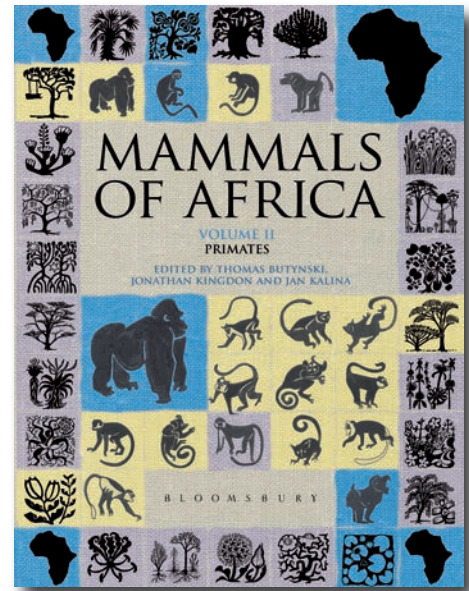
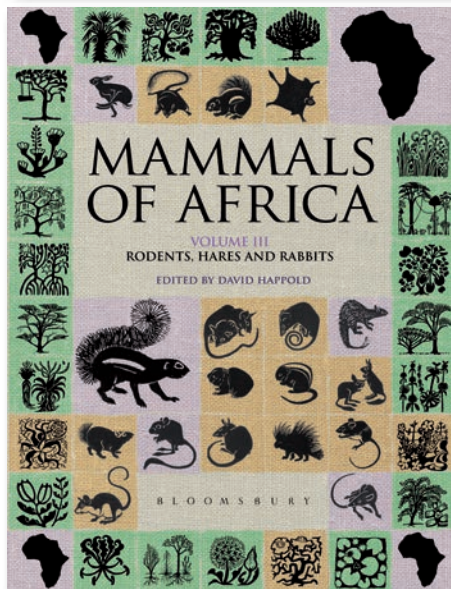


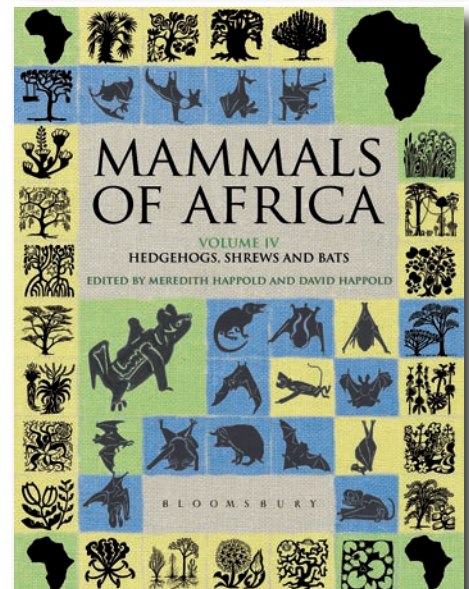
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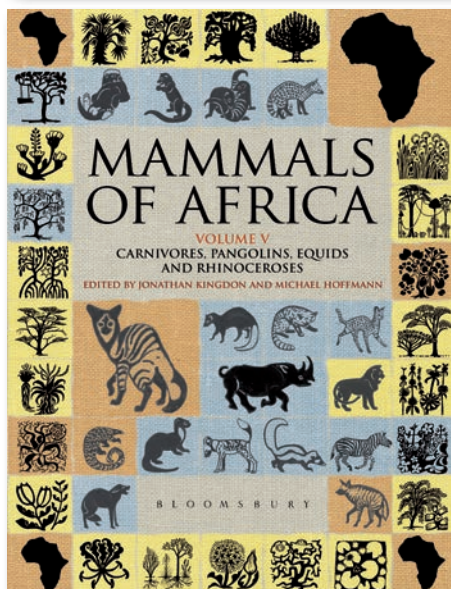
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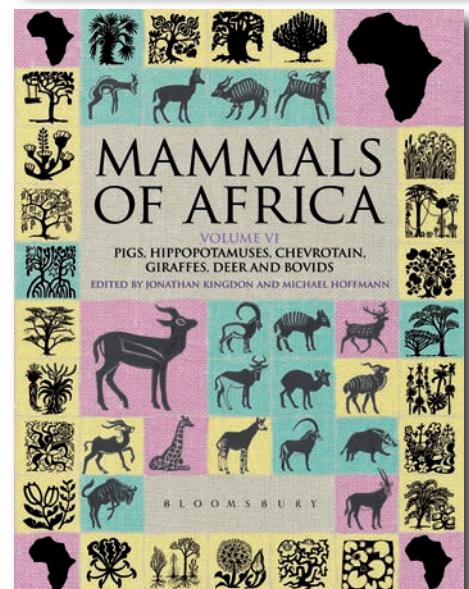
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MAMMALS OF AFRICA

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INTRODUCTORY CHAPTERS AND AFROTHERIA



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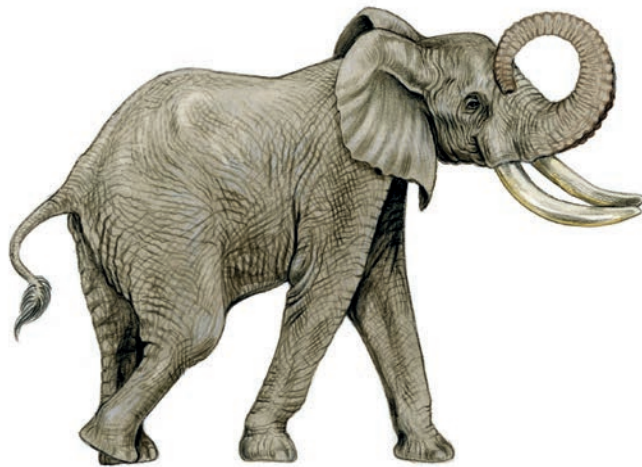
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THOMAS BUTYNSKI, MEREDITH HAPPOLD AND JAN KALINA



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PEN AND INK ILLUSTRATIONS OF SMALL AFROTHERIA BY MEREDITH HAPPOLD

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ABOVE LEFT: Jan Kalina.

ABOVE: (from left to right) Jonathan Kingdon, Thomas Butynski, Meredith Happold, David Happold and Andrew Richford.

LEFT: Jonathan Kingdon (left) and Mike Hoffmann.

Acknowledgements for Volume I

Jonathan Kingdon

When Andrew Richford at Academic Press first took up my suggestion of a Handbook of African Mammals (partly modelled on *The Birds of Africa*, which he had edited), neither of us anticipated that it might take as long to reach print as it has. Even so the journey has been deeply rewarding in terms of scientific and intellectual stimulus and my gratitude to the authors and editors that have joined me in this enterprise is immense. Above all, my fellow-editors, Mike Hoffmann and Andy Richford, have offered a quality of fellowship that has been unprecedented in a lifetime of many shared endeavours. Tom Butynski, Jan Kalina, and David and Meredith Happold have also been splendid collaborators, and Tom a true companion and stimulating friend on the field trips we have shared. In assuming the task of drawing the many line drawings for the small mammal skulls, Meredith Happold relieved me of much labour, for which I am most grateful. Likewise, David and Meredith Happold, in taking exclusive charge of editing all small mammal profiles, significantly reduced the burden on other editors. This has freed us all to concentrate on our chosen areas of interest. Nigel Redman, David and Namrita Price-Goodfellow, and Elaine Leek have been wonderful collaborators in bringing these volumes to print. I am deeply grateful for their enthusiasm and hard work.

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In the long chain of events that eventually led to the decision to embark on an inventory and handbook of the mammals of Africa Julian Huxley was an early but profoundly formative influence. On retirement as the founding Director of UNESCO, he revisited many

African countries in 1960 to update a previous landmark report on progress in Science and Education on our continent. During his visit to the Makerere University Zoology Field Course at Mweya, in western Uganda I was asked to guide him and the students. In the evening, as we listened to the choruses of hippos as they left the water to go grazing, Julian quizzed me about my local background and biological interests, remarking 'you should do something with the knowledge you have acquired'. Subsequently he helped shepherd me through the first two volumes of my *East African Mammals: An Atlas of Evolution in Africa*. His passionate interest in that enterprise was a legacy that helped drive my own determination to inform others about the mammals of our continent, their evolution and their relevance in the unfolding quest to discover the historical and prehistoric roots of our own humanity.

What and who inspires a youngster's interests is often arbitrary. I remember with affection Saidi Batale, who took me hunting hyraxes and cane-rats when I was six years old. Crawling over the rocks of Mwanza Bay with him, watching otters, mongooses and tomb bats laid foundations for my lifetime interest in the natural history of my home continent. As a schoolboy, banished to England, it was mutual loneliness and longing for the tropics that brought me and Percy Willoughby Lowe together. I became an eager sounding board for his reminiscences of scientific collecting expeditions, some of them made at the beginning of the twentieth century (several African mammals are named after him, notably a guenon from West Africa, gerbils and a bat from the Jebel Marra in Sudan and a genet from Tanzania). He put me in touch with C.H.B Grant and R.W. Hayman at the British Museum (Natural History). Soon thereafter, at Percy's and their behest, I, too, was collecting specimens and I still have a certificate of thanks, issued by the British Museum: I was 16. My friendship with Percy made discoveries and events that happened long before I was born tangible. Whenever I handle the bird and mammal specimens that he so carefully preserved and read his handwritten labels I am moved by more than memories of an endearing old man. I give thanks for the spirit of scientific enquiry and intellectual adventure that sent Percy (and before him, William Bates, Alfred Wallace and Charles Darwin) to remote places, to all our benefit. Their spiritual descendants are now countless but all the contributors and most readers of this work will be quick to acknowledge our communal debt to these pioneers and to the many workers in universities, laboratories, museums and conservation societies who strive to maintain the momentum of biological science in an age of ecological and economic barbarism.

I had the good fortune to have known 'Iodine' Ionides, an avid naturalist and collector, for many years a colleague of my father and Chief Game Warden in the Southern Province of Tanganyika (my essay

on polymorphism in Giant Sengis in this volume owes much to our discussions and to the carefully transcribed field notes that he sent me in the early 1960s and to the specimens that he collected). Many aspects of our science still depend upon past and present observers and collectors of specimens and records. They are often inadequately acknowledged and in addition to Percy Lowe I should especially mention Tony Archer, Richard Gicheru, Robert Glen, David Harrison, Paul Bates, Peter Mwangi, Andy Williams and Raphael Abdullah (and his father, Ali) all of whom have made exceptionally important contributions in this regard.

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It has been very reassuring that so many institutions, worldwide, have been sufficiently interested in the mammals of Africa to display some of the drawings and paintings that illustrate these volumes. I am grateful to the following for hosting these works, many of them major exhibitions: the Smithsonian Institution in Washington, USA, the Los Angeles County Museum, California, Duke University, North Carolina, the Senckenberg Museum in Frankfurt, Germany, Justus Leibig University, Geissen, Germany, the Natural History Museum in Geneva, Switzerland, the Zoological Society of London, The Barbican Centre, London, the Royal Society (1982 Darwin Centenary), the Royal Geographic Society, the Commonwealth Centre and the Wellcome Trust HQ all in London; the Ashmolean Museum, Oxford, University of Oxford Zoology Dept, the University of Oxford Natural History Museum, the Cambridge University Zoological Museum, exhibits in Bristol, Bath, Bury St Edmunds, Rolle College, Exmouth, Port Lympne, Pangolin Gallery, Chalford and the Welshpool gallery, Wales, Brunel University, Edinburgh, the Uganda Museum and Makerere University, Kampala, the Sorsbie and Watatu galleries and Kenyatta University, Kenya, the Windhoek Museum, Namibia, the South African Wildlife Society, Johannesburg, the British Council in Dar-es-Salaam, Tanzania, the British Council in Kyoto, Japan and the CSIRO Forest Research Centre in Atherton, Australia. The commissioning and response to these exhibits have demonstrated a widespread enthusiasm for the mammals of Africa and for their study. Apart from helping fund my work, the responses to these exhibitions have reinforced my confidence in the worth of such endeavours. Thanks also to the librarians in many institutional libraries, including Maria Garruccio of Bioversity International.

Many years ago Peter Medawar reviewed a proposal in which I sought to study some of the principles involved in visual signalling systems through a study of guenon monkeys. He said 'make sure you have a real biological point to make; don't just make a parish register'. That advice has been incompletely followed in *MoA*: we *have*, unashamedly, made parish registers but Peter's advice was taken to heart and a great many biological points have been made too.

Among the many people who have contributed data, ideas, practical help and facilitated the growth and realization of this project over the years the following are remembered with much gratitude:

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CHAPTER ONE

Mammals of Africa: *An Introduction and Guide*

David Happold, Michael Hoffmann, Thomas Butynski and Jonathan Kingdon

Mammals of Africa is a series of six volumes that describes, in detail, every extant species of African land mammal that was recognized at the time the profiles were written (Table 1). This is the first time that such an extensive coverage has been attempted; all previous books and field guides have either been regional in coverage, or have described a selection of mammal species – usually the larger species. These volumes demonstrate the diversity of Africa's mammals, summarize what is known about the distribution, ecology, behaviour and conservation status of each species, and serve as a guide to identification.

Africa has changed greatly in recent decades because of increases in human populations, exploitation of natural resources, agricultural development and urban expansion. Throughout the continent, extensive areas of forest have been destroyed and much of the forest

that remains is degraded and fragmented. Savanna habitats have been altered by felling of trees and development for agriculture. Many of the drier areas are threatened with desertification. As a result, the abundance and geographic ranges of many species of mammals have declined – some marginally, some catastrophically, some to extinction. Hence, it seems appropriate that our knowledge of each species is recorded now, on a pan-African basis, because the next few decades will see even more human-induced changes. How such changes will affect each mammalian species is uncertain, but this series of volumes will act as a baseline for assessing future change.

The study of African mammals has taken several stages. During the era of European exploration and colonization, the scientific study of African mammals was largely descriptive. Specimens that were sent to museums were described and named. As more specimens became available, and from different parts of the continent, there was increasing interest in distribution and abundance, and in the ecological and behavioural attributes of species and communities. At first, it was the largest and most easily observed species that were the focus of most studies, but as new methodologies and equipment became available, the smaller and more cryptic and secretive species became better known. Many species were studied because of their suspected role in diseases of humans and livestock, and because they were proven or potential 'pests' in agricultural systems. During the past decade or so, there has been greater emphasis on the genetic and molecular characteristics of species. All these studies have produced a wealth of information, especially during the past 40 years or so. These volumes are not only a distillation of the huge literature that now exists on African mammals, but also of much unpublished information.

Readers will notice that there is a huge discrepancy among species in the amount of information available. Some species have been studied extensively for many years, especially the so-called 'game species', some species of primates, and a few species that are widespread and/or easily observed. In contrast, other species are known only by one or a few specimens, and almost nothing is known about them. Likewise, some areas and countries have been well studied, while other areas and countries have been neglected. During the preparation of these

Table 1. The mammals of Africa.

Order	Number of families	Number of genera	Number of species
Hyracoidea	1	3	5
Proboscidea	1	1	2
Sirenia	2	2	2
Afrosoricida	2	11	24
Macroscelidea	1	4	15
Tubulidentata	1	1	1
Primates	4	25	93
Rodentia	15	98	395 ^a
Lagomorpha	1	5	13
Erinaceomorpha	1	3	6
Soricomorpha	1	9	150
Chiroptera	9	49	224
Carnivora	9	38	83
Pholidota	1	3	4
Perissodactyla	2	3	6
Cetartiodactyla	6	41	93
16	57	296	1116^b

^aIncluding five introduced species. ^bSpecies profiles in *Mammals of Africa*.

Table 2. The six volumes of *Mammals of Africa*.

Volume	Contents	Number of species	Editors
I	Introductory chapters. Afrotheria (Hyraxes, Elephants, Dugong, Manatee, Otter-shrews, Golden-moles, Sengis and Aardvark)	49	Jonathan Kingdon, David C. D. Happold, Michael Hoffmann, Thomas M. Butynski, Meredith Happold and Jan Kalina
II	Primates	93	Thomas M. Butynski, Jonathan Kingdon and Jan Kalina
III	Rodents, Hares and Rabbits	408	David C. D. Happold
IV	Hedgehogs, Shrews and Bats	380	Meredith Happold and David C. D. Happold
V	Carnivores, Pangolins, Equids and Rhinoceroses	93	Jonathan Kingdon and Michael Hoffmann
VI	Pigs, Hippopotamuses, Chevrotain, Giraffes, Deer and Bovids	93	Jonathan Kingdon and Michael Hoffmann

volumes, the editors have often been surprised by the wealth of information about some species when little was anticipated, and by the paucity of information about others, some of which were assumed to be 'well known'. In addition to presenting information that is based on sound scientific evidence, the aims of these volumes are to point out where there are gaps in knowledge and to correct inaccurate information that has become embedded in the literature. For most taxa, the detail provided in the species profiles allows accurate identification.

Mammals of Africa comprises six volumes (Table 2). The volumes consist mainly of species profiles – each profile being a detailed account of the species. They have been edited by six editors who distributed their work according to the orders with which they were most familiar. Each editor chose authors who had extensive knowledge of the species (or higher taxon) and, preferably, had experience with the species in the field. Each volume follows the same general format with respect to arrangement, subheadings and contents. Because *Mammals of Africa* has contributions from 356 authors (each with a different background and speciality) and each volume was edited by one or more editors (each with a different perspective), it has not been possible or even desirable to ensure exact consistency throughout. Species profiles are not intended to be exhaustive literature reviews, partly for reasons of space. None the less, they are written and edited to be as comprehensive as possible, and to lead the reader to the most important literature for each species. Inevitably, not all information available could be accommodated for the better-known species, and so such profiles are a précis of available knowledge. Extensive references in the text alert the reader to more detailed information.

In addition to the species profiles, there are profiles for the higher taxa (genera, families, orders, etc.). Thus, there is a profile for each order, for each family within the order, for each genus within the family and for each species within the genus. For some orders there

are additional taxonomic levels, for example, tribes (e.g. in Bovidae), subgenera (e.g. in *Procolobus*) and species-groups, or 'superspecies' (e.g. in *Cercopithecus*). The taxonomy used in these volumes mostly follows that presented in the third edition of *Mammal Species of the World: A Geographic and Taxonomic Reference* (Wilson & Reeder 2005), although authors have employed alternative taxonomies when there were good reasons for doing so. Volume I differs from the other volumes in that it contains a number of introductory chapters about Africa and its environment, and about African mammals in general.

The continent of Africa

For the purposes of this work, 'Africa' is defined as the continent of Africa (bounded by the Mediterranean Sea, the Atlantic Ocean, the Indian Ocean, the Red Sea and the Suez Canal) and the islands on the continental shelf, which, at some time in their history, have been joined to the African continent. The largest of the 'continental islands' are Zanzibar (Unguja), Mafia and Bioko (Fernando Po). All 'oceanic islands', e.g. São Tomé, Príncipe, Annobón (Pagulu), Madagascar, Comoros, Seychelles, Mauritius, Socotra, Canaries, Madeira and Cape Verde are excluded, with the exception of Pemba. Pemba is included because of its close proximity (ca. 50 km) to the mainland.

The names of the countries of Africa are taken from the *Times Atlas* (2005). The Republic of Congo is referred to as 'Congo' and the Democratic Republic of Congo (formerly Zaire) as 'DR Congo'. Smaller geographical or administrative areas within countries are rarely referred to except for Provinces in South Africa, which are used extensively in the literature. A political map of Africa, and of the Provinces of South Africa, is given (Figure 1), as well as a list of the 47 countries together with their previous names, which are used in the older literature on African mammals (Table 3).

Africa is the second largest continent in the world (after Asia), but it differs from other continents (except Australia and Antarctica) in being essentially an island. At various times in the past, Africa has been joined to other continents – a situation that has had a strong influence on the fauna and flora of the continent. Africa is a vast continent (29,000,000 km², 11,200,000 mi²) that straddles the Equator, with about two-thirds of its area in the northern hemisphere and one-third in the southern hemisphere. As a result, Africa has many varied climates (with seasons in each hemisphere being 6 months out of phase), many habitats (including deserts, savannas, woodlands, swamps, rivers, lakes, moist forests, monsoon forests, mountains and glaciers), and altitudes ranging from 155 m (509 ft) below sea level at L. Assal, Djibouti, in the Danakil (Afar) Depression, to 5895 m (19,341 ft) on Mt Kilimanjaro, Tanzania. Africa is comprised of 47 countries, some of which are very large (e.g. Sudan [2,506,000 km²; 967,000 mi²], Algeria [2,382,000 km², 920,000 mi²] and Congo [2,345,000 km², 905,000 mi²]), and others that are relatively small (e.g. Djibouti [23,200 km², 9000 mi²], Swaziland [17,400 km², 6700 mi²] and The Gambia [11,300 km², 4400 mi²]). The human population of each country also varies greatly, from about 346/km² in Rwanda to only about 2.5/km² in Namibia. With its great size and varied habitats, Africa supports a high biodiversity, including a large number of species of mammals. Likewise, most countries have a high diversity of mammals (especially when compared with temperate countries).



Figure 1. (a) Political map of Africa; (b) provinces of South Africa; (c) altitudes and major rivers of Africa. South Sudan and Somaliland are not identified as separate countries in the text.

Table 3. The countries of Africa: names, areas and human population density.

Country name	Area (km ²) '000	Area (miles ²) '000	Human population '000 (2006)	People per km ²
Algeria	2,382	920.0	33,500	14.1
Angola (includes Cabinda)	1,247	481.0	15,800	12.7
Benin * [Dahomey]	113	43.0	8,700	77.0
Botswana [Bechuanaland]	582	225.0	1,800	3.1
Burkina Faso * [Upper Volta; Burkina]	274	106.0	13,600	49.6
Burundi [part of Ruanda-Urundi (= part of Belgian Congo)]	27.8	10.7	7,800	280.5
Cameroon [includes former French Cameroon, German Cameroon and part of Eastern Nigeria]	475	184.0	17,300	36.2
Central African Republic #	623	241.0	4,300	6.9
Chad [Tchad]	1,284	496.0	10,000	5.8
Congo [Republic of Congo]	342	132.0	3,700	10.8
Côte d'Ivoire * [Ivory Coast]	322	125.0	19,700	61.2
Democratic Republic of Congo [Belgian Congo; Congo (Kinshasa); Zaire]	2,345	905.0	62,700	26.7
Djibouti [French Somaliland]	23.2	9.0	800	34.5
Egypt	1,001	387.0	75,400	75.3
Equatorial Guinea # (includes Rio Muni [Spanish Guinea] and Bioko I. [Fernando Po])	28.1	10.8	500	17.8
Eritrea (formerly part of Ethiopia)	94	36.0	4,600	48.9
Ethiopia [Abyssinia]	1,128	436.0	74,800	66.3
Gabon #	268	103.0	1,400	5.2
The Gambia	11.3	4.4	1,500	132.7
Ghana [Gold Coast]	239	92.0	22,600	94.6
Guinea *	246	95.0	9,800	39.8
Guinea-Bissau [Portuguese Guinea]	36	13.9	1,400	38.9
Kenya	580	224.0	34,700	59.8
Lesotho [Basutoland]	30.4	11.7	1,800	59.2
Liberia	111	43.0	3,400	30.6
Libya	1,760	679.0	5,900	3.6
Malawi [Nyasaland]	118	46.0	12,800	108.5
Mali *	1,240	479.0	13,900	11.2
Mauritania *	1,030	412.0	3,200	3.1
Morocco [includes former Spanish Morocco and French Morocco]; (now also includes Western Sahara = former Spanish Sahara)	447	172.0	32,100	71.8
Mozambique [Portuguese East Africa]	802	309.0	19,900	24.8
Namibia [South-west Africa]	825	318.0	2,100	2.5
Niger *	1,267	489.0	14,400	11.3
Nigeria	924	357.0	134,500	145.6
Rwanda [part of Ruanda-Urundi (= part of Belgian Congo)]	26.3	10.2	9,100	346.0
Senegal *	197	76.0	11,900	60.4
Sierra Leone	71.7	27.7	5,700	79.5
Somalia [†] [British Somaliland and Italian Somaliland; Somali Republic]	638	246.0	8,900	13.9
South Africa	1,220	471.0	47,300	38.7
Sudan § [Anglo-Egyptian Sudan]	2,506	967.0	41,200	16.4
Swaziland	17.4	6.7	1,100	63.2
Tanzania [German East Africa; Tanganyika] (now includes Zanzibar I., Mafia I. and Pemba I.)	945	365.0	37,900	40.1
Togo [Togoland]	56.8	21.9	6,300	110.9
Tunisia	164	63.0	10,100	61.6
Uganda	236	91.0	27,700	117.4
Zambia [Northern Rhodesia]	753	291.0	11,900	15.8
Zimbabwe [Southern Rhodesia]	391	151.0	13,100	33.5
Totals/mean density	29,448	11,383	902,600	56.8

Former names are listed in chronological order in square brackets, with the oldest name listed first. Obsolete names are listed because much of the older literature refers to past colonial entities. * = formerly part of French West Africa. # = formerly part of French Equatorial Africa. § At the time of going to press, the country of Sudan had been divided into two: the Republic of Sudan in the north, and the Republic of South Sudan in the south. [†]The former British Somaliland is now a self-declared state under the name of the Republic of Somaliland, but remains internationally unrecognized.

Africa may also be categorized into Biotic Zones (see Chapter 5, Figure 3, p. 62). A Biotic Zone is defined as an area within which there is a similar environment (primarily rainfall and temperature) and vegetation, and which differs in these respects from other Biotic Zones. Africa can be divided into 13 Biotic Zones, two of which may be divided into smaller categories. The Biotic Zones concept provides a general assessment of the environmental conditions in which a species lives, as well as providing an assessment of the geographic distribution of the species. In a similar way, the Rainforest Biotic Zone (see Chapter 5, Figure 5, p. 69) and the South-West Arid Biotic Zone may be divided into regions and sub-regions that reflect the different biogeographical distributions of species, each region/sub-region having a community of mammals and other animals that is different to any other. Details of the Biotic Zones of Africa, and the Regions and Sub-regions of the Rainforest and South-West Arid Biotic Zones, are given in Chapter 5. The Biotic Zones map is reprinted in the Introductions to volumes II–VI of this series.

The Afrotheria of Africa

This volume, Volume I, is devoted to the orders Hyracoidea (hyraxes), Proboscidea (elephants), Sirenia (Dugong and Manatee), Afrosoricida (otter-shrews and golden-moles), Macroscelidea (sengis or elephant-shrews) and Tubulidentata (Aardvark), which collectively comprise the Afrotheria. In Africa, these orders contain 49 species (i.e. about 4% of all African mammals). Of these, 10 species are large to very large and 39 species (Afrosoricida and Macroscelidea) are small to very small. Some species described in this volume have been studied in detail and are well known; others, particularly the smaller species, have not been well studied, often because of their rarity and small geographic ranges.

Since the texts for this volume were prepared, two new species have been described within the order Macroscelidea:

Rhynchocyon udzungwensis Rathbun & Rovero, 2008, *J. Zool., Lond.* 274: 127. Distribution: Vikongwa River Valley, Ndundulu Forest, West Kilombero Scarp Forest Reserve, Udzungwa Mountains, Iringa Region, Tanzania [7°48.269' S, 36°30.355' E (Arc 1960 datum)], at 1350 m a.s.l. Remarks: location is c. 15 km south-east of Udekwa Village, Iringa Region, Tanzania. (Reference: Rovero *et al.* 2008).

Elephantulus pilicaudus Smit, 2008. *J. Mammal.* 89: 1263. Distribution: Vondelingsfontein Farm, Calvinia, Northern Cape Province, South Africa (31°48' S, 19°49' E), at 1449 m a.s.l.

The editors of the species profiles in this volume are Jonathan Kingdon and Michael Hoffmann (Hyracoidea, Proboscidea, Sirenia and Tubulidentata; 10 species), and David and Meredith Happold (Afrosoricida and Macroscelidea; 39 species).

Species profiles

Information about each species is given under a series of subheadings. The amount of information under each of these subheadings varies greatly between species; where no information is available, this is recorded as 'No information available' or words to this effect. The sequence of subheadings is as follows:

Scientific Name (genus and species) The currently accepted name of the species.

Vernacular Names English, French and German names are given, as available. The first given English name is the preferred vernacular name for the species; alternative names are given in parentheses for some species. Wilson & Cole (2000) list proposed vernacular names for all the world's mammals; most of these names were also given

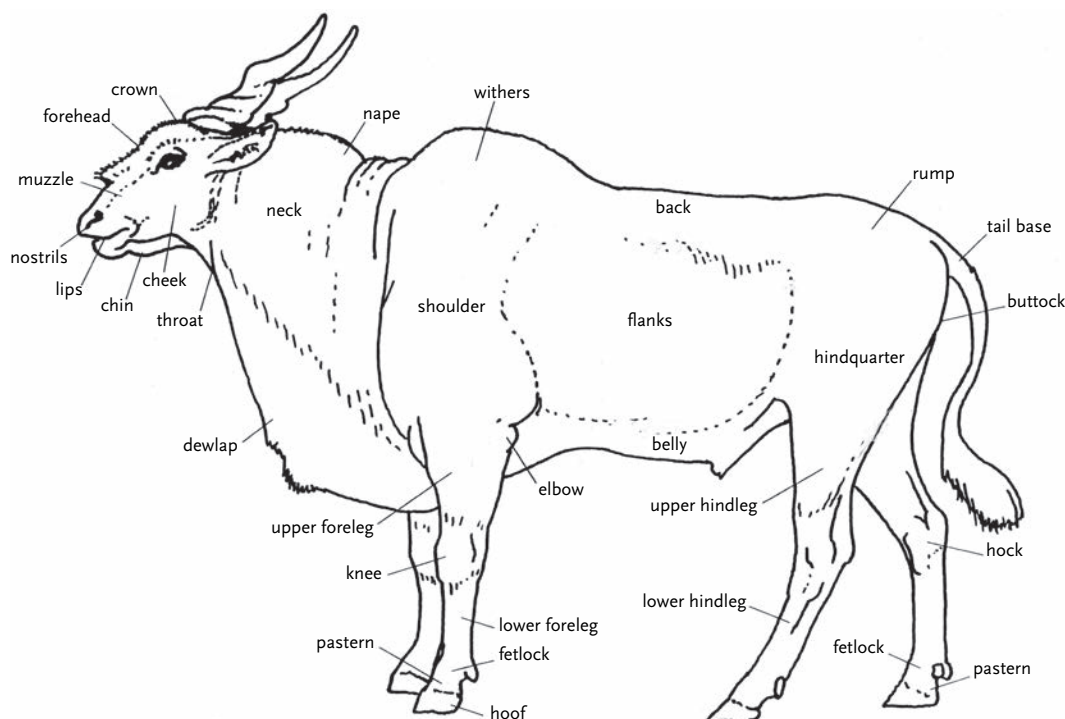
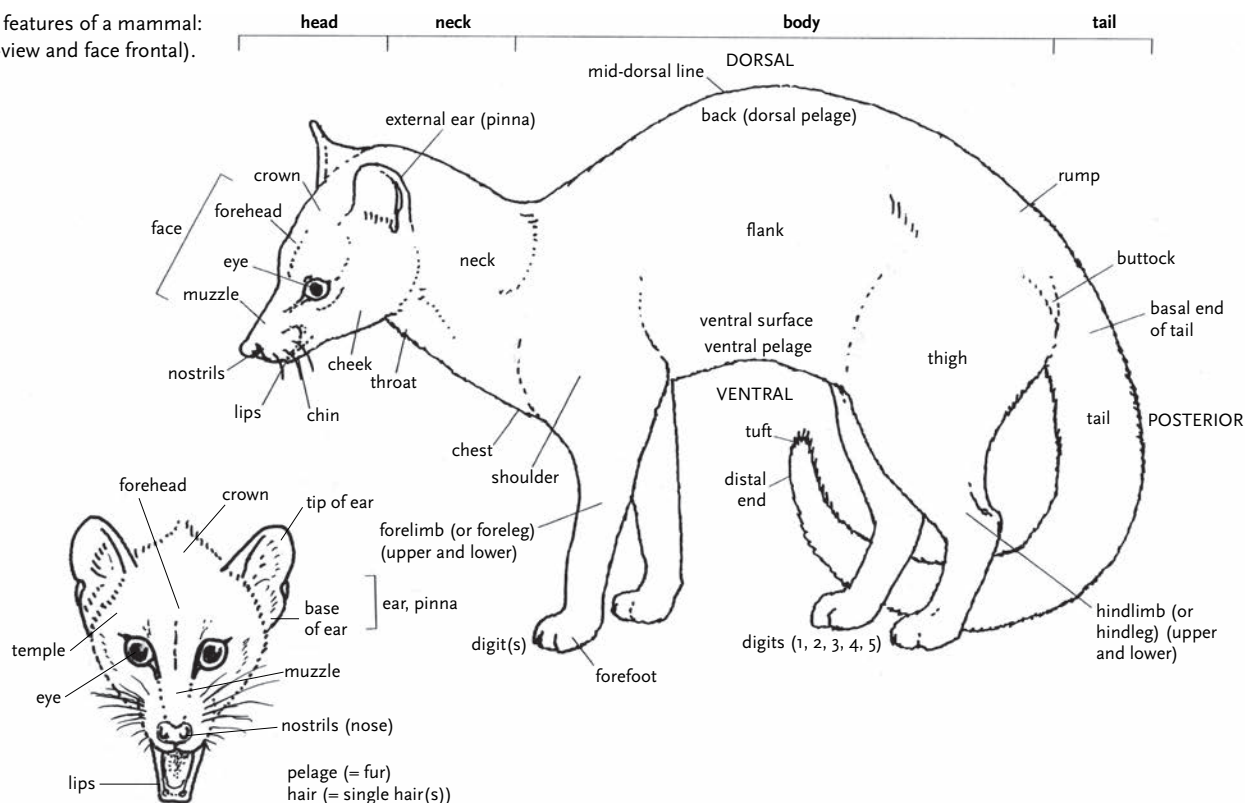


Figure 2. External features of a mammal: Common Eland *Tragelaphus oryx*.

Figure 3. External features of a mammal: *Genetta* sp. (side-view and face frontal).



in the third edition of *Mammal Species of the World* (Wilson & Reeder 2005). Although these works have been consulted, the names used have not always been adopted in *Mammals of Africa*. French names were either provided by authors, or taken from Gunther (2003).

Scientific Citation This provides the full scientific name of the species, i.e. genus name, species name, authority name and date of authority. Parentheses around the authority's name and date indicate that the species was originally named in a different genus to its present generic allocation. The scientific name is followed by the publication where the species was described, and the location where the type specimen (or type series) was obtained. Most of this information is taken from Wilson & Reeder (2005).

Taxonomy This section contains information on taxonomic problems, if any, associated with the species, and its relationship with other species in the genus. For some species, there is considerable information about these topics; for others, there may be nothing. A list of synonyms (without the taxonomic authority for each) and the number of subspecies (if any) is presented, mostly taken from Wilson & Reeder (2005). The chromosome number is given if available, and in some cases this is followed by other information relevant to the chromosomes.

Description This section, together with the illustrations, provides the reader with adequate information to identify the species. The section begins with a brief overall description of the species, including an indication of size. This is followed by a detailed description of the external features of the species' head (and parts of the head), dorsal pelage, legs, feet, ventral pelage, and tail (in this order), as well as any special characteristics unique to the species.

For some species, diagnostic characteristics of the skull are given. The characters described in this section are common to all subspecies of this species (unless otherwise noted). The mammary formula, i.e. the number and arrangement of nipples in adult females, is noted wherever this feature varies between the taxa being discussed.

In the profiles of the Afrosoricida and Macroscelidea, the word 'comparatively' is used in the context of describing the size of one character compared with the size of the same character in a *different* species. The word 'relatively' is used in the context of describing the size of one character relative to the size of a different character in the *same* species. This is usually expressed as a percentage, e.g. Tail 80% of HB. In contrast, authors of profiles in other orders may have given these words more generalized meanings.

Geographic Variation Variation within the species may be of two sorts: (a) clinal variation without subspecies, or (b) subspecific variation. If (a), there is a description of the character(s) that alter clinally across the geographic range of the species. If (b), each of the subspecies is listed with its geographic range and the characters that distinguish it from other subspecies of the species. For some species, subspecies have been described that are no longer considered to be valid; in some cases, such names may be listed but without further comment.

Similar Species Species that are sympatric or parapatric with the species under consideration, and with which it may be confused, are listed along with diagnostic characteristics (additionally, readers may refer to profiles of the similar species in question). In some instances, species that are allopatric in distribution are also included.

In the profiles of the Afrosoricida and Macroscelidea, when two similar species are distinguished on the basis of their size, one is only said to be 'larger' or 'smaller' than the other if there is no

Figure 4. External features of a hypothetical golden-mole.

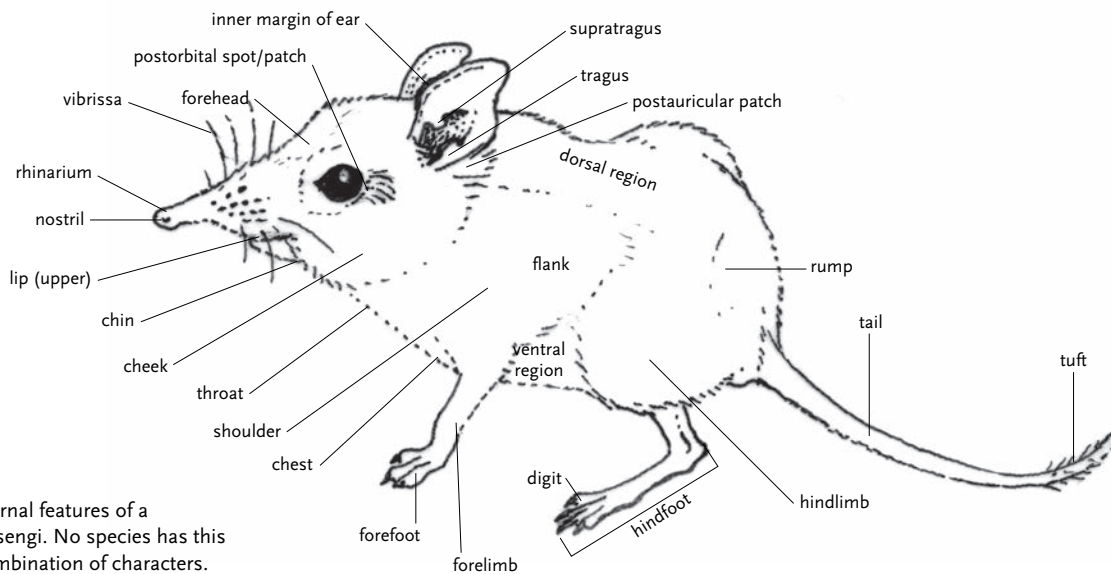
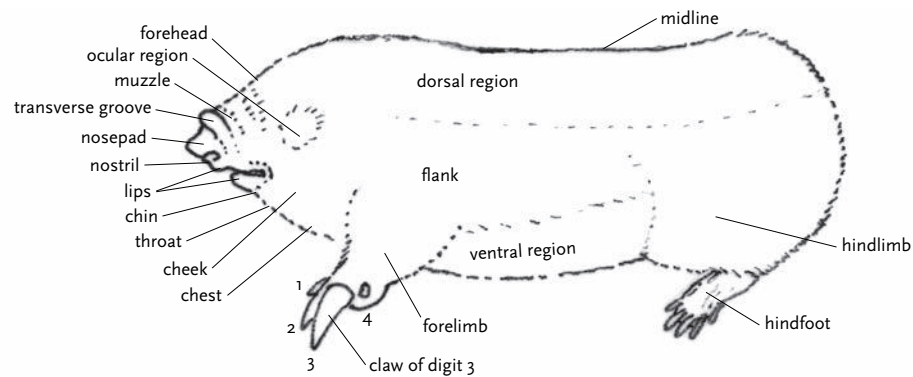


Figure 5. External features of a hypothetical sengi. No species has this particular combination of characters.

overlap in the size ranges of the two species. If there is overlap but the means are different, it is stated that one is 'larger on average' or 'smaller on average' than the other. In contrast, authors of profiles in other orders may have used 'larger' or 'smaller' in both of the above situations.

Distribution The first sentence 'Endemic to Africa' informs the reader that this is an African species and does not occur on any other continent; if a species also occurs outside Africa, this is noted at the end of this section. The next sentence usually gives the Biotic Zone (or Zones) where the species has been recorded; this provides the reader with a general impression of where the species occurs in Africa and the sort of habitat where the species occurs. Finally, the countries (or parts of countries) where the species has been recorded are generally listed; sometimes other data (such as altitude range and habitat) are also included. As a general rule, descriptions of the range for species with very restricted distributions are more precise in terms of information given (including, for example, geographic coordinates) than for more widespread species, where a more generalized range statement is adequate. A distribution map (see below) augments the information given here.

Habitat This section provides a description of the range of habitats where the species lives. Details of plant communities, plant

species, vegetation structure, soil type and/or structure and water availability, etc. (if available) are also recorded. Other information may include average annual rainfall, altitudinal limits and seasonal variation in habitat characteristics.

Abundance A general indication of abundance in the habitat. This may be unquantified, such as abundant, common, uncommon, rare, or phrases such as 'rarely seen but frequently heard', etc. For better-known species, abundance may be expressed as estimates of density (e.g. number/ha or number/km²), or relative abundance within the community (e.g. 'comprised 40% of small mammals captured', 'the second most numerous species'); for the better-known rare species, actual numbers of individuals for the species may be given. Other information may include seasonal changes in density, frequency of observations, or the relative abundance of specimens in collections.

Adaptations This section describes morphological, physiological and behavioural characteristics, which show how the species uniquely interacts with its environment, conspecifics and other animals. This section may also describe species-specific adaptations for feeding, locomotion, burrowing, mechanisms for orientation, production of sound, sensory mechanisms and activity patterns. In some instances comparison with related or convergent species allows the unique

adaptations of the species under discussion to be detailed or highlighted.

Foraging and Food The first sentence briefly describes the food habits of the species (e.g. insectivorous, carnivorous, granivorous, etc.). This may be followed by the method of collecting food (foraging), size of home range and daily distance moved. The diet is then described either by a list of the taxa of animals or plants consumed, and/or as a quantitative measure based on direct observations or of examination of the contents of the stomach or the faeces.

Social and Reproductive Behaviour Topics in this section may include group structure (whether solitary, social, or colonial), group size and composition; agonistic and amicable behaviour, comfort behaviour, etc.; home-range (including quantitative data), territorial behaviour, courtship and mating behaviour, behaviour of young, parental–young interactions; presence of helpers, vocalizations, and interactions with other species (mammals, birds, etc.).

Reproduction and Population Structure This section begins with an assessment of reproductive strategy (if known) and the times/seasons of the year when individuals are reproductively active (pregnancy and lactation in females, active spermatogenesis in males). Other information may include length of gestation, times/seasons of births, including peaks of births, litter-size, birth-weight and size, spacing of litters, growth and time to weaning, maturity, longevity and mortality rates. Reproductive strategies, if known, are described with respect to locality, food availability and population density. Population structure (sex ratio, adult/young ratio, abundance of different cohorts in the population at different times of the

year) may be described, and related to seasonal variations in reproduction and environmental variables.

Predators, Parasites and Diseases The known predators, parasites and diseases are listed. Additional information is given if the species is a host to diseases that affect humans and domestic stock, and if it is utilized as food for humans ('bushmeat').

Remarks This subheading subsumes five of the above subheadings (Adaptations, Foraging and Food, Social and Reproductive Behaviour, Reproduction and Population Structure, and Predators, Parasites and Diseases) in those instances where there is little or no information available.

Conservation The conservation status of the species is stated, as given by IUCN – International Union for Conservation of Nature Red List of Threatened Species (version 2011.2). The IUCN Red List categories follow the definitions given in the *IUCN Red List Categories and Criteria Version 3.1* (Table 4); for those species classified as threatened (Vulnerable, Endangered and Critically Endangered), readers may obtain detailed reasons for the classification on the IUCN Red List website. If a species is listed on Appendix I or Appendix II under CITES (Convention on International Trade in Endangered Species; www.cites.org), this is also indicated. For some species, additional information, such as presence in protected areas, major threats and current or recommended conservation measures are provided.

Measurements A series of morphological measurements is provided. For each species there is a standard set of measurements. The abbreviations for each measurement are given in the Glossary. A measurement is cited as the mean value (with minimum value

Table 4. Definitions for the IUCN Red List categories (from IUCN – Red List Categories, Version 3.1).

Category	Description
Extinct (EX)	A taxon is Extinct when there is no reasonable doubt that the last individual has died. A taxon is presumed Extinct when exhaustive surveys in known and/or expected habitat, at appropriate times (diurnal, seasonal, annual), throughout its historic range have failed to record an individual. Surveys should be over a time-frame appropriate to the taxon's life-cycles and life form.
Extinct in the Wild (EW)	A taxon is Extinct in the Wild when it is known only to survive in cultivation, in captivity or as a naturalized population (or populations) well outside the past range. A taxon is presumed Extinct in the Wild when exhaustive surveys in known and/or expected habitat, at appropriate times (diurnal, seasonal, annual), throughout its historic range have failed to record an individual. Surveys should be over a time-frame appropriate to the taxon's life-cycle and life form.
Critically Endangered (CR)	A taxon is Critically Endangered when the best available evidence indicates that it meets any of the criteria A to E for Critically Endangered, and it is therefore considered to be facing an extremely high risk of extinction in the wild.
Endangered (EN)	A taxon is Endangered when the best available evidence indicates that it meets any of the criteria A to E for Endangered, and it is therefore considered to be facing a very high risk of extinction in the wild.
Vulnerable (VU)	A taxon is Vulnerable when the best available evidence indicates that it meets any of the criteria A to E for Vulnerable, and it is therefore considered to be facing a high risk of extinction in the wild.
Near Threatened (NT)	A taxon is Near Threatened when it has been evaluated against the criteria but does not qualify for Critically Endangered, Endangered or Vulnerable now, but is close to qualifying for (or is likely to qualify for) a threatened category in the near future.
Least Concern (LC)	A taxon is Least Concern when it has been evaluated against the criteria and does not qualify for the Critically Endangered, Endangered, Vulnerable or Near Threatened categories. Widespread and abundant taxa are included in this category.
Data Deficient (DD)	A taxon is Data Deficient when there is inadequate information to make a direct, or indirect, assessment of its risk of extinction based on its distribution and/or population status. Data Deficient is not a category of threat. Listing of taxa in this category indicates that more information is required and acknowledges the possibility that future research will show that a threatened classification is appropriate.
Not Evaluated (NE)	A taxon is Not Evaluated when it has not yet been evaluated against the criteria.

to maximum value in parentheses) and sample size. For some, the standard deviation (mean \pm 1 S.D.) is given instead of the range. For most measurements, data for males and females are combined but where there is sexual dimorphism, measurements for males and females are given separately. Where possible, measurements also detail the localities where the specimens were obtained, and the source of the data. Sources are either cited publications, or specimens in museums, or unpublished information from authors or others. The acronym BMNH corresponds to 'Natural History Museum, London, UK [formerly British Museum (Natural History)]'. Most museum records are provided by the author of the profile; others – when an author did not have the measurements or did not have the opportunity to visit museums – were provided by the editor(s).

Key References A select list of references, which provides more general information on the species. Each reference is given in full in the Bibliography.

Author The name of the author, or authors, is given at the end of each profile. All profiles should be cited using the author name(s).

Tables For selected taxa (mainly families and genera) tables provide details of the main characteristics of these taxa and can be used as an aid to identification.

Higher taxon profiles

The profiles for orders, families and genera are less structured than for the species profiles. Each profile usually begins with a listing of the taxa in the next lower taxon; for example, each family profile lists the genera in that family. An exception to this arrangement is where a taxon has only one lower taxon. Higher taxa profiles provide the characteristics common to all members of that taxon. Some of these characteristics may not be repeated in lower taxon profiles (unless essential for identification).

Distribution maps

Each species profile, with a very few exceptions, contains a pan-African map showing the geographic range of the species. Most maps were provided by the author of the profile and were compiled from literature records and museum specimens; some maps were provided by the editor(s) when it was not possible for the author to do so. We are grateful to the IUCN SSC African Elephant Specialist Group for permission to reproduce the map of the Savanna and Forest Elephants from the African Elephant database 2007. Each map shows the boundaries of the 47 countries of Africa, some of the major rivers (Nile, Niger–Benue, Congo [with the tributaries Ubangi, Lualaba and Lomani], Zambezi and Orange), and Lakes Chad, Tana, Turkana (formerly Rudolf), Albert, Edward, Victoria, Kyoga, Kivu, Tanganyika, Malawi, Mweru, Bangwuela and Kariba. The geographic distribution of a species is indicated as:

- red shading = current range (or ranges)
- × = isolated locations considered to be separate from the main geographic range(s); some locations indicated by × may include two or more closely spaced locations
- red arrow = recorded from the island indicated by the arrow

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CHAPTER TWO

Thinking Mammals: An Introduction to African Mammals in Science, Natural History and Culture

Jonathan Kingdon

Darwin saw clearly that the succession of life on this planet was not a formal pattern imposed from without, or moving exclusively in one direction. Whatever else life might be, it was adjustable and not fixed. It worked its way through difficult environments. It modified and then, if necessary, it modified again, along roads which would never be retraced.

As the only thinking mammals on the planet – perhaps the only thinking animals in the entire sidereal universe – the burden of consciousness has grown heavy upon us. Nevertheless, in the nature of life and in the principles of evolution we have had our answer. Of men elsewhere, and beyond, there will be none forever.

Loren Eiseley, *The Immense Journey*, 1946

Because we are thinking animals and because we depend so much upon animals for our subsistence and economies, it is impossible for us *not* to think about the rest of animal life (although, of course, many urban people actively avoid such thought and do not come into contact with non-human animals). That said, *how* people think about, behave towards, talk and write about animals has always said more about the upbringing, personality, culture and history of the humans concerned than it can possibly tell us about an evolved being as complex and interesting as a mammal. A work such as this recognizes the many potentialities for distortion that come with that legacy, but the scientific principles and purposes it serves require that they be minimized. We have brought scientific methods to bear but, none the less, our work is still an artefact, a collaborative product by many authors. We, in turn, are products of our time, place and culture, all humble students of beings whose depths we are still ill-equipped to plumb.

When those mammals number many hundreds of species from every part of a vast continent, anyone interested in them, individually or severally, must depend upon all those naturalists and scientists who have provided us with records. What form those records have taken ranges from systematic details in pocket books or computers, tables of measurement, maps, drawings, film and other images, to dead or living specimens, and surely anecdotes, scribbles on napkins or scraps of paper etc. as well. In any effort to synthesize such diverse sources of knowledge authors, editors and readers of a work such as this must

extract some sort of truth-seeking portrait from a rich mix of reportage embedded in very varied cultural histories.

We also depend upon the serendipity that sometimes puts a passionate naturalist in a particular corner of Africa where she gets to tell us more about one sort of animal than had ever been learned in all of history. Names may seem invidious among a long line of illustrious naturalists, but it was Jane Goodall who introduced wild-living chimpanzees to the world, George Schaller who transformed our view of gorillas while David Macdonald created both interest and empathy for meerkats and foxes, but there are many others to whom we all owe deep debts.

While we have no option but to copy, assemble and integrate what other people have reported about the animals, many of us, especially those with first-hand experience of particular species, such as Jane, George and David, will be able to summon up, in the mind's eye, still richer internal visions of that animal's physical existence. But no matter how rich, how wide-ranging, deep and inspiring any one person's knowledge and writing is, it will belong to a time and place as will their experience. The fast growth of science itself ensures that all of us are in some sense pioneers that will very soon be overtaken, but that same growth will ensure that much of what goes on now, as before, will eventually become redundant. For knowledge to grow and deepen, the animals and their environments must continue to exist across the generations. African mammals incorporate many realities that are still hidden



Head of Blue Buck *Hippotragus leucophaeus* (from skins and contemporaneous documents).

from us, but for future humans, better equipped than we are, they may reveal much that is now unknown simply by *being* the animals they are.

In the effort to match verbal and other images to living, behaving mammals we exercise a very human faculty, but it is essential that we remember the ephemerality of our observations. Three centuries ago a hunter described a quality that he thought was unique to his quarry, he wrote, 'The coat looked like blue velvet in life but faded to lead colour in death'. Another hunter, who was also an amateur artist, tried to render its living appearance in water-colour, tinting his paper with cerulean blue. Appropriately this South African mammal was called 'Blue Buck', but by 1779 it was extinct. Something blue was gone and even the lead colouring of a few remaining skins now looks more like dust. The words of someone who had witnessed a quality that belonged only to life are more eloquent than the remaining dusty skins and skulls.

In the growth of science, skins and skulls, ideally deposited in an accessible museum, provided the first records upon which names and descriptions could be based. As science has progressed the range of recordings has vastly increased, but has it become any less cadaverous? Had that hunter had a tape-recorder would he merely have preserved the last cry of the Blue Buck? With an electronic tag would he have preserved an oscillogram of its heart's last beat? Of Africa's mammals many more will leave just such eccentric records of their existence in museums, recorders and in published words. For many species that is all that those with a curiosity about the mammals of Africa will find in the future.

While we have no choice but to be children of our time, attempting to place our work in some sort of historical perspective helps us define what is new about our own time. If we are self-conscious enough we may, perhaps, be less content to be passive witnesses to blue tints turning to leaden grey.

So where do texts and images of African mammals begin? Drawings and paintings, finer, more authoritative and better observed than almost anything depicted today, ornament many cave and rock-shelter

walls across Africa, testifying to the intensity of observation and importance of large mammals for our ancestors. It was images, but mainly words, woven into tales about Africa's most dramatic mammals that made a historical progression (but also a verbal chain that resembled 'Chinese whispers') from campfires in Africa itself, to markets around the Mediterranean, to be translated eventually into books, mainly illuminated or printed in Europe and Asia. A few species of North African mammals were physically transported to the circuses and menageries of ancient Rome where they became 'curiosities' just as they did later in northern European menageries. In China and India royal courts marvelled at giraffes and zebras. That legacy long ago made some African mammals familiar to the rest of the world. What child has not heard of lions, zebras and elephants? Their likenesses fill storybooks and plaster school-room walls, just as they ornamented the very first maps of Africa, but most people are still more familiar with images and stories about African mammals than they are with any sort of reality.

The curiosity and awe that fuelled gossip in tenth-century souks, that marketed medieval bestiaries, created a hunger for zoos in nineteenth-century Europe and went global with twentieth-century wildlife films, is not entirely separable from the scientific curiosity that finds expression in this book. Certainly the history of books about African mammals faithfully records the dominant preoccupations of their authors and of the times in which they were published. From our descendants we can expect a cold-eyed examination of today's technological state and the position our current culture took on our relationship with other animals. Even our own profile accounts in these volumes will not escape such scrutiny.

Before the invention of books, stories about animals were as ephemeral as the memories of those who heard them. Books changed that, but because they were invented far from Africa it need surprise no one that whatever facts might have been there to begin with became mostly myth and fable. Beast-based fables, such as those told by the slave Aesop about 2600 years ago, contained moral messages that eventually found their way into books. One of the most interesting examples of myth-creation or, perhaps, myth-reinforcement, concerned one-eyed giants, Cyclopes, that were reputed to have inhabited certain caves in Sicily. Bolstering, or, perhaps, originating, belief in these Titanic monsters were elephant skulls that were found in the same caves, with the nasal orifice interpreted as a single eye-socket in the forehead of large, but otherwise somewhat humanoid skulls! The rhinoceros, familiar enough to many Africans and South Asians, became transformed into the mythological unicorn in ancient China, Vietnam and northern Europe and acquired various attributes, including that of a horned symbol of fertility. Such ideas were still in circulation in Renaissance Italy, where Leonardo da Vinci imagined unicorns falling asleep in the laps of virgins! Likewise, two giraffes carried to Beijing in 1433 were acclaimed as magical 'Qilins', their capture and harnessing being paraded as emblematic of the Chinese Emperor's supreme power. By the time stories, body-parts or actual animals had found their way to the primitive cultures of Europe and Asia they were transformed by many similarly grotesque expectations or perversions.

The most pervasive and damaging of all cultural artefacts was a belief in several Mediterranean monotheistic cultures that animals were explicitly placed on earth for man's exploitation and that exotic animals were manifestations of 'thoughts' in the mind of an anthropomorphic creator god. The main 'purpose' of animals was their moral and symbolic role in a mental universe, they were essentially

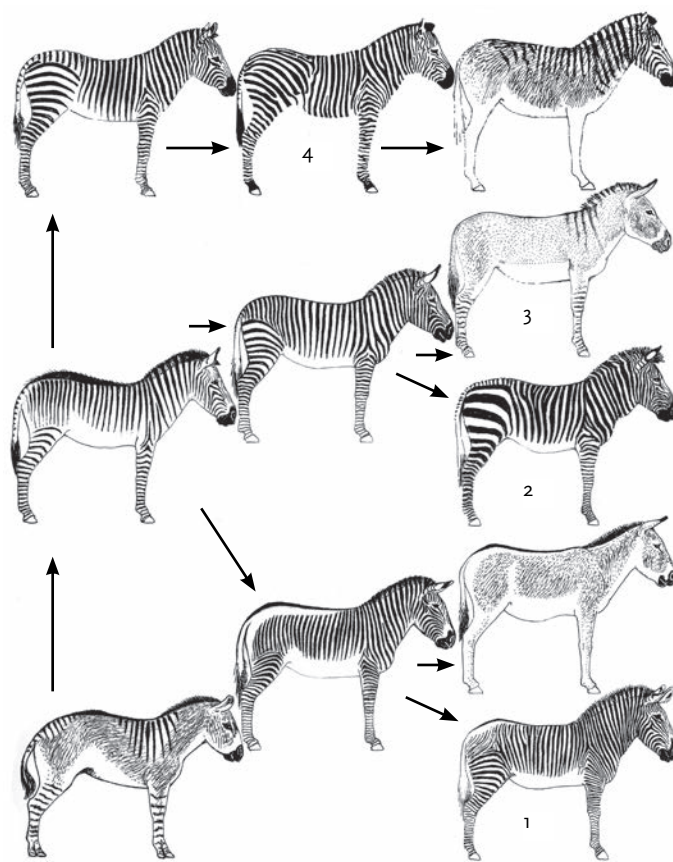
avatars, embodiments of concepts: thus monkeys, leopards, foxes, goats and rats were all manifestations of evil or 'the devil' in early Christian iconography, while purity found expression in a stoat! It was even believed that an animal went extinct when its 'creator' ceased to think about it! This anthropocentric (almost 'post-modern') tradition is still predominant in the thinking of large numbers of people, and it is still being reinforced by a variety of atavistic cultural thought-police.

In a history of the development of books and ideas about African mammals such ideas found expression in medieval 'bestiaries'. These emerged, from much earlier traditions, as the first of some four or five major phases. Intensely interesting as products of their feudal theocratic times, they now have little or no scientific interest. Likewise, traditional parables, typified by Aesop's fables, were among the first books to be published in Europe. Descendants of this tradition, in which animal characters speak for human stereotypes, continue to flourish, often in the form of cartoons, sometimes brilliantly funny but more often silly stories with cutesy names. Film, TV and DVD have, to a large extent, overtaken the book in this tradition.

Two rather different sorts of books and records emerged as European empires expanded into Africa, but the boundary between them was sometimes blurred. The year 1758 saw the publication of Linnaeus' tenth edition of *Systema Naturae*, where many African mammals were named and described systematically for the first time. This open-ended system wherein every organism could be placed, depended partly on written descriptions, partly on preserved specimens. Linnaeus, his contemporaries and his followers begged travellers to send them specimens to describe and their collection became a major *raison d'être* for many expeditions and one of the expressions of what has been called the scientific 'Enlightenment'.

Collecting specimens and measurements were among the primary objectives of the voyage of *The Beagle*, a small British navy survey vessel that circumnavigated the world between 1831 and 1836. Although it only docked in Africa for two weeks and was but one of innumerable exploratory expeditions sent out by European imperial powers, one passenger on *The Beagle*, Charles Darwin, ultimately changed humanity's perception of its relationship with the rest of nature. His ideas and writing continue to be relevant to how African mammals are viewed and valued.

The science of biology has many historical roots but Darwin's *The Origin of Species*, published in 1859, put the study of plants and animals, including humans, on an entirely new footing. While Darwin provided numerous examples from nature to exemplify the many dimensions of evolution by natural selection, most of his illustrations were drawn from Europe, Asia and the Americas, Africa being little-known to the outside world at that time. On his visit to Cape Town he learned that more species of plants were crowded together in the Cape of Good Hope than in any other quarter of the world and he took as serious, and in my view a more perceptive, an interest in African zebras than any contemporary scientist. He collected abundant evidence that mules and other inter-specific equid hybrids all tended to show striping on legs and shoulders, even when both parents showed none, and he witnessed, at first hand, barring on the legs and shoulders of individual horses. He wrote: 'I venture confidently to look back thousands of generations, and I see an animal striped like a zebra, but perhaps otherwise very differently constructed, the common parent of our domestic horse' (Darwin 1859). It has taken well over a century for comparable sensitivity and deep prehistorical insight to be brought to bear on the study, not just of zebras, but of African mammals as a whole.



Darwin's prediction corroborated? Tentative relationships between five equine lineages (after Orlando *et al.* 2009). This chart assumes (as Darwin did) that extant equines (right column and top middle) had striped ancestors. Reconstruction of common ancestor for all lineages centre left column.

Hypothesis: vertical stripes originated in ancient equid ancestor as modest 'grooming targets' on croup and shoulder. Stripes then spread to the rest of the body, neck and head (lower left). Increased contrast (black and white) made broadside views of the entire animal highly visible to conspecifics.

Separate banding of the lower legs extended upwards. When enlarged, horizontal stripes on hindquarters enhance the signal value of overall striping because the optical spacing of such stripes is visible at greater distances and is maintained regardless of viewing angle. This improvement in visual clarity appears to have been a later development in zebroid patterning. Ancestors of the three zebra species probably entered Africa in sequence (as indicated by numbers). Extant equine species, right column, from top: *Equus quagga*, *E. africanus*, *E. zebra*, *E. hemionus* and *E. grevyi*.

Later, with the rise of imperialism, trophies as well as specimens became the lure. Collecting trophies imitated and extended feudal hunting practices as a display of power and privilege. Books from this period were sometimes titled 'Records of Big Game'; others were essentially memoirs of shooting trips, but several, notably Frederick Courtenay Selous' reminiscences (Selous 1881, 1893, 1896) and President Teddy Roosevelt's two books, included some useful scientific information within a mindscape that envisaged eastern Africa as a land teeming with 'beasts of the chase'. The latter, best-sellers in their time, are particularly interesting for Roosevelt's ability to combine an almost medieval imagination with factual records. More than 150 forms of mammals were collected and named and the Roosevelt collection in the American Museum of Natural History remains one of the major reference collections of African mammals in the world. Yet Roosevelt introduced 'African Game Trails' (Roosevelt 1909), recalling his visceral:

joy of hunting the mighty and terrible lords of the wilderness, the cunning, the wary and the grim. ... there are dread brutes that feed on the flesh of man; and among the lower things that crawl, and fly, and sting, and bite, he finds swarming foes far more evil and deadly than any beast or reptile. ... there are creatures which are the embodiments of grace; and others whose huge ungainliness is like that of a shape in a nightmare.

(Roosevelt 1909)

Contemporary mockery of such conceits needs to be tempered by the realization that many contemporary perceptions are no less inconsistent and primitive.

A symbolic change in vocabulary took place in the mid-twentieth century when 'game' became 'wildlife'. This cultural phase coincided with the independence of African countries, the spread of television and the development of mass tourism bringing large numbers of visitors to the newly formed National Parks of Africa. Parks, field guides, research stations and very large numbers of tourists provide the contexts, rationales and economic support in which much of contemporary mammalogy takes place.

Now new perspectives are developing and the sort of seriousness that Darwin and before him Lucretius had brought to bear on their view of nature has begun to re-emerge from the shadows. The most recent revolution in the way African mammals are perceived can be quite as anthropocentric as any earlier manifestation. It is strongly reinforced by contemporary genetics and palaeontology, which have demonstrated, without ambiguity, the genetic affinity of humans with other mammals, indeed with all of organic life.

In this view of life, animals and humans are infinitely complex genetic accretions that reflect countless adaptations to the environments and biotic communities in which they evolved over huge stretches of time. Of course there is a downside to contemporary preoccupation with molecular science. It is still a closeted subculture, its safe benches very far from the world inhabited by the animals themselves. (Academic leadership in leading universities and research centres often remains as short-sighted as ever, more often than not favouring molecules over ecological, behavioural and whole-organism biology.) However, this phase must eventually give way to matching genomes with the behaviour and ecological adaptedness that the genes actually code for.

There are important philosophical dimensions to the huge expansion in knowledge that has been led by molecular science. We desire and pursue knowledge but we know that the enquiring mind is but one expression of being, one faculty of the processes that have given us life, one small detail of the process that generated meerkats, gorillas, chimpanzees and the people who tell us about them. Greater is the desire for life itself. We all desire existence, as it is, and for its own sake, whether we are one in a rare band of foragers or members of a race numbering seven billion today or ten billion in 50 years time. In that we differ not at all from any other mammal, but in coming to terms with our exploding numbers and our cultures' exclusive preoccupation with our own rights and indifference to the survival of other mammals we face new ethical dilemmas.

It is in such perspectives that African mammals have acquired a special interest in the twenty-first century. We now know that embedded within the various communities of African mammals there were, in recent prehistory, a diversity of bipedal primates that

included our own ancestors among their numbers. Unveiling the details of their evolutionary progression is a science still in its infancy but it is attracting some of the best minds of our time. We hope that *Mammals of Africa* will be a useful tool in the study of human origins, but most mammalogists would assert that their subjects need no human dimension to be of all-absorbing interest in their own right.

Beyond the present lie still deeper dimensions to the study of mammals. Because every one of us is a mammal we should, theoretically, be able to bring a large measure of self-knowledge to bear on the task of thinking about other mammals. When a mammal eats, drinks, excretes, copulates, gives birth, socializes, sniffs the air, trembles, dreams or sleeps, our personal experience of those activities is there to give us some insight as to what is going on in that other mammal – or is it? In fact that apparently straight-forward comparison is subverted by human culture. Eating, drinking, socializing, giving birth and all the rest are activities that have been so appropriated and ritualized by culture that most people perceive their expression in other animals as funny, embarrassing or, in many instances, offensive, even obscene and horrible. That horror, well illustrated by Queen Victoria's response to seeing an orang-utan ('frightful and painfully and disagreeably human') will continue to subvert the development of comparative psychology. It will slow the quest to explore how our fellow mammals think, and it will delay the changes in ethics that must be integral to our exploration of other minds.

When a culture persuades its adherents that other animals are obscene or funny when they perform the same functions as ourselves, that indoctrination effectively blocks both knowledge and empathy. Many cultures go still further, categorizing particular mammals as 'unclean', demonic or comical and have dogmas that enforce automatic responses of revulsion, fear or laughter when confronted by such animals or their images. It is just such indoctrination that blocks entire cultures from any appreciation of mammals as worthy subject-matter for adult intellect. Many, perhaps most, cultures permit children to indulge their natural interest in animals but then enforce coming-of-age customs that 'put away childish things', including fascination with animals. It is just such cultural denigration that has made an adult concern with animals into very much of a minority interest and our intellectual life is the poorer for it.

The biographies of several eminent scientists reveal how biological science and natural history at school allowed them to hang on to their 'childish' fascination with the natural world and later helped emancipate them from cultural brain-washing, while offering them a way of making a living as professional scientists (Wilson 1994, Hamilton 1996). While there is a respectable niche for biology and biologists in most modern societies, their subject-matter, animals, particularly wild ones, have retained their atavistic cultural association with childhood.

In Africa and elsewhere there is also a strong and negative association between living in a landscape inhabited by wild animals and in what is perceived as an 'undeveloped' past or, worse still, present. Such primitive attitudes are still sufficiently widespread for biologists themselves to feel the need to dress their science in 'adult', 'developed' robes, voluntarily narrowing the real scope of their discipline. Biologists have also had to create recognized niches within the larger society. These pressures have been strongest in countries that are still dominated by non-scientific cultures. Among the consequences are an allocation of biological science and natural

history to privileged enclaves: intellectual and physical ghettos outside the mainstream. As a result there are very few countries in Africa where animals, other than domesticated ones, merit much serious interest in the society at large.

For cultures that are intrinsically non-scientific (a majority), science has proved too useful for it to be proscribed, but a hostility that is specific to biology remains, strongly reinforced by predominantly non-secular education systems. Any serious enquiry into the existential meaning of the animal life that is all around us challenges pre-scientific orders of knowledge. It should not be forgotten that as recently as 1619, the Italian philosopher Lucilio Vanini, originally a Carmelite friar, was burned alive by the Inquisition for suggesting, among other heresies, that humans might have originated from apes: the institutions responsible for his murder are still influential (Namer 1980). The current guardians of non-scientific education/indoctrination know, and fear, biology's potential to subvert the dogmas of the past. They have a vested interest in keeping animals funny or grotesque and 'for children only' and their hostility to biology remains a huge obstacle to the scientific education and enlightenment of millions of young people in Africa and elsewhere.

Mammals of Africa is a handbook and inventory of the mammalian fauna of a continent. Other mammalian inventories of other continents have been published and are important for what they can tell us about the biological history and evolution of the modern world. Mammals, world wide, are of absorbing interest in many other ways but over and beyond the many insights that are essentially global, the mammal communities of Africa deserve special attention for several uniquely compelling reasons, some of which have been touched on above and in other introductory chapters.

For a start, the diversity of orders, families and genera is far higher than that of any other continent as our lists and tables confirm. Some likely explanations for such mammalian richness are discussed elsewhere (in several other introductory chapters), but much more remains to be discovered, so among the functions of these volumes are the advertisement of such lacunae and the provision of base-lines for just such studies.

The ecological and economic impact of mammals, especially of the many and numerous species of large mammals, impinges on rural African people in more significant ways than on peoples of other continents. Of all continents, Africa has the longest history of humans exploiting mammals as wild food. Hunting, both traditional and modern, legal and illegal, continues to play a significant part in human social relations, nutrition and recreation. When it comes to the husbandry of crops and livestock (activities that are much more recently developed than subsistence hunting), the impact of mammals is also pervasive. For centuries agriculturists have done their best to exclude wild mammals from their fields. As destroyers of their labour and of human subsistence most wild animals, quite naturally, were, and continue to be viewed collectively as, 'pests' or 'vermin'. Most field biologists will have encountered this total antithesis between their own fascination with the details of a wild animal's behaviour and the all-embracing disgust with which peasant farmers view the same subject. As agriculture expands, this ever-enlarging conflict of interest is still far from any sort of sensible resolution. On present trajectories it can only culminate in the extermination of many species of mammal, as has happened on all other continents.

Only a profound change in current cultural attitudes can deflect such a disaster. It has long been obvious that modern agriculture is rapidly destroying mammalian habitats right across the continent, yet, to date, no effective or compensatory demands have been required of large scale agricultural development. The ancient farmers' pioneering vision of 'reclaiming' fields and pastures from the 'wilderness' remains unchallenged in spite of two major innovations in a newly global civilization. One change is a vast amplification in the scale, scope and destructiveness of agricultural development due to science, technology and new agricultural machines, chemicals, genetic manipulation and the opening of international markets for African products. By the same token, science has emerged as humanity's most universal cultural achievement and our species' fastest-moving intellectual frontier. Yet, while science has also articulated many of the strongest arguments for conservation, it is still rare to find local people giving much value to any other 'use' of a landscape than for agriculture or commercial forestry. Provincial, nationalistic and sometimes precariously ephemeral, the political cultures of contemporary Africa have not been equipped to re-evaluate the role of modern agriculture. International institutions have been little better at re-thinking sensible limits for agriculture's and forestry's scope and role in the twenty-first century.

While it has always been known that all cultivated plants and animals have 'wild' ancestors, the complex ecosystems in which cultivars and domestic stock evolved still fail to elicit any serious interest from those who determine land-use policies. Likewise, recognition that our own 'wild' ancestors had evolutionary contexts that are profoundly relevant for humanity's future self-knowledge has yet to influence how we use land. Because uncontrolled hunting and the unimpeded progress of agricultural development is rapidly diminishing biodiversity and must eventually cut us off (together with all domesticated species and varieties) from our biological roots it is essential and urgent that agriculture's claims to monopolize land-use and land-use planning be challenged.

It is our generation that must take up that challenge and ensure that adequate samples of all natural ecosystems be preserved for future enjoyment, study and analyses by our descendants. We already know that they will have techniques infinitely superior to those available to us. It is the responsibility of our generation not only to put firm, scientifically defensible limits upon agricultural expansion. We must also initiate demands for revenue from the commercial use of land, on the argument that this is proper compensation for the valuable resources that have been and continue to be destroyed. Such revenue, demanded as of right, should fund the conservation of natural ecosystems and must eventually augment, perhaps even displace, the current dependence of conservation on 'charity'.

The title and content of this essay has contrasted the substantial reality of Africa's surviving mammals with the apparent insubstance and mutability of policies, books, records and thoughts. As all thoughts about animals must originate in actual encounters, there are a few easily listed situations in which people interact with animals directly, animal to animal. All the rest (and all that rest is mountainous) is second-hand, whether it be published science, hear-say, cultural baggage, camp-fire folk-lore or outright mythology. Reminding ourselves of the very limited ways in which humans can interact physically with animals helps keep the vast conceptual mountains we have erected around them in some sort of perspective. The practical

utility of seeing just how few these physical interfaces are is that it helps highlight what challenges are faced when we try to learn or think about animals. (It also shows what difficulties conservation faces.) The interfaces may be physical, as often as not culminating in death, but each one also has great potential for distortion of ideas about what animals *are*:

- 1 Nuisances, pests and parasites: crop-raiding mammals and human measures to deter, punish or kill them. Distortion through anger or fear.
- 2 Hunter and prey: the animal pursued, killed, eaten and processed. Distortion through appetite, the thrills of the chase or social braggadocio.
- 3 The human as prey: predators finding meat where they may. Distortion through terror.
- 4 Aids to hunting morphing into companionship: artificial selection morphing wolves into dogs. Distortion through sentiment.
- 5 Domestication: tended livestock as stored meat, milk, transport, power or pest-control. Multiple sources of distortion.
- 6 Animals as avatars, vehicles for symbol or myth: animals or their trophies kept or hunted for attributed ideas. Multiple sources of distortion.
- 7 Animals as subjects of scientific study: observation, capture and/or experiment; excavation of fossils and extrapolation through comparative anatomy. Involuntary sources of distortion include abstraction and generalization but this is the one area where thinkers are most deliberately conscientious about minimizing distortion. It is also an area where the welfare of animals has sometimes been neglected, to great shame and loss of popular support for science.

In sum, by far the most significant difference between mammal communities in Africa and those of other continents is the fact that humans and most of their primate ancestors have been an integral part of these communities for many millions of years. We *are* African mammals. An ancient lack of awareness of Africa, certainly of evolution in Africa, once deprived people of any possibility of correctly answering central puzzles of human existence: ‘where do we come from?’ ‘where is our ancestral home?’ ‘from what natural communities did we emerge?’ and ‘what is our place in the natural communities of the future?’

We cannot know how cultures will view or portray the mammals of Africa in the future but we can be certain there will always be people that seek truth in the concrete realities of living communities of animals and plants and in their decipherable histories. That quest will always be preferable to the culturally generated constructs and myths that have so grievously distorted our understanding in the past.

Science represents the single most radical and systematic departure from the myth-making of the past. It is a very specific manifestation of human thinking and one of its many triumphs has been analysis and formulation of the abstract principles that govern natural processes, including those that originated and sustain our own existence and survival. The educated public has had ample demonstrations that biodiversity has arisen by genetic drift and natural selection operating on populations that have somehow become separated and distinct. Behind such necessarily generalized insights the earth’s many predictabilities have been punctuated by what can only be called accidents – asteroids

arriving from outer space, the eruption of mountains and volcanoes, switches in ocean currents or the collision of continents. As Loren Eiseley remarked (in the opening to this essay) the catalogue of chaotic events that is prehistory has also created the very particular conditions, the specific opportunities, to which the ancestors of today’s mammals adapted. It is in the very nature of life to be a triumphant response to chaos and happenstance.

One of the primary tasks science has set itself is to reconstruct the long drawn-out manoeuvres of a single mammal lineage, our own, through all this accident-strewn terrain. Science has brought us close to the starting point for an entirely new appreciation for the role chance has played in the evolution and differential survival of humans and hominins. The hominin radiation was no less a proliferation of experiments in adaptation than were the Pan-African radiations of antelopes, mice, mongooses and mangabeys. Science now has to address the question of why only one member of that fecund radiation now survives.

If ‘strategic intelligence’ played its part in the survival of *Homo sapiens* its beginnings are sure to lie in just a few of the innumerable permutations of climate and geography acting on just one of many populations. The many skills of other hominins were eventually trumped by those of just one species. Knowing that evolution takes place in real space and real time forces us to survey Africa’s geography and dig her soils for clues as to exactly where the earliest ancestors of that singular lineage first emerged. Increasingly, the signs point to the territory south of the Limpopo but at this juncture it is, perhaps, the change in thinking that is as significant as the locality. We are discovering new significance, new depths of meaning, in the details of Africa’s history and geography and in the minutiae of behaviour and ecology. Sadly, opponents of science’s questioning effectively deprive the majority of young Africans of contact and participation in an unprecedented and exhilarating expansion of knowledge in which Africa and its mammals have taken centre-stage.

Darwin, alone in seas of incomprehension even greater than in our own time, wrote

No one ought to feel surprise at much remaining as yet unexplained in regard to the origin of species and varieties, if he makes due allowance for our profound ignorance in regard to the mutual relations of all the beings which live around us. ... Yet these relations are of the highest importance, for they determine the present welfare, and, as I believe, the future success and modification of every inhabitant of this world.

(Darwin 1859)

In trying to mitigate our ignorance and seeking answers to such questions in the light of contemporary science biologists are not alone. All thinking people now face a challenge that could only have surfaced in our time but it is a challenge that will not go away. Discovering our place in nature is a major frontier in contemporary thought and because of it we have no option but to be thinking mammals: our very survival depends upon it. New frameworks of thinking about mammals are developing and must go on developing in the minds and actions of the self-defined ‘Thinking Mammal’.

In the quest to provide modern scientific answers to so many puzzles we hope that this work will make a contribution and promote a deeper respect for mammals, including illumination of our own status, as one among many other African mammals.

CHAPTER THREE

The Evolution of a Continent: Geography and Geology

Daniel Livingstone & Jonathan Kingdon

I look at the natural geological record as a history of the world imperfectly kept and written in a changing dialect; of this history we possess the last volume alone ... of this volume, only here and there a short chapter has been preserved; and of each page, only here and there a few lines.

Charles Darwin, *The Origin of Species*, 1859

Geographic background

Africa is a large continent. With Arabia, with which it formed one land mass through most of its history, it has an area of almost 33,000,000 km², greater than that of Europe, Australia and the United States combined. It extends over 73 degrees of latitude, almost equally split north and south of the Equator. It extends from one temperate zone to the other and includes the full array of tropical and sub-tropical climates in between.

As described in detail in Chapter 5, the Congo cuvette and West Africa contain, or recently contained, large blocks of evergreen or deciduous forest, and there are smaller areas of forest elsewhere, but woodland, wooded grassland, grassland and various kinds of wetland, thicket, scrub, alpine moorland and other types of vegetation cover most of the continent.

Africa is home to the largest and two of the driest deserts on earth, and, on the seaward slopes of Mt Cameroon, receives one of the earth's highest rainfalls. Rainfall over much of the continent is low, and not only in the sub-tropical trade wind belts: desert conditions occur within 2 degrees of the Equator in Kenya. High African mountains carry glaciers even close to the Equator (although they are melting fast in the face of global warming; Kaser & Osmaston 2002, Mote & Kaser 2007). During the Quaternary ice ages glaciers were more extensive and descended to much lower altitudes (Osmaston 1967, 1989 and see Chapter 4, p. 43). Furthermore, Africa has spanned the southern temperate, southern sub-tropical, tropical and northern sub-tropical belts throughout the last 100 million years.

The evolutionary history of Africa's fauna cannot be understood only in terms of present geography or environment but needs to be viewed within the perspective of the evolving geological and

environmental history of the continent (King 1962, Fage 1963, Janis 1993, Adams *et al.* 1999, Denton 1999; and see Chapters 4, 5 and 6). The way in which the continent was formed shapes the physical surfaces that support life, and its tectonic history shaped the origins of its mammalian fauna (Maglio & Cooke 1978, Kumar & Hedges 1998). Here we first consider some of the gross features of Africa's physical geography and geology, interleaving discussion of some of the implications for mammalian evolution and biology.

Plate tectonics: separations and collisions of continents

No geologic development of the last hundred years has had so great an effect on our understanding of the earth as the discovery that continents have moved around on its surface. The continents are the surface expression of crustal plates, which sometimes move together, colliding to form super-continent and throwing up mountain ranges, or sometimes split apart to form an array of more or less separate land-masses such as we see in the world around us today. The remarkably exact match between Africa's western coastline and the eastern margin of South America has been noticed ever since they were first mapped. That correspondence was the first evidence for the longitudinal fracture of an earlier land mass and its break-up into drifting continents and islands. A compelling body of evidence now shows that not only Africa and South America, but also India, Australia, Antarctica and Madagascar were once parts of the single southern super-continent Gondwana.

Still earlier, in the Permian (223–190 mya) a single land-mass called Pangaea had formed, only to become bisected, around 180

						PRECAMBRIAN	
mya	Epochs		mya	Periods		mya	Eras
	Pleistocene 1.6		70	65.5	245	570	PROTEROZOIC
5	Pliocene 5.3						
10	late				280	1000	
15	Miocene mid	100	Cretaceous		286		
20	early				320		
25	23				360		PROTEROZOIC
30	Oligocene late				360	2000	
30	early	150		144	400		
40	late		Jurassic		408		
40					440		
50	Eocene mid	200			450		ARCHEAN
50	early				500	3000	
60	55.8		Triassic	208	505		
65.5	Palaeocene	245			570	3750	

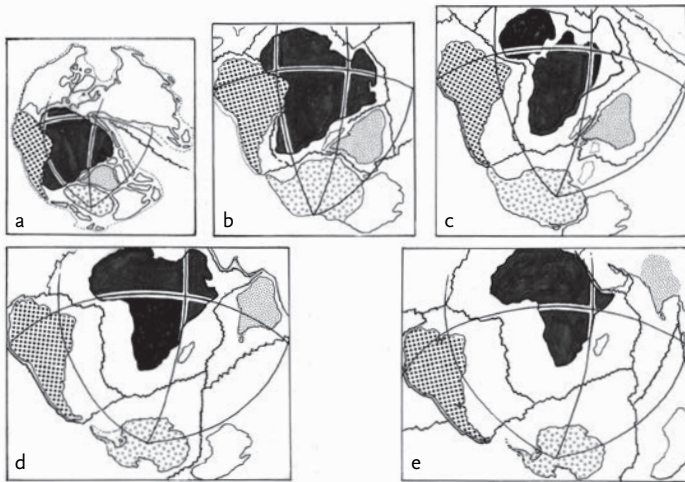
Timescale chart. Shows Eras, Periods and Epochs from the Archean (3750 mya) to the Present. Geological timescale currently estimated as: Palaeocene 65.5–55.8 mya; Eocene 55.8–33.9 mya; Oligocene 33.9–23.0 mya; Miocene 23.0–5.3 mya; Pliocene 5.3–1.8 mya; Pleistocene 1.8 mya to present day.

mya, by the Sea of Tethys to give rise to Gondwana in the south and Laurasia in the north. Where continents are moving away from each other, as the New World has moved away from the Old during formation of the Atlantic Ocean, their past positions are relatively clear. Lava welling up along the mid-oceanic ridge bears the signature of the earth's magnetic field at the time it solidified. That magnetic field has undergone a series of reversals, which have been mapped in great detail by oceanographers at sea and dated radiometrically by stratigraphers on land. We therefore have a good understanding of the times when Africa separated from North and South America and when it separated from the rest of Gondwana. We have also learned much about the break-up of that southern super-continent into Australia, Antarctica, India and Madagascar.

Things are much more complicated where plates collide, and in the case of Africa's relationship with Eurasia it is just such continental connections that are of central interest to mammalogists. Unfortunately there is no simple palaeomagnetic chronology to draw on, and the collisions disrupt or destroy geological evidence from the times of merger. The details of collision between Africa and Eurasia are, and are likely to remain, much fuzzier than the details of Gondwana's break-up (Dercourt *et al.* 2000). None the less, it is known that Africa's northward movement slowed or halted after about 37 mya and that some form of connection or corridor permitted faunal exchange by about 27 mya. Actual suturing between Arabia and Asia was as late as 16.5–15 mya.

Africa is unusual in having stayed very largely in the same attitude, and at similar latitudes, since the origin of mammals, with only some 20 degrees of northward movement and a small measure of counter-clockwise rotation. While North and South America drifted away from Europe and Africa, and while Australia, Madagascar and India split away from Antarctica and drifted to their present positions, Africa moved much less. Other continents and plates drifted away to collide with each other, throwing up such mountain ranges as the Andes, the Cordillera and the Himalayas, but Africa, by comparison, held its place. None the less, collision with Europe between 37–15 mya has thrown up one folded mountain range, the Atlas and Tell Mts, of the type so common elsewhere and, in Europe, the northward movement of Africa moulded the Mediterranean and played its part in pushing up and folding the Alps (Stampfli *et al.* 2001).

The splitting of continents is driven by currents deep within the mantle of the earth and its earliest manifestation on the surface is doming above 'plumes', which create 'hotspots'. There are several such domes in contemporary Africa, the highest and most extensive being Ethiopia (King & Ritsema 2000, Rogers *et al.* 2000, Pik *et al.* 2003, Goudie 2005). When domes eventually split open the cracks become rift valleys that gradually widen (Pritchard 1979). The South Atlantic Ocean is the best example of a long, north–south rift valley that opened up and let the sea in. The Red Sea, a rift valley that opened up to let in the Indian Ocean about 10 mya (Hempton



Reconstruction of Africa's tectonic history from circa 250 mya to the present. Africa's northward progression and Equator's southward shift and tilt indicated by three notional degrees of longitude in relation to Equator.
 a. Pangea at circa 250 mya.
 b. Gondwana breakup at 115 mya.
 c. Africa disconnected on all sides and Saharan shallow sea at 80 mya.
 d. Continental plates widen west, east and south of Africa at 39 mya.
 e. Distribution of former Gondwanan continents and plates at Present. In part after Smith *et al.* (1994) and de Wit *et al.* (1999).

1987), exemplifies an early phase in the creation of oceans. It is also a reminder that the further fragmentation of Africa, the central core of ancient Gondwana, continues: today's rift valleys are future seas and oceans.

One result of continent formation is that the upwarps that once lifted the margins of rift valleys remain close to their parent land-mass's new shore-line. This is most vividly illustrated by both sides of the Red Sea, which are lined by long north-south mountain chains that end abruptly along typical rift valley escarpments. The margins of the Atlantic rift valley are also still visible in a long chain of raised ground along most of the length of Africa's western edge but its former escarpments have been worn away by more than 100 million years of erosion by rivers and modified by subsequent flexure of the land surface within Africa. During the Cretaceous these rift margins were still high mountains that yielded montane floras (R. Morley pers. com.). Fracture of the continent's eastern coast was still earlier, so former uplift is only perceptible in ancient hills and mountains close to the Tanzanian and Mozambique coast.

Sometimes the fusion of continents is permanent, as India's suture onto Asia; sometimes it is intermittent, as Afro-Arabia's connections with Eurasia. Collision of India with the Asian land mass began more than 50 mya but major uplift began about 23 mya (Aitchison *et al.* 2005). This had a profound indirect influence on Africa and its fauna because, by throwing up the Himalayas, this collision created a rain-shadow stretching from the Gobi Desert and Sinkiang through Persia and Arabia to the Sahara. This effect was augmented by plate movement further east, which disrupted the movement of heat from the Pacific towards India and Africa. It is thought that from the early Miocene onward moisture off the Pacific was intercepted by South-east Asia (Cane & Molnar 2001).

Whatever the causes, an extensive belt of dry land required all migrants into or out of Africa to cross an unforested, often arid or

semi-arid corridor more than 30 degrees north of the Equator. The most significant tectonic events for our understanding of today's mammalian fauna were those that brought Africa into physical contact with Eurasia. These began no earlier than about 23–27 mya. The evolution of mammals was probably influenced strongly by closure of the Straits of Gibraltar between the Mediterranean Basin and the Atlantic Ocean between 5.6 and 5.32 mya (Clauzon *et al.* 1996, Duggen *et al.* 2003). Named the Messinian Salinity Crisis, the near-total evaporation of the Mediterranean created a vast, deep depression, floored with salt lakes and pans and bounded by the cliffs of continental shelves, that could have been even a more formidable barrier than the Mediterranean Sea itself. While the Messinian probably created a dry land corridor between continents it also saw the start or intensification of desert conditions in the Sahara, yet another obstruction for inter-continental migration.

While the position of continental plates is now well understood, the roles of mantle plumes, superplumes, downwellings and their influence on changing land and sea levels remain little known. None the less, the earliest formation of Antarctic ice in the early Oligocene (32–30 mya) was linked with falls of between 30 and 90 m in sea level. We still rely on records of the first appearance of fossils from newly immigrant fauna to suggest how Africa exchanged mammalian stocks with the rest of the world. Such new arrivals imply some form of physical bridge shortly before their fossils appear in Africa for the first time.

Continental origins of placental mammals

In recent decades it has become clear that primitive mammals and proto-mammals were a significant part of the vertebrate fauna of the world for a very long time during the Mesozoic (65.5–225 mya). Taking into account the sources of various ancestral mammals and the biotic communities in which placentals would later evolve, we should not forget the Mesozoic history of the continent, part of which was spent as an integral part of the megacontinent Pangea, and part as a component of the southern super-continent Gondwana.

Over all of this time mammals were less important than dinosaurs and other reptiles, and most of those ancient mammals were very different from modern placentals (Kemp 1982, Rose 2006). Mesozoic mammals known before the present decade were small, unspecialized, insectivorous and apparently nocturnal, but recent discoveries show that by the middle Jurassic some were highly specialized for aquatic life (Ji *et al.* 2006), by the late Jurassic some were fossorial (Luo & Wible 2005) and by the lower Cretaceous some were large enough to prey on small dinosaurs (Hu *et al.* 2005). Mesozoic mammals that have been collected in Africa so far do not show such flamboyant specialization (Jacobs *et al.* 1988, Krause *et al.* 2003, Kielan-Jawarowska *et al.* 2004).

Today there is a gathering consensus, fuelled mainly by new, robust molecular phylogenies, that extant superorders of placental mammals emerged at about 105 mya according to Springer *et al.* 2003 and Bininda-Emonds *et al.* 2007. The basic distinction between Eutherian (placental) and Metatherian (marsupial) stocks is even older; fossils of both have been found in lower Cretaceous beds with an age of 125 million years (Ji *et al.* 2002, Luo *et al.* 2003), essentially doubling the age of these two groups. Genetics and palaeontology now broadly agree that the fundamental split between marsupial and placental

mammals was established by 125 mya (Bininda-Emonds *et al.* 2007, Murphy *et al.* 2007, Wible *et al.* 2007). Most early placental lineages have gone extinct but at least one that gave rise to the modern radiations survived. Where it survived and then diversified has been disputed but the bulk of current evidence suggests Asia, which is consistent with the sparse geological record for mammals in Africa. No marsupial survives in Africa, although marsupials are known from African beds of early Oligocene age (Crochet *et al.* 1992).

After South America's break-away about 100 mya, Africa (at that time including Arabia) began a long period of almost total separation from all other continents. The influence of this isolation on the history of African mammals has only begun to be appreciated in recent years (Kumar & Hedges 1998).

That protracted isolation underpinned the evolution of such striking indigenous elements as the Afrotheria (elephants, hyraxes, sirenians, aardvarks and others), all of which evolved in Africa during this period (Springer *et al.* 1997). This rather limited spectrum of mammals, all of which are very specialized today, looks much more like the progeny of a very early chance colonist than the vestiges of an indigenous placental parent population (Seiffert *et al.* 2004). Zack *et al.* (2005) have claimed that some Palaeocene hoofed mammals in North America are close relatives of one extant sub-group of Afrotheria, the macroscelidians (sengis or elephant shrews) but Tabuce *et al.* (2007) have shown that hyraxes and macroscelids were already well differentiated by the Eocene and that the Afrotheria must have evolved in Africa from a very much earlier common ancestor, possibly allied to a hysodontid condylarth.

The established approach to the history of evolutionary divergence used to be totally dependent on the morphological fossil record. Unfortunately the absence of evidence for a particular lineage at a particular place and time is not evidence for its actual absence. The oldest known fossil of a mammal taxon shows that the mammal had evolved by its time, but leaves open the possibility of a long previous history that goes undetected, perhaps because conditions were not conducive to fossilization, or because relevant fossils have not yet been found and identified. Also, preservation of mammal skeletons is seldom close to complete (Maglio & Cooke 1978). Fossil teeth are singularly informative, but where only teeth are available, as is often the case (especially for the earlier part of mammalian evolutionary history), the identity and phylogenetic position of the mammal that chewed with them may be less than certain.

Until recently fossil mammals in Africa had mostly come from a very few sites, most of them Miocene or later and all of them after the K–T event at 65.5 mya. In effect the fossil record indicated that the orders of mammals were of Cenozoic age. Mesozoic mammals seemed to be small unspecialized creatures that came into their own after the demise of dinosaurs. Released from the competition and predation of those dominant reptiles, mammals were seen to have evolved and diversified very rapidly during the early Cenozoic.

The idea of such a late development of mammals lost some of its credibility when it was demonstrated that by the early Cenozoic, Africa, South America, Antarctica, Australia, India and Madagascar were separated by wide water gaps from each other and from the rest of the world. Molecular methods show that the fundamental divergences between the orders of mammals are much older (Bininda-Emonds *et al.* 2007, Murphy *et al.* 2007). Even such closely related orders as rodents and lagomorphs diverged close to the

Cretaceous/Palaeocene boundary (Asher *et al.* 2005). Although the full-blown modern orders may be mostly Cenozoic in age, the underlying differences between those orders arose well back in the Cretaceous.

Estimates of the times of divergence can still be wildly discrepant. It is not uncommon for the molecular estimate for the separation of two evolutionary stocks to be very much older than that provided by the oldest known fossils. In mammals the discrepancy seems to get worse and worse as we investigate older and older divergences. This is particularly well illustrated by the primate tree shown in Volume II.

Where the details of fossil or extant anatomy have been well studied or reviewed in the light of new knowledge, the most recent molecular phylogenies have turned out to be broadly accordant with morphological and palaeontological ones (Archibald 2003). There have been several major surprises, notably recognition of the superorders Afrotheria, Laurasiatheria and Euarchontoglires (Hedges 2001, Madsen *et al.* 2001), and also some within lower-level taxonomic groups, such as the Carnivora. The cheetah lineage *Acinonyx*, which evolved in North America, probably as the main predator of American pronghorns and deer, seems to have gone through more than one intercontinental exchange (Johnson *et al.* 2006). Similarly, ancestral zebras and canids originated in North America. Such histories raise still-to-be-resolved questions of how and when such lengthy dispersals took place.

It is likely that two major taxa, notably the ancestors of today's caviomorph rodents and platyrrhine anthropoids, crossed from Africa to South America. It has been suggested that these were the outcome of chance rafting events; a less likely explanation could be movement across oceanic rises when they were above sea level.

There were also movements between Africa and the separated parts of East Gondwana. Carnivores, tenrecids and primates moved between Africa and Madagascar during the Palaeogene. In the case of Madagascan strepsirrhine primates an Asian origin has been suggested (Marivaux *et al.* 2001) but is generally considered unlikely. Angiosperm plants suggest dispersal from Gondwanan Africa to India as it drifted north to Asia during the Cretaceous and Palaeocene (see Chapter 4), and it is remotely possible that some African mammals might have reached India as it drifted north to Asia; if so, no fossil or other evidence has been found. The only hint of an early placental mammal in Gondwana has been the recent discovery of some teeth in Australia that were attributed to a mesozoic erinaceid (over 100 million years old, Rich *et al.* 1997). Placental mammals appear to be of Laurasian origin.

Africa–Eurasia connections and disconnections

With such a history one might expect the original fauna of Africa to consist mostly of species inherited from Pangaea, and to resemble that of Gondwana more than that of Laurasia. There are, in fact, some vertebrates, such as lungfish, and some ancient plant lineages, that seem to be descended from Gondwanan ancestors. For the most part, however, the vertebrates of Africa are more like those of Eurasia than those of the rest of Gondwana (this similarity between African and Laurasian biotas is apparent even well back into the Mesozoic, when dinosaurs were a significant part of all the continental faunas),

but a high proportion can be attributed to more recent invasions or exchanges. Gheerbrant and Rage (2006) have provided an enlightening treatment of the history and affinities of the African vertebrate fauna. They show that a continuous long-lasting land connection was not re-established between Africa and any part of the outside world until the Miocene, when intermittent attachments of Afro-Arabia to Asia were formed.

Mammalian exchanges in north-western Africa appear to have been small in scale and infrequent, which suggests that the water gap between north-west Africa and Iberia has functioned as a barrier; no direct exchanges between Europe and North Africa have been demonstrated before the Messinian (5.7–5.3 mya) (Kowalski & Rzebik-Kowalska 1991, Thomas *et al.* 1982). However, the palaeogeographic maps of Smith *et al.* (1994) do suggest the possibility of a route that did not necessarily involve crossing a

deep strait. On this restless earth there are few bits of land that have been such close and constant companions as Spain and North Africa. Sometimes bits of Africa have been attached to Spain, with the water barrier lying south of them. Other times bits of Spain have been closer to Africa than to Europe, with the water barrier lying north of them.

Likewise, part of southern Italy and Sicily are the northward extension of a basin that in the late Miocene became detached from the North African shelf and sutured onto the rest of Italy (Stampfli *et al.* 2001, Rook *et al.* 2006). Like other Gondwanan fragments, notably India and parts of Indonesia and Australia, that have become embedded in or close to their northern continental neighbour, these chips off continents could have rafted placental mammals but, so far, there is no evidence that they did.

Apparently connections were never sufficiently sustained between Africa and Eurasia for a wholesale exchange of fauna, like the one that followed establishment of the Isthmus of Panama, but exchanges were frequent enough, and significant enough, to create many faunistic resemblances between Africa and Eurasia.

Biogeographers distinguish between three types of dispersal:

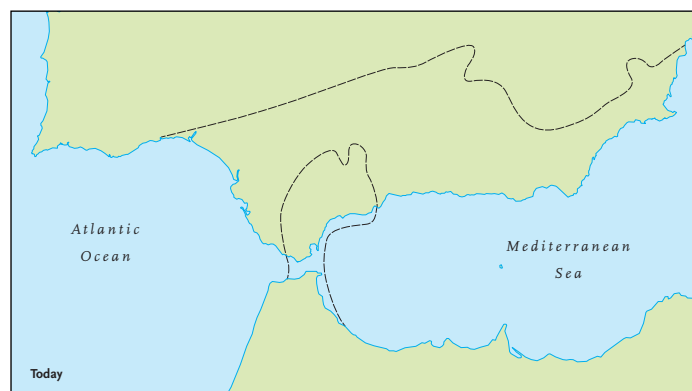
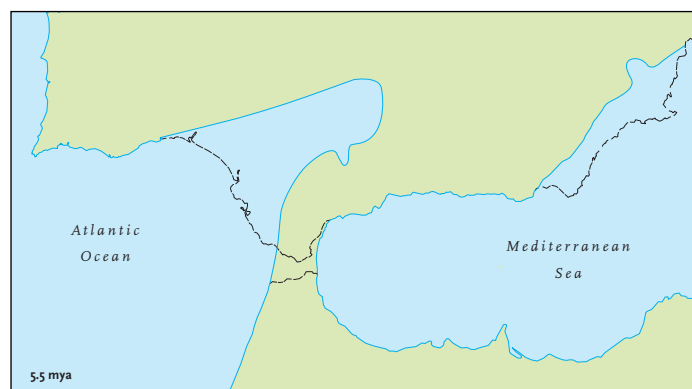
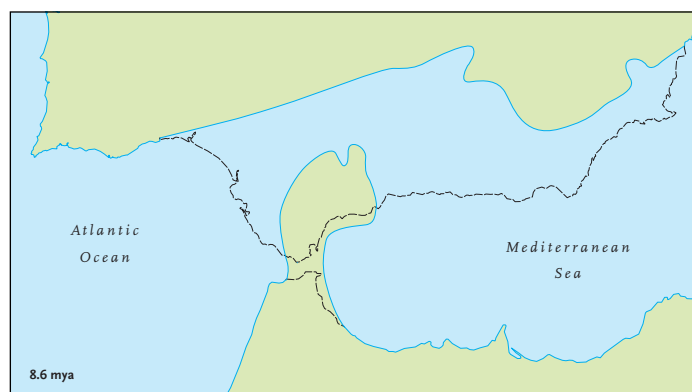
- 1 Along **corridors** that permit the passage of most or all of a biota.
- 2 Across **filter bridges** that selectively admit only a small part of the total biota.
- 3 **Sweepstake** dispersal over wide water gaps by accidents too rare to be observed but significant over geologic time and certainly very significant in terms of potential for genetic proliferation of the immigrant.

Sweepstake routes probably account for a very small number of colonizations, such as the ancestral founders of the afrotherians, the anthropoid and strepsirrhine primates, creodonts, anthracotheres and some rodent groups. All these appeared, or can be extrapolated to have appeared, in Africa well before solid land connections arose in the Miocene.

Since the start of the Miocene, Africa and Eurasia have sometimes been joined by filter bridges, via the Middle East (as they are now), at Gibraltar, and possibly via sills and islands to southern Europe. These later filter bridges selected for mammals that could live in grassland, desert, dry thickets or woodlands, such as antelopes and their predators. Although longer-lasting than bridges across the Mediterranean to Europe, the Middle Eastern route was always too dry for mesic vegetation and obligate forest dwellers. Such equatorial forest species as Okapi, Bongo and Gorilla had Eurasian ancestors that were all non-forest types and have adapted to a forest environment within the last 10 million years (Stewart & Disotell 1998, Kingdon 1990, 2003).

The three dispersal categories are not entirely discrete and can grade into each other. Intercontinental dispersal of flightless terrestrial mammals can sometimes be regarded as sweepstake events, especially the earlier ones, but most later biotic exchanges probably took place over filter bridges.

Rafting is the usual mechanism invoked to permit sweepstake colonization, and the most likely sweepstake migrants would be small and able to live in the branches of drifting trees or on floating islands. It should not be common among large mammals less well suited to long survival on a floating island and it has been rare even



Sketch maps of supposed coastline of NW Africa (Morocco) with Eurasia (Spain) at 8–6 mya, 5.5 mya (Messinian) and Present. (After Smith *et al.* 1994 and others.) Black dotted lines indicate putative changes in coast lines.

in the dispersal of squirrels (Mercer & Roth 2003). Sweepstake dispersal seems to have permitted chameleons to reach Africa from Madagascar and lemurs, carnivores and hippopotamus to go the other way. These dispersals were rare accidents – all the carnivores of Madagascar are descended from one immigrant species (Yoder *et al.* 2005). When several groups of mammals cross an intercontinental water barrier at about the same time there is reason to suspect that they may have used island way-stations to aid their passage. Islands too small and land bridges too transitory to appear on the maps of palaeogeographers could have permitted the movement of primates, creodonts and some rodents between Eurasia and Africa in the late Cretaceous or early Palaeogene.

Although there is no basic difference between crossing from one island to another and from one continent to another, distances between islands are commonly shorter, making sweepstake dispersal between islands more likely. It is worth noting, however, that Spain and North Africa have never been far apart since late-Cretaceous time. Water gaps between the various parts of Europe were commonly wider albeit less lasting (Smith *et al.* 1994). The earliest exchanges were possibly between western Europe and Africa. Then a second route opened up to Asia, and finally, with establishment of more frequent land connections, many more mammals passed between Asia and Africa.

Sea level changes further complicate the picture of inter-continental connections, especially where the sea is shallow and the submarine slope gentle. A small change in sea level can make an enormous difference in the ability of mammals to spread from one continent to another, or to island-hop between them. Smith *et al.* (1994) provide a sobering evaluation of the evidence on which such summaries as theirs are based. In addition to the problems of colliding plates and changing sea level, it is not always easy to recognize a past shoreline in the geologic record. Uncertainties too small to be of interest to plate dynamicists can be vital to mammalogists.

After about 23 mya faunal exchanges with other continents brought in additional ancestral mammalian stocks, such as a succession of carnivores, antelopes, giraffes, pigs and hippo-like mammals, all groups that are characteristic of Africa's fauna today.

When the fauna of a smaller system meets that of a larger one the smaller system tends to lose out. This is what has happened time and again to the fauna of oceanic islands (Cox & Moore 2000), but species that have evolved life strategies that are exceptionally well-adapted to local conditions tend to endure. When fauna from Asia entered Africa the outcome was not necessarily ruinous for the mammals already in Africa. Placental carnivores probably contributed to wiping out African creodont predators, despite their rich diversity, their specializations and the size advantage of the largest ones (which could be 3 m long! – Rasmussen *et al.* 1989). But among the Afrotheria, which had until that time succeeded only in sending tenrecids to Madagascar, the Proboscidea spread with great success to every continent but Australia and Antarctica.

Africa, of course, is a big and diverse system, so its fauna was adapted to many different habitats and to the competitive and predatory pressures that came with them (Grubb 1999). Among larger mammals, Africa's success in colonizing the outside world, though impressive, was limited mostly to three groups: elephants (Proboscidea), monkeys, apes and hominins (Anthropoidea) and, rather later, antilopine ancestors of the sheep and goats (Caprini).

Changing landscapes on a stable continent of ancient rocks

Africa appears to have moved rather little with respect to the earth's axis of rotation during the last 200 million years, and, while its northward movement was instrumental in creating the European Alps, since their formation Africa seems to have been relatively stable with respect to the convective circulation of the mantle. None the less it has had a highly dynamic geological history.

From at least 65 until 30 mya it was a relatively low-lying continent with widespread deep weathering (Schluter 2006). Exposed Precambrian surfaces are of great extent and are known as the 'Precambrian Shield'. These surfaces are not always flat and have been subject to tectonic forces that have either perforated and overlaid them with lava, as in Ethiopia, down-warped them as in the Zambezi valley (Thomas & Shaw 1991, Goudie 2005) or up-warped them along numerous swells, notably those in East Africa and around the Congo basin.

In other continents large areas of low-lying land have previously been submerged beneath the sea by various combinations of rising sea level and tectonic warping. Africa, too, is thought to have had a well developed seaway during the late Cretaceous (the Trans-Saharan Seaway), which was caused by plate tectonic suture between the Niger Delta area and Libya, temporarily separating Africa into two terranes. The suture failed in the Maastrichtian/Palaeocene, when the Niger Delta began to form. Since 30 mya much of Africa has lain at too high an altitude to be flooded by either local or world-wide changes in sea level. Small areas of marine sediment occur here and there around the African coast, but marine sediment also occupies much of low-lying northern Africa, especially under the Sahara Desert, which is extensively underlain by marine sedimentary rocks. Most of the African continent, however, is composed of very old metamorphic, volcanic and plutonic rocks, covered in places by a thin and discontinuous mantle of much younger fluvial, lacustrine and terrestrial deposits.

There is a sharp physiographic contrast between highland southeastern Africa, most of which is a plateau 1000 m or more above sea level, and north-western Africa, much of which lies below 500 m (King 1962, Hamilton 1982). As summarized earlier, many of Africa's uplands, particularly those close to the continent's margins, derive from ancient uplift left over from the break-up of Gondwana, but some of these have been augmented by much later tectonics. In terms of understanding complex mammalian biogeography the distinction between ancient massifs and more recent volcanic mountains is crucial, even when the two are very close to one another. For example the base of volcanic Mt Kilimanjaro is less than 20 km from the relatively low but ancient Pare/Usambara mountain chain, yet the latter shelters very many endemic animals and plants while Kilimanjaro has very few, all recently evolved. Thus the 'older' Angola Pied Colobus *Colobus angolensis*, which occurs down the coast, also occurs in the Usambaras, while the 'newer' Guereza Colobus *Colobus guereza* has colonized Kilimanjaro from the north-west (Kingdon 1971). The Usambara and Pare mountains belong to a wide scatter of ancient continental margin hills and mountains, which, together with choice forested localities on the coastal littoral, including Zanzibar I., are rich in endemic organisms.



Map of Precambrian surfaces in Africa.

Volcanism and the emergence of swells and basins

Before 30 mya continuous volcanism was largely restricted to Cameroon, although there was volcanic activity for about 10 million years close to the place where the southern Ethiopian Rift crosses the Kenya–Ethiopia border, and for shorter periods elsewhere. Around 30 mya volcanism began simultaneously in many parts of the continent wherever rising hot mantle plumes reached the crust (Burke 1996).

Plume-driven continental doming and rifting of Miocene and later age, especially in East Africa and Cameroon, punctuates the broader pattern of extensive surfaces of Precambrian Shield (Cox 1989, Goudie 2005). By thrusting up blocks of older rocks, such as Rwenzori, and by generating volcanoes such as Cameroon, Elgon, Kenya, Kilimanjaro and Rungwe, rifting has provided a sprinkling of high mountains across Africa, as well as creating its rift valleys and, through the formation of deep trenches, warpage and craters, many of its lakes. The high mountains rise from a plateau of much lower altitude, and are limited in areal extent (UNESCO 1971). Only in Ethiopia has Cenozoic volcanism produced an extensive highland area. All of the rift-associated highlands, extensive or not, date just from the mid-Tertiary, with domes first forming about 45 mya (Pik *et al.* 2003) but actual rifting starting about 30 mya (Burke 1996). The geologically young domes have been characterized as ‘hotspots’; while the mantle plumes that lie beneath them have acquired geological names, Ethiopia has been thrust up by the Afar plume, the Drakensberg mountains rise above the Karoo plume and the Angolan Bie plateau lies above the Parana plume (Gilchrist & Summerfield 1990, Moore & Blenkinsop 2002). Other significant hotspots are the Hoggar, Tibesti and Darfur massifs, the Adamawa uplands of Cameroon and, of course, the string of uplands associated with the East African Rift Valleys (King & Ritsema 2000, Goudie 2005). The latter probably derive from more than one plume (Rogers *et al.* 2000) but the entire East African rift system has been attributed to



Present-day topography showing 1000 m contour.

the continent’s northward movement over a single very extensive plume (Ebinger & Sleep 1998). The opening of the eastern rift has been dated to 15 mya (Grove 1983).

With the appearance of doming a pattern of basin and swell structures became established over much of Africa. Many of the swells are capped with volcanoes, and one might be tempted to attribute their height to accumulation of volcanic rocks. Some of them, however, such as those around the Congo and Kalahari basins, have no volcanoes on their crests; it seems likely that all the swells result from flexure due to low-density melted rocks beneath them.

The swells, volcanoes and rifting, all of which started at about the same time, might have been influenced by collision of the African plate with Eurasia (which may also have helped keep the African plate from moving farther north). However, King & Ritsema (2000) have shown that mantle plumes are directly responsible for most of the basin/swell topography of Africa. They are also likely influenced by the onset of new imminent plate boundaries along the East African Rift (Burke 1996) and the formation of constructive plate margins. Although there are similar structures on the surfaces of Mars and Venus, the swell and basin form of the African continent is unique on earth and may be a product of the formation of new plate/terrane boundaries.

Basins and lakes

The swell and basin topography of Africa has had a profound effect on the hydrology of the continent. During dry periods depressions tended to be basins of internal drainage, but during wet ones some of the basins overflowed and cut rivers to the sea (Beadle 1974).

Every major African basin has had one or more sumps where waters form freshwater or salty lakes (now or at some time in the past). Over geological time the location of such sumps can change with the wholesale tilting of land surfaces or they can be drained

by deep-cutting gorges or down-warps; uplift tends to hide or dismember the evidence for previous drainage basins (Partridge & Maud 1987).

Lake 'Mega-Chad' has periodically occupied much of the Chad Basin. The Niger inland delta covers a sizeable area of the southern portion of the Eldjoug Basin while the smaller Taodeni depression lies much further north. Likewise, Tidikelt is the principal south-westerly sump for the Sahara (or Gabes) Basin while the lakes around Nefta drain the north-east (Griffin 2002). The Sudd swamps were, according to Salama (1987), a lake in the Tertiary and this region has remained a well-established sumpland for the southern part of the Sudan Basin. In south-western Africa the Okavango and neighbouring sumplands collect waters near the centre of the kidney-shaped Kalahari/Cubano Basin while the Etosha pan lies close to its north-western margin (Buch 1997). In East Africa the effect of swells and basins on river drainage has been greatly complicated by activity of the Great Rifts, all of which have a scatter of rift valley lakes along their lengths. Ponding of the water of rivers that formerly flowed eastward to the Indian Ocean began the process that created the Lake Victoria basin. Following uplift to the east, further uplift along the Western Rift reversed flow of the then-westerly flowing Nzoia-Katonga and Mara-Kagera rivers, eventually closing exits to east and west. Thus, intercepted by uplift associated with both Eastern and Western Rifts, these rivers and Lake Victoria eventually added their waters to the northward-flowing main Nile.

It was once thought that Lake Victoria was about 1 million years old, but Kendall (1969) showed that it was saline and fell below the level of the Nile outlet prior to 12,500 years. Stager *et al.* (1986) and Johnson *et al.* (2000) showed that the level of the lake had fallen so much that it could have held water only in the deepest part of the basin as mapped on the Admiralty charts. Johnson *et al.* (2000) believed that the Admiralty chart incorporated serious sounding errors, and this has been supported by further echo-sounding (R. Hecky, personal communication). The main lake was completely dry prior to 12,500 years ago, although there may have been some standing water in the estuaries of rivers running off Mt Elgon. Johnson *et al.* (2000) found a thickness of sediment consistent with an age of 400,000 years for the basin. A claim that the Nile outlet was not established until well into the Holocene was inconsistent with the data of Kendall (1969) and with the isotopic signature of downstream beds along the Nile (Talbot *et al.* 2000). Lake beds of Miocene age at Rusinga have no genetic connection to the modern lake.

Even shallow ephemeral lakes, such as the present Lake Victoria, the former Mega-Chad and the still earlier 'Lake Congo', can act as temporary boundaries of mammal ranges. The much deeper tectonic lakes of the Rift provide longer-lasting boundaries, probably for several million years, even though they have not been as large as they are today through all of that time (Scholz *et al.* 2007).

More significant has been the longer-term role of shallow basins in providing habitat for the evolution of swamp species such as the Marsh Cane-rat *Thryonomys swinderianus*, Marsh Mongoose *Atilax paludinosus*, Sitatunga *Tragelaphus spekii* and reed antelopes of the genera *Redunca* and *Kobus*. The habits, ecology and distribution of such animals provide clues as to their geographic origin. For example, the Sitatunga is a shade-loving browser and it ranges all through the Congo Basin swamps, where it probably evolved, but

extended its range after becoming a swamp specialist. By contrast, take the distribution of the grass-eating Southern Lechwe *Kobus leche*, strictly limited by its swamp specializations to the sumplands of upper Zambezia while the Nile Lechwe *Kobus megaceros* is similarly restricted to the Sudd. The isolation of two Lechwe species, each equally specialized, in two well-separated regions only makes sense in the context of the Lake Victoria basin having been as extensive an area of grassy swamps as the upper Zambezi region is today. The open, grassy swamps of the Lake Victoria basin in its recent past may therefore have been the focal centre for the common ancestral Lechwe and just possibly represented their place of origin.

Thought to have held an extensive 'Lake Congo' in the Pliocene (Beadle 1974), the Congo Basin differs from all others in its immense extent (currently 3.7 million km² but once larger still) and in being the principal and perennial captor of Africa's equatorial rainfall. The significance of this can be gauged by the river's annual discharge, which is 1400 billion m³. No other African basin can compare with the Congo for the amount of water falling on and flowing through it, even during relatively dry periods. The basin and river are central to African geography and to the dynamics of mammalian evolution because the river, wherever its course may have run in the past, is a major barrier to dispersal (currently from north southwards or from the south northwards) and different sections of the basin, with different climates, have been perennial foci for distinct communities of forest fauna and flora.

Today its immense water-capture spills over falls, narrows and rapids into the Atlantic Ocean, where it has created a spectacular submarine canyon cut into the narrow continental shelf and, beyond it, a wide deep-sea fan. Beadle (pers. com. to J.K.) thought that all these features were indicative that the present exit of the Congo R. was not very ancient and was due to backward erosion by a short Atlantic river that captured the Congo Basin's waters during a period when water or lake levels were particularly elevated within the basin. Burke (1996) suggested that this might have happened at some time during the last 30 million years but Beadle considered a Pliocene date more likely.

Most of the rain falling on equatorial Africa falls into the Congo Basin and this probably dates back to the continent's separation from South America more than 100 mya. The present course of the Congo R. may not have had enough time to build up a delta fan above sea level but past courses were, potentially, the major source of sediments along the Atlantic coast. It may therefore be significant that between 80 and 35 mya the present R. Niger's immense delta in the Gulf of Guinea was mainly fed by waters flowing westwards down the widely and deeply eroded Benue R. (Goudie 2005). Although there have been periods when the Chad Basin emptied into the Benue, it seems less likely that the waters that gouged out the Benue came down from the north than that the Benue then connected with the Congo, the major source of water and sediment out of Africa. Such a scenario is made less improbable when it is remembered that only a very slight uplift along the spine of today's Central African Republic would have been sufficient to interrupt and reverse northward flow by the Congo R.

Still earlier there might have been other exits for the bulk of Africa's equatorial rain. For example, the main Atlantic site for sediment during the upper Cretaceous was the mouth of the very deep-cut Ogooué R. (Uenzelmann-Nebel 1998). It is, therefore,

KEY**1. Domes (plumes) and Rift Valley swells**

hp	Hoggar
tbp	Tibesti
dp	Darfur
rsp	Red Sea dome
afp	Afar plume
kyp	Kenya rift dome
tap	Tanganyika rift dome
map	Malawi rift dome
adp	Adamawa (Cameroon)
pap	Parana plume
nap	Namibian uplands
kop	Karoo plume

2. Pressure fold-belt ranges

ats	Atlas Mountain
mus	Muscat Ranges
cape	Cape Ranges

3. Basins

SaB	Sahara
L-EB	Libya-Egypt
Ed B	Eldjoui
CB	Chad
SuB	Sudd
IB	Iraq
RaKB	Rub-al-Khali
ZB	Congo-Zaire
Cu-KaB	Cubango-Kalahari

4. Depressions

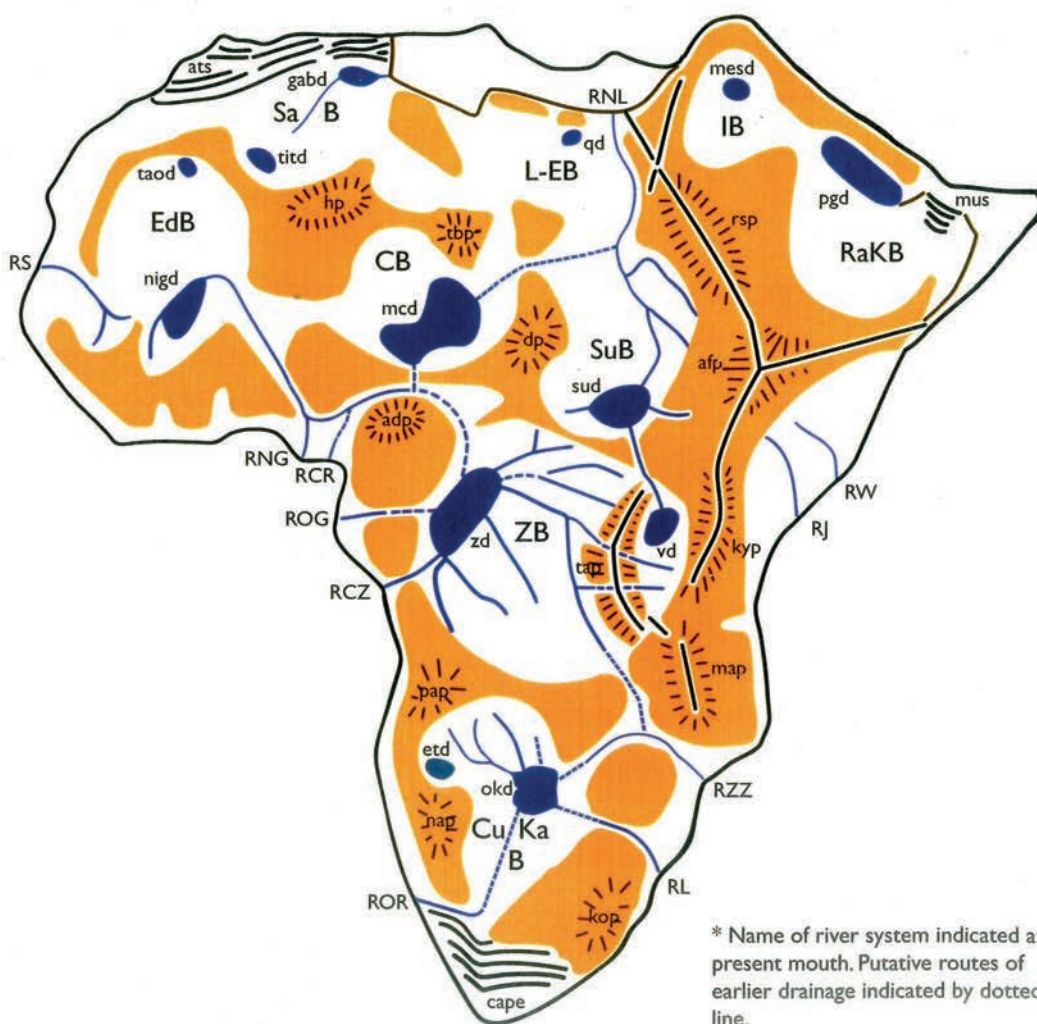
taod	Taoudeni
titd	Tidikelt
gab	Graves
qd	Qattara
nigd	Niger
mcd	Mega-Chad
sud	Sudd

mesd	Mesopotamia
pgd	Persian Gulf
zd	Congo/Zaire
vd	Lake Victoria
etd	Etosha
okd	Okavango

5. Drainage lines*

RS	Senegal
RNG	Niger
RCR	Cross
ROG	Ogoe
RCZ	Congo/Zaire
ROR	Orange
RL	Limpopo
RZZ	Zambezi
RJ	Juba
RW	Webshebele
RNL	Nile

Afro-Arabian landmass showing plumes, swells and three pressure fold-belt ranges. Also shown are depressions within nine major basins. Overspills are indicated by the courses of present and putative past rivers. Timespan: Palaeocene to Present. (In part after Holmes 1965, Burke 1996 and Goudie 2005.)



possible that the much less significant Ogoe Basin formerly connected with the main Congo Basin and captured its vast volumes of water. Goudie (2005) has sketched in a still earlier drainage pattern in which Congo Basin waters once flowed south-east, exiting in the Indian Ocean. This reversal of direction of flow would be consistent with the substantial uplift that has been associated with formation of the Rift Valley system, raising surfaces and blocking southward flow. Goudie (2005) has stressed that such scenarios for former drainage

patterns are highly speculative but that they are informed by a new appreciation of how unstable Africa's crust has been and by new data from radar scanning by satellites.

Further south, the Cubango-Kalahari Basin, an internal basin during dry periods, probably spilt over, successively, in three different directions during wet ones. McCarthy (1983) has suggested a south-westerly pitch, at which time waters exited into the far south Atlantic at the mouth of today's Orange R. Drainage south-

east into today's Limpopo R. has been suggested by De Wit *et al.* (2000). Down-warping in the 'Gwembe trough' (Caprivi-Kariba area) probably helps explain how the present Zambezi captured the Cubango drainage, as late as the Pliocene to mid-Pleistocene (Thomas & Shaw 1991, Goudie 2005).

African rivers

Africa's river basins have their origins in the development of broad depositional basins that are fringed by uplifted ridges or plateaux (Butzer & Cooke 1982). Beginning well back in the Palaeozoic, but continuing up to the present, uplift around the margins of these basins has been well illustrated by Holmes (1965).

Swells have changed the drainage patterns of Africa profoundly, with flows being directed to basins of internal drainage (Holmes 1965, Goudie 2005). Uplift anywhere leads to runoff, uplift along continental margins, inland domes and swells creates interior basins (Holmes 1965, Moore & Larkin 2001), and one of the most striking features of Africa's topography is its inland basins. The swells and basins have affected the drainage pattern of the continent, by diverting river flows into the basins, and by periodically shifting the course of rivers over the swells.

Falconer (1911) first observed that many contemporary river courses seem very youthful: this has been generally and widely confirmed. Burke (1996) believes that the drainage pattern of southern Africa has been changed by river capture due to rising swells, which has continued at least into the last million years.

In addition to the gross pattern of some ten or so major basins, some minor drainage basins have developed down the eastern side of Africa and their tree-lined rivers seem to be of significance for the dispersal and speciation of moisture-dependent mammals previously isolated in eastern African coastal or montane forests (Kingdon 2003).

Because rivers sometimes form the boundaries of mammal ranges, sometimes routes of dispersal, their age and history since initial establishment are of special interest to mammalogists. The Congo R. is by far the most important in this respect but, as the previous section showed, its history has been complex. None the less, most distributions can be related to its present course and topography and these are discussed shortly as well as in individual species profiles. So long as the Congo R. has flowed into the Atlantic (which is certainly throughout the rise of mammals) it has represented a barrier to movement between the areas north and south of it. There may have been periods that were sufficiently dry to bring arid habitats close to both left and right banks yet it is striking that non-volant arid-adapted taxa in southern Africa have closer ties with the Horn of Africa than they do with the Sahara, in spite of the latter being physically closer. Except for large powerful swimmers or chance 'rafters' the lower Congo R. has long represented a nearly impassable obstacle to any exchange between northern and southern arid-adapted mammals.

The Nile is illustrative of the difficulties of tracing the history of Africa's rivers. At 7000 km, the Nile is the longest river in the world, draining 3.2 million km² (Said 1981), but it was not always so and its great length is essentially a product of the very unstable, south-north East African rift system which has tended to block any flow to the east from central Africa.

The present lower Nile follows the western margins of the Red Sea up-warp and thus likely dates from the time of initiation of this up-warp. Prior to the initiation of the eastern Africa/Red Sea rift system the basin of the present Nile was probably covered by five or more separate hydrographic units (Butzer & Hansen 1968). Burke (1996) noted that there was no great river reaching the north coast of Africa in the area of the present Nile Valley during deposition of the late Eocene and early Oligocene sediments of the Fayum but that a great delta lay 200 km south of the present Nile Delta during the early Miocene.

Goudie (2005) lists three distinct stages in the Nile's formation, starting with a Saharan Gulf system between 40 and 24 mya. This was followed by the second Qena stage in which uplift of the Red Sea margin reversed the flow of the Wadi Qena. The third stage saw the development of the modern Nile system.

During the Messinian (5.6–5.32 mya, when the Mediterranean Sea evaporated, forming a colossal trench) the Nile cut a gorge, the Messinian Canyon, which was four times as deep as the Grand Canyon in Arizona. This downcut the Miocene Nile Delta as far south as 24 degrees and, when the Mediterranean refilled, deep marine sediments, from about 5.0 mya, formed in a long, narrow arm of the Mediterranean that reached Aswan (Krijgsman *et al.* 1999, Goudie 2005).

The present Nile, as a perennial river, is extremely young. Although most of the water in the lower Nile comes from the Blue Nile and the Atbara (where the north-westerly tilt of the Red Sea Rift and western Ethiopian highlands captures virtually all the rain), their flow is strongly seasonal. The river is sustained as a year-round stream by the much smaller but steadier discharge that leaves Lake Albert. The Nile became a seasonally flowing river at the height of the last glaciation between about 20,000 and 12,500 years ago when the level of Lake Albert fell below the level of the Nile outlet, so there was no discharge of water from the upper part of the Nile catchment (Harvey 1976, Richardson *et al.* 1978, Adamson *et al.* 1980). Discharge from the Blue Nile and the Atbara would have been reduced by the same climatic change that lowered the surface of L. Albert. There is reason to believe that similar circumstances prevailed many times during the Quaternary. There is also evidence for a much bigger river at other times in the Quaternary (Said 1981). From the point of view of a freshwater fish, and probably from the point of view of a mammal wishing to cross the Nile Valley without drowning or being eaten by crocodiles, the Nile is 12,000 years old rather than 30 million years.

It has been suggested from radar evidence that a westward-flowing river across the eastern Sahara formerly drained much of the Nile catchment to the Atlantic (McCauley *et al.* 1982), but Burke & Wells (1989) point out that this is inconsistent with the large delta of the Nile and the lack of one at the putative Atlantic outlet. Shared aquatic fauna implies physical connection between the Nile and Niger basins via Chad, probably most recently during the wet early Holocene, but we perceive no effect of such connection on mammalian biogeography.

Africa has two other major rivers, the Niger and Zambezi. The sedimentary record of the Niger Delta suggests that the delta has been in place since the mid-Eocene (R. Morley pers. comm.). At present the Niger drains to the ocean, but in dryer times it probably lost some of its catchment. Urvoy (1942) thought that the upper

Niger had once run into the Saharan Lake Azaouad but then became deflected by the build-up of sand dunes. Talbot (1980) suggested that Lake Chad formerly emptied into the Benue R., the Niger's main tributary. That connection does not operate today, so the Benue has a relatively small catchment area, but the watershed between the Benue and Chad basins is very tenuous. A possible earlier connection between the Benue and the Congo has already been mentioned.

The Zambezi in its present form is another relatively new river. Its most westerly tributaries, arising on the margins of the Cubango basin, once drained south and then emptied to the west (McCarthy 1983) and De Wit *et al.* (2000) have suggested that this section was once part of the palaeo-Limpopo. The down-warpage that channelled the present river down its present course and over the Victoria Falls took place, according to Thomas & Shaw (1991), between the late Pliocene and mid-Pleistocene (perhaps around 1.8 mya). It is just possible that the eastern limits of some species, such as the Cape Fox *Vulpes chama*, Meerkat *Suricata suricata* and the Yellow Mongoose *Cynictis penicillata*, became established or were influenced at a time when the Zambezi exited further south but it is more likely that ecological and competitive factors explain their present ranges.

Large rivers have acted as major barriers so that some non-swimming species that have dispersed from a place of origin north or south of, say, the Congo or east/west of the Nile, often have these rivers as a boundary. Some typical examples are the Giant Forest Hog *Hylochoerus meinertzhageni*, which is distributed from Guinea to Kenya and Ethiopia, yet is never found south of the Congo. Likewise there is no evidence that the Gorilla *Gorilla gorilla* ever existed south of the river and there are numerous other examples (White-bellied Duiker *Cephalophus leucogaster*, Giant Genet *Genetta victoriae*, some squirrels and others). By the same token, animals dispersing from a southern or south-eastern source fail to cross to the north bank. Typical examples are the Bonobo *Pan paniscus* and the Four-toed Sengi *Petrodromus tetradactylus*. There is the interesting possibility that some of the species restricted to north of the Congo might derive from ancestral stocks that had come into Africa and gradually adapted to the conditions found north of the river (which very approximately coincides with the Equator) and never succeeded in reaching or adapting to the south bank.

The Nile, in spite of its intermittent flows in the past, seems to have inhibited the most recent colonists from the east, such as the Bushy-tailed Jird *Sekeetamys calurus* and the Nubian Ibex *Capra nubiana*, neither of which have succeeded in invading land west of the river.

One very minor river that seems to mark the western or eastern boundary of some forest mammals is the Cross R. in south-eastern Nigeria: the list includes the Western Gorilla *Gorilla gorilla*, Olive Colobus *Procolobus verus*, Preuss's Red Colobus *Piliocolobus preussi*, the Drill *Mandrillus leucophaeus* and Grey-cheeked Mangabey *Lophocebus albigena*. While this probably has more to do with ecological factors the possibility should be borne in mind that this stream marks the course of a much more formidable barrier-river in the past.

Lesser river valleys often act as dispersal routes, not barriers, and this is particularly relevant for rivers connecting the highlands of eastern Africa with the Indian Ocean. Here an arid belt that periodically connected the Horn of Africa with the Kalahari has served to separate the coastal and far eastern mountain forests from those in central Africa. Galleries of forest growing on the banks

or in the valleys of such rivers have been sufficient to create links, only subsequently to be broken. Such cycles of connection and disconnection via rivers have probably been major facilitators of speciation or subspeciation in tropical Africa and distribution patterns imply very long lasting results. Thus the Suni *Nesotragus moschatus*, a basal antelope that most resembles the ancestral Neotragini, has an eastern coastal distribution from the Equator to South Africa. This dwarf antelope lives well inland and up into montane areas, having dispersed along many riverine forests, including the Rufiji and Zambezi valleys. Ancestral populations gave rise to forest colonists that spread much further west, notably Bates's Pygmy Antelope *Neotragus batesi* and the Royal Antelope *N. pygmaeus*, that live within the equatorial forest belt. Some eastern African littoral mammals, squirrels (Sciuridae), monkeys (Cercopithecidae) and sengis (Macroscelidae) suggest comparable histories in which coastal or Eastern Arc forest forms have used riverine gallery forests to reach suitable habitats further west.

Such dispersals can flow both ways and the Two-spotted Palm Civet *Nandinia binotata*, which has a very extensive distribution in West and central African forests, still occupies riverine strips close to its effectively disjunct eastern African distribution. As both the Neotragini and Nandiniidae are ancient lineages it is clear that such peculiar ranging patterns could have origins going back to the Miocene.

The chemical composition of African lake and river waters is dominated by incongruent solution reactions between soil water and silicate rocks rather than the congruent solution of marine carbonates that is dominant in most of the world. Two consequences of this are likely to affect mammal distribution and abundance. First, African waters are rich in sodium and potassium, poor in calcium and magnesium, which would handicap cervids in their competition with bovids. Cervids have a foothold in Africa, but only in the Atlas Mts, where calcium-rich marine sediments are common. Secondly, sodium fluoride is three orders of magnitude more soluble than calcium fluoride, so African waters are unusually rich in that halogen. It is probably no coincidence that our own African species requires so much fluoride for dental health that we commonly suffer from caries on other continents (Livingstone 1963, Garrels & MacKenzie 1971, Kilham 1972, 1990).

Mountains and uplands as corridors and centres of endemism

Apart from the Atlas Mts, Africa lacks folded mountain belts but it does have a series of domes and raised uplands that run, in a slightly disjunct way, on both sides of the great north-south rift valleys and these provide opportunities for dispersal by upland mammals, or even specifically 'Rift' species.

As in the Americas, the distribution of African biota, including mammals, reveals that, during cool periods, many so-called 'temperate species' (some of recent Eurasian origin) have dispersed south along this raised continental spine while biotas that have evolved in temperate South Africa have dispersed to the north when conditions were right. Along the way there are pockets of upland habitats in north-eastern, eastern and southern Africa, which appear to conserve relictual pockets of once extensive populations.

Choice localities within these mountains and uplands have permitted species to accumulate because, with minimal movement, established and well-adapted species can survive under relatively consistent local climates in relatively stable habitats. The more long-established of these are generally described as 'archaeo-endemics'. Examples of such archaeo-endemics are readily found among the seven genera and many species of golden-moles (Chrysochloridae) of the South African Cape.

Centres of endemism can also attract 'pre-adapted' species from relatively widespread parental stocks. For example, high-altitude moorlands growing on ground recently released by the melting of glaciers in Ethiopia have been colonized by various temperate-adapted murine mice. Living under conditions that are unlike any elsewhere in Africa, these mice have speciated rapidly. Such recent arrivals, when identifiable, can be labelled as 'neo-endemics'. Examples of neo-endemic rodent genera from Ethiopia are *Stenocephalomys* and *Desmomys*. The Giant Root-rat *Tachyoryctes macrocephalus* is another rodent with ancestors of known recent Eurasian origin.

Like the Galapagos Is., the isolated East African Arc highlands exemplify a much wider scatter of 'Centres of Endemism'. The latter consist of very varied eco-geographic foci, all ecological 'islands' that enjoy the common feature of relative stability in a continent that has suffered many climatic and tectonic vicissitudes. An important feature of highlands such as the Udzungwa and Uluguru Mountains, which are sufficiently high and close enough to the Indian Ocean to enjoy relatively reliable rainfall, is the existence of sufficient physiographic and geological complexity for humid habitats to survive in a region where the overall climate has been very unstable. These habitats and their inhabitants tend to depend on the maintainance of a narrow spectrum of temperatures, rainfall and soil types. Whenever the global climate changed, the topographic complexity of these mountainous regions ensured that established ecological communities could endure simply by slipping up or down the catena or by retreating into particularly sheltered valleys. One of the most striking and exciting examples of this phenomenon is the very recent discovery, in the Udzungwa Mts, Tanzania, of numerous endemic species of animals and plants, all restricted to three isolated forests, Ndundulu, Luhomero and Mwanihana (Butynski & Ehardt 2003, Rovero & Rathbun 2005, Rovero *et al.* 2005, Burgess *et al.* 2007). Because of the detailed topography of these highest reaches of the Udzungwa mountain chain these forests have escaped the near total deforestation (mostly by fire) around them.

Rift valleys

Rift valleys are the product of uplift as well as downthrust. Oligocene marine beds were raised to 3000 m at the centre of the Ethiopian Dome (Butzer & Cooke 1982). This is the earliest and most northerly of a series of domes that have split open along their crests, mostly north-south. The most notable rift, L. Tanganyika, 650 km long with its surface close to 700 m above sea level, is 1434 m deep. Its waters extend almost as far below sea level as they do above and are underlain by deep deposits much of which was laid down after rifting began. This multiple half-graben basin (Rosendahl 1988), like L. Malawi, acts as a defining boundary for the distribution of many mammals.

These lakes, and the longitudinal rift valleys of which they are a part, act as physical boundaries. That role is modified by biological influence: most of the land to the west is warm, wet, forested lowland while most of the higher, drier, cooler land to the east is not forested. The forest/non-forest divide is a major defining separation for most organisms in tropical Africa and this ecological divide modifies the physical effect of the rift valleys as physical barriers. In Uganda, formerly extensively forested, many forest organisms skirted mountains, lakes and rift valleys to extend their ranges eastwards, some as far as the Nile, others as far as Mt Elgon or Mt Kenya. Within East Africa the Somali arid corridor seems to have been a more decisive barrier between western and eastern forest biota than the more permeable rift valleys and mountains, which also have approximately north-south alignments.

Regardless of whether the boundary of their range is primarily ecological or physical, many forest species get no further east than the very physical boundaries of Lakes Tanganyika, Kivu, Edward and Albert. To name but a few of the more obvious ones: Agile Mangabey *Cercocebus agilis*, Dent's Monkey *Cercopithecus denti*, Demidoff's Galago *Galagoides demidoffi*, Beecroft's Anomalure *Anomalurus beecrofti*, Long-nosed Mongoose *Xenogale naso* and White-bellied Duiker *Cephalophus leucogaster*.

A very different physical and ecological boundary lies between the highlands of Ethiopia and those of East Africa, notably Mt Kenya and Mt Nyiru, which lie only about 250 km south of the Ethiopian piedmont. This region, the Marsabit district, is low and dry and Clayton (1976) has drawn attention to its significance as a major dividing line between African grasses. For mammals and many other organisms the primary importance of this divide is that during glacial periods Eurasian immigrants were able to move south into Africa along the raised ground that lines the western side of the Red Sea Rift (Kingdon 1990). While there were substantial glaciers on the heights of Ethiopia the surrounding uplands were so extensive that a variety of cool habitats were available for such immigrants and they remained and even became dominant long after the glaciations were over, becoming unique Ethiopian endemics in the course of time. The best known examples of Eurasian mammals that followed this route are the Ethiopian Wolf *Canis simensis*, the Walia Ibex *Capra walie* and root-rats of the genus *Tachyoryctes*.

The great height of the Ethiopian dome and of the string of lakes and grassy valleys that floor its 600 km-long rift has ensured that many tropical life forms are effectively eliminated during each glaciation. This 'sterilization' of the landscape probably favours cool-adapted biota that are relatively generalized but may be less resistant to intense competition. A great abundance of hominin fossils has been excavated along the Ethiopian Rift system; perhaps the bipedal apes were effective and rapid colonists of such habitats whenever glaciation ameliorated. The relative rarity of tropical primate species (and of their diseases) might have been among the keys opening the Ethiopian Rift Valley floor to hominins.

Another rather surprising traveller along Rift Valley walls, but in the opposite direction, is Smith's Red Rock Hare *Pronolagus rupestris*. Recent research (Robinson *et al.* 2002) has shown that hares belonging to this exclusively south-eastern genus are the most conservative of all hares and rabbits. Despite being early invaders from Eurasia, perhaps in the earlier Miocene, *Pronolagus* spp. found in the extreme south of Africa a refuge from the competition of more

advanced hares and, perhaps, from hare-specific predators. During favourable climatic cycles, the marked preference of *P. rupestris* for steep rocky hillsides has made the recently slumped walls of the Rift Valleys an appropriate path for northward expansion.

Deserts

Morphologically, the desert areas of Africa have the same swell and basin substrate as the rest of Africa. The physical surfaces of this substrate, however, are profoundly altered by break-down into rocks, pebbles, sand and silt, creating very different types of desert and very diverse habitats for mammals.

The best known desert in Africa and, at over 10 million km², the largest in the world, is the Sahara. Recurrent desert conditions have prevailed there at least since 7 mya (Schuster *et al.* 2006). Evidence for xerophytic plants in the Sahara dates back to the Pliocene (Kowalski & Rzebik-Kowalska 1991). Daily fluctuations of temperature can exceed 35 °C. Nocturnal temperatures can hit –10 °C and diurnal ones can reach 56 °C. Typical precipitation in the centre of the Sahara is 3–12 mm but the 150 mm isohyet is commonly used to demarcate its southern border. All the major Saharan endemic mammals are true desert-adapted species but where there is evidence for their evolution this implies either post-Miocene Asiatic origin (some gerbilline and dipodid rodents and foxes) or *in situ* evolution since the onset of the Messinian (Addax and Oryx).

The various physical surfaces found in the Sahara provide habitats for mammals and all have Arabic names that have been widely adopted in English and other languages. Hills and mountains are called jebels; stony plateaux are hamadas; rocky basins that conserve springs or rock pools are guelta while other small depressions are daya; more extensive depressions, typically of gypsum or clay, are called sebkha while saltflats or ephemeral salt lakes are shotts. Alluvial plains are reg; seasonal water-courses are wadis and areas of sand, sometimes covering great areas and forming wind-blown dunes that can be hundreds of metres high are called ergs or great ergs. Although specific desert types can be extensive these names give expression to the diversity of habitats that exist within the Sahara.

In spite of its immense size, the Sahara may not, however, be the oldest arid area in Africa. Aridity in the extreme south-west of Africa may have fluctuated over time but the conditions that cause such aridity have been in place for at least the last 10 million years when the cold South Atlantic Benguela current first formed (Siesser 1980, Denton 1999). Indeed some aridity in south-western Africa was likely earlier still because the polar ice-sheet and circumpolar current developed about 23–20 mya, according to Barker & Burrell (1977). Even then, cool surface temperatures in the South Atlantic would have reduced precipitation in south-western Africa and encouraged general adaptive trends towards drought resistance. Namibian desert plants and animals tend to confirm the greater age of their adaptations compared with those in the Sahara. For example, the Sahara has no equivalent to the sand-burrowing Grant's Golden-mole *Eremitalpa granti* (which is an afrothere). The Namibian endemic Pygmy Rock Mice *Petromyscus* spp. derive from a particularly ancient rodent group, the Petromyscinae; their poorly approximate equivalents in the Sahara derive from much more recent murine immigrants.

True desert is of very limited extent in the Horn of Africa but many Somali animals and plants exhibit adaptations to generally arid conditions that are likely to originate well before the Messinian. For example, molecular clocks suggest that the arid-adapted Beira *Dorcatragus megalotis*, a local endemic, differentiated from its closest relatives about 9 mya and dik-diks *Madoqua* spp., small arid-adapted antelopes, have been a distinctive lineage for even longer.

Adaptations to desert-living are described in the profiles of many species. In addition to selection for physiologies that save water and resist heat or anatomies that facilitate escape from predators or heat by leaping, digging or aestivating, some desert animals have adapted to physical niches that allow them to combine shelter from the elements with escape from predation. For example, several species, from totally unrelated taxa, retreat into rock crevices in the desert. The most striking of these is the Noki (Dassie Rat) *Petromus typicus*, which has a broad, flat skull and malleable body selected for squeezing into very narrow spaces. Other rodents, such as some dormice species and the Pygmy Rock Mice *Petromyscus* spp., show similar flattening but a bat has taken this adaptation to its extreme. A Horn of Africa endemic, the Flat-headed Bat *Platymops setiger* has a wafer-thin skull and body that almost approaches two-dimensionality!

Among larger mammals one of the least remarked-upon adaptations to desert living is physical mobility and modification of the feet for difficult substrates. Before their near extermination by humans, long-legged desert antelopes made extensive seasonal migrations between seasonal pastures and some species have hooves modified to cope with loose sand while the Beira has rubbery hooves that provide traction over pebbly hillsides.

In the past a belt of dry country has connected the arid north-east Horn of Africa with the Kalahari/Namib south-west (Kingdon 1971, Coe & Skinner 1993). At the present time this corridor is barely discernible but it would seem to owe its existence to a rain-shadow that periodically lay behind the chain of mountains that runs from the Usambaras, Ulugurus and Uzungwas on down both sides of L. Malawi to the Manica and other uplands of Zimbabwe. This long chain of higher ground intercepts moisture blowing in from the Indian Ocean and this desiccating influence is likely to have been amplified during arid climatic phases. Higher ground may have made this extremely narrow corridor less than absolute but it seems to have been an enduring and influential feature of African biogeography. This arid corridor constitutes a line of fracture between Central and Eastern forest communities and has been called 'Kingdon's line' (Grubb *et al.* 1999) and its influence is extensively discussed in other chapters as well as individual species profiles. Kingdon (2003) has argued that this barrier likely provided the essential separating mechanism between the ancestors of modern apes to its west and the earliest ancestors of modern people to its east. If that view proves correct this inconspicuous geographic barrier will deserve very much more attention than it has received to date. Some species common to both the north-eastern and south-western arid zones are the springhares *Pedetes* spp., Caracal *Caracal caracal*, Aardwolf *Proteles cristatus*, Bat-eared Fox *Otocorys megalotis*, dik-diks and the oryxes *Oryx* spp. None of these is adapted to true desert but their discontinuous distribution suggests that areas of very dry *Acacia* bush have, at various times, been sufficiently continuous between these two areas to connect them.

Fossil mammals and fossil sites

While physical and geological features of Africa's contemporary and past landscapes can be shown to have shaped many aspects of mammalian biology and distribution, the single most important interface between contemporary mammalogy and geology is the fossil record (Benton 2000). The palaeontological literature on African mammals is immense and good introductions to it are provided by Cooke (1968, 1972), Hopwood & Hollyfield (1954), Turner & Anton (2004), Werdelin & Sanders (2010) and Kielan-Jaworowska *et al.* (2004). Among the many contributions of that literature is the principal evidence for human evolution from primate ancestors in Africa. It has also revealed a very incomplete but very detailed record of first and last occurrences of extinct species and groups and, of course, provided concrete evidence for the first occurrences of incoming biota from Eurasia.

Of surviving placental lineages, Afrotheria dominate the scene, so our brief survey of fossils begins with Afrotheria and then follows the sequence of *Mammals of Africa*.

Afrotheria

The semi-aquatic, tapir-like *Moeritherium* from the Eocene/Oligocene beds at Fayum in Egypt offers many insights into the first beginnings of the elephants Proboscidea. The further evolution of proboscids into ever larger and taller forms is well illustrated by fossils of *Gomphotherium* and *Stegotetrabelodon* from several north-east African sites. Mastodon (*Mammutus*) fossils appear at about 22 mya but their lineage eventually went extinct. The living elephant genus, *Loxodonta* (in the form of *L. cooki*), first appears in the late Miocene. The dentally more advanced *Elephas recki*, closely allied to modern Indian Elephants, appears later, in the early Pliocene. Hyracooids first appear in North Africa but continue to be common and diverse in many later African deposits. A giant form, *Gigantohyrax*, lasted into the Pliocene in South Africa and a very robust form resembling living hyraxes, *Prohyrax*, is a common and widespread fossil.

Another fossil, named *Myohyrax* because it was initially mistaken for a hyrax, is actually an early, herbivorous macroscelid, hinting at the ultimate common roots of all Afrotheria. A fossil belonging to the modern Sengi genus *Rhynchocyon* (*rusingae*) has been found in 17 mya deposits on Rusinga I. in Lake Victoria. Observers of modern *Rhynchocyon* should bear in mind that the very peculiar life-form that these sengis manifest has been around at least 17 mya! Aardvarks somewhat similar to the living species, *Orycteropus gaudreyi* and *Leptorycteropus guilielmi*, date from 7–5 mya.

Fossil sirenians that were already adapted to sea-going have been found outside Africa from about 50 mya. Such extreme specialization and divergence at this early date hints at a bench-mark for the likely pre-Cenozoic beginnings of afrothere evolution.

Primates

According to Sige *et al.* (1990), the earliest fossil primate appears in Africa at Adrar Mgom in Morocco, dated to about 60 mya. Other early primates, *Azibius trerki* and *Biretia piveteaui*, have also come from North Africa (Bonis *et al.* 1988), dated to the Eocene (55–34 mya). The earliest currently recognized anthropoid has been dated to about 49 mya and thereafter there is a rich primate fauna, including early anthropoids, throughout the Eocene/Oligocene beds at Fayum in Egypt. There have even been claims for a Tarsier, *Afrotarsier*, from about 35 mya. Apart

from this single fragmentary fossil Tarsiers are an exclusively Asian group, so doubts have been raised as to its real identity.

In East and South Africa a rich record illustrates the differentiation between proto apes and proto monkeys and of the Colobine/Papionine split covering an almost continuous record from the early Miocene to the Holocene. *Victoriapithecus* spp., ancestors for most of today's monkeys, first appear about 15 mya in East Africa.

Rodentia

The great diversity of living rodent groups owe their variety to a succession of invasions out of Eurasia. The earliest fossil zegdomyids and hystricognaths date from the Eocene (50–35 mya) in Fayum. Also from North Africa are Eocene records of phiomysids, notably *Protophiomys algeriensis*. It is therefore likely that more than one primitive rodent lineage was already present before the Miocene invasions. Among possible descendants of the Zegdomyids are the anomalurids *Nementschamys lavocati*, *Megapedetes* and *Parapedetes*. Among the latter are numerous Ctenodactyla and Thryonomyidae.

Lagomorpha

It is probable that the ancestral stocks of *Pronolagus* and *Bunolagus* differentiated from a primitive stock entering Africa during the early Miocene, but currently the earliest hare is the mid-Miocene *Kenyalagomys mellalensis*.

Chiroptera

Although bats are known to have been numerous and diverse by the Eocene they are currently best represented by living genera in the middle Miocene (17–11 mya) of North Africa, with *Rhinolophus*, *Hipposideros*, *Tadarida* and various megadermids and vespertilionids all represented. Bat radiations are thought to be post-KT. No bat families are exclusive to Africa but Nycteridae almost certainly evolved in Africa, emerging from a common ancestor with the globally distributed Emballonuridae.

Erinaceomorpha and Soricomorpha

Hedgehogs and crocidurine shrews are known from the mid-Miocene onwards. One hedgehog, *Gymnurechinus comptolophus*, from Rusinga has been dated to about 17 mya. *Protechinus salis* from Morocco has a similar age.

Carnivora

The now extinct Creodonta were already present in the Palaeocene and some hung on after the arrival of modern lineages. Among the earliest of modern types are two that have gone extinct: 'half-dogs' (Hemicyonina) and 'bear-dogs' (Amphicyoninae).

Felids, in the form of various large or largish sabre-toothed forms, tend to dominate the early Neogene record. The ancestors of living forms have tended to arrive as separate invaders but it would appear that the Caracal *Caracal caracal*, the African Golden Cat *Profelis aurata* and the Serval *Leptailurus serval* may have differentiated within the continent from a single ancestor. The first fossil lion appears at 3 mya and the leopard at 3.4 mya.

Mustelids and viverrids were among the earlier invaders. Among the fossil mustelids a very large predator *Ekorus ekakeran* has been found at Lothagam (about 6 mya). A distinctive viverrid is *Kanuites*, which resembles *Genetta*. Bears made a brief appearance in the late Pliocene.

Canids, which originated in North America, were the last carnivore group to arrive in the late Miocene.

Pholidota

Pangolins are known from Eurasia well before their first appearance as fossils in Africa during the mid-Miocene in Kenya and Pliocene in Uganda.

Perissodactyla

The extinct chalicotheres were among the earlier perissodactyls and they survived in various forms from about 20 mya to 2 mya. Rhinoceros species have been successful and diverse members of the African fauna from the early Miocene onwards. Equids, all of North American origin, arrived as three-toed hipparions in the late Miocene while fossils of modern Equus species first appear at 2.5 mya.

Cetartiodactyla

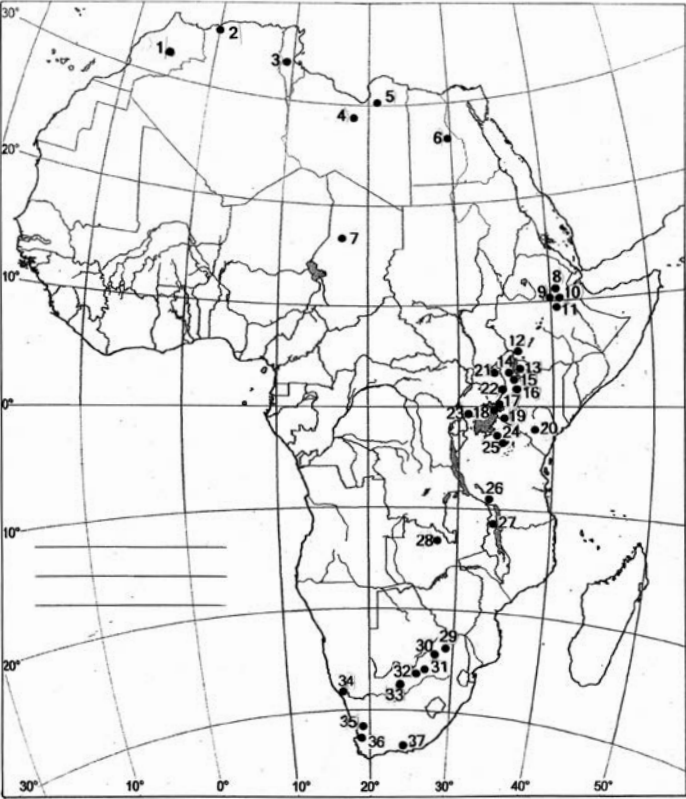
Anthracothers, a now extinct group but probably linked to hippos and whales, are among the earliest fossil mammals, being found in North Africa from the Eocene (Coiffait *et al.* 1984). The earliest

pig fossils date from 17.5 mya and the dominant *Nyanzochœrus*/*Noyochœrus* lineages subsequently went extinct. The earliest fossil hippopotamids date to the early Miocene. Ancestral chevrotains and primitive giraffids arrived around 22 mya. Cervids only make an appearance about 1 mya. The first fossil of a primitive antelope, *Eotragus*, is recorded from about 18 mya (Thomas 1979), but it is likely that the ancestor of today's African antilopine radiation arrived still earlier. The first fossil of a tragelaphine bovine dates to 14.5 mya. All living members of the genus *Tragelaphus* probably derive from a common ancestor entering Africa at about this time.

Fossil sites

Sites that contain important mammal fossils in Africa have a wide scatter but are mainly concentrated in a very few countries. The best-known sites for fossils are clustered in geologically favoured parts of East, north-east, southern and northern Africa. Many of these are Miocene to Holocene and have become well known because key hominin fossils have been found there. Apart from strictly commercial explorations, the search for human origins in Africa has driven much of what palaeontological activity there has been.

Sites yielding earlier mammal fossils are still rare, the best known being in Egypt, Algeria and Morocco. New sites, dating from the Palaeocene onwards, in the North Songwe valley, Tanzania, promise to yield new material representative of mammalian evolution closer to the centre of Africa, rather than from its peripheries. Some of the best known or most fossil-rich sites are listed below to demonstrate their uneven spread in space and time.



Fossil sites in Africa. 1. Beni Mellal 14 mya; 2. Bou Hanifa 11 mya (+ Ternefine 0.6 mya); 3. Bled ed Dourah 14–10 mya (+ Ichkeul 2 mya); 4. Jebel Zelten 22 mya; 5. Sahabi 5 mya; 6. Fayum 40–30 mya; 7. Totos-Menalla 7–5 mya (+ Koro Toro 3.2 mya); 8. Hadar 3 mya; 9. Middle Awash (Aramis) 4.4 mya; 10. Bodo 0.6 mya; 11. Bouri 2.5 mya; 12. Omo 4.5–1 mya; 13. Allia Bay 3.9 mya; 14. W. Turkana 1.5–3.5 mya; 15. Lothagam 7–5 mya; 16. Kanapoi 4 mya; 17. Maboko 15 mya; 18. Rusinga & Mwangano 17 mya; 19. Fort Ternan 14 mya; 20. Ologesailie 0.8 mya; 21. Moroto 18–20? mya; 22. Bukwa 9? mya; 23. Nsongezi 0.9 mya; 24. Olduvai 2–0.2 mya; 25. Laetoli 3.8–3 mya; 26. Songwe 57–50? mya; 27. Chiwondo 4–1.6 mya; 28. Kabwe 0.2 mya; 29. Makapansgat 3 mya; 30. Gondolin 2–1.5 mya; 31. Drimolin 2–1.5 mya; 32. Sterkfontein Valley 3.5–1 mya; 33. Taung 2.5 mya; 34. Oranjemund 150,000–100,000 ya; 35. Oudrif Permian–Holocene; 36. Langebaanweg 5.2–2.5 mya; 37. Klasies 110,000–75,000 ya.

Adrar Ngom – Morocco	60 mya
Quaratzate – Morocco	58 mya
Chambi – Tunisia	53 mya
Dra – Algeria	50 mya
Bir el Ater – Algeria	40 mya
Fayoum – Egypt	40–31 mya
Jebel Zelten – Libya	22 mya
Moroto – Uganda	20.6 mya
Beni Mellal – Morocco	17 mya
Testour – Tunisia	17 mya
Turkana Basin (Kenya and Ethiopia)	17–0.5 mya
Rusinga & Mfwangano – Kenya	17 mya
Maboko – Kenya	15 mya
Fort Ternan – Kenya	14 mya
Arris Drift – South Africa	14 mya
Bled ed Douarah – Tunisia	12–10 mya
Oued Zra – Morocco	10 mya
Lothagam – Kenya	7–5 mya
Chad Basin – Chad	7–5 mya
Sahabi – Libya	5 mya
Langebaanweg – South Africa	5 mya
Aramis – Ethiopia	4.4 mya
Kanapoi – Kenya	4.1 mya
Turkana Basin – Kenya	4.5–1 mya
Chiwondo – Malawi	4–1.6 mya
Laetoli – Tanzania	3.8–3 mya
Hadar – Afar Ethiopia	3–2.5 mya
Sterkfontein/Makapansgat – South Africa	3.5–1 mya
Olduvai – Tanzania	2–1 mya

STRATIGRAPHY AND DATING

The discipline of geology developed first in Western Europe and later in Africa. Despite enormous progress Darwin's 1859 assessment of the geologic record is still accurate all over the world, but especially in Africa.

Radiometric dating now makes it possible to correlate the eras, periods and epochs of Phanerozoic time (the last 542 million years) and also to date them. Note on p. 28 especially the great length of Cretaceous and of Miocene time. Some non-radioactive processes provide especially precise correlation between different bodies of rock. For example, periodic changes in the motion of the earth around the sun and shifts in orientation and intensity of the earth's magnetic field affect the whole world at the same time.

Fossiliferous marine sediments are not widespread in Africa so we are particularly dependent on the new methods to correlate sedimentary deposits in which our mammals are found. Had we a good sequence of widespread terrestrial deposits we would be able to

erect a stratigraphy based on terrestrial fossils. Occasionally that can be done. Pig fossils helped to straighten out the confusing radiometric dating of hominid-bearing sediments around Lake Turkana (Cooke 1978, White & Harris 1977, Harris 1991). For the most part, however, we depend on radiometric dating of volcanic deposits below, above and between the rocks in which fossil mammals occur.

Several terms common in the literature are not included in our figure. **Holocene** is sometimes called **Recent**, **Holocene** combined with **Pleistocene** is frequently referred to as **Quaternary**, and the pre-Pleistocene part of the Cenozoic used to be called **Tertiary**. All of geologic time has been subdivided much further but in this chapter the only such subdivision we use is **Messinian** (5.75–5.3 mya), during which the Mediterranean was cut off from the world ocean and evaporated largely or completely. Several Saharan desert-adapted mammal species seem to have evolved then.

Recent discoveries and future prospects

The current revision of the International Geological Map of Africa (Commission for the Geological Map of the World, 1985–1990) provides an overview of knowledge of the geology of the continent. Comparison of the enormous outcrop area of Mesozoic and even more of Cenozoic rocks with the very small number of sites from which most of the mammal record comes suggests immediately that the palaeontological exploration of Africa has hardly begun.

Not all of those rocks are fossiliferous, of course, and finding those that are is much easier in regions too dry for a continuous and heavy cover of vegetation. It is also easier to find significant fossils in a countryside where relief and erosion expose them for inspection. Less commonly in Africa than in some other parts of the world, discovery is also aided by the exposures produced by human engineering or mining activities.

Research driven by curiosity about human origins shows what can be achieved by serious prospecting. No doubt a comparable effort devoted to non-hominid mammals would bring similar rewards. Unfortunately the mineral resource in greatest demand, petroleum, requires direct searching of such small volumes of rock that it is unlikely to provide many fossil mammals, although it can provide useful background information about the mammalian environment. Some other minerals, such as alluvial gold and diamonds, and even humble limestone, have yielded a steady trickle of information significant to mammalogists. One might argue that the greatest contribution of economic geology to African mammalogy was recruiting L. B. S. Cooke to vertebrate palaeontology. In any case, there is no discernible current increase, nor any prospect of a spectacular future increase, in the flow of information about mammals and their past from economic geology.

The most spectacular progress of the past decade has come from the interaction of palaeontology and molecular genetics and the development of statistical methods for handling their data (see, for example the papers by Stanhope *et al.* 1998, Eizirik *et al.* 2001, Hedges 2001, Murphy *et al.* 2001a, b, Jaeger 2003, Springer *et al.* 2003, 2004, Jaeger & Marivaux 2005, Bininda-Emonds *et al.* 2007 and others already cited in this chapter). At the same time the classical methods of

vertebrate palaeontology have continued to enrich our understanding of African mammals and their history. Note for example Suwa *et al.* (2007) describing gorilla-like teeth from a late Miocene ape in Ethiopia and McBrearty & Jablonski's description of a fossil chimpanzee (2005), Seiffert *et al.*'s (2005) account of Africa's higher primate radiation, Sige *et al.*'s discovery of a late Palaeocene omomyid primate from Morocco (1990), and Kappelman *et al.*'s use of Oligocene mammals from Ethiopia to constrain the time of faunal exchange between Afro-Arabia and Eurasia (2003).

Two features of the African landscape have special promise for understanding the history of African mammals and their environment. Deep tectonic, volcanic and meteoritic lakes contain a very detailed stratigraphic record covering up to about 5 million years of Cenozoic time. That is long enough to embrace all of hominid evolution and reach back to the separation of chimpanzee and human evolutionary lines. Cores have already been raised that cover the last million years at L. Malawi and L. Bosomtwe in Ghana (Scholz *et al.* 2007). Bones of mammals are not likely to be found in useful quantities in those slender cores, but the environment is well represented in them by fossil pollen grains, diatoms and grass cuticles. At its best, the sediment in these lakes provides a discernible record of each individual year. Using Darwin's analogy we are likely to read each individual letter of a record covering the last million years, although we are likely to find that even in meteoritic impact lakes, where the record is most complete, an occasional word is missing.

The extensive basins between plume-driven swells, such as the Congo and Kalahari Basins, are the other special African resource. At present there is no immediate prospect of tapping the rich mammal record they must surely contain. Most have not been uplifted and exposed as a consequence of collisions between continental plates, like the Cenozoic beds of Eurasia and America, and excavating deposits that are many thousands of metres in thickness is still prohibitively expensive.

Could we tap the possibilities of those basins, however, we would be able to answer questions about the ancestral stock of afrotherians and anthropoid primates, and possibly about filter bridge connections across the Mediterranean, that puzzle us today.

CHAPTER FOUR

Africa's Environmental and Climatic Past

Robert J. Morley & Jonathan Kingdon

When an icy mantle gradually crept over much of the northern hemisphere, the greater part of the animal life must have been driven southward, causing a struggle for existence which must have led to the extermination of many forms, and the migration of others into new areas. But these effects must have been greatly multiplied and intensified if, as there is good reason to believe, the glacial epoch itself... consisted of two or more alternations of warm and cold periods.

Alfred Russel Wallace, *Man's Place in the Universe*, 1903

In this review we have three primary concerns:

- 1 To reconstruct the broadest features of the environments that ancestral mammals had to adapt to, notably in relation to the major division of African fauna and flora into humid (or forest-adapted) and arid (or non-forest-adapted) species and groups.
- 2 Given the very high proportion of contemporary mammal groups that have ancestral roots in, or have a history of exchange with, Eurasia, to understand the nature of those past environments that facilitated or inhibited such exchanges between the two land masses. It is also important to correlate such environments with estimated times of connection and disconnection.
- 3 To identify those features of change that may help us understand the biology, distribution and immediate history and ancestry of contemporary species.

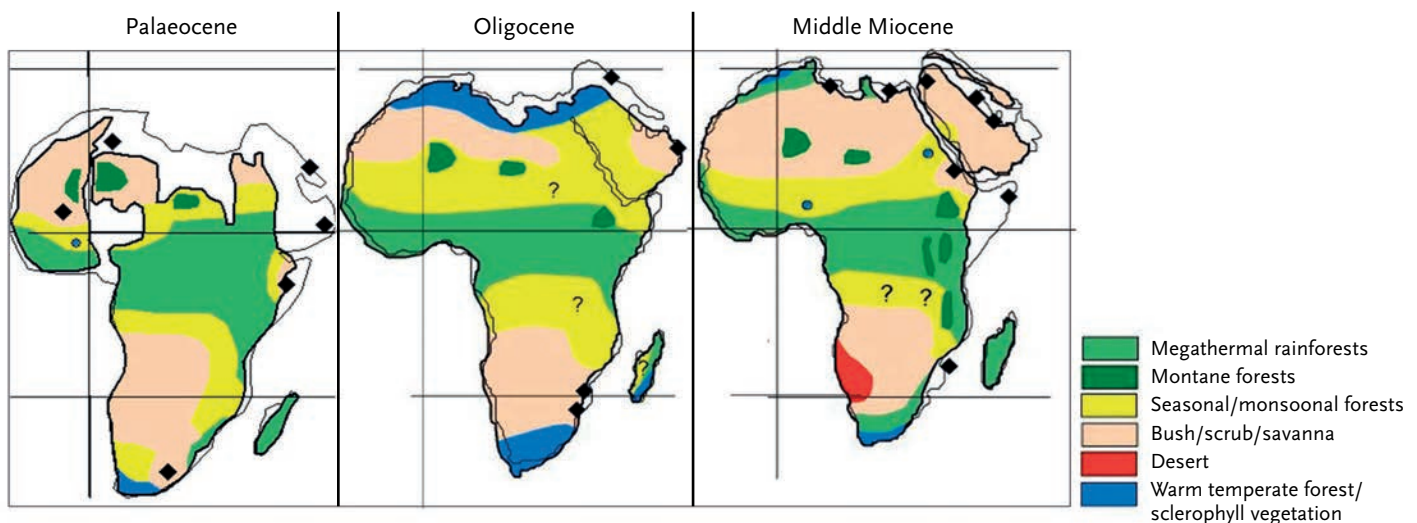
There are many very puzzling mammal distribution patterns as well as many unexplained peculiarities in the biology of living species that clearly have their roots in their ancestral pasts. To explain these alone requires deep perspectives in time: some can be explained on relatively short-term time-scales within the range of tens to hundreds of thousands of years, relating to the climatic perturbations of the Quaternary ice age, but others need to be considered on a much longer time-scale.

At generic or other higher taxonomic levels, time-frames on scales of millions or tens of millions of years need to be considered, taking us back to the mid-Cretaceous (105 mya) when placental mammals are thought to have emerged (Bininda-Emonds *et al.* 2007, Murphy *et al.* 2007), to later differentiation of the major lineages and further

radiation of mammals at the beginning of the Tertiary period (65 mya) following the extinction of the dinosaurs. Newly found fossils in China and Mongolia reveal that eutherian mammals were already established during the early Cretaceous (96–130 mya), and thus diversified substantially earlier than was formerly thought (Lopatin 2006). We have therefore begun this review from the beginning of the Cretaceous period, from which time the flowering plants first appeared, and subsequently came to dominate the vegetation of the continent.

Today, the vegetation and climate of the African continent contrasts markedly with the archipelagic region of South-East Asia and the Neotropics in that it is characterized by widespread deserts, such as the Sahara, the Horn of Africa and the Kalahari (see map p. 53), and huge stretches of savanna and open woodland, but relatively smaller areas of forest (Moreau 1963a, b, 1969, Kingdon 1971, 1990, White 1983). Africa has only one-fifth of the global total of tropical rainforest, despite having by far the largest land area within the tropical zone. South America and South-East Asia, instead, have comparatively more extensive tropical rainforests and fewer dry regions.

The flora of the African tropics is also less diverse than its other tropical counterparts. For instance, Africa has fewer species of palms than the tiny island of Singapore, and is also poor in Annonales, orchids and rainforest undergrowth taxa, epiphytes and lianes; there is also only one species of bamboo. In contrast to the relative poverty of tropical African flora, the southern tip of the continent has a very rich and diverse temperate flora, characterized by the Fynbos of the western Cape, a diversity only approached elsewhere in temperate areas of Western Australia.



Tentative vegetation maps for the Palaeocene, Oligocene and middle Miocene (from Morley 2000 with modifications). (In all maps palaeogeography and palaeocoastlines after Smith *et al.* 1994.) Occurrences of evaporites and bauxites (diamond symbols) from Boucot (unpublished).

Left map: Late Palaeocene/early Eocene thermal maximum.

Centre map: Oligocene, following the terminal Eocene cooling event.

Right map: Middle Miocene, coinciding with the Miocene thermal maximum.

The vertebrate fauna adapted to African forests also tends to differ from its Asian and American equivalents in that numerous species and groups have non-forest sibling species (Moreau 1966, Kingdon 1971, 1990, Schiøtz 1975). Conversely, neotropical and South-East Asian forest faunas are largely derived from forest-dwelling ancestors. The scarcity of larger organisms that can be shown to have a long and unbroken record of forest-adapted ancestry implies a tenuous hold for this habitat in Africa's past. Another mammalian group, the golden-moles (Chrysochloridae), that has recently been shown to derive from the very earliest radiation of afrotherian mammals (Stanhope *et al.* 1998), is best represented in temperate southern Africa, suggesting that long-term relative stability for temperate habitats in Africa may also be significant.

These contrasting differences between Africa and its tropical counterparts, and between tropical and temperate Africa, are the result of their different geological and climatic histories, involving a variety of time-scales (Morley 2000). The scenario presented here sets out to provide a background within which the evolution and diversification of African mammals can be investigated and visualized.

Palaeovegetation as the setting for mammalian evolution

This review of vegetational history and climate has been augmented by continent-wide vegetation reconstructions modified from Morley (2000), and constructed from palaeobotanical and palynological data, together with data from climatically sensitive lithologies, such as evaporites and coals, coupled with and utilizing climate modelling techniques of Parrish & Barron (in press). Data on the occurrence of bauxites from Boucot *et al.* (2008) have also been used in this reconstruction because bauxites form under hot, strongly seasonal climates and are therefore good climate indicators (albeit difficult to date). For generalized maps for the Palaeocene, Oligocene and Middle Miocene see above.

Cretaceous climate and vegetation

The African continent formed part of Pangaea during the Jurassic (180 mya) and became part of Gondwana in the earlier early Cretaceous (130 mya). During these periods it lay further south than today but still straddled the Equator (Smith *et al.* 1994). However, the climate of the region was relatively uniform (as shown by macrofossil and pollen floras summarized in global maps by Vakhrameev 1992). The vegetation of North and central Africa was characterized by woody members of the gymnosperm families Araucariaceae and Cheirolepidaceae (latter now extinct), perhaps with an understorey of ephedroid plants and some ferns. The absence of coal deposits (which reflect periods of ever-wet climate) for the entire African Jurassic and Cretaceous suggests that ever-wet climates over this period were absent, and Parrish *et al.* (1982) and Parrish (1987) have interpreted this as indicating the widespread occurrence of monsoonal climates (i.e. alternate wet and dry seasons) across the African land mass. Southernmost Africa, south of about 40° latitude, probably bore a more mesic vegetation with austral affinities, especially southern gymnosperms, such as *Dictyozamites*, *Nilssonia* and *Araucarites* (Vakhrameev 1992).

First appearance of flowering plants

A more distinctive climatic gradient became established across the continent in the later early Cretaceous (128–96 mya), until the early late Cretaceous (96–85 mya). This roughly coincided with the time of initial appearance and subsequent radiation of angiosperms across the region and their eventual rise to dominance over other groups. It is likely that the emergence and earliest differentiation of placental mammals was also taking place at about this time, probably in the Eurasian land mass (Beard 2004, Bininda-Emonds *et al.* 2007).

This period coincides with the global Cretaceous 'thermal maximum' (Barron & Washington 1985), when equatorial climates were considerably warmer than at present, with equatorial oceanic

temperatures being 5° warmer than modern oceans (Zachos *et al.* 2003). There was a clear climatic gradient at about palaeolatitude 20° N and S (Crane & Lidgard 1990), in the vicinity of the subtropical high pressure zones, probably reflecting belts of drier climates (Morley 2000), and with more humid (but not ever-wet) climates becoming established in the region of the palaeoequator (Doyle *et al.* 1982). Comparison of climatic inferences drawn from mid-Cretaceous palynomorph data with computer-derived climatic models are often in conflict in that the climate models propose often moist, seasonal low latitude climates (Barron & Washington 1982), but fossil data infer uniformly drier climates (Herngreen *et al.* 1996). A possibility is that although moisture may have been freely available at this time, higher temperatures may have resulted in overall moisture deficiency, registered by plants as indicating aseasonal aridity (Morley 2000); equatorial climates at the time of the radiation of the flowering plants would therefore have no present day analogue.

The first flowering plants (magnolialian dicots and monocots) probably became established in ephemeral habitats such as river flood-plains, and eudicots, the main clade of non-magnolialian dicots, exhibited an important centre of radiation in Africa during the Aptian (113–108 mya) (Doyle *et al.* 1977). These diversified rapidly during the Albian (108–96 mya), to become dominant over other plants during the Cenomanian (96–88 mya). Possibly this diversification and expansion reflects adaptation of flowering plants from flood-plains to most other habitats. The earliest radiations of mammals (according to Bininda-Emonds *et al.* 2007, between about 100 mya and 90 mya) seem therefore to have coincided with the sudden appearance of many new habitats and food sources that could have provided the setting for mammalian emergence, adaptation and diversification. There is currently no fossil evidence for the presence of placental mammals in Africa at that time but molecular clocks (most notably Bininda-Emonds *et al.* 2007 and Murphy *et al.* 2007) imply that an early common ancestor of the Afrotheria and South American Xenarthra might have been present around 90 mya.

Development of the rainforest canopy

The development of canopied tropical rainforest is of central interest because one of the most fundamental distinctions among many African taxa, including mammals, is between forest and non-forest species. Resemblances between African and Asian forest biota tempted earlier scientists to posit direct rainforest connections or corridors between these distant regions, connections that are now thought to be false. While the need to explain the resemblances remains, answers based on the adaptability of migrants promise to be more interesting and complex than explanations based on hypothetical forest corridors.

During the late Cretaceous, following the separation of Africa from South America, and also parallel with a phase of global cooling, the pattern of monsoonal climates across Africa began to change, and a more zonal climate regime came into place with the stabilization of the intertropical convergence zone to the equatorial belt. This led to the development of ever-wet climates at equatorial latitudes, indicated, for instance, in Nigeria by the presence of coal deposits from the Campanian (84–74.5 mya) (and possibly Coniacian 88 mya) onward (Reyment 1965). These wet climates resulted in a remarkable change in vegetation, thought to reflect the first development, on

a global scale, of the rainforest canopy, which is nowhere better illustrated than in West Africa. The appearance of tall trees is indicated by the presence of large-girth angiosperm wood (Duperon-Laudoueneix 1991), the occurrence of large-seeded angiosperms (large seeds being a necessary advantage for germination below the forest canopy) and also appearance of the first climbers, such as members of Passifloraceae and Icacinaceae (Chesters 1955), indicate that the main building blocks of the rainforest canopy were in place at this time, a development considered by Rubitski (2005) as one of the major stages in the development of all land plants. The gradual diversification of this vegetation is illustrated by the pollen record, which shows a steady increase in numbers of pollen types up to the end of the late Cretaceous (Boltenhagen 1976), and this has been proposed to reflect evolutionary adaptations that were associated with development of the forest canopy (Niklas *et al.* 2003).

Just a few years ago the idea that grasslands occurred in the late Cretaceous would not have been taken seriously. However, the recent discovery of diverse grass phytoliths in dinosaurian coprolites from India (Prasad *et al.* 2005) suggests that grasslands were probably extensive in the Indian subcontinent during the late Cretaceous, and it is therefore possible that grasslands were similarly present, and perhaps extensive, on the African Plate, but this is still a contentious conclusion.

During the late Cretaceous and early Tertiary (70–60 mya) Africa was an island continent, separated from South America by the widening Atlantic Ocean, and from Eurasia by the Sea of Tethys. However, the pollen record shows that numerous plant dispersals were taking place with South America (Morley 2003), presumably by island-hopping or by physical drifting on 'floating islands'. Dispersals were also taking place with Eurasia, for the latest Cretaceous of North Africa yields common Normapolles pollen (Kedves 1971, Meon 1990), which forms the dominant pollen group of western Eurasia and eastern North America at this time (Herngreen *et al.* 1996). The absence of this group from equatorial Africa, and of more southern elements from the north, such as hexaportricolpate pollen (probably derived from Didymelaceae, a family widespread across equatorial Africa in the late Cretaceous but now restricted to Madagascar), emphasizes that a strong climate zonation must have been in place across the African continent in the latest Cretaceous (Morley 2000).

While it is remotely possible that placental mammals had arisen earlier in Gondwana, it is now thought more likely that the first placental mammal got into Africa after the mid-Cretaceous. This would have been the ancestral afrothere (which might have been semi-aquatic) and presumably also arrived by island-hopping, sweepstake or rafting dispersal. The distant but exclusive affiliation of Afrotheria with South American Xenarthra suggests that the latter, in turn, rafted across the proto-Atlantic, then very narrow.

Widespread destruction following meteorite impact

The end of the Cretaceous period was heralded by a massive meteorite impact (Alvarez *et al.* 1980) in the Yucatan Peninsula in Mexico (Hildebrand *et al.* 1991). This collision, known as the K–T event, affected both fauna and flora globally, with the destruction of 38% of marine animal genera (Raup & Sepkowski 1984), including all ammonites, pliosaurs, mososaurs and ichthyosaurs, together with dinosaurs and pterodactyls on land. The destruction

that followed this impact affected both vegetation and environment globally, with wildfires causing massive destruction and short-term climate change during which sunlight was, perhaps, cut out over several years (Alvarez *et al.* 1980). African tropical rainforests did not escape, indicated by a 40% loss of pollen types across the Cretaceous–Tertiary boundary (Morley 2000, Fig. 5.15c) and the total loss of equatorial lowland gymnosperms. The effect of this meteorite impact on the flora and fauna of Africa was clearly quite dramatic, and many new niches must have become available virtually overnight, especially with the removal of generalist dinosaurian herbivores and carnivores.

Clearly a wide range of placental mammals survived the event. According to the molecular clocks devised by Bininda-Emonds *et al.* (2007), Springer *et al.* (2003) and Murphy *et al.* (2007), at least 20 major placental lineages had already differentiated before K–T. This discovery contradicts previous assumptions, which were based on an apparent lack of fossils before the K–T event, which was generally supposed to have accelerated the diversification of mammals in the early Tertiary (but see Wible *et al.* 2007 for a contrary view). In Africa the only living placental lineage present before the K–T event is currently thought to have been restricted to the Afrotheria and, probably, bats (Seiffert 2006). If molecular clocks are any indication it is also just possible that early Anthrozoidea had also arrived in Africa before K–T.

Earlier Tertiary (Palaeocene to Eocene) climate and vegetation

Data on the vegetation and climate for the Palaeocene and Eocene of Africa are sketchy, and reconstructing palaeoclimates and vegetation is problematic, and open to different interpretations of detail.

Based on pollen diversity data, following the K–T extinction the African flora went through a period of rapid diversification during the Palaeocene and Eocene (Morley 2000, Fig. 5.15c). Palynological and macrofossil data from northern, equatorial and southern Africa is best explained in terms of a climatically driven latitudinal zonation of vegetation across the continent through this period, and that the zonation was least marked during the late Eocene when global climates were cooling, and closed rainforests were extensive at equatorial latitudes, but best developed prior to this.

Palaeocene

During the Palaeocene (see left map p. 44), the equatorial climate is thought to have been less moist than in the latest Cretaceous. It was also probably seasonal, since coals, which were extensively present in the West African Maastrichtian (74–65 mya), are absent. Geomorphological evidence also points to seasonal climates, on the basis of the widespread distribution of bauxites and ferruginous crusts of Palaeocene–Eocene age across equatorial Africa (Guiraud & Maurin 1991). Around the coasts palynological data indicate that mangroves were well developed, and included the palm *Nypa*. Based on pollen data, other palms were also prominent at low latitudes.

Several lines of evidence suggest closed, mesic forests in widely scattered localities. Seward (1935) has described a mesophyll macroflora from the early Palaeocene of the Red Sea, an area which has also yielded wood of megathermal rainforest trees, such as

Myristicoxylon princeps (Myristicaceae) (Boureau *et al.* 1983). Marine sediments of Palaeocene age from Yemen have yielded diverse *Ctenolophon* pollen (Krutzsch 1989), from the rainforest tree family Ctenolophonaceae (a useful ecological indicator type), which was also particularly prominent in Cameroun at this time (Salard-Cheboldaëff 1990). *Ctenolophon* pollen is, however, absent from the Palaeocene of the nearby Niger Delta, despite its presence there in the latest Cretaceous (Germeraad *et al.* 1968), and conditions there may have been less favourable for rainforests than during the latest Cretaceous. Other Palaeocene pollen records suggesting the presence of closed mesic forests are forthcoming from Senegal (Caratini *et al.* 1991, Morley 2000). It is also likely that open vegetation is indicated by the presence of pollen of Gramineae, which occurs in modest frequencies in Nigeria (Adegoke *et al.* 1978), although it is equally possible that Gramineae were primarily dwellers of swamps at that time. Data therefore provide limited evidence for closed forest and possibly open woodland within the equatorial zone, and that palm-dominated swamps were probably extensive in low-lying areas.

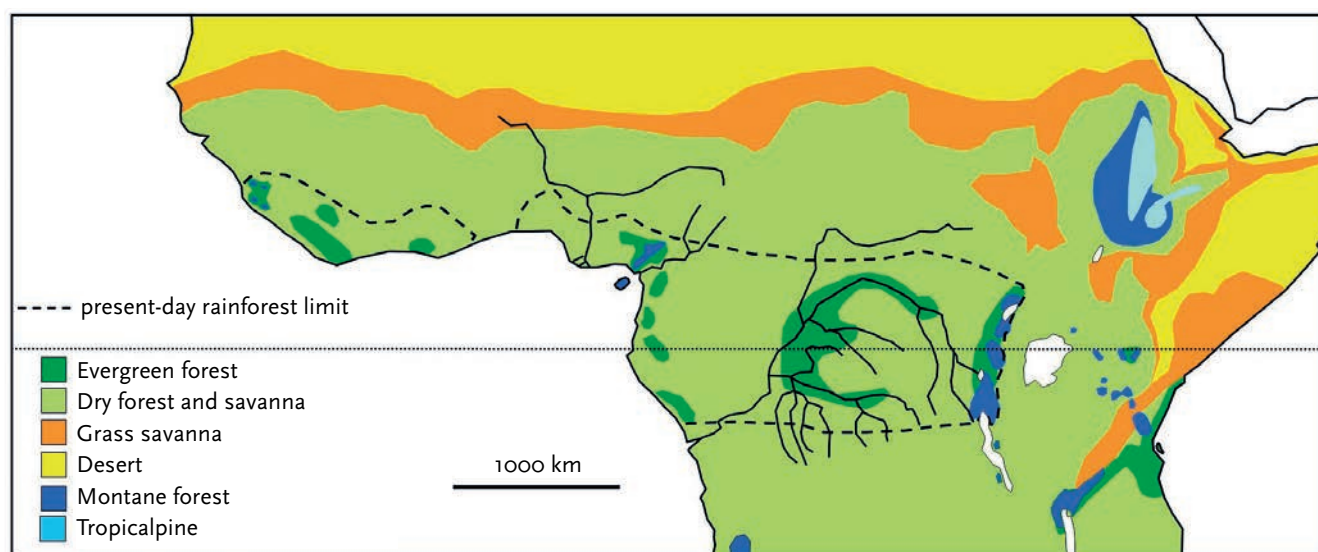
Limited evidence for Palaeocene vegetation to the north of the equatorial belt is available from fossil woods from Algeria and pollen from Tunisia. Louvet (1971) recorded wood comparable to that of the rainforest emergent *Entandrophragma angolense*, together with wood of several Leguminosae, from the Palaeocene of Algeria (in Boureau *et al.* 1983), but pollen analytical studies from North Africa suggest that Eurasian elements were also widespread components of the vegetation (e.g. Meon 1990). Floristic differences with the equatorial belt, shown by the absence of many characteristic low palaeolatitudinal pollen types in North Africa, suggest that the Saharan region formed a major biogeographic divide even at this time. This divide might have included upland areas, centred on the regions of Tibesti and Hoggar (Axelrod & Raven 1978) and might have been defined by arid climate.

Floras in southern Africa also differed from those of the equatorial zone, and included many southern hemisphere elements. In the Cape floral region, palynological studies at Arnot by Scholtz (1985) suggest the presence of open-canopied, dry, warm temperate forest with *Araucaria*, *Casuarina* and Proteaceae, and an understorey of Epacridaceae, Ericaceae, Restionaceae and Gunneraceae but without *Nothofagus*. Within the earliest Tertiary, the South African flora thus showed a close relationship with the Australian region, emphasizing the antiquity of the Cape Floristic Kingdom.

The only fossil placentals currently known to have been present in Africa during the Palaeocene are afrotheres, the primate *Altiasius*, a few supposed 'insectivores' (todralestids and, possibly, adapisoriculids) and some basal hyaenodontid creodont carnivores (E. Seiffert, pers. comm.). However, the only sites from this period are marine or shoreline so the samples may not be very representative.

Palaeocene/Eocene Tertiary thermal maximum

Evidence for African vegetation at the time of the late Palaeocene/early–middle Eocene thermal maximum is particularly meagre. However, there is good palynological data for floristic diversity change over this event from Colombia by Jaramillo *et al.* (2007) and Davis *et al.* (2005) and it is likely that, in the broadest terms, equatorial South America and Africa would have shown some parallels. The short-lived thermal maximum marking the Palaeocene/Eocene boundary



Vegetation of low latitude Africa for last glacial maximum. West and central African refugia from Maley (1996). Present text for eastern African refugia. Savanna and desert limits modified from Anhufer *et al.* (2006).

was caused by a sudden release of large volumes of the greenhouse gas methane from deep water hydrates, affecting temperatures globally (Pancost *et al.* 2007). The resulting rapid temperature rise at this time resulted in a further reduction of biotic diversity and the virtual elimination of the Colombian Palaeocene flora. Floristic diversity then increased rapidly, with maxima during the middle and late Eocene (Jaramillo *et al.* 2007). A similar scenario is likely for equatorial Africa (see illustration p. 51).

Reconstruction of African low-latitude vegetation during the early and middle Eocene is open to different interpretations. Bauxites occur commonly at very low latitudes, and this suggests that monsoonal climates may have been in place (see left map p. 44). A leaf flora recently described from a mid-Eocene crater lake from Tanzania, about palaeolatitude 15°S, suggests the presence of wooded rather than forest vegetation with near-modern precipitation estimates for this area (Jacobs & Herendeen 2004). The plant community was dominated by caesalpinoid legumes and was physiognomically comparable to miombo woodland. Coetzee (1993) indicated that microfossil assemblages from the Palaeocene–Eocene boundary point to a significant change in the lowland vegetation, and suggested the co-existence of a mosaic of dry and humid forest, with savanna woodland extending over most of the Congo Basin. This suggestion is to some extent supported by the data of Salard-Cheboldaëff (1990) from Cameroun, which showed that Gramineae pollen was common there together with forest elements. A change to drier, probably strongly xerophytic, vegetation in Egypt is likely on the basis of palynological studies by Kedves (1971), who showed that the earliest Eocene vegetation was dominated by Gramineae and cycads.

Fossil wood and seed determinations from North Africa, discussed by Boureau *et al.* (1983), suggest that mangroves were well developed there in coastal districts, with records of the palm *Nypa* from various localities, and fossil woods from probable Rhizophoraceae and Sonneratiaceae from Libya. In this region a coastal forested zone bordered by mangroves gave way to a more open, seasonal forest inland, with gallery forests along rivers (Boureau *et al.*

1983). Palynological studies from North Africa, however, continue to emphasize floristic differences from the equatorial region, through the presence of a significant Laurasian warm temperate element (Kedves 1971, 1986). Although some pollen of tropical elements, such as *Crudia* or *Isoberlinia* and *Acacia* (Leguminosae), was represented, the majority of those taxa characteristic of equatorial Africa were missing.

Late Eocene

A major change occurred in the equatorial African flora during the late Eocene (37–34 mya) with the sudden appearance of pollen of many extant taxa, particularly of legumes, most of which occur, sometimes as dominants, in extant African rainforests. The new appearances included the bat-pollinated tree *Parkia*, suggesting that nectivorous bats were already well established at this time. At about 37 mya fossil anthracotheres first appear (E. Seiffert pers. comm.); as these Eurasian hippo-like animals may have been partially aquatic their appearance implies origin by some form of island-hopping or rafting. The rainforest tree *Ctenolophon* reappeared in Nigeria, after an apparent absence in the earlier Eocene and Palaeocene (Germeraad *et al.* 1968), suggesting a wetter climate, and Gramineae became less common in Cameroun (Salard-Cheboldaëff 1990). To the north, palynological analyses by Kedves (1971) show some significant changes in the vegetation of Egypt, although pollen of warm temperate taxa, such as caryoid and myricoid pollen, dominate, together with pollen of cycads. Pollen of tropical tree taxa are much more common than previously, and can be referred to Sapotaceae, Bombacaceae, Mimosaceae and Palmae.

Differences between North African and equatorial vegetation is also shown by mangroves, which were characterized by *Nypa*, Rhizophoraceae and ancestral Sonneratiaceae in North Africa. West African mangroves began to diversify; in addition to Nypoidae, they also included *Pelliciera rhizophorae* (Theaceae), now restricted to the Panamanian isthmus and Pacific Colombia, and probably the brackish water palm *Oncosperma*, now restricted to South-East Asia (reflected by the presence of the pollen type *Racemonocolpites hians*).

Oligocene to mid-Miocene climate and vegetation

In equatorial regions generally, there was a marked floristic change at the end of the Eocene, paralleling the disappearance of tropical-aspect forests from the mid-latitudes as a result of global cooling. In Africa the rainforest flora subsequently underwent a significant phase of modernization in the Oligocene, with the first appearances of many extant genera from this time (Morley 2000). However, the overall trend was of extinction (Morley 2000, Fig. 5.14b). Particularly notable was the disappearance of many palms, especially of the brackish water Nypoidae (*Nypa* and *Proxapertites*). However, the overall diversity decrease suggests that all vegetation types were affected by the terminal Eocene event. Detailed palynological datasets over the Eocene–Oligocene boundary that might explain these changes are not available for equatorial Africa, but from South-East Asia there is clear evidence for much cooler and drier climates during the Oligocene, driven by global temperature changes (Morley *et al.* 2003), which also resulted in a reduction in species richness there. For Colombia, palynomorph diversity data by Jaramillo *et al.* (2007) also shows a dramatic reduction in floristic diversity. A similar pattern is likely for the African equatorial flora.

Oligocene

Mapping Oligocene vegetation in Africa relies heavily on global climate models, which suggest that temperate climates and vegetation were extensively in place within northern and southern areas (see centre map p. 44).

Unpublished palynological data from the Niger Delta (summarized in Morley 2000, p. 140) suggest that drier climates characterized the late Oligocene (28.5–23 mya). Grass pollen maxima, suggesting a widespread expansion of grasses, coincide with periods of lower sea levels. The late Oligocene phases of increased representation of grasses were not so pronounced as those of the late Neogene, and it is most likely that grasses formed the understorey of open woodland, rather than forming open grasslands.

There is clear evidence for a significant drying at the end of the Eocene in Egypt. Kedves (1971) showed that whereas late Eocene palynomorph assemblages are characterized by Eurasian warm temperate and megathermal elements, these were replaced in the earliest Oligocene by probable Chenopodiaceae/Amaranthaceae and Gramineae, with all of the megathermal elements, except Palmae, being absent. It is therefore most likely that in Africa the terminal Eocene event resulted in the expansion of drier and cooler climates, and an associated widespread retraction of tropical forests toward the palaeoequator. The character of North African Oligocene vegetation is also revealed by wood and leaf fossils, particularly from Algeria, Libya and Egypt, reviewed by Boureau *et al.* (1983). They suggest that in the Oligocene, North Africa was characterized by a mosaic of savanna, open forests and gallery forests, with continuous forest developing locally in low lying coastal areas. Mangroves would have fringed coastlines.

Eocene–Oligocene mammals

Although there were many changes in plant communities from the late Eocene to early Oligocene, especially at low latitudes, faunal changes are poorly known. Sieffert (2006) found less change between faunas from Fayum in the late Eocene, and Oligocene (37–29.5 mya) and

the late Oligocene (26.5–23 mya) from the Chilga region of Ethiopia (Kappelman *et al.* 2004). It has been suggested that African faunas therefore might have been less affected by the climate changes that elsewhere seem to have resulted in widespread extinctions (Prothero 1994). The dominant mammalian groups present at Fayum (and some at Chilga) were paenungulates (Embrithopoda, Proboscidea and Hyracoidea), arsinotheres, anthropoid primates and creodont carnivores. It is possible that other mammalian groups may have inhabited rain-forested areas at this time, of which there is no fossil record. This is particularly likely for hystricognath rodents, which first appear as fossils at the Eocene/Oligocene boundary (E. Sieffert pers. comm.) but may have made their first appearance in Africa earlier.

Early and mid-Miocene, Neogene thermal maximum

From the mid-Tertiary onward, the African land mass underwent a phase of uplift, with flexure of the pre-Miocene surface into a number of warps and basins (see p. 35) and the initiation of the East African Rift Valley (Baker *et al.* 1972). During the early Miocene, global temperatures once again began to increase, reaching a maximum within the earliest mid-Miocene.

In the earliest Miocene, prior to Neogene uplift and volcanism, when the continental divide was low, climates were moist over most of equatorial Africa, with rainforests extending more or less from coast to coast (Andrews & Van Couvering 1975). This is suggested by mammalian fossils preserved in early Miocene deposits east of the divide, that include forest dwellers. Palynological studies from southern Sudan suggest the presence of rainforest vegetation during the Oligo-Miocene (Awad & Brier 1993, Awad 1994), and a rich leaf flora of early Miocene age described from Rusinga I., L. Victoria by Chesters (1957), was thought to represent lowland rainforest by Andrews and Van Couvering (1975).

It was probable, however, that various biogeographic barriers existed between the east and west throughout the Tertiary, in order to account for the restriction of certain wood and leaf fossils to East and North Africa, especially to explain the presence of fossils of Asian Dipterocarpaceae in East Africa (Chiarugi 1933, Bancroft 1935) but to the west their absence, a divide that has a long history. Grubb *et al.* (1999) drew a line that represents the optimal separation of overlapping centre/western and eastern forest faunal elements. By analogue of Wallace's line in South-East Asia they termed this intra-continental biotic divide 'Kingdon's line'. This is discussed in more detail in Chapter 3 on evolution.

At the beginning of the early Miocene, West African mangrove swamps recruited two new taxa, *Rhizophora* (Rhizophoraceae) and the parent plant of the *Verrutricolporites rotundiporus* group of pollen (Lythraceae or Sonneratiaceae) that substantially modified coastal vegetation. Both of these taxa dispersed from South America (Morley 2000, 2003). *Rhizophora* subsequently became the most important element of West African mangroves, and pure swamps of this genus must have been extremely widespread, to account for the abundance of its pollen in marine sediments, especially during phases of Neogene rising sea levels. The parent plants of the *Verrutricolporites rotundiporus* pollen group are likely to have been derived from ancestral *Sonneratia* spp. (characteristic of South-East Asian mangroves), and thus early and mid-Miocene mangroves were much more diverse than those of the present day.

Early Miocene extinctions and the expansion of grasslands

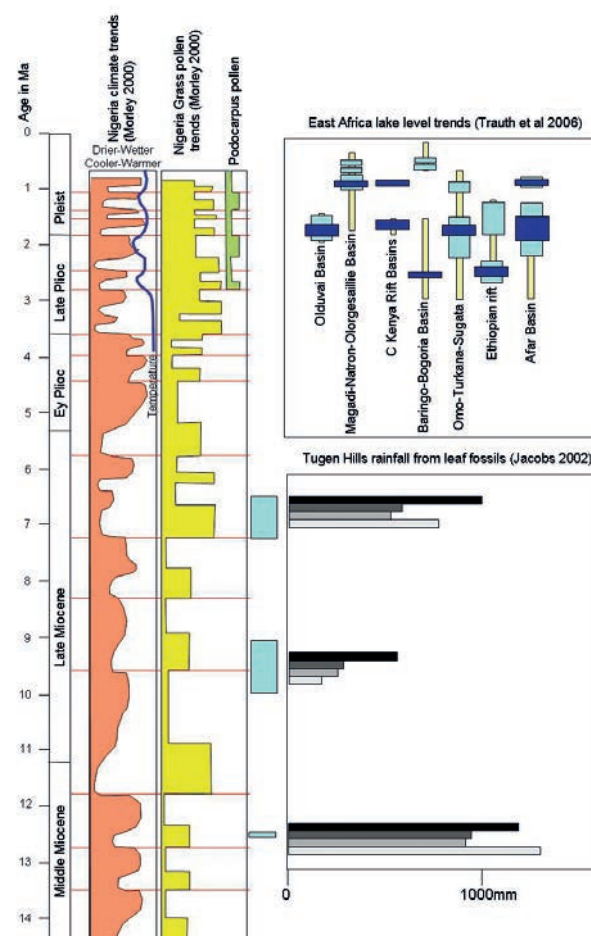
The palynological record from both the Niger Delta and Cameroon suggests a gradual change in the character of low latitude vegetation during the course of the Miocene, with successive extinctions of rainforest taxa (Legoux 1978, Morley 2000). During this time, Gramineae pollen, suggesting open grassy woodland or savanna, increases in representation, especially at times of low sea levels, with the first evidence of burning (from the presence of charred Gramineae cuticle) at about 15 mya, in the Middle Miocene (Morley & Richards 1993), widespread natural burning becoming successively more common during the mid-Miocene. Drier conditions are suggested over a wide area of the Niger catchment, with the expansion of open woodland and savanna at the expense of rainforests.

Rainforests in East Africa also became greatly reduced during this period and were replaced by open woodland and grassland. The character of mid-Miocene grass-dominated vegetation and gallery forest in East Africa has been reconstructed by Retallack *et al.* (1990) and Retallack (1992a, b), through the study of plant fossils and palaeosols associated with the *Kenyapithecus* site, which is dated at about 14 mya. He interprets a mosaic of early successional woodland, grassy woodland and wooded grassland and observed that mid-Miocene grassland ecosystems differed substantially from modern grasslands in that although the grass subfamily Chloridoideae and supertribe Paniceae were common, there was no evidence for the supertribe Andropogonae, which is now dominant in seasonally arid, overgrazed and burned African grasslands. Tooth enamel studies of mammalian faunas from Fort Ternan also suggest that East African mid-Miocene vegetation differed from Serengeti-type wooded grassland (Cerling *et al.* 1997) in that most food sources consisted of a C₃ diet, whereas modern tropical grasslands are dominated by C₄ grasses. Janis (2003) indicated that mid-Miocene ungulates represent a diversity of browsers that is unlike that found in any present-day environment, which is thought to reflect vegetation growing under conditions of greater CO₂.

The change from dominance of forests to the widespread development of woodland and savanna during the Miocene has generally been attributed to global cooling. However, upwarp of the African Plate following the formation of the East African rift is also important, and has recently been discussed by Sepulchre *et al.* (2006).

Vegetation and climate in northern and southern Africa

There is little evidence for moist forests within North Africa during the Miocene, which from the pollen record of Kedves (1971) was characterized by woodland and savanna. However, in South Africa, mesothermal to megathermal, mesic forests extended as far south as the southern tip of Africa during periods of warmer climate and high sea levels (Coetzee 1978). She recorded two periods, which she interpreted as within the early Miocene, about 19 mya, and mid-Miocene, 14–16 mya, when palm-dominated vegetation was widespread at the Cape. These intervals are associated with the occurrence of pollen of the primitive angiosperm *Drimys* (Winteraceae) and of the now endemic Madagascan rainforest tree family Sarcocaulaceae (Coetzee & Muller 1984). This suggests that during warmer, moist periods, the Cape vegetation bore similarities to the present day humid forests of Madagascar. It is possible that conservative mammals, such as the Cape Grysbok *Raphicerus melanotis*



Some indicators for climatic change in Africa. The two columns on the left show temperature fluctuations since the mid Miocene as inferred from Gramineae and *Podocarpus* pollen abundance in Niger Delta (modified from Morley 2000).

Top right: East African lake level data from Trauth *et al.* (2005).

Lower right: Rainfall inferred from leaf fossils in Tugen Hills (Jacobs 2002).

(which displays characteristics of the very earliest types of antelope), became adapted to what were once more extensive habitats, but are now relicts inhabiting the drier end of the Cape vegetation spectrum (Kingdon 1982, 1990).

Malagasy-like forests were also probably widespread along the east coast of southern Africa, but not in the west, since the west coast experienced a very dry climate after the inception of the cold circum-polar current, which began to flow at about the Oligocene–Miocene boundary, about 23 mya (Barker & Burrell 1977) and development of polar ice in the Antarctic (Van Zinderen Bakker 1975). According to Denton (1999), the Benguela current in its present configuration formed about 10 mya.

During intervening times, temperate woodland, with southern hemisphere gymnosperms *Podocarpus*, *Microcachrys*, *Widdringtonia* and drier, sclerophyllous vegetation, with *Casuarina*, were widespread. Sub-tropical evergreen forest patches with Cunoniaceae and Proteaceae survive today as refugia in gulleys in the mountains of the Cape region, and may be relicts of the tropical aspect rainforests which were widespread during the Miocene.

The extent of austral-affinity warm temperate vegetation in South Africa has been greatly influenced by the northward drift of the African

Plate into the southern hemisphere high pressure zone. In the Oligocene and early Miocene, most of South Africa would have occurred south of this zone (Morley 2000: Fig. 13.5), permitting the expansion of forests with common megathermal elements during the mid-Miocene thermal maximum. During the late Miocene and Pliocene, the combination of northward drift of the African Plate coupled with a strengthening of the southern hemisphere high pressure zone, opportunities for austral warm temperate communities of animals and plants became substantially reduced, with the result that today, they are restricted to just a few localities across the Cape region. Recent molecular studies on this flora suggest that the diversity of species can be partially attributed to rapid late Neogene evolution (Richardson *et al.* 2001, Linder 2003, Klak *et al.* 2004). It is probable that an enlarged source area for this flora, prior to the later phases of northward drift of the African Plate, was also influential in the development of this uniquely diverse flora. The diversity of Afrotherian golden-moles in southern Africa and the peculiarities of their distribution are also suggestive that the beginnings of that diversity lay in the once more extensive range of southern temperate environments.

Interchange of African and Eurasian mammals and its relation to plant dispersal

The first interchange of Eurasian and African mammals, long believed to have taken place in the mid-Miocene, following the collision of the African and Asian Plates, is now thought to have taken place in the earliest Miocene at about 23 mya (Jolivet & Facenna 2000) but immigration of single taxa, presumably by sweepstake or rafting, took place earlier, notably ancestral anomalurids and ctenohystriid/hystriognaths. It is possible that these taxa are uniquely African in origin, the former giving rise to extant anomalures and springhares, the latter to such ancient endemics as gundis, mole-rats and cane rats. Late Eocene fossil rodents, *Protaphiomys algeriensis* (thought to belong to the cane rat lineage, Thryonomyidae) and an anomalurid, *Nementschamys jebeli*, have been found in Algeria (Jaeger *et al.* 1985) and are consistent with African origins (as estimated by molecular clocks), which imply an invasion during the early Eocene (Adkins *et al.* 2001, Montgelard *et al.* 2002, Stepan *et al.* 2004). These discoveries support suppositions for very early, sweepstake arrivals of single ancestors for major rodent radiations. Still earlier fossil ctenohystriid rodents have been unearthed recently from 37 million-year-old deposits in the Fayum (E. Seiffert pers. comm.). These are currently undescribed and show little diversity, implying that their arrival in Africa might not have been much earlier (E. Seiffert, pers. comm.).

At about 23 mya the earliest documented major faunal exchange between Africa and Eurasia is likely to have brought in the common ancestor of all African antelopes (Antilopinae) as well as those of cricetomyine (and, perhaps, proto-gerbilline) rodents (Adkins *et al.* 2001, Stepan *et al.* 2004). Following this time, and particularly during the mid-Miocene (18–15 mya), many Eurasian mammals, such as tragelaphine bovines, shrews, carnivores, perissodactyls, Anthracotheres and giraffids, dispersed into Africa, and some Afro-Arabian mammals, such as some elephant, primate and porcupine emigrants, successfully migrated in the opposite direction.

Such interchanges are not apparent from the record of plant fossils, at least, with respect to tropical taxa. This is probably due to the presence of strong latitudinal vegetational zonation that restricted dispersal between higher and lower latitudes, a constraint

that operated from the terminal Eocene onwards. Only the appearance of the conifer *Juniper* within the East African highlands (noted by Bonnefille 1984) and *Alnus* in North Africa (Kedves 1971) can be considered candidates for such dispersal. Latitudinal belts of arid climate and vegetation may have been breachable for the more versatile of mammals but it seems very likely that, for more sensitive species, dry habitats represented a barrier that was not easily crossed in either direction. For example, duikers, galagos and other forest mammals have never made it out of Africa and there are Eurasian forest mammals, such as tapirs, tupias and tarsiers, that were equally inhibited from colonizing Africa.

The situation for mammals may differ from plants in that most, perhaps all successful mammalian immigrations up to the Miocene probably derived from a very few, single ancestral invaders, not some major influx, and their ecological restriction may have been less constraining. For some mammal immigrants, particularly later ones, a broad latitudinal belt of arid land delayed or inhibited colonization of more southerly regions, thus shaping the pattern of evolutionary radiation in Africa, a phenomenon that is discussed in more detail in Chapter 6 on evolution.

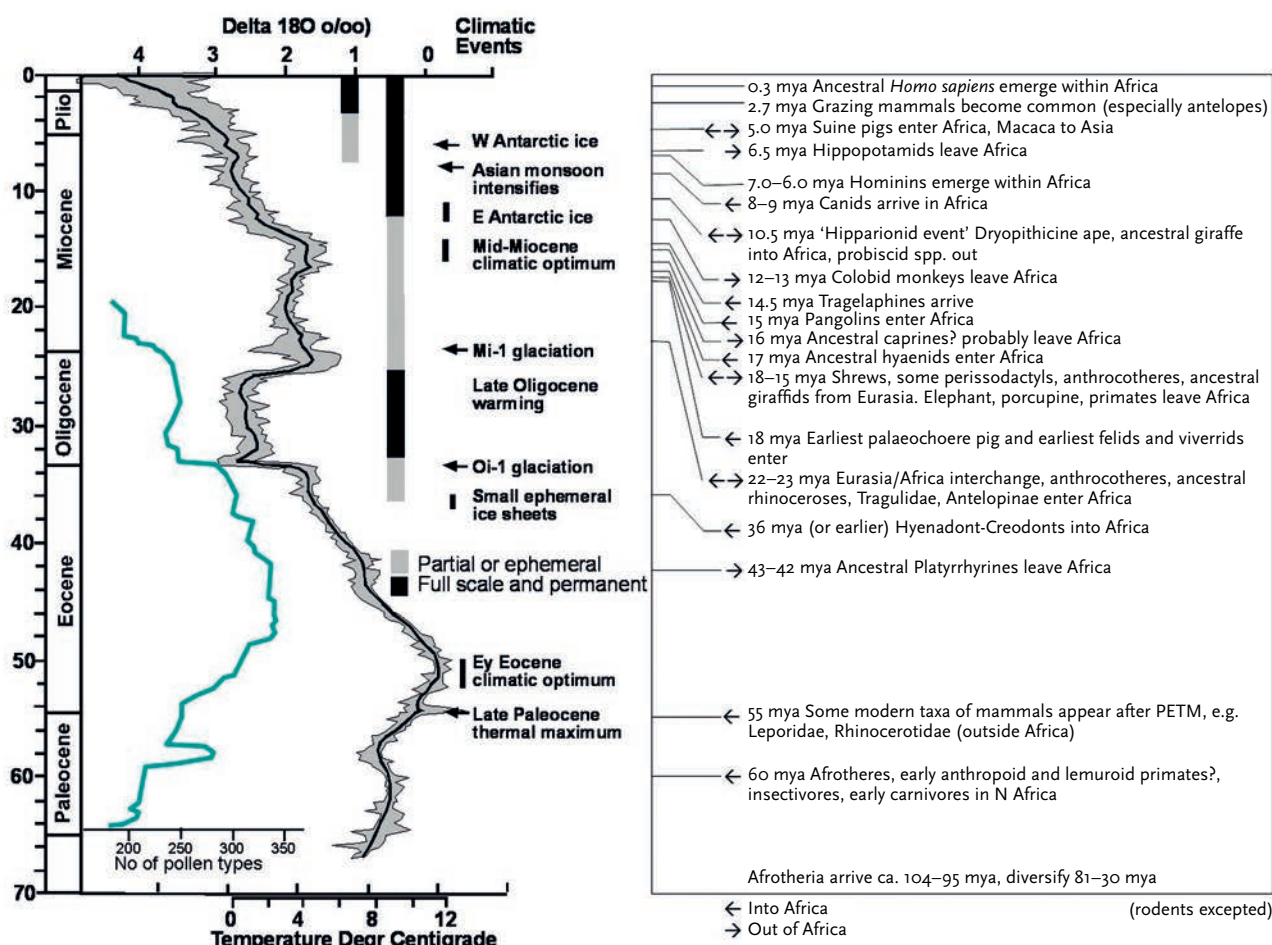
As noted above, members of the group Afrotheria dominated Africa's fauna throughout the mid-Tertiary, but today South Africa has retained more afrotherians (notably the Chrysochloridae or golden-moles) than any other region. A possible dimension to this very marked biogeographic pattern is that the equatorial rainforest belt, acting as a barrier between afrotherians and their ecological competitors, inhibited Eurasian taxa from invading southerly niches (certainly up to the uplift of East Africa in the mid-Miocene). A similar dynamic may have operated with the bathyergid mole-rats (blesmols), which are less ancient than golden-moles, but none the less, represent an early endemic rodent radiation which is now predominantly southern and south-eastern in distribution.

Late Miocene and Pliocene climate and vegetation

Late Miocene

The late Miocene was a time of global cooling, with a widespread build-up of ice in Antarctica (Abreu & Anderson 1998, Zachos *et al.* 2001). A detailed record of the effects of global temperature fluctuations on the vegetation of equatorial Africa is forthcoming from palynological analyses of deep boreholes from the Niger Delta (Morley & Rosen 1996, Morley 2000). This delta, being located on the northern edge of the rainforest belt, between the Dahomey Gap and the Cameroon–Gabon rainforest block is in a very sensitive position for recording climatic change in West Africa (Poumot 1987, Morley & Richards 1993). From East Africa, sites display at best only an intermittent palynological record (Bonnefille 1984) but benefit from well-preserved leaf floras, which provide detailed palaeoclimate data for short time intervals (Jacobs 1999, 2002).

Palynological records from deep Niger Delta boreholes display alternating maxima of rainforest and Gramineae pollen (Morley 1996, 2000). These reflect successive periods of expansion of grasslands, possibly across the Niger Delta, and a parallel reduction in range of rainforests. The grasslands, probably open savannas, were maintained by natural fires, since the fossil grass pollen is generally



Global temperature curve based on C18 by Zachos *et al.* (2001), and South American (Colombia) pollen diversity by Jaramillo *et al.* (2007). The timing of main mammal appearances, migrations and emergences are tentatively indicated.

accompanied by charred Gramineae cuticle, which suggests burning (Morley & Richards 1993). The many fluctuations of pollen from savanna to rainforest closely parallel sea level fluctuations that have been identified by sequence stratigraphy (Morley & Rosen 1996), testifying to their significance operating on a regional scale.

The first major dry phase at the beginning of the late Miocene was characterized by the frequent presence of Gramineae pollen and by the common occurrence of pollen of Caesalpiniaceae, suggesting a combined expansion of savanna and open woodland, and this coincided with the most pronounced of the Neogene sea level falls at about 11.7 mya (Hardenbol *et al.* 1998). Characteristic rainforest and freshwater swamp taxa became common only after sea levels subsequently rose to their previous maximum levels, the climate became more moist and mangrove swamps expanded. During this time, mangrove communities actually underwent a remarkable reduction in diversity, losing sonneratioid taxa and also the possible brackish water palm *Oncosperma* possibly associated with phases of late Miocene sea level fall and increased aridity.

The late Miocene is an important period for the emergence of the common ancestor for humans and African apes. While this was long thought to represent an endogenous African development, it is now considered more likely that a species of Eurasian tree ape or woodland dryopithecine entered Africa at about 10.5 mya (Stewart & Disotell 1998, Heizemann & Begun 2001, Kingdon 2003). This was a major

episode of intercontinental faunal exchange that is known as the Hipparionid event, when there appears to have been a good connection between Africa and Eurasia when sea levels were low. Among the incomers was the porcupine *Hystrix* and an ancestral murine rodent (Misonne 1969, Stepan *et al.* 2004), various carnivores, giraffes, caprines and tetraconodont pigs (Harris & White 1979, Pickford 1993): among the likely outgoing stocks were colobine monkeys (Stewart & Disotell 1999) and some afrotherian emigrants.

The alternating climates of this period are likely to have been of relevance for the speciation of many equatorial mammals, including the emergent hominins, because climate change fragmented both forest and non-forested areas into temporary islands that expanded and contracted. The moist equatorial islands, in particular, probably followed patterns that were repeated over and over again with predictable major centres in the far west (Upper Guinea), Cameroon/Gabon and central Africa (i.e. eastern Congo Basin) (Moreau 1966, Kingdon 1971, 1990, 2003, Hamilton 1976 and see map p. 55).

The most obvious effects of such isolation of populations would have been to reinforce the distinctness of isolates but another dynamic also operated. Each time changing climates altered the vegetation of an ecological island from, say, savanna woodland to moist forest, its inhabitants became engulfed in forest and had to adapt to the new conditions or die out. Although former 'corridors' that might have isolated non-forest organisms within what are today forest

areas and the adaptation of such organisms to true forest have to be extrapolated, there are numerous examples of 'engulfed' organisms, especially in the Congo Basin and Gabon/Cameroon region. Among primates, the example of the ancestral gorilla is discussed in more detail in Chapter 6. The Sun-tailed Guenon *Allochrocebus solatus*, a very localized, now forest-dwelling species from a small region of the Ogooue River Valley, also exemplifies just such an engulfed species inasmuch as this very terrestrial primate exhibits several hints of previous adaptation to drier environments (Dutrillaux *et al.* 1982, Kingdon 1997).

The broader continental pattern of interaction between past climates and habitats is also relevant to any attempt to reconstruct human origins and prehistory. At the core of any evolutionary radiation is the isolation of populations, and the bisection of Africa into an upland, cooler and drier south-eastern zone versus a lowland, warmer and wetter centre-western zone is germane to any consideration of continent-wide patterns of evolution. This is discussed in further detail in Chapter 6. Another corridor between separate arid regions occurs in East Africa; the Somali arid zone has probably been of biogeographic significance at least since the mid-Miocene uplift that created the East African highlands and their associated rift valleys. This corridor has long been one of the defining major features of African biogeography, with naturalists noting the close Horn/Namib affinities between such arid-adapted mammals as oryxes and dik-diks and, among birds, bustards, sandgrouse and larks (Lydekker 1908, Moreau 1952, 1963a, Kingdon 1971, 1990, Coe & Skinner 1993). The role of this corridor in separating forest communities has had less emphasis and the recognition that there was a temporal dimension, with older biota occupying the coastal region and ancient crystalline mountains of eastern Tanzania and younger forest biota on the volcanoes and moister areas of central and western Kenya and Uganda, is more recent (Kingdon 1971, 1990).

The East African dry corridor has periodically connected the Horn of Africa with the deserts of extreme south-west Africa and the entire eastern region can be predicted to have been strongly perturbed by almost every major episode of climatic change since the earliest Miocene (see profiles of *Madoqua* and *Oryx* spp. in Volume VI). Because equatorial lowlands are demonstrably the preferred habitat of all the larger diurnal primates many of them would probably span the continent had there not been climatic and tectonic interruptions, albeit periodic, that broke the continuity of these forests (see map p. 55).

Because many primates are dependent on a year-round supply of fruit, aridity can be predicted to have eliminated all but the hardiest of primates from much of the East African interior. The East African coastal region and montane piedmonts, by contrast, have been very favourable habitats for primates, even up to the very recent past, and it is here that the earliest woodland-adapted Miocene apes would have found a narrow but particularly favourable environment. The fossil record shows that between 6 mya and 1 mya most of the many populations of hominins had an eastern distribution. It is therefore plausible that the eastern coastal region and favourable habitats inland are the most likely settings in which mainly terrestrial, highly 'manual' (and eventually bipedal) habits first developed, in relative isolation, in a Miocene tree ape population (Kingdon 2003). Anthropologists have, for many years, identified climate change as a dominant force driving the evolution of hominins. The biogeographic, ecological and behavioural contexts in which hominins evolved have

had less attention and, by the nature of the evidence, largely remain areas of conjecture and extrapolation (as with so much of hominin prehistory).

In West Africa, periods of expansion of open vegetation with grasslands became more pronounced after about 7.0 mya. The pollen record shows the presence of abundant Gramineae and Cyperaceae, and the presence of charred Gramineae cuticle fragments with the fossil pollen indicates that the grasslands were regularly subject to burning, and thus may have resembled modern savannas in many areas, with dry, or seasonal climate vegetation increasing in diversity.

Late Miocene leaf floras from the Tugen Hills in Kenya studied by Jacobs (2002) and Jacobs & Deino (1996) have been dated at 9–10 mya (from Waril) and 6.6 mya (from Kapturo), respectively. The older of the two localities suggests an open vegetation structure and a climate with a pronounced dry season, whereas the younger suggests a woodland or dry forest setting. Jacobs (2002) suggests from these data that there was not a unidirectional change from forest to open environments in the Kenya Rift Valley during the late Miocene (as is often proposed to explain the evolution of hominids in Africa). As with the Niger catchment, it is more likely that a succession of alternating wetter and drier phases occurred, with an overall trend toward cooler and drier climates, in line with global trends. The Waril locality would thus tie in well with the West African expansion of open vegetation from 9 to 11.7 mya, whereas the 6.6 mya Kapturo assemblage would tie in with the phase of wetter climates from 6.5 to 7 mya recorded from the Niger Delta. Intervening wet phases might also account for the occurrence of 'rainforest' elements far north of their current distribution, such as the occurrence of late Miocene fossils of a waterbird, *Podica*, at L. Chad, which is exclusive to forest-fringed waters (Louchart *et al.* 2005).

Isotopic, C_3/C_4 analyses from the Tugen Hills suggest that late Miocene vegetation in the East African rift was derived from a mix of C_3 and C_4 plants, and that open grasslands at no time dominated this portion of the Rift Valley (Kingston *et al.* 1994). They suggest that the vegetation through this period was ecologically diverse, and that there was no single shift from more closed C_3 to more open C_4 grassland habitats. Two factors need to be considered when interpreting such datasets: first, how complete is the stratigraphic succession (a sequence stratigraphic approach could bring to attention the likelihood of repeated stratigraphic gaps); and secondly, it must be borne in mind that the succession for this part of the East African Rift Valley may not be representative of African environments as a whole, especially since palynological data from the Niger Delta indicate that widespread grasses contributed to African vegetation long before the late Miocene (Morley 2000).

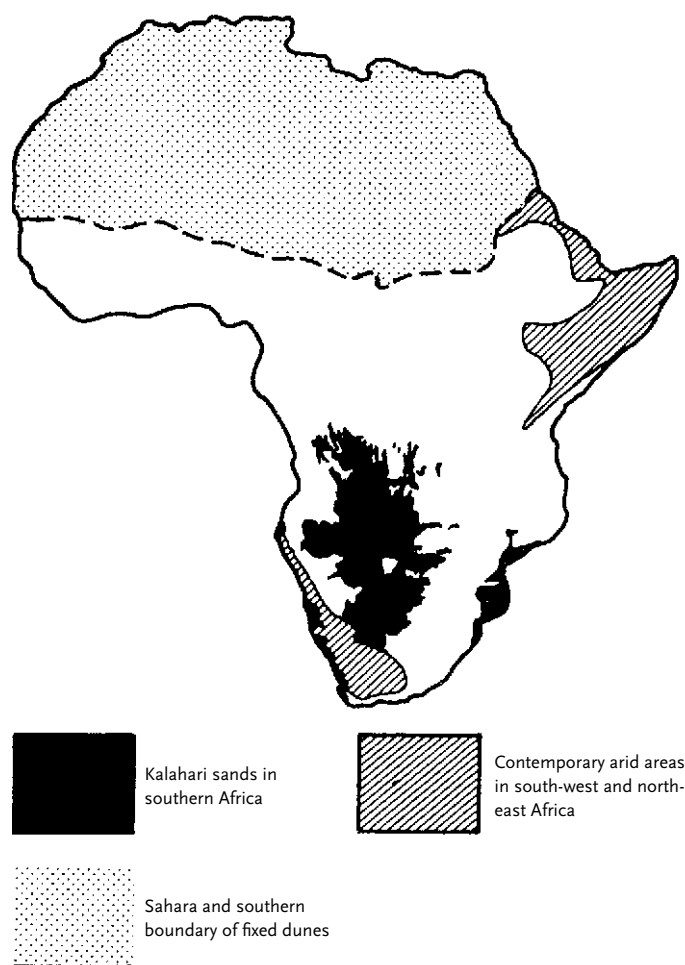
Pliocene and late Pliocene cooling and aridification

The early Pliocene (5–3.5 mya) was characterized by moist climates, the expansion and diversification of rainforests, and the contraction of savanna. The expansion of rainforests was greatest at the end of the early Pliocene, when they extended northward along the coast with palynological signals as far as northern Senegal (Leroy & Dupont 1994).

It should be borne in mind that rainforest elements reach Senegal even today, as extremely wet rain seasons counterbalance the effects of long intervening dry seasons. The late Pliocene (3.5–1.6 mya) however, saw much more pronounced climatic changes, with marked

drying and cooling. A drying phase at 3.2 mya was followed by a much more pronounced period of desiccation at 3.0 mya, both being accompanied by the marked expansion of grasslands, reduced floristic diversities and numerous regional extinctions. At about 2.7 mya, coinciding with the onset of glaciation in the northern hemisphere, a sudden change to a cooler climate resulted in the expansion of *Podocarpus* into West Africa (Morley 2000, 2003), indicated by pollen records (first brought to attention by Knaap 1972). This was the first evidence for a gymnosperm to occur in West Africa since the end of the Cretaceous. These changes took place during successive wet–dry oscillations. Recent studies based on isotope data, by Trauth *et al.* (2005) for East Africa, clearly show the intervening periods of increased humidity associated with these oscillations, with periods of increased humidity from 2.7 to 2.5 mya, and 1.9 to 1.7 mya.

Studies of the last glacial/interglacial cycle (Dupont & Wienelt 1996, Maley 1996) suggest that *Podocarpus* was common in West Africa at times when climates are cooler than at present, but still moist, at which time cloud forest was probably widespread (Maley 1987, 1989, 1996), and it is thought that such conditions must have created a suitable pathway for the dispersal of *Podocarpus milanjanus* from upland areas in East Africa via Angola and Gabon. Opportunities for dispersal of this species may also have been assisted as a result of the late Miocene–early Pliocene uplift of the African Plateau (King 1962).



Evidence for extreme aridity in Africa. Wind-blown sands extend from the Sahara to form fixed dunes well south of their present limits. To the south, Kalahari sands underlie contemporary forest.

Aridification was a continent-wide feature of the late Pliocene. Studies of ODP site 658 offshore of Senegal by Leroy & Dupont (1994) indicate an increase in trade wind activity between 3.3 and 2.5 mya, with a marked phase of aridification after 3.2 mya. Further aridification occurred around 2.7 mya, with desert conditions developing after 2.6 mya. Similarly, Bonnefille (1984), using palynological data, records a change to much drier conditions after 2.5 mya for East Africa. The pattern of expansion of open, wooded and savanna habitats and of aridification, with major phases of expansion at the beginning of the late Miocene (after 11.7 mya) then again at about 7 mya, followed by the Messinian (5.75–5.3 mya) and yet again within the mid-Pliocene, after 2.7 mya, corresponds with fossil evidence that browsing mammals, notably antelopes, were widespread and numerous during the late Miocene, while grazers supposedly only became prominent in the fossil record from the mid-Pliocene (Turner 1995). However, the ability of particular ungulate lineages to digest grass evolved at different rates and times, with Perissodactyla, for example, becoming grass-eaters much earlier than other taxa. Grass-eating equids were well represented as fossils substantially earlier than the Pliocene.

Quaternary climate and vegetation

The role of past climates in determining distributions and limiting species to specific localities was recognized early (Lonnberg 1929, Wayland 1940). Discontinuities in the geographic distributions of African birds (Moreau 1963b, 1966) and rainforest plant species (Hamilton 1976, Brenan 1978, White 1983) were proposed to reflect the restriction of rainforests to refugia during the driest and coolest periods of the last glacial, from which they subsequently spread during the Holocene (Mayr & O'Hara 1986). For mammals, accumulations of species in favourable localities were attributed to multiple phases of connection and disconnection (largely driven by climatic changes), with representatives of successive faunal and climatic eras superimposed upon one another within such local centres (Kingdon 1971, 1990). Early palynological studies from the East African highlands provided little evidence either to support or refute such suggestions (e.g. Coetzee 1967, Livingstone 1967, Hamilton 1982); they mainly showed that during the last glacial maximum, montane vegetation zones were depressed altitudinally by 1000 m or more.

Quaternary distribution of forests and forest faunas

Subsequent palynological data from low altitude sites and from marine cores are, however, now providing clear evidence for the retraction of rainforests during the time of the last glacial maximum and of the occurrence of refugia (Anhuf *et al.* 2006). Lake Bosumtwi in Ghana (Maley & Livingstone 1983, Maley 1989, 1991, 1996) and L. Barombi Mbo in Cameroun (Brenac 1988, Maley 1996) are currently surrounded by closed forests, but pollen records show that the area surrounding L. Bosumtwi was unforested during the time of the last glacial maximum, whereas L. Barombi Mbo, close to the Cameroon–Gabon Refuge, was surrounded by open forest, with grassland at the same time. Similarly, palynological studies of a deep marine core offshore the Dahomey Gap, to the south-west of the Niger Delta, indicate that during the period of the last glacial, savanna was much more extensive in the Niger Delta catchment than today, and also that rainforests formed a continuous

belt from Cameroun to Guinea during the early Holocene (Dupont & Wienelt 1996), tying in with wetter early Holocene climates from North and East Africa suggested from high lake levels (Street-Perrott & Grove 1976). Offshore cores from West Africa also show that during the last glacial maximum, the savanna belts substantially shifted to the south (Hoogheemstra & Agwu 1988), correlating with evidence for low lake levels across the Sahara, in Mauritania, Ethiopia, Sudan and the East African highlands (Street-Perrott & Grove 1976).

On the other hand, palynological studies from a core offshore Ghana recorded the presence of rainforests on adjacent coasts throughout the last glacial maximum (Lezine & Vergnaud-Grazzini 1993), and pollen analyses from Uganda (Sowunmi 1991) and Burundi (Bonnefille & Riollet 1988) provide evidence for forest continuity in areas proposed as forest refuges. In both these instances rainforest pollen assemblages contain a mixture of lowland and montane elements, suggesting that during glacial maxima, rainforests contained a mixture of lowland and lower montane taxa, as suggested also for the Amazon Basin by Colinvaux *et al.* (1999) and Bush & Silman (2004). A recent review of palaeoecological data from equatorial Africa by Bonnefille (2006) emphasizes that patterns of floristic diversity seen in rainforests cannot be explained by simple replacement of rainforest by savanna during glacial periods, but that more complex processes must have been in place that are currently poorly understood.

Studies from offshore cores are also beginning to show the nature of vegetation change in equatorial Africa during the last interglacial and beyond. The offshore Niger Delta deep-sea core studied by Dupont & Wienelt (1996) showed that rainforest vegetation during the last interglacial (Oxygen isotope stage 5e, 120,000–110,000 years ago) was very similar to that of the Holocene, and that at that time also, rainforests were probably continuous along the coastal region of the Gulf of Guinea. During stages 5d–a (110,000–74,000 years ago), however, although rainforests were still widespread, there was some expansion of woodland, but most notably, mountainous *Podocarpus* forest expanded in Cameroun and possibly Nigeria, as a result of some degree of lowering of temperatures, but without major changes in rainfall. It is unlikely, however, that rainforests extended far beyond their Holocene limits at any time during the Quaternary, for a core from L. Oku, which occurs in the Guinea Savanna belt, in a tectonic depression at the southern end of the Benue Trough (7°N) in Nigeria (Medus *et al.* 1988), has yielded a sedimentary succession of late Pliocene and Pleistocene age (Morley 2000), which shows rapid fluctuations of Gramineae and Cyperaceae pollen and provides evidence for fluctuations of savanna grasslands, marshes, gallery forests and montane vegetation over the last 2.7 million years, but without evidence for rainforests.

A legacy of 'glacial' forests with a mixture of upland and lowland taxa may find some reflection in the distribution of some mammal species, notably those that are equally well adapted to lowland rainforest and montane habitats, but such adaptability is far from universal. Examples of mammals that appear to be relatively insensitive to altitude are guenon monkeys belonging to the very widely distributed Gentle Monkey *Cercopithecus mitis* complex that commonly inhabit both habitats, sometimes, but not always, showing subspecific differences that correspond with altitude. Likewise, Lord Derby's Anomalure *Anomalurus derbianus* inhabits equatorial lowland and montane forests from the Atlantic to the Indian Ocean coasts.

The Bushbuck *Tragelaphus scriptus* and Two-spotted Palm Civet *Nandinia binotata* show similar versatility while several other species

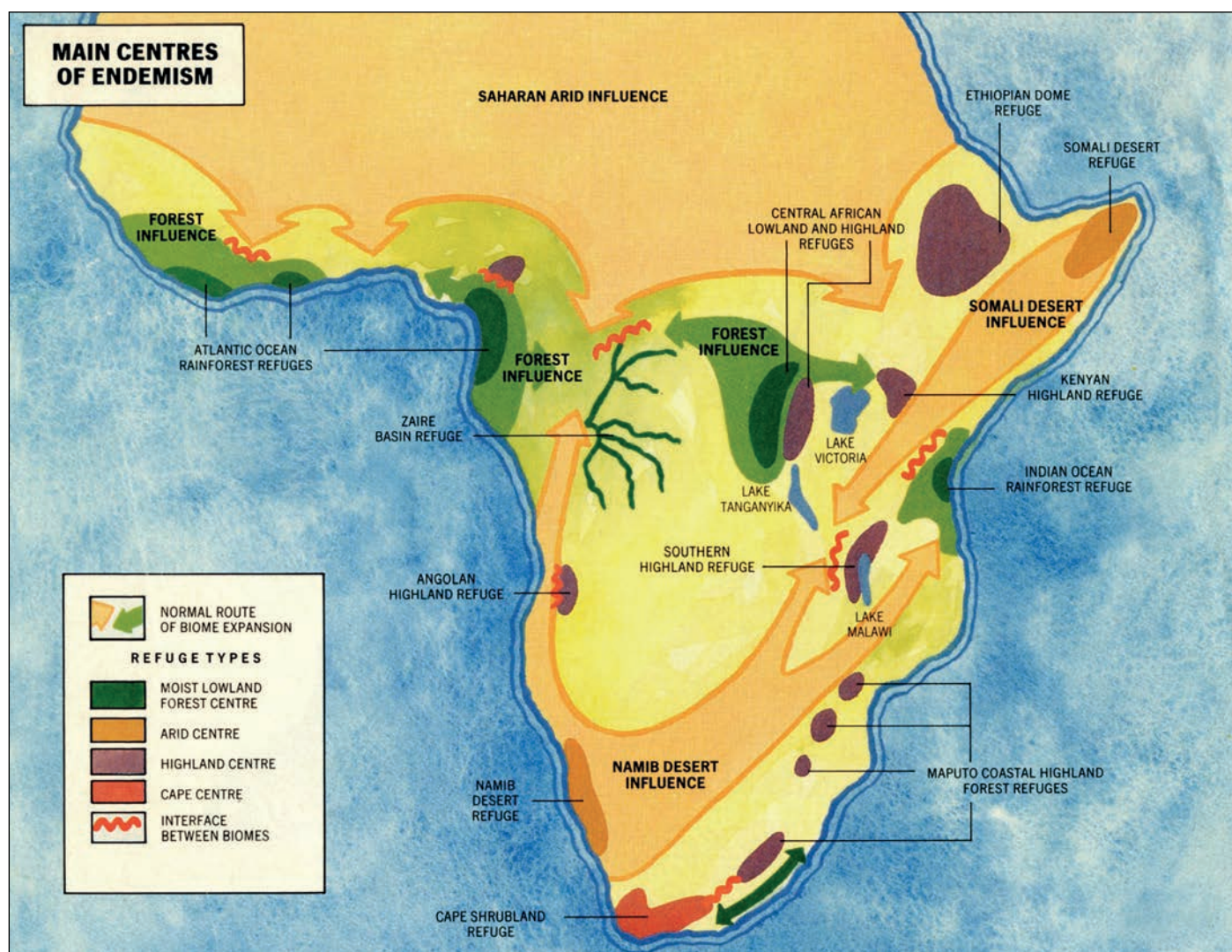
are more restricted in overall range but seem equally indifferent to altitude, notably the Chequered Sengi *Rhynchocyon cirnei*, the African Golden Cat *Profelis aurata*, Alexander's Cusimanse *Crossarchus alexandri*, the Giant Forest Hog *Hylochoerus meinertzhageni*, the Black-fronted Duiker *Cephalophus nigrifrons* and the Bongo *Tragelaphus eurycerus*. It could be significant that some of these species represent relatively conservative taxa that have survived a succession of climatic fluctuations and have presumably had ample time to adapt to cooler, drier uplands as well as humid hot lowland forests (but this is unlikely to be a universal explanation).

Two pied colobus species that are both found in lowland as well as montane forests, *Colobus angolensis* and *C. guereza*, exhibit a geographic separation that has strong temporal implications. The former species is, on morphological grounds, 'older' and has a somewhat spotty distribution from Angola to the East African coast, mainly south of the Equator. *Colobus guereza*, on the other hand, seems to derive more recently (probably from a common ancestor with *C. vellerosus* in Upper Guinea) and lives mainly north of the Equator (and north of the Congo R.), where its range is generally more continuous.

It is not always easy to discriminate between older and younger branches of a single radiation, but the biogeographic pattern of older forest fauna south of the Equator and more recent communities north of it seems to hold for a number of species (Kingdon 1971 and see pp. 85–6 this volume). None the less, 'older' species are not always in retreat and at least one species of the chequered Giant Sengi (*Rhynchocyon cirnei*), unlike other *Rhynchocyon* species, seems to have been able to recolonize ground lost to periodic aridity as well as make accommodations to less than total forest cover. (This situation is discussed in some detail in Chapter 6, p. 75.)

As described in Chapter 3, the equatorial Congo R. has served as a massively influential and long-established barrier to non-volant or non-aquatic animals. Coupled with former shifts in the position and extent of the Sahara Desert's southern boundaries, the distributions of forest mammals are likely to have been significantly affected. Thus, forest communities north of the Congo R. (and broadly north of the Equator) may have been impoverished or partially extirpated by climate changes in the past while forest areas south of the river were less affected by such changes. If forests sandwiched between the Sahara and the Congo R. were seriously degraded, they were probably open to relatively recent, eastward recolonizations from wetter 'refugia' closer to the coast and from the southernmost parts of western Africa. Expansions westwards from a central African refugium are also likely. Some such effects are discernible at the subspecific level among Bushbuck populations (Moodley & Bruford 2007).

Speciation and subspeciation may well proceed within larger rainforest blocks so long as the subdivisions enjoy quite specifically distinct environmental features such as peculiar seasonal patterns or regionally distinctive plant and animal associations (Kingdon 1990). In the case of guenons, every population is bounded by some identifiable form of permanent or temporary barrier. When such barriers are breached due to climatic shifts, some populations show signs of hybridizing when brought back into contact, while others appear to maintain their distinctness. Whether any given population maintains its genetic distinctness may have as much to do with species-specific behaviour, mediated through such local peculiarities as 'head-flagging' or signalling with mask-like facial patterns, as with external environmental factors (Kingdon 1981 and see pp. 83 & 116 this volume).



Main centres of endemism in sub-Saharan Africa. Showing N–S, S–N expansion and contraction of arid foci and E–W, W–E expansion and contraction of humid foci. Intermediate ecotypes (often narrow) are typically located along interfaces between these biomes and on piedmonts of upland massifs.

The influence of past climates in blurring or accentuating the lowland/montane forest divide is well illustrated by a complex of closely related squirrels from eastern Africa. Red Bush Squirrels, *Paraxerus palliatus* are almost exclusively eastern African lowland forest squirrels ranging from Somalia to South Africa, but there is a single very distinctive form *P. p. swynnertoni* that lives in montane forests in the Manica highlands (Chirinda). Another exclusively montane squirrel, *P. vincenti*, is also closely related but lives only on Namuli Mountain, Mozambique. Further north and, for the most part, deeper into the interior, the speciating process has gone still further with a number of isolated montane *Paraxerus* populations that have, in the past, been very variously grouped as species or subspecies (*byatti*, *laetus*, *vexillarius*, *lucifer*). A plausible sequence of events was that a single ancestral squirrel population was widespread in eastern Africa during a period when forests were relatively extensive and the distinctions between montane and lowland forest were less marked than today. During one, or more likely, several fluctuations of climate, montane and lowland populations became physically separate and each subsequently adapted to the conditions within their respective enclaves.

Montane forests are generally cooler and less diverse in numbers of species, including plant foods, predators, pathogens and competitors. Of special current interest in this context is the 2004 discovery of a new primate genus, *Rungwecebus kipunji*, in the Southern Highlands of Tanzania (25°S) where it ranges up to 2500 m. A partial explanation for the survival of this very isolated, wholly montane and very puzzling population could lie in their former stranding, after changes in climate, in a region with fewer species of fruiting plants, much colder temperatures and fewer competitors. It would seem that this precariously rare species exists on the very edge of a tropical primate's environmental tolerance. If the consequences of diminished dietary resources but fewer other constraints in south-temperate or cooler montane areas are examined in the context of climatic change there are conclusions that are of central significance for an understanding of primates, for their conservation and for exploration of early human origins.

In respect to the latter, account needs to be taken of earlier periods than the Quaternary, but it is evident that early hominin fossils in South Africa are direct evidence for our own lineage escaping some of the constraints that govern many other African primates. It should

be borne in mind that the role of climate might, in such instances, be over-ridden by the influence of other factors, such as changes in diets, the development of innovative food-getting behaviours, diminished competition and changes in susceptibility to diseases.

'Refugia' as centres of endemism

A recent review by Anhufer *et al.* (2006) emphasizes that African rainforests experienced much greater retraction during the last glacial compared to the same latitude in the Neotropics, and that rainforests retracted to a limited number of regions, which can be clearly mapped (see p. 55). There is unequivocal palynological evidence from equatorial Africa to support certain aspects of Pleistocene refuge theory, unlike the situation in South America. Five such forest refuges are now recognized (see p. 47), Upper Guinea in West Africa, Cameroon–Gabon (or Biafran Bight), the 'Central Refuge' in eastern DR Congo (Kingdon 1971) and the Congo Basin (Colyn 1991, Maley 1996) with an East African 'Zanj' (or 'Zanzibar–Inhambane') centre of forest endemism strung out along the East African coast (White 1983, Kingdon 1971, 1990a). The effects of climate change most likely help explain the paucity of 'wet climate' plant groups, such as palms, understorey shrubs, epiphytes and lianes. It is likely that this demonstrable loss of diversity has been caused by particular stresses that have hit communities adapted to ever-wet climates rather than those adapted to more seasonality. Several factors may apply in explaining this diversity loss. First, it is possible that during previous glacial maxima rainforest refugia may have become too small to maintain previous diversity levels. Second, the high relative elevation of the African continent (Morley 2000: Fig. 5.1), steep continental slopes and lack of continental shelves or low-lying littorals suggest that during cool/dry climate episodes lowland rainforests may have had limited opportunities to find refuge within appropriate low altitudinal zones (Morley 2000). These factors may also help to explain the scarcity of mammals in Africa that can be shown to have a long, unbroken, forest-adapted ancestry.

However, forest is not the only habitat to provide 'refuge'. At the opposite extreme desert-dwelling animals and plants are no more able to make rapid adaptation to an abundance of rain than forest organisms are to aridity. In between these extremes are more subtle, often seasonal or temperature-dependent regimes that also centre on refugial 'islands' (often mountain blocs) where there are less obviously specialized endemics. Many mammal distributions reflect the reality of diverse, climatically determined 'refuges' in which the successions of past changes have played crucial roles:

It is the absence or moderation of exterminating climates that favours an accumulation of many species. Such accumulation has been most favoured in highly diversified or stratified landscapes. In such localities animals and plants could escape any minor change by shifting a few kilometres up or down some valley or further along some coastal plain. How specialized or different species become is influenced by how long that environment has been stable.

(Kingdon 1990: p. 17)

That long-term stability (rather than simple allopatric speciation following forest fragmentation) has shaped speciation in 'refuge' areas has also been proposed for birds and plants (Fjeldsa and Lovett 1996, Morley 2000). The broad pattern of climatic change in the equatorial zone (with successive retractions and expansions of rainforests) has

been in place back to at least the late Miocene, so the main 'refugia' are likely to be at least this old.

The major 'centres of endemism' (sometimes made up of clusters of 'refugia') are relatively few and their location can, in every case, be analysed in terms of their geo-climatic position on the continent and their relationship to climate changes in the past. The southernmost Cape of Good Hope centre of endemism has already been mentioned and numerous mammal species are endemic to this regional centre of ancient temperate climate, notably the Cape Mole-rat *Georychus capensis*, African White-tailed Rat *Mystromys albicaudatus*, Riverine Rabbit *Bunolagus monticularis* and Cape Grysbok *Raphicerus melanotis*. Adjacent, but distinctive in being an arid focus, are the Namibian deserts and sub-deserts, which also have a number of very distinctive mammalian endemics, exemplified by the Round-eared Sengi *Macroscelides proboscideus*, Damara Ground Squirrel *Xerus princeps* and Noki (Dassie Rat) *Petromus typicus*.

The closest biotic affinities of this centre are often in the Horn of Africa, where the Somali centre of endemism is notably rich in a variety of more or less arid-adapted species, often concentrated in narrow strata of specialized vegetation. Well-defined centres of endemism are sometimes focused on single mountain blocks such as the (dry) Ethiopian Dome and (wet) Rwenzori Mts, or more fractured mountain chains such as the volcanoes and scarps bordering the Western or Albertine Rift and the 'Eastern Arc' and 'Southern Highlands' mountains of Tanzania. There are also quite extensive uplands in Cameroon and the Angolan Scarp and smaller, but biogeographically significant isolated massifs at Nimba in upper Guinea, Namuli, Mulanje and Inyanga in Zambezia and the Saharan massifs of Hoggar, Tibesti, Aïr and Jebel Marra.

All these regions have distinctive bird or mammal endemics but the disparate mountains of eastern and north-eastern Africa are exceptionally rich in endemic mammals (and birds), many of which probably have histories of speciation and adaptation that go further back well before the Quaternary.

Correspondingly, for mammals of woodland, savanna and even drier habitats, the pattern of retracting rainforests would have opened up repeated north–south corridors across Gabon and East Africa during glacial periods. During particularly warm humid periods these routes could subsequently have been severed by the expansion of rainforests or gallery-laced habitats across much of the equatorial zone. Although some species, notably the larger, more mobile ones, such as bats, the larger carnivores and Roan Antelopes *Hippotragus equinus*, somehow managed to sustain single species, with (superficially) insignificant variation, across the entire extent of African savannas, other populations north and south of the Equator have been isolated by the forest belt, particularly in the west, or by lakes and rivers. This process would have encouraged speciation of woodland and savanna mammals within a similar time-frame. Such differences are common, as is well exemplified by members of the Hartbeest *Alcelaphus buselaphus* complex (see Volume VI), but, as might be expected for relatively recent changes, a high proportion of such differences between northern and southern savanna species is at the level of subspecies.

Correlating the distributions and biology of surviving mammal species with the climatic events that have shaped them is a science in its infancy. This review advertises many unresolved puzzles but further investigation of mammalian biology in the perspectives of new information about past environments and past evolutionary events represents a rich field of enquiry for future scholars.

CHAPTER FIVE

The Biotic Zones of Africa

David Happold & J. Michael Lock

Africa is a continent of diversity and contrast. The altitude varies from sea level to over 5000 m. The vegetation includes deserts, rainforests, woodlands, bushlands, shrublands, grasslands, alpine heathlands and grasslands, and swamps. There are numerous streams and rivers; most flow to the coast but some flow into huge swamps where the water evaporates. Virtually every part of the continent has a seasonal climate. This great diversity in altitude, vegetation and climate is one of the main reasons why there are so many species of mammals in Africa. Every one of them has evolved a set of characteristics that enables it to live in its environment, and the many environments in Africa have resulted in many ways of living. The environments of Africa can be broadly classified on their major characteristics. Such a classification provides a framework that allows an understanding of the distribution and characteristics of each species of mammal. Combinations of climate, vegetation and topography (which collectively determine the 'environment') enable Africa to be classified into biotic zones. Before describing these biotic zones, it is worth considering briefly the factors that determine their distribution.

The environment

Geology and soils

Much of the southern half of Africa is underlain by very ancient rocks (the 'Basement Complex') that have been exposed to weathering for many millions of years. Consequently the rocks themselves are only rarely visible at the surface. Because of this long period of weathering, the soils developed from these rocks are generally low in mineral nutrients for both plants and animals. In such areas, sites where minerals are concentrated ('salt-licks') are often sought after by animals. The long period of weathering also means that there can be large variations in soil type with topography – valley bottom, slope and ridge-top soils are often very different. The northern half of Africa mostly lies at lower altitudes and parts of it are covered with more recent sedimentary rocks. Even here, though, the effects of prolonged weathering often obscure the underlying rocks. Along the Rift Valleys, and in the Ethiopian Highlands, soils are often derived from recent volcanic materials and are much richer in mineral nutrients.

Climate

Because Africa straddles the Equator, the areas to the north and south are essentially mirror images of one another; corresponding areas have similar seasonal patterns, but displaced by six months. The extreme northern and southern parts of the continent have a winter-rainfall ('Mediterranean') climate with hot dry summers and cool moist winters. Moving towards the Equator, there is an arid zone in which rain is sparse and unpredictable. Because of the shape of the African continent and the proximity of Arabia, this zone is much more extensive in the north, and maritime influence is much greater in the south. In south-western and north-western Africa the general aridity is reinforced by cold water upwelling offshore. This reduces convective rainfall and can cause great local aridity, sometimes partially mitigated by regular fogs that condense on suitable surfaces.

The main part of Africa, here referred to as tropical Africa (i.e. between the Tropic of Cancer and the Tropic of Capricorn) has a climate that is influenced and determined by the Intertropical Convergence Zone. At and between the Tropics the sun is overhead at midday on at least one day each year. Briefly, the portion of the Earth's surface where the sun is overhead at midday is heated more than regions to the north and south. In this zone of greatest heating, the hot air rises and rain is generated as the air expands, cools and loses its water-holding capacity. The rising air is replaced by warm moist air that blows in from the north and south, but is deflected by the Earth's rotation to produce the north-east and south-east 'trade winds'. The air that rises at the Equator, having lost its moisture, flows polewards at high altitudes and finally descends as a dry air mass, producing the sub-tropical dry belts (e.g. the Sahara). Because of the tilt of the Earth's axis, the sun appears to move north and south during the course of the year. The sun is overhead at noon (12:00 h) on 21 December at 22° S (southern summer solstice), at the Equator on 21 March and 22 September (the equinoxes) and on 22 June at 22° N (northern summer solstice). This apparent movement of the sun produces a rain belt that moves with the sun (actually, a month or so behind it). This rain belt is a broad one, taking about three months to move across any point along its path. At the northern and southern ends of its passage, therefore, there is a single wet season each year. Thus there are two seasonal cycles, six months apart; the 'boreal cycle' in the northern hemisphere (with rainfall sometime

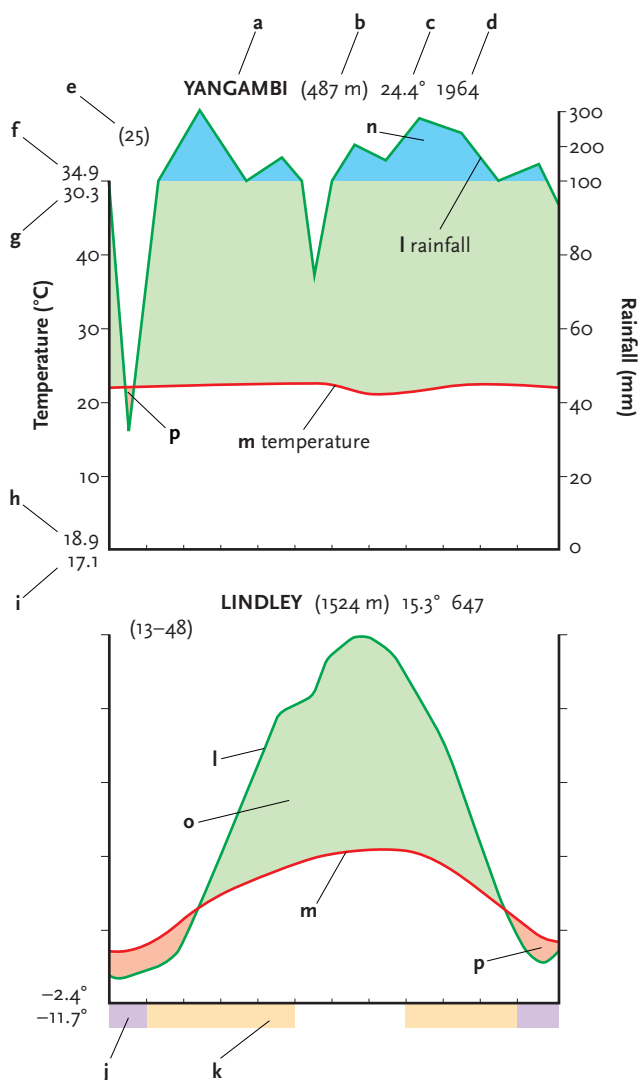


Figure 1. **Key to Climate diagrams.** Abscissa: Months of year (Northern Hemisphere, January–December; Southern Hemisphere, July–June); warmest seasons in the centre of diagram. Ordinate (left): Temperature in degrees Centigrade (each division = 10 °C). Ordinate (right): Rainfall in millimetres (each division = 20 mm from 0–100 mm, and 100 mm thereafter). Ordinate numerals are normally omitted from each graph. Data is not available for all locations.

(a) Name of locality. (b) Altitude of locality (metres above sea level). (c) Mean annual temperature (°C). (d) Mean annual rainfall (mm). (e) Number of years of observation. (f) Absolute maximum temperature. (g) Mean daily maximum of hottest month. (h) Mean daily minimum of coldest month. (i) Absolute minimum of coldest month. (j) Months with a mean daily minimum below 0 °C (purple bar). (k) Months with an absolute minimum below 0 °C (beige bar). (l) Monthly means of rainfall in millimetres (green line). (m) Monthly means of temperature (red line). (n) Months when monthly rainfall is more than 100 mm/month = perhumid season (blue shading). (o) Months when monthly rainfall is less than 100 mm/month and when the rainfall curve is above the temperature curve = humid season (green shading). (p) Months of relative drought when the rainfall curve is below the temperature curve (pale orange). Modified from Walther (1978) and White (1983).

between April and October, with a peak in about August) and an 'austral' cycle in the southern hemisphere (with rainfall sometime between December and April, with a peak about February). Along the Equator, there tend to be two wet seasons (Mar–May and Aug–Nov), corresponding approximately to the equinoxes. In areas of very

high rainfall these may merge so that rain falls almost throughout the year, but in Africa there are virtually no areas that do not experience at least a brief dry season of four to six weeks during the year.

In most of tropical Africa, diurnal temperature variations are generally much greater than seasonal variations. Indeed, the climate of high mountains in tropical Africa has been described as 'winter every night and summer every day'. Temperatures tend to be highest at the beginning of the wet season, when cloud cover is low and early showers have washed the smoke haze out of the atmosphere.

However, the diurnal temperature range is often greatest during the dry season, when low atmospheric humidity and low cloud cover allow rapid radiative cooling during the night. As is usual, temperature falls with increasing altitude; this 'lapse rate' is variable, but a figure of 0.5 °C per 100 m is a useful approximation. Within the tropics, frosts are virtually unknown at low altitudes, but occur regularly above about 2500 m (Hedberg 1964). Snow can fall above 4000 m, and glaciers descend to this level on the Rwenzori Mts.

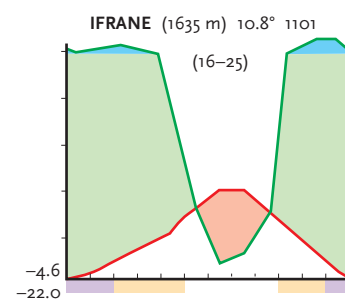
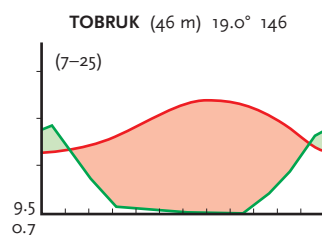
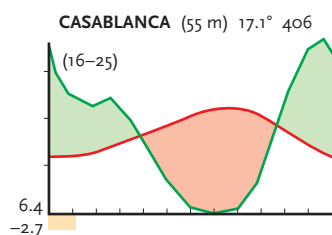
The ways in which climatic variations interact can be shown graphically by the use of climate diagrams (Walter & Lieth 1967, Walter 1978). These are plotted so that 20 mm of precipitation is equivalent to each increase of 10 °C above zero (Figures 1 & 2). Using this convention, periods when the rainfall curve falls below that of temperature can be regarded as times of relative drought, and periods when the rainfall curve is above that of temperature, as relatively moist. Periods when the monthly rainfall exceeds 100 mm are regarded as perhumid, and here the scale is reduced so that one scale division equals 100 mm of rainfall. Each of these three conditions is indicated by different shadings in the diagrams so that the overall climate, and seasonal changes in climate, are easily recognizable. By and large, plant growth is likely to be relatively rapid during the moist and perhumid periods, and slow, spasmodic or absent during periods of drought. A glance at the climate diagram of a particular location (Figure 2) provides a good indication of the type of vegetation that may be expected, as well as showing the environment that is experienced by the mammals that live there.

Fire

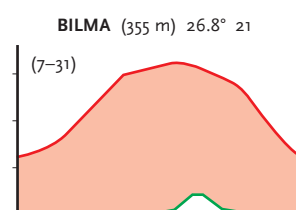
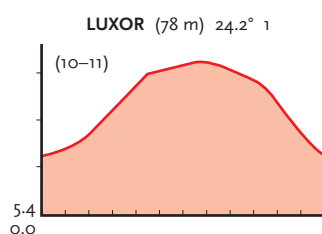
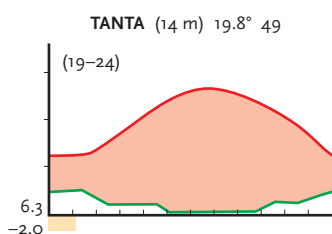
In a highly seasonal climate, vegetation dries out and becomes flammable during the dry season. Fires are a regular feature of the more seasonal types of African vegetation. In most of seasonal Africa a high proportion of the land surface is burned each year. Some fires are ignited by lightning. However, there can be little doubt that fire frequency has increased since the advent of humans, first as humans learned to use naturally occurring fires, then again when they began to make fire themselves, and finally, even more with the introduction of the safety match (Lock 1998). Fires tend to be hotter and fiercer in regions of higher rainfall, as long as there is a marked dry season, because vegetation productivity is greater and hence there is a higher standing crop to burn.

Many plant species in regularly burned vegetation are highly adapted to fire. Many grasses have awned seeds; the hygroscopic movements of the awn buries the seed in the soil, often out of the

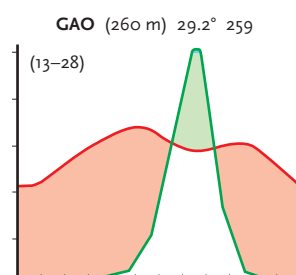
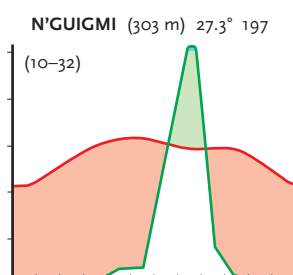
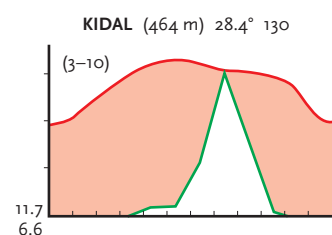
1 Mediterranean Coastal Biotic Zone



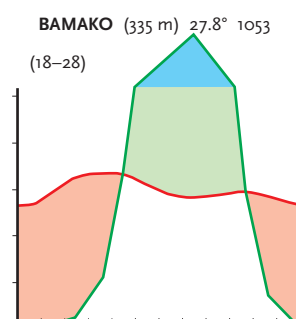
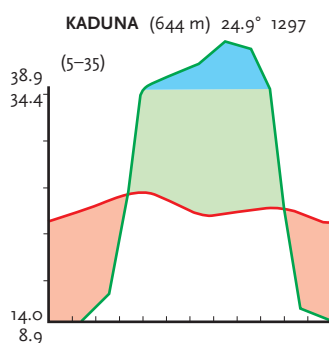
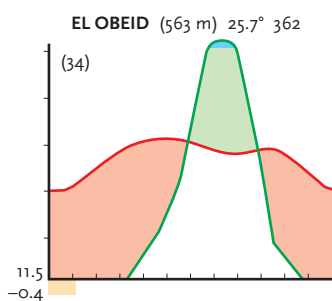
2 Sahara Arid Biotic Zone



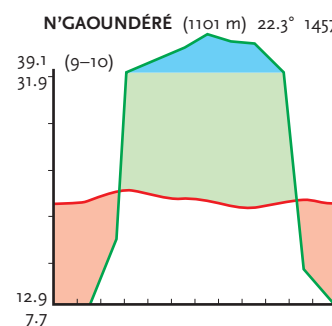
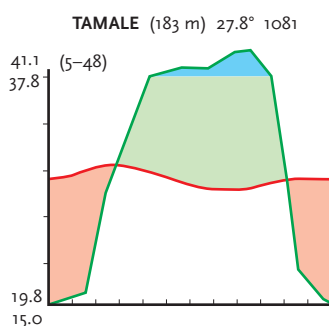
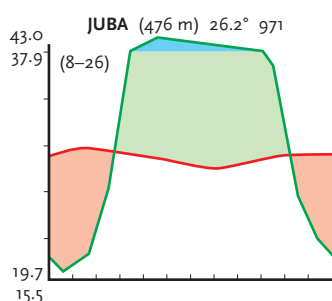
3 Sahel Savanna Biotic Zone



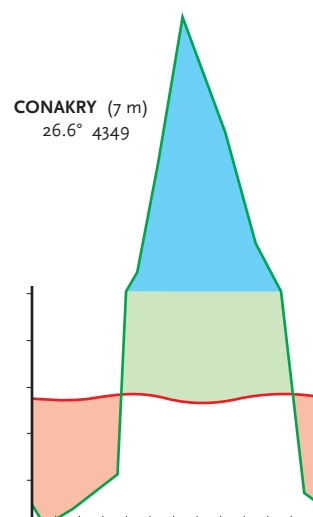
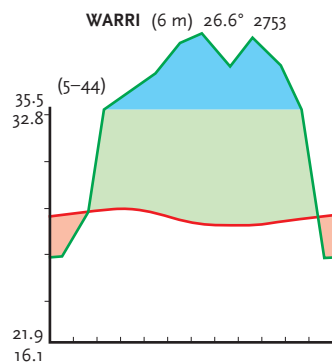
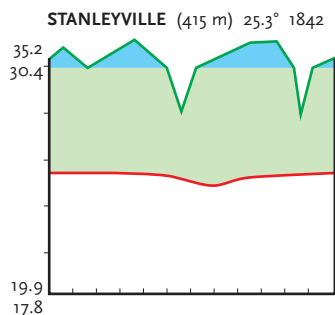
4 Sudan Savanna Biotic Zone



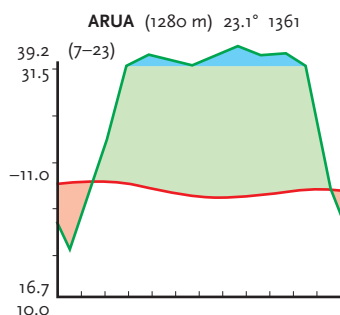
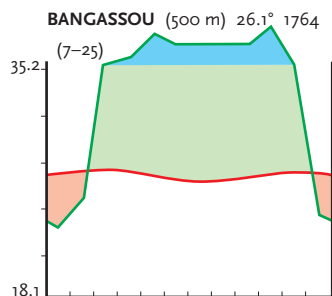
5 Guinea Savanna Biotic Zone



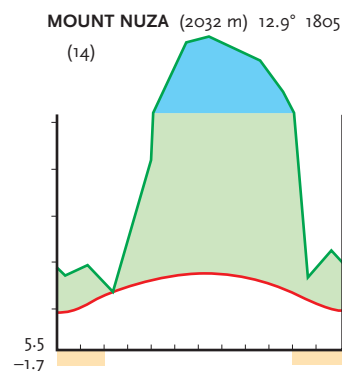
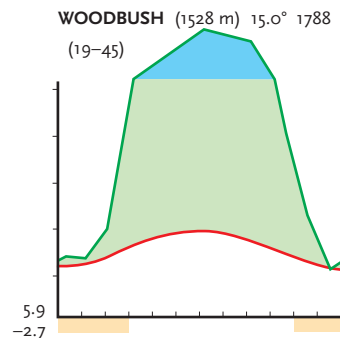
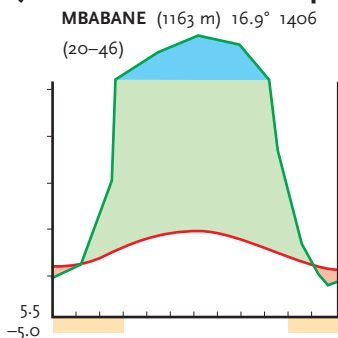
6 Rainforest Biotic Zone



6a Rainforest–Savanna Mosaic

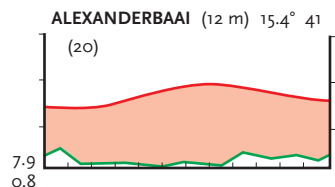


7 Afromontane–Afroalpine Biotic Zone

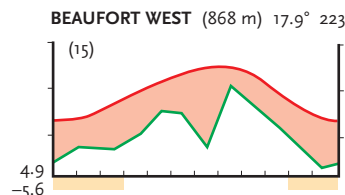


11 South-West Arid Biotic Zone

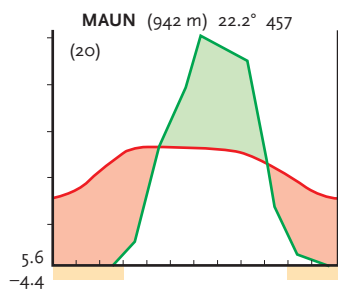
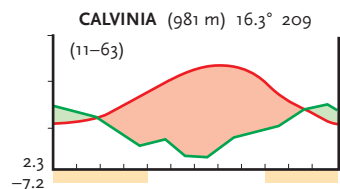
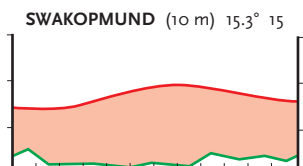
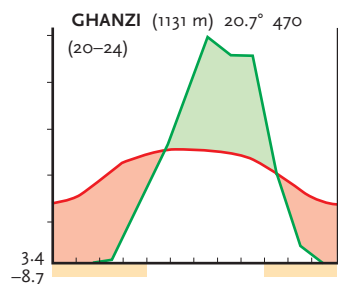
Namib



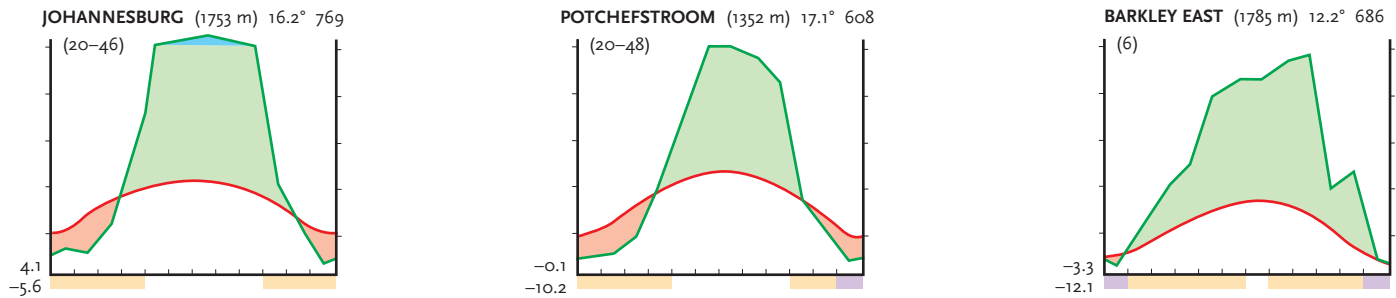
Karoo



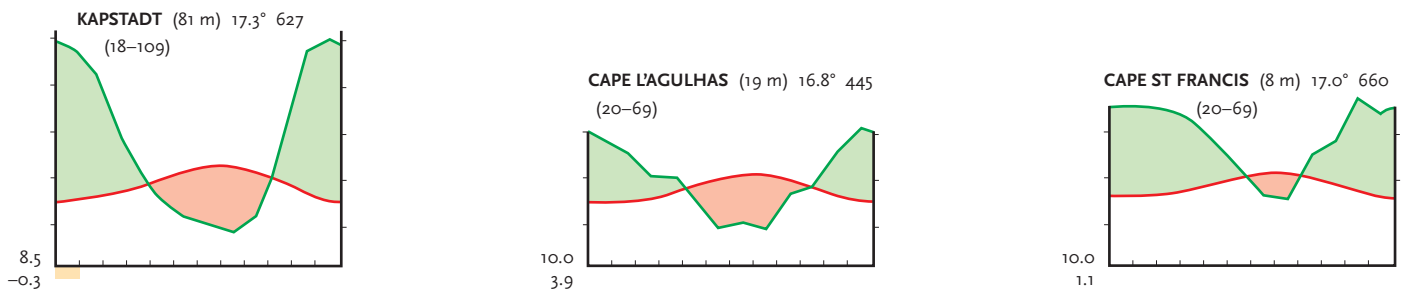
Kalahari



12 Highveld Biotic Zone



13 South-West Cape Biotic Zone



OPPOSITE AND ABOVE: Figure 2 (continued). Climate diagrams for selected localities arranged according to Biotic Zones.

heat of the fire (Lock & Milburn 1971). Clumped grasses have their growing points below ground level in the depths of the clump. Many trees have thick, furrowed corky bark that insulates the growing tissues from the heat of a fire. Some plants are stimulated by fire, and flower afterwards even if no rain falls. Others take advantage of the clearance of the vegetation to flower early before the taller species grow up. Adjacent areas of unburned forest and regularly burned savanna have very few species in common. Regularly burned areas, particularly those burned late in the dry season when the fires are hottest, have reduced densities of trees.

Fires have a major influence on mammals. A few may be killed by the fire and scavengers are often seen patrolling a burned area after the fire has passed. Large mammals can move much faster than a fire, while small ones can often take refuge in holes in the ground or inside termite mounds. Soil is an excellent insulator, and under more than 2 cm of soil there is almost no change in temperature during a fast-moving fire. However, once the vegetation cover has been removed and the sun shines directly onto the soil surface, soil temperatures are often much higher than prior to the fire. Fire destroys forage, but regrowth is usually fairly quick, and areas burned are generally not so large as to preclude local movements to nearby unburnt grasslands. It is often assumed that fire destroys valuable forage. In fact, by the early dry season, a very high proportion of the nutrients in the grass will have been transferred to the root system and stem bases, leaving the above-ground parts with a low nutrient content. Seasonal variations in grass growth and nutrient content are a major cause of some of the great mammal migrations of Africa, such as those in the Serengeti (Sinclair & Norton-Griffiths 1979) and southern Sudan (Howell *et al.* 1988). Small terrestrial mammals that cannot migrate exhibit seasonal changes in diet, seasonal changes in populations numbers (higher mortality when resources are scarce, high natality when resources are abundant) and limited local movements to preferred environments.

Biotic zones and mammalian biology

Africa may be divided into a number of biotic zones (Figure 3) and the distribution of mammals is often closely related to the distribution of these biotic zones. For example, the distributions of many species of desert rodents agree closely with the distribution of the arid biotic zones, and the distributions of rainforest arboreal species closely follow the distribution of rainforest. However, the relationship is not always exact. Many mammalian species occur in several biotic zones, indicating that they have a wide environmental tolerance. In contrast, others have a very limited tolerance and are found in only part of a biotic zone, suggesting that their distribution is determined by local conditions. For example, a species that requires cool temperatures and an arboreal habitat will occur only in montane forests. The limiting factors that prevent such a species expanding its distribution may be higher temperatures and an absence of trees in adjacent areas. Of course, such factors may not act directly on the species itself but rather on the plants upon which it is dependent. Precise analysis of such factors, as well as of competitive interactions with other species, is extremely difficult.

When a particular feature of the environment exceeds the level of tolerance of a species (e.g. the temperature on a long-term basis is too hot or too cold, the water supply becomes inadequate, the vegetation structure changes, or appropriate food is no longer available), populations may become locally extinct. The exact nature of 'limiting factors' is different for every species, and hence the geographic distribution of every species is different. The geographic distribution of a species (as shown in each distribution map) may be thought of as being composed of three parts:

- 1 'Core Area', where conditions for survival are optimal. Here, population numbers are maintained, and the birth rate approximates



Figure 3. The biotic zones of Africa. The numbers refer to the biotic zones as described in the text.

the death rate. There may be temporary peaks and slumps in population numbers, but, on average, population numbers are maintained at the carrying capacity of the area.

- 2 'Peripheral Area', on the edge of the geographic range, where conditions are not optimal all the time or in all locations. Sometimes, when conditions are temporarily favourable, the geographical range may increase; at other times it may contract.
- 3 'Relict Areas', where populations survive in isolated patches, sometimes far removed from the Core Area. Such patches were joined to the Core Area in the past, but are now isolated because of changes in climate and the activities of humans. Relict populations survive because their environment is the same as in the Core Area, even though now separated by unsuitable habitats. The best examples are several species of rainforest mammals that live in small relict patches of rainforest within savannas, sometimes several hundreds of kilometres from the present boundary of the rainforest zone. For all species, the outer limits of distribution are where environmental conditions exceed the limits of tolerance, or where geographical and historical barriers have prevented colonization.

The characteristics of any biotic zone have a profound effect on the biology and structure of mammalian communities. Thus for any biotic zone, there are communities and species that are 'typical' or 'representative'. Over the course of evolution, the mammals of a particular biotic zone have evolved characteristics (often shared by many species) that are of value for living in that biotic zone. In addition, different species have evolved to exploit different niches within a biotic zone, so there may be several sets of characteristics that are typical. In a rainforest, for example, there are many species that are arboreal; but other species are highly adapted for life on the

ground. There are four major ways in which mammalian species and communities are affected by the characteristics of biotic zones:

- 1 The number of species, and the composition of the mammalian community, is strongly affected by the structure and resources of the biotic zone. If a biotic zone is very extensive, the species composition is likely to vary in different regions due to natural variations in vegetation and climate. In general, the richest biotic zones (i.e. those with many plant species, great variation in plant structure and high annual plant productivity) contain the highest number of mammalian species, and the least productive biotic zones have the smallest number of species. Because there are many mammalian species in most biotic zones, the interactions between the species and the environment, and between the species themselves, are numerous and complex. The expansion and contraction in the area of biotic zones (resulting from past climatic fluctuations), and the presence of rivers and mountains that have acted as barriers to movement, have also had significant effects on species composition.
- 2 The number of individuals and their biomass is also determined by the complexity of the biotic zone and the availability of resources. In order to exploit the varied food resources in biotic zones, mammals have developed many ways of ingesting and digesting food. Within a community, each species differs in its diet; the differences may be large (such as between a herbivore and a carnivore) or very slight (such as closely related species eating slightly different proportions of a particular food). The result is that many food resources are exploited, thus increasing the numbers of individuals and biomass that can be sustained of each species.
- 3 Many of the characteristics of species are determined by the biotic zone. Most desert mammals, for example, have evolved mechanisms to cope with shortages of water. These may be physiological, morphological or behavioural, but all of them enable survival in an arid environment. The relative importance of each of these mechanisms is usually associated with the size of the mammal – what is possible for a small mammal is not possible for a large mammal, and vice versa. In rainforests, many species are arboreal and have morphological adaptations for climbing, swinging and gliding – all of which are inappropriate for species living in a treeless region. The relationship between the characteristics of an animal and its habitat is so close that it is easy to infer where and how it lives from its physiological and morphological characteristics.
- 4 The period of the year when a species is able to reproduce is closely related to the seasonal changes in temperature and in the availability of water and food. Mammals time their reproduction so that the young are born when conditions are optimal for the survival of the mother and young. The timing of mating and length of time for gestation have evolved in relation to the size of the species, the length of time required for foetal development and the stage of development when the young are born. For some species, mating occurs at a time when environmental conditions are at their worst – but the young are born when conditions are at their best. Smaller species, with shorter gestations, are the most responsive to environmental change; larger species (because of their longer gestations) are the least responsive because gestation may last over several seasons. For most species, young are born at a well-defined period of the year that is more or less constant

from year to year. Some species give birth to their young over a period of several months, whereas other species give birth during a restricted period of only a few weeks. Populations increase rapidly when the young are born (particularly in those species that have large litters in quick succession) and then decline because of natural mortality, particularly when environmental conditions deteriorate. The reproductive strategies (and hence life-cycles) of species vary greatly depending on their phylogeny, size and diet, so that a community composed of many species also shows great variation even though all species live under the same environmental conditions.

- 5 For individual mammals, seasonal and annual changes in the characteristics of a biotic zone affect where the individual lives, whether it has to move from one place to another, whether it will reproduce, the composition of its diet, and whether it lives or dies. These changes affect populations in a similar way, controlling the increases and decreases in numbers and the very existence of the population itself. Each species profile in these volumes refers, directly or indirectly, to the biotic zone (or zones) where the species lives. All of the characteristics of a biotic zone impinge, to a greater or lesser extent, on the biology and life-style of every species of mammal.

The biotic zones

Concept and definition

Biotic zones, as used here, are defined by a combination of physiognomic vegetation type and phytogeographic area. Both of these defining terms are used here in the sense of White (1983). Biotic zones can be defined as follows (Rutherford & Westfall 1986):

- 1 They refer to broad continental patterns and large natural areas, and are normally mapped at scales of 1 : 1,000,000 or greater. They do not adequately describe small-scale local variations in the environment. They generally have a characteristic climate.
- 2 The climax vegetation of each biotic zone is characterized by a particular physiognomy. Thus, in forest, the vegetation is dominated by trees, arranged in several layers, usually associated with dependent growth forms such as epiphytes and lianas. The physiognomy of a plant community is independent of floristic composition, which may vary considerably within a small area because of slight variations in slope and drainage, and the consequent changes in soil type. Such catenary variation, for example, does not invalidate the general characteristics of a biotic zone. Successional stages of growth (as when forest is cleared and is in the process of regrowing) are also not considered as biotic zones, although they may be important to mammals. The major physiognomic vegetation types recognized by White (1983) are forest, woodland, bushland and thicket, shrubland, grassland and afroalpine. There are, of course, intermediates between most of these (such as wooded grassland) but for our purposes these need not be considered.
- 3 White (1983) divided Africa into a number of 'phytochoria' – areas with similar floras. The highest level of this classification is the Regional Centre of Endemism. To qualify as such, a region must not only have a high proportion of endemic species (White used 50%), but also a substantial number of these endemic plant species (White

used a figure of 1000). Although these definitions have been applied somewhat elastically, they remain useful when used with caution. White's major phytochoria in Africa, which he termed 'Regional Centres of Endemism', are: Guineo-Congolian, Zambezan, Sudanian, Somalia–Masai, Cape, Karroo–Namib, Mediterranean and Afroalpine. The Afroalpine is exceptional in being discontinuous ('archipelago-like', to use White's expression). He recognized Transition Zones between many of these phytochoria, and also three Regional Mosaics (RM), where elements from several Regional Centres mingle – the Lake Victoria RM, the Zanzibar–Inhambane RM and the Tongoland–Pondoland RM. White only named and mapped Transition Zones where they were large, sometimes larger than some Regional Centres of Endemism. He defined them as having few endemic species and with the majority of their species occurring in adjacent phytochoria. The Regional Mosaics are more complex, with mosaics of different physiognomic vegetation types and floristic relationships, and more endemism than in the Transition Zones. Dowsett-Lemaire & Dowsett (1998) have shown that there is a close correlation between forest bird species distribution and the Guineo-Congolian and Afromontane chorological categories. They conclude that 'Frank White's phytochoria provide zoologists with an excellent environmental framework, a prerequisite for studies of biodiversity, endemism, and species conservation'. The names for biotic zones used in *Mammals of Africa* are those in common usage in the regions concerned; the equivalent in White's terminology is, however, also given (Table 5).

- 4 Within some biotic zones, human activity has altered the physiognomy of the vegetation, but for our purposes this is regarded as a temporary perturbation. Although the changes wrought by humans have had a detrimental effect on most species of mammals (and many other animals), they have favoured a few by allowing an increase in numbers and an extension of geographic range.
- 5 While the boundaries between biotic zones are drawn on any map as hard lines, one must always remember that a line on a map separating Zone A from Zone B will, on the ground, separate A with patches of B, from B with patches of A (Keay 1959a). The 'change-over' from one zone to another may take 50–100 km, or more; the changes may be subtle and only recognizable by a gradual change in the percentage occurrence of a few dominant plant species. Even where the plant structure between adjacent zones is very different, such as between rainforest and savanna, patches typical of one zone may be found deep inside the other.

The biotic zones of Africa

There have been many attempts to classify the vegetation of Africa. The most widely accepted classifications of vegetation for the whole of the continent are those of Keay (1959a) and White (1983). There have also been many regional classifications, such as those of Acocks (1975) and Rutherford & Westfall (1986) for South Africa, Greenway (1973) for East Africa, Rosevear (1953) for West Africa and Keay (1959b) for Nigeria. In some respects, the biotic zones of Africa north and south of the Equator are mirror images. The various biotic zones form bands that roughly follow the lines of latitude. The rainforests that span the Equator are followed by successive bands of savanna, then by deserts or arid conditions, and finally by temperate environments. This simple banding is modified by the effects of the oceans in coastal regions, and by the

Table 5. The biotic zones and mosaics of Africa as used in *Mammals of Africa*. The vegetation zones, vegetation number and vegetation types (following White 1983) are given for each of the Biotic Zones and Mosaics.

Biotic Zones and Mosaics	Vegetation Zone	Vegetation Type	
		No.	Name
1. Mediterranean Coastal BZ	A	10	Mediterranean sclerophyllous forest.
	B	55	Sub-Mediterranean semi-desert grassland and shrubland.
		49	Transition from Mediterranean <i>Argania</i> scrubland to succulent semi-desert shrubland.
		10	Mediterranean sclerophyllous forest (small patches only).
2. Sahara Arid BZ	C	71	Regs, hamadas, wadis.
		70	Desert dunes with perennial vegetation.
		67	Absolute desert.
		69	Desert dunes without perennial vegetation.
		72	Saharomontane vegetation (small patches).
		-	Oases
3. Sahel Savanna BZ	D	54a	Northern Sahel semi-desert grassland and shrubland
	E	43	Sahel <i>Acacia</i> wooded grassland and deciduous bushland.
		62	Edaphic grassland mosaic with <i>Acacia</i> wooded grassland.
		75	Herbaceous swamp and aquatic vegetation (around Lake Chad).
4. Sudan Savanna BZ	F	29a	Sudanian undifferentiated woodland.
		30	Sudanian undifferentiated woodland with islands of <i>Isoberlinia</i> .
		29b	Ethiopian undifferentiated woodland.
		62	Edaphic grassland mosaic with <i>Acacia</i> wooded grassland (in east).
		63	Edaphic grassland mosaic with communities of <i>Acacia</i> and broad-leaved trees (patches only).
5. Guinea Savanna BZ	G	27	Sudanian woodland with abundant <i>Isoberlinia</i> .
(The Sudd [included mostly into the eastern end of Guinea Savanna BZ])	I	61	Edaphic grassland in Upper Nile Basin.
		64	Edaphic grassland in Upper Nile Basin with semi-aquatic vegetation
6. Rainforest BZ	Ja	1a	Guinea-Congolian lowland rainforest (wetter types)
	Jb	2	Guinea-Congolian lowland rainforest (drier types).
	Jc	8	Swamp forest
		9	Mosaic of swamp forest and wetter lowland rainforest
6a. Northern Rainforest-Savanna Mosaic	H	11a	Guinea-Congolia/Sudanica mosaic of lowland rainforest and secondary grassland.
6b. Eastern Rainforest-Savanna Mosaic	M	11a	Lake Victoria mosaic of lowland rainforest and secondary grassland.
6c. Southern Rainforest-Savanna Mosaic	N	11a	Guinea-Congolia/Zambezia mosaic of lowland rainforest and secondary grassland.
		14	Mosaic of lowland rainforest, Zambezan dry evergreen forest and secondary grassland.
		60	Edaphic and secondary grassland on Kalahari Sand.
		31	Mosaic of wetter Zambezan woodland and secondary grassland.
7. Afromontane–Afroalpine BZ (discontinuous; shaded black)	Y	19a	Afromontane undifferentiated montane vegetation
		38	Evergreen and semi-evergreen bushland and thicket (Ethiopian Highlands only)
	Z	23	Mediterranean montane forest and altimontane shrubland
8. Somalia–Masai Bushland BZ	K	54b	Somalia-Masai semi-desert grassland and shrubland.
	L	42	Somalia-Masai <i>Acacia-Commiphora</i> deciduous bushland and thicket.
9. Zambezan Woodland BZ	O	25	Wetter Zambezan miombo woodland dominated by <i>Brachystegia</i> , <i>Julbernardia</i> and <i>Isoberlinia</i> .
	Pa	28	<i>Colophospermum mopane</i> woodland and scrub woodland.
	Pb	26	Drier Zambezan miombo woodland dominated by <i>Brachystegia</i> and <i>Julbernardia</i> .
		29c	N Zambezan undifferentiated woodland.
		29d	S Zambezan undifferentiated woodland.
		22a	Mosaic of dry deciduous forest and secondary grassland.
		60	Edaphic and secondary grassland on Kalahari Sand.
10. Coastal Forest Mosaic BZ	Q	16a	East African coastal mosaic: Zanzibar-Inhambane.
		16b	East African coastal mosaic: forest patches.
		16c	East African coastal mosaic: Tongaland-Pondoland.

Biotic Zones and Mosaics	Vegetation Zone	Vegetation Type	
		No.	Name
11. South-West Arid BZ	R	35a	Zambezian Transition from undifferentiated woodland to <i>Acacia</i> deciduous bushland and wooded grassland.
11a	S	44	Kalahari <i>Acacia</i> wooded grassland and deciduous bushland.
11a		56	Kalahari/Karoo-Namib transition.
11b	U	51	Bushy Karoo-Namib shrubland.
11b	V	74	Namib Desert.
11c	Wa	53	Dwarf Karoo shrubland.
11c	Wb	57b	Transition from Karoo shrubland to Highveld grassland.
11c		57a	Montane Karoo grassy shrubland.
11c		51	Bushy Karoo-Namib shrubland.
11c		52	Succulent Karoo shrubland.
12. Highveld BZ	T	58	Highveld grassland.
13. South-West Cape BZ	X	50	Cape shrubland (Fynbos) (with central island of 51 Bushy Karoo-Namib shrubland)

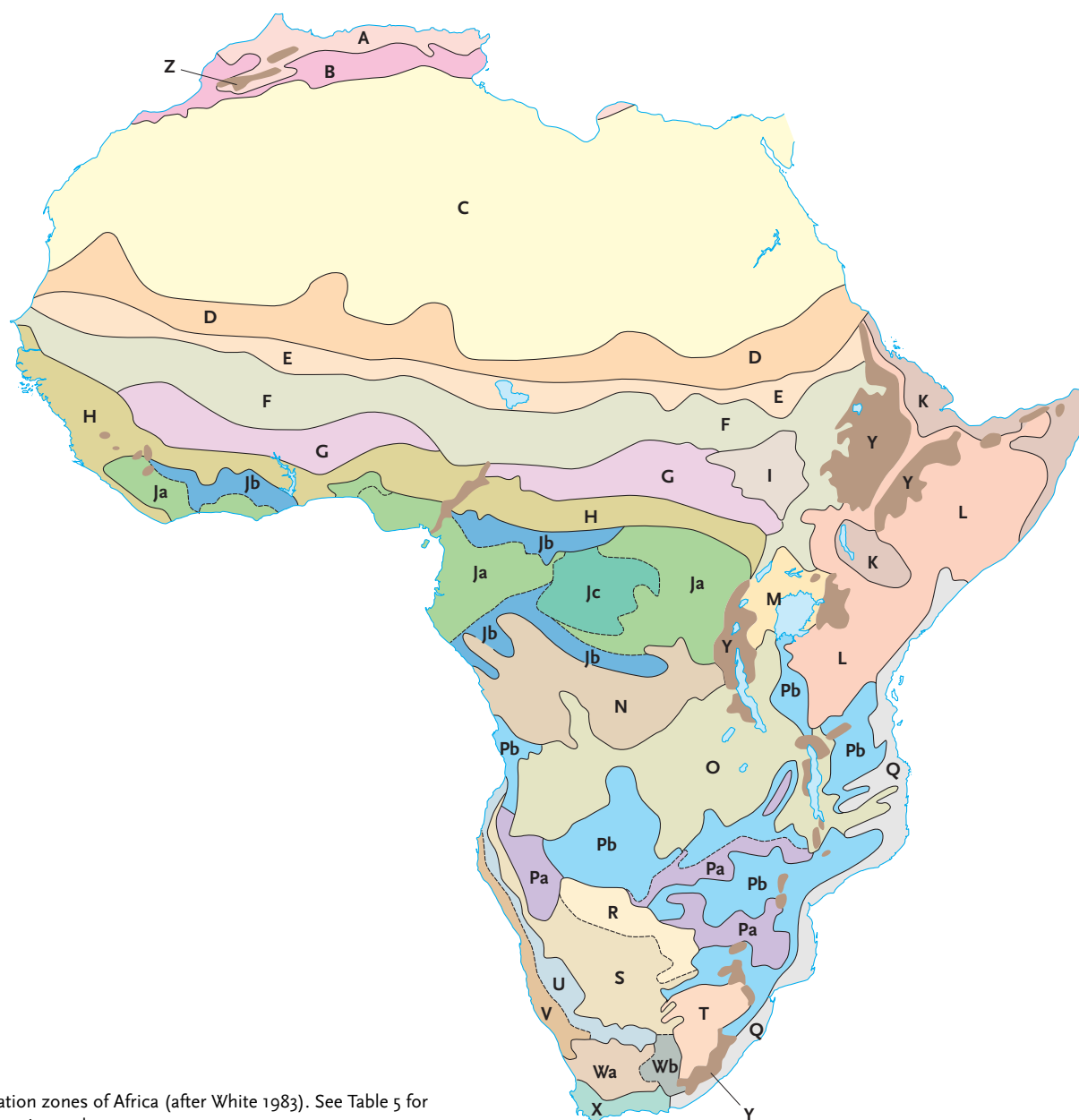


Figure 4 . The vegetation zones of Africa (after White 1983). See Table 5 for explanation of the lettering codes.

highlands and plateaux that are so characteristic of the eastern side of the continent. Overall, however, there is considerable similarity in environments at equivalent latitudes in both the northern and southern hemispheres of the continent. Hence it is not surprising that ecologically equivalent animals (though of different species) occur in both hemispheres in equivalent biotic zones; this is especially noticeable in the drier savannas and arid environments.

Thirteen biotic zones, and one azonal biome, are recognized; brief details of each are given below. In each zone, four principal characteristics are described: plant structure and composition, plant biomass and production, rainfall and water availability, and temperature. The biotic zones are mapped in Figure 3, and the climatic characteristics of each is represented in Figure 2. Further information on each biotic zone and its vegetation is provided in Table 1 and Figure 4. The biotic zone (or zones) where each mammalian species is known to occur is recorded in the 'Distribution' section of each species profile. The term 'biotic zone' is abbreviated to BZ in each profile.

(1) MEDITERRANEAN COASTAL BIOTIC ZONE

(White's Mediterranean Regional Centre of Endemism)

The Mediterranean Coastal zone occurs only north of about 31°N in Morocco and 33°N in Algeria and Tunisia. A small outlier occurs in Jebel el Aktar (formerly Cyrenaica) in Libya. The climate is typically Mediterranean, with hot, dry summers during which no rain may fall for 4–5 months (May to Aug–Sep). The winters, by contrast, are cool and wet. Most of the rain (700–1000 mm) falls in winter (Nov–Mar), when the temperature may drop to around freezing at night. The coastal plain may originally have been covered by forest in which *Pistachia atlantica* and *Celtis australis* were probably important, with evergreen oak *Quercus ilex* and cork oak *Q. suber* occupying the drier sites. Degradation of the forests by repeated clearance and an increase in fire frequency produces a shrubby thicket in which most of the species, such as mastic tree *Pistachia lentiscus* and wild olive *Olea europaea*, have small tough leaves.

Further inland is a chain of mountains and plateaux – the High Atlas, Middle Atlas and Saharan Atlas (collectively called the Maghreb by local people) – which stretches for about 2000 km, bordered on the north by the coastal plain and on the south by the Sahara Desert. Most of this land is over 1500 m, parts are above 3000 m and the highest peak (in Morocco) is 4165 m. The climate in the mountains follows the same seasonal pattern as on the plains, but in the winter there are frosts at night for 6–8 months of the year, and snow occurs on the higher peaks (and hence is more similar to that of the Afromontane–Afroalpine Biotic Zone). Above the lowland forests, from about 1400 m, is a belt of coniferous forest in which North African Cedar *Cedrus atlantica* and Aleppo Pine (*Pinus halepensis*) may dominate. Above the treeline (around 3000 m) there is often a zone of low spiny cushion-forming shrubs ('hedghog heath').

The phytogeographic affinities of North Africa are generally with Europe and the rest of the Mediterranean basin, rather than with tropical Africa. Although parts of the central Sahara were considerably wetter several thousand years ago (so that at least some mammals were able to cross it), the great differences between the flora north and south of the desert suggest that it has long been a substantial barrier to movement of plant species.

(2) SAHARA ARID BIOTIC ZONE

(White's Sahara Regional Transition Zone)

The arid zone of the Sahara Desert stretches from the Atlantic Ocean to the Red Sea, and north to the Mediterranean in Libya and Egypt. Its physical characteristics are extremely varied and include ergs (seas of sand with little or no vegetation where the sand is mobile), hamadas (wide plateaux covered with small stones or boulders), regs (smooth sand or clay plains covered with fine gravel) and rocky massifs. Surface water is virtually absent, but scattered throughout the Sahara are natural oases where ground water reaches the surface. Originally these probably supported a shrubby plant community in which the doum palm *Hyphaene thebaica* and species of tamarisk *Tamarix* may have been prominent, but have now been replaced by planted date palms *Phoenix dactylifera*. Pools of water support typical marsh plants such as reed-mace or cat-tail *Typha latifolia* and reed *Phragmites australis*.

The climate throughout the whole of the zone is extremely harsh. Temperatures vary greatly annually and diurnally. In summer, air temperatures are typically 35–45 °C during the day and 15–20 °C at night; in winter, the night temperatures may be close to 0 °C. Rainfall is sparse, unpredictable and variable throughout, generally averaging 75 mm or less per year. On the northern margin of the zone, rain falls during the winter (Jan–Mar), and towards the southern edge, during the summer (Aug–Sep). In the central Sahara, between 18 and 30°N, the mean annual rainfall is less than 20 mm. Average figures are, however, almost meaningless because there may be no rain for years and then the equivalent of several years of the 'average annual rainfall' can fall in a few hours. When this happens, normally dry wadis flow for a few hours or days, and the water percolates deeply into the sand. The seeds of ephemeral desert plants such as *Neurada procumbens*, and grasses such as species of *Aristida*, germinate to give a temporary flush of green. This type of vegetation is important to animals because it dries quickly, retaining much of its nutritive value, and remains for years as 'standing hay'. Perennial plants are restricted to places where water accumulates. Shrubs and trees are rare and restricted to well-watered sites such as outwash fans. Here species of acacia (*Acacia tortilis*, *A. ehrenbergiana*) are often accompanied by the perennial grass *Panicum turgidum*. Phytogeographically, the Sahara is a transition zone. As one moves south, species of Mediterranean affinity, such as annual species of *Astragalus* (Leguminosae) are gradually replaced by species of African affinity, such as *Zornia glochidiata* (Leguminosae).

In the eastern Sahara, the Nile R. provides water throughout the year to a narrow strip of fringing vegetation and irrigated crops. The strip varies in width through the year from a few metres to a few kilometres with the annual rise and fall of the river dependent upon rainfall further south. Many species which live in mesic habitats to the north and south of the Sahara are found close to the Nile. The strip of vegetation along the river also acts as a passageway for birds that migrate between Europe and Africa.

(3) SAHEL SAVANNA BIOTIC ZONE

(White's Sahel Regional Transition Zone)

The Sahel Savanna, like the Sahara Arid Biotic Zone, stretches from the Atlantic to the Red Sea. It forms an intermediate zone between the arid environments of the Sahara and the mesic environments of sub-tropical Africa. The climate is semi-arid, with rain during the hot

summer. The climate is very hot for most of the year (especially Mar–Jun), cooler during the wet season (see below) and coolest during ‘winter’ (Nov–Feb). There is considerable diurnal temperature fluctuation, especially during the winter. Annual rainfall varies from 100 mm falling in 1–2 months (Aug–Sep) at the northern edge, to 350–400 mm falling in 3–4 months (Jul–Oct) at the southern edge. Interannual variability in rainfall is high, but less so than in the Sahara. The variations are linked to the well-known El Niño – Southern Oscillation climatic cycles. There is considerable evidence for a long-term decline in the rainfall of the Sahel. The landscape is fairly featureless over much of the zone, with the exception of isolated mountains like Jebel Marra in Sudan.

The vegetation is mainly a sparse woodland or wooded grassland in which species of acacia (*Acacia tortilis*, *A. laeta*), *Commiphora africana* and members of the caper family (Capparidaceae) are the commonest woody plants. Most of the grasses are annuals; cram-cram *Cenchrus biflorus* and *Schoenfeldia gracilis* are common species. The perennial grass *Andropogon gayanus* has been much reduced by cultivation and overuse. Fires are relatively uncommon because there is usually insufficient fuel to support them.

(4) SUDAN SAVANNA BIOTIC ZONE

(the northern part of White’s Sudanian Regional Centre of Endemism)

The Sudan Savanna stretches from the Atlantic Ocean to the Ethiopian Highlands and to northern Uganda. The climate is less arid than in the Sahel Savanna Biotic Zone. Seasonal temperature variations are not so extreme (the mean annual temperature lies between 24 and 28 °C), average annual rainfall is higher (500–800 mm), the wet season lasts for 4–6 months (May–Oct) and there is less annual variability in rainfall. Some months may have more than 100 mm of rain. Annual rainfall increases from north to south, as in the Sahel Savanna Biotic Zone. These slight differences in the climate from that of the Sahel Biotic Zone allow higher and more regular plant productivity.

Because of its higher and more reliable rainfall, the Sudan Savanna Biotic Zone is much more intensively farmed than in the Sahel to the north. Large areas are almost completely cleared of natural vegetation, leaving a ‘farmed parkland’ where useful trees such as *Parkia biglobosa*, baobab *Adansonia digitata* and apple-ring acacia *Faidherbia* (*Acacia*) *albida* are retained among the crops of maize, millet, sorghum and groundnuts.

Vegetation destruction by cultivation has been so widespread in this region that it is very difficult to be certain of the nature of the original vegetation. As far as can be ascertained from relict patches, it is essentially transitional between the Sahel to the north in which most of the trees have finely divided leaves, and the Guinea Savanna to the south in which most trees have broad undivided leaves (Clayton 1963). Areas in which the soils are too poor and stony for satisfactory cultivation often support sparse woodland where *Combretum* spp. and *Anogeissus leiocarpus* are usually the prominent trees. Grazing and cultivation may lead to the elimination of *Anogeissus* and its replacement by a low *Combretum*-dominated scrub. Other heavily used areas can develop into dense *Acacia* thicket during the fallow period. Seasonally wet valleys are characterized by the shrub *Mitragyna inermis* and a ground flora of moisture-loving grasses and sedges.

(5) GUINEA SAVANNA BIOTIC ZONE

(including the southern half of White’s Sudanian Regional Centre of Endemism and the northern parts of his Guineo-Congolia/Sudania Regional Transition Zone)

The Guinea Savanna Biotic Zone is the band of savanna that lies immediately to the north of the rainforest. It extends from the edge of the rainforest in the west of West Africa to north-western Uganda. Some typical trees of the Guinea Savanna include *Daniellia oliveri*, *Isoberlinia doka* and *Cassia sieberiana*. East of the Nile in Uganda there are extensive woodlands, sometimes referred to as ‘Tall grass–low tree savannas’. Although similar in physiognomy, these woodlands lack the species listed above; instead, the dominant trees are the shea nut tree *Vitellaria* (*Butyrospermum*) *paradoxum* and species of *Terminalia* and *Combretum* (which are also found in the true Guinea Savanna). This zone, together with the Sudan and Sahel Savanna Biotic Zones, may be collectively referred to as the ‘northern savannas’.

The climate of the Guinea Savanna Biotic Zone is wetter than further north. Mean annual rainfall is 800–1500 mm and the wet season lasts for 7–8 months (Mar–Oct), sometimes with a ‘short dry season’ in July and August. The usual vegetation is open woodland, with a dense grass layer. The commonest grass species mainly belong to the genus *Hyparrhenia* and attain a height of 2–3 m by the end of the wet season. As the dry season progresses they wither and die. Intense annual fires are usual in much of this zone; fire reduces most of the grass to ash or charred stems, and stimulates the growth of new grass before the next wet season. This new grass provides nutritious food for herbivores at a time when the grass in unburnt areas is unpalatable and poor in nutrients.

Most trees are 10–20 m tall, with a few up to 30 m. Most of the trees have thick fire-resistant bark, and at least some have seed germination mechanisms that bury the growing point in the soil where it is protected from the heat of fires (Jackson 1974). Two forms of Guinea Savanna can be distinguished: northern and southern (Keay 1959b). The southern part is characterized by trees such as *Daniellia oliveri*, *Lophira alata* and *Azelia africana*. All three species have similar ‘sister species’ in the rainforests. The northern part is characterized by trees such as *Isoberlinia doka*, *I. dalzielii* and *Monotes kerstingii*. These northern Guinea Savannas are physiognomically similar to those of the Zambezian Woodland Biotic Zone south of the Equator.

The balance between woodland and rainforest in the southern part of the Guinea Savanna Biotic Zone, close to the forest margin, is a delicate one. Long-term experiments (see Lock 1998 for a list and summary) show that burning early in the dry season, before the grass layer is completely dry, damages the trees rather little and allows the survival of tree seedlings, so that tree density slowly increases, even to the point where grasses are partially suppressed so that fires become much less intense. If there is a nearby source of seed from forest tree species, they may begin to invade and the vegetation will begin to change to forest. The complete exclusion of fire has a similar but faster effect, but is in practice difficult to achieve. On the other hand, fires that occur late in the dry season when the grass layer is fully dry are much hotter, often damage adult trees and also kill their seedlings, so that the balance of the vegetation shifts from trees to grassland. Further north, far from the forest margin, similar but much less marked changes occur; here, sources of forest tree seeds are usually absent, and the main

change in the absence of fire is an increase in the density of savanna trees.

This region, intermediate between rainforest and savanna, with vegetation whose nature probably depends on human intervention (particularly fire frequency and timing) over a long period, is often called 'Derived Savanna' or 'Forest–Savanna Mosaic'. It is a very extensive area which surrounds the Rainforest Biotic Zone, but it is not a Biotic Zone in itself; here it is referred to as the Northern Rainforest–Savanna Mosaic, Eastern Rainforest–Savanna Mosaic and Southern Rainforest–Savanna Mosaic (labelled as 6a, 6b and 6c in Figures 2 & 3, and Table 1). It provides a mixture of forest and savanna habitats, often with sharp boundaries so that the plant species composition changes almost completely over a hundred metres (or less). Over the last few millennia the position of this boundary has certainly changed a good deal and its position continues to be labile. Swaine *et al.* (1976) show that, in Ghana, the nature of the mosaic may be linked to the underlying rocks. On sandstones, the forest extends into the savanna along streams in a dendritic pattern. On finer-grained rocks, there is often forest along streams but also on hilltops, with savanna restricted to the intervening slopes. The Mosaics contain a mammalian fauna comprising selected species from the Rainforest Biotic Zone (which live in the rainforest habitat) and from the Guinea Savanna Biotic Zone (which live in the savanna habitat); the mosaics are as important biogeographically as the zones themselves.

Forested habitats in the Rainforest–Savanna Mosaics contain a mixture of rainforest and savanna trees; they occur, in ribbon-like fashion, along the edges of rivers and streams (often far from the edge of the rainforest), and are variously referred to as 'riverine forest', 'riparian forest' or 'gallery forest'. Some occur as isolated patches (or islands) completely surrounded by savanna and are referred to as 'relict forest'.

(6) RAINFOREST BIOTIC ZONE

(White's Guineo-Congolian Forest, with outliers in his Lake Victoria Regional Mosaic and Zanzibar–Inhambane Regional Mosaic, and elsewhere; montane forest is dealt with under the Afromontane Biotic Zone)

The Rainforest Biotic Zone extends for about 4500 km across West and central Africa, eastwards into western Uganda and western Tanzania. There are also areas of forest in the coastal regions of eastern and south-eastern Africa. Many wide rivers pass through the zone, and mammalian communities on one side of a river often differ from those on the other side, suggesting that some of these rivers may be important barriers to the movement of some species. On the basis of their mammalian fauna (as well as other faunas), the rainforest may be divided into regions and sub-region (Happold 1996; Figure 5).

The climate of the Rainforest Biotic Zone is warm and humid. The annual mean maximum temperature is about 30°C and the minimum is about 20°C; the daily range is only a few degrees, although this diurnal variation is greater than the annual between-month variation. The annual rainfall is 1600–2000 mm – rather low in comparison with areas of tropical rainforest in other parts of the world. Two areas on the edges of the zone receive a higher rainfall – a large area of Cameroon near Mt Cameroon receives more than 3000 mm per annum, and at least one small area receives

10,000 mm. Here there is a short and irregular dry season of 4–6 weeks in December and January. In Guinea, Sierra Leone and Liberia there is an area along the coast that receives 3000–4000 mm of rain annually; this falls during a wet season lasting 8–10 months, with a marked dry season between December and March. In the Congo Basin, and along the West African coast, there tend to be two rainfall peaks separated by two short periods of 1–2 months (Dec–Jan and Jun–Jul) of lower rainfall. At the wettest localities on the coast, and throughout much of the forests of the Congo Basin, rain falls in every month of the year with more than half the months recording more than 100 mm each month.

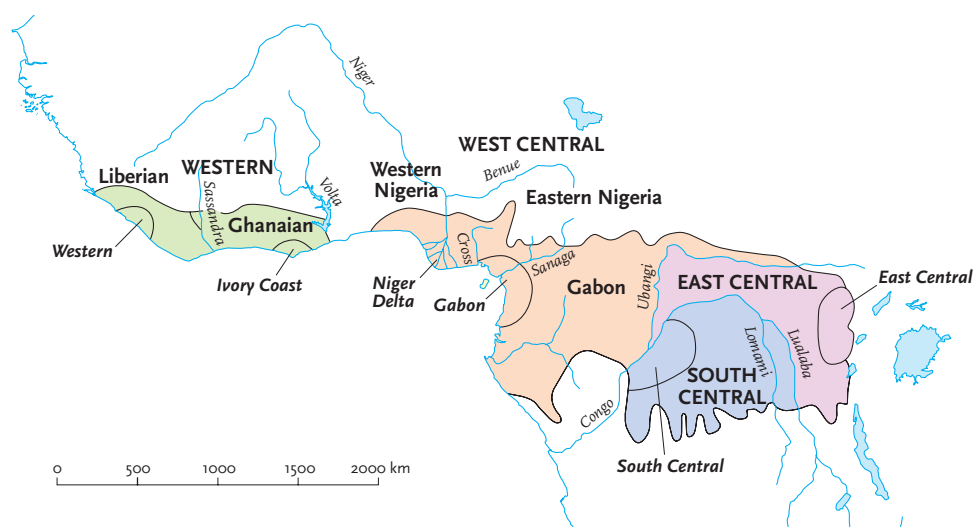
Although the general climate of the rainforest is uniform, there are important variations at different levels within the forest. Absolute temperatures, diurnal fluctuations in temperature and humidity, wind flow and light levels are much greater in the canopy than near the ground. In the understorey, temperature may not vary by more than a degree or two over 24 hours, humidity is uniformly high and air movement is minimal. Such differences effectively produce a variety of environments within a small area, and may go some way to explaining the great diversity of species in rainforest.

Forest vegetation is generally multilayered. The largest trees, 60–100 m tall and with broad crowns, project above the general canopy and are known as emergents. The main canopy trees, also with broad crowns, form a continuous upper layer, generally at 30–40 m above the ground. Below these are smaller trees with more vertically elongated crowns. Some of these are young individuals that may eventually reach the canopy, but some remain small even at maturity. Closer to the ground there are pygmy trees (with a single main stem) and shrubs (branched into several stems at the base), often 1–3 m tall. In undisturbed forests there are few herbs growing on the forest floor, and it is generally easy to walk. Disturbance in the canopy lets in more light and encourages the growth of herbs and young woody plants, so that walking can be difficult. Other plants that are important in the rainforest are the lianas (woody climbers). These often ascend to the crowns of the tallest trees, relying on them for support and linking the crowns of adjacent trees one to another. Epiphytes are frequent in rainforest, attaining their greatest abundance in the wetter forests, particularly those that have only a short dry season, or that grow in sites where mists are frequent. Many of the epiphytes are ferns or orchids, relying on their host tree only for support and drawing no nutrients from it.

Another tree growth habit is that of the strangler. In Africa, most stranglers are figs (*Ficus* spp.), whose fruits are an important food for many mammals. The seeds of figs germinate above the ground, often where a branch forks from the main trunk. The plant grows as an epiphyte at first, but also produces long roots that eventually reach the ground. Once rooted in the ground, the fig grows faster, and its roots enlarge to form a network around the trunk of the host. Eventually the host tree dies, leaving the fig as a free-standing tree with a hollow trunk.

The tree flora of the rainforest is extremely diverse. It is also different from that of Asian and South American rainforests. The family Dipterocarpaceae, which is well represented in South-East Asia, is virtually absent from Africa. The only group that can be regarded as characteristic of African forests is the subfamily

Figure 5. The Rainforest Biotic Zone showing the regions, sub-regions and refugia. Regions are indicated in capital letters; sub-regions are indicated in lowercase letters; refugia are indicated in lowercase italics (after Happold 1996 and references therein).



Caesalpinioideae of the Leguminosae. Members of this subfamily are common both in the canopy and in the understorey, and in some areas they form almost monospecific stands. The forests of Uganda ironwood (*Cynometra alexandri*) in western Uganda and the Ituri region of DR Congo, and *Gilbertiodendron dewevrei* in western DR Congo and southern Cameroon, are examples. Apart from these single-species dominated forests, it is not particularly meaningful to distinguish the normal and more diverse forest types by using the names of trees that are often rare. Classifications such as that of Hall & Swaine (1976, 1981) used moisture status, combined with the degree of deciduousness (e.g. Wet Evergreen; Dry Semi-Deciduous). Hall & Swaine (1976, 1981) found the greatest plant diversity in the wettest forests and the lowest in the driest; they also showed that their Ghanaian forests were less diverse than those of South-East Asia and this is true of African forests in general. They also found a relationship between tree height and rainfall, with the trees in somewhat drier and more seasonal forest type being tallest, and both drier and wetter forests having a lower maximum tree height. This may be due to nutrient availability; in areas of high rainfall many of the mineral nutrients in the soil are leached out.

Gaps caused by tree falls, as well as those caused by clearance for cultivation, occur throughout the rainforest. Old trees fall, often in the strong winds that accompany storms at the beginning of the wet season. Because tree crowns are often tied together by lianas, the fall of one tree may bring down others to produce a substantial gap. Initially the vegetation of gaps is dominated by quick-growing herbs, often of the ginger family (Zingiberaceae). This lush vegetation is attractive to elephants as well as to gorillas and other primates, and their continued foraging visits may prolong the life of the clearing. In general, however, colonization by fast-growing tree species such as *Musanga cecropioides* and *Trema orientalis* is rapid; both have fruits that are eaten by primates, birds and bats so that their seeds are distributed widely over the forest. These trees are, however, relatively short-lived (perhaps 20–30 years), and are rapidly replaced by slower-growing species that can regenerate in shade. Within a century, a former gap will usually be indistinguishable from its surroundings.

Within the Rainforest Biotic Zone, seasonally flooded or waterlogged valleys often support swamp forests in which species

composition is completely different from that of dry-land and upland forests. Palms, including species of *Raphia*, and the climbing rattan, *Calamus deeratus*, are often common. Both have abundant fruits that are eaten by many animal species. Other specialized forest types include those found on and around granite inselbergs – isolated rounded rock outcrops – within the Rainforest Biotic Zone. Here, species characteristic of drier regions can often be found far outside their normal range, just as rainforest tree species occur around springs within the Guinea Savanna Biotic Zone, often far from the Rainforest Biotic Zone. Finally, there are mangrove forests, regularly inundated by seawater; these usually have only a few species, mostly belonging to the genera *Rhizophora* or *Avicenna*.

Seasonal changes in rainforest are not as great or as obvious as in the savanna, but most species of plants show seasonal cycles in relation to slight variations in climate. Deciduousness, in particular, is often used to describe forest types but in fact there is a complete gradation from fully evergreen to almost fully deciduous forests. Hall & Swaine (1981) found that even in the driest forest types the canopy trees were fully deciduous. Species of plant vary in their times of leafing, flowering and fruiting so that there is generally some form of plant food available for animals throughout the year. However, the few detailed studies of forest phenology (e.g. Tutin 1998) show not only that there are large variations in fruit availability in each month of the year, but also that this availability may vary greatly from one year to the next. Thus animals that rely on fruits for food will have to switch from the fruits of a particular suite of species in one month to those of other species in the next month. Swaine & Hall (1986) found in a Ghanaian forest that species with fleshy fruits showed less seasonal fluctuation in fruiting than those species with explosive or wind-dispersed fruits.

Recent destruction of rainforest by humans has resulted in many 'savanna-like' habitats within the Rainforest Biotic Zone, often linked to each other by roads and urban areas. These are often dominated by vigorous-growing elephant grass (*Pennisetum purpureum*) and spear grass (*Imperata cylindrica*). These, as well as the natural treeless patches sometimes found around rock outcrops, can provide habitats for some savanna species of animals and plants within the Rainforest Biotic Zone.

(7) AFROMONTANE—AFROALPINE BIOTIC ZONE

(White's Afromontane Archipelago-like Regional Centre of Endemism, and Afroalpine Archipelago-like Region of Extreme Floristic Impoverishment)

This biotic zone is found on the mountains of Africa south of the Sahara. It differs from all other zones because it is broken up into a series of widely dispersed areas. In West Africa these are few and far between – the Fouta Djallon in Guinea, Mt Nimba on the Liberian border with Guinea and Côte d'Ivoire, Bioko I. (Equatorial Guinea) and Mt Cameroon and associated highlands to the north in Cameroon. The most extensive highland area in Africa lies in Ethiopia. The Ethiopian Plateau is volcanic in origin and lies mainly between 1500 and 3000 m, although some massifs reach 4000–4300 m. It is divided into eastern and western halves by the Eastern (or Gregorian) Rift Valley, and numerous deep and spectacular gorges cut into the margins of the plateau. The streams originating on the plateau are the sources of several large rivers – the Blue Nile, the Awash, the Juba and the Wabe Shebelle – that flow into the arid lowland environments that surround the plateau. Moving south, most of the highland areas are volcanic and associated with the Rift Valley. Mount Kenya, Mt Elgon, the Aberdare Range and Mt Kilimanjaro are close to the Eastern (Gregorian) Rift Valley. Mountains associated with the Western (or Albertine) Rift include the Virunga Mts and the Kungwe–Mahali Mts and the mountains bordering L. Kivu and L. Tanzania. The Rwenzori Mts on the Uganda–DR Congo border, although associated with the Western Rift Valley, are not volcanic. In eastern Tanzania there are also several massifs that are neither volcanic nor associated with the Rift Valley; these include the Usambara, Uluguru and Uzungwa Mountains, all rich in endemic animals and plants and collectively referred to as the Eastern Arc Mts. The Livingstone Mts in south-west Tanzania, and the Nyika Plateau (both associated with the Gregorian Rift Valley in Malawi) and Mt Mlanje (a large non-volcanic mountain, not associated with the Rift Valley, in south-east Malawi), may form 'stepping-stones' between the mountains of eastern Africa and the Drakensberg Range and the Knysna highlands of South Africa. Finally, although they barely attain 2500 m, the Angolan highlands near Huambo are rich in endemic plants and birds.

The environment of the Afromontane zone differs in a fairly predictable way from the lowlands. Mean temperature falls with increasing altitude at about 0.5 °C per 100 m. In the clear air of the high mountains there are very large diurnal fluctuations, such that the climate of the alpine zone (see below) has been described as 'summer every day and winter every night'. Above about 4000 m, snow is present throughout all, or most, of the year. Glaciers exist on the Rwenzori Mts, on Mt Kenya and on Mt Kilimanjaro. Rainfall increases with altitude up to a certain level (generally corresponding to the height normally attained by the daily cloud cover) and then declines. For example, the saddle between the two peaks of Mt Kilimanjaro has a very low annual rainfall of around 150 mm and is largely barren; it has been described as a high altitude desert (Greenway 1965). Within the montane forest zone (see below) precipitation occurs partly by rainfall, but to a greater extent by the interception of moisture droplets from mist.

Because of the change in climate with altitude, the vegetation of mountains is zoned. The position of each vegetation zone varies on each mountain depending on the height, aspect and latitude of the mountain. A particular vegetation zone may not occur on all

mountains, and it may have different altitudinal limits on different mountains. Different aspects of the same mountain may show differences in the altitudinal limits of the vegetation zones.

Montane forest generally begins at about 1500 m but this is an arbitrary limit. As a rule, montane forest is shorter in stature than lowland rainforest. Lianas are often more abundant than in the lowlands, as are epiphytes because of the greater incidence of mist in montane forests. Characteristic tree genera of montane forest include *Podocarpus*, *Ilex*, *Ocotea*, *Nuxia* and *Olea*; many of these are widespread, occurring from the Cape (Knysna) to Ethiopia. On dry mountains such as those of northern Somalia and Kenya, there may be juniper *Juniperus* forests.

Above the montane forest there may be a zone dominated by bamboo *Arundinaria alpina*. Few other species grow with the bamboo, and the tangle of fallen stems makes them difficult to traverse. Bamboo flowers gregariously over large areas and then dies, replacing itself by seed.

Above the bamboo, or above the montane forest, there is a zone of thicket or small trees commonly called the giant heath zone. The commonest plants belong to the genus *Erica* (including the species formerly placed in *Philippia*), and some species may be 7 m tall. This zone is moist and misty, and the trunks and branches of the trees, and the ground, are usually covered with thick mats of mosses and liverworts.

The uppermost vegetation zone, the Afroalpine zone, is physiognomically remarkable, and is characterized by the giant lobelias *Lobelia* and giant groundsels *Dendrosenecio*, which are characterized by their huge leaf rosettes. Most *Lobelia* species do not form a tall trunk, although their inflorescences can be up to 5 m tall. Some *Dendrosenecio* species, on the other hand, form substantial trunks up to 6 m tall, covered either by a thick layer of dead leaves, or thick corky bark. The ground vegetation is varied, with grasses, broad-leaved herbs and small shrubs. Many of these belong to, or are closely related to, temperate genera.

The vegetation of the high plateaux of Ethiopia generally follows the patterns outlined above. However, the extensive areas of fairly level ground, the fertile soils developed from volcanic rocks, and the fairly reliable rainy seasons have encouraged human settlement and cultivation. In some parts, the natural vegetation has now been cleared and replaced with a patchwork of small fields of cereal and pulse crops. The remaining patches of natural vegetation can be found along streams and marshes, on rocky hills and on steep slopes and cliff ledges.

(8) SOMALIA—MASAI BUSHLAND BIOTIC ZONE

(White's Somalia–Masai Regional Centre of Endemism)

This zone is centred on the Horn of Africa. To the north it is bounded by the foothills of the Ethiopian Highlands. To the south it merges into the Zambezian Woodland zone and to the west it bounds on to the moister woodlands of northern Uganda – an impoverished extension of the Guinea Savanna Biotic Zone (see above). A thin extension of the zone stretches northwards between the Red Sea and the Ethiopian Highlands and joins the northern part of the Sahel Biotic Zone. There is growing evidence that the Horn of Africa has a long history of both aridity and isolation, and both its flora and fauna are rich in endemics. It is sometimes distinguished as the Somali Arid Biotic Zone. The landscape varies between hot arid plains, rugged

barren hills and dry savannas. The mountains along the northern edge of the Horn are an extension of the Ethiopian Highlands, but are lower and drier, with a tendency to winter rains. Southwards and westwards this region includes large areas of grassland and wooded grassland at altitudes of up to 1700 m; these areas include some of the major national parks of East Africa (e.g. Amboseli N. P., Tsavo N. P., Serengeti N. P.). These may appear very different to the much drier bushlands of the Horn, but are linked to them by a continuum of vegetation types and by a similar climate. They are, however, poorer in both endemic plants and endemic mammals.

The main climatic characteristic of this region is the unpredictability of the rainfall. Its equatorial position means that there are usually two wet seasons (Mar–May and Sep–Nov) but either or both of these can and often do fail. In general, the rainfall declines in both total quantity and reliability northwards and eastwards. The extreme tip of the Horn (Cape Guardafui) has a mean rainfall of 21 mm, and much of lowland northern Somalia has annual means of less than 200 mm. Further inland and at higher altitude, the rainfall may be much higher, with up to 1000 mm at Nairobi.

The dry bushlands of the Horn are dominated by two tree genera – *Acacia* and *Commiphora*. Both have many species in this region. *Commiphora* spp. are characteristic of the drier parts of the region. For much of the year they are grey and leafless, but they rapidly produce leaves as soon as there is rain. *Acacia* species are especially widespread and several form vegetation communities that are easily recognized and characteristic of the region, particularly the more mesic parts outside the Horn. The whistling thorn *Acacia drepanolobium*, with its swollen spine-bases ('ant-galls'), occurs in shallow seasonally waterlogged valleys on black soil. *Acacia tortilis* forms the flat-topped trees scattered in the open grasslands. *Acacia xanthophloea* is the yellow-barked 'fever-tree' that occurs beside rivers and lakes. The vegetation of the drier parts of the Horn tends to be heavily grazed. Perhaps in response to this, numerous plant genera that are herbs elsewhere in Africa have woody representatives in the Horn, and many species are spiny. Grasses in this part of the region tend to be annual, and appear after rain. In the highland and more mesic regions, however, the open grasslands are dominated by perennial species, particularly the red oat-grass *Themeda triandra*. This species has awned seeds that bury themselves in the ground (Lock & Milburn 1971), and it appears to be encouraged by regular fires.

The characteristics of the vegetation of this region that most affect animals arise from the unpredictability of the rainfall. A good wet season produces copious grass and a good flush of leaves and young stems on the trees and shrubs. There may, however, then be a period of many months with little or no rain during which animals either have to subsist on what is left or migrate. Trees and shrubs tend to carry nutritious leaves and young growth for longer than grasses and it is perhaps no coincidence that many of the larger herbivores in this area are browsers. In the wetter upland grasslands, the higher biomass of grass is able to support a high biomass of animals. In Serengeti N. P., the characteristic large herds of herbivorous mammals have regular migrations. The herds travel from area to area, exploiting each area when the grasses have attained their most nutritious stage of growth. As a result, the grasslands can support a higher biomass of animals than if the herds stayed at the same place throughout the year.

The Somalia–Masai Bushland Biotic Zone is assumed to have expanded and contracted during the dry periods of the Quaternary.

The drier parts of the savanna south of the Ethiopian Highlands now merge into the easternmost parts of the Guinea Savanna Biotic Zone. When the rainforests were more extensive, they may have reached almost to the foothills of the Ethiopian Highlands, and would have blocked any movement of savanna and arid-adapted animals between northern and southern savannas. During dry periods, there was a wide band of savanna, perhaps rather dry (the so-called 'dry corridor' or 'drought corridor'), which linked the northern and southern savannas. In the past, the opening and closing of the 'dry corridor' helps to explain the present disjunct distributions of some species of savanna mammals.

(9) ZAMBEZIAN WOODLAND BIOTIC ZONE

(White's Zambezan Regional Centre of Endemism)

The savanna woodlands of Africa south of the Equator cover a vast area. They form the 'southern savannas' and are the southern equivalent to the Guinea and Sudan Savannas north of the Equator. To the north they interdigitate with the forests of the Congo Basin; to the north-east they merge gradually into the Somalia–Masai bushlands and grasslands and to the south they grade into the drier shrublands and grasslands of the South-West Arid Biotic Zone and the upland grasslands of the Highveld. There are a number of highland 'islands', as well as several large lakes, associated with the Rift Valley, and extensive areas of seasonal and permanent swamp in the area of the headwaters of the Congo and Zambezi rivers. Soils in the southern part of the region are particularly poor because they are underlain by Kalahari Sands. These are wind-blown deposits dating from the cold dry stages of the Quaternary period, when arid conditions extended much further north than they do now.

The climate is remarkably uniform throughout the Zambezan Woodland Biotic Zone. There is a single wet season that lasts for 5–7 months (Oct–Apr). Annual rainfall is generally 700–1200 mm. The dry season lasts for 5–7 months and coincides with the cooler months of the year. The seasonal pattern of rainfall is thus similar to that of the Guinea and Sudan Savannas, but displaced by six months. Temperatures in the southern savannas are strongly influenced by altitude and season. In the north, the daily minimum and maximum temperatures in *Brachystegia* woodland (Liwonde, Malawi, 500 m) are 21–33 °C in the hot dry season, 15–27 °C in the cool dry season and 23–30 °C in the wet season. These contrasting seasons each provide different environments for plants and animals; in the wet season, water is freely available and plant growth is rapid, but in the dry season water is scarce or unavailable and plant growth is limited. Some plants survive as seeds but the majority of the grasses and herbaceous plants survive as underground parts. Fires are common during the dry season, destroying much of the above-ground parts of the grass.

The vegetation that is most widespread in this region is woodland, often referred to by its local name of 'miombo'. The most abundant and widespread components of this woodland are species of *Brachystegia* and *Isobrerlinia*, both trees belonging to the subfamily Caesalpinioideae of the Leguminosae. They generally form a light but fairly continuous canopy at 15–20 m. On the Kalahari Sands, however, there is a more mixed woodland from which *Brachystegia* and *Isobrerlinia* are often absent and in which *Cryptosepalum pseudotaxus* and *Baikiaea plurijuga* are often prominent. In the areas of highest rainfall, a woodland physiognomically similar to Guinea Savanna

and locally referred to as 'chipya' is widespread. Again, *Brachystegia* and *Isoberlinia* are absent, and the tree assemblage is more varied, including *Burkea africana*, *Parinari curatellifolia*, *Pericopsis angolensis*, *Pterocarpus angolensis* and *Combretum* spp. The ginger *Aframomum albobolaceum* and bracken fern (*Pteridium aquilinum*) are widespread and characteristic, growing among the grasses.

The topography, developed for the most part on an ancient land surface, tends to be gently undulating, and the different parts of the landscape bear different vegetation types. Miombo woodland occupies the gentle slopes and plateaux of this region. The broad, shallow, seasonally waterlogged valleys, with black clay soils, have either grassland or sparse and open woodland of small *Acacia* trees standing in tussocky grasslands with numerous small ephemeral herbs between the tussocks. The hilltops are often crowned by inselbergs bearing specialized succulent-leaved plants and often surrounded by denser woodland or thicket that benefits from the run-off water from the rocks as well as the mineral nutrients derived from them. A further source of habitat diversity in the woodland is the presence of large termite mounds. Such mounds are common throughout most savanna zones of Africa, but here they are especially large and prominent. They are often covered by dense thickets, frequently less completely deciduous than the main woodland, and also much richer in species. As well as providing a less seasonal food source, the holes at the base of these mounds provide a valuable refuge for animals.

The trees of the main canopy are deciduous. The leaves fall early in the dry season, and as the humidity drops, so the pods on the trees burst open and release their seeds. Some weeks before the beginning of the wet season, the trees flush into new leaf, and many also flower. The ground vegetation begins its main period of growth at this time, although some species flower during the dry season, sometimes apparently stimulated by fire. During the wet season the grasses continue to grow, and most flower late in the wet season.

At the southern, drier edge of this zone, *Brachystegia* and *Isoberlinia* tend to be replaced by *Colophospermum mopane*, another tree in the same family (Fabaceae–Caesalpinioideae), which gives its name to the 'mopane' woodlands. Mopane woodland tends to grow in hotter and drier areas than miombo, and it can tolerate soils in which there are high concentrations of sodium. This is a tolerance rather than a preference – mopane grows better on ordinary soils but it is susceptible to competition from other species. There is usually little grass in mopane woodland and, indeed, if the woodland is opened up (by, for example, heavy browsing by elephants), an increase of grass cover can lead to fire damage to the trees.

(10) COASTAL FOREST MOSAIC BIOTIC ZONE

(White's Zanzibar–Inhambane Regional Mosaic and his Tongaland–Pondoland Regional Mosaic)

This biotic zone is a thin strip of low-lying land extending along the coast of eastern Africa between the ocean and the higher country of the interior. It begins in southern Somalia and ends in KwaZulu–Natal, South Africa. Much of this area is fairly flat but there are isolated hills. The lower reaches of large rivers such as the Tana, Rufiji, Rovuma, Zambezi, Sabi and Limpopo flow into extensive estuaries at the coast. Included in this biotic zone are the offshore islands, of which the largest are Pemba, Zanzibar and Mafia Is.

The climate is warm and humid for most of the year, and strongly influenced by the monsoons of the Indian Ocean. The annual rainfall

is 800–1900 mm, according to locality. In the northern part of the area there tend to be two rainy seasons (Apr–Jun and Oct–Dec), but from southern Tanzania southwards there is a single wet season (Nov–May), which lasts for about six months. However, a little rain falls in all months of the year and the effect of the dry season is mitigated by the humidity from the sea. The proximity of the ocean also helps to maintain an even temperature throughout the year.

The vegetation of this biotic zone has been heavily cleared and cultivated for a long time, and little of the original vegetation remains. Many of the surviving fragments owe their preservation to being sacred groves ('kayas') that are preserved by local people for their mystical significance, as well as acting as a source of fuel, poles and medicinal plants. Forest was probably formerly widespread, and the fragments that remain suggest that it was originally a mixed forest. Many of the tree species are endemic to this biotic zone, but many also have close relatives in the Guineo-Congolian forests. Whether this indicates a former connection between these forests and the main Guineo-Congolian forests remains uncertain. Many of the species are endemic to the region; in the forests around Amani, in the East Usambara Mts, at 1250 m, about 40% of the plant species are endemic. The general stature of the vegetation is lower than that in Guineo-Congolian forest, with few emergents exceeding 35 m in height. Further south, the longer dry season leads to floristic impoverishment, so that the forests of Mozambique and KwaZulu–Natal are much less species-rich than those of northern Tanzania and southern Kenya. However, interesting endemic trees have recently been discovered in coastal central Mozambique. Swamp forests occur close to the river estuaries; those dominated by *Barringtonia racemosa* are somewhat salt-tolerant, and occur on the landward side of the true mangrove forests.

The drier areas bear thicket vegetation, spiny and often leafless during the drier parts of the year. In areas where there has been extensive cultivation, the vegetation is a mosaic of tall grasslands, crops and patches of fruit-bearing trees such as coconut *Cocos*, mango *Mangifera* and cashew *Anacardium*. There may also be isolated trees from the original forest, left either for shade or because they have some other use.

(11) SOUTH-WEST ARID BIOTIC ZONE

(White's Karoo–Namib Regional Centre of Endemism, with part of his Kalahari–Highveld Regional Transition Zone)

The South-West Arid Biotic Zone is the southern equivalent of the Sahara Arid Biotic Zone, but because of the influence of the Indian and Atlantic Oceans, aridity is less marked here than in the Sahara where the land masses of Asia and the Arabian Peninsula intercept any rain that may be coming from the east on the trade winds. In southern Africa, the eastern side of the continent receives moist air from the Indian Ocean and is therefore far from arid. On the western side, however, the presence of the cold waters of the Benguela Current close inshore mean that any onshore winds bear little moisture, except as fog. Much of the region is arid throughout the year. As in the Sahara Arid Biotic Zone, the northern and southern edges have different patterns of rainfall. At the northern and eastern edges of the region, rain falls during the summer (Dec–Mar), while at the southern edge it does so during the cool winter season (May–Sep). At the southern margin there may be 200–300 mm of winter rain each year, and at the eastern margin, up to 400 mm of

mainly summer rain. Throughout the region, and particularly in the areas with the lowest rainfall, there is great variation from year to year. Temperatures, in general, are not as high as in the arid zones north of the Equator, probably because of the moderating effects of the sea. Daily maximum temperatures range from 25–30 °C during the summer (Nov–Feb) and 10–15 °C during the winter (Jun–Jul). Away from the coast, there are large daily fluctuations in temperature and frosts occur in several months of the year. In the Kalahari Gemsbok N. P., for example, the daily mean maximum and minimum temperatures are 36 and 19 °C respectively in summer, and 22 and 0 °C in winter.

The South-West Arid Biotic Zone may be divided into three subzones: the Namib, the Karoo and the Kalahari. All are arid to varying degrees but in rather different ways. Briefly, the Namib has extremely low rainfall, the Karoo has low and rather unpredictable rainfall and the Kalahari has more rain but very permeable sandy soils that mean that surface water is very scarce. As in the arid zones north of the Equator, the landscape is varied, and includes extensive sand dunes, plains with very low sparse scrubby vegetation and seasonal river beds that contain water after heavy rain and have a more luxuriant vegetation.

The Kalahari Desert subzone (11a) occupies a great basin between the Highveld to the east and the Windhoek Mts to the west. Much of the basin lies between 850 and 1000 m and is largely devoid of hills, mountains or rock outcrops. The whole area is underlain by deep sands of varying age, and the drainage is largely internal. The Okavango R. flows into the northern part of the Kalahari and disappears into the sands. Surface water for drinking is very scarce. Annual rainfall is generally 250–500 mm and falls mainly in the summer. The winters are dry and cold, with frost at night. The natural vegetation of the sandy soils of much of the region is wooded grassland. Most of the grasses are perennial (although overgrazing may alter the balance towards annuals). The trees are mainly species of *Acacia* in the south, with more species with broad leaves (such as species of *Commiphora* and *Combretum*) in the north. Areas with more stony or gravelly soils are usually covered by bushland in which *Tarchonanthus camphoratus* is prominent.

The Namib Desert subzone (11b) forms a coastal strip extending from north-western South Africa through Namibia to the extreme south-west of Angola. For most of its length it is about 100 km wide. Over the whole area, annual rainfall averages less than 100 mm and over much of the area it is very much lower, with less than 10 mm per annum on the coast at Swakopmund. When rains occur, they tend to fall in the winter in the south and in the summer in the north. In the driest areas there may be virtually no measurable rain in some years. Particularly near the coast, this extreme aridity is mitigated by frequent fogs. These form offshore over the cold waters of the Benguela Current and are blown inland during the night. Condensation from these fogs can provide water in quantities sufficient to be useful to animals although it is only useful to plants where it is concentrated in some way, as near rock outcrops. The waters of the Benguela Current are highly productive, with some of this productivity being transferred to the land through the activities of birds and seals. The vegetation of the Namib Desert is extremely sparse. Gravel desert may support many lichens, but higher plants are mostly ephemeral

succulents and grasses that appear only after years with exceptionally heavy rain. The extensive sand dune areas are usually virtually free of vegetation. However, drainage lines may carry perennial vegetation, even including trees in the most favoured sites.

The Karoo subzone (11c) occupies the northern parts of South Africa, mainly within the Northern Cape Province. It lies between the winter rainfall zone of the Cape and the summer rainfall of the Highveld and the Zambebian woodlands to the north. Even if the rain falls mainly in the summer or winter, there is often significant precipitation in the other parts of the year, and sometimes the normal rainfall distribution may be reversed. Much of the Karoo lies above 800 m, and frosts may occur during several months in winter. Much of the Karoo is fairly level and has clay-rich soils, which tend to accumulate salts.

The vegetation of the Karoo is mainly a low shrubland. Many of the shrubs and herbs have either succulent leaves or succulent stems. The main family in this vegetation is the Mesembryanthemaceae. These are usually small herbs with thick, succulent leaves, sometimes cryptic – they may be coloured and shaped so that they resemble stones. Flowering takes place mainly in response to rain. There are also scattered larger plants, some of them almost of tree stature; most of these grow among rocks or in other places where some extra water is available from run-off. Among these are species of *Aloe*, including *A. pillansii* that attains 10 m, and the more drought-resistant species of *Acacia* such as *A. redacta* and *A. erioloba*. There are also many annuals (more strictly ephemerals), many of them in the family Compositae, that germinate in response to heavy rain and produce the carpets of flowers for which the southern parts of the region are famous. Grasses are present, but not abundant; it is possible that they have declined with increasing grazing of these areas by domestic stock.

(12) HIGHVELD BIOTIC ZONE

(Most of White's Kalahari–Highveld Regional Transition Zone)

This biotic zone occupies the interior plateau of South Africa. Most of the plateau is gently undulating country of low relief, usually above 850 m, although at its eastern and western margins it reaches nearly 2000 m.

Its inland position means that it is generally a region of low rainfall, with an annual total of about 250 mm in the south-west and about 650 mm in the south-east. The rain falls in a single rather extended summer wet season between November and May. The seasons are well defined and the generally high elevation of the plateau means that average temperatures, even in summer, are relatively low. The mean maximum of the warmest month is 20–25 °C. Frosts occur throughout the zone between April and September, and may be severe.

The vegetation of the Highveld Biotic Zone, between 1200 and 2200 m, is grassland. There are many species, but the most widespread and conspicuous is *Themeda triandra* (red oat grass). It is possible that the dominance of this species has been increased by regular burning, which it withstands well. Heavy grazing can lead to the loss of *Themeda* and its replacement by grasses such as *Aristida* and *Chloris* spp. Species of *Hyparrhenia*, which are characteristic of the warmer seasonal grasslands of the Zambebian Woodland and Guinea Savanna Biotic Zones, are absent.

On the Kalahari Sand, which underlies much of the western and north-western parts of this biotic zone, the characteristic vegetation

is wooded grassland. In the drier southern parts, the main trees are species of *Acacia*, with other genera including *Combretum* and *Commiphora* in the wetter northern parts. The main grasses are species of *Antheophora*, *Eragrostis*, *Panicum* and *Schmidtia*.

(13) SOUTH-WEST CAPE BIOTIC ZONE

(White's Cape Regional Centre of Endemism)

The South-West Cape Biotic Zone is a small but very distinctive biotic zone occupying the south-west corner of the African continent. In a climatic sense, and in the physiognomy of its main vegetation, it is the southern analogue of the Mediterranean Coastal Biotic Zone. The region is also diverse geologically and topographically, with several mountain ranges trending generally east–west, and a variety of underlying rocks including sandstones (such as that which makes up Table Mountain), granites, shales and limestones.

The climate of the southern and south-western parts of the zone is a winter rainfall season (Apr–Sep), with warm summers and cooler winters. Because of the proximity of the sea, there is some rain in every month and, probably for the same reason, the temperature extremes are not great. Annual rainfall is 400–600 mm in the centre of the zone, but considerably less to the north on the western side. Eastwards, the seasonal rainfall pattern changes, and at East London there is summer rainfall (Oct–Apr). Rainfall increases rapidly with altitude, so that the annual total for Table Mountain (761 m) is 1780 mm while that of Cape Town (12 m) is 630 mm. Frosts occur regularly inland and on the mountains, but not at the coast, and at the highest altitudes snow falls regularly but does not persist.

The Cape flora is extremely rich. Within White's (1983) Cape Centre of Endemism, there are over 7000 plant species (of which over half are endemic) in an area of 71,000 km². Some genera, such as the heathers (*Erica*), have undergone prolific speciation (now some 650 species). Many of the very species-rich genera are small shrubs, but geophytes (plants with bulbs and other underground organs) are also abundant.

The main vegetation type of this biotic zone is locally referred to as 'fynbos'. It is a dense shrubland 1–3 m tall, made up of plants with drought-resistant small thick leaves. The best-known components of fynbos are members of the Proteaceae, particularly *Protea*, as well as *Leucadendron* and *Leucospermum*. Members of the Ericaceae, Leguminosae-Papilionoideae and Compositae are also prominent. Grasses are not an important component of the vegetation now, but it has been suggested that they were commoner before the introduction of domestic stock. Many of the grass-like plants belong to a completely different family, the Restionaceae. Fynbos is very vulnerable to invasion by species from other parts of the world with similar climates: Australian species of *Acacia* and Mediterranean species of *Pinus* are particularly invasive.

Fire is probably an essential factor in the maintenance of fynbos. Although a burned area may appear devastated after a fire, many species sprout from the base of the stems, or germinate from seeds that are protected within fruits or inflorescences and are released when a fire occurs. Other species flower in response to a fire. Many species are now known to lose vigour or even die if they are not burned.

(14) AQUATIC ENVIRONMENTS

Although not a biotic zone as such, aquatic habitats in Africa are an important ecological entity for mammals and other animals. Most of

the rivers of Africa have a fringe of distinctive vegetation. In many savanna habitats, long strips of forest occupy the river banks and valleys, providing pathways from the main parts of the rainforest into the savanna. In drier regions, where rivers may not flow all the year, there is often a fringe of forest or thicket, surviving on water deep in the river bed. Fast-flowing rivers are usually devoid of submerged vegetation (except for the highly specialized moss-like Podostemaceae), although some plants may grow in the slower reaches if the water is not too deep or too turbid.

Lakes in Africa are essentially of two types. Most of the Western Rift Valley lakes, such as L. Albert, L. Edward, L. Kivu, L. Tanganyika and L. Malawi, are deep and have steeply sloping shores with little shallow water. Such lakes often lack much of a distinctive vegetation fringe, and there is also usually little submerged vegetation. Other lakes, such as L. Victoria, L. Kyoga and L. George in Uganda, L. Chad on the Chad–Nigeria–Cameroon border, and L. Mweru wa Ntipa in Zambia are shallow and much more productive. The margins of shallow lakes have extensive beds of tall swamp plants such as papyrus *Cyperus papyrus*, reed *Phragmites australis* and reed-mace *Typha domingensis*, which provide shelter, but are of little value as food. Animals can live in these reed-beds during the day, and move out to feed on swamp grasses during the night. Shallow water areas are also densely vegetated with species rooted in the bottom mud (e.g. water-lilies *Nymphaea*) or free-floating, such as the Nile cabbage *Pistia stratiotes* and the introduced water hyacinth *Eichhornia crassipes*. Again, these species are little used as food by animals, but they provide valuable shelter during the day, and also harbour large numbers of fish that are much preyed upon by some mammals.

Flood-plains are important for some African mammals. The major flood-plains are the Inland Delta of the Niger, the Sudd Region of the Nile in southern Sudan, L. Bangweulu and the Luangwa Valley in Zambia, and the Okavango Swamps in Botswana. In all of these except the Okavango, a central river flows throughout the year; but during the wet season, the river rises and bursts its banks flooding huge areas of the surrounding plains. In the Okavango, the river flows into the swamps, where it eventually disappears. River flooding may be supplemented by direct flooding from heavy rain, as many of these areas lie on impervious clay soils. The fringing swamps of the river are usually dominated by giant swamp herbs, such as papyrus. The seasonally flooded grasslands are gradually exposed during the dry season as the river levels fall. Grazing animals are able to follow the flood as it recedes, feeding as they go on the newly exposed grasses, most of which are specialized swamp species such as *Oryza* (wild rice) and *Echinochloa*. In southern Sudan, these seasonally flooded grasslands are a key dry season resource for several mammalian species, including the Nile Lechwe *Kobus megaceros*, White-eared Kob *Kobus kob leucotis*, Tiang *Damaliscus lunatus tiang* and several species of small rodents. Likewise, the seasonally flooded grasslands of southern tropical Africa are a crucial resource for the Red Lechwe *Kobus leche*.

A final type of aquatic habitat is the saline or alkaline lake. These are characteristic of the Eastern Rift Valley. Here salts are leached from the fresh alkaline volcanic rocks and are washed into basins of internal drainage where they accumulate. Most of these lakes are too saline to be used as drinking water (although there are often springs of fresh water at their margins). As such they do not provide a very useful habitat for many mammals although they may be used as a refuge and for wallowing and bathing. Scavengers may also find rich pickings along their shores.

CHAPTER SIX

Mammalian Evolution in Africa

Jonathan Kingdon

The theory of evolution by cumulative natural selection is the only theory we know of that is in principle capable of explaining the existence of organized complexity. Even if the evidence did not favour it, it would still be the best theory available! In fact the evidence does favour it ... Cumulative selection, by slow and gradual degrees, is the explanation, the only workable explanation that has ever been proposed, for the existence of life's complex design.

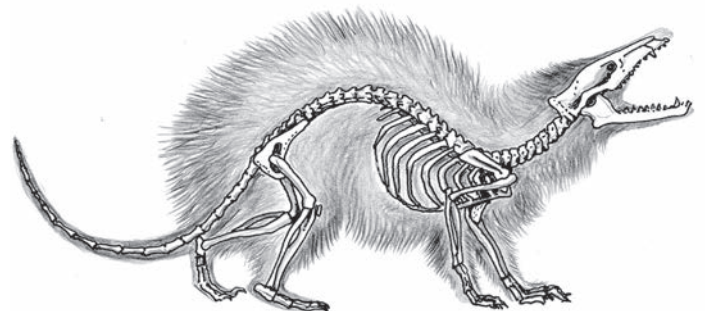
Richard Dawkins, *The Blind Watchmaker*, 1986

Beginnings

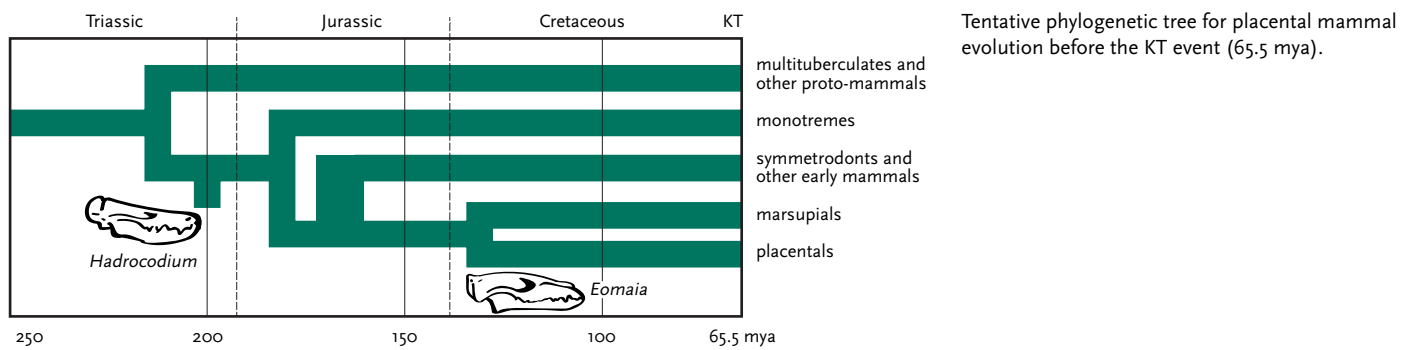
Australia suits kangaroos, Antarctica suits penguins. With 17 of the world's 20 orders of terrestrial mammals – more than any other continent – Africa certainly suits mammals. Does this imply that the first mammals were African? Is Africa the place to find evidence for the evolution of aardvarks, antelopes, apes, bats, giraffes and zebras from a common ancestor? On current knowledge the answer must be no. Placental mammals are unlikely to have originated in Africa and, if they did, the obliteration of any traces of early beginnings has been extraordinarily thorough. However, the fact that so many types have flourished and diversified, once their ancestors did get here, has to be an evolutionary theme of major significance.

While the mammals of Africa are celebrated for their distinctiveness and variety, the reasons for such diversity have been quite slow to emerge and one of the purposes of these volumes, and of our introductory chapters, is to synthesize a large body of new research and explanations drawn from a broad spectrum of disciplines. Our introductory chapters discuss the roles of geography and geology, vegetation, climatic changes, behaviour and morphology in mammalian biology. This chapter explores the continent as a very singular theatre of mammalian evolution, a perspective that complements its other purpose, which is to identify some fundamental features of the evolutionary process that seem particularly well illustrated by African mammals. In profiles of living species, with standardized topic headings, some aspects of evolution can be easily overlooked. Among them are considered discussions of selection, by predators, by disease, by sexual competition, by inter- or intra-specific competition or mate selection. The importance of co-evolution and the role of, say, elephants in shaping the habitats within which many *other* mammals have evolved also invite discussion; so size and co-evolution are among the topics that are discussed in this chapter.

What was the first placental like? Externally it probably differed scarcely at all from earlier non-placentals because its special physiological advantages were internal, not external. A generalized outline of the earliest mammal as a small, possibly very small, probably nocturnal and at least partially arboreal animal remains a plausible model in spite of that characterization having been around for well over a hundred years (Matthew 1904, Simpson 1937, Romer 1945, Cartmill 1974). Now there is a fossil to confirm this general outline. In 2002 Ji *et al.* described a 125-million-year-old proto-placental mammal, *Eomaia scansoria* (meaning literally 'climbing dawn-mother'), from China, which was clearly semi-arboreal (in some respects resembling a dormouse in size and appearance: see below). The disparate characteristics of supposed stem mammals are also consistent with some such ancestral placental emerging on the Eurasian land mass some time after 150 mya (Bininda-Emonds *et al.* 2007). However, the discovery of *Eomaia* serves to remind us that all living placentals derive from just one of more than a dozen lineages, all but one of which have become extinct (Wible *et al.* 2007).



Reconstruction of *Eomaia scansoria*, a furry early Cretaceous placental mammal.



What distinguishes the present state of mammal studies is that we are becoming better equipped now than at any time in the past to get past loose generalities and explore some of the specifics of mammalian evolution. Apart from fossils such as *Eomaia*, the main source of new information about mammalian origins has derived from the construction, by geneticists from around the world, of molecular phylogenetic trees for all the orders and families of mammals. For several major groupings such strong implications of continental origin have emerged that some now have continental names, notably the Afrotheria and Laurasiatheria. The more modern trees are accompanied by a time-scale deriving from molecular clocks. Fossils have provided crucial cross-checks or calibration and, when sufficiently abundant and diverse, have generally ended up supplementing and confirming the likely truth of some of the most recent molecular trees.

While the power of genetics and palaeontology to reveal evolution in action is incontestable it is important to remember that innovations in science, notably molecular techniques, take many years to develop and the conclusions or hypotheses that derive from a newly emergent branch of science can be subject to error and initially have to be treated as provisional. This is particularly so for dating, but none the less, the broad thrust of contemporary molecular science has been one of the most illuminating of all advances in the history of science. Some radically revised taxonomies have emerged from all this activity in contemporary genetics, and many of the taxonomic recommendations of these molecular scientists have been adopted or adapted in this work.

Changing time-tables for mammalian origins

As is detailed in the chapter on Africa's geological history, it has long been known that Pangaea, the supercontinent, had resolved into two major land masses by about 150 mya. Gondwana (of which Africa was the central and most stable part) lay to the south while Laurasia embraced the present three northern continents in what was initially a more or less contiguous continental mass. The sea of Tethys lay in between. Correlating continental tectonics with placental emergence is clearly central to understanding the timing of mammalian evolution in general but it is particularly significant for understanding mammalian evolution in Africa.

The Eutherian protoplacental fossil *Eomaia scansoria*, mentioned above, comes from the Yixian formation in southern China and has

been dated at 125 mya (Ji *et al.* 2002). This extraordinary fossil, jacketed in fossil hair and without a single bone missing, post-dates the placental/marsupial divide and although its lineage is extinct it serves to reinforce the likelihood of a semi-arboreal and Asiatic origin for placental mammals. The age of this fossil accords with recent molecular clock datings, which suggests placental and marsupial mammals diverged 150–180 mya (Bininda-Emonds *et al.* 2007, Meredith *et al.* 2011). Both fossil and molecular dates are a lot earlier than was estimated in the twentieth century and make it more probable that primitive placentals emerged *after* Pangaea had begun to break up into northern and southern land masses. The Chinese fossils hint very strongly that Asia was the placentals' motherland, but even more persuasive has been the fact that a high proportion of phylogenetic trees and most of the 'stem' mammal groups root in Asia. Furthermore, all but one supercohort of extant African mammals can trace ultimate origins to non-African roots (and even those, the Afrotheria, might have still earlier origins in the northern continental masses).

Mammals of Africa has been compiled during a period of unprecedented scientific discovery. When the project was begun it was still possible to argue that Africa, its precursor mega-continent Gondwanaland, or even the still earlier supercontinent Pangaea, were equally plausible sites for the emergence of placental mammals. Yet within the few years that this book has been in preparation, such evidence as there is, and mainstream scientific opinion, has swung strongly against placental mammals originating in Africa or, indeed, anywhere in the southern continents, although that position is still robustly defended and the possibility must remain open (Montgelard *et al.* 2002, Murphy *et al.* 2007). Admittedly, the appearance of supposed placental fossil teeth and mandibles in Australia has given some support to the idea of southern origins. The teeth are said to have belonged to a hedgehog-like mammal from about 110 mya (Rich *et al.* 1997), and if correctly identified as a placental could imply a Gondwanan origin for all modern mammals. It would also imply their early total extinction and up to now there is no other evidence for placentals ever having lived in ancient Australia and further complicates our ability to interpret the significance of these few teeth. In Africa ancient placental fossils are even scarcer and the earliest reported so far only date from about 60 mya (Gheerbrandt *et al.* 2005). In spite of such tentative hints at southern beginnings, the weight of both fossil and molecular evidence is now in favour of Asia as the place of origin for placental mammals (Archibald 2003, Beard 2004, Robinson & Seiffert 2004).

The primary radiations

The taxonomic revisions that have emerged from contemporary genetics (Murphy *et al.* 2001a, b, 2007, Waddell *et al.* 2001, Huchon *et al.* 2002, Bronner *et al.* 2003, Bininda-Emonds *et al.* 2007) all recognize a radiation, within Africa, of the newly recognized and newly named 'Afrotheria' (Springer *et al.* 1997). This 'supercohort', a grouping of seven orders, derives from a single ancestor in Africa and is extensively discussed elsewhere in this volume.

While the earliest molecular separations (dated to about 105 mya, by some authorities) were between ancestral Eurasian mammals, Afrotheria and the South American Xenarthra (another supercohort), this does not necessarily mean simultaneous continental separation. This is because molecular trees can only sample living species and putative Eurasian representatives of the early lineages that reached Africa and South America probably went extinct long ago. A current estimate of the time when a common afrotherian ancestor might have arrived in Africa suggests some time between 80 and 92 mya (Springer *et al.* 2003). The likelihood of a common afrotherian ancestor deriving from a gene pool that was already established in Africa is now thought to be very low. An ultimate Asian ancestry for the afrotheres and (much later) for the anthropoid primates is made less improbable by tens of millions of years being more than adequate time for the occurrence of chance raftings or island-hoppings between the Asian and African land masses, however far apart they might have been then.

Following these earliest radiations Eurasian mammals divided into two supercohorts: Laurasiatheria, named after the parental land mass, and the Supraprimates (or 'Euarchontaglires'), which allies two particularly ancient groups, primates and rodents. There has been considerable disagreement over extrapolated ages for these two Asian complexes but one of the most recent estimates for their divergence is about 97 mya (Bininda-Emonds *et al.* 2007). Until very recently placental mammals were assumed to have made their main radiations after the demise of the dinosaurs, at the K–T boundary, some 65 mya ago, a time when the broad configuration of today's continental masses was already recognizable (a view that is still held by some scientists, for which see Wible *et al.* 2007). It now seems more likely that the basal placental stock had begun to differentiate into distinct adaptive lineages well before any mammals had reached an Africa that was then surrounded by ocean on all sides. None the less, it is important to remember that the very earliest placental immigrant to Africa did not face an ecological vacuum. It is, indeed, more than likely that it arrived in a continent that was without placentals, but there were abundant dinosaurs and a variety of proto-mammals that would have narrowed the choice of niches into which the new arrivals could expand (Rose 2006).

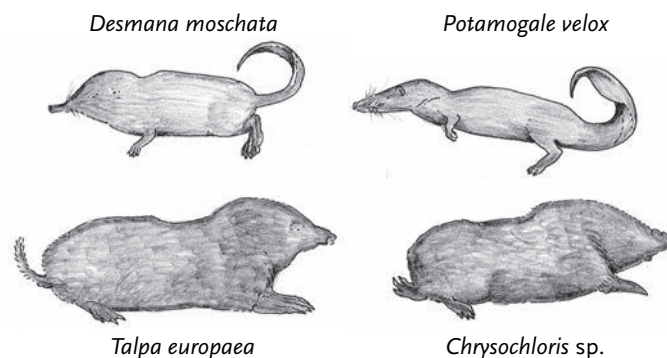
The colonization of continents: Africa's afrotheres

When Springer *et al.* (1997) first revealed that the genes of what were once thought to be completely unrelated orders of living placental mammals had a common (and exclusively African) evolutionary history the association of elephants and their kin with sengis (elephant-shrews) and golden-moles was greeted with

surprise, even disbelief. The Afrotheria embrace a very disparate assortment of seven major mammal orders: hyraxes, elephants, sirenian dugongs and manatees, the Aardvark, sengis (elephant-shrews), golden-moles and (disputedly) otter-shrews, and they are discussed in detail in the appropriate profiles. Although Afrotheria may well represent the oldest surviving group of all living placentals, the implication of a Gondwanan origin for all placentals does not necessarily follow (Montgelard *et al.* 2002, Springer *et al.* 2003, Murphy *et al.* 2007). If, as now seems most likely, modern placentals arose on the Laurasian land mass, the presence of the most primitive of all living types in the southern continents can only be explained by very early 'sweepstake' raftings. A continental bifurcation of the earliest placentals has been proposed by Murphy *et al.* (2007), the Eurasian branch labelled 'Boreoeutheria' and the Afrotheria/Xenarthra common lineage dubbed the 'Atlantogenata'. In this scenario a very small, and possibly semi-aquatic, proto-afrothere island-hopped or drifted from Laurasia to Africa across the Sea of Tethys. It has also been suggested that the Afrotheria might derive from some very early condylarth-like Euramerican ancestor (Tabuce *et al.* 2007).

On current evidence the afrotherian ancestor was the earliest placental to become truly endemic to Africa and its extraordinary radiation into such diverse forms is a clear manifestation of the African continent's prolonged isolation from other continents. Indeed, many afrotheres, both extant and fossil, show remarkable convergences with mammals that derive from totally different groups. Some early elephants in Africa appeared to resemble Eurasian and American tapirs in their anatomy (but probably more aquatic in their habits). Golden-moles resemble unrelated Eurasian moles *Talpa* spp. as well as marsupial moles *Notoryctes* spp. Otter-shrews *Potamogale* spp. resemble the Eurasian desmans *Desmana* spp., which are insectivorous, aquatic moles. In each instance such non-African equivalents of Afrotheria are unknown in Africa and were presumably unable to colonize that continent in the face of an established competitor. The hyraxes are also survivors of another ancient endemic lineage that was once a dominant herbivore type in Africa. In their case incoming Eurasian artiodactyls eventually replaced them in all but their rock and tree fastnesses, where most hard-hoofed antelopes could not compete.

As placental mammals with the longest history in Africa, it would seem that some Afrotheria acquired an adaptive advantage



Comparisons between Afrotheres and unrelated species with convergent features: African Otter-shrew *Potamogale velox* and Eurasian Aquatic Mole *Desmana moschata*; African 'Golden Mole' *Chrysochloris* sp. and Eurasian Mole *Talpa europaea*.

because they occupied specialized niches that no later invaders could displace them from. This would seem to have been the case for sengis (elephant-shrews) Macroscelidea. Numbering some 16 extant species, all long-legged, long-nosed and insectivorous, the divergence between the smaller, more arid-adapted Macroscelidinae and the somewhat larger forest-adapted *Rhynchocyon* has been estimated at 42 mya (Douady *et al.* 2003). This has confirmed that all sengi species share an extremely conservative body form. (The *Rhynchocyon* radiation offers a fascinating expression of one of the basics of evolution, predator-selection, to be discussed shortly.)

Of other mammal groups that co-existed with the Afrotheria, the extinct *Arsinotherium*, creodonts, primitive rodents, two marsupials and primates, are the only ones known as fossils, although bats were almost certainly about. Anthropoid primates, long assumed to be archetypically African, now seem more likely to have arisen from a very tiny and very primitive Asian primate that somehow rafted to Africa between 45 and 60 mya (Sige *et al.* 1990, Beard 2004).

How do mammals speciate within Africa?

While it was rare geological and climatic events, and perhaps chance raftings, that established Eurasian mammals in Africa the founders of surviving lineages were selected somewhat less randomly. The exact environmental conditions within ephemeral, often narrow or discontinuous connecting corridors (or, perhaps, island chains) probably filtered out all but a few appropriately adapted species. The filtering effect was further biased in favour of populations that naturally lived close to the temporary corridor or bridge at the time the corridor opened.

Such restrictions on lineage founders would have contrasted strongly with the wide ranges of environments open to their now pan-African descendants but it would be wrong to envisage subsequent radiations spontaneously adapting to such a diverse choice of habitats. Various lines of evidence suggest that the most likely course of events is an initial wide-ranging prevalence eventually followed by fragmentation of that population, primarily in response to climatic changes. This situation was not only faced by an incoming immigrant mammal – any species that had temporarily become very widespread in the continent found itself in a comparable situation. Some predictable patterns of speciation emerge wherever we have some evidence for the break-up of any once widespread population. Near ubiquity can occur at any time and the accretion of species in Africa implies layer upon laminated layer of super-imposed radiations going back to the earliest mammalian invasions of Africa. The older the radiation, the fewer the surviving lineages become, thus it is among more recently successful groups that we find the clearest evidence for speciation.

Some initial conclusions about how radiations happen can be deduced from examining a series of widespread species (or closely related species groups) and relating their subdivisions to the continent's geography. When reliable phylogenetic trees can be dated and correlated with known fluctuations in climate, and when knowledge of adaptive traits within such entities are added to the equation we can conclude that adaptation to different environmental conditions must have been directly dependent on and a consequence of past physical and reproductive isolations under differing environmental conditions.

These patterns are clearest when a radiation is relatively recent and when the founding ancestor's arrival can be dated.

Are all African mammals immigrants?

The comparison of dated fossils from Eurasia and Africa has revealed that virtually all the other species of living mammals in Africa descend from a succession of invasions (often accompanied by some two-way exchanges) that only assumed major proportions after Africa regained physical contact with Eurasia. Dates for the earliest connections are contested but the earliest clear evidence for a major, multiple influx of mammal taxa is as late as 27 mya, at which time fossils of several rodent, perissodactyl and carnivore groups and chevrotains, Tragulidae, appear for the first time. The dates for later tectonic connections and disconnections are becoming better known as are fluctuations in both global and local climates (see Chapter 4 on climate change). Wherever these events can be tied in to the first appearance of Eurasian taxa in African deposits it becomes possible to chart an increasingly diverse spectrum of mammals that has derived from a staggered succession of invasions.

We can now learn, for example, which groups have radiated within the continent and which derive more directly from immigrants. Perhaps most astonishing of all is to discover that because of Africa's extreme isolation during the most critical periods of mammalian diversification, a sizable proportion of today's mammals derive from single ancestral species that somehow found their way to this vast continental 'island' across substantial distances of ocean. The continent's mammalian diversity has therefore built up through a steady accretion, augmentation, replacement and extinction of species.

One type of accretion derives from a succession of invasions from Eurasia and these invaders, even after becoming distinct, tend to maintain most of the characteristics that ensured their success *before* they found their way to Africa. Many can be called neo-endemic (or, while still indistinguishable from their Eurasian stock, *actual* immigrant species). Another form of accretion has taken place as particular types of mammal have speciated *within* the continent. These can often be called true endemics (and the older ones archaeo-endemics). There are numerous intermediate grades between the oldest archaeo-endemic and the newest of immigrants but the polarities are real.

The existence of these two major sources of diversity becomes particularly significant in discriminating between (1) mammal types that show adaptations specific to some peculiarly African set of conditions and (2) mammals that live in ways that demonstrably evolved on other continents. Of the latter the most obvious are recent arrivals still restricted to northern Africa, carnivores such as foxes, jackals and cats and some generalized rodents. Of mammals that have evolved in Africa, humans are an obvious example, but while it is true that we are predominantly African there are undoubted Eurasian interludes to our animal past that involve both immigration and emigration and these, as well as our African-ness, will deserve serious attention if we are ever to come to grips with humanity's evolutionary history. Understanding speciation within Africa involves some sort of reconstruction of what happens to new immigrants once they have arrived.

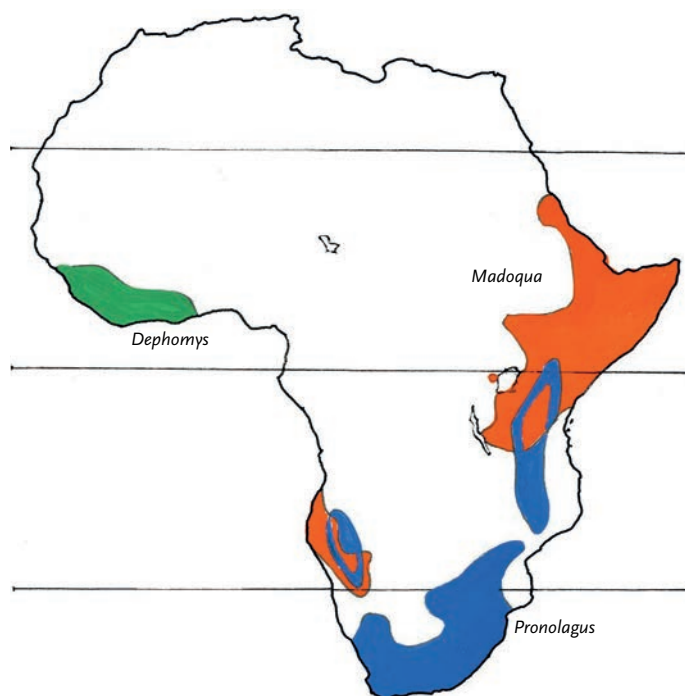
The centre-west versus south-east divide

One of the starting points in the process of speciation is the break-up of a previously single population into two or more separate parts (Mayr 1970). If each part maintains its genetic separation it will come to be different, if only through neutral genetic drift. Given that any mammal population in Africa exists in a landscape where no two places are ever exactly the same and given that habitats are altered by changes in climate, selection for locally adaptive traits will differ in each of two or more parts.

Time and again successful mammal types such as baboons, porcupines or giraffes have dispersed across Africa only to break up into recognizable regional subpopulations. This pattern repeats itself at numerous different levels from cryptic demes that are only now being revealed by molecular analysis, to distinct allopatric species-pairs. Within long-established taxa such as primates and antelopes, adaptation to local differences has eventually culminated in the evolution of genera (or even tribes), each now exclusive, or nearly so, to a region or ecotype. Examples are dik-diks *Madoqua* spp. in the north-east, rock hares *Pronolagus* spp. in the south and dephua mice *Dephomys defua* in the far west. Even among higher taxa, which are necessarily older, with histories that are more difficult to reconstruct, there can be hints that the differentiation between, say, one subfamily and another had its roots in gross regional separation followed by local adaptation.

Are there consistent patterns to this process? Has Africa's peculiar geography imposed its own rules upon the evolutionary history of mammals as a whole? There are, of course, innumerable patterns, but in sub-Saharan Africa one gross bifurcation repeats itself with many slightly different variations. It is a differentiation between populations occupying the latitudinally oriented equatorial centre-west and those in the longitudinally oriented south-east. Today this split roughly corresponds to the difference between lowland forest and upland non-forest, or, latitudinally, boreal and austral communities. Because of this, distribution patterns are commonly treated as direct expressions of adaptation to major contemporary habitat differences. While this may be quite correct there are other, less proximate dimensions to this gross subdivision of a continent. Outlines of differentiation, from family level downwards, suggest that this centre-west/south-east bifurcation (which broadly follows Africa's 'inverted L shape') has been profoundly influential in the evolution of mammals at every level and way back in time.

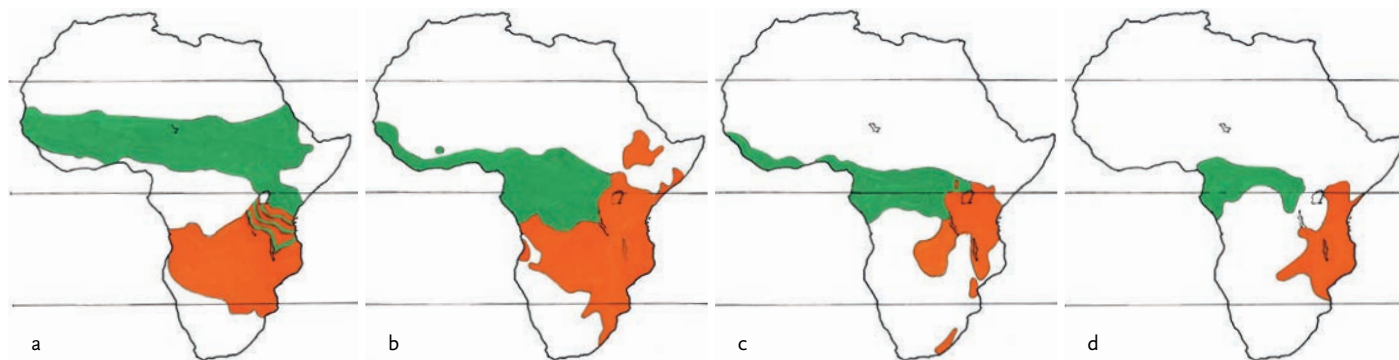
It might be expected that whatever split single populations into two would be a consistent and well-defined discontinuity between



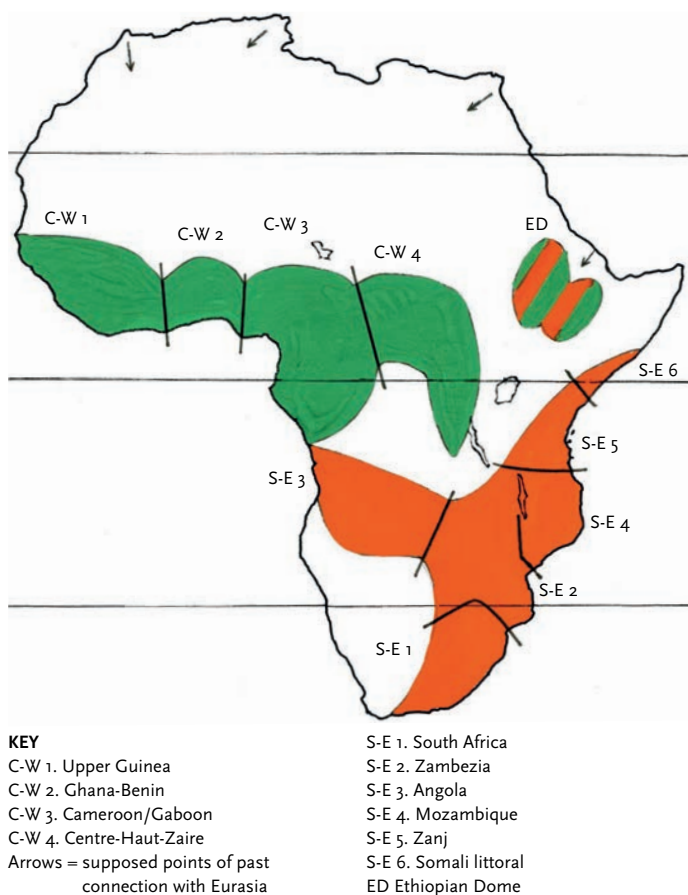
Simplified map showing regional foci of distributions of the genera *Madoqua*, *Pronolagus* and *Dephomys*.

the two regions. To some extent the agencies for just such definition are there: the Nile and Congo Rivers, L. Tanganyika, the Rwenzori Mts, the Rift Valleys, the Somali arid zone or the main rainforest block itself. All can demonstrably act as physical or ecological barriers for various species. Which boundary or barrier is most decisive for a living population varies. Which dividing mechanism can be deduced as playing the major role in any one evolutionary history may differ from its contemporary expression as well as differing from one geological era to another.

The centre-west/south-east divide is exemplified in several antelope species, some rodent duos and two non-forest galago species that have different forms occupying broadly north-western and south-eastern savanna distributions. The Common Eland *Tragelaphus oryx* once inhabited most of southern and eastern Africa while its less derived cousin, the Giant Eland *T. derbianus* ranged through the moister wooded belts south of the Sahara. For these groups the forest belt, assisted by hurdles such as the Nile, the Rift Valley or the East African highlands, are obvious separating mechanisms.



Simplified species distribution maps of (a) *Galago*, (b) *Potamochoerus*, (c) *Dendrohyrax* and (d) *Bdeogale* showing centre-west/south-east divides.



Division of sub-Saharan Africa into two major evolutionary realms. 1. Humid, latitudinal 'Centre-West' (C-W). 2. Drier longitudinal 'South-East' (S-E).

It is postulated that populations originally confined within either realm may extend into intervening areas (most notably to the Ethiopian Dome) or may eventually spread more widely as new species.

Past changes in climate, augmented by geographic barriers, have subjected each realm to further (and changing) subdivisions or conjunctions.

Forest-adapted taxa also separate out along similar lines. The Red River Hog *Potamochoerus porcus*, which inhabits the equatorial forest, is essentially separated from its close relative the Bushpig *P. larvatus* by the Albertine Rift and by the southern edges of the rainforest (the latter a particularly blurry boundary). Likewise, the Western Tree Hyrax *Dendrohyrax dorsalis* ranges right across the main forest belt while the Southern Tree Hyrax *D. arboreus* is its south-eastern equivalent. Among duikers, the *Cephalophus callipygus/weynsi* group inhabit the main forest block, the *C. natalensis/harveyi* group the south-eastern woodlands and forests. There are centre-west and south-eastern populations of bushy-tailed mongooses *Bdeogale* spp., some sun squirrels *Heliosciurus* spp. and various smaller rodents. Some closely related genera also follow this pattern; for example the forest pygmy antelopes, the Royal Antelope *Neotragus pygmaeus* and Bates' Pygmy Antelope *N. batesi* have an eastern relative, the Suni *Nesotragus moschatus*. To merit generic differentiation this separation is clearly of very long standing, revealing a phenomenon with a history that can be measured in millions of years.

Entire groups of animals are wholly or nearly exclusive to one of these regions; notably sengis (Macroscelidae), blesmols or 'mole-rats' (Bathyergidae), rock-hares or the Bat-eared Fox *Otocyon megalotis* in the south-east; forest pangolins (Pholidota), rope squirrels *Funisciurus* and many primate groups in the centre-

west. The list could go on and could easily invoke species, genera and families of reptiles, amphibians, birds and other biota. The exact boundaries of living species have less importance than the implication of a major bifurcation, which reasserts itself at almost every taxonomic level.

The persistence of this pattern suggests that there has been a perennial (but also permeable) divide for both forest and non-forest communities through most of the Cenozoic evolutionary history of African biota. I have argued elsewhere (Kingdon 2003), and summarize shortly, the idea that this divide, in one of its many permutations, was also central to the initial separation between ancestral apes and ancestral hominins. I have also argued elsewhere in this work (Volume II, p. 27) that the Oligocene split between hominoids and cercopithecoids and the Miocene parting between colobines and cercopithecines involved some such geographic polarization.

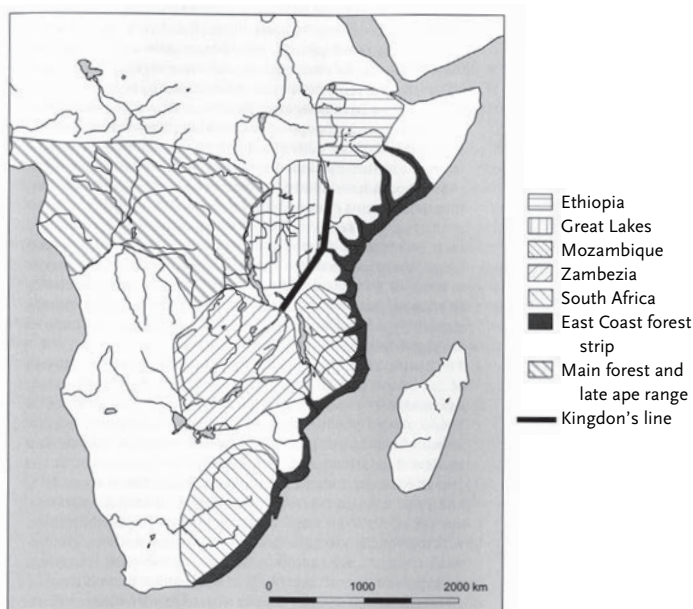
If we return to the starting point, a hypothetical, single primary population with sufficient adaptability to spread very widely (but not into waterless true desert), there are important differences between its centre-western and south-eastern wings that are due to Africa's intrinsic shape and to its tectonic history as well as to climatic and environmental differences. Whether forest-adapted or not, the centre-westerners live within a long but relatively narrow latitudinal belt of mainly humid lowlands with boreal seasonality to influence their life-cycles and breeding. The Atlantic Ocean (with water temperatures that are known to have fluctuated periodically) is the ultimate source of rainfall throughout. Habitats range from near-desert to rainforest with no clear or lasting boundaries between very long east-west strips.

By contrast, the south-easterners live along a north-south axis that can range over as much as 45 degrees of latitude of mainly hilly lands and plateaux with austral seasons and seasonal rainfall (coming off an Indian Ocean that has less labile temperatures). Mountain ranges tend to intercept much of the rain, creating rain shadows and a very varied ecological mosaic. Some of these highlands are Mesozoic, most are post-Oligocene but the region as a whole has been decidedly cooler and drier than in the moist lowlands of the centre-west.

Differences between these two regions go back well beyond the Oligocene and have been very marked for all the period in which mammals have been populating Africa. The climatic and ecological differences would have promoted differentiation within even the most ubiquitous population, but the discontinuities and physical barriers listed above have certainly served to accelerate local adaptation, separate gene pools and define boundaries and sub-boundaries.

Bifurcations upon bifurcations

Ideas about the driving forces behind speciation are subject to a large measure of scientific fashion and, in any case, modes of speciation are, in themselves, diverse (White 1978). Recent years have seen much emphasis on climate-driven 'turnover pulses' and sudden spasms of evolution, supposedly in direct response to changes in climate. Many of the latter have now been shown to have been so numerous as to defy our ability to tie any one climate change to particular evolutionary events. What has been neglected is awareness of sustained, incremental adaptation among



Map of east and central Africa indicating five ecologically discrete hinterlands or river basins inland from the east coast forest strip. Some hinterlands might have sheltered distinct types of hominins and other mammal populations (after Kingdon 2003).

pre-existent taxa to, say, wetter or drier conditions, or to more or less competition, disease or predation in some corner or block of their range. Because the evolutionary products of this bifurcation flow, ebb and change it is tempting to suppose that the sudden appearance of a novel form as a fossil represents a 'pulse'. Such sudden appearances are, instead, an artefact of the pin-prick sampling and semi-arbitrary dispersion of fossil sites in relation to two vast, interacting sub-regions of Africa and still further ecological fragmentation within them.

When new species suddenly appear in a layered bed of fossils it is therefore much more likely that changes in climate have permitted former regional isolates to expand their range than that these apparently 'new' species manifest a sudden evolutionary 'pulse'. It is in this context that the centre-west and south-east divide finds special significance. Each block can be further subdivided and within each such compartment there are evidently further opportunities for bifurcation, even multiplication. For example, the northern and southern ends of the south-eastern block are in separate hemispheres and 40 degrees of latitude apart. Likewise, the westernmost lowlands of the 5000 km-long centre-west block have suffered repeated ecological isolation due to fingers of Saharan aridity periodically probing southwards while its easternmost mountains remained perennially wet. In spite of these and other subdivisions assisting further speciation or subspeciation, the significance and tangible existence of a single major divide in Africa cannot be over-emphasized.

There are many inferences suggesting that 'pre-adapted' populations from one block, or some part of it, are able to spread out from their enclave when conditions favour them or shrink back when events turn against them. For instance, there are many examples of relictual extant fauna and flora that appear to have common and widespread fossil predecessors. Likewise, species that are montane isolates in eastern Africa are less constrained

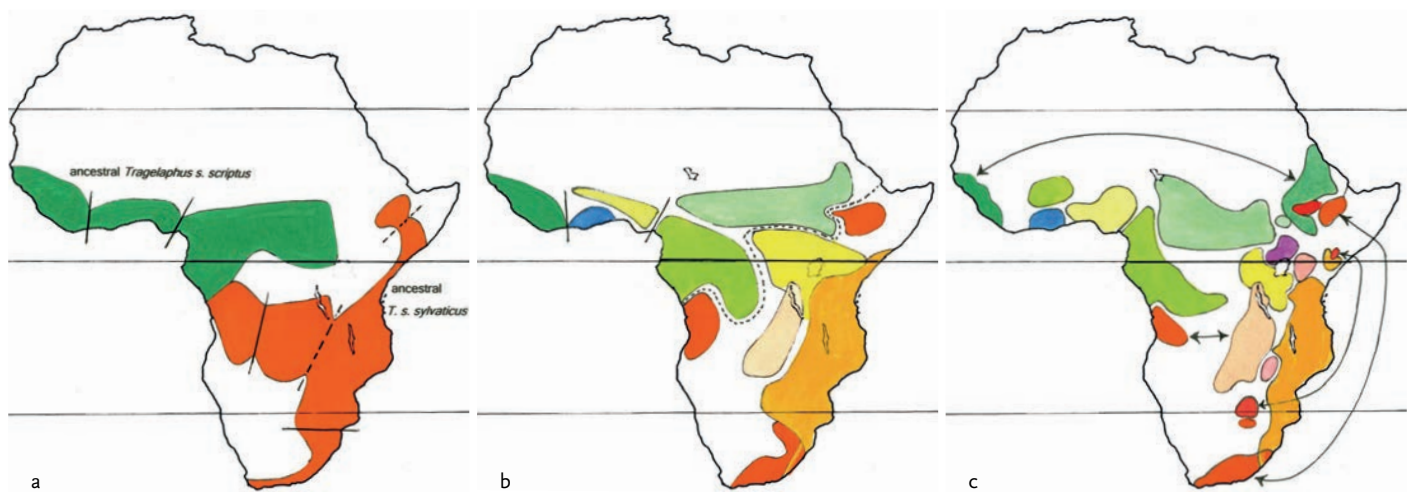
in temperate South Africa, with the clear implication that such species ranged more widely through the south-east during cool, glacial periods. While there are many more dimensions to evolutionary success than mere adaptation to more or less rain or higher/lower temperatures, adaptation to wet/warm and cold/dry polarities is a realistic way of throwing the main mechanisms of evolution into high relief. At its crudest, the centre-west/south-east divide represents, on the massive scale of an entire continent, a geographic and ecological polarization. It need surprise no one that no two species ever coincide exactly in their distribution and that patterns of spread, retreat and further speciation or subspeciation are as varied as there are taxa.

In the past, south-east and centre-west populations have been periodically separated by a barrier that is mainly climatic and geographic. In the context of the present discussion arid habitats and their inhabitants can be regarded as a labile, crude negative interposed between the two blocks. This, of course, debases the inhabitants of that dry corridor, which have also speciated with their own polar centres in the south-west and in the north-eastern Horn of Africa. The dynamics of speciation among these arid or semi-arid adapted species is discussed further in relation to geographic factors in Chapter 3 and climatic ones in Chapter 4. Here it is sufficient to point out that relatively small, but ancient arid foci in the Horn and south-west (and the much larger but more recent Sahara) have expanded and ebbed many times. At each expansion aridity has presented numerous physiological and environmental challenges to animals and plants adapted to more humid habitats and conditions. Periods of aridity have also served to reinforce the isolation of forest communities in more consistently moist enclaves or refugia.

One of the most instructive explorations of incipient speciation, subspeciation and genetic diversification has been provided by a recent study of the Bushbuck *Tragelaphus scriptus* by Moodley & Bruford (2007). The choice of this pan-sub-Saharan species for such a study was apt because it is very unusual in the number of its regional subpopulations, in the extent of its range, in its relatively sedentary habits and in its tolerance of a wide spectrum of temperatures, rainfalls, altitudes and habitats, including forest. The Bushbuck's 'generalist' tragelaphine niche and relatively small body size (about 50 kg) corresponds to an optimum found in many of the most successful species of antelopes and deer, world-wide.

The gross partitioning between what is commonly called the 'harnessed' bushbuck (*scriptus* type) in the centre-west and the 'sylvan' bushbuck (*sylvaticus* type) in the south-east has been known and discussed for a century or more, but Moodley & Bruford's revelation of the very complicated patterns of affinity within each of these two polar mega-populations is unprecedented. Gene profiles reveal that some of these discrete subpopulations must have retreated into small enclaves while others seem to have expanded their ranges. See-sawing interactions along the boundaries between *scriptus* and *sylvaticus* types imply that boundaries are mobile, with environmental changes favouring, say, some types of Sahelian *scriptus* at one time, or particular East African *sylvaticus* groups at another.

This study is complicated by uncertain genetic affinities between bushbuck and the south-eastern Nyala *T. angasi* and centre-western Bongo *T. eurycerus*, but it has demonstrated that terminal level haplogroups have diversified most at the centre of each mega-



a. Hypothetical map of ancestral *Tragelaphus s. scriptus* and ancestral *T. s. sylvaticus*.
 b. Hypothetical map of later subdivisions of both ancestral *Tragelaphus scriptus* populations (based on data extrapolated from Moodley & Bruford 2007).
 c. Distribution of 23 *T. scriptus* haplogroups identified by Moodley & Bruford (2007).

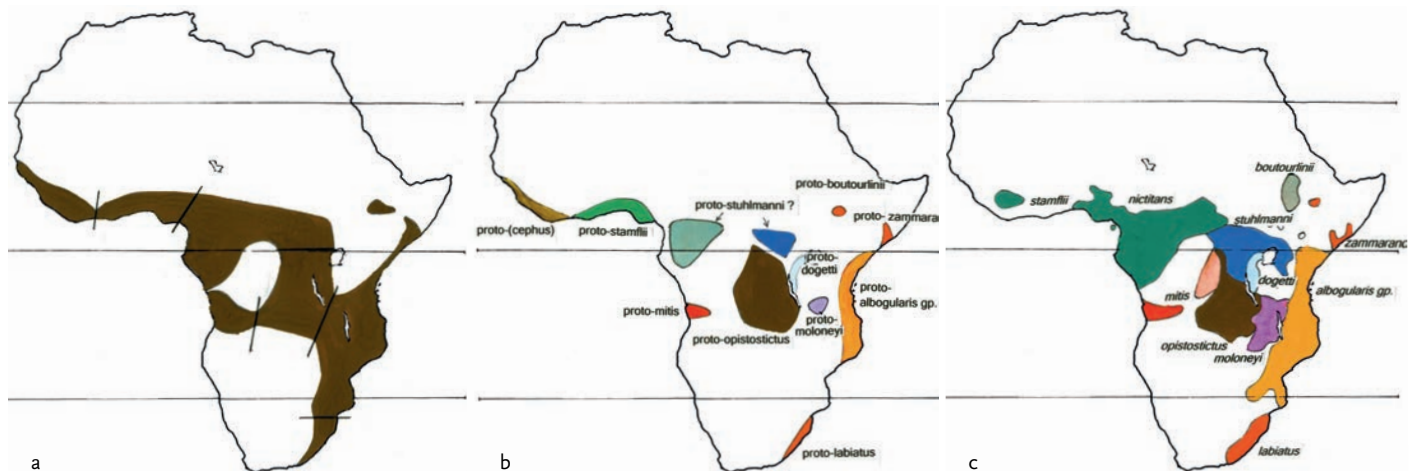
population's range while, very significantly, the outermost extremities of the Bushbuck's overall range shelter basal haplogroups that are indicative of a more generalized ancestral state. This is because the haplotypes most isolated from later genetic contact have the least complex history and so tend to retain more of the oldest genetic signature. Thus the most westerly of all the *scriptus* haplotypes is effectively closest to the ancestral type. On the south-eastern half of the continent conservative *sylvaticus* haplotypes occur in three outlying distributional 'polyps', namely in the extreme south, the extreme north-east and the extreme north-west of *sylvaticus* range (see diagrammatic maps of this process above).

Regional diversification of Bushbuck populations is of intrinsic interest because it exemplifies and holds within it the potential for even further speciation. A mega-bifurcation can lead on to still further bifurcations and then still more. This is the process that has generated the extraordinary diversity of species in Africa.

The Bushbuck pattern closely resembles what seems to have happened in other widespread groups. Most notable in this regard

is a pattern of morphological resemblances and differences among Gentle Monkeys *Cercopithecus (nictitans)* group, which awaits an ongoing comparative genetic study that will, hopefully, be comparable with that of the Bushbuck. In this complex of widely scattered regional populations distinctions between full species, incipient species, subspecies and regional demes are particularly difficult to draw: a radiation that graphically illustrates evolution as a very finely tuned, on-going process. It is already clear that it was an earlier, smaller-bodied outlier of this group that gave rise to the *C. (cephus)* radiation. Other populations now subsumed within the *C. (nictitans)* group may eventually be shown to be scarcely less distinct.

Recent molecular studies imply that the species that most closely links the *C. (nictitans)* group to the rest of the *Cercopithecus* guenon radiation is the little-known and secretive Owl-faced Monkey *C. hamlyni*, living mainly in the eastern Congo basin (Dutrillaux *et al.* 1988, Tosi *et al.* 2005). This has several interesting implications. One is confirmation that *C. (nictitans)* was likely to have shared a common origin in the Congo basin forests. Another implication is that *C.*



a. Hypothetical map of common ancestral population to the *Cercopithecus (nictitans)* and *C. (cephus)* radiations.
 b. Hypothetical map of later subdivisions of above population.
 c. Distribution of currently recognized populations in the *C. (nictitans)* group.

hamlyni, having continued to refine local species-specific adaptations within its area of origin, might represent some sort of modified survivor of a previous common ancestor linking *C. (nictitans)* with the rest of the guenon radiation.

To complicate matters, there may be yet further layers of relictual populations left over from the spread of *C. (nictitans)* over a range that now stretches very far from its place of origin. For example, there are reasons to suppose that, after *C. hamlyni*, another layer of relict populations might be represented by the swamp-forest-loving *C. (n.) m. opistostictus* and *C. (n.) m. heymsi*. Both are currently classed as subspecies of *C. (nictitans) mitis* but a difference in chromosome count in the former (Dutrillaux *et al.* 1982), if confirmed, might merit recognition as a separate species.

The evolutionary layering of populations does not stop here. Like the Bushbuck, Gentle Monkeys have centre-western populations (*C. (n.) nictitans* and *C. (n.) mitis*) and a south-eastern complex (commonly grouped under *C. (n.) albogularis*). Also like the Bushbuck, Gentle Monkeys seem to have reached out, at some very early stage of their expansion, to the furthestmost extremities of forest. Thus *C. (n.) n. stamflii*, from West Africa, *C. (n.) a. labiatus*, from South Africa, *C. (n.) boutourlini* from Ethiopia and the dwarfed *C. (n.) a. zammaranoi* from the Juba R. in Somalia, closely resemble the Bushbuck pattern in that all these four extremities probably shelter more conservative populations than those from more central regions. These relictual populations out on the margins of *C. (nictitans)* overall range imply a genetic conservatism that must qualify any attempt to cluster taxa on purely geographic criteria.

New species emerge from changes in size: dwarfing

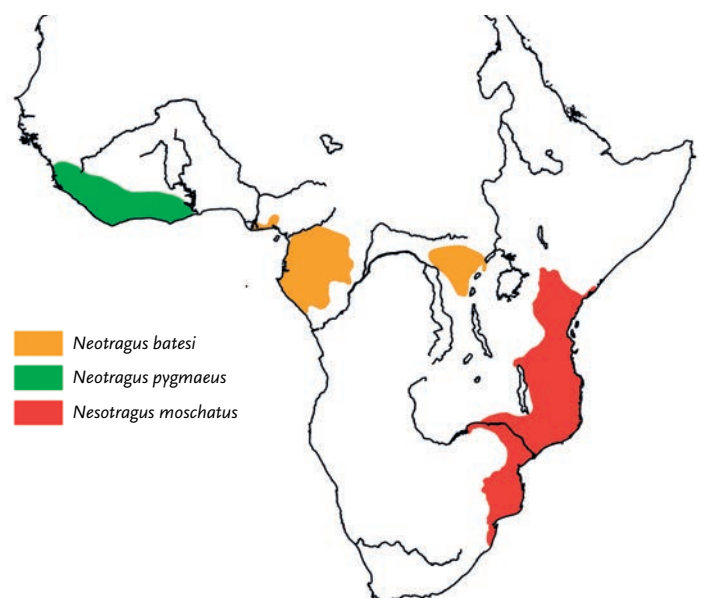
Among functional traits that are selected for in marginal areas during hard times is diminished body size. Large bodies can be a severe constraint under such conditions, and in the case of Gentle Monkeys it seems likely that a trend towards dwarfing in far western Africa resulted in emergence of the most recently evolved of all forest monkeys, members of the *C. (cephus)* group, which are also among the smallest. Regional diversification of Gentle Monkeys is of intrinsic interest but hypothetical dwarfing in the extreme west and demonstrable dwarfing in the extreme north-east serve to illustrate that even within a single species, or species-group, a potential exists for smaller bodied animals to make their own radiations. For the *C. (cephus)* group, small size opened new opportunities and the radiation of some ten regional populations is discussed in the *C. (cephus)* species-group profile in Volume II. Suffice here to point out that the extraordinary diversity of facial patterns in this group would seem to be the product of population fragmentation taking place, due to an accident of forest contraction at the very moment when selection for visual distinctiveness was at its most critical (Kingdon 1980). Such elaborations of facial patterns not only seem to have a large element of arbitrariness in their designs, their very diversity seems to be largely an accident of timing.

Selection for dwarfing is best known on islands; rapid and drastic reductions in the size of elephants have been well documented on Mediterranean islands such as Sicily, Cyprus and Malta. In such circumstances it has been plausibly argued that small individuals survive best because resources are less consistently available in

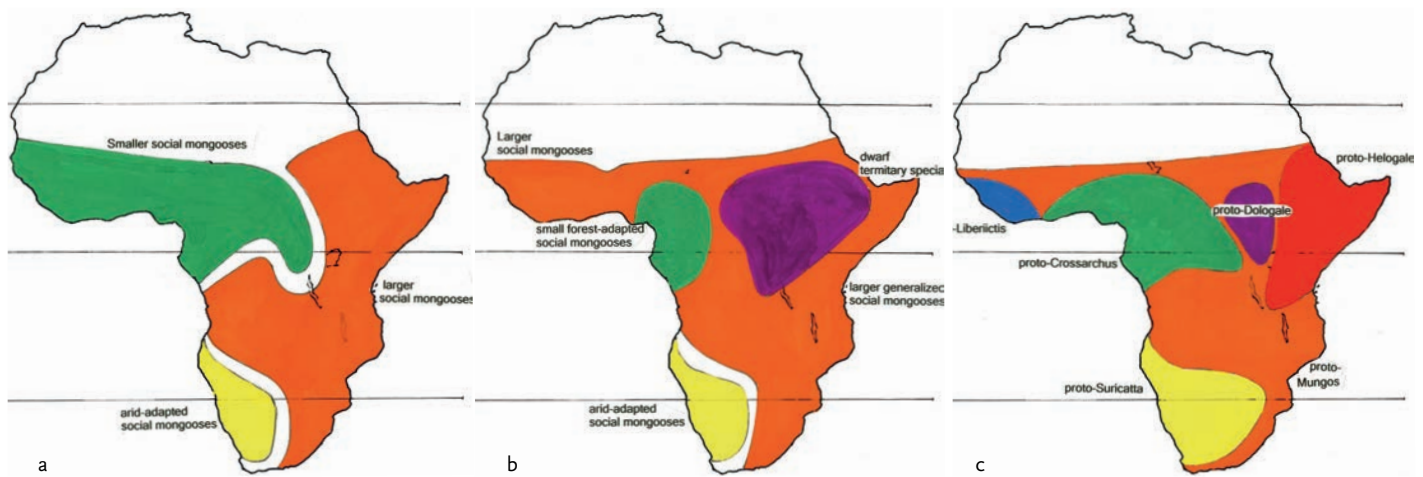
bulk and/or because smaller animals can sustain themselves best on small home-ranges. Dwarfing is one manifestation of a more general characteristic, which is commonly summarized as character displacement (Hutchinson 1959). All members of the forest guenon genus *Cercopithecus* exemplify displaced variations on a common guenon template; the effect has been to pack many more monkey species into the African forest canopy. Variables other than size concern growth patterns, dietary preferences, physiological tolerance levels, relative speed of movement or alertness and other less obvious differences. The range of sizes among arboreal forest monkeys tends to be strongly constrained and narrowed by the weight-bearing tolerances of canopy and other branches.

Size can alter functional behaviour and social signals. For example, among bats that emit ultrasonic bursts of sound through their nostrils it has been shown that the frequency of pulses correlates with body size (actually nose-size as expressed in the distance between the two nostril emitters). Thus Horseshoe Bats, Rhinolophidae, produce CF wavelengths that measure twice the distance between their nostrils (Mohres 1953). It seems improbable that living bats would preserve evidence for a phylogenetic size differentiation along centre-western or south-eastern axes but there are differently sized species of *Rhinolophus* that do conform with such geography and this perspective might merit further examination.

Reduced body size and the centre-west/south-eastern divide are both involved in the evolution of duikers (see Volume VI). The Suni has already been mentioned as a typical south-easterner while its even more diminutive relatives, dwarf antelopes of the genus *Neotragus* are centre-westerners, inhabiting parts of the rainforest belt. In this instance it was probably forest shade that indirectly first induced extreme dwarfing through the scarcity of young foliage on the forest floor. A longer-term evolutionary effect was to entrench tiny bovids in a habitat where a very significant dietary change could take place. Such surviving dwarfs illustrate a dynamic that also played out in the evolution of duikers. It is understandable that leaf-eating antelopes in a forest should become restricted to the rare spots



Distribution map of Suni *Neotragus moschatatus* with the ranges of its nearest relatives in the forest (after Kingdon 1997).



a. Hypothetical map of a common ancestral population of social mongooses separating into three major divisions.
 b. Hypothetical map of further regional and ecological specialization among social mongoose populations.
 c. Schematic map of postulated regional origins for six genera of social mongooses.

where ground-level herbage is fed by sunlight penetrating the canopy and that very small bodies are more easily sustained by relatively scarce and patchily distributed food. However, the most abundant fresh green growth on the forest floor consists of fragments dropped by arboreal animals in the canopy. Scavenging for these rather than browsing directly off plants would have introduced the very earliest proto-duikers to a mode of feeding that was mainly dependent on guilds of canopy animals. Because fallen fruits and other products of the canopy are both more abundant and more nutritious than sun-starved leaves, selection would have favoured those miniature antelopes that became more frugivorous or reliant on dropped plant-parts. The extant spectrum of duikers is a living demonstration that appropriate behavioural, physiological and anatomical adjustment developed by small increments. Once such adjustments to frugivory and omnivory had been made these very small antelopes could then become larger and the course of their radiation is followed in some detail in the appropriate profiles.

Another example of dwarfing involves a phylogenetic decline in size among several genera of social mongooses. Other than living in places with both predators and abundant bolt-holes, sociality in mongooses has no other obvious ecological correlates and various authors (Rasa 1977, Rood 1983, 1990, Macdonald & Nel 1986, Clutton-Brock *et al.* 1999) have demonstrated that social living has, indeed, evolved in response to selection by predators, especially raptors. Attrition in social mongooses tends to be severe (Creel 1996) and social mongooses produce large numbers of young and expend much energy in maximizing reproduction, sharing care for the young and sharing socially beneficial vigilance. Apart from alarm calls and flight, anti-predator behaviour includes 'rescues' and coordinated responses to predators (Rood 1975, 1986, Kingdon 1977).

Recent molecular studies have shown that *Mungos*, the genus to which the common and widespread Banded Mongoose *M. mungo* belongs, has its closest affinities with the rainforest-adapted and apparently relictual Liberian Mongoose *Liberiictis kuhni* (Veron *et al.* 2004). Both these long-clawed excavator-foragers average about 400 mm in head-and-body length and weigh about 2 kg and they live in complex social groups (Booth 1960, Ewer 1973, Rood 1975, 1986, Kingdon 1977).

According to Veron *et al.* (2004), the common ancestor of the *Mungos*–*Liberiictis* lineage also gave rise to another species of social mongoose, which was probably smaller and had a very wide range. Its descendants split along the classic centre-west/south-east divide: *Crossarchus* became forest animals while the Dwarf Mongoose *Helogale parvula* occupied the south-east. The centre-westerners have several resemblances with the Liberian Mongoose but have head-and-body lengths of about 350 mm and weigh about 1 kg; adult *Helogale* measure about 250 mm and weigh 300 g – real dwarfs!

The point has been made that social mongooses, as a class, are not tied to specific habitats, so the common ancestor of *Crossarchus* and *Helogale*, like the Bushbuck, can be predicted to have been a single very wide-ranging species. It is likely that the relict offshoot of an early ancestor to *Helogale* (and closer to its shared ancestry with *Crossarchus*) survives in the form of yet another genus, the rare central African Pousargues' Mongoose *Dologale dybowskii*. Intermediate between *Crossarchus* and *Helogale* in size and general morphology, this species also bridges both regions geographically and ecologically. Very significantly, the few observations of this species suggest a close association with termitaries (Hayman 1936, Kingdon 1977). This observation is relevant to the apparent paradox that *Helogale parvula*, the species with the greatest exposure to predators, is the smallest, but Rasa (1977), Creel (1996) and others have pointed out that there are special ecological and behavioural reasons for this. Even more than other social mongooses, *Helogale parvula* is assailed by very many predators: the profile in this work names 13 as recorded instances, but there are many more, including raptors, reptiles and larger carnivores, and escaping them calls for vigilance, a quick response to warning cries and speedy decamp to a nearby refuge. Their dispersal through the landscape correlates closely with a high density of termitaries. Of several constraints on size, the major one is probably the need to fit or flit down narrow termitary ventilation chimneys (serving as ubiquitous bolt-holes as well as social dens). In other habitats, notably in the forests of the centre-west, refuges come in many forms and sizes whereas ventilation shafts have quite narrow ranges of variance. If termitary chimneys are the evolutionary determinant of *Helogale* body size their pre-existence was essential

to the evolution of dwarfing. In effect evolution of the two *Helogale* species, and their dwarfing, were tied to the behaviour and activity of other social animals, termites. Termites provided essential but highly structured refuges from the raptors and carnivores that would otherwise have exterminated the mongooses. The pre-existence of other animals and the ecological impact of their behaviours is a much neglected topic in evolutionary biology. Wherever they occur in Africa termite-mounds are an integral part of the landscape, while the termites themselves possibly represent the largest biomass of any single class of animal, but, in the past, elephants must have run them a close second.

Pioneers in gigantism: afrotherian elephants – elephant activity defines habitats

It is well known that the first motor roads in Africa, as well as countless traditional tracks, followed the courses of elephant paths. Even today, in the few areas where elephants survive in landscapes that are still friendly to them, there are networks of paths that clearly express the logic of elephant needs. Over tens of thousands of years paths to water and to separate dry and wet season pastures have followed subtleties of relief as expertly as ever did any Roman engineer. Traditional elephant paths are familiar landmarks in such landscapes, as are 'stations', to which many generations of elephants have returned, again and again, for social or operative reasons, or as broadcast/reception posts on strategic ridges or hilltops.

In the evolution of hominids, especially flesh-footed, soft-toed hominins, elephant paths were probably as important to their survival as termitary chimneys have been for the evolution of dwarf mongooses. The association between elephants and specific localities is still expressed in numerous place-names, Njoro, Njoko, Ndoto, Embu, Mbungu, Nyamandhlovu, to name but a few, (even in Europe titles such as Kaiser and Tsar are said to ultimately derive from an ancient North African name for the elephant, *Casius*). Another respect in which elephant species, living and extinct, are likely to have shaped the lives of other mammals is their 'gardening' of the landscape. Many, probably most large plant species are unable to survive sustained and heavy browsing by elephants. Some have evolved chemical or mechanical deterrents in their leaves, bark or trunks, others, like several *Acacia* species, have developed a tolerance for very severe wounding and can re-sprout from stumps or mangled coppicing. The long-term effects of such 'gardening' were to limit the range of available plant species in elephant-dominated landscapes, creating communities of plants and animals that were much less diverse than they might otherwise have been. This might have been especially important for hominins because plant impoverishment greatly reduces the scope for both frugivorous and folivorous primates, reducing both competition and susceptibility to primate diseases in hominins. Species such as browse rhinos *Diceros bicornis* have been observed to decline under the influence of elephants steadily degrading the woody vegetation on which the rhinos were dependent. Among the effects, very numerous elephants would have opened up the vegetation and fast-growing grasses and herbs would have been favoured over vulnerable trees and bushes. There can be

little doubt that many grazing antelopes and rodents were among the beneficiaries and it is possible that the southward expansion, perhaps even speciation, of arid-adapted antelopes, such as Thomson's Gazelle *Eudorcas thomsonii* and those of the Grant's Gazelle *Nanger (granti)* complex might have been assisted by the modification of such habitats by past populations of proboscids.

It has been widely observed that when the impact of numerous elephants is/was augmented by fire the trend towards open grassland accelerates. Elephants alone, or fire alone may be insufficient to destroy some very resistant woodland types, but when both combine grassland tends to become progressively more open. Given that humans and their ancestors are likely to have been the major setters of fires certain combinations of past behaviour in *Homo* and *Loxodonta* probably shaped the ecology of substantial areas of Africa and may even have influenced the very recent evolution of the Hartbeest *Alcelaphus* as the dominant grassland antelope species. The presence of elephants can also deter predators so that much smaller animals take advantage of elephant herds at, say, waterholes, to gain access to water. In all such examples it is not always possible to separate opportunism from the potential for co-evolution, but the important point is that the gigantic size of elephants has undeniably helped shape the conditions under which other plants and animals have evolved, including human ancestors.

Mammalian radiations within Africa

When Eurasian immigrants entered Africa they commonly brought with them a heritage of adaptation to temperate climates and ecotypes. That legacy would sometimes have put constraints upon expansion, but where the immigrant had decisive advantages over established populations it would eventually widen its range and diversify. Most immigrants probably began by favouring the habitats that most resembled those of their region of origin or of the bridging corridor that allowed them into Africa. As a consequence, drier, cooler zones, especially in uplands or on mountains could be expected to (and demonstrably do) shelter some of the more conservative members of immigrant lineages. As remarked earlier, highlands also harbour species that flourished and probably had wider ranges during earlier periods of cooler climate.

For mammal immigrants that had successfully entered northern Africa and moved south, a significant challenge was presented by the continent's equatorial girdle, the single largest area of equatorial habitat on earth. The difficulties involved were far from trivial: there were established competitors and predators of which the immigrant had no evolutionary experience and the environment was dominated and shaped by large numbers of giant animals, notably endemic species of elephants. There were also physiological and behavioural challenges for animals entering moist, hot habitats from relatively dry cool ones.

Greater than any other obstacle was the existence of numerous tropical diseases. Disease is a primary agent in evolution so the relative susceptibility of mammals to Africa-specific (or extra-African) diseases, will, undoubtedly, become a very significant topic for research in the future. When immigrant populations encountered the habitats of equatorial Africa they met diseases against which their recent evolutionary history offered no defence. Both evolutionary

and biogeographic patterns in Africa are likely to have cryptic subtexts in which disease has played a critical, if not central role (W.D. Hamilton, pers. comm.).

The tragelaphine example

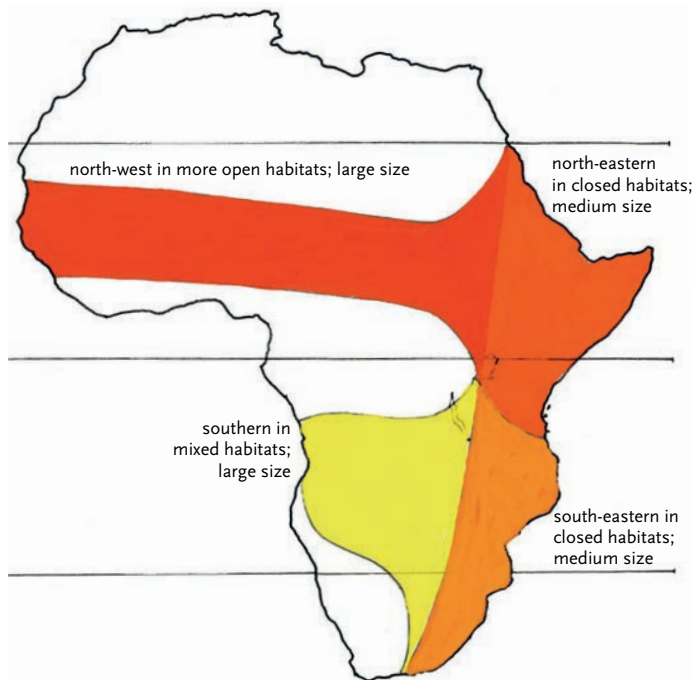
To illustrate the dynamics of adapting to novel habitats, take the relatives of the Bushbuck, the Tragelaphini or spiral-horned antelopes. Now widespread and diverse in sub-Saharan Africa, they are known to have speciated from a common ancestor that left Eurasia some 14 mya. A recent molecular study (Willows-Munro *et al.* 2005) has provided a genealogical tree that offers clues to the sequences and eco-climatic determinants behind this very successful radiation and some suggestive correspondences between the conservativeness or innovative adaptedness of species and their eco-geographic distribution. Of this distinctive group of mainly browsing bovinines, two very similar species, the Nyala *Tragelaphus angasii* and the Lesser Kudu *T. imberbis*, are close to the stem of the entire radiation. Extrapolating from tragelaphine morphology and fossils we can infer that these two are probably more like their Asiatic ancestor than any other extant species. Their separation, in dry enclaves at opposite ends of eastern Africa, is probably of long standing but thicket-dwelling and leaf-browsing plus, perhaps, their strongly residential habits, are likely to be common, conservative retentions. Taken together, this closely related pair can be regarded as contemporary relicts still occupying favoured pockets of a once more extensive south-eastern range.

Other tragelaphines have moved further from their ancestral niche and, of these, the species that derive most directly from their common ancestor are the Greater Kudu *T. strepsiceros* and the Mountain Nyala or Gedemsa *T. buxtoni*. An appreciable increase in size is apparent in these two species and fossil relatives of the Greater Kudu were

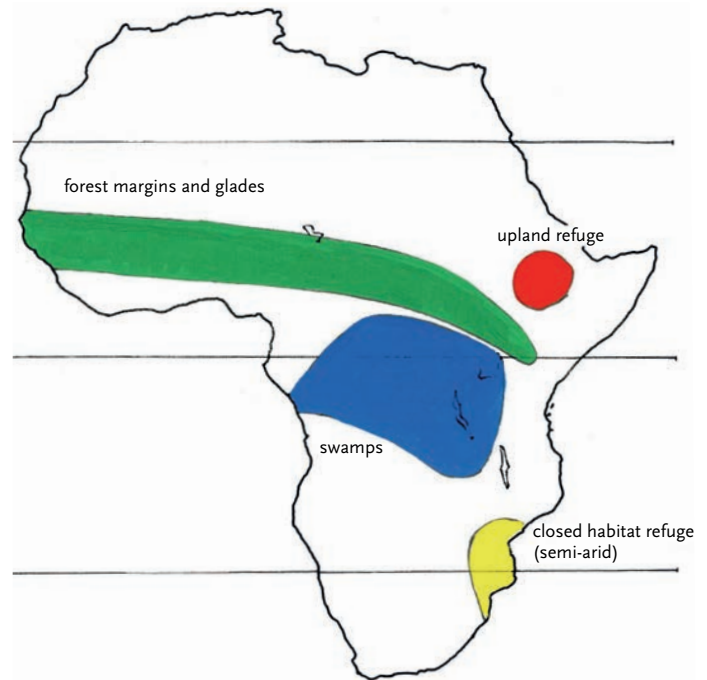
bigger still. This trend towards larger size can be correlated with the development of more mobility, larger ranges and a wholesale shift out of closed woody environments. It is a trend that culminates in the two species of eland, which can weigh close to one ton, lead nomadic lives in savannas or relatively open woodlands and have already provided an illustration of the centre-west/south-east divide (for further discussion see the species and genus profiles and Kingdon 1982, Matthee & Davis 2001 and Willows-Monro *et al.* 2005).

The more conservative tragelaphines, Lesser Kudu and Nyala, conform to the expectation that early descendants of incoming immigrants prefer the drier and sometimes cooler habitats of eastern and southern Africa. Overcoming the adaptive challenges of lower, warmer and wetter habitats would have taken more time. The spatial dimension of such an expansion had to be westwards along the centre-western axis and this is what two apparently more advanced species did. Willows-Munro *et al.* (2005) identified the Bongo *T. eurycerus* and Sitatunga *T. speikii* as members of a tragelaphine 'closed forest group' and confirmed that the two are particularly closely related (for example they produce fertile hybrid offspring in captivity). Although their distribution ranges overlap extensively, the two species have differentiated both morphologically and ecologically in substantial and very significant ways (see the species profiles).

Today the shaggy Sitatunga inhabits deep swamps, most notably those in the forests of the Congo Basin, and it has evolved long thin legs and splayed hooves to aid it in walking over mud and compacted vegetation in search of herbaceous and fresh leafy growth. The ancestors of the Sitatunga were unlikely to have moved into such habitats 'voluntarily'. Instead, like the Dwarf Mongoose's reliance on termitaries, swamp or swamp forest would have been adopted by relatively slow, defenceless animals as a refuge from predators:



Map 1. Schematic map of adaptive trends in early tragelaphines to Boreal/Austral, drier/wetter, more open/closed environments. Note larger body sizes in drier west (retained by *Tragelaphus derbianus* in N-W, *T. strepsiceros* in S-W); medium size in eastern thickets (retained by *T. imberbis* in N-E, *T. angasii* in S-E).



Map 2. Schematic map of adaptive trends in later tragelaphines to: 1. forest margins and glades along northern margins of forest belt (retained by *Tragelaphus eurycerus*); 2. swamps in or near forest (retained by *T. speikii*, especially south and east of forest belt).

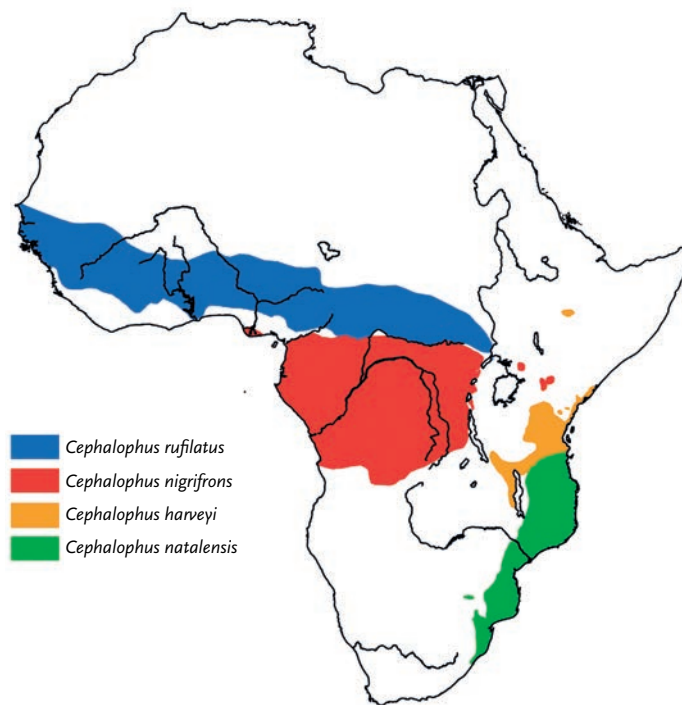
selection through predator-evasion. Only slowly, step by step, have swamps become a permanent, preferred and exclusive habitat and the Sitatunga's long-term survival must have been facilitated by an important property of swamps. They are a relatively predictable environment and persist because they are dependent more on impeded drainage than on local climate. In a vast, relatively shallow river basin where many tributaries flow, sluggishly, from east to west, swamps stretch, as an enduring and predictable habitat, from central Africa to the Atlantic. While extreme climatic fluctuations had the capacity to eliminate entire communities over very extensive areas, and probably did, swamp communities still survived wherever the drainage profile was right.

Another type of ecological continuity exists in the same central African forests. Ground-level growth needs sunlight and the agencies that fell forest trees to produce fresh new plant growth are predictable. Trees fall for many reasons and they create 'chablis' or temporary clearings that attract browsing animals. These open areas are rarest and most temporary in the areas of highest rainfall; they are commonest on or close to forest margins, where elephants and fires knock the forest back, or beside impervious substrates where trees find it harder to grow. Bongos *T. eurycerus* have learned to exploit ephemeral but very nutritious sources of new growth around forest clearings and along forest margins. However rich they are at any one time, such resources are unpredictable and they require exceptional mobility of their consumers. In the process of acquiring just such mobility, the Bongo has modified both its behaviour and its morphology, some of which parallel strategies adopted by elands (for which consult the species profiles).

The adaptive shifts by ancestral sitatungas and bongos into specialized forest subtypes therefore seem to have taken place along identifiable ecological (and latitudinally aligned) gradients. One has taken place at the wettest end of the catena while the other follows 'forest edges' or, more generally, 'the forests' edge'. The common ancestor of the Bongo and Sitatunga probably resembled the extinct, but formerly widespread *T. nakuae*, and molecular trees suggest that the Bushbuck, which currently occupies the 'generalist' tragelaphine niche, has derived from the same stock.

It is interesting that two duikers have followed a similar trajectory to the Sitatunga/Bongo bifurcation in exactly the same region. The splay-hooved Black-fronted Duiker *Cephalophus nigrifrons* favours Congo Basin swamps while its closest relative, the 'edge-loving' Red-flanked Duiker *C. rufilatus* prefers secondary growth along the northern margins of the same river catchment. Both species occupy the rich, complex forests of the Congo Basin where the resources available to duikers are partitioned out between multiple species and both are classic centre-westerners. As with the tragelaphine Bongo/Sitatunga pair, the genes of *nigrifrons/rufilatus* suggest they are among the most recently evolved species in their group and in both instances, only a less specialized common ancestor could have given rise to such contrasting life-styles. Their earlier origins conform with the centre-west/south-east model in that their known closest relatives are the generalized, non-specialist (and therefore more conservative) Natal/Harvey's duiker complex, *C. natalensis* and *C. harveyi*, which live in the patchy, impoverished forests of south-eastern Africa.

Tracing the origins as well as the fate of more generalized ancestors is central to understanding how adaptive niches proliferate in African habitats (particularly when the adaptor has immigrant ancestry).



Eco-geographic speciation in duikers: *Cephalophus nigrifrons/rufilatus* in west; *Cephalophus harveyi/natalensis* in south-east.

Recent immigrants and how they fare in Africa

The most recent arrivals can be identified by their close affinity with relatives in Eurasia. For example, the (Barbary) Red Deer *Cervus elaphus* has been present in north-west Africa for less than a million years, likewise, various rodents such as the Long-tailed Field Mouse *Apodemus sylvaticus*, Garden Dormice *Eliomys* spp., the Four-toed Jerboa *Allactaga tetradactyla* and some Asian gerbils (Gerbillinae), the Palestine mole-rat *Nannospalax ehrenbergi* and the Red Fox *Vulpes vulpes* are all Eurasian species with marginal extensions of range into northern Africa. The polecat and two species of weasels (all *Mustela* spp.) are also recent arrivals that have failed to penetrate beyond the northern fringes of the Sahara, essentially outliers of species that are widespread and successful in Eurasia.

Eurasian immigrants that have yet to push their frontiers very far south are the Rhizomyidae (root-rats), mainly a Himalayan and South-East Asian group. Their African representative, *Tachyoryctes*, has speciated into a variety of forms and is locally very successful and abundant yet only known at present from the upper reaches of some north-eastern African uplands. One constraint may be their own recent Eurasian origins; another inhibition to expansion might be the presence of competitors, in this case from an Africa-evolved equivalent, the blesmols, Bathyergidae, which are known to be a very ancient African 'mole-rat' lineage.

A corollary to the fortunes of immigrants was their impact on established species and communities. Each new incursion introduced new competitive challenges and, in many instances, new predators. A long succession of immigrant carnivores presented challenges to all but the largest mammals as Eurasian herpestids, mustelids, ursids, viverrids, felids and finally canids found their way into Africa. Here were new fields for their particular, often highly specialized, predatory

talents, so, with more excavation of dated fossil mammal assemblages, we can expect to see the rise and fall of both predators and their prey documented in increasing detail. While canids, in particular, were likely to have hit all those species that were vulnerable to such fast and intelligent predators, not all canids were a universal success.

All canids in Africa have relatively shallow roots in the continent but the Ethiopian Wolf *Canis simensis* may have the youngest pedigree of all because its closest affinities have been ascribed to Eurasian wolves and its arrival can be linked with one or other of the more recent glacial periods. It remains restricted to tundra-like habitats on the highest reaches of the Ethiopian Dome. Other immigrants with unequivocally northern temperate roots have managed to establish enclaves in the extreme south. These include the southern Cape Fox *Vulpes chama*, with close relatives in Eurasia and North Africa. Both these last examples emphasize how forbidding the equatorial region can be for northern-adapted mammals, yet other mammal lineages have eventually succeeded in adapting to the diverse habitats of tropical Africa, many of them emphatically different from anything in neighbouring parts of Eurasia. The restriction of particular species to identifiable vegetation types encourages the assumption that the primary influence on adaptation is environmental. In the proximate sense this may be true but it can be demonstrated that the technique that an established lineage brings to the task of making a living is decisive in its success. For example, Leopards *Panthera pardus* are successful over a wide spectrum of habitats and their ability to over-ride local climatic differences is due to the efficacy of their generalized predatory habits. Regardless of where they originated, leopards are no less successful in Africa than in Eurasia.

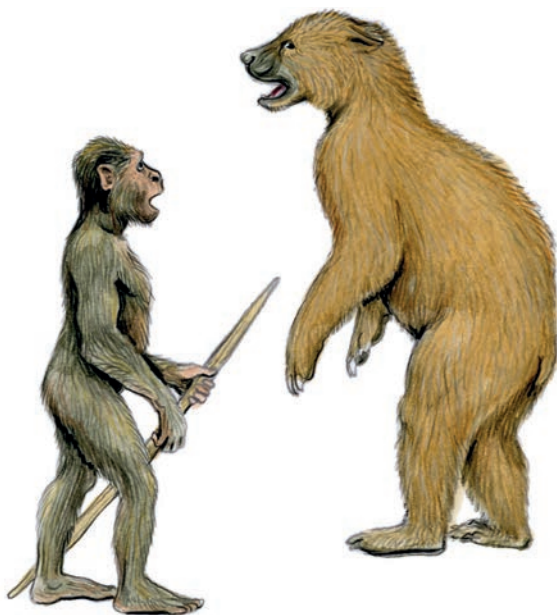
There are some apparent anomalies; bears have been widely successful in both temperate and tropical Eurasia as well as the Americas, but not in Africa. Why? An extinct fossil bear *Indarctos* occurred in Libya and a rather athletic brown bear *Agriotherium africanus* is known from the very early Pliocene in Ethiopia and South Africa. Both north-east and southern Africa have consistently temperate climates but the brevity of bear presence in Africa correlates with, and could have much to do with, the emergent

radiation of bipedal apes or hominins in the same areas. Fossil hominins seem to have particularly favoured these cooler regions and, as relatively large omnivores, they were already well established in Africa at the time of these bear invasions. It is therefore plausible that hominins and bears shared similar dietary and climatic tastes, implying that ecological overlap between them was substantial and led to the bears being eventually out-competed by hominins.

The Ethiopian and East African uplands resemble South Africa in being an essentially temperate region, but differ in straddling and extending north of the Equator. In the case of Ethiopia's higher reaches these represented an extreme southern extension of northern glaciated habitats at the time when colder temperatures probed deep into Africa. During northern ice ages any incoming Eurasian invaders would have found upland north-east Africa especially inviting because environments existed there that were broadly comparable with those in the invader's region of origin and also had the virtue of less competition from established mammals. Actual glaciers are inimical to all life, but in the aftermath of extensive glaciation, especially over high upland plateaux, their retreat exposes extensive areas of sterilized, new and 'empty' land. In particular, the higher regions of the Ethiopian Dome became available for animals that could tolerate low temperatures. The example of invading root-rats of the genus *Tachyoryctes* has been mentioned.

Because habitats on the higher reaches of Ethiopia are subject to very distinct climates and are isolated from equivalent habitats both outside and within Africa, many animal and plant populations have speciated there with exceptional rapidity. During glacial maxima the glaciated peaks would have been effectively sterile, but tundra-like belts would have radiated out over all the surrounding mountain belts and piedmonts, creating corridors for cool-adapted species. The more mobile of these colonized other uplands and a few (notably birds such as Wattled Cranes *Grus carunculatus* and bald ibises *Geronticus* spp.) got as far as temperate South Africa. During warmer interglacial periods inter-connecting corridors disappeared, leaving smaller subpopulations of temperate-adapted species stranded on higher massifs. The massifs included Cameroon in the west, Ethiopia in the north-west and a wide scatter of mountains southward down the eastern side of Africa, mainly following the Rift Valley. The flow of species was in both directions, with incomers drifting south and a few southerners drifting north. A well-known example (of a predominantly southern montane species) is the Mountain Reedbuck *Redunca fulvorufula*, which favours dry uplands between about 1500 and 5000 m on mountains as far apart as South Africa, northern Tanzania, Ethiopia and Cameroon.

A long succession of climatic swings, connecting and disconnecting populations, has provided the primary mechanism for local populations to become distinct. As a result most members of these montane communities are likely to have deeply laminated genealogical histories that current research techniques are still unable to untangle. None the less, geographic foci for distinct speciations can be identified. For example, in north-eastern Africa niches for small herbivorous rats are dominated by four closely related 'grass rat' genera, *Arvicanthis*, *Pelomys*, *Mylomys* and *Desmomys*. As entire biota ebbed and flowed up and down the flanks of the vast Ethiopian Dome, 'grass rat' populations must have made opportunistic excursions back and forth from this major region and these pulses from an identifiable focal point must have influenced the evolution of some 15 species of 'grass rats'. A similar north-eastern bias is evident in some of the omnivorous murid genera. Other aspects of these murid radiations are discussed further below.



Hominins and bears – competitors? Extinct African bear *Agriotherium africanus* and Nutcracker Hominin *Paranthropus boisei*.

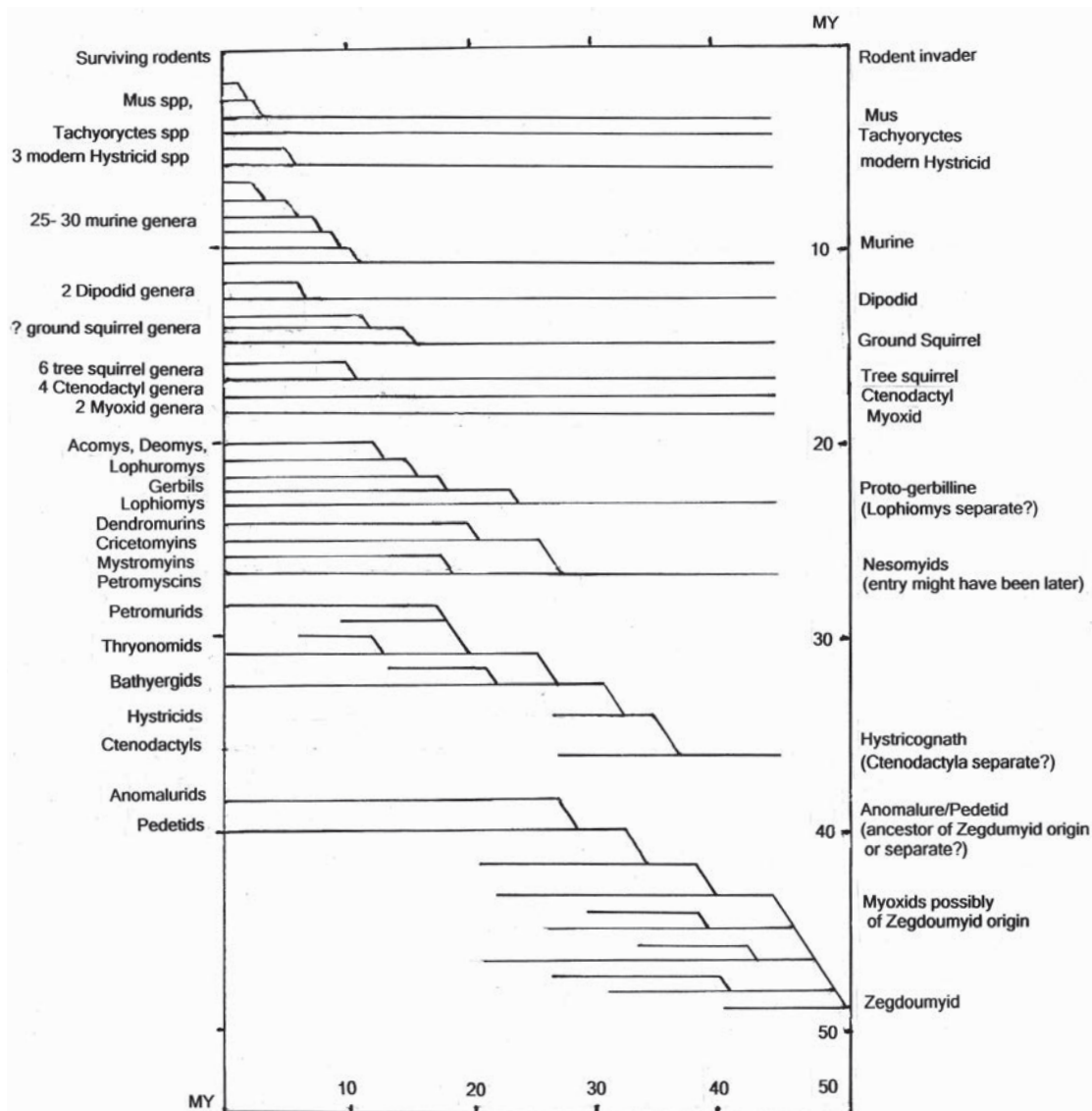
Rodent serial invaders

The special opportunities that Africa offers to incoming mammals and their subsequent fortunes over time can be illustrated with a brief summary of the likely history of rodents on this continent, as reconstructed from fossils and recent molecular studies. There is now persuasive evidence that the rodent fauna of Africa breaks down into about a dozen invasions, of which at least five or six are major groupings, each of which plausibly derives from a single ancestral species and each of which invaded Africa at a different period and then radiated. The groups can be listed (in the sequence of their supposed time of arrival in Africa with dates approximated from Adkins *et al.* 2001, Huchon *et al.* 2002, Montgelard *et al.* 2002, Jansa & Weksler 2004, Steppan *et al.* 2004, and E. Seiffert pers. comm.).

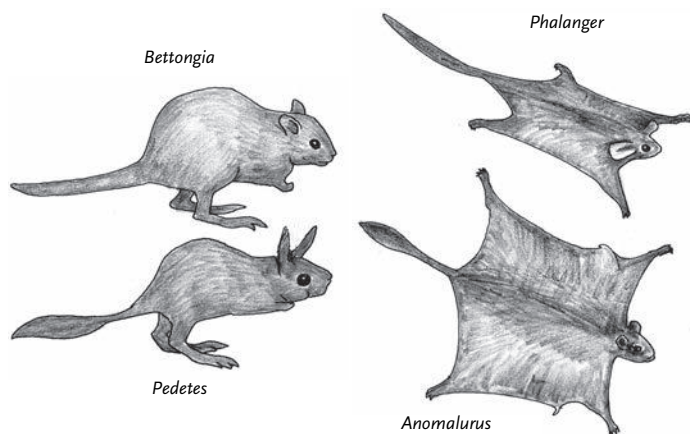
Zegdomyids, possible anomalurid ancestors, are first found fossilized at 50 mya, so a Palaeocene arrival is possible. After a major gap in the fossil record, definitive anomalurids are found in Africa at 37 mya. Protophiomys-grade hystricognathous rodents are also present by 37 mya (at Fayum and Bir el-Ater) and a major radiation of phiomyid and thryonomyid rodents seems to have taken place

between 34 and 29 mya in the Jebel Qatrani Formation (E. Seiffert pers. comm.). Then, after another major gap in the African record, an ancestral Nesomyid arrives, probably between 25 and 27 mya. Soon after this immigration, Proto-Gerbillinae arrive about 21–23 mya and, finally, at about 10.5 mya African murines arrive, to produce the largest of all rodent radiations. In each case, likely arrival would have taken place well before occurrence as fossils.

Given the quite numerous total of immigration events, it is tempting to conclude that opportunities for successful immigration were frequent, easy and involved the incursion of multiple ancestral species each time. Such a conclusion does not square with the fossil evidence and the sheer diversity of descendants deriving from single ancestors implies that such events were rare and generally quite widely spaced. The earliest radiations of rodents took place outside Africa, possibly as early as the late Cretaceous, 66–88 mya (Adkins *et al.* 2001, 2003, Bininda-Emonds *et al.* 2007, Meredith *et al.* 2011). By the Eocene rodents had already split into proto-anomalure, proto-squirrel and proto-porcupine (hystricognath) lineages. The last vestiges of the anomalurid radiation survive in the gliding anomalures (*Anomalurus* and allies) and hopping springhares (*Pedetes*),



Schematic table of procession of rodent radiations from supposed single invaders. Note the late entry of modern hystricids, ctenodactyls and myoxids, possibly preceded by much earlier African radiations (in part after Montgelard *et al.* 2002, Jansa & Weksler 2004, and courtesy of Erik Seiffert, Louise Roth, John Mercer and David Happold.)



Silhouettes of Australian marsupial *Bettongia* and African springhare *Pedetes*, and Australian marsupial *Phalanger* and African anomalure *Anomalurus*, illustrating convergence between the arboreal and terrestrial members of ancient Australian and African taxa.

both of which are herbivorous. (Since the Eocene, Australian arboreal marsupials have evolved gliding forms several times and, at an equally early date, the same phalanger lineage has also given rise to the hopping bettongs (*Bettongia*), so the anomalure–springhare duo are less than unique in the breadth of their ecological span! It is, perhaps, not surprising that subsequent rodent invaders have been unable to supplant such super-specialists, particularly since several anomalurids are of relatively large size for a rodent.

Another rodent radiation, of which five families survive, mostly largish herbivorous specialists, are grouped together in the Ctenohystrica or Nesomyids (Montgelard *et al.* 2002). This disparate group may or may not include desert rock-dwellers, the gundis (Ctenodactylidae) (genetically thought to be the most primitive type); the porcupines (Hystricidae); the subterranean and sometimes eusocial blesmols or African mole-rats (Bathergidae) (Jarvis *et al.* 1994); the flat-skulled Noki (Dassie Rat) *Petromus typicus* (single survivor of a once diverse group, the Petromuridae); and two species of large, valley-grass-eating specialists, cane rats of the family Thryonomyidae.

Fossil precursors of the Noki were unremarkable rodents, yet the only survivor of this once abundant lineage has transformed its anatomy by flattening and widening both body and skull, betraying thereby how strong selection has been for survival in a relatively open, predator-rich terrain, where the only shelter is in narrow horizontal rock crevices. The Noki also illustrates why older lineages are more likely to be found in marginal or demanding, difficult habitats. In such places selection is severe and operates on many fronts so that, over time, a large number of incremental changes are needed to survive predation. Appropriate adaptations then become partly a function of time lived in such habitats. Both the Noki and some Saharan gundis are extremely localized, a restriction that is consistent with long tenancy and the likelihood that their ancestors were long ago out-competed in more generalized rodent niches (with those competitors generally being the descendants of later rodent immigrants).

Another rodent species arrived in Africa, possibly at the end of the Oligocene, this time a small mouse; it was probably somewhat of a climber and adapted, initially, to the relatively benign climatic conditions of the period. If its descendants are anything to judge by,

they were a lot more sluggish in their movements and activity than advanced rodents (such as common rats). The descendants of this mouse penetrated most habitats and, having reached Madagascar, became dominant rodents there, a status that their descendants, the Nesomyinae, still retain. Like other rodent groups that arrived relatively early, their African survivors are now highly specialized, or, in two cases, *Leimacomys* and *Delanymys*, relicts on the verge of natural extinction.

The more successful specialists have taken advantage of small size to become very adept climbers on grass or fine herbage stems (the climbing mice *Dendromus* spp. and allies) or exploiters of tiny crevices in desert rocks (pygmy rock mice *Petromyscus* spp.). The one lineage that has increased in size, the pouched rats or Cricetomyinae, have evolved a unique foraging strategy that seems to compensate for their relatively slow reactions and movements. Very large cheek pouches permit these rats to gather volumes of food at the safest time (generally at night) and return to a secure refuge, where the gatherers may spend many days consuming their store. The largest of these are the celebrated Giant Pouched Rats *Cricetomys* spp. All these rats and mice are mainly vegetarian.

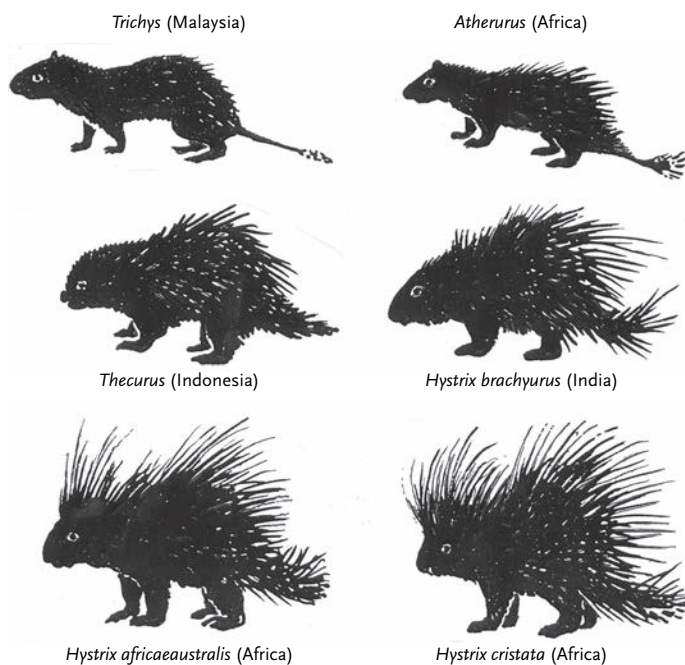


Head of Gambian Giant Pouched Rat *Cricetomys gambianus* showing partially filled cheek-pouches.

Once established in Africa, emigrant Ctenohystrica went on to make a sweepstake colonization of South America, possibly in the late Eocene, where they have been particularly successful, while an early member of the Old World porcupines ‘returned’ to Eurasia and speciated still further. Later in this discussion, I draw attention to the ‘return’ of previously African primate lineages to Asia and then a still later ‘re-return’ to Africa. The porcupines have followed a similar peripatetic history, with the most recent returnees giving rise to the largest, most prickly species, *Hystrix cristata* and *H. africae australis*.

In spite of their spiny armour being so familiar an example of animal defence, the selective transformation of rodent dorsal fur into a barrage of long sharply pointed spikes on porcupines is still astonishing. As a vivid demonstration of selection being driven by predators the entire transformation can still be seen in a comparison of living porcupine species. The least prickly of species remains a relatively nondescript and smallish rodent while the largest is the most fiercely spinous, implying, incidentally, that predators may have been the main constraint on rodents getting very large. Porcupines are not the only rodents to shield themselves with prickles and another example is discussed shortly.

Some time after the Giant Pouched Rat’s ancestor got into Africa, another immigrant arrived, probably about 20–22 mya. This was a



Silhouettes of African and Asian porcupines illustrating a gradient in relative spyness.

mouse that could be described as an unspecialized proto-gerbil. This time the ancestral form was likely to have had more omnivorous habits, was probably already adapted to dry conditions and, again, judging by many of its descendants, was fast and active. Initially, a continental divide might have kept proto-gerbils (Gerbillinae) in Eurasia from the proto-spiny mice (*Acomys* and allies) that are more nearly wholly African. The gerbils have continued to cross back and forth between Eurasia and Africa, a mobility that must be helped by resistance to the heat and drought typical of the north-east African corridors with Asia. Today gerbils are common and very successful inhabitants of all the drier habitats of Africa and western Asia. In their progressive adaptation to the difficulties presented by drought, heat and multiple predators their evolutionary history probably parallels some features of the Noki and pygmy rock mice, but these are more fecund, faster and more generally adaptable rodents.

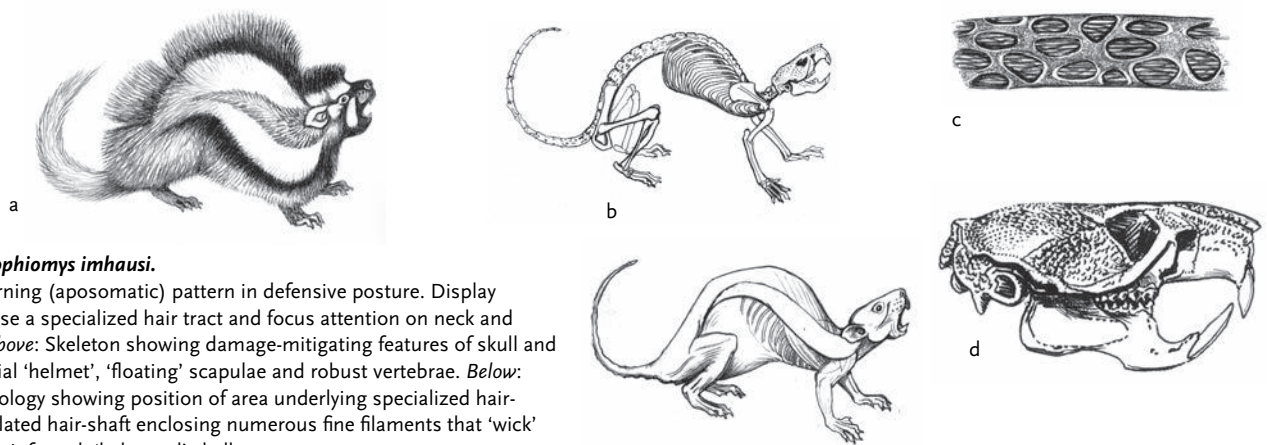
The revelation of a genetic relationship between the short-legged, short-muzzled and mainly arid-adapted spiny mice *Acomys* spp. and the long-legged, long-muzzled and forest-dwelling Link Rat *Deomys ferrugineus* came as a surprise to field biologists (Jansa & Weksler 2004). None the less there are resemblances in the springy, flattened, finely grooved (and probably predator-deterrent) hairs, large, mobile ears, pointed muzzle and adept use of the hands to handle invertebrate foods. Furthermore, the molecular clock suggests more than 12 million years have elapsed since divergence of the spiny mice and Link Rat lineages (Steppan *et al.* 2004). This discovery is of considerable interest because it shows how animals can be totally transformed by the adoption of new niches. In this case a rodent with dry-country gerbil-like ancestors has (in common with some of the brush-furred mice *Lophuromys* spp.) adapted to equatorial forest. Within the forest, *Deomys* ranges through relatively dry areas during the rains but descends into valley bottoms during the dry season, where its long legs are clearly an advantage in shallows and it can hunt invertebrates along swamp-forest margins.

The food resources in this rather linear habitat were clearly the primary incentive for this rodent's shift into forest. At the overall landscape level, many swamps dry out seasonally and tend to be dependent on the vagaries of climate but, within the forest zone, where evaporation is reduced by a canopy, or along the larger forest galleries, even during the driest climatic cycle, there are always obstructions to the free flow of water. Sometimes these dams, which hold back water and create swamp forest, are of substantial extent, sometimes they are extremely local, but they serve as refuges and 'concentration zones' for a very wide range of water-dependent organisms. It is the long-term durability and predictability of this habitat that ensures a rich invertebrate fauna and attracts such predators as can cope with a wet and densely obstructed substrate and find prey that is seldom on the surface. *Deomys* shares a preference for invertebrate foods (including indigestible ants) with its closest relatives, *Acomys* and *Lophuromys*, but it has enlarged their common sensory apparatus; the whiskers are almost shrew-like in their length and fineness, the ears are enormous and highly mobile and the long barrel of a nose is extremely sensitive to scent clues; this barrage of detectors clearly enhances its success as a hunter of invertebrates. While the divergence of *Deomys* from its more arid-adapted cousins involves an ecological shift, the biogeographic dimension of its earliest beginning brings us back to the south-east/centre-west divide, with *Deomys* ancestors likely inhabiting the centre-west and proto-*Acomys* the south-east and north.

The evolution of this seasonal swamp-forest specialist from more generalized *Acomys*-like cousins is doubly interesting because there are extremely close parallels among some of the descendants of yet another rodent colonist, the last to enter and radiate widely in Africa. Furthermore, there is good evidence that the most *Deomys*-like of the later arrivals already puts substantial competitive pressure on *Deomys* wherever the two species overlap in range.

An even more extraordinary adaptive history surrounds the Crested or Maned Rat, *Lophiomys imhausi*. According to Jansa & Weksler (2004), this sluggish long-haired rodent, which can weigh nearly a kilo, probably shares ancient origins with the proto-gerbillines and, in common with the spiny mice and relatives, has modified hairs. In the case of *Lophiomys* its flank hairs are probably the most complex of all mammalian hairs. Tips and bases are solid, normal hairs but the central shaft is inflated with a strong outer cylinder perforated by abundant vacuoles. This outer cylinder encloses numerous long, fine fibres that together act as a 'wick'. These wicks ensure rapid absorption of secretions and once hairs are saturated the open lattice-work ensures that the hairs cannot be touched without direct contact with the secretion. These hairs grow in tapered, leaf-shaped tracts running from behind the ears across each flank to the groin. The animal can expose these tracts by means of specially modified dermal muscles, which erect the animal's long, externally dull grey fur upwards above it and deflect it downwards below it. This flaring of the fur, which is triggered by any external interference or attack, reveals bold black and white bands on the longer hairs that grow above and below the shorter spongy flank hair. The effect of this striking pattern is somewhat zorilla-like but effectively serves to outline the flank tracts. The rat pulls its head back into its shoulders, hisses loudly and turns its flared tract towards its adversary, as if actively inviting a bite!

This visual display is not the only hint of anticipating an attack – the cranium of *Lophiomys* has evolved a 'double hull' or cranial 'helmet'



Crested Rat *Lophiomys imhausi*.

a. External warning (aposematic) pattern in defensive posture. Display serves to expose a specialized hair tract and focus attention on neck and shoulder. b. *Above*: Skeleton showing damage-mitigating features of skull and skeleton: cranial 'helmet', 'floating' scapulae and robust vertebrae. *Below*: Schematic myology showing position of area underlying specialized hair-tract. c. Vacuolated hair-shaft enclosing numerous fine filaments that 'wick' secretion. d. Reinforced, 'helmeted' skull.

The molecular and physiological details of this mammal's toxin-management systems have significant future implications for human health, making it potentially one of the most important and interesting rodents in Africa.

of reinforced bone. The temporal muscles (which attach to the top or sides of the cranial capsule in all other rodents) are, in this case, totally encased under a canopy of dense, carunculated bone. Rugose, 'pimpled' bone extends over the bridge of the nose, the back of the bullae and, significantly, over most of the external surfaces of the occiput. This skull reinforcement is unique to this species. *Lophiomys* has an extraordinarily dense, tough and close-textured dermis, which is resistant to all but the sharpest of teeth, beaks or claws. It has an exceptionally robust, flexible and elongated vertebral column (with three extra thoracic and one extra lumbar vertebrae), all with enlarged bodies and short spines apparently designed to enhance the amplitude and flexibility of lateral movements. Further peculiarities are near-atrophy of the clavicle, effectively freeing the broad scapulae, apparently to act as shield-plates over the neck and thorax when the shoulders are hunched. These 'floating shoulder-blades' are made all the more mobile by particularly well-developed attachment muscles, notably the trapezius, latissimus dorsi, levator anguli scapulae and brachiocephalicus (see Kingdon 1974, 1983). The lips and tongue are also prominent and well developed. Beneath all these specific external features are yet further adaptations unique to *Lophiomys*. Its stomach has weakly sacculated into five compartments (Vorontsov 1967), implying a complex digestive physiology. Consistent with the role of some mammal salivas in producing proteins that can bind to plant polyphenols, *Lophiomys* has large salivary glands. Circumstantial evidence suggests that both the salivary glands and stomach might be adapted to metabolize plant toxins.

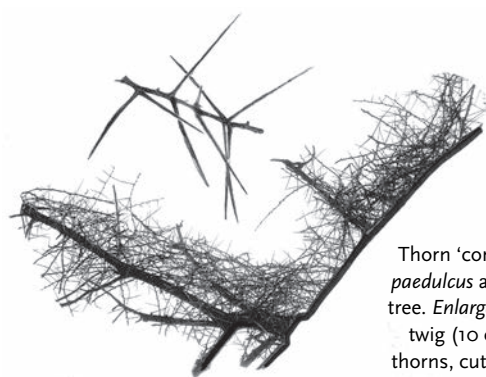
This apparently random assortment of adaptations is connected by the single evolutionary thread of predator-selection. Dogs that attempt to bite *Lophiomys* exhibit every symptom of being poisoned by contact with the hairs and, in some cases, die with startling rapidity, apparently from heart failure. How could a rat, which seldom shows much propensity to bite back itself (in spite of much hissing and snapping), inflict such a deadly response? And how could such a fast effect on the predator have evolved? The answer lies in an astonishing case of association between this mammal and very toxic plants belonging to the Apocynaceae, notably *Acokanthera* spp. In East Africa *Lophiomys* is found in rough or hilly areas, mostly

between 1100 and 2300 m where these locally very common evergreen trees grow in thickets, low-canopy forests or in stony grassland mosaics and gullies. In common with primates and birds, *Lophiomys* feed on the non-poisonous berries of *Acokanthera* but unlike them *Lophiomys* tolerates chewing the bark and roots, which contain higher concentrations of Ouabain, a cardiac glycoside or cardenolide that precipitates pain and cardiac dysrhythmia in many vertebrates. Natural selection has led *Lophiomys* to exploit the susceptibility to Ouabain in its principal predators, mammalian carnivores, while sharing a general insensitivity to Ouabain among many fellow rodents. *Lophiomys* has evidently enhanced its own tolerance of the same toxins to the point where it can chew up and slaver Ouabain/saliva colloid for absorption into its flank hairs (Kingdon *et al.* 2011).

There are abundant instances of insects and some birds utilizing plant toxins to deter or poison their predators, but this is the first instance of something comparable evolved by a mammal. So, while further details of the exact relationship between rat and plant await further research, the genetic basis for Ouabain-control metabolism has obvious implications for therapy in humans and other mammals. Even the barest outlines of this toxic defence hint at the power of predation to select for very unusual defences in prey species.

Another peculiar example of a predator-driven defence strategy has evolved in a founding population of the last, and most extensive radiation from a Eurasian rodent invader. Its ancestor was essentially a generalist and it arrived, together with a number of other Eurasian mammal immigrants, at about 10.5 mya. On entering Africa it found a continent that was populated by the descendants of up to nine previous rodent radiations, but this Eurasian murine clearly possessed many of the attributes that have ensured the almost world-wide success that *Rattus*-like rats enjoy today.

According to Misonne (1969), this ancestral stock has a direct and morphologically little-changed descendant in the acacia rats *Thallomys* spp. Consistent with their semi-arid Eurasian origins these rats range through the drier parts of eastern and southern Africa, from Ethiopia to the Kalahari, preferring thorny acacia woodlands where they are both terrestrial and arboreal. In spite of their generalized and conservative morphology these *Acacia* folivores have evolved an energy-consuming behaviour that must have been predator-selected no less than the prickles of porcupines or the poisonous-ness of *Lophiomys*. Like miniature beavers, *Acacia* Rats expend much time and energy gnawing, cutting and carrying thorny twigs of *Acacia*,

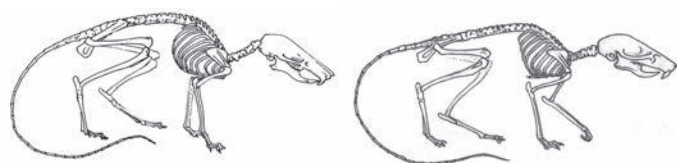


Thorn 'corridor' built by *Thallomys paeudulus* along branches of Acacia tree. Enlarged: a single typical thorn twig (10 cm long) with nine 8 cm thorns, cut, carried and woven into 'corridor' by *T. paeudulus*.

typically *A. tortilis* and *A. xanthophloa*, each twig being up to 15 cm long (about the rat's body length). The rat then transports these twigs and interlaces them in dense self-made thorn tangles that snake over the branches of their home trees and connect arboreal nests with terrestrial burrows. The rats travel along these thorn corridors and it would seem that this corridor-making behaviour has served to artificially extend the one pre-existent property of their food-trees that protects them from predators, principally genets and owls – a barricade of thorns. If Misonne was correct about their conservative genotype then it would seem that the main evolutionary innovations in this species have been behavioural and digestive, leaving the morphology of an already successful invader largely unchanged.

The ancestor of all African murines soon diverged into two lineages separated by dietary preference. For one, the *Praomys* group, adaptable omnivory was probably the established norm and was retained or refined. For the other, the 'grass rats', *Arvicanthis* + allies, the vegetable resources of a continent were sufficient to induce a return towards the primary adaptive niche of rodents: the more-or-less exclusive gnawing and eating of plants.

In the centre-west region, mainly in rainforest, another, related branch of omnivorous rats/mice, *Praomys* and *Hylomyscus* spp., emerged (the latter becoming mainly arboreal) together with several much more specialized terrestrial relatives. I have mentioned how the long-legged, long-headed *Deomys ferrugineus*, aberrant ally of the *Acomys* lineage, became transformed by forest dwelling. Among the *Praomys* group an equivalent transformation took place. The swamp-forest-dwelling Long-footed Rat *Malacomys longipes* has very similar habits and morphology to *Deomys* and the convergence is so close that it clearly involves competition. In a comparison of the status of rats and mice in two Uganda swamp-forests, I found *Deomys* captures accounted for 28.5% of omnivorous rodents where *Malacomys longipes* was absent and only 5% in a swamp-forest where the latter was present (Kingdon 1974).



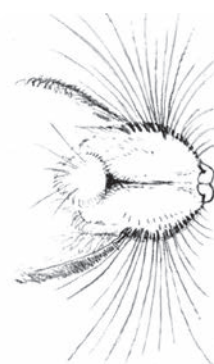
Skeletons of *Deomys ferrugineus* (left) and *Malacomys longipes* (right) illustrating close convergence in proportions of limbs and skulls.

The general conclusion to be drawn from these examples (and many less obvious ones among other mammals) is that most

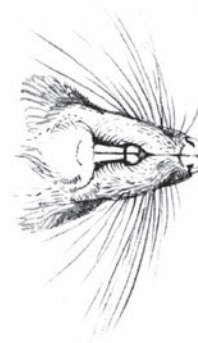
immigrant colonists begin as successful generalists because the narrowness of bridges into Africa seldom favour specialists. Initially the main species to suffer from the new invader are generalists that established themselves after earlier colonizations. In the case of advanced murines, they are more fecund, faster, tougher, more active and aggressive than their nesomyid and proto-gerbilline precursors and possibly have more efficient digestive and immune systems. As the recent invaders penetrated more and more habitats and speciated they became adapted to a steadily widening range of specialized environments, often in well-defined biogeographic zones. As specialization proceeds, competition with earlier forms can have many interesting outcomes, some of them culminating in extinction for the more archaic competitor. Others appear to lead on to still greater specialization and sometimes, especially in older species, further contraction into narrower or more difficult geographic and/or ecological zones (as has happened with *Thallomys* in genet and owl-infested thorn bush).



Colomys goslingi



Malacomys longipes



Comparison between *Colomys goslingi* and *Malacomys longipes* mouths and whisker patterns.

In a very recent adaptation to aquatic habits, yet another murine, the velvet-furred African Water Rat *Colomys goslingi* exemplifies a trend that has gone much further in the Australian Water Rat *Hydromys chrysogaster*. Even so, its muzzle has become hugely swollen and its very long whiskers arrayed into an otter-like splay that contrast strongly with those of its closest relative, the less aquatic *Malacomys*. Given more time, *Colomys* would probably evolve into a still more otter-like form and further complicate the ecology of water-side and swamp-adapted small mammal communities. Similar patterns of adaptation can be discerned in the biology of other mammals but patterns of competitive replacement are seldom as clear-cut as they seem to be among rodents.

Stranded in the south, stranded in the east

A factor that is discussed more fully in Chapter 3 is the northward migration and tilting of the Afro-Arabian land mass. This continental drift has diminished the area of Africa that lies south of the Tropic of Capricorn and this history may help explain why numerous endemic animals and plants are today restricted to very small ranges in the Cape of Good Hope. The ranges of ancient temperate-adapted species must have been greater in the past simply because a higher proportion of the continent lay within the southern-temperate zone. This can be taken to imply that formerly there were also greater numbers of species in these southern temperate groups (and fossils provide some limited support for this). The timing of evolutionary radiations within these southern endemics is currently unknown, but their speciation is likely to have been quite protracted.

Of contemporary mammal groups with overall ranges that are likely to have contracted the best examples are the ancient afrotherian Chrysochloridae or golden-moles and the archaic 'mole-rats' or blesmols Bathyergidae. If external catastrophies, such as major volcanic eruptions, have played their part in the survival of ancient groups then it could be no accident that both these groups are subterranean. Of seven genera of Chrysochloridae (embracing 21 species) only two genera occur outside southern Africa and both are montane or relictual. Of the remainder, all occupy precise, often very localized South African habitats with rather little overlap of ranges. In parcelling out a very limited area into numerous specialized species-ranges these southern golden-moles therefore resemble 'island' taxa (Birds of Paradise on Papua, say). The implications and effects of progressive contraction in a region that once covered a significant proportion of an entire continent deserves much more intensive examination than it has received so far. As their range gradually contracted did the number of golden-mole taxa (or lineages) remain much the same? Did they become fewer, or have they speciated more recently and become more diverse? Further knowledge of the biology of contemporary species will hopefully help answer such questions.

Golden-moles are by no means the only group of African mammals that have a well-defined 'regional centre of endemism'. If latitude and cooler, more seasonal climates have made southern Africa into an ecological enclave for some ancient afrotheres, long established peculiarities of climate and topography have created a similar set of small enclaves in tropical East Africa. The periodically semi-arid Somali-Kalahari corridor has served to cut off forest and montane-adapted species on or close to the eastern seaboard from forest communities in central and western Africa. The eastern coastal forests are intimately connected with the montane forests that grow mainly on eastern faces of mostly ancient massifs scattered from the L. Malawi region north-eastwards to the Usambara Mts and Taita hills in Kenya.

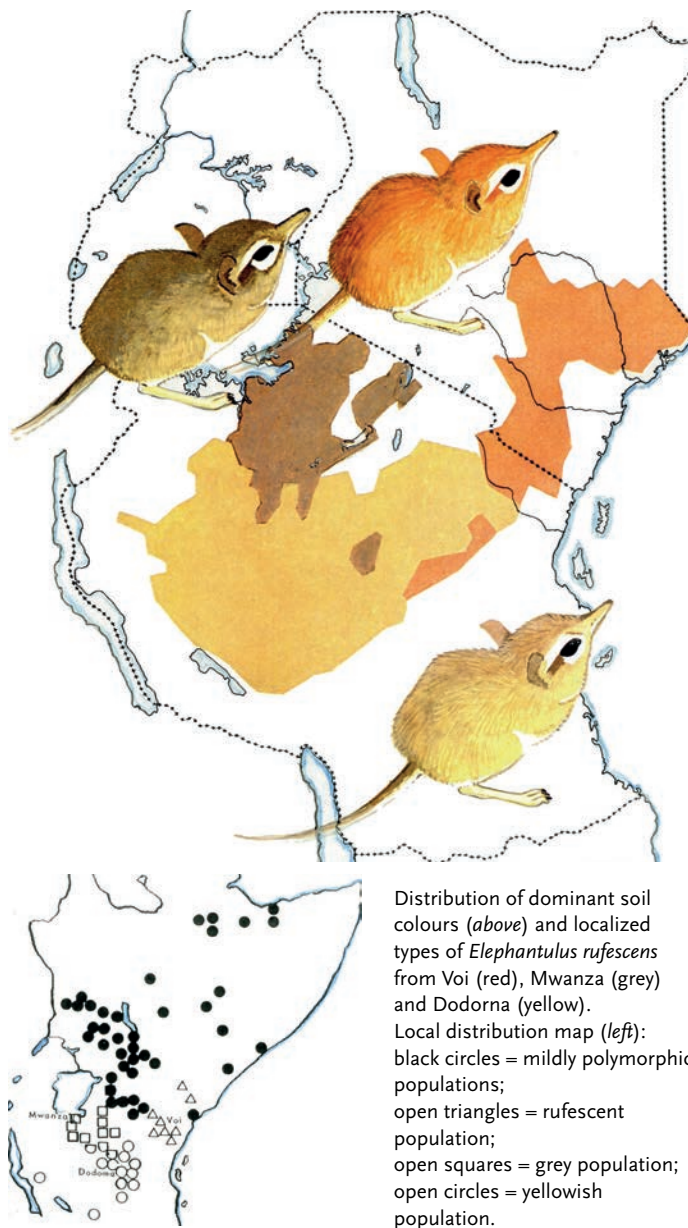
It is at the more tropical end of this montane/coastal complex of forests that another relictual group of afrotherians, like some golden-mole species in the Cape, maintain a precarious hold on existence. There are five species of giant sengi: Black-and-Rufous Giant Sengi *Rhynchocyon petersi*, on Zanzibar I. and parts of the adjacent coast; Golden-rumped Giant Sengi *R. chrysophygus* and an as yet undescribed species *Rhynchocyon sp. nov.* on the Kenya coast; *R. udzungwensis*, a newly discovered species known only from three

small forest blocks in the Udzungwa Mts; and the widespread Chequered Giant Sengi *R. cirnei* (*R. udzungwensis* and *R. sp. nov.* are too recently described to be profiled in this work).

These five species illustrate how predators can drive evolutionary change through differential selection on their prey in different environments. This finds external expression in very interesting differences in coat colouring: relatively uniform in some populations, highly polymorphic in others.

Colour and pattern selection by predators

Before exploring this complex situation, the role of predator-selection can be exemplified in its simplest terms by another Macroscelid, the so-called Rufous Sengi *Elephantulus rufescens*. Over much of its range this species is mildly polymorphic in colour, its pelage exhibiting various shades of sandy, tinted browns.



However, in three localized populations in the southern part of this species' (north-eastern) African range, dorsal coat colours exactly match local soil colour. This mainly diurnal species inhabits relatively open habitats with a scatter of acacia bushes and thickets and the ground becomes bare during the dry season, the period when predation from raptors is most intense. This indicates that predators selectively remove the least cryptic individuals. Over time they strongly influence and progressively refine the colour traits of the survivors.

All sengis are difficult to see and their behaviour is singularly well suited to being cryptic. At the slightest disturbance they 'freeze', only darting away at great speed when they have located the source of a sound or movement. Unlike *Elephantulus*, *Rhynchocyon* species are predominantly forest floor ant-eaters and are the largest and longest-nosed of all sengis. Their colouring and patterning is varied but there are ecological and biogeographic contexts that suggest their diverse patterns of black, red, yellow and grey have also been evolved by selective predation, but in a more nuanced way than in *Elephantulus rufescens*.

The ranges of *R. petersi*, *R. udzungwensis*, *R. sp. nov.* and *R. chrysopygus* are small, discrete but quite tightly clustered. Like many other organisms endemic to the forests east of the Somali arid corridor, they only survive in very small enclaves on the strip of equatorial coast opposite and north of Zanzibar, or in moist pockets on the mountains commonly described as 'the East African Arc'. Researchers on a wide

range of biota agree that the fragmentation of these relictual forests is of very long standing (Moreau 1952, 1963, Hamilton 1982, Lovett & Waser 1993, Burgess & Clarke 2001, Burgess *et al.* 2007). None the less, the four species of forest *Rhynchocyon* are sufficiently alike for them to have presumably differentiated from a common ancestor that had flourished when forests were more widespread and continuous. That the period may have been very remote is made more plausible by the existence of this genus as a fossil in the early Miocene some 20 mya. Of the four species, *R. udzungwensis*, which is a substantially larger animal, is likely not only to be the most conservative species (as deduced from some suggestive features of its coat pattern) but its provenance appears to put it close to the geographic centre of the entire *Rhynchocyon* radiation. It is therefore plausible to suggest that *R. udzungwensis* retains more features of a common ancestor than any other species.

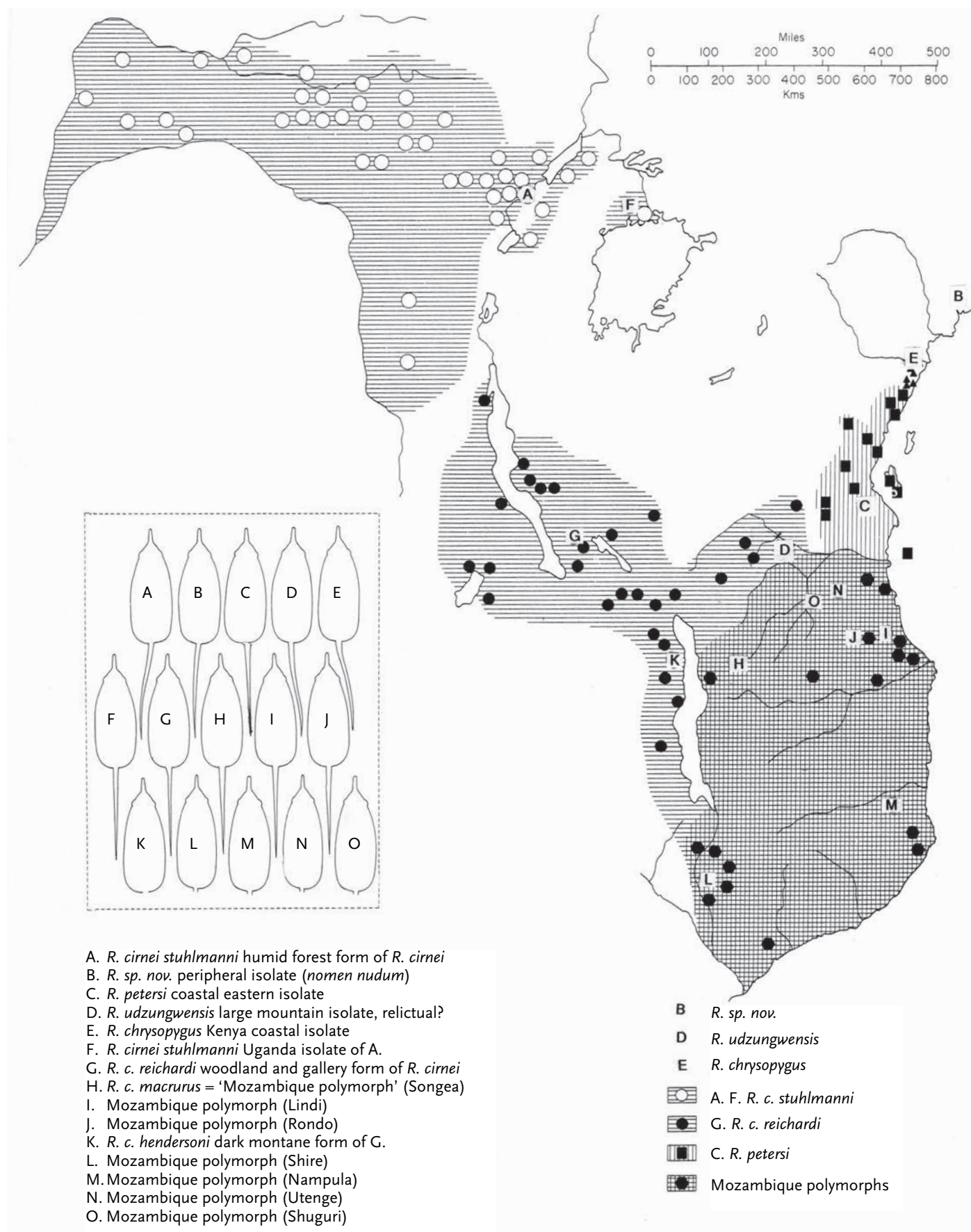
Both *R. udzungwensis* and *R. petersi* live under high, thick, evergreen canopies and the absence of both species outside small enclaves of permanently well-shaded forest implies that they are restricted, probably to a large degree, by predators. *Rhynchocyon chrysopygus* and *R. sp. nov.*, isolated in a narrow northern tongue of low canopy coastal forest, close to an arid hinterland, live under broken, partly deciduous canopies through which some light commonly penetrates. Adults of *R. chrysopygus*, of the Zanzibar population of *R. petersi* and of some polymorphic *R. cirnei*, have pronounced crests on their necks and crowns. The crest is longest (and most mobile) in *R. sp. nov.* (B. Agwanda pers. comm.). Rathbun (1979a) has suggested that the yellow patch may also serve as an intra-specific signal for *R. chrysopygus*.

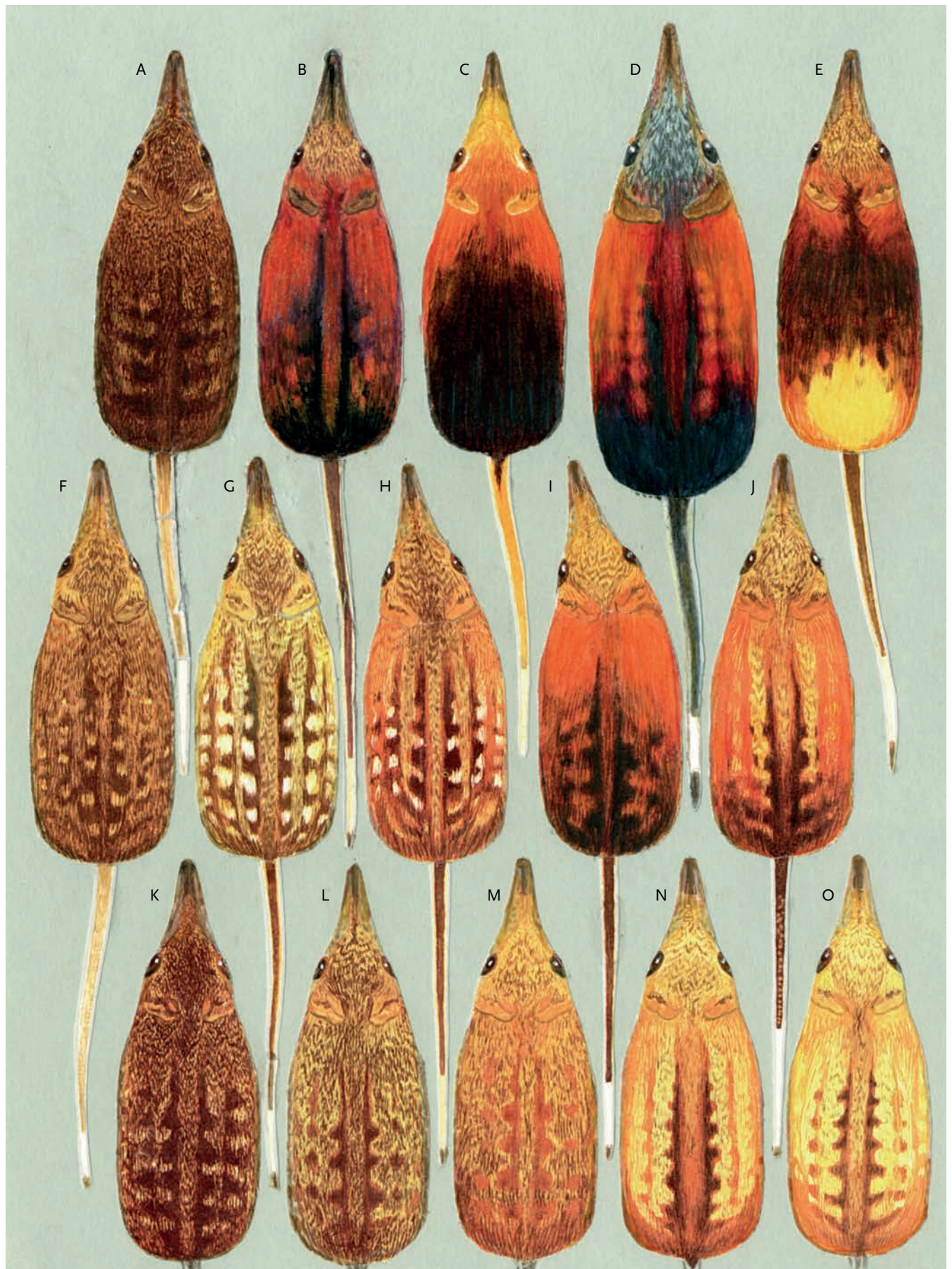
The fifth species of giant sengi, *R. cirnei*, is completely unlike the four species locked into their enclaves. Instead it has a very extensive range that breaks down into three very large geographic blocks, each about 500,000 km² in extent. In two of these blocks the local morph is, in each case, quite consistent in colouring but in the third, which covers Tanzania south of the Rufiji–Kilombero Rivers and all of Mozambique north of the Zambezi, there is an astonishing variety of patterns, which I once mistakenly attributed to hybridization (Kingdon 1974). It now seems more likely that these patterns are influenced by predators *failing* to select for a single colour pattern (just as Rufous Sengi *E. rufescens* living on mosaics of differently coloured soils do not match any one soil-type). The polymorphism of Chequered Sengi *R. cirnei* in this region is likely to be strongly influenced by their living under very varied light levels in an extremely diverse mosaic of habitats. These habitats include grassland, if only seasonally. Mozambique and southern Tanzania differ from many other parts of Africa in having six months of rains (that derive directly from the adjacent Indian Ocean) falling on both coast and uplands in the interior. The entire region is therefore webbed by mostly perennial rivers that are substantial enough to sustain narrow gallery forests within a patchwork of thickets, woodlands and savannas.

Unlike other regions of Africa where large areas have types of plant cover that respond quite uniformly to climatic changes, the basic diversity of the Mozambique mix is likely to have been maintained over many fluctuations in climate because of its proximity to the Indian Ocean. Under such consistently varied conditions raptor-selection was less likely to favour any single type of pattern. Thus some individuals living in dense forest in coastal Tanzania are almost entirely shades of red or have black or mahogany rumps and red flanks. These Sengis often exhibit patterns of dark longitudinal streaks between paler red dorsal blotches. In drier, more exposed areas there has been selection for lighter spotting and paler agouti streaking.



Pattern elements common to most *Rhynchocyon* spp. illustrated by dorsum of new-born Golden-rumped Giant Sengi *R. chrysopygus*.

Pelage patterns and corresponding map and key of *Rhynchocyon* spp. distribution.

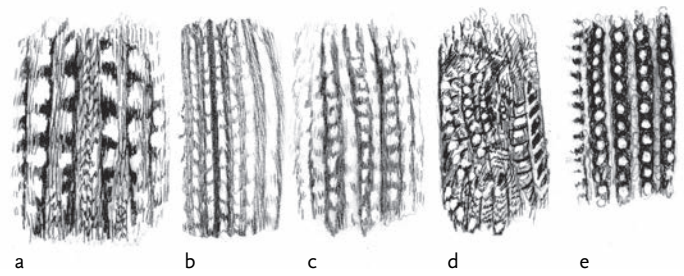


The occurrence of redder colouring between the Rufiji and Rovuma Rivers and more agouti towards the Zambezi was once interpreted as a north–south cline (Corbet & Hanks 1968), and these authors' observation that northern morphs are most like their northern neighbours has acquired new significance in light of the very recent discovery of *R. udzungwensis* and *R. sp. nov.* Francesco Rovero (pers. comm.) has recorded traces of spotting and striping on the backs and flanks of some individuals of *R. udzungwensis*, demonstrating the existence of minor pattern polymorphisms even within this very small and confined population. Some individuals have a particularly close resemblance with some *R. cirnei* morphs living in its immediate vicinity, implying that both species originally sprang from a common parental population restricted to the eastern seaboard and 'Eastern Arc' mountains. Indeed, *cirnei* may well have begun as the southernmost extension of an exclusively tropical forest-adapted animal with a quite limited eastern distribution.

I contend that the explanation for ecological success in *R. cirnei*, as well as the polymorphism of its easternmost population, lies in the likelihood that riverine forest galleries in Mozambique and southern Tanzania were maintained over many climatic cycles, probably over many millions of years and over the greater part of this very substantial area. This provided long-term continuity of a predictable, reliably stable habitat for a large population of giant sengis. The crucial distinction, for this discussion, is that forest galleries are unlike solid blocks of forest in being linear and are nearly always emarginated by drier, more open country. During the long wet season, habitats beyond the forest margin become a rich source of invertebrate prey, with dense grass cover making the margins only slightly less safe than the forest itself. Contemporary *R. cirnei* do, indeed, move out into grassland during the wet season (J. Kingdon pers. obs.) but it has to be significant that they encounter more than three times as many raptor species; all fifteen or so of them potential predators.

Convergence in predator-selected pattern

So what of the two other *R. cirnei* populations? Inland from ecologically diverse Mozambique/southern Tanzania there is an upland region where the temperatures are cooler, rivers are narrower and the savannas and miombo woodlands that surround them are more uniform and less diverse. It is here that a much more consistently patterned morph, *R. cirnei reichardi*, has evolved. The ground colour in this subspecies is a freckled light olive agouti that is similar in tone and micro-structure to that of numerous other cryptic mammals. The dark longitudinal bars that occur in various permutations on the polymorphs from further east are, in *reichardi*, ordered into six 'strips' that run from shoulder to rump. Each dark strip is punctuated by five to seven white or off-white 'spots' (actually irregularly shaped blotches) that observably derive from very variable lighter-toned blotches in the eastern polymorphs. This disposition of light and dark markings closely resembles the pattern evolved by various American ground squirrels and by some African maculated grass-mice of the genus *Lemniscomys*. There are even some lizard and bird species that have feather or scale patterns organized along very similar optical principles. The patterns of all, sengis, squirrels, mice, lizards and birds, conform to highly abstracted principles of camouflage in which the disposition of three tones, light, dark and intermediate, are ordered within systematic grids that reflect



Convergences in cryptic, predator-selected patterns. a. *Rhynchocyon cirnei reichardi* (Afrotherian sengi). b. *Lemniscomys macculus* (African murid rodent). c. *Spermophilus tridecemlineatus* (American ground squirrel). d. *Caprimulgus pectoralis* (African nightjar bird). e. *Cnemidophorus* sp. (whiptailed lizard).

a structured equivalent to the probabilities of light-distribution in real environments. Pattern elements that are mutable in the polymorphs have, in *reichardi*, become consistent and 'geometrized'. During their evolution by natural (aka predator) selection, all the taxa listed above have shared a common vulnerability and all have been weeded out according to how closely their patterns match the statistical breakdown of three tones in their environment.

Evolution of the grid structure is probably favoured by more than one factor, genetic and physiological ones included. I contend that this development correlates with a narrower range of environmental settings within which the sengis are vulnerable to hawks. In this respect the complex grid pattern of *reichardi* has an outcome that does not differ in principle from selection for soil-matching in monotonous *E. rufescens*. It is just that the larger animal must break up its colouring and body outlines to achieve similar 'invisibility' in a more cluttered setting.

It would seem that once the genetic coding for a systematic grid-like pattern has been established, predation very quickly fine-tunes it. Predators select against any mismatch with the average light-levels of the environment so that the overall tonality of the pattern goes down or up according to the probabilities of lighter or darker backgrounds in different localities. This helps explain why, within the overall range of *reichardi*, much darker forms occur in montane forests (typified by *R. cirnei hendersoni*, for which see figure K on p. 97).

The tonal versatility that is implicit in the *reichardi* pattern-type has helped it to spread over very extensive areas west of L. Malawi and around both shores of L. Tanganyika. Outwitting hawks may not be the only advantage that *R. cirnei* has over its strictly forest-adapted cousins; presumably it has physiological adaptations to drier, perhaps colder conditions as well. Whatever its hidden attributes, I contend that its ecological advantages have permitted this type of sengi to reach, and then colonize, an enormous block of lowland rainforest north and east of the Congo R. Here I see giant sengis 'returning' to an ecological setting and light levels that are comparable with those in which its *udzungwensis*-like ancestors evolved. In effect, the tonalities of all three components of the grid pattern have darkened to the point where the whole animal is as dark, sometimes even darker than *R. udzungwensis* and *R. sp. nov.* The type for this Congolese population is called *R. cirnei stuhlmanni*, but even within this major population there are lighter morphs along the drier north-eastern margins of its range. Paler brown, with more visible spots, the tonality of *stuhlmanni* from Uganda presumably correlates with higher light levels in evergreen forests that are less consistent in the density of their shade.

Although the north-eastern Congo Basin and Uganda are demonstrably good habitat for *Rhynchocyon* today, the radiation pattern outlined here implies that this extensive equatorial region might have been devoid of giant sengis before the arrival of *stuhlmanni's reichardi*-like ancestors. At the grossest level of explanation past changes in climate could be implicated, but this also implies phases of extreme vulnerability to past climatic changes in *Rhynchocyon*. If so, this only serves to emphasize what unique combinations of circumstance must have allowed *R. udzungwensis* to survive in its tiny enclave.

Finally, the ecological success of *reichardi* has allowed it to spread to the point where its range now actually surrounds the three forests where *udzungwensis* survives. Indeed, *reichardi* now occurs in forests that are said to be indistinguishable from those in which *udzungwensis* lives and only 25 km distant.

The presence of such a successful, and presumably newer, species so close to such a conservative and rare type could imply several things. The most likely is that the forest blocks in which *udzungwensis* survives have an unbroken history that goes back for immense stretches of time while those in which *reichardi* occurs may be 'regrown' secondary forests. A more unsettling possibility is that *reichardi* has been steadily advancing at the expense of *udzungwensis* as the extent of forests has steadily shrunk around them. In any event the differing status of these two sengi species makes them into very valuable indicators for both past and current change in African environments.

This summary analysis of a hypothetical but ecologically and morphologically plausible evolutionary radiation suggests that the details of a living species' biology and distribution can help shed light on events that have taken millions of years to unfold. The example of an African radiation following the incursion of a Eurasian primate will be discussed shortly but, first, consider some more general features of the African continent as a theatre of primate evolution.

Primate histories

If Africa suits mammals, Africa certainly suits primates, and things about this continent have favoured the radiation and multiple speciation of bush-babies, colobus monkeys and Cercopithecinae, or 'cheek-pouch monkeys', and, in the past, apes or proto-apes. Today, living higher primate species are at their most diverse in Africa and it is also clear that all the anthropoid primates that currently live in Asia are derived from African ancestors that reached Asia during the Miocene by means of at least three, possibly more, emigrations. The likely timing of those events and the classes of emigrants can be summarized as follows:

Approx. 20 mya	At least one, possibly two, species of proconsul-like 'proto-ape' left Africa and gave rise to the gibbon, orang-utan and related lineages in Eurasia (this almost certainly included the ancestors of extant African hominoids).
Approx. 13 mya	An ancestral colobine ancestor left Africa and gave rise to Asiatic Leaf-monkeys.
Approx 10.5 mya	Eurasian apes very abundant in Europe: at least one form likely to have entered Africa and given rise to modern African apes and hominins.
After 10 mya	Macaque ancestor left Africa and radiated across Asia.

As was emphasized earlier, continental exchanges are generally rare and commonly involve no more than a single species, which then radiates within its new continental home. Of even greater importance for primate evolution, especially for our understanding of the evolution of modern African apes and humans, has been the return, back into Africa, of a Eurasian primate. A return passage is still hotly contested but the evidence for a Eurasian lineage of ape giving rise to both modern African apes and humans has been cogently and persuasively argued by Stewart & Disotell (1998). These authors have shown that alternative explanations for the indisputable common genetic ancestry of African hominids and the orang-utan would all involve more exchanges between Asia and Africa than are plausible (or necessary) to explain the facts.

Of the known invasions out of Eurasia that have been listed above, one, at about 10.5 mya, brought in several examples of large-bodied Eurasian fauna, which implies a particularly solid, broad land connection at that time (Hempton 1987). This is the most likely time of arrival for a Eurasian dryopithecine tree ape. When it came to penetrating the more tropical regions of Africa with their well-established and diverse primate fauna, a Eurasian ape coming from a temperate or semi-temperate background would have suffered similar delays or constraints to other mammals. Expansion south was easiest at times when the pattern of seasonal changes most resembled those of the Mediterranean (where dryopithecines were particularly abundant between about 12 and 9 mya). Such expansion was therefore favoured most during cool, dry periods, when arid or semi-arid corridors cut into the forest belt, sometimes linking northern arid-adapted communities with southern ones. This scenario is central to attempts to understand the evolutionary origins of gorillas.

Interpreting their distribution, biology and history poses many questions, but my explanation for their present pre-eminence in central Africa begins with an early proto-gorilla population (almost certainly of dryopithecine ancestry) entering just such a temporary 'corridor' that passed through today's Cameroon and Gabon (Kingdon 2003). When the climate became warmer and more humid these apes would have become engulfed in forest and this engulfed population became the putative ancestors of today's gorillas. Gorillas are still most abundant in this region, where it is proposed that their ancestors first adapted to true forest-living. The situation is not without precedent; there are other primates that seem to have non-forest ancestors, notably drills *Mandrillus* spp., Sun-tailed Guenons *Allochrocebus solatus* and the Squirrel-Galagos *Sciurocheirus* complex, and all of them now inhabit this region, most of them exclusively. This evolutionary pathway from non-forest into forest is but a detail in a much larger and much repeated feature of Africa's biogeographic history.

Geographical axes and the biogeography of speciation under changing climates

I began this chapter by pointing out that the success of mammals in Africa, like that of many other animals, was partly due to such a large portion of the continent being equatorial and tropical but not necessarily permanently forested. I went on to discuss the south-east and centre-west continental divide. Beyond pointing out that climatic changes subdivide these blocks and alter the boundaries between them, I have deferred until now discussion of the mechanism that

has given rise to extraordinary levels of diversity in groups such as primates, rodents, mongooses and antelopes. It is a mechanism that is driven by climate change. Dry habitats expand or contract on a north–south axis under the influence of dry, cold climates. These are associated with northern ice-ages and a substantial lowering of sea levels. It is at these times that arid-adapted communities in northern and north-eastern Africa make contact and exchange fauna and flora with arid south-western Africa: Oryx and dik-dik antelopes and bat-eared foxes are much cited examples (Lonnberg 1929, Moreau 1963, Kingdon 1971, Coe & Skinner 1993, and see map p. 55).

At the opposite extreme, forests in Africa expand and contract along an east–west, equatorial axis. Warm, wet periods cause forests and forest communities to expand and join up only to retreat into enclaves, large and small, when the droughts return. The (*cephus*) monkeys provide a particularly vivid example of the diversification of forest-adapted mammals across the main forest zone (see Vol. II) and red colobus *Piliocolobus* spp. are another example of speciation within today's apparently continuous forest belt. There can be little doubt that the isolation of forest blocks and of the animal populations that live in them has been influential in causing evolutionary change. However, it is not only forest and desert animals that expand and contract. Populations belonging to every adaptive permutation between true desert forms and exclusive forest forms shift the boundaries of their ranges during periods of climate change. This frequently involves isolation in discrete pockets of territory, especially on the slopes of mountains and uplands. These periodic disjunctions and reconnections between populations have clearly provided a major mechanism for speciation in Africa and help explain the extraordinary diversification of mammals that was emphasized at the beginning of this chapter.

The diversity of African mammals and primates includes *Homo sapiens*, a species that has evolved during the same period, over the same continental mass and by the same processes as other mammals (Cartmill 1974). Even more significant, it is a species that is the product of the same back-and-forth exchanges between continents that have brought several 'returnees', such as porcupines, some caprine and cat lineages and rousette bats, 'back' into Africa from Eurasia.

The dryopithecine tree ape that is the most likely ancestor of African great apes and humans (Stewart & Disotell 1998, Kingdon 2003) would have entered Africa during a well-known period of connection: the 'Hipparionid Event' at about 10.5 mya. This was precisely the time that the *Rattus*-like ancestor of today's murine rodents is thought to have entered Africa (Steppan *et al.* 2004). Like that immigrant rodent generalist, it was probably able to spread widely at first, especially in the northern and eastern parts of Africa that most resembled their western Eurasian homeland. Even as its range expanded, it is to be expected that differences between the south-east and centre-west, overlaid by fluctuations in climate, soon led to some differentiation in that founding stock. The earliest speciating event that can be plausibly reconstructed was that of proto-gorillas in the Gabon–Cameroon 'corridor' (as summarized earlier). At much the same time, or perhaps a little later, increasing aridity was likely to have isolated another population of dryopithecine-like apes east of the Somali–Kalahari arid corridor that was discussed earlier.

Reconstructing the subsequent fortunes of African ape and hominin descendants has to be, by the sparse nature of the evidence,

a highly speculative enterprise, but whatever the true course of events, it must have followed similar patterns to those that underlie the history of other speciating organisms in Africa. In any event, the very eastern distribution of fossils implies a marked preference for this region by early hominins after their differentiation from the ancestors of African apes. An eastern bias is still reflected in the distribution of many fauna and flora and, among mammals, the Suni and Red Bush Squirrel *Paraxerus palliatus* are species that are limited to the long, narrow strip of rather dry forests, thickets and mosaics that are sustained by rain coming off the Indian Ocean. Even some birds with immigrant origins, for all their mobility, seem capable of retaining a preference for those regions or habitats closest to those of their source. Thus the Trumpeter Hornbill *Bycanistes bucinator*, a bird with close affinities to some Oriental hornbills, has a mainly eastern and south-eastern distribution. Likewise the monarch flycatchers *Erythrocerus holochlorus* and *E. livingstonei* have a close Oriental relative, *Culicicapa*, and an eastern coastal forest distribution, and there are other similarly suggestive avian distribution patterns.

For forest-adapted eastern littoral species the main pathways across the semi-arid belt and on into the interior are up the forested banks of major rivers. Because major rivers tend to be well spaced out, what could be called 'basin evolution' is not easily separable from latitudinal stratification. In effect the inhabitants of major river basins, such as those of the Limpopo, Zambezi, Rufiji and Web Shebelle, can become distinct populations. 'Basin evolution' has been examined for its explanatory powers in relation to the proliferation of hominins and a sequence of speciation events (that are broadly consistent with the fossil record) has been proposed in a previous work (Kingdon 2003).

If that model of evolution is correct, the emergence of hominins could be said to have hinged on nothing more than sudden aridification of a long tract of land that became interposed between our ancestors in the east from those of apes in the west. So far as we can tell, whatever has happened to those two lineages over the last 7 million years has been predicated upon a 'mere' accident of geology and climate.

Every creature alive is the product of a unique history. The statistical probability of its precise reduplication on another planet is so small as to be meaningless. Life, even cellular life, may exist out yonder in the dark. But high or low in nature, it will not wear the shape of man. That shape is the evolutionary product of a strange, long wandering through the attics of the forest roof and so great are the chances of failure that nothing precisely and identically human is likely ever to come that way again.

(Eiseley 1946)

However much we live for the present, we need history and prehistory to retrace that 'strange, long wandering', if only in our minds. For the first time ever, we have the technical tools and intellectual frameworks to begin that journey. It was a wandering that wove in and out of the mammalian communities of Africa. We need all the descendants of those communities in order to understand how mammals, including humans, have speciated in Africa and evolved their particular characteristics. This is a science in its infancy and only a lot more excavation and analysis of genes, fossils and behaviour will reveal the true depth and breadth of the process that has given us, and all other African mammals, our life and existence.

CHAPTER SEVEN

Classification: A Mammalian Perspective

Colin Groves & David Happold

Classification in its widest sense is the ordering of organisms into groups on the basis of their relationships (Simpson 1961). Two other terms are frequently used in relation to the classification of organisms: 'systematics' is the scientific study of the kinds and diversity of organisms, and 'taxonomy' is the theoretical basis for classification. Actually, these three concepts grade into one another, in practice if not in principle, and they are sometimes regarded as loose synonyms. In particular, taxonomy is no longer regarded as merely a theoretical study, and 'a taxonomy' is used in very much the same way as 'a classification'. It is hard to insist on different meanings for the three terms any more, though it remains correct to say that they imply different degrees of inclusiveness. A fourth word commonly used in the context of biological classification is 'nomenclature'. In this case, the concept has a different sphere of concern, and its distinctness must be carefully maintained; nomenclature is a system of rules to determine what name shall be used for a taxon.

Species Concepts

The basis of all biological studies is the species. According to the Biological Species Concept, a species is a population (or series of populations) that does not interbreed under natural conditions with other such populations. The qualification 'under natural conditions' is important because there are well acknowledged species that can be persuaded to breed in captivity but that do not interbreed in the wild. In fact, some species that are considered to be genuinely distinct may commonly cross to form fertile hybrids (for example, between the two species of wildebeest, *Connochaetes taurinus* and *C. gnou*; Fabricius *et al.* 1988); so it is not true that hybrids between distinct species are necessarily sterile.

In some situations, closely related species that do not usually interbreed and whose geographical ranges join or overlap may occasionally form hybrids. When this happens, there are narrow zones where hybrids occur infrequently, but since there is little backcrossing, there seems to be little or no gene-flow between the parent forms.

Examples of hybridization in the wild between African mammals of distinct species, or what many would consider distinct species, include a hartebeest *Alcelaphus*–tsessebe *Damaliscus* hybrid (a single instance but noteworthy because it is intergeneric; Selous 1893) and several records of baboon *Papio*–gelada *Theropithecus* hybrids, also intergeneric (Jolly *et al.* 1997). A further example is the presence of a number of hybrid zones between different taxa of baboons (Jolly 1993). The difficulty with taxa that hybridize is whether they should be regarded as two species or as a single species that exhibits considerable geographic variability. In the case of the baboons, Jolly (1993) considered that the taxa were conspecific (i.e. they belong to a single species, namely *Papio hamadryas*) whereas Groves (2001) maintained that they were separate species. These examples illustrate that an exact definition of what constitutes a species under the BSC is not as simple as it seems.

Two other concepts – the Recognition Species Concept and the Phylogenetic Species Concept – have been developed to accommodate those situations that seem to be contrary to the Biological Species Concept and on which the concept offers no guidance. The Recognition Species Concept assumes that members of a species share a common fertilization system. The meaning of 'a common fertilization system' can be interpreted in a variety of ways. In a study of galagos (Galagidae), it has been shown that vocalizations are the main determinators in bringing potential mates together, and so may be regarded as the principal mechanism for this 'common fertilization system'. Although the characters that may comprise a 'common fertilisation system' are debatable, this method can only be employed in the field and can not be used for museum specimens.

Both the Biological Species Concept and the Recognition Species Concept are *process* concepts, which recognize a species according to the process by which it is maintained. But it is not always – in fact, not even usually – easy or possible to detect that process. But it is possible to recognize a *pattern* that may identify a population as a species which differs diagnostically from other populations. This pattern concept is known as the Phylogenetic Species Concept. A diagnosable taxon is one that can infallibly be recognized from all others (as far as the available evidence goes), implying that there are fixed genetic differences that

separate it from any other taxon. Any character, as long as it can be reasonably inferred to have a genetic basis, is suitable, e.g. morphology, vocalization, karyotype, nuclear DNA sequences, etc. Interbreeding between species, or its absence, is not a criterion under the Phylogenetic Species Concept; the examples mentioned above, even the baboon hybrid zones, would not affect the status of the hybridizing taxa as full species, as they are none the less diagnosably distinct.

Under the Phylogenetic Species Concept, many more taxa merit species status than under the Biological Species Concept – perhaps twice as many in some groups of land vertebrates. Under the Biological Species Concept there are no criteria for deciding on the species status of allopatric populations; no conceivable evidence will permit an objective evaluation. Under the Recognition Species Concept, the criteria are more often available and potentially more nearly objective, but they change from group to group, and it may need an unattainable degree of knowledge to decide what counts as a suitable series of criteria. Under the Phylogenetic Species Concept, the categorization is as clear-cut as the available evidence allows.

A species, consequently, is a population (or series of populations) diagnosable by one or more unique, fixed, heritable character states.

Subspecies

Two populations within a species may be separable because some or many of the individuals that comprise each of these populations differ in body size, body proportions or colouration, and it may be worthwhile distinguishing them taxonomically. Such populations may be considered to be subspecies within a species. Just how small a proportion of individuals can differ for the populations to be deemed subspecifically distinct? Most taxonomists would probably follow the rule-of-thumb proposed by Mayr (1963): that is, 75% of individuals in a population should be distinguishable from all other members of the same species. Statistically, this is equivalent to a 90% non-overlap between two populations, and is especially useful in morphometric comparisons.

Subspecies replace one another across the geographic range of the species; they never overlap and hence are never sympatric. They are not variants within a single population in a single location. A species does not have just one subspecies: it has two or more, or it has none. If a species has no subspecies, it is termed monotypic; if it is divided into subspecies, it is termed polytypic.

If, for example, two taxa differ only on average (according to the 75% rule), they may be termed subspecies within a single species; but if they differ absolutely so they do not overlap in one or more characters they should be named as separate species. It is quite normal in classification for a taxon originally described as a subspecies to be reclassified as a species in the light of new information, and for two species to be replaced by a single species with two subspecies using one of the names originally designated. For example, the Forest and Savanna Elephants were long considered to be two subspecies of a single widespread species, the African Elephant (*Loxodonta africana*), and were called *L. a. cyclotis* and *L. a. africana* respectively. A recent revision (Grubb *et al.* 2000), subsequently supported by genetic evidence (Roca *et al.* 2001, Rohland *et al.* 2010), showed that they differ diagnostically, and hence they are now classified as two species (*L. africana* and *L. cyclotis*, respectively).

Subspecies, of course, are merely points along a scale of differentiation at which it becomes convenient to provide separate

names, whether subspecies or species. The objective demarcation is between subspecies and species, not between subspecies and populations with less divergent gene frequencies.

The Hierarchy of Classification

Organisms are classified in a descending series of less and less inclusive categories called ‘ranks’. These categories are ‘nested’, that is to say each one belongs only to one higher category. There is general agreement that in some way taxonomy must reflect their phylogenetic affinities.

The tenth edition (1758) of Linnaeus’s *Systema Naturae* is taken as the starting point for all biological nomenclature. The hierarchy of taxonomic ranks, from highest to lowest, is: Kingdom, Phylum, Class, Order, Family, Genus and Species. These are referred to as the obligatory ranks, and it is mandatory to classify each species with respect to them. An example is as follows. The class Mammalia are in the phylum Chordata (which also includes the fish, amphibians, reptiles and birds, as well as the so-called ‘protochordates’, the sea-squirts and lancelets). The class Mammalia is, in turn, divided into many orders – 29 according to the most recent reckoning (Wilson & Reeder 2005), including the Lagomorpha (hares), Rodentia (rodents), Primates (humans, apes, monkeys, lemurs), Carnivora (carnivores), Proboscidea (elephants), Chiroptera (bats) and others. Each one of these orders is further divided into one or more families, each family into one or more genera, and each genus into one or more species. Thus the order Lagomorpha has two living families, the Leporidae (hares and rabbits) and Ochotonidae (pikas). The Leporidae contain ten genera including *Lepus* (hares), *Oryctolagus* (rabbits) and *Pronolagus* (rock hares). In Africa, the genus *Lepus* contains five or six species, the genus *Oryctolagus* contains one species and the genus *Pronolagus* contains four species. When a classification is viewed from the species upwards, the classification of the Cape Hare *Lepus capensis* is species *capensis*, genus *Lepus*, family Leporidae and order Lagomorpha. The name of any species is a binomial name, which includes the genus name and the species name (see Nomenclature). All species within a genus have a set of shared derived character states that places them in a single higher taxon (a genus in this case), indicating that they are the exclusive descendants of a common ancestor. A family contains one or more genera, which, likewise, have a set of shared derived character states. Thus all species in a genus are more similar, and more closely related, to each other than they are to species in another genus in the family (or indeed any other genus in any other family); the implication of ‘closely related’ is that they are a monophyletic group (the exclusive descendants of a common ancestor).

Sometimes finer levels of discrimination are required and so it is necessary to insert subordinate ranks below obligatory ones; these are typically ‘sub-’ ranks, with ‘infra-’ ranks below that. This results in a more complicated (but more precise) classification. The 29 orders of mammals are not evenly inter-related, and the Mammalia are divided into two subclasses: the Prototheria (for the order Monotremata alone) and Theria for the other 28 orders. The Theria are in turn divided into two infraclasses: Metatheria (for the marsupials, of which there are seven orders) and the Eutheria (for the placentals, of which there are 21 orders). A classification can be very unbalanced and there is no necessity to have even approximately equal numbers of subordinate categories in a major taxonomic group.

Other subordinate ranks can be used in some circumstances. Superorders can be used to group related orders together (and come below infraclasses); in the past, other ranks (such as megorders, parvorders, grandorders, mirorders, cohorts) have been used when needed. By far the most common of these splitting practices is to insert the ranks of ‘tribe’ and ‘subtribe’ below the subfamily in order to group related clusters of genera, and subgenera to group related clusters of species.

Any taxonomic group, at whatever level, is referred to as a taxon (*pl. taxa*). The order Lagomorpha is a taxon, so is the genus *Lepus*, so is the species *Lepus capensis*.

Splitting and lumping

Disagreements about how to classify species are not uncommon. A ‘splitter’, who divides up a genus into several different genera, can be accused of failing to see the wood for the trees; while a ‘lumper’, who combines several genera into one all-inclusive genus, risks missing worthwhile information. At the species level, splitting and lumping have rather different connotations from the generic level or above, and because at the species level we have a hope of introducing much more objectivity, it is better not to use the terms ‘splitting’ and ‘lumping’ for species taxonomy, but to reserve them for more restrictive and more inclusive arrangements of genera and families.

Nomenclature

The naming of animals (by their scientific names) is controlled by the *International Code of Zoological Nomenclature*, now on its fourth edition. The *Code* ‘has one fundamental aim, which is to provide the maximum universality and continuity in the scientific names of animals compatible with the freedom of scientists to classify animals according to taxonomic judgements’ (International Commission on Zoological Nomenclature, 1999). After taxonomists have completed a taxonomic investigation, any changes to names or status of a taxon are subject to the rules laid down in the *Code*. ‘Changing the names’, which so many non-taxonomists complain about, is generally a result of an advance in taxonomic understanding, which thereby *automatically mandates* a nomenclatural decision, which may involve changing some names.

The basic principle of zoological nomenclature is priority: the earliest name given to a taxon is the one that should be used for it, so long as the name is *available*. To be available, a name must pass certain criteria:

- It must have been published.
- It must not predate 1758, as the tenth edition of Linnaeus’s *Systema Naturae* is the official starting point of the system.
- The work in which the name was introduced must have used binomial nomenclature.
- It must have been accompanied by a description or a bibliographic reference to one (otherwise the name is called a *nomen nudum* and it cannot be used).
- It must be unique: two species in the same genus cannot bear the

same specific name; two genera in the animal kingdom cannot bear the same generic name. Two nominal taxa with the same name are called *homonyms*.

- From the year 2000 onwards, it must be accompanied by a set of formalities: it must be specifically stated to be new, and must have a *type specimen* (see below).

Ironically a name does not have to be in any way appropriate. The name of the Hartebeest *Alcelaphus buselaphus* means ‘elk-stag ox-stag’, but the animal does not in any meaningful way resemble an elk, an ox, or a stag!

The *Code* provides rules and guidelines for the names of a taxon within a species-group (species and subspecies), genus-group (genera and subgenera) and family-group (superfamilies, families, subfamilies, tribes and subtribes). Some of these are described in the following paragraphs. There are no rules for other ranks such as orders.

In nomenclature, a species has two names (a binomial): the name of the genus followed by the name of the species. A subspecies has three names (a trinomial): the generic, the specific and the subspecific. The name of a genus, or of a species or subspecies (the binomial or trinomial), is either written in italics or is underlined. The genus name always begins with a capital letter, but species and subspecies names are always in lower case even if the name commemorates a person (*wilkinsoni*) or a geographic region (*africanus*). If a large genus is divided into subgenera, the subgenus name may be included in parentheses (e.g. *Tadarida (Mops) condylura*). One of the subspecies – the one found at the type locality and which includes the type specimen, is *nominotypical*, and repeats the species name (e.g. *Pan troglodytes troglodytes*; *Cephalophus nigrifrons nigrifrons*; *Otomys sloggetti sloggetti*); other subspecies that are found elsewhere are given a separate trinomial name (e.g. *Otomys sloggetti turneri*, *O. s. robertsi*). Under the principle of coordination, the names given to species and subspecies are interchangeable, so if a subspecies is found actually to be a full species it retains the same name, but as a binomial not a trinomial. Some of the bushbucks that have been described as subspecies of *T. scriptus* may, in fact, be distinct species; if so, the subspecies *Tragelaphus scriptus sylvaticus* would change its name to *Tragelaphus sylvaticus*. Likewise, if a genus is divided into subgenera, one of them is the *nominotypical* subgenus and bears the same name as the genus. If a family is divided into subfamilies, one of them is the *nominotypical* subfamily and bears the same name as the family, except that it ends in *–inae* instead of *–idae*; and there may also be *nominotypical* tribes and subtribes (which end in *–ini* and *–ina*, respectively).

When a species or subspecies is first named, it must be represented by a type specimen (the original specimen that was used for the original description of the taxon) and a type locality (the place where the type specimen was collected). Every genus, species and subspecies has a type locality and a type specimen. For each of the genera and species described in *Mammals of Africa*, the full citation of the taxon is given. The citation consists of the binomial scientific name of the species, the name of the describer and the date (year) when the description was published, the name of the publication where the description was published, and finally the details of the type locality. Thus for the Golden-rumped Sengi, the full citation is: ‘*Rhynchocyon chrysopygus* Günther, 1881. *Proceedings of the Zoological Society of London* 1881:164. Mombasa, Kenya’.

From this information, the interested reader can find the original description, which give the details of the taxon (size, pelage colour, skull characteristics, etc.) and the distinctive characters, which, in the describer's view, separate the taxon from other similar and related taxa (though subsequent research will often have modified the describer's original ideas).

The specific name is unique to any organism, which is why biologists always use the scientific name of a species rather than its common or vernacular name (see later). For example, the squirrel named *Heliosciurus gambianus* is a unique name. There is only one *gambianus* in the genus *Heliosciurus* and there is only one *Heliosciurus* in the family Sciuridae (or any other family or order). A specific name may however be used in conjunction with another genus; besides *H. gambianus*, there is *Cricetomys gambianus* (a rat), *Mungos gambianus* (a mongoose) and *Nycteris gambianus* (a bat); and *gambianus* is used as a specific name in many other non-mammalian animals.

Names in a species-group, a genus-group and a family-group are separate: a specific name (the second name in a binomial) cannot be 'upped' to generic rank. On the other hand, by the *principle of coordination*, a name given to a subspecies is deemed to have been given to a potential species, and vice versa; a name given to a genus is deemed to have been given to a potential subgenus and vice versa; and a name given to a family is deemed to have been given to a potential subfamily, tribe, subtribe or superfamily. So subspecies can be 'upped' to species rank or species downgraded to subspecific rank – and so on.

In some instances, the name of the describer and the date are placed within parentheses, which indicates that the species was originally described in a different genus to that in which it is now placed. For example, *Bunolagus monticularis* (Thomas, 1903) means that Thomas in 1903 ascribed *monticularis* to a genus other than *Bunolagus* (in fact, he described it as *Lepus monticularis*), whereas *Lepus capensis* Linnaeus, 1758 has no parentheses because Linnaeus ascribed it right from the start to the genus *Lepus*. Two authors with the same surname are usually distinguished by a single initial. Thus in *Pronolagus crassicaudatus* (I. Geoffroy, 1832) the 'I.' distinguishes Isidore Geoffroy St. Hilaire (usually shortened just to Geoffroy) from his father Étienne, who would be referred to as E. Geoffroy.

Scientific names are Latin or latinized; so a specific name, if the species name is an adjective, must agree in gender with the generic name. Thus, when the Savanna Elephant was transferred to a new genus, the former *Elephas africanus* became *Loxodonta africana*. Specific names may also be nouns in apposition and so not subject to gender agreement (so *pardus* in *Panthera pardus* does not become '*parda*'); or they may be genitives, as in *Galago gallarum* ('galago of the Galla people'). When a species is named after its discoverer or someone it is intended to honour, the name is a reflection of this: if the person is a male, *-i* is added to the person's name (*smithi*); if a female, *-ae*; and if two or more people, *-orum*. In the past, other terminations were occasionally used (e.g. *Tragelaphus oryx pattersonianus*, which, by the rules of nomenclature, cannot now be corrected to *pattersoni*).

The suffix at the end of the higher ranks indicate the status of the rank. A family name ends in *-idae*, a subfamily in *-inae*, a tribe in *-ini* and a subtribe in *-ina*. A superfamily ends in *-oidea*. A family-group name is formed from the (latinised stem of) the name of one of the included genera: so, Sciuridae from *Sciurus* and Bovidae from *Bos* (stem *Bov-*). The genus concerned does not have to be a valid genus, though usually it is; nor does it have to be the earliest named genus.

The *Code* is not entirely problem-free, and the International Commission on Zoological Nomenclature is constantly being asked to adjudicate on certain tough problems such as when a well-known name is threatened by the discovery of a long-forgotten name (*nomen oblitum*) which is thought to have priority. Applications to the Commission, and the Commission's Opinions, are published in the *Bulletin of Zoological Nomenclature*.

Types

A type specimen is the one to which the name of a taxon in a species-group is irrevocably attached. Usually, the type was designated or otherwise fixed as the type when the taxon was described (and is known as a holotype); but there may have been two or more specimens used by the original describer, and just one of these may have been designated to be 'the type' subsequent to the original description of the taxon (in which case it is known as a lectotype). Occasionally it is necessary, to sort out some vexing problem of nomenclature, to provide a type specimen retrospectively, using a specimen unknown to the original describer: this is known as a neotype. Every species and subspecies has a type locality, the locality at which the type specimen was collected. If the type locality is unknown, a subsequent reviser may fix it by fiat. A topotype (which may be collected later than the holotype) is any specimen from the type locality of the taxon.

There are types for a genus-group and family-group, but these are taxa rather than specimens. The type of a genus is a species; the type of a family is a genus.

Type specimens are extremely valuable because they are the basis for the naming and description of a species. Some type specimens are very old (dating from two centuries ago, or even more), others (for newly described species and subspecies) are barely a few years old. In museums, type specimens are kept under lock and key and are identified as types by red labels. Ironically, some types are not typical of the species they represent – because, by chance, the collector collected an individual which was atypical of the population as a whole. But once a type has been selected, it always remains as the type specimen.

Synonymy

Whereas homonyms are the same name given to two different taxa, synonyms are different names given to the same taxon. The earliest synonym is the senior synonym; the others are junior synonyms.

Up to about 1850, international communications were so poor that it was not uncommon for different authors to name the same taxon independently, even (in the case of taxa of the species-group) using the same type specimen. These names, objectively referring to the same taxon, are called objective synonyms.

Names given to putative taxa, which at the time were considered to be distinct but which subsequently were considered not to be distinct, are subjective synonyms. The senior subjective synonym is the name to be used for the taxon, but it is of course possible that one or more of the junior subjective synonyms may be removed from synonymy if subsequently it is considered that it represents a valid taxon. This illustrates the difference between nomenclature, an objective, artificial but nevertheless very useful system, and taxonomy, a subjective

study reflecting how we view the natural world. Because a currently recognized species may have one or more junior synonyms (by which the species was referred to in previous works), the names of junior synonyms are given for each species described in *Mammals of Africa*. The full citation for a synonym includes the name, describer's name and date of publication; in *Mammals of Africa* only the synonym name is given; additional details (describer's name, date, etc.) are provided by Allen (1939), Ansell (1989), Wilson & Reeder (1993, 2005) and Hoffmann *et al.* (2009).

A word is necessary here about the nomenclature of domestic animals. For fairly obvious reasons, the domestic form of a particular animal was often described and given a scientific name before any wild representatives were known, so that the name given to the domestic form has priority. This, however, creates enormous problems for subspecific taxonomy, biogeography and so on, and a ruling of the International Commission on Zoological Nomenclature published in 2003 stipulates that a name given to a domesticate should not be used for a wild taxon; the domestic species should either be included within the wild species or, preferably, treated for convenience as a separate species (which it is in one way, and is not in another). The history of the problem, the meaning of the ruling and the philosophy behind it, are recounted by Gentry *et al.* (2004). It explains, for example, why the African Wild Ass is called *Equus africanus* (von Heuglin & Fitzinger, 1866), rather than *Equus asinus* Linnaeus, 1758 – the latter name applies to the domestic ass or donkey.

The higher categories

The higher categories are, in essence, phylogenetic branches. To say that *Civettictis* and *Genetta* belong to the Viverridae, and *Crocuta* to the Hyaenidae, is to say that *Civettictis* and *Genetta* share a more recent common ancestor than either does with *Crocuta*. It is astonishing that, until very recently, there were no criteria for deciding on precise ranks above the species level. In general, these were set by some authority's fiat in the nineteenth or even the eighteenth century, and changed by incremental creep thereafter. The question has very rarely been asked, for example, why the Bovidae is ranked as a family, rather than as an order or a genus?

Recently, the idea of a relationship between a taxon's rank and its time depth (the time since it became separate from its sister-group) has been revived. For example, one can ask 'When did the family Lorisidae originate?' This question can mean either 'When did divergence between the family Lorisidae and its sister-group (probably family Galagidae) occur?', or 'When did the last common ancestor of the modern genera of Lorisidae live?' Goodman *et al.* (1998) suggested that, in mammals, a genus should have separated from its sister genera at least 4–6 mya (back to the Miocene–Pliocene boundary), and a family from its sister families about 22–23 mya (i.e. close to the Oligocene–Miocene boundary). Their elaborate scheme gives expected time depths for orders, semiorders, suborders, infraorders, superfamilies, families, subfamilies, tribes, subtribes, genera and subgenera. A simpler arrangement is to restrict the idea to the obligatory ranks (order, family, genus, as total groups) only (Groves 2001); the subordinate categories are inserted where needed merely to divide up a large, unwieldy obligatory taxon. Avise & Johns (1999) broadened such a scheme to comparisons with other

animal groups, specifically the cichlid fish of L. Victoria, which have a far shallower time depth than primates at corresponding ranks, and fruit-flies, which unexpectedly have a far deeper one. These authors envisaged either a gradual convergence of ranking schemes, or else the development of a new temporal-banding system alongside the Linnaean system.

It is probably too soon to expect even a mammal-wide consistency in fitting rank to time depth, but if any progress is to be made beyond the present state of subjectivity, then some such system must come. A problem, of course, is that it could not possibly apply to species, and a break between the taxonomy of species and that above the species level will become accentuated.

Methods of taxonomy

A – Collecting

Taxonomy has traditionally been the preserve of morphologists. Most of the world's natural history museums are devoted to storage cabinets full of specimens of animals and plants (preserved dry or in alcohol and not on exhibit to the public). Here generations of biological taxonomists have spent their careers, measuring and examining specimens with the naked eye, under the microscope, or by X-ray. In the case of mammals, the specimens are overwhelmingly skins and skulls; postcranial bones are scarcer and soft parts scarcer still. In the eighteenth and early nineteenth centuries, mammalian skins were usually stuffed and mounted in life-like postures. Later, when storage space came to be increasingly scarce, they came to be stored either as flat, opened-out skins or as slightly padded-out skins (called 'puppet skins') filled with cotton-wool or tow.

The morality of collecting biological specimens has rarely been discussed in the literature. Until the early twentieth century, much of the mammalian material in museums was supplied by people who were, in effect if not by designation, big-game hunters; it was opportunistic and unsystematic, and of course large mammals predominated. Most specimens, in fact, were not made available to museums but were kept as trophies, or even left where they fell. Major P.H.G. Powell-Cotton was one of a very few collectors who kept his entire bag (mainly African), which is today still available for study. Even Powell-Cotton, however, collected mainly what interested him (Primates, Carnivores and Ungulates) and in places that he enjoyed visiting (Cameroon, Sudan, Ethiopia, and DR Congo). Collectors in the twentieth century tried to address the imbalance between large and small mammals by collecting many of the smaller species such as rodents, insectivores and bats. This was perhaps appropriate in another way, too, as the tide of public opinion was turning – people who would loudly deplore the ruin of an elephant would have little objection to the collection of a dozen or so mice. At the same time, wildlife conservation was becoming a necessity, and collecting large species was becoming less and less ethical.

Given that we cannot do without collections, what should our guidelines be? It goes without saying that we should avoid collecting anything, whether large or small, that is of conservation concern, even if it is legal in the country concerned. It also goes without saying that collection methods should always be humane, but this is a much harder area to define. Should we avoid collecting intelligent species, whose cognition is closer to our own? It may seem

anthropomorphic, but it seems reasonable to conclude that species whose mental condition is more like ours – such as chimpanzees and gorillas, perhaps some other primates, and maybe elephants – have more claim to our moral concern than do other species. Other questions that should be considered concern an individual mammal's position in its social group, and its reproductive status. The human social setting must also be taken into account; it does not set a good example if foreigners collect and hunt when the local people are enjoined not to hunt (and if they do so, suffer legal penalties).

B – Sources of evidence

There is no substitute for minute analysis of morphological features when making a careful taxonomic analysis. Do, for example, individuals from different geographic regions have different patterns of basicranial foramina, shapes of the naso-frontal suture, or molar cusp arrangement? If they do, and the differences are consistent, then we classify them as different species; according to the Phylogenetic Species Concept, a diagnostic (100%) difference in just a single character, as long as there is a reasonable inference that the difference has a genetic basis, is sufficient to confirm their status as separate species. If they differ on average, but not absolutely, in one or more characters, then we might conclude that they are separate subspecies. Disentangling sympatric species (i.e. species with overlapping geographic ranges) can be much more problematic; here, we look for congruent patterns of variation in two or more characters.

At the level of species and below, morphometrics is often an extremely useful technique. Univariate or bivariate metrical comparisons may help in the construction of useful identification keys, but great care should be taken to exclude purely phenotypic effects, which may be caused by variations in diet, rainfall and temperature in different habitats. Similarly, differences in shape may be simply consequences of size differences, because of unsuspected allometric relationships. Multivariate analysis may not altogether get over this problem but, if phenotypic plasticity can be safely excluded, different techniques of multivariate morphometrics can be extraordinarily revealing.

At and above the species level where by definition character states are reticulate, cladistic analysis is essential for organizing basic phenetic information into a phylogenetic framework. Such an analysis results in a matrix of many different characters (often up to quite a large number), each of which is coded by its presence or absence or 'state'. A number of computer programs are available for analysing large sets of data, resulting in a cladogram, which is not itself an evolutionary tree but can be readily converted into one. The cladogram can in turn be converted into a taxonomic classification using the principle that taxa ought to be ranked according to the recency of common ancestry.

Behavioural characters have always been used in taxonomy, but have come into their own mainly since the 1930s, after the genesis and spread of ethology. A book such as Estes (1991) is an invaluable starting point for the use of ethological characters of African mammals in taxonomy. There are many examples where behavioural characteristics (e.g. displays, vocalizations, social organization) are species-specific and hence can be shown to be important in maintaining species boundaries and preventing wholesale

hybridization between closely related species. Two taxa that appear morphologically similar (at least to humans), and which may have been considered as populations within a single species, may exhibit quite different behavioural characteristics, which would indicate that they are indeed separate species. Behavioural characteristics should not be used solely as a criterion for species determination, but in conjunction with other evidence.

Chromosome morphology, amino-acid sequencing and DNA sequencing have been successively added to the methodology of the taxonomist since the 1960s. It is necessary to emphasize that these new methods have not replaced traditional methods, but have been added to them. There has sometimes been a distressing tendency to assume that if no difference can be found between two well-established taxa in a 100+ base-pair sequence, then the craniodental or pelage character differences somehow do not exist, or do not count. Presumably most gross morphological differences do have a genetic basis; failure to find differences in a studied sequence means simply that this basis lies elsewhere within the genome. Claims that a certain level of genetic distance between two taxa indicates a specific difference (while less than this indicates only subspecific, and more than this indicates generic difference) must be taken as a guideline only, because, as discussed above, whether a taxon ranks as a species or not depends not on 'degree of difference' but on diagnosability.

It must be acknowledged that phylogeography (the study of the principles and processes governing the geographic distributions of genealogical lineages [Avice 1994]) has proved extremely fruitful in enlarging our understanding of the processes of geographic differentiation within species, although so far it is mainly mitochondrial DNA that has been used as evidence. When karyotypes or DNA sequences of a particular taxon are published, it is essential there be some guarantee that the taxon has been correctly identified. A photograph, or a note of a museum voucher number, would serve to do this.

Case studies of species and subspecies

African elephant

Grubb *et al.* (2000) examined the case of the African elephant. The Savanna Elephant and the Forest Elephant have, at least since the mid-twentieth century, always been classified as two subspecies of a single species – *Loxodonta africana africana* and *L. a. cyclotis*, respectively. They are strongly different, and many of the differences are fixed and diagnosable. Each subspecies occupies a wide geographic range, over which it is homogeneous: they make no morphological approach to one another towards the boundaries of their ranges. By the criteria of the Phylogenetic Species Concept, they are distinct species, and Grubb *et al.* (2000) designate them as such: *Loxodonta africana* and *L. cyclotis*. Examining specimens from the very border of their ranges, Groves & Grubb (2000) found that in some regions they almost certainly interbreed, while in other regions there is no evidence that they do. Because their geographic ranges do meet, the Biological Species Concept interbreeding criterion can in principle be applied (suggesting only one species), but the results are inconsistent. There is no equivocation, however, according to the Phylogenetic Species Concept.

Bushpig and African buffalo

The taxonomy of two other species, Bushpig and African Buffalo, is analogous to that of the African elephant (Groves 2000). The Bushpig (*Potamochoerus larvatus*) and the forest-living Red River Hog (*P. porcus*) are not known to interbreed where their ranges meet; and hence they rate as distinct species under both Phylogenetic Species Concept and Biological Species Concept. Among the African buffaloes (*Syncerus*), the Cape Buffalo and Forest Buffalo, like the elephants, seem to interbreed in some regions and not in others and hence it seems reasonable, once again, to refer them to two distinct species under the PSC: *Syncerus caffer* and *S. nanus*, respectively. The case has been confused because the normally forest-living *S. nanus* extends well into the West African savannas and has there developed a subspecies, *S. c. brachyceros*, which converges, but only superficially and only to a slight degree, towards *S. caffer*.

Bushbuck

The most difficult case is that of Bushbuck. Traditionally, only one species has been recognized, *Tragelaphus scriptus*, but Groves (2000) suggested, on the basis of an earlier analysis by Grubb (1985), that there are actually several species of Bushbuck (and see Moodley & Bruford 2007). There is a small species (*T. scriptus*) with well-marked white stripes and spots throughout adult life, found in both rainforest and in the bush savanna in West Africa, and as far east as the Nile; and there is a large species (*T. sylvaticus*), in which the white marks nearly disappear in adults and the males become very dark, found throughout most of southern and eastern Africa. Their ranges not only abut but even interdigitate in Sudan, Uganda and north-eastern DR Congo, and it is remarkable that they have never, since the early twentieth century at least, been recognized to be distinct species. There are two complicating factors. The first is the existence of three other distinctive taxa (*decula*, *fasciatus* and *meneliki*) in the Horn of Africa and along the East African coast. While perfectly distinct from the two widespread species and from each other, two of them show superficial convergence with one or other of the widespread species (*fasciatus* has white marks like *T. scriptus*, *meneliki* is very dark like males of *T. sylvaticus*). Under the Phylogenetic Species Concept, there would in fact be as many as five species. The second complicating factor is the presence of a population (*ornatus*) in southern DR Congo and western Zambia that, on the face of it, looks like an intergrade or widespread hybrid between *T. scriptus* and *T. sylvaticus*. Yet the East African evidence suggests five species. Occasionally, the useful system formulated by Linnaeus, which has served so well for 250 years, comes up against the reality that evolution is a dynamic process.

Vernacular or common names

Most non-scientists prefer to use the vernacular (or common) name of a mammal rather than the scientific name. The problem with vernacular names is that a species may have several vernacular names, even within a single language, and several species may have the same vernacular name. When the vernacular names in different languages are taken into account as well, a species that is known unambiguously by its two-word scientific name, may be known by 10, 20, or more

vernacular names. It is clearly impractical to include all vernacular names in *Mammals of Africa*. Because of the widespread use of the English language in Africa, the preferred English vernacular name is given for each species. For some species, alternative English vernacular names are given in parentheses. French and German vernacular names are also provided if available; but many of the smaller species do not have vernacular names in these languages. In general, it is much better and more precise to refer to a species by its scientific name.

The English vernacular names used in these volumes are not necessarily the most well-known names. Using as many published works as possible, and especially the names proposed by Wilson & Cole (2000) and Wilson & Reeder (2005), *Mammals of Africa* has chosen what is considered to be the best and most accurate vernacular name for each species. Whenever possible, the following criteria have been used: (a) part of the vernacular name of a species should include the vernacular name of the genus, a name that is shared by all members of the genus; (b) no two genera can share a generic vernacular name, but additional words can be added to provide uniqueness (e.g. African, Gambian, etc.); (c) a vernacular name should be the translation of scientific name (e.g. *Myotis* = Mouse-eared); and (d) a vernacular name, likewise, should be a translation of the scientific name of the species and hence reflect the wishes of the describer. Well-established vernacular names may, however, be retained if they are firmly engrained in the literature. It has not always been possible to follow these criteria, but in general, the vernacular names used in *Mammals of Africa* bring a measure of consistency and logic to a rather chaotic naming system.

In the past, vernacular names have normally been written in a variety of ways. For example, the vernacular name for *Epomophorus gambianus* has been written as Gambian epauletted fruit bat, Gambian epauletted fruit-bat, or Gambian Epauletted Fruit Bat (note the variation in the use of capital letters and hyphens). But there are ambiguities; is this a fruit-bat with epaulets, or a bat that feeds on epauletted fruits? The modern convention, used here, is that all words in a vernacular name begin with a capital letter, except where two words are joined by a hyphen (as in Fruit-bat), and that hyphens are used where the first word is adjectival to the second. Wherever possible, the vernacular name of the genus is included as part of the name of the species, so that all species in a genus are linked together by part of their vernacular names. The vernacular name of a particular species is adjectival to the vernacular name of the genus. Thus the genus *Dendromus* has the vernacular name of 'Climbing Mouse' and the vernacular names of some species within this genus are Kivu Climbing Mouse (for *Dendromus kivuensis*), Grey Climbing Mouse (for *D. melanotis*) and Nyika Climbing Mouse (for *D. nyikae*). In some instances, when these criteria were applied, a vernacular name became too long and complicated, so a shortened easier-to-remember name has been used. Likewise, well established and well-known vernacular names were maintained to ensure continuity and simplicity, e.g. Lion, Serval, Gerenuk, etc. However, in the case of some species, it has been necessary to add a qualifier to avoid any possibility of ambiguity, hence Greater Kudu (for *Tragelaphus strepsiceros*) and Lesser Kudu (*T. imberbis*), and Common Warthog (*Phacochoerus africanus*) and Desert Warthog (*P. aethiopicus*).

Classification and *Mammals of Africa*

The classification used in *Mammals of Africa* mostly follows that given by Wilson & Reeder (2005), but authors were given the liberty to follow a different classification if there were good, and published, reasons for doing so. Hence the genera, species and subspecies may, in some instances, differ from those given in earlier publications on African mammals and in Wilson & Reeder (2005). Of course, taxonomy is often controversial (as explained above), so parts of the classification used in *Mammals of Africa* may in time prove to be incorrect. This is inevitable as new information comes to light and our knowledge of African mammals increases.

The sequence of orders presented in the six volumes mostly follows the 'classical' tradition that has evolved during the last two centuries. There have however been some significant changes. Until about 100 years ago, for example, the Lagomorpha (hares and rabbits) were included within the Rodentia (squirrels, rats, mice and their allies) but are now placed in their own order. The Insectivora is no longer considered as a natural group, and is now divided into four separate orders: the Macroscelidea (elephant-shrews or sengis), Soricomorpha (shrews, moles and their allies), Erinaceomorpha (hedgehogs and their allies) and Afrosoricida (golden-moles, tenrecs and otter-shrews). The sequence of presentation of families within orders, and genera within families, mainly follows Wilson and Reeder (2005) and reflects in a very general way the phylogenetic relationships between them. But for some taxa, the sequence of presentation is pragmatic rather than phylogenetic, e.g. the genera within the family Muridae (Rodentia) are arranged by subfamily, and then alphabetically by genus; within each genus, species are also listed alphabetically.

It does not necessarily follow that a new hypothesis in respect of relationships (and hence classification) is correct; in the 1980s it was suggested, on the basis mainly of brain structure and neurology, that

the fruit-bats (Megachiroptera) were more closely related to primitive primates than to the microbats (Microchiroptera). If proved to be correct, it would mean that the Chiroptera were diphyletic in origin rather than monophyletic. A great deal of fascinating research was generated as a result of the hypothesis (see e.g. Pettigrew 1986, 1991); but in the end, the similarities of fruit-bats to primitive primates was shown to be due to convergence and not to a common ancestry. Hence the hypothesis was discarded and the Chiroptera are still regarded as monophyletic.

The Proboscidea (elephants), Hyracoidea (hyraxes) and Sirenia (manatee and dugongs) have, for a long time, been placed next to each other because of their unexpectedly close phylogenetic relationship. Recent research has shown that these three orders, together with the Afrosoricida (golden-moles, otter-shrews and tenrecs), Macroscelidea (elephant-shrews or sengis) and Tubulidentata (Aardvark) belong to a superordinal grouping called Afrotheria. The Afrotheria, as the name suggests, is thought by its proposers to have originated and diversified within Africa, and hence to be a very 'African' group of mammals. Although the earliest fossils so far assigned to the Afrotheria are actually North American (Asher *et al.* 2003), the superorder today is more diverse in Africa and Madagascar than elsewhere; in fact, two of the orders (Tubulidentata and Macroscelidea) are entirely confined to the African continent, one occurs only in Africa and Madagascar (Afrosoricida), one extends beyond Africa only as far as the Levant and the Middle East (Hyracoidea), and two (Proboscidea and Sirenia) are more widespread as well as occurring in Africa. The Afrotheria hypothesis was proposed by Stanhope *et al.* (1998) on molecular grounds and subsequent molecular studies have substantiated it; on the other hand, Asher *et al.* (2003) could find no morphological characters that would unequivocally characterize such a grouping although there did not seem to be any glaring incongruities, while most recently Wible *et al.* (2007) succeeded in validating Afrotheria on the morphological level.

CHAPTER EIGHT

Behaviour and Morphology

Jonathan Kingdon & Fritz Vollrath

Morphology is the most interesting department of natural history and may be said to be its very soul. What can be more curious than that the hand of a man, formed for grasping, that of a mole for digging, the leg of the horse, the paddle of the porpoise and the wing of the bat, should all be constructed on the same pattern, and should include the same bones in the same relative positions? ... The explanation is manifest in the theory of the natural selection of successive slight modifications. ... The innumerable species, genera, and families of organic beings, with which this world is peopled, have all descended, each within its own class or group, from common parents, and have all been modified in the course of descent.

Charles Darwin, *The Origin of Species*, 1859

How does morphology relate to behaviour?

Humans, golden-moles, zebras, sea cows (sirenians), bats as well as many more mammals are profiled in considerable detail in the volumes that follow. Grasping, digging, galloping, paddling and flying are patterns of behaviour that have given rise to all these modification of limbs following ‘the course of their descent from a common parentage’.

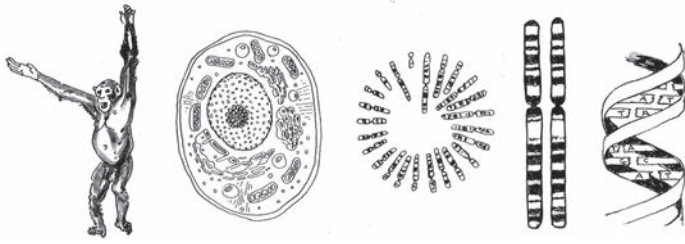
Contemporary evolutionary science brings many new perspectives to Darwin’s words and insights, and one concerns the relationship between function and form, or, more precisely, the relative primacy between behaviour and morphology. It would seem counter-intuitive to allocate a primary formative role and priority to ephemeral, insubstantial behaviour (often belittled as ‘mere’ behaviour) over the physical substantiality of living animals and their bodies, bones and fossils. And yet it is so. Many authors within *Mammals of Africa*, under the heading ‘Adaptations’, have described specific morphological peculiarities and linked them with the species-specific behaviours of which they seem to be the agents. This is appropriate because, over evolutionary time-spans, behaviour in its most comprehensive sense has driven morphology. In addition, as the fossil record so vividly illustrates, morphology, too, is not the static state of being that it seems to be from an immediate, contemporary perspective. Rather it is the manifestation of an organism’s adaptive condition at a given moment in time and as such it is, to a greater or lesser degree, fluid and subject to continuous change, but at a much slower rate than is behaviour, which is inherently flexible and able to respond immediately to challenges.

This chapter aims to demonstrate the link between what animals *do* and the structures that have evolved to increase the efficiency

and effectiveness of that behaviour. Given the great diversity of expressions of form, we also seek to reconcile that extraordinary plasticity with the common body plan that underlies all mammal morphology. To this end we present a selection of behavioural and mechanical dimensions to ‘form and function’ as well as providing a guide to the terminologies employed in the description of anatomical and morphological features.

Instead of using its conventional near-synonym, the more ancient and more anthropocentric ‘Anatomy’, Darwin used the word ‘Morphology’ to create an important new association. From bald description and operative comparison of shape Darwin went on to add functional explanations. These, of course, required both implicit and explicit integration of the only rational explanation for the great diversity of morphologies, which was the mechanism that brought them into being – natural selection.

‘Morphology’ was a relatively new word in Darwin’s time. Indeed, the ‘science of shape’ had been founded by the great German naturalist, poet and thinker Goethe, in 1790, not long before Darwin’s birth (1809). At the time it was a particularly inviting field of study in Europe and America because museums, zoos and wealthy naturalists were making ever more diverse collections of animals (or their cadaverous relics) available for scientific study. The specimens, in turn, were interesting and exciting because many were newly discovered, exotic and in need of examination, classification and explanation. While the specimens were relatively easy to collect and export, their behaviour and ecology were left behind where they came from, typically unrecorded or with only marginal comments. One privilege of our own generation has been to be among the first to study animal behaviour, in depth, and in the knowledge that this apparent ‘insubstance’ has been a driving force in the evolution of animals and their wonderful diversity of form.



Today, expressions of the 'science of shape' embrace internal organs, tissues, cells, enzymes and molecules. A living mammal contains multiple 'shapes', each of them expressions of self-regulating systems that range from gene to whole body. A chimp body contains about 100 trillion cells; each cell has a nucleus; each nucleus has 48 paired chromosomes; of every pair, one chromosome is from each parent; chromosomes consist of packed strands of DNA. Genes are DNA segments coded to make proteins.

Knowledge of exotic animal behaviour was rudimentary in the nineteenth century but major differences in, say, locomotion, were so obvious that Darwin could confidently choose grasping, digging, galloping, paddling and flying as examples of activities that could become more efficient through the 'selection of successive slight modifications' in the limbs that served these activities or behaviour patterns. As our opening quotation emphasizes, linking form to function was integral to Darwin's thinking. A more contemporary expression of that preoccupation – working out how functional behaviour gives rise to morphological form – remains central to the interest and significance of an inventory of mammalian diversity such as *Mammals of Africa*.

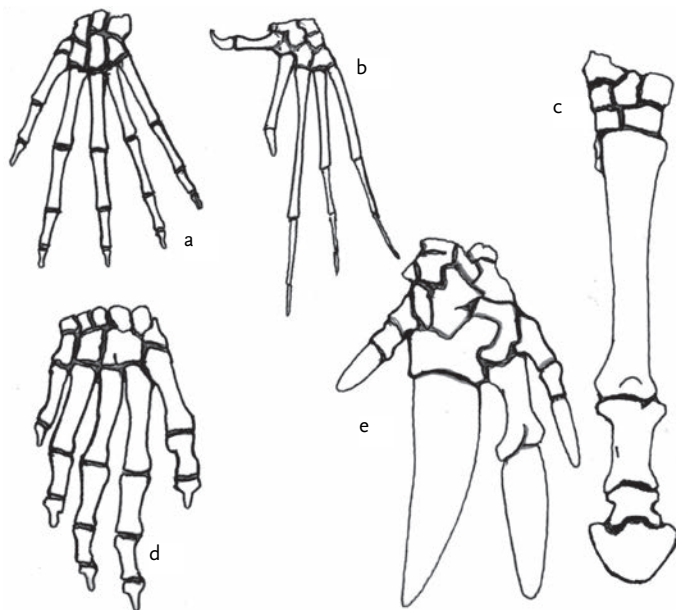
In addition to relating anatomical form to activities and behaviour, Darwin also closely observed how morphologies had specific regional contexts (islands, of course, being of special interest) and he demonstrated how the shapes of animals and plants were adapted to what we would now call ecological niches. He also observed and compared the morphology of living and fossil forms. As we begin to refine our understanding of African environments and explore their

many changes over time we can begin to appreciate how mammals have had to modify their behaviour and, ultimately, their anatomy to survive change, competition and other vicissitudes. For Darwin, the soul of natural history was comparative morphology. For contemporary scientists and naturalists his metaphysical metaphor would have to include behaviour and genes, the 'insubstances' that so closely approximate to traditional concepts of soul or spirit.

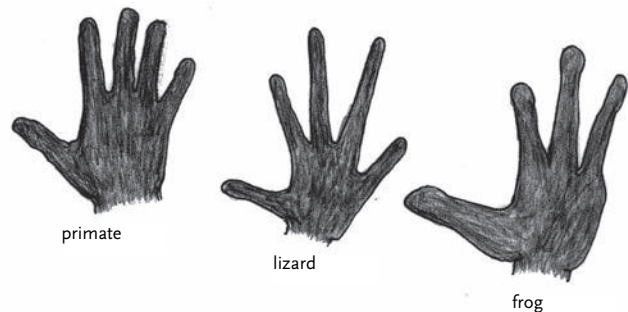
It is worth remembering that in the nineteenth century exploring and comparing morphologies and making deductions from the clues they provided was as novel and revealing as DNA fingerprints are today. The comparison of DNA patterns has become a new material base for contemporary taxonomy. We can already see that the 'science of shape' is gaining many new and important insights from the 'science of the shapers of shape'. Some of these essentially new connections will be explored in this chapter and in the volumes that follow.

Behavioural shifts give rise to morphological change

The ancestral five-digit mammalian forelimb has been morphed through infinitely small incremental changes into all the very different behavioural functions that Darwin listed and many, many more. This shift by one utilitarian morphology into another (probing finger to pounding hoof) demonstrates that within specific physiological constraints most gross features of mammalian anatomy are capable of surprising modification and, ultimately, total functional transformation. In trying to understand and recreate the many steps in such transformation, comparisons cannot be superficial. Taking Darwin's example of primate hands; lizards, frogs and even salamanders have fingered hands and feet, the latter usually having five digits. These resemblances *do* denote evolutionary relationship, but at levels so deep as to confirm that morphology is only comprehensible if grounded in the broadest ethological, physiological, anatomical and genetic contexts and in an explicitly evolutionary framework. Non-scientific systems that make superficial associations between like and somewhat alike, especially on the basis of a single feature such as 'hands', would link humans with newts and geckos while limbless lizards would join eels and worms. 'All true classification is genealogical; that community of descent is the hidden bond that naturalists have been unconsciously seeking, and not some unknown plan of creation, or enunciation of general propositions, and the mere putting together and separating of objects more or less alike' (Darwin 1859: 420). Only rigorous scientific methods can emancipate us from primitive, traditional systems that based their



Manus: a. human *Homo sapiens*, b. fruit bat *Stenonycteris lanosus* (foetal), c. zebra *Equus quagga*, d. Dugong *Dugong dugon* and e. golden-mole *Chrysochloris* sp.



Outlines of primate, lizard and frog hands.

taxonomies on single or arbitrary criteria, such as ‘hands’, which are not that different from basing classifications (and value systems) on ownership, economic worth, castes and ‘clean’ or ‘unclean’ animals.

Once the complex of characteristics that unites mammals and distinguishes them from other vertebrates have been identified (the diagnostic features of mammals are dealt with elsewhere), it is the mutability of virtually every feature that becomes of central concern for the ‘science of shape’.

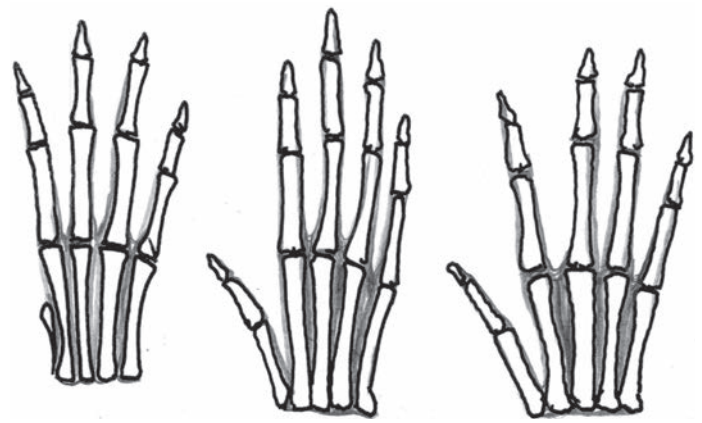
Of course the most obvious diversity of form (in mammals as in other organisms) concerns differences between different orders and families of mammals. Throughout the class Mammalia, diversity of form is based upon the modification of already existent structures. This can involve elaboration, such as the extension of digits into the struts of a bat’s wing, or reduction, as in the paring away of all but one digit in a horse or zebra’s limb.

How does this happen? What are the forces at work that can turn a little shrew-like hand into the bat’s spreading wing over a few million years? Begin with one, apparently rather obvious observation: morphology tends to be conservative but behaviour is not; our children bear our likeness but their behaviour differs from ours in innumerable and trend-setting ways. Furthermore, as conditions are constantly changing, the existence of behavioural plasticity becomes essential, particularly when changes are sustained generation after generation. Individual adaptability, together with natural selection for appropriate behaviour are fundamental to the evolutionary process and to the evolution of diversity. Since behaviour is the primary strand of our argument we can categorize it under headings similar to those used in these volumes to describe the biology of species: locomotion, foraging, communication, social facilitation, predator avoidance etc. Consider then, some examples of how changes in structures have derived from shifts in specific behaviour patterns.

Innovations in locomotion or limb-use

It was, perhaps, because humans make their own bodies the vehicle and prototype for most of their ideas about nature that naturally thumb-less monkeys so horrified early naturalists that they called them *colobus*, Greek for ‘cripple’! The history of science’s slow progress towards some sort of objective detachment is littered with this sort of visceral subjectivity. The real reasons for suppressing the thumb have to do with the adoption, by one lineage of ancestral monkeys, of a leaf diet and an elegant energy-saving form of arboreal locomotion. No digital manipulation is required of a leaf-eating monkey because, for the most part, it is easier to eat floppy material directly off the tree rather than handle it. A further, and related reason for doing without a thumb is that the remaining fingers have been aligned into a robust, weight-bearing *hook* that can support a body that has become exceptionally heavy because the stomach has been transformed into a copious, leaf-fermenting vat. A monkey that must catapult its barrel of a body across breaks in the canopy puts very different stresses on its hands than a smaller, slimmer primate that combines rapid traverses across the tops of fine branches with fast capture and manipulation of small insects.

Even within a single closely related group of the latter type of monkey, relatively modest differences in proportion can be instructive. African guenons, of the genus *Cercopithecus*, include a large-bodied,



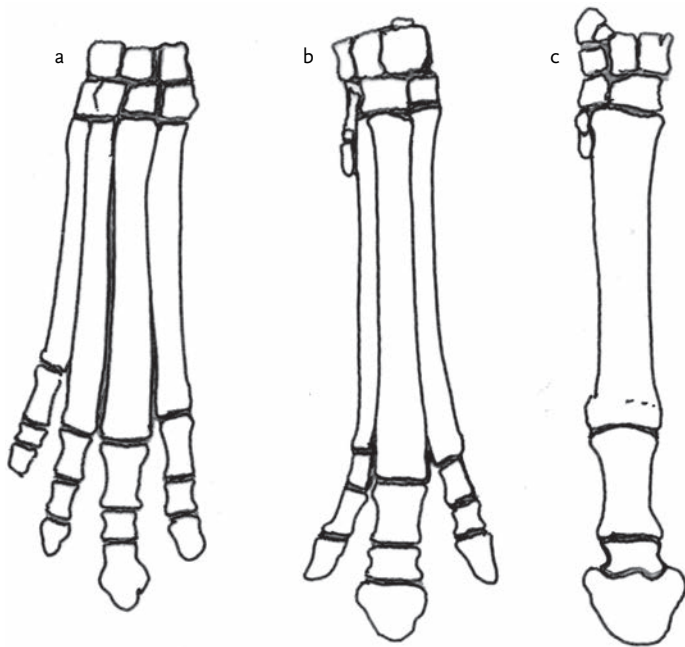
Right manus of, from left to right, *Procolobus rufomitatus*, *Cercopithecus nictitans* and *C. pogonias*.

relatively slow species, Putty-nosed Monkey *C. nictitans*, which has long, slender fingers and a short, weak thumb (probably for similar reasons to the colobus) and Crowned Monkey *C. pogonias*, a small-bodied, fast omnivore with a compact, small hand and a relatively strong thumb. The latter is an adept snatcher of agile insects on thinner branches and twigs in the canopy, the former is a heavier animal that eats both fruit and leaves and prefers thicker branches in the shade where less active arthropod (animal) prey are discovered under bark or on trunks (Gautier-Hion 1978, Struhsaker & Leland 1979, Kingdon 1980, 1988).

Detailed studies of the behavioural ecology of primates can reveal proximate, species-specific adaptations of this sort but they can also help resolve larger evolutionary questions. Fully arboreal African monkeys were long assumed to be archaic while more terrestrial species were regarded as later, more derived forms that had descended from the prototypical arboreal niche (Schwartz 1928). A combination of detailed comparative anatomy and molecular studies has shown this to be an inversion. Instead, it was semi-terrestrial guenon ancestors that effectively re-colonized the forest canopy (Kingdon 1971, 1988, Dutrillaux *et al.* 1982). In the process they modified (or even remodified) the proportions of their hands.

The ancestors of one semi-terrestrial monkey took to exploring potentialities for life along the 5000 km southern borders of the Sahara desert. This exposed successive generations to an ever-fluctuating frontier where trees were frequently scarce. By seeking to make a living in steppes where trees were rare, alongside a variety of fleet predators, the ancestors of the Patas Monkey *Erythrocebus patas* had to become extremely fast *in spite of* possessing typically primate hands and feet. This ecological and behavioural shift led to elongation of the entire length of the limbs, including the bones of the hands and feet. The Patas Monkey has become a sort of ‘primate greyhound’ and, in adopting an almost wholly terrestrial existence, has paralleled some of the modifications typical of other fast, light quadrupeds, such as jackals *Canis* spp. and the Cheetah *Acinonyx jubatus*. Elongation has not been the only change. Because it takes no weight during running, the thumb has greatly reduced but has been saved from disappearing altogether because of its residual usefulness for manipulating food.

Elongation of limbs and simplification of extremities are evident in all fast cursorial mammals but the trend has been most extreme in horses and zebras. Fortunately the equids have an exceptionally rich and continuous fossil record; and the progressive reduction and



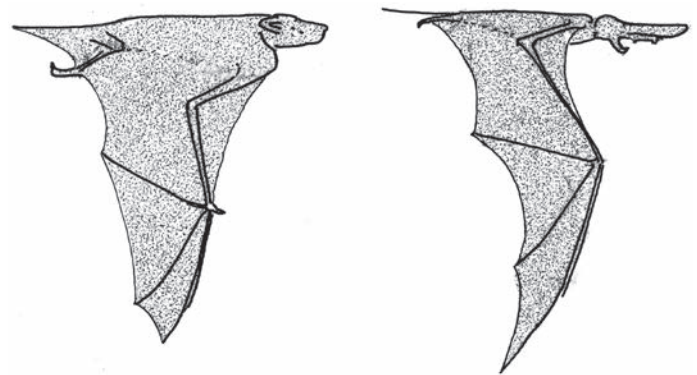
Evolution of zebra foot. a. *Hyracotherium* (early 4-toed equid); b. *Miohippus* (Miocene 3-toed equid); c. *Equus* (modern 1-toed equid).

eventual loss of all but one digit is beautifully illustrated by fossils that range from the Eocene to the Holocene.

The most extreme differences in the proportions of 'hands' are to be found among bat wings. The shortest wing, relative to the size of the bat, belongs to Moloney's Mimic Bat *Mimetillus moloneyi*, the longest to the Large-eared Giant Mastiff Bat *Otomops martiensseni*. Moloney's Mimic Bats are small and agile, living under loose bark, with body and skull appropriately flattened to this end. Nowhere is the formative role of behaviour in shaping morphology clearer than in *M. moloneyi*. In scurrying in and out of their loose bark refuges or in clambering up tree trunks to get to an elevated launching pad the short forearm and stubby little thumb are almost as active as the

forelimb of a true quadruped. This agility is achieved by a unique folding pattern of the digits, the more distal of which have been secondarily shortened. The proximal digits of the wing are of the same length as the forearm and fold neatly under it in such a way as to minimize any risk of snagging. Behind these digits the very short distal ones fold away within the tightly furled umbrella of this very versatile hand-wing. These bats can open up to become highly mobile on their one-fingered forearm or, like a deck-chair, fold up into a flat, inconspicuous and easily stored package. (There are some similarities here to the Central American vampire bat, *Desmodus*, which has to sneak up on, and run away from, bigger mammals to suck blood.)

Sloughing tree bark represents a significant microhabitat for bats but it is intrinsically temporary and subject to predation from primates, birds and snakes. Under such constraints Moloney's Mimic Bat has developed a forelimb that combines flight with some of the mechanical advantages of a climber's limb. Among the costs are a need to take frequent rests (because such a short wing requires very fast and tiring wing-beats) and the need to take off from a height, because of the initial drop before lift can be achieved. The Large-eared Giant Mastiff Bat, instead, has long, pointed, sickle-shaped wings that allow it to fly very fast, very high, over great distances. It is the migratory swift, *Apus*, of the bat world, with wings that have the highest aspect ratio of any African bat and the greatest elongation of digits in any mammal.

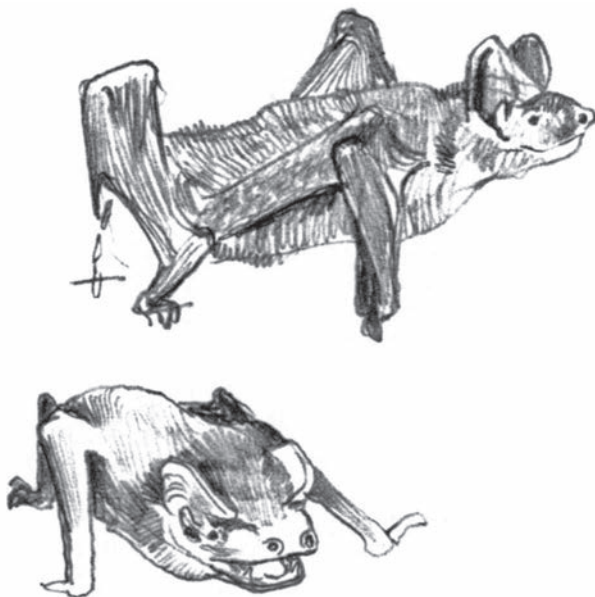


Wing outlines of *Mimetillus moloneyi* (left) and *Otomops martiensseni* (right).

Changes in foraging or food processing

Limbs and bodies can change proportions for many reasons and elongation of any feature is always a significant change. Lamarck had the idea that giraffes grew long necks by stretching them. Lamarck was right: but not in the way he imagined. Lengthening necks by stretching them is not the inherited adaptation that Lamarck envisioned. However, inhabiting an environment and adopting a habit where there are rewards for neck elongation could very well have become a trait that spread through some ancient ancestral population of proto-giraffes. This behaviour could be consistently rewarded if it offered unique access to plentiful food resources that were untapped by other herbivores.

Giraffes stretch their necks because they seek to browse from the tips of high branches or from the tops of lower canopies. This is their foraging niche. It is a niche where they have few competitors and no competitor at all within their current morphological guild, which is that of heavy-weight, selective browsing ruminant.



Mimetillus moloneyi sketches.



Diagram of head of Giraffe *Giraffa camelopardalis* showing ossicones, tongue, vertebrae, etc.

Incidentally, necks also power uniquely giraffid 'necking' contests that help settle inter-male competition for females (Coe 1967, Simmons & Scheepers 1996). The weight of male heads increases by osteoblastic processes very similar to the evolutionary ones that gave rise to ossicones in the first place (Kingdon 1979).

Even today giraffe necks vary individually in relative length. Length is governed by the time neck-growing genes are in operation. Thus necks are actually lengthened by extension in the activity of genes that control growth and length.

Browsing, like all food-getting, is behaviour, and the earliest, possibly okapi-like, giraffes would have had to stretch their necks to reach the choicest sprouts and buds. Perhaps this behaviour was learned, perhaps it became inherited, or, more likely, the two became concerted, as with the giraffe-antelope or Gerenuk *Litocranius walleri*, which reaches for nutritious herbage on higher branches by standing on its hindlegs, thereby augmenting its already exceptional reach. Proto-giraffes were also likely to have inherited a proclivity for out-reaching other browsers but the nutritional rewards allowed an already large animal to get still larger. One advantage of eating young, nutritious growth that other browsers could not reach would have been less of the toxins that many plants generate in response to browsing and more of the concentrated nutrients of sprouts that were always exposed to the sun. Such specific preferences allowed higher-reachers to crop better forage and hence breed more and stronger offspring with just those traits that had enhanced the survival of their parents and their lineage.

Continued natural selection over very many generations would have fine-tuned foraging behaviour together with a longer and more muscular tongue and, eventually, and in concert with a longer neck, a stronger heart and valved arteries (to cope with sudden surges of blood pressure). All these morphological changes would have been the consequence of minor initiatives in foraging behaviour, not the other way round, so that it is logical to conclude that behaviour was the innovator while pre-existent morphology was the constraint: behaviour was the evolutionary motor while morphology was a sort of anchor, serving to ensure that the many other advantages of being a two-toed ruminant were retained. The constraint of pre-existent structures is nowhere more apparent than in the giraffes' laryngeal nerve, which

originally linked the brain and larynx, a distance of a few centimetres. Because this nerve always loops around an aorta that has remained close to the heart, elongation of the neck in evolutionary time has required an ever longer detour of the recurrent laryngeal nerve until in modern giraffes it runs several metres down the entire length of the neck before ascending all the way back to reach the larynx.

While giraffes exemplify the role of foraging behaviour in shaping an ecological niche and the role of ecology in shaping morphology, it is only the most conspicuous example for an impressive radiation of African herbivores. Notably the ruminants, which, in addition to the giraffes, embrace those most typically African animals, the bovids, which encompass about a dozen distinct lineages, including the many forms of antelope.

Bovids are interesting because they demonstrate a great diversity of foraging niches that are the result of very early behavioural specializations coupled with morphological adaptations that then became the hallmark of their descendant lineage. They range from the rabbit-sized Royal Antelope *Neotragus pygmaeus* to the cow-sized Common Eland *Tragelaphus oryx* and they occupy quite distinct foraging niches. These centre on a combination of dietary types, ecological strategies and physiological refinements that have allowed them to radiate into a variety of special habitats. For example, large-bodied African Buffalo *Syncerus caffer* are mobile large-scale grazers in moist but climatically unstable habitats whereas small-bodied dik-diks *Madoqua* spp. are high-quality browsers able to survive on small, permanent territories in waterless scrublands because of their special physiology. By contrast, oryx and kin (Hippotragini) are relatively large-bodied mobile grazers able to live in arid or impoverished habitats but at low densities, while the Impala *Aepyceros melampus* is a medium-sized specialist in living along woodland/grassland ecotones, able to switch from grass to browse and sustain locally high densities.

Ever more refined, behaviour-led adaptations are evident in the duikers (Cephalophini), where individual species specialize in following particular patterns of fruit-fall. Thus a broad-mouthed species, the Bay Duiker *Cephalophus dorsalis*, ranges far and wide at night, seeking larger, rarer, fruits, while the diurnal, very localized and territorial Weyn's Duiker *C. weynsi* concentrates on the richest, most diverse forest zones where, by being attentive to the movements of primates and hornbills, they can rely on a year-round rain of nutritious plant-parts, particularly fruits and flowers.

The entire radiation of African bovids can be understood in terms of behavioural adaptation to different ecological situations and the adoption of modes of making a living, often within the constraints of a very particular and demanding habitat.

Quite minor shifts in foraging technique can give rise to interesting changes in anatomical details. For example, needle-clawed galagos *Euoticus* spp. have become different from their closest relatives through a greater dependence on tree exudates as their major source of sustenance. As a preponderance of gums ooze from tree trunks and very large branches the galagos need to spread-eagle their limbs and get a tight grip on the bark while levering chunks of gum away with their incisor teeth. To be able to accommodate this specialist foraging behaviour, originally flat, blunt finger-nails have developed sharp points allowing a firm, embedded grasp.

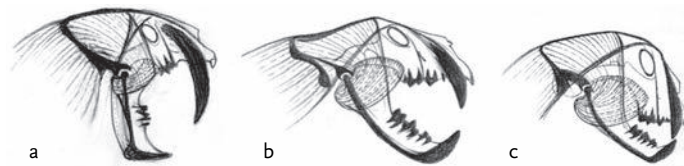
It is common enough to see shape vary among individuals, but Liers *et al.* (1990) recorded skull growth patterns varying seasonally within a local population of the common Multimammate Mouse

Mastomys natalensis. In the same population, Fadda & Liers (2009) measured significant differences in skull proportions between entire generations born during wet and dry years. They found that a prolonged drought had lasting effects on the shape of adult skulls. While most of the skull of the much smaller drought generation was simply scaled-down this did not extend to the brain, which was larger, relative to the rest of the skull, making for different proportions between the two generations.

Suppose that a discrete population of such 'large-brained' mice lived under drought over a very long period while a geographically separate population enjoyed a consistently benign climate. On morphological criteria alone the two might merit being treated as separate species. Indeed, with enough time and enough geographic separation speciation could be the outcome.

On the other hand, without the two elements of time and genetic separation such drought-induced differences represent little more than an entire generation becoming runts. Nevertheless, this example implies that, given enough time and isolation, species can emerge from common and natural physiological responses to environmental difference.

Carnivore skulls and teeth provide particularly good examples of foraging (in this case scavenging or killing) techniques that shape morphological form. For example, compare the skull shape, chewing muscles and teeth of, say, the insect-swallowing hyaenid Aardwolf *Proteles cristatus* with those of a bone-crunching hyaena or put the throttle-clamp of a Cheetah next to the killing bite of a Lion or the slicing stab of the recently extinct African Sabre-tooth *Megantereon*.



Skulls and tooth orientation in three felids, indicating different killing techniques.

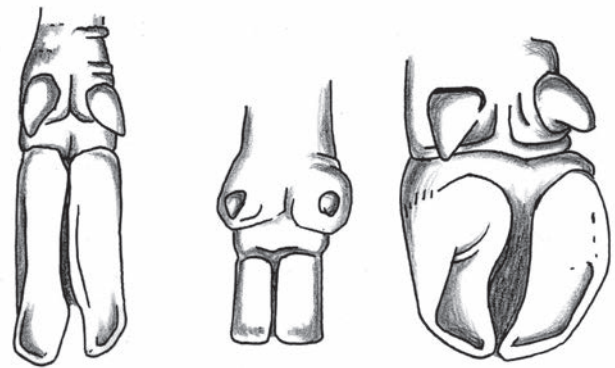
- Megantereon* sp. Sabre-tooth. Stabbing strike by enlarged upper canines. Principal force exerted by neck muscles.
- Panthera leo*, Lion. Canine bite. Deep pincer action by long canines in both jaws.
- Acinonyx jubatus*, Cheetah. Sustained clench by short, bunched jaw muscles. Clamp on throat of prey enhanced by steep angle of face and down-turned maxilla (after Kingdon 1977).

Such comparisons of the species-specific buttressing of skulls display the mechanics of leverage around the front or back ends of the tooththrow (or the atrophy of both in the Aardwolf). Remembering that every structure is 'the sum of many contrivances', each with a long evolutionary history, all predicated on highly specific behaviours, every head shape can be seen to manifest the physiology and mechanics of a species-specific killing or food-gathering technique. Lion, hyaena and other heads are telling illustrations of Darwin's insight into the dynamics of carnivore evolution. 'Some carnivores, ...being enabled to feed on new kinds of prey, either dead or alive; some inhabiting new stations, climbing trees, frequenting water, and some, perhaps, becoming less carnivorous. The more diversified in habits and structure the descendants of our carnivorous animal became the more places they would be enabled to occupy.' How Darwin would have relished watching all these

species going about their predatory businesses, wild yet unafraid of their human observers, in Serengeti or Kruger National Parks!

Shifts in environment/habitat

All habitats have borders and some, like rivers, are essentially linear. It is along these margins or ecotones that mammals living in neighbouring zones most readily (and literally) shift from one habitat to another, but it is probably climatic change that has had the greatest influence in forcing animals to adapt to different habitats. Our earlier example of the Patas 'greyhound' is but one of many. At the other extreme, in a continent that has been dry for much of its history, swamps have tended to be ephemeral or, if of longer duration, have been quite localized. The one antelope group that has been best placed to invade swamps has been the waterbuck tribe, or Reduncini, which made an early accommodation to living along grassy drainage lines. By shifting down the catena into the permanently flooded sumplands (perhaps mainly to mitigate predation), this type of antelope has given rise to the lechwes, *Kobus leche* and *K. megaceros*. Aside from cryptic physiological adaptations, their most obvious adaptation is the development of long, splayed hooves. These limit the animals' ability to live anywhere other than in marsh and it is significant that lechwes of any sort have not survived or spread outside Africa's two most extensive regions of swamp.



Hooves of, from left to right, *Kobus megaceros*, *Oreotragus oreotragus* and *Syncerus caffer* compared.

Another antelope that is quite severely constrained by the development of specialized toes is the Klipspringer *Oreotragus oreotragus*. These animals are also likely to have made their initial accommodation to an ostensibly impossible habitat; steep, rocky country (probably in an extensive region of deeply dissected mountains, such as Ethiopia). Their invasion of such a difficult habitat for a hoofed animal was probably driven as much by the need to find refuge from predators as the rewards of forage up among the crags, kloofs and kopjes. Indeed, in some parts of its range the Klipspringer tends to descend and leave these refuges to feed, yet it always returns to ruminate, rest or sleep among the rocks and cliffs. Its behaviour of leaping about cliffs has led to the development of rock-gripping rubbery hooves, a specialist adaptation that can be seen to a much lesser extent in other antelopes that also live in stony habitats.

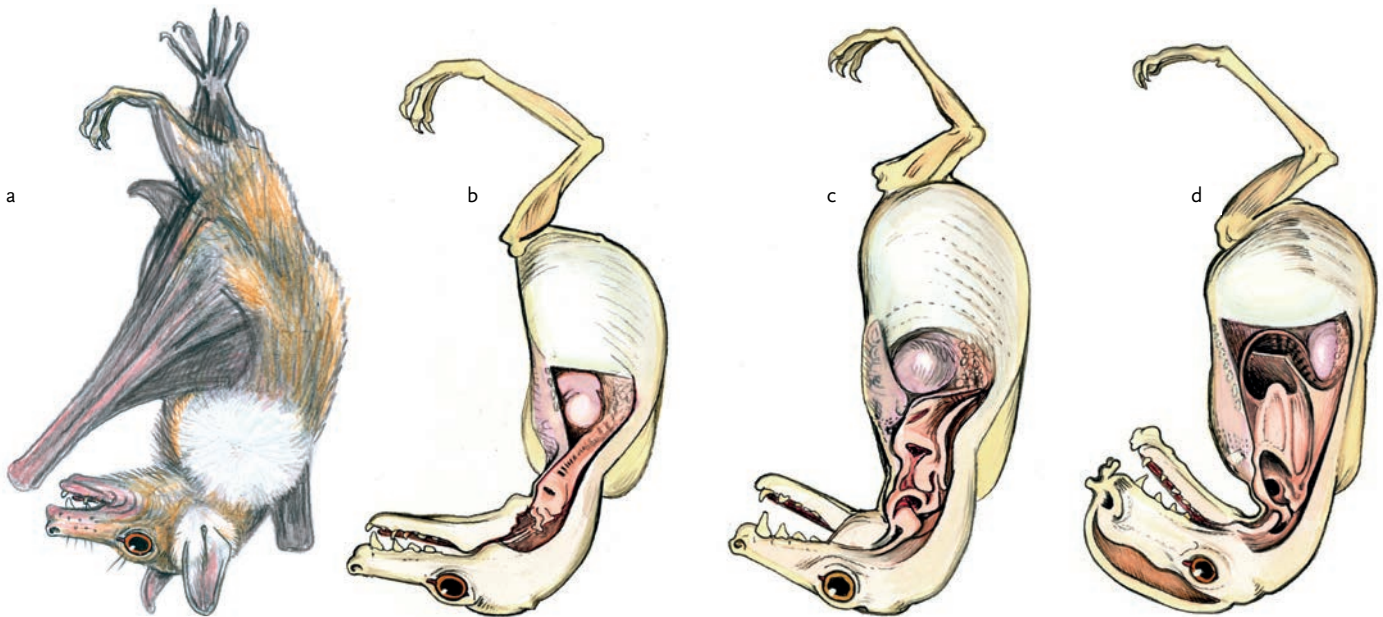
Shifts or innovations in communication and in the balance of senses

Fruit bats are dependent on a dispersed food supply that is often narrowly seasonal in availability as well as being highly unpredictable in abundance between seasons and years. For some fruit bats efficient exploitation of such a shifting mosaic of fruit demands quite substantial seasonal movement and dispersal over an extensive terrain. The resulting semi-nomadic 'camping' life-style poses problems for bats that require to keep in touch with one another.

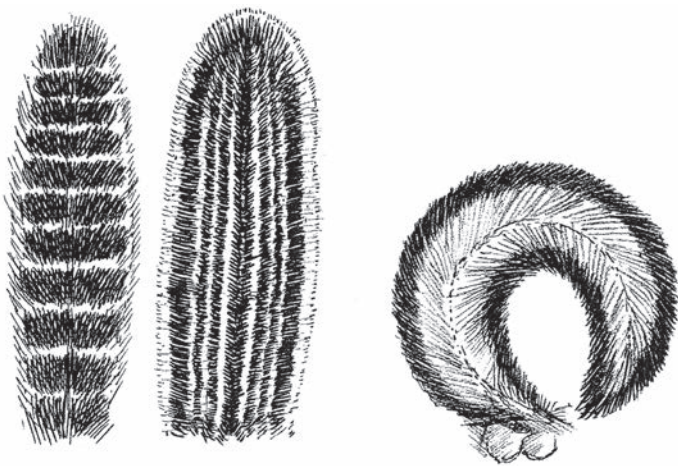
Their primary solution has been enhanced vocal communication, and three species of epomophorine bats illustrate three types of morphological adaptations to facilitate the amplification of advertising calls. Wahlberg's Fruit Bat *Epomophorus wahlbergi* has a loud clinking call, somewhat like a particularly resonant frog's croak. Franquet's Fruit Bat *Epomops franqueti* has a substantially louder and rather 'musical' call. The Hammer-headed Fruit Bat *Hypsignathus monstrosus* has such a loud blaring honk that on a still night it can be heard over several kilometres. In each instance the vocal apparatus devoted to the generation and amplification of sound is enlarged. *Epomophorus wahlbergi* has a larger voice-box than other bats but it comfortably fits in the throat in the space between chin and chest. *Epomops franqueti* has a voice-box sufficiently large to invade the chest and has clearly reorganized its breathing to increase the air pressure passing through the enlarged structure. In the case of *H. monstrosus*, the largest bat in Africa, the vocal apparatus has so enlarged that it has displaced heart, lungs and diaphragm, with the vast larynx doubled up like a tuba. To further amplify and project the sound, there are sacs on each side of the neck and a two-chambered pouch that is anchored on the enlarged nasal rostrum. *Hypsignathus* males have effectively become flying loud-hailers and the morphological modifications to this end have so reshaped their heads as to earn their 'monstrous' epithet.

While the last species seems to rely solely on a vocal signal, both *Epomophorus* and *Epomops* have augmented the call with scent and visual signals. Because vocalizing is the major signal mode, scent and vision are subordinate. In this instance this subordination is particularly obvious because these bats have developed scent-pouches containing evertible white 'plumes' or soft hair tufts on their shoulders. These 'epaulettes' effectively advertise the call. The logic behind the 'choice' of such a peculiar site to develop a visually advertised glandular area becomes obvious when the bat makes its call. As a diaphragm-pumping muscular spasm forces air through the voice-box it simultaneously flexes the shoulders and this spasm opens the epaulette, thereby dispensing a puff of scent from the brilliantly white hairs that are rooted in the glandular pocket that underlies it. In this way the bat sends out vocal, visual and olfactory signals more or less simultaneously, with the last two advertisements totally predicated upon the first, primary vocal signal. The interaction of behavioural selection (for a louder call) with a physiological constraint (having to 'heave' the chest and flex the shoulders) have here led to the evolution of a novel way to signal with scent and then on to a visual device associated with both the vocal and olfactory signals' source.

Many scented signals are distributed by way of faeces, and/or related methods. Tails are obvious dispensers for anal scents and many mammals with anal glands frisk or wave their tails in a variety of ways. Indeed, the tails of most genet species are boldly banded in black and white (in similar fashion to a barber's pole), strongly suggesting a coupling of visual and olfactory advertisement. Often these gestures, too, are advertised visually by conspicuous colouring or movement and nowhere is this more obvious than in the squirrels. In the case of giant squirrels *Protoxerus*, the upper side of the tail has narrow white and broad black bars that run from side to side whereas the underside is marked with equidistant, longitudinal black and white stripes. This difference in pattern indicates that a depressed tail sends an opposite visual signal to an elevated one.

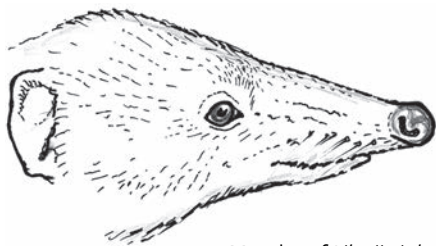


The evolution of a flying loud-speaker. Shape determined by signal-generating apparatus. Bisections of heads and thoraxes of:
a. & b. *Epomophorus*, showing some elaboration of the vocal tract and eversion of the white 'epaulette' signal.
c. *Epomops*, showing significant enlargement of larynx.
d. *Hypsignathus*, showing larynx enlargement has displaced the entire chest cavity.

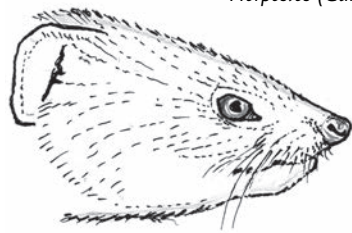


Tail patterns of *Protoxerus stangeri*, upper and lower sides, and *Funisciurus pyrrhopus* symmetrical tail curl.

Shifts in behaviour, i.e. the functional balance of senses (or changes in the relative importance of any one sensory activity), are given away when one member of an identifiable lineage exhibits a diminution or enlargement of its ears, eyes or nose. Thus the disproportionately big ears of the Serval *Leptailurus serval*, which lives much of its life in long grass, betray a dependence on hearing scurrying rodents, while the large eyes of Black-footed Cats *Felis nigripes* signify exclusively nocturnal habits. Likewise, the long snout of the earthworm-finding Liberian Mongoose *Liberiictis kuhni* contrasts dramatically with the short muzzle of the partially arboreal and more 'visual' Slender Mongoose *Herpestes sanguineus*.



Muzzles of *Liberiictis kuhni* (above) and *Herpestes (Gallerella) sanguineus* (below) compared.

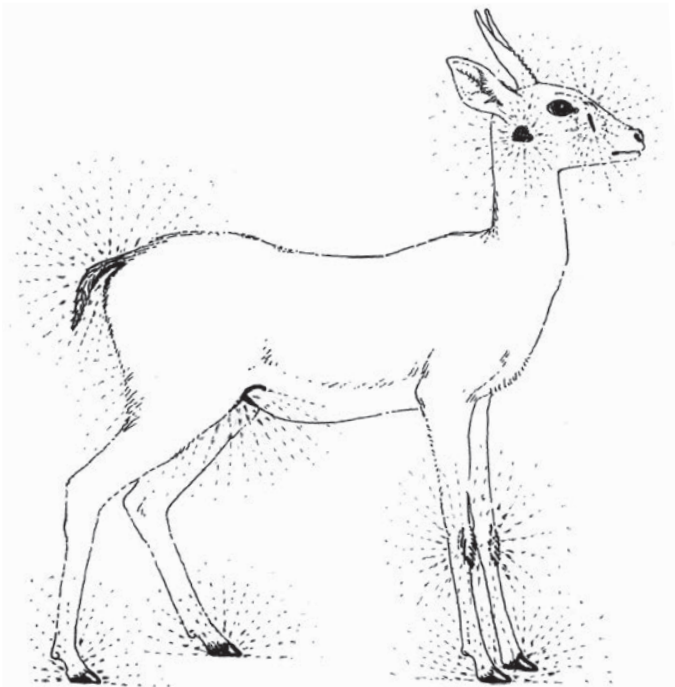


A more subtle manifestation of behaviour-driven sensory shift is exemplified by a group of small-bodied, very fast, guenon monkeys that garner much of their food on the smaller, outermost branches of the forest (mostly small fruits, flowers, budding leaf growth and active arthropods). By shifting out into this more exposed habitat, members of the moustached or red-tailed monkey group, the *Cercopithecus (cephus)* species complex, have gained access to a rich (but generally more dispersed) food supply but have also acquired substantial problems. An obvious hazard is greater exposure to eagles, which demands greater vigilance by all members of a social

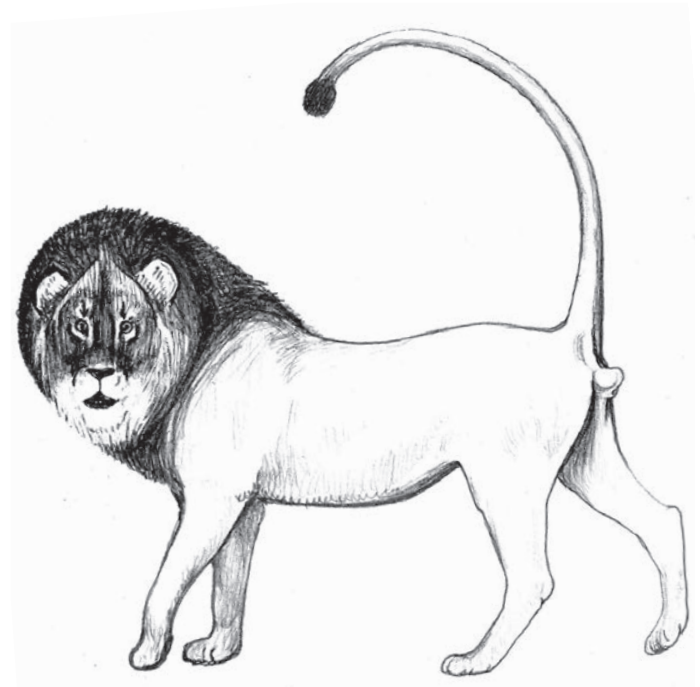
group and heightened visual awareness. Abundant but scattered resources require a dispersed foraging pattern and this, in turn, elicits problems for social behaviour because group members are spatially separated and this physical separation compromises a primary social greeting among guenons. This greeting consists of turning round and 'presenting' (an often distinctively coloured) genital region for both visual and tactile inspection. Enlarging the distance between individuals not only diminishes the value of tactile communication but (because grooming and genital signals have less utility) dispersal also facilitates female escape from males. Male frontal approaches are all too easily seen as threatening to females, which makes male inspection and mating with females more difficult, thus complicating efficient reproduction. Given these anti-social traits in *C. (cephus)* groups, any behaviour that can offset centrifugal tendencies is likely to be favoured by natural selection. 'Presenting' becomes all the more difficult and impractical while group members are scattered through a lattice of thin branches and it is futile to turn round, on precarious twigs, to present the genital pole to an out-of-reach partner!

Unlike many other guenons, *C. (cephus)* monkeys lack coloured or patterned signals on their rear ends, and they seem to pay less attention to that pole of the body than other monkeys. Instead, these monkeys have elaborated highly conspicuous face patterns, which act as 'flags' when they flick their faces in ritualized 'eye-avoidance' gestures. Significantly, flicking the head to avoid staring is an appeasing gesture that is roughly equivalent to 'presenting' as a reassurance. When the behaviour and morphology of these monkeys is compared with that of other guenons it would seem that *C. (cephus)* monkeys have switched a major primate social signal flag from 'back to front' (see profile of this super-species). This interpretation of *C. (cephus)* biology implies that specific behaviours, namely, foraging for small, nutritious items in the outermost foliage of trees, has favoured small bodies and a dispersed foraging pattern; this, in turn, has devalued tactile genital signals but favoured visual frontal ones. Thus the previously minor or inconspicuous gesture of eye-avoidance (which helped dampen aggression and ease inter-sexual communication) has been up-graded and visual signals have developed on the face to advertise the gesture. Morphological characters, such as coloured skin or deflected hair tracts, have evolved in the *C. (cephus)* group as a direct consequence of their behavioural shift from predominantly tactile to visual communication.

There are many other examples of a species making an apparent ecological shift that has demanded changes in what the animal does to survive in a new setting. These changes, in turn, have led to the evolution of interesting anatomical or physiological peculiarities. For example, any enlargement of a species' body size or of its home-range can severely challenge pre-existent adaptations. Thus the Oribi *Ourebia orebi* shares facial and other skin glands with various, much smaller, dwarf antelopes (Neotragini) that inhabit forested or thicket mosaics. Among the dwarf antelopes these glands are sufficient to mark out relatively small, exclusive territories in relatively stable, closed habitats. Oribi, instead, have come to inhabit more open grasslands that are subject to annual fires and are decidedly unstable. The Oribi's evolutionary response seems to have been to enlarge and intensify the effectiveness of skin glands, to multiply their number and to diversify their positions on the body. Thus Oribis have enormous face glands, very active



Oribi *Ourebia ourebi* indicating multiple sources of scent signals.



Male Lion *Panthera leo* strut displays body in tip-toed side-view, but head and mane head-on.

inguinal and pedal glands, scented knee-tufts and a patch of 'hot-plate-type' glandular skin below the ear. Each of these gland types dispenses and distributes scent in a slightly different way. Extended territories demand more frequent and dispersed scent marks but each territorial male Oribi also accompanies his female to ensure that she is exposed to a continuous barrage of his various scents (Monfort & Monfort 1974). This intensification of tending behaviour probably helps to deter defection by the female and may offset increased demands on the male's capacity to mark his territory. The sheer diversity of scent-production in a male Oribi combined with persistent monitoring of the female may also habituate the latter to prefer the scent of their shared living space and thus remain rather than defect and choose another male.

Changes in social structure

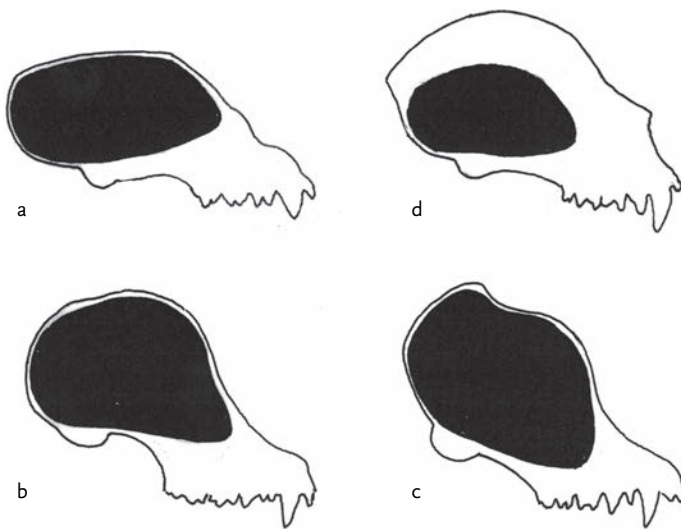
When previously solitary mammals become more social many residual details of ancestral behaviour can become problematic. Thus territorial species must modify or suppress territorial behaviour, as a result offsetting the centrifugal force of intra-specific aggression. When such aggression is gender-specific then interesting differences can appear in the appearance or morphology of the sexes, especially when aggression is, paradoxically, enlisted in the task of becoming social!

Take Lions *Panthera leo*, which are very frequently social and probably derive from ancestors with habits that would have resembled those of the solitary Leopard *Panthera pardus*. Lion sociality is built upon the retention and intensification of female-offspring bonds coupled with a fierce antagonism, amounting to xenophobia, from all pride members towards unrelated Lions, especially female ones (Schaller 1972, Bertram 1975). Thus young females remain with

their mothers and aunts, having every reason to avoid wandering while being under no pressure to leave. Males, instead, leave their natal pride as they mature and then wander, often in sibling pairs or groups, until they can oust the males of another pride and impose themselves upon that pride's resident females (and typically start by killing all young, thus bringing the newly acquired females into oestrous as fast as possible; Bertram 1973). Imposition of male supremacy is demonstrably helped by the males' larger size but it would seem that the sheer ferocity of female xenophobia makes any ambiguity about gender something to be avoided.

Stressing that male Lion manes serve a primarily visual, not a physiological function, Kingdon (1977) correlated manes with a lateral, head-up, tip-toe display that is exclusive to males and mainly directed at females. In this behaviour strutting makes the actor look as tall and as large as possible while manes become primarily a head-enlarging device. Noting that male Lions are the principal source of fresh genes and the manes of prime-age males come into particular prominence during the 'lion strut', Kingdon (1990, 1997) suggested that manes and strutting combine to serve as an intimidating, intra-specific, anti-incest mechanism. Morphology and behaviour combine to assist mobile males to identify themselves as non-females and to impose themselves on the more sedentary and matrilineal females.

Other species that have become social have developed very different, almost opposite, trends. For example, the Bongo *Tragelaphus eurycerus* is, almost certainly, a social descendant of relatively solitary ancestors in which the horned males were larger than the hornless females. The development of horns in Bongo females probably reinforces female hierarchy within the herd while also ensuring some ability to protect the young. Similar trends are apparent in elands, *T. oryx* and *T. derbianus*, where females are also well horned and of imposing size in spite of remaining smaller than males.

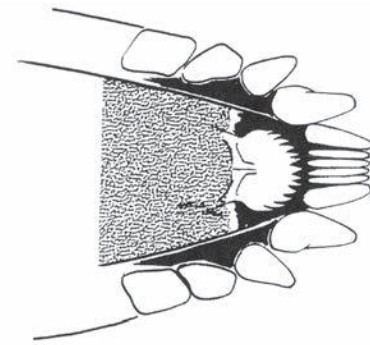


Relative brain-size in four bats. Exceptionally large brains are typified by *Cardioderma* (a), *Kerivoula* (b) and *Miniopterus* (c). A relatively smaller brain is typified by *Hipposideros commersoni* (d).

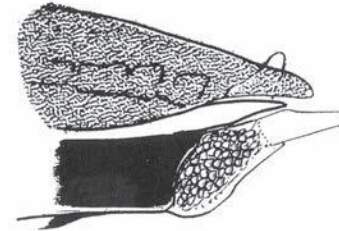
Increasing social complexity: brains and bonding

If changes in all morphological structures are initiated by changes in behaviour, alterations in the size or shape of brains can be no exception. Some echo-locating bats have, compared to the size of their bodies, very large brains. Among those with larger brains are the Heart-nosed Bat *Cardioderma cor*, species of woolly bats *Kerivoula* and long-fingered bats *Miniopterus*. What these very different bats have in common is that all are social and all have complex but emphatically different ways of finding and catching food. In *Miniopterus schreibersii*, a migratory species that ranges from Africa and Europe to China and Australia, young are born with large brains, develop very fast and are deserted by their mothers at about six months (Dwyer 1968) and disperse very widely, whereas adults are more sessile. Able learners (in orientation and the capture of food as well as in social interaction) are likely to have been selected for. Thus improving the ability to acquire, process and store information, from an early age, must have been one of the primary reasons that brains enlarged in any lineage. Primates, like bats, are already large-brained animals but still further enlargement in the ape and most especially in the human lineage signifies a fundamental shift in which foetal rates of brain growth continue for about a year after birth and brains still keep growing until puberty. Among humans there has been especially pronounced elaboration of the visual apparatus of the brain (Le Gros Clark 1959) as well as those parts of the brain that service the hands (Penfield & Rasmussen 1950).

One of the primary behavioural mechanisms that promotes sociality in mammals is one-on-one grooming of the fur with teeth or fingers. In primates, as with most mammals, the primary purpose of grooming, especially self-grooming, is the maintenance of a healthy skin and pelage. In the case of bush-babies (Galagidae) and pottos (Lorisidae), the development of 'incisor-combs' has increased the efficiency of their grooming and fur-cleansing behaviour. In the more social higher primates grooming is probably as important socially as it is in pelage-maintenance. Indeed, some monkeys seem to produce



Incisor comb and sublingual in galagos.



musk-scented sebum flakes at the roots of the fur, expressly to serve as 'grooming-bait' (Kingdon 1971). A much more elaborate development, putatively of 'visual bonding' out of physical nibble-grooming, is described in the profile of subgenus *Hippotigris* spp.

Reproductive behaviour shaping sexual attributes

The most common outcome of male competition for females is through direct trials of strength and endurance. When there are few constraints on increasing size and a big pay-off in terms of numbers of females inseminated there can be very rapid selection for gross sexual dimorphism. This is most marked in the Cape Fur Seal *Arctocephalus pusillus*, where very large numbers of females come ashore to give birth and copulate in choice 'rookeries' off the coast of south-west Africa. Here very many females are mated by a small number of powerful males. Each generation of seals reinforces selection for larger size and greater vigour but seal numbers are known to fluctuate widely, so it is likely that relative measures of sexual dimorphism also fluctuate. In *A. pusillus* the current level of male dimorphism by weight is approximately five to one.

The frequency with which males fight is another measure of male competition, and this is often an expression of the relative density of males during the rut. Thus substantial differences in the weight and shape of antelope horns can be correlated with relative density at this time. For example, within the Bohor Reedbuck *Redunca redunca* (generally well spaced out in territories) one locality on the banks of the Nile supports a dense concentration for the duration of the rut. Here horns are appreciably longer and heavier than anywhere else in the overall range of Bohor Reedbuck. Likewise, among Hartbeest populations, the Lelwel *Alcelaphus buselaphus lelwel* and the Kanki *A. b. major* often live at very high densities and have ultra-stout, tightly twisted, hook-like horns on extended pedicels while populations living at lower densities tend to have lighter, less complex horns that have shorter pedicels. At a grosser level antelopes that are small, well



Female Gelada Baboon *Theropithecus gelada* showing sexual swellings and vesicle-bordered chest and neck.

spaced-out and territorial thus experience encounters with a very few, and typically well-known, neighbours. These species tend to have small spiked horns and their contests tend to take the form of a regular testing of condition; their social structure tends toward well-established pairs, as typified by the dik-diks. By contrast, the males of harem species, such as Impala *Aepyceros melampus* and Kob *Kobus kob* have evolved heavy, lyre-shaped horns, which are used in frequent, bruising, and sometimes fatal, fights.

Among many extraordinary examples of behaviour shaping unique, species-specific structures is the transfer in female Gelada Baboons *Theropithecus gelada* of an anatomical signal indicating oestrus from the back to the front of the animal. In many higher primates, including chimpanzees and baboons, females advertise receptivity with conspicuous genital swellings. The most likely reason for female Geladas developing a partial 'necklace' of pink vesicles on their chests is the fact that they forage squatting and shuffling along on their haunches. Shuffling conserves warmth and saves energy in a cold, nutrient-poor environment but removes from view a prime indicator of reproductive condition. The conspicuous vesicles wax and wane with oestrus, thus providing an alternative signal of receptivity.

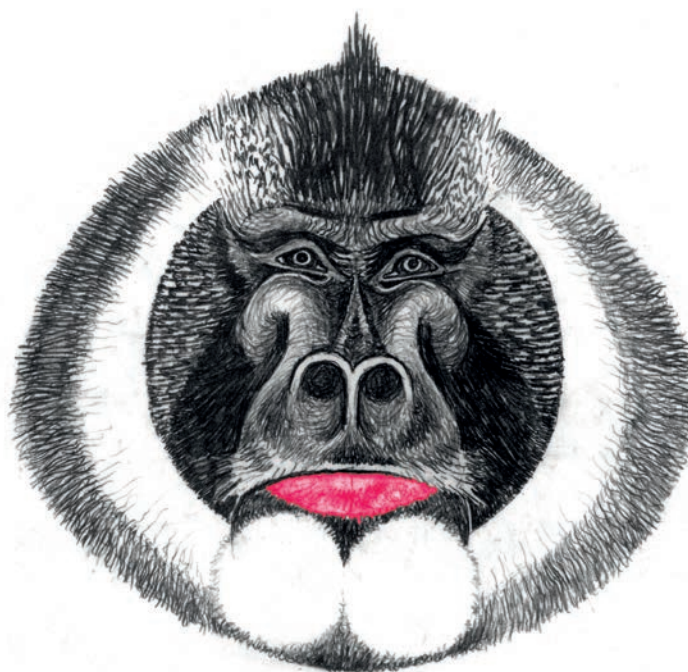
Many other African monkeys elaborate sexual differences in sex-specific structures, in size and in visual appearance, but few exceed drills and mandrills, *Mandrillus*, in the exaggeration of masculine features. In both species, the much larger males posture and strut with dominant individuals staring down potential rivals. Elaborate symmetry in the frontal aspect of a healthy, fully mature male Drill, *M. leucophaeus*, suggests that intra-specific selection (and more exactly, selection through the pattern-extracting susceptibilities of visual neurones in viewers) has favoured geometry and the evolution of an impressive and uniquely specific black, white and red facial mask.

Predator pressures and avoidance

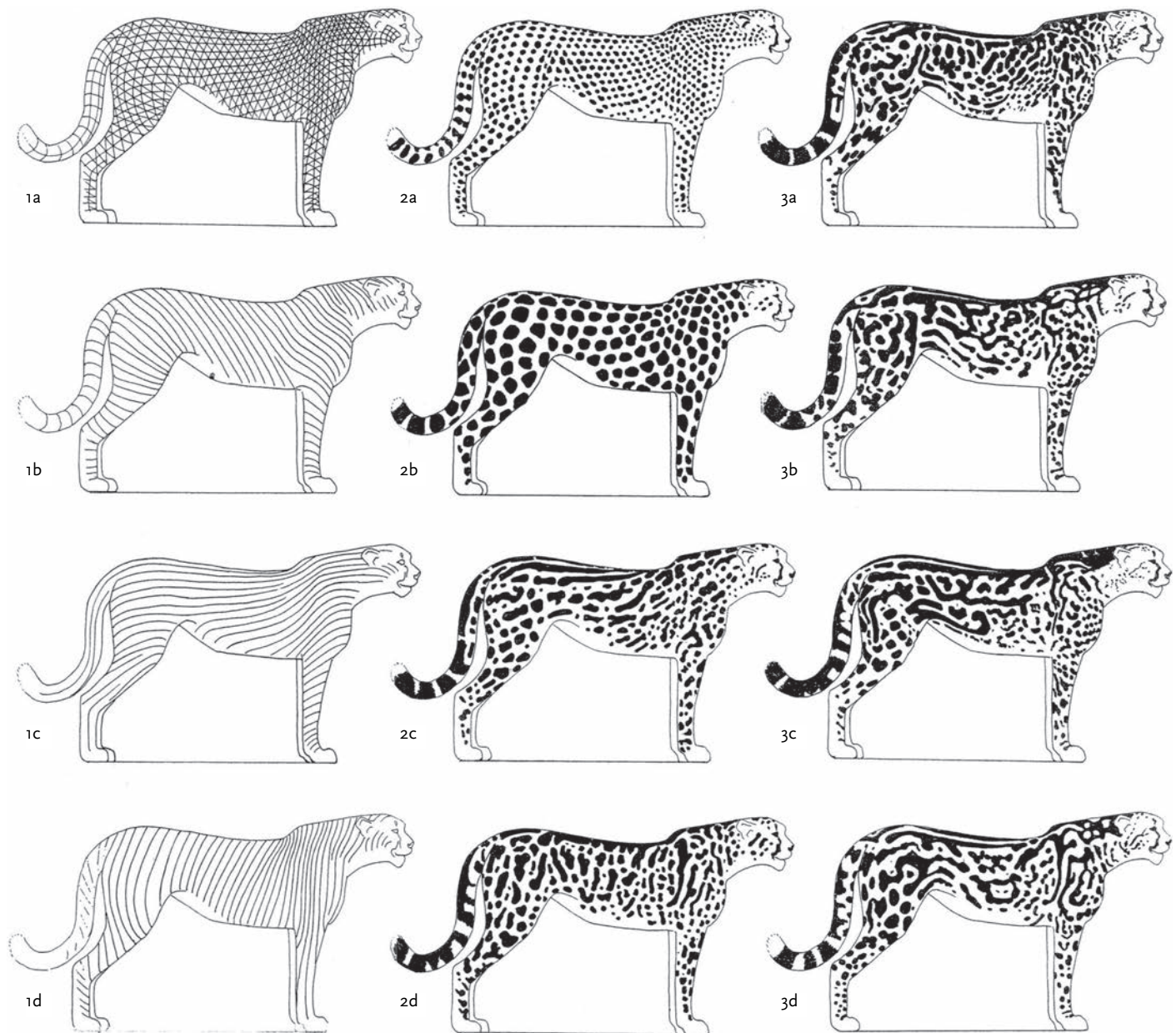
Both predators and their prey are shaped by evolutionary 'arms races': among the morphological features are improvements or changes in

camouflage. The pelage of many stalking predators has been selected to be as inconspicuous as possible so that they can sneak up closer to their prey. Likewise brownish agouti patterns, flecked and spotted pelage have evolved in rats, sengis and hares to aid blending in with the surroundings. Likewise, another strategy to escape predation is to minimize exposure, for example, by collecting and storing food in caches. Many rodents employ this strategy but the pouched rats and pouched mice (*Cricetomyinae*) have taken this to extremes, with cheek pouches that can hold as much as, or more, than their stomach. The need, by a slow, arboreal/terrestrial rodent (the Gambian Giant Pouched Rat *Cricetomys gambianus*) to minimize the time it spends foraging has led to particularly capacious cheek pouches. The 'cheek-pouch monkeys' (*Cercopithecinae*) have evolved similar structures and techniques. The practice of transporting food in bulk for later, more leisurely consumption is also found among ruminants who quickly accumulate forage, which is later processed by 'chewing the cud' at leisure, often hidden away from the feeding grounds where they may be more vulnerable.

Both the bodies and the skulls of the petromurid rodent *Petromus* and several other crevice-dwelling species, notably the bats *Mormopterus* spp., *Platymops setiger* and *Mimetillus moloneyi*, have flattened to accommodate to narrow refuges, as was outlined earlier. As for more direct protection against predator attack, enlargement of dorsal hairs to the point where they become spines reaches its extreme in crested porcupines, but hedgehogs (*Erinaceidae*) and some spiny mice *Acomys* spp. are less extreme examples. Scales have evolved to provide pangolins (*Manidae*) with a protective armour and the Zorilla *Ictonyx striatus* has evolved impressive anal stink-glands together with conspicuous black and white colouring, which advertises its noxious presence.



Male Drill *Mandrillus leucophaeus* illustrating the symmetrical geometry surrounding the muzzle and mouth.



Spot patterns of the Cheetah *Acinonyx jubatus* serve to disrupt the visual impact of body mass and outline. Stalking prey mainly during daylight in open, well-lit habitats, the optimum size and frequency of spots is roughly equivalent to the average distribution of pixel spots on digitized images of Cheetah habitat. The Cheetah's pelage is effectively a visual abstraction of its environment. Approximately 60% of the Cheetah's total spotted areas are light coloured. Dark tones comprise about 40%.

Cheetah spots are distributed over all surfaces exposed to the view of potential prey. Spot sizes vary and counts range from 8 to 24 spots per 100 cm². Analyses of normal Cheetah patterns reveal that spots are aligned along a multi-stranded grid.

1a. shows a grid superimposed upon the outline of a Cheetah profile and shows the tight, relatively even, multi-directional spacing of alignments. 1b. isolates alignments that are mainly diagonal, 1c. horizontal alignments and 1d. mainly vertical alignments.

Analysis of aberrant patterns among so-called 'King Cheetahs' reveals that the genetic control of such patterns effectively consolidates single small spots into larger amalgams without changing the broad ratio of 60% light to 40% dark.

Were all smaller spots to be amalgamated within the same equal-distance grid that governs normal Cheetah patterns, this would result in the hypothetical polka-dot pattern shown in 2b., which would be highly conspicuous and is unknown in nature. Instead, break-down in the genetic control of spot-spacing results in spots amalgamating along particular linearities of the overall grid as well as at random.

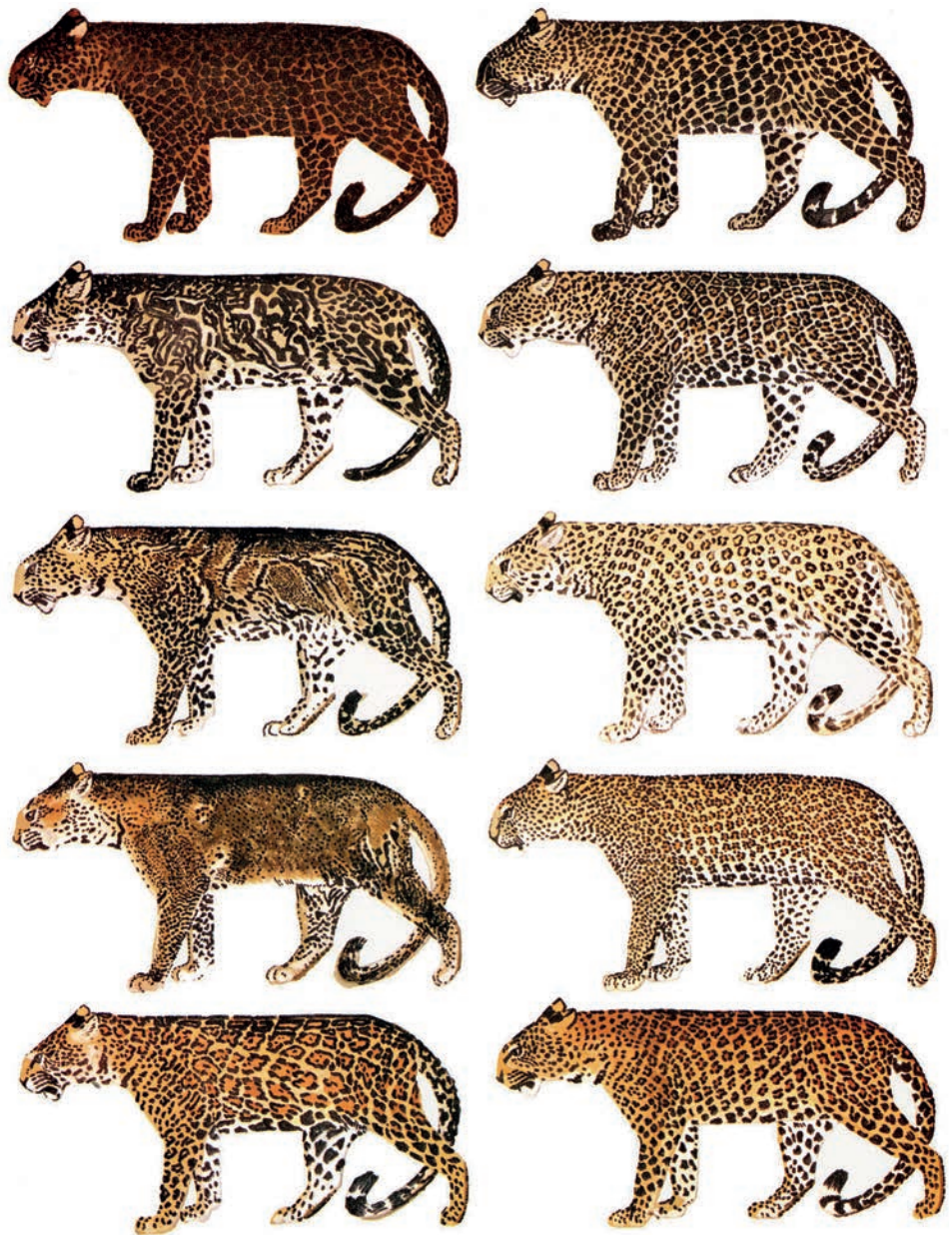
2c. and 2d. are collages in which horizontal (2c.) and vertical (2d.) pattern elements have been extracted from photos of 15 different King Cheetah morphs. 3a. to 3d. show actual patterns on four King Cheetah individuals. Note retention of very small areas of normal spotting (3a.), some horizontal consolidation (3b.), some 'polka-dotting' (notably on haunches of 3c.) and typical 'marbling' (3d.).

Note that normal Cheetah patterns show less regional variance in spot counts and tonal ratios compared to taxa with broader habitat tolerances (such as Leopards and some genet species, Kingdon 1977).

Pattern 'maps' of Leopards *Panthera pardus*.

Left-hand column = polymorphism (from top):
 Melanistic morph (Black Panther);
 'Marbled' morph;
 'Panelled' morph;
 'Freckled' morph;
 'Jaguar-like' morph.

Right-hand column = regional types (from top):
 Amalgamated rosettes, Ethiopian Highlands;
 'Mosaic' pattern, Rwenzori Mts;
 Pale, open network, Somalia;
 Multiple, small rosettes, Zanzibar Island
 (exterminated);
 Most widespread type (Mount Elgon).



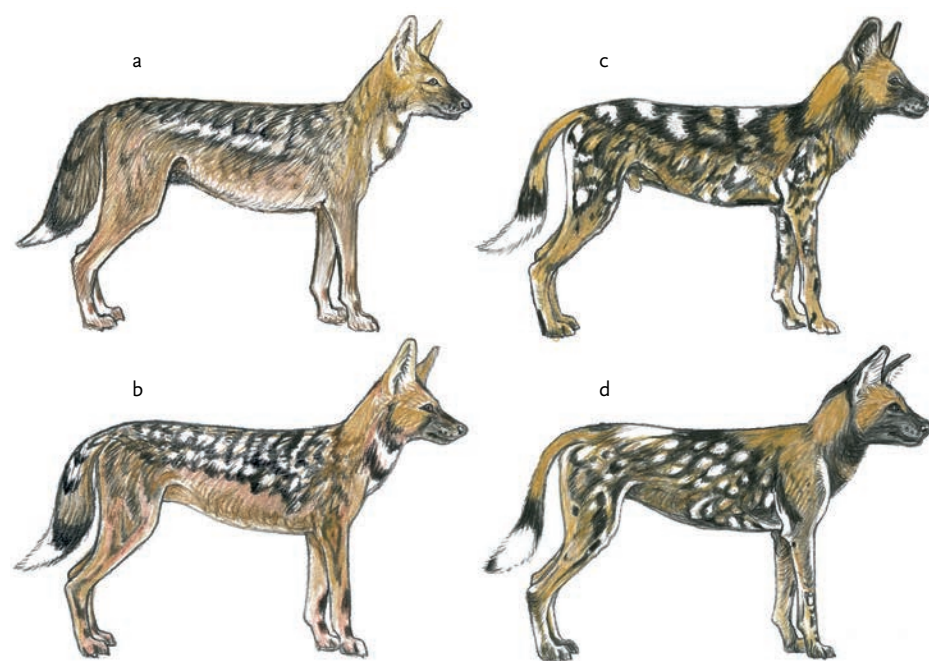
Diversity and transformations of camouflage

In direct apposition to aposomatic signals are the many manifestations of 'camouflage'. Predators that are effective stalkers of their prey must evolve patterns that complement their stalking behaviour. In the case of Leopards, pattern variations show some correspondence with the very varied regions that they inhabit. Thus Leopards from the arid Horn of Africa have widely spaced, open-centred rosettes on a pale yellowish background. By contrast, the black spotting on rosettes of Leopards from dark, moist montane forests in Ethiopia have amalgamated into densely packed blotches (see figure above).

In each case the basic grid of rosettes would seem to have been modified in correspondence with very different vegetation types and light levels. The particular mimesis of the Leopard's coat appears to be the dapple of leaves and their shadows, the setting within which Leopards spend most of their time. Dark and light areas of the coat are

dispersed in an abstract conformation that breaks tones up into broad averages of area and contrast. The groupings of spots into rosettes resembles the ink-spot clusters found in colour photographs after passing through a mechanical screen or scanner (Kingdon 1977).

The typical Cheetah pattern of isolated spots follows similar principles but has no relationship to leaf mimesis. It also represents an abstract mathematical averaging-out of relative tones in the Cheetah's more grassy habitat (see figure opposite). Among both Leopards and Cheetahs there are individual variants commonly described as 'aberrant'. Yet it can be demonstrated that natural selection for just such marbled variations can take place. For example, some so-called 'King Cheetahs' as well as some 'aberrant' Leopards have patterns that approximate to the Asiatic Marbled Cat *Pardofelis marmorata*. Leopard variants, in particular, can individually resemble the patterns of Clouded Leopards *Neofelis nebulosus*, Ocelots *Leopardus pardalis* and Jaguars *Panthera onca*. These non-African felids also vary, both regionally and individually, in their coat patterns.



Pelage pattern formation in African Wild Dog *Lycaon pictus*. a. Generalized, semi-cryptic formation in genus *Canis* as expressed in various jackals and wolves. b. Similar pattern becoming more conspicuous through enhanced tonal contrast. c. *Lycaon* pelage in which *Canis*-like format has been dislocated but elements are still perceptible. d. *Lycaon* pelage in which dislocation has generated typical 'marbling' (individual from Longido, N Tanzania).

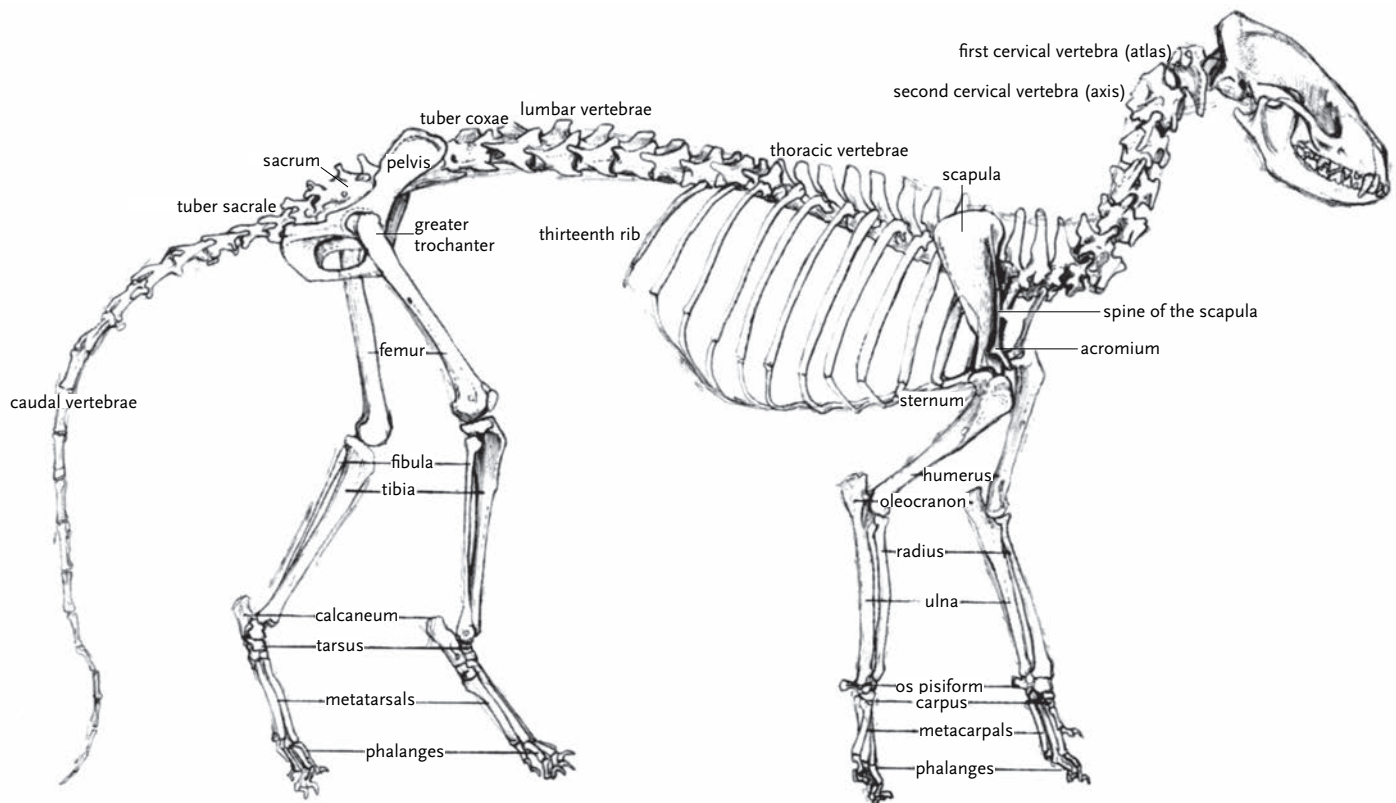
In these instances, selection would still seem to function as 'camouflage', yet there is one more carnivore example in which marbled or blotched patterns vary with every individual as well as showing regional trends. It would seem likely that the swirling, blotchy black, white and yellow patterns of African Wild Dogs ('Painted Dogs') *Lycaon pictus* have evolved by a process analogous to that of the 'aberrant' felids. If this analogy holds, the *Lycaon pictus* pattern may represent the semi-random elaboration of ancestrally more structured and quieter patterns, such as the flank and dorsal stripes of jackals and more subtle colouring on the faces, legs and tails of Wolves *Canis lupus* and Dholes *Cuon alpinus*. Unlike the felid examples, African Wild Dogs are coursers, pursuing their prey in the open and cannot, by any ordinary use of the term, be described as 'camouflaged'. Furthermore, elaborate social behaviours in *Lycaon pictus* provide a plausible explanation for the evolution of their extraordinary tri-coloured mottle pattern, which resembles the sort of polymorphism of some domestic animals. Schaller (1972) interpreted this pattern as helping scattered pack members to keep in visual contact and maintain the group cohesion, but did not volunteer how this might have evolved or operate. More specifically, one of us has linked the adaptive value of a pattern that breaks up the body's contours directly to the social disciplines that maintain pack cohesion (Kingdon 1977).

Significantly, for a species where the vulnerable young are left in a den while the adults go hunting, wandering pups elicit strong responses from adults: observers have noted that provisioning adults returning to the den not only tend to disgorge meat in favour of those pups that stick together, they may even bite or harass stragglers. The behaviour of adults, especially provisioning ones, would therefore seem to influence survival in *Lycaon pictus* and it has been suggested that this interaction is sufficient to select for a unique form of 'camouflage': one that favours those pups that 'blend in' best with the rest of their noisy, hyperactive litter (Kingdon 1977). At the moment of maximum reward and maximum risk, a pup's immediate and actual environment becomes a cluster of prostrate begging siblings.

The mud walls of a den's mouth are not the pups' immediate visual setting; instead it is the tactile, mobile, alive mass of fellow pups. In this parent-selector-driven context Kingdon (1977) argued that the mottled pattern is an aberrant form of camouflage, but one that instead of being predator-selected has its origin in social behaviour.

By begging, small pups, from the age of one month, can coerce adults to disgorge meat and this behaviour continues into adult life as a social greeting and a system whereby the weaker can influence the stronger without either party resorting to unrestrained biting (Kuhme 1964). Thus, prostration is a tactic that combines access to food with insurance against attack; both the beggar (paradoxically the 'aggressor') and the provider (inhibited from aggression by the beggar's behaviour) co-operate in a ritualized expression of interdependence. Schaller (1972) suggested such exhibitions of 'friendly aggressiveness' induced cohesion, especially during 'meets' or 'social rallies'. Kingdon (1977) contended that an 'aberrant' and highly conspicuous, contour-breaking pattern serves as the main visual cue for such cohesion. At such times adult dogs readily switch their behavioural role from typical 'dependent beggar' to typical 'coerced provider' and then back again. In the process, temporary alliances are formed between individuals and the alert, excited conditions that precede embarking on a hunt seem to be facilitated (Kuhme 1965). The pups' collective dependence on adult providers seems to have carried over into a mechanism that helps maintain interdependence and pack cohesion. Coat patterns, by 'dissolving' the individual contours of these most social of dogs, are integral to the signalling environment in which they interact and survive as a visually undifferentiated group.

The complex genetic recipe that encodes for the coat patterns of African Wild Dogs, Marbled Cats, Clouded Leopards or domestic 'sports' must include, within its complexity, residues of symmetrical regularities in distant ancestors. The larger message is that every genetic history embraces increment upon increment of selection for 'aberrant' individuals. In evolutionary biology, aberrant is a word to be used with caution.



African Civet *Civettictis civetta* skeleton (above) and skull (right).

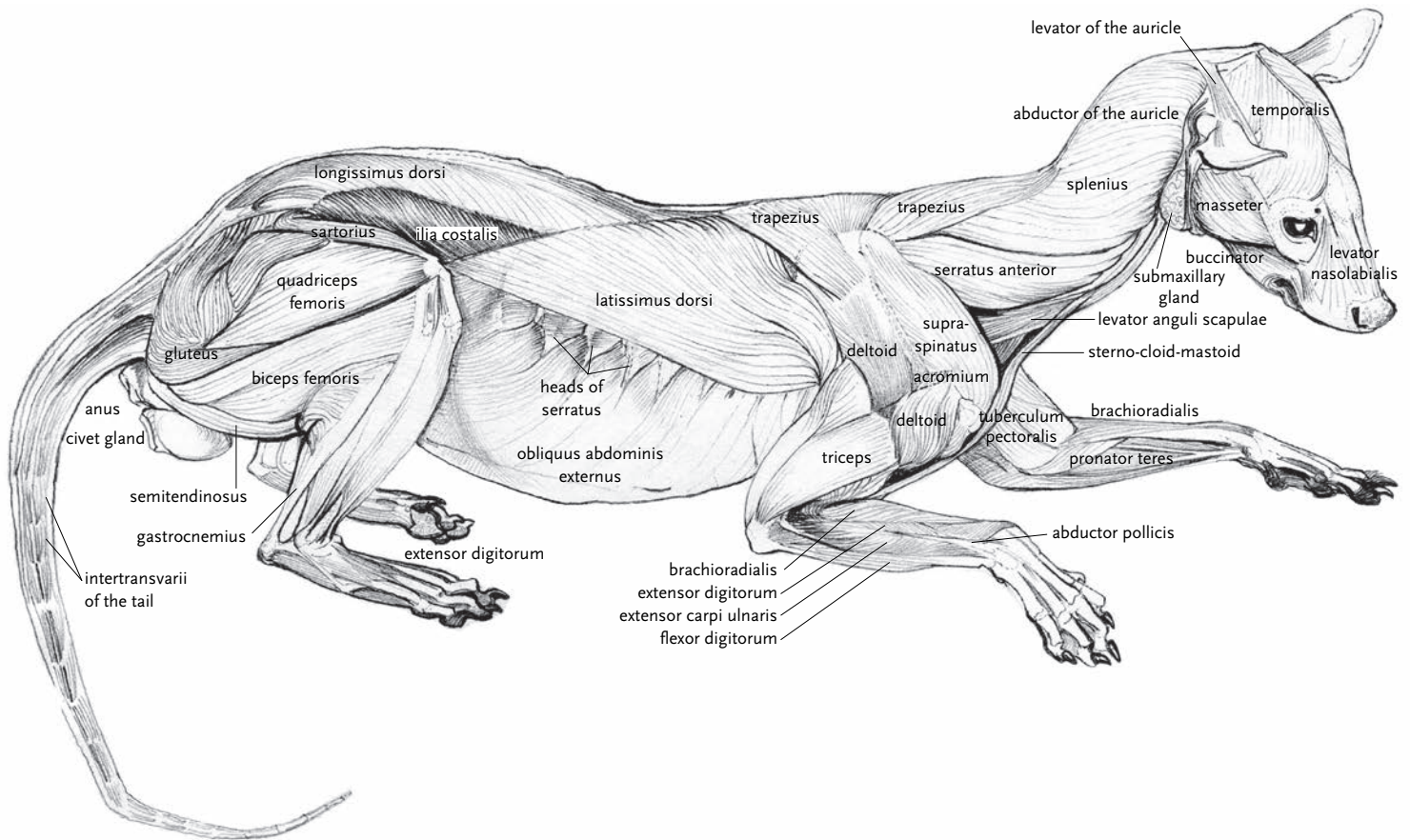
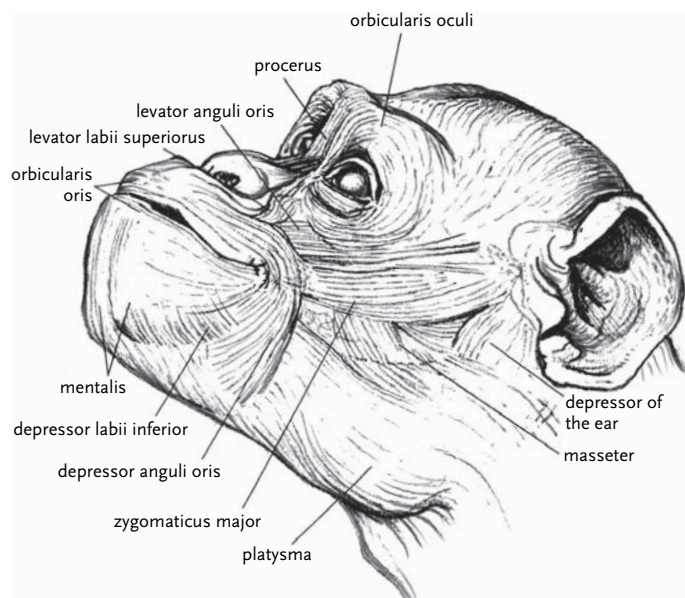
Tool-language and morphological metaphors

All examples given so far demonstrate that it is not possible to describe mammals, let alone discuss their structure, without invoking the relationship between form and function (thus we have used similes such as umbrellas and deck-chairs). In relating functional behaviour to the complex structures that the behaviour has helped engender, it is often difficult to avoid technical language and we have provided pictorial guides to body parts, to the names of all major bones and to the larger and more obvious muscles of mammals. Sometimes jargon can be side-stepped, but it is significant that attempts to modernize or Anglicize terminology are often little more than simple restatements of the Greek or Latin words we have inherited to describe the many and various parts of an animal. The reasons for this convergence lie in the difficulty of finding words that translate our understanding of form into functions, mechanisms and geometries that we can readily envision and which we already understand. Latin names actually help comprehension by preventing too literal a mental match while at the same time expressing the link between *nomen*, form and function. Thus *pelvis* is Latin for basin, *bulla* is bubble, *fibula* means clasp or attachment and *masseter* simply means chewer; all are technical terms that describe and (more importantly) suggest familiar artefacts as well as functions.

At a higher level of metaphor, biologists have struggled to conceptualize how the total architecture of organisms, from the gene to the protein and tissue, relates to the structured living behaviour of individuals that belong to those entities that we call 'species'. Theoretically minded biologists have invented a telling simile for all living organisms in designating them as 'self-regulating

machines' or 'homeostatic systems'. Although easily dismissed as overly mechanistic, these are examples of what the great biologist J. Z. Young called 'tool language' (Young 1957). Tool language is a large part of the terminology of modern biology and is almost inescapable whenever we try to formulate ideas about natural phenomena in general and functional morphology in particular.

When it comes to naming whole classes of mammals, especially extinct ones, palaeontologists sometimes have rather little to go by, but the names they invent must still allow comparison with more familiar animals. For some little-known, very early extinct species, teeth are the *only* part of the skeleton to have survived so that some important groups of early mammals are actually named after the shape of their teeth: creodonts ('flesh-teeth'), tribosphenids ('three cusps') and multituberculates ('many cusps'). Among living orders several have also been named in reference to their teeth, notably the rodents ('gnaw-teeth'), edentates ('toothless') and tubulident ('mini-tube-teeth'). Even when limited to diagnosis or nomenclature, dental and mandibular structures are intensely useful but, as Darwin emphasized, dental, cranial or general anatomy only becomes central to biology when the evolutionary and functional meaning of structures

African Civet *Civettictis civetta* myology.Chimpanzee *Pan troglodytes* head myology.

are revealed. And for teeth, again this means also the behaviour of choosing food as well as grabbing and chewing it.

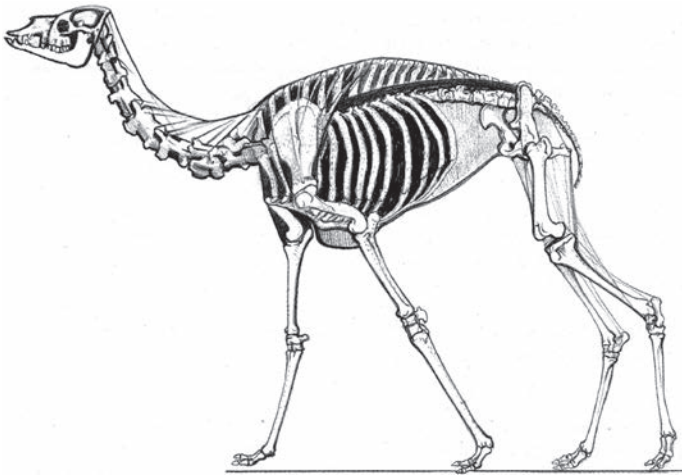
Tool language is often best applied to component parts where there are extraordinary elaborations of limbs, heads, faces and tails. Less easily changed structures do exist, for example, the vertebral column, but even this most fundamental of vertebrate structures

varies in interesting ways. An examination of the backbone and the varied relationship between body mass and limbs can serve as a useful introduction to the architecture of mammals, as we shall consider next.

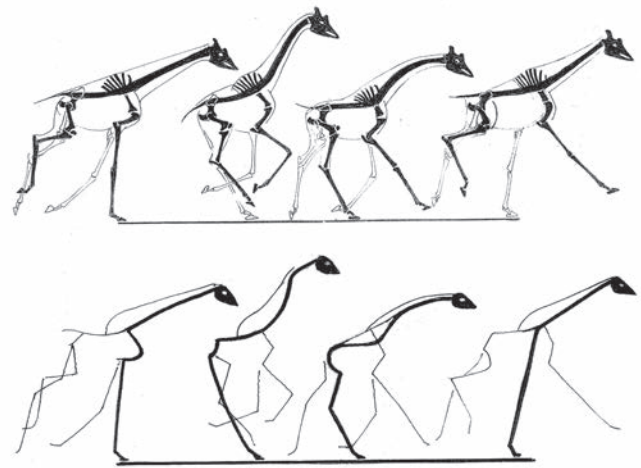
The mechanics of morphology: struts, levers and bridges

In a typical quadrupedal mammal the vertebral column is arched between supporting legs, which, when static, have some analogy with bridge piers while the form of the vertebral column itself can be compared with a suspension bridge. The bodies of the vertebrae are the bridge's beam, or compression member, while the muscles and ligaments of the back serve as its cables or tension members (Thompson 1911). The vertebrae are generally heaviest and the muscles greatest in the small of the back, especially if the load is not spread out over ribs, limbs or pelvis. The vertebral spines and interspinous ligaments represent a web of struts and ties that give both strength and lightness to the back. The spines vary in height, the tallest being where the bending moments are concentrated. In many ungulates the head is cantilevered out on a long neck and, because of this extra load, as much as three-fifths of the animal's total weight may be taken on the forelegs. The spines are generally longest over the shoulders, where they serve as struts, absorbing the weight of the head through the tension members of the *ligamentum nuchae* and *sacrospinalis*. Variations on this pattern can be illustrated by wildebeest, giraffes, rhinos and Cheetahs.

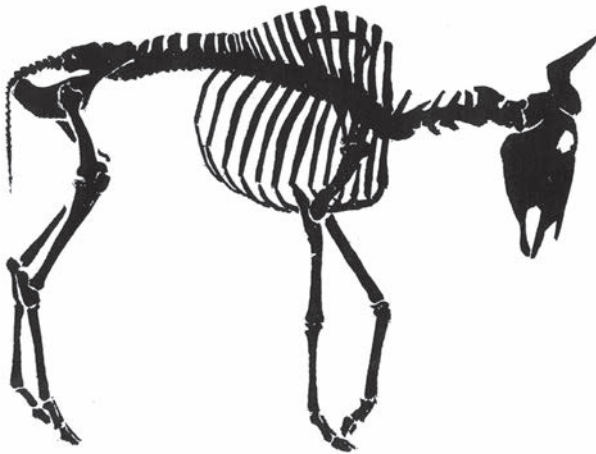
The cantilevered head and tall thoracic spines of the Common Wildebeest *Connochaetes taurinus* provide the closest analogy with



Camel skeleton and neck tendons to show 'suspension-bridge' structure. 65% of camel's weight is carried on its forelegs (after Kingdon 1990).



Silhouettes of cantering Giraffe *Giraffa camelopardalis* illustrating mechanical leverage of mammalian limbs.



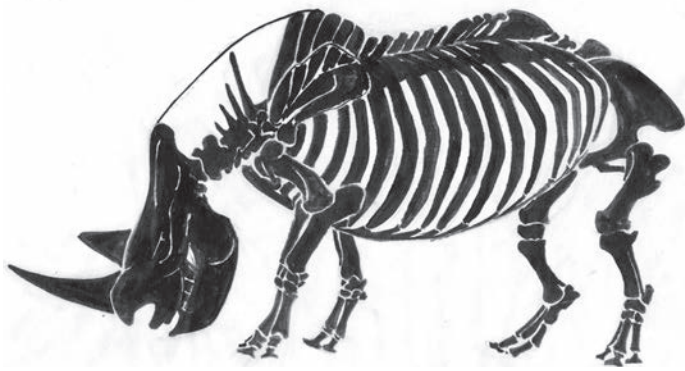
Silhouette of skeleton of Gnu *Connochaetes taurinus* to compare with diagram of cantilevered girder as used in bridge building.

a bridge. In engineering terms, if not in superficially aesthetic ones, the wildebeest is one of the most elegant and economically built of mammals while the giraffe is one of the most eccentric. Demonstrating that vertebral columns do not have to be horizontal, the weight of a bull giraffe's heavy, bony head is borne, for the most part, vertically, down the robust, elongated nuchal vertebrae and on down the forelegs but also out along the sloping back. However, the neck is not always under vertical compression, indeed, walking and browsing, certainly running, can cantilever the head and neck out quite horizontally. This exerts immense forces along the very highly developed and powerful *ligamentum nuchae*. The thoracic spines help spread this weight backwards and thus keep the animal in equilibrium. None the less, balance in such a long-necked and long-legged animal



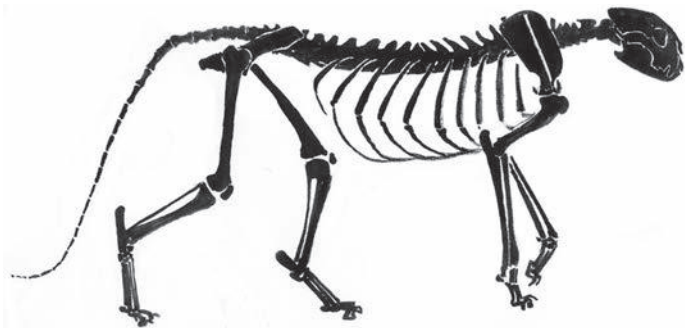
Silhouette of skeleton of Giraffe *Giraffa camelopardalis*.

can be problematic and I have seen a running Giraffe that was jostled by a neighbour go crashing to the ground. Likewise, one contestant among neck-fighting males can occasionally get knocked down.



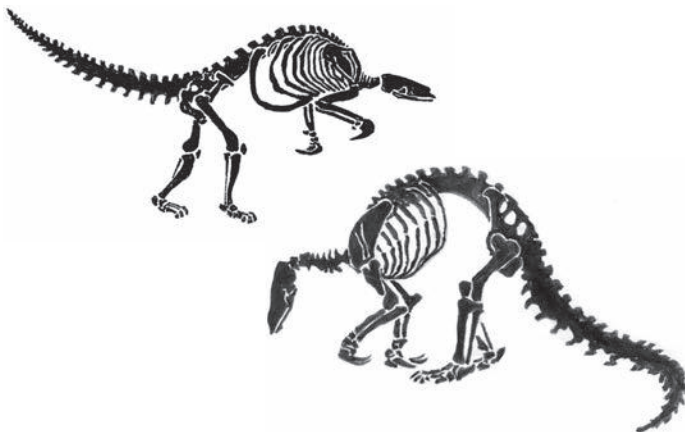
Silhouette of skeleton of White Rhino *Ceratotherium simum*.

The White or Grass Rhinoceros *Ceratotherium simum* possesses one of the heaviest of quadrupedal arches and the proportion of the animal's overall weight that is taken on the hindlegs is greater than in Giraffes, camels and other front-heavy animals. This is partly due to large, heavy muscles and bones in the back legs having to provide much of the propulsive power when the animal runs or gallops. The double demand for strength and flexibility in the White Rhino's shoulder is manifest in the broad, blade-like thoracic spines, which have slots to accommodate the spine behind when the vertebrae are compressed.

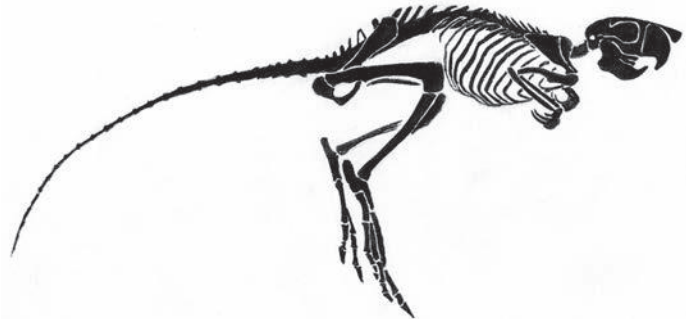


Silhouette of skeleton of Cheetah *Acinonyx jubatus*.

The Cheetah *Acinonyx jubatus* represents a lightly built extreme of the quadrupedal bridge, with flexibility of the back at a premium. When the animal is standing and relaxed the back tends to hang slightly in a long, loose arc.



Silhouette of skeleton of Ground Pangolin *Smutsia temminckii* in bipedal action (left) and silhouette of skeleton of quadrupedal Giant Pangolin *Smutsia gigantea* (right).



Silhouette of skeleton of Southern African Springhare *Pedetes capensis*.

The front part of an animal is not the only end capable of being a cantilever. The vertebrae of the tail, notably in the pangolins (Manidae), can be the most numerous and the most heavily built in the entire vertebral column. This is because the tail acts as a protective sheath when the animal curls up, a supportive strut while digging, a principal limb in the climbing forms and a posterior cantilever in the bipedal Ground Pangolin *Smutsia temminckii*. Thus tails can serve as clubs or protective shields while other mammals use them as flags, limbs or fly-whisks. In common with many other animals, the tail of the Southern African Springhare *Pedetes capensis* is a balancer. This essentially bipedal animal can, in mechanistic terms, be described as a single balanced cantilever. Unlike most mammals, it is the lumbar and sacral spines, not the thoracic, that are the longest and strongest. This is because it is the hindlimbs, not the tiny folded-up forelimbs, that absorb all the pressures of hopping and jumping.

The most drastic reorientation of the vertebral column has taken place in the evolution of true bipedalism in humans and in many species of now extinct hominins. The driving force behind the adoption of such a rare and finely balanced posture and gait was almost certainly due to the hands and manipulative behaviour having become the indispensable interface between hominin ancestors and their environment. These ancestors were likely to have been terrestrial 'squat-foragers', feeding in a somewhat similar fashion (but with a wider range of foods) to modern Geladas (Jolly 1970). Some confirmation of this squat-foraging phase in hominin evolution comes from 'platform-like' feet (with angled big-toes serving as stabilizing struts) in an early hominin, *Ardipithecus ramidus* (Lovejoy *et al.* 2009). Like all the other morphological specializations reviewed above, our ancestors' too, were behaviour-driven; further details (and alternative explanations) concerning this extraordinary transformation of the primate skeleton are explored in Kingdon (2003).



Left to right: Skeletons of Human *Homo sapiens*, 'Ground Ape' *Ardipithecus* and Gorilla *Gorilla Gorilla* in squatting positions showing differing proportions and morphology of pelvis, lumbar column, limbs and feet (in part after Kingdon 2003).

Attaching limbs: balls and sockets, bandages and other ties – different origins for fore- and hindlimbs are significant

Mammalian limbs, while acting as levers and supports for the body, have assumed a great variety of secondary functions, such as seizing and holding, feeling, digging, hanging and, in some mammals, flying and swimming. The body is supported and levered along by a variety of means, on toes or toe, on the soles or even on the elbows and wrists in some bats. The limbs are balanced by forces exerted by the weight of the body (and that of the upper part of the limb itself) bearing down through the limb and against the ground. During movement, strains within the body and limbs shift continuously and these strains are met by muscles that act as instantly adjustable ties and braces. Each muscle has an antagonist, another muscle or a ligament. The shape of these is determined by function, those for fast action being long and parallel, those exerting force being bundles of short-grouped fibres. Because limb bones are under compression, they are effectively struts. Their attachment to muscles can be direct or through tendons that can be attached on either side of the hinges or fulcrums that allow individual bones to join others in manoeuvrable, crane-like limbs.

The weight-bearing, supportive limbs of mammals are a distinct improvement on the lateral, only temporarily supportive ones of, say, reptiles and amphibians. The morphology of mammalian limbs has incorporated the evolutionary changes that were necessary to accomplish weight-bearing. In the forelimb, when the elbow swung back under, or in line with, the body, the hand unit had to rotate forwards. This phylogenetic shift forced the radius to twist around the ulna, a modification that the muscles also had to accommodate to. In the hindlimb no substantive change to a reptile-like ball and socket joint was needed but the swing of the knee forward and beneath the body necessitated a sharp bend in the orientation of the femoral head. The hindlimbs carry the weight of the body directly, bone to bone, through the femoral–pelvic socket joint.

The forelimbs have no direct bony connection with the main body mass, except for those mammals (primates, bats and digging animals) that have retained a collar bone or clavicle. This bone serves as a tie, stopping compression of the two limbs across the thorax. Both the clavicle and the scapula are modified remnants of the early synapsid shoulder girdle. In mammals that dig, fly, swim or run the stress of those behaviours are absorbed onto the barrel of the body via the scapulae. In typical, heavily quadrupedal mammals the scapulae transfer the stress of the body's weight to the supporting limb via muscles. The trunk of the body is attached to the scapulae by a hammock-like muscle-complex called the *serratus anterior*. The shoulder is pulled back by a fan-shaped sheet muscle, the *latissimus dorsi*, that links the humerus to the dorsal fascia. The entire shoulder is pulled forward by the *pectoralis*, which connects the humerus, scapula and clavicle to the median line of the chest; this is the main muscle powering flight in bats, digging in digging species and thumping an opponent in human boxers. Among bats the size of pectoral muscles is a direct measure of flight power and a strong, long-distance sustained flyer such as the Midas Free-tailed Bat *Tadarida midas* has much thicker, longer chest muscles than a short distance, short-flight bat, such as Moloney's Mimic Bat. The scapula is held to the body on its upper edge by the *rhomboid*, bound over by the thinner, more superficial *trapezius*. Other strap or 'bandage' muscles are the *levator scapulae*, which

connect the scapula to the upper nape and skull. The *sternocleidomastoid* is a sheet muscle running from the back of the skull to the shoulder joint and the *basihumeral* is a strap running from the skull to the humerus and clavicle. Scapula and humerus are bound together by ligaments and also by the *supraspinatus* and *infraspinatus*. The *deltoid* both moves the foreleg and helps bind the shoulder into a compact functional mass. The shoulder joint is given extra stability and control by the *biceps*, *triceps teri* and *teres major*. The *biceps* and *triceps* muscles run from shoulder to elbow and help to flex or extend the entire forelimb. The humerus is generally broad and flat at its lower end, providing a powerful hinge joint with the two bones of the lower arm, ulna and radius. The olecranon, or 'funny bone', of the ulna protects and locks this hinge while the slender, rounded top end of the radius simply rotates at its junction with the rounded capitulum of the humerus. This combination of complex, large-headed ulna and simple, small-headed radius is reversed at the bones' lower ends. Here the radius broadens and provides the main attachment with the hand while the ulna slims down to a relatively feeble connection on the outer margin of the wrist. Because of this arrangement mammal forelimbs are unlike those of any other animal. The upper arm is effectively attached to the ulna, the hand or paw is attached to the radius and the two long bones swivel around each other so that the hand can be prone, supine or any position in between.

In primates and other animals with relatively conservative, highly manoeuvrable forelimbs the radius and ulna are two separate bones. In most ungulates the radius and ulna are fused and the muscles below the elbow have become semi-tendinous and then extend as tendons to the toe or toes, thus reducing the weight that has to be moved in running. The bones of the hand or forefoot have an original arrangement of three proximal carpals, a central carpal, five metacarpals followed by five digits of two or three phalanges. As Darwin's 'curiosities' exemplify, mammal forefeet range from single-toed horses to bat wings and porpoise flippers.

The hindlimbs usually mimic the forelimbs but in spite of their similarity they have quite different origins. Parts of the forelimbs derive from structures that were integral to the early vertebrate head, thus the pectoral fins were actually tethered to the head in early fishes. When tetrapods developed forelimbs from these fins, which became detached from the skull, one pair of gill arches was dragged away to become the scapulae. Forelimbs are mainly served by cervical nerves, close to the brain. From early vertebrate history, forelimbs helped adjust sense-driven decisions about the pace and direction of forward movement. By contrast it was vertebrae and associated bones from towards the tail that first differentiated into hind fins and eventually hindlimbs and pelvis. Like the rest of the rear end, their primary function was propulsion and that function is still evident in the hindlimbs of a majority of modern mammals.

The pelvis is a light, strong, balanced structure, the ilia sometimes fused onto the sacrum (which is part of the vertebral column) but sometimes capable of independent flexion. Together with the sacrum, the paired iliac bones form a ring through which sexual and excretory ducts pass. Ball and socket joints on either side allow the hindlimbs plenty of movement without loss of strength. The most powerful movement is that of 'kicking-off' and a complex of flexors and tensors concentrated in the upper leg exert power and control of movement. These are the *gluteus*, *biceps*, *gracilis*, *semimembranosus* and *semitendinosus*. The lower leg muscles are greatly reduced in most species and are primarily tendinous in all running species.

The morphology of heads and their evolutionary origins

The concentration of disparate activities that are welded together in vertebrate skulls would seem extraordinary were it not so familiar. The further elaboration of head shapes, especially by horns, antlers, tusks and ossicones, has provided humans with symbols and trophies from the earliest times, yet remain a poorly explored aspect of morphology. It is partly our human fascination with heads and partly the superior survivorship of teeth that has ensured that fossil heads dominate palaeontological collections and provide the data for much of our knowledge of the evolution of heads.

Because the fore-ends of primitive chordates and vertebrates were the first to encounter both food and obstacles, basic sense organs and a 'mouth' developed there. The polarity of organisms and their symmetrical organization crosses all the higher taxa (Wainwright 1988). The need to respond to light, chemical, electric or vibrational signals led to the differentiation of cells until they developed into eyes, nose and ears, each encapsulated in compartments that shared the upper part of what became the skull. The lower section of this structure became a hinged mandible and eventually both jaws developed teeth. In many predatory vertebrates, from the most primitive to the most advanced, the size of jaws closely reflects the size and toughness of the prey. Furthermore, a gross expression of animal proportions is the size of heads relative to the size of bodies.

Apart from whales, the most extreme examples of disproportionately large or small heads are to be found in bats. This is partly because the head and jaws get little or no heavy-duty help from the limbs in the behaviour patterns of capturing and processing prey. Thus Moloney's Mimic Bat, a species that only takes small, soft-bodied prey, has no need for a large head while the Heart-nosed Bat *Cardioderma cor* seizes robust, often vertebrate, prey with its large jaws and must quickly subdue it with deep, damaging bites powered by massive jaw muscles. The head of the former is about one-seventh of the combined head-body volume, whereas *Cardioderma* heads are closer to a quarter!

One of the most fundamental expressions of cranial morphology concerns the sizes of sensory activities in the head. It is in the relative

sizes of compartments and in permutations of connecting bridges, struts and welds that the species-specific morphology of mammal heads becomes obvious. Wherever sufficient data exist on the ecology and behaviour of species, we find superb and detailed examples of forms evolving morphological modifications that serve very precise behavioural functions. This is particularly obvious in the relative sizes of, say, orbits, olfactory equipment and auditory bullae in mammal skulls. Even more explicit are the functional shapes of eyes, ears, noses and sensory whiskers in mammals as different as a galago, a Bat-eared Fox *Otocyon megalotis*, an Aardvark *Orycteropus afer* or an Aquatic Genet *Genetta piscivora*.



Thomas's Galago
Galagoides thomasi

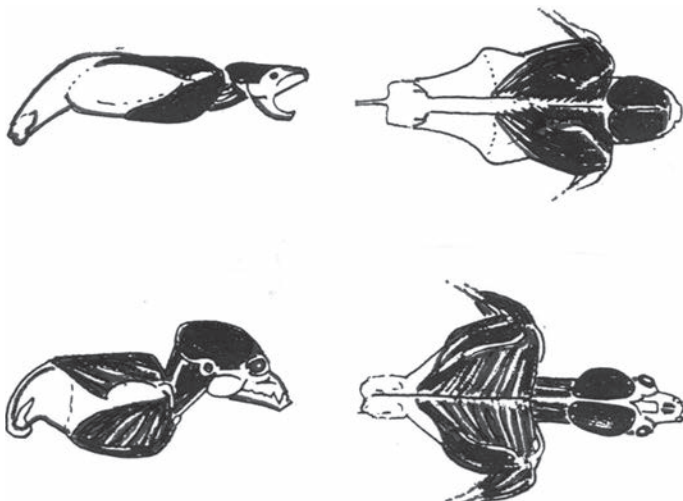
Bat-eared Fox
Otocyon megalotis



Aardvark *Orycteropus afer*

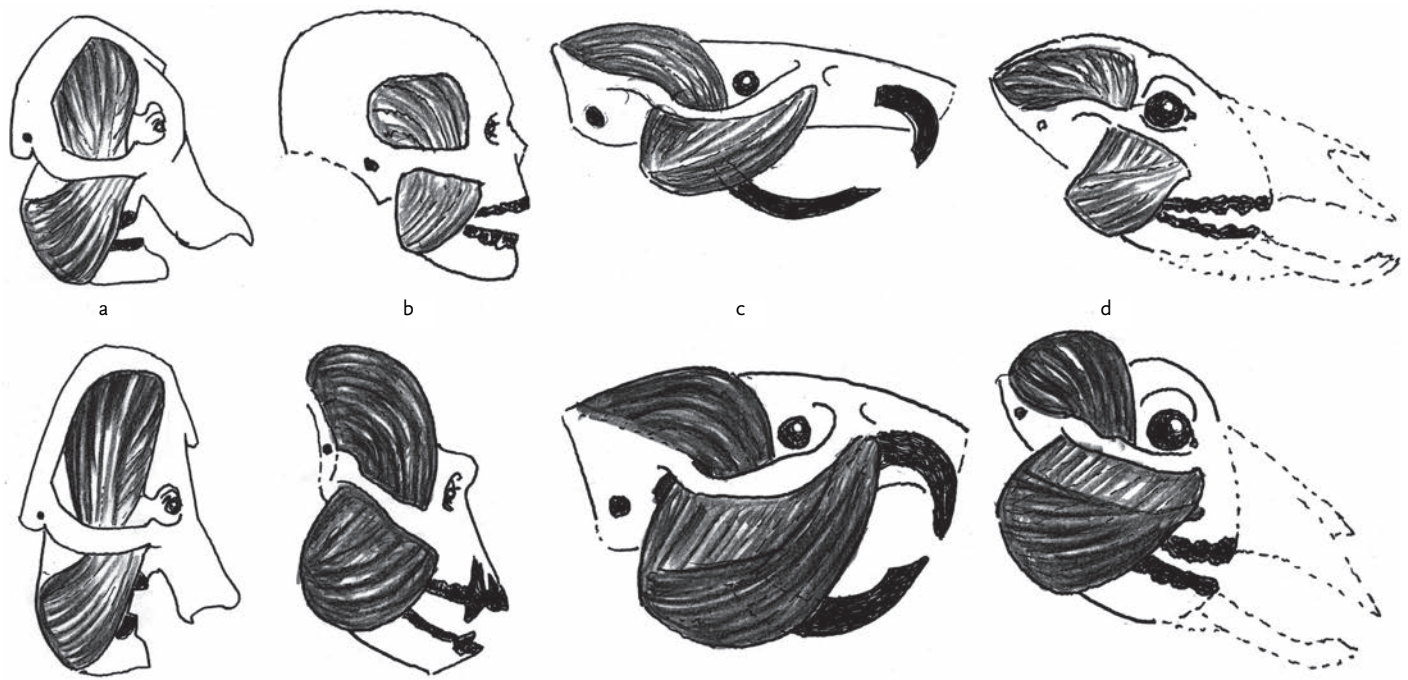


Aquatic Genet
Genetta piscivora



Head/body proportions in Mimic Bat *Mimetillus moloneyi* and Heart-nosed Bat *Cardioderma cor* (after Kingdon 1974).

Heads to illustrate super-development of different sensory faculties.



Skull outlines of four pairs of related mammal species, showing the role of chewing muscles (masseter and temporalis) influencing skull shape. Weaker chewers (top row) have shallow muscle attachments on relatively gracile skulls; powerful chewers (lower row) have robust skulls with deep muscle attachments.

a. African Elephant *Loxodonta africana* and Pleistocene Elephant *Elephas recki*. b. Human *Homo sapiens* and Western Gorilla *Gorilla gorilla*. c. Link Rat *Deomys ferrugineus* and Giant Squirrel *Protoxerus stangeri*. d. Bushbuck *Tragelaphus scriptus* and Mountain Reedbuck *Redunca fulvorufula*.

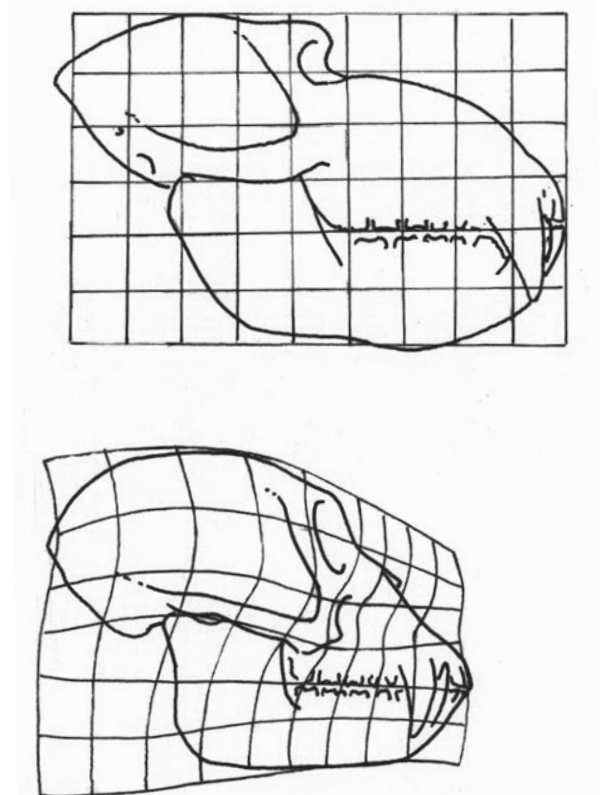
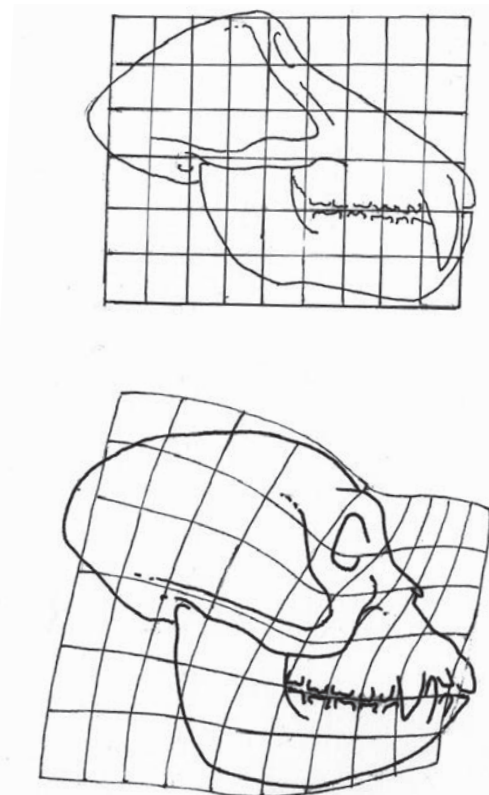
Head-shape and chewing

The mechanics of jaw function are nowhere more simple and explicit than in the Savanna Elephant *Loxodonta africana*, which has a back-and-forth mode of chewing with very little sideways action. The short, heavy mandible hangs from the *temporalis* muscle as if it were the chair of a swing. Here the 'ropes' of the *temporalis* are at right-angles to the lower tooth rows that resemble the chair's seat. The swing seat is pulled back towards the chest, in a loose, easy arc, by the *digastric* muscle. Coming forward again it closes over the mouthful of food and, clamping hard against the upper toothrow, grinds forward under the combined force of *masseter* and *temporalis* muscles.

In one of those confounding inversions of expectation, modern African elephants are, in terms of dentition and diet, relatively primitive. Until quite recently (about 19,000 years ago) the commonest and most widespread elephant species in Africa was *Elephas recki*, a close relative of the Indian elephant. Its fossils are abundant and widespread, from South Africa to the Sahara. *Elephas recki* (like its Indian congener *E. indicus* and its Nordic relative, the mammoth, *Mammuthus*) was a dentally advanced species with very deep, multi-plated molars that could masticate coarse, abrasive foods more efficiently than *Loxodonta africana*. However, it is not just teeth and their bony buttressing that take the strain of chewing. More force must be exerted on tougher foods and that force must be exerted by larger, longer muscles. And increased muscle forces reshape the bones onto which they are attached, such is the adaptability of bone form and function. In the case of elephant skulls, this resulted in the phylogenetic elevation of paired, honeycombed arches that absorb all the forces of chewing and cowl the braincase like a bonnet (tool language again). Although *E. recki* had a rather small skull relative to its body, its forehead was immense and a large part of this

enlargement can be confidently correlated with the behavioural need to enlarge the temporal muscles in order to exert more force on a formidable battery of chewing teeth. Comparing the skulls and teeth of *L. africana* and *E. recki* provides a vivid illustration of how changed diets (often triggered by climate change) drive modifications to tooth and skull structure. New stresses and strains on teeth call for changed mechanics in the skull, the external expressions of which are distinctive head shapes and silhouettes. Understanding the mutability of bones is, in turn, impossible without taking into account changes in the muscle forces exerted upon the bones. The interplay between behaviour, diet, teeth, the mechanics of mastication and the gross morphology of bones and muscles are evident in comparison between a dissection of an extant Savanna Elephant's head with a reconstruction of the same muscles on an *E. recki* skull.

Another simple demonstration of 'function and form' emerges from comparing the head proportions of two similar-sized antelopes: the Bushbuck *Tragelaphus scriptus* and Mountain Reedbuck *Redunca fulvorufula*. The former has a slender head with long-lipped mouth; the latter's head is short-mouthed and wedge-shaped. These differences begin with tooth proportions. The soft-foliage-eating Bushbuck has modest, shallowly rooted masticatory teeth set in equally shallow jaws, but the broad-leaved shrubs and herbs that it eats need a wide maw. The tough-grass-eating Mountain Reedbuck instead has heavily crenellated cheekteeth that are firmly rooted in a well-reinforced, deep-jawed skull and mandible. It is the expansion of teeth and their rooting, together with massive *masseter* and *temporalis* muscles, that open up that mandibular wedge. It is the nibbling of tough grasses that calls for that tight, short-lipped, muscular mouth. The external expressions of such dietary differences are an elongated sleek face in the Bushbuck, a relatively short, chunky face for the Mountain Reedbuck (see drawings).



Cartesian co-ordinates on skull profiles illustrate phylogenetic retraction of the muzzle of the Baboon Mangabey *Lophocebus* compared with its closest relative, the baboon *Papio* (top left), and Drill Mangabey *Cercocebus* compared with its closest relative, the Drill *Mandrillus* (top right).

Linking morphological form and function with genetics

At a time when genetics is the primary conceptual preoccupation of biology, and in a culture that is visually dominated by surface photography, general interest in the functional morphology of animals and the elucidation of their 'hidden' anatomy has gone into a decline that surely would have disappointed Darwin. Yet many new discoveries in molecular science only pique a broader interest in their implications. Eventually genetic peculiarities need to be understood in terms of the structures for which they code and the behaviours that employ them. Eventually we will want to relate gene codes to whole animals living in real landscapes and in the context of deep evolutionary time.

For example, among the genes that govern the production of the muscle protein myosin there is one that serves to build powerful jaw muscles in many mammals. This gene, *MYH16*, is fully intact in most higher primates but has recently been shown to have mutated in humans in such a way as to disable some of its muscle-building capacity (Stedman *et al.* 2004). Furthermore, the application of molecular clock techniques has dated the first appearance of this disabling mutation to 2.7–2.1 mya, broadly the same period when some fossil hominins show a substantial reduction in relative jaw size. Since the action and development of muscles are major determinants of bone shape and size this sudden decline in the architecture of hominin mandibles some 2.5 mya can now be ascribed to mutation in an identifiable, muscle-building gene. The *MYH16* mutation could only spread in those prehistoric populations because selection favouring powerful *masseter* muscles must have been relaxed. Less

need for powerful chewing muscles must have been influenced by significant shifts in foraging patterns, possibly the use of fire, tools and dietary changes. Although this is the first time that genetics, palaeontology and anatomy have been linked up in this way (Currie 2004), we can be confident that many more such instances will be discovered in the future.

To illustrate how contemporary science might integrate genetic information with morphology, diet, ecology and social behaviour, consider monkey jaws. Humans are not the only primates to have suffered a phylogenetic decline in the size of their muzzle. Two monkey lineages with even more prominent muzzles than apes, i.e. baboons *Papio* spp. and drills *Mandrillus* spp., have incisors and canines that project out from the male cranium about as far as is structurally possible without risking frequent fracture. Independently, ancestral populations belonging to each of these large, predominantly terrestrial monkey types have given rise to smaller-bodied, arboreal lineages, namely the baboon-mangabeys *Lophocebus* spp., the drill-mangabeys *Cercocebus* spp. and, probably, the newly discovered Kipunji *Rungwecebus kipunji* (Cronin & Sarich 1976, Davenport *et al.* 2006). The arguments in support of this phylogenetic shrinkage of jaws are presented in Volume II. Morphologically, these changes have involved remodelling of the skull as phylogenetic, backward migration of the entire tooththrow has forced the jugal plate (on which the molars were previously dependent for support) to buckle backwards and inwards, creating peculiar suborbital fossae. Once thought to be the principal diagnostic marker for a single mangabey lineage, its functional purpose was earnestly puzzled over. Now that separate origins have been demonstrated for the three genera by genetic analysis, it is apparent that suborbital fossae are simply convergent by-products of evolutionary change. Buckling

and dimpling of the jugal plate is an artefact of shifting skull parts and the 'fossae' are apparently without any direct functional significance in themselves. Some of the best examples of comparable remodelling of the skull can be found among whales, but these need not concern us here.

How muscles shape bone morphology

As demonstrated by the examples of elephants and antelopes, the size of a muscle can have a profound influence on the shape of the bones to which it is attached. Nowhere is this more pronounced than in the relationship between chewing muscles and the architecture of muzzles and skulls. The comparison between jowly early hominins and weakly jawed *Homo* is paralleled by clearly defined differences between two closely related porcupines. In the African Brush-tailed Porcupine *Atherurus africanus* the evolution of a weakly developed temporal muscle in this fruit-eater was probably as much due to softer foods as it was in *Homo*. It can be predicted that this decline was also mediated by the rodent equivalent of the *MYH16* gene. When the skull morphology of this porcupine is compared with that of an Asian equivalent, the Long-tailed Porcupine, *Trichys fasciculata*, there are precise correlations between the size of temporal muscles and the development of angular and temporal processes: prominent development in the strong gnawer *Trichys* and absence in the weak masticator *Atherurus*.

On a short-term (rather than the evolutionary) scale, behaviour-driven morphological change can be demonstrated through experiment. The role of temporal muscles in drawing out angular processes on mandibles and erecting temporal ridges on top of the cranial vault has been investigated in rats. Rats fed an exclusively soft diet have chewing muscles up to 13% lighter than those of rats on a hard diet and the angular process is also measurably reduced in size (Moore 1965). When the temporalis muscle is removed in very young rats both temporal ridges and angular processes entirely fail to develop (see right from Horowitz & Schapiro 1951).

Describing morphology and profiling adaptation in *Mammals of Africa*

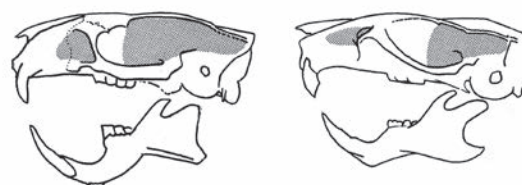
Practical concern for morphology and anatomy is expressed by the authors and editors of these volumes in various ways. To begin with, describing appearance requires verbal and conceptual skill, even to convey a minimal appreciation of an animal's shape and substance. The task is eased when the proportions, colours, shapes and sizes of one species are compared with those of another or others; indeed, the description of morphology leans heavily on the comparison of forms. However, any comparison of 'unfamiliar' animals with 'familiar' ones involves assumptions, not only about what species are familiar but also about what attributes constitute familiarity. Furthermore, verbal descriptions suffer from being linear processions of itemized attributes that all too easily become purely prescriptive: a cobbled amalgam of parts passing for a whole. Because any single individual of a single species possesses an immense, almost uncountable number of attributes, all descriptions have to be drastically condensed to a conventional summary of supposedly diagnostic attributes. Offsetting the atomistic limitations of language, and the apparent



Dorsal views of skulls of Brush-tailed Porcupine *Atherurus africanus* (left) and lab rat *Rattus rattus* (right) in which the right temporal muscle was removed in infancy.



Lateral views of skull and mandible of Brush-tailed Porcupine *Atherurus africanus* (left) and right mandible of lab rat *Rattus rattus* (right) in which the temporal muscle was removed in infancy.



Lateral views of skulls of Asiatic Porcupine *Trichys fasciculata* (left) and lab rat *Rattus rattus* (right).

sterility of listing itemized components, are prime reasons to invoke the 'familiar'. Authors forced to itemize often seek to retrieve some sense of the whole animal by referring to other animals that already exist as whole entities in the psychological gestalt of their readers. The problems faced by authors trying to translate their data and perceptions of a unique type of animal form into a verbal summary are therefore very real, and they are no easier to solve within the prescriptions of a handbook than those of field guides (to appreciate the perils see *Primates* and *Barbary Macaque* texts in Van den Brink 1967). Of course, field guide texts have to be drastically pruned but the condensation is merely a matter of degree; even the most comprehensive descriptions fall far short of reality.

Most biologists and naturalists share Darwin's desire to explore the biological 'meaning' of animal design: they seek to interpret form in terms of function and selective advantage. 'When we regard every production of nature as one which has had a history: when we contemplate every complex structure and instinct as the summing up of many contrivances, each useful to the possessor; ... when we thus view each organic being, how far more interesting, I speak from experience, will the study of natural history become' (Darwin 1859). It is partly in response to this Darwinian exhortation that all species profiles in *Mammals of Africa* include the heading 'Adaptations'. Herein authors are free to describe and interpret the behavioural, morphological and physiological adaptations that are unique to the species that is being profiled. Many of these adaptations involve secondary, tertiary, even umpteenth modifications of already intricate structures.

That the mammals of Africa should take so many diverse forms, yet be constructed on the same pattern and by a comprehensible process of natural selection, beginning with small changes in behaviour: what could be more curious? What could be more intellectually thrilling?

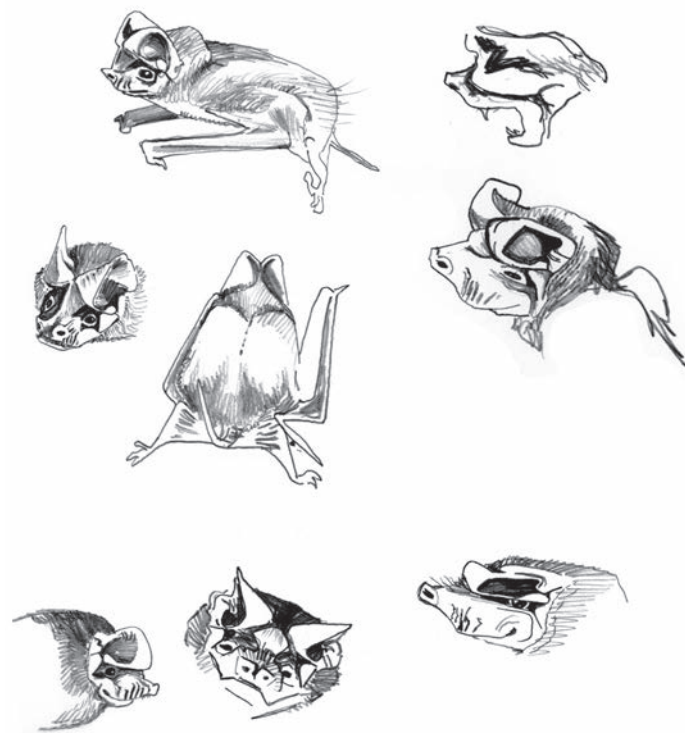
Illustrating morphology in *Mammals of Africa* (a postscript by Jonathan Kingdon)

Comprehension of mammalian biology can be deepened and supplemented by a variety of graphic media from maps, diagrams, histograms, gene charts, videos, photographs to all sorts of pictorial illustration. These modes of representation are sometimes self-sufficient for the sort of information they seek to propagate. However, Mitchell (1994) has pointed out that representation (in both modern and postmodern senses) becomes a conceptual issue when there are perceptible ruptures between image and text, and that illustrated texts can be better conceived not as a juxtaposition of two separate media but as composite synthetic works.

In these volumes the text is augmented by maps and drawn illustrations. A large number of the latter derive from a very long-term enterprise that has generated very many thousands of drawings (Kingdon 1971–1982, 1983, 1997). One of the reasons for preparing my *East African Mammals: An Atlas of Evolution in Africa* and my field and pocket guides was to enlist graphic imagery as a mode of exploration and discovery in itself. With my pencil I set out to record, both in field and laboratory, the morphology, functional anatomy and behaviour of many little-known mammals in the confidence that my audience would share with me a Darwinian excitement in making discoveries. Many of the smaller mammals that I observed or trapped had never been drawn, let alone photographed before and some of my work actually had the character of ‘first contact’ documents. Some 40 years after publication of the first volume of my *Atlas* these exploratory documents have been greatly augmented, often in close collaboration with the authors of this work, who have helped extend this enterprise into another millennium. We have been assisted by new forms of graphic aids that were inconceivable when I was drawing animals in the 1950s and 1960s (among the most exciting are camera-trap and space-tracking systems).

None the less, the greater part of an animal's structure is hidden under its coat, and photographs, however beautiful, seldom offer more than a hint of what lies beneath the surface. Of course, single-view drawings are similarly constrained but there is much greater scope for the isolation and presentation of those features that are most diagnostic of a species' appearance. Where the production of drawings has included detailed anatomical records of dissection and progressive stripping down to the skull and skeleton, such representations gain in authority. In the corpus of work from which these illustrations have been selected, there were more than 300 such published dissections, and several hundred skulls and other anatomical details were also drawn. The skull drawings have been augmented here by many hundreds more but these have been rendered in a more conventional format to assist comparability between taxa.

Verbal language is not our only artefact in the effort to study and conceptualize ‘meaning’ in the physical existence of mammals. Anatomically correct drawing, particularly when backed up by dissection and field sketches of ephemeral behaviour and postures, can augment description with a useful type of non-verbal functional analysis. Unfortunately, most expressions of contemporary visual media are designed for instant absorption and the habit of taking time to carefully examine both real objects and man-made pictorial images has become exceptional. Most of the drawings in this work are the outcome of sustained and time-consuming contemplation and analysis of representative individuals of particular species, with particular

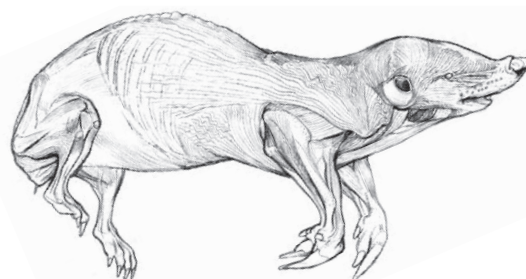


Sketches of *Tadarida thersites* showing the mutability of ear shape.

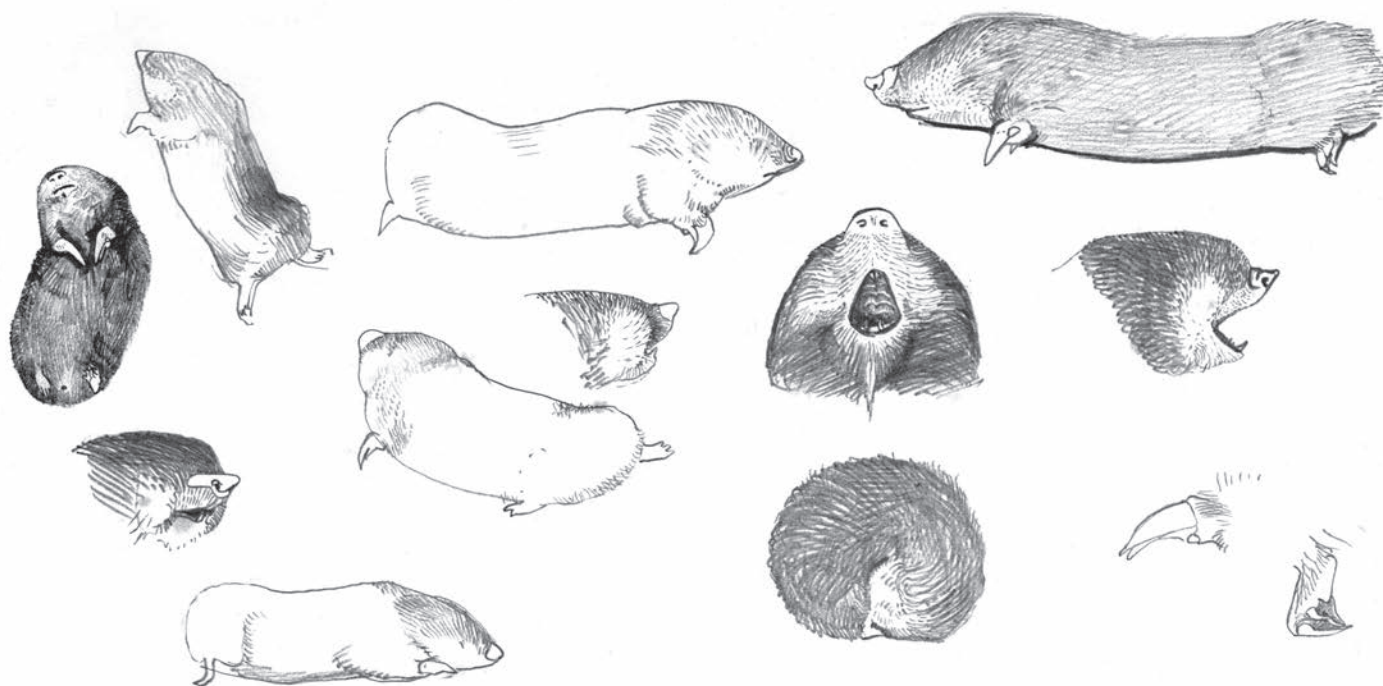
attention to the relative proportions of functional components. Many of the drawings were made under quite trying conditions in the field, during floods, heat-waves, downpours, out in the open, under canvas, in contention with innumerable insects or in the relative comfort of a vehicle. In the final production of coloured illustrations I have sought to recognize and display as many subtle intimations of uniqueness as are possible in a single image. In *East African Mammals* these were augmented by line drawings of relevant details of anatomical form and sheets of sketches that illustrated behaviour and posture. Similar augmentation has been applied to some of the species profiled in this work.

We now know that small changes in diet or in the techniques whereby food is processed are tied in with evolutionary changes in ecology and behaviour, and, ultimately, with the morphology of teeth, heads, limbs and backbones. At a more general level the comparison of species, one with another, helps suggest how physical aspects of the environment (such as the composition of food or an ecological shift) elicit changes in behaviour, which drive the evolution of appropriate adaptive structures as expressed in the details of animal form.

The problems of representation are nowhere better exemplified than with the Afrotherian golden-moles. In spite of the pretty metallic fur that has given them their name, their appearance within museum drawers or even in photographs, is of featureless oval blobs. Such apparent ‘shapelessness’ to superficial photographic or human lenses



Myology of Stuhlmann's Golden-mole *Chrysochloris stuhlmanni*.



Action drawings of Stuhlmann's Golden-mole *Chrysochloris stuhlmanni*.

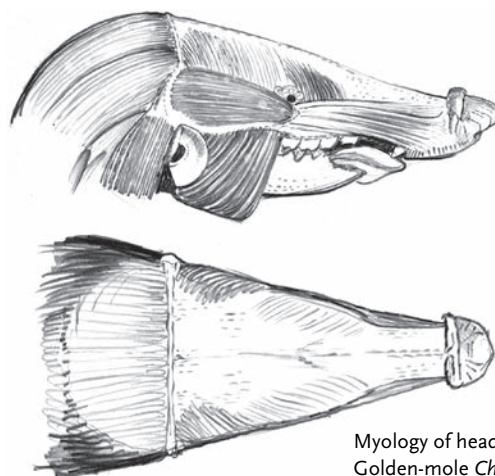
is profoundly misleading. Golden-moles are no less highly evolved than Aardvarks or elephants. Closer inspection of living animals, let alone careful dissection of their myology, reveals an energetic digger perfectly adapted to a subterranean existence.

Exposed outside their burrows, tiny clawed feet row their bodies over the surface without ever lifting their bellies off the ground. The spade-shaped snout can be forced deep into the soil or into interstices, whereupon one or two fingers, armed with sharp claws, are brought forward into the nose-made crevice and a very powerful opening-up action follows as the robust cranium and nose push up and the hard claws tear down and back.

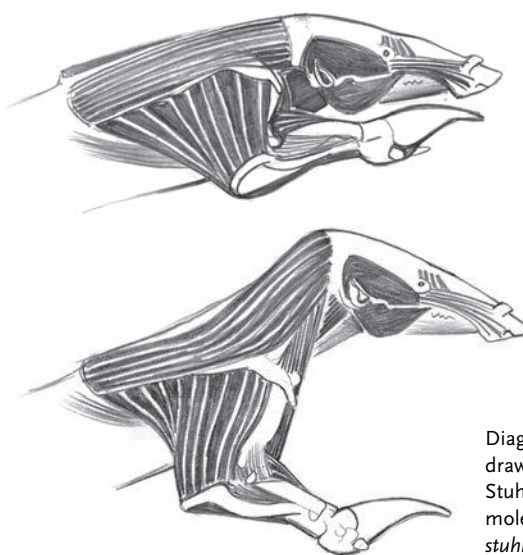
Something of the golden-mole's vitality can be conveyed by sketches of the living animal *in natura* but simplified anatomical diagrams can enhance appreciation of the fitness of highly modified bones and muscles for probing and digging functions. A quick sketch of a Giant Golden-mole *Chrysospalax trevelyani* skeleton (see overleaf) positioned to display its digging action illustrates the streamlined anatomy of a superbly designed digging machine beneath that metallic, blobby oval. Golden-mole genera vary in sizes, in the proportions of heads in relation to body length and in the details of skulls, claws and limbs. Appreciation of such differences can be enhanced by matching colour images of their relatively bland external appearance with schematic 'x-ray' equivalents (see overleaf) in which diverse body sizes and body proportions become obvious and bleached skull outlines hint at interesting differences that are specific to each genus.

For a while, conservative biologists rejected the recent discovery that golden-mole genetics placed them unambiguously within the (almost as recently discovered) 'Afrothere' radiation. However, such contention has dropped away as more and more analyses have demonstrated the intrinsic power of the burgeoning new science of molecular phylogeny.

As the physiological and anatomical functions of genes are explored perhaps we should trust that one day it will be molecular science

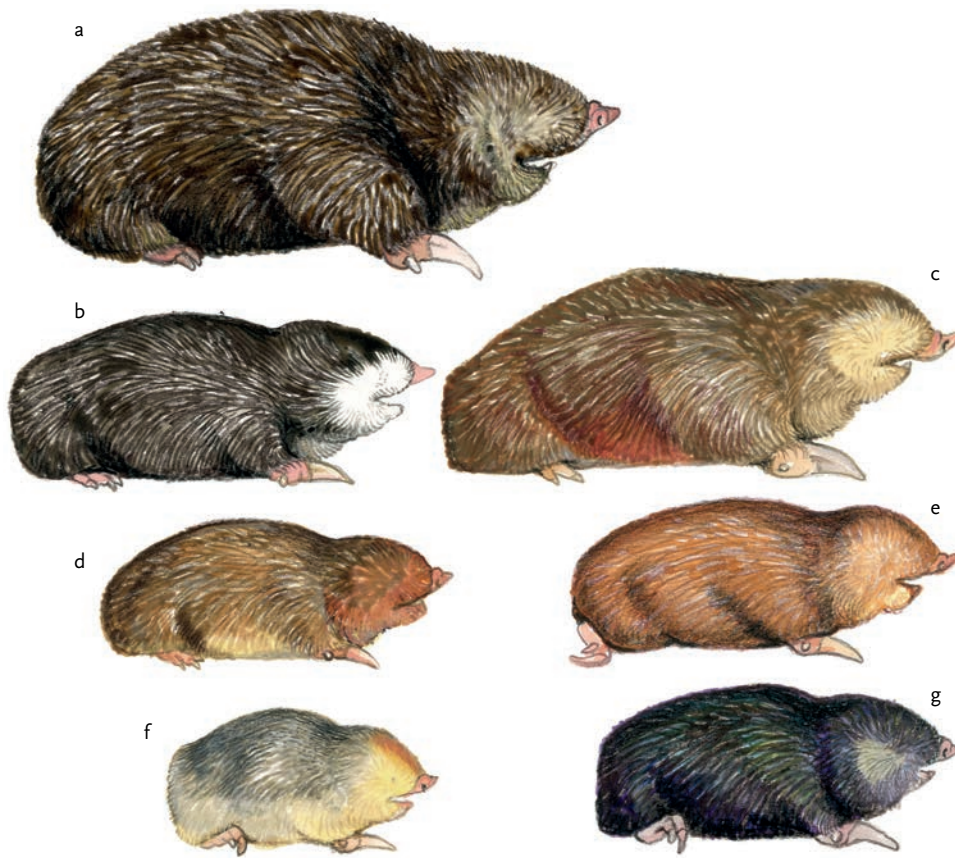


Myology of head of Stuhlmann's Golden-mole *Chrysochloris stuhlmanni*.

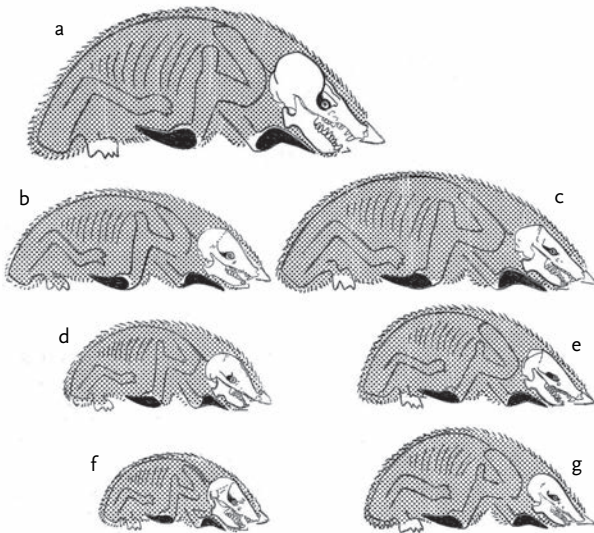


Diagrammatic myology drawings of a digging Stuhlmann's Golden-mole *Chrysochloris stuhlmanni*.

LEFT AND BELOW LEFT: a. Rough-haired Golden-mole *Chrysospalax villosus*. b. Cape Golden-mole *Chrysochloris asiatica*. c. Hottentot Golden-mole *Amblysomus hottentotus*. d. De Winton's Golden-mole *Cryptochloris wintoni*. e. Yellow Golden-mole *Calcochloris obtusirostris*. f. Grant's Golden-mole *Eremitalpa granti*. g. Duthie's Golden-mole *Chlorotalpa duthieae*.



BELOW: Giant Golden-mole *Chrysospalax trevelyani* digging.



that leads a renaissance in morphological studies and on to a deeper appreciation of how form is shaped by function and functional behaviour!

As the richest and most diverse region for mammals on Earth and the context for our own emergence and existence as human beings, Africa's living and fossil fauna can be expected to offer many new insights into evolution and a great diversity of absorbing aesthetic experiences. We can expect numerous new ways of representing biological insights to be developed in the years to come but I hope the pioneering intentions of the drawings/documents on offer here will continue to help viewers formulate a deeper and more contemplative appreciation for their subjects.



Ventral view of the skeleton of Stuhlmann's Golden-mole *Chrysochloris stuhlmanni* showing strut-like clavicles.

Class MAMMALIA

Few people today can deny that they, too, are mammals. Yet ancient and pre-scientific traditions, that drew un-crossable mental lines between humans and other mammals, still persist, thereby barring the most direct and simple way of defining and appreciating what it is to be a mammal. In all essentials for life and reproduction they are like us and we are like them.



Suckling female Gorilla *Gorilla gorilla*.

Such a starting-point can bring both objective scientific analysis and some measure of empathy to bear on the task of defining what it is to be a mammal. The most fundamental diagnosis includes the meaning of the name itself: mammals are animals whose mothers have mammary glands – mammae that have the evolutionary origin of being modified cutaneous glands (Darwin 1859). Being suckled is actually but a detail of the two adaptations that have ensured the world-wide success of mammals: one is drawing energy and nutrients

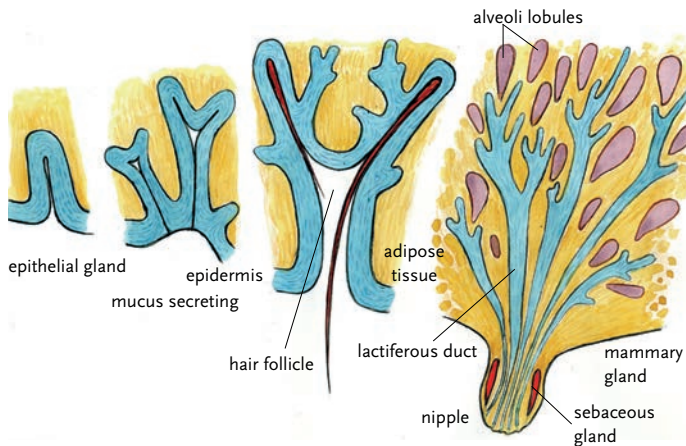
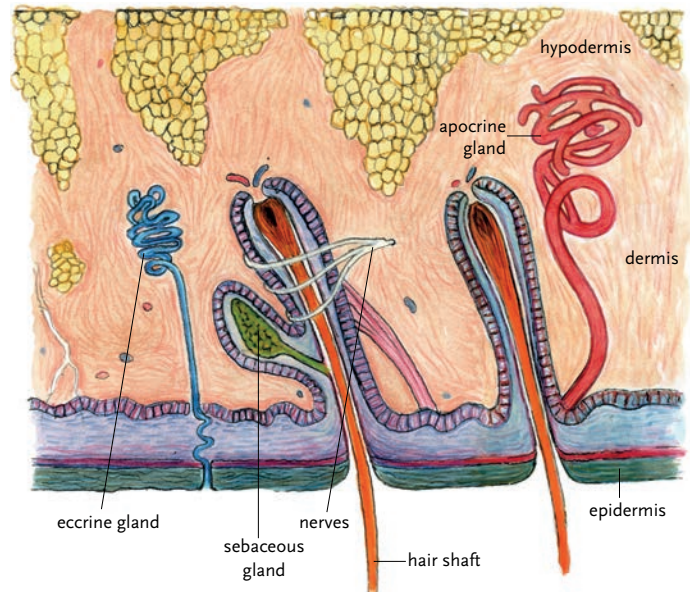


Diagram of possible evolutionary origins of mammary glands. Following the suggestion that mammae were derived from cutaneous glands (Darwin 1859), Oftedal (2002) suggested that milk-secreting glands derived from modified hair-follicles associated with apocrine-like glands. Vorbach *et al.* (2006) have shown that milk-production probably derived from an inflammatory response that involved immuno-protective proteins in skin glands.

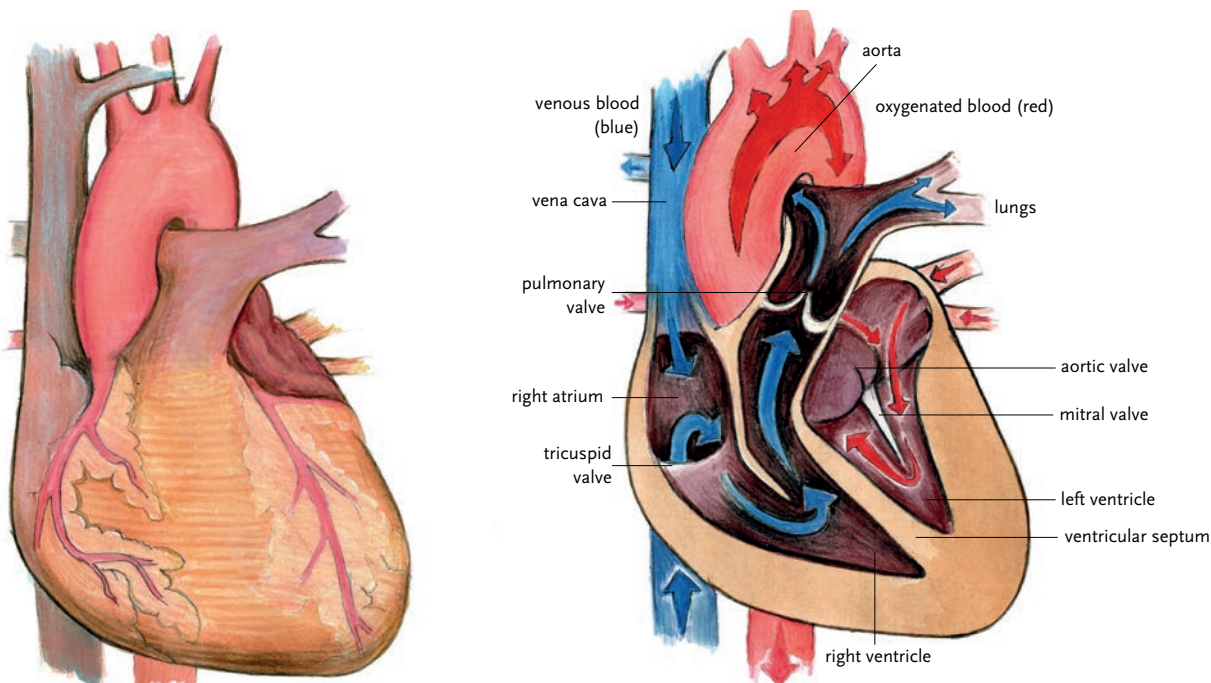


Microstructure of a typical mammalian hair and associated nerves, sebaceous, eccrine and apocrine glands in dermal tissues.

from the mother's body both before and after birth. The other is having an energetic warm-blooded body, a property called homeothermy. Mammals have a higher metabolic rate than other animals (excepting birds) because they have evolved internally stable temperatures, mediated by warm blood, which circulates very efficiently thanks to several unique adaptations. This makes them rather independent from the disciplines of the environment; much more so than most other animals, and hence mammals are also found at climatic and geographic extremes. Homeothermy allows consistently faster and sustainable movement, so that mammals are among the fastest of all running, leaping, flying and swimming animals.

The most obvious external manifestation of temperature-regulation consists of fur, hair or bristles that take many different forms, including scale-like and horn-like structures and may even have degenerated, leaving some mammals partly or wholly naked (see illustration p. 206). A less labile and more universal and fundamental regulator for the high metabolic turnover associated with high, endotherm body temperature is the mammalian four-chambered heart. This complex muscular organ keeps out-going, lung-oxygenated blood separate from blood that returns, spent of its oxygen, after energizing working muscles and actions. Immediately below the lungs is a thick, membranous diaphragm that is tightly attached to the inner walls of the thoracic cavity. Assisted by rhythmic contractions of the rib-cage and its muscles, the diaphragm helps pump the lungs, drawing fresh air in to oxygenate the blood and then expels 'used' air that includes carbon dioxide.

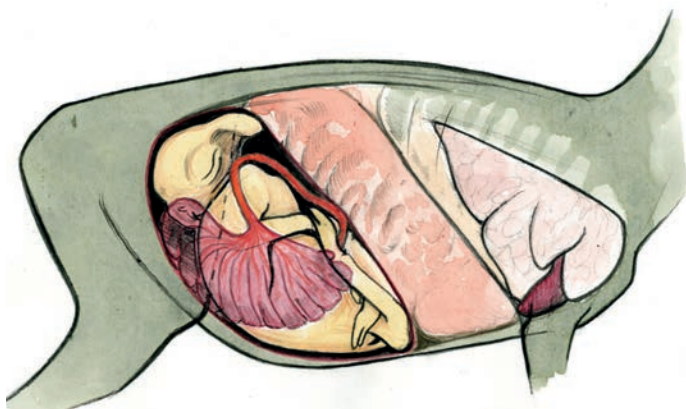
All African mammals are placental and the evolution of this mode of reproduction (which probably originated in Eurasia) is unique to placental or 'Eutherian' mammals. It overcomes several disadvantages



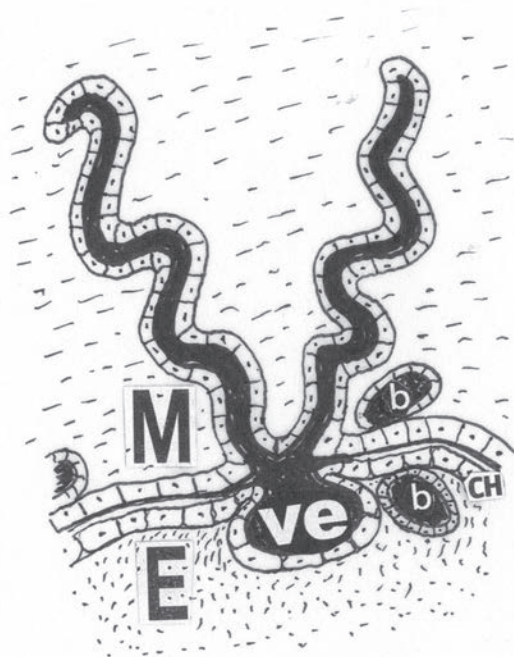
Typical mammalian heart showing venous blood (blue) flowing into right atrium through tricuspid valve into right ventricle, then via pulmonary valve and pulmonary arteries into lungs. Oxygenated blood (red) returns into left ventricle via mitral and aortic valves into aorta and on to arterial blood supply.

that are inherent in the eggs that are laid by other vertebrates: notably the egg's store of nutrients is finite, the period of development within an egg is relatively brief, the embryo is totally separated from the mother's metabolism at a very early stage of development and the developing embryo cannot void metabolic wastes through the egg's shell or membrane (Fox 1999). This combination inhibits or delays the building of energy-costly structures, such as brains. Indeed, Martin (1990) has pointed out that the resources supplied through the placenta are crucial in determining the eventual size of the brain. The existence of foreign (paternal) genes in the embryo may have been one reason for separating the embryo from the mother in a self-contained egg thus insulating the foetus from being rejected by the mother's metabolism as a foreign body. Exactly how the placenta overcame this last problem during its evolution remains a controversial topic (Cohen & Larsson 1988), but it is central to what the placenta represents as an evolutionary advance. Placentas are, of course, the defining adaptation for placental mammals.

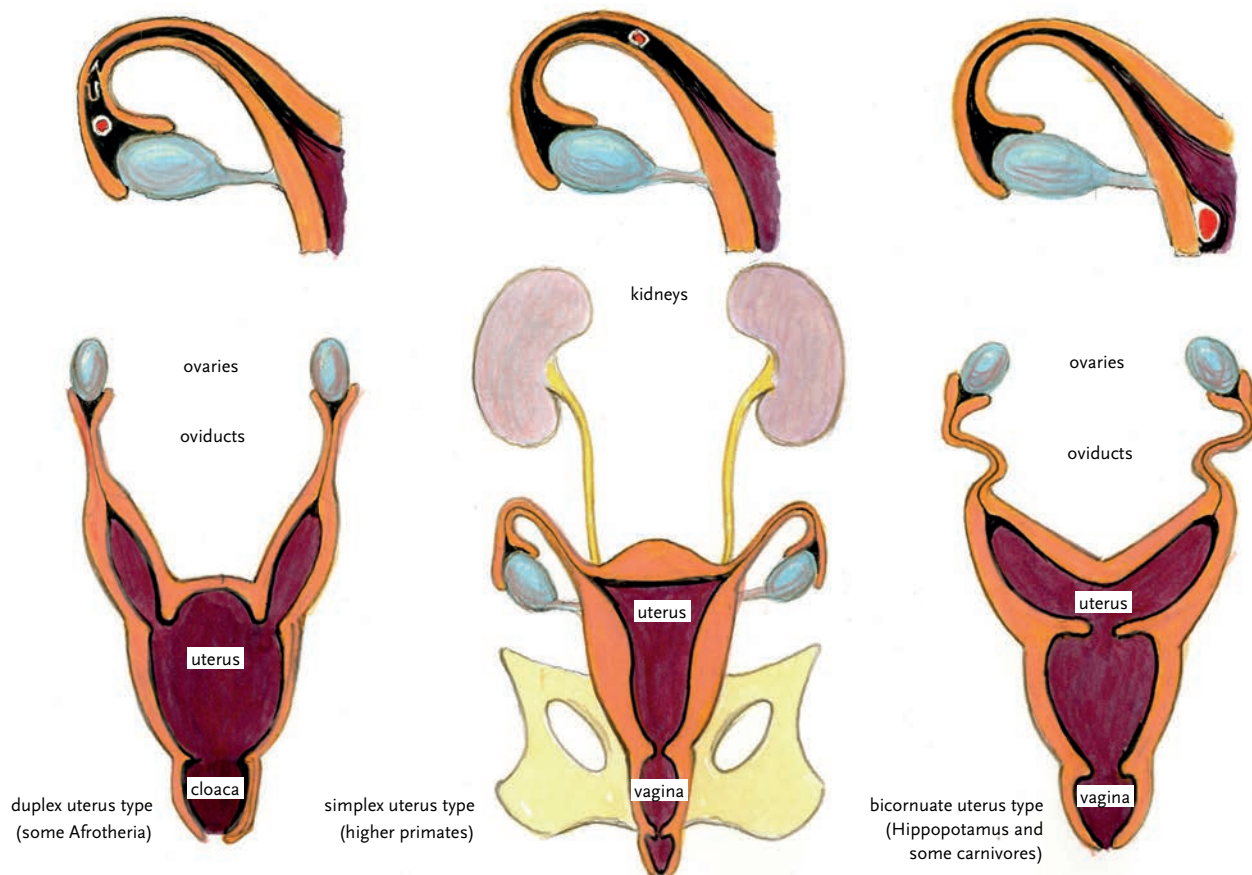
The placenta begins as a disc-shaped tissue that issues from the earliest stages of embryo development and acts as the interface between foetus and mother. It secretes hormones that prepare the uterus wall to accept the foetus and it produces immunosuppressive proteins that are thought to inhibit maternal rejection of the foetus (Larsson *et al.* 1994). Placental cells fuse to develop a complex, multinucleated tissue called placental syncytium, which has multiple projections that



Placenta and foetus of an antelope (*Madoqua* sp.) showing position, size and form of placenta at near full-term.



Details of interlacing between the maternal (M) and embryonic (E) tissues in the placenta. b = blood vessels on both portions of placenta; CH = chorion outer membrane of foetal portion; ve = vesicle/invagination below villi accessing maternal blood supply.

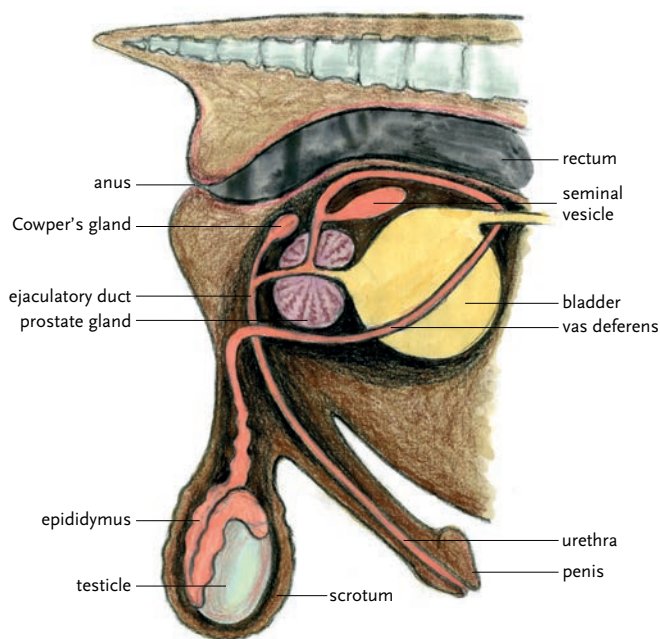


ABOVE: Course of the ovum (red) from the ovary (blue) to implantation in the uterus. BELOW: Types of female reproductive tracts.

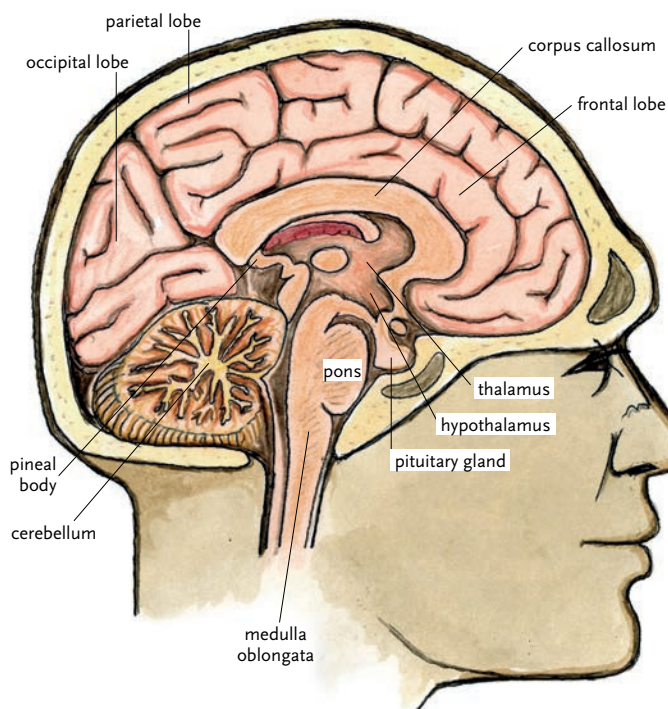
probe deeply into the uterine lining and actually invade the mother's blood vessels. Once it is firmly embedded in the wall of the uterus, the placenta develops a rich network of blood vessels that taps into the female's vascular circulation. Connected to the placenta via its umbilical cord, the foetus not only absorbs oxygen and nutrients from its mother, it also discharges its own metabolic wastes into her

system via the placenta (see figure, opposite below right). As well as allowing the foetus to share its mother's nutritional, respiratory and excretory circulation, the placenta produces multiple hormonal controls, including oestrogen, progesterone and gonadotrophin. It has been suggested that an embryonic association with an endogenous retrovirus (ERV) might have mediated the earliest beginnings of the placenta by becoming encoded into mammalian DNA (Larsson *et al.* 1994). This could explain why the mother is inhibited from rejecting the foetus, an idea that has been hotly contested, but research on the properties and origins of the placenta continue, with the gene coding for syncytin now identified in the human genome (Mallet *et al.* 2004). Immediately after birth, the placenta is shed.

Mammals have specialized in maternal care: first there is the womb and all its placental properties. This is followed by another key feature (but shared with the marsupials that are so conspicuously absent in contemporary Africa) that is secreting milk from the mammae. This necessitates days, months (or even years in the case of elephants) of direct maternal contact and protection. In many species, protection (sometimes bi-parental) extends well beyond weaning and effectively augments the physiological adaptations that make mammals relatively independent of the environment. Social structures in some mammal species mimic or extend parent-like security to most members of the group. In humans, the mammalian traits of (i) detachment from ecological systems and from many rigours of the environment, and (ii) social dependency have been extended by technology, psychological management and social institutions well past adulthood, even into old age. Thus it can be argued that humans have evolved to become the most mammalian



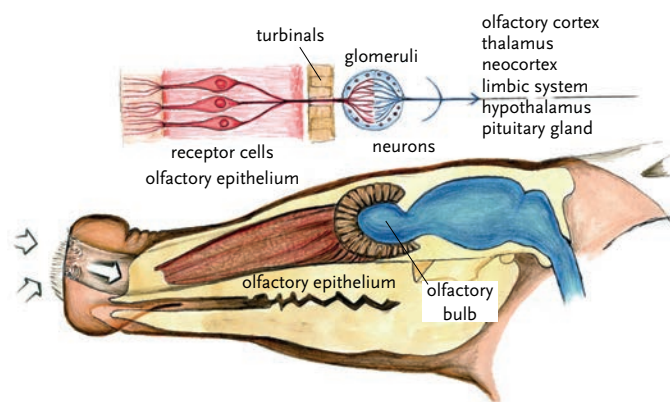
Male mammalian reproductive tract.



Principal components of the mammalian brain (typified by *Homo sapiens*). Signals are exchanged between the brain and the peripheral nervous system via the spinal cord.

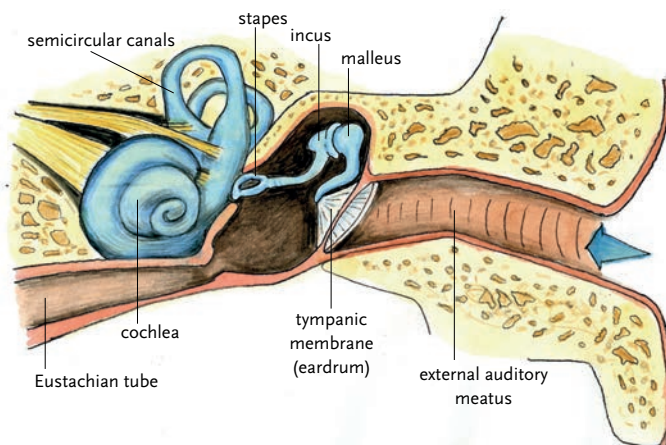
of all mammals by prolonging parental/social dependency and by extending relative independence from the environment – both of which features are, after all, typically mammalian strategic traits!

While a mammal shares a highly adapted brain with many other types of animal, the mammalian brain is relatively larger and more complex (especially the cerebellum). Perhaps more than any other morphological trait, the brain and its multiple functions is most developed in primates. And, within the primates, the brain has evolved



Mammalian olfaction pathways typified by Aardvark *Orycteropus afer*. Odour molecules entering nasal cavity bind to hair-like terminals (cilia) on trigeminal receptor cells embedded in olfactory epithelium covering thin turbinal bones.

Neuron extensions in receptors transmit olfactory information through the cribriform plate to the brain's olfactory bulb. Glomeruli within the olfactory bulb transform information coded in receptor cells and permit exchange with mitral and granule cells. Mitral and other neurons send information to the brain and activate appropriate responses in limbic, endocrine and autonomous nervous systems.



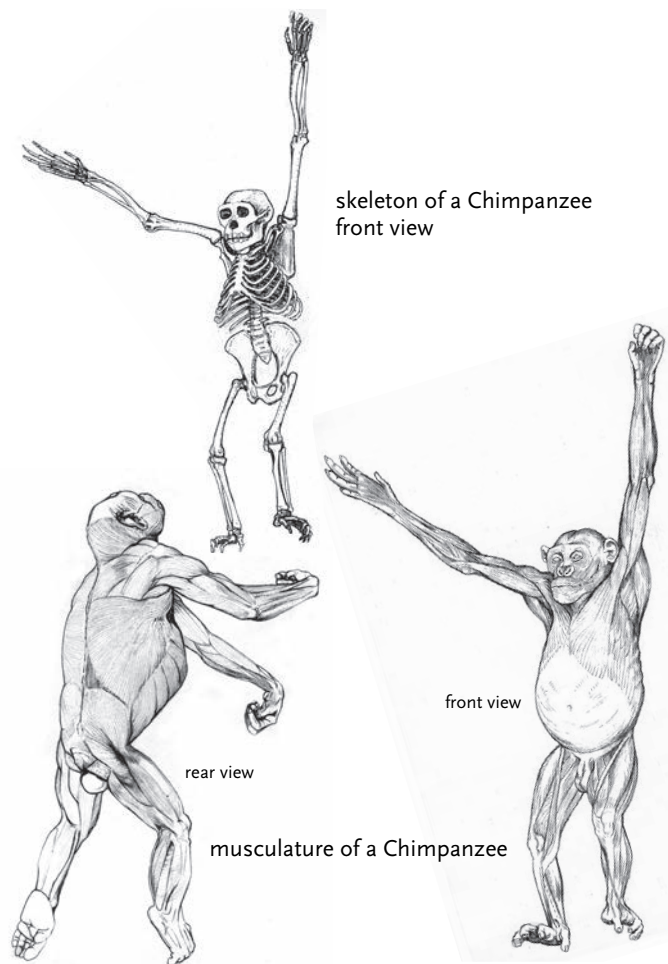
Mammalian auditory system. Incoming sound waves registered on the eardrum are transmitted via the malleus, incus and stapes to the cochlea, where auditory nerve endings translate sound waves into electrical signals for transmission to the brain. Of all biota, mammalian auditory capacity is the most refined. There is exceptional sensitivity to very high and very low pitch.

its largest relative size in the humans. Other mammals, especially some cetaceans, elephants and bats, also have highly developed brains with capacities and ranges of functions that still remain largely unknown. However, none of these brains, well adapted as they have to be, matches the cognitive capacities of the human brain.

Mammals share their basic sensory systems with birds and reptiles; and are actually inferior to many bird and lizard species in visual acuity and in sensitivity to optical wave-range. However, most mammals (excepting primates and some bats) have very superior olfactory apparatus to birds and reptiles and consequently are able to navigate in a world of scent. In concert with this specific sensitivity, mammals have developed numerous glands that are rich in olfactory information.

Mammals also have evolved great sensitivity to sound, and their hearing capacities are far superior to reptilian equivalents. The evolutionary origins of the hearing apparatus have been reconstructed from a rich fossil record of the ancestry of mammals. This documents the transformation of bony components (originally part of the mandible) and the migration of these modified bones and their attachment to the base of the cranium. Indeed, the development of refined hearing in mammals is one of the most telling of all examples of the modification of one set of structures, by infinitely slow, incremental steps, to serve an entirely new purpose. In mammals, hearing not only serves in the finding of food, the identification of conspecifics and the detection of predators, it also has been greatly (and independently) developed and modified to serve as super-sensitive sonar in the bats and cetaceans. The range of sensitivity to sound signals has been greatly extended at both ends of the sound spectrum in rodents, insectivores and elephants (to mention a few of the best-known examples) as well as bats and cetaceans. Thus sound, in mammals, has been co-opted to serve in orientation, spatial awareness and social cohesion as well as numerous other communicative purposes.

The exact configuration of senses differs from one mammal taxon to another. Scent, hearing, sight and touch are balanced in permutations that are unique to each species, and that balance finds a gross expression in the shape of mammal skulls, heads, skeletons and myology (see Chapter 8, p. 109). Each of these faculties has developed by small increments from the less specialized sensory



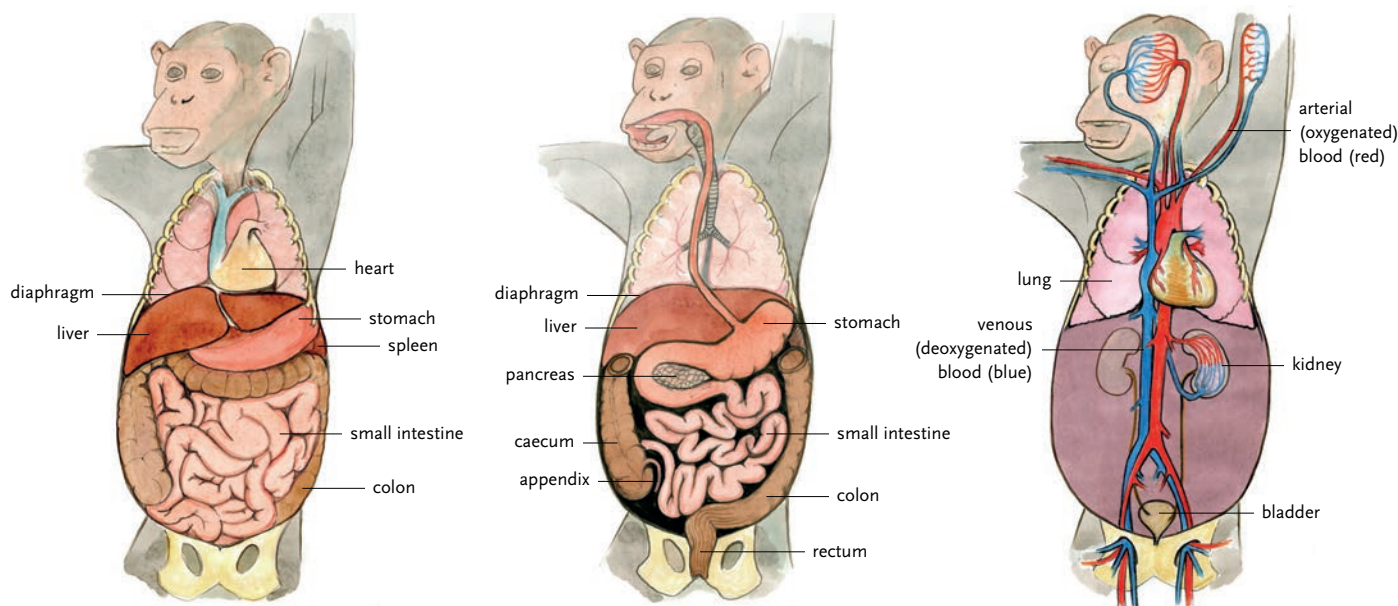
A mammal's musculature, skeleton, sensory, neural and vascular systems, reproductive, urinary and digestive tracts are all discrete 'homeostatic systems' contained within its skin and all obfuscated by its pelage.

apparatus that preceded them. Even at quite a refined level the proportions of subtle differences in the skull proportions of primates, rodents, foxes, antelopes and other speciose groups can all be related to similar shifts in the balance of senses. Likewise, the relative sizes and functional activities of mammal bodies and musculature are expressed in their proportions and gross anatomy.

Contours of bodies conceal ever more complex metabolic systems, respiratory, vascular, hormonal, digestive, excretory, reproductive and nervous systems, each subjects for distinct scientific disciplines. During the course of evolution the interweaving of these self-regulating systems has generated odd but essential structures such as a secondary palate and a valvular pharynx (both of which serve to keep nasal and oral passages separate). A series of schematic illustrations (below, mostly drawn from a single individual, a young chimpanzee) can only hint at the maze of interwoven pipes, cables, tubes and organic machines that lie beneath *any* mammal's bland exterior.

Teeth and the details of their structure have long been a staple in the diagnosis of mammals (McKenna 1975, Hillson 1986). Much effort has been expended on reconstructing the structure of ancestral mammalian teeth. A good fossil record of cynodont and early mammaliaforms shows that the differentiation of peg-like teeth into distinct classes of specialized form, namely incisors, canines, premolars and molars, long predates the emergence of mammals. Such differentiation is known as heterodonty (Novacek 1986).

A practical reason for emphasis on teeth is that they survive well after death, both in extant and extinct taxa. Their usefulness for phylogeny also derives from the fact that dentition is usually species-specific and is always highly diagnostic at higher taxonomic levels. Even the rise of molecular phylogenies cannot displace the



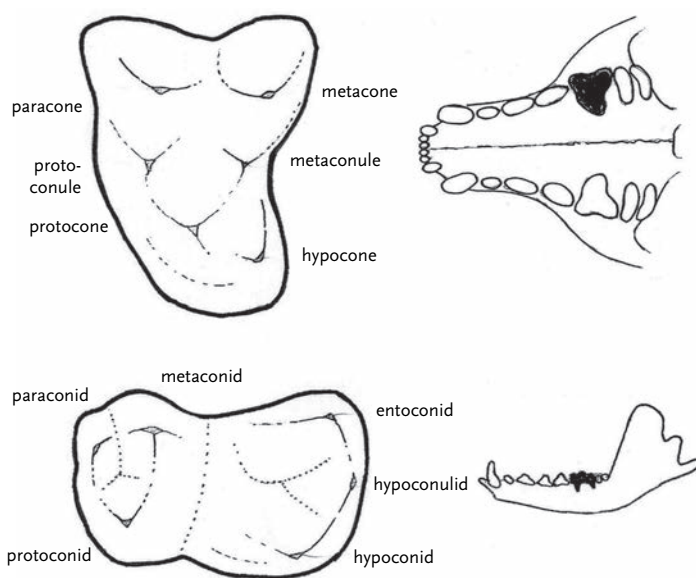
LEFT: Schematic representation of viscera: shows relative positions and sizes of heart, lungs, liver, stomach and gut in a Chimpanzee.

CENTRE: The respiratory and digestive tracts in a Chimpanzee, showing bronchial trees at lower end of trachea reach all parts of lungs. Pathway of oesophagus (connecting mouth and stomach), stomach and pancreas, small and large intestines (mid-section of latter cut away), appendix and colon/anus. Note glottis serves to separate oral and nasal passages in pharynx (all simplified).

RIGHT: Schematic representation of circulatory and renal systems in a Chimpanzee. Heart, lungs, diaphragm and blood vessels combine to send oxygenated blood (red) to body tissues, including kidneys. Veins return de-oxygenated blood (blue) to lungs where carbon dioxide is removed and the cycle repeats.

importance of teeth as indicators of affinity. Differences in the shape of teeth, no less than any other aspect of morphology or behaviour are outcomes from the struggle for subsistence itself. Getting access to, or processing food demands teeth, and their description has even led to the naming of entire groups, such as rodents or tubulident.

The primitive dental condition in early placental mammals can be expressed in the dental formula of $I^{3/3} C^{1/1} P^{4/4} M^{3/3} = 48$. This represents a reduction from earlier conditions (Novacek 1986) but the details need not concern us here. The molar teeth of nearly all extant mammals derive from an ancestral tribosphenic structure (Bown & Kraus 1979). None the less, this origin can be wholly lost in the complex transformations that have evolved since the Mesozoic. Teeth, both deciduous 'milk' teeth and adult 'permanent' teeth, are therefore essential to mammalian diagnostics and dental descriptions and illustrations are an important part of the group and species profiles that follow (see figure below).



Terminology for dental cones on a generalized mammalian molar: maxilla above, mandible below.

Comparing anatomical, physiological and functional systems with those of other animal forms is part of defining the Mammalia but, given that reptiles, amphibians and birds all share a common ancestry with us, how long have mammals been distinct and when did they diverge?

What distinguishes all mammals from, say, reptiles and birds, is a common heritage that stretches back over 300 million years (Cifelli 2001, Rose 2006). Placental mammals parted from the marsupial mammals some time between 145 and 135 mya (Luo *et al.* 2002, Wible *et al.* 2007). To appreciate the magnitude of these time frames, and of the shared distinctiveness of both mammalian clades, we may remember that it is only about 9–6.5 million years since humans shared a common ancestry with our closest living primate relatives (Sarich & Wilson 1967) and that the dinosaurs were supreme until only 65.5 mya.

Today the diagnostic characteristics that distinguish modern mammals from reptiles and birds are numerous and clear-cut. The differences between any pair of living animals (an ostrich versus a lizard, a lion versus a crocodile or a human compared with a galago) encompass an enormous array of genetic, anatomical, physiological and psychological details. These are strong differences between

end-members of long-separate lineages but fossils suggest that the differences were not always so clear-cut. The levels of comparison that are possible between living survivors diminish once lineages that have become extinct are taken into consideration. And immense numbers of extraordinary and interesting animals, especially types of mammals and proto-mammals, have gone extinct (see Hopson & Crompton 1969, Kemp 2005, Rose 2006). Luckily the accidents that have given us the rich 'History Book' of fossils do at least allow mineralized extinct teeth to be compared with teeth in living mammals, fossil bones with living bones and many other extrapolations can nowadays be made about the behaviours that gave rise to so many peculiarly shaped anatomies.

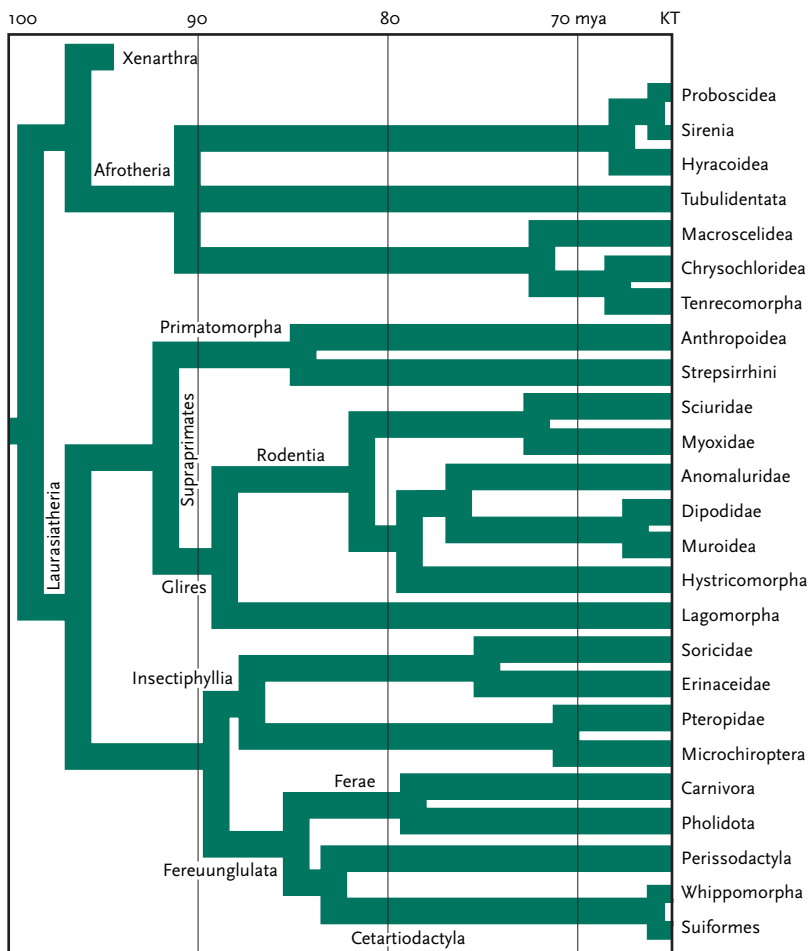
The more ancient of our mammalian (or reptile-like) ancestors, were they not all extinct, would have seemed somewhat similar to one another, with their resemblances deriving from their common ancestry among the amphibian-like Protothyrids (Carroll 1988). Until quite recently it was common to find mammals described as descending from reptiles. This is incorrect, in spite of many close resemblances in the earliest ancestors of both groups. Mammals and reptiles have had separate lineages since the Carboniferous, about 300 mya (Rose 2006).

The synapsids, the ancestors from which all mammals descended, used to be called 'mammal-like reptiles' (Romer 1945). However, synapsids are now known to have been a separate lineage from that of the reptiles. Synapsids, during more than 200 million years of separate evolution, radiated into a great variety of distinct forms (Hopson & Crompton 1969, Kemp 1983, Hopson 1994, Benton 1999). Within this phylogenetic 'bush', cladistic analysis of fossil morphology has traced the ancestors of modern mammals through primitive synapsids to pelycosaurs, then therapsids and, by the Triassic, to the cynodonts, which, while being more mammal-like and ancestral to modern mammals, were still not classed as mammals (Rose 2006). By the late Triassic, multituberculates had evolved and were to become the dominant mammaliaforms throughout the Jurassic. It was at this time and later, during the Jurassic, that a great variety of mammal types, including egg-laying monotremes (which survive in Australasia) and symmetrodonts (all now extinct), evolved.

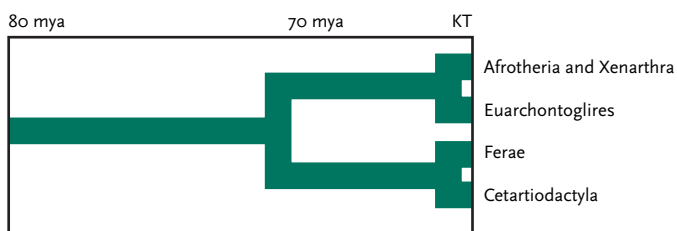
Among the earliest and best preserved fossils of an early mammal is *Hadracodium*. One of the smallest mammals ever known, it was estimated (Luo *et al.* 2001) to weigh little more than 2 g, close to the weight of a tadpole! Possibly a crevice-dweller, its skull was peculiarly flat and wide. The outline of its skull and its 195 mya position on the mammalian tree are shown on p. 76. By the early Cretaceous there was a great diversity of mammalian types, including the ancestors of placental and marsupial mammals, which diverged at about this time (Bininda-Emonds *et al.* 2007, Wible *et al.* 2007).

The best fossil of an early placental mammal is a Chinese find, the 125-million-year-old *Eomaia scansoria*, in which not one bone is missing and even the dense fur has been preserved (Ji *et al.* 2002, illustrated on p. 75). This animal was partly arboreal and, although not directly related to any living lineage, its presence in the Xixian formation strongly supports suggestions that the earliest eutherian mammals were of Asian origin. The outline of its skull and position on the mammalian tree is also shown in our early mammalian tree.

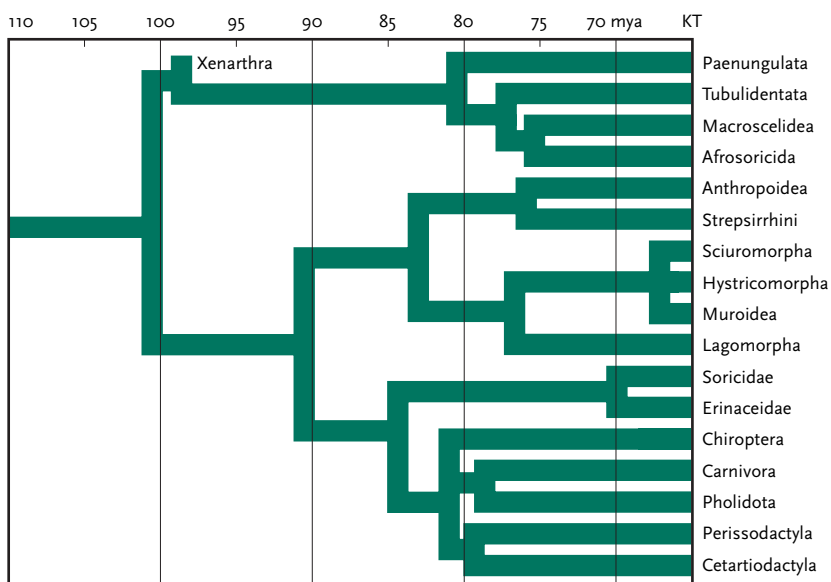
No fossils of anywhere near this age have been found so far in Africa. In Morocco there is a single good Palaeocene site at Ouarzazate (about 60 mya). The evolution of mammals in Africa and the sparse fossil record is discussed in our chapters on African



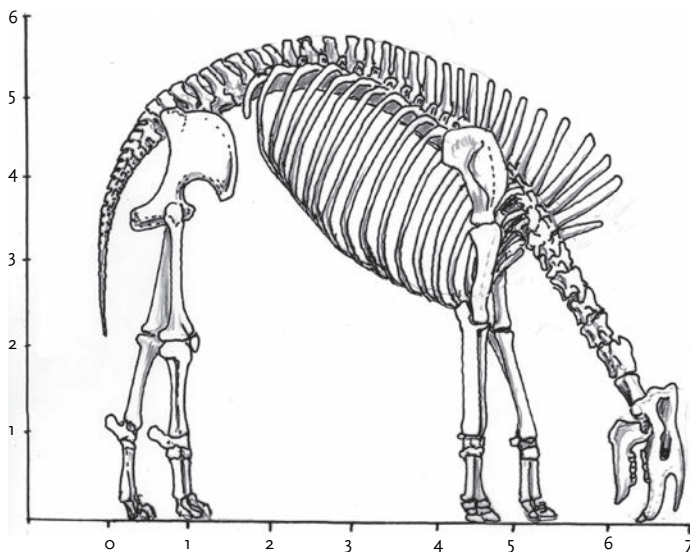
The 'short-fuse model', one of three alternative phylogenetic trees for placental mammals before the KT event (65.5 mya) (after Bininda-Emonds *et al.* 2007). Some dates are modified by O. R. P. Bininda-Emonds (pers. comm. 2009).



The 'explosive' model, one of three alternative versions of mammalian radiation before the KT event (65.5 mya) (after Wible *et al.* 2007).



The 'long-fuse' model, one of three alternative versions of mammalian radiation before the KT event (65.5 mya) (after Meredith *et al.* 2011).



The largest land mammal known: the rhinocerotid *Paraceratherium* (height and length indicated in metres).

geology and on the evolution of African mammals (pp. 27 and 75). However, it must be appreciated that much remains to be discovered about the evolution of mammals, especially the timing and speed of their radiations. Very different concepts have been elaborated, and in keeping with the palaeontologists' geological background, the three principal models for mammalian evolution have acquired rock-breaking names: the Explosive, the Short-fuse and the Long-fuse models!

The Explosive model has become identified with the geological evidence for a late and sudden explosion of mammal types after the K–T asteroid impact of 65.5 mya (best known for being the event in which dinosaurs became extinct) (Alroy 1999, Benton 1999, Foote *et al.* 1999). The post-K–T 'explosive' model is best exemplified by Wible *et al.* (2007). The Short-fuse model depends upon molecular clock interpretations of the primary diversification of placental mammals taking place during the Cretaceous (Kumar & Hedges 1998, Bininda-Emonds *et al.* 2007). The Long-fuse model is an amalgam of the previous two in suggesting that the stem taxa for most of today's orders probably diverged during the Cretaceous but most of the elaborations we see in modern mammals are after the K–T event (Springer *et al.* 2003, Douady & Douzery 2003, Meredith *et al.* 2011).

Inasmuch as we have tried to illustrate the most likely radiation of mammals, we have often referred to Bininda-Emonds *et al.* (2007). Detailed comparisons of the genotypes of all known orders of mammals, as pioneered by Bininda-Emonds and by other molecular biologists, have permitted the erection of entirely new supraordinal taxa: superorders, cohorts and supercohorts. Their adoption has been far from universal and both the new taxonomic names and their existence are contested. However, their identification has been backed up by robust and authoritative arguments accompanied by molecular clocks that vary greatly in their calibration of divergence times. These phylogenetic trees have served to emphasize that the evolutionary branching of mammal orders, families and species has taken place in real time and in real continental or local settings. Many of these assessments will need revision, but we have included three tentative trees (see p. 141) as pioneering efforts to understand the mammalian radiations.

Under this phylogeny, Mammalia breaks down into four supercohorts, namely Afrotheria, Xenarthra, Supraprimates (also known as Euarchontaglires) and Laurasiatheria. These, in turn have been subdivided into cohorts and superorders, descending ultimately to the species, portrait profiles of which are our ultimate product and purpose. In the text that follows each supercohort merits a profile (excepting Xenarthra, which is exclusively American) and our opening texts and volume concern the Afrotheria: the one group that has best claim to be endemic to the African continent.

The primacy of maternal care and prolonged dependency has had particular emphasis in the definition of Mammalia: this emphasis is also evident in much of the behaviour of mammals, especially where it concerns their social lives. Unlike most reptile and bird mothers, a mammalian mother must care for her offspring; that is, after all, why she has a womb and mammae! To ensure that the young (and their lactating mothers) have access to the best resources that are available and at the optimal times of year, there has been selection for a wide range of very different types of social systems. In spaced-out, often residential patterns of land-use, several or single females enter or share the territories of single males. Competition among the latter tends to ensure that the best resources have been won by vigorous territory-holders. Where resources are more dispersed or seasonal, females can enjoy enhanced protection and access to food within groups that have enlarged male hierarchies. Yet another strategy has been either a sustained or a semi-permanent association with a male or males that actually help raise offspring (typically their own only). Long-term pair-bonding has developed in some species (notably wild dogs *Lycaon*, where the sexes are of similar size and appearance).

Male competition can have conspicuous consequences for male external appearances. Weaponry, in the form of horns, tusks or antlers, accompanied by loud calls and/or pungent scents and emphatic displays of patterns or structures have been developed to defend territories or rank. Age-graded gigantism has evolved in the males of hierarchical species, such as gorillas, fur-seals, giraffes and elands.

African mammals have provided much material for evolutionary theory, from Darwin, noting the abundance of spotted and striped felids to invoke just such an evolutionary ancestry to explain patterned lion cubs (Darwin 1859) to Richard Dawkins using gazelles and Cheetahs to illustrate an evolutionary 'arms-race' (Dawkins 1986). Jenny Jarvis has revealed fundamental connections between the ecology and behaviour of blesmols (mole-rats) and the evolution of complex social structures (Jarvis *et al.* 1992, Jarvis 1993). John Crook and Robin Dunbar have explored many socio-biological aspects of evolution from their studies of African primates (Crook & Gartlan 1966, Dunbar 1988) while Dorothy Cheney and Robert Seyfarth have begun to plumb the depths of primate communication with baboons and vervet monkeys (Seyfarth & Cheney 1984, Cheney & Seyfarth 1990, 2007). The list could run on and on.

The diversity of ways in which mammals have evolved ways of living, become social or communicated subtle information with one another are all areas of active ongoing research. We report on this explosion of interest in African mammals and on the multifaceted attempts to understand how the extraordinary variety of mammals has evolved. Here are important strands of thought among the many that are discussed in the volumes that follow.

Jonathan Kingdon

Supercohort AFROTHERIA

Afrotheria Stanhope, Waddell, Madsen, de Jong, Hedges, Cleven, Kao & Springer, 1998. *Proc. Nat. Acad. Sci. (USA)* 95: 9971

Modern placental mammals have not always inhabited Africa, and very recent fossil discoveries have raised, once again, the central question of just where the first placentals arose. At the centre of this controversy is the very new revelation, initially from molecular evidence, of a single and unexpectedly diverse evolutionary radiation of mammals that is so unequivocally African it has been named the Afrotheria ('African mammals'). This radiation includes three orders that have long been recognized as being related and of African origin, namely the elephants (order Proboscidea), manatees and dugongs (order Sirenia) and hyraxes (order Hyracoidea). They have now been joined by four other groups: the Aardvark (order Tubulidentata); sengis or elephant-shrews (order Macroscelidea); golden-moles (family Chrysochloridae) and tenrecs and otter-shrews (family Tenrecidae), now grouped in the new order, Afrosoricida (Stanhope *et al.* 1998). Some authors have argued that this new order should be called Tenrecoidea or Tenrecomorpha, but both of these names present taxonomic difficulties (Bronner & Jenkins 2005).

Are these animals modern derivatives of the very earliest placental mammals or are they later products of the Afro-Arabian landmass's known physical isolation? We know now that Afro-Arabia became separated, sequentially, from Eurasia, Indo-Madagascar and then South America by plate tectonics that opened up the Tethys Sea and proto-Atlantic in the later Mesozoic. Understanding the origins of placentals and of the afrotherian radiation is inseparable from the geological history of continents. That mammals confined to a single continent should radiate into highly diverse forms is entirely consistent with a very lengthy isolation, but was the afrotherian common ancestor native or immigrant? This question can only be answered with absolute certainty by more fossils from appropriate periods, but in the interim the biogeographic significance of both placental and afrotherian origins continues to be a matter of debate.

Some scholars have argued that the presence of two Gondwanan branches (Afrotheria and the endemic South American order Xenarthra) favours a Gondwanan, and possibly even African, origin for placental mammals (Murphy, Eizirik, O'Brien *et al.* 2001). Others cite the presence of much more primitive Late Cretaceous placentals and marsupials in Asia as evidence for a northern origin (Archibald 2003, Robinson & Seiffert 2004, Wible *et al.* 2007). If placental mammals did originate in Asia, as now seems most likely, then basal afrotherians must have dispersed to the Afro-Arabian landmass some time between the predicted origin of placentals (~108 mya) and the putative origin of afrotherians (~80 mya) (Springer *et al.* 2003).

A broad acceptance of Afrotheria has rendered traditional taxonomies obsolete, but it is interesting to retrace some earlier insights and intuitions. The present work is one of the first to attempt to come to grips with some of the implications and introduce readers to the many new questions that these discoveries raise. As for traditional ideas about relationships, they had to be founded on whatever evidence was available at the time, which often did not amount to much. The evidence is still incomplete but the molecular revolution that has unearthed the reality of Afrotheria is but part of a global effort to construct genealogical trees for all biota.

People familiar with wild animals, especially hunters and herders, in Africa and elsewhere, have often recognized that similar species or similar attributes imply ancestry. Thus fishermen, finding ivory tusks in elephant-like Dugong skulls sometimes called them 'elephants of the sea'. Scientific comparisons of the anatomy of elephants and hyraxes with dugongs and manatees, living and fossil, led to the recognition that these superficially very different animals shared a common ancestry (Simpson 1945). This conclusion had been greatly facilitated by the recovery of numerous fossils of these large mammals, primarily from the late Eocene beds of the Fayum Depression in Egypt (Andrews 1906). Following Simpson (1945), this taxonomic clustering is now referred to as the Paenungulata, and has subsequently come to be strongly supported by a vast array of genetic data (Springer *et al.* 1999, Murphy *et al.* 2001a, Amrine-Madsen *et al.* 2003, Murata *et al.* 2003, Nikaido *et al.* 2003, Nishihara *et al.* 2005, Meredith *et al.* 2011).

Determining the affinities of the Aardvark, sengis, otter-shrews and golden-moles has long been much more difficult because their early fossil record is either scarce or non-existent. The Aardvark shares a number of morphological features with similarly myrmecophagous pangolins (order Pholidota) and xenarthrans, and as such was historically aligned with these taxa, although more recently there have been suggestions that it might be more closely related to 'ungulates' – paenungulates, perissodactyls and/or artiodactyls (Novacek 1986, 1992, Shoshani 1986).

While the oldest possible fossil of Macroscelidea is from the early Eocene, about 50 mya (Hartenberger 1986, Tabuce *et al.* 2007) and that of primitive tenrec and/or golden-mole relatives may be Palaeocene or Eocene (Seiffert 2010, Goswami *et al.* 2011), aardvarks do not appear in the fossil record until the early Miocene, about 20–18 mya (MacInnes 1956, Patterson 1975). From the time of their initial discovery, these groups have always puzzled biologists, and have been very unsatisfactorily allocated to various other mammalian higher taxa, never with any confidence. Apart from the rarity of their fossils, a major reason for much of this confusion has been the combination of apparently primitive features and extreme specializations (or 'autapomorphies'), and their resulting transformation into swimming, digging and leaping 'insectivores'.

Insectivora has long served as a taxonomic waste-paper basket into which all small, apparently primitive, invertebrate-eating mammals were thrown. Thus, sengis, golden-moles and tenrecs once joined solenodons, shrews, moles, hedgehogs (and, early in the history of taxonomy, even tree shrews and flying lemurs) in the Insectivora (Wagner 1855). The menotyphlan insectivores (i.e. those with caeca – the flying lemur, tree shrews and sengis) were subsequently elevated to their own orders (Gill 1872, Butler 1956), leaving behind the remaining insectivorans, which were also placed in their own order, Lipotyphla (Butler 1972). However, the lipotyphlan assemblage has long been an unstable one. Following their eviction from the Insectivora, sengis came to be aligned either with the rabbits, hares and pikas (order Lagomorpha) (McKenna 1975, Szalay 1977) or with lagomorphs and rodents together (Glires) (Novacek 1986). Only with the recovery of early fossil macroscelideans

(Hartenberger 1986, Simons *et al.* 1991) was it recognized that their origins might lie with some 'ungulate' group.

Fortunately, technological advances have allowed scientists to rapidly sequence and compare large amounts of DNA, and a much more accurate, objective and less obfuscated analysis of the affinities of all biota has become possible. As noted, these data have confirmed the paenungulate clustering of elephants, hyraxes, and dugongs and manatees, but, much more importantly, have also revealed that paenungulates are the larger representatives of an extremely important and very ancient endemic African radiation that includes many very small mammals as well. A close relationship between aardvarks and paenungulates was first suggested by an analysis of eye lens crystallins (de Jong *et al.* 1981) that would also later provide the first biochemical evidence for the sengis' close relationship with paenungulates (de Jong *et al.* 1993). Analyses of mitochondrial and nuclear gene sequences subsequently expanded this group to include the golden-moles (Lavergne *et al.* 1996, Springer *et al.* 1997) and tenrecs (Stanhope *et al.* 1998). An ancient, single origin for this assemblage is now supported by numerous protein and nucleotide sequences (Amrine-Madsen *et al.* 2003, Meredith *et al.* 2011) as well as rare genomic changes such as protein sequence signatures (Van Dijk *et al.* 2001), unique deletions (Madsen *et al.* 2001, Scally *et al.* 2001), short interspersed nuclear elements or 'jumping genes' (SINEs, Nikaido *et al.* 2003, Nishihara *et al.* 2005) and chromosomal rearrangements (Robinson *et al.* 2004).

Afrotheria has attracted a considerable amount of controversy or scepticism because its members share so little superficial anatomical similarity (Springer *et al.* 2004). Currently, about the only morphological characters uniting Afrotheria involve the reproductive tract, including undescended testicles (the testicond condition) in males (Werdelin & Nilsson 1999) and a four-lobed allantoic sac in females (Mess & Carter 2006), although some homoplasy exists in both traits. Sanchez-Villagra *et al.* (2007) have argued that afrotherians are specialized in having more thoracolumbar vertebrae than other placental mammals. There has also been intense speculation about the sequence and adaptive significance of phylogenetic branching within the supercohort (Seiffert 2002, 2007, Robinson & Seiffert 2004, Asher & Seiffert 2010). This interest stems primarily from the fact that living and extinct macroscelideans share a number of apparently specialized craniodental and postcranial features with paenungulates that are not seen in tenrecs and golden-moles. The position of macroscelideans relative to these taxa depends on whether molecular or anatomical data are considered. Phylogenetic analyses of afrotherians that use morphology suggest that sengis are more closely related to paenungulates than to the other afrotherian insectivores (Seiffert 2003, 2007), and imply that the lipotyphlan features of golden-moles and tenrecs were likely to have been present in the last common afrotherian ancestor. However, recent analyses of various types of genetic data (Amrine-Madsen *et al.* 2003, Waddell & Shelley 2003, Robinson *et al.* 2004, Nishihara *et al.* 2005, Meredith *et al.* 2011) support a fundamentally different arrangement that aligns aardvarks and sengis with golden-moles and tenrecs in an assemblage that has been named 'Afroinsectiphillia' (Waddell *et al.* 2001). If this latter result is correct, then it could be the case that the resemblances between sengis and paenungulates represent primitive features within Afrotheria and that the afrotherian common ancestor would have been more like a small paenungulate than a lipotyphlan.

The above possibility is attractive in that it implies morphological support for Afrotheria, but the ultimate answer is unlikely to be so clear-cut, because at least some of the shared features of paenungulates and sengis are sure to be due to convergent evolution within the ancient afrotherian radiation. The best way to test these competing hypotheses will be to search for Late Cretaceous mammals in Africa from beds that span the time period since the living afrotherians are thought to have first appeared – about 80 mya (Springer *et al.* 2003, Meredith *et al.* 2011).

If Afro-Arabia had been sufficiently isolated from Eurasia throughout the Cretaceous, then the afrotherian common ancestor could have arrived on an African continent that was otherwise devoid of placental mammals and, presumably, of marsupials as well. Unfortunately, at present, we really do not know just how isolated Afro-Arabia was during this time period because very few vertebrate fossils (and no mammals – aside from a single tailbone!; Nessov *et al.* 1998) have been found in Late Cretaceous sediments in Africa. Were the Afro-Arabian continent as decisively isolated as is currently thought, its placental afrotherian colonist must have had some tolerance for exposure at sea. Whether this implies possession of semi-aquatic habits must remain conjecture.

However, the extraordinary morphological variation observable among past and present members of Afrotheria would appear to be consistent with an original, ancestral dispersal into a Late Cretaceous Afro-Arabia that had few, if any, eutherian mammal competitors. Estimates of divergence dates within Afrotheria indicate that the living orders radiated quickly (Springer *et al.* 2003), presumably invading vacant niches that would also come to be occupied by distantly related placental mammals on other continents. Several mammal lineages from outside Africa and members of the Afrotheria share many similar or convergent adaptations. These are listed and discussed further below, but they include myrmecophagy (various ant-eating mammals versus afrotherian Aardvarks), fossoriality (various mole-like animals versus afrotherian golden-moles), the zalambdodont pattern of molar cusps (solenodons versus afrotherian tenrecs and golden-moles), large-scale aquatic habits (whale and hippo-like mammals versus afrotherian sirenians), small-scale semi-aquatic faunivory (several placentals and one marsupial versus afrotherian potamogales), cursoriality (at small body size) (a diversity of mammals versus afrotherian sengis), and spines (true hedgehogs versus afrotherian tenrecid hedgehogs in Madagascar).

Likewise, hyracoids share enough detailed morphological similarities with perissodactyls that a close relationship between the two orders has been championed by morphologists until very recently (Prothero *et al.* 1988, Fischer 1989). Another convergence has only been revealed recently; this shows that the diverse radiation of extinct hyraxes contained cursorial bovid-like forms (Rasmussen & Simons 2000). Early proboscideans such as *Moeritherium* were likely to have had life-styles directly comparable with those of somewhat aquatic tapirs (Kingdon 1979). The most parsimonious explanation for the evolution of detailed morphological convergences is that these adaptations evolved in response to similar selection pressures on disjunct landmasses. Otherwise, direct competition between taxa with such similar evolutionary trajectories would have led to character displacement or early extinction in their evolutionary histories. It is for these and other reasons, we are unconvinced by the recent arguments of Asher *et al.* (2003) and Zack *et al.* (2005) that

posit afrotheria orders originating on northern continents, alongside demonstrably convergent clades.

A major argument against Holarctic origins for Afrotheria is the implication that most afrotherian lineages dispersed to Afro-Arabia independently, via crossings of the Tethys Sea, at times when such dispersals would have been highly unlikely. Although it is clear that primates had arrived in Afro-Arabia by the late Palaeocene, ~56 mya (Sigé *et al.* 1990) and rodents had invaded Africa by the early or middle Eocene, perhaps as early as 50 mya (Vianey-Liaud *et al.* 1994, Marivaux *et al.* in press), these colonizations do not offer compelling evidence for a 'sweepstake' route that could also explain multiple afrotherian arrivals. Primates and rodents are, for whatever reason, remarkably adept at colonizing distant landmasses; for instance, members of both groups managed to subsequently colonize the distant South American landmass from Africa whereas no other mammals have. Primate and rodent groups have also crossed the Mozambique Channel to colonize Madagascar.

In evaluating the hypothesis of extra-African origins for Afrotheria, the likelihood that all the different members of a diverse, closely related group of mammals such as Afrotheria would have coincidentally (and successfully) crossed the Tethys Sea independently, is almost infinitesimal. In spite of morphological resemblances, hypotheses that taxa such as hyopsodontids, phenacodontids and leptictids should be aligned with afrotherians now have to be rejected in spite of the fact that such extinct taxa have left behind no DNA. Affinities suggested on the basis of a few widely distributed morphological features are no different from the taxonomic arrangements that have been erroneously erected over the course of the last two centuries. Had perissodactyls, lagomorphs, pholidotans or solenodontids gone extinct and left no DNA perhaps their few resemblances could have bolstered claims that these taxa too were afrotherians, aligned with hyracoids, sengis, aardvarks and tenrecs, respectively? It may also be the case that previous phylogenetic studies simply did not adequately sample the morphological information that has been provided by the radiation of living and extinct mammals. This possibility would appear to be supported by the recent outgroup- and character-rich analysis of Wible *et al.* (2007), which, unlike the studies of Asher *et al.* (2003) and Zack *et al.* (2005), placed North American taxa such as *Hyopsodus*, *Meniscotherium* and *Phenacodus* far outside of the afrotherian radiation rather than placing them as stem paenungulates.

The oldest, undisputed members of afrotherian orders appear in the Palaeocene of north-west Africa, where the earliest proboscidean *Eritherium* is now known (Gheerbrant 2009). However, Palaeocene African mammals are still scarce, deriving largely from a few micromammal sites in Morocco. These have produced numerous insectivores (Gheerbrant 1992, 1994, 1995, Gheerbrant *et al.* 1998), and a few isolated specimens of creodonts (Gheerbrant 1995, Solé *et al.* 2009) and primates (Sigé *et al.* 1990), as well as some indeterminate fragments of condylarth teeth. It is possible that some of the late Palaeocene insectivores are actually aligned with the tenrecid-chrysochlorid clade (Seiffert 2010, Goswami *et al.* 2011) but it is not yet possible to identify possible late Palaeocene stem members of the Tubulidentata on the basis of isolated teeth, because the only undoubted fossil aardvarks appear in the early Miocene with essentially modern, specialized, enamel-less, peg-like teeth (MacInnes 1956). One possibility is that the order traces back to the peculiar ptolemaïds, which are now known from the late Eocene,

early Oligocene, and early Miocene of Africa (Cote *et al.* 2007, Seiffert 2007).

The remarkable diversity that is now evident among Palaeocene and early Eocene proboscideans (Gheerbrant *et al.* 2002, 2005, Gheerbrant 2009) is consistent with molecular estimates of divergence dates within Paenungulata, which would place proboscidean origins well back into the Palaeocene (Springer *et al.* 2003). For the next 35 million years or so, paenungulates would dominate Africa's large mammal fauna with morphologically diverse hyracoids, proboscideans and the extinct embrithopods occupying a variety of browsing and grazing niches. Afrotherian dominance was first challenged (apparently, not too seriously) by a trans-Tethyan dispersal of the semi-aquatic anthracotheriid artiodactyls, which first appear in Africa as fossils during the earliest part of the late Eocene, about 36 mya. None the less, paenungulates continued to be the dominant large-bodied herbivores in Africa until at least the latest Oligocene, about 25 mya, shortly after which the first major exchange of fauna took place between Africa and Eurasia. There is still no evidence for any other artiodactyls or perissodactyls having dispersed from northern continents before this time (Kappelman *et al.* 2003, Rasmussen & Gutierrez 2009). There is still no evidence for lagomorphs or eulipotyphlans in Africa until the Miocene. No other group of placental mammals is known to have existed in Africa before the Afrotheria. Still important elements of the continent's fauna, they represent a continuous presence for at least 50 million years and perhaps as much as 80 million years.

The molecular and palaeontological data provide a broad view of the phylogenies and biogeographical relationships of the different clades making up the Afrotheria, but these data fail to tell us much about the ecological relationships of current afrotherians. Two features of the extant afrothere fauna are striking. First, compared with other placental radiations, species diversity is low (with the exception of the tenrecs on Madagascar and, to a lesser degree, the golden-moles in southern Africa). Secondly, the extant species are



Comparisons between an Afrothere and an unrelated species with convergent features: Marsupial Banded Ant-eater *Myrmecobius fasciatus* (above) and Giant Sengi *Rhynchocyon* sp. (below).

very highly specialized in terms of their morphology or ecology or both, and this specialization is probably related to low species diversity and to the advantages, for such lineages, of a long head-start in adapting to difficult niches.

Currently, there are about 78 species of extant afrotheres, including three elephants (though there is some controversy regarding current recognition of two African species), four sirenians (dugongs and manatees), five hyraxes, one armadillo, 15 sengis, 30 tenrecs and 21 golden-moles. As was pointed out earlier, many, if not most of these, have ecologically convergent forms on other continents, but some do not and there are generally quite plausible reasons for both the presence and the lack of convergences. For example, the afrotherian golden-moles are remarkably similar to the marsupial moles (genus *Notoryctes*) and various Holarctic talpid moles, adaptive niches in which an early occupation of the continent has to be particularly advantageous, given how much body modification is necessary. The afrotherian armadillo is broadly comparable to the Giant Anteater *Mymecophaga tridactyla* of South America in size and habitat, while afrotherian hyraxes, particularly the higher altitude forms, have many ecological similarities with the pikas (family Ochotonidae) in Eurasia and North America. The three afrotherian species of Potamogalinae are convergent with various aquatic soricid shrews and desmans in the Holarctic region and with the marsupial Duck-billed Platypus *Ornithorhynchus anatinus* – in Australia. Interestingly, the only tenrecs on the African continent are the three highly specialized aquatic potamogales while the 27 others are confined to the island of Madagascar, where they occupy ecological positions similar to a diversity of Australasian marsupials, Caribbean solenodons and a variety of shrews and hedgehogs from other areas and continents. Although the larger sengis (*Rhynchocyon*) superficially resemble bandicoots and the solenodons of Cuba and Espanola, the smaller species (e.g. *Elephantulus*) do not have many resemblances with other small mammals. In addition, sengi life history sets them apart from any other group of mammal, with features that are uniquely African and might best be thought of as a cross between a miniature antelope and small anteater! Despite such specializations, sengis occupy the extremes of terrestrial habitats – from gravel plains of the Namib Desert and boulder fields in north-west Africa to tropical forests of central and eastern Africa.

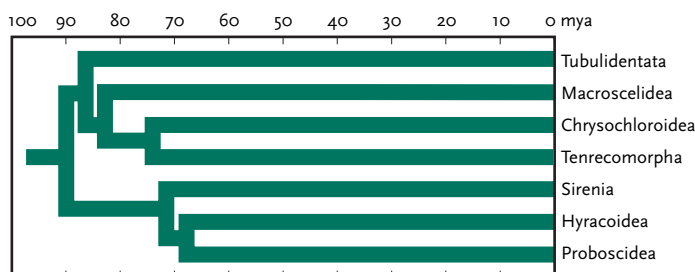
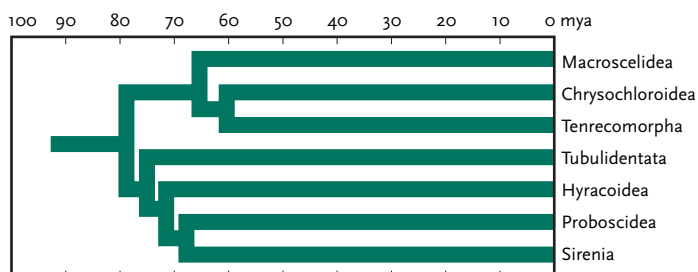
All the smaller afrotheres continue to be restricted to the Afro-Arabian region, plus Madagascar, but the two clades with representatives with the largest body mass dispersed to other continents. The elephants were well represented in North America and Asia and the sirenians radiated into the world's tropical oceans at a very early date, in addition to the North Pacific, and the Amazon

River system. Although elephants and sirenians are wide-ranging, they are both morphological specialists. In addition, sirenians are obligate aquatic herbivores and as such have no ecological equivalents outside the afrotherian radiation.

The palaeontological record suggests that the highly specialized nature of extant afrotheres may not have been so marked in the past. For example, the diversity of sengis in the Miocene included six subfamilies, which included several herbivores, based on the morphology of their dentition. Only two subfamilies are extant, and all taxa in these two subfamilies have retained somewhat hypsodont dentition as well as a caecum, which strongly implies herbivorous ancestors. The herbivorous macroscelideans became extinct in the Mio-Pliocene; perhaps they could not effectively compete with newly arriving rodents, hares and ungulates coming in from the north. The extant sengis seem to have escaped competition with these invaders by secondarily becoming invertebrate specialists, especially anteaters, where a head-start in adapting to ant chemistry must be an advantage. Likewise, the palaeontological history of hyraxes suggests that only those species that were rupicolous or arboreal were able to escape competitive extinction with hares, rodents and ungulates.

A similar argument does not explain the high species diversity, in the very recent past, of elephants and dugongs and manatees compared with their current sorry status, and most available evidence suggests that prehistoric humans might have played a decisive role in some of their extinctions. The diversity of tenrecs on Madagascar apparently suffered less from the impact of incoming rodents, undoubtedly because there was no competition for food between the herbivorous rodents and insectivorous tenrecs. Golden-moles similarly escaped competition from other insectivores by being fossorial. It thus appears that an important factor in the relatively small number of extant afrotheres is their ecological specialization, which allowed them to avoid extinction in the face of invading faunas from outside Africa. Although this specialization has served the extant afrotheres well in the past, their low species diversity, often accompanied by highly restricted distributions and ecological specialization, makes many forms especially vulnerable to another wave of extinctions – at the hands of humans. This is especially the case with the potamogales, several golden-moles and the forest-dwelling sengis. These taxa all occupy highly restricted habitats that are being increasingly degraded by human activities. Because of the low species diversity of the extant afrotheres, extirpations will have an especially severe impact on an already depauperate group.

Jonathan Kingdon, Erik R. Seiffert, Blair Hedges & Galen Rathbun



Tentative phylogenetic relationships of afrotherian mammals (left) based on a combined analysis of DNA from living species and morphology of living and extinct species (after Seiffert 2007), and (right) based on analysis of genomic data alone (after Meredith *et al.* 2011).

Cohort PAENUNGULATA

Cohort Paenungulata Simpson 1945. Bulletin of the American Museum of Natural History 85: 131.

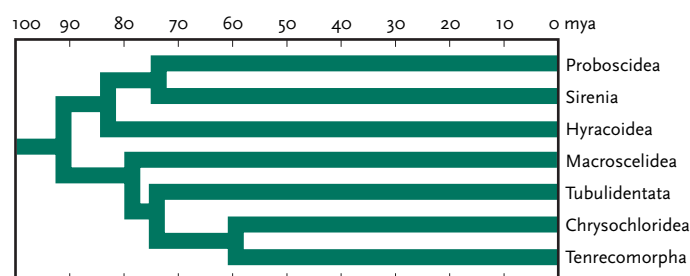
A close relationship between hyraxes, manatees and dugongs, elephants and the extinct Palaeogene order Embrithopoda was first explicitly recognized by Gregory (1910), thanks in large part to fossil discoveries made in the late nineteenth and early twentieth centuries in the Fayum Depression of northern Egypt (Andrews 1906). Simpson eventually coined the name Paenungulata for this clade, but also included a variety of other extinct taxa whose affinities are now believed to lie elsewhere. The taxon Paenungulata has since been used by different authors to include very different assemblages of living and extinct placentals (Lucas 1993), but is now generally recognized as the afrotherian radiation that produced the orders Hyracoidea, Sirenia, Proboscidea, and the extinct Embrithopoda and Desmostylia (e.g. Gheerbrant *et al.* 2005a). In the past, many morphologists aligned paenungulates with perissodactyls in a clade called Altungulata or Pantomesaxonia, and some authorities have even favoured a closer relationship of hyracoids to perissodactyls than to tethytherian paenungulates (sirenians and proboscideans), but molecular data have now firmly established that the derived morphological features that perissodactyls share with paenungulates are evolutionary convergences (Springer *et al.* 2004).

The tiny Palaeocene proboscidean *Eritherium*, from Morocco, is the oldest undoubted paenungulate (Gheerbrant 2009). More derived proboscideans (*Daouitherium* and *Phosphatherium*) and the oldest known hyracoid (*Seggeurius*) have been found in earliest Eocene sediments of the same basin (Ouled Abdoun) (Gheerbrant *et al.* 2003, Gheerbrant *et al.* 2005b). By the earliest Eocene, hyracoids are morphologically distinct and there is already considerable morphological diversity within Proboscidea, suggesting that the evolutionary histories of both clades will eventually be traced much farther back into the early Palaeocene. As yet basal sirenians are missing from the early African record, and the oldest forms are from

the early middle Eocene of Jamaica (Savage *et al.* 1994). However, by that time, sirenians already exhibit clear morphological adaptations for an aquatic existence.

With the recognition of Afrotheria, a number of the morphological features that have been proposed as evidence for paenungulate monophyly now must be re-evaluated. For instance, one of the key features that was thought to align paenungulates to the exclusion of other 'ungulates' is a serial arrangement of the carpal and tarsal bones (i.e. no contact between the astragalus and the cuboid in the foot, and no contact between the lunar and unciform in the wrist) (Rasmussen *et al.* 1990). However, there is also no astragalar–cuboid contact in most other afrotherians (aardvarks, tenrecs, golden-moles), and there is no lunar–unciform contact in tenrecs, golden-moles and primitive sengis or elephant-shrews. As such, the serial carpus and tarsus could either be primitive within Placentalia or could represent afrotherian synapomorphies, but these characters can no longer be confidently interpreted as paenungulate synapomorphies. Other features, such as testicondy, a zonary placenta, the cup-like astragalar cotylar fossa (which articulates with an enlarged medial malleolus of the tibia), enlargement of the central upper incisors and caudal extension of the jugal to the glenoid fossa, are also seen in various other non-paenungulate afrotherians, suggesting a more ancient origin for these characters. Placement of the orbit over the premolars, which is seen in living and extinct tethytherians and extant procaviid hyracoids, is absent in primitive fossil hyracoids and so likely evolved convergently within Paenungulata.

Paenungulates can be distinguished from other afrotherians by a number of derived dental features and muscular arrangements (Shoshani 1993), in addition to postcranial characters such as loss of the clavicle and metacromion, an increase in the number of rib-bearing thoracic vertebrae, loss of the humeral entepicondylar foramen (though present, perhaps secondarily, in the early proboscidean *Numidotherium*), and, possibly, wide and flaring iliac alae. Amastoidy remains as a probable cranial synapomorphy of Paenungulata, while other possible synapomorphies include loss of lacrimal–palatine contact, presence of an alisphenoid canal, presence of a piriform fenestra rostral to the petrosal, a weakly excavated subarcuate fossa and a vertical to anterior orientation of the mandibular ascending ramus. However, these, and many other, candidate cranial synapomorphies of Paenungulata must be tested with fossil evidence from early stem and crown paenungulates.



Alternative tree of phylogenetic relationships of afrotherian mammals based on a combined analysis of DNA from living species and morphology of living and extinct species, showing recovery of Tethytheria within Paenungulata (after Asher *et al.* 2003).

Erik R. Seiffert

Order HYRACOIDEA – Hyraxes

Hyracoidea Huxley, 1869. An Introduction to the Classification of Animals. Churchill, London. viii + 147 pp.

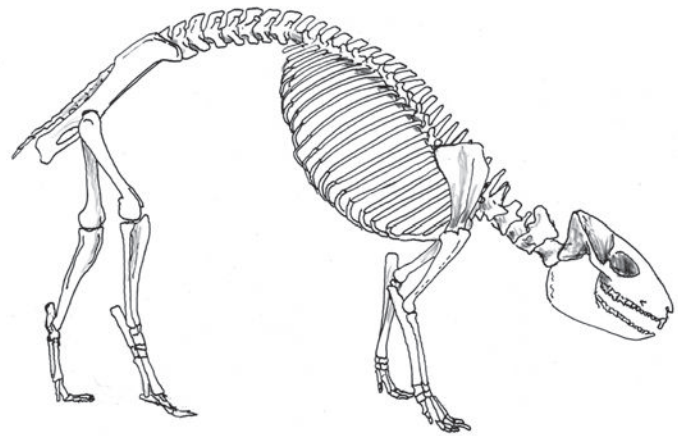
Procaviidae (3 genera, 5 species)	Hyraxes	p. 150
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Myology of *Dendrohyrax dorsalis*.

The order Hyracoidea includes five families: the wholly extinct families Geniohyidae, Saghatheriidae, Pliohyracidae and Titanohyracidae (Pickford 2004), and the family Procaviidae, which contains both living and extinct genera (Hahn 1934, Meyer 1978, Jones 1984, Carroll 1988). The extant taxa include three genera: *Dendrohyrax* (three species), *Heterohyrax* (one species) and *Procavia* (one species), although the number of species in each genus is a matter of contention (Bothma 1971, Schlitter 1993, Shoshani 2005).

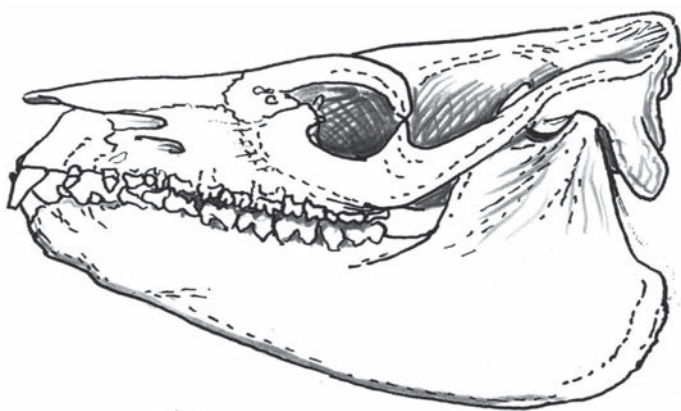
Hyraxes are small mammals (1.8–5.5 kg), the size of a guinea-pig, but without a visible external tail. The ears are small and rounded. Colour varies from light grey to dark brown. In the centre of the back there is a dorsal spot, with long (probably scent-dispersing) hairs that are of different colour than the rest of the body (white, cream, pale orange, russet-brown, or black), and that surround a glandular structure. The degree of piloerection of the dorsal hairs functions as a signal of alarm and threat while the dorsal gland secretions have general social, and possible sexual, functions (Sale 1970a). Length of the naked dorsal gland has been used as a diagnostic, albeit not always consistent, feature for distinguishing species (Bothma 1971). Tactile hairs or vibrissae up to 80 mm long are widely distributed over the body (Sale 1970a). The limbs are plantigrade; the forefoot has four digits and the hindfoot three. All the digits end in broad, flat hoof-like nails. The inner toe of the hindfoot has a long curved claw-like nail utilized for grooming. The soles are naked and covered by thick epithelium kept moist by glands (Dobson 1876, Sokolov & Sale 1981). Special arrangements of muscles enable shaping of the soles into air-tight cups for improved gripping. There are numerous thoracic and lumbar vertebrae (27–30) and 20–21 bear ribs. There are no clavicles (Sclater 1900). Nipples usually include one pectoral pair and two inguinal pairs, but variations are known (see profile Procaviidae).



Oligocene hyracoid, *Saghatherium*.

In profile, the procaviid skull is relatively high, with the mandible contributing more height than the cranium; there is no prominent sagittal crest, and the rostrum is blunt. Crania of adults measure 65–118 mm long, 30–35 mm tall and 50–63 mm wide. Unique to Hyracoidea, the parietal contributes to the dorsal postorbital process (Meyer 1978); the lingual process of the hyoid apparatus is derived from the basihyoid (Flower & Lydekker 1891, Gasc 1967). The cranium has the postorbital bar complete (*Dendrohyrax*) or incomplete (*Heterohyrax* and *Procavia*), and temporal ridges that converge or form a sagittal crest (*Procavia* and *Heterohyrax*), or are far apart (*Dendrohyrax*). The dental formula is $I^{1/2}, C^{0/0}, P^{4/4}, M^{3/3} = 34$, although *Procavia* often has the lower first premolar absent. The upper incisors are long, growing from persistent pulps, and are uniquely triangular in cross-section; the lower incisors are chisel-shaped. The cheekteeth are lophodont and separated from the incisors by a large diastema (Thomas 1892). Molars show some general similarities with perissodactyls (Osborn 1907, McKenna 1975, Fischer 1989). Fossil forms retained primitive double-rooted canines and have dental formulae similar to primitive eutherian mammals, $I^{3/3}, C^{1/1}, P^{4/4}, M^{3/3} = 44$ (Osborn 1907).

Members of the order are characterized by several unusual features, including: a stomach divided into two chambers (a cardiac, non-glandular section and a pyloric, glandular section); two large conical supplementary caeca (a structure encountered frequently in birds); a highly subdivided liver; absence of a gall bladder; duplex uterus; and abdominal testes (Flower & Lydekker 1891, Sclater 1900, Glover & Sale 1968, Rahm & Frewein 1980). The unbranched caecum acts as a fermentation chamber that produces large amounts of volatile fatty acids that serve as an energy source, and about which there has been much discussion in the literature (Clemens 1977, Clemens & Maloiy 1978, Engelhardt *et al.* 1978, Leon 1980, Eloff & VanHoven 1985). Hyraxes have very efficient renal function, and have a high capacity for concentrating urea and electrolytes and excreting large amounts of undissolved calcium carbonate (Meltzer 1973, Rübsamen *et al.* 1982). All species defaecate in specific spots

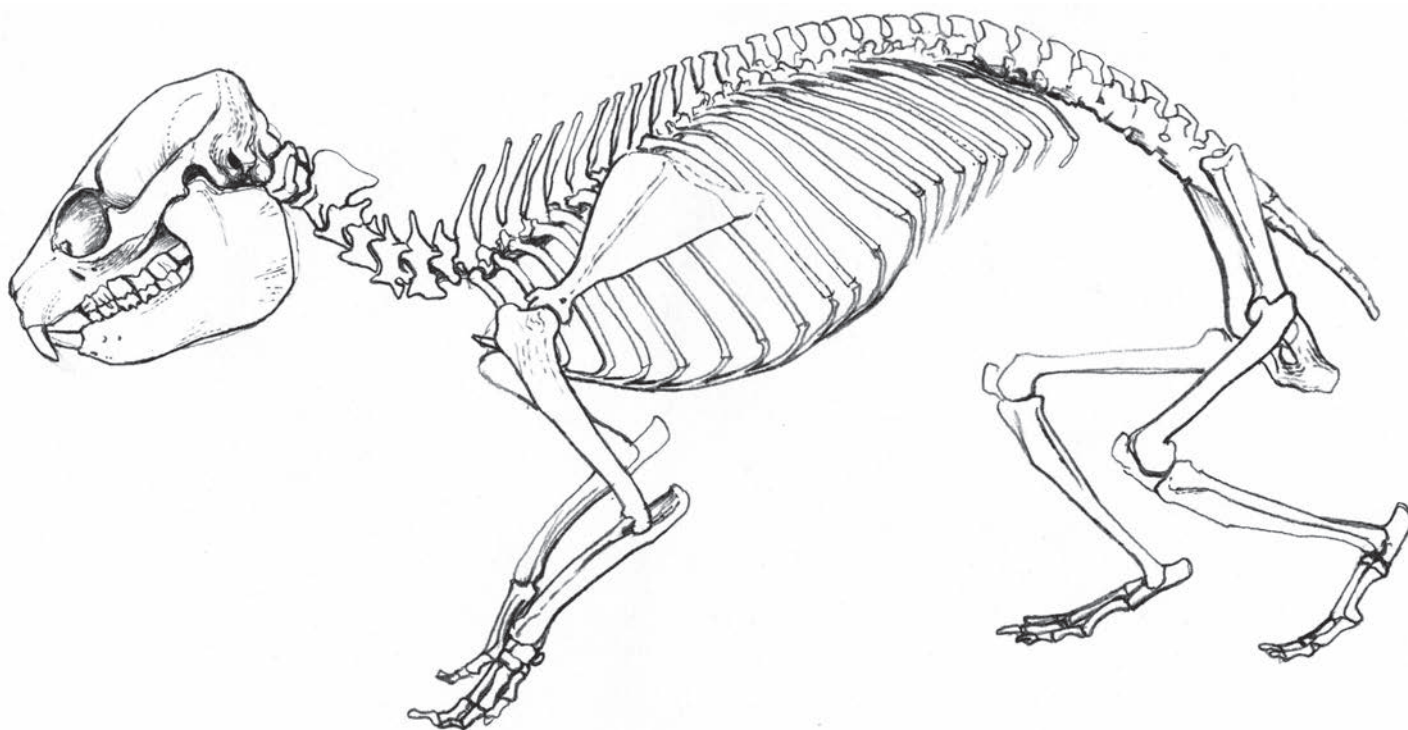
Skull of *Megalohyrax*.

and many species use latrines (Kingdon 1997). The accumulated deposits of crystallized calcium carbonate whiten the cliff faces below latrines; these crystals were used as medicine (hyraceum) by several South African tribes and by Europeans (Hahn 1934). Hyraxes have a poor ability to regulate their body temperature and a low metabolic rate for their body size. Body temperature is maintained mainly by behavioural thermoregulation, including gregarious huddling, long periods of inactivity and basking (Taylor & Sale 1969, Sale 1970b, Bartholomew & Rainy 1971). The pupil of the eye in several species (*Procavia*, *Heterohyrax*) has an umbraculum, a shield that allows a basking individual to stare into the sun (Millar 1973) and thereby detect aerial predators. All three genera are highly vocal (Fourie 1977, Hoeck 1978a). A long gestation period (6–8 months) is another peculiar characteristic (Sale 1965a).

The early fossil record of Hyracoidea is restricted to Afro-Arabia and begins in the earliest Eocene (~55 mya) of Morocco, where a single lower molar of the genus *Seggeurius* has been found

(Gheerbrant *et al.* 2003). Fragmentary jaws and a few upper teeth of *Seggeurius* and *Microhyrax* are known from younger (~50 million-year-old) sites in Algeria (Court & Mahboubi 1993, Tabuce *et al.* 2001). *Seggeurius* and *Microhyrax* were small species and had very simple, unmolarized premolars; they lack the coronoid canal found in later hyracoids. Much larger contemporaries of these early forms are only known from a few upper molars (Sudre 1979), and suggest considerable early diversity. The latest Eocene was witness to the acme of the hyracoid radiation; a single locality of this age in Egypt has revealed remains of eight hyracoid species ranging in size from small procaviids to small horses. This ~34 million-year-old community shows great morphological disparity, and included cursorial bovid-like forms, tapir-like species and a few taxa with greatly inflated, hollowed out mandibles (Meyer 1978, DeBlieux *et al.* 2006). One of the latter genera, *Thyrohyrax*, was otherwise very similar to later fossil procaviids in its craniodental and postcranial morphology and might have been broadly ancestral to that group. Hyracoids remained the dominant small- to medium-sized mammalian herbivores in Afro-Arabia until the early Miocene, when many species were replaced by immigrant artiodactyls and perissodactyls (Kappelman *et al.* 2003). Early and middle Miocene species included archaic large genera such as *Afrohyrax* and *Brachyhyrax* (Pickford 2004), and more specialized genera such as *Paraplioxyrax* (Pickford 1996, 2003), and the smaller, more procaviid-like *Prohyrax*. Some hyracoid lineages migrated out of Africa in the later Neogene (e.g. Chen 2003), but ultimately went extinct. Several specimens of *Heterohyrax* have been described from the late Miocene in Namibia, including *Heterohyrax auricampensis*, which has an estimated age of 10–9 mya, and whose molar teeth can barely be distinguished from living *Heterohyrax* species (Rasmussen *et al.* 1996).

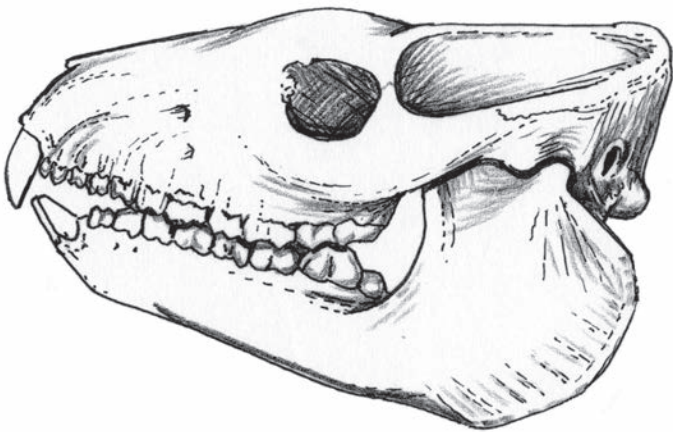
Jeheskel Shoshani, Paulette Bloomer & Erik R. Seiffert

Skeleton of *Procavia capensis*.

Family PROCAVIIDAE
HYRAXES

Procaviidae Thomas, 1892. Proc. Zool. Soc. Lond. 1892: 51.

<i>Dendrohyrax</i> (3 species)	Tree Hyraxes	p. 152
<i>Heterohyrax</i> (1 species)	Bush Hyrax	p. 161
<i>Procavia</i> (1 species)	Rock Hyrax	p.165



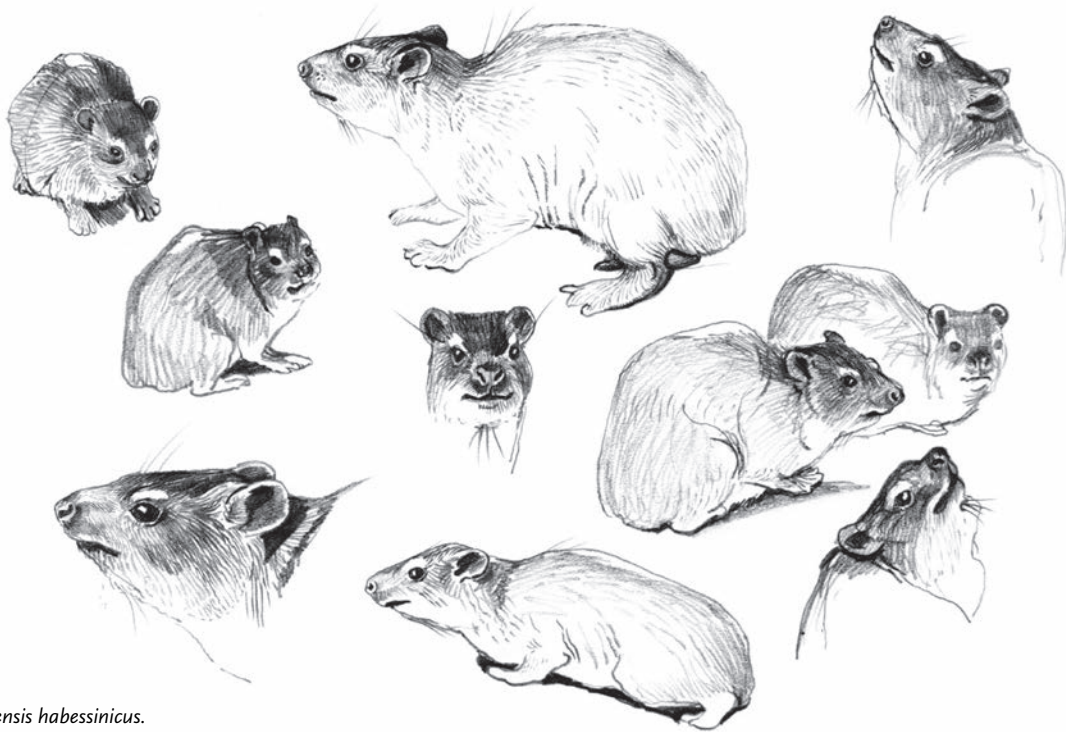
Skull of *Myohyrax hendeyi*.

The odd appearance of the hyrax has caused considerable taxonomic confusion. The superficial similarity of hyraxes to rodents led Storr (1780) mistakenly to link them with guinea pigs of the genus *Cavia*, and he thus placed Rock Hyraxes in the genus *Procavia* (meaning ‘before the guinea pigs’) and in the family Procaviidae. Later, the mistake was discovered and the group was given the equally misleading name of hyrax, which means ‘shrew mouse’. The name

‘dassie’, colloquially used in English in parts of southern Africa, is Afrikaans and is derived from the Dutch *das* or badger, the name applied by the Dutch settlers in the Cape to this species.

In Phoenician and Hebrew, hyraxes were/are known as *shaphan*, meaning ‘the hidden one’. Some 3000 years ago, Phoenician seamen explored the Mediterranean, sailing westward from their homeland on the coast of Syria. They found land where they saw small mammals, which they thought were hyraxes, and so they called the place ‘I-shaphan-im’ – Island of the Hyrax. The Romans later modified the name to Hispania. But the animals were really rabbits, not hyraxes, and so the name ‘Spain’ derives from faulty observation (Hahn 1934)!

Most authors recognize three distinct extant genera: *Procavia*, *Heterohyrax* and *Dendrohyrax* (Allen 1939, Swynnerton & Hayman 1950, Roberts 1951, Bothma 1971, Hoeck 1978a, Meester *et al.* 1986, Schlitter 1993, Shoshani 2005), although *Heterohyrax* has sometimes been treated as a subgenus of *Dendrohyrax* (Ellerman *et al.* 1953, Roche 1972, Ansell 1978, Corbet 1978). Generic delineation has traditionally been based on differences in dentition and skull characteristics, although colouration, mammary formulae, penis structure, behaviour and ecological differences also distinguish the three genera (see Table 6, p. 151). Numerous species and subspecies of hyrax have been described, and there remains little consensus regarding the number of species in each genus (Bothma 1971, Schlitter 1993, Shoshani 2005). Preliminary molecular phylogenetic data indicate high levels of intraspecific variation within *Procavia* and *Heterohyrax*. The three genera are genetically distinct and *Dendrohyrax* appears to be basal (Prinsloo & Robinson 1992, Prinsloo 1993).



Sketches of *Procavia capensis habessinicus*.

Table 6. Major differences among the three genera of hyrax (modified after Shoshani 1992, based on sources given below).

	<i>Procavia</i> Rock hyrax	<i>Heterohyrax</i> Bush hyrax	<i>Dendrohyrax</i> Tree hyrax
Distribution	Africa and the Middle East	Africa only	Africa only
Habitat	Rocky outcrops	Rocky outcrops and trees	Trees
Food	More grazer than browser	More browser than grazer	Mostly browser
Activity period	Diurnal	Diurnal	Nocturnal
Sociality	Gregarious, associates with <i>Heterohyrax</i>	Gregarious, associates with <i>Procavia</i>	Less gregarious, little association with other genera
Head + body length (cm)	39–58	32–56	40–55
Body weight (kg)	1.8–5.5	1.3–3.6	1.6–4.0
Body colour	Yellowish to greyish, brown and dark; buff underparts	Brown mixed with white and black; whitish underparts	Dark brown to blackish; greyish underparts
Facial marks	Dark patch around eye	White patch above eye	No marks around eye
Cranium, post-orbital bar	Not complete	Not complete	Complete
Cranium, profile on top	Flat	Flat	Depression above orbit
Cranium, temporal lines	Converge	Do not converge, with narrow gap between them	Do not converge, with wide gap between them
Cheekteeth	Hypsodont (high crown)	Brachyodont (low crown, intermediate)	Brachyodont (lower crown than <i>Heterohyrax</i>)
Cheekteeth	Length of upper molar tooththrow (M^{1-3}) greater than length of premolar tooththrow P^{1-4}	Length of upper molar tooththrow (M^{1-3}) about equal to length of premolar tooththrow P^{1-4}	Length of upper molar tooththrow (M^{1-3}) shorter than or about equal to length of premolar tooththrow P^{1-4}
Lower first premolar	Sometimes absent	Present	Present
Mandible, ascending ramus	Broad	Narrow	Narrow
Mandible, coronoid process	Same level as condyle or slightly above it	Higher than in <i>Procavia</i>	Higher than in <i>Procavia</i>
Uterus type	Duplex (similar to that found in rodents, lagomorphs and Aardvark)	Bicornuate (similar to that found in ungulates)	Bicornuate (similar to that found in ungulates)
Penis: distance from anus	34–36 mm	65–82 mm	17–25 mm
Penis: form	Simple, widens towards tip, flattened in cross-section	Complex, with an appendage at its tip, round in cross-section	Simple, curved, narrow towards tip, flattened in cross-section
No. of nipple pairs	1 pectoral, 2 inguinal	1 pectoral, 2 inguinal (or 2 inguinal pairs only)	1 inguinal (but sometimes 1 pectoral only, or 1 inguinal and 1 pectoral, or 2 inguinal)
Litter size	2–4	2–4	1–2

Sources: Hahn 1934, Mendelssohn 1965, Coetzee 1966, Glover & Sale 1968, Dorst & Dandelot 1970, Bothma 1971, Roche 1972, Meltzer 1973, Hoeck 1978a, 1982a, 1989, Jones 1978, Corbet 1979, Smithers & Wilson 1979, Hoeck *et al.* 1982, Olds & Shoshani 1982, Meester *et al.* 1986, Dor 1987, Yom-Tov & Tchernov 1988, Kingdon 1997, Barry & Shoshani 2000, and unpublished observations of J. Shoshani and J. M. Milner

Procavia is the most widely distributed of the genera and the only representative outside the African continent, being present in parts of the Arabian Peninsula and the Middle East. *Procavia* and *Heterohyrax* are rock dwelling, gregarious and diurnal, while *Dendrohyrax* is arboreal, less gregarious and nocturnal (Bothma 1964, 1971, Hoeck 1978a). *Procavia* is predominantly a grazer whereas *Heterohyrax* and *Dendrohyrax* mostly browse (Turner & Watson 1965, Hoeck 1975, Lensing 1983, Kingdon 1971, 1997). These dietary preferences are reflected in the dentition, with *Procavia* having hypsodont molars, and *Heterohyrax* and *Dendrohyrax* having brachyodont molars. *Procavia* also has an upper molar tooththrow (M^{1-3}) that is longer than that of the premolar tooththrow (P^{1-4} , with P^1 sometimes absent), whereas in the other genera the length of P^{1-4} is just less than or equal to length of M^{1-3} (*Heterohyrax*) or exceeds the length of M^{1-3} (*Dendrohyrax*) (Bothma 1971, Meester *et al.* 1986). The penis of *Heterohyrax* is more complex than those of *Procavia* and *Dendrohyrax*, and the distance between the anus and the preputial opening in an adult ♂ is 65–82 mm, which is two to three times longer than in the other

genera (Coetzee 1966, Hoeck 1978a); mean distance between anus and preputial opening is 35 mm in *Procavia* and 20 mm in *Dendrohyrax* (Coetzee 1966, Hoeck 1978a).

The origin of Procaviidae remains something of a mystery. Eocene–Oligocene *Thyrohyrax* is probably more closely related to procaviids than to other Palaeogene genera (Rasmussen & Simons 1988, Seiffert 2003), but this genus also exhibits some bizarre specializations, such as an internal mandibular chamber, that appear to exclude it from procaviid ancestry. In some ways Miocene *Prohyrax* helps to bridge the morphological gap between *Thyrohyrax* and extant procaviids, but it too appears to be only a distant relative of the procaviids. Various extinct members of the procaviid crown group have been identified, including species of *Heterohyrax* (Rasmussen *et al.* 1996), *Procavia* (Churcher 1956) and the extinct genus *Gigantohyrax* (Kitching 1965), which was about three times larger than the extant procaviids.

Jeheskel Shoshani, Paulette Bloomer & Erik R. Seiffert

GENUS *Dendrohyrax*

Tree Hyraxes

Dendrohyrax Gray, 1868. Ann. Mag. Nat. Hist., ser. 4: 1–48.

This genus includes three species of hyraxes: the Eastern Tree Hyrax *D. validus*, from montane parts of East Africa; the Western Tree Hyrax *D. dorsalis*, from West Africa and central Africa; and the Southern Tree Hyrax *D. arboreus*, ranging from C Kenya to the Eastern Cape Province in South Africa. The validity of *D. validus* as a distinct species from *D. arboreus* has been questioned by some authors (e.g. Bothma 1971), and Shoshani (2005) considered the latter species to include *D. validus*.

Compared with other hyraxes, all members of the genus are arboreal, less gregarious and nocturnal (Bothma 1964, 1971, Hoeck 1978a). Calls of all three species show a degree of geographical variation (Roberts 1999). Length of upper molar tooththrow (M^{1-3}) is approximately the same length as that of upper premolar tooththrow (P^{1-4}).

Paulette Bloomer

Dendrohyrax arboreus SOUTHERN TREE HYRAX (SOUTHERN TREE DASSIE)

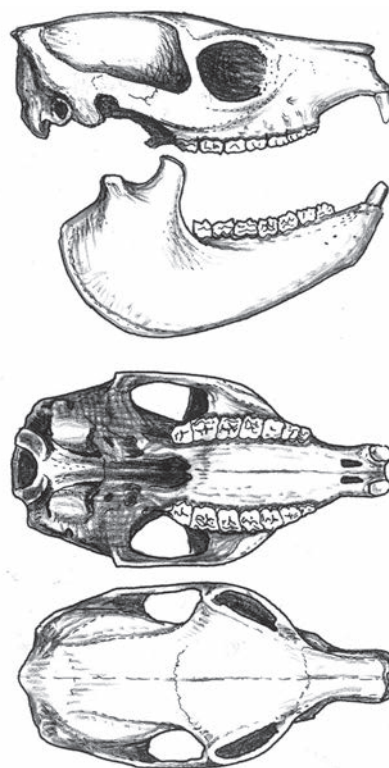
Fr. Daman d'arbre; Ger. Baumschliefer

Dendrohyrax arboreus (A. Smith, 1827). Trans. Linn. Soc. Lond. 15: 468. Forests of Cape of Good Hope, Western Cape Province, South Africa.Southern Tree Hyrax *Dendrohyrax arboreus ruwenzorii*.

Taxonomy Eight subspecies were recognized by Bothma (1971). All appear similar, but are distinguished by altitudinal range, habitat or geographic area, and possibly by vocalizations. Montane populations tend to be more distinctive in pelage characteristics. Taxonomic confusion has led to several subspecies having synonyms within the genera *Procavia* and *Heterohyrax*. Recognition of subspecies here is provisional, following Bothma (1971), pending a more detailed investigation employing vocalizations and molecular data. Shoshani (2005), who did not recognize subspecies, included Eastern Tree Hyrax *D. validus* as a synonym of this species. Synonyms: *adolfo-friederici*, *bettoni*, *braueri*, *crawshayi*, *helgei*, *mimus*, *ruwenzorii*, *scheelei*, *scheffleri*, *schubotzi*, *stuhlmanni*, *vilhelmi*. Chromosome number: $2n = 54$ (Prinsloo & Robinson 1991).

Description Superficially guinea-pig-sized and shaped, with short, sturdy legs, no external tail, and soft, dense pelage. General colouration grey or brown, but quite variable, and may appear grizzled due to buff band below black tips of guard hairs. Individuals from high rainfall areas have darker pelage (Bothma 1967). Head often darker than rest of the body and ventral pelage very pale, creamy or white. Short white hairs fringe the ears. Black whiskers up to 80 mm in length, and a patch of long hairs on the eyebrows. Distinct creamy white dorsal patch of longer erectile hairs (45–50 mm) in the middle of the back marks the large bare dorsal apocrine gland. The length of the bare dorsal gland has been suggested as a diagnostic feature

for this species (e.g. Bothma 1971, Jones 1978, both of whom cite a length of 23–30 mm). However, animals from Rwanda have a dorsal spot ranging in length from 17 to 48 mm ($n = 19$) (J. M. Milner pers. obs.), suggesting large overlap in length between Southern Tree Hyrax and Eastern Tree Hyrax and some overlap between large Southern Tree Hyrax individuals and Western Tree Hyrax *D. dorsalis*. Soles of feet are padded, generally with black skin although pink feet have been reported from Ngorongoro (H. N. Hoeck pers. comm.). Females have varying number of nipples: usually there is one inguinal pair, but sometimes there is only one pectoral pair, or one inguinal pair with the addition of one pectoral pair, or otherwise two pairs inguinal (Rudnai 1984a).

Lateral, palatal and dorsal views of skull *Dendrohyrax arboreus*.

Upper incisors are widely separated, long, curved and triangular in section. Outer pair of lower incisors retains tricuspid condition in adults. Upper diastema 15–17 mm, much wider than in *Procavia* but similar to *Heterohyrax*.

Geographic Variation

- D. a. adolfi-friederici* (including *schubotzi* and *helgei*): montane E DR Congo, Rwanda, Burundi, SW Uganda.
D. a. arboreus: Eastern Cape Province and KwaZulu–Natal (South Africa), C Mozambique.
D. a. bettoni (including *scheffleri* and *vilhelmi*): S Kenya.
D. a. braueri: NW Zambia and S DR Congo; also presumably the form in NE Angola.
D. a. crawshayi: C Kenya.
D. a. mimus: NE Zambia, W Malawi, WC Tanzania.
D. a. ruwenzorii: Rwenzori Mts. In open rocky habitat; one pair inguinal and one pair pectoral nipples.
D. a. stuhlmanni (including *scheelei*): SE DR Congo, Kenya, Tanzania. One pair inguinal and one pair pectoral nipples.

Kingdon (1971) drew attention to a possible hybridization zone between Southern Tree Hyrax and Western Tree Hyrax in S Uganda. He interpreted this in terms of a recent expansion of range, by the Western Tree Hyrax, eastwards as far as the Victoria Nile. Both species, as well as apparent hybrids, are known from this area.

Similar Species

- D. dorsalis*. Generally has shorter, coarser pelage; yellowish-white dorsal spot; longer dorsal patch (42–72 mm); rostrum naked; conspicuous white spot beneath chin; one pair inguinal mammae. Sympatric or parapatric in S Uganda and along the western border of DR Congo, where hybridization may occur.
D. validus. Yellow or russet-brown dorsal spot; naked rump patch 20–40 mm (though see notes above); one pair inguinal nipples. Isolated montane and coastal forests of Tanzania/Kenya, as well as Pemba and Zanzibar Is.
Heterohyrax brucei. Sympatric in NE DR Congo and NW Uganda. For further distinguishing characteristics see Table 6, p. 151.
Procavia capensis. Distributed widely in sub-Saharan Africa, with isolated population in North Africa, in a wide range of habitats. For further distinguishing characteristics see Table 6, p. 151.

Distribution Endemic to Africa. Patchily distributed in forested areas of central and eastern mainland Africa, from C Kenya as far south as Eastern Cape and KwaZulu–Natal provinces of South Africa. Occurs relatively widely in Uganda, C and SW Kenya, Tanzania, E and SE DR Congo, Rwanda and throughout Zambia (excluding the areas west of the Zambezi R.) (Kingdon 1971, Ansell 1978). Although occurs widely in Malawi (Ansell & Dowsett 1988), distribution east of L. Malawi is uncertain. Several authors (e.g. Skinner & Chimimba 2005) comment on the lack of records from Angola, but the species certainly does occur, having been noted earlier by Hayman (1963) and De Barros Machado (1969); distribution in the north-east of this country is mapped by Crawford-Cabral & Veríssimo (2005). Shortridge (1934) makes reference to this species from the Caprivi, but this appears unsubstantiated, and Smithers (1971) did not record this species from Botswana. May occur in NW Mozambique, otherwise confined to the central area south of the Zambezi R. (Smithers &



Lobão Tello 1976). In South Africa, recorded from the southern and southern-central forests of KwaZulu–Natal and along the coast of the Eastern Cape, as far west as the Sundays R. (about 27° E). Also never recorded in Zimbabwe, although they almost certainly do occur (Smithers & Wilson 1979), or the Limpopo Province of South Africa.

Habitat Associated with well-developed woodland or forest. In South Africa occurs in Afromontane forests and better-developed forests and thickets of the Eastern Cape and KwaZulu–Natal provinces (Lawes *et al.* 2000). At the western coastal limit, occurs in milkwood-dominated coastal forests (Gaylard 1994), while further north in C Mozambique occurs in lowland evergreen forests as well as in the evergreen riverine forests of the Save R. (Smithers & Lobão Tello 1976, Skinner & Chimimba 2005). In East Africa also occurs in drier *Acacia* woodland and in rocky alpine and sub-alpine habitats. Across its range, found from sea level to sub-alpine areas of the Bufumbira and Rwenzori Mts (Kingdon 1971).

In both southern and eastern Africa this species is dependent on tree cavities, epiphytes or dense matted forest vegetation for shelter (Milner & Harris 1999b, Lawes *et al.* 2000, Gaylard & Kerley 2001, Skinner & Chimimba 2005). A decrease in numbers in southern Africa has been attributed to loss of structure within habitat, rather than forest size (Castley & Kerley 1993), although forest patches should be over 5 ha and less than 0.25 km from other larger forest patches to ensure a high probability of occupancy (Lawes *et al.* 2000). Preferred trees for denning are usually canopy trees in an intermediate stage of decay (i.e. >50% of the tree's material alive), and that have multiple cavity entrances. In the Eastern Cape den trees were 4–8 m in height (and often the tallest trees at a site), with diameters typically 40–80 cm and trunks angled between 45 and 67°; they were also preferred food trees. Preferred species include *Podocarpus falcatus*, *Schotia latifolia*, *Sideroxylon inerme*, *Rhus chirindensis*, *Andrachne ovalis* and *Apodytes dimidiata* (Gaylard & Kerley 2001). In East Africa selected trees are significantly larger (height

and diameter) than other trees in the area. Preferred species in SW Kenya include *Podocarpus latifolius*, *Schefflera* spp., *Juniperus procera* and *Olea africana* (Milner 1994), and *Hagenia abyssinica* in the Virunga Mts (Milner & Harris 1999b), due to their tendency to form cavities and support epiphytes. Southern Tree Hyraxes have been recorded sheltering in termitaria in East Africa (Kingdon 197, Rudnai 1992).

Abundance Heard calling more frequently than they are seen. Southern Tree Hyraxes spend long periods inactive in the high canopy or tree holes and so often escape notice. Locally abundant in the Virunga Mts (13.4/ha; Milner & Harris 1999a) and Rwenzori Mts, where they live at a high density and many apparent family groups live close together (Kingdon 1971). Such high densities contrast strongly with other parts of East Africa. A rough estimate in SW Kenya suggests a density of at least 1.2/ha (Milner 1994). In southern Africa, where *D. arboreus* is considered rare (Lawes *et al.* 2000), relative density has been estimated using playbacks of recorded vocalizations, as well as by means of counts of latrines in cavity trees (i.e. Catch Per Unit Effort; Gaylard 1994): 0.07–0.29 latrines/man hour searching were found in the Eastern Cape Province of South Africa.

Adaptations Predominantly nocturnal, perhaps as an adaptation to human disturbance or diurnal avian predators (Rudnai 1984b), although in some parts of the range they are active by day. Generally quite inactive, likely a consequence of a low metabolic rate and a low-quality folivorous diet. Energy requirements are also minimized by a thick pelage and by thermoregulatory behaviour such as sun basking and the use of tree cavities, especially during inclement weather. In contradiction to this, ♂♂ in particular may be active in the canopy at night, despite low temperatures. *Dendrohyrax arboreus* is thought to be thermolabile, like other hyracoids.

Like other members of the genus, Southern Tree Hyraxes are arboreal and well adapted for climbing, having excellent agility and feet that have both a strong grip and can be easily supinated. They spend most of their time above ground level and feed principally in the high canopy (Gaylard & Kerley 1997). However, they have been observed on the ground foraging during daylight hours, giving birth and when sick (J. Rudnai, pers. comm.).

Most other adaptations are as for other hyracoids. Long white hairs around the large dorsal gland are erectile and raised under conditions of excitement (Sale 1970a). Hyraxes may assume a characteristic defensive position when threatened, turning the back and rump towards the enemy and spreading the hair around the dorsal gland to expose the naked glandular area. The animal also protects itself from smaller predators by furiously biting with its very large incisors. During aggressive interactions the upper lip is curled and the teeth are bared. Rubbing of the dorsal gland on branches has been observed in dry season, presumably as a means of territorial marking.

Foraging and Food Exhibits a dietary preference for mature foliage, hairy leaf petioles and woody tips of branches; eating poor quality, but abundant, items may minimize search effort whilst maximizing intake. In the Virunga Mts, leaves of *Hagenia abyssinica*, *Hypericum revolutum*, *Senecio maranguensis*, *Galium ruwenzoriense* and *Pleopeltis excavata* formed the bulk of the diet (Milner & Harris

1999a). Important dietary species include *Podocarpus latifolius*, *Schefflera volkensii*, *Ilex mitis*, *Ficus natalensis*, *Acacia albida* and *Juniperus procera* in East Africa (Hoeck 1978a, Milner 1994) and leaves of *P. falcatus*, *Schotia latifolia*, *Cassine aethiopica*, *Euclea natalensis*, *Eugenia capensis zeyheri* in the Eastern Cape Province of South Africa (Gaylard & Kerley 1997). A low diversity of dietary plant species is consumed. In the Ngorongoro Crater, Southern Tree Hyraxes have also been recorded feeding on fig fruits (H. N. Hoeck pers. comm.). There is no evidence that they feed on insects. A primary feeding peak takes place in the evening, after dark; in the Virunga Mts, a second feeding peak occurs later in the night and appears to be more common among ♂♂, whilst ♀♀ are more likely to feed during the daytime.

Social and Reproductive Behaviour Southern Tree Hyraxes are solitary animals, although ♀♀ with offspring (often sitting on the mother's back) may be encountered; occasionally may be seen in family groups or pairs. The same ♂ has been observed with several ♀♀. In the Virunga Mts, home-range size varies between 150 and 2550 m², with young animals occupying the smallest areas (Milner & Harris 1999b). Tree density may influence range size. Female territories overlap, often with individuals of a different generation, possibly parents or offspring. Male territories overlap those of ♀♀, but the extent of male/male overlap is not clear. Seasonal variation in range size has not been investigated. Evidence from ranging patterns suggests that the mating system may be one of facultative polygyny; an exception to this general pattern is the semi-social rock-dwelling *D. a. ruwenzorii* that lives at an altitude of 3900 m, above the treeline.

Southern Tree Hyraxes defaecate in regular sites forming latrines, which are often found inside hollow trees. Each animal will use more than one latrine and several individuals may share each latrine. An average of 2.2 latrines per hyrax were found in the Virunga Mts (J. M. Milner pers. obs.). The social or territorial significance of latrines is unknown.

Southern Tree Hyraxes have a very loud and distinctive call, thought to be of territorial significance. It consists of a series of deep croaks (winding up) followed by a loud penetrating scream. Anecdotal reports suggest loud calls vary regionally, presumably by subspecies. Calls seem to be highly seasonal, and are heard regularly in the dry season in the early evening and middle of night. Calls can be heard as a wave passing through the forest as individuals respond to their neighbours. Both ♂♂ and ♀♀ call, ♀♀ only in the absence of a mate (Rudnai & Frere 2000). Whilst occasional calls may be heard outside the dry season, they tend not to elicit a wide response. Calling activity is not influenced by lunar phase. A large number of other less conspicuous sounds are also made (Rudnai & Frere 2000).

Courtship lasts 2–10 days in captivity (Rudnai 1998). Copulation has been observed in the dry season, preceded by the ♀ snarling at the advancing ♂, with the dorsal spot erect.

Reproduction and Population Structure Timing of the birth season is uncertain. Data from the Rwenzori Mts suggest a birth peak in Apr/May (Sale 1969), which agrees with observations of mating in Oct in the Virunga Mts (Milner & Harris 1999a) and the seasonal nature of calling and territorial marking. However, O'Donoghue (1963) found no apparent birth season in the Rwenzori Mts. Taylor (1998) collected two gravid ♀♀ in KwaZulu–Natal during Mar and Apr with two and three foetuses, respectively.

The gestation period is very long for such a small mammal, in the order of 7.5–8 months (Kingdon 1971). At birth, young are highly precocious, and weigh approximately 200 g. Young are weaned at 3–7 months and reach maturity at 20–30 months (Rudnai 1998). The reproductive strategy appears to be one of few young, with small litter-sizes (1–3; Rudnai 1984a, Taylor 1998) and low mortality rates, leading to a low ratio of juveniles to adults (0.2 : 1 in Virunga Mts; Milner & Harris 1999a). Miscarriage rate in captive animals is high (Rudnai 1998). A female-biased sex ratio (0.3 ♂♂ to 1 ♀ [n = 17] in the Virunga Mts) is presumably caused by differential dispersal and mortality rates. Longevity is at least 14 years in captivity (J. Rudnai pers. comm.).

Predators, Parasites and Diseases Known predators include Leopards *Panthera pardus*, African Golden Cats *Profelis aurata*, Servals *Leptailurus serval*, Caracals *Caracal caracal*, genets (*Genetta* spp.), African Civets *Civettictis civetta*, pythons (*Python* spp.), African Hawk-eagles *Hieraaetus spilogaster*, Crowned Hawk-eagles *Stephanoaetus coronatus* (e.g. see Boshoff *et al.* 1994) and large owls.

Southern Tree Hyraxes are subject to infection by a number of ectoparasites from the family Mallophaga (Roberts 1951). These parasites are host-specific and the presence of particular species of the parasitic family Mallophaga, in particular, may be used to identify hyracoid species (Roberts 1951). One captive animal died of *Toxoplasmosis* (Olubayo & Karstad 1983).

Conservation IUCN Category: Least Concern. CITES: Not listed.

Threats to this species include snaring for meat and skins (see, for example, Milner 1994), although the extent of this has not been evaluated, and loss of forest habitat. Populations of Southern Tree Hyraxes are now very fragmented, with limited gene flow among populations. Overall, the species has a relatively wide distribution, is present in several protected areas, and is generally not believed to be at immediate risk of extinction.

Measurements

Dendrohyrax arboreus

HB: 502 (441–566) mm, n = 14

T: 0 mm

HF: 62 (45–69) mm, n = 14

WT: 2.00 (1.17–2.65) kg, n = 14

Rwanda, excluding juveniles (Milner & Harris 1999a)

HB: 475 (428–520) mm, n = 9

T: 0 mm

HF: 63 (59–67) mm, n = 10

E: 32 (29–36) mm, n = 8

Southern Africa (Bothma 1967)

Key References Gaylard 1994; Gaylard & Kerley 1997, 2001; Hoeck 1978a; Kingdon 1971; Milner & Harris 1999a, b; Rudnai 1984a, b, 1998; Skinner & Chimimba 2005.

Jos M. Milner & Angela Gaylard

Dendrohyrax dorsalis WESTERN TREE HYRAX

Fr. Daman d'arbre; Ger. Westlicher Baumschliefer

Dendrohyrax dorsalis (Fraser, 1855). Proc. Zool. Soc. Lond. 1854: 99 [1855]. Bioko, Equatorial Guinea.

Taxonomy Six subspecies have been recognized (Rahm 1969, Bothma 1971, Jones 1978), though these are in need of revision. Synonyms: *adametzi*, *aschantiensis*, *beniensis*, *brevimaculatus*, *congoensis*, *dorsalis*, *emini*, *latrator*, *marmota*, *nigricans*, *rubriventer*, *stampflii*, *sylvestris*, *tessmanni*, *zenkeri*. Chromosome number: not known.

Description Small stocky animal, not unlike a guinea-pig, but larger. Coat thick, coarse, dark-brown and black with diffused lighter yellowish hairs; long sensory hairs (vibrissae) are scattered

throughout the pelage. Pale cream morphs are also known (Kingdon 1971). Rostrum naked. Ears small and rounded and may be tipped with white. There is a conspicuous white spot beneath the chin, and an obvious large, yellowish-white dorsal spot concealing a naked dorsal scent gland (42–72 mm long). Tail short and does not extend past the end of the body. Foot-pads are black, ridged and flexible. One pair of inguinal nipples.

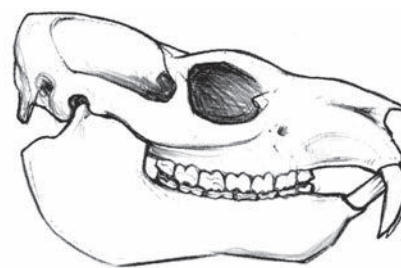
Geographic Variation

D. d. dorsalis: Bioko I.

D. d. sylvestris: coastal forests from Sierra Leone to the lower Niger R. in Nigeria.



Western Tree Hyrax *Dendrohyrax dorsalis*.



Skull of *Dendrohyrax dorsalis*.

D. d. nigricans: lower Niger R. in Nigeria to N Angola.

D. d. latrator: C DR Congo.

D. d. emini: N and E DR Congo.

D. d. marmota: N Uganda. Some hybridization may occur with the Southern Tree Hyrax *D. arboreus* in S Uganda. Kingdon (1971) suggested that the softer fur of *D. d. marmota* might be a product of long-term hybridization with *D. arboreus*.

Subspecific boundaries are not well established, but geographic variation in call structure is discernible, even between fairly close populations, though not as marked as between more isolated populations of *D. validus* (see *D. validus* profile). Call structure of different populations differs enough to possibly serve as a useful character for distinguishing subspecies. Inter-individual differences in calls may also be marked enough to allow discrimination of individuals based on calls (A. Gautier-Hion pers. comm.). Representative sonograms of calls from three *D. dorsalis* populations – forest of Minwo, Ebom, S Cameroon; Abidjan, S Côte d'Ivoire; and Makokou Forest, NE Gabon – illustrate population differences (Roberts 1999).

Similar Species

D. arboreus. Longer and softer pelage; creamy-white dorsal spot; naked rump patch given as 23–30 mm, though some Rwandan specimens to 48 mm (J. M. Milner pers. comm.); one pair inguinal nipples, but sometimes one pair pectoral and one pair inguinal or one pair pectoral or two pair inguinal). Sympatric or parapatric in S Uganda and along the western border of DR Congo, where some hybridization may occur.

D. validus. Yellow or russet-brown dorsal spot; naked rump patch 20–40 mm; one pair inguinal nipples. Not sympatric, being confined to isolated montane and coastal forests of Tanzania/Kenya, as well as Pemba and Zanzibar Is.

Heterohyrax brucei. Sympatric in NE DR Congo and NW Uganda. For distinguishing characteristics of genus see Table 6, p. 151.

Procapia capensis. Distributed widely in sub-Saharan Africa, with isolated population in North Africa, in a wide range of habitats; F. Dowsett-Lemaire (pers. comm.) recorded Rock Hyrax in sympatry with *D. validus* in Kalakpa Reserve, E Ghana. For distinguishing characteristics of genus see Table 6, p. 151.

Distribution Endemic to Africa. West and central Africa, from Sierra Leone through to S Sudan and N Uganda and southwards to Cabinda (Angola) and C DR Congo. Although Jones (1978) gave the range as 'from Gambia to the Niger River', Grubb *et al.* (1998) note there is no confirmed record west of Sierra Leone, but the species is recorded from near Somoria in NE Guinea (Ziegler *et al.* 2002). Absent from the Dahomey Gap, there being no records from east of the Volta R. in Ghana or from Togo (Grubb *et al.* 1998). Present on Bioko Is.

Habitat Usually found in moist lowland forests and moist savannas to an altitude of around 1500 m, but recorded in montane habitats up to 3500 m (Malbrant & Maclatchy 1949). Also from small and degraded forest fragments.

Abundance Individuals maintain territories, but population densities and structure are poorly known. Observations from Tâi N.

P., Côte d'Ivoire, provide a rough estimate of 1–2 individuals per square kilometre based on nocturnal calling records (S. Shultz pers. obs.). However, it is likely that actual densities are similar to other species in the genus (see *D. arboreus* and *D. validus* profile).

Adaptations Western Tree Hyraxes are extremely competent climbers and are able to ascend smooth tree trunks up to 50 cm in diameter (Richard 1964). Their limbs and body are flexible and can be contorted to navigate through complex branches (Rio & Galat 1982). The grip is strong, and the feet can be easily supinated. Captive animals have been observed climbing on vines and wires, and even up door frames.

Grooming, using the lower incisors and the inner digit of the hindfoot, is common, and captive animals groom each other regularly, particularly on the face and neck (Jones 1978). Kingdon (1971) has suggested that the dorsal gland is important for marking territories and home-ranges, as well as for interspecific identification. Captive animals have been seen to rub the gland against objects such as doors or trees, and ♀♀ excrete cinnamon-smelling oil from their dorsal gland prior to mating. When disturbed or exhibiting aggression, these animals exhibit piloerection of the hair around the gland, at the same time emitting odoriferous secretions.

Foraging and Food Herbivorous, consuming mostly fruit, twigs, shoots, bark and leaves (Rahm 1966, Kingdon 1971). Most activity occurs in the canopy, but they descend to the ground to forage and move between trees. They are predominantly nocturnal, emerging regularly at dusk with another period of activity shortly before daylight (Richard 1964).

Social and Reproductive Behaviour Primarily solitary but groups of two and three can be found (typically mother and subadult young). Spends the day resting in holes at the top of large trees (Malbrant & Maclachy 1949). Tree hyraxes have small home-



Dendrohyrax dorsalis



Sketches of *Dendrohyrax dorsalis*.

ranges, with each defended male territory overlapping those of several smaller female ranges. Individuals use middens, defaecating repeatedly at the bases of trees.

As with other tree hyraxes, Western Tree Hyraxes produce very loud, distinct calls. Call structure is characterized by long cries, repeated between 22 and 42 times at gradually increasing amplitude and intervals, reaching a loud climatic crescendo at end. Among captive animals, Rahm (1969) observed that at the beginning of each call there was a sequence of very faint, almost inaudible units that only showed up faintly on oscillograms. Both ♂♂ and ♀♀ call, the latter more often when solitary. Hyraxes call throughout the night, but with marked peaks in late evening (20:00–22:00h) and early morning (04:00–05:00h), corresponding to activity patterns (Rahm 1969). There is some seasonal variation in both calling frequency and schedules. They are also heard to call during the day, typically after being disturbed.

Tree hyraxes have been observed raising their dorsal crest, 'tutting' and licking their lips when alarmed (F. Maisels pers.

comm.). Captive animals are often quite aggressive and will charge and snap at other individuals (Jones 1978).

Reproduction and Population Structure Both mating and birth peaks tend to coincide with the dry season (Kingdon 1971), but offspring may be born throughout the year. In Gabon and Cameroon, births are primarily during Mar and Apr, and from May to Aug in S and W DR Congo, while in the eastern part of the range (Uganda) young are born throughout the year (Kingdon 1971). Gestation period is eight months. One or two young are born; they are precocious, fully furred and fairly large, with birth-weights of 180–380 g (Mollaret 1962, Roche 1962). Jones (1978) recorded one captive animal attaining adult body size by 120 days and another at more than 200 days. Longevity in captive animals is likely similar to the Southern Tree Hyrax *D. arboreus*.

Predators, Parasites and Diseases Known predators include Crowned Hawk-eagles *Stephanoaetus coronatus* and possibly also larger eagle-owls *Bubo* sp. or hawk-eagles *Hieraaetus* sp. The species has been documented in very low proportion in the diet of both Leopards *Panthera pardus* (1.4%; Hoppe-Dominik 1984) and Crowned Hawk-eagles (approx. 2%; Shultz 2002) in Tāi N. P. Chimpanzees *Pan troglodytes* have also been documented capturing and killing adults (Hirata *et al.* 2001), but have not been seen to eat them.

West African specimens have been found to have various nematode parasites (*Crossophorus collaris*, *Libyostrongylus alberti*, *Hoplodontophorus flagellum*, *Theileriana brachylaima*) (Dekeyser 1955). Fain & Lukoschus (1981) recorded a new species of psoroptid tick from DR Congo.

Conservation IUCN Category: Least Concern. CITES: not listed.

Apparently widespread and common in large forest tracts, and present in a number of protected areas, such as Tāi N. P. and the National Park of Upper Niger (Guinea); however, they are probably sensitive to intensive habitat degradation and fragmentation. They are also killed for their fur and for food, and have been recorded in a number of bushmeat markets; Fa *et al.* (2000) actually recorded a significant increase in the number of carcasses of this species found in bushmeat markets in Bioko I. between 1991 and 1996. The status of this species should be closely monitored in the future.

Measurements

Dendrohyrax dorsalis

HB: 440–570 mm, n = 14

HF: 70–90 mm, n = 14

E: 21–30 mm, n = 14

WT: 1850–4500 g, n = 14

Origin unknown (Jones 1978); mean not given

Key References Jones 1978; Kingdon 1971; Malbrant & Maclatchy 1949; Rahm 1969.

Susanne Shultz & Diana Roberts

Dendrohyrax validus EASTERN TREE HYRAX

Fr. Daman d'arbre; Ger. Östlicher Baumschliefer

Dendrohyrax validus True, 1890. Proc. U. S. Nat. Mus. 1890: XIII: 228. Mt Kilimanjaro, Tanzania.Eastern Tree Hyrax *Dendrohyrax validus*.

Taxonomy Four subspecies have been recognized in Tanzania (Swynnerton & Hayman 1950), namely *D. v. validus*, *D. v. terricola* (including the form *vosseleri*), *D. v. neumanni* and *D. v. schusteri*. Bothma (1971) recognized three subspecies (including the form *schusteri* in *D. v. terricola*), but also listed *D. v. vosseleri* as distinct, although he indicated it was probably synonymous with *D. v. terricola*. Based on variation in loud-calls, there are distinct vocal profiles that correspond with at least three 'call zones' (see below), which have been identified by Roberts (2001). These may represent subspecific differences or even species-level divisions. Tree hyraxes, previously unknown there, have now been recorded in Ethiopia. Distinguished by apricot brow-spots and mottled white and apricot undersides, a new species or new subspecies of *D. validus* is likely (A. Mekonnen, pers. comm.). This brings into question the current taxonomy of the species, suggesting that a major revision of this group is overdue, all the more so since Shoshani (2005) considered this species a synonym of the Southern Tree Hyrax *D. arboreus*. We provisionally follow Swynnerton & Hayman (1950) in listing four subspecies, recognizing that more than one full species may emerge with further study of the genes and vocalizations of local populations. Synonyms: *adersi*, *neumanni*, *schusteri*, *terricola*, *validus*, *vosseleri*. Chromosome number: not known.

Description Small, robust mammal, similar in shape to a guinea-pig, but typically slightly larger. No discernible tail; dusky-brown feet with blunt, nailed toes, and a distinctive dorsal scent gland 20–40 mm long marked by a yellow to russet-brown, or cinnamon-coloured patch of erectile hairs (True 1890, Bothma 1971, Kingdon 1971). Hairs around the nostrils, eyes, feet and outsides of the ears are dusky-brown. Ears rounded, small to moderately sized and internally have a tuft of yellowish-white hairs. Hair covers the muzzle as far as the nostrils and there is a narrow, hairless, border around the nostrils extending to the margin of the lip (True 1890). Pelage is dense, soft and long-furred (Kundaali 1976a, b). Colour varies greatly within the species, though generally dorsal pelage is cinnamon-brown darkening to dusky-brown or black, especially around the head. Most dorsal hairs are muted chocolate-brown at base, with a bright cinnamon subterminal ring and brown or black tip. Among these are

numerous longer, straight, shining hairs coloured entirely dusky-brown or black. Around the head, subterminal rings on hairs are paler, giving the forehead and cheeks a greyer tinge. Undersides are paler, with hairs coloured chocolate-brown at the base and tinged at the ends cinnamon-brown to paler yellowish-white, especially between the hind legs (True 1890). One pair inguinal nipples only.

Skull depressed, slightly expanded at the posterior with an elongated muzzle and rectangular nasal bones. Orbit is completed by the fusion of the processes of the frontal and zygomatic bones. The coronoid process of the mandible is rectangular and angled forward forming a 45° angle with the molars, with the upper margin almost in line with the margin of the ramus posterior to the condyle (True 1890).

Geographic Variation

D. v. validus: Mt Meru and Mt Kilimanjaro.

D. v. terricola (including *vosseleri*): Taita Hills, Pare and Usambara Mountains.

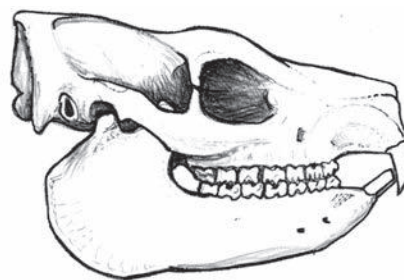
D. v. schusteri: Uluguru Mts and (possibly) Udzungwa and Rubeho Mountains.

D. v. neumanni (including *adersi*): Zanzibar, Pemba and Tumbatu Is.

Compared with Southern and Western Tree Hyraxes, the calls of the Eastern Tree Hyrax show radically more apparent and dramatic geographical variance. Roberts (2001) identified three distinct vocal profiles, falling into three 'call zones': offshore islands, including Zanzibar and Pemba; southern mountains, including the Uluguru, Udzungwa and Rubeho Mountains; and northern mountains, including the Taita Hills, Pare and Usambara Mountains. No data were available from Mt Meru and Mt Kilimanjaro, although J. Kingdon (pers. comm.) suggests call patterns from these populations are akin to those recognized from the Taita Hills and Pare Mts.

The clear differences in vocal profiles between call zones can best be illustrated by comparing spectograms of vocalizations. On Zanzibar and Pemba Is, one call type has been recorded: a discrete (i.e. having an essentially constant pattern each time it is heard) 'knock' sequence with a distinctive crescendo and decrescendo pattern and characterized by an initial unit of relatively high amplitude followed by 2–4 less powerful (sometimes almost inaudible) units, prior to the main element of the call.

In the Uluguru, Udzungwa and Rubeho Mountains there are two frequently heard call types: (1) 'hac-phrases', which occur as

Skull of *Dendrohyrax validus neumanni*.

volleys of relatively monotonous short phrases of five or six units, constituting a short, sharp resonant 'hac' sound, which animals appear to exchange on an ad hoc basis; and (2) diagnostic 'hac-pingpong' sequences, in which animals emit a series of 'hac-phrases', building to a longer climactic 'pingpong' sequence which, as the name suggests, sound very similar to a bouncing pingpong ball and which seem to occur above a certain level of arousal. J. E. Topp-Jørgensen (pers. obs.) reports hearing high-pitched screams in the Udzungwa Mts uttered during fighting and another call type that starts with two rapid series of between 6 and 12 single 'hacs' followed by single or double 'hacs' uttered for up to three minutes. The latter call correlated with increasing density and could be related to increased competition.

In the Taita Hills, Pare and Usambara Mountains, call patterns vary more compared with the other two, the most diagnostic being the 'strangled-thwack' call-type, with a unique phrased-unit structure, i.e. composed of audible and observable sub-units, rather than individual units as in the other zones.

Similar Species

D. dorsalis. Generally has shorter, coarser pelage; yellowish-white dorsal spot; longer dorsal patch (42–72 mm); rostrum naked; conspicuous white spot beneath chin. Rainforests of West and central Africa.

D. arboreus. Generally grey or brown colouration, may appear grizzled, and head frequently darker than body; creamy-white dorsal spot; naked rump patch given as 23–30 mm (J. M. Milner pers. comm.), so not a reliable diagnostic character. One pair inguinal nipples, but sometimes one pair pectoral and one pair inguinal, or one pair pectoral or two pairs inguinal. Forested areas of central and eastern mainland Africa as far south as the Eastern Cape Province, South Africa.

Heterohyrax brucei. Recorded in montane forest habitat within the range of *D. validus* (Topp-Jørgensen *et al.* 2008; A. Perkin pers. comm.). For further distinguishing characteristics see Table 6, p. 151.

Procavia capensis. Distributed widely in sub-Saharan Africa, with isolated population in North Africa, in a wide range of habitats. For further distinguishing characteristics see Table 6, p. 151.

Distribution Endemic to Africa. Of all tree hyrax species, the Eastern Tree Hyrax has the most restricted and patchy geographic range, being limited to montane forests on the slopes of Mt Kilimanjaro and Mt Meru, and the Eastern Arc Mountains – a chain of isolated forest remnants on crystalline mountain blocks running from the Taita Hills in S Kenya to the Udzungwa Mts in S Tanzania; also present in coastal forests of Tanzania, S Kenya and offshore islands (Seibt *et al.* 1977, Pakenham 1984, Kingdon & Howell 1993, Burgess *et al.* 2000, Cordeiro *et al.* 2005). Swynnerton & Hayman (1950) documented *D. v. validus* on Mt Kilimanjaro and Mt Meru; *D. v. terricola* in the East Usambara (Amani, Monga), West Usambara (Lushoto, Magamba), and both North and South Pare Mountains; *D. v. neumanni* in coastal forests on the islands of Pemba, Unguja (Zanzibar) and Tumbatu; and *D. v. schusteri* in the Uluguru Mts (Bagilo, Mkarazi, Nyange, Nyingwa, Vituri). Burgess *et al.* (2000) indicated the species occurs on Mafia I., presumably a lapsus for Pemba (Kock & Stanley 2009). Seibt *et al.* (1977) reported the first record of the Eastern Tree Hyrax in Kenya, recording a population inhabiting a



Dendrohyrax validus

fossil reef area close to the shore at Vipingo, a small village north of Mombasa. Recently, between 1993 and 2005, the species has also been recorded from Nguu, and Rubeho Mts (Tanzania) (Eltringham *et al.* 1998, Cordeiro *et al.* 2005, J. Kingdon pers. comm., A. Perkin pers. comm.). It possibly occurs in Ethiopia.

Habitat Confined to moist lowland and montane forest, and occupies a wide altitudinal range from sea level to 3070 m on Mt Kilimanjaro, where it occupies a continuous belt of forest between 1700 m and 3070 m (Kundaali 1976b). Favoured tree species on Kilimanjaro include *Ocotea usambarensis*, *Schefflera volkensii*, *Nuxia congesta*, *Podocarpus* spp. and *Ficus thonningii* (Kundaali 1976a, b, Grimshaw *et al.* 1995). In the Eastern Arc Mts, Cordeiro *et al.* (2005) recorded this species from several forest reserves at elevations between 900 m and 2000 m. In the Nilo F. R. it seemed most common in forest at lower elevations (900–1300 m), but was rarer in stunted forest on ridges and at 1500 m (where the absence of large, mature trees for nest holes may have been a limiting factor). Similarly, at Kindoroko F. R. it was commonly heard at 1500–1800 m, but less so above these elevations. *D. validus* is also reported to den where there are large boulders on Mt Kilimanjaro (Umbwe route), and in the Eastern Arcs and adjacent lowland sites (e.g. Kihansi) (N. Cordeiro pers. comm.). It possibly occurs in Ethiopia.

Abundance Locally abundant. As with other tree hyrax species, Eastern Tree Hyraxes are rarely seen, but can frequently be heard calling. Based on circular plot counts of calls, densities of up to 17 ind/ha have been estimated in undisturbed, closed-canopy forest in the Udzungwa Mts, and up to 12 ind/ha in moderately disturbed, closed-canopy forest (Topp-Jørgensen *et al.* 2008). Abundance varies greatly and seems to correlate negatively with open-canopy structure and hunting (Topp-Jørgensen *et al.* 2008). In forests at higher altitudes, where predation levels appear to be low, Eastern Tree Hyraxes can become the dominant herbivore in especially

favoured patches, with biomass densities in the order of 75 kg/ha (J. Kingdon pers. comm.).

Evidence suggests the species is highly susceptible to disturbance. In the Udzungwa Mts, logging has a significant impact on population numbers, especially where hunting also occurs (Topp-Jørgensen & Pedersen 2001). In disturbed forests, individuals call less frequently, a feature associated with either severely reduced population densities or stress-induced behavioural change. Overall, high population densities (i.e. calling frequency) appear to be linked to isolated, undisturbed forest patches (Topp-Jørgensen *et al.* 2008). These findings support those of Kundaeli (1976b) on Mt Kilimanjaro: highest densities were estimated at an elevation of 2310 m, where disturbance from logging was low. Food within the forest was found to be generally abundant and not a factor regulating population density. However, access to, and availability of, specific cavity-bearing tree species for shelter was found to limit densities, and at this elevation preferred tree species, such as *Ocotea usambarensis* on the southern slopes, and *Nuxia congesta* on the western slopes, were abundant, though at lower elevations were exploited intensively. Using the density of defaecation sites as a measure, population numbers were higher on the southern and western slopes – average of 23 individuals/ha and 13 individuals/ha, respectively – compared with the northern (seven individuals/ha) and eastern (where only one defaecation site was recorded) slopes. This again was linked to variance in the abundance and presence of preferred shelter trees. Population density on Mt Kilimanjaro is also regulated by other factors, such as the solitary nature of these hyraxes and high intraspecific intolerance, and the fairly constant thermal and microclimatic conditions in the forest (Kundaeli 1976b).

Adaptations Like other tree hyrax species, the Eastern Tree Hyrax appears to be secondarily nocturnal, as indicated by its reliance on vocal and olfactory signals for communication, intensely solitary behaviour and observed activity patterns. However, these hyraxes have no specific physical adaptations to a nocturnal existence (e.g. there is no *tapetum lucidum* for enhanced vision or enlarged ears). They are predominantly arboreal, and very adept climbers, spending most of their time feeding and resting above the ground, but come down when looking for a mate or sometimes to forage. Thick pelage, long periods of inactivity and thermoregulatory behaviour (e.g. use of tree cavities and sun basking) minimize energy requirements. Kundaeli (1976b) suggests they are reliant on a constant environment and are unable to cope with rigorous or changeable climatic conditions.

Foraging and Food Eastern Tree Hyraxes are browsers, feeding almost entirely on leaves. They feed predominantly above the ground, but occasionally come down to forage on soft-tissued climbers and herbs (Kundaeli 1976a, b). Some feeding may occur during the day, but intense feeding occurs at dusk and again just before dawn.

At the top of its altitudinal range in the Udzungwa Mts, this species can live at very high densities (estimated from calls to be in excess of 20 per ha) in low canopy (15–20 m) mist forest where a very rare and localized species of African Violet *Saintpaulia grotei* grows abundantly, often rooted in decayed hyrax faeces. The plants appear to escape the very heavy browsing of hyraxes in this habitat, suggesting that the herb is distasteful to the hyraxes. The plants seem to derive competitive, as well as nutritional, advantages from their

association with the hyraxes, suggesting that the herb and herbivore might have co-evolved (J. Kingdon pers. comm.).

Social and Reproductive Behaviour Essentially solitary, with animals nesting, foraging and travelling independently, but social relations are maintained by vocal calls and scent marking signals. On Mt Kilimanjaro most shelter trees are occupied by only one animal, except for ♀♀ with young or where a tree has more than one independent cavity (Kundaeli 1976b). No data are available regarding male and female territories, male–male behaviour, dispersal patterns, and behaviour of young.

Calling appears to be the dominant means of communication. Eastern Tree Hyraxes call throughout the night, with peak periods just after dusk and before dawn (Cordeiro *et al.* 2005). It is unclear whether there are seasonal differences or whether climate or moon phase affects calling activity. No large differences were noted in calling frequency over an eight-month period between Jul and Mar, although on misty days calling may be delayed by up to 15 mins (J. E. Topp-Jørgensen pers. obs.). Sometimes vocal during the day, but mainly inactive, resting very still on a platform near an escape hole (Kundaeli 1976a, b). Like other tree hyrax species, defaecation and urination takes place from the same vantage point, forming middens, usually at the base of trees (Kundaeli 1976a). In the Udzungwa Mts middens can cover several square metres and cover trunks and the surrounding ground with a very strong-smelling, thick, tarmac-like coat. As a result of hunting, daytime call frequency, sun basking and the use of middens is reduced even in lightly disturbed areas (Topp-Jørgensen & Pedersen 2001).

Reproduction and Population Structure Peak in births is probably around Aug, and both mating and birthing seasons appear to coincide with dry seasons at least for the Kilimanjaro area. There is a very long gestation period of around 7.5 months (Kundaeli 1973, cited in Kundaeli 1976a, b). A single young is the norm (but occasionally two are born), and the young are highly precocious. No data are available on suckling behaviour, age of sexual maturity, lifespan and population structure.

Predators, Parasites and Diseases Known predators include Leopards *Panthera pardus*, genets *Genetta* spp., Two-spotted Palm Civets *Nandinia binotata*, Servals *Leptailurus serval*, African Civets *Civettictis civetta*, Crowned Hawk-eagles *Stephanoaetus coronatus* and African Rock Pythons *Python sebae*. There is no known information on parasites or diseases.

Conservation IUCN Category: Least Concern. CITES – Not listed.

The major threats to this species are severe forest loss and fragmentation, and hunting. Individuals can persist in closed-canopy forests of less than 1 square kilometre; however, logging, including selective logging of large trees, removes potential shelter trees, destroys arboreal pathways and makes animals more vulnerable and prone to ground trapping (Topp-Jørgensen *et al.* 2008). Clear pathways through the undergrowth (runnels) also appear over time where tree hyraxes are active, which make them vulnerable to local hunters. Eastern Tree Hyraxes are hunted for their meat and skins, and easily trapped using snares set at the head of a runnel near the base of a tree. They may also

be clubbed, speared, or run down by dogs having been 'smoked out' or following the felling of a den tree (a common method employed in the Udzungwa Scarp F. R.) or extracted from holes between boulders using a stick or spear (Topp-Jørgensen & Pedersen 2001).

Kundaali (1976a) recorded 4708 legally caught hyraxes between May 1972 and July 1973 on Mt Kilimanjaro. Hunting was banned in Tanzania in 1973; however, it still continues and most, if not all, hunting of tree hyraxes in Tanzania is illegal. They are trapped for their meat and pelts to make karosses ('hyrax blankets') (Kundaali 1976a), which, while much reduced in availability since the 1970s, can still be bought in Arusha, Tanzania. In the Udzungwa Mts both over-harvesting by local people and felling of den trees suggest significant effects on population numbers (Topp-Jørgensen & Pedersen 2001).

Protected areas from which this species has been recorded include the Udzungwa Mts and Kilimanjaro National Parks, Arusha National Park as well as several forest reserves in the Eastern Arc Mts of

Tanzania, such as Nilo, Kindoroko and Nguru North Forest Reserves (see Cordeiro *et al.* 2005).

Measurements

Dendrohyrax validus

HB: 470–588 mm (n = 5)

HF: 58–64 mm (n = 5)

E: 12.5–15.5 mm (n = 5)

WT: 2.5–3.0 kg

Measurements: Kilimanjaro and Taveta, Tanzania (True 1890)

Weight: Kilimanjaro, Tanzania (Kundaali 1976a)

Key References Cordeiro *et al.* 2005; Kingdon 1971; Kundaali 1976a, b; Seibt *et al.* 1977.

Diana Roberts, Elmer Topp-Jørgensen & David Moyer

GENUS *Heterohyrax*

Bush Hyrax

Heterohyrax Gray, 1868. Ann. Mag. Nat. Hist., ser. 4, 1–50.

Heterohyrax is a monotypic genus, represented only by the Bush Hyrax, or Yellow-spotted Rock Hyrax, *H. brucei*. Two additional forms, *antineae* and *chapini*, have been considered distinct species (e.g. Bothma 1971; and see Schlitter 1993), but the former is a *Procavia* (see Hoffmann *et al.* 2008). Like *Procavia*, *Heterohyrax* is rock dwelling, gregarious and diurnal. Relative to other hyraxes, the penis of *Heterohyrax* is more complex than those of either *Procavia* or *Dendrohyrax*, characterized by an appendage at its tip and being round

in cross-section, and the distance between the anus and the preputial opening in an adult ♂ is 65–80 mm, some two to three times longer than in the other genera (Coetzee 1966, Hoeck 1978a). Length of upper molar tooththrow (M^{1-3}) is less than the length of the upper premolar tooththrow (P^{1-4}) (Bothma 1971).

Paulette Bloomer

Heterohyrax brucei BUSH HYRAX (YELLOW-SPOTTED HYRAX)

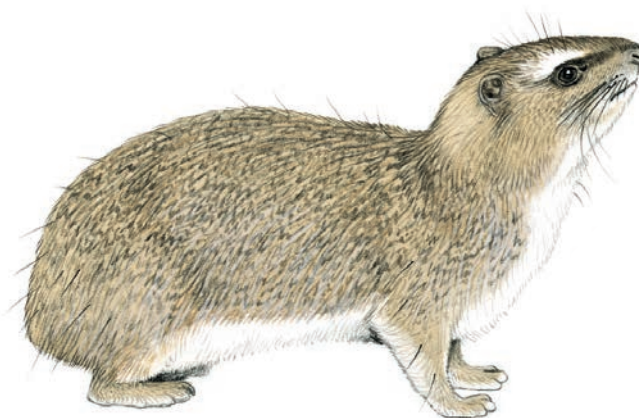
Fr. Daman d'arbuste; Ger. Buschschliefer

Heterohyrax brucei (Gray, 1868). Ann. Mag. Nat. Hist., ser. 4, 1: 35–51. Ethiopia.

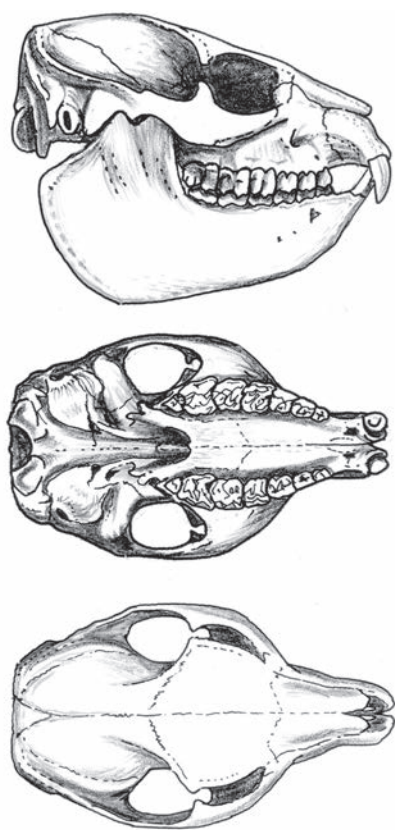
Taxonomy Although the type species was originally designated *Dendrohyrax blainvillii*, *Heterohyrax blainvillii* was proposed as a provisional name (Gray 1868; see Barry & Shoshani 2000). Allen (1939), Roberts (1951) and others considered *Hyrax syriacus* the prior name for this species, but Ellerman *et al.* (1953), Bothma (1971) and Meester *et al.* (1986) referred this form to *Procavia*, such that *brucei* becomes the earliest available name.

More than 20 subspecies have been described from Africa, and two additional forms, *antineae* and *chapini*, were treated as distinct species by Bothma (1971). *Heterohyrax antineae*, from the Ahaggar Mts, was maintained as a distinct species by Bothma (1971) and Schlitter (1993), and included in the synonymy of *H. brucei* by Barry & Shoshani (2000). However, this form is likely conspecific with an earlier described form of *Procavia* (*bounhioli*) (Hoffmann *et al.* 2008). *Heterohyrax chapini* (described by Hatt 1933) from Matadi in SW DR Congo, not far from the mouth of the Congo R., supposedly characterized by the presence of only two pairs of inguinal nipples, is also now more commonly treated as conspecific with *H. brucei* (Roche 1972, Schlitter 1993, Barry & Shoshani 2000, Shoshani

2005). Barry & Shoshani (2000) and Shoshani (2005) recognized 25 subspecies for the African continent, including both *antineae* and *chapini*. Although no consensus exists on whether all of these subspecies are conspecific, sequences of the mitochondrial DNA



Bush Hyrax *Heterohyrax brucei*.



Lateral, palatal and dorsal views of skull of *Heterohyrax brucei*.

cytochrome *b* gene indicate that at least *H. b. hindei* in the central portion of the range and *H. b. ruddi* and *H. b. granti* from Zimbabwe and South Africa are highly distinct and may represent cryptic species (P. Bloomer pers. comm.).

Synonyms: no fewer than 34 synonyms are listed by Shoshani (2005), many of which have been considered subspecies (see Bothma 1971, Barry & Shoshani 2000). Chromosome number: $2n = 54$ (Prinsloo & Robinson 1991). Karyotype marked by 20 acrocentric, two subtelocentric, two submetacentric and two metacentric autosomal pairs. The X chromosome is the largest submetacentric and the Y is a very small acrocentric.

Description Small to medium-sized, short-legged mammal with rudimentary tail, round ears, and rabbit-like appearance and movement. Lateral and dorsal colour ranges from grey in arid regions to dark reddish-brown in more mesic climates (Skinner & Chimimba 2005). Some individuals in isolated populations can be white-spotted (Hoeck 1982a). A small, linear creamy to yellow spot in the midline of the back surrounds the dorsal gland, but in some subspecies it may be lacking. Ventral colour white or creamy in distinct contrast to the sides, back, head and rump. Eyebrows strikingly white to creamy (paler than in *Procavia*) and conspicuous at a distance. Vibrissae (up to 90 mm long on the snout) evident on the snout, above the eyes, under the chin, along the back and sides, on the abdomen and on fore- and hindlimbs. Ears more prominent than in other hyraxes, the eyes bulge and the head is flat dorsally. Guard hairs are softer than in *Procavia*, black-tipped, and up to 30 mm long. Underhairs are basally brown or grey and terminally buffy. The anal-preputial distance in ♂♂ is 65–82 mm, two or three times longer than in

other genera. Anatomy of the penis is complex, with an appendage at the tip and round in cross-section, and measures greater than 60 mm when fully erected (Coetzee 1966, Glover & Sale 1968, Hoeck 1978a, c). Females typically have one pair of pectoral and two pairs of inguinal nipples (although in some animals, such as the isolated form *chapini*, the pectoral pair is absent) (Hatt 1933, Roche 1962, Bothma 1971, Hoeck 1977a). Males and ♀♀ are, on average, of similar size, although ♀♀ are sometime larger than ♂♂ (Smithers & Wilson 1979).

The single pair of tusk-like upper incisors is ridged or triangular in cross-section in ♂♂ (Thomas 1892), but rounded in ♀♀. A diastema (10–16 mm long in adults; Thomas 1892, Bothma 1971) precedes the short-crowned molariform cheekteeth (Meyer 1978) that bear transverse cusps (lophodont condition, resembling those of the family Rhinocerotidae; Skinner & Chimimba 2005) adapted for a herbivorous diet. The length of the upper premolar tooththrow, P^{1-4} is just less than or equal to that of the upper molar tooththrow, M^{1-3} (Bothma 1971).

Geographic Variation Substantial geographic variation in coat colour has been recorded from across the range of this species, and has led to a proliferation of described forms. Bothma (1966) recorded the high degree of individual variation in coat colour in southern Africa (and see Skinner & Chimimba 2005). We provisionally list the 24 subspecies and their country type localities, following Barry & Shoshani (2000) and Shoshani (2005), but excluding the form *antineae*, which is here considered a *Procavia*. Many will probably not hold up to taxonomic scrutiny:

H. b. albipes: Kenya.
H. b. bakeri: NE DR Congo,
 S Sudan and NW Uganda.
H. b. bocagei: Angola.
H. b. brucei: Ethiopia.
H. b. chapini: DR Congo.
H. b. dieseneri: Tanzania.
H. b. frommi: Tanzania.
H. b. granti: South Africa.
H. b. hindei: Kenya.
H. b. hoogstraali: Sudan.
H. b. kempfi: Kenya.
H. b. lademanni: Tanzania.

H. b. manningi: N Malawi, N and
 E Zambia.
H. b. mossambicus: Mozambique.
H. b. munzneri: Tanzania.
H. b. princeps: Ethiopia.
H. b. prittwitzii: Tanzania.
H. b. pumilus: Somaliland.
H. b. ruddi: Mozambique.
H. b. rudolfi: Ethiopia.
H. b. somalicus: Somaliland.
H. b. ssongaeae: Tanzania.
H. b. thomasi: Sudan.
H. b. victoria-njansae: Tanzania.

Hatt (1933), in describing *H. chapini* from near Matadi, just north of the Angolan border in SW DR Congo, considered this form to be not closely related to the Angolan hyraxes, later (1936) commenting that *bocagei* 'is quite different in its longer, thicker pelage, smaller size, broader teeth, proportionately broader skull, elevated supraorbital ridges, shorter muzzle and flatter basicranium.'

Similar Species

Procavia capensis. Sympatric across much of its range in sub-Saharan Africa, except in West Africa where *Heterohyrax* is absent. For further distinguishing characteristics of genus see Table 6, p. 151.
Dendrohyrax arboreus. Sympatric in S Kenya and N Tanzania. For distinguishing characteristics of genus see Table 6, p. 151.
Dendrohyrax dorsalis. Sympatric in NE DR Congo and NW Uganda. For distinguishing characteristics of genus see Table 6, p. 151.

Dendrohyrax validus. Restricted to isolated montane and coastal forests of Tanzania/Kenya, as well as Pemba and Zanzibar Is. For distinguishing characteristics of genus see Table 6, p. 151.

Distribution Endemic to Africa. Widely distributed in Africa from Sudan and Eritrea through the Horn of Africa south to the Limpopo Province in South Africa (Barry & Shoshani 2000, Skinner & Chimimba 2005). Isolated populations in SW DR Congo (*H. b. chapini*; Hatt 1933) and Angola (*H. b. bocagei*; Crawford-Cabral & Veríssimo 2005). Records of this species in North Africa, specifically Egypt, along the Red Sea coast, and from the Hoggar Mts of Algeria, are erroneous and relate to *Procavia* (Hoffmann *et al.* 2008).

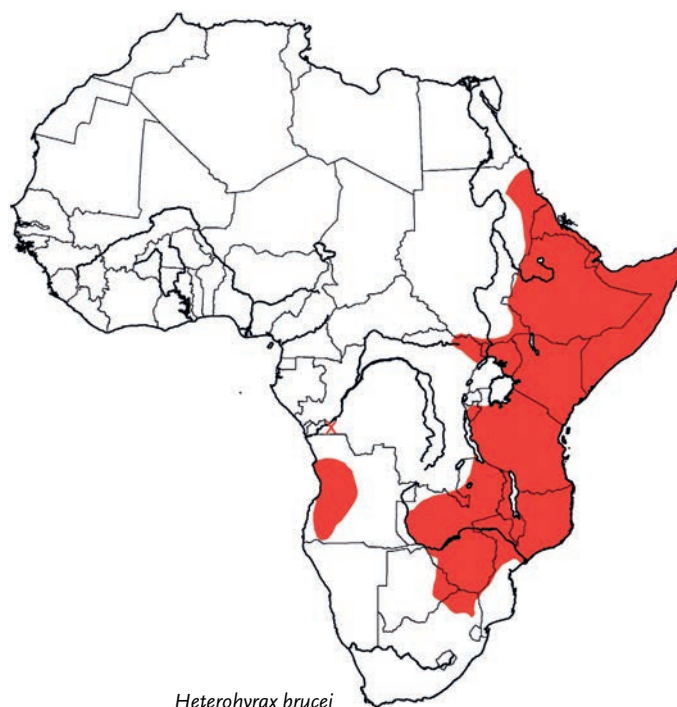
Habitat Restricted to rocky kopjes (inselbergs), krantzes and piles of large boulders with openings of at least 11 cm in height and 1 m² of floor space (Sale 1966). Kopjes provide a constant, moderate temperature (17–25 °C) and humidity (32–40%) and protection from fire (Turner & Watson 1965). Sometimes found also in forests along rivers in East Africa (H. N. Hoeck, pers. obs.). In East Africa, individuals range to 3800 m altitude (Kingdon 1971).

Bush Hyraxes are frequently found in the company of Rock Hyraxes *Procavia capensis*, sometimes even inhabiting the same rock crevices (Hoeck 1975, Barry 1994, Skinner & Chimimba 2005). This heterospecific association varies seasonally in Zimbabwe, but is especially evident during synchronous parturition in Mar (Barry & Mundy 2002).

Abundance Often conspicuous and common in appropriate habitat. Densities in the Matobo N. P. in Zimbabwe ranged from 0.5 to 1.1 individuals/ha (1.2–2.6/ha of kopje) from 1992 to 1996 (Barry & Mundy 1998), and rose to 1.9/ha (4.5/ha of kopje) in 1998 after several years of good rains (R. E. Barry pers. obs.). In Serengeti N. P., densities reached 75/ha of kopje in allopatry and 28/ha in local sympatry with the Rock Hyrax (Hoeck 1982a, 1989, H.N. Hoeck pers. obs.). Rainfall, through its effect on fecundity, appears to be the factor primarily responsible for annual fluctuations in abundance (Barry & Mundy 1998).

Adaptations A dorsal gland lies beneath a raised patch of skin approximately 1.5 cm long in adults that is surrounded by the dorsal spot of erectile hairs. The gland in sexually active, mature adults consists of lobules of glandular tissue, each lobule constituted by 25–40 alveoli of secretory epithelium surrounding a lumen (Sale 1970a). The gland is odoriferous and may function in mating and recognition of the mother by young (Sale 1965a, 1970a). During courtship the ♂ erects the hairs of the dorsal spot, exposing the dorsal gland. Pilo-erection of the dorsal spot functions as an alarm or threat signal to hyraxes and other animals nearby; dorsal hairs are erected during mating behaviour and when animals are aroused.

As with all hyraxes, the digits have flat, hoof-like nails except for the second digit of the pes, which has a long, curved claw for grooming; in addition, the four lower incisors are comb-like for grooming the fur (Hoeck 1982b). The soles have thick, rubbery pads with numerous skin glands that increase the grip for climbing (Dobson 1876, Meyer 1978, Sokolov & Sale 1981); Bush Hyraxes are agile climbers and good jumpers (Hoeck 1977b). The pupil of the eye, as in Rock Hyrax, houses an umbraculum, a shield that allows a



Heterohyrax brucei

basking individual to stare into the sun (Millar 1973) to detect aerial predators.

The weight-specific metabolic rate is low, with a thermoneutral zone of 24–35 °C (Bartholomew & Rainy 1971). Body temperature typically ranges from 35 to 37 °C, but fluctuates up to 7 °C in response to changes in air temperature. At air temperatures above 25 °C body temperature is maintained by evaporative water loss from the nostrils, soles of the feet, panting, salivating and grooming (Taylor & Sale 1969, Bartholomew & Rainy 1971). Water is conserved by the production of small volumes of urine and faeces (Maloiy & Eley 1992). The highly concentrated urine, together with faeces at communal latrines, forms a dark, crystalline residue called 'klipstreet' or 'hyraceum' (Turner & Watson 1965, Eley 1994). Little free water is consumed because of the low metabolic rate, low urine volume, and thermal lability (Maloiy & Eley 1992); most water is obtained from their food.

Huddling and stacking of individuals conserves heat (Sale 1970b). Behavioural thermoregulation is achieved by early morning and late afternoon basking on the surface, and by retreating to the rocks and shaded areas in midday to avoid heat and desiccation (Sale 1966, Taylor & Sale 1969).

Foraging and Food Bush Hyraxes are obligate browsers (DeNiro & Epstein 1978, Walker *et al.* 1978), spending more than 80% of foraging time browsing on twigs and bark of woody species and leaves, buds, flowers and fruits of trees, bushes and forbs (Hoeck 1975, 1977b, 1982c); they only very rarely consume grass. Plants most commonly foraged in Serengeti N. P. include *Acacia tortilis*, *Allophylus rubifolius*, *Cordia ovalis*, *Grewia fallax*, *Hibiscus lunarifolius*, *Ficus glumosa*, *F. ingens*, *Iboza* sp. and *Maerua triphylla* (Turner & Watson 1965, Hoeck 1975). In Zimbabwe the plants most frequently eaten were *Combretum molle*, *Elephantorrhiza goetzei*, *Flueggia virosa*, *Strychnos usambarensis*, *Kirkia acuminata*, *Croton gratissimus* and *Mundulea sericea*; *Rhus leptodictya* and *Commiphora marlothii* also are taken by juveniles (Barry & Shoshani 2000).

Activity pattern is diurnal, with most feeding occurring between 07:30 and 11:00h and between 15:30 and 18:00h (Kingdon 1971, Hoeck 1975), but occasionally to 21:00h (Turner & Watson 1965). Individuals may feed alone or in a group (Sale 1965b). Group feeding can occur up to 50 m from the centre of the colony, although casual feeding rarely occurs at distances more than 20 m from the den site. Feeding bouts average 20 min and last no longer than 35 min. Individuals can climb vertical trunks of trees and balance on thin branches (Hoeck 1977b) in order to feed on the outermost leaves (Hoeck 1982c).

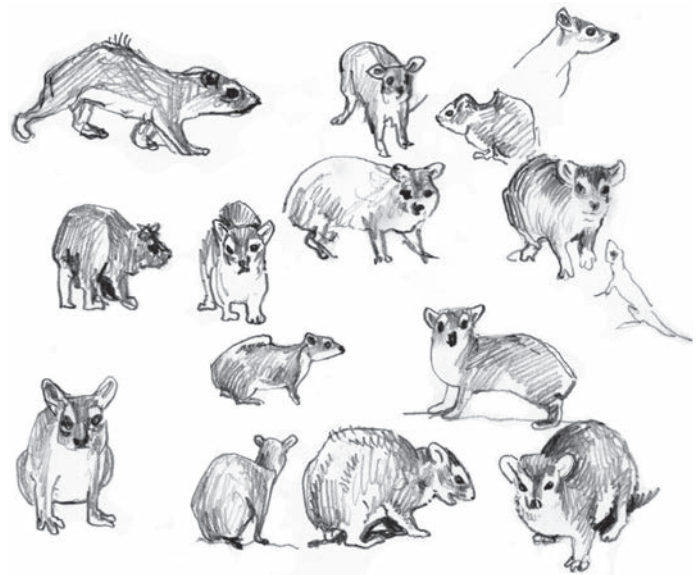
Social and Reproductive Behaviour Bush Hyraxes are gregarious (Sale 1970b), and group size can reach 34 individuals. The social unit is a polygynous harem, with a territorial adult ♂, up to 17 adult ♀♀, and juveniles (Hoeck 1977a, 1982b, Hoeck *et al.* 1982). Territorial ♂♂ threaten other ♂♂ by movement or changes in posture (raising head and shoulders), showing large incisors, grinding molars, growling, snapping, chasing or biting, and erecting hairs around the dorsal gland (Glover & Sale 1968, Hoeck *et al.* 1982). Appeasement is communicated with the hair and body flat and rump presented (Kingdon 1997). Latrines, located near sleeping quarters, are revealed as visible white stains resulting from deposits of urine rich in calcium carbonate (Estes 1991).

Bush Hyraxes have a highly structured repertoire of calls, indicating predator detection, contact, threat and distress; some of these calls are recognized by Rock Hyraxes (Hoeck 1982b) and Klipspringers *Oreotragus oreotragus* (Kingdon 1997). Loud territorial calls are frequent during the mating season (Hoeck 1982b); the territorial call of adult ♂♂ is shrill and long, lasting about 1.5 sec, and given repeatedly for up to 5 min (Hoeck 1978a).

Territorial ♂♂ copulate more often than non-territorial ♂♂ and mate preferentially with ♀♀ older than 28 months of age. Peripheral ♂♂ exhibit a dominance hierarchy and mate more often with young ♀♀ (Hoeck *et al.* 1982). The ♂ emits a shrill cry as he approaches to mate, and the ♀ erects her dorsal spot hairs. The ♂ sniffs the female's vulva, rests his chin on her rump, then slides onto her back as he makes thrusting movements followed by intromission in 3–5 minutes. A second copulation may occur after 1–3 hours (Hoeck 1978a, c).

Mothers suckle only their own young (Hoeck 1977a, 1982b). Young play with conspecifics, and sometimes with young Rock Hyraxes at heterospecific nurseries, by nipping, biting, climbing, pushing, fighting, chasing and mounting (Hoeck 1978b, Caro & Alawi 1985, Barry 1994). Young in nurseries are attended by their own mothers, and by mothers of other young, non-maternal conspecifics, or even Rock Hyrax individuals (Barry 1994). Females join the adult female group at sexual maturity (approximately 16 months of age), but male offspring disperse between 12 and 30 months of age (Hoeck 1982a). However, dispersal of ♀♀ also has been recorded in the Serengeti N. P.; dispersing ♀♀ prevent inbreeding and are mainly responsible for long-distance gene transfer between kopjes (Gerlach & Hoeck 2001).

Reproduction and Population Structure Females come into oestrus once or twice per year for up to three days, perhaps repeatedly during four weeks. Oestrus in ♀♀ in a family group is synchronized. Gestation lasts 26–30 weeks. In Serengeti N. P., two distinct birth seasons, after the long and short rains, were observed



Sketches of *Heterohyrax brucei*. Note erectile fur tract above dorsal gland.

(Hoeck 1982a). Birth pulses occur from Feb to Mar, just before the rains, in Kenya (Sale 1969), and in Mar, two months after peak rainfall, in Zimbabwe (Barry 1994).

Litter-size averages 1.6 in Tanzania (Hoeck 1982a), 1.7 in Kenya (Sale 1969) and 2.1 in Zimbabwe (Barry 1994; and see Smithers & Wilson 1979). Females may bear young every other year (Barry 1994). Young are precocious at birth and weigh 220–230 g (Skinner & Chimimba 2005). Young nurse for 1–5 months and sexual maturity is achieved at 16–17 months of age (Hoeck 1977a). Maximum recorded life-span in the wild is a little more than 11 years in ♀♀ (Hoeck 1989), similar to records in captivity (Weigl 2005).

Sex ratios ranged from 1 male : 1.6–3.2 females (Hoeck 1982a, Hoeck *et al.* 1982). However, in Zimbabwe sex ratios of captured individuals and those that were prey to Verreaux's Eagles *Aquila verreauxii* did not differ from 1 : 1 (Barry & Mundy 1998). Density of this population was estimated at 0.5–1.1 individuals/ha (1.2–2.6/ha of kopje) over a five-year period. This population comprised 19.4–27.5% juveniles, 7.2–13.1% subadults and 62.9–73.7% adults. Juvenile mortality was estimated at 52.4–61.3%.

Predators, Parasites and Diseases The principal predator is Verreaux's Eagle, with more than 90% of the diet in this species made up of Bush Hyraxes and Rock Hyraxes; in Zimbabwe adults were selected disproportionately by Verreaux's Eagles (Barry & Barry 1996). Other predators include large snakes, Leopards *Panthera pardus*, Martial Eagles *Polemaetus bellicosus* and other raptors (Turner & Watson 1965, Wilson 1969, Grobler & Wilson 1972, Smith 1977, Hoeck 1982a, Gargett 1990, Aumann & Chiweshe 1995).

Bush Hyraxes are susceptible to viral pneumonia and tuberculosis (Sale 1969). The sarcoptic mite that causes mange can heavily reduce colonies (Hoeck 1982a). Individuals can harbour the flagellate *Leishmania* (Ashford 1970, Ashford *et al.* 1973) and nematode *Crossophorus collaris* (Barry & Shoshani 2000). Their role as hosts of *Leishmania* is thought to be of epidemiological significance in the transmission of leishmaniasis to humans, especially in Ethiopian villages close to rocky inselbergs (Ashford 1970). Ectoparasites

collected from live-captured individuals in Zimbabwe included ixodid ticks (*Rhipicephalus distinctus* and *Haemaphysalis leachii*), fleas (*Procatiopsylla*), lice (*Proclignognathus*) and ear mites (*Acomatacarus*) (Barry & Shoshani 2000). Individuals often dust-bathe to remove ectoparasites.

Conservation IUCN Category: Least Concern. CITES: Not listed.

Bush Hyraxes are readily snared and, in parts of southern Africa, their pelts are used to make karosses (blankets), with resultant dramatic declines in the density of local populations. However, overall the species is widespread and present in several well-managed protected areas across its range.

Measurements

Heterohyrax brucei

TL (♂♂): 434 (382–469) mm, n = 28

TL (♀♀): 430 (325–472) mm, n = 65

WT (♂♂): 1.75 (1.40–2.10) kg, n = 57

WT (♀♀): 1.84 (1.30–2.41) kg, n = 133

Serengeti N. P. (Hoeck 1982a)

TL (♂♂): 497 (465–530) mm, n = 5

TL (♀♀): 516 (485–560) mm, n = 12

HF s.u. (♂♂): 68 (65–70) mm, n = 5

HF s.u. (♀♀): 69 (65–73), n = 12

E (♂♂): 32 (30–33) mm, n = 5

E (♀♀): 32 (29–34), n = 12

WT (♂♂): 3.01 (2.72–3.18) kg, n = 5

WT (♀♀): 3.01 (2.32–3.63) kg, n = 12

Zimbabwe (Smithers & Wilson 1979)

Key References Barry & Shoshani 2000; Hoeck 1982a, 1989; Hoeck *et al.* 1982; Skinner & Chimimba 2005.

Ronald E. Barry & Hendrik N. Hoeck

GENUS *Procavia*

Rock Hyrax

Procavia Storr, 1780. Prodr. Meth. Mamm., p. 40.

Several authors (Olds & Shoshani 1982, Schlitter 1993, Shoshani 2005) considered the genus *Procavia* to be monospecific, and the precedent set by these authors has been provisionally followed in this work. However, other authors have recognized additional species in the genus, including: Cape Hyrax *P. capensis*, Abyssinian Hyrax *P. habessinica*, Johnston's Hyrax *P. johnstoni* and Western Hyrax *P. ruficeps* (Hahn 1934, Kingdon 1971); Bothma (1971) added a fifth species, the Kaokoveld Hyrax *P. welwitschii*, which had been treated as a form of *Heterohyrax* (Shortridge 1934, Roberts 1951). More recent studies on geographic variation in mitochondrial DNA in South Africa indicate that there are at least two species within what conventionally has been regarded as *P. capensis* (Prinsloo & Robinson 1992) and mtDNA gene sequences also suggest the distinctiveness of the more northern taxa, *P. syriaca* and *P. johnstoni* (Prinsloo 1993, P. Bloomer & T.J. Robinson unpubl.). The monospecificity of the genus *Procavia* is, therefore, debatable and further research is required to resolve the taxonomy.

Like *Heterohyrax*, *Procavia* is rock dwelling, gregarious and diurnal, but unlike other hyraxes, it is predominantly a grazer, and has hypsodont molars. The length of the upper molar tooththrow M^{1-3} is much greater than that of the upper premolar tooththrow P^{1-4} (Bothma 1971).

Paulette Bloomer & Hendrik N. Hoeck



Lateral, palatal and dorsal views of skull of *Procavia capensis*.

Procavia capensis ROCK HYRAX (KLIPDASSIE)

Fr. Daman de roches; Ger. Klippschliefer

Procavia capensis (Pallas, 1766). Misc. Zool., p. 30. South Africa, Western Cape Prov., Cape of Good Hope.Rock Hyrax *Procavia capensis*.

Taxonomy Most taxonomic treatments recognize 17 subspecies (Roche 1972, Olds & Shoshani 1982, Shoshani 2005), although the status of many of these subspecies is dubious. Several of these subspecies have been elevated to the level of distinct species. Synonyms: more than 65 synonyms are listed by Shoshani (2005). The form *antineae* from Algeria, often considered as a form of *Heterohyrax*, is a *Procavia* (Hoffmann *et al.* 2008; and see Olds & Shoshani 1982). Chromosome number: $2n = 54$ (Hungerford & Snyder 1969). The X chromosome is the largest, with a submedian centromere; the Y chromosome is a very small acrocentric.

Description Small- to medium-sized, solidly built, small mammal. There is extensive variation in coat colour, which varies widely throughout geographic range from a yellowish-buff to a dark brown; this variation has been associated with mean annual rainfall patterns (Bothma 1966; and see Geographic Variation). Pelage dense, up to 25 mm long, with grizzled appearance due to banding of the hairs (dark at the base, with a lighter band of varying width and a black tip). Underfur short, soft and thick. Underparts are lighter in colour than the upper, and the hair is slightly longer and lacks the banding. Long black vibrissae (tactile hairs) 60–70 mm in length (though longer on the face) are widely distributed over the body, probably for orientation in dark fissures and holes (Sale 1970a). Rock Hyraxes have a dorsal gland (see Social and Reproductive Behaviour), surrounded by a creamy, yellow-coloured (typical of *P. c. ruficeps*) or brown to black (typical of *P. c. capensis*) margin of hairs that can be fanned when the animal is excited; this dorsal margin is not conspicuous in the Rock Hyrax of southern Africa. Females have three pairs of nipples: one pair pectoral and two pairs inguinal (Hahn 1934). Mean distance between anus and penis is 35 mm ($n = 41$) (Coetzee 1966, Hoeck 1978a, 1982b). Males and ♀♀ are approximately the same size.

Characteristic features of the skull of this species include: widely spaced and anteriorly situated eye sockets; well-developed interparietal; small tympanic bullae; premaxillae form a tubercle between the incisive foramina; coronoid process is small and recurved; hyoid bone is unusually scoop-shaped in structure. Zygomatic arches are broad and heavily built, indicative of a powerful

set of masseter muscles that operate the lower jaw (Olds & Shoshani 1982, Skinner & Chimimba 2005). In contrast to the typically hyracoid dentition, dental formula is typically $I^{1\frac{1}{2}}_2, C^{0/0}, P^{4/3}, M^{3/3} = 32$, although specimens from northern parts of Africa often have the first lower premolar present (as in Bush Hyrax *Heterohyrax brucei*). The length of the upper molar tooththrow M^{1-3} is much greater than that of the premolar tooththrow P^{1-4} (Bothma 1971). The two upper, ever-growing incisor teeth, one on each side, are separated by about the width of one tooth. The upper incisors are tusk-like, ridged or triangular in cross-section in ♂♂, but rounded in ♀♀ (Hahn 1934).

Geographic Variation As noted earlier, no fewer than 17 subspecies have been recognized (Olds & Shoshani 1982, Shoshani 2005). The validity of many of these is doubtful, while some may actually represent distinct species. Recognized subspecies on the African continent and the origin of their type localities include:

<i>P. c. antineae</i> : Algeria.	<i>P. c. mackinderi</i> : C Kenya.
<i>P. c. bamendae</i> : SW Cameroon.	<i>P. c. matschiei</i> : N Tanzania.
<i>P. c. capensis</i> : Cape of Good Hope, South Africa.	<i>P. c. pallida</i> : N Somalia.
<i>P. c. capillosa</i> : Western Bale Province, Ethiopia.	<i>P. c. ruficeps</i> (Hemprich & Ehrenberg, 1832, not Thomas, 1892): NE Sudan.
<i>P. c. erlangeri</i> : Somalia.	<i>P. c. scioanus</i> : CE Ethiopia.
<i>P. c. habessinicus</i> : NW Ethiopia.	<i>P. c. sharica</i> : C Chad.
<i>P. c. jacksoni</i> : C Kenya.	<i>P. c. syriaca</i> : 'Syria' (but possibly Lebanon).
<i>P. c. johnstoni</i> : C and S Malawi.	<i>P. c. welwitschii</i> : SW Angola.
<i>P. c. kerstingi</i> : Togo–Benin border.	

The average size of adult Rock Hyraxes varies greatly across Africa, and seems to be closely linked to average annual precipitation, which in turn affects the availability of food (Klein & Cruz-Urbe 1996); size increases up to a mean annual rainfall of 700 mm and decreases thereafter. On the other hand, Yom-Tov (1993) found size variation in the skulls of Rock Hyraxes from different regions to be positively correlated with temperature, indicating that this species conforms to Bergmann's Rule.

Similar Species

Dendrohyrax arboreus. Forests in East and central Africa south to the Eastern Cape Province of South Africa. For distinguishing characteristics of genus see Table 6, p. 151.

D. validus. Isolated montane and coastal forests of Tanzania/Kenya, as well as Pemba and Zanzibar Is. For distinguishing characteristics of genus see Table 6, p. 151.

D. dorsalis. Forests of West and central Africa. For distinguishing characteristics of genus see Table 6, p. 151.

Heterohyrax brucei. Sympatric across much of the range, though absent from West Africa. For distinguishing characteristics of genus see Table 6, p. 151.

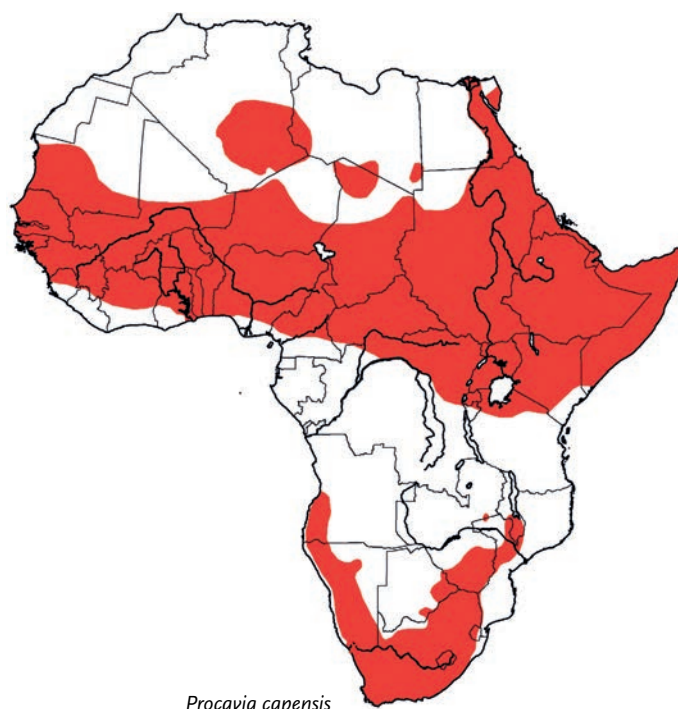
Distribution Rock Hyraxes have a wide distribution in Africa. Their range is frequently given as from Senegal and S Mauritania through S Algeria and Libya to Egypt and then southwards to southern Africa, but their distribution is very discontinuous (and see Habitat). The precise northerly limit is not clearly defined, though the species is recorded in S Algeria (see De Smet 1989, Kowalski & Rzebik-Kowalska 1991) and parts of Libya, such as the Akakus Mts and Libyan Tibesti (Hufnagl 1972). In Egypt, the species only occurs east of the Nile R. Previously unrecorded from Zambia (Ansell 1978), until Osborne's (1987) record from the south-east on the border with Mozambique. In southern Africa, Rock Hyraxes are absent from much of Botswana except the eastern parts, while in Zimbabwe they occur only in the southern parts (Smithers 1971, Smithers & Wilson 1979). There is what appears to be a very distinct break in distribution between S Malawi and N Tanzania (see Kingdon 1971, 1997; not shown in Olds & Shoshani 1982 or Skinner & Chimimba 2005), and this potential discontinuity requires further investigation.

Extralimital to the African continent, Rock Hyraxes occur in S Sinai, Oman, Yemen, Saudi Arabia (probably occurring throughout the mountainous western regions), Jordan, Israel and Lebanon (Olds & Shoshani 1982, Harrison & Bates 1991). Reports of their presence in Turkey are in error (Kryštufek & Vohralík 2001). Although the form *syriaca* was described from 'Mount Lebanon, Syria', the occurrence of this species in Syria remains equivocal (D. Kock pers. comm.).

Habitat Rock Hyraxes occupy a wide range of habitats, from arid deserts to rainforest, and from sea level to the alpine zone of Mt Kenya (3200–4300 m; Coe 1962, Young & Evans 1993). However, as their name implies, Rock Hyraxes are dependent on the presence of rocky outcrops (kopjes), mountain cliffs or loose boulders that provide suitable refuge in the form of crevices and crannies in which to shelter ('The high mountains are for the wild goats; the rocks are a refuge for the conies'; Psalms 104: 18). The nature of the refuge environment differs substantially across Africa, but rock outcrops appear to be favoured due to the extensive networks of crevices and fissures, access to safe foraging areas and good vantage points (Turner & Watson 1965, Davies 1994). Overall the refuge environment provides stability compared with the surrounding habitats where conditions are more extreme (see Adaptations). However, Rock Hyraxes have also been found in erosion gullies (e.g. in the Karoo, a habitat they have colonized recently), in culverts under roads and holes in stone-walls, and even in the holes of other species such as Aardvark *Orycteropus afer* and Suricate *Suricata suricatta* (Roberts 1951). These refuges seem to be common in areas where overpopulation of rocky habitats occurs, and at these times individuals they may traverse considerable distances between areas of suitable rocky habitat (Kolbe 1967, Lensing 1983).

In several parts of Africa (e.g. the Serengeti N. P. in Tanzania, Matobos N. P. in Zimbabwe and the northern parts of South Africa), Rock and Bush Hyraxes occur together and live in close associations on rock outcrops (Hoeck 1975, 1982a, b, Barry & Mundy 1998, 2002, P. Bloomer pers. obs.).

Abundance Rock Hyrax densities depend upon a combination of several abiotic (rainfall and availability of holes and hiding places) and biotic factors, such as interspecific and intraspecific competition for



Procapra capensis

food, predation and parasites (Hoeck 1989). In Serengeti N. P., Rock and Bush Hyraxes are the most important resident herbivores of the kopjes. The population density of Rock Hyraxes ranged from 5 to 56 animals/ha and group size varied from 2 to 26 individuals (Hoeck 1982a), while in the Matobo N. P. densities were 0.73–0.94/ha (Barry & Mundy 1998). In South Africa, major differences have been reported between regions, with density estimates ranging from 35/km² in the semi-arid Karoo N. P. (Davies 1994) to 376/km² in the Mountain Zebra N. P. (Fourie 1983). On Mt Kenya, where Rock Hyraxes are considered the most conspicuous mammals, average density has been estimated at 20–100 animals/km² (Young & Evans 1993).

As observed by Meltzer (1967) and Hoeck *et al.* (1982), larger and often more mobile family groups with associated peripheral ♂♂ (up to 80 individuals) are possible in areas where resources are favourable. Long-term observations in the Serengeti and Matobos show that Rock Hyrax populations fluctuate and while some kopjes show stable occupation over more than 20 years, small colonies are prone to extirpation (Hoeck *et al.* 1982, Hoeck 1989, Barry & Mundy 1998). These cycles of extinction and recolonization have also influenced the levels of genetic variability within and among Rock Hyrax colonies in the Serengeti, with Rock Hyraxes showing very low allelic diversity and heterozygosity at microsatellite loci (Gerlach & Hoeck 2001; and see Reproduction and Population Structure).

Adaptations Rock Hyraxes are well adapted to life in a rocky environment. Their feet are not adapted for digging, but rather the padded soles ensure increased traction and allow Rock Hyraxes to negotiate steep and often smooth rock surfaces with great ease; while the animal is running, the feet sweat, which greatly enhances its climbing ability (Sale 1970a, Fischer 1992). Hyraxes are able to move through very narrow crevices and crannies: George & Crowther (1981) found that the mean slot height (151 mm [n = 69])

through which they move is just over twice the mean skull height (66.1 mm [$n = 45$]). Hole/crevice size may bear some relation to the size of predators in the local area (Sale 1966). Rock Hyraxes are also good tree climbers.

The eye of the hyrax has a peculiar shield called an 'umbraculum' that allows them to stare at the sun; Millar (1973) has suggested this has evolved in response to predation by Verreaux's Eagles *Aquila verreauxii*. Hyraxes are the predominant prey of these eagles (Gargett 1990, Davies 1994, Barry & Barry 1996; and see Predators, Parasites and Diseases) and, being somewhat thermolabile, they often bask in the sun, thereby exposing themselves to attack (Millar 1973).

The extent to which the Rock Hyraxes meets energetic requirements depends on the interaction of ambient temperature, food quality and availability, and foraging efficiency in the presence of predators. The extent to which each of these factors influences behaviour differs on a daily and seasonal basis (Sale 1970b, Louw *et al.* 1972, Brown & Downs 2005). Basal metabolic rate, lower critical temperature and thermal conductance all vary inversely with body size, and are intimately related. The metabolic rate climbs precipitously with decreasing body weight. Hyraxes conserve energy by having a low metabolic rate and a labile body temperature. The metabolic rate is 30% lower than that predicted on a weight basis while the labile body temperature (which can drop by several degrees at night; Sale 1970a, Louw *et al.* 1972) suggests a strategy adopted by larger animals such as the Common Eland *Tragelaphus oryx*. The labile body temperature is activated by acclimatization and not by a rhythmic daily drop in body temperature (McNairn & Fairall 1984). Body temperatures are regulated mainly by gregarious huddling, long periods of inactivity, and basking. Although their physiology allows Rock Hyraxes to exist in very dry areas and use food of relatively poor quality, they are dependent on shelters (boulders and tree cavities) that provide relatively constant temperature and humidity (Turner & Watson 1965, Bartholomew & Rainy 1971, Rübsamen *et al.* 1982). Turner & Watson (1965) succinctly described kopjes as 'islands of constant environmental conditions surrounded by a sea of environmental extremes'. The Rock Hyrax form on Mt Kenya has much longer and darker fur than its lowland relatives, apparently an adaptation to extreme cold (Coe 1962).

Diet includes a significant amount of grass, and as grass is a relatively coarse material (because of phytoliths or plant opal), the molars and premolars are hypsodont, i.e. they have high crowns with relatively shorter roots. Hyraxes do not ruminate, but because of the complex morphology of their gut they are able to digest fibres as efficiently as ruminants. The morphology of the digestive tract of Rock Hyraxes differs from most other mammals. Its design is well suited for digestion of fibrous diets by means of microbial fermentation. The stomach is divided into a non-glandular part with very slow movements and a glandular part that rapidly mixes the digesta. The large intestine has two fermentation chambers: the caecum, which rapidly mixes the digesta, and the colonic sac, which efficiently, but slowly, mixes digesta. Between these chambers runs the connecting colon. No retrograde transport is observed in any part of the large intestine (Rübsamen *et al.* 1982, Bjornhag *et al.* 1994). There is no gall bladder (Olds & Shoshani 1982).

Rock Hyraxes are typically independent of free drinking water, obtaining their moisture requirements from their food. However,

when water is available, they drink regularly. Their efficient kidneys allow them to exist on a minimal moisture intake (Louw *et al.* 1972). In addition, they have a high capacity for concentrating urea and electrolytes and excreting large amounts of undissolved calcium carbonate (Rübsamen *et al.* 1982).

Food and Foraging Diet comprises a variety of grasses, forbs and shrubs, favouring new shoots, buds, fruits and berries (Sale 1965b, Hoeck 1975). In Serengeti N. P., Rock Hyraxes were observed feeding on 79 plant species. The animals have a high seasonal adaptability: in the wet season they showed a high preference for grasses (78%), but in the dry season when grasses became parched and poor in quality they browsed (57%) extensively, and more or less in proportion to the foliage density of each vegetation class. They were observed to feed on 24 grass species such as *Panicum maximum*, *Pennisetum mezianum* and *Themeda triandra* and dicotyledonous plants such as *Cordia ovalis*, *Maerua triphylla*, *Hoslundia opposita*, *Iboza* sp., *Hibiscus lunarifolius*, *Ficus ingens*, *Solanum incanum*, *Grewia fallax* and *Acacia tortilis* (Hoeck 1975).

In studies in southern Africa, Rock Hyraxes exhibited similar seasonal preferences. In Namibia, a study of diet composition from two areas found that grasses were eaten only in significant quantities at the end of the hot, dry season and at the beginning of the wet season (Lensing 1983). Some 35 grass species were consumed, including: *Antheophora pubescens*, *Aristida congesta*, *Cynodon dactylon*, *Enneapogon scaber*, *E. brachystachyus*, *Eragrostis trichophora*, *Stipagrostis hirtigluma* and *S. uniplumis*. The most important dicotyledonous plants in the diet were *Acacia mellifera* and *Ziziphus mucronata*. Fourie & Perrin (1989) found that although they used a wide variety of plant species, ten species constituted more than 80% of the dietary biomass: *Acacia karroo*, *Olea europaea*, *Felicia filifolia*, *Grewia occidentalis*, *Cussonia paniculata*, *Maytenus heterophylla*, *Pentzia* spp., *Clematis brachiata*, *Lycium oxycarpum* and *Diospyros lycoides*. Leaves of trees and shrubs formed the major portion of the diet (being browsed throughout the year), whereas grazing was largely dependent on the seasonal availability of grasses. Examination of $C^{13} : C^{12}$ ratios of carbonate and collagen fractions of bone (DeNiro & Epstein 1978) and microwear patterns of the molariform teeth (Walker *et al.* 1978) confirm that Rock Hyrax switch between grazing and browsing at different times of the year. Rock Hyraxes are thus highly adaptable in contrast to the more specialist browsing Bush Hyraxes. In areas of sympatry, differential feeding behaviour of the two species, especially in the wet season, may limit interspecific competition (Turner & Watson 1965). However, Hoeck (1975) did not find clear niche separation between the two species and reported no instances of interspecific aggression even during the dry season when both species browse.

Sale (1965c) reported an instance of Rock Hyraxes feeding on a poisonous plant *Phytolacca dodecandra*, and they are also known to eat *Lobelia* spp. that are also toxic. However, there are a number of plant species that they avoid, such as *Anthoxanthum nivale*, *Sedum ruwenzoriense* and *Carduus keniensis* (Coe 1962, Young & Evans 1993).

Rock Hyraxes are predominantly diurnal, though they are sometimes active at night. It is not unusual to find them feeding at any time of the day, although there are peaks in the mid-morning and mid-afternoon during warm periods. In winter, peak periods are later, or may become a single extended period (Sale 1965b,

Hoeck 1975, Davies 1994, Brown & Downs 2005). Feeding activity mostly comprises group feeding during which the group often assumes a fan-like orientation that may serve to avoid conflict or to spot predators (Sale 1965b). Often a few individuals act as sentinels during group feeding because feeding away from their refuges makes them vulnerable to attack by predators (Davies 1994). Group feeding is intensive, usually only lasting on average 20 min. Rock Hyraxes usually do not spend more than two hours feeding each day (Sale 1965b). Kingdon (1997) suggested that the disproportionately large jaws are an adaptation to enable intensive feeding. Davies (1994) observed that the daily average distance travelled during group feeding was 169–572 m in the Karoo N. P. (South Africa), but Rock Hyraxes seldom feed more than 15–20 m away from shelter. Kotler *et al.* (1999) showed that the sentinel behaviour during group feeding can allow hyraxes to feed further away from their crevices. Casual feeding by single individuals occurs more sporadically and at any time of the day, usually only a short distance away from the protection of crevices (Sale 1965b, Davies 1994).

Social and Reproductive Behaviour Rock Hyraxes are gregarious (Sale 1970a), living in cohesive and stable family groups or colonies numbering as many as 80 individuals and consisting of 3–7 related adult ♀♀, one adult territorial ♂, dispersing ♂♂, subadult ♀♀ and the juveniles of both sexes. Their numbers vary depending on the size of the kopje: smaller kopjes or rocky outcrops support only a single colony, but larger kopjes may support several family groups, each occupying a traditional range.

There are four classes of mature ♂: territorial, peripheral, and early and late dispersers. Territorial ♂♂ are the most dominant, and repel all intruding ♂♂ from an area largely encompassing the females' core area. Their aggressive behaviour towards other adult ♂♂ escalates particularly in the mating season (when the weight of their testes increases 20-fold; Millar 1972) and when they monopolize all receptive ♀♀. Peripheral ♂♂ are those unable to settle on small kopjes, but on large kopjes they can occupy areas on the periphery of the territorial male's territories. Males are solitary, and the highest ranking among them takes over a female group whenever a territorial ♂ disappears; some studies have reported regular replacement of the dominant ♂. The females' home-ranges are not defended and may overlap. Rarely, an adult ♀ from outside a group will be incorporated into the family group (Hoeck 1982a, Fourie & Perrin 1987a, Davies 1994).

The early dispersers – the majority of juvenile ♂♂ – leave their birth sites at 16–24 months old, soon after reaching sexual maturity. The late dispersers leave a year later, but before they are 30 months old. Individual Rock Hyraxes have been observed to disperse over a distance of at least 2 km, although it has been suggested that gene flow over distances greater than 10 km is unlikely (Hoeck 1982a, b, 1989). However, the further a dispersing animal has to travel across open country, where there is little cover and few hiding places, the greater its chances of dying, either through predation or as a result of its inability to cope with temperature stress (Hoeck 1982a, b, 1989, Gerlach & Hoeck 2001; and see Predators, Parasites and Diseases). Fourie & Perrin (1987a) reported shorter dispersal distances, indicating that the nature of the rocky habitat and the intervening vegetation between habitat islands would strongly influence dispersal distance.

More than 90% of the day is spent resting. Heaping, where several individuals are stacked on top of each other, is observed inside crevices and also outside during very cold conditions. Young can often be observed showing this kind of behaviour with their mother. Even though it can also be observed inside crevices, huddling behaviour is the most common interaction during group resting. This is especially observed early in the morning when the hyraxes first emerge from their crevices to sun themselves. During warmer times of the day, inactive periods consist of solitary resting (Sale 1970b). Hyrax behaviour is directly linked to daily temperature fluctuations and their physiology (Sale 1970b, and see Adaptations). Some of the resting time is spent self-grooming using the lower incisors and the curved claw on the second digit. Grooming and dust-bathing help rid Rock Hyraxes of ectoparasites (see Predators, Parasites and Diseases). Rock Hyraxes urinate and defaecate in latrines. As they have the habit of urinating in the same place, crystallized calcium carbonate forms deposits that whiten the cliff faces below latrines. The precipitated calcium oxalate where urine soaks through the dung heaps and then crystallizes where it seeps out, was used as medicine (hyraceum) by several South African tribes and by European settlers (Hahn 1934, N. Fairall pers. comm.).

Although Rock Hyraxes are gregarious, low levels of intraspecific aggression play an important role in maintaining colonial life (Olds & Shoshani 1982, Kingdon 1997). Visual communication in the form of flaring of the hairs surrounding the dorsal gland and several typical postures is observed. Piloerection of the dorsal spot can either signal alarm (45°) or threat (90°) (Sale 1970a, Fourie & Perrin 1987a). These clear signals and stereotypical appeasement behaviour limit serious aggressive encounters between individuals (Sale 1970b); agonistic behaviour is mostly observed between ♂♂ during the breeding season (Hoeck *et al.* 1982, Fourie & Perrin 1987a). Olfactory communication functions during reproduction and to establish mother–infant bonds (Sale 1970b). Fourie (1977) recorded 21 vocal and four non-vocal sounds. The multitude of grunts, growls, snarls, spits, snorts and squeals are used in a variety of contexts, but most commonly in showing aggression, appeasement or defensive retreat. The alarm call in the form of a sharp bark is characteristic and differs from that of *Heterohyrax* and *Dendrohyrax*. A repetitious bark appears to function in transmitting territorial and sexual signals. The alarm calls used by the sentinels, especially during group feeding, appear to be specific to the particular threat (Sale 1965b, Davies 1994). Males are more vocal during the breeding season and they also use dorsal gland secretions for signalling (Hoeck 1978a, Kingdon 1997). During this time the dominant territorial ♂♂ monitor urine deposits routinely in search of receptive ♀♀ and most copulations are observed between the territorial ♂♂ and adult ♀♀; peripheral ♂♂ most often mate with subadult ♀♀ (Hoeck *et al.* 1982, Fourie & Perrin 1987a). Fourie & Perrin (1987a) observed receptive ♀♀ approaching the dominant ♂ and signalling their readiness to mate through flaring of the dorsal spot hairs, sniffing the male's anogenital region and presentation of their hind-quarters. Hoeck (1978a) observed ♂♂ initiating mating through a mating call, 'weaving head movements' and dorsal spot flaring, followed by brief copulation. Hoeck *et al.* (1982) reported instances where ♀♀ mated with more than one territorial ♂ and with peripheral ♂♂.

The young are born inside the rock crevices, but despite initial bonding with the mother (Sale 1970a), parental care is minimal

(Olds & Shoshani 1982). Juveniles form nursery groups that often engage in social play; both juveniles and subadults have a much larger area of activity compared with the territorial and peripheral adults (Fourie & Perrin 1987a).

Where Rock and Bush Hyraxes occur together, they huddle in single mixed groups in the early mornings after spending the night in the same holes. They also use the same urination and defaecation sites. Parturition tends to be synchronous (Barry 1994). Newborns are greeted and sniffed intensively by members of both species, and they form a nursery group and play together. Most of their vocalizations are also similar (Hoeck 1982b). However, Bush and Rock Hyraxes do differ in key behavioural patterns. They do not interbreed because their mating behaviour is different and they have a different reproductive anatomy. The male territorial call, which might function as a 'keep out' sign, is also different (Hoeck 1978a).

Reproduction and Population Structure There is a single breeding season per year and for both ♂♂ and ♀♀ this represents a very short period of sexual activity (Millar 1971). In South Africa, Fourie & Perrin (1987b) reported male sexual activity from Feb–May with a peak in Apr; testes mass increased dramatically during this time (with a more than ten-fold difference between active and quiescent ♂♂). Females have a mean oestrous cycle length of 13 days ($n = 12$; Gombe 1983) and Hoeck *et al.* (1982) observed that ♀♀ may cycle several times over a seven-week period. Gestation is 212–240 days, which is exceptionally long relative to body size. It may represent a plesiomorphic characteristic given the much larger body sizes of some of the ancestral hyrax species or it may reflect the adaptive advantages of producing precocial young (Millar 1971).

Within a family group, the pregnant ♀♀ all give birth within a period of about three weeks; this birth synchrony appears to be a mechanism to avert predation by predators such as eagles (Barry 1994, Barry & Barry 1996). Some authors have suggested that parturition may be linked to rainfall or photoperiod. For example, in most areas in South Africa the breeding season is in late summer (with a peak in Apr), but with a shift from earlier conception in the south-west (Jan–May) relative to the north-east (May–Jul). This results in a shift in births from the end of Aug in the south-west to the end of Mar in the north-east (Millar 1971, Stuart & Stuart 1984, Fourie & Perrin 1987b). In Serengeti N. P., Hoeck (1982a) recorded births from Mar–May while Mendelssohn (1965) found that most of the births in Israel occurred in Apr, supporting photoperiod as one of the proximate causes. Stuart & Stuart (1984) suggested that the timing of the breeding season reflects adaptation to more favourable temperatures for the newborn young. In the arid areas of NW South Africa they reported conception from Sep–Nov and parturition from May–Jul.

The number of young per ♀ varies between 1 and 4 (mean 2.4) in Serengeti N. P. (Hoeck 1982a). In southern Africa, a ♀ with six embryos has been collected, and mean litter-sizes recorded include: 3.3 in the Western Cape (Millar 1971); 2.7 in Mountain Zebra N. P., Eastern Cape ($n = 95$) (Fourie & Perrin 1987b); 2.4 in the Free State (range 1–5; $n = 49$) (Van der Merwe & Skinner 1982); and 2.37 in Zimbabwe ($n = 19$) (Barry 1994). Sale (1969) and Fourie & Perrin (1987b) suggested an increase in litter-size with latitude while several authors demonstrated a relationship between litter-size and female age; first breeders have only 1–2 young (Fairall *et al.*



Sketches of *Procavia capensis mackinderi*.

1986), ♀♀ 2–8 years of age produce the largest litters, followed by a decline in older ♀♀ (Fourie & Perrin 1987b). Millar (1971) indicated that nutritional conditions would affect both litter-size and age at first breeding.

Young are fully developed at birth, fully haired and with eyes open. They are capable of agile movement within a few days and can ingest solid food within a few weeks (Mendelssohn 1965). Birth-weight varies to some degree depending on the number in the litter (mean: 195 g) and the average litter weight (581 g) is high relative to female body weight (Millar 1971). Suckling young assume a strict teat order (Hoeck 1977a). Weaning occurs at 1–5 months (mean: 3 months, Millar 1971), though Young & Evans (1993) mention one individual still suckling at nine months. Both sexes reach sexual maturity at about 16–17 months of age (Millar 1971, Hoeck 1982a). Millar (1971) reported some ♀♀ breeding at five months of age and according to Fourie & Perrin (1987b) ♂♂ reach sexual maturity at 28–29 months. The findings of the latter study suggest that there is a difference between physiological and behavioural sexual maturity in ♂♂; the dominant ♂ effectively prevents mating by sexually mature young ♂♂.

The sex ratio is equal at birth and up to two years of age, whereafter ♀♀ sometimes tend to outnumber ♂♂ (Millar 1971, Hoeck 1982a, Fourie & Perrin 1987a). A high level of juvenile mortality has been recorded by Fourie (1983) and Davies (1994) and appears to be an important factor controlling the dynamics of hyrax populations. Adult ♀♀ live significantly longer than adult ♂♂ and may reach an age of over ten years (Hoeck 1982a, Kingdon 1997); in captivity, animals have lived to more than 14 years (Weigl 2005).

Upon sexual maturity, ♀♀ usually join the adult female group, while ♂♂ disperse before they reach 30 months. Greenwood (1980) proposed that most mammalian species display male-biased dispersal. This was confirmed for Rock Hyraxes by observation in several studies (Hoeck 1982a, 1989, Hoeck *et al.* 1982, Fourie & Perrin 1987a, Davies 1994), and although adult dispersal was also recorded, juvenile male dispersal appeared to be of particular importance. However, preliminary results involving microsatellite

DNA analysis of Rock Hyraxes in Serengeti N. P. showed no sex bias and revealed extremely low levels of genetic variation within and between neighbouring colonies (Gerlach & Hoeck 2001). Prinsloo & Robinson (1992) also suggested, on the basis of the patterns of geographic variation of maternally inherited mtDNA, that there are high levels of historical connectedness among localities in South Africa. Additional molecular markers are needed to reconcile direct and indirect estimates of dispersal and gene flow.

Although occupancy of some habitat islands remains stable over time (Hoeck 1982a, Hoeck *et al.* 1982), most regions are characterized by fluctuations in the numbers of Rock Hyraxes and probably function as metapopulations with local extinction and recolonization events. This is reflected by colonies occupying kopjes in the Serengeti, where low levels of allelic diversity and heterozygosity at eight hyrax-specific microsatellite loci suggest the influence of metapopulation dynamics and population bottlenecks (Gerlach & Hoeck 2001). Davies (1994) suggested that the dynamic population structure of Rock Hyraxes is a consequence of their unpredictable environment.

Predators, Parasites and Diseases Rock Hyraxes form the most important prey in the diet of Verreaux's Eagle *Aquila verreauxii* (Gargett 1990). Because ♂♂ are forced to disperse when mature, one- to two-year-old (as well as old) ♂♂ are particularly at risk of predation. Boshoff *et al.* (1991) found that juveniles constituted 11–33% of the remains of *Procavia* in the nests of Verreaux's Eagles in the Western Cape, and Barry & Barry (1996) found that juveniles comprised 18% of remains in the Matobo N. P., Zimbabwe. Rock Hyraxes also form a main component of the diet of Crowned Hawk-eagles *Stephanoetus coronatus* (Boshoff *et al.* 1994). Other predators include Martial Eagles *Polemaetus bellicosus* and Tawny Eagles *Aquila rapax*, Leopards *Panthera pardus* (particularly on Mt Kenya), Lions *P. leo*, Caracals *Caracal caracal*, jackals *Canis* spp., Spotted Hyenas *Crocuta crocuta* and snakes (Coe 1962, Turner & Watson 1965, Palmer & Fairall 1988).

There is an extensive literature on the variety of external parasites (ticks, biting and sucking lice, mites and fleas) that have been collected from Rock Hyraxes (see for example, Hoogstraal & Wassef 1981, Horak & Fourie 1986, and references therein). In the study by Horak & Fourie (1986), only ten individuals of some 10,000 ticks recovered belonged to species that could infest domestic livestock. Dust-bathing probably helps keep parasite burdens relatively low. Rock Hyraxes also harbour a number of internal parasites, including nematodes and cestodes (see, for example, Fourie *et al.* 1987), which could play a role in hyrax mortality in some areas. Fourie *et al.* (1987) investigated the seasonal variation in the densities of both ecto- and endo-parasites on Rock Hyraxes in the Mountain Zebra N. P. in South Africa, and found that ♀♀ showed significant seasonal differences in tick and biting lice densities, with these being highest in the summer (also the time of the highest tick densities). This difference between the sexes was related to social structure (♀♀ being more social than ♂♂, making them vulnerable to increased infestation rates) and to the decreased physiological condition of ♀♀ (see Fourie & Perrin

1985) during the summer. No significant seasonal differences were noted in endoparasite densities.

In Serengeti N. P. the 'sarcoptic mite', which causes mange, is an important cause of mortality for Rock Hyraxes (Hoeck 1982a), and ♀♀ that matched these symptoms have been seen on Mt Kenya (Young & Evans 1993). In Kenya and Ethiopia, Rock Hyraxes might be an important reservoir for the parasitic disease leishmaniasis (Ashford 1970).

Conservation IUCN Category: Least Concern. CITES: Not listed.

Although this species is subject to some localized hunting and may have been extirpated in some small localities, it has a wide distribution on the African continent (and extraliminally). Currently it is present in a number of protected areas across its range, and is generally not believed to be at any risk of extinction in the wild.

Measurements

Procavia capensis johnstoni

HB (♂♂): 484 (395–578) mm, n = 41

HB (♀♀): 496 (439–539) mm, n = 33

HF (sexes combined): 656 mm, n = 63

E (sexes combined): 320 mm, n = 63

WT (♂♂): 3.0 (1.8–4.5) kg, n = 66

WT (♀♀): 3.2 (2.0–5.4) kg, n = 57

WT (subadult): 1.3 (0.2–2.6) kg, n = 86

Serengeti N. P., Tanzania (Hoeck 1982a, H. N Hoeck unpubl.)

Procavia capensis capensis

TL (♂♂): 476 (376–560) mm, n = 26

TL (♀♀): 499 (415–628) mm, n = 31

HF c.u. (♂♂): 67 (56–91) mm, n = 26

HF c.u. (♀♀): 66 (62–78) mm, n = 30

E (♂♂): 32 (28–37) mm, n = 25

E (♀♀): 32 (27–38) mm, n = 28

WT (♂♂): 2.8 (1.5–4.3) kg, n = 10

WT (♀♀): 3.26 (1.8–4.3) kg, n = 12

Former Transvaal, South Africa (Rautenbach 1982)

Smithers & Wilson (1979) give the average weight for ♂♂ as 3.52 kg (range 3.21–4.65, n = 10) and for ♀♀ as 3.09 kg (range 2.47–3.46, n = 10).

Procavia capensis

GLS (♂♂): 92.0 (83.5–104.2) mm, n = 80

GLS (♀♀): 89.8 (79.9–98.6) mm, n = 99

GWS (♂♂): 54.0 (49.1–64.9) mm, n = 86

GWS (♀♀): 51.8 (41.7–60.2) mm, n = 99

Southern Africa (Yom-Tov 1993)

Key References Barry & Mundy 1998, 2002; Bothma 1971; Coe 1962; Fourie & Perrin 1987a, b; Hoeck 1975, 1982a, b, 1989; Millar 1971, 1973; Rübsamen *et al.* 1982; Sale 1965b, 1966, 1970a, b.

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Superorder TETHYTHERIA

Superorder Tethytheria McKenna, 1975. In: *Phylogeny of the Primates* (Luckett W. P. and Szalay F. S., eds), p. 42.

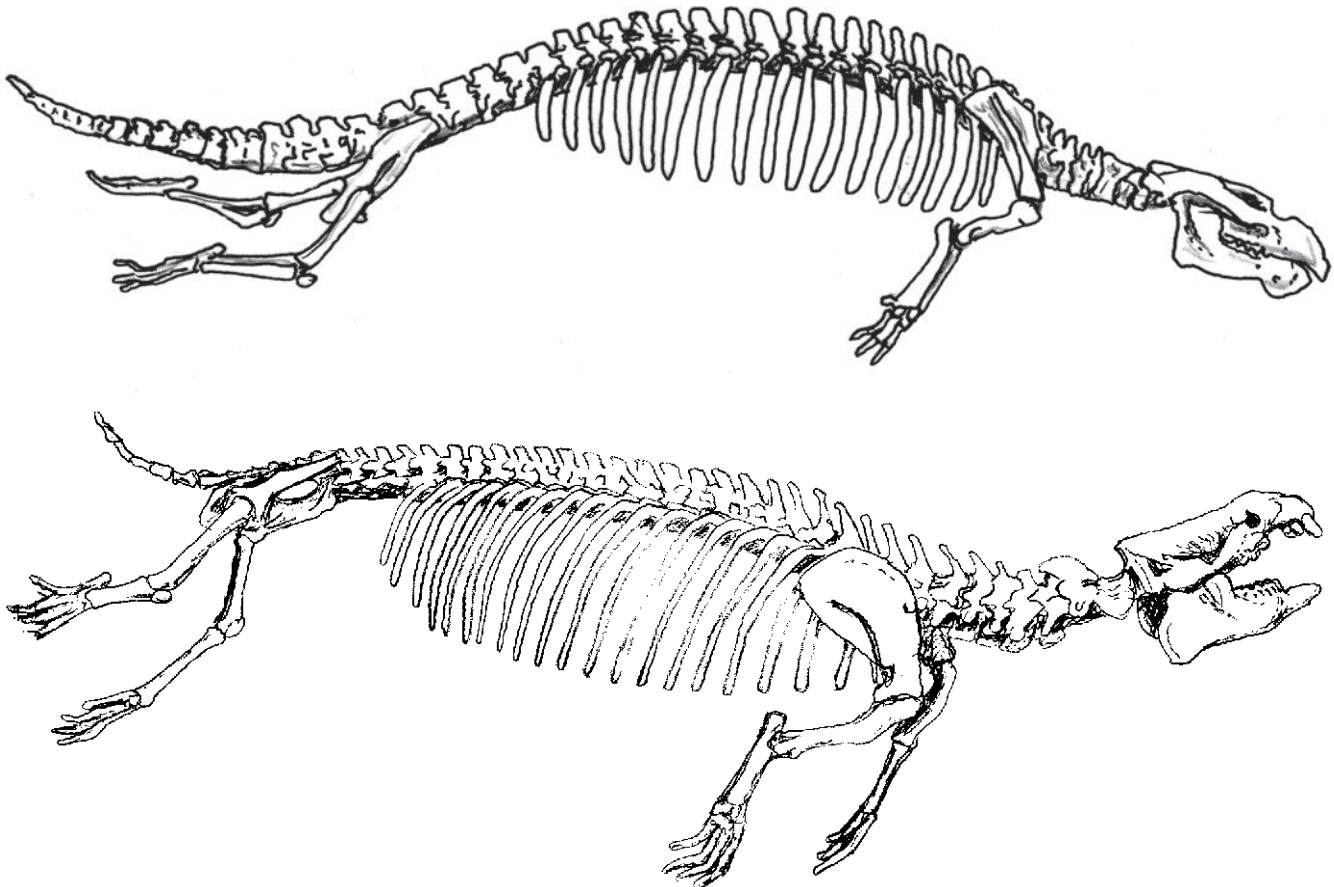
The superorder Tethytheria contains the extant orders Proboscidea and Sirenia and the extinct order Desmostylia; the extinct order Embrithopoda and family Anthracobunidae are often included as well (Gheerbrant *et al.* 2005a). Like so many other supraordinal nomina currently being used in placental systematics, Tethytheria is not only a phylogenetic hypothesis but also a biogeographic hypothesis, and implies that the origin and early evolution of tethytherians occurred in or around the ancient Tethys Sea, which isolated Afro-Arabia from Europe and Asia throughout the Palaeogene.

A close relationship of proboscideans and sirenians to the exclusion of Hyracoidea has long been suggested by various forms of morphological data and was first articulated by Henri M. D. de Blainville (who used the now-abandoned taxon ‘Gravigrades’) in 1834. Surprisingly, with the advent of molecular systematics this phylogenetic hypothesis has not come to be similarly well supported by genomic data. Though one large DNA dataset supports Tethytheria (Poulakakis & Stamatakis 2010), another dataset incorporating DNA and amino acids supports a Hyracoidea+Proboscidea clade (Meredith *et al.* 2011). A single retroposon provides support for a hyracoid–sirenian clade, but none have been found that support

Tethytheria (Nishihara *et al.* 2005, Poulakakis & Stamatakis 2010). Furthermore, some morphological features that were thought to be tethytherian synapomorphies (Fischer 1990) have been revealed as probable convergences by a better early fossil record of proboscidean and sirenian evolution (Court 1994, Gheerbrant *et al.* 2005b).

The remaining morphological evidence for Tethytheria is nevertheless still compelling, and includes both skeletal and soft-tissue evidence (Fischer & Tassy 1993, Shoshani 1993). There is also some palaeontological evidence for a shared semi-aquatic tethytherian ancestor, as the earliest proboscideans, such as *Eritherium*, *Phosphatherium* and *Daouitherium*, are from marine deposits, and morphological adaptations and isotopic signatures for a semi-aquatic existence are also evident in later genera such as *Moeritherium* (Liu *et al.* 2008). Desmostylians were clearly dedicated to such a life-style. In light of this evidence, a closer relationship of hyracoids and proboscideans, or of hyracoids and sirenians, would imply that ‘tethytherian’ features are either primitive within Paenungulata, or evolved convergently among early sirenians and proboscideans.

Erik R. Seiffert



Two early aquatic tethytheres: skeleton of an extinct quadrupedal sirenian, *Pezosiren* (above), and the skeleton of a proboscidean, *Moeritherium* (below).

Order PROBOSCIDEA – Elephants

Proboscidea Illiger, 1811. Prodrum systematis mammalium, p. 96.

Elephantidae (1 genus, 2 species)	Elephants	p. 176
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Traditionally (since Illiger 1811) the category or rank of ‘order’ has been used for Proboscidea. McKenna & Bell (1997), following a cladistic classification, proposed a new category (‘parvorder’) for Proboscidea. For reasons of stability, we retain the ordinal category here, even though the category parvorder conveys a cladistic message.

The order Proboscidea consists of approximately ten families, 45 genera and 185 species and subspecies. Of these only two or three species are living, all classified in the family Elephantidae. The living elephants include the African and the Asian species. The African group incorporates the Savanna (or African Bush) Elephant *Loxodonta africana* and the Forest Elephant *L. cyclotis*, although this taxonomy is not agreed upon by all scientists.

At the time when Illiger (1811) coined the named Proboscidea, only the living elephants, the extinct American mastodon (named ‘*Elephas americanus*’ by Kerr in 1792) and the woolly mammoth (named ‘*Elephas primigenius*’ by Blumenbach in 1799) were well known. Illiger used the familiar proboscis or trunk as the distinguishing character for this order of mammals (‘proboscis’ is of Greek origin and it means ‘before the mouth’). Today, we recognize some extinct proboscidean species, none of which is believed to have possessed a proboscis, for example *Moeritherium lyonsi*, *Phosphatherium escuilliei*, *Daouitherium rebouli* and *Numidotherium koholense*. It is, therefore, necessary to define the synapomorphies or shared-derived characters for all proboscideans, extinct and extant. Four proboscidean synapomorphies are recognized by Gheerbrant *et al.* (2005): (1) a well-developed zygomatic process of the maxillary bone, which contributes significantly to the ventral of the orbit and the zygomatic arch (in other mammals the maxilla contributes little or none to the ventral border of orbit); (2) internally, the periotic bone has a relatively large size of the mastoid portion (*pars mastoidea*) compared with the *pars cochlearis*; (3) the hypoconulid cuspid of the lower teeth is in the labial position (in other mammals the hypoconulid is either at the centre or on the lingual side of the tooth); and (4) a retracted optical foramen in the orbitotemporal fossa towards the posterior of the cranium. Note that in Gheerbrant *et al.*’s (2005) analysis members of extinct Anthracobunidae are not closely related to Proboscidea.

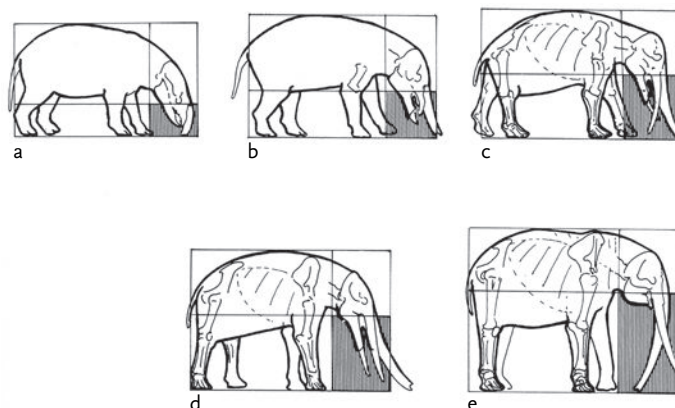
Classification of the Proboscidea is incomplete mostly because of the paucity of post-cranial elements for early members of this order, and thus there are not enough distinguishing characters assigned to early taxonomic units within the order. Shoshani *et al.* (2001) proposed the name Plesielephantiformes as a sister taxon to Elephantiformes; this suggestion was incorporated in one of the most recent classifications of the Proboscidea (Shoshani & Tassy 2005). In this scheme, the position of Moeritheriidae remains uncertain. The unity of Plesielephantiformes was based on the lophodonty of cheekteeth in members of Numidotheriidae, Barytheriidae and Deinotheriidae, a hypothesis that is not supported for all members of Plesielephantiformes, based on a parsimony analysis by Gheerbrant *et al.* (2005). None the less, E. Gheerbrant (pers. comm.) proposes that lophodonty of cheekteeth may be a synapomorphy

for Plesielephantiformes, with some extra homoplasies (with the currently available characters, the most parsimonious solution is that lophodonty is a primitive trait for Proboscidea).

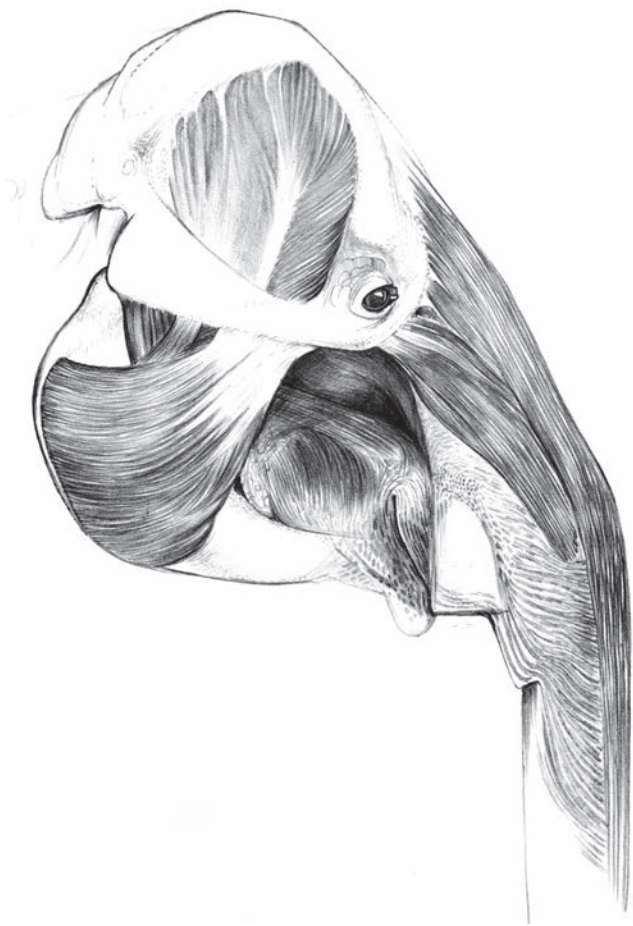
Within the Proboscidea there are shared-characters for the clade of Elephantimorpha, that is, Mammutida (true mastodons) and Elephantida (gomphotheres, stegodontids and elephantids). These characters are typical of the living elephants and they include: forwards displacement of premolars and molars as though they were moving on a slow conveyor belt, columnar arrangement of long bones in limbs (graviportal, in most taxa), and a well-developed proboscis (Shoshani 1996, Tassy 1996). Elephantimorpha probably originated in Africa during the late Oligocene, about 28–27 mya (Kappelman *et al.* 2003, Sanders *et al.* 2004, Shoshani *et al.* 2006b). Forwards displacement of cheekteeth and graviportal adaptation are easily detected on bones and teeth of extinct taxa, yet a soft tissue like the proboscis has to be inferred. The presence of a developed proboscis in extinct forms is conjectured based on the elevated position of the single external naris, the dorsal contact between premaxillae and frontal bones, that the premaxillae make an ascending process for the mesethmoid cartilage in the nasal fossa, and the large infraorbital canals on either side of the face.

Among early members of Proboscidea, Deinotheriidae may have had graviportal limbs (Osborn 1936); however, recent data may lead to different interpretations. A convergent evolution between Deinotheriidae and more advanced proboscideans cannot be definitely ruled out. Deinotheres are also believed to have had a trunk (possibly also evolved in convergence: but note there is no ascending process of the premaxillae in the nasal fossa). Although often depicted in older literature with a developed proboscis (Osborn 1936), Harris (1975), Tassy (1998) and Markov *et al.* (2001) proposed that a shorter trunk than that of the living elephants was probably more likely possessed by deinotheres.

Evolutionary trends of proboscideans from the earliest fossilized member (*Eritherium azzouorum* that lived in the late Palaeocene



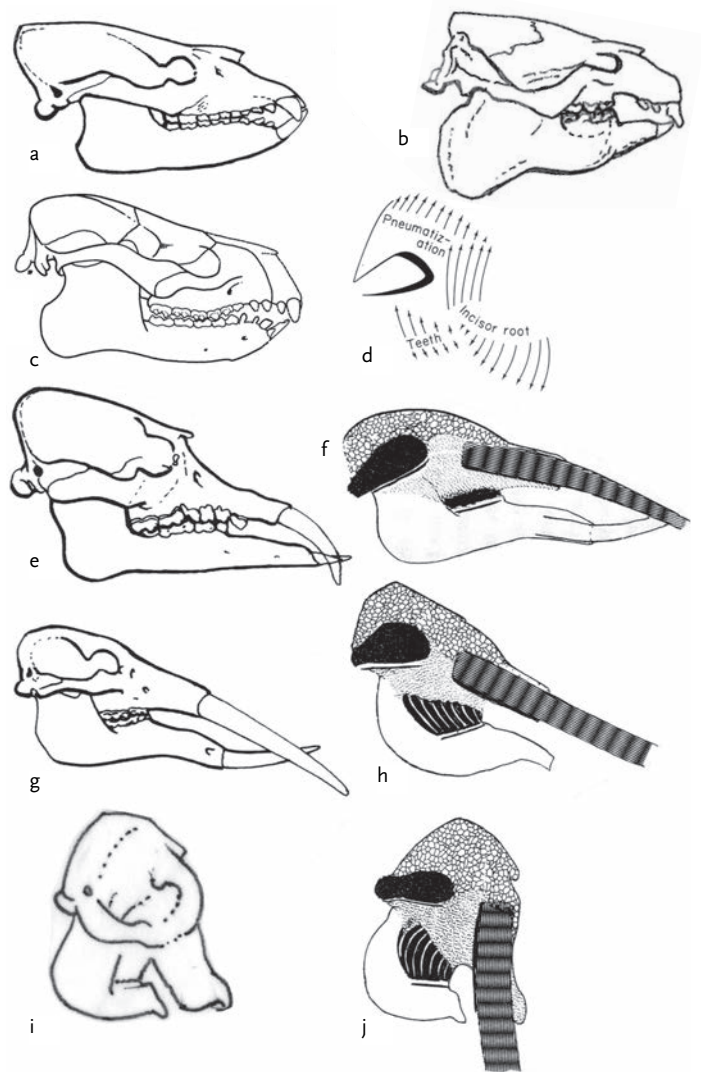
Changes of proportions in the evolution of Proboscidea. Horizontal line indicates rising level of mouth. Texture indicates principal feeding zone. a. Reconstruction of ancestral proboscidean. b. *Phiomia*. c. *Gomphotherium*. d. *Stegotetrabelodon*. e. *Loxodonta africana*.



Myology of *Loxodonta africana* head.

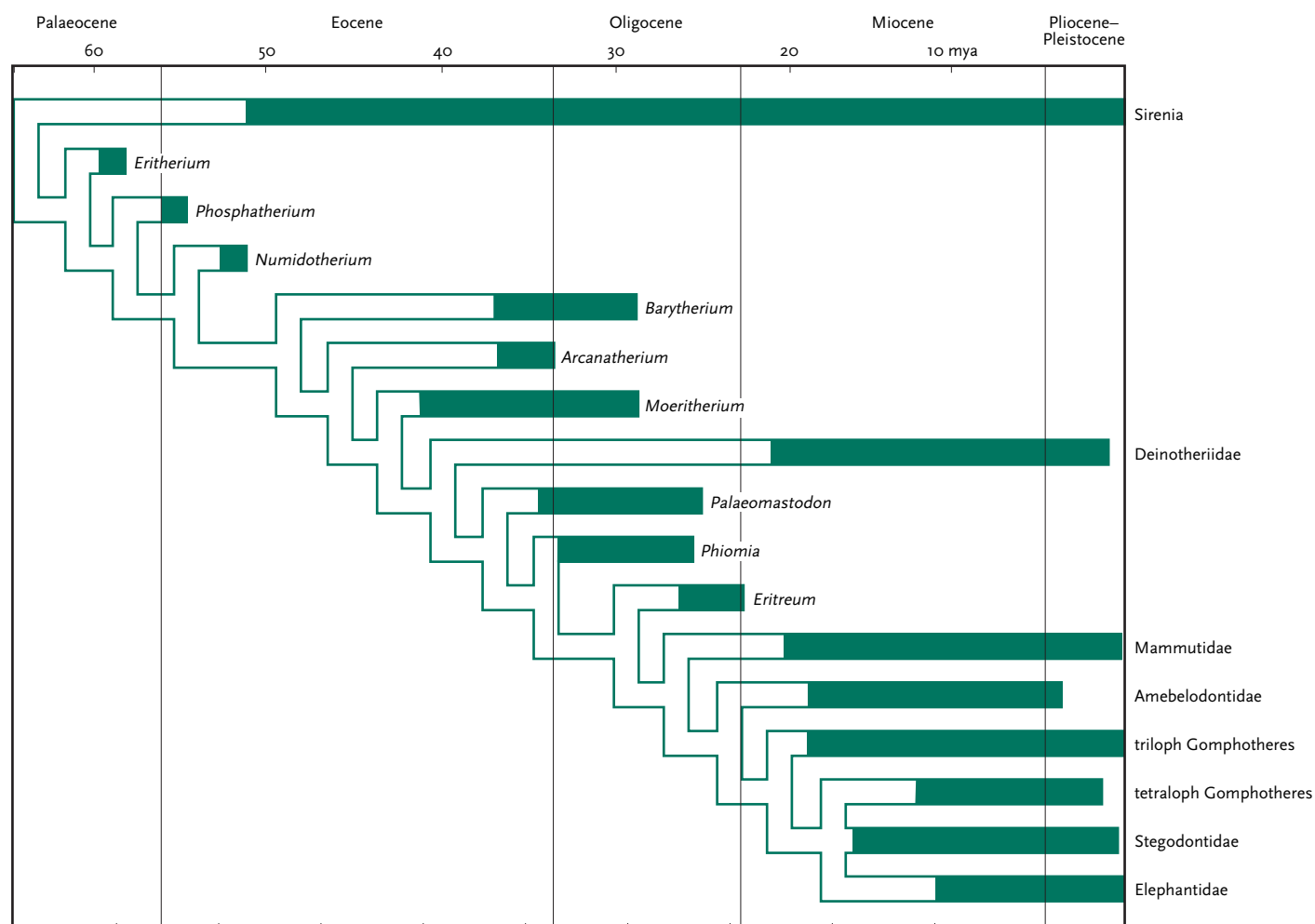
epoch, about 60 mya; Gheerbrant 2009) to the present, include: increase in the number of lophs or plates on premolars and molars; shift from regular tooth replacement (deciduous teeth to permanent teeth) to horizontal displacement of premolars and molars; increase of tusk size (proboscideans have the largest teeth of any mammals, living and extinct); development of a trunk, or proboscis; increase of trunk length; and a ten-fold increase in the encephalization quotient (EQ). All these trends can be summarized as – overall increase in body size. Evolutionary processes incorporate gigantism (over 4 m shoulder height) and dwarfism (only 1 m tall), co-evolution of infrasonic communication and the ability to store water in the pharynx (Shoshani 1998). *Phosphatherium escuilliei* was about the size of a dog (10–15 kg), but it was not a dwarf; it did not have a trunk, tusks, nor horizontal displacement of premolars and molars. Nevertheless, *Phosphatherium* was a proboscidean since it possessed unique proboscidean characters such as a well-developed zygomatic process of the maxillary bone (Gheerbrant *et al.* 2005). The elephant adult brain averages 4783 g, the largest among living and extinct terrestrial mammals; during evolution, EQ has increased by ten-fold, 0.2 for extinct *Moeritherium*, ~2.0 for extant elephants (details in Shoshani *et al.* 2006a).

Despite our increasing knowledge of the early history of the Proboscidea, there is still much uncertainty concerning the place of origin of this group of mammals. Fossils of Proboscidea have been recovered from all continents except for Antarctica, Australia and some oceanic islands. Numidotheres (e.g. *Phosphatherium*,



Proboscidean incisors and toothrow in relation to brain and basi-cranial axis. a. Ancestral proboscidean as reconstructed in Kingdon (1979). b. *Moeritherium trigodon*. c. Eocene *Phosphatherium escuilliei*. d. Directions of increases in pneumatization, of changes in orientation of incisors and in size of molars. e. *Phiomia*. f. *Gomphotherium*. g. *Gomphotherium*. h. *Elephas planifrons*. i. *Loxodonta africana*. j. *Loxodonta africana* ('c' after Gheerbrant *et al.* 2005).

Daouitherium and *Numidotherium*), for example, were found in north-west Africa, in the early-middle Eocene. Africa is believed to have been isolated from other continents during most of the Palaeogene (Palaeocene, Eocene and Oligocene), and thus its fauna during these geological epochs was endemic. E. Gheerbrant (pers. comm.) has suggested that Palaeogene proboscideans are representative of the whole African province, and that proboscideans are of African origin (see also Gheerbrant 1997, Gheerbrant *et al.* 1998). Yet, a late Oligocene member of the Elephantimorpha was described in Pakistan by Antoine *et al.* (2003). We thus consider migration and dispersal patterns of the earliest proboscideans from north-west Africa during the Palaeogene to be uncertain. However, one possibility emerges that the northern shores of the Mediterranean Sea (a remnant of the ancient Tethys Sea) might be the place of origin of Proboscidea (for this discussion, members of Anthracobunidae are excluded). North-east Africa (Egypt, Libya) and Arabian Peninsula (Oman) embodied environmental conditions where fossils of *Moeritherium*,



Tentative schematic phylogenetic tree of proboscidean evolution. Dark bands indicate known fossil taxa. White tree indicates supposed relationships (after Tassy 1996 & Gheerbrant & Tassy 2009).

Barytherium, *Omanitherium*, *Palaeomastodon* and *Phiomia* have been found in the late Eocene to Oligocene sediments. It seems plausible that north-eastern African proboscideans may have migrated to the Horn of Africa (late Oligocene) and to East Africa (Miocene) where centres of radiations of some proboscideans (including deinotheres and gomphotheres) are believed to have taken place (see Sanders *et al.* 2010).

Another later centre of radiation of extinct gomphotheres is believed to have occurred in Asia. From the Horn of Africa (again following the geological evidence we have thus far), it is suggested that some proboscideans (possibly gomphotheres stock) migrated to what is today the Saudi Arabian peninsula (late Oligocene to early Miocene) and from there towards the general area of what is today Pakistan. *Elephas maximus*, originally from East Africa, spread into Asia and Europe during the Pliocene. The living African

elephants (*L. africana* and *L. cyclotis*) are believed to have originated in eastern Africa and did not migrate out of the continent. Like the classification and the evolutionary tree, maps of dispersals are subject to constant changes with the discovery of new fossils and/or different interpretations of old material.

The Proboscidea have been grouped together with members of the order Sirenia (manatees and sea cows) in the superorder Tethytheria (which also contains the extinct order Desmostylia; Gheerbrant *et al.* 2005). The Tethytheria and order Hyracoidea form the Paenungulata. However, Tethytheria is not well supported by genomic data; for example, one recent study incorporating DNA and amino acids supports a Hyracoidea+Proboscidea clade (Meredith *et al.* 2011). Refer to the higher-level profiles for further discussion.

Jeheskel Shoshani & Pascal Tassy

Family ELEPHANTIDAE

ELEPHANTS

Elephantidae Gray, 1821. London Med. Repos. 15: 305.

<i>Loxodonta</i> (2 species)	African Elephants	p. 178
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Elephantidae is one of approximately ten families in the order Proboscidea, comprising about 30 species, three of which are extant, one species being found in Asia and two in Africa. Fossil remains of extinct taxa have been recovered from Africa, Asia, Europe and North America, dating to as early as the late Miocene. The fossil record of the living genera (*Loxodonta* and *Elephas*) also goes back to the late Miocene, between 7.3 and 5.4 mya (Maglio 1973, Shoshani & Tassy 1996, Todd & Roth 1996, Tassy 2003).

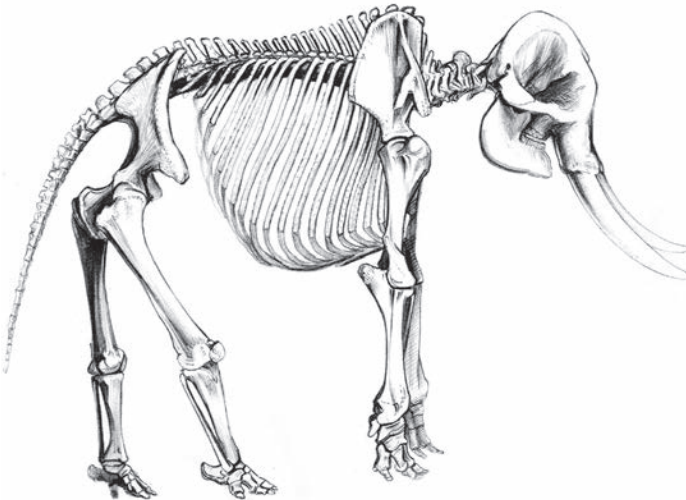
Maglio (1973) divided the Elephantidae into two subfamilies: Stegotetrabelodontinae (with two genera – *Stegotetrabelodon* and *Stegodibelodon*) and Elephantinae (with four genera – *Primelephas*, *Loxodonta*, *Elephas* and *Mammuthus*). This system has been followed by most other authors (e.g. Coppens *et al.* 1978, Shoshani & Tassy 1996). Kalb *et al.* (1996) included *Stegolophodon* and *Stegodon* in the family Elephantidae. Saegusa (1996) classified the last two genera in the Stegodontidae (and see Tassy 1996 and Shoshani 1996). Shoshani & Tassy (2005) and Shoshani *et al.* (2007) added *Palaeoloxodon* to the Elephantinae, a hypothesis originating with Osborn (1942). Synapomorphies of Elephantidae (excluding stegodontids) include lophes and lophids modified into columnar laminae (Tassy 1996, pp. 41, 44) and hypsodont molars (Shoshani 1996, p. 175).

Relationships among Elephantidae taxa, living and extinct, have been presented by Aguirre (1969), Maglio (1973), Coppens *et al.* (1978), Tassy & Darlu (1987), Froehlich & Kalb (1995), Kalb *et al.* (1996), Shoshani (1996), Shoshani *et al.* (1998) and Tassy (1996), to name a few more recent authors. In general, most authors agree on a cladistic relationship among members of the subfamily Stegotetrabelodontinae and among the basal taxa of Elephantinae (*Primelephas*). Disagreements concerning the relationships among *Loxodonta* (extant), *Elephas* (extant) and *Mammuthus* (extinct) can be summarized in two hypotheses. The first is the traditional, morphology-based hypothesis that *Elephas* and *Mammuthus* are closer to each other than either is to *Loxodonta*, cladistically expressed as (*Loxodonta* (*Mammuthus*, *Elephas*)). This hypothesis was advanced by the morphological studies of Maglio (1973), Tassy & Darlu (1987), Kalb *et al.* (1996), Shoshani (1996), Tassy (1996) and by molecular studies (e.g. Yang *et al.* 1996, Ozawa *et al.* 1997). The second, more recent, molecular-based hypothesis noted that *Loxodonta* and *Mammuthus* are closer to each other than either is to *Elephas*, cladistically expressed as (*Elephas* (*Mammuthus*, *Loxodonta*)), and proposed by Debruyne (2001), Debruyne *et al.* (2003a) and Thomas *et al.* (2000). Most recent studies (Krause *et al.* 2006, Poinar *et al.* 2006, Rogaev *et al.* 2006, Rohland *et al.* 2010) that include larger molecular data for the extinct mammoth corroborate the traditional hypothesis of (*Loxodonta* (*Mammuthus*, *Elephas*)). Shoshani *et al.* (2007) also corroborate the traditional hypothesis based on independent data from the hyoid apparatus.

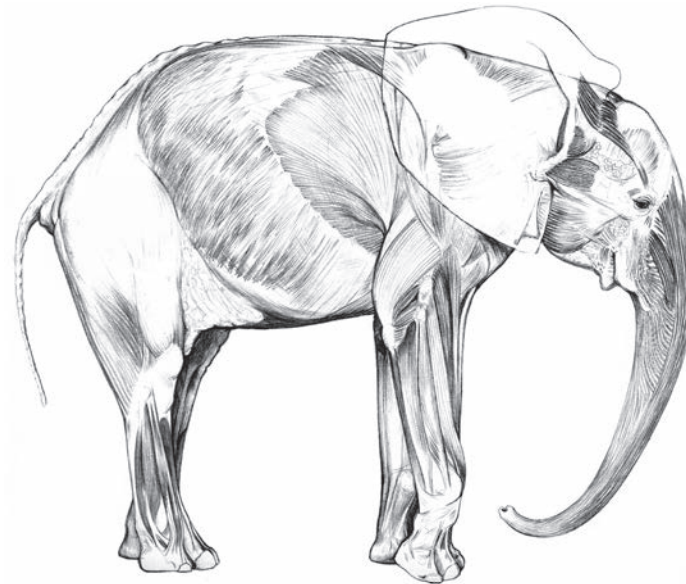
Molecular studies also contribute to better understanding of species composition within Africa. Until recently, the African elephant was divided into two subspecies, *L. africana africana* and *L. a. cyclotis* (Sikes 1971). However, recent taxonomic revision suggests

dividing the African elephant into two species: the Forest Elephant (*L. cyclotis*) and the Savanna Elephant (*L. africana*). However, not all authors agree on this classification (see genus profile for further discussion).

Common features for the living elephants include large size (*Loxodonta* is the largest living terrestrial animal, reaching a height of 4 m at the shoulder and a weight of 6 tonnes); longevity (elephants can live to about 80 years); and presence of trunk or proboscis (not all extinct proboscideans had a trunk). The proboscis is a combination of the upper lip and nose, the two nostrils continue throughout the length of the trunk; the trunk is a multi-purpose prehensile organ and is probably the most important appendage for survival. The skin (dermis and epidermis) can reach 32 mm in thickness, yet it is sensitive, movable and the body is covered with little hair and bristles (most hair is on head and tail, young elephants are more hairy than adult). The



Skeleton of *Loxodonta africana*.



Superficial myology of *Loxodonta africana*.

limbs are columnar with graviportal stance; the sole of the forefoot is larger (used for support) and round, that of the hindfoot (used for support and propulsion) is oval. In addition, newly born and juvenile elephants have relatively 'flat' soleprints, or very few features may be observed. With age, more and more soleprint features are evident and in adults, traditional hunters have long recognized that soleprints are unique for individual elephants (Shoshani *et al.* 2004).

The cranium is pneumatized (filled with air sinuses), thereby reducing the weight of the cranium (Badoux 1961), while providing ample attachment for the nuchal and masticatory muscles. The external nares (where the trunk begins) are elevated. A secondary acoustic meatus is present, as are the alisphenoid canal and the mandibular coronoid canal. The hyoid apparatus consists of five bones. Premolars and molars are composed of plates (lamellae) held together with cementum, the inside of each plate contains dentine, surrounded by enamel, lozenge-shaped in *Loxodonta* (hence the name) and in compressed loops in *Elephas* ('*Elephas*' means huge arch). Up to 15 plates are present in *Loxodonta* and 29 in *Elephas*. The molars are very large (the last molar can weigh over 5 kg); dental formula is: $I^{1/0}$, $C^{0/0}$, $P^{3/3}$, $M^{3/3}$ = 26; chewing teeth (premolars and molars) exhibit forward or horizontal displacement, a feature also shared by non-Elephantidae taxa, but not with all proboscideans; and very large tusks. Tusks are used for defence, offence, display and feeding. Tusks are enlarged incisors (elephants have the longest teeth of any living or extinct mammals), with a record of 345 cm long for an African elephant. Tusks of elephants exhibit a unique and complex pattern of criss-crossing lines called Schreger pattern, also known as 'engine turning' or guillochage (see Fig. 2.7, p. 15 in Shoshani 1996); this pattern is also present in dentine of cheekteeth (summarized from Laursen & Bekoff 1978, Shoshani & Eisenberg 1982, Roth & Shoshani 1988, Shoshani 1996, 2000, Shoshani & Tassy 1996, Shoshani *et al.* 2007).

The vertebral formula is: Cervical 7 (for *Loxodonta* and *Elephas*), Thoracic 20–21 (for *Loxodonta*), 19–20 (for *Elephas*), Lumbar 3–4 (for *Loxodonta*), 3–5 (for *Elephas*), Sacral 4–6 (for *Loxodonta*), 3–5 (for *Elephas*), Caudal 18–33 (for *Loxodonta*), 24–34 (for *Elephas*). The radius and ulna are separate, permanently crossed in pronation position; the tibia and fibula are also separate and the latter articulates with the calcaneum. The ilium is almost vertically expanded laterally, and the acetabular fossa is directed downwards. Both manus and pes are pentadactyl, the manus is larger than the pes, and there is a serial bone arrangement in the carpus, and in the pes the astragalus does not articulate with the cuboid and lacks the astragalar foramen. The long bones generally lack medullary marrow cavities, instead a mesh of cancellous bone allows passage of blood vessels for haematopoietic functions (Shoshani 1996). The epiphyses on long bones fully fuse at about 30 years in females and about 35–40 years for males (Roth 1984). Unlike most mammals, the mandibular fossa is not a convex–concave form, but a double convex part with a double concave cushion of fibrous tissue in between condyle and mandibular fossa (Shoshani *et al.* 1982).

Elephants are adapted to a variety of habitats from desert to mountain-tops, and exhibit nocturnal, diurnal and crepuscular activity patterns to avoid harassment and hunting. Their predators include Lion *Panthera leo*, Tiger *P. tigris* and humans; calves have been preyed upon by crocodiles. Long distance communication between and among herds is achieved by powerful calls containing infrasonic frequencies (5–24 Hz). The degree of development of senses changes with age. Elephants have an excellent sense of hearing, an

acute sense of smell, very good sense of touch, unknown sensitivity to taste (seems to be selective) and poor sense of vision, though it is good in dull light. Living elephants migrate long distances in search of food (an adult elephant requires 100–250 kg per day) and water (an adult elephant requires 75–150 l per day) and to reduce or avoid inbreeding. Elephants are keystone and super-keystone species. They are herbivorous (*Loxodonta* is more browser than grazer and *Elephas* is more grazer than browser), social mammals that live in herds led by the matriarch, where the young have the opportunity to be in close contact with the adult and copy or learn the art of survival. Gestation period lasts 18–24 months and the newly born are precocious and able to follow their mothers shortly after birth; they suckle from nipples (not teats) at the axillary mammae. Elephants exhibit complex behaviours, including altruism, tool using and tool making. Both Asian and African elephants have been trained for domestic chores and antics; it has been suggested, however, that the Asian species can perform more complex functions than the African (summarized from Gordon 1966, Sikes 1971, Douglas-Hamilton & Douglas-Hamilton 1975, Moss 1988, Western 1989, Shoshani & Tassy 1996, Meng *et al.* 1997, Payne 1998, Shoshani 2000).

Unlike in other mammals, the vulva is situated between the hindlegs (not under the tail). Having the vulva between the hindlegs may have evolved to accommodate less falling distance for the newborn. The testes are intra-abdominal (a primitive, not derived character). Unique to Elephantidae (*Loxodonta*, *Elephas*, *Mammuthus* and probably other extinct elephantids taxa) is the presence of the temporal gland, located subcutaneously midway between the eye and the ear opening; bull elephants secrete from the temporal glands during a physiological condition called musth during which blood testosterone levels are high and elephants are more aggressive than when not in musth. Also unique to Elephantidae and probably to other proboscideans are the presence of the pharyngeal pouch and the associated function of water storage and sound production. In time of stress (e.g. hot weather and absence of water), Asian and African elephants insert their trunk into their mouths and draw stored water from this pouch and douse themselves; because of their large volume compared with the relatively small surface area, it is difficult for elephants to keep their body cool (Shoshani 1998).

An elephant's heart has a double apex (a feature also common in Sirenia) and paired anterior venae cavae; it can reach 28 kg. Body temperature is 97–99° F (36–37° C) but it can fluctuate about five degrees to conserve energy during thermoregulation. The left lung is slightly smaller than the right, both lungs have several deep fissures and there is little or no plural cavity. The digestive system is not very efficient (about 44% of the food eaten is digested, the rest passes out with the faeces). The soft palate is short and there is no uvula. The stomach is simple (not chambered), intestines reach 30 m, the caecum is sacculated and acts as a fermentation chamber, and the anal flap is present (apparently unique to *Loxodonta*, *Elephas*, *Mammuthus*) (summarized from Todd 1913, Benedict 1936, Short 1962, Laursen & Bekoff 1978, Shoshani & Eisenberg 1982, Roth & Shoshani 1988, Shoshani 1996, 1998, 2000, Shoshani & Tassy 1996, Isaza 2006, Mikota 2006).

Brain weight of a newly born elephant is about 50% of adult brain weight. The elephant brain is the largest among living and extinct terrestrial mammals, with an average weight of 4.78 kg for adults ($n = 16$). The cerebrum and cerebellum are extremely convoluted (more than that of man), and the temporal lobe is proportionally large

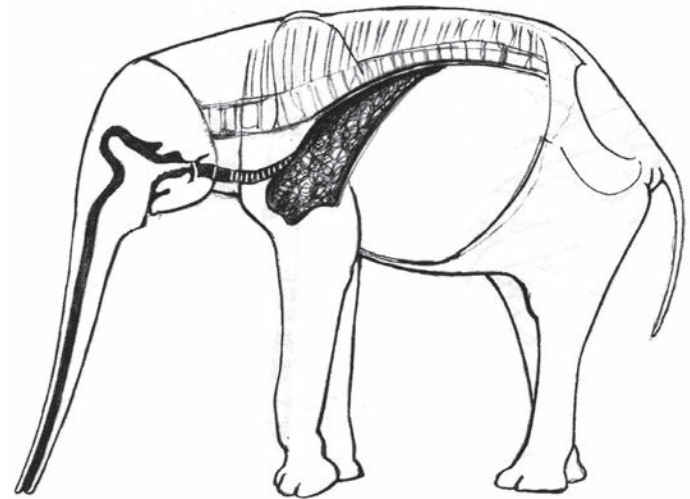
and bulges laterally and ventrally. The capacity to store data in elephants is about three times larger than in humans. Average encephalization quotient (EQ, the ratio of actual brain size to expected brain size for a given body size) for mammals = 1 (Jerison 1973). The EQ for elephants ranges from 1.13 to 2.36 ($n = 16$), with an average of 1.88, and with an average of 2.14 for Asian elephants and 1.67 for African; 2.1 for ♀♀ ($n = 4$) and 1.3 for ♂♂ ($n = 3$). Among mammals, those that use and make tools include humans, elephants and chimpanzees; all have a high EQ (details in Shoshani *et al.* 2006a).

Visible, and easily detected, differences between the African and the Asian species include: the shape of the back (which, in profile, is concave in *Loxodonta* and convex or straight in *Elephas*); the ear of the African elephant is large and exceeds the height of the neck and its dorsal end folds medially, whereas in the Asian species, the ear is small, does not exceed the height of the neck and its dorsal end folds laterally.

Living African and Asian elephants are geographically separated and do not interbreed. In captivity, however, animals are artificially placed together, and hybrids among animals that will never meet in the wild are possible. The only known hybrid between a male African elephant and a female Asian elephant was conceived in Chester Zoo, England in 1978 (Howard 1979). 'Motty' lived only 10 days. Immunological experiments confirmed that Motty's tissue behaved like that of a mule, corroborating that it was a hybrid between *L. africana* and *E. maximus* (Lowenstein & Shoshani 1996). These results are not totally surprising since the diploid chromosome number in somatic cells for both elephant species is 56 (Hungerford *et al.* 1966, Norberg 1969).

Of all the living and extinct species and subspecies of Proboscidea (approximately 185), only two extant genera, with three species, are alive today. The vast majority of living elephant populations are continuously decreasing due to shrinking range or habitat fragmentation, and therefore they are listed by CITES as either in Appendix I or Appendix II.

Jeheskel Shoshani & Pascal Tassy



Lungs and air passages of Savanna Elephant *Loxodonta africana*.

GENUS *Loxodonta* African Elephants

Loxodonta Anonymous, 1827. The Zoological Journal (London) 3: 140–143.

Note: F. Cuvier was the author of the original description of this genus in 1825 (Cuvier 1825 in E. Geoffroy St-Hilaire & F.G. Cuvier, *Hist Nat. Mammifères*, 3 (52): 2) but he used the name 'Loxodonte' in French, which is an invalid format in scientific publications (Article 11(b) of the International Code of Zoological Nomenclature), and thus the emended Latinized form of *Loxodonta* by an anonymous author in 1827 takes precedence.

The current work recognizes two living species of *Loxodonta*: the Savanna Elephant *Loxodonta africana*, characteristic of the savannas of southern and East Africa, and the Forest Elephant *L. cyclotis*, formerly widespread across the equatorial forest of central and western Africa up to Sierra Leone, but now surviving in fragmented populations under threat by poaching and habitat loss (Blake *et al.* 2007). Morphologically, Forest Elephants are smaller, with more slender and straighter tusks, a protuberant mandibular symphysis and smaller ears (Table 7); other morphological differences between the two taxa are given by Grubb *et al.* (2000), who considered *L. cyclotis* to be more primitive than *L. africana*.

The taxonomic validity of two species that were previously considered to be conspecific continues to be debated. During the colonial era there was a profusion of claims for different races of African elephants (Noack 1906, Frade 1931, Dollman 1934, Bourdelle & Petter 1950, Blancou 1962; and see Spinage 1994 for review) but the prevailing view over the past 50 years has been to recognize

only two valid subspecies, the forest *L. a. cyclotis* and the savanna *L. a. africana*. None the less, local demes with distinctive features have long been recognized (notably in Namibia and the Rufiji delta) and genetic variation has been demonstrated for several subpopulations (Georgiadis *et al.* 1994, Barriel *et al.* 1999, Comstock *et al.* 2002, Nyakaana *et al.* 2002). Very small forms of *cyclotis*, formerly described in central DR Congo, were once supposed to belong to distinct pygmy forest elephants (described as *Loxodonta pumilio*), but these populations are not now thought to form a distinctive clade on either morphological or molecular grounds (Groves & Grubb 2000a, Debruyne *et al.* 2003b).

Frade (1931, 1955) was among the few earlier authors to recognize two species of African elephants, and several recent authors have presented morphological, ecological and molecular evidence in support of this classification (Groves & Grubb 2000b, Grubb *et al.* 2000, Roca *et al.* 2001, 2004, Rohland *et al.* 2010). Transitional morphological forms between typical savanna and typical forest elephants exist in peripheral zones in Central/East Africa (see Groves & Grubb 2000b, Grubb *et al.* 2000, Roca *et al.* 2004). In their interpretation of hybridism, two schools of thinking have emerged: the first posits that hybridization is ancient and the two forms are indeed separate species (Roca *et al.* 2001, 2004, 2005); the second regards the hybridization as active and the two forms are subspecies with a geographical cline from east to west (Debruyne 2005a, b). Geographical extension of more than two units, however named, is an alternative (Eggert *et al.* 2002).

On the basis of skull differences, Grubb *et al.* (2000) noted that hybrids between the *Loxodonta* forms were ‘occasional’ and they supposed that the area of sympatry was narrow. Had they recognized a wider area of sympatry or interaction between the *Loxodonta* species

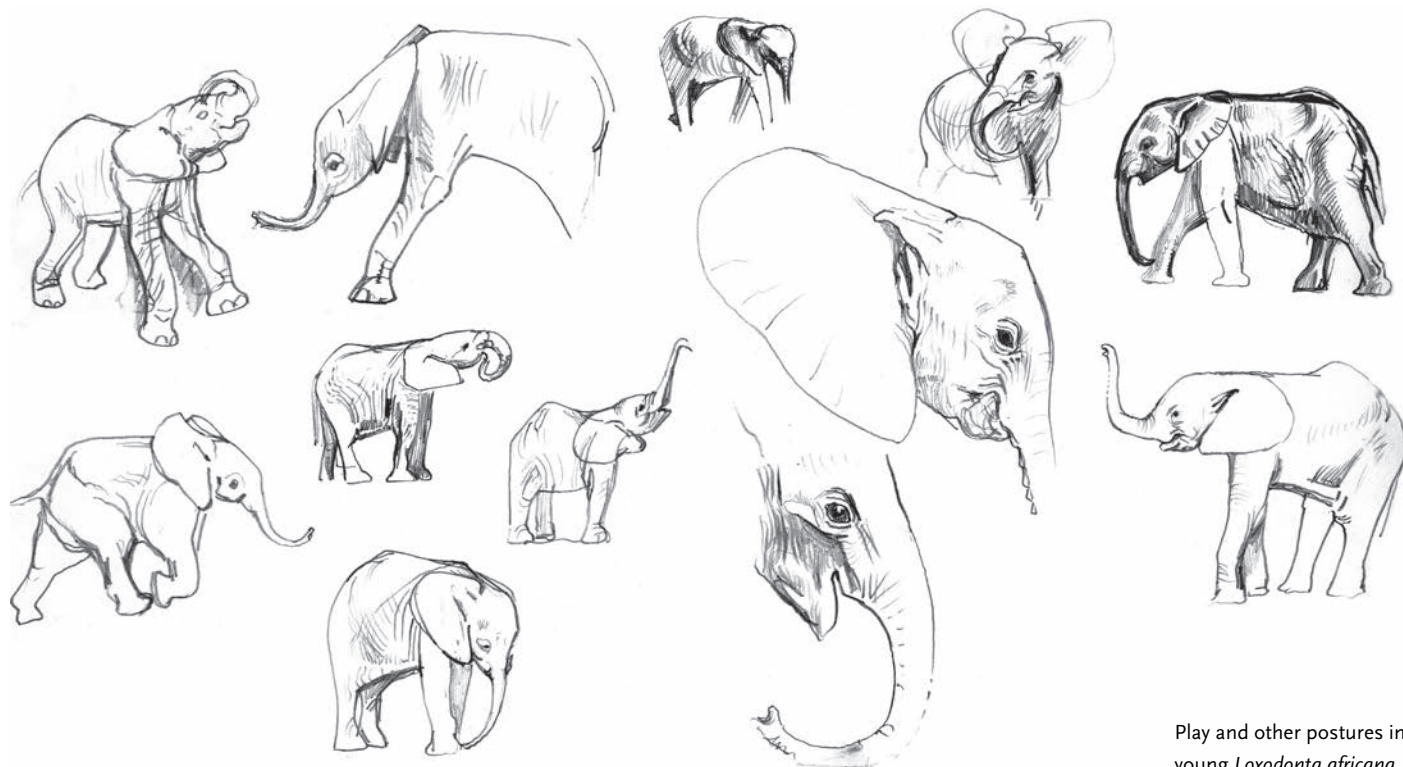
Table 7. Major differences between species of *Loxodonta*.

	<i>L. africana</i> (Savanna Elephant)	<i>L. cyclotis</i> (Forest Elephant)
Weight	4000–6500 kg	2000–4500 kg
Height at shoulder (♂♂)	3.2–4.0 m	2.4–3.0 m
Skin	On average lighter	On average darker
Shape and size of ears	Triangular, extend below line of neck	Rounder, usually do not extend below line of neck
Skull, rostrum	More flared	Less flared
Skull, cranium	Much pneumatized	Less pneumatized
Skull, nasal aperture	Narrower	Wider
Skull, anterior end of rostrum	Slight dorsal cavity	Deep dorsal cavity
Skull, occipital plane	Slopes forward	More upright
Skull, mandible	Shorter, taller	Longer, lower
Skull, mandibular condyles	More rounded	Transverse–oval
Tusks	Curved out and forward, thicker	Straighter, downpointing, slender
Cheekteeth	High-crowned	Lower-crowned
Number of nail-like structures ('toes') in adults	Forefeet 4 or 5 Hindfeet 3, 4 or 5	Forefeet 5 Hindfeet 4 or 5

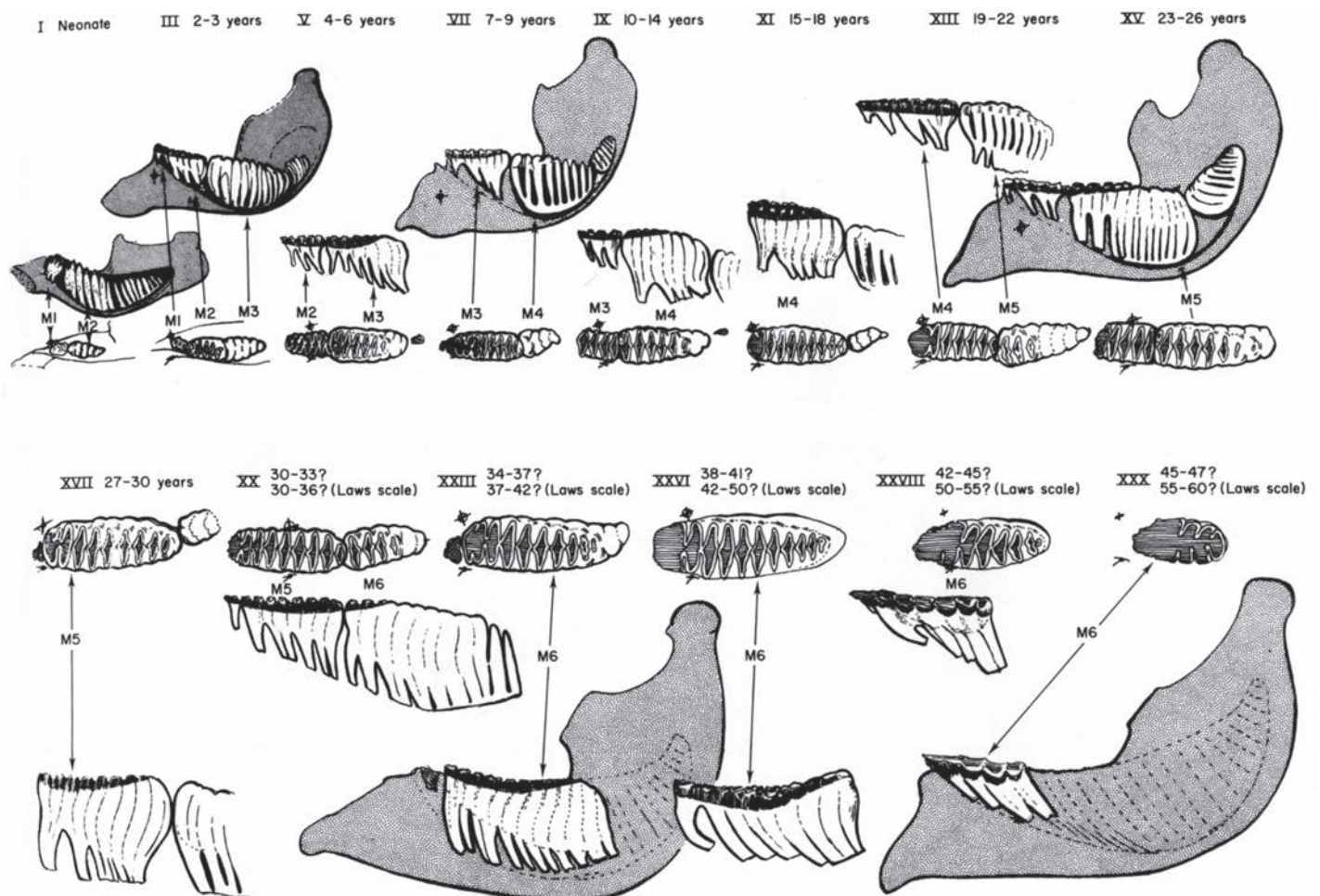
Source: Adapted from Grubb *et al.* (2000)

or subspecies then they might have drawn different conclusions. The genetic situation is actually much more complicated, with extensive introgression of Forest Elephant haplotypes in populations that are of morphologically Savanna Elephant type now generally acknowledged (e.g. at Garamba, see Roca *et al.* 2004). Nuclear and mtDNA profiles show cytonuclear dissociations that reveal male and female genomes with different evolutionary histories. A nearly continent-wide study showed that *L. africana* bulls are recurrently backcrossing with female hybrids to progressively replace the *cyclotis* nuclear genome over an extremely wide, not narrow, zone of hybridization (Roca *et al.* 2004).

Fossil remains of *Loxodonta* are restricted to Africa. The earliest known member of the genus has been described from the late Miocene (ca. 5–7 mya) in Kenya and Uganda with the specimens consisting of some primitive isolated teeth showing emergence of the typical loxodont enamel loop (the generic name *Loxodonta* refers to the lozenge shape of the enamel loops on chewing surfaces of the molars). These have been labelled '*Loxodonta* sp. indet. (Lukeino stage)' (Tassy 1986, 1994). Sanders (2007) has described a new loxodont species (*Loxodonta cookei*) dated to the latest Miocene–early Pliocene, ca. 5.0 mya from the Varswater Formation at Langebaanweg, South Africa. This species is distinguished from *L. adaurora* by having anterior and posterior accessory central conules, and from other loxodont elephants by its primitive retention of permanent premolars, lower crown height, fewer molar plates, thicker enamel and lower lamellar frequency. Together with this newly described species, the total number of loxodont fossil taxa is ten. Approximately, from oldest to youngest, they are: '*Loxodonta* sp. indet. (Lukeino stage)', *L. cookei*, *L. adaurora adaurora*, *L. a. kararae*, *L. exoptata*, *L. atlantica angammensis*, *L. a. atlantica*, *L. a. zulu*, *L. cyclotis* and *L. africana*. Beden (1983) employed the name '*Loxodonta schneideri*' from Chad instead of *Stegodibelodon schneideri* described by Coppens (1972); corrected usage of *S. schneideri* was reinstated by Shoshani & Tassy (1996). More common in the latest



Play and other postures in young *Loxodonta africana*.



Toothwear and progression in *Loxodonta africana*, following Laws (1966). Roman numerals = 'Laws age scale'. (M1 to M3 equivalent to milk molars in non-proboscids.) Molariform teeth are numbered 1 to 6 – all deciduous.

Miocene and early Pliocene (ca. 5–4 mya) of East Africa are *Loxodonta adaurora* and *L. exoptata* described on the basis of dental and skeletal remains (Maglio 1970, 1973, Beden 1983, 1987). The molars, with a lesser marked lozenge, indicate that *L. adaurora* is probably an early offshoot of the genus. The subspecies *L. adaurora kararae* is a pygmy chronological subspecies described in the latest Pliocene of Kenya at Koobi Fora and the Omo (Shungura) in Ethiopia (Beden 1983). The discovery of *L. a. kararae* has demonstrated that Kingdon's (1979) query whether *L. cyclotis* might not be a dwarfed ecological isolate of *L. adaurora* was not a rhetorical question.

A large species, *Loxodonta atlantica* (larger and with more derived molars than those of *L. africana*), is known from the latest Pliocene of Yayo (Chad) and Omo (Ethiopia) and, in the form of *L. atlantica angammensis*, up to the late Pleistocene (Maglio 1973, Beden 1987). Numerous fossils of *L. atlantica atlantica* show that this was a widespread species, known from northern Africa, to eastern and southern Africa. Although the living species *L. africana* must have been present in Africa together with *L. atlantica*, the former is not known as a fossil before the late Pleistocene of South Africa and Chad.

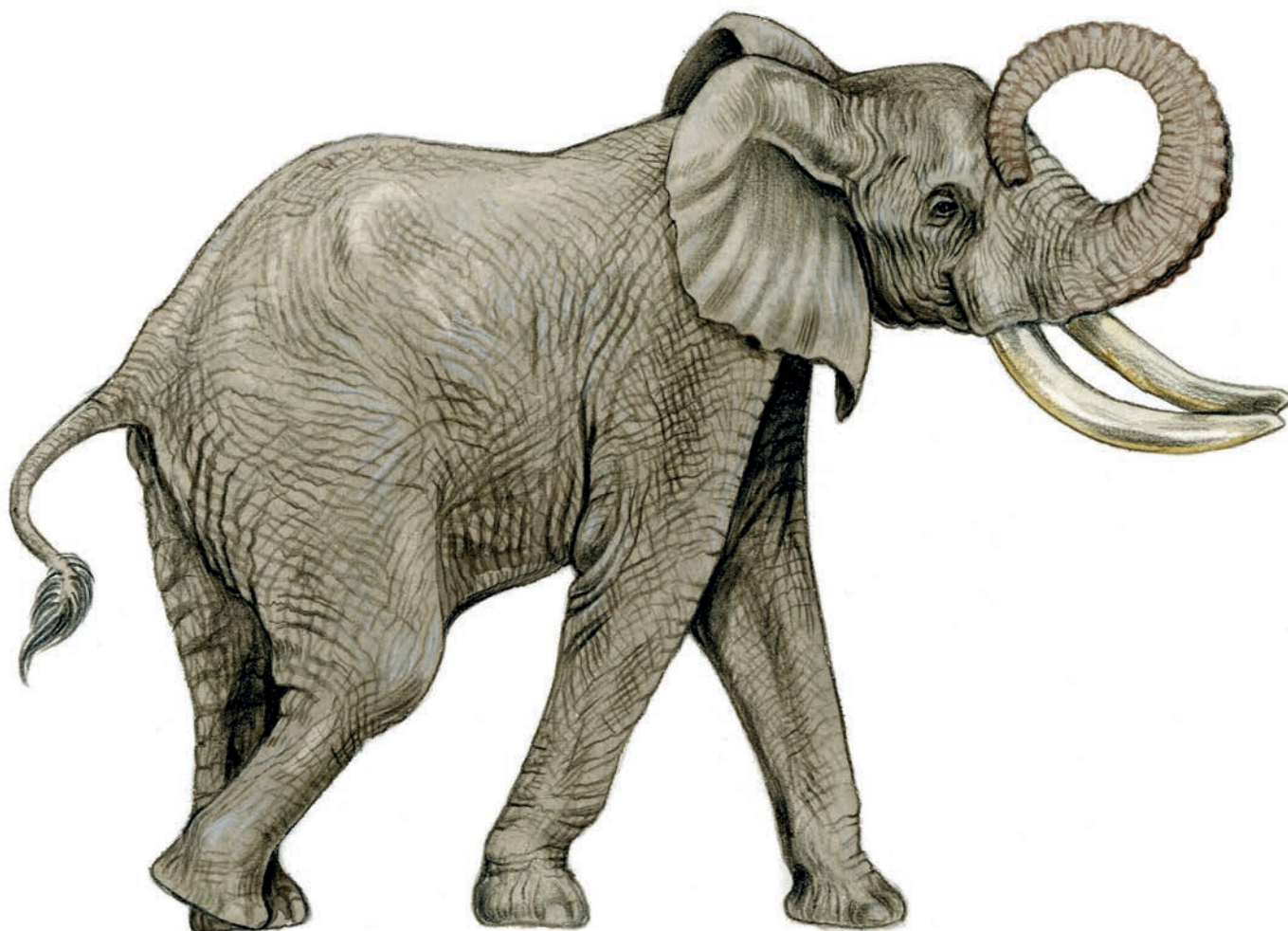
Although *L. adaurora* had exceptionally large, vertically embedded tusks it shared a typical globular cranium with the extant species (i.e. the profile was rounded compared with the flatter and more elongated frontal profile of gomphotheres and primitive elephantids). Compared with *Elephas* (and *Mammuthus*) the frontoparietal area is

concavo-convex. Maglio (1973) observed that *Loxodonta* was the first of the three genera to evolve the short, facially flexed skull that became typical for all later elephants; it evolved more than 2.5 mya before the others. In spite of this early specialization in cranial architecture, 'little change in the dentition occurred in the entire history of the genus and it would seem that this particular combination of cranial and dental specialisations was sufficient for this group' (Maglio 1973).

Six cheekteeth succeed one another in a one-by-one progression. In adult elephants, no more than one and a half teeth are in use. The forward surface of each molar is worn down progressively (while their roots also get resorbed as they wear down). Mandibular tooth rows broadly mirror their antagonists in the upper jaw but the latter travel at a steeper angle. Laws (1966) documented the form and progression of loxodont teeth in the lower jaw of *L. africana*, correlating tooth-wear stages with age-classes. These have provided the basis for population studies of the species ever since, and have been revised by Lee *et al.* (2012).

In terms of behaviour and social structure, *L. africana* and *L. cyclotis* principally differ in that the daughters of Savanna Elephants never leave their mothers. This results in large, stable matriarchal families, while in Forest Elephants daughters leave their mothers once they achieve puberty (see species profiles).

Pascal Tassy & Jeheskel Shoshani



Savanna Elephant *Loxodonta africana*.

***Loxodonta africana* SAVANNA ELEPHANT (AFRICAN BUSH ELEPHANT)**

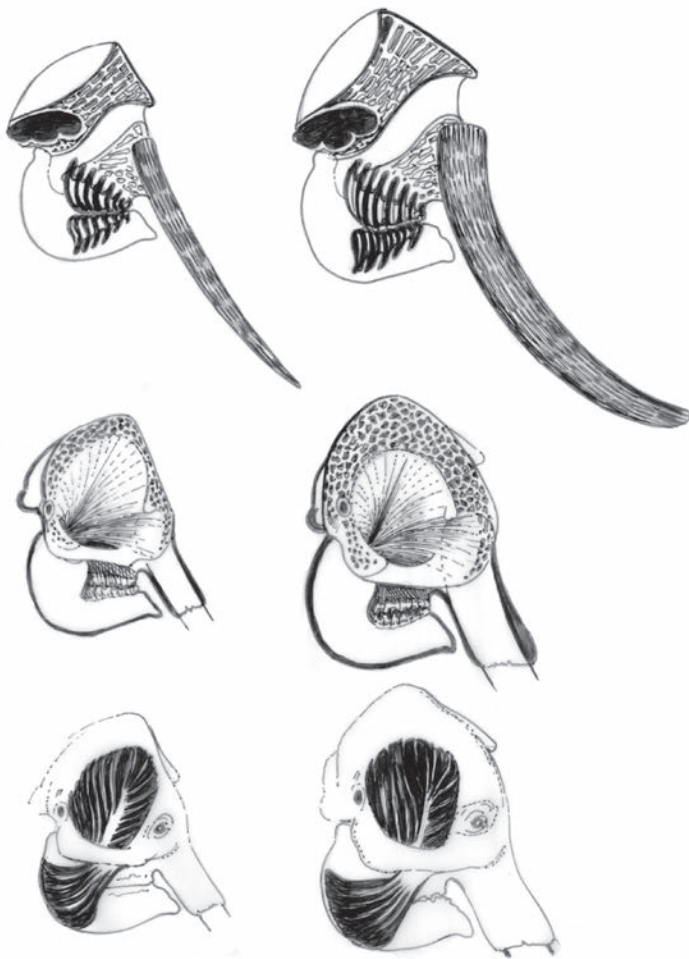
Fr. Elephant d'Afrique; Ger. Afrikanischer Elefant

Loxodonta africana Blumenbach, 1797. Handb. Naturgesch., 5th Ed., p. 125. Restricted to the Orange River, South Africa, by Pohle (1926).

Taxonomy The colonial era brought a profusion of claims of different races of African elephants (see genus profile). Ansell (1974) recognized four subspecies within his *africana* section (see also Laursen & Bekoff 1978, Spinage 1994), but their validity is doubtful. Shoshani (2005) recognized a single monotypic species. Synonyms: *angolensis*, *berbericus*, *capensis*, *cavendishi*, *cornaliae*, *hannibali*, *knochenhaueri*, *mocambicus*, *orleansi*, *oxyotis*, *peeli*, *pharaohensis*, *rothschildi*, *selousi*, *toxotis*, *typicus*, *zukowskyi*. Chromosome number: $2n = 56$; the normal karyotype has 25 acrocentric/telocentric and two metacentric/submetacentric autosomal pairs. The X chromosome is a large submetacentric; the Y chromosome is small and acrocentric (Hungerford *et al.* 1966, Wallace 1978, Houck *et al.* 2001).

Description The largest of land animals, weighing as much as 6 tonnes, the Savanna Elephant is easily identifiable in having a trunk, tusks, large ears and pillar-like legs. The massive head is relatively larger and broader in older ♂♂ than in younger ♂♂ and ♀♀. The ears are extremely large, as much as 1.2 m across by 2 m vertical. The prehensile trunk, a fusion of nose and upper lip and made up of

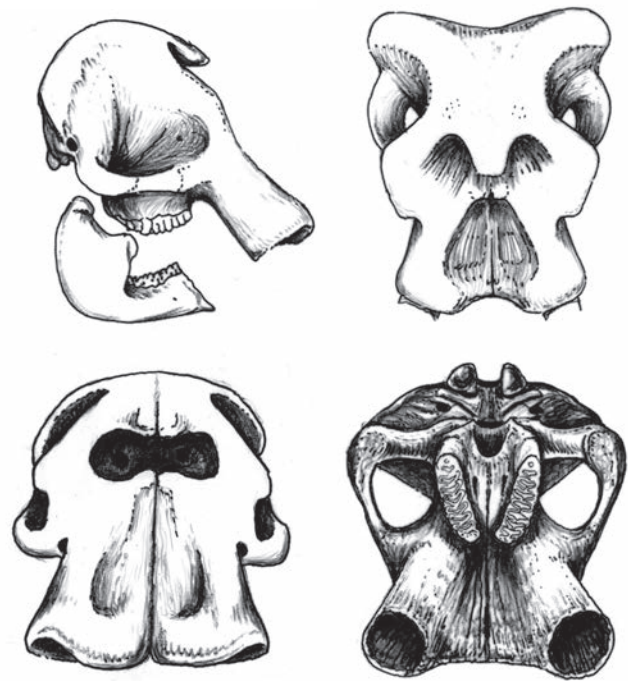
approximately 150,000 subunits of muscles (Shoshani 1997), contains two nostrils and is equipped with two finger-like tips. The wrinkled skin, which reaches a thickness of 30–40 mm on the legs, forehead, trunk and back, is dark to pale grey or brown, and, in rare instances, depigmented patches can be seen. Newborn elephants may be covered in reddish-brown hair. Adults retain coarse bristles up to 40 mm long on the trunk and chin and as abraded remnants in the crevices of skin over much of body. Tail hair varies in length from stubble to shiny black hairs up to 500 mm long; the tail itself may reach a length of 1.0–1.5 m in adults. The limbs are pillar-like. Elephants walk tip-toed on five digits and one sesamoid predigit, all encased in hoops of tissue, skin and nail-like structures above a cushion of fibro-fatty tissue. As elephants adopted the 'tip-toed' stance 40 mya, the sesamoid bone was co-opted to help support the elephant's weight (Hutchinson *et al.* 2011). 'Toenails' vary from five on both fore- and hindfeet to four on the forefeet and three on the hind. The smooth but cracked soles leave recognizable tracks, with larger circular forefeet and smaller oblong hindfeet. The length of the hindfoot is a reliable indication of shoulder height (Poole 1982, Western *et al.* 1983, Lee & Moss 1995).



Three aspects of skull structure in female (left) and male (right) *Loxodonta africana*. (Above) Cross section showing brain capsule, honeycomb bone and rooting of incisor and molar. (Middle) Cranial buffering with honeycomb revealed by 'shaved' surface. (Below) Masseter and temporalis muscles.

Sex in elephants can be determined by the shape of the forehead (in profile rounded in ♂♂ and more angular in ♀♀), the presence of mammary glands (two between the forelegs), the thickness and shape of the tusks (thicker and more conical in ♂♂), the slope of the underbelly (sloping downward toward the hindlegs in adult ♂♂; more curved in ♀♀) and the genitals. There is no scrotum, and testes are internal. In nulliparous ♀♀ breast development commences in the fifth month of first pregnancy and is clearly visible by the tenth month (Mutinda 1994). Thereafter, ♀♀ are typically either lactating or pregnant (though inter-calf-intervals may increase substantially and sometimes cease later in life) and breasts are visible (Poole 1989a).

The skull is massive and rounded, the relatively small brain cavity situated low down at the back of the skull. The maxillary and premaxillary bones extend well below the level of the upper toothrow, forming bony supports on either side for the bases of the tusks. In the female skull there is a distinct nuchal eminence not present in that of the male. A small interparietal bone is present at birth, but fuses with the surrounding cranial bones at an early age. The cranium is pneumatized (filled with air sinuses), with a 'honey-combed' structure and, in an adult bull, may be as much as 300–400 mm thick at the frontal region. The orbits are situated towards



Loxodonta africana skull. Profile and frontal views (left). Dorsal and palatal views (right).

the front of the skull. The structure of the cranium and mandible is discussed in detail by Van der Merwe *et al.* (1995).

The tusks are modified upper incisors composed of layered dentine (ivory, which shows a cross-grained matrix). The tusk is preceded by a deciduous tooth, which consists of a crown, root and pulpal cavity, the formation of which is completed soon after birth. The deciduous tooth reaches a maximum length of 5 cm but does not erupt through the skin and is later pushed aside and resorbed (Raubenheimer *et al.* 1995). The presence, absence, length, shape and orientation of tusks are subject to much variation both within and between populations. In the Kruger N. P. (South Africa) research has shown that in bulls, tusk growth accelerates with age, while in cows it ceases at about 40 years of age, after which tusk size may even decline probably due to wear (I. Whyte & A. J. Hall-Martin unpubl.). Broken tusks have been observed to grow back rapidly even among older females (J. Poole pers. obs.). Elephants use their tusks for gathering food, digging, defence, offence and display, and it is not unusual for one of the tusks to be subject to greater wear than the other. Both sexes have tusks, although tusklessness occurs naturally (rarely in ♂♂) in low proportions (~2–4%; Poole 1989a) and appears to be increasing (Jachmann *et al.* 1995). In heavily poached areas, tusklessness may reach up to 45% in some female age classes (Poole 1989a). In the Addo Elephant N. P. (South Africa) 98% of the ♀♀ are tuskless (Whitehouse 2002), due to previous heavy exploitation for ivory.

During the course of their lifetime, elephants grow six grinding teeth, known as molars I–VI, which grow and move forward, replacing each other in both upper and lower jaws, one by one, with each successive molar longer and wider than the previous one (Laws 1966). In young and subadult individuals two molars normally occur on each side of the upper and lower jaws and are in use at the same time. Molar displacement and wear has been used as a means of ageing African elephants, based on the following general patterns of eruption: M1 at birth to 0.5 years; M2 partially in wear at 2 years; M3 at 2.5 years, full

tooth at 4 years; M4 at 6–8 years, in full wear at 15 years; M5 at 18, full tooth at 25 years; and M6 at 32–34 years, full tooth at ~45 years (Laws 1966, revised by Lee *et al.* 2012). However, there is variation in the rate in which molars come into full wear (e.g. Lindeque 1991).

Hanks (1979) developed a useful visual method for obtaining quick age assessments in the field, based on body size within a family unit; the relative size of footprints and faecal boli may also be useful (Western *et al.* 1983, Jachmann & Bell 1984). Other studies have also investigated patterns of age determination in African elephants, expanding on Laws' earlier pioneering work (Johnson & Buss 1965, Laws 1967, Sikes 1966, 1967, Krumrey & Buss 1968, Fatti *et al.* 1980, Lang 1980, Lark 1984, Jachmann 1985, 1988, Lindeque 1991) in African elephants. Recent work by Shrader *et al.* (2006), based on ten populations in five countries across southern and eastern Africa, confirms the work of earlier studies that the growth patterns of Savanna Elephants are similar across large areas of Africa. Growth curves indicated that shoulder height can provide an accurate estimation of the age of ♀♀ up to 20 years (215 cm) and ♂♂ up to 36 years (290 cm) (Lee & Moss 1995).

Geographic Variation Savanna Elephants can vary dramatically in size across their range, and a number of subspecies have been described based on external features, including the ears (e.g. Lydekker 1907). Regional differences probably reflect a combination of local adaptation (especially in the case of desert populations), founder effects and genetic drift in what sometimes appear to be self-contained gene pools. Savanna Elephant populations show modest levels of phylogeographic subdivision, based on composite microsatellite genotype, an indication of recent population isolation and restricted gene flow between locales (Comstock *et al.* 2002).

Similar Species

L. cyclotis. Smaller body size, with straighter, more downward-pointing tusks and smaller rounder ears. Distributed in the Guinea-Congolian rainforests.

Distribution

Historical Distribution Elephants once inhabited virtually the entire African continent. Neolithic rock paintings from 10,000–12,000 years ago reveal that elephants once existed through much of the Sahara Desert and North Africa (Coulson 2001), but climatic fluctuations might have excluded them from some waterless regions during very arid periods. From ancient historical writings it is clear that elephants occurred from the Mediterranean coast in North Africa (Bryden 1903) and the species is believed to have survived into the first few centuries AD in the Atlas Mts and along the Red Sea coastline and Nubia. At the time of first contact with non-aboriginal people, the distribution of elephants broadly spanned the entire continent south of the Sahara (Mauny 1956, Douglas-Hamilton 1979).

Current Distribution Today, Savanna Elephants are extirpated throughout the region north of the Sahel, and are restricted to south of the Sahara, occupying only 20% of their historic range. Their distribution is patchy and fragmented. The main cause for range decline is habitat loss and poaching for ivory during the last two centuries. In West Africa, where range loss has been most severe, Savanna Elephant populations exist in small, fragmented and isolated enclaves in the Sahelian zone, along forest edge, woodlands and savanna. A relict



population of desert-living elephants occurs in Gourma, Mali (Blake *et al.* 2003, Bouché *et al.* 2009). In central Africa, Savanna Elephants are known to occur in N Central African Republic and N Cameroon, and there is reportedly a narrow zone of hybridization in NE DR Congo (and perhaps in S Central African Republic). In Chad, the only central African range state having only Savanna Elephant populations, elephants occur in Sudanian woodland in the south and in the drier Sahelian Acacia wooded grasslands further north; there are no elephants in the Saharan north of the country (Blanc *et al.* 2007).

In Eastern Africa, Savanna Elephants occupy both forest and savanna habitats. Populations in Uganda, Ethiopia, Eritrea, Somalia and Rwanda are remnant and highly fragmented, while larger ranges and populations still occur in Sudan, Kenya and, particularly, Tanzania. Southern Africa is home to most of Africa's Savanna Elephants where they occur in fragmented ranges, although elephants have been extirpated from Lesotho. The largest remaining population in an unbroken range includes parts of Namibia, N Botswana, Zimbabwe, Zambia and Angola (Blanc *et al.* 2007). Small relict populations of forest-living Savanna Elephants occur along the eastern coast of Africa from Kenya's Arabuko-Sokoke and Shimba Hills forests to the Knysna forest in the Western Cape, South Africa. Many new, but fragmented, populations have been established in South Africa through translocations from Kruger N. P.

Habitat Savanna Elephants occur in virtually every habitat type on the African continent from sub-deserts to swamps, lowland rainforests, gallery and montane forests, upland moors, flood-plains, savannas and various types of woodlands, and range from sea level to as much as 4875 m (Grimshaw *et al.* 1995). Ability to utilize such diverse and contrasting habitats is possible because they are relatively unspecialized herbivores. Preferred habitat such as wooded savanna provides both browse and grass with access to water. Shade and cover for protection and water availability can have an important impact on elephant movements and distribution (Nellemann *et al.* 2002).

Table 8. Estimated numbers of Savanna Elephants, including West Africa.

	Estimate	95% CL ±	Guesstimate		Range covered %	Area (km ²)
			From	To		
Estimates from surveys	496,000	36,500			42	883,000
Estimates from low quality surveys and guesses			32,500	45,000	21	448,000
Unassessed range					37	767,000
Total range					100	2,098,000

Source: African Elephant Database 2007, courtesy of the IUCN/SSC African Elephant Specialist Group

In rare cases, elephants have become adapted to desert conditions, for example, in Gourma, Mali (Blake *et al.* 2003), and the Kaokoveld and Damaraland in Namibia (Leggett 2004). The best-studied population is in NW Namibia, where elephants cope with seasonally scarce vegetation and water by moving over large seasonal ranges of approximately 650 km and have home-ranges of up to 12,600 km² (Viljoen 1987, 1989, Viljoen & Bothma 1990, Lindeque & Lindeque 1991, Leggett *et al.* 2003, Leggett 2006a).

Abundance Elephants are least common at high altitudes and in hot deserts where access to water is limited. Densities also tend to be low in dense forest and open grasslands. Mixed woodlands with plenty of grass and browse provide year-round forage and may allow population densities to reach over 5/km² (e.g. Lake Manyara N. P., Tanzania). However, such cases are exceptional and are unlikely to be sustainable over the long term. In most savannas, elephant densities range from 0.5 to 2/km² with densities in forests usually lower. Large spatial and temporal differences in local density are not uncommon due to both environmental and social factors.

A continent-wide assessment of population size for Savanna Elephant (Table 8) is complicated by countries having both Forest and Savanna elephants. None the less, using the results from the African Elephant Status Report (Blanc *et al.* 2007) it is possible to arrive at a general continental population estimate. Such an assessment makes three general assumptions, namely: that central Africa is the only place where Forest Elephants occur; that there are no *cyclotis*–*africana* hybrids anywhere; and that the only Savanna Elephants that occur in central Africa are those in Chad and N Central African Republic. It is quite likely that all three assumptions are incorrect, and that an unknown number of

elephants here allocated to the forest kind are in fact Savanna Elephants (or hybrids) and vice versa. However, given the relatively wide error margins in the estimates, the fact that these figures are rounded, and that there remain considerable amounts of range for which no estimates of abundance are available for either taxon, it is likely that any incorrect allocation would get lost in the general imprecision.

As noted above, determining country-level estimates is complicated, and so we report here only on those countries where available national estimates are very clearly *L. africana* only. For this reason, below we omit discussion of national estimates for all of West Africa (noting only that a recent aerial count in the Gourma region of Mali produced a minimum of 344 elephants; Bouché *et al.* 2009) and several countries elsewhere around the forest rim that likely harbour hybrids (such as Cameroon, Central African Republic and Uganda). In addition, we do not consider national estimates for those countries in which the proportion of surveyed range is so small as to render the national estimate meaningless (e.g. Angola, with population estimates available for only 5% of estimated elephant range in the country). We caution further that increasing levels of ivory poaching since 2007 may render these estimates inaccurate.

The largest number of Savanna Elephants in Africa is found in southern Africa, with a population of nearly 321,000, nearly twice as high as East Africa, mainly in the six countries of Botswana, Zimbabwe, Zambia, South Africa, Namibia and Mozambique (Blanc *et al.* 2007; Table 9). The largest population survives in Botswana, where recent estimates put the population at around 150,000 animals surviving in an area of about 100,000 km², followed by Zimbabwe with approximately 90,000 animals (Blanc *et al.* 2007). Today, Malawi has fewer than 3000 elephants, while Swaziland (where the resident

Table 9. Country and regional elephant numbers for southern Africa.

Country	Elephant numbers				Range area (km ²)	% of regional range
	Definite	Probable	Possible	Speculative		
Angola	818	801	851	60	406,946	31
Botswana	133,829	20,829	20,829	0	100,265	8
Malawi	185	323	632	1,587	7,538	1
Mozambique	14,079	2,396	2,633	6,980	334,786	26
Namibia	12,531	3,276	3,296	0	146,921	11
South Africa	17,847	0	638	22	30,455	2
Swaziland	31	0	0	0	50	0
Zambia	16,562	5,948	5,908	813	201,247	15
Zimbabwe	84,416	7,033	7,367	291	76,931	6
Total	297,718	23,186	24,734	9,753	1,305,140	39

Source: Blanc *et al.* (2007)

Table 10. Country and regional elephant numbers for eastern Africa.

Country	Elephant numbers				Range area (km ²)	% of regional range
	Definite	Probable	Possible	Speculative		
Eritrea	96	0	8	0	5,293	<1
Ethiopia	634	0	920	206	38,365	4
Kenya	23,353	1,316	4,946	2,021	107,113	12
Rwanda	34	0	37	46	1,014	0
Somalia	0	0	0	70	4,526	<1
Sudan	20	0	280	0	318,239	36
Tanzania	108,816	27,937	29,350	900	390,366	44
Uganda	2,337	1,985	1,937	300	15,148	2
Total	137,485	29,043	35,124	3,543	880,063	26

Source: Blanc *et al.* (2007)

population was extirpated around the 1890s; Monadjem 1998) has the smallest population of only 31 individuals.

In eastern Africa, elephant range spans more than 880,000 km², of which 80% is accounted for by Tanzania and Sudan (Blanc *et al.* 2007; Table 10). Eastern Africa suffered massive declines of elephants between 1960 and 1990 when 85–98% of the elephants were killed for ivory; some populations have never recovered. Rwanda, Eritrea and Somalia contain only tiny fragmented elephant populations (estimated to number fewer than 300 individuals between them) and even these are thought to be in decline. Elephants were exterminated from Burundi in the 1980s. Sudan boasts a large elephant range, and although Blanc *et al.* (2007) indicated that elephants numbered only 300 individuals, a survey by Fay *et al.* (2007) estimated the population at ~7000. Despite huge losses, Tanzania and Kenya remain strongholds for East African elephants with estimates of 135,000 and 25,000, respectively (Blanc *et al.* 2005, 2007), although current poaching is likely to have eroded these figures. Uganda's elephants (including some Forest Elephant populations) have recovered from a few hundred to nearly 3000 individuals today after a decline of almost 99% (according to the Uganda Wildlife Authority in 2002). Elephant range in some parts of East Africa has been significantly affected by armed conflict and civil disturbances. In other areas it is being reduced by expanding human settlement.

In Chad, the only central African country known to harbour Savanna Elephants only, Blanc *et al.* (2007) estimated the population at nearly 6000 animals, with by far the largest population in Zakouma N. P. However, poaching has had a significant impact on this figure, with the population in Zakouma now at an historical low (Poilecot 2010, Bouche *et al.* 2011).

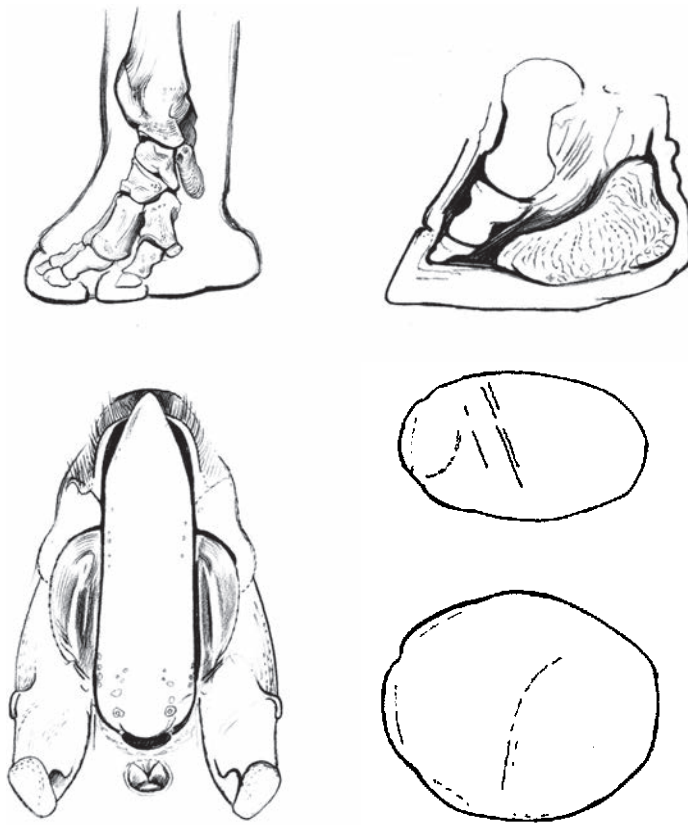
Adaptations Elephants exhibit some characteristics that have long been interpreted in terms of an aquatic or semi-aquatic ancestry (Andrews 1906, Matsumoto 1923, Osborn 1936, Janis 1988, Gaeth *et al.* 1999), a view initiated by the undoubted relationship between proboscids and sirenians and by the ambiguity of an Eocene fossil, *Moeritherium*, which has been variously allied with one or other order. This has stimulated enquiry into the possibility of retentions from an ancient aquatic ancestry in living elephants. Among the suggestions are the development of a trunk, internal testes and the development of nephrostomes in the mesonephric kidney (Gaeth *et al.* 1999). The latter authors also noted that nephrostomes, briefly present during

early stages of foetal development in many mammals, might last longer during a particularly long gestation; as Shoshani & Tassy (2005) have pointed out, this carries no implication of an aquatic phase. Supposedly related to the development of a trunk, two additional adaptations have been noted. Living adult elephants have little or no pleural cavity, and the lungs are fused to the chest wall and diaphragm. This adaptation is thought to be a protection against the high negative intra-thoracic pressures attained when water has to be sucked up the trunk before drinking (Todd 1913, Short 1962). Any connection with an aquatic origin is contradicted by wholly aquatic sirenians having normal lungs with pleural cavities (Rommel & Reynolds 2000).

As elephants ventured into more arid lands in the Miocene, the pharyngeal pouch, a structure unique to elephants, was naturally selected for water storage. Elephants are able to store 4.5 l of water in this pouch located at the base of the tongue. During hot weather elephants can be observed to withdraw water stored there by inserting the trunk up to the pharynx, extracting water therein and spraying it over their backs, under body and ears (Kingdon 1979, Shoshani 1997). While this behaviour has been observed elsewhere, desert-dwelling elephants use this method routinely (Leggett 2004). Several other behavioural adaptations allow elephants to survive very harsh environments, including the ability to go without water for periods of up to five days (Viljoen & Bothma 1990, Leggett 2006b) and young obtaining moisture by eating the moist dung of adults. Another interesting thermoregulatory mechanism involves adult animals urinating on sand and then both the young and old scooping and throwing urine-soaked sands over their bodies (Leggett 2004). Finally, Kahl & Armstrong (2000a) observed juveniles drinking urine excreted by adult elephants during a severe drought in Zimbabwe.

Elephants use their ears in display, in sound localization and as a cooling mechanism. The skin on the backs of the ears is very thin and is laced with numerous blood vessels, which, when fanned, help to reduce the elephant's overall body temperature. Wright & Luck (1984) measured water loss from the skin of a 1200 kg elephant and concluded that it was capable of losing an average of 0.23 l of water/m²/h (despite the fact that the skin lacks sweat glands). The estimated surface area was 11 m², so that some 2.5 l of water would be lost per hour.

Being large bodied, elephants are naturally able to produce low frequency sounds, but several adaptations have allowed them to produce even lower frequencies (down to 5 Hz). First, the trunk itself



Top left: *Loxodonta africana* carpal area showing toes contained within hoop of tissue, skin and nail.

Top right: Foot profile to show pad of elastic tissue.

Lower right: Footprints of left hindleg (above) and left foreleg (below).

Lower left: Foetal lower jaw and tongue, showing remarkable length.

adds about 3 m on to the length of the resonating chamber. Second, the hyoid apparatus is attached to the skull by muscles, tendons and ligaments, rather than bones as in most other mammals. This looser arrangement allows for a greater movement and flexibility of the larynx and, therefore, facilitates the production and resonance of low-frequency sounds (Shoshani 1998). Third, the looser arrangement also houses the pharyngeal pouch that permits a further enlargement of the resonating chamber by lowering the loosely attached larynx.

The long ear canal, large tympanic membrane and massive ossicles of elephants reflect special adaptation to low-frequency hearing. The enormous cranium has allowed the evolution of an outer ear canal of about 20 cm in length, thus providing adequate protection for its very large tympanic membrane that in turn allows the high signal-to-noise ratios so important at very low frequencies (Nummela 1995). Massive ossicles seem to occur in animals that receive acoustic information through bodily vibrations (Reuter *et al.* 1998). Elephants and sirenians are unique among modern mammals in having reverted to a reptilian-like cochlear structure (Fischer 1990, O'Connell *et al.* 1998). Since the cochlear structure of reptiles facilitates a keen sensitivity to vibrations it has been suggested that the similar structure in elephants allows them to detect vibrational signals, too (O'Connell *et al.* 1998).

The trunk serves an obvious role in the acquisition of food and water and in tactile communication, but it is also important in chemical communication, for tactile investigation of the

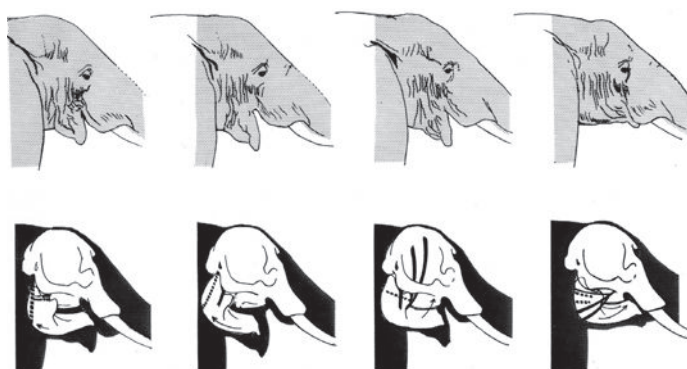
environment, olfaction and vomerolfaction (Rasmussen & Schmidt 1998). The tip of the trunk houses two types of vibrissal hairs, small corpuscles and free nerve endings. These features allow the trunk tip to detect vibrations, finely manipulate objects and transfer liquids (Rasmussen & Munger 1996). Within the nasal cavity are seven turbinates specialized for olfaction and detection of hormones emanating from urine, faeces, and from secretions of the trunk, mouth and temporal glands. The tip of an elephant's trunk has densely packed cells known as Pacinian corpuscles that are sensitive to vibrations (Rasmussen & Munger 1996). Elephants often make use of the trunk to throw objects or materials such as mud, soil and vegetation in aggressive encounters and for exploration (Wickler & Seibt 1997), and are reputed to be able to throw with great precision (Chevalier-Skolnikoff & Liska 1993, J. Poole pers. obs.).

Also unique to elephants is the temporal gland, derived from apocrine sweat glands (Estes & Buss 1976), located subcutaneously on the side of the face with its orifice located between the ear and the eye. In Savanna Elephants the gland appears to have different functions in ♂♂ and ♀♀. Females, less frequently young ♂♂ and rarely adult ♂♂ secrete a dark, watery liquid when they are socially aroused, frightened, or subjected to a variety of stresses (Poole & Granli 2003, J. Poole pers. obs.); adult ♂♂ alone secrete a more viscous, chemically distinct substance during their annual period of sexual activity known as musth (Poole 1987).

The brains of *Loxodonta africana* rank among the highest for absolute and relative mass, cortical expansion and complexity, features comparable only to those of some of the Cetacea, man (Cozzi *et al.* 2001) and the great apes. The elephant's brain weighs up to 6 kg (averaging 4.8 kg; Shoshani *et al.* 2006a) and an EQ (encephalization quotient – the ratio between the observed and expected brain weight for a defined body weight; Jerison 1973) of 1.7 to 2.1 (Eisenberg 1981, Shoshani 1998, Shoshani *et al.* 2006a) is comparable with the larger primates. Their large and convoluted neocortex associated with a relatively low density of neurons may indicate that cognitive faculties concentrated in long-term processing and in synthesizing a great diversity of input over time (Hart *et al.* 2008). Hakeem *et al.* (2009) have documented the presence of a type of nerve cell (e.g. Von Economo Neurons) that, in great apes and the Cetacea, has been associated with neural circuitry involved in social awareness and, potentially, Theory of Mind.

The extremely large and convoluted temporal lobes and underlying hippocampus of the elephant's brain likely function in their prodigious memories (for places, individuals and events) and their ability to navigate over long distances (Shoshani 1998, Hakeem *et al.* 2005). A flood of recent publications indicates that elephants are self-aware (Plotnik *et al.* 2006), and capable of a wide range of higher-level cognitive behaviours such as: empathizing with others (Douglas-Hamilton *et al.* 2006, Bates *et al.* 2008a); rudimentary teaching (Bates *et al.* 2010) suffering from the long-term effects of trauma (Bradshaw *et al.* 2005); distinguishing between the many voices (McComb *et al.* 2000) and scents (Bates *et al.* 2008b) of their relatives and companions; making subtle discriminations between predators (Bates *et al.* 2007); recognizing the bones of their own species (McComb *et al.* 2006); using simple tools (Hart *et al.* 2001); social learning (Lee & Moss 1999); and vocal imitation (Poole *et al.* 2005).

Foraging and Food Though primarily browsers, elephants are mixed feeders and can switch to a grass-dominated or browse-



Loxodonta africana chewing cycle. Above: stills from film. Below: diagrams of a single cycle of mandible action.

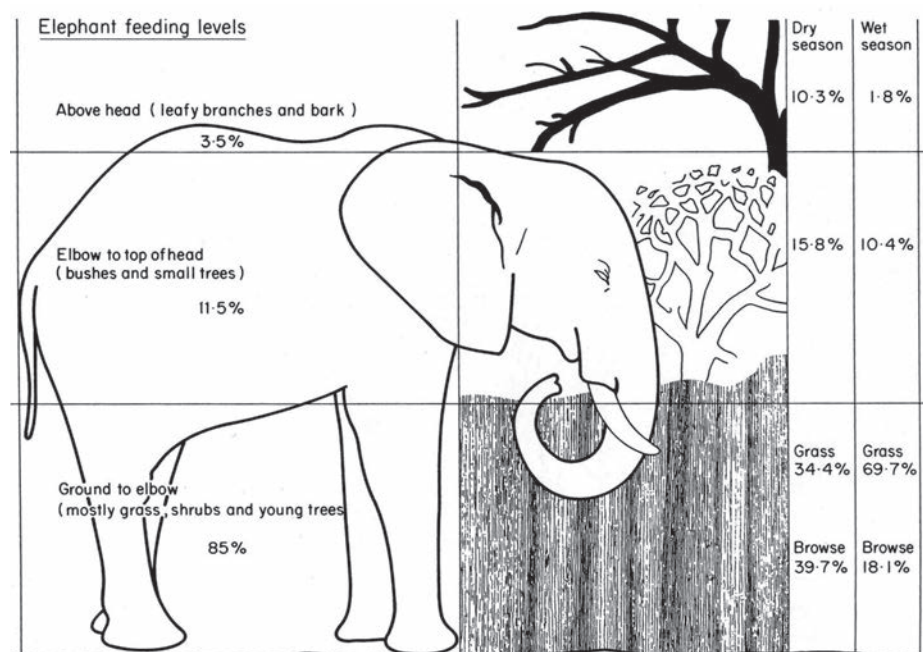
dominated diet depending on which provides the highest ratio of protein to fibre; thus, diet changes with season and habitat (e.g. Buss 1961, Laws *et al.* 1975, Williamson 1975). Seasonal movement patterns through different habitats reflect an attempt to achieve the most nutritious diet. Grass predominates in the wet season and woody plants in the dry season. In Kruger N. P., studies involving stable carbon isotope analysis of faeces reveal that elephant populations from the northern part of the park consistently eat higher proportions of grass (40%) during the dry season than do their southern counterparts (10%) (Codron *et al.* 2006; and see Vogel *et al.* 1990). The wet-season diets of elephants from northern and southern parts include similar amounts of grass (50%), because elephants in the south, but not in the north, ate significantly more grass during this time. Codron *et al.* (2006) postulate that the relative homogeneity of woody vegetation in the north of Kruger N. P. (where the variable, and questionable, nutritive value of the dominant Mopane *Colophospermum mopane* may deter browsing) may force elephants to opt for alternative food sources like grass throughout the year. The wider diversity of woody plant species in southern Kruger N. P. allows elephants to exploit this browse more

efficiently, especially during the dry season when grass production is low (Codron *et al.* 2006).

Among woody plant resources, forbs and shrubs form the main component of the diet, and elephants will pull down entire trees to consume leaves and bark. The bark of certain trees, such as several *Acacia* species (*Acacia tortilis*, *A. xanthophloea*, *A. nigrescens*) and *Marula* *Sclerocarya birrea* is especially favoured; preferred species have strong, pliable bark, which is associated with a high proportion of fibres (Malan & Van Wyk 1993). The bark is loosened with the tusks and then stripped off. Elephants will also take the roots of certain woody species such as *Combretum* spp., *Dalbergia melanoxylon* and *Terminalia* spp.

Due to their large size and digestive system specialized for rapid throughput of coarse vegetation, elephants satisfy their dietary requirements by consuming considerable quantities of food each day (40–80 kg dry mass, or 1–2% of their body weight; Lindsay 2011). To accomplish this elephants feed for 60% of a 24-hour day and are active for 18–24 hours. While adults usually rest standing up during the day, at night they frequently sleep lying down for a few hours. Foraging is achieved with their incredibly versatile trunk, efficiently selecting individual items of fruit, tugging up tufts of grass, or stripping the bark off tree trunks. The 2–3 pairs of lozenge-shaped molars crush the forage by sliding forwards and backwards. Digestion is inefficient and elephant dung is fibrous. Lactating ♀♀ eat proportionately more than non-lactating ♀♀, and bulls consume greater browse content than cows.

Elephants need to drink in the order of 160 l per day. Dependence on water can force elephants to remain in less preferred, and even degraded, habitats during the dry season, and this may be the driving force behind the seasonal movements and annual migrations (some up to hundreds and even thousands of kilometres) observed in many populations. When freshwater is not available, elephants will drink brackish water, although this has proved fatal if water salinity is unusually high. Weir (1972) found that the largest congregations of elephants in Hwange N. P. gathered at man-made waterholes where the water was rich in sodium (adult elephants require 75–100 g salt



per day); sodium content was usually correlated with carbonate and bicarbonate alkalinity. Elephants also utilized local concentrations of water-soluble sodium in the soil (a practice termed geophagy, the eating of saline or calcareous soils). Ruggiero & Fay (1994) recorded geophagia of enriched termitarium soils, where sodium may be a major attraction, and elephants are well known for making use of the salt licks in the caves of Mt Elgon, where they pry off chunks of the cave walls with their tusks and consume the volcanic agglomerate (Redmond 1982). In Hwange N. P., ♀♀ consume more mouthfuls of soil and spend a greater part of their activity budget feeding on soil than do ♂♂, as they probably have greater requirements due to pregnancy and lactation (Holdo *et al.* 2002). Holdo *et al.* (2002) found that soils consumed by elephants differed from other soils primarily in their high sodium content, and that elephants in non-Kalahari-sand habitats generally do not appear to create or use licks, probably because they are able to obtain their sodium requirements from ubiquitous sodium-rich water supplies (which do not occur naturally in Kalahari-sand habitats).

The activity of elephants can have a dramatic effect on the existing vegetation, and studies of the 'elephant problem' have dominated the literature since the 1970s. In eastern and southern Africa, savanna woodlands have been changed to less wooded grasslands and treeless grasslands (Buechner & Dawkins 1961, Savidge 1968, Laws 1970, Laws *et al.* 1975, Cumming *et al.* 1997). Diverse ecosystem hypotheses have been proposed to explain the elephant habitat interactions from equilibrium theory to stable cycles and multiple stable states. For such long-lived organisms as elephants and trees, quantifying relationships over many decades is virtually impossible as disturbances such as poaching or range contraction become superimposed on the interaction and obscure processes. However, modelling and empirical studies of the Masai Mara ecosystem have provided insights. Dublin *et al.* (1990) proposed that elephants and fire interact in woodlands to drive the change in state to grasslands, while elephants alone can maintain the grassland state. In this ecosystem two equilibria are possible: high tree density and low elephant density, or low tree density and high elephant density. Other states are not stable and reversion to one of the other states will occur. A change in state from high tree density is dependent on an exogenous force, fire, while elephants can maintain the low tree density once the change in state has occurred. Research in other sites suggests that woodlands can be converted to grassland by elephants alone if the density of elephants is high enough. Such changes have occurred in Murchison Falls N. P. in Uganda and Tsavo N. P. in Kenya. Very high local densities, and occupancy by bulls, can accelerate the process. In the Mwaluganje Elephant Sanctuary in the Shimba Hills ecosystem of Kenya, elephants concentrate in a deciduous forest where local densities can exceed 6/km² compared with 1.5/km² for the entire ecosystem. The killing of trees by debarking and pushing, primarily by bulls, has resulted in woodland decline (Kahumbu 2002). Similar findings in other bull areas have been reported in the Ngorongoro Crater, Tanzania and Nazinga Ranch, Burkina Faso.

In Kruger N. P., concern over excessive impacts of elephants on vegetation and biodiversity led to culling, which aimed to keep the population at around 7000 individuals ($\pm 2.5/\text{km}^2$). This policy was partially successful in minimizing these impacts, but even at this level, elephants induced detectable changes, including elimination of

certain species from some landscapes and changes from tree savannas to shrub savannas in others (reviewed by Whyte *et al.* 2003).

It is believed that in the past the elephant–habitat relationship was spatially dynamic, influenced by climatic variation and successional patterns that involved other herbivores and Pleistocene hunter-gatherers and more recent man. Vegetation modification caused by elephants is a normal activity and can contribute to beneficial changes in habitat diversity and biomass turnover. Confinement and concentration of elephants in declining ranges in parts of Africa has caused elevated densities and striking changes that can be detrimental to species diversity and can be a major cause of concern for wildlife management authorities.

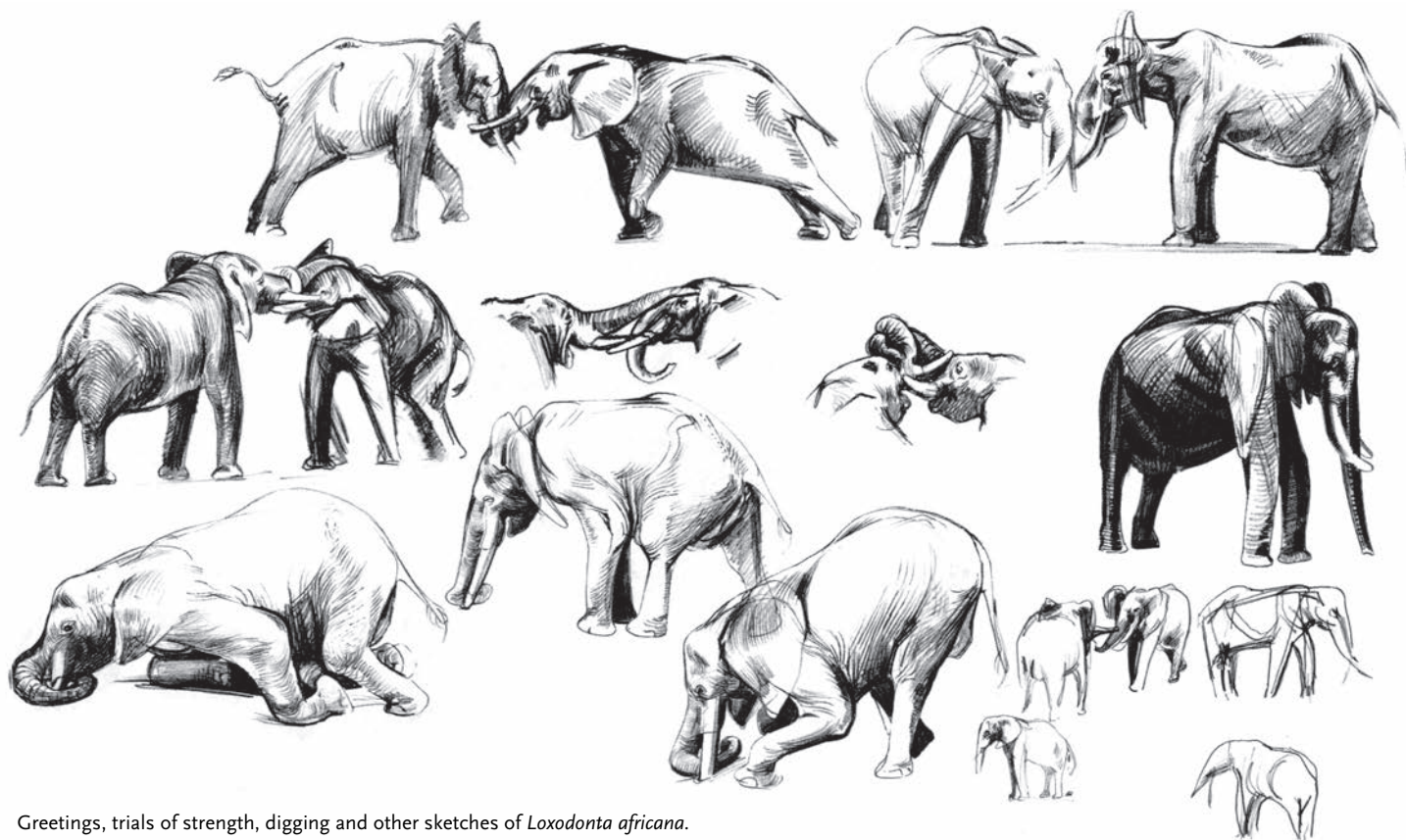


Pacing *Loxodonta africana*, note placing of hindfoot on spot vacated by forefoot.

Social and Reproductive Behaviour The social network of Savanna Elephants is unusually large, radiating out from the mother–offspring bond through family, bond group, clan, subpopulation, to independent adult ♂♂, and beyond the population to strangers (Moss & Poole 1983, Archie *et al.* 2005, Wittemyer *et al.* 2005, Moss & Lee 2011). Their fluid society is characterized by group fission and fusion: the membership of groups changes often, forming and splitting along lines that may be predicated on the basis of close social bonds, kinship, home-range, season and, in the case of ♂♂, their reproductive state. Fission–fusion sociality combined with the close and enduring cooperative social relationships as found in elephants is rare in the animal kingdom (Archie *et al.* 2005).

The social lives of adult ♀♀ and ♂♂ are very different. The basic social unit of adult ♀♀ and young elephants is the family group or unit (Douglas-Hamilton 1972). Family size ranges from two, a mother and her youngest calf, to 45 or more individuals and may span four generations of related individuals (Moss 1988, Moss & Lee 2011). Rarely, families may be composed of unrelated individuals (Archie *et al.* 2005). Families vary in their degree of cohesion. Over time families may split to form bond groups or, sometimes, fuse to form new families (Moss & Lee 2011). Bond groups may comprise as many as five family units. Members of a family or a bond group may be distinguished by their pattern of greeting behaviour, coordinated movement and strong affiliative and protective behaviour toward one another. Families using the same dry season home-range have been referred to as belonging to a clan (Moss & Poole 1983). These individuals meet on a regular basis. Elephants are able to discriminate between these more familiar and less familiar elephants on acoustic characteristics alone (McComb *et al.* 2000). Elephants are also able to use scent to discriminate between individual family members and keep track of their specific locations (Bates *et al.* 2008b). In addition, they are able to discriminate between different groups of humans, reacting more fearfully to the scent of those groups who represent a possible threat than to those groups who do not (Bates *et al.* 2007).

During drier periods when food is scarce elephants tend to split up into small groups composed of families or fragments of families. However, when food resources become more plentiful, these smaller



Greetings, trials of strength, digging and other sketches of *Loxodonta africana*.

groups amalgamate and elephants are more likely to be seen in larger aggregations. These groupings may represent entire families, portions of a bond group, several bond groups or even the portions of several clans and independent adult ♂♂ (Poole & Moss 1989).

Group size varies from lone ♂♂ to aggregations of several hundreds or thousands of individuals (although as a consequence of poaching aggregations of more than a few hundred elephants are extremely rare). Group size varies tremendously depending upon the season, habitat type and population. In general, forest or thick bushland tend to support smaller groups of elephants, while large aggregations of elephants are more likely to be observed in open bush or wooded grassland.

Males begin to spend time away from their families at ~ 9 years old and by about 14 years of age they have left their natal families (Lee & Moss 1999). Newly independent ♂♂ usually spend several years in the company of other families near to their natal clan area, either associating with one particular family or moving from family to family, before they embark on their lives as fully adult ♂♂ (Lee *et al.* 2011b). As adult ♂♂ their lives fluctuate between periods of sexual activity and inactivity (Poole 1982, 1987, 1989b).

Elephants are not territorial, but ♀♀ are wary in their use of areas 'belonging' to the families of other clans (J. Poole pers. obs.). Home-range size varies tremendously from 50 km² to more than 12,000 km². To a large extent the variation can be accounted for by habitat type; elephants living in harsh desert environments typically have the largest home-ranges (see Habitat). Home-range also varies considerably within populations and individual preference, tradition, inter-family relationships, sex, habitat and human activities, all play a role in determining patterns of occupancy (Croze & Moss 2011). In the Kruger N. P. ranges of adult ♀♀ varied in size between

86 km² and 2776 km², with a mean of 880 km² (Whyte 2001b). In N Botswana home-range size rose significantly with increased distance to dry season surface water, and migratory herds travelled up to 200 km in search of water during the dry season; home-range size averaged 1091 km² (range 447–3309, n = 9) and 1699 km² (range 52–6412, n = 9), using satellite collars and radio collars, respectively (Verlinden & Gavor 1998). In N Kenya, home-ranges ranged from 102 to 5527 km² (n = 20) (Thouless 1996), while in the more arid environments of Namibia, they varied between 2136 and 10,738 km², with a mean of 5860 km² (minimum convex polygon; Lindeque & Lindeque 1991; and see Leggett 2006a).

Female elephants typically utilize their 'clan area' during the dry season and expand beyond this area to meet other clans during periods of food abundance (Moss & Poole 1983, Poole & Moss 1989). Adult males utilize a 'bull' or 'retirement area' during sexually inactive periods, but leave this area during sexually active periods to search over a wide area for receptive females (Moss & Poole 1983, Poole & Moss 1989). At independence young ♂♂ leave their family's clan area and over a period of decades gradually define their own particular 'bull area'. Chiyo *et al.* (2011) found that associations in bull areas were positively correlated with genetic relatedness, suggesting that kinship influences patterns of male associations.

By age 30 the majority of ♂♂ have experienced their first musth (range 17–34; average first musth 28; Poole *et al.* 2011). Musth is a period of heightened sexual and aggressive activity (Poole & Moss 1981, Hall-Martin & Van der Walt 1984), characterized by a distinct posture, the musth walk, swollen and secreting temporal glands, the dribbling of strong smelling urine (Poole & Moss 1981, Poole 1987) and a very low frequency vocalization, the 'musth rumble' (Poole 1987, 1999a, Poole *et al.* 1988). During musth, male elephants experience

dramatic surges of circulating testosterone (Hall-Martin & Van der Walt 1984, Poole *et al.* 1984), interact aggressively with other large adult ♂♂, particularly those in musth, and spend much of their time searching for, attempting to gain access to, or guarding oestrous ♀♀ (Poole 1987, 1989b, c, Poole & Moss 1989). The duration of musth is age-related; musth periods are asynchronous and each male is on his own particular cycle (Poole 1987). Musth has a dramatic effect on the relative dominance ranks of ♂♂ (see Poole 1989b); with few exceptions, a musth ♂, whether large or small, ranks above all non-musth ♂♂. Musth ♂♂ interact aggressively whenever they meet, and the presence of an oestrous ♀ is not a prerequisite for a fight (Poole 1989b).

Females come into oestrus about once every 4.5 years (Moss 2001), though in other populations longer intervals have been observed. Behavioural oestrus lasts 4–6 days (Moss 1983, Poole 1989c). Diagnostic behaviours include wariness, the oestrous walk, the chase, mounting, mating, guarding and consort behaviour (Moss 1983, Poole 1989c). During early and late oestrus the ♀ is pursued and sometimes mounted, usually unsuccessfully, by young, non-musth ♂♂; the ♀ is guarded and mated by a musth male(s) during the mid 2–3 days of peak oestrus. Owing to the intense competition from older ♂♂ (Poole 1989b) and strong female preferences for mature individuals (Moss 1983, Poole 1989c), young ♂♂ have very limited mating opportunities during peak oestrus. Once a ♀ goes into consort with a musth ♂ mating occurs relatively infrequently (~ several times per 24 hrs) and lasts about 45 seconds. A mated ♀ rumbles repeatedly with a series of ‘post-copulatory’ or ‘oestrous’ rumbles (Poole *et al.* 1988). Her calling is typically joined by loud and excited rumbles, trumpets and roars by nearby elephants (usually members of her family) and is known as the ‘mating pandemonium’ (Poole *et al.* 1988, Poole 1989c, Poole & Moss 1989).

With the exception of musth, relationships between elephants are, in general, remarkably amiable. Within families and bond groups interactions are, as a rule, highly cooperative and interactions between non-relatives are seldom unfriendly. However, the relative level of agonistic and amiable behaviour differs from population to population depending upon the availability of resources. In areas where water, minerals or high quality food is limited or unevenly distributed, agonistic behaviour is more common (J. Poole pers. obs.). Among sexually inactive ♂♂ relationships are ‘gentlemanly’, while those between sexually active ♂♂, particularly those in musth, become highly aggressive and combative (Poole 1987). Older ♂♂ are larger and are generally dominant to younger ♂♂ (Poole 1989b).

Agonistic and affiliative displays take many forms (Poole & Granli 2011). Very simply, an elephant may threaten another by attempting to appear larger, approaching closer and using a variety of threatening ear and trunk postures, vocalizations and/or secretions. Submissive behaviour involves attempting to appear smaller, adopting avoidance behaviour and is associated with another set of ear and trunk postures as well as particular vocalizations (Langbauer 2000; for a full description and images see <http://www.ElephantVoices.org> and Poole & Granli 2011). The survival of calves is, to a great extent, dependent upon the strength of bonds between individual family members and these are maintained by frequent acoustic, chemical and tactile demonstrations of friendly affiliation and solidarity.

Elephants communicate with one another using visual and tactile displays, and vocal and chemical signals. Visuals and tactile displays use

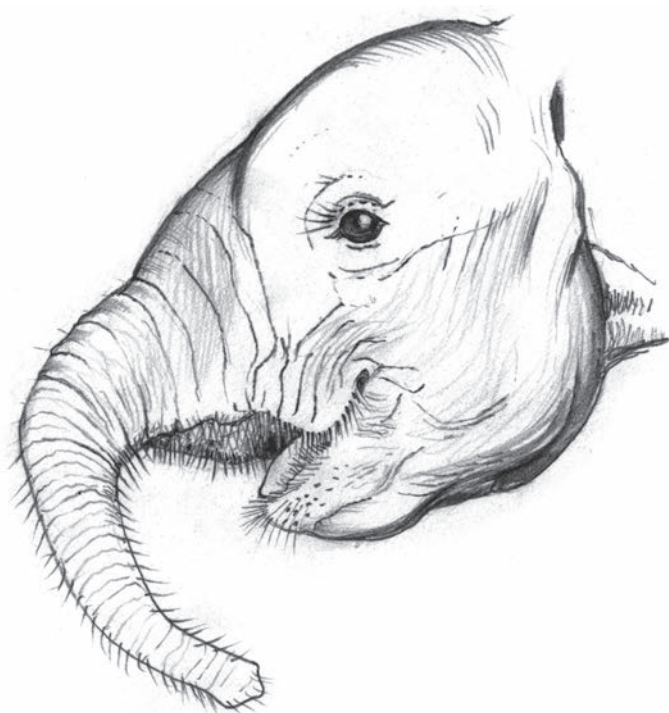
a combination of trunk, ear, limb and body postures and movements and signal a broad range of agonistic, defensive and affiliative gestures and complex emotional responses (an extensive description of the different postures and gestures can be viewed on www.ElephantVoices.org; Poole & Granli 2011; see also Kahl & Armstrong 2000b). Sources of chemical signals include fluids from the anogenital tracts and the temporal glands, and saliva, mucus secretions from the eye, ear and interdigital glands may also be involved (Rasmussen & Schmidt 1998). Chemical signals play an essential role in elephant social and reproductive communication and have been the subject of in-depth study (e.g. Rasmussen *et al.* 1996, Rasmussen & Schmidt 1998, Rasmussen & Krishnamurthy 2000, Rasmussen & Wittemyer 2002).

Vocal communication has also been intensively studied. Savanna Elephants produce a broad variety of sounds with components ranging from 9 Hz to over 9000 Hz; Poole 2011), including very low frequency rumbles and higher frequency trumpets, snorts, screams, barks, roars, cries and other calls (Berg 1983, Poole *et al.* 1988, Poole 1994, Langbauer 2000, Soltis *et al.* 2005a, b, Poole 2011). Elephants are able to coordinate their movements by communicating with powerful, very low frequency sounds (Payne *et al.* 1986, Poole *et al.* 1988, Langbauer *et al.* 1991, Garstang *et al.* 1995, Larom *et al.* 1997, McComb *et al.* 2000). Elephants communicate a broad range of complex messages related to interactions of an agonistic, defensive, affiliative, parental care, mating and social nature. Recently, Poole *et al.* (2005) discovered that elephants are capable of vocal production learning (imitation) and posit that this rare talent may have evolved to facilitate social bonding and cohesion in the elephants’ highly dynamic fission–fusion society.

Elephants can recognize the specific voices of other elephants up to 2.5 km away, though more usually at distances of 1–1.5 km (McComb *et al.* 2002). Under certain conditions, such as exist in the Etosha N. P. in the dry season, elephants may hear the calls of conspecifics at distances exceeding 10 km (Garstang *et al.* 1995). Furthermore, when an elephant vocalizes with a low frequency rumble an exact replica of this signal propagates separately in the ground (O’Connell *et al.* 1998) and elephants respond appropriately to this signal component (O’Connell *et al.* 2006, 2007).

Comfort behaviour includes: water-bathing; mud-wallowing; dust-bathing; scratching the body by rubbing on trees, logs or anthills; scratching the body (sometimes to remove parasites) with sticks or other objects held in the trunk; swinging the tail, trunk or branches held in the trunk to repel insects; yawning; stretching; exhaling loudly or ‘blowing’ through the trunk; rubbing the ears with the curved distal portion of the trunk; placing the tip of the trunk over the end of a trunk to reduce the itching; scrunching up the trunk and making a ‘squelching’ sound to reduce itchiness in the trunk; and ear-flapping to cool the body.

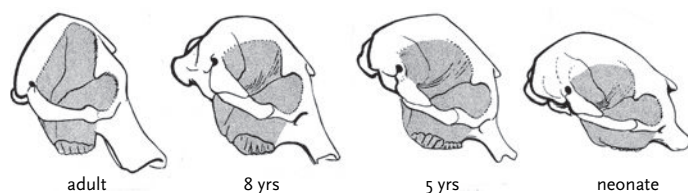
Birth may take place wherever the ♀ finds herself, but typically occurs in the company of other family members and most often at night. Elephants usually give birth standing with bent hindlegs, but may lie down prior to the birth. Signs of an imminent birth may include: kneeling down or squatting (straining during contraction); lying down and getting up again; kneeling, getting down on all four legs; kicking backwards; beating bushes; vaginal secretions; frequent urination; intense interest by other family members (smelling and vocalizing) in the vaginal orifice and secretions of the pregnant ♀; swollen vulva; and a bulge protruding under the tail (foetus in birth canal) (Moss 1992, Poole 1996, 1999b). The actual birth happens



Vibrissae around mouth and trunk of foetal *Loxodonta africana*.

quickly, and the foetus is propelled forward with considerable force. The infant is usually born partially covered by the foetal sac and placenta. Mother and other family members use their tusks to gently free the infant from the birth sac, and show great interest in the placenta, carrying it about, tossing it in the air and swinging it back and forth with their trunks. With assistance from its mother and other adult ♀♀ an infant is usually able to stand within 15 minutes of birth. The birth itself is a momentous occasion for an elephant family and is accompanied by intense rumbling, screaming and trumpeting that may last up to 40 minutes (Poole 1999b, J. Poole pers. obs.). Young ♀♀ between the ages of three and eight years old show intense interest in newborn calves, following the mother and infant around and offering comfort and assistance (Moss 1992).

Young elephants depend on their mothers for milk for two years. After this age, they can support themselves on solid foods, although most calves will carry on sucking for as long as the mother will tolerate it. During the first five years of life, calves develop their social skills and form relationships with members of their family. Sons and daughters are treated differently by mothers and develop sex-specific behaviour early in life (Lee 1986, Lee & Moss 1999). Sons are more exploratory, seek out playmates from unfamiliar families, and are allowed by mothers to suck more frequently than are daughters. Daughters are more socially interactive within the family, and are



Changes in skull form with age in *Loxodonta africana*.

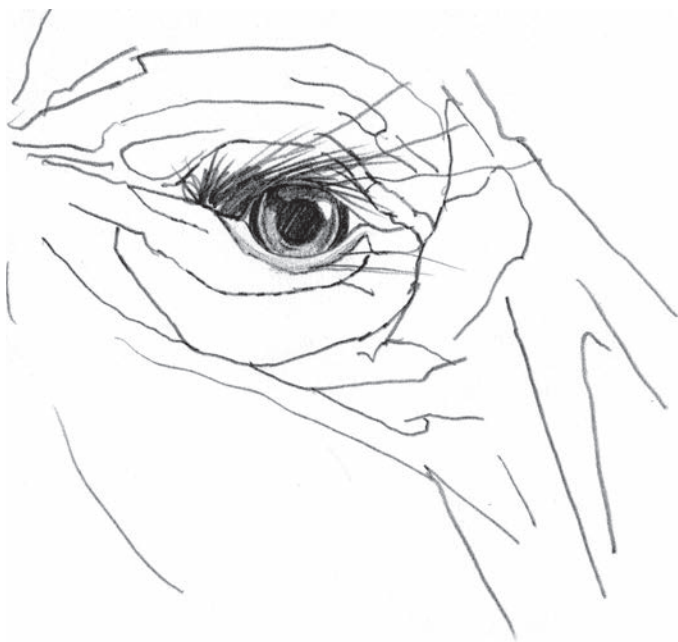
less demanding of milk from their mothers. The young ♀♀ within a family play a critical role in the survival of calves, shepherding them, protecting them from obstacles or stresses in the environment and ensuring that calves are safe from predators (Lee 1987).

Elephants may show unusual interest in and/or irritation with other species. Infants and calves enjoy chasing birds, monkeys and other small mammals in play. Larger calves and juveniles, too, will playfully chase a variety of animals including birds, warthogs, antelopes (including buffalo), hyaenas and primates. Adults tend to have a more competitive interaction with other species, displacing other animals at waterholes, putting an end to the cavorting of wildebeests, chasing predators (Lions *Panthera leo*, Spotted Hyaenas *Crocuta crocuta*) and scavengers (jackals, vultures) off kills or away from the vicinity of the family. Elephants are one of the few herbivores that purposefully kill other species, for example, by stepping on birds, hares and other small mammals that have startled them, and goring, and kneeling on, people and their livestock. Young orphaned elephants introduced to wildlife parks have displayed intense aggression towards White Rhinos *Ceratotherium simum* (e.g. Slotow & Van Dijk 2001, Slotow *et al.* 2001; and see Berger & Cunningham 1998). The killing of other animals appears to cause an elephant great distress, resulting in highly aggressive and unusual behaviour, refusal to leave the body, uprooting and trampling of vegetation in the vicinity of the body, and even covering the body in vegetation (J. Poole pers. obs.). Elephants have even been observed to chase Lions and Spotted Hyaenas off a wildebeest kill and then stand over the dead animal (N. Njiraini pers. comm.).

Reproduction and Population Structure The longest study of demography among free-ranging Savanna Elephants comes from the Amboseli population where data have been collected from individuals of known age and identity for 35 years (Moss 2001, Lee *et al.* 2011a). The information that follows comes largely from this study supplemented with additional information from other regions.

The pattern of breeding varies with habitat type and rainfall conditions, though most authors report some seasonality of births coinciding with the months of high rainfall (Hanks 1969, Laws & Parker 1968, Laws 1969, Sherry 1975, Smuts 1975, Craig 1984, Lindeque 1988). In Amboseli where 1030 birth dates were known to within two weeks, births occurred in every month, but 81% occurred between Nov and May (Moss 2001). In general, ♀♀ conceive when they are in good condition during periods of higher food availability. Birth rates show peaks and troughs over time and in some populations (Moss 2001) ♀♀ become synchronized in a 4–5 year cycle of conceptions and births.

Gestation has been calculated as 660 days (Perry 1953, Laws *et al.* 1975, Moss 1983, Poole *et al.* 2011). Twinning is rare. In Amboseli, where the live births of 1192 individuals have been recorded (Moss 2001), one case of twins was observed (0.08%), and Smuts (1975) recorded only two sets of twins out of more than 350 embryos and foetuses examined in Kruger N. P.; however, the incidence was much higher in Etosha N. P. (10%; Lindeque 1988). A female in Kruger N. P. known as MaMerle produced successive sets of twins all of which survived up to weaning age and beyond (I. Whyte pers. obs.). Weight at birth has been estimated at 120 kg (Perry 1953), though they may be lighter (75 kg; Smuts 1975) or heavier. Shoulder heights



Skin folds and lashes around eye of *Loxodonta africana*.

of newborn calves in Amboseli measure 79 cm for ♀♀ and 85 cm for ♂♂. These are somewhat smaller than the minimum measures at Kruger N. P. (85 cm for ♀♀, 92 cm for ♂♂). Growth is most rapid in the first five years of life and growth rates of ♂♂ and ♀♀ diverge after age two. Males are consistently larger than ♀♀ by 5–6 years of age. There are interesting differences between populations in growth rates, which affect adult size. Males reach 2 m in height at seven years in Kruger N. P. and at ten years in Amboseli, while ♀♀ reach this height after nine years in Kruger N. P. and 14 years in Amboseli (Kruger: I. Whyte pers. obs.; Amboseli P. Lee pers. obs.). Growth in body size continues for most of adult life accentuating these differences between the sexes, due to late epiphyseal fusion of long bones, and absent fusion of vertebrae and scapula (Haynes 1991; see also Roth 1984). Full adult height is reached at about 30 years for ♀♀, while ♂♂ continue to grow in height and mass well into their 50s (Poole 1989b, Lee & Moss 1995; and see Lindeque & Van Jaarsveld 1993). Males tend to be over 30% taller and double the weight of ♀♀ (Laws 1966, Lee & Moss 1995).

Elephant calves typically cease to suck when the next calf is born (Lee & Moss 1986), and examination of elephant cows at culls in Kruger N. P. showed that most lactate constantly (Smuts 1975, I. Whyte pers. obs.). As a result 'weaning' is an extended and gentle process (Lee & Moss 1986). There are subtle differences between the sexes of calves in weaning, with sons being allowed to suckle whenever they emit a vocal protest, while mothers are somewhat less tolerant of daughters. Given that the inter-calving period in Kruger N. P. was calculated at 3 years and 8 months (Whyte 2001a), this also represents the average age at weaning. In cases where the inter-calving period is extended, age at weaning would probably be extended accordingly.

Mean inter-birth interval varies from population to population depending upon food availability and other factors, and ranges from 2.9 to 9.1 years (Eltringham 1982; upper range: 9.5, Viljoen 1988). In nutritionally stressed populations, mean inter-birth interval tends

to be long (Laws *et al.* 1975). In the Amboseli population inter-birth interval averaged 4.5 years, while in the Addo population inter-birth interval was 3.8 years. In Kruger N. P. the interval was estimated at 3.7 years from a culled sample of 966 adult ♀♀ (Whyte 2001b), comparable with that in Etosha N. P. (3.9; Lindeque 1988). Inter-birth interval is considerably shortened by the death of a calf (Moss 2001). In Amboseli a ♀ has been known to produce a calf as quickly as 22 months after a birth if the first calf dies and 27 months after the birth of a surviving calf (Moss 2001).

Fecundity is fairly constant between the ages of 16 and 40 and then declines slightly, though ♀♀ over 60 can still give birth (Moss 2001). In Kruger N. P., fecundity declines in older cows, but several between 50 and 60 years were pregnant (Freeman *et al.* 2008). Unlike in Addo Elephant N. P. (Whitehouse & Hall-Martin 2000), ♀♀ in Amboseli were able to reproduce until the end of their life-span (Moss 2001). Breast development is a good indication that a ♀ is either pregnant or lactating and thus lack of breast development is an indication that she is neither. In populations that are suffering from high levels of poaching the proportion of ♀♀ of reproductive age with developed breasts can be much lower. For instance, in the Mikumi population in 1989, 31% (n = 35) and 75% (n = 16) of ♀♀ aged 15–19.9 and 20–24.9 years had developed breasts compared with 87% (n = 23) and 92% (n = 26), respectively, in the Amboseli population in the same year (Poole 1989a).

Many studies have estimated birth rate by counting the number of calves less than one-year-old at a given time as a proportion of population size and using this figure as an index of recruitment (Buss & Savidge 1966, Laws 1966, Calef 1988). However, such instantaneous counts can reflect short-term patterns of peaks and troughs and thus produce misleading estimates of population growth rates. Second, these estimates do not take into account the high rate of mortality among calves under one year of age. Thirdly, the method assumes that the estimates of calves' ages are accurate, which is questionable as calves just under or just over 12 months are easily misclassified. Over the course of 25 years in the Amboseli study population, growth rate averaged 2.17%, although lower (–7.42%) and higher (up to 11.3%) were witnessed in any particular year (Moss 2001). Between 1975 and 1994 when the entire Kruger N. P. was fenced and immigration and emigration were thus limited, the observed rate of increase averaged 6.6% per year, though fluctuations of between –2.9% and +14.8% were recorded during this period (Whyte 2001b).

The age of first birth varies across populations (Eltringham 1982). In Amboseli most ♀♀ gave birth for the first time between the ages of 14 and 15 years (median 14.1; Moss 2001). The youngest first birth was 8.9 years and the oldest 21.6 years (Moss 2001). In Kruger N. P. the youngest first birth was 9 years while 93% of 14-year-olds were either pregnant or lactating (Whyte 2001b).

Puberty in males is marked by the first production of sperm at ~ 14 years and sexual maturity, the production of sperm in quantity, by 17 years old (Laws 1969). At this age ♂♂ are only half their full adult weight and cannot compete with older ♂♂ for access to ♀♀ (Poole 1989b). Between the ages of 20 and 25, free-living ♂♂ have begun to show behavioural signs of sexual cycles, and by 29 years of age most ♂♂ have experienced their first musth period (Poole 1987). The duration of musth increases with the age of the ♂ (from days to weeks in younger ♂♂ to 3–4 months in older ♂♂) until approximately 50 years of age, when ♂♂ appear to enter a slow

reproductive decline (Poole *et al.* 2011). They are still reproductively active at age 60 (Poole *et al.* 2011). Genetic paternity confirms that older ♂♂ in musth father at least 75% of elephant calves (Hollister-Smith *et al.* 2007). Genetic paternity studies have also shown that despite the roving mating strategy of ♂♂ and the fluid sociality of both sexes, elephants avoid breeding with their close maternal and paternal relatives (Archie *et al.* 2007).

Elephant calves are born at a 1 : 1 sex ratio (Smuts 1975, Whyte 2001b, Moss 2011). Calf mortality in Amboseli averages around 10% in the first year of life (Moss 2001) while average annual natural mortality in Kruger N. P. has been estimated at around 3.2% per annum (Whyte 2001b). Males tend to have higher mortality than ♀♀ throughout much of their lives. While 84% of ♀♀ reach the age of ten years, only 75% of ♂♂ reach this age, and while 82% of ♀♀ survive to the age of first reproduction (14 years), only 39% of ♂♂ survive to the age when they regularly enter musth for the first time and are likely to start obtaining regular matings (Moss 2001).

Males have higher mortality than ♀♀ throughout most of their lives. Life expectancy at birth is 41 years for ♀♀ and 24 years for ♂♂ (Moss 2001). However, in the absence of human-induced mortality, female life expectancy increases to 54 years and males' life expectancy to 39 years. Maximum life-span for Savanna Elephants is unknown, but is at least 65 years for ♀♀ and at least 60 years for ♂♂ (Moss 2001). Since longevity is partly determined by viable molar teeth, animals with exceptionally abrasive diets may, theoretically, have shorter natural life-spans. In captivity, maximum recorded longevity is 53–54 years of age for a wild-born ♀ that was still living (Weigl 2005).

Predators, Parasites and Diseases Non-human predators include Spotted Hyenas and Lions. Although mortality caused by these predators is probably rare and primarily limited to calves and immature individuals, healthy elephants up to age 15 have been reported killed by Lions (e.g. Joubert 2006, Loveridge *et al.* 2006). The extent to which Spotted Hyenas and Lions affect mortality pat-

terns varies by season and locality depending upon the elephant's condition, predator population size and their sources of other suitable prey. Elephants do, however, treat both species as a threat and respond to them with aggression.

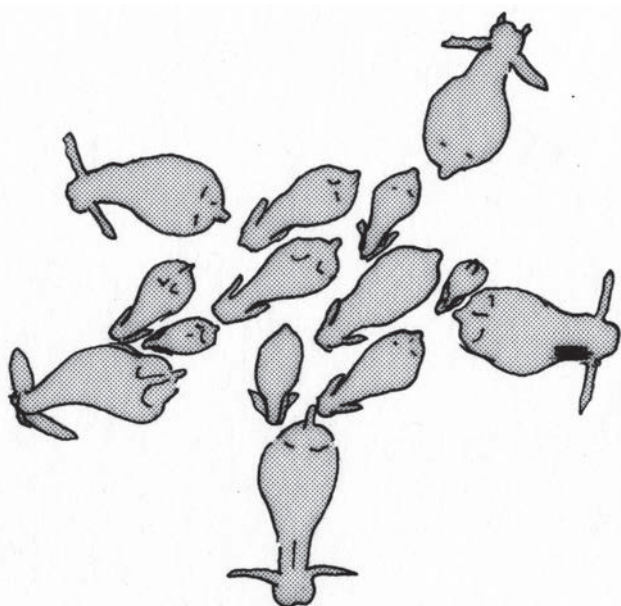
Elephants are affected by a number of diseases and ailments. Of all of these, only anthrax *Bacillus anthracis* has been shown to have the potential of limiting an elephant population, and this only in Etosha N. P. (Lindeque & Turnbull 1994). In the Kruger N. P., sporadic outbreaks of anthrax have caused some mortality. In addition, the *Picornia* virus, which causes encephalomyocarditis (EMC) and is transmitted by rodents (Grobler *et al.* 1995), has caused some deaths. No cases of foot-and-mouth disease or bovine tuberculosis have ever been recorded in free-living elephants. Other conditions known to affect elephants include heart diseases, twisted gut, septicaemia and cancerous growths.

A condition known as 'floppy' or 'flaccid trunk syndrome' (FTS), which is caused by a deterioration of the nerves of the trunk, has been recorded at Kariba, Zimbabwe (Kock *et al.* 1994) and Kruger N.P. The condition is progressive, leading to total paralysis of the trunk, which can be fatal as feeding becomes severely impaired. Little is yet known about its causes, but it is suspected that plant toxins and/or pollutants may be involved. In the Amboseli population one or two elephants are seasonally afflicted by a condition known as 'twisting disease', which causes the affected individual to walk with some difficulty and an unnatural gait. Since this condition is only observed during and following the rains and most often in adolescents, plant toxins or a virus are plausible causes. In addition, starvation is not uncommon during periods of severe drought.

Elephants are infested by a host of internal parasites. Condy (1974) and Round (1968) have listed 33 species from 25 genera and 14 families (and see Bauer & Styoe 1985). None of these is known to be fatal, but may contribute to mortality in individuals in poor condition. External parasites include ticks (21 species from four genera), the louse *Haematomyzus elephantis*, ear mites (*Loxonoetis bassoni*, *Otanoetis wetzeli*) and biting flies, including flies, mosquitoes, horse flies, warble, bot and bloodsucking flies (among them tsetse flies) (Zumt & Wetzel 1970, Sikes 1971, Fain 1983).

Conservation IUCN Category: Vulnerable A2a. CITES: Appendix I in 1989, but the populations of the following Range States have since been transferred back to Appendix II with specific annotations: Botswana (1997), Namibia (1997), South Africa (2000) and Zimbabwe (1997).

Although it is known that earlier humans were capable of killing elephants and mammoths, it is not known what effects they may have had on elephant populations, though it has been speculated that humans may have had a limiting role. However, the activities and practices of modern humans are an extremely important and limiting factor for adult elephants and indirectly, therefore, on immature elephants (Poole 1989a). The Waata people of the Tsavo region (Kenya) were renowned hunters of elephants using bows and poisoned arrows and may even have had a limiting effect on elephant population growth in that area (Ville 1995). In more recent times it is the commercial pursuit of ivory and the expansion of human settlements that has led to the contraction of the range of African elephants (Cumming *et al.* 1990, Milner-Gulland & Beddington 1993).



Defensive formation in *Loxodonta africana*.

Although elephant range has undergone considerable contraction, elephant populations occur in a number of protected areas across the continent, with recent evidence of an overall increase in numbers (Blanc *et al.* 2005, 2007). In southern Africa, protected areas known to hold important populations of Savanna Elephants include: Niassa G. R. (Mozambique); Nyika N. P. (Malawi); Etosha N. P. (Namibia); Chobe N. P., Moremi G.R. and Tuli (Botswana); North and South Luangwa, Kafue N. P. (Zambia); Gonarezhou N. P., Hwange N. P. and surrounds, and Matusadona N. P. (Zimbabwe); and Addo Elephant N. P., Kruger N. P., Klaserie G. R., Timbavati G. R., Sabi-Sand G. R., Madikwe G. R. and Tembe Elephant Reserve (South Africa). In East Africa, important protected areas include: Omo, Mago and Gambella National Parks (Ethiopia); Aberdare N. P., Mt Kenya N. P., Amboseli, Masai Mara N. R. and Tsavo N. P. (Kenya); Nimule N. P. (Sudan); and Katavi N. P., Mikumi N. P., Ruaha N. P., Rungwa G. R., Selous G. R. and Tarangire N. P. (Tanzania) (Blanc *et al.* 2007). Zakouma N. P. in Chad has been an important stronghold for Savanna Elephants in the central African region but is under intense poaching pressure. The arid-adapted population in Gourma is partly formally protected in the Douentza Elephant Reserve. The 'W' N. P. that straddles the borders of Benin, Niger and Burkina Faso, together with adjacent protected areas, represents the largest elephant range in West Africa (Blanc *et al.* 2007).

Despite their presence in many protected areas, the majority of elephant range is not within protected areas; about 70% and 72% of their range falls outside protected areas, in eastern and southern Africa, respectively (Blanc *et al.* 2007). However, in some countries, such as South Africa, extensive human development precludes the occurrence of elephants outside public and private conservation areas, with the result that about 85% of the range falls within protected areas (Blanc *et al.* 2007). In these confined areas, the impacts of elephants on biodiversity can be dramatic (e.g. Coetzee *et al.* 1979, Moolman & Cowling 1994, Scholes *et al.* 2003) and some argue that such populations can only be constrained by reduction of elephant numbers or limitation of population growth (e.g. via contraception). There are a few options for such management, but all of them pose ethically and morally taxing dilemmas that have been examined by Whyte (2001b) and Whyte & Fayrer-Hosken (2008). It is expected that more and more conservation areas across Africa will be faced with these difficult decisions as human developments expand.

Historically, significant changes in elephant populations and ranges have occurred. In southern Africa, elephants were almost hunted to extinction by the end of the nineteenth century. South Africa contained only a few remnant fragments, which occurred in the Kruger N. P., Addo Elephant N. P., Knysna Forest and Tembe Elephant Park. From these meagre remnants, the national population has increased to nearly 18,000 (Blanc *et al.* 2007), with many new public and privately owned conservation areas being established, most of which have acquired their elephant herds through translocations from Kruger N. P. Genetic inbreeding has occurred in Addo due to the population bottleneck there, though this issue is now being addressed through the introduction of adult bulls from the Kruger N. P. All of these areas are now formally conserved, which has resulted in population increases except in the Knysna area where numbers have declined almost to the point of extirpation.

Poaching continues to pose a significant threat to elephants and has hampered conservation efforts in most parts of Africa. Equally

worrying is the growing conflict with humans, which has come about due to human population growth and resulting loss of elephant range and habitat. The 1989 international ban on trade in ivory was a turning point for many populations, though the decision remains highly controversial. A partial re-opening of the ivory trade was approved in 1997 despite the fact that growing demand for ivory in the East continued to threaten elephants in many parts of Africa. Concerns that legal trade would stimulate markets and provide a cover for laundering of illicit ivory led to the implementation in 2000 of a continent-wide monitoring system known as MIKE (Monitoring of Illegal Killing of Elephants). The MIKE was established to determine the effects of CITES decisions on elephants in 50 sites across Africa. The limited and controlled ivory stockpile sales that occurred in 2008 may have contributed positively to elephant conservation in some parts of southern Africa, but it may also have intensified poaching threats in other populations. Indeed, soaring demand for ivory in the Far East (e.g. Vigne & Martin 2011) has caused a marked upsurge in elephant poaching that has the potential to threaten elephant populations across the continent.

Measurements

Loxodonta africana

HF (♂ range 10–65 yr): 360–540 mm

HF (♀ range 10–65 yr): 340–470 mm

Sh. ht (♂): 2.9–3.7 m

Sh. ht (♀): 2.5–3.0 m

Amboseli N. P. (Lee & Moss 1995)

Maximum recorded shoulder height for a ♂ is the Fenykoevi elephant from Angola (housed in the Smithsonian Museum), which stood 4.0 m (Haynes 1991). The largest ♂ measured in Kruger N. P. stood 3.45 m; for females, 2.74 m, but they seldom exceed 2.55 m (I. Whyte pers. obs.).

WT (♂): up to 6048 kg

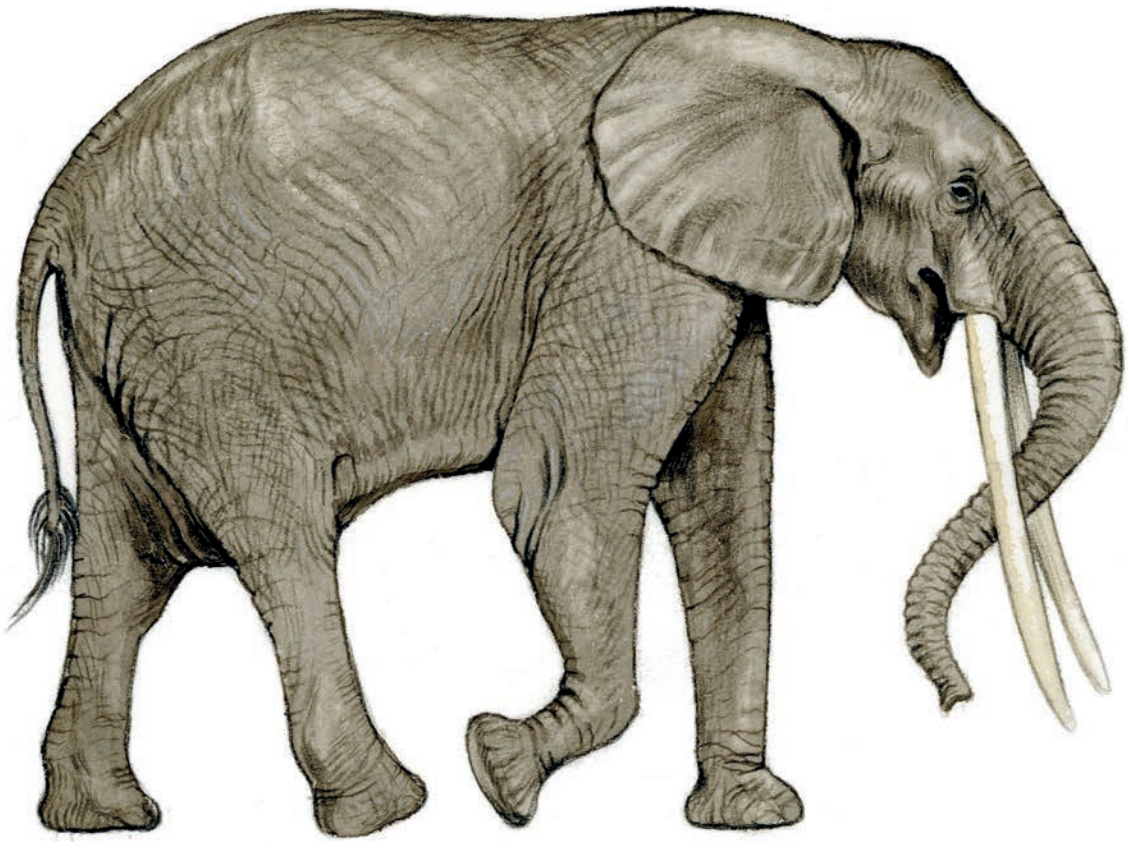
WT (♀): up to 3232 kg

Moss (1976) recorded that the heaviest bull elephant on record had a mass of 6569 kg.

The heaviest pair of tusks on record, now housed in the collections of the British Museum of Natural History, are from Mt Kilimanjaro with a mass of 102.7 kg (3.11 m long) and 97.0 kg (3.19 m long). In Kruger N. P., which is well known for its large tuskers, the heaviest female tusk weighed was 10.7 kg but they rarely exceed 7.0 kg (I. Whyte & A. J. Hall-Martin unpubl.). Mean tusk mass for bulls exceeding 50 years of age was 40 kg, and the heaviest male tusks recorded in Kruger N. P. were from a bull known as 'Mandleve' and weighed 73.5 kg and 69 kg, respectively. The longest tusk recorded from a ♂ in Kruger N. P. was 2.64 m from a 55-year-old. Several tusks exceeding 50 kg are on display in the elephant museum at Letaba restcamp in Kruger N. P.

Key References Blanc *et al.* 2007; Laws 1966, 1967, 1970; Laws *et al.* 1975; Lee 1986, 1987; Lee & Moss 1986, 1995, 1999; Lee *et al.* 2011a; Lindeque 1988, 1991; Moss 1981, 1988, 2001; Moss & Poole 1983; Moss *et al.* 2011; Poole 1982, 1987, 1989a, b, c; Spinage 1994; Whyte 2001a, b.

Joyce Poole, Paula Kahumbu & Ian Whyte



Forest Elephant *Loxodonta cyclotis*.

Loxodonta cyclotis FOREST ELEPHANT

Fr. Eléphant de Forêt; Ger. Waldelefant

Loxodonta cyclotis (Matschie, 1900). Sitzb. Ges. Naturf. Fr. Berlin, p. 194. Yaunde, S Cameroon.

Taxonomy Monotypic. Originally described as a subspecies of the Savanna Elephant *Loxodonta africana* by Matschie (1900), but recent morphological and genetic studies (Grubb *et al.* 2000, Roca *et al.* 2001, 2004, Comstock *et al.* 2002, Rohland *et al.* 2010) confirm the earlier assertions of Frade (1931, 1955) that the Forest Elephant is a distinct species (but see Debruyne 2004, 2005a). Eggert *et al.* (2002) propose a third lineage that includes both Forest and Savanna Elephants of West Africa.

There have been persistent reports of a pygmy elephant (*Loxodonta pumilio*) (Noack 1906) that shares the same habitat as the Forest Elephant (Morrison-Scott 1947). However, there is no genetic evidence for the existence of such a species (see Debruyne *et al.* 2003b). The long-standing belief in a separate race or species was based on sightings of solitary juvenile and subadult Forest Elephants: their small stature and precocial tusk development misled observers into believing they were adults. Behavioural observations make it clear that 'pygmy' elephants are actually immature Forest Elephants (Western 1986, Groves & Grubb 2000a, A. Turkalo pers. obs.), although this view was still disputed until quite recently (Eisentraut & Bohme 1989, Anon 1990, Bohme & Eisentraut 1990). Synonyms: *albertensis*, *cottoni*, *fransseni*, *pumilio*. Chromosome number: $2n = 56$ (Hungerford *et al.* 1966).

Description Forest Elephants have many features in common with their Savanna counterparts (most of which are not repeated in this account), but they are markedly smaller in stature, with adult ♀♀ averaging 2 m and ♂♂ 2.4 m at the shoulder. Ear shape has been described as being more rounded and smaller than that of the Savanna Elephant, although there is a wide variation in shape and size. Some Forest Elephants possess ears that are similar to those of Savanna Elephants, with lobes extending well below the chin line. The body colour is generally described as grey, but variations in colour vary from grey to yellow to reddish with the yellow and red colouration usually due to mud wallowing. Newborns possess a noticeable sparse body hair covering (black), but this disappears as the elephant matures. Hair remains present in adults but is sparse and is noticeable in the tail, and in ♀♀ sometimes a 'beard' on the chin is discernible. Tail length varies from half of the rear rump height to longer tails whose hairs touch the ground. The tail is covered in thick skin ending in an asymmetric lobed tip, bordered by long, coarse black hairs (20–200 mm). There is also a difference in the number of 'toenails' or nail-like structures between the Savanna and Forest species. Generally, Forest Elephants have five nails on the front feet and four on the rear, whereas in the Savanna species the front feet have four and the rear three.

Tusks of adult ♂♂ are generally longer and thicker than those of adult ♀♀, this characteristic being easily discerned even in infant and juvenile Forest Elephant ♂♂. Forest Elephant ivory differs from the ivory of the Savanna Elephant in both colour and hardness. Described as 'pink' or 'hot', Forest Elephant ivory is harder, making it the preferred material for carvings. Generally, male Forest Elephants carry thinner tusks than Savanna Elephants, although there is a wide variation in tusk morphology among Forest Elephants.

Geographic Variation None recorded.

Similar Species

L. africana. Larger and taller, with larger more triangular-shaped ears, and heavier, more curved tusks.

Distribution

Historical Distribution Forest Elephants are assumed to have occurred throughout the Guinea-Congolian region of West and central Africa. The limits of past and present distribution remain vague because of intergradations between Forest Elephants and Savanna Elephants along the northern and eastern fringes of the West African and Congo Basin forests (Roth & Douglas-Hamilton 1991). In Garamba N. P., DR Congo, three individual elephants showed genotypes with a combination of Forest and Savanna alleles, suggesting a history of limited hybridization in the ancestors of this population (Roca *et al.* 2001).

Current Distribution Forest Elephants are widespread in the remaining forests of the Guinea-Congolian forests. The majority of elephant range in central Africa is inhabited by Forest Elephants, with Savanna Elephants occurring in N Cameroon, N Central African Republic and Chad (Blanc *et al.* 2007). However, the distribution of elephants in the forests of central Africa is shrinking at an accelerated rate as roads, railways, pipelines and mining and logging companies penetrate forests that were formerly difficult to access, making it easier for hunters to find and kill them. Loss of elephant range in DR Congo has been especially acute over the past several decades as rapidly expanding human populations move into some of the most important elephant landscapes, especially in the eastern forest zone (see Conservation).

In West Africa, elephants are now found in 35 small, isolated forest patches with a median area of 800 km² (AfESG 2003).

There are reports of cyclotiform elephants in tongues of riverine forest far into the savanna zone of N Central African Republic and in the Sudanian savanna zone of N Togo (Stalmans & Anderson 1992). Elephants in the mountains of Kenya are Savanna Elephants (Roca *et al.* 2001). See profile of Savanna Elephant (p. 183) for distribution map.

Habitat In central Africa, Forest Elephants inhabit the large contiguous forest tracts, and are also found in areas of overlapping savanna and forest in Lopé in Gabon, Odzala in the Republic of Congo, and in the northern forest savanna mosaic of DR Congo. In West Africa, Forest Elephants are now confined to forest fragments.

Abundance The central African forests, which contain the least disturbed habitats, often support high elephant densities. Although few elephants may be seen close to roads and villages, densities increase with distance from roads to well over 1/km² in some remote forests (e.g. Barnes *et al.* 1991, 1997, Hall *et al.* 1997, Thomas *et al.* 2001). Little is known about how the population in central Africa changed during the nineteenth and twentieth centuries when they were under heavy pressure for ivory. The creation of protected areas and the enactment of legislation outlawing commercial hunting for ivory during the past few decades has not been particularly effective due to political instability in the region and the expansion of extractive industries, which has opened up previously inaccessible areas of the rainforest.

Gabon, the only central African country to have been surveyed completely (Barnes *et al.* 1995, 1997, Blanc *et al.* 2007), and the most politically stable country in the region, is thought to have the largest Forest Elephant population, with probably in the order of 25,000 individuals (Blanc *et al.* 2007). The vast forests of DR Congo have the potential to hold many thousands of elephants, possibly as many as 20,000 (Blanc *et al.* 2007, J. Hart pers. comm.), but ivory poaching was intense during the 1970s and 1980s in even the most remote forests (Alers *et al.* 1992). With the recent expansion of the bushmeat trade, elephants are now being killed for meat as well as for ivory (Mubalama & Mapilanga 2001, Blanc *et al.* 2007). Elephants in many remote forests have been nearly or totally eliminated in the years of civil war and political instability spanning the turn of the twenty-first century (J. Hart pers. comm.). Cameroon, Central African Republic and Congo all contain sizeable populations of elephants, but few reliable figures exist. Elephants in Equatorial Guinea may number as many as 1300 individuals, but the majority (~90%) of elephant range in this country remains unsurveyed and this is little more than an informed guess (Blanc *et al.* 2007).

As with Savanna Elephants, a continent-wide assessment of population size for Forest Elephants is complicated by countries having both Forest and Savanna Elephants, and the unclear status of elephants in West Africa. None the less, using the results from the African Elephant Status Report (Blanc *et al.* 2007), and the same general assumptions used to calculate the Savanna Elephant population estimate (see species profile), it is possible to arrive at a general estimate for Forest Elephants in central Africa (here taken to exclude elephant populations from N Central African Republic and Chad) (Table 11).

Table 11. Estimated numbers of Forest Elephants, excluding West Africa.

	Estimate	95% CL ±	Guesstimate		Range covered (%)	Area (km ²)
			From	To		
Estimates from surveys	9500	4200			1	15,500
Estimates from low-quality surveys and guesses			100,000	160,000	29	362,500
Unassessed range					70	860,000
Total range					100	1,238,000

Source: African Elephant Database 2007, courtesy of the IUCN/SSC African Elephant Specialist Group

Few surveys were conducted in West African forests before 2000 and most estimates of population size were guesses that suggested a median population size of 50 and a median density of 0.08 elephants/km² (AFESG 1999). Recent surveys show large variations in density, e.g. 0.04 and 0.64/km² in two Ghanaian forests (EBM 2000, Danquah *et al.* 2001). Many West African Forest Elephant populations are probably not viable because of their small numbers, unbalanced sex ratios and distorted age structures (Barnes 1999).

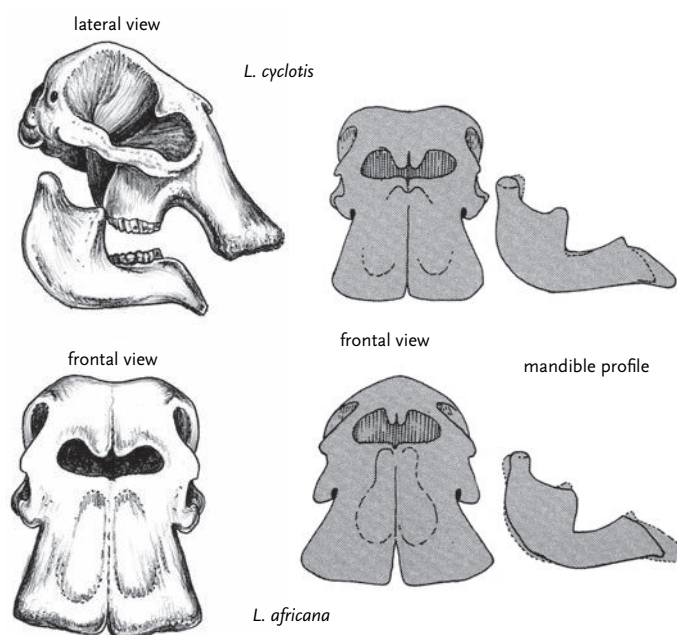
The most common method of estimating Forest Elephant numbers is by means of dung counts (e.g. Barnes *et al.* 1997, Hall *et al.* 1997, Walsh & White 1999). Transects are distributed across the study area according to a specified survey design and elephant dung-piles recorded by distance sampling (Buckland *et al.* 2001). The resulting estimates of dung-pile abundance can then be combined with defaecation rate and dung decay rates to give estimates of elephant numbers with confidence limits. The estimates from dung counts are as accurate as those from other methods and give narrower confidence limits than aerial sample surveys (Barnes 2001, 2002). Jachmann (1991) concluded that dung counts should be the preferred method for estimating elephant numbers in all situations.

Work on the use of acoustical methods to monitor and census Forest Elephant was initiated in 2000 at the Dzanga clearing in the Central African Republic (Payne *et al.* 2003). Further work is now in progress to establish the extent to which the rates and patterns of calls of Forest Elephants reflect their numbers, group structure and reproductive health. This information will provide the basis of an acoustical monitoring programme through which much can be learned about the locations, demography and condition of Forest Elephant populations throughout central and West Africa.

Estimates of small populations usually have wide confidence limits that make it difficult to detect changes in animal numbers (Barnes 2002). Advances in DNA technology now provide a reliable method for estimating the numbers of elephants in small forests such as those in West Africa. DNA is extracted from samples of dung and individual elephants are identified by multilocus genotyping. The data from a series of collections can be analysed by mark-recapture methods to give estimates of elephant numbers (Eggert *et al.* 2003).

Adaptations Most of the adaptations described for Savanna Elephants apply also to Forest Elephants. As with their Savanna relatives, both sexes possess temporal glands located on each side of the head at eye level. Temporal glands are most noticeable in adult ♂♂ undergoing musth ('rut'). During this period these glands swell and a secretion (known as temporin) streams down the side of the head. In Forest Elephant ♀♀, temporal gland secretion is seldom observed, and when it does occur is thought to be related to stress (A. Turkalo pers. obs.).

Forest Elephant crania are also exceptionally thick and pneumatized, which effectively reduces the weight of the cranium (Badoux 1961). The honeycomb structure of the cranium serves several primary functions: it allows the angles and areas of attachment for both nuchal and masticatory muscles to achieve optimal mechanical advantage, it allows the tusks to be aligned vertically (at right-angles to the basi-cranial axis), it favours mobility of the head, and also serves as a 'shock absorber' (especially insulating the brain) in those instances when elephants feed by shaking fruits out of trees

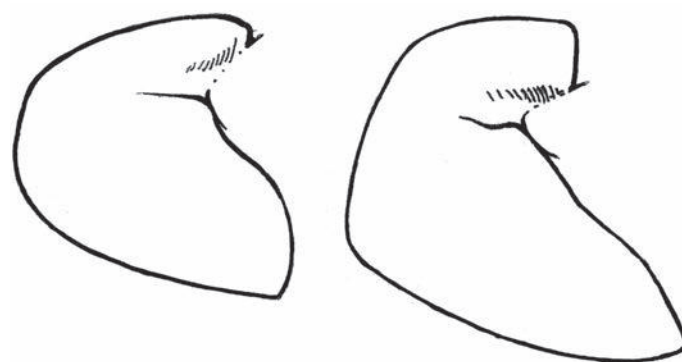


Skulls of *Loxodonta* spp. compared

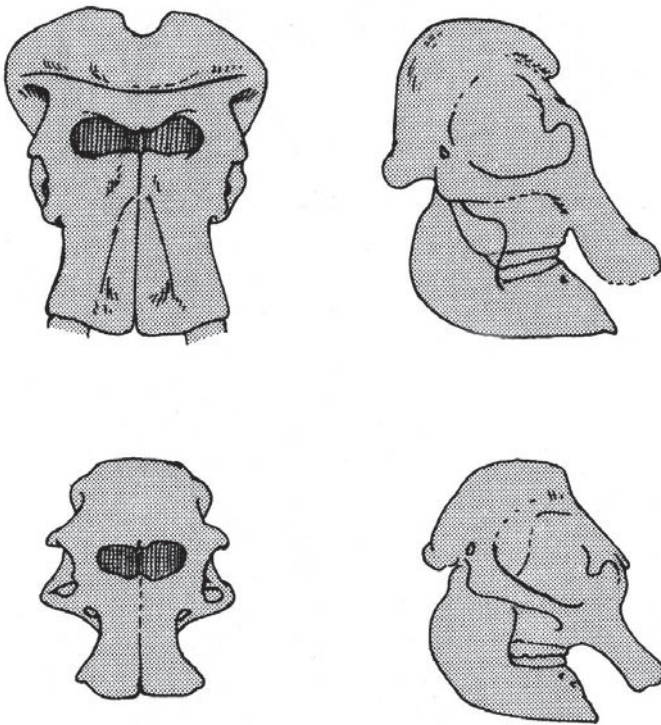
by ramming their heads against tree trunks (or, during conflicts, against each other) (Maisels *et al.* 2002, A. Turkalo pers. obs.).

Elephant hearing and communication is highly developed and their auditory range extends to low frequency sounds below that of human hearing (>20 Hz). Forest Elephants have been recorded emitting frequencies as low as 5 Hz (S. Gulick pers. comm.). These low frequency sounds are used to communicate over long distances, especially in locating family members. At the Dzanga Clearing in Central African Republic where Forest Elephants have been studied for the last decade, observations in and around the clearing demonstrate that family groups locate one another by means of both audible sounds as well as infrasonic vocalizations. Extensive calling between elephants allows groups to keep track of each other and to coordinate their movements (A. Turkalo pers. obs.).

Foraging and Food The diet of the Forest Elephant consists of a wide variety of plant parts including leaves, fruit, pith, bark, lianas and fruit. Grass, a rare occurrence in the forest, found mostly in and around forest clearings, is also occasionally consumed but forms a very small portion of the diet. Forest Elephants are highly frugivorous and studies in Gabon (White 1994), Congo (Blake



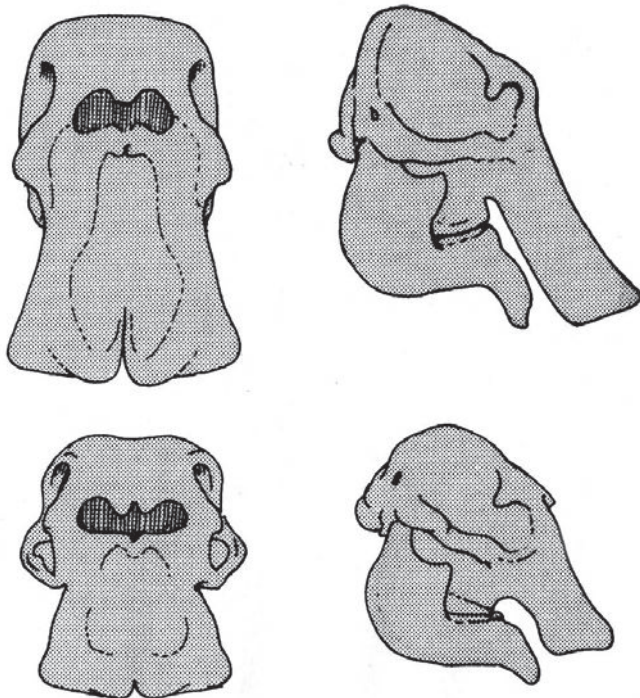
Ear shape in *Loxodonta cyclotis* (left) and *L. africana* (right).



Skull outlines of dwarfed island elephant, *Elephas falconeri* (below) with its mainland equivalent, *E. namadicus* (above).

2002) and Côte d'Ivoire (Short 1981) showed they were observed to consume between 20 and 70 species of fruit, with favoured fruit species including members of the families Sapotaceae, Tiliaceae, Moraceae and Marantaceae (White *et al.* 1993, Maurois *et al.* 1997, Blake 2002).

Successful germination of many fruit species is linked to elephant digestion, which in turn plays an important role in the species



Is *L. cyclotis* (below) a dwarfed ecological isolate of extinct *L. adaurora* (above)?

composition of the forest (Hawthorne & Parren 2000, Blake *et al.* 2009). The availability of fruits plays an important part in the month-to-month movements of Forest Elephants (Short 1983, White 1994, Theuerkauf *et al.* 2000b). A marked difference in diet occurs between the dry and wet seasons, the wet season diet being particularly rich in fruit in the central African forests, transitioning to leaves and bark in the dry season. In contrast, in West African forests fruit is more abundant in the dry season (Theuerkauf *et al.* 2000b, Danquah & Oppong 2006). The months when fruit is least abundant in West African forest fragments are those when crops are maturing in the farmland outside, so tempting elephants into farmers' fields.

Forest clearings rich in minerals also play an important role in Forest Elephant diet. Elephants have been observed to spend many daylight hours ingesting soils in these clearings where minerals may act as a buffer in their diet in the digestion of secondary plant compounds (Klaus *et al.* 1998, Houston *et al.* 2001). They also use their pillar-like feet and tusks to dig for water that is rich in mineral salts in forest clearings.

From data collected from collared elephants in the Dzanga-Ndoki and Nouabale-Ndoki National Parks, elephants feed most intensively during the day and at night they rest near water points (Blake 2002).

Social and Reproductive Behaviour Forest Elephants are highly social, the basic social unit comprising a family group of several related adult ♀♀ and their young. Initial studies of Forest Elephants showed that they form small family groups averaging three individuals (Merz 1986, White *et al.* 1993, Turkalo 1996, Querouil *et al.* 1999, Theuerkauf *et al.* 2000a), but a long-term study of known individuals at the Dzanga clearing in Central African Republic has shown that Forest Elephants, like their savanna counterparts, also form large, extensive family units that can number up to 20 individuals (A. Turkalo pers. obs.). The lack of natural predators in the forest permits Forest Elephants to form less cohesive family groups unlike in the savanna, where family group members remain close together as a defensive strategy against predation (Western 1986).

Unlike the Savanna Elephant, adult Forest Elephant ♂♂ have not been observed in 'bachelor herds' but only as solitary individuals. Younger ♂♂, juveniles and subadults form loose, non-permanent groups that may last one to several days (A. Turkalo pers. obs., F. Maisels pers. obs.). In forest clearings, which are used extensively by Forest Elephants seeking mineral salts, which are essential to their diet, male hierarchy is tested and established around large holes that are excavated by ♂♂ in their search for high-quality minerals. Aggression is regularly observed in the competition for minerals, but very few injuries are incurred.

From a long-term data set of 15 years, gathered at the Dzanga clearing, Central African Republic, and from four radio-collared elephants in the same area, ranging behaviour varies greatly between individuals (Blake 2002, A. Turkalo pers. obs.). Forest Elephants can have a minimum convex polygon home-range of up to 2000 km² and move an average of 7.8 km/day. One individual ranged more than 25 km in less than 48 hours (Blake 2002). By their habitual use of the same paths, they create wide trails in the forest (Vanleeuwe & Gautier-Hion 1998).

Observations at the Dzanga clearing reveal that some ♀♀ are resident, spending more time in the area, whereas ♂♂ noticeably spend less time in the area of the clearing. Larger ♂♂ are more likely to visit the clearing during the dry season during the peak musth season, when they come in search of mineral salts and oestrous ♀♀.

Musth, a phenomenon well documented in male Savanna Elephants, has been observed regularly at the Dzanga clearing. The most obvious musth signs are temporal gland secretion accompanied by a steady urine dribble, resulting in a characteristic pungent body odour. Musth has been observed only in the largest ♂♂ in the Dzanga population. The majority of bulls undergoing musth are observed during the dry seasons, the longest dry season occurring in Dec–Mar, and a shorter dry season occurring during Jul–Aug. The length of musth in ♂♂ is thought to last for at least two months. Musth occurs in individual ♂♂ during the same time period each year (A. Turkalo pers. obs.).

During the guarding of an oestrous ♀ by the ♂, the ♂ stays in close contact with the ♀ allowing her access to (otherwise) unavailable resources such as choice mineral access points otherwise dominated by ♂♂ in the area. The guarding and mating generally lasts for approximately two days during which time the ♂ copulates with the receptive ♀ a couple of times. After the short oestrous period the ♂ leaves the ♀ to go in search of other potential mates (A. Turkalo pers. obs.).

Newborns are immediately mobile after birth and stay in close contact with their mothers and other family members. Allomothering is tolerated by mothers and is performed by older female siblings as well as unrelated subadult and adult ♀♀ (A. Turkalo pers. obs.).

Reproduction and Population Structure Sexual maturity is attained between the ages of 12 and 14 years in ♀♀. Males probably reach sexual maturity at the same age as ♀♀, but become sexually active much later (A. Turkalo pers. obs.). Oestrous occurs during the entire year, but the peak periods are during the two dry seasons (A. Turkalo pers. obs.). Oestrous in free-ranging Forest Elephant ♀♀ is thought to last several days, as in Savanna Elephants (A. Turkalo pers. obs.).

One young is born after a gestation of approximately 660 days (similar to the savanna species). During the 15 years of a long-term study at the Dzanga clearing in Central African Republic, some 675 newborn calves have been recorded to known ♀♀ and twins have never been observed (A. Turkalo pers. obs.). Weaning is dependent on the mother; some calves have been observed suckling until the age of five (A. Turkalo pers. obs.). From the Dzanga clearing dataset, the inter-birth interval has been calculated at four years or less ($n = 69$) (A. Turkalo pers. obs.) and the sex ratio is 52% female and 48% male (A. Turkalo pers. obs.). Maximum potential life-span in Forest Elephants is thought to approximate that in the Savanna species: 50–60 years.

Predators, Parasites and Diseases Unlike Savanna Elephants, Forest Elephants have no major natural predators. Leopards *Panthera pardus* may prey upon newborn calves (Blake 2004), but since calf mortality is low at 3% (A. Turkalo pers. obs.) this phenomenon is probably rare in the forest environment. Orphaned calves above the age of two years have been observed to survive with siblings or even independently.

Forest Elephants show little sign of disease. Anthrax, which has been associated with mortality in Savanna Elephants, has never been recorded in Forest Elephant populations. Tumorous growths have been observed in a population of Forest Elephants at the Dzanga clearing (A. Turkalo pers. obs.). Infections resulting from wounds incurred from fighting or tree falls during feeding have also been observed but rarely do these infections result in death (A. Turkalo pers. obs.). Although internal parasites have been well documented in Savanna Elephants, little work has been done on the forest species (Chabaud & Rousselot 1956, Kinsella *et al.* 2004). Kinsella *et al.* (2004) collected faecal samples from six African Forest Elephants from the Nouabale-Ndoki N. P., Congo, and the Dzanga-Sangha N. P., which revealed the presence of a schistosome, *Bivitellobilharzia* sp., a tracheal nematode, *Mammomonagamus* sp., and a complex of intestinal strongylids and ciliates. The nematode genera *Decrusia* and *Equinurbia* were also reported for the first time from African elephants, and the ciliate genus *Latteuria* for the first time from wild elephants. One elephant was found freshly dead from natural causes, and 12 species of intestinal parasites (two bot fly larvae, one trematode and nine nematodes) were collected during a complete necropsy.

Conservation IUCN Category: Not listed (included in *Loxodonta africana*, since the view of the African Elephant Specialist Group is that premature allocation into more than one species may leave hybrids in an uncertain conservation status). CITES: Appendix I (see below).

The 1989 CITES Conference of the Parties (COP) voted to transfer African elephants (no distinction being made between Savanna and Forest Elephants) from Appendix II to Appendix I. Although the Savanna Elephant populations of Botswana, Namibia, South Africa and Zimbabwe have since been returned to Appendix II, all Forest Elephant populations remain on Appendix I. Therefore, all commercial trade in Forest Elephant products, such as ivory, meat and hide, between countries is banned. Sport hunting of Forest Elephants is not covered by this ban, and certain countries, such as Cameroon, wish to manage some of their elephants for safari hunting.

Forest Elephants in central Africa roam through vast forests that stretch along the Equator from the Atlantic coast to the Congo–Nile divide. Human densities are sparse over large parts of the central African forest and elephants were numerous in the first half of the twentieth century (Roth & Douglas-Hamilton 1991). During the 1970s and the 1980s, the heavy hunting of central African elephants for ivory was hidden from the outside world by the forest canopy. Comparisons of heavily poached and relatively undisturbed forests suggest large numbers of elephants were killed (Michellmore *et al.* 1994). Poachers used motorized canoes to penetrate the most remote forests of DR Congo (Alers *et al.* 1992). Commercial logging is advancing rapidly, and logging roads open these formerly remote and inaccessible areas for settlement. Elephants avoid roads, and as the road network expands, the area of undisturbed habitat diminishes (Barnes *et al.* 1997). Government wildlife agencies continue to be ineffective as a result of economic and social conditions and the expansion of the bushmeat trade has promoted the market for elephant meat (Blake & Hedges 2004). Poaching for ivory continues, despite the international ban on the ivory trade (Blake *et al.* 2007). Protection is weak in national parks and reserves because of the general lack of resources. Nevertheless, elephant densities remain

higher inside the national parks than outside, showing that they still have an important role to play in conservation (Blake *et al.* 2007).

Automatic weapons have proliferated in central Africa because of civil war and strife in Rwanda, DR Congo, Congo and the Central African Republic. As a result of this unrest, refugees have been displaced into areas where elephants were previously undisturbed and it is this loss of their former habitat that is becoming the greatest threat to the last of the great elephant populations of the forest zone (J. Hart pers. comm.).

DR Congo has a human population estimated at 67 million in 2011 (largest national sub-Saharan population after Nigeria and Ethiopia), and despite conflict this population is growing at 2.8% or more annually. Most large forests in DR Congo are visited by people, and even occupied at a light level in relation to fishing, hunting and artisanal mining. Many of these same forests are 'empty' or severely depleted of wildlife, including significant portions of the country's largest forest parks (Salonga, Bili-Uere, Okapi, Maiko and Kahuzi lowlands). Elephants are among the most obvious of the depleted species and have been eliminated, or nearly so, from large areas of their historic range. Range shrinkage continues, and is accelerating in the east (Ituri, Maiko, Kahuzi) (J. Hart pers. comm.). The numbers of Forest Elephants will continue to decline in central Africa unless the expansion of the road network into remote forests can be limited, the trades in ivory and bushmeat can be brought under control, and the remote national parks protected effectively because they are likely to become the last refuges for Forest Elephants (Blake *et al.* 2007).

In West Africa, Forest Elephants are restricted to small forest patches and reserves that are isolated by agriculture from other elephant habitats. In Côte d'Ivoire many of the smaller populations were extirpated during the years of peak poaching in the 1970s and 1980s (Barnes 1999). Elephant numbers have declined significantly in many sites in Côte d'Ivoire even since the ivory trade ban came into effect (Fischer 2005, Hoppe-Dominik *et al.* 2011). While inbreeding, distorted sex ratio and age structures will compromise the long-term viability of the remaining small populations, in the short and medium term it is human–elephant conflict, habitat loss and hunting for meat and ivory that will determine the fate of these elephants. As the human

population expands, conflict between elephants and people will intensify because they compete for the same land resources (Parker & Graham 1989). The increasing hectareage of agriculture attracts crop-raiding elephants out of forest reserves, and the suffering of farmers turns rural communities against the concept of conservation (Boafo *et al.* 2004).

Today, Forest Elephants occur in several important protected areas and national parks in the central African region, including: Dja Faunal Reserve, Nki F. R., Abong-Mbang F. R., Boumba-Bek F. R., Lobeke N. P. and Mongokele F. R. (Cameroon); Dzanga-Ndoki N. P., Bangassou F. R. (Central African Republic); Monte Alén N. P. (Equatorial Guinea); Nouabale-Ndoki N. P., Conkouati N. P., Odzala N. P. (Congo); Lopé N. P., Minkebe N. P., Moukalaba N. P., Ivindo N. P., Mpassa N. P., Louango N. P., Mwagne N. P., Waka N. P., Biringou N. P. (Gabon); and Salonga N. P., Kahuzi Biega N. P., Maiko N. P., Okapi N. P. and Garamba N. P. (DR Congo).

Measurements

Loxodonta cyclotis

HB (♂ ♂): 244.2 (214.0–290.0) cm, n = 103

HB (♀ ♀): 198.4 (176.0–234.0) cm, n = 170

Dzanga-Ndoki N. P., Central African Republic (A. Turkalo pers. obs.)

Maximum shoulder height measured at the Dzanga clearing was 2.8 m (n = 810) (A. Turkalo pers. obs.). Shoulder height measurements of Forest Elephants from Louango in Gabon were considerably smaller than those obtained at Dzanga, with a maximum measurement of 2.16 m (n = 53) (Morgan & Lee 2003).

Record tusk length in Forest Elephants is unknown because no subspecies are listed for record purposes. The longest estimated tusk length in a ♂ observed at the Dzanga clearing in Central African Republic is 1.8 m (A. Turkalo pers. obs.).

Key References Barnes *et al.* 1997; Blake 2002; Blake *et al.* 2007; Blanc *et al.* 2007; Merz 1986; Querouil *et al.* 1999; Theuerkauf *et al.* 2000a, b.

Andrea Turkalo & Richard Barnes

Order SIRENIA – Dugongs, Manatees

Sirenia Illiger, 1811. Prodrromus systematis mammalium et avium ... Berlin: C. Salfeld: 140–141.

Dugongidae (1 genus, 1 species)	Dugongs	p. 203
Trichechidae (1 genus, 1 species)	Manatees	p. 209

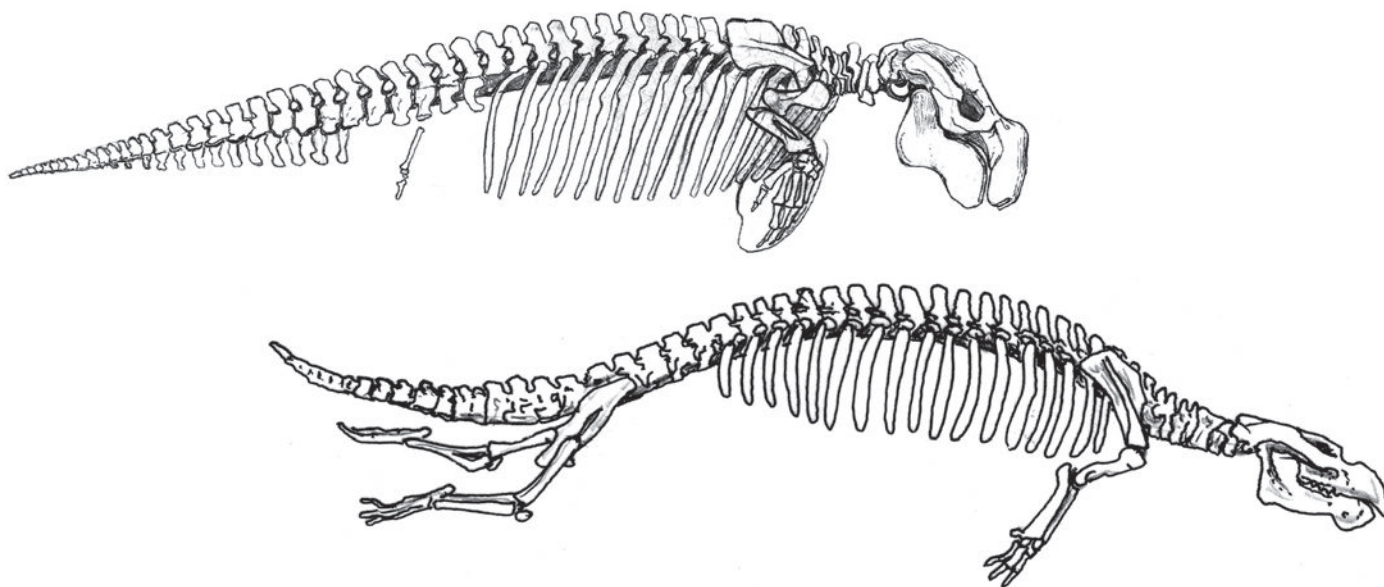
The order Sirenia comprises four families: two extinct dating to the Eocene (Prorastomidae and Protosirenidae) and two extant: the Dugongidae and the Trichechidae. Sirenians are the only living group of herbivorous marine mammals. The name Sirenia alludes to legends of ‘sirens’ or mermaids, thought (rightly or wrongly) to have been inspired by manatees or dugongs. *Dugong* is a Filipino Malay name for the animal; *Trichechus*, from Greek *trichos* meaning ‘hair’, was bestowed on these nearly-hairless mammals to distinguish them from other ‘fish’ when they were still classified among the latter. The order is represented in Africa by only two species, the Dugong *Dugong dugon* and the West African Manatee *Trichechus senegalensis*.

Except for the earliest forms, which were amphibious quadrupeds (Domning 2001a), sirenians also resemble cetaceans in their fish-like body form, lack of an external ear pinna, short neck, flipper-like forelimbs, loss of hindlimbs, stiffening of the body by a subdermal connective-tissue sheath of helically wound fibres, and propulsion by a horizontally expanded tail fin. The tail fin is triangular and cetacean-like in dugongids, but retains a more primitive paddle shape in manatees. There is never a dorsal fin, and there are two separate nostrils rather than a single blow-hole. The enlarged, prehensile upper lip is a ‘muscular hydrostat’ formed by variously oriented muscles (Marshall *et al.* 1998, 2003). All body hairs are sinus hairs (specialized tactile organs), especially the elaborately developed facial vibrissae, some of which are also prehensile (Reep *et al.* 2002). The thorax and lungs are elongate and the diaphragm is nearly horizontal, placing the buoyant lungs wholly dorsal to the abdominal organs. The ventricles of the heart form separate lobes. The skeleton typically shows both extensive pachyostosis (increase

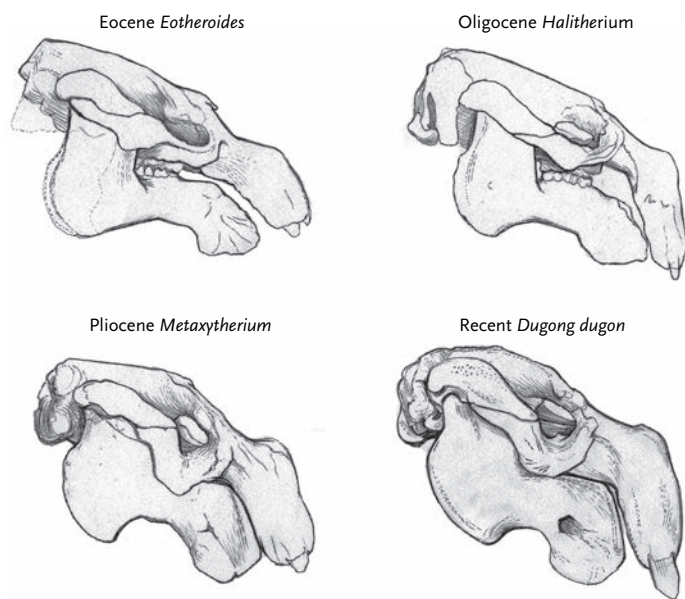
in bulk of individual elements, especially the ribs) and osteosclerosis (increased proportion of compact to cancellous bony tissue). These conditions provide ballast to neutralize the buoyancy of the lungs, which do not collapse during submergence in these shallow-diving animals (Domning & de Buffrénil 1991). Body sizes have ranged from about 2 m to 9 or 10 m in extinct forms.

The skull is distinguished by enlarged premaxillae that contact the frontals and form a more or less down-turned rostrum, a large mesorostral fossa for the narial passages and musculature, reduction or loss of nasals and lacrimals, lack of paranasal air sinuses, lack of a postorbital bar, a massive zygomatic arch, fusion of parietals and supraoccipital into a thick, dense skullcap (usually with pronounced temporal crests but no sagittal crest), and strongly developed pterygoid processes. There is a ring-shaped ectotympanic, not forming a bulla; the periotic is massive and enclosed in a socket in the squamosal. The mandible is heavy, with a long, laterally compressed, down-turned symphysis that primitively bore parasagittally aligned incisor–canine tooththrows. The infraorbital and mental foramina are large, to accommodate the nerves and vessels supplying the fleshy, mobile snout and lips.

The primitive dental formula comprises three incisors, a single canine, five premolars and three molars above and below; whether the five premolars represent a retention of the primitive eutherian condition, or a synapomorphic reversal to that condition, is still unresolved (although optimization of premolar number onto mammalian cladograms derived from morphological or molecular [or both] types of data indicates that the presence of five premolars is apomorphic). Incisors and canines are reduced or (in most forms) absent, except for the single pair of enlarged upper first incisors which form tusks in many species. A pair of horny masticating pads covers the symphyseal parts of the upper and lower jaws.



Fossil skeleton of an extinct quadrupedal sirenian, *Pezosiren* (below) compared with the skeleton of the extant *Dugong dugon*.

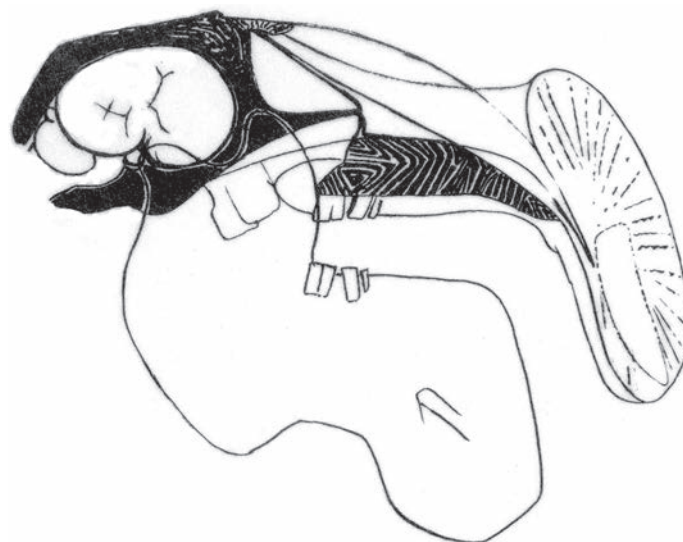


Sirenian evolution.

Replacement premolars are reduced in number or lost in post-Eocene sirenians, but at least some deciduous premolars are usually present in immature individuals. Molars are low-crowned, primitively bunodont and more or less bilophodont, with anterior and posterior cingula on uppers and posterior cingula (usually enlarged on M_3 to form a hypoconulid lophule) on lowers. However, in the extant forms, the cheek dentition is radically modified (degenerate molars in the Dugong, supernumerary ones in manatees).

Forelimb elements are less modified than in cetaceans. The shoulder, elbow, wrist and finger joints are freely movable, though radius and ulna are ankylosed and some of the carpals tend to be fused. The deltoid crest and bicipital groove of the humerus are large in most sirenians including the Dugong, but tiny or absent in manatees. Five digits are present; the first is reduced and the fifth enlarged. Hyperphalangy is not normally seen. A clavicle is lacking. Usually no more than three or four of the 14–21 pairs of ribs are connected to the sternum, which in all but protosirenids comprises only one to three elements. There is normally no fusion of vertebrae. Seven cervicals are present, except in *Trichechus*, which has only six (Giffin & Gillett 1996). In most forms the pelvis is attached by a ligament to a single sacral vertebra, but in modern manatees even this connection is no longer as distinct, and the three post-thoracic vertebral regions cannot be clearly distinguished. The vertebral formulae for the extant African species are C 7, T 18–19, L 3, S 1, Ca 26–32 in the Dugong and C 6, T 17–18, L–Ca 25–26 in the West African Manatee.

The fossil record of the Sirenia is substantial and nearly cosmopolitan (Domning 2001b), including important finds in North Africa (Domning *et al.* 2010). The oldest and most primitive sirenians are *Prorastomus* and *Pezosiren* from the early Middle Eocene of Jamaica, ca. 50 mya (Savage *et al.* 1994, Domning 2001a). These pig-sized quadrupeds already displayed aquatic adaptations, and probably spent more time in the water than the modern hippopotamus, feeding as well as resting there. Most later sirenians were marine and consumed mainly sea-grasses. The Dugong's closest fossil relatives are found in the Caribbean; they may have dispersed between there and the Indian Ocean (around the Cape of Good Hope) in just the last 2 million years,



Dugong dugon: cross-section of skull. Note massive bony capsule around brain and incisor embedded in down-turned Os intermaxillare and matching downturn in mandible.

so there is a possibility of finding their fossil remains on the coast of West Africa (Domning 1995). The euryhaline *Trichechus* evolved in South America and probably also crossed the equatorial Atlantic to West Africa only in the late Pliocene or Pleistocene (Domning 2005).

The Sirenia are clearly a well-defined, strictly monophyletic group. Morphological evidence links them firmly with proboscideans (elephants) and some extinct groups in a taxon called Tethytheria (McKenna 1975, Shoshani 1993, Gheerbrant *et al.* 2005), indicating that these animals probably share an Old World origin. However, there is little molecular support for Tethytheria – the longest concatenations of mitochondrial and nuclear genes actually reject the clade (Amrine-Madsen *et al.* 2003, and see Meredith *et al.* 2011). Molecular support is stronger (though morphological support is weaker) for the more inclusive taxon Paenungulata (Tethytheria + Hyracoidea). Recent molecular studies have raised the hypothesis of Afrotheria, which associates the Paenungulata with macroscelideans, tubulidentates, chrysochlorids, and tenrecs. This is a radically different view, in that it places sirenians and other paenungulates among the most basal lineages of modern placentals, rather than higher up among the hoofed mammals as in morphology-based trees (e.g. Thewissen & Domning 1992).

Sirenians, like the sea-grasses and mangroves on which they feed, evidently originated in the region of the Tethys Sea, the former east–west seaway separating the northern and southern continents. However, they quickly dispersed throughout the Tethyan realm and have remained pantropical ever since – with the notable exception of the lineage leading to the extinct Steller's Sea-cow (*Hydrodamalis*), which adapted to the temperate and cold waters of the North Pacific. This persistent tropicity very likely accounts for the depleted diversity of the Sirenia, given the global cooling of the last few million years.

A comprehensive annotated bibliography of the order is provided by Domning (1996) and recent reviews of Sirenian evolution are found in Domning (2002) and Domning *et al.* (2010).

Daryl P. Domning

Family DUGONGIDAE

DUGONG

Dugongidae Gray, 1821. London Med. Repos. 15: 309.

<i>Dugong</i> (1 species)	Dugong	p. 203
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The family Dugongidae includes a single extant species (Rice 1998, Marsh 2002, Shoshani 2005), the Dugong *Dugong dugon*, which has an extremely large range, being found in coastal waters of at least 48 countries, from East Africa to Vanuatu (Reynolds & Odell 1991, Marsh *et al.* 2002). Despite their wide range, discontinuities in habitat, as well as the impact of localized human activities, cause the species to be sparsely and discontinuously distributed in most regions; in fact, 'throughout much of its range, the Dugong is believed to be represented by relict populations separated by large areas where its numbers have been greatly reduced or where it is already extirpated' (Marsh *et al.* 2002).

Dugongids appeared in the Eocene and were more diverse in the fossil record than is the case today. Most sirenian species that have existed over time were, in fact, members of the family Dugongidae. In addition to the extant Dugong, the family was represented until recently by the Steller's Sea-cow *Hydrodamalis gigas*, which was exterminated by human hunters by 1768 (Reynolds & Odell 1991).

The most thorough, multifaceted and long-term studies of Dugongs have been done in Australia. In the absence of specific information from elsewhere, scientists and managers tend to use information from Australian Dugongs when considering conservation and management in other specific parts of the Dugong's range (see species profile *Dugong dugon*).

Like other sirenians, Dugongs are herbivores. However, unlike other species in the order, Dugongs are obligate bottom feeders, due to their extreme rostral deflection. As a consequence of this adaptation, together with their mostly marine distribution, Dugongs appear to be highly dependent on the integrity of sea-grasses (Marsh 2002, Marsh *et al.* 2002). In fact, Dugong life history attributes (e.g.

age at sexual maturation; inter-calf interval) appear to be relatively plastic (see Boyd *et al.* 1999), in part due to changes in availability of sea-grass resources for food. For example, in some locations, ♀♀ may not reach sexual maturity until they are 17 years old, whereas in other locations sexual maturation may be reached as young as six years of age (see species profile). Typical K-strategists, Dugongs live to be at least 73 years old, and the maximum rate of population increase is low. Population models estimate the maximum rate of population increase to be about 5% per year at best (Boyd *et al.* 1999).

The dependence on sea-grasses by Dugongs has been noted. Conversely, Dugongs appear to function as cultivation grazers whose grazing actually increases the productivity of local sea-grass meadows (Preen 1995a). Dugongs possess adaptations associated with herbivory, such as expanded hindgut capacity, the presence of gut microflora for cellulolysis, and a variety of specialized cellular arrangements in the digestive system (see, for example, Marsh *et al.* 1977). In addition, they possess attributes that facilitate an existence in the marine environment: large size (up to approximately 3 m) for thermoregulation; fusiform body shape; a split fluke for locomotion; smooth skin; and general reduction in external protuberances. Although sensory biology of Dugongs has not been well studied, it is likely that they have functional specializations to facilitate communication, navigation and habitat selection. Marsh (2002) and Marsh & Dutton (see species profile) summarize the diagnostic characteristics of Dugongs; Pabst *et al.* (1999) and Marshall (2002) also provide general information regarding Dugong adaptations. Recent volumes by Marsh *et al.* (2011) and Hines *et al.* (in press) provide comprehensive overviews of dugong ecology and conservation.

John E. Reynolds, III

GENUS *Dugong*

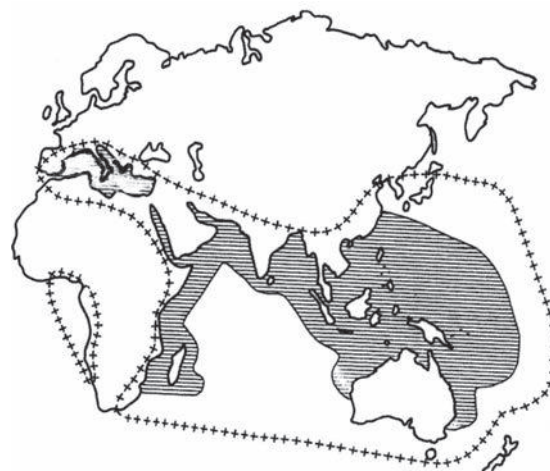
Dugong

Dugong Lacépède, 1799. Tab. Div. Subd. Orders Genres Mammifères 14: 17.

The genus *Dugong* is monotypic, represented by the Dugong *Dugong dugon* (Shoshani 2005), which has a wide distribution in tropical coastal waters from East Africa to Vanuatu within the latitudes of about 26–27° north and south of the equator.

Helene Marsh

Old World distribution of Dugong past and present (shaded) and Potamogetonaceae (+++++).



Dugong dugon DUGONG

Fr. Le Dugong; Ger. Dugong

Dugong dugon (Müller 1776). Linne's Vollstand. Natursyst. Suppl., p. 21. Cape of Good Hope to the Philippines.*Dugong dugon* adult male.

Note: there is much information published on Dugongs from outside Africa. The following account, based primarily on data from Africa, is supplemented by relevant information available from other parts of their range.

Taxonomy Monotypic. Synonyms: *australis*, *cetacea*, *dugung*, *hemprichii*, *indicus*, *lottum*, *tabernaculi*. Chromosome number: $2n = 50$.

Description Rotund cetacean-like body with flippers and flukes that resemble those of a dolphin without a dorsal fin. Head resembles that of a walrus without the long tusks (Bryden *et al.* 1998). Head distinctive, with mouth opening ventrally beneath broad, flat muzzle. Eyes located on side of head, small and not prominent. Externally, ears consist of small openings on either side of head. Adults grey in colour, but may appear brown from the air or from a boat. Older 'scarback' individuals may have large areas of unpigmented skin on the back above the pectoral fins. Flippers are short (up to 420 mm, average 330 mm; Spain & Heinsohn 1975) and, unlike those of the West African Manatee *Trichechus senegalensis*, lack nails. Hind flippers are absent. Fluke is triangular, like that of a whale, unlike that of manatees (*Trichechus* spp.), which have a paddle-shaped tail. Dugongs exhibit little sexual dimorphism in size. Anal and genital apertures are contiguous in ♀♀. In ♂♂ genital aperture is about halfway between anus and umbilicus. Testes are abdominal (Marsh *et al.* 1984a). Two mammary glands, each opening via a single teat,

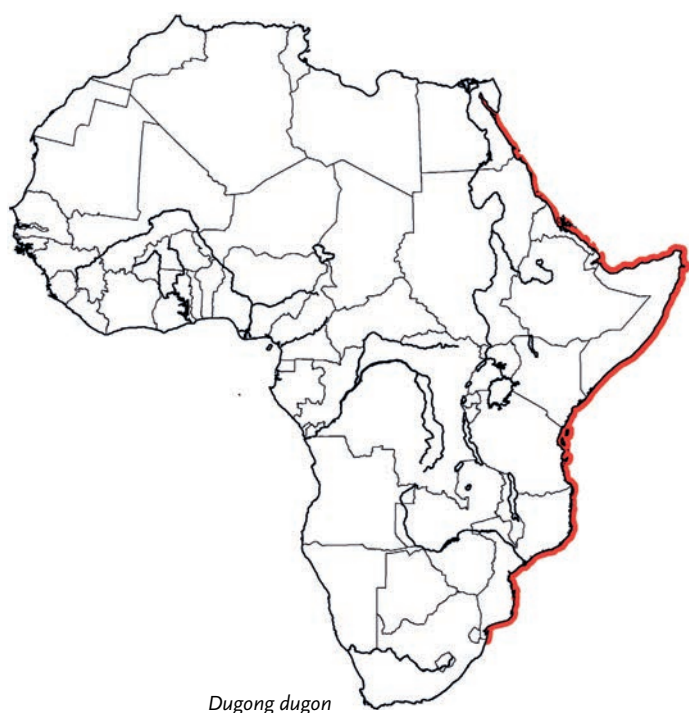
Lateral, palatal and dorsal views of skull of *Dugong dugon*.

are situated in the 'armpit' or axilla; mammaries are somewhat reminiscent of the breasts of human ♀♀.

Tusks of mature ♂♂ and some old ♀♀ erupt on either side of the head for up to about 30 mm (Marsh 1980). Molar teeth are simple and peg-like. A Dugong has a total of six cheekteeth (premolar and molar) in each quadrant of its jaw during its life, but these are never all erupted and in wear simultaneously. Three premolars are present at birth; old animals have only two pairs of teeth (molars two and three), and these may grow throughout life (Marsh 1980).

Geographic Variation None recorded.

Similar Species No other extant members of the Family Dugongidae. The Dugong's closest living relatives in the order Sirenia are the manatees of the family Trichechidae, but no members are sympatric.

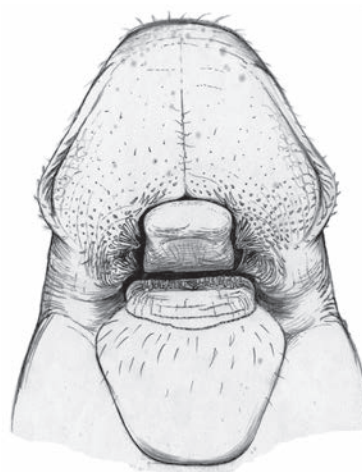


Dugong dugon

Distribution African range extends from the Red Sea and Gulf of Aden to Mozambique (Marsh *et al.* 2002) and Dugongs have been recorded as vagrants as far south as 50 km north of Durban, KwaZulu–Natal (Skinner & Chimimba 2005). There is little information on current Dugong distribution and abundance along the African Red Sea. Dugongs have been reported off the coasts of Egypt (Vincent 1996, Hanafy *et al.* 2006), Sudan and Djibouti (Robineau & Rose 1982), Somalia (Travis 1967, Cockcroft & Young 1998) and, based on anecdotal reports of live sightings and the location of skulls, are thought to occur in most areas along the coast of Eritrea (Marsh *et al.* 2002). In 2003 and 2004, information was collated through literature reviews, questionnaire surveys and opportunistic sightings, and confirmed the continued existence of small numbers of Dugongs in Kenya, Tanzania, Mozambique, Madagascar, Seychelles and the Comoros Archipelago (Moheli and Mayotte Is.) and established the regional significance of the Bazaroto Archipelago in Mozambique as important Dugong habitat (WWF Eastern African Marine Ecoregion 2004). Dugongs have disappeared from Mauritius and are believed never to have occurred in Réunion.

Extralimital to the African continent and the Red Sea region, the Dugong has a range that spans at least 40 countries and territories in tropical and sub-tropical coastal and island waters including the Arabian Gulf, the coast of India and Sri Lanka, South-East Asia, Taiwan, north to Okinawa in Japan, and east through Papua New Guinea to Vanuatu, between about 26 and 27° north and south of the Equator (Nishiwaki & Marsh 1985, Marsh *et al.* 2002, 2011). Their historic distribution is believed to have been broadly coincident with the tropical Indo-Pacific distribution of its food plants, the phanerogamous sea-grasses of the families Potamogetonaceae and Hydrocharitaceae (Husar 1978) (see illustration on p. 203).

Habitat Dugongs frequent coastal waters. Large concentrations of Dugongs tend to occur in wide shallow protected bays, wide shallow mangrove channels (Hughes & Oxley Oxland 1971) and in



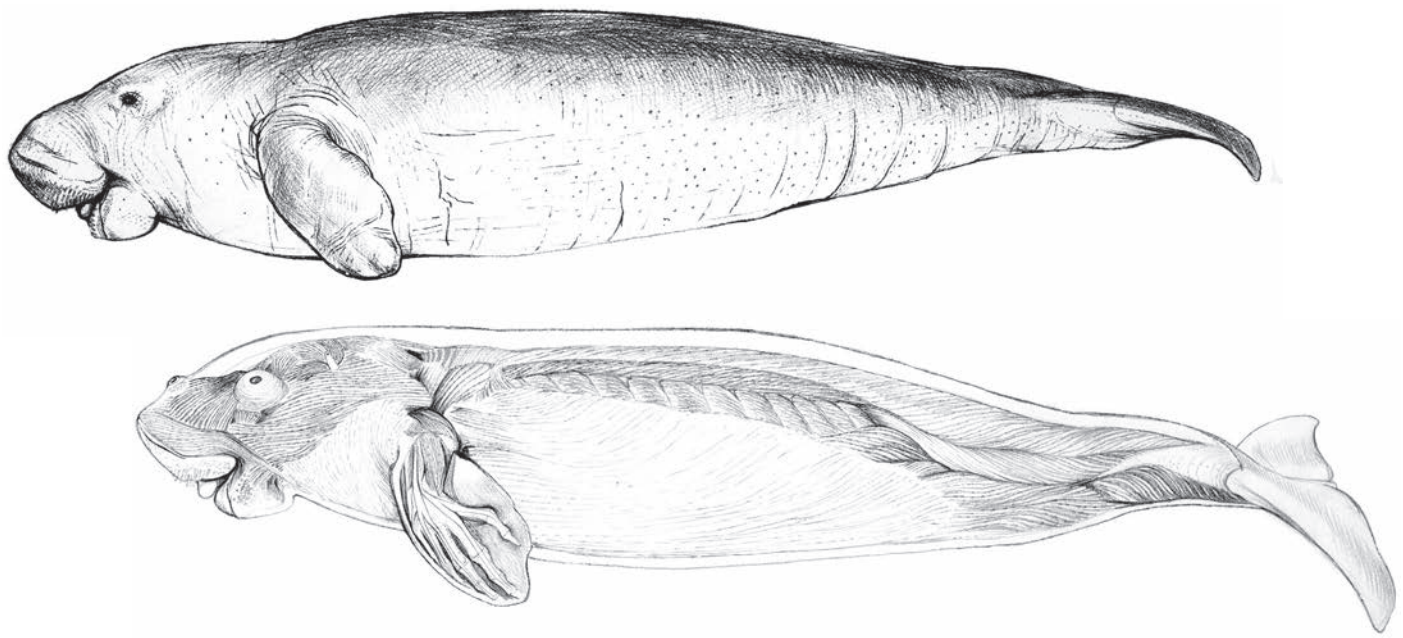
Frontal view of *Dugong dugon* muzzle showing bristles around the oral cavity and intermaxillary rostrum. Embedded in an expansive and flexible complex of oral muscles and skin.

the lee of large inshore islands where there are sizeable sea-grass beds (Heinsohn *et al.* 1977). Dugongs are also regularly observed in deeper water further offshore in Australia in areas where the continental shelf is wide, shallow and protected (e.g. Marsh *et al.* 1997), and where deepwater sea-grass beds occur. Dugong feeding scars have been observed at depths of up to 33 m in sea-grass beds in the Great Barrier Reef region (Lee Long & Coles 1997). Around the Lamu archipelago, fishermen reported that Dugong used to be numerous in deeper waters beyond the reef during periods when the sea was calm (Nov–Mar) where they were believed to be feeding on *Syringodium* and *Cymodocea ciliata*. When the sea became rough, Dugongs moved into shallower, more sheltered bays within the reef, at which time they were feeding on *Halophila* and *Zostera* spp. and *Halodule uninervis*. Similar seasonal movements were reported by fishermen around Mafia I. (Kingdon 1971).

Abundance Anecdotal data suggest that Dugong populations have suffered steep declines in most countries in East Africa since the 1960s (Kenya and Tanzania) and 1980s (Madagascar and Mayotte), while in Mozambique the decline has apparently escalated since the end of the civil war in 1992 (WWF Eastern African Marine Ecoregion 2004). On the basis of the apparent similarity between the distribution of suitable Dugong habitats along the African and Arabian coasts of the Red Sea, Preen (1989a) estimated that the African side could potentially support a population similar in size to that along the Arabian coast, estimated at 4000 in 1986.

The number of Dugongs worldwide is unknown, but there are likely to be more than 100,000 individuals. However, this rather large number is somewhat deceptive if one considers the conservation status of Dugongs in particular countries. Of this estimate there are likely to be some 85,000 animals in Australia (Marsh 2002) and several thousand in the Arabian Gulf; however, in many parts of the species' original range, Dugongs survive only in very small numbers (i.e. a few tens or hundreds of individuals).

Adaptations Dugongs are highly adapted to the marine environment in which they spend their entire lives as evidenced by their relatively large size, streamlined body, whale-like tail, paddle-like forelimbs (flippers) and absence of hindlimbs (Bryden *et al.* 1998). In common with other sirenians, the skeleton of the Dugong is comprised of extremely dense bone that presumably functions to

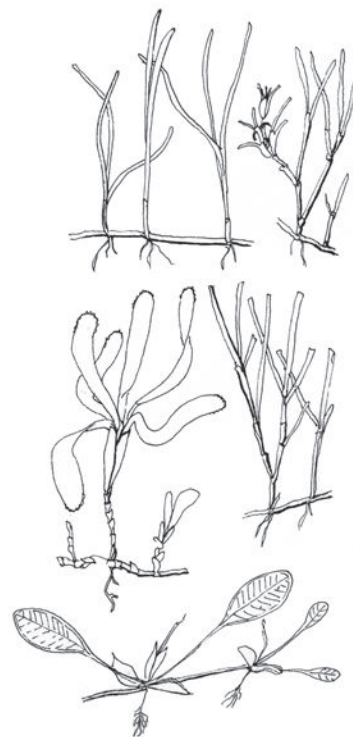


Dugong dugon. The lower image shows the myology. Note that a thick layer of blubber covers all body musculature. The eyes and auditory orifice reach the surface through approximately 25 mm of blubber.

help overcome buoyancy problems while bottom-feeding. Body hair is sparse but the hairs and bristles on the Dugong's head, particularly around the lips and mouth, are highly developed sensory organs that presumably help Dugongs detect their sea-grass food. The Dugong's mouthparts are highly adapted to bottom-feeding on vegetation and the mechanism whereby the muzzle and lips 'rake' food into the mouth has been described and illustrated in Kingdon (1971). The two nostrils are on top of the anterior end of the snout, which allows the Dugong to breathe with very little of the head above the water. The nostrils cannot be closed completely, but contraction of muscles surrounding the nasal ducts closes the ducts. The eyes have no eyelids but are protected by nictitating membranes and are lubricated by oil glands.

Foraging and Food Dugongs are sea-grass specialists, uprooting whole plants when they are accessible leaving long serpentine furrows bare of sea-grass in sea-grass meadows (Anderson & Birtles 1978). When the whole plant cannot be uprooted, they feed only on the leaves (Anderson 1982). In some places, Dugongs prefer 'weedy' or 'pioneer' species of sea-grass, especially species of the genera *Halophila* and *Halodule* (Marsh *et al.* 1982); *Halodule uninervis* is mentioned in most studies that have investigated the diet of the species in the African range (Gohar 1957, Hughes & Oxley-Oxland 1971). These sea-grasses are low in fibre, high in available nutrients and easily digested. Off the Kenya coast, Kingdon (1971) reported seasonal movements between 'pastures' and correlated alterations in Dugong diet. These were attributed to seasonal change in marine flora, which, in turn, could be related to seasonal fluctuations in water temperature and the roughness of the sea. Thus, deep water sea-grasses, notably *Cymodocea* and *Syringodium*, are allegedly preferred by Dugongs Nov–Mar, when seas are calm and warm, while shallow-water, in-shore species such as *Halodule*, *Halophila* and *Zostera* are apparently grazed Apr–Oct, when the sea, off-shore, is very rough and cold and avoided by Dugongs.

Experiments simulating Dugong grazing indicate that feeding Dugongs alter both the species composition and nutrient qualities of sea-grass communities (Preen 1995a). Dugongs are known to practise coprophagy, at least in captivity, and they have been known to feed on invertebrates in some areas (Kingdon 1971, Preen 1995b). Dugongs have an enlarged hindgut with a rich microflora enabling them to digest cellulose and other fibrous carbohydrates (Nishiwaki & Marsh 1985); they retain low-fibre material for extended periods of time within the long, tubular hindgut thereby digesting all the fibrous material (Lanyon & Marsh 1995).

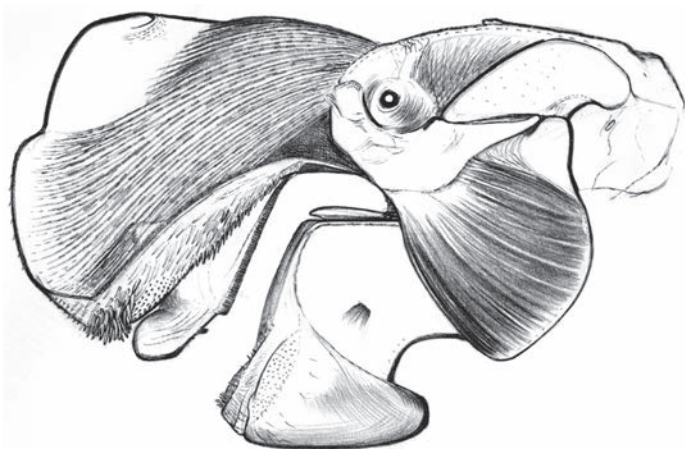


Zostera capensis (left) and *Syringodium* sp. (right)

Cymodocea ciliata (left) and *Halodule uninervis* (right)

Halophila sp.

Principal sea-grasses eaten by *Dugong dugon* in African waters.



Myology of the facial musculature of *Dugong dugon*. Note the horny bristles around the mouth and embedded in highly developed levator labii muscle.

Social and Reproductive Behaviour Knowledge of the social behaviour of Dugongs is rudimentary. The habits and habitats of Dugongs make them difficult to observe and the lack of distinct size classes or obvious sexual dimorphism limits our capacity to interpret observational data on Dugong behaviour. The only defined long-lasting social unit is the cow and her calf (Anderson 1981); most sightings even in areas of high Dugong density are of one or two animals. Travis (1967) reported a group of more than 500 dugongs off the S Somalia coast, and Kingdon (1971) recorded congregations of over 100 off the Kenyan coast; large aggregations of up to several hundred animals still occur (but outside Africa) (Marsh 2002). Little is known of the structure and function of Dugong herds, but Preen (1995a) reported that grazing helped maintain sea-grass meadows at the stage favoured by Dugongs.

There are no data on long-range Dugong movement patterns in African waters, but such movements can be inferred based on sightings in the Seychelles in 2001 (Marsh *et al.* 2002). Seventy Dugongs fitted with satellite-monitored and GPS transmitters in sub-tropical and tropical waters of Australia exhibited a large range of movements. For example, 26 individuals were relatively sedentary (moved <15 km from the capture site) while 44 moved distances of up to 560 km from their capture sites (Sheppard *et al.* 2006). Regional movements were classified as those greater than 100 km, while local movements were less than 15 km. Local movements were generally tidally driven and represented commuting between and within sea-grass beds. Large-scale movements were rapid and apparently directed at reaching a specific and distant site. Radio-tracked Dugongs that were travelling rarely were far from the coast. Some animals caught close to the high latitude limits of the Dugongs' range on the Australian east coast in winter apparently undertook long distance movements to escape water temperatures less than about 18 °C (Sheppard *et al.* 2006). Preen (2004) sighted large herds of Dugongs in winter in the Arabian Gulf, in contrast to their dispersed distribution in summer. He suggested that Dugongs may aggregate around thermal springs in winter, entailing large-scale movements of approximately 400 km from their summer habitats.

Mating behaviour of Dugongs is variable. Herds of mating Dugongs have been observed at several locations along the N Australian coasts. Presumed groups of ♂ ♂ engage in bouts of violent fighting before attempting to mount a presumed ♀ (Preen 1989b). In contrast, in

South Cove in Shark Bay, Western Australia, presumed male Dugongs defended mutually exclusive small temporary breeding territories or leks to attract ♀ ♀ (Anderson 1997). There are no reports of Dugong mating behaviour in African waters.

Vocalizations of Dugongs, which sound like bird chirps, span the 3–18 kHz bandwidth (Anderson & Barclay 1995). An audiogram conducted on one captive Dugong in Australia suggested a minimum hearing range of 4–32 kHz (D. Ketten pers. comm.).

Diving behaviour of 15 Dugongs has been documented using time-depth recorders by Chilvers *et al.* (2004). Overall, the Dugongs spent about half of their daily activities within 1.5 m of the sea surface and 72% in less than 3 m. Their mean maximum dive depth was 4.7 m, mean dive duration was 2.6 min, and the average number of dives per hour was 11. The maximum dive depth recorded was 20.5 m, the maximum dive time in water >1.5 m was 12.3 min.

Reproduction and Population Structure Studies in Australia indicate that Dugongs are long-lived with a low reproductive rate, long generation time, and a high investment in each offspring (Marsh 1980, Marsh *et al.* 1984b, Boyd *et al.* 1999, D. Kwan pers. comm.). Females do not bear their first calf until they are at least six years of age and up to 17 years old. Gestation is approximately 13 months (Boyd *et al.* 1999). Usual litter size is one; Dugongs only rarely give birth to twins. Neonates are 1.1–1.25 m in length ($n = 18$) and weigh 27–35 kg ($n = 53$) (Marsh 1995). The calf suckles for 18 months or so, and the period between successive births is very variable; estimates range from 2.5 to 7.0 years (Boyd *et al.* 1999, D. Kwan pers. comm.). Dugongs start eating sea-grasses soon after birth, and grow rapidly during the suckling period. Population simulations indicate that a Dugong population is unlikely to be able to increase in size more than 5% per year (Boyd *et al.* 1999). This makes the Dugong highly susceptible to over-exploitation by humans. Body weight at puberty is about 250 kg.

Like the teeth of other marine mammals, Dugong tusks accumulate 'growth layer groups' that are used to estimate age, rather like the growth rings of a tree. The oldest Dugong was estimated to be 73 years old when she died (Boyd *et al.* 1999).

Predators, Parasites and Diseases Given the Dugong's life history, natural mortality rates must generally be low. In Australian waters, there are reports of Dugongs being attacked by sharks (Heithaus 2001), killer whales (Anderson & Prince 1985) and crocodiles. Dugongs are susceptible to a wide range of diseases, some of them infectious or parasitic (Campbell & Ladds 1981, Marsh *et al.* 2000). Blair (1981) describes a range of Dugong parasites. There is no information available from Africa.

Conservation IUCN Category: Vulnerable A2bcd. CITES: Appendix I. CMS: Appendix II.

Dugongs are vulnerable to human impacts because of their life history and their dependence on sea-grasses that are restricted to coastal habitats, and which are often under pressure from human activities. In Africa, Dugongs continue to be threatened by direct human exploitation, habitat loss and destruction, and incidental capture during fishing operations in this region (Marsh *et al.* 2002, WWF Eastern African Marine Ecoregion 2004). From an ecological perspective, the Red Sea is considered to be one of the least damaged bodies of water in the world. None the less, oil spills have occurred in the Red Sea, and



Sketches of *Dugong dugon*. Note the crescent-shaped valvular nostrils, and how the ventral surface follows the same plane as the grazing mouth.

are thought to affect Dugongs through the degradation of sea-grass beds (Preen 1989a). Coastal developments include oil-related industrial centres and tourist resorts. Inadequate environmental standards at oil facilities and the de-ballasting of ships in the Red Sea are all potential threats to sea-grass areas (Marsh *et al.* 2002).

Coastal East African countries are experiencing massive population increases and demographic changes that are resulting in environmental degradation that affects critical near-shore Dugong feeding areas (Cockcroft *et al.* 1994, Wamukoya *et al.* 1996a, b). Sea-grass beds are also being destroyed by trawl nets (Wamukoya *et al.* 1996a, b). Artisanal fisheries mostly operate in inshore waters along the East African coast. These fisheries involve the use of dynamite and/or seine, drift and bottom set gill nets from small traditional boats (Cockcroft *et al.* 1994). The density of gill nets along the coast is high. There are no records of the numbers of Dugongs taken as bycatch in these fisheries; however, surveys, including interviews with fishermen, have revealed that Dugongs are taken in the drift gill net fishery (Guissamulo & Cockcroft 1997). Incidentally captured Dugongs are eaten by fishermen, and eating Dugong is not forbidden in most Muslim communities. In non-Muslim countries the meat may be disguised as pork and sold in restaurants (Dutton 1994). Although legislation now bans Dugong hunting, it is considered to

be one of the factors that has caused the decline in Dugong numbers along the south coast of Kenya (Wamukoya *et al.* 1995, Wamukoya, Mirangi *et al.* 1996, Wamukoya *et al.* 1996a, b). Dugongs are afforded legislative protection in most countries in the region. However, most governments have neither the resources nor the capacity to monitor all activities in the marine and coastal zones (WWF Eastern African Marine Ecoregion 2004). The fact that Dugongs range across national borders argues for the development and implementation of regional and international conservation efforts.

Measurements

Dugong dugon

HB (♂ ♂): 2.4 (2.2–3.31) m; n = 18

WT: 250–570 kg

Australian waters (Spain & Heinsohn 1975, Marsh 1995, Lanyon *et al.* 2010)

Key References Boyd 1999; Kingdon 1971; Marsh *et al.* 2002, 2011; Nishiwaki & Marsh 1985; WWF Eastern African Marine Ecoregion 2004.

Helene Marsh & Paul Dutton

Family TRICHECHIDAE

MANATEES

Trichechidae Gill, 1872. *Smithson. Misc. Coll.* 11 (1): 14.

<i>Trichechus</i> (1 species)	Manatees	p. 210
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The family Trichechidae includes three extant species of manatees (Rice 1998, Reynolds & Powell 2002, Shoshani 2005): the West Indian Manatee *Trichechus manatus*, Amazonian Manatee *T. inunguis* and West African Manatee *T. senegalensis*. Only the latter occurs in Africa. Domning & Hayek (1986) provide evidence that two subspecies of West Indian Manatee exist, namely the Florida Manatee (*T. m. latirostris*) and the Antillean Manatee (*T. m. manatus*). Little genetic data have been published, but Garcia-Rodriguez *et al.* (1998) found 15 haplotypes among West Indian Manatees and suggest three, rather than two lineages.

On current evidence, the first truly manatee-like sirenians (*Potamosiren*) appeared 15 mya, during the Miocene. Extant species are found from the SE USA into Brazil (*T. manatus*), the Amazon R. and tributaries in Brazil, Peru, Ecuador and Colombia (*T. inunguis*), and from S Mauritania to Angola (*T. senegalensis*). Around the mouth of the Amazon R., West Indian and Amazonian manatees may interbreed, as their ranges overlap (Vianna *et al.* 2006).

Manatees are extremely derived anatomically and physiologically (e.g. Pabst *et al.* 1999, Marshall 2002, Reynolds *et al.* 2002, Rommel & Reynolds 2002). The best-studied taxon is the Florida Manatee; in many cases, information available for this subspecies is assumed, in the absence of corroborating data, to apply for other trichechids. Reviews of manatee functional morphology appear in the references cited above.

All living manatees are large animals. The West Indian Manatee is the largest species, with some individuals approaching 1500 kg in weight and 4 m in length. The smallest species is the Amazonian Manatee, which measures less than 3 m and weighs less than 500 kg. Manatees lack pelvic limbs (although vestiges of pelvic bones remain) and have paddle-like pectoral flippers. The body is streamlined (fusiform) with a single, rounded fluke for locomotion. No dorsal fin is present. The skeleton is pachyosteosclerotic; this feature, coupled with the thick, dense integument, provides ballast. The elongated hemidiaphragms and lungs are important in buoyancy control (Rommel & Reynolds 2000). The nostrils are located on the dorsal tip of a somewhat streamlined head. Compared with many other marine mammals, manatees swim slowly and dive only to shallow depths and for short periods of time (< 20 min). The epidermis is somewhat rough in the West Indian Manatee and West African Manatee, but it is much smoother in the Amazonian Manatee. The latter species also tends to possess white-pink areas on the belly. Another external difference in the Amazonian Manatee is the lack of nails at the tips of the pectoral appendages.

Manatees are non-ruminating herbivores (Reynolds & Rommel 1996) that possess a greatly enlarged hindgut (especially the large intestine, which can exceed 20 m in length and 150 kg in weight), a single stomach, a capacious duodenum and an elongated but narrow

post-duodenal small intestine. Manatees may consume up to 7% of their body weight per day, but Amazonian Manatees are thought to fast during the dry season for periods of up to 200 days, when vegetation is unavailable to them. Associated with their consumption of large amounts of often-gritty vegetation, manatees possess enlarged, flexible lips equipped with prehensile and tactile vibrissae and moved by a muscular hydrostat; supernumerary molariform teeth that are replaced throughout the lifetime of an individual; and unusual histology of the mucosae of the gastrointestinal tract organs.

The distribution of Florida Manatees is limited by cold weather in winter and perhaps by access to freshwater to drink. The latter limitation may well apply to other taxa. Although manatees possess vascular, counter-current heat exchangers, their inherently low metabolic rates (20–30% lower than expected) influence their ability to withstand cold conditions. Although trichechids are considered totally aquatic, they may voluntarily haul themselves partially out of the water to feed. Amazonian Manatees are confined to freshwater, and there are no known records of the species in salt water, whereas the other species are euryhaline in their distribution, occupying rivers, embayments and coastal marine habitats where sea-grass meadows or other aquatic vegetation is available.

The sensory biology of manatees is not well studied (Glaser & Reynolds 2003). Acoustics is likely to be the most important mode of communication among manatees. Vision is relatively poor, the ability to communicate and select habitat using chemical signals is likely but undemonstrated, and the use of innervated hairs on the body may provide signals similar in nature to those from a lateral line in fishes.

The social structure of manatees is not well understood. In Florida, a loose, fission–fusion society exists (Wells *et al.* 1999). In terms of their life history attributes (Reynolds & Powell 2002), Florida Manatees are K-strategists that may live as long as 60 years, reach sexual maturity as early as two years of age for ♂♂ and 3–4 years for ♀♀, and generally produce a single calf once every 2.5–3 years. Manatees are sperm competitors (Reynolds *et al.* 2004) and display promiscuous breeding. Sexual dimorphism is lacking, although Florida Manatees ♀♀ appear to be heavier, on average, than ♂♂.

The only taxon for which good population data exist is the Florida Manatee, and even for this subspecies, uncertainties in counts and population trends exist. As a general rule, survival of manatees worldwide is jeopardized by a range of current threats (incidental taking in fishing gear, habitat loss, watercraft collisions, hunting and pollution), as well as future threats associated with human population growth and human activities (Reynolds 1999). Recent volumes by Marsh *et al.* (2011) and Hines *et al.* (in press) provide comprehensive overviews of manatee ecology and conservation.

John E. Reynolds, III

GENUS *Trichechus*

Manatees

Trichechus Linnaeus, 1758. Syst. Nat., 10th Edn, 1–34.

The genus *Trichechus* includes three species: West African Manatee *T. senegalensis*, Amazonian Manatee *T. inunguis* and West Indian Manatee *T. manatus* (Shoshani 2005). As their names suggest, only the first occurs in African waters. The generic name originates from the Greek words *trichos* (hair) and *ekhō* (to have) pertaining to the sparse hairs covering manatees. The West Indian and West African species

are most similar in anatomy and morphology, although recent genetic analysis suggests closer phylogeny with the Amazonian species (Parr & Duffield 2002, Vianna *et al.* 2006).

James A. Powell

Trichechus senegalensis WEST AFRICAN MANATEE

Fr. Lamantin; Ger. Seekuh, Manati

Trichechus senegalensis Link, 1795. Beitr. Naturgesch. 1 (2): 109. Senegal.West African Manatee *Trichechus senegalensis*.

Taxonomy Monotypic. Synonyms: *africanus*, *australis*, *nasutus*, *owenii*, *stroggylonurus*, *vogelii*. Chromosome number: not known.

Description West African Manatees are heavy, adapted to aquatic life with a fusiform shape, broad back and no dorsal fin. Head is small compared with overall body size. Eyes are small and protrude slightly. No external ears. Muzzle blunt and rostrum only slightly deflected downward. Muzzle has massive, movable lip pads that manipulate and grasp vegetation aided by the stiff bristles. Skin colour is grey but can vary from greenish to brown to black depending on growths of epiphytic algae. Manatees in coastal waters may have barnacle growth. The thick skin is tough, slightly rough and underlain by fat; the body is covered by sparse, fine, evenly distributed hairs. Hindlimbs absent, moveable pectoral limbs are paddle-like, used for orienting the body, holding food and 'walking' on the bottom. Each pectoral flipper possesses 3–4 fingernails on the lateral, distal edge. Manatees possess a large, horizontally flattened, rounded tail. Male genital aperture is located near the middle of the ventrum and genital slit for ♀♀ is near the anus just anterior to the peduncle. There are two axillary nipples. Skull is

generally broad, with a shortened, slightly deflected snout. Nasal bones variable in form. Cheekteeth brachyodont. Five to seven functional teeth are present at any time in each jaw; teeth are continually replaced by horizontal migration from the back of the jaw to compensate for tooth-wear caused by their abrasive diet of grasses and aquatic plants.

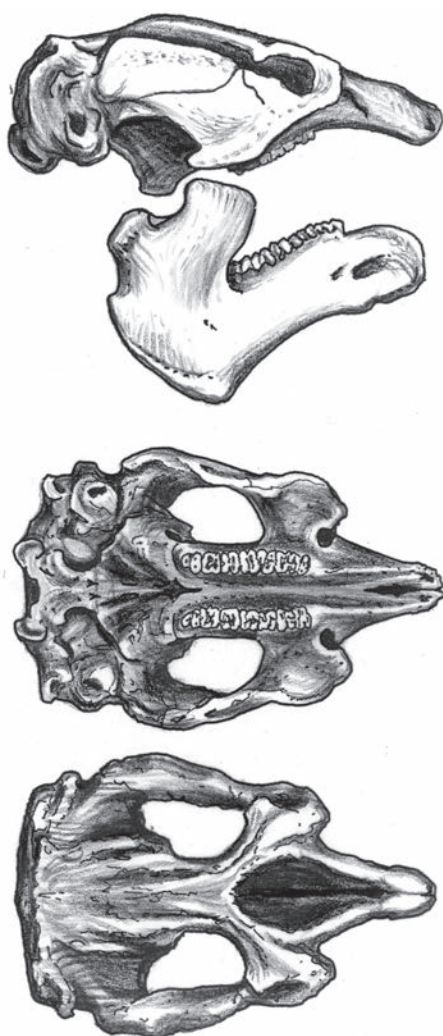
Geographic Variation None recorded.

Similar Species

Dugong dugon. Tail bifurcated similar to Cetacea; muzzle large and disc shaped; peduncle oval in cross-section along dorsal axis (whereas manatees have oval peduncle in cross-section along lateral axis). Strictly marine, feeding on sea-grasses. Indian Ocean coasts only.

Distribution Widely distributed along coastal regions, rivers, estuaries and lagoons of West Africa from S Mauritania to the Cuanza

*Trichechus senegalensis*



Lateral, palatal and dorsal views of skull of *Trichechus senegalensis*.

and Longa Rivers, Angola (Husar 1978, Nishiwaki 1984, Grigione 1996, Powell 1996, Morais 2006). Ascends many hundreds of kilometres up rivers and can be found offshore in shallow coastal regions such as the Bijagos Archipelago (Guinea Bissau) and Casamance (Senegal) where there are abundant sea-grasses. Isolated populations cut off from the sea are found in L. Volta, Ghana, above the Volta hydroelectric dam and the upper reaches of the Niger R. as far as Guinea. Occur along the entire length of the Gambia R., penetrating into Senegal where there are records as far upstream as Niokolo-Koba N. P. (Grubb *et al.* 1998). In Chad, manatees are present in L. Léré and L. de Tréné along the Mayo-Kebbi, Bahr Keeta and Baniangi Rivers; manatees are also reported from the Baniangi, Logone and Chari river tributaries of L. Chad. Sightings of manatees reported from L. Chad itself but no confirmed records (Ita 1994). Manatees have penetrated the Niger R. as far upstream as Segou, Mali, which represents a distance of some 2000 km (Hatt 1934).

Habitat Wide variety of marine and freshwater habitats, including shallow coastal areas, estuaries, lagoons, small tidal rivers and hundreds of kilometres up larger freshwater rivers (Husar 1978). Some populations are completely cut off from the sea by natural barriers such as cataracts or by human structures such as

hydroelectric and salinity dams. In arid regions where water levels vary considerably between wet and dry seasons, manatees survive drier periods by seeking refuge in deeper pools and seasonally connected lakes, such as Pandam L. in Nigeria or moving downriver (Sikes 1974). Preferred habitats are sheltered estuaries, large, freshwater rivers and shallow coastal regions with freshwater input (Husar 1978). In some areas they co-exist with Common Hippopotamus *Hippopotamus amphibius* (J. Powell pers. obs.).

Abundance Elusive and largely nocturnal, manatees are inconspicuous though present throughout much of their historic range. Recent information and surveys indicate manatees persist in many areas thought previously extirpated (Powell 1996), although numbers appear low throughout. Populations are probably depressed due to their low reproduction rate and human-related mortality preventing populations from building.

Adaptations Manatees are well adapted to their aquatic habitat, being fusiform in shape with a large, rounded tail. Their forelimbs form flippers that tuck in closely to the body when swimming forward. Otherwise, the flippers are used to manoeuvre by sculling and 'walking' along the bottom. Male West Indian Manatees *Trichechus manatus* clasp the ♀ with the flippers during sexual pursuit and cavorting. The muscular lip pads are used to grasp vegetation, aided by stiff bristles that help manipulate food toward the mouth. The body is covered by fine, evenly spaced hairs that, in the West Indian species, have been found to detect subtle pressure differences and vibrations (Reep *et al.* 2002). Internally, manatees have thick, heavy (pachyostotic) bones, which, together with dense skin, help create ballast. The arrangement and orientation of the lungs and diaphragm assist with buoyancy control.

Foraging and Food Food consists of submerged vegetation, emergent plants, overhanging bank growth and floating plants. Fruits and nuts falling into the water are also consumed. Preferred food items include aquatic plants such as *Eichornia crasipes* and *Cymodocea nodosa*, bank sedges such as *Vossia* sp. and *Echinochloa* sp., and leaves of mangroves (*Rhizophora* sp.). The manatees grasp bank grasses with their lips and twist the grass stem at a node until it breaks free. Feeding sign is often easy to observe where there are sections of twisted and broken grass stems mixed among intact bank growth. Food is digested by hindgut fermentation similar to horses and elephants. Husar (1978) estimated that a free-ranging adult could consume as much as 8000 kg of aquatic vegetation in one year. Manatees are considered a pest on rice in Guinea-Bissau and Sierra Leone during the flood season (Reeves *et al.* 1988, Powell 1996).

Fishermen in Senegal and Sierra Leone report manatees 'sucking' the flesh off fish entangled in nets, though this is not confirmed (Reeves *et al.* 1988, Powell 1996). Powell (1978) observed similar behaviour by the West Indian species in Jamaica.

Radio tracking manatees in Côte d'Ivoire indicated that manatees feed almost exclusively at night (Powell 1996). On average, they spent 4–6 hours feeding, sometimes travelling several kilometres between daytime resting areas and feeding areas. Manatees would frequently return to the same areas to feed for several consecutive nights. It is believed that the nocturnal feeding and travelling pattern may be a response to hunting pressure.



Sketch of *Trichechus senegalensis*.

Social and Reproductive Behaviour Little information is available on the social and reproductive behaviour of West African Manatee. Current knowledge is based on tagging studies and inferences from other manatee species. Males and ♀♀ are largely solitary, but may loosely aggregate at preferred feeding and resting sites; the strongest association is between a ♀ and her calf. Groupings of manatees occur in mating herds, when ♀♀ are in oestrus and followed by a consort of several ♂♂. Radio tagging information from Côte d'Ivoire showed seasonal aggregations occurring just before the rainy season in a certain section of a small tributary (Powell 1996). It is speculated that this aggregation may be related to reproductive behaviour. These observations are consistent with Howell (1968), who reported that manatees breed seasonally in weedy swamps and lagoons at the end of the dry season.

Movements are known to occur in response to changes in seasonal water levels and salinities. In drier periods where river levels fluctuate dramatically, manatees move downstream or, if blocked access, seek deeper pools or lakes connected to main rivers. Where manatees inhabit larger, tidally influenced rivers, they will spend extended time upstream during the dry season in lower salinities (Powell 1996).

Reproduction and Population Structure Typically one young, although, extrapolating from fishermen reports and from what is known of West Indian Manatees, twins may be rare. Gestation is 12–13 months, calving interval probably similar to other manatees at 2.5–3.0 years, with calves remaining with ♀♀ for 1–1.5 years. Newborn calves are about 1 m in length (Cadenat 1957). Howell (1968) reported seasonal breeding/births before the onset of the wet season, although newborn calves have been reported throughout the year (Dekeyser 1952, Cadenat 1957).

Predators, Parasites and Diseases There are no known predators or diseases for West African Manatees, although large

crocodiles may occasionally predate calves or injured individuals. Their thick, extremely tough hide may help to protect them from potential predators. Shark predation on West Indian Manatees has been reported (Falcon-Matos *et al.* 2003, J. Powell pers. obs.), but there are no documented cases for West African Manatees.

Only two internal parasites have been recorded for the West African Manatee. The trematode *Chiorchis fabaceus* inhabits the lumen of the caecum and colon (Baylis 1936), and is shared by all three manatees (Beck & Forrester 1988). A new ascaridoid nematode, *Heterocheilus domningi*, was identified from a manatee collected from the lower Congo R. (Sprent 1983) and is very similar to *H. tunicatus* known from the other two species (Sprent 1983, Beck & Forrester 1988). Two ectoparasites have been recorded: *Chelonibia manati* also found on the West Indian Manatee, and *Platyelaps hexastylus* (Beck & Forrester 1988).

Conservation IUCN Category: Vulnerable A3cd; C1. CITES: Appendix II. CMS: Appendix II.

Protected by specific laws in all countries where they occur in Africa, although enforcement of laws is minimal. Sanctuaries and reserves established that include protection of manatees and their habitat include: Parc National des Oiseaux de Djoudj, Parc National de Basse Casamance, Delta du Saloum (Senegal), Baboon Island N. P., Kiangs West N. P. (Gambia), Ilhas de Orango N. P., João Vieira e Poilão Marine N. P. (Guinea-Bissau), National Park of Upper Niger (Guinea), Azagny N. P., Iles Eotiles N. P. (Côte d'Ivoire), Digya N. P. (Ghana), 'W' N. P. (Burkina Faso/Niger/Benin), Kainji L. N. P., Pan Dam Wildlife Reserve (Nigeria), Reserve de Faune de Douala-Edea, Korup N. P. (Cameroon), Konkouati N. P. (Congo R.) and five recent national parks in Gabon. Hunting of manatees for their meat, oil and use of body parts for medicinal purposes exists throughout their range. Hunting techniques include harpooning, trapping by a variety of methods, netting in large mesh nets, and catching them on large hooks baited with cassava. Incidental/accidental mortality occurs when manatees become entangled in fishing nets, shark nets, hook lines or stranded when water levels drop (Powell 1996). In Guinea Bissau, Silva & Araújo (2001) reported 209 deaths between 1990 and 1998; of these, 72% died in fishing gear, 13% were hunted, 4% stranded at low tide and for 11% the cause of death was undetermined.

Measurements

Trichechus senegalensis

HB (♂♂): 2.56 (1.77–3.34) m, n = 14

HB (♀♀): 2.59 (2.25–3.03) m, n = 11

Senegal (Cadenat 1957, Dupuy & Maigret 1978, Diop 1984), Sierra Leone (Cole & Okera 1976), Côte d'Ivoire (Powell 1996), Gabon (Peck unpubl.), Nigeria (Dollman 1933) and Gambia (Itoh & Tsuyuki 1974)

Note: there are no known published body weights available for West African Manatee, but it is possible to estimate body weight by extrapolating from a dataset of 2.0–3.35 m long Antillean Manatees (*Trichechus manatus manatus*) from Belize (J. A. Powell *et al.* unpubl.), which weighed 166–640 kg (n = 51).

Key References Husar 1978; Powell 1996.

James A. Powell

Cohort AFROINSECTIPHILLIA

Cohort Afroinsectiphillia Waddell, Kishino & Ota, 2001. *Genome Informatics* 12: 148.

The afrotherian clade that contains the Aardvark (order Tubulidentata), sengis (order Macroscelidea) and tenrecs and golden-moles (order Afrosoricida) has been named Afroinsectiphillia, which means ‘African insect-lovers’. The monophyly of this curious assemblage is now supported by phylogenetic analyses of large genomic datasets (Amrine-Madsen *et al.* 2003, Murata *et al.* 2003, Poulakakis & Stamatakis 2010, Meredith *et al.* 2011), and two types of rare genomic changes (Robinson *et al.* 2004, Nishihara *et al.* 2005, Poulakakis & Stamatakis 2010), but the three major afroinsectiphillian lineages show little superficial morphological similarity. Indeed, Afroinsectiphillia is more notable for its great morphological disparity, in that it contains small-bodied cursors (sengis) that may be descended from herbivorous ancestors; semi-aquatic carnivores (African otter-shrews and Malagasy *Limnogale*); arboreal, spiny and shrew-like tenrecs in Madagascar; and a number of large- and small-bodied fossorial taxa. Digging adaptations are a recurring theme within Afroinsectiphillia, having evolved independently at least three times (in the Aardvark, golden-moles and Malagasy rice tenrecs).

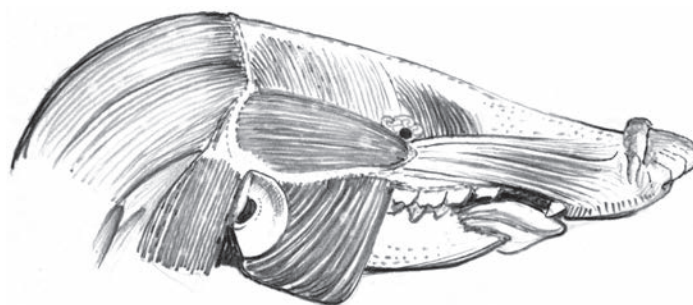
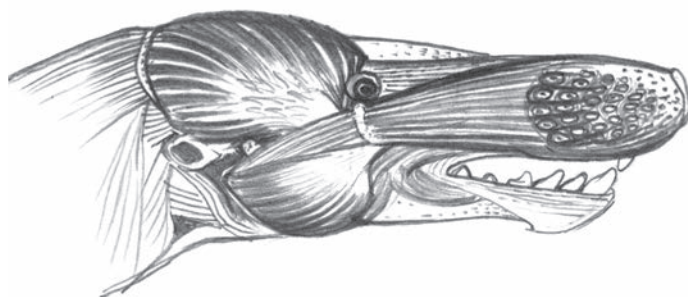
Genetic data suggest that the last common ancestor of the extant afroinsectiphillians lived about 75 mya, in the Late Cretaceous – unfortunately during a huge gap in Afro-Arabia’s fossil record of mammalian evolution. However, some of the oldest placental mammal-bearing sites in Africa, which are about 56 million years old (late Palaeocene), have produced possible fossil afrosoricids (Seiffert

2010, Goswami *et al.* 2011), and distant relatives of the living sengis are known from Eocene localities that are 50–45 million years in age. Undoubted fossil aardvarks are not known until about 18 mya, in the early Miocene, but the extinct order Ptolemaiida, known from Eocene and Oligocene deposits in Egypt and the early Miocene of East Africa, might be more closely related to Tubulidentata than to other afrotherian orders (Seiffert 2007).

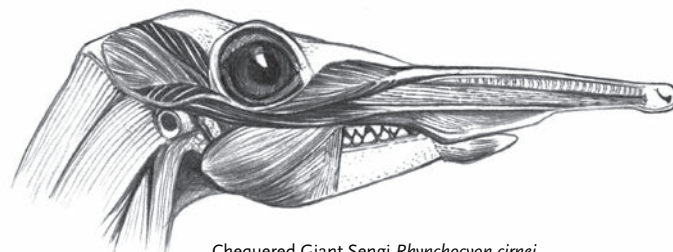
Perhaps because of their very poor early fossil records, the interrelationships of afroinsectiphillian orders remain unclear. One option, favoured by the largest available DNA datasets, places sengis closest to afrosoricids in the superorder Afroinsectivora (Amrine-Madsen *et al.* 2003, Poulakakis & Stamatakis 2010, Meredith *et al.* 2011); however, rare genomic changes have alternatively provided support for both a sengi–Aardvark clade (Robinson *et al.* 2004) and an Aardvark–afrosoricid clade (Nishihara *et al.* 2005), neither of which have been assigned a higher-level taxonomic name. For now, it is probably best to recognize Afroinsectiphillia and Afrosoricida, and to wait for more data to resolve the position of the Aardvark and sengis relative to afrosoricids.

Erik R. Seiffert

Giant Otter-shrew *Potamogale velox*



Stuhlman's Golden-mole
Chrysochloris stuhlmanni



Chequered Giant Sengi *Rhynchocyon cimei*



Aardvark *Orycteropus afer*

Myology of representatives of the Afroinsectiphillia.

Order AFROSORICIDA – Tenrecs, Otter-shrews, Golden-moles

Afrosoricida Stanhope *et al.* 1998. Proc. Natl Acad. Sci., USA 95: 9967–9972.

Tenrecidae		
Potamogalinae (2 genera, 3 species)	Otter-shrews	p. 216
Chrysochloridae (9 genera, 21 species)	Golden-moles	p. 223

Stanhope *et al.* (1998) erected the Afrosoricida as a new order to name a clade comprising two families: Chrysochloridae or golden-moles (9 genera, 21 species) of sub-Saharan Africa, and Tenrecidae. The Tenrecidae comprise four subfamilies: the tenrecs (3 subfamilies, 8 genera, 27 species) of Madagascar and Comoros Islands (not included in *The Mammals of Africa*), and the otter-shrews (subfamily Potamogalinae; 2 genera, 3 species) of Africa. The African representatives of the Order (Chrysochloridae and Tenrecidae [subfamily Potamogalinae]) comprise 11 genera and 24 species. The Afrosoricida was born out of the final sundering of the Insectivora (also referred to as Lipotyphla), an order that was recognized for many decades, but which recent molecular evidence now shows to be polyphyletic. This profile deals only with the taxa on the continent of Africa; general information on the Tenrecidae of Madagascar may be found in Nowak (1999) and Olson & Goodman (2003). See Bronner & Jenkins (2005) for a taxonomic review of the Afrosoricida.

Biological Characteristics of African Afrosoricida

The two families of the order represented in Africa have very different morphological characteristics. The otter-shrews (family Tenrecidae, subfamily Potamogalinae) are semi-aquatic with an elongated body, long muscular tail (ca 80% of HB), water-repellent pelage, small ears, long vibrissae and short limbs. One species has webbed digits. Otter-shrews are fairly small (mean HB: ca. 140 mm to ca. 320 mm) and are similar in general shape to otters (order Carnivora) although smaller in size. All species live in streams (rather than big waterways) in rainforest and montane forest habitats in West and central Africa. They are generally uncommon and rarely seen. Golden-moles (family Chrysochloridae) are subterranean and highly adapted for life underground. Golden-moles are mostly small in size (mean HB of ca. 80–110 mm, with a range of HB ca. 60 mm to ca. 220 mm, according to the species), body shape is fusiform or cylindrical and the head merges with the body without an obvious neck. External ears are absent; eyes are degenerate and covered with skin. The tail is absent and limbs are very short. Forelimbs are well developed with large digits and nails (especially Digit 3). Most species of golden-moles live in grasslands, semi-deserts and highland areas of southern Africa; two species live in rainforests of central and eastern Africa, and one species in semi-desert habitats of the Horn of Africa.

Species of the Afrosoricida are insectivorous and/or carnivorous. Golden-moles eat insects and earthworms, and otter-shrews eat crabs, aquatic insects, shrimps and fish. Typically, all species have a large set of teeth: 36–40 in golden-moles and 40 in otter-shrews: the incisor and canine teeth are pointed, but the canine is not enlarged as in the Carnivora. Premolar and molar teeth are multi-cusped for crushing and cutting the prey. The social organization of afrosoricids is not well known. As far as is known, otter-shrews and golden-moles are solitary, although the home-ranges of individual otter-shrews may overlap. Reproductive strategies, likewise are not well known; litter-size is small (1–2) and most species have restricted reproductive seasons, the timing of which varies according to the species and the environment; a few species of golden-moles may breed throughout the year.

Populations are often isolated because of restricted distributions and the limited mobility of individuals: otter-shrews are confined to streams and golden-moles are confined to suitable patches of soil. Demes of golden-moles (as for many subterranean mammals) show considerable morphological variation, which has resulted in many named forms (most now considered as synonyms). Movement of individuals to suitable new habitats is difficult for otter-shrews and golden-moles because of their strict environmental requirements and their inability to travel across unsuitable habitats.

Phylogenetic Relationships The Insectivora, as traditionally recognized, included the shrews (Family Soricidae), hedgehogs (Family Erinaceidae), true moles (Family Talpidae), elephant-shrews or sengis (Family Macroscelididae), tree-shrews (Family Tupaiidae), solenodons (Family Solenodontidae), golden-moles (Family Chrysochloridae), tenrecs (Family Tenrecidae) and several extinct families. It was a poorly defined group, essentially a taxonomic wastebin for various ‘undifferentiated’ insectivorous forms assumed to be the ancestral stock from which other placental mammals radiated. The Insectivora was rendered obsolete, first by the removal of the elephant-shrews to the Order Macroscelidea and the (non-African) tree-shrews to the Order Scandentia, and more recently by the allocation of golden-moles, tenrecs and otter-shrews to the Order Afrosoricida. The remnants of the Insectivora are now allocated to the Order Soricomorpha (shrews, true moles and [non-African] solenodons) and the Erinaceomorpha (hedgehogs).

A close phylogenetic affinity between golden-moles and tenrecs (including otter-shrews) was first proposed more than a century ago, and has been supported by several authors (e.g. Butler 1956), but their recent grouping in the Afrosoricida has evoked controversy. Ironically, this controversy is not about the putative close relationship between the Chrysochloridae and Tenrecidae, which has little morphological support despite overwhelming molecular evidence. Instead, it concerns the name ‘Afrosoricida’, and the inclusion of this order within the recently erected supraordinal group named ‘Afrotheria’.

The name 'Afrosoricida', which literally means 'African shrew-like mammals', is still controversial, and has been rejected by some authors who instead advocate using the names 'Tenrecomorpha' or 'Tenrecoidea' for the clade containing golden-moles and tenrecs. The term 'Afrosoricida' is deemed inappropriate because it suggests a close relationship between shrews and golden-moles and/or tenrecs, and also because it engenders confusion with the shrew subgenus *Afrosorex*. Despite the tendency during the nineteenth and twentieth centuries to include shrews, golden-moles and tenrecs in the same order (Insectivora), or even in the same suborder (Soricomorpha; e.g. Butler 1988), there is now robust morphological and molecular evidence against any close phylogenetic relationship between shrews and the clade containing golden-moles and tenrecs (Asher *et al.* 2003). Consequently, there has been widespread reluctance (especially among shrew biologists) to accept the name 'Afrosoricida'.

Some authors have argued that Tenrecoidea McDowell, 1958 pre-dates Afrosoricida and is the valid name for the clade containing golden-moles and tenrecs (e.g. Malia *et al.* 2002). However, Tenrecoidea Simpson, 1931 was first erected as a superfamily to group several families with 'zalambdodont' cheekteeth (i.e. cheekteeth with three main cusps connected by a V-shaped crest), but excluded chrysochlorids, which were instead assigned to a separate superfamily (Chrysochloridea Broom, 1915). McDowell's (1958) restriction of Tenrecoidea to include only golden-moles and tenrecs radically changed Simpson's grouping concept, violated the principle of reasonable emendation (Simpson 1945: 33) and also his recommendation that superfamily names (ending in -oidea) should be avoided.

A colloquial derivative of 'Tenrecoidea', the term 'tenrecoid', has also been widely misused in the scientific literature for vaguely defined groupings of extant and extinct taxa putatively characterized by zalambdodont cheekteeth. However, it is now known that some of these taxa are not technically zalambdodont, and that zalambdodonty may have arisen independently several times (Broom 1916). This further militates against the nomenclatorial use of 'Tenrecoidea' and 'tenrecoid', regardless of taxonomic rank.

'Tenrecomorpha' Butler, 1972, named as a suborder to accommodate the tenrecs (but not golden-moles), has also been used for the clade containing golden-moles and tenrecs (e.g. Bronner *et al.* 2003). However, 'Tenrecomorpha' has most consistently been used to include only tenrecs (e.g. MacPhee & Novacek 1993) and consequently is better applied at the subordinal level to distinguish between the Tenrecidae and Chrysochloridae, in accordance with both morphological and molecular data suggesting early divergence of these families. The name 'Afrosoricida', although inappropriate, implies the most specific and least confusing phylogenetic grouping concept; it is also a name that is already embedded in the primary scientific literature (Bronner & Jenkins 2005).

Until very recently, the inclusion of Afrosoricida within the supraordinal taxon Afrotheria remained controversial. Numerous studies (employing a variety of sophisticated analytical procedures), which have utilized an impressive suite (>17 kbp) of mtDNA and nuclear gene data by independent research groups, have all found strong probabilistic support for an affinity with the Afrotheria (e.g. Stanhope *et al.* 1998, Murphy *et al.* 2001b). Various molecular synapomorphies uniting all afrotheres (including Afrosoricida) have also been identified; the probability that these arose convergently is infinitesimally small (e.g. Van Dijk *et al.* 2001).

Analyses of morphological data, in contrast, have yielded largely equivocal results regarding an affinity between Afrosoricida and the Soricomorpha. MacPhee & Novacek (1993), however, showed that the only morphological characters that support the grouping of the Afrosoricida with the other families formerly included in the Insectivora are shared primitive characters (symplesiomorphies), which are lacking in the other families, rather than synapomorphies that define and combine them. Monophyly of the Insectivora is only weakly supported by cladistic analyses of morphological data (Asher 1999) and phylogenetic analyses of combined molecular and anatomical data (the latter also from some extinct taxa) strongly support the inclusion of afrosoricids within Afrotheria (e.g. Asher *et al.* 2003). The order Afrosoricida, together with the orders Macroscelidea (sengis) and Tubulidentata (aardvark), has been placed in the Cohort Afroinsectiphillia (Waddell *et al.* 2001, Amrine-Madsen *et al.* 2003) – the 'African insect lovers' – within the Superorder Afrotheria. Further information on Afrotheria is given on p. 143.

Despite the overwhelming molecular evidence for the existence of a clade containing golden-moles and tenrecs, there is surprisingly little morphological support for a close relationship between these families beyond their joint possession of zalambdodont cheekteeth – the homology of which is uncertain given that zalambdodonty has arisen independently several times (Broom 1916). The only non-dental characteristics used previously to defend a grouping of chrysochlorids and tenrecids are either symplesiomorphic or equivocal (MacPhee & Novacek 1993). Golden-moles and tenrecs also diverge markedly in the characters of the male reproductive system, and golden-moles possess many unique adaptations for burrowing (Butler 1988). The absence of morphological synapomorphies to support the monophyly of the Afrosoricida probably reflects the independent evolution of sophisticated phenotypic specializations over the millions of years since the time when golden-moles and tenrecs diverged from each other, thus obscuring any morphological similarities that might offer clues to the ancestry encoded in their genes.

Gary N. Bronner

Family TENRECIDAE
TENRECS, OTTER-SHREWS

Tenrecidae Gray, 1821. London Med. Repos. Rec. 15: 301.

<i>Micropotamogale</i> (2 species)	Pygmy Otter-shrews	p. 216
<i>Potamogale</i> (1 species)	Giant Otter-shrew	p. 220

(African genera only)

The family Tenrecidae is endemic to Madagascar and Africa, and characterized by the presence of a caecum, zalambdodont dentition (molars with a V-shape pattern in most species), a cloaca-like anogenital opening, testes positioned close to the kidney or in an intra-abdominal position, and skull without zygomatic arches. Dental formula: $I\ 3/3, C\ 1/1, P\ 3/3, M\ 3/3 = 40$.

The family was formerly allocated to the order Insectivora, suborder Lipotyphla. Based on molecular data, Stanhope *et al.* (1998) evidenced a phylogenetic relationship with Elephants and Hyraxes rather than with other members of the Insectivora, and Emerson *et al.* (1999) confirmed a close relationship with the Chrysochloridae. The Tenrecidae together with the Chrysochloridae (or golden-moles) are now allocated to the order Afrosoricida and separated from other families previously in the Insectivora (i.e. Soricidae, now placed in the order Soricomorpha; Erinaceidae, now in the order Erinaceomorpha).

Of the four subfamilies in the family (see Order profile above), the Potamogalinae is the only subfamily endemic to continental Africa. It contains only the otter-shrews, comprising two genera and three species, all distributed within the Rainforest BZ. They are semi-aquatic mammals looking like small otters with an enlarged flat muzzle, a slender body and a strong tail. They are good swimmers; one species uses the tail and the others use the limbs for propulsion. The characters of the subfamily include: eyes small; ears proportionally narrow; mystacine vibrissae very strong, 3–4 on the cheek, one over the eyes and four (three lateral and one median) on the chin; nose leathery with two opercula for closing the nostrils when diving, without philtrum; pelage shiny, due to the strong overhairs with a

large terminal shield (hair apex enlarged like a lance) as in desmans and otters; tail relatively long (75–85% of HB), base enlarged and very strong; and, in one species, digits of fore- and hindfeet webbed. Syndactyly of Digits 2 and 3 of the hindfoot provides a ‘comb’ for grooming pelage, a character not found in *Limnogale*, the aquatic tenrec of Madagascar. The skull is narrow, without zygomatic arches. One pair of incisors (I^1) in upper jaw and one pair (I_2) in lower jaw are very large for catching prey (and appear caniniform); canine teeth are small. Tooth replacement is rather slow (Kuhn 1964). Skull lacks lacrimal ducts (Butler 1978, Asher 2000). The postcranial skeleton is similar to that of Tenrecs, but without clavicles and with the pubic bones separated.

Otter-shrews were first considered to represent a family (Potamogalidae) within the Order Insectivora. Most authorities now allocate them to the Potamogalinae as a subfamily within the family Tenrecidae (Heim de Balsac & Bourlière 1955, Hutterer 1993, Bronner & Jenkins 2005). Molecular data suggest that otter-shrews belong to the Afrotheria clade (Van Dijk *et al.* 2001), which also contains the Tenrecs (Stanhope *et al.* 1998; see also order profile). In a morphological analysis (Asher 1999), the Potamogalinae clustered with *Limnogale*. In contrast, molecular data (Douady *et al.* 2002) suggest that the Potamogalinae form a sister-group with the tenrecs of Madagascar (Tenrecinae and Oryzorictinae) confirming the conclusion of McDowell (1958), who grouped these two families in the taxon Afrosoricida (=Tenrecoidea).

Two genera of otter-shrews are recognized: *Potamogale*: large size (HB: >170 mm); tail very thick at base and flattened laterally on terminal half; hindfeet not webbed (1 sp.); and *Micropotamogale*: small size (HB: <170 mm); tail not flattened laterally; hindfeet webbed (1 sp.) or not webbed (1 sp.).

Peter Vogel

Subfamily POTAMOGALINAE – Otter-shrews

Potamogalinae Allman, 1865. Proc. Zool. Soc. Lond. 1865: 467.

This subfamily contains two genera and three species, all indigenous to the African continent. Full details of the subfamily are given in the family Tenrecidae profile above.

GENUS *Micropotamogale*
Pygmy Otter-shrews

Micropotamogale Heim de Balsac, 1954. C. R. Acad. Sci. Paris 239: 102. Type species: *Micropotamogale lamottei* Heim de Balsac, 1954.

The genus *Micropotamogale* contains two species of otter-shrews: one lives in West Africa and the other in E DR Congo. Both species have restricted distributions in the Rainforest BZ and montane forests.

The genus is characterized by its adaptations for aquatic life: small elongated body, small size (HB: <170 mm, mean weight ca. 78–100 g) and a tail that is not flattened laterally (cf. *Potamogale*). One species in the genus has webs between the digits of the fore- and

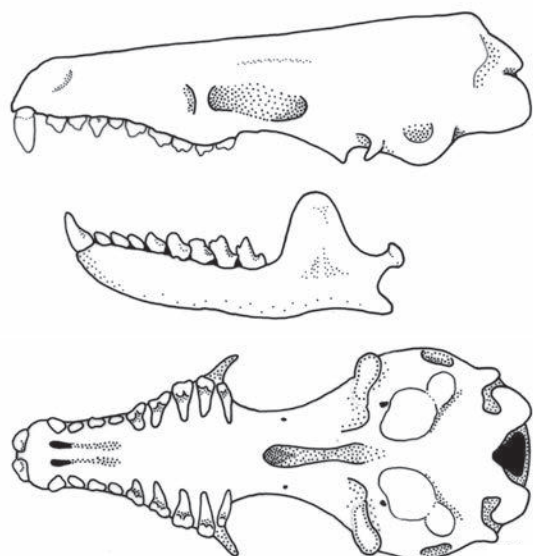


Figure 4. Skull and mandible of *Micropotamogale lamottei* (BMNH 73.170).



Micropotamogale ruwenzorii.

to premolars; premolars simple, molars zalambdodont (V-shaped pattern on occlusal surface) (Figure 4). The zalambdodont pattern of teeth is a plesiomorphic character, confirming relationship with the tenrecs. (See also family profile.) Dental formula: $I^{3/3}, C^{1/1}, P^{3/3}, M^{3/3} = 40$.

The two species are distinguished by size, presence/absence of webbing on the feet, and geographical distribution.

Peter Vogel

Micropotamogale lamottei NIMBA OTTER-SHREW (PYGMY OTTER-SHREW)

Fr. Micropotamogale du Mont Nimba; Ger. Kleine Otterspitzmaus

Micropotamogale lamottei Heim de Balsac, 1954. C. R. Acad. Sci. Paris, 239: 102. Ziela, Mt Nimba, Guinea. 550 m.

Taxonomy Considered by Heim de Balsac (1956) as the most primitive form of the Potamogalinae. Synonyms: none. Chromosome number: $2n = 38$ (Vogel *et al.* 1977).

Description Small blackish-brown otter-like mammal, with slender body. Dorsal pelage dense, glossy, brown to blackish-brown; hairs grey to whitish-grey at base, blackish-brown at tip; underfur woolly, grey with brown tips. Ventral pelage similar to dorsal pelage, but when dry slightly speckled by brighter tips to hairs. Head with enlarged snout and numerous stiff vibrissae. Nostrils on upper surface of the leathery rhinarium, closed when diving. Eyes very small. Ears rather short, only little longer than pelage hairs. Fore- and hindlimbs short; narrow digits not webbed and not bordered by stiff hairs. Syndactyly of Digits 2 and 3 of hindfeet form a comb. Tail relatively long (ca. 77% of HB), slightly thickened at base, covered by short dark hairs; not laterally flattened and without visible skin scales. Skull: see genus profile. Nipples: 2 (pectoral) + 1 (abdominal) + 1 (inguinal) = 8.

Geographic Variation None recorded.

Similar Species

M. ruwenzorii. Similar size; ventral pelage grey, pale brown or whitish; feet broad, feet with webs between digits; E DR Congo only.

Potamogale velox. Much larger; ventral pelage white, feet not webbed; tail thick, laterally flattened; Cameroon to E DR Congo.



Micropotamogale lamottei

Distribution Endemic to Africa. Rainforest BZ (Western Region). Known only from Mt Nimba in Liberia, Guinea (Kuhn 1964) and W Côte d'Ivoire (Vogel 1983), and the mountains of the Putu Range, Liberia (Kuhn 1971). Very restricted; most distant localities only 380 km apart.

Habitat Very small creeks, larger streams and small swamps in primary and secondary rainforest in hilly country (Vogel 1983). Also occurs in regions where primary and secondary forest has been replaced by cocoa and coffee plantations, provided dense vegetation remains along streams. May occur in rice cultures (Kuhn 1964).

Abundance Generally uncommon; density usually low; very rare where hills not present. In the Nimba region, drowned animals collected by fishermen from fish bownets suggest a density of about one otter-shrew per 10 km². In 1970, otter-shrews were frequently found close to villages; by 1990, rarely found within 3–5 km of villages (P. Vogel, pers. obs.).

Adaptations Efficient swimmer and diver, even though tail and feet are not specially adapted for aquatic life (Guth *et al.* 1959) compared with the other two species of otter-shrews. Nimba Otter-shrews can remain underwater for more than 10 minutes (when escaping from danger) by lowering the metabolic rate. The strong sensitive vibrissae are used for locating underwater prey. The narrower feet and thinner tail (when compared with *M. ruwenzorii*) probably allows these otter-shrews to have broader ecological niche compared with other species of otter-shrews.

Foraging and Food Foraging occurs along the river banks and also in open water. The diet is mainly crabs and catfish, with a few insects (Kuhn 1964) and tadpoles (Vogel 1983). Crabs are carried onto land for eating; the crab is then attacked from behind, minimizing the chances of being bitten by the pincers, and the skeleton is crushed at the junction of the cephalothorax and abdomen (Vogel 1983). In captivity, food consumption was about 40 g fish/day.

Social and Reproductive Behaviour Evidence from the rare captures, and from predatory behaviour, suggest that Nimba Otter-

shrews are rather solitary and territorial. However, a pair kept over several months in the same enclosure did not exhibit aggressive behaviour (Vogel 1983).

Reproduction and Population Structure Litter size (births and embryo numbers): 2.6 (1–2), mode 2, n = 11 (Kuhn 1971, Vogel 1983, P. Vogel unpubl.). Gestation: >50 days. At birth, young naked, but whiskers present; dorsal pelage present Day 11; eyes open Day 23, first solid food eaten Day 40 (n = 1; P. Vogel unpubl.).

Predators, Parasites and Diseases Endoparasites: *Molineus eburneus* (Nematoda: Trichostrongyloides) recorded from the intestine (Vaucher *et al.* 1979). Ectoparasites: mites *Orycterovenus liberiensis* and *O. minor* (Fain *et al.* 1974).

Conservation IUCN Category: Endangered.

Suitable habitat is threatened by mining and agricultural development and by increased human activities. Mining activities in Liberia have devastated large regions of suitable habitat (Nicoll & Rathbun 1990), and wetland rice agriculture introduced in 1980 to the Nimba region has resulted in large-scale habitat destruction (P. Vogel unpubl.).

Measurements

Micropotamogale lamottei

HB: 141 (120–155) mm, n = 15

T: 108 (95–134) mm, n = 15

HF: 20 (19–21) mm, n = 15

E: 10 (9–11) mm, n = 13

WT: 78 (32–95) g, n = 6

GLS: 35.9 (32.4–38.1) mm, n = 16

GWS: n. d.

I¹–M³: 15.4 (14.2–16.2) mm, n = 16

Côte d'Ivoire (P. Vogel unpubl.)

Only adults with complete dentition

Key References Guth *et al.* 1959, 1960; Kuhn 1964; Vogel 1983.

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Micropotamogale ruwenzorii RWENZORI OTTER-SHREW

Fr. Micropotamogale du Rwenzori; Ger. Mittel Otterspitzmaus

Micropotamogale ruwenzorii (de Witte and Frechkop, 1955). Bull. Inst. Roy. Sci. Nat. Belg. 31 (84): 9.

W slopes of Mt Rwenzori, DR Congo. 1100–1200 m.

Taxonomy Originally described in the genus *Potamogale*, later assigned to a new genus *Mesopotamogale* now considered as a subgenus (Guth *et al.* 1960, Verheyen 1961d, Corbet 1974b). Presence of webbed feet (cf. *Potamogale velox*, *M. lamottei*) suggests that this species could represent a separate genus (P. Vogel, pers. obs.). Subspecies: none. Chromosome number: not known.

Description Small brown otter-like mammal, with a more compact body than the other species of otter-shrews. Dorsal pelage dark brown, woolly underfur grey with brown tips. Ventral

pelage grey, pale brown or whitish. Head with a large flat muzzle and numerous stiff vibrissae. Rhinarium leathery. Eyes very small. Ears small but clearly visible, not concealed by pelage. Limbs short; fore- and hindfeet broad and bordered with stiff hairs, webs between digits. Syndactyly of Digits 2 and 3 of hindfeet form a comb. Tail (ca. 84% of HB) bicoloured, with many small scales and well covered with short hairs, dark brown (as dorsal pelage) above, pale brown or cinnamon below; in section, oval at its basal part, then circular towards tip; covered with sparse hairs, scales of the skin present. Tail is stronger than in *M. lamottei*. Skull: see genus

profile. Nipples: uncertain; probably the same as *M. lamottei* (i.e. $2 + 1 + 1 = 8$).

Geographic Variation None recorded.

Similar Species

Micropotamogale lamottei. Similar size; ventral pelage dark; feet not webbed; tail not laterally flattened; Liberia, Guinea and Côte d'Ivoire.

Potamogale velox. Larger (HB: 224–410 mm); ventral pelage white, feet not webbed; tail thick, laterally flattened.

Distribution Endemic to Africa, Rainforest BZ (East Central Region). Recorded only in Kivu and Rwenzori regions of E DR Congo and W Uganda (Rahm 1966).

Habitat Streams of varying size in Rainforest BZ from 800 to 900 m ($n = 4$) and in montane forest up to 2200 m ($n = 4$) (Rahm 1960). Also recorded from streams in gallery forest surrounded by secondary savanna (elephant grass) from 1000 to 1200 m.

Abundance Little quantitative information; locally not rare.

Adaptations The webbed feet suggest a strong adaptation for aquatic life. Both fore- and hindfeet have webs between the digits. The forefeet are relatively large; Digit 1 and Digit 5 are elongated (Verheyen 1961a). Similar morphological adaptations are found in only a few other insectivorous small mammals such as *Limnogale mergulus* (Tenrecidae), *Nectogale elegans* (Soricidae) and *Galemys pyrenaica* (Talpidae) – all of which are separated from related species without webbed feet at the generic level. Swimming is by paddling with the fore- and hindlimbs (as in a dog). The feet may be used synchronously when diving (Rahm 1961) in a similar way to the Pyrenean Desman *Galemys pyrenaica* (Niethammer 1970). The tail does not appear to be used for propulsion. There are several periods of activity each night; grooming occurs after each activity period (Rahm 1961). The anatomy of the species has been studied by Verheyen (1961a, b, c, d).

Foraging and Food Carnivorous and insectivorous. Foraging occurs in water. The preferred prey are crabs with a carapace width < 5 cm, aquatic insects, oligochaete worms and fish (*Clarias*, etc.). An otter-shrew weighing 135 g eats ca. 80 g of food per night. Manipulation of food is performed only with the mouth, not with the forefeet. Faecal pellets (ca. 2–5 cm long, diameter 0.9 cm) contain fragments of chitin from the crab and insect prey (Rahm 1961).

Social and Reproductive Behaviour No information.

Reproduction and Population Structure Embryo number: 1 ($n = 2$) or 2 ($n = 1$) (Rahm 1960, H. Stephan pers. comm.). Young



Micropotamogale ruwenzorii

(HB: ca. 80 mm) recorded in Apr in Kivu region, DR Congo ($n = 2$, labels, RMCA).

Predators, Parasites and Diseases Parasitized by ticks (*Ixodes dawesi*), but only where syntopic with *Potamogale velox* (Arthur 1965, U. Rahm pers. comm.).

Conservation IUCN Category: Near Threatened.

May be threatened by destruction of suitable habitats. Previously assessed as Endangered.

Measurements

Micropotamogale ruwenzorii

HB: 163 (130–200) mm, $n = 26$

T: 136 (123–150) mm, $n = 25$

HF: 28 (26–29) mm, $n = 10$

E: 11 (10–14) mm, $n = 12$

WT: 98 (75–135) g, $n = 10$

GLS: 36.8 (33.8–39.4) mm, $n = 4$

GWS: 16.8 (15.5–17.8) mm, $n = 4$

I^1 – M^3 : 17.7, 18.5 mm, $n = 2$ (adults only)

Central Africa (Rahm 1960, 1961, 1966, U. Rahm unpubl., H. Stephan in litt.)

Key References Rahm 1960, 1961; Verheyen 1961a.

Peter Vogel

GENUS *Potamogale*

Giant Otter-shrew

Potamogale du Chaillu, 1860. Proc. Boston Soc. Nat. Hist. 7: 363. Type species: *Cynogale velox* du Chaillu, 1860.

Potamogale is a monotypic genus, widely distributed in the Rainforest BZ of central Africa. The genus is characterized by its adaptations for aquatic life, large size (mean HB: ca. 320 mm, mean weight ca. 650 g),

tail thickened at the base and laterally flattened on the distal half, and without webs between the digits of the fore- and hindfeet. Skull: elongated and narrow, without zygoma; upper incisors canine-like; canines small, similar to premolars; premolars simple, dilambdodont (W-shaped pattern on occlusal surface) (Figure 5). The dilambdodont pattern of the molar teeth is a character interpreted as derived (see also family profile). Dental formula: $I \frac{3}{3}, C \frac{1}{1}, P \frac{3}{3}, M \frac{3}{3} = 40$.

Peter Vogel

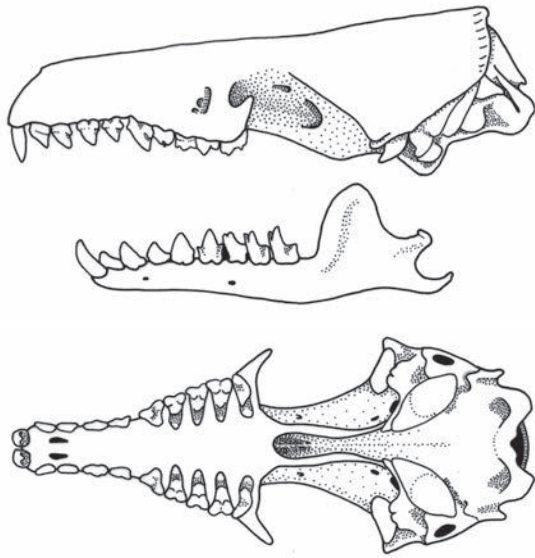


Figure 5. Skull and mandible of *Potamogale velox* (BMNH 26.11.1.64).



Potamogale velox.

Potamogale velox GIANT OTTER-SHREW

Fr. Potamogale; Ger. Große Otterspitzmaus

Potamogale velox du Chaillu, 1860. Proc. Boston Soc. Nat. Hist., 7: 363. Ogowe River, Gabon.

Taxonomy Synonyms: *allmeni*, *argens*. Subspecies: none. Chromosome number: not known.

Description Slim and elongated like an otter, with a flattened head and large muzzle with stiff white vibrissae. Pelage soft, dense and shiny, with thick underfur. Head and dorsal pelage chocolate- or tobacco-brown; hairs white at base, rich chocolate-brown at tip. Dense white underfur; white colour of hairs and underfur does not show through to surface of pelage. Flanks similar, with some white-tipped hairs. Ventral pelage pure white, underfur cream. Colour of dorsal and ventral pelage clearly delineated on lower flanks. Eyes small. Large leathery rhinarium. Ears small but proportionally longer than in otters. Mouth set back from tip of head. Fore- and hindfeet relatively short; five digits on each limb, without webs between digits. Syndactyly of Digits 2 and 3 of hindfeet form a comb. Postaxial border of hindfoot with a wide cutaneous fold. Tail relatively long (ca. 80% of HB), same colour as dorsal pelage; basal part of tail as thick as hind part of body, distal half laterally compressed with sharp dorsal keel. Dense long pelage of body extends on first quarter of the tail, remaining part densely covered with very short adpressed hairs. Skull: see genus profile. Nipples: 2 (pectoral) + 1 (abdominal) + 1 (inguinal) = 8 (Dubost 1965).



Potamogale velox

Geographic Variation None recorded.

Similar Species

Micropotamogale ruwenzorii. Much smaller; hindfeet with webs between digits; tail not flattened laterally; sympatric in E DR Congo and W Uganda.

Micropotamogale lamottei. Much smaller; hindfeet without webs between digits; tail circular in section; Liberia, Guinea and Côte d'Ivoire.

Distribution Endemic to Africa. Widespread in Rainforest BZ (except for Western Region and West Central Region [Western Nigeria sub-region]). Recorded from Nigeria (east of Cross R.) eastwards to W Uganda and W Kenya, and southwards to C Angola and N Zambia (Corbet 1974a). Sea level to 1800 m. Isolated record from rainforest at Kakamega, Kenya (00° 17' N, 34° 47' E).

Habitat Streams in equatorial rainforests. Lives along rather small slow-flowing forest streams, forest pools and mountain torrents where banks provide habitats for nest chambers (Nicoll & Rathbun 1990). Also along streams bordered by gallery forest. Normally does not occur in large rivers, although one was found in the Ivindo R., Gabon, where the river was several hundred metres wide.

Abundance Mean density in good habitats may be one territorial animal/0.5–1.0 km length of stream; maximum densities of about one individual/100 m of river (Dubost 1965).

Adaptations Very efficient swimmer. Swimming is effected by horizontal undulations of the thick muscular tail, as in fish and crocodiles. These undulations are produced by contractions of the gluteus muscle of the rump, which extends backwards into the tail (an exceptional feature for a tail). Forelimbs are not used for propulsion. This method of swimming is unique amongst aquatic mammals (cf. seals and whales swim by undulations in a vertical plane). Moving on land is rather clumsy. Body pelage is groomed with the comb-like structure formed by fusion of Digits 2 and 3 of the hindfeet. Nocturnal with several bouts of activity each night (Dubost 1965, Nicoll 1985); rests during daytime in burrow in river bank. When disturbed, escapes into the water. Movements over long distances always by water, never by land.

Foraging and Food Forages in water, feeding only on aquatic prey. Hunts by diving, each dive lasting for only several seconds. Prey located using the sensitive vibrissae and odour; eyes apparently not used to locate prey. Analysis of stomach contents and faeces show that diet is mainly fish, crabs, shrimps and water insects; frogs are



Potamogale velox.

rarely eaten (Dubost 1965). In captivity eats 15–20 crabs per night (Durrell 1953).

Social and Reproductive Behaviour Latrines probably used to mark boundaries of territory (Dubost 1965). The den, with the nest chamber, is entered from below or above water level and is usually placed under a tree.

Reproduction and Population Structure Reproduction during wet and dry seasons. Litter size: 1 ($n = 3$) or 2 ($n = 2$). Probably two litters/year (Dubost 1965).

Predators, Parasites and Diseases Seven species of Nematoda are known from the digestive system: *Molineus grassei* (Chabaud *et al.* 1966), *Galeiceps cucullus* (Chabaud *et al.* 1967), *Molineus amberti*, *M. brosetti*, *Parastrongyloides callipygus*, *Procamallanus potamogalei* and *Spinitectus menzalei* (Hugot 1979). *Ixodes dawesi*, a tick specific to the Potamogalinae, has been found in several geographic regions (Arthur 1965).

Conservation IUCN Category: Least Concern.

In Cameroon (and probably elsewhere) forest clearance and soil erosion cause murkiness and opaqueness of the water in forest streams, and has resulted in local extinction of some populations (Nicoll 1985). Previously assessed as Endangered.

Measurements

Potamogale velox

HB: 320 (305–337) mm, $n = 10$

T: 269 (235–290) mm, $n = 10$

HF: 43 (39–46) mm, $n = 10$

E: 21 (15–23) mm, $n = 10$

WT: 656 (517–780) g, $n = 7$

GLS: 63.7 (60.5–66.3) mm, $n = 10$

GWS: 26.2 (25.1–27.5) mm, $n = 10$

I^1 – M^3 : 30.6 (29.2–32.5) mm, $n = 10$

Measurements: DR Congo (Mede, Nipa and Kananga; AMNH)

Weight: Several sources

Key References Dubost 1965; Durrell 1953; Nicoll 1985.

Peter Vogel

Family CHRYSOCHLORIDAE

GOLDEN-MOLES

Chrysochloridae Gray, 1825. Ann. Philos., n.s. 10: 335.

<i>Amblysomus</i> (5 species)	Golden-moles	p. 226
<i>Calcochloris</i> (3 species)	Golden-moles	p. 233
<i>Carpitalpa</i> (1 species)	Arends's Golden-mole	p. 237
<i>Chlorotalpa</i> (2 species)	Golden-moles	p. 239
<i>Chrysochloris</i> (3 species)	Golden-moles	p. 242
<i>Chrysospalax</i> (2 species)	Golden-moles	p. 246
<i>Cryptochloris</i> (2 species)	Golden-moles	p. 250
<i>Eremitalpa</i> (1 species)	Grant's Golden-mole	p. 252
<i>Neamblysomus</i> (2 species)	Golden-moles	p. 255

Golden-moles are endemic to sub-Saharan Africa, where nine genera and 21 known species (Table 12) inhabit a wide spectrum of altitudinal, climatic and vegetational habitats from deserts to savanna grasslands and montane forests. Most species occur only in southern Africa and many have restricted geographic ranges; only three species occur elsewhere. All species are subterranean, but some forage in litter on the surface.

The family name Chrysochloridae refers not to the pelage colour, which varies from black to pale tawny-yellow, but to the iridescent sheen of coppery green, blue, purple or bronze of their pelage. Morphologically, golden-moles display a high degree of structural conformity comprising both primitive as well as highly specialized mammalian characters (Hickman 1990). Unique characters of chrysochlorids include a hyoid-dentary articulation, extremely enlarged malleus bones in the middle ear of some species that permit great sensitivity to underground vibrations (Mason & Narins 2001), a third bone in the forearm (possibly an ossified tendon), a reduction in the number of phalanges in the fore- and hindfeet, and muscle arrangements not paralleled in the Mammalia (MacPhee & Novacek 1993).

All species have compact fusiform or lozenge-shaped bodies, short and powerful forelimbs and no external tail, although internal caudal vertebrae are present. The dense pelage consists of backward-set guard hairs that are moisture-repellent, and woolly underfur for insulation. The skin is thick and tough, particularly on the head. Eyes are vestigial and covered by skin, and the optic nerve is degenerate. External ear pinnae are absent and ear openings are covered by dense hairs. The muzzle is obtuse and terminates in a leathery nosepad that protects the nostrils, and is used, together with the webbed hindfeet, to shovel soil. In some species, the nostrils also have foliaceous projections that prevent sand from entering the nasal passages during burrowing. The wedge-shaped head is used to push and pack soil loosened by the robust pick-like digging claws of the forelimbs, which are powered by extremely muscular forequarters. There are four digits on the forefoot and five on the hindfoot. The claw on Digit 3 of the forefoot is usually the largest, while those on Digits 1 and 2 are shorter and have more slender claws. Digit 4 is vestigial in all but one species, and bears a minute nail- or knob-like claw. The digits of the hindfeet are linked by small membranes, and each has only a small claw. Nipples: $2 + 2 = 4$ in all species.

The skull is conical with a broad braincase, complete zygomatic arches and an elongated snout without any marked interorbital

constriction. Cheekteeth are high-crowned and zalambdodont with three main cusps arranged in a triangle. Dental formula is $I^{3/3}, C^{1/1}, P^{3/3}, M^{2-3/2-3} = 36-40$. The first premolars (P1) are either bicuspid and sectorial like the preceding teeth, tricuspid like the other molars, or pseudo-molariform (tricuspid but lacking a posterior crushing basin), but this varies considerably with toothwear. The lower molars of some taxa bear a talonid (low ledge), which occludes with the protocone cusp of the upper molars to provide a small grinding surface, and the cheekteeth interdigitate closely providing a shearing action to slice through prey. The third upper molars (M^3), when present, are either tricuspid (similar to other molars) or minute and peg-like, this to a large extent depending on toothwear (and thus age). The incidence of the M^3 or M_3 molars varies considerably in some taxa (Bronner 1995b). This reflects the almost random sequence of tooth replacement in chrysochlorids, rendering dental formula inadequate for diagnostic purposes. The length of the upper tooth row is measured from canine to upper second molar ($C-M^2$), or canine to upper third molar ($C-M^3$) for those species that retain M^3 . In chrysochlorids, the suture between premaxilla and maxilla bone fuses early in life, and hence the canine tooth (which is similar in size to the incisor teeth) may be difficult to discern; it is the fourth tooth from the front of the skull (the first three are incisor teeth).

Several genera of chrysochlorids have an enlarged malleus located in a bony bulla that is often visible externally on the surface of the skull. In *Chrysochloris* and *Cryptochloris* the malleus is elongated and club-shaped, and the caput (head) is housed in a bulla evident as a pronounced temporal bulla (*Chrysochloris*), or smaller subtemporal bulla (*Cryptochloris*). *Eremitalpa* and *Chrysospalax* have an enlarged spherical ('pea-shaped') malleus housed in an anteriolateral expansion of the skull visible as a swelling in the region of the zygomatic arch, rather than a distinct bulla. In *Chlorotalpa* and *Carpitalpa*, the malleus is somewhat inflated and bulbous ('pear-shaped'), but is accommodated entirely within the skull so no external bulla is evident – a condition found also in *Amblysomus* and *Neamblysomus*, which have a small and unspecialized ('normal') malleus similar to those of most other mammals. These specializations of the middle ear are related to their extraordinary sensitivity to vibrations, which are used to detect prey and avoid predators. The enlarged malleus bones in *Eremitalpa* and *Chrysospalax*, which are the heaviest (in relation to body size) among all mammals, may be an adaptation for surface foraging since increased malleus mass enhances sensitivity to higher frequencies of sound than are normally experienced underground (Mayer *et al.* 1995).

Physiologically, chrysochlorids are unusual in mammals in displaying daily and seasonal torpor (Kuyper 1985) or almost complete poikilothermy. They have a high thermal conductance and do not thermoregulate when at rest, thereby considerably reducing energy requirements. Body temperature in the thermal neutral zone is lower than expected for similar-sized mammals, and they are moderate (*Chrysochloris asiatica*, *Amblysomus hottentotus*) to extreme (*Eremitalpa granti*) thermoconformers (Seymour *et al.*

Table 12. Characteristics of the species in the family Chrysochloridae. (n. d. = no data)

Species (subfamily) ^a	Length of claw on Digit 3 of forefoot (range) (mm) ^c	Basal width claw of Digit 3 of forefoot (range) (mm) ^c	HB mean (range) (mm) ^c	GLS mean (range) (mm) ^c	Colour of dorsal pelage	M ³ present (P) or absent (A)	Notes
<i>Amblysomus corriae</i> (A)	13–15	4.5–5.6	119 (108–130) 115 (109–130)	27.4 (25.4–28.9) 26.7 (25.3–28.6)	Smoky-black to reddish-brown	A	South Africa (Western and Eastern Cape Provinces)
<i>Amblysomus hottentotus</i> (A)	13–16	4.3–6.6	123 (114–135) 118 (104–135)	26.5 (25.0–27.7) 25.9 (24.6–27.7)	Chestnut-red to brownish-black	A (usually)	South Africa (coastal and parts of highveld), Swaziland
<i>Amblysomus marleyi</i> (A)	10.5–13	3.7–4.4	102 (96–105) 101 (90–120)	23.9 (23.1–24.6) 23.5 (22.4–24.7)	Dark reddish-brown	A (usually)	South Africa (KwaZulu–Natal)
<i>Amblysomus robustus</i> (A)	14–17	5.3–7.2	131 (118–143) 128 (109–138)	30.8 (29.9–32.0) 28.8 (27.2–29.7)	Dark reddish-brown	A (usually)	South Africa (Mpumalanga Province)
<i>Amblysomus septentrionalis</i> (A)	14–15.7	5.3–6.6	127 (114–135) 125 (105–145)	29.0 (27.2–30.5) 17.9 (16.8–19.5)	Dark reddish-brown	A	South Africa (Mpumalanga Province, ?NE Free State)
<i>Calcochloris leucorhinus</i> (A)	9–11.5	2.3–4	63, 126 (n=2)	21.7 (19.5–22.8) 22.2 (21.0–23.1)	Dark brown to slaty-grey	P (usually)	Angola, DR Congo, Cameroon, Central African Republic
<i>Calcochloris obtusirostris</i> (A)	7–9	<3.5	100 (88–110) 93 (82–110)	22.6 (20.8–24.2) 21.5 (19.0–23.6)	Yellowish-orange to dull reddish-brown	A	South Africa (KwaZulu–Natal), S Mozambique, SE Zimbabwe
<i>Calcochloris tytonis</i> (A)	n. d.	n. d.	n. d.	n. d.	n. d.	P	S Somalia
<i>Carpitalpa arendsi</i> (C)	9–12	3.5–4	124 (115–141) 121 (115–139)	27.7 (26.8–29.0) 27.3 (25.3–28.6)	Blackish-brown	P	E Zimbabwe (Inyanga Highlands)
<i>Chlorotalpa duthieae</i> (C)	7–9	3.5–4	106 (95–125) 102 (96–130)	23.8 (22.9–24.5) 22.8 (22.0–23.9)	Reddish-brown	P	South Africa (Eastern and Western Cape Provinces)
<i>Chlorotalpa sclateri</i> (C)	8–9	3–4.5	101 (83–135) 102 (82–123)	23.6 (21.8–27.4) 23.4 (21.2–26.7)	Glossy reddish-brown	P	South Africa (widespread)
<i>Chrysochloris asiatica</i> (C)	10–12	3.5–4.6	105 (100–115) 100 (94–114)	22.9 (22.1–23.6) 22.5 (21.1–25.4)	Blackish to slate-grey	P (usually)	South Africa (western areas)
<i>Chrysochloris stuhlmanni</i> (C)	11	3–4.2	113 (106–123) 107 (103–111)	26.9 (24.8–28.1) 25.9 (24.3–28.3)	Blackish-brown	P	Uganda, Kenya, Tanzania, Cameroon (mostly montane)
<i>Chrysochloris visagiei</i> (C)	n. d. ^b	4.1	106 (n=1)	22.8 (n=1)	Tawny-olive	P	South Africa (Northern Cape Province – type locality only)
<i>Chrysospalax trevelyani</i> (C)	17–19	7	222 (215–235) 216 (208–229)	41.7 (41.0–42.4) 41.6 (39.9–43.2)	Glossy brown	P	South Africa (Eastern Cape Province)
<i>Chrysospalax villosus</i> (C)	15–17	4–6	163 (148–175) 143 (127–160)	33.9, 34.9 (n=2) 33.8 (33.4–34.6)	Yellowish-brown (variable)	P	South Africa (highland areas)
<i>Cryptochloris wintoni</i> (C)	10.3–10.5	4	86, 92 (n=2)	21.3, 22.0 (n=2)	Pale slate-grey	P	South Africa (Northern Cape Province)
<i>Cryptochloris zyli</i> (C)	10	4	82 (n=1)	21.7, 22.2 (n=2)	Lead-grey	P	South Africa (type locality only)
<i>Eremitalpa granti</i> (C)	9–12	3.7–4.9	82 (76–86)	19.5 (18.6–20.4) 16.6 (15.5–18.2)	Tawny-olive to greyish-olive	P (very small)	South Africa (Western Cape Province), S Namibia
<i>Neamblysomus gunningi</i> (A)	12.5–14	4.3–4.9	125 (121–132) 122 (111–132)	28.4 (27.1–29.3) 27.5 (27.0–27.8)	Reddish-brown	P (usually)	South Africa (Drakensberg Mts)
<i>Neamblysomus julianae</i> (A)	8.5–10	3.6–4.3	101 (94–111) 99 (92–111)	23.2 (22.4–23.6) 22.5 (21.8–23.5)	Cinnamon-brown to reddish-brown	A (usually)	South Africa (scattered)

^a A = subfamily Amblysominae (malleus bone of middle ear typically mammalian in shape and not expanded). C = subfamily Chrysochlorinae (malleus bone of middle ear enlarged to form a spherical or club-like shape).

^b Probably similar to *C. asiatica*.

^c Single line of numerals: sex not recorded. Two lines of numerals: upper line, males; lower line, females.

1998). The low metabolic rate of *C. asiatica* is achieved by lowering the body temperature, whereas in *E. granti* it is also the result of intrinsic metabolic depression. Lowered metabolism and efficient renal function effectively reduce water requirements to the extent that all species are independent of drinking water (Fielden *et al.* 1990a). Far from being ‘primitive’ characters, such physiological specializations allow chrysochlorids to survive in permanently or seasonally inclement habitats where temperatures are extreme and food is often scarce.

Limited reproductive data available suggest that most species breed throughout the year, perhaps with a peak in the wetter months when prey is more abundant, and may be polyoestrous (Bernard *et al.* 1994). Although these are r-selected characters, other facets of their breeding biology (small litter-sizes [mean = 2] and extended postnatal development) are more typical of a specialized, K-selected reproductive strategy.

Like most subterranean mammals, chrysochlorids are ecological specialists with low vagility. The limited data suggest that all species are opportunistic foragers feeding primarily on earthworms, termites, insect pupae and/or millipedes, although a variety of other prey items, including small vertebrates, are sometimes eaten. Most are solitary and subterranean, constructing semi-permanent burrow systems comprising two tiers: subsurface tunnels (visible from above as raised ridges of soil) for foraging, and deeper tunnels connecting chambers used for resting and raising young, the entrances to which are sometimes marked by small mounds on the ground surface (Roberts 1951, Kuyper 1985). An exception to this is the ‘Shark of the Dunes’ – the small Namib Golden-mole *Eremitalpa granti namibensis* which ‘swims’ through the desert sands, often emerging onto the surface to reduce the energetic costs of subterranean travel (Narins *et al.* 1998). The Giant Golden-mole *Chrysospalax trevelyani* is also primarily a surface forager, but in indigenous forests, and is the only species that shows any indication of sociality.

Unlike other mammals, golden-moles have a southern African centre of diversity with only three species occurring outside this region: *Calcochloris leucorhinus* and *Chrysochloris stuhlmanni* in the Rainforest BZ of central Africa; and *Calcochloris tytonis*, in the Somalia–Masai Bushland BZ. The 18 species in southern Africa fall into two broad ecological groups: an arid-adapted group of five species which occur in semi-desert (*Eremitalpa* [1 sp.], *Cryptochloris* [2 spp.]), karoo (*Chrysochloris visagiei*) or moister fynbos habitats (*Chrysochloris asiatica*) along the south-west coast; and a mesic-adapted group of 13 species inhabiting forests, savanna woodland and temperate grassland habitats in the eastern part of the sub-region (*Chrysospalax* [2 spp.], *Chlorotalpa* [2 spp.], *Calcochloris* [1 sp.], *Carpitalpa* [1 sp.], *Neamblysomus* [2 spp.] and *Amblysomus* [5 spp.]). Only two species (*Amblysomus hottentotus* and *Chrysochloris asiatica*) are widespread and show marked geographic variation in size and colour. Populations are often restricted to patches of suitable habitat with friable soils and abundant invertebrate prey, so that the distribution of demes is clumped, even within widespread species. Different species seldom coexist and compete for resources, even though their distributions

may appear broadly sympatric. Where two species occur in the same area, they tend to occupy different micro-habitats, probably as a result of ecological displacement. Many of the genera and species in the family are of conservation concern: 11 species (out of 21) and eight genera (out of nine) are placed in various ‘Threatened’ categories of IUCN because of their rarity, small geographic range and the destruction of their habitats.

Many anatomical specializations shown by extant taxa are evident also in fossils from the early Miocene, and are so numerous and unusual that golden-moles have been described as ‘spectacularly autapomorphic’ and worthy of ordinal (Chrysochloridea *sensu* Broom 1916) or subordinal (Chrysochloromorpha *sensu* MacPhee & Novacek 1993) status. These proposals have received little attention, however, and until recently chrysochlorids were generally regarded to be only specialized members of the order Insectivora, with possible affinities to the tenrecs of Madagascar based on their joint possession of zambododont cheekteeth. However, contemporary studies of mitochondrial and nuclear gene sequences have conclusively demonstrated that chrysochlorids and tenrecs form a clade worthy of ordinal status (Liu *et al.* 2001, Madsen *et al.* 2001, Murphy *et al.* 2001a). Stanhope *et al.* (1998) named this clade the Afrosoricida (African shrew-like mammals), a somewhat inappropriate name since it contains no soricids and could engender confusion with *Afrosorex* (a subgenus of *Crociodura* [see Hutterer 2005]). Divergence between golden-moles and tenrecs probably occurred about 50 mya, with the result that they share few morphological synapomorphies, warranting their allocation to distinct suborders (for which the names Tenrecomorpha and Chrysochloridea should be used).

Many previous taxonomic revisions of chrysochlorids were largely intuitive, or based on only elementary statistical evaluation of few specimens, leading to conflicting classifications that obscured rather than resolved inter-specific relationships. Based on phylogenetic analyses of morphometric and cytogenetic variation in three genera, Bronner (1995b) proposed a new classification including a newly described species (Bronner 2000, see also Bronner & Jenkins 2005). Following Simonetta (1968), two subfamilies may be recognized, albeit with differing species allocations: Chrysochlorinae, in which the malleus bone of the middle ear is enlarged with a spherical or club-like shape (*Carpitalpa* [1 sp.], *Chlorotalpa* [2 spp.], *Chrysospalax* [2 spp.], *Chrysochloris* [3 spp.], *Cryptochloris* [2 spp.] and *Eremitalpa* [1 spp.]) and Amblysominae in which the malleus is not expanded and has the typical mammalian shape (*Amblysomus* [5 spp.], *Neamblysomus* [2 spp.] and *Calcochloris* [3 spp.]). Here the genera, and species within each genus, are listed alphabetically (see also Table 12).

In the Descriptions, an indication of the size of each species is recorded comparatively to other species in the family. The size categories, based on mean head and body length (HB), are: Very small: <92 mm; Small: 100–115 mm; Medium-sized: 116–125 mm; Large: ca. 150 mm; Very large: >500 mm.

Gary N. Bronner

GENUS *Amblysomus*

Golden-moles

Amblysomus Pomel, 1848. Arch. Sci. Phys. Nat. Geneve 9: 247. Type species: *Chrysochloris hottentotus* A. Smith, 1829.

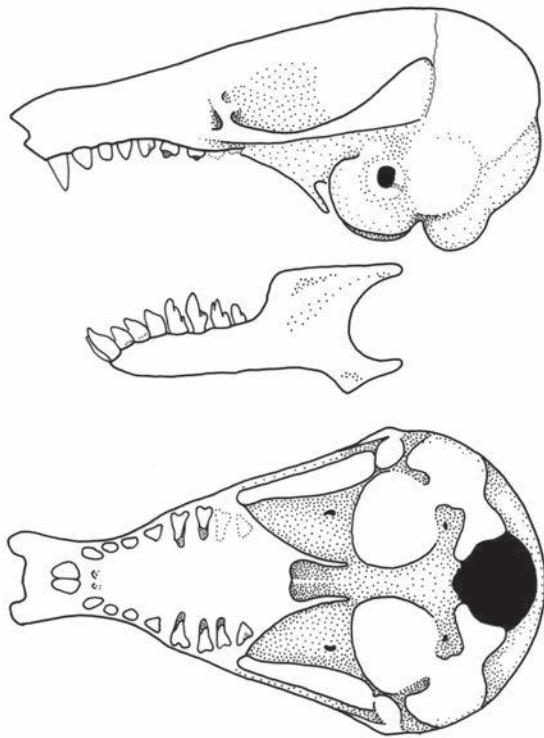


Figure 6. Skull and mandible of *Amblysomus corriae* (BMNH 5.6.5.6).

Gary N. Bronner

Amblysomus corriae FYNBOS GOLDEN-MOLE

Fr. Taupe dorée de fynbos; Ger. Fynbos-Goldmull

Amblysomus corriae Thomas, 1905. Abstracts, Proceedings of the Zoological Society of London 20: 5; Proceedings of the Zoological Society of London 2: 57. Knysna, Western Cape, South Africa.

Taxonomy Traditionally grouped with populations from Zululand in *A. iris*. However, Bronner (1996) showed that the Zululand populations represent only a subspecies (*iris*) of the widespread Hottentot Golden-mole, *A. hottentotus*. The Western Cape populations represent the distinct species *A. corriae*, which includes two subspecies: *A. c. corriae* and *A. c. devilliersi*, which was formerly recognized as a subspecies of *A. hottentotus*. Although distinguishing between these forms using live specimens is difficult, they can be diagnosed with 95% accuracy using a craniometric technique (Bronner 1996). Since *A. corriae* is now considered as a distinct species, the colloquial name 'Zulu Golden-mole' is no longer suitable. Roberts (1951) referred to *A. corriae* as the 'Knysna golden mole', but Broom (1907a) used this name for *Chlorotalpa duthieae*. *Amblysomus corriae* also occurs far from Knysna, and hence this name is not appropriate, and should be replaced with one that more accurately reflects the biogeographic affinity of the species with the fynbos (South-West Cape BZ). Synonyms: *devilliersi*, *swellendamensis*. Subspecies: two. Chromosome number: $2n = 30$, $FN = 56$ (Bronner 1995a).

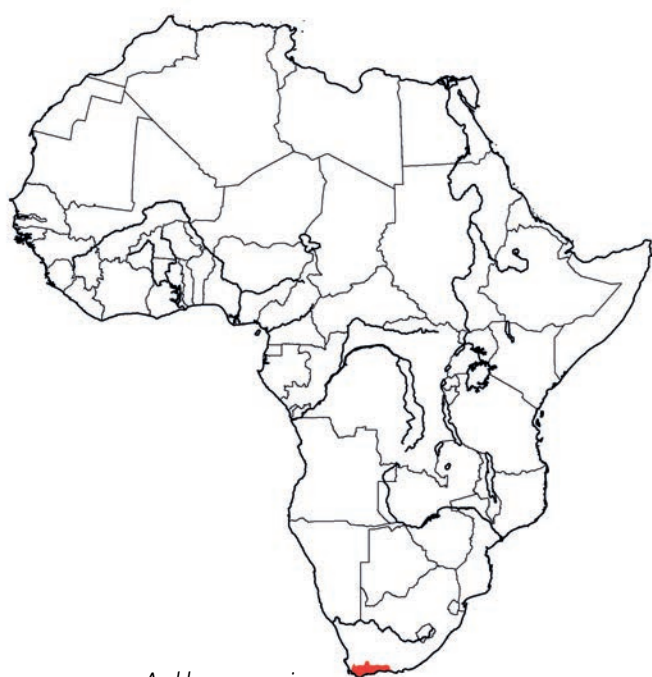
The most diverse genus of the Chrysochloridae, with five mesic-adapted species endemic to the south-eastern parts of South Africa. Species in the genus occur in habitats ranging from fynbos and coastal afro-montane forests of the South-West Cape BZ to grasslands, woodlands and montane scrub in southern African savanna. One species, *A. hottentotus*, is widespread in southern Africa, and the others have restricted geographic distributions. Some previous authors synonymized *Chlorotalpa*, *Neamblysomus* and/or *Calcochloris* under this genus (Roberts 1951; Simonetta 1968; Petter 1981), but phylogenetic analyses of morphometric and cytogenetic data confirm that these are distinct genera (Bronner 1995a, b).

Body fusiform; size ranges considerably from small to medium-sized. Skull elongated (breadth <70% of GLS), zygomatic arches without broad plates sweeping backwards, the malleus of the inner ear relatively small and unspecialized, and the palate relatively narrower (<29% of GLS) compared with that in *Neamblysomus*. M^3 usually absent, molar talonids are well-developed and the first premolars are sectorial (bicuspid) rather than molariform (tricuspid) (Figure 6). The five species are distinguished by body size, colour of pelage, form and size of claw on Digit 3 of forefoot and chromosomal properties (Bronner 1995a). Multivariate analyses of skull measurements may be necessary to discriminate between *A. hottentotus*, *A. septentrionalis* and *A. robustus*.

Description Medium-sized species, similar to *A. hottentotus* in general appearance but with darker colouration. Dorsal pelage smoky-black to reddish-brown. Ventral pelage brownish-grey to pale orange. Hairs 8–9 mm long, dark slaty-grey at base with brownish-grey subterminal bands and iridescent blackish-brown or reddish-brown tips. Muzzle and cheeks somewhat paler than back, sometimes with small buffy eye-spots. Foreclaws marginally more slender than in *A. hottentotus*; claw on Digit 3 largest (13–15 mm long, 4.5–5.6 mm wide at base). Skull: malleus not enlarged; bulla not externally evident; M^3 absent (see also family and genus profiles). Males on average slightly larger and heavier than ♀♀, but sexes do not differ markedly in cranial proportions.

Geographic Variation

A. c. corriae: Coastal plain below the Outeniqua, Kouga and Baviaanskloof mountain ranges, from George in Western Cape Province northwards along coast to Humansdorp in Eastern Cape Province. Dorsal pelage uniformly smoky-black; ventral pelage



Amblysomus corriae

pale brownish-grey without conspicuous reddish-brown tinge seen on flanks and abdomen of *A. hottentotus*.

A. c. devilliersi: Stellenbosch and Paarl in Western Cape Province, eastwards to slopes of Langeberg mountains near Riversdale, and northwards to Hawequas Forest near Worcester, but not into the arid Karoo. Dorsal pelage reddish-black, redder on flanks; ventral pelage reddish-brown to pale orange as in *A. hottentotus*. Considerable variability exists in extent of reddish-brown on dorsal pelage. Some individuals have subtle rufous tinge on flanks, whereas others have reddish-brown colouration extending almost to mid-dorsal region so that blackish colouration is restricted to narrow band along the back. This variability may be related to the stage of moulting.

Similar Species

Chlorotalpa duthieae. Skull smaller (GLS: 22.9–24.5 mm); claw on digit 3: 7–9 mm; M³ present.

Chrysochloris asiatica. Often smaller (HB: 94–115 mm); skull smaller (GLS: 21.1–25.4 mm); pelage less rufous; M³ present; malleus enlarged and club-shaped; bulla pronounced and projecting through temporal surface of skull.

Distribution Endemic to Africa. South-West Cape BZ. Recorded from Boland region of Western Cape Province along the coast to Humansdorp in Eastern Cape Province, where it is replaced by *A. h. hottentotus*.

Habitat Sandy soils and soft loams in Mountain Fynbos, Grassy Fynbos and Renosterveld of South-West Cape BZ. Also in afromontane forest and southern African savanna along the southern Cape coast. Coexists with *Chrysochloris asiatica* in Stellenbosch, but favours richer

and wetter soils (Broom 1907a). Exists in broad sympatry with *Chlorotalpa duthieae* along the southern Cape coast, but trapping data suggest they select different micro-habitats, *A. corriae* preferring forest fringes and associated fynbos, and *C. duthieae* preferring deeper forest. Thrives in gardens, cultivated lands and livestock paddocks. Present also in exotic plantations, but at lower densities.

Abundance Locally common, but no quantitative data.

Adaptations See profile Family Chrysochloridae.

Foraging and Food Insectivorous. Stomach contents of three individuals comprised only small earthworms. Forages in subsurface tunnels, mainly at night. Sometimes emerges to capture prey on the soil surface, but drags it below ground before eating, often making soft 'chirruping' vocalizations.

Social and Reproductive Behaviour Solitary, except for ♀♀ raising young.

Reproduction and Population Structure Pregnant ♀♀, each with two embryos (1L, 1R) have been captured in Aug, May and Dec, suggesting aseasonal polyoestry. Young altricial and hairless at birth. Gestation period unknown.

Predators, Parasites and Diseases Regularly caught by Barn Owls *Tyto alba* and by domestic cats and dogs. No information on parasites and diseases.

Conservation IUCN Category: Near Threatened.

Conserved in many protected areas in South Africa.

Measurements

Amblysomus corriae

HB (♂♂): 119.7 (108–130) mm, n = 19

HB (♀♀): 115.4 (109–130) mm, n = 24

T: 0 mm

HF (♂♂): 14.7 (12–16) mm, n = 19

HF (♀♀): 13.9 (12–15) mm, n = 24

E: 0 mm

WT (♂♂): 56 (46–62) g, n = 10

WT (♀♀): 47 (46–64) g, n = 13

GLS (♂♂): 27.4 (25.4–28.9) mm, n = 20

GLS (♀♀): 26.7 (25.3–28.6) mm, n = 25

GWS (♂♂): 15.9 (15.1–16.9) mm, n = 20

GWS (♀♀): 15.5 (14.7–16.9) mm, n = 25

C–M² (♂♂): 6.3 (5.6–6.8) mm, n = 17

C–M² (♀♀): 6.2 (5.6–7.0) mm, n = 24

A. c. corriae, Knysna/Humansdorp, South Africa (Bronner 1995b)

Key References Bronner 1996; Broom 1907a; Roberts 1951.

Gary N. Bronner

Amblysomus hottentotus HOTTENTOT GOLDEN-MOLE

Fr. Taupe dorée de Hottentote; Ger. Hottentotten-Goldmull

Amblysomus hottentotus (A. Smith, 1829). Zoological Journal 4: 436. 'Interior parts of South Africa'
(taken as Grahamstown, Eastern Cape Province, South Africa, following Roberts 1951).

Taxonomy Originally described in the genus *Chrysochloris*. Traditionally taken to include populations that Bronner (1996, 2000) recognized as valid species, namely *A. septentrionalis*, *A. robustus*, *A. marleyi* and *A. corriae* (in part). Synonyms: *affini*, *albifrons*, *albirostris* (*nomen dubium* of Wagner, 1841 and of Broom, 1908), *holosericea*, *iris*, *littoralis*, *longiceps*, *meesteri*, *natalensis*, *pondoliae*, *rutilans*. Subspecies: five. Chromosome number: $2n = 30$, $FN = 56$ (Bronner 1995a).

Description Medium-sized species with considerable geographic variation in size, and marked variability in pelage colour both within and between populations. Dorsal pelage chestnut-red, brownish-black or reddish-black, becoming more rufous on flanks. Ventral pelage bright brown, reddish-brown or dull orange, sometimes with a dark brown mid-ventral line from throat to belly. Extent of reddish tinge is highly variable within populations. Muzzle paler than dorsal pelage with buffy-white to yellowish-orange patches on cheeks, extending laterally to above the subdermal eyes, and often coalescing behind the nosepad. Dorsal surface of hindfeet blackish to light buffy-rufous. Albinistic specimens with dorsal and ventral pelage cinnamon-brown to pale yellow (rarely recorded). Claws of forefeet moderately developed, claw on Digit 3 largest (13–16 mm long and 4.3–6.6 mm at base), claw on Digit 2 much shorter (6–8 mm), claw on Digit 1 about half as long as that on Digit 2. Digit 4 vestigial with a knob-like claw. Skull: malleus not enlarged; bulla not externally evident; zygomatic arches without broad plates sweeping backwards. M^3 are present in less than 2% of individuals and their occurrence often varies between jaw quadrants. If present, they are small and their morphology ranges from triconid (molariform) to peg-like depending on toothwear. Molar talonids well developed, except in specimens from southern Mpumalanga Province. Dental variability is random and localized rather than geographic by nature, and may reflect the irregular sequence of tooth replacement in chrysochlorids (Roberts 1951, Bronner 1996, 2000). Sexual size dimorphism pronounced, ♂ larger on average than ♀ in external and cranial measurements. Skull: see family and/or genus profiles.

Geographic Variation Size varies clinally in relation to altitude and ambient temperature in the inland part of the geographic range. Five subspecies recognized, but discrimination difficult owing to intergradations in size (Bronner 1996).

- A. h. hottentotus*: Eastern Cape Province from Van Stadens R. in the south to Great Fish River Valley in north; inland to Elandsberge, Winterhoekberge, Suurberge and Winterberge mountains. Intermediate in size between *A. h. longiceps* and *A. h. iris*; interpterygoid region narrower (<28% of greatest palate width) than in *A. h. pondoliae* (>29%).
- A. h. pondoliae*: Great Fish River Valley in Eastern Cape Province northwards along KwaZulu–Natal coast to Umdloti R. near Durban; inland to Drakensberg foothills near Elliot and Maclear,

where it is replaced by *A. h. longiceps*. Second largest subspecies.

- A. h. iris*: Zululand, from Umdloti R. in the south (where it intergrades with *A. h. pondoliae* in the vicinity of Verulam) north-eastwards to L. St Lucia and Cape Vidal (where it is replaced by *Calcochloris obtusirostris*). Pelage darker, reddish-black to dark brown, with a rufous tinge present variably on flanks and ventral pelage. Smallest subspecies with a length of 107–125 mm. Claws gracile, basal width of foreclaw of Digit 3 <5.5 mm, as opposed to >6 mm in *A. h. longiceps*. Mandibular ramus narrower (<60% of palate width) than in *A. h. pondoliae* (60–64%).
- A. h. longiceps*: Interior of KwaZulu–Natal Province, from Underberg in the south to Van Reenen in the north, and marginally into the Free State to Harrismith and Clarens. Recorded from W Swaziland, but these specimens may be *A. septentrionalis*. Largest subspecies (total length 120–141 mm), similar in size to *A. septentrionalis* and *A. robustus*, from which it can be distinguished craniometrically (Bronner 2000). Claws robust, foreclaw of Digit 3 >6 mm at base, in contrast to <5.5 mm in *A. h. pondoliae*. Mandibular ramus wider (>65% of palate width) than in *A. h. pondoliae*.
- A. h. meesteri*: Graskop and Mariepskop districts of northern Drakensberg escarpment, southwards to White R. Similar in size to *A. h. pondoliae*, but distinctive in that pelage is reddish-brown with a mid-dorsal band of reddish-black. Molar talonids absent or only weakly developed.

Similar Species

- A. septentrionalis* and *A. robustus*. Slightly larger; not separable from *A. hottentotus* using any single skull measurement but can be distinguished using a multivariate craniometric technique (Bronner 1996).
- A. marleyi*. Claw on Digit 3 of forefoot usually shorter (10.5–13 mm) and narrower (3.7–4.4 mm at base). Skull almost always shorter (23.1–24.7 mm).
- Chlorotalpa sclateri*. On average smaller (HB: 102 [82–135] mm); claw on Digit 3 of forefoot 8–9 mm long; M^3 present.
- Chrysospalax trevelyani*. Much larger (HB: 208–235 mm, GLS: 39.9–43.2 mm); pelage coarser; malleus enlarged; zygomatic arches with broad plates sweeping backwards.
- Chrysospalax villosus*. Usually larger (HB: 127–175 mm); skull larger (GLS: 33.4–34.9 mm), pelage coarser, malleus enlarged; zygomatic arches with broad plates sweeping backwards.
- Neamblysomus julianae*. Usually smaller (HB: 92–111 mm); skull smaller (GLS: 21.8–23.60 mm); pelage less red; subtle chromosomal differences (Bronner 1995a).

Distribution Endemic to Africa. Coastal Forest Mosaic BZ and parts of Highveld BZ. Recorded from Swaziland and South Africa (Eastern Cape and KwaZulu–Natal Provinces, and S Mpumalanga Province below the Drakensberg escarpment, with a marginal intrusion into NE Free State). Marginal intrusion into the South-West Cape BZ (Fynbos and Karoo biomes) in the southern parts of range.



Amblysomus hottentotus

Habitat Wide variety of woodland and grassland habitats, and also in afro-montane forests and marshes.

Abundance Locally common in suitable habitats, as well as in gardens, golf courses and cultivated lands. Densities of up to 25 individuals/ha recorded in optimal habitat. Particularly abundant in moist soils near rivers and dams, but also found far from water provided the substrate is friable and not too rocky.

Adaptations Individuals construct two-tier burrow systems: subsurface tunnels used for foraging, and deeper (10–50 cm) tunnels connecting grass- or leaf-lined nests in spherical (15–20 cm diameter) chambers, with two or three spiralling boltholes (29–94 cm deep). Mounds are sometimes thrown up at the junction of the subsurface and deeper tunnel systems. Deeper tunnels are excavated at a rate of up to 9 m daily, and are also used for foraging in dry winter months when invertebrate prey is scarce near the soil surface. Subsurface tunnels are 9.5–240 m long, and may be extended by 4–12 m/day depending on prey abundance and substrate friability, and are used predominantly for foraging during the wet summer months. Burrow systems tend to be more extensive in less fertile habitats.

Activity is for periods of up to two hours by day and night, interspersed with periods of inactivity lasting 3–5 hours. Peak activity is at dawn, sunset and around midnight. Soil temperatures in burrow systems range from 0.8 to 32 °C. Optimal thermal conditions for activity are 23–33 °C, which corresponds with the thermoneutral zone. Individuals enter torpor if ambient temperature drops below 15 °C, or exceeds 30 °C, resulting in a markedly reduced metabolic rate and significant energetic saving. They coexist with Common Mole-rats *Cryptomys hottentotus*, which they tolerate in their burrows, presumably since they do not compete for food; joint occupancy reduces the energetic costs of burrow maintenance. Other species occupying active burrow systems include the Red Toad *Bufo carens*, Wolf-spider *Harpactira* sp., crickets, isopods, scarabid beetles and annelids (Kuyper 1979, 1985, Hickman 1990).

Foraging and Food Carnivorous and insectivorous. The diet is soil-dwelling invertebrates, particularly earthworms. In KwaZulu–Natal, 97% of stomachs contained only earthworms and minute (<0.5%) finely ground vegetable matter, while the contents of the remaining 3% included up to 5% insect remains, especially scarabid beetle larvae (McConnell 1986). Diet sometimes includes slugs, snails, crickets, insect pupae and spiders (Kuyper 1985). Individuals consume up to 90% of their body weight daily (McConnell 1986), but this estimate, based on captive animals, seems extreme and is temperature dependent. In captivity, they have been observed to eat garlic and geophytes, but this was probably coincidental since their digestive tracts are not specialized for herbivory.

Social and Reproductive Behaviour Adults are solitary and fight aggressively with individuals of either sex by wrestling their opponent using the foreclaws, and biting at the abdomen. Fighting is often accompanied by high-pitched squeaks. Individuals actively defend their burrow systems. Some amount of home-range overlap is tolerated, and dominant moles sometimes take over neighbouring burrow systems to increase their home-range. Courtship involves chirruping vocalizations, head-bobbing and foot stamping by ♂, and rasping and squealing vocalizations by ♀ (Kuyper 1985).

Reproduction and Population Structure Reproduction and recruitment of young occur throughout the year, but at low levels, with a peak in the wet summer months. Females show aseasonal polyoestrus and a postpartum oestrus, and spermatogenesis in ♂ is continuous, reflecting the relatively constant microclimate of their subterranean niche (Bernard *et al.* 1994). Litter-size: 1–3 (mode 2). At birth, young hairless, HB 47 mm, weight ca. 4.5 g. Short, dark-brownish dorsal pelage is evident when 17 g and HB 72 mm, but ventral surface remains naked and teeth unerupted. Pale ventral pelage first appears when HB 80 mm and weight ca. 27 g. Eviction from the maternal burrow occurs when 35–40 g (Kuyper 1979, 1985).

Populations show low levels of genetic diversity, as reported also for other subterranean mammals; this may reflect selection pressures for homozygosity in the largely homogeneous underground environment (Filipucci *et al.* 1991).

Predators, Parasites and Diseases Predators include snakes, owls, white storks, otters, genets, mongooses and jackals. Often also killed by domestic cats and dogs, but seldom consumed. No information on parasites or diseases.

Conservation IUCN Category: Least Concern.

Measurements

Amblysomus hottentotus

HB (♂ ♂): 123.6 (114–135) mm, n = 20

HB (♀ ♀): 118.6 (104–135) mm, n = 21

T: 0 mm

HF (♂ ♂): 14.4 (13–19) mm, n = 21

HF (♀ ♀): 14.3 (12–18) mm, n = 20

E: 0 mm

WT (♂ ♂): 56.6 (37–85) g, n = 15

WT (♀ ♀): 50.1 (37–60) g, n = 19

GLS (♂ ♂): 26.5 (25.0–27.7) mm, n = 22
 GLS (♀ ♀): 25.9 (24.6–27.7) mm, n = 24
 GWS (♂ ♂): 16.0 (15.1–17.4) mm, n = 24
 GWS (♀ ♀): 17.1 (16.1–19.0) mm, n = 25
 C-M² (♂ ♂): 6.7 (6.2–7.2) mm, n = 19
 C-M² (♀ ♀): 6.5 (6.0–7.1) mm, n = 24

South Africa (G. Bronner unpubl.)

Key References Bronner 1996; Hickman 1990; Kuyper 1985.

Gary N. Bronner

Amblysomus marleyi MARLEY'S GOLDEN-MOLE

Fr. Taupe dorée de Marley; Ger. Marleys Goldmull

Amblysomus marleyi Roberts, 1931. Ann. Transvaal Mus. 14: 225. Ubombo, KwaZulu–Natal, South Africa.

Taxonomy Traditionally recognized as a subspecies of *A. hottentotus*; now elevated to species rank based on its smaller size, more gracile build and different pelage colour (Bronner 1996). While generally smaller than *A. hottentotus* from further south along the coast, discriminating between these species using external measurements is difficult because of an overlap in size. Multivariate analyses of morphometric data provides unequivocal diagnosis (Bronner 1996). Synonyms: none. Chromosome number: 2n = 30, FN = 56 (Bronner 1995a).

Description Small golden-mole with a delicate build and fine claws on the forefeet. Dorsal pelage very dark reddish-brown. Ventral pelage dullish-orange to greyish-brown. Muzzle and cheeks paler than dorsal pelage often with broad white band behind nosepad that extends to region above the eyes. Throat paler and redder than flanks (Roberts 1931). Guard hairs dark grey distally and yellowish at base, except for uniformly off-white hairs on muzzle. Claw on Digit 3 of forefoot largest (10.5–13 mm long, 3.7–4.4 mm wide at base). Skull: malleus not enlarged; bulla not externally evident; zygomatic arches without broad plates sweeping backwards, M³ usually absent (see also family and genus profiles). Males on average slightly larger than ♀ ♀; sexual size dimorphism does not appear to be pronounced, but this may be an artefact of small sample sizes.

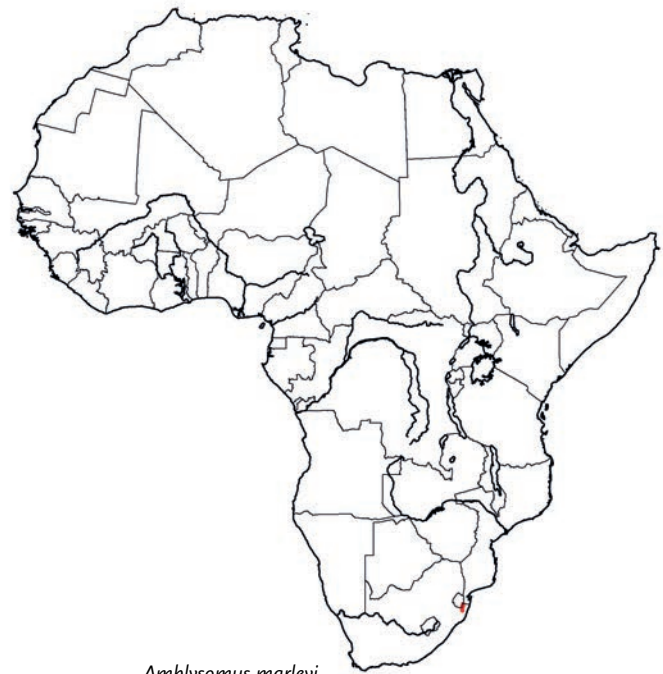
Geographic Variation None recorded.

Similar Species None within the geographic distribution of the species.

Distribution Endemic to Africa. Coastal Forest Mosaic BZ. Known only from two isolated localities (Ubombo and Ingwavuma) on eastern slopes of Lebombo Mts in KwaZulu–Natal Province. Owl pellet remains from near Weenen, ca. 250 km SW of type locality, appear to represent this species, suggesting that it may be more widespread than currently recognized.

Habitat Moist grasslands and indigenous forests in Natal Lowveld, Bushveld and Lebombo Arid-Mountain Bushveld of southern African savanna. Does not occur below the mountains on the Mozambique plain, where it is replaced by the Yellow Golden-mole *Calcochloris obtusirostris*. Also occurs in gardens.

Abundance Common in localized patches of suitable habitat with soft soils; cryptic and rarely encountered. No quantitative data on abundance.



Amblysomus marleyi

Adaptations Like other members of this genus, constructs two types of burrows: subsurface tunnels used for foraging and deeper tunnels leading to nesting chambers under rocks and roots of trees. The entrances to deep tunnels are sometimes marked by small mounds of soil.

Remarks Insectivorous, but no quantitative analysis of diet. Solitary.

Predators, Parasites and Diseases No information.

Conservation IUCN Category: Endangered.

Given the restricted range of the species, the fragmented nature of populations and adverse impacts of humans on its habitat, this species is appropriately classified as Endangered.

Measurements

Amblysomus marleyi

HB (♂ ♂): 102.0 (96–105) mm, n = 4

HB (♀ ♀): 100.6 (90–120) mm, n = 9

T: 0 mm

HF (♂ ♂): 12.3 (11–13) mm, n = 4

HF (♀ ♀): 11.4 (10–13) mm, n = 9

E: 0 mm
 WT (♂): n. d.
 WT (♀): n. d.
 GLS (♂♂): 23.9 (23.1–24.6) mm, n = 4
 GLS (♀♀): 23.5 (22.4–24.7) mm, n = 8
 GWS (♂♂): 15.3 (14.8–16.0) mm, n = 4
 GWS (♀♀): 14.6 (13.9–16.0) mm, n = 8

C–M² (♂♂): 5.8 (5.6–6.2) mm, n = 5
 C–M² (♀♀): 5.6 (5.3–6.1) mm, n = 7
 Ubombo/Ingwavuma, KwaZulu–Natal, South Africa.

Key References Bronner 1996; Roberts 1951.

Gary N. Bronner

Amblysomus robustus ROBUST GOLDEN-MOLE

Fr. Taupe dorée robuste; Ger. Robuster Goldmull

Amblysomus robustus Bronner, 2000. Mammalia 64: 42. Verloren-Vallei Nature Reserve, Dullstroom, Mpumalanga Province, South Africa.

Taxonomy A monotypic species, with a unique chromosome number amongst chrysochlorids (Bronner 1995a). Easily confused with *A. septentrionalis* (2n = 34; FN = 62) and *A. hottentotus longiceps* (2n = 30; FN = 56), which it resembles in overall size and pelage colour (Bronner 1996), but can be diagnosed craniometrically using a technique outlined in Bronner (2000). Synonyms: none. Chromosome number: 2n = 36, FN = 68.

Description Medium-sized golden-mole, and largest species in genus. Dorsal pelage dark reddish-brown with bright reddish-brown flanks. Ventral pelage orange. Yellowish-orange cheek patches extend laterally to above sub-dermal eyes. Claws on forefeet strongly developed, claw on Digit 3 largest (14–17 mm long and 5.3–7.2 mm wide at base). Juveniles resemble adults but dorsal pelage is greyish-brown, becoming dullish-orange on the flanks. Sexual size dimorphism pronounced, ♂♂ on average larger than ♀♀ in most measurements. Skull: see family and/or genus profiles.

Geographic Variation None recorded.

Similar Species

A. septentrionalis and *A. hottentotus*. On average slightly smaller; not separable from *A. robustus* using any single skull measurement but can be distinguished using a multivariate craniometric technique (Bronner 1996).

Chrysospalax villosus. On average larger (HB: 151 [127–175] mm); skull larger (GLS: 33.4–34.9 mm); pelage finer; malleus enlarged; zygomatic arches with broad plates sweeping backwards.

Neamblysomus julianae. Usually smaller (HB: 92–111 mm); skull smaller (GLS: 21.8–23.60 mm); pelage less red; subtle chromosomal differences (Bronner 1995b).

Distribution Endemic to Africa. Highveld BZ. Recorded only from the Steenkampsberge mountains in the Belfast and Dullstroom districts of E Mpumalanga Province, South Africa.

Habitat Montane grasslands and marshes in Moist Sandy Highveld Grassland (Brendenkamp & van Rooven 1996). Prefers friable soils, from sands to quite heavy clays. Avoids shallow substrates along rocky ridges (which may act as dispersal barriers) and waterlogged areas.

Abundance Common in suitable natural habitats, also in gardens, orchards and cultivated lands.

Adaptations These golden-moles are robust, with strong claws that enable them to subsist in the heavier soils common on the highveld. In this respect they differ from most other species of *Amblysomus*, which are restricted to sands and soft loams at lower altitudes. They are active mainly in late afternoon and night, and are torpid during the heat of day. Burrow systems are two-tiered comprising subsurface tunnels for foraging and deeper tunnels (20–80 cm) with nest chambers. Burrows sometimes extend upwards into rotting trees, which may provide an abundant source of invertebrate prey and refuge in areas where burrows become waterlogged during heavy rains. Subsurface activity declines during the dry winter season when prey is scarce, and individuals may enter prolonged torpor spanning several days or confine their foraging to deeper tunnels.

Foraging and Food Insectivorous, with a preference for earthworms (n = 2). Golden-moles forage for soil-dwelling invertebrates in subsurface tunnels, mainly at night. In captivity, they consume a wide variety of living invertebrate and vertebrate prey, such as mealworms, kingworms, earthworms and baby mice, but ignore dead prey.



Amblysomus robustus

Social and Reproductive Behaviour No information, except that adults are usually solitary. Individuals confined together fight vigorously, regardless of sex, but this may also be due to stress while in captivity.

Reproduction and Population Structure Pregnancies and lactation recorded in late summer to early autumn (Mar and Apr) suggest that breeding occurs primarily during the wet summer season.

Predators, Parasites and Diseases No information.

Conservation IUCN Category: Vulnerable.

Should be classified as Data Deficient. While the geographic range of the species is limited, and the vegetation type in which it occurs is heavily transformed, insufficient information exists on the status of populations to justify allocation to a threatened category. A persistent population decline seems unlikely since it is common in habitats modified by humans.

Measurements

Amblysomus robustus

HB (♂ ♂): 131.7 (118–143) mm, n = 6

HB (♀ ♀): 127.7 (109–138) mm, n = 7

T: 0 mm

HF (♂ ♂): 18.5 (18–19) mm, n = 6

HF (♀ ♀): 15.9 (13–18) mm, n = 7

E: 0 mm

WT (♂ ♂): 72, 98 g, n = 2

WT (♀ ♀): 61, 73 g, n = 2

GLS (♂ ♂): 30.8 (29.9–32.0) mm, n = 7

GLS (♀ ♀): 28.8 (27.2–29.7) mm, n = 14

GWS (♂ ♂): 19.2 (18.6–20.4) mm, n = 7

GWS (♀ ♀): 17.6 (16.6–18.2) mm, n = 14

C–M² (♂ ♂): 7.4 (7.1–7.6) mm, n = 6

C–M² (♀ ♀): 6.9 (6.0–7.3) mm, n = 14

Verloren–Vallei/Dullstroom, Mpumalanga Province, South Africa (Bronner 2000)

Key References Bronner 1996, 2000.

Gary N. Bronner

Amblysomus septentrionalis HIGHVELD GOLDEN-MOLE

Fr. Taupe dorée de montagne; Ger. Highveld-Goldmull

Amblysomus septentrionalis Roberts, 1913. Ann. Transvaal Mus. 4: 73. Wakkerstroom, Mpumalanga Province, South Africa.

Taxonomy Traditionally classified as a subspecies of the Zulu Golden-mole *A. iris*. Now considered as a valid species with a unique chromosome number amongst chrysochlorids; closely related to *A. hottentotus* and *A. robustus*, from which it can be discriminated craniometrically (Bronner 1996, 2000). Synonyms: none. Chromosome number: 2n = 34, FN = 62 (Bronner 1995a).

Description Medium-sized golden-mole similar in size and pelage colour to *A. robustus* from further north in Mpumalanga Province, and *A. h. longiceps* from further south in the interior highlands of KwaZulu–Natal. Dorsal pelage dark reddish-brown, light reddish-brown on flanks. Ventral pelage pale brown to orange. Guard hairs yellowish at base, dark grey subterminally. Pale yellow cheek patches extend laterally to above subdermal eyes. Claws on forefeet well developed, but slightly smaller than in *A. robustus*, claw on Digit 3 largest (14.0–15.7 mm long, 5.3–6.6 mm at base). Skull: malleus not enlarged; bulla not externally evident; zygomatic arches without broad plates sweeping backwards; M³ absent (see also family and genus profiles). Sexual dimorphism pronounced, ♂ ♂ on average larger than ♀ ♀.

Geographic Variation Size varies clinally in relation to altitude and ambient temperature (Bronner 1996). Although consistent craniometric differences exist between populations, sample sizes are too small for a thorough analysis of geographic variation and no subspecies are recognized.

Similar Species

A. hottentotus and *A. robustus*. Not separable from *A. septentrionalis* using

any single skull measurement but can be distinguished using a multivariate craniometric technique (Bronner 1996).

Chlorotalpa sclateri. On average smaller (HB: 102 [82–135] mm); claws less robust, claw on Digit 3 of forefoot 8–9 mm; M³ present.

Chrysospalax villosus. HB on average larger (HB: 151 [127–175] mm); skull larger (GLS: 33.4–34.9 mm); pelage less fine; malleus enlarged; bulla visible externally; zygomatic arches with broad plates sweeping backwards; M³ present.

Neamblysomus julianae. Usually smaller (HB: 92–111 mm); skull smaller (GLS: 21.8–23.60 mm); pelage less red; subtle chromosomal differences (Bronner 1995a).

Distribution Endemic to Africa. Highveld BZ. Recorded from Mpumalanga Province from Wakkerstroom northwards to Ermelo and Barberton. Populations from NE Free State (Heilbron/Parys) and Swaziland (Piggs Peak/Mbabane) may represent this species.

Habitat Grasslands and edges of marshes in high-altitude southern African savanna. Known only from Moist Sandy Highveld Grassland and Wet Cold Highveld Grassland. Restricted to friable soils in valleys and on mountainsides, where individuals may co-exist with the Rough-haired Golden-mole *Chrysospalax villosus*. Found in thickets of Oldwood trees *Leucosidea sericea* on the banks of streams in valleys, but avoids scrubby vegetation in kloofs and along rocky ridges, where it is replaced by *Chlorotalpa sclateri*.

Abundance Locally common in suitable habitats; also in gardens and cultivated lands.



Amblysomus septentrionalis

Adaptations The sturdily built body and well-developed claws allow these golden-moles to exist in heavier soils than most other species. Individuals construct two-tier burrow systems: subsurface tunnels used for foraging and deeper (15–30 cm) tunnels connecting grass-lined nests. Activity peaks at night, and declines rapidly after dawn when individuals enter daily torpor until late afternoon. Subsurface activity is reduced during dry winter months.

Foraging and Food Soil-dwelling invertebrates, particularly earthworms and pupae.

Social and Reproductive Behaviour No information, except that adults are solitary.

Reproduction and Population Structure Limited data

suggest that pregnancies may occur throughout the year, but mostly in the wet summer months (Nov–Mar). Litter-size: 1–2. At birth, young are altricial and raised in grass-lined nests (Roberts 1951, Bernard *et al.* 1994).

Predators, Parasites and Diseases Striped Weasels *Poecilogale albinucha* sometimes prey on these golden-moles. Domestic dogs and cats also kill them regularly, but appear to find them unpalatable. Also recorded from pellets of the Barn Owl *Tyto alba*, indicating that individuals may venture out onto the ground surface, particularly after heavy rains. No information on parasites or diseases.

Conservation IUCN Category: Near Threatened.

While the geographic range of this species is restricted, a persistent population decline seems unlikely since it thrives in habitats modified by humans.

Measurements

Amblysomus septentrionalis

HB (♂ ♂): 128.6 (114–135) mm, n = 12

HB (♀ ♀): 125.3 (105–145) mm, n = 25

T: 0 mm

HF (♂ ♂): 15.3 (13–20) mm, n = 11

HF (♀ ♀): 14.7 (12–17) mm, n = 21

E: 0 mm

WT: 52–86 g, n = 3

GLS (♂ ♂): 29.0 (27.2–30.5) mm, n = 16

GLS (♀ ♀): 28.2 (26.2–30.0) mm, n = 25

GWS (♂ ♂): 17.9 (16.8–19.5) mm, n = 16

GWS (♀ ♀): 17.1 (16.1–19.0) mm, n = 25

C–M² (♂ ♂): 7.0 (6.2–7.4) mm, n = 11

C–M² (♀ ♀): 6.9 (6.5–7.2) mm, n = 19

Ermelo/Wakkerstroom, Mpumalanga Province, South Africa (Bronner, 1996)

Key References Bronner 1996; Roberts 1951.

Gary N. Bronner

GENUS *Calcochloris*

Golden-moles

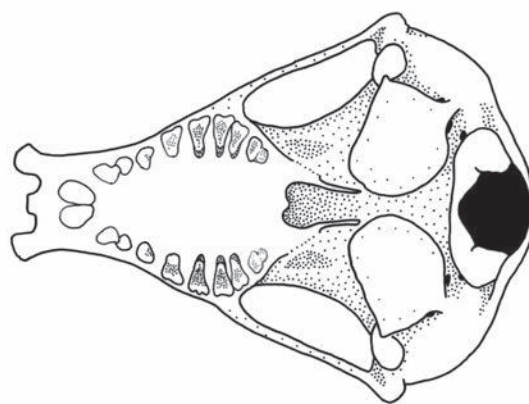
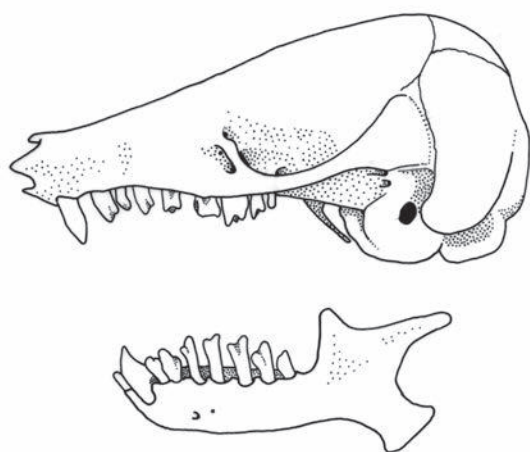
Calcochloris Mivart, 1867. J. Anat. Physiology, London 2: 133. Type species: *Chrysochloris obtusirostris* Peters, 1851.

This genus includes three small species from widely separated parts of Africa. One species (*C. leucorhinus*) lives in primary rainforest and montane forests of central Africa, and another (*C. obtusirostris*) in the sandy soils of eastern South Africa and Mozambique. The third species (*C. tytonis*) is known only from owl pellets in Somalia. See also Family Chrysochloridae.

The diagnostic characters of the genus are a mixture of those in other genera. Body shape fusiform. Claws on forefeet slender and short; claw of Digit 3 largest (7–9 mm long and 2.5–3 mm wide at base), those on Digits 1 and 2 much shorter. Digit 4 vestigial with a short (2 mm) claw. The skull is short and broad (breadth >70% of GLS) with a broad palate (30–35% of GLS). Zygomatic

arches without broad plates sweeping backwards. First premolars are tricuspid and lower molars lack talonids (as in *Chrysochloris*). The malleus is small and unspecialized (as in *Amblysomus*), so no external bulla is visible. M³ are either absent (*C. obtusirostris*) as in *Amblysomus*, or present (*C. leucorhinus* and *C. tytonis*) as in *Chrysochloris* and *Chlorotalpa* (Figure 7).

Considering the mixture of characters within the genus, it is not surprising that previous authors differed greatly in their treatment of the three species, which have been assigned to either *Chrysochloris* (Broom 1907a), *Amblysomus* (Simonetta 1968, Petter 1981) or *Calcochloris* (Meester 1974). In phylogenetic analyses based on multivariate morphometrics, *C. obtusirostris* and *C. leucorhinus*

Figure 7. Skull and mandible of *Calcochloris obtusirostris* (BMNH 6.11.5.26).

consistently grouped together in a separate clade, supporting their allocation to a distinct genus. The allocation of *C. tytonis* to this taxon was based only on qualitative characters (hyoid and malleus morphology) since no mensural data were available, and its taxonomic status remains uncertain (Bronner 1995b). The name

Calcochloris antedates *Chrysotricha*, a name commonly used for this genus until 1953 (Meester 1974). The three species are distinguished by colour and geographic location.

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Calcochloris leucorhinus CONGO GOLDEN-MOLE

Fr. Taupe dorée du Congo; Ger. Kongo-Goldmull

Calcochloris leucorhinus (Huet, 1855). Nouv. Arch. Mus. Hist. Nat., Paris 8: 8. 'Gulf of Guinea Coast, Congo'.

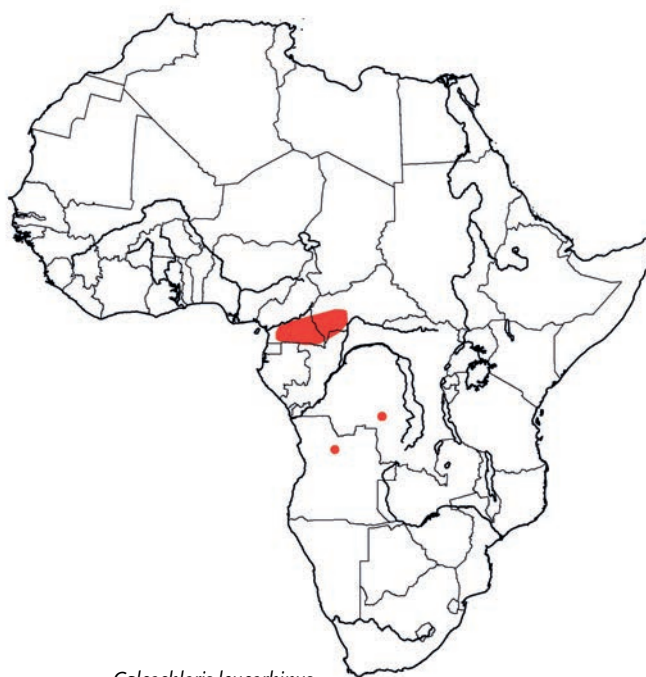
Taxonomy Historically placed in three different genera: included with *Calcochloris obtusirostris* in *Amblysomus* by Simonetta (1968) and Petter (1981), primarily on the basis of malleus morphology ('normal' cf. inflated); in *Chryschloris* on the grounds of dental characters (Allen 1939); and in *Chlorotalpa* (Meester 1974) owing to the absence of a temporal bulla and the presence of M^3 . Craniometric analyses indicate, however, that *C. leucorhinus* should provisionally be included in *Calcochloris* (Bronner 1995b). Synonyms: *cahni*, *congicus*, *luluanus*. Subspecies: two. Chromosome number: not known.

Description Small species, similar in size to *C. obtusirostris*. Dorsal pelage darkish-brown to slaty-grey. Ventral pelage similar to dorsal pelage, but paler. Muzzle with creamy-whitish mask extending laterally to almost the ear. Hairs fine, ca. 7 mm on back. Claws on forefeet very slender, claw on Digit 3 largest and narrow (9–11.5 mm long, 2.5–3 mm wide at base). Skull: malleus not inflated, so that there is no distinct subtemporal bulla; zygomatic arches without broad plates sweeping backwards; M^3 usually present, resembling other cheekteeth; first premolar completely molariform but narrower than in *C. obtusirostris* (see also family and genus profiles). Sample sizes too small to evaluate sexual size dimorphism.

Geographic Variation Two subspecies have been described, but their validity is uncertain:

C. l. leucorhinus: DR Congo southwards to N Angola. Lower premolars with well-developed talonids; includes *congicus* and *luluanus* (Meester 1974).

C. l. cahni: Cameroon and Central African Republic. Talonids feeble on $P_{1,2}$, absent on P_3 and M_3 . Although the pelage of some *C. l. cahni* is paler than in *C. l. leucorhinus*, one individual from Cameroon has a darker colouration suggesting that colour differences between subspecies are not consistent.



Calcochloris leucorhinus

Similar Species

Chrysochloris stuhlmanni. Skull larger (GLS: 24.3–28.31 mm); malleus enlarged; temporal bulla pronounced and protruding through temporal surface of skull. Might be sympatric but full extent of distribution not known.

Distribution Endemic to Africa. Rainforest BZ (West Central Region [Gabon sub-region] with limited extension into the Northern Rainforest–Savanna Mosaic, and two outliers in Southern Rainforest–Savanna Mosaic). Recorded only from scattered localities in Angola, DR Congo, Cameroon and Central African Republic.

Habitat Lowland equatorial forests and montane forests.

Remarks Apparently no other information available.

Conservation IUCN Category: Data Deficient, previously Least Concern.

Measurements

Calcochloris leucorhinus

HB: 63, 126 mm, n = 2

T: 0 mm

HF: 9, 10 mm, n = 2

E: 0 mm

WT: n. d.

GLS (♂ ♂): 21.7 (19.5–22.8) mm, n = 4

GLS (♀ ♀): 22.2 (21.0–23.1) mm, n = 4

GWS (♂ ♂): 19.2 (18.6–20.4) mm, n = 7

GWS (♀ ♀): 17.6 (16.6–18.2) mm, n = 14

C–M³ (♂ ♂): 5.9 (5.6–6.5) mm, n = 6

C–M³ (♀ ♀): 6.7 (4.7–6.4) mm, n = 7

Museum specimens throughout geographic range (Bronner 1995b)

Key References Bronner 1995b; Simonetta 1968.

Gary N. Bronner

Calcochloris obtusirostris YELLOW GOLDEN-MOLE

Fr. Taupe dorée jaune; Ger. Gelber Goldmull

Calcochloris obtusirostris (Peters, 1851). Bericht Verhandl. K. Preuss. Akad. Wiss., Berlin 16: 467. Inhambane, coastal Mozambique.

Taxonomy Originally described in the genus *Chrysochloris*. A polytypic species with three subspecies, all of which were once regarded as valid species. Synonyms: *chrysillus*, *limpopoensis*. Subspecies: three. Chromosome number: 2n = 28, FN = 56 (Bronner 1995a).

Description Small species, distinctive among golden-moles in having underfur that is orange at base, instead of slaty-grey. Dorsal pelage yellowish-orange to dull reddish-brown, owing to a progressive increase in grizzled-brown hair tips. Ventral pelage less variable, yellowish-orange to bright brownish. Muzzle, throat and chin yellowish-white with fewer brown-tipped hairs. Nostrils with unique foliaceous projections. Pelage colour becomes darker and more grizzled with time between moults. Claws on forefeet very slender and flattened. Claw on Digit 3 largest (7–9 mm long, <3.5 mm wide at base), claws on Digits 1 and 2 about same length. Digit 4 small with a short (2 mm) claw. First premolars molariform, canines bicuspid. M³ absent, molar talonids absent or feeble. Sexual size dimorphism pronounced, ♂♂ on average larger than ♀♀ in most cranial measurements. Skull: see family and/or genus profiles.

Geographic Variation Morphological differences between subspecies are subtle and distinguishing between them is difficult owing to intergradations in size:

C. o. obtusirostris: Inhambane and Gaza districts in Mozambique westwards to Changane and Save river systems and to SE lowlands of Zimbabwe and Northern Province of South Africa.

C. o. limpopoensis: Masiene district of Mozambique southwards along coast to Maputo. Larger than other subspecies (GLS: >22.5 mm), with a wider rostrum (>7.2 mm) than in *C. chrysillus* and more gracile claws than in *C. o. obtusirostris*.

C. o. chrysillus: southern Mozambique Plain from Maputo to Maputaland (north of L. St Lucia) in N KwaZulu–Natal, South Africa; rostrum <7.1 mm.

Similar Species

Carpitalpa arendsi. Larger (HB: 115–141 mm; GLS: 25.3–29.0 mm); M³ present; pelage darker. Highlands of E Zimbabwe and W Mozambique near Zimbabwe border.



Calcochloris obtusirostris

Distribution Endemic to Africa. Extreme southern part of Zambezian Woodland BZ. Distribution closely follows the limits of the Mozambique sands. Recorded from Inhambane in Mozambique southwards to N KwaZulu–Natal Province, South Africa, and inland to the great escarpment and south-eastern lowveld of Zimbabwe.

Habitat Sandy soils in savanna. In KwaZulu–Natal, *C. o. chrysillus* occurs in Coastal Bushveld–Grassland and Subhumid Lowveld Bushveld. In E Mozambique, *C. o. limpopoensis* occurs in miombo savanna, and in Mozambique and adjacent parts of Zimbabwe (with a marginal intrusion into the Nyadu Sandveld of Kruger N. P.), *C. o. obtusirostris* occurs in *Acacia* and mopane savanna.

Abundance Locally common but no accurate information on densities.

Adaptations The unique foliaceous projections on the nostrils prevent sand entering during burrowing. Nest chambers are located amongst the roots of trees, from where subsurface tunnels lead off for up to 50 m to foraging areas. Deeper tunnels (up to 20 cm below surface) are reused and regularly maintained. If disturbed in subsurface tunnels, these golden-moles burrow deeply downwards in a spiralling pattern. They are particularly active after rains. Watering the soil surface stimulates activity by captive individuals, which sometimes move at a surprising speed in and out of the sand in a porpoise-like fashion (Roberts 1936).

Foraging and Food Mostly insectivorous. Forage in subsurface tunnels, mainly at night. Prey includes tenebrionid larvae, termites, grasshoppers, flies, moths and small lizards. Highly sensitive to vibrations emitted by live prey (Roberts 1936).

Social and Reproductive Behaviour Adults solitary. Emit high-pitched squeaks when agitated or handled.

Calcochloris tytonis SOMALI GOLDEN-MOLE

Fr. Taupe dorée de Somalie; Ger. Somalia-Goldmull

Calcochloris tytonis (Simonetta, 1968). *Monitore Zoologico Italiano* 2 (Suppl.): 31.

Giohar (= Villaggio Duca degli Abruzzi), southern Somalia.

Taxonomy and Description Originally described in the genus *Amblysomus* on the basis of size and structure of the malleus (Simonetta 1968). Subsequently included in *Chlorotalpa* by Meester (1974) based on the presence of M^3 , but included here in the genus *Calcochloris* because the few characters available for this species suggest that it may be closely related to *Calcochloris leucorhinus* (Bronner 1995b). However, *C. tytonis* is known only from a partially complete specimen in an owl pellet, and no measurements are available. It should therefore be regarded as *incertae sedis* until more specimens are available. The incidence of third molars is a primitive character that sheds no light on phylogenetic relationships among chrysochlorids.

Geographic Variation None recorded.

Reproduction and Population Structure Breeding individuals recorded in Oct ($n = 3$) and Jan ($n = 1$), suggesting that reproduction takes place primarily in wet summer months. Litter-size: 2 ($n = 1$). Gestation period unknown.

Predators, Parasites and Diseases No information.

Conservation IUCN Category: Least Concern.

Occurs in several protected areas. Its cryptic nature allows it to coexist successfully with humans.

Measurements

Calcochloris obtusirostris

HB ($\sigma \sigma$): 100.3 (88–110) mm, $n = 17$

HB ($\phi \phi$): 93.3 (82–110) mm, $n = 15$

T: 0 mm

HF ($\sigma \sigma$): 11.3 (10–13) mm, $n = 17$

HF ($\phi \phi$): 11.6 (9–14) mm, $n = 13$

E: 0 mm

WT ($\sigma \sigma$): 28.1 (25–33) g, $n = 9$

WT ($\phi \phi$): 24.5 (15–37) g, $n = 11$

GLS ($\sigma \sigma$): 22.6 (20.8–24.2) mm, $n = 21$

GLS ($\phi \phi$): 21.5 (19.0–23.6) mm, $n = 17$

GWS ($\sigma \sigma$): 16.1 (15.4–16.8) mm, $n = 23$

GWS ($\phi \phi$): 15.5 (13.8–16.8) mm, $n = 18$

C– M^2 ($\sigma \sigma$): 6.1 (5.9–6.3) mm, $n = 10$

C– M^2 ($\phi \phi$): 5.9 (5.6–6.2) mm, $n = 10$

Museum specimens throughout geographic range (Bronner 1995b)

Key References Bronner 1995b; Roberts 1936

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Similar Species None within the known geographic distribution of the species.

Distribution Endemic to Africa. Somalia–Masai Bushland BZ. Known only from the type locality.

Habitat Dense bush and savanna of the Somali Peninsula (Agnelli *et al.* 1988).

Abundance No information.

Remarks The holotype was recovered from the pellet of a Barn Owl *Tyto alba*. Apparently no other information on this species.

Measurements None available.

Conservation IUCN Category: Critically Endangered.

Key References Bronner 1995b; Meester 1974; Simonetta 1968.

Gary N. Bronner



Calcochloris tytonis

GENUS *Carpitalpa* Arends's Golden-mole

Carpitalpa Lundholm, 1955. Ann. Transvaal Mus. 22: 285. Type species: *Chlorotalpa (Carpitalpa) arendsi* Lundholm, 1955.

A monotypic genus including only Arends's Golden-mole *Carpitalpa arendsi* from afro-montane forests and high-altitude grasslands of E Zimbabwe and adjacent parts of Mozambique. Body shape fusiform. Claws on forefeet gracile, claw of Digit 3 largest (9–12 mm long) but slender (3.5–4.0 mm at base), claws on Digits 1 and 2 much shorter. Digit 4 absent. Skull elongate (breadth <65% of GLS, with a narrow palate 28–29% of GLS). Zygomatic arches without broad plates sweeping backwards. Small, tricuspid M^3 present, upper premolars semi-molariform but crushing basin not fully formed (Bronner 1995b). Definitive characters of this genus are the possession of a club-shaped malleus that, although enlarged, does not project through the temporal region of the skull as a bulla. In this respect it resembles the smaller species of *Chlorotalpa* from South Africa, from which it is distinguished by a relatively narrower skull and absence of well-developed talonids on the lower molars (Figure 8).

Lundholm (1955) described this taxon as a subgenus of *Chlorotalpa*, as well as the subgenus *Kilimaltalpa* for *C. stuhlmanni* from East Africa. Simonetta (1968) elevated *Carpitalpa* to generic rank to include *Kilimaltalpa*. Meester (1974) assigned *C. arendsi* to *Chlorotalpa* and *C. stuhlmanni* to *Chrysochloris*, commenting that differences between the species of *Chlorotalpa* did not warrant subgeneric separation. Phylogenetic analyses of morphometric data, however, confirm that *C. arendsi* has diverged considerably from the *Chlorotalpa* species and *Chrysochloris (Kilimaltalpa) stuhlmanni*, necessitating its allocation to a separate genus (Bronner 1995b).

Gary N. Bronner

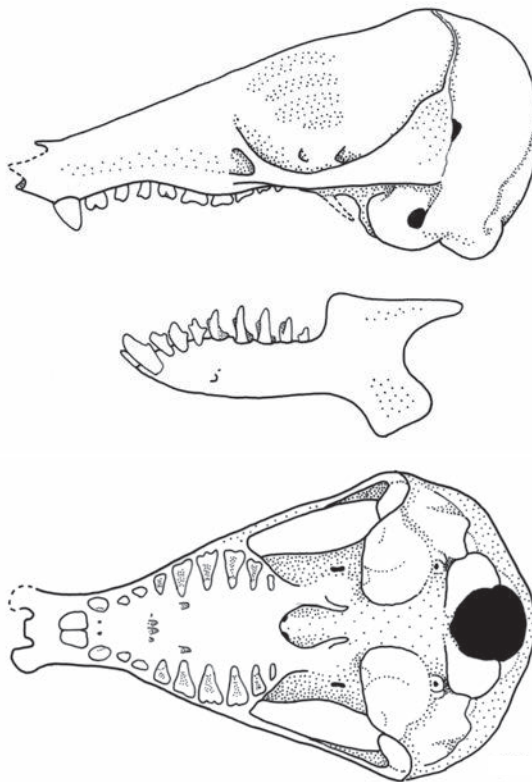


Figure 8. Skull and mandible of *Carpitalpa arendsi* (TM 12965, based on photo by T. Kearney).

Carpitalpa arendsi ARENDS'S GOLDEN-MOLE

Fr. Taupe dorée d'Arends; Ger. Arends Goldmull

Carpitalpa arendsi (Lundholm, 1955). Ann. Transvaal Mus. 22: 285. Pungwe Falls, Inyanga, Zimbabwe.**Taxonomy** Synonyms: none. Chromosome number: not known.**Description** Originally described in the genus *Chlorotalpa*. Medium-sized golden-mole with a comparatively strong build, similar in size and cranial proportions to *Neamblysomus gunningi*. Dorsal pelage brownish-black, ventral pelage greyish-brown, with a distinct violet or silver sheen. Underfur dark grey. Muzzle paler; eye patches whitish. Males on average slightly larger than ♀♀ but sexual dimorphism in cranial size is not pronounced (Bronner 1995b). Skull: M³ present (see family and genus profiles).**Geographic Variation** None recorded.**Similar Species***Calcochloris obtusirostris*. Smaller (HB: 82–110 mm, GLS: 19.0–24.2 mm); M³ absent; pelage paler. Lowlands of Zimbabwe and Mozambique.**Distribution** Endemic to Africa. Zambezian Woodland BZ. Restricted to the Inyanga Highlands of E Zimbabwe between latitudes 18°S and 20°S, and altitudes of 850–2000 m. Also recorded in W Mozambique in the highlands close to the Mozambique–Zimbabwe border.**Habitat** Loamy soils, with detritus, in montane grasslands and forest fringes (Smithers & Wilson 1979). Also recorded in roadside verges and gardens.**Abundance** Locally common.**Remarks** Arends's Golden-moles construct subsurface tunnels that radiate outwards from roots of trees and clumps of grass into open areas. They are most active in gaps between grass tussocks where they coexist with vlei rats *Otomys irroratus*. After rains, they may forage and travel on the surface of the ground (Smithers & Wilson 1979). In open areas, burrowing may kill the grasses (Lundholm 1955). Insectivorous; also eats earthworms (Smithers & Wilson 1979).**Predators, Parasites and Diseases** No information.**Conservation** IUCN Category: Vulnerable.*Carpitalpa arendsi***Measurements***Carpitalpa arendsi*

HB (♂♂): 123.6 (115–141) mm, n = 11

HB (♀♀): 121.2 (115–139) mm, n = 11

T: 0 mm

HF (♂♂): 14.2 (14–16) mm, n = 9

HF (♀♀): 13.2 (12–16) mm, n = 11

E: 0 mm

WT (♂♂): 53 (43–70) g, n = 6

WT (♀♀): 50 (43–56) g, n = 5

GLS (♂♂): 27.7 (26.8–29.0) mm, n = 7

GLS (♀♀): 27.3 (25.3–28.6) mm, n = 8

GWS (♂♂): 16.8 (16.2–17.5) mm, n = 7

GWS (♀♀): 16.6 (15.8–17.2) mm, n = 8

C–M³ (♂♂): 7.1 (6.5–7.6) mm, n = 7C–M³ (♀♀): 7.3 (6.9–7.7) mm, n = 8

Museum specimens throughout geographic range (Bronner 1995b)

Key References Bronner 1995b; Lundholm 1955; Smithers & Wilson 1979.

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GENUS *Chlorotalpa*

Golden-moles

Chlorotalpa Roberts, 1924. Ann. Transvaal Mus. 10: 64. Type species: *Chrysochloris duthieae* Broom, 1907.

The genus *Chlorotalpa* contains two small species endemic to South Africa. The two species have different habitat requirements and geographic ranges. Sclater's Golden-mole *C. sclateri* lives in a variety of montane grasslands and forested kloofs inland. Duthie's Golden-mole *C. duthieae* lives in sandy habitats of coastal forests.

Body-shape fusiform. Claws on forefoot long and slender, claw on Digit 3 largest (7–9 mm long), claws on Digits 1 and 2 much shorter. Digit 4 minute with a small nail. *Chlorotalpa* resembles *Amblysomus* in general appearance and skull morphology, but is markedly smaller with weaker claws on the forefeet. Skull elongate (breadth 62–66% of GLS) with a narrow palate (<30% of GLS). Zygomatic arches without broad plates sweeping backwards. Small molariform M³ present, lower cheekteeth have well-developed talonids. The malleus is somewhat inflated and pear-shaped, but does not protrude through the temporal region of the skull to form a bulla; in size and shape, it is intermediate between the club-shaped malleus of *Chrysochloris* and the small, unspecialized malleus of *Amblysomus* (Mayer *et al.* 1995), suggesting that *Chlorotalpa* is transitional between these genera (Figure 9).

Some authors have disputed the use of dental formulae for diagnosing genera amongst golden-moles, and thus have synonymized *Chlorotalpa* under *Amblysomus*. The consistent differences in the morphology of the malleus between these taxa, however, correlate with subtle but complex differences in the configuration of the temporal region of the skull, which must be regarded as taxonomically important. These two genera also differ in chromosomal properties (Bronner 1995b). The two species in the genus are distinguished by pelage colour and habitat requirements.

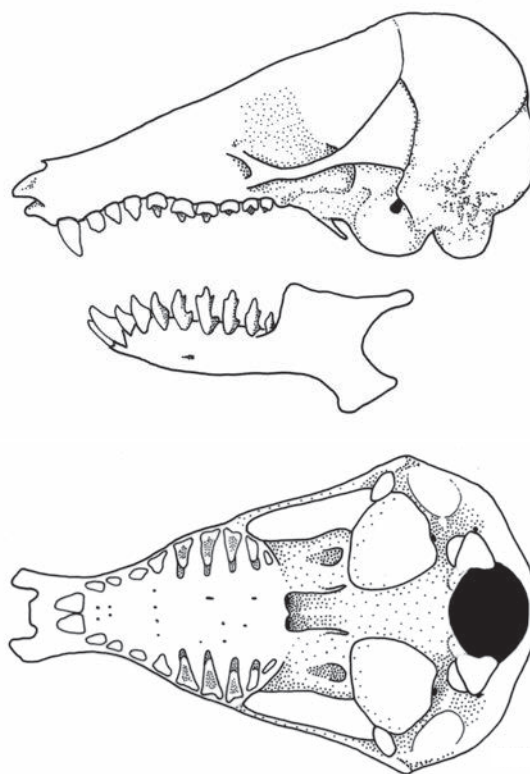


Figure 9. Skull and mandible of *Chlorotalpa duthieae* (BMNH 5.13.10.1).

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Chlorotalpa duthieae DUTHIE'S GOLDEN-MOLE

Fr. Taupe dorée de Duthie; Ger. Duthies Goldmull

Chlorotalpa duthieae (Broom, 1907). Trans. S. Afr. Phil. Soc. 18: 292. Knysna, Western Cape Province, South Africa.

Taxonomy Originally described in the genus *Chrysochloris*. A monotypic species that some authors (Ellerman *et al.* 1953, Simonetta 1968) treated as a subspecies of *C. sclateri*, but constant differences in pelage colour and chromosomal properties, and their preference for quite dissimilar environments, indicate that they are distinct species (Bronner 1995b). Synonyms: none. Chromosome number: 2n = 30, FN = 60 (Bronner 1995a).

Description Small golden-mole, with a delicate build and slender claws on the forefeet. Dorsal pelage uniformly reddish-black or brownish-black. Ventral pelage with less lustre. Throat and chest greyish. Hairs 8–9 mm long, pale at base, with dark grey subterminally. Muzzle paler than dorsal pelage with buffy-white patches extending to ocular region (Roberts 1951). Nosepad with rounded outer edge, section behind transverse groove narrow (1.5–2 mm). Claw on Digit 3 of forefoot largest (7–9 mm long, 3.5–4.0 mm wide at base).

Sexual size dimorphism marked, ♂♂ significantly larger than ♀♀ in most cranial measurements (Bronner 1995b). P1 tricuspid rather than sectorial, P¹ lack protocones. Well-developed talonids invariably present on lower molars. Skull: see also family and/or genus profiles.

Geographic Variation Individuals from Knysna are generally larger than those from further east, but geographic variation is not sufficiently marked to warrant recognition of subspecies.

Similar Species

Amblysomus corriae. Skull larger (GLS: 25.3–28.9 mm); claw on Digit 3 longer (13–15 mm); M³ absent.

Distribution Endemic to South Africa. South-West Cape BZ. Occurs along the coast from George in Western Cape Province to Port Elizabeth in Eastern Cape Province, South Africa.



Habitat Alluvial sands and sandy loams in afro-montane and coastal forests. Coexists with *Amblysomus corriae* in parts of the range, but trapping data suggest these species select different micro-habitats, *A. c. corriae* apparently favouring fynbos and forest fringes, and *C. duthieae* favouring deeper forest. Thrives in cultivated areas and gardens.

Abundance Locally common but no quantitative data.

Adaptations Constructs predominantly shallow subsurface tunnels that radiate outwards from nests located under the roots of trees.

Foraging and Food Forages in subsurface tunnels and amongst leaf litter, mainly at night. Limited observations suggest the diet comprises mainly earthworms ($n = 2$ stomachs).

Social and Reproductive Behaviour Adults solitary.

Reproduction and Population Structure Only one pregnancy recorded, in early summer (Nov). Litter-size: 2 (1L, 1R).

Predators, Parasites and Diseases Recorded from pellets of Barn Owls *Tyto alba*, suggesting occasional surface activity. Also caught by domestic cats and dogs.

Conservation IUCN Category: Vulnerable.

Within its limited distribution, adequately conserved in numerous protected areas.

Measurements

Chlorotalpa duthieae

HB (♂ ♂): 105.7 (95–125) mm, $n = 10$

HB (♀ ♀): 101.9 (96–130) mm, $n = 11$

T: 0 mm

HF (♂ ♂): 11.6 (9–14) mm, $n = 9$

HF (♀ ♀): 11.6 (9–13) mm, $n = 9$

E: 0 mm

WT (♂ ♂): 33.0 (26–41) g, $n = 3$

WT (♀ ♀): 26.0 (20–27) g, $n = 3$

GLS (♂ ♂): 23.8 (22.9–24.5) mm, $n = 8$

GLS (♀ ♀): 22.8 (22.0–23.9) mm, $n = 10$

GWS (♂ ♂): 14.9 (14.4–15.8) mm, $n = 8$

GWS (♀ ♀): 14.3 (13.7–15.2) mm, $n = 10$

C-M³ (♂ ♂): 7.1 (6.5–7.6) mm, $n = 7$

C-M³ (♀ ♀): 7.3 (6.9–7.7) mm, $n = 8$

Knysna, Nature's Valley and Port Elizabeth, South Africa (Bronner 1995b)

Key References Bronner 1995b; Broom 1907a; Roberts 1951.

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Chlorotalpa sclateri SCLATER'S GOLDEN-MOLE

Fr. Taupe dorée de Sclater; Ger. Sclaters Goldmull

Chlorotalpa sclateri (Broom, 1907). Ann. Mag. Nat. Hist., ser. 7, 19: 263. Matjiesvlei, Beaufort West, Western Cape Province, South Africa.

Taxonomy Originally described in the genus *Chrysochloris*. Differs markedly in colour from *C. duthieae*, although these species are indistinguishable cranially. Synonyms: *guillarmodi*, *montana*, *shortridgei*. Subspecies: four. Chromosome number: $2n = 30$, $FN = 60$ (Bronner 1995a).

Description Small golden-mole with a stocky build and slender claws on the forefeet. Dorsal pelage glossy reddish-brown, darker along mid-line. Ventral pelage dull greyish with rufous tinge. Hairs short, 10–12 mm long and rather coarse. Lips and cheeks creamish-yellow with pale patches extending to above the subdermal eyes and forming a band above the nose pad. Nose pad rounded without obtuse corners as in *Chrysochloris asiatica*. Claw on Digit 3 of forefoot largest (8–9 mm

long, 3.0–4.5 mm wide at base). Skull: M³ present; P¹ tricuspid, resembles other cheekteeth, P¹ lacks protocone; lower molars with well-developed talonids (see also family and genus profiles). Males on average slightly larger than ♀ ♀, but sexual dimorphism not pronounced.

Geographic Variation Distributional limits of the four subspecies are unclear owing to poor geographic sampling, but their known ranges are separated by expanses of seemingly inhospitable habitat suggesting that they may be geographically isolated.

C. s. sclateri: Beaufort West in Western Cape Province north-eastwards

along Koueveldberge and Sneeuwege mountains to Graaff-Reinet in Eastern Cape Province. Palate relatively longer (>53% of GLS) than in *C. s. guillarmodi*.

C. s. shortridgei: known from only Sutherland in Northern Cape Province, but may range eastwards along Nieuweveldbeerg mountains toward Beaufort West in Western Cape Province. Slightly larger than other subspecies with wider rostrum (>4.7 mm) than *C. s. sclateri* (<4.5 mm).

C. s. guillarmodi: Herschel and Lady Grey in Eastern Cape Province north-eastwards through Lesotho, with a marginal intrusion into E Free State and KwaZulu-Natal (Taylor *et al.* 1994). Palate <51% of GLS, shorter than in *C. s. sclateri* and *C. s. montana*.

C. s. montana: known from only Wakkerstroom in Mpumalanga Province, but may range southwards along the Low Drakensberg to intergrade with *C. s. guillarmodi* near Harrismith or Clarens. Palate significantly longer (>12.2 mm) than in *C. s. guillarmodi* (<12 mm).

Similar Species

Amblysomus septentrionalis. On average larger (HB: 126 [105–145] mm); claws more robust, claw on Digit 3 of forefoot 14–15.7 mm; M^3 absent.

Distribution Endemic to Africa. Highveld BZ and South-West Arid BZ. Recorded from Sutherland in Northern Cape Province, South Africa north-eastwards through Eastern Cape Province and Lesotho to E Free State, W KwaZulu-Natal and S Mpumalanga Provinces.

Habitat Restricted to high-altitude grasslands, scrub and forested kloofs in the Karoo and Grassland biomes. *Chlorotalpa s. shortridgei* occurs in Escarpment Mountain Renosterveld. *Chlorotalpa s. sclateri* and *C. s. guillarmodi* in South-eastern Mountain Grassland with marginal intrusion into Wet Cold Highveld Grassland. *Chlorotalpa s. montana* is known from only North-eastern Mountain Grassland where it favours forested kloofs rather than valley grasslands where *A. septentrionalis* is the commoner species.

Abundance Locally common, but no quantitative data.

Adaptations Small size and weak digging claws generally limit the distribution of these golden-moles to light, sandy soils, although they may also invade heavier clays when wet after rains. They construct predominantly shallow subsurface tunnels especially among roots of trees, or in clumps of rocks, where the nesting chambers are located (Roberts 1951). Active mainly at night, but also for short periods during the day, especially after rain.

Foraging and Food Carnivorous and insectivorous. Forages for invertebrates in subsurface tunnels that meander outwards from nesting areas for distances of up to 45 m. Feeds predominantly on earthworms and insect larvae.

Social and Reproductive Behaviour Adults solitary.

Reproduction and Population Structure Pregnancies recorded during the wet summer months (Dec and Jan). Litter-size: 2 (1L, 1R). Young born in grass-lined nests (Roberts 1951). Females have a postpartum oestrus (Bernard *et al.* 1994); this may



Chlorotalpa sclateri

assist in maximizing breeding success during the short period in summer when rainfall and temperatures are high enough to sustain an abundant supply of food.

Predators, Parasites and Diseases Regularly caught by dogs and cats. No information on wild predators, diseases or parasites.

Conservation IUCN Category: Least Concern, previously Vulnerable.

Although widely distributed, the geographic range is highly fragmented and many of its habitats may have been degraded by overgrazing.

Measurements

Chlorotalpa sclateri

HB (♂ ♂): 100.9 (83–135) mm, n = 16

HB (♀ ♀): 102.2 (82–123) mm, n = 13

T: 0 mm

HF (♂ ♂): 12.7 (10–16) mm, n = 15

HF (♀ ♀): 11.5 (9–13) mm, n = 13

E: 0 mm

WT (♂ ♂): 36.4 (22–54) g, n = 11

WT (♀ ♀): 32.5 (22–48) g, n = 7

GLS (♂ ♂): 23.6 (21.8–27.4) mm, n = 16

GLS (♀ ♀): 23.4 (21.2–26.7) mm, n = 13

GWS (♂ ♂): 15.4 (14.5–17.6) mm, n = 16

GWS (♀ ♀): 15.1 (14.1–16.9) mm, n = 13

C-M³ (♂ ♂): 6.3 (5.8–6.9) mm, n = 15

C-M³ (♀ ♀): 6.3 (5.6–6.9) mm, n = 14

Museum specimens throughout geographic range

Key References Bernard *et al.* 1994; Broom 1907b; Roberts 1951.

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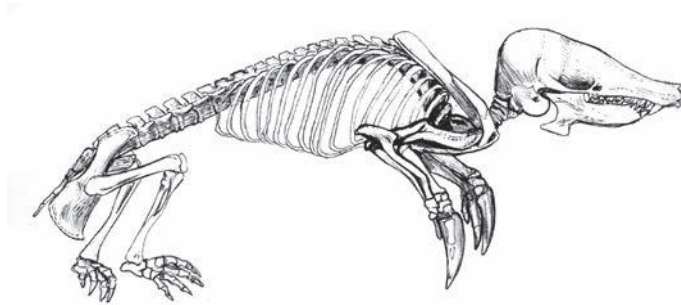
GENUS *Chrysochloris*

Golden-moles

Chrysochloris Lacépède, 1799. Tabl. Mamm., p. 7. Type species: *Chrysochloris capensis* Lacépède, 1799 (= *Talpa asiatica* Linnaeus, 1758).



Chrysochloris stuhlmanni.



Skeleton of *Chrysochloris stuhlmanni*.

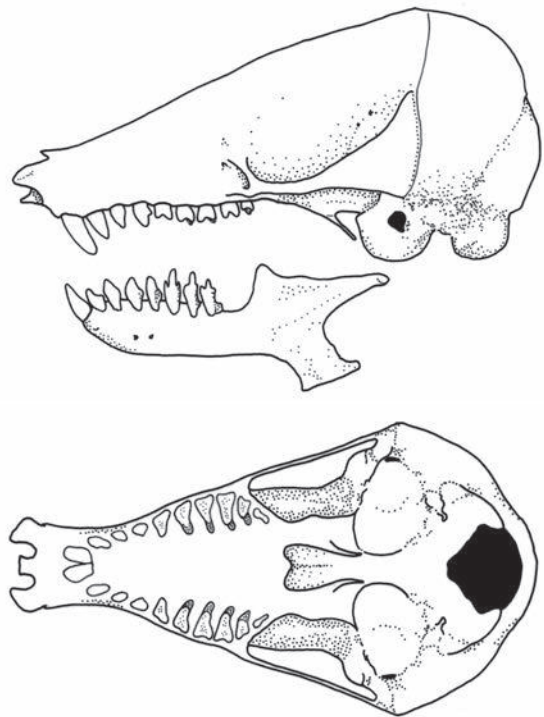


Figure 10. Skull and mandible of *Chrysochloris stuhlmanni* (based on Simonetta 1968).

The genus *Chrysochloris* contains three small species from the geographical extremes of the range of golden-moles in sub-Saharan Africa. The Cape Golden-mole *C. asiatica* (which Linnaeus mistakenly assumed to have come from Siberia) is endemic to sandy soils of SW South Africa, and Stuhlmann's Golden-mole *C. stuhlmanni* occurs on mountains in central and eastern Africa. Visagie's Golden-mole *C. visagiei* is known only from the type locality in Northern Cape Province of South Africa (Meester 1974).

Body shape is fusiform. Claws on the forefeet are slender, the claw of Digit 3 is markedly larger (10–12 mm long) than that on Digit 2 (5–8 mm) and Digit 1 (3–4.5 mm). Digit 4 is vestigial. The most distinctive feature of this genus is the possession of an enlarged, club-shaped malleus orientated vertically and housed in a bony bulla that projects through the temporal surface of the skull (Broom 1907a). Zygomatic arches without broad plates sweeping backwards. In *C. asiatica* and *C. visagiei* the skull is short and broad (breadth >70% of GLS) with a wide palate (30–32% of GLS), though not to the same extent as in *Eremitalpa* and *Cryptochloris* (palate width >35% of GLS). The skull of *C. stuhlmanni* is elongate (breadth <65% of GLS) with

a narrow palate (26–28% of GLS), as in the genera *Amblysomus* and *Chlorotalpa*. Pelage colour varies substantially, both within populations (*C. asiatica*) and geographically. Small M^3 present in most specimens (but consistently absent in some populations); morphology ranges from tricuspid to peg-like depending on toothwear. Incidence of molar talonids is variable, being either well-developed (*C. stuhlmanni*) or absent (*C. asiatica* and *C. visagiei*) (Figure 10).

The two species that are comparatively well-known, *C. asiatica* and *C. stuhlmanni*, live in different habitats and have different geographic ranges. *Chrysochloris asiatica* lives in sandy soils in semi-arid habitats of South Africa; *C. stuhlmanni* lives in montane forest soils at higher altitudes in eastern Africa. Both species feed mainly on earthworms.

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Chrysochloris asiatica CAPE GOLDEN-MOLE

Fr. Taupe dorée du Cap; Ger. Kap-Goldmull

Chrysochloris asiatica (Linnaeus, 1758). Syst. Nat., 10th edn, 1: 53. 'In Sibiria', taken as the Cape of Good Hope, South Africa.

Taxonomy Originally described in the genus *Talpa*. A monotypic species in need of revision. Previous authors recognized up to eight subspecies based on considerable geographic variability in size and colour, but this may be largely clinal by nature (Meester

1974). Synonyms: *auratus*, *aurea*, *bayoni*, *capensis*, *calviniae*, *concolor*, *damarensis*, *dixonii*, *elegans*, *inaurata*, *minor*, *namaquensis*, *rubra*, *shortridgei*, *taylori*, *tenuis*, *visserae*. Subspecies: none. Chromosome number: $2n = 30$, $FN = 56$ (Bronner 1995a).

Description Small dark species with pale markings on the muzzle. Dorsal pelage blackish, slaty-grey to brownish-grey, olive-brown, or drab silver. Ventral pelage somewhat paler than dorsal pelage, blackish to pale creamy-grey or greyish-white, tips of hairs often paler on chest and greyer on abdomen. Muzzle and chin creamy-yellow with a profuse admixture of whitish hairs, becoming paler on cheeks, often with whitish eye patches. Underfur dense and slate-grey. Younger animals duller and more greyish. Albino individuals pale to golden-brown (rarely recorded). Nosepad narrow, 9–10 mm long with blunt corners. Claws on forefeet gracile, claw on Digit 3 largest (10–12 mm long, 3.5–4.6 mm wide at base), claw on Digit 2 shorter (5.5–7.2 mm) and claw on Digit 1 very short (3–4.5 mm). Digit 4 reduced to a minute tubercle. Skull broad (breadth 70–78% of GLS) with a relatively wide palate (30–32% of GLS). Malleus enlarged and club-shaped, temporal bulla well-developed. M^3 usually present, though occasionally absent in some individuals from Little Namaqualand; morphology varies from triconid (like other cheekteeth) to peg-like depending on toothwear. Molar talonids absent. Skull: see also family and/or genus profiles. Adult ♂♂ on average larger than ♀♀, but extent of sexual dimorphism has not been evaluated statistically.

Geographic Variation Colour and size vary geographically. Individuals from Cape Peninsula are larger and darker with blackish-grey pelage sometimes suffused with dark brown; those from Little Namaqualand are smaller, with pale pelage, which becomes paler (olive-brown to pale brownish or drab silver) from south to north. Malleus size and shape also vary geographically (Broom 1907a, 1946). These differences may, however, be adequately explained by clinal variation in colour (darker to paler) and size (larger to smaller) from south to north (Meester 1974). Almost complete intergradation between darker and paler colour extremes evident at some localities (Shortridge 1942), suggesting that variation may also have a substantial within-population component.

Similar Species

Amblysomus corriae. Often larger (HB: 108–130 mm), skull larger (GLS: 25.3–28.9 mm); pelage more rufous; M^3 absent, claw on digit 3: 13–15 mm; malleus not enlarged, bulla not visible externally.

Cryptochloris zyli and *Cryptochloris wintoni*. Slightly smaller (HB: < 92 mm); claws on Digits 1, 2 and 4 of forefoot better developed; palate relatively wider (>35% of GLS); malleus enlarged; bulla small.

Eremitalpa granti. Much smaller (HB: 76–86 mm, GLS: 18.6–20.4 mm); body lozenge-shaped, claws on Digits 1, 2 and 4 of forefoot not so markedly shorter than that on Digit 3; skull relatively much broader (breadth > 85% of GLS); malleus pea-shaped, less enlarged; bulla not visible externally.

Distribution Endemic to Africa. Western parts of South-West Arid BZ (Karoo) and South-West Cape BZ. Ranges from the Cape Peninsula (Western Cape Province) eastwards across Cape Flats to Bredasdorp and Swellendam, and northwards along the Atlantic coast to Port Nolloth in Northern Cape Province. Occurs inland to Ceres, Worcester and Stellenbosch in the south, and Calvinia, Garies and Kamieskroon in the north, but not in the arid Karoo. One specimen (type of '*C. damarensis*') recorded from Damaraland



Chrysochloris asiatica

in Namibia, but likely incorrect and collected in Little Namaqualand (Meester 1974).

Habitat Sandy soils in a wide variety of vegetation types, most commonly in Renosterveld, Fynbos and Strandveld Succulent Karoo. Common in gardens and cultivated lands; readily invades lawns. Coexists with *A. hottentotus* at Stellenbosch, but prefers drier, sandier soils (Broom 1907a).

Abundance Locally common.

Adaptations Cape Golden-moles make subsurface tunnels, which radiate outwards from bushes or clumps of rocks where nests are located. Occasionally they burrow deeper and throw up small mounds of soil. Activity is mainly at night, particularly after rains. Surface activity declines markedly during the dry summer months (Nov–Mar). Adaptive hypothermia and thermolability reduce energetic requirements and prevent overheating in the closed burrow systems, particularly during dry periods or in arid environments where food resources may be limited. Resting metabolic rate is 68% of that predicted for insectivorous mammals. Individuals may enter torpor if ambient temperature drops below 9 °C, resulting in a five-fold reduction in energy requirements. Assimilation efficiency is high, about 86%, as in other insectivorous and carnivorous mammals (Withers 1978, Bennett & Spinks 1995).

Foraging and Food Insectivorous and carnivorous. Diet includes earthworms, sow-bugs, centipedes, insect larvae and millipedes. Observed to venture onto sandy beaches, presumably to feed on amphipods and isopods associated with rotting kelp (Bennett & Spinks 1995).

Social and Reproductive Behaviour Solitary except for ♀♀ raising young. Aggressive towards conspecifics; agonistic encounters involve 'rolling' and biting.

Reproduction and Population Structure Newborn young recorded in Jun, Jul and Aug, suggesting that breeding is restricted to the wet winter months. Litter-size: 1–3. At birth, young are about 47 mm long, altricial and practically hairless. Postnatal development slow. Pups are suckled by their mother for 2–3 months. Teeth do not erupt until the individual is nearly mature (Broom 1907a).

Predators, Parasites and Diseases Remains are common in pellets of Barn Owls *Tyto alba*, indicating substantial surface activity. Often killed by domestic cats, which seldom eat the carcass, perhaps because of the tough skin and musky secretions of the large anal glands. Disliked by gardeners and green-keepers because their subsurface tunnels are deemed unsightly and often cause plants to wilt and die. No information on parasites and diseases.

Conservation IUCN Category: Least Concern.

Protected in many conservation areas and able to thrive in habitats modified by humans.

Measurements

Chrysochloris asiatica

HB (♂ ♂): 105.4 (100–115) mm, n = 10

HB (♀ ♀): 99.6 (94–114) mm, n = 10

T: 0 mm

HF (♂ ♂): 12.6 (9–14) mm, n = 9

HF (♀ ♀): 11.9 (11–14) mm, n = 10

E: 0 mm

WT: n. d.

GLS (♂ ♂): 22.9 (22.1–23.6) mm, n = 9

GLS (♀ ♀): 22.5 (21.1–25.4) mm, n = 12

GWS (♂ ♂): 17.6 (16.1–19.0) mm, n = 10

GWS (♀ ♀): 17.1 (16.1–19.2) mm, n = 11

C–M³ (♂ ♂): 6.2 (5.4–6.7) mm, n = 5

C–M³ (♀ ♀): 6.4 (6.2–6.5) mm, n = 4

Throughout geographic range and literature records

Key References Bennett & Spinks 1995; Broom 1907a; Meester 1974.

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Chrysochloris stuhlmanni STUHLMANN'S GOLDEN-MOLE

Fr. Taupe dorée de Stuhlmann; Ger. Stuhlmanns Goldmull

Chrysochloris stuhlmanni Matschie, 1884. Sber. Ges. Naturf. Freunde Berlin, p. 123. Ukonjo and Kinyawang, Rwenzori region, Uganda.

Taxonomy A polytypic species subjected to markedly different taxonomic treatments. Lundholm (1955) created the subgenus *Kilimatalpa* within *Chlorotalpa* for this species, whereas Simonetta (1968) placed it in the genus *Carpitalpa*, but assigned one of the subspecies (*tropicalis*) to the genus *Chlorotalpa*. Meester (1974) included *stuhlmanni* in *Chrysochloris* based on the morphology of the malleus, an arrangement followed by Bronner (1995b) who, in addition, assigned it to the subgenus *Kilimatalpa* based on significant divergence from *asiatica* in cranial shape. Synonyms: *balsaci*, *fosteri*, *tropicalis*, *vermiculus*. Subspecies: five but of dubious validity. Chromosome number: not known.

Description Small species, resembling *C. asiatica* in general appearance but with a comparatively narrower and longer skull (breadth <65% of GLS compared to >75%) as in *Amblysomus*. Dorsal pelage blackish-brown, dull brown, greyish-brown or fawn, with silvery sheen. Ventral pelage somewhat paler, sometimes with a russet tint. Pelage shows geographic variation in colour (see below). Muzzle and cheeks often with whitish or russet patches that join across upper lip. Claws on forefeet gracile: claw on Digit 3 of forefoot largest (ca. 11 mm long, 3.0–4.2 mm wide at base), claw on Digit 2 shorter (ca. 8 mm long), claw on Digit 1 shortest (ca. half length of Digit 2). Digit 4 vestigial. Skull elongate (breadth 57–65% of GLS) with a narrow palate (26–27% of GLS). Temporal bulla housing enlarged, club-shaped malleus less developed than in *C. asiatica*. Small, tricuspid M³ present, molar talonids well-developed but sometimes reduced to feeble ledges by toothwear. See also family and genus profiles. Extent of sexual dimorphism in body size cannot be evaluated because of small samples available for study.

Geographic Variation The validity and geographic limits of subspecies are uncertain owing to the few specimens available.

C. s. stuhlmanni: Rwenzori Mts along border of Uganda and DR Congo, from Mt Rwenzori southwards to Rutshuru and Rukiga district of Rwanda.

C. s. fosteri: Mt Elgon, Uganda and Cherangani Hills, Kenya. Dorsal pelage dull-brown to grey, not so bright-brown as in *stuhlmanni*; ventral pelage more greyish.

C. s. tropicalis: Uluguru mountains and Rungwe district, Tanzania. Dorsal pelage glossy blackish-brown; ventral pelage slightly paler with a rufous tint in inguinal region.

C. s. vermiculus: Yambuya and Kisangani, N DR Congo. Size smaller, similar to *Calcochloris leucorhinus*, but without white facial markings; dorsal pelage pale brown to fawn; ventral pelage slightly paler. Known only from a preserved skin, and therefore *incertae sedis*. Possibly only a geographic variant of *C. leucorhinus*, which occurs 320 km south-west at Bokongu in C DR Congo.

C. s. balsaci: Mt Oku, Cameroon.

Similar Species

Calcochloris leucorhinus. Skull smaller (GLS: 19.5–23.1 mm); malleus small and unspecialized; bulla not visible externally. Might be sympatric but full extent of distribution not known.

Distribution Endemic to Africa. Eastern Rainforest–Savanna Mosaic (Mt Elgon, Uganda and Cherangani Hills, Kenya), Afromontane–Afroalpine BZ (Uganda, E DR Congo), northern edge of Zambezian Woodland BZ (one locality in N Tanzania), Rainforest



Chrysochloris stuhlmanni

BZ (one locality in E DR Congo) and Northern Rainforest–Savanna Mosaic (one locality in Cameroon; Lamotte & Petter 1981). Distribution disjunct and largely restricted to mountain ranges (except *C. s. vermiculus*).

Habitat Well-drained soils at high altitudes, from 1700 to 3500 m. Widespread in montane grasslands, bamboo thickets and ericaceous vegetation, as well as in *Podocarpus* and *Hagenia*/*Hypericum* woodlands. Prefer light soils with sparse vegetation cover.

Abundance Locally common but no quantitative data. Less common in heavily grazed grasslands above 3000 m; avoids exotic plantations (Duncan & Wrangham 1971).

Adaptations Nocturnal. Individuals make subsurface tunnels about 4 cm below the surface but also, in forests, in leaf litter. Food distribution and soil penetrability are important factors governing dispersion. In swampy areas they make branched, interconnecting tunnels with small (6–8 cm diameter) unlined chambers in thick layers (10–15 cm) of sphagnum moss, seldom penetrating the heavy peaty soils below. In better-drained areas, burrowing activity is concentrated in clumps of vegetation that are connected by unbranched tunnels, and small mounds of soil are formed above ground (Duncan & Wrangham 1971, Jarvis 1974). When alarmed, reported to make a ‘noise similar to that emitted by the puff-adder’ (St Leger 1931), possibly as a threat display.

Foraging and Food Carnivorous and insectivorous. Earthworms and insect (mainly dipteran) larvae form the bulk of the

diet, supplemented with myriapods, molluscs and small crustaceans (presumably isopods). Analyses of stomach contents: 100% contained earthworms, 50% contained insect larvae, 12% contained adult insects (n = 8; Duncan & Wrangham 1971, Jarvis 1974).

Social and Reproductive Behaviour Duncan & Wrangham (1971) reported that burrow systems are used by more than one individual, since two golden-moles were caught in one trap in a tunnel that showed signs of renewed use a week later. These two individuals may, however, have been a mother and her near-adult youngster, or the later capture could reflect colonization of the vacant burrow system by another individual.

Reproduction and Population Structure Parous ♀♀ recorded in Jul, each with one embryo in the left uterine horn (n = 3; Duncan & Wrangham 1971). Gestation period not known. At birth, young are altricial and hairless, and remain with the mother for 2–3 months (Kingdon 1974).

Predators, Parasites and Diseases Predation pressure is low and does not seem to affect distribution. Ectoparasites include two species of fleas: *Xiphiopsylla* sp., which also occurs on the mole-rat *Tachyoryctes splendens*; and a species of *Ctenophthalmus* allied to *C. cophurus*, probably transferred to *C. stuhlmanni* by sympatric burrowing rodents (particularly *Lophuromys flavopunctatus*; Duncan & Wrangham 1971). Heligmosomatine nematodes recorded in alimentary tract (Jarvis 1974).

Conservation IUCN Category: Least Concern.

Measurements

Chrysochloris stuhlmanni

HB (♂♂): 112.8 (106–123) mm, n = 5

HB (♀♀): 106.5 (103–111) mm, n = 4

T: 0 mm

HF (♂♂): 12.6 (10–12) mm, n = 5

HF (♀♀): 11.2 (10–12) mm, n = 4

E: 0 mm

WT (♂): 42 g, n = 1

WT (♀): n. d.

GLS (♂♂): 26.9 (24.8–28.1) mm, n = 7

GLS (♀♀): 25.9 (24.3–28.3) mm, n = 6

GWS (♂♂): 16.2 (14.7–17.2) mm, n = 8

GWS (♀♀): 15.8 (14.3–17.2) mm, n = 6

C–M³ (♂♂): 6.5 (5.8–6.9) mm, n = 7

C–M³ (♀♀): 6.6 (6.0–7.4) mm, n = 6

Museum specimens throughout geographic range

Key References Duncan & Wrangham 1971; Jarvis 1974; Kingdon 1974.

Gary N. Bronner

Chrysochloris visagiei VISAGIE'S GOLDEN-MOLE

Fr. Taupe dorée de Visagie; Ger. Visagies Goldmull

Chrysochloris visagiei Broom, 1950. Ann. Transvaal Mus. 21: 238. Gouna, 86 km east of Calvinia. Northern Cape Province, South Africa.

Taxonomy Simonetta (1968) treated *visagiei* as a subspecies of *C. asiatica*. The shape of the malleus differs from that of *C. asiatica* (Broom 1950), but also varies geographically within *C. asiatica*, so this character cannot be considered diagnostic. The holotype may be merely an aberrant *C. asiatica* (Meester 1974); more specimens are needed to clarify the status of this taxon. Synonyms: none. Chromosome number: not known.

Description Small species known only from the ♀ holotype specimen. Dorsal pelage pale tawny-olive, hairs grey with fawn tips. Underfur slaty-grey. Ventral pelage somewhat paler, greyish, with fewer tawny hairs. Muzzle and upper lip much paler than back. Forefeet as in *C. asiatica*; claw of Digit 3 largest (4.11 mm wide at base), Digit 4 vestigial with a small nail. Skull with well-developed temporal bullae, malleus club-shaped but shorter and broader (length:breadth <2) than in *C. asiatica* (length:breadth >3) (Broom 1950). Small, tricuspid M³ present, molar talonids absent. Skull: see also family and/or genus profiles.

Geographic Variation None recorded.

Similar Species None within the geographic distribution of the species.

Distribution Endemic to Africa. South-West Arid BZ (Karoo). Known only from the type locality.

Habitat Bushmanland Nama-Karoo.

Abundance No information.

Remarks Apparently no other information available.

Conservation IUCN Category: Data Deficient, previously Critically Endangered.

A survey (in 2002) of the type locality yielded no signs of golden-moles, and the habitat (gravel plains) is atypical of chrysochlorids. This raises the possibility that the species is either extinct, or that the original specimen was translocated to the type locality accidentally by humans.

*Chrysochloris visagiei***Measurements***Chrysochloris visagiei*

HB: 106 mm, n = 1

T: 0 mm, n = 1

HF: 12 mm, n = 1

E: n. d.

WT: n. d.

GLS: 22.8 mm, n = 1

GWS: 17.5 mm, n = 1

C-M³: 6.5 mm, n = 1

Holotype ♀

Key Reference Broom 1950.

Gary N. Bronner

GENUS *Chrysochalax***Golden-moles***Chrysochalax* Gill, 1883. Standard Nat. Hist. 5 (Mamm.): 137. Type species: *Chrysochloris trevelyani* Günther, 1875.

The genus *Chrysochalax* contains the two largest species of golden-mole, both endemic to eastern parts of South Africa. The Giant Golden-mole *C. trevelyani* lives in indigenous forests, whereas the Rough-haired Golden-mole *C. villosus* lives in densely vegetated mesic grasslands. Both species forage above ground to a greater

extent than do other golden-moles. The Giant Golden-mole shows some social behaviour (an unusual character in golden-moles).

Apart from their larger size, these species are distinguished by a long, shaggy pelage with very coarse guard hairs. The claws on the forefeet, although obviously larger than in other species, are long

but slender, perhaps reflecting the habit of these golden-moles of constructing only short tunnels and foraging mainly above ground. Skull elongate (breadth: 60–65% of GLS) with a relatively broad palate (30–35% of GLS). The unique feature of the skull is broad plates that develop posteriorly from the zygomatic arches and sweep backwards over the cranium. A sagittal crest for the insertion of strong temporal muscles used in chewing is pronounced, especially in *C. trevelyani* (Figure 11). The malleus is enlarged and pea-shaped, and housed in a large bony bulla (up to 7 mm diameter) that protrudes anteriolaterally at the level of the zygomatic arch to incorporate the glenoid joint, so that the whole side of the skull bulges outwards. This may be an adaptation for surface foraging since increased malleus mass enhances sensitivity to higher frequencies of sound than are normally experienced underground (Mayer *et al.* 1995). Dentition comprises 40 teeth (tricuspid M^3 present), similar in morphology to those of more generalized species (such as *Chrysochloris asiatica*). Larger, lower molars have well-developed talonids. These characters suggest that these are the most primitive of the golden-moles, yet also highly specialized (Roberts 1951). *Chrysoxalax villosus* was long referred to the genus *Bemataiscus*, but differences between these forms do not warrant more than specific distinction (Meester 1974). The two species are distinguished by the colour and texture of the pelage, size and habitat preference.

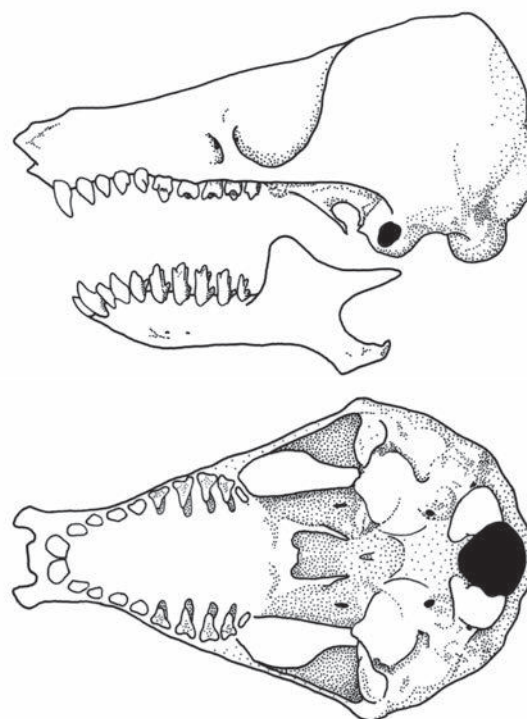


Figure 11. Skull and mandible of *Chrysoxalax trevelyani* (based on Simonetta 1968).

Gary N. Bronner

Chrysoxalax trevelyani GIANT GOLDEN-MOLE

Fr. Taupe dorée géante; Ger. Riesengoldmull

Chrysoxalax trevelyani (Günther, 1875). Proc. Zool. Soc. Lond. 1875: 311.
Pirie Forest, King Williams Town, Eastern Cape Province, South Africa.

Taxonomy Synonyms: none. Chromosome number: $2n = 30$, $FN = 56$ (Bronner 1995a).

Description Originally described in the genus *Chrysochloris*. Very large golden-mole, the largest in the family. Dorsal pelage dark glossy-brown, yellowish-brown or greyish-brown. Ventral pelage similar, but paler. Head slightly darker than back, cheeks with yellowish patches above subdermal eyes. Guard hairs long and coarse, up to 20 mm on back, greyish-yellow at base, dark brown with a yellow tinge at tip. Throat, chest and underparts of forelimbs dull yellow; hairs shorter than on dorsal pelage. Underfur dense, buffy-grey. Claws on forelimbs powerful and pick-like; claw on Digit 3 of forefoot largest (17–19 mm long, 7 mm wide at base), claw on Digit 2 slightly smaller, claw on Digit 1 very small. Digit 4 reduced to a small tubercle with a rounded claw. Skull with broad plates that develop posteriorly from the zygomatic arches and sweep backwards over the cranium; M^3 present (see also family and genus profiles). No apparent sexual size dimorphism, but this may be an artefact of small samples available for study.

Geographic Variation There is considerable inter- and intra-population variation in pelage colour; colour variation within demes is as great as between populations and therefore no subspecies are recognized (Broom 1907a).

Similar Species

Amblysomus hottentotus. Much smaller; finer pelage; malleus bones not enlarged; lacks the broad plates sweeping back from the zygomatic arches.

Distribution Endemic to Africa. Coastal Forest Mosaic and Afromontane–Afroalpine BZs. Recorded in Eastern Cape Province from East London northwards along coast to Port St Johns, and inland to Amatola and Koglogha Mountains near King Williams Town, Stutterheim and Hogsback. May be locally extinct in many places where it occurred formerly.

Habitat Coastal and Afromontane Forests. Sometimes also penetrates into grasslands adjoining forests (Maddock 1986).

Abundance Locally common but with a clumped dispersion. Greatest abundance in forest patches with soft soils, well-developed undergrowth and deep litter layers. Avoids steep slopes and rocky terrain.

Adaptations Giant Golden-moles make numerous short (1–13 m) tunnels amongst roots of trees; entrances are left open and connected by well-defined surface runways (Maddock 1986). Individuals may move up to 130 m along surface runways during a night, but sometimes forage within only a few metres of the burrow

*Chrysospalax trevelyani*

from which they emerged. They readily enter water and swim using forefeet as paddles (Ranger 1927). Activity is mainly at night, from shortly after dusk until dawn, although diurnal activity occurs on cool cloudy days. In captivity, they are mainly nocturnal with short peaks of activity from 16:00h to 20:00h, and again from 23:00h to 01:00h (Maddock & Hickman 1985). Activity reduced during dry winter months (Apr–Aug). Torpor is induced if captive individuals are subjected to low temperatures.

Foraging and Food Forages mainly above ground in leaf litter using small runways that meander off from main tracks linking burrow entrances. Foraging areas marked by characteristic signs of rooting where they stir up soil and leaves in search of prey. Diet comprises earthworms, particularly giant earthworms (*Microchaetes* spp.; Roberts 1951), although in parts of their range where giant earthworms do not occur they feed primarily on oniscomorph millipedes (Duckworth & Hickman 1985).

Social and Reproductive Behaviour These are the only chrysochlorids showing any indication of sociality (Hickman 1990). An unconfirmed report of several adult individuals dug out of the

same nest in Jul suggests that small groups may overwinter together in burrows.

Reproduction and Population Structure A pregnant ♀ with two embryos was reported by Hickman (1990). Bronner (1992) recorded the birth of a single altricial pup in Oct. Postnatal development is slow, suggesting extended periods of parental care. During copulation, ♂ mounts ♀ from the back in a dog-like fashion.

Predators, Parasites and Diseases Feral dogs, associated with rural subsistence communities, are known predators. At Nqadu Forest, four individuals were killed by a pack of dogs during one evening in 1990, suggesting that they are comparatively defenceless against groups of predators. Their tough, loose skins are difficult to puncture with the result that the dogs seldom consume the carcasses.

Conservation IUCN Category: Endangered.

Suitable forest habitats have been fragmented and degraded by poor agricultural practices, bark-stripping of trees for traditional medicines, collection of firewood, burning, and by the development of commercial plantations, urbanization and coastal resorts.

Measurements

Chrysospalax trevelyani

HB (♂ ♂): 222.0 (215–235) mm, n = 7

HB (♀ ♀): 215.8 (208–229) mm, n = 4

T: 0 mm

HF (♂ ♂): 24.3 (20–28) mm, n = 8

HF (♀ ♀): 23.4 (21–27) mm, n = 5

E: 0 mm

WT (♂): 470 g, n = 1

WT (♀ ♀): 410, 500 g, n = 2

GLS (♂ ♂): 41.7 (41.0–42.4) mm, n = 5

GLS (♀ ♀): 41.6 (39.9–43.2) mm, n = 7

GWS (♂ ♂): 26.2 (25.7–27.4) mm, n = 5

GWS (♀ ♀): 25.9 (24.2–27.4) mm, n = 6

C–M³ (♂ ♂): 9.7 (9.4–9.9) mm, n = 5

C–M³ (♀ ♀): 9.8 (9.7–10.2) mm, n = 4

Museum specimens throughout geographic range

Key References Hickman 1990; Maddock 1986; Roberts 1951.

Gary N. Bronner

Chrysospalax villosus ROUGH-HAIRED GOLDEN-MOLE

Fr. Taupe dorée à poil dur; Ger. Rauhaar Goldmull

Chrysospalax villosus (A. Smith, 1833). S. Afr. Quart. J. 2: 81. Towards Natal (near Durban), KwaZulu–Natal, South Africa.

Taxonomy Originally described in the genus *Chrysochloris*. Synonyms: *dobsoni*, *leschae*, *rufopallidus*, *rufus*, *transvaalensis*. Subspecies: six, of uncertain validity. Chromosome number: not known.

Description Large golden-mole with extremely coarse pelage. Dorsal pelage yellowish-brown or greyish-brown to dark slaty-grey

(see below for geographic variation). Ventral pelage paler, especially on abdomen. Throat dull yellowish-white. Head slightly paler than back, face and muzzle buffy-grey, often with a dark patch around the horny nose pad. Upper lips and chin yellowish-white suffused with brown. Guard hairs glossy and sparsely distributed, 18–21 mm long on back; greyish-brown at base, with broad medial band of

yellowish-brown or reddish-brown, and narrow dark-brown tip. Underfur slaty-grey, dense and woolly, about two-thirds length of guard hairs. Claws on forelimbs weaker than in *C. trevelyani*; claw on Digit 3 long (15–17 mm long and 4–6 mm at base), claw on Digit 2 slightly smaller, claw on Digit 1 about one-third the length of Digit 2. Digit 4 reduced to small tubercle with short claw (ca. 1.5 mm long). No apparent sexual dimorphism but this may be an artefact of small samples available for study. Skull with broad plates that develop posteriorly from the zygomatic arches and sweep backwards over the cranium; malleus enlarged; bulla large and protruding laterally; M^3 present (see also family and genus profiles).

Geographic Variation Meester (1974) listed six subspecies distinguished mainly by subtle differences in pelage colour, but the validity of these subspecies is uncertain.

- C. v. villosus*: 'Near Durban', KwaZulu–Natal. Pelage yellowish-brown faintly brindled with dark brown, flanks and abdomen greyish-brown.
- C. v. dobsoni*: Pietermaritzburg and KwaZulu–Natal midlands. Probably a synonym of *villosus*; pelage yellowish-brown, brown or brownish-grey.
- C. v. leschae*: St Cuthberts, Tsolo, to Tabase, Eastern Cape Province. Dorsal pelage uniformly dark brown; ventral pelage slightly paler.
- C. v. rufopallidus*: Wakkerstroom northwards to Belfast, Mpumalanga Province. Pelage pale yellowish-red; hairs on back comparatively short, 14–16 mm long.
- C. v. rufus*: Spitzkop, Sabie district, Mpumalanga Province. Pelage rich reddish-brown with dark grey underfur; smaller than *C. v. transvaalensis*, with shorter claws on forefeet (Meester 1953a).
- C. v. transvaalensis*: Pretoria and Witwatersrand. Pelage pale reddish-brown. (Includes *pratensis*.)

Similar Species

Amblysomus hottentotus, *Amblysomus septentrionalis* and *Amblysomus robustus*. All to some extent smaller in HB (HB lengths: 104–145 mm); skulls smaller (GLS: 24.6–32.0 mm); pelage finer; malleus not enlarged; bulla not evident externally; zygomatic arches without broad plates sweeping backwards; M^3 usually absent.

Distribution Endemic to Africa. Highveld BZ and parts of Afromontane–Afroalpine BZ. Distribution disjunct, recorded only from scattered localities in Eastern Cape, KwaZulu–Natal, Gauteng and Mpumalanga Provinces, South Africa.

Habitat Sandy soils in grasslands, meadows and along edges of marshes. Occurs in Moist Upland Grassland, Moist Cool Highveld Grassland, Rocky Highveld Grassland and North-eastern Mountain Grassland. Recorded from gardens and parklands; also found in dense stands of kikuyu grass *Pennisetum clandestinum* adjoining natural grasslands.

Abundance Extremely rare and secretive. Difficult to detect owing to predilection for dense grasslands with abundant cover.



Chrysospalax villosus

Adaptations These golden-moles construct short burrows, the entrances to which are left open with loose soil piled up at back and sides (like the holes of crabs). Well-defined surface runways lead to foraging areas, which show the characteristic signs of rooting where soil is turned up by the horny nose. Short (30–70 cm) burrows with two entrances are made periodically along surface tracks, where the moles 'dip' into the ground; these probably serve as bolt-holes if alarmed. They have an extraordinary sense of direction, and dash unerringly and rapidly into the nearest burrow entrance at the slightest sign of danger. Sometimes shams death when handled.

Foraging and Food Insectivorous. Roberts (1951) stated that these golden-moles forage above ground at night, and only after rains. Foraging in underground burrows seems probable given the unpredictability of rains and periodic droughts.

Social and Reproductive Behaviour No information.

Reproduction and Population Structure No information, except that ♀♀ give birth to two young.

Predators, Parasites and Diseases No information on predators. Lawrence (1944) recorded a new species of ectoparasitic mite (*Schizoptes*) on this species.

Conservation IUCN Category: Vulnerable.

Only three specimens were collected during the 23-year period 1980–2003. The widespread practice of allowing cattle to graze in marshes and dense grasslands near water during dry winter months leads to trampling and a loss of cover, and this undoubtedly impacts severely on this species. Some areas in which they formerly occurred (eg. Pretoria West) have been completely transformed by urbanization.

Measurements*Chrysopalax villosus*

HB (♂ ♂): 163.0 (148–175) mm, n = 4

HB (♀ ♀): 142.8 (127–160) mm, n = 6

T: 0 mm

HF (♂ ♂): 14.3 (14–17) mm, n = 4

HF (♀ ♀): 17.1 (13–20) mm, n = 6

E: 0 mm

WT (♂ ♂): 137.7 (108–160) g, n = 3

WT (♀ ♀): 93, 105 g, n = 2

GLS (♂ ♂): 33.9, 34.9 mm, n = 2

GLS (♀ ♀): 33.8 (33.4–34.6) mm, n = 5

GWS (♂ ♂): 20.5 (19.6–22.2) mm, n = 3

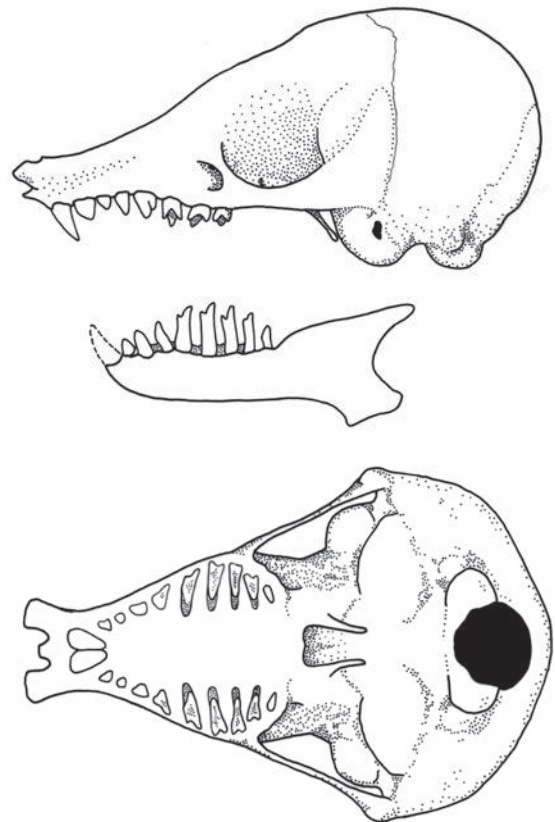
GWS (♀ ♀): 21.9 (19.6–23.1) mm, n = 5

C–M³ (♂ ♂): 7.4 (7.1–7.7) mm, n = 4C–M³ (♀ ♀): 7.2 (6.4–8.1) mm, n = 5

Museum specimens throughout geographic range

Key References Meester 1953; Roberts 1951.**Gary N. Bronner****GENUS *Cryptochloris*****Golden-moles***Cryptochloris* Shortridge and Carter, 1938. Ann. S. Afr. Mus. 32: 284. Type species: *Cryptochloris zyli* Shortridge and Carter, 1938.

The genus contains two very small species, *C. zyli* and *C. wintoni*, which differ mainly in colour of the pelage, and are known only from only a few specimens collected at the type localities on the Namaqualand coastal plain in South Africa. Like Grant's Golden-mole (genus *Eremitalpa*), the body is lozenge-shaped, in contrast to the fusiform shape of other genera. The most distinctive external feature is the possession of a large digging pad (possibly supported by a radial sesamoid bone) at the base of Digit 1 of the forefoot, so that the forefoot is much broader than in other species. The forefeet bear long slender claws; claw on Digit 3 long (10–11 mm long, 4.0–4.5 mm wide at base), claws on Digit 1 and 2 only slightly shorter than Digit 3, claw on Digit 4, while moderately developed, is more gracile than in *Eremitalpa*. The skull is short and broad (breadth 70–76% of GLS) with a very wide palate (35–37% of GLS), but slightly narrower than in *Eremitalpa*. Zygomatic arches without broad plates sweeping backwards. The olfactory region is conspicuously inflated and much wider than the anterior part of the cranium (Figure 12). The malleus is club-shaped and enlarged, although not to the extent seen in *Chrysochloris*, with the result that only small subtemporal bullae are present. Tricuspid M³ present; lower molars lack talonids. These characters suggest that *Cryptochloris* is intermediate between *Eremitalpa* and *Chrysochloris* (Shortridge 1942). Simonetta (1968) regarded *Cryptochloris* as a synonym of *Chrysochloris*. The two species are distinguished by pelage colour, morphology of forelimbs and shape of the malleus.

**Gary N. Bronner** Figure 12. Skull and mandible of *Cryptochloris zyli* (based on Simonetta 1968).***Cryptochloris wintoni* DE WINTON'S GOLDEN-MOLE**

Fr. Taupe dorée de De Winton; Ger. De Wintons Goldmull

Cryptochloris wintoni (Broom, 1907). Ann. Mag. Nat. Hist., ser. 7, 19: 264.

Port Nolloth, Little Namaqualand, Northern Cape Province, South Africa.

Taxonomy Originally described in the genus *Chrysochloris*. Some authors (e.g. Simonetta 1968) regarded this monotypic species and *C. wintoni* as only subspecifically distinct, but these taxa differ

consistently in pelage colour and malleus morphology, indicating that they are not conspecific (Meester 1974). Synonyms: none. Chromosome number: not known.

Description Very small species resembling *Eremitalpa granti* in size and colour. Dorsal pelage pale slaty-grey with yellowish tinge becoming more intense on forehead, cheeks and lips; hairs whitish, grey at base, broad fawn at tips. Ventral surface slightly paler than dorsal pelage, hairs whitish at tips. Body foreshortened and lozenge-shaped. Nosepad 4 mm long, ca. 8 mm wide, corners rounded, anterior digging portion more prominent than in *C. asiatica*. Claw on Digit 3 largest (10.3–10.5 mm long and 4 mm wide at base), claw on Digit 2 shorter (5.0–7.0 mm), claw on Digit 1 also shorter (4.5–4.8 mm). Claw on Digit 4 small (1.5 mm long). Skull: malleus moderately enlarged, club-shaped with head more bulbous than in *C. zyli* (Broom 1907a, b, Roberts 1951); bulla small; M^3 present (see also family and genus profiles). Small sample sizes preclude any evaluation of sexual dimorphism.

Geographic Variation None recorded.

Similar Species

Eremitalpa granti. Smaller (HB: 76–86 mm, GLS: 18.6–20.4 mm); claw on Digit 4 of forefoot longer (3–4 mm); olfactory region of skull not markedly inflated.

Chrysochloris asiatica. Larger (HB: 94–115 mm); claws on Digits 1, 2 and 4 markedly smaller than on Digit 3; palate relatively narrower (30–32% of GLS); malleus more enlarged so that the temporal bulla is more pronounced.

Distribution Endemic to Africa. South-West Arid BZ (Namib Desert). Recorded only from the type locality at Port Nolloth, Northern Cape Province, South Africa.

Habitat Coastal dunes and adjacent sandy areas in Strandveld Succulent Karoo.

Abundance Extremely rare; known from only three specimens and not captured for over 50 years.

Remarks Apparently no other information available.

Conservation IUCN Category: Critically Endangered.



Known only from the type locality, situated in a region that is being markedly transformed by alluvial diamond mining.

Measurements

Cryptochloris wintoni

HB: 86, 92 mm, n = 2

T: 0 mm

HF: 10.3, 10.5 mm, n = 2

E: 0 mm

WT: n. d.

GLS: 21.3, 22.0 mm, n = 2

GWS: 15.5, 16.2 mm, n = 2

C– M^3 : n. d.

Type locality (Broom 1907a, Roberts 1951)

Key References Broom 1907a, b.

Gary N. Bronner

Cryptochloris zyli VAN ZYL'S GOLDEN-MOLE

Fr. Taupe dorée de Van Zyl; Ger. Van Zyls Goldmull

Cryptochloris zyli Shortridge and Carter, 1938. Ann. S. Afr. Mus. 32: 284.
Compagnies Drift, Little Namaqualand, Western Cape Province, South Africa.

Taxonomy Some authors (e.g. Simonetta 1968) regarded this monotypic species as only subspecifically distinct from *C. wintoni*. However, these taxa differ consistently in pelage colour and malleus morphology, indicating that they are not conspecific (Meester 1974). Synonyms: none. Chromosome number: not known.

Description Very small species with violet metallic sheen restricted to coarser guard hairs, giving the pelage a spangly

appearance. Dorsal pelage dense and short, dark lead-grey; underfur smoky-grey. Ventral pelage similar to dorsal pelage, but drab. Face with well-defined whitish markings (admixed with slightly darker hairs) extending posteriorly to above the subdermal eyes. Claw on Digit 3 long (10.0 mm long, 4 mm wide at base), claws on Digits 1 and 2 of forefoot subequal to Digit 3 so that these three claws meet almost in a point. Claw on Digit 4 small (2.0 mm long) and narrow. Skull: malleus club-shaped but smaller

and less bulbous than in *C. wintoni* and *C. asiatica*; M^3 present (see also family and genus profiles). Small sample sizes preclude any evaluation of sexual dimorphism.

Geographic Variation None recorded.

Similar Species

Eremitalpa granti. Dorsal pelage tawny-olive to greyish-yellow, finer in texture. Digit 4 of forefoot with a broad scraper-like claw, 3–4 mm long and 2–3 mm wide at base.

Chrysochloris asiatica. Larger (HB: 94–115 mm); claws on Digits 1, 2 and 4 of forefoot markedly smaller than that on Digit 3; malleus more enlarged so that the temporal bulla is pronounced.

Distribution Endemic to Africa. South-West Arid BZ (Karoo). Recorded only from the type locality near Lamberts Bay, South Africa. Possibly ranges northwards along coast to the Olifants R.

Habitat Coastal dune belt and adjacent sandy areas in Strandveld Succulent Karoo.

Abundance Extremely rare; known from only three specimens (Helgen & Wilson 2001).

Remarks When handled, individuals may emit high-pitched squeaks or sham death (Shortridge 1942).

Predators, Parasites and Diseases No information.

Conservation IUCN Category: Endangered.

Known only from the type locality (situated in a region that is being markedly transformed by alluvial diamond mining) and one other locality.



Cryptochloris zyli

Measurements

Cryptochloris zyli

HB: 82 mm, n = 1

T: 0 mm

HF: 12 mm, n = 1

E: 0 mm

WT: n. d.

GLS: 21.7, 22.2 mm, n = 2

GWS: 15.0, 15.2 mm, n = 2

C– M^3 : 8.0 mm, n = 1

South Africa (Shortridge 1942, Helgen & Wilson 2001)

Key References Broom 1946; Helgen & Wilson 2001; Shortridge 1942.

Gary N. Bronner

GENUS *Eremitalpa* Grant's Golden-mole

Eremitalpa Roberts, 1924. Ann. Transvaal Mus. 10: 63. Type species: *Chrysochloris granti* Broom, 1907.

A monotypic genus endemic to the South-West Arid BZ. Grant's Golden-mole *E. granti* is the smallest of the golden-moles, and inhabits loose sands along the west coast of South Africa and Namibia. Highly specialized for life in the Namib Desert, hence its alternative vernacular name, the Namib Golden-mole.

The body is foreshortened and lozenge-shaped, the claws of the forefeet are long and slender as in *Cryptochloris*. The skull is broader than in any other species (breadth >85% of GLS) with a very wide palate (35–38% of GLS) (Figure 13). Snout short, lacking the marked inflation of the olfactory region seen in *Cryptochloris*. Zygomatic arches

without broad plates sweeping backwards. Malleus enlarged and pea-shaped, housed in enlarged epitympanic recess that inflates the internal laminae of the squamosal and temporal bones, but not conspicuous externally. Minute tricuspid M^3 present, but incidence varies among jaw quadrants. Molar talonids absent. Similarities in middle ear structure with *Chrysospalax* probably arose independently in response to a similar mode of foraging predominantly above ground (Mayer *et al.* 1995). Other characters are given in the species profile.

Gary N. Bronner

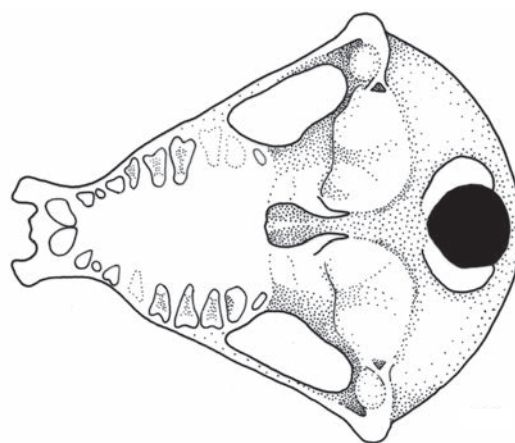
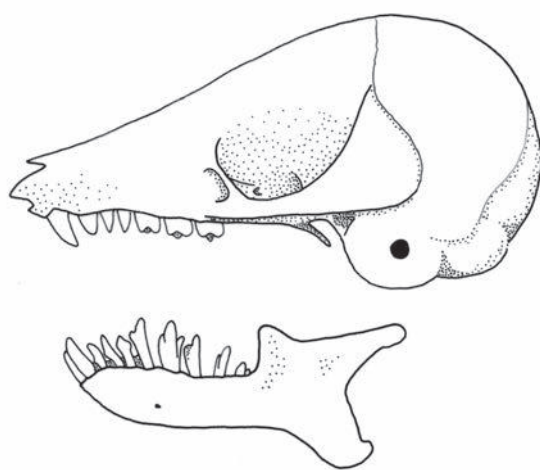


Figure 13. Skull and mandible of *Eremitalpa granti* (BMNH 75.2006).

Eremitalpa granti GRANT'S GOLDEN-MOLE (NAMIB GOLDEN-MOLE)

Fr. Taupe dorée de Grant; Ger. Grants Goldmull

Eremitalpa granti (Broom, 1907). Ann. Mag. Nat. Hist., ser. 7, 19: 265. Garies, Little Namaqualand, Northern Cape Province, South Africa.

Taxonomy Originally described in the genus *Chrysochloris*. Synonyms: *cana*, *namibensis*. Subspecies: two. Chromosome number: not known.

Description Very small golden-mole with a lozenge-shaped body. Pelage silky, 7–12 mm on back, up to 20 mm on flanks. Dorsal pelage tawny-olive to greyish-yellow, flanks paler with intense yellowish tinge; guard hairs grey at base, upper third pale brownish-yellow, darker brown at tip. Ventral pelage greyish-brown to fawn. Forehead and cheeks pale yellow, sometimes with pale pinkish-buff around nosepad. Claw on Digit 3 of forefoot largest (9–12 mm long, 3.7–4.9 mm wide at base), claw on Digit 1 flattened and nearly as long (4–5 mm) as on Digit 2 (5–8 mm) but noticeably narrower. Digit 4 vestigial but with a broad scraper-like claw (3–4 mm long, 2–3 mm wide at base). Hindfoot with prominent thickened pad. Skull: relatively broad (breadth >85% of GLS); malleus pea-shaped, enlarged; bulla not visible externally; M^3 present but minute (see also family and genus profiles).

Geographic Variation

E. g. granti (includes *E. g. cana*): St Helena Bay along coast to Port Nolloth, and inland to Garies. Larger; pelage less yellowish, hairs longer (8–13 mm at mid-back); skull significantly longer (18.6–20.4 mm) and narrower than in *E. g. namibensis* (breadth 79.9–88.3% of GLS).

E. g. namibensis: Orange R. northwards along coast to Walvis Bay, and inland as far as ProNamib. Smaller; pelage with more intense yellowish tinge, hairs shorter (6.5–7 mm at mid-back); skull shorter (16.8–19.4 mm) and relatively broader than in *E. g. granti* (breadth: 85.3–95.7% of GLS).

Similar Species

Cryptochloris zyli. Dorsal pelage lead-grey with violet metallic sheen, coarser in texture. Claw on Digit 4 of forefoot shorter (2.0 mm) and narrow.

Cryptochloris wintoni. Larger (HB: 86–92 mm, GLS: 21.3–22.0 mm, $n = 2$); claw on Digit 4 of forefoot shorter (1.5 mm); olfactory region of skull markedly inflated.

Chrysochloris asiatica. Much larger (HB: 94–115 mm, GLS: 21.1–25.4 mm); body fusiform; claws on Digits 1, 2 and 4 of forefoot markedly shorter than that on Digit 3; skull relatively less broad (breadth 70–78% of GLS); malleus club-shaped, more enlarged; bulla pronounced and visible externally.

Distribution Endemic to Africa. South-West Arid BZ (Namib Desert and Karoo). Confined to the west coast of southern Africa, from St Helena Bay (Western Cape Province, South Africa) northwards to Walvis Bay (Namibia).



Eremitalpa granti

Habitat Strandveld Succulent Karoo and Namib Desert. Prefers soft, shifting sands of dunes but also present in inter-dune valleys with quite dense vegetation providing sand is not too consolidated.

Abundance Densities are low owing to the arid, energy-sparse conditions of the environment.

Adaptations The broad, hollowed-out claws are adapted for burrowing in loose sand, and the thickened pads on the hindfeet facilitate walking on the sand surface. Primarily nocturnal with occasional bouts of afternoon activity, especially in winter. Activity patterns vary adaptively in relation to environmental conditions, particularly temperature and prey availability. Nocturnal activity related primarily to maintenance of body temperature and water balance rather than predator avoidance (Fielden *et al.* 1992). Diurnal activity involves subsurface sand-swimming, which leaves U-shaped furrows or raised ridges if sand is moist. During the heat of the day, rests under the roots of bushes or dune grasses at depths of up to 50 cm underground, and becomes active in the early afternoon during cool winter days. Surface locomotion at night reduces energetic costs of foraging in an energy-sparse environment, and appears to be more common in sparsely vegetated areas. Some burrows are re-used, presumably those leading to nests where young are raised, or those leading to foraging areas.

The senses are poorly developed, except for touch and sensitivity to vibrations, the latter due to the extraordinary development of the middle ear (Mason & Narins 2001). Energetic requirements are reduced, when necessary, by inactivity, adaptive hypothermia, extreme thermolability and intrinsic metabolic suppression. Assimilation efficiency is high (79%) as in other insectivorous mammals (Seymour *et al.* 1998). Maintenance of water balance is facilitated by a reduction in body temperature and metabolic rate, behaviour (nocturnal activity and surface foraging) and efficient renal function (Fielden *et al.* 1990a).

Foraging and Food Insectivorous and carnivorous. The length of foraging pathways, and foraging tactics, depend on prey dispersion. For example, Grant's Golden-moles may forage over distances of 5–695 m/night (Fielden *et al.* 1990b) and as far as 5800 m (Holm 1969). Average foraging distance is 1412 m (Seymour *et al.* 1998). Surface activity is interspersed with head dips into sand every 3–5 m, presumably to sense seismic cues (Narins *et al.* 1998) or vibrations emitted by prey. Detection of prey is effective over only short distances; search pattern is non-random and is effective at locating localized patches where prey is abundant. Sand-swimming predominates once patches of prey are detected, and when searching beneath the roots of plants. The subspecies *E. g. namibensis* is a highly selective feeder specializing on termites (*Psammotermes allocerus*). Analysis of stomach contents ($n = 16$): 89% contained termites, 37% beetle larvae, 30% adult beetles and 26% contained root material. Termites comprise 95% (by weight) of stomach contents despite the

low biomass of termites relative to other potential invertebrate prey, and their clumped dispersion in subterranean nests under clumps of dune grasses. Ingestion of roots may not be entirely incidental (Fielden *et al.* 1990b). Web-footed geckos (*Palmatogecko rangei*), legless lizards and sand-burrowing skinks may also be eaten (Roberts 1951).

Social and Reproductive Behaviour Adults solitary, but tracks of several individuals have been found in the same area on the same night suggesting that a certain amount of home-range overlap is tolerated. Unlike most other golden-moles, individuals housed together do not fight or display signs of aggression. Whether this is indicative of greater sociality than in other chrysochlorids, or simply an artefact of captivity, is uncertain.

Reproduction and Population Structure Pregnancies recorded in Oct and Nov. Litter-size: 1–2. Placentation and early embryology is typical of eutherian mammals but with some primitive features (Hickman 1990).

Predators, Parasites and Diseases Nocturnal predators include Barn Owls *Tyto alba* and Spotted Eagle-owls *Bubo africanus* and small terrestrial carnivores. Black-backed Jackals *Canis mesomelas* and Striped Polecats *Ictonyx striatus* (and possibly also genets *Genetta genetta*) follow furrows and ridges and then dig for the golden-moles. Diurnal predators include Crows *Corvus alba* and Pale Chanting Goshawks *Melierax canorus* (Fielden *et al.* 1992). Acanthocephalan cystacanths (Origacanthorhynchidae) recorded in the peritoneal cavity (Hickman 1990).

Conservation IUCN Category: Least Concern, previously Vulnerable.

The coastal sands inhabited by *E. g. granti* are mined extensively for alluvial diamonds.

Measurements

Eremitalpa granti granti

HB: 81.5 (76–86) mm, $n = 17$

T: 0 mm

HF: 10.5 (9–12) mm, $n = 7$

E: 0 mm

WT: 23 (15–30) g, $n = 17$

GLS: 19.5 (18.6–20.4) mm, $n = 46$

GWS: 16.6 (15.5–18.2) mm, $n = 46$

C–M³: 5.5 (5.2–5.7) mm, $n = 5$

Measurements: Port Nolloth, South Africa (Meester 1964)

Key References Fielden *et al.* 1990b, 1992; Narins *et al.* 1998; Seymour *et al.* 1998.

Gary N. Bronner

GENUS *Neamblysomus*

Golden-moles

Neamblysomus Roberts, 1924. Ann. Transvaal Mus. 10: 64. Type species: *Chrysochloris gunningi* Broom, 1908.

This genus contains two species endemic to South Africa. Gunning's Golden-mole *N. gunningi* is found in montane forests of the Drakensberg range, and Juliana's Golden-mole *N. julianae* lives in bushveld habitats of northern South Africa. Body shape fusiform. Claws on forefoot long and slender. Skull elongate (breadth 60–68% of GLS) with narrow palate (<30% of GLS). Zygomatic arches without broad plates sweeping backwards. There is a small, unspecialized malleus bone in the middle ear (so no temporal or lateral bullae is visible externally) as in *Amblysomus* spp. (Figure 14). M^3 present or absent. Lower molars

lack well-developed talonids, but a lower tricuspid or peg-like M_3 is present, although variable amongst jaw quadrants (*N. gunningi*) or populations (*N. julianae*). Previous authors synonymized *Neamblysomus* under *Amblysomus* (see Meester 1974). Subtle cranial and dental divergence between these genera has, however, been accompanied by karyotypic differentiation (Bronner 1995b). The two species can be distinguished by size, pelage colouration and skull width.

Gary N. Bronner

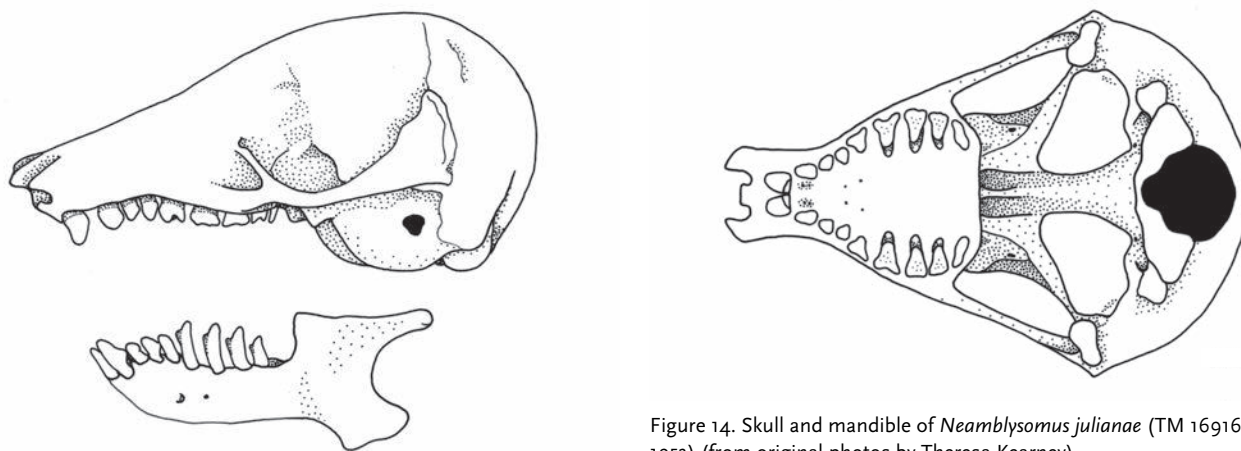


Figure 14. Skull and mandible of *Neamblysomus julianae* (TM 16916 and TM 1953) (from original photos by Theresa Kearney).

Neamblysomus gunningi GUNNING'S GOLDEN-MOLE

Fr. Taupe dorée de Gunning; Ger. Gunnings Goldmull

Neamblysomus gunningi (Broom, 1908). Ann. Transvaal Mus. 1: 14. Woodbush Hill, Soutpansberg district, Limpopo Province, South Africa.

Taxonomy Originally described in the genus *Chrysochloris*. Assigned to *Neamblysomus* by Roberts (1924), Allen (1939), Roberts (1951) and Bronner (1995b) although some authorities, including Ellerman *et al.* (1953) and Meester *et al.* (1986), placed it in *Amblysomus*. Synonyms: none. Chromosome number: $2n = 30$, $FN = 56$ (Bronner 1995a).

Description Medium-sized species, similar in build and appearance to *A. hottentotus*, but with more slender foreclaws. Dorsal pelage dark reddish-brown. Ventral pelage fawn, throat and cheeks yellowish-brown. Claw on Digit 3 of forefoot largest (12.5–14.0 mm long, 4.3–4.9 mm wide at base), claw on Digit 2 much shorter (6.0–7.5 mm), claw on Digit 1 smaller still and narrow. Digit 4 reduced to a small tubercle with a knob-like claw. Skull elongate (breadth 60–63% of GLS) with narrow palate (28–30% of GLS). Molars lack well-developed talonids except in some young individuals. M^3 present variably, with a triconid appearance (similar to other molars) in younger individuals, reduced and peg-like in appearance with increasing toothwear. See also family and genus profiles. Males slightly larger on average than ♀♀, but sexes do not differ markedly in cranial size (Bronner 1995b).

Geographic Variation None recorded.

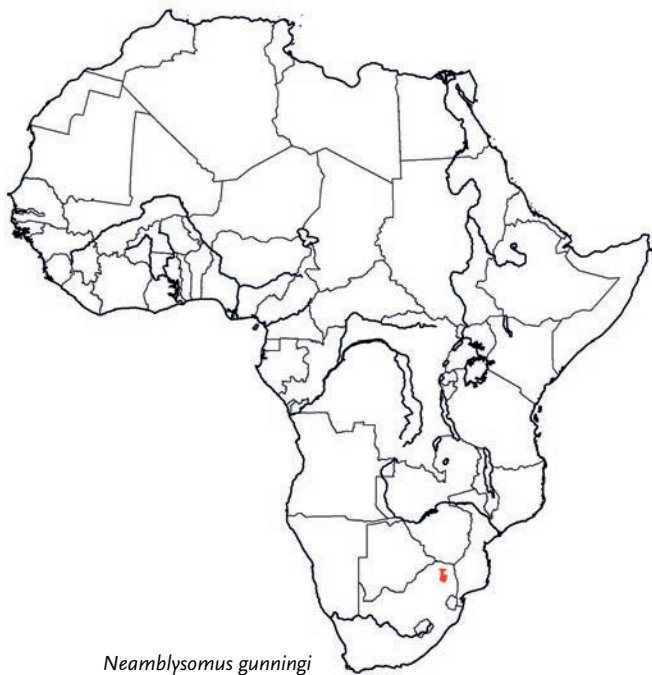
Similar Species

A. septentrionalis and *A. hottentotus*. More robust claws; molar talonids well developed; M^3 usually absent; subtle chromosomal differences.

N. julianae. Smaller (HB: 92–111 mm, GLS: 21.8–23.6 mm); skull often narrower (GWS: 14.7–16.7 mm), breadth 67–70% of GLS; lighter (WT: 21–35 g); pelage paler.

Distribution Endemic to Africa. Extreme south of the Zambezi Woodland BZ. Recorded only from the far northern Drakensberg escarpment, between Haenertsburg, New Agatha and Tzaneen, Limpopo Province, South Africa.

Habitat Afromontane forest and adjacent grasslands in North-Eastern Mountain Grassland. Also occurs in cultivated lands and young pine plantations, where it coexists with Hottentot Mole-rats *Cryptomys hottentotus*.

*Neamblysomus gunningi*

Abundance Locally common; most numerous in moist soils near water-courses and ponds.

Adaptations Burrow systems comprise deep tunnels (15–30 cm) and shallow subsurface tunnels used for foraging at night. Entrances to deep tunnels are marked by mounds of soil. Individuals enter torpor during the day. Particularly active after rains.

Foraging and Food Carnivorous. Forage for invertebrates in subsurface tunnels, and sometimes emerge onto the surface briefly to stir up leaf litter in search of prey. Contents of three stomachs contained only the remains of earthworms. Captive individuals readily eat mealworms (tenebrionid larvae), crickets and baby mice.

Social and Reproductive Behaviour Adults solitary.

Reproduction and Population Structure Pregnancies recorded in Feb, Apr and May suggesting that breeding occurs primarily during the wet summer season.

Predators, Parasites and Diseases No information.

Conservation IUCN Category: Endangered.

The distribution of populations is highly localized and preferred habitats are threatened by commercial forestry operations. In the former Transvaal Province, this species was given the highest regional priority score for mammals (Freitag & van Jaarsveld 1997).

Measurements

Neamblysomus gunningi

HB (♂ ♂): 125.4 (121–132) mm, n = 9

HB (♀ ♀): 122.4 (111–128) mm, n = 8

T: 0 mm

HF (♂ ♂): 15.3 (14–18) mm, n = 9

HF (♀ ♀): 14.0 (13–17) mm, n = 8

E: 0 mm

WT (♂ ♂): 62.8 (56–70) g, n = 6

WT (♀ ♀): 51.0 (39–56) g, n = 4

GLS (♂ ♂): 28.4 (27.1–29.3) mm, n = 11

GLS (♀ ♀): 27.5 (27.0–27.8) mm, n = 6

GWS (♂ ♂): 17.3 (16.1–18.2) mm, n = 11

GWS (♀ ♀): 16.6 (15.9–16.9) mm, n = 6

C–M² (♂ ♂): 7.1 (6.7–7.3) mm, n = 10

C–M² (♀ ♀): 7.0 (6.8–7.2) mm, n = 7

Throughout geographic range

Key References Broom 1908; Freitag & van Jaarsveld 1997.

Gary N. Bronner

Neamblysomus julianae JULIANA'S GOLDEN-MOLE

Fr. Taupe dorée de Juliana; Ger. Julianas Goldmull

Neamblysomus julianae (Meester, 1972). Ann. Transvaal Mus. 28: 35. The Willows, Pretoria, Gauteng Province, South Africa.

Taxonomy Originally described in the genus *Amblysomus* and retained there by Meester *et al.* (1986) but assigned to *Neamblysomus* by Bronner & Jenkins (2005). Synonyms: none. Chromosome number: 2n = 30, FN = 56 (Bronner 1995a).

Description Small species with a gracile build and very slender claws on the forefeet. Dorsal pelage cinnamon-brown to reddish-brown, slightly darker along middle of back; flanks fawn. Ventral pelage fawn to dull reddish-brown. Guard hairs off-white or yellowish at base, slaty-grey medially, reddish-brown or fawn at tip. Muzzle, cheeks and throat speckled with uniformly off-white hairs. Whitish facial patches sometimes present near ocular region. Claw on Digit 3 of forefoot largest (8.5–10.0 mm long, 3.6–4.3 mm wide at base), claw on Digit 2 slightly shorter (5.8–6.7 mm), claw of Digit 1 much shorter barely reaching the insertion of the second claw. Digit 4 vestigial with a knob-

like claw. Skull comparatively short with very wide braincase (breadth 67–70% of GLS) and a relatively wide palate (30–32% of GLS). Molar talonids either absent or only weakly developed. M³ usually absent. M₃ present variably, smaller than other molars with a peg-like appearance. Skull: see also family and/or genus profiles. Males slightly heavier than ♀ ♀, and slightly (but significantly) larger in six cranial measurements. Sexual size dimorphism thus does not seem to be pronounced, but this may be an artefact of small sample sizes.

Geographic Variation Consistent colour and dental differences exist between populations from geographical extremes of the geographic range. Individuals from two western populations (Pretoria and Nylsvley), located ca. 125 km apart in central South Africa, have a pale cinnamon-brown dorsal pelage and fawn-coloured ventral pelage, and lack lower M₃. Specimens from

Kruger N. P., located ca. 400 km further east, have a dark reddish-brown dorsal pelage and dull reddish-brown ventral pelage, and have minute M_3 . Sample sizes are too small for a thorough assessment of intra-specific variation.

Similar Species

N. gunningi. Larger (HB: 111–132 mm, GLS: 27.0–29.3 mm); skull often broader (GWS: 15.9–18.2 mm), breadth 60–63% of GLS; heavier (WT: 39–70 g); pelage darker.

Amblysomus hottentotus, *A. septentrionalis* and *A. robustus*. HB usually larger; skulls larger (GLS: 24.6–32.0 mm); pelage redder; subtle chromosomal differences (Bronner 1995a).

Distribution Endemic to Africa. Extreme south of the Zambezian Woodland BZ. Recorded from three isolated localities in South Africa: The Willows (type locality), Shere and Tierpoort in Pretoria, Gauteng Province; Nylsvley Provincial Nature Reserve in Limpopo Province; and Numbi Gate, Pretoriusskop and Matjuluwana districts of Kruger N. P., Mpumalanga Province. Skulls from owl pellets at Witkoppen Cave, ca. 25 km east of Nylsvley Nature Reserve, clearly represent this species, suggesting that it may occur more widely throughout the sandy Sprinkbok Flats. A specimen of this species caught in March 2003 at Malelane in Mpumalanga indicates that it may also be more extensive in the lowveld than previously thought.

Habitat Confined to sandy soils, often pockets of weathered sandstone associated with rocky ridges. The population on Nyl flood-plain occurs in Clay Thorn Bushveld and the population at Pretoria in Rocky Highveld Grassland; in Kruger N. P. occurs in Sour Lowveld Bushveld. Common in well-irrigated gardens. Absent from grasslands on the heavier soils of the Mpumalanga escarpment where the larger-sized *A. septentrionalis* and *A. robustus* occur.

Abundance Locally common, but no quantitative data.

Adaptations The delicate foreclaws and gracile build limit these golden-moles to light, sandy soils. Their small size allows them to burrow through narrow spaces between underground rocks. They enter daily torpor from shortly after dawn until late afternoon. Surface activity increases dramatically after rains. They emit high-pitched squeaks when agitated or handled.

Foraging and Food Forages in shallow subsurface tunnels for invertebrate prey during late afternoon and night. Subsurface foraging activity declines markedly during the dry winter months (May–Sep). However, captive individuals remain active on a daily basis suggesting that the reduction in subsurface activity is the result of foraging being restricted to deeper tunnels, rather than prolonged torpor. No information exists on diets of free-ranging individuals.

Social and Reproductive Behaviour Adults solitary. Fight viciously when confined together, regardless of sex.

Reproduction and Population Structure Breeding individuals have been found in Jul, Aug and Nov–Feb, suggesting aseasonal



Neamblysomus julianae

polyoestry and sustained but low levels of reproduction throughout the year. Litter-size: 2.

Predators, Parasites and Diseases Remains have been found in pellets of Barn Owls *Tyto alba*, reflecting the tendency of these golden-moles to forage on the surface. Often captured by domestic cats and dogs.

Conservation IUCN Category: Vulnerable.

The type population is being severely impacted by intensive urbanization and sand mining. In the former Transvaal Province, this species was given the highest regional priority score for mammals (Freitag & van Jaarsveld 1997).

Measurements

Neamblysomus julianae

HB (♂ ♂): 100.5 (94–111) mm, n = 7

HB (♀ ♀): 99.2 (92–111) mm, n = 6

T: 0 mm

HF (♂ ♂): 13.4 (12–14) mm, n = 7

HF (♀ ♀): 12.0 (9–14) mm, n = 6

E: 0 mm

WT (♂ ♂): 30 (21–35) g, n = 5

WT (♀ ♀): 26 (23–29) g, n = 5

GLS (♂ ♂): 23.2 (22.4–23.6) mm, n = 7

GLS (♀ ♀): 22.5 (21.8–23.5) mm, n = 8

GWS (♂ ♂): 16.0 (15.4–16.7) mm, n = 7

GWS (♀ ♀): 15.4 (14.7–16.2) mm, n = 8

C-M² (♂ ♂): 5.9 (5.7–6.1) mm, n = 6

C-M² (♀ ♀): 5.7 (5.5–5.9) mm, n = 4

Tierpoort, Shere and The Willows districts, Pretoria, South Africa

Key References Bronner 1995a, b; Freitag & van Jaarsveld 1997.

Gary N. Bronner

Order MACROSCELIDEA – Sengis (Elephant-shrews)

Macroscelidea Butler, 1956.

Macroscelididae (4 genera, 15 species)	Sengis	p. 261
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The order Macroscelidea contains one family with four genera and 15 species, which are widely distributed in southern, eastern, central and north-west Africa. Representatives of the order live in forests, woodlands, bushlands and semi-arid habitats, but not in sandy deserts. The order, both extant species and fossils, is endemic to Africa.

The taxonomy of the order follows Corbet & Hanks (1968) and Corbet (1974b), and more recently Schlitter (1993, 2005). The order contains a single family, Macroscelididae, with two subfamilies (Table 13). The Rhynchocyoninae (giant sengis) has a single genus *Rhynchocyon* and is comprised of three comparatively large species that live in forests and woodlands of eastern and central Africa. The second subfamily, Macroscelidinae (soft-furred sengis), contains three genera: (a) *Petrodromus*, with a single species, which occurs throughout most of central, eastern and southern Africa; (b) *Macroscelides*, also with a single species, which is confined to the Cape Province of South Africa and W Namibia; and (c) *Elephantulus*,

with ten comparatively small species that occur in semi-arid habitats and which, together, have a wide geographic range extending from southern Africa, through eastern Africa, to the Horn of Africa, and a single isolated species in NW Africa (Table 14). Most species of *Elephantulus* have comparatively small geographic ranges.

The most obvious character of sengis (or elephant-shrews) is the elongated, trunk-like and very mobile snout, which ends with a small rhinarium enclosing the nostrils. The snout is often moved up, down and sideways testing the environment for odours. The broad upright ears turn frequently, scanning for sounds, and the large eyes enable the location of small prey and potential predators. The forefeet and legs are of moderate length but the hindlimbs are elongated and slender, facilitating the characteristic rapid quadrupedal bounding (not bipedal hopping) locomotion of sengis; in *Rhynchocyon* both fore- and hindlimbs are especially elongated, as in small antelopes (Evans 1942). *Macroscelides* and *Elephantulus* possess five digits on both fore- and hindfeet, *Petrodromus* has five digits on each forefoot and four on each hindfoot, and *Rhynchocyon* has four digits on both fore- and hindfeet. The relatively long tail is sparsely covered with short hair, which in

Table 13. Principal diagnostic characters of the two subfamilies of Macroscelididae (after Corbet & Hanks 1968).

Character	Rhynchocyoninae (<i>Rhynchocyon</i>)	Macroscelidinae (<i>Elephantulus</i> , <i>Macroscelides</i> , <i>Petrodromus</i>)
Head and body size	Large (HB: ca. 250 mm)	Medium or small (<200 mm)
Pelage	Slightly coarse, sparse and boldly patterned	Soft, dense, not boldly patterned
Number of digits on forefoot/hindfoot	4/4	5/4 (<i>Petrodromus</i>), 5/5 (<i>Elephantulus</i> , <i>Macroscelides</i>)
Digit 5 of forefoot	Very short	Long
Nipples	Abdominal only	Nuchal, pectoral and (sometimes) abdominal
Post-anal gland	Present	Absent
Tip of nasal bones of proboscis	Partly ossified	Wholly cartilaginous
Postorbital process of skull	Present	Absent
Bony palate of skull	Not perforated	Perforated
Paraoccipital processes of skull	Well-developed	Rudimentary
Upper incisor teeth	Absent or rudimentary, non-functional	Present, functional
Upper canine teeth	Very large	Small
Shape of pupil of eye	Circular	Vertically elongate

Table 14. Genera in the family Macroscelididae.

Genus	Digits on forefoot	Digits on hindfoot	Head and Body length (mm) ³	Tail length (mm) ³	Greatest length of skull (mm) ³	Nipples ⁴	Pectoral gland ⁶	
<i>Elephantulus</i> (10 spp.)	5	5	114–135	98–157	33.5–37.6	1+1+1 = 6	0 or 2	
<i>Macroscelides</i> (1 sp.)	5	5	110 (104–115)	121 (107–134)	33.7 (32.1–34.8)	1+1+1 = 6	0	
<i>Petrodromus</i> (1 sp.)	5	4 ²	192 (163–210)	166 (156–187)	56.1 (54.3–58.5)	1+1+0 = 4	1	
<i>Rhynchocyon</i> (3 spp.)	4 ¹	4 ²	240–270	230–243	67.6–67.6	0+0+2 = 4	0	

¹ Digit 1 (= pollex or thumb) absent

² Digit 1 (= hallux or 'big toe') absent

³ Mean and range (*Macroscelides*, *Petrodromus*). Mean of smallest species – mean of largest species (*Elephantulus*, *Rhynchocyon*)

⁴ antebrachial + pectoral + abdominal/inguinal (on each side) = total both sides

⁵ Canine-M3 in *Rhynchocyon*; upper incisors absent or rudimentary (Data for *R. cirnei* only)

⁶ 0 = absent. 1 = slightly developed, 2 = well-developed (mostly after Corbet & Hanks 1968)

⁷ Gland is postanal, at tail insertion; large and round in shape.

some species forms a small terminal tuft. Scent glands, which are important for chemical communication, are present on several parts of the body (Corbet & Hanks 1968, Rathbun 1979, Faurie 1996); principally these are the pectoral gland (absent in *Rhynchocyon* spp.), subcaudal gland, post-anal gland (*Rhynchocyon* spp. only), pedal gland and sebaceous glands. The presence or absence of each of these glands varies according to species. Testes are internal and thus ♂♂ lack a scrotum, but the prepuse is prominent near the base of the sternum (Woodall 1995a). The dental formula is $I^{0-3}/_3, C^1/_1, P^4/_4, M^2/_2-3 = 42$ at maximum (see also genus profiles and Figure 15).

Skull is tall with dome-shaped cranium, and well developed complete zygomatic arches. Orbits are large, with moderate interorbital constriction. Rostrum moderately long. Tympanic region not inflated except in *Macroscelides*. Palate with broad short anterior palatal foramina, and complex posterior palatal foramina (usually four pairs of foramina) in *Elephantulus*, *Macroscelides* and *Petrodromus*; no foramina in *Rhynchocyon*. Toothrow long, without diastema (similar to that in other Afrotheria and in Soricomorpha); toothrow diverges posteriorly so bony palate is considerably wider at level of molar teeth than at level of incisors. Dental formula either $I^3/_3, C^1/_1, P^4/_4, M^2/_2-3 = 40$ or 42 in *Elephantulus*, *Macroscelides* and *Petrodromus*; or $I^0/_3, C^1/_1, P^4/_4, M^2/_2-3 = 34$ or 36 in *Rhynchocyon* where upper incisors absent or rudimentary and usually not erupted. Incisors small and subequal (except in *Petrodromus* where I1 is large and caniniform). Canine small and incisiform except in *Rhynchocyon* where large and caniniform. Upper premolars and molars (four or six in each ramus) large, increasing in size posteriorly, sectorial with well-developed cusps; brachydont or slightly hypsodont; dilambdodont; P¹ usually small and simple; P⁴ large and subequal to M¹ (Figure 15). Mandible long and slender, with posteriorly pointing angular process; tall coronoid process (especially in *Elephantulus*, *Macroscelides* and *Petrodromus*).

Sengis are primarily insectivorous, feeding on a wide variety of small invertebrates. The prey are captured by the long tapering tongue that can be extended beyond the tip of the nose, and masticated by the sectorial teeth, in a similar way to other small insectivorous mammals. The digestive tract is of moderate length, as expected for an insectivore, but unlike most insectivores, sengis have a functional caecum (Woodall & Mackie 1987). The caecum perhaps denotes a partly herbivorous diet in some species and it may also reflect the phylogeny of sengis. Most species are socially monogamous and live on home-ranges (sometimes territories) of

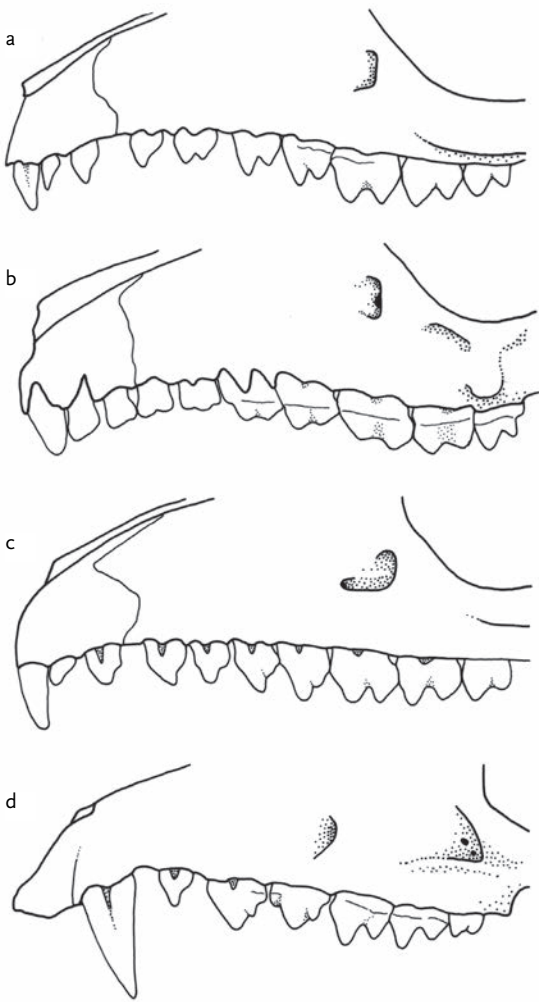


Figure 15. Upper left toothrow of each genus of sengis. (a) *Elephantulus*. (b) *Macroscelides*. (c) *Petrodromus*. (d) *Rhynchocyon*. (BMNH specimens; see Figs 16, 18, 19, 20.)

up to 100 ha (usually less), depending on the species and habitat occupied (Rathbun 1979, Rathbun & Rathbun 2006). Sengis are polycyclic, but primarily crepuscular or diurnal, sheltering in rock crevices, shallow burrows or on comparatively exposed trails at the bases of bushes (*Macroscelidinae*), while others build leaf nests on the forest floor (*Rhynchocyoninae*).

	Subcaudal gland ⁶	Tympanic bullae	I-M ³ (mm) ³	Notes
	1 or 2	Not inflated or moderately inflated	17.0–20.6	Widespread in southern and eastern Africa; one species in NW Africa.
	2	Very inflated	15.6 (14.9–16.3)	Namibia and South Africa. Head broad (GWS/GLS = >60%; other genera <60%)
	n. d.	Small	29.3 (28.1–30.5)	Widespread in eastern, southern and central Africa. Forelimbs longer relative to hindlimbs than in other genera.
	0 ⁷	Small or not inflated	28.9 (27.4–29.9) ⁵	One species widespread in central and eastern Africa; two species mostly restricted to coastal East Africa.

Reproduction may occur throughout the year in tropical regions, but is seasonal at higher latitudes (Neal 1995). Gestation is comparatively long for such small mammals (4–6 weeks) and is probably related to the precocious state of neonates. There are 2–3 pairs of nipples (antebrachial/pectoral, and abdominal/inguinal) arranged differently according to genus. Litter-size is 1–4 (depending on the species). The eyes are open at birth and the young can walk within a few hours in the Macroscelidinae (Rathbun 1979), but in the Rhynchocyoninae neonates are less developed and nest-bound for about two weeks (Baker *et al.* 2005). Four species of sengis (*Elephantulus edwardii*, *E. brachyrhynchus*, *E. myurus*, *Macroscelides proboscideus*) are known to have the unusual characteristic of polyovulation (also recorded in several species of mammals belonging to other orders) in which the ovaries produce many more eggs at each ovulation than is required for implantation (11 species examined; Tripp 1971). The reason for polyovulation in these species is uncertain.

The fossil and extant Macroscelidea include six subfamilies (two extant) with 14 genera (four extant) (Holroyd & Mussell 2005). The earliest macroscelid fossils come from the early Eocene (ca. 55 mya), but by the Pliocene (ca. 4 mya), all but the two extant subfamilies have disappeared from the fossil record, and the genera *Elephantulus*, *Macroscelides* and *Rhynchocyon* have first appeared (Butler 1995). *Miorhynchocyon* arose in the early Miocene (ca. 23 mya), and it closely resembled present-day giant sengis in many respects (Novacek 1984). *Petrodromus* is not present in the fossil record until the mid-Pleistocene (ca. 1.0 mya). The dentition from most of the older fossils suggests a herbivorous diet. Indeed, the Pliocene macroscelid genus *Myohyrax* was initially misidentified as a hyracoid because of its highly hypsodont dentition (Patterson 1965).

The taxonomic relationship of sengis with other mammals has been confusing. The historical arrangement was to include them as a family, the Macroscelididae, within the order Insectivora. When the order was split into the two suborders, the Liptotyphla and Menotyphla, the family was assigned with the Tupaiidae (the ‘tree-shrews’ of India and South-East Asia) in the suborder Menotyphla.

Another view, based on morphology and osteology (Novacek 1982, Novacek & Wyss 1986), is that the Macroscelididae are more closely related to the Lagomorpha (hares and rabbits) than to the Insectivora or the Tupaiidae (McKenna 1975). The current view is that the Macroscelididae is the only family in the order Macroscelidea (Butler 1956), and that the Tupaiidae is a separate order, the Scandentia – both families and orders now quite separate from the Insectivora. The vernacular name, ‘elephant-shrew’, refers to the elongated snout reminiscent of the proboscis of elephants, and their historical relationship to true shrews (order Soricomorpha; formerly Soricidae, order Insectivora); recently, the alternative vernacular name ‘sengi’ has gained credence because it better reflects their unique phylogeny (Rathbun & Kingdon 2006).

The molecular evidence for sengis belonging to an early African radiation of placental mammals, called the Afrotheria, is overwhelming (see Chapter 7 ‘Classification: a Mammalian Perspective’, p. 101). Afrotheria include the elephants (order Proboscidea), dugongs and manatees (order Sirenia) and hyraxes (order Hyracoidea), which together are referred to as the Paenungulata, the Aardvark (order Tubulidentata), the sengis (order Macroscelidea) and the tenrecs and golden-moles (order Afrosoricida). Although morphological evidence in support of this radiation is less convincing, the Afrotheria hypothesis is focusing considerable interest on fossils (e.g. Zack *et al.* 2005) and morphological traits (e.g. Carter *et al.* 2004), which will undoubtedly result in a better understanding of this extraordinary group of African mammals. The order Macroscelidea, together with the orders Afrosoricida (otter-shrews, golden-moles and the Malagasy tenrecs) and Tubulidentata (Aardvark), has been placed in the Cohort Afroinsectiphilia (Waddell *et al.* 2001, Amrine-Madsen *et al.* 2003) – the ‘African insect lovers’ – within the Superorder Afrotheria. Further information on Afrotheria is given in Volume 1 of *The Mammals of Africa*.

An extensive bibliography (750 citations) of the scientific literature on sengis was given by Rathbun & Woodall (2002).

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Table 15. Species in the genus *Elephantulus*.

Species	Pectoral gland	Eye-ring	Postorbital patch of dark fur	Canine tooth	Upper incisor teeth	
<i>E. brachyrhynchus</i>	Absent	Present	Absent	molariform	I ¹ and I ³ larger than I ²	
<i>E. edwardii</i>	Absent	Present	Absent	molariform	I ¹ –I ³ similar in size, or I ² slightly smaller	
<i>E. intufi</i>	Absent	Present	Absent	pointed	I ¹ –I ³ similar in size	
<i>E. myurus</i>	Absent	Present	Absent	small, pointed	I ¹ much larger than I ² and I ³	
<i>E. rozeti</i>	Absent	Absent	Absent	molariform	I ² smaller than I ¹ and I ³	
<i>E. rupestris</i>	Absent	Indistinct	Absent	slightly molariform	I ² smaller than I ¹ and I ³	
<i>E. fuscus</i>	Absent	Present	Absent	molariform	I ¹ larger than I ² and I ³ ; I ² and I ³ similar in size	
<i>E. fuscipes</i>	Present	Indistinct	Absent	molariform	I ¹ –I ³ similar in size	
<i>E. revoili</i>	Present	Present	Present	molariform	I ¹ –I ³ similar in size	
<i>E. rufescens</i>	Present	Present	Present	slightly molariform	I ² smaller than I ¹ and I ³	

¹ Bicoloured = dark above, white or pale below

Family MACROSCELIDIDAE
SENGIS (ELEPHANT-SHREWS)

Macroscelididae Bonaparte, 1838. Nuovi Ann. Sci. Nat. 2: 111.

<i>Elephantulus</i> (10 species)	Sengis	p. 261
<i>Macroscelides</i> (1 species)	Round-eared Sengi	p. 276
<i>Petrodromus</i> (1 species)	Four-toed Sengi	p. 279
<i>Rhynchocyon</i> (3 species)	Giant Sengis	p. 282

The characteristics of the family are given in the order profile above. The family contains four genera and 15 species. The genera in the family, and each species in each genus, are described alphabetically. In

the Descriptions, an indication of the size of each species is recorded comparatively to other species in the family. The size categories, based on mean head and body length (HB), are: Very small: 90–139 mm; Small: 140–189 mm; Medium-sized: 190–139 mm; Large: 140–189 mm; and Very Large: 190–340 mm.

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GENUS *Elephantulus*
Sengis

Elephantulus Thomas and Schwann, 1906. Abst. Proc. Zool. Soc. Lond. 1906 (33): 10. Type species: *Macroscelides rupestris* A. Smith, 1831.

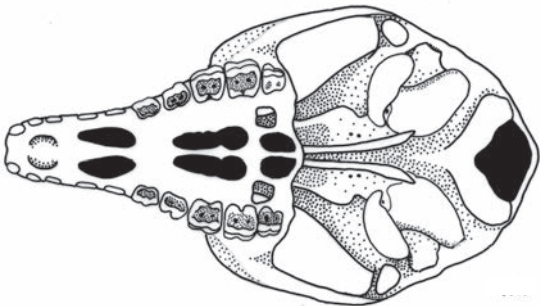
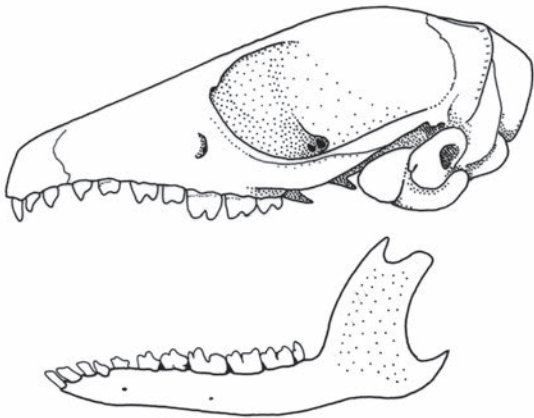


Figure 16. Skull and mandible of *Elephantulus brachyrhynchus* (BMNH 21.11.3.43).

Elephantulus contains ten species (Table 15) distributed throughout southern, eastern and north-west Africa. Five of these species occur only in southern Africa, three only in eastern Africa, one in both eastern and southern Africa, while one occurs only in north-west Africa. Most species have a comparatively restricted geographic range. All species are terrestrial; most live in savanna habitats, but *E. edwardii*, *E. myurus*, *E. rupestris* and *E. rozeti* are rupicolous.



Elephantulus rufescens.

Mean Tail length (as % of HB)	Tail colour; tuft at tip ¹	Distribution and notes
90	Bicoloured, no tuft	Widespread central and eastern Africa. Supratragus simple
130	Bicoloured, small tuft	South Africa
105	Bicoloured (dorsal hairs with black tips), small tuft	Namibia, Botswana, Angola, South Africa. Golden patch behind each ear
110	Bicoloured, no tuft	Southern Africa
110	Bicoloured, small tuft	North-western Africa
115	Bicoloured, well-developed tuft	South Africa, Namibia
90	Bicoloured, no tuft	Malawi, Mozambique, Zambia. Supratragus twisted
67–75	Bicoloured, no tuft	Uganda, NE DR Congo, S Sudan
120	White (dorsal hairs with brown tips), small tuft	Somalia
105	Dark brown, no tuft	Somalia, EC Ethiopia, SE Sudan, Kenya, E Uganda and NC Tanzania



Species in the genus are characterized by small size (HB less than ca. 160 mm), large head and eyes, long ears, long limbs with five digits on each fore- and hindfoot, and three pairs of nipples. Skull characters include upper toothrow (I–M³) less than 22 mm, upper incisors present, upper canines small, bullae not greatly inflated, I¹ and I³ not sectorial, and postorbital process absent. The dental formula is $I^{3/3}, C^{1/1}, P^{4/4}, M^{2/2} = 40$ in most species, or $I^{3/3}, C^{1/1}, P^{4/4}, M^{2/3} = 42$ in *E. brachyrhynchus*, *E. fuscipes* and *E. fuscus*. Subcaudal and pectoral glands present in some species. Some of these characters are shared with other genera of sengis. See also family profile and Figures 15 and 16.

Elephantulus spp. are mainly crepuscular with bouts of activity during day and night, suggesting that they are polycyclic (Rathbun 1979; Woodall *et al.* 1989). Some use runways to travel between

shelters and foraging areas. None is known to use nesting material. They are primarily insectivorous. Most species that have been well studied are monogamous and the male–female pair defends a territory (Rathbun & Rathbun 2006). Metabolism and thermoregulation has been studied in some species: in *E. intufi*, basal metabolic rate is lower than expected for a species of this size, and T_b can be maintained over a wide range of ambient temperatures (even when T_a is ca. 5 °C); cold temperatures elicit torpor in some species. Those species living in arid environments perhaps have specialized kidneys to aid water conservation. Although they all have long limbs and are extremely agile and can run exceedingly fast, they do not hop on their rear legs. Most species of *Elephantulus* communicate with each other by scent-marking, but also with rapid foot-drumming of the hindfeet on the substrate. Reproductive rate is slow because of the comparatively

long gestation, small litter-size (1–4) and limited seasonal breeding especially at higher latitudes (Neal 1995).

Some species of *Elephantulus* show considerable geographic variation in pelage colouration, which has given rise to the description of many taxa (see especially *E. intufi*, *E. rufescens*, *E. rupestris*). The genus was described by Thomas & Schwann (1906) when they split the genus *Macroscelides* into three genera: *Macroscelides* (enlarged tympanic bullae, two lower molars), *Elephantulus* (normal-sized bullae and two lower molars) and *Nasilio* (normal-sized bullae and three lower molars; *brachyrhynchus*, *fuscipes*, *fuscus* only). Allen (1939) and Roberts (1951) also regarded *Nasilio* as a separate genus. In contrast, Ellerman *et al.* (1953) placed it as a subgenus of *Elephantulus*. Currently, *Nasilio* is not recognized as a genus or subgenus (Corbet & Hanks 1968) and the species formerly in this genus are now referred to *Elephantulus*. Although the different species of *Elephantulus* are often difficult to distinguish morphologically, they are genetically distinct with a high degree of divergence in some species (Raman

& Perrin 1997); *Elephantulus* is considered to be distinct from the genera *Macroscelides* and *Petrodromus* using genetic criteria. However, recent genetic and morphological evidence suggests that *E. rozeti* in NW Africa is more closely related to *Petrodromus* than *Elephantulus* (Douady *et al.* 2003).

The species are distinguished on the basis of presence/absence of a pectoral gland, the form of the supratragus, the relative size of the tympanic bullae, the shape of the premaxillary suture, the number of molar teeth in the mandible and the presence and form of cusps on premolars. A key to all ten species is given by Koontz & Roeper (1983), and to nine species (excludes *E. fuscus*) by Corbet & Hanks (1969) (Table 15).

A new species, *Elephantulus pilicaudus* from South Africa, was described in 2008 (Smit *et al.* 2008, see also p. 16) after this text was submitted to the publishers.

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Elephantulus brachyrhynchus SHORT-SNOUDED SENGI (SHORT-SNOUDED ELEPHANT-SHREW)

Fr. Macroscélide à nez court; Ger. Kurznasen-Elefantenspitzmaus

Elephantulus brachyrhynchus (A. Smith, 1836). Report of the Expedition for Exploring Central Africa 1834: 42 [1836].
(The country between L. Latakoo [= Kuruman, Northern Cape Province, South Africa] and the Tropic [= in Botswana]).

Taxonomy Originally described in the genus *Macroscelides* and later assigned to the genus *Nasilio* on the basis of three lower molars rather than two as in most other *Elephantulus* spp. (Corbet & Hanks 1968). Other forms previously considered within this species include *fuscus* and *fuscipes* (both now valid species), *malosae* (now a synonym of *E. fuscus*) and *schinzi* (now a synonym of *E. intufi*) (Corbet 1974b). Molecular and genetic studies suggest low levels of polymorphism in *E. brachyrhynchus*, although higher than in other species of *Elephantulus* (Raman & Perrin 1997). Allozyme and isozyme data link *E. brachyrhynchus* with *E. intufi* and *E. rupestris*, and support the retention of *brachyrhynchus* in the genus *Elephantulus* rather than in the separate genus *Nasilio*, as proposed on the basis of dentition (Corbet 1974b). *Elephantulus brachyrhynchus* probably diverged early within the genus *Elephantulus* (Corbet 1974b). Subspecies: none. Chromosome number: $2n = 26$ (Stimson & Goodman 1966, Tolliver *et al.* 1989).

Description Small sengi with relatively short snout, eye-ring, and buff patch behind ears. Dorsal pelage reddish- or yellowish-brown, but variable (see below); dorsal hairs ca. 10 mm, dark grey at base, brown at tip; some scattered longer black-tipped hairs. Ventral pelage whitish; ventral hairs grey at base, white at tip. Head large, with short snout, large eyes, indistinct white eye-ring, white upper lip. Ears large, rounded at tip, with small supratragus which is not twisted backwards (Figure 17, cf. *E. fuscus* and *E. fuscipes*). Usually with buff patch behind ears. No dark spot behind eye. Pectoral gland absent, subcaudal gland present. Fore- and hindlimbs whitish. Hindlimbs elongated; five digits; soles brown and naked. Tail relatively long (ca. 90% of HB), but comparatively short for an *Elephantulus* sp.; bicoloured, dark above, paler below; without tuft. Skull: I^1 and I^3 larger than I^2 ; M_3 present (also in *E. fuscus* and *E. fuscipes*; see profile genus *Elephantulus*). Nipples: $1 + 2 = 6$.

Geographic Variation Considerable clinal variation in colour of pelage. Dorsal pelage reddish-yellow or pale buffy-grey (Namibia and Botswana), dark greyish-brown (higher altitudes of Malawi), rufous-grey (Zambia) and grey (East Africa).

Similar Species

E. fuscus. HB and HF similar size; pectoral gland absent; I^1 larger than I^2 and I^3 ; supratragus twisted; Malawi, Mozambique and Zambia; probably allopatric.

E. fuscipes. HB slightly larger, HF slightly smaller; pectoral gland present, poorly developed; I^1 , I^2 and I^3 similar in size; supratragus large and twisted; Uganda, NE DR Congo, S Sudan; marginally parapatric.

E. myurus. HB slightly larger, HF considerably longer (ca. 39 mm); pectoral gland absent; I^1 much larger than I^2 and I^3 ; M_3 absent; South Africa, Zimbabwe; sympatric in part of range.

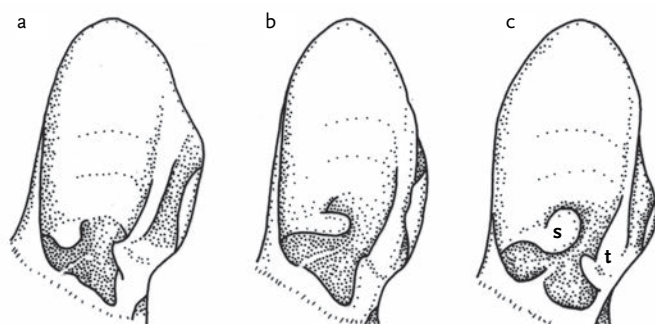
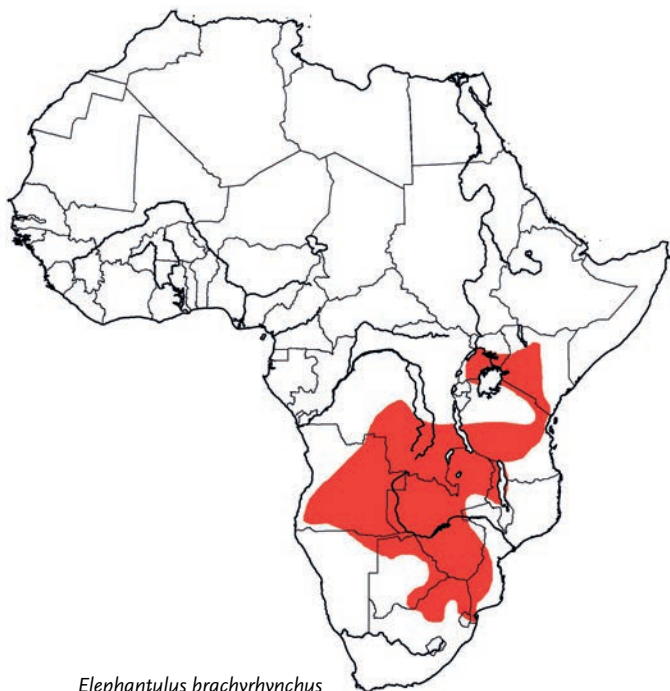


Figure 17. Left ear of (a) *Elephantulus brachyrhynchus*, (b) *E. fuscus* (as *E. brachyrhynchus* – atypical form) and (c) *E. fuscipes* (after Corbet & Hanks 1968). s = supratragus; t = tragus.

*Elephantulus brachyrhynchus*

Distribution Endemic to Africa. Zambezan Woodland BZ, adjacent areas of Somalia–Masai Bushland BZ and Eastern and Southern Rainforest–Savanna Mosaics. The most widely distributed species of sengi. Recorded from NE Swaziland, South Africa (N Transvaal), S Mozambique, Zimbabwe, N and E Botswana, NE Namibia, N Malawi, Zambia, S DR Congo, Angola and northwards to Tanzania, Kenya and Uganda. The taxonomic status of populations in Malawi, Mozambique and Zambia are uncertain; they perhaps represent *E. fuscus*.

Habitat Savanna habitats where there is thick cover, long grass and shrubs in riparian woodlands. Lives on sandy ground or on hard substrate but not on rocks (cf. some other *Elephantulus* spp.). Prefers mixed woodland dominated by *Colophospermum mopane*, *Combretum apiculatum*, *C. zeyheri* and *Erythroxylum zambesiacum* in Zimbabwe, where herbs and grasses are abundant and ground cover is good, even during the dry season (Neal 1995). Also occurs in *Brachystegia jullbernardia* mixed woodland (miombo), *Combretum–Terminalia–Eragrostis* low woodland on talus slopes, and *Commiphora–Combretum* wooded bushland thickets (Neal 1995).

Abundance Locally common but usually at low densities. Distances recorded between consecutive captures of individuals in Tanzania are comparatively short (mean \pm 1 S.D. = 42.3 ± 38.3 m; median 32 m; $n = 65$) and not significantly different between the sexes (Leirs *et al.* 1995).

Adaptations Terrestrial; diurnal with most activity at dawn. Runs swiftly, dashing from cover to cover. Shelters in dense cover, but does not dig burrows. Sunbathes (especially in morning) to increase body temperature and to save energy expenditure. In captivity, metabolic rate is 73–94% of that expected (on basis of body size) and T_b is $34.2\text{--}37.7^\circ\text{C}$ (Perrin 1995). When T_a is $>35^\circ\text{C}$, hyperthermia does not occur because of increased

evaporative water loss. Insulation and vasomotor control is also important in controlling body temperature (Perrin 1995). Skin glands on many parts of the body produce secretions used for communication with conspecifics (Faurie 1996). Foot-drumming is common; typically, there are 10–30 drums/bout (with some irregular bouts), drum intervals of 30–40 msec, 100–200 msec between bouts, and <10 bouts per series; the length of a series ranged from 200 msec to 5 sec (Faurie *et al.* 1996). A sharp high-pitched squeal is uttered when fighting, and the alarm call is shrill and penetrating. ‘Mew’ vocalizations are 545 msec long and have a fundamental of 1.65 kHz (Faurie 1996).

Foraging and Food Insectivorous. In Zimbabwe (Neal 1995), ants and termites are the principal prey, and occasionally plant matter, including leaves and seeds, is eaten ($<2\%$ by volume). However, in Tanzania, Leirs *et al.* (1995) recorded the diet (based on analysis of stomach contents) as $47.2 \pm 5.3\%$ invertebrates and $51.7 \pm 5.2\%$ green plant material (macroscopic analysis), and 40.1% invertebrates and 47.2% green plant material (microscopic analysis). Small amounts of fruits and seeds were also eaten.

Social and Reproductive Behaviour Adults typically occur in monogamous pairs and are territorial (Neal 1995). Their social structure appears to be similar to that described for *E. rufescens* (Rathbun 1979). Males and ♀♀ display aggressive territorial behaviour (Faurie 1996).

Reproduction and Population Structure Females show partial polyovulation, producing a mean of 8.5 ova/ovary (range 0–23, $n = 16$) at each ovulation (Tripp 1971); this condition is intermediate between those species that do not polyovulate (most sengis) and those that show extreme polyovulation (*E. edwardii*, *E. myurus*, *P. macrosceles*).

In Zimbabwe, young are born throughout the year (Neal 1995), although the percentage of pregnant ♀♀ varies throughout the year (40% in Feb to 100% in Oct and Nov). Litter frequency is reduced in the cool winter months when insect food is less abundant; average interval between litters is 90 days during the cool dry season and about 60 days during the warmer period of the year (Neal 1995). Mean embryo number varies with season: 1.40 during the cool dry season, 1.74 during the hot dry season and 1.76 in the warm wet season (Neal 1984a). Mean embryo number also varies with the weight of the ♀: smaller ♀♀ (<40 g) have a smaller number of embryos (mean 1.1 [cool dry season] to 1.7 [warm wet season]); and larger ♀♀ (>40 g) have a larger number of embryos (mean 1.6 [cool dry season] to 1.9 [warm wet season] and 2.0 [hot dry season]) (Neal 1995). In Tanzania, the percentages of pregnant ♀♀ each month were mostly lower than in Zimbabwe, and there were several months of the year when the pregnancy rate was 0% (Mar, May, Jun, Jul [no sample], Sep, Nov and Dec) (Leirs *et al.* 1995). Embryo number: 1.4 (1–2), $n = 10$. At birth, young are precocial, fully furred and the eyes are open; young can run almost immediately after birth, and development is rapid (Faurie 1996). The overall sex ratio in a wild population did not differ from parity (Leirs *et al.* 1995).

Predators, Parasites and Diseases Owls *Tyto alba* and *T. capensis* are known predators (Vernon 1972).

Conservation IUCN Category: Least Concern.

The most widely distributed sengi with no known significant threats.

Measurements

Elephantulus brachyrhynchus

TL (♂♂): 213.8 (202–225) mm, n = 9

TL (♀♀): 212.0 (205–218) mm, n = 4

T (♂♂): 98.9 (91–110) mm, n = 9

T (♀♀): 95.3 (88–101) mm, n = 4

HF (♂♂): 29.9 (29–31) mm, n = 9

HF (♀♀): 28.8 (27–30) mm, n = 6

E (♂♂): 21.1 (20–24) mm, n = 9

E (♀♀): 20.7 (20–21) mm, n = 6

WT: n. d.

GLS (♂♂): 33.5 (32.4–34.3) mm, n = 9

GLS (♀♀): 32.8 (32.2–33.8) mm, n = 5

GWS (♂♂): 18.1 (17.6–18.8) mm, n = 9

GWS (♀♀): 17.5 (16.8–18.5) mm, n = 5

I¹–M³ (♂♂): 17.0 (16.4–17.6) mm, n = 9

I¹–M³ (♀♀): 17.0 (16.8–17.2) mm, n = 6

Southern Africa (Rautenbach & Schlitter 1977)

Key References Corbet & Hanks 1968; Faurie 1996; Leirs *et al.* 1995; Neal 1995; Perrin 1995.

Mike Perrin

Elephantulus edwardii CAPE SENGI (CAPE ELEPHANT-SHREW)

Fr. Macroscélide du Cap; Ger. Kap-Elefantenspitzmaus

Elephantulus edwardii (A. Smith, 1839). Illustrations of the Zoological Society of South Africa, Mammals: p1. 14. Oliphants River, Western Cape Province, South Africa. Corbet & Hanks (1968) assume the type locality refers to the river that flows into the Atlantic, since the species has subsequently been found in this region, and not to the Oliphants River in the Outdtschoorn District where the species has not been recorded.

Taxonomy Originally described in the genus *Macroscelides*. Ellerman *et al.* (1953) treated *edwardii* as conspecific with *E. myurus* (which they called *E. rupestris*), although there are a number of dental characters that separate the two species (Rautenbach & Nel 1980). The degree of heterozygosity of allozymes and isozymes is very low (Raman & Perrin 1997), suggesting a close relationship with *E. myurus*. Synonyms: *capensis*, *karoensis*, *rupestris*. Subspecies: none. Chromosome number: 2n = 26 (Tolliver *et al.* 1989).

Description Small greyish-coloured sengi, similar to *E. rupestris* and *E. myurus*. Pelage long, soft and silky. Dorsal pelage greyish-brown, turning to ashy-grey tinged with pale tawny on flanks. Ventral pelage greyish-white to white. Head large; snout black above, white laterally. Eyes large with white eye-ring. No spot behind the eye. Ears large, rounded at tip; yellowish-brown patch behind each ear. Tragus and supratragus slightly developed. Pectoral gland absent, subcaudal gland present. Hindlimbs elongated; five digits. Tail long (ca. 130% of HB) with very short hairs, black above, paler below near body but distal third black; hairs longer at tip forming small tuft. First lower premolar single-rooted (cf. double-rooted in *E. myurus*). M₃ absent. Females may be slightly larger than ♂♂ (Stuart *et al.* 2003). Nipples: 1 + 2 = 6.

Geographic Variation There is some variation in pelage colour between populations at extreme ends of the range (Corbet & Hanks 1968).

Similar Species

E. rupestris. Ventral pelage paler; orange-buff rather than yellow-buff behind the ears; tail on average longer, more hairy, distal third not completely black.

E. myurus. Ventral pelage paler; inconspicuous buffy patch behind ears; tail on average longer, less tufted, not black; less truncated supratragus.

Distribution Endemic to Africa. South-West Arid BZ (Karoo) and South-West Cape BZ. Recorded from SW and C Cape in the east to the Little Karoo in the west. Eastern and western parts of range are not disjunct (Rautenbach 1978; C. Stuart pers. comm.), as illustrated in older publications (Corbet & Hanks 1968).

Habitat Rocky areas on mountains, small rocky outcrops and flat rock sills adjacent to vegetated areas of dwarf shrubs, and hard sandy ground with sparse cover.

Abundance Locally common.



Elephantulus edwardii

Adaptations Terrestrial; adapted to rocky habitats. Mainly nocturnal (Woodall *et al.* 1989), but also crepuscular and diurnal (Stuart *et al.* 2003), suggesting they are polycyclic (Leon *et al.* 1983). Sunbathes on cool days. Foot-drumming includes both regular and irregular bouts with enough variation that makes it difficult to distinguish this species from others (Faurie *et al.* 1996). Various vocalizations ('clicks' and 'mews'), and secretions from perianal and pedal scent glands, are used presumably for social interactions and for marking territories (Faurie 1996). Metabolic and water turnover rates are only slightly lower than expected, based on body size (Leon *et al.* 1983).

Foraging and Food Insectivorous. Feeds mainly on ants (Stuart *et al.* 2003) and termites, but also on other arthropods. Stuart *et al.* (2003) observed animals flipping hyrax dung to feed on exposed insects. While foraging on insects attracted to the flowers of *Protea humiflora*, the Cape Sengi acts as a significant pollen vector (Fleming & Nicolson 2002). Captives can be kept on a commercial cereal mixture (Pronutro) plus vitamins and minerals and mealworms (Leon *et al.* 1983). The digestive traits of Cape Sengis are typical of an insectivore, although the assimilation of termites was surprisingly low considering their importance in the diet (Woodall & Currie 1989).

Social and Reproductive Behaviour Probably monogamous and territorial. Occurs singly or in male–female pairs, or as a mother with young (C. Stuart pers. comm.). Captives must be maintained singly or as monogamous pairs due to aggression (Leon *et al.* 1983).

Reproduction and Population Structure Females polyovulate, producing a mean of 44 ova/ovary (range 31–55, $n = 3$) at each ovulation (Tripp 1971). Young tend to be born in the warmer and wetter months: Sep–Jan in the western part of their range and into February further east (Stuart *et al.* 2003). Litter-size: 1–2 (usually 2). Birth interval: ca. 30 days. Neonates weigh 9–11 g, are highly precocial at birth and gain about 0.6 g per day until they reach about 65% of adult weight at Day 30 (Dempster *et al.* 1992, Stuart *et al.* 2003).

Predators, Parasites and Diseases Ectoparasites include five species of ticks (Fourie *et al.* 1995, Stuart *et al.* 2003) and the louse *Polyplax biseriata* (Stuart *et al.* 2003).

Conservation IUCN Category: Least Concern.

Although this species is endemic to South Africa, it occupies rocky habitats that are comparatively immune to most human disturbances at present.

Measurements

Elephantulus edwardii

TL (♂ ♂): 249.3 (230–273) mm, $n = 9$

TL (♀ ♀): 250.8 (230–275) mm, $n = 11$

T (♂ ♂): 131.3 (115–145) mm, $n = 9$

T (♀ ♀): 130.7 (116–149) mm, $n = 11$

HF (♂ ♂): 35.0 (33–37) mm, $n = 9$

HF (♀ ♀): 34.8 (33–39) mm, $n = 12$

E (♂ ♂): 29.2 (27–33) mm, $n = 9$

E (♀ ♀): 29.5 (26–33) mm, $n = 11$

WT (♂ ♂): 46.5, 47.5 g, $n = 2$

WT (♀ ♀): 52 (46–67) g, $n = 5$

GLS (♂ ♂): 35.3 (33.0–38.0) mm, $n = 9$

GLS (♀ ♀): 34.9 (33.5–37.0) mm, $n = 12$

GWS (♂ ♂): 19.6 (19.1–20.5) mm, $n = 8$

GWS (♀ ♀): 19.3 (18.7–20.3) mm, $n = 12$

I¹–M³ (♂ ♂): 18.2 (17.1–19.9) mm, $n = 9$

I¹–M³ (♀ ♀): 18.3 (17.5–20.8) mm, $n = 12$

Measurements: southern Africa (Rautenbach & Schlitter 1977)

Weights: South Africa (G. B. Rathbun unpubl.)

Key References Corbet & Hanks 1968; Dempster *et al.* 1992; Leon *et al.* 1983; Raman & Perrin 1997.

Mike Perrin & Galen B. Rathbun

Elephantulus fuscipes DUSKY-FOOTED SENGI (DUSKY-FOOTED ELEPHANT-SHREW)

Fr. Macroscélide à pattes sombres; Ger. Dunkelfuß-Elefantenspitzmaus

Elephantulus fuscipes (Thomas, 1894). Ann. Mag. Nat. Hist., ser. 6, 13: 68. N'doruma, Niam-Niam country, NE DR Congo.

Taxonomy Originally described in the genus *Macroscelides*. Similar to *E. brachyrhynchus*, and probably forms an allopatric pair with *E. fuscus* (Corbet & Hanks 1968). Synonyms: none. Chromosome number: not known.

Description Small dark brown sengi. Dorsal pelage dark brown; hairs dark grey to black, brown at tip; many longer black-tipped hairs especially on dorsum giving pelage a dark saturated appearance, Flanks paler. Ventral pelage whitish-grey; hairs grey at base, white at tip. Head large, without hairy rhinarium (cf. *E. rufescens*). Eyes large, with indistinct white eye-ring and without postorbital dark patch. Ears large, rounded at tip, with swollen supratragus, which is twisted backwards on a constricted stalk (to a greater extent than in *E. fuscus*, cf. *E. brachyrhynchus*; see Figure 17). No buff patch behind ears. Pectoral gland present, but poorly developed and only visible

when hairs on chest are parted; subcaudal gland slightly developed. Hindfoot elongated; five digits. Tail relatively short (ca. 67–75% of HB), bicoloured, almost black above; without terminal tuft. M₃ present (also in *E. brachyrhynchus* and *E. fuscus*; see profile genus *Elephantulus*). Nipples: 1 + 2 = 6.

Geographic Variation Pelage colour of individuals at Niangara, DR Congo, at the end of the wet season are brighter and more rufous than those from Faradje several months after the wet season; however, this colour change is not constant and it is uncertain whether such variations are seasonal or geographic (Allen, J. 1922).

Similar Species

E. brachyrhynchus. Dorsal pelage reddish-brown; pectoral gland absent; lacks twisted supratragus.

E. rufescens. Dorsal pelage paler; pectoral gland present; hairy rhinarium; facial pattern includes dark spot behind eye; M_3 absent.
E. fuscus. Pectoral gland absent; similar form of supratragus; Malawi, Mozambique and Zambia only.

Distribution Endemic to Africa. Restricted areas of Northern Rainforest Mosaic and adjacent Eastern Rainforest–Savanna Mosaic. Recorded from SW Sudan, NE DR Congo and Uganda. Marginally sympatric, but not syntopic, with *E. brachyrhynchus* and *E. rufescens*.

Habitat Woodland savanna.

Abundance Uncertain; generally rarely collected and probably uncommon; appears to be common at selected localities in NE DR Congo.

Remarks Apparently no other information available. One pregnant ♀ with one embryo in Mar (Faradje, NE DR Congo; label, RMCA).

Conservation IUCN Category: Data Deficient, previously Least Concern.

Little is known about the status of this species; Nicoll & Rathbun (1990) provisionally assessed it as 'Safe'.

Measurements

Elephantulus fuscipes

HB: 135.2 (126–148) mm, $n = 5$

T: 91.8 (86–100) mm, $n = 6$

HF: ca. 27–28 mm

E: n. d.

WT: 59.8 (52–77) g, $n = 6$



Elephantulus fuscipes

GLS: 32.6 (35.6–36.6) mm, $n = 4$

GWS: 17.3 (16.9–17.9) mm, $n = 3$

I^1 – M^3 : 18.2 (17.8–18.9) mm, $n = 4$

Body measurements and weight: RMCA

Skull measurements: Uganda, SW Sudan, NE DR Congo (BMNH)

Key Reference Corbet & Hanks 1968.

Mike Perrin

Elephantulus fuscus DUSKY SENGI (DUSKY ELEPHANT-SHREW)

Fr. Macroscélide foncé; Ger. Dunkle-Elefantenspitzmaus

Elephantulus fuscus (Peters, 1852). Reise nach Mossambique, Zoologie 1, Säugethiere, p. 87. Boror, near Quelimane, N Mozambique.

Taxonomy Originally described in the genus *Macroscelides*. Corbet & Hanks (1968) included *fuscus* as a synonym of *E. brachyrhynchus* but Corbet (1974b) points out that the two taxa appear to be sympatric in the vicinity of Tete, Mozambique, and accordingly treats them as separate species. Synonyms: *malosae*. Subspecies: none. Chromosome number: not known.

Description Small sengi very similar to *E. brachyrhynchus*. Dorsal pelage dark brown. Ventral pelage dark grey. Head large. Eyes large, with white eye-ring. Ears large, rounded at tip, with swollen supratragus, which is twisted backwards on a constricted stalk (but to a lesser extent than in *E. fuscipes*, cf. *E. brachyrhynchus*; see Figure 17). Pectoral gland absent; subcaudal gland present. Hindfeet elongated; five digits; soles dark and naked. Tail relatively long (ca. 90% of HB), black above in mid-dorsal line, paler below. Skull: infraorbital foramen is diagonal in lateral view and triangular when viewed anteriorly. M_3 present (also in *E. brachyrhynchus* and *E. fuscipes*; see profile Genus *Elephantulus*). Nipples: $1 + 2 = 6$.

Geographic Variation None recorded.

Similar Species

E. brachyrhynchus. Very similar; supratragus swollen and not twisted backwards; infraorbital foramen oval in shape; not sympatric.

Distribution Endemic to Africa. Zambezian Woodland BZ. Recorded from Mozambique (Lower Zambezi Valley in the Vila Pery, Beira and Tete districts), S Malawi and SE Zambia (Meester *et al.* 1986).

Habitat Grassland with scattered bushes and trees on a sandy substrate (Smithers & Lobão Tello 1976).

Remarks Little is known about this species, although its biology is presumed to be similar to *E. brachyrhynchus*.

Conservation IUCN Category: Data Deficient, previously Least Concern.



Little is known about the status of this species; Nicoll & Rathbun (1990) provisionally assessed it as 'Safe'.

Measurements

Elephantulus fuscus

HB: 114.0 (105–125) mm, n = 5

T: 102.8 (86–116) mm, n = 5

HF: 28.6 (28–30) mm, n = 5

E: 19.9 (19.5–20) mm, n = 5

WT: 45, 46 g, n = 2

GLS: 33.9 (32.7–35.5) mm, n = 7

GWS: 17.8 (17.2–18.4) mm, n = 5

I¹–M³: 17.3 (16.3–17.9) mm, n = 7

Zambia and Malawi (BMNH, D.C. D. Happold unpubl.)

Key References Corbet 1974b; Corbet & Hanks 1968; Meester *et al.* 1986.

Mike Perrin

Elephantulus intufi BUSHVELD SENGI (BUSHVELD ELEPHANT-SHREW)

Fr. Macroscélide des régions sèches; Ger. Trockenland-Elefantenspitzmaus

Elephantulus intufi (A. Smith, 1836). Report of the Expedition for Exploring Central Africa 1834: 42 [1836].

Flats beyond Kurrichane, Marico district, North West Province, South Africa.

Taxonomy Originally described in the genus *Macroscelides*. Ellerman *et al.* (1953) included all the forms now considered as *E. rupestris* (Corbet & Hanks 1968) within *E. intufi*. Genetic studies suggest that this species is most closely related to *E. rupestris* (Raman & Perrin 1997). Morphological variation within and between populations of *E. intufi* is low (Matson & Blood 1997). Synonyms: *alexandri*, *schinzi*, *kalaharicus*, *mossamedensis*, *namibensis*, *campbelli*, *mchughi*, *omahekensis*, *canescens*. Subspecies: none. Chromosome number: 2n = 26 (Tolliver *et al.* 1989).

Description Small pale-coloured sengi, with white eye-ring. Pelage long and dense; hairs ca. 12 mm on mid-dorsal line. Dorsal pelage yellowish-buff; hairs dark grey, with yellowish-buff tip; long black-tipped guard hairs (especially on the rump). Flanks paler. Ventral pelage white or greyish-white; hairs white, grey at base. Head large. Eyes with white eye-ring. Ears large, rounded at tip, buffy, with conspicuous long white hairs on inner margins. Golden-buffy patches behind each ear. Pectoral gland absent, subcaudal gland possibly present. Hindlimbs elongated; five digits; soles of hindfeet naked, pale brown. Tail relatively long (ca. 105% of HB), dense short white hairs (with black tips) above, white below; no tuft at tip. M₃ absent. No evidence of sexual dimorphism (Matson & Blood 1997). Nipples: 1 + 2 = 6.

Geographic Variation Individuals from the eastern and southern parts of the geographic distribution tend to be paler than those from N Namibia (Corbet & Hanks 1968).

Similar Species

E. myurus. Almost always larger in size; soles of feet black; NE South Africa and Zimbabwe.

E. rupestris. On average larger in size; dorsal pelage brownish; eye-ring less conspicuous; tail tufted with long black tuft at tip; tail relatively longer; Eastern Cape Province, South Africa, and W Namibia.

This species and *E. rupestris* are often difficult to distinguish in the field, especially where the two occur in close proximity where bushveld habitat meets rock outcrops (Tolliver *et al.* 1989).

Distribution Endemic to Africa. South-West Arid BZ (Kalahari Desert and parts of Namib Desert). Recorded from Namibia, SW Angola, S Botswana and South Africa (adjacent to the borders with Namibia and Botswana).

Habitat Arid habitats with low shrubs and scattered grasses, usually on compact sandy soils.

Abundance Widespread, but usually not abundant or dense and often rare (G. B. Rathbun pers. obs.).

Adaptations The behavioural ecology of this species is similar to *E. rufescens* of eastern Africa (Rathbun 1979). In Namibia (Rathbun & Rathbun 2006, G. B. Rathbun pers. obs.), Bushveld Sengis normally shelter at comparatively exposed sites at the bases of bushes or under



large boulders, and may temporarily use rodent burrows to escape disturbances. Their activity is polycyclic, with crepuscular peaks. Like many *Elephantulus*, they build and maintain paths through the surface litter with sweeping actions of the forefeet; the paths connect basking, sheltering and feeding areas within the home-range.

Bushveld Sengis are well adapted to their arid environment in aspects of their thermal biology and metabolism. Basic metabolic rate is 73–94% of that expected in relation to size; T_b is maintained at 33.5–37.7°C over a wide range of T_a (5–30°C), even during cold nights (Perrin 1995). Hyperthermia is prevented at high temperatures by evaporative water loss, which may be as high as 156% of the normal rate for short periods, and by behavioural means (habitat selection, inactivity, etc.). When T_a is cool, T_b is maintained by resting in (warmer) burrows, vasoconstriction and good insulation. Torpor has not been reported.

Communication with conspecifics probably includes foot-drumming, scent-marking and vocalizations (high-pitched alarm squeak and soft 'purrs' [Faurie 1996, G. B. Rathbun pers. obs.]). Foot-drumming is highly variable (Faurie *et al.* 1996) and probably is a graded response to stressful situations (G. B. Rathbun pers. obs.).

Foraging and Food Insectivorous. Feeds primarily on ants. Also catches larger prey, which are carried to the safety of cover for ingestion. Sometimes eats some plant material.

Social and Reproductive Behaviour In Namibia (Rathbun & Rathbun 2006), opposite sex pairs share highly overlapping home-ranges that are exclusive of neighbours; mate-guarding by ♂♂

results in social monogamy. Average territory area of ♂ is 0.47 ha compared to 0.32 ha for ♀♀. Pairs shelter separately and interact infrequently and, except for brief polygamous associations, remain paired for life.

Reproduction and Population Structure Reproduction may be seasonal in the southern part of the range, corresponding with the warm and wet months of Aug–Mar (Skinner & Smithers 1990), but is nearly year-round in Namibia (Rathbun & Rathbun 2006). Litter-size: 1–2. Mean embryo number in Botswana: 1.9 ($n = 9$; Smithers 1971). Young are precocious at birth; the mother only visits neonates infrequently to nurse, and there is no direct or indirect paternal investment (Rathbun & Rathbun 2006).

Predators, Parasites and Diseases Barn Owls *Tyto alba* are a known predator (Vernon 1972) and the Horned Adder *Bitis caudalis* also preys on Bushveld Sengis (G. B. Rathbun pers. obs.). Ectoparasites include one species of ixodid tick, *Rhipicephalus parvus* (Fourie *et al.* 1995).

Conservation IUCN Category: Least Concern.

The unspecialized habitat requirements and comparatively wide distribution of the species in southern Africa suggest that it is not threatened at present. Nicoll & Rathbun (1990) provisionally assessed it as 'Safe'.

Measurements

Elephantulus intufi

TL (♂♂): 237.7 (218–246) mm, $n = 7$

TL (♀♀): 244.3 (238–254) mm, $n = 4$

T (♂♂): 118.3 (102–128) mm, $n = 7$

T (♀♀): 121.8 (117–131) mm, $n = 4$

HF (♂♂): 32.7 (32–39) mm, $n = 10$

HF (♀♀): 34.0 (32–36) mm, $n = 6$

E (♂♂): 23.7 (22–25) mm, $n = 10$

E (♀♀): 24.0 (23–26) mm, $n = 6$

WT (♂♂): 45.9 (43–54) g, $n = 12$

WT (♀♀): 45.7 (35–62) g, $n = 15$

GLS (♂♂): 33.8 (32.7–35.0) mm, $n = 10$

GLS (♀♀): 34.2 (33.0–35.0) mm, $n = 6$

GWS (♂♂): 19.3 (18.9–19.8) mm, $n = 8$

GWS (♀♀): 19.6 (19.0–20.0) mm, $n = 5$

I^1 – M^3 (♂♂): 17.1 (16.3–17.7) mm, $n = 10$

I^1 – M^3 (♀♀): 17.3 (16.7–13.2) mm, $n = 6$

Measurements: southern Africa (Rautenbach & Schlitter 1977)

Weight: Omaruru, Namibia (G. B. Rathbun unpubl.)

Key References Corbet & Hanks 1968; Ellerman *et al.* 1953; Meester *et al.* 1986; Rathbun & Rathbun 2006; Smithers 1971.

Mike Perrin & Galen B. Rathbun

***Elephantulus myurus* EASTERN ROCK SENGI (EASTERN ROCK ELEPHANT-SHREW)**

Fr. Macroscélide oriental; Ger. Östliche Klippen-Elefantenspitzmaus

Elephantulus myurus Thomas and Schwann, 1906. Proceedings of the Zoological Society, London 1906: 586. Woodbush, Limpopo Province (formerly NE Transvaal), South Africa.

Taxonomy Originally described as a subspecies of *E. rupestris*, but recognized as specifically distinct by Roberts (1935). *Elephantulus myurus* is closely related to *E. rupestris* on the basis of allozyme and isozyme comparisons, although it also shows affinities with *E. edwardii* (Raman & Perrin 1997). Synonyms: *jamesoni*, *mapogonensis*, *centralis*, *fitzsimonsi*. Subspecies: none, although *fitzsimonsi* may represent a valid subspecies (race) (Corbet & Hanks 1968). Chromosome number: $2n = 30$ (Ford & Hamerton 1956).

Description Small greyish sengi with white eye-ring. Dorsal pelage buffy-grey, soft and woolly, becoming greyer towards the rump. Flanks paler and greyer than dorsal pelage. Ventral pelage white or pale grey. Pectoral gland absent; subcaudal gland present. Head large, with large eyes and conspicuous white eye-ring. Ears large, brown, rounded at tip, with fringe of white hairs in inner margin. Buffy patch behind ears not conspicuous. Hindlimbs long; five digits; soles of hindfeet black. Tail relatively long (ca. 110% of HB), with sparse short hairs, dark above, paler below, without tuft at tip. M_3 absent. Nipples: $1 + 2 = 6$.

Geographic Variation Very little variation, although the length of the upper toothrow decreases clinally to the north (Corbet & Hanks 1968).

Similar Species

E. rupestris. Dorsal pelage greyish-brown; comparatively conspicuous buffy patch behind ears with rufous-yellow hair at the base of the ears; tail hairy with black tuft at tip; South Africa and W Namibia; only marginally sympatric.

Distribution Endemic to Africa. Zambezi Woodland BZ and parts of the Highveld BZ. Recorded from South Africa (NE Eastern Cape Province northwards to KwaZulu-Natal and former Transvaal), Lesotho, Zimbabwe, SE Botswana and SW Mozambique. Not recorded from Swaziland (Monadjem 1998).

Habitat Rocky outcrops on hill slopes, kopjes or piles of boulders in semi-arid environments. Holes and crannies in rocks that are used for shelter are essential for survival. Partially sympatric with *E. brachyrhynchus*, which lives in adjacent sandy, flat ground.

Abundance Locally common with marked interannual changes in density depending on the amount of rainfall. Densities may be high (88/ha) when insect abundance peaks during periods of average rainfall, but decline quickly to small isolated groups (even in prime habitats) when rainfall is low (Du Toit 1993). Tends to be commoner where there are large boulders and rock debris, and less common in isolated rock outcrops and unbroken hill slopes.

Adaptations Terrestrial, in rocky habitats. Predominantly diurnal, with a peak of activity at dawn, but also active at night



(Woodall *et al.* 1989). Shelters in crevices and under rocks, without building any nest (Du Toit 1993). Extremely agile, capable of jumping from rock to rock. Eastern Rock Sengis are well adapted to semi-arid environments: the structure of the kidney shows characters for conserving water (Downs 1996); when T_a is cold, these sengis become hypothermic and enter torpor (Perrin 1995). Deep torpor occurs when T_b is 5°C ; during deep torpor (which does not exceed 24 h in length) oxygen consumption drops to just 2% of basal metabolic rate (Lovegrove *et al.* 2000a, b).

As in many other species of *Elephantulus*, communication is probably by foot-drumming, scent-marking and vocalizations, which includes a 'mew' with a fundamental of 1.47 kHz that averages 468 msec (Faurie 1996). Foot-drumming is performed during social encounters and also to indicate alarm; some drumming traits are probably specific to Eastern Rock Sengis (Faurie *et al.* 1996).

Foraging and Food Insectivorous. The diet is mostly small insects, especially termites and ants. Forages from cover, with quick hops to seize prey; large prey (the size of a large grasshopper) is carried into cover for ingestion. The caecum is small, but definitely plays a role in the digestion of protein (Woodall & Mackie 1987).

Social and Reproductive Behaviour Mate-guarding by ♂♂ results in social monogamy (Ribble & Perrin, 2005). Pair bonding is weak, and unattended ♀♀ may be temporarily attended by an adjacent monogamous ♂ (Ribble & Perrin 2005), similar to *E. rufescens* (Rathbun 1979) and *E. intufi* (Rathbun & Rathbun 2006).

Reproduction and Population Structure The reproductive biology of this species is documented in a large series of papers by Van der Horst & Gillman (e.g. 1941) and Van der Horst (e.g. 1946, 1954); ♀♀ polyovulate, producing a mean of 49 ova/ovary (range 25–89, n = 50) at each ovulation (Tripp 1971). Young are born during the warm, wet summer (Sep–Mar). Gestation: ca. eight weeks. Embryo number: 1.7 (1–2) in Botswana (Smithers 1971); 1.9 (1–2) in South Africa (Tripp 1971). Young are precocial at birth and independent at a young age; ♀♀ become sexually mature at five or six weeks of age. Males have relatively small, abdominal testes, which are reproductively active throughout the year, but with a significant reduction in sperm numbers and viability during winter (Apr–Jun), when reproduction stops (Woodall & Skinner 1989).

Predators, Parasites and Diseases Known predators include Barn Owls *Tyto alba* (Vernon 1972), Cape Eagle-owls *Bubo capensis mackinderi* (Gargett & Grobler 1976) and Rhombic Skaapsteker *Psammodromus rufescens* (Van Wyk, 1988). Parasites include eight species of ticks and two non-tick arthropods (Fourie *et al.* 1995).

Conservation IUCN Category: Least Concern.

This species occupies rocky habitats that are in little danger of modification from human activities and the species is comparatively widespread in southern Africa.

Measurements

Elephantulus myurus

TL (♂♂): 275.1 (239–288) mm, n = 21
 TL (♀♀): 276.3 (264–292) mm, n = 13
 T (♂♂): 147.3 (135–160) mm, n = 21
 T (♀♀): 147.2 (137–159) mm, n = 13
 HF (♂♂): 39.5 (38–42) mm, n = 24
 HF (♀♀): 39.3 (37–41) mm, n = 13
 E (♂♂): 26.6 (25–28) mm, n = 24
 E (♀♀): 26.5 (25–28) mm, n = 13
 WT n. d.
 GLS (♂♂): 38.5 mm, n = 22*
 GLS (♀♀): 38.1 mm, n = 6*
 GWS (♂♂): 20.4 (19.5–21.2) mm, n = 20
 GWS (♀♀): 20.1 (19.4–20.4) mm, n = 7
 I¹–M³ (♂♂): 20.6 (19.9–21.2) mm, n = 25
 I¹–M³ (♀♀): 20.6 (20.0–21.3) mm, n = 12
 Southern Africa (Rautenbach & Schlitter 1977)
 *Minimum and maximum not available

Key References Corbet & Hanks 1968; Faurie *et al.* 1996.

Mike Perrin & Galen B. Rathbun

Elephantulus revoili SOMALI SENGI (SOMALI ELEPHANT-SHREW)

Fr. Macroscélide de Somalie; Ger. Somali-Elefantenspitzmaus

Elephantulus revoili (Huet, 1881). Bull. Soc. Philomath. Paris, ser. 7, 5: 96. Medjourtine, NE Somalia.

Taxonomy Originally described in the genus *Macroscelides*. A clearly defined but little-known species, closely related only to *E. rufescens* (Corbet & Hanks 1968). Synonyms: none. Subspecies: none. Chromosome number: not known.

Description Small sengi with distinctive facial pattern, and fairly long hairy tail ending in a small tuft. Dorsal pelage pale brown to pinkish-grey; hairs grey or black at base, brown or pinkish-grey at tip; black-tipped guard hairs. Flanks paler. Ventral pelage whitish-grey; hairs black on basal third, white on terminal two-thirds. Head large; rhinarium hairy below. Eyes large, with narrow white eye-ring and dark postorbital patch that extends back to below ear. Ears grey-brown; dark buffy patch behind ears. Pectoral gland present, marked by dense fringes of short white hair. Subcaudal gland present. Hindfeet elongated; five digits. Tail relatively long (ca. 120% of HB); hairs white with brown tips; longer at terminal end forming small tuft at tip. Dorsal pelage of juveniles paler than in adults, with more yellow and less grey. M₃ absent. Nipples: 1 + 2 = 6.

Geographic Variation Individuals from the south of the geographic distribution tend to be paler, with hairs grey at base (rather than black) and fewer black-tipped guard hairs, than individuals from the north.

Similar Species

E. rufescens. On average slightly smaller, darker in colour; tail less hairy; distribution mostly further south in East Africa.

Distribution Endemic to Africa. Somalia–Masai Bushland BZ. Recorded from N coast of Somalia between 44° 00' E and 44° 20' E; isolated specimens from Run, Garoe, Somalia (48° 17' N, 48° 20' E).



Elephantulus revoili

Possibly sympatric with *E. rufescens* but in different habitats. Occurs above 1300 m in northern part of range.

Habitat Stony ground in montane habitats.

Abundance Possibly rare; very few specimens have been collected.

Remarks Apparently no other information available.

Conservation IUCN Category: Data Deficient.

Little is known about the status of this species or its habitat. The small geographic range may be cause for concern.

Measurements

Elephantulus revoili

HB: 132 (122–148) mm, n = 6

T: 157 (144–167) mm, n = 6

HF: 37.3 (34–39) mm, n = 6

E: 24.3 (23–25) mm, n = 5

WT: n. d.

GLS: 37.6 (36.4–38.7) mm, n = 6

GWS: 20.8 (18.6–21.9) mm, n = 6

I¹–M³: 19.2 (17.3–21.0) mm, n = 5

Somalia (Corbet & Hanks 1968, BMNH)

Key Reference Corbet & Hanks 1968.

Mike Perrin

Elephantulus rozeti NORTH AFRICAN SENGI (NORTH AFRICAN ELEPHANT-SHREW)

Fr. Macroscélide de Rozet; Ger. Nordafrikanische Elefantenspitzmaus

Elephantulus rozeti (Duvernoy, 1833). Mem. Soc. Hist. Nat. Strasbourg 1 (2) art. 4: 18. Near Orana, Algeria.

Taxonomy Originally described in the genus *Macroscelides*. This species is not conspecific with *E. rufescens* (Corbet 1974b), as suggested by Ellerman *et al.* (1953). Based on molecular genetics and penis morphology *E. rozeti* is more closely related to *Petrodromus* than to other *Elephantulus* (Douady *et al.* 2003). Synonyms: *atlantis*, *clivorum*, *deserti*, *moratus*. Subspecies: two. Chromosome number: 2n = 28 (Matthey 1954).

Description Small sengi. Pelage long, soft and silky; hairs 12–14 mm on mid-dorsal line. Dorsal pelage yellowish-brown to pale buffy-brown; hairs black at base, brown or buff at tip; some longer hairs with black tips. Flanks paler. Ventral pelage greyish-white; hairs black at base, white at tip. Rhinarium naked. Eyes large, but smaller than other *Elephantulus*, without eye-ring. Ears large, rounded at tip, with large tragus; buffy patch behind ears (sometimes inconspicuous). Postorbital dark spot absent. Pectoral gland absent; subcaudal gland present and especially well developed. Hindfeet elongated; five digits. The only species of *Elephantulus* with very rugose interdigital pads. Tail relatively long (ca. 110% of HB), hairy, dark above, paler below, with small pencil at tip. M₃ absent. Nipples: 1 + 2 = 6.

Geographic Variation Corbet & Hanks (1968) recognize two subspecies:

E. r. rozeti: Morocco and Algeria north of the Atlas Mts. Dorsal pelage dark; hairs with brown tip ca. 2 mm; I¹–M² on average longer (mean 17.7 [17.0–18.8] mm).

E. r. deserti: Tunisia and Morocco south of the Atlas Mts (but not into the desert). Dorsal pelage pale greyish-buff, brown tips 3–4 mm; I¹–M² on average shorter (mean 16.9 [16.5–17.6] mm).

Similar Species This is the only species of sengi in North Africa. No close physical resemblance with any other *Elephantulus* species.

Distribution Endemic to Africa. Mediterranean Coastal BZ of

NW Africa from SW Morocco/Western Sahara to Tunisia and W Libya. Altitudinal range: sea level to 1600 m, and occasionally to 2725 m (Cuzin & Séguignes 1990). The Atlas Mts divide the western part of the range into a coastal region with typical Mediterranean climate, and a drier southern region continuous with the Sahara Desert. In NE Algeria and Tunisia, the range is more likely to be continuous from the coast to the edge of the desert (Corbet & Hanks 1968).

Habitat Semi-arid rocky areas, including outcrops, mountainsides and scree slopes; often adjacent to bush-scrub and grassland habitats (Cabrera 1932, Séguignes 1988).



Elephantulus rozeti

Abundance Widespread and locally common, but not abundant. Can maintain high population densities in optimal habitat (M. R. Perrin unpubl.).

Adaptations Terrestrial. Mainly crepuscular and nocturnal, although may sunbathe for short periods of time (Aulagnier & Thévenot 1986). Shelters among rocks and boulders where T_a remains comparatively constant and is neither too hot nor too cold, or in burrows made by other species. During summer, they are mainly active at dusk and from 02:00h to 04:00h, but in winter, activity is mainly during the day from 10:00h to 16:00h (Séguignes 1983). Prominent subcaudal gland probably used for scent-marking (Cabrera 1932). Locomotion is similar to other sengis; bipedal hopping has not been observed (Cabrera 1932).

T_b varies from 32°C in the shade to 37°C in the sun, and individuals actively move from shade to sun as a means of controlling T_b . In experimental conditions, when T_a is about 20°C, enters torpor and is capable of arousing spontaneously. When T_a is 10–19.5°C, T_b is the same as T_a , and individuals are incapable of arousal until T_a increases to above 20°C (Séguignes 1983). Sandbathes by rubbing head and body in sandy soil accompanied by vigorous kicking of the hindlimbs, similar to other *Elephantulus* species.

Foraging and Food Insectivorous. Forages at base of rock scree and boulders for insects.

Social and Reproductive Behaviour No data available.

Reproduction and Population Structure Mating occurs Jan–Apr, and young are born Mar–Jun. At higher altitudes in Morocco, young are born later (Apr). Gestation: ca. 75 days (longer than for other small sengis). May produce two litters/year at low altitudes, but only one litter/year at higher altitudes. Embryo number: 2.4 (1–4), $n = 48$; mode 2. In 48 ♀♀, the number of embryos/female was 1 ($n = 2$), 2 ($n = 28$), 3 ($n = 15$) and 4 ($n = 3$). Females producing two young/litter contributed 49% of young. Young are

born with eyes open and with hair, and can eat insects while still suckling (Séguignes 1989). Reproduction is constrained by the comparatively short period of warm weather (spring, summer) and the comparatively long gestation. The mean embryo number and maximum embryo number is greater than in other sengis.

Predators, Parasites and Diseases Remains of these sengis are commonly found in owl pellets in Algeria (Kowalski & Rzebik-Kowalski 1991). They are also preyed upon by rock-dwelling snakes (M. R. Perrin unpubl.). A remarkable number of endoparasites have been described (Seurat 1913, 1914, Delanoe 1931, Fain & Lukoschus 1976, Quentin 1978, 1979, Quentin & Seureau 1978, Kolebinova 1979).

Conservation IUCN Category: Least Concern.

Little is known about the status of this species; Nicoll & Rathbun (1990) provisionally assessed it as 'Safe' because the rocky habitats where it lives are rarely disturbed by humans.

Measurements

Elephantulus rozeti

HB: 108.1 (100–120) mm, $n = 14$

T: 113.4 (105–137) mm, $n = 14$

HF: 31.8 (30–34) mm, $n = 13$

E: 24.6 (21–27) mm, $n = 14$

WT: 45.3 ± 1.4 g, $n = 7$

GLS: 33.8 (32.7–34.8) mm, $n = 8$

GWS: 19.9 (19.2–20.5) mm, $n = 8$

I^1-M^3 : 17.5 (16.8–18.8) mm, $n = 8$

Measurements: Morocco and Algeria (BMNH)

Weight: Morocco and Algeria (M. R. Perrin unpubl.)

Key References Aulagnier & Thévenot 1986; Cabrera 1932; Corbet & Hanks 1968; Séguignes 1983, 1988, 1989.

Mike Perrin & Galen B. Rathbun

Elephantulus rufescens RUFIOUS SENGI (RUFIOUS ELEPHANT-SHREW)

Fr. Macroscélide roux; Ger. Rotbraune Elefantenspitzmaus

Elephantulus rufescens (Peters, 1878). Monatsb. K. Akad. Wiss. Berlin 1878: 198. Ndi, Taita, Kenya.

Taxonomy Originally described in the genus *Macroscelides*. Corbet & Hanks (1968) do not recognize any subspecies, although Corbet (1974b) recognizes six subspecies (see below). This is a clearly defined species not closely resembling any other except *E. revoili*. Review of taxonomy and biology given by Koontz & Roeper (1983). Synonyms: *boranus*, *delicatulus*, *dundasi*, *hoogstraali*, *mariakanae*, *ocularis*, *peasi*, *phaeus*, *pulcher*, *rendilis*, *renatus*, *somalicus*. Subspecies: six. Chromosome number: $2n = 34$ (Robbins & Baker 1978).

Description Small sengi with distinctive facial pattern. Pelage dense, hairs ca. 10 mm on mid-dorsal line. Dorsal pelage rufous, grey, buff or yellowish (according to locality – see below); hairs dark grey, grey-buff on terminal quarter. Ventral pelage pure white. Head large, with hairy rhinarium (a character shared only with *E.*

revoili). Eyes large, with conspicuous white eye-ring that enlarges to form a large white eyebrow; dark postorbital patch extends to below ear. Ears large, rounded at tip; buff or whitish-buff postauricular area present. Pectoral gland present, surrounded by short woolly white hairs. Subcaudal gland present, but rudimentary. Hindlimbs elongated; five digits. Feet white in adults (brown in juveniles), with dark claws. Tail relatively long (ca. 105% of HB), dark brown, sparsely haired, without tuft at tip. M_3 absent. Nipples: $1 + 2 = 6$.

Geographic Variation Six subspecies are recognized by Corbet (1974b):

E. r. boranus: S Ethiopia.

E. r. dundasi: N Kenya, Uganda and Sudan.

E. r. peasi: E Ethiopia.
E. r. pulcher: N Tanzania.
E. r. rufescens: SE Kenya.
E. r. somalicus: N Somalia.

Colour variation may be related to the type and colour of the soil. Kingdon (1974: plate opp. p. 65) refers to a 'red population' in SE Kenya (= *rufescens*?), a 'grey population' in NW Tanzania (= *pulcher*?) and a 'yellow population' in C Tanzania. Intermediate forms are also present. Within a single population, there may be individual variation in respect of some skull characters (supernumerary teeth, number of accessory cups on premolars, length of palatal foramina). However, the level of variation is low, lower than in other *Elephantulus* spp. (Matson *et al.* 1984).

Similar Species

E. revoli. On average slightly larger; dorsal pelage pale brown to pinkish-grey; tail with tuft at tip; Somalia only. Both species have a hairy rhinarium and similar distinctive facial pattern.

Distribution Endemic to Africa. Somalia–Masai Bushland BZ. Recorded from Somalia, EC Ethiopia, extreme SE Sudan, Kenya, E Uganda and N Tanzania (southwards at least to Ruaha R.).

Habitat Dry woodland and bushland; open wooded steppe and grassland, where there are thickets that can be used for shelter.

Abundance Comparatively common in suitable habitats.

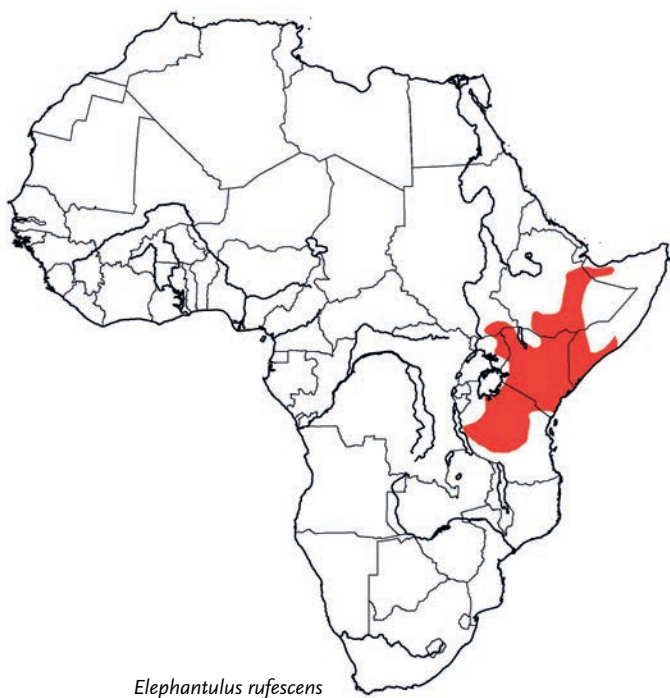
Adaptations Terrestrial. Active at all times of the day and night (polycyclic); in SE Kenya peaks of activity were crepuscular (06:00 to 09:00h, and 16:00 to 19:00h) with the least activity at mid-day (Rathbun 1979). Typical daylight activity budgets for an individual ♀ (and ♂): 30% (13%) foraging, 21% (40%) trail clearing, 24%

(30%) locomotion, 13% (13%) social interactions, 6% (0%) inter-specific interactions, 2% (1%) grooming and 3% (1%) combined activities (Rathbun 1979). When active, individuals travel between sheltering places (just a simple depression under a bush) along well-defined trails, which are maintained by 'sweeping' with the forefeet, by biting grass and small twigs, and pushing larger debris out of the way with the forefeet and forehead. Burrows generally are not used (Rathbun 1979). Body temperature is maintained at 34–38 °C when T_a is 10–35 °C (Perrin 1995). Sunbathing occurs frequently, especially in the early morning (Rathbun 1979). Basal metabolic rate is 82% of expected for weight (Thompson & Nicoll 1986). Both sexes scent-mark with pectoral and pedal glands (Rathbun & Redford 1981, Koontz 1984). Foot-drumming probably functions in both intra- and inter-specific communication, the latter perhaps as a predator invitation signal (Roeper 1981).

Foraging and Food Insectivorous. Foraging takes place on trails or on nearby (1–2 m) barren areas for a few seconds to a few minutes; foraging often alternates with trail clearing. When foraging in leaf litter, the nose is used as a probe while the forefeet clean away obstructing leaves and twigs. Prey is captured by rapid in-and-out flicking of the very long tongue (Rathbun 1979). The principal invertebrate prey (decreasing frequency of stomach content) in SE Kenya are harvester termites (*Odontotermes*), black ants, beetles, crickets and grasshoppers, spiders and silverfish. During the wet season, the fruits of a shrub (*Premna resinosa*) form a small part of the diet along with some green plant matter. Rufous Sengis are selective feeders; termites and ants form ca. 75% of the diet, but comprise only about 40% of the available invertebrates (Rathbun 1979). The diet in Meru National Park (C Kenya) is similar: arthropods (mainly termites and ants) form 93 to >99% of the diet, depending on the season; 0–7% is stem and leaf matter (Neal 1984b).

Social and Reproductive Behaviour Socially monogamous. In SE Kenya, home-ranges of ♂♂ and ♀♀ are congruent and vary in area from 0.16 ha to 0.52 ha. Where the habitat was not saturated, the home-ranges of most pairs were contiguous with those of neighbouring pairs (Rathbun 1979). Pairs defend their home-ranges (same-sex specifically). The pair association is stable and may last for as long as the individuals live, perhaps 2–3 years. Pair-bonding behaviour is infrequent and the ♀ is dominant over the ♂ (Rathbun 1979). Sexual interactions are brief, facilitated by familiarity between the ♂ and ♀ (Lumpkin & Koontz 1986). Vaginal marking by the ♀ occurs during oestrus, which is nearly the only time when pairs are inseparable (Rathbun 1979, Lumpkin *et al.* 1982). Male mate-guarding, rather than indirect paternal investment (trail maintenance), is probably responsible for their social monogamy (Rathbun & Rathbun 2006).

Reproduction and Population Structure Reproduction occurs throughout the year (Rathbun 1979, Neal 1982). In Meru N. P., Kenya, pregnancy rate was 65–100% (monthly $n = 2–17$), and was highest in wet season and lowest in the dry season. Mean embryo number varies with the weight of the ♀: smaller ♀♀ (<40 g) have only single embryos; larger ♀♀ (>40 g) have a mean embryo number of 1.51 (range: 1–2; $n = 37$) (Neal 1982). However, there were no seasonal changes in embryo number or recruitment of young into the population (Neal 1982). Females



Elephantulus rufescens

do not superovulate. Placenta: haemochorial (Oduor-Okello *et al.* 1980). Gestation: 57 days. Birth wt: ca. 10 g. Average daily gain ca. 1.0 g (Rathbun *et al.* 1981). Birth-sites are at comparatively exposed locations on the surface at the base of a shrub; no nesting material is used. At birth, young are highly precocial and remain at the birth-site for the first 1–2 days. Mean birth interval is 56–65 days ($n = 7$). Juveniles are weaned by Day 30 and both parents aggressively drive the young from their territory when the next litter is born. Juveniles either disperse to a vacant territory, try to establish a new one, or fall prey to predators. Mortality of young is high: survival to 100 days of age is ca. 40% (Rathbun 1979). Annual potential productivity is 8.3 young/annum (Neal 1982).

Predators, Parasites and Diseases In Kenya, only Speckled Sand Snakes *Psammophis punctulatus* are known predators (Rathbun 1979). In Serengeti N. P., Tanzania, 0.8% of owl pellets ($n = 345$) contained sengi bones (Laurie 1970). Three species of *Rhipicephalus* ticks, one species of sucking louse (Fourie *et al.* 1995) and a mite (Fain & Lukoschus 1976) have been recorded. Several endoparasites are also known (Hoogstraal *et al.* 1950, Kolebinova 1981).

Conservation IUCN Category: Least Concern.

Little is known about the status of this species; Nicoll & Rathbun (1990) provisionally assessed it as 'Safe'.

Measurements

Elephantulus rufescens

HB: 128.3 (102–199) mm, $n = 22$

T: 134.5 (111–163) mm, $n = 22$

HF: 33.8 (30–54) mm, $n = 22$

E: 25.0 (22–39) mm, $n = 22$

WT: 57.3 (47.1–70.2) g, $n = 16$

GLS: 36.1 (35.2–37.2) mm, $n = 12$

GWS: 20.1 (19.4–20.8) mm, $n = 12$

I¹–M³: 17.6 (17.2–18.1) mm, $n = 12$

Body measurements and weight: Kibwezi, Kenya (G. B. Rathbun unpubl.)

Skull measurements: Cherangani Mts, Kenya (Matson *et al.* 1984)

References Corbet 1974b; Neal 1982, 1984b; Rathbun 1979.

Mike Perrin & Galen B. Rathbun

Elephantulus rupestris WESTERN ROCK SENGI (WESTERN ROCK ELEPHANT-SHREW)

Fr. Macroscélide occidental; Ger. Westliche Klippen-Elefantenspitzmaus

Elephantulus rupestris (A. Smith, 1831). Proc. Zool. Soc. Lond. 1830–1831: 11.
Mountains near the mouth of the Orange River (= Little Namaqualand [Shortridge 1934]).

Taxonomy Originally described in the genus *Macroscelides*. According to Corbet & Hanks (1968), 'Ellerman *et al.* (1953) included this species in *E. intufi* and used the name *rupestris* for the species that we call *E. myurus* and *E. edwardii*. This error was caused by confusion over type specimens. Meester *et al.* (1986) recognized *rupestris* as a valid species, as do Corbet & Hanks (1968). Morphological analysis shows that there is little variation within and between populations (Matson & Blood 1997). Allozyme and chromosomal studies suggest that *E. rupestris* is closely related to *E. intufi* (Tolliver *et al.* 1989), and allozyme and isozyme data generally show a close relationship to *E. myurus* (Raman & Perrin 1997). Synonyms: *barlowi*, *gordoniensis*, *kobosensis*, *montanus*, *okombahensis*, *tarii*, *typus*, *vandami*. Subspecies: none. Chromosome number: $2n = 26$ (Wenhold & Robinson 1987).

Description Small sengi with broad patch of rufous or yellowish-brown hair behind ears. Dorsal pelage greyish-brown or rufous-brown, becoming grey on flanks; hairs dark grey, with rufous-brown at tip; some longer hairs with black tips especially on mid-dorsal line. Ventral pelage greyish-white; hairs grey at base, tip white. Head large with elongated snout, narrow black line dorsally. Eyes large; eye-ring indistinct. Ears large, rounded at tip, with distinct patch of rufous hair from base to nape of neck. Pectoral gland absent; subcaudal gland present. No dark spot behind the eye. Hindlimbs elongated; five digits. Soles of hindfeet naked, black. Tail relatively very long (ca. 115% of HB), black above, paler below, with black tuft at tip. M₃ absent. Mean measurements of ♀♀ slightly larger than for ♂♂. Nipples: 1 + 2 = 6.

Geographic Variation All named forms show variation in pelage colour.

Similar Species

E. myurus. Ventral pelage greyer; eye-ring conspicuous; tail without tuft at tip; South Africa, Zimbabwe.

E. intufi. Ventral pelage greyish-white; eye-ring present; tail usually shorter, paler, with small tuft at tip; Namibia, S Botswana.

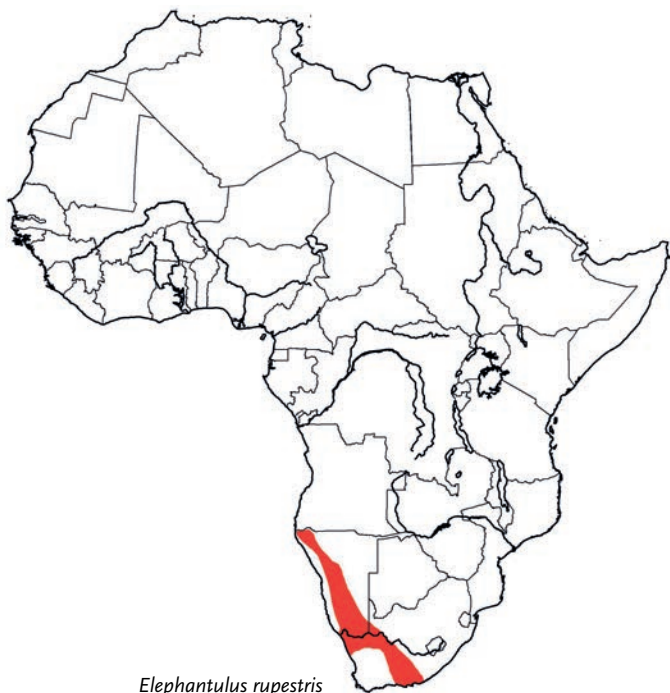
E. edwardii. Ventral pelage greyish-white; eye-ring present; tail black above, distal one-third completely black with small tuft at tip; western parts of South Africa.

Elephantulus rupestris and *E. intufi* are often difficult to distinguish in the field, especially where the two occur in close proximity where bushveld habitat meets rock outcrops (Tolliver *et al.* 1989).

Distribution Endemic to Africa. South-West Arid BZ (Namib Desert and Karoo) and parts of South-West Cape BZ. Recorded from South Africa (Eastern Cape Province to Little Namaqualand, where isolated populations occur) and W Namibia (Kaokoveld to just south of the border with Angola). Absent from NE Namibia and Western Cape Province of South Africa.

Habitat Rocky kopjes and outcrops or piles of boulders in arid and semi-arid areas.

Abundance No information.



Adaptations Little is known about this species. Terrestrial, and adapted to living among rocks. Predominantly crepuscular. Locomotion quadrupedal, often characterized by habitual use of specific routes across rock surfaces. Vocalizations ('mews' and 'clicks'), foot-drumming and scent marking are used, probably for communication (Faurie 1996). Foot-drumming is characterized by 30–50 drums/bout (more than in other *Elephantulus* spp.), drum intervals of 15–25 msec, and one bout/series; the length of a series is 1–1.5 sec (Faurie *et al.* 1996). This species is more active and less aggressive than other related species (Faurie 1996).

Foraging and Food Insectivorous. Principal prey are ants and termites.

Social and Reproductive Behaviour Probably similar to *E. myurus*. Often trapped as male–female pairs (Withers 1979),

and thus probably monogamous and territorial, as in other sengis (Rathbun & Rathbun 2006).

Reproduction and Population Structure Little information. In Namibia, ♀♀ were pregnant in Sep. Embryo number: 1–2 (Shortridge 1934). Females may produce several litters each year.

Predators, Parasites and Diseases Barn Owls *Tyto alba* are known predators (Vernon 1972). Ectoparasites include ten species of fleas, 11 species of ixodod ticks and one species of mite (Fourie *et al.* 1995).

Conservation IUCN Category: Least Concern.

The rocky habitats of this species are not subject to human interference, and are comparatively widely distributed in southern Africa.

Measurements

Elephantulus rupestris

TL (♂♂): 269.0 (239–292) mm, n = 24

TL (♀♀): 274.5 (255–292) mm, n = 19

T (♂♂): 145.5 (122–166) mm, n = 24

T (♀♀): 149.7 (137–163) mm, n = 19

HF (♂♂): 36.5 (34–38) mm, n = 26

HF (♀♀): 37.1 (35–39) mm, n = 20

E (♂♂): 26.0 (22–29) mm, n = 26

E (♀♀): 26.4 (24–38) mm, n = 20

WT: n. d.

GLS (♂♂): 36.5 (35.0–37.9) mm, n = 21

GLS (♀♀): 36.9 (35.6–38.6) mm, n = 17

GWS (♂♂): 20.0 (19.2–20.9) mm, n = 24

GWS (♀♀): 20.0 (19.1–20.9) mm, n = 16

I¹–M³ (♂♂): 19.1 (18.2–20.1) mm, n = 26

I¹–M³ (♀♀): 19.1 (18.4–19.7) mm, n = 20

Southern Africa (Rautenbach & Schlitter 1977)

Key References Corbet & Hanks 1968; Matson & Blood 1997; Meester *et al.* 1986.

Mike Perrin

GENUS *Macroscelides*

Round-eared Sengi

Macroscelides A. Smith, 1829. Zoological Journal, London 4: 435. Type species: *Macroscelides typus* A. Smith, 1829.



Macroscelides proboscideus.

The genus is monotypic (Table 13) and occurs only in semi-arid and arid environments of Cape Province, South Africa, W Namibia and SW Botswana. The genus is characterized by small size (HB usually less than 120 mm), five digits on fore- and hindfeet, three pairs of nipples, very inflated tympanic bullae (visible dorsally on the skull) and two molars on each mandible (Figure 18). Further information is given in the species profile. The single species is *Macroscelides proboscideus*.

Mike Perrin

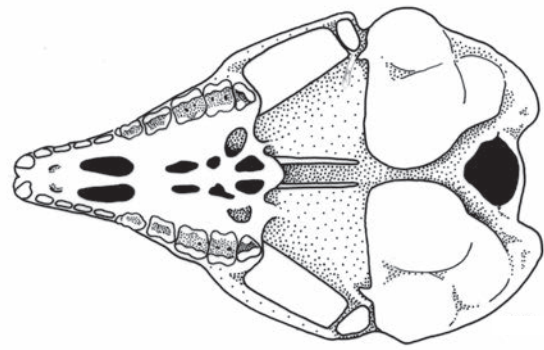
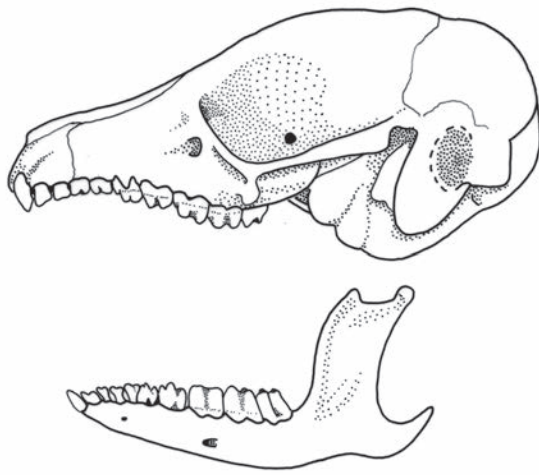


Figure 18. Skull and mandible of *Macroscelides proboscideus* (BMNH 25.1.2.11).

Macroscelides proboscideus ROUND-EARED SENGI (ROUND-EARED ELEPHANT-SHREW)

Fr. Macroscélide à oreilles courtes; Ger. Kurzohr-Rüsselspringer

Macroscelides proboscideus (Shaw, 1800). Gen. Zool. Syst. Nat. Hist. 1 (2), Mammalia, p. 536. Cape of Good Hope (specified as Roodewal, Oudthoorn, Cape Province [now Western Cape Province] by Roberts 1951).

Taxonomy Originally described in the genus *Sorex*. The only species in the genus *Macroscelides*. Synonyms: *ausensis*, *brandvleiensis*, *calvinensis*, *chiversi*, *flavicaudatus*, *harei*, *hewetti*, *isabellinus*, *jaculus*, *langi*, *melanotis*, *typicus*, *typus*. Subspecies: uncertain. Roberts (1951) recognized ten subspecies, based on pelage colouration, although only *flavicaudatus* in the north of the range may be valid, perhaps even at the species level (Corbet & Hanks 1968). The status of the form *melanotis* is uncertain: it is now considered to be conspecific with *M. proboscideus* because the specimen from Benguela, Angola, was a misidentified *E. intufi*, and the location of the holotype from Namibia was supposedly from South Africa (Corbet & Hanks 1968). The genetic distance between *M. proboscideus* and *Petrodromus tetradactylus* is comparatively low (0.323), implying a close relationship between these two species (Tolliver *et al.* 1989, Corbet 1995). Chromosome number: $2n = 26$ (Wenhold & Robinson 1987).

Description A small round-bodied sengi with a round face and round ears. Pelage long (up to 17 mm), soft and silky and rather fluffy-looking. Dorsal pelage buffy-grey to greyish-brown; hairs black at base with buffy-grey tip. Flanks yellowish-brown. Ventral pelage greyish-white; hairs black at base with white tip. Head large with long thin snout. Eyes moderate (smaller than in most *Elephantulus*), without white eye-ring. Ears broad and rounded (shorter than in most *Elephantulus*), white on inner edges and without buffy patch behind ears; tragus large; supratragus well-developed, but not twisted. Pectoral gland absent; subcaudal gland present. Hindlimbs elongated; five digits. Tail long (ca. 105% of HB), proximal half dark above, paler below; distal half all black with longer hairs forming tuft at tip. Skull with very enlarged tympanic bullae (which can be felt on the dorsal posterior part of the head). Nipples $1 + 1 + 1 = 6$.

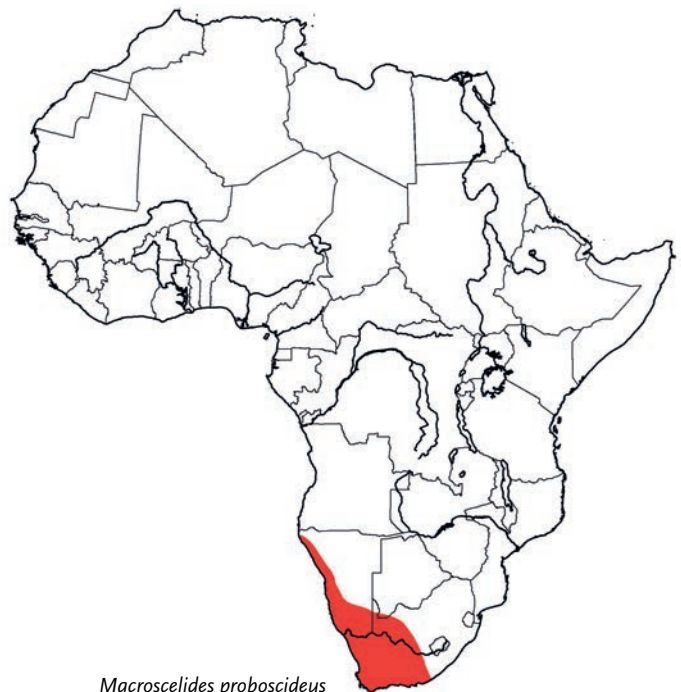
Geographic Variation Individuals from the Cape Province, South Africa, have darker pelage than those from Namibia, which are pinkish in the Namib Desert. According to Corbet & Hanks (1968)

this variation is clinal, but darker specimens recently trapped near the type location for *melanotis*, east of the Namib Desert in Namibia (M. Griffin pers. comm.), suggest that this is not always the case.

Similar Species

Elephantulus spp. (*E. edwardii*, *E. rupestris*, *E. intufi*). Large ears not rounded at tip; supratragus small; tympanic bulla not enlarged; white eye-ring present; buffy colour behind ears.

Distribution Endemic to Africa. South-West Arid BZ (Namib Desert and Karoo) and South-West Cape BZ. Recorded from



Macroscelides proboscideus

Northern, Western and Eastern Cape Provinces, South Africa (as far west as Grahamstown), W Namibia and extreme SW Botswana.

Habitat Desert and semi-arid regions. In the Namib Desert, associated with boulders and small rocky outcrops on gravel plains, where vegetation is exceedingly sparse. In the Karoo, found where gravel and sandy plains are well vegetated with low bushes and scrub. Livestock grazing reduces population numbers of this sengi (Eccard *et al.* 2000).

Abundance Locally common but not abundant. Numbers and densities may fluctuate over time, but quantitative data are lacking.

Adaptations Terrestrial. Highly cursorial (ca. 20 km/h), especially when running on trails (which are sometimes hundreds of metres in length) (Sauer 1973). Mainly nocturnal and crepuscular (Woodall *et al.* 1989, Roxburgh & Perrin 1994). Shelters under bushes, rocks, boulders, or scree (depending on habitat). May dig their own burrows (Sauer 1973) or use existing burrows.

The digestive tract is well adapted to an omnivorous diet (Woodall 1987, Kerley 1995, Spinks & Perrin 1995). The stomach is a simple unilocular glandular sac, the intestines are long and there is a functional caecum containing a diverse microflora (as in many purely herbivorous mammals). The characters of the digestive system change seasonally in response of the seasonal changes in diet (Woodall 1987).

Temperature regulation is atypical for a small mammal adapted to arid habitats (Roxburgh & Perrin 1994). T_b remains fairly constant (35–37.8 °C) over a wide range of T_a (5–38 °C) and is regulated behaviourally by basking, sheltering, and altering activity patterns. Vasodilation is also used when T_a is high. Evaporative water loss is comparatively low. Metabolic rate is close to the weight-specific prediction. Individuals enter torpor in cold weather (Roxburgh & Perrin 1994) and when deprived of food (Lovegrove *et al.* 1999).

The kidneys show adaptations to conserve water, with the pelvic region enlarged and elongated for efficient reabsorption of fluid. However, the kidneys are not as efficient at concentrating urine as those of *Elephantulus*. Captive sengis can maintain weight without drinking water when insects are available (Downs 1996). It is likely that in the wild, these sengis obtain all their water from their food. In these respects, they exhibit many similarities to arid-adapted small rodents.

Foraging and Food Omnivorous, feeding mainly on insects and herbage. In the Karoo of South Africa, the diet was 63.0% insects, 36.7% herbage, and a trace of seeds (Kerley 1995). At other locations, the proportion of insects was 46–88%, with considerable individual and seasonal variation. The consumption of insects was highest in Oct–Nov (77.4%, $n = 8$) and lowest in Jun–Jul (45.5%, $n = 4$). In captivity, Round-eared Sengis are also omnivorous (Unger & Schratte 2000).

Social and Reproductive Behaviour In the Namib Desert, home-ranges are up to 1.0 km², with varying degrees of overlap between loosely associated male–female pairs (Sauer 1973) that result in various degrees of social monogamy, depending on habitat and the population density (Rathbun & Rathbun 2006). Well-defined straight trails are maintained through gravel and substrate litter that connect shelters and feeding areas (Sauer 1973). Nesting material is not used in nests, and ♀♀ visit the highly precocial neonates infrequently (once a day?) to suckle. At about Day 5, the mother begins provisioning young with invertebrates collected in her cheeks (Sauer 1973). There is no direct paternal investment. Scent-glands (Faurie 1996) and foot-drumming (Faurie *et al.* 1996) are probably important in communication.

Reproduction and Population Structure Females polyovulate, producing 21 ova/ovary ($n = 2$) at each ovulation (Tripp 1971). In the Karoo of South Africa (Bernard *et al.* 1996), spermatogenesis and births occur throughout the year, but most pregnancies occur in the summer months (Sep–Feb), although a few occur in early winter. Oestrous cycle: ca. 10 weeks; gestation: ca. 56 days. Litter-size: 1–2 (Trautmann & Carbone 1991). At birth, young are highly precocial (Unger 2000), as in other Macroscelidinae; they are fully haired, and the eyes are open. Female suckles young for ca. 2 weeks, stops provisioning (see above) at ca. Week 3 and the young are independent at ca. Week 6 (Sauer 1973).

Predators, Parasites and Diseases Barn Owls *Tyto alba* are known predators (Vernon 1972). Ectoparasites include three species of fleas (Fourie *et al.* 1995).

Conservation IUCN Category: Least Concern.

Measurements

Macroscelides proboscideus

HB: 110.1 (104–115) mm, $n = 13$

T: 121.4 (107–134) mm, $n = 13$

HF: 34.1 (32–36) mm, $n = 13$

E: 22.2 (20–25) mm., $n = 13$

WT (♂♂): 38.0 (32–47) g, $n = 4$

WT (♀♀): 38.4 (31–47) g, $n = 5$

GLS: 33.7 (32.1–34.8) mm, $n = 13$

GWS: 21.0 (20.2–21.8) mm., $n = 13$

I¹–M³: 15.6 (15.0–16.3) mm, $n = 13$

Measurements: South Africa (BMNH)

Weight: South Africa (Smithers 1983)

Key References Corbet & Hanks 1968; Raman & Perrin 1997; Roxburgh & Perrin 1994; Sauer 1973; Woodall 1987.

Mike Perrin & Galen B. Rathbun

GENUS *Petrodromus*

Four-toed Sengi

Petrodromus Peters, 1846. Bericht Verhandl. K. Preuss. Akad. Wiss. Berlin 11: 258. Type species: *Petrodromus tetradactylus* Peters, 1846.



Petrodromus tetradactylus.

This monotypic genus (Table 13) is a comparatively unspecialized representative of the family. Characters of the genus include the narrow skull (proportionally the narrowest in the family); smallest braincase, smallest bullae and olfactory chamber; and the most constricted interorbital region (Figure 19). It also has proportionally longer forelimbs than hindlimbs compared with other sengis (Evans 1942). Based on molecular techniques and morphology, *Petrodromus* forms a distinct clade with the monospecific genus *Macroscelides* (Tolliver *et al.* 1989, Corbet 1995, Raman & Perrin 1997). However, more recent morphological and molecular data indicate that *Elephantulus rozeti* is more closely related to *Petrodromus* than to other *Elephantulus* (Douady *et al.* 2003). *Petrodromus* is the largest member of the subfamily Macroscelidinae, and is distinguished from other genera by five digits on forefoot, four digits on hindfoot (Digit 1 absent), and two pairs of nipples. In size, it is intermediate between the small to medium-sized *Macroscelides* and *Elephantulus* and the very large *Rhynchocyon* (Corbet & Hanks 1968). Dental formula is $I^{3/3}$,

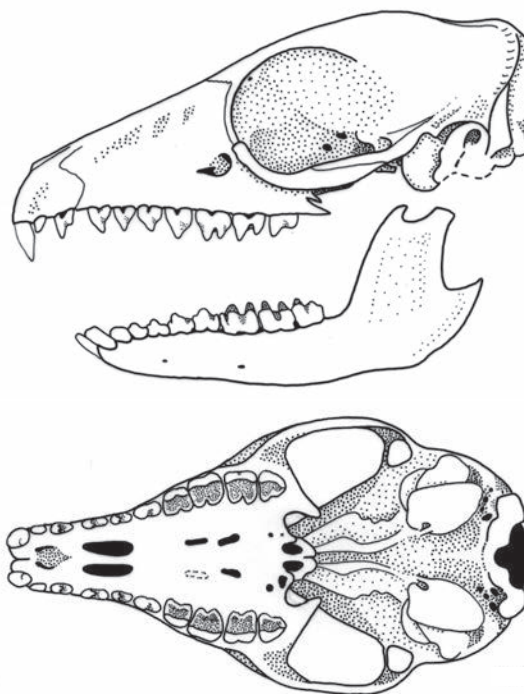


Figure 19. Skull and mandible of *Petrodromus tetradactylus* (BMNH 20.10.10.19).

$C^{1/1}, P^{4/4}, M^{2/2} = 40$. The first upper incisors are slightly recurved and over twice as long as the other incisors and canines. *Petrodromus* does not polyovulate (Tripp 1971). The 'pseudo-ungulate' habit and behaviour is less developed than in the three species of *Rhynchocyon*.

The single species is *Petrodromus tetradactylus*.

Galen B. Rathbun

Petrodromus tetradactylus FOUR-TOED SENGI (FOUR-TOED ELEPHANT-SHREW)

Fr. Pétródrome à quatre orteils; Ger. Vierzehen-Elefantenspitzmaus

Petrodromus tetradactylus Peters, 1846. Bericht Verhandl. K. Preuss. Akad. Wiss., Berlin 11: 258. Tette, Mozambique.

Taxonomy A varied species with one or two forms that may prove to justify specific rank (Corbet & Hanks 1968). Synonyms: *beirae*, *matschie*, *mossambicus*, *nigriseta*, *occidentalis*, *robustus*, *rovumae*, *sangi*, *schwanni*, *sultani*, *swynnertoni*, *tordayi*, *tumbanus*, *venustus*, *warreni*, *zanzibaricus*. Subspecies: nine (Corbet 1974b). Chromosome number: $2n = 28$, with eight pairs of metacentric and submetacentric chromosomes. Distinguished from all other Macroscelidea by presence of a small pair of subtelocentric autosomes on chromosomes 4 and 13 (Tolliver *et al.* 1989).

Description Medium-sized sengi with four digits on hindfoot and conspicuous facial markings. Pelage soft and dense. Dorsal pelage

varied: rusty-red, buffy-grey, or dark brown to grey. Dark wide mid-dorsal stripe is present in some forms; naked patch on rump at base of tail. Flanks buff or orange or pale grey. Ventral pelage white. Head large with moderately long snout; dark brown or black patch from behind eye to base of ear. Eye large, with distinctive white eye-ring. Ears broad and upright, rusty-brown to buffy-yellow. Limbs elongated and slender; forefeet with five digits, hindfeet with four digits (Digit 1 absent). Tail relatively long (ca. 85% of HB), slender, black above, paler below, sparsely haired; stiff bristles (see Adaptations) on the underside of the distal third in some forms. Pectoral gland slightly developed; subcaudal gland absent. Little or no sexual dimorphism. Nipples: 2 (one antebrachial, one pectoral) + 0 (inguinal) = 4.



Geographic Variation Colour and pattern variation in this species is extensive, and complex, and not well understood (see incomplete descriptions in Corbet & Hanks 1968). Some of the nine subspecies are provisional because further information may indicate clinal variation (Corbet & Hanks 1968, Corbet 1974b).

- P. t. beirae*: C Mozambique, south of Zambezi R.
- P. t. rovumae*: E Tanzania and N Mozambique.
- P. t. schwanni*: coast of S Mozambique.
- P. t. sultani*: coast of SE Kenya and NE Tanzania.
- P. t. swynnertoni*: Chimanimani Mts, E Zimbabwe.
- P. t. tetradactylus*: Malawi, Zambia, E DR Congo, W Tanzania, Ruanda.
- P. t. tordayi*: C and W DR Congo, NE Angola.
- P. t. warreni*: N KwaZulu–Natal, South Africa and Mozambique.
- P. t. zanzibaricus*: Mafia and Zanzibar Is.

Similar Species

Elephantulus rufescens. On average smaller, with distinct pectoral gland; similarly distinct white eye-ring with a dark posterior patch on cheek; nearly sympatric with *P. tetradactylus* in Kenya.

Distribution Endemic to Africa. Zambezian Woodland BZ, Coastal Forest Mosaic BZ and Southern Rainforest–Savanna Mosaic where rainfall exceeds about 700 mm/year, and from sea level to ca. 1400 m (Corbet & Hanks 1968). One subspecies (*tordayi*) in Rainforest BZ of DR Congo. Recorded from SE Kenya, S Uganda, Tanzania, Mozambique, Zambia, Malawi, SE Zimbabwe, DR Congo, E Congo, NE Angola and NE South Africa (KwaZulu–Natal Province). Also Mafia and Zanzibar Is.

Habitat Dense woody thickets in forests, closed canopy woodlands, rocky outcrops and riparian areas. In Kenya, sometimes sympatric and syntopic with *Rhynchocyon chrysopygus*, but the two species avoid competition because Four-toed Sengis prefer denser cover, prey on different invertebrates and are crepuscular rather than diurnal (FitzGibbon 1995).



Petrodromus tetradactylus

Abundance Widely distributed. In parts of the Arabuko–Sokoke Forest, Kenya, abundance varies according to habitat. Most abundant in habitats dominated by *Cynometra* trees, moderately abundant in *Afzelia* habitats and least abundant in *Brachystegia* habitats. In *Afzelia* habitats, the estimated density was 2.1 animals/ha (FitzGibbon 1995). Although comparatively common locally, these sengis are not easy to see because they are crepuscular and secretive. The most obvious evidence of their presence is the loud sound that they make by foot-drumming on the substrate (especially when disturbed), and their network of narrow paths through the leaf litter (Ansell & Ansell 1969, Kingdon 1974, Rathbun 1979).

Adaptations Terrestrial. Four-toed Sengis are highly cursorial and very alert. They are active at all times of the day, mainly at dawn and dusk, and usually rest in the middle of the day. The level of activity at night is uncertain, but may continue to at least 22:25h (FitzGibbon 1995). Movement is normally by walking and running; not by ricochets as reported in many accounts. A network of narrow paths is made through the leaf litter, and is maintained by sweeping motions with the front feet. Paths are also used to reach feeding areas, and to flee disturbances (Kingdon 1974, Rathbun 1979). These sengis do not build or use nests, but instead rest and groom on favoured sections of path. To escape predators, they sometimes retreat into hollow tree trunks or logs, and into holes in the ground (Ansell & Ansell 1969).

T_b is 33–37.5°C, generally 1–2°C lower than in smaller *Elephantulus* spp. Because of the larger size of this species, oxygen consumption/g body weight and evaporative water loss/g body weight is lower than in *Elephantulus* (Perrin 1995). The kidneys are unable to produce concentrated urine (cf. the arid-adapted sengis) so, when water is scarce, temperature regulation is effected by vasodilation and selection of comparatively cool micro-climates. When fed mealworms in captivity in the absence of drinking water, body weight can be maintained (Downs 1996). The stiff bristles along the underside of the tail probably function to spread sweat and sebaceous gland products on the substrate during scent marking (Jennings & Rathbun 2001). Other forms of communication include foot-drumming (similar to most Macroscelidinae), and soft purrs and chirps. Captured animals sometime scream loudly (Jennings & Rathbun 2001).

Foraging and Food Insectivorous and omnivorous. Prey is located by scuffing and disturbing leaf litter with the hindfeet and long mobile nose. The tongue is very long and used to glean exposed prey (Kingdon 1974). In coastal Kenya, prey (in decreasing order of importance) consists of beetles, termites, plant matter, centipedes, ants, crickets, millipedes and spiders (Rathbun 1979, FitzGibbon 1995). In other areas, ants and termites are the principal prey, together with some green plant material, seeds and fruits (Ansell & Ansell 1969).

Social and Reproductive Behaviour Appears to be solitary or to live in pairs (Brown 1964). Home-ranges in the Arabuko–Sokoke Forest, Kenya, dominated by *Afzelia* trees, averaged 1.2 ± 0.2 ha (FitzGibbon 1995). Although it is suspected that Four-toed Sengis form monogamous pairs for life, little is actually known

of their social behaviour (Rathbun 1979, FitzGibbon 1995). Captive animals are best maintained as opposite sex pairs to reduce intra-specific aggression, which suggests that they may be territorial and monogamous in the wild (Jennings & Rathbun 2001).

Reproduction and Population Structure Birth of young appears to vary according to location and climate. Young have been recorded for most months of the year in eastern Africa (Jennings & Rathbun 2001). In Zambia, foetuses have been recorded in Jan, Jul and Oct (Ansell 1960). In southern Africa, breeding occurs mainly during the wet months of Aug–Oct (Smithers 1983). Litter-size: 1, occasionally 2. At birth, young weigh about 31.5 g, are highly precocial and are able to walk within hours of birth (Tripp 1971, Rathbun 1979). Four-toed Sengis have not been successfully bred in captivity (Nicoll & Rathbun 1990).

Predators, Parasites and Diseases Predators include the Gabon Viper (*Bitis gabonica*), domestic cats and probably raptors and native carnivores (Ansell & Ansell 1969, Jennings & Rathbun 2001). Ectoparasites include ticks (9 spp.), lice (1 sp.), mites (2 spp.) and fleas (2 spp.) (Fourie *et al.* 1995). Blood parasites include *Trypanosoma petrodromi*, *Plasmodium brodeni* and filarial worms (Jennings & Rathbun 2001).

Conservation IUCN Category: Least Concern.

Most subspecies are widely distributed and thus in little danger of extinction. The subspecies *sangi* (included in *P. t. sultani* by Corbet 1974b) is restricted to the Taita Hills in Kenya, and may be endangered or already extinct due to loss of forest habitat (Nicoll & Rathbun 1990). The Giriama people of Kenya trap Four-toed Sengis for meat with snares and deadfall traps. FitzGibbon *et al.* (1995) found that about 15 individuals/km²/year were being harvested, a rate that they believe is sustainable. The subspecies *beirae* is considered ‘rare’ based on its restricted distribution in KwaZulu–Natal, South Africa (Jennings & Rathbun 2001).

Measurements

Petrodromus tetradactylus

HB: 192.9 (163–210) mm, n = 33

T: 166.4 (156–187) mm, n = 33

HF: 54.8 (51–58) mm, n = 33

E: 35.9 (34–39) mm, n = 33

WT: 198.3 (129–250) g, n = 11

GLS: 56.1 (54.3–58.5) mm, n = 12

GWS: 29.4 (28.1–30.5) mm, n = 12

I¹–M³: 29.3 (28.1–30.5) mm, n = 12

Upper canine: 3.98 (3.53–4.90) mm, n = 12

Body measurements and weight: Arabuko–Sokoke Forest, Kenya (G. B. Rathbun unpubl.)

Skull measurements: Kenya (BMNH)

Key References Corbet & Hanks 1968; FitzGibbon 1995; Jennings & Rathbun 2001; Perrin 1995; Rathbun 1979.

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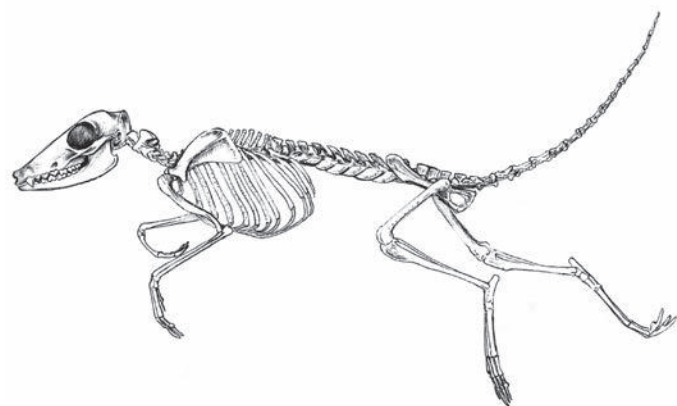
GENUS *Rhynchocyon*

Giant Sengis

Rhynchocyon Peters, 1847. Bericht Verhandl. K. Preuss. Akad. Wiss., Berlin 12: 36. Type species: *Rhynchocyon cirnei* Peters, 1847.



Rhynchocyon cirnei.



Skeleton of *Rhynchocyon petersi*.

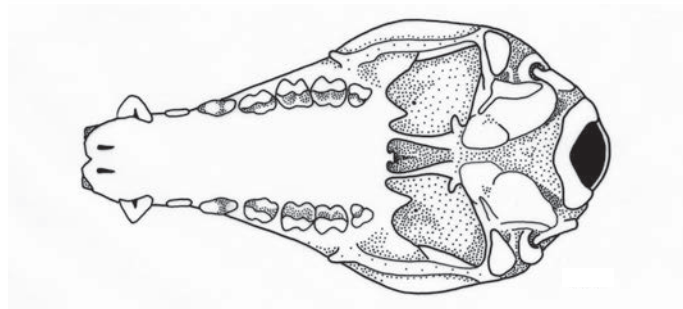
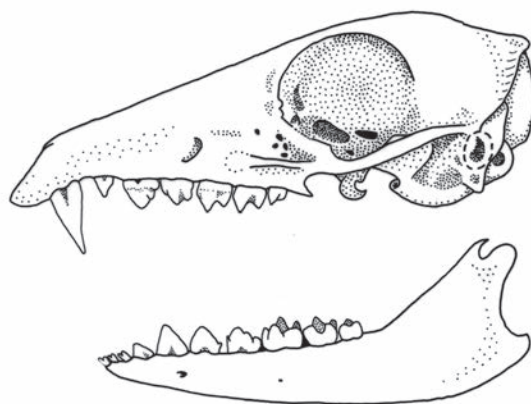


Figure 20. Skull and mandible of *Rhynchocyon cirnei* (BMNH [4287], RMCA 90-042-M-200).

The genus *Rhynchocyon* contains three species that live in woodlands and forests of central and eastern Africa. The species are allopatric: one (*R. cirnei*) is widespread and the other two (*R. chrysopygus* and *R. petersi*) have restricted distributions. The genus is placed in a separate subfamily (Rhynchocyoninae, see Tables 13 and 14) to the other genera of sengis (see order Macroscelidea).

The three species in the genus have very similar and somewhat bizarre morphology that gives the impression of a cross between a miniature antelope, anteater and rodent. The genus is characterized by large size (the largest of all sengis), narrow body (ungulate-like), long and spindly legs, long rodent-like tail and sparse, slightly coarse, brightly coloured and patterned pelage. The feet are digitigrade, with four digits on forefoot (a unique character of this genus), four digits on hindfoot and long claws (especially on three well-developed front digits). The sole of the metatarsal has hair, and there is no carpal pad. The eyes are large and dark, with a round pupil. The pinnae are hairless, moderate in size and carried upright. The nose is extremely elongated and flexible (trunk-like rather than rigid), with the nostrils at the tip, and the small mouth is set well behind the nostrils; the tip of the nasal bones is ossified (cf. other genera of sengis). Pectoral gland absent, post-anal gland well developed, large and round. Females have two pairs of nipples, both abdominal/inguinal. The dental formula is $I^{0-1/3}, C^{1/1}, P^{4/4}, M^{2/2} = 34-38$. The

presence/absence of upper incisors varies according to species and individuals. If present, upper incisors are rudimentary and may not even be visible; the single upper incisor may be present on both sides or on only one side of the upper jaw (see Corbet & Hanks 1968) (cf. *Elephantulus*, *Macroscelides* and *Petrodromus*, which have well-developed upper incisors). Other characteristics of the teeth include notched lower incisors, large upper canines, and progressively complex cheekteeth ending with hypsodont and dilambdodont molars (Figure 20). Palatal foramina are absent. The many differences between *Rhynchocyon* and the other genera of sengis are listed by Corbet & Hanks (1968).

These large sengis are terrestrial and exclusively diurnal. When not active, they shelter in large terrestrial nests made of leaves. They feed exclusively on arthropods and other small invertebrates, which they gather by excavating in the soil and litter with the claws of the forefeet. Many of their characters, such as their alert, high-strung nature and swift cursorial half-bounding gait, are reminiscent of a small ungulate (Evans 1942). Their morphological and behavioural characters are quite unlike those usually exhibited by other small insect-eating mammals (Kingdon 1974, Rathbun 1979).

The genus is the sole extant representative in the subfamily Rhynchocyoninae (Corbet & Hanks 1968), which dates from at least the early Miocene (Butler 1995). The three species are most easily distinguished by the colour and pattern of the pelage.

A distinctively coloured *Rhynchocyon* was camera-trapped in the NE Udzungwa Mts of Tanzania (Rovero & Rathbun 2006) and was described as a new species (*Rhynchocyon udzungwensis*) in 2008

(Rovero *et al.* 2008, see also p. 16), after this text was submitted to the publishers.

Galen B. Rathbun

***Rhynchocyon chrysopygus* GOLDEN-RUMPED GIANT SENGI (GOLDEN-RUMPED ELEPHANT-SHREW)**

Fr. Macroscélide à croupe dorée; Ger. Goldrücken Rüsselhündchen

Rhynchocyon chrysopygus Günther, 1881. Proc. Zool. Soc. Lond. 1881: 164.

River Mombaça, corrected by Moreau *et al.* (1946) to Mombasa, Kenya.



Rhynchocyon chrysopygus.



Rhynchocyon chrysopygus

Taxonomy Generally considered a full species (Corbet & Hanks 1968), although Kingdon (1974) once treated it as an ‘incipient species’ of *R. cirnei*. This view was based mainly on indistinct dark stripes at the leading edge of the rump patch of some adults and most neonates, which are reminiscent of the prominent dorsal stripes of *R. cirnei*. Synonyms: none. Subspecies: none. Chromosome number: not known.

Description Large sengi with prominent yellow rump. Dorsal pelage maroon or russet-brown to dark rufous with bright yellow rump, which has slightly longer hairs than rest of body. Ventral pelage rufous. Head grizzled yellowish-brown; neck tending to maroon. Snout very long, eyes large. Ears broad, upright, naked and black. Fore- and hindlimbs black and long, four digits on forefoot, four digits on hindfoot, all with well-developed claws. Tail long (ca. 85% of HB), thick at base tapering to tip, with short, sparse hairs, black above, paler below; tip of tail with irregular white patch. Some individuals have indistinct dark central stripes at the anterior edge of the rump patch, reminiscent of the pattern in *R. cirnei*. Pectoral gland absent; post-anal gland well developed. No sexual dimorphism in body size, but ♂♂ have longer canines and thicker rump skin than ♀♀. Nipples: 0 + 2 = 4.

Geographic Variation None recorded.

Similar Species This is the only sengi with a yellow patch on the rump.

Distribution Endemic to Africa. Coastal Forest Mosaic BZ. Occurs only in small and fragmented forests in the coastal region of Kenya from south of the Tana R. southwards, through Arabuko–Sokoke Forest, to Rabai near Mombasa (FitzGibbon 1994).

Habitat Coastal semi-deciduous forest, woodlands with a more-or-less closed canopy, coral rag scrub, and abandoned and overgrown agricultural lands with a closed canopy. Thick leaf litter is characteristic of all habitats.

Abundance Mostly a rare species with a restricted distribution, although may be locally common in a few favoured habitats. In Arabuko–Sokoke Forest maximum densities are about 75 individuals/km² in comparatively undisturbed forest habitats dominated by *Azizelia* trees. Densities are lower in less desirable habitats, including forest edges and near human settlements. Total population in Arabuko–Sokoke Forest is estimated at about 22,000 (FitzGibbon 1994).

Adaptations Terrestrial and diurnal. Golden-rumped Sengis build nests of leaves where they rest, singly, during the night. When building a nest, a cup-shaped hole about 8 cm deep is dug in the soil and dead leaves are arranged to form a lining; additional leaf material is

dragged and piled on top of the nest forming a pile about 15 cm high and 50 cm in diameter. There is no proper entrance; the sengi just burrows in at the side and the leaves settle down again. In time, the leaves weather and the nest is inconspicuous. Usually each member of a pair (see below) builds and uses several nests (Rathbun 1979).

These sengis leave their nests just before dawn and return just before sunset; they are active most of the day except for a mid-day rest period (FitzGibbon 1995). During the day, they spend, on average, nearly 80% of their time foraging, 12% walking, 4% resting and a little time building nests and interacting with conspecifics (Rathbun 1979). Walking is the main form of locomotion; when disturbed, an individual either freezes, or runs for about 10 m before stopping. When in danger, they either (a) walk away slowly while slapping the tail on the leaf litter, (b) run away while stotting in a similar way to an antelope, or (c) flee in the typical half-bounding gait. When necessary, they can run extremely swiftly (up to ca. 27 kph) (Rathbun 1979). Unlike *Petrodromus* and some *Elephantulus* spp., this sengi does not build trails.

The distinctively coloured rump-patch, with its associated thick dermal shield, may serve to attract bites from pursuing conspecifics during agonistic encounters; the thickness of the dermal shield probably gives protection against serious bites from a conspecific. Similarly, the distinct rump patch may serve as a predator invitation signal by enticing would-be predators to prematurely expose themselves to sengi foraging on the forest floor (Rathbun 1978). The senses of smell, sight and sound are acute. There is no information on metabolism, temperature regulation and water conservation in this species.

Foraging and Food Insectivorous. Prey is located by probing in dense leaf litter with the long flexible snout, and small prey and food fragments are flicked up with the long extensible tongue (Rathbun 1979). Earthworms are excavated from the soil with the strong claws of the forefeet, leaving distinctive 3 cm-deep conical holes. Large prey, such as earthworms and centipedes, are pinned to the ground with a forefoot, and then awkwardly ingested. The principal prey (in decreasing order of importance) are beetles, centipedes, termites, crickets, ants, spiders and earthworms (Rathbun 1979). The density of this sengi is positively correlated to the abundance of spiders (FitzGibbon 1995), although spiders comprise only a small proportion of the diet.

Social and Reproductive Behaviour Facultatively monogamous and territorial. Territories are 1.5–5.0 ha, territories of ♂♂ being slightly larger than those of ♀♀. Both sexes mark their territories with secretions from a post-anal gland (Rathbun 1979, FitzGibbon 1995, 1997). The territories of a monogamous pair overlap to large extent, but there is little overlap with the territories of neighbouring pairs. Males intrude on neighbouring territories more frequently than do ♀♀. Territorial defence is sex-specific, male–male aggression being most common. The ♀ of a pair is closely followed by her mate during oestrus for 1–2 days, otherwise the pair rarely interact. Male mate guarding is probably responsible for their monogamous social structure (Rathbun & Rathbun 2006). Individuals spend each night, and rest intervals during the day, in separate leaf-litter nests on the forest floor. Different nests are used every few nights (FitzGibbon & Rathbun 1994). Vocalizations include

very soft chattering between conspecifics and a loud distress scream when captured. The tail is noisily slapped on the dry leaf litter every 1–2 seconds in conflict situations.

Reproduction and Population Structure Golden-rumped Sengis are reproductively active throughout the year, with an average interval between births of 82 days. Gestation: ca. 42 days. Litter-size: 1. Weight at birth: ca. 80 g. The precocial neonate remains in the nest until about Day 14, when it is weaned. Young remain on the parental territory indefinitely, eventually finding a vacant territory or becoming prey. Longevity is about 3–4 years (Rathbun 1979).

The structure of the penis is unique among sengis, being composed mostly of connective tissue rather than vascular bodies (Woodall 1995b). The spermatozoa are also distinct from other sengis in that they have the shortest spermatozoon and the fewest gyres (Woodall 1995b, Woodall & FitzGibbon 1995). Whether the placenta is chorioallantoic or endotheliochorial is not clear (Cutler *et al.* 1998). Golden-rumped Sengis have rarely been maintained, and have never bred, in captivity.

Predators, Parasites and Diseases A wide variety of large snakes, raptors and mammalian carnivores are known or suspected predators (Rathbun 1979). Ectoparasites include two species of fleas and one species of tick (Fourie *et al.* 1995).

Conservation IUCN Category: Endangered.

The decline in numbers is associated with reduction in area, and in the extent and quality of habitats. FitzGibbon *et al.* (1995) estimate that about eight individuals/km² are harvested for meat by local people in the Arabuko–Sokoke Forest, a harvesting rate that they believe is sustainable. However, forest destruction for agricultural and urban development, and logging for building materials, wood carving and charcoal production, is a serious threat to their habitat (Rathbun & Kyalo 2000).

Measurements

Rhynchocyon chrysopygus

HB: 277.9 (218–304) mm, n = 80

T: 240.5 (213–270) mm, n = 80

HF 74.0 (68–79) mm, n = 80

E: 33.5 (30–38) mm, n = 80

WT: 534.8 (410–690) g, n = 40

GLS: 67.6 mm, n = 1

GWS: 36.2 mm, n = 1

C–M³: 27.8 mm, n = 1

Canine length (♂♂): 5.0 ± S.E. 0.2 mm, n = 53

Canine length (♀♀): 3.1 ± S.E. 0.1 mm, n = 44

Arabuko–Sokoke Forest, Kenya.

Body measurements and weight: G.B. Rathbun unpubl.

Canine lengths: FitzGibbon 1995

Skull measurements: BMNH

Key References Corbet & Hanks 1968; FitzGibbon 1994, 1995, 1997; Rathbun 1978, 1979; Rathbun & Kyalo 2000; Woodall & FitzGibbon 1995.

Galen B. Rathbun

***Rhynchocyon cirnei* CHEQUERED GIANT SENGI (CHEQUERED ELEPHANT-SHREW)**

Fr. Macroscélide de Cirne; Ger. Geflecktes-Rüsselhündchen

Rhynchocyon cirnei Peters, 1847. Bericht Verhandl. K. Preuss. Akad. Wiss., Berlin 12: 37. Quelimane, Bororo District, Mozambique.

Taxonomy Corbet & Hanks (1968) suggest that six allopatric forms can be recognized and that further collecting may demonstrate clinal variation linking some of these forms; they also suggest that allopatric *R. c. stuhlmanni* from DR Congo and Uganda may be a separate species. Synonyms: *claudei*, *hendersoni*, *macrurus*, *melanurus*, *nudicaudata*, *reichardi*, *shirensis*, *stuhlmanni*, *swynnertoni*. Subspecies: six. Chromosome number: not known.

Description Large sengi with distinctive pattern of lines and spots on back and flanks. Dorsal pelage very variable (see below), buff to dark brown; three longitudinal stripes from mid-back to base of tail on either side of mid-dorsal line; two central lines are nearly continuous, while second and third lines on each side often broken into pale and dark spots. In some races, the darker background obscures the stripes so only a faint pattern is visible. Ventral pelage whitish. Head with long snout, grizzled yellow or cream. Ears upright, naked. Fore- and hindlimbs elongated, buff; four digits on forefoot, four digits on hindfoot, all with well-developed claws. Tail long (ca. 90% of HB), nearly hairless, white at tip. Pectoral gland absent; post-anal gland well developed. No sexual dimorphism except for longer and wider canines in ♂♂. Nipples: 0 + 2 = 4.

Geographic Variation Six subspecies (or races) distinguished by sometimes subtle variation in pelage colouration and pattern (Corbet 1974b, Kingdon 1974 especially plate p. 42).

- R. c. cirnei*: Mozambique. Dorsal spots pale chestnut.
- R. c. hendersoni*: Livingstonia, N Malawi. As *R. c. reichardi*, but entire pelage very dark.
- R. c. macrurus*: SETanzania and perhaps N Mozambique. Dorsal pelage rufous, chequered pattern prominent on inland specimens but obscured by dark pelage from those near coast.
- R. c. reichardi*: N Malawi, NE Zambia, SE DR Congo, SW Tanzania. Dorsal pattern of dark and pale spots.
- R. c. shirensis*: S Malawi. Dorsal spots blackish-chestnut, white spots absent.
- R. c. stuhlmanni*: NE DR Congo, Uganda (and perhaps near Bangui, Central African Republic). Similar to *reichardi*, but dorsal pelage very dark so that the spots and stripes may be obscured; tail nearly white.

Similar Species

- R. chrysopygus*. Large yellow patch on rump; some individuals have indistinct stripes on back.
- R. petersi*. Mid-back to rump jet black and face grizzled rufous-orange; pale orange tail and orange-brown ears; some individuals with indistinct stripes at anterior margin of the black colouration.

No other species of sengi has distinctive stripes on the back and flanks.

*Rhynchocyon cirnei*

Distribution Endemic to Africa. Rainforest BZ (East Central Region) and restricted parts of Zambezan Woodland and Somalia–Masai Bushland BZs. Recorded from Mozambique north of the Zambezi R.; highlands associated with the Rift Valley in Malawi, Zambia and Tanzania; W Uganda; STanzania; DR Congo between the Congo and Ubangi rivers (Corbet & Hanks 1968).

Habitat Montane and lowland forests, closed-canopy woodlands and riparian thickets where substrate is usually covered with dense leaf litter.

Abundance Widespread, but no detailed information.

Adaptations Terrestrial and diurnal. Builds leaf-litter nests on the forest floor (Allen & Loveridge 1933). Highly cursorial (Lawrence & Loveridge 1953, Ansell & Ansell 1973). Based on numerous short accounts of fleeting observations, the natural history of this species is probably similar to the better-known Golden-rumped Sengi. However, for such a widespread species, very little is known about its biology.

Foraging and Food Stomachs of specimens from montane region of NE Zambia contained beetles, bees or wasps, fly larvae, and bugs (Ansell & Ansell 1973).

Social and Reproductive Behaviour In NE Zambia, all sightings were of solitary individuals, except for one pair (Ansell & Ansell 1973).

Reproduction and Population Structure Litter-size usually one, with twin foetuses reported from Zambia, Malawi and Uganda (Lawrence & Loveridge 1953, Brown 1964, Ansell & Ansell 1973).

Predators, Parasites and Diseases The chequered pattern of the pelage is probably related to camouflage from predators (Kingdon 1974). Forest Cobras *Naja melanoleuca*, Robust Chimpanzees *Pan troglodytes* and African Golden Cats *Profelis aurata* are known predators. Mbuti Pygmies and local people near Kisangani, DR Congo, harvest Chequered Sengis for meat. Ectoparasites include one species of flea, a species of dipteran fly and several species of *Ixodes* ticks (Fourie *et al.* 1995). The blood protozoan *Sarcocystis* sp. has also been found (Keymer 1971).

Conservation IUCN Category: Near Threatened.

Of special concern are two subspecies: *R. c. hendersoni* is restricted to an isolated montane forest in Malawi, and may be threatened with extinction from habitat destruction (Nicoll & Rathbun 1990); and *R. c. cirnei* (known only from the holotype) in coastal Mozambique. Habitat loss may also threaten the other subspecies with restricted distributions. Chequered Sengis are not known to have been successfully bred in captivity (Nicoll & Rathbun 1990), although it is rumoured that they have been successfully maintained in private collections.

Measurements

Rhynchocyon cirnei

HB: 272.7 (242–303) mm, n = 67

T: 243.4 (220–265) mm, n = 66

HF: 85.7 (81–91) mm, n = 67

E: 31.0 (29–34) mm, n = 67

WT: 352.0 (320–420) g, n = 10

GLS (♂♂): 67.6 (62.2–70.8) mm, n = 39

GWS (♂♂): 36.1 (33.5–38.0) mm, n = 39

C–M³: 28.9 (27.4–29.9) mm, n = 12

Canine length (♂♂): 3.4 (3.3–3.5) mm, n = 5

Canine length (♀♀): 2.2 (1.7–2.3) mm, n = 5

Body and skull measurements: *R. c. stuhlmanni* from Niapu, DR Congo (Allen, J. 1922)

Weight and canine lengths: *R. c. reichardi* from NE Zambia (Ansell & Ansell 1973)

C–M³: BMNH

Note: *R. c. reichardi* (mean values: HB = 242.0 mm, T = 213.8 mm, HF = 66.8 mm, E = 29.5 mm, n = 10; Ansell & Ansell 1973) is on average smaller than *R. c. stuhlmanni*.

Key Reference Corbet & Hanks 1968.

Galen B. Rathbun

Rhynchocyon petersi BLACK-AND-RUFIOUS GIANT SENGI (BLACK-AND-RUFIOUS ELEPHANT-SHREW)

Fr. Macroscélide de Peters; Ger. Schwarzbraunes Rüsselhündchen

Rhynchocyon petersi Bocage, 1880. Journ. Sci. Math. Phys. Nat., Lisboa 1 (7): 159. Mainland Tanganyika (Tanzania), opposite Zanzibar I.



Rhynchocyon petersi.

Taxonomy Corbet & Hanks (1968) suggested that there may be a cline between this species and *R. cirnei*. In contrast, Kingdon (1974) suggested a hybrid zone between the two taxa, because some individuals of *R. petersi* have indistinct dorsal stripes reminiscent of the pattern in *R. cirnei*; on this basis *R. petersi* may be considered as an 'incipient species' of *R. cirnei*. Synonyms: *adersi*, *fischeri*, *usambara*. Subspecies: two. Chromosome number: not known.

Description Large black and orange-rufous coloured sengi. Pelage bright and shiny. Dorsal pelage (from shoulder blades to rump and thighs) black; upper back and flanks orange to rufous-orange or dull maroon (see Geographic Variation). Ventral pelage orange to rufous-orange. Head with well-developed snout, orange-brown; forehead grizzled, tinged with rufous. Ears upright, orange-brown. Fore- and hindlimbs long, orange-brown; four digits on



Rhynchocyon petersi

forefoot, four digits on hindfoot, all with well-developed claws. Tail pale orange, nearly hairless, with faint irregular white area near tip. Pectoral gland absent; post-anal gland well developed. Nipples: $0 + 2 = 4$.

Geographic Variation

R. p. petersi: Tanzania (mainland) and Kenya. Pelage of shoulders, flanks and ventrum orange-rufous; head yellowish.

R. p. andersi: Zanzibar and Mafia Is. Pelage of shoulders, flanks and ventrum dull maroon; head rufous.

Similar Species No other species of sengi has the distinctive black and orange-rufous dorsal pelage and grizzled rufous face, nor the orange-coloured skin on tail and ears.

Distribution Endemic to Africa. Coastal Forest Mosaic BZ and marginally in adjacent BZs. Recorded from Tanzania and Kenya (in the 'Eastern Arc' mountains and coastal forests from the Rabai Hills near Mombasa, Kenya, to just south of Dar es Salaam, Tanzania). Also Zanzibar and Mafia Is.

Habitat Evergreen and semi-deciduous forests, dense woodlands, coral rag scrub and abandoned and overgrown agricultural lands with closed canopies where there is a thick covering of leaf litter.

Abundance Mostly a rare species with a fragmented and restricted distribution. Maximum densities, estimated from transect surveys of nests, between $19/\text{km}^2$ and $79.3/\text{km}^2$ (Hanna & Anderson 1994, Coster & Ribble 2005).

Adaptations Little is known about this species. Terrestrial and diurnal. Very keen senses, highly cursorial (Allen & Loveridge 1927).

Foraging and Food Insectivorous, but no details except that soldier ants (*Dorylus* spp.) are eaten in Nkuka Forest, Tanzania (Allen & Loveridge 1933). Captive animals successfully maintained on a diet of dry cat food supplemented with crickets and mealworms (Baker *et al.* 2005).

Social and Reproductive Behaviour Generally observed as solitary individuals, and presumed to be facultatively monogamous (as for Golden-rumped Sengi). In captivity, kept as monogamous pairs. Multi-sex groups show greater tolerance between unrelated adult ♀♀ than between ♂♂ (Baker *et al.* 2005).

Reproduction and Population Structure Based on captive animals (Baker *et al.* 2005), gestation ca. 40 days, litter-size 1–3. Young not as precocial as in species of Macroscelidinae. Neonates remain in a leaf nest for about 3 weeks and are visited only by the mother once each day. The ♂ does participate in rearing the young. Interval between births about 80 days.

Predators, Parasites and Diseases Ectoparasites include three species of fleas and three species of ixodid ticks (refs in Fourie *et al.* 1995).

Conservation IUCN Category: Vulnerable.

The geographic range is small, and there is continuing decline in area and quality of habitats. Fragmentation of habitats is due to urban and agricultural expansion into forests, many of which are already small and isolated (Nicoll & Rathbun 1990). Extraction of timber for woodcarving, firewood and charcoal production are also threats to habitats (Hanna & Anderson 1994). In 2000, Black-and-rufous Sengis from Tanzania were imported to North American zoos, where they have bred successfully (Baker *et al.* 2005).

Measurements

Rhynchocyon petersi

HB (♂): 324 mm, $n = 1$

HB (♀♀): 275, 270 mm, $n = 2$

T (♂): 230 mm, $n = 1$

T (♀♀): 240, 213 mm, $n = 2$

HF (♂): 71 mm, $n = 1$

HF (♀♀): 67, 83 mm, $n = 2$

E (♂): 31 mm, $n = 1$

WT: n. d.

GLS: n. d.

GWS: n. d.

C–M³: n. d.

Measurements (♂♂): Allen & Loveridge 1927

Measurements (♀♀): Hollister 1918, Loveridge 1922

Key References Corbet & Hanks 1968; Hanna & Anderson 1994; Nicoll & Rathbun 1990.

Galen B. Rathbun

Order TUBULIDENTATA – Aardvark

Tubulidentata Huxley, 1872. A Manual of the Anatomy of Vertebrated Animals. New York: D. Appleton, pp. 288–289.

Orycteropodidae (1 genus, 1 species)	Aardvark	p. 289
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The order Tubulidentata consists of a single family, the Orycteropodidae, and one extant species, *Orycteropus afer*. Tubulidentata is the only order of mammal to be represented by a single extant species. The name Tubulidentata derives from the unique microstructure of the orycteropodid teeth: each tooth consists of hundreds of tubes of dentine agglomerated and surrounded by cement. The name Orycteropodidae and *Orycteropus* derives from Greek ‘*orukter*’ and ‘*pous*’ meaning ‘digging foot’, referring to the Aardvark’s adaptations for digging.

All Tubulidentata, fossil and extant, share the same following osteological characters. The skull is long, roughly tubular, particularly elongated on the snout and widest at the level of the jugals. Maxilla, premaxilla, frontal and nasal bones are well developed. The nasal bones are triangular in shape, broaden caudally but are never fused. The lacrimal bone presents a rostral development and the lacrimal foramen is situated on the border of the orbit. The frontal bones bulge dorsally in front of the orbit as a result of the highly developed nasal chamber where the olfactory bulbs are contained. The position of the anterior border of the orbit in relation to the upper toothrow differs among living and extinct species. The parietals are fused in one unit at maturity. In Tubulidentata, a part of the parietal bone joins the alisphenoid so that frontal and squamosal are not in contact. There is no sagittal crest and only faint temporal ones. The lambdoid crest, between the parietal and occipital bones, can be straight or V-shaped (in dorsal view) according to species. In juvenile Aardvarks an interparietal bone is present between the parietal and the occipital bones, but this disappears (fuses) by adulthood. The zygomatic arch is complete but slender and the orbit is only separated from the temporal fossa by a postorbital process (i.e. there is no postorbital bar). The palate is long and narrow. The palatine bone is elongated, presents two post-palatine foramina and ends caudally in a strong post-palatine torus. The tympanic cavity is simple: the tympanic bone is annular, and there is no auditory bulla. The mastoid bone is visible laterally and caudally. Moreover, post-temporal and mastoid foramina are present on its caudal aspect. The body of the mandible is very slender and broadens at the level of the molars. The mandibular symphysis is rarely complete. On the ascending ramus, the coronoid process is long and projects over the condylar process, which can be flat or concave according to species. Likewise, the mandibular fossa on the cranium is flat or has a tubercle.

The humerus shows a very broad distal epiphysis, possesses a deltoid tuberosity and a well-developed deltoid crest (except in two extinct species). The vertebral formula for the extant Aardvark is Cervical 7, Thoracic 13, Lumbar 8, Sacral 6, Caudal 25–28. In some fossil forms (e.g. *Amphiorhycteropus abundulafus* from Chad), and at the juvenile stage of the extant form, the number of sacral vertebrae is only five. The pelvis is large and characterized by a dorso-caudal extension of the iliac bone. The sacrum does not enter into contact with the ischium. The pubic symphysis is unreduced in comparison with other digging mammals (MacPhee 1994). The proximal epiphyses of the tibia and fibula are fused, and the diaphysis of the tibia is bent. Scaphoid and centrum are fused (Clark & Sonntag 1926) and the pollex (Digit 1) has

disappeared, so that the hand has only four digits. The tarsus is serial (the talus does not articulate with the cuboid); the talus retains an astragalar foramen and its distal articulation surface is ball-like, supported by a distinct neck. The hindfoot, which can be plantigrade when the animal is digging, possesses five toes. A detailed anatomical description was originally given in a monograph of *Orycteropus afer*, divided in a series of three papers (Sonntag 1925, Sonntag & Woolard 1925, Clark & Sonntag 1926).

The oldest known unquestionable members of Tubulidentata are *Myorycteropus minutus* (Pickford 1975) and *M. africanus* (MacInnes 1956) from the early Miocene (more precisely, between 20 and 18 mya) of Kenya. However, they already show the peculiar tubulidentate tooth structure, and are probably dedicated diggers. Therefore, the Tubulidentata must have diverged from the eutherian mammal lineage earlier, during the Palaeocene or, more likely, the Cretaceous. The phylogenetic position of the Tubulidentata has been heavily discussed since the first description of the extant Aardvark in 1766, but even more during the last 20 years. The presupposed (but incorrect) absence of teeth, and most of all the myrmecophagous diet, led many authors to include the Tubulidentata in the (now obsolete) order ‘Edentata’, along with pangolins, armadillos, sloths and South American anteaters. The extensive work by Sonntag (Sonntag 1925, Sonntag & Woolard 1925, Clark & Sonntag 1926) on the anatomy of the extant Aardvark demonstrated that this placental mammal must be placed in an order on its own. Resemblances between Aardvarks and other ant-eating mammals (e.g. Xenarthra, pangolins) are in fact likely due to convergent evolution. Since then, mammalian phylogenies, based on morphological characters and fossil record, supposed that Tubulidentata belonged to the higher-level taxon Ungulata (Thewissen 1985, Novacek 1989, Shoshani & McKenna 1998). However, over the past two decades, molecular analyses have led to the description of a supraordinal clade of mammals, the Afrotheria, which has regrouped Proboscidea, Hyracoidea, Sirenia, Macroscelidea, Afrosoricida and the Tubulidentata (see, for example, Springer *et al.* 1997, Stanhope *et al.* 1998, Asher *et al.* 2003). Afrotheria is considered to be a group of placental mammals that originated in Africa in the late Cretaceous. Among the Afrotheria, the position of Tubulidentata needs further clarification (see Robinson & Seiffert 2004).

According to the fossil record, the earliest Eurasian fossil aardvarks have been found in the early middle Miocene of Turkey (Van der Made 2003). Therefore, they must have dispersed from Africa into Eurasia before or around that period like numerous other mammals (see Rögl 1999). The widest distribution area of the order spans Africa, Europe (France, Italy, Moldavia, Greece, Turkey) and Asia (Iran, Pakistan). However, Tubulidentata became extinct from Eurasia before the end of the Pliocene, thus restricting their distribution to the African continent. Fossil records (Romer 1938), as well as archaeological clues (Keimer 1944, Frechkop 1946, Manlius 2002), suggest that Aardvarks were, until recently, present north of the Sahara. The extant species lives now only in sub-Saharan Africa.

Thomas Lehmann

Family ORYCTEROPODIDAE

AARDVARK

Orycteropodidae Gray, 1821. London Medical Repository 15 (1): 305.

Orycteropus (1 species)	Aardvark	p. 289
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The only family in the order Tubulidentata, comprising a single extant species, the Aardvark *Orycteropus afer*. Patterson (1975) subdivided the Orycteropodidae into two subfamilies. The Plesiorycteropodinae are represented by a single genus, *Plesiorycteropus*, including sub-fossil taxa that lived around 1000 years ago on Madagascar, and represented by two species: *P. madagascariensis* and *P. germainepetterae*. However, MacPhee (1994) argued that this genus does not belong to the Tubulidentata, but rather represents an order on its own: Bibymalagasias. More recent analyses (Lehmann 2004) tend to confirm that there is only one subfamily of Tubulidentata, namely the Orycteropodinae. The subfamily comprises at least four genera (Lehmann 2009). Two of these, *Myorycteropus*, from the early Miocene of Rusinga and Mfangano in Kenya, and *Leptorycteropus*, from the late Miocene of Lothagam also in Kenya, are monospecific and extinct. Pickford (1975, 2004) proposed that the genera *Myorycteropus* and *Leptorycteropus* were synonyms of a third genus, the extant *Orycteropus*, but their validity is borne out by other authors (Van der Made 2003, Lehmann *et al.* 2005, Lehmann 2009). A recent revision of the family (Lehmann 2009) split *Orycteropus* in two based on a cladistic analysis of morphological characters, and in so doing created the genus *Amphiorhycteropus*. Consequently, whereas the genus *Orycteropus* was until recently known by 12 extinct species and only one living species, the latest classification recognizes two Pliocene and one extant African species in *Orycteropus*, and includes five species known from middle Miocene to Pliocene in Africa and Eurasia in *Amphiorhycteropus* (Lehmann 2009).

The following features characterize the extant Aardvark and the members of the genus *Orycteropus*: large species with an elongated snout, absence of incisors or canines, rectangular and 8-shaped outline of the molars, large deltoid crest, broad distal epiphysis of the humerus, button-like bicipital tuberosity of the radius, articular axis of the sigmoid notch of the ulna perpendicular to the diaphysis, six sacral vertebrae, presence of a falciform process on the tibia, and talus as long as broad with a concave cotylar fossa.

However, in the smaller extinct *Leptorycteropus*, the canines are preserved, the deltoid crest is not strongly developed, the distal epiphysis of the humerus is reduced, the pubis is oriented medio-ventrally, five vertebrae form the sacrum, there is no falciform process on the tibia and the tibial crest is short. In contrast to *Orycteropus*, *Myorycteropus*, which is 50% smaller than the extant Aardvark, shows upper teeth that stand vertical in their alveoli, a low mandibular angle, an articular axis of the sigmoid notch of the ulna oblique to the diaphysis, a *caput femoris* not oriented medio-laterally, no falciform process on the tibia, a short tibial crest with a real cnemial tuberosity and a vertical cotyloid facet on the talus. Finally, *Amphiorhycteropus* can be distinguished from the other genera by a V-shaped nuchal line, the anterior border of the orbit situated at the level of the M², molars trapezoidal in shape, a pointed bicipital tuberosity on the radius, a proximo-distally elongated talus, and a mandibular angle superior to 73°.

Thomas Lehmann

GENUS *Orycteropus*

Aardvark

Orycteropus E. Geoffroy St. Hilaire, 1796. Extrait d'un mémoire sur le *Myrmecophaga capensis*, Gmellin. Bulletin de la Société Philomathique de Paris, no. 50, pp. 1–2 [see Lehmann 2007 for discussion about the various incorrect former attributions of authority and date to this genus].

Orycteropus is a monotypic genus, represented by a single extant species, the Aardvark *Orycteropus afer*, distributed throughout sub-Saharan Africa in a wide range of habitats including grassland, all savanna types, semi-arid Karoo (South Africa) and some forests but not desert.

Patterson (1975) included five extinct species of *Orycteropus* in the genus with confidence, noting that others required more complete specimens for clarification. Since then, a new species has been described, some additional material has been discovered, and the genus has been split in two, with the description of *Amphiorhycteropus* (see Lehmann *et al.* 2004, Lehmann 2009). Thus, including fossil forms, the genus currently comprises three described species, all known only from Africa so far: *O. afer* (extant, Africa), *O. crassidens* (Kenya) and *O. djourabensis* (Chad). Following Patterson (1975) and

Lehmann (2009), three forms previously included in *Orycteropus* – cf. *Myorycteropus minutus*, cf. *Amphiorhycteropus pottieri* and cf. *A. seni* – are considered with reservation pending the availability of further material. The species *O. pilgrimi* has been shown to be a synonym of *A. browni*.

The oldest established record for the extant Aardvark is from the Palaeolithic of Algeria (Romer 1938) or perhaps the early Pliocene of South Africa (Langebaanweg; Pickford 2005). Historically, the genus appeared in East Africa some 7 mya. It soon spread over the whole continent, reaching Chad by 4 mya, and replaced all former taxa (Lehmann 2008, 2009).

Thomas Lehmann & Andrew Taylor

Aardvark *Orycteropus afer*.***Orycteropus afer* AARDVARK (ANTBEAR)**

Fr. Oryctérope; Ger. Erdferkel

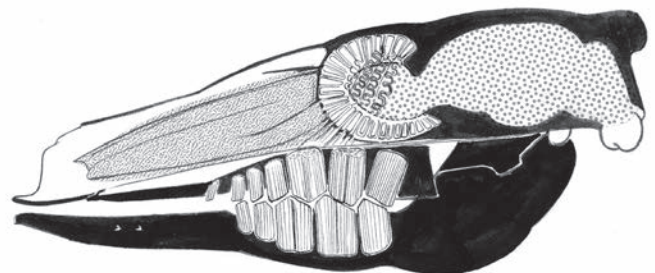
Orycteropus afer Pallas, 1766. Miscellanea Zoologica 64. Cape of Good Hope, Western Cape, South Africa.

Taxonomy There are 18 subspecies recognized, based primarily on colour, size and degree of frontal inflation, but this number is almost certainly too high, and the scarcity of material makes it difficult to determine the status or the limits of distribution of subspecies (Meester 1971). The name Aardvark derives from Dutch and means 'earth pig'. Synonyms: *adametzi*, *aethiopicus*, *albicaudus*, *angolensis*, *erikssoni*, *faradius*, *haussanus*, *kordofanicus*, *lademanni*, *leptodon*, *matschiei*, *observandus*, *ruvanensis*, *senegalensis*, *somalicus*, *wardi*, *wertheri*. Chromosome number: $2n = 20$ (Benirschke *et al.* 1970, Yang *et al.* 2003).

Description Medium- to large-sized species with heavy arched body and greyish-brown appearance. Head appears small relative to body, particularly in large specimens. Long tubular muzzle ends in a soft, swollen snout, with numerous bristle-like hairs inside mobile nostrils. Dark-brown eyes, small for the size of the animal, with vibrissae below lower eye-lashes. Ears long and tubular, commonly held upright. Thick neck, wider than head. Dorsal pelage grey and sparse with irregular bare patches. Flank pelage less sparse, becoming thicker and longer on legs and rump; pelage on legs black. Body colour may be influenced by colour of local soils. Legs stocky and powerful, with four toes on each forefoot and five on each hindfoot. Strong nails present on all toes; those on forefeet longer and more robust than those on hindfeet. All toes are united by webbing to varying degrees. Webbing on the forefeet is greatest between Digits 1 and 2; on the hindfeet webbing is greatest between Digits 2 and 3. Only digital pads are present; plantar and carpal pads are missing. Tail thick at base, tapering to a narrow tip. There is no sexual dimorphism. One abdominal pair and one inguinal pair of nipples. Scent glands resembling scrotal sacks occur in the groin

area of both sexes. The orifices of these are long slits opening on either side of the vulva in ♀♀ and just behind the prepuce in ♂♂. The sacs are short and wide and filled with a yellow secretion smelling like the anal glands of mustelids. In ♂♂, the penis is short and shaped like a truncated cone. The genital orifice of the ♀ is a long cleft behind the centre of the genital eminence and is preceded by a large cordate posteriorly bilobed plate, the clitoris.

The dentition is heterodont and diphyodont, with a highly variable permanent dental formula of $I^{0/0}$, $C^{0/0}$, $P^{2-4/2-4}$ (usually $3/2$), $M^{3/3} = 20-28$. In contrast with numerous mammals, the third molars of the Tubulidentata erupt at an early stage of the ontogenesis and are thus not a good criterion for age determination. The tubulidentate teeth have no enamel and grow continuously from open roots. A digitation of the pulp runs inside each tube and produces centripetal layers of dentine until closure of the tube upon the surface. The premolars are peg-like whereas the molars are

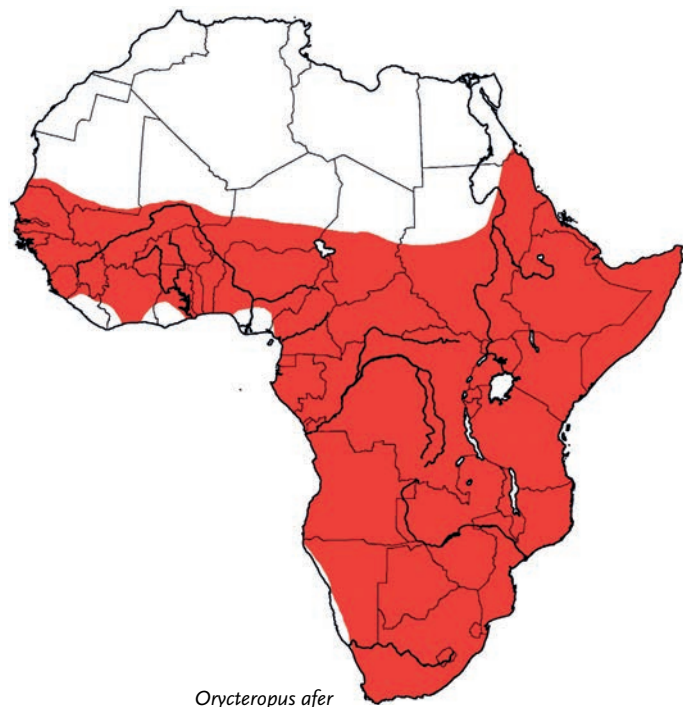
Mid-line section of *Orycteropus afer* skull.

bicolumnar (8-shaped in occlusal view) with longitudinal grooves on each side.

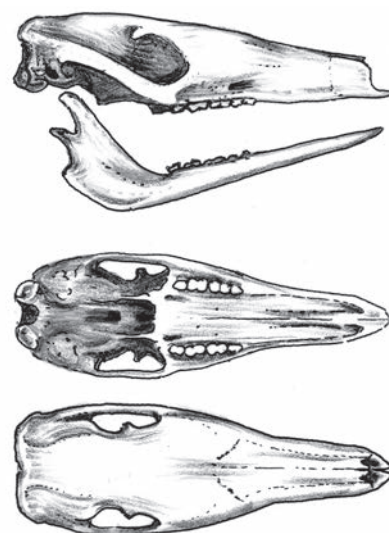
Geographic Variation Numerous subspecies have been described, but the validity of many of these is in doubt (see Taxonomy). For example, Smithers (1971) synonymized the form *albicaudus* from Botswana, a form stated to have a very short tail and to be pure white, in the nominate *afer*. The form *erikssoni* was described as a large forest form from the Congo, characterized by short hairs, short ears and large claws, with the skull large, the anterior base of the zygoma narrow and the mandible slender, and was said to differ unmistakably in many features from East African and southern African animals (Hatt 1934).

Similar Species The Aardvark is unlikely to be confused with any other species.

Distribution Endemic to Africa. Widespread, but localized, south of the Sahara from Senegal to Ethiopia and south to South Africa, being absent from the Sahara and Namib Deserts (Kingdon 1971, Shoshani *et al.* 1988, Skinner & Chimimba 2005). Not recorded from Lesotho (Lynch 1994), but they almost certainly do occur. Although sometimes shown as absent from the forests of the Congo Basin (e.g. Shoshani *et al.* 1998), Aardvarks are in fact widely distributed throughout the region (Hatt 1934, Schouteden 1948, Rahm 1966, Pagès 1970, Carpaneto & Germe 1989, J. Hart pers. comm.); for example, in Congo they occur in savannas and forests from at least the Bateke Plateaux northwards to the border with Cameroon and the Central African Republic (F. Maisels pers. comm.), while in Gabon they have been camera-trapped in the Ivindo N. P. (and a skull was found in Minkebe N. P.) (P. Henschel pers. comm.). Distribution in West African rainforests is poorly known (Grubb *et al.* 1998). The distribution of the Aardvark is largely determined by the distribution of suitable ant and termite species (see Foraging and Food).



Orycteropus afer



Lateral, palatal and dorsal views of skull of *Orycteropus afer*.

In Pre-Dynastic Egypt, the Aardvark occurred in the Nile Delta as has been proved by faithful representations on jugs of that period, and in paintings in tombs (Keimer 1944, Manlius 2002).

Habitat Present in a wide range of habitats, including grassland, all savanna types, woodlands and thickets, semi-arid Karoo (South Africa) and the transition zones (savanna-forest) of West Africa; also known from all the forested zones of central Africa except, seemingly, swamp forests (F. Maisels pers. comm.). Recorded in submontane forests of the Udzungwa Mts (Rovero & De Luca 2007) and to elevations of 3200 m in the Bale Mts of Ethiopia (Yalden *et al.* 1996). Their preferred habitat is flat or gently sloping ground that is not too rocky, which facilitates the digging of burrows and excavation of ant nests. Steep slopes are sometimes utilized, mainly in traversing areas. Presence of ants and termites is vital. The presence of free-standing water is not essential.

Abundance Locally common, but rarely seen due to nocturnal and evasive behaviour. Densities in the Nama Karoo of South Africa were estimated at 1–2/km² (Taylor & Skinner 2003). Densities vary according to abundance of prey. Burrows are often the only indication of presence; however, high burrow densities do not imply high Aardvark densities because many burrows are abandoned.

Adaptations Many adaptations of the Aardvark are associated with their myrmecophagous diet and digging specialization. Aardvarks are nocturnal and find both food and refuge underground. Prey is located by a highly developed sense of smell. The macrosmatic brain, and the fact that Aardvarks have very large olfactory lobes, with more olfactory bulbs than any other eutherian mammal, suggest that olfaction is probably the most developed sense (Shoshani *et al.* 1988). These are contained within the turbinates of the nasal cavities (Sonntag & Woollard 1925). The enlarged olfactory lobes result in a slight swelling of the skull just in front of the eyes. When foraging for food, bristle-like hairs inside the nostrils help prevent soil particles from being inhaled (Pocock 1924). The tongue is long (ca. 30 cm), vermiform and specialized for penetration of narrow tunnels of ant and termite nests. Large salivary glands provide

Frontal view of mouth and nostrils of *Orycteropus afer*.Myology of *Orycteropus afer*. Note short, thick muscles on limbs and large, hard nails.

copious amounts of saliva, facilitating the adherence of small prey but also soil. Cheekteeth are present even though most food is swallowed without chewing. The muscular stomach usually suffices for digestion. However, Aardvarks do occasionally chew specific types of prey, with the ant species *Messor capensis* being one example. They also have a large caecum, unusual for a myrmecophagous mammal. Hearing is acute, with the middle ear having a large tympanic membrane (Hunt & Korth 1980) and the detection of ambient noises facilitated by the long mobile ears; the ears are not generally used for prey location. Ears are kept erect mainly by the stiffness of the inflected margins of the lower half of the pinna, rather than being strengthened by additional cartilage. They can be folded flat during burrowing. Eyesight is poor, dark-adapted with no colour vision, and there is no tapetum (Franz 1908, Sonntag & Woollard 1925). The outer layer of the cornea is greatly keratinized to defend against the bites of ants. The skin shows a strong development of the dermis reticular layer as well as a thick epidermis (Sokolov *et al.* 1995) that helps protect against penetration of biting mandibles of the prey. Sensory hairs on the face below the eyes serve to alert the individual to obstacles and help prevent damage to the eyes during burrowing and foraging.

Aardvarks are digitigrade and are well known for their prodigious digging activities. The musculature of the forelimb is highly developed (see Thewissen & Badoux 1986) and the joints are strengthened. For instance, the distal epiphysis of the metacarpal bones presents a strong vertical crest that prevents uncontrolled latero-medial movement of the digit. The radius is shorter than the humerus. The brachial index (length of radius as a percentage of the length of humerus) is always less than 75% (Lehmann 2004), a condition that, according to MacPhee (1994), characterizes fossorial mammals. The powerful forelimbs and robust nails allow excavation of heavy soils and hard epigeal termitaries. The hindlimbs provide a firm base while digging, and are used to shovel soil backwards along passages and out of burrows. The sturdy tail provides additional support while digging. Nails could potentially inflict serious wounds on small carnivores, but are ineffective against the largest predators. Aardvarks are fast runners, attaining speeds of up to 40 km/h and escape predation by entering burrows. In the Karoo, burrows generally occur in clusters;

in one extreme case 58 burrows occurred in an area 40 m × 200 m. These burrows were not interconnected and most were abandoned (A. Taylor pers. obs.). Densities of up to 15 burrows/ha have been recorded in the Rwenzori N. P. in Uganda (Melton 1976). Aardvarks regularly change burrows. New burrows may be used for only one night, or for more than a month, but the average length of tenancy in South Africa is between five and nine days (Taylor & Skinner 2003). When changing burrows, old ones are often renovated rather than new ones excavated (though this may depend on the substrate).

Burrows normally have one entrance, although occasionally they have more. Out of 18 burrows excavated in Uganda, 13 had one entrance, two had two entrances, two had three entrances and one had five (Melton 1976). In the Karoo, Aardvarks under observation always exited burrows from the same entrance they entered, implying that each had only one exit/entrance hole (Taylor & Skinner 2003). Burrows descend steeply before levelling out, may turn in any direction and often extend over 10 m in length. With diameters of 350–450 mm, tunnels are generally just broad enough for Aardvarks to move through. They often fork and terminate with an enlarged chamber used for sleeping and giving birth. Depths of 3 m in soft soil are easily achieved. In some areas Aardvarks have to contend with freezing temperatures at night. Their sparse hair and lack of body fat is not adapted for this, but the use of deep burrows buffers them from the cold. Burrow temperatures vary less than ambient temperatures, being warmer in cold weather and cooler in hot weather. As an Aardvark pushes its way through a burrow, soil is displaced behind it, creating an additional barrier to temperature extremes as well as predators. Aardvark body temperatures vary between 34° C when they are inactive inside burrows, and 37° C when they are active on the surface (Taylor & Skinner 2004).

Aardvarks become active soon after dusk. They are normally active all night in summer, for periods of up to eight hours or more, and return to their burrows before dawn. In winter they become active earlier and in cold areas such as the Karoo sometimes emerge in the afternoon (Taylor & Skinner 2003). They then often return to their burrows before midnight at ambient temperatures of approximately 2° C. Activity patterns become shorter, lasting up to seven hours. Nearer the Equator, activity periods are more consistent.

Foraging and Food Aardvarks predominantly prey on ants and termites, digging them out of the ground or from epigeal termitaries. Geographical variation in ant and termite faunas leads to variation in the prey species eaten. Ant genera so far identified as food items include *Aenictus*, *Alaopone*, *Anoplolepis*, *Camponotus*, *Crematogaster*, *Dorylus*, *Messor*, *Monomorium*, *Pheidole*, *Solenopsis*, *Tetramorium* and *Typhlopone*; termite genera include *Allodotermites*, *Basidentitermes*, *Cubitermes*, *Hodotermites*, *Macrotermes*, *Microhodotermites*, *Odontotermites*, *Pseudacanthotermites* and *Trinervitermes*.

As well as ants and termites, Aardvarks are also known to eat the pupae of dung beetles (*Scarabaeidae*). Adult scarab beetles lay their eggs in dung and store them up to 40 cm below the surface, from where Aardvarks dig them up. Evidence for this comes from stomach contents, direct observation of diggings for the larvae, spoor and dung in eastern and southern Africa (Kingdon 1971, P. Lindsey pers. comm.).

The most detailed studies of feeding ecology have been carried out at Tussen die Riviere N. R. in the Free State, South Africa (Taylor *et al.* 2002). Here more ants are eaten than termites, with a dietary

Aardvark *Orycteropus afer* sketches.



ratio of four ants to one termite. These proportions have not been determined elsewhere. The ant *Anoplolepis custodiens*, which is an abundant species, comprises about 70% of the total number of prey eaten. The termite *Trinervitermes trinervoides*, with its many epigeal termitaries, makes up about 20% of the diet. There are 13 other prey species known from this site, but they constitute a small proportion (about 10%) of the diet.

Seasonal changes in diet have been recorded, but reports are conflicting. In Uganda, Aardvarks are reported to eat fewer termites in the dry season than in the wet because the termites become quiescent and are harder to obtain (Melton 1976). In the Karoo, the termite *T. trinervoides* becomes quiescent in winter (May–Aug), but they confine themselves in termitaries where they are highly concentrated and more easily extracted. Aardvarks regularly target termitaries at these times and consume large quantities of termites. They do not feed from termitaries between Oct and Mar (Taylor *et al.* 2002).

Aardvarks move slowly when foraging, keeping their nose close to the ground and can be heard sniffing continuously. When a nest is located, they push their snouts flat against the ground while continuing to sniff. They then either start digging frantically to reach the prey or move on foraging. All this time the ears are held erect, indicating that hearing is probably only used for predator detection. Mammals that use sound to locate prey, such as the Bat-eared Fox *Otocon megalotis*, always cup their ears forwards and downwards in the direction of the prey.

Aardvarks feed in discreet bouts of short duration, moving from one ant or termite nest to the next. Most feeding bouts vary between 10 sec and 2 min, but feeds from termitaries may last over 30 min. On average, Aardvarks make about 25 separate feeds per hour and may feed from over 200 nests in one night. Foraging speeds vary between 0.5 and 1.0 km/h (Taylor 1998). There are almost always some ants or termites left active on the surface at the end of a feed because the Aardvark's tongue is not adapted to lapping them off the surface.

Aardvarks feed from subterranean nests that vary in depth from shallow scratches at the surface to depths of over 1 m. Digs of approximately 200 mm are the norm. Very deep excavations are normally restricted to deep-living termite species such as *Hodotermes mossambicus* and such feeds may last over 30 min. In the case of *Trinervitermes* termitaries, Aardvarks dig into the centre of the mound and below ground level where large numbers of workers and larvae are concentrated.

Mechanical and chemical defences of ants and termites often play an important role in the feeding behaviour of myrmecophagous mammals. When the number of soldiers gets too high, other myrmecophagous mammals are forced to stop feeding, but this is not generally so for Aardvarks. Some ants, such as *Dorylus helvolus*, do bite hard enough to cause discomfort, but the attempts of most species are ineffective. The chemical defences of termites such as *Trinervitermes* spp., which deter many potential predators, do not stop Aardvarks either. On the contrary, these species are eaten in large numbers and many soldiers are ingested.

While active, Aardvarks spend the majority of their time searching for food. The small size of their prey requires them to consume hundreds of thousands of ants and termites per night, and this necessitates them spending all their time foraging to satisfy their energy requirements. Nightly foraging distances are governed by ant

densities. In the Karoo, it is not unusual for them to travel 4 km or more per night (Taylor 1998), although Melton (1976) recorded distances of up to 14 km per night in Uganda (though these latter estimates were based on spoor and may not be reliable).

There have been reports of Aardvarks eating the fruits of a geocarpic plant, the Aardvark Cucumber *Cucumis humifructus* (Meeuse 1958). Seeds from this species have been found in faeces and the plant has been found growing at the entrance of burrows where droppings are often deposited. Due to its unique habit of forming fruit underground, fruits of this plant need to be dug up for dispersal. It has been suggested that the Aardvark devours the fruit for its moisture content and the consumed seeds are then dispersed by the Aardvark with the added bonus of being deposited in manure, but this has yet to be observed directly. Aardvarks, however, fulfil their water requirements from ants and termites, so this argument seems implausible. In addition, Aardvarks lack the mouthparts necessary to break open the tough rind of the fruit. An alternative hypothesis is that seed harvesting ants store the seeds of the Aardvark Cucumber in their nests and then Aardvarks consume these seeds coincidentally when eating the ants. Kingdon (1971) reports that fungus gardens of termitaries are rejected in the wet season, but may be eaten in the dry season.

Commensal feeding associations have been recorded. The Aardwolf *Proteles cristatus*, which is unable to open termitaries itself, exploits the ability of the Aardvark to do so. During winter in South Africa *Trinervitermes trinervoides* remain within their termitaries where Aardwolves cannot reach them. This considerably reduces the amount of food available and Aardwolves lose condition. At these times they often follow Aardvarks and feed on freshly exposed termites (Taylor & Skinner 2000). When Aardvarks become active during the day, Southern Anteater-chats *Myrmecocichla formicivora* hang around and feed on ants from freshly opened nests (Taylor & Skinner 2001). Similar associations are known with Clapper Lark *Mirafra apiata* (Vernon & Dean 1988) and baboons (J. Kingdon pers. comm.).

Social and Reproductive Behaviour Aardvarks are solitary with very limited contact between conspecifics. When a ♂ and ♀ are in close proximity, they detect each other by sound and smell. On approach they sniff each other vigorously, especially around the base of the tail. On contact they occasionally rear up on their hindlegs as part of the investigative process. Interactions are short, usually lasting less than 10 min. If sexual interest is shown, the interaction may last longer.

Home-range areas are 200–300 ha in the Karoo (Taylor & Skinner 2003), but could be larger in areas with lower prey abundance. No seasonal variation is recorded, although non-cyclic spatial shifts in home-ranges do occur. The degree of territoriality is unknown. Meetings between adult ♂♂ have not been observed, so the degree of antagonism is unrecorded. However, one young habituated ♂ behaved very nervously when a large adult ♂ was close by, and repeatedly hid inside burrows for short periods. This young animal appeared to perceive the adult by scent. Although densities are low, home-ranges are not mutually exclusive. Limited overlap occurs between ♂♂ and ♀♀, ♂♂ and ♂♂, and ♀♀ and ♀♀. Scent glands produce a viscous, strong-smelling liquid that is regularly used by both sexes to scent-mark throughout their home-ranges. In ♀♀ the gland opens on either side of the vulva and in ♂♂ they open just behind the prepuce. Scent-marking is achieved by wiping the

gland over freshly excavated soil at feeding sites, burrow entrances and faecal scrapes.

During three consecutive years in the Karoo, mating occurred in Oct and Nov; one observation was also made in May. During copulation, the ♂ hangs on tightly to the ♀ with his forefeet, the claws inflicting numerous scratches on the back and flank of the ♀. Several attempted mountings may occur in a short space of time, with each lasting up to 15 sec. Behaviour of mothers with young is unknown in the wild. In captivity, young first follow their mother out of the nesting chamber at about 18 days. Females consume faeces and urine excreted by babies and have been observed to scent-mark them. It is not known how long young remain in the burrow with their mother, nor the age when the young disperse and become totally independent.

Although Aardvarks do not interact directly with other species, their burrows are utilized by many other species. Unused burrows provide sleeping shelter for warthogs, porcupines, Aardwolves, pangolins, jackals, genets, Black-footed Cats *Felis nigripes*, mongooses and any mammals small enough to enter (Smithers 1971). Hyaenas and African Wild Dogs *Lycaon pictus* may use them to shelter their young. They are even known to provide roosts for bats, notably *Nycteris* spp. Snakes and lizards are also important users of burrows, as are some birds such as the Southern Anteater-chat and Blue Swallow *Hirundo atrocaerulea*, which make nesting chambers in the roof of the burrow entrance. Excavated termitaries also provide shelter for many snakes and lizards as well as nests for small mammals such as the Southern African Pygmy Mouse *Mus minuotoides* and Lesser Dwarf Shrew *Suncus varilla* (Smithers 1971, A. Taylor pers. obs., S. Cilliers pers. comm.). Aardvarks never share burrows with conspecifics, but have been known to share a burrow with porcupines, probably in a separate chamber (A. Taylor pers. obs.).

Aardvarks do not vocalize, although young animals may make a bleating sound when stressed.

Reproduction and Population Structure Information about reproduction is available mostly from captive animals, supplemented by limited observations from the wild. Births in the wild have been reported from May to Jun in Ethiopia, early Nov in Uganda (Kingdon 1971), Oct and Nov in DR Congo (Shoshani *et al.* 1988) and May to Aug in southern Africa (Smithers 1983). In the Karoo, mating in Oct and Nov extrapolates to births in Jul (A. Taylor pers. obs.). One young, occasionally two, are born after an average gestation of 35 weeks (range 33.5–37.0) (Chicago Zoological Park records). Babies are born alert and active, weighing 1.8 kg (range 1.40–1.95 kg) (Chicago Zoological Park records). Captive animals grow quickly, reaching 10 kg after seven weeks, and 40 kg after just seven months; wild animals grow much more slowly. One captive ♂ gained only 9 kg in one year (23 kg to 32 kg). Population structure is poorly known, but meagre evidence from the Karoo suggests it is 1 ♂ to 1 ♀ (Nel *et al.* 2000). One captive specimen lived to nearly 30 years (Weigl 2005).

Predators, Parasites and Diseases Lions *Panthera pardus*, Leopards *Panthera leo*, Spotted Hyaenas *Crocuta crocuta* and African Rock Pythons *Python sebae* are the main predators of the Aardvark, although smaller predators may take young. Shoshani *et al.* (1988), reviewing the literature available at the time, list a number of ectoparasites including ticks, such as *Haemaphysalis muhsami*, *Hyalomma impressum* and a number

of species of the genus *Rhiphicephalus*; sucking lice (*Haematopinus notophallus* and *Hybophthirus notophallus*), a flea (*Echidnophaga larina*) and various flies. Endoparasites include flagellates (*Trichomonas* sp. and *Trypanosoma* spp.); an amoeba (*Entamoeba* sp.); a thorny headed worm (*Nephridiacanthus longissimus*); various roundworms and a pentastome (*Armillifer armillatus*). Diseases are unknown.

Conservation IUCN Category: Least Concern. CITES: Not Listed.

Although reduced in areas where their habitat has been altered as a result of human activities, the Aardvark has a wide, nearly pan-African distribution, south of the Sahara, occurs in many well-managed protected areas, and is not currently believed to be threatened. In central and West Africa, numbers may be declining as a result of the expansion of human populations, habitat destruction and hunting for meat. Hatt (1934) recorded indigenous hunters in the Congo killing Aardvarks trapped in burrows, and Mbuti pygmies in the Ituri Forest in DR Congo are reported smoking them out of their burrows (Carpaneto & Germe 1989). The meat is prized, including the skin; many parts of the Aardvark, such as the claws and teeth, are used to make bracelets, as charms and curios, and for some medicinal purposes (Carpaneto & Germe 1989).

Measurements

TL (♂ ♂): 1600 (1490–1750) mm, n = 15 TL (♀ ♀): 1580 (1400–1730) mm, n = 16
T (♂ ♂): 544 (443–620) mm, n = 15
T (♀ ♀): 539 (464–630) mm, n = 16
HF c.u. (♂ ♂): 256 (240–268) mm, n = 15
HF c.u. (♀ ♀): 247 (225–280) mm, n = 16
E (♂ ♂): 180 (167–210) mm, n = 15
E (♀ ♀): 177 (165–185) mm, n = 16
WT (♂ ♂): 53.3 (41.3–64.5) kg, n = 15
WT (♀ ♀): 51.4 (40.4–57.7) kg, n = 16
Zimbabwe (Smithers & Wilson 1979)

TL (♂ ♂): 1721 (1640–1785) mm, n = 4
TL (♀ ♀): 1770 (1610–1850) mm, n = 6
T (♂ ♂): 637 (610–720) mm, n = 4
T (♀ ♀): 644 (580–700) mm, n = 6
HF c.u. (♂ ♂): 276 (270–290) mm, n = 4
HF c.u. (♀ ♀): 270 (263–275) mm, n = 6
E (♂ ♂): 169 (162–175) mm, n = 15
E (♀ ♀): 171 (158–180) mm, n = 16
GLS (♂ ♂): 253 (252–254) mm, n = 3
GLS (♀ ♀): 247 (240–255) mm, n = 6
GWS (♂ ♂): 92 (84–98) mm, n = 4
GWS (♀ ♀): 92 (85–96) mm, n = 6
NE DR Congo (Hatt 1934)

Hatt (1934) recorded a ♂ specimen from the forests of Congo (which he attributed to the form *O. a. erikssoni*) with measurements: TL: 1980 mm; T: 760 mm; and HF c.u.: 300 mm.

Key References Kingdon 1971; Melton 1976; Shoshani *et al.* 1988; Skinner & Chimimba 2005; Taylor 1998; Taylor & Skinner 2000, 2001, 2003, 2004; Taylor *et al.* 2002.

Andrew Taylor

Glossary

abbrev. = abbreviation

adj. = adjective

cf. = *confer*, compare with; as opposed to

Lat. = Latin

n. = noun

pl. = plural

q.v. = *quod vide*, 'which see'

v. = verb

acetabulum: the concave socket (fossa) in the pelvic bone in which the head of the femur articulates.

acrocentric: describes a chromosome which has the centromere (*q.v.*) very near one end and which therefore appears to have only one arm (= telocentric (*q.v.*) for practical purposes).

ad libitum: (*Lat.*) as much as one likes; having unrestricted access to a resource (e.g. water or food).

aestivate: state of torpor (*q.v.*) induced by cold or drought; usually associated with a reduced metabolic rate and inactivity.

afroalpine: describes habitats and/or vegetation occurring above the treeline on African mountains. Includes montane grassland and heathlands.

afromontane: refers to mountainous regions in Africa, e.g. afromontane forests and afromontane grasslands.

Albertine Rift Valley: *see* Rift Valley (*q.v.*).

allele: an alternative form of a gene. A diploid organism carries two alleles (which may be same or different) for each gene locus. At any one locus, there may be several possible alleles (although only two are present in a single organism).

allelomimetic behaviour: behaviour in social animals in which each animal does the same thing as those nearby.

Allen's Rule: A rule that states that structures in endotherms such as limbs (which are more prone to heat loss) are reduced in size by means of natural selection over time in cooler climates (to reduce heat loss).

allogrooming: grooming behaviour directed at another individual. *cf.* autogroom (*q.v.*).

allomothering: non-parental mothering; caring for young by individuals (male or female) that are not the parents of the young.

allopatry (*adj.* **allopatric**): the situation where populations of the same or different species have non-overlapping geographic ranges; refers also to populations of the same, or different, species that are geographically separated. *cf.* sympatry (*q.v.*); syntopy (*q.v.*).

allozyme: one of a number of forms of the same enzyme having different electrophoretic properties and which are encoded by alternate alleles at the same genetic locus.

altimontane: collective term for the belts of ericaceous and afroalpine vegetation on the high mountains of tropical East Africa (White 1983).

altricial: describes young born in an undeveloped state. *cf.* precocious (*q.v.*).

altruism: behaviour which enhances the reproductive and genetic fitness of another individual at the expense of its own.

alveolus (*pl.* **alveoli**, *adj.* **alveolar**): small cavity; socket that houses the root of a tooth.

amastoidy: a condition characteristic of paenungulate mammals in which the mastoid process is concealed by the expansion and overlap of the squamosal.

angular process: process at the posterior lower corner of the mandible; situated ventral to the coronoid process (*q.v.*).

ante-orbital: in front of the orbit (*q.v.*).

antebrachial: anterior to the arm (forelimb).

anterior palatal foramina: the two foramina (*q.v.*) on the ventral part of the skull.

apomorphy (*adj.* **apomorphic**): situation in which a novel character evolves from a pre-existing character. In cladistics (*q.v.*), an apomorphic character shared among two or more species (synapomorphy [*q.v.*]) indicates shared descent from a common ancestor and hence monophyly (*q.v.*). *cf.* plesiomorphy (*q.v.*).

arboreal: living above the ground (in trees and shrubs). *cf.* scansorial (*q.v.*); terrestrial (*q.v.*).

auditory bulla: *see* tympanic bulla.

auditory meatus (*pl.* **auditory meati**): the external opening of the ear; the passage leading from the tympanic membrane (ear drum) to the external ear.

autapomorphy: derived trait uniquely characteristic of a taxon.

autogroom: grooming behaviour in which an individual grooms itself. *cf.* allogroom (*q.v.*).

autosomal: pertaining to any chromosome other than the sex chromosomes.

bachelor herd: a herd comprised entirely of males, usually mature, but of mixed age.

baculum (*pl.* **bacula**, *adj.* **bacular**): the os penis, or penis bone, which supports the penis in some mammals.

bai (*pl.* **bais**): an opening or clearing.

basal metabolic rate: metabolic rate required for survival in the thermal neutral zone (*q.v.*); a state that requires the lowest expenditure of energy when at rest.

basicranium: the base of the skull.

basisphenoid: cranial bone in middle of base of skull; the median posterior part of the sphenoid bone, forming part of the floor of the braincase.

Bergmann's Rule: The theory that the size of a warm-blooded animal in a single, closely related, evolutionary line, increases along a gradient from warm to cold temperatures.

bicuspid: having two points or cusps (particularly of teeth).

bifid: divided by a shallow notch.

bilophodont: describes cheekteeth having two transverse ridges.

bipedal: body supported by the two hindlimbs; movement not using the forelimbs.

blastula: a hollow ball of undifferentiated cells (derived from a

- fertilized ovum by cell division), which represents one of the earliest stages of embryonic development.
- BP:** (*abbrev.*) before the present.
- brachyodont:** describes a premolar or molar tooth with low crowns. *cf.* hypsodont (*q.v.*).
- braincase (= cranium):** that part of the skull housing the brain; the part of the skull posterior to the front line of the orbits. *cf.* rostrum (*q.v.*).
- buccal:** On the cheek side of the mouth or teeth or penetrating to the cheek or sometimes used broadly as pertaining to the cavity of the mouth.
- bullae:** *see* tympanic bulla.
- bnodont:** describes molar teeth, entirely covered by enamel, that have low, rounded, hill-like cusps (as opposed to sharp, pointed cusps). (*cf.* hypsodont, lophodont).
- bushmeat:** meat for human consumption derived from non-domesticated mammals, birds and reptiles taken from their natural habitats and domiciles.
- bushveld:** savanna vegetation type characterized by a grassy ground layer and a moderately dense upper layer of shrubs and scattered trees.
- BZ:** (*abbrev.*) Biotic Zone.
- C or c:** (*abbrev.*) canine tooth; upper case denotes adult dentition, lower case denotes deciduous dentition (milk teeth). *See also* canine.
- C–M¹, C–M², C–M³:** in golden-moles, the length of the upper tooththrow, measured from the most anterior part of the canine to the most posterior part of the most posterior molar. For golden-moles, the most posterior molar is M² or M³.
- c.u.:** (*abbrev.*) (*Lat. cum unguis* = with nail) measurement of the hindfoot when length of the nail on the claw is included in the measurement. Usually hindfoot is measured without the claw because claws may be broken or worn. When length of claw is included, it is conventional to record as 'HF c.u.'. *cf.* s.u. (*q.v.*)
- caecum (pl. caeca):** a blind-ending pouch in the alimentary canal (often enlarged as a fermentation chamber) located at the junction of the small and large intestines.
- canine:** the most anterior tooth on the maxilla bone and in a similar position on the mandible; situated immediately posterior to the incisors; if incisors are absent, the most anterior tooth in the jaw. Unicuspid; tall and pointed in most mammals. Never more than one canine on each side of each upper and lower jaw; absent in some taxa.
- caniniform:** having shape and appearance of a canine tooth.
- carotid:** pertaining to the carotid artery located in the front of the neck through which blood from the heart flows to the brain.
- caudal:** pertaining to the tail; in the direction of the tail.
- Cenozoic (= Cenozoic Era):** geological era, ca. 65 mya to today, comprising the Quaternary and Tertiary Periods: the Age of Mammals.
- central Africa:** Cameroon (south of the Sanaga R.), Central African Republic (but only south of ca. 7° N), Equatorial Guinea, Gabon, DR Congo (except SE). Mainly rainforest habitats and rainforest–savanna mosaics.
- centromere:** the part of a chromosome where sister chromatids are linked together during mitosis.
- cerebellum:** the part of the hindbrain that controls and coordinates motor movements, posture, balance and muscle tone.
- cerebrum (= cerebral hemispheres):** the anterior part of the brain that is involved in voluntary movements, processing sensory information, olfaction, learning, memory, communication and other functions.
- cervical:** pertaining to the neck.
- cf.** (in general usage): compare or compare with. In the context of descriptions, implies a difference or contrast: e.g. 'In *Elephantulus edwardii*, first lower premolar single-rooted (*cf.* *E. myurus* in which the first lower premolar is double-rooted).'
- cf.** (in taxonomy): precedes the specific name if there is uncertainty in the assignment.
- cheekteeth:** the premolar (*q.v.*) and molar (*q.v.*) teeth combined.
- choana (pl. choanae):** the openings of the internal nostrils on the skull, situated immediately posterior to the bony palate.
- chromosome:** one of the thread-like bodies within the nucleus of a cell, which carry the genes (genetic material) in linear order; each chromosome is composed of one long molecule of DNA (and two long molecules at cell division). Chromosomes occur in pairs (one from each parent) and are visible as rod-like bodies in cells that are dividing. The total number of chromosomes in a cell is expressed as the diploid number (2n).
- cingulum (pl. cingula):** ridge around the base of the crown of a tooth.
- CITES:** (*abbrev.*) Convention on International Trade of Endangered Species of Wild Fauna and Flora; an international treaty set up to ensure that international trade in wild animals and plants does not threaten the survival of species in the wild. It accords varying degrees of protection to more than 33,000 species of animals and plants. Appendix I lists species that are the most endangered among CITES-listed animals and plants. Appendix II lists species that are not necessarily now threatened with extinction but that may become so unless trade is closely controlled. Appendix III is a list of species included at the request of a Party that already regulates trade in the species and that needs the cooperation of other countries to prevent unsustainable or illegal exploitation.
- clade:** branch of a phylogenetic tree containing the set of all organisms descended from a common ancestor.
- cladistic (analysis):** a methodology that provides a classification in which organisms are grouped in terms of the time when they had a common ancestor.
- cline (adj. clinal):** in context of geographic variation, a gradual and sequential change of a character(s) without a significant break such as would justify division into separate subspecies or species.
- cloaca:** the single common opening for faeces, urine and genital products; not present in mammals except that a cloaca-like structure is present in some species of Tenrecidae.
- cochlea (pl. cochleae, adj. cochlear):** a hollow structure, spirally coiled like a snail's shell, situated in the skull and containing the internal organ of hearing.
- comparatively:** in profiles of Afrosoricida and Macroscelidea, used in the context of describing the size of one character compared with the size of the same character in a different species. Sizes described as small, medium or large (if range is divided into three) or very small, small, medium, large, very large (if range is divided into five). *cf.* relatively (*q.v.*).
- competitive exclusion:** the principle that two different species cannot indefinitely occupy the same ecological niche.

concatenation: a chain of linked elements.

concave: having a curvature that curves inwards; having an outline or a surface curved like the interior of a circle or sphere. *cf.* convex (*q.v.*).

concavity: a concave depression in an outline or surface.

conductance: in thermal biology, the rate at which heat passes across a temperature gradient, e.g. the density and thickness of the pelage affects the rate at which body heat passes from the body to the outside. Thick pelage, which traps and holds air, results in low thermal conductance.

condylar process: process at the posterior upper corner of the mandible, which forms the lower hinge of the jaw articulation; fits into the glenoid fossa (*q.v.*) of the skull.

condylarth (*adj.*): as in the Condylarthra, an extinct order of mammals.

condyle: a rounded process on a bone, which articulates with a socket-like concavity in another bone.

congeneric: belonging to the same genus.

conspecific: belonging the same species. *cf.* heterospecific (*q.v.*).

contiguous: touching; sharing a boundary (as in geographic ranges).

convex: having a curvature that bulges outwards; having an outline or a surface curved like the exterior of a circle or sphere. *cf.* concave (*q.v.*).

coprophagy: the eating of faeces. Includes the eating of an individual's own faeces as they are voided from the anus.

coronoid canal: a foramen (canal) in the coronoid process (*q.v.*) of the mandible.

coronoid process: angular pointed process on the upper margin of the mandible, situated anteriorly to the condylar process (*q.v.*); does not participate in the jaw articulation.

corpus luteum (*pl. corpora lutea*): a glandular mass of tissue on the surface of an ovary, that develops after the extrusion of an ovum from a Graafian follicle (*q.v.*); secretes the hormone progesterone.

cotype: originally synonymous with syntype but now used as synonym of paratype (*q.v.*).

CR: (*abbrev.*) *see* crown–rump length.

cranial profile: the shape of the cranium (that part of the skull which surrounds the brain) when viewed from the side.

craniodental: pertaining to the skull and teeth.

cranium: that part of the skull housing the brain. Also called braincase.

crepuscular: at, active in, twilight, when light intensity is higher than at night but lower than during the day. *cf.* diurnal (*q.v.*); nocturnal (*q.v.*).

Cretaceous Period: period (within the Mesozoic Era); 146–65 mya.

crown: (1) top of head; (2) exposed part of a tooth (visible above gum), especially the grinding surface.

crown–rump length (CR): distance from the crown of head to the rump of a foetus (i.e. maximum length of a foetus in its natural form).

cursorial: pertaining to running.

cusp (*adj. cuspidate*): a prominence or sharp point, such as on the occlusal surface of some teeth. *See also* t.

cutaneous: (*adj.*) pertaining to the skin.

Cyrenaica: a region of North-East Libya. Includes the Cyrenaican Plateau and that part of the Mediterranean Coastal Biotic Zone

between the plateau and the sea, as well as drier terrain south of the plateau.

cytochrome b: a protein involved in electron exchange in the mitochondria. It is the product of a gene in the mitochondrial genome. The sequence of this gene is often compared between species in phylogenetic studies to infer relatedness.

cytogenetics (*adj. cytogenetic*): the study of the microscopic structure of chromosomes, especially the mapping of genes.

cytonuclear (*adj.*): pertaining to the nucleus and the cytoplasm of a cell.

Dahomey Gap: the geographic region where savanna habitat extends southwards to the West African coast in E Ghana, Togo, Benin (formerly Dahomey) and extreme SW Nigeria. The presence of savanna forms a break (or gap) in the extensive Rainforest Biotic Zone, which extends along the West Africa coast from Sierra Leone to Cameroon. The Dahomey Gap is an important biogeographical barrier separating the faunas to the east and west of the Gap.

deciduous teeth: *see* milk teeth (*q.v.*).

delayed implantation: a means of lengthening the interval between copulation and parturition by delaying the implantation of the blastula (*q.v.*), so that both copulation and parturition can occur in the most optimal seasons. Development to blastula stage is followed by a period of halted development lasting several weeks or months; then the blastula implants and embryonic development proceeds normally, usually without any further interruption, until the young is born.

deme: a unit of population which is interbreeding and which is separate from any other such population.

dental formula: a simple numerical method of denoting the number of incisor (I), canine (C), premolar (P) and molar (M) teeth on one side of the upper jaw and lower jaw, and the total number of teeth. For example, the dental formula of a primitive mammal is $I^{3/3}, C^{1/1}, P^{4/4}, M^{3/3} = 44$, which means there are three incisors, one canine, four premolars and three molars on each side of the upper jaw and also the lower jaw, making a total of 44 teeth. The formula may also be expressed in the form $^{3143}/_{3143} = 44$. Each incisor, premolar and molar is numbered according to its position in the tooth row; superscript numbers indicate upper jaw, subscript numbers indicate lower jaw (mandible) e.g. P^4 (upper fourth premolar), M_2 (lower second molar).

dentine: the substance, also known as ivory, comprising tusks (*q.v.*) and the interior hard part of vertebrate teeth. Lies under the enamel of teeth (but may be exposed if the enamel wears) and surrounds the pulp chamber and root canals.

diastema: space in the mouth between the incisor teeth and cheekteeth in those mammals that feed on grasses, herbs etc. (e.g. rodents, hares, rabbits, ruminants, etc.).

dichromatism: condition in which members of a species show one of only two distinct colours or colour-patterns.

dilambdodont: molar tooth with W-shaped ridges. *cf.* zalambdodont (*q.v.*).

dimorphism: *see* sexual dimorphism.

diphyly: the derivation of a taxon from two separate lines of descent. *cf.* monophyly (*q.v.*).

diploid number (2n): total number of chromosomes (including sex chromosomes) in a somatic cell of an organism.

- distal:** the end of any structure furthest away from the mid-line of the body or furthest from the point of its attachment. *cf.* proximal (*q.v.*).
- diurnal:** at, active in, daytime; when light intensity is high. *cf.* crepuscular (*q.v.*); nocturnal (*q.v.*).
- DNA:** (*abbrev.*) deoxyribonucleic acid; the very large self-replicating molecule that carries the genetic information of a chromosome; each molecule is composed of two complementary chains of DNA.
- DNA hybridization:** technique of comparing the similarity between two DNA molecules by reassociating single strands from each molecule and determining the extent of double-helix formation. In phylogenetics, this technique is used to determine the relatedness of two or more taxa.
- dorsoventral (dorsoventrally):** from dorsal to ventral surface; from back to belly of an animal.
- E:** (*abbrev.*) length of external (outer) ear (= pinna), measured from tip of ear to the posterior point of the ear conch. Length and shape usually affected by preservation.
- East Africa:** Kenya, Uganda, Rwanda, Burundi and Tanzania.
- eastern Africa:** SE Sudan, Ethiopia, Eritrea, Djibouti, Somalia, Kenya, Uganda, Tanzania, Malawi (but only south of L. Malawi and east of the Shire R. Valley) and Mozambique (but only east of Malawi and north of the Zambezi R.).
- ecotype:** a genetically distinct geographic variety or population within a species, which is adapted to specific environmental conditions.
- ectoparasite:** a parasite that lives on the exterior of an organism (e.g., ticks, fleas, lice). *cf.* endoparasite (*q.v.*).
- ectotympanic:** a bony element within the middle ear that supports the tympanic membrane or eardrum.
- edaphic:** influenced by conditions of soil or substratum.
- emargination:** a distinct notch or indentation.
- embryo number:** number of foetuses within the uterus or uteri of the female (as assessed by autopsy). Expressed as mean number (with range from minimum to maximum, and sample size). *cf.* litter-size (*q.v.*).
- enamel:** hard material that forms a cap over the dentine component of a tooth; usually the most visible part of a tooth.
- encephalization quotient (EQ):** a measure of comparative brain size or weight defined as the ratio of the actual brain weight to the expected brain weight predicted for an animal of a given body weight.
- endemic:** restricted to, peculiar to, or prevailing in, a specified country or region.
- endoparasite:** a parasite that lives in the interior of an organism (e.g., nematodes, cestodes, blood parasites). *cf.* ectoparasite (*q.v.*).
- entotympanic:** an independent ossification found in the floor of the tympanic cavity in various extant and extinct eutherian groups, including, for example, Scandentia, Chiroptera, Dermoptera, Hyracoidea, Pholidota, Xenarthra, Carnivora, and Macroscelidea.
- Eocene:** geological Epoch (within the Tertiary Period); 55–38 mya.
- epiphysis (pl. epiphyses):** any part of a long bone that is formed from a different centre of ossification and which later fuses with the bone to form its terminal part.
- epitympanic recess:** a hollow located on the roof of the middle ear.
- erg:** a large, relatively flat area of desert covered with wind-swept sand with little or no vegetation cover (sometimes referred to as a dune sea).
- evaporative water loss:** the loss of water from the body through the skin and/or the lungs. A mechanism used by mammals to reduce T_b (*q.v.*) when T_a (*q.v.*) is high. Excessive evaporative water loss may lead to dehydration if free (drinking) water is unavailable.
- exfoliating:** shedding flakes (e.g. of bark), or breaking into relatively thin slabs (e.g. of granitic rock).
- exoccipital condyles:** a pair of projections from the occipital bone on either side of the foramen magnum (*q.v.*) which articulate with the first of the spinal vertebrae.
- extant:** living at the present time. *cf.* extinct.
- F. R.:** (*abbrev.*) Forest Reserve.
- facultative:** having the capacity to switch from one mode of life or action to another depending on conditions or circumstances. *cf.* obligate (*q.v.*).
- female-defence polygyny:** a mating system in which males control access to females directly, usually by virtue of female gregariousness (Emlen & Oring 1977).
- fenestra (pl. fenestrae):** opening in a bone, or between two bones.
- flank:** the side of the body of a mammal.
- FN:** (*abbrev.*) *see* fundamental number.
- foliaceous:** (*adj.*) resembling the leaf of a plant.
- folivore (adj. folivorous):** an animal that eats leaves.
- foot-drumming:** activity of banging/drumming the soles of the hindfeet on the substrate to produce a noise used for communication between individuals; footdrums vary in length, intensity and form according to species; a frequent means of communication in sengis.
- foramen (pl. foramina):** an aperture (which is usually small, round or elliptical) in a bone, or between bones, for the passage of a nerve, blood vessel or muscle.
- foramen magnum:** the large opening at the posterior end of the skull through which the spinal cord passes.
- forest island:** *see* relict forest.
- fossorial:** adapted for digging; burrowing. *cf.* subterranean (*q.v.*).
- founder effect:** the loss of genetic diversity that occurs when a new isolated population is derived from a very small number of individuals.
- fovea:** small pit or depression.
- frontal bone:** one of a pair of bones forming the anterior part of the braincase.
- frugivorous:** fruit-eating.
- fundamental number (FN):** an ambiguous term sometimes defined as (1) the total number of chromosomal arms in the full chromosomal complement of an organism (i.e. including the sex chromosomes), or (2) the total number of chromosomal arms found in the autosomal chromosomes only (i.e. excluding the sex chromosomes). When only the autosomal chromosomes are included, some authors (but not all) use aFN instead of FN to avoid ambiguity.
- fusiform:** elongated and tapering at both ends.
- fynbos:** the heath shrublands characteristic of the Cape Floristic Kingdom (within the South-West Cape Biotic Zone) of South Africa. Dominant plants are sclerophyllous, evergreen, low (<3 m), bushy and fine-leaved, but there are also scattered

taller bushes and, less often, very widely spaced trees. Contains an exceptionally high number of endemic species of plants. The three main components on nutrient-poor sandy soils are species of Ericaceae, Restionaceae and Proteaceae. Also includes 'renosterveld' (*q.v.*) (dominated by species of Asteraceae) on nutrient-rich silt or clay soils.

G. R.: (*abbrev.*) Game Reserve.

gallery forest: type of forest outlier (in a savanna region) found in narrow sheltered valleys and ravines on hillsides, where soils are moist enough, and conditions humid enough, to support rainforest trees (Rosevear 1953).

genetic drift: in population genetics, refers to changes in the frequencies of genes in small, isolated populations that occur with time, as a result of random sampling events as opposed to natural selection.

genotype: genetical term to describe the genetic constitution of an individual inherited from its parents. *cf.* phenotype (*q.v.*).

genus (*pl. genera*): taxonomic division superior to species and subordinate to family.

geocarpic: having fruit mature underground.

geophagy (= geophagia): the eating of saline or calcareous soil.

gestation: the development of embryo/foetus, which takes place in the uterus; the period during which this development takes place. The gestation period is defined as the interval between conception and parturition (birth). Strictly speaking, the gestation period is not the interval between copulation (mating) and parturition (birth), although many authors take it to be this interval. The gestation period (*sensu stricto*) may be lengthened by reproductive delays, such as delayed implantation (*q.v.*).

glans penis: the bulbous tip of the penis.

glenoid (= glenoid fossa): the cavity (fossa) in the squamosal bone of the skull for the articulation of the condyle of the mandible (lower jaw) in mammals; visible on lateral and/or ventral views of skull depending on the taxon.

GLS: (*abbrev.*) greatest length of skull, measured from anterior end of incisor teeth or nasal bone (whichever is most anterior) to the posterior end of the skull (occiput, occipital condyles or auditory bullae, whichever is most posterior).

Gondwana (= Gondwanaland): the southernmost of the two Mesozoic (*q.v.*) supercontinents that later fragmented (as a result of continental drift) into the landmasses of Africa, Madagascar, Antarctica, Australia, South America, the Indian subcontinent and the Arabian peninsula.

Graafian follicle: the structure in the mammalian ovary which contains the developing ovum, and from which the ovum is released at the time of ovulation.

gracile: lightly built. *cf.* robust.

graminivore (*adj. graminivorous*): feeding on grasses.

granivore (*adj. granivorous*): an animal that eats grains and seeds.

graviportal: having limbs adapted to bearing great weights (as in elephants).

gregarious: living together in groups, flocks, herds.

Gregorian Rift Valley: *see* Rift Valley.

guard hair: long thin bristle-like hairs, mainly on the back and flanks, which project beyond the soft hairs of the pelage; when present, conspicuous but never as numerous as soft hairs; probably tactile in function.

gular: pertaining to the upper part of the throat (the gula) as in gular gland, gular pouch, gular region.

GWS: (*abbrev.*) greatest width of skull, usually measured across the widest point of the zygomatic arches (*q.v.*).

haematopoietic (*n. haematopoensis*): pertaining to the formation of blood cells from stem cells.

hallux: the first digit of the hindlimb.

hammada: flat plain covered with pebbles of various sizes on a hard substrate in an arid environment. Much of the Sahara Desert is formed of hammada.

haplotype: the set of alleles borne on one of a pair of homologous chromosomes; a group of genes that is inherited together from a single parent.

HB: (*abbrev.*) length of head and body (measured from the tip of the nose to the most posterior point of the pelvis (anterior to the first tail vertebra).

hemidiaphragm: half of the diaphragm, the muscle that separates the chest cavity from the abdomen and that serves as the main muscle of respiration.

hermaphrodite (*adj. hermaphroditic*): an individual having both male and female reproductive organs.

heterospecific: (*adj.*) belonging to different species. *cf.* conspecific (*q.v.*)

heterothermic: condition when the body temperature fluctuates in relation to the ambient temperature T_a (*q.v.*). *cf.* homeothermic (*q.v.*).

heterozygosity: a measure of the genetic variation in a population, expressed through the presence of different alleles (*q.v.*) at one or more loci on homologous chromosomes.

HF: (*abbrev.*) length of hindfoot (measured from the 'ankle bone' to the tip of the longest digit usually without including the claw). *See also* c.u.; s.u.

high forest: rainforest that has matured, stabilized and reached the climax stage of succession.

highveld: high plateaux characteristic of inland southern Africa, dominated by grasses.

Holocene: geological Epoch (within the Quaternary Period) (*q.v.*) following the Pleistocene Epoch (*q.v.*); ca. 11,000 mya to today. Sometimes referred to as the 'Recent' Epoch.

holotype (= type): the single specimen designated or indicated by the original author of the original description of a new species or subspecies, to be the standard reference to the essential characters of the new taxon. *See also* cotype (*q.v.*), lectotype (*q.v.*), neoparatype (*q.v.*), neotype (*q.v.*), paratype (*q.v.*), syntype (*q.v.*), topotype (*q.v.*) and type locality (*q.v.*).

home-range: the area (expressed in square metres, or square kilometres) routinely used by an animal for its day-to-day activities and requirements, and which contains the resources required for survival and reproduction. Within the home range there may be a 'core area' or 'centre of activity', which is utilized more frequently than other parts (e.g. 80% or 90% of known time-based observations). *cf.* territory (*q.v.*).

homeothermic: describes an organism having a body temperature that is maintained at a constant level (within limits), independently of the ambient temperature T_a (*q.v.*). For the limits, see upper and lower critical temperatures [*q.v.*]. *cf.* heterothermic (*q.v.*).

- homoplasy:** similarity between different organisms or taxa resulting from evolution along similar lines (e.g. convergent evolution) rather than descent from a common ancestor.
- homozygous** (*n.* homozygosity): describes a diploid organism that has inherited the same allele of any particular gene from each of its parents. *cf.* heterozygous.
- hyoid:** a small bone or bones in the throat located at the base of the tongue and supporting the muscles of the tongue.
- hyperthermia:** elevation of body temperature above normal limits due to increase in T_a (*q.v.*) or increase in metabolic rate. *cf.* hypothermia (*q.v.*).
- hypoconulid:** the most posterior cusp on the lingual (inner) side of a lower molar tooth.
- hypothermia:** drop in body temperature below normal limits; occurs in some small mammals when T_a (*q.v.*) falls, and is a means of conserving energy in cold weather. *cf.* hyperthermia (*q.v.*).
- hypsodont:** describes a premolar or molar tooth with high crowns; has short roots. *cf.* bunodont, lophodont.
- I or i:** (*abbrev.*) incisor (*q.v.*) tooth or teeth; upper case denotes adult dentition, lower case denotes deciduous dentition (milk teeth). *See also* incisor.
- I.** (*pl.* **Is.**): (*abbrev.*) Island.
- I¹-M³:** (*abbrev.*) the length of the upper toothrow from the anterior end of the first upper incisor to the posterior end of the last molar. In taxa where the last molar is M¹ or M² (instead of M³), the measurement is I¹-M¹ or I¹-M².
- implantation:** the embedding of a blastula (*q.v.*) in the lining of the uterus.
- incertae sedis:** (*Lat.*) refers to a taxon of uncertain status and that is perhaps taxonomically invalid.
- incisive foramen** (*pl.* **foramina**): paired foramina located at the anterior end of the bony palate, just posterior to the incisor teeth.
- incisor:** tooth rooted in the premaxillary bone (most anterior bone of upper jaw) and in an equivalent position in the mandibular bone (lower jaw); always anterior to the canine teeth, if present. The number and form of the incisor teeth varies in different species. *See also* dental formula (*q.v.*).
- infraorbital foramen** (*pl.* **foramina**): foramen that connects the orbit (eye-socket) with the rostrum (premaxilla and maxilla bones); this foramen contains the masseter medialis muscle in some taxa. Also referred to as ante-orbital foramen and antorbital foramen.
- infrasonic:** describes sounds with frequencies below the range that can be heard by humans.
- infundibulum:** a funnel-shaped cavity or depression.
- inguinal:** situated in the groin, that is the area between the lower lateral part of the abdomen and the thigh.
- inner:** nearest to mid-line of body, e.g. inner incisor, inner margin of ear.
- insectivore** (*adj.* **insectivorous**): an animal that eats insects.
- inselberg:** isolated rocky hill; term used mainly in western Africa. *See also* jebel (*q.v.*); kopje (*q.v.*), krantz (*q.v.*).
- inter-aural:** between the ears.
- inter-digital:** between the digits (e.g. interdigital gland).
- inter-orbit (= inter-orbital constriction):** narrowest part of the skull between the orbits when viewed dorsally at the level of the frontal bones.
- interparietal:** bone (not paired) on dorsal surface of the skull, lying between and partly posterior to the parietal bones.
- interpterygoid region:** the region between the two plate-like pterygoid bones (*q.v.*) that form part of the roof of the mouth.
- inter-specific:** between different species.
- intra-specific:** within one species; between members of the same species.
- intromission:** insertion of the penis into the vagina during copulation.
- Isoptera:** taxonomic order containing the termites (within the phylum Insecta).
- isozyme:** any one of several different forms of an enzyme encoded by the same or different genes and which each differ in properties such as optimum pH or isoelectric point.
- iteroparous:** repeated reproduction throughout a season or a lifetime (*cf.* semelparous – reproduces once and then dies).
- ivory:** *see* dentine.
- jebel (= gebel):** isolated rocky hill in savanna and arid habitats; term used mainly in northern Africa. *See also* inselberg (*q.v.*); kopje (*q.v.*).
- jugal:** bone of the skull which forms the middle part of the zygomatic arch (*q.v.*); anteriorly joins the maxillary process (*q.v.*) of the maxilla bone and posteriorly joins the squamosal process of the squamosal bone.
- K-selection:** selection for characteristics suitable in stable environments (slow development of young, small litter size, relatively long time to maturity, relatively long life span) *cf.* r-selection (*q.v.*).
- Kaokoveld:** area of sandstone and lava hills of the Namib Desert (Biotic Zone 11b) in NW Namibia, inland from the Skeleton Coast.
- Karoo:** southern African term for grassy dwarf shrubland on the semi-arid central plateau of the western half of South Africa at altitudes of 500–2000 m.
- karyogram:** a photographic representation of a karyotype (*q.v.*) as it appears at mitosis. Individual chromosomes are arranged in pairs from largest to smallest.
- karyological:** pertaining to the nucleus and chromosomes.
- karyotype:** the chromosomes in the cell of an animal. *See also* karyogram.
- kloof:** a deep, narrow valley or gorge.
- kopje:** rocky hill with boulders, rock crevices and sparse vegetation; term used mainly in southern Africa. *See also* inselberg (*q.v.*); jebel (*q.v.*); kranz (*q.v.*).
- krantz** (*pl.* **krantzes**): a wall of rock encircling a mountain or summit; hence any precipitous or overhanging wall of rocks.
- L:** (*abbrev.*) Lake.
- labial:** pertaining to the lips; situated near the lips; on the outer side of the teeth within the mouth. *cf.* lingual (*q.v.*).
- labially:** in the direction of the lips. *cf.* lingually (*q.v.*).
- lachrymal bone:** small bone in skull situated at the upper anterior margin of the orbit, near the lachrymal (tear) gland.
- lambdoid crest:** *see* supraoccipital crest.
- lamina** (*pl.* **laminae**): in the context of premolar and molar teeth, a transverse row of cusps which form a transverse ridge of bone and dentine across the tooth.
- larynx (= voice box):** the structure in the throat of mammals that produces sound.

- Laurasia:** the northernmost of the two Mesozoic (*q.v.*) supercontinents that later fragmented (as a result of continental drift) into the landmasses of Europe, Asia (excluding the Indian subcontinent) and North America.
- lectotype:** a specimen chosen from syntypes (*q.v.*) to stand as 'the type' of a species or subspecies when no holotype (*q.v.*) was designated by the author who described the new species or subspecies.
- lek:** a traditional site where males gather for the sole purpose of attracting and courting females, and to which females come for the sole purpose of mating with the male of their choice.
- limiting factor:** the principle that the growth or functioning of an organism is limited when any essential factor (or resource) is lacking or in short supply, regardless of the quantity available of any other factor (or resource). The principle may also be applied to the proliferation and/or distribution of a population or species.
- lingual:** pertaining to the tongue; situated near the tongue; on the inner (tongue) side of the mouth. *cf.* labial (*q.v.*).
- lingually:** in the direction of the tongue. *cf.* labially (*q.v.*).
- Lipotyphla** (*adj.* **lipotyphlan**): a suborder of the order Insectivora comprised of shrews, moles, hedgehogs, tenrecs and golden-moles; now considered to be polyphyletic and therefore not currently recognised as a valid taxon.
- litter-size:** number of young born to a female. Expressed as mean number (with range from minimum to maximum, and sample size). *cf.* embryo number (*q.v.*).
- localized movements:** movements of an animal within part or all of its home-range within a single day or within a limited period of time. *cf.* migration (*q.v.*); nomadic movements (*q.v.*).
- longitudinal:** lengthwise; running in a head to tail direction. *cf.* transverse (*q.v.*).
- lophodont:** molar teeth having the crowns formed in transverse crests or ridges (*cf.* bunodont).
- lordosis:** dorsi-flexion of the spine, often performed by females prior to copulation.
- lower critical temperature:** the lowest ambient temperatures at which the animal must increase its metabolic rate to maintain a constant body temperature. If ambient temperature decreases further, and the animal is unable to increase its metabolic rate sufficiently to maintain a constant body temperature, it will enter hypothermia and may eventually die. *cf.* upper critical temperature.
- lowveld:** savanna at lower altitudes below the Great Escarpment of South Africa, with vegetation consisting of a grassy lower layer and a woody upper layer of shrubs and/or trees, at either high density (woodland) or intermediate density (bushveld, *q.v.*).
- lumbar:** describes vertebrae between the thoracic vertebrae and the sacrum; vertebrae of the lower back in humans.
- M:** (*abbrev.*) molar tooth or teeth. *See also* molar (*q.v.*).
- Maghreb:** *see* North-West Africa (*q.v.*).
- malleus:** the most external bone of the three ossicles of the middle ear, the handle of which is joined to the ear drum.
- mandible:** lower jaw.
- mandibular ramus:** one of the two branches (sides) of the mandible (*q.v.*); the two rami are joined at the mandibular symphysis (*q.v.*).
- mandibular symphysis:** the junction, marked by a small vertical ridge, where the left and right sides of the mandible are fused.
- masseter muscle:** one of the muscles which raises the lower jaw, e.g. during chewing. Particularly well developed and powerful in herbivores.
- mastoid:** one of a pair of bones, often with a prominent process, situated near the posterior end of the skull behind the auditory meatus (*q.v.*).
- matriarchal:** describes social groups dominated and/or led by a female (often one of the oldest females in the group).
- maxilla** (*pl.* **maxillae**): one of the pair of bones in the skull that forms that part of each upper jaw in which the canine (*q.v.*) (if present) and cheekteeth (premolars and molars) (*q.v.*) are rooted.
- maxillary process:** projection of bone from the maxilla, which forms the anterior portion of the zygomatic arch (*q.v.*); usually oriented vertically to the anterior–posterior line of the skull.
- maxillary:** pertaining to the maxilla (*q.v.*).
- meatus:** a passage or channel; the opening of a passage.
- medial:** situated in the middle.
- Mesozoic (= Mesozoic Era):** geological era; ca. 250–ca. 65 mya, comprising the Triassic, Jurassic and Cretaceous Periods: the Age of Reptiles.
- metabolic rate:** *see* basal metabolic rate (*q.v.*).
- metabolic water:** water produced by oxidative processes within the body; an important source of water for arid-adapted mammals when free (drinking) water and water within the food is in short supply or unavailable.
- metacarpals:** the long bones of the hand, situated between the carpal bones of the wrist and the proximal phalanges of the fingers.
- metacentric:** describes a chromosome with the centromere (*q.v.*) at or very near the middle of its length, so there are two arms of equal or almost equal length (ratio not greater than 1 : 1.1). *cf.* submetacentric (*q.v.*).
- metacromion:** a process projecting backward and downward from the acromion (the lateral triangular projection of the spine of the scapula that forms the point of the shoulder and articulates with the clavicle of the scapula) of some mammals.
- metapopulation:** in population dynamics and ecology, a group of spatially separated populations of the same species which interact at some level.
- metatarsals:** the long bones of the foot, situated between the tarsal bones of the ankle and the most proximal phalanges of the toes.
- microsatellite locus** (*pl.* **microsatellite loci**): a region within a DNA sequence where short sequences of one, two, three or four of the nucleotides (A [adenine], T [thiamine], G [guanine] and C [cytosine]) are repeated consecutively; e.g. ACACAC, CAACAA. The number of times a sequence is repeated varies between individuals, within populations of a species, or between species which makes microsatellite loci useful tools in systematics (*q.v.*).
- migration:** movements of species that travel, predictably and more-or-less directly, from one habitat to another (and back again), along predetermined routes, in response to seasonal changes in climate, food supply or any other resource. *cf.* localized movements (*q.v.*); nomadic movements (*q.v.*).
- milk teeth:** teeth occurring in newborn mammals, or appearing soon after birth, and preceding the permanent teeth of the adult animal. Also called deciduous teeth.
- Miocene:** geological Epoch (within the Tertiary Period); ca. 23–5 mya.

- miombo:** a vernacular name applied to trees in the genus *Brachystegia*; a type of savanna woodland in the Zambezi region where *Brachystegia* spp. are the commonest trees or one of the commonest trees.
- mitochondrial DNA:** the small amount of DNA contained within the mitochondria of a cell.
- molar:** grinding or cutting tooth rooted in the maxilla bone and the mandible; there are usually one, two or three molar teeth in each ramus of the jaw. Together with the premolars, if present, they form the 'cheekteeth'. The number and form of the molar teeth varies in different species. Not preceded by deciduous (milk) teeth.
- molariform:** similar in form to a molar tooth; used to describe the form of the premolar teeth in some taxa.
- monoestrous:** Generally, having one oestrus cycle (*q.v.*) during a single reproductive season. In some taxa, having one litter per year. *cf.* polyoestrous (*q.v.*).
- monogamous:** having only one mate, usually for the whole of an animal's lifetime.
- monogamy** (*adj.* **monogamous**): a mating system in which one male mates with one female. Neither sex has the opportunity of monopolizing additional members of the opposite sex. Fitness often maximized through shared parental care (Emlen & Oring 1977). *cf.* polygyny (*q.v.*).
- monophyletic:** describes a taxonomic group descended from a common ancestor that was itself a member of that taxonomic group, and including *all* the descendants of that ancestor (Groves 2001). *cf.* paraphyletic (*q.v.*); polyphyletic (*q.v.*).
- monophyly:** derivation of taxa from a common ancestor. *cf.* diphyly (*q.v.*), polyphyly (*q.v.*).
- monospecific:** describes a genus containing only one known species. *See also* monotypic (*q.v.*).
- monotypy** (*adj.* **monotypic**): describes a taxon containing only one immediately subordinate taxonomic unit, e.g. a monotypic family contains only one genus; a monotypic genus contains only one species. *cf.* polytypy (*q.v.*).
- mopane:** a vernacular name applied to the tree *Colophospermum mopane*; a type of savanna woodland in the Zambezi region in which *C. mopane* is the commonest species of tree.
- Mt:** (*abbrev.*) Mount.
- mtDNA:** (*abbrev.*) mitochondrial DNA (*q.v.*).
- Mts:** (*abbrev.*) Mountains.
- multiparous:** describes either the birth of more than one offspring at once, or a female that has given birth two or more times.
- muzzle:** the snout; the nose and jaws of a mammal.
- mya:** (*abbrev.*) millions of years ago.
- myrmecophagy** (*adj.* **myrmecophagous**): the eating of ants and/or termites.
- mystacine vibrissae:** vibrissae (*q.v.*) resembling a moustache.
- n. d.:** (*abbrev.*) no data.
- N. P.:** (*abbrev.*) National Park.
- N. R.:** (*abbrev.*) Nature Reserve (not National Reserve).
- naris** (*pl.* **nares**): a nostril.
- Neogene Period:** geological period and system; 23.03 ± 0.05 to 2.5 mya, comprising the second part of the Cenozoic Era.
- neonate:** a newly born animal.
- neoparatype:** any specimen described at the same time as the neotype (*q.v.*).
- neotype:** a specimen selected as the type in cases where the primary types are definitely known to be lost or destroyed.
- nipple:** external opening of mammary gland. Nipple number and position vary according to the taxon, but are consistent within a species. Nipples arranged in pairs, one of the pair on each side of body. Nipple number (if given) is: the number and the position of the nipples on one side of the body, and the total number for both sides. For example, in golden-moles, nipple number is: 1 (abominal) + 1 (inguinal *q.v.*) = 4.
- nocturnal:** at, active in, the night; when light intensity is at its lowest; between sunset and sunrise. *cf.* crepuscular (*q.v.*); diurnal (*q.v.*).
- nomadic movements:** irregular and unpredictable movements, from one locality to another, made by species living in unpredictable habitats. *cf.* localized movements (*q.v.*); migration (*q.v.*).
- nomen dubium:** when the available evidence is not sufficient to permit the identification of a species, its name is considered to be a *nomen dubium* and therefore not available for taxonomic purposes.
- nomen nudum:** a name which is not valid because, when it was originally published, the organism to which it referred was not adequately described, defined or sketched. The name is therefore invalid because it is impossible to associate it indisputably with any specific organism.
- nominate subspecies:** the subspecies that bears the name of the species to which it belongs (e.g. *Amblysomus corriae corriae*), only brought into existence by the creation of one or more other subspecies in the same species (e.g. *Amblysomus corriae devilliersi*).
- North Africa:** those parts of Mauritania, Morocco, Algeria, Tunisia, Libya and Egypt that are north of the Sahara Desert.
- North-Central Africa:** Southern Chad and southern Sudan, west of the Nile R. and south of the Sahara. Mainly savanna habitats.
- North-West Africa (= Mahgreb):** those parts of Mauritania, Morocco, Algeria, Tunisia and NW Libya which are north of the Sahara Desert.
- nosepad:** area of naked, thickened dry skin which surrounds and protects the nostrils in Golden-moles; used for pushing and moving soil during tunnel excavation.
- nuchal:** pertaining to the nape of the neck.
- nulliparous:** not having given birth.
- obligate:** obligatory; limited to one mode of life or action irrespective of conditions or circumstances. *cf.* facultative (*q.v.*).
- occipital condyles:** the pair of smooth, rounded processes of the occipital bone at the posterior end of the skull on either side of the occipital foramen which acts as a hinge between the head and the neck.
- occiput:** the posterior part of the skull, above the foramen magnum (*q.v.*).
- occlusal:** pertaining to the biting surface of a tooth.
- oestrous cycle:** the reproductive cycle in most non-pregnant female mammals, comprising recurring physiological changes induced by reproductive hormones.
- oestrus** (*adj.* **oestrous**): The period when a female is sexually receptive.
- Oligocene:** geological Epoch (within the Tertiary period), ca. 38–23 mya.
- omnivore** (*adj.* **omnivorous**): an animal that eats a wide range of foods.

- orbit:** bony cavity (eye-socket) in which the eye is situated.
- oscillogram:** a visual representation (graph) of sound waves in which amplitude (sound wave pressure) is plotted on the vertical axis, and time on the horizontal axis (*cf.* sonogram *q.v.*).
- osteophagia:** the chewing on bones engaged in by herbivorous animals suffering from a deficiency of phosphorus and calcium in their diet.
- outer:** furthest from the mid-line of the body.
- ovulation:** the release of female gametes (ova, eggs) from the ovary.
- ovum:** the female gamete or egg cell.
- owl pellets:** waste material, normally in an egg-like shape, regurgitated by owls, which contains undigested fragments of bone, hair, feathers and scales etc. from the prey; for mammalogists, useful in determining indirectly the species of small mammals in a habitat.
- P or p:** (*abbrev.*) premolar tooth or teeth; upper case denotes adult dentition, lower case denotes deciduous dentition (milk teeth). *See also* premolar.
- pachyosteosclerosis:** a thickening of the bones of the ribs and vertebrae, resulting in unusually solid bone structure with little to no marrow.
- Paenungulata** (*adj.* **paenungulate**): a taxon (belonging to the Supercohort Afrotheria) that includes the elephants (Proboscidea), manatees and dugongs (Sirenia), hyraxes (Hyracoidea) and two extinct orders.
- Palaearctic:** a zoogeographic region comprising Europe, North Africa and Asia (except for southern portion of the Arabian Peninsula and tropical and sub-tropical parts of the Oriental Region).
- Palaeocene:** geological Epoch (within the Tertiary Period); 65–55 mya.
- palatal foramen** (*pl.* **palatal foramina**): a foramen (*q.v.*) in the palatine bone.
- palate:** the roof of the mouth. The anterior part (hard palate) comprises the bony palate (formed by the premaxillae, maxillae and palatine bones), and a covering mucous membrane. The posterior part (soft palate) is composed only of muscular tissue covered by a mucous membrane.
- Paleogene:** geological period and system; 65.5 ± 0.3 to 23.03 ± 0.05 mya, comprising the first part of the Cenozoic Era.
- papilla** (*pl.* **papillae**, *adj.* **papillate**): a small projection or protuberance.
- paraoccipital process:** narrow strut-like bone which projects ventrally from the paraoccipital bone on the posterior part of the skull.
- parapatry** (*adj.* **parapatric**): the situation where two or more species have geographic ranges that are contiguous (*q.v.*) but do not overlap. This abutting may be along a line of habitat discontinuity, ecotone, or altitudinal/climatic contour, but may also arise from competitive exclusion of one (or both) by the other.
- paraphyletic:** describes a taxon containing units that have evolved from a single ancestral taxon but which do not contain all of the descendents of the most recent common ancestor.
- paratype:** a specimen collected at the same time and place as the holotype (*q.v.*) and designated by the original authority as such. There may be one or more paratypes.
- parietal:** one of the pair of bones forming the vault of the braincase, situated between the frontal and the occipital bones.
- parous:** having given birth.
- parturition:** the act of giving birth.
- pectoral:** pertaining to or situated on the chest.
- pedal glands:** glands which are situated in the feet opening between the hooves.
- pelage:** the hairy, woolly or furry covering of the body in mammals. The pelage variously consists of hairs, guard hairs and underfur according to the species.
- petrophily** (*adj.* **petrophilic**): occupying habitats dominated by large boulders.
- phalanx** (*pl.* **phalanges**): one of the bones in a finger.
- pharynx** (*adj.* **pharyngeal**): the passage leading from the oral and nasal cavities in the head to the oesophagus and larynx (*q.v.*).
- phenotype:** the visible characters of an individual resulting from the interaction between the genotype (*q.v.*) and the environment.
- philopatry:** the tendency to remain in or consistently return to the place where one was born.
- philtrum:** a medial vertical cleft or groove in the rhinarium (*q.v.*) extending from between the nostrils to the upperlip.
- phylogenetics:** pertaining to the line of descent of a taxon; a method of classification that attempts to show the evolutionary relatedness of organisms.
- phylogeny** (*adj.* **phylogenetic**): the evolutionary history and line of descent of a species or higher taxonomic unit.
- piloerection:** the erection of hairs which occurs as a means of conserving heat (*see* temperature regulation) and, in some mammals, as a threat display.
- pinna** (*pl.* **pinnae**): the external (outer) ear.
- placental scars:** scars on the inner surface of the uterus of a mammal; the site where a placenta was attached during pregnancy. The number of placental scars can give an indication of the number of litters that a female has had (when the average number of young/litter is known).
- placentation:** the formation, type and structure of the placenta; the arrangement of placentae.
- plantar:** of the sole of the foot.
- plantigrade:** describes locomotion during which the entire sole of each foot touches the ground.
- Pleistocene:** geological Epoch (within the Quaternary Period); ca. 1.7 mya to 10,000 year ago.
- plesiomorphy:** (*adj.* **plesiomorphic**): in cladistics (*q.v.*), describes a pre-existing character state across a wide taxonomic grouping. Sharing of that state (symplesiomorphy [*q.v.*]) amongst a subset of taxa within the wider grouping is not indicative of monophyly (*q.v.*). *cf.* apomorphy (*q.v.*).
- pleural cavity:** the body cavity occupied by the lungs.
- Pliocene:** geological Epoch (within the Tertiary period), ca. 5–2 mya.
- poikilothermic:** the condition when the body temperature varies with the surrounding ambient temperature.
- pollex:** digit 1 ('thumb') of forefoot ('hand').
- polygyny** (*adj.* **polygynous**): a mating system in which one male mates with several females. *See* resource-defence polygyny; female-defence polygyny. *cf.* monogamy (*q.v.*).
- polymorphism** (*adj.* **polymorphic**): the existence, within a species or population, of individuals having different forms (colour, size, shape etc.).

- polyoestrous:** Generally, having two or more oestrous cycles (*q.v.*) during a single reproductive season. In some taxa, having more than one litter/year. *cf.* monoestrous (*q.v.*).
- polyovulation:** production of many ova (and hence many corpora lutea) during a single oestrus; sometimes called 'superovulation'; recorded in some species of sengis.
- polyphyletic:** describes a taxon derived from two or more ancestral sources; not of a single, immediate line of descent (Mayr *et al.* 1953). *cf.* monophyletic (*q.v.*).
- polyphyly:** derivation of a taxon from two or more ancestral sources. *cf.* monophyly (*q.v.*).
- polytypy** (*adj.* **polytypic**): a taxon that has several taxa in the next lower taxonomic category, e.g. a polytypic family contains two or more genera, a polytypic genus has two or more species. *cf.* monotypy (*q.v.*).
- postauricular:** behind the external ear (pinna).
- postorbital:** behind (posterior to) the orbit.
- postorbital process:** the bony projection arising from upper rim of orbit and projecting outwards and downwards around the posterior of the orbit.
- postpartum oestrus:** an oestrus cycle immediately after (or very soon after) parturition and while lactating.
- precocious** (= **precocial**): describes young born in a well developed state enabling them to move around and forage soon after birth. *cf.* altricial (*q.v.*).
- premaxilla** (*pl.* **premaxillae**): one of a pair of bones at the anterior end of the skull which bears the incisor teeth.
- premolar:** tooth on the maxilla bone situated immediately anterior to the molar teeth; usually preceded in time by deciduous (milk) tooth; multi-cusped. Structure and function of premolar teeth vary according to species.
- preorbital:** anterior to the eye.
- prepuce** (*adj.* **preputial**): the skin surrounding and protecting the head of the penis; foreskin.
- preputial gland:** a gland situated adjacent to the penis or vaginal opening.
- primiparous:** a female that has given birth only once. *cf.* multiparous (*q.v.*).
- promiscuity:** a mating system in which each male mates with several females and each female mates with several males.
- protocone:** The main inner (lingual) cusp of an upper molar tooth.
- protuberant:** projecting forward (bulging) beyond the surrounding surface.
- proximal:** nearest to the body or to the mid-line of the body; nearest to the point of attachment. *cf.* distal (*q.v.*).
- proximate cause:** a cause that produces an effect directly without any intervening agency.
- pterygoid process:** one of a pair of narrow, ventrally projecting processes of the pterygoid bones situated immediately posterior to the bony palate and forming the walls of the mesopterygoid fossa (*q.v.*).
- pterygoid:** one of a pair of cranial bones forming part of the roof of the mouth.
- pubic bone:** anterior inferior part of the pelvis, articulating with its opposite number in the anterior midline at the pubic symphysis.
- Quaternary Period:** period within the Cenozoic Era; 2 mya to today, comprising two epochs: the Pleistocene and Holocene (Recent) (*q.v.*).
- r-selection:** selection for characteristics suitable in unstable fluctuating environments (rapid development of young, large litter size, relatively short time to maturity, relatively short life span) *cf.* K-selection (*q.v.*).
- R.:** (*abbrev.*) River.
- ramus:** one half (left or right) of the lower jaw or mandible.
- relatively:** in profiles of Afrosoricida and Macroscelidea, used in the context of describing the size of one character relative to the size of a different character in the same species. Usually expressed as a percentage. e.g. Tail 80–90 % of HB. *cf.* comparatively (*q.v.*).
- relict forest:** a forest that persists where local conditions are favourable after the disappearance of forest from the surrounding area as a result of climate change or human activity. Relict forests include those at the base of inselbergs that are watered by rainwater running off the inselberg, and forests growing in graveyards and sacred sites that are protected. Sometimes known as forest islands.
- relict population:** one that persists where local conditions are favourable after the extinction of the species from at least part of its former range.
- Renosterveld:** a dominant vegetation type in the Cape Floristic Region (*q.v.*), and characterized by the dominance of members of the Daisy Family (Asteraceae), specifically one species - *Renosterbos* *Elytropappus rhinocerotis*, from which the vegetation type gets its name.
- reproductive capacity:** number of young produced by a female during the breeding season.
- reproductive chronology:** the timing and duration of events, such as spermatogenesis, copulation, ovulation, gestation, parturition, lactation and reproductive inactivity, throughout the year.
- reproductive strategy:** the strategy adopted to maximise reproductive success, determined primarily by litter-size and reproductive chronology (*q.v.*).
- resource-defence polygyny:** a mating system in which a male controls access to several females indirectly, by monopolizing critical resources (Emlen & Oring 1977).
- retarded embryonic development:** a means of lengthening the interval between copulation and parturition so that both events can occur in the most optimal seasons. The implanted embryo enters a period of retarded (slowed) growth which may last 4–8 months, after which development proceeds normally.
- reticulation** (*adj.* **reticulated**): having a net-like pattern.
- rhinarium:** area of naked moist skin surrounding the nostrils.
- ridge** (= **commissure**): in teeth, a ridge connecting two cusps.
- Rift Valley:** deep valley extending from the Red Sea through Ethiopia and East Africa to Malawi; formed ca. 12 mya by subsidence of the valley floor and uplifting of the edges to form mountains and highlands. Four parts: (1) Ethiopian Rift Valley dividing the Ethiopian plateau into two parts; (2) Albertine Rift Valley (Western Rift Valley) in Uganda, E DR Congo and W Tanzania; (3) Gregorian Rift Valley (Eastern Rift Valley) in N Kenya, C Kenya and N Tanzania; (4) Malawian Rift Valley – the extension of the

- Albertine Rift Valley in Malawi. The Rift Valleys are noted for their many deep and beautiful lakes.
- riparian:** growing on or living on the banks of streams or rivers.
- riverine forest:** forest growing along the banks of a river or stream where conditions are moister than in the surrounding area. Sometimes referred to as 'fringing forest'.
- Robertsonian fusion:** a chromosomal event involving the apparent fusion of non-homologous single armed (telocentric *q.v.*) chromosomes to form a bi-armed (metacentric *q.v.* or submetacentric *q.v.*) chromosome. Modern studies have revealed that all chromosomes have two arms, even if the smaller one is not detectable by light microscopy. Consequently, the term Robertsonian translocation is becoming more commonly used than Robertsonian fusion.
- rostral:** pertaining to the rostrum.
- rostrum:** that portion of the skull anterior to the front line of the orbits and supporting the upper part of the muzzle, comprised of the nasals, premaxillae and maxillae bones.
- rupicolous:** rock-living.
- sacrum** (*adj. sacral*): the fused vertebrae to which the pelvic girdle is attached.
- sagittal crest:** longitudinal crest of raised bone on the mid-dorsal line of the cranium.
- scansorial:** climbs or scrambles over logs and in low vegetation close to the ground. *cf.* terrestrial (*q.v.*); arboreal (*q.v.*).
- sclerophyllous:** describes vegetation having hard leaves that are resistant to drought.
- scrotal:** pertaining to, or within, the scrotum (*q.v.*).
- scrotum:** an external sac containing the testes and epididymides in male mammals.
- sebkha:** A geological feature, in North Africa, which is a smooth, flat, plain usually high in salt (also sabkha).
- sectorial:** adapted for cutting.
- selenodont:** molar teeth having longitudinal crescent-shaped ridges.
- Senegambia:** Senegal and Gambia.
- sensu lato:** (*Lat.*) in a broad sense.
- sensu stricto:** (*Lat.*) in a strict sense.
- sensu:** (*Lat.*): in the sense of.
- sex ratio:** the number of males to the number of females, usually expressed as a proportion to one male, e.g. 1 : 1 (equal numbers of males and females), 1 : 0.5 (= twice as many males as females), 1 : 2 (= twice as many females as males).
- sexual dimorphism:** observable (phenotypic) difference(s) (e.g. in colour, size or form) between the males and females of a species or higher taxon.
- Sh. Ht.:** (*abbrev.*) shoulder height.
- sibling species:** pairs or groups of true species that are reproductively isolated, but genetically closely related and so similar in appearance that they are difficult to separate solely on the basis of morphological characters.
- side-stripe:** longitudinal stripe(s) of contrasting colour on each flank, usually from shoulder to rump or upper part of hindlimbs. May be bordered by additional side-stripe above and below.
- singleton:** a neonate which is born singly as opposed to being one of a larger litter.
- sister species:** species that are thought to have arisen from a single dichotomous splitting event.
- sonogram:** a visual representation (graph) of sound in which frequency is plotted on the vertical axis, and time on the horizontal axis; can be analysed manually or with computer programs (*cf.* oscillogram *q.v.*).
- South-Central Africa:** Angola, SE DR Congo, Zambia and Malawi (but only west of L. Malawi and the Shire R. Valley).
- southern Africa:** south of the Cunene and Zambezi Rivers, i.e. Namibia, Botswana, Zimbabwe, southern Mozambique and South Africa (after Smithers 1983).
- species:** populations(s) of closely related and similar organisms, which are capable of interbreeding freely with one another, and cannot or typically do not interbreed with members of other species.
- sperm:** any male gamete; the male cell which fuses with a female gamete (ovum, egg cell) to produce a fertilized egg or zygote from which an embryo will develop.
- spermatogenesis:** the formation of sperm in the testes.
- s.u.:** (*abbrev.*) (*Lat. sans unguis* = without claw) sometimes added as a suffix to the hindfoot measurement to emphasize that HF has been measured without the claw. However, since this is the standard method of measurement, most authors write 'HF', not 'HF s.u.'. *cf.* c.u. (*q.v.*).
- sub, sub-:** prefix meaning under, signifying beneath or ventral to (as in anatomical features) or south of (as in sub-Saharan); less than (as in subsonic); not quite, nearly, almost, somewhat (as in subequal, subtriangular). In taxonomy, indicates a group just below the status of the taxa immediately following it (e.g. a genus may contain two or more subgenera).
- subauricular:** below the ear.
- subcaudal:** below the tail.
- subdermal:** just below the skin.
- submetacentric:** describes a chromosome with the centromere (*q.v.*) somewhat nearer one end than the other, so there are two arms of somewhat unequal length (ratio 1 : 1.2–1.9). *cf.* metacentric (*q.v.*); subtelocentric (*q.v.*).
- subspecies:** a geographically localized and isolated subdivision of a species, which differs genetically, morphologically and taxonomically from other subdivisions of the species.
- subtelocentric:** describes a chromosome with the centromere (*q.v.*) much nearer one end than the other, so there are two arms of very unequal length (ratio 1 : >2).
- subterminal:** just below the end or tip.
- subterranean:** living permanently below the ground; *cf.* fossorial (*q.v.*).
- suckling:** the act of a mother giving milk directly from her breast (mammary glands) to her young. Mothers suckle; their young suck.
- sulcus** (*pl. sulci*): a groove, fissure or furrow.
- superovulation:** *see* polyovulation (*q.v.*).
- supinate:** to turn or rotate the hand or forearm, or the hindlimb and foot.
- supracaudal:** above the tail.
- supraoccipital crest:** ridge of bone, oriented transversely across the back of the skull, at the junction of the parietal and/or supraoccipital bones and the occipital bone. Sometimes referred to as the lambdoid crest.
- supraorbital ridge:** ridge of bone along upper rim of orbit (eye-socket).

- supraorbital:** above (dorsal to) the orbit.
- supraordinal:** describes a taxon above the level of the order.
- supratragus:** in some species of sengis, a fleshy lobe on inner lower surface of outer ear situated above the tragus.
- sympatry** (*adj.* **sympatric**): the situation where populations of two or more different species have overlapping geographic ranges; refers also to populations of two or more species whose geographic ranges are partly or wholly overlapping. They may or may not interact. *cf.* allopatry (*q.v.*); syntopy (*q.v.*).
- symplesiomorphy:** a primitive or ancestral character shared by two or more groups, which is inherited from ancestors older than the last common ancestor.
- synapomorphy** (*adj.* **synapomorphic**): situation in which a homologous character is present in two or more taxa and is thought to have originated in their most recent common ancestor. *See also* apomorphy.
- syndactyly:** of digits; whole of part fusion of two or more digits (e.g. Digits 2 and 3 of the hindfoot in otter-shrews).
- synonym:** one or more different names for the same taxonomic unit. A synonym may be a 'senior synonym' (the oldest name), or a 'junior synonym' (a more recent name), which is no longer considered as valid. May be used to refer to all names that have been associated, at some time in the past, with the taxonomic unit as currently understood.
- syntopy** (*adj.* **syntopic**): describes the situation where two or more species use the same or similar habitats and activity times. They may or may not interact. *cf.* allopatry (*q.v.*); sympatry (*q.v.*).
- syntype:** any specimen, or one of a series of specimens, used to designate a species when a holotype (*q.v.*) and paratype(s) (*q.v.*) have either not been selected, or have been lost or destroyed.
- systematics:** the science of arranging organisms in a way that reflects their evolutionary relationships; such relationships may be expressed as a phylogeny (*q.v.*). Often defined (somewhat incorrectly) as a synonym of taxonomy (*q.v.*).
- T:** (*abbrev.*) length of tail, measured from anterior of the first caudal vertebra to the posterior end of the last caudal vertebra (excluding any tufts, bristles etc. at tip of tail).
- T_a:** (*abbrev.*) ambient temperature; the temperature in which an animal is living. *cf.* T_b (*q.v.*).
- talonid:** heel at the posterior end of a lower molar tooth.
- tapetum lucidum:** light-reflecting layer behind or in the retina of the eyes of some vertebrates which reflects light back through the retina thereby increasing the sensitivity of the eye to dim light.
- taxon** (*pl.* **taxa**): any defined unit (e.g. family, genus, species, subspecies) in the classification of organisms.
- taxonomy:** the science of biological nomenclature; the study of the rules, principles and practice of naming and classifying species and other taxa. Sometimes considered as an integral part (and near synonym) of systematics (*q.v.*).
- T_b:** (*abbrev.*) body temperature; the temperature of the core (central) part of an animal. *cf.* T_a (*q.v.*).
- telocentric:** describes a chromosome that appears to have a terminal centromere (*q.v.*) and therefore only one arm. Modern studies have revealed that all chromosomes have two arms but the smaller arm of telocentric chromosomes is not visible under a light microscope.
- temporalis:** a broad radiating muscle arising from the coronoid process (*q.v.*) of the lower jaw and attaching to the upper part of the skull.
- termitarium** (*pl.* **termitaria**): a place where termites (Insecta: Isopoda) live. Often a large mound of modified hard soil. The shape and size of a termitarium is unique to each species of termite.
- terrestrial:** living on the ground. *cf.* arboreal (*q.v.*); scansorial (*q.v.*).
- territory:** an area defended by an individual against certain other members of the species, usually by overt aggression or advertisement; territory is marked by the urine, faeces or glandular secretions of the territory's owner. *cf.* home-range (*q.v.*).
- Tertiary Period:** geological period, 65–2 mya, comprising five epochs: Palaeocene, Eocene, Oligocene, Miocene and Pliocene (*q.v.*); followed by the Quaternary Period (*q.v.*).
- testes:** the male gonads, or testicles, in which spermatozoa are formed and in which the male hormone is produced.
- Tethys Sea:** the sea separating the two supercontinents, Gondwana (*q.v.*) and Laurasia (*q.v.*) during much of the Mesozoic Era before the opening of the Indian and Atlantic oceans during the Cretaceous Period (*q.v.*).
- thermal conductance:** a measure of the ability of substances (including pelage) to transfer heat.
- thermolability** (*adj.* **thermolabile**): the ability of a homeotherm (e.g. camel) to allow its body temperature to vary over a 24-hour period, without either hibernating or aestivating.
- thermoneutral zone:** the range of body temperatures within which an animal does not have to increase its metabolic rate to increase T_b (*q.v.*) (when T_a (*q.v.*) is low) and reduce T_b (when T_a is high).
- thermoregulation:** regulation of body temperature, either by metabolic or behavioural means (or both simultaneously) so that T_b (*q.v.*) is kept more or less constant.
- thoracic:** pertaining to, or situated upon, the chest.
- through-put time:** time taken for food to pass through the digestive tract.
- tibia** (*pl.* **tibiae**): one of the two bones forming the lower leg (the shin bone); part of hindlimb between knee and ankle.
- TL:** (*abbrev.*) total length from tip of snout to posterior end of tail. Equivalent to the head and body length and tail length added together. *See also* HB (*q.v.*) and T (*q.v.*).
- toothrow:** Generally, the row of teeth from the most anterior incisor tooth to the most posterior molar. In golden moles, the row of teeth from the canine to the most posterior molar. Sometimes used in contexts of specific types of teeth, e.g. premolar toothrow, molar toothrow.
- topotype:** any specimen from the type locality (*q.v.*), i.e. the same locality as that from which the holotype (*q.v.*) was taken.
- topotypical:** pertaining to the type locality (e.g. a topotypical population is one found at the type locality).
- torpor** (*adj.* **torpid**): a state in which there is a (usually short-term) reduction of metabolic rate and a lowering of T_b (*q.v.*) when T_a (*q.v.*) declines; arousal from torpor occurs when T_a increases and without high energy costs to the individual. Torpor is associated with a state of inactivity and reduced responsiveness to stimuli. Torpor lasts for only short periods of time (hours or days). *cf.* hibernation.

- tragus:** a cartilaginous structure, usually small, projecting from the inner side of the external ear just anterior to the auditory meatus (*q.v.*).
- transverse:** in a direction across the body from side to side. *cf.* longitudinal (*q.v.*).
- Triassic Period:** period (within the Mesozoic Era); 248–208 mya. The first mammals appeared in this period.
- triconid:** describes a molariform tooth having three cusps.
- tricuspid:** having three points or cusps (particularly of teeth).
- trifid:** divided into three by two emarginations (*q.v.*).
- tubercle:** a small rounded protuberance.
- tusks:** long, continuously growing incisor or canine teeth that protrude (usually in pairs) beyond the mouth in some mammals including elephants (in which the tusks are incisors), and warthogs and other pigs (in which the tusks are canines); comprised of dentine (ivory). Some mammals, e.g. hyraxes, have ‘tusk-like’ incisors.
- tympanic bulla** (*pl.* **tympanic bullae**): one of a pair of usually rounded bony capsules, on underside of skull (one on each side), housing structures of the middle and inner ear in many mammals. Also called auditory bulla (*q.v.*).
- type description:** the original description of a species; the original description of the holotype (and paratype[s] if included).
- type locality:** the locality from which a holotype (*q.v.*), lectotype (*q.v.*) or neotype (*q.v.*) was collected. Also called topotypical locality.
- type population:** the population from which the holotype was selected.
- type series:** the holotype and all specimens collected at the same place and time and used, together with the holotype, to describe a new species.
- type species:** usually the species that was the first to be described under the name of a new genus. Not all genera had a designated type species when they were first created; in such cases, other rules determine which species will be the type species.
- type specimen:** *see* holotype.
- umbraculum,** a membrane that shades the pupil of the eye allowing basking hyraxes to stare into the sun without harm.
- underfur:** dense and often woolly layer of the pelage, situated close to the skin and below the soft hairs and guard hairs; usually short and present in those species which experience lower T_a .
- unicuspid:** having one cusp or point (particularly of teeth).
- upper critical temperature:** the highest ambient temperatures at which the animal must increase its metabolic rate to maintain a constant body temperature. If the ambient temperature increases above the upper critical temperature and the animal is unable to cool itself, it will enter hyperthermia and may eventually die. *cf.* lower critical temperature.
- uvula:** the conical projection from the posterior edge of the soft palate that plays a role in the articulation of sounds and the closing the nasopharynx during swallowing.
- vagility:** the ability to move about, disperse or migrate.
- vagrant:** an individual that has been found well outside the normal geographic range of its species, e.g. a bat or bird that has been wind-borne, or an animal that has been transported as a stowaway on a ship, to a distant locality.
- vascularized:** infiltrated with capillaries.
- vasoconstriction:** constriction of the capillaries of the blood system near the surface of the skin in order to reduce the rate of heat loss through the skin; a mechanism used by many mammals to conserve heat when T_a (*q.v.*) is low. *cf.* vasodilation (*q.v.*).
- vasodilation:** the dilation (or opening) of the capillaries of the blood system near the surface of the skin in order to increase the rate of heat loss through the skin; a mechanism used by many mammals to cool themselves when T_a (*q.v.*) is high. *cf.* vasoconstriction (*q.v.*).
- veld:** Afrikaans word, used mainly by southern African biologists, to refer to a wide variety of grassland vegetation types typically used for grazing. *See also* bushveld, highveld, lowveld.
- vertebra** (*pl.* **vertebrae**): any of the bones that make up the backbone.
- vertebral formula:** the number of vertebrae in each part of the spine, from anterior to posterior: the parts are cervical (C), thoracic (T), lumbar (L), sacral (S), caudal (Ca).
- vestigial:** small and imperfectly developed; a structure having a smaller and more simple form than the corresponding structure in an ancestral species.
- vibrissa** (*pl.* **vibrissae**): long stiff hairs on the face, especially around nostrils and lips; often associated with the perception of tactile sensation; ‘whiskers’.
- vlei:** southern African term for a marsh or swamp, either permanent or seasonal.
- wadi:** a desert valley, usually dry at the surface except after heavy rainfall.
- water turnover:** the rate at which water (fluids) is utilized and replaced in the body per unit time (normally expressed as ml/kg body weight/day); the amount of water an animal processes through its body each day. Water turnover is related to water availability, the urine concentrating ability of the kidney, amount of protein in the diet and T_a (*q.v.*). Water turnover rates are characteristically low in arid-adapted mammals when compared with non arid-adapted mammals.
- West Africa:** ca. south of 18° N from Senegal to the Sanaga R. in Cameroon, and Bioko I. (Equatorial Guinea) (Rosevear 1965).
- WT:** (*abbrev.*) weight (mass) of an individual, usually expressed in grams (g) or kilograms (kg).
- xiphisternum:** The posterior segment, or extremity, of the sternum (sometimes called the xiphoid process).
- zalambdodont:** cheekteeth with three main cusps connected by crests (ectolophs) forming a V-shape; largest cusp is at the apex of the V (on the lingual or tongue side of the tooth); assumed to be derived from the primitive tribosphenic teeth found in some extinct early mammals. *cf.* dilambdodont (*q.v.*).
- ZW:** (*abbrev.*) *see* zygomatic width.
- zygomatic arch:** one of a pair of cheekbones, formed of the maxillary process anteriorly, jugal bone medially and squamosal bone posteriorly. Ranges from massive, broad, widely flared and bony, to frail, slender and cartilaginous. When present, provides protection to the eyes and orbits. Also called zygoma.
- zygomatic width (ZW):** greatest width between the outer aspect of one zygomatic arch to the equivalent position on the opposite zygomatic arch. *See also* GWS.

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Chapter 5. The Biotic Zones of Africa

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JONATHAN KINGDON AND JAN KALINA

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Dedication

This volume is dedicated to Carly and Jake Butynski, the children of Jan Kalina and Tom Butynski.

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photograph by Jan Kalina

ABOVE LEFT: Jan Kalina.

ABOVE: From left to right: Jonathan Kingdon, Thomas Butynski, Meredith Happold, David Happold and Andrew Richford.
LEFT: Jonathan Kingdon (left) and Michael Hoffmann.

Acknowledgements for Volume II

Tom Butynski

It was a long time ago (1998) that Jonathan Kingdon* invited me to serve as an editor for the 'Mammals of Africa Project'. At that time we imagined that the Project would be handily completed in seven years. That was not to be! *Mammals of Africa* would take twice that long to bring to press. I hope that you will agree with me that the six volumes arising from this project were well worth the long wait.

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*Author in Volume II

Mammals of Africa:

An Introduction and Guide

David Happold, Michael Hoffmann, Thomas Butynski and Jonathan Kingdon

Mammals of Africa is a series of six volumes that describes, in detail, every extant species of African land mammal that was recognized at the time the profiles were written (Table 1). This is the first time that such an extensive coverage has been attempted; all previous books and field guides have either been regional in coverage, or have described a selection of mammal species – usually the larger species. These volumes demonstrate the diversity of Africa's mammals, summarize what is known about the distribution, ecology, behaviour and conservation status of each species, and serve as a guide to identification.

Africa has changed greatly in recent decades because of increases in human populations and the related exploitation of natural resources, agricultural development and urban expansion. Throughout the continent, extensive areas of forest, woodland and savanna have been destroyed and much of what remains is degraded and fragmented. Many of the drier areas are threatened with desertification. As a result, the abundance and geographic ranges of many species of mammals have declined – some marginally, some catastrophically, some to extinction. Hence, it is appropriate that our knowledge of each species is recorded now, on a pan-African

basis, because the next few decades will see even more human-induced changes. How such changes will affect each mammalian species is uncertain, but this series of volumes will act as a baseline for assessing future change.

The study of African mammals has taken several stages. During the era of European exploration and colonization, the scientific study of African mammals was largely descriptive. Specimens that were sent to museums were described and named. As more specimens became available, and from different parts of the continent, there was increasing interest in distribution and abundance, and in the ecological and behavioural attributes of species and communities. At first, it was the largest and most easily observed species that were the focus of most studies, but as new methodologies and equipment became available, the smaller and more cryptic and secretive species became better known. Many species were studied because of their suspected role in diseases of humans and livestock, and because they were proven or potential 'pests' in agricultural systems. During the past decade or so, there has been greater emphasis on the genetic and molecular characteristics of species. These studies have produced a wealth of information, especially during the past 40 years or so. These volumes are not only a distillation of the huge literature on African mammals, but also of much previously unpublished information.

There is a huge discrepancy among species in the amount of information available. Some species have been studied extensively for many years, especially the so-called 'game species', some species of primates and a few species that are widespread and/or easily observed. In contrast, other species are known only by one or a few specimens, and little has been written about them. Likewise, some areas and countries have been well studied, while other areas and countries have been neglected. During the preparation of these volumes, the editors have often been surprised by the wealth of information about some species when little was anticipated, and by the paucity of information about others, some of which were assumed to be 'well known'. In addition to presenting information that is based on sound scientific evidence, the aims of these volumes are to point out where there are gaps in knowledge and to correct inaccurate information that has become embedded in the literature. For most taxa (including all primates), the detail provided in the species profiles allows accurate identification.

Mammals of Africa comprises six volumes (Table 2). The volumes consist mainly of species profiles – each profile being a detailed

Table 1. The mammals of Africa.

Order	Number of families	Number of genera	Number of species
Hyracoidea	1	3	5
Proboscidea	1	1	2
Sirenia	2	2	2
Afrosoricida	2	11	24
Macroscelidea	1	4	15
Tubulidentata	1	1	1
Primates	4	25	93
Rodentia	15	98	395 ^a
Lagomorpha	1	5	13
Erinaceomorpha	1	3	6
Soricomorpha	1	9	150
Chiroptera	9	49	224
Carnivora	9	38	83
Pholidota	1	3	4
Perissodactyla	2	3	6
Cetartiodactyla	6	41	93
16	57	296	1116^b

^a Including five introduced species. ^b Species profiles in *Mammals of Africa*.

Table 2. The six volumes of *Mammals of Africa*.

Volume	Contents	Number of species	Editors
I	Introductory chapters. Afrotheria (Hyraxes, Elephants, Dugong, Manatee, Otter-shrews, Golden-moles, Sengis and Aardvark)	49	Jonathan Kingdon, David C. D. Happold, Michael Hoffmann, Thomas M. Butynski, Meredith Happold and Jan Kalina
II	Primates	93	Thomas M. Butynski, Jonathan Kingdon and Jan Kalina
III	Rodents, Hares and Rabbits	408	David C. D. Happold
IV	Hedgehogs, Shrews and Bats	380	Meredith Happold and David C. D. Happold
V	Carnivores, Pangolins, Equids and Rhinoceroses	93	Jonathan Kingdon and Michael Hoffmann
VI	Pigs, Hippopotamuses, Chevrotain, Giraffes, Deer and Bovids	93	Jonathan Kingdon and Michael Hoffmann

account of the species. They have been edited by six editors who distributed their work according to the orders with which they are most familiar. Each editor chose authors who had extensive knowledge of the species (or higher taxon) and, preferably, had experience with the species in the field. Each volume follows the same general format with respect to arrangement, subheadings and contents. Because *Mammals of Africa* has contributions from 356 authors (each with a different background and speciality), and because each volume was edited by one or more editors (each with a different perspective), it has not been possible or even desirable to ensure exact consistency throughout. Species profiles are not intended to be exhaustive literature reviews, partly for reasons of space. None the less, they are written and edited to be as comprehensive as possible, and to lead the reader to the most important literature for each species. Inevitably, not all information available could be accommodated for the better-known species, and so, such profiles are a précis of available knowledge. Extensive references in the text alert and guide the reader to more detailed information.

In addition to the species profiles, there are profiles for the higher taxa (genera, families, orders, etc.). Thus, there is a profile for each order, for each family within the order, for each genus within the family, and for each species within the genus. For some orders there are additional taxonomic levels, for example, tribes (e.g. in Bovidae), subgenera (e.g. in *Procolobus*), and species-groups, or 'superspecies' (e.g. in *Cercopithecus*). The taxonomy used in Volume II mostly follows that presented in Grubb *et al.* (2003), although, in a few cases, the editors adopted an alternative taxonomy when there were good reasons for doing so. Volume I differs from the other volumes in that it contains a number of introductory chapters about Africa and its environment, and about African mammals in general.

The continent of Africa

For the purposes of this work, 'Africa' is defined as the continent of Africa (bounded by the Mediterranean Sea, the Atlantic Ocean, the Indian Ocean, the Red Sea and the Suez Canal) and the islands on the continental shelf. The largest of the 'continental islands' are Zanzibar (Unguja), Mafia and Bioko (Fernando Po). All 'oceanic islands', e.g. São Tomé, Príncipe, Annobón (Pagulu), Madagascar, Comoros, Seychelles, Mauritius, Socotra, Canaries, Madeira and Cape Verde, are excluded with the exception of Pemba, which is included because of its close proximity (ca. 50 km) to the mainland.

The names of the countries of Africa are taken from the *Times Atlas* (2005). The Republic of Congo is referred to as 'Congo', and the Democratic Republic of Congo (former Zaire) as 'DR Congo'. Smaller geographical or administrative areas within countries are rarely referred to except for Provinces in South Africa, which are used extensively in the literature. Maps showing the political boundaries of Africa (Figure 1a), the Provinces of South Africa (Figure 1b), and the major physical features of Africa (Figure 1c) are provided, as is a list of the 47 countries together with their previous names as used in the older literature on African mammals (Table 3).

Africa is the second largest continent in the world (after Asia), but it differs from other continents (except Australia and Antarctica) in being essentially an island. At various times in the past, Africa has been joined to other continents – a situation that has had a strong influence on the fauna and flora of the continent. Africa is a vast continent (29,000,000 km², 11,200,000 mi²) that straddles the Equator, with about two-thirds of its area in the northern hemisphere and one-third in the southern hemisphere. As a result, Africa has many varied climates (with seasons in each hemisphere being six months out of phase), many habitats (including deserts, savannas, woodlands, swamps, rivers, lakes, moist forests, monsoon forests, mountains and glaciers), and altitudes ranging from 155 m (509 ft) below sea level at L. Assal, Djibouti, in the Danakil (Afar) Depression, to 5895 m (19,341 ft) on Mt Kilimanjaro, Tanzania. Africa is comprised of 47 countries, some of which are very large (e.g. Sudan, 2,506,000 km², 967,000 mi²; Algeria, 2,382,000 km², 920,000 mi² and Democratic Republic of Congo, 2,345,000 km², 905,000 mi²) and others that are relatively small (e.g. Djibouti, 23,200 km², 9,000 mi²; Swaziland, 17,400 km², 6,700 mi²; and The Gambia, 11,300 km², 4,400 mi²). The human population of each country also varies greatly, from about 346/km² in Rwanda to only about 2.5/km² in Namibia. With its great size and varied habitats, Africa supports a high biodiversity, including a large number of species of mammals. Likewise, most countries have a high diversity of mammals (especially when compared with temperate countries).

Africa can be divided into 'biotic zones' (Figure 2). A biotic zone is defined as an area within which there is a similar environment (primarily rainfall and temperature) and vegetation, and which differs in these respects from other biotic zones. Thirteen biotic zones are recognized, two of which may be divided into smaller categories. The biotic zones where each species of mammal has been recorded are listed in each profile for several reasons. They indicate the environmental conditions in which the species lives and they provide data with which the geographic distribution can be explained and predicted. Furthermore, the number of biotic zones exploited by a species indicates its level of habitat tolerance and



Figure 1. (a) Political map of Africa; (b) provinces of South Africa; (c) altitudes and major rivers of Africa. South Sudan and Somaliland are not identified as separate countries in the text.

Table 3. The countries of Africa: names, areas and human population density.

Country name	Area (km ²) '000	Area (miles ²) '000	Human population '000 (2006)	People per km ²
Algeria	2,382	920.0	33,500	14.1
Angola (includes Cabinda)	1,247	481.0	15,800	12.7
Bénin * [Dahomey]	113	43.0	8,700	77.0
Botswana [Bechuanaland]	582	225.0	1,800	3.1
Burkina Faso * [Upper Volta; Burkina]	274	106.0	13,600	49.6
Burundi [part of Ruanda-Urundi (= part of Belgian Congo)]	27.8	10.7	7,800	280.5
Cameroon [includes former French Cameroon, German Cameroon and part of Eastern Nigeria]	475	184.0	17,300	36.2
Central African Republic [#]	623	241.0	4,300	6.9
Chad [Tchad]	1,284	496.0	10,000	5.8
Congo [Republic of Congo]	342	132.0	3,700	10.8
Côte d'Ivoire * [Ivory Coast]	322	125.0	19,700	61.2
Democratic Republic of Congo [Belgian Congo; Congo (Kinshasha); Zaire]	2,345	905.0	62,700	26.7
Djibouti [French Somaliland]	23.2	9.0	800	34.5
Egypt	1,001	387.0	75,400	75.3
Equatorial Guinea [#] (includes Rio Muni [Spanish Guinea] and Bioko I. [Fernando Po])	28.1	10.8	500	17.8
Eritrea (formerly part of Ethiopia)	94	36.0	4,600	48.9
Ethiopia [Abyssinia]	1,128	436.0	74,800	66.3
Gabon [#]	268	103.0	1,400	5.2
The Gambia	11.3	4.4	1,500	132.7
Ghana [Gold Coast]	239	92.0	22,600	94.6
Guinea *	246	95.0	9,800	39.8
Guinea-Bissau [Portuguese Guinea]	36	13.9	1,400	38.9
Kenya	580	224.0	34,700	59.8
Lesotho [Basutoland]	30.4	11.7	1,800	59.2
Liberia	111	43.0	3,400	30.6
Libya	1,760	679.0	5,900	3.6
Malawi [Nyasaland]	118	46.0	12,800	108.5
Mali *	1,240	479.0	13,900	11.2
Mauritania *	1,030	412.0	3,200	3.1
Morocco [includes former Spanish Morocco and French Morocco; (now also includes Western Sahara = former Spanish Sahara)]	447	172.0	32,100	71.8
Mozambique [Portuguese East Africa]	802	309.0	19,900	24.8
Namibia [South-west Africa]	825	318.0	2,100	2.5
Niger *	1,267	489.0	14,400	11.3
Nigeria	924	357.0	134,500	145.6
Rwanda [part of Ruanda-Urundi (= part of Belgian Congo)]	26.3	10.2	9,100	346.0
Senegal *	197	76.0	11,900	60.4
Sierra Leone	71.7	27.7	5,700	79.5
Somalia [‡] [British Somaliland and Italian Somaliland; Somali Republic]	638	246.0	8,900	13.9
South Africa	1,220	471.0	47,300	38.7
Sudan [§] [Anglo-Egyptian Sudan]	2,506	967.0	41,200	16.4
Swaziland	17.4	6.7	1,100	63.2
Tanzania [German East Africa; Tanganyika] (now includes Zanzibar I., Mafia I. and Pemba I.)	945	365.0	37,900	40.1
Togo [Togoland]	56.8	21.9	6,300	110.9
Tunisia	164	63.0	10,100	61.6
Uganda	236	91.0	27,700	117.4
Zambia [Northern Rhodesia]	753	291.0	11,900	15.8
Zimbabwe [Southern Rhodesia]	391	151.0	13,100	33.5
Totals/mean density	29,448	11,383	902,600	56.8

Former names are listed in chronological order in square brackets, with the oldest name listed first. Obsolete names are listed because much of the older literature refers to past colonial entities. * = formerly part of French West Africa. [#] = formerly part of French Equatorial Africa. [§] At the time of going to press, the country of Sudan had been divided into two: the Republic of Sudan in the north, and the Republic of South Sudan in the south. [‡] The former British Somaliland is now a self-declared state under the name of the Republic of Somaliland, but remains internationally unrecognized.



Figure 2. The biotic zones of Africa.

the extent to which it is vulnerable to loss of a particular habitat. The Rainforest Biotic Zone and the South-West Arid Biotic Zone are divided into regions and sub-regions that reflect the different biogeographical distributions of species, each region/sub-region having a community of mammals and other animals that is different to any other. Details of the biotic zones of Africa, and the regions and sub-regions of the Rainforest Biotic Zone and South-West Arid Biotic Zone, are given in Chapter 5 of Volume I of *Mammals of Africa*.

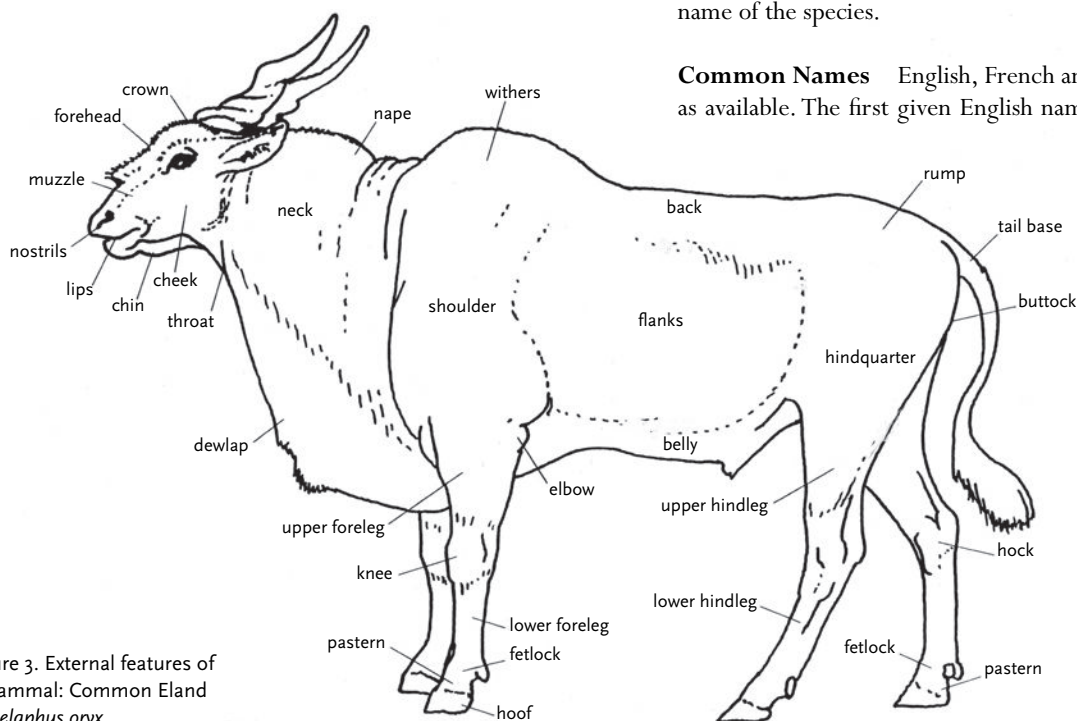


Figure 3. External features of a mammal: Common Eland *Tragelaphus oryx*.

The primates of Africa

This volume, Volume II, is devoted to the order Primates. The order Primates, using the taxonomy adopted for this volume, contains four families, 25 genera and 93 species. About 8% of Africa's species of mammal are primates.

Since the texts for this volume were prepared, one new species of primate has been described:

Lesula *Cercopithecus lomamiensis* J. Hart, Detwiler, Gilbert, Burrell, Fuller, Emetsu, T. Hart, Vosper, Sargis & Tosi, 2012. *PLOS ONE* 7(9): e44271, p. 4. *Type locality*: Near Lohumonoko (01°01'S, 24°25'E; 470 m asl), west bank, Lomami R., Central Basin, Democratic Republic of Congo. *Taxonomy*: Member of the Owl-faced Monkeys Group *Cercopithecus* (*hamlyni*). *Distribution*: Between Lomami R. and Tshuapa R., C DRC (01°01'–01°26'S, 24°25'–25°02'E; 440–715 m asl). Area of occurrence: ca. 17,000 km². See map on p. 341. *Habitat*: Mature terra firma evergreen forest. *Description*: Slender, medium-sized, long-limbed monkey. Recalls Owl-faced Monkey *C. hamlyni* but facial skin pinkish-grey to tan-brown; vertical nose stripe cream or indistinct; chin, throat and chest yellowish-buff; posterior 30–50% of dorsum with prominent, amber, median stripe (brightest at base of tail); tail tuft absent. Further information on *C. lomamiensis* is presented in Hart *et al.* (2012). See illustration on p. 344.

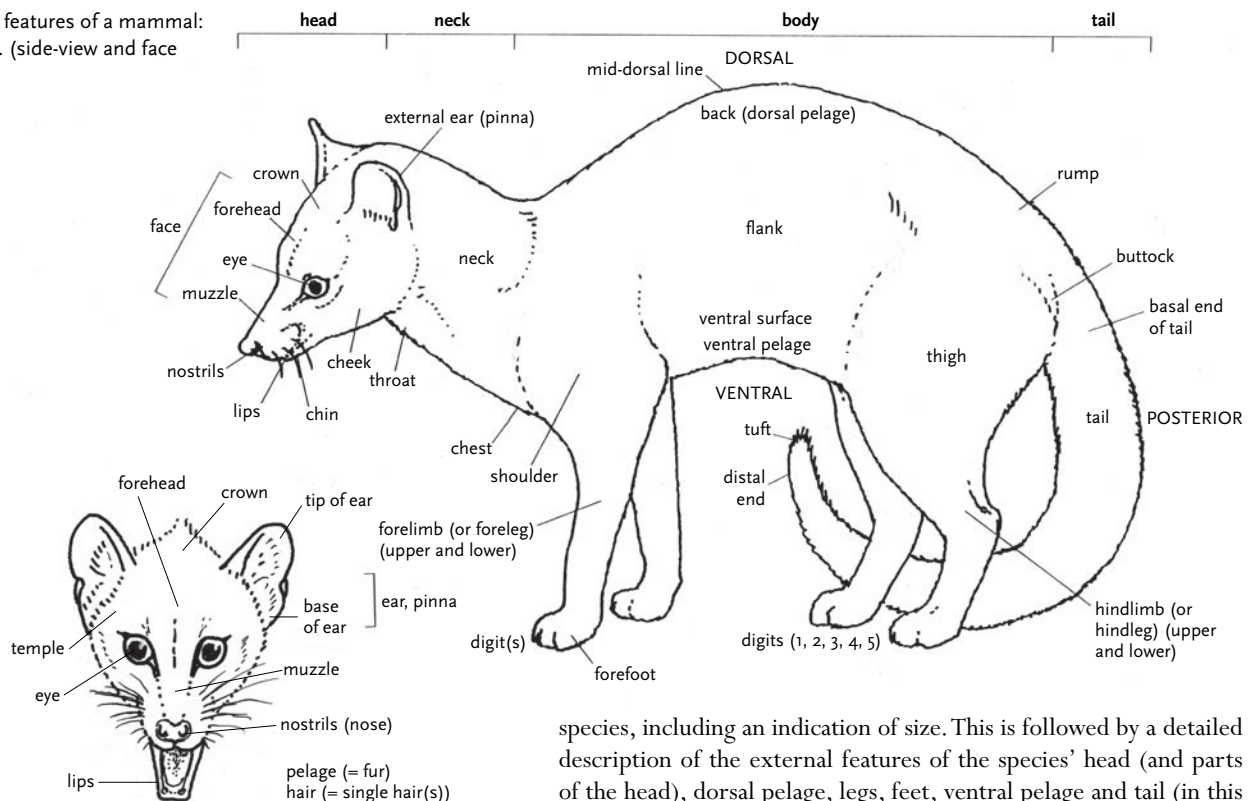
Species profiles

Information about each species is given under a series of subheadings, the amount of information under each of which varies greatly among species; where no information is available, this is recorded as 'No information available' or similarly. The sequence of subheadings is:

Scientific Name (genus and species) The currently accepted name of the species.

Common Names English, French and German names are given, as available. The first given English name is the preferred common

Figure 4. External features of a mammal: Genet *Genetta* sp. (side-view and face frontal).



(vernacular) name for the species; alternative names are given in parentheses for some species. Most of the English common names used in this volume are taken from Grubb *et al.* (2003). The French and German common names derive from various sources or are direct translations of the English vernacular.

Scientific Citation This provides the full scientific name of the species, i.e. genus name, species name, authority name and date of authority. Parentheses around the authority's name and date indicate that the species was originally named in a different genus to its present generic allocation. The scientific name is followed by the publication where the species was described and the type locality (i.e. where the type specimen [or type series] was obtained). Most of this information is taken from Wilson & Reeder (2005).

Taxonomy This section contains information about previous scientific names of the species, taxonomic problems, and the relationship with other species in the genus. For some species, there is considerable information about these topics; for others, there may be nothing. Synonyms are listed in alphabetical order (without the taxonomic authority for each unless essential for clarity) and the number of subspecies (if any) is presented, mostly taken from Grubb *et al.* (2003) and Wilson & Reeder (2005). The chromosome number is given if available and, in some cases, this is followed by other information relevant to the chromosomes. In late 2006, a revised edition of the *Atlas of Mammalian Chromosomes* was published (O'Brien *et al.* 2006), but it was not possible to incorporate the findings of that important work here.

Description This section, together with the illustrations, provides the reader with adequate information to identify the species. The section begins with a brief overall description of the

species, including an indication of size. This is followed by a detailed description of the external features of the species' head (and parts of the head), dorsal pelage, legs, feet, ventral pelage and tail (in this order), as well as any special characteristics unique to the species. For some species, diagnostic characteristics of the skull are given. The mammary formula (i.e. the number and arrangement of nipples) is noted wherever this feature varies among the taxa being discussed. The characters described in this section are common to all subspecies of this species (see also Geographic Variation). Characters that are diagnostic to the genus are not usually repeated in a species profile; hence, higher taxa profiles should also be consulted.

Geographic Variation Variation within the species may be of two sorts: (a) clinal variation without subspecies, or (b) subspecific variation. If (a), then there is a description of the character(s) that alter clinally across the geographic range of the species. If (b), each of the subspecies is listed with its geographic range and the characters that distinguish it from all other subspecies of the species.

Similar Species Species that are sympatric or parapatric with the species under consideration, and with which it may be confused, are listed along with diagnostic characteristics and geographic ranges (additionally, readers may refer to profiles of the similar species in question). In some instances, similar species that are allopatric are also included.

Distribution The first sentence is often 'Endemic to Africa', indicating that the species is found (in the wild) only in Africa. If a species also occurs outside Africa (and, hence, is not endemic), this is noted at the end of this section. The next sentence usually gives the Biotic Zone(s) where the species has been recorded; this provides the reader with a general impression of where the species occurs in Africa and the sort of habitats where the species lives. Finally, the countries (or parts of countries) where the species has been recorded are listed. As a general rule, descriptions of the range for species with very restricted

distributions are more precise in terms of information given (including, for example, geographic coordinates) than for more widespread species, where a more generalized range statement is adequate. A distribution map (see below) augments the information given here.

Habitat This section provides a description of the habitat, or range of habitats, where the species lives. Details of plant communities, plant species, vegetation structure, water availability, etc. (if available) are also presented. Other information may include average annual rainfall, average annual rainfall limits, altitudinal limits, temperature limits and seasonal variation in habitat characteristics.

Abundance A general indication of abundance of the species in its habitat(s). This may be unquantified, such as ‘abundant’, ‘common’, ‘uncommon’, ‘rare’, or phrases such as ‘rarely seen but frequently heard’. For better-known or rare species, abundance may be expressed as estimates of density (e.g. number/ha or number/km²), or relative abundance (e.g. ‘the second most numerous species’).

Adaptations This section describes morphological, physiological, and behavioural characteristics that show how the species uniquely interacts with its environment, with conspecifics and with other animals. This section may also describe species-specific adaptations for feeding, locomotion, production of sound, sensory mechanisms and activity patterns. In some instances, comparison with related or convergent species allows the unique adaptations of the species under discussion to be detailed or emphasized.

Foraging and Food The first sentence briefly describes the food habits of the species (e.g. insectivorous, folivorous, granivorous, omnivorous). This may be followed by the method of collecting food (foraging), size of home-range and daily distance moved. The diet is then described either by a list of the taxa of animals or plants consumed,

and/or as a quantitative measure based on direct observations, or of examination of the contents of the stomach or the faeces.

Social and Reproductive Behaviour Topics in this section may include social organizations (e.g. solitary, social, or colonial), group size, group composition, agonistic and amicable behaviour, comfort behaviour, territoriality, courtship and mating, parental behaviour, parent–young interactions, presence of helpers, vocalizations, and interactions with other species (mammals, birds, etc.).

Reproduction and Population Structure This section begins with an assessment of the reproductive strategy (if known) and the times/seasons of the year when there is reproductive activity (mating, pregnancy, birth, lactation). Other information may include length of gestation, litter-size, birth-weight and size, birth intervals, birth rates, time to weaning, time to maturity, longevity, mortality rates, sex ratios and adult/immature ratios.

Predators, Parasites and Diseases Predators, parasites and diseases are listed. Additional information is given if the species is a host to diseases that affect humans and domestic stock, and if the species is hunted by humans (‘bushmeat’).

Remarks This subheading subsumes the last five of the above sub-headings in those cases where there is little or no information available.

Conservation The conservation status of the species in 2012 is stated, as given by the *IUCN Red List of Threatened Species*. The IUCN Red List ‘degree of threat categories’ follow the definitions and criteria given in the *IUCN Red List Categories and Criteria Version 3.1* (www.iucnredlist.org). The categories are listed in Table 4. For those species classified as ‘threatened’ (i.e. ‘Vulnerable’, ‘Endangered’, ‘Critically Endangered’), readers can obtain detailed reasons for the classification by going to

Table 4. Definitions for the IUCN Red List categories (from IUCN – Red List Categories, Version 3.1).

Category	Description
Extinct (EX)	A taxon is Extinct when there is no reasonable doubt that the last individual has died. A taxon is presumed Extinct when exhaustive surveys in known and/or expected habitat, at appropriate times (diurnal, seasonal, annual), throughout its historic range have failed to record an individual. Surveys should be over a time frame appropriate to the taxon’s life-cycles and life-form.
Extinct in the Wild (EW)	A taxon is Extinct in the Wild when it is known only to survive in cultivation, in captivity or as a naturalized population (or populations) well outside the past range. A taxon is presumed Extinct in the Wild when exhaustive surveys in known and/or expected habitat, at appropriate times (diurnal, seasonal, annual), throughout its historic range have failed to record an individual. Surveys should be over a time frame appropriate to the taxon’s life-cycle and life-form.
Critically Endangered (CR)	A taxon is Critically Endangered when the best available evidence indicates that it meets any of the criteria A to E for Critically Endangered, and it is therefore considered to be facing an extremely high risk of extinction in the wild.
Endangered (EN)	A taxon is Endangered when the best available evidence indicates that it meets any of the criteria A to E for Endangered, and it is therefore considered to be facing a very high risk of extinction in the wild.
Vulnerable (VU)	A taxon is Vulnerable when the best available evidence indicates that it meets any of the criteria A to E for Vulnerable, and it is therefore considered to be facing a high risk of extinction in the wild.
Near Threatened (NT)	A taxon is Near Threatened when it has been evaluated against the criteria but does not qualify for Critically Endangered, Endangered or Vulnerable now, but is close to qualifying for (or is likely to qualify for) a threatened category in the near future.
Least Concern (LC)	A taxon is Least Concern when it has been evaluated against the criteria and does not qualify for the Critically Endangered, Endangered, Vulnerable or Near Threatened categories. Widespread and abundant taxa are included in this category.
Data Deficient (DD)	A taxon is Data Deficient when there is inadequate information to make a direct, or indirect, assessment of its risk of extinction based on its distribution and/or population status. Data Deficient is not a category of threat. Listing of taxa in this category indicates that more information is required and acknowledges the possibility that future research will show that a threatened classification is appropriate.
Not Evaluated (NE)	A taxon is Not Evaluated when it has not yet been evaluated against the criteria.

the IUCN Red List website. Some species have changed status due to improved knowledge, taxonomic revision, or the impact of threatening processes or conservation actions. Readers can obtain detailed reasons for the past and present status of a species by going to the IUCN Red List website. If, in 2012, a species was listed on Appendix I or Appendix II under CITES (Convention on International Trade in Endangered Species; www.cites.org), this is also indicated. For some species, additional information is provided, such as presence in protected areas, major threats, and current or recommended conservation measures.

Measurements A series of morphological measurements is provided. For each species there is a standard set of measurements provided for adult males and adult females. The abbreviation and definition for each measurement is given in the Glossary. A measurement is cited as the mean value, range (given in parentheses) and sample size. For some, the standard deviation (mean \pm 1 S.D.) is given instead of the range. Where possible, information is given on the location(s) where the specimens were obtained and the source of the data. Sources are either cited publications, specimens in museums, or unpublished information from authors or others. Acronyms for museums referred to in this volume are given in Table 5.

Key References This is a list of the more important references for the species. Each reference is given in full in the Bibliography.

Author The name of the author, or authors, is given at the end of each profile. All profiles should be cited using the author name(s).

Higher taxon profiles

The profiles for orders, families and genera are less structured than for species. Each profile usually begins with a listing of the taxa in the next lower taxon; for example, each family profile lists the genera in that family. An exception to this arrangement is where a taxon has only one lower taxon. Higher taxa profiles provide the characteristics common to all members of that taxon; these characteristics are usually not repeated in the lower taxa profiles (unless essential for identification).

Distribution maps

Each species profile contains a pan-African map showing the geographic range of the species. Most maps were provided by the author(s) of the profile and were compiled from literature records, museum specimens, and unpublished sources; some maps were provided by the editors. Maps in this volume were checked (and modified if necessary) by the members of the Africa Section of the 'Primate Taxonomy for the New Millennium' workshop held in Orlando, Florida, in February 2000 (Grubb *et al.* 2003). This workshop was organized by the IUCN/SSC Primate Specialist Group, The IUCN Global Mammal Assessment, and Conservation International. Each map shows the boundaries of the 47 countries of Africa, some of the major rivers (Nile, Niger–Benue, Congo [with the tributaries Ubangi, Lualaba and Lomani], Zambezi and Orange), and Lakes Chad, Tana, Turkana (formerly Rudolf), Albert, Edward, Victoria, Kyoga, Kivu, Tanganyika, Malawi, Mweru, Bangwuela

Table 5. Museum acronyms.

Acronym	Museum name
AM	Amatole Museum, King William's Town, South Africa (formerly Kaffrarian Museum)
AMNH	American Museum of Natural History, New York, USA
BMNH	Natural History Museum, London, UK [formerly British Museum (Natural History)]
CM	Carnegie Museum of Natural History, Pittsburgh, USA
CUMV	Cornell University Museum of Vertebrates, Ithaca, New York, USA
FMNH	Field Museum of Natural History, Chicago, USA
LACM	Los Angeles County Museum, Los Angeles, USA
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, USA
MNHN	Museum National d'Histoire Naturelle, Paris, France
NMK	National Museums of Kenya, Nairobi, Kenya
NMZB	Natural History Museum of Zimbabwe, Bulawayo, Zimbabwe
PCM	Powell-Cotton Museum, Birchington, UK
RMCA	Royal Museum for Central Africa, Tervuren, Belgium
TM	Transvaal Museum, Pretoria, South Africa
USNM	United States National Museum of Natural History, Smithsonian Institution, Washington DC, USA
ZFMK	Zoologisches Forschungsmuseum, Alexander Koenig, Bonn, Germany

and Kariba. The map projection is Transverse Mercator, with the following parameters: False Easting: 0; False Northing: 0; Central Meridian: 20; Linear Unit: metre; Datum: Clarke 1866.

The geographic distribution of a species is indicated as:

- red shading = current range(s). When presented, different colour shading denotes subspecies.
- × = isolated locations considered to be separate from the main geographic range(s). Some locations indicated by × may include two or more closely spaced locations.
- ? = locality of uncertain validity; relevant information usually in text.
- coloured arrow = presence on the island indicated by the arrow.

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Supercohort SUPRAPRIMATES (EUARCHONTOGLIRES)

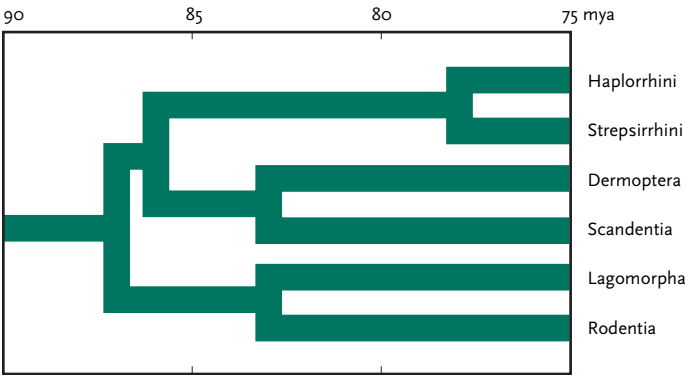
Supraprimates Waddell, Kishino & Ota, 2001. *Genome Informatics* 12: 141–154.

Euarchonta	Primates and allies	p. 22
Glires	Rodents, Hares	See <i>Mammals of Africa</i> , Volume III

Efforts to understand the relationship of primates to other mammals have exercised biologists for more than 100 years. Based primarily on comparative anatomy, the deepest levels of affinity eluded success until the advent of molecular phylogeny. The latest genetic studies reveal some unexpected affinities, refute others and, in at least one case, broadly confirm a supposed taxonomic relationship that is of long standing. Thus, Gregory (1913) clustered primates with tree-shrews (Scandentia), colugos or flying lemurs (Dermoptera) and bats (Chiroptera). The bat connection is firmly rejected by all molecular studies while the long-suspected, but hotly disputed, link between primates and tree-shrews receives some support (Waddell *et al.* 2001). The colugos, however, turn out to have the closest genetic affinities with primates, followed by Scandentia (Murphy *et al.* 2001, Bininda-Emonds *et al.* 2007, Perelman *et al.* 2011). More distant than either tree-shrews or colugos, rodents and lagomorphs are the next closest relatives of primates (Eizirik *et al.* 2001, Murphy *et al.* 2001).

These previously hidden subtleties of relationship elicit a need for taxonomic expression at various supraordinal levels. As such, Waddell *et al.* (2001) propose a supercohort named ‘Supraprimates’ to group primates, flying lemurs, tree-shrews, rodents and lagomorphs. Other authors apply the name ‘Euarchontoglires’ to the same grouping (Madsen *et al.* 2001, Murphy *et al.* 2001, Van Dijk *et al.* 2001). A still higher level of grouping is mooted by Hedges *et al.* (1996) and Eizirik *et al.* (2001), who link ‘Euarchontoglires’ and ‘Laurasiatheria’ in ‘Boreoeutheria’ to stress their putative common origin in the northern continents.

A continental dimension for taxonomy has long had obvious meaning for endemic groups such as kangaroos in Australia, golden-moles in Africa and armadillos in South America, but formal expression through archaeocontinental names for mammal groupings is essentially new and reflects a heightened awareness that geographic separation is a fundamental part of evolution (Hedges *et al.* 1996). This innovation has come about because there is now general recognition that the splitting of Pangaea into Laurasia and Gondwana, and subsequent fragmentation of the latter into the southern continents, had consequences for the evolution of placental



Tentative phylogenetic tree for the Supraprimates (after Springer *et al.* 2003).

mammals (Scally *et al.* 2001). While controversy still surrounds allocation of these supraordinal groupings to specific land masses, they are founded upon the most plausible interpretation of the evidence currently available: Supraprimates (Euarchontoglires) embraces Primates, Dermoptera, Scandentia, Rodentia and Lagomorpha.

Molecular clocks suggest that the primary divergence between Supraprimates and their closest other supercohort, the Laurasiatheria, was during the mid-Cretaceous, between 102 mya (Bininda-Emonds *et al.* 2007) and 92 mya (Kumar & Hedges 1998). Within Supraprimates, the Euarchonta/Glires split is estimated at about 98 mya by Bininda-Emonds *et al.* (2007) but later by others.

While the timing of such divergences remains open to question, the relationships among major groupings have found closer agreement. The phylogenetic tree that is presented here follows Bininda-Emonds *et al.* (2007); hopefully, the broad pattern of its branching will not undergo further major changes even if the putative times of divergence eventually need revision.

In the absence of fossils, any reconstruction of what a 100-million-year-old common ancestor of all supraprimates might have looked like must be extremely tentative. This ancestor was probably small, nocturnal and semi-arboreal: superficially it may have resembled a small opossum or dormouse (but without the specializations of contemporary marsupials or rodents).

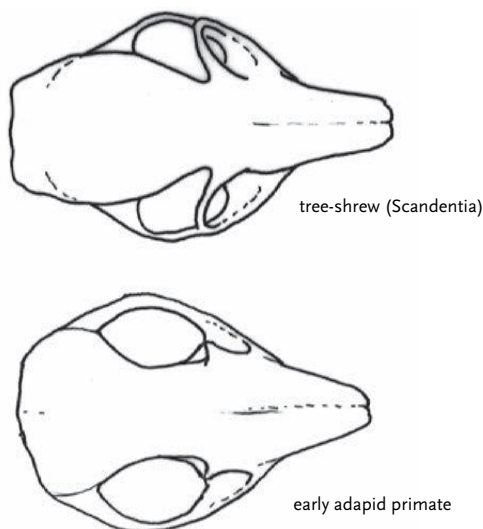
Jonathan Kingdon

Cohort EUARCHONTA

Euarchonta Murphy, Elzirik, O'Brien, Madsen, Scally, Douady, Teeling, Ryder, Stanhope, de Jong & Springer, 2001. *Science* 294: 2348–2351.

This newly erected category associates the primates, on the basis of genetic similarities, with two non-African taxa: the Oriental tree-shrews (Scandentia) and the South-East Asian colugos (flying lemurs) (Dermoptera).

Discussion of possible affinities with tree-shrews has a long and interesting history, beginning with observations by Parker (1885) in which he first noted resemblances. Gregory (1910, 1913) went on to erect the taxon 'Archonta', which grouped primates with tree-shrews, colugos and bats. Following detailed surveys of tree-shrew morphology by Carlsson (1922) and Le Gros Clark (1924, 1934), Simpson (1945) went so far as to include tree-shrews within Primates, remarking that the former were 'either the most primate-like insectivores or the most insectivore-like primates', and 'the use of [tree-shrews] to represent the earliest primate or latest pre-primate stage of evolution is as valid and useful and subject to as much caution as is any use of living animals to represent earlier phylogenetic stages'. Subsequent taxonomists disagreed and removed tree-shrews from Primates (Roux 1947, Van Valen 1965, Szalay & Delson 1979).



Skull outlines of a tree-shrew (Scandentia) and an early adapid primate (after Martin 1990).

Controversies over classification are less interesting than understanding degrees and levels of relationship, so the new molecular techniques have had the special virtue of making the construction of phylogenetic trees more objective and plausible. As Martin (1990) remarked, an objective assessment of the phylogenetic relationship between tree-shrews and primates is actually a valuable test case in understanding primate origins. The fact that tree-shrews and colugos are both exclusively Asian taxa and have never been found, even as fossils, outside Asia, provides some confirmation that tree-shrews and colugos, as well as primates, diverged from common ancestors in Asia during the mid-Cretaceous, some 100–93 mya.

Tree-shrews fall on the more primitive side of the Euarchonta/Rodentia divide, so it is interesting that several Oriental squirrels have extraordinary resemblances with sympatric tree-shrews, a convergence that was first noted by Shelford (1916). New recognition that rodents have an ancient relationship with primates and tree-shrews does not make such resemblances any less expressive of convergent evolution in separate lineages, but it does imply substantial continuity in the niche structure of tropical forests – as does the continuous presence of tarsiers since the mid-Eocene, 40 mya (Gebo *et al.* 2000). Opportunities for small, nest-making omnivores (tree-shrews eat mainly arthropods and small fruits) with a weight range of 45–350 g, occur at all levels of the forest, including the floor, where one genus, *Urogale*, spends most of its life.

Attempts to envisage primate, rodent, placental or marsupial ancestors by referring to mammals that look like 'primitive insectivores' have long been a part of grappling with evolution. Romer (1966) wrote, 'it may well be that in tree-shrews we see the most primitive of living placentals – forms not too distant from the common base of all eutherian stocks'. Martin (1990) was more specific, noting that tree-shrews conform to the expectation of an intermediate between primitive insectivore and advanced primate.

In spite of recognizing a genetic affinity, the new molecular trees and their associated clocks are a reminder that primates and tree-shrews have pursued separate evolutionary paths for more than 90 million years.

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Superorder PRIMATOMORPHA

Primatomorpha Waddell, Kishino & Ota, 2001. *Genome Informatics* 12: 141–154.

This taxon has been erected in recognition that the closest and most exclusive genetic affinity between primates and any other living mammal is with the South-East Asian colugos (Cynocephalidae, Dermoptera). Cronin & Sarich 1980 were the first to report monophyly between these two groups (and tree-shrews). In naming 'Primatomorpha', Waddell *et al.* (2001) gave formal expression to this relationship within the Euarchonta.

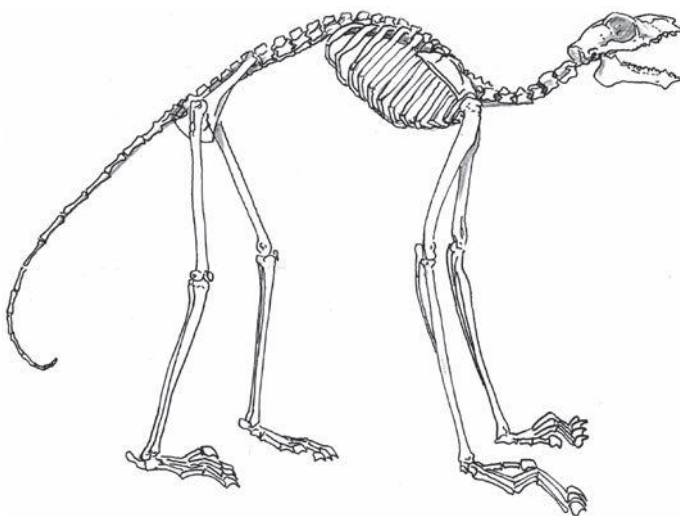
Colugos, of which there are two species, weigh 1–1.7 kg and have developed skin webbing between their limbs and tail as a gliding membrane or patagium. They are vegetarian, eating leaves, shoots, flowers and sap, and have very long, lightly built limbs, large clawed feet and hands, and a wide, flat head that resembles that of a lemur, hence their alternative name, 'flying lemur'.

It would seem that modification of skin to provide a 'vol-plane' is a relatively simple development and has evolved independently in many animals, including amphibians, reptiles and mammals. Among Australian possums the gliding membrane has evolved several times. The closest living relative of one form, the Greater Glider *Petauroides volans*, is the non-gliding Lemuroid Possum *Hemibelideus lemuroides*, not one of several other gliding possums. The habitat that favours gliding is open, broken-canopy woodlands where the branches of trees are not in contact. Here, arboreal animals that need to range widely must either become semi-terrestrial or evolve the capacity to glide from tree to tree.

This the ancestors of colugos did, but *when* gliding developed and at what stage of evolution in the colugo lineage is not known. It is possible, however, that among the diverse forms of proto-primates a gliding form emerged and that the colugo derives directly from that very early radiation. The pre-existence of efficient gliding mammals (anomalures in Africa, squirrels and colugos in Asia) has probably deterred primates from evolving gliding forms. Indeed, there is no evidence for there ever having been any kind of gliding primate.

Resemblances, such as there are, between lemurs (Lemuriformes) and colugos suggest that the common ancestor of dermopterans and primates was not strikingly different from either in their facial morphology and slender limbs.

Jonathan Kingdon



Skeleton of colugo (Dermoptera, Cynocephalidae, *Cynocephalus*).

Profile and portrait views of colugo *Cynocephalus* sp. to compare with extant lemur *Lemur* sp. (bottom).

Order PRIMATES – Primates

Primates Linnaeus, 1758. *Systema Naturae*, 10th edn, vol. 1.

Hominidae (3 genera, 5 species)	Great Apes, Humans	p. 32
Cercopithecidae (15 genera, 68 species)	Old World Monkeys (Cercopithecids)	p. 92
Lorisidae (2 genera, 3 species)	Lorises, Potto, Angwantibos	p. 391
Galagidae (5 genera, 18 species)	Galagos (Bushbabies)	p. 404

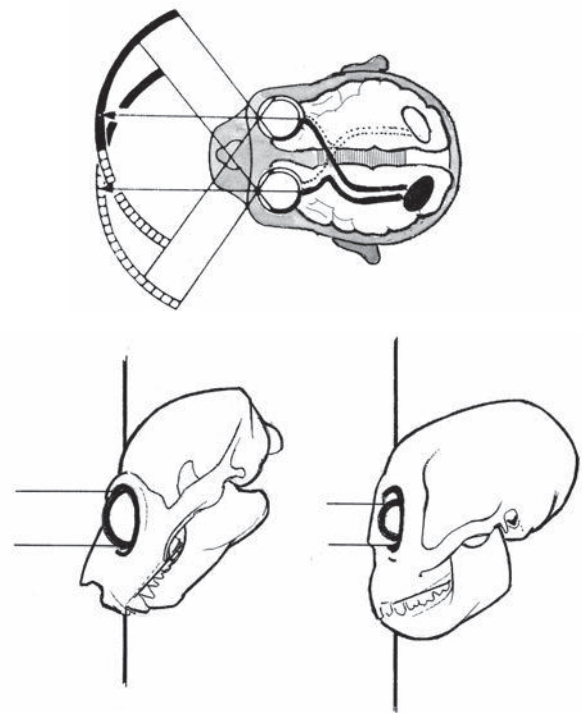
Because every reader of these pages is a primate, the origins, diversity and radiation of our ancient mother-order have a peculiarly personal significance. Our historical search for self-knowledge now includes reaching back to chart *our* particular place within a family tree that we share with many other primate species, all related but to very varying degrees. Thus, describing primates and primate fossils accurately, and analysing their affinities and biology are particularly challenging and important tasks.

Comparisons between one species and another, one group and another group, are an essential part of the scientific process, but such comparisons need extensive information on as many and as diverse species (both living and extinct) as possible. This volume has been designed to assist that process but it should be emphasized, from the start, that our knowledge is still extraordinarily, almost shamefully, incomplete for such an important group of mammals. The scale of our ignorance (but also the pace of recent discovery) can be gauged by the fact that a popular inventory of African primates published 28 years ago listed 43 species in 13 genera (Haltenorth & Diller 1980), while the most recent and most exhaustive review listed 95 species in 22 genera (Groves 2001). The taxonomy followed in this volume is a close (but not exact) match with the latter work and with Grubb *et al.* (2003).

There are several reasons for this more than two-fold increase in recognized species, aside from the idiosyncrasies of authors. Molecular scientists have been a major influence in elevating the taxonomic status of already-described forms, and greater sensitivity to the significance of differences among populations has been another factor, but the actual scientific discovery of new forms of primates in the wild has also swelled the numbers since 1980. As a consequence, while this inventory of primates represents the most up-to-date review of all the known primates of Africa, it should still be regarded as provisional. In addition to increasing numbers, there are changes in how relationships are understood, sometimes precipitated by the discovery of new fossil primates. In general, ideas about primate origins have developed faster since 1980 than at any previous time.

What explains the extraordinary abundance of primate species in Africa? Primates are essentially tropical and mainly arboreal animals. Africa is, at the grossest level of generalization, the largest area of equatorial land on earth and this fact could be taken as sufficient to explain primate abundance. However, it is the particular dispersal of humid-to-arid habitats and, as climates have fluctuated, the changing boundaries of major habitat blocks that helps explain the extraordinary diversity of primates. This evolutionary mechanism has been explored in some of the introductory chapters in Volume I of *Mammals of Africa*, as well as in some of the family and genus profiles in this volume.

How many primate species are there in Africa, and how are they related to one another? The table above enumerates the families,



Stereoscopic vision in primates.

Top: Whole field of vision registered separately on left and right sides of retinas. Some optic fibres from right half of *both* retinas transmit to right brain hemisphere. Likewise, retinal impulses from left half of *both* retinas travel to left side of brain's visual cortex. Cross-over takes place in chiasma (at base of midbrain). Processing takes place in the lateral geniculate bodies of the thalamus at the back of the brain (in part after Ankel-Simons 2000).

Bottom left: Visual orientation in tilted head of a strepsirrhine, the Potto *Perodicticus potto*.

Bottom right: Less tilted head of a haplorrhine, the red colobus monkey *Procolobus*. Stereoscopic vision is likely facilitated by reduction of the olfactory apparatus.

genera and species that we recognize. The diagnostic attributes of primates are seldom clear-cut, largely because they retain many basal mammalian features. Even so, all, or nearly all primates share certain traits or trends. These are as follows:

- 1 A tendency for the brain, from foetus to adult, to be proportionally large.
- 2 Forward rotation and convergence of the eyes, and stereoscopic vision.
- 3 Loss of one pair of incisors and one pair of premolars. Thus, the dental formula for the majority of African primates is 2123/2123.
- 4 Nails rather than claws on most digits (a few non-African primates have claws on most digits).
- 5 Spreadable fingers on grasping hand, with a divergent and opposable thumb in most species.
- 6 Spreadable toes on grasping foot, with divergent big toe (hallux).
- 7 Compared to most other mammals (and allowing for size), slower foetal growth, longer gestation times and longer lives.

Some of these trends have been taken to their furthest degree in humans and great apes, implying that they are among the most 'primate-ish' of all primates!

Among the diagnostic characteristics common to all primates are highly versatile hands with soft finger pads, long digits, relatively short palms, and very flexible wrists attached to long, relatively slender arms. It is of interest that primates possess an elaborated type of nerve ending, Meissner's corpuscles, in the digital pads. These are, otherwise, found only in arboreal marsupials. This detail is of particular relevance for human evolution because these corpuscles give a special sensitivity to the hands and fingers.

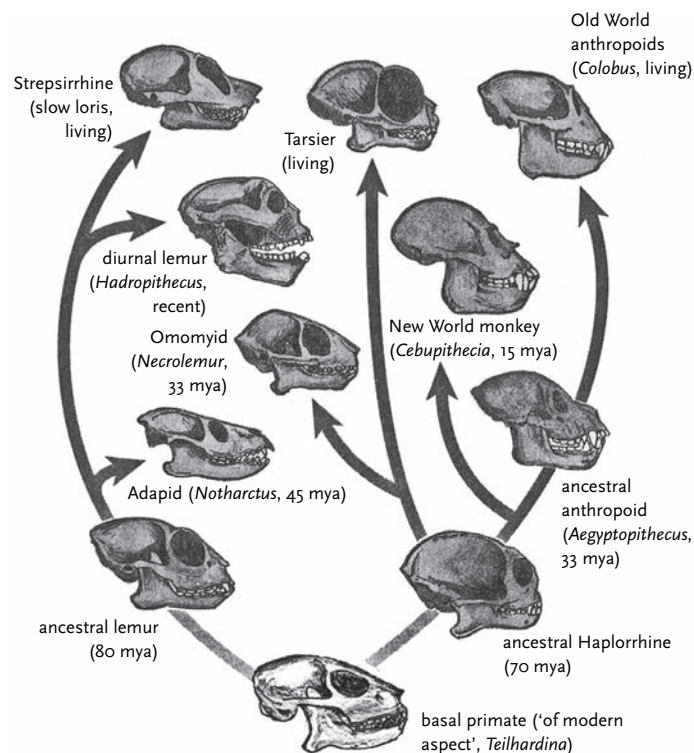
Although primates have 'hands' on all limbs (and were once called 'quadrumanes'), the feet are a lot less versatile than the hands. The feet, however, have flexible ankles attached to powerfully muscled legs that, for a majority of species, propel the animal by running, leaping or bounding, mainly on branches and stems. In combination, the limbs provided a firm base for movement in all directions and through highly obstructed environments.

Primates represent one of the basal or near-basal orders of placental mammals; the first primates presumably shared many traits with the earliest placental mammals. Matthew (1904), Martin (1990), Sussman (1991) and Cartmill (1992) consider it likely that all the earliest placentals were to some extent arboreal, and Lewis (1983) discusses the evidence for the hands and feet of early placental mammals being adapted to a combination of arboreal and terrestrial habits.

Primates are an old group, originating at least as early as the Cretaceous, and, according to molecular analyses, share a common early ancestry with the Asian tree shrews and flying lemurs (Bininda-Emonds *et al.* 2007). These authors date the emergence of Primates as an order at ca. 94 mya (mid-Cretaceous) and calculate that the supercohort Supraprimates (or Euarchontoglires) separated from its sister supercohort (Laurasiatheria) ca. 102 mya. Murphy *et al.* (2001) place the latter divergence at 88–79 mya, while Wible *et al.* (2007) place it after 65.5 mya (late Cretaceous).

While the earliest mammals may have emerged in cooler environments (see Mammalia, Volume I), primates are, today, overwhelmingly tropical, so the initial divergence between primates and other mammals (or, possibly, between Supraprimates and the rest) may have been partly geographic or latitudinal: probably within the Asiatic land mass. In terms of habitat, the extremities of tropical trees and shrubs represent, by volume, a high proportion of the plants' biomass and occupation of space, a space almost continuously loaded with leaves, fruit and invertebrates (the latter being the likely food of the earliest primates). The differentiation of primates from other mammals probably involved a decisive adaptation to living in trees. Life within a dense lattice of fine branches, twigs and twiglets demanded flexible leverage, an efficient grasp and speedy reaction times. To this end, all primates have realigned their limb joints and articulations, evolving ingenious swivel points in the limbs and neck, a firm pelvic girdle, exceptionally dexterous, clasping hands and feet, and a relatively energetic life-style.

There is some agreement among scientists that primates arose as arboreal, and perhaps nocturnal, placental mammals taking the form of very small, visually oriented invertebrate-eaters, possibly foraging quite systematically through the fine foliage. Cartmill (1974) supposed that 'the last common ancestor of the extant



Outline of primate phylogeny showing skulls of five extant and six extinct lineages and likely phyletic relationships (after Martin 1990, Ross 1996).

primates, like many extant prosimians, subsisted to an important extent on insects and other prey, which were visually located and manually captured in the insect-rich canopy and undergrowth of tropical forests'.

There has been some controversy, which has yet to be resolved, as to which early mammals can legitimately be termed primates. Thus 'euprimates' and 'plesiadapoids' occupy uncertain positions close to the evolutionary roots of primates. These controversies affect arguments about the timing of primate origins and diversification, as well as the diagnostic features of the order. Apart from offering some broad generalities about primate affinities and characteristics, our discussion by-passes such controversies here by beginning with an outline of the known history of primates in Africa.

Widespread confusion has surrounded the crucial issue of how the order Primates should be broken down into its very diverse component parts. The most thorough early classification of primates ('quadrumanes') was by É. Geoffroy (1812a, b). He divided primates into two informal 'families', apes and monkeys ('singes' and 'lemuriens'). The first 'family' he divided into Catarrhini and Platyrrhini; all of the second 'family' he included in a third group, Strepsirrhini. Haeckel (1874) originated the distinction between 'half-monkeys' (or 'Prosimiae') and 'monkeys' (or 'Simiae'), based loosely on the schemes devised earlier by Illiger (1811) and É. Geoffroy (1812a, b). He lumped, under Prosimiae, tarsiers, a variety of living lemurs, and fossil forms.

One of the earliest authors to align the tarsiers with monkeys and apes, rather than with lemurs, was Pocock (1918), who divided the primates into two grades, one comprising the lemurs, for which he revived É. Geoffroy's (1812b) name 'Strepsirrhini' (but spelling it with a single 'r'), the other including tarsiers and anthropoids, for which

he coined the name ‘Haplorhini’ [*sic*]. Initially, much more influential was Simpson’s (1945) revival of the Prosimii/Anthropoidea division, which was followed by Le Gros Clark (1959). Among mid-twentieth century authors, only Hill (1953) adopted Pocock’s insight.

Groves (1989) revived Pocock’s scheme, abandoning Prosimii as a scientific category and dividing Primates into two extant suborders, Strepsirrhini and Haplorrhini. This arrangement, in which major taxa correspond to groups (clades) defined by exclusive common ancestry (Hennig 1950) has found wide acceptance and is followed in this volume. Strepsirrhini and Haplorrhini are generally agreed terms, but there is some disagreement about the best term to label the monkey and ape clade within the Haplorrhini. The name Simiiformes, proposed by Hofstetter (1982), has not found wide acceptance – nearly all biological anthropologists use Anthropoidea instead of Simiiformes. While we find Hofstetter’s (1982) arguments for using Simiiformes cogent, we go with the flow and, in this work, use Anthropoidea in its place.

Central to the division of primates into Strepsirrhini and Haplorrhini are differences in the structure of their skulls and eyes, which relate to ancestral adaptations to night or day vision. However, the South-East Asian tarsiers, which are certainly Haplorrhini, are believed to be secondarily nocturnal (i.e. they derived from diurnal ancestors) (Cartmill 1970, Groves 1989, Ross 1996). This hypothesis has, however, yet to find unequivocal support from the fossil record. Dentally, tarsiers are extremely conservative but in the skull (notably the enormous orbits) and in the limbs (in particular the elongation of the calcaneus and navicular, and the extensive fusion of the tibia and fibula) they are extraordinarily specialized. Some measure of the age of Primates can also be gauged from recovery of fossils ascribed to the extant tarsier genus as *Tarsius eocaenus* from 45 mya (mid-Eocene) deposits in China (Beard *et al.* 1994).

On present fossil evidence, strepsirrhines appear in Africa later than anthropoids, but the great diversity of lemurs in Madagascar must derive from an African source. This suggests that the earliest African lemuroids have escaped being found as fossils (Seiffert *et al.* 2004). The ultimate common roots between the Asiatic lorises (subfamily Lorisinae) and African lorises (subfamily Perodicticinae) can hardly be in question but Asian lorises form a monophyletic clade separate from that formed by African pottos *Perodicticus* and angwantibos *Arctocebus*. The Lorisidae split probably occurred during the early Miocene (23 mya; Goodman *et al.* 1998). The Asian and African lorisid clades show a large measure of convergence; for example, each has a larger, plumper representative (*Nycticebus* in Asia, *Perodicticus* in Africa) and a smaller, more slender representative (*Loris* in Asia, *Arctocebus* in Africa). This has sometimes led primatologists into misunderstanding the true phylogeny and its biogeographic significance. Only Africa, however, has the active, long-legged forms known as galagos or bushbabies (family Galagidae).

The degree to which primates differ in terms of night vision (in nocturnal species) and colour vision (in diurnal species) remains an area of active research. This topic is discussed further in the profiles of Strepsirrhini and Haplorrhini.

While many anatomical features of living primates are advanced, some strepsirrhine species retain very unspecialized teeth. The anterior dentition (‘toothcomb’) is, however, a dramatic modification of the ancestral primate pattern (selection for the comb derives in most, if not all, species from the need to keep specialized, scent-

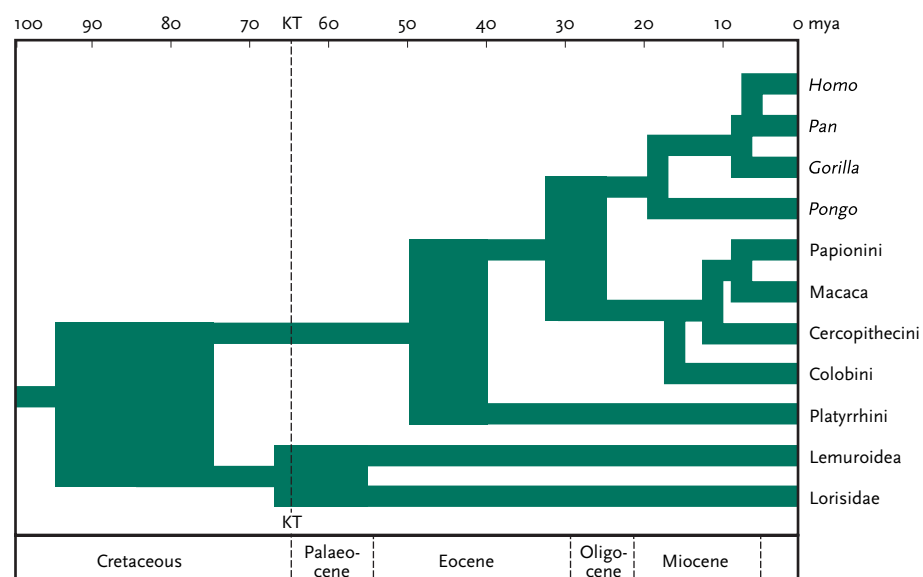
dispensing fur in prime condition). In adapting to a frugivorous/ folivorous diet, from an originally insectivorous one, most African anthropoids developed blunter, more robust teeth set in more compact tooththrows with the two mandibular components fused at the chin (only a few very large, non-African strepsirrhines have fusion of the symphysis).

For more than half a century the earliest fossils of monkeys that were plausible ancestors for both Old World and New World monkeys all came from 36–30 million-year-old (late Eocene–early Oligocene) deposits in Egypt (Andrews 1906, Simons 1963). The oldest likely primate fossil from Africa is the rather fragmentary *Altiatlasius* from Morocco (Sigé *et al.* 1990), at 57 million years old (late Paleocene), but its relationships remain uncertain. *Altiatlasius* was assigned by its describers to the extinct haplorrhine family Omomyidae. Gunnell & Rose (2002) suggest, however, that *Altiatlasius* might belong to an, as yet, poorly known separate radiation of early primates. Unfortunately, few primate-containing fossil deposits occur in Africa until the late Eocene.

In 1992, a tiny, apparently anthropoid primate, *Algeripithecus minutes*, was discovered in Algeria and dated to 45–40 mya (mid-Eocene) (Godinot & Mahboubi 1992). This, and later Egyptian fossils, show that a radiation of higher primates was already under way by the mid-Eocene. Seiffert *et al.* (2005a) describe the most complete early Anthropoidea from 37-million-year-old deposits in the Fayum, including two species of marmoset-sized *Biretia*, both with dentition that was consistent with their being within the ancestral lineage of later anthropoids. Noting that one of these, *Biretia megalopsis*, had enlarged orbits (implying nocturnal habits), E. Seiffert (pers. com.) considers this diversification of niches another indication that Anthropoidea were already long-established in Africa by the late Eocene (37 mya). Early occurrence, a diversity of species, their absence from the much more numerous and widely representative Eurasian deposits, plus the sheer abundance of diverse primates in the African Miocene (24–5 mya), has long supported the idea that most of the anthropoid primates, as we know them today, developed exclusively in Africa. This proposition remains true for the more derived forms but now needs significant qualification when it comes to ultimate origins. It is now theoretically admissible that one of the earliest of all placental mammals after the afrotheres to arrive from Asia was an ancestor for the higher primates.

The recent discovery in eastern Asia of fragments of very small primates, *Eosimias*, makes it more likely that the earliest haplorrhines were not African (Ni *et al.* 2004). Combining tarsier-like and non-tarsier haplorrhine traits, the Eosimiidae are known from the mid-Eocene (ca. 45 mya) deposits in Burma and China (Beard *et al.* 1994). This supports the proposal that Asia was their place of origin and undermines the assumption of African roots for all the higher primates (Gebo *et al.* 2000, Beard & Klinger 2005, Ciochon & Gunnell 2006). *Eosimias* is unlikely to be the descendant of an immigrant out of Africa (partly because of the continent’s extreme isolation in the Eocene). If, as its discoverers claim, *Eosimias* is a very primitive anthropoid ‘monkey’, the earliest origins of anthropoids must lie in Asia, which is also where tarsiers, the closest relatives of anthropoids live (as well as the tree shrews and flying lemurs, the primates’ closest relatives). Fossil tarsiers of similar age to *Eosimias* have also been found in Asia. Even the fact that living tarsiers survive only in tropical Asia implies support for the idea

Tentative composite phylogenetic tree for African primates (assembled from Steiper & Young 2006, Bininda-Emonds *et al.* 2007, Janečka *et al.* 2007).



that, at the very least, a proto-anthropoid ancestor entered Africa from Eurasia. The supposed divergence between Asian eosimiids and African anthropoids has now been narrowed to some time during the Paleocene (65.5–55.8) (Ciochon & Gunnell 2006). Just how tarsier-like that ancestor was remains debatable, but the ultimate immigrant status of anthropoid primates in Africa has become much more plausible than it was a few years ago.

North African fossil primates are few. Unless we include *Altatlasius* as a precursor, early fossil strepsirrhines have yet to be found. The fossil primates documented so far in Africa are localized and far from the supposed equatorial heartland. None the less, it can be inferred that primates flourished in Africa throughout the Oligocene (33.9–23.0 mya). The catarrhine–platyrrhine split almost certainly occurred in Africa before founders of the platyrrhine branch (now exclusively American) drifted across a much narrower Atlantic Ocean in the Eocene, some 43 mya (Steiper & Young 2006). Primates with anatomy comparable to that of some of the Egyptian fossils are thought to have founded the platyrrhine or New World primate fauna (Dagosto 2002).

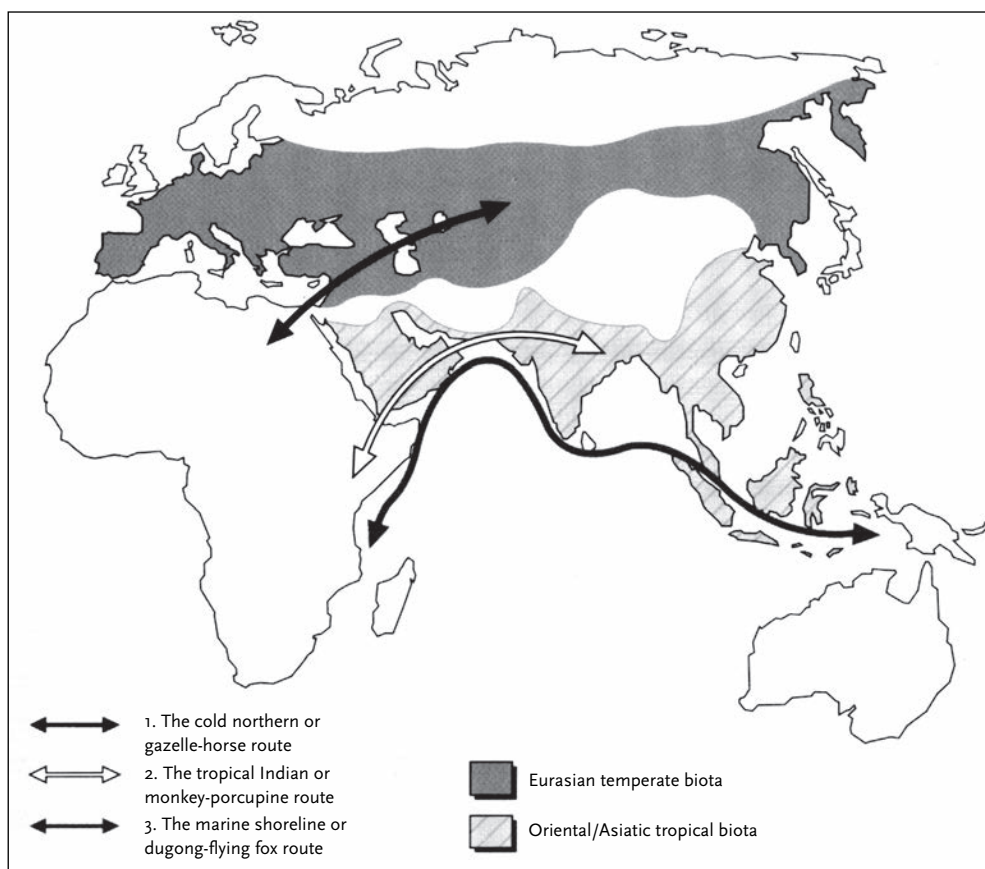
Some time in the mid-to-late Oligocene (28–25 mya), the early catarrhines gave rise to two lineages; one ancestral to cercopithecoid monkeys, the other to apes. The descendants of both branches were so successful that they eventually colonized other continents. Although the primate fossils from Egypt are relatively diverse, whatever richness there may have been throughout the rest of Africa is unknown until the latest Oligocene. This 10-million-year break, from which there are effectively no fossils, must have been a critical time for primate evolution.

A series of important Miocene sites in Kenya and Uganda document the separation of Cercopithecoidea and Hominoidea, and also an astonishing abundance and diversity of catarrhine lineages that have since gone extinct. Of these, the most notable is the diverse and abundant family of ‘ancestral apes’ or ‘proto-apes’, the Proconsulidae. An important diagnostic detail, manifesting an advance in forelimb versatility, is the hinging of the humerus on the ulna. It is this detail that allows the Proconsulidae to be classed in Hominoidea, although they differed both from apes and monkeys in many other respects (Walker & Shipman 2005).

A few Miocene catarrhines are known by nearly complete skeletons, showing that some were arboreal but slow and quadrupedal (*Afropithecus*), others were arm-swingers (*Nacholapithecus*) and yet others were mainly terrestrial (*Equatorius*) (Walker & Shipman 2005). *Griphopithecus*, a very close relative of *Equatorius*, may represent, and certainly exemplifies, the sort of early modern ape that spread out of Africa and flourished in Eurasia, where its remains have been recorded from deposits dated 17.0–16.5 mya (mid-Miocene) in Turkey and Germany (Begun 2000, Heizmann & Begun 2001).

Molecular data suggest that the hominoid ape lineage split from the cercopithecoid monkey lineage some time during the mid- to late Oligocene (31–23 mya). Interestingly, hominoids are abundant in north-east African Miocene fossil sites, cercopithecoids are rare. Why the discrepancy? Were cercopithecoid monkeys more abundant anywhere else? Africa is a vast continent with comparatively few fossil sites, so it is not altogether surprising that fossils of early Cercopithecoidea have so far escaped discovery. This is especially so if southern or south-eastern Africa was the region for their differentiation (the rationale for which is discussed in Volume I, p. 80 and in subsequent profiles, pp. 90 & 155). The pre-eminence of apes was eventually overtaken by cercopithecoids. So far as we can deduce from fossils, the pioneers of this lineage were the now extinct Victoriapithecinae. Prior to 10 mya (mid-Miocene), this lineage split into the Colobinae and the Cercopithecinae. Colobinae fossils are common until the Pleistocene (1.8 mya) but virtually all fossil species of colobine eventually went extinct. Still later, the cheek-pouch monkeys, the Cercopithecinae (another lineage with likely south-eastern Africa origins that are hidden from the fossil record) came to dominate the scene, as they do today. These developments are discussed in the profiles that follow.

African forests of today contain five main primate groups: anthropoid apes, colobines, cercopithecines, lorises and galagos. Their distinctness at the generic level from Asian primate communities has been influenced by a biogeographic peculiarity. This is the existence of a ‘filter’, a semi-arid belt lying between Africa and Asia, that has blocked exchanges between forest-adapted faunas since the Oligocene (25 mya) and possibly even earlier. In particular, no forest-dependent primate has entered or left Africa since at least the Oligocene.



Africa–Eurasia diffusion routes. Primates probably followed the ‘tropical’ route.

The semblance of such an exchange might be suggested by tree-living mammals, such as squirrels that exist on both sides of the barrier, but all such immigrants can be shown, or inferred, to have derived from ancestors that were not wholly forest-adapted. These founding stocks were sufficiently versatile to cross by way of the narrow corridors that have periodically connected Asia and Africa. The filter has operated both ways, with less forest-limited primates leaving Africa to found Asian radiations. This, undoubtedly, explains the presence of apes, colobines and macaques in Asia, and may also apply to the lorises.

A significant complication of this pattern is that once an immigrant from Eurasia had dispersed as far south as the tropics, it was faced by an established community of true rainforest mammals. A combination of competition, disease and pre-adaptation to non-forest environments probably inhibited or slowed down successful invasion of the forest. On the other hand, for populations living in non-forest corridors, fluctuating climates must have periodically engulfed non-forest populations living in drier ‘corridors’ as forests expanded from both sides of the corridor. Such enforced exposure of Eurasian immigrants to African forest conditions would have exerted strong selective pressure and probably assisted the process of adapting (or ‘re-adapting’!) to forest life.

From the perspective of human evolution, the most significant of all these exchanges was the emigration of African apes to Eurasia during the early Miocene (19–17 mya, when the ‘filter’ was less arid) and the eventual ‘return’ of a versatile Eurasian ape about 10.5 mya ago, or earlier. This ‘out-of-Africa-and-back’ exchange best explains the evolution of modern apes and hominins in Africa (Stewart & Disotell 1998, Begun *et al.* 1997, Kingdon 2003). The immigrant

might have resembled *Anoiapithecus brevirostris*, a Eurasian tree-ape that shared its ancestry with the orang-utans (*Pongo*), or, perhaps, a descendant of the same lineage as *Pierolapithecus catalaunicus*. This medium-sized ape was recently described from a fossil in Spain from 13.0–12.5 mya (mid-Miocene) and is distinguished by having short, straight digits and mobile, typically ape-like, shoulders. Whatever its precise origins, the immigrant ape was ancestral to at least three distinctive lineages. One led to the gorilla (*Gorilla*) clade, while the other two led to the closely related chimpanzee (*Pan*) and human (*Homo*) clades. The success of this ape might have been helped by a well-developed strategic intelligence.

Such an interpretation is hotly contested by some authors (Wrangham & Pilbeam 2001, Bernor *et al.* 2004), who believe that modern African apes derive from a resident African lineage. This is discussed elsewhere in this volume (see p. 35).

The separation of primate lineages into arboreal equatorial populations living, for the most part, in the forests of Central and West Africa (an area unseparated by natural barriers from drier habitats to the north), and terrestrial or semi-terrestrial ones (baboons, savanna monkeys and some galagos) in southern and south-eastern Africa, has many historical, evolutionary and ecological dimensions that have yet to be addressed. The nature of this forest/non-forest, centre-west/south-east dichotomy has many implications for our understanding of the dynamics of primate evolution even though contemporary species are distributed over much wider areas. We hope that the profiles in this volume help stimulate the further research that is needed.

Jonathan Kingdon & Colin P. Groves

Suborder HAPLORRHINI – Haplorrhines: Tarsiers, Monkeys, Apes, Humans

Haplorrhini Pocock, 1918. Proc. Zool. Soc. Lond. 3: 719–741.

In Africa, the Haplorrhini embraces all the Catarrhini or Old World monkeys, great apes and humans. The other (extralimital) members of this group are the Platyrrhini (or New World monkeys) and the Tarsiidae, or Oriental tarsiers. In Africa there are two families, 18 genera and some 73 species of haplorrhines.

Today the majority of species are confined to forests in the tropics but a few species, notably the baboons and savanna monkeys, occupy the temperate south and relatively dry areas south of the Sahara, sometimes with striking success. Of others, only humans have escaped the ecological constraints that limit the ranges of most contemporary African haplorrhines.

Haplorrhines have all the traits enumerated in the profile of Primates but have larger brains than Strepsirrhini and, in general, are of larger size, with more species having partial or wholly terrestrial habits.

All African species are diurnal. In general, diurnal and frugivorous species have greater acuity in daylight vision (having differentiated the structures of the inner eye to become more sensitive to colour and to particular wavebands). Most platyrrhines (except for howler monkeys *Alouatta*) have only a single medium/long-wave-sensitive locus, which is on the X chromosome, but there are two or (in some species) more alleles at this locus, so that whereas all males are dichromats, some (or even most) females are trichromats. In catarrhines (and independently in *Alouatta*) the medium/long-wave-determining locus has split into two, so that potentially all individuals are trichromats, males as well as females. Many interesting contributions on this topic are found in *Anthropoid Origins: New Visions* (Ross & Kay 2004). One genus of South American monkeys, the owl monkeys *Aotus*, has become nocturnal (filling the galago niche in Amazonian forests). Interestingly, *Aotus* eyes and orbits have greatly enlarged and reverted to becoming close to monochromatic, so the animals have greatly reduced colour vision. This reversion and the differences between Old World and New World monkey vision raises many interesting questions about the selective forces operating on primate visual apparatus (Jacobs 1993, Wright 1996).

The South American monkeys also include a dwarf marmoset that illustrates a very significant evolutionary process, heterochrony or, in this case, paedomorphosis by progenesis (Groves 1989), that could also be operating, but not so obviously, among some African primates, notably talapoin monkeys (*Miopithecus* spp.), and possibly Dryad Monkey *Cercopithecus dryas*. Most marmosets have a cryptic agouti-patterned coat and 'babyish' paedomorphic appearance while they are juveniles and the Pygmy Marmoset *Callithrix pygmaea* is no exception, being dull khaki and growing at the same rate as its larger congeneric, the Common Marmoset *C. jacchus*. At about 12 months old, Pygmy Marmosets suddenly stop growing and abruptly become sexually mature. They stay this way for the rest of their lives, resembling dwarfed, immature versions of their closest relative. Natural selection can, therefore, alter the setting of biological clocks over a large number of features, as in this case, or can operate on



Infant Patas Monkey *Erythrocebus patas*. Typical signs of paedomorphism are a diminished face and an enlarged brain.

a very few features, or perhaps a single feature, in others. Thus, selection for particular features, in this case ones that already exist in the ontogeny of the animal (e.g. small size, cryptic coat colour and squeaky vocalizations) can serve to open new niches within an established primate community.

A similar mechanism may well have operated among the ancestors of *Miopithecus*, where the adults most resemble juvenile Patas Monkeys *Erythrocebus patas* (see illustration p. 251). While both *Miopithecus* and *Erythrocebus* have, today, greatly diverged both morphologically and ecologically, it appears that they derive from a common ancestor (Dutrillaux *et al.* 1980). Paedomorphism in talapoin monkeys may, therefore, have its roots in a similar selective process as that which gave rise to the Pygmy Marmoset.

Similar processes are also likely to have operated in the evolution of another haplorrhine lineage, that of the Hominae. Modern Humans have many paedomorphic traits that are most easily illustrated with comparisons between adult human faces and those of juvenile apes. In this instance, juvenile appearance may be but one aspect of traits that have been favoured by selection, the others being less easily characterized aspects of juvenilia, such as psychological interdependency, curiosity, playfulness, susceptibility to social learning, and attraction to other group members. In any event, there is sufficient evidence to suggest that heterochrony and selection for paedomorphic traits is common in the Haplorrhini, with substantial implications for understanding the evolution of morphology and behaviour in this major group of mammals.

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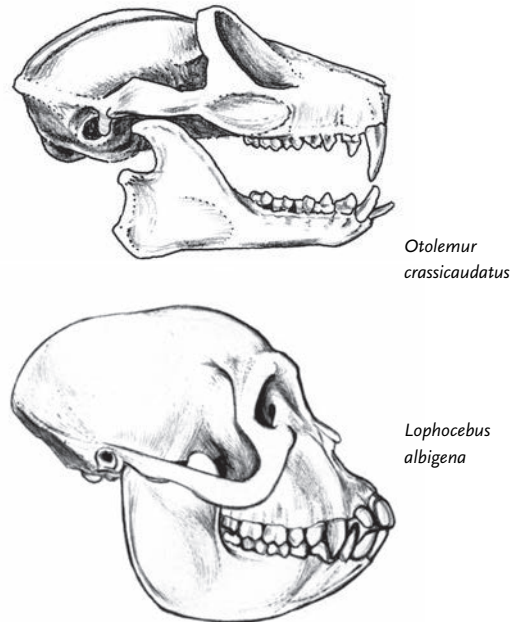
Hyporder ANTHROPOIDEA (Infraorder: SIMIIFORMES) – Anthropoids: Monkeys, Apes, Humans

Anthropoidea Mivart, 1864. *Medical Times* 1: 672.

Within the suborder Haplorrhini, the hyporder Anthropoidea (or infraorder Simiiformes) serves to distinguish the Old World monkeys, the New World monkeys (extralimital) and the hominoids from the infraorder Tarsiiformes and a third, extinct, infraorder, the Omomyiformes, which embraces a large group of fossil primates. This distinction reflects the biogeographic history behind the radiation of Primates. Although a fragmentary tarsier fossil, *Afrotarsius*, has been described from the Oligocene (33.9–23.0 mya) of Egypt, and another fragment from Ethiopia, their identification is challenged by Beard & Klinger (2005), who consider that the Tarsiiformes are an exclusively Eurasian group, a region in which the living and diverse genus *Tarsius* has been supposed to occur continuously since at least 45 mya (mid-Eocene).

By comparison with Strepsirrhini, Anthropoidea can be diagnosed by less reliance on scent and more on vision. They lack a reflecting tapetum and have a greater degree of colour vision. The lachrymal bone lies within the orbit rather than outside it. The two halves of the mandible fuse together early in life (probably associated with a more vertical action of the incisors, which number two in each quadrant). Canine teeth tend to be larger and have deeper rooting. The three molars of each quadrant tend to have a squarer form. Most anthropoids are larger than most extant strepsirrhines.

From an African perspective, the presence of Anthropoidea goes back to some uncertain and hotly contested dates when a small ancestor to all the living members of this group found its way to a peculiarly isolated African land mass. E. Seiffert (pers. comm.) thinks it possible that fossil fragments of *Altiasius* from 56-million-year-old late Paleocene deposits in North Africa (Ouarzazate Basin) could be stem anthropoids (also see Godinot & Mahboubi 1992, Beard & Klinger 2005, Seiffert *et al.* 2005a). This implies that anthropoid origins could be as early as the late upper Cretaceous. Steiper & Young (2006) calculate a molecular divergence date of 77.5 mya within a range of 97.7–67.1 mya (mid- to late Cretaceous), while Pennisi (2007) provides an estimate of 71 mya. These dates are much older than those proposed by Ciochon & Gunnell (2006), who put the divergence between Asian Eosimiids and Anthropoidea in the Paleocene (65.5–55.8 mya), and Gillman (2007), who estimates a 57-million-year-old origin for the Anthropoidea. Miller *et al.* (2005) think the fossil evidence showing a late Eocene presence in North Africa accords with an African origin for anthropoids. Tabuce & Marivaux (2005), instead, propose a mid-Eocene migration of an anthropoid ancestor to Africa.



Skulls of strepsirrhine *Otolemur crassicaudatus* and anthropoid *Lophocebus albigena*. Simple rings surround strepsirrhine eyes whereas *Lophocebus* eye sockets are typical of all anthropoids in enclosing the eyes in bony cups.

After radiating within Africa, a single rafting established the ancestor of all New World primates in South America. The date of this event (in which the most plausible agency would have been a floating 'island' of forest trees) has been dated to 42.9 (52.4–37.3) mya (mid- to late Eocene) by Steiper & Young (2006). At 44 mya, Pennisi (2007) offers an estimate that is well within this range and a time when the Atlantic was very much narrower than it is today, particularly between today's Guinea coast and north-eastern Brazil. Gillman (2007) has, instead, estimated 32 mya (early Oligocene), when the Atlantic had become quite wide.

Among the Catarrhini, the two superfamilies, the Cercopithecoidea and the Hominoidea, diverged within Africa during the Oligocene, a radiation that is discussed in following profiles. Much later, and in succession, apes, colobines, macaques and hominins emigrated to Asia, as is detailed in the following profiles. This poses numerous challenging puzzles, which are only beginning to be addressed by scientists today.

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Parvorder CATARRHINI – Catarrhines: Old World Monkeys, Apes, Humans

Catarrhini Pocock, 1918. *Proc. Zool. Soc. Lond.* 3: 719–741.

Catarrhini embraces the descendants of some primates that remained and flourished in Africa after the ancestors of Neotropical monkeys had left. Later, during the Oligocene (33.9–23.0 mya), this lineage gave rise to the two superfamilies Cercopithecoidea and Hominoidea.

As the name implies, the catarrhines share simple down-pointing (Greek *kata*) nostrils, which have only a narrow septum between them, a feature that distinguishes them from the New World

platyrrhine, or ‘flat-nosed’ monkeys. Other features shared by all catarrhines are the reduction of the premolars to just two in each half of each jaw, and the development of true opposability of the thumb, such that the thumb can be rotated until its pulp faces that of the index finger.

Colin P. Groves

Superfamily HOMINOIDEA – Anthropoids: Apes, Humans

Hominoidea Gray, 1825. *Annals of Philosophy* 10: 338.

The superfamily Hominoidea embraces all the surviving apes, including gibbons and humans, as well as some fossil groups that have left no descendants (Afropithecidae, Oreopithecidae, Proconsulidae). In this, as in other aspects of primate higher taxonomy, we follow Groves (1989, 2001).

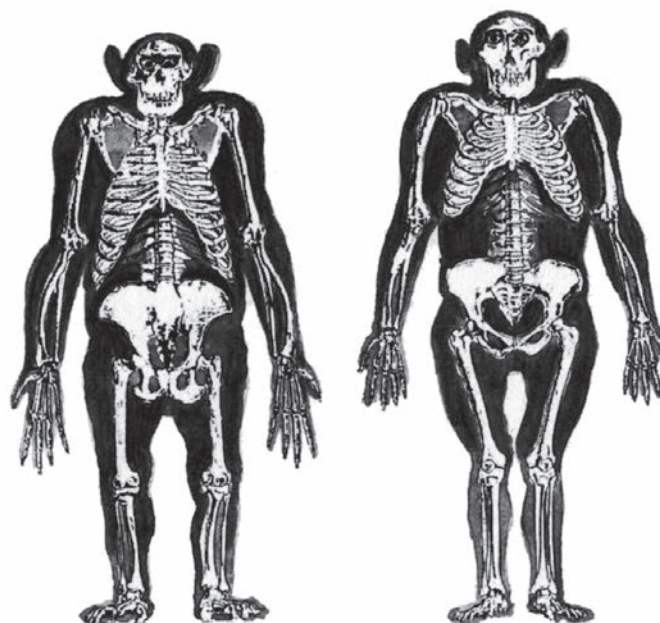
Of living primates, we include the extralimital orang-utans (*Pongo*), together with the African great apes (*Gorilla* and *Pan*) and humans (*Homo*), in the family Hominidae, but we exclude gibbons (Hylobatidae). We place the African biogeographic entity (African apes and humans) in the subfamily Homininae and reserve the tribe Hominini for the many taxa of bipedal apes and proto-humans that flourished in Africa until quite recent times. For Africa, the Hominoidea comprises three extant genera and five extant species.

Conservative and homocentric taxonomists argue that these rankings give far too little taxonomic weight to the peculiarity of humans. Until relatively recently, humans had been placed in their own family, leaving the great apes in a paraphyletic family Pongidae; such an arrangement sacrifices the (phylogenetic) information content of taxonomy for mere convenience, with an anthropocentric flavour.

A school of taxonomists who argue for a strict time-ranked classification (Schneider *et al.* 1997, Goodman *et al.* 1998) would rank Hominoidea as no higher than a family because this grouping probably diverged from the Cercopithecoidea later than the Oligocene/Miocene boundary (23 mya; see temporal/phylogenetic tree of hominoid relationships on p. 27). Strict adherence to such a system might well, as Goodman *et al.* (1998) argued, put humans and chimpanzees in the same genus and would lump many very distinctive primates in a small number of genera. While this may, in the end, prove to be justified, in the interim we feel it best to remain conservative. We have, therefore, retained most well-established genera and subgenera, and even recognized some controversial new ones.

The divergence between hominoids and cercopithecoids is of special interest because, on present evidence, it occurred *within*

Africa at a time when the continent was particularly isolated from other land masses. From fossil anatomy we can correlate differences in body form and gait with several ecological, climatic and behavioural differences. The late Oligocene (23 mya) was a period of global cooling, preceded by the first formation of an Antarctic ice-sheet and a substantial retraction of tropical forest in Africa (see ‘Africa’s Environmental and Climatic Past’, Chapter 4, Volume I). The proto-cercopithecoids seem to have adapted to these changes in climate by becoming longer-backed, more terrestrial, faster, and better able to forage and escape predators in more open habitats.



Body proportions as displayed in schematic skeletons of (left) Robust Chimpanzee *Pan troglodytes* and (right) *Australopithecus (Praeanthropus) afarensis*.

The biogeographic dimension to this divergence can be related to the outline discussed in the introductory chapter on mammalian evolution (Chapter 6, Volume I). Because a large proportion of dry, more temperate Africa was south of the Equator during the Oligocene (more so than today because the continent has meanwhile drifted northwards), there are good grounds for supposing that the cercopithecoids had mainly south-eastern origins.

In this divergence, the hominoid lineage can be seen as the more conservative in the sense that they remained the most committed arborealists, with very mobile joint articulations and compact, short-backed trunks. Certainly some forms became adapted to less than wholly forested habitats, but, in general, the early apes seem not to have readily accommodated to habitats where travelling and foraging on the ground was required. Because closed forests, with year-long supplies of plant and animal foods, are ultimately dependent on tropical temperatures and rainfall, apes, then as now, probably preferred equatorial forests and/or dense woodlands along a centre-

west axis. It is, therefore, possible that a catarrhine ancestral stock split along latitudinal lines and that hominoids dominated northern and equatorial Africa (remembering that there was no Sahara desert at that time!), while the earliest cercopithecoids were of south-eastern provenance. That it was hominoids, not cercopithecoids, that first got out of Africa (ca. 19 mya) lends increased weight to this hypothesis.

The Hominoidea are easily distinguished from their closest relatives, the Cercopithecoidea, by such characters as the lack of a tail, the broad rib cage with the scapula at the back, and the greatly enhanced rotatory ability of the shoulder joint. The Hominoidea lack the outstanding dental specialization of the Cercopithecoidea – the bilophodont molars (and premolars, the sectorial anterior lower premolar, of course, excepted); the morphology of the postcanine dentition in the Hominoidea retains an overall plesiomorphic condition.

Colin P. Groves & Jonathan Kingdon

Family HOMINIDAE

HOMINIDS: GREAT APES, HUMANS

Hominidae Gray, 1825. Annals of Philosophy 10: 344.

Homininae		
<i>Gorilla</i> (2 species)	Gorillas	p. 35
<i>Pan</i> (2 species)	Chimpanzees	p. 53
<i>Homo</i> (1 species)	Humans	p. 74

The Hominidae, in the sense that we use it in this volume, follows the taxonomic arrangements of Groves (2001). This taxon essentially clumps all the larger apes, Asiatic and African, and humans. Linnaeus (1758) placed humans in the order Primates, but most of his successors demurred, preferring to set apart ‘man’ in a separate order, Bimana. The most conspicuous exception was Gray (1825), who first recognized and named the family Hominidae, which he divided into two sections, as follows:

- † Tail none. 1. Hominina: *Homo*. 2. Simiina: *Troglydites*, Geoff. *Simia*, Lin. *Hylobates*, Illiger.
- †† Tail long or short (section containing Old World monkeys).

Troglydites was the generic name at that time used for the chimpanzee, and *Simia* for the orang-utans, while *Hylobates* is the generic name still in use for one of the genera of gibbons. Gray was thus well ahead of his time, not only in including humans in the Primates, and in the group we would now call catarrhines, but in the same family as the great and lesser apes. Today, it is almost universal to place the great apes in the Hominidae, and has been so since the 1980s, but it was not until the last years of the twentieth century that the gibbons were also included in the Hominidae (Goodman *et al.* 1998), although they are still more usually placed in a separate family, Hylobatidae, though within the super family Hominoidea along with the Hominidae and some fossil families.

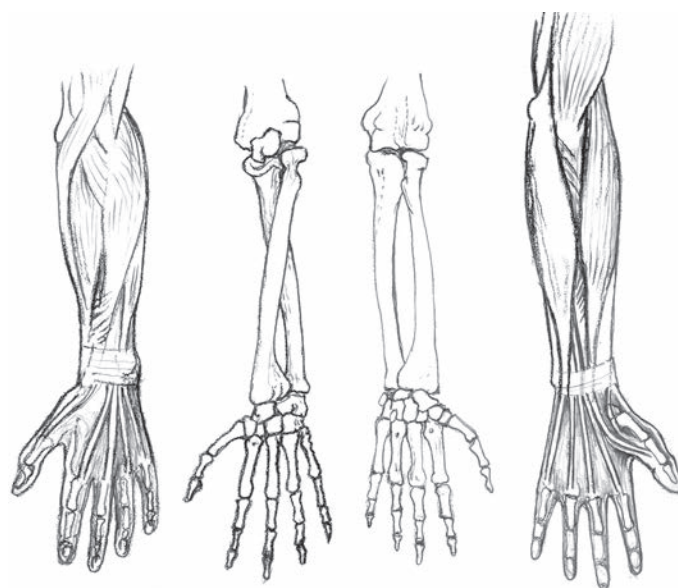
The origins of this group are deeply controversial, with some scientists believing that the ‘great apes’ arose and differentiated

within Africa and only later entered Asia. Stewart & Disotell (1998), however, showed that, according to the fossil evidence, although the Hominidae probably arose within Africa, an initial diversification in Asia is much more parsimonious. Certainly the evidence for gibbons (Hylobatidae) being of wholly Asian origin is generally accepted (there has never been any evidence for African gibbons or proto-gibbons). Furthermore, Eurasian fossils (notably *Oreopithecus* and *Lufengpithecus*) imply that the Ponginae (to which the orang-utan belongs) and gibbons share common Eurasian roots. It seems more probable, therefore, that the African apes arose from a Eurasian ‘returnee’ than that they arose from an unknown lineage within Africa.

The family Hominidae contains not only *Gorilla*, *Pan*, *Homo* and *Pongo*, but also many fossil forms, notably *Sivapithecus*, *Dryopithecus* and *Graecopithecus* in Asia and a variety of later African fossil taxa (see profiles for Homininae and Hominini). Today, Asian and African apes range through quite restricted localities within the total rainforest and neighbouring areas of their respective continents. This restriction is undoubtedly partly due to competition with other primates, including humans. Ranges are also likely to have been pruned by climatic fluctuations, even tectonic events. In addition, the heavyweights, orang-utans and gorillas, seem to be poor dispersers, a limitation that earlier, lighter and more versatile apes, such as *Dryopithecus* spp., seem to have escaped. For example, *Dryopithecus* fossils are extremely widespread and numerous in Europe between 13 and perhaps as little as 9 mya (mid-Miocene). The possible significance of such differences is discussed in the Homininae profile. It suffices here to point out that a newly discovered great ape, the nearly 10-million-year-old *Nakalipithecus nakayamai* (Kunimatzu *et al.* 2007), from a late Miocene deposit in Kenya, most resembles the Eurasian *Ouranopithecus* and is consistent with the ‘returnee hypothesis’ (Disotell & Tosi 2007).

The most obvious features shared by all members of the family Hominidae include the relatively shortened, more robust canine teeth of the males, the presence of at least the rudiments of a metaconid (second cusp) on the anterior lower premolar, the reduced hair density on the body, the reduction in the number of thoracolumbar vertebrae and the short and stout vertebral bodies, the deep mandible (especially its symphysis), and the separation of the wrist bones from the ulna by a meniscus (giving the wrist greater flexibility).

Colin P. Groves & Jonathan Kingdon



Pronation and supination of the human hand is made possible by rotation of the ulna and radius.

Subfamily HOMININAE – Hominins: African Great Apes, Humans

Homininae Gray, 1825 *Annals of Philosophy* 10: 338.

This subfamily is primarily made up of a large number of fossil genera (extinct hominins, australopithecines and others), with only Modern Humans and African apes surviving. Groves (2001) and Grubb *et al.* (2003) list two species of *Gorilla*, two species of *Pan* and one species of *Homo*. We follow the same arrangement here. These five species are the sole survivors of a much larger intra-African radiation of large apes and hominins.

The detailed anatomy of this African radiation shows the following differences from their close Asiatic relatives, the orang-utans (*Pongo*). The premolar row is shortened compared to the molars. The forearm is shortened, the brachial index being below 100. In the wrist, os centrale is fused to the scaphoid; the talus (astragalus) is nearly as broad as it is long; the calcaneus has a long, broad 'heel'. The axillary organ, a coalescence of apocrine glands in the armpit, is large and elaborated. The scalp is more densely haired than the body. The intestine is long, more than nine times the head and body length. These features appear to be related to a more semi-terrestrial life compared with a basic rainforest arboreal niche, and some de-emphasis (notably among some gorilla populations and among humans and their ancestral lineage) of frugivory. The broad talus and the developed 'heel' indicate efficient locomotion on the ground, and the shortened forearm and more compact wrist strongly suggest a weight-bearing role for the forelimbs. Tolerance of non-forest environments is suggested by the thickly haired scalp, and the importance of a complex, compact social organization is indicated by the development of the axillary scent organ. The ability to subsist on terrestrial herbaceous vegetation (THV), during periods of scarcity of more preferred foods, is implied by the reversal of molar/premolar emphasis and by the lengthened gut.

In gorillas and chimpanzees, the 'weight-bearing role of the forelimbs' involves knuckle-walking, a unique form of locomotion seen in no other mammal. The weight of the foreparts is borne on the medial phalanges of the hand: not only is the proximal/medial joint held at a right-angle, but the entire wrist region must be held rigid, resisting the compressive forces that would tend to hyperextend the joints. There are both a specialization of the mid-carpal articulation (known as conjoint rotation) and a prominent dorsal ridge on the distal end of the radius, helping to stabilize the wrist and hand in knuckle-walking position. Given that gorilla and chimpanzee are not sister-groups, but rather chimpanzee and humans together form a sister-group to gorilla, it may be that the ancestor of the gorilla and the ancestor of the chimpanzee independently developed knuckle-walking specializations. The alternative hypothesis, that the common ancestor of the Homininae developed these specializations and that they were lost somewhere along the human lineage, is, however, more parsimonious. This prediction was verified by the Richmond & Strait's (2000) analysis of the distal radius of *Australopithecus anamensis* and *A. afarensis*, mid-Pliocene (3.6 mya) members of the human lineage, in which they demonstrated the persistence of knuckle-walking traits.

Based on molecular data, the Ponginae and Homininae lineages separated 16.5–12.5 mya (mid-Miocene), gorilla and human–chimpanzee diverged 12.0–7.1 mya (late Miocene), and the human–chimpanzee split occurred 7.0–5.5 mya (Raaijmakers *et al.* 2005, Perelman *et al.* 2011, Roos *et al.* 2011, Scally 2012). There is claim (Suwa *et al.* 2007) of a possible gorilla ancestor, *Chororapithecus*, from Ethiopia, dating at 10.5–10.0 mya (the claimed dental similarities to the gorilla are real enough, although more evidence is needed to show whether they are genuine synapomorphies or convergence).

The differences between surviving African apes and Modern Humans formerly seemed much greater than could easily be explained. None the less, when ape and human anatomy was examined in detail virtually all the physical differences were long ago shown to be ones of changed proportion or differing linear dimensions. In almost every case these changes have come to be

plausibly correlated with environmental or behavioural changes during the evolution of both African apes and humans. Meanwhile, an ever-richer treasure-trove of fossils has revealed a diverse number of Homininae, illustrating many intermediate forms between apes and humans, as well as some surprising offshoots (see Hominini and illustrations on p. 71).



Hands and 'small object precision handling', as the interface with their environment, drove hominin evolution.
Left: Top to bottom, ten drawings of ape hands. *Right:* Top to bottom, six drawings of human hands.

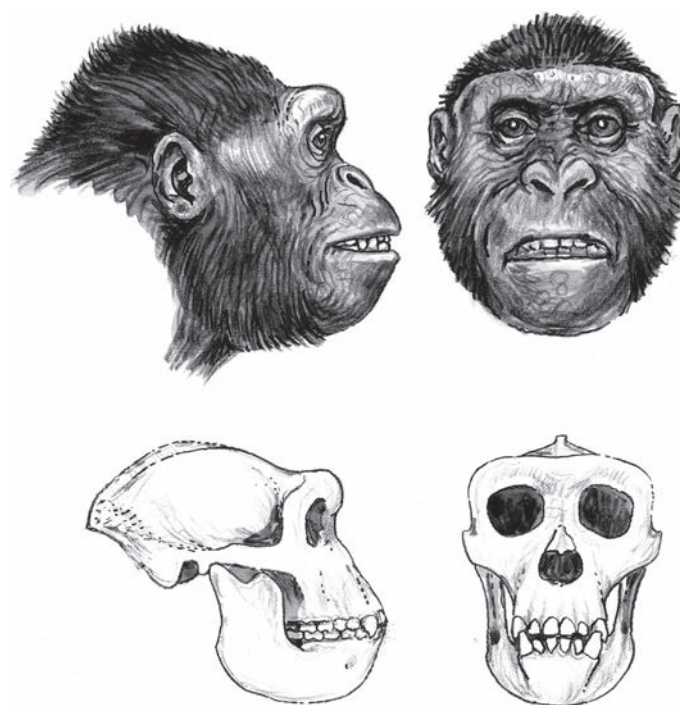
Reconstruction of 'Toumai' *Sahelanthropus tchadensis*.

Top: Supposed appearance.

Bottom: Skull (as reconstructed in Kingdon 2003).

Prominent among these fossil members of the Homininae are some European genera, notably *Anoiapithecus*, and also *Dryopithecus* and *Ouranopithecus*, which are robust with heavily built facial skeletons, including supraorbital tori. The second of these (the correct name may in fact be *Graecopithecus*), known from approximately 9 mya deposits in Greece, may be a very primitive member of the gorilla lineage, but, as Begun (2002) has pointed out, the similarities – mainly related to robusticity – may be symplesiomorphic. This makes sense in the light of the extreme robusticity shown by the controversial *Sahelanthropus*, which has been represented as the earliest evidence for separation of the human lineage (Brunet *et al.* 2002). It has also been argued, however, that *Sahelanthropus* is not clearly a member of any of the separate hominine lineages but rather represents a 'pre-split' population close to the common stock of African apes and humans (Kingdon 2003, Wolpoff *et al.* 2006).

Colin P. Groves & Jonathan Kingdon



Tribe GORILLINI

Gorillas

Gorillini Frechkop, 1943. Exploration du Parc National Albert, Mission S. Frechkop (1937–1938). 1. Mammifères, p. 11.

Because there has been a generally felt need to differentiate humans and bipedal apes from quadrupedal ones, the former have tended to be placed in the tribe Hominini. This has left the affinities of quadrupedal apes unanswered. Groves (1986) has pointed out that cladistic rules absolutely prohibit the clustering of gorillas *Gorilla* spp. and chimpanzees *Pan* spp. into a single group that does not include Modern Humans *Homo* (as was proposed by Andrews 1987). Any cladistically acceptable arrangement, therefore, requires there to be two tribes: Gorillini and Panini. As far as the living fauna is

concerned, both tribes are synonymous with the genera *Gorilla* and *Pan*, and for most intents and purposes are effectively redundant. The diagnosis that follows is, therefore, appropriately brief. The tribe Gorillini has a single extant genus. A second genus, *Chororapithecus*, provisionally allocated to this tribe, is known from the late Miocene (10.5–10.0 mya) (Suwa *et al.* 2007) and is mentioned in the profile for *Gorilla*.

Colin P. Groves

GENUS *Gorilla*

Gorillas

Gorilla I. Geoffroy, 1852. Comptes Rendus de l'Académie des Sciences, Paris 34: 84.

Polytypic genus. In the latter half of the nineteenth century and early twentieth century, a large number of species and subspecies of the genus *Gorilla* were described. Coolidge (1929) united all of them into a single species, *Gorilla gorilla*, with two subspecies, namely *G. g. gorilla* and *G. g. beringei*, regarding all the other named taxa as synonyms of one or the other. Subsequent authors have mostly maintained the single-species arrangement; the main exception being Schultz (1934), who regarded Coolidge's two subspecies as distinct species, although it seems that he may have inadvertently allocated a few specimens to the wrong species. It was not until over half a century later that Groves (2000b), once again arguing for the adoption of a Phylogenetic Species Concept, separated *G. gorilla* and

G. beringei at the full species level. Diagnoses of these two species, and their subspecies, are given in Groves (2001).

A brief history of gorilla taxonomy, with something of the rationale behind the original description of the different species in the early phase of gorilla taxonomy, is presented in Meder & Groves (2005).

Gorilla gorilla (Western Gorilla) is found mostly in lowland forest from the Congo–Oubangui R., DR Congo, westwards to the coast. The Sanaga R., Cameroon, is the northern border of the continuous area of distribution. There are outlying populations to the north-west in the Ebo Forest to the north of the Sanaga R. and in the montane forests of Cross River District on the Cameroon–Nigeria border. *Gorilla beringei* (Eastern Gorilla, including, but not limited to, the

famous Mountain Gorilla) is confined to the forests, both lowland and montane, of Kivu District (CE DR Congo), the montane forests of the Virunga Mts (where DR Congo/Rwanda/Uganda meet), Bwindi Impenetrable Forest (SW Uganda) and, from here, westward across the Uganda/DR Congo border into the Sarambwe Forest.

The genus *Gorilla* is characterized by extreme sexual dimorphism, mature ♂♂ weighing at least two-and-a-half times as much as mature ♀♀, with much larger sagittal crests (very rarely absent in adult ♂♂, and present in only about 20% of adult ♀♀) and larger nuchal crests. Both sexes are dark in colour, the naked skin of the face, ears, chest, palms and soles being jet black (with occasional deep pigmented spots on the palms and soles); the pelage is jet black in *G. beringei*, and a deep blackish-brown, often with a red crown, in *G. gorilla*. In both species the mature ♂ has a grey to white 'saddle' on the dorsum; between the shoulders and the rump in *G. beringei*, but spreading back to the thighs in *G. gorilla*. Infants have a narrow white tuft of hair above the anus. The ears are remarkably small, but lobed. The nostrils are large, slightly raised above the level of the nose and upper lip, and often 'padded'.

The skull is not unlike that of *Pan* spp., but can be distinguished by the more anteriorly prominent, rounded supraorbital torus, continued from side to side across the glabella with almost no break. The lateral orbital pillars are likewise prominent and rounded. The interorbital pillar has a median ridge, which runs down the internasal suture.

The incisors are narrow and unspecialized, both upper and lower. The canines are elongated in adult ♂♂, more than in *Pan*. The molars are characterized by high crystalline cusps, with prominent crests running between them; the enamel is somewhat wrinkled, and thin, so that the dentine 'horns' penetrate considerably into the cusps. The cusps are peripherally situated on the occlusal surfaces, so that the central basin is wide; the upper molars have wide but short proximal and distal foveae, separated by the crests from the central basin. These features indicate an enhanced shearing function, related to their dependence on terrestrial herbaceous vegetation in the diet.

The thorax is very broad, widening very considerably from first to last rib. All vertebrae, but particularly the lumbar, are short and broad. The iliac crests are extremely broad, second only to *Homo*. The intermembral index (ratio of arm bones to leg bones) is about 112–120, higher than in *Pan*. The knuckle-walking characters are well developed, the hands are short and wide. The toes are short; the length of the heel, the length of the sole and the relative lack of divergence of the great toe are second only to *Homo* among the Hominoidea. These, and other terrestrial adaptations, have been described in detail, illustrated and tabulated by Sarmiento (1994).

Compared to other hominids, growth and development in gorillas is surprisingly rapid. Though the gestation averages 257 days compared to 228 days for Robust Chimpanzees *Pan troglodytes* (and 240 days for orangutans *Pongo* spp.), all the other parameters are shorter than for other hominids: interbirth interval (between surviving infants) around 4.2 years in *G. beringei* and 5.2 years in *G. gorilla*, compared to 5.4 years or more in *P. troglodytes*; age at weaning 4 years or less in *G. beringei*, 5–6 years in *G. gorilla*, cf. 4–5 years in *P. troglodytes*; menarche at 7.0–7.5 years in *G. beringei* and 6.5–8.5 years in captive *G. gorilla*, cf. 10–11 years in *P. troglodytes*; menstrual cycle 28 days in *G. beringei* and 32–33 days in captive *G. gorilla*, cf. 36 days in *P. troglodytes* (Groves & Meder 2001). Male gorillas reach the 'blackback' stage, when they are sexually but not physically (or

socially) mature, at age ten years in *G. gorilla*, perhaps even earlier in *G. beringei*, and reach the 'silverback' stage of full physical maturity at 18 years in *G. gorilla* (Breuer *et al.* 2009) and perhaps only 15 years in *G. beringei* (Watts & Pusey 1993). Groves & Meder (2001) calculated mean ages at death for *G. b. beringei* reaching maturity as follows: ♀♀: Virunga Mts, 24 years (but 32 years according to Harcourt & Stewart 2007a); ♂♂: Virunga Mts, 20–27 years (25 years according to Harcourt & Stewart 2007a). This compares with *P. troglodytes* at Gombe (W Tanzania) and Kibale (SW Uganda), where a ♀ who reaches maturity can be expected to survive into her early or mid-30s, and a ♂ to 29 years (Gombe) and 41 years (Kibale).

These are, of course, mean figures, but maximum achieved ages also seem low for *G. beringei*, the mid-40s, compared with the 50s in *P. troglodytes*. About ten years may have to be added to these maxima for captive individuals, although Harcourt & Stewart (2007a) note that gorillas run through their life history stages at much the same rate in captivity as in the wild, whereas chimpanzees grow and reproduce at much faster rates in captivity. These life history parameters are surprising because one would predict late weaning and age at maturity, long interbirth intervals and long life in large-bodied primates (Harvey *et al.* 1987). Groves & Meder (2001) argue that gorillas may be considered in the traditional sense to be r-selected. One would also, according to this scheme, predict large brain size, but in gorillas the encephalization index is actually less than for other hominids.

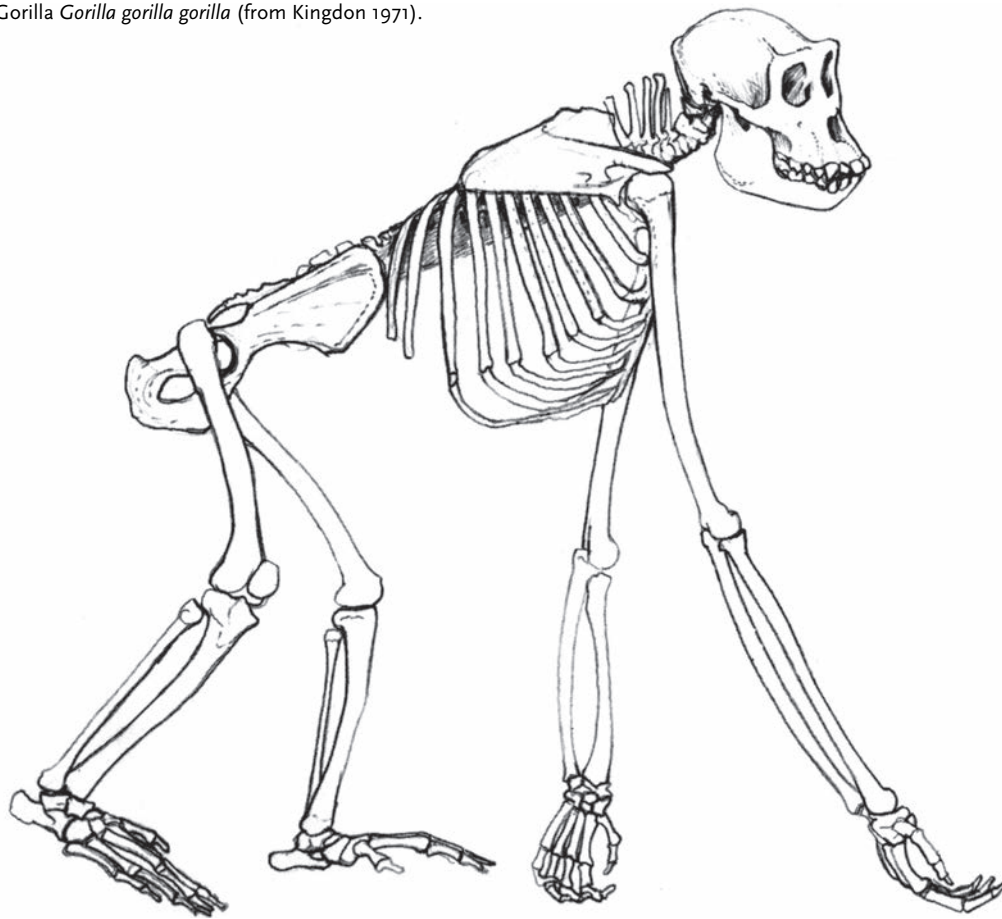
Until the twenty-first century, the gorilla lacked a fossil record. This recently changed: Pickford & Senut (2005) described a few, mostly fragmentary, teeth from Kapsomin and Cheboit in the Lukeino Formation of the Tugen Hills, Kenya, the same sites (dating to 5.9 mya) where the earliest known hominin, *Orrorin tugenensis*, occurs. More recently still, Suwa *et al.* (2007) described a new genus and species, *Chororapithecus abyssinicus*, from Chorora, Ethiopia, dated at somewhat over 10 mya; this has the characteristic crest formation, peripheral cusps and short mesial fovea of modern gorillas, but thicker enamel and lower cusps, and less developed crista obliqua, suggesting a primitive, presumably ancestral, morphology.

The distribution of gorillas today is strikingly disjunct: that of *G. gorilla* extends east as far as the Oubangui R., whereas that of *G. beringei* does not begin until east of the Lualaba R., DR Congo. Even within their distributional areas, both species show patchy distributions. *Gorilla g. gorilla* populations are quasi-continuous from the Congo R. estuary to the Sanaga R., then there is a considerable gap to the range of *G. g. diehli* to the north-west. *Gorilla beringei* populations are also quasi-continuous in the Kivu lowland and mountain regions of E DR Congo, while those of the Virunga Mts (i.e. *G. b. beringei*) and the Bwindi–Sarambwe Forest represent further isolates.

What caused the enormous gap between the distributional areas of the two species, and how long has it existed? Thalmann *et al.* (2005), using mtDNA, calculate that the two species separated 1.3 mya, and later (Thalmann *et al.* 2007), using 16 noncoding autosomal sequences, give a range of 1.6–0.9 mya. A more recent study puts the divergence time at 1.75 mya (Sclay *et al.* 2012). This presumably marks the time of some geographic disjunction, and Thalmann *et al.* (2007) point to geological changes during that period. Yet the fact that some of these mtDNA lineages are shared between the two species indicates that there has been more recent gene flow between them, i.e. that the ranges have been in contact again at one or more times since their



Individuality in the faces of gorillas *Gorilla*. Facial differences vary with region, age, sex and emotion (from Kingdon 1990).

Western Lowland Gorilla *Gorilla gorilla gorilla* (from Kingdon 1971).

initial separation. Thalmann *et al.* (2007) argue that this more recent gene flow was male-mediated and asymmetrical (predominantly from *beringei* to *gorilla*), and ceased about 77,700 years ago.

It is possible that the ranges of the two species may have approached each other again very recently. First, some (the exact number, whether three or four, is unclear) gorillas were said to have been shot near Bondo, on the Uele R., DR Congo, in 1898. As discussed by Hofreiter *et al.* (2003), these specimens, now housed in the Museum for Central Africa in Tervuren (Belgium), are indistinguishable morphologically from *G. gorilla* (despite having been referred to a distinct subspecies), and a mtDNA sequence obtained from one of them is nested within sequences of that species. There are uncertainties connected with the provenance of at least some of the specimens, and Hofreiter *et al.* (2003) doubt whether the locality is accurate, although this would not necessarily follow from their findings. It is certainly plausible that *G. gorilla* followed the expansion of the western central African rainforests north of the Grand Cuvette of the Congo R. during climatic amelioration at the end of the Pleistocene (10,000 years B.P.), and that one or more population isolates might have remained in northern DR Congo until very recently.

The question of what might limit the distribution of gorillas has been raised by Groves (1971), who noted that gorillas seem to largely avoid both marshy forest and monodominant *Gilbertiodendron* forest. The latter forest type has little ground vegetation, and permanent residence in that type of forest by most terrestrial herbivores, such as gorillas, is difficult or impossible. Hart *et al.* (1989) argue that

monodominant forests of this type are those that have remained undisturbed over relatively long periods. Strikingly, charcoal samples from what are now *Gilbertiodendron* dominated formations in the Ituri Forest indicate that these areas were mixed forest less than 1000 years ago (Hart, T. B. *et al.* 1996). The implication is that, over the course of long periods of climatic stability and minimal environmental (including human) disturbance, shade-tolerant species of poor dispersal ability, such as *Gilbertiodendron dewevrei*, would very gradually spread and take over from the mixed forest, limiting, if not excluding, herbivores such as gorillas.

When looking at distribution maps, it is striking that, with very few exceptions, red colobus monkeys *Procolobus* spp. occur only where gorillas do not. The gorilla heartlands of the western central African region and the Kivu/Central African Rift region are almost without red colobus, which on the contrary are abundant in the closed-canopy monodominant forests where gorillas are unable to exist. They appear to coexist only in a few regions: Kahuzi-Biega and Itombwe (E DR Congo), Ebo Forest, Ngotto (SW Central African Republic) and east of Motaba (NE Congo). It would be of great interest to know whether their apparent coexistence in these regions is broad-scale only, and the two taxa maintain separate micro-habitats, or whether there are indeed places where a silverback gorilla may look up and see a red colobus looking down at him.

Colin P. Groves

Gorilla gorilla WESTERN GORILLA

Fr. Gorille de l'Ouest; Ger. Westlicher Gorilla

Gorilla gorilla (Savage in Savage & Wyman, 1847). Boston Journal of Natural History 5: 417. Gabon Estuary, Mpongwe country, Gabon.

Taxonomy Polytypic species. The history of gorilla taxonomy is a long and complicated one, and is covered in detail by Groves (1966, 2003) and Sarmiento & Oates (2000). An overview of the taxonomy of the *Gorilla* spp. is presented in the Mountain Gorilla *Gorilla beringei* profile. Two subspecies of *G. gorilla* are recognized: Western Lowland Gorilla *G. g. gorilla* and Cross River Gorilla *G. g. diehli*.

Formally referred to as *G. g. gorilla*, recent morphological and molecular studies indicate that the Cross River Gorilla is as different from *G. g. gorilla* as is *G. b. beringei* from some populations of Grauer's Gorilla *G. b. graueri* (Oates 1998, Sarmiento & Oates 2000, Oates *et al.* 2003). Time of divergence ca. 17,800 years ago (Thalmann *et al.* 2011). As such, *G. g. diehli* was revived by Sarmiento & Oates (2000) and widely supported (Groves 2001, 2005c, Grubb *et al.* 2003, Oates *et al.* 2007, Sunderland-Groves *et al.* 2007, Nicholas *et al.* 2009, Oates 2011). Taxonomic status of gorilla populations in Ebo/Ndokbou, SW Cameroon, awaits clarification (Groves 2005a).

Synonyms: *adotes*, *africanus*, *castaneiceps*, *diehli*, *elliotti*, *gigas*, *gina*, *halli*, *hansmeyeri*, *jacobi*, *matschiei*, *mayêma*, *savagei*, *schwarzi*, *uellensis*, *zenkeri*. Chromosome number: $2n = 48$ (Romagno 2001).

Description Very large (adult ♂♂ ca. 170 kg, adult ♀♀ ca. 60 kg), small-eared, tailless, brown-grey or brownish-black, mostly terrestrial primate. Well-developed supraorbital ridges. Nose large, flattened. Nostrils large. Nasal septum with projection ('lip') above. Nasal openings nearer to mouth than to orbits. Eyes small, dark brown. Ears small, flat, black or brown. Pelage brownish-grey or brownish-black except crown, which is often brownish to reddish-brown. Bare skin of face, hands and feet black. Length, colour and distribution of hair variable. Adult ♂♂ have well-developed sagittal crest and completely greyish-silver 'saddle' on the back (i.e. 'silverback') and often on the thighs. Adult ♀♀ ca. 35% the weight of adult ♂♂ and lack a well-developed sagittal crest.

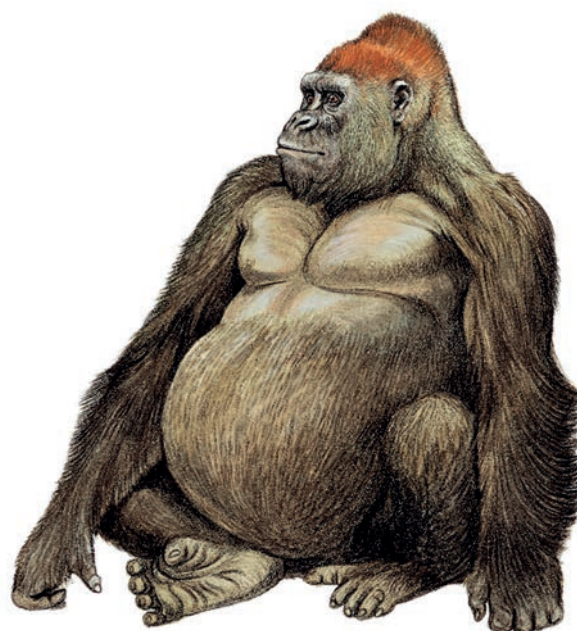
Western Lowland Gorilla *Gorilla gorilla gorilla* adult female and young.**Geographic Variation**

G. g. gorilla Western Lowland Gorilla. Occupies all of the range of *G. gorilla* except that portion in the Cross R. area on the Nigeria–Cameroon border. Longer/larger skull measurements. Adult ♂♂ from the 'coastal sample' ($n = 71$), which represent the smallest of the *G. g. gorilla* subpopulations: mean greatest length of skull = 296 mm (S.D. = 16.6); mean cranial length = 196 mm (S.D. = 13.7); face height = 146 mm (S.D. = 10.1); but relatively narrow mean biorbital breadth = 136 mm; and mean bizygomatic breadth = 174 mm (Groves 2001). Cheektooth surface area for adult ♂♂ from various sites: mean = 1098 mm² (S.D. = 103, range 954–1369, $n = 58$). Cheektooth surface area for adult ♀♀ from various sites: mean = 915 mm² (S.D. = 66, range 775–1042, $n = 28$) (Sarmiento & Oates 2000, Sarmiento 2003).

G. g. diehli Cross River Gorilla. Confined to the upper Cross R. forest on the Nigeria–Cameroon border. Shorter/smaller skull measurements (Sarmiento & Oates 2000, Groves 2001). Adult ♂♂ ($n = 25$): mean greatest length of skull = 183 mm (S.D. = 13.7); mean cranial length = 183 mm (S.D. = 13.7), face height 140 mm (S.D. = 7.4); but relatively broader mean biorbital breadth = 136 mm; and mean bizygomatic breadth = 176 mm (Groves 2001). Cheektooth surface area for adult ♂♂: mean = 957 mm² (S.D. = 84, 807–1159, $n = 32$). Cheektooth surface area for adult ♀♀: mean = 839 mm² (S.D. = 72, range 707–960, $n = 17$) (Sarmiento & Oates 2000, Sarmiento 2003).

Similar Species

Pan troglodytes. Sympatric below ca. 2300 m. Smaller (adult ♂♂ <55 kg). Ears relatively large. Sagittal crest absent or weakly

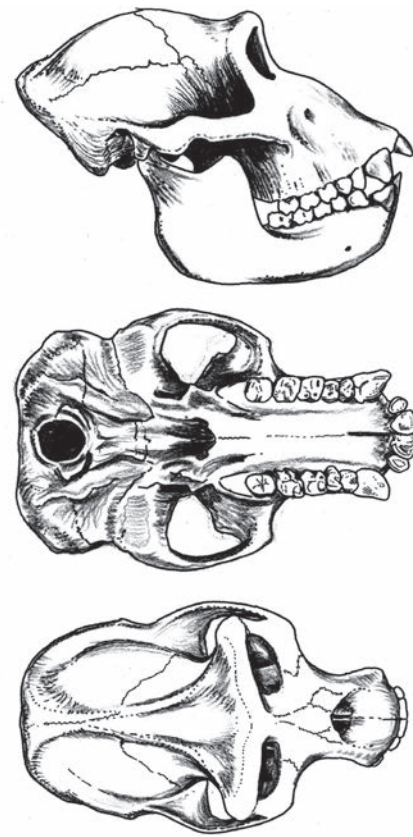
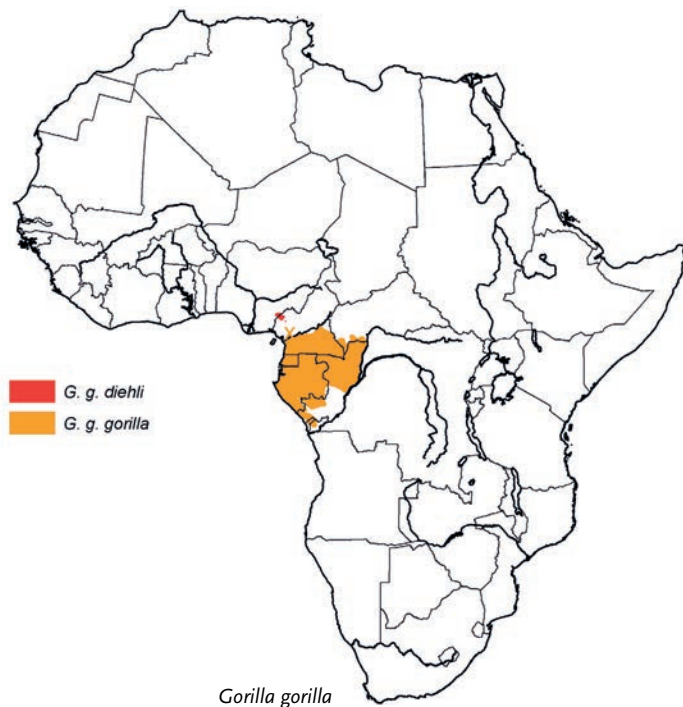
Western Lowland Gorilla *Gorilla gorilla gorilla* adult male.

developed in adult ♂♂. Nasal openings nearer to orbits than to mouth.

Distribution Endemic to western central Africa; Rainforest BZ. *Gorilla g. gorilla* distributed over six or seven countries from south of Sanaga R. south through S Cameroon, SW Central African Republic, mainland Equatorial Guinea (Rio Muni/Mbini) and Gabon, into extreme N Angola (Cabinda enclave) to Congo R., and east into W Congo and across the Sangha R. to about the Oubangui R. Western boundary is the Atlantic Ocean. The northern and southern boundary roughly defined by limits of the closed forest. Once resident in SW DR Congo, but probably now transitory in DR Congo. Extent of occurrence roughly 700,000 km² (Butynski 2001).

Gorilla g. diehli is the most northern and western subspecies of gorilla. Restricted to the upper Cross R. region on the Nigeria–Cameroon border about 260 km north of the range of *G. g. gorilla* (Lee *et al.* 1988, Oates 1998, Sarmiento & Oates 2000), and about 250 km north of the recently discovered gorilla population in the Ebo Forest, Cameroon (Oates *et al.* 2003, Sunderland-Groves *et al.* 2007). Extent of occurrence during the 1800s ca. 22,000 km² (Butynski 2001, E. Sarmiento pers. comm.) but geographic range greatly reduced to roughly 4000 km² (Oates 2011). There are at least 11 localities at which *G. g. diehli* occurs and these are believed to represent three subpopulations (Groves 2002, Bergl 2006, Bergl & Vigilant 2007, Oates *et al.* 2007, Sunderland-Groves *et al.* 2007, Nicholas *et al.* 2009, Bergl *et al.* 2011). Present area of occupancy ca. 400 km² (Oates *et al.* 2007). Recent molecular research indicates that at least occasional emigration of individuals occurs among the scattered subpopulations (Bergl & Vigilant 2007).

Habitat *Gorilla g. gorilla* is present in primary and secondary lowland forest, swamp forest, and submontane forest from sea level to at least 624 m (Equatorial Guinea; H. Ruffler & M. Murai pers. comm.). Especially common where ground vegetation is dominated



Lateral, palatal and dorsal views of skull of Cross River Gorilla *Gorilla gorilla diehli* adult female.

by monocotyledonous plants such as *Haumania liebrechtsiana*, *Megaphrynium macrostachyum*, *Raphia* spp. and *Sarcophrynium* spp. (Rainey *et al.* 2009). *Gorilla g. diehli* occurs from 200 to 2000 m and is now largely restricted to rough terrain in submontane forest, although sometimes in lowland forest between hills (Sarmiento & Oates 2000, Oates *et al.* 2003, Sunderland-Groves *et al.* 2003, Bergl 2006, Oates 2011). In the Cross R. catchment area mean annual rainfall ranges from about 1800 to 4500 mm, mean monthly minima temperature ranges from ca. 14 to 25 °C and mean monthly maxima temperature ranges from ca. 24 to 36 °C (Sarmiento 2003).

Abundance The majority of *G. g. gorilla* are in Gabon and Congo. The number in Gabon was estimated at 28,000–42,000 in the early 1980s (Tutin & Fernandez 1984). Congo had a similar number in 1989–1990 (Fay & Agnagna 1992). Cameroon held ca. 15,000 *G. g. gorilla* in 1998 (L. Usongo pers. comm.). Equatorial Guinea (Rio Muni/Mbini) supported >3000 *G. g. gorilla* in 2011 (H. Ruffler & M. Murai pers. comm.). In 2009, total number of *G. g. gorilla* estimated at >150,000 (F. Maisels pers. comm. in Pain 2009). This is considerably more than earlier estimates by Harcourt (1996), Kemf & Wilson (1997), Butynski (2001) and Plumptre *et al.* (2003a) of 111,500, 111,000, 95,000 and 110,000, respectively. The current number of *G. g. gorilla* is not known because (1) much of the range has never been surveyed, (2) much of the survey data are now out-dated, and (3) commercial hunting and the Ebola virus have dramatically reduced numbers during the past two decades (Ferriss 2005, Tutin *et al.* 2005).

There are ca. 200–300 *G. g. diehli* (Oates *et al.* 2003, 2007, Sunderland-Groves *et al.* 2007, Nicholas *et al.* 2009, Bergl *et al.* 2011). Only ca. 0.2% of *G. gorilla* are *G. g. diehli*, making this the rarest subspecies of gorilla.

Typical density of *G. g. gorilla* is 0.25 weaned ind/km², although they occur at higher densities in Marantaceae and swamp forests. At some sites there are 3–25 gorillas/km², while poor habitat may host as few as 0.1/km² (Poulsen & Clark 2004, Rainey *et al.* 2009). Half of breeding group members are immatures (Lokoué 48%, Maya 56%; Gatti *et al.* 2004). At two sites in Congo, 5% of the population is solitary ♂♂ (Magliocca *et al.* 1999, Parnell 2002a).

Adaptations Diurnal and semi-terrestrial. *Gorilla g. gorilla* forages intensively early in the day in the vicinity of nest-sites (Williamson *et al.* 1990), alternating periods of feeding and travel throughout the day. *Gorilla gorilla* has less time available for resting and socializing than *G. beringei* due to its frugivorous diet (Doran-Sheehy *et al.* 2004). Feeding is the primary impetus for climbing (Remis 1998). Gorillas are modified brachiators (Napier 1963), and *G. g. gorilla* exhibits more suspensory features than *G. beringei* with broad scapulae, and relatively short phalanges and metacarpals (Doran 1997b). *Gorilla g. gorilla* is an agile climber, more arboreal and more gracile than *G. b. beringei*, with longer, more slender limbs. Immatures and adults both brachiate and walk quadrupedally along branches (Williamson 1988). Solitary adult ♂♂ climb more than adult ♂♂ in groups (Remis 1998). Adult ♀♀ climb more than adult ♂♂ (Doran & McNeillage 1998). Will wade across streams and in swamps bipedally using outstretched arms for balance (Parnell 2002b).

Gorilla g. gorilla is similar to the Robust Chimpanzee *Pan troglodytes* in craniodental (Shea 1983) and gut morphology (Chivers & Hladik 1980). Adaptations to frugivory include relatively narrow mandibular corpus and symphysis, and smaller area for masseter attachment than *G. b. beringei* (Uchida 1998, Taylor 2002). Shearing crests on molars are reduced and incisors broad compared to more folivorous *G. b. beringei* (Doran & McNeillage 1998).

The simple stomach does not have the capacity for fermentation, but *G. gorilla* is anatomically equipped to digest fibre and consume foods containing digestion inhibitors through a combination of large body size and surface area of the gut, and retention of digesta in the gut to maximize absorption of nutrients (Chivers & Hladik 1980, Rogers *et al.* 1990, Remis 2000). The caecum is small with a vermiform appendix; the colon is large and morphologically complex (Chivers & Hladik 1980, Caton 1999), and contains many cellulose-digesting entodiniomorph ciliates (Landsoud-Soukate *et al.* 1995). *Gorilla gorilla* tolerates high levels of fibre, total phenols and condensed tannins in its food (Calvert 1985, Rogers *et al.* 1990). In captivity mean gut retention time is 50 h (range 16–136; Remis 2000). *Gorilla gorilla* does not have the gut specializations required to digest seeds (Chivers & Hladik 1980, Andrews & Aiello 1984).

Gorilla gorilla relies on physical strength to break open termite mounds and other food sources, and does not use tools to access foods. Tremendous strength allows these animals to snap off fruit-laden terminal branches to carry to safer feeding spots. It also enables access to resources that are not available to other frugivores, for example, they bite into the hard protective shell of *Detarium macrocarpum* to eat the seeds (Williamson *et al.* 1990).

Finding enough good quality food, especially patchily distributed fruit, is a challenge for *G. gorilla*. Dozens of types of fruit are produced in lowland forest but individual trees bear fruit for only a few days or a few weeks of the year. Thus, greater intelligence is needed to efficiently exploit food sources in lowland tropical forests than in *G. b. beringei*'s more heterogeneous and less complex montane environment. *Gorilla gorilla* is likely to have similar capacity to *Pan troglodytes* for mental mapping, to remember locations, and to exploit ephemeral fruit sources by anticipating ripening (Williamson 1988). *P. troglodytes* has an acute memory of location and perception of relative distances (Menzel 1973), and uses spatial memory and mental mapping (Boesch & Boesch 1984). *Gorilla g. gorilla* possesses extensive knowledge of food resources and animals travel long distances to find rare foods (e.g. travelled 4 km in two days to feed on *Treculia obvoidea*, Tutin 1997a). An indication of species differences in brain function is asymmetry of cerebral hemispheres (Groves & Humphrey 1973).

Adult ♂♂ have laryngeal air sacs in the chest cavity that produce resonance when the chest is beaten with open palms of the hands (Schaller 1963, Dixson 1981).

Gorilla g. gorilla builds a nest to sleep in every night; animals pull, bend and break the stems of vegetation and arrange them around and under their bodies. Materials used for construction depend on local plant availability. The majority of ground nests are constructed from *Aframomum* spp. and species of Marantaceae. In the Likouala Swamps of Congo, most nests are made of the fronds of *Raphia* sp. (Blake *et al.* 1995). Tree nests are built by folding branches to form a bed of leaves at the centre, and built by all age–sex classes. Adult ♂♂ likely build fewer tree nests than smaller individuals (Remis 1998). Nesting on or above ground is determined by availability of raw materials, likelihood of rain, or disturbance by elephants *Loxodonta* spp. (Tutin *et al.* 1995). Proportion of tree nests varies among sites (Lac Tété, Congo *terra firma* forest, 3%, n = 719 [Poulsen & Clark 2004]; Bai Hokou, Central African Republic, 17%, n = 1123 [Remis 1993]; Odzala, Congo, 18%, n = 630 [Bermejo 1999]; Lopé, Gabon, 35%, n = 2435 [Tutin *et al.* 1995]). Tree nests are more prevalent in habitats where herbs are scarce (Ngotto, Central African Republic, 61%, n = 145 [Brugière & Sakom 2001]; Lac Tété, swamp forests, 66%, n = 719 [Poulsen & Clark 2004]; Petit Loango, Gabon, 73% on ground, n = 110 [Furuichi *et al.* 1997]). Day nests are resting places moulded between bouts of feeding. These are simpler and less flattened than night nests, since they are used for shorter periods.

Foraging and Food Herbivorous, folivore–frugivore. Tutin (2003: 299) described *G. gorilla* as 'folivores who like fruit'. All age classes feed in trees, up to 30 m above ground. Animals adopt both sitting and standing positions for feeding. They bend terminal branches within reach, often without breaking them. Fruits and leaves are plucked with the lips, or pulled off by hand and transferred to the mouth. When fruit abundance is low adult ♂♂ remain on the ground rather than expending energy to climb (Remis 1999). Adult ♂♂ also bend and break saplings to access foliage, fruit or vines (Williamson *et al.* 1990). When feeding on the ground, group members spread out at distances of up to 500 m. Animals will wade in swamps to forage on aquatic herbs, and sit in water chest-deep for up to 2 h. They wash sediment from aquatic plants before ingestion by waving handfuls of plants back and forth in the water (Parnell

2002b). In Gabon, they occasionally cross open savanna to eat fruits of shrubs (Williamson *et al.* 1990).

Gorilla gorilla eats fruit, seeds, leaves, stems, bark, shoots, roots, petioles, bracts, vine tendrils, invertebrates and earth, with striking similarities across sites. The diverse diet of *G. g. gorilla* with an important fruit component is closer to the diet of *P. troglodytes* than to *G. b. beringei* (Tutin *et al.* 1991a). Average dietary diversity is 148 food species (range 100–180; Rogers *et al.* 2004). The feeding strategy of *G. g. gorilla* requires it to consume leaves to meet protein needs, even when fruit is abundant (Tutin & Fernandez 1994). Staple foods are pith of *Aframomum* spp. and leaves and shoots of Marantaceae (primarily *Haumania* spp.), which are abundant, accessible, and available year-round. *Gorilla gorilla* is highly selective; for example, animals eat the easily digestible stem- and leaf-bases of *Megaphrynium macrostachyum* and *Haumania liebrechtsiana* but discard the remainder of the plant. They consume leaves high in protein, ripe succulent fruit high in soluble sugars and low in tannins (Rogers *et al.* 1990, Remis *et al.* 2001), and freshwater herbs high in protein and minerals such as sodium and potassium (Magliocca & Gautier-Hion 2002, Doran-Sheehy *et al.* 2004). Unripe fruit and leaves high in digestion inhibitors are avoided.

Fruit is widely available in lowland habitats, thus *G. g. gorilla* is more frugivorous than *G. beringei* (Williamson *et al.* 1990, Doran & McNeilage 2001). *Gorilla gorilla* eats fruits from up to 100 species (Tutin *et al.* 1997a). Fruit is the most diverse food category at all sites studied (range 44–70% of food species; Rogers *et al.* 2004). When abundant, fruit forms the bulk of the diet, although quantitative data are not available and consumption is measured by faecal analysis (fruit remains recorded in 90–100% of faecal samples, Rogers *et al.* 2004). However, the first study of *G. g. gorilla* by direct observation indicates that degree of frugivory may be lower than previous estimates (Doran-Sheehy *et al.* 2006). Seeds of ripe fruits are ingested with pulp, but rarely digested, thus *G. g. gorilla* is an important seed disperser (Tutin *et al.* 1991b). An exception is in Likouala, where *G. g. gorilla* feeds heavily on *Gilbertiodendron dewevrei* seeds during mast fruiting (Blake & Fay 1997), but processing of seeds is time-consuming and individuals have difficulty picking up small seeds on the ground (Tutin *et al.* 1997a). In Gabon, immature seeds of *Dialium lopense* are reingested through coprophagy (Rogers *et al.* 1998).

In Gabon, *G. gorilla* feeds sporadically in streams and marshes on semi-aquatic Marantaceae, *Marantochloa cordifolia*, *M. purpurea* and *Halopogon azurea* (Williamson *et al.* 1988). In Congo, animals make extensive use of waterlogged or permanently flooded swamp forest where preferred foods are aquatic *Hydrocharis chevalieri* and sodium-rich sedges *Rhynchospora corymbosa* and *Cyperus* sp. (Magliocca & Gautier-Hion 2002, Parnell 2002b). In Likouala and Lac Télé swamps, staple foods are *Raphia* sp. palm fronds and *Pandanus candelabrum*, respectively (Blake *et al.* 1995, Poulsen & Clark 2004). Fallback foods are always available but tend to be lower quality (pith, leaves, barks and fibrous fruits) and are ignored when ripe succulent fruits are available (Rogers *et al.* 1994, 2004). For example, *Duboscia macrocarpa* and *Klainedoxa gabonensis* are tough, dry fruits eaten in large quantities only when other fruits are lacking (Williamson *et al.* 1990).

Gorilla g. gorilla consumes >20 species of invertebrate, mostly social ants and *Cubitermes* termites. Weaver ants *Oecophylla longinoda*

are ingested in convenient nests, containing eggs, larvae, pupae and adults. Remains of ants have been recorded in 31% of faeces (Williamson *et al.* 1990). The gorillas are more insectivorous in areas dominated by secondary forest, where *Crematogaster* (ants) and *Thoracotermes* (termites) are also eaten (Deblauwe *et al.* 2003). Insectivory seems to occur at about the same rate at four sites: Lopé, Belinga, Ndoki and Dzanga-Sangha (Tutin & Fernandez 1992, Deblauwe *et al.* 2003). Termites are the most commonly observed food item and eaten on 91% of days (Cipolletta *et al.* 2007). Geophagy has been observed at natural salt-licks with a high concentration of sodium (e.g. Williamson *et al.* 1990).

The diet of *G. g. gorilla* varies seasonally. The amount of fruit eaten is positively correlated with rainfall and the availability of ripe fruit trees (Goldsmith 1996, Remis 1997b). When fruit is abundant, it constitutes most of the diet (68%), but only 30% in the dry season (Tutin *et al.* 1991a). In the dry season more fibrous vegetative matter is eaten, including shoots, young leaves and bark. *Milicia excelsa* bark is eaten only during the dry season (Williamson *et al.* 1990, Tutin *et al.* 1997a).

Little is known about the diet of *G. g. diehli*. Diet includes fruit, leaves, stems, piths, invertebrates and soil, but fruit is preferred when available (Oates *et al.* 2003). The habitat of *G. g. diehli* is notable for strong seasonality, with a prolonged (4–5 month) dry season during which fruit becomes scarce and diet shifts to bark, leaves and pith of terrestrial herbs (Oates *et al.* 2003). *Landolphia* leaves are the staple food at Afi, Nigeria (Rogers *et al.* 2004).

Ranging patterns are shaped by the availability of particular foods, and *G. g. gorilla* travels widely between patchily distributed fruit trees (Tutin 1996, Remis 1997b, Goldsmith 1999). Mean distance travelled each day by *G. g. gorilla* was 1.1–2.6 km (Lopé 1105 m, range 220–2790, $n = 80$ [Tutin 1996]; Bai Hokou 2588 m, range 342–5237, $n = 85$ [Goldsmith 1999]; Bai Hokou 1527 m, median = 1450, range 250–3300, $n = 431$ [Cipolletta 2004]; Mondika 1904 m, range 1485–2651, $n = 94$ [Doran & McNeilage 2001]; Mondika 2014 m, range 400–4860, $n = 334$ [Doran-Sheehy *et al.* 2004]). Mean daily travel distance for one group of *G. g. diehli* was 1270 m, 600–3700, $n = 75$ (McFarland 2007).

Gorilla gorilla adopts a low-cost energy strategy during periods of fruit scarcity by decreasing day range and shifting diet towards abundant but lower quality leaves and woody vegetation. For example, at Bai Hokou, shorter distances are travelled by *G. g. gorilla* during dry season months: dry 1326 m (S.D. = 432, $n = 149$) vs. wet 1595 m (S.D. = 642, $n = 177$) (Cipolletta 2004).

Gorilla g. gorilla home-ranges are large (Lopé 7–14 km² annual, $n = 3$ groups, total 21.7 km² for ten years, $n = 1$ group [Tutin 1996]; Bai Hokou 10.6 km² annual, range 7.5–13.3, $n = 3$ groups [Cipolletta 2004]; Mondika 15.4 km², one group, one year [Doran-Sheehy *et al.* 2004]). Annual home-range of one group of *G. g. diehli* at least 13.1 km², but probably closer to 20 km². Total home-range roughly 30 km² (McFarland 2007).

Social and Reproductive Behaviour *Gorilla gorilla* is social, living in stable, cohesive groups with one adult ♂, several ♀♀ and their offspring. One-male breeding groups are the norm in *G. g. gorilla* (Levréro *et al.* 2006). The ♂ : ♀ ratio in groups is 1 : 3 (Parnell 2002a, Douadi *et al.* 2007) with, on average, four immatures per group (Gatti *et al.* 2004). Basic group structure is

similar across sites and between gorilla species, one main difference being that multimale groups are rare in *G. g. gorilla*, although known at Lopé and Lossi (Tutin *et al.* 1992, Bermejo 1999). Average *G. g. gorilla* group size is similar to *G. b. beringei* (Maya: 11.2, range 2–22, $n = 31$ [Magliocca *et al.* 1999]; Mbeli: 8.4, range 2–16, $n = 14$ [Parnell 2002a]; Lokoué: 8.2, range 3–15, $n = 37$ [Gatti *et al.* 2004]). Groups with >20 individuals known only at two sites in Congo (maximum = 32 [Bermejo 1999, Magliocca *et al.* 1999]). *Gorilla g. diehli* group size is smaller (<6 weaned individuals), although one group of ca. 20 individuals known at Afi (Oates *et al.* 2003). No evidence of fission–fusion (Parnell 2002a), but *G. g. gorilla* groups are less cohesive, both in group spread and occurrence of subgrouping, than *G. b. beringei* groups (Doran & McNeillage 1998).

Both ♂♂ and ♀♀ disperse from natal groups (Stokes *et al.* 2003, Robbins *et al.* 2004). Transfers are facilitated by extensive overlap of home-ranges (Tutin 1996, Bermejo 2004). Before reaching sexual maturity, ♂♂ go through a bachelor stage that can last several years as a solitary individual or in a non-breeding group (Gatti *et al.* 2004, Levréro *et al.* 2006). One-third of adult and subadult ♂♂ are solitary (Maya 32% [Magliocca *et al.* 1999]; Lokoué 34% [Gatti *et al.* 2004]). However, at Mbeli the youngest age at which a ♂ became solitary was 14.6 years (Breuer *et al.* 2009). Non-reproductive and all-male groups observed at three sites (Bai Hokou, Lokoué, Mbeli). A merger of immature ♂♂ and a solitary adult ♂, and immigration of immature ♂♂ into non-reproductive groups, were observed at Lokoué (Gatti *et al.* 2004). Rates of ♂ emigration from *G. g. gorilla* groups are higher than from *G. b. beringei* groups, and even immature ♂♂ sometimes transfer between mixed-sex groups (Robbins *et al.* 2004). Females do not live alone, but seek the protection of an adult ♂ (Stokes *et al.* 2003, Klailova 2011). Females can join another breeding group or a solitary ♂, the latter case leading to the formation of a new group (Stokes *et al.* 2003). The youngest adult ♂ observed to acquire a ♀ at Mbeli was 18 years old (Breuer *et al.* 2009). Group integrity is maintained by mutual dependence between adult ♂♂ and adult ♀♀, based on infant protection (Stokes 2004). When the adult ♂ in a single-male group dies, the group typically disintegrates.

Little is known of *G. gorilla* intra-group behaviour. A study at Mbeli found that interactions between ♂♂ were limited to feeding displacements, all of which were initiated and won by the dominant ♂. Herding and intimidation of ♀♀ by adult ♂♂ occurred, and relationships were characterized by ♂ agonism and ♀ submission (Parnell 2002b). Interactions between adult ♀♀ are predominantly agonistic and described as ‘proximity intolerance’. Females are not seen to form coalitions, and immigrant ♀♀ are harassed by resident ♀♀ (Parnell 2002b). Grooming is a common intra-group behaviour in *G. b. beringei*, but at Mbeli grooming and other forms of social support were rarely observed between adult ♀♀ (Stokes *et al.* 2003, Stokes 2004). Affiliative behaviour is all but absent among adults with the exception of the mother–infant dyad (Parnell 2002b).

The dominant ♂ has a protective role, defending ♀♀ and offspring from other adult ♂♂ and predators. When aroused, adult ♂♂ bark or scream and emit a pungent odour before chest-beating, charging, thumping the ground and breaking vegetation to intimidate human observers (Williamson 1988, Klailova 2011).



Western Lowland Gorilla *Gorilla gorilla gorilla* adult male posturing in lateral ‘head and shoulder display’.

Dramatic ‘splash displays’ observed in *G. gorilla* at Mbeli, ♂♂ leaping into streams or slapping the water’s surface with their hands to intimidate potential rivals for ♀♀ (Parnell & Buchanan-Smith 2001). Females and immatures will chest-beat or hand-clap to attract the attention of the dominant ♂ in fearful situations (Fay 1989). *Gorilla g. diehli* observed to throw fistfuls of grass at humans in display contexts (Wittiger & Sunderland-Groves 2007). The vocal repertoire of *G. g. gorilla* includes loud calls, such as question barks, threat barks, screams and roars (Williamson 1988), and soft calls, such as several types of belch vocalization (Klailova 2011). Olfactory communication is important for *G. g. gorilla* but has only recently been the subject of field research (Klailova 2011).

Gorilla gorilla is non-territorial; ranges are not defended and no group has exclusive access. Range overlap between neighbouring groups is extensive (Doran-Sheehy *et al.* 2004). Where baïs are present, one group’s home-range may overlap with those of as many as 36 other groups (Gatti *et al.* 2004). *Gorilla g. gorilla* avoids encounters with other groups or lone ♂♂ by changing direction and departing from sites where other gorillas have been heard (Cipolletta 2004). Solitary *G. g. gorilla* ♂♂ pursue groups for days, presumably in attempts to acquire mates (Tutin 1996, Bermejo 2004). At Bai Hokou, home-range expansions occurred when a group acquired a new ♀ (Cipolletta 2004).

Several groups of *G. g. gorilla* may make use of a bai at the same time (Parnell 2002a, Gatti *et al.* 2004, Magliocca & Gautier-Hion 2004), consequently inter-group encounters are four times more frequent than for *G. b. beringei* groups. Encounters tend to be neutral or pacific (Doran-Sheehy *et al.* 2004, 2006); groups exchange chest-beats and vocalizations, but levels of ♂ agonism are low with peaceful intermingling of groups (Parnell 2002a). High visibility in baïs and the ease of ‘policing’ by the dominant ♂♂ are thought to create an unusually tolerant social dynamic (Parnell 2002b). High tolerance between groups has also been described by Bermejo (2004) and Magliocca & Gautier-Hion (2004).

The bai environment also favours interactions with other species, including the Forest Elephant *Loxodonta cyclotis*, Forest Buffalo *Syncerus caffer nanus*, Sitatunga *Tragelaphus speki* and Slender-snouted Crocodile *Crocodylus cataphractus*. *Gorilla g. gorilla* monitor the location and activity of Forest Elephants and other animals, but generally avoid them. Gorillas were seen to approach a group of Forest Elephants only once, displaying and causing the elephants to flee. Adult ♂♂ also displaced Forest Buffalo by displaying at them (Parnell 2002b). Females and juveniles displayed alarm towards Slender-snouted Crocodiles by clapping their hands or barking, and seeking proximity of the adult ♂. At Lopé, gorillas sometimes leave nest sites during the night to avoid elephants (Tutin *et al.* 1995).

Gorilla g. gorilla is sympatric with *P. t. troglodytes* throughout its range, and shows high dietary overlap (Tutin *et al.* 1997a, Morgan & Sanz 2006). The outcome of encounters between the two apes is thought to depend upon the size and composition of their respective groups, with one species usually displacing the other (Tutin & Fernandez 1987), but *G. g. gorilla* and *P. t. troglodytes* in Goulougo, Congo, feed in the same fruiting trees. Co-occupancy occurs on a regular basis and has lasted for an average of 46 minutes (18–150, $n = 8$) (Morgan & Sanz 2006).

Reproduction and Population Structure Length of the menstrual cycle in wild *G. g. gorilla* is unknown; 32 days in captivity (range 24–42, $n = 25$; Nadler cited in Groves & Meder 2001). Average length of gestation in captivity is 257 days (range 234–289, $n = 80$; Meder 1991 cited in Groves & Meder 2001), which is close to 255 days in wild *G. beringei*. Schaller (1963) provides birth-weights of 1.7–2.4 kg for four *G. gorilla* born in captivity.

Average age of infants when last seen to suckle is 4.7 years (median = 4.8 years, range 3.1–6.1 years, $n = 25$; Breuer *et al.* 2009). Greater age at weaning relative to *G. beringei* is thought to be a consequence of the frugivorous diet of *G. g. gorilla* (Stokes 2004, Nowell & Fletcher 2007) and results in lower birth rates and longer interbirth intervals. Preliminary data indicate that birth rates for *G. g. gorilla* are lower than for *G. b. beringei*; Lossi 0.18 births/adult ♀/year ($n = 12$) and Mbeli 0.20 births/adult ♀/year ($n = 32$). When the infant survives, average interbirth interval at Mbeli is 5.2 years ($n = 3$) and at Lossi median is 5.0 years (range 4–6 years, $n = 3$) (Robbins *et al.* 2004). Infant mortality in *G. g. gorilla* is higher in later years of infancy than during the first year (Nowell 2005). Preliminary rates of first-year mortality from two sites are 8% (Lossi, $n = 12$) and 29% (Mbeli, $n = 23$). Mortality rate increases to 22% (Lossi, $n = 9$) and 50% (Mbeli, $n = 23$) for infants up to 3 years of age (Robbins *et al.* 2004). Adult ♂♂ gain reproductive benefits from infanticide by shortening the time to impregnate the mothers. Infanticide has been inferred at Mbeli and Lokoué (Stokes *et al.* 2003, Gatti *et al.* 2004).

Age at first reproduction of *G. g. gorilla* in captivity is 6.8–9.7 years for ♀♀ and 6.0–9.5 for ♂♂ (Groves & Meder 2001) but is likely to be much later in wild populations. Wild *G. g. gorilla* grows more slowly than wild *G. b. beringei* (Taylor 1997). Breuer *et al.* (2009) estimate that wild *G. g. gorilla* become subadults at 7.5 years, ♀♀ become adult at 10 years, and ♂♂ become fully mature at 18 years of age. It seems likely that seasonality and spatial variation in food result in later maturation.

Predators, Parasites and Diseases Due to its large size, *G. gorilla* has only two predators of any significance. Humans are, by far, the primary predator of *G. gorilla*, killing animals for their meat, body parts and in retaliation for damage to crops (Wolfheim 1983, Lee *et al.* 1988, Bowen-Jones 1998, Rose *et al.* 2003). Leopards *Panthera pardus* are important predators at some sites, with *G. gorilla* accounting for 4–9% of biomass consumed ($n = 261$ scats; Henschel *et al.* 2005, 2011).

Gorilla gorilla, like *G. beringei*, is susceptible to numerous parasites and diseases (Butynski & Kalina 1998, Homsy 1999, Butynski 2001, Woodford *et al.* 2002, Ferriss 2005, Ryan & Walsh 2011). This topic is addressed in the profile for *G. beringei*.

Conservation IUCN Category (2012): *G. gorilla* Critically Endangered; *G. g. gorilla* Critically Endangered; *G. g. diehli* Critically Endangered. CITES (2012): Appendix I.

The threats to *G. gorilla* are reviewed in detail by Ferriss (2005). The primary threats are commercial bushmeat hunting (largely facilitated by logging activities) and disease (in particular the Ebola virus). Since the 1970s, vast tracts of remote forest with high densities of *G. g. gorilla* have become accessible through the establishment of a system of logging roads and the availability of logging trucks and other vehicles. With this opening up of the range of *G. g. gorilla*, large numbers of commercial hunters, loggers and other people have entered the region, and logging camps and villages have been established. Logging of primary forest is expected to continue over much of the range of *G. g. gorilla* with the result that all large tracts of forest are expected eventually to be exposed to logging and commercial bushmeat hunting (Lee *et al.* 1988, Bowen-Jones 1998, Minnemeyer 2002, Rose *et al.* 2003). Walsh *et al.* (2005) estimated that from 1983 to 2000, the number of *G. g. gorilla* in Gabon declined by around 56% – primarily as a result of commercial hunting.

The most recent threat to *G. g. gorilla* is disease, especially the Ebola virus. Since the early 1990s, Ebola has caused several massive *G. g. gorilla* die-offs in the most remote parts of the species' range (Huijbregts *et al.* 2003). These include some of the most important sites for the conservation of *G. g. gorilla*; Lopé N. P., Minkébé N. P. and Mwagné forest block in Gabon, and Odzala N. P. in NW Congo. The Ebola epizootic wave is moving eastward at ca. 45 km/year. As such, Ebola is expected to reach most of the remaining range of *G. g. gorilla* within the next decade (Walsh *et al.* 2003, 2005, Lahm *et al.* 2006). Ebola causes ca. 95% mortality within populations of *G. g. gorilla* (Bermejo *et al.* 2006, Caillaud *et al.* 2006). A conservative estimate is that ca. 33% of the total protected area population of *G. g. gorilla* has been killed by Ebola over the past 13–14 years. In short, since the early 1980s, hunting for the commercial bushmeat trade and outbreaks of Ebola virus have largely eliminated *G. gorilla* from vast areas of intact forest and caused a rapid decline in numbers elsewhere.

While it is hoped that the sites mentioned above that have been affected by commercial hunting and Ebola will eventually recover (Ryan & Walsh 2011), there remain a few strongholds that have yet to be much affected by hunting and where Ebola has not as yet reached. Among these are the Sangha Trinational Complex of Central African Republic, Cameroon and Congo, the Lac Tété/Likouala complex in Congo, the Dja Conservation Complex and Boumba-Bek/Nki Complex in Cameroon, and the Loango/Moukalaba-Doudou/Gamba Complex in Gabon (Tutin *et al.* 2005). Tourism based on

gorilla-viewing is increasing within the range of *G. gorilla*, but this activity needs to be carefully implemented and closely monitored (Klailova *et al.* 2010, Macfie & Williamson 2010).

Since 2000, *G. g. diehli* has been ranked as one of the world's most threatened primates (Sunderland-Groves *et al.* 2007, Nicholas *et al.* 2009). Most of the surviving 250–300 *G. g. diehli* are in 11 small subpopulations occasionally linked by immigration (Bergl & Vigilant 2007), and most are outside of protected areas and engulfed by a dense human population. Thus, this subspecies is at risk from inbreeding, various human activities (e.g. hunting and habitat loss) and disease. In Nigeria, *G. g. diehli* occurs in the Okwangwo Division of Cross River N. P. and Afi Mountains Wildlife Sanctuary, but fragmentation, degradation and loss of habitat to agriculture continue at a rapid rate, even within the Cross River N. P. In Cameroon, *G. g. diehli* occurs in the Kagwene Gorilla Sanctuary and in the 'proposed' Takamanda N. P. All four of these sites, additional sites and connecting lowland sites, need to be protected and effectively managed if *G. g. diehli* is to survive over the long term (Oates *et al.* 2003, 2007, Sunderland-Groves *et al.* 2007, Nicholas *et al.* 2009, Bergl *et al.* 2011). (See also Thalman *et al.* 2012.)

Measurements

Gorilla gorilla

Standing ht (♂ ♂): 1670 (1380–1760) mm, n = 25

Girth (♂ ♂): 1430 (1320–1690) mm, n = 19

Arm span (♂ ♂): 234 (202–272) mm, n = 17

Arm length (♂ ♂): 1120 mm, n = 8*

Leg length (♂ ♂): 770 mm, n = 8*

Napier & Napier (1967), after Groves (1970)

*Range not given

HB (♂ ♂): (1030–1070) mm, n = 3

HB (♀ ♀): n.d.

T (both sexes): 0 mm

HF (♂ ♂): (289–312) mm, n = 3

HF (♀ ♀): n.d.

E (♂ ♂): (56–60) mm, n = 3

E (♀ ♀): n.d.

WT (♂ ♂): 168 (145–191) kg, n = 11

WT (♀ ♀): 63 (58–72) kg, n = 3

GLS (♂ ♂): 299 (259–340) mm, n = 264

GLS (♀ ♀): 232 (206–264) mm, n = 170

GWS (♂ ♂): 178 (155–201) mm, n = 259

GWS (♀ ♀): 147 (132–173) mm, n = 166

Measurements from various localities (C. P. Groves pers. comm.).

G. g. gorilla and *G. g. diehli*: for various long bone, hand bone, foot bone, vertebral, cranial, facial, and dental measurements and indices, see Sarmiento *et al.* (1996) and Sarmiento & Oates (2000).

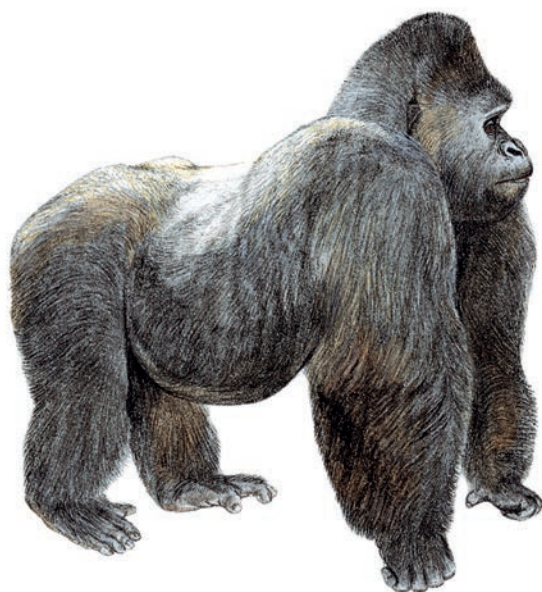
Key References Butynski 2001; Caldecott & Miles 2005; Dixon 1981; Ferriss 2005; Harcourt & Stewart 2007a; Oates 2011; Oates *et al.* 2007; Taylor & Goldsmith 2003; Tutin *et al.* 2005; Walsh *et al.* 2007.

E. A. Williamson & Thomas M. Butynski

Gorilla beringei EASTERN GORILLA

Fr. Gorille de l'Est; Ger. Östlicher Gorilla

Gorilla beringei Matschie, 1903. Sitzb. Ges. Naturf. Fr. Berlin, 257. Mt Sabinyo, Rwanda.



Mountain Gorilla *Gorilla beringei beringei* adult male.

Taxonomy Polytypic species. The history of gorilla taxonomy is a long and complicated one, and is covered in detail by Groves (1966). As early as 1961, Vogel resurrected *beringei* to full species status and put forth a taxonomy in which there are two species of gorilla (Western Gorilla *Gorilla gorilla* of western central Africa and the Eastern Gorilla *Gorilla beringei* of eastern central Africa), and two subspecies (Mountain Gorilla *G. b. beringei* and Grauer's [= Eastern Lowland] Gorilla *G. b. graueri*). None the less, until the mid-1990s, Vogel's (1961) taxonomy was largely ignored in favour of a one species, three subspecies taxonomy: *G. g. gorilla*, *G. g. beringei* and *G. g. graueri* (Groves 1966, 1970, 1986, Dandelot 1974, Jenkins 1990, Kingdon 1997). *Gorilla g. gorilla* is separated from *G. b. beringei* and *G. b. graueri* by ca. 900 km of lowland forest. Since the early 1990s, mitochondrial DNA sequence data (but not the nuclear DNA sequence data; Jensen-Seaman 2000) have emerged that indicate that genetic differences between gorillas living in these two regions are slightly greater than the differences between the Robust Chimpanzee *Pan troglodytes* and the Gracile Chimpanzee (= Bonobo) *Pan paniscus*, and that the difference approaches the level of genetic divergence exhibited between *Pan* and *Homo* (Morell 1994, Ruvolo *et al.* 1994, Garner & Ryder 1996, Uchida 1996, Ryder *et al.* 1999). The genetic distance, together with a number of newly identified ecological, behavioural and morphological differences (e.g. lower molar size

differences; Uchida 1998), suggest more diversity among gorillas than can be accommodated by a single species taxonomy; but, crucially, many of these differences appear to be fixed in the genetic sense, i.e. the two species are diagnosably different as required by the Phylogenetic Species Concept. As such, Vogel's (1961) taxonomy has been resurrected and is the currently accepted view (Ruvolo *et al.* 1994, Groves 1996, 2001, 2005c, Sarmiento & Butynski 1996, Ryder *et al.* 1999, Grubb *et al.* 2003). Molecular research suggests that *G. b. beringei* and *G. b. graueri* diverged ca. 400,000 years ago (Vigilant & Bradley 2004).

Gorillas of Bwindi Impenetrable N. P., SW Uganda, are often referred to as 'Mountain Gorillas', but their taxonomy remains uncertain (Groves 1966, 2001, Jenkins 1990, Sarmiento & Butynski 1996, Sarmiento *et al.* 1996, Kingdon 1997, Sarmiento 2000, Grubb *et al.* 2003, Ferriss *et al.* 2005). As such, in this profile, the gorillas of this population are referred to as 'Bwindi Gorillas' *G. beringei* ssp.?

Synonyms: *beringeri* (*lapsus*), *graueri*, *manyema* (*lapsus*), *mikenensis*, *rex-pygmaeorum*. Chromosome number: $2n = 48$ (Mai 1983).

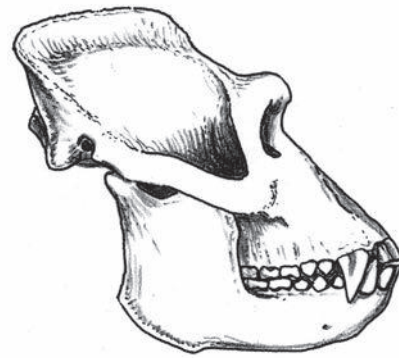
Description Very large (adult ♂♂ >155 kg, adult ♀♀ >80 kg), small-eared, tailless, black, mostly terrestrial primate. Well-developed supraorbital ridges. Nostrils large. Nasal openings nearer to mouth than to orbits. Eyes small, flat, dark brown. Ears relatively small, black or brown. Bare skin of face, hands and feet black. Bare skin of chest, grey or black. Length, colour and distribution of hair variable. In general, individuals living at higher altitudes have longer hair than those living at lower altitudes. Pelage typically (dull or shiny) black, but sometimes with brown or reddish tint. Schaller (1963) describes one adult ♀ with a brown crown, one with a brown rump and one with brown hair between the breasts. Pelage becomes increasingly greyish-silver with age in both sexes, but especially in ♂♂. Pelage shortest on back and longest on arms, reaching 200 mm in some adult ♂♂ (Schaller 1963).

Adult: Adult ♂♂ older than 12 years are especially large, have well-developed sagittal crest and completely greyish-silver 'saddle' on the back (i.e. 'silverback'). Old ♂♂ completely greyish-silver except for the arms, which remain black (Schaller 1963). Adult ♀♀ about half the weight of adult ♂♂ and lack a well-developed sagittal crest.

Infant: Skin at birth pinkish-grey or medium-brown becoming dark brown or black by ca. 1.5 months. Newborns with soft, black, relatively sparse hair on head, dorsum and outside of arms and legs, while rest of the body essentially bare. Hair growth increases at ca. 2 months. Ventrums covered with hair at 3 months. Pelage of inside of forearms and inside of legs sparse until 6–7 months. Rump with white (pygal) tuft of hair at birth that persists until >4 years of age. Crown becomes brown at ca. 1.5–2.5 months and then black again by 8–9 months (Schaller 1963).

Geographic Variation

G. b. beringei Mountain Gorilla. Virunga Mts. Hair longer, tending towards jet black or bluish-black, rarely with brownish or reddish tones. Pelage on crown longer, shaggier. Face wider. Nostrils more ovate and angular, strongly outlined above and well defined. Upper lip (alae) weakly padded. Cranial height longer. Facial height and palate breadth of ♂ shorter. Hallux longer. Humerus



Mountain Gorilla *Gorilla beringei beringei* adult male skull.

shorter. Clavicle longer. Scapula with vertebral border pulled outward at root of scapular spine, sinuous (Groves 1966, 2001, Jenkins 1990). Although it is often stated that *G. b. beringei* is larger than *G. b. graueri*, the available data on body size do not support this.

G. b. graueri Grauer's Gorilla. West of the Western Rift Valley. Hair, shorter, black, often with brownish or reddish tones. Pelage on crown shorter, less shaggy. Face narrower. Nostrils rounded, not strongly outlined above. Upper lip (alae) strongly padded. Cranial height shorter. Facial height and palate breadth of ♂ longer. Hallux shorter. Humerus longer. Clavicle shorter. Scapula with vertebral border relatively straight, not sinuous (Groves 1966, 2001, Jenkins 1990).

G. b. ssp.? Bwindi Gorilla: known only from Bwindi Impenetrable N. P. with a few individuals entering Sarambwe Forest across the border in DR Congo (see below). See Sarmiento *et al.* (1996) for details of morphology.

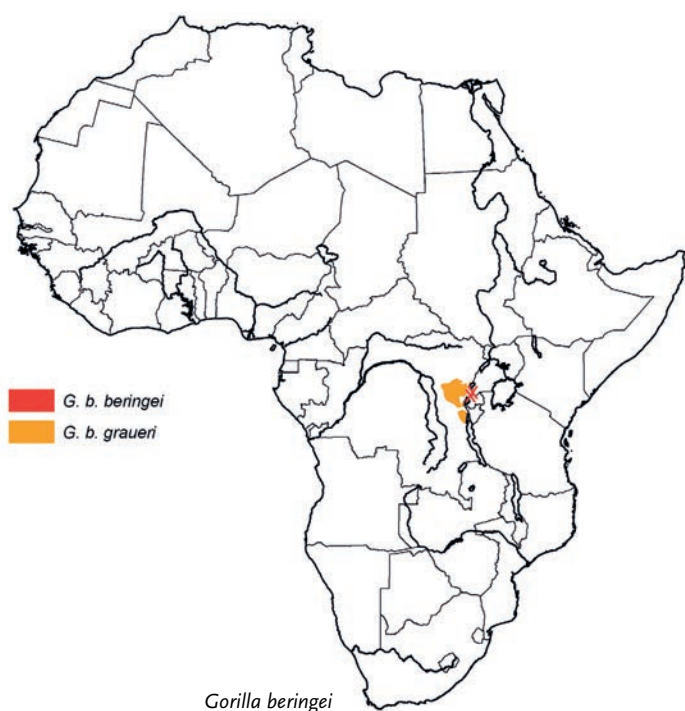
Similar Species

Pan troglodytes. Sympatric below ca. 2300 m. Smaller (adult ♂♂ <55 kg). Ears relatively large. Sagittal crest absent or weakly developed in adult ♂♂. Nasal openings nearer to mouth than to mouth.

Distribution Endemic to extreme NW Rwanda, extreme SW Uganda and E DR Congo; Rainforest and Afromontane–Afroalpine BZs. *Gorilla b. beringei* restricted to one population in the Virunga Mts, where the borders of Uganda, Rwanda and DR Congo meet (Sholley 1991). This subspecies/population occupies an area of 447 km² (Owiunji *et al.* 2005), previously given as 375 km², within an altitude range of 1850–4100 m, but typically <3800 m (Harcourt & Fossey 1981, Vedder & Weber 1990, Butynski 2001, Ferriss *et al.* 2005).

Bwindi Gorillas occupy an area of ca. 215 km² within the Bwindi Impenetrable N. P. and range in altitude from ca. 1400 to 2500 m (IGCP/M. Gray pers. comm.). A small number of Bwindi Gorillas cross the Uganda–DR Congo border to enter the Sarambwe Forest, but no Bwindi Gorillas are resident there. Bwindi Impenetrable N. P. is ca. 25 km to the north of the Virunga Mts, with the intervening area densely settled by people (>300 people/km²) and intensively cultivated.

Gorilla b. graueri has a discontinuous distribution in eastern DR Congo from the Lualaba R. eastward to the Western Rift. Its



northern limit is the headwaters of the Lindi (= Ulindi) R. and the Mitumba Mts (Mt Tshiaberimu) off the north-west corner of L. Edward. Its southern limit is the Itombwe Mts off the north-west corner of L. Tanganyika (Hall *et al.* 1998a, Butynski 2001). *Gorilla b. graueri* is endemic to DR Congo (unless the Bwindi Gorilla is of this subspecies). Subspecific status of some other gorilla populations generally referred to as *G. b. graueri* remains equivocal, such as the population on Mt Tshiaberimu to the north-east of L. Edward (Groves & Stott 1979, Sarmiento & Butynski 1996). *Gorilla b. graueri* ranges in altitude from 600 to 2900 m (Ferriss *et al.* 2005) and has a geographic range of roughly 112,000 km² (Butynski 2001). In 1963 the area occupied was ca. 21,000 km² but declined greatly over the subsequent 35 years to ca. 15,000 km² in the early 1990s (Hall *et al.* 1998a). For *G. b. graueri*, the area occupied is roughly 13% of the geographic range, reflecting the subspecies' current highly fragmented distribution.

In 1908 three gorilla skulls were obtained from local people at Bili (near Bondo) on the right bank of the Uele R. ca. 500 km north-north-west of the nearest present-day known distribution for *G. beringei*. It is not known whether these skulls originated from this locality or were carried there (Schaller 1963, Groves 1966) from distant populations to the west or east. Surveys in the Bondo region over the past decade have failed to locate any gorillas. Whether these skulls are those of *G. beringei* or of *G. gorilla* remains unclear at this time (Groves 1966, 2001).

Habitat Primary and secondary lowland, mid-altitude (= transition), montane and bamboo forests, as well as afromontane vegetation (Schaller 1963, Butynski 1984, Harcourt 1996, Sarmiento *et al.* 1996, Ferriss *et al.* 2005). Altitude limits ca. 600–4100 m. In the Virunga Mts, *G. b. beringei* makes frequent use of *Hagenia abyssinica* and *Hypericum revolutum* woodland where the canopy is open and there is a dense, tall, herbaceous ground layer in which *Galium* climber *Galium ruwenzoriense*, Wild Celery *Peucedanum linderi*, Thistle

Carduus nyassanus, Nettle *Laportea alatis*, Stinging Nettle *Urtica massaica*, *Rubus* spp., *Mikania chenopodiifolia* and *Mimulopsis excellens* are often abundant. Bamboo *Sinarundinaria alpina* covers large areas, either in monodominant stands or mixed with widely scattered trees, often *Podocarpus latifolius* and *H. abyssinica*. The montane forest is comprised largely of the trees *H. abyssinica*, *P. latifolius*, *Morella salicifolia*, *Prunus africana*, *Myrsine melanophloeos*, *Ilex mitis*, *Nuxia congesta*, *Agarista salicifolia*, *Pittosporum spathicalyx*, *Bersama abyssinica*, *Xymalos monospora*, *Dombeya torrida*, *Croton macrostachyus*, *Neoboutonia macrocalyx* and *Maesa lanceolata*.

In the Bwindi Impenetrable N. P., as well as over much of the range of *G. b. graueri* to the west of the Western Rift, some of the more common emergent (21–>37 m) tree species are *P. latifolius*, *Prunus africana*, *Parinari excelsa*, *Newtonia buchananii*, *Entandrophragma excelsum*, *Chrysophyllum gorungosanum* and *Symphonia globulifera*. The more common middle stratum (9–21 m) tree species include *C. macrostachyus*, *N. macrocalyx*, *Albizia gummifera*, *Carapa procera*, *Faurea saligna*, *Harungana madagascariensis*, *Macaranga capensis kilimandscharica*, *Olea capensis* ssp. *macrocarpa*, *Polyscias fulva*, *Strombosia scheffleri* and *Syzygium guineense*. The following are among the more common understorey (<9 m) trees: *Alchornea hirtella*, *Cyathea manniana*, *Myrianthus holstii*, *Tabernaemontana pachysiphon*, *Vepris nobilis*, *Galiniera saxifraga*, *Musanga leo-errerae*, *Xymalos monospora*, *Maesopsis eminii* and *Vernonia* spp. The more common species of vines, herbs, shrubs and ferns in the ground layer are often Bracken Fern *Pteridium aquilinum*, *Mimulopsis arborescens*, *Smilax anceps*, *Urera hypselodendron*, *Piper capense*, *Brillantaisia* spp., *Aframomum* spp., *Impatiens* spp., *Palisota* spp. and *Laportea* spp.

Mean annual rainfall over the range of *G. beringei* is ca. 1500–2500 mm, perhaps reaching 3000 mm at the highest altitude used by *G. beringei* on Mt Kahuzi. Temperatures range from ca. –4 °C to ca. 32 °C.

Abundance In 1989 there were ca. 324 *G. b. beringei* in the Virunga Mts (Sholley 1991). A 2000 census of this population led to an estimate of 359–395 individuals (Kalpers *et al.* 2003), while a 2003 census estimated 380 individuals (Gray *et al.* 2009). A census, conducted in 2010, yielded an estimate of 480 individuals (Gray *et al.* 2011).

Bwindi Gorillas numbered ca. 300 individuals during the early 1990s (Butynski & Kalina 1998, Butynski 2001) and in 1997 (McNeilage *et al.* 2001). A census in 2002 resulted in an estimate of 320 individuals (McNeilage *et al.* 2006), while a 2006 census found ca. 300 gorillas (Guschanski *et al.* 2009).

Surveys conducted from 1989 to 1995 indicate that there were about 16,900 *G. b. graueri* (8660–25,500) in at least 11 populations. Roughly 86% of these lived in the Kahuzi-Biega N. P. – Kasese region. Approximately two-thirds are within the Kahuzi-Biega N. P. and Maiko N. P. (Hall *et al.* 1998a, b). There is concern that there has been a substantial decline in the number of *G. b. graueri* as a result of poaching related to coltan ore mining and of the warfare that has engulfed the whole of the range of *G. b. graueri* from the late 1990s until the present (Ferriss *et al.* 2005).

The above surveys indicated that the total number of *G. beringei* is roughly 17,500 individuals. Of the ca. 17,500 *G. beringei*, roughly 96% are *G. b. graueri*, 2% are *G. b. beringei* and 2% are Bwindi Gorillas. *Gorilla beringei* is, by far, the rarest of Africa's four species of great ape (Butynski 2001, Caldecott & Miles 2005).

The density of *G. b. beringei* in the Virunga Mts was ca. 1.0 ind/km² in 2003 (Kalpers *et al.* 2003) and ca. 1.3 ind/km² in 2010 (Gray *et al.* 2011). The density of the Bwindi Gorilla in the Bwindi Impenetrable N. P. is ca. 1.4 ind/km² (Butynski 2001, McNeilage *et al.* 2001, 2006, Guschanski *et al.* 2009).

Adaptations Diurnal and semi-terrestrial. *Gorilla beringei* deposits large amounts of fibrous dung on leaving the nests to begin feeding soon after sunrise. Animals spend ca. 50% of daylight hours feeding and the remainder resting (Watts 1988). During heavy or persistent rain the gorillas stop eating and seek shelter in dense vegetation or under fallen tree trunks. The long, dense pelage effectively sheds rain. Predominant mode of adult locomotion is knuckle-walking quadrupedalism (Doran 1997b), for which the forearm and hand are modified (Tuttle & Watts 1985). *Gorilla b. beringei* has shorter arms and less divergent big toes than *G. g. gorilla*, but terrestriality is not obligate (Remis 1998); modified brachiators (Napier 1963) with broad scapulae and relatively short phalanges and metacarpals, but only 3% of daily activity of *G. b. beringei* takes place in trees (Tuttle & Watts 1985). Age-class differences are apparent in suspensory behaviour: adult ♂♂ spend 2% of time above ground, adult ♀♀ 7%, juveniles 13% (Doran 1997b).

Gorilla b. beringei is adapted to high altitude where temperatures drop below freezing at night: thick, black hair and large body retain heat; extremities (ears, hands, feet, penis) are small so heat loss is reduced. The wide nostrils allow the animal to breathe more easily at high altitude (Dixson 1981).

Gorillas have a generalized hominoid morphology (Shea 1983) and physiology (Chivers & Hladik 1984) but show craniodental and gastrointestinal specializations associated with an herbivorous diet. A highly developed sagittal crest in ♂♂ indicates a powerful jaw musculature for crushing. The high crested molar surfaces and narrow central incisors are adaptations for shearing leaves (Groves 1986, Uchida 1996). *Gorilla b. beringei* has a wide mandibular corpus and symphysis, a large area for masseter attachment, with incisor–molar and cusp area proportions adapted for feeding on fibrous vegetation (Taylor 1997, Uchida 1998). These features are more pronounced in *G. b. beringei* than in *G. b. graueri* (Uchida 1996).

The stomach is simple and non-fermenting. The relatively long small intestine and enlarged hindgut (Caton 1999) enable *G. beringei* to subsist on a bulky diet high in structural carbohydrates (Watts 1996). The caecum is small with a vermiform appendix and the colon is complex with specialized fermentation chambers. Together, the caecum and colon provide a large surface area for absorption of nutrients (Chivers & Hladik 1980). Large body size and long gut retention times also facilitate digestion of fibre (Remis 2000). *Gorilla beringei* tolerates high levels of fibre, total phenols and condensed tannins in food (Waterman *et al.* 1983).

Gorilla beringei does not use tools, relying on physical strength to tear apart food items. These gorillas do, however, learn complex techniques for gathering food with bimanual coordination of the hands. Many foods with stings (e.g. nettles) or spines are processed in a sequence of precision movements (Byrne & Byrne 1993).

Adult ♂♂ have laryngeal air sacs in the chest cavity that produce resonance when the chest is beaten with open palms of the hands (Schaller 1963, Dixson 1981).

Like all great apes, *G. beringei* builds a nest in which to sleep at night by bending or breaking vegetation (twigs and branches of

trees, and stems of herbs and grasses, including bamboo). Many different species of plants are used for nest construction. There have been numerous studies of nest-building: *G. b. beringei* almost always nests on the ground (Kabara, DR Congo 97% ground nests, n = 2488, Schaller 1963). *Gorilla b. graueri* in the highlands also nests mostly on the ground (88%, n = 3547), but in the lowlands, 40% of nests (n = 375) are found in trees (Yamagiwa 2001). Much of this difference in the use of trees as nest sites may have to do with the fact that tree density is many times higher in the lowlands than in the highlands. Lighter-bodied individuals nest at greater average heights: immatures 15 m above ground, adult ♀♀ 12 m, compared to adult ♂♂, 4 m (Yamagiwa 2001). Variation in nest structure correlates with habitat type, but there is no significant difference in the proportion of tree to ground nests between wet and dry seasons (Yamagiwa 2001). Day nests are resting places moulded between bouts of feeding. These are simpler and less flattened than night nests, since they are used for shorter periods (Schaller 1963). *Gorilla b. beringei* feeds for the first few hours of the morning, then takes leisurely rest periods in the middle of the day (Harcourt 1978, Fossey 1983).

Foraging and Food Herbivorous. Upon rising from their night nests, gorillas spread out to forage. Animals sit on their haunches, or eat while walking (travel-feed). *Gorilla b. beringei* is terrestrial for 96% of feeding time (Watts 1984). Adults climb for only 4% of feeding time, immatures feed in trees 18% of the time (Fossey & Harcourt 1977). Adult ♂♂ eat ca. 30 kg of vegetation per day. There is little competition between individuals, as food is generally abundant. *Gorilla b. beringei* is a selective eater, choosing specific plant parts and often foraging on rare species (Vedder 1984, Watts 1984). The diet is high in protein (3.5–25.38% dry weight) and low in acid detergent fibre and condensed tannins (Waterman *et al.* 1983).

There is considerable variation between and within the diets of the various populations of *G. beringei* (Yamagiwa *et al.* 2003, Ganas *et al.* 2004). Diets consist of young and mature leaves, stems, fruits, seeds, bark, pith, wood and insects (Yamagiwa *et al.* 1994, Stanford & Nkurunungi 2003, Ganas *et al.* 2004). *Gorilla b. beringei* is more folivorous than *G. b. graueri*. In the Virunga Mts, herbaceous foods are abundant and ubiquitous, predominantly leaves and stems (93% food intake). Here >75% of diet is comprised of three species: *G. ruwenzoriense*, *P. linderi* and *C. nyassanus* (Watts 1984). Bamboo shoots, a highland food (above ca. 2300 m), are a seasonal, highly preferred, food that is eaten when available, sometimes comprising as much as 90% of the diet (Casimir & Butenandt 1973, Vedder 1984). Highland populations of *G. b. graueri* also eat large quantities of the basal parts of the sedge *Cyperus latifolius* (Casimir 1975).

Diversity of the plant diet increases with decreasing altitude as the plant diversity of the habitat increases. Lowest number of species consumed was recorded for *G. b. beringei* in Rwanda (62 species; Watts 1996), and highest for Bwindi Gorillas at Buhoma (140 species; Ganas *et al.* 2004). *Gorilla b. graueri* is intermediate, with many more species eaten in the lowlands than in the highlands of Kahuzi-Biega N. P. (121 species vs. 79 species; Yamagiwa *et al.* 2003). Fruit availability is also inversely correlated with altitude and reflected in gorillas' degree of frugivory (Goldsmith 2003, Ganas *et al.* 2004). Fruit consumption by *G. b. beringei* is negligible due to lack of suitable fruit in the environment (Vedder 1984, Watts 1984,

McNeillage 2001). *Gorilla b. graueri* feeds on more species of fruit than sympatric *P. troglodytes* (Yamagiwa *et al.* 2003). Fruit remains are present in 89–96% of faecal samples. Fruit accounts for 25% of food species in highlands, 40% in lowlands (Yamagiwa 2004). Diet of Bwindi Gorillas is more similar to *G. b. graueri* than to *G. b. beringei*, due to greater overlap in food availability (Robbins *et al.* 2006). Fruit remains are found in 66–82% of faecal samples, forming ca. 26% of species in the diet (Ganas *et al.* 2004). By volume, fruit accounts for ca. 25% of diet; the most important species is *M. holstii* (seeds found in 20% of faecal samples; Stanford & Nkurunungi 2003). Fruit is eaten on 60–80% of days (Robbins & McNeillage 2003, Ganas *et al.* 2004).

Gorilla b. beringei diet changes little during the year (Watts 1998c). Only bamboo shoots are limited by season (Casimir & Butenandt 1973, Vedder 1984). Seasonality of diet increases as altitude declines (Yamagiwa *et al.* 1994, Nkurunungi *et al.* 2004, Robbins & McNeillage 2003). Fruit intake correlates with availability (Stanford & Nkurunungi 2003), and varies interannually (Robbins *et al.* 2006). *Gorilla b. graueri* and Bwindi Gorillas rely on fibrous items as fallback foods, which are always available, but eaten only when is fruit scarce (Ganas *et al.* 2004). All subspecies of *G. beringei* consume insects. *Gorilla b. beringei* does so rarely as ant availability decreases with increasing altitude (Watts 1989a). *Gorilla b. graueri* in the lowlands consumes ants and termites frequently (ants in 37% of faecal samples, $n = 171$; Yamagiwa *et al.* 1991). There are few sex or age differences in the diets of *G. beringei*, but in Bwindi Gorillas smaller individuals are more insectivorous (2% of faecal samples from adult ♂♂ contain ants, compared to 13% adult ♀♀, 11% juveniles, Ganas & Robbins 2004). Individuals in some groups ingest earth a few times a year (Mahaney *et al.* 1990). Geophagy coincides with feeding on plants containing high levels of toxins (Mahaney *et al.* 1995). *Gorilla b. beringei* also eats dung (Harcourt & Stewart 1978). The functions of coprophagy are unclear, but adult ♀♀ and juveniles sometimes compete for the dung of adult ♂♂ (E. A. Williamson pers. obs.).

Gorilla beringei subspecies move ca. 1 km each day, but differences are known. Daily travel distances are greater in lowland than in highland areas. *Gorilla b. beringei* is surrounded by food, so travels ca. 570 m/day (range 190–3000 m, $n = 116$; Watts 1991b). Mean day range for *G. b. graueri* in the highlands is ca. 851 m (range 239–3570 m, $n = 225$) but these gorillas travel farther in the lowlands in search of fruit (mean = 1531 m, range 142–3439 m, $n = 8$; Yamagiwa *et al.* 2003). Bwindi Gorilla groups travel ca. 716 m/day (range 242–2055 m, $n = 109$; Stanford & Nkurunungi 2003).

Gorilla beringei home-range size varies widely. *Gorilla b. beringei* range is smallest as herbaceous food densities are exceptionally high (annual home-range 3.1–33.8 km², $n = 11$ groups; McNeillage 1995, Watts 1998b, IGCP/M. Gray pers. comm.). *Gorilla b. graueri* in the lowlands requires a larger area than in the highland sector but size of home-range is unknown (Yamagiwa *et al.* 2003). Estimates for the highlands vary widely: 23–31 km² ($n = 1$ group; Casimir & Goodall cited in Yamagiwa 1999) to 13–17 km² ($n = 1$ group; mean = 14.1 km²; Yamagiwa *et al.* 2003). Total area used over eight years was 42.2 km². Bwindi Gorilla home-ranges are comparable to *G. b. graueri* and *G. g. gorilla*: annual home-range 16–28 km² (mean = 22 km², 45.5 km² for 6 years, $n = 1$ group; Robbins *et al.* 2006). *Gorilla b. beringei* group home-ranges overlap 24–72% ($n = 6$ groups;

Watts 1998b). Overlap is similarly ‘extensive’ for *G. b. graueri* and Bwindi Gorilla (Yamagiwa *et al.* 2003, Ganas & Robbins 2005). Availability of particular foods influences ranging even where food is abundant (Casimir & Butenandt 1973, Vedder 1984, Watts 1998b). *Gorilla b. beringei* shows no seasonal patterns of range use except for increased time spent in the bamboo zone when shoots are present (Vedder 1984, Watts 1998c). *Gorilla b. graueri* increases travel to access preferred fruits, and increases range during the dry season (Yamagiwa *et al.* 1996). The limited distribution of bamboo causes seasonal shifts in ranging (Casimir & Butenandt 1973). Ranging patterns are also influenced by social factors such as inter-group encounters, mate-searching and acquisition of group members. Mate competition has a strong short-term effect (Watts 1998c), at times concealing the influence of ecological factors. Home-ranges of solitary ♂♂ are larger than would be necessary to meet nutritional requirements as they follow groups in attempts to acquire ♀♀ (Yamagiwa 1986, Watts 1994). Groups also range farther after interactions with other social units, and aggressive encounters can cause abrupt shifts in range (Watts 1998c).

Social and Reproductive Behaviour *Gorilla beringei* is social and lives in stable, cohesive, polygynous groups composed of several ♀♀, their offspring and at least one adult ♂ (i.e. ‘silverback’). Groups are one-male, multimale or non-reproductive (containing no adult ♀♀). Multimale groups in the Virunga Mts, exceptionally, have up to eight adult ♂♂. Some adult ♂♂, but no ♀♀, become solitary.

Gorilla beringei group sizes range from 2 to >50 individuals with a mean of roughly 10 (*G. b. beringei*: mean 12.5, median 10.5, 2–47, $n = 36$ [Gray *et al.* 2011]; *G. b. graueri* highlands: mean 9.7, 2–36, $n = 25$ [Inogwabini *et al.* 2000]; *G. b. graueri* lowlands: mean 6.8, 2–31, $n = 41$ [calculated from Hall *et al.* 1998b]. See also Amsini *et al.* (2008) and Hart *et al.* (2007). Bwindi Gorilla: mean 11.3, 3–25, $n = 27$ [McNeillage *et al.* 2006]). In the Virungas, habituated groups are larger than unhabituated groups (14.5 vs. 8.4, Gray *et al.* 2011). One *G. b. graueri* group with >40 individuals (Yamagiwa 1983), one *G. b. beringei* group with >50 individuals (Gray *et al.* 2010) and one Bwindi Gorilla group with >32 individuals (T. Butynski pers. obs.). Polygynous *G. b. graueri* groups sometimes fission temporarily into subgroups and nest apart, each subgroup with at least one adult ♂ (Yamagiwa 2001). Subgrouping is most frequent during fruiting seasons (Yamagiwa *et al.* 2003).

Typical *G. b. beringei* group composition is one adult ♂, five adult ♀♀, and their offspring (Harcourt & Stewart 2007b). Multimale groups form when maturing ♂♂ remain in their natal group. Both *G. b. beringei* and Bwindi Gorillas have a significant proportion of multimale groups (*G. b. beringei* 36% [Gray *et al.* 2010]; Bwindi Gorillas 44% in 2002 [McNeillage *et al.* 2006] compared to *G. b. graueri* ca. 10% [Yamagiwa *et al.* 2003, 2009, 2012]). One adult ♂ dominates the ♂ hierarchy. Adult ♀♀ are ‘dispersal-egalitarian’, forming neither hierarchies nor coalitions (Sterck *et al.* 1997). Affiliative behaviour between adult ♂♂ is rare. Competition among adult ♂♂ is intense and aggression between ♂♂ is likely when ♀♀ are in oestrus (Harcourt *et al.* 1980). Most intra-group aggression is between adult ♀♀, and is usually limited to aggressive vocalizations. Rarely does aggression between adult ♀♀ escalate beyond screaming as adult ♂♂ intervene to end disputes. Interactions between adult ♂♂ and



Bwindi Gorillas *Gorilla beringei* ssp. resting.

adult ♀♀ are limited to interventions, exchanges of vocalizations, aggressive displays by ♂♂ towards ♀♀, and appeasement behaviour by subordinates. Most affiliative behaviour is between related ♀♀, who maintain close proximity and groom each other.

Grooming is a common intra-group behaviour in Mountain Gorillas. Most grooming is between mothers and offspring, but is also extended, in reducing frequency, to maternal relatives, paternal relatives and unrelated individuals. Juveniles groom each other and also groom the dominant ♂; adult ♀♀ are known to groom dominant ♂♂, and adolescent ♂♂ sometimes groom adult ♀♀ (Schaller 1963, Harcourt 1979a, b, Fossey 1983, Watts & Pusey 1993, Fletcher 1994). Grooming almost certainly serves a social purpose in terms of reinforcing such bonds as exist between individuals, but is ultimately related to the removal of ectoparasites, dry skin flakes and vegetation.

Gorilla beringei ♂♂ and ♀♀ are both philopatric, but most emigrate from their natal group (Robbins 1995, Watts 2000a). Some ♀♀ are known to reproduce within their natal group (31%, $n = 29$) and many reproduce in more than one group (56%, $n = 27$; Watts 1996). Half of *G. b. beringei* and most *G. b. graueri* ♂♂ emigrate from their natal group by age 15 years (range 9.6–14.4, $n = 6$; Robbins 1995, Yamagiwa & Kahekwa 2001). Maturing ♂♂ who emigrate either spend time in an all-male group, or remain solitary and attempt to attract ♀♀. Solitaries, however, are rarely successful at establishing groups (Robbins 1995, Watts 2000a, E. A. Williamson pers. obs.). Adult ♂♂ in multimale groups are often related, and subordinate ♂♂ in these groups sire a small proportion of offspring (Bradley *et al.* 2005, Yamagiwa *et al.* 2012).

Adult social bonds are strongest between ♀♀ and ♂♂. Most ♀♀ are unrelated and do not associate regularly with each other (Watts 1996). Adult ♀♀ associate with adult ♂♂ as a means to avoid infanticide by extra-group ♂♂ (Watts 1989b, Yamagiwa *et al.* 2009, 2012). Most infanticides occur when a mother is not

accompanied by an adult ♂ (Watts 1989b). Infanticide shortens the time for mothers to become fertile again and accounts for 26% of infant deaths ($n = 19$; Robbins & Robbins 2004). Multimale groups are more stable; if the dominant ♂ in a multimale group dies, a subordinate takes over and the group remains intact (Robbins 1995). Habituated groups of *G. b. beringei* are almost all multimale (Kalpers *et al.* 2003).

Copulation is initiated by both sexes. Females initiate 63% by approaching, staring and reaching towards the ♂. Males initiate through approach, display and 'train-grunt' vocalization (Watts 1991a). Copulations are brief (median = 80 sec, range 30–310 sec, $n = 251$; Watts 1991a). Dominant ♂♂ perform most copulations. Subordinate ♂♂ also mate but are often harassed by a dominant adult ♂. Newborns cling to the mother's hair, suckle and are carried ventrally. Infants are highly dependent on their mothers at birth and unlikely to survive if orphaned before three years of age. During the first few months, infants have a white tail tuft and travel in a ventro-ventral position. Travel on the mother's back (dorsal ride) starts at 1–2 months and climbing at 6–12 months (Fossey 1979). From ca. six months infants spend increasing amounts of time away from the mother (Fletcher 2001). Play begins when the infant is ca. nine months old, peaks during juvenility and decreases during adolescence (Fletcher 1994). Infants manipulate vegetation at eight months, build clumsy nests by 18 months, but sleep in the mother's nest until age three years (Fossey 1979). They become independent at 3.5–4 years, eating solid food and building their own nests. By four years their locomotion is roughly adult (Tuttle & Watts 1985).

The dominant ♂ has a protective role, defending ♀♀ and offspring from other adult ♂♂ and predators with intimidating displays (Schaller 1963). Immatures are attracted to the dominant ♂ as the group's focal point during both feeding and resting periods (Stewart 2001). As time spent near the mother decreases in late infancy, time spent in proximity to the dominant ♂ increases. Adult ♂ frequently intervenes during aggressive conflicts between immatures, which serves to protect immatures from high levels of aggression (Watts 1997, Stewart 2001).

More than 16 *G. b. beringei* vocalizations have been identified. The vocal repertoire and sound production within groups is dominated by adult ♂♂ (92% of all vocalizations; Marler & Tenaza 1977). When encountering another group, adult ♂♂ convey alarm or threat by barks, roars and screams, usually accompanied by displays (Schaller 1963, Fossey 1972). Over half of within-group vocalizations are exchanges with neighbours (Harcourt & Stewart 2001). When *G. b. beringei* feeds, individuals disperse and often cannot see each other in the dense vegetation. At such times they emit belch vocalizations to maintain contact within the group, and 'close calls' are thought to be important for spacing. Close calls seem to coordinate group movement by signalling intent (Harcourt & Stewart 1996). Other vocalizations include threat barks during aggressive displays, question barks, a mildly aggressive cough-grunt, infant whimpers, breathy chuckles during play, staccato whimpers during copulation, 'humming', 'singing' and hoots (Schaller 1963, Fossey 1972, Harcourt & Stewart 1996, Sicotte 2001).

Chest-beats are provoked by excitement and used in many contexts from play to intimidation within groups, to communication between groups (Schaller 1963, Dixson 1981). All age classes charge, but only adult ♂♂ produce the full displays incorporating charges,

chest-beats, strutting, screams or barks, hoot-series (vocalizations), ground-thumping and vegetation throwing. The 'stiff-legged strut' is described as 'showing off' (Schaller 1963). Adult ♂♂ emit a musky odour from axillary glands in the armpit in situations of excitement or fear (Schaller 1963), and all age classes produce diarrhoeic dung when stressed or afraid. Inter-group encounters, where adult ♂♂ exchange chest-beats and vocalizations, are aggressive contests for adult ♀♀, not for food (Sicotte 1993). Groups usually try to avoid each other, but when inter-group encounters occur over two-thirds of them induce aggressive interactions between adult ♂♂ (Harcourt 1981, Sicotte 1993). When these escalate to physical contact, the fights are intense (Harcourt 1981, Watts 1989b) and sometimes fatal (E. A. Williamson pers. obs.). Adult ♂♂ in multimale groups cooperate by herding to prevent ♀♀ from emigrating (Sicotte 1993).

Gorilla beringei is sympatric with *P. troglodytes* over all but the highest altitudes of their geographic range. The diets of *G. beringei* and *P. troglodytes* overlap but they show different foraging strategies when fruit is scarce, and there is little evidence of inter-specific feeding competition (Yamagiwa *et al.* 1996, Stanford & Nkurunungi 2003). *Gorilla b. beringei* shows curiosity and is gentle on the rare occasions that they interact with other animals (E. A. Williamson pers. obs.), unless they encounter potential dangers (e.g. poachers, Cape Buffalo *Syncerus caffer*), at which times adult ♂♂ actively defend other group members.

Reproduction and Population Structure The median length of the menstrual cycle in *G. b. beringei* ♀♀ is 28 days (mean = 28.8, range 20–39, $n = 25$; Watts 1991a). Females are proceptive for 1–4 days (Watts 1991a). Ovulation is at the mid-cycle, and mating occurs near peak oestrogen concentrations (Czekala & Sicotte 2000). *Gorilla b. graueri* ♀♀ menstrual cycles are slightly longer at 33.2 days (Yamagiwa & Kahekwa 2001). Nulliparous ♀♀ have small sexual swellings but parous ♀♀ show no external signs of oestrus (Czekala & Sicotte 2000).

Gestation lasts ca. 255 days (Watts 1991a, Czekala & Sicotte 2000, Yamagiwa & Kahekwa 2001). There is no evidence of seasonality in births for *G. b. beringei* ($n = 206$; Gerald 1995, Watts 1998c), but there appears to be a May–Jul birth peak for *G. b. graueri* ($n = 47$; Yamagiwa *et al.* 2012). *Gorilla beringei* typically give birth to a single infant. Twins are rare, but have been born into the Virunga and Kahuzi-Biega populations; however, there is only one known case of both twins surviving (Meder 2004). Birth weight ca. 2 kg. Sex ratio at birth is 1 : 1 ($n = 214$; Robbins *et al.* 2007). Birth rate is 0.22–0.28 births per adult ♀ per year, or about one birth per adult ♀ every 4.4 years ($n = 101$; Gerald 1995, Steklis & Gerald-Steklis 2001). Females surviving to adulthood (60%) have an average reproductive lifespan of 14 years and produce a mean of 4.6 offspring that survive to beyond infancy (Gerald 1995).

Females are not fertile whilst suckling young and lactational anoestrus lasts ca. three years. *Gorilla b. beringei* mean inter-birth interval is close to four years when the previous sibling survives (median 3.9 years, S.D. = 0.7 years, $n = 62$). If an infant dies before weaning, another is born two years later (S.D. = 1.1 years, $n = 39$; Gerald 1995). *Gorilla b. graueri* has a slightly longer interval of 4.6 years (range 3.4–6.6, $n = 9$) between surviving offspring, or 2.2 years when an infant dies (range 1.4–2.7, $n = 3$; Yamagiwa

& Kahekwa 2001). Infants are weaned at 3–4 years (median = 43 months, range 22–62 months, $n = 5$; Stewart 1988, Fletcher 2001).

Gorilla b. beringei grows faster than *G. g. gorilla* (Taylor 1997). Age at fertility in ♂♂ is unknown, but ♂♂ do not copulate until age 9–10 years (Watts 1991a). *Gorilla b. beringei* ♂♂ show a growth spurt and develop secondary sexual characteristics from ten years of age, but are not fully grown until 15 years (Watts 1991b, Watts & Pusey 1993). *Gorilla b. beringei* ♀♀ reach sexual maturity and first copulate at 7.0–7.5 years (Groves & Meder 2001), but experience ca. two years of adolescent sterility before first conception (Watts 1991a). *Gorilla b. graueri* has a similar sterile subadult period (Yamagiwa & Kahekwa 2001, Yamagiwa *et al.* 2003). Mean age at first parturition is 10.2 years in *G. b. beringei* (range 8–13, $n = 42$; Gerald 1995), and 10.6 years in *G. b. graueri* (range 9.1–12.1, $n = 6$; Yamagiwa & Kahekwa 2001). In *G. b. beringei* the ♂ : ♀ ratio is 1 : 1.7 and of immatures : adults is 1 : 1.2 in a population of 255 individuals (based on Kalpers *et al.* 2003).

Mortality rates are highest for infants and older adults (Gerald 1995). *Gorilla b. beringei* infant mortality is greatest in the first six months (18%, $n = 151$; Gerald 1995) and 34% in first three years ($n = 65$, Watts 1991a). Rates are similar in *G. b. graueri* (20% in first year, 26% in first three years, $n = 46$; Yamagiwa & Kahekwa 2001). Mortality is highest in the wet season due to increase of respiratory infections (200% higher than predicted; Watts 1998c). About 60% of *G. b. beringei* survive to age eight years (Gerald 1995). Survivorship is constant from the young adult age-class (8–12 years) through the mature adult age class (12–20 years) and drops thereafter. Adult ♂♂ die relatively young, perhaps because of competition among them (Groves & Meder 2001). About 32% of ♂♂ die at 24–30 years, compared to only 8% for ♀♀ (Gerald 1995). The oldest known *G. b. beringei* individual died at 45 years of age (Robbins & Robbins 2004).

Predators, Parasites and Diseases Due to its large size, *G. beringei* probably has only two predators of any significance. Humans are, by far, the primary predator of *G. beringei*, killing them for their meat, body parts and in retaliation for damage to crops (Plumptre *et al.* 2003a). Several cases of *G. beringei* predation by Leopards *Panthera pardus* are described by Schaller (1963).

Gorilla beringei is susceptible to numerous diseases and parasites, including: common cold, pneumonia, whooping cough, influenza, hepatitis A and B, Epstein–Barr virus, chicken pox, smallpox, bacterial meningitis, tuberculosis, diphtheria, measles, rubella, mumps, yellow fever, yaws, paralytic poliomyelitis, encephalomyocarditis, schistosomiasis, giardiasis, filariasis, strongyloidiasis, cryptosporidiosis, shigellosis, salmonellosis, *Capillaria hepatica*, *Entamoeba coli*, *E. histolytica*, *Endolimax nana*, *Ancylostoma* sp., *Oesophagostomum* sp., *Acanthocephala* sp., *Cyclospora* sp., *Chilomastix* sp., *Iodamoeba buetschlii* and *Sarcoptes scabiei* (Ashford *et al.* 1990, 1996, Durette-Desset *et al.* 1992, Butynski & Kalina 1998, Homsy 1999, Butynski 2001, Woodford *et al.* 2002, Ryan & Walsh 2011). See also Conservation.

Conservation IUCN Category (2012): *G. beringei* Endangered; *G. b. beringei* Critically Endangered; *G. b. graueri* Endangered. CITES (2012): Appendix I as *G. gorilla*. Listed as an 'Endangered Species' under the US Endangered Species Act of 1973.

Threats to *G. beringei* all relate to the high human population density within the geographic range and human requirements for natural resources, especially land for agriculture, timber and bushmeat. Populations of *G. beringei* are being increasingly fragmented, isolated and destroyed directly through unsustainable hunting (i.e. poaching), and indirectly through habitat degradation, loss and fragmentation (Lee *et al.* 1988, Kemf & Wilson 1997, Bowen-Jones 1998, Hall *et al.* 1998a, Butynski 2001, Plumptre *et al.* 2003a, Rose *et al.* 2003, Ferriss *et al.* 2005, Yamagiwa *et al.* 2012). Such fragmented populations are susceptible to extinction not only from further habitat loss and over-exploitation, but also from random (stochastic) genetic and demographic changes, and from environmental catastrophes such as disease.

While much has been written about the impact of habitat loss and hunting on populations of *G. beringei*, less has been said about the known and potential impacts of disease on this species. Disease, including parasites, is another major concern as transmission from humans to *G. beringei* occurs and has the potential to be catastrophic. Because *G. beringei* is phylogenetically close to humans, this species is highly susceptible to numerous human diseases (see Predators, Parasites and Diseases, and Homsy 1999, Butynski 2001, Woodford *et al.* 2002, Ferriss *et al.* 2005, Palacios *et al.* 2011). Many of the diseases to which *G. beringei* is susceptible are fatal or cause morbidity, with severe consequences for normal behaviour and reproduction. Of particular concern at this time is the fact that, each year, thousands of tourists from hundreds of localities around the world, step out of crowded, poorly ventilated airplanes and airports and within 1–2 days are close to, and sometimes touching, habituated *G. beringei* (Butynski & Kalina 1998, Sandbrook & Semple 2006, Macfie & Williamson 2010, Ryan & Walsh 2011). These visitors can carry exotic strains of pathogens while not yet showing clinical signs of disease. The risk is that humans will transfer a disease to an immunologically naïve population of *G. beringei*, triggering an epidemic. Both of the *G. beringei* populations that are now the focus of intensive tourist viewing are already small and highly threatened: the Virunga Mts populations with ca. 480 individuals, and the Bwindi Impenetrable N. P. population with ca. 300 individuals. Each day, ca. 75% of the individuals in the Virunga population are visited by people (tourists, researchers, guides, porters, rangers and military escorts).

The risks and consequences of disease transmission between humans and *G. beringei* are predicted to become increasingly serious if once-stable ecosystems and large (genetically diverse) populations of *G. beringei* are fragmented, reduced and stressed by humans. Small populations are likely to have diminished genetic variation, one result of which is increased vulnerability to infectious diseases. In the case of *G. beringei* the stress involved with the habituation process and frequent visits by people may further challenge their well-being, compromising their ability to respond normally to disease. The introduction of a human-borne infection into small, stressed, genetically depressed populations of *G. beringei* could lead not only to the extinction of the population but also (where the subspecies is represented by but one population) to the extinction of the subspecies (Butynski & Kalina 1998, Butynski 2001).

Identifying and implementing actions to minimize and reduce the major threats to *G. beringei* have been the focus of many workshops, articles and books (e.g. Schaller 1963, Dixon 1981, Lee *et al.* 1988, Butynski 2001, Caldecott & Miles 2005, Ferriss *et al.* 2005, Pain

2009) and will not be reviewed here. The major protected areas whose effective management is critical to the long-term survival of *G. beringei* are Kahuzi-Biega N. P., Maiko N. P., Itombwe Nature Reserve and Virunga N. P. in DR Congo, Bwindi Impenetrable N. P. and Mgahinga Gorilla N. P. in Uganda, and Volcanoes N. P. in Rwanda.

Research priorities for *G. beringei* at this time are: (1) new surveys to determine the present distribution and numbers of *G. b. graueri*; (2) more research on the impacts of tourism on the ecology and behaviour of *G. b. beringei* and the Bwindi Gorilla; and (3) a detailed assessment of the taxonomic status of the gorillas of Mt Tshiaberimu and Bwindi Impenetrable N. P.

Measurements

Gorilla beringei

WT (♂ ♂): 165 (?–?) kg, n = 5

WT (♀ ♀): 90 (?–?) kg, n = 3

G. b. beringei and *G. b. graueri* from various sites combined (Sarmiento *et al.* 1996)

G. b. beringei

Standing ht (♂ ♂): 1700 (1610–1710) mm, n = 5

Girth (♂ ♂): 1490 (1380–1630) mm, n = 8

Arm span (♂ ♂): 2310 (2000–2760) mm, n = 8

Arm length (♂ ♂): 1050 (970–1110) mm, n = 5

Leg length (♂ ♂): 660 (610–710) mm, n = 2

HB (♂ ♂): 1105 (1010–1200) mm, n = 2

T (both sexes): 0 mm

HF (♂ ♂): 305 (286–320) mm, n = 10

E (♂ ♂): 58 (50–65) mm, n = 6

WT (♂ ♂): 152 (120–191) kg, n = 7

WT (♀ ♀): 84 (70–98) kg, n = 2

GLS (♂ ♂): 311 (287–342) mm, n = 19

GLS (♀ ♀): 247 (237–260) mm, n = 11

GWS (♂ ♂): 183 (179–197) mm, n = 19

GWS (♀ ♀): 148 (140–154) mm, n = 10

Virunga Mts. Compiled primarily by C. P. Groves (1966, pers. comm.) from numerous sources. Includes one adult ♂ collected by E. Heller in 1925. Details taken from E. Heller's notes, which are on deposit at FMNH (J. Kerbis pers. comm.). One ♀ WT from C. A. Whittier (pers. comm.).

G. b. graueri

Standing ht (♂ ♂): 1820 (1690–1960) mm, n = 6

Girth (♂ ♂): 1540 (1420–1600) mm, n = 4

Arm span (♂ ♂): 2510 (2340–2700) mm, n = 3

Arm length (♂ ♂): 990 (860–1100) mm, n = 3

Leg length (♂ ♂): 795 (790–800) mm, n = 2

HB (♂ ♂): 1090 (1040–1140) mm, n = 4

T (both sexes): 0 mm

HF (♂ ♂): 297 (287–312) mm, n = 4

E (♂ ♂): 52 (50–54) mm, n = 4

WT (♂ ♂): 159 (150–209) kg, n = 4

WT (♀ ♀): 76 (73–80) kg, n = 2

GLS (♂ ♂): 302 (276–334) mm, n = 43

GLS (♀ ♀): 243 (219–258) mm, n = 31

GWS (♂ ♂): 182 (167–200) mm, n = 40

GWS (♀ ♀): 149 (135–164) mm, n = 29

Various sites in E DR Congo. Compiled by C. P. Groves (1966, pers. comm.) from numerous sources. Includes one adult ♂ collected by E. Heller in 1924. Details taken from E. Heller's notes, which are on deposit at FMNH (J. Kerbis pers. comm.).

See Sarmiento & Oates (2000) and Sarmiento (2003) for cheektooth surface area data for six *G. beringei* populations. See Sarmiento *et al.* (1996) for various long bone, hand bone, foot bone, vertebral, cranial, facial, and dental measurements and indices for *G. beringei* and Bwindi Gorilla.

Key References Butynski 2001; Dixson 1981; Ferriss *et al.* 2005; Fossey 1983; Homsy 1999; Kalpers *et al.* 2003; Robbins *et al.* 2001; Sarmiento *et al.* 1996; Schaller 1963; Taylor & Goldsmith 2003; Yamagiwa *et al.* 2009, 2012.

E. A. Williamson & Thomas M. Butynski

Tribe PANINI

Chimpanzees

Panini Delson, 1977. *Journal of Human Evolution* 6: 450.

As outlined in the tribal designation of Gorillini, the need for a tribe that is effectively synonymous with the genus is dictated by a generally accepted need to separate bipedal and quadrupedal apes

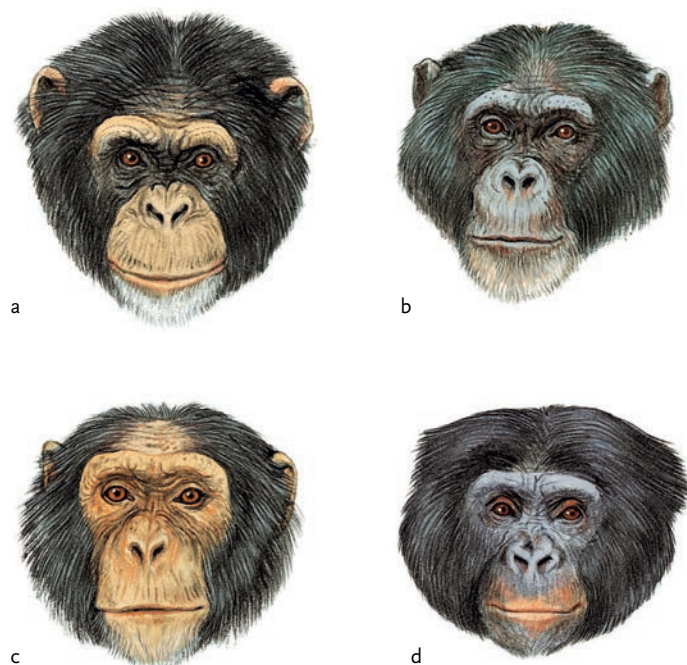
(Groves 1986). The tribe Panini consists of a single genus; hence its definition and characterization is the same as that for *Pan* (below).

Colin P. Groves

GENUS *Pan*

Chimpanzees

Pan Oken, 1816. *Lehrbuch der Naturgeschichte*, ser. 3 (2): 11.



(a) Western Chimpanzee *Pan troglodytes verus*. (b) Eastern Chimpanzee *Pan troglodytes schweinfurthii*. (c) Central Chimpanzee *Pan troglodytes troglodytes*. (d) Gracile Chimpanzee (Bonobo) *Pan paniscus*.

Polytypic genus endemic to the forests of tropical Africa. There are two species in this genus: the Robust or Common Chimpanzee *Pan troglodytes* and the Gracile Chimpanzee, also known as the Bonobo or Pygmy Chimpanzee, *Pan paniscus*. The latter was described as a subspecies of chimpanzee by Schwarz (1929), and elevated to the

rank of species by Coolidge (1933). The last shared ancestor was ca. 1.8 mya (Gondet *et al.* 2011). A suggestion that the West African *P. troglodytes verus* might also be ranked as a distinct species (Morin *et al.* 1994) has not been widely adopted.

The differences between the two species of chimpanzees relate primarily to body build: *P. paniscus* is much more slender (i.e. 'gracile'), with an especially small round head and heavy, pillar-like legs. As such, the intermembral index (ratio of arm length to leg length) for *P. paniscus* is about equal to 100, whereas the intermembral index is >100 in *P. troglodytes*. Infant *P. troglodytes* have pink faces that gradually darken with age, often developing conspicuous freckles and large tan spots, becoming black at or after maturity; infant *P. paniscus* already have black faces, except around the mouth, and this does not essentially change with age. Both species go bald on the scalp with age, ♀♀ earlier and usually more extensively than ♂♂.

Compared to *Gorilla*, *Pan* differs as follows. Size is much smaller (large chimpanzee ♂♂ weigh about as much as small gorilla ♀♀), and sexual dimorphism is not so marked, chimpanzee ♂♂ being (in most populations) little larger than ♀♀. The ears are conspicuously larger, and in adults generally remain bronze rather than black. The nose is both shorter and narrower, though an approach to the 'squashed tomato' nostrils of many gorillas may be made. The arms are relatively shorter (intermembral index, even in *P. troglodytes*, is lower), the hand is much longer and narrower, the thorax is narrower, the vertebral border of the scapula is much shorter, the iliac crests lack the expansion, the calcaneum is shorter, the feet are narrower, the toes are longer, and the hallux (great toe) is more slender and more divergent. The pelage is almost invariably jet black; adult ♂♂ lack a 'silverback' saddle, although with extreme age both sexes become grey, first on the lower back and thighs, the greyiness later

spreading to other parts of the body. Like gorillas, infant chimpanzees have a whitish tuft above the anus.

The skull can be distinguished from that of gorillas, first, by the smaller size (the greatest length of the skull is rarely above 220 mm, whereas even in ♀ gorillas it is rarely below 250 mm), and, secondly, by the flattening of the upper face. The supraorbital tori, though often dorsoventrally expanded, are more or less flattened on their anterior surface (as well as being separated in the midline by a depression at glabella), and the lateral orbital pillars are also wide and flat; in particular, the interorbital space is very wide and flat, and there is no median nasal ridge.

In the dentition, the enamel is thin. The maxillary incisors are distinctive: broad, thick at the base and with a strong lingual tubercle, deeply incised around the base. Lateral incisors are similar to the central ones. The canines of ♂♂ are not as elongated as in ♂ gorillas, and canine dimorphism is less. Cheekteeth are bunodont, with the cusps low but fairly well defined, without the sharp crests of *Gorilla*, so that, for example, the central basins of the maxillary molars are not strongly interrupted by the crista obliqua.

It is safe to suppose that the ancestral *Pan* ranged over a larger geographic area and was less restricted in its choice of habitats than the two species are today. Furthermore, on the basis of recent historical evidence, Kortlandt & Van Zon (1969) concluded that *P. troglodytes* also occupied a broader spectrum of habitats, and they envisaged earlier populations occupying semi-open habitats. These authors emphasized the part played by humans and proto-humans in constraining and progressively diminishing the chimpanzee's ecological niche.

If this is correct, the geographic and ecological range of *Pan* evidently contracted greatly as the apes relinquished more open habitats to hominins, and such a history has important implications for understanding the behaviour and even the morphology of contemporary populations. For example, their ability to climb tall rainforest trees with apparent ease may be a skill that has been superimposed during the last 5 million years or so over an older, less specialized semi-arborealism. Recent discovery of a half-million-year-old fossil chimpanzee in Kenya (McBrearty & Jablonski 2005), in the Kapthurin Formation, where early human fossils are also found, may take the prediction of such evolutionary changes out of the realm of speculation and into scientific documentation.

The exploitation by *Pan* of fruit or seeds in tall emergent trees within the forest has provoked debate on how making use of this particularly demanding resource might have had a precedent in earlier *Pan* habitats, such as open woodlands. For a majority of primates, the canopy of the rainforest is the main resource: a second 'floor' above the relatively barren, deeply shaded ground below. Competition for all types of food is intense here but the spaced-out emergents above this crowded floor are less accessible to smaller primates for two reasons. One is the physical challenge of climbing thick trunks, the other, more decisive inhibitor, is exposure to predators. Even if, as Kortlandt & Kooij (1963) and others have suggested, *Pan* was originally less of a true forest animal, its exploitation of spaced out large woodland trees (something that still occurs) would have 'pre-adapted' these large-bodied, powerfully muscled apes to make use of forest emergents (Kingdon 2003). Such an interpretation is consistent with the exceptional development of the forelimbs and strength of the chimpanzee's long, curved fingers. In relation to their putative hominin competitors, these traits would have closed off



Central Chimpanzee *Pan troglodytes troglodytes* adult male.



Gracile Chimpanzee (Bonobo) *Pan paniscus* adult male.

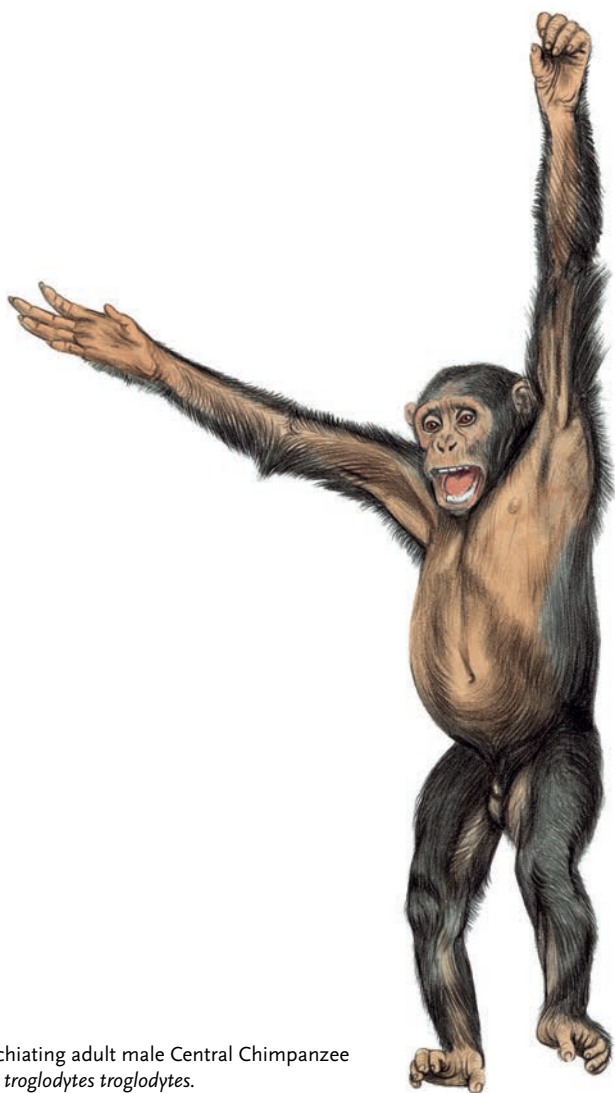
any possibility of chimpanzees becoming bipedal. For that outcome an opposite trend – reduction, not amplification – of the forelimb would have been necessary.

All *P. troglodytes* populations so far studied have turned out to be partially carnivorous, hunting monkeys (predominantly red colobus *Procolobus* spp.) in particular, also occasionally small ungulates such as duikers *Cephalophus* spp. and *Philantomba* spp., Bushbucks *Tragelaphus scriptus* and young Bushpigs *Potamochoerus larvatus*. Hunting is often a cooperative affair and, like many other aspects of chimpanzee behaviour, differs in its cultural norms from place to place. This, as well as the fission–fusion community social organization, patterns of tool-use and tool-making, and so on, speaks of a behavioural heritage that in many respects parallels that of humans – or were these features already characteristic of the common ancestor, as parsimony would suggest?

The first identified chimpanzee fossil (consisting of teeth only) was, as described above, found in the Baringo region of Kenya, in deposits only slightly less than 545,000 years old (McBrearty & Jablonski 2005). Schwartz & Tattersall (2003) suggested that some isolated teeth from the Plio-Pleistocene (ca. 1.8 mya) of Koobi Fora, east of L. Turkana, Kenya, a well-known site of early hominins, may also actually be proto-chimpanzee, including one of the teeth (1590F) usually ascribed to a specimen of *Homo rudolfensis*. If this is so, it implies that we should also look for other representatives of the Panini in early hominin deposits.

Pan troglodytes ROBUST CHIMPANZEE (COMMON CHIMPANZEE)

Fr. Chimpanzé commun; Ger. Gemeiner Schimpanse

Pan troglodytes (Blumenbach, 1775). De generis humani varietate nativa, p. 37. Mayoumba, Gabon.

Brachiating adult male Central Chimpanzee
Pan troglodytes troglodytes.

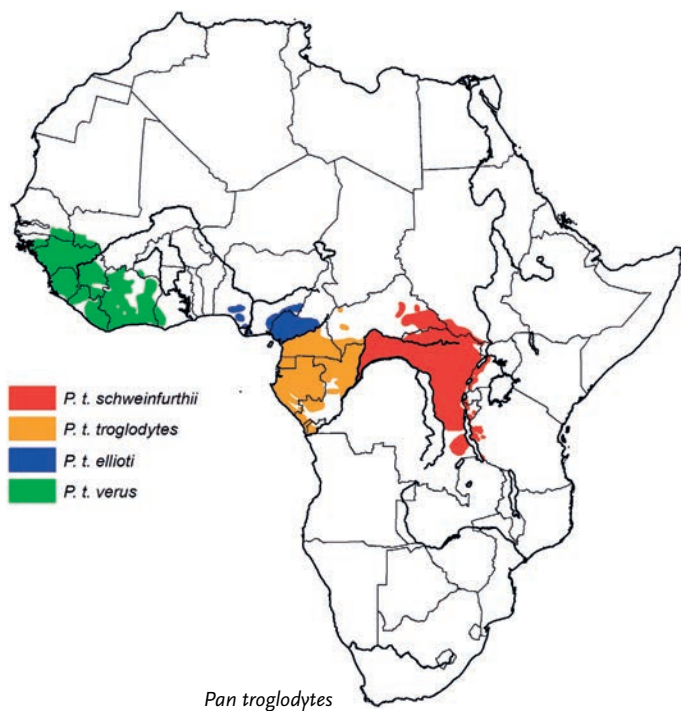
Taxonomy Polytypic species. There is a complicated history of generic, specific and subspecific classification, resulting from both broad anatomical similarities among African and Asiatic ape taxa, and from considerable inter-individual variation in colouring and facial features within *Pan*. Most common former classifications substituted the generic names *Anthropopithecus*, *Troglodytes* or *Simia* and/or the species name *satyrus* (Hill 1969, Jenkins 1990, Groves 2001). The type specimen, no longer in existence and given the name *Simia troglodytes*, was likely *P. t. troglodytes* (Hill 1969). Current designation as a single species can be traced to Schwarz (1934, using the species name *satyrus*) and Allen (1939), who both included the Gracile Chimpanzee (or Bonobo) *Pan paniscus* within *Pan troglodytes*. Coolidge's (1933) classification of the Gracile Chimpanzee into a separate species is widely accepted today. One genetic study suggests that the Western Chimpanzee has diverged sufficiently to be designated as a full species, *Pan verus* (Morin *et al.* 1994). Modern taxonomic usage is fairly

consistent, though genetic similarities prompted some researchers to suggest that *Pan* could be regarded as a subgenus of *Homo* (Wildman *et al.* 2003). Genetic studies put the divergence of the *Homo*–*Pan* clade in the late Miocene (ca. 8–6 mya) (Caccone & Powell 1989, Ruvolo 1997, Perelman *et al.* 2011, Roos *et al.* 2011). No confirmed cases of hybridization between *P. troglodytes* and any other ape taxon.

Synonyms: *adolphi-friederici*, *africanus*, *angustimanus*, *aubryi*, *calvescens*, *calvus*, *castanomale*, *chimpanse*, *cottoni*, *elliotti*, *fuliginosus*, *fuscus*, *graueri*, *heckii*, *ituricus*, *ituriensis*, *jocko*, *koolookamba*, *lagaros*, *leucoprymnus*, *livingstonii*, *mafuca*, *marungensis*, *nahani*, *niger*, *ochroleucus*, *oertzeni*, *pan*, *papio*, *pfeifferi*, *pongo*, *purschei*, *pusillus*, *rarihilosus*, *reuteri*, *satyrus*, *schneideri*, *schubotzi*, *schweinfurthii*, *steindachneri*, *tschego*, *vellerosus*, *verus*, *yambuyae*. The complete genome has been sequenced (Chimpanzee Sequencing and Analysis Consortium 2005). Chromosome number: $2n = 48$ (Young *et al.* 1960).

Description Moderately large, robustly built, knuckle-walking ape. Sexes alike in colour but adult ♀♀ have smaller canines, narrower shoulders, and are about 80% as heavy as adult ♂♂. Face, ears, hands and feet of infants pink, generally darkening to brown or black in adults; often with a dark 'mask' in juveniles. Head prognathic with pronounced brow ridges. Face and centre of forehead primarily bare and framed by hair. Iris orange-brown to dark brown. Sclera brown (rarely, white). Ears completely or partially bare, human-like in general shape but relatively large, and can face forward or lay flat against the side of the head. Upper and lower lips highly flexible and strong. Hands long and slender with short, opposable thumb. Metacarpals and phalanges curved. Fingers and palms hairless. Grasping feet with broad soles and short toes. Sole and toes hairless. Forelimbs slightly longer than hindlimbs. Tail absent. Pelage long, coarse, dark brown to black. Many older adults with light brown or grey hair on the lower back, legs and/or chin. Immatures with tuft of white hair above the anus.

Geographic Variation Three subspecies widely recognized (Groves 2001, Becquet *et al.* 2007). Genetic (Gonder *et al.* 1997, 2006, 2011, Stone *et al.* 2010, Bowden *et al.* 2012) and molar morphometric (Pillbrow 2006) data strongly support the designation of a fourth subspecies, *P. t. elliotti* (formerly *vellerosus*; Oates *et al.* 2009, Morgan *et al.* 2011, Oates 2011), and point to weak divergence between *P. t. troglodytes* and *P. t. schweinfurthii* (Gonder *et al.* 2011). Hill (1969) described a fifth subspecies, *P. t. koolokamba*, the Gorilla-like Chimpanzee; this designation has no current credence, as both historical (Schwarz 1939) and modern (Groves 2001) experts define these specimens within *P. t. troglodytes*. Based on a recent craniometric study, Groves (2005b) argues for two subspecies within what is presently *P. t. schweinfurthii*; a north-eastern subspecies (*P. t. schweinfurthii*) and a south-eastern subspecies (*P. t. marungensis*). This is, however, not supported by the genetic evidence (Gonder *et al.* 2011). Others argue that subspecies designations are not warranted (Fischer *et al.* 2006). Resolution of these issues awaits



greater understanding of gene flow among populations and studies at the known and probable geographic limits or contact zones for each taxon (Jolly *et al.* 1995, Won & Hey 2005).

Here, four subspecies are recognized, following the current IUCN classification (Grubb *et al.* 2003). All subspecies are best diagnosed based on the locality of collection or sighting; we provide some general phenotypic characteristics of each subspecies, though individual phenotypic variation is extensive enough to preclude diagnostic field criteria to distinguish the taxa.

P. t. verus Western Chimpanzee or Upper Guinea Chimpanzee. South-eastern Senegal and S Mali south-east to either the Dahomey Gap (Bénin) or Niger R. Tend towards profuse white 'beards'. Darkly pigmented circumocular and/or nasal 'mask' develops rapidly. Face often maintains some pink colouration into adulthood. Face typically broad across forehead with ears large, prominent and pale. Hair of scalp parting along midline. Palms and soles pale with irregular patches of darker pigment on digits.

P. t. ellioti Elliot's or Gulf of Guinea or Nigerian-Cameroon Chimpanzee. Southern Nigeria and W Cameroon, probably from the Dahomey Gap (Bénin) or Niger R. south to the lower Sanaga R. (Morgan *et al.* 2011, Oates 2011). Recognized based on mtDNA (Gonder *et al.* 1997, 2011) and molar morphometric (Pilbrow 2006) evidence. Relative to *P. t. verus*, ears small and lie close to head; top of head rounder; brow ridge straighter, more gracile build; face, hands and feet uniform black in adults (Oates 2011).

P. t. troglodytes Central Chimpanzee or Lower Guinea Chimpanzee. Sanaga R. south-east to Ubangi R. and south to Congo R. Skin, including face, ears, palms and soles, tends to be uniformly dark brown or black in adulthood. Ears small to medium. Tends to quickly develop prominent bald patches on the forehead.

P. t. schweinfurthii Eastern Chimpanzee or Long-haired Chimpanzee. Ubangi R. east across DR Congo, north of Congo R. and east of



Eastern Chimpanzee *Pan troglodytes schweinfurthii* juvenile.

Lualaba R. to SW Tanzania. Slightly smaller in body size than other subspecies. Hair long, particularly around the face and shoulders. Facial pigmentation ranges from pale brownish-pink to brown or greyish-black in adulthood, with traces of pink evident primarily near the lips in some individuals. Face typically longer than *P. t. verus*. Palms and soles usually brick red to bronze.

Similar Species

Pan paniscus. Parapatric. Limited to central Congo Basin, DR Congo, south of the Congo R. More gracile, ca. 15% lighter. Head small and round. Mouth region contrastingly pink. Face black at birth. Upper molar rows not parallel.

Gorilla gorilla and *Gorilla beringei*. Sympatric. Larger (adult ♂ >130 kg). Ears relatively small and black. Sagittal crest well developed in adult ♂♂. Nasal openings nearer to mouth than to orbits.

Distribution

Historical Distribution The historical geographic range of *P. troglodytes* is roughly 2.3 million km² (Butynski 2003), comprising 25 countries. Probably extirpated from Bénin, Burkina Faso and Togo, but confirmation needed. On the verge of extirpation from Senegal and Ghana. Extirpated from large areas within most countries.

Current Distribution Endemic to equatorial Africa. Rainforest BZ. Occurs in 22 or 23 countries from Senegal east to SW Tanzania, from ca. 13°N to 7°S (Butynski 2001, 2003).

Habitat Most habitats are mosaics, particularly of moist evergreen or semi-deciduous forest, swamp forest, gallery forest, woodlands, colonizing forest and grassland. Preferred habitats are mature forests, though colonizing forests are frequently used. Altitudes range from sea level to at least 2949 m (Nyungwe Forest, Rwanda; Gross-Camp *et al.* 2009). Mean annual rainfall is typically

over 1400 mm (summarized in: Kortlandt 1983, Butynski 2001). A few populations, including those at Fongoli and Mt Assirik, Senegal (*P. t. verus*), and Ugalla (Tongwe), Tanzania (*P. t. schweinfurthii*), utilize drier, open grassland and woodland habitats (Itani 1979, McGrew *et al.* 1981, Pruetz 2007). Associated and important plant species cannot be generalized across sites, though the density of Robust Chimpanzees seems to vary positively with the density of large trees bearing fleshy fruit (Balcomb *et al.* 2000).

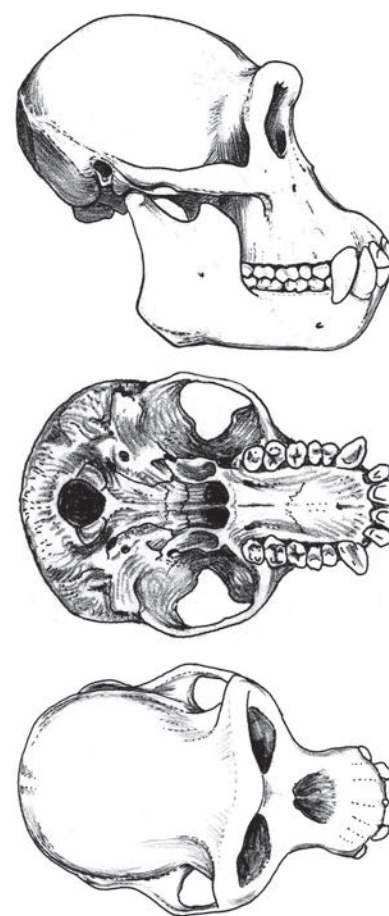
Abundance Estimates of abundance are rough given that only a small portion of the species' range has ever been surveyed, and that most of the survey data were collected well over a decade ago. Abundance data for many areas may now be overestimates due to recent catastrophic disease outbreaks, heavy hunting and habitat loss (see Conservation). These figures may also be misleading due to highly fragmented habitats; e.g. Uganda contains 4000–5700 Robust Chimpanzees, but many of these are in small populations (<500 individuals) that may have low long-term viability (Plumptre *et al.* 2003b). Densities are <1 ind/km² in most areas, with 2–8 ind/km² in some protected areas (Kormos *et al.* 2003, Plumptre *et al.* 2003b, Oates 2011). The following figures represent the most recent population estimates (Butynski 2003, Plumptre *et al.* 2010, Morgan *et al.* 2011):

- P. t. verus* 21,300–55,600. Largest populations are in Côte d'Ivoire, Guinea, Sierra Leon and Liberia. Senegal, Ghana and Guinea-Bissau each hold fewer than 1000 individuals.
- P. t. ellioti* 3500–9000. Largest population is probably in Cameroon.
- P. t. troglodytes* 70,000–116,500. Largest populations are in Congo (10,000), Cameroon (31,000–39,000) and Gabon (27,000–64,000). Angola, Central African Republic and DR Congo each hold fewer than 1000 individuals
- P. t. schweinfurthii* 76,4000–119,600. Largest populations are in Uganda (4000–5700) and DR Congo (70,000–110,000). Sudan, Burundi and Rwanda each hold fewer than 500 individuals.

Adaptations Diurnal and semi-terrestrial. Active 10–13 h per day (Wrangham 1977, Lodwick *et al.* 2005). Although Robust Chimpanzees feed mostly in trees, they travel all but the shortest distances on the ground, where they also do most of their resting and grooming. Arboreal locomotion is primarily via vertical climbing, palmar walking on the tops of tree limbs, quadrumanous clambering and, rarely, brachiation; terrestrial locomotion is by quadrupedal knuckle-walking (forelimb bears weight through the dorsal surface of knuckles and medial phalanges rather than palm). Skeletal features, including mobile shoulder joint, narrow scapula and triangular rib cage are adaptations for efficiency in arboreal foraging via vertical climbing, grasping support and arm-hanging. Terrestrial bipedal walking is rare, e.g. during play and aggressive displays, or when carrying food (Hunt 1994, Videan & McGrew 2002, Carvalho *et al.* 2012).

Relatively large incisors (Shea 1983), with elongated cutting surfaces relative to molar teeth (Pickford 2004), are likely adaptive for tearing into large, fleshy fruits. Male canines ca. 25–40% greater in height than in ♀♀, functioning in intrasexual competition (Leutenegger & Shell 1987, Plavcan & van Schaik 1992).

All populations use tools that provide access to important foods such as termites ('fished' for with modified twigs and grass stems; McGrew 1994, Sanz *et al.* 2004, Fowler & Sommer 2007, Abwe &



Lateral, palatal and dorsal views of the skull of Eastern Chimpanzee *Pan troglodytes schweinfurthii* adult male.

Morgan 2008), hard-shelled nuts (smashed open with stones, logs or sticks; Boesch & Boesch 1983, Sakura & Matsuzawa 1991) and honey (McGrew 1994, McLennan 2011). Some tools are widely distributed, such as sponges made by chewing leaves or moss to absorb drinking water (Sugiyama 1995, Lanjouw 2002). However, most are restricted to a few populations or even individuals, such as those involved in aggression (e.g. sticks used to club others; Wrangham & Peterson 1996). Variation in tool use may be explained by a combination of ecological, genetic and cultural factors (Whiten *et al.* 1999, Gruber *et al.* 2009, Langergraber *et al.* 2011).

Self-medication is evidenced by two distinct behaviours. Swallowing of whole, often folded, hispid leaves is practised by many populations, and likely expels intestinal parasites through physical action (Wrangham 1995, Huffman 1997). Chewing of bitter pith is well known in one site (Mahale, Tanzania), and is suspected to control gut pathogens via ingestion of steroid glucosides (Huffman & Seifu 1989; Jisaka *et al.* 1992).

Adults sleep in nests that they construct or refine each evening, or rest in by day (Goodall 1962). Tree nesting is most common, though some communities also utilize ground nests (e.g. Maughan & Stanford 2001). Mean nest heights of 10–20 m are reported from most sites (Fruth & Hohman 1994, 1996), though nest height can vary substantially within populations (e.g. Budongo, Uganda: 2.5–32.5 m, n = 601, Brownlow *et al.* 2001). Males tend to nest at lower heights than ♀♀ (Brownlow *et al.* 2001), perhaps due to their

weight. Robust Chimpanzees are selective in tree species and habitat types utilized for nesting; they prefer areas of high, dense vegetation and different tree species from those they feed from, though the particular species used varies by site (Fruth & Hohman 1994). Nests are frequently constructed at sites adjacent to recent feeding sites (Goodall 1986). High temperatures can lead individuals to seek refuge in less open portions of the habitat. Caves are sometimes used in the warmer, more open habitats in Fongoli, Senegal (Pruetz 2007).

Robust Chimpanzees spend the majority of their waking hours in the pursuit of food. An average of ca. 55% of the day is spent foraging (Gombe, Tanzania: 46–60% in four seasons, Wrangham 1977, Budongo: 49%, Newton-Fisher 1999b). Resting (ca. 25%), travelling (ca. 14%) and allogrooming (ca. 6%) are the next most frequent activities (Wrangham 1977).

Foraging and Food Omnivorous. Ripe fruit specialists. Ripe fruit pulp is both an important and preferred food, comprising ca. 60% of the diet in most populations, whether measured as a proportion of feeding time, items used, or gross weight. Diet in any given month consists of 0–90% fruit (e.g. Hladik 1977, Nishida & Uehara 1983, Emery Thompson & Wrangham 2008a, Watts *et al.* 2012a, b). Leaves or piths are major supplemental foods, particularly during months of low ripe fruit availability. Small amounts of unripe fruit, seeds, flowers, bark, wood, shoots, sap, honey, insects, eggs and vertebrate prey are also consumed. Red colobus monkeys *Procolobus* spp. are the most frequent mammalian prey reported (Struhsaker 2010, Lwanga *et al.* 2011); Robust Chimpanzees in the wild also consume Guerezas *Colobus guereza*, Blue Monkeys *Cercopithecus mitis stuhlmanni*, Red-tailed Monkeys *Cercopithecus ascanius*, Olive Baboons *Papio anubis*, Yellow Baboons *Papio cynocephalus*, Vervets *Chlorocebus pygerythrus*, Uganda Grey-cheeked Mangabeys *Lophocebus ugandae*, lesser galagos *Galago* spp., dwarf galagos *Galagoides* spp., Bushbucks *Tragelaphus scriptus*, Bushpigs *Potamochoerus larvatus*, Sunis *Nesotagus moschatus*, duikers *Cephalophus* spp. and *Philantomba* spp., White-tailed Mongooses *Ichneumia albicauda*, Bush Hyraxes *Heterohyrax brucei*, and a variety of rodents, birds, and tadpoles (Goodall 1986, Newton-Fisher *et al.* 2002, Watts & Mitani 2002, O'Malley 2010). Partial and complete cannibalization of chimpanzee infants has also been observed (Arcadi & Wrangham 1999). Hunting is performed almost exclusively by adult ♂♂, though ♀♀ and adolescents sometimes follow a hunt closely and kill incapacitated animals. Though individuals come across potential prey items frequently, the probability of attempting a hunt (and of succeeding) varies with seasonal food availability, the number of adult ♂♂ travelling together, and the presence of low or broken canopy that thwarts prey escape (Watts & Mitani 2002, Gilby 2004, Gilby & Wrangham 2007). Participation of highly skilled hunters promotes investment of other ♂♂ in hunting (Gilby *et al.* 2008).

Feeding typically begins shortly after dawn, declines at midday and resumes in the late afternoon before nesting. Fruits tend to be eaten earlier in the day than lower quality resources like leaves (Hladik 1977, Wrangham 1977).

Robust Chimpanzees in the wild do not often share food or provide direct provisioning to offspring, though young offspring can take bites from the mother's mouth or hand. Meat is the major shared food item, though portions are not shared by all group members, or even by all of the hunting party. Though it has been argued that meat may be used as a currency for social bonding (Nishida *et al.*

1992) or sexual access (Stanford *et al.* 1994), studies suggest that sharing is mainly a response to costs imposed by intensive begging or harassment (Wrangham 1975, Stevens & Gilby 2004).

Mean day ranges vary from 1.9 km/day (mothers at Kibale Forest, Uganda, Pontzer & Wrangham 2004) to 4.6 km/day (adult ♂♂ at Gombe, Wrangham 1977). In addition to community-level variation (e.g. at Taï, Côte d'Ivoire: 2.1 km/day in Middle Community, 4.2 km/day in South Community, Herbinger *et al.* 2001), ♂♂ range farther than ♀♀ within communities (e.g. at Kibale, 2.0 km/day for adult ♀♀ without clinging infants, 2.4 km/day for adult ♂♂, Pontzer & Wrangham 2004). Day range is expected to vary with the location and abundance of food resources, as well as with age and physical condition (Wrangham 1977, Herbinger *et al.* 2001, Pontzer & Wrangham 2004). On rare occasions, an individual may travel more than 10 km in a single day (Wrangham 1975), while sick, injured, or heavily pregnant individuals sometimes do not move at all in a day.

Home-ranges typically vary from 6–32 km² (e.g. Wilson 2001, Williams *et al.* 2002b). In low-density populations, community ranges can be >200 km². Ranges of individual ♂♂ are large and broadly overlapping, whereas ♀♀ often limit ranging to smaller core areas or 'neighbourhoods' within the community range (Hasegawa 1990, Wilson 2001, Emery Thompson *et al.* 2007a). Males are highly territorial; encounters near borders can result in killing of extra-community ♂♂, ♀♀ or infants (reviewed in: Arcadi & Wrangham 1999, Wilson & Wrangham 2003). Males modify vocal and grouping behaviour in accordance with this risk (Wilson *et al.* 2007); small parties, and particularly ♀♀ with dependent infants, avoid borders (Chapman & Wrangham 1993, Williams *et al.* 2002b). Groups of ♂♂ actively patrol border areas (Watts & Mitani 2001) and respond with agonistic approach to vocalizations of strangers (Wilson *et al.* 2001). Given the significant risk involved, encounters with neighbouring ♂♂ are only initiated when the aggressors have a clear numerical advantage (Wilson *et al.* 2001). Home-range size at Gombe is positively associated with ♀ reproductive rates, suggesting that ♂♂ defend territories to increase resources available to reproductive ♀♀ (Williams *et al.* 2004).

Social and Reproductive Behaviour Robust Chimpanzees are social, with a fission–fusion social organization in which the members of an expanded social network ('community') form smaller temporary associations ('parties') (Nishida 1968, Sugiyama 1968). Party size can vary as a function of food patch size and availability, presence and number of cycling ♀♀ with sexual swellings, and social affinities of community members (e.g. Wrangham *et al.* 1996, Doran 1997a, Matsumoto-Oda 1999b, Pepper *et al.* 1999). Most communities contain 20–60 individuals, including multiple breeding ♂♂ and ♀♀ and their offspring. However, communities can number >140 individuals or, in particularly disturbed habitats, <20 individuals (Reynolds 2005, Watts 2007).

Males are philopatric. Some ♀♀ remain in their natal community, though most transfer during adolescence (Pusey 1980). Females rarely transfer after their first birth, though cases have been noted in three communities (Nishida *et al.* 1990, Williams *et al.* 2002b, Emery Thompson *et al.* 2006a). Sexually attractive swellings of the anogenital region (see Reproduction and Population Structure) likely facilitate transfer into a new community (Nishida 1979, Boesch & Boesch-Achermann 2000).

Overt aggression among ♀♀ is rare, with daily feeding competition reduced by foraging in smaller parties and maintaining more differentiated core areas than those of ♂♂ (Wrangham 2000b, Williams *et al.* 2002a). Female–female aggression intensifies when foraging areas are challenged, such as upon new immigrations, and can include severe attacks on other ♀♀ and infanticide attempts on their infants (Townsend *et al.* 2007, Kahlenberg *et al.* 2008, Pusey *et al.* 2008). Though subtly expressed, ♀♀ form linear dominance relationships that are correlated positively with age (Pusey *et al.* 1997, Wittig & Boesch 2003b, Kahlenberg *et al.* 2008). Males form linear dominance hierarchies; high-ranking ♂♂ are more aggressive than low-ranking ♂♂ and have higher testosterone and cortisol levels (Muller 2002, Muller & Wrangham 2004a, b). Male status competition frequently involves strategic alliances between two or more ♂♂ who affiliate preferentially and cooperate in aggressive contests (Goodall 1986, Newton-Fisher 1999a, Mitani *et al.* 2000a). Male aggression occurs most often in the contexts of sexual competition, reunion after ♂♂ have been travelling separately and unresolved dominance relationships (Goodall 1986, Muller 2002). Males also direct both mild and severe aggression at ♀♀, particularly during oestrous periods (Matsumoto-Oda & Oda 1998, Muller *et al.* 2007). The majority of aggressive interactions involve charging or stationary displays directed at specific individuals or as a generalized demonstration of strength and size. Display hallmarks are piloerection and erratic or exaggerated behaviours that emphasize size or strength, such as bipedal charges, pant-hoot vocalizations, tree-limb dragging, ground-stamping, ‘drumming’ on tree buttresses, flinging rocks, slapping at individuals in passing and shaking vegetation or hitting others with it. Despite these animals’ potential to inflict serious damage, severe aggression within groups is rare (Goodall 1986). However, within-community lethal attacks on mature ♂♂ have been observed at three field sites (Kitopeni *et al.* 1995, Fawcett & Muhumuza 2000, Watts 2004), and within-community infanticides by ♂♂ have been reported from five sites (Wrangham *et al.* 2006).

Males are more gregarious than ♀♀ (Doran 1997a, Pepper *et al.* 1999, Wrangham 2000b, Emery Thompson & Wrangham 2006), though this sex difference varies by community; while ♀♀ in East Africa generally travel in small parties (Wrangham 2000b), larger parties among ♀♀ in Tai are attributed to protection from Leopard *Panthera pardus* predation (Lehmann & Boesch 2005). Affiliation rates among adult ♂♂ are higher than among adult ♀♀ (Watts 2000c, Arnold & Whiten 2003). While ♂♂ maintain a larger number of social relationships, ♀♀ may form a small number of strong relationships with other kin or non-kin ♀♀ while rarely associating with others (Lehmann & Boesch 2008, Wakefield 2008).

Grooming is the principal affiliative behaviour and is commonly mutual, with partners grooming simultaneously or in succession. Rank has some effects on grooming distribution, particularly across age–sex classes, but reciprocity is high, especially among adult ♂♂. Males have more grooming partners than ♀♀ but tend to concentrate most grooming on a few major partners, often those near them in the hierarchy (Boesch & Boesch-Achermann 2000, Watts 2000b, c). Among ♂♂ grooming can be exchanged for support in agonistic interactions (Watts 2002). Grooming can be used to reconcile conflicts, ease tension, or console others, as can conciliatory behaviours such as embracing, social mounting, reaching out a hand or the back of the wrist, touching another’s genitals, or

placing an open mouth on the partner in a mock bite (De Waal & Van Roosmalen 1979, Goodall 1986). Reconciliation occurs in only about 15% of conflicts among wild groups (Arnold & Whiten 2001, Kutsukake & Castles 2004), and individuals with stronger social relationships reconcile more often (Wittig & Boesch 2003a).

Sexual behaviour is concentrated during morning hours, peaking just after individuals emerge from nests and at mid-day after feeding has slowed (Tutin 1979, Wallis 2002). Mating is promiscuous; ♀♀ copulate hundreds of times for each birth, usually with all ♂♂ in the community (Wrangham 2002). Female copulation rates while in oestrus vary from approx. 0.4–5/h, dependent on ♀ fecundity and the number of potential ♂ partners (Emery Thompson 2005, Watts 2007). During the periovulatory period, ♀♀ behave proceptively to fewer ♂♂ and resist more (Matsumoto-Oda 1999a, Stumpf & Boesch 2005), which appears to be a response to ♂ coercive aggression rather than explicit ♀ choice (Muller *et al.* 2007, 2011). Males most frequently initiate copulations, particularly when ♀ conception risk is high (Goodall 1986, Emery Thompson & Wrangham 2008b); this can involve direct approach and chasing or solicitation of ♀ approach by displaying an erect penis and swaggering, stamping his feet, flicking his penis, shaking or bending branches, nodding his head, waving his arms, or clipping bunches of leaves with his teeth. Females initiate copulations or respond to solicitations by presenting their swollen genital areas, often while crouching down and backing towards the ♂. Copulations are brief (mean = 7 seconds, range 2–13 seconds, *n* = 132; Nishida 1997). Most are dorsoventral, with the ♂ holding the ♀ with one hand or leaning back for balance while thrusting his pelvis forward. Females often scream near the end of copulation and/or dart away before or after ejaculation.

Most mating is opportunistic in bisexual parties, but high-ranking ♂♂, alone or in pairs, often mate-guard, preventing other ♂♂ from gaining access to the ♀ (Tutin 1980, Tutin & McGinnis 1981, Watts 1998a). Male relationship strength impacts mating tolerance (Duffy *et al.* 2007). A third ♂ strategy is to form a consortship with a ♀, leading her away from the rest of the community for days or weeks (Tutin & McGinnis 1981). Long-term data from Gombe suggested that fewer than one-quarter of conceptions could have occurred in consortships, though this is presumably an effective strategy for particular ♂♂ (Wallis 1997).

Play occurs in individuals of all ages, peaking between two and four years (Goodall 1968, Clark 1977). Before infants are able to move independently, mothers tickle them or apply soft bites. Gradually, individuals play with other juveniles, as well as with adult ♂♂ and related adult ♀♀. Play often consists of tickling, wrestling and chasing, as well as mock-biting, somersaulting, swinging and slapping at one another, and flinging objects. Sticks are sometimes carried and treated as ‘dolls’, particularly by juvenile ♀♀ (Kahlenberg & Wrangham 2010). Related or unrelated nulliparous ♀♀ provide occasional alloparental care in short bouts (typically 4–10 minutes). Mothers rarely interact with unrelated offspring, but can be aggressive to them (Nishida 1983). Adults, usually male–male or male–female dyads, also play together, often beginning with ‘finger-wrestling’ behaviour with outstretched arms that can escalate into more intense tickling, gentle wrestling, or slow circular chasing (Goodall 1986).

In populations that use tools to fish for termites or crack nuts, juvenile development includes learning of tool use. Juveniles begin



Eastern Chimpanzees *Pan troglodytes schweinfurthii*.

these extractive techniques at ca. 2–4 years, taking several years to achieve proficiency. Females spend more time observing their mothers use tools and practise more often, reaching proficiency sooner than ♂♂ who spend more time in social play (Boesch & Boesch-Achermann 2000, Lonsdorf *et al.* 2004).

Robust Chimpanzees have a broad vocal repertoire, with many graded or hybridized calls (Goodall 1986). A major species-typical vocalization is the ‘pant-hoot’, incorporating a build-up of low booming sounds followed by series of high-pitched whoops, usually in chorus with others. Pant-hoots are given in many situations of excitement, such as when joining a group and during displays; pant-hoots carry over long distances (ca. 1 km for a single caller; J. Mitani pers. comm.), and parties often respond to each other’s calls. Acoustic structure of calls varies across populations (Mitani *et al.* 1999). Males of adjacent communities produce acoustically different calls, independent of genetic relatedness, suggesting the role of vocal learning (Crockford *et al.* 2004). Within communities, pant-hoot structure varies among individuals, and individual calls are often stereotyped enough for experienced human observers to identify the caller (Marler & Hobbett 1975, Mitani *et al.* 1996). During pant-hoot displays, ♂♂ often drum on tree buttresses with hands and feet, providing a secondary acoustic signal that carries at least as far as the vocal signal. The temporal patterning of drumming, like the pant-hoot itself, varies both inter-individually and across populations (Arcadi *et al.* 1998). The ‘pant-grunt’ is given at close range as a signal of deference when a higher-ranking individual approaches or threatens aggression; it is often accompanied by other signs of submission. High-pitched screaming is common in the context of aggression or other threat. Acoustic characteristics of screams differ between aggressor and victim, and vary with severity of attack, though this can be exaggerated in eliciting support from high-ranking individuals (Slocombe & Zuberbühler 2005, 2007). ‘Hoo’ vocalizations signify curiosity or mild distress, while shrill ‘wraah’ barks indicate alarm (e.g. sighting of a snake or strange individual) and short ‘barks’ are given as threats. Juveniles make a variety of whimpers and loud, protesting cries, in addition to panting ‘laughs’ given during play. Soft grunts are given in many contexts; good food sources elicit excited grunts. Exaggerated lip smacking and tooth clapping often occurs during grooming.

Facial expressions are equally diverse and graded (Goodall 1986, Parr *et al.* 2005). A ‘play face’ is indicated by an open mouth with lower teeth exposed and upper teeth usually covered. During displays and agonism, lips are pressed tightly together so that the mouth bulges out. Slight fear or submission can be indicated with a ‘fear grin’ in which lips are drawn back and teeth exposed. More intense fear is shown with an open mouth, lips retracted and both upper and lower lips exposed, with or without screaming. Begging and infant protests are often accompanied by a ‘pout-face’, extension and flattening of the upper lip while the lower lip is drawn back slightly. In older individuals both lips are extended and spread open during excitement or mild distress, with or without accompanying pant-hoot or hoo vocalizations.

Outside of hunting, individuals rarely interact with other species, though interspecific grooming and play have been observed with other primate species (*P. cynocephalus*, Goodall 1986; *C. ascanius*, Tinka & Reynolds 1997). Despite their dominant body size, Robust Chimpanzees are occasionally attacked by monkeys (*P. cynocephalus*, Eastern Red Colobus *Procolobus rufomitratus*, Goodall 1986; *C. guereza*, Newton-Fisher *et al.* 2002).



Eastern Chimpanzee *Pan troglodytes schweinfurthii* adult male.

Reproduction and Population Structure Cycling ♀♀ display exaggerated swelling of the anogenital tissue for approximately 10–12 days of a cycle that averages 35 days in length (Tutin 1980, Wallis 1997, Matsumoto-Oda 1999b, Emery Thompson 2005). Fully tumescent swelling size varies from 60 to 450 cm² in the dorsal area (Emery & Whitten 2003, Deschner *et al.* 2004); larger swellings are associated with higher fecundity and greater ♂ sexual interest (Emery & Whitten 2003, Deschner *et al.* 2004). Copulations are almost entirely confined to the period of maximal sexual swelling. Ovulation is most likely during the last six days of swelling; copulation rates with adult ♂♂ and possessive mating by dominant ♂♂ increase during this period (Hasegawa & Hiraiwa-Hasegawa 1990, Matsumoto-Oda 1999a, Deschner *et al.* 2003, Emery Thompson 2005). Sexual swellings sometimes also occur during pregnancy (Wallis & Goodall 1993).

Males have a long filiform penis (length when erect: mean = 14.4 cm, range 10–18 cm, n = 11, captivity, Dixson & Mundy 1994). Testes are also large (combined weight, captive specimens, mean = 119 g, n = 3; Schultz 1938; mean = 158 g, n = 10; Dixson & Mundy 1994) and capable of producing large quantities of highly motile sperm. A portion of ejaculate coagulates to form a sperm plug in the ♀ reproductive tract that can prevent another male’s sperm from entering (Dixson & Anderson 2002).

Breeding is not strictly seasonal in that births can occur in all months of the year. However, long-term reproductive patterns reveal seasonal variation in births and the number of oestrous ♀♀; timing of these peaks varies by population and cannot be strictly attributed to climatic features such as rainfall (Nishida *et al.* 1990, Wallis 2002). For example, at Gombe, higher copulation rates and two-thirds of conceptions occur in the drier half of the year (May–Oct); at Budongo, conceptions peak (50%) in the three driest months of the year (Dec–Feb), but reach their nadir (11%) in the second, milder dry season (Jun–Aug) (Wallis 2002). Conception timing and the number of oestrous ♀♀ is closely related to utilization of high-quality food resources, many of which are themselves seasonally unpredictable (Emery Thompson & Wrangham 2008a).

Mean gestation length is ca. 230 days both in captivity (range 202–261 days, $n = 56$; Yerkes 1943, Martin *et al.* 1978, Shimizu *et al.* 2003) and in the wild (range 207–259, $n = 42$; Wallis 1997, M. Emery Thompson pers. obs.). Females near term are often increasingly solitary and lethargic, and may withdraw from social contact in the peripartum period (Pusey *et al.* 2008). Obvious labour lasts between 40 minutes and 8 h and typically takes place in an arboreal nest (Keeling & Roberts 1972, Pusey *et al.* 2005a). In captivity, infants weigh ca. 1.7 kg (range 0.9–2.4 kg, $n = 57$) at birth (Leigh 1996, Hamada & Udono 2002). Most births are singletons, though twins do occur; survival of both twins is rare in the wild.

The average inter-birth interval following surviving offspring is ca. 5–6 years (range 23–132 months, $n = 288$ intervals; Emery Thompson *et al.* 2007b). The majority of the birth interval is spent in lactational amenorrhoea (Gombe: mean = 46 months, range 29–68 months, $n = 28$, Wallis 1997; Mahale: mean = 55 months, range = 33–74 months, $n = 38$, Nishida *et al.* 2003; Tai: mean = 23 months, range = 2–60, $n = 26$, Deschner & Boesch 2007).

Growth in captive ♀♀ continues until ca. 12 years and continues about 1 year longer in ♂♂, who grow faster and with a more apparent growth spurt in late adolescence (Gavan & Swindler 1966, Leigh & Shea 1995). Dental and postcranial analyses both illustrate that wild individuals grow markedly slower and mature later than captive individuals (Kimura & Hamada 1996, Zihlman *et al.* 2007).

Adolescence in both sexes entails changes in association, as individuals begin to travel in separate parties from their mothers. Females begin experiencing minor, irregular swellings at ca. eight years, with larger, cyclic swellings emerging at ca. 10–11 years (Wallis 1997, Goodall 1986, Nishida *et al.* 2003). During puberty, ♀♀ begin to associate more frequently with unrelated ♂♂, and transfer usually follows the first full swelling (Pusey 1979, 1980, Stumpf *et al.* 2009). First births occur at ca. 14 years (range = 9–23 years, Wallis 1997, Boesch & Boesch-Achermann 2000, Nishida *et al.* 2003, Sugiyama 2004). Puberty in ♂♂, beginning at approximately eight years, entails substantial growth in muscle mass and testicular volume, along with increases in aggressive behaviour and affiliation with adult ♂♂. By the end of adolescence, around 15 years, ♂♂ are dominant to all ♀♀ and juveniles.

Paternity studies suggest that high-ranking ♂♂ father the majority of offspring (Constable *et al.* 2001, Vigilant *et al.* 2001, Boesch *et al.* 2006, Newton-Fisher *et al.* 2010). This is likely due mostly to intensified competition and increased mate-guarding by dominant ♂♂ in the periovulatory period (Emery Thompson & Wrangham 2008b). Females also have considerable variance in reproductive success. Dominant ♀♀ at Gombe have higher birth and infant survival rates, and faster-maturing daughters, than do subordinate ♀♀ (Pusey *et al.* 1997). The location of a female's core area can also influence her reproductive rate as a result of uneven access to resources within heterogeneous habitats (Williams *et al.* 2002b, Emery Thompson *et al.* 2007a).

Life expectancy at birth is less than 15 years, with about 20% mortality in the first year; life expectancy at maturity (age 15 years) is another 15 years (Hill *et al.* 2001). Males have significantly higher mortality rates as infants and as adults (Hill *et al.* 2001).

Maximum life-span is probably >60 years in the wild (R. Wrangham pers. obs.), and some captive individuals (including 'Cheeta' of *Tarzan* fame) are thought to have reached their 70s. Births

to ♀♀ aged 40 years or over are noted from five wild populations with the eldest mother aged mid-50s (Emery Thompson *et al.* 2007b, Jones *et al.* 2010); the maximum age of birth exceeds 60 years in captivity (A. Halloran pers. comm.). Senescence and accumulating health deficits lead to declining birth rates in the fourth decade (Emery Thompson *et al.* 2007b), and advancing age is associated with longer cycles, shorter oestrus periods, and changes in pituitary hormone production (Graham 1979, Nishida *et al.* 2003, Videan *et al.* 2006). However, recent studies of birth rates and ovarian follicle depletion suggest that few Robust Chimpanzees reach menopause (Emery Thompson *et al.* 2007b, Jones *et al.* 2007). This may help explain why ♂ chimpanzees prefer older ♀♀ as mates (Muller *et al.* 2006).

Sex ratios at birth tend to be slightly female-biased (e.g. 1 : 1.27 at Tai, Boesch & Boesch-Achermann 2000; 1 : 1.14 at Mahale, Nishida *et al.* 1990; 1 : 1.04 at Gombe, Goodall 1983). Mature ♀♀ typically outnumber mature ♂♂, though this varies markedly between populations (e.g. 1 : 3 at Tai, Boesch & Boesch-Achermann 2000; 1 : 1.3 at Ngogo, Pepper *et al.* 1999) and within populations over time (between ca. 1 : 1 and 1 : 3 within 15 years at Gombe, Goodall 1983; and Budongo, Townsend *et al.* 2007). Adult:immature ratios show no consistent trends across populations (e.g. 1 : 1.3 during stable period at Tai, Boesch & Boesch-Achermann 2000; 1.3 : 1 at Ngogo, Pepper *et al.* 1999), a result of the variable proportion of mature ♂♂; ratios of adult ♀♀ to immatures range between 1 : 1 and 1 : 2 (Goodall 1983, Pepper *et al.* 1999, Boesch & Boesch-Achermann 2000).

Predators, Parasites and Diseases Most common causes of 'natural' mortality are respiratory diseases, diarrhoeal or wasting diseases, within-species aggression and, in some locations, predation (see next section, Goodall 1986, Hill *et al.* 2001, Nishida *et al.* 2003, Williams *et al.* 2008). Robust Chimpanzee skeletons exhibit high incidence of trauma, suggesting that falls from the canopy contribute significantly to morbidity and mortality (Jurmain 1997, Carter *et al.* 2008). In many locations, human activities, including hunting and accidental snaring, are major sources of mortality (see Conservation).

Many populations appear to be untroubled by natural predators, but Leopard attacks can be a major source of mortality in the Tai Forest, accounting for 39% of deaths during one 3-year time span (Boesch 1991). See also Henschel *et al.* (2005, 2011). A transient pride of Lions *Panthera leo* preyed upon at least six chimpanzees at Mahale (Tsukahara 1993). In a population of free-ranging, rehabilitant chimpanzees, predation by Nile Crocodiles *Crocodylus niloticus* is strongly suspected in at least two deaths (Brewer-Marsden *et al.* 2006).

Because Robust Chimpanzees are phylogenetically close to humans, they are highly susceptible to many human infectious diseases, including parasites and, especially, viruses. Many of these diseases are fatal or cause morbidity, with severe consequences for normal behaviour and reproduction (Wallis & Lee 1999, Butynski 2001, Köndgen *et al.* 2008).

Robust Chimpanzees are particularly susceptible to frequently deadly respiratory illnesses, especially pneumonia, influenza and tuberculosis (Goodall 1986, Wallis & Lee 1999, Nishida *et al.* 2003, Reynolds 2005, Köndgen *et al.* 2008). Various forms of diarrhoeal disease or wasting illnesses are commonly reported (Goodall 1986,

Nishida *et al.* 2003); severe peritonitis has been diagnosed in some of these individuals (D. Koehler in Goodall 1986, W. Boardman *et al.* in Reynolds 2005). Lethal outbreaks of scabies (A. Pusey in Wallis & Lee 1999), poliomyelitis (Goodall 1986), anthrax (Leendertz *et al.* 2004) and Ebola haemorrhagic fever (Formenty *et al.* 1999, Leroy *et al.* 2004) also occur. Ebola outbreaks have been particularly devastating (Ryan & Walsh 2011). A single outbreak in Tai Forest in 1994 killed 25% of the community under study (Formenty *et al.* 1999); an outbreak in the Congo probably killed the majority of chimpanzees in Lossi Sanctuary (Leroy *et al.* 2004, Bermejo *et al.* 2006). While transmission to humans can occur while handling dead chimpanzees, the rapid, high mortality of infected apes suggests they are not a reservoir of the virus (Formenty *et al.* 1999).

Pan t. troglodytes and *P. t. schweinfurthii* each harbours a distinct strain of the simian immunodeficiency virus (SIV) (Santiago *et al.* 2002, Nerrienet *et al.* 2005); viral phylogenetic analyses point to *P. t. troglodytes* as the reservoir for HIV-1 in humans with at least three independent transmission events (Gao *et al.* 1999, Keele *et al.* 2006). The handling and consumption of Robust Chimpanzees as bushmeat is the likely source of transmission and remains a continuing threat for transmission of rapidly evolving viruses (Hahn *et al.* 2000).

The wide range of intestinal parasites found in faecal samples of free-ranging individuals include hookworms (*Necator*), pinworms (*Probstmayria*, *Enterobius*), whipworms (*Trichuris*), other nematodes (esp. *Oesophagostomum*, *Strongyloides*, *Physaloptera*), amoeba (*Entamoeba*, *Iodamoeba*), thorny-headed worms (*Prosthenorchis*), tapeworms (*Bertiella*) and flagellates (esp. *Chilomastix*) (e.g. File *et al.* 1976, McGrew *et al.* 1989a, Ashford *et al.* 2000, Krief *et al.* 2005). *Giardia* infections also occur and are suspected to have arisen from contact with human faeces (Ashford *et al.* 2000). Ciliates (esp. *Troglodytella*) are routinely present and may be digestive symbionts (Collet *et al.* 1984). Malarial infection also occurs; the endemic *Plasmodium reichenowi* is a close relative of the *P. falciparum* parasite common in humans (Escalante & Ayala 1994).

Conservation IUCN Category (2012): Endangered. All subspecies Endangered. CITES (2012): Appendix 1.

Though Robust Chimpanzees are, in theory, protected from international trade by CITES regulation and from hunting by national laws in most or all range countries, unsustainable hunting for 'bushmeat' is widespread, particularly in West Africa and central Africa, and represents a primary threat to species survival. Commercial logging intensifies hunting pressure by providing roads that allow hunters to penetrate deep into the forest and extract meat for urban markets (Butynski 2001, Kormos *et al.* 2003, Walsh *et al.* 2003, Morgan *et al.* 2011). While eating of primates is taboo in much of East Africa, chimpanzees are killed while crop-raiding and by immigrant hunters and traders (Wrangham 2001). They are also incidental victims of snares and steel-jaw traps intended to capture other species. One-third of mature chimpanzees in the Budongo study community (Reynolds 2005) and 27% in Kanyawara (Wrangham 2000a) exhibit snare injuries ranging from missing finger segments to severely deformed or missing hands and feet; lethal infections also occur (Wrangham & Goldberg 1997, Reynolds 2005). Given that these field sites maintain active snare removal programmes, it is likely that animals at other unmonitored sites within reach of human hunters suffer even more snare-related injuries and deaths.

Habitat destruction and degradation due to agricultural expansion, timber extraction and mining threatens the long-term survival of Robust Chimpanzees and other forest-dependent species. Chimpanzees suffer these effects disproportionately due to large home-range requirements, strict territoriality and slow reproductive rate. Gallery forests are a key habitat in savanna areas as they serve as ecological corridors among otherwise fragmented populations (Fleury-Brugière & Brugière 2010).

When habitat loss puts apes in close proximity and frequent contact with human populations, outbreaks of tuberculosis, Ebola and other anthropogenic illnesses are serious threats (Wallis & Lee 1999, Butynski 2001).

Capture and trade of infant Robust Chimpanzees for use as pets, research and entertainment results in a large number of deaths due to trauma and malnourishment of captured infants and killing of associated chimpanzees during capture (Kormos *et al.* 2003). Efforts to confiscate and rehabilitate orphaned chimpanzees have quickly filled existing sanctuaries. While rehabilitated chimpanzees have shown prospects for survival in natural environments under limited monitoring (Goossens *et al.* 2005, Brewer-Marsden *et al.* 2006), reintroduction efforts are limited by funds as well as by the availability of appropriate habitat not already inhabited by chimpanzees or under threat by humans.

The combined pressures from human interference result in an inverse relationship between Robust Chimpanzee densities and proximity to major cities (Walsh *et al.* 2003). Habitat loss and fragmentation, and ever-increasing human populations, all bring more chimpanzees into close contact with humans (Wrangham 2001), one result of which can be extremely quick and severe decline of chimpanzee populations (Campbell *et al.* 2008a).

Measurements

Pan troglodytes schweinfurthii

HB (♂ ♂): 834 (770–925) mm, n = 7

HB (♀ ♀): 783 (700–850) mm, n = 4

T (both sexes): 0 mm

HF (♀ ♀): 220 mm, n = 1

E (♂ ♂): 77 (66–95) mm, n = 4

E (♀ ♀): 64 (60–67) mm, n = 3

WT (♂ ♂): 41.7 (28–56) kg, n = 43

WT (♀ ♀): 34.4 (20–46) kg, n = 50

GLS (♂ ♂): 192.8 (188–201) mm, n = 9

GLS (♀ ♀): 184.4 (175–194) mm, n = 7

GWS (♂ ♂): 132.6 (123–142) mm, n = 9

GWS (♀ ♀): 121.3 (115–128) mm, n = 7

Cranial volume (♂ ♂): 385.8 (323–408) ml, n = 4

Cranial volume (♀ ♀): 389.5 (354–406) ml, n = 6

HF, E and HB: DR Congo (AMNH specimens, Allen 1925)

WT: Range given for all specimens, mean equally represents four populations – Mahale, Tanzania (Uehara & Nishida 1987), Gombe, Tanzania (Pusey *et al.* 2005b, A. Pusey pers. comm.), Kibale, Uganda (Carter *et al.* 2008) and eastern DR Congo (Rahm 1967). WT from Mahale, Kibale and DR Congo is similar (♂ ♂: 43 kg, ♀ ♀: 35 kg), but Gombe population ca. 10% lighter (♂ ♂: 39 kg, ♀ ♀: 31 kg).

Cranial volumes: Gombe, Tanzania (Morbeck & Zihlman 1989)

Other cranial measurements: various localities (AMNH, NMNH, BMNH, FMNH specimens, Shapiro 1995)

Pan troglodytes verus

T (both sexes): 0 mm

HF (♂ ♂): 247 (S.D. = 11.2) mm, n = 7

HF (♀ ♀): 234 (S.D. = 9.6) mm, n = 6

WT (♂ ♂): 47.0 (46–49) kg, n = 3

WT (♀ ♀): 41.6 kg, n = 3

GLS (♂ ♂): 191.1 (183–201) mm, n = 10

GLS (♀ ♀): 184.6 (171–194) mm, n = 11

GWS (♂ ♂): 131.3 (121–139) mm, n = 10

GWS (♀ ♀): 121.9 (115–132) mm, n = 12

HF: measurements from ca. 12-year-old captive individuals, may include other subspecies (Yerkes Regional Primate Research Center, Gavan 1971)

WT: various localities (Morbeck & Zihlman 1989, Smith & Jungers 1997)

Cranial measurements: Côte d'Ivoire, Liberia, Sierra Leone (AMNH specimens, Shapiro 1995)

Pan troglodytes troglodytes

HB (♂ ♂): 855 (800–959) mm, n = 8

HB (♀ ♀): 806 (702–905) mm, n = 36

T (both sexes): 0 mm

WT (♂ ♂): 59.7 kg, n = 5

WT (♀ ♀): 45.8 kg, n = 4

GLS (♂ ♂): 197.6 (190–209) mm, n = 16

GLS (♀ ♀): 186.5 (175–199) mm, n = 11

GWS (♂ ♂): 132.1 (122–152) mm, n = 50

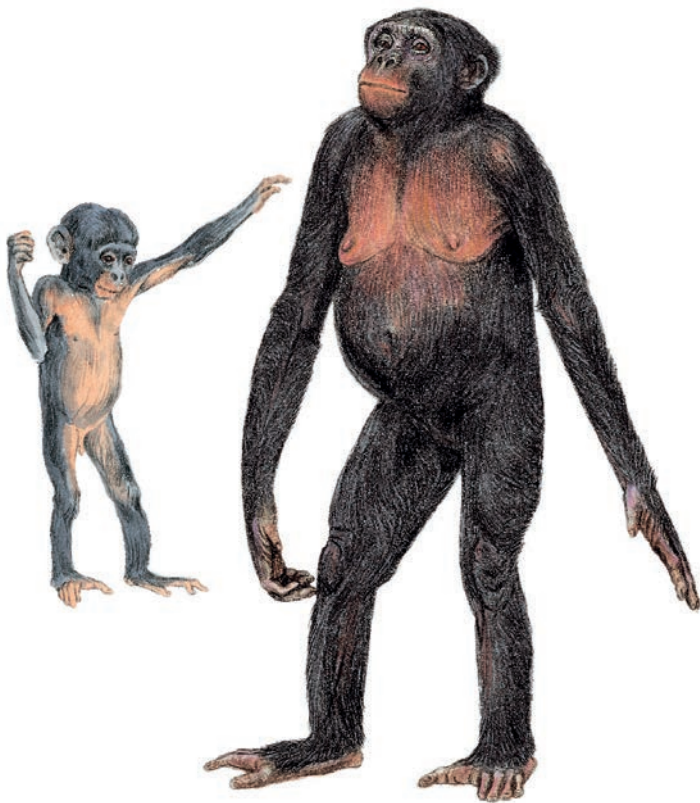
GWS (♀ ♀): 120.5 (112–134) mm, n = 44

HB, WT: Western Africa, may include some *P. t. verus*. No range given for WT (primarily PCM specimens, Shea 1981, Jungers & Susman 1984, Smith & Jungers 1997, Groves 2001)

Cranial measurements: various localities (RMCA specimens, Cramer 1977; AMNH specimens, Shapiro 1995)

Key References Boesch & Boesch-Achermann 2000; Boesch *et al.* 2002; Goodall 1986; Kormos *et al.* 2003; McGrew *et al.* 1996; Nishida 1990; Wrangham *et al.* 1994; Oates 2011.**Melissa Emery Thompson & Richard W. Wrangham*****Pan paniscus* GRACILE CHIMPANZEE (BONOBO, PYGMY CHIMPANZEE)**

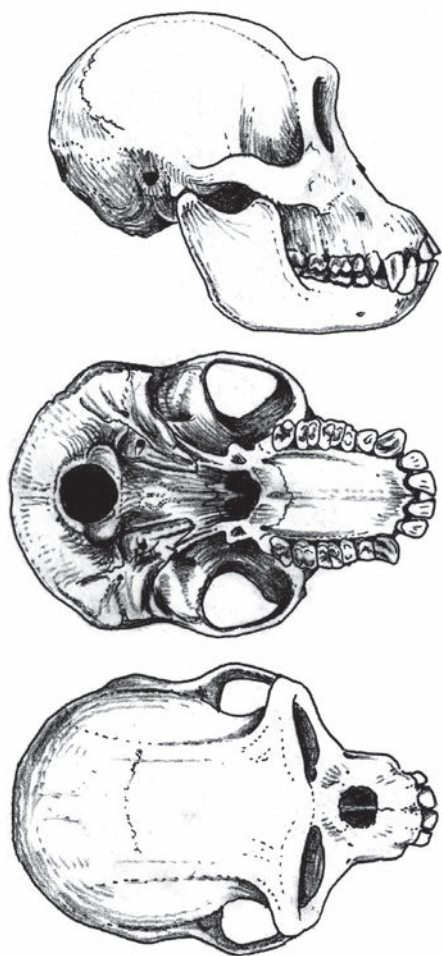
Fr. Bonobo; Ger. Bonobo

Pan paniscus Schwarz, 1929. Rev. Zool. Bot. Afr. 16: 4. South of the upper Maringa R., 30 km south of Befale, DR Congo.Gracile Chimpanzee (Bonobo) *Pan paniscus* infant (left) and adult female (right).

Taxonomy Monotypic species. In 1929, Schwarz designated the Gracile Chimpanzee as a subspecies (*Pan satyrus paniscus*) of the Robust (or Common) Chimpanzee *Pan troglodytes*. Thompson (1997) suggested that the first description of the Gracile Chimpanzee occurred in 1887 (*Troglodytes niger* var. *marungensis* Noack 1887) from a specimen collected in the Marungu Mts, west of L. Tanganyika. DNA analyses have, however, identified the specimen as *Pan troglodytes schweinfurthii* (J. Eriksson pers. comm.). Coolidge (1933) raised the Gracile Chimpanzee to a species, *Pan paniscus*. The original common name was 'Pygmy Chimpanzee', but the term 'Bonobo' came into regular use after Heck (1939) reported what he mistakenly thought to be an indigenous term. Some primatologists now prefer the name 'Gracile Chimpanzee' as this is the most descriptive common name for *P. paniscus*. Debate continues over which of the several common names is most appropriate (Gijzen 1974, White 1996, Kortlandt 1997, Kano & Nishida 1999, Butynski 2001).

Studies on nuclear DNA (Reinartz 1997) and mitochondrial DNA (Eriksson *et al.* 2004) from wild-born specimens show varying levels of genetic structuring among the eastern, northern and west-central populations of *P. paniscus*. Likely barriers to gene flow are the large rivers that transverse the species' range, especially the Lomami R. in the east (Eriksson *et al.* 2004). In captivity, a *P. paniscus* ♂ and *P. troglodytes* ♀ have produced offspring but it is not yet known whether these are fertile (Vervaecke & Van Elsacker 1992). Synonyms: none. Chromosome number: 2n = 48 (Chiarelli 1962a) exhibiting species distinctive karyotypic patterns (Gijzen 1974, Bogart & Benirschke 1977).

Description A black, forest-dwelling great ape that resembles *P. troglodytes* but is more gracile (Jenkins 1990). Sexes alike in colour. In the



Lateral, palatal and dorsal views of skull of Gracile Chimpanzee (Bonobo)
Pan paniscus adult male.

wild, adult ♀ ♀ about 73% as heavy as adult ♂ ♂. Females in captivity average 82% of males' weight. This is comparable to body weight dimorphism in the Eastern Chimpanzee *P. t. schweinfurthii* and humans (Parrish 1996). Despite its common name 'Pygmy Chimpanzee', *P. paniscus* is not a diminutive form of chimpanzee; the range in body size and weight overlaps (up to 85%) that of *P. t. schweinfurthii*. Head rounded with small brow. Face black, even in infants. Lips light to pink, contrasting with face. Ears small, close to sides of the head. Head hair flattened with long horizontal tufts of hair surrounding the face. Body covered by long silky black hair (except for face, hands, feet and genitalia). Anal tuft white. Upper molar rows curved. Features such as smaller head, less prominent canine teeth, white tail tuft and low degree of sexual dimorphism are considered by some primatologists to be juvenile characteristics indicating paedomorphic evolution (Gijzen 1974, Kuroda 1979, 1980, Kano 1992).

Geographic Variation None recorded.

Similar Species None within the known geographic range of *P. paniscus*.

Pan troglodytes. Parapatric with *P. paniscus*. More robust, ca.15% heavier. Head large, vault flattened, face prognathic, brow ridge well developed. Skull length greater (♂ ♂: mean = 198 mm, range = 182–213 mm, n = 23; ♀ ♀: mean = 186 mm, range



Pan paniscus

= 172–198 mm, n = 19) (Jenkins 1990). Mouth region not contrastingly pink. Chin beard noticeably white in adults. Anal tuft black in subadults and adults. Face pink at birth turning black by maturity. Upper molar rows parallel.

Distribution Endemic to central Congo Basin, DR Congo. Rainforest BZ. Distribution delimited by two large river systems: Congo-Lualaba River System on west, north-west, north and east, and Kwa-Kasai-Sankuru River System on south-west and south. Limits of distribution uncertain south-east of Sankuru and Lomami headwaters. Current distribution poorly known as surveys not conducted over most of the species' range and most records >20 years old. Today *P. paniscus* has a patchy, highly fragmented distribution (Butynski 2001). Rare or absent where human population density is high (Kano 1984, 1992, Reinartz *et al.* 2006). Surveys in the central portion of the range confirm presence at: North and South Sectors of Salonga N. P. (Reinartz 2003, Blake 2005, Reinartz *et al.* 2006, 2008, Grossman *et al.* 2008), Lui Kotal on the western edge of Salonga N. P. (Hohmann & Fruth 2003c, Mohneke & Fruth 2008), Wamba (Furuichi & Mwanza 2003, Idani *et al.* 2008), Lomako (Dupain *et al.* 2003), Lukuru (Thompson & Tshina-tshina 2003), Kokolopori north-east of Wamba (Thompson *et al.* 2003), and south of Lokoro (J. Eriksson pers. comm.). In the eastern extent of the range, *P. Paniscus* occurs between the Lomami R. and Congo-Lualaba R. (Hohmann & Eriksson 2000, Vosper *et al.* 2007). Five remnant populations have been confirmed at the extreme western end of the range: three between Lac Tumba and Lac Mai Ndombe (Mwanza *et al.* 2003, Inogwabini *et al.* 2007, 2008), and two between the Congo R. and Kwa-Kasai R. (Inogwabini *et al.* 2007).

Habitat Mosaic of low, dry, semi-deciduous forest punctuated by monotypic stands of primary evergreen forest, swamp forest and secondary forest (Evrard 1968, Boubli *et al.* 2004). In the drier and higher elevations of the southern portion of the range, the forest is

increasingly interposed by grasslands. Optimal habitat is dense, humid, mixed mature, semi-deciduous lowland forest on *terra firma* soils with herbaceous understorey (Marantaceae, Zingiberaceae) (Kano 1983, Kano & Mulavwa 1984, Kortlandt 1995, Reinartz *et al.* 2006). *Pan paniscus* can, however, utilize a wide variety of habitat types, including young and old secondary forest, grassland, marsh grasslands, seasonally inundated and swamp forests, and agriculture (Sabater Pi & Vea 1990, Thompson-Handler *et al.* 1995, Hashimoto *et al.* 1997). Altitudinal range: 300–565 m. Annual temperature range: 19–30°C. Annual rainfall range: 1670–2210 mm (Kano 1992, Thompson 1997).

Abundance The majority of the survey data for *P. paniscus* are two decades old and vast areas of the potential range, estimated at 343,000 km² (Butynski 2001), have never been surveyed (Thompson-Handler *et al.* 1995, Dupain & Van Elsacker 2001b). Population estimates are based on density estimates ranging from 0.25 ind/km² (Thompson 1997) to 0.40 ind/km² (Kano 1984) and extrapolated to the probable occupied area. Because of widespread hunting by humans and loss of habitat, the area occupied by *P. paniscus* at present is believed to be far less than the potential historical range. The most recent estimates are that there are between 20,000 and 50,000 individuals (Butynski 2001, Dupain & Van Elsacker 2001b).

Adaptations Semi-terrestrial and diurnal. *Pan paniscus* is considered more of a true forest ape than *P. troglodytes* and, as such, many of the morphological characters that separate *P. paniscus* from *P. troglodytes* are described as adaptations to differences in the habitats they occupy (Susman 1984a). Compared to *P. troglodytes*, *P. paniscus* has narrower shoulders, chest and hips, longer legs, nearly equal leg and arm lengths, a greater proportion of leg to body mass resulting in a lower centre of gravity, and a higher propensity to walk bipedally (Zihlman 1980, 1996, Susman 1984a, Thompson 2002). However, recent studies that extend the range of *P. paniscus* into drier forest/savanna mosaic habitats challenge this assumption (Thompson 2002).

When arboreal, *P. paniscus* engages in more leaping and diving types of movements than does *P. troglodytes* (Doran 1996). Whether or not *P. paniscus* is more arboreal than *P. troglodytes*, as once believed, is open to question. *Pan paniscus* is said to engage in bipedal behaviour more often than *P. troglodytes*, especially when carrying objects, entering water, to peer over tall grasses and during friendly social behaviour (whereas *P. troglodytes* is more likely to engage in bipedalism during aggressive interactions). Webbing that sometimes occurs between the toes of *P. paniscus* may be related to their willingness to enter water to forage. Molars of *P. paniscus* are more flattened than those of *P. troglodytes*, providing a greater grinding surface area. This may allow higher consumption rates of terrestrial herbaceous vegetation by *P. paniscus*, which may be associated with decreased individual feeding competition and larger social groups (Malenky & Stiles 1991). However, measurements of mandibular traits do not indicate that *P. paniscus* is necessarily adapted to a coarser and more fibrous diet than *P. troglodytes* (Taylor 2002).

Tool-using behaviour of *P. paniscus* differs from that of *P. troglodytes* (Hohmann & Fruth 2003a). The ability of *P. paniscus* to make and use tools is clear from observations of the extensive use of tools by captive individuals (Takeshita & Walraven 1996), as well as the complexity of their manipulation of objects in the wild during nest-building and arboreal bridging (Fruth & Hohmann 1993, Ingmanson

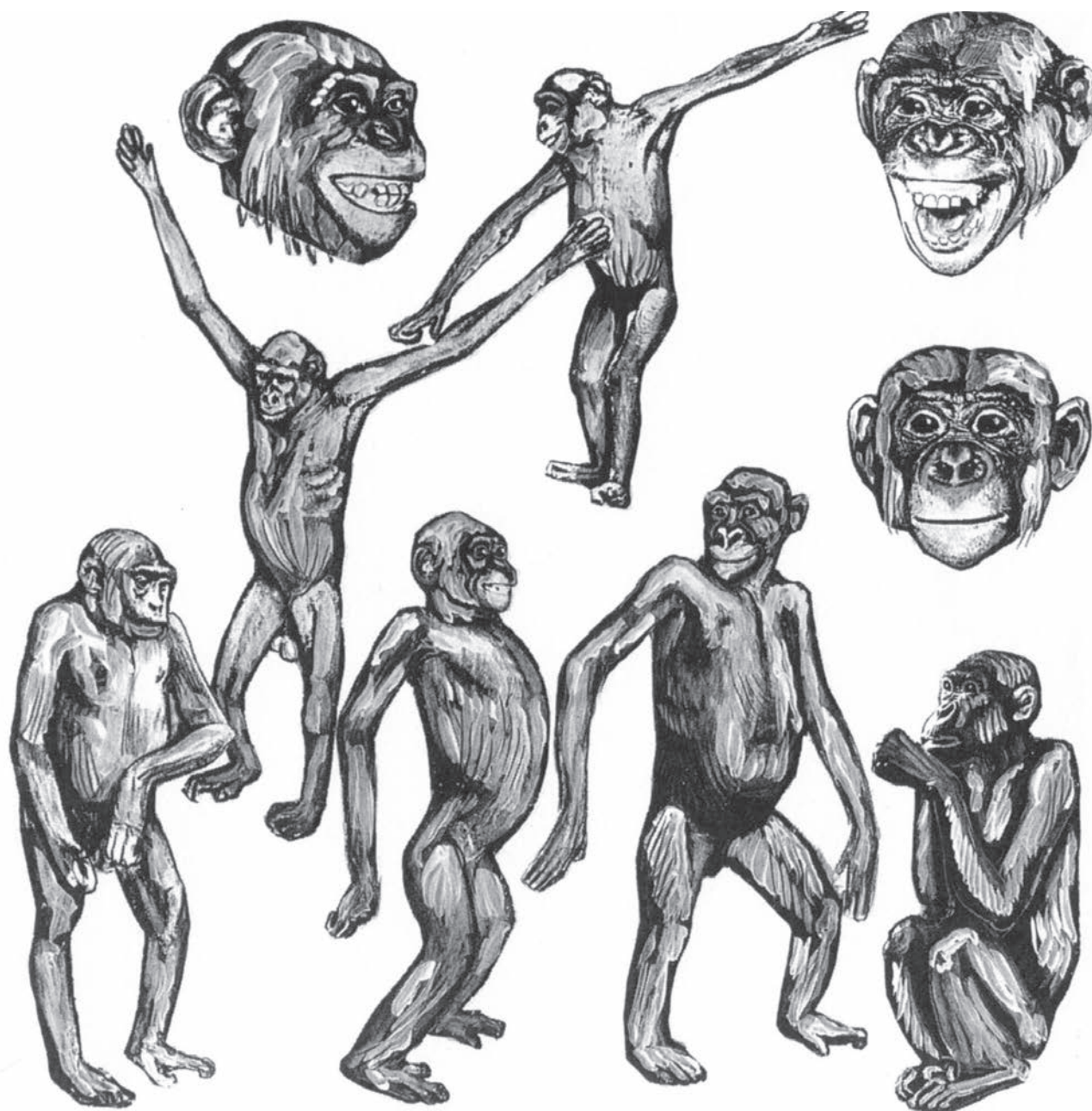
1996). *Pan paniscus* rarely use tools for food acquisition. However, they do incorporate tools into social communication, such as branch-dragging by adults (see Social and Reproductive Behaviour), or by infants during social play (Ingmanson 1988, 1996). In addition, *P. paniscus* occasionally makes and uses napkins, fly swatters, tooth picks and other items, and drapes vegetation over the head and shoulders to provide protection during heavy rains (Kano 1982, Fruth & Hohmann 1993, Ingmanson 1996).

Foraging and Food Omnivorous. *Pan paniscus* spend up to 40% of their time foraging/feeding. Most foraging occurs within groups while in trees (White 1989). At Lomako and Wamba, group size is positively correlated with food patch size and food abundance (White 1989, Kano 1992, Mulavwa *et al.* 2008, Furuichi *et al.* 2008), but studies in Salonga do not reveal any correlation (Hohmann *et al.* 2006).

Fruits, located most often in the canopy, constitute 54–83% of the diet. Fruits of Apocynaceae vines, *Pancovia*, *Dialium*, *Polyalthia* and *Annonidium*, are particularly common in the diet. Leaves comprise 15–21% (Caesalpinaceae, Papilionaceae) of the diet, and seeds, piths, shoots and animals constitute the remainder (Badrian & Malenky 1984, Kano & Mulavwa 1984, White 1992, Idani *et al.* 1994). Diet is high in protein, low in tannins and, compared to *P. troglodytes*, is relatively low in sugar and crude fat (Hohmann *et al.* 2006). Terrestrial herbaceous vegetation (predominantly Marantaceae) is an important source of protein (Malenky & Stiles 1991). When foraging on herbs, *P. paniscus* quietly splinter off into subgroups in search of shoots and petioles of *Haumania liebrechtsiana*, *Megaphrynium macrostachyum* and *Aframomum* spp. Fruit consumption (and species consumed) varies according to availability (Kano & Mulavwa 1984), whereas Marantaceae herbs are utilized at approximately the same levels throughout the year (Malenky & Stiles 1991). *Pan paniscus* occasionally eat marshland herbs and grasses (Uehara 1990), and sub-aquatic algae and vegetation (Thompson 2002). Coprophagy is practiced but is rare (Sakamaki 2010).

Although ‘cooperative hunting’ has never been observed, duikers (*Cephalophus* spp. and *Philantomba monticola*), anomalures *Anomalurus* spp., shrews, snakes and many invertebrate species are eaten (Ihobe 1992, Kano 1992, Hohmann & Fruth 1993). Patterns of meat eating, meat sharing and prey search image appear to vary among populations (Hohmann & Fruth 2003a). *Pan paniscus* travel 0.4–6.0 km per day while foraging in forest habitat (Kano 1992). Once a food patch is located, group feeding is often preceded by vocalizations and animated movements as food is collected and consumed (Kuroda 1980, Kano 1992). Food begging and sharing are frequent (Fruth & Hohmann 2002). Adults may reach out a hand slowly toward the possessor’s food, and may touch and grin. The possessor responds either by ignoring or by giving the beggar a portion of the food. Copulations between ♂♂ and ♀♀, as well as homosexual encounters, are frequent during feeding times (e.g. ♀♀ engage in intensive genito-genital rubbing).

Social and Reproductive Behaviour Social. As for *P. troglodytes*, the community or unit-group is the largest mixed-sex social unit, whose members maintain a closed social network. Community’s members share a discrete, large home-range (22–60 km²), but extensive overlap between communities (40–66%) may exist and there may be seasonal and yearly variations in home-ranges (Van Elsacker *et al.* 1995). Communities contain 10–22 individuals



Distinctive proportions of Gracile Chimpanzee (Bonobo) *Pan paniscus*; longer limbs and more slender than Robust Chimpanzee *Pan troglodytes* (gouache from photographs).

in Lomako and 30–120 individuals in Wamba (Kano & Mulavwa 1984). There are almost equal numbers of adult ♂♂ and adult ♀♀ in Wamba (Kano 1992), whereas in at least one Lomako community, the adult sex ratio is strongly female-biased (Fruth 1995, Hohmann *et al.* 1999). Entire communities come together less often at Lomako than at Wamba (Kano 1992, F. J. White 1992, Fruth 1995). Through fission and fusion, membership of parties changes in varying degrees within days, hours or even minutes. By contrast, membership of communities changes only with the birth or death of members, or permanent inter-group transfer.

Smallest functional unit of *P. paniscus* daily life is the party, defined as individuals remaining in sustained proximity to one another, or

within earshot of each other (Hashimoto *et al.* 2003), or travelling and foraging together (Van Elsacker *et al.* 1995). Larger, more stable parties are seen in Wamba, with on average 13 individuals (Kano 1992), than in Lomako, with about five individuals on average (1–16) (Hohmann & Fruth 2002). Parties usually contain mature individuals of both sexes, with more ♀♀ than ♂♂ (Kano 1982, F. J. White 1988, Fruth 1995, Hohmann & Fruth 2002).

Pan paniscus lives in fission–fusion communities or unit-groups (Kano 1992). Unit-groups have recognizable members, with ♀ transfer out of, and ♂ residency in, the natal group. A possible case of fusion of unit-groups was observed at Wamba following population disruption related to human activities (Hashimoto *et al.*

2008). In comparison to *P. troglodytes* in East Africa, *P. paniscus* unit groups tend to be more cohesive and larger. Strong social bonds exist among ♀♀ and ♂♂, and among ♀♀ (Furuichi 1997, Furuichi *et al.* 1998, Hohmann *et al.* 1999, Hohmann & Fruth 2002, Stevens *et al.* 2006). Relative to *P. troglodytes*, *P. paniscus* has low levels of aggression, both between and within unit groups. However, violent acts do sometimes occur during encounters of different unit groups (Hohmann & Fruth 2002). Males and ♀♀ both form dominance hierarchies within the group (Furuichi 1997, Vervaecke *et al.* 2000a, Stevens *et al.* 2007). Unrelated ♀♀ form social bonds with each other and support each other against aggression by ♂♂ (Kano 1992, Parrish 1996, Vervaecke *et al.* 2000b). The bond between mothers and their adult sons is very strong, long lasting and may play a role in the dominance hierarchy. In one unit-group at Wamba, ♂♂ rarely became alpha-male until their mother achieved alpha status (Kano 1992, Furuichi 1997).

Sexual behaviour occurs in almost all age–sex categories, including infants (Hashimoto 1997), and plays an important role in the non-reproductive social cohesion of a group, i.e. maintaining male–female coexistence (Kano 1992). Compared with *P. troglodytes*, *P. paniscus* ♀♀ exhibit sexual swellings that extend beyond the ovulatory period (Thompson-Handler 1990, Heistermann *et al.* 1996, Vervaecke 1999, Furuichi & Hashimoto 2002). Adult copulations are not limited to time of ovulation, but the majority of copulations occur at maximum swelling, a period that is loosely linked to the fertile phase (Furuichi 1987, Kano 1989, Vervaecke 1999, Reichert *et al.* 2002). Takahata *et al.* (1996) showed that adult *P. paniscus* ♂♂ at Wamba do not copulate more than adult *P. troglodytes* ♂♂ at Mahale (*P. paniscus*: 0.10–0.21/h; *P. troglodytes*: 0.20–0.29/h), that adolescent *P. paniscus* ♂♂ copulate less frequent than adolescent *P. troglodytes* ♂♂, and that adult *P. paniscus* ♀♀ copulate at an equal rate to adult *P. troglodytes* ♀♀. Only adolescent *P. paniscus* ♀♀ copulate more frequently than adolescent *P. troglodytes* ♀♀. Copulations also occur between adult ♀♀ and juvenile ♂♂, though rarely between mothers and sons (Kano 1992). Adult ♂♂ mount and thrust, and occasionally penetrate juvenile ♀♀, but the frequency of penetration increases as ♀♀ reach adolescence and begin exhibiting sexual swellings. Adult ♂♂ also use genital stimulation toward infants as an apparent means of soothing them (Hashimoto 1997). Sexual contact between adult ♂♂ takes the form of mounting, often reciprocally, rump–rump touching and, on rare occasions, penile fencing.

Sexual activities between adult ♀♀ have been much studied (Hohmann & Fruth 2002, 2003b, Fruth & Hohmann 2006). Genito-genital (G-G) rubbing occurs when two ♀♀ embrace ventrally and move their hips laterally, rubbing the labia and clitoris together (Kano 1992). Females engage in G-G rubbing during periods of excitement, such as greeting and feeding. This behaviour may serve as a mechanism for social bonding between the ♀♀, allowing them to cooperate and share feeding spaces without aggression. Young ♀♀ who first enter a group quickly seek out the dominant ♀♀ and engage in G-G rubbing (Idani 1991).

Kuroda (1984) describes the use of a rocking gesture by free-living *P. paniscus* to request closer proximity to one another. Ingmanson (1996) describes the use of branch-dragging to convey complex information related to coordinating group movement, such as direction and timing of movement.

Reproduction and Population Structure Most of the demographic data for *P. paniscus* come from Wamba, where free-living *P. paniscus* have been food provisioned and studied for 20 years (Kano 1992, Furuichi *et al.* 1998). In both species of *Pan*, mature ♀♀ have continuous cyclic ovarian activity accompanied by overt swelling of the anus and labia, reaching maximal volume and turgidity in the period around ovulation. In wild *P. paniscus*, swelling cycles and menarche first occur at 9–12 years of age (Kano 1992); in captivity, they occur, on average, at 8.2 years (range = 6.0–11.2 years, *n* = 9; Thompson-Handler 1990). Onset of menarche is generally followed by 2–3 years of adolescent sterility (Van Elsacker *et al.* 1997). In *P. paniscus*, the period of swelling is longer than the window of fertility, and the end of the period of maximal swelling and the timing of ovulation are weakly associated (Heistermann *et al.* 1996, Reichert *et al.* 2002). Wild adult ♀♀ at Wamba showed maximal swelling during 48% of the cycle (Kano 1992), while wild adolescent ♀♀ showed maximal swelling most of the time (Kano 1984). Swelling in *P. paniscus* may conceal rather than signal ovulation (Kano 1992, Reichert *et al.* 2002) leading to longer periods of ♀ sexual receptivity in *P. paniscus* than in *P. troglodytes* (Thompson-Handler *et al.* 1984, Furuichi & Hashimoto 2002).

In wild ♀♀, the mean interval between two successive maximal swellings is 42 days (range = 37–49, *n* = 3; Furuichi 1987). In captivity, the mean length of the menstrual cycle is 34 days (range = 31–51 days, *n* = 6; Heistermann *et al.* 1996). If conception does not occur, there are 1–3 days with slight vaginal bleeding (Vervaecke 1999, Vervaecke *et al.* 1999). In contrast to *P. troglodytes*, where the labia are entirely flat during non-fertile phases of a normal cycle, the labia are flat only in some captive adults during the latter half of pregnancy and/or early lactation (Vervaecke 1999). Captive ♂♂ reach sexual maturity at an average age of ca. seven years (Thompson-Handler 1990). However, DNA analyses confirm the paternity of captive ♂♂ as young as five years of age (Leus *et al.* 2003, Reinartz *et al.* 2003). In captivity, gestation averages 234 days (range = 229–238, *n* = 3) from hormonally detected ovulation, or 246 days (range = 227–277, *n* = 11) from last menses (Harvey 1997). Single young are most frequent; twins are exceptional. Newborns weigh ca. 1.5 kg (range = 1.2–1.8, *n* = 13; Mills *et al.* 1997).

Age of ♀♀ at first birth ca. 12–13 years in the wild (Kano 1992), and 14.2 years (*n* = 6) (Kuroda 1989) and 10.5 years in captivity (8–15 years, *n* = 20; De Lathouwers & Van Elsacker 2003, 2005, Reinartz *et al.* 2003). At Wamba, mean birth interval is 4.8 years (*n* = 28; Furuichi *et al.* 1998). At Lomako, however, the median birth interval may be as long as nine years (B. Fruth pers. comm. in Knott 2001). Mean birth interval in captivity is 4.93 years (range = 1.88–7.60, *n* = 34; De Lathouwers & Van Elsacker 2003, 2005). The infant is generally weaned at the birth of the next sibling. In the wild, births occur throughout the year with a peak (57%) in Mar–May (*n* = 15) and a low period (43%) from Oct–Feb (Furuichi *et al.* 1998). Furuichi *et al.* (1998) reported a 4.5% first-year mortality for infants at Wamba (*n* = 22 infants); however, this rate is the lowest reported for any great ape and may be a sampling artefact. In captivity, 16% of *P. paniscus* infants are stillborn (De Lathouwers & Van Elsacker 2003). Of live born infants, 21% die during the first year (*n* = 155 infants) (Reinartz *et al.* 2003) and 84% of live-born offspring survive until five years of age (*n* = 51) (De Lathouwers & Van Elsacker 2003, 2005, Reinartz *et al.* 2003).

Sex ratios:

♂ : ♀ ratio: 1 : 1.1 (n = 70; Kitamura 1983). 1 : 1.3 (n = 69; Kuroda 1979). 1 : 2.1 (n = 22) for Group 1; 1 : 1.6 (n = 23) for Group 2; 1 : 1.1 (n = 9) for Group 3 (White 1988).

Adult ♂ : adult ♀ ratio: 1 : 1.1 (n = 31; Kano 1982). 1.1 : 1 (n = 32) for Group 1; 1 : 0.9 (n = 39) for Group 2 (Kano 1987).

Adolescent ♂ : adolescent ♀ ratio: 1 : 1.6 (n = 13; Kano 1982). 1 : 1.6 (n = 18) for Group 2 (Kano 1987). In captivity, no sex ratio bias at birth (64 : 73 : 4 = ♂ : ♀ : unknown; n = 141; De Lathouwers 2004).

Females in the wild typically emigrate from their natal group at ca. 7–8 years. Males remain in their natal group and retain a lifelong bond with their mother (Kano 1992). Maximal life-span is unknown for wild *P. paniscus*, and is >50 years in captivity (Leus *et al.* 2003, Reinartz *et al.* 2003).

Predators, Parasites and Diseases Except where local taboos against hunting still exist, humans are the main predator of *P. paniscus* throughout the range, and present rates of off-take are unsustainable (Thompson-Handler *et al.* 1995, Butynski 2001, Dupain & Van Elsacker 2001a, Reinartz *et al.* 2006, Hart *et al.* 2008, Idani *et al.* 2008). Natural predators probably include Leopards, African Crowned Eagles *Stephanoaetus coronatus* (Horn 1980, Kano 1983), Nile Crocodiles *Crocodylus niloticus* and Central African Rock Pythons *Python sebae*.

Because of its close genetic relationship to humans and frequent close contact with humans, *P. paniscus* is highly susceptible to numerous human diseases, including the following (reviewed Butynski 2001, Woodford *et al.* 2002): colds, pneumonia, influenza, tuberculosis, measles, mumps, hepatitis A and B, bacterial meningitis, diphtheria, yellow fever, whooping cough, poliomyelitis, encephalomyocarditis, and haemorrhagic fevers such as Ebola. Thus, the species is vulnerable to the diseases/epidemics manifested in surrounding human populations. Near Wamba *P. paniscus* has displayed leprosy- and herpes-like lesions, and a high incidence of limb abnormalities (Kano 1992). Internal parasites in wild *P. paniscus* include *Troglodytella* sp., *Capillaria* sp., *Trichuris* sp., *Strongyloides* sp., dicrocoeliid eggs and strongylid eggs resembling hookworm eggs (Hasegawa *et al.* 1983). Illnesses in newly orphaned *P. paniscus* commonly include severe diarrhoea (attributed to or exacerbated by parasites), infections (gram-negative bacteria), gum disease, severe psychological stress, immune suppression and life-threatening malnutrition (Messinger & Bi-Shamamba 1997, D. Messinger pers. comm.). Their parasites include *Ancylostoma* spp., *Trichomonas intestinalis*, *Strongyloides* spp., *Entamoeba histolytica*, whipworms, tapeworms, mites and lice (Messinger & Bi-Shamamba 1997, Butynski 2001). Captives are sensitive to respiratory infections and laryngeal air sacculitis (Rietschel & Kleeschulte 1989).

Conservation IUCN Category (2012): Endangered. CITES (2012): Appendix I.

Population decline is primarily the result of unsustainable hunting due to the combination of several key factors, including a growing

bushmeat trade (Butynski 2001, Dupain & Van Elsacker 2001a, Rose *et al.* 2003), the disappearance of traditional taboos against eating *P. paniscus* (Furuichi & Mwanza 2003), the uncontrolled infusion of firearms into the region combined with the occupation of once-remote areas by soldiers and displaced people during civil wars (Draulans & Van Krunkelsven 2002, Amman *et al.* 2003) and the lack of law enforcement. Formerly dense populations of *P. paniscus* (e.g. Lomako) may have suffered a decline of up to 75% as a consequence of the civil war and concomitant increases in hunting (Amman *et al.* 2003, Dupain *et al.* 2003). Trade in orphans for pets is a continuing problem (C. André pers. comm.) Massive habitat destruction stems from logging and agriculture. While logging in DR Congo has not yet reached the levels of other central African countries (Wolfire *et al.* 1998), where logging occurs it has caused habitat destruction, population fragmentation and a dramatic increase in bushmeat hunting (Butynski 2001, Dupain & Van Elsacker 2001a, Rose *et al.* 2003).

There is only one national park designated for *P. paniscus* protection, the Salonga N. P. It is not yet clear whether this Park harbours a viable population (Reinartz *et al.* 2006). Conservation priorities are: (1) to assess the distribution/abundance of *P. paniscus* in order to identify major populations; (2) to determine the degree of population fragmentation and the ecological factors affecting distribution; and (3) to direct resources toward law enforcement, support for protected areas and creation of additional protected areas.

In captivity, *P. paniscus* has the smallest population of all the great ape species: 168 individuals worldwide (excluding African sanctuaries). With intensive genetic and demographic management, the captive population can be self-sustaining for up to five generations (Reinartz *et al.* 2003).

Measurements*Pan paniscus*

HB (♂ ♂): 780 (730–830) mm, n = 4

HB (♀ ♀): 740 (700–760) mm, n = 4

T (both sexes): 0 mm

HF (♂ ♂): 22 (21–22) mm, n = 4

HF (♀ ♀): 22 (20–22) mm, n = 4

E (both sexes): 63 (55–72) mm, n = 7

WT (♂ ♂): 45 (37–61) kg, n = 7

WT (♀ ♀): 33 (27–38) kg, n = 6

GLS (♂ ♂): 163 (150–171) mm, n = 28

GLS (♀ ♀): 163 (142–172) mm, n = 31

Data from museum specimens from various localities in DR Congo (HB, WT: Jungers & Susman 1984; HF, E: Coolidge & Shea 1982; GLS: Jenkins 1990)

Key References Butynski 2001; Furuichi & Thompson 2008; IUCN & ICCN 2012; Kano 1992; Susman 1984b; Thompson-Handler *et al.* 1995.

Gay E. Reinartz, Ellen J. Ingmanson & Hilde Vervaecke

Tribe HOMININI

Hominins

Hominini Gray, 1825. *Annals of Philosophy* 10: 338.

An international scramble to find human and proto-human fossils, especially in Africa, has begun to flesh out the concrete, physical evidence for human evolution. Tracing the past fortunes of the Hominini, therefore, promises to become one of the best documented, and certainly the single most arresting, example of the process that has given rise not only to us but to all the astonishing diversity of life on Earth. It is this that makes the Hominini one of the most fascinating taxa among African mammals.

By the same token, this is a fast-moving field of enquiry and the wide scatter and fragmentary nature of most fossil hominins creates difficulties when it comes to listing and describing the substantial number of fossil forms belonging to this tribe.

The following genera are commonly recognized in the Hominini: *Sahelanthropus* Brunet *et al.*, 2002 ('Toumai'). Late Miocene (7–6 mya). Resemblances with gorillas *Gorilla* spp., chimpanzees *Pan* spp. and hominins suggest it might predate hominin emergence. While

possibly not Hominini, *Sahelanthropus* is listed here because it is a highly significant fossil for our understanding of hominin emergence.

Orrorin Senut *et al.*, 2001 (Millennium Human Ancestor). Late Miocene (ca. 6 mya).

Ardipithecus White *et al.*, 1995 (Ground Apes). Late Miocene to early Pliocene (5.8–4.4 mya). Also see White *et al.* (1994, 2009).

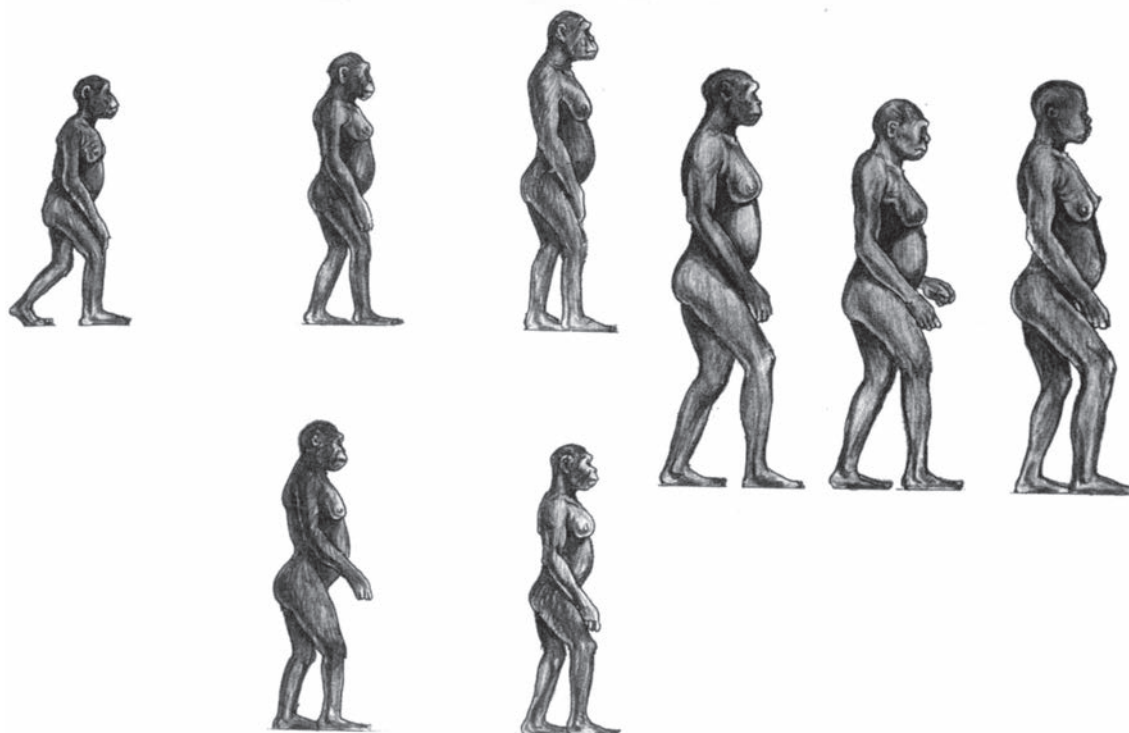
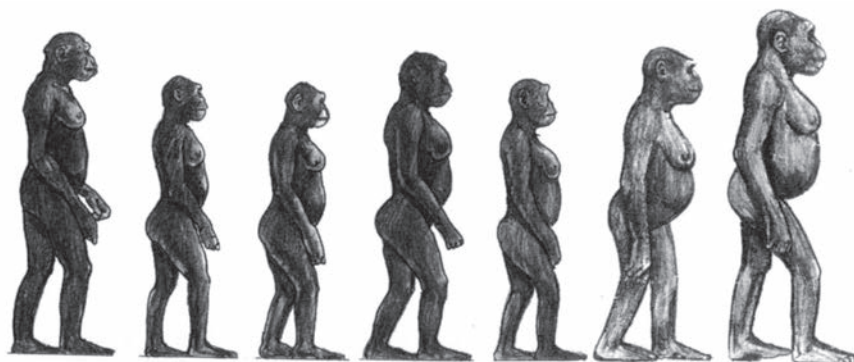
Praeanthropus Weinert, 1950 ('Lucies'). Early to mid-Pliocene (4.2–3.0 mya).

Australopithecus Dart, 1925 (Southern Ape and South Africa Man-ape). Mid- to late Pliocene (4.2–2.0 mya).

Kenyanthropus Leakey *et al.*, 1995 (Kenya Flat-face Man). Mid-Pliocene (ca. 3.5 mya).

Paranthropus Broom, 1938 ('Nutcracker Man'). Mid-Pliocene to early Pleistocene (2.6–1.4 mya).

Homo Linnaeus, 1758 (Early to Modern Humans). Mid-Pliocene (2.4 mya) to present day.



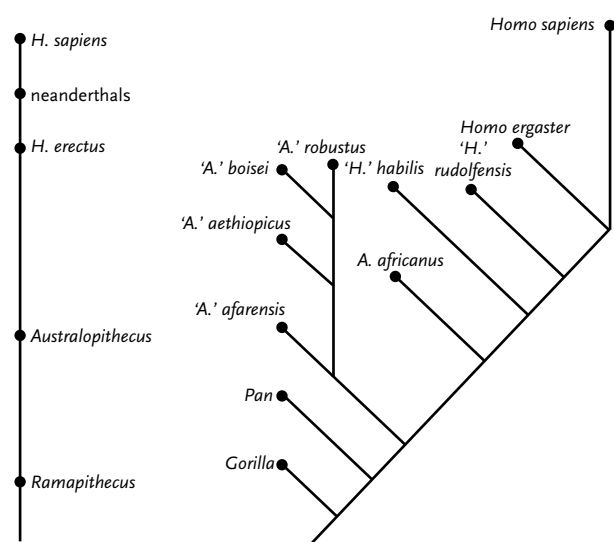
The certainty of ancestors – the uncertainty of ancestry (from Kingdon 2003).

Top row:
Australopithecus
(*Praeanthropus*) *anamensis*,
A. (P.) afarensis,
A. (P.) bahrelghazali,
A. (P.) aethiopicus,
A. (P.) garhi,
A. (P.) robustus,
A. (P.) boisei.

Middle row, left:
Orrorin tugenensis,
Kenyanthropus platyops,
Homo rudolfensis.

Middle row, right:
Homo ergaster,
H. heidelbergensis,
H. sapiens.

Bottom row, left:
Australopithecus africanus,
Homo habilis.

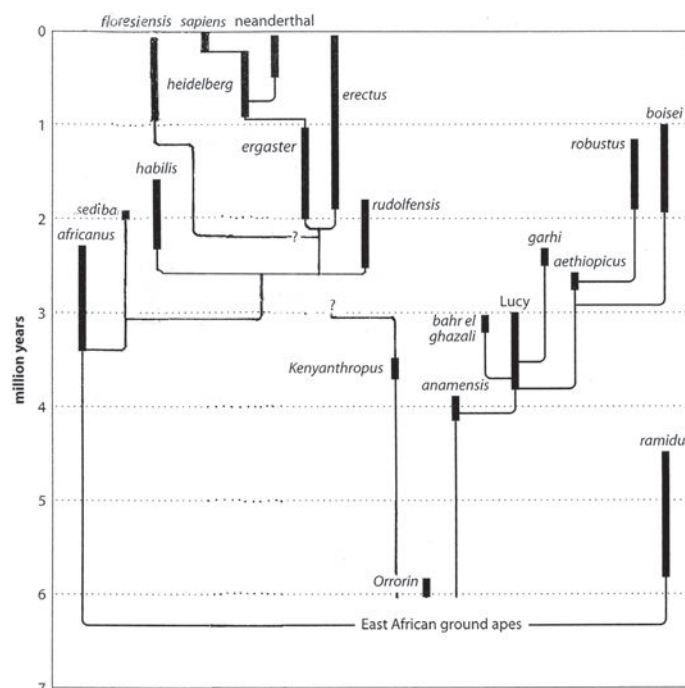


Changing perceptions of Human ancestry. Left: Loring Brace (1971). Centre: Olson (1981)/Falk (1988). Right: Hominin genealogy according to the 'Evolution by Basin Model' (modified after Kingdon 2003).

This classification includes at least three paraphyletic genera, that are presumed to incorporate successive lineal ancestors of *Homo*. There has, however, been much reshuffling of species from one genus to another, especially as some authorities do not recognize *Paranthropus* as separate from *Australopithecus*, and yet others think that a further genus, *Praeanthropus*, may be distinct from *Australopithecus* (Strait *et al.* 1997, Kingdon 2003). Recently, it has been proposed that all the described species in the Hominini should be incorporated into a single genus, *Homo*, which of course would lead to the tribe itself being redundant except that it does serve to separate bipedal humans from quadrupedal apes.

One must avoid the mistake of assuming that human evolution was unilineal, one species succeeding another in unbroken advance. This assumption, in as far as it still survives, is a legacy of the historical origins of the subject itself – among (mainly medically trained) anatomists, not among evolutionary biologists. It is only since the 1970s that it has become clearer that, just like most other mammals whose fossil record is at all well-known, multiple species of hominins arose, coexisted for a while and mostly became extinct without issue: a bush not a ladder.

The characteristics of the Hominini include highly manipulative hands, specializations for habitual upright posture, bipedal locomotion, and extreme reduction of the canine teeth (involving a particular shortening of the pointed tip, but also raising of the mesial and distal 'shoulders', to render the canine almost incisiform in both jaws). An intermediate stage of the development of the postural/locomotor specializations appears to be illustrated by *Ororin*; in which canine reduction (including reduction of sexual dimorphism) can be seen in the stepwise sequence *Ardipithecus kadabba* – *Ardipithecus ramidus* – *Australopithecus* (*Praeanthropus*) *anamensis* – *Australopithecus* (*Praeanthropus*) *afarensis* (using 'traditional' generic designations). While intense interest in the origins of our own species has led to extraordinary squabbles, taxonomic instability, and disagreements on phylogeny based on anatomical salami-slicing, there is no doubt that it has led to the



human fossil record being one of the best represented (and, despite all the controversies, best understood) of any mammal lineage. Dated phylogenetic trees serve to illustrate both the growth in the number of taxa thought to be distinct, and significant conceptual progress from the 'ladder' model of evolution (Loring Brace 1971) to the much more complex and bushy trees of contemporary thinking. Given that the fossil record is always incomplete, all trees are essentially provisional and tentative, and can be seen as steps in a series of successive approximations.

Beyond the number of genera, note the geographical range of fossils and presumed habitats of this family. Prior to some 2.5–2.0 mya (after the emergence of the genus *Homo*), all representatives of the Hominini appear to have been African. With few exceptions, these Pliocene hominins are known from just two regions: the Rift Valley of eastern and north-eastern Africa, and the caves of the Transvaal highveldt. Throughout their evolutionary history, Hominini have been typical of south-eastern Africa. Partly the reflection of a paucity of fossil sites, this bias shows up in numerous other organisms and supports the supposition that the primary split between proto-hominins and quadrupedal apes had a geographic and ecological base (Kingdon 1993, 2003).

What caused only one of the lineages of hominins listed above (i.e. *Homo*) to persist and survive? Part of the answer must extend back to an exploration of how the earliest ancestors of humans might have responded to some of the challenges posed by the environment of their region/ecology of origin. Among the influential modifications made in response to specific local ecologies and climates, we can infer adjustments in behaviours such as social organization and modes of communication. Eventually, certain acquired characteristics allowed *Homo* to spread and out-compete other hominins. Tracing the regional specifics of adaptation, therefore, remains a central strand in the study of hominin and human prehistory. As such, discovering exactly where the human lineage emerged within the vastness of Africa is a quest

of the greatest importance and gives a special value to conserving the full spectrum of African habitats and species.

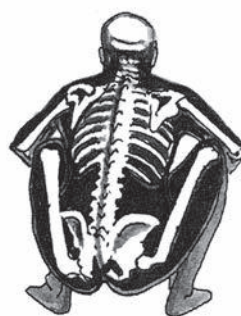
Implied habitats favoured by early hominins are generally wooded and close to water, although some sites represent more closed forest, later ones were adjacent to more open plains. Diets (known as far as the early stages are concerned from stable isotope analysis) were, perhaps, largely vegetarian, including both fruits and underground parts. The latter is clearly consistent with the terrestriality of hominins but also implies the means to excavate. The unearthing or capture of small but numerous food items is implied by hominins having highly manipulative hands (possibly assisted on occasion by crude digging tools). Termite feeding has been convincingly proposed and it can be argued that sustained use of the hands for collecting terrestrial and sub-terrestrial mini-foods was the initial driving factor in the emergence of hominins (Kingdon 2003). Because apes, as well as other primates, prefer a seated position while foraging over prolonged periods for small items on or under the ground, it is reasonable to suppose that this 'squat-foraging' posture (as in Geladas *Theropithecus gelada*) became the norm for the earliest (probably south-eastern African) ground apes. The habitual adoption of such a foraging posture has substantial long term implications inasmuch as natural selection is likely to favour a number of anatomical changes. A stable squatting position on the ground favours flatter, broader feet that can provide a firmer platform for long-armed, mobile forequarters. The latter would have been inhibited because the rib cage of a typical, top-heavy, ape is closely tied to the broad, high blades of the pelvis and the lumbar region is exceptionally weak and inflexible. The fossil record confirms that the development of a functional articulation between the thorax and the pelvis was one of the earliest innovations of hominins. The rib cage became narrower, shorter and flatter (from front to back) while the iliac blades of the pelvis retracted to form a more compact structure that was no longer integrated into a single body mass. Elongation

and strengthening of the lumbar region (including an increase in the number and robustness of lumbar vertebrae) allowed a 'waist' to develop. The most plausible rationale for this change is that a seated ape needs to twist and flex its body during squat-foraging. Another implication for this behaviour becoming habitual is that selection would favour the head becoming more vertically positioned above, rather than oblique to the spinal column. All these changes in early hominins are commonly correlated with bipedalism but can be even more strongly argued as evolutionary adaptations to squat-foraging.

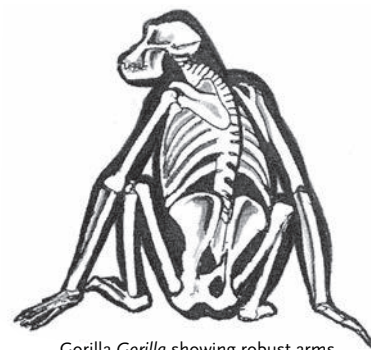
If an intensification of terrestrial foraging *with the hands* was the motor of Hominin evolution then a seated position for this activity is demonstrably necessary. Previous difficulties for a quadruped attempting to rear up on two legs became negligible once the entire body had become rebalanced (more or less vertically) above a ground-based pelvic basin. Corroboration for a squat-foraging phase in hominin evolution can be inferred from the pelvis, spinal column, skull and feet of the earliest known and best-documented hominin, *Ardipithecus ramidus*. This species retained long ape-like arms but had a basin-like pelvis, a strong lumbar column with an increased number of larger vertebrae, a typically hominin foramen magnum and, surprisingly, the long legs of a slow but habitual walker (Lovejoy *et al.* 2009). Emerging from the inner aspect of their broad, splayed feet were rigid, strut-like 'big toes'. While such feet were crudely functional for both tree-climbing and walking their obviously platform-like structure was somewhat anomalous for both activities. Such a structure not only suggested a squatting ancestry but implied that squatting (on both flat ground and on branches) was still a functional activity for this long-armed, big handed terrestrial biped. It can now be argued that the combination of

RIGHT: Proportions in three hominids while in a squatting posture.

Reconstruction of a Ground Ape
Ardipithecus ramidus adult female.



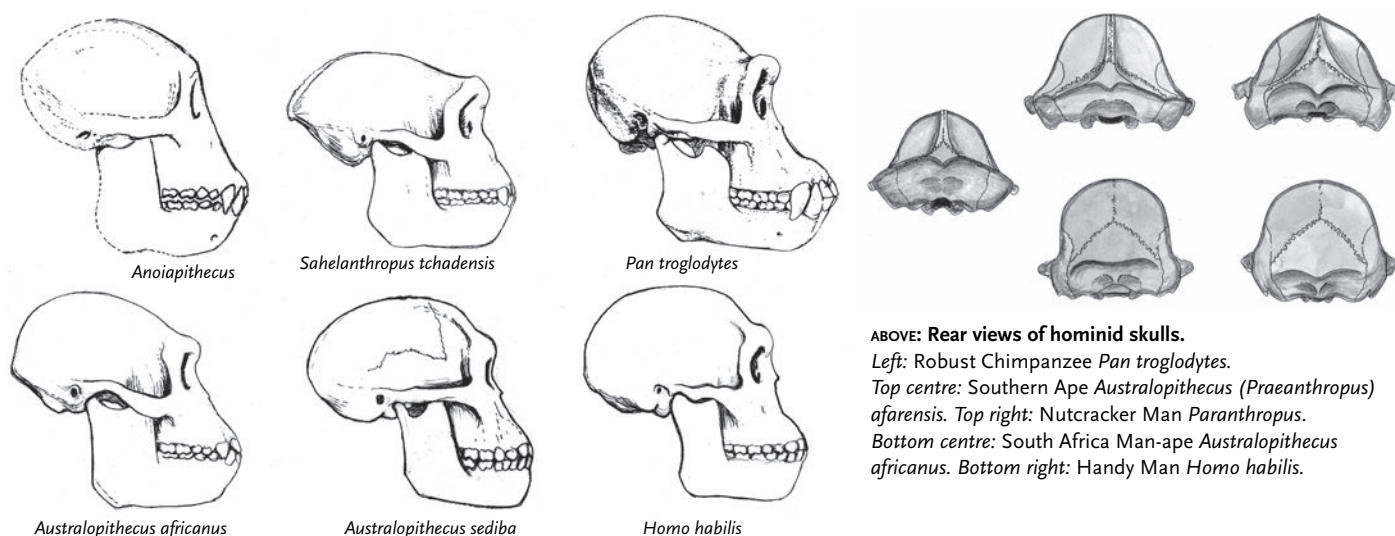
Modern Human *Homo sapiens*
showing contracted pelvis,
robust legs and gracile arms.



Gorilla *Gorilla* showing robust arms,
short legs and tall, plate-like pelvis.



Ground Ape *Ardipithecus ramidus* showing long
arms and splayed feet (pelvis uncertain) (derived
from J. Matterness in White *et al.* 2009).



ABOVE: Rear views of hominid skulls.

Left: Robust Chimpanzee *Pan troglodytes*.
 Top centre: Southern Ape *Australopithecus* (*Praeanthropus*) *afarensis*. Top right: Nutcracker Man *Paranthropus*.
 Bottom centre: South Africa Man-ape *Australopithecus africanus*. Bottom right: Handy Man *Homo habilis*.

Hominin skulls.

Top left: Generic *Anoiapithecus*. Top centre: 'Toumai' *Sahelanthropus tchadensis* (in part after Zollikofer et al. 2005). Top right: Robust Chimpanzee *Pan troglodytes*. Bottom left: South Africa Man-ape *Australopithecus africanus*. Bottom centre: *Australopithecus sediba*. Bottom right: Handy Man *Homo habilis*.

features displayed by *A. ramidus* renders previous models involving any sort of direct leap from quadrupedalism to bipedalism obsolete.

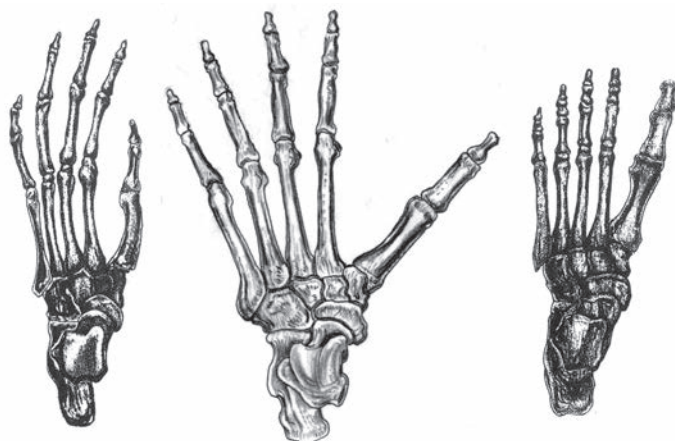
Among later hominins, legs became longer still (and, eventually, arms shortened) and some species moved out into more open habitats. Large mammals began to be hunted by some hominins, having first, perhaps, been scavenged. As early hominins adapted to various and wider ranges of habitat, necessary changes in behaviour induced strong selection for appropriate incremental changes in physiology and morphology. At least three major lineages can be identified and as many as six or more hominin species might have existed in and out of Africa at any one time (though not in the same locality). One branch (including the famous 'Lucy' *Australopithecus* [or *Praeanthropus*] *afarensis*) culminated in the *Paranthropus* or 'nutcracker humans'. This

lineage dominated the scene 4–2 mya but was eventually replaced by the *Homo* lineage that were relative late-comers.

It now seems likely that, among a diverse scatter of hominins, the southern-most, more temperate-adapted species, *Australopithecus* (*Praeanthropus*) *africanus* and *Australopithecus sediba*, gave rise to the *Homo* lineage. It has been argued that strong seasonality in the hilly or mountainous habitats of *A. africanus* demanded exceptionally versatile social and strategic responses (Kingdon 2003). Global fluctuations in climate eventually permitted the descendants of these hominins (originally exclusive to South Africa) to spread northwards and eventually to enter Eurasia, where they proliferated still further. Because such studies are hostage to the availability of rare fossils, reconstructing progressive changes in a wide scatter of hominins through space and time, especially those of the *Homo* lineage, poses one of the most difficult but fascinating challenges in contemporary science.

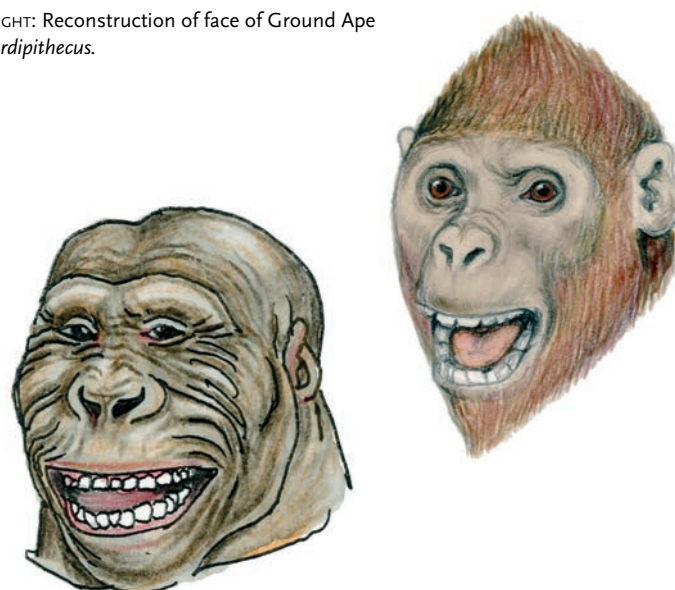
Jonathan Kingdon & Colin P. Groves

RIGHT: Reconstruction of face of Ground Ape *Ardipithecus*.



Three grades of hominid feet.

Left: Robust Chimpanzee *Pan troglodytes* climbing foot with curved digits.
 Centre: Ground Ape *Ardipithecus* walk-climb foot retains phylogenetically earlier 'platform' structure from a squatting phase of evolution.
 Right: Modern Human *Homo sapiens* walking/running foot with re-aligned large toe.



Reconstruction of the original Nutcracker Man *Zinjanthropus* (now *Australopithecus* [*Paranthropus*] *boisei*).

GENUS *Homo*

Humans

Homo Linnaeus, 1758. *Systema Naturae*, 10th edn, 1: 20.

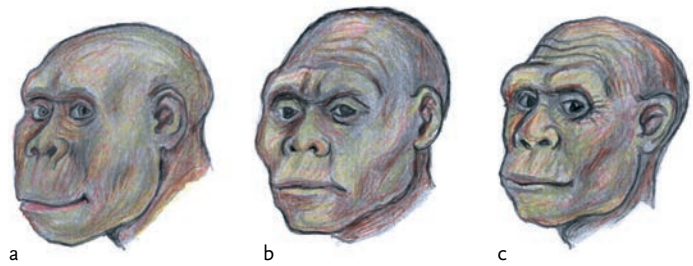
<i>Homo sapiens</i> Modern Human	<i>Homo floresiensis</i> 'Hobbit'
<i>Homo heidelbergensis</i> 'Heidelberg'	<i>Homo habilis</i> 'Handy Man'
<i>Homo neanderthalensis</i>	<i>Homo rudolfensis</i> 'Rudolf Man'
Neanderthal	
<i>Homo ergaster</i> 'Work Man'	
<i>Homo erectus</i> Erect Man (might include the un-named 'Denisova DNA species')	

There are scientists who, citing how recently our evolution has taken place and seeking uniform time-criteria for taxonomy, have proposed including chimpanzees *Pan* spp., even gorillas *Gorilla* spp., in *Homo*. This has not found, and remains unlikely to find, general acceptance. The genus *Homo*, by current definition, embraces a single living species – ourselves. All of us are, in a very basic sense, African mammals because the emergence and tenancy in Africa of our ancestors was probably about twice as long as Modern Human presence anywhere else (200,000–300,000 years in Africa versus <100,000 years outside Africa). Before the evolution of *Homo sapiens* (in the narrowest usage of that name), there were a variety of populations that lived in and outside Africa; these were mostly less gracile in body-build and, although unmistakably human, some had quite apish faces.

The oldest of these, at about 2 mya, was named from a ♀ specimen of a small species named *Homo habilis*, or 'Handy Man'. The name was coined because she was found close to a cache of stone tools, which she (at the time thought to be he!) had supposedly made. Such are the quirky beginnings of names, but the fossils they describe are a concrete archaeological reality. Likewise, the progression and spread of *Homo* clearly begins with a population of African humans of which *H. habilis* is the only one that is well represented in fossil form. A second hominid, usually allocated to the genus *Homo*, is *H. rudolfensis* 'Rudolf Man'. Known from fewer, and slightly earlier, sites on the shores of L. Rudolf (= L. Turkana) and L. Malawi, this flat-faced animal was appreciably larger than *H. habilis*. *Homo rudolfensis* may represent a regional or temporal variety belonging to the *habilis* group or might belong to a separate lineage. Such are the current uncertainties.

Post-*habilis* human evolution is then documented by an ever-wider, more numerous and diverse collection of bones and artefacts, bearing testimony to a succession of populations inside and outside of Africa. Whether any of these are direct ancestors to Modern Humans is rather less certain than that many varieties of humans have flourished in Africa over the past 2 million years.

The earliest specimens of *H. habilis* are hard to distinguish from the South African Man-ape *Australopithecus africanus* (especially since most of them are very fragmentary) and they are even more similar to the recently discovered South African fossil *Australopithecus sediba* (Berger *et al.* 2010). Both of these Man-apes appear to have been restricted to southern Africa. The most widespread species at any one time, and the best represented in any one region, are likely to be those best adapted to peculiarities of the time and of the locality. This means that many of the best-known fossils are not necessarily (indeed, are often unlikely to be) the direct ancestors of Modern



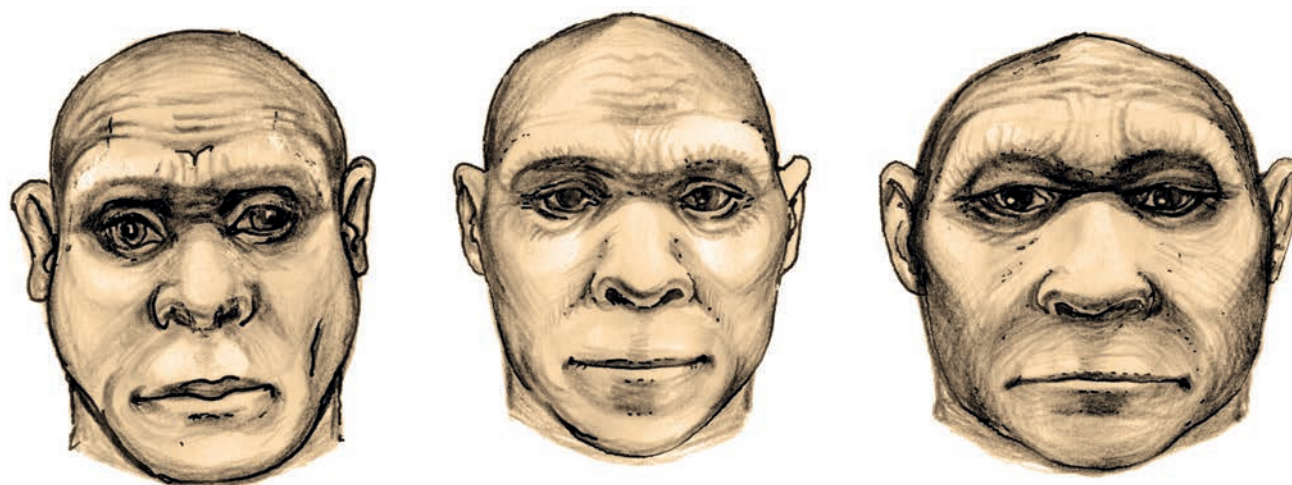
Reconstructed heads of three near contemporaries: (a) '*H.* *rudolfensis*'; (b) '*H.* *habilis*'; (c) '*H.* *ergaster (erectus)*'.

Humans. This makes deciphering the precise course of human evolution challenging because the actual fossils are usually best taken as illustrative of trends rather than documenting actual ancestry.

The proliferation of populations within the genus *Homo* continues to pose many problems but the radiation of *Homo* is as certain as that of any other of the many mammal radiations described in these volumes. As for other mammals, fossils are no longer the only sources of information; the genes of living people are a guide to what is now the most complex diaspora of mammals on earth. DNA has even been extracted from the bones and tissues of extinct humans (notably 'Neanderthal' *Homo neanderthalensis*) and, more recently, from the single bone of an unknown species from the Altai Mts, east-central Asia (Krause *et al.* 2010). Such discoveries hugely augment what we know, and can learn, about human origins.

It now seems highly likely that a population of early humans, possibly very similar to *H. habilis*, spread first to North Africa and the Arabian Peninsula, then much farther into Eurasia. Exactly where the next type of early human emerged (from a complex of populations of common ancestry with *H. habilis*) remains conjectural, but it was most likely to have taken place in, or near, the Afro-Arabian/Eurasian interface. Here, more open and strongly seasonal environments would have favoured larger body-sizes, lengthening of the legs, the adoption of more animal foods in the diet, and tighter, more secure social systems. The complex of fossil humans that would seem to broadly conform with this characterization have generally been lumped as *Homo erectus* 'Erect Human'. The discovery of *H. erectus* in Java in 1891 and *Homo pekinensis* 'Pekin Man' in China in 1927, led their discoverers and followers to believe that Asia was the ancestral land of humans. Since then the fossils of many other closely related humans have been discovered, of which the African type, *Homo ergaster* 'Work Man', is probably closest to the main line of subsequent descent than any other type (Groves 1989).

The *H. erectus* complex embraces a wide scatter of very different fossils and all testify to the rapid expansion of a highly successful type of pioneering human. With the help of fire, *H. pekinensis* types colonized cold northern habitats, while *H. erectus* (or even a close precursor) may well have invented rafts or boats in the SE Asian Peninsula. These local populations differentiated into distinctive forms to which authors have variously given specific or sub-specific



Three species (subspecies?) of *Homo erectus* type. Left: Work Man *Homo ergaster*. Centre: Pekin Man *Homo pekinensis*. Right: Erect Man *Homo erectus* (Java) (in part after De Beer 1964).

names, *erectus*, *soloensis*, *modjokertensis*, *ngangdongensis*, *trinilensis* and *sangiranensis* in Java, and *pekinensis*, *sinensis* and *hexianensis* in N China. In spite of persistent attempts to link such regional types of early humans with contemporary races of Modern Humans, recent research has been almost unanimous in dismissing what came to be called ‘the multiregional hypothesis’. None the less, it remains possible, even probable, that later human types occasionally hybridized with earlier ones and that some regional types might have retained or preserved older traits where these were adaptive.

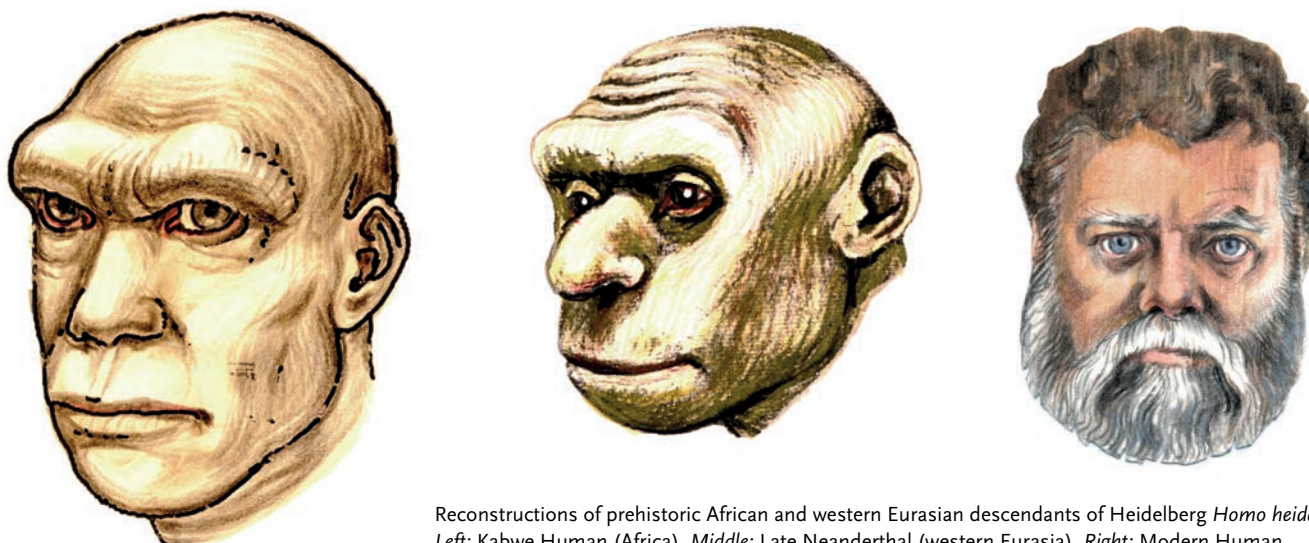
Among the most interesting of Asian fossils is *Homo floresiensis* ‘Hobbit’, a diminutive and very primitive human from the island of Flores in Indonesia. Possibly linked to an Asian dispersal of *Homo habilis*-like populations as early as 2 mya, this species succeeded in crossing a deep water trench to colonize Flores more than 1 mya (Brumm *et al.* 2010). If this was the product of deliberate rafting it would be another instance of the capabilities of our early precursors or near-precursors being grossly underestimated by scientists. Accidental rafting during a tsunami, however, seems more probable.

Later human fossils are relatively rare, very unevenly scattered, and subject to much individual variation. As such, there has been a great proliferation of names. Among them, *Homo heidelbergensis*

‘Heidelbergers’ and allies have come to be regarded as the most convincing intermediate forms between *H. erectus* and fully Modern Humans (Groves 1989).

Apart from the incompleteness of the fossil record, the radiation of *Homo* is made much more complex by the influence of a factor that operates scarcely at all for most other mammals. Young *Homo* grow up in a physical world that is mediated almost entirely by artefacts. Instead of interacting directly with the climate, soil, trees and water, or with their food and prey, *Homo* put a great variety of interfaces between themselves and all these manifestations of nature. These interfaces consist of stone, wood, and other tools, string, skin blankets and leather clothes, containers, and diverse uses of fire to heat, cook, hunt and clear land. Long ago, the habitat of *Homo* ceased to be a particular vegetation type but rather a micro-habitat created around a camp or settlement, regardless of how briefly such sites were inhabited. Some of the many consequences of humans creating self-made habitats are explored in the following profile, demonstrating how faculties that evolved in Africa to cope with local challenges opened the way for an eventual colonization of the entire earth.

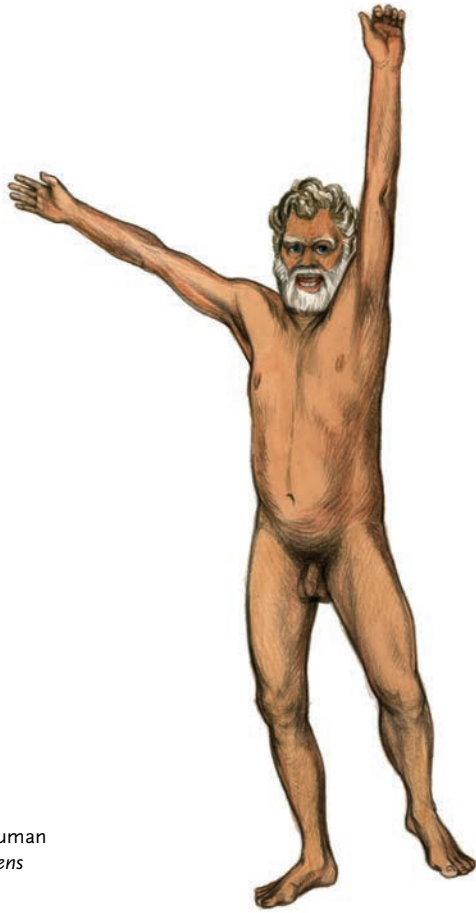
Jonathan Kingdon



Reconstructions of prehistoric African and western Eurasian descendants of Heidelberg *Homo heidelbergensis*. Left: Kabwe Human (Africa). Middle: Late Neanderthal (western Eurasia). Right: Modern Human.

Homo sapiens MODERN HUMAN

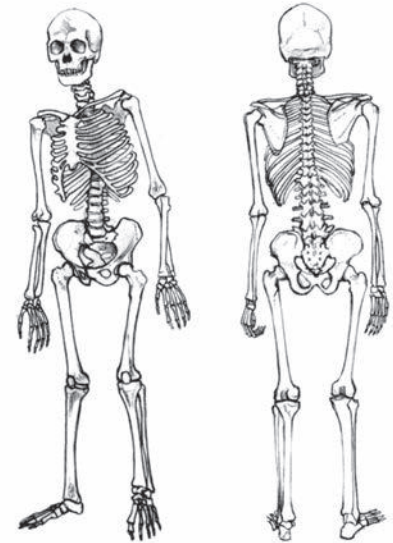
Fr. Homme modern; Ger. Moderner Mensch

Homo sapiens Linnaeus, 1758. *Systema Naturae*, 10th edn, 1: 20.

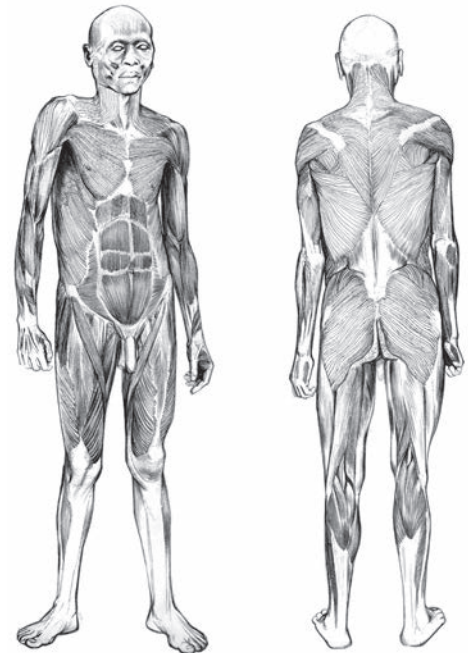
Modern Human
Homo sapiens
adult male.

Taxonomy Monotypic species. Linnaeus described *Homo sapiens* in the tenth edition of his *Systema Naturae* in 1758. In this founding document of taxonomy he classified humans as one of four genera in the order Primates; the others were *Simia*, *Lemur* and *Vespertilio* (the latter being bats that, in his view, were primates!). The huge orang-utan *Pongo* spp. became the archetypal 'monkey' with the contradictory name *Simia pygmaeus* (because the type specimen derived from the remains of an immature captive). For a university lecturer in botany who belonged to a religious tradition that regarded humans as the singular creation of a single god, it took some courage to devise and publish a classification system in which humans were subsumed within a category that included apes, monkeys, lemurs and bats.

Since 1758, subdivision of the primates has been in continuous flux. As such, the placement of humans within the order has also varied and shifted substantially. Linnaeus's primary split into 'Simians' (*Simia*) and 'Prosimians' (*Lemur*) transmuted into Anthropoidea and Prosimii. Within Anthropoidea, *Homo* was the only genus in the family Hominidae. Today, *H. sapiens* is generally regarded as belonging to the suborder Haplorrhini (which embraces all tarsiers, monkeys and apes) and to the superfamily Hominoidea, a taxon we share with all the other apes. Combining evidence from fossils and molecular clocks reveals that Old World monkeys and anthropoid apes diverged in Africa about 30 mya (early Oligocene).



Front and rear views
Modern Human
Homo sapiens.



Myology of Modern
Human *Homo sapiens*
adult male.

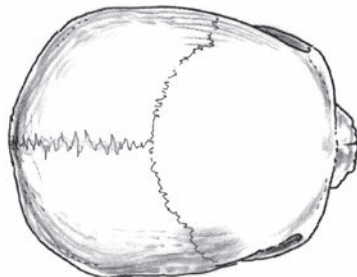
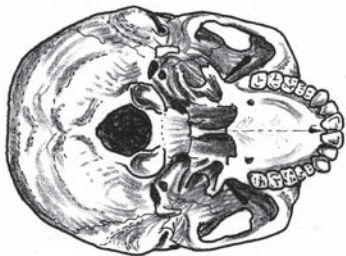
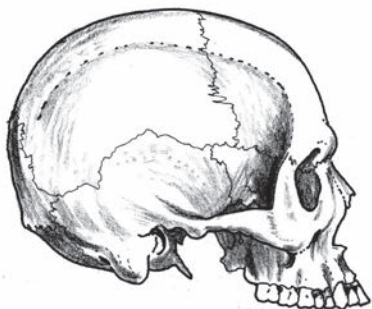
We still occupy the family Hominidae, but molecular evidence makes it clear that all the great apes belong there too: we even share the subfamily Homininae with the African apes leaving only the tribe Hominini reserved for living and fossil humans and all the extinct bipedal apes (Groves 2001). Although other species of *Homo* exist as fossils, and there are occasional calls for the chimpanzees *Pan* spp. to be included in our genus, the general consensus is that we are the only surviving species of *Homo*. Groves (2001) lists >30 published names for proposed species or subspecies of living or extinct *Homo*. Most are of merely historical interest but some of the fossil forms provide rich and incontrovertible evidence for the reality of human evolution in Africa.

Of the other species of *Homo* that exist as fossils, the earliest, *Homo habilis* 'Handy Man', is known from about 2.5 mya and *Homo erectus* 'Erect Man' at 2 mya. There is good fossil and molecular evidence to suggest that our own species, *Homo sapiens* 'Modern Human', emerged only ca. 250,000–300,000 years ago.

The placement of *Homo sapiens* within current mammalian systematics is as follows:

- Class Mammalia
 - Subclass Eutheria
 - Order Primates
 - Suborder Haplorrhini
 - Parvorder Catarrhini
 - Superfamily Hominoidea
 - Family Hominidae
 - Subfamily Homininae
 - Tribe Hominini
 - Genus *Homo*
 - Species *Homo sapiens*

Lists of synonyms for *H. sapiens* are available in Groves (2001, 2005a). Modern Humans have 46 chromosomes, two less than chimpanzees *Pan* spp. and gorillas *Gorilla* spp., which have 48. However, this anomaly is due to the human chromosome 2 being an end-to-end fusion of two ape chromosomes, a fact revealed by the banding patterns on human chromosome 2 (Yunis & Prakash 1982).



Lateral, palatal and dorsal views of skull of adult Modern Human *Homo sapiens*.

Description A uniquely bipedal, large, primate with a peculiar distribution of hairy patches on the head and limb axia, but otherwise a general tendency to greatly reduced hairiness. Surface features, such as hair type, skin/eye/hair colour and nose shape, vary both individually and regionally. Sexual dimorphism is moderate; adult ♀ being, on average, smaller than adult ♂.

Modern Humans resemble the great apes closely in much of their anatomy and physiology (a fact that has led to the use of chimpanzees as human proxy experimental subjects in medical, pharmaceutical and cosmetic laboratories). The fossil record now offers evidence for many of the steps leading from our common ancestry with chimpanzees and gorillas. It is in the proportions of limbs and head that chimpanzees, gorillas and humans differ most; humans having elongated legs, shortened arms and face, and enlarged cranium. The hands of African great apes also differ substantially from those of humans and have probably become progressively more specialized for weight-bearing and climbing. The functional significance of some human peculiarities is discussed in 'Adaptations'.

Geographic Variation Modern Humans vary greatly in external appearance and this variation has both individual and regional roots. The majority of Modern Humans have skins that are various shades of light brown, with dark brown eyes and straight, black hair. Two



North-east Africans.

Top from left: Maasai adult male and juvenile male; El Molo male youth; Oromo middle-aged female; Samburu elderly female.

Bottom from left: Maasai elderly male and middle-aged male; Rendille elderly male; two Maasai adult males.



Eurasians.

Top from left: West European middle-aged male (profile and frontal); German Jewish youth; West European middle-aged female (frontal and profile).

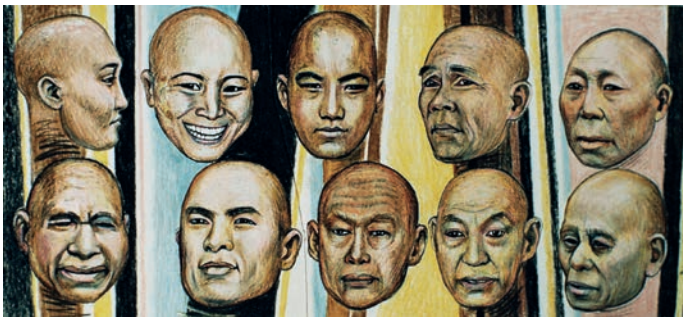
Bottom from left: North European elderly male; Central European middle-aged male; Western European adult male; Middle Eastern adult female (Kurd); Pakistani adult male.

**Melanesians.**

Top from left: New Guinea (Cogdala) adult male; New Guinea (Huli) adult male; New Guinea (Highlander) middle-aged male; New Guinea (Telefol) adult female.

Bottom from left: Solomon Islander adult female; Vanuatuan middle-aged male; New Guinea (Kewa) adult male; New Guinea (Duna) adult female.

major departures from this primary type involve opposite trends towards 'super-pigmentation' or 'depigmentation'. A gene that plays a major role in depigmentation is the theomine gene SLC24A5, which Lamason *et al.* (2005) estimated to have arisen a mere 6000–12,000 years ago. The roots of this trait can be confidently located in the Baltic region of northern Europe and is typified by blonde hair and skin, and blue eyes. The opposite trend, with dark brown or black skin and eyes, spiralling hair and distinctive physiognomic features, is now most widespread in Africa but this genetic package of characteristics might have arrived there in prehistoric times after originating in Melanesia (Haddon 1919, Kingdon 1993, 2003). Eyes are also subject to significant differences in shape, some being the product of subcutaneous deposits of fat that probably serve to protect the eye-balls, insulating them from extremes of cold and shielding them from bright reflectance off snow. Such traits can sometimes be traced to selection for useful traits under extreme conditions, as in the higher reaches of the Andes and Tibet, where the thin air poses problems for pregnant women. Still other manifestations of regional

**ABOVE: East Asians.**

Top from left: Siberian adult female; Yunnan adult female; Nepalese male youth; Vietnamese adult male; Siberian middle-aged female.

Bottom from left: Alaskan (Inuit) middle-aged male; Central Asian (Kazakh) adult male; South Chinese middle-aged male; North Chinese middle-aged male; Japanese elderly male.

RIGHT: Andamanese.

Top from left: Young adult females.

Bottom from left: Young adult female; young adult male; adult female.

**Australians.**

Top from left: Queensland middle-aged female; Tasmanian middle-aged female; Queensland youth; Arnhemland female; West Australian elderly female.

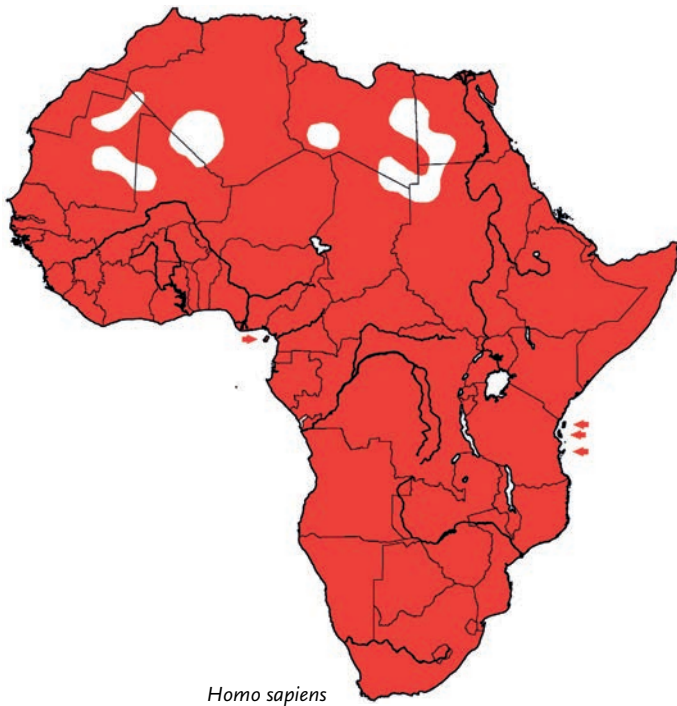
Bottom from left: Queensland adult male; South Australian elderly male; Central Australian elderly male; Arnhemland adult and middle-aged males.

**South-East Asians (Negrito).**

Top from left: Philippine (Aeta) middle-aged male; Malayan (Batek) young adult female; Malayan (Semang) adult male.

Bottom from left: Malayan (Semang) adult male; Malayan (Batek) adult male; Philippine (Aeta) middle-aged female.



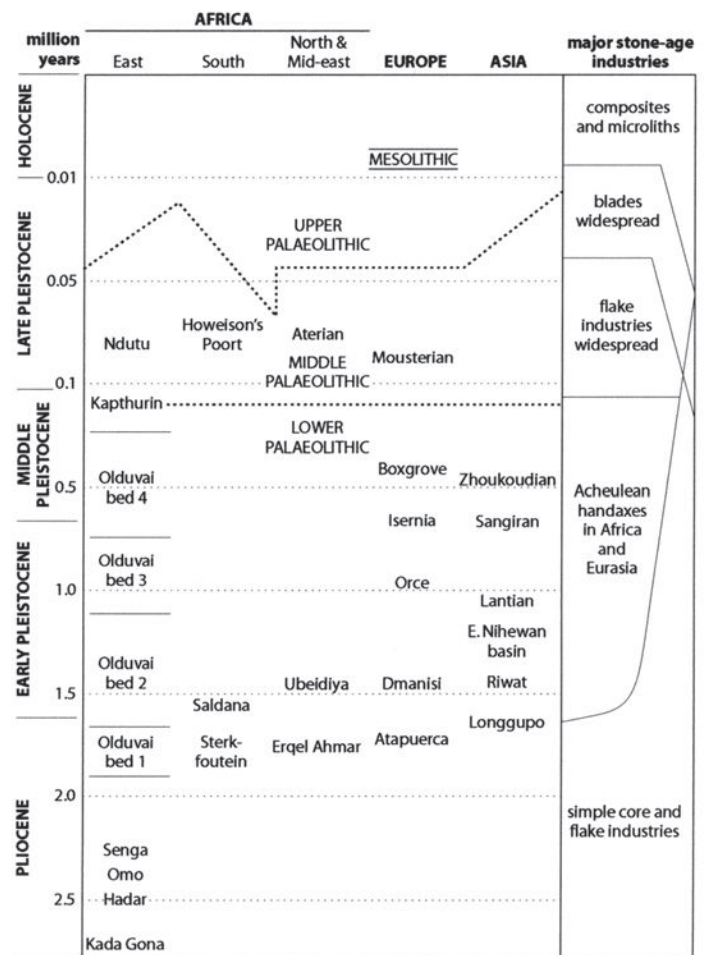


difference can be traced to founder-effects, as when a very small number of immigrants has colonized an island or spread widely over a continent.

Similar Species Humans are broadly sympatric with all six species of great apes. Resemblances with orang-utans, chimpanzees and gorillas offer many evolutionary insights but the erect posture, hairlessness and large cranium of modern humans prohibit any confusion in identification.

Distribution Modern Humans occur in all African biotic zones and inhabit every continent. A primary reason to include humans in a continental mammal inventory is that *Homo sapiens* evolved, exclusively, over millions of years, within African mammal communities. We can be sure that prehistoric distributions of primates represented complex patterns of ecological partitioning, exclusion, competition, constraints (and, possibly, facilitation) for almost every species of primate. At various stages of their evolution, proto-humans and extinct humans were integral to these patterns of interaction. Few surviving species, either primate or non-primate, have escaped the legacy of human competition/exploitation of commonly used resources. Furthermore, this human onslaught has been strung out, step-by-step, habitat-by-habitat and region-by-region.

It is, therefore, interesting to find some African Middle Stone Age industries (dated 250,000–45,000 years BP, and once commonly referred to as 'Stillbay') that were mainly confined to upland, temperate and semi-arid zones. Here, tool types were remarkably similar from the Cape to the Horn of Africa, suggesting a well-dispersed, mainly savanna-dwelling population that used relatively uniform techniques. Then, about 42,000 years ago, living sites became much more numerous and began to extend into low-lying and humid parts of central and West Africa (Anciaux de Faveaux 1955, Clark 1967, 1982, Isaac 1982). At this time, tool-kits became



Palaeolithic sequences and artefact types from African archaeological sites (diagram modified after Gowlett 1992).

more varied and numerous, representing many regional variants. The implications are of expanding, less habitat-specific populations (perhaps even 'tribes') devising a variety of new techniques to exploit an expanding range of environments. In spite of 42,000 years being deep in prehistory, that expansion of numbers and range could be seen as one of several starting points for the modern era. It suggests a substantial enlargement of our ancestors' capacity to exploit resources that were previously not used. Because equatorial lowlands are hotbeds of primate diseases, it is possible that disease-resistance in a particular human population was a decisive factor in this ecological expansion (Kingdon 1993). This expansion of range also seems to mark a significant leap in an invasive, 'niche-thieving' dynamic that has continued to typify human interactions with the rest of nature. The present era undoubtedly marks another, much more comprehensive and sudden, technological and demographic leap.

If such archaeological discoveries could be plotted through time, and investigated in terms of staged expansions into once unpopulated regions and into previously unexploited ecosystems, there would likely be important insights to our understanding of the biology of many mammal species. It may eventually be possible to reconstruct long-term patterns of ecological change and extinction induced by human activities. When such reconstructions are attained, it is

predicted that a deeper understanding of mammalian biology in Africa will emerge. The archaeological record provides reminders that the impact of human numbers, and of the ever-expanding technological inventiveness of humans, has deep roots, and that we are witnesses to but one moment in a very protracted human assault on the natural environment – and on all species that live in these environments.

Habitat Human habitats are essentially self-made and the invention of clothing, harnessing of fire, ability to make tools and to construct shelters and transport systems, etc., means that modern humans have come to occupy the entire range of contemporary terrestrial habitats. This ecological annexation has proceeded step-by-step, incrementally. It has long been recognized that when humans lack appropriate technologies, their ecological niches and impacts are narrower, even though prehistoric modern humans were no different in physique or intellect to contemporary people. Thus, the invasion of rainforests, deep swamps, high mountains and polar regions is probably relatively recent, whereas savannas, especially African savannas, represent an archetypal habitat for *Homo sapiens*.

When such insights are referred to actual species it can be appreciated that bovids, such as the Hartebeest *Alcelaphus buselaphus*, Wildebeest *Connochaetes taurinus* and Common Eland *Tragelaphus oryx*, evolved within savanna habitats where humans were already a factor in natural selection. Thus, human activities, such as grass-burning or intensive hunting around waterholes in dry seasons or during arid climatic phases, could have favoured one antelope versus another, and shaped some details of their behaviour and evolution (and may have caused the extinction of especially vulnerable species). By contrast, a forest bovine, such as the Bongo *Tragelaphus eurycerus*, or a desert antelope, such as the Addax *Addax nasomaculatus*, evolved in effectively human-free environments. In all instances, there are implications for our understanding of the species' biology and conservation status today.

Our historic and prehistoric interactions with predators also raise numerous questions. Many species of large predator have gone extinct in Africa as elsewhere. We can only guess at some of the reasons for these extinctions but once humans became effective predators in their own right it is certain that they became a significant factor shaping predator communities. From detailed studies of predator guilds in several parts of Africa (e.g. Serengeti N. P. in Tanzania, Kruger N. P. in South Africa, Bale Mountains N. P. in Ethiopia) we know there are highly structured specializations in prey type and killing technique, as well as systematic appropriation of prey. These may be the evolutionary outcomes of ancient interactions or 'arms races' between different predators, but the exact spectrum or balance of carnivores in any one place at any one time is the direct product of locality-specific competition. The constraints on early humans, and the two-way dynamics of human interaction with Lions *Panthera leo*, Leopards *Panthera pardus*, Cheetahs *Acinonyx jubatus*, Wild Dogs *Lycaon pictus*, Spotted Hyaenas *Crocuta crocuta*, Black-backed Jackals *Canis mesomelas* and other large, savanna-living, predators, have scarcely begun to be examined in this context.

It is even more important to understand the dynamics of our evolutionary interactions with close relatives, especially chimpanzees and gorillas. Assuming ancient periods of physical separation (because our common ancestor could not have speciated without that), there are likely to have been other times when expanding and contracting ranges (probably correlated with climatic changes as well

as technological innovation) brought formerly separate lineages into contact again. Of special interest are those ancient times when the burgeoning lineages of early Hominini and early *Pan* were a lot more alike than they are today. At such early times we can assume that ancestral chimpanzees and ancestral hominins retained some residual overlap in their ecological preferences. What happened during these early interactions is crucial for understanding the nature of our biological differences. Extrapolating from what we know about ecological partitioning in general, it is likely that direct competition within these early zones of overlap served to define ecological boundaries among the species. Thus, chimpanzees may well have been forced to become more decisively forest-dwellers and more specifically 'big tree climbers' as a direct consequence of ancestral exclusions by our own lineage (and, perhaps, other primates) in the distant past. In Africa, understanding the differing susceptibilities of antelopes, carnivores, or the great apes, whether prey, predator, or competitor, needs to be informed by the history or pre-history of their interaction with humans and proto-humans.

Abundance At about 7 billion (US Census Bureau 2007), humans are today, by far, the most abundant primate on earth. Humans are currently in an unprecedented phase of demographic expansion, especially in Africa. The UN estimated projections of future global population range from 7.6 and 9.8 billion for 2050, while projections for 2150 are as high as 30 billion. Increasing densities, unbalanced age distributions and newly urban societies have transformed, or destroyed, traditional economies and modes of behaviour. Nomadic foragers and hunters used to live in small, mobile, family-sized functional groups. Pastoralists also had to be mobile but tended to operate more expansive clan systems with the young men in warrior groups. Settled farming societies varied greatly but generally had enlarged family groups because their labour-intensive crops could support more children and plants needed more hands to be cultivated and harvested (Butzer 1971, Flannery 1973). City living, on the other hand, tends to favour nuclear families operating within large social aggregations that are controlled by clan-like kings, religious figures, or other leaders (Harris 1978). Some of the biological underpinnings of human societies are explored under 'Social and Reproductive Behaviour'.

Rapid increase in numbers and huge expansions in the geographic range of humans has involved the extirpation of many subspecies and several species of large mammals in Africa, notably the Blue Buck *Hippotragus leucophaeus* in South Africa and the Red Gazelle *Gazella rufina* in North Africa. A currently fashionable myopia promotes the idea that most human enterprises need not have adverse effects on the survival of mammals, large and small. On the contrary, an exponential increase in human numbers can only lead to further extirpation of species, most particularly those species that occupy small areas in localities with large (and/or lawless) human populations. Current trends suggest that burgeoning human populations will soon cause the extermination of some, or all, of the following species of mammals in their natural habitats: Pennant's Red Colobus *Procolobus pennantii*, Preuss's Red Colobus *Procolobus preussi*, Tana River Mangabey *Cercocebus galeritus*, Sclater's Monkey *Cercopithecus (cephus) sclateri*, Red-bellied Monkey *Cercopithecus erythrogaster*, Preuss's Monkey *Allochrocebus preussi*, Drill *Mandrillus leucophaeus*, Rondo Dwarf Galago *Galgoides rondoensis*, Golden-rumped Sengi *Rhynchocyon chrysopygus*, Ethiopian Wolf *Canis simensis*, Wild Ass *Equus africanus*, Grevy's Zebra *Equus grevyi*,

Aders's Duiker *Cephalophus adersi*, Hirola Antelope *Beatragus hunteri*, Dama Gazelle *Nanger dama*, Slender-horned Gazelle *Gazella leptoceros*, Scimitar-horned Oryx *Oryx dammah* and Addax *Addax nasomaculatus*, to name but a few. The activities of humans are, of course, also having a severe negative impact on the world's birds, amphibians, reptiles, fishes, plants, and species in other taxonomic groups.

Adaptations Primarily diurnal and terrestrial. Some of the adaptations that most distinguish Modern Humans are best appreciated by comparing characteristics (some obvious, others more cryptic) with equivalent features of modern apes and fossil hominins. *Homo sapiens* is the last survivor of a great diversity of extinct hominins that are becoming ever more richly documented by the fossil record. These fossils demonstrate the tangible reality of human evolution and often offer hints as to how some of our uniquely human adaptations were acquired.

The earliest of these fossils, 'Toumai' *Sahelanthropus tchadensis*, is a well-preserved 6–7 million-year-old hominid skull. This skull combines characteristics of Modern Humans, chimpanzees and gorillas, confirming Darwin's 1871 prediction that Africa was the most likely home of the *Homo sapiens* lineage, and that chimpanzees and gorillas are our closest living relatives. The somewhat younger 'Millennium Human Ancestor', *Orrorin tugenensis* (6 mya), has a much more fragmentary skull, but is probably closer to the human line of descent.

The next oldest hominin fossils belong to the 'Ground Apes', *Ardipithecus kadabba* and *Ardipithecus ramidus*, of Ethiopia. The earliest specimens of *kadabba* are ca. 5.8 mya, the youngest specimens of *ramidus* are ca. 4.4 mya. These eastern apes lived in riverine forests and woodlands in a relatively dry region of eastern Africa. Extrapolating from equivalent contemporary East African riverine forests and woodlands, the ground was likely to have been a richer source of forage than the treetops. As is summarized below, this detail hints at the driving force that initiated hominin divergence and the emergence of Modern Humans. Since genetic isolation is an essential part of speciation, eastern provenances for these and subsequent fossil hominins suggest that an arid corridor allowed the earliest hominins to diverge in isolation from the much larger populations of apes occupying central and West Africa.

In apparent concert with our upright stance, humans have developed strong, flexible 'waists' that separate and balance a slab-shaped thorax above a basin-like pelvis; chimpanzee and gorilla rib cages are splayed and conical, their lower margins bound closely to broad pelvic plates in a single, oblique and top-heavy body mass. These anatomical differences are now associated with bipedalism in humans and quadrupedalism in chimpanzees and gorillas. However, the initial divergence in body proportions, especially the slimming down of shoulders and chest, was likely to have begun with the adoption, by our earliest ground ape ancestors, of a 'squat-foraging' mode. This was a posture in which the upper body became less top-heavy and the vertebral column became more upright. The detailed adaptations of the *Ardipithecus* ground apes remains to be elucidated but it is clear that any 'squat-foraging' primate gleaning for small food items, both plant and animal, on the forest floor, must have employed increasingly dextrous fingers (Kingdon 2003).

The actual size of our hands is, proportionally, somewhat smaller than in chimpanzees and gorillas, but we should not equate



'Penfield homunculus' (adapted from brain maps in Penfield & Rasmussen 1950 and from a figure in Dawkins 2004).

anatomical size with functional significance. This has been illustrated in an original and interesting way. In 1950, Penfield & Rasmussen published a paper on the human cerebral cortex that offered a graphic demonstration of how important hands are for *H. sapiens*. These authors mapped two aspects of brain function: one represented the ratios of the brain devoted to controlling muscles, the other mapped equivalent ratios for the sense of touch. In each instance, the hands occupied hugely disproportionate parts of the brain. The 'homunculus' that emerged from this exercise was grotesquely 'hand-heavy', as were the parts of the face given over to vocalization: tongue, lips and jaws (see illustration above). A significant conclusion emerging from the evidence that hands were of paramount importance in human evolution is that skills in manipulation help explain the emergence of bipedalism. Once deft, food-gathering hands became the prime adaptive specialization of ground apes, and once the vertebral column began to be rebalanced, it was inevitable that bipedalism would develop. To gather and handle a wide variety of mainly small food items is not entirely without precedent (some African and South American monkeys are highly manipulative). What was new was the combination of direct finger-gathering with indirect tool-use (we can infer the latter from numerous instances of its existence, in rudimentary form, in chimpanzees). More important, this specialization in tool-assisted foraging represented an entirely novel way of interacting with the external world. Bipedality allowed the descendants of ground apes to become more mobile, but this was far from being an instant conversion. There is telling evidence from fossils to suggest that two-legged walking and running took a long time to improve, let alone perfect. Long, forager's arms had to shorten while apish squatter's legs took several million years to become long, powerfully muscled legs. Throughout this period, trees

and cliffs are likely to have continued to be important as sources of refuge and shelter, especially at night.

T. Butynski (pers. comm.) points out that the distributions of dry country monkeys (i.e. Patas Monkey *Erythrocebus patas*, savanna monkeys *Chlorocebus* spp., baboons *Papio* spp.), as well as some populations of Robust Chimpanzee *Pan troglodytes*, are dependent on surface water and on safe sleeping sites. Noting that (1) habitats away from drainage lines tend to produce much the same foods over large areas, and (2) that no monkey or ape exploits this vast supply of food, he envisages significant opportunity for, and selective pressures on, early hominins to exploit these foods, including meat. The expansion of the geographic range of early hominins into this enormous 'empty niche' was likely dependent on (1) the ability to carry resources (e.g. food, water, building poles and tools) that bipedalism allows for, (2) the ability to make water containers, build shelters, hunt large prey and avoid and/or defend against predators that tool-use and complex vocal communication enable, and (3) the ability to use fire for cooking, warmth, hunting and defence. In short, development of bipedalism, tool-use, complex language and control of fire among early hominins allowed for the much greater exploitation of the natural resources (especially food) of the vast, waterless, African savannas and bushlands.

The swollen braincase of Modern Humans is one of the last obvious innovations to emerge. We are fortunate to have a rich fossil record demonstrating progressive enlargement of human brains, most of which took place over the last 2 million years. People are often struck by how 'human' young primates are. This is to invert the situation: humans resemble big-headed baby primates because selection has to operate upon pre-existent traits and processes. So humans are 'neotenuous' or 'paedomorphic' primates in their bulging foreheads, reduced teeth, chewing muscles and, above all, in many aspects of their behaviour. Neoteny is essentially a consistent alteration in the timing of various developmental processes. For example, if brains are to enlarge, the bony plates that surround and protect them need to remain loose long enough to accommodate this enlargement. The mechanism allowing this to happen is retention and extension of the juvenile phase of development and suppression of some adult features, such as massive ♂ brow-ridges. Neoteny and the extension of childhood have a central role to play in the development of human social systems. These are further explored under 'Social and Reproductive Behaviour'.

Other adaptive peculiarities of *H. sapiens* do not fossilize, among them important physiological properties of the skin and hair. Most notable of these is the superabundance of eccrine glands in *H. sapiens*, a characteristic that is as diagnostic of Modern Humans as speech or bipedalism (Sokolov 1982). Eccrine glands are found in many mammal species with a soft skin interface between themselves and the ground or branches on which they walk or climb. The fine watery eccrine secretions that exude from the palms of primates, carnivores etc., are seldom found anywhere else but on finger-pads and paws. Their primary role seems to be to condition, protect and cleanse these sensitive, exposed, wound- and infection-prone surfaces from contamination or harm. Human eccrine secretions even possess antibiotic properties (Randerson 2001). Another important property is to increase the sensitivity and micro-traction of fingers and palms. This is a significant virtue for contemporary humans (a sensitivity greatly enhanced by dense mosaics of Meissner's corpuscles

embedded in the skin surfaces of primate fingers). Human hands, especially the fingertips, are so sensitive that skills such as reading Braille, sewing, servicing watches or computers, or playing small, complex musical instruments, can quickly be learned. (Incidentally, most of these talents would have had prehistoric equivalents in terms of finely tuned manual skill.) Finally, evaporation of the water in eccrine secretions also produces a pronounced cooling effect.

Today, this last property of eccrine secretions seems the most obvious advantage. 'Sweating' and cooling must have been a major evolutionary benefit when our ancestors moved into more exposed habitats and undertook high-exertion activities such as walking long distances while carrying food and water. However, it was probably the cleansing functions of eccrine glands that first favoured their initial spread and multiplication in apes and their near total replacement of other glands in Modern Humans. In terms of hair and skin hygiene, humans have effectively abandoned the relatively dry, oil-based system employed by many other mammals. Instead they have enlisted the water-greedy eccrine glands to cleanse and cool a relatively naked skin. A possible connection between nakedness and eccrine glands is discussed further under 'Social and Reproductive Behaviour'.

The adaptive property, which is most frequently thought to distinguish humans from other animals, is the development of a mind capable of articulating and sharing knowledge and feelings with others. In 1837, Charles Darwin made a jotting in his notebook: 'man is a species like any other. The mind is a function of body. He who understands baboons would do more towards metaphysics than Locke' (Browne 1995). Ever since, scientists have been exploring the many ways in which mind is a function of body – and baboons, like other African primates, continue to offer us insights into one of the most difficult of all evolutionary puzzles.

Foraging and Food Omnivorous. In their wild forms, most foods eaten by humans were or are shared with other species: fruits with fruit-bats, palm dates with palm civets, roots with root-rats, honey with Honey Badgers, and meat with Lions, Leopards and Spotted Hyaenas. In many instances, plants that are now cultivated and eaten by humans co-evolved with non-human consumer species that served the plant as disperser or pollinator. Where such animals have been entirely displaced by humans the latter could, in an evolutionary sense, be said to be 'thieves', but that could probably be said of many other instances of evolutionary displacement. Human perspectives invert this, so wild animals that attempt to share resources with us are dubbed 'pests'. Humans have developed a battery of devices that effectively withhold potential foods from other animals. We have typically mammalian instincts about attacking or excluding competition.

Conflicts between *H. sapiens* and other mammals pose fundamental problems for the long-term survival of many mammal species. As the texts of these volumes exemplify, food resources are often partitioned to some degree among the animals that consume them, and the consumers have prescribed tastes and genetically determined food-getting techniques that are unique to the species. Humans, instead, have emancipated themselves from a limited range of species-specific foods and have, with the help of various tool-assisted techniques, devised numerous ways of protecting, obtaining, preserving, processing and altering otherwise unavailable or inedible foods. These characteristics are part of our evolved repertoire. Thus,

skills in cultivating, breeding, processing, and protecting edible plants and animals are not new, nor is the capacity to consume a wide range of species (Ucko & Dimbleby 1969). So, is this merely a vastly enlarged expansion in tool-assisted omnivory? If it is argued that the consumption of a continuously expanding harvest has long been characteristic of our evolutionary career, can we project its momentum on into the future? Will we reach a point where there will be no plants or animals that are not, in some sense, consumable? Is such a state desirable? Perhaps unease with that question lurks in ideological arguments as to how 'naturally vegetarian' or 'naturally carnivorous' humans are? In many languages the word for meat is also used for animal (i.e. 'nyama' in Kiswahili) and 'going the way of all flesh' (dying) also includes humans in the same animal commodity.

Lee (1968) documented contemporary, subsistence-based, human hunter-gatherer societies eating far more, and larger, vertebrate prey than any other primate. In an effort to arrive at some (implicitly retrospective) averages, Lee (1968) sampled 58 such societies from many latitudes and in many parts of the world. With one exception, he found that all these societies derived at least 20% of their diet from hunting mammals (mean ca. 35%). He, therefore, postulated that, on average, prehistoric humans derived 30–40% of their diet from the meat of mammals. In spite of many prehistoric societies having scant, or only seasonal, access to fish, Lee added a mean of 26% of fish into postulated prehistoric diets. He concluded that mammals and fish comprised 61% of the diet of prehistoric humans. Given that other vertebrates and invertebrates were not considered, Lee's estimate of 61% of animal matter was a conservative value.

Butynski (1982c), reviewing vertebrate predation by contemporary primates, including humans, showed that while animal matter is a major component of the diets of many species of primates (sometimes 30–70% of the diet), almost all of this derives from invertebrates. Animal matter comprises only 1–4% of the diet of baboons and chimpanzees (far less than this in gorillas). The hunting of vertebrates by non-human primates is an uncommon, albeit widespread, behaviour. Butynski (1982c) points out that chimpanzees and humans are the only primates known to occasionally kill their prey by flailing it against a hard surface and to carry meat for distances of >1 km. No primate other than humans is known to prey upon animals larger than itself. Chimpanzees and baboons seldom kill prey weighing more than 6 kg, and 10 kg appears to be close to the upper limit. In contrast, humans often kill prey many times their weight. The frequent hunting and utilization of large mammals by humans appears to have been enabled by the addition of complex vocal communication, bipedalism, fire-use and weapon-use to a basic primate hunting pattern.

One probable outcome of this 'hominin hunting pattern' was the hunting of vertebrates (especially mammals) as a major activity and 'way of life'. This appears to have resulted in a dramatic (perhaps 30–35-fold) increase in the consumption of meat from vertebrates, an increase perhaps already evident >2.5 mya. The hominin hunting pattern comprises adaptations not shared with any extant non-human primate nor, presumably, with any pre-hominid ancestor. The hominin hunting pattern allowed for the exploitation of a new, very different, and vast food-niche (see above) in which there was little or no competition with other primates – although there was probably important competition with several large African predators (Butynski 1982c).

There is no consensus concerning the diet of early hominins. As such, anthropologists argue passionately about just how frugivorous, omnivorous or carnivorous prehistoric hominins were, notably for more recent periods, when diets reflected the local availability of plant and animal foods. The issues are certainly relevant to understanding hominin divergence from our common ancestor with the other apes but are still far from being resolved. Knowing that hands were used for food-gathering and that early hominin hands differed from those of other apes, we can safely infer that diet was involved. The most likely difference was that the ground apes were omnivorous and foraged for small items on the ground whereas ape ancestors were predominantly arboreal eaters of relatively large fruits.

It may be too much to hope that an appreciation for the initial divergence between the human and ape lineages being founded on small dietary differences could translate into greater sympathy for African apes and for their present plight. Even so, insisting that apes be recognized as fellow primates, our closest living relatives, has to be preferable to treating them as an exotic food, as they are in the restaurants of several West African and European cities (Peterson & Ammann 2003, Rose *et al.* 2003). Human appetites, not just gastronomic ones, threaten a great many of the mammals described in this work. If some recognition emerges that Modern Humans are an integral part of Africa's mammalian fauna, and that chimpanzees and gorillas are our cousins, then consumption of chimpanzees and gorillas may eventually come to be seen as closer to a form of genocidal cannibalism than to gourmet dining.

The ability of contemporary societies to ship ape and other carcasses to far away markets is an essentially modern and new challenge but it is part of a much larger trend. As all types of human impact on the environment grow, agriculture (for the most part primitive, but increasingly machine- and chemical-dependent) demands more and more land and excludes more and more species. In rich countries, trade, research and transport have spread access and knowledge of foods to an ever-expanding market. In poor countries, population growth and hunger drives continuous agricultural expansion and unsustainable exploitation of many local foods that were previously ignored or only eaten *in extremis*. As wild foods decline, the ultimate loss is of local ecological integrity and diversity, and an increasing and permanent impoverishment of the natural world. The great Australian writer and scientist, Tim Flannery, has dubbed us the 'Future Eaters' (Flannery 1994).

There are three major forces, which, if they continue to follow present trajectories, will extirpate many species of the larger mammals in Africa. One is the increasing numbers of humans with the need and, increasingly, the means, to inhabit virtually the entire land surface of Africa. Concurrently, the single most direct force exterminating large mammals is the widespread and unregulated commercial bushmeat trade. The third major force is the use of ever-increasing areas of land for commercial crops such as beef, sugar, oil-palm, cereals, coffee, tea, fruits and vegetables, timber, even flowers, and concomitant appropriations of water sources. Were we to articulate the interests of other mammals as though they were comparable with our own interests, or were we to entitle natural ecosystems the 'right' to survive, the progressive turn-over of all lands to the purposes and interests of a single species could only be called theft. The ultimate effect of additive theft by one species is denial of the 'right' of other species and natural communities to

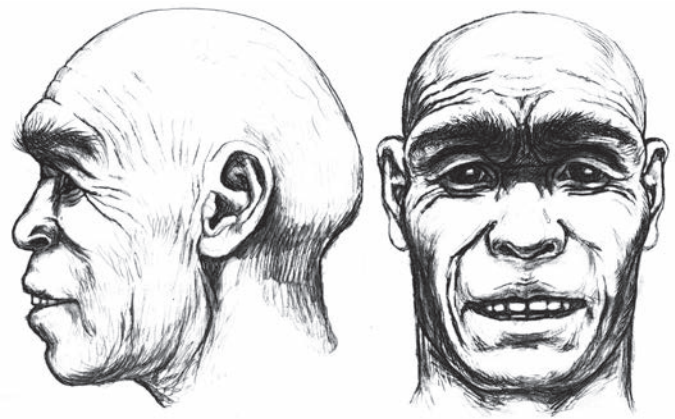
exist. Of course, few humans can acknowledge such an extreme characterization of their actions but, in ecological terms, humans are actively stealing the niches of other animals. As such, we should at least consider what can be done to mitigate our destructive ecological role and evolutionary status as 'niche-thieves'.

At the international level, land-use policies are seldom ecologically based. Both national and international bodies concerned with feeding human populations continue to value the soils and climates of remaining non-agricultural land only in terms of their potential for crops or livestock. The ambassador of a major Western nation, on visiting a small African national park of almost unprecedented ecological diversity and of a natural biological richness that dwarfed that of his own country, enthused publicly about the area's potential for conversion to vineyards. (Although his advocacy of viticulture was not taken up, the size of the park was subsequently drastically diminished and the excised areas were, indeed, given over to agriculture, much of it for the production of alcohol.) For the ambassador nothing could conceivably transcend the value of wine. His mental imposition of a Western wish-landscape over a real, but unfamiliar, African one illustrated the imprinting power of culture. He also exemplified the almost total, worldwide, absence of ecological insight or training in contemporary public leadership.

Political leadership is still oblivious to some of the most policy-relevant findings of modern science. Studies of Africa's indigenous flora and fauna have demonstrated that no agronomic or pastoral system devised by humans has ever, or will ever, begin to compare with natural ecosystems for inherent productive efficiency and for the progressive diversification of ecological niches. Accelerating degradation of African landscapes by so-called 'modern' agriculture, and drastic over-grazing by livestock, must eventually persuade thoughtful people to seek knowledge of the natural structure of African ecosystems and induce respect for the rich landscapes that preceded today's spreading ecological deserts.

All aspects of human welfare and all domesticated plants ultimately depend upon our need to understand their evolutionary history. The realization is growing that all plants and animals, including ourselves and our domesticates, have spent significant periods of evolutionary time subject to precise ecological parameters and confinement to quite precise geographic regions. There are innumerable potentialities for human exploitation in the adaptations of highly specialized biota. There are also many foods and condiments that were once part of human resource use in Africa that are being displaced by imported plants (Maguire 1980, Peters *et al.* 1992, O'Brien & Peters 1998). The workings of the evolutionary process tie our time and place to past and future, and tie our survival to all the animals and plants on which we depend, fruit, oil-palm, rice, wheat, maize, livestock, fish and many more, every one of which owes its existence to the same over-arching process. Many out-moded and, originally, non-African agricultural and pastoral practices will eventually have to be scaled down or even abandoned. In the meantime, maintaining viable mammal communities is integral to the long-term objective of ensuring that Africa develops locally relevant, not primitive or exotic, systems of resource use.

Social and Reproductive Behaviour Social. In the past, human societies differed from those of other primates in the prolonged dependence and extreme vulnerability of their young, and in the



Reconstruction of the 'Idaltu Human', one of the earliest and most complete fossil skulls of a Modern Human *Homo sapiens*.

high level of dependence of mothers on a social system that enhanced security for all. Early human societies would also have differed from those of most apes in that both sexes and all ages were more similar in physique. If human ♂♂ show less difference from human ♀♀ (and all ages and sexes are neotenous compared to, say, ♂ gorillas or ♂ chimpanzees), what significance does this have for society?

For a start, as a result of exceptionally helpless babies, every member of a human social group was more vulnerable than its ape equivalent; even adult ♂♂, always a minority, shared an interest in finding security within a group of relatively helpless ♀♀ and children. If all classes were in some sense juvenilized, a group-wide, shared, sense of vulnerability would have selected for behaviour that put the whole group at an advantage. Many animal societies find security in numbers and coordinated activities, but human group activities have more than a simple defensive role. At an early stage, ancestral human groups probably modified originally defensive behaviour into a more deliberate, systematic and proactive engagement with any aspect of the environment that might provide food or other resources. Thus, human societies became oriented to the systematic 'removal of obstacles' (including overcoming the evolved defences of plants and animals) in order to gain group-access to resources. The development of scrapers, cutters, crushers and diggers by early humans are all evidence for skills that serve this central feature of the human ecological niche (Renfrew 1973, Gowlett 1992; see p. 79).

One manifestation of neoteny in recent human societies is the extension of childhood psychology and assumptions into adulthood. Perhaps the most fundamental social purpose served by the dependence of infants on parents is social subordination. Juveniles generally follow parental example and practice, and societies of all sorts benefit from any traits that subordinate individual behaviour to the immediate needs of the group. In small family-like groups, subordination to biological parents may last as long as the parent lives. Ancestor cults in many societies bear witness to the fact that even after the death of a parent their memory is a source of psychological authority that has been integrated into specific social structures. In larger groups, that subordination tends only to continue if the offspring benefits from the status of its parent, parents or long-dead ancestor. This does not mean that psychological dependence on protective adult authority disappears. Within an enlarged group, any leader can assume a pseudo-parental role and it is in the varied ways in which 'pseudo-parents'



Ritualized intimidation displays.

Left: Adult male gorilla *Gorilla* (accompanied by a bout of chest-beating).

Centre: Robust Chimpanzee *Pan troglodytes* (short noisy charge, sometimes waving branch).

Right: Adult male Modern Human *Homo sapiens* ('Haka').

manipulate infantile psychological dependency that neoteny finds social expression (Chagnon 1975). The ways in which leaders bolster their power by assuming parent-like authority varies greatly but some general patterns are shared across all cultures.

At the ontogenetic and psychological level, a sense of continued defence by parents comforts individuals and helps smooth the transition from safe juvenile to much more vulnerable young adult. At broader historical and social levels, the transfer of each child's individual dependence upon one or two mortal, ageing parents, to generic, socially sanctioned, parent-like leaders, was a relatively small step among groups with small family-like structures. In larger, more highly organized societies, this fundamental carry-over of childhood dependence provided opportunities for the emergence of chiefs or monarchs (Bloch 1966). Once such powers were consolidated, and social structures became multi-generational, veneration for a symbolic parent lost its association with single individuals. Typically, monarchs, intent on defending or extending their own and their descendants' power, have tended to install agents charged with disseminating acceptance of their leadership by whatever means (Carneiro 1970). The most effective way of achieving this objective was to stress the parental properties of the monarch or, if the monarch was old or dead, to deify their memory. In this way, symbolic parenthood became 'eternal' and metaphysical. Most societies devise elaborate coming-of-age rituals that are designed to appropriate the allegiances and energies of their youth. The transition into adulthood is emphasized, but the neotenous psychology of dependency on the groups' 'pseudo-parents' continues and is, if anything, intensified.

Allied with coercive force of arms, a dynasty's warriors, 'guards' and agents could impose veneration for their own pseudo-parent over a much wider area. With the development of media (initially books), the power of a local dynasty could be augmented and spread exponentially. Furthermore, it served the interests of dynastic agents

to extend the veneration of a pseudo-parent, both to themselves and to the books that had become the instrument of their success and power: thus even books, obviously human artefacts, became 'sacred' in some 'Cultures of the Book'!

Among contemporary societies, the North Korean dynasty and its apparatus is an instructive cartoon of this process. Elsewhere, one-time agents of dynastic power and privilege long ago became priesthoods of various denominations. All depend on some degree of entrenched veneration for a symbolic parent, and their priesthoods provide obvious opportunities for ambitious leaders, who, wittingly or unwittingly, exploit a neotenous mammalian trait for their own social ends. There are few social institutions that are untouched by this dynamic.

Physiological mechanisms mediate all animal life, and biochemical agents trigger or suppress most of the behaviours that dominate social relations among mammals. In terms of social structures, the primary function of aggression is to optimize the spacing of individuals or groups. As such, aggression is centrifugal in nature (Marler 1965, Freid *et al.* 1968). Aggression is controlled by hormones, particularly testosterone among ♂♂, which drive individuals to confront competing or intruding conspecifics (usually other ♂♂). Centripetal tendencies, instead, are mediated by hormones that induce conciliatory, even submissive behaviour. In their relationship to social behaviour in humans, hormones have not been significantly modified – in spite of their social utility being no longer obvious. Specific and local manifestations of these chemically driven behaviours have acquired abstract, culture-specific names, such as 'hate', 'anger', 'obsequiousness', 'capitulation' and, at the broader, social level, find expression in phrases such as 'the enemy', 'war-mongering', or 'religious intolerance'.

The most reductionist explanation for much animal behaviour, including human behaviour, is that it is 'territorial', but territorialism has many expressions. Humans, like other mammals, need access

to adequate water and food, and space secure and ample enough for reproduction, play, sleep, waste disposal, etc. Like any other mammal, humans require space – territory – and they, like any other mammal, will fight for it, at national, tribal, family or individual levels, against any entity that would deny them. A single mammalian species now regards Africa as its ‘own’ territory and has plans to use and ‘develop’ every hectare of Africa’s surface for its own purposes. Thus all large mammals in Africa (and most small ones too), as well as the entire ecosystems on which they depend, exist on borrowed time. They exist on borrowed time because they are powerless to defend their lives and livelihoods against all these human needs. They are helpless to defend their space from a species that is now equipped to take away their entire livelihood, even its physical substrate, shipping it away on flatbed logging trucks. The fact is, that over the greater part of the continent, wild mammals and wild places are not just memories, they are forgotten, and with that forgetfulness, 99.9% of human history has disappeared beyond recall.

Humans emerged as a singular component of the natural communities that are now being destroyed. At the present time, our knowledge of that immensely long and influential phase of our history and prehistory is minuscule because current political, social and intellectual cultures put no value on such knowledge. Most humans, today, are much more ignorant of nature than their precursors were. In the future, ‘neo-knowledge’ of ecological processes will have to become an important strand of scientific education. Such scientifically informed education systems will also need to reappraise fundamental assumptions about culture, race, history and identity. It is in understanding the ecological underpinnings of human societies that we can begin to explain many expressions of variation among human cultures, societies and religions. In every instance there had to be a resource base to support whatever permutations of human society evolved. In every instance, food, technology and demography have all been linked and in a constant state of flux and change (Renfrew 1974). In every part of the world that Modern Humans inhabit, external ecological constraints, as well as internal social ones, have shaped cultural evolution. In adapting to naturally complex ecosystems and to increasingly complex social environments, humans devised ever-greater complexity (Freid 1967, Sahlins 1972). Thus, as human numbers increased and as humans spread ever more widely, the organic evolution of biodiversity and biocomplexity has been paralleled, or mimicked, by the cultural evolution of increasing complexity in human societies.

In the context of this work, it is useful to remember that other mammals have had a huge historical influence on African peoples. For millions of years before any animal or plant was domesticated, mammals were a primary food resource for hunter-gatherer populations. Indeed, it appears that a major difference between humans and all other primates is the amount of meat in the diet, especially mammals, and the hunting patterns by which they acquired these prey (Lee 1968, Butynski 1982c; see ‘Foraging and Food’). Modern Humans have spent, by far, the greatest part of their existence as hunter-gatherers; a time in which human knowledge of plants and animals was much greater than it is for the majority of contemporary humans.

When cattle were first domesticated, some 10,000 years ago, peoples’ relationship with the land, particularly grassland, changed (Zeuner 1963). New pastoral societies with new land-management techniques, such as firing the savannas, emerged in Africa and their demographic fortunes changed radically because domestic stock

can generally support a higher density of people than hunting (Epstein 1971). In southern Africa, some Khoi-San peoples retained a foraging economy while others adopted pastoralism. The subsequent fortunes of the foraging San and the pastoral Khoi (near annihilation for the former, semi-integration into modern economies for the latter) are reminders of how vulnerable foragers become when non-foragers want the land they inhabit. The Khoi’s adoption of an economy that



People in the Sudd, S Sudan. Impressions from a sketch-book.

was perceived as intrinsically 'inferior' by the San ensured the Khoi's survival and an increase in their numbers while the San succumbed to more powerful economies. Within our lifetime, external forces have systematically dismantled the last vestiges of a way of life that sustained our ancestors for hundreds of thousands of years (Lee 1972). As a San hunter once put it, 'the string has been broken'.

Mammals of all sorts had hundreds of thousands of years to accommodate to sustained hunting by humans and this may help to explain why so many species have managed to survive in Africa. Elsewhere, notably in Australia and the Americas, many so-called 'naïve' mammal species became extinct soon after humans invaded their realms (Flannery 1994, 2001). For the indigenous African herbivores, the arrival of exotic livestock brought new elements of competition. For the larger carnivores, pastoral humans represented a shield denying them access to a source of meat that has continued to expand at the expense of their original prey base.

If carnivores have lost out to pastoralism, herbivores have lost even more to agriculture as their own attempts to consume cultivars have turned them into 'pests'. Even more significant, the expansion of agricultural peoples has progressively eaten into all sorts of natural ecosystems, in many instances obliterating the natural vegetation and faunas of entire regions.

Both the numbers of humans and the complexity of their societies have continued to enlarge. Recently created 'sovereign states' are already being drawn into a web of global institutions that are in the process of transforming the scale of basic human enterprises. Among these enterprises is the ancient practice of studying and enumerating resources. Within the bounds of their territories, foragers knew the whereabouts, habits, sometimes the numbers, of the animals and plants on which they depended (Roth 1897). Pastoralists kept a tally of all their animals and knew intimately their physical needs. Farmers monitored and recorded many details of their crops and livestock. Today, international bodies, such as United Nations Food and Agriculture Organization (FAO), have globalized these practices. The editors and authors of this work, together with organizations such as The Wildlife Conservation Society (WCS), IUCN, WWF, Fauna and Flora International (FFI) and the Zoological Society of London (ZSL), are engaged in the vast and endlessly incremental task of studying and conserving the mammalian communities of the world, communities of which *H. sapiens* is an organic and integral part. This volume is a contemporary expression of human concern and interest in the mammals of Africa. Many of these mammals helped sustain our ancestors: hopefully they will continue to sustain our descendants.

Reproduction and Population Structure Human gestation lasts about nine months. It is theoretically possible for human numbers to double in <20 years. In the contemporary world, societies differ widely in their birth and survival rates. Many of the factors determining the reproduction and demography of Modern Humans are culturally determined, but many parameters remain biologically constrained in ways that do not differ from those of other mammals.

With the onset of puberty, humans of both sexes, like other primates, develop an interest in sexual activity. While eventual reproduction is usually the outcome, social manipulation usually plays a decisive role in the pairing process, with parents, families and convention enforcing control over their youths' reproductive potential for whatever social advantage can be extracted. Such

controls have usually acquired both moral and socially strategic connotations that strongly influence the choice of partners. Numerous works of art, such as *Romeo and Juliet*, have explored the joys and tragedies of sexual attraction and its social manipulation.

In spite of births having been decoupled from seasons, in most societies there are still reported to be birth peaks after wars, or nine months after spring public holidays! As among other mammals, there is an intimate relationship between food and reproductive success, birth-weights, growth rates and survivorship. In all aspects of our reproductive biology – growth, maturity, longevity, birth, and mortality rates – we are typically mammalian and, more specifically, we are recognizably African primates.

Predators, Parasites and Diseases In Africa, humans have probably always been regular prey for Lions and other large carnivores. There is a fundamental difference between the attitudes and behaviour of people that have no experience of being threatened by Lions, Leopards or hyaenas and those who have. Rural people are frequently at risk (or may perceive themselves or their livestock as being so). Thus, with the spread of humans and their domesticates the pressure on potential predators mounts, leading to an attrition that has already led to widespread local extinction of carnivores. It is an attrition that has been greatly speeded-up by the availability of cheap poisons, firearms and traps.

Disease is still a major selective factor in human biology, no less than it is for other mammals (Black 1975). To mention only two examples, the impact of malaria and AIDS on the well-being of African human populations is enormous. It is essential to understand the biology of such diseases if we are to mitigate the suffering they cause. Other African mammals are highly relevant to that task: for example, there is a type of malaria that is specific to a particular species of African murine rodent (Vincke 1950). This is one example of a self-contained host–parasite relationship that can be reproduced and studied in miniature form in the laboratory.

AIDS is a disease that has jumped from its original hosts, several African primate species, into the one African primate that has a world-wide population. Thus, *H. sapiens* has served the virus well in spreading it widely and in providing millions of hosts (and the epidemic is still far from peaking). Only a much greater knowledge of African ecology and of the primates that also harbour AIDS will allow us to come to grips with this disease and understand its deep evolutionary roots.

While indigenous diseases will undoubtedly continue to pose threats to humans and their domesticated animals, disease reservoirs in domesticates are now an increasingly common threat to wild animals. Disease has always been a universal for mammals and, as the leading agent of natural selection, disease has profoundly shaped what an animal is. Disease has certainly shaped *H. sapiens*, sometimes in unexpected ways.

It is likely that prehistoric population densities and resource-use patterns had a direct influence on human biology (Armalegos & McArdle 1975), and on the evolution of one of our most species-specific characteristics – nakedness. For example, epidemiological challenges must soon have arisen when foraging groups of early *Homo* assembled for any significant period of time in particularly resource-rich localities. This is because large groups soon accumulate waste and excreta, and these, in turn, quickly attract a variety of noxious

organisms, especially in the tropics. Since diseases and parasites are among the most influential and fastest agencies in natural selection, greater exposure to contamination would soon select for the individual humans that were most resistant to opportunistic skin infections. The skin-cleansing and antibiotic role of eccrine glands, one of our primary peculiarities, was pointed out earlier and the possibility was mentioned that eccrine gland multiplication in humans is linked with decreased hairiness. It is not simply that eccrine glands have increased and the size and density of hairs have decreased. The decrease in hairiness combines with a drastic decline, in humans, of the apocrine and sebaceous glands that are directly attached to hair follicles in most mammals. These fatty glands have disappeared from extensive areas of the human body and, in many peoples, so has a dense growth of thick hair. However, the high level of variation in degree of hairiness in Modern Humans supports the idea that hair reduction might be a relatively recent and incomplete evolutionary development. If there is a direct connection between reduced hair cover, increased eccrine glands and more exposure to skin infections, self-cleansing must be part of the explanation. We may be naked for no more glamorous a reason than that our ancestors were a dirty lot!

Conservation IUCN Category (2012): not listed. CITES (2012): not listed.

When a world leader proclaims, 'the planet is not at risk, WE are!', the possibility that *Homo sapiens* might be an 'endangered species' is quite explicit (Havel 2007). Emergent diseases, nuclear war, climate change, over-population, or the impact of volcanics or an asteroid are all possibilities, but the core of Havel's argument is that we must study and respect the natural processes that govern life on earth in order to survive as a species. He identifies, as the central problem, the comprehensive appetites of our species and all the industries that serve them.

'Conservation' is a word and a concept created by the intellect and emotions of contemporary humans. It is diametrically opposed to many of the consumptive appetites of humans so that practical conservation, whether it is for the long-term well-being of humanity or for the survival of other species, comes into unavoidable conflict with all the human institutions and practices that serve those appetites. In Africa, the conservation of mammals has a species-specific dimension that is rarely appreciated because so few people are willing to acknowledge their status as one more African mammal, still less acknowledge the possibility of our own extinction.

Understanding human origins in Africa is a discipline in its infancy. Integral to the growth of that understanding will be the reconstruction of human and pre-human ecological niches using existent plant and animal communities of Africa as living models and exemplars. Even if there were no other motive for conservation (and there are many reasons), this self-centred reason would be sufficient to justify current efforts to conserve the entire spectrum of African mammals and their habitats.

In terms of rationales for conservation, these have been iterated and re-iterated by distinguished thinkers and by leading conservation bodies, world-wide. In the contemporary world, we have frequent reminders of our commonality with other mammals; reminders that come from innovations in medicine, from frequent new fossil discoveries and from the laboratories of geneticists, all reinforcing the message of genetic commonality with the rest of nature. These

reminders are welcome for many reasons, but especially because they awaken a more general recognition that we need to develop universal human ethics and practices that include an awareness of the existential needs of animals. After all, the vast majority of our ancestors were governed by just such underpinnings of their existence; yet the extermination of species continues to gather momentum.

How can humans develop ethical attitudes towards other animals and towards the environment? And how can we develop ethical institutions and legislations to ensure that mammals, and the environments that sustain them, survive an unprecedented increase in human numbers? Plans for the future can be predicated upon little more than hope: hope that the present nationalistic era of economic, political and religious barbarism will eventually evolve into a more rational and benign relationship with the global environment and with other species. That evolution will depend upon the spread, rather than the suppression, of biological self-knowledge and a heightened awareness of our commonality with other forms of life. In spite of many discouraging trends, there are reasons for qualified optimism. The most promising sign of change is the articulation of a new philosophical position by a new breed of world leaders. In a 2007 address entitled 'The planet is not at risk. We are', Vaclav Havel (2007) wrote: 'We must return again and again to the roots of human existence and consider our prospects in centuries to come ... equally important is support for education, ecological training and ethics – a consciousness of the commonality of all living beings and an emphasis on shared responsibility. We will either achieve an awareness of our place in the living and life-giving organism of our planet, or we will face the threat that our evolutionary journey may be set back thousands or even millions of years.'

There is, therefore, a growing recognition of indebtedness to nature for all our plant and animal products, and for a range of natural services from water and living space to processes such as natural pollution control, pollination, seed dispersal and soil fertility. That indebtedness requires payment and compensation no less than to a local council or police force. As the annual payment of land and property taxes becomes ever more universal, there must be an explicit provision for conservation. 'Must' because all land has ultimately been taken from some natural ecosystem, and because long-term human interests demand that all such ecosystems should be preserved in some parts of their natural range. A share of taxes is the surest, most principled, equitable and practical way of funding both the conservation of ecosystems and their in-depth study.

At the local level we are already seeing that anyone's so-called right to own and use land is being qualified as more and more countries and local authorities tax both the ownership and the tenancy of land and property. Even more important, most countries now put a time-limit on ownership by imposing substantial death duties on land and property. Wherever this is enforced, the act of purchasing or inheriting land has ceased to be a final and absolute indulgence to be protected by force or by inequitable laws. The right to own and use land is being replaced by a much healthier principle in which 'owning' changes into something more like a secure form of 'borrowing'. Liability for land or property taxes, payable to the state or other local authorities, is, therefore, becoming an entrenched practice that will certainly continue to spread and is likely, in the long run, to become global. Furthermore, the switch from traditional ideas of outright, heritable ownership towards concepts of stewardship of borrowed

assets is increasingly being applied regardless of whether the land is in individual, communal or corporate hands.

Implicit in such change is acceptance of an individual owner's fiscal responsibility to a wider world: the tax payer is helping fund the infrastructure that surrounds his property. A wholly anthropocentric interpretation of an owner's responsibilities and privileges limits the owner's debt to the human services that are enjoyed. Now there is the dawning awareness that owners are borrowing from much older 'infrastructures'. In Africa, where subsistence has been much more obviously wrested from nature by force, it is to nature that future debts will have to be paid.

The relative costs and benefits of feckless, reckless exploitation of all and every natural resource for immediate gain will eventually come under formal assessment and judgement. As all natural resources, particularly biota and habitats, become rarer and more restricted, it will become essential, if they are not to disappear altogether (as so many already have), to preserve and fund their preservation, not as voluntary responses to eccentric lobbyists, but as necessary acts in the public interest. Funding will depend upon an equitable taxation system. Taxes are needed that would directly fund the conservation and study of all that is being destroyed, not just in forests, not just in Africa, but world-wide. The beneficiaries of taxes, as well as the payers and dispensers, will have to be involved at local, national and global levels.

The beneficiaries of taxation of land and property could be primarily within the country or region within which such taxes are generated, but this ought to be qualified by the nature of the lands' products. Thus, tax on cattle ranches in Argentina or Australia should also contribute to research and conservation of ruminants in continents and countries where bovids are indigenous, rather than to artificially sustained, imported exotics. More significant and complex in terms of revenues and their allocation would be a 'conservation share' of taxes on consumer goods. Consumers will eventually have to pay tax on all goods that have ultimate origins in nature. Such goods will be taxed on the principle that the natural ecosystems within which such products evolved (or the ecosystems displaced by their cultivation or production) must be conserved, and the level of tax graded not only by the value of the product itself but also by the value of what the product has displaced. Thus, consumers of any product will contribute materially towards the preservation of the conditions within which that product was able to evolve as well as to the ecosystems its production has displaced. A significant part of the revenue generated by such taxes would return to the regions of origin of such products. Thus, taxes on coffee and palm-oil products, world-wide, would generate funds both for the conservation and study of African forests, where coffee and palm-oil originated, and for the conservation of South American or South-east Asian forests, which have been decimated by clearance for coffee or palm-oil plantations. Likewise, consumers of beef, milk or leather products will be taxed in order to sustain the ecosystems in which large herbivores evolved and continue to evolve. At present such consumers are actively contributing to the rapid extermination of wild herbivores and the destruction of their habitats, especially in Africa. To call such a situation short-sighted or immoral is an understatement; at present both the consumption and production of these goods enjoy far too many subsidies and bonanzas, and the enormous real costs have been concealed for far too long. The time for calling the producers' bluff is overdue, and revealing their deceit may require

some forceful expressions of public dismay at the behaviour of these industries and their apologists.

There are central issues of equity involved. Those who benefit from the products of nature and those who benefit from the land that has been taken from nature should contribute to the systematic preservation and study of viable samples of all the world's major ecosystems. Although the enterprises that are currently permitted to steal and profit from nature without having to pay anything in return will initially throw tantrums, they will be the first to boast of their largesse and take pride in the results once such taxes are put in place. And put in place they eventually will have to be, however long it takes. An ever-growing and ever-more-influential minority is becoming aware that the conservation of natural communities and ecosystems is far too important an enterprise to be left to charity alone. In the world we live in, systematic and sustained taxation on the exploitation of nature is the only form of compensation, barring charity, that we can realistically expect. As for the scale and rating of such compensation, it should be sufficient to permanently maintain and protect viable and widely scattered samples of all natural ecosystems across the whole of Africa and across other continents as well. The pioneer mentality that once applauded the seizure and conversion of so-called 'wilderness' will eventually have to change and mutate. The descendants of 'pioneers' will about-face and supervise, tax, or even outlaw such behaviour as being against the common good. This will be, or already is, a difficult transition as yesterday's heroes are made to stand accused in today's dock.

We employ police, detectives, judges and prison systems to deal with thieves or vandals that steal or destroy the carefully husbanded goods of more prudent persons or ancestors. We now need to enlarge the remit of such institutions to deal with thieving from Nature, our ancient but perennial parent. The conservation of natural ecosystems and species is, therefore, not some aesthetic folly of the rich and privileged, it is a profound expression of the will of intelligent humans to survive through knowledge. Only knowledge can save humans from their own follies and from becoming one more endangered species.

Measurements

Homo sapiens

Total Height (♂ ♂): 170 (95–215) cm (max. 272 cm)

Total Height (♀ ♀): 160 (91–>200) cm

HB (both sexes): est. (73–83) cm

T (both sexes): 0 cm

HF (both sexes): est. 22 (15–33) cm

E (both sexes): est. 63 (22–55) mm

WT (♂ ♂): 80 (35–>100) kg (max. 419 kg)

WT (♀ ♀): 66 (30–>100) kg (max. 730 kg)

Marked regional and temporal variation, from small, light-weight Twa and San to tall Nuer and Dinka people. Upper weights distorted by dietary habits and hormonal condition. Maximum weights cited are from exceptionally obese, effectively immobile individuals. Figures given here averaged from diverse sources. For detailed figures see Ruff (2002).

Key References Darwin 1859; Jones *et al.* 1992; Kingdon 1993, 2003; Stringer & Andrews 2005.

Jonathan Kingdon

Superfamily CERCOPITHECOIDEA – CERCOPITHECOIDS: OLD WORLD MONKEYS

Cercopithecoidea Gray, 1821. London Medical Repository 15: 297.



Myology of Olive Baboon *Papio anubis* sub-adult male.

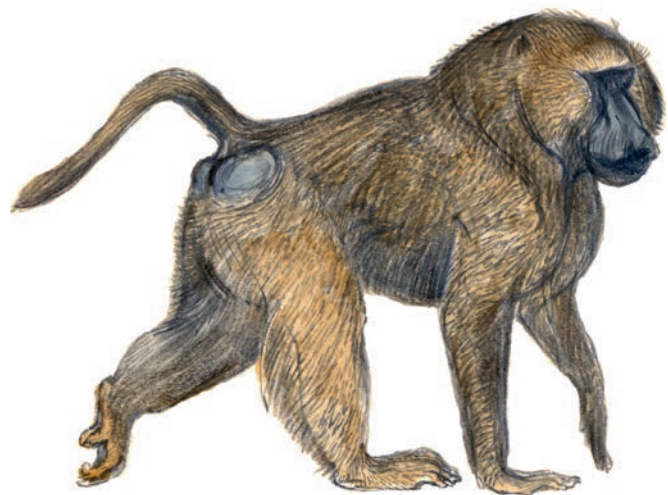
The superfamily Cercopithecoidea includes a single living family, Cercopithecidae, which embraces the subfamilies Colobinae ('leaf monkeys') and Cercopithecinae ('cheek-pouched monkeys'). Cercopithecoidea also includes at least one extinct family, Victoriapithecidae.

While the split between cercopithecoids and hominoids (apes) poses questions, the split clearly took place within Africa. There are two sources of information for dating the divergence between the cercopithecoid and hominoid lineages. The first, inferred from fossils, produces an estimate of 23.3 mya (late Oligocene) (Walker & Shipman 2005). The second method, using molecular clocks, gives a substantially earlier (late Eocene–early Oligocene) estimate of 30.5 (36.4–26.9) mya (Steiper & Young 2006) and 31.6 mya (Perelman *et al.* 2011), although Roos *et al.* (2011) provide an estimate of 26.5–21.9 mya, which is similar to the estimate based on fossils.

It may be significant that the end of the Eocene (33.9 mya) saw a marked change in climate, and that much of the Oligocene was drier and cooler, with forest retreating to the equatorial region (see Chapter 4 in Volume I). Among the Cercopithecoidea there are indications that their common ancestor was less than wholly arboreal, and that their emergence was probably linked to substantial and extensive aridity. In both fossil and living cercopithecoids, the primary indications of a less arboreal ancestral phase are an elongation of the back combined with more fore–aft movement in the limbs. Both of these alterations are correlated with fast movement on the ground. A terrestrial ancestry is unambiguous both for Cercopithecinae (many of which are still strongly terrestrial) and for Colobinae (in spite of being almost entirely arboreal today). Apart from a relatively rich fossil record, which confirms their early terrestrial bias, colobines share many



Colobinae. Colobus monkeys (red colobus *Procolobus*).

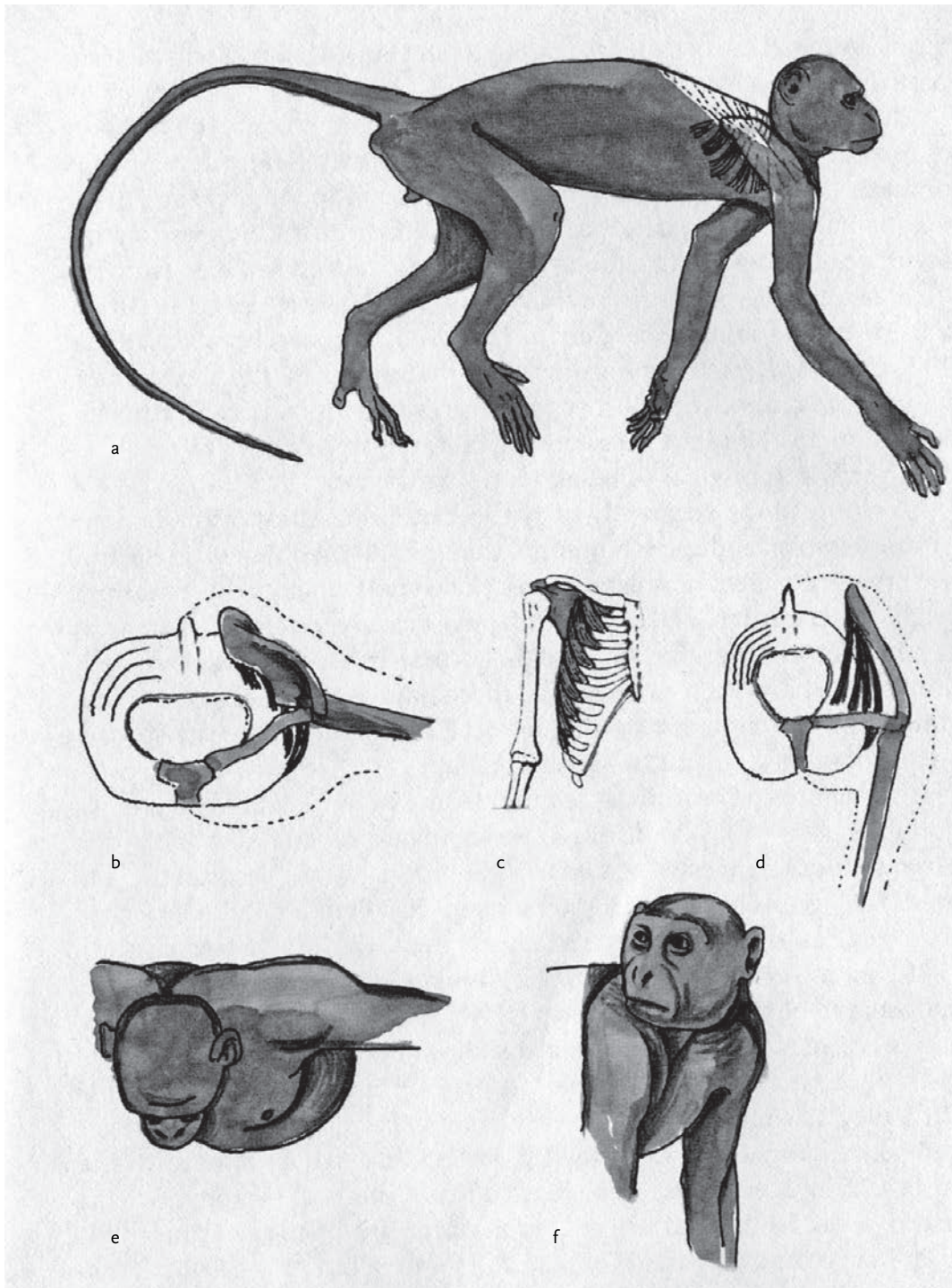


Cercopithecinae. Cheek-pouched monkeys (baboon *Papio*).

anatomical features with cercopithecines (quadrupedal adaptations of the postcranial skeleton and, in particular, the striking bilophodonty of the molar teeth). In spite of the great dietary specialization of most contemporary species of Colobinae, a few extant species retain enough ecological flexibility to betray their common origins with Cercopithecinae (particularly evident in the semi-terrestrial *Semnopithecus* spp. langurs of South Asia).

As for an intra-African separation between proto-cercopithecoids and proto-hominoids, the latter were the first to leave Africa and this has phylogenetic as well as biogeographic implications. Thus, at the time of their emigration during the early Miocene (ca. 20 mya), Hominoidea seem to have had a more northerly and equatorial range in Africa while the earliest Cercopithecoidea were, putatively, differentiating in the drier, more temperate south-east (which, at that time, was farther south and more extensive than today).

The features that colobids and cercopithecids have in common are dietary: not only the bilophodont cheekteeth, but also, apparently, an ability to detoxify plant secondary compounds in the gut. This is an ability that hominoids lack and which gave the Old World monkeys a marked ecological advantage.



Anatomical reflections of 'branch-running' and brachiating.

In quadrupedal branch-running, the monkey long serratus muscle and scapula are approximately vertical (a, d and f).

In brachiating, the ape serratus muscle and scapula wrap around the trunk (b, c and e).

In addition, there are cranial and dental features indicative of a dietary shift in which a frugivorous diet had to accommodate to more seeds/nuts. This would have been consistent with greater seasonality in the south. Cercopithecoid bilophodonty has been analysed in terms not only of increasing the surface for grinding harder foods but also the construction of reinforced, wedge-like cusps that could crack and open nut shells and break-up hard seeds (Kay 1975, Maier 1977, Benefit & Pickford 1986). The entire skull had to withstand occlusal forces and provide the anchorage for more powerful mandibular muscles (Benefit 1999). This led to loss of the maxillary sinus and more heavily reinforced buttressing of the

mandibles. Thus, all Cercopithecoidea share locomotory, digestive, dental and cranial specializations. It is possible that these traits evolved in response to a diminished choice of foods, especially fruit, in south-east Africa. These traits may have begun to evolve before colobines and cercopithecines diverged, and before any movement out of their south-eastern enclave. However, the first cercopithecoid lineage to move back into the equatorial belt would have had to face competition from their abundant and diverse tropical precursors, the apes. This competitive challenge may have given the proto-colobines a selective advantage, which led to further accentuation of the dietary trait. Just such a break-out of south-eastern isolation could

have generated the phylogenetic split within the Cercopithecoidea and initiated a distinctive colobine lineage. Meanwhile, the parent population, still isolated in the south-east, would have been free of competition from apes but subject to its own selective forces (mostly in relation to predation and socially driven pressures in habitats that were harsher and more seasonal).

Such a staged history would be consistent with colobines getting out of Africa later than the apes, yet several million years earlier than the cercopithecines. Thus, south-eastern origins for the Cercopithecoidea would not only account for the primary split

in a common anthropoid ancestor, it also helps explain why apes were the first to leave Africa and why colobine ancestors were next (because they were the first to move north-east). Eventually, colobines and cercopithecines both had Eurasian diasporas, which then radiated extensively, especially in tropical South-east Asia. More detailed accounts of the features that distinguish colobines from cercopithecines are given in their respective profiles and in the species profiles.

Jonathan Kingdon & Colin P. Groves

Family CERCOPITHECIDAE

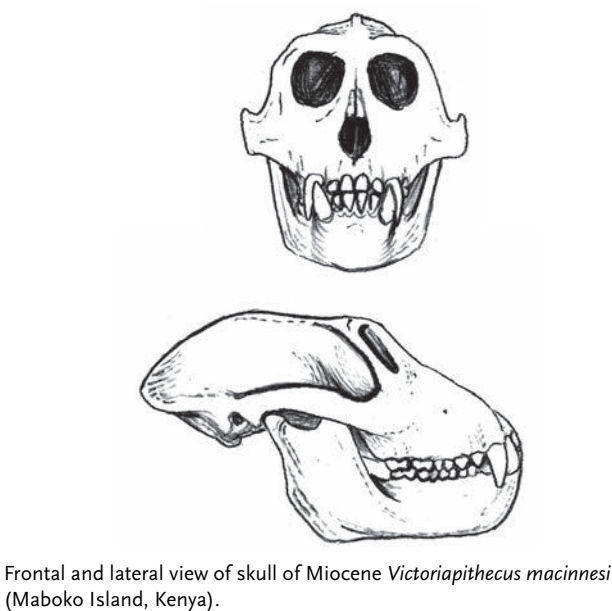
CERCOPITHECIDS: OLD WORLD MONKEYS

Cercopithecidae Gray, 1821. London Medical Repository 15: 297.

| | | |
|--|--|--------|
| Colobinae (2 genera with 2 subgenera, or 3 genera; about 12 species) | Colobus Monkeys (Colobine Monkeys) | p. 93 |
| Cercopithecinae (13 genera, 56 species) | Cheek-pouched Monkeys (Cercopithecine Monkeys) | p. 155 |

Until recently, cercopithecine monkeys and colobine monkeys were generally distinguished at the familial level (i.e. Cercopithecidae and Colobidae). Thus, most references before 2000 use Cercopithecidae in this sense. With the rise of molecular phylogenetics and a gradually improving fossil record, the objective dating of evolutionary divergences at various higher taxonomic levels has become, for the first time, possible. This offers taxonomists a temporal criterion to determine the taxonomic rank to which any one group can be allocated. In the provisional temporal ranking of taxa suggested by Goodman *et al.* (1998), the emergence of a family should take place in the late Oligocene (28–25 mya), while subfamilies should emerge in the early Miocene (23–22 mya). Fossil and molecular data combine in suggesting that the cercopithecine monkeys and colobine monkeys diverged from a common ancestor in the early to mid-Miocene (14–18 mya; Perelman *et al.* 2011, Roos *et al.* 2011), which, on the new criteria, precludes the two taxa from being ranked any longer as families. We, therefore, adopt Cercopithecidae as the sole extant family within the Cercopithecoidea, the other potential taxa being extinct fossil lineages (notably the lineage or ‘plesion’ to which *Prohylobates* belonged and another to which Victoriapithecine monkeys might have belonged).

The family Cercopithecidae embraces some 23 genera within a very diverse group of African and Eurasian monkeys. These include the colobine monkeys or ‘leaf-monkeys’, subfamily Colobinae, and the cercopithecine monkeys or ‘cheek-pouched monkeys’, subfamily Cercopithecinae. The Cercopithecinae includes two tribes: the long-tailed African guenons and their allies, Cercopithecini, and the large-muzzled African baboons, drills and other baboon-like monkeys, Papionini. The Papionini also includes the predominantly Asian genus *Macaca*, which is thought to be of African origin and to have emigrated



Frontal and lateral view of skull of Miocene *Victoriapithecus macinnesi* (Maboko Island, Kenya).

to Asia before 5 mya (late Miocene) (Stewart & Disotell 1998).

Features distinguishing Cercopithecidae from Hominidae are quadrupedal locomotor apparatus, with arms not much shorter than the legs, somewhat elongated lumbar spine, and bilophodont cheekteeth, which initially operate as a series of transverse ridges along the toothrow and, with wear, leave a series of enamel loops that prolong the life of the teeth.

Among *living* groupings, Cercopithecidae effectively share all their characteristics with Cercopithecoidea. Therefore, consult the Cercopithecoidea profile for the characteristics that distinguish Cercopithecidae in its new, post-2000, sense. The features of subfamilies and genera are presented under the appropriate taxonomic headings.

Colin P. Groves & Jonathan Kingdon

Subfamily COLOBINAE – Colobines: Colobus Monkeys

Colobinae Jerdon, 1867. Mammals of India, p. 3.

| | | |
|--|---|--------|
| <i>Colobus</i> (5 species) | Black Colobus Monkey,
Black-and-white Colobus
Monkeys | p. 95 |
| <i>Procolobus</i> (The 2 subgenera are
often ranked as full genera) | Olive Colobus Monkey,
Red Colobus Monkeys | p. 120 |
| (<i>Procolobus</i>) (1 species) | Olive Colobus Monkey | p. 121 |
| (<i>Piliocolobus</i>) (6 or more species) | Red Colobus Monkeys | p. 125 |

Colobus monkeys are medium-sized, variously coloured monkeys with big bodies and small heads. One species is all black, some black-and-white, some have red and orange tints, and one species is dull olive. At close quarters their most distinctive peculiarity is a lack of thumbs. Amputation of digits is a mutilation for humans, hence the monkeys' anthropocentric name, from the Greek, *kolobos*, meaning 'mutilated'. Thumblessness and dietary specialization represent the two adaptations that most clearly separate the extant African colobines from other cercopithecoid monkeys. The progressive development of these peculiarities over time poses questions of the greatest biological interest (Hartwig 2002).

There are a dozen recognized species in the African branch of Colobinae and these belong to three genera or subgenera, the Black-and-white Colobus-Group *Colobus*, the Olive Colobus *Procolobus* (subgenus *Procolobus*) and the Red Colobus-Group *Procolobus* (subgenus *Piliocolobus*). There are seven Asian genera, all of which derive from an African source following an emigration at about 12–11 mya (mid-Miocene; Perelman *et al.* 2011, Roos *et al.* 2011). Molecular phylogenetic evidence indicates that the African colobine radiation started by the late Miocene with the Black-and-white Colobus-Group splitting from the Olive Colobus/Red Colobus-Group by 9.9–6.8 mya (Ting 2008a, b, Perelman *et al.* 2011, Roos *et al.* 2011). The last common ancestor for Olive Colobus and Red Colobus is estimated at 6.4 mya (Ting 2008a, b) and 6.9 mya (Perelman *et al.* 2011, Roos *et al.* 2011). The chromosome count for all African colobines that have been examined thus far is $2n = 44$ (Romagno 2001).

Today, African colobus monkeys are almost exclusively equatorial and wholly arboreal, but the fossil record and their emigration to Asia demonstrate that, in the past, their ecology was more diverse, their geographic distribution much greater and their diversity more rich. Fossil colobines from the late Miocene and Pliocene show that they were then semi-terrestrial, and some are thought to have been wholly terrestrial, while at least one fossil species, *Mesopithecus* from the late Miocene of Eurasia, had a sizeable thumb. Jablonski (2002) and Leakey & Harris (2003) provide an exhaustive review of current knowledge of the fossil colobines and summarized the evidence available for African colobines.

The earliest fossils date from the late Miocene (Benefit 1999) and several fossil genera have been described, notably *Microcolobus* (according to Elton 2007 the earliest fossil colobine at about 9 mya), *Kuseracolobus*, *Rhinocolobus*, *Dolichopithecus* and *Cercopithecoides*. An exceptionally large Pliocene form, *Paracolobus chemeroni*, was likely predominantly terrestrial, as was *Dolichopithecus* (Delson 1994, Benefit & Pickford 1986). To date, no fossil colobines have been

reliably allocated to the living genera or subgenera, and most fossil forms did not give rise to extant species.

The divergence between Cercopithecinae and Colobinae has been variously estimated at ca.14 mya (Stewart & Disotell 1998) and 16.2 mya (17.9–14.4) (Raaum *et al.* 2005); the latter range seems more likely when it is remembered that by 11 mya well-developed colobines were probably present in Asia (Stewart & Disotell 1998, Tosi *et al.* 2005). The beginning of the mid-Miocene coincided with a period of warming just before a more general period of global cooling. Such an amelioration of climate might have allowed the colobine ancestor to detach itself from its parental population, putatively in south-eastern Africa, and move into the equatorial belt. This may help explain why colobines had such a substantial head-start over cercopithecines, not only in colonizing Asia but also in reaching outlying areas north of the equator. The first fossil cercopithecoid in North Africa was a late Miocene colobine, *Libypithecus*. The colobine emigration to Asia took place about 11 mya, whereas the eastward spread of *Macaca* was 4 million years later.

It seems plausible, therefore, that when the colobine ancestor moved north-west to share evergreen equatorial forests with a variety of mostly larger (and possibly more strategic-minded) proto-apes, their advantage lay in being 'digestion specialists' that could cope with food types that were too difficult for the proto-apes, such as plants that protected their seeds and leaves with distasteful or toxic secondary compounds (Montgomery 1978). Later, when colobines and cercopithecines came into direct competition, the colobines' dietary specializations became even more pronounced. This development gains some credence when it is remembered that at least one Asian genus, the partly terrestrial *Semnopithecus*, retains a less specialized digestive physiology. Further evidence for this progressive, staged, digestive specialization is registered in changes in the dentition of colobine fossils during the Pliocene (Benefit 1999). Judging from the relative abundance of their fossils, Colobinae were only overtaken by Cercopithecinae (in Ethiopia, which must have been very much of a peripheral outpost for them, even then) as late as 4.0–3.5 mya. At the early Pliocene site at Aramis, Ethiopia, White *et al.* (1994) calculated that colobines were 12 times as abundant as cercopithecines, but they had become much rarer by 3.3 mya (Benefit 1999).

The mainly Pliocene radiation of Cercopithecini, particularly of guenons, which embrace a range of body sizes similar to colobines, seems to have progressively narrowed the niche for colobines. This is most obvious in Africa, where colobines originated and have the longest history of interaction with other monkeys.

Thumblessness and dietary specialization represent the two adaptations that today separate the African colobines from other cercopithecoid monkeys. Only in monkeys wholly committed to living in dense forest would the hands become modified into flexible hooks. Many fossil colobines were not only more terrestrial, living in less than true forest, but they had thumbs. The evolution of hands, such as those possessed by modern African colobines, involved the alignment of the long fingers into a single, narrow, curved arc (where a thumb would actually obstruct its branch-gripping function).



Peters's Angola Colobus *Colobus angolensis palliatus*.

Because their hands have lost the ability to manipulate isolated, droppable objects or living prey, colobus prefer to take material off a plant directly into the mouth. Thus thumblessness implies that colobines became almost wholly arboreal and vegetarian at much the same time; but when? It is likely that these were relatively late developments, probably strongly influenced by competition from cercopithecines (but see Ting 2008a, b). The rise of cercopithecines eventually excluded colobines from all their earlier, more terrestrial niches, at the same time leading to still stronger selection for specialized digestion of chemically protected plant parts.

The complex, sacculated stomach of colobus monkeys holds up to one-third of their total body-weight in food. They are 'foregut-fermenters' and digestion requires long rests to allow bacterial fermentation of a sort that is similar to that of ruminants and other purely herbivorous animals (except that colobines do not regurgitate and chew cud). The bacteria are short-lived and protein from their dead bodies provides a large proportion of easily absorbable nutrients for the monkey (R. Hofmann pers. comm.). There is clearly a history of co-evolution between African colobines and the trees in their disparate habitats. A prominent part of most colobine diets consists of leguminous plants, the leaves and fruits of which are exceptionally well protected by chemicals. Because of this peculiar chemistry, and because legumes have dominated African forests, the processing of legume toxins must have been an important factor in the evolution of African colobine digestion (Oates *et al.* 1977, Montgomery 1978, Moreno-Black & Bent 1982). Although long referred to as 'leaf-monkeys', colobines are better described as 'processors of difficult plant material' and their diet includes fruits, seeds, petioles and flowers, as well as leaves, but most species actively avoid ripe,

soft, colourful fruit, preferring unripe fruits, seeds and seed-pods (Oates *et al.* 1977). There are significant differences among colobine species in the proportions of fruits and seeds that they eat, as is well exemplified in the profiles that follow.

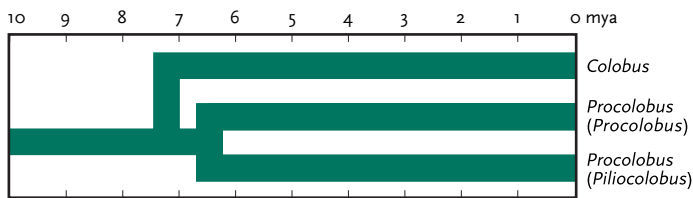
While colobines share the primary feature of a toxin-processing and leaf-digesting chambered stomach, the members of the Black-and-white Colobus-Group have the most advanced digestive capacity and a correspondingly extensive distribution through moist evergreen forests. The Olive Colobus *Procolobus verus* with, apparently, a less advanced ability to cope with fibrous old leaves and plant secondary compounds, is much more restricted in its small West African range. Monkeys belonging to the widely scattered, but patchily distributed, Red Colobus-Group appear to be intermediate.

Colobine teeth are only moderately modified for a leafy diet, being essentially higher-cusped and higher-crowned specializations on the general cercopithecoid pattern (Strasser & Delson 1987). Generic modifications do occur. For example, the cheekteeth of *Piliocolobus* and *Procolobus* tend to be relatively narrower than those of *Colobus*. In *Procolobus*, the third lower molar is usually six-cusped, whereas in the other genera it is, as in most other cercopithecoids, five-cusped. The central incisors in both jaws are short and broad in *Procolobus* and *Piliocolobus*, but long and comparatively narrow in *Colobus*. The unworn lateral incisors are caniniform; in *Procolobus* and *Piliocolobus* their points are acute and are directed laterally, but in *Colobus* they are more obtuse and are directed medially. In *Procolobus* the incisors have a prominent lingual cingulum with a distinct lingual tubercle. The unusually robust teeth of Black Colobus *Colobus satanas* may be seen as adaptations to considerably more hard seeds in the diet (Oates & Trocco 1983).

Apart from the dental characters mentioned above, there are well-marked differences among the three African colobine groups in the skull. *Procolobus* develop sagittal crests in adult ♂♂, whereas *Colobus* never do. In *Piliocolobus* the orbits are angular, with thick supraorbital ridges interrupted by a notch or channel; there are well-marked suborbital fossae; and the choanae and interpterygoid fossa are deep and narrow. In *Colobus* the orbits are more rounded, with supraorbital ridges that are usually less marked and generally run uninterrupted above each orbit without marked notches; the facial skeleton is relatively flat on either side of the nasal aperture, without suborbital fossae; and the choanae and interpterygoid fossa are low and wide. In most respects, *Procolobus* resembles *Colobus* cranially, except that, like *Piliocolobus*, there are marked suborbital fossae. Differences among the three groups were first described in detail by Verheyen (1962), although some of the characters he ascribed to *Piliocolobus* apply only to central African species.

There are also characteristic differences among species both within *Colobus* and *Piliocolobus*. In particular, the skulls of *C. satanas* and Guereza *Colobus guereza* are very distinctive (see illustrations pp. 98 & 113).

Lumping all colobus monkeys under a single genus, *Colobus*, was common practice until recently. Indeed, all our principal authors have, over time, shifted positions on colobine taxonomy. In their earlier works Groves (1970), Kingdon (1971) and Struhsaker (1975) all followed the authorities of that time (Booth 1954, 1958a, b, Verheyen 1962, Napier & Napier 1967) in referring to various regional forms of red colobus as subspecies of the Western Red Colobus *Colobus badius*. Initially, the arrival of molecular taxonomy scarcely changed this: Cronin & Sarich (1975) divided colobines into three equal genetic lineages, the African *Colobus*, and the Asian *Pygathrix* and *Presbytis*.



Tentative phylogenetic tree of extant colobines (after Ting *et al.* 2008a).

Groves (1989) subdivided African colobines into two genera, *Colobus* and *Procolobus*, and he further subdivided the latter into the subgenera *Procolobus* and *Piliocolobus*. Since 1989, the generic or subgeneric name, and further subdivisions, of red colobus monkeys have been at variance (Grubb *et al.* 2003, Groves 2007b, Ting 2008a, b, Roos *et al.* 2011). Readers should be aware that opinions on the taxonomic status of red colobus and the number of species contained within this entity are still contentious, even among the editors and authors of this work.

In adopting the subgenera *Procolobus* (*Procolobus*) and *Procolobus* (*Piliocolobus*) the editors and authors of this work have arrived at a provisional compromise. In this volume, T. Struhsaker, P. Grubb and K. Siex treat *Piliocolobus* as a subgenus of *Procolobus*; they have written profiles of the three taxa designated as *P. rufomitratus*, *P. gordonorum* and *P. kirkii*. Further profiles, designated as *P. badius*, *P. pennantii* and *P. preussi*, are presented by other authors. Of the forms described herein as subspecies of *P. rufomitratus*, C. P. Groves, J. Kingdon and T. Butynski recognize that complex, and the not easily explained interactions (perhaps hybrid zones) that exist between the best-defined regional populations. They suspect, however, that some of the forms within *P. rufomitratus* merit full species status (notably *tholloni*, *foai*, *tephrosceles*, *oustaleti*). Readers will appreciate that little is known about red colobus biology in general, especially at the

molecular level, and that, as such, colobine taxonomy remains in a state of flux (Grubb *et al.* 2003, Groves 2007, Ting 2008a, b, Roos *et al.* 2011).

Regardless of current controversies, the red colobus diaspora embraces a complex of 18 or more identifiable populations that have long posed major puzzles for scientists. Red colobus are recognizable by their distinctive colouring, with red caps or red patches on the crown being the norm in almost all species. Crown hair forms complex crests and crisp whorls in some species (notably *badius*, *pennantii*, *tephrosceles*, *rufomitratus*), but can be lank and unstructured in other species. A black band between orbits and ears is obvious in most populations and spreads up onto the brows or down onto the cheek in some eastern and central Congo Basin populations (notably *rufomitratus*, *tephrosceles*, *tholloni*) and in the Niger Delta population *epieni*. The distribution of red or black patches on the body and limbs is highly variable; some populations are quite drab, such as *P. rufomitratus* and *P. pennantii*, while others (notably *P. kirkii*, *P. gordonorum*, *P. tholloni*) are brightly coloured. *Procolobus gordonorum* has two main morphs, one rather drab and blackish, the other more colourful and contrasty in pattern, but both typically have red crown hair forming a 'toupee'. The relevance of this polymorphism, which occurs within groups throughout their range, would be worth study, especially in relation to the selective effects of differing levels of predation and population densities. *Procolobus foai* is also highly variable; it may be that what are now classified as the four or five subgroups of this taxon are actually hybrid swarms occupying zones in between the distributions of formerly more distinct taxa (Colyn 1991).

Other features of the Colobinae are presented in the genus and species profiles.

Jonathan Kingdon & Colin P. Groves

GENUS *Colobus*

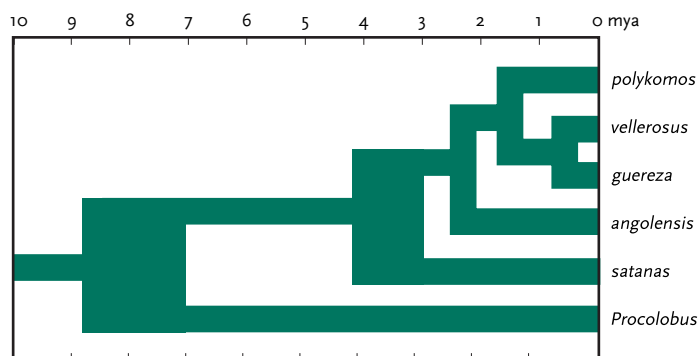
Black-and-white Colobus Monkeys

Colobus Illiger, 1811. *Prodromus Systematis Mammalium et Avium*, p. 69.



Western Guereza *Colobus guereza occidentalis*.

Polytypic genus endemic to the forests of tropical Africa. Until recently it was common to find the name *Colobus* applied to all extant African colobines, including some fossil species (see Subfamily Colobinae). The Black-and-white, or Pied, Colobus-Group of the genus *Colobus* consists of five species: Black Colobus *Colobus satanas*; Angola Colobus *C. angolensis*; King Colobus *C. polykomos*; White-thighed Colobus *C. vellerosus*; and Guereza Colobus *C. guereza*. Apart from the bold black-and-white colouring, this genus is distinguishable from *Piliocolobus* and *Procolobus* by its conjoined ischial callosities, by the absence of sexual swellings in ♀♀ and by the absence of perineal organs in ♂♂. All species have very loud calls ('roars') that emanate from an enlarged larynx and subhyoid sac that are unique to *Colobus*. The stomach has three chambers that offer, within the colobines, the most advanced mode of digestion of difficult vegetation types. The skulls are different from species to species and, to a lesser extent, from population to population (Hull 1979). For detailed discussion and diagnosis of the significance of features unique to *Colobus*, see Oates *et al.* (1994). With the exception of *C. satanas*, the infants of all species are white at birth.



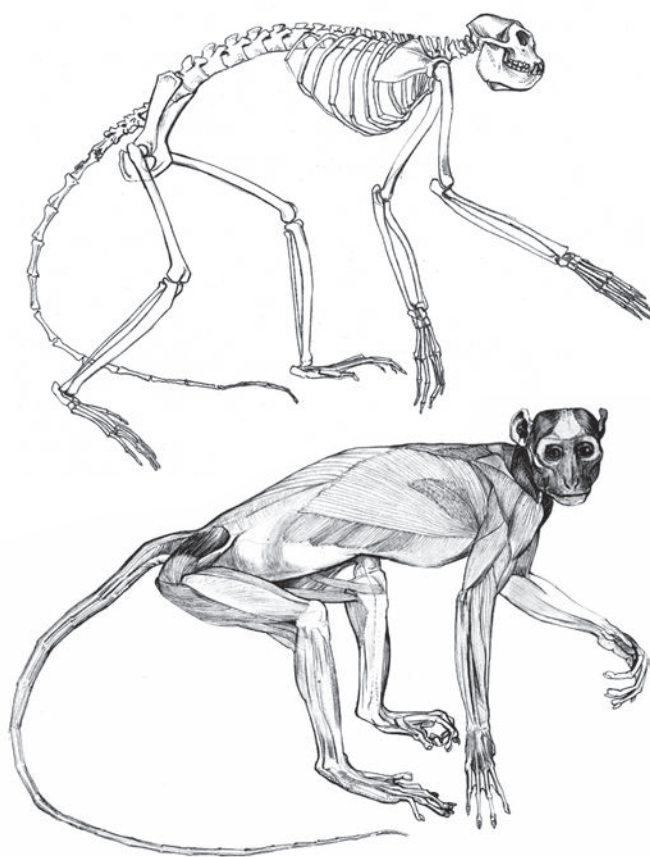
Tentative phylogenetic tree for extant *Colobus* spp. (after Ting 2008a).

Colobus species include much mature green leaf in their diet. This enlargement of the dietary range has allowed two species, *C. guereza* and *C. angolensis*, to range well outside the main forest block into forest mosaics, galleries and degraded evergreen vegetation in eastern, north-eastern and south-central Africa. Both of these species have been particularly successful in colonizing montane forest habitats, where they grow thicker, longer pelage. Earlier expansions, presumably during wetter, warmer periods, have left isolated populations on mountain massifs in eastern Africa and some of these are distinct subspecies. *Colobus satanas* and *C. polykomos*, specialized seed-eaters, are much more restricted to high forest, though their preferred diets enable them to subsist in swamp forest and other forests with extremely poor soils.

Taking the ability to digest chemically protected plant material as the primary adaptation in Colobinae, *Colobus* is clearly the most advanced genus. As such, the other African genera must derive from earlier branches of the colobine tree. Awaiting further study are differences among populations of the same *Colobus* species within and outside the main forest block. Other monkey species, including other colobine genera and guenons, are relatively few outside the main forests, whereas competition from the large guilds of primates within equatorial forests is intense. Comparing *C. angolensis* in the



Western Guereza *Colobus guereza occidentalis* neonate.



Top: Skeleton of Guereza Colobus *Colobus guereza*.

Above: Myology of Western Guereza *Colobus guereza occidentalis*.

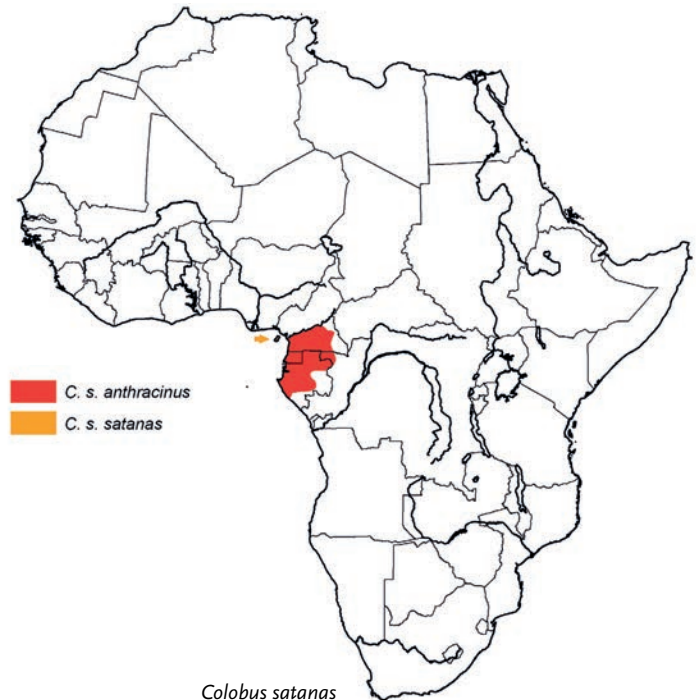
southern Congo Basin with *C. angolensis* in NW Tanzania could be revealing, as could comparisons between *C. guereza* east and west of the Eastern (Gregory) Rift. In the Semliki and north Rwenzori forests, SW Uganda, *C. angolensis* lives in montane forest and *C. guereza* lives in lowland forest. *Colobus guereza* has possibly played a role in the recent disappearance of *Procolobus* in this area (the main influences being hunting, forest clearance and degradation).

In the coastal littoral and 'Eastern Arc' montane and forested areas of East Africa there is a north-south partition between *C. guereza* and *C. angolensis*, the latter occupies all the coastal and gallery forests of S Kenya and Tanzania, while *C. guereza* occupies forests north and west of the Pare Mts up to 2900 m (notably Mt Kilimanjaro, Mt Meru, Mt Kenya and the Aberdares) (T. Butynski pers. comm.). This suggests a dynamic in which a possibly more physiologically advanced *C. guereza* expanded from the west (and only north of the Congo R.), possibly displacing *C. angolensis* in some localities but not in others, although there are areas of overlap between the two *Colobus* species in E DR Congo (e.g. Ituri Forest). Such localities could be rewarding for the study of niche formation in competitive primate communities. *Colobus*, therefore, offers numerous opportunities for study of dynamics in African ecosystems (Struhsaker 1975).

Recent molecular evidence indicates that the five extant *Colobus* spp. diverged between 3.5 mya (mid-Pliocene) and 0.2 mya (end of the Pleistocene) with *C. satanas* being the first extant species to diverge and *C. polykomos* and *C. vellerosus* being the last to diverge (Ting 2008a, b).

Colobus satanas BLACK COLOBUS

Fr. Colobe noir; Ger. Schwarzer Stummelaffe

Colobus satanas Waterhouse, 1838. Proc. Zool. Soc. Lond. 1837: 57 [1838]. Fernando Po (=Bioko I.), Equatorial Guinea.Black Colobus *Colobus satanas* adult female.*Colobus satanas*

Taxonomy Polytypic. Two subspecies (Grubb *et al.* 2003). Formerly considered a subspecies of King Colobus *Colobus polykomos* (e.g. Haltenorth & Diller 1977), but the distinctive phenotypic, cranial, dental and vocal features warrant species status (Dandelot 1974, Hull 1979, Oates & Trocco 1983). The full species status of *C. satanas* is now widely accepted (Groves 2001, 2005c, 2007b, Grubb *et al.* 2003). Grubb (1978) suggested that *C. satanas* represents an ancestral form of *Colobus* spp. This is supported by recent molecular evidence that indicates that within the Black-and-white Colobus-Group, *C. satanas* was the first to diverge (Ting 2008a, b). Synonyms: *anthracinus*, *limbarenicus*, *metternichi*, *municus*, *zenkeri*. Chromosome number: $2n = 44$ (Gregory 2008).

Description Large, black, arboreal monkey with heavy body and long limbs and tail. Entirely black (including bare skin areas). Sexes identical in colour. Adult ♀ *C. s. satanas* about 80% as heavy as adult ♂ (Butynski *et al.* 2009). Head with crest of hairs. Ears with extremely irregular outline. Tail with tuft of hairs at base but not at tip. Dorsal outline of braincase in lateral view is saddle-shaped. Skull less prognathous than for other *Colobus* spp. (Groves 2001). Individual with aberrant coat colour (white and black areas irregularly mixed) described from Bioko I., Equatorial Guinea (González-Kirchner 1997a). Infants brown.

Geographic Variation

C. s. satanas Bioko Black Colobus. Bioko I. endemic. Pelage long and thick. Smaller; tail ca. 16% shorter; hindfoot ca. 10% shorter, body weight about 10% less (see below).

C. s. anthracinus Gabon Black Colobus. Mainland Africa. Pelage short and thin. Larger.

Similar Species None within geographic range.

Distribution Endemic to western central Africa. Rainforest BZ. Restricted to rainforests of Bioko I., Equatorial Guinea, Cameroon south of Sanaga R., south through coastal Rio Muni (Equatorial Guinea) to SW Gabon, and east to W Congo. Eastern and southern limits poorly known (Groves 2001). Early in the 20th century one specimen collected east of 14° E and two specimens collected north of 03.5° N (Napier 1985). There are no data to suggest that the Black Colobus is still present this far east or north. On Bioko I. now apparently occurs in two populations: one centred on the Pico Basilé (central part of the island) and one in southern one-third of the island (Butynski & Koster 1994). Three populations in Rio Muni: one on left bank of Uoro-Mbini R. between Niefang and Macizo de los Montes Mitra, one in the mountains near Cabo San Juan (ca. 01° 15' N, 09° 30' E) and one in the Nsoc-Nzomo area (ca. 01° 55' N, 11° 00' E) (González-Kirchner 1994). Distribution patchy in Gabon; in Monts de Cristal and in Minkébé area. Not known whether present between these two areas. In south present in the Massif du Chaillu. In west present between Monts Doudou and Atlantic coast. Distribution limits to east uncertain. Not known between left bank of Ivindo R. and right bank of Ogooué R. Present in Lopé N. P. and adjacent Forêts des Abeilles (Malbrant & Maclatchy 1949, Blom *et al.* 1992, Lahm 1993, White 1994, Brugière *et al.* 2002). In Congo possibly restricted to area between

eastern boundary of Odzala N. P. and Gabon border (Carpaneto 1995, M. Fay pers. comm.).

Habitat Primary and old secondary moist forest. Coastal forests to montane forest to heathland on Bioko I., from sea level to 3000 m (Butynski & Koster 1994). On the mainland, observed from sea level to 800 m (in Waka N. P., C Gabon; Abitsi 2006, F. Maisels pers. comm.). Absent in degraded and young secondary forests but in gallery forests. Presence of tall trees essential as the species preferentially uses the upper canopy: 36% and 40% of time is spent higher than 30 m at Makandé, central Gabon (Fleury 1999), and on Bioko I., respectively (González-Kirchner 1997b). Mean annual rainfall for sites at which *C. satanas* occurs ranges from ca. 1500 mm (Lopé, Gabon; White 1994) to >10,000 mm (south Bioko; Butynski & Koster 1994).

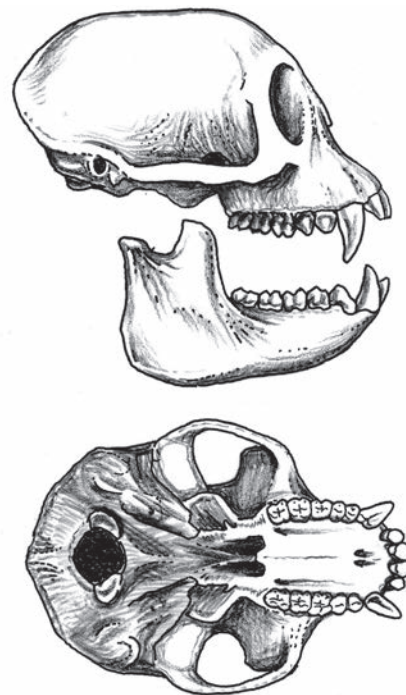
Abundance *Colobus s. anthracinus* common in non-hunted areas but abundance can vary markedly within a given area. For example, in the Lopé N. P., densities vary from 11 ind/km² in primary forest (Brugière 1998) to 30 ind/km² in gallery forest (Harrison 1986). Over the species' geographic range, densities vary from 7 ind/km² in Forêt des Abeilles, Makandé (Brugière *et al.* 2002) to 30 ind/km² in Douala Edea F. R., Cameroon (McKey 1978).

On Bioko I., *C. s. satanas* encountered at the rate of 0.02 groups/km along 373 km of transect during an island-wide survey in 1986 (Butynski & Koster 1994). Other encounter rates on Bioko are as follows: 0.18 groups/km in 2008 along 44 km of transect in Gran Caldera de Luba; 0.14 groups/km in 2008 along 49 km of transect on south slope of Pico Basilé; and 0.39 groups/km in 2009 along 48 km of transect and 0.32 groups/km in 2010 along 50 km of transect at Badja North, SW Bioko (T. Butynski, G. Hearn, M. Kelly & J. Owens pers. obs.). These last-mentioned three sites are remote and receive relatively low levels of hunting. Also, there has been little to no anthropogenic impact on the habitats at these sites. As such, these encounter rates are likely close to what can be expected for undisturbed populations of *C. s. satanas*.

Adaptations Diurnal and arboreal. The Black Colobus is the most granivorous of all *Colobus* spp. Seed eating is an adaptive strategy as seeds are high in nutrients and more palatable than leaves. Polyspecific associations of Black Colobus with Cercopithecidae monkeys permit a higher consumption of seeds (Gautier-Hion *et al.* 1997). Geophagy occurs when the consumption of leaves is high. Chemical analysis shows that the soils eaten have sodium and magnesium contents significantly higher than non-eaten forest soils (Fleury 1999).

When the tree species composition of the forest induces both seasonal food shortage and episodic intra-annual severe bottlenecks in food supplies (as in forest dominated by the irregular mass fruiting Caesalpiniceae tree species), Black Colobus shift to a semi-nomadic ranging behaviour over a large home-range (Fleury & Gautier-Hion 1999). This is the least costly strategy to cope with the low carrying capacity of the habitat.

Black Colobus spent 37–60% of the daylight hours in inactivity, 22–27% handling and ingesting food, 4–32% moving and 4–10% in social interactions (McKey & Waterman 1982, Fleury 1999). Grooming is the predominant social interaction (38%), while



Lateral and palatal views of skull of Black Colobus *Colobus satanas* adult male.

agonistic interactions account for only 7%. Typical daily activity pattern includes the following sequence (from sun rise to sun set): moving (short distance), feeding, resting, moving (long distance), feeding and resting (Fleury 1999).

Foraging and Food Granivorous-folivorous. At Makandé (Gabon, 00°40'S, 11°54'N) foraging activities peak between 07:00h and 08:00h, and 15:00h and 17:00h. This corresponds to the most active period of the day. Black Colobus often remained within small areas for several days while intensively exploiting a few individual trees. This is followed by days when they move farther, to other food patches in which they linger (Fleury & Gautier-Hion 1999). Mean distance travelled/day is 852 m (range 20–1980, n = 24) at Makandé, 510 m (range 40–1100) at Lopé (Gabon, 00°30'S, 11°40'E) and 459 m (range 100–800) at Douala-Edéa (Cameroon, 03°20'N, 10°00'E). Daily travel distance increases with increasing seed intake and decreases with increasing leaf intake at Makandé and Lopé (Fleury & Gautier-Hion 1999). In contrast, at Douala-Edéa, daily travel distance increased with increasing mature leaf intake because mature leaves were rare and patchily distributed plant species (McKey 1979). Home-range size at Makandé (573 ha) was three times that of a group at Lopé (184 ha) and eight times that of a group at Douala-Edéa (69 ha) (McKey 1979, Harrison & Hladik 1986, Fleury 1999).

Seeds and leaves (young and mature) account, respectively, for 56% and 38% of the diet at Makandé, 64% and 26% at Lopé and 53% and 38% at Douala-Edéa (McKey 1978, Harrison 1986, Gautier-Hion *et al.* 1997). Consumption of leaves increases when availability of seeds decreases. Mature leaves are eaten when young leaves are scarce. Foods rich in minerals and nitrogen, but low in lignin and secondary compounds, are preferred (McKey *et al.* 1981). Seed consumption increases when Black Colobus feed in mixed-species groups with (frugivorous) Putty-nosed Monkeys *Cercopithecus*

(n.) *nictitans*, Crowned Monkeys *Cercopithecus (m.) pogonias* and Grey-cheeked Mangabeys *Lophocebus albigena* (Gautier-Hion *et al.* 1997). At Makandé, the three most often eaten plant food species are *Petrocarpus soyauxii* (Fabaceae), *Dialium pachyphyllum* (Caesalpiniaceae) and *Aucoumea klaineana* (Burseraceae), but their use varies among years (Fleury 1999).

Opportunistic observations on Bioko I. suggest that Black Colobus there eat few, if any, seeds. Here, the flower buds of *Tabernaemontana brachyantha* (Apocynaceae) and the leaves of *Schefflera mannii* (Araliaceae) appear to be particularly important foods. On Bioko I., Black Colobus sometimes come to the ground to feed (T. Butynski pers. comm.).

Social and Reproductive Behaviour Social. Groups have 2–6 adult ♂♂ and 2–7 adult ♀♀. Mean group size 13 (range 5–30, $n = 13$; Sabater Pi 1973a, McKey, Eisentraut in Oates 1994, Fleury 1999). Adults always more numerous than immatures (at Makandé, mean percentage of immatures/group is 30% ($n = 3$). Allomothering observed several times at Makandé.

Group home-ranges overlap. At Makandé up to seven groups shared the same space. Overlap of a group's home-range by other groups reaches 65% (Fleury & Gautier-Hion 1999). At Makandé encounters between Black Colobus groups occurred more often than expected by chance. Encounters mainly occur at food patches and are peaceful. Short chases and counter-chases occur, are rare, and involve from one to five adult ♂♂ in each group (Fleury & Gautier-Hion 1999). Males transfer between groups more often than do ♀♀. Integration into the new group is instantaneous (Fleury 1999).

At Makandé, Black Colobus were in association with one or more other species of primate (*C. nictitans*, *C. pogonias*, Moustached Monkey *Cercopithecus (c.) cephus* and *L. albigena*) 14% of the time ($n = 3$ groups). At this site a single *C. pogonias* (♂) was integrated into a group of Black Colobus and interspecific grooming with that individual occurred (Fleury & Gautier-Hion 1999).

The Black Colobus is less vocal than are other *Colobus* spp. and the vocal repertoire is less extensive. A high volume, low frequency (0.5–1.5 kHz) loud-call (the 'roar') is produced by both sexes. The roar is given mainly in response to potential or identified danger. Other vocalizations include 'squeals' that are often produced before roars, and 'caws' that are given during agonistic encounters (Fleury 1999). The roar is not used as a territorial loud-call as in other *Colobus* spp. (Fleury 1999). Oates & Trocco (1983) found that among *Colobus* spp., *C. satanas* has the most distinct roar.

On Bioko I., roars often heard at night, especially during the hour before dawn. Once the male(s) of one group begins to roar, the ♂♂ of 1–3 distant groups often begin to roar. A 'soft honk' is frequently given as an intragroup contact call that can be heard to ca. 50 m. A 'loud, sharp honk' is given as an alarm/warning call that can be heard to >150 m. The loud, sharp honk often elicits a bout of roaring and 'aint' alarm/warning calls from other members of the group (T. Butynski pers. comm.).

Reproduction and Population Structure Black Colobus ♀♀ have a slight raising of the bare black area adjacent to the perineum during the mating and birth periods (Oates & Trocco 1983, Fleury 1999). Females solicit copulations using a



Adult Black Colobus *Colobus satanas*.

presentation posture. Length of gestation unknown. At Makandé (Fleury 1999) and Douala-Edea (McKey 1979), most births occur during the second half of the year, but the sample is low ($n = 12$). Only one infant born at a time. At Makandé the inter-birth interval is longer than two years ($n = 7$ ♀♀). Suckling occurs for at least eight months. Age of maturity not known, but estimated at >4 years (Fleury 1999).

The overall ♂ : ♀ ratio for one group at Makandé over two years varied from 1 : 1.3 to 1 : 1.8. When adults only are considered, the ♂ : ♀ ratio varied from 1 : 1.2 to 1 : 1.4 at Makandé (Fleury 1999), 1 : 2.0 to 1 : 5.0 at Douala-Edéa (McKey 1979), and 1 : 2.5 to 1 : 5.0 at Lopé (M. Harrison pers. comm.).

The adult/immature ratio for one group at Makandé over two years varied from 1 : 0.2 to 1 : 0.5. Birth rate in this group was 0.29 births/year/adult ♀. No deaths occurred in this group during the 2-year study (Fleury 1999). Birth-weight not known; a 2–3-week-old infant weighed 770 g (Fleury 1999). Longevity not known.

Predators, Parasites and Diseases Leopards *Panthera pardus* are known predators (Henschel *et al.* 2005, 2011). Robust Chimpanzees *Pan troglodytes* and African Crowned Eagles *Stephanoaetus coronatus* are probable predators. Predation rates probably low as no case of predation observed during the monitoring of groups at Makandé, Lopé or Douala-Edéa. Diseases and parasites unknown.

Conservation IUCN Category (2012): Vulnerable as *C. satanas* and as *C. s. anthracinus*. Endangered as *C. s. satanas*. CITES (2012): Appendix II.

Main threats are logging, forest clearance for agriculture and hunting by humans. Populations persist in logged forests as long as logging does not significantly alter the structure and composition of the forest (Brugière 1998). The Black Colobus is unable to thrive in degraded secondary forest but persists in a mosaic of secondary and primary forest. It is highly vulnerable to hunting because of its large body size, its relative inactivity and the relative lack of fear of humans. From 1998 to 2005, between 170 and 380 Black Colobus were sold each year at the Malabo Market, Bioko I. (Hearn *et al.* 2006). See also Fa *et al.* (2000), Fa & Garcia Yuste (2001), Kumpel *et al.* (2008) and Mora *et al.* (2009).

The Black Colobus occurs in protected areas in Cameroon: Douala-Edea Faunal Reserve (1283 km²) (not present in Dja Faunal Reserve; probably extirpated from Campo-Maan N. P.); in Gabon: Lopé N. P. (4910 km²), Monts de Cristal N. P. (1200 km²), Minkébé N. P. (7567 km²); in Equatorial Guinea, Bioko I: Pico Basile N. P.

(330 km²), Gran Caldera & Southern Highlands Scientific Reserve (510 km²); in Rio Muni: Monte Alén N. P. (2000 km²). There are no Black Colobus in the world's zoos.

Measurements

Colobus satanas

C. s. satanas

HB (♂ ♂): 595 (510–675) mm, n = 37
 HB (♀ ♀): 576 (500–680) mm, n = 48
 T (♂ ♂): 759 (690–840) mm, n = 37
 T (♀ ♀): 742 (600–825) mm, n = 47
 HF (♂ ♂): 174 (160–188) mm, n = 38
 HF (♀ ♀): 170 (154–190) mm, n = 46
 E (♂ ♂): 32 (28–40) mm, n = 38
 E (♀ ♀): 30 (26–36) mm, n = 47
 WT (♂ ♂): 10.3 (7.3–13.1) kg, n = 12
 WT (♀ ♀): 8.2 (6.6–10.0) kg, n = 7
 Upper Canine (♂ ♂): 15 (10–18) mm, n = 28
 Upper Canine (♀ ♀): 6 (4–10) mm, n = 43
 Lower Canine (♂ ♂): 11 (6–14) mm, n = 28
 Lower Canine (♀ ♀): 5 (3–8) mm, n = 43
 GLS (♂): 108 mm, n = 1
 GWS (♂): 80 mm, n = 1
 GLS (♀): 105 mm, n = 1

GWS (♀): 74 mm, n = 1

Bioko I., Equatorial Guinea (Butynski *et al.* 2009). Skull measurements by T. Butynski (pers. obs.)

C. s. anthracinus

HB (♂ ♂): 654 (580–710) mm, n = 8
 HB (♀ ♀): 607 (465–690) mm, n = 5
 T (♂ ♂): 902 (830–1000) mm, n = 9
 T (♀ ♀): 892 (820–970) mm, n = 6
 HF (♂ ♂): 196 (180–210) mm, n = 9
 HF (♀ ♀): 184 (170–195) mm, n = 5
 E (♂ ♂): 28 (20–46) mm, n = 5
 E (♀ ♀): 44, 50 mm, n = 2
 WT (♂ ♂): 11.1 (9.0–13.2) kg, n = 10
 WT (♀ ♀): 9.4 (6.0–10.9) kg, n = 5

Data from various locations; HB, T, HF, E and ♀ WT (Malbrant & Maclatchy 1949, Fleury 1999, O'Leary 2003); ♂ WT (Malbrant & Maclatchy 1949, Harrison 1986, Fleury 1999, Delson *et al.* 2000)

Key References Fleury 1999; Fleury & Gautier-Hion 1999; Harrison & Hladik 1986; McKey 1978; McKey *et al.* 1981; Oates 2011.

Marie-Claire Fleury & David Brugière

Colobus polykomos KING COLOBUS (WESTERN PIED COLOBUS, WESTERN BLACK-AND-WHITE COLOBUS)

Fr. Colobe magistrat; Ger. Weißbart-Stummelaffe

Colobus polykomos (Zimmermann, 1780). Geogr. Gesch. Mensch. Vierf. Thiere 2: 202. Sierra Leone.

Taxonomy Monotypic species. Between 1927 and 1983, *polykomos* and White-thighed Colobus *vellerosus* were considered subspecies of *C. polykomos* (Rahm 1970, Hull 1979), because W. P. Lowe had collected specimens of an intermediate subspecies, *C. polykomos dollmani* in 1927 in Côte d'Ivoire (Oates & McGraw 2009). Oates & Trocco (1983) conclude that *vellerosus* and *polykomos* are separate species and that *dollmani* represents a hybrid swarm. Groves *et al.* (1993) argue that *dollmani* is more closely related to *C. vellerosus* than to *C. polykomos*. Groves (2001, 2005c, 2007b) and Grubb *et al.* (2003) list *dollmani* as a synonym of *C. vellerosus*. Groves (2007b) lists *ursinus* as a synonym of *C. polykomos*. Synonyms: *comosa*, *polycomos*, *regalis*, *tetradactyla*, *ursinus*. Chromosome number: 2n = 44 (Gregory 2008).

Description Large, long tailed, thumbless, black-and-white, arboreal monkey. Sexes alike in colour but ♂ ♂ have slightly longer canines (Plavcan 1999). Adult ♀ about 84% as heavy as adult ♂. Face furless and black. Nose slightly bent, long. Top of head, sides of face and throat greyish-white. Front of shoulders and forearms with straggly, long greyish-white hair. Body and limbs black. Tail long ca. 170% of HB, not tufted. Males have small testes compared to *Procolobus* spp. (Oates 1994). Callosities of ♂ ♂ joined and fringed by one large white triangle, which sometimes continues to the genitalia, while ♀ ♀ have two smaller triangles. Infants predominantly white for first 41–53 days. Full adult colouration attained at 97–120 days (Mearns & Pidgeon 1978).

Geographic Variation None recognized but see Oates & McGraw (2009).

Similar Species

Colobus vellerosus. Perhaps parapatric in vicinity of Bandama R. Face encircled by thick ruff of white fur. Shoulders lack epaulettes or with a few white hairs. Thighs with broad white stripe on proximal two-thirds.

Distribution Endemic to coastal West Africa. Rainforest BZ.

Historical Distribution The forest zone along the coast of Côte d'Ivoire, Liberia, Sierra Leone, Guinea, Guinea-Bissau and scattered forest patches in Senegal, up to 14°N (Booth 1954, 1958b, Rahm 1970, Oates & Trocco 1983). Reports of skins in Gambia are questionable (Oates & Trocco 1983). Eastern boundary: Sassandra R., Côte d'Ivoire (starting at 06°W).

Current Distribution Guinea (Barnett *et al.* 1994, Ziegler *et al.* 2002, Eriksson & Kpoghomov 2006), Sierra Leone (Harding 1984a), Liberia (Waitkuwait 2003), Côte d'Ivoire (Oates *et al.* 1990, Oates 1994), and a few remaining sites in Guinea-Bissau (C. Sousa pers. comm.). Extinct in Senegal. *Colobus polykomos-vellerosus* hybrid population between Sassandra R. and Bandama R. is likely restricted to one site (Gonedelé Bi *et al.* 2006, 2012), if it still exists (Oates & McGraw 2009).



King Colobus *Colobus polykomos* adult male.

Habitat Lowland forests: wet evergreen, moist evergreen, moist semi-deciduous and dry semi-deciduous forest. Also in riparian forests in savanna and patches of dry forest well outside the major moist forest blocks (Oates 1977b). Mean annual rainfall and mean annual temperature range from 3000 mm and 27°C at Tiwai and Gola, Sierra Leone, to 1830 mm and 26.5°C at Banco, Côte d'Ivoire, to 300 mm with 24.5°C in Nimba Mts, Liberia and Guinea

(Korstjens & Dunbar 2007). Range in altitude from near sea level to 800 m at Mt Nimba (Galat-Luong & Galat 1990).

Abundance Common where habitat available and hunting pressure low. About 5.6 groups/km² (50 individuals/km²) in undisturbed forest at Tiwai, Sierra Leone (Dasilva 1989, Oates *et al.* 1990), and 2.8 groups/km² (47 individuals/km²) in Tãï, Côte d'Ivoire (Korstjens 2001, but see Galat & Galat-Luong 1985 who calculated 23.5 ind/km², n = 2, in Tãï based on their home-range estimates). Densities drop dramatically for areas where poaching is common, such as in Tãï N. P. away from research areas (Refisch & Koné 2005, A. Korstjens pers. obs.).



Colobus polykomos

Adaptations Diurnal and arboreal. *Colobus polykomos* spends ca. 52% of time in closed canopy, ca. 33% in emergents and ca. 15% in lower strata both at Tãï (Galat & Galat-Luong 1985, n = 2242; see also McGraw 1996, 1998a, McGraw & Sciulli 2011) and at Tiwai (Dasilva 1989). Comes to ground to forage on fallen seeds of *Pentaclethra macrophylla*, to cross forest clearings and for conspecific inter-individual chasing. Regularly found at forest fringes. Remains inactive for long periods and hides in thick tangles of lianas. Sits while feeding and often sprawls over a bough while resting (McGraw 1998c). In Tãï spends ca. 40% of time on boughs, ca. 47% on medium-sized branches and only ca. 13% on thin branches (Galat & Galat-Luong 1985, n = 2117; see also McGraw 1996, 1998b, c). Postures, such as hunching and sunbathing (spends 39% of time in the sun; A. Galat-Luong pers. obs.), and travel distances optimize energy intake and expenditure according to climatic conditions and food availability (Dasilva 1992, 1993). Annual activity budget in Tãï and Tiwai, respectively: resting 54–55% and 61%, feeding 16–31% and

28%, moving 13–23% and 9%, and socializing 6–8% and 1% (Galat-Luong 1983, $n = 2233$; Dasilva 1989, Korstjens 2001). Rests 53% of time out of reach of leaves (A. Galat-Luong pers. obs., $n = 522$) and prefers tall bare trees for sleeping but does not regularly use the same sleeping-trees (Dasilva 1989, A. Korstjens pers. obs.).

Foraging and Food Folivorous–frugivorous. Forages primarily on leguminous trees and lianas. In Tāi (Korstjens *et al.* 2007) and Tiwai (Davies *et al.* 1999) the annual diets were, respectively, 28% and 30% young leaves, 20% and 27% mature leaves, 48% and 36% fruits (33% hard seeds and 3% whole fruits in Tiwai) and 3% and 3% flowers. In Tāi Galat & Galat-Luong (1985) found 53% leaves, 32% fruits, 4% flowers and 10% miscellaneous (e.g. lichen) ($n = 209$ food item intakes). In Tāi and Tiwai the most frequently consumed food is *Pentaclethra macrophylla* seeds (Dasilva 1989, 1994, Korstjens 2001, Korstjens *et al.* 2007). The long canines are used to strip open the wooden pods of these and similar unripe fruits to reach the hard seeds inside (A. Korstjens pers. obs.). In Tāi the number of food species is low compared to sympatric Western Red Colobus *Procolobus badius badius* and Olive Colobus *Procolobus verus* (Korstjens 2001, Korstjens *et al.* 2002). Mean daily travel distance is 677 m (range 200–1241 m, $n = 54$; Korstjens 2001, Korstjens *et al.* 2007) in Tāi and 860 m (range 350–1410, $n = 72$; Dasilva 1989, 1992) in Tiwai. Daily travel distances increase during the months in which *P. macrophylla* seeds are the main food and decrease when high quality food is scarce at Tāi and Tiwai. Detailed lists of plant food species are presented in Dasilva (1992, 1994) and Korstjens (2001).

Despite similar mean group sizes (see below), mean annual home-range size is 77.4 ha (range 71.5–83.3, $n = 4$) in Tāi (but see Galat & Galat-Luong 1985, who found mean home-range size of 37.5 ha [range 29–46 ha, $n = 2$] in Tāi) and 22 ha ($n = 1$) in Tiwai (Dasilva 1989, Oates 1994). Home-ranges of conspecific groups overlap 20–22% in Tāi. Due to similar percentage overlap with three to five groups, no group had an area of exclusive access in its home-range (Korstjens *et al.* 2005).

Social and Reproductive Behaviour Social. Lives in groups of 5–19 individuals, mean = 16.2 ($n = 10$) in Tāi and 12.5 in Tiwai ($n = 2$), with 1–3 adult ♂♂ (in Tāi eight of ten groups had one ♂, and 1–3 adult ♂♂ in Tiwai where most groups had two adult ♂♂) and 4–6 adult ♀♀ (Galat & Galat-Luong 1985, Dasilva 1989, Korstjens 2001). A few solitary ♂♂ have been seen in Tāi but none in Tiwai (Galat & Galat-Luong 1985, Dasilva 1989, Korstjens 2001).

Agonistic interactions among adult ♀♀ are rare (Dasilva 1989, Korstjens *et al.* 2002) but, with 0.60 interactions/focal observation hour in Tāi, more common than in *C. vellerosus* (P. Sicotte pers. comm.) or in Black-and-White Colobus *C. guereza* (Fashing 2001c). Aggression among adult ♀♀ is most frequent during foraging, especially over items that require a long handling time such as seeds from wooden pods (Korstjens *et al.* 2002). Aggression between the sexes is rare, but adult ♂♂ displace adult ♀♀ (Dasilva 1989, Korstjens 2001). Clear dominance relationships exist among adult ♂♂ (Dasilva 1989). Proximity between individuals: Tāi, 35% of time is spent within 2 m of conspecifics; Tiwai, 48% within 2.5 m of conspecifics. Grooming is the main affiliative interaction (see ‘time budget’). Adult ♀♀ groom up to ten times more and spend up to twice as much time with neighbours than adult ♂♂ (Dasilva 1989,



Adult King Colobus *Colobus polykomos*.

Korstjens 2001). Males spend little time together and are often at the periphery of the group.

Inter-group interactions occur once every 6.6 and 8.0 observation days in Tāi and Tiwai, respectively. Inter-group encounters range from simple proximity (12% of 83 encounters in Tāi and 33% of nine encounters in Tiwai), to displays (25% and 0%), or fights and chases (63% [Korstjens *et al.* 2005] and 67% [Dasilva 1989]). Female participation in inter-group conflicts, generally rare in colobus monkeys (Oates 1977c, Struhsaker & Leland 1979, Fashing 2001c), is common in Tāi (52% of 83 encounters [Korstjens *et al.* 2005]) but was not observed in Tiwai (Dasilva 1992). In Tāi, ♀♀ are more often aggressive during the months when they eat *P. macrophylla* seeds. Adult ♂♂ perform forays to other groups (average of once every 20 days in Tāi) and chased members of the target group in 75% of 16 forays. One to six adult ♀♀ joined the ♂ in 25% of the forays, but ♀♀ never attacked the target group. Forays were especially frequent when the target group had young infants (see Sicotte & MacIntosh 2004 for similar observations on *C. vellerosus*). Males often threaten ♂♂ from other groups with a ‘stiff-legged display’ and by bouncing through the trees.

Vocalizations are rare and most are soft. The most conspicuous vocalization is the loud-call (‘roar’). The roar has similar general characteristics in the different *Colobus* species, but has a faster pulse rate and higher pitch in *C. polykomos* compared to *C. vellerosus* and *C. guereza* (Oates & Trocco 1983, Oates *et al.* 2000b). Roars occur throughout the day, and unlike in *C. guereza* (Marler 1969), morning choruses are relatively rare in *C. polykomos* (Dasilva 1989, A. Korstjens pers. obs.). Most roars are produced in response to a predator threat. Roar characteristics differ according to the type of predator (i.e. Leopard *Panthera pardus* or African Crowned Eagle *Stephanoaetus coronatus*) that is perceived (Schel *et al.* 2009). Roars are often contagious (i.e. other groups respond with a roar). Although most complete roars are performed by ♂♂, ♀♀ do sometimes roar in Tāi in response to a threat (A. Korstjens & A. Galat-Luong pers. obs., E. C. Nijssen pers. comm.). Roars are rarely given during inter-group encounters (Dasilva 1989, A. Korstjens pers. obs.). Females and ♂♂ jointly threaten, mob and alarm-call when threatened by humans or predators but ♂♂ are the more aggressive (Korstjens *et al.* 2005).

Females disperse at least occasionally and ♂♂ disperse as a rule (Dasilva 1989, Nijssen 1999, Korstjens 2001). Sexual behaviour is rarely observed. Females in all reproductive states (cycling, pregnant, lactating) copulate. Females have no sexual swellings and

solicit copulations by presenting. Copulatory vocalizations do not occur (Dasilva 1989). In Tiwai all three ♂♂ in a three-male group mated with ♀♀ (most mates were pregnant/lactating ♀♀ [Dasilva 1989]); in Tai, only the dominant ♂ was observed to mate in a bi-male group (A. Korstjens pers. obs.).

Infant handling is common and is most often performed by juvenile and nulliparous ♀♀. Lactating ♀♀ whose infants are being handled seem to be able to devote more time to feeding (Dasilva 1989, E. C. Nijssen pers. comm.). *Colobus polykomos* spent 28% of time in a polyspecific association (both in Tai and Tiwai), which is no more than expected by chance (Whitesides 1989, Höner *et al.* 1997). However, in Tai, encountered primate groups often contain *C. polykomos* (68% of encounters of groups, $n = 37$); associations with Diana Monkeys *Cercopithecus (d.) diana* and red colobus being the most frequent (Galat & Galat-Luong 1985). Red colobus solitary ♂♂ and solitary ♀♀ regularly associate for several days or weeks with *C. polykomos* groups (Korstjens *et al.* 2007). Inter-specific social interactions include grooming, playing and aggression (Galat-Luong 1983, Deffernez 1999). *Colobus polykomos* sometimes handle Olive Colobus infants (A. Korstjens pers. obs.) and ♀ red colobus sometimes handle *C. polykomos* infants (Fimbel 1992); in both cases, both parents try to get the infant back (A. Korstjens pers. obs.).

Reproduction and Population Structure Inter-birth interval: mean \pm S.D. = 25.5 ± 5.0 months; median = 25.0 months (Tai, $n = 4$; A. Korstjens pers. obs.); mean = 24 months (Tiwai, $n = 4$; Dasilva 1989). Births occur throughout the year ($n = 6$) in Tai (A. Korstjens pers. obs.), but only during Dec–Feb (i.e. dry season) in Tiwai ($n = 9$) (Dasilva 1989). Gestation: ca. 165 days (147–178, $n = 5$) at Jersey Zoo (Mallinson 1973). Birth-weight is 597 g (Ross 1991). One infant is born; twins not reported. Infants feed from their mothers for at least five months and rarely suckle after one year (Dasilva 1989, Korstjens 2001). One of four ♀♀ in Tai had their first infant at four years of age, but the other three did not reproduce for the first 6–7 years (after which they disappeared from their natal group). Females are receptive for 3–7 days and can have five consecutive receptive periods (A. Korstjens pers. obs.). Maximum recorded life-span in captivity is 30.5 years (Ross 1988).

Predators, Parasites and Diseases Main predators in Tai Forest are Robust Chimpanzees *Pan troglodytes* (Boesch & Boesch-

Achermann 2000), African Crowned Eagles (Shultz *et al.* 2004), Leopards (Hoppe-Dominik 1984, Zuberbühler & Jenny 2007) and humans (Refisch 2000). Robust Chimpanzees are estimated to catch 1.4% (Korstjens 2001), Leopards 7.0% and African Crowned Eagles 2.1% (Shultz *et al.* 2004) of the *C. polykomos* population each year in Tai. Although viraemia is longer in *C. polykomos* than in cercopithecines, the role of *C. polykomos* in Yellow Fever transmission should be less important because the proportion of immature individuals is lower (Galat & Galat-Luong 1997).

Conservation IUCN Category (2012): Vulnerable. CITES (2012): Appendix II.

Local populations of *C. polykomos* are threatened throughout the range due to habitat loss and hunting by humans (McGraw 2007b). Human consumption of *C. polykomos* in the Tai region is 1.4 ind/km²/year (11.7 kg/km²/year) while maximal sustainable harvest is estimated at 0.9 ind/km²/year (Refisch & Koné 2005). *Colobus polykomos* is the fourth primate species to disappear from the Tai region because of human activity (Galat & Galat-Luong 1997). In this region high population densities are only maintained near research stations (Refisch & Koné 2005). Tai N. P., Nimba MAB Reserve, National Park of Upper Niger (Guinea) and Tiwai are the main refuges. Survive also in ‘sacred woods’ in Côte d’Ivoire and Guinea (Galat & Galat-Luong 1997, Gonedelé Bi *et al.* 2006, 2012).

Measurements

Colobus polykomos

HB (♂♂): 1530, 1590 mm, $n = 2$

T (♂♂): 900, 940 mm, $n = 2$

HF (♂♂): 190, 200 mm, $n = 2$

E (♂♂): 20, 25 mm, $n = 2$

WT (♂♂): 9.9 (8.0–11.7) kg, $n = 5$

WT (♀♀): 8.3 (6.6–10.0) kg, $n = 10$

Body measurements: Côte d’Ivoire and Liberia (O’Leary 2003)

WT: Tiwai, Sierra Leone (O’Leary 2003)

Key References Dasilva 1989; Galat & Galat-Luong 1985; Korstjens 2001; Korstjens *et al.* 2007; McGraw *et al.* 2007; Oates 1994, 2011.

Amanda H. Korstjens & Anh Galat-Luong

Colobus angolensis ANGOLA COLOBUS (ANGOLA BLACK-AND-WHITE COLOBUS, ANGOLA PIED COLOBUS)

Fr. Colobe noir et blanc d’Angola; Ger. Angola-Mantelaffe

Colobus angolensis Sclater, 1860. Proc. Zool. Soc., Lond. 1860: 245. 483 km inland from Bembe, Angola.

Taxonomy Polytypic species. Seven subspecies: Colyn (1991) described five subspecies in the Congo Basin. Dandelot (1974) and Hull (1979) recognized a subspecies from Kenya and Tanzania. There is an unnamed subspecies in W Tanzania (Nishida *et al.* 1981). Subspecies are distinguished by pelage, cranial measurements (Hull 1979), habitat type and geographical distribution (Groves 2007b). Molecular data support recognition of *sharpie* (McDonald & Hamilton 2010). Synonyms: *adolphi-friederici*, *benamakimae*, *cordieri*, *cottoni*, *langheldi*, *maniamae*, *mawambicus*, *nahani*, *palliatius*, *prigoginei*,

ruwenzorii, *sandbergi*, *sharpie*, *weynsi*. Chromosome number: $2n = 44$ (Dutrillaux *et al.* 1981, Wienberg & Stanyon 1998).

Description An arboreal, black-and-white monkey with long white cheek-hairs and white ‘epaulettes’. Sexes alike in colour. Adult ♀ about 80% as heavy as adult ♂. Crown and neck black. Face black across the orbital region and nose. Narrow line of white hairs form a ‘brow-band’ above the eyes. Ears black. Pelage under chin grizzled. Long, flowing white hairs (‘whiskers’, 6–10 cm)

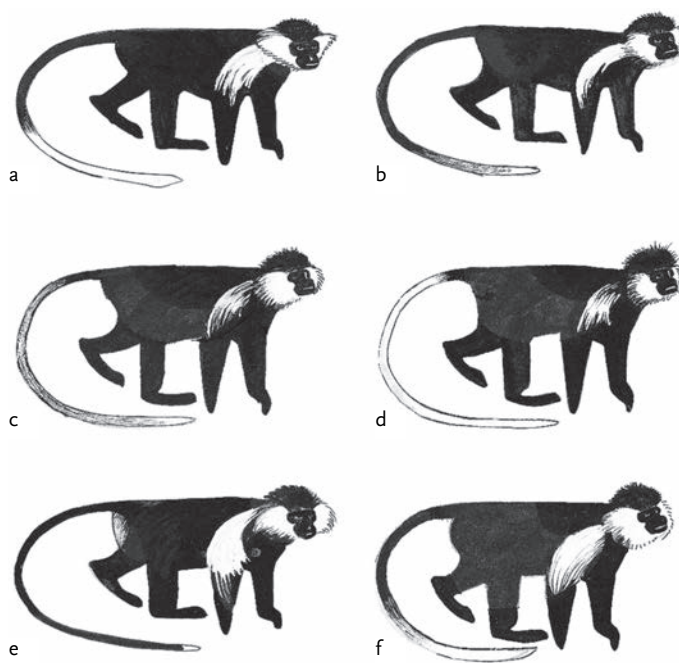


Peters's Angola Colobus *Colobus angolensis palliatus* adult male (Southern Highlands, Tanzania).

extending from temples and cheeks, and from shoulders and upper forelimbs ('epaulettes', 15–30 cm long). Thumb absent. Dorsum, ventrum and flanks black; forelimbs and hindlimbs black. Tail black in basal region and mid-section, gradually lightening onto the distal region with a terminal tuft of white hairs. Ischial callosities pink, fringed with white hairs; callosities fused into a central ridge in ♂♂. Subspecies differ in the length and extent of epaulettes, and white hair coverage on the brows, cheeks, tail and callosities. Three subspecies (*angolensis*, *ruwenzorii* and *palliatus*) have a white 'pubic band' of hair between the legs. Pubic band absent in the other four subspecies. In newborn infants the face is pink and pelage completely white. Infants' face and pelage change colour gradually; they acquire the black-and-white pattern characteristic of adults by the age of 3.5–4.0 months (Bocian 1997).

Geographic Variation The following seven subspecies are recognized by Groves (2001, 2007b) and Grubb *et al.* (2003). Descriptions presented here are based on Colyn (1991) and Groves (2001):

- C. a. angolensis* Sclater's Angola Colobus. Synonyms: *benamakimae*, *maniemae*, *sandbergi*, *weynsi*. DR Congo, Angola and perhaps NW Zambia; Congo Basin, south and west of the Congo/Lualaba R., extending south-west through the Kasai and Kwango Basins (Colyn 1991) to the Luando R., Angola (Machado 1969). May be present in north-western tip of Mwinilunga District, Zambia (Ansell 1974). Extreme south-east record is from the Lusiji R. area (SE Baluba Province, DR Congo; Colyn 1991). White 'whiskers' and broad white epaulettes, forming a continuous band on each side of the body and sometimes covered by long black hairs. Narrow medial stripe of white hairs in the pubic region. Distal 30–70% of tail white. The rest of the body is black.
- C. a. cottoni* Powell-Cotton's Angola Colobus. Synonyms: *mawambicus*, *nahani*. DR Congo; east bank of the Congo R., extending north to the Uele R. Range delimited in the west by the Itimbiri R. basin; in the south by the Lindi R.; in the east by the forest/savanna ecotone extending from L. Albert to L. Edward (Colyn 1991). White cheek-whiskers well-developed, more so than epaulettes, with which they form a continuous narrow band on either side; no white in pubic region; distal half or so of tail greyish to greyish-white. *Colobus a. cottoni* × *ruwenzorii* hybrids occur near the south-east limit of *cottoni* distribution (Colyn 1991).



Subspecies of Angola Colobus *Colobus angolensis*: (a) Sclater's Angola Colobus *C. a. angolensis*. (b) Powell-Cotton's Angola Colobus *C. a. cottoni*. (c) Cordier's Angola Colobus *C. a. cordieri*. (d) Prigogine's Angola Colobus *C. a. prigoginei*. (e) Rwenzori Angola Colobus *C. a. ruwenzorii*. (f) Peters's Angola Colobus *C. a. palliatus*.

- C. a. cordieri* Cordier's Angola Colobus. DR Congo. South from the Ulindi R. to the Elila R., and from the Lualaba R. east to Shabunda, Bukavu and Mwenga. Cheek whiskers poorly developed, forming a continuous band with epaulettes; no white in pubic region; tail wholly greyish except for proximal 5–8 cm. *Colobus a. cordieri* × *ruwenzorii* hybrids occur along east limit of *cordieri* distribution (Colyn 1991).
- C. a. prigoginei* Prigogine's Angola Colobus. DR Congo. Holotype from Mt Kabobo (=Misotshi-Kabogo), ca. due west of Kigoma on the west side of L. Tanganyika. Unconfirmed, but may be present between L. Tanganyika and L. Mweru (Ansell 1974). Similar to *C. a. cordieri* but tail yellowish-white instead of greyish; pelage long and silky.
- C. a. ruwenzorii* Rwenzori Angola Colobus. Synonym: *adolphi-friederici*: Western Rift, from DR Congo and Uganda south to Rwanda, Burundi and NW Tanzania. Cheek whiskers and epaulettes forming a broad, continuous white band, sometimes overlain with long black hairs; a 6–10 cm wide band of white or greyish hairs in pubic region; distal 5–10 cm of tail greyish.
- C. a. palliatus* Peters's Angola Colobus. Synonyms: *langheldi*, *sharppei*. SE Kenya and Tanzania. Not in Malawi (Ansell 1974, Ansell & Dowsett 1988). Epaulettes large; white pubic band broad in ♂♂, narrow or absent in ♀♀. Distal 30% of tail white; white band on forehead broad and continuous with full cheek-whiskers; occipital hairs lengthened; coat long, thick and soft.
- C. a. ssp. nov.* Mahale Mountains Angola Colobus. Mahale Mts, W Tanzania. Pelage similar to that of *C. a. palliatus* and *C. a. ruwenzorii* but lacks white pubic band. Tail greyish only at the tip (Nishida *et al.* 1981, Groves 2001, 2007b, Grubb *et al.* 2003).

Similar Species

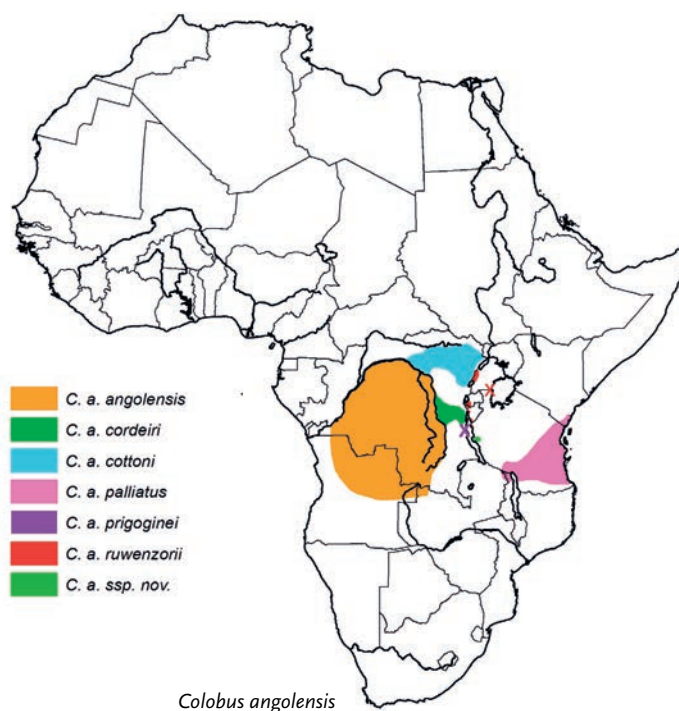
Colobus guereza. Sympatric in the N Congo Basin. White hair coverage of tail is far greater; longer epaulettes form a continuous mantle (cape) across the shoulders, flanks and back. Muscle development on head of ♂♂ is marked, giving 'double-humped' appearance.

Distribution Endemic to equatorial Africa. Rainforest, Afro-montane–Afroalpine and Coastal Forest Mosaic BZs. Forested habitats from the central Congo Basin east to the Rwenzori Mts and L. Victoria, then south to W Rwanda, W Burundi, and north-west side of L. Tanganyika. An isolated population in Mahale Mts N. P. on the east side of L. Tanganyika. From Congo/Lualaba R. and Itimbiri R., south to NW Angola and, perhaps, NW Zambia. Colyn (1991) reports a hiatus in *C. angolensis* distribution east of the Congo/Lualaba R. in the area between the Lindi R. and Ulindi R. Hart & Sikubwabo (1994), however, saw *C. angolensis* in Maiko N. P. It is, therefore, possible that the northern boundary of the hiatus lies farther south at either Maiko R. or Lowa R. Also present in the coastal forests of S Kenya and E Tanzania, through the Eastern Arc Mts and Selous G. R. to the Southern Highlands, perhaps into NE Zambia. Ansell (1974) and Ansell & Dowsett (1988) unable to substantiate reports of presence in N Malawi (e.g. Misuku Hills).

Habitat Restricted to forests and forest fragments. Across the species' geographical distribution, mean annual rainfall ranges from ca. 1100–1800 mm; average annual minimum and maximum temperatures are ca. 11 °C and ca. 26 °C; altitude ranges from sea level in East Africa to 2415 m in Nyungwe Forest, Rwanda (Bocian 1997, Anderson *et al.* 2007c, Fashing *et al.* 2007b).

Lowland subspecies of the Congo Basin (*angolensis*, *cottoni* and *cordieri*) inhabit evergreen and semi-deciduous forest, including swamp and seasonally flooded areas. Distribution associated with forests dominated by leguminous trees, particularly the Caesalpinioideae. Most populations of *C. a. ruwenzorii* inhabit montane forest of the Western Rift, although also in gallery forest on the western edge of L. Victoria. *Colobus a. prigoginei* and *C. a. ssp. nov.* in montane forest. *Colobus a. palliatus* in montane forest, coastal forest, coastal scrubland and mangrove. In the Ituri Forest, DR Congo, a high density of mature, broad- and deep-crowned trees, including *Cynometra alexandri*, *Julbernardia seretii*, *Gilbertiodendron dewevrei*, *Erythrophloeum suaveolens* and *Cassia mannii* results in a relatively closed-canopy forest. Canopy height reaches 30–40 m, with emergents >40 m. Caesalpinioideae accounts for ca. 47% of sampled trees (Bocian 1997). *Colobus a. cottoni* prefers mature mixed forest where its preferred food trees are common, particularly *C. alexandri*, *Celtis mildbraedii*, *Alstonia boonei* and *E. suaveolens*. Monodominant stands of *G. dewevrei* occur throughout Ituri (Hart *et al.* 1989), but *C. a. cottoni* is uncommon in this forest type (Bocian 1997). In forest inhabited by *C. a. angolensis* in Salonga N. P., DR Congo, Caesalpinioideae accounts for 39% of sampled trees. Soil here is very acidic (pH = 4.13), sandy (87%) and nutrient-poor (Maisels *et al.* 1994).

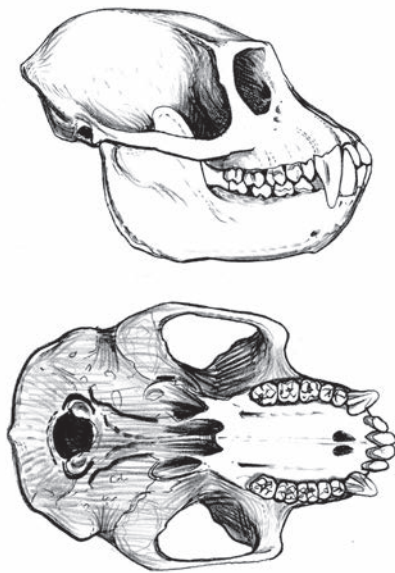
In the Diani Forest, Kenya, *C. a. palliatus* is common in tall (>10 m), closed-canopy coastal forest; uncommon in coastal shrub; rare in mangrove and bush-farmland. *Colobus* occupancy of forest fragments is determined by fragment size and degree of canopy cover. In unprotected areas beyond the Shimba Hills National Reserve groups occupy fragments as small as 1–3 ha (Anderson



2005). Primarily dependent on indigenous tree species for food, but can survive in heavily degraded forest patches if favoured tree and shrub species are still present. *Colobus a. palliatus* is adaptable; in modified habitats like Diani, it has incorporated exotic tree species into the diet (e.g. *Azadirachta indica*, *Delonix regia*), and will travel through bush-farmland to gain access to relict indigenous trees in degraded cultivated areas (Anderson 2005).

Abundance Surveys for *C. a. palliatus* conducted in Kenya during 2001 found 55 isolated populations in coastal forest fragments. Total Kenyan population is estimated at between 3100 and 5000 individuals. Density varies widely among sites and is significantly affected by forest area, forest loss over 12 years and the availability of 14 major food tree species. The Shimba Hills National Reserve protects both the largest forest and largest *C. angolensis* population in Kenya; density in the reserve is estimated to be 2.9 ± 0.52 groups/km² or 15.3 ± 2.88 ind/km². Density in the Diani Forest estimated to be 31 ind/km²; in the Mwache F. R., six ind/km²; colobus are absent from some forest fragments (Anderson *et al.* 2007c). Surveys in Tanzania from 1971–76 found 42 isolated *C. a. palliatus* populations (Rodgers 1981). There are at least 10,000 individuals in Udzungwa Mts, SC Tanzania (Rovero *et al.* 2009). Estimates of *C. angolensis* abundance are not available for populations in the Congo Basin or Western Rift. In the Okapi Faunal Reserve (central Ituri Forest, DR Congo) density in mature mixed forest is estimated to be 1.2 ± 0.38 groups/km² or 16.7 ± 5.28 ind/km²; density in *Gilbertiodendron*-dominant forest is estimated to be 1.1 ± 0.45 groups/km² or 7.0 ± 2.88 ind/km² (Bocian 1997).

Adaptations Diurnal and arboreal. Like other colobines, *C. angolensis* shows morphological and physiological adaptations to a folivorous diet; i.e. a sacculated stomach in which leaves can be retained separately for fermentation, and molars with high shearing crests that are effective in tearing leaves.



Lateral and palatal views of skull of Angola Colobus *Colobus angolensis* adult male.

Intensive feeding bouts begin at sunrise and continue until mid- to late morning, followed by a resting period. In Ituri, *C. a. cottoni* begins a second series of feeding progressions in mid-afternoon, continuing to travel and feed until 17:30–18:30h, then settling into sleeping trees for the night (Bocian 1997). At Diani *C. a. palliatus* rests and feeds alternately from 06:00–18:30h. Resting always occurs in the primary and secondary canopy layers in particular trees within easy access to food sources (Moreno-Black & Maples 1977). Similarly, individual sleeping trees are consistently used throughout the year. Intensive periods of ‘sun-basking’ behaviour occur, particularly following feeding bouts (and rainy periods), with a plethora of resting positions observed (J. Anderson pers. obs.). In the Nyungwe F. R. (Rwanda), *C. a. ruwenzorii* forms unusually large groups of >300 individuals; the abundance of high quality mature leaf forage is thought to facilitate such group formation (Fimbel *et al.* 2001).

In response to aerial predators (e.g. African Crowned Eagle *Stephanoetus coronatus*) *C. angolensis* conceals itself in dense tree crowns, remaining motionless and silent until the predator is gone (C. Bocian pers. obs.).

Foraging and Food Folivorous. Feeds primarily on leaves and seeds, although fruit pulp, flowers and lichens are also consumed. In the Ituri Forest *C. a. cottoni* consumes more leaves than seeds (leaves, 51% of feeding observations; seeds, 22%; flowers, 7%; fruit pulp, 5%; lichen, 0.4%; $n = 2457$ observations). Preferred food items include *Amphimas pterocarpoides* flowers, *C. mildbraedii* leaves, *Celtis zenkeri* leaves and *Lecaniodiscus cupanioides* seeds. Peak seed consumption occurs in Aug and Sept (58% and 70%, respectively, of feeding observations) coinciding with high availability of *C. alexandri* and *E. suaveolens* seeds. Peak leaf consumption occurs in Nov and Mar (82% and 73%, respectively; Bocian 1997). Daily travelling distance of *C. a. cottoni* increases when availability of primary food is low. In this habitat *C. a. cottoni* roams extensively in search of food (mean daily travel distance is 983 m, range 312–1914 m, $n = 52$ days); cumulative home-range of the study group was still increasing in size, beyond 371 ha, after one year (Bocian 1997).

In the Salonga N. P. *C. a. angolensis* consumes more seeds than leaves (seeds, 50% of feeding observations; leaves, 27%; fruit, 17%; flowers, 6%; $n = 486$; Maisels *et al.* 1994). Here the forest is a mosaic of swamp, seasonally flooded and well-drained ground. Leguminous species, dominant here and in the Ituri Forest, have protein-rich seeds but poor-quality mature leaves (Maisels *et al.* 1994, Bocian 1997). In the Congo Basin frequently consumed food plants include *C. alexandri*, *E. suaveolens*, *A. pterocarpoides*, *Dialium* sp., *Guibourtia demeusei*, *Angylocalyx pinnaertii*, *Millettia* sp., *Piptadeniastrum africanum*, *Albizia* sp. (all Leguminosae), *C. mildbraedii*, *C. zenkeri*, *Ongokea gore*, *Strombosiaopsis tetrandra*, *Strombosia* sp., *Alstonia boonei*, *Xylopia aethiopica* and *Pycnanthus angolensis* (Maisels *et al.* 1994, Bocian 1997).

In Kenya *C. a. palliatus* is predominantly folivorous (leaves, 57%; fruit, 21%; seeds, 11%; flowers, 11%; Moreno-Black & Maples 1977). Frequently consumed plants include *Adansonia digitata*, *Lannea welwitschii*, *Cussonia zimmermannii*, *Combretum schumannii*, *Drypetes* spp., *Trichilia emetica*, *Milicia excelsa*, *Millettia usaramensis*, *Zanthoxylum* sp., *Lecaniodiscus fraxinifolius*, *Lepisanthes senegalensis*, *Sideroxylon inerme*, *Grewia* sp. and *Ficus* sp. (Lowe & Sturrock 1998, Anderson *et al.* 2007a).

In the Nyungwe Forest one group of *C. a. ruwenzorii* was primarily folivorous (leaves, 66%; fruit, 17%; petioles, 6%; flowers, 5%; lichen, 5%; $n = 14,259$; Fimbel *et al.* 2001). A nearby group, however, consumed a more varied diet in which leaves (38%), lichen (32%) and seeds (20%) were all major components; other items eaten included whole fruits, petioles, bark, flowers and soil (Vedder & Fashing 2002). This population, in which groups sometimes exceed 300 individuals, relies heavily on an abundant supply of high-quality mature leaves, particularly the common terrestrial scrambler *Sericostachys scandens* (Fimbel *et al.* 2001). Home-ranges are enormous at Nyungwe, with one group occupying 26.5 km² over a 2-year period before suddenly moving 13 km south of their former range. This ranging behaviour is unprecedented among *Colobus* spp. and may be linked to the need to allow time for depleted food patches to regenerate after large groups have foraged in them (Fashing *et al.* 2007b).

In Kenya, *C. a. palliatus* groups move through mangrove, perennial crops and wooded shrubland to forage on indigenous food trees. Leaf buds and young leaves of *Rhizophora mucronata*, *Heritiera littoralis* and *Ceriops tagal* are also consumed (Anderson *et al.* 2007b).

With the exception of *C. a. ruwenzorii* at Nyungwe, *C. angolensis* feeds mainly in the mid canopy (21–30 m high) and, to a lesser extent, at lower levels (11–20 m high) in mature mixed forest; *C. a. cottoni* and *C. a. palliatus* rarely come to the ground, and only do so to eat soil (Bocian 1997, J. Anderson pers. obs.) or to move between forest fragments.

Social and Reproductive Behaviour Social. *Colobus a. cottoni* in the Ituri Forest lives in groups of 6–20 individuals. In mature mixed forest mean group size is 13.9 animals; groups typically consist of 2–5 adult ♂♂, 2–8 adult ♀♀, 0–2 subadults and 0–5 immature animals ($n = 8$ groups; Bocian 1997). Groups of *C. a. angolensis* in Salonga N. P. range in size from 3–7 individuals ($n = 5$ groups; Maisels *et al.* 1994). Groups in the Udzungwa Mts comprise 2–14 individuals (Rovero *et al.* 2009). *Colobus a. palliatus* in Kenya live in groups of 2–13 individuals (mean = 6, $n = 136$). Groups are typically comprised of one adult ♂, two adult ♀♀ and an array of subadults, juveniles and infants. Single-male groups are far more common (88% incidence) than multimale groups (11% with two

♂♂, 1% with three ♂♂; $n = 190$; Anderson *et al.* 2007c). This demographic pattern may be maintained by a high degree of adult ♂ dispersal (solitary ♂ to group ratio 1 : 7).

At Nyungwe, at least two groups of >300 *C. a. ruwenzorii* individuals have been observed (Fimbel *et al.* 2001, Fashing *et al.* 2007b). Oates (1974) reported much smaller groups of *C. a. ruwenzorii* in the Sango Bay Forests (Uganda): one group of at least 30 and another of at least 51 individuals; this second group was judged to be an association of three smaller groups. Nishida *et al.* (1981) reported a group of about 30 *C. angolensis* (now named *ssp. nov.*) in the Mahale Mts.

Social bonds are strong among adult ♀♀ in the same group, who commonly groom each other and rest near each other in clusters with young animals. Grooming and resting in proximity is also common among adult ♂♂ in the same group, who appear to maintain a dominance hierarchy (Bocian 1997). In Ituri Forest encounters between two groups are common, often leading to the formation of temporary aggregations or 'super-groups'. These associations, during which groups rest, feed and/or travel in proximity (<50 m of each other) may last for several hours or for more than one day (Bocian 1997). Aggressive interactions during group encounters occur when one or more adult ♂♂ of one group attempt to 'infiltrate' a cluster of animals in the other group. Extra-group ♂♂ are chased away by a 'team' consisting of several adult ♂♂ or of adult ♂♂ and ♀♀. Persistent attempts provoke confrontations between ♂♂, which may involve snarling, grappling and sometimes biting (Bocian 1997). Similarly, in the Diani Forest, adult ♀♀ within a group mount defensive attacks against invading satellite ♂♂ who attempt group takeovers (J. Anderson pers. obs.).

Colobus a. cottoni groups do not have areas of exclusive use, nor do they exhibit territorial behaviour. Group ranges are completely overlapped by those of other conspecific groups (Bocian 1997). Although Fimbel *et al.* (2001) suggest that some *C. angolensis* populations exhibit a fission–fusion type of social organization, we found no evidence of this in either *C. a. cottoni* in Ituri Forest or *C. a. palliatus* in Diani Forest. *Colobus a. palliatus* groups are territorial in undisturbed mature forest and do not tolerate other conspecific groups within their home-range (J. Anderson pers. obs.). Territorial displays (e.g. exaggerated jumping, roaring and 'stiff-leg' displaying) by adult ♂♂ are common (D. L. Patel pers. comm.). However, in degraded or disturbed habitat, such as in Diani Forest, groups tolerate home-range overlap with neighbouring groups, while ♂♂ are unusually 'silent', rarely partaking in daily territorial roaring (J. Anderson pers. obs.). In Ituri Forest several adult ♂♂ in a *C. a. cottoni* group will engage in a group display of jumping and roaring, but this behaviour is infrequent and has only been observed in response to alarming or arousing stimuli (Bocian 1997). An earlier study of *C. a. palliatus* in Diani Forest also reports that ♂ roaring is rarely heard (Moreno-Black & Bent 1982). In contrast, roaring displays occur daily in *C. a. ruwenzorii* groups in the Nyungwe Forest; many adult ♂♂ in a group participate in such displays that include branch-shaking, leaping and chasing (Fimbel *et al.* 2001).

Courtship and mating behaviour differs considerably between the two subspecies for which information is available. Adult ♀ *C. a. cottoni* typically do not solicit copulations; rather, adult ♂♂ grab ♀♀ and appear to copulate forcibly. Mating is not monopolized by one adult ♂ (Bocian 1997). In *C. a. palliatus* the adult ♂ (and alpha-

males in multimale groups) monopolizes all mating with ♀♀ in his group. Copulation is solicited by the ♀, with increased approaching, grooming of the ♂ and presenting during this time (J. Anderson pers. obs.).

Female *palliatus* leave the group to give birth alone, although sometimes the ♀ is accompanied by a related subadult or juvenile ♀. Infant handling by other group members (including adult ♂♂) is extremely common. Frequency of this behaviour diminishes as the infant's coat colour changes from white, through grey, to black and white at about three months of age. Subadult ♀♀, however, continue their interest in carrying infants far longer than other group members (J. Anderson pers. obs.). This 'aunting' behaviour also occurs in *C. a. cottoni* ♀♀ (Bocian 1997). Small subadults, juveniles and older infants frequently play with each other, although juveniles also play with adult ♂♂ and adult ♀♀. Juveniles and infants huddle with adult ♀♀ during rest periods and storms (Bocian 1997).

Roaring vocalizations are produced by adult ♂♂ as part of a display, or in truncated form during agonistic encounters among ♂♂ (Bocian 1997, Oates *et al.* 2000b). Other than roaring, the only other vocalizations noted in the species are the squeals of infants and young juveniles. Non-vocal sounds produced include snorting (which seems to indicate surprise or mild alarm) and 'tongue-clicking'. The latter sound is like an exaggerated opening of the mouth with a lip-smack. Tongue-clicking is frequently used between group members before approaching one another, and is given in both affiliative and aggressive contexts (J. Anderson pers. obs.).

In Diani Forest *C. a. palliatus* commonly associates with Sykes's Monkeys *Cercopithecus (n.) mitis* throughout the day; the two species frequently gather together in the evenings to rest in adjacent trees. Although rare, interactions occur between juvenile *C. a. palliatus* and Vervet Monkeys *Chlorocebus pygerythrus*. *Colobus a. palliatus* frequently respond to alarm calls of *C. m. albobularis* and will cooperate in ousting Yellow Baboons *Papio cynocephalus* or predators from their territories (J. Anderson pers. obs.). They will also chase Silvery-cheeked Hornbills *Bycanistes brevis* from feeding and sleeping trees. Interspecific play occurs between *C. a. palliatus* and *C. m. albobularis* juveniles (J. Anderson pers. obs.) and, in Ituri Forest, between *C. a. cottoni* and Blue Monkey *C. m. stuhlmanni* juveniles (C. Bocian pers. obs.). Also in Ituri *C. a. cottoni* frequently rest or feed in proximity to Guerezas *Colobus guereza*, Blue Monkeys *C. m. stuhlmanni*, Red-tailed Monkeys *Cercopithecus (c.) ascanius*, Wolf's Monkeys *Cercopithecus (m.) wolfi* and Grey-cheeked Mangabeys *Lophocebus albigena*; they are seen less often in association with Western Red Colobus *Procolobus badius* and Agile Mangabeys *Cercocebus agilis* (Bocian 1997).

Reproduction and Population Structure In *C. a. cottoni* sexually mature ♀♀ show a slight perineal swelling for several days each month (Bocian 1997); menstrual cycles are not always synchronized among all group ♀♀. Although ♀ *C. a. palliatus* have no perineal swelling the ischial callosities become slightly redder prior to labour and birth (J. Anderson pers. obs.). Gestation not known. There is no distinct birth season in the Ituri, Nyungwe and Diani Forest populations (Bocian 1997, Fimbel *et al.* 2001, Anderson 2005). Females give birth to a single offspring, although one case of twinning occurred in Diani Forest (the second infant died, however, after a few weeks) (J. Anderson pers. obs.). Infants are usually weaned at one year, although suckling can extend to 18–24 months

(J. Anderson pers. obs.). Females are fully-grown by 5–6 years of age; ♂♂ by about seven years of age. Sexual maturity is probably reached before full growth is attained. Infanticide occurs in *C. a. palliatus*. Invading adult ♂♂ will kill one or all of the infants and juveniles up to three years of age within the group (J. Anderson pers. obs.). Infanticide not observed in *C. a. cottoni*.

In Diani Forest average *C. a. palliatus* adult ♀ : ♂ ratio in groups is 2.3 : 1.2. Immature to adult ♀ ratios in groups average 2.1 : 2.3 (n = 56; Anderson 2005). Longevity in captivity is up to 36 years, but much less in the wild. Average interbirth interval in captivity is 441 days (range 348–567, n = 11; Anderson, L.K. 2001). Birth and mortality rates not known.

Predators, Parasites and Diseases In Ituri Forest predators include Leopards *Panthera pardus* and African Crowned Eagles; *C. guereza* and *C. angolensis cottoni* make up 1% of the composition of Leopard scats (Hart, J. A., et al. 1996). During Bocian's Ituri study an African Crowned Eagle killed a *C. guereza* adult ♀ and infant and a *C. ascanius* adult ♂. Circumstantial evidence suggests Robust Chimpanzees *Pan troglodytes* kill and eat *C. a. ruwenzorii* at Nyungwe; black or brown and white hairs (believed to be from *C. angolensis ruwenzorii* or l'Hoest's Monkey *Cercopithecus lhoesti*) were found in seven chimpanzee scats (Fashing et al. 2007b). In East Africa predation by Leopards and raptors is also probable; the high density of human settlements in this region have also resulted in *C. angolensis* deaths via domestic dogs and by road traffic accidents (Anderson et al. 2007b).

Ectoparasites of *C. a. palliatus* include *Sarcoptes scabiei*. Endoparasites include nematodes *Trichuris* spp., *Strongyloides* spp. (including *S. fulleborni*), *Enterobius vermicularis* and *Trichostrongylus* spp., and protozoa *Entamoeba coli*, *Entamoeba histolytica*, *Balantidium coli* and *Cyclospora colobi* (Obadha 1999, Eberhard et al. 2001, Okanga 2004, Gillespie et al. 2005b).

Conservation IUCN Category (2012): Least Concern as a species; *C. a. ruwenzorii* – Vulnerable; *C. a. prigoginei* – Endangered. CITES (2012): Appendix 2).

C. a. prigoginei appears to be the most threatened subspecies. This 'Endangered' subspecies is endemic (as far as is known) to the forests of Mt Kabobo (=Misotshi-Kabogo). A one-month biodiversity survey of these forests in 2007 by a large team encountered *C. a. prigoginei* but once. The one observation was made from camp. None were observed along 133 km of transect/reconnaissance walk (Plumptre et al. 2008).

Indigenous Mbuti in the central Ituri Forest are net-hunters and probably have little impact on primate populations; however, where guns are available, they are used for hunting in other parts of Ituri. It is likely that humans are hunting *C. angolensis* throughout eastern DR Congo, Rwanda and Burundi due to prolonged instability and violence in the region since the 1994 war. The movement of refugees into DR Congo has resulted in forest degradation and habitat loss for *C. angolensis*. Subspecies *C. a. cottoni* and *C. a. cordieri* will continue to lose habitat as settlements move deeper into the moist forest zone. In Tanzania continued degradation and fragmentation of forest habitat is the major threat to *C. angolensis* (Rovero et al. 2012). In Kenya there is a major degree of resource overlap in coastal forest fragments between human extraction of lumber, charcoal, fuel wood,

building poles and carving wood, and *C. a. palliatus* food resource requirements; major food tree species such as *M. usaramensis*, *C. schumannii* and *L. fraxinifolius* are particularly targeted. Forest clearance for tourism development and agriculture is ongoing. As the area and quality of coastal forests declines, colobus crop-raiding and resultant human wildlife conflict may become an additional problem (Anderson et al. 2007a). Illegal hunting for pelts is still reported in Tanzania and Kenya (Anderson et al. 2007c, Rovero et al. 2012).

Priority conservation actions include: improved forest protection in East and central Africa to incorporate coastal mangrove within existing habitat preservation and *C. a. palliatus* conservation strategies; promote alternative wood resources for local and tourism sectors; encourage local efforts to enrich agricultural matrix among forest fragments through tree planting schemes; promote existing cultural values of *C. a. palliatus* and its habitat, including benefits through small-scale eco-tourism; and conduct a detailed assessment of the distribution, abundance and conservation status of *C. a. prigoginei*.

Measurements

Colobus angolensis palliatus

HB (♂♂): 665 (520–740) mm, n = 17

HB (♀♀): 563 (480–660) mm, n = 15

T (♂♂): 794 (560–897) mm, n = 17

T (♀♀): 782 (720–853) mm, n = 15

HF (♂♂): 172 (130–210) mm, n = 17

HF (♀♀): 158 (130–180) mm, n = 15

E (♂♂): 44 (30–85) mm, n = 28

E (♀♀): 44 (30–70) mm, n = 28

WT (♂♂): 8.9 (6.0–11.5) kg, n = 16

WT (♀♀): 7.1 (5.0–8.5) kg, n = 15

Wakuluzu Friends of the Colobus Trust, Diani, Kenya

Key References Anderson et al. 2007a, b, c; Bocian 1997; Fashing et al. 2007b; Fimbel et al. 2001; Maisels et al. 1994.

Carolyn M. Bocian & Julie Anderson



Angola Colobus *Colobus angolensis* adult male.

Colobus vellerosus WHITE-THIGHED COLOBUS (GEOFFROY'S PIED COLOBUS, URSINE COLOBUS)

Fr. Colobe de Geoffroy; Ger. Geoffroy-Stummelaffe

Colobus vellerosus (I. Geoffroy, 1830). Bulletin des Sciences Naturelles et de Géologie 22: 318. Type locality not known.White-thighed Colobus *Colobus vellerosus* adult male.

Taxonomy Monotypic species. Analyses of cranial morphology, coat colour and ♂ loud-calls ('roar') confirm that the White-thighed Colobus is a separate species from the King Colobus *Colobus polykomos* (Oates & Trocco 1983, Groves 2001). *Colobus vellerosus* ♂ loud-calls are closest to those of the Guereza *Colobus guereza* (Oates *et al.* 2000b). Groves (2007b) lists *ursinus* as a synonym of *C. polykomos*. Synonyms: *bicolour*, *dollmani*, *leucomeros*. Chromosome number: $2n = 44$. Composed of metacentric and submetacentric chromosomes (Dutrillaux *et al.* 1981, Romagno 2001).

Description Arboreal, medium-sized, black-bodied monkey with long, all-white, slightly tufted tail. Tail 124–152% of HB (Groves *et al.* 1993). Sexes alike in colour pattern. Adult ♀ about 80% as heavy as adult ♂. Face encircled by broad white ruff. Thigh with grey patch. White epaulettes absent, but shoulder hair of ♂ ♂ markedly longer than hair on the rest of the body (10–15 cm), marginally longer in ♀ ♀ (Booth 1958b). In ♀ ♀ there is white fur around callosities broken at the perineum and underside of tail base. In ♂ ♂ there is no break. Infants white at birth and gradually change to various shades of grey (7–11 weeks of age). Black-and-white pelage by 12 weeks.

Geographic Variation Hybrids with *C. polykomos* occur, or did occur, between Sassandra R. and Bandama R. in Côte d'Ivoire (Groves *et al.* 1993, Groves 2007b, Gonedelé Bi *et al.* 2006, 2012, Oates & McGraw 2009, Oates 2011). These hybrids are phenotypically much closer to *C. vellerosus* than to *C. polykomos* (Groves *et al.* 1993).

Similar Species None within geographic range.

Distribution Endemic to West Africa. Rainforest BZ. From Comoe R., SW Burkina Faso, and the Bandama R. and Nzi R., Côte d'Ivoire, east through Ghana, Togo, Bénin to W Nigeria (Booth 1958a, Oates & Trocco 1983, Sayer & Green 1984, Happold 1987, Groves 2001, Galat & Galat-Luong 2006b, Gonedelé Bi *et al.* 2010, Oates 2011). In the north the range follows riverine forests into the Guinea savanna (Sayer & Green 1984, Grubb *et al.* 1998, Fischer *et al.* 2000). Historic range estimated at 381,000 km² (Eeley & Foley 1999).

Habitat Mainly in primary evergreen and semi-deciduous forests, but also secondary forests and riverine forests. In inundated (swamp) forests in extreme SE Côte d'Ivoire, SW Ghana (W. S. McGraw pers. comm.) and Bénin (Sinsin *et al.* 2002a, Assogbadjo & Sinsin 2007).

Abundance Declining and uncommon. In Côte d'Ivoire McGraw *et al.* (1998a) surveyed five Forest Reserves (Bossematie, Mabi, Yaya, Songan and Ehy); only in Yaya were there confirmed sightings of *C. vellerosus*, although subsequent surveys confirmed *C. vellerosus* in Ehy Swamp Forest (W. S. McGraw pers. comm.). Up to

*Colobus vellerosus*

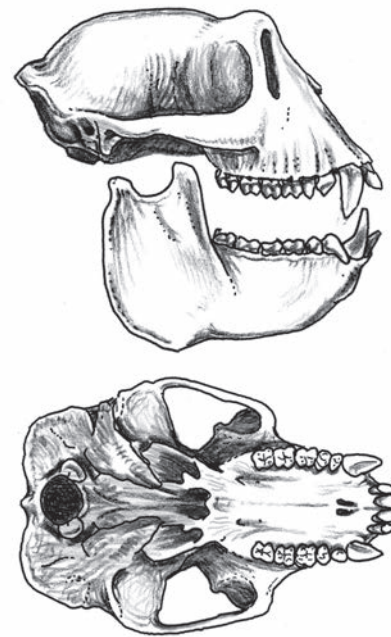
1996 sightings of *C. vellerosus* were frequent in Comoé N. P., but the species has become rare since; ♂ roaring also ceased to be heard in recent years (Fischer *et al.* 2000). See Gonedélé Bi *et al.* (2010, 2012). In Ghana *C. vellerosus* was common in Bia N. P. and Ankasa Resource Reserve (Asibey 1978). Already rare in Bia N. P., Ankasa Resource Reserve and Kakum N. P. in 1993 (Struhsaker & Oates 1995). However, the population in Boabeng-Fiema Monkey Sanctuary (BFMS) is increasing and was estimated at 275 individuals in 19 groups in 2007 (Wong & Sicotte 2006, K. Kankam pers. comm.). Forest pockets around BFMS also support small populations (90 individuals in ten groups in 2007; B. Kankam pers. comm.). The local people's perception of *C. vellerosus* is that it is rare or locally extinct (Ntiama-Baidu 1998). Other recent sightings include Krokosua Hills F. R., Attandanso Resource Reserve, Yoyo F. R. (Oates *et al.* 2000a) and Mole N. P. (T. Saj pers. obs.), but the population status at these sites is unknown. In Togo reported in Keran and Fazao-Malfacassa National Parks (Asibey 1978) and recently confirmed in Fazao-Malfacassa and Yikpa-Gigbé (Campbell *et al.* 2008b). In Bénin, in Forêt Classée de Lama (Nobimé & Sinsin 2007), Lokoli Forest (Sinsin *et al.* 2002a, Assogbadjo & Sinsin 2007) and Kikélé Sacred Grove (Inoussa & Nobimé 1997). Reported, but not confirmed, at other sites (Campbell *et al.* 2008b).

Status in Bénin is unknown. At least one group sighted in the Forêt Classée de Lama (G. Altherr pers. comm.) in 2002, and one group of 5–7 animals in the Lokoli Forest near Bohicon in 2001–02 (Sinsin *et al.* 2002a). Also reported recently in Mont Kouffé Forest, Wari Maro Forest (B. Sinsin pers. comm.), Kikélé Sacred Grove (Inoussa & Nobimé 1997) and Pénessoulou Forest (G. S. Djossou pers. comm. to J. A. Teichroeb & G. Campbell pers. comm.). In W Nigeria *C. vellerosus* was common until the 1960s near the border with Bénin, but it is now possibly extirpated (Happold 1987). Between 1997 and 2001, I. Faucher (pers. comm.) travelled extensively in SW Nigeria and did not observe *C. vellerosus* despite looking for primates and sighting several other species.

Adaptations Diurnal and arboreal. Adaptations similar to other black-and-white colobus.

Foraging and Food Folivorous. At BFMS the main food items are: mature and young leaves (79%), fruits and seeds (11%), flowers and buds (6%), seedpods (4%). These are taken mainly from middle and upper storey of trees in the families Moraceae, Bombacaceae and Mimosaceae. Main seasonal difference in diet relates to the proportion of mature leaves, which (for one group) varied from 100% of monthly feeding records in the wet season to 0% in the dry season. Seeds and unripe fruits are consumed when available in the dry season (e.g. *Albizia zygia*, *Aubrevillea kerstingii*, *Trilepisium madagascariense*) (Saj 2005). This is similar to the finding of D. K. Olson for *C. vellerosus* in Bia (cited in Oates 1994). At BFMS groups travel ca. 300 m a day (range 65–604 m, $n = 96$ days for two groups). In Bia mean daily range was 307 m (range 75–752 m; Curtin & Olson 1984 cited in Oates 1994). *Colobus vellerosus* travel on the ground when arboreal routes are lacking (Booth 1956b, Jeffrey 1975, T. L. Saj & P. Sicotte pers. obs.) and can apparently move between forest fragments (Wong & Sicotte 2006).

The mean activity budget for three groups at BFMS (Aug–Nov 2000 and 2001) shows resting in 59% of records, feeding in 24%, moving in 15% and social behaviour (primarily grooming and



Lateral and palatal views of skull of White-thighed Colobus *Colobus vellerosus* adult male.

copulations) in 3% of records. Resting occurs frequently throughout the day. Feeding increases slightly in the early morning, at mid-day and at the end of the afternoon (Teichroeb *et al.* 2003).

Social and Reproductive Behaviour Social. Mean group size is 15.1 in BFMS and 10.3 in surrounding fragments (range 3–38, $n = 21$ groups; Saj *et al.* 2005, Wong & Sicotte 2006). These numbers are consistent with information in Jeffrey (1975), Martin (1991) and from B. Sinsin (pers. comm.). Galat & Galat-Luong (1980) and A. Galat-Luong (pers. obs.) observed groups of 3, 4, 6, 10 and 11 individuals (mean = 6.8) in Comoé N. P., as well as a solitary adult ♂. Single-male and multimale groups occur. In BFMS and surrounding fragments the ♀ : ♂ ratio ranges from 0.9 to 1.5, whereas the percentage of immatures in the population ranges from 28% to 44%. All-male groups occur (Saj & Sicotte 2005). There are low frequencies of aggression and affiliation within groups. The range of agonistic interactions over food per adult in two groups was 0.005–0.013/h (459 h of observation). The range of agonistic interactions for all contexts per adult in two groups was 0.007–0.036/h (459 h of observation). Time spent grooming between adults varied from 0.8% to 1.2% in two groups. Between 79% and 98% of this grooming took place between ♀ ♀ (Saj 2005). Males and ♀ ♀ use the 'stiff-leg' display, a low intensity aggressive behaviour (Oates 1977c). Inter-group encounters (in which ♂ ♂ are more aggressive than ♀ ♀) range from mere proximity to severe aggression (Sicotte & MacIntosh 2004). Loud-calls are rarely heard during encounters, rather they are heard at dawn and dusk, and during the day in the absence of encounters.

At Bia N. P., a wet semi-deciduous forest, a group of 13–18 individuals had an annual home-range of 31 ha (Olson 1986). One study group also used a smaller area of their home-range in the dry season (Curtin & Olson 1984 cited in Oates 1994). In BFMS, a dry semi-deciduous forest, home-range sizes for 11 months for groups

of 8 and 33 individuals was 11 ha and 12 ha, respectively. Minimum known total home-range overlap for two groups with neighbouring groups ($n = 5$) ranged from 43% to 46% (Saj 2005). Population density at BFMS is 119 animals/km² (Wong & Sicotte 2006).

One association in Comoé N. P. comprised groups of *C. vellerosus*, Lesser Spot-nosed Monkey *Cercopithecus (c.) petaurista*, Lowe's Monkey *Cercopithecus (m.) lowei* and White-naped Mangabey *C. lunulatus* (A. Galat pers. comm.). *Colobus vellerosus* associates occasionally with Campbell's Monkey *Cercopithecus (m.) campbelli* (W. S. McGraw pers. comm.). In BFMS *C. vellerosus* responds to alarm calls from *C. campbelli*. Play and aggressive interactions also take place between individuals of both species.

Females have no sexual swellings, frequently solicit copulations and when multiple ♂♂ are in the group, mate promiscuously (Saj & Sicotte 2005). Extra-group copulations occur (Teichroeb *et al.* 2005). About 38% of infant mortality at BFMS during 2003–2005 was due to infanticide by non-resident adult males, one result of which was reduced interbirth intervals for the mothers (Teichroeb & Sicotte 2008, Teichroeb *et al.* 2009).

Reproduction and Population Structure Length of gestation about six months. Breeding does not seem to be seasonal. One young born at a time. Twins not reported. Infants are white for 5–6 weeks after birth ($n = 5$). Time to weaning is unknown. Infant handling by adult and subadult ♀♀ occurs up to 12 weeks. Youngest infants are the most attractive, although grey infants are handled the most (Brent 2005, Brent *et al.* 2007).

Longevity, birth and mortality rates unknown. In BFMS, ♂ tenure is short (mean 15.8 months, range = 3–>52, $n = 29$). All the ♂♂ observed from infancy to adulthood ($n = 10$) dispersed from their natal group. Female transfer also occurs (Saj & Sicotte 2005, Teichroeb *et al.* 2009).

Predators, Parasites and Diseases Leopards *Panthera pardus* and Lions *Panthera leo* prey on *C. vellerosus* in Comoé N. P. (Bodendorfer *et al.* 2006). African Crowned Eagles *Stephanoaetus coronatus* and Robust Chimpanzees *Pan troglodytes* are predators of colobus at other sites and probably also prey on *C. vellerosus*. At BFMS *C. vellerosus* reacts by grunting and crouching when large birds fly close to the canopy. Human hunting is undoubtedly the primary source of predation.

Conservation IUCN Category (2012): Vulnerable. CITES (2012): Appendix II.

See Abundance above. *Colobus vellerosus* is hunted for its coat and meat. In the 1890s an estimated 190,000 skins were exported from Ghana. In the early twentieth century the trade averaged 17,000 per year (Grubb *et al.* 1998). Since the 1970s *C. vellerosus* has been protected by law in Ghana and Bénin, and partially protected in Côte d'Ivoire, Togo and Nigeria (De Klemm & Lausche 1987). However, poaching occurs and specimens are sometimes found in local markets (Côte d'Ivoire: McGraw *et al.* 1998, Fisher *et al.* 2000, Gonedelé Bi *et al.* 2010, 2012; Ghana: Ntiemoa-Baidu 1998; Bénin: P. Neuenschwander pers. comm.; W Nigeria: Happold 1987).

Loss of habitat is the other primary threat. Forested habitats are now rare in Togo, Bénin and SW Nigeria. Wolfheim (1983) suggests that *C. vellerosus* may be able to adapt to low levels of logging, but a comparison of the population densities in four Forest Reserves and in Bia N. P. in Ghana found that even low level timber exploitation was associated with a reduced population density (Martin & Asibey 1979 cited in Martin 1991). Better enforcement of hunting laws, better habitat protection and more protected areas are necessary. Where local taboos against hunting *C. vellerosus* are effective, populations can increase. Small-scale ecotourism programmes may encourage further conservation efforts (e.g. BFMS, Ghana; Kikélé, Bénin). Outside West Africa, *C. vellerosus* is not reported to occur in zoos (Reichler 2001).

Measurements

Colobus vellerosus

HB (♂♂): 663 (600–670) mm, $n = 4$

HB (♀♀): 623 (600–670) mm, $n = 4$

T (♂♂): 865 (830–930) mm, $n = 4$

T (♀♀): 834 (730–904) mm, $n = 4$

HF (♂♂): 196 (190–210) mm, $n = 4$

HF (♀♀): 183 (175–190) mm, $n = 4$

E (♂♂): 33 (31–38) mm, $n = 4$

E (♀♀): 35 (31–38) mm, $n = 4$

WT (♂♂): 8.5 (range unknown) kg ($n = 3$)

WT (♀♀): 6.9 (range unknown) kg ($n = 5$)

Body measurements: W Ghana (Jeffrey 1975)

Weight: Oates *et al.* (1994) from BMNH and MNHN

Key References Booth 1958a; Grubb *et al.* 1998; Oates 2011; Oates & Trocco 1983; Saj *et al.* 2005.

Tania L. Saj & Pascale Sicotte

Colobus guereza GUEREZA COLOBUS (BLACK-AND-WHITE COLOBUS, ABYSSINIAN COLOBUS)

Fr. Colobe guéréza; Ger. Guereza

Colobus guereza Rüppell, 1835. Neue Wirbelt. Fauna Abyssin. Gehörig. Säugeth., p. 1. Damot region, Gojjam, Ethiopia.

Taxonomy Polytypic species. Nine subspecies recognized by Rahm (1970), six by Dandelot (1974) and eight by Napier (1985), Groves (2001, 2007b) and Grubb *et al.* (2003). Long referred to as *Colobus abyssinicus*, following Oken (1816), who named it *Lemur abyssinicus*. In 1956, however, the International Commission on Zoological Nomenclature ruled (Opinion 417) that Oken's name was invalid (Napier 1985). Synonyms: *abyssinicus*, *albocaudatus*,

brachychaites, *caudatus*, *dianae*, *dodingae*, *elgonis*, *escherichi*, *gallarum*, *ituricus*, *kikuyuensis*, *laticeps*, *managaschae*, *matschiei*, *occidentalis*, *percivali*, *poliurus*, *roosevelti*, *ruppelli*, *rutschuricus*, *terrestris*, *thikae*, *uellensis*. Chromosome number: $2n = 44$ (Bigoni *et al.* 1997).

Description Large, robustly-built, arboreal colobine monkey, with striking, glossy, black-and-white pelage and a 'roar' loud-call.



Western Guereza *Colobus guereza occidentalis* adult male.

Distinguished from other *Colobus* species by mantle (or cape) of long white hairs that extend from shoulders to flanks and across the lower back. Adult ♀ about 68–84% as heavy as adult ♂, depending on the subspecies. Lower brow, cheeks, chin and throat white, forming a circumfacial ruff. Crown, upper back, limbs, hands, feet and ventrum jet black. Tail with white tuft on tip. Extent of white on tail, length and bushiness of terminal tuft and length of mantle vary with subspecies. Sexes similar in colour, except ring of white pelage circling the ischial callosities is complete in ♂♂ and incomplete in ♀♀. Infants have an entirely white pelage and pink skin. Adult pelage and black skin appear by 14–17 weeks. In adults crown of head has double-humped appearance resulting from muscle development, especially marked in adult ♂♂, whose crowns are up to 1.5 times as large as those of adult ♀♀. Photographs of *C. guereza* from sites in Kenya and Tanzania available at: www.wildsolutions.nl

Geographic Variation The following eight subspecies are recognized by Napier (1985), Groves (2001, 2007b) and Grubb *et al.* (2003). Data on percentage of the tail that is white were provided by P. Grubb (pers. comm.) based on the examination of 132 specimens at the BMNH.

- C. g. guereza* Omo River Guereza. Ethiopian Highlands west of Rift Valley, south to lowlands in the Omo Valley. Mantle hair relatively long, covering ca. 20% of tail. Tail much longer than HB: proximal part of tail grey; distal ca. 53% silvery white (S.D.=6.4, range=38–62, n=13).
- C. g. gallarum* Djaffa Mountains Guereza. Ethiopian Highlands east of Rift Valley. Proximal part of tail black with scattered grey hairs increasing distally; distal ca. 55% white and bushy (S.D.=6.7, range=45–61, n=5).
- C. g. occidentalis* Western Guereza. Donga River Valley, Nigeria, south through Cameroon to NE Gabon and Congo, and east through Central African Republic to N DR Congo, SW Sudan and W Uganda. Hair of mantle and tail tip creamy-white. Tail ca. 40% longer than HB: distal ca. 40% creamy-white (range=25–51, n=64).
- C. g. dodingae* Dodinga Hills Guereza. Imatong Mts, SE Sudan. Hair of mantle slightly creamy. Similar in pelage and craniometrics to *C. g. occidentalis*, with which it was grouped by Dandelot (1974).

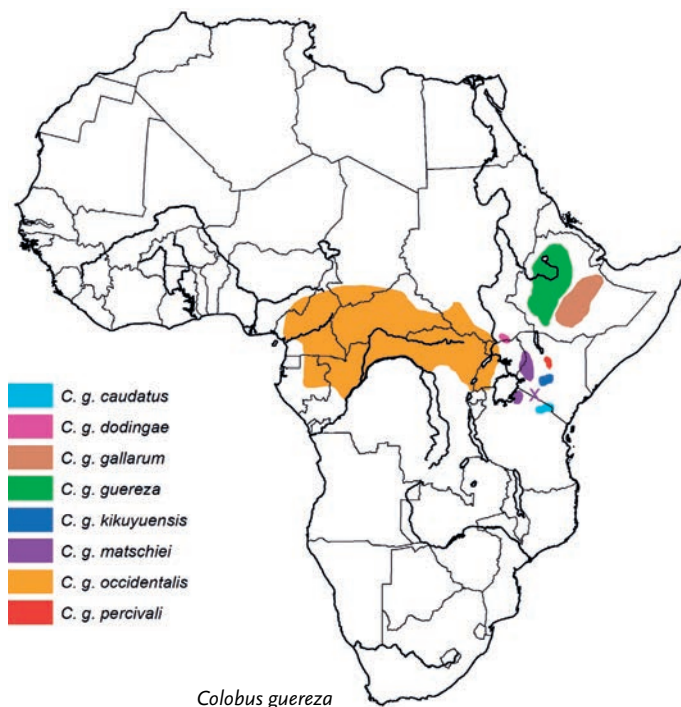
Tail about same length as HB: distal ca. 46% creamy-white and not very bushy (S.D.=4.5, range=40–55, n=10).

- C. g. percivali* Mt Uargues Guereza. Mathews Range (=Waragess =Uargess), C Kenya. Mantle hair long, creamy-white, covering 20–25% of tail. Tail longer than HB: distal ca. 72% (n=1) white and bushy.
- C. g. matschiei* Mau Forest Guereza. Kenya, Uganda and Tanzania, from Mt Elgon east to Rift Valley (including Kakamega Forest, Mau Forest, and forests near L. Nakuru and L. Naivasha) and south-west to Grumeti R. of western Serengeti in NW Tanzania. Tail longer than HB: proximal part black; distal ca. 47% white (S.D.=55, range=36–58, n=16).
- C. g. kikuyuensis* Mt Kenya Guereza. Kenya, east of Rift Valley including Mt Kenya, Aberdares Range and Ngong Hills. Mantle long and luxuriant, covering ca. 25–30% of tail. Tail relatively short, length about equal to HB: proximal part grey or black with scattered grey hairs increasing distally; white tuft very bushy. Distal ca. 78% of tail white (S.D.=3.5, range=71–83, n=19).
- C. g. caudatus* Mt Kilimanjaro Guereza. N Tanzania, including Mt Kilimanjaro and Mt Meru. Mantle even longer than on *C. g. kikuyuensis*. Male loud-call ('roar') higher pitched than *C. g. occidentalis* (Oates *et al.* 2000b). Proximal part of tail black with scattered grey hairs; white tuft comprising ca. 80% of tail length. Tail longer than HB: distal ca. 82% of tail white (S.D.=7.7, range=71–88, n=4).

Similar Species

Colobus angolensis. Angola, Congo Basin, SW Rwanda, SW Uganda, SE Kenya and Tanzania. Lacks white mantle (veil) and well-developed tail tuft (Oates 1994).

Distribution Endemic to equatorial Africa. Rainforest and Afromontane–Afroalpine BZs. The most widespread of the black-and-white colobus monkeys, the Guereza occupies woodlands and



Colobus guereza

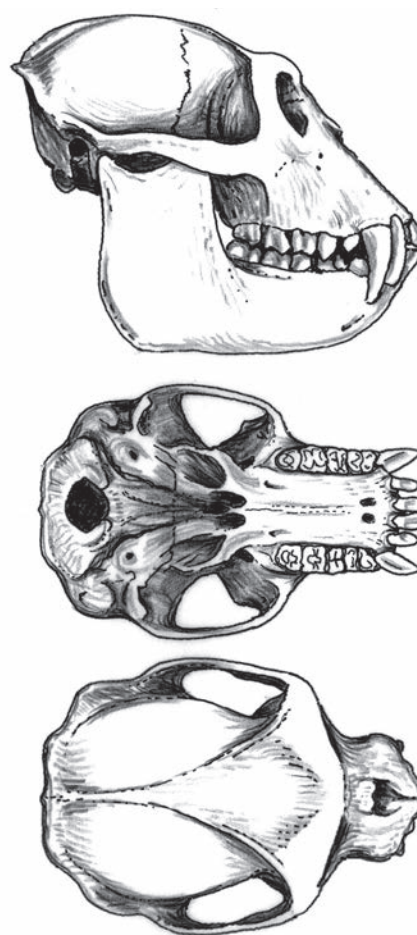
forests from E Nigeria (ca. 10° E) across the northern fringe of the Congo Basin to eastern Africa, as far east as ca. 42° E in Ethiopia. The northern limit is ca. 14° N in Ethiopia and the southern limit is ca. 03° S in Tanzania. In western Africa the southern limit is just south of the Equator in Gabon and Congo. Guerezas occur from ca. 200 m asl in Cameroon to at least 3300 m in Ethiopia (Oates 1977b). Present from 1900–2900 m on the Aberdares Range, C Kenya (Butynski 1999), and from 1800–2900 m on Mt Kilimanjaro, N Tanzania (T. Butynski pers. comm.). A ‘mummified’ individual found at 4700 m on Mt Kenya (Young & Evans 1993), and a carcass found at 4680 m in a cave on Mt Kilimanjaro (Guest & Leedal 1954), but both records are well above the typical range for this species at these two sites. Subspecies distributions given above under Geographic Variation.

Habitat Guerezas inhabit a wide array of forest types, including lowland and medium-altitude moist forest, montane forest, swamp forest, dry forest, gallery forest and disturbed forest (Oates 1994, 2011, Fashing 2007, Fashing *et al.* 2012). Mean annual rainfall varies considerably across this range of habitats, from 700 mm in N Central African Republic (Fay 1985), to 1100–1200 mm in gallery forest in East Africa and Ethiopia (Oates 1977a, R. Dunbar pers. comm.), to 2220 mm in Kakamega, Kenya (Cords 1987b).

Abundance Guerezas often attain higher densities than most of the primates with which they are sympatric. Densities tend to be particularly high in small patches of forest along lakes and rivers (315 animals/km²: Bole, Ethiopia [Dunbar 1987]; 347 animals/km²: Kyambura Gorge, SW Uganda [Krüger *et al.* 1998]; 396 animals/km²: L. Naivasha, Kenya [Rose 1978, M.D.]; 800 animals/km²: Murchison Falls, Uganda [Leskes & Acheson 1970]), and particularly low in large areas of undisturbed moist forest (3 animals/km²: Ituri Forest, DR Congo [Bocian 1997]; 4.5 animals/km²: Kibale Forest (Ngogo), SW Uganda [Struhsaker 1997]). Guerezas attain intermediate densities in moist forest areas that have been subjected to low to moderate levels of human disturbance (100 animals/km²: Kibale Forest (Kanyawara) [Oates 1974]; 150–168 animals/km²: Kakamega Forest, W Kenya [Fashing & Cords 2000, Fashing *et al.* 2012]; four to >10 groups/km² in the montane forest of the Aberdares Range [Butynski 1999]).

Adaptations Diurnal and arboreal. Because they reach such high densities in many gallery forests and forest fragments, Guerezas are believed to be specially adapted to life in these forests (Oates 1977a, 1994). They thrive on the colonizing deciduous tree species and lianas characteristic of these forests, possibly because these plant species invest their energy more in rapid growth than in secondary compounds and lignin for their leaves (Oates 1977a). Even in continuous moist forests, Guerezas prefer areas of secondary growth and forest edge (Butynski 1985, Thomas 1991, Bocian 1997). For example, in the moist montane forest at Bwindi, Uganda, Guerezas are confined to the edge of the forest and appear to be absent at distances >2.8 km into the forest (Butynski 1985).

Like other colobines, Guerezas are characterized by an enlarged forestomach in which microbial fermentation of food occurs (Kay & Davies 1994). They may be especially good at digesting high-fibre food items; a study by Watkins *et al.* (1985) found that



Lateral, palatal and dorsal views of skull of Western Guereza *Colobus guereza occidentalis* adult male.

captive Guerezas fed on a high-fibre diet exceeded the digestive efficiency predicted for ruminant mammals of the same body size. Their capacity for subsisting on mature leaves during times of preferred food scarcity (Oates 1977a, Fashing 2004) may explain why Guerezas are sometimes able to achieve extraordinarily high densities (e.g. Leskes & Acheson 1970, Dunbar 1987, Krüger *et al.* 1998).

As a result of their relatively leafy diet and digestive adaptations, Guerezas also have a particularly sedentary life-style; they spend at least half of the day resting at all three sites where their activity patterns have been studied extensively (Kibale Forest, Uganda [Oates 1977a]; Ituri Forest, DR Congo [Bocian 1997]; Kakamega Forest, Kenya [Fashing 2001a]). Their tendencies to lead inactive life-styles, sunbathe in the canopy during the cool early morning and hunch over during rainstorms (Oates 1977a, Fashing 2001a) suggest that Guerezas may be adopting a strategy of behavioural thermoregulation similar to that of their West African congener King Colobus *Colobus polykomos* (Dasilva 1993).

In many habitats Guerezas sometimes travel and feed on the ground. This behaviour is particularly noticeable in forest galleries in savanna, where they move hundreds of metres on the ground between forest patches (Oates 1977a, c, Fay 1985), but it has also been observed in moist forest habitats, where they sometimes come to the ground to consume swamp plants or soil (Oates 1978; Fashing *et al.* 2007a).

In a craniometric study Hull (1979) found Guerezas to differ markedly from other black-and-white colobus species in their teeth, palate and jaws. For instance, Guerezas have relatively smaller incisors and longer molars than the other species, dental features that may be correlates of a more leafy diet.

Foraging and Food Folivorous. Extensive studies of Guereza diets have been conducted at four field sites (Kibale, Uganda; Ituri, DR Congo; Kakamega, Kenya; Budongo, Uganda). The results of these studies suggest that Guerezas exhibit impressive dietary flexibility. Guerezas tend towards extreme folivory at Kibale (Oates 1977a, Wasserman & Chapman 2003, Chapman *et al.* 2004) and Ituri (Bocian 1997), while their diets are more evenly balanced between leaves and fruit at Kakamega (Fashing 2001b) and Budongo (Plumptre 2006). Few primates are as folivorous as Guerezas at Kibale where up to 89% of the annual diet consists of leaves (Chapman *et al.* 2004), while at Kakamega, fruit accounts for up to 44% of the annual diet, and up to 81% of the diet in months when fruit is abundant (Fashing 2001a, b).

Unlike other *Colobus* species (McKey 1978, Harrison 1986, Dasilva 1994, Maisels *et al.* 1994), Guerezas consume primarily pulpy fruits rather than seeds (Dunbar & Dunbar 1974a, Fashing 2001b; A. Plumptre pers. comm.). In the case of both leaves and fruits Guerezas tend to focus on abundant species (Oates 1977a, Fashing 2001b). Furthermore, the total number of plant species consumed annually is generally low (Ituri 31 spp. [Bocian 1997]; Kakamega >37 spp. [Fashing 2001b]; Kibale 43 spp. [Oates 1977a]). Often a single species plays a major role in the diet of Guerezas: plant parts (mostly young leaves) of *Celtis gomphophylla* (syn. *C. durandii*) (Ulmaceae) comprised 50% of the annual diet for Guerezas at Kibale (Oates 1977a) and plant parts (mostly mature leaves) of *Prunus africana* (Rosaceae) made up 19% of the annual diet for Guerezas at Kakamega (Fashing 2001b, 2004). In addition to being the most frequently consumed items in the annual diet of Guerezas at Kakamega, *P. africana* mature leaves were also the primary fallback resource for Guerezas at this site, accounting for as much as 50% of the diet during months of fruit scarcity (Fashing 2004).

The chemical basis of food choice has been unusually well studied in Guerezas. Guerezas typically select food items that are high in protein, low in fibre, or both (Bocian 1997, Chapman *et al.* 2004, Fashing *et al.* 2007a). Secondary compounds also sometimes play a role in Guereza food choice, with most items high in condensed tannins tending to be avoided at Kibale (Oates *et al.* 1977) and Kakamega (Fashing *et al.* 2007a), but not at Ituri (Bocian 1997). Most minerals do not appear to strongly influence food choice, though there are several exceptions (Rode *et al.* 2003, Fashing *et al.* 2007a). Guerezas at both Kibale and Kakamega select for food items high in zinc, and engage in long journeys to access rare resources such as herbaceous swamp plants or *Eucalyptus* (Myrtaceae) bark that are rich in sodium (Oates 1978, Rode *et al.* 2003, Fashing *et al.* 2007a, Harris & Chapman 2007).

Guerezas typically engage in several prolonged feeding bouts spaced throughout the day with particularly sharp increases in time spent feeding occurring in the late afternoon at Kibale (Oates 1977a) and Chobe, Uganda (Oates 1977a), and in the mid- to late afternoon at Ituri (Bocian 1997). Feeding bouts are generally

followed immediately by long periods of rest, which are presumed to be necessary if Guerezas are to ferment and extract nutrients from their leafy diets (Oates 1977a).

In forest habitats group daily travel distances are relatively low (Kibale: mean = 535 m, range 288–1004 m, n = 60 days on one group [Oates 1977a]; Kakamega: mean = 588 m, range 166–1360 m, n = 185 days on five groups [Fashing 2001a]; Ituri: mean = 609 m, range 268–1112 m, n = 55 days on one group [Bocian 1997]). Unlike many other primates Guerezas do not appear to substantially alter their daily travel distance in response to temporal fluctuations in food availability (Oates 1977a, Bocian 1997, Fashing 2001a, b). Instead, Guereza ranging patterns may be influenced more by the distribution of the rare, sodium-rich resources, such as herbaceous swamp plants and *Eucalyptus* bark, that they periodically make long journeys to access (Oates 1977a, Fashing 2001a, Fashing *et al.* 2007a, Harris & Chapman 2007). They have also been seen out in freshly burned grassland, apparently eating ash or charcoal (Kingdon 1971). These journeys require some groups to cover much greater distances than others depending on how far a group's usual ranging area is from the high-sodium resources (Harris & Chapman 2007). This disparity among groups in distance to sodium-rich resources may help explain why Guereza daily path lengths and home-range sizes are not typically correlated with group size (Fashing 2001a, Fashing *et al.* 2007a, Harris & Chapman 2007). It is also possible, however, that the lack of a correlation between group size and ranging variables reflects an absence of scramble competition over food within most Guereza groups (Fashing 2001a).

Home-range areas of groups vary widely from 1.5 ha at Murchison Falls, Uganda (n = 1, Leskes & Acheson 1971) to 100 ha at Ituri (n = 1, Bocian 1997). Mean home-range areas at other sites include: Limuru, Kenya: 2.0 ha, n = 1 (Schenkel & Schenkel-Hulliger 1967); Bole, Ethiopia: 2.0 ha, range 1.4–3.6 ha, n = 10 (Dunbar 1987); Kyambura Gorge, Uganda: 3.7 ha, range 1.7–6.2 ha, n = 24 (Krüger *et al.* 1998); L. Naivasha, Kenya: 4.8 ha, n = 1 (Rose 1978); L. Shalla: Ethiopia, 5.6 ha, range not reported, n = 6 (Dunbar 1987); Entebbe, Uganda: 7.5 ha, range 6.4–9.3 ha, n = 3 (Grimes 2000); Kibale: 13.7 ha, range 8.8–18.8 ha, n = 6 (Harris 2005); Budongo, Uganda: 14 ha, range 7.3–21.3, n = 25 (Suzuki 1979); Kakamega: 18 ha, range 16–20 ha, n = 2 (Fashing 2001a); Kibale: 28 ha, n = 1 (Oates 1977a). Even at sites where home-ranges are relatively large (e.g. Kakamega, Kibale, Ituri), groups tend to concentrate their activities within a smaller 'core area' of their range (Oates 1977a, c, Bocian 1997, Fashing 2001a, Harris 2005). At Kibale, Harris (2006a, Harris *et al.* 2010) found that core areas featured a greater abundance of food per unit area than other portions of her groups' home-ranges.

Comparisons across Guereza study sites suggest that home-ranges become compressed into increasingly smaller areas as population density increases (Dunbar 1987, Fashing 2001a). Range overlap between groups is often high in moist forests where densities are intermediate (Kibale: 74% overlap [Oates 1977b], 83% overlap [Harris 2005]; Kakamega: >67% overlap [Fashing 2001a]), but tends to be much less extensive in moist forests where densities are low (Ituri: 22% overlap, Bocian [1997]; Budongo, Uganda: overlap not reported, but can be inferred from ranging and density data to have been minimal [Suzuki 1979]), and in gallery forests where densities are high (Chobe, Uganda: 10% overlap [Oates 1977a]; Bole, Ethiopia:

'relatively little' overlap [Dunbar & Dunbar 1974a]). The extensive range overlap at Kibale and Kakamega may be due in part to the convergence by many groups on small patches of rare resources at these sites (swamp plants and soil at Kibale, and *Eucalyptus* bark and soil at Kakamega) (Oates 1977c, 1978, Fashing 2001a, Fashing *et al.* 2007a, Dierenfeld *et al.* 2007).

Social and Reproductive Behaviour Social. Guerezas live in groups that typically include 1–2 adult ♂♂, 1–6 adult ♀♀ and their dependent offspring (Oates 1994, Fashing 2007). Adult ♂♂ not belonging to bisexual groups appear to travel most often alone or in pairs, though larger all-male groups of up to four animals occur (Oates 1974, P. Fashing pers. obs.). Bisexual groups range in size from two (Marler 1969, Suzuki 1979) to 23 individuals (Fashing 1999). Mean group size tends to be larger in large forest blocks than in small fragments and gallery forests (Dunbar 1987, Onderdonk & Chapman 2000, Fashing 2007). Groups in large forest blocks are more likely to include multiple ♂♂ (Oates 1994, Fashing 2007). The extent to which multimale groups are stable has been debated. Dunbar & Dunbar (1976) and Oates (1994) contend that multimale groups are only the temporary results of immigration and maturation within the group, while von Hippel (1996) argues that multimale groups can be stable over long periods and are, in fact, the typical social unit for Guerezas inhabiting large moist forest blocks.

Long-term, intermittent, longitudinal monitoring of Guereza populations in two large moist forests suggests that the extent to which multimale groups predominate and are long-lasting varies among forests. Over a recent 28-year period at Kakamega, five of six censuses of Guereza group composition indicated that 50% or more of the groups surveyed contained multiple ♂♂ (1980: 50%, $n = 6$ [Cords in Mulhern 1991]; 1990: 100%, $n = 2$ [Mulhern 1991]; 1992: 89%, $n = 18$ [von Hippel 1996]; 1997–98: 40%, $n = 5$ [Fashing 2001a]; 2004: 80%, $n = 5$; 2008: 83%, $n = 6$ [P. Fashing pers. obs.]). Furthermore, P. Fashing (pers. obs.) found that one recognizable adult ♂ at Kakamega remained subordinate in a multimale group for at least seven years, suggesting that the composition of multimale groups sometimes remains stable over long periods. On the other hand, studies over the past three decades at Kibale indicate that multimale groups are consistently less common than uni-male groups (1971–72: 14–29%, $n = 7$ [Oates 1977c]; 1992–93: 43%, $n = 40$ [Teelen 1994]; 2002–03: 17%, $n = 6$ [Harris 2006a]) and do not appear to be stable in composition over time (Oates 1977c).

Affiliative behaviour is common while agonism is rare within Guereza groups (Leskes & Acheson 1971, Dunbar & Dunbar 1976, Oates 1977b, Struhsaker & Leland 1979, Dunbar 1987, Fashing 1999, 2001a, Harris 2005). Grooming is the most frequent affiliative behaviour among Guerezas and they spend up to 15% of their time engaged in this behaviour (Kakamega: 6% [Fashing 2001a]; Kibale: 6% [Oates 1977b], 15% [Harris 2005]). Adult ♀♀ are the primary groomers in most groups at Kibale and Kakamega (Oates 1977b, Fashing 2001a, Harris 2005), although in groups where they are present, juvenile ♀♀ frequently groom others at Kakamega as well (P. Fashing 2001a, pers. obs.). Adult and juvenile ♂♂ groom others only rarely both at Kibale and Kakamega (Oates 1977c, Fashing 2001a, Harris 2005). Adult ♀♀ are typically the primary recipients of grooming (Oates 1977b,

Fashing 2001a), although Harris (2005) found that adult ♂♂ in Kibale often received more grooming than most adult ♀♀. Amongst adult ♀♀ within a group, there is considerable inter-individual variation in the extents to which they groom and are groomed by others (Oates 1977b, Harris 2005, P. Fashing pers. obs.). Oates (1974) noted that the smallest adult ♀♀ in his study group at Kibale received far less grooming than other adult ♀♀. This pattern was also observed in the group for which social relationships were most carefully studied at Kakamega (P. Fashing pers. obs.).

Agonism is typically uncommon within Guereza groups (Kibale: one incident every 8.7 h [Oates in Struhsaker & Leland 1979]; one incident every 9.1 h [Harris 2005]; Kakamega: no incidents during 16,710 scan samples and only occasional incidents outside scan samples [Fashing 2001a]). Still, Harris (2005) found that, at Kibale, displacements amongst adult ♀♀ occurred more often than expected in the context of feeding, and that ♀♀ displacing others fed more often than expected in the immediate aftermath of the displacement. Harris (2005) also noted that some adult ♀♀ had consistently unidirectional dominance relationships with other ♀♀ in their groups. These results suggest that, despite their reliance on a highly folivorous diet, contest competition over food occurs amongst ♀♀ within Guereza groups at Kibale (Harris 2005), albeit at a low rate.

Relationships between Guereza groups are typically antagonistic (Oates 1977a, c, Fashing 1999, 2001c, 2007, Harris 2005, 2006b, 2010). Patterns of home-range defence vary widely across habitat types, across forests of similar habitat type, and even within individual forests over time. Defence of the entire range appears typical of Guerezas in gallery forests where ranges are small (Dunbar 1987), while groups in large moist forests, where ranges are larger, tend to focus on defending only portions of their range (Oates 1977c, Fashing 1999, 2001c, Harris 2005). Guerezas in the large moist forest at Kakamega consistently engage in site-specific home-range defence, most staunchly and successfully defending those portions of their range they occupy most often (Fashing 1999). In the large moist forest at Kibale, Oates (1977c) found that the outcomes of most encounters were also location-specific, though some encounters appeared to be decided by inter-group dominance relationships instead. In another study at Kibale 30 years later, Harris (2006b) found that inter-group dominance relationships were the decisive factor influencing the outcomes of most encounters and that her six study groups could be ordered into a linear transitive dominance hierarchy based on competitive ability during encounters.

Males are the most aggressive group members during inter-group encounters, with ♀♀ only occasionally playing aggressive roles (Oates 1977b, Fashing 2001c, Harris 2010). Male inter-group aggression appears related primarily to the defence of food resources, although in some instances aggression may also be related to mate guarding (i.e. direct defence of mates [Fashing 2001c, Harris 2010]). The occasional ♀ aggression that occurs during encounters is probably related to resource defence, although during most encounters ♀♀ appear to rely on ♂♂ to do the bulk of the resource defence (Fashing 2001c, Harris 2010). Fashing (2001c, 2007) suggests that Guereza ♂♂ may engage in inter-group resource defence as a means of indirect mate defence; ♀♀ may be more likely to mate with, and less likely to transfer away from, ♂♂ who successfully defend food sources for their group.



Western Guereza *Colobus guereza occidentalis*.

One of the most distinctive sounds in the forests of equatorial Africa is the loud-call of the ♂ Guereza. This call, termed a 'roar' (Schenkel & Schenkel-Hulliger 1967), can be heard as far as 1.6 km away from its source (Marler 1969). Males uttering roars often simultaneously engage in a ritualized jumping display. Roars are most often given around dawn, when they are usually contagious, with ♂♂ from across the forest joining in once one ♂ begins roaring (Schel & Zuberbühler 2012). Dawn roars have been postulated to serve as inter-group spacing calls (Marler 1969, Waser 1977b) and/or as a form of male–male competition (Oates & Trocco 1983, Oates *et al.* 2000a, Harris *et al.* 2006). Roars are also sometimes given during the day when they appear to function primarily as predator alarm calls (Marler 1972, Oates 1994, Schel *et al.* 2009, 2010, Schel & Zuberbühler 2009). Kingdon (1971) noted roaring in response to nocturnal earthquakes and found that some groups in western Uganda called at about 03:00h with some frequency. Occasionally given at night, the function of these nocturnal roars is unclear.

In a study of captive ♂ Guerezas, Harris *et al.* (2006) found that the mean formant dispersion (i.e. difference, in Hz, between frequency bands) of the roars uttered by individual ♂♂ was significantly inversely correlated with their body mass. Harris (2006b) also reported that the mean formant dispersion of roars by ♂♂ in the wild at Kibale could be used to predict the outcome of encounters between groups. The lower the mean formant dispersion of a male's roars, the more likely his group was to win encounters with other groups. Guereza roars thus appear to be honest signals of body size, which may reflect ♂ competitive ability (Harris 2006b, Harris *et al.* 2006).

Allomaternal behaviour is common in Guerezas with juvenile ♀♀ and nulliparous adult ♀♀ particularly interested in carrying the infants of other ♀♀. This behaviour has been most thoroughly investigated in captive animals (Wooldridge 1969, Emerson 1973, Horwich & Manski 1975, Horwich & Wurman 1978). At Kibale, infants are handled most by non-mothers in their first 1–2 weeks of life, when they have all-white coats and are still completely dependent on others for all locomotion (Oates 1977c). Rate of infant transfers to allomothers during this stage is ca. 3–5 incidents/h at Kibale. Infants and, to a lesser extent, their mothers sometimes attempt to resist transfers to allomothers, and infants often squeal and flail about under the care of allomothers until their mothers come to retrieve them (Oates 1977c). Adult ♂♂ rarely engage in infant care, with all observed instances resulting from infants approaching ♂♂ and clinging to them (Oates 1977c, P. Fashing pers. obs.). However, individual juvenile ♂♂ occasionally seek out young infants to hold and carry, though much less frequently than ♀♀ (P. Fashing pers. obs.).

Most of what is known about Guereza mating behaviour comes from a recent study at Kibale (Harris & Monfort 2006). During this study, 334 solicitations for copulation were observed, of which 85% were accepted. Females and ♂♂ played the role of solicitor almost equally often. Twenty-three per cent of copulations were harassed by other group members, most commonly subadult ♂♂, though adult ♀♀ and juveniles occasionally harassed copulations as well. When a ♀ is in oestrus, copulatory rate can be high; one ♀ copulated with a particular ♂ 29 times in 64 min (Harris & Monfort 2006). Based on this report and a smaller sample of copulatory events observed

at Kakamega, Guerezas appear to be multiple mounters (Harris & Monfort 2006, Fashing 2007).

The percentage of time Guerezas spend in close proximity with other primate species (i.e. in polyspecific associations) varies across forests, though rarely reaches the frequencies observed among cercopithecines (Waser 1987, Cords 1990, Enstam & Isbell 2007). At Kakamega and Kibale, where polyspecific associations were defined as occasions when members of two species were within 50 m of one another, Guerezas spent 24% (P. Fashing pers. obs.) and 40% (Harris 2005) of their time in these associations, respectively. Guerezas most often formed these associations with Blue Monkeys *Cercopithecus (n.) mitis stuhlmanni* at Kakamega (P. Fashing pers. obs.) and with Uganda Red Colobus *Procolobus rufomitratus tephrosceles* at Kibale (Harris 2005). Polyspecific associations were defined differently at Bole where they were considered to occur only when the two closest members of different species are nearer to one another than are the two most widely separated group members of the same species. By this definition, Guerezas spent 11% of their time in polyspecific associations at Bole, most often with Grivets *Chlorocebus aethiops* (Dunbar & Dunbar 1974a).

Reproduction and Population Structure Unlike the Olive Colobus *Procolobus verus*, red colobus *Procolobus* spp., the Angola Colobus *Colobus angolensis* and the Black Colobus *Colobus satanas*, Guereza ♀♀ lack sexual swellings (Oates 1994, Bocian 1997). Ovarian cycle length, based on hormonal monitoring of three ♀♀ at Kibale, is ca. 24 days (range 15–27 days; Harris 2005). Most copulations at Kibale occurred from five days before to three days after the estimated date of ovulation. In some groups at Kibale multiple ♀♀ are sometimes simultaneously in oestrus (Harris & Monfort 2006). Females in captivity first give birth at 4.5–5.0 years of age after a gestation period of ca. 170 days (Rowell & Richards 1979). Gestation in the wild is ca. 152 days (range 142–161 days) based on hormonal monitoring of three ♀♀ at Kibale (Harris & Monfort 2006). Only singletons have been recorded. Birth-weight averages 445 g (Harvey *et al.* 1987). Inter-birth intervals are ca. 17 months at Kakamega (Fashing 2002), and 22–25 months at Kibale (Oates 1977c, Harris & Monfort 2006). No birth season observed at either Kibale or Kakamega, though there was some synchrony of births within study groups at Kakamega (Oates 1977b, Fashing 1999, 2002). Rowell & Richards (1979) suggest that Guerezas breed rapidly and aseasonally because their specialized digestive system releases them from the selective pressures imposed on other monkeys by seasonal food shortages. Few data are available on ♂ reproductive parameters.

Groups nearly always contain more adult ♀♀ than adult ♂♂ (Oates 1994, Fashing 2007). Average adult ♀ to adult ♂ ratios in groups were 3.4 : 1.4 at Kibale (n = 7 groups; Oates 1977c) and 3.8 : 2.4 at Kakamega (n = 5 groups; Fashing 2007). Immature to adult ♀ ratios in groups were 6.5 : 3.4 at Kibale (n = 7 groups; Oates 1977c) and 6.8 : 3.8 at Kakamega (n = 5 groups; Fashing 2007). Ten of 11 adult ♀♀ in three closely monitored groups gave birth during a 17-month study at Kakamega (Fashing 2002). Only one of these infants disappeared during the study period, suggesting that infant survivorship is high at this site (Fashing 2002). Infant mortality attributed to falls and infanticide (Oates 1977b), though the latter has been observed only at Kibale (Onderdonk 2000, Harris



Mt Kilimanjaro Guereza *Colobus guereza caudatus* adult male.

& Monfort 2003, Chapman & Pavelka 2005). Chapman & Pavelka (2005) suggest that infanticide risk may act as the primary constraint on group size among Guerezas at Kibale. Longevity in the wild is unknown, though Guerezas live to at least 23 years and 9 months in captivity (Jones 1982).

Male Guereza emigrate from their natal groups after adolescence and ♀♀ may occasionally transfer between groups (Harris *et al.* 2009). Bachelor ♂♂ and, to a lesser extent, all-male groups consisting of adult and/or subadult ♂♂ occur at Kibale and Kakamega, indicating that ♂♂ spend considerable periods living outside bisexual groups after dispersing (Oates 1977c, Fashing 1999). An all-male group with four members was regularly observed following one of P. Fashing's (pers. obs.) study groups at Kakamega over several weeks before eventually joining it permanently. An adult ♀ and her small juvenile who did not belong to any of the Kakamega study groups were also observed following and occasionally approaching one of Fashing's groups on several consecutive days but then were not seen again. Two members of another Kakamega study group, an adult ♂ and a large juvenile ♀, became increasingly peripheral to their group over several weeks before disappearing permanently. They are assumed to have transferred. There is also evidence from Kakamega that adult ♀♀ take an active role in expelling other adult ♀♀ from their group (P. Fashing pers. obs.). On several occasions over a 2-day period adult ♀♀ cooperated in holding down an adult ♀ group-mate while biting and hitting her until she fell to the forest floor. After the last instance of aggression from her ♀ group-mates, the victim fled through the undergrowth and was never observed in the group again.

Predators, Parasites and Diseases The primary predator on Guerezas appears to be the African Crowned Eagle *Stephanoaetus coronatus*, though the intensity of Crowned Eagle predation differs widely among sites. For example, Guerezas accounted for 39% of the prey of Crowned Eagles at Kanyawara study site in Kibale Forest (Skorupa 1989). However, just 12 km away at Ngogo, Guerezas comprised only 4% of the Crowned Eagle's diet (Mitani *et al.* 2001). Mitani *et al.* (2001) suggest that this disparity may be the result both of Guereza densities being higher at Kanyawara and inter-individual variation in hunting behaviour between Crowned Eagle pairs at the two sites.

Robust Chimpanzees *Pan troglodytes* prey on Guerezas at both Kibale (Mitani & Watts 1999, Watts & Mitani 2002) and Budongo

(Suzuki 1975). However, the rate of chimpanzee predation at Kibale is low with Guerezas accounting for only 4% of the chimpanzee's mammalian prey items (Watts & Mitani 2002). Leopards *Panthera pardus* probably also prey on Guerezas at low rates: Hart, J.A. *et al.* (1996) found that Guerezas and Angola Colobus combined comprised only 1% of the prey items in Leopard scats at Ituri, DR Congo; such remains could arise from Leopards scavenging African Crowned Eagle kills.

Guerezas appear to use several tactics to avoid predation. For example, adult ♂♂ give loud-calls ('roars') when they detect a predator. These vocalizations may help intimidate the predator and alert group-mates (Marler 1972, Schel *et al.* 2009, 2010). In the case of African Crowned Eagles, ♂ Guerezas may also use physical threats to intimidate them. P. Fashing (pers. obs.) once witnessed a ♂ Guereza chase off an Crowned Eagle perched quietly in the same tree as the ♂ and his group; the ♂ Guereza repeatedly raced to within 1 m of the Crowned Eagle and lunged at it. Another tactic Guerezas may use to avoid predation is to cluster together on moonlit nights, presumably to reduce their chances of being detected. Consistent with this assertion is von Hippel's (1998) finding that the number of sleeping trees occupied on a given night by members of a Guereza group in Kakamega Forest is significantly inversely correlated with the fullness of the moon. Lastly, aside from their loud-calls, most Guereza vocalizations are relatively quiet, a characteristic that reduces their conspicuousness to predators.

Ten species of gastrointestinal parasites were present in 476 faecal samples collected from Guerezas at Kibale: *Trichuris* sp., *Entamoeba coli*, *Entamoeba histolytica*, *Oesophagostomum* sp., *Strongyloides fulleborni*, *Ascaris* sp., *Colobenterobius* sp., *Bertiella* sp., an unidentified Strongyle, and a species in the Dicrocoeliidae. Prevalence (percentage of faecal samples in which a parasite was present) exceeded 10% only for *Trichuris* sp., which was found in 79% of the samples (Gillespie *et al.* 2005b).

A preliminary study of 23 Guereza faecal samples from Kakamega revealed nine species of parasites: *Trichuris* sp., *E. coli*, *E. histolytica*, *Heterophyes* sp., *Fasciola* sp., *Schistosoma* sp., an unidentified Strongyle, an unidentified hookworm and an unidentified worm. Like at Kibale, *Trichuris* sp. was among the most prevalent parasites and was found in 87% of samples from Kakamega. Other parasites present in at least 10% of samples from Kakamega were *E. coli*, *E. histolytica*, *Heterophyes* sp., *Fasciola* sp., the unidentified Strongyle and the unidentified hookworm (P. Fashing, C. Ashira & I. Farah pers. obs.).

Many of the parasites found among Guerezas at Kibale also occur commonly among the human population in W Uganda. However, no differences were found in parasite prevalence between Guerezas living in anthropogenically disturbed (logged) forest and those inhabiting undisturbed forest (Gillespie *et al.* 2005b). Still, when Chapman *et al.* (2005) examined the effects of immigration of Guerezas from a fragment cleared by humans into a second fragment where Guereza parasite loads were already being monitored, they found that, over the next five years, *Trichuris* sp. infection prevalence and intensity increased while Guereza density declined.

Conservation IUCN Category (2012): Least Concern. *C. g. percivali*: Endangered. *C. g. gallarum*, *C. g. dodingae* and *C. g. matschiei*: Data Deficient. All other subspecies: Least Concern. CITES (2012): Appendix II.



Western Guereza *Colobus guereza occidentalis* adult male.

Guerezas have traditionally been hunted for ceremonial purposes by many African peoples, including the Kuria, Chagga, Kikuyu, Samburu and Luhya. Guerezas were also hunted heavily for their skins to supply the European fur market in the nineteenth century, and in the twentieth century to make rugs for the tourist trade (Oates 1977b). The Guereza skin trade was outlawed in Kenya and Ethiopia in the 1970s (Dunbar & Dunbar 1975a, Oates 1977b), though Guereza pelts and rugs were still found on sale illegally in an Addis Ababa souvenir shop as recently as 2003 (P. Fashing pers. obs.). Although primates are not often hunted for their meat in the African savanna zone, or in much of East Africa, Guerezas are hunted as food in the forest zone; in western equatorial forests they are threatened, along with other large forest primates, by the bushmeat trade. For instance, Fay (1985) reported that Guerezas were still abundant in gallery forests in the Manovo–Gounda–St Floris N. P. in the savanna zone of Central African Republic, while they had been nearly extirpated in the southern, forested, portion of the country.

Perhaps the most threatened subspecies is *C. g. percivali*, which is endemic to the Mathews Range F. R. (940 km²) where this subspecies remains widespread from 1400–2000 m. Incidence of loud calls indicates that some sites support at least three groups/km². It appears that the habitat and the primates of the Mathews Range are better protected now than in the recent past (Mwenge 2008, De Jong & Butynski 2010a).

The Guereza is one of the few primate species that generally responds well to some habitat disturbance (Fashing *et al.* 2012), actually attaining higher densities in logged than in undisturbed areas at Kibale (Skorupa 1986, Struhsaker 1997, Chapman *et al.* 2000) and Budongo (Plumptre & Reynolds 1994). However, intensive logging and forest clearance for agriculture are as much a threat to Guerezas as they are to other forest-dependent primates (Chapman *et al.* 2003, 2007).

Measurements

Colobus guereza

HB (♂♂): 615 (543–699) mm, n = 20

HB (♀♀): 576 (521–673) mm, n = 22

T (♂♂): 667 (521–826) mm, n = 20

T (♀♀): 687 (528–797) mm, n = 22

Specimens in BMNH; localities not listed (Napier 1985)

C. g. occidentalis

HB (♂♂): 593 (535–690) mm, n = 16

HB (♀♀): 554 (485–640) mm, n = 13

T (♂♂): 811 (670–885) mm, n = 16

T (♀♀): 773 (715–825) mm, n = 13

HF (♂♂): 191 (175–207) mm, n = 16

HF (♀♀): 179 (165–190) mm, n = 13

E (♂♂): 44 (37–50) mm, n = 16

E (♀♀): 40 (35–43) mm, n = 13

WT (♂♂): 9.3 (6.8–11.3) kg, n = 46

WT (♀♀): 7.4 (5.4–10.9) kg, n = 46

Body measurements: various localities in E DR Congo (Allen 1925)

Weight: numerous localities (Delson *et al.* 2000)

C. g. guereza

WT (♂♂): 13.5 (12.4–14.4) kg, n = 3

WT (♀♀): 9.2 (8.2–10.1) kg, n = 3

Specimens from Ethiopia in MNHN (J. F. Oates pers. obs.).

C. g. matschiei

WT (♂♂): 9.9 (8.2–11.8) kg, n = 15

WT (♀♀): 8.3 (6.4–10.2) kg, n = 15

Several localities (Delson *et al.* 2000)

Key References Fashing 2001a, c; Harris 2006a, b, 2010; Oates 1977a, c, 2011.

Peter J. Fashing & John F. Oates

GENUS *Procolobus*

Olive Colobus Monkey, Red Colobus Monkeys

Procolobus de Rochebrune, 1887. Faune de Sénégal. Suppl. Vert., Mamm. 1: 95.



Tshuapa Red Colobus *Procolobus rufomitratu tholloni* adult male.

Polytypic genus endemic to the forests of tropical Africa. Two subgenera provisionally recognized (*Procolobus* and *Piliocolobus*), one species of Olive Colobus and 18 taxa of red colobus monkeys. The number of species of red colobus monkeys is controversial but six are profiled in this volume. For further details, see profiles for the subgenera *Procolobus* and *Piliocolobus*, and Struhsaker (1981b, 2010), Colyn (1991), Grubb *et al.* (2003), Groves (2001, 2007b), Ting (2008a, b), Cardini & Elton (2009) and Oates (2011).

Recent molecular data indicate that *Procolobus* and *Piliocolobus* diverged prior to the late Miocene (6.9–6.4 mya) (Ting 2008a, b, Roos *et al.* 2011). If the suggested divergent time standard for genera of 6–4 mya is adopted, *Piliocolobus* should be considered a genus based on its divergence from *Procolobus* at least 6 mya (Goodman *et al.* 1998, Groves 2001).

All members of the genus *Procolobus* share the following characters:

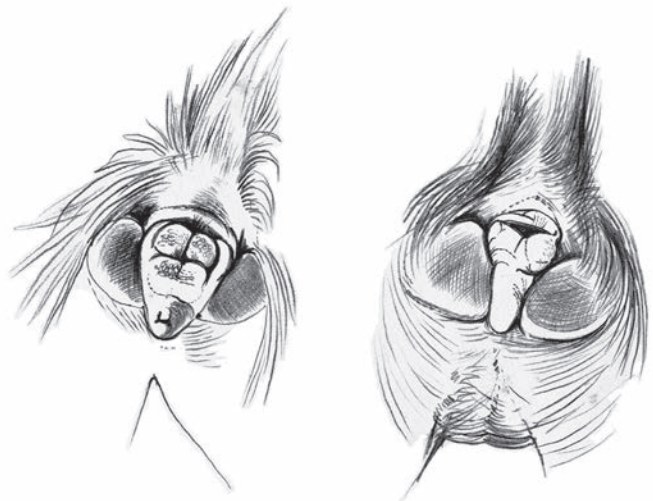
- 1 Four-chambered stomach. This differs from the three-chambered stomach of *Colobus*. All Colobinae have cellulolytic bacteria that allow consumption and digestion of large quantities of leaves and seeds.
- 2 A sagittal crest in most adult ♂♂, and a larger nuchal crest in ♂♂.
- 3 Enlarged supraorbital ridges.
- 4 Larynx reduced in size (not enormously enlarged as in *Colobus*), subhyoid sac absent and pterygoid fossa deepened.

- 5 Adult and subadult ♀♀ have perineal swellings that vary in size over time. There is tremendous inter-taxa variation in the maximum size of these swellings, with the largest so far recorded being found in *P. badius temminckii*, *P. badius badius*, *P. preussi*, *P. rufomitratu oustaleti* and *P. gordonorum*, and the smallest in *P. rufomitratu tephrosceles*, *P. r. rufomitratu* and *P. kirkii*.
- 6 Males of all ages have a perineal organ that superficially resembles the very smallest swellings of adult ♀♀.
- 7 Ischial callosities are separate in both sexes.

Pelage colour usually includes varying amounts of reddish-brown or orange, depending on the taxon. Coat colour is often highly variable, even amongst members of the same social group. Cranial differences are considerable, and the two putative subgenera are considered by many authors (Kingdon 1997, Jablonski 1998, Groves 2001, 2005c, 2007b) to be generically distinct. In his monograph on cranial morphology, Verheyen (1962) separated the Olive Colobus *Procolobus verus* as a distinct genus while uniting red colobus with black-and-white colobus in the genus *Colobus*.

Procolobus eat relatively little animal food and rarely drink water (e.g. from tree-holes), obtaining most water from food. They are largely diurnal although some activities, such as copulation, sometimes occur at night. Their forest habitats are highly variable in rainfall and tree species composition, ranging from the dry and seasonal forests (mean annual rainfall of ca. 1050 mm for *P. b. temminckii* at Fathala, S Senegal; Gatnot 1976) to the extremely wet forests of S Bioko I., Equatorial Guinea (ca. 10,000 mm mean annual rainfall) in the case of *P. p. pennantii*. Found from sea level (e.g. *P. p. pennantii* on Bioko I. and *P. kirkii* on Zanzibar [Unguja] I.) to ca. 2200 m (*P. gordonorum* in the Udzungwa Mts, Tanzania).

Peter Grubb, Thomas T. Struhsaker & Kirstin S. Siex



Ashy Red Colobus *Procolobus rufomitratu tephrosceles* perineal and anal region in adult female (left) and adult male (right).

Subgenus *Procolobus* Olive Colobus Monkey

Procolobus de Rochebrune, 1887. Faune de Sénégalambie. Suppl. Vert., Mamm. 1: 95.

Monotypic subgenus endemic to the moist forests of West Africa. Subgenus *Procolobus* embraces a single species, the Olive Colobus *P. verus*. *Procolobus verus* is restricted mainly to high forest in West Africa, though occurring also in some gallery forests, for example along the Benue R., Nigeria (its easternmost distribution). This is the smallest of all extant African colobines. Pelage dull olive greyish-green or olive-brown comprised of agouti-banded hairs. *Procolobus verus* has a swept-up crest and distinctively cow-licked hair on the crown, hairy ears, and a glans penis covered in minute papillae. Differs from the subgenus for red colobus monkeys, *Piliocolobus*, in numerous cranial features (Verheyen 1962, Groves 2001, Cardini & Elton 2009). Some of these are:

- 1 Facial skeleton not so prognathous, premaxillae vertical; supraorbital ridges thin, curved; margins of pyriform aperture sharp; an incipient anterior nasal spine; posterior palatal canals deeply sunk in fossae; wide choanae and pterygoid fossa, with flat basisphenoid floor.
- 2 Symphyseal foramen present in mandible. This is a rare feature in 'higher primates'.
- 3 Maxillary incisors have a lingual cingulum and tubercle; lateral incisors are rather caniniform. Lower M3 have a tuberculum sextum.

- 4 Second and fourth fingers are remarkably shortened, and the second finger has a peculiarly claw-like nail.

Subgenus *Procolobus* shares the following features with *Colobus*: shallow, wide interpterygoid fossa and other features of the basicranium, and oval orbits with thin supraorbital arches. This subgenus, however, lacks the subhyoid sac and enlarged larynx that characterize the very vocal *Colobus* species. No other colobines, living or fossil, have been allocated to this subgenus.

Of behavioural peculiarities, mothers carrying their young in the mouth or the young clinging to the mother's neck. These are assumed to be primitive or conservative behaviours, although these habits could have been selected through infants being consistently weak or inefficient in their grasp of the mothers' short, slippery hair. Characteristically, *Procolobus* are quiet and inconspicuous, and their groups form long-term associations with those of sympatric *Cercopithecus* spp., especially Diana Monkey *Cercopithecus* (d.) *diana*. Other features of this subgenus are given in the profile for *P. verus*.

Peter Grubb & Colin P. Groves

Procolobus verus OLIVE COLOBUS (VAN BENEDEN'S COLOBUS)

Fr. Colobe de van Beneden; Ger. Grüner Stummelaffe

Procolobus verus (van Beneden, 1838). Bull. Acad. Sci. Belles-Lettres Belg. 5: 347. 'Africa'.

Taxonomy Monotypic species. Sometimes treated as a monotypic genus (see below), but most authors currently recognize the Olive Colobus as a monotypic subgenus within *Procolobus*, a genus that also contains the subgenus *Piliocolobus*, the red colobus monkeys (Grubb *et al.* 2003).

Van Beneden's original description placed the Olive Colobus in the genus *Colobus*, but it was allocated to its own genus, *Procolobus*, by de Rochebrune (1887). Pocock (1935) recognized the close affinities of the red colobus monkeys and the Olive Colobus by 'provisionally'

assigning the red colobus monkeys to *Procolobus*, with *verus* as the type species. This arrangement has been supported by several later authors, including Kuhn (1967), Grubb *et al.* (2003) and Oates (2011). Others, however, see *Procolobus* as a monotypic genus (Dandelot 1974, Corbet & Hill 1980, Kingdon 1997, Groves 2001, 2005c, 2007b). Synonyms: *chrysurus*, *cristatus*, *olivaceus*. Chromosome number: not known.

Description Small, olive-brown, arboreal monkey. Smallest colobine monkey. Adult ♀♀ same colour as adult ♂♂. Adult ♀♀ average about 91% the weight of adult ♂♂. Head small and rounded. Face naked, dark grey. Eyes surrounded by obvious 'spectacles' of bare, puckered, grey skin. Ears large. Crown with short sagittal crest, which is particularly noticeable in adult ♂♂. Thumbs extremely reduced. Hands long. Feet especially long, exceeding in length both the thigh and the crus. Detailed anatomical description given by Hill (1952). Dorsal pelage varies from light reddish-brown to dark greyish-brown, sometimes with a slight olivaceous tinge. Ventrums dull grey to whitish. Testes large, contained in a pendulous scrotum. Glans of the penis unique among anthropoids in bearing small horny spicules. Adult ♀♀ have large cyclical circumvulval swellings, which reach a length of >6 cm. Perineal swellings present in juvenile ♂♂. Infants similar to adults in colour.



Olive Colobus *Procolobus verus* adult male.

Geographic Variation None recorded.

*Procolobus verus*

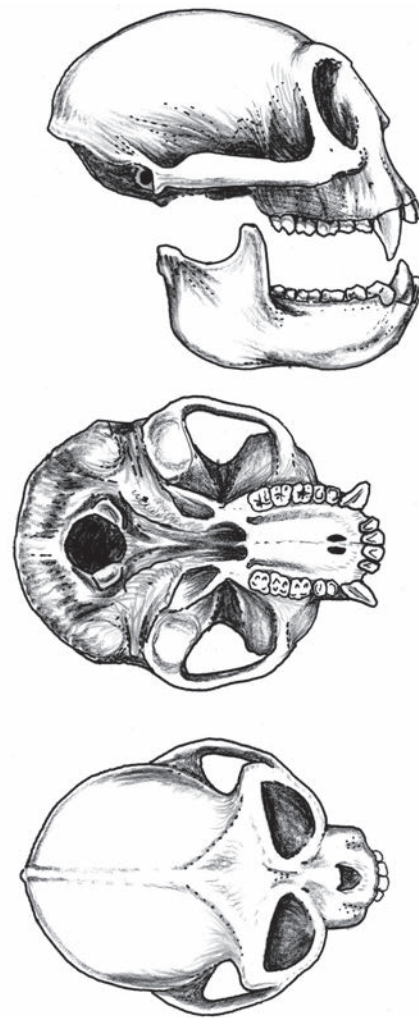
Similar Species None within geographic range.

Distribution Endemic to West Africa. Rainforest BZ. Restricted to coastal forests from Sierra Leone eastward to just east of the Niger R. in Nigeria. Although most records are south of 08° N (Oates 1981, Wolfheim 1983, Grubb *et al.* 1998), the Olive Colobus occurs as far north as 09° N in the Comoé N. P., Côte d'Ivoire (Fischer *et al.* 2000). Recent records for areas where this monkey had not been recorded previously (Dahomey Gap of S Bénin [Oates 1996b, Campbell *et al.* 2004, Nobime *et al.* 2011]; Niger Delta [Anadu & Oates 1988, Powell 1995]) suggest that the Olive Colobus may be more widespread than has been suspected, and that its apparent rarity may be due in part to its crypticity.

Current distribution probably similar to the historical distribution, but populations are today fragmented within this range as a result of deforestation by humans. The distribution of the Olive Colobus shows remarkable general correspondence to that of another endemic West African mammal, the Pygmy Hippopotamus *Choeropsis liberiensis*.

Habitat Lowland moist forest, swamp forest and forest galleries in the derived savanna/dry forest zone. Most abundant in riverine forest (Oates 1981). Presence in the Niger Delta confirmed only for the seasonally flooded forest of the upper Delta (Powell 1995). In Bénin the habitat in the Lama Forest is seasonally inundated. The sacred forest where the Olive Colobus occurs at Togbota is in the lagoon of the Ouémé R. Annual rainfall (and its distribution) within the species' range is extremely variable, from over 3000 mm with a 4-month dry season at Tiwai I., Sierra Leone, to ca. 2000 mm with a 3–4 month dry season in Tāi N. P., Côte d'Ivoire, to <1200 mm with a 5-month dry season in the Ayangba region of E Nigeria.

Abundance Generally rare, although density in one area of Tāi N. P. was ca. 14–21 ind/km² (Galat & Galat-Luong 1985, Korstjens



Lateral, palatal and dorsal views of skull of Olive Colobus *Procolobus verus* adult male.

2001). On Tiwai I., where Olive Colobus are relatively abundant, the estimated density was 7–8 ind/km² (Oates *et al.* 1990, Whitesides *et al.* 1988). In Kakum, Ghana, 0.06–0.19 groups encountered per km of transect walked (Oates *et al.* 2000a).

Adaptations Diurnal and arboreal. Olive Colobus appear to have a proclivity for areas with thick undergrowth and abundant lianas, such as river margins, secondary forest and canopy gaps (Booth 1957, Kuhn 1964, McGraw & Sciulli 2011). The Olive Colobus is a cryptic animal that is hard to detect because of its small size, its drab colouration, its habit of remaining inactive for long periods in thick growth, its tendency to live in small, dispersed groups and its quietness (most calls are soft, and they are given infrequently). Olive Colobus use their long hind-limbs to leap (20% of locomotor time is spent leaping compared to 18% for red colobus *Piliocolobus* spp., 14% for black-and-white colobus *Colobus* spp., and <11% for *Cercopithecus* spp. in Tāi; McGraw 1998a).

Olive Colobus are almost always seen in close proximity to groups of other monkeys, especially *Cercopithecus* spp., with which they may maintain prolonged association. This has been viewed as an anti-predator strategy (Booth 1957, Whitesides 1989, Oates & Whitesides 1990). The ranging patterns of individuals are strongly

influenced by the movements of the other-species group with which they are travelling.

Like other colobine monkeys, Olive Colobus have a large, sacculated stomach, including a bacterial fermentation chamber. Like red colobus, the stomach has a distinct four-part structure (Kuhn 1964). A study of second-molar anatomy by Kay (1981) found Olive Colobus to have the thinnest enamel and the greatest relative shearing crest development of any catarrhine primate. These anatomical features are correlates of the highly folivorous diet of this species (see below).

One of the most remarkable behavioural features of this unusual monkey is the method of carrying the infant. Unlike any other monkey or ape, infants are carried in the mother's mouth, as first reported by Booth (1957). At Tiwai and Tãi this behaviour continued until infants were at least ten months old, and infants were never seen clinging to the mother's ventrum; the mother typically held the infant by the skin of its flank, with the infant tucked against her neck and its tail wrapped around her neck and upper back (Oates 1994). Booth (1957) suggested that this behaviour occurs because the infant would have difficulty clinging to its mother's belly given its rudimentary thumb and her sparse ventral pelage, and would be in danger of being dislodged as the mother moves through thick vegetation.

Foraging and Food Folivorous. The Olive Colobus appears to be entirely vegetarian, but feeding often occurs in thick, low growth in the forest, where details of what is being ingested are hard to observe. While feeding, members of a social group are frequently highly dispersed, and mingled with monkeys of other species. In Tãi the home-range of two groups was 29 ha and 33 ha (Galat & Galat-Luong 1985), while Korstjens (2001) found the annual home-range of two groups at the same site to be 54 ha and 58 ha (Korstjens *et al.* 2007). At Tiwai I., a group associating with a group of Diana Monkeys *Cercopithecus (d.) diana* had a home-range of 28 ha (Oates 1994).

Olive Colobus travel and activity patterns are strongly influenced by the behaviour of the other monkey species with which they associate, and therefore vary considerably from place to place. As a result of their frequent association with *Cercopithecus* spp., Olive Colobus often travel longer distances each day than do most colobines. Daily mean travel distance in Tãi was 1202 m (± 297 , $n = 12$; Korstjens 2001, Korstjens *et al.* 2007). Annual activity budgets in Tãi (A. H. Korstjens & R. Noë pers. obs.) and Tiwai I. (J. Oates pers. obs.): 16% and 28% feeding, 50% and 39% resting, 30% and 26% moving, and 4% and 7% socializing (mainly grooming). McGraw (1998a) gives for Tãi: 13, 30, 19 and 6, respectively. At Tãi McGraw (1998a) found Olive Colobus to spend 64% of their time in the understorey (between 5 and 15–20 m), while at Tiwai I. 59% of observations were in the middle canopy at 10–19 m (Oates & Whitesides 1990). Both at Tãi and at Tiwai, Olive Colobus used lower heights in the canopy for foraging than travelling; 85% of Tãi foraging records were from the understorey or below, compared to 72% for travel (McGraw 1998a, see also McGraw & Sciulli 2011). At Tiwai 54% of feeding records came from below 15 m compared to 32% for travel (Oates & Whitesides 1990). Occasionally Olive Colobus come to the ground to cross tree gaps, and they sometimes forage on the ground on fallen fruits and on termite hills (Korstjens & McGraw pers. obs.). In Tãi they spend far more time on the ground (6%) than conspecific Western Red Colobus *Procolobus badius badius* (0.1%) or King Colobus *Colobus polykomos* (0.4%) (McGraw 1996,



Olive Colobus *Procolobus verus*.

1998c). There appears to be little variation in activity patterns during the day except for a peak in feeding in the afternoon, especially after 16:00h (Deschner 1996, J. Oates pers. obs.).

Based on 521 observations of feeding at Tiwai I., the composition of the Olive Colobus diet was 59% young leaves, 15% other leaves or leaf parts, 14% seeds, 7% flowers and 4% whole fruits or fruit pulp (Oates 1988a). Of 991 observations on feeding at Tãi, 91% were leaves or leaf parts, and 9% fruit or seeds (Korstjens 2001, Korstjens *et al.* 2007). Most of the leaves and seeds eaten by Olive Colobus at these two sites came from second-growth, riverbank or understorey trees (e.g. *Myrianthus libericus*, *Napoleona leonensis*, *Plagiosiphon emarginatus*, *Rinorea longicuspis*, *Scyttopetalum tieghemii*, *Strephonema pseudocola* and *Terminalia ivorensis*) and from lianas (see Korstjens 2001 for a detailed list of tree species used at Tãi).

Social and Reproductive Behaviour Social. Although Olive Colobus are social, grouping patterns are highly variable and fluid. Across the species' range in West Africa, group sizes range from 2 to 15 individuals. In Tãi, groups ranged in size from 3 to 14, with a mean of 7.1 ($n = 17$, Galat & Galat-Luong 1985; $n = 6$, Korstjens & Schippers 2003, Korstjens & Noë 2004). In the few cases where group composition has been assessed, 1–3 adult ♂♂ were present. Two adult ♂♂ were present in two, and three adult ♂♂ in one of six groups in Tãi (Galat & Galat-Luong 1985, Oates 1994, Korstjens & Schippers 2003, Korstjens & Noë 2004). Groups show frequent changes in composition, especially through ♀♀ transfer and natal dispersal by both sexes. For instance, a group at Tiwai contained two adult ♂♂, five adult ♀♀, one juvenile and three infants in Apr 1983, but by Nov 1985 contained only one adult ♂, one adult ♀ and one juvenile (Oates 1988a). During 4.5 years of observation in Tãi, one adult ♀ transferred into a group every 3.9 adult ♀ observation years; for ♂♂ this value was only one per 6.8 adult ♂ observation years. Of 11 juveniles monitored at Tãi, none matured in their natal group. New groups formed around solitary adult ♂♂ who were associated with a Diana Monkey group (Korstjens & Schippers 2003, Korstjens & Noë 2004, Korstjens *et al.* 2007). Related to the weak group cohesion, Olive Colobus show relatively low levels of intra-group affiliative behaviour; grooming is more common between ♂♂ and ♀♀ (especially around the time of mating activity) than among ♀♀. Overt agonistic behaviour is rare.

It is unclear whether Olive Colobus groups defend territories. However, adult ♂♂ have a distinctive high-pitched 'laughing' call, rendered by Hill & Booth (1957) as 'hoo hoo hoo hoo yow yow wee wee yow', rising in pitch to the penultimate syllable and dying away on the last. Both at Tāi and at Tiwai, Olive Colobus adult ♂♂ accompanying different Diana Monkey groups approach each other and exchange laughing calls, accompanied by much of side-to-side head-bobbing threatening gestures (Korstjens & Noë 2004) while the Diana Monkey groups have territorial encounters. Olive Colobus ♀♀ generally remain hidden in the vegetation and do not get involved in these conflicts. However, Korstjens & Schippers (2003) observed three ♀♀ with swellings giving sexual presents to ♂♂ of neighbouring groups during such encounters. In two of these cases the male(s) who were presented to mated with the proceptive ♀, while in the third case the ♂ chased the ♀ away (Korstjens & Schippers 2003, Korstjens & Noë 2004).

Females with sexual swellings are often followed closely by adult ♂♂, sometimes throughout the long receptive period (median 17 days; see below). Mating is frequent (sometimes >40 times/day) during these consortships. If there is more than one adult ♂ in the group, both may mate with the ♀ within five minutes. In Tāi a group is visited by a solitary ♀ (of unknown origin) with a sexual swelling, on average, once every 57th observation day (Korstjens & Schippers 2003, Korstjens & Noë 2004). These ♀♀ typically mate with male(s) of the group and disappear again within three weeks (Korstjens & Schippers 2003, Korstjens & Noë 2004).

Reproduction and Population Structure The large perineal sexual swellings of Olive Colobus ♀♀, and the large testes and penile spicules of ♂♂, are mentioned above. Female swellings last 14–20 days, median 17 days ($n = 7$), and can recur monthly (Korstjens & Noë 2004). At Tiwai, where the rainy season usually occurs from May to Oct, almost all observed copulations occurred during Mar–Aug, and ♀♀ with large sexual swellings were seen only in Jun–Aug. Very small infants were seen only in Nov–Apr, with the majority estimated to have been born in Jan, during the pronounced Dec–Mar dry season. In Tāi the rainy season occurs during Sep–Oct and the dry season from Dec to Feb. Here, ♀♀ with large swellings occur throughout the year, but births ($n = 13$) are most common during Oct–Feb, and never observed during May–Sep (Korstjens & Noë 2004). These observations suggest a typical colobine gestation of about six months, with births (only singletons observed) primarily during or close to the dry season. Young leaves are most abundant in the Tiwai forest in Feb–Mar (late dry season) and May–Jun (early rains) (Davies *et al.* 1999).

Few data on population structure are available, but social groups usually contain more adult ♀♀ than ♂♂. Six groups in Tāi had a mean of 1.5 adult ♂♂ (range 1–3) and 3.0 adult ♀♀ (range 1–5) per group (Korstjens & Schippers 2003, Korstjens & Noë 2004). In Tāi inter-birth intervals range from 1.2 to 2.0 years (mean 1.6, $n = 6$); juveniles are generally weaned at ca. one year of age, but one juvenile survived the loss of its mother at an age of 8.4 months (Korstjens & Schippers 2003). The only ♂ monitored from birth until attaining secondary sexual characteristics matured at an age of 3.7 years (Korstjens 2001, Korstjens & Schippers 2003).

Predators, Parasites and Diseases The cryptic appearance and behaviour of the Olive Colobus, combined with its strong

tendency to associate with other forest monkeys, are thought to have evolved as devices to lower predation risk. African Crowned Eagles *Stephanoetus coronatus*, Leopards *Panthera pardus* and Robust Chimpanzees *Pan troglodytes* prey on Olive Colobus (Boesch & Boesch 1989, Buzzard 2004, Shultz *et al.* 2004, Shultz & Thomsett 2007, Zuberbüler & Jenny 2007). No Olive Colobus remains were found in an analysis of 215 Leopard scats in Tāi (Hoppe-Dominik 1984). During a 7-year study in Tāi, Boesch & Boesch (1989) recorded only two attempts by chimpanzees to hunt Olive Colobus, compared with 110 attempts to hunt Western Red Colobus. This study occurred where the density of Western Red Colobus is estimated to be about eight times greater than that of Olive Colobus. Korstjens (2001) estimated that, each year, chimpanzees capture 0.9% of the Olive Colobus population, compared with 3.2% of Western Red Colobus, and 1.4% of Western Black-and-white Colobus in the same area. Shultz *et al.* (2004) calculated predation rates in Tāi of 1.0% of the Olive Colobus population per year by Leopards, and 4.8% by African Crowned Eagles.

Conservation IUCN Category (2012): Near-Threatened. CITES (2012): Appendix II.

The main threat to Olive Colobus is loss of habitat. Fortunately, this monkey does well in secondary forest and farm bush. Olive Colobus are shot, but, partly due to their strong smell, small size and cryptic nature, they are not a major target of hunters. Consequently, Olive Colobus are often one of the few remaining species in heavily hunted forests in Côte d'Ivoire and Ghana (Oates *et al.* 2000a, Refisch & Koné 2005, McGraw 2007b). Priority action for the long-term survival of the Olive Colobus is better control of hunting. Important areas for conservation are the larger protected areas, especially Tāi and Sapo, and smaller or interesting ones like Tiwai and Kakum in Ghana. The more eastern populations need attention; for instance, there is no effective conservation area for Olive Colobus within Nigeria.

Measurements

Procolobus verus

HB (♂♂): 458 (430–480) mm, $n = 8$

HB (♀♀): 465 (435–490) mm, $n = 6$

T (♂♂): 594 (570–640) mm, $n = 8$

T (♀♀): 610 (570–640) mm, $n = 6$

HF (♂♂): 136 (130–145) mm, $n = 8$

HF (♀♀): 135 (125–143) mm, $n = 7$

E (♂♂): 28 (26–31) mm, $n = 8$

E (♀♀): 27 (26–29) mm, $n = 7$

WT (♂♂): 3.8 (3.3–4.4) kg, $n = 7$

WT (♀♀): 3.6 (2.9–4.1) kg, $n = 5$

Ghana (Booth 1957)

WT (♂♂): 4.7 (4.0–5.7) kg, $n = 23$

WT (♀♀): 4.3 (3.6–5.4) kg, $n = 11$

Numerous sites. Based on the dataset presented in Delson *et al.* (2000) minus the four specimens taken from Booth (1957)

Key References Booth 1957; Hill 1952; Korstjens 2001; Korstjens *et al.* 2007; McGraw *et al.* 2007; McGraw & Sciulli 2011; Oates 1988a, 1994, 2011; Oates & Whitesides 1990.

John F. Oates & Amanda H. Korstjens

Subgenus *Piliocolobus*

Red Colobus Monkeys

Piliocolobus de Rochebrune, 1887. Faune de Sénégalie. Suppl. Vert., Mamm. 1: 96.

Some taxa of red colobus:

- (a) Temminck's Red Colobus *Procolobus badius temminckii*.
- (b) Niger Delta Red Colobus *Procolobus (pennantii?) epieni*.
- (c) Tana River Red Colobus *Procolobus rufomitratatus rufomitratatus*.
- (d) Preuss's Red Colobus *Procolobus preussi*.
- (e) Ashy Red Colobus *Procolobus rufomitratatus tephrosceles*.
- (f) Udzungwa Red Colobus *Procolobus gordonorum*.
- (g) Tshuapa Red Colobus *Procolobus rufomitratatus tholloni*.
- (h) Kivu Red Colobus *Procolobus rufomitratatus foai*.
- (i) Zanzibar Red Colobus *Procolobus kirkii*.

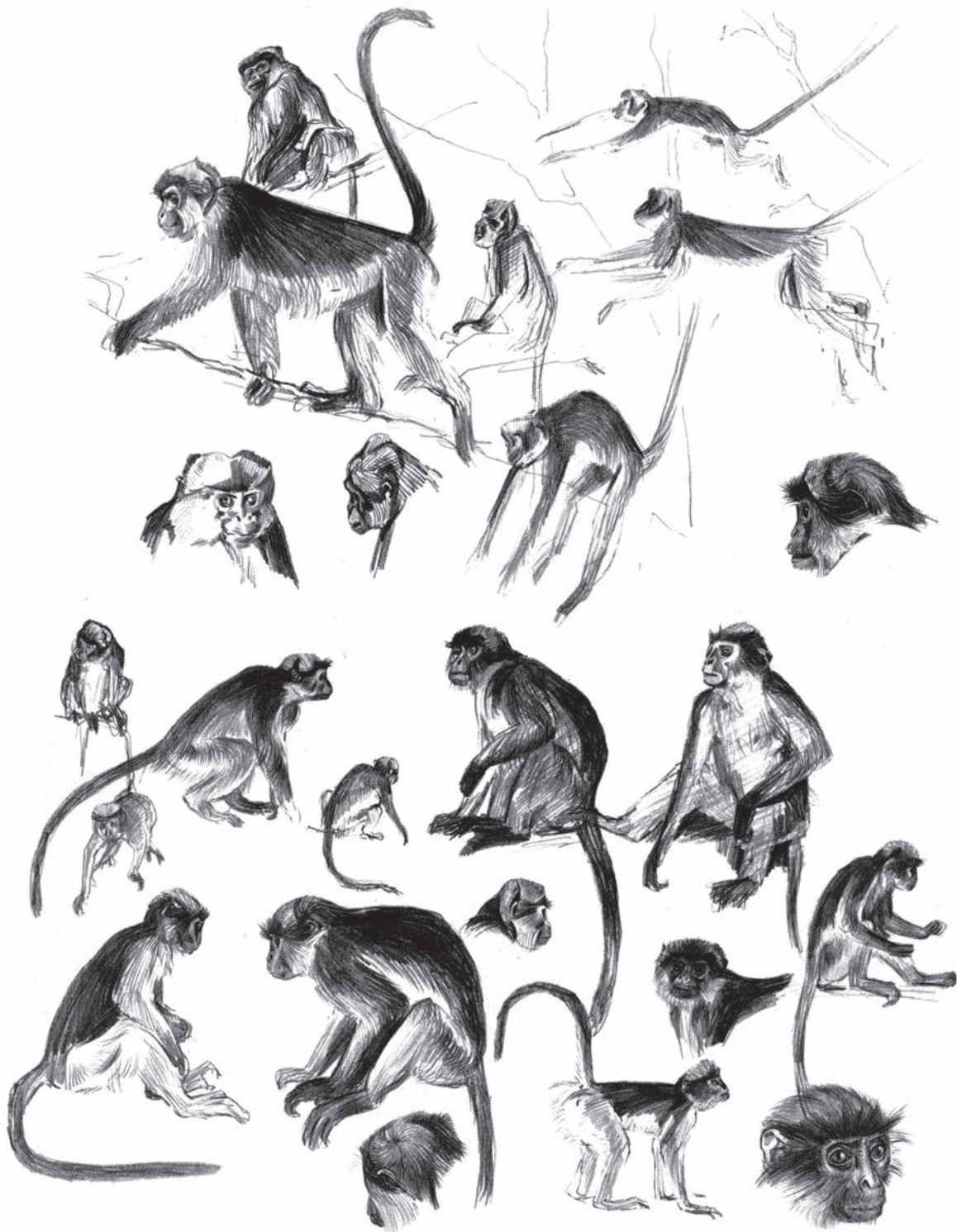


Polytypic subgenus endemic to the forests of tropical Africa. The various taxonomies applied to this subgenus are reviewed in Grubb *et al.* (2003) and in Ting (2008b). This volume, very provisionally, recognizes six species of red colobus monkeys and 18 taxa:

- P. badius* Western Red Colobus. Includes *P. b. badius*, *P. b. temminckii* and *P. b. waldroneae*.
- P. preussi* Preuss's Red Colobus.
- P. pennantii* Pennant's Red Colobus. Includes *P. p. pennantii*, *P. p. bouvieri* and possibly *P. p. epieni*.
- P. rufomitratatus* Eastern Red Colobus. Includes *P. r. rufomitratatus*, *P. r. tholloni*, *P. r. oustaleti*, *P. r. langi*, *P. r. ellioti*, *P. r. lulindicus*, *P. r. foai*, *P. r. parmentieri* and *P. r. tephrosceles*.
- P. gordonorum* Udzungwa (or Iringa) Red Colobus.
- P. kirkii* Zanzibar Red Colobus.

The last ancestor for *Procolobus* and *Piliocolobus* is estimated at 9.4–4.4 mya (Roos *et al.* 2011) and 9.1 mya (Perelman *et al.* 2011). *Piliocolobus* differs from nominotypical *Procolobus* in numerous cranial features (Verheyen 1962, Groves 2001, 2007b, Cardini & Elton 2009). These include the following:

- 1 Jaws prognathous; strong straight supraorbital ridges; suborbital fossa present; pyriform aperture margins rounded; no anterior nasal spine; posterior palatal canals shallow; choanae and pterygoid fossa narrow, and basisphenoid crested and bordered laterally by gutters.
- 2 Mandible lacks a symphyseal foramen; upper incisors with no incisor cingulum or tubercle; no tuberculum sextum on posterior lower molar.
- 3 Pelage usually includes varying amounts of reddish-brown or orange, depending on the taxon, and most taxa lack agouti



Ashy Red Colobus *Procolobus rufomitratus tephrosceles*.

banding. The second and fourth fingers are not shortened, and all fingers have flat nails.

Red colobus monkeys have long presented one of the thorniest taxonomic problems among the African primates (Grubb *et al.* 2003, Ting 2008a, b, Cardini & Elton 2009, Struhsaker 2010). There is little doubt that they are a monophyletic group, within which there is a

complex pattern of variation distributed across many allopatric forms (none are sympatric) spread across equatorial Africa from Senegal and Bioko I., Equatorial Guinea, to Zanzibar I., Tanzania. However, these different forms show more variability than would be expected from a single species. In colour pattern, some populations of red colobus differ at least as much as related species of *Colobus* or *Cercopithecus*, and there are probably many different species (Kingdon 1997, Groves

2001, 2005c, 2007b). Regional variation in vocalizations also suggest that there are several species. Struhsaker (1981b, 2010) grouped 12 red colobus taxa on the basis of similarities in 11 calls that are common to one or more of these taxa. An additional six taxa, for which the vocal repertoire remains unknown, were placed in a particular group on the basis of geographical distribution, coat colour, cranial features, and the opinions of others. The resultant seven groups are:

(*temminckii*, *badius*, *waldroneae*) (*preussi*) (*pennantii*) (*bouvieri* ?status) (*epieni*, *tholloni*, *foai*, *langi*, *lulindicus*, *oustaleti*, *elliotti* = *semlikiensis*?, *parmentieri*, *tephrosceles*, *rufomitratu*s) (*gordonorum*) (*kirkii*).

*Procolobus rufomitratu*s is very diverse, because of cranial features and considerable geographic isolation. The nominate form *P. r. rufomitratu*s has itself been treated as a distinct species, yet in vocalizations and colour pattern it is particularly similar to its nearest (but distant) neighbour to the west, *P. r. tephrosceles*. Populations of *P. r. sceles*, *P. r. elliotti* and *P. r. oustaleti* are in close proximity near the border of DR Congo and Uganda, and have suggestive similarities in colour pattern as well as in vocalizations. *Procolobus r. oustaleti* is particularly variable and may be divisible into further races.

The subspecies *P. r. langi*, *P. r. elliotti* (including *semlikiensis*), *P. r. lulindicus* and *P. r. foai* intergrade in a complex pattern (Colyn 1991), and not all are considered valid by some authors (Groves 2001, 2007b, Struhsaker 2010). These four subspecies, together with *P. r. parmentieri*, make up the informal *foai*-Subgroup, whose distribution is constrained by the Aruwimi–Ituri and Lomami Rivers, and Western Rift Valley.

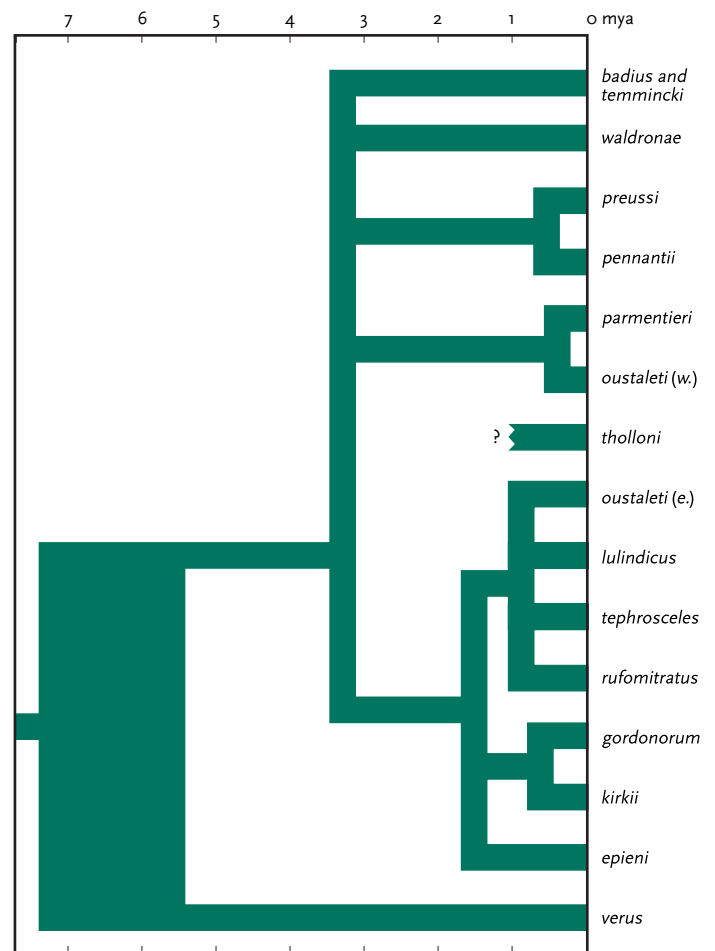
Procolobus r. tholloni is treated as a species by Groves (2001, 2007b) and is unlike other red colobus in the extent of its bright orange colouration. According to Colyn (1991) and Struhsaker (2010), however, *tholloni* is related to the *foai*-Subgroup within the *P. r. (rufomitratu*s) Group.

Procolobus gordonorum is akin to *P. kirkii* in vocalizations (Struhsaker 2010) and some aspects of the pelage and cranium (Cardini & Elton 2009). Molecular data indicate that *P. gordonorum* and *P. kirkii* diverged ca. 0.6 mya (Ting 2008a, b).

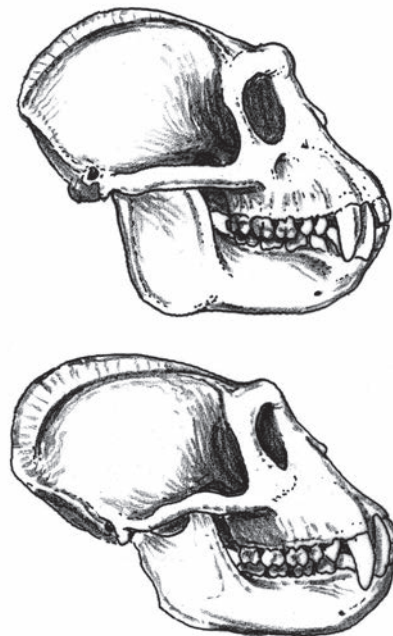
Procolobus p. preussi is regarded as a separate species by some authors (Groves 1989, 2001, 2005c, 2007b, Kingdon 1997, Oates 2011) as it is distinctive and separated from the nearest population of *P. pennantii* (i.e. *P. p. pennantii* on S Bioko I.) by ca. 250 km (Oates *et al.* 2004), which includes the ca. 32 km stretch of water (Atlantic Ocean) that separates Bioko I. from Cameroon. The molecular data indicate that *pennantii* and *preussi* diverged ca. 0.3 mya (Ting 2008a, b). *Mammals of Africa* treats *preussi* as a full species (for details, see the *P. preussi* profile). Thus, the number of species of red colobus tentatively recognized in this volume is six.

After the profiles in this volume were prepared for publication, Ting's (2008b) dissertation on *Procolobus* molecular systematics became available. Here are some of the more important findings put forth in this dissertation:

1. The close relationship between *badius* and *temminckii* is further supported by a divergent time estimated to be 0.3 mya.



Tentative phylogenetic tree for extant red colobus *Procolobus* (after Ting 2008a, b).



Red colobus adult male skulls showing short muzzle (Oustalet's Red Colobus *Procolobus rufomitratu oustaleti*) (above) and long muzzle (Tshuapa Red Colobus *Procolobus rufomitratu tholloni*) (below).

2. The form *epieni* (Niger Delta) appears to be much more closely related to the red colobus of central and East Africa (e.g. *rufomitratus*, *kirkii* and *gordonorum*) than to those of West and west-central Africa (e.g. *pennantii* and *preussi*). This supports the relationships as discerned from the data on vocalizations (Struhsaker 2010). Unlike earlier taxonomies, however, Ting (2008b) treats *epieni* as a full species. This is based on the considerable (i.e. species-level) mitochondrial divergence that he observed for *epieni*.
3. The form *waldronae* may represent a relatively ancient and distinct mitochondrial lineage, perhaps with a divergent time of 3 mya. If so, this supports the taxonomies of Dandelot (1974) and Groves

(2007b), which, based on pelage and morphology, give *waldronae* full species status.

4. The available molecular data do not support the designation of either *preussi* or *gordonorum* as presented in this volume.

See Struhsaker (2010) for additional information on the taxonomy, demography, behaviour, ecology and conservation of *Procolobus* spp., particularly *P. t. tephrosceles*.

Peter Grubb, Thomas T. Struhsaker & Kirstin S. Siex

Procolobus badius WESTERN RED COLOBUS (BAY COLOBUS)

Fr. Colobe bai d'Afrique occidentale; Ger. Westafrikanischer Stummelaffe

Procolobus badius (Kerr, 1792). Animal Kingdom, p. 74. Sierra Leone (probably Sherbro I.).



Bay Colobus *Procolobus badius badius* adult male.

Taxonomy Polytypic species. *Procolobus badius* formerly comprising most or all red colobus (Schwarz 1928a, Napier & Napier 1967, Wolfheim 1983, Napier 1985). Here restricted to three West African subspecies: *P. b. temminckii*, *P. b. badius* and *P. b. waldronae* (Kingdon 1997, Groves 2001, 2005c, Grubb *et al.* 1998, 2003). Note that 'waldroni' is 'corrected' to 'waldronae'. Relatedness of *temminckii*, *badius* and *waldronae*, supported by studies of Struhsaker (1981b, 2010), Ting (2008a,b) and Cardini & Elton (2009). Dandelot (1974), Groves (2007b) and Oates (2011) consider *waldronae* to be a full species. Rahm (1970) regarded *P. preussi* as a subspecies of *P. badius* but Groves (1989) pointed out that *preussi* is distinct and, subsequently, treated this taxon as a species (Groves 1993, 2001, 2005c, 2007b), as have Kingdon (1997), Cardini & Elton (2009), Struhsaker (2010), Oates (2011) and the present volume. Synonyms: *ferruginea*, *ferruginosus*, *fuliginosus*, *rufo-fuliginosus*, *rufoniger*, *temminckii*, *waldronae*. Chromosome number: $2n = 44$ (Romagno 2001).

Description Medium-size, arboreal monkey with crown and back the same colour, no whorl of hair behind ears, cheeks the same colour as lower limbs, and tail not red. Sexes alike in colour. Only slight sexual dimorphism; mean weight of adult ♀♀ about 92% that of adult ♂♂. Canines of adult ♂ only moderately larger than

those of adult ♀. Face relatively flat, dark bluish-grey to black with pink margins around mouth, eyes and nostrils (although contrast less prominent in some older animals). Area surrounding nostrils appears raised or swollen (although individuals vary in the degree to which nasal margins are raised, particularly in *C. b. waldronae*). Crown glossy black or ashy-grey, with red, if any, confined to small areas above and behind ear or behind brow. Cheeks, sides of neck, lower limbs, inner limbs, flanks, hands and feet orange-ochre to deep mahogany-red. Ventrums orange-ochre, mahogany-red, or whitish, depending on the subspecies. Dorsum, upper arms and upper legs glossy black or ashy-grey. Tail red, reddish-brown, or black. Unlike other *Procolobus* (*Piliocolobus*) species, there is little or no white in the pelage and 'crown whorls' are absent. Infant dorsum grey; tail with reddish tint; ventrum whitish (Groves 2007b).

Geographic Variation

P. b. badius Bay Colobus or Upper Guinea Red Colobus. S Guinea, Sierra Leone and Liberia to W Côte d'Ivoire. Nostrils raised on a swelling of nasal septum. Cheeks, flanks, lower limbs, ventrum, hands and feet mahogany-red. Dorsum and upper limbs glossy black. Tail dark brown over basal half, black distally, or all black. Perineal region and inside of thighs with patch of white hairs. Adult ♀ has large sexual swelling.

P. b. temminckii Temminck's Red Colobus. SW Senegal, Gambia, Guinea-Bissau and Guinea. Much the same pattern as *P. b. badius* but considerably paler or 'washed-out'. Face dusky, grey to grey-black with pinkish circum-orbital patches and muzzle patches from the lower lip to the top of the nostrils (Starin 1991). Cheeks, sides of neck, lower limbs, hands, feet, sides of belly orange-ochre (north-west extreme of range) to russet-brown or red (south part of range). Brow and nape with patches of orange-ochre. Dorsum, upper limbs and thighs slaty to ashy-grey (north-west extreme of range) to charcoal or black (south part of range). Tail rusty or orange-brown. Fingers and toes rufous. Midline of underlimbs and ventrum light orange-red to grey to whitish. Perineal region and insides of thighs with patch of white hairs. Geographically variable; in particular, animals in the relatively dry, open, Fathala Forest, Delta N. P., SW Senegal, at the north-west extreme of the

range are much paler than those from all (wetter) sites farther south (Galat-Luong & Galat 2005, A. Galat-Luong & G. Galat pers. comm.).

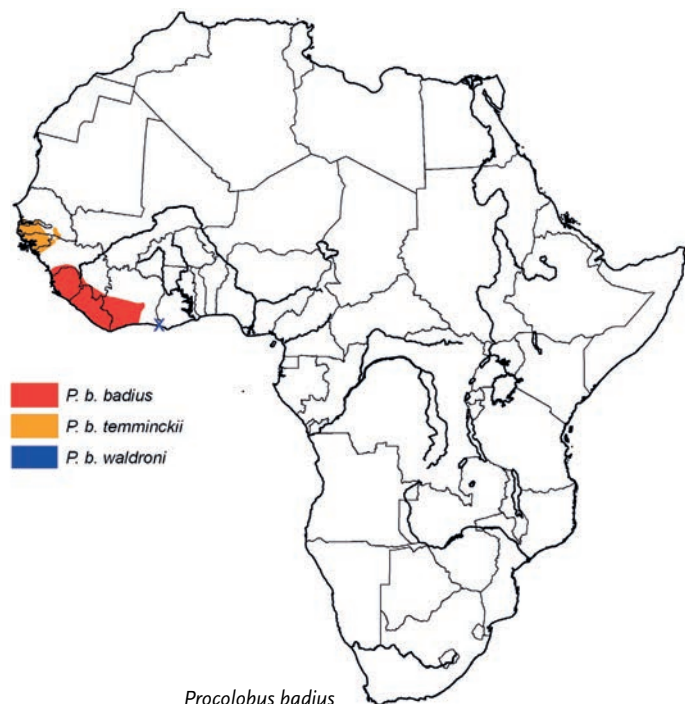
P. b. waldronae Miss Waldron's Red Colobus. SC Côte d'Ivoire to SW Ghana. Similar to *P. b. badius* but (1) nose flatter, without raised fleshy base, (2) tail all black, (3) forehead and outer thighs mahogany-red, (4) ears with reddish tuft above, (5) brow with reddish patch behind, and (6) scrotum white.

Similar Species None within geographic range.

Distribution Endemic to West Africa. Rainforest BZ, including the 'Northern Rainforest-Savanna Mosaic'. From SW Senegal and Gambia southeastwards to SW Ghana (Booth 1956b, 1958b, Rahm 1970, Wolfheim 1983, Lee *et al.* 1988, Groves 2007b). Distribution maps for *P. badius* in Ghana, Sierra Leone and Gambia presented in Grubb *et al.* (1998). Distribution map for *P. badius temminckii* over the northern part of the range (Senegal and Gambia) presented in Galat *et al.* (2009). Known northern limit (SW Senegal) for *P. b. temminckii* is 13° 50' N. Known western limit (SW Senegal) for *P. b. temminckii* is 16° 30' W. Known eastern limit (SC Senegal) for *P. b. temminckii* is 13° 15' W (Gatinot 1974, 1976). In fringing or gallery forests in Gambia, Senegal and Guinea-Bissau.

P. b. badius: Sierra Leone, adjacent parts of SE Guinea and Liberia to Nzi-Bandama R. System, W Côte d'Ivoire. Known limits are from 09° 00' N, 12° 35' W (Rokupr, Sierra Leone) to the Bandama R. (Groves 2007b).

P. b. temminckii: S Senegal, Gambia, E and S Guinea-Bissau, NW Guinea and NW Sierra Leone (Galat *et al.* 2009). In SC Guinea Bissau, present east of the Rio Grande (Rio Corubal) at Catio (Monard 1938), and close to the border with Guinea in the Cantanhez Forest and Cacine Basin (Gippoliti & Dell'Omo 1996).



Mapped from the Fouta Djallon in Guinea (Booth 1958b), from which no other published records are available. Reported from NW Sierra Leone (Harding 1984a) but otherwise geographically isolated from *P. b. badius*.

P. b. waldronae: from Nzi-Bandama R. System SC Côte d'Ivoire eastwards to SW Ghana. Separated from *P. b. badius* by the Nzi-Bandama R. System. Now perhaps extinct (see below).

Habitat *Procolobus b. badius* and *P. b. waldronae* prefer undisturbed, dense, primary, moist lowland forest with tall, emergent trees (Booth 1956b, 1958b, Struhsaker 1975, Wolfheim 1983, Grubb *et al.* 1998, Galat-Luong & Galat 2005). *Procolobus b. temminckii* is unusual among red colobus (with the exception of the Tana River Red Colobus *Procolobus rufomitratus rufomitratus* of Kenya) in that it inhabits relatively dry, 'fringe', deciduous forest and savanna woodland and gallery forest, although also present in moist, dense, lowland forest, mangrove forest (swamp) and perennial gardens (Booth 1958b, Struhsaker 1975, Gatinot 1976, Dupuy & Verschuren 1977, Gunderson 1977, Starin 1981, 1991, Harding 1984a, b, Galat-Luong & Galat 2005, Galat *et al.* 2009, McGraw & Sciulli 2011). At Saloum Delta N. P., SW Senegal (13° 41' N, 16° 30' W, 76 km², 6–16 m asl), on the north-western extreme of the geographic range of *P. b. temminckii* (and of the range for the genus *Procolobus*), groups were encountered 60% of the time in closed habitat and 39% of the time in open habitat (n = 213, Galat-Luong & Galat 2005).

Mean temperature in Fathala Forest is 26.5 °C and mean annual rainfall was 1050 mm during 1950–70 (Gatinot 1976, 1977), 904 mm during 1963–73, and 738 mm during 1987–97 (Galat-Luong & Galat 2005, Galat *et al.* 2009). The wet season is from Jun–Oct. *Procolobus b. temminckii* is present in Abuko Nature Reserve (107 ha, 5–16 m asl, 13° 24' N, 16° 00' W), W Gambia, where the mean daily minimum temperature is ca. 20 °C, mean daily maximum temperature is ca. 30 °C. During the course of one year, the lowest temperature recorded was 11 °C (Jan), and the highest was 41 °C (Mar). Mean annual rainfall was 1181 mm (range 582–1854) from 1946–79, but has declined by >300 mm per year since 1979 (Galat *et al.* 2009). The single wet season is from mid-Jun to mid-Oct, with Aug being the wettest month (Gunderson 1977, Starin 1994, 1999). Mean relative humidity ranges from 51% (Feb) to 87% (Aug) (Gunderson 1977). *Procolobus b. temminckii* also in the Kilimi area (240 km², ca. 200 m asl, 09° 43' N, 12° 32' W), NW Sierra Leone. Here, mean daily temperature is between 21 °C and 27 °C, and temperatures range from 18 to 38 °C. Mean annual rainfall is ca. 2160 mm (Harding 1984a, b). Most populations of *P. b. temminckii* are found <50 m asl (A. Galat-Luong & G. Galat pers. comm.). The highest reported altitude is ca. 200 m asl (Kilimi area, Harding 1984).

Procolobus b. badius occurs in Tai Forest, SW Côte d'Ivoire (4540 km², 125–370 m asl), where mean annual rainfall is ca. 1990 mm, and mean monthly minimum and maximum temperatures are ca. 20 °C and 30 °C, respectively. The wet season here is from Mar through Oct (Galat & Galat-Luong 1985). At Mt Nimba, Guinea, *P. b. badius* known to occur from near sea level to ca. 900 m (Galat-Luong & Galat 1990). During the dry season, mean temperature at high altitude varies between 15 °C and 20 °C, and to below 10 °C during the wet season. Mean annual rainfall is ca. 2500 mm (A. Galat-Luong & G. Galat pers. comm.).

Abundance Density of *P. b. temminckii* 45–480 ind/km² in W Senegal (Gatinot 1975). Gunderson (1977) found 310–880 ind/km² in Abuko Nature Reserve, while a later study by Starin (1991, 1994) found 124 ind/km². Density in Pirang Forest Park (64 ha), W Gambia, was 81 ind/km² (Galat-Luong 1988). Density of *P. b. badius* is 180 ind/km² in Taï N. P., Côte d'Ivoire, and 49–70 ind/km² at Tiwai I., Sierra Leone (Oates *et al.* 1990). Galat & Galat-Luong (1985) recorded a density of 37 ind/km² in Taï Forest. See also Zuberbühler & Jenny (2007) and N'Goran *et al.* (2012). Of the seven species of monkeys in Taï, *P. b. badius* is the most common, comprising about 33% of the monkey population. These densities are not typical of most parts of the range as *P. badius* is intensively hunted in many areas. *Procolobus b. waldronae* has been effectively exterminated by habitat loss and hunting (see Conservation section).

Adaptations Diurnal and arboreal. In Abuko Nature Reserve, during the dry season, there are activity/foraging peaks from 8:00–10:00h and from 16:00–18:00h. The activity peaks were much less prominent during the wet season (Gunderson 1977).

During a 30-year study of *P. b. temminckii* in Fathala Forest, Galat-Luong & Galat (2005) identified five changes in behaviour that enhanced the survivorship of the ca. 560 individuals in that population. In spite of a >50% reduction in the area of forest and a >30% decline in woody species diversity, the size of this populations dropped by only 12% between 1974–76 and 2002. They attributed this survival to five major adaptive shifts, namely: (1) increased frugivory; (2) greater terrestriality; (3) a higher tendency to form polyspecific associations with Green Monkeys *Chlorocebus sebaeus*; (4) increased use of more open habitat; and (5) adoption of mangrove forest as both a refuge and source of food.

'Gloger's Rule' states that colour tones darken with increasingly humid environments. Both *P. b. badius* and *P. b. waldronae* live in relatively tall, dense, dark primary moist forest. The colouring of *P. b. badius* and *P. b. waldronae* represents an extreme among red colobus, being made up of intensely black upperparts and strongly contrasting mahogany-red cheeks, lower limbs and ventrum. The geometry of these contrasts and the intensity of fully saturated black and red pigmentation suggest intra-specific selection for strong visual emphasis of gestures and of positioning of the limbs. The evolution, in many taxa of animals, of bright species-specific colouring is correlated with ritualized positional behaviours and displays. It appears that intra-specific selection for unambiguous postures and gestures (in the relatively dense and dark primary moist forest) has been stronger in *P. b. badius* and *P. b. waldronae* than has selection for crypsis against predators. This cannot be said for *P. b. temminckii*. This subspecies has a pale grey and ochre tinted pelage and occupies much drier, more open, lower canopy forests on the north-western margins of the species' range. Here, far better visibility and selective pressures imposed by visual predators (e.g. African Crowned Eagle *Stephanoaetus coronatus* and Leopard *Panthera pardus*) are likely explanations for the 'faded' tints that show much less colour or tonal contrast.

Foraging and Food Folivorous. *Procolobus b. temminckii* spends ca. 21% of time feeding, although this varies on a monthly basis (range 13.8–34.7%) (Starin 1991). Fruits and seeds comprise the

majority of the diet for *P. b. temminckii* (35.9% in Fathala Forest and 41.6% in Abuko Nature Reserve), followed by young leaves (24.0% and 26.2%, respectively), leaf buds (17.5% and 8.7%, respectively), mature leaves (5.4% and 11.7%, respectively) and floral parts (8.7% and 8.6%, respectively) (n = 1488; Gatinot 1977). In a second study in Fathala Forest, the diet comprised 56.7% young leaves, 18.8% fruits, 13.4% leaf buds, 6.3% mature leaves, 0.8% flowers and 4.0% other items (n = 1875; Diouck 1999). Fruit dominates the diet during the rainy season, young leaves and leaf buds during the dry season in Abuko Nature Reserve (Starin 1991). All three of these studies found that *P. b. temminckii* eats far more fruit and seed than reported for other forms of *Procolobus*. In contrast, one study in Taï Forest, found that leaves comprised the bulk of the diet of *P. b. badius* (83.5%), followed by fruit (10.4%) (n = 230 observations; Galat & Galat-Luong 1985). A second study, however, found that fruit comprised ca. 30% of the diet (Korstjens *et al.* 2007).

In Abuko Nature Reserve, items from 105 plant species are consumed (Starin 1991), but only 39 plant species were reported consumed in Fathala Forest (Gatinot 1977). In Fathala Forest, the top ten, top five and top one food species account for 89.9%, 77.5% and 43.6% of the annual diet, respectively (Gatinot 1977, n = 1 group). Here the most frequently eaten species was *Erythrophleum guineense*, followed by *Pterocarpus erinaceus*, *Ficus glumosa* and *Detarium senegalense*. A second study in Fathala Forest found that leaves are most often eaten from *E. guineense*, *Terminalia macroptera*, *Dichrostachys glomerata*, *P. erinaceus* and *Celtis integrifolia* (Galat-Luong & Galat 2005). In Abuko Nature Reserve, the diet is more diverse, with the top ten, top five and top one food species accounting for 61.2%, 44.1% and 12.6%, respectively (n = 1 group). The most common food species in Abuko Nature Reserve include *Parinari excelsa*, *Ficus trichopoda*, *D. senegalense*, *Parkia biglobosa* and *Pseudospondias microcarpa*. Feeding on soil from termite mounds occurs at Abuko Nature Reserve (Starin 1991).

In Fathala Forest, Gatinot (1975) found *P. b. temminckii* at a mean height of 9.4 m, while Diouck (1999) found the mean height to be 5.1 m during the wet season and 5.8 m during the dry season (n = 7077 records). In Abuko Nature Reserve, 61% of observations (n = 99) in canopy. In Pirang Forest Park, 80% of observations (n = 298) in canopy. In Taï N. P., 92% of observations (n = 1903) in canopy (Galat-Luong 1988). See also McGraw (1998, 2007).

Procolobus b. temminckii in Fathala Forest, Pirang Forest Park and Abuko Nature Reserve live in a much more open habitat (i.e. dry forest, gallery forest and woodland). The amount of time spent on the ground varied from 1 to 4% for Fathala Forest (Diouck 1999), 2.4% for Pirang Forest Park (n = 298) and 15% for Abuko Nature Reserve (n = 99; Galat-Luong 1988, Galat-Luong & Galat 2005). At Fathala Forest, groups sometimes move >2 km across open ground to temporarily occupy small patches of isolated forest (Galat-Luong 1988).

Size of group home-ranges for *P. b. temminckii* was 9.0–19.7 ha (n = 7) in Fathala Forest (Gatinot 1975, Diouck *et al.* 1996, Galat-Luong & Galat 2005) and 4.3–12.8 ha in Abuko Nature Reserve (n = 3; Gunderson 1977). A later, long-term (5.5 years) study in Abuko Nature Reserve found group home-ranges of 11–34 ha (mean = 22 ha, n = 3). The main study group had a home-range of 34 ha, of which >60% was shared with two other groups. A second

group, with a home-range of 11 ha, shared >62% of its home-range with other groups (Starin 1991, 1994). Home-range size for one group of *P. b. badius* in Tai Forest was 100 ha (Galat & Galat-Luong 1985). See also Korstjens *et al.* (2007).

Social and Reproductive Behaviour Social. Live in multimale-multifemale groups. Mean size of *P. b. badius* groups in Tai Forest was 36.8 (8–70, $n=17$); Galat & Galat-Luong 1985), but groups of >90 animals occur (Korstjens *et al.* 2007). Groups of 20–>60 present in Gola F. R., Sierra Leone (Davies 1987). Groups of >100 in Sierra Leone up to the 1950s (Grubb *et al.* 1998). Mean size of *P. b. temminckii* groups in Fathala Forest was 29 (14–62, $n=22$) in 1973 (Gatinot 1975), 18 (9–38, $n=14$) in 1990–94 and 16 in 1996–2002 (Galat-Luong & Galat 2005). In Abuko Nature Reserve, mean group size was 34 (24–40, $n=3$) in one study (Gunderson 1977). A later study found mean group size at Abuko Nature Reserve to be 23 (14–32, $n=5$; Starin 1991, 1994). Mean size of three groups in the Pirang Forest Park was 18 (17–20). All eight groups observed in Cantanhez Forest comprised >25 individuals (Gippoliti & Dell’Omo 1996). Mean size of five groups in Kilimi area was 7.5, with the largest group comprising 20 individuals (Harding 1984a, b). Solitary individuals reported in Abuko Nature Reserve, Fathala Forest, Cantanhez Forest and Kilimi area (Harding 1984, Starin 1994, Gippoliti & Dell’Omo 1996, Galat-Luong & Galat 2005).

In Abuko Nature Reserve, groups of *P. b. temminckii* contain 1–5 adult ♂♂ and 9–14 adult ♀♀ plus young (Starin 1991, 1994). Group adult sex ratio varies from 2.0 to 7.0 ♀ : ♂ ($n=16$; Gatinot 1977, Starin 1991). No apparent bias in infant sex ratio ($n=28$ infants; Starin 1991). In Tai Forest, one group of 32 *P. b. badius* had three adult ♂♂ and 13 adult ♀♀, while a group of 37 had about nine adult ♂♂ and ten adult ♀♀. Mean number of adult ♀♀ per adult ♂ was 3.3 ($n=6$ groups). Mean number of immatures per adult was 0.7 ($n=10$; Galat-Luong & Galat 2005).

Procolobus b. temminckii spend ca. 52% of the time resting, 21% feeding, 13% moving, 7% playing and 6% grooming ($n=1$ group; Starin 1991). Time spent in resting and feeding varies more among individuals than among age-sex classes. Adult ♀♀ are the predominant groomers and adult ♂♂ are the main recipients of grooming. Play is conducted mainly by infants and juveniles, mostly in the trees (only ca. 1% of play occurs on the ground). Infant ♂♂ play more than do infant ♀♀; conversely juvenile, subadult and adult ♀♀ play more than do ♂♂ of the same age categories (Starin 1991). See McGraw (1996, 2007a) and McGraw & Sciulli (2011) for activity budget and positional behaviour of *P. b. badius* in Tai Forest.

Procolobus b. temminckii subadult ♂♂ and (surprisingly) subadult ♀♀ both move between groups. During one long-term (5.5 years) study at Abuko Nature Reserve, 12 subadult ♀♀ permanently emigrated from their natal group, ten subadult ♀♀ permanently immigrated, and six subadult ♀♀ temporarily moved into or out of the focal group (Starin 1991, 1994). Movement of ♀♀ appears to be voluntary and not the result of overt competition and aggression. Their transfer is immediate and with little aggression. Of the 11 subadult ♀♀ who left the focal group, eight travelled in the immediate company of age mates; not spending time as solitary or extra-group ♀♀. Ten of these 11 ♀♀ eventually ended up in a

group with at least one fellow natal group mate. In contrast, six of seven subadult ♂♂ in the focal group were aggressively forced out of the group. All six spent time as ‘adolescent exiles’ and four, perhaps five, returned to their natal group once a resident adult ♂ died or disappeared. Males prefer to rejoin their natal group, probably because joining a ‘strange’ group can be fatal. Two ♂♂ were killed, and another two ♂♂ were probably killed, while attempting to join an alien group. Both of the attacks that led to killings were initiated and maintained by the resident adult ♀♀, and the killings were, in each case, conducted by a single adult ♂ and multiple adult ♀♀. In addition, six solitary ‘alien’ ♂♂ were chased from the focal group. In all instances the initial aggressive response was by immature ♀♀ and immature ♂♂ screaming, or by adult ♀♀ screaming and/or chasing the alien ♂. Exiled ♂♂ lived alone, with an older ♂, with a ♀, or with a natal group ♂ for >1–26 months before joining a group ($n=7$).

The great majority of copulations with fully swollen ♀♀ are performed by one ♂. These ‘chief copulators’, however, usually change from breeding season to breeding season (Starin 1994).

Group composition varies over the short term with the formation, by adult ♀♀, of subunits, indicating a fission-fusion sociality (Gunderson 1977, Starin 1991, 1994, Diouck *et al.* 1996, Galat-Luong & Galat 2005). Territorial behaviour not observed although aggressive encounters between groups occur. Adult ♂♂ and adult ♀♀ both participate in these aggressive inter-group encounters (Starin 1991, 1994, Galat-Luong & Galat 2005). For further detail on social and reproductive behaviour see Gatinot (1977), Starin (1991, 1994, 2001) and Galat-Luong & Galat (2005).

From 1990–2002, Galat-Luong & Galat (2005) found *P. b. temminckii* groups in Fathala Forest to be in polyspecific associations during 35.7% of 171 encounters; 10.5% of these associations were with Patas Monkeys *Erythrocebus patas* and 89.5% were with *C. sabaeus*. All three species were in association on one occasion. Pourrut *et al.* (1996), during 114 encounters with groups of *P. b. temminckii* in Fathala Forest, found *P. b. temminckii* + *C. sabaeus* 39% of the time, and *P. b. temminckii* + *C. sabaeus* + *E. patas* 6% of the time. No observations were made of *P. b. temminckii* + *C. patas* only. Diouck (1999) encountered 64 polyspecific associations at Fathala Forest. Of these, 95% were of *P. b. temminckii* + *C. sabaeus*, 3% were of *P. b. temminckii* + *E. patas* and 2% were of all three species. In Kilimi area, *P. b. temminckii* were consistently associated with King Colobus *Colobus polykomos* (Harding 1984a). In Tai Forest, *P. b. badius* groups in polyspecific associations during 87% of 67 encounters; most frequently with Diana Monkey *Cercopithecus (d.) diana* (55% of encounters), followed by Lesser Spot-nosed Monkey *Cercopithecus (c.) petaurista* (43%) and Campbell’s Monkey *Cercopithecus (m.) campbelli* (31%) (Galat & Galat-Luong 1985). See also McGraw *et al.* (2007).

Procolobus badius has a distinctive vocal repertoire (Struhsaker 1975, 1981b, 2010). *Procolobus b. temminckii* give the following calls: ‘chirp’, ‘nyow (bark)’, ‘yelp’, ‘squeal (scream)’, ‘sneeze (cough)’, ‘sqwack’, ‘rraugh’, ‘whine’, ‘quaver’, ‘wa-ah!’, ‘wa!’, ‘woo’, ‘ack’, ‘eh!’ and ‘copulation quavers’, most of which are shared with *P. b. badius*. The vocal repertoires of *P. b. temminckii* and *P. b. badius* do, however, differ somewhat. For example, the ‘wa-ah’ and ‘whine’ of *P. b. temminckii* are not known to be given by *P. b. badius* (Struhsaker 1975, 2010, Starin 1991, Galat-Luong & Galat 2005). The ‘chist’ and ‘wheet’ are notably absent from the vocal repertoire of *P. badius*. See



Temminck's Red Colobus *Procolobus badius temminckii* adult female (left) and Bay Colobus *Procolobus badius badius* adult male (right).

Struhsaker (1975, 1981b, 2010) and Starin (1991) for information on the circumstances and functions of some of these vocalizations.

Reproduction and Population Structure Male *P. b. temminckii* in Abuko Nature Reserve begin reproducing at ca. 28 months (range 26–30, $n = 4$). Females begin reproducing at ca. 34 months (range 30.8–38.8, $n = 4$), with the first infant born at ca. 50 months (range 24–60, $n = 4$). Mean inter-birth interval is 29.4 months (range 27.8–32.0, $n = 4$). Adult ♀♀ exhibit large sexual (perineal) swellings during which mating and conception occur. Full swelling lasts 4–8 days (mean = 5.4 days, median = 5 days, $n = 23$). Mean length of gestation is about 173 days ($n = 2$). Pregnant ♀♀ do not appear to avoid strenuous exercise or stressful situations. Up until the time of birth they take part in intense inter-group chases, attacks, and fights with alien (intruder) ♂♂. Eight of nine infants at Abuko Nature Reserve were born during the night or early morning (19:00–07:00h), while only one was born during the daylight hours (sometime between 07:45 and 13:00h). Six of seven nulliparous ♀♀ left the group for a period of 1–9 days after giving birth. In contrast, none of the seven multiparous ♀♀ left the group just before or after giving birth. Neonates are licked clean and the placenta is probably eaten by the mother immediately after being expelled (Starin 1988, 1991).

The majority of conceptions in Abuko Nature Reserve take place during times of high precipitation and humidity, rising temperatures, increasing day length, and when diets are rich in fruit and flowers. Births are seasonal, occurring primarily during the dry season. There is considerable intra-group synchrony in the time of births. Infant mortality is high (ca. 21%) during the first five months of life ($n = 28$). After the first five months, mortality for ♂♂ was 0% up until their third or fourth year, and mortality for ♀♀ was 0% well into adulthood. These data agree with data collected elsewhere in Abuko Nature Reserve; of the 13 non-focal group deaths, the majority were young ♂♂. There is strong indirect evidence for infanticide (dead infants with canine puncture wounds). In one group, of six infants below the age of six months that died or disappeared, two (perhaps three) were the victims of infanticide. Live to at least 16 years in the wild (Starin 1991, 1994).

Male *P. b. temminckii* are multiple mounters. Although the majority of ♀♀ mate with many ♂♂, including ♂♂ from other groups, they prefer the dominant ♂ (who receives the most sexual advances and the least rejections). Masturbation uncommon but observed both among ♂♂ and ♀♀ at Abuko Nature Reserve (Starin 2004).

Predators, Parasites and Diseases Four percent of 215 Leopard scats in Tāi N. P. held *P. b. badius* (Hoppe-Dominik 1984). In another study, 10% of 215 scats held *P. b. badius* (Zuberbühler & Jenny 2007). Here, 80% of the prey of Robust Chimpanzees *Pan troglodytes* were *P. b. badius* (Boesch & Boesch-Achermann 2000; see also Bshary 2007). *P. troglodytes* kill ca. 3–4% of this population each year (Shultz *et al.* 2004). Predation by African Crowned Eagles on *P. b. badius* is well documented for Tāi N. P. (Shultz 2001, McGraw *et al.* 2006a, Shultz & Thomsett 2007). Shultz *et al.* (2004) estimate that 8% of the *P. b. badius* in Tāi N. P. are killed each year by the above-mentioned three predators. Humans are, however, the primary predator (Koné & Refisch 2007, McGraw *et al.* 2007; see Conservation section). In Abuko Nature Reserve, from 1978–1983, Nile Crocodile *Crocodylus niloticus* and Central African Rock Python *Python sebae* account for 40% of known deaths of *P. b. temminckii*; two young adult ♂♂ killed by *C. niloticus* and two adult ♀♀ killed by *Python sebae*. In addition, two adult ♀♀ appeared to have died of snakebite. *Python sebae* is thought to be the most important predator for *P. b. temminckii* at this site (Starin, 1989, 1991, 1992).

The following parasites were found in 57 *P. b. temminckii* faecal samples at Fathala Forest: strongyles (present in 38.1% of faecal samples), strongyloides (5.0%) and amoeba (1.4%). There was no evidence for ascaris or trichurus. *Procolobus b. temminckii* living in core gallery forests (where they do not need to move on the ground and where human presence is less frequent) had a much lower incidence of infection (i.e. at least one of the above-listed parasites was present in 4.3% of 24 faecal samples) than those living in more open habitats and where human presence is frequent (e.g. forest boundaries and near camps where at least one of the above-listed parasites was present in 37.5% of 33 faecal samples). Whitish individuals, and individuals with areas lacking hair, observed near the largest neighbouring village. This may be the result of severe parasitism or of inadequate intake of at least one nutrient (A. Galat-Luong & G. Galat pers. comm.).

In Abuko Nature Reserve, ulcers on the penis, scrotum and groin observed on all *P. b. temminckii* breeding ♂♂ (and on some subadult ♂♂), and external mouth ulcers seen on at least five juvenile ♀♀ (Starin 2004). Mouth ulcers also reported for *P. b. temminckii* in Fathala Forest (A. Galat-Luong & G. Galat pers. comm., E. Starin pers. comm.). Mouth ulcers on ♀♀ and genital ulcers on ♂♂ present at Bijilo Forest Park, Kiang West N. P. and River Gambia N. P., Gambia (E. Starin pers. comm.).

Conservation IUCN Category(2012): Endangered as *P. badius*, *P. b. badius* and *P. b. temminckii*. Critically Endangered as *P. b. waldroneae*. CITES (2012): Appendix II.

Numbers of all three subspecies have declined throughout the range in recent decades, but details on population size and extent of decline are lacking for most sites (Wolfheim 1983, Lee *et al.* 1988). Details on the distribution of *P. b. temminckii* at the north end of the range provided by Galat *et al.* (2009), along with the reasons for the decline of this species in this region. Surviving populations are widely scattered and isolated. *Procolobus b. badius* and *P. b. waldroneae* appear to be particularly sensitive to habitat degradation and fragmentation. Like all *Procolobus* spp., *P. badius* is extremely vulnerable to hunting (Davies 1987, Lee *et al.* 1988, Starin 1989, Grubb *et al.* 1998, Struhsaker 1999, 2005, 2010, Oates *et al.* 2000a, McGraw & Oates

2002, 2007, N'Goran *et al.* 2012). This is because *Procolobus* spp. are (1) large and, therefore, provide much meat for the cost of a shotgun shell, (2) conspicuous as they are brightly coloured, noisy and live in large groups, and (3) they are often slow to detect danger or to flee from dangers (Davies 1987).

Survival of the westernmost population of *P. b. temminckii* in the Fathala Forest and Abuko Nature Reserve illustrates that some populations have the capacity to adapt their behaviour to limited levels of habitat change (see Galat-Luong & Galat 2005, Galat *et al.* 2009, and Adaptations section).

The extinction, or near extinction, of *P. b. waldronae* illustrates how vulnerable all red colobus species are in countries that exert little or no control over bushmeat hunting and the destruction of forest (Oates *et al.* 1997, McGraw 1998d, 2005, McGraw *et al.* 1998b). The known range of *P. b. waldronae* in Ghana has been searched since 1993, but no living animals have been found. Although the search continues, the last material evidence for the existence of *P. b. waldronae* in Ghana was obtained in 1972 in the form of a skin (Struhsaker & Oates 1995, Oates *et al.* 1997, Oates 2006). In early 2002, another hunter's skin raised hopes that a population of *P. b. waldronae* might still survive in or near the Ehy (=Tanoé) Forest (300 km²), extreme SE Côte d'Ivoire (McGraw & Oates 2002, 2007). Subsequent surveys, however, failed to find any evidence that *P. b. waldronae* is not extinct (Koné 2004, Koné & Akpatou 2005, McGraw 2005, Koné *et al.* 2007a, b, Oates 2011, Gonedelé Bi *et al.* 2012). The Ehy Forest seems to be the only place where a small population of *P. b. waldronae* might survive, but this forest is being logged, cleared for oil palm plantations, and heavily hunted by Ivorian and Ghanaian hunters. An urgent survey of the Ehy Forest has been called for. If extinct, *P. b. waldronae* is 'the first recorded extinction of a widely recognized primate taxon in the twentieth century, and human hunting rather than habitat loss has almost certainly been the primary cause of the monkey's extinction' (Oates *et al.* 2000a, p. 1530).

At least seven species of threatened primates occur in the same forests as *P. badius*. These include White-thighed Colobus *Colobus vellerosus* (Vulnerable), Roloway Monkey *Cercopithecus (d.) roloway* (Critically Endangered), White-naped Mangabey *Cercocebus lunulatus* (Critically Endangered) and Robust Chimpanzee *Pan troglodytes* (Endangered) (Gonedelé Bi *et al.* 2012). All of these species would benefit from actions taken to ensure the survival of *P. badius*, especially the protection of habitat and the strict enforcement of hunting laws. Development and effective implementation of a 'Red Colobus Action Plan' should have a high conservation priority (Oates 1996a, Oates *et al.* 2000a, McGraw & Oates 2002, 2007).

Some of the most important sites for the survival of *P. badius* are:

P. b. temminckii: Niokolo Koba N. P. (8175 km²), Fathala Forest (76 km²) in Saloum Delta N. P., Forêt Classée de Patako (55.8 km²), Forêt Classée de Sangako (21.4 km²) and Basse Casamance N. P. (5.0 km²), Senegal; Kiang West N. P. (110 km²), Bama Kuno Forest Park (9.3 km²), River Gambia N. P. (= Baboon I.) (5.8 km²), Katilenge (= Kahlenge) Forest Park (3.2 km²), Abuko Nature Reserve (1.1 km²), Pirang Forest Park (0.6 km²) and Bijilo Forest Park (0.5 km²), Gambia; Basin of the Tombali, Cumbija and Cacine Rivers, including the Cantanhez Forest (650 km²), Guinea Bissau. Details on the distribution and conservation status of *P. b. temminckii* in Senegal and Gambia are given in Galat *et al.* (2009), along with the reasons for the decline of the populations of *P. b. temminckii* in this region.

P. b. badius: Taï N. P. (3400 km²) Côte d'Ivoire; Grebo National Forest (2603 km²), Sapo N. P. (1308 km²), North Lorma National Forest (712 km²), Liberia; Gola Forest (748 km²), Loma Mountains Non-hunting Forest Reserve (332 km²; now under consideration for national park status) and Tiwai I. (12 km²), Sierra Leone; Réserve Naturelle Intégrale des Monts Nimba (= Nimba UNESCO Man and Biosphere Reserve) (218 km²), Guinea.

P. b. waldronae: Tanoé Swamps Forest (= 'Ehy Forest and vicinity'; ca. 300 km²), Côte d'Ivoire. This is thought to be the only site in which this subspecies might still exist. The conservation of this site is of particular concern at this time as there are plans to cut this forest in order to establish an oil palm plantation. Important populations of *C. lunulatus* and *C. (d.) roloway* also here. See: <http://www.manifeste-fmt.org/>

Measurements

Procolobus badius

P. b. badius

HB (♂ ♂): 611 (584–627) mm, n = 3

HB (♀ ♀): 562 (500–635) mm, n = 6

T (♂ ♂): 676 (635–706) mm, n = 3

T (♀ ♀): 715 (630–800) mm, n = 6

HF (♂ ♂): 159 (152–173) mm, n = 3

HF (♀ ♀): 175 (165–185) mm, n = 6

E (♂ ♂): 29 (25–33) mm, n = 3

E (♀ ♀): 31 (27–34) mm, n = 6

WT: (♂ ♂): 8.4 (6.4–9.6) kg, n = 17

WT: (♀ ♀): 7.8 (5.0–10.0) kg, n = 37

GLS (♂ ♂): 105.0 (100–106) mm, n = 5

GLS (♀ ♀): 98.0 (93–105) mm, n = 10

GWS (♂ ♂): 78.3 (74–82) mm, n = 4

GWS (♀ ♀): 72.7 (70–75) mm, n = 9

Linear measurements from Verheyen (1962), Allen (1925) and BMNH

WT from Delson *et al.* (2000)

P. b. temminckii

HB (♀): 522 mm, n = 1

T (♀): 730 mm, n = 1

HF (♀): 166 mm, n = 1

E (♀): 35 mm, n = 1

WT: n. d.

GLS (♂ ♂): 99, 101 mm, n = 2

GLS (♀ ♀): 93.4 (88–103) mm, n = 5

GWS (♂): 77 mm, n = 1

GWS (♀ ♀): 68.5 (66–71) mm, n = 5

Verheyen (1962), Allen (1925) and BMNH

P. b. waldronae

HB (♂ ♂): 499 (435–570) mm, n = 8

HB (♀ ♀): 496 (415–565) mm, n = 8

T (♂ ♂): 603 (500–686) mm, n = 8

T (♀ ♀): 555 (515–750) mm, n = 8

HF (♂ ♂): 162 (150–174) mm, n = 8

HF (♀ ♀): 164 (146–175) mm, n = 8

E (♂ ♂): 29 (20–38) mm, n = 8

E (♀ ♀): 30 (27–34) mm, n = 8

WT: (♂ ♂): 6.4 (6.3–6.5) kg, n = 2
 WT: (♀ ♀): 5.8 (5.5–6.0) kg, n = 2
 GLS (♂ ♂): 101 (92–109) mm, n = 8
 GLS (♀ ♀): 95.3 (92–101) mm, n = 15
 GWS (♂ ♂): 79.5 (72–86) mm, n = 8
 GWS (♀ ♀): 71.2 (67–73) mm, n = 15

Linear measurements from Verheyen (1962), Allen (1925) and BMNH
 WT from Delson *et al.* (2000)

Key References Galat & Galat-Luong 1985; Galat *et al.* 2009; Galat-Luong & Galat 2005; Gatinot 1977; McGraw *et al.* 2007; McGraw & Sciulli 2011; Oates 2011; Starin 1991, 1994; Struhsaker 2010.

Thomas M. Butynski, Peter Grubb & Jonathan Kingdon

Procolobus preussi PREUSS'S RED COLOBUS

Fr. Colobe bai de Preuss; Ger. Preuss-Stummelaffe

Procolobus preussi (Matschie, 1900). Sitzb. Ges. Naturf. Fr. Berlin, p. 183. Barombi, Elephant L., N Cameroon.



Preuss's Red Colobus *Procolobus preussi* adult female.

Taxonomy Monotypic species. Taxonomic history of *P. preussi* summarized by Grubb *et al.* (2003) and Ting (2008b). Cranium distinct (Groves 2001, Cardini & Elton 2009). Based on morphological and phenotypic characters, Schwarz (1928a), Allen (1939), Rahm (1970), Napier (1985) and Grubb (1990) treat *preussi* as a subspecies of *P. badius*. There are, however, some phenotypic characters (e.g. pale inner limbs and ventrum, agouti-speckled dorsum) that suggest affinity to Pennant's Red Colobus *Procolobus pennantii*. In addition, the geographic range of *preussi* is >1000 km from the nearest population of *P. badius* and the region in between holds several well-

recognized geographic barriers to primate distribution (e.g. major rivers). Moreover, the geographic range of *preussi* lies relatively close to, and between, the ranges of the Bioko Red Colobus *P. p. pennantii* and the Niger Delta Red Colobus *P. p. epieni*. As such, Grubb *et al.* (2003) provisionally include *preussi* as a subspecies of *P. pennantii*. This is referred to as the 'Western Assemblage of Red Colobus' or '*Procolobus pennantii*-Subgroup'. This close relationship is supported by molecular data, which place *P. preussi* closest to *P. p. pennantii* with a divergence time of 0.3 mya (Ting 2008a, b). A close relationship between *P. preussi* and *P. pennantii* is, however, not supported by the data on vocalizations. The vocal repertoire of *preussi* is distinct but with closest affinity with *P. badius* (Struhsaker 1981b). Vocal repertoire of *P. preussi* overlaps the vocal repertoires of *P. b. badius* and *P. b. temminckii* by 58%, and that of *P. p. pennantii* by only 32% (Struhsaker 2010). Dandelot (1974) viewed the differences among *preussi*, *badius* and *pennantii* as species-level differences and concluded that *preussi* is a full species. This was followed by Groves (1993, 2001, 2005c, 2007b), Kingdon (1997), Cardini & Elton (2009), Struhsaker (2010) and Oates (2011), and is the taxonomy used here. This very localized form might represent a stabilized hybrid that arose in the contact zone between more westerly and easterly parent populations. Chromosome number: not known.

Description Medium-sized arboreal monkey with orange-rufous cheeks, limbs and tail. As far as is known, colouration of adult ♂ like adult ♀. The few body measurement data available suggest that there is little, if any, sexual dimorphism, except that the adult ♂ appears to be slightly more robust than the adult ♀. Face quite flat, dark grey with pink margins around mouth and nose. Nostrils 'swollen' at base like *P. badius*. Fur dense, more frizzy than other red colobus species. Cheeks and sides of neck orange-rufous. Brow to ears and upper cheeks black. A whorl above brows, but no whorls above ears. Crown and temples with longish pelage that is swept back to cover ears. Crown, nape, shoulders, back, rump and base of tail blackish, blackish-grey, or greyish-brown with fawn or deep red bands or tips to hairs (i.e. agouti-speckled). Dorsum may become greyer posteriorly. Flanks and limbs orange-rufous or sandy, becoming dark brown-black on hands with tendency for digits to be black. Limbs white on inner surface. Ventrums pinkish-buff or pale red-gold, this colour going narrowly up throat to chin. Tail all rusty; sometimes sandy or reddish with brown-black, light grey, or blond over distal ca. 25%. Perineal organ of adult ♂ not

conspicuous. Adult ♀ has prominent clitoris and very large, pink, sexual swelling (Struhsaker 1975). Neonate black above, light grey below. Vocally distinct (Struhsaker 1981b).

Geographic Variation None, but individual variation exists in the intensity and extent of orange and red.

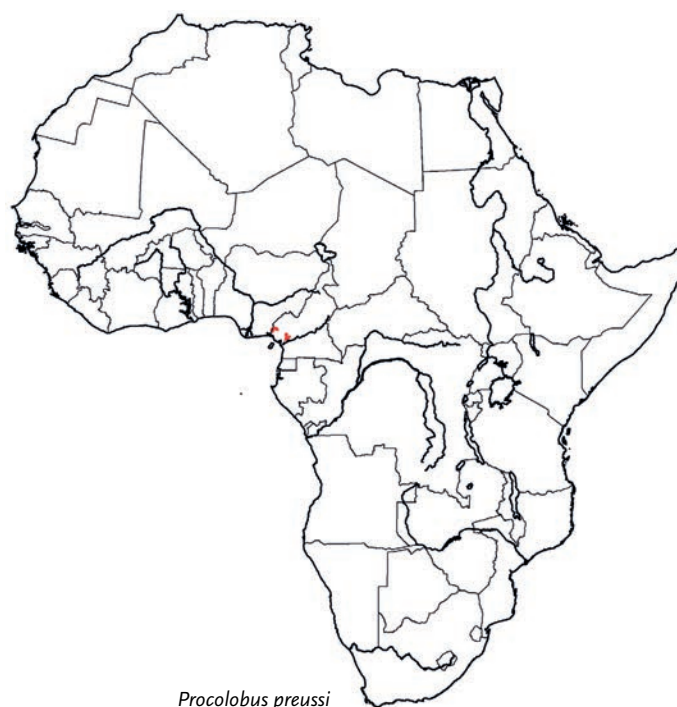
Similar Species Sympatric monkeys are unlikely to be confused with this colobine species.

Cercopithecus (c.) *erythrotis*. Sympatric. Reddish nose and ears. No red, rufous or orange on limbs.

Distribution Endemic to a small region between Cross R. in extreme SE Nigeria south-eastward to Sanaga R. in SW Cameroon (Eisentraut 1973, Napier 1985, Lee *et al.* 1988, Oates 1996a, Grubb *et al.* 2000, Dowsett-Lemaire & Dowsett 2001, Oates *et al.* 2004). Rainforest BZ. In 1988 and 1999 observed north-east of Ekonganaku (05°04'N, 08°39'E) in the Ikpan Block of the Oban Division (2800 km²) of Cross River N. P., Nigeria (Oates 1996a, Grubb & Powell 1999, Grubb *et al.* 2000). In 1977 thought to be confined in Cameroon to the region along the border with Nigeria; south of the Ikon-Mamfe Road (04°24' to 05°36'N, 08°48' to 09°20'E) in an area of ca. 7200 km² (S. Gartlan pers. comm. to Lee *et al.* 1988). Within this area, confirmed only for Korup N. P. (04°53' to 05°28'N, 08°42' to 09°16'E; 1260 km²) at this time but in 1977 present in Ejagham Council F. R. (749 km²) off the north boundary of Korup N. P. (S. Gartlan pers. comm. to Lee *et al.* 1988). *Procolobus preussi* last reported in this forest in 1996 (Usongo 1996). About 80 specimens collected in Yabassi District and Ndokfass District, S Cameroon, by P. C. M. Merfield in 1939 (Napier 1985). In 2001 observed in the Ndokbou Forest (>1000 km²) and Ebo Forest (1400 km²; 04°30'N, 10°30'E), Yabassi region, just to the north of the Sanaga R. South-east limit probably near Ebo (04°10'N, 10°16'E. Also near Toubassala, south-east of Mt Nlonako (Dowsett-Lemaire & Dowsett 2001, F. Dowsett-Lemaire pers. comm.). Reported to be in the Bakossi Mts and in Banyang Mbo during the 1990s (I. Faucher pers. comm. to F. Dowsett-Lemaire). This species probably widespread from the Cross R. to Ebo in the recent past. It is somewhat surprising that *P. preussi* does not occur on the foothills of Mt Cameroon, especially given the proximity of *C. pennantii* on Bioko I. to the west.

Habitat Coastal lowland forest and mid-altitude forest (Lee *et al.* 1988, Dowsett-Lemaire & Dowsett 2001, Oates *et al.* 2004). Appears to prefer primary forest and old secondary forest (Usongo & Amubode 2001, Linder 2008). Lowest known altitude is roughly 50 m (J. Linder pers. comm.). Maximum altitude reported for *P. preussi* is ca. 1000 m (Ebo Forest at southern end of range; F. Dowsett-Lemaire pers. comm.). Although Korup N. P. ranges from near sea level to 1079 m (Mt Yuhun), *P. preussi* not known to occur below 50 m or above 300 m (in north-east Korup N. P.; J. Linder pers. comm.).

Dominant plant family at Korup N. P. is Leguminosae (especially the subfamily Caesalpiniaceae). Other major families are Annonaceae, Euphorbiaceae, Rubiaceae, Scytopetalaceae, Myristicaceae, Olacaceae, Verbenaceae and Sterculiaceae (Gartlan *et al.* 1986, Linder 2008). One major refuge for *P. preussi* is Korup N. P. where 1700 plant species have been recorded. Nearly 500 tree



Procolobus preussi

species have been recorded for south Korup N. P. The structure of the tree community at some sites in Korup N. P. that are occupied by *P. preussi* is described in detail by Linder (2008). *Procolobus preussi* lives in one of the wettest areas of Africa; rainfall >500 mm during most months at some sites (Gartlan & Struhsaker 1972, Struhsaker 1975, Sarmiento & Oates 2000). Mean annual rainfall at south end of Korup N. P. is ca. 5460 mm and mean annual rainfall at north end of Korup N. P. is ca. 2700 mm, about one-third of which falls in Jul and Aug (Gartlan *et al.* 1986, Linder 2008). Over the historic range of *P. preussi* there is a short dry season during Dec–Feb. In this region humidity is usually above 90% and temperatures range from 15 to 33°C. In south Korup N. P., monthly temperature ranges from a mean minimum of 23.7°C to a mean maximum of 30.2°C (Gartlan *et al.* 1986). August is the coolest month and Feb is the hottest month.

Abundance Gartlan & Agland (1980) estimated that fewer than 8000 *P. preussi* survived in 1980. Oates (1996a) estimated that 10,000–15,000 were present in Korup N. P. in 1996. No estimates exist for the Yabassi region, but it is said to be 'widespread' (Dowsett-Lemaire & Dowsett 2001: 5). British museums hold at least 80 *P. preussi* specimens collected from the Yabassi region in 1939 alone. This strongly suggests that *P. preussi* was once common in this region (Napier 1985).

In 1970, T. Struhsaker (pers. comm. in Linder 2008) encountered 0.15 groups of *P. preussi*/h in south Korup N. P., making this one of the most frequently recorded species of primate in this region. In Korup N. P., in 2004–05, Linder (2008) encountered 0.04 groups/km during 352 km of census. In south Korup N. P., Dunn & Okon (2003) encountered 0.06 groups/km in 2001–03 during 420 km of census, while Linder (2008) encountered 0.05 groups/km during 243 km of census here in 2004–05. In north Korup N. P., Edwards (1992) encountered 0.07 groups/km in 1990 during 74 km of census. She estimated 0.52 groups/km² (quadrat method) and 0.56 groups/km² (line transect method), or 26–28 individuals/

km². In this same region, Linder (2008) encountered 0.05 groups/km during 74 km of census in 2004–05 and estimated 0.46 groups/km² and 23 individuals/km² (line transect method).

Adaptations Diurnal and arboreal. The colouring of *P. b. badius*, which has some resemblances with that of *P. preussi*, is discussed in the profile of that species and the point is made that strong colour contrasts can serve intra-specific communication. Red, especially, acts as a strong contrast with green vegetation (Sumner & Mollon 2003). It is interesting, therefore, that the most conspicuous feature of *P. preussi* is its bright orange-rufous tail. *Procolobus preussi* is not the only cercopithecoid monkey to evolve such a brightly coloured tail; members of the *Cercopithecus (cephus)* group, including the sympatric *C. erythrotis*, also have bright orange-rufous tails. In the latter there are behaviour patterns to suggest that tail postures and movements provide information about dominance ranking. Whether this is also the case for *P. preussi* is not known. Orange-rufous limbs presumably help enhance the visibility of limb postures and gestures.

Of 13 groups of *P. preussi* encountered during surveys in Korup N. P., 92% were in association with groups of at least one other species of monkey (Struhsaker 2000a). These large associations are believed to enhance predator detection and avoidance, and to provide foraging advantages (Gartlan & Struhsaker 1972, Struhsaker 2000a).

Foraging and Food Folivorous, dependent on emergent trees for food (S. Gartlan pers. comm. to Lee *et al.* 1988). Prefers the upper strata (Linder 2008). Seventeen species of plants belonging to nine families observed eaten by *P. preussi* in Korup N. P. (Usongo & Amubode 2001). Species and plant part most eaten were young leaves of *Lecomtedoxa klaineana* (27%) and *Xylopia aethiopica* (22%). Families Sapotaceae and Annonaceae constituted about 50% of total food items. Information on the nutritive values (e.g. crude protein, crude fibre, ether extract, nitrogen-free-extractable and total ash) of some of the food items is presented in Usongo & Amubode (2001).

Social and Reproductive Behaviour Social. Little-studied. Struhsaker (1975, 2000a) reports mean group size in Korup N. P. >47 (range >24–80). All of his 36 encounters with *P. preussi* in Korup N. P. were with groups (i.e. no solitary individuals were encountered). More recently (2001–03) Dunn & Okon (2003) observed groups of >100 individuals in south Korup N. P. and found a mean group size of 35 (range = 10–130, n = 23). Has the most complex vocal repertoire of all *Procolobus* spp., including several calls not found amongst other red colobus taxa. The calls given by *P. preussi* include the 'nyow', 'yowl' and 'copulation quaver' (Struhsaker 1975, 1981b, 2010).

Reproduction and Population Structure Few data. Females probably have largest sexual swelling of any species of *Procolobus*, reaching an estimated 25–33% of the female's body volume (Struhsaker 1975) and measuring at least 33 cm lengthwise and 45 cm in circumference (F. G. Merfield pers. comm. in Napier 1985). Sexual swelling of ♀ pink. Females give a quavering copulation call before, during and after mating (Struhsaker 1981b, Oates 1994).

Predators, Parasites and Diseases No information, but likely predators include Leopards *Panthera pardus*, African Golden Cats

Profelis aurata, Robust Chimpanzees *Pan troglodytes*, Central African Rock Pythons *Python sebae* and Nile Crocodiles *Crocodylus niloticus*. The African Crowned Eagle *Stephanoaetus coronatus* is probably the most significant natural predator of *Procolobus* spp. (Struhsaker 2000a, 2010), but any such predation has long been dwarfed by heavy hunting by humans.

Conservation IUCN Category (2012): Critically Endangered. CITES (2012): Appendix II.

Procolobus preussi still present in one protected area in Nigeria, the Oban Division of Cross River N. P., which is contiguous with Korup N. P. (J. Oates pers. comm.). The largest known population occurs in Korup N. P. A second population (of unknown distribution and size) is present in Ndokbou Forest and Ebo Forest but this population is not protected. The bushmeat trade, logging and habitat loss have reduced and extirpated populations over the past 40 years (Lee *et al.* 1988, Oates 1996a, Linder 2008, Linder & Oates 2011). Hunting of critical populations of *P. preussi* continues at a high level in Oban Division of Cross River N. P. (J. Oates pers. comm.), in Korup N. P. (Oates 1996a, Linder 2008) and in the Yabassi region (Dowsett-Lemaire & Dowsett 2001). *Procolobus preussi* is one of the most common monkeys for sale in the bushmeat markets in the vicinity of Korup N. P. (Linder 2008). As a result of hunting, *P. preussi* is now extirpated from many areas, including most, if not all of the Korup Support Zone, of which the Ejagham Council F. R. is a part (Waltert *et al.* 2002, Steiner *et al.* 2003). Although there remains considerable habitat for *P. preussi*, national and international conservation bodies have proved helpless to protect *P. preussi* from the pressures of the bushmeat trade (Bowen-Jones & Pendry 1999, Oates 1999, Linder 2008). The main recommendations for the long-term conservation of *P. preussi* are (1) to stop hunting at all sites and to successfully implement the current human resettlement projects for Korup N. P., (2) to conduct surveys to better determine the distribution and abundance of *P. preussi*, especially in Cross River N. P., Ejagham Council F. R. and Yabassi region, and (3) to up-grade the conservation status of Ebo Forest, Ndokbou Forest and Nlonako Forest and provide them with high levels of protection against hunters.

Measurements

Procolobus preussi

HB (♂ ♂): 560, 630 mm, n = 2

HB (♀): 620 mm, n = 1

T (♂ ♂): 750, 760 mm, n = 2

T (♀): 750 mm, n = 1

WT (♂): n. d.

WT (♀): 7.3 kg, n = 1

GLS (♂ ♂): 111 (107–121) mm, n = 9

GLS (♀ ♀): 108 (102–115) mm, n = 21

GWS (♂ ♂): 84 (81–87) mm, n = 9

GWS (♀ ♀): 80 (75–83) mm, n = 21

Powell-Cotton Museum (C. P. Groves pers. comm.) except GLS and GWS for two ♂ ♂ and two ♀ ♀ at BMNH (P. Grubb pers. comm.)

Key References Lee *et al.* 1988; Linder 2008; Oates 2011; Struhsaker 2010; Usongo & Amubode 2001.

Thomas M. Butynski & Jonathan Kingdon

***Procolobus pennantii* PENNANT'S RED COLOBUS (BIOKO RED COLOBUS)**

Fr. Colobe bai de Pennant; Ger. Pennant-Stummelaffe

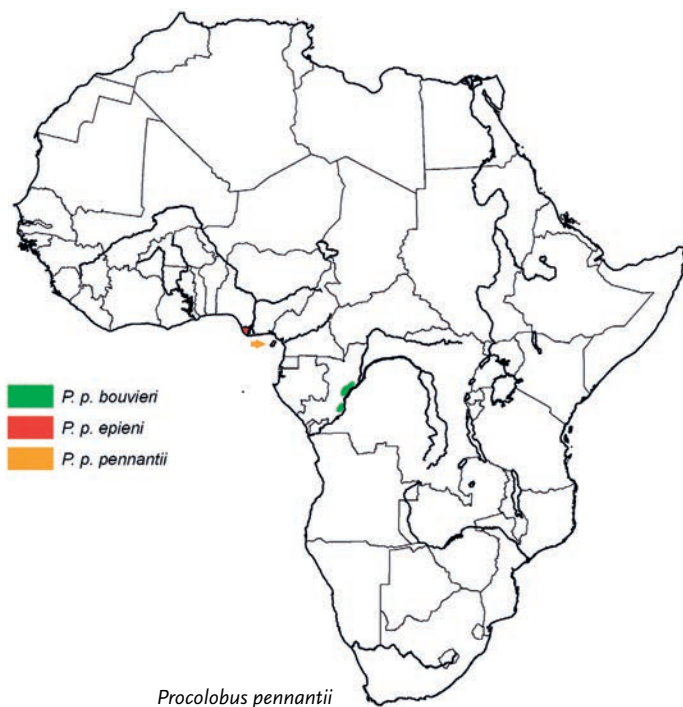
Colobus pennantii (Waterhouse, 1838). Proc. Zool. Soc. Lond. 1838: 57. Fernando Po (= Bioko I.), Equatorial Guinea.

Taxonomy Polytypic species, here taken to include three subspecies, *pennantii*, *bouvieri*, *epieni*. See taxonomic reviews in Grubb *et al.* (2003) and Ting (2008a, b). Dorst & Dandelot (1970) took *P. pennantii* to encompass all red colobus other than *badius* and *temminckii*. Groves (1993) followed a similar course but excepted *preussi* and *rufomitratus* (and restored *waldroneae* to *badius*). Dandelot (1974), Napier (1985) and Grubb (1990) restricted *P. pennantii* to include *bouvieri*. Kingdon (1997) and Groves (2001, 2005c) took *P. pennantii* to include both *bouvieri* and, provisionally, *epieni*. This is the taxonomy adopted here. Grubb *et al.* (2003) placed *preussi*, *bouvieri* and *epieni* in *P. pennantii*. Vocal repertoire (Struhsaker 2010) and molecular data (Ting 2008b) suggest that *epieni* is more closely related to the red colobus of East Africa than to *P. pennantii*. Groves (2007b) and Oates (2011) treat *pennantii*, *preussi*, *bouvieri* and *epieni* as full species. Polymorphic in *epieni* and *pennantii*, less certain in *bouvieri* – but likely (Colyn 1993). Synonyms: *bouvieri*, *epieni*, *likualae*. Chromosome number: not known.

Description Medium-size, arboreal, reddish and black monkey with white cheeks. A highly variable species. For *P. p. pennantii*, adult

♀ ♀ have, on average, slightly greater body linear measurements than adult ♂ ♂. Adult ♀ ♀ are, however, more gracile than adult ♂ ♂, as indicated by their body weight, which is about 94% that of the adult ♂ ♂. Canines of adult ♂ ♂ more than twice as long as for adult ♀ ♀ (see measurements below). Muzzle relatively short (Verheyen 1962). Facial skin black with contrasting pink eyelids, nostrils and lips (most visible in younger animals). Cheeks and throat whitish, dirty white, or pale grey. Crown black or deep brown. Back and tail variable in extent of black, red or brown, but sometimes entirely black. Flanks and limbs predominantly orange or reddish. Ventrums whitish, dirty white, or faint peach. Hands and feet black. Unusual for red colobus in that *P. p. epieni* exhibits traces of agouti freckling on the crown and back. One infant *P. p. pennantii* estimated to be <1 month of age had body and tail black (with some slight mixing of white hairs), except for whitish fringe around face and some white on shoulders and thighs. Face bare, black (no pink skin). Ears, inner limbs, top of hands and top of feet bare, pink. Ventrums thinly covered with whitish hairs (T. Butynski pers. obs.). *Procolobus p. pennantii* is the only taxa of *Procolobus* in which newborns have an entirely black face (T. Struhsaker pers. comm.).

Pennant's Red Colobus *Procolobus pennantii pennantii* adult male.



Geographic Variation Subspecies are very isolated geographically (Colyn 1991, Grubb & Powell 1999, Oates *et al.* 2004, Groves 2007b). Few specimens for each of the three subspecies. As such, the full range of variation within each subspecies is not known.

P. p. pennantii Bioko Red Colobus. Bioko I., Equatorial Guinea. Face with black skin (no pink skin). Pelage around eyes and over bridge of nose sooty. Cheek whiskers long, white, dirty white, or grey. Temples and ears blackish. Crown blackish; no whorls. Hairs of mantle black with orange bands. In the field, the human eye is drawn to the white cheeks and their strong contrast with the blackish temples, ears and crown. Shoulders, upper back, sides, outer limbs variable; orange-brown to blackish-brown. Lower back, hips, lower arms, lower legs and upper-side of tail blackish or blackish-brown, sometimes with infusion of orange. Whitish on outer side of arm restricted to a fringe extending from chest; rest of front and outside of arm orange-brown. Flanks and front of legs orange-brown. Throat, chest, belly, upper outer arms and inner arms and legs dirty white, pale-grey, to faint peach. Black of hands and feet extends somewhat up outside of limbs. Tail varies from all black to black over proximal 50–70%, and deep reddish-brown over the distal 50–30%, becoming increasingly reddish towards tip. Preliminary field observations (T. Butynski pers. obs.) suggest some sexual dimorphism in colour of pelage; most noticeably, adult ♂♂ have a faint peach ventrum, and extensive bright orange-brown (chestnut) on sides and dorsum, while adult ♀♀ have a dirty white ventrum, less extensive, paler orange-brown on sides, and dorsum blackish-brown.

P. p. bouvieri Bouvier's Red Colobus. Between lower Léfini R. and lower Sangha R., Congo, at ca. 00–1° S. Stiff, black superciliary band extends to ears. Crown deep brown or reddish without whorls. Ears with a small tuft behind. Mantle hairs blackish and unbanded. Blackish zone down neck, shoulders and back, becoming greyer and broadening on the rump and extending onto the tail. Rest of

upperparts, outer arms and outer legs russet. Inside of lower legs black. Tail mostly golden-brown.

P. p. epieni Niger Delta Red Colobus. West sector of Niger Delta. Facial skin black to pinkish-grey; some pink skin sometimes on muzzle. Eyelids pinkish (J. L. R. Werre pers. comm.). Crown black with conspicuous hair-whorls behind and over ears. Hairs of mantle black with orange bands. Whitish of underparts extends to outer side of arms, limiting orange-brown to the back of the outer arms. Front of forearms white. Black of hands and feet not extending up limbs. Dorsal pelage agouti-speckled in part (Grubb & Powell 1999, Werre 2000).

Similar Species No similar sympatric species, but two similar subspecies parapatric with *P. p. bouvieri*.

Procolobus rufomitratatus oustaleti. North and east of the Sangha R. Back dark smoky-brown to olive-brown to coppery red. Ventrums paler than dorsum (but not white or dirty-white).

Procolobus rufomitratatus tholloni. East and south of the Congo R. Circumfacial hair short, black, except on lower cheeks where whitish. Back orange-russet all over. Feet dark brown. Tail red for proximal ca. 70%, then brown with blackish tuft.

Distribution Endemic to west-central Africa. Rainforest BZ. Discontinuously small distributions in Bioko I., Nigeria and Congo (Oates *et al.* 2004). See details above under Geographic Variation.

Habitat Moist forest. *Procolobus p. pennantii* in primary lowland, mid-altitude and montane forest from sea level to at least 1500 m in montane forest on the southern one-third of Bioko I. (on Pico Biao). Hunters claim that this species is found to >1800 m in *Schefflera*-dominant forest on Pico Basile (Butynski & Koster 1994, T. Butynski pers. obs.). González-Kirchner (1997b: 99) states that 'The Pennant's Red Colobus was always observed under 2000 m above sea level' but he does not actually state the highest level at which he observed this species. He also states that *P. p. pennantii* prefer primary montane forest. *Procolobus p. pennantii* is largely absent from degraded or secondary forest, but this is likely due entirely to heavy hunting of this monkey in such habitats. *Procolobus p. bouvieri* on the margins of major rivers, but habitat-use poorly known. *Procolobus p. epieni* in mangrove swamps of Niger Delta (Werre & Powell 1997). Annual mean rainfall ranges from ca. 2000 to >10,000 mm.

Abundance In 1986, the highest density (0.6 groups/km) of *P. p. pennantii* occurred in the Gran Caldera de Luba, SW Bioko (T. Butynski pers. obs.). Other encounter rates are 0.18 groups/km in 2008 along 44 km of transect in the Gran Caldera de Luba, and 0.31 groups/km in 2009 along 48 km of transect and 0.34 groups/km in 2010 along 50 km of transect at Badja North, SW Bioko (T. Butynski, G. Hearn, M. Kelly & J. Owens pers. obs.). The Gran Caldera de Luba and Badja North are remote sites where hunting is relatively uncommon and there are no other anthropogenic impacts. As such, the encounter rates at these two sites are likely close to what is expected for an undisturbed population of *P. p. pennantii*. This species has been extirpated from much of Bioko as a result of unsustainable hunting with shotguns (Hearn *et al.* 2006). Large

Niger Delta Red Colobus *Procolobus pennantii epieni* adult male.



groups of colobus, presumed to be *P. p. bouvieri*, have been seen on the right bank of the Congo R. in recent years (R. O'Hanlon pers. comm.). Museum specimens indicate that the range of *P. p. bouvieri* covers a linear distance of at least 200 km. Thus, even if *P. p. bouvieri* is primarily a riverine species, which is uncertain, it seems likely that there are still substantial numbers along the western bank of the Congo and its tributaries (e.g. Sangha R. and Léfini R.).

Adaptations Diurnal and arboreal. This species poses puzzling questions as to what adaptive or maladaptive features restrict the

distinctive subspecies to two or three widely separated geographic locations. Their situation contrasts strongly with their eastern neighbour, *P. r. oustaleti*, which is well distributed across a vast range. Likewise, their western neighbour, the Western Red Colobus *Procolobus badius*, was highly successful and until the twentieth century had a more or less continuous distribution from Senegal to Ghana. The present very restricted populations of *P. pennantii* imply that the species has suffered some biological inhibition that has prevented it from expanding out of its current enclaves. Understanding that adaptive shortcoming is highly relevant to

ensuring the future conservation of this red colobus monkey. Some measure of its relictual status is the distance of ca. 1200 km between the range of *P. p. epieni* in the Niger Delta and that of *P. p. bouvieri* on the right bank of the Congo R. There are no known populations of *Procolobus* over these 1200 km. The presence of *P. p. pennantii* on Bioko I. is puzzling since the population on the mainland opposite Bioko I. is that of Preuss's Red Colobus *Procolobus preussi* – which appears to have a different affinity, being morphologically closer to *P. badius*. Furthermore (assuming that *P. p. epieni* belongs in *pennantii*) *P. preussi* is interposed between it and *P. p. bouvieri*; how did it get there? (Possible explanations for this anomalous distribution are discussed in the profile of *P. preussi*.) Is *P. pennantii* an early form of red colobus that has been widely displaced by later, more adaptable species? Could competition from *Colobus satanas* have displaced *P. pennantii* throughout the intervening area? Perhaps, but the diets of these two species probably differ considerably, and the two species are sympatric on Bioko I. – so why not on the mainland? On Bioko I. González-Kirchner (1997b) found that these two species use the various levels of the forest strata to different extents. On present evidence, *P. pennantii* would appear to be a particularly poor disperser but the cause of its inability to 'regain lost ground' remains unknown. Kingdon (1997) noted the exceptional floristic and faunal richness of the Bight of Bénin, particularly the diversity of primates, and he listed competition with other primates, climate change, past hunting and species-specific disease pandemics as possible influences. Whatever the causes, they are not likely to have been recent.

While it is obvious that all red colobus species have a common ancestor, the timing of their dispersal across equatorial Africa, and the details of their speciation pattern, await a comprehensive molecular study. When molecular trees of the red colobus group are eventually constructed, it seems likely that *P. pennantii* will be seen to belong to an early, possibly conservative, lineage. While all living species of red colobus, under current conditions, appear to be slow dispersers, *P. pennantii* seems to be the poorest colonist of them all. This conclusion is reinforced by their survival close to the focal centre of primate evolution in Africa, presumably the area where they might be expected to have had the longest tenancy. This suggests that their occupation of Bioko I. was the result of an early colonization that took place before the species' decline on the mainland.

Foraging and Food Folivorous. No detailed studies have been made of *P. pennantii*. This species is unlikely, however, to differ from other red colobus species in the broader outlines of its diet. See the profiles for the other *Procolobus* spp. However, the three subspecies of *P. pennantii* live under quite different ecological regimes (especially rainfall), with likely implications for their diet and feeding habits. The main tree species in their diets are likely to differ considerably.

Procolobus p. pennantii covers the altitudinal range from sea level to at least 800 m on Bioko I., and the range may be as much as 1800 m. On Bioko this species is present in coastal forest, 'monsoon forest' (rainfall >10,000 mm/year), mid-altitude (transition) forest and montane forest (Butynski & Koster 1994). Over this range, the composition of the tree community differs greatly, meaning that the diet of *P. pennantii* must also differ greatly over a horizontal distance of ca. 10 km. Therefore, *P. p. pennantii* is likely to have a more diversified diet than *P. p. bouvieri* or *P. p. epieni*, both of which live

at relatively low altitude on relatively flat ground. Sightings of *P. p. bouvieri* have been mostly along the margins of major rivers but it should be remembered that the pre-eminence of river transport in the Congo Basin could give a false idea of the ecological limits of *P. p. bouvieri*. *Procolobus p. epieni* is likely to have the most localized and peculiar diet, living, as it does, in a lowland delta close to the sea. From what is known of seasonal phenology in such littoral habitats it is possible that green fruit is taken more during the wet season while leaves and buds are the staple food during the dry season.

Procolobus p. pennantii spends most of its time in the mid-canopy at ca. 15–30 m above the ground, but does forage in the upper canopy to >45 m (González-Kirchner 1997b) and, at least occasionally, on the ground (Struhsaker 2000a, T. Butynski pers. obs.). Observed feeding on flower buds of *Allophylus africanus* (T. Butynski pers. obs.).

Social and Reproductive Behaviour Social. *P. p. pennantii* groups seem to typically have >20 individuals and some have >30 individuals (Butynski & Koster 1994). Counts of 14 groups by Struhsaker (2000a) yielded a mean size of ca. 14 individuals (range = 5–<30). Groups have 1–3 adult ♂♂ (Struhsaker 2000a) but the majority of groups probably have but one adult ♂ (T. Butynski pers. obs.).

Of 17 encounters with *P. p. pennantii*, 24% were with solitary individuals (Struhsaker 2000a). In another study, none of the ten encounters were with solitary individuals (Butynski & Koster 1994). Group spread sometimes >100 m but usually much less than this (T. Butynski pers. obs.).

Procolobus p. pennantii observed in polyspecific associations with Bioko Black Colobus *Colobus satanas satanas*, Bioko Red-eared Monkey *Cercopithecus (c.) erythrotis erythrotis* and Golden-bellied Crowned Monkey *Cercopithecus (m.) pogonias pogonias*. Of ten encounters during censuses conducted in 1986, *P. p. pennantii* in association with groups of other species of primate 40% of the time. Similarly, of 13 encounters in SW Bioko in 1992, Struhsaker (2000a) found that 38% of the *P. p. pennantii* groups were in a polyspecific association. During surveys conducted on Bioko in the Gran Caldera de Luba in 2008, two (25%) of the eight *P. p. pennantii* groups encountered were in a polyspecific association (Butynski & Owens 2008). Polyspecific associations are thought to confer anti-predator and foraging advantages to the participants (Struhsaker 2000a).

The vocal repertoire of *P. p. pennantii* has the least overlap with other taxa of *Procolobus*. The calls given include: 'chist', 'nyow', 'copulation quaver' and 'convex'. The '2-unit honk', '2-unit chist', 'nasal scream' and 'nasal sqwack' are very distinctive calls unique to *P. p. pennantii*. *Procolobus p. epieni* gives the 'wheet', a call which is absent from the vocal repertoire of *P. p. pennantii* (Struhsaker 1981b, 2010).

The loud, squeaky 'eeeyak' and loud 'honk' calls of *P. p. pennantii* are highly variable in length and intensity. Both calls appear to be given only by adult ♂♂. The 'eeeyak' can be heard to >250 m and the 'honk' to >400 m. The 'honk' may be the loudest call given by any *Procolobus* spp. and probably serves some of the same functions as the loud calls of adult ♂♂ of other primate taxa (e.g. *Colobus* spp., *Lophocebus* spp., *Cercopithecus* spp.). These calls are given in times of excitement (e.g. intra-group aggression, loud noise from a falling tree, detection of a human). Adult ♀♀ give sharp 'ik' and soft 'honk'

warning calls. Soft 'whistles' also given; these may be analogous to the 'wheats' of mainland *Procolobus* spp. (T. Butynski pers. obs.).

Reproduction and Population Structure Few data available. Adult ♀♀ exhibit large perineal swellings, sometimes protruding to >6 cm (T. Butynski pers. obs.).

Predators, Parasites and Diseases The Central African Rock Python *Python sebae* is a likely predator of all three subspecies of *P. pennantii*, perhaps particularly of *P. p. pennantii*, which frequently moves on the ground, as Leopards *Panthera pardus*, African Golden Cats *Profelis aurata* and Nile Crocodiles *Crocodylus niloticus* are all absent from Bioko I. These are all, however, likely predators of *P. p. epieni* and *P. p. bouvieri*. Likewise, the African 'monkey-eating eagle', the African Crowned Eagle *Stephanoaetus coronatus*, is absent from Bioko I. but is expected to be second only to humans as the primary predator of *P. p. epieni* and *P. p. bouvieri*.

Conservation IUCN Category (2012): Critically Endangered as *P. pennantii*, *P. p. epieni* and *P. p. bouvieri*, and Endangered as *P. p. pennantii*. CITES (2012): Appendix II.

Procolobus p. epieni listed as one of the world's 25 most threatened primates in 2008 (Oates & Werre 2009). *Procolobus p. pennantii* previously (2004–08) listed as one of the world's 25 most threatened primates (Butynski *et al.* 2007). *Procolobus p. pennantii* probably has the most restricted range of all of Bioko's 11 species of primates, and is now only known for certain from an area of <400 km² on the south-west of the island, within the Gran Caldera and Southern Highlands Scientific Reserve (510 km²). *Procolobus p. pennantii* is extremely threatened by bushmeat hunting, most notably since the early 1980s when a commercial bushmeat market appeared in the capital city of Malabo (Butynski & Koster 1994). Hearn *et al.* (2006) estimated numbers killed for bushmeat at 550 and 350 in the years 2004 and 2005, respectively, and a decline of more than 40% in the population over the 20 years from 1986 to 2006. The average price paid in the Malabo market for an adult *P. p. pennantii* in 2006 was about US\$42. This is well over twice as much as the cost of the readily available, high-quality, whole chicken, pork and beef at the same market. Similar high prices are paid on Bioko for all seven species of monkeys and for both species of duikers. Bushmeat on Bioko is, obviously, now a 'luxury food' (Hearn *et al.* 2006). Probably all of the *P. p. pennantii* killed on Bioko at this time are coming from within the Gran Caldera and Southern Highlands Scientific Reserve, but small numbers may persist in the most remote and rugged parts of Bioko's other protected area, the Pico Basile N. P. (330 km²). The continued high flow of primates, duikers and other wildlife into the Malabo Bushmeat Market indicates that neither 'protected area' is receiving adequate protection from the government of Equatorial Guinea.

The red colobus monkeys of West Africa and west-central Africa are probably more threatened than any other taxonomic group of primates in Africa. This is partly due to the fact that red colobus are especially sensitive to habitat degradation and vulnerable to hunters (Oates 1996a, Oates *et al.* 2000a, Waltert *et al.* 2002, Struhsaker 2005). None of the few protected areas in which *P. pennantii* occurs is well protected. Of very high priority for the conservation of *P. pennantii* is (1) immediate field surveys to determine the current distributions and abundance of *P. p. epieni* and *P. p. bouvieri* and, at

the same time, (2) rigorous protection of all of those populations that are known to exist.

Providing adequate protection to viable populations of these three subspecies of red colobus would greatly assist the conservation of numerous sympatric threatened taxa. Among primates, these include: Bioko Preuss's Monkey *Allochrocebus preussi insularis*; *C. e. erythrotis*; *C. p. pogonias*; Bioko Stampfli's Putty-nosed Monkey *Cercopithecus (n.) nictitans martini*; Bioko Black Colobus *Colobus satanas satanas*; Bioko Drill *Mandrillus leucophaeus poensis*; Western Chimpanzee *Pan troglodytes verus*; and Nigeria Chimpanzee *P. t. vellerosus*. If a concerted effort is to be made to save all of the diversity present within the red colobus, then the major international conservation NGOs will need to focus their efforts on this taxonomic group and work closely with national conservation NGOs and national protected area authorities.

Measurements

Procolobus pennantii

P. p. pennantii

HB (MM): 505 (470–554) mm, n = 12

HB (FF): 519 (470–583) mm, n = 48

T (MM): 587 (520–630) mm, n = 12

T (FF): 639 (600–710) mm, n = 48

HF (MM): 154 (142–162) mm, n = 12

HF (FF): 158 (140–176) mm, n = 51

E (MM): 30 (26–35) mm, n = 12

E (FF): 30 (26–33) mm, n = 50

WT intact (MM): 11.0 kg, n = 1

WT intact (FF): 10 kg, n = 1

WT eviscerated (MM): 6.2 (5.2–8.0) kg, n = 9

WT eviscerated (FF): 5.8 (5.0–7.0) kg, n = 38

Upper canine (MM): 17 (15–20) mm, n = 12

Upper canine (FF): 7 (4–12) mm, n = 41

Lower canine (MM): 12 (10–16) mm, n = 12

Lower canine (FF): 5 (3–8) mm, n = 40

GLS (MM): 112 (109–117) mm, n = 3

GLS (FF): 106 (106–107) mm, n = 2

GWS (MM): 91 (90–92) mm, n = 3

GWS (FF): 71 (71–72) mm, n = 2

Bioko I., Equatorial Guinea (Butynski *et al.* 2009). Skull measurements from Eisentraut (1973), P. Grubb (pers. obs.) and T. Butynski (pers. obs.).

P. p. bouvieri

GLS (♀): 108 mm, n = 1

GWS (♀): 78 mm, n = 1

Congo (BMNH, P. Grubb pers. obs.)

P. p. epieni

GLS (♂): 106 mm, n = 1

GWS (♂): 78 mm, n = 1

Niger Delta, Nigeria (P. Grubb pers. obs.)

Key References Butynski & Koster 1994; González-Kirchner 1997b; Hearn *et al.* 2006; Oates 2011; Oates & Werre 2009; Struhsaker 2000a, 2010.

Thomas M. Butynski, Peter Grubb & Jonathan Kingdon

Procolobus rufomitrat EASTERN RED COLOBUS

Fr. Colobe bai à tête roussee; Ger. Ostafrikanischer Stummelaffe

Procolobus rufomitrat (Peters, 1879). Monatsb. K. Preuss. Akad. Wiss. Berlin 1879: 829. Muniuni, Tana R., Kenya.

Taxonomy Polytypic species. Taxonomy extremely complex and much debated (Thorington & Groves 1970, Rahm 1970, Dandelot 1974, Napier 1985, Groves 1989, 2000a, 2001, 2007b, Colyn 1991, Kingdon 1997, Gautier-Hion *et al.* 1999, Grubb & Powell 1999, Grubb *et al.* 2003, Struhsaker 2010). As treated here, includes at least eight subspecies: Tana River Red Colobus *P. r. rufomitrat*; Ashy (or Uganda) Red Colobus *P. r. tephrosceles* (synonym: *gudoviusi*); Tshuapa (or Thollon's) Red Colobus *P. r. tholloni*; Oustalet's Red Colobus *P. r. oustaleti* (synonyms: *brunneus*, *nigrimanus*, *powelli*, *schubotzi*); Kisangani Red Colobus *P. r. langi*; Lulindi River Red Colobus *P. r. lulindicus*; Kivu Red Colobus *P. r. foai* (synonym: *graueri*); and Lomami River Red Colobus *P. r. parmentieri*. A ninth, Semliki Red Colobus *P. r. ellioti* (synonym: *semlikiensis*), may represent a very large hybrid swarm between the latter five taxa (Verheyen 1962). Most early authorities considered all to be subspecies of a single species of red colobus *Colobus badius* (e.g. Schwarz 1928a, Rahm 1970, Haltenorth & Diller 1980). Dorst & Dandelot (1970) confined *badius* to a single western species while a second species, *pennanti*, embraced all the rest of the red colobus forms. Groves (1989) regarded the nominate population, *P. rufomitrat*, from the lower Tana R., Kenya, to be a species in its own right and most of the forms listed above as subspecies of a single 'Central species', *P. pennantii*, ranging from the Bight of Bénin to Zanzibar I. Groves (2001) again kept *Tana rufomitrat* as a separate species, one of nine in the following red colobus subgroup; *tholloni*, *foai* and *tephrosceles* were also given specific status. Groves (2001) placed, *ellioti*, *langi*, *lulindicus*, *oustaleti*, *parmentieri* and *semlikiensis* as subspecies or synonyms of *Piliocolobus* (*Procolobus*) *foai*. Kingdon 1997 had followed a similar course but provisionally allied *tephrosceles* with *oustaleti* and other populations from north and east of the Congo R. (DR Congo), clustering them as subspecies of a Central African Red Colobus *P. oustaleti*. Gautier-Hion *et al.* (1999) divided *P. r. oustaleti* into six subspecies, and placed *foai*, *langi*, *lulindicus*, *parmentieri*, *powelli*, *nigrimanus*, *oustaleti*, *semlikiensis* and *tholloni* as subspecies of Pennant's Red Colobus *Procolobus pennantii*. See authors listed above and Napier (1985), Colyn (1991), Grubb *et al.* (2003), Groves (2007b) and Struhsaker (2010) for reviews and additional details. Synonyms: see above. Chromosome number: unknown.

Description A medium-sized, arboreal monkey with variable amounts of reddish-brown or orange-brown on top of the head, back, tail and lateral surface of the arms and legs, and paler ventrum. Males generally same or similar colour as ♀♀. Adult ♂♂ of some subspecies up to ca. 25% heavier than adult ♀♀ (e.g. 9–12.5 kg vs. 7–9 kg for *P. r. tephrosceles*; Kingdon 1971, Struhsaker 1975), but this size difference is not present in all subspecies (e.g. *P. r. rufomitrat*; T. Struhsaker pers. obs.). In all subspecies, ♂♂ have larger canines, and nuchal and sagittal crests (Verheyen 1962, P. Grubb pers. obs.).

Colour and patterning highly variable among subspecies and often so within a subspecies, such as *tephrosceles*, *oustaleti* and particularly in the *ellioti*/*semlikiensis* hybrid swarm. See Geographic Variation for information on extent of phenotypic variation. Back and tail often dark-grey, lacking any red or brown depending on subspecies. Tail typically

tufted, especially in adult ♂♂. *Procolobus r. tholloni* is the most brightly coloured subspecies with bright orange or reddish over most of the dorsum. Hair usually of medium length. Face dark grey or blackish in most subspecies, but *tholloni* distinct from the others by having light skin around the eyes, nose and mouth, but not as contrasting as in the Udzungwa Red Colobus *Procolobus gordonorum* or Zanzibar Red Colobus *Procolobus kirkii*. *Procolobus r. tholloni* is also distinguished by its more prognathous skull. See Verheyen (1962), Napier (1985), Colyn (1991), Kingdon (1971, 1997), Gautier-Hion *et al.* (1999), Groves (2001) and Grubb *et al.* (2003) for detailed descriptions, illustrations and discussions of the complex of subspecies here recognized within *P. rufomitrat*.

Newborns differ in colour from adults, are all dark grey to blackish on the dorsum and top of head, and light grey below. All newborns so far described for the subspecies within *P. rufomitrat* (*tephrosceles*, *oustaleti*, *tholloni*) have distinct pink lips and noses that are joined by a pink stripe. These pink parts of the face contrast sharply with the otherwise dark face. This facial pattern is lost in *P. r. tephrosceles* at about 3–4 months of age, but not lost in *P. r. oustaleti* until about 2–3 years. Red and brown colours do not appear in the pelage until about two months of age in *P. r. tephrosceles*, but may appear earlier in *P. r. tholloni*. Adult colouration in *P. r. tephrosceles* occurs at about 3.5 months (Struhsaker 1975 and unpub. data).

There is tremendous variation in colour and other phenotypic characters between and within the subspecies of this subgroup (see above). For example, *P. r. tephrosceles* in the Mbisi Forest of S Tanzania has longer hair than in Kibale, Uganda, and a much higher incidence of stump tails. Fifteen per cent of the Mbisi adults and subadults in a sample of 35 had stump tails, whereas none was seen amongst juveniles (Rodgers *et al.* 1984). These characters are attributed to the high altitude (2400 m) and southerly latitude (07° 40' S) that result in much colder temperatures at Mbisi. Sexual dimorphism, particularly in body size, is most pronounced in *P. r. tephrosceles* and least in *P. r. rufomitrat*.

Geographic Variation

P. r. rufomitrat Tana River Red Colobus. Lower Tana R. forests, Kenya.

Predominantly greyish-brown dorsum. Darker on shoulders and



Tana River Red Colobus *Procolobus rufomitrat rufomitrat* adult male.



Oustalet's Red Colobus *Procolobus rufomitrat oustaleti* adult male.

tail, but paler on rump and lateral surface of limbs. Crown and nape dull orange contrasting with black brow and dark greyish-black face. 'Cow-lick' (whorl) of stiff hairs behind each ear. Dorsum dull greyish-brown to charcoal grey. Ventrums greyish-white.

P. r. tephrosceles Ashy or Uganda Red Colobus. Border of Western Rift in SW Uganda and W Tanzania from Kibale N. P., SW Uganda, to Mbisi F. R., SW Tanzania (ca. 00° 41' N to 07° 55' S; Davenport *et al.* 2007). Resembles *rufomitrat* but much more robust; back and tail dark grey to black; lighter grey sides and ventrum; arms and legs grey with varying amounts of brown on lateral surface especially on the upper or proximal part of the arm; brown usually absent from hindlegs; facial whiskers grey. Face greyish; cap rusty-red with whorled hair above/behind ear (sometimes edged with a black tuft) conspicuous in some individuals. Black on brow extends to ears, sometimes up onto crown. Some ♂ develop conspicuous cape on shoulders. Considerable variation in colour.



Tshuapa Red Colobus *Procolobus rufomitrat tholloni* adult male.

P. r. tholloni Tshuapa or Thollon's Red Colobus. South of the Congo R. east to Lomami R., and south to the Kasai-Sankuru R., DR Congo. Circumfacial hair short, black, except on lower cheeks where hair is whitish. Muzzle square and prominent. Crown deep brown or chestnut, upperparts and outer surfaces of limbs orange-russet. Ventrums whitish with yellowish tone. Upper surfaces of hands and feet dark brown. Tail red for about 70% of its length, terminal tuft black.

P. r. oustaleti Oustalet's Red Colobus. North of Congo R. from Sangha R. in west across the Oubangui R. east to L. Albert. Northern limit is the gallery forests north of the Uele R. and Congo/Nile watershed in S Sudan. South-east limit is the Aruwimi-Ituri R., DR Congo. Medium sized. Highly variable colouration, but predominantly reddish-brown. Crown reddish-brown; face dark. Dorsum varies from dark smoky-brown to olive-brown to coppery-red to dark mahogany. Ventrums paler than dorsum. Hands and feet often black. Tail light brown to black.

P. r. langi Kisangani Red Colobus. Lowland forest east of Congo R. from about Bumba to Boyoma Falls. North of Maiko R. to valley of Aruwimi R., east to piedmont of Western Rift Highlands. Crown, shoulders and front legs deep orange, reddish or chestnut. Dorsum, hindlegs and tail blackish. Ventrums grey.

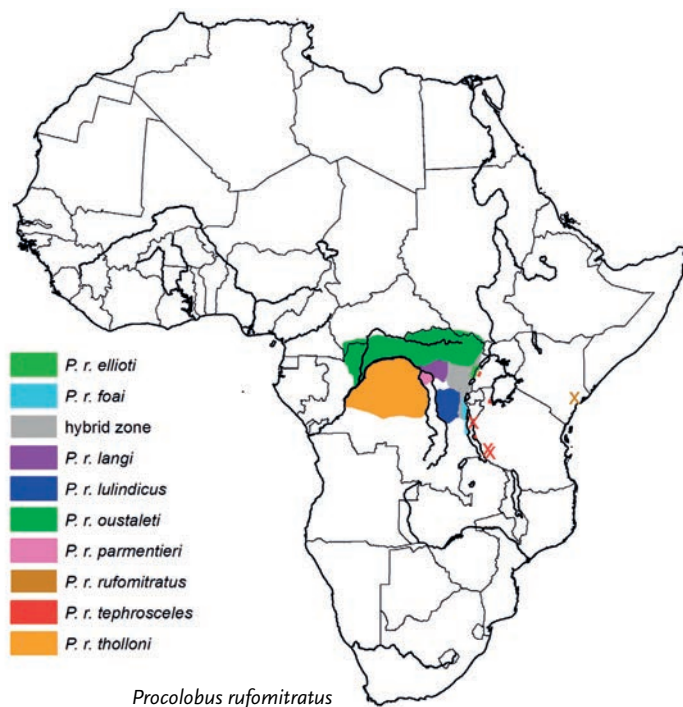
P. r. lulindicus Lulindi River Red Colobus. Riverine (lowland) forest subspecies. Western limit is the Lualaba R. Between Lova-Oso R. in north and Elila R. in south, DR Congo. Crown reddish. Crest poorly developed. Brow-band black. Ears with prominent tufts at base. Proximal dorsum blackish. Distal dorsum and legs reddish. Ventrums greyish. Hands, feet and tail blackish. Pelage short.

P. r. foai Kivu Red Colobus. Montane forest species. Between Lova R. on west side of L. Kivu and ca. 6° S on west shore of L. Tanganyika, E DR Congo. Pelage long, with 'ragged' appearance. Ears with prominent tufts at base. Cheeks often streaked with dark brown freckles. Brows black beneath red tuft on forehead; crown reddish. Proximal dorsum blackish. Distal dorsum reddish. Ventrums greyish. Limbs, hands and feet unicolour, light reddish, paler than distal dorsum. Tail reddish.

P. r. parmentieri Lomami River Red Colobus. Between Lomami R. and Lualaba R., south to Ruiki R. and Lutanga R. Face black with pinkish lips, chin and base of nose. Ears with prominent tufts at base. Frontal band black. Crown brownish-red without crest. Mid-back, shoulders and upper arms black, rest of dorsum and lateral side of arms and legs brick red. Ventrums and throat whitish. Feet and hands black.

P. r. ellioti Semliki Red Colobus. From Congo-Lualaba R. east to Semliki Valley, and west shore of L. Edward. Northern limit the Aruwimi-Ituri R. Southern limit the Maiko R. Highly variable subspecies and probably represents a large hybrid swarm involving *langi* and *semlikiensis* (Colyn 1993). Apart from an orange cap there is no consistent coat colour or pattern (Lorenz von Libernau, L. 1917, Colyn 1993, T. Struhsaker pers. observ.). Predominantly reddish-brown. Crown orange-red. Proximal dorsum and shoulders generally reddish. Saddle grey or reddish tones, hindlegs and tail dark brown, grey or black. Arms rusty orange or grey. Forearms orange-red or charcoal grey.

Similar Species None within geographic range.



Distribution Endemic to central and East Africa. Rainforest, Afromontane–Afroalpine and Coastal Forest Mosaic BZs. From the Sangha R. in W Central African Republic, east to the lower Tana R. in E Kenya, north to S Central African Republic and S Sudan, and south to N Zambia and SW Tanzania (Kingdon 1971, Rodgers 1981, Colyn 1991, 1993, Gautier-Hion *et al.* 1999, Groves 2001, 2007b, Struhsaker 2010). Subspecies distributions given above under Geographic Variation.

Habitat In a variety of forest types, including gallery forest, forest-miombo mosaic, old-growth lowland, mid-altitude and montane moist forest, degraded secondary forests, and raphia palm swamps (Struhsaker 1975, Marsh 1978, 1981, Rodgers *et al.* 1984, Maisels *et al.* 1994, Chapman & Chapman 2000). Present at altitudes from ca. 20 m (lower Tana R., Kenya; Butynski & Mwangi 1994) to 2420 m (Mbizi Forest, SW Tanzania; T. Davenport pers. comm.). Most of the research on *P. rufomitratus* has focused on *P. r. tephrosceles* in Kibale Forest, W Uganda, and on *P. r. rufomitratus* in floodplain/ground water forests along the lower Tana R., E Kenya. In Kibale they are most abundant in moist, old-growth, evergreen forest with emergent trees reaching 50 m in height. Prominent trees in this habitat include: *Parinari excelsa*, *Aningeria altissima*, *Celtis durandii*, *C. africana*, *Markhamia platycalyx*, *Uvariopsis congensis*, *Funtumia latifolia*, *Lovoa swynnertonii*, *Mimusops bagshawei*, *Albizia grandibracteata*, *Newtonia buchananii* and *Piptadeniastrum africanum* (Struhsaker 1975, Chapman & Chapman 2000, Isbell 2012). Common trees in the Tana R. forests include *Sorindeia madagascariensis*, *Ficus sycomorus*, *Diospyros mespiloformis*, *Albizia gummifera* and *A. glaberrima*. Except for the drier lower Tana R. site, *Procolobus rufomitratus* usually occurs where annual rainfall is >1000 mm.

Abundance Extremely common at some sites and rare at others. Population densities of *P. r. tephrosceles* in Kibale range from about 25 to 300 ind/km² (Struhsaker 1975, 1997, Skorupa 1988, Chapman & Chapman 1999, Chapman & Lambert 2000, Teelen 2005). Densities of *P. r. rufomitratus* along the Tana R. range from 33 to 253 ind/km²

(Marsh 1978, Decker 1994a, Mbora 2003). Moderate to heavy levels of selective logging result in very reduced population densities in Kibale (Struhsaker 1975, 1997, Skorupa 1986) that persist for at least several decades (Chapman *et al.* 2000, Struhsaker 2005). Unusually high rates of predation by Robust Chimpanzees *Pan troglodytes* in Kibale, and at Gombe, Tanzania, have also led to major reductions in *P. r. tephrosceles* populations (Wrangham & Bergmann-Riss 1990, Stanford 1998, Mitani & Watts 1999, Mitani *et al.* 2000b, Struhsaker 2005, Teelen 2005). Struhsaker (2005) estimates that there are at least 17,000 *P. r. tephrosceles* in Kibale alone, plus a few thousand more in the small and isolated forests of W Tanzania.

Forest destruction and fragmentation along the lower Tana R. has led to very significant population declines of *P. r. rufomitratus*, which may now number fewer than 1500 individuals (Butynski & Mwangi 1994, 1995, Decker 1994a, Wieczkowski & Mbora 2000, Mbora 2003, Struhsaker 2005). There are no population estimates for other subspecies of *P. rufomitratus*, but *P. r. oustaleti* and *P. r. tholloni* are likely the most numerous because of their vast geographic ranges and large amount of habitat remaining.

Adaptations Diurnal and arboreal. See the subgenus and genus *Procolobus* profiles, as well as the Subfamily Colobinae profile for anatomical and physiological adaptations.

Foraging and Food Folivorous. Daily travel distance for *P. r. tephrosceles* in Kibale is highly variable within and between groups, ranging from ca. 180 to 1185 m. During a 15-month sample period, the daily travel distance of one group of 22 individuals ranged from 222 to 1185 m. Average daily travel distance among five groups in Kibale was between 500 m and 600 m (Struhsaker 1975, Struhsaker & Leland 1987). Daily distances are similar amongst the smaller groups living in the drier and more seasonal riparian forests of the Tana R., Kenya (Decker 1994a). There is disagreement as to whether or not group size affects travel distance (Struhsaker & Leland 1987, Gillespie & Chapman 2001, Struhsaker 2010, Isbell 2012).

Mean annual home-range size varies from ca. 35 ha (Kibale) to 100 ha (Gombe) for *P. r. tephrosceles* (Clutton-Brock 1975, Struhsaker 1975, Struhsaker & Leland 1987), whereas they are only 4–19 ha for *P. r. rufomitratus* in the riverine forest patches along the Tana R. (Decker 1994a). Territoriality is absent amongst the populations studied and groups often have extensive, if not complete, overlap in home-ranges (Struhsaker 2000b). Exceptions exist in heavily logged areas of Kibale where there is little overlap in home-ranges and inter-group encounters are rare (Skorupa 1988, Struhsaker 2000b).

Feeding occurs throughout the day, but is frequently alternated with periods of rest and travel (Struhsaker 1975, Marsh 1981). Time spent feeding during the daylight hours is ca. 23–30% for *P. r. rufomitratus* (Decker 1994a) and ca. 45% for *P. r. tephrosceles* (Struhsaker 1975). Young leaves dominate (ca. 30–50%) the diets of all three subspecies for which there are data, i.e. *P. r. tephrosceles* at Kibale (Struhsaker 1975, 1978b, Clutton-Brock 1975, Chapman & Chapman 2000, Isbell 2012), *P. r. rufomitratus* at Tana R. (Marsh 1981, Decker 1994a) and *P. r. tholloni* at Salonga N. P., DR Congo (Maisels *et al.* 1994). Mature leaves are eaten to a much lesser extent and even then it is usually the petioles and not the lamina that are consumed (Struhsaker 1975, 1978b). In the Salonga N. P., DR Congo, *P. r. tholloni* eats large quantities of seeds (31% of diet). Seeds sometimes dominate the diet

of *P. r. tephrosceles* in Kibale for periods of several weeks (T. Struhsaker pers. obs.). Hundreds of tree and liana species are fed upon. Some of the common food species are: (1) *P. r. tephrosceles*: *C. africana*, *C. durandii*, *N. buchananii*, *M. platycalex*, *Aningeria altissima*, *Milletia dura*, *L. swynnertonii*, *P. excelsa* and *A. grandibracteata*; (2) *P. r. rufomitratu*: *F. sycomorus*, *Sorindeia obtusifoliolata*, *Acacia robusta*, *A. gummifera* and *Pachystela brevipes*; and (3) *P. r. tholloni*: *Guibourtia demeusei*, *Dialium* sp., *Symphonia globulifera*, *Cynometra pedicellata*, *Gilbertiodendron dewevrei* and *Daniella pynaertii*. *Procolobus r. tephrosceles* of Kibale occasionally eats soil from the castings of subterranean termites (T. Struhsaker pers. obs.).

Social and Reproductive Behaviour Social. Groups of *P. r. tephrosceles* average about 45–50 individuals (range 8–80) in Kibale, and 55–59 individuals (range 30–82) in Gombe (Struhsaker 1975, 2000a, b). Groups smaller in the high-altitude and disturbed Mbisi Forest with means of ca. 25 (range <14–30; Rodgers *et al.* 1984) and 40.6 (30–56; Davenport *et al.* 2007). One group of *P. r. tholloni* numbered at least 60 individuals (Maisels *et al.* 1994). Groups of *P. r. rufomitratu* are much smaller, averaging 18 individuals in the 1970s (Marsh 1979), 11 in the late 1980s and early 1990s (Decker 1994a) and 10 (4–31) in 1999–2000 (Mbora 2003). Fission–fusion occurred in a *P. r. tephrosceles* group in a heavily logged area (Skorupa 1988, Struhsaker 1997, 2000a), and for another group in an unlogged part of Kibale (Chapman & Chapman 2000).

Groups of *P. r. tephrosceles* in Kibale and Gombe usually contain several adult ♂♂ (mean = 7–8, range 1–13), but the smaller groups in Mbisi appear to have fewer adult ♂♂ (Struhsaker 2000a, b). Similarly, the large groups of *P. r. oustaleti* in the Ituri Forest, DR Congo, have several adult ♂♂ (T. Struhsaker pers. obs.). *Procolobus r. rufomitratu* at Tana R. is exceptional in that most groups have only one adult ♂ and never more than two (Marsh 1979, Decker 1994a).

Groups of *P. rufomitratu* in Kibale and Gombe contain many adult ♀♀ (mean = 18, range 2–32) and the adult sex ratio (♀ : ♂) averages 2.1 : 1 in Kibale and 1.9 : 1 in Gombe (range 0.6–34, *n* = 16; Struhsaker 2000a, b, 2010). Adult sex ratios are much higher in the one-male groups of *P. r. rufomitratu* at Tana R., averaging 7.3 : 1 in the 1970s (Marsh 1979) and 5.1 : 1 in the late 1980s and early 1990s (Decker 1994a). In general, about 35–50% of group members are immature. Solitary adult and subadult ♂♂ are uncommon. Temporary all-male parties have been seen only in *P. r. rufomitratu* (Marsh 1979).

Amongst *P. r. tephrosceles* in Kibale and *P. r. rufomitratu* at Tana R., all ♀♀ leave their natal groups. Parous ♀♀ transfer between groups and this can occur several times in a lifetime. Even ♀♀ with 1–2-year-old juveniles occasionally transfer between groups. Female transfers appear to be immediate without any aggression (Marsh 1979, Struhsaker & Leland 1979, 1985, Struhsaker & Pope 1991). In contrast, although about half of the *P. r. tephrosceles* ♂♂ in Kibale leave their natal groups, they are rarely able to join other groups. Most of them disappear and presumably die. Males remaining in their natal groups form a coalition among themselves. There is a dominance hierarchy within these ♂ coalitions, which is expressed through displays, and priority of access to food and space. The highest-ranking ♂ undertakes most, but not all, of the copulations. Females sometimes mate with more than one ♂. Red colobus are multiple mounters, i.e. a complete copulation with ejaculation is preceded by a series of incomplete mounts by the same ♂ on the same ♀. No vocalizations are given during copulation, but ♀ *P. r. tephrosceles* often shake their heads and forequarters back

and forth near the end of a complete copulation, perhaps indicating orgasm. Among *P. r. tephrosceles*, copulating pairs are often harassed by other adult ♂♂ and juveniles.

Male dominance ranks and mating success change over time. In Kibale no ♂ has been dominant and the main copulator for more than ca. 3–4 years, but some ♂♂ were reproductively active for nearly 12 years (Struhsaker 1975, 2000b, Struhsaker & Pope 1991). Coalitions of ♂♂ in neighbouring groups fight one another and the outcome of these encounters may be important in determining patterns of ♀ transfer. Females do not usually participate in these fights nor those within groups (Struhsaker 1975). In contrast, *P. r. rufomitratu* along the Tana R. is exceptional in that adult ♂♂ are much less tolerant of one another and groups usually contain only one or, occasionally, two adult ♂♂. On the Tana ♂♂ are able to immigrate and take over groups from incumbent ♂♂. All-male groups are uncommon and unstable in the Tana population (Marsh 1979).

Allogrooming is common and adult ♀♀ are the primary groomers. In contrast, allomothering is extremely rare (Struhsaker 1975). Only once was a *P. r. tephrosceles* ♀ seen carrying another female's infant. She carried this infant along with her own infant for several days until one of the infants disappeared (T. Struhsaker pers. obs.). Play amongst immatures is common during their first two years. The vocal repertoire size of *P. r. tephrosceles* is complex and may contain more than 25 different calls, many of which are components of a graded system (Marler 1970, Struhsaker 1975, 2010). The repertoires of *P. r. oustaleti*, *P. r. ellioti* and *P. r. rufomitratu* are less well studied, but they appear identical to *P. r. tephrosceles* (T. Struhsaker pers. obs.). It appears that *P. r. rufomitratu* on the Tana vocalize much less than the other subspecies of *P. rufomitratu* (Struhsaker 1975). This may be a consequence of their smaller, one-male, social groups.

Polyspecific associations are common for *P. rufomitratu* and have been particularly well documented for the *P. r. tephrosceles* of Kibale. During line transects 72% of all encounters with red colobus groups in unlogged forest were with other monkey species (Struhsaker 2000a). Although they associated with five other monkey species in Kibale, they most typically associated with Red-tailed Monkeys *Cercopithecus (c.) ascanius*. It appears that these associations are formed primarily in response to predation pressure from African Crowned Eagles *Stephanoaetus coronatus* and secondarily to habitat quality, the cost to benefit ratio of foraging together, convergence at common foods and by chance alone (Struhsaker 1981a, 2000b, Chapman & Chapman 2000).

Reproduction and Population Structure Adult ♀♀ have perineal swellings, which are very large (ca. 7–10 × 7–10 cm) in *P. r. oustaleti* (T. Struhsaker pers. obs.) and much smaller (ca. one-third this size) in *P. r. tephrosceles* and *P. r. rufomitratu* (Struhsaker 1975). These swellings appear to occur during oestrus and ovulation, but also occur at other times, such as during pregnancy (Struhsaker & Leland 1985, T. Struhsaker pers. obs.). Oestrous *P. r. tephrosceles* may give off olfactory cues because ♂♂ often nuzzle a female's perineum before mounting her (Struhsaker 1975).

Gestation length is ca. 6–7 months (Struhsaker & Leland 1985). Copulations and births occur in all months, but at Kibale most *P. r. tephrosceles* births occurred during three relatively wet months (Apr, May and Nov) and one dry month (Jun) (Struhsaker 1997). Likewise, no seasonality in births was observed during an 18-month study of *P. r. rufomitratu* (Marsh 1978). Single births are the rule and no twins have

been recorded. Weight at birth unknown, but an infant *P. r. tephrosceles* estimated to be <4 months old weighed 0.5 kg (Struhsaker 1975). The average inter-birth interval for 16 recognizable *P. r. tephrosceles* in Kibale over 18 years was 24.4 months ($n = 73$ births to 16 ♀♀) and 27.5 months when cases of neonatal mortality were excluded (Struhsaker & Pope 1991). A similar inter-birth interval appears to occur among the *rufomitratus* of the Tana R. based on ratios of infants per adult ♀ (Marsh 1979, Decker 1994a, Struhsaker *et al.* 2004). Weaning is a gradual process and is usually complete in *P. r. tephrosceles* by about 12–18 months. Reproductive and physical maturity are reached in about 5.0–5.5 years both in ♂ and ♀ *P. r. tephrosceles* (Struhsaker & Leland 1985, Struhsaker & Pope 1991).

Infanticide by one ♂ was observed during a long-term study of a multimale group of *P. r. tephrosceles* (Struhsaker & Leland 1985) and suspected in *P. r. rufomitratus* when a ♂ replaced the resident ♂ (Marsh 1979). In both cases the evidence supported the hypothesis that infanticide is a reproductive strategy. Mowry (1995) observed possible infanticidal behaviour by a ♂ *P. r. rufomitratus*, but the infant survived the attack.

Population structure is essentially the same as that given for group composition because solitaries are uncommon. Maximum longevity is unknown, but one adult ♀ *P. r. tephrosceles* was observed for nearly 15 years. Because she was fully adult at the initiation of observations, she was probably at least 20 years old when she died (Struhsaker & Pope 1991). Mean annual birth rate in *P. r. tephrosceles* is 0.49 (Struhsaker & Pope 1991). Mean survivorship to adulthood is estimated as 39%. Assuming a 1 : 1 sex ratio at birth, survivorship to adulthood was 47% for ♀♀ and 34% for ♂♂ (Struhsaker & Pope 1991).

Predators, Parasites and Diseases Major predators on *P. r. tephrosceles* are African Crowned Eagles (Struhsaker & Leakey 1990, Mitani *et al.* 2001) and Robust Chimpanzees (Wrangham & Bergmann-Riss 1990, Stanford 1998, Mitani & Watts 1999, Mitani *et al.* 2000b, Struhsaker 2005, 2010, Teelen 2005, Lwanga *et al.* 2011). A herpes-like disease afflicted some *P. r. tephrosceles* in Kibale and apparently killed five out of ten adult ♂♂ in one group over a 2.5 year period (Struhsaker 2000b). Predation by humans is particularly important in DR Congo, e.g. *P. r. tholloni* (Thompson 2000, Struhsaker 2010).

Conservation IUCN Category (2012): Least Concern as *P. rufomitratus*. Endangered as *P. r. rufomitratus* and *P. r. tephrosceles*. Other subspecies Near Threatened, Least Concern or Not Evaluated. CITES (2012): Appendix I for *P. r. rufomitratus*. Other subspecies Appendix II.

Procolobus r. rufomitratus listed as one of the world's 25 most threatened primates since 2002 (Mbora & Butynski 2007, 2009). The main threat to *P. r. rufomitratus* is habitat loss due primarily to agricultural clearing and extraction of forest products by local communities (Butynski & Mwangi 1994, 1995, Wiczowski & Mbora 2000, Decker 1994a, Mbora 2003, Moinde-Fockler *et al.* 2007) and secondarily to alteration of river flow volume and cycles by five hydroelectric power dams upriver (Hughes 1985, Butynski 1995b). Less than 35% of the *P. r. rufomitratus* population is legally protected within the Tana River Primate National Reserve, but even there the habitat is insecure because of inadequate law enforcement (Butynski & Mwangi 1994, 1995, Wiczowski & Mbora 2000). Given the small size, grave threats, and presence of another endemic, Endangered, primate (Tana River Mangabey *Cercocebus galerritus*), the

forests of the lower Tana R. represent the most important site in East Africa for primate conservation actions (De Jong & Butynski 2012). A small subpopulation of *P. r. rufomitratus* was discovered in 2009 at the north end of the Tana Delta (Hamerlynck *et al.* 2012).

The largest population of *P. r. tephrosceles* is in the Kibale N. P. where the habitat is well protected. In Kibale and Gombe, however, the greatest threat to *P. r. tephrosceles* is predation by Robust Chimpanzees, where it is estimated that they kill between 6% and 40% of these monkeys annually (Stanford 1998, Watts & Mitani 2002, Teelen 2005). As a result, *P. r. tephrosceles* populations have declined in both of these national parks in the last 20–25 years (Struhsaker 2005). The Kibale population should be monitored on an annual or semi-annual basis. Status surveys should be done of smaller populations of *P. r. tephrosceles* in areas such as Mahale Mountains N. P., Mbisi F. R. and the Biharamulo region of Tanzania.

Nothing is known of the population status of the other subspecies of *P. rufomitratus*. The very extensive range of some, such as *P. r. oustaleti* and *P. r. tholloni*, suggests their conservation status might not be as dire as those taxa living farther east. Thompson (2000), however, describes the very extensive and intensive hunting pressure on *P. r. tholloni*, which has likely increased with continuous expansion of the bushmeat trade and its extension into rapidly growing urban centres, with the proliferation of weapons and ammunition, all associated with the long-standing conflicts and insecurity in DR Congo. The same problem likely applies to other subspecies of *P. rufomitratus* living in DR Congo. Obvious conservation actions include: more conservation areas; greater law enforcement, conservation education and surveys to better understand the status and conservation problems facing the *P. rufomitratus* of DR Congo.

Measurements

Procolobus rufomitratus

P. r. tholloni

HB (♀♀): 580, 600 mm, $n = 2$

T (♀): 690 mm, $n = 1$

HF (♀♀): 150, 170 mm, $n = 2$

E (♀): 35 mm, $n = 1$

WT estimated to be in lower range for red colobus at 7–10 kg (average WT estimate for red colobus at 8–12 kg)

From Allen (1925) and BMNH

P. r. oustaleti (cf. *powelli*)

HB (♂♂): 540 (455–590) mm, $n = 17$

HB (♀♀): 524 (480–565) mm, $n = 12$

T (♂♂): 726 (650–800) mm, $n = 17$

T (♀♀): 713 (645–790) mm, $n = 12$

HF (♂♂): 186 (170–198) mm, $n = 17$

HF (♀♀): 182 (170–202) mm, $n = 12$

E (♂♂): 39 (35–42) mm, $n = 17$

E (♀♀): 37 (35–40) mm, $n = 12$

WT estimated to be in mid to low range for red colobus at 8–11 kg

From Allen (1925) and BMNH

P. r. oustaleti (cf. *brunneus*)

HB (♂♂): 550, 560 mm, $n = 2$

HB (♀♀): 490 (450–520) mm, $n = 5$

T (♂♂): 630, 770 mm, $n = 2$

T (♀♀): 580 (430–650) mm, $n = 5$

HF (♂♂): 160, 195 mm, n = 2
 HF (♀♀): 163 (154–172) mm, n = 5
 E (♂♂): 25, 35 mm, n = 2
 E (♀♀): 32 (29–35) mm, n = 5
 From Allen (1925) and BMNH

P. r. oustaleti (cf. *brunneus*)
 HB (♂♂): 582 (525–610) mm, n = 10
 HB (♀♀): 559 (510–585) mm, n = 5
 T (♂♂): 714 (633–785) mm, n = 10
 T (♀♀): 709 (650–750) mm, n = 5
 HF (♂♂): 191 (180–200) mm, n = 10
 HF (♀♀): 189 (183–203) mm, n = 5
 E (♂♂): 40 (38–42) mm, n = 10
 E (♀♀): 39 (35–42) mm, n = 5
 WT (♀♀): 5.4 (S.D. = 0.5) kg, n = 21
 Linear measurements from Allen (1925) and BMNH
 WT from Gevaerts (1992). Based on 21 non-pregnant adult ♀♀ *P. rufomitrat* from bushmeat markets in Bondo, Kisangani and Kindu, DR Congo. These are likely to be mostly *P. r. oustaleti*, but probably also include some *P. r. langi*, *P. r. lulindicus*, *P. r. parmentieri*, and perhaps other subspecies. Range not given.

P. r. tephrosceles
 HB (♂♂): 615 (584–648) mm, n = 5
 HB (♀): 584 mm, n = 1
 T (♂♂): 691 (660–724) mm, n = 5
 T (♀): 686 mm, n = 1
 HF (♂♂): 182 (171–191) mm, n = 5
 HF (♀): 171 mm, n = 1
 E (♂♂): 35 (32–41) mm, n = 5
 E (♀): 29 mm, n = 1
 WT (♂): 10.5 kg, n = 1
 WT (♀): 5.8 kg, n = 1
 Kibale Forest, Uganda (Struhsaker 1975)

P. r. ellioti (cf. *semlikiensis*)
 HB (♂♂): 512 (480–540) mm, n = 5
 HB (♀♀): 520 (500–540) mm, n = 3
 T (♂♂): 640 (540–750) mm, n = 5
 T (♀♀): 643 (600–680) mm, n = 3
 HF (♂♂): 168 (160–189) mm, n = 5
 HF (♀♀): 170 (165–175) mm, n = 3
 E (♂♂): 31 (29–33) mm, n = 5
 E (♀♀): 30 (29–30) mm, n = 3
 From Allen (1925) and BMNH

P. r. rufomitrat
 WT: (♂♂): 9.7 (9.0–10.0) kg, n = 3
 WT: (♀♀): 7.2 (6.0–8.0) kg, n = 7
 Lower Tana R., Kenya (Delson *et al.* 2000)

P. r. tholloni
 GLS (♂♂): 113.6 (108–119) mm, n = 16

GLS (♀♀): 104.4 (97–111) mm, n = 26
 GWS (♂♂): 84.4 (78–90) mm, n = 16
 GWS (♀♀): 72.9 (66–78) mm, n = 26
 Kunungu, DR Congo (Colyn 1991)

P. r. oustaleti
 GLS (♂♂): 112.2 (108–118) mm, n = 17
 GLS (♀♀): 104.5 (98–109) mm, n = 17
 GWS (♂♂): 87.8 (84–92) mm, n = 18
 GWS (♀♀): 76.2 (72–82) mm, n = 16
 Akenge, DR Congo (Colyn 1991)

P. r. oustaleti
 GLS (♂♂): 108.3 (105–112) mm, n = 7
 GLS (♀♀): 103.3 (100–106) mm, n = 3
 GWS (♂♂): 86.9 (84–90) mm, n = 6
 GWS (♀♀): 75.4 (73–78) mm, n = 2
 Zokwa, DR Congo (Colyn 1991)

P. r. oustaleti
 GLS (♂♂): 114.4 (110–120) mm, n = 12
 GLS (♀♀): 104.2 (99–108) mm, n = 13
 GWS (♂♂): 90.3 (87–93) mm, n = 11
 GWS (♀♀): 76.8 (72–80) mm, n = 12
 Faradje, DR Congo (Colyn 1991)

P. r. oustaleti
 GLS (♂♂): 111.8 (107–115) mm, n = 7
 GLS (♀♀): 101.5 (99–105) mm, n = 4
 GWS (♂♂): 86.2 (82–89) mm, n = 7
 GWS (♀♀): 77.6 (74–81) mm, n = 4
 Oubangui, DR Congo (Colyn 1991)

P. r. langi
 GLS (♂♂): 103.1 (98–109) mm, n = 31
 GLS (♀♀): 98.9 (94–104) mm, n = 32
 GWS (♂♂): 78.3 (74–86) mm, n = 31
 GWS (♀♀): 69.8 (66–72) mm, n = 32
 Batiakuya, DR Congo (Colyn 1991)

P. r. lulindicus
 GLS (♂♂): 107.8 (98–113) mm, n = 24
 GLS (♀♀): 100.4 (94–107) mm, n = 13
 GWS (♂♂): 81.5 (75–86) mm, n = 22
 GWS (♀♀): 70.8 (68–76) mm, n = 13
 Mulongo, DR Congo (Colyn 1991)

P. r. foai
 GLS (♂♂): 113.0 (107–120) mm, n = 18
 GWS (♂♂): 86.0 (82–93) mm, n = 18
 Baraka Region, DR Congo (Colyn 1991)

P. r. parmentieri
 GLS (♂♂): 112.0 (105–118) mm, n = 31
 GLS (♀♀): 104.7 (101–109) mm, n = 32
 GWS (♂♂): 86.0 (79–91) mm, n = 29
 GWS (♀♀): 75.4 (69–80) mm, n = 32

Mabobi, DR Congo (Colyn 1991)

P. r. ellioti
 GLS (♂♂): 108.3 (99–116) mm, n = 32
 GLS (♀♀): 100.2 (90–107) mm, n = 27
 GWS (♂♂): 84.4 (71–91) mm, n = 28
 GWS (♀♀): 73.2 (68–79) mm, n = 27
 Hybrid zone, DR Congo (Colyn 1991)

P. r. ellioti (cf. *semlikiensis*)
 GLS (♂♂): 110.3 (108–114) mm, n = 9
 GWS (♂♂): 84.9 (81–92) mm, n = 9
 Semliki R., DR Congo (Colyn 1991)

P. r. tephrosceles
 GLS (♂♂): 110.8 (105–115) mm, n = 12
 GLS (♀♀): 99.3 (95–103) mm, n = 4
 GWS (♂♂): 84.0 (79–88) mm, n = 11
 GWS (♀♀): 73.5 (71–77) mm, n = 4
 Uganda (Verheyen 1962, BMNH)

P. r. tephrosceles
 GLS (♂♂): 108.7 (105–112) mm, n = 9
 GWS (♂♂): 84.6 (80–88) mm, n = 9
 Semliki R., DR Congo (Colyn 1991)

P. r. tephrosceles
 GLS (♂♂): 116.0 mm, n = 1
 GWS (♂♂): 88.0 mm, n = 1
 Nyamanzi R., Tanzania (Verheyen 1962, BMNH)

P. r. tephrosceles
 GLS (♂♂): 119.0 mm, n = 1
 GWS (♂♂): 94.0 mm, n = 1
 Mbizi Forest, Ufipa, Tanzania (Verheyen 1962, BMNH)

P. r. tephrosceles
 GLS (♀♀): 96.0 mm, n = 1
 GWS (♀♀): 70.0 mm, n = 1
 Ruiga Bay, Tanzania (Verheyen 1962, BMNH)

P. r. rufomitrat
 GLS (♂♂): 106.5 (101–111) mm, n = 4
 GLS (♀♀): 92.0 (91–94) mm, n = 5
 GWS (♂♂): 83.3 (80–87) mm, n = 4
 GWS (♀♀): 68.0 (66–70) mm, n = 5
 Lower Tana R., Kenya (Verheyen 1962, BMNH, J. Wierzchowski & T. Butynski pers. comm.)

Key References Colyn 1991; Decker 1994a; Maisels *et al.* 1994; Marsh 1978; Struhsaker 1975, 2010; Struhsaker & Pope 1991.

Thomas T. Struhsaker & Peter Grubb

Procolobus gordonorum UDZUNGWA RED COLOBUS (IRINGA / UHEHE / GORDON'S RED COLOBUS)

Fr. Colobe bai d'Udzungwa; Ger. Udzungwa-Stummelaffe

Procolobus gordonorum (Matschie, 1900). Sitzb. Ges. Naturf. Fr. Berlin, p. 186. Udzungwa Mts, Iringa, Tanzania.Udzungwa Red Colobus *Procolobus gordonorum* adult male.*Procolobus gordonorum*

Taxonomy Monotypic species. The Udzungwa (= Uzungwa) Red Colobus has been considered a subspecies of Western Red Colobus *Procolobus badius*, Pennant's Red Colobus *Procolobus pennantii*, Tana River Red Colobus *Procolobus rufomitratus* or Zanzibar Red Colobus *Procolobus kirkii*, or as a full species, *P. gordonorum* (Groves 2001, 2005c, 2007b, Grubb *et al.* 2003). Molecular (Ting 2008a, b) and craniometric (Cardini & Elton 2009) data indicate a close relationship with *P. kirkii*. Synonyms: none. Chromosome number: unknown.

Description Medium-sized arboreal monkey with a tricolour pattern of contrasting blackish, whitish and reddish. Sexual dimorphism not pronounced, although adult ♂ has longer canines, slightly larger, more robust and broader head, and thicker tail than adult ♀. Female has a prominent clitoris. Nose and lips pinkish. Cheeks white. Face dark grey to black. Crown cap extensive like an inverted bowl or toupee varying in colour from bright orange-red, brilliant rufous, to red-brown; this colour sometimes extending down the neck, separated from white cheeks by thick black band along brow and temples. Body hair of moderate length, somewhat longer on shoulders. Upper parts, including limbs and most of tail, predominantly glossy black to charcoal grey, with silver-white hairs invading the lower hindlimbs. Anterior edge of shoulders and underparts, including insides of limbs, throat and underside of first 20 cm of tail, whitish. Feet black. In one sample 2% of the monkeys had reddish lumbar-sacral patch. Top of the head of one adult or subadult ♀ entirely grey without any orange-red. Entire back of one adult ♀ orange-red like top of head. Some tails entirely orange-red, while others only partly orange-red or white (Struhsaker & Leland 1980, Ehardt *et al.* 1999, A. R. Marshall pers. comm., T. Struhsaker pers. obs.). Infants up to ca. 3–4 months of age have face dark grey

or blackish while nose and mouth are pale pink like adults. Head and back black. Ventrums grey.

Geographic Variation No pattern of geographic variation observed over the small geographic range of this species, but much intra-specific variation present (see Description).

Similar Species None within geographic range.

Distribution Endemic to south-central Tanzania. Afroalpine BZ and moist evergreen and semi-deciduous forests and miombo woodland adjacent to these forests. Populations occur throughout the Udzungwa Mts, including the following forests in the Udzungwa Mountains N. P.: Mwanihana (probably largest population), Iwonde, Mlale, Matundu and Luhombero; and in the following Forest Reserves: W Kilombero (including Ndundulu, Nyumbanitu, Ukami, Iyondo), Matundu, Udzungwa Scarp, Nyanganje, Kiranzi-Kitungulu and New Dabaga/Ulangambi. Also collected or reported from the non-reserved forests of Muhanga/Boma la Mzinga and Mbongolo that are south of Dabaga. Also in the Kilombero Valley at the eastern base of the Udzungwa Mts in the following forest patches: Magombera, Kiwanga and Kalunga (this forest is now gone). Also in gallery forest along the Msolwa R. south of the railway to its confluence with the Kilombero R., including the Ibiki and Msitu ya Kinjugu Forests (Struhsaker & Leland 1980, Rodgers 1981, Rodgers & Homewood 1982, Decker 1994b, Ehardt *et al.* 1999, Dinesen *et al.* 2001, Struhsaker *et al.* 2004, Marshall *et al.* 2005, P. Grubb pers. obs.). Probably now

extinct in the Lukoga Forest as this forest was essentially destroyed in 1998 (Ehardt *et al.* 1999).

Habitat *Procolobus gordonorum* occurs in a wide variety of forest types ranging in altitude from ca. 250 to 2200 m (Struhsaker & Leland 1980, Rodgers & Homewood 1982, Ehardt *et al.* 1999, Dinesen *et al.* 2001, Struhsaker *et al.* 2004, Marshall *et al.* 2005), including lowland old-growth, secondary and montane forests of the Udzungwa Mts and miombo *Brachystegia* spp. woodland adjacent to old-growth or secondary forest in the lower parts of the Mwanihana forest and elsewhere. Most abundant in low to medium altitude mixed evergreen and semi-deciduous forests (ca. 300–700 m) of the Mwanihana Forest where the canopy attains heights of 30–40 m and annual precipitation is 2000–2500 mm. Prominent tree species in this habitat include: *Parinari excelsa*, *Albizia gummifera*, *Erythrophleum suaveolens*, *Afrosersalia cerasifera*, *Parkia filicoidea*, *Bequartiodendron natalensis*, *Lettowianthus stellatus*, *Chlorophora excelsa*, *Anthocleista grandiflora* and several *Ficus* spp. (F. Rovero & A. R. Marshall pers. comm.). Also in drier, more seasonal forest types (i.e. semi-deciduous, gallery and ground-water forests in the Kilombero Valley).

Abundance Common at some sites. Most recently, Rovero *et al.* (2009) estimated 25,000–35,000 animals. Group encountered rates 0.11/km and 0.46/km at two sites in Udzungwa Mts (Rovero *et al.* 2012) and 1.28/km in Magombera Forest (Rovero *et al.* 2009). Population density varies widely and may be lower at higher altitudes (Dinesen *et al.* 2001, Marshall *et al.* 2005). Rovero *et al.* (2006) estimate 180–245 ind/km² in the low to medium altitude forests of Mwanihana. This means that the largest interbreeding population is likely greater than 2000 individuals. Preliminary estimates indicate at least 1000 in the 10 km² Magombera Forest (A. R. Marshall pers. comm., T. Struhsaker pers. obs.). Uncommon in the more seasonal, lowland gallery forest along the Msolwa R.

Adaptations Diurnal and arboreal. *Procolobus gordonorum* eat soil from the ground and from arboreal termite tunnels in the Mwanihana Forest (A. R. Marshall & A. Pucci pers. comm., T. Struhsaker pers. obs.), presumably for minerals and/or to adsorb anti-feedants and toxins, thereby assisting digestion and nutrient absorption. The daily activity pattern consists of several periods of feeding, travel and social behaviour that alternate with periods of rest.

Foraging and Food Folivorous. Feeding occurs off and on throughout the day and constitutes ca. 34–41% of the diurnal time budget (Rovero 2003). In a preliminary study groups moved 200–600 m/day (F. Rovero pers. comm.). Tree leaves are the most common foods. In Magombera Forest (270 m) foods included: young leaves of *Ochna* sp., mature leaf petioles of *Parkia filicoidea* and unripe, medium-sized fruit of *Treculia africana* (Struhsaker & Leland 1980). In Mwanihana Forest (ca. 700 m) Wasser (1993) recorded 45 plant food species, with the most commonly eaten being: *A. cerasifera*, *A. gummifera*, *Tabernaemontana pachysiphon*, *Uapaca paludosa*, *P. filicoidea*, *E. suaveolens*, *Lagynias pallidiflora* and *Entada pursaetha*. Leaf petioles constituted more than 60% of the feeding observations and 99% of these were mature petioles. Young leaves were the second most common food items (ca. 17%). Rovero (2003) studied two groups

in the Mwanihana Forest, one at ca. 700 m and one at ca. 300 m, and found that leaf lamina (mainly young leaves) were the most frequently items eaten (71% of feeding observations). Leaf petioles constituted only 13% of the diet. He recorded at least 52 plant food species. The most common were: *Parinari excelsa*, *Saba comorensis*, *Antiaris toxicaria* and *Sorindeia madagascariensis*. There are no data on seasonal changes in diet, age and sex differences in diet, on food availability, or on home-range size.

Social and Reproductive Behaviour Social. *Procolobus gordonorum* lives in groups of 7–83 animals (mean = 36.3, S.D. \pm 15.1, n = 60). Solitary individuals, including adult ♂♂ and adult ♀♀ with clinging infants, are uncommon (Struhsaker *et al.* 2004). No all-male associations observed. Group size is largest in large blocks of moist, old-growth, mixed evergreen and semi-deciduous forest, and smallest in small patches of drier, more seasonal, semi-deciduous and degraded forests (Struhsaker *et al.* 2004). Groups in highly degraded forests appear to have fission–fusion societies (Struhsaker *et al.* 2004). Social groups in Mwanihana Forest (large, moist, mature, mixed evergreen and semi-deciduous) have more adult ♀♀ per adult ♂♂ than those in the smaller, highly degraded and semi-deciduous Kalunga Forest (4.1 vs. 3.1), but this difference is not statistically significant (Struhsaker *et al.* 2004). Adults and subadults constitute ca. 65–69% of the group, and juveniles and infants ca. 31–35% (Struhsaker *et al.* 2004).

Little is known about the social behaviour of this species (Struhsaker & Leland 1980), but T. T. Struhsaker's unpublished observations are summarized here. Adult ♂♂ give 'leaping-about' displays while vocalizing. Adult ♂♂ give stylized presentations of their hindquarters to one another and the presenter sometimes squeals. Immatures also present their hindquarters to adult ♂♂, and sometimes adult ♂♂ present to adult ♀♀. These stylized presentations are like those of the Uganda Red Colobus *P. rufomitratus tephrosceles* (Struhsaker 1975). Adult ♂♂ within a group are tolerant of one another and often sit together. Fighting between ♂♂ of a group not seen, but supplantations over potential mates do occur. Preliminary evidence indicates that adult ♂♂ form the stable core of the group – like the groups of *P. r. tephrosceles*. Aggression between adult ♀♀ is rare. Social grooming is common and adult ♀♀ are the primary groomers.

Copulation occurs as a series of mounts with thrusting (up to at least ten mounts). The final mount of the series is terminated with a pause when ejaculation is assumed to occur. The male's feet remain on the substrate and do not grasp the female's ankles. He grasps the female's body with his hands along her sides near her back and hips. Often the ♀ shudders during the thrusting or when the ♂ is pausing (ejaculating?). This shudder may indicate orgasm. No vocalizations have been heard before, during or after copulation. Before mounting, the ♂ sometimes muzzles the female's perineum and/or briefly handles her swelling and/or clitoris with his fingers. Females being mounted usually have large perineal swellings (see below) (Struhsaker & Leland 1980). Small juveniles sometimes harass copulating pairs of adults and will even grab the adult ♂ while he is mounted. Harassed ♂♂ sometimes slap toward and supplant these juveniles. Once an adult ♀ slapped twice toward a young adult ♀ with perineal swelling who was being repeatedly mounted by an adult ♂. Eventually, the ♂ left the young ♀ and suckled from the

aggressive adult ♀. Adult ♂♂ supplant one another for priority of copulation with swollen ♀♀.

Allomothering is not observed. Mothers seem to be the only ones that carry and groom infants. Play is common among small and medium-sized juveniles.

Group ranges overlap extensively, with no indication of territoriality (T. Struhsaker pers. obs.). Groups of *P. gordonorum* associate with other primate species up to 90% of the time. Most associations are with Peters's Angola Colobus *Colobus angolensis palliatus* and Sykes's Monkey *Cercopithecus (n.) mitis* (Struhsaker & Leland 1980, Wasser 1993, Ehardt *et al.* 1999). Juvenile *P. gordonorum* play with juvenile baboons *Papio cynocephalus* on the ground. Young baboons mount and thrust adult ♀ and juvenile *P. gordonorum*. Juvenile *P. gordonorum* also groom juvenile baboons. Once, a juvenile baboon approached and tried to touch an infant *P. gordonorum* that was clinging to its mother, but the mother turned away and soon left with her infant (A. R. Marshall pers. comm., T. Struhsaker pers. obs.).

At least eight types of vocalizations are recognized in *P. gordonorum* (Struhsaker & Leland 1980, Struhsaker 2010). The longest, most complex and variable calls are those given by adult ♂♂ (nasal 'shriek-squawks' and 'quavers'). No detailed systematic study has been done on the context and probable function of these vocalizations, but the long calls of ♂♂ often seem to be associated with the initiation of group progressions. The vocal repertoire of *P. gordonorum* is most like that of *P. kirkii*.

Reproduction and Population Structure Adult ♀♀ have very large pink perineal swellings (ca. 10 × 10 cm, T. Struhsaker pers. obs.). This is apparently related to ovulation because swollen ♀♀ have complete copulations with adult ♂♂. These swellings are larger than those of any of the other East African red colobus taxa, but like those of adult ♀ Temminck's Red Colobus *Procolobus badus temminckii* in Gambia and Senegal, Upper Guinea Red Colobus *Procolobus badius badius* in Taï Forest, Côte d'Ivoire, and Preuss's Red Colobus *Procolobus preussi* in Korup N. P., Cameroon (Struhsaker 1975). Gestation length is not known. There is no pronounced birth season. Young infants, swollen adult ♀♀ and copulations occurred during all study months, i.e. Feb, Jul, Aug, Sep and Oct (Struhsaker & Leland 1980, T. T. Struhsaker pers. obs.).

Single births are the rule. No twins observed. Inter-birth intervals are not known, but ratios of infants to adult ♀ are lower in the small, semi-deciduous and heavily degraded Kalunga Forest (mean = 0.19 infants/adult ♀, n = 5 groups) than in the larger and more mature Mwanihana Forest (mean = 0.41 infants/adult ♀, n = 12 groups, or in the ground-water, and more evergreen, Magombera Forest (mean = 0.53 infants/adult ♀, n = 6 groups (Struhsaker *et al.* 2004). These ratios suggest that fecundity is adversely affected by forest degradation and loss of food trees.

Growth rates and age of physical and sexual maturity are unknown. However, long-term studies of *P. r. tephrosceles* in Kibale show that most juveniles stop nursing by 18–24 months of age, corresponding to the 2-year inter-birth interval in that population. Although older ♂♂, including adults, do suckle from adult ♀♀ in Kibale, this was extremely rare (T. Struhsaker pers. obs.). In contrast, nursing by large juvenile ♂♂ and adult ♂♂ was observed at least six times among *P. gordonorum* during relatively few hours of observation (T. Struhsaker

pers. obs.). All these observations were in degraded forest and may reflect nutritional stress resulting in a longer period of suckling and longer inter-birth intervals. No large juvenile or subadult ♀♀ were observed suckling, suggesting greater investment by mothers in their sons than in their daughters.

Population structure is probably the same as that of social groups. Mortality rates are unknown, but, unless the sex ratio is very skewed at birth, mortality must be higher among ♂♂ than ♀♀ because the adult sex ratio is 3–4 ♀♀ per ♂ in social groups. Solitary adult ♂♂ are not common enough to account for this difference. Group composition and ratios of juveniles to adult ♀♀ indicate that mortality rates among medium-sized juveniles and subadult ♂♂ are slightly higher in small, semi-deciduous and degraded forests than in larger, more mature, evergreen forests (Struhsaker *et al.* 2004). There is no information on longevity.

Predators, Parasites and Diseases The African Crowned Eagle *Stephanoaetus coronatus* is common throughout the range of *P. gordonorum* and is likely its most important predator. Although no cases of predation have been observed, *P. gordonorum* and all other species of primate in the Udzungwa Mts and Kilombero Valley give strong vocal responses to these eagles whenever they are nearby. Leopards *Panthera pardus* are common in many areas of the Udzungwas and they too may prey upon *P. gordonorum*. The local Wahehe people reportedly hunt *P. gordonorum*, particularly in the western and south-western parts of the range. There is no published information on diseases and parasites.

Conservation IUCN Category (2012): Endangered. CITES (2012): Appendix II.

Owing to its highly fragmented habitat, the largest population of *P. gordonorum* may number no more than 2000 individuals (Rodgers & Homewood 1982), but more recent estimates (Rovero *et al.* 2006) indicate that the Mwanihana population may be much larger than that. Forest fragments (and separation of *P. gordonorum* populations) within the Udzungwa Mts are maintained largely by fires. These fires prevent forest regeneration and the rejoining of forest patches (Ehardt *et al.* 1999, Dinesen *et al.* 2001, Marshall *et al.* 2001, Struhsaker *et al.* 2004). The majority of these fires are probably started by poachers. *Procolobus gordonorum* is adversely affected by logging, farming and other human activities that degrade and destroy forests (Struhsaker *et al.* 2004). Populations of *P. gordonorum* within the Udzungwa Mountains N. P. are reasonably secure, while those in Forest Reserves and on public land are not. The small forest remnants in the Kilombero Valley are particularly vulnerable. Here the local people are degrading and destroying forest through the removal of trees for timber, firewood, charcoal, building poles and farmland. For example, the Lukoga and Kalunga Forest Reserves have been destroyed over the past decade (Ehardt *et al.* 1999, T. Struhsaker pers. obs.). The Magombera Forest Reserve was officially reduced from ca. 11–15 km² to 6 km² in 1980 to provide land to settlers. However, Landsat images taken in 1999 indicated the size of Magombera to be ca. 10–11 km². In 2002 the remainder of this important forest (that holds more than 1000 *P. gordonorum* and several endemic species of plants) was almost destroyed when the government of Tanzania agreed to relocate squatters there from the nearby Kilombero Sugar Estate. Fortunately the international

conservation community launched a successful appeal that averted this destruction. None the less, Magombera remains under serious threat, as do all Forest Reserves where there is ineffective protection (e.g. Udzungwa Scarp, West Kilombero and Matundu). Hunting of *P. gordonorum* by humans is reported to occur, but there are no data on its extent.

Conservation priorities for *P. gordonorum* are: (1) annexation of the following Forest Reserves to the Udzungwa Mountains N. P.: W. Kilombero (including: Ndundulu, Nyumbanitu, Ukami, Iyondo), Udzungwa Scarp, Matundu and Nyanganje; (2) annexation of the following forests to the Selous G. R.: Magombera, Ibiki and all other forest remnants along the Msolwa R.; (3) prevention of fire to allow forest expansion and establishment of corridors between forest blocks, thereby facilitating the dispersal and increase of forest-dependent species, including *P. gordonorum*; (4) more effective law enforcement to prevent fires, illegal logging and poaching. Research priorities for *P. gordonorum*: (1) demographic and ecological studies to determine densities, natality and recruitment, demographic trends, and correlates with various ecological conditions and forest types; (2) long-term monitoring of populations to determine population

trends at various sites under various ecological conditions; (3) studies to determine ecological requirements and to facilitate forest regeneration and expansion.

Measurements

Procolobus gordonorum

HB (♀ ♀): 600, 655 mm, n = 2

T (♀ ♀): 640, 685 mm, n = 2

HF (♀ ♀): 170, 180 mm, n = 2

E (♀ ♀): 35, 35 mm, n = 2

WT: n. d.

GLS: 101, 105 mm, n = 2

GWS: 75, 80 mm, n = 2

Field measurements for two adult ♀ ♀ at MCZ (C. P. Groves pers. comm.).

Key References Dinesen *et al.* 2001; Ehardt *et al.* 1999; Struhsaker 2010; Struhsaker *et al.* 2004.

Thomas T. Struhsaker, Peter Grubb & Kirstin S. Siex

Procolobus kirkii ZANZIBAR RED COLOBUS (KIRK'S RED COLOBUS)

Fr. Colobe bai de Zanzibar; Ger. Sansibar-Stummelaffe

Procolobus kirkii (Gray, 1868). Proc. Zool. Soc. Lond. 1868: 180. Zanzibar I., Tanzania.



Zanzibar Red Colobus *Procolobus kirkii* adult female.

Taxonomy Monotypic. Originally named *Colobus kirkii*. Once considered a subspecies of Western Red Colobus *Procolobus badius* and of Pennant's Red Colobus *Procolobus pennantii* (e.g. Schwarz 1928a). Now widely recognized as a full species (Groves 2001, 2005c, 2007b, Grubb *et al.* 2003). Species designation supported by craniometric (Cardini & Elton 2009) and molecular data (Ting 2008a, b), as well as by differences in the vocal repertoire (Struhsaker 2010). Synonyms: none. Chromosome number: not known.

Description Medium-sized, long-tailed monkey with striking tricoloured coat pattern. Smallest of the *Procolobus* spp. and relatively

paedomorphic (Cardini & Elton 2009). Sexes similar in colour and size but adult ♀ ♀ have slightly greater body linear measurements than adult ♂ ♂. Adult ♀ ♀ are, however, more gracile than adult ♂ ♂, as indicated by their slightly lower body weight and much smaller skull. Face and ears black with varying degrees of pink on nose and lips. Fringe around face of long white hairs, sometimes mixed with straw-coloured hairs; fringe usually longer above eyes, shorter on cheeks and chin. Crown and lower back dark brown, rufous, or reddish-brown to orange. Shoulders and upper back black, although in some individuals entire back red-brown. Throat and ventrum white or pale grey sprinkled with black hairs. Legs black with some grey on lateral surface, white or grey on medial surface. Lower hindlimbs grey and black on lateral surface. Hands and feet black. Tail ventral surface white or grey mixed with blond, dorsal surface rufous sometimes blond over distal one-third. Colour variation often pronounced among adults of same social group. No sexual dichromatism. Relative to adult ♀ ♀, adult ♂ ♂ have broader shoulders, much larger skulls, longer canines, more robust muzzle and well developed sagittal and nuchal crests (which are lacking in adult ♀ ♀). Infants: nose and lips pink; face black fringed with long white hairs; top of head, back and lateral surface of limbs black; ventrum white. Red and brown colours appear at ca. 3 months of age.

Geographic Variation None recorded.

Similar Species None within geographic range.

Distribution

Historical Distribution Endemic to Zanzibar (Unguja) I., Tanzania. Probably once occurred throughout Zanzibar I. Presumably at higher



densities on the west and central portions of the island, where deeper, more fertile soils supported higher forest, and at lower densities in the coral thicket forests of the east coast (Pakenham 1984).

Current Distribution Mainly confined to the south-central portion of Zanzibar I. in Jozani-Chwaka Bay N. P. (JCBNP), the adjacent agricultural areas to the south, and the coral thickets and mangrove swamps of Uzi I. 10 km to the south-west. At very low densities in isolated populations in the coral thickets along Zanzibar's eastern coast from Kiwengwa in the north to Mnyambiji in the south. On the west coast there is a small isolated group in the mangrove swamps of Maji Mekundu, and a translocated population of ca. 56 individuals in Masingini F. R. (Struhsaker & Siex 1998a, b). Fifteen *P. kirkii* (5 ♂♂, 10 ♀♀) introduced to Ngezi-Vumawimbi Nature F. R., NW Pemba I., Tanzania, in 1973. Here there were ca. 15–30 *P. kirkii* in 2000 (Camperio Ciani *et al.* 2001b) and 35–40 in 2011 (Butynski & De Jong 2011).

Habitat The core of the *P. kirkii* population is in the 5 km² of evergreen ground-water and seasonally flooded forest in JCBNP and a ca. 40 ha area of perennial gardens and fallow land adjacent to Jozani. Lower numbers occur in the dry coral thickets east and west of the ground-water forest and in the mangrove swamps to the north and south. *Procolobus kirkii* lives at 0–110 m. Temperatures range between 18 and 34°C. Annual rainfall is bimodal and averages 1600 mm (range 1000–2500 mm; Pakenham 1984). Each of these habitats is dominated by two to three tree species (Hall *et al.* 1992, Mturi 1993, Siex & Struhsaker 1999b). The ground-water forest is dominated by *Calophyllum inophyllum*, *Pandanus rabaiensis* and *Polysphaeria parvifolia*; the coral thickets by *Elaeodendron schlechteranum*, *Encephalartos hildebrandtii* and *Mystroxydon aethiopicum*; the perennial gardens by *Terminalia catappa* and *Cocos nucifera* (Hall *et al.* 1992, Siex 2003). There is little overlap in tree species composition among these distinct habitats.

Abundance Total population size is ca. 1500–2000 individuals, concentrated in and around JCBNP (Struhsaker & Siex 1998b). Highest densities occur in ca. 40 ha of agricultural lands adjacent to the southern border of JCBNP (784 ind/km², range 418–1209 in 1999). These high densities are due to population compression following destruction of adjacent habitat rather than to intrinsic growth (Siex 2003). *Procolobus kirkii* are rarely found in gardens located more than 2 km from Jozani Forest. In the southern portion of Jozani Forest the density of *P. kirkii* is 176 ind/km² (range 153–199; Siex & Struhsaker 1999b, Siex 2003). Density in the coral thickets adjacent to Jozani Forest is probably less than 50 ind/km² (Siex & Struhsaker 1999b). Densities appear to decrease with increasing distance from Jozani Forest.

Adaptations Diurnal and arboreal. *Procolobus kirkii* in groups in Jozani Forest and adjacent agricultural areas spend ca. 45% of the day resting (range 39–48%, *n* = 7 groups) and 29% of the day feeding (range 25–32%, *n* = 7 groups) regardless of population density. However, in agricultural areas where *P. kirkii* densities are highest, groups spend less time moving (mean = 6%, range 6–6%, *n* = 4 groups) than in Jozani Forest (mean = 12%, range 11–14%, *n* = 3 groups), and more time involved in social activities (mean = 15%, range 12–17%, *n* = 4 groups vs. 7%, range 6–8, *n* = 3 groups), and in intra-group aggression (mean = 2%, range 0.5–2.2, *n* = 4 groups vs. 0.3%, range 0.1–0.5, *n* = 3 groups; Siex 2003).

Unlike mainland species of *Procolobus*, or *P. kirkii* groups living in forest habitats (which are almost exclusively arboreal), *P. kirkii* groups living in agricultural areas spend ca. 10% of time on the ground (range 6–15%, *n* = 4 groups). In agricultural areas groups spend ca. 23% of total feeding time on the ground (range 14–32%, *n* = 4 groups). Time spent feeding on herbs on the ground varies monthly (range 0–69%, *n* = 4 groups) and peaks during the long dry season (May–Sep) when young leaves in trees are scarce (Siex 2003).

Procolobus kirkii living in perennial gardens (Cooney & Struhsaker 1997, Struhsaker *et al.* 1997, Siex 2003) and Guerezas *Colobus guereza* living in forest fragments around Kibale Forest, W Uganda (C. A. Chapman pers. comm.) are the only non-human primates known to eat charcoal in the wild. The charcoal is possibly to adsorb compounds, such as phenolics, which can be toxic and/or interfere with digestion. This behaviour in *P. kirkii* using agricultural areas may allow this species to feed more extensively on foods that are nutritious but high in phenolic content. In turn, this may partly account for its high population density in this habitat (Cooney & Struhsaker 1997, Struhsaker *et al.* 1997). Water consumption is extremely rare in *P. kirkii* groups in ground-water forest, agricultural areas and coral thickets. Drinking is, however, common (almost daily) in *P. kirkii* groups that utilize mangrove forests. Sources of water include dew and rain on leaves and tree trunks, and in holes of trees and coral stones. Frequency of drinking is directly related to time spent feeding in mangrove forests (K. Nowak pers. comm., K.S. Siex pers. obs.).

Foraging and Food Folivorous. Majority of feeding occurs in two bouts, early morning and late afternoon. Home-ranges in densely populated agricultural areas south of Jozani Forest are smaller (mean = 12.6 ha, range 7.5–16.5 ha, *n* = 4 groups) than

in the ground-water forest of Jozani (mean = 25.3 ha, range 23.3–26.8 ha, $n = 3$ groups). Average daily travel distances moved in the agricultural area are shorter (mean = 310 m, range 280–358 m, $n = 4$ groups) than in Jozani (mean = 565 m, range 507–614 m, $n = 3$ groups; Siex 2003). Young leaves and leaf buds comprise 50–60% of the annual diet (Mturi 1991, 1993, $n = 3$ groups; Siex 2003, $n = 7$ groups), but this varies from 7 to 96% on a monthly basis. In Jozani unripe fruit (predominantly *Ficus sycomorus*) accounts for 24% of the monthly diet (range 0–88%, $n = 3$ groups), but for only 5% (range 0–27%, $n = 4$ groups) in the adjacent agricultural areas. In the agricultural areas herbs comprise 15% (range 0–47%, $n = 4$ groups) of the monthly diet and are important in the May–Sep dry season when food from trees is less abundant (Siex 2003).

Food plants include 63 tree species (Mturi 1993, Siex 2003) and eight herbaceous species (Siex 2003). A few species dominate the diet. The top ten, top three and top one food species account for 85–99%, 43–85% and 17–53% of the annual diet, respectively (Mturi 1991, 1993, $n = 3$ groups; Siex 2003, $n = 7$ groups). The most common food species in the ground-water forest include *Casuarina equisetifolia*, *F. sycomorus*, *Bridelia micrantha* and *Vitex doniana*, whereas in the agricultural areas they are *Terminalia catappa*, *C. nucifera*, *Mangifera indica*, *Flueggia virosa*, *Bridelia micrantha* and *Ficus sur* (Siex 2003). A large portion of the diet, particularly in the agricultural areas, comes from exotic and crop species, mainly *C. equisetifolia*, *T. catappa*, *C. nucifera* and *M. indica*. Many food trees in the agricultural areas appear overbrowsed, probably a consequence of the *P. kirkii* population being compressed (Siex 2003, 2005).

Social and Reproductive Behaviour Social. Mean size of groups in ground-water forest and the adjacent agricultural areas is ca. 30 individuals (range 7–85, $n = 15$). Groups in coral thickets and mangrove forests are smaller (mean = 16, range 5–30, $n = 11$; K. Nowak pers. comm., K. S. Siex pers. obs.). Groups contain 1–10 adult ♂♂ (mean = 2.5, $n = 15$), 3–40 adult ♀♀ (mean = 10.6, $n = 15$) and 2–40 young (mean = 12.0, $n = 15$) (Mturi 1991, Siex & Struhsaker 1999b, Siex 2003, K. S. Siex pers. obs.). In contrast to the Ugandan Red Colobus *Procolobus rufomitratus tephrosceles* in Kibale Forest, where ♀♀ are the primary dispersers between groups, ♂ and ♀ *P. kirkii* both transfer.

Groups are not territorial and overlap in home-ranges is greater in the agricultural areas than in the ground-water forest. Almost complete overlap by multiple groups occurs in the agricultural areas (some areas shared by up to seven groups), whereas groups in the forest have exclusive use of up to 69% of their range (range 35–69%, $n = 3$; Siex 2003). Inter-group encounters in the agricultural areas range from complete tolerance to intense aggression by individuals of all ages and both sexes. Two groups may tolerate one another on one day and then behave aggressively towards one another on the next. In contrast, inter-group encounters in Jozani are less frequent, usually consisting of one group quietly supplanting another. Aggressive encounters between groups in Jozani are rare and only involve adult ♂♂, who give vocal and branch-shake displays (Siex 2003). Groups in Jozani divide into two or more foraging parties ca. 50% of the time, whereas groups in the agricultural areas are very cohesive. These differences may be due to contrasts in resource distribution and population densities. Larger, more cohesive groups may have competitive advantages in

the agricultural areas where food is more uniformly distributed, and where population densities and inter-group competition are higher (Siex & Struhsaker 1999b).

Social activities consist mainly of grooming and play. Adult ♀♀ are the predominant groomers (82% of grooming). Dependent juveniles and infants are the main groomees (55%), followed by adult ♀♀ (24%) and adult ♂♂ (16%). Play involves mainly infants and young juveniles. When older juveniles or adults participate, play is usually focused on these individuals, i.e. younger individual(s) play-attack the older one (Siex 2003). Females often copulate with several ♂♂. All adult ♂♂ in a group copulate, but dominant ♂♂ have a higher frequency of copulation. Aggression between ♂♂ over a ♀ is infrequent. Infants and juveniles often harass copulating adults (Siex 2003). Alloparenting, not reported for other taxa of red colobus, occurs rarely in the agricultural subpopulation of *P. kirkii* (Siex 2003).

Six distinct vocalizations are recognized. Long (>11 sec) spectrographically complex and variable bouts of 'warble' calls are given by adult ♂♂. The warble is distinct from the calls of other species of red colobus and are among the most complex vocalizations of any non-human primate. Sonograms of warble calls indicate two resonators operating simultaneously, a rare phenomenon among vertebrates. These long bouts of calling are typically given by adult ♂♂ prior to the onset of group progressions, among ♂♂ within groups and among ♂♂ of different groups during inter-group encounters (Struhsaker & Leland 1980, Struhsaker 1981b, 2010).

Procolobus kirkii associates with the Zanzibar Sykes's Monkey *Cercopithecus mitis albogularis* ca. 25% of the time (Struhsaker 2000a). These two species groom one another and play together. In Ngezi, preliminary observations suggest *P. kirkii* are frequently, if not almost always, in association with 'forest-living' Pemba Vervet Monkeys *Chlorocebus pygerythrus nesiotus* (Y. de Jong & T. Butynski pers. comm.).

Reproduction and Population Structure Females exhibit perineal swellings that may indicate oestrus and/or pregnancy. Both swollen and unswollen ♀♀ copulate. Length of gestation unknown. Births occur throughout the year, but most (84%) are Jul–Dec, with a birth peak in Oct in Jozani Forest (33% of births in Jozani Forest) and in Dec in the agricultural areas (24% of births in agricultural areas). This overlaps the end of the long dry season and the short wet season (Oct–Dec), the period of maximum food availability (Siex & Struhsaker 1999b, Siex 2003). Single births are the norm, but in 1999 three sets of twins were observed in the agricultural subpopulation. An unconfirmed fourth set of twins was reported in 1998. An estimated 2% of all recorded births ($n = 150$ births) between 1992 and 1999 were twins (K. S. Siex pers. obs.). There are no records of twins for other red colobus taxa. Birth-weight and size unknown. Inter-birth intervals range from ca. 32–35 months in the agricultural areas (mean = 34, $n = 5$ groups, ca. 100 adult ♀♀ over two 1-year periods), and 26–55 months in Jozani (mean = 41, $n = 5$ groups, ca. 85 adult ♀♀ over two 1-year periods) (Siex & Struhsaker 1999b, Siex 2003). Although the majority of ♀ young are weaned by two years, some ♂♂ suckle until they are sexually mature at ca. 4–5 years. Group adult sex ratio varies between habitats and over time (range 2 : 13.7, ♀ : ♂, $n = 15$), as does the ratio of young (infants and pre-dispersal juveniles) per adult ♀ (1.0 in the agricultural areas and 0.73 in Jozani) (Siex & Struhsaker 1999b, Siex

2003). Survivorship of infants and small juveniles varies between habitats and over time. Based on data from 1992–96 and 1999, ca. 35% and 43% of infants ($n = 15$ groups, $n = 150$ infants) survived the first 26 months in the agricultural areas and Jozani, respectively (Siex & Struhsaker 1999b, Siex 2003).

Predators, Parasites and Diseases Historically *P. kirkii* was most likely preyed upon by the Zanzibar Leopard *Panthera pardus adersi*, now probably extinct. There are no large eagles on Zanzibar. Occasionally *P. kirkii* are killed by humans, vehicles and dogs. No obvious external parasites were found on 69 anaesthetized *P. kirkii*. Faecal samples from approximately 55% of these individuals were infected by at least one of three helminths: *Strongyloides* in 52% of the individuals, and *Trichostrongyle* and *Trichuris* each infected 17% of the individuals. Some had secondary and tertiary infections (17% and 2%, respectively) of these three helminths (M. Eberhard & K. Glander pers. comm., K. S. Siex pers. obs.). In a second study of faecal samples from 38 individuals 26% were infected by *Trichuris*, 13% by *Trichostrongyle*, 50% by *Entamoeba* and 3% by *Giardia*. Secondary and tertiary infections were found in 21% and 3% of the individuals, respectively (J. R. Broderon & A. K. Prestwood pers. comm., T. Struhsaker pers. obs.).

Conservation IUCN Category (2012): Endangered. CITES (2012): Appendix I. *Procolobus kirkii* is one of Africa's most threatened primates because less than 2000 individuals remain in a very restricted area (Struhsaker & Siex 1998b). The main threat is habitat destruction due to cutting for building poles, fuel, charcoal production and conversion to agriculture. *Procolobus kirkii* is sometimes killed as a perceived agricultural pest. As Zanzibar's human population grows at ca. 5% per year due to intrinsic growth and immigration, these threats will intensify. Approximately half of the remaining *P. kirkii* population is outside of JCBNP where their habitats are unprotected. Of particular importance are the groups in the agricultural areas directly south of JCBNP. These groups are important both to the survival of the species and as a significant economic resource (Siex & Struhsaker 1999a, Siex 2005). In 2002 tourists paid ca. \$100,000 in fees to visit *P. kirkii* in these agricultural

areas. This revenue is shared with the local community. As *P. kirkii* population densities increase in this area due to population compression resulting from habitat destruction elsewhere, human–wildlife conflicts are likely to increase. Consequently, it is recommended that this parcel of 100 ha be purchased and annexed to JCBNP. In addition, legal protection should be given to Kiwengwa Forest, the coral thickets and mangrove forests of Uzi I. and other isolated forest patches inhabited by *P. kirkii*, and habitat corridors established between these patches and JCBNP. Recommendations for the management of *P. kirkii* on Pemba I. are presented in Butynski & De Jong (2011).

Measurements

Procolobus kirkii

HB (♂ ♂): 494 (415–555) mm, $n = 25^*$

HB (♀ ♀): 513 (448–555) mm, $n = 23^*$

T (♂ ♂): 624 (550–670) mm, $n = 25^*$

T (♀ ♀): 655 (564–745) mm, $n = 23^*$

HF (♂ ♂): 158 (140–170) mm, $n = 26$

HF (♀ ♀): 161 (146–171) mm, $n = 25$

E: n. d.

WT (♂ ♂): 7.0 (5.5–9.4) kg, $n = 26$

WT (♀ ♀): 6.8 (5.5–8.4) kg, $n = 25$

GLS (♂ ♂): 98.2 (92–104) mm, $n = 7$

GLS (♀ ♀): 91.2 (87–94) mm, $n = 10$

GWS (♂ ♂): 74.8 (73–77) mm, $n = 7$

GWS (♀ ♀): 67.9 (62–70) mm, $n = 7$

From Unguja I. Body measurement data from live, immobilized, individuals (K. Glander & K. Siex pers. obs.)

GLS and GWS from Verheyen (1962) and BMNH compiled by P. Grubb (pers. comm).

*Adult ♀ ♀ have significantly longer HB and T measurements than adult ♂ ♂ (t -test, $p = 0.030$ and 0.003 , respectively).

Key References Mturi 1991, 1993; Siex 2003; Siex & Struhsaker 1999a, b; Struhsaker 2010.

Kirstin S. Siex & Thomas T. Struhsaker

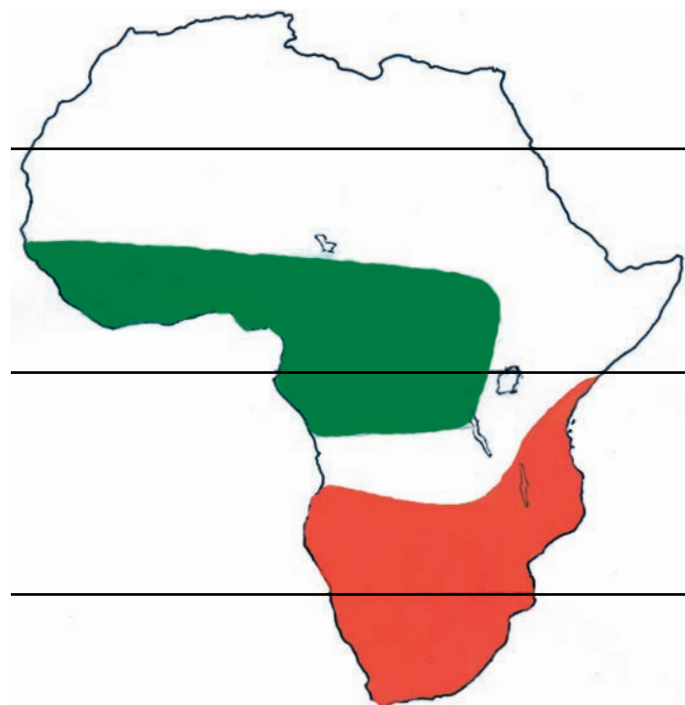
Subfamily CERCOPITHECINAE – Cercopithecines: Cheek-pouched Monkeys

Cercopithecinae Gray, 1821. London Medical Repository 15: 297.

| | | |
|-----------------------------------|--------------------------|--------|
| Papionini | Papionins | p. 157 |
| <i>Macaca</i> (1 species) | Macaques | p. 159 |
| <i>Cercocebus</i> (7 species) | Drill-mangabeys | p. 165 |
| <i>Mandrillus</i> (2 species) | Mandrills | p. 190 |
| <i>Lophocebus</i> (6 species) | Baboon-mangabeys | p. 204 |
| <i>Rungwecebus</i> (1 species) | Kipunji | p. 211 |
| <i>Papio</i> (5 species) | Baboons | p. 217 |
| <i>Theropithecus</i> (1 species) | Gelada | p. 239 |
| Cercopithecini | Guenons (Cercopithecins) | p. 245 |
| <i>Allenopithecus</i> (1 species) | Allen's Swamp Monkey | p. 248 |
| <i>Miopithecus</i> (2 species) | Talapoin Monkeys | p. 251 |
| <i>Erythrocebus</i> (1 species) | Patas Monkey | p. 256 |
| <i>Chlorocebus</i> (6 species) | Savanna Monkeys | p. 264 |
| <i>Allochrocebus</i> (3 species) | Mountain Monkeys | p. 290 |
| <i>Cercopithecus</i> (20 species) | Arboreal Guenons | p. 303 |

This subfamily (formerly family) embraces all the non-colobine African monkeys (as well as the mainly Asian macaques, *Macaca*, with one African species, the Barbary Macaque *Macaca sylvanus*). Cercopithecinae is comprised of two tribes, 13 genera with 56 species in Africa. Cercopithecinae vary greatly in size, colour and shape, ranging from the miniature, round-headed talapoin *Miopithecus* spp. to heavily built, long-faced baboons *Papio* spp., drills *Mandrillus* spp. and the Gelada *Theropithecus gelada*. Cercopithecinae embraces 13 African genera, of which the largest number of species belongs to the tribe Cercopithecini: forest guenons *Cercopithecus* spp., savanna monkeys *Chlorocebus* spp., mountain monkeys *Allochrocebus* spp., talapoin monkeys *Miopithecus* spp., the Patas Monkey *Erythrocebus patas* and the Allen's Swamp Monkey *Allenopithecus nigroviridis*. The larger, more terrestrial, large-muzzled baboons (*Papio* spp., *Mandrillus* spp. *T. gelada*) and the baboon-like monkeys (*Macaca* spp., drill-mangabeys *Cercocebus* spp., baboon-mangabeys *Lophocebus* spp. and Kipunji *Rungwecebus kipunji*) are grouped in the tribe Papionini (formerly subfamily Papioninae). The macaques are thought to be of African origin and to have emigrated to Asia about 5 mya ago (late Miocene; Stewart & Disotell 1998).

The divergence between Cercopithecinae and Colobinae occurred ca. 17.9–14.1 mya (mid-Miocene), and the split between cercopithecins and papionins at 11.6 (12.9–10.3) mya (Raum *et al.* 2005, Perelman *et al.* 2011, Roos *et al.* 2011). The earliest fossil documenting the Cercopithecinae–Colobinae split, the colobine *Microcolobus*, dates to 10–11 mya. As *Microcolobus* is a morphologically very primitive colobine, it suggests that the lower limit of the dates put forth for the divergence between Cercopithecinae and Colobinae is the more likely. That both divergences took place within Africa, raises questions as to what geographic, climatic and ecological factors were involved. In spite of the early Miocene record being relatively sparse and localized, it is sufficient to show that Victoriapithecine monkeys were diverse and relatively generalized, surviving as a recognizable entity from about 20 to 14 mya (early to mid-Miocene). The common cercopithecine–colobine lineage probably arose from some south-eastern Africa population of omnivorous/frugivorous Victoria monkeys.



Schematic map showing the possible role of Equatorial Realm and South-eastern Realm in the differentiation of Colobinae and Cercopithecinae.

The likelihood of a cercopithecine origin in southern Africa receives some implicit support from the fossil record. Seven endemic species have been recorded from the Plio-Pleistocene in the far south of Africa in spite of temperate regions normally being not greatly favoured by primates. While it might be expected that eastern Africa would be a preferred region for cercopithecines, fossil sites there remain poor in species, even during the later Pliocene, and fossil colobines, which are almost absent in the south, number six species in Plio-Pleistocene East Africa (Benefit 1999). The distribution and frequency of cercepithecoid fossils in Ethiopia shows that Cercopithecinae only overtook Colobinae as late as 3.3 mya (mid-Pliocene; Benefit 1999).

Kingdon (this volume, pp. 92–3) thinks that physical and ecological separation between a previously common cercopithecoid population in south-eastern Africa and a pre-colobine population that successfully expanded into the equatorial region was the most likely mechanism initiating the divergence between cercopithecins and colobins. The estimated timing is significant because it corresponds to tectonic events combined with major climatic shifts. Very warm, wet conditions were widespread at about 16 mya (see Volume I, Chapter 4). An expansion of forests, and with them, the broadly continuous spread of a common parental population would have been facilitated by such a humid climate. Interruption by tectonic uplift in central-eastern Africa and the drying out of formerly moist forest areas could have re-isolated the populations living in the south-east and exerted new selective pressures on the proto-cercopithecine ancestor. The likelihood that such an ancestor tended to be centred in

the south-east is heightened by still earlier and sustained drying-out of the south-west due to the circumpolar current having a cooling, drying effect from about 20 mya onwards (Barker & Burrell 1977 and see Volume I, Chapter 4).

The fact that contemporary cercopithecins and colobins differ most in dietary and digestive physiology suggests that these differences began with and might be explained by the nature of their physical separation. The biggest differences, apart from the obvious ones connected with latitude, seasonality and temperatures, would have concerned competition and disease (Elton 2007). For equatorial monkeys, the co-existence and competition of abundant, often larger-bodied and well-established ape-like primates would have defined the newcomers' niche (see Colobinae). Isolated south-eastern monkeys, by contrast, would have had less, perhaps no, competition from apes as well as less exposure to primate-specific diseases. Omnivorous diets would have been favoured by the strong seasonality of fruiting in the south-east.

Cheek-pouches have given this group their vernacular name, and their possession is the single most diagnostic feature that distinguishes Cercopithecinae from their sister subfamily, Colobinae. These exceptionally elastic buccal sacs (see illustration below) represent an adaptation whereby rapidly gathered food items can be

stored for later processing. Partly because there is scant need for cheek-pouches when food is dispersed through the forest canopy this feature has been explained as the legacy of a semi-terrestrial stage in their ancestry (Napier & Napier 1967). Exposed to greater risk from predators but also subject to more intense intra-group competition for scarcer food items, selection for the development of inaccessible 'shopping baskets' was an ingenious solution to both pressures. Cheek-pouches gave advantages to animals that could harvest rapidly and then chew and swallow in trees and at leisure. Likewise, a tighter social structure, possibly induced by sustained predation, would have favoured individuals able to rapidly ingest food items without having them snatched away by necessarily competitive conspecifics.

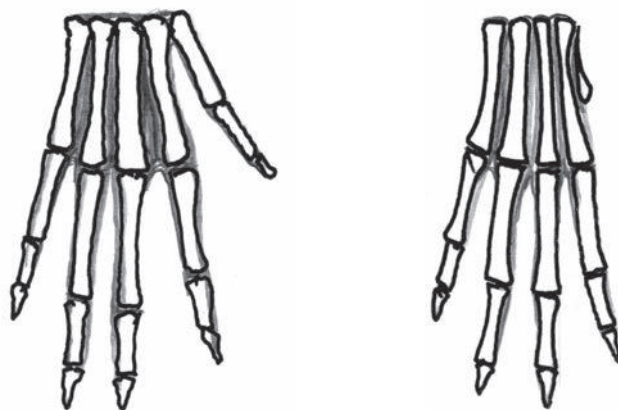
Cercopithecine ancestors would seem to have developed differences in size and skull structure between ♂♂ and ♀♀, both living in polygynous social groups. Among ♂♂, large, impressive and well-armed fighters would have been favoured, leading to strong sexual selection (which was only reversed among late derivative lineages, such as the arboreal guenons).

The hands of cercopithecins are less modified than those of colobines. The lower incisors lack lingual enamel, and the face and nasal bones tend to be elongated (Strasser & Delson 1987). Strasser (1988, 1994) has noted that the feet are 'mesaxonic'. That is, the central digit is the longest and extreme flexibility at the ankle is made possible by a convex distal astragalocalcaneal facet that is acutely angled to the navicula (Kingdon 1988a) and the entire plantar border of the astragalus is occupied by the medial malleolar facet.

Jonathan Kingdon & Colin P. Groves



Schematic myology of Blue Monkey *Cercopithecus mitis stuhlmanni* showing distended cheek-pouches.



Hand skeleton of a cercopithecine (Mona Monkey *Cercopithecus mona*) (left) compared with that of a colobine (Eastern Red Colobus *Procolobus rufomitratu*) (right).

Tribe PAPIONINI

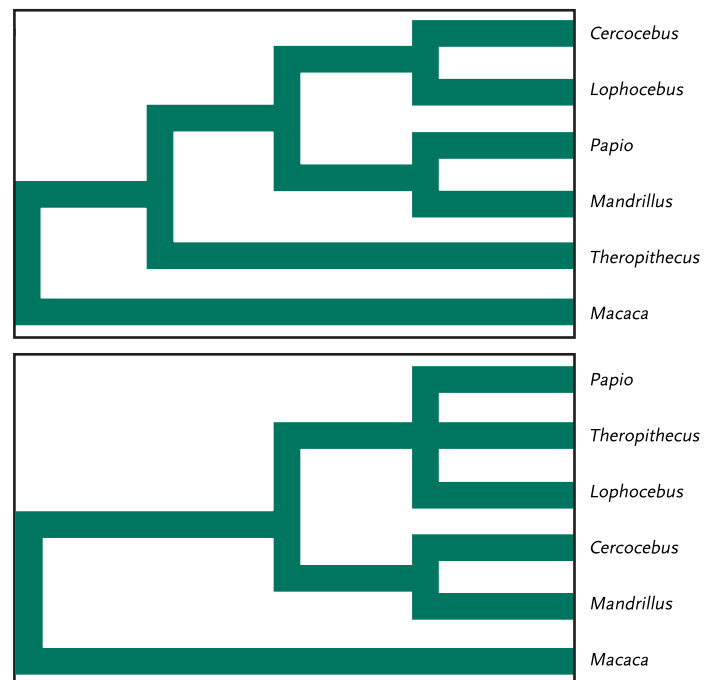
Papionins: Macaques, Drill-mangabeys, Mandrills, Baboon-mangabeys, Kipunji, Baboons, Gelada

Papionini Burnett, 1828. Q. J. Lit. Sci. Arts Lond. 4.

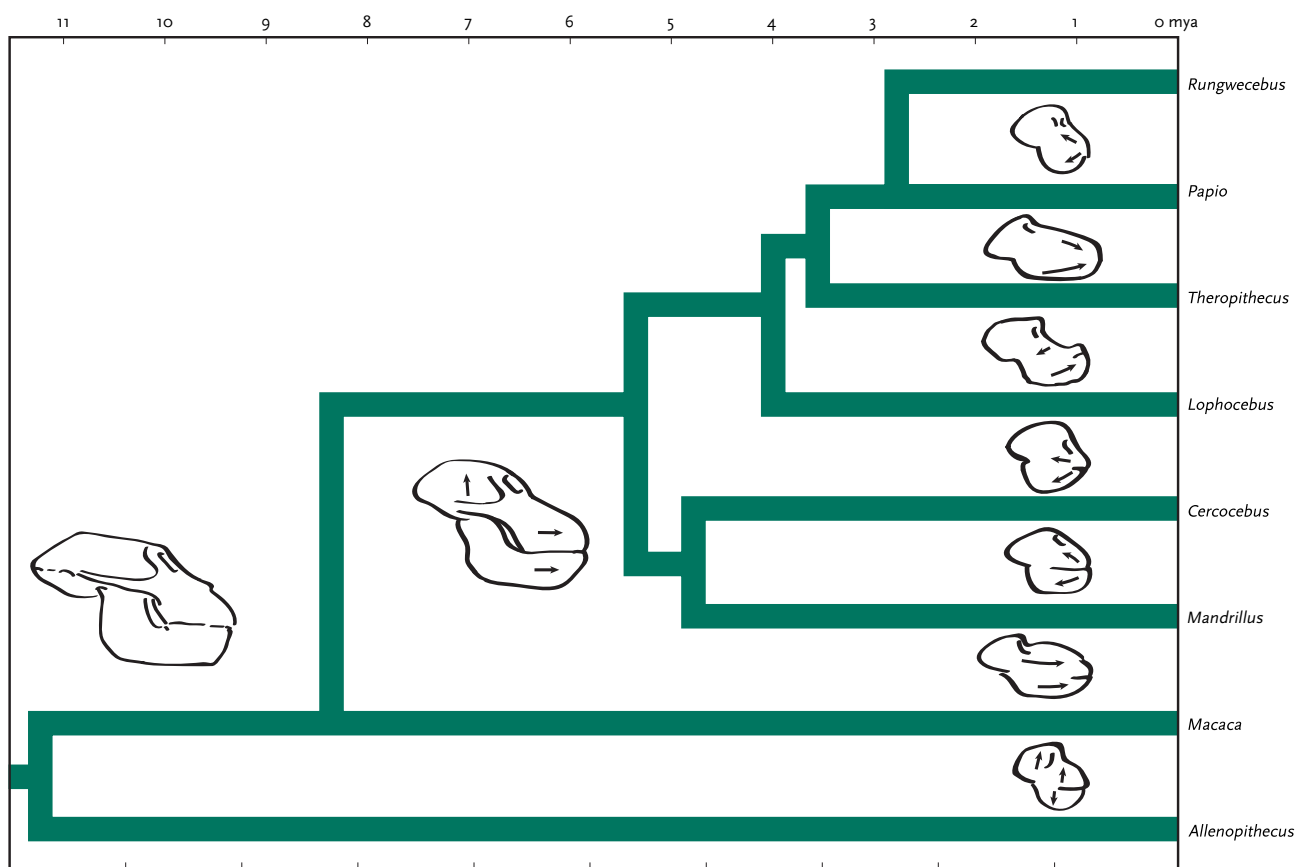
Olive Baboon *Papio anubis*.

The papionins are medium to large-sized monkeys. They include the macaques *Macaca* spp. of Eurasia and North Africa, and the Gelada *Theropithecus gelada*, Kipunji *Rungwecebus kipunji*, drill-mangabeys *Cercocebus* spp., mandrills *Mandrillus* spp., baboon-mangabeys *Lophocebus* spp. and baboons *Papio* spp. of tropical and temperate Africa. The number of genera is seven and the number of species in Africa is 23. All are quadrupedal, with well-developed thumbs, and with forelimbs and hindlimbs more equal in length than in most other cercopithecids. Tails range from absent to long. Unlike their sister taxa in the tribe Cercopithecini, all studied papionins have the diploid complement of $2n = 42$ chromosomes. Also, unlike cercopithecins, papionine fossils are frequently found in deposits from the mid-Miocene onwards, and include at least three, and probably more, genera that are now extinct (Freedman 1957, Delson 1988, Frost 2001). *Macaca* and *Papio*/*Theropithecus* diverged ca. 5.1 mya according to Perelman *et al.* (2011), but 10.0–5.1 mya according to Roos *et al.* (2011).

A prominent ♀ sexual swelling localized in the genital region is probably ancestral for papionins (and for cercopithecins), and is retained in most tropical and sub-tropical papionine species. Of all non-human primate tribes, Papionini is most heavily weighted towards species that conduct much of their activity on the ground. This has enabled *Macaca* spp. and *Papio* spp. to occupy, and diversify in, the widespread, seasonally dry woodland and savanna habitats of tropical and temperate Africa and Eurasia. A few genera (*Cercocebus*,



Two interpretations of papionin relationships. *Top*: Earlier morphological tree (Strasser & Delson 1987). *Bottom*: Later molecular tree (Harris & Disotell 1998).



Tentative phylogenetic tree for Papionini (partly after Tosi *et al.* 2005). Arrows suggest directions of cranial extension or contraction.

Mandrillus, *Lophocebus*, *Rungwecebus*), however, are committed to tropical rainforest habitats, and some of these species are highly arboreal (*Lophocebus*, *Rungwecebus*).

All Papionini are diurnal, and most live in large, perennial social groups that include multiple adults of both sexes. In some species, groups have a complex, multi-layered internal social structure. In most papionine species the great majority of ♂♂ disperse from their natal group before breeding, while ♀ philopatry results in a group structure based on persistent, ranked, matrilineages.

Of the seven extant papionine genera that are currently recognized, all but *Macaca* are confined to the Ethiopian Faunal Realm, and of these ‘afro-papionins’ (Jolly 2007), only *Papio* currently extends beyond sub-Saharan Africa (into SW Arabia).

The afro-papionins range in size and build from the massive *Mandrillus* spp. and *Papio* spp. to the smaller and more lightly built *Lophocebus* spp., *Cercocebus* spp. and *R. kipunji*. Diverse as they are, the afro-papionins share features of cranial and genital structure, and molecular evidence confirms that they form a single clade that is the sister-group of the Eurasian macaques. These two groups are sometimes named as subtribes (Macacina and Papionina). That the macaques have no particular relatives in sub-Saharan Africa suggests that their ancestral stock left that region before its papionine fauna diversified extensively. Fossil evidence suggests that a macaque-like common ancestor of the afro-papionins, inhabited woodlands rather than equatorial forest, adapted to foraging both on the ground and in the trees, and rapidly diversified into an array of larger (and, therefore, longer-faced), more terrestrially committed, somewhat baboon-like, species.

The living afro-papionins comprise two distinct stocks that survived from this diversity – one branch includes only *Cercocebus* and *Mandrillus*, the other includes *Papio*, *Theropithecus*, *Lophocebus* and *Rungwecebus* (Davenport *et al.* 2006, Zinner *et al.* 2009a). These relationships – now supported by some details of morphology, as well as strong molecular evidence – mandate the splitting of two long-accepted groups, *Papio* + *Theropithecus* + *Mandrillus* (‘baboons’ *sensu lato*, occasionally lumped into a single genus, *Papio*), and *Cercocebus* + *Lophocebus* (‘mangabeys’, traditionally combined as genus *Cercocebus*). To complicate matters further, initial molecular evidence suggests that *Rungwecebus*, which morphologically is a mangabey similar to *Lophocebus*, is a sister-taxon of *Papio* (Davenport *et al.* 2006) that apparently occasionally hybridized with *Papio* long after the two genera diverged (Zinner *et al.* 2009a, Burrell *et al.* 2009)!

Since each branch of the afro-papionins includes both large, long-faced, ground-foraging ‘baboons’, and smaller, short-faced, more arboreal ‘mangabeys’, some convergent evolution must have occurred. Kingdon (1997, and see above) suggests that the ancestral afro-papionin was large and long-faced, in which case the features shared by mangabeys evolved at least twice, and three times if *Rungwecebus* is descended from a *Papio*-like ancestor. If, on the other hand, the ancestral afro-papionin was mangabey-like (Jolly 2007), then large body size (along with long faces, which follow automatically by processes of allometric growth) evolved at least twice, in *Papio* + *Theropithecus*, and in *Mandrillus*. Detailed study of the genetic basis of body mass variation in the different lineages holds the best promise of solving this puzzle.

Clifford J. Jolly

GENUS *Macaca*

Macaques

Macaca Lacépède, 1799. Tableau des Divisions, Sous-Divisions, Ordres et Genres des Mammifères 4.

The genus *Macaca* embraces a large number of Asiatic forms and a single African species, the Barbary Macaque *Macaca sylvanus*. Because the group is so varied and widespread in Asia it was long assumed that *M. sylvanus* was a late immigrant into Africa. Molecular analysis suggests, instead, that *M. sylvanus* arose directly from an African parental population from which the entire Asiatic radiation derives (Stewart & Disotell 1998). *Macaca sylvanus* is, therefore, likely to inhabit part of the range of the genetic founders of this genus, implying that *Macaca* may have originally arisen as a specifically trans-Saharan population of an otherwise typically tropical African monkey population. A fossil

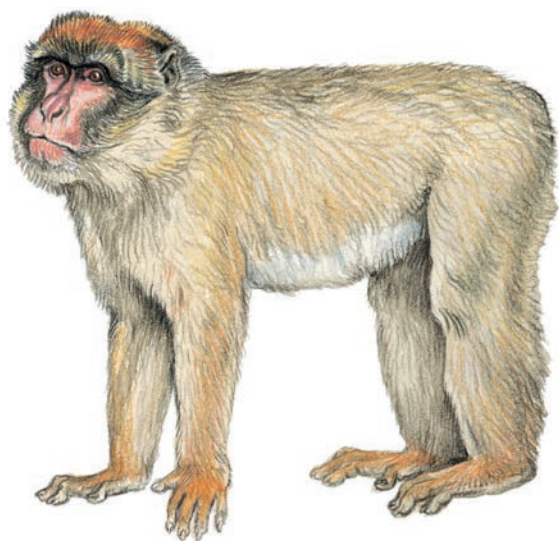
genus with (symplesiomorphic) resemblances to *Macaca* is known from Pliocene (5.3–1.8 mya) sites in East and South Africa – *Parapapio*. Although there is now no doubt that the genus *Macaca* is indeed monophyletic, undoubted synapomorphic conditions for the genus are hard to find. The most convincing one is the presence of maxillary sinuses; as all other Old World monkeys lack these sinuses, their presence in *Macaca* most parsimoniously interpreted as a uniquely derived condition, developed convergently with the Hominoidea.

Colin P. Groves & Jonathan Kingdon

Macaca sylvanus BARBARY MACAQUE (BARBARY APE)

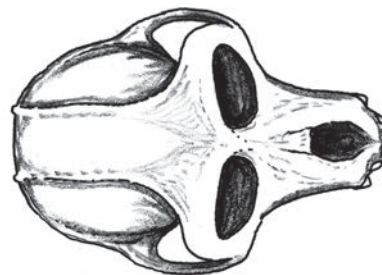
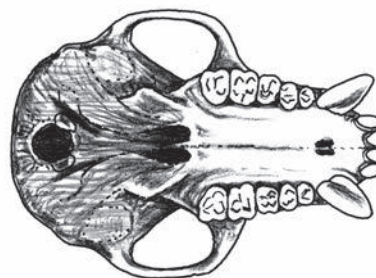
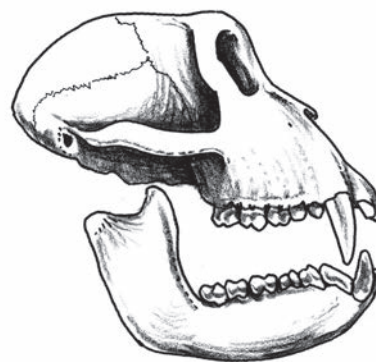
Fr. Magot; Ger. Berberaffe

Macaca sylvanus (Linnaeus, 1758). Systema Naturae, 10th edn, 1: 25. 'Barbary coast', North Africa.



Barbary Macaque *Macaca sylvanus* adult male.

Taxonomy Monotypic species. Known and named by ancient Phoenicians, Etruscans, Egyptians and Greeks, including Aristotle. *Macaca sylvanus* is the only species of macaque found outside Asia, and the only representative of this group in Africa. Fossils found throughout Europe establish *M. sylvanus* as an important component of the fauna during glacial and inter-glacial periods. Genetically, *M. sylvanus* is recognized as a sister-group of Asian macaque species (Morales & Melnick 1998). Intra-specific genetic variation in the species indicates that Algerian mtDNA haplotypes are more divergent than Moroccan ones (Modolo *et al.* 2005), and that the present disjunct clustering of haplotypes may be a product of Pleistocene and Holocene climate changes that resulted in periodic forest fragmentations and interconnections. Haplotype evidence also indicates that the Gibraltar population is a result of artificial introduction of monkeys from the Rif and Akfadou (Algeria) regions.



Lateral, palatal and dorsal views of skull of Barbary Macaque *Macaca sylvanus* adult male.

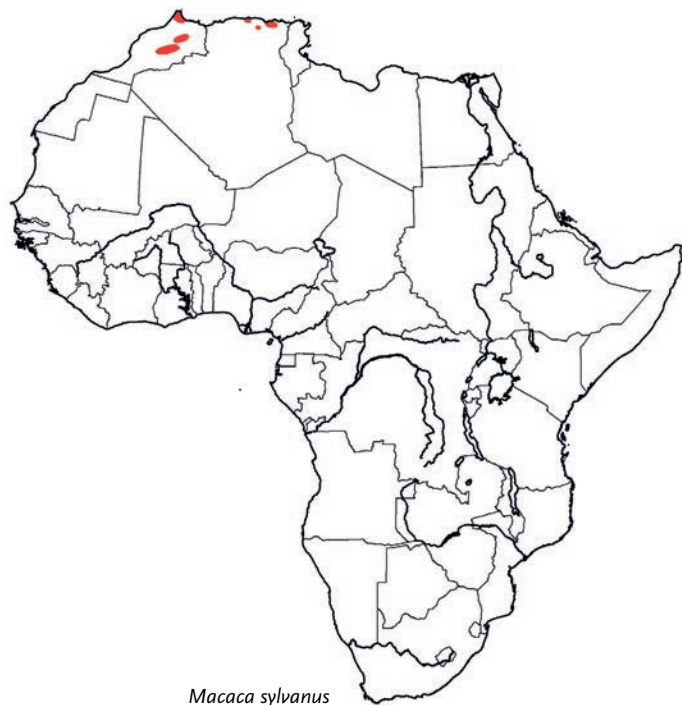
Synonyms: *ecaudatus*, *inuus*, *pithecus*, *pygmaeus*. Chromosome number: $2n = 42$ (Dutrillaux *et al.* 1982a, Romagno 2001).

Description Medium-sized, heavy-set, semi-terrestrial monkey. Sexes alike in colour. Adult ♀ about 68% as heavy as adult ♂. Sides of the face bounded by streaks of dark brown hair, while the face is thinly haired and lightly pigmented. Crown variegated as on the back, but tends to be more brightly coloured. Tail vestigial and inconspicuous; may be absent. Dorsum of subadults and adults typically strongly variegated, pale (buffy to golden-brown to burnt orange) and dark (blackish). Ventrums and legs thinly haired, pale buff to whitish. At birth, dorsum blackish, and ventrum pelage thin and slightly paler (Deag & Crook 1971, Fa 1984e). The gradual transition from blackish infantile pelage to variegated brownish juvenile pelage begins at ca. 45 days of age and is completed by ca. 145 days of age. Pelage length in juveniles is less than in subadults and adults, but the colouration is generally similar. *Macaca sylvanus* is the only macaque in which the ischial callosities of the ♂ meet in the midline, a presumably symplesiomorphic feature with the sub-Saharan African Papionini.

Geographic Variation Erythristic forms reported in Morocco (Panouse 1957, Aulagnier & Thevenot 1986), but geographic patterns in pelage have not been studied. No body mass differences detected between Algerian and Moroccan forms (Fooden, 2007).

Similar Species None within geographic range.

Distribution Endemic to extreme North Africa. Mediterranean Coastal BZ. Extant natural populations of *M. sylvanus* are disjunctly distributed in the Atlas and Rif Mountains in Morocco and Algeria from ca. 31°15'N to 36°45'N, and ca. 07°45'W to 05°35'E. Moroccan and Algerian populations separated by a gap of ca. 700 km, and narrower gaps separate populations within Morocco and Algeria. Holocene extinction records ($n = 28$ populations) indicate that



distributional gaps were narrower within historic times, and that the range recently extended east of Algeria to ca. 10° E into Tunisia (Joleaud 1931). This pattern is not a result of habitat selection as presumed by Taub (1977), but a consequence of range restriction and isolation in the higher altitude habitats as demonstrated by Fa (1984d). No non-human primate is sympatric with *M. sylvanus* (Aulagnier & Thevenot 1986, Kowalski & Rzebik-Kowalska 1991, Majolo *et al.* 2013).

The population on Gibraltar is not native. There is no mention of *M. sylvanus* in ancient commentaries on Gibraltar (Joleaud 1931, McDermott 1938). The oldest known reference to monkeys on Gibraltar is in an eighteenth century document preserved in the British Museum (Sayre 1862, cf. Buffon 1789) that indicates that 'a great quantity' of Barbary Macaques were introduced into the British garrison in 1740 (Busk 1877, Trouessart 1905, Fa 1981). Additional introductions occurred in 1813 and 1860 (Fa & Lind 1996). In 1925 the population was reduced to three individuals (Kenyon 1938), and in 1938–45 major restocking occurred (Fa 1984d). A recent study of mtDNA variation in the existing Gibraltar population indicates that this population includes individuals of both Moroccan and Algerian ancestry (Modolo *et al.* 2005).

Lydekker (1893–1894) and Forbes (1894) indicated that, during the nineteenth century, *M. sylvanus* inhabited southern Spain in the vicinity of Gibraltar. This appears to have been an error (Joleaud 1931, cf. Kelaart in Newman 1846). In a subsequent publication, Lydekker (1916) omitted Spain from the species' distribution. *Macaca sylvanus* from European parks were deliberately released at three localities in Morocco during the 1980s (de Turckheim & Merz 1984, Fa, 1986a). The most successful re-introduction was in 1985, when more than 40 formerly captive individuals were deliberately released near Nador, a northern coastal town at ca. 35°00'N, 03°00'W (Chivers 1984, Aulagnier & Thevenot 1986, Anonymous 1988).

Habitat Habitats occupied by *M. sylvanus* include Atlas Cedar *Cedrus atlantica* forest, Moroccan Fir *Abies maroccana* forest, and oak forests (Evergreen Oak *Quercus ilex*, Portuguese Oak *Quercus faginea*, Algerian Oak *Quercus canariensis*, Cork Oak *Quercus suber*), scrub, grassland and rocky ridges dominated by herbaceous vegetation. The known altitudinal distribution is 400–2300 m; over half of the 62 altitudinal records are at or above 1800 m (Fa *et al.* 1984, Fooden 2007).

Climate in the range of *M. sylvanus* is essentially Mediterranean, but greatly modified by altitude. At lower altitudes, in semi-arid scrub, mean annual rainfall is low (<400 mm) and concentrated during winter months; summers are very dry and hot (>30°C; Trewartha 1981, Fa 1982). At altitudes >1500 m mean annual precipitation is >800 mm, with much of this falling as snow from Dec to Mar (snow may fall Sep–May). In Deag's (1984) Aïn Kahla (Middle Atlas, Morocco) study area, snow fell during 39 days and lay on the ground in appreciable quantities for 82 days. Complete snow cover has a marked effect on the monkeys' feeding behaviour (Fa 1982, Deag 1984, Mehlman 1984). Winter temperatures in the Moyen Atlas and Rif Mountains are consistently low and drop to –18°C (Deag 1984, Drucker 1984, Mehlman 1984). Summer temperatures here are high, however, at >30°C.

Abundance In 1984, Fa *et al.* (1984) estimated the total natural population of *M. sylvanus* to be 14,000–23,000 individuals (9000–17,000 in Morocco, 5000–6000 in Algeria). In 1992, Lilly

& Mehlman (1993) indicated that the total population had declined to 10,000–16,000 individuals and, in 2005, Modolo *et al.* (2005; cf. Camperio Ciani & Palentini 2003) reported a further decline from 10,000 individuals. The number of *M. sylvanus* in Morocco declined from 4000–5000 individuals in 2005 to ca. 3000 individuals in 2008 (Van Lavieren & Wich 2010, A. Camperio Ciani pers. comm.). The Rif Mountains macaque populations, assessed in 1980 by Fa (1982) to be >1000 individuals in five sub-populations, were recently surveyed by Waters *et al.* (2007) and found to hold only ca. 300 individuals. The current situation for *M. sylvanus* in Algeria is unstudied. Current world wild population ca. 5000–6000 (Majolo *et al.* 2013).

Population density in *M. sylvanus* (12–70 ind/km²) apparently attains its maximum in relatively undisturbed cedar or mixed cedar/oak habitats (Deag 1984, Ménard & Vallet 1996, Van Lavieren & Wich 2010). As expected, degraded habitats, particularly those in the Moroccan Rif, support population densities that are much lower at (0.4–4.5 ind/km²; Mehlman 1989).

Adaptations Diurnal and semi-terrestrial. *Macaca sylvanus* is a highly adaptable species that is found in a variety of habitats with very different climates. The species exhibits much ecological plasticity (Ménard 2003). Fa (1994) discusses anatomical gut characteristics that correlate with *M. sylvanus*'s high herbaceous diet.

Macaca sylvanus spends most of the daylight hours on the ground; reported mean frequency of daytime terrestriality varies from 68% to 83% in Morocco, and from 58% to nearly 100% in Algeria. Infants and juveniles tend to be less terrestrial than adults (Merz 1976, Deag 1985, Ménard 1985, Ménard & Vallet 1986, Machairas *et al.* 2003). At Afennourir and Cèdre Gouraud (=Gouroud), Morocco, juveniles were 70% terrestrial and adult ♂♂ were 81% terrestrial (Machairas *et al.* 2003). Frequency of terrestriality also varies seasonally (Deag 1985, Ménard & Vallet 1986, 1997). Flee into trees to escape danger (Merz 1976, Deag 1985). Sleep in trees (Taub 1977, de Turckheim & Merz 1984, Mehlman 1989, Hammerschmidt *et al.* 1994) or in caves on rocky cliffs (MacRoberts & MacRoberts 1971, Alvarez & Hiraldo 1975, Fa *et al.* 1984, Mehlman 1984). Alvarez & Hiraldo (1975) report that *M. sylvanus* in the Rif Mountains migrate to lower altitudes during winter, but this is anecdotal.

Foraging and Food Omnivorous. Home-ranges of groups of *M. sylvanus* are, on average, smallest (18 ha, 12–25, n = 2) in the Moroccan Moyen Atlas (Fa 1986b, Drucker 1984), largest (804 ha, 307–1200, n = 6) in the Moroccan Rif (Fa 1986b, Mehlman 1989) and intermediate (280 ha, 39–424, n = 3) in the Algerian Grand Kabylie (Ménard *et al.* 1990, Ménard & Vallet 1996). Group home-ranges frequently overlap in all three areas (Deag & Crook 1971, Rumsey & Whiten 1972, Ménard & Vallet 1997, Mehlman 1989). A group in cedar-oak forest (Tigounatine-Djurdjura, Algeria) with a home-range of 376 ha shared 48% of its home-range with other groups, while a group in deciduous oak forest (Akkfadou) with a home-range of 424 ha shared 80% of its home-range with other groups (Ménard & Vallet 1996).

Day ranges vary considerably from site to site and from day to day at each site. In cedar-oak forest day ranges were 473–3240 m (mean 1856, n = 115 days) at Tigounatine-Djurdjura, 892–2274 m (mean 1583, n = 41 days) at Aïn Kahlaj and 1401–4188 m (mean 2794, n = 40 days) at Seheb, Middle Atlas, Morocco. In deciduous oak

forest at Akfadou, day range was 799–3472 m (mean 2336, n = 104 days) (Ménard & Vallet 1997, N. Ménard pers. comm.).

Diet of *M. sylvanus* includes a wide variety of plants (Fa 1984b). In the Moroccan Moyen Atlas at least 107 species of plants are eaten (cf. Deag 1983, Drucker 1984); in the Moroccan Rif, at least 100 species are eaten (Fa 1983a, Mehlman 1988); and in the Algerian Grand Kabylie, at least 130 species are eaten (cf. Ménard 1985, Ménard & Vallet 1986, 1996). The 100 species of food plants in the Moroccan Rif constitute 51% of 195 species of seed plants identified as present in that area. Similarly, the 130 species exploited in the Algerian Grand Kabylie constitute 48% of 271 species identified as present in that area. Also consumes fungi, lichens, mosses and animals (Deag 1983, Fa 1984b, Ménard 1985). Agricultural crops have been raided by *M. sylvanus* since at least the early sixteenth century (Leo Africanus 1896 edition, Mehlman 1988).

Eats flowers, fruits, seeds, seedlings, leaves, buds, bark, gum, stems, roots, bulbs and corms (Fa 1984b, Mehlman 1988, Ménard & Qarro 1999). Fa (1994) compared *M. sylvanus* diets with other *Macaca* spp. to show the species' high reliance on herbaceous plants, in comparison to the more frugivorous Asian macaques. Diet of *M. sylvanus* shows high seasonal variation (Deag 1983, Mehlman 1984, Ménard 1985, Ménard & Vallet 1986). Diet also varies by habitat. Seeds and leaves are the main foods (ca. 60–75%) in lowland oak forests in the Algerian Grande Kabylie (Ménard & Valet 1986), but more fruits are consumed in the Moroccan Moyen Atlas (Deag 1983, Drucker 1984, Ménard & Qarro 1999). In the higher altitude coniferous forests they eat large volumes of fir and cedar leaves during periods of high snowfall when conditions impede them from feeding on ground vegetation (Deag 1983, Drucker 1984, Mehlman 1988).

Animal prey includes snails, earthworms, scorpions, spiders, centipedes, millipedes, grasshoppers, termites, water striders, scale insects, beetles, butterflies, moths (including larvae), ants (including nests) and tadpoles (Fa 1983a, 1984b, Mehlman 1984, 1988, Ménard & Vallet 1986). Semi-free-ranging *M. sylvanus* monkeys pursue and/or catch birds, Red Squirrels *Sciurus vulgaris* and young European Rabbits *Oryctolagus cuniculus* but have not been observed to eat them (Kaumanns 1978, de Turckheim & Merz 1984); mice are, apparently, ignored.

Feeding occupies an average of 24% and 25% of daytime hours at two localities in the Moroccan Moyen Atlas (Fa, 1986b, Machairas *et al.* 2003), and also occupies 24% and 25% of daytime hours at two localities in the Algerian Grande Kabylie (Ménard & Vallet 1997). In winter, water may be obtained by eating snow (de Turckheim & Merz 1984, Mehlman 1988).

Social and Reproductive Behaviour Social. Mean size of 68 groups is 27.1 individuals (7–88). Mean group size is smallest (18.3 individuals, 10.0–27.5, n = 27) in the Moroccan Rif, largest (50.2 individuals, 27–88, n = 8) in the Algerian Grande Kabylie and intermediate (28.6 individuals, 12–40, n = 33) in the Moroccan Moyen Atlas. Group size generally is stable, but it is unstable in the population that inhabits a rocky habitat in the Djurdjura Mts, Algeria (Ménard *et al.* 1985, 1990, Ménard 2002); in this marginal habitat, groups frequently split into subgroups that subsequently reunite in various combinations. Solitary ♂♂, as far as 7 km from the nearest group, occur in the Moroccan Rif (Mehlman 1985, 1986).

Within natural groups, the number of adult ♂♂ averages only slightly less than the number of adult ♀♀. The ratio of adult ♂♂ to adult ♀♀ averages 0.70 in the Moroccan Moyen Atlas, 0.99 in

the Moroccan Rif and 0.84 in the Algerian Grande Kabylie (Whiten & Rumsey 1974, Taub 1980a, Fa 1982, 1986b, Deag 1984, Drucker 1984, Ménard *et al.* 1986, 1990, Mehlman 1989, Ménard & Vallet 1993a, Hammerschmidt *et al.* 1994, Ménard & Qarro 1999, Camperio Ciani & Machairas 2003, Machairas *et al.* 2003).

Most studies of *M. sylvanus* groups indicate that their composition is reasonably constant. Adult ♀♀ to immatures (infants and babies) ratio at Aïn Kahla, Moyen Atlas (Deag 1984) was 1:0.9 (1:0.5–1:1.2, $n = 5$), and 1:1.3 and 1:1.4 for the same area in a later study (Taub 1978). For the Rif Mountain groups studied by Mehlman (1984), the adult ♀:immature ratio averaged 1:1.2. The proportion of immatures in Algerian groups varied between 0.41–0.59 at Tigounatine, and 0.42–0.58 at Akfadou, according to the year (Ménard & Vallet 1996).

During the mating season, pairs of ♂♂ and oestrous ♀♀ form consortships (i.e. temporary sexual associations) in the course of which copulations occur (Taub 1978, 1980a, de Turckheim & Merz 1984, Fa 1986b). The duration of consortships varies from <1 min to 93 min (median 13, $n = 297$ consortships) in the Moroccan Moyen Atlas (Taub 1980a), and from ca. 1–240 min (85% less than 8 min) in Gibraltar (Fa 1986b). In Morocco the formation of most consortships is initiated by ♀♀ (55%; ♂♂ 28%; mutually originated 17%), and ♀♀ also are responsible for the termination of most consortships (72%) (Taub 1980a, Todt & Pohl 1984, Small 1992). The mean rate of exchange of consortship partners by ♀♀ in the Moroccan Moyen Atlas is one per 19.9 min (Taub 1980a, Small 1992, Paul *et al.* 1993). In a group that included six mature ♀♀ and 11 mature ♂♂, ♀♀ consorted with a mean of 6.1 ♂♂ per day (3–10 ♂♂; Fa 1986b, Small 1993, Ménard *et al.* 2001).

As in other *Macaca* spp., the ♂ typically mounts the ♀ dorsoventrally by gripping her trunk and shanks with his hands and feet, respectively (Fooden & Aimi 2005). *Macaca sylvanus* is a single-mount ejaculator. That is, copulations usually are restricted to a single mount–dismount sequence, during which the ♂ ejaculates following a brief series of pelvic thrusts (Taub 1980a, 1982, Mehlman 1986, Kuester & Paul 1989, 1992, Van den Bergh 1991, Semple 1998). The mean (S.D.) duration of 205 copulations in Aïn Kahla group was 8.7 (± 1.1) sec (6–14), and the mean number of pelvic thrusts to ejaculation was 9.1 (± 1.8 , 5–21; Taub 1980a, Mehlman 1986, Kuester & Paul 1989, 1992). The mean interval between consortship formation (see above) and onset of copulation was 2.3 min (<1–16 min).

Harassment of copulating pairs by other group members was not observed at Aïn Kahla (Taub 1980a), but 100 incidents of harassment by ♀♀ were observed in the Salem, Germany, semi-natural population (Kuester & Paul 1996). Of these harassment incidents, only 5% resulted in successful displacement of the harassed target. During the peak mating season at three Algerian localities, Ménard *et al.* (1985) observed an average of 1.1–1.3 copulations/h. During the concluding phase of copulation the ♀ utters a characteristic series of loud, low frequency grunts (Taub 1980a, Todt & Pohl 1984, Paul 1989, Van den Bergh 1991, Small 1992, Todt *et al.* 1995, Semple 1998). Males apparently are able to detect differences among copulation calls produced by ♀♀ at different stages of the oestrous cycle (Pohl & Todt 1984, Semple & McComb 2000, Fischer & Hammerschmidt 2002).

Interactions between infants and older ♂♂ are more frequent in *M. sylvanus* than in most *Macaca* spp. or *Papio* spp. (Fa 1984e, Taub 1985, Maestripieri 1998, Thierry 2000). Lahiri & Southwick (1966), who studied two newborn infants in captive groups for 12 weeks,

found that the infants consistently associated with the dominant ♂♂ in their respective groups for ca. 8% of the observation hours; during these interactions, the infants were held, groomed, or carried by the dominant ♂♂. Similar interactions between infants and adult ♂♂ (without grooming, however) were observed during a six-month study on Gibraltar (MacRoberts 1970, MacRoberts & MacRoberts 1971, Burton 1972).

In addition to dyadic male–infant interactions, Deag & Crook (1971), who studied natural *M. sylvanus* groups for two months in the Moyen Atlas, Morocco, observed triadic interactions involving one infant and two older ♂♂. In these interactions one of the ♂♂ (typically lower ranking) carried an infant to another ♂ (typically higher ranking) and presented the infant to that ♂. Deag & Crook hypothesized that presence of the infant tended to reduce tension between the low-ranking ♂ and the nearby high-ranking ♂. Accordingly, Deag & Crook designated dyadic interactions as ♂ care and triadic interactions as ‘agonistic buffering’.

Evidence concerning possible harm to infants in male–infant interactions is equivocal. Taub (1980b) reports that older ♂♂ handled infants carefully and that infants in the 535 interactions that he observed in the Moyen Atlas sustained no injuries. However, Fa (1986b) indicates that three infant deaths on Gibraltar were the result of ‘kidnapping’ by the dominant ♂, and Paul & Kuester (1988) attribute at least nine infant deaths at Salem to a similar cause. At Kintzheim, France, ♂♂ may carry and otherwise interact with dead infants in approximately the same way that they interact with live infants (Merz 1978). The functional significance of triadic male–infant interactions has been vigorously debated. On one side of this debate an exploitative agonistic-buffering function has been assigned to these triadic interactions (Deag & Crook 1971, Deag 1980, Small 1993, Paul & Kuester 1996). On the other side, an altruistic kin-investment function has been proposed (Taub 1975, 1978, 1980b, 1984, 1990, Smith & Pfeffer-Smith 1982, Taub & Redican 1984, Riechelmann *et al.* 1994). Recent genetic studies do not indicate that male–infant triads preferentially consist of closely related individuals (Kuester & Paul 1986, 2000, Paul *et al.* 1992, 1996, Ménard *et al.* 1992, 2001).

Macaca sylvanus is not territorial. As noted above, home-range overlap among groups can be extensive (up to at least 80%). Of 13 observed contacts between groups, only three (23%) were agonistic (Deag & Crook 1971, Mehlman & Parkhill 1988). Inter-group encounters at Riffian are described by Mehlman & Parkhill (1988) as either ‘neutral’ (in which little inter-group interaction took place) or ‘intermediate’ (in which one group slowly approaches another, causing it to retreat without any overt agonism exhibited). Deag (1973) observed similar inter-group encounters and displacement in the Moyen Atlas, with inter-group agonism being uncommon.

Fischer & Hammerschmidt (2002) provide an overview of *M. sylvanus* vocalizations using spectrographic displays of calls linked to accompanying facial gestures and the contexts in which each call is given, with special regard to the age and sex of the caller. The vocal repertoire of *M. sylvanus* mainly consists of ‘screams’, ‘shrill barks’, ‘geckers’, and low-frequency ‘pants’ and ‘grunts’, with gradation within and between call types. *Macaca sylvanus* typically produce series of several consecutive calls. Habitat, social structure and phylogenetic descent affect the morphology of the repertoire and call diversity in comparison to other species. Brum *et al.* (2005) report that *M. sylvanus* utter specific vocalizations while monitoring interactions

of other group members. As they did not direct other behaviours to the interacting group members, these vocalizations were referred to as 'vocal comments'. Most adult ♂♂ and adult ♀♀ of two studied groups produced low-amplitude calls when observing close contact interactions of other group members. The acoustic features of these calls varied with characteristics of the situation suggesting that such calls might not be directed towards the agents of the situation, but towards other group members. The vocal comments may signal the callers awareness of the observed interaction and possibly attract the attention of others to the situation.

Reproduction and Population Structure Although morphology of the glans penis and uterine cervix provides important taxonomic characters relevant to species relationships in the genus *Macaca* (Fooden 2006), little information is available concerning these structures in *M. sylvanus*. The glans in *M. sylvanus* is bilobed and relatively broad, as in the *silenus* taxonomic group (Fooden 1975). Hill (1974) provides measurements of two *M. sylvanus* bacula: length 11.2 mm, 11.5 mm; dorsoventral diameter 3.1 mm, 3.5 mm; and transverse diameter 2.2 mm, 2.0 mm.

During the mating season, *M. sylvanus* ♀♀ exhibit coordinated reproductive cycles of sexual skin swelling, oestrous behaviour and menstruation. During subsequent mating seasons, the swellings increase in area and thickness and often become bluish-grey until age ca. 7–15 years, after which the swellings gradually decrease in size, ultimately becoming inconspicuous beyond age ca. 20 years. At the stage of maximal development, the area of the circumanal swelling (ca. 200 cm²) is approximately four times as large as the area of the lateral vulval swellings (Fa 1984a, Möhle *et al.* 2005).

Of 12 ♀♀ in the Gibraltar population that were closely monitored during the 2001–02 mating season, ten exhibited two cycles of tumescence and detumescence, and two exhibited three cycles. Tumescence is associated with an increasing faecal oestrogen level, and detumescence is associated with an increasing faecal progesterone level. Ten of the monitored ♀♀ became pregnant during one of their cycles, and all ten of these ♀♀ exhibited a post-conception tumescence. The median interval between successive tumescence peaks was ca. 32 days (27–44 days; Möhle *et al.* 2005).

The oestrous cycle consists of a period of ♀ proceptive/receptive sexual behaviour, marked by a gradually increasing copulation rate, abruptly followed by a period of ♀ sexual inactivity (Kuester & Paul 1984a, 1989, Ménard *et al.* 1985, Paul & Kuester 1987, Small 1990b). Maximal copulation rate in an oestrous cycle is correlated with maximal sexual swelling/turgescence. Most ♀♀ exhibit two oestrous cycles per mating season (Small 1990b, Semple 1998). A female's first oestrous cycle of the season tends to be the longest, including 2–4 weeks (rarely 6 weeks) of sexual activity and ca. 2 weeks of sexual inactivity; subsequent oestrous cycles include about 1 week of sexual activity. Most ♀♀ are probably fertilized during the first oestrous cycle of the season (Kuester & Paul 1984b). During an oestrous cycle, several ♀♀ in the same group (five of 13 in one group; six of 14 in another) may be concurrently sexually active (cf. Ménard *et al.* 1985, Semple 1998).

The menstrual cycle in *M. sylvanus* has a median length of ca. 32 days (27–44, *n* = 10), including a median duration of menstrual bleeding of four days (Panouse 1957, Möhle *et al.* 2005). The median interval between the last day of maximal sexual skin swelling and the first day of menstruation is 16 days (12–18, *n* = 11; Möhle *et al.* 2005).

al. 2005). Post-conception bleeding occurs at ca. 3 weeks after fertilization (Kuester & Paul 1984a, Möhle *et al.* 2005).

In the Salem semi-natural population, gestation length was measured as the interval between the date of an infant's birth and the date of its mother's last copulation during a conceptional oestrus (Didier & Rode 1936, MacRoberts & MacRoberts 1966, Kuester & Paul 1984a, Paul & Kuester 1987). The mean (S.D.) gestation period for 67 ♀ infants was 165.3 (± 4.6) days (145–178), and for 56 ♂ infants was 163.2 (± 5.4) days (145–177). The difference between the mean gestation periods of ♀ infants and ♂ infants is statistically significant (*p* < 0.02; Paul & Kuester 1987). Weight at birth is ca. 450 g (Small 1990a). In a composite sample of 874 births reported in semi-natural populations, twinning frequency is 0.8%. Viability of *M. sylvanus* twins is low; of the ten pairs reported, six pairs were stillborn, 2.5 pairs died within eight days after birth and only 1.5 pairs survived.

Matings in natural populations of *M. sylvanus* are restricted to Sep–Apr (wet season), with a mating peak during Nov–Jan. Births in natural populations are restricted to Feb–Sep. Birth seasons vary locally. The median birth date at Akfadou (3 May) is significantly earlier than that at nearby Tigounatine (19 May) (Ménard & Vallet 1996).

In the Algerian Grand Kabylie, ♀♀ typically do not produce their first infants until >5 years of age (18 of 32 ♀♀), which indicates that these ♀♀ generally do not become sexually mature (capable of pregnancy) until >4.5 years of age (Ménard *et al.* 1985, Ménard & Vallet 1996). Only 1 of 37 ♀♀ (3%) in this population produced an infant at age four years, and none of 43 ♀♀ produced an infant at age three years. Males in the Algerian Grand Kabylie are capable of ejaculatory copulation at age 5–7 years, although they are not yet full grown (Ménard *et al.* 1985). The same is true of ♂♂ in the Moroccan Moyen Atlas (Deag 1980).

Macaca sylvanus infants begin to experiment with solid foods at age ca. 45 days and, during the next few months, mothers begin to resist nursing attempts by their infants (Burton 1972, Rumsey & Whiten 1972, Fa 1984e), although an infant generally continues to nurse sporadically until ca. 1 year of age or longer (if its mother does not produce a new infant). An orphan in a natural population was fully capable of feeding itself at age 6–8 months (Deag 1980, Kuester & Paul 1984a, Paul & Thommen 1984a, b, Ménard *et al.* 1985). In the Salem semi-natural population, older mothers wean their infants later than younger mothers (Paul *et al.* 1993).

Of 1040 *M. sylvanus* newborns, 538 were ♂♂ and 502 were ♀♀ (♂ : ♀ ratio = 1.07). Although the overall difference is not statistically significant (*p* > 0.10), the number of ♂ newborns equals or exceeds that of ♀ newborns in five of the seven available samples. Neonatal sex ratio is related to maternal rank in the Salem sample (Paul & Kuester 1990): the ♂ : ♀ sex ratio for newborns by high-rank mothers (102/74 = 1.38) significantly exceeds that for infants produced by low-rank mothers (86/95 = 0.91; *p* < 0.05); sex ratio for newborns of mid-rank mothers is intermediate (92/96 = 0.96).

The longest life-span reported for *M. sylvanus* ♀♀ in the semi-natural population at Salem is ca. 30 years (Burton & Sawchuk 1974, 1982, cf. Paul *et al.* 1993). The longest life-span reported for ♂♂ at Salem is 25 years (Kuester *et al.* 1995). The mean post-reproductive life-span for ♀♀ is around six years (3–8) in seven individuals at Salem that died after reaching estimated ages of at least 25 years (Paul *et al.* 1993). The post-reproductive life-span in a 25-year-old ♂ at Salem (see above) was one year (Kuester *et al.* 1995).

The mean annual birth rate in *M. sylvanus* is 0.59 in three natural groups (Mehlman 1989, Ménard & Vallet 1993b) and 0.70 in five semi-natural groups (Burton & Sawchuk 1982, Fa 1984d, Small 1990a, Paul *et al.* 1993, Fa & Lind 1996, Kümmerli & Martin 2005). Among factors known to affect the birth rate are natural food supply (Ménard & Vallet 1993b), age and parity of sexually mature ♀♀ (Paul & Thommen 1984a, Paul & Kuester 1988, Paul *et al.* 1993, Ménard & Vallet 1996), and human disturbance of semi-natural groups (Fa 1988). The mean annual death rate in three semi-natural populations ranged from 3.4% to 5.8% (Fa 1984d).

The mean annual population growth rate in two natural Algerian populations of *M. sylvanus* varies from 4.8% in a deciduous oak forest at Akfadou to 14.6% in a cedar–oak forest at Tigounatine. The annual growth rate in the Tigounatine population approaches that reported in the provisioned captive population maintained at Salem (18.3%).

Predators, Parasites and Diseases There are few records of ill health for wild *M. sylvanus* populations. Deag (1984) reported on the general good health of his study groups, although ailments such as coughs, sneezing and vomiting were recorded. Injuries and malformations were relatively rare. There was also a low incidence of wounding during mating seasons, reflecting the less aggressive nature of *M. sylvanus* in comparison to other macaques (Ruehlmann *et al.* 2005). *Macaca sylvanus* in Gibraltar have suffered from disease outbreaks (such as gastro-enteritis, viral pneumonia), probably as a consequence of higher densities and, at times, inadequate provisioning (Fa 1986b).

Under natural conditions the Leopard *Panthera pardus* and Barbary Lion *Panthera leo leo* probably were the major predator of *M. sylvanus* when these three species were broadly sympatric (Aulagnier & Thevenot 1986, Fa 1986a). Large eagles presumably also are predators; *M. sylvanus* respond to Golden Eagles' *Aquila chrysaetos* approach with alarm calls (Mehlman 1984); domestic dogs elicit a similar response, but Red Foxes *Vulpes vulpes* and Common Jackals *Canis aureus* do not (Ménard *et al.* 1986). In semi-free-ranging European populations, *M. sylvanus* give alarm calls in response to snakes, raptors and dogs (Paul & Kuester 1988, Fischer & Hammerschmidt 2002). In a European zoo an infant was killed by a hawk (Salzert 1978).

Conservation IUCN Category (2012): Endangered. CITES (2012): Appendix II.

The main factor responsible for the decline in the number of *M. sylvanus* is apparently anthropogenic destruction of habitat (Fa 1986a, Camperio Ciani *et al.* 2005, Majolo *et al.* 2013). Habitat loss and degradation caused by human consumption of wood, fire, clearing for cultivation, and over-grazing by sheep and goats have been inferred as major reasons for the decline of the species (Taub 1977, Fa *et al.* 1984, Camperio Ciani 1986, Ménard & Vallet, 1993a, Van Lavieren & Wich 2010). Because water shortage has become more severe in the last ten years, shepherds inhabiting forest habitats have been forced to settle near water sources. The shepherds' enclose open water sources with cement wells to extract water for their herds. As a result, *M. sylvanus* and other wildlife are excluded from water sources. This may force the monkeys to strip bark in order to obtain water (Ménard & Qarro 1999, Camperio Ciani *et al.* 2001a).

Live trade of *M. sylvanus* is presumed important, though not high. Most specimens taken from the wild are for the international pet

trade. In the 1960s, a large number of *M. sylvanus* were captured for use in laboratories in Casablanca, Tangier and Spain, but this is no longer permitted in Morocco. *Macaca sylvanus* are frequent captured and sold as pets in Morocco with reports of capture for the international pet trade dating back to 1977 (Deag 1977). Van Lavieren (2004, 2008) found that trade has increased markedly and estimates that 300 infants are taken annually from the wild in Morocco. This number now greatly exceeds the maximum sustainable offtake and thus poses a threat to wild populations (Van Lavieren & Wich 2010).

Macaca sylvanus receives some protection in Morocco under national and international legislation. Capture and sale of *M. sylvanus* is prohibited by the National Hunting Regulation (Art. 8). Collection and export of *M. sylvanus* are regulated by a system of permits in Morocco, but enforcement of the legislation is inadequate. The National Eaux et Forêts is the responsible authority. Deag (1977) mentions a maximum quota for trade of 100 macaques annually in Morocco. In 2000, the European Union suspended imports of *M. sylvanus* from Algeria and Morocco because such trade was deemed to have a harmful effect on the conservation status of the species.

Most *M. sylvanus* habitats in Algeria are found within protected areas. This is not the case in Morocco. The large population in the Rif Mts is partially included in Talassemtane N. P., but this Park is too small to support many macaques. The many *M. sylvanus* that are in oak forests and scrub are not in protected areas (Waters *et al.* 2007). A planned national park in the Moyen Atlas cedar/mixed forests would protect a substantial proportion of Moroccan *M. sylvanus*. In both Morocco and Algeria, the national forestry departments are responsible for management and protection of flora and fauna. However, the Moroccan National Eaux et Forêts until recently believed that *M. sylvanus* numbers in the Moyen Atlas forests were too high (due to the disappearance of predators), and that macaques are responsible for the degradation of cedar forests through their bark stripping behaviour. Suggestions have been made in the past to cull and/or translocate some of the monkeys. These actions would be premature without a thorough scientific investigation into the still unresolved conflict issues.

Measurements

Macaca sylvanus

HB (♂♂): 634 ± 25.7 (605–653) mm, n = 3

HB (♀♀): 557 ± 11.5 (540–566) mm, n = 4

T (♂♂): 14 ± 12.2 (0–22) mm, n = 3

T (♀♀): 1 ± 2.0 (0–4) mm, n = 4

HF (♂♂): 179 ± 7.9 (170–185) mm, n = 3

HF (♀♀): 168 ± 1.7 (166–170) mm, n = 4

E (♂♂): 51 ± 1.2 (50–52) mm, n = 3

E (♀♀): 10 ± 1.0 (8–12) mm, n = 18

WT (♂♂): 14.5 ± 1.8 (10.0–18.0) kg, n = 33

WT (♀♀): 9.9 ± 1.0 (8.0–12.0) kg, n = 18

GLS (♂♂): 136 ± 2.3 (133–138) mm, n = 5

GLS (♀♀): 119 ± 5.5 (114–126) mm, n = 4

From various museums (Fooden 2007).

Key References Fa 1984e; Fooden 2007; van Lavieren & Wich 2010.

John E. Fa

GENUS *Cercocebus*

Drill-mangabeys (White-eyelid Mangabeys)

Cercocebus É. Geoffroy, 1812. Ann. Mus. Hist. Nat. Paris 19: 97.

Large, semi-terrestrial monkeys endemic to the moist forests of equatorial Africa. The most useful characters for distinguishing among the seven species of *Cercocebus* are the shape of the crest on the crown, and colour of the face, eyelids, crown, dorsum and ventrum. The number of species in this diverse genus has been long debated. In the past the species of *Cercocebus* were allocated to two taxonomic groups – indeed, formerly only two species were recognized (e.g. Schwarz 1928d, Allen 1939, Dandelot 1974, Wolfheim 1983). Booth (1956a) recognized five species, while Hill (1974) recognized three species. Note, however, that the Sanje Mangabey *Cercocebus sanjei* was not discovered until 1979, and not named until 1986. More recently, Groves (1993) and Grubb *et al.* (2003) provisionally recognized three species, but anticipated that more might be recognized given further study. Six species were recognized by Kingdon (1997) and Groves (2001, 2005c). Seven species are recognized here.

The genus *Cercocebus* is more restricted in content than was once thought. Studies by Barnicot & Hewett-Emmett (1972) and Cronin & Sarich (1976) found that the blood proteins of the *albigena/aterrimus*-Group are distinctly different from the *agilis/torquatus*-Group, and morphological investigations by Groves (1978) showed that the Grey-cheeked Mangabey '*Cercocebus albigena*' and the Black Mangabey '*Cercocebus aterrimus*' are closer to *Papio* than to *Cercocebus*. On this basis, Groves revived the name *Lophocebus* for these two species. Differences included the flat, instead of upturned, nasal bones; the facial skeleton more flexed on the braincase; the skull broader in general; the very elongated auditory tube; and the suborbital fossa. The suborbital fossa, the main feature that was formerly considered to unite all mangabeys, is less deep anteroposteriorly than in *Lophocebus* but the dorsoventral and mediolateral diameters are greater. Variations in suborbital fossa depth (which they term 'maxillary excavations') are discussed in McGraw & Fleagle (2006).

Fleagle & McGraw (2002) have shown that in some features of the postcranial skeleton, *Cercocebus* resembles *Mandrillus* and differs from all other Papionini in many respects. Notably, the scapula is supero-inferiorly deep compared to its dorsoventral length, the humerus has an exceptionally broad deltoid plane with projecting medial and lateral crests, the ilium is broad basally, and the medial lip of the patellar groove is at least as prominent as the lateral. The same authors also pointed out that, as in *Mandrillus*, *Cercocebus* have greatly enlarged posterior premolars, doubtless reflecting their reliance on hard nuts and seeds collected from the forest floor (Hoshino 1985, Fleagle & McGraw 2002). Molecular studies (Cronin & Sarich 1976, Disotell *et al.* 1992, Goodman *et al.* 1998) converge in indicating that *Cercocebus* have a closer genetic affinity with the Drill *Mandrillus leucophaeus* and Mandrill *Mandrillus sphinx* than with *L. albigena* or *L. aterrimus* (i.e. 'Baboon-mangabeys', Kingdon 1997).

The morphological feature that was considered diagnostic and to unite *Cercocebus* and *Lophocebus*, the peculiar suborbital fossa, has no perceptible function and is best interpreted as a buckling of the jugal plate and the result of phylogenetic retraction in a long-jawed ancestor. First interpreted in these terms by Kingdon (1971) (who linked these retractions and reduced body size with significant

changes in socio-sexual behaviour), this explanation is also considered probable by C. J. Jolly (pers. comm.) but they differ in their views of the likely sequence of evolutionary events that led to lighter build, retracted muzzles and more arboreal habits both in *Cercocebus* and *Lophocebus*.

Kingdon thinks that the facial shortening in the two mangabey groups is convergent (a view endorsed by Groves, 2001), and that *Papio*, *Mandrillus* and *Theropithecus* all represent highly differentiated descendants of a common, long-faced, ancestor living 7–9 mya (late Miocene), possibly of south-eastern African origin. Kingdon envisages sustained forest dwelling in an already large-muzzled, sexually dimorphic *Mandrillus*-like lineage giving rise to *Cercocebus* as a lighter-bodied, more arboreal and westerly taxon. That the shorter-muzzled mangabeys might have derived from longer-muzzled types was first proposed by Dobroruka & Badalec (1966); by this reckoning, the most conservative skull structure within *Cercocebus* is found in the Red-capped Mangabey *Cercocebus torquatus*, a species that occupies a 2500 km long arc from Bénin to the Congo R. Here they live in moist forests, mostly within 200 km of the coast. Within a generally western vicinity, Kingdon envisages an early *Cercocebus* lineage altering its social and spatial relations (probably fewer expressions of inter-male competition among smaller-bodied animals in substantially diminished and more stable home-ranges). Later, populations expanded in all directions but most notably eastwards to the Indian Ocean. Also, judging from the recent discovery of a mid-Pliocene *Cercocebus*-like mangabey in Sterkfontein, South Africa, mangabeys once penetrated deeply to the south, presumably during periods of particularly benign climate (Gilbert 2007). Apart from changing climates, the ultimate influence on what is now a highly fragmented and relictual distribution for *Cercocebus* spp. (especially the two easternmost species, Tana River Mangabey *C. galeritus* and *C. sanjei*) is probably the rise of competing species of cercopithecines (guenons), most particularly members of the generalized Gentle Monkeys-Group *Cercopithecus (nictitans)*, which ranges over much of tropical and south-eastern Africa.

C. J. Jolly (pers. comm.) also thinks that competition from cercopithecines was a significant factor in afro-papionin evolution and that there were always many semi-terrestrial cercopithecids throughout the African Neogene. He envisions the spread of open habitats giving rise to a more terrestrial, long-faced 'baboon' resembling the fossil genus *Parapapio*, and that this stock underwent facial retraction. Unlike Kingdon, however, he thinks that facial retraction happened only once, and that it was *Cercocebus* mangabeys that gave rise to *Mandrillus*, which re-acquired long faces and a larger body. Likewise, he sees 'pre-*Lophocebus*' mangabeys (which would have resembled *Cercocebus*) giving rise to *Papio* (initially in the southern savannas), to *Theropithecus* (initially in the northern savannas), and to (arboreal) *Lophocebus* in the forests of central Africa. In Jolly's view, *Mandrillus* and *Papio* became large-bodied and long-faced convergently. In this way he explains why all mangabeys look cranially much alike – because they are conservative. They do not look like macaques, because of the 'cranial retraction' phase in

their common ancestor; Nakatsukasa (1994b, 1996) also thought that most features of mangabeys were derived from larger, more terrestrial ancestors. Patterns of shape variation in papionins and the bearing of cranial differences on their biogeography, phylogeny and systematics have been further discussed by Singleton (2002), Leigh *et al.* (2003) and Frost *et al.* (2003).

Groves takes a slightly different view, noting striking, presumably symplesiomorphic, resemblances between the two extremities of the genus, Sooty Mangabey *Cercocebus atys* in the extreme north-west and *C. sanjei* in the extreme south-east. Central African Agile Mangabey *Cercocebus agilis* also retains a very plesiomorphic morphology. Centrifugal speciation mechanisms have produced two highly autapomorphic centrally distributed species: *C. torquatus*, a derivative of the *atys*–*sanjei* axis, and Golden-bellied Mangabey *Cercocebus chrysogaster*, derived from *C. agilis* and convergent on *Mandrillus*.

Cercocebus share with *Mandrillus* a nasal ridge that runs between the zygomatic arch and the incisors; vastly inflated in *M. sphinx*, this ridge is most prominent in *C. torquatus* (Gilbert *et al.* 2006, McGraw & Fleagle 2006, Gilbert 2007). These authors also note that *Mandrillus* spp. and *C. torquatus* exhibit virtually identical orientations and development of the temporal lines. Based on these cranial features, they suggest that the shorter-muzzled *C. agilis* exhibits primitive cranial morphology while *C. torquatus* and *Mandrillus* spp. display the derived condition. Jolly (2007) has also suggested that the foraging behaviours and social structures of *Mandrillus* spp. are presaged in *Cercocebus*.

This is a diametrically opposite conclusion from that of Kingdon, who regards *M. sphinx*, *M. leucophaeus*, *C. torquatus* and *C. chrysogaster* as four divergent lineages but all more conservative than the five shorter-muzzled (and slightly more arboreal) *Cercocebus* spp. He notes that large-bodied primates that move about in large groups rely upon resources that are seasonal in abundance and widely dispersed, requiring large ranges that cross many vegetation types. These expansive subsistence strategies are most likely to develop in habitats with strongly seasonal climates and clumped sources of food. As such, the majority of baboon-like monkeys, both extant and fossil, come from non-forest habitats, where they probably originated, and that were most widespread during drier periods. Because masting and other expressions of localized and temporary abundance also occur in forests there are opportunities (over the course of several climatic fluctuations and through evolutionary time) for *Mandrillus*-like primates to transplant or adopt similar expansive patterns of land use within the forest zone. Thus large groups of large imposing ♂♂ can intimidate both predators and competitors in forests just as well as in woodlands, thickets and savannas and exaggerated ♂ dimorphism can be selected for in any of these habitat types.

Only very rich resources can sustain an expansive system that can regularly bring many hundreds of animals together. That fact helps explain the restriction of *Mandrillus* to the wettest and most highly diversified area of forest in Africa. Once an ancestral *Mandrillus*-like lineage had become established in such an area residual limitations in their expansive strategy would have become most apparent on the margins of their range. Here conditions would have become less predictable, especially during arid phases of climate. Here ancestral *Mandrillus* would have been subject to selection for more intensive, efficient and localized use of resources, especially when fruit sources become fragmented. These more marginal conditions,

even if ‘temporary’, would have favoured selection for more cryptic, smaller-bodied animals living in smaller groups in smaller home-ranges, often within sub-types of vegetation. Such animals would have had less use for intense inter-male competition resulting in strong selection for greatly reduced ♂ dimorphism. These would have been plausible geographic, ecological and behavioural contexts for the emergence of *Cercocebus*. In the now well-studied cranial morphology of *Cercocebus* and *Lophocebus* Kingdon envisages a common trend for sexually dimorphic, long-muzzled baboon-like ancestors with expansive subsistence strategies giving rise to retracted-muzzled mangabey-like primates with more intensive ways of living and not the other way round. In spite of such controversies, all authors, including Grubb (1978, 1982), are in general agreement that *C. torquatus* is a sister taxon of *Mandrillus*. It can be predicted that additional molecular data will eventually settle which of these scenarios is the more likely.

Goodman *et al.* (1998) and Perelman (2011) calculated that *Cercocebus* and *Mandrillus* separated only 4–5 mya (early Pliocene), too recently to qualify for generic separation under their proposed criteria. If *Cercocebus* and *Mandrillus* are to be combined, and one of us (C. G.) supports this, the prior name is *Cercocebus*. If this date, derived from molecular clock techniques, is correct, it would have occurred during a short period of warmer and wetter climate, during which forests probably expanded after the prolonged and widespread aridity of the Messinian period (and establishment and spread of the Sahara). Not only would formerly isolated forests have spread and connected, but adaptation to forest-living and a trend towards more arboreal habits (particularly in marginal or terrestrial primates) would have been favoured. This would support the supposition that the main expansion of *Cercocebus*, notably for the antecedents of today’s eastern species, would have been during this more benign part of the mid-Pliocene and before cold and aridity set in again later in the Pliocene. It seems likely that the two eastern species of *Cercocebus* that remain today (i.e. *C. galeritus* and *C. sanjei*) first became isolated and diverged during the arid late Pliocene.

Some resemblance between the distinctive ‘whoop-gobble’ loud-calls of *Lophocebus* and *Cercocebus* has been invoked as evidence for a close relationship between these two genera, but sonograms demonstrate a closer structural resemblance between the loud-calls of *Cercocebus* and *Mandrillus* than with those of *Lophocebus* (Gautier 1999). The ‘whoop’ is a separate component that alerts all neighbours to pay attention to the coming species-specific ‘gobble’ (for which listeners have to wait several seconds). The ‘whoop’ only has to be loud. As such, the attention-getting first part of the loud-call (i.e. the ‘whoop’) can derive from any pre-existent loud-call.

The two more widespread West African species, *C. atys* and *C. torquatus*, are phenotypically very different from one another (*contra* Groves 1978). If, as we suspect, they are *not* sister species, then the species that is geographically and, to some degree, phenotypically intermediate between them, White-naped Mangabey *Cercocebus lunulatus*, poses numerous questions. The differences among *atys*, *torquatus* and *lunulatus* are consistent. There are no specimens obtained from within the geographic range of *lunulatus* that could be taken for a specimen of *atys* or *torquatus*, or that even vary in their direction. Keeping *lunulatus* as a subspecies of *atys* is therefore meaningless. The intermediate condition of *lunulatus* raises at least three possibilities. First, that *lunulatus* is a species of hybrid origin that has long since

stabilized as a homogeneous entity. Second, that *lunulatus* represents a population that has conserved an intermediate condition in the evolution of *atys* from a shared ancestry with *torquatus*. This condition could be characterized as a progressive cline, *atys*–*lunulatus*–*torquatus*, going from primitive to derived or vice versa. Third, and least likely, *lunulatus* could be a population conserving features of an ancestor common to both *atys* and *torquatus*. See McGraw & Fleagle (2006) for a discussion of clinal distribution of characters.

The curious phenotypic and geographic aspects of this genus defy any simple hypothesis of interrelationships. The identification of *Parapapio*, from the mid-Pliocene of Sterkfontein, South Africa, as *Procercopithecus* (Gilbert *et al.* 2006, Gilbert 2007) is of great interest here. The mid-Pliocene was, as noted above, a time of forest expansion as the climate became wetter and warmer. The South African occurrence of a proto-mangabey would, if correct, indicate that the distribution of this genus has contracted hugely over time and reinforces the possibility that species that are geographically closest to one another at the present time are not necessarily the most closely related (e.g. *C. torquatus* and *C. agilis*, *C. galleritus* and *C. sanjei*).

Cercopithecus chrysogaster is a particularly puzzling species: in its robust build, considerable sexual dimorphism, slightly elongated

skull, shorter tail and reddish-gold throat and ventrum, it is the most *Mandrillus*-like of the *Cercopithecus* spp. How to interpret these resemblances remains contentious. Field studies of this threatened species would be of considerable interest and might help resolve whether *C. chrysogaster*'s *Mandrillus*-like characteristics are indicative of a convergent, conservative or shared derived condition.

Members of the genus are all semi-terrestrial, feeding on hard seeds and invertebrates that abound on the forest floor (especially in the case of *C. agilis* and *C. galleritus*) after the recession of floods in the riverine environments that they favour. *Cercopithecus* and *Mandrillus* both forage for nuts and other hard objects using their hands and arms with a fast and muscular style. There are, according to Groves (1978), Nakatsukasa (1994b, 1996), Fleagle & McGraw (1999, 2002), adaptive features in their limb anatomy that are not found in *Lophocebus*, *Papio* or *Theropithecus* (see above). The stiff-legged stance and the tail, which is characteristically held stiffly forward over the back from an angle at the base, contrast strongly with the flexible gait and exceptionally long, ragged and mildly prehensile tail of *Lophocebus*.

Jonathan Kingdon & Colin P. Groves

Cercopithecus galleritus TANA RIVER MANGABEY

Fr. Mangabé de la Tana; Ger. Tana-Mangabe

Cercopithecus galleritus Peters, 1879. Monatsb. K. Preuss. Akad. Wiss. Berlin 1879: 830. Mitole, Tana R., Kenya (02° 10' S, 40° 10' E).



Tana River Mangabey *Cercopithecus galleritus* adult male.

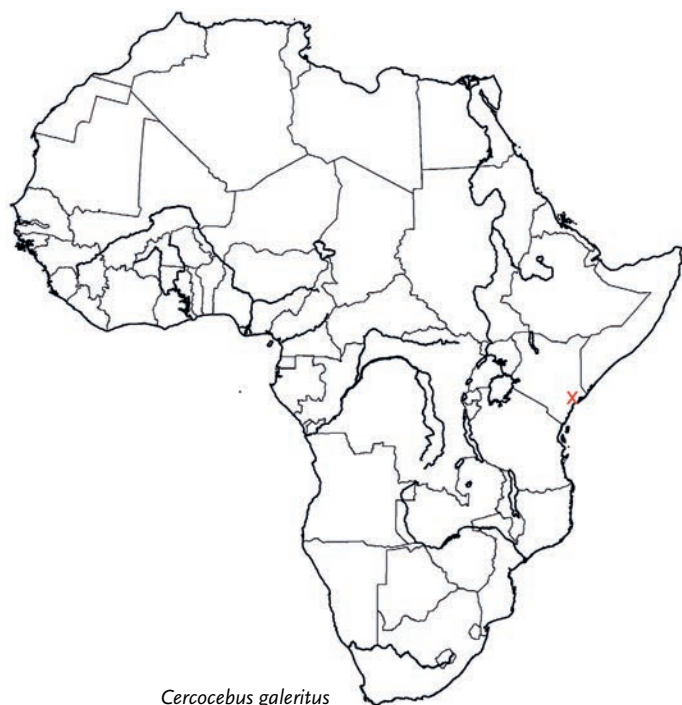
Taxonomy Monotypic species. Originally given full species status by Peters (1879), and that classification retained by Elliot (1913b), Dobroruka & Badalec (1966), Groves (1978, 2001, 2005c) and Kingdon (1997). Considered by some to be a subspecies *C. g. galleritus*, with the conspecifics Sanje Mangabey *C. g. sanjei*, Golden-bellied Mangabey *C. g. chrysogaster* and Agile Mangabey *C. g. agilis* (Schwarz 1928d, Dandelot 1974, Hill 1974, Napier 1981, Grubb *et al.* 2003). Synonyms: none. Chromosome number: 2n = 42 (Groves 1978).

Description Medium-sized, long-tailed, gracile, semi-terrestrial, pale greyish-brown monkey with conspicuous crest on crown and white eyelids. Sexes alike in colour. Adult ♀ has HB and tail measurements ca. 75% as long as adult ♂. Pelage long, coarse, wavy and dull. Face bare, black skin rimmed with white pelage. Cheeks and temples whitish. Eyelids bright white, contrasting with face. Forehead white, hair projecting forward. Ears black. Crest on crown with long (>100 mm), limp, medium grey to blackish-brown hairs, parted down the middle, sweeping back and to the sides, and falling over the ears. Dorsum pale yellowish-grey to greyish-brown, tinged olive. Throat and ventrum yellowish-white. Ventrum pelage long and sparse. Outer lower forelimbs dark grey to blackish-brown. Inner limbs white to yellowish-grey. Hands and feet dark grey to blackish-brown. Tail dark grey to blackish-brown with paler terminal ca. 25%. Tail with slight tuft. Hairs of crown, neck and shoulders annulated. Callosities joined in ♂♂ and separate in ♀♀. Occasionally holds tail in 'question-mark' pose above the back. Infants with pink face, ears and limbs, and without the characteristic crest on crown.

Geographic Variation None recorded.

Similar Species None within the small geographic range of this species.

Distribution Coastal Forest Mosaic BZ. Endemic to flood-plain forests along 60 km of the lower Tana R., SE Kenya, from Kanjonja in the north to Tana Delta in the south (01° 24' S to 02° 24' S, 40° 06' E to 40° 19' E, 20–40 m asl) (Butynski & Mwangi 1994, 1995, Hamerlynck *et al.* 2012).

*Cercocebus galeritus*

Habitat Flood-plain forest and adjacent woodland and bushland. Forest within the geographic range occurs in 71 fragments that range in size from 1 to 1100 ha and comprise a total forest area of ca. 37 km². In 1994 mangabeys inhabited 27 of these forests and occupied a total area of ca. 26 km² (Butynski & Mwangi 1994, 1995). Mangabeys move up to 1 km through non-forest habitat between forests (Wieczkowski 2010). Flood-plain forest comprised of plant species from four floristic regions, and characterized by high inter-forest species variation that is determined by forest location on the flood-plain (Medley 1992). The most common tree species are *Phoenix reclinata* (13%), *Polysphaeria multiflora* (12%), *Garcinia livingstonei* (7%) and *Sorindea madagascariensis* (5%) (percentages are of all trees ≥ 10 cm DBH sampled in 49,850 m² in 31 forests; D. Mbora & J. Wieczkowski pers. obs.)

Forest size and density of trees > 10 cm DBH are the only variables that are significantly positively correlated with mean number of mangabey groups/forest (Wieczkowski 2004).

Lower Tana R. is a highly seasonal environment. Mean annual rainfall 470 mm (120–1020 mm; Decker 1994a). Rainfall mostly limited to Mar–Jun and Nov–Dec. Mean monthly minimum daily temperatures are 17–25 °C, and mean monthly maximum daily temperatures are 30–38 °C (Butynski & Mwangi 1994). The coolest months are Jul–Sep and the hottest months are Oct–Jun.

Abundance Common within its small ca. 26 km² range. Densities within individual forests range from 0–6.8 animals/ha. Density within the entire forested area of the range is ca. 0.45 animals/ha. A total of 48 groups located during a survey of the entire range in 1994 when the total population was estimated at 1000–1200 animals (Butynski & Mwangi 1994). This is a decline from the 1975 estimate of 1200–1600 (Marsh 1978). Changes in the size of this population from 1972–94 are summarized in Butynski & Mwangi (1994).

Adaptations Diurnal and semi-terrestrial. Spends 56% of time on ground, 32% of time in vegetation to 10 m, and 12% of time

above 10 m ($n = 1$ group; J. Wieczkowski pers. obs.). *Cercocebus* spp. have a dental morphology and muscular jaws believed to be adapted to eating seeds and hard nuts (Fleagle & McGraw 2002). This interpretation is supported by the preponderance in the diet of seeds (Kinnaird 1990a, Wieczkowski 2003) that have high crushing resistance values (Wieczkowski 2009). Also adapted to the seasonality of fruit availability, and the temporal and spatial heterogeneity of its habitat, through flexibility in diet, grouping, ranging patterns and inter-group interactions (Homewood 1976, Kinnaird 1990a, Wieczkowski 2003). Spends more time foraging and moving when food less available, and more time in social behaviours when food more available (Kinnaird 1990a).

Foraging and Food Frugivorous. Average time spent feeding (eating and foraging) is 58% (46–65, S.D. = 8, $n = 6$ groups; Homewood 1976, Kinnaird 1990a, Wieczkowski 2003). Time spent eating is fairly constant throughout day, while foraging peaks morning and mid-day (Kinnaird 1990a). Feeds predominantly on the ground and up to 2 m (Homewood 1978a). Average daily travel distance for 431 sample days is 1511 m (1040–2618, S.D. = 562, $n = 10$ groups). Annual home-ranges ca. 17, 19, 20, 30, 47, 51, 53, 57, 70 and 101 ha (mean = 46.5 ha). Amount of overlap with neighbouring groups varies from 25% (70 ha range) to 36% (53 ha range) to 100% (17 and 19 ha ranges) (Homewood 1976, Kinnaird 1990a). Home-range size varies negatively with habitat quality and population density, and positively with group size (Homewood 1976, Kinnaird 1990a, Wieczkowski 2005b, Mbora *et al.* 2009).

Predominantly eats seeds and fruit, but also stems, leaves, insects and fungi. Adult ♀ observed with a small bird that was discarded (M. F. Kinnaird pers. comm.) and adult ♂ photographed repeatedly pulling an adult African Wood Owl *Strix woodfordii* from a tree-hole but left without killing the owl (Schuetz & Razakarivony 2004). Average annual diet is 44% fruit (26–71, S.D. = 18, $n = 6$ groups) and 32% seed (7–46, S.D. = 16, $n = 6$ groups; Homewood 1976, Kinnaird 1990a, Wieczkowski 2003), although there appears to be a shift to a preponderance of seeds in the latter two studies: fruit 32% (26–36, S.D. = 5, $n = 4$ groups) and seeds 42% (34–46, S.D. = 5, $n = 4$ groups). Eats unripe, ripe and dry fruit and seeds (Homewood 1976, Kinnaird 1990a, Wieczkowski 2003).

Observed feeding on total of 96 species of plants, though eight species each individually account for $> 10\%$ of the annual diet (*Aporrhiza paniculata*, *Acacia robusta*, *Diospyros mespiliformes*, *Ficus sycomorus*, *Hyphaene compressa*, *Pachystela msolo*, *Phoenix reclinata* and *Saba comorensis*) (Homewood 1976, Kinnaird 1990a, J. Wieczkowski pers. obs.). Species and items in the monthly diet closely follow the fruiting seasons of the top food species. High food availability from Nov–Apr; low food availability from Jun–Oct (Homewood 1976, Kinnaird 1990a).

Social and Reproductive Behaviour Social. Lives in multifemale groups with one or more adult ♂♂. Changes in group size from 1972 to 1992 are summarized in Butynski & Mwangi (1994). Mean group size has fluctuated over time: 26 (17–36, $n = 4$; Homewood 1976); 20 (15–28, $n = 7$; Kinnaird & O'Brien 1991); and 31 (6–62, $n = 17$; J. Wieczkowski pers. obs.). Mean for all years is 27 animals/group, consisting of a mean 2.2 adult ♂♂, 7.0 adult ♀♀, 2.4 subadult ♂♂, 2.0 subadult ♀♀, 9.6 juveniles and 3.3 infants ($n = 9$; Kinnaird & O'Brien 1991, J. Wieczkowski pers. obs.).

Agonistic behaviour includes eyelid flashes, lunges, chases, grabs, bites, grapples, branch shaking and vocalizations. These are described by Gust (1994), who did not observe damaging contact or serious wounding during a 210 h, 6-week study. Amicable behaviour includes stylized presentations, grooming and play. Territorial behaviour varies temporally. When fruit is scarce, groups avoid one another, using different areas of their overlapping ranges. When fruit is abundant and uniformly distributed, groups often move and feed together for several hours. When fruit is patchily distributed and defendable, territorial behaviour is exhibited. This includes approaching the other group, which may lead to an aggressive encounter. Aggressive encounters have site-dependent outcomes (Kinnaird 1990a, 1992b).

The dominant ♂ secures the majority of copulations with oestrous ♀♀ (Kinnaird 1990b). Copulation described by Gust (1994).

Adult ♂♂ emit a loud, long 'whoop-gobble' call that aids in inter-group spacing. Mean duration of the whoop-gobble is 90.5 sec (S.E. = 10.0, n = 136; Gust 1994). About 66% of whoop-gobbles are given between 06:30h and 11:00h (n = 562; Kinnaird 1992b). This call is audible to a distance of >1 km. Other vocalizations include 'screams' and 'wherrs' that are given during aggressive encounters (Gust 1994), as well as 'grunts', a bleating contact call and various alarm calls (J. Wiczowski pers. obs.).

Does not form polyspecific associations with other species of primates. Although often found with Pousargues's White-collared (Sykes's) Monkey *Cercopithecus mitis albitorquatus*, associations do not occur more often than expected by chance (Homewood 1976). Sometimes grooms Sykes's Monkey and the Tana River Red Colobus *Procolobus rufomitratus rufomitratus* (J. Wiczowski pers. obs.). Interactions with Yellow Baboon *Papio cynocephalus* are variable (fights, avoidance, supplants, toleration). Seen mounting and grooming Harvey's Duiker *Cephalophus natalensis harveyi* on several occasions (Homewood 1976, M. F. Kinnaird pers. comm., J. Wiczowski pers. obs.).

Reproduction and Population Structure Adult ♀♀ exhibit large, monthly, oestrous swellings lasting 4–5 days (Kinnaird 1990b). Mean gestation is 180 days (S.E. = 4.49, n = 7 pregnancies; Kinnaird 1990b). Details of parturition given in Kinnaird (1990b). Single births during Aug–Apr (Kinnaird & O'Brien 1991), generally a time of high food availability (Homewood 1976; Kinnaird 1990a). Twins not observed. About 63% of adult ♀♀ give birth during a given year (9–100%, n = 6 groups; Homewood 1976, Kinnaird 1990b). Infants suckle until 6–10 months; inter-birth interval is 18–24 months (Homewood 1978b). Infanticide by adult ♂♂ during dominance turnovers is thought to occur (Kinnaird 1990b). Post-conception sexual swelling lasting 8–9 days occurs after the first two months of pregnancy (mean = 62 days, S.E. = 3.6, n = 7), and two of seven pregnant ♀♀ under study copulated at this time (Kinnaird 1990b).

Based on studies of closely related species, ♀♀ probably first breed at ca. 6.5 years. Males probably first breed at seven years. Longevity estimated at 19 years (Homewood 1976, Kinnaird & O'Brien 1991). Adult ♂ to adult ♀ ratio in groups ranges from 1 : 2 to 1 : 6 (n = 9 groups). Adult and subadult ♂ to adult and subadult ♀ ratio in groups ranges from 1 : 1.2 to 1 : 6 (n = 11 groups). Adult to young (subadult, juvenile and infant) ratio in groups ranges

from 1 : 0.8 to 1 : 2.8 (n = 9 groups; Homewood 1976, Kinnaird & O'Brien 1991, J. Wiczowski pers. obs.). In one well-studied group of 20 mangabeys, two out of four adult ♂♂, and one out of five infants died in one year (Homewood 1976).

Predators, Parasites and Diseases Central African Rock Python *Python sebae* thought to be the most common and important predator (Homewood 1976, M. F. Kinnaird pers. comm., J. Wiczowski pers. obs.). Likely predators include African Crowned Eagles *Stephanoaetus coronatus* (Wiczowski *et al.* 2012), Martial Eagles *Polemaetus bellicosus*, Nile Crocodiles *Crocodylus niloticus* (Homewood 1976, J. Wiczowski pers. obs.) and Leopards *Panthera pardus*. An adult ♀ attacked by an (unidentified) eagle died of her wounds two days later. Twelve nematodes (*Abbreviata* sp., *Ascaridia galli*, *Capillaria* sp., *Heterakis* sp., *Oesophagostomum* sp., *Physaloptera* sp., *Streptopharagus* sp., *Strongyloides fuelleborni*, *Toxascaris* sp., *Toxocara* sp., *Trichostrongylus* sp. and *Trichuris trichura*) and three protozoans (*Entamoeba coli*, *E. histolytica*, *E. hartmani*) found in mangabey faecal samples from 82 individuals. The most common parasites were *E. coli* (20% of individuals), *T. trichura* (20%), *Heterakis* sp. (10%) and *Trichostrongylus* sp. (6%). *Entamoeba histolytica*, pathogenic in humans, was found in 1% of individuals (Mbora & Munene 2006).

Conservation IUCN Category (2012): Endangered. CITES (2012): Appendix I.

Ranked in 2002 as one of the world's 25 most threatened primates (Konstant *et al.* 2003). Greatest threat is forest degradation through taking of forest products and loss of forest for farmland (Butynski & Mwangi 1994, 1995), both of which increased dramatically after 1994 (Wiczowski & Mbora 2000, Wiczowski 2005a, Moinde-Fockler *et al.* 2007). Of special concern is decimation of local *P. reclinata* populations by humans (Kinnaird 1992a, Wiczowski & Mbora 2000); this palm is the mangabey's top food resource (Homewood 1976, Kinnaird 1992a, Wiczowski & Kinnaird 2008). Between 1994 and 2000, ca. 30% of the forest cover within the range of *C. galleritus* was lost to clearance for agriculture (Butynski & Mwangi 1994, Wiczowski 2005a). There was a 20% loss of forest inside the Tana River Primate National Reserve (TRPNR; 169 km²) and a 41% loss of forest outside this Reserve. In addition to *C. galleritus*, there is another Endangered primate that is endemic to the forests of the lower Tana R., *P. r. rufomitratus*. As such, the forests along the lower Tana R. represent the most important site in East Africa for primate conservation actions (De Jong & Butynski 2012). The history of research and conservation actions on behalf of *C. galleritus*, *P. r. rufomitratus* and the forests of the lower Tana R. is reviewed in Butynski & Mwangi (1994) and Wiczowski (2005a).

A five-year Kenya Wildlife Service (KWS) and Kenya Forest Department Project, funded by World Bank's Global Environmental Facility (GEF), was initiated in 1996 to enhance conservation and protection of the biodiversity and forests of the lower Tana R. Unfortunately, this potentially important project was terminated prematurely due to poor project management. This left the responsibility for the conservation and protection of the Tana River's biodiversity and forests entirely to KWS.

The TRPNR was gazetted in 1976 in approximately the northern half of the distribution of *C. galleritus* and *P. r. rufomitratus* (Marsh 1976). Officially a County Council Reserve, the Tana River County

Council had given management authority of the Reserve to KWS. In February 2007 the High Court of Kenya ruled in favour of Tana R. residents who brought a lawsuit stating the Reserve had been gazetted without their permission. Therefore, the TRPNR must be degazetted. Consequently, none of the habitat of *C. galeritus* or *P. r. rufomitratus* is legally protected. The residents say that they are interested in creating a community wildlife sanctuary but the way forward for the formal establishment of a community wildlife sanctuary and its effective management is unclear at this time (Mbora & Butynski 2007, Allen & Mbora 2012).

Habitat degradation and loss along the lower Tana R. has been further exacerbated by the failure of the 250 km² Tana Delta Irrigation Project's (TDIP) rice-growing scheme (under the administration of the Tana and Athi Rivers Development Authority [TARDA] with financing from Japan International Cooperation Agency [JICA]) to protect forest patches on their land. Some of the best forest habitat for *C. galeritus* and *P. r. rufomitratus* has been lost to TDIP (Butynski & Mwangi 1994, Moinde-Fockler *et al.* 2007). Now TARDA is promoting the establishment of a 400 km² sugar-cane plantation in the Tana Delta and of a 300 km² sugar-cane plantation slightly up-stream of the Delta. Beyond this, two jatropha biofuel farms (500 km², 280 km²) are being proposed for near the Delta (Hamerlynck *et al.* 2012). These new plantations will result in loss of forest, a large influx of people and an increase in the demand for forest resources, thereby putting even more pressure on the last remaining habitat for these two threatened monkeys (Mbora & Butynski 2007, Hamerlynck *et al.* 2012).

Priorities for research on *C. galeritus* include long-term monitoring and ecological studies in the southern half of the geographic range.

Priority conservation actions include habitat protection, community conservation education, establishment of forest corridors, planting of woodlots, creation of a permanent field research station at Mchelelo, and surveys of the newly discovered population in the Tana Delta (Butynski & Mwangi 1994, Wiczowski 2005a).

Measurements

Cercocebus galeritus

HB (♂ ♂): 600, 620 mm, n = 2

HB (♀): 450 mm, n = 1

T (♂ ♂): 620, 730 mm, n = 2

T (♀): 520 mm, n = 1

HF (♂ ♂): 158, 160 mm, n = 2

HF (♀): 133 mm, n = 1

E (♂): 39 mm, n = 1

E (♀): 32 mm, n = 1

WT (♂ ♂): n.d.

WT (♀): ca. 3.7 kg, n = 1

GLS (♂ ♂): 123 (122–127) mm, n = 5

GLS (♀ ♀): 107 (106–107) mm, n = 3

GWS (♂ ♂): 82 (79–84) mm, n = 5

GWS (♀ ♀): 70 (68–72) mm, n = 3

Tana R. (Elliot 1913b, Allen & Lawrence 1936, C. P. Groves pers. comm., T. Butynski & J. Wiczowski pers. obs.)

Key References Butynski & Mwangi 1994; Homewood 1976; Kinnaird 1990a; Wiczowski 2003, 2004, 2010.

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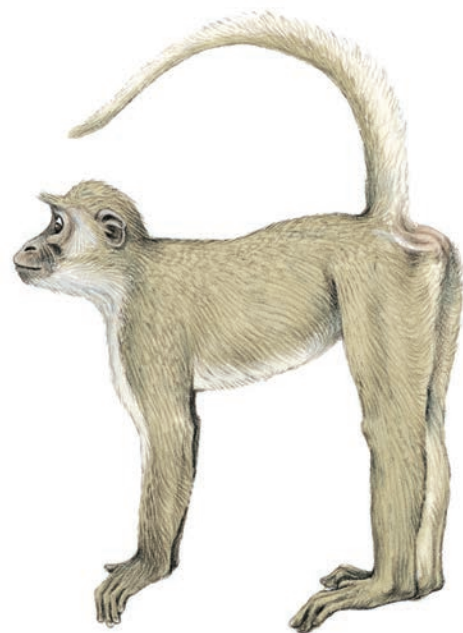
Cercocebus agilis AGILE MANGABEY

Fr. Mangabé agile; Ger. Olivmangabe

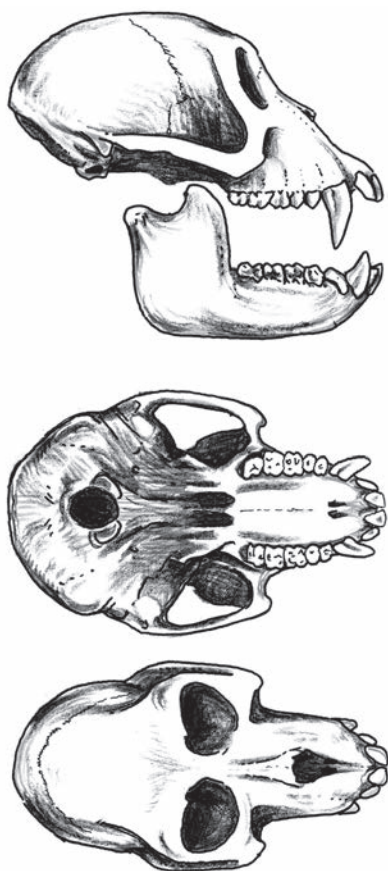
Cercocebus agilis Milne-Edwards, 1886. Revue Scientifique 12: 15. Republic Poste des Ouaddas (junction Oubangui R. and Congo R.), DR Congo.

Taxonomy Monotypic species. Often considered a subspecies of *Cercocebus galeritus*, along with other subspecies *galeritus*, *sanjei* and *chrysogaster* (Dandelot 1974, Napier 1981, Gautier-Hion *et al.* 1999, Grubb *et al.* 2003). Groves (1978) revised the genus, resurrecting *Cercocebus agilis*. (See also Groves 2001, 2005c.) Synonyms: *fumosus*, *hagenbecki*, *oberlaenderi*. Chromosome number: 2n not known, but probably 42, as for all Papionini for which chromosome number has been determined (Romagno 2001).

Description Medium-sized, lanky, brownish-grey, semi-terrestrial monkey with long tail. Sexes alike in colouration. Adult ♀ ♀ ca. 60% the weight of adult ♂ ♂. Muzzle moderately prognathic with short vibrissae. Face, ears, palms and soles black. Capacious cheek-pouches. Eyelids pale grey, but not as light as in Red-capped Mangabey *Cercocebus torquatus*. Face with white border formed by light bases to the hairs. Crown with whorl of hairs radiating 360° out from naked whitish skin, parting (creating a projecting brow). Crown, dorsum, outer limbs and upper tail heavily speckled brownish-grey, darkest on crown and lower limbs; hairs short, fine and agouti-banded. Chin, throat, inner limbs, ventrum and undertail unspeckled yellowish-white. Tail long



Agile Mangabey *Cercocebus agilis* adult male.



Lateral, palatal and dorsal views of skull of Agile Mangabey *Cercocebus agilis* adult male.

(ca. 140% of HB) and tapered, with variable presence of a whitish terminal tuft. Tail often carried arched or horizontal above the back, with tip almost touching the head. Ischial callosities separate in ♀♀, continuous in ♂♂. Infants born with red faces, which become black over time.

Geographic Variation Groves (1978) distinguishes a light morph and a dark morph, based on pelage colour; these co-occur, in different proportions, throughout the range of the species. Although four taxa (*agilis*, *hagenbecki*, *fumosus* and *oberlaenderi*) were described from different parts of the range in the early 1900s, Groves assessed that the level of geographic variation is not sufficient to warrant subspecies differentiation. Body size is larger in the west of the species' geographic range (Groves 2001).

Similar Species

Cercocebus torquatus. Geographic range to the west of *C. agilis*; only zone of contact is around Mevo/Sangmelima, Cameroon (Gautier-Hion *et al.* 1999). Crown chestnut. Collar white.

Lophocebus albigena. Widely sympatric with *C. agilis*. Pelage dark brown, longer and scruffier. Mane (= cape = mantle) over neck and shoulders.

Distribution Endemic to equatorial central Africa. Rainforest BZ. From SE Cameroon, NE Gabon, SW Central African Republic and N Congo to E DR Congo (Gautier-Hion *et al.* 1999). In Gabon from left bank of Ivindo R. as far south as Koungou Waterfalls, and



Cercocebus agilis

possibly along Mvounou R. (S. Lahm pers. comm.). Unclear how far west the range extends in the Minkebe area of N Gabon, although present on Sing R. and Nouna R. (S. Lahm pers. comm.), and on Mvounou R., a tributary of the Ntem R. (L. White pers. comm.). Western limit thought to be Lobo R., around Sangmelima, ca. 75 km west of Dja R., Cameroon (Gautier-Hion *et al.* 1999), but recently reported farther west at Campo-Ma'an N. P., SW Cameroon (Matthews & Matthews 2002, Etoga & Foguekem 2009). Distribution extends north in Cameroon to Nyong R. In Central African Republic the range extends north following the forest limit between Nola and Berberati, dipping down into the Ngotto Forest near Mbaiki. Agile Mangabeys were in the hills outside Bangui, but the forest there had been heavily degraded (N. Shah pers. obs.) so now probably absent there. From Bangui the distribution is to south of the left bank of Oubangui R., south of Gbadolite, DR Congo, then north again to the forests around Bangassou (A. Blom pers. comm.). Between the Oubangui R. and Congo R., DR Congo, distribution uncertain, as forests are highly fragmented and have not been much surveyed. Hicks (2010), however, found them in most areas surveyed north and south of Uele R. between Mbomu R. to the north and Rubi/Itimbiri R. to the south in the area around Aketi and Bambesa. Present almost as far east as Garamba (E. de Merode pers. comm.). The eastern limit in DR Congo likely the forest-savanna ecotone. Southern limit in DR Congo not clear: present in Ituri Forest north to Nepoko Forest and south of the Ituri R. (Hart & Thomas 1986) and in the Maiko N. P. (Hart & Sikubwabo 1994) but not in the Kahuzi-Biega lowlands (J. Hart pers. comm.). In Congo southern limit probably the limit of the forest block, around Likouala R., as this species is not found in forest fragments along Alima R. (A. Gautier-Hion pers. comm.), nor at Léfini or Konkouati. Reports (Sabater Pi & Jones 1968) of Agile Mangabeys in Equatorial Guinea (Rio Muni) require verification.

Habitat Often in riverine, seasonally inundated, or swamp forests, but can inhabit *terra firma* forest exclusively in some places.

Uses both primary and secondary forests, but prefers habitat with dense ground vegetation. Uses all forest strata, from ground to canopy. Occasionally in more open *Gilbertiodendron*-monodominant forest (Shah 2003, Devreese 2011). Travels and forages primarily on the ground, but climbs into trees to find fruit and to sleep. Large groups may spend more time on ground (72%; Devreese 2011) than small groups (12–22%; Quris 1975, Shah 2003). Adult ♂♂ more terrestrial than adult ♀♀ (36% vs. 24% of time on ground; Shah 2003).

Abundance More often heard than seen, and thought to be uncommon throughout most of its range. Difficult to estimate densities due to human hunting pressure, its semi-terrestrial nature and preference for habitats with dense ground vegetation. Quris (1975) estimated a density of 6.7–12.5 ind/km² along riverbanks in swamp forest in NE Gabon. At Mondika, in Ndoki Forest, S Central African Republic/N Congo, density ca. 6.9 ind/km² (Shah 2003) in terra firma forest. In Ituri Forest, DR Congo, Thomas (1991) estimated 0.25 groups/km², or ca. 2 ind/km², whereas Kambale Saambili (1998) estimated 38.3 ind/km² in the same area. In 1999, D. Brugière (pers. comm.) found 0.92 groups/km², or ca. 18.9 ind/km² in a narrow strip of flooded forest along the Mbaéré R. in the Ngotto Forest, Central African Republic. Densities ranged from 0.4 to 2.0 groups/km² (or ca. 7.2–41.0 ind/km²) in different stretches of this habitat; densities related to human hunting pressure. At this site Agile Mangabeys are restricted to a narrow strip of flooded forest along the river (i.e. not the entire flooded forest habitat).

Adaptations Diurnal and semi-terrestrial. Capacious cheek-pouches for storing food, and extra-laryngeal air sacs for long-distance vocalizations. Large molarized posterior premolars with thick enamel for crushing seeds, and well-developed forelimb flexor muscles for aggressive manual foraging (Fleagle & McGraw 1999, 2002).

Fruits and seeds are available to Agile Mangabeys on a longer temporal scale than for other sympatric monkeys, since they are able to consume many fruits before they are ripe and then dig up seeds that persist on the forest floor for months after the fruiting season. Additionally, they procure food at all forest levels, from the ground to the canopy, expanding their food niche relative to strictly arboreal monkeys.

Foraging and Food Frugivorous. Agile Mangabeys spend 64–76% of feeding time eating fruits, including seeds (Quris 1975, Kambale Saambili 1998, Shah 2003, Devreese 2011). At Mondika, of those observations where foods could be identified, 76% were fruit (including seeds), 16% pith and shoots of terrestrial herbs, 5% invertebrates, 2% mushrooms and 2% roots (Shah 2003). At Bai Hokou, SW Central African Republic: 68% fruit (including seeds), 21% plant structural parts, 6% animal matter and 5% mushrooms (Devreese 2011).

Agile Mangabeys eat a wide variety of fruits and seeds in ripe, unripe and over-ripe (i.e. rotting) stages. They also consume old seeds and nuts, which persist on the forest floor for months, or that they find by digging up or by sifting through Forest Elephant *Loxodonta cyclotis* dung (Ekondzo & Gautier-Hion 1998, N. Shah pers. obs.) or Western Gorilla *Gorilla gorilla* dung (N. Shah pers. obs.). They use their powerful jaws, broad cheekteeth and thick dental enamel to open tough pods and fruits, crunch hard seeds, and their incisors to scrape a hole to open lignified fruits. These morphological adaptations allow them to consume foods that most other monkeys cannot access.

During a one-year study at Mondika, the three species of fruit most eaten by Agile Mangabeys were *Diospyros pseudomespilus*, *Erythrophleum ivorense* and *Anonidium mannii*. The second-most-eaten category of food was the protein-rich shoots and terminal tips of Marantaceae herbs, especially *Haumania danckelmaniana* (Kambale Saambili 1998, Shah 2003). *Raphia* shoots are also often eaten (Quris 1975). Other plant food items include mushrooms, roots, tubers, seedlings and flowers. Animal prey includes termites, centipedes, butterflies, millipedes, beetles, gastropods, birds' eggs, rodents and small snakes (Shah 2003, Devreese 2011, A. Todd pers. comm.).

Agile Mangabeys hunt larger mammals at Bai Hokou (Knights *et al.* 2008, L. Devreese pers. comm.). Prey taken include infant Blue Duikers *Philantomba monticola*, infant Water Chevrotain *Hyemoschus aquaticus* and infant Peters' Duikers *Cephalophus callipygus*. Preliminary data indicate that infant Blue Duikers are taken ten times as often as other prey. Only adult ♂ Agile Mangabeys were observed to hunt these species. Hunts are opportunistic and solitary, and meat sharing has not been observed (although other individuals will take dropped pieces of meat). Preliminary data yield an average of 2–3 hunts/month (0–6; Knights *et al.* 2008).

For a small group at Mondika, about 33% of the time is spent feeding, 31% travelling, 13% inactive, 10% engaged in social/sexual behaviour, 8% foraging and 5% in other behaviours (Shah 2003). Adult ♀♀ spend more time searching for food (i.e. foraging and travelling) than adult ♂♂ (39% vs. 26%; Shah 2003). For a very large group at Bai Hokou (ca. 130 animals), about 25% of time spent feeding, 42% travelling, 10% inactive, 6% in social/sexual behaviour, 15% foraging, and 3% in other behaviours (Devreese 2011). Average daily travel distance is 1155 m (390–1985, n = 54) in terra firma at Mondika (Shah 2003), and 1215 m (n = 12, range unreported) in inundated habitat in NE Gabon (Quris 1975). For the much larger group at Bai Hokou, average daily travel distance is ca. 3884 m (Devreese 2011) to 3200 m (n = 79, range unreported; C. Cipolletta pers. comm.). During periods of fruit scarcity, Agile Mangabeys at Mondika travel longer distances, spend more time on the ground and spend a greater proportion of time searching for food (Shah 2003). Home-range for the group at Mondika was >303 ha (Shah 2003). The group in NE Gabon had a long and narrow home-range of 200 ha, following the course of a marshy river (Quris 1975). The very large group at Bai Hokou ranged over 1500 ha (L. Devreese pers. comm., A. Todd pers. comm.).

Social and Reproductive Behaviour Social. Group sizes vary enormously. Difficult to obtain accurate group counts, because of Agile Mangabeys' terrestrial locomotion in habitats with dense undergrowth. Smaller group counts are 8–18 individuals in NE Gabon (n = 1; Quris 1975), 21 individuals at Mondika (n = 1; Shah 2003), 24 individuals in Ituri Forest (9–55, n not given; Kambale Saambili 1998) and ca. 20 individuals in the Ngotto Forest (D. Brugière pers. comm.).

Large groups (50 to >200 animals) are occasionally reported in SE Cameroon (Uongo & Fimbel 1995), in NE Gabon (Quris 1975), in Ituri Forest (Kambale Saambili 1998) and in SW Central African Republic (A. Turkalo pers. comm., C. Cipolletta pers. comm., N. Shah pers. obs.). It is not always clear whether these counts represent larger groups, temporary aggregations of groups, or greater population densities. At Bai Hokou one group maintained a size of ca. 125 individuals for several months, appeared to merge with another group and maintained a size of ca. 230 individuals for 2 years, dropped to 134 for several months, then increased to 330 individuals (C. Cipolletta, A. Todd, K. Knights, M. Santochirico & L. Devreese pers. comm.).

Smaller groups have one adult ♂ (Quris 1975), while larger groups are age-graded or multimale (Quris 1975, Shah 2003, Devreese 2011). One group at Mondika comprised two adult ♂♂, two subadult ♂♂, 7–8 adult ♀♀ and 11 juveniles and infants (Shah 2003). At Bai Hokou the group of ca. 230 individuals comprised 32 adult ♂♂ and 22 subadult ♂♂ (M. Santochirico pers. comm.), and when it was 134 individuals there were 19 adult ♂♂ and 48 adult ♀♀ (Devreese 2011). In NE Gabon ♂♂ and ♀♀ both transferred between groups during inter-group encounters. Solitary ♂♂ were observed at this site (Quris 1975). In NE Gabon neighbouring groups have overlapping home-ranges. Here, a group of 7–18 individuals with a long and narrow home-range along a river had extensive overlap with other groups (Quris 1975), whereas at Mondika, a group of 21 individuals had a home-range of >303 ha in terra firma forest, with minimal overlap with other groups (Shah 2003).

Relations between conspecific groups are variable: sometimes affiliative, with individuals intermingling in temporary associations called 'supergroups' (Quris 1975, Shah 2003), and at other times agonistic (Shah 2003). During these agonistic encounters, adult ♂♂ vocalize, display and chase ♂♂ of other groups. It is not clear whether relations with the same neighbouring groups are affiliative at some times, and agonistic at others, or whether relations with certain neighbouring groups are always affiliative, and with others always agonistic. Groups temporarily fragment into subgroups (Quris 1975, Kambale Saambili 1998, L. Devreese pers. comm.).

Adult ♀♀ display oestrous swellings and have visible menses. Males sometimes mate-guard oestrous ♀♀. There can be high levels of aggression between ♂♂ over an oestrous ♀ (N. Shah pers. obs.). Weaning conflicts between mothers and their offspring begin when infants are about seven months old, but ♀♀ occasionally nurse offspring as old as 18 months. Infants are sometimes carried by adult and subadult ♂♂, particularly in tense encounters between ♂♂, where they potentially serve to buffer aggression (N. Shah pers. obs.).

Adult ♂♂ emit long-range vocalizations, beginning with a loud 'whoop' (very similar to the 'whoop' of the sympatric Grey-cheeked Mangabey *Lophocebus albigena*) followed by a 'gobble' or 'cackle'. These calls, audible to observers at up to 1000 m, are thought to play a role in both intra-group coordination and inter-group communication (Quris 1973, 1980). Most 'whoop-gobbles' (or 'whoop-cackles') are emitted around dawn. Individuals within a group also communicate using a variety of other vocalizations, including a soft 'contact' grunt that is audible only to ca. 25 m and that is thought to help maintain group cohesion in dense understorey (N. Shah pers. obs.).

Agile Mangabeys occur in polyspecific associations with other primate species 11% of the time at Mondika (Shah 2003) and 6% of the time in NE Gabon (Quris 1976), but these are usually short-lived associations, often at shared feeding trees. Inter-specific interactions are generally neutral, but occasionally may be agonistic or affiliative. Agile Mangabeys sometimes supplant or chase other monkeys (e.g. *L. albigena*, Putty-nosed Monkeys *Cercopithecus nictitans*, Moustached Monkeys *Cercopithecus cephus*, Crowned Monkeys *Cercopithecus pogonias*) out of feeding trees (Shah 2003). Juveniles, however, occasionally engage in reciprocal grooming bouts with adult ♂♂ and juveniles of other monkey species (e.g. *C. cephus* and *C. pogonias*) (Shah 2003). Other animals, such as guineafowl (several species), Red River Hogs *Potamochoerus porcus* and various species of duikers (*Philantomba monticola*, *Cephalophus* spp.), often forage with Agile Mangabeys. Agile Mangabeys react to alarm calls of all of these species (A. Todd, M. Santochirico & N. Shah pers. obs.).

Reproduction and Population Structure When in oestrus, ♀♀ have perineal swellings that they sometimes present to ♂♂. Gestation is ca. 24 weeks in captivity (E. Dols pers. comm.). At Mondika one ♀ gave birth six months after she was last observed copulating (N. Shah pers. obs.). One infant is born at a time. Twins not reported. Birth-weights are not available. Inter-birth intervals at Mondika are greater than 21 months (N. Shah pers. obs.). In NE Gabon infants are born in Dec–Feb (Quris 1975). At Mondika births occur during two periods: Dec–Feb and Jun–Aug (N. Shah pers. obs.). At Bai Hokou, ca. 60 km to the north of Mondika, births occur in May–Aug (K. Knights & M. Santochirico pers. comm.). Infants are weaned at 7–18 months at Mondika (N. Shah pers. obs.) and at about six months in captivity (E. Dols pers. comm.). In a small group at Mondika the ratio of adults and subadults to juveniles was 1 : 1, and the ratio of adult ♂♂ to adult ♀♀ varied from 1 : 3.5 to 1 : 4.0 (Shah 2003). In a group of 134 animals at Bai Hokou, the ratio of adult ♂♂ to adult ♀♀ was 1 : 2.6 (Devreese 2011). Longevity in the wild not known. One animal in captivity lived to 21 years of age (E. Dols pers. comm.).

Predators, Parasites and Diseases Gabon vipers *Bitis gabonica*, Leopards *Panthera pardus* and African Crowned Eagles *Stephanoaetus coronatus* are known predators of Agile Mangabeys (A. Todd & L. Devreese pers. comm.). Central African Rock Pythons *Python sebae* and cobras (*Naja* spp.) unsuccessfully attacked Agile Mangabeys (A. Todd pers. comm.).

Agile Mangabeys carry high levels of parasites, such as *Entamoeba histolytica*, *Entamoeba coli*, *Balantidium coli*, *Iodamoeba butschlii* and trichomonads. All of these parasites are transmitted back and forth between humans and the monkeys (Lilly *et al.* 2002). Agile Mangabeys also harbour a strain of simian immunodeficiency virus (SIV) (Apetrei *et al.* 2002).

Conservation IUCN Category (2012): Least Concern. CITES (2012): Appendix II.

The primary threat to Agile Mangabeys is hunting for the bushmeat trade. Because of their semi-terrestrial habits, they are vulnerable to snare hunting. A secondary threat is habitat loss, degradation and fragmentation. Agile Mangabeys are notorious crop

raiders (Kambale Saambili 1998), which may make them vulnerable to reprisals in areas where they live close to plantations.

Measurements

Cercocebus agilis

HB (♂ ♂): 572 (500–625) mm, n = 6

HB (♀ ♀): 489 (440–530) mm, n = 5

T (♂ ♂): 684 (570–760) mm, n = 6

T (♀ ♀): 530 (450–600) mm, n = 5

HF (♂ ♂): 169 (153–180) mm, n = 5

HF (♀ ♀): 139 (130–150) mm, n = 4

E (♂ ♂): 370 (350–400) mm, n = 5

E (♀ ♀): 360 (340–400) mm, n = 3

Various localities (Hill 1974)

HB (♂ ♂): 550 (?–?) mm, n = 11

HB (♀ ♀): 465 (?–?) mm, n = 11

T (♂ ♂): 745 mm, n = 11

T (♀ ♀): 635 mm, n = 11

WT (♂ ♂): 8.8 (4.8–10.0) kg, n = 7

WT (♀ ♀): 5.4 (4.3–6.2) kg, n = 5

Makokou area, Gabon (Gautier-Hion *et al.* 1999)

WT (♂ ♂): 9.0, 10.0 kg, n = 2

WT (♀ ♀): 4.3, 6.2 kg, n = 2

Ngotto Forest, Central African Republic (Colyn 1994)

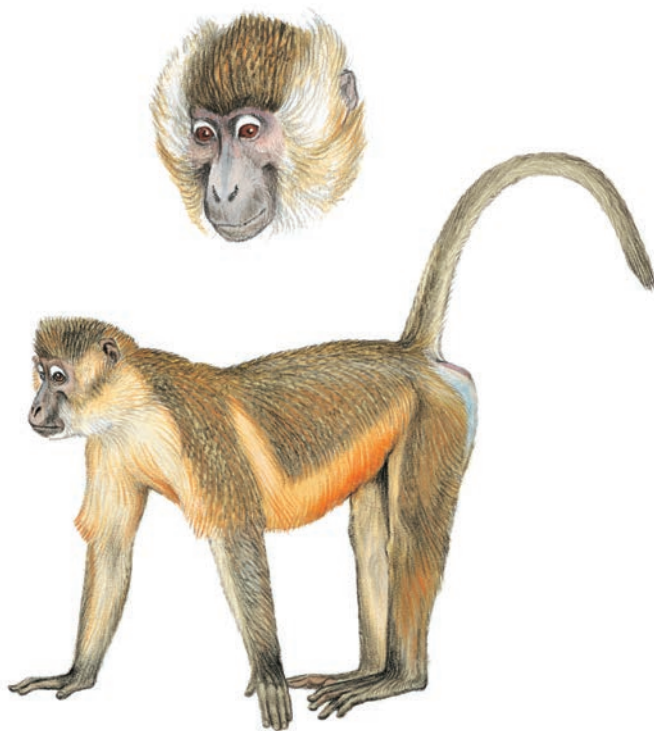
Key References Devreese 2011; Gautier-Hion *et al.* 1999; Groves 1978; Kambale Saambili 1998; Quris 1975; Shah 2003.

Natasha F. Shah

Cercocebus chrysogaster GOLDEN-BELLIED MANGABEY

Fr. Mangabé à ventre doré; Ger. Goldbauchmangabe

Cercocebus chrysogaster Lydekker, 1900. Novitates Zoologicae 7: 279. Upper Congo, DR Congo.



Golden-bellied Mangabey *Cercocebus chrysogaster* young adult male.

Taxonomy Monotypic species. Originally given full species status by Lydekker (1900), and that classification retained by Elliot (1913b), Dobroruka & Badalec (1966), Kingdon (1997) and Groves (2001, 2005c). Also classified as *Cercocebus galeritus chrysogaster* (Schwarz 1928d, Dandelot 1974, Hill 1974, Napier 1981, Grubb *et al.* 2003) and as *Cercocebus agilis chrysogaster* (Groves 1978, 1993, Gautier-Hion *et al.* 1999). Synonyms: none. Chromosome number: 2n = 42 (Dutrillaux *et al.* 1979).

Description Robustly built monkey with a golden-yellow to orange-gold or reddish-gold belly. Only mangabey without a brow (frontal) fringe. Adult ♀ like adult ♂, but less robust and smaller; body weight ca. two-thirds that of adult ♂. Muzzle robust. Bare skin of chin, lips, muzzle, face and ears dark brown to blackish. Eyes brown. Eyelids whitish or pinkish. Cheek whiskers cream-yellow, long and swept back from near corner of mouth to behind ears giving a 'mutton-chop' appearance, especially in mature ♂ ♂; pelage bordering face and sides of head off-white. Light cream to reddish patch behind ears. Forehead lacks parting or whorl in adults, but whorl present in some juvenile museum skins (Groves 1978). Crown and neck brownish-olive to reddish-olive, speckled with black, tipped yellow or light orange. Shoulders, back, flanks and outer limbs colour of crown and neck but paler and less speckled, especially on the flanks and outer hindlimbs. Inner forelimbs light yellow or pale orange proximally, becoming cream towards wrists and ankles. Inner hindlimbs light reddish-gold. Hands and feet grey, dark greyish-brown to blackish. Throat, front of upper arms and chest pale orange to light reddish-gold, darker towards midline. Shoulders and upper arms of adult ♂ with a mane (= cape = mantle) of long, thick pelage. Belly light yellow to golden-yellow to reddish-gold, becoming brighter towards the lower belly. Belly with median fringe of long hairs. Rump broad, poorly furred. Buttocks of adult ♂ each have a patch of cream-white pelage and a patch of pink bare skin to either side of base of tail; absent in ♀ ♀. Ischial callosities wide, light pink, rosy-pink, or violet-grey; fused in ♂ ♂, separate in ♀ ♀. Broad ring of off-white pelage around ischial callosities. Tail pelage short; above speckled like dorsum at base, rest unspeckled grey or sooty-black, paler below, especially near base. Tail about equal in length to HB. Penis bright scarlet. Scrotum bluish.

Infant colouration differs from adult; head pelage black, skin pale pink and belly pale beige or white. A golden band appears on forehead at ca. 8 weeks of age and adult colouration gradually expands over the head; skin darkens to greyish-brown by 14 weeks

with contrasting non-pigmented eyelids visible by 20 weeks (Field 2007).

Sexes markedly dimorphic in size (Dorst & Dandelot 1970, Groves 1978); adult ♂♂ noticeably more robust, with canines about three to four times longer than in adult ♀♀ (Field 2007). GLS for adult ♀ (n = 2) is 82% that of adult ♂ (n = 9; Groves 1978). In captive animals weight of adult ♀♀ ca. 62% that of adult ♂♂, and HB length of ♀♀ ca. 83% that of ♂♂ (Field 2007).

Geographic Variation Upon examination of 15 study skins, the only variation that Groves (1978: 17) found was that the one specimen from the westernmost locality (Luaza) had a belly that 'is hardly yellow at all,' in sharp contrast to the golden-yellow or bright orange colouration on the belly of the other 14 specimens. Both this specimen, and the one from the south-easternmost locality (between Lusambo and Pania), were only weakly speckled on the flanks.

Similar Species None within geographic range.

Distribution Endemic to the western and central Congo Basin, DR Congo. Rainforest BZ. Geographic distribution not well-known. There is no evidence for *C. chrysogaster* in the NE Congo Basin; absent in the Lomako Forest and in the 70,000 km² 'Maranga-Lopori-Wamba Landscape' as indicated by extensive ground surveys in the region and by the absence of *C. chrysogaster* from among the ca. 12,000 carcasses examined in the Basankusu (01° 13' N, 19° 49' E) bushmeat market. This market is fed largely by hunters operating in forests along, and between, the Maranga and Lopori Rivers (J. Dupain pers. comm.). Based on a specimen from Irebu Village (00° 37' S, 17° 45' E), the western limit is the Congo R. (Schouteden 1944a, Hill 1974). A specimen from Lulonga (= Lubonga) Village suggests that the north-west limit (and northern extreme) is the lower Lulonga R. (ca. 00° 24' N, 18° 14' E; Groves 1978, Gautier-Hion 1999). *Cercocebus chrysogaster* is present, but uncommon, in the bushmeat market south of Lulonga R. at Mbandaka (00° 03' N, 18° 15' E; J. Hart pers. comm.). Absence of *C. chrysogaster* from the Basankusu bushmeat market (see above) to the north of the Lulonga R. indicates that this species does not occur along the upper reaches of the Lulonga R., nor north of the Lulonga R. Distribution appears to be south-south-east from Lulonga R. (Groves 1978) to Momboyo R. at about Imbonga Village (00° 41' S, 19° 39' E; J. Hart pers. comm.), and then to the Lokoro R. at Luikotale Village (which is the western boundary of the South Sector of the Salonga N. P.). J. Eriksson (pers. comm.) found *C. chrysogaster* to be uncommon at Luikotale, but already more common just 10 km to the west, and fairly abundant ca. 50 km to the west at Lokolama Village and Mimia Village, as well as between Lokolama and the right bank of the Lukénie R. at Oshwe. From Luikotale, the range appears to extend south-east to the Ngendo R. (ca. 03° 28' S, 21° 13' E), a northern tributary of the Lukénie R. Inogwabini & Thompson (2004) state that *C. chrysogaster* occurs west of the Ngendo R., but not to the east. From here the distribution becomes particularly poorly known, but at some point the range probably meets the Sankuru R. to the south. The distribution likely extends east along both the Lukénie and Sankuru Rivers to at least Samangwa Village (04° 14' S, 24° 06' E). The south-east limit



Cercocebus chrysogaster

appears to be between Lusambo Village and Pania Village (05° 00' S, 23° 24' E). At least four specimens obtained in the vicinity of Samangwa, Lusambo and Pania (Schouteden 1944a, Hill 1974, Groves 1978). Samangwa is only ca. 75 km from the west bank of the Lomami R. As such, Hill (1974) suggests that the Lomami R. is the likely eastern limit for *C. chrysogaster*. Known south-west limit, based on a specimen, is Luaza Village (03° 25' S, 17° 11' E) on the Kwilu R., a southern tributary of the Kasai R. One specimen collected at Oshwe (03° 23' S, 19° 30' E) on the south bank of the Lukénie R. (Schouteden 1944a, Hill 1970, Groves 1978, Gautier-Hion *et al.* 1999), and J. Eriksson found *C. chrysogaster* to be common here. Inogwabini & Thompson (2004) did not find *C. chrysogaster* east of 20° 30' E along the Kasai-Sankuru R. and, thus, believe that the Lukénie R. is the southern boundary for *C. chrysogaster* in this region, not the Kasai-Sankuru R. as indicated by Gautier-Hion *et al.* (1999).

The information available suggests that *C. chrysogaster* may occur in two populations (a western population and an eastern population), or else these two ranges are connected by a narrow corridor that runs along, or in the vicinity of, the Lukénie R. and/or Sankuru R. A. Gautier-Hion (pers. comm.) notes that there are patches of savanna to the south of the South Sector of the Salonga N. P. and that this presence of unsuitable habitat may account for what appears to be a fragmented distribution for *C. chrysogaster* in this region. It is of conservation importance that *C. chrysogaster* appears to be absent from the North Sector of Salonga N. P. (Gautier-Hion *et al.* 1999, G. Reinartz pers. comm., J. Hart pers. comm., J. Thompson pers. comm.). J. Hart (pers. comm.) and his colleagues undertook surveys over much of Salonga N. P. (36,560 km²), encountered >200 groups of primates and never observed *C. chrysogaster*. J. Thompson (pers. comm.) conducted surveys in the southern half of the South Sector of Salonga N. P. and never encountered *C. chrysogaster*. The map in Gautier-Hion *et al.* (1999) shows *C. chrysogaster* as present in the South Sector of Salonga N. P., although this map is based on information collected from interviewees and not on the authors'

direct observations of *C. chrysogaster* in this region (A. Gautier-Hion pers. comm.). If *C. chrysogaster* is present anywhere in the Salonga N. P. it is most likely in the south-west corner of the South Sector on the Lula R. between Luikotale Village and the Ngendo R.

Not known to be sympatric with Agile Mangabey *Cercocebus agilis*, the two species being separated by the Congo R. (Groves 1978, Gautier-Hion *et al.* 1999).

Habitat Prefers seasonally flooded and swamp forests (Groves 1978, Gautier-Hion *et al.* 1999, Inogwabini & Thompson 2004). Can be common in secondary forest (J. Eriksson pers. comm.). The altitude limits of the distribution of *C. chrysogaster* are ca. 300 and 500 m (Inogwabini & Thompson 2004).

Abundance Few data. What information is available strongly suggests that *C. chrysogaster* not only has a small and fragmented distribution, but that the area actually occupied is small.

Adaptations Diurnal and semi-terrestrial (Hill 1974, Gautier-Hion *et al.* 1999). Not studied in the wild. J. Eriksson (pers. comm.) is of the opinion that *C. chrysogaster* moves mainly on the ground.

Foraging and Food Unknown. Kingdon (1997) suggests diet is largely frugivorous. J. Eriksson (pers. comm.) observed *C. chrysogaster* eating seeds out of Forest Elephant *Loxodonta cyclotis* dung and often saw duikers *Cephalophus* spp. foraging within *C. chrysogaster* groups.

Social and Reproductive Behaviour Social. No detailed information available on social structure or social organization from wild populations. Gautier-Hion *et al.* (1999) suspect that group size averages ca. 15 animals, if similar to *C. agilis*. J. Eriksson (pers. comm.) estimated group size for *C. chrysogaster* as often >100 animals, and sometimes had the impression that groups might be between 200–300 animals (in the vicinity of Lokolama, Mimia and Oshwe).

Data from captive heterosexual pairs of *C. chrysogaster* indicate sex differences in behaviour, with ♂♂ displaying significantly more aggression, and ♀♀ more social grooming and vocalization (Mitchell *et al.* 1988). Posture is more similar to that of macaques (*Macaca* spp.) than to other *Cercocebus* spp. (Hill 1974), and overall appearance reminiscent of some of the more robust macaque species; these are the strong impressions one gets upon seeing this species for the first time (T. Butynski & C. L. Ehardt pers. obs.). Unlike all other mangabeys, immatures and adults both carry the tail in a backward arch with the tip directed at the heels. While apparently never arched high over the shoulders and/or back (Dandelot 1974, Kingdon 1997), the tail may be swung forward at such an acute angle that the mid-part of the tail touches a shoulder and the tip touches an upper arm (T. Butynski pers. obs.). In captivity at least one aggressive display involves a wide yawning expression with the upper lip pulled back, all teeth showing, and eyebrows raised (Hill 1974, T. Butynski pers. obs.).

One vocalization is described by Hill (1974: 165) as ‘a deep guttural croak, somewhat like a baboon’s bark’. A rapid, low, ‘ooh-ooh-ooh-ooh’ given by a captive ♂ in what appears to be greeting behaviour (C. L. Ehardt & T. Butynski pers. obs.). A ‘ha-ha-ha-’ call

given in aggressive situations (Mitchell *et al.* 1988). Not known to give the ‘whoop-gobble’ loud-call of some other *Cercocebus* spp.

Reproduction and Population Structure No data available from wild populations. Data on reproductive parameters collected on five captive ♀♀ (two wild-caught). Two ♀♀ began cycling at 2.5 and 2.6 years with first menses at 2.7 years; menses heavy and highly visible. Mean menses is three days. Oestrous cycles average 30.7 days (20–51, n = 149 cycles), with duration of peak perineal swelling averaging 5.8 days (2–22, n = 151 cycles). First pregnancy at 4.9 years (Walker *et al.* 2004).

Gestation ca. 5.8–5.9 months (n = 2 births). Mean interval from parturition to resumption of swelling 8.6 months (5.5–10.0, n = 3 ♀♀). Inter-birth interval for captive ♀♀ with infants surviving >1 month averages 19.9 months (16.6–24.8, n = 4 ♀♀ producing nine births; Walker *et al.* 2004). There is a post-conception swelling. Females solicit adult ♂ cage-mates during periods of post-conception swelling, and copulations have occurred at this time (Walker *et al.* 2004, Field 2007). No twin births observed in captivity (n = 15). Birth-weight of one individual was 750 g (Field 2007). No pronounced birth season in captivity (Field 1995a, 2007).

Predators, Parasites and Diseases No information. Most important predators are likely to include Leopards *Panthera pardus* and African Crowned Eagle *Stephanoaetus coronatus*. Humans are undoubtedly the most important predator (see below).

Conservation IUCN Category (2012): Data Deficient. CITES (2012): Appendix II.

As indicated above, and in Inogwabini & Thompson (2004), it now appears that *C. chrysogaster* has a considerably smaller range and lower numbers than once believed. Assessment by the IUCN Primate Specialist Group at this time would likely find that *C. chrysogaster* deserves threatened species status. Habitat degradation and loss, as well as hunting by humans, are major threats (Wolfheim 1983, Inogwabini & Thompson 2004). Hunting rates are high, as indicated by the many *C. chrysogaster* on the streets of Kinshasa and elsewhere, both for meat and the pet trade; it is also an agricultural pest in some areas. Young are often kept as pets as they seem to tame readily (Inogwabini & Thompson 2004, G. Reinartz pers. comm., J. Eriksson pers. comm.). Sixteen wild- and captive-born *C. chrysogaster* (seven ♂♂, nine ♀♀) are present in six North American zoos (Field 2007); four European zoos currently house ten ♂♂ and 18 ♀♀ (ISIS 2007). This is one of Africa’s least-known primates and, potentially, one of Africa’s most unique primates. Research is needed on all aspects (distribution, abundance, ecology, conservation status, threats) of this likely threatened monkey.

Measurements

Cercocebus chrysogaster

T (♂♂): 510 (470–550) mm, n = 4

T (♀♀): 460 mm, n = 1

WT (♂♂): 11.6 (10.1–13.6) kg, n = 4

WT (♀♀): 9.0 kg, n = 1

Captive individuals at Sacramento Zoo (L. Field pers. comm.)

HB (♂): 790 mm, n = 1

T (♂): 430 mm, n = 1

HF (♂): 130 mm, n = 1
 Locality not stated (Elliot 1913b)

HB (♂♂): 530 mm
 HB (♀♀): 440 mm
 T (♂♂): 540 mm
 T (♀♀): 450 mm
 WT (♂♂): 11–15 kg
 WT (♀♀): 8 kg

Based on an unknown number of captive individuals at various sites (Field 2003); ranges and sample sizes not available

GLS (♂♂): 131 (129–134) mm, n = 9

GLS (♀♀): 105, 109 mm, n = 2

GWS (♂♂): 85 (82–89) mm, n = 9

GWS (♀♀): 67, 68 mm, (n = 2)

From various localities (RMCA) (Groves 1978, C. P. Groves pers. comm.)

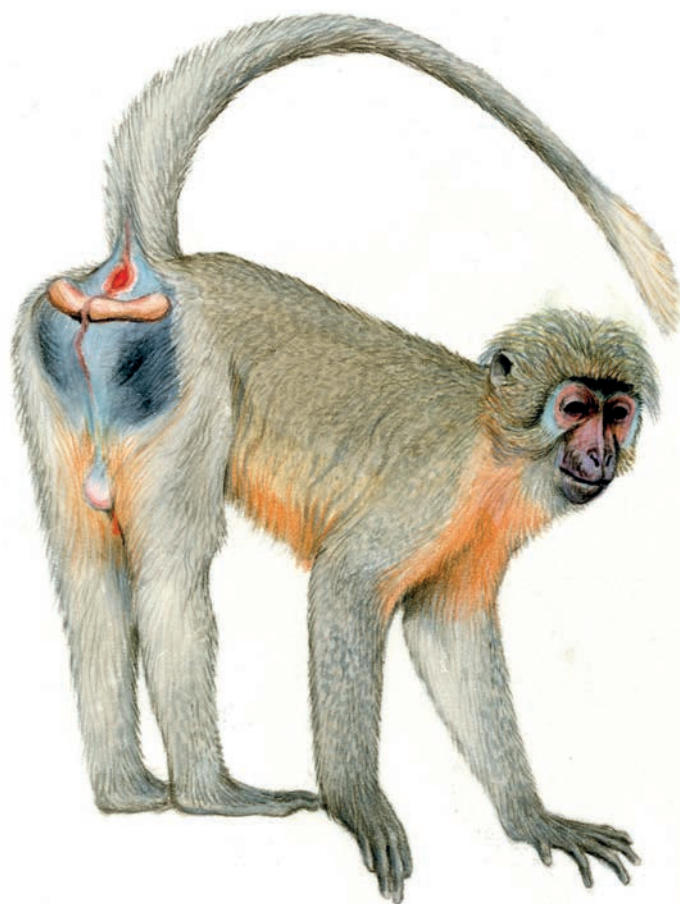
Key References Elliot 1913b; Gautier-Hion *et al.* 1999; Groves 1978.

Carolyn L. Ehardt & Thomas M. Butynski

Cerrocebus sanjei SANJE MANGABEY

Fr. Mangabé Sanje; Ger. Sanje-Mangabe

Cerrocebus sanjei Mittermeier, 1986. In: Else & Lee (eds), Primate Ecology and Conservation, p. 338. Sanje Waterfall, Mwanihana Forest, Udzungwa Mts, Tanzania.



Sanje Mangabey *Cerrocebus sanjei* adult male.

Taxonomy Monotypic species (Kingdon 1997, Groves 2001, 2005c). Originally considered a subspecies (*Cerrocebus galeritus sanjei*) (Homewood & Rodgers 1981). No museum specimen exists and no holotype has been designated. Synonyms: none. Chromosome number: 2n = unknown, but 42 for all *Cerrocebus* spp. and *Lophocebus* spp. for which the chromosome number determined (Dutrillaux *et al.* 1979, T. Disotell pers. comm.).

Description Medium-sized, long-tailed, semi-terrestrial, grizzled-grey monkey. Sexes alike in colour. Adult ♂♂ moderately larger than ♀♀, but no body measurements exist against which to accurately assess sexual dimorphism. Muzzle grey to dark grey, moderately projecting with numerous dark vibrissae. Face pale pinkish and grey. Eyelids slightly less pigmented, pale beige, contrasting with surrounding skin. Skin on forehead and under eyes pale pinkish-cream. Cheek skin along hair line pale blue. Skin on body bluish-white, with skin on hands, feet and ears dark greyish. Crown hairs long, slightly parted along midline or forming a slight whorl, with shorter seam of hair extending forward along the brow. Hairs on crown, brow and extending back around face blackish at base, then dark greyish-brown. (Note: Previous descriptions of crown hairs swept back and upward to give a 'bouffant' appearance are inaccurate. These were based on the appearance of the crown of a captive adult ♂ at the Mount Meru Game Sanctuary, Arusha, Tanzania, which did not resemble any observed free-living animal. The 'bouffant' crown of this captive might have been due to the fact that it received a haircut as a juvenile pet and/or repetitive rubbing of the crown against the wire mesh of its cage.) Dorsum hairs long, light creamy-grey at base, then a darker grey band followed by a yellowish-orange band and black tip. Ventrums hairs long, pale orange. Pelage darker grey or blackish on distal part of limbs and on hands and feet. Paracallosal skin greyish with pink tinge. Ischial callosities pink; fused in ♂♂, separate in ♀♀. Tail long, grey, with slight tuft at tip. Infants have dark greyish-black coat and pink skin on face, ears, hands and feet.

Geographic Variation None recorded.

Similar Species None within geographic range.

Distribution Coastal Forest Mosaic and Afromontane–Afroalpine BZs. Endemic to two forests within the Udzungwa Mts, SC Tanzania: Mwanihana Forest (7°40'–7°57'S, 36°46'–36°56'E) within Udzungwa Mountains N. P. (UMNP), and Udzungwa Scarp F. R. (USFR; 7°39'–7°51'S, 35°51'–36°02'E) (Rodgers & Homewood 1982, Ehardt *et al.* 1999, 2005, Dinesen *et al.* 2001). The area of closed



canopy in the Mwanihana Forest is ca. 131 km², while that in the USFR is ca. 100 km². Reported presence in Ndundulu Forest in West Kilombero F. R. (Dinesen *et al.* 2001) resulted from misidentification of the Kipunji *Rungwecebus kipunji* (Jones *et al.* 2005, Ehardt & Butynski 2006a, b). Historical distribution may have included lowland forests of the Kilombero Valley below the south-eastern escarpment of the Udzungwa Mts (Homewood & Rodgers 1981).

Habitat In mosaic habitats and moist forest at altitudes from ca. 300–1800 m (Rodgers & Homewood 1982, Ehardt *et al.* 1999, 2005, Dinesen *et al.* 2001, Rovero *et al.* 2009). Occasionally observed in low altitude (300–500 m) miombo *Brachystegia* spp. woodland near human habitation and bordering secondary forest; reported to raid crops in these areas. Most abundant in mosaic habitats composed of mid-altitude (transitional) mixed evergreen and semi-deciduous forest, and in tall evergreen forest with canopy heights 40–50 m. One habituated study group ranges 700–900 m altitude in Mwanihana Forest. Main habitats and some of the common tree species within each of the habitats present within the home-range of this group of Sanje Mangabeys are summarized as: mature primary evergreen forest with canopy to 40 m (*Parinari excelsa*, *Tabernaemontana pachysiphon*, *Bombax rodhagnaphalon*, *Lagynias pallidiflora*); dominant *Tabernaemontana* forest with closed canopy to 15 m (*Anthocleista grandiflora*, *Harungana madagascariensis*, *Ficus* spp.); dry slopes covered in bracken fern *Pteridium aquilinum* and *Rubus* spp. with scattered trees to 15 m (*Bridelia micrantha*, *Vernonia mariacancia*, *Vitex doniana*, *Annona senegalensis*); and valley bottoms with predominant *Aframomum* spp. Other prominent trees in less-disturbed evergreen forest include: *Albizia gummifera*, *Parkia filicoidea*, *A. grandiflora* and *Treulia africana*. Sanje Mangabeys are frequently encountered in forested valleys near streams and rivers, which are numerous in both Mwanihana Forest and USFR. Annual rainfall along the south-eastern escarpment of the Udzungwa Mts varies 1500–2500 mm, with a distinct dry season May–Nov (Lovett *et al.* 1988).

Abundance Size of fragmented population uncertain but estimated at <1300 animals (Ehardt *et al.* 1999, 2005). Greatest abundance may be in Mwanihana Forest. Ehardt *et al.* (2005) estimate 200–270 animals in USFR and 700–900 animals in Mwanihana Forest. Line-transect censuses located 0.155 groups/km in USFR (S. D. = 0.223, n = 134 transects, total 479 km) and 0.058 groups/km in Mwanihana Forest (S. D. = 0.125, n = 180 transects, total 702 km; Rovero *et al.* 2012). These transects yield estimates of 1050–1400 animals in 30–40 groups for USFR, and 1750–2100 animals in 50–60 groups for Mwanihana Forest, giving a world population of ca. 2800–3500 animals (Rovero *et al.* 2009).

Adaptations Diurnal and semi-terrestrial. Occupies all forest strata, but most often <10 m above ground. Spends ca. 50% of time on the forest floor (Ehardt *et al.* 2005). Percentage time in different canopy strata for the habituated study group in Mwanihana Forest is as follows: lower canopy (3–6 m height) 10%; middle canopy (7–15 m height) 7%; upper canopy (>15 m height) 34% (C. L. Ehardt pers. obs.). Sleeps in large (>30 m tall), clumped trees such as *P. excelsa*. Study group in Mwanihana Forest utilized eight areas of tall trees for sleeping, scattered through their large home-range; each site might or might not be used during consecutive nights (C. L. Ehardt pers. obs.).

Adult ♂♂ emit ‘whoop-gobble’ loud-calls, audible to >1 km, which likely function as a group-spacing mechanism. These are given at all times of the day, but are most common in early morning, with ca. 70% given before 12:00h. Whoop-gobbles are frequently given in sleeping trees before the group begins foraging, and when conspecific groups are encountered. Other vocalizations include: high-pitched, repetitively emitted ‘barks’ given when the group is alarmed, which may differ in structure depending on the source of the threat (alarm calls); low volume, low frequency, short duration ‘moo’ calls that group members emit periodically when the group is spread out and resting (contact calls); multi-syllabic ‘hee-aw’ calls by oestrous ♀♀ after ♂ ejaculates and ♀ runs forward, breaking copulatory mounted position (post-copulatory calls); and rapidly repeated ‘geckers’ given by infants and young juveniles, especially in context of weaning (C. L. Ehardt pers. obs.).

Foraging and Food Omnivorous. Forages in all strata of the forest, but most often on the ground and in understorey trees and shrubs (Ehardt *et al.* 2005). On the forest floor Sanje Mangabeys manually search through leaf litter and decomposing wood for invertebrates, fallen seeds and nuts, and fungi, as well as dig for subterranean roots as deep as 500 mm (e.g. *Costus* sp.). The Sanje Mangabey has large posterior premolars, which are similar to other *Cercocebus* mangabeys (Fleagle & McGraw 2002), used to crack open hard seeds and nuts (e.g. *P. excelsa*) (C. L. Ehardt pers. obs.). Groups often fission into foraging parties, regrouping ≤6 h later (Ehardt *et al.* 2005). Invertebrates, such as ants, millipedes, slugs and snails, are taken from epiphytes in the branches of trees, and from rotting wood and leaf litter. When foraging on abundant fruit in single trees (e.g. *Ficus* sur), or on large fruits that cannot be consumed quickly, Sanje Mangabeys frequently place whole fruits or chunks of fruit in their cheek-pouches and move into other trees to process and consume. Also observed to place *P. excelsa* nuts gathered while moving along the forest floor into cheek-pouches to consume in trees, often in

early evening when moving toward sleeping trees (C. L. Ehardt pers. obs.).

Diet includes fruit pulp (ca. 50% of diet items consumed; $n = 5084$ food item scores over 19 months), seeds and nuts (27%), invertebrates (6%), shoots and stalks (4%), fungi (4%), mature and young leaves (4%), flowers (2%) (C. L. Ehardt pers. obs.). Consumed in smaller relative amounts (each $\leq 1\%$ of total diet items) are buds, petioles, herbs, roots, bark, lichen, tree gum or latex, birds, amphibians and reptiles (e.g. frogs and chameleons), and several invertebrates, such as snails and crabs found in or near rivers and streams (Wasser 1993, Ehardt *et al.* 2005, C. L. Ehardt pers. obs.). Plants utilized by non-systematically observed groups (near Sanje River Falls, ca. 600 m in Mwanihana Forest [Wasser 1993]), and by one study group at 700–900 m in the Sonjo River Valley in Mwanihana Forest (Ehardt *et al.* 2005, C. L. Ehardt pers. obs.), are: *Acacia polyacantha*, *Acacia siberiana*, *Aframomum* sp., *A. gummifera*, *A. senegalensis*, *A. grandiflora*, *Antiaris toxicaria*, *B. micrantha*, *Celtis gomphophylla*, *Costus* sp., *Diospyros natalensis*, *Dovyalis* sp., *Dracaena mannii*, *Entada rheedii*, *Ficus cyathistipula*, *F. sur*, *Ficus vallis-choudae*, *H. madagascariensis*, *Hoslundia* sp., *Kigelia africana*, *L. pallidiflora*, *Lettowianthus stellatus*, *Macaranga capensis*, *Mangifera indica*, *Milicia excelsa*, *Olyra* sp., *Oxytenanthera abyssinica*, *P. excelsa*, *P. filicoidea*, *Psychotria capensis* subsp. *riparia*, *Rhaphiostylis beninensis*, *Saba comorensis*, *Sorindeia madagascariensis*, *Strombosia scheffleri*, *Syzygium cumini*, *T. pachysiphon*, *Tarennia pavettoides*, *Toddalia asiatica*, *T. africana*, *Trema orientalis*, *Tricholysia* sp., *Trilepisium madagascariensis*, *V. mariacancia*, *V. doniana* and *Voacanga africana*. Foraging occurs most frequently in the morning, early afternoon, late afternoon and early evening (groups tend to rest for 1–2 h at mid-afternoon).

Home-range of Mwanihana Forest study group is ca. 2 km and overlaps that of two conspecific groups (Ehardt *et al.* 2005, C. L. Ehardt pers. obs.). Rovero *et al.* (2009) report home-ranges of 4–6 km² with overlap of home-range with up to three other groups. No evidence of territoriality. Intra-specific group encounters produce frequent ‘whoop-gobble’ vocalizations and alarm calls, with occasional chasing/fleeing. Mean daily path length ca. 1350 m (500–1650 m, $n = 190$ days; C. L. Ehardt pers. obs.).

Social and Reproductive Behaviour Social. Groups are multimale/multifemale. From 3–8 adult ♂♂ in Mwanihana study group; ♀♀ are philopatric. Group size counts and estimates in Mwanihana range from 1 to 40 individuals (mean 10, Wasser 1993; mean = 15, $n = 14$, Ehardt 2001). Rovero *et al.* (2009) report that mean group size is between 40 and 60 individuals. The study group in Mwanihana increased from 39 to 58 animals across ca. 3.5 years (C. L. Ehardt pers. obs.); another group in UMNP grew from 35 to 49 members over five years (Jones *et al.* 2006). Solitary adult ♂♂ occur (Homewood & Rodgers 1981, Wasser 1993, Dinesen *et al.* 2001, Ehardt 2001, Ehardt *et al.* 2005). In 2005 the study group of 47 animals in Mwanihana was comprised of five adult ♂♂ (number fluctuated from two to five), 23 adult ♀♀, ten subadults, five juveniles and four clinging infants (ratio adult ♂♂ to adult ♀♀ = 1 : 4.6; immatures to adults = 1 : 1.47) (C. L. Ehardt pers. obs.).

Groups form polyspecific associations with most of the other diurnal primate species in the Udzungwa Mts (Udzungwa Red Colobus *Procolobus gordonorum*, Peter’s Angola Colobus *Colobus angolensis palliatus*, Sykes’s Monkey *Cercopithecus mitis*) (Wasser 1993, Ehardt *et al.* 2005). One adult ♀ Udzungwa Red Colobus moved and foraged

with the Mwanihana Forest study group of Sanje Mangabeys for three consecutive days; interactions between this ♀ and group members were infrequent, although juvenile and subadult Sanje Mangabeys groomed her (C. L. Ehardt pers. obs.). In Mwanihana Forest Sanje Mangabeys were in polyspecific associations for ca. 28% of the sightings; the most frequent interspecific association for the Sanje Mangabeys was with Sykes’s Monkeys (ca. 52%, $n = 25$), ca. 54% of which involved a single adult ♂ Sykes’s Monkey. Associations with Udzungwa Red Colobus (28% of mangabey sightings) and Peter’s Angola Colobus (20% of mangabey sightings) were less frequent. Sanje Mangabey groups also associate with Natal Red Duiker *Cephalophus natalensis* and Crested Guineafowl *Guttera pucherani* (C. L. Ehardt pers. obs.).

Oestrous adult ♀♀ copulate with multiple adult ♂♂; adolescent and juvenile ♂♂ mount young adult ♀♀ in first oestrus without interruption by adult ♂♂. Dominant adult ♂ observed numerous times travelling and resting with an infant clinging to his ventrum. Male emits low, repetitive ‘ooh-ooh-ooh grunts’ when infant is clinging, especially following locomotion and before ♂ sits and infant dismounts. Male arches tail up and over back with tip at crown or side of head when giving the vocalization. Mother of infants follows behind ♂ and retrieves infant when it dismounts (C. L. Ehardt pers. obs.).

Reproduction and Population Structure Little known. Females exhibit perineal swellings and emit post-copulatory vocalizations; ♂♂ are single-mount ejaculators. Infants are carried on the ventrum during the first year; young juveniles sometimes carried ventrally for short distances. Singletons usually born, but one set of twins born in the habituated study group in Mwanihana Forest ($n = >12$ births). No pronounced mating/birth seasons, although birth peaks may exist; births in the habituated Mwanihana study group were not highly clumped across the year-long study but did not occur in all months (C. L. Ehardt pers. obs.).

Predators, Parasites and Diseases Predators include African Crowned Eagles *Stephanoaetus coronatus*, which are common in the Udzungwas and seen or heard on ca. 50% of observation days in Mwanihana Forest (Ehardt *et al.* 1999, 2005). Sanje Mangabeys give an alarm call when an eagle is detected. An adult African Crowned Eagle ♀ was attacked and killed by an adult Sanje Mangabey ♂ as the bird attacked a subadult mangabey feeding in a *Ficus* tree (Jones *et al.* 2006). Other predators known to take primates in the Udzungwa forests are Leopards *Panthera pardus*, Lions *Panthera leo*, various venomous snakes, and humans (see below). There is no information on parasites or other diseases.

Conservation IUCN Category (2012): Endangered. CITES (2012): Appendix II.

Sanje Mangabeys are threatened due to habitat loss and alteration, continued fragmentation of their small populations, and hunting by local people (Ehardt *et al.* 2005, Ehardt & Butynski 2006a, Rovero 2007, Rovero *et al.* 2012). Hunted with dogs and nets by local non-Muslim people (Homewood & Rodgers 1981). Hunting is largely controlled in UMNP, but mangabeys are sometimes caught in snares (A. R. Marshall pers. comm., C. L. Ehardt pers. obs.), that were likely set for other prey such as small antelope.

Concern for the persistence of this Tanzanian endemic monkey is great, especially given that ca. 40–50% of the world’s population

resides outside of UMNP, in the poorly protected USFR. The two most important actions that can be taken on behalf of the long-term conservation of the Sanje Mangabey are to upgrade the status of USFR to that of a Nature Reserve, and to establish the 'Mngeta Conservation Corridor' as this would link USFR with the southern forests of UMNP (Marshall *et al.* 2007, Rovero *et al.* 2012).

Measurements

Cercocebus sanjei

GLS (♀ ♀): 104, 113 mm, n = 2

GWS (♀ ♀): 72, 76 mm, n = 2

No body measurements available, and only two skulls, both collected in Mwanihana Forest, one by A. R. Marshall and one by F. Rovero.

Key References Ehardt 2001; Ehardt & Butynski 2006a; Ehardt *et al.* 1999, 2005; Homewood & Rodgers 1981; Rovero *et al.* 2011; Wasser 1993.

Carolyn L. Ehardt & Thomas M. Butynski

Cercocebus atys SOOTY MANGABEY (SMOKY MANGABEY)

Fr. Mangabé fuligineux; Ger. Russmangabe

Cercocebus atys (Audebert, 1797). Histoire Naturelle des Singes et des Makis 4 (2) 13. West Africa.



Sooty Mangabey *Cercocebus atys* adult male.



Cercocebus atys

Taxonomy Monotypic species. Considered by some to be a subspecies of the Red-capped Mangabey *Cercocebus torquatus* (Dandelot 1974, Groves 1978, Napier 1981, Grubb *et al.* 1998) but not by most authorities, particularly in recent years (Booth 1956a, 1958b, Hill 1974, Oates 1996a, Kingdon 1997, Groves 2001, 2005c, Grubb *et al.* 2003). Type locality given as 'Indes orientales' but type label is marked 'Afrique occidentale' (Schwarz 1928d). White-naped Mangabey *Cercocebus lunulatus* often treated as a subspecies of *C. atys* (e.g. Booth 1956a, 1958b, Groves 1978, 2001, 2005c, Kingdon 1997, Grubb *et al.* 2003) but recognized as a species by Oates (2011) and here. Synonyms: *aethiopicus*, *aethiops*, *fuliginosus*. Chromosome number: $2n = 42$ (Brown *et al.* 1986).

Description Medium-size, slender, slate-grey (sometime light brown) monkey with long limbs and tail. Sexually dimorphic. Body

weight of adult ♀ ♀ about 60% that of adult ♂ ♂. Sexes similar in colour. Muzzle and ears blackish. Whiskers light grey. Face greyish-pink or pinkish. Eyelids off-white (not pure white). Iris olive. Crown usually without crest or whorl. Dorsum usually slate-grey though light brown in some individuals. Ventrums and inner limbs cream to light grey. Hands, feet and top of tail slightly darker grey than dorsum. Palms and soles black. Scrotum pinkish. Sexual skin of ♀ rosy pink. Depressions in the skull's suborbital region combined with facial prognathism give a hollow-cheeked appearance. Infants and juveniles like adults, though suborbital excavation not as pronounced.

Geographic Variation None recorded.

Similar Species

Cercocebus lunulatus. Between Sassandra and Volta Rivers. Nape (posterior crown) with concentric, V-shaped, or oval whitish

patch. Whorl of hairs on crown. Crown hairs without straw-coloured band. Ventrums pure white. Distinct, dark spinal stripe.

Distribution Rainforest BZ. Endemic to Upper Guinea Forests from Niadiou Village, Senegal (12° 30' N, 16° 05' W; Struhsaker 1971a) to the Nzo–Sassandra River System, Côte d'Ivoire (Wolfheim 1983, Kingdon 1997, Grubb *et al.* 1998, Groves 2003).

Habitat Primary forest preferred, but present, even abundant, in secondary forest. In high forest, gallery forest, coastal forest, *Raphia* palm swamp and mangrove, and farm bush. Probably always near water (Booth 1956a, Oates *et al.* 1990, Fimbel 1994b, Grubb *et al.* 1998, McGraw & Sciulli 2011). A frequent crop raider able to effectively utilize cultivated areas (Hill 1974, Fimbel 1994b).

Abundance One of the more common monkeys in West Africa (Wolfheim 1983, Kingdon 1997). Surveys and reports from Côte d'Ivoire, Liberia and Sierra Leone suggest that this species' abundance is due to its ability to exploit a variety of habitat types (Davies 1987, Oates *et al.* 1990, Fimbel 1994a). Reported densities are 11.9 ind/km² at Tai N. P., Côte d'Ivoire (McGraw & Zuberbühler 2007), and 38.5 ind/km² on Tiwai I., Sierra Leone (Oates *et al.* 1990). The following estimates are based on a 2006–08 study in Tai N. P. (3300 km²); 10.5 ind/km², 0.64 groups/km², and total of ca. 63,000 individuals (N'Goran *et al.* 2012).

Adaptations Diurnal and predominantly terrestrial. Males have large canines. Light-coloured eyelids are flashed as threats during agonistic encounters. During these threats ♂♂ commonly arch the tail over the rump in combination with yawns to display canines. The high masticatory forces needed to crush hard nuts are evident in various craniodental characteristics: these monkeys possess powerful jaws and teeth, their premolars are greatly expanded and the cheekteeth become heavily worn at early ages (Fleagle & McGraw 1999, Daegling *et al.* 2011, McGraw *et al.* 2011, 2012). Features of the humerus, ulna and radius reflect the frequent and aggressive use of the forelimbs to search for and process foods from the forest floor (Nakatsukasa 1996, Fleagle & McGraw 1999, 2002).

When alarmed on the ground, Sooty Mangabeys jump into short trees. Flight from predators, however, occurs on the ground. Experimental evidence from the Tai Forest indicates that of the seven sympatric cercopithecids present, *C. atys* is the best at detecting ground predators from the greatest distance (McGraw & Bshary 2002).

Vocal repertoire consists of 19 distinct vocalizations including 'grunts', 'twitters', 'screams' and 'growls' (Range & Fischer 2004). Copulation calls given by ♀♀ only. Adult ♂♂ give 'whoop-gobble' long/loud call, that is similar to whoop-gobbles given by *Lophocebus* (Struhsaker 1971a, Waser 1982). Males and ♀♀ both give distinct alarm calls to snakes (e.g. Gabon Viper *Bitis gabonica*, Black-necked Spitting Cobra *Naja nigricollis*), African Crowned Eagles *Stephanoaetus coronatus* and Leopards *Panthera pardus* (Range & Fischer 2004).

Foraging and Food Omnivorous. Foraging occurs at all forest levels but most food is obtained from the forest floor and includes fallen fruits and seeds, mushrooms, insects and leaves (Bergmueller 1998,

Fleagle & McGraw 2002, McGraw & Zuberbühler 2008, McGraw *et al.*, 2011). In Tai N. P., spends 67% of time, 85% of travel, and 71% of foraging on the ground (McGraw 2007a). Mean home-range size for groups in Tai N. P. is 4.92 km² with the largest home-range being 8.0 km². Average daily path length for one group followed for 58 days was 2.2 km (0.8–3.8) (Rutte 1998). Sooty Mangabeys have spatial memory of fruiting states of trees and this helps shape foraging routes (Janmaat *et al.* 2006). Two particularly important foods are *Sacoglottis gabonensis* and *Anthonata fragrans* (Bergmueller 1998, Rutte 1998, Daegling *et al.* 2011, McGraw *et al.* 2011).

Considerable foraging time is spent pawing through the leaf litter on the forest floor looking for fallen fruits, nuts and seeds. Skeletal adaptations of the forelimb and dentition reflect this reliance on manual foraging and seed predation. Compared to arboreal mangabeys (genus *Lophocebus*), the forelimb bones of *C. atys* possess much larger muscle markings indicative of frequent and aggressive use of forelimbs to access food on or near the ground. In these respects, the foraging ecology and accompanying morphology of *Cercocebus* are similar to those of Drills *Mandrillus leucophaeus* and Mandrills *Mandrillus sphinx* (Fleagle & McGraw 1999, 2002).

Social and Reproductive Behaviour Highly social. Live in large, multimale, multifemale groups with a complex social organization. Typical groups number 75–100 individuals. One group of 120 individuals studied for 10 months consisted of 6–10 adult ♂♂, 24–34 adult ♀♀, 29–34 juvenile ♂♂, 17–26 juvenile ♀♀ and 4–22 infants (Range & Noë 2002, 2004, Range 2005, 2006). The group's core consists of related ♀♀; ♂♂ disperse from their natal groups. Home-ranges overlap significantly with those of neighbouring groups. Territorial encounters between groups are infrequent and inter-group spacing appears to be maintained by the whoop-gobble calls of adult ♂♂. During inter-group encounters, both sexes may engage in threats and chases though such incidents usually involve ♀♀ only (F. Range pers. comm.). Non-resident adult ♂♂ are often seen travelling and foraging alone. The dominance system in captive *C. atys* is not based on maternal dominance rank (Bernstein 1976, Ehardt 1988, Gust & Gordon 1994, Gust 1995). In contrast, studies on grooming partners and association frequencies of free-ranging populations in Tai N. P. indicate that the dominance system is matrilineal-based (Range & Noë 2002, Range *et al.* 2007).

Polyspecific associations with arboreal monkeys are common but there are no data quantifying the frequency of these associations. Arboreal monkeys often respond to the presence of Sooty Mangabeys by descending and foraging to lower forest levels, including the ground (McGraw & Bshary 2002). In captivity and the wild, ♀♀ typically carry infants but ♂♂ also do so (Busse & Gordon 1984, W. S. McGraw pers. obs.).

Reproduction and Population Structure Visible changes in sexual skin of ♀♀ include a bright pinkening in the peri-anal region and correspond to ovulation (Gust 1995). Gestation (captivity) is ca. 175 days and a single infant is born (n = 198; Gust *et al.* 1990, Gordon *et al.* 1991). Twins have not been reported (Gust *et al.* 1990). There is a distinct mating season in Tai N. P. from Jun–Oct and the birth season is Oct–Mar (n = 52 births) with a peak during the Dec–Feb dry season. Interbirth interval ca. 2 years (Range *et al.* 2007). Females (captivity) first reproduce at 3.1 years (Ross 1991). Males

(captivity) reach sexual maturity at ca. 7 years (Gust & Gordon 1991, Gust *et al.* 1998). Birth rate (captivity) is 0.92. Maximum life-span (captivity) is 18 years (Ross 1991).

Predators, Parasites and Diseases Sooty Mangabeys frequently preyed upon by African Crowned Eagles *Stephanoaetus coronatus* and Leopards *Panthera pardus* (Shultz *et al.* 2004, McGraw *et al.* 2006a, Shultz & Thomsett 2007, Zuberbühler & Jenny 2002, 2007). Occasionally eaten by Robust Chimpanzees *Pan troglodytes* (Boesch & Boesch-Acherman 2000). The Sooty Mangabey is the primate reservoir of HIV-2, a less common strain of the AIDS virus. Transmission of this disease to humans probably occurred the first half of the twentieth century and involved the butchering of monkeys killed for consumption (Hirsch *et al.* 1989, Chen *et al.* 1996, Hahn *et al.* 2000, Lemey *et al.* 2003, Silvestri 2005).

Conservation IUCN Category (2012): Near threatened. CITES (2012): Appendix II.

There are no recent census data on the species, but numbers are undoubtedly decreasing owing to habitat loss and poaching (McGraw 2007b, Oates 2011). Dwindling habitat has forced this monkey to exploit cultivated lands, where farmers hunt them with dogs.

Measurements

Cercocebus atys

HB (♂): 580 mm, n = 1

HB (♀ ♀): 500 (470–520) mm, n = 3

T (♂): 600 mm, n = 1

T (♀ ♀): 580 (520–645) mm, n = 2

HF (♂): 157 mm, n = 1

HF (♀ ♀): 146 (145–147) mm, n = 3

E (♂): 28 mm, n = 1

E (♀ ♀): 31 (26–35) mm, n = 3

WT (♂ ♂): 10.6 (9.5–11.4) kg, n = 4

WT (♀ ♀): 6.2 (5.6–7.0), kg, n = 4

GLS (♂ ♂): 132 mm, n = 11

GLS (♀ ♀): 115 mm, n = 2

GWS (♂ ♂): 87 mm, n = 11

From various localities. Linear body measurements from Hill (1974).

Body weights from Oates *et al.* (1990) and W. S. McGraw (pers. obs.).

Skull measurements from Groves (1978); ranges not provided.

Key References Bergmueller 1998; Fleagle & McGraw 2002; Gust *et al.* 1990; McGraw & Zuberbühler 2008; McGraw *et al.* 2007; Oates 2011; Range & Noë 2002.

W. Scott McGraw

Cercocebus lunulatus WHITE-NAPED MANGABEY (WHITE-CROWNED MANGABEY)

Fr. Mangabé couronné; Ger. Weißcheitelmangabe

Cercocebus lunulatus (Temminck, 1853). Esquisses Zoologiques sur la Côte de Guinée, p. 37. Forest along Boutry R., Gold Coast [Ghana].



White-naped Mangabey *Cercocebus lunulatus*.

Taxonomy Monotypic species. Described, named and first recognized as a species by Temminck (1853). This designation subsequently supported for many years by a number of taxonomists, including Pocock (1906) and Elliot (1913b), and is the taxonomy used by Oates (2011) and in this profile (see below). Note that the type locality, 'Boutry R.' is better known (at least today) as the 'Ankobra R.' with Princes' Town (= 'Butri') at its mouth.

Treated as a subspecies of the Red-capped Mangabey *Cercocebus torquatus* by Schwarz (1928d) and others, including Dandelot (1974), Groves (1978d) and Napier (1981). More recently regarded as a subspecies of the Sooty Mangabey *Cercocebus atys* by Booth (1956a, b, 1958b), Dobroruka & Badalec (1966), Hill (1974), Grubb (1978, 1982), Kingdon (1997), Groves (2001, 2005c), Grubb *et al.* (2003) and McGraw & Fleagle (2006).

Grubb (1978, 1982) and McGraw & Fleagle (2006) argue that *lunulatus* derived from *C. atys* and that *C. torquatus* derived from *lunulatus*. However, both phenotypically and morphologically, *lunulatus* appears to be intermediate to *C. atys* and *C. torquatus* (Groves 1978, 2001) – although the number of available *lunulatus* specimens for study is small. For example, *lunulatus* is intermediate in colour of the eyelids, colour and banding of the hairs of the crown, colour of the dorsum, ventrum, tail and limbs, extent of white on the head and neck, development of the dorsal stripe, and size of the skull (perhaps also size of the body). In addition, the geographic distribution of *lunulatus* lies between *C. atys* and *C. torquatus*. As such, C. P. Groves, J. Kingdon and W. S. McGraw (pers. comm.) now suspect that *lunulatus* derived from an ancient hybridization between *C. atys* and *C. torquatus*. Synonyms: none. Chromosome number: $2n = 42$ (Groves 1978).

Description Medium-sized, gracile, brownish-grey monkey with long limbs and tail, and white or off-white patch on posterior of crown (i.e. nape). Sexes similar in colour but ♀ ♀ smaller; skull

measurements of adult ♀ ca. 90% that for adult ♂♂ (Groves 1978). Adult ♀♀ body weight ca. 54% that of adult ♂♂. Face and ears pinkish. Muzzle sometimes light grey (A. Galat-Luong pers. comm.). Eyelids off-white. Whiskers form horizontal crest half-way down cheeks with convergence of dark grey hairs of upper cheek with upwards-directed white hairs of lower cheek. Forehead with line of sparse, black, vibrissal hairs. Anterior of crown with blackish-brown whorl; hairs not banded or speckled straw-yellow. Nape with large V-shaped, oval, or crescent-shaped patch of pale yellowish-white or white, bordered with black. Parietal-occipital and temporal lines bounding crown brownish-black or indistinct. Dorsum variable, from pale gold-blond to dark sooty-grey (A. Galat-Luong pers. comm.). Flanks, outer limbs, tail tip and underside of tail usually brownish-grey or smoky-grey, sometimes yellowish-brown. Dorsal stripe from neck to tail distinct, dark brown to greyish-brown. Dark flanks sharply demarcated from light underparts. Tail dark grey or blackish above and on sides – almost as dark as dorsal stripe. Hands and feet brownish-black, only slightly darker than outer limbs. Sides of head, front of shoulders, throat, ventrum and inner legs pure silvery-white, sometimes yellowish-white on belly. Throat and upper chest sometimes yellow (A. Galat-Luong pers. comm.). Callosities pink. Sexual skin of adult ♀ bright rosy pink. Juvenile with dorsum more yellowish or reddish, especially on limbs; nape-patch slightly rusty (Hill 1974). Infant born with pale skin on face, hands and feet, and without dorsal stripe or white patch on nape. Dorsal stripe and white on nape begin to appear at about four days and about ten weeks, respectively (Field 1995a).

Geographic Variation None recorded.

Similar Species

Cerrocebus atys. Apparently narrowly sympatric. West of Nzo-Sassandra R. System, Côte d'Ivoire. Booth (1958b) observed both *C. atys* and *C. lunulatus*, but no intermediate forms, between the Nzo R. and Sassandra R. in the vicinity of Guiglo (06° 31' N, 07° 30' W; on Lac de Buyo near mouth of Nzo R.). Groves (1978), however, reports an intermediate (hybrid?) specimen from this region that lacks the white on the nape yet has a whitish ventrum. Nape black or blackish. Hairs of crown with straw-coloured band. Crown without a whorl. Dorsal stripe absent or indistinct. Ventrum light grey. More robust (A. Galat-Luong pers. comm.).

Distribution Endemic to Côte d'Ivoire, Ghana and Burkina Faso. Rainforest BZ. Distribution highly fragmented. East of Nzo-Sassandra River System, W Côte d'Ivoire, from coast north to near Guiglo (ca. 06° 44' N, 07° 20' W), and near Goudi (ca. 06° 07' N, 05° 06' W, near Lamto along Bandama R.; Bourlière *et al.* 1974), eastward into SW Ghana where southern limit is the coast, eastern limit known to approach to ca. 55 km of the Volta R., northern limit is the Afram R. (Booth 1958b) and north-east limit is the Digya N. P. (07° 23' N, 00° 37' W; R. Dowsett & F. Dowsett-Lemaire pers. comm.; S. Gatti & S. Wolters pers. comm. to J. Oates). From the distribution map in Grubb *et al.* (1998), northern limit in Ghana does not reach the Tain R., or the towns of Wenchi or Techiman, and is at ca. 07° 24' N.

Formerly 'regularly' encountered in forest islands and gallery forest of the Comoé N. P., Côte d'Ivoire (Mühlenberg & Steinhauer-



Burkart 1982, G. Galat & A. Galat-Luong pers. comm.). Present as an isolated population along the Comoé R. in southern Comoé N. P. (ca. 09° 01' N, 03° 44' W; Fischer *et al.* 2000). Present also in a newly discovered, and apparently isolated, population along the Comoé R., ca. 140 km farther up river in AGEREF/Comoé-Léraba Reserve, SW Burkina Faso (09° 55' N, 04° 37' W; Galat & Galat-Luong 2006b). Mangabeys reported to be to the north of Guiglo between Nzo R. and Sassandra R. on Mt Péko and in Mt Sangbé N. P. If present, the species of *Cerrocebus* there needs to be determined (G. Campbell pers. comm.).

Extent of occurrence roughly 51,000 km² (Y. de Jong & T. Butynski pers. obs.) but area of occupancy much less than this.

Habitat In primary and secondary moist forest, mangrove, coastal forest, gallery forest and inland swamps, especially *Raphia* palm swamps. Of 11 encounters in Comoé N. P., seven in gallery forest, three in forest islands and one on a cliff (G. Galat pers. comm.). B. Kunz (pers. comm.) encountered *C. lunulatus* 22 times in Comoé N. P. and estimates that these represented four or five groups. Sixteen encounters in or on the edge of gallery forest, three in savanna, and three in or on the edge of forest islands. Apparently always in or near damp or wet habitats (e.g. palm swamps and seasonally flooded forest). Enters rice paddies and farm bush (Booth 1956a, 1958b). Mean annual rainfall over geographic range of *C. lunulatus* ca. 900 mm in SW Burkina Faso to 2000 mm on coast of Ghana and Côte d'Ivoire. Mean annual temperature over geographic range ca. 25–28 °C. Altitudinal range is from near sea level to roughly 300 m (e.g. at Comoé N. P.; F. Fischer pers. comm.).

Abundance Already rare throughout most of range during 1990s (see Conservation). 'Regularly' encountered in forest islands and gallery forest of the Comoé N. P. Of the 183 groups of primates encountered by G. Galat & A. Galat-Luong (pers. comm.) during 1980–86, 11% were *C. lunulatus*. Of the eight species of diurnal

primates in Comoé N. P., *C. lunulatus* was the fourth most abundant behind the Olive Baboon *Papio anubis* (34%), White-thighed Colobus *Colobus vellerosus* (19%) and Lowe's Monkey *Cercopithecus lowei* (12%).

Density in gallery forest of the Comoé R., in AGEREF/Comoé–Léraba Reserve, is about 5 ind/km² (G. Galat & A. Galat-Luong pers. comm.). In the protected areas in Ghana where Magnuson (2002) found *C. lunulatus*, the encountered rate was 0.03–0.08 groups/km. Observed seven times during 2006–08 in Ankasa Resource Reserve, Ghana (0.07/h, $n = 2468$ h; 0.002/km, $n = 3704$ km; Gatti 2009).

Adaptations Diurnal and semi-terrestrial. Sleeps in trees in gallery forest or on forest islands.

Foraging and Food Omnivorous. In AGEREF/Comoé–Léraba Reserve group home-range extends for >1.5 km in the ca. 100 m wide gallery forest along the Comoé R. and adjacent savanna. *Cercocebus lunulatus* enters savanna for a distance of ca. 1 km to feed in fruiting trees (G. Galat & A. Galat-Luong pers. comm.). One group of ten individuals at AGEREF/Comoé–Léraba Reserve had a home-range of >2 km² (G. Galat & A. Galat-Luong pers. comm.).

Cercocebus lunulatus probably spends the majority of its time on the forest floor but uses all forest strata. In Comoé N. P. eats ripe fruits of *Lannea welwitschii*, *Tamarindus indica* and *Dialium guineense*, unripe and ripe fruits of *Lannea acida* and *Diospyros mespiliformis*, unripe fruit and leaves of *Sarcocephalus latifolius*, unripe seeds of *Daniellia oliveri*, *Cynometra megalophylla* and *Parkia biglobosa*, flower buds of *Ceiba pentandra* and the bases of green grasses (B. Kunz pers. comm.). Eats maize and rice in Ghana (Booth 1958b, Jeffrey 1970), and fruits of *Saba senegalensis* and *Dialium guineense* in Burkina Faso (Galat & Galat-Luong 2006b).

Social and Reproductive Behaviour Social. Groups of 3–23 animals in Comoé N. P.; one group of 23 comprised six infants in May 1998 (Fischer *et al.* 2000). Here, B. Kunz (pers. comm.) made complete counts of three groups (23, 25–30, 58 individuals, mean = ca. 36). Two groups in AGEREF/Comoé–Léraba Reserve comprised six and 13 individuals. The group of 13 comprised one adult ♂, four adult ♀♀, seven young and one clinging infant (A. Galat-Luong & G. Galat pers. comm.). In Ghana hunters commonly report historic sightings of groups of >50 individuals (L. Magnuson pers. comm.).

Vocalizations include: 'chirps', 'shreeks', 'coh coh' grunts, 'woof woof' grunts, 'whoop-gobbles' and 'karakoo' barks. Whoop-gobble and karakoo barks only given by adult ♂♂. Whoop-gobble + karakoo bark bouts include 2–8 whoops followed by 10–75 sec silence, followed by four to many karakoo barks. The karakoo barks may continue to be given for >20 min. For some karakoo bark bouts, the last call is a 'karakoo oo oo'. Whoop-gobble + karakoo barks most frequent at night (01:00–05:00h) in series of two or three bouts, and in the early morning (05:00–07:45h). Duets of numerous whoop-gobbles occur between two groups, with only the last whoop-gobble followed by karakoo barks (A. Galat-Luong & G. Galat pers. comm.). In captivity ♀ emits 'coh' call before copulation and ♂ emits 'oh oh oh' call during copulation (A. Galat-Luong pers. comm.). In AGEREF/Comoé–Léraba Reserve territorial conflicts include whoop-gobbles and karakoo barks of adult ♂, karakoo bark

choruses of other adults and of subadults, chirps of young and other individuals, and contact fights between adults (A. Galat-Luong & G. Galat pers. comm.).

In Comoé N. P., G. Galat & A. Galat-Luong (pers. comm.) observed *C. lunulatus* in associations with other species of monkey 4% of the time ($n = 183$ encounters); *C. lowei*, Lesser Spot-nosed Monkey *Cercopithecus petaurista*, *P. anubis* and *C. vellerosus*. *Cercocebus lunulatus* was sometimes in association with up to at least three other species at one time; for example, with *C. lowei*, *C. petaurista* and *P. anubis*, or *C. lowei*, *C. petaurista* and *C. vellerosus*. In AGEREF/Comoé–Léraba Reserve *C. lunulatus* forms polyspecific associations with Green Monkeys *Chlorocebus sabaeus* (Galat & Galat-Luong 2006a). In Ghana observed with *C. lowei* and Roloway Monkeys *Cercopithecus roloway* (L. Magnuson pers. comm.).

Inter-specific interactions include supplantation of an adult ♀ + clinging infant *C. lowei*; whoop-gobble + karakoo bark bouts in response to Patas Monkey *Erythrocebus patas* and *P. anubis* barks; and karakoo bark-induced *C. lowei* loud-calls (A. Galat-Luong & G. Galat pers. comm.). On one occasion B. Kunz (pers. comm.) observed several Olive Baboons chase 3–5 *C. lunulatus* from a fruiting *D. mespiliformis* in which they were feeding. On another occasion one *C. lunulatus* fed near a group of Olive Baboons on unripe pods of *P. biglobosa*.

Cercocebus lunulatus in captivity spontaneously use sticks (tools) to scratch (groom) themselves in order to decrease stress. Sticks 10–40 cm long are prepared by removing the leaves and twigs. If the stick is too long it is broken into two pieces. Two sticks may be used simultaneously, either hand + hand, or hand + foot. Body parts that are difficult or impossible to reach with the hands or feet are scratched (e.g. inside of the ears) (Galat-Luong 1984, A. Galat-Luong pers. comm.).

Reproduction and Population Structure Minimum length of oestrous cycle in captivity is 19 days. Gestation is reported as 152–180 days (Field 1995b). Gestation at London Zoo and Dublin Zoo reported as 5.5–6.0 months and 5.0 months, respectively (A. Payne pers. comm.). Flamingo Land reports a gestation of 5.5 months. Over 51 births in captivity, including 36 at Ménagerie du Jardin des Plantes (G. Pothet pers. comm.). Thirty-seven per cent of the 51 infants born in captivity died, most of them when <2 months of age. Only single infants reported as live births but stillborn twins observed at Flamingo Land (D. Cross pers. comm.). Birth weights at Ménagerie du Jardin des Plantes ranged 400–580 g (sample size not provided; G. Pothet pers. comm.). Female at Dublin Zoo lived to ca. 31 years (S. Devaney pers. comm.).

Predators, Parasites and Diseases Humans, by far, are the most important predator for *C. lunulatus* (Oates *et al.* 1997, McGraw & Oates 2002). Commonly hunted with the use of dogs in Ghana (L. Magnuson pers. comm.). Found in seven Leopard *Panthera pardus* scats ($n = 371$) collected in Comoé N. P., accounting for 1.4% of the prey items and 1.2% of the prey biomass consumed. Not found in any of the Leopard scats ($n = 188$) collected in Marahoué N. P., Côte d'Ivoire, nor in any of the Lion *Panthera leo* scats ($n = 89$) collected in Comoé N. P. (Bodendorfer *et al.* 2006). Probable predators of *C. lunulatus* include African Crowned Eagles *Stephanoaetus coronatus*, Robust Chimpanzees *Pan troglodytes* and Central African Rock Pythons *Python sebae*.

In Comoé N. P. *C. lunulatus* has been observed mobbing a Leopard – while giving karakoo barks and in association with *C. vellerosus* and *C. lowei*. In another instance, gave karakoo barks in response to a Martial Eagle *Polemaetus bellicosus* attack on *C. lowei* and *C. petaurista* (while *C. lowei* and *C. petaurista* gave loud-calls). While giving karakoo barks, the adult ♂ looked up towards the sky and stayed in an open situation, chest exposed, while the members of his group hid or fled (G. Galat & A. Galat-Luong pers. comm.).

Conservation IUCN Category (2012): Endangered as *C. a. lunulatus*. CITES (2012): Appendix II.

Considered to be one of the world's most threatened primate taxa (McGraw *et al.* 2006b). Galat & Galat-Luong (2006a) estimate the wild population to total <1000 individuals. The Upper Guinean Forest in which *C. lunulatus* lives has been reduced by >90% as a result of logging and agriculture (Asibey 1978, McGraw *et al.* 2006b). Hunting is intensive throughout the range (Wolfheim 1983, Oates *et al.* 1997, 2000a, McGraw & Oates 2002, Galat & Galat-Luong 2006a, Oates 2006, 2011, Gonedélé Bi *et al.* 2012). In Ghana in the late 1960s to mid-1970s *C. lunulatus* present in Sefwi Wiawso, Sukusuku, Dadieso F. R. and Yoyo F. R., abundant in Ankasa Resource Reserve and Nini-Suhien N. P., and rare in Bia N. P. (Jeffrey 1970, Asibey 1978, Wolfheim 1983). Oates *et al.* (1997) surveyed nine sites during 1993–95 in SW Ghana and never encountered *C. lunulatus*. They concluded (p. 142) that, 'Based on hunters' reports, our guess is that this species is still present in several areas, but in very low numbers.'

In Ghana, *C. lunulatus* in Ankasa Resource Reserve, Nini-Suhien N. P., Draw River F. R., Krokosua Hills F. R., Boi Tano F. R., Dadieso F. R. and Yoyo F. R. during the 1990s and early 2000s but rare at all sites (Abedi-Lartey 1999, Oates *et al.* 2000a, Magnuson 2002). More recently, Oates (2006) surveyed four forests in SW Ghana: Mamiri F. R., Boi Tano F. R., Krokosua Hills F. R. and Bia N. P. and Resource Reserve. He concluded that *C. lunulatus* had been extirpated from all four sites. In 2004–05, R. Dowsett & F. Dowsett-Lemaire (pers. comm.) spent six months in Ghana surveying birds in all of the Ghana Wildlife Division's protected areas and received convincing reports for *C. lunulatus* in only three areas: Atewa Range F. R., Cape Three Points F. R. and Digya N. P. (3478 km²). S. Gatti (pers. comm. to J. Oates) observed *C. lunulatus* at Cape Three Points F. R. and Digya N. P. in Dec 2006. Still present, but rare, in Ankasa Resource Reserve in 2006–08 (Gatti 2009).

In Côte d'Ivoire, reported in Marahoué N. P., Dassioko F. R., Niegre F. R., Comoé N. P. and Ehy Forest (= Tanoé Swamp Forest; Fischer *et al.* 2000, McGraw & Oates 2002, McGraw *et al.* 2006b, Koné *et al.* 2007a, b), but see Gonedélé Bi *et al.* (2012). In Burkina Faso, in the AGEREF/Comoé-Léraba Reserve, there is a small, isolated population restricted to the gallery forest of the Comoé R. It appears that this is a recently established population. Previous surveys of the mammals of the AGEREF/Comoé-Léraba Reserve never recorded *C. lunulatus* (Bousquet 1992), and local people, including park rangers and hunters, did not know this monkey until its discovery by Galat & Galat-Luong (2006a, b) in 2005. In the area where one group was observed in 2005, at least three groups were present 1.5 years later. Galat & Galat-Luong (2006a, b) suggest that

C. lunulatus was able to move into AGEREF/Comoé-Léraba Reserve in ca. 2004 from Comoé N. P. as a result of a corridor of protected area that was created between the two parks and that became effective in ca. 2004.

Priorities for the conservation of *C. lunulatus* are to: (1) upgrade the Nini-Suhien N. P./Ankasa Resource Reserve/Draw River F. R. complex to one national park; (2) consolidate Bia N. P. and Bia Resource Reserve into one national park; (3) greatly improve protection of all sites in which *C. lunulatus* occurs; and (4) conduct surveys to further assess the status of forest primates at the above sites as well as Atewa Range F. R., Cape Three Points F. R., Digya N. P. and Ehy Forest (Oates 1996a, 2006, 2011, Oates *et al.* 1997, McGraw *et al.* 2006b, Koné *et al.* 2007a, b, R. Dowsett & F. Dowsett-Lemaire pers. comm.). Several sites where *C. lunulatus* is present are also sites important for the Endangered *C. rolaway* and the Vulnerable *C. vellerosus* (Magnuson 2002, McGraw *et al.* 2006b, Oates 2006, 2011). Any actions that protect *C. lunulatus* and *C. rolaway* may, however, already be too late to save another taxon that once occurred at some of these sites, the Critically Endangered, probably extinct, Miss Waldron's Red Colobus *Procolobus badius waldronae* (Oates *et al.* 2000a, McGraw & Oates 2002).

There are ca. 50 *C. lunulatus* in ten European zoos. The West African Primate Conservation Action Project (WAPCA) focuses on primate protection and reproduction in Ghana.

Measurements

Cercocebus lunulatus

HB (♂): 550 mm, n = 1

T (♂): 680 mm, n = 1

HF (♂): 180 mm, n = 1

E (♂): 43 mm, n = 1

GLS (♂♂): 136, 140 mm, n = 2

GLS (♀): 124 mm, n = 1

GWS (♂♂): 91, 93 mm, n = 2

GWS (♀): 80 mm, n = 1

Various localities (Hill 1974, Groves 1978, pers. comm.).

HB (♂♂): 640 (520–730 mm, n = 3

HB (♀♀): 520, 560 mm, n = 2

T (♂♂): 680, 740 mm, n = 2

T (♀): 680 mm, n = 1

HF (♂♂): 170, 180 mm, n = 2

HF (♀): 155 mm, n = 1

E (♂♂): 43, 45 mm, n = 2

E (♀): 40 mm, n = 1

WT (♂♂): 9.9 (7.1–11.8) kg, n = 7

WT (♀♀): 5.3 (3.9–6.3) kg, n = 8

From captives at Paris Zoo (n = 3; C. P. Groves pers. comm.), London Zoo (n = 3; A. Payne pers. comm.) and Ménagerie du Jardin des Plantes (n = 12; G. Pothet pers. comm.).

Key References Galat & Galat-Luong 2006a, b; McGraw & Fleagle 2006; McGraw *et al.* 2006b; Oates 2011; Oates *et al.* 1997.

Thomas M. Butynski

Cercocebus torquatus RED-CAPPED MANGABEY (WHITE-COLLARED MANGABEY)

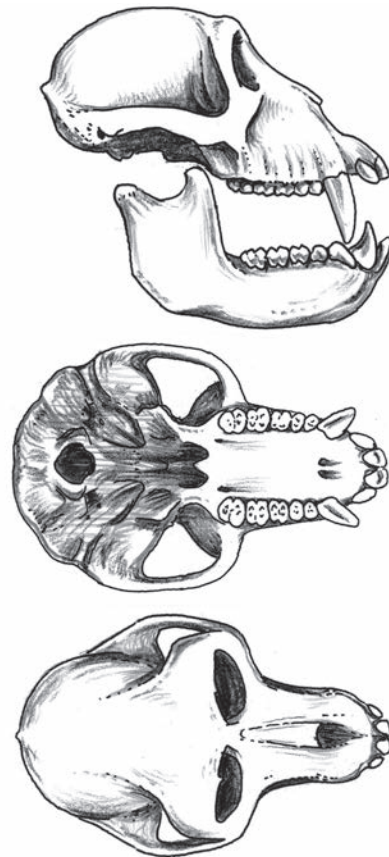
Fr. Mangabé à collier blanc; Ger. Rotkopfmangabe

Cercocebus torquatus (Kerr, 1792). Animal Kingdom, p. 67. West Africa.Red-capped Mangabey *Cercocebus torquatus* adult male.

Taxonomy Monotypic species (Kingdon 1997, Groves 2001, 2005c). Previously classified at the subspecies level, *Cercocebus torquatus torquatus*, with the Sooty Mangabey *C. t. atys* and the White-naped Mangabey *C. t. lunulatus* comprising the other two subspecies (Dorst & Dandelot 1970, Groves 1978). Synonyms: *collaris*, *crossi*. Chromosome number: $2n = 42$ (Dutrillaux *et al.* 1979).

Description Large, slate-grey, moderately long-muzzled, semi-terrestrial monkey with red crown and white collar. Sexes alike except markedly dimorphic in size. Adult ♀♀ weigh about 55% as much as adult ♂♂. Face skin dark grey to black with eyelids bright white and sharply contrasting with face skin. Ears naked, dark greyish-black, extending above white collar. Crown russet to dark maroon-red, outlined by the white collar and broad temporal line, and may show whirl or slight medial partition. Chin, sides of the neck, cheeks and throat white. Cheek stripe grey, of variable thickness, separating white cheeks from white throat. Whiskers white, short, directed backward. Nape with white patch. Dorsum chestnut brown to dark grey with darker dorsal stripe. Outer limbs darker grey at distal end and on feet. Ventrums and inner limbs sharply-demarcated white. Hands and feet with brownish-black skin. Tail darker grey than dorsum, whitens distally with white tuft. Callosities brownish-pink, fused in ♂, separate in ♀. Skin and pelage colour different in infants: skin of face, hands and feet pink; eyelids lighter than face skin. Head auburn. Dorsum brownish-grey. Crown red by four months of age; full adult colouration by five months (Field 1995a).

Suborbital fossae shallow relative to other *Cercocebus* spp., whereas the paranasal ridges are the most pronounced of the *Cercocebus* spp. (McGraw & Fleagle 2006). These features, and the presence of straight temporal lines are, among the *Cercocebus* species, the most similar to

Lateral, palatal and dorsal views of skull of Red-capped Mangabey *Cercocebus torquatus* adult male.

Mandrillus. This suggests that *C. torquatus* is the sister taxon to *Mandrillus* within the *Cercocebus*–*Mandrillus* clade (McGraw & Fleagle 2006).

Geographic Variation Skull size and breadth substantially variable across populations, although not in a pattern justifying distinct subspecies (Groves 1978). Length of white on tail also variable (90–235 mm) across populations (Hill 1974, Groves 1978).

Similar Species None within geographic range.

Distribution Endemic to West Africa. Rainforest BZ. From W Nigeria (from west of Niger R.) through Cameroon (east as far as E Dja Reserve), Equatorial Guinea (Rio Muni), and the Gabon coast (to south of Nyanga R. in Mayumba N. P.) into S Congo (Conkouati-Douli N. P.) (Rosevear 1953, Gartlan & Struhsaker 1972, Hapold 1973, Schlitter *et al.* 1973, Blom *et al.* 1992, Groves 2001, Oates 2011). Distribution patchy across range. Almost all populations within 350 km of the coast (Maisels *et al.* 2007b).

Western limit uncertain. Hapold (1973) stated that the Red-capped Mangabey occurs in forest relics in the derived savanna zone of W Nigeria, near the Dahomey Gap (e.g. within the Igangan F. R.).



Cerrocoebus torquatus

Schlitter *et al.* (1973) state that the species might occur in remnant forests west of the Nigerian border in Bénin. This is supported by Campbell *et al.* (2008b), who obtained verbal reports of Red-capped Mangabeys in SE Bénin.

Habitat Occupies a variety of habitat types, although principally relatively wet habitats: swamp forest or seasonally/intermittently inundated forests, mangroves, lowland riverine and coastal forest. Also in primary and secondary *terra firma* dry forest, and utilize agricultural areas such as rice fields and gardens (Sabater Pi & Jones 1967, Jones & Sabater Pi 1968, Gartlan & Struhsaker 1972, Hill 1974, Napier 1981, Garcia & Mba 1997, Gautier-Hion *et al.* 1999, Cooke 2005). Garcia & Mba (1997) observed Red-capped Mangabeys frequently associated with nipa palm trees *Raphia* spp. in riparian forests along the Uolo R. and Laña R. in Monte Alén N. P., Equatorial Guinea. The majority of sightings by Sabater Pi & Jones (1967) were in lowland forests (<350 m asl) of the coastal region, in riverine forest and confluences of rivers and the ocean, or in swamps characterized by tangles of red mangrove *Rhizophora mangle* roots and stands of *Pandanus* sp., with dense closed canopies 10–12 m high composed of plants such as *Raphia* spp., *Sclerosperma mannii*, *Mitragyna ciliata*, *Oxytenanthera abyssinica* and *Cytosperma senegalense*. Vegetation near the coast of Rio Muni where Red-capped Mangabeys were observed was 10–25 m plants such as *Phoenix reclinata*, *Cocos nucifera*, *Canavalia ensiformis*, *Urena lobata*, *Pennisetum purpureum* and *Terminalia cattappa* (Jones & Sabater Pi 1968). Annual rainfall across the geographic range of Red-capped Mangabeys ca. 1400–3200 mm with wet seasons from Mar to May (minor) and Sep to Dec (major) (Mitani 1991, Blom *et al.* 1992, Garcia & Mba 1997). Found at altitudes from sea level along the Atlantic coast to <1000 m, with most reported locations below 500 m.

Abundance Abundance decreases from west to east both in Cameroon and Gabon (Matthews & Matthews 2002); rarely encountered east of Campo Forest in Campo-Ma'an N. P., S

Cameroon (Mitani 1990), and apparently absent in SE Cameroon (Lobéké N. P.) (Davenport & Usongo 1997). Although Gartlan & Struhsaker (1972) found Red-capped Mangabeys in E Dja Reserve, later surveys here did not locate them (Ngandjui 1997). Struhsaker (1972) reported this species as 'common' in both Douala-Edéa R. and Korup N. P. Densities have since declined: 0.23 groups/km² in 1999; 0.14 groups/km² in 2000 (Waltert *et al.* 2002); 0.01 groups/km² in 2004–05 (Linder 2008); 0.02 groups/km² in 2006–08 (Astaras *et al.* 2011). Matthews & Matthews (2002) reported 0.51 groups/km² in Campo Forest, and significantly higher densities in areas of lower levels of human disturbance (0.71 groups/km² on Dipikar I., with minimal disturbance, vs. 0.36 groups/km² in a heavily exploited logging concession area; $p < 0.01$). These censuses indicated Red-capped Mangabeys were largely restricted to the coastal areas, only reaching 80–100 km inland. In Gabon, early reports also suggested that Red-capped Mangabeys are less abundant in the interior (Malbrant & Maclatchy 1949). Non-systematic surveys confirmed this observation in the protected areas of Moukalaba and Sette Cama; Red-capped Mangabeys were reported to be 'abundant' although restricted in distribution to areas near the coast (Blom *et al.* 1992). Cooke (2005) found Red-capped Mangabeys to be the most abundant cercopithecoid near the village of Sette Cama, south of Loango N. P., Gabon. Morgan (2007) encountered 36 groups in Loango N. P. and estimated mean group density at 0.97 groups/km² in this coastal protected area.

Generally rare in the interior of Equatorial Guinea (Jones & Sabater Pi 1968, Garcia & Mba 1997), but locally abundant. Declining in all areas of Equatorial Guinea (C. Jones pers. comm. in Wolfheim 1983). In Nigeria, rare or not abundant west of the Niger R. (Happold 1973, Schlitter *et al.* 1973). In Okomu N. P., SW Nigeria, White (1988) found ca. 85 groups, although the area was threatened by hunting and habitat alteration, worsened by the negative consequences of a programme of agricultural development assistance to migrant farmers (Oates 1995). Here, in 2008–09, Akinsorotan *et al.* (2011) found 0.1 groups/km² and 2.2 groups/km². Surveys (since 1995) in S Nigeria indicate that the Red-capped Mangabey is locally extinct or rare in a number of areas of the Niger Delta and Akwa Ibom (Z. Tooze pers. comm.).

These observations support Kingdon's (1997) evaluation that the Red-capped Mangabey was once a widespread, successful species that is declining from all areas where habitat loss to agricultural expansion and intensive hunting occur.

Adaptations Diurnal and semi-terrestrial (Jones & Sabater Pi 1968, Mitani 1989, Gautier-Hion *et al.* 1999). Red-capped Mangabeys spend considerable time on the ground, frequently descend to the ground to feed or to flee when alarmed, and utilize forest strata from the ground to 40 m high in the canopy (Jones & Sabater Pi 1968, Mitani 1989, 1991). In Campo Forest, the vertical distribution of Red-capped Mangabeys differed by activity patterns: 'escape' (fleeing observers) occurred on the ground in 85% of 21 observed instances; 'move' (locomotion) and 'socio-rest' (including both grooming and resting) were recorded most frequently at 0–5 m (ca. 58% of 185 observations and ca. 63% of 161 observations, respectively); whereas 'feed' (search, approach, manipulation, consumption of food) correlated positively with distribution of fruit production, with a mode height of 25–30 m (Mitani 1989).

Red-capped Mangabeys, like other semi-terrestrial *Cercocebus* spp., exhibit a suite of skeletal and dental features associated with foraging on the forest floor for sparsely distributed, hard object foods, such as nuts and seeds, which require extensive gnathic processing – features and associated ecological behaviour shared with *Mandrillus* (Hoshino 1985, Rogers *et al.* 1996, Kingdon 1997, Fleagle & McGraw 1999). These features include greatly enlarged upper and lower posterior premolars that approach the first molars in size and that function to open and process seeds and nuts (Fleagle & McGraw 2002). The expanded premolars are used by Red-capped Mangabeys to process seeds of *Guibourtia tessmannii*, *Lacouli carlifolia* and *Craibia laurentii* in Sette Cama (Cooke & McGraw 2007).

The robust, well-developed forelimb skeletal morphology is functionally adaptive for extensive, forceful manual foraging in forest litter and rotting wood as well as for vertical climbing. The similarly developed hindlimb and hip skeletal features further facilitate the vertical climbing of tree trunks by species in the *Cercocebus*–*Mandrillus* clade of African papionins (Fleagle & McGraw 2002). Jones & Sabater Pi (1968) describe Red-capped Mangabeys ascending vines head first with hand-over-hand movements, and descending from arboreal substrates by backing down utilizing similar hand-over-hand movements. Similar locomotory behaviour in the Sanje Mangabey *Cercocebus sanjei* (C. L. Ehardt pers. obs.).

Foraging and Food Omnivorous. Forages on the forest floor and in the canopy. In Campo Forest, forages in the lowest strata (0–5 m) for monocotyledonous shoots and young leaves of shrubs; foraging for fruit is most frequent in the canopy (ca. 57% of 103 observations at 25–30 m) (Mitani 1989, 1991). Group fissioning into foraging parties of variable age/sex composition was noted by Jones & Sabater Pi (1968) in Rio Muni and by Mitani (1989) in Cameroon. Mitani (1989) reported mean foraging group size of 21.11 ± 2.55 (range 14–38, $n = 9$) and foraging group age/sex composition (ratio adult ♂♂ to adult ♀♀ to immatures) as 1 : 1.2 : 1.9. Ranging area varied seasonally with spatial distribution of fruiting trees in this study, averaging ca. 50% of the annual home-range size in each of the wet/dry seasons sampled over 15 months.

Home-range of one study group in Cameroon encompassed 247.4 ha over 15 months and partially overlapped (ca. 30%) the ranges of two conspecific groups, although neighbouring groups avoided one another (Mitani 1989). A three-month study of two groups of Red-capped Mangabeys in Sette Cama found home-ranges of ca. 2 km² and day ranges of ca. 1 km (Cooke & McGraw 2007).

Diet consists largely of fruit and seeds/nuts, supplemented with leaves; monocotyledon shoots, stems and roots; flowers (e.g. *Halopegia azurea*); grasses (e.g. *Haumania danckelmaniana*); mushrooms; and insects (Jones & Sabater Pi 1968, Mitani 1989, Gautier-Hion *et al.* 1999). Red-capped Mangabey groups raid crops, including Cacao and Ground-Nut plantations (Jones & Sabater Pi 1968, Wolfheim 1983). In Cameroon, fruit was the major food item consumed across all seasons (ca. 60% of diet), there was no seasonal difference in species diversity of food fruits or number of fruit species eaten, and the seasonal range size of groups correlated with the spatial distribution of fruiting trees. The study group's fruit diet came predominantly (73%) from only five plant species: *Grewia coriacea*, *Anthonotha cf. cladantha*, *Sacoglottis gabonensis*, *Scorodophoeus zenkeri* and *cf. Khaya ivorensis*. Seeds were the second most consumed food, contributing 20% of the diet for this



Red-capped Mangabey *Cercocebus torquatus* adult male showing bright white eyelids.

study group (Mitani 1989). In Rio Muni, Red-capped Mangabeys utilize *Raphia vinifera* and *Ancistrophyllum secundiflorum* in the swamp forest areas of their range, and *Antrocaryon klaineianum*, *Chytranthus macrophyllus*, *Ficus hochstetteri* and *Pycnanthus angolensis* in primary and secondary forest areas (Jones & Sabater Pi 1968).

Social and Reproductive Behaviour Social. Groups are multimale-multifemale, ♀♀ are philopatric and solitary ♂♂ occur (Jones & Sabater Pi 1968, Mitani 1989). In SW Cameroon mean group size ca. 19 (S.D. = 3; sample size not reported; Matthews & Matthews 2002). Twenty-five individuals in one study group; adult ♂ to adult ♀ ratio of 1 : 1.75 (Mitani 1989). In Rio Muni, group sizes were 14–23 individuals ($n = 11$ groups, Jones & Sabater Pi 1968), and 20–60 individuals (mean = 35, $n = 5$, C. Jones, pers. comm. in Wolfheim 1983). Morgan (2007) encountered ten groups in censuses of Loango N. P. and reported mean group size of 17.7 (S.E. = 1.18).

Polyspecific associations common. Red-capped Mangabeys associate with Wolf's Monkey *Cercopithecus wolffi*, Moustached Monkey *Cercopithecus cephus*, Red-bellied Monkey *Cercopithecus erythrogaster*, Putty-nosed Monkey *Cercopithecus nictitans* and De Brazza's Monkey *Cercopithecus neglectus* (Jones & Sabater Pi 1968, Oates 1985, Mitani 1991, Cooke 2005). Associates infrequently with Talapoin Monkey *Miopithecus talapoin* in Rio Muni (Jones & Sabater Pi 1968). Most frequent association in Campo Forest was with *C. wolffi* ($n = 30$ of the 49 two-species associations observed for Red-capped Mangabey groups); association with Mandrill *Mandrillus sphinx* ($n = 4$) also exceeded expected frequency based on numbers of foraging groups for each taxon. Here, Red-capped Mangabey groups exhibited seasonal variation in frequency of polyspecific associations (mean = 7.11, $p < 0.05$), forming more associations during the two dry seasons (Mitani 1991).

'Whoop' vocalizations given in series, which may be in quick succession and descending in tone; may be similar to the initial portion of the 'whoop-gobble' loud call of several other mangabey species, but the 'gobble' portion not given. A two-syllable 'bark' is emitted both by ♂♂ and ♀♀, most frequently in the early morning and without evident eliciting stimuli (Cashner 1972, Waser 1982). Jones

& Sabater Pi (1968) report that Red-capped Mangabeys in their study area ceased vocalizing when groups were disturbed by their presence; this contrasts with other mangabey species that respond to disruption with distinctive loud ('alarm') calls (Waser 1982).

Reproduction and Population Structure The following reproductive parameters are from captive Red-capped Mangabeys. Males become sexually dimorphic at about five years. Females begin to cycle at 2.2–3.0 years of age; cycle length 30–33 days. First conception at 3.3 years; mother's age at first birth ca. 6.5 years. Gestation 170–175 days. Birth interval reported as 13 months by Harvey *et al.* (1987) and as 16 months by Field (2007). Females exhibit dark pink, prominent perineal swellings during oestrus. Post-conception swellings also occur, 1.5–2 months into pregnancy; these swellings appear similar to those of a normal ovulatory cycle but stay at maximum tumescence longer and detumescence is slower, lasting 15–25 days (Harvey *et al.* 1987, Field 1995a). No evidence of mating/birth seasonality. No twin births recorded for North American captive populations (Jones & Sabater Pi 1968, Field 2007).

Maximum recorded ages in captive Red-capped Mangabeys of known birth dates are 26 years for ♂♂, 24+ years for ♀♀ (Field 1995a).

Predators, Parasites and Diseases African Crowned Eagles *Stephanoaetus coronatus* and Leopards *Panthera pardus* are known predators. Human hunters are undoubtedly the Red-capped Mangabey's most significant predator in many areas (Mitani 1989, Blom *et al.* 1992, Fa & Garcia Yuste 2001, Waltert *et al.* 2002, Willcox & Nambu 2007). Wild populations in Nigeria and Cameroon harbour novel simian immunodeficiency viruses (SIV) (Beer *et al.* 2001, Telfer *et al.* 2003) and novel simian T-cell lymphotropic viruses (STLV) (Meertens *et al.* 2002). These are similar to those found in wild populations of *Mandrillus*, further emphasizing the phylogenetic closeness of *Cercocebus* and *Mandrillus* (Beer *et al.* 2001, Telfer *et al.* 2003), and may facilitate research addressing disease ecology and immunology of related human viral pathogens (HIVs and HTLVs).

Conservation IUCN Category (2012): Vulnerable. CITES (2012): Appendix II.

Although Red-capped Mangabeys reside in a number of legally protected areas (e.g. Korup N. P. [ca. 1253 km²] and Campo-Ma'an N. P. [ca. 2640 km²]; Okomu N. P. [ca. 181 km²]; Loango N. P. [ca. 1550 km²]; Monte Alén N. P. [ca. 2000 km²]; and Conkouati-Douli N. P. [ca. 5045 km²]), high levels both of hunting for the bushmeat trade and habitat alteration/destruction persist. The causes are many, but include insufficient law enforcement and ill-designed development schemes that destroy the natural resource base and that conflict with effective conservation.

Populations of Red-capped Mangabeys have declined considerably, or have been extirpated, in many places, a situation exacerbated by the species' restricted distribution and often low densities. They are widely hunted using shotguns, and their semi-terrestrial behaviour subjects them to additional risk from snares, which may have been set for other animals such as Blue Duikers *Philantomba monticola*, other duikers *Cephalophus* spp., Emin's Giant Pouch Rat *Cricetomys emini* and cane rats *Thryonomys* spp. In many areas, such as along the Cameroon-Nigerian border, hunting is the major cause of primate declines (Oates

1999), feeding what has become a billion-dollar bushmeat industry. In addition, a portion of the range is within the Guinean Forests of West Africa Biodiversity Hotspot, a region that has already lost >85% of its original forest cover. Continued high levels of deforestation due to commercial and slash-and-burn agriculture, logging and large-scale mining are significant contributors to continued forest degradation, loss, fragmentation in the region, including the coastal forest and swamp forest habitats preferred by Red-capped Mangabeys. Protected areas within the range of the Red-capped Mangabey are inadequate in number, size, connectivity and levels of law enforcement; improving conservation will require multi-national cooperation, extensive effort to reverse historically deep patterns of land use, and curtailment of the highly destructive bushmeat trade.

In 2007 there were 27 Red-capped Mangabeys (14 ♂♂, 13 ♀♀) in eight North American zoos (Field 2007) and 50 (30 ♂♂, 20 ♀♀) in ten European zoos (ISIS 2007).

Measurements

Cercocebus torquatus

HB (♂♂): 634 (584–665) mm, n = 4

HB (♀): 500 mm, n = 1

T (♂♂): 737 (670–790) mm = 3

T (♀): 590 mm, n = 1

WT (♂♂): 10.6 (8.8–12.5) kg, n = 4

WT (♀): 5.8 kg, n = 1

Various localities (Malbrandt & MacLachy 1949)

HB (♂♂): 584 (457–666) mm, n = 6

HB (♀♀): 510 (420–563) mm, n = 7

T (♂♂): 669 (499–760) mm, n = 6

T (♀♀): 574 (460–639) mm, n = 7

GLS (♂♂): 136 (121–142) mm, n = 7

GLS (♀♀): 115 (108–123) mm, n = 5

Various localities (Hill 1974)

GLS (♂♂): 138.2 mm, n = 5

139.9 mm, n = 11

140.0 mm, n = 4

140.5 mm, n = 2

146.6 mm, n = 13

155.0 mm, n = 1

GLS (♀♀): 116.1 mm, n = 4

119.3 mm, n = 6

118.7 mm, n = 3

121.0 mm, n = 4

GWS (♂♂): 89.5 mm, n = 5

90.0 mm, n = 2

92.9 mm, n = 11

94.5 mm, n = 4

95.0 mm, n = 1

95.2 mm, n = 13

Various localities (Groves 1978).

Key References Jones & Sabater Pi 1968; Mitani 1989, 1991; Oates 2011.

Carolyn L. Ehardt

GENUS *Mandrillus*

Mandrills

Mandrillus Ritgen, 1824. *Natürliche Eintheilung der Säugethiere*, p. 33.

The first published description and depiction of either a Drill or a Mandrill was by Gesner (1554), who referred to it as a kind of wolf. Gesner's description was the chief basis for the Linnaean name *Simia sphinx*. To straighten out the nomenclature, a neotype for the name *sphinx* was nominated. For a summary of this unusual taxonomic history see Napier (1981).

Mandrillus includes two species of 'forest baboon': the Drill *Mandrillus leucophaeus* and the Mandrill *Mandrillus sphinx*. The ♂♂ are among the most extreme and flamboyant examples of sexual dimorphism among primates, indeed, among mammals. In spite of this distinction there are arguments for this genus to be subsumed in the much less spectacular and monkey-like genus *Cercocebus*. One of us (C. P. G.) finds these arguments compelling although in this instance we adhere to traditional nomenclature. Molecular study puts the time of divergence between *Mandrillus*/*Cercocebus* and *Papio*/*Lophocebus* at 6.7 mya (late Miocene; Perelman *et al.* 2011).



Left: Mandrill *Mandrillus sphinx* adult male grimace.

Right: Drill *Mandrillus leucophaeus* adult male head tilt.

Drills and Mandrills are heavily built, baboon-like animals with long muzzles and very short, forward-tilted tails that help to emphasize the colourful genital area. Although their pelage is a grizzled olive, the broad, mostly hairless rumps of ♂♂ in both species are brightly coloured, as are their facial areas, which have been elaborated into species-specific 'masks'. The faces and proportions of the much smaller ♀♀ resemble small, short-tailed baboons but are distinguished by contracted, drabber versions of the male's face-mask. Males of both *Mandrillus* spp. have long faces with nasal ridges that connect the zygomatic plate with the canines and incisors. This elongated facial skeleton protrudes in front of the braincase with no downward deflection, unlike *Papio*. Large bony paranasal ridges extend the length of the muzzle on either side of the nasal bones; these ridges undergo rapid secondary enlargement in some adult ♂♂ (Elton & Morgan 2006), and they also differ between the two species. The bony paranasal ridges are hollow, inflated and creased in *M. sphinx* and are covered in white and blue, sometimes red, skin.

This, together with the red skin that covers the nasal bone, apparently mimics and enhances an expression that resembles a carnivore-like 'snarl'. In *M. leucophaeus* the ridges are smooth and shiny black, forming a contrast to the bright red streak below the lower lip. Above and behind the brows and eye sockets, the forward parts of large temporal muscles are attached to ridges on a flat but anteriorly broadened frontal bone. These superior temporal lines are sharply set off from the surface of the braincase; they begin on the posterior side of the lateral edges of the supraorbital ridges, and converge gradually, overhanging the postorbital constriction before reaching the braincase. This arrangement correlates with an exceptionally powerful bite on a tooththrow that is strengthened by enlargement of the premolars (Hoshino 1985, Fleagle & McGraw 2002).

Externally, the genus is characterized by large, forward-facing nostrils, pointed ears with a hairless patch behind, noticeable circumoral vibrissae and a large sternal gland whose sticky secretion, in breeding ♂♂, continuously saturates the breast hair. Morphologically *Mandrillus* spp. differ from *Papio* spp. and most other papionins in that they have distinctive shoulder-blades, upper arms, knees and pelvis, all modifications that assist in manipulation of vegetation and the substrate in their search for food, much of which is hidden (Hoshino 1985, Nakatsukasa 1994a, 1996, McGraw & Fleagle 2006).

Sexual dimorphism in body size is greater in this genus than in any other monkey, possibly greater than for any other primate. Asymptotic body mass in wild Mandrill ♀♀ is 8.9 kg, in ♂♂ 30.4 kg, a ratio of more than 3 : 1.

These two allopatric species are confined to the Ogooué R. Basin and a broad coastal strip running between the mouth of the Congo R. and the Sanaga R. (Mandrill), and between the Sanaga R. and the Cross R. (Grubb 1973). Also on Bioko I. (Drill). There are two noteworthy features about this limited distribution. One is that the range of these two species coincides with the highest rainfall in Africa. The other peculiarity is that to the immediate east of their distribution the presently continuous forest belt has been vulnerable to degradation during past arid periods, creating a dry corridor that has periodically connected the northern and southern savannas. Both these environmental peculiarities may have a bearing on our understanding of the origins of *Mandrillus*, of extreme constriction in the distribution of this genus and on the evolution of their subsistence strategy. It is noteworthy that three loriform genera, *Arctocebus*, *Euticus* and *Sciurocheirus*, are restricted to much the same general area.

Mandrillus ranges may not have shrunk greatly in historic times, although populations within those ranges have declined and become fragmented. There are no recorded instances of them living far from their present overall distribution around the Bight of Bénin. As such, any hypothetical retraction over a more extensive area would have had to be prehistoric.

This limited distribution (originally, perhaps, some 10% of the forest zone) is in striking contrast with the wide ranges of many other forest primates and with the pan-sub-Saharan range of

mainly savanna-living baboons *Papio*, which share similar foraging patterns to *Mandrillus*, with many animals covering extensive areas (>50 km²). The *Mandrillus* social structure is unlike that of *Papio* in that huge 'hordes' of >600 individuals may assemble in which ♀♀ preponderate. They are also unlike baboons in their highly seasonal breeding and polygynous mating.

In common with *Papio*, *Mandrillus* are heavy, mainly terrestrial primates that periodically move about in large groups. They rely upon two types of foods: the first are fruits or nuts that are of high nutritional value, often well dispersed throughout the forest at appropriate seasons and best harvested, as they ripen, by smaller, equally dispersed groups of monkeys. The second type of food consists of ubiquitous vegetation, old dropped kernels and invertebrates under the leaf litter, or seasonal masting over extensive areas of forest. These allow *Mandrillus* spp. to gather in very large numbers that then comb through and strip an area of everything edible before they move on, en masse. A prime advantage in mass-feeding is gaining access to a resource while predators are effectively intimidated, an imposition that is assisted by the physical size and leonine, masked heads of ♂♂ in both species.

The striking ecological success of *Papio*, the limited contemporary range of *Mandrillus*, and the abundance of baboon-like fossils from savanna habitats over the entire Plio-Pleistocene, all suggest that *Mandrillus* derived from a less forest-adapted type of papionin. None the less, today *Mandrillus* spp. are well adapted members of a rich forest primate community.

The limited range of *Mandrillus* today is of special interest because in some respects it seems relictual, being only viable in the wettest forests. Climatic fluctuations, opening and closing the Cameroon/Gabon 'corridor' provide, in theory, a mechanism for the 'entrapment' of originally non-forest organisms. The location of this corridor immediately adjacent to *Mandrillus* range suggests a possible geographic locus and hints at ecological and climatic conditions that might have facilitated the emergence of a unique genus of 'forest baboons'. The nature and timing of that emergence is currently unknown. If it involved the transfer of a baboon-like ancestor from non-forest into forest, this emergence might have been linked to a warm phase in the mid-Pliocene (3.6 mya) or, just conceivably, to warmer, moister conditions in the very late Miocene (5–6 mya). The timing of such events is crucial for our understanding of *Mandrillus* origins because there are currently fundamental disagreements as to whether *Mandrillus* is the earlier basal type for its close sister group, *Cercocebus*, or whether the relationship between the two genera is reversed (see pp. 165–6 and below).

Mistakenly classed as baboons *Papio* by some authors (Hilzheimer 1906, Elliot 1909b, Haltenorth & Diller 1980), *Mandrillus* has a different genetic profile from *Papio* (Cronin & Sarich 1976, Disotell *et al.* 1992, Goodman *et al.* 1998). C. J. Jolly (pers. comm.) describes the *Lophocebus/Papio/Theropithecus* and *Mandrillus/Cercocebus* stocks as ultimately derived from smallish, moderately long-faced ancestors much like the fossil genera *Parapapio* or *Pliopapio*. A species of this

stock underwent facial retraction, as proposed by Kingdon (1971), that culminated in a common, ancestral mangabey stem. The *Cercocebus* branch of this stem gave rise to the current diversity within the genus, and also to *Mandrillus*. The latter, in Jolly's view, became larger-bodied and longer-faced convergently with *Papio*, itself an offshoot of the other mangabey branch, from which *Lophocebus* and *Theropithecus* also derived.

Kingdon (1971, 1997) agrees with a long-term separation of *Papio* and *Mandrillus* lineages, and also concurs in *M. sphinx*, *M. leucophaeus*, Red-capped Mangabey *Cercocebus torquatus* and Golden-bellied Mangabey *Cercocebus chrysogaster* being closely related but sees them as four divergent lineages that are more conservative than the five shorter-muzzled *Cercocebus* spp. Like Dobroruka & Badalec (1966) and Nakatsukasa (1994a, 1996), Kingdon proposed that shorter-muzzled mangabeys derived from longer-muzzled types. In his view, *Mandrillus* might represent the response of a *Parapapio*-like population to the exceptional humidity (and probable spread of forests) in the later Miocene. From this perspective the *Cercocebus* radiation derived from a once more diverse and more widely distributed *Mandrillus*-like lineage, and Kingdon considers that a number of behavioural, ecological and morphological patterns accord best with this suggestion.

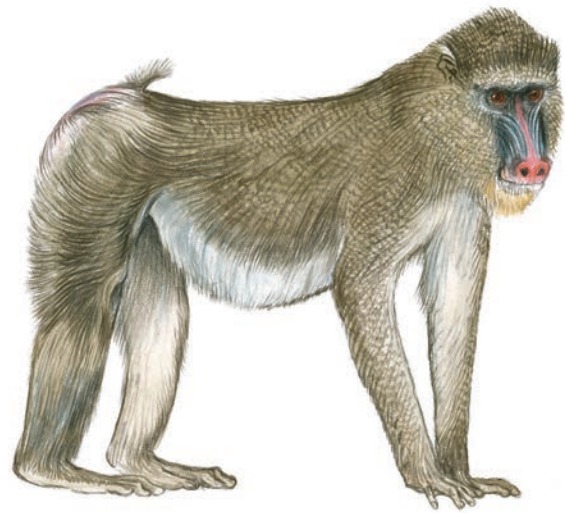
Resolving this issue is of considerable theoretical importance. *Mandrillus* appears to follow an expansive foraging strategy broadly similar to that of *Papio*, which is of demonstrable utility in non-forest habitats. The behavioural and morphological resemblances between *Mandrillus* and *Papio* would, in this instance, derive from a shared ancestry and an adaptive starting point that is relatively early, not late. In the second instance, if this mode of existence evolved independently within the forest, and *Mandrillus* derived from substantially smaller, forest-dwelling mangabey ancestors, then the degree of convergence with baboons invites much closer attention to the morphological details and evolutionary increments behind such an exclusively *intra-forest* transformation. It also invites attention to the particular properties of the forests around the Bight of Bénin to determine what unique features might have favoured this development there and nowhere else. This option necessarily implies that *Mandrillus* is of late, relatively recent evolutionary origin, a conclusion that would tie the evolution of each species to extremely localized conditions. Older origins, in which baboon-like features are more likely retentions (rather than convergences), accords better with what otherwise appears to be a relictual status.

It is interesting that *Mandrillus* shares its range with one of the mangabeys, *C. torquatus*, which, though not itself the most drill-like of these mangabeys (that status belongs to the more robust *C. chrysogaster*), is the largest and longest-faced. Simultaneous field studies on these two sympatric, closely related, semi-terrestrial, hard-object-feeding monkeys should be revealing.

Jonathan Kingdon & Colin P. Groves

Mandrillus sphinx MANDRILL

Fr. Mandrill; Ger. Mandrill

Mandrillus sphinx (Linnaeus, 1758). Systema Naturae, 10th edn, 1: 25. Dja R., Bitye, Cameroon.Mandrill *Mandrillus sphinx* adult male.Mandrill *Mandrillus sphinx* adult female.

Taxonomy Monotypic species. Based on morphological similarities, *Mandrillus sphinx* has often been erroneously referred to as *Papio sphinx*, but compelling genetic and morphological analyses during the 1990s (Disotell 1993, Fleagle & McGraw 1999) show *Mandrillus* to be closer to the terrestrial mangabeys *Cercocebus* spp. than to *Papio*. Synonyms: *burlacei*, *ebolowae*, *escherichi*, *hagenbecki*, *insularis*, *latidens*, *madarogaster*, *maimon*, *mormon*, *pennanti*, *planirostris*, *schreberi*, *suilla*, *tessmanni*, *zenkeri*. Chromosome number: $2n = 42$ (Romagno 2001).

Description Large, stocky, short-tailed, terrestrial monkey with a facial mask of bare red, white and blue skin. Extreme sexual dimorphism, becoming apparent at about four years of age. Fully mature adult ♂♂ (>10 years old) weigh 3–4 times more than adult ♀♀.

Adult ♂: head and neck pelage dark brown with highly contrasting white flashes behind the small brown or pink ears. These flashes are exaggerated by pads of fat on the skull, pushing out the ear and increasing the visibility of the white hair and white skin. Face brightly coloured, with dark red skin covering the prominent brow ridge, nasal ridge and nostrils. Skin around the eyes generally dark brown to black, though in some ♂♂ red colour can spread throughout the face. Eyes hazel-brown with pale skin on the upper lids, highly visible when the animal blinks. Two elongated patches of white skin puckered into 6–10 parallel (paranasal) ridges, run either side of the nose, supported by bony protuberances of the maxillary bone and mimicking a dog-like snarling expression. The troughs of

these paranasal folds are bright blue. White begins to appear on the paranasal ridges at about six years of age. As the paranasal ridges grow, the blue in the troughs is eclipsed by the expanding white ridges. By ten years, the muzzle is completely white, with the blue visible only at the edges of the ridges (i.e. deep within the troughs). When the adult ♂ 'snarls', the blue helps to accentuate the snarl. The blunt muzzle is sparsely haired white, blending into a golden yellow beard and ruff around the face. A triangular crest of erectile hair from the brow ridge to apex of the sagittal crest appears almost black when the animal is agitated. Hair around the face and neck is much longer than the body hair, giving the impression of a disproportionately large head in fully mature ♂♂, and a heavy, 'bear-like' profile. Dorsum and limbs brown to grey. Ventrums white and long-haired. Penis bright red, hairless, not visible in a walking animal though easily visible, and often displayed, in a seated animal. Scrotum bright pink. Perianal skin bright red. Buttocks and upper thighs almost hairless, coloured iridescent blue, blending through purple to pink towards the edges of the hairless patch. Colour intensity and size of bald patch vary among animals. Tail short, 60–100 mm long, held erect, dark brown to black above, sometimes pale grey below. Anal callosities fused in ♂♂; not highly visible in older ♂♂ with full colouration.

Adult ♀: head, neck and body pelage dark brown to mid-grey. No white ear flashes. Skin on face dark blue, occasionally with red in the brow ridge. Paranasal ridges much smaller and less prominent than in the ♂ and generally dark blue with occasional red mottling. Paranasal ridges of the ♀ gradually fade back to blackish-grey as she ages. Faces of old ♀♀ have a 'faded' look but there is no exact age at which this begins. Some adult ♀♀ never have much blue on the paranasal ridges. No white on face, though full cheek pouches can give the temporary impression of a white ruff around the throat. Dorsum and limbs brown to grey. Ventrums light brown to pale grey. Perianal skin red. Adult ♀♀ display a red sexual tumescence around

the vulva during ovulatory cycles. Some ♀♀ have slight thinning of the hair and a pale bluish colouration of the skin on the buttocks. This trait is highly variable, though ♀♀ never attain the iridescent blue colouration of ♂♂, nor develop red colouration on the buttocks. Anal callosities on buttocks unfused and easily visible from behind.

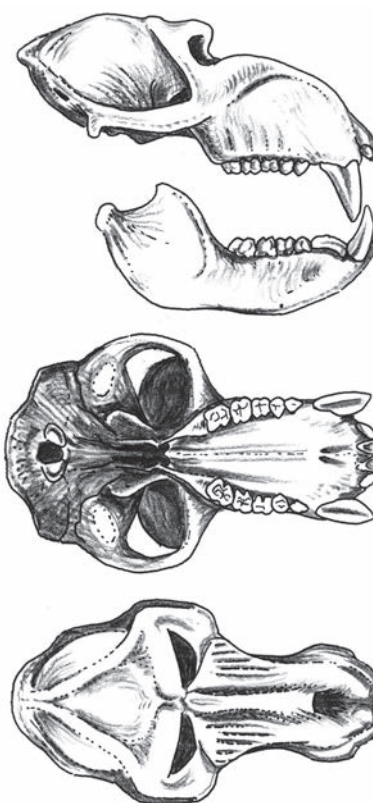
Infants and juveniles: born with pink faces, darkening to black masks and crowns around 2–4 months of age. Large pink ears and face, and white hair on the limbs, easily visible when carried ventrally. Pelage darkens at 5–13 weeks of age to olive and this colour is typical of juveniles under three years old. Head, neck and back pelage relatively thick. Prominent beard yellow, pointed 'goatee', that diminishes around three years of age. Ventrums pale grey to white. Colouration develops in the face and genitals around three years of age, with full adult characteristics in ♀♀ at around four years, and in ♂♂ at around ten years of age. From 3–5 years the paranasal ridges are bluish in both sexes. Unless the penis (red) is seen, the sexes are indistinguishable until 5 years.

Geographic Variation No subspecies recognized although recent phylogeographic analyses show a genetic divergence between populations north and south of the Ogooué R., Gabon (Telfer *et al.* 2003). Individuals from these populations show no reproductive isolation when brought into contact in captivity (Wickings *et al.* 1993).

Similar Species

Mandrillus leucophaeus. Allopatric at Sanaga R., Cameroon. Black facial mask with well-defined edge contrasting with white skin. Beard absent.

Distribution Endemic to western central Africa. Rainforest BZ. Confined to the rainforests of Gabon west of the Ivindo and Ogooué Rivers upstream of their confluence, Cameroon south of the Sanaga R., Equatorial Guinea and coastal Congo, north of Pointe Noire.



Lateral, palatal and dorsal views of skull of Mandrill *Mandrillus sphinx* adult male.

Probably absent from the Ogooué Delta and Lagoons region of coastal Gabon.

Habitat Confined to closed canopy rainforests, Mandrill groups only cross open habitat for short distances (<200 m), though lone ♂♂ sometimes venture farther. Long grass savannas are avoided. Within forest, preference for mature and riparian forest types with clear understorey. Avoids dense herbaceous ground cover, such as in 'Marantaceae' forest. The entire range of the Mandrill is characterized by fairly high rainfall (1500–4000 mm/year) and the occurrence of two wet and two dry seasons per year, each of roughly three months duration. The timing of these seasons is, however, different in the parts of the range north and south of the Equator.

Abundance No reliable population estimates are available. Simple extrapolation from the only accurately measured mean group size of 620 ± 167 (325–845, $n = 6$) and home-range size of ca. 89 km², gives a density of 7.0 ind/km² (6.5–11.2) for the Lopé N. P., Gabon, in the centre of the species' range (Abernethy *et al.* 2001, 2002, White 2007). This mean group size has remained stable at Lopé over 11 years of study. Densities are likely lower outside protected areas.

Adaptations Diurnal and mainly terrestrial. Modified canines and premolars allow efficient shearing of tough pods and seeds. Premolars of the lower jaw are extended and have a modified labial edge forming a flat plate for shearing seeds against the lingual surface of the long upper canines. A well-developed sagittal crest anchors strong jaw musculature, increasing bite force and ability to crack

hard seeds. Upper canines in ♂♂ have an extremely sharp caudal edge and measure 3–5 cm long. All canines are deeply grooved on the rostral surface, possibly to reduce weight whilst maintaining strength in such large teeth. Bite wounds received during male–male fights in the breeding season are common and can be fatal (W. Karesh pers. comm.).

Extreme sexual dimorphism, and the evolution of bright coloured skin patches and specialized vocalizations in breeding ♂♂ may be display adaptations to avoid costly direct conflict during intense competition between ♂♂ (Wickings & Dixon 1992, Abernethy *et al.* 2002). Adult ♂♂ have highly vascularized bony protrusions of the maxillary bones running parallel to the nasal bone. These uplift and exaggerate the visibility of the coloured skin of the face. Fatty deposits behind the ears and on the buttocks similarly serve to increase the visibility of coloured skin patches.

Foraging and Food Omnivorous. Opportunistic omnivores, specializing on fruit, seeds and insects. Mandrills have a wide dietary niche. One group used 48 different foods in a ten-day period (Rogers *et al.* 1996). Dung analysis of 3156 samples from two groups over a period of five years in Lopé showed 76 species of plant used, from which fruit pulp (contained in 76% of samples), seeds (52%), leaves (57%) or other fibres (90%) had been consumed, as well as insect matter (88%) and occasional meat from small mammals, reptiles, crustaceans, or fish (<1% in total). These results are broadly similar to those from other areas (Hoshino 1985, Lahm 1986). There is no strong influence of seasonality on the overall composition of the diet, though the species making up the fruit and seed content vary through the year. Diet shifts towards ripe fruit in times of abundance and towards seeds in times of fruit scarcity (White 2007).

Mandrill hordes (large aggregations of animals) travel continuously, moving an average of 4.2 km per day (0.5–11.2, $n = 92$ day ranges over two years). Bouts of relatively stationary foraging are rare, usually confined to early morning (06:00–07:00h) and late afternoon (17:00–18:00h), whilst opportunistic foraging occurs throughout the travel period from around 07:00–17:00h daily. Group spread during foraging can be over 6 ha, but is more usually around 1–2 ha (White 2007, K. Abernethy & L. White pers. obs.). Most time is spent foraging on the ground, often searching extensively through leaf litter, presumably for fallen seeds, fungi, invertebrates and small vertebrates. Mandrill horde trails are easily seen in the dry season as patches of leaves are swept aside across a swathe of forest floor. Mandrills forage arboreally for fruit and seeds, concentrating particularly on small fruited species such as *Uapaca*, *Dialium* and *Diospyros* species, Oil Palm *Elaeis guineensis* nuts and the large unripe seeds of leguminous trees such as *Pentaclethra macrophylla*. Sugary fruit pulps are often actively rejected when feeding on fruits to extract the seeds (White 2007, K. Abernethy & L. White pers. obs.). Crop-raiding is frequently reported, particularly in dry seasons when fruit crops in the forest are poor (Lahm 1993). Root crops, such as manioc or sweet potato, are frequently targeted. Adult ♂♂ leave the hordes outside the breeding season, possibly to reduce feeding competition with ♀♀ and young, but do not appear to have a significantly different diet when solitary.

Mandrill hordes seem to inhabit relatively exclusive home-ranges. In Lopé a horde of 620 animals used an annual home-range of ca. 89 km² of forest, but changed their range slightly each year, to use an area of approximately 182 km² over six years. Home-ranges rarely

overlap the range of a neighbouring horde (White 2007). Aggressive encounters between individuals occur, but there is no clear evidence of defensive territoriality and intergroup aggression has never been documented (K. Abernethy pers. obs.).

Social and Reproductive Behaviour Social. In Lopé N. P., Mandrill ♀♀ and young (♀ offspring under four years and ♂♂ to approximately five years of age) live in very large hordes of 400–850 animals (mean 620 ± 167 , $n = 6$). Group sizes of 400+, similar to those found at Lopé, are reported for the Minkébé, Waka, Ivindo and Moukalaba Doudou National Parks and the Lékédi Sanctuary, Gabon (P. Henschel, M. Starkey, S. Lahm, C. Mbina & P. Peignot pers. comm.). Much smaller group sizes (80–150 ind) reported for areas in the north of the range during the 1970s and 1980s (Jouventin 1975, Hoshino *et al.* 1984). These may, however, have been due to difficulty of observation, or to group reduction through hunting pressure.

Horde composition in Lopé is typically ca. 15% infants under one year old, 35% juveniles of 2–3 years, 30% adult ♀♀ and 20% subadult ♂♂ (4–9 years old). Adult ♂♂ join the group only during the breeding season, in proportion to the numbers of available breeding ♀♀: a maximum of 21 breeding ♂♂ (2.6% of group members) seen in a horde of 804 Mandrills that included 49 ♀♀ showing sexual tumescence and likely to be fertile (Abernethy *et al.* 2002).

The ♀ hordes appear to have a highly flexible structure and may separate into subgroups for periods of a few days to several weeks at any time of the year, though often this is following disturbance by humans or other predators. Thirty-five radio-collars placed in a horde in Lopé N. P. from 1998 to 2007 (ongoing study) show that subgroups have highly flexible sizes and memberships. Subgroups rarely stay separated for more than a few weeks, though the horde may only reunite for a few days before re-splitting into different subgroups, and the entire horde may only travel together for a small part of the year. Subgroup sizes and subgrouping frequencies are spatio-temporally related to ripe fruit abundance. Adult ♂♂ are only seasonally associated with the hordes and, outside the breeding season, live as solitary individuals (Abernethy *et al.* 2002, White 2007).

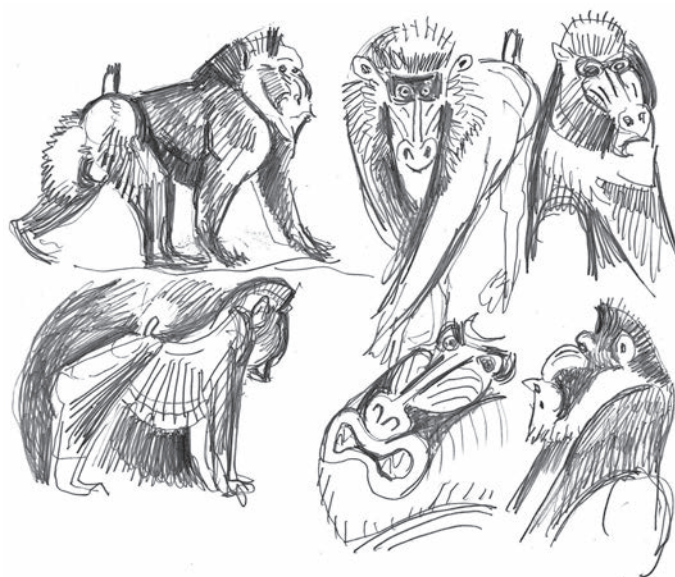
Horde or subgroup leadership is unclear in wild Mandrills. As adult ♂♂ are not permanent members of the horde, it is unlikely that they play a role in leadership. Observations of travelling hordes have not shown any consistent pattern of leading individuals, although there is a tendency for younger ♂♂ and ♀♀ without offspring to be towards the front of the group, ♀♀ carrying ventral infants towards the middle of the horde, and juveniles bringing up the rear. Although these patterns are very variable, they are clear enough to imply organization of the entire horde as one unit, rather than multiple subunits. Mandrill hordes travel terrestrially. Although they are agile climbers, they are not good jumpers, lacking the balance brought by a long tail. As such, they do not travel arboreally. When alarmed, all Mandrills drop to the ground and run swiftly, bunched together. Hordes can travel several kilometres in less than one hour in order to escape human predators and will usually move in silence during escape flights. Offspring are carried ventrally for all travel during the first 3–5 months of life and, periodically, at moments of stress or fast travel thereafter. Young become fully independent at ca. two years of age, when the next offspring is born. Males play no role in infant care or defence. Juvenile ♀♀ carry infants in the wild, possible orphaned individuals or closely related individuals, but

this behaviour is rare and breeding ‘helpers’ are not used. At around two years of age infants are fully weaned and often travel and forage in juvenile groups of 6–10. When stressed, however, they return to their individual mothers (K. Abernethy pers. obs.).

When adult ♂♂ are with the hordes they are most often following and mate-guarding sexually receptive ♀♀, spread throughout the group. The number of adult ♂♂ within a horde is not related to overall horde size, but highly correlated to the number of sexually receptive ♀♀ present, as defined by visible sexual tumescences (Abernethy *et al.* 2001). Adult ♀♀ move away from adult ♂♂ by climbing on to thin branches inaccessible to the heavier ♂♂, but ♀ ability to freely choose mates seems restricted. Adult ♂♂ may enter and leave the horde several times during a breeding season, travelling with the ♀♀ for between two days and six months, depending on accessibility of sexually receptive ♀♀ and competition with other ♂♂. Male–male competition is fierce and the secondary sexual characters are likely to play a large role in ♂ reproductive success (Setchell & Dixson 2001). Males rejoin the same horde up to four years in succession. Adult ♂♂ can move between neighbouring hordes either within or between breeding years, but this happens infrequently (only two visits to neighbouring groups documented during ten years radio tracking of 21 breeding ♂♂). Male dispersal away from the natal horde likely occurs during the subadult phase of ♂ development, as ♂♂ 6–9 years of age are solitary. No information exists, however, on the behaviour of wild subadult ♂♂ during this period. Females are not known to disperse between hordes, and genetic analyses indicate that ♀♀ within hordes are highly related.

Females vocalize frequently, using a complex repertoire of calls. Most obvious are long, shrill ‘wraaaaahh’ screams, used to maintain contact across large group spreads. The frequency of these calls increases when the horde is travelling, and especially when directional changes are made, or when subgroups are inadvertently separated from the main horde. Female screams may be heard by the human ear over 1 km away across open ground and up to 600 m in the forest. Chuckling or burbling contact calls are not so loud and appear to be used to maintain group cohesion during foraging. Aggressive hissing is often heard between ♀♀ engaged in squabbles over food items. Mature ♂♂ in the horde emit a constant deep grunting throughout the day when in the presence of sexually receptive ♀♀. Breeding ♂♂ begin to vocalize around dawn and continue until group activity stops at dusk. The grunting frequency and volume increase if the animals are agitated in conflict and are thought to serve as a display signal to reduce direct conflict between ♂♂, and possibly also to influence ♀ choice. Males do not grunt when solitary, nor when there are no sexually receptive ♀♀ in the horde. Alarm calls may be given by any group member, although those emitted by juveniles are often ignored by others. The alarm call is a short cough, repeated and developing into an ‘uh-HUH’ as agitation increases. Small, questioning coughs, accompanied by head bobbing are often used to investigate new objects and precede true alarm calls, especially by juveniles (Hoshino 1985, K. Abernethy pers. obs.).

Other primate species often travel with Mandrills as the horde moves through their range, presumably gaining from increased vigilance and predator deterrence by the large horde. As Mandrill diet overlaps in part with that of each of the sympatric primate species, some inter-specific feeding competition is likely, although the nomadic behaviour of the Mandrills serves to reduce the



Mandrill *Mandrillus sphinx* adult males.

intensity of competition with any one other group. Insect-eating birds, particularly White-crested Hornbills *Tropicranus albocristatus*, also follow foraging Mandrills. Although Mandrills eat meat, active hunting of even small mammals is rare. As such, monkeys are commonly seen mingling with Mandrill hordes. At Lopé, Western Grey-cheeked Mangabeys *Lophocebus albigena* move with Mandrill groups during at least 40% of days, and Putty-nosed Monkey *Cercopithecus nictitans*, Moustached Monkey *Cercopithecus cephus* and Crowned Monkey *Cercopithecus pogonias* also often associated with Mandrills. Ogilby's Duiker *Cephalophus ogilbyi*, Peter's Duiker *Cephalophus callipygus*, Blue Duiker *Philantomba monticola* and Red River Hog *Potamochoerus porcus* forage within Mandrill hordes, showing no avoidance of the Mandrills (K. Abernethy pers. obs.).

Adult ♂♂ and adult ♀♀ both have a sternal gland. Adult ♂♂ use this gland to scent-mark tree trunks by rubbing the chest against the bark in a series of upward thrusts from a semi-seated position. The significance of such marks in communication is poorly understood but may have a role in maintaining the exclusivity of home-ranges.

Reproduction and Population Structure Adult ♂♂ have extreme secondary sexual characters; brightly coloured skin on face, genitals and hindquarters, large size (3–4 times the weight of ♀♀) and loud vocalizations used exclusively during the reproductive period. These characters appear costly to evolve and are likely to have been selected through the enhanced reproductive success of individuals with the most extreme characters (Setchell & Dixson 2001, Setchell *et al.* 2001).

Females of a horde have semi-synchronous reproductive seasons, though sexual activity can continue through 5–6 months of the year in a horde of several hundred animals. The breeding season across the southern range of the Mandrill (south of the Ogooué R.) is between late May and early Nov. Breeding is polygynous, with ♂♂ serially guarding receptive ♀♀ in the group throughout the breeding season. Gestation is around 24 weeks (Wickings & Dixson 1992) and births are concentrated in the short dry season, around Dec–Jan in the southern range, though possibly at a different time in the northern

range. A single infant is born, weighing ca. 500–600 g. Sex ratio at birth is 1 : 1 in the semi-free ranging group in Franceville (Wickings & Dixon 1992) and is likely to also be 1:1 in the wild. Inter-birth intervals in the wild appear to be around two years; ♀♀ carrying infants have not been observed with one-year-old offspring, nor with sexual tumescence, indicating that young are not born in successive years. The inter-birth interval, however, may be longer than two years. Young are fully weaned around two years of age, and are sexually mature at four years in ♀♀ and ten years in ♂♂ (Wickings & Dixon 1992, Wickings *et al.* 1993, K. Abernethy & E. Wickings pers. obs.).

Males do not hold harems nor dominate one-male units, but mix through the group, interacting with one ♀ at a time. Genetic analyses of paternity in a captive colony showed extremely skewed reproductive success rates in ♂♂, with dominant individuals fathering almost all offspring in a group (Wickings *et al.* 1993). Whilst differential reproductive success among wild ♂♂ is certain, it is highly improbable that one ♂ maintains exclusive access to a horde of several hundred ♀♀ in the wild.

The different rates and timing of sexual maturity for ♂♂ and ♀♀, and the different ages during which they are sexually active, combined with the breeding system, form an inbreeding avoidance mechanism that is unique to Mandrills (or, possibly, to *Mandrillus*). Females begin to breed at four years, with an inter-birth interval of about two years, up to 12–14 years. Males only breed between 10 and 14 years; thus a father cannot breed with his daughter, who will not have matured before his death. Even the first son of a mother will not breed until after her death at 14 years (when he will be just 10 years). A Mandrill can only have a full-sibling if his/her father manages to survive to breed two (or just possibly four) years later, finds the same horde and breeds with the same ♀. In the rare case that this happens, these siblings could only mate if the older one is ♂ and the younger is ♀ (otherwise she would be too old [post-reproductive] before he is mature). This differential maturation mechanism means that Mandrills (1) do not need to rely on kin recognition to avoid inbreeding and (2) that hordes require only low levels of immigration/emigration to maintain genetic diversity (K. Abernethy pers. obs.).

Maximum longevity in captivity is 31 years and 8 months (Jones 1982). Radio-telemetry studies of wild animals in Lopé indicate a life-span of around 12–14 years in the wild (based on 15 ♂♂ and three ♀♀ collared at >10 years of age; K. Abernethy & L. White pers. obs.).

Predators, Parasites and Diseases Mandrills are known prey of humans, Leopards *Panthera pardus* and Central African Rock Pythons *Python sebae*. Mandrill remains found in 5.6% of forest Leopard scats in their range (3.1% of ingested biomass; n = 196; Henschel 2001; see also Henschel *et al.* 2011). Predation on Mandrills by Leopards shows a significant skew to the Mandrill breeding season, possibly because ♂ calling allows Leopards to track groups more easily at this time. A census of markets selling bushmeat in Gabon, which covers 60% of the Mandrill's range, showed that 2.2% of the wild animals harvested for the commercial meat trade were Mandrills. These data indicate a minimum off-take of 2000 Mandrills per year for human consumption in Gabon (Abernethy *et al.* 2001). Mandrills comprised ca. 3% of bushmeat eaten by villagers at three sites in Gabon (Foerster *et al.* 2011).

Wild Mandrills carry two strains of Mandrill-specific simian immunodeficiency virus (SIV), that are closely related to the human

HIV virus (Souquière *et al.* 2001), and two strains of mandrill specific STLV-1 (Makuwa *et al.* 2004). Neither virus has, however, been shown to develop the auto-immunodeficiency syndrome (AIDS) provoked by the virus in humans. Parasite loads are not known to be high despite living in large social units. Epidemic deaths of Mandrills from disease, including Ebola virus outbreaks in central Africa during 1996, 2000, 2002 and 2006, are not documented. This may be due to lack of research.

Conservation IUCN Category (2012): Vulnerable. CITES (2012): Appendix I.

Gabon banned all primate hunting in July 2002 and the Mandrill is nationally protected in Cameroon and Congo. None the less, populations likely to be declining through hunting and through habitat loss. Most of the species' range is currently allocated as commercial timber concession (Global Forest Watch 2009). Management of hunting on sustainably managed and eco-certified logging concessions is becoming more widespread. If hunting were managed over large areas it could markedly reduce one of the greatest current threats to Mandrills. Mandrills are found in at least 14 protected areas in central Africa: Campo Ma'an N. P. in Cameroon, Monté Alén N. P. in Equatorial Guinea, the Minkébé, Monts de Cristal, Lopé, Moukalaba-Doudou, Waka, Mayumba, Ivindo and Mont Birougou National Parks, Wonga-Wongue Presidential Reserve, Lékédi Sanctuary, and Mont Iboundji Sanctuary in Gabon, and the Conquati-Douli N. P. in Congo. These areas cover ca. 13% of the species' range.

Old, climatically stable, clear understorey forests seem to be the most important habitat for Mandrills, as well as large contiguous forest blocks that allow several hordes to be in reproductive contact. Preservation of forest cover and reduction of bushmeat hunting in the Crystal Mountains (Monte Alén N. P., Monts de Cristal N. P.), Massif du Chaillu (Lopé N. P., Waka N. P., Birougou N. P.), and the uplands of Moukalaba-Doudou N. P. are key areas for the long-term conservation of the Mandrill. A research programme on ecology, genetic variation and population trends was initiated in Lopé N. P. in 1998 in order to establish a national conservation plan for the Mandrill and this programme is still under way.

Measurements

Mandrillus sphinx

HB (♂♂): 860 (840–900) mm, n = 12

HB (♀♀): 570 (530–610) mm, n = 6

T (♂♂): 72 (60–100) mm, n = 11

T (♀♀): 47 (40–60) mm, n = 12

HF (♂♂): 223 (210–230) mm, n = 5

HF (♀♀): 163 (150–170) mm, n = 4

E (♂♂): 45 (30–60) mm, n = 8

E (♀♀): 38 (30–50) mm, n = 9

WT (♂♂): 30.4 (25–36) kg, n = 11

WT (♀♀): 8.9 (7–11) kg, n = 10

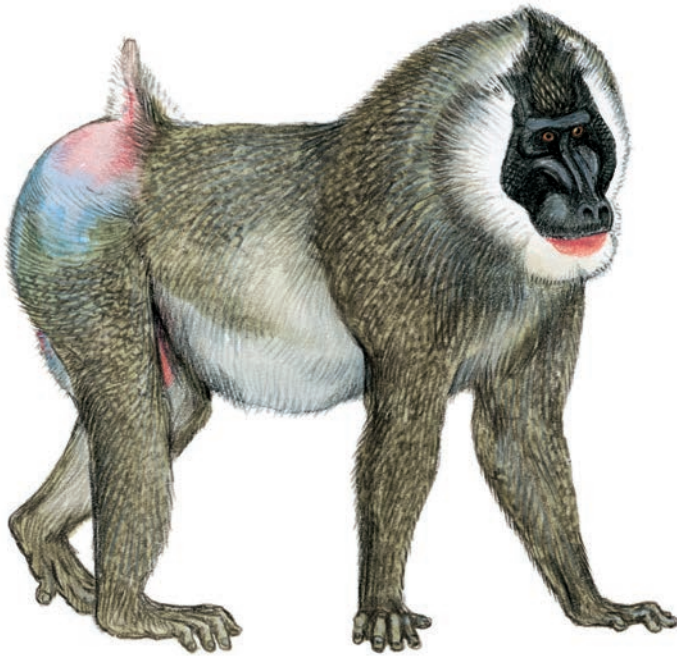
Lopé N. P., Gabon, 1998–2002 (K. Abernethy, W. Karesh & L. White pers. obs.)

Key References Abernethy *et al.* 2002; Harrison 1988b; Lahm 1986; Telfer *et al.* 2003.

Katharine Abernethy & Lee J.T. White

Mandrillus leucophaeus DRILL

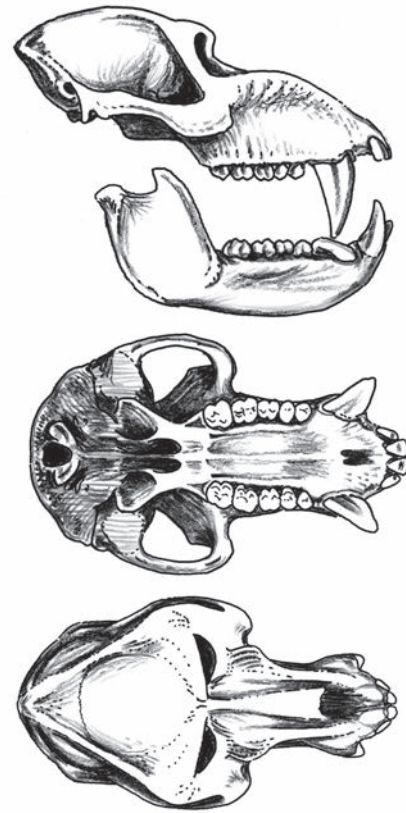
Fr. Drill; Ger. Drill

Mandrillus leucophaeus (F. Cuvier, 1807). Ann. Mus. Hist. Nat. Paris 9: 477. Africa.Drill *Mandrillus leucophaeus* adult male.

Taxonomy Polytypic species. Two subspecies recognized: Mainland Drill *Mandrillus leucophaeus leucophaeus* on the African mainland and Bioko Drill *M. l. poensis* on Bioko I. (Napier 1981, Groves 2001, 2005c, Grubb *et al.* 2003). No reliable evidence that Drills occur south of Sanaga R. Thus, *M. l. mundamensis* is a synonym of *M. l. leucophaeus* (Grubb 1973, Harrison 1988b). Formerly placed by some in genus *Papio*, but *Mandrillus* is more closely related to the semi-terrestrial drill-mangabeys *Cercocebus* than to either baboons *Papio* or the arboreal baboon-mangabeys *Lophocebus* (Dutrillaux *et al.* 1982a, Muleris *et al.* 1986, Disotell *et al.* 1992, Disotell 1994, Goodman *et al.* 1998, Fleagle & McGraw 1999, McGraw & Fleagle 2006). Synonyms: *cinerea*, *drill*, *livea*, *mundamensis*, *poensis*, *sylvestris*, *sylvicola*, *?variegata*. Chromosome number: $2n = 42$ (Chiarelli *et al.* 1979b, Romagno 2001).

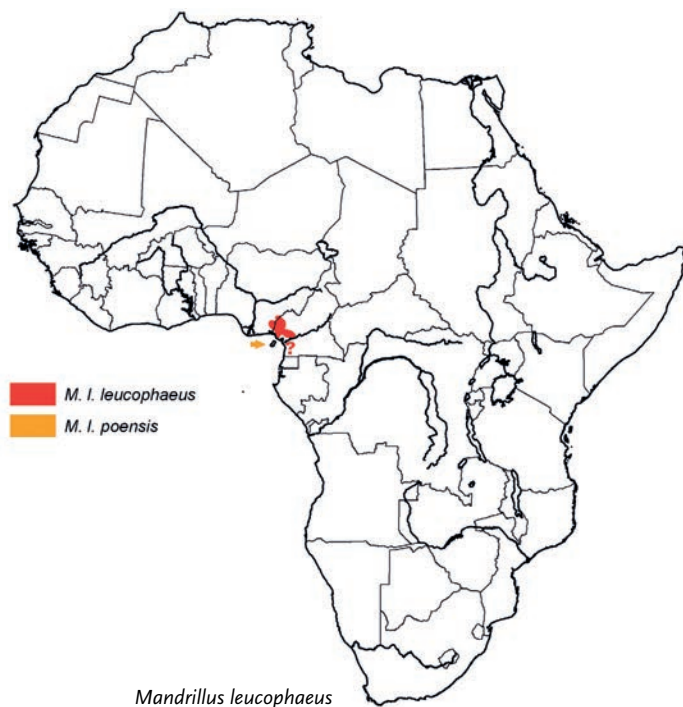
Description Large, robust, short-tailed, semi-terrestrial, highly sexually dimorphic monkey. Adult ♂♂ two-fold (*M. l. poensis*) to three-fold (*M. l. leucophaeus*) heavier than adult ♀♀.

Adult ♂: muzzle elongated, smooth, almost hairless, with single paranasal ridge on either side. Front of muzzle with sparse white whiskers. Lower lip black, marked below with reddish-pink to scarlet strip that may extend 20–30 mm onto chin. Face naked, shiny black, fringed on sides (but not brow) with yellowish-tan fur extending onto chin; hair on chin white only in mature animals. White skin sharply demarcated from black, mask-like face, washed with pink on cheek edge in heavily-coloured ♂♂. Beard absent. Ears naked, black; bare skin behind ears white. Forehead and crown with

Lateral, palatal and dorsal views of skull of Drill *Mandrillus leucophaeus* adult male.

modest, dark brown or blackish medial, semi-erectile crest. Dorsum light brown to greyish-brown with gold overtones (*M. l. leucophaeus*) or blackish-grey (*M. l. poensis*). Dorsal stripe faint, darker brown. Shoulders and upper back with loose mane of longer hair. Hands and feet mixed black and buff. Tail short (<13 cm), with pink skin showing through brown hair; darker tip. Centre of chest between nipples with longer greyish hairs that serve secretions from sternal scent gland. Ventrums and insides of limbs white to greyish-white, more sparsely haired toward rear of body. Skin on inside of thighs and groin reddish-pink to scarlet. Penis sheath scarlet. Penis pink. Scrotum may be pink or lavender, depending on age and condition. Ischial callosities light pink. Skin around anus from tail to callosities deep red. Rump naked, pink grading to blue and lavender. Adult ♂ skin colour varies greatly among individuals, and during the course of life (E. Gadsby pers. obs.).

Adult ♀: like adult ♂ except as noted here. Much smaller (see Measurements below) and without coloured skin, dorsal stripe and elongated hairs on chest or mane. Sternal scent gland less active than in ♂♂. Up to four years of age ♂♂ and ♀♀ look the same. Hair on cheeks yellowish-white. Hair on chin yellowish-white, except in old ♀♀ where it is white. Hair on dorsum same colour in ♀♀ as in ♂♂. Skin on groin pale pink.



Infant: ears, face, hands and feet with white/pink skin. Pelage silvery-grey, with black 'infant cap'. Infant pelage replaced gradually over 3–6 months, to eventually resemble the colour of adult ♀♀. Face darkens to black by 4–6 months (E. Gadsby pers. obs.).

Geographic Variation

M. l. leucophaeus Mainland Drill. Endemic to SE Nigeria and SW Cameroon. Larger than *M. l. poensis*. For adult ♂, HB ca. 12% longer; E ca. 22% longer; HF ca. 14% longer; T ca. 22% longer; WT ca. 60% heavier. Compared to adult ♂ *M. l. poensis*, skull of adult ♂ *M. l. leucophaeus* is longer (192–231 mm); braincase wider (84–102 mm); upper tooththrow longer (54–56 mm). More sexually dimorphic. Adult ♂ about three-fold heavier than adult ♀. See Measurements below. Hairs on sides of crown banded yellow and black. Dorsum greyish-brown.

M. l. poensis Bioko Drill. Endemic to Bioko I., Equatorial Guinea. Smaller than *M. l. leucophaeus* (see above). Compared to adult ♂ *M. l. leucophaeus*, skull of adult ♂ *M. l. poensis* is shorter (186–207 mm); braincase narrower (78–94 mm); tooththrow shorter (45–50 mm). See Measurements below. Less sexually dimorphic. Adult ♂ about two-fold heavier than adult ♀. Hairs on sides of crown yellowish-brown with only the tip black. Dorsum blackish-grey.

Similar Species

Mandrillus sphinx. Allopatric at Sanaga R., Cameroon. Paranasal ridges longitudinally grooved and bluish in adult ♀. Adult ♂ with nasal ridge, nostrils and lips bright red; paranasal ridges longitudinally grooved, white with faint sky-blue troughs. Cheek whiskers and pointed beard yellow to orange.

Distribution Endemic to SE Nigeria, SW Cameroon and Bioko I., Equatorial Guinea. Rainforest BZ. Perhaps the smallest geographic range of any medium-large African mammal. *Mandrillus l. leucophaeus*

occurs from the Cross R., Nigeria as far north-west as 06° 27' N, 08° 57' E (E. Gadsby pers. obs.); as far north-east as 06° 14' N, 09° 33' E, and south-east to the Sanaga R., Cameroon (Grubb 1973, Wolfheim 1983, Dowsett-Lemaire & Dowsett 2001, Oates *et al.* 2004). Range includes forested areas of the Cross R. drainage. Presently confirmed east along Sanaga R. as far as 10° 53' E (B. Morgan pers. comm.) but not farther than the Mbam R. Reports of Drills south of the Sanaga R. probably cases of mistaken identity (Grubb 1973, Harrison 1988b). Historic range <50,000 km² on mainland. Mainland range fragmented into 11 or more habitat islands. With ongoing habitat loss, probably <25,000 km² now available to the Drill, of which the majority lies in Cameroon (Gadsby & Jenkins 1998, E. Gadsby pers. obs.).

On Bioko I. (2017 km²), *M. l. poensis* present on lower slopes of Pico Basile and over much of the southern one-third of the island, including the Gran Caldera Volcánica de Luba (Schaaf *et al.* 1990, Butynski & Koster 1994, González-Kirchner & Sainz de la Maza 1996). Drills on Bioko now believed to be all of the same population. The present extent of occurrence is unlikely to be greater than 800 km² (T. Butynski pers. obs.).

Habitat Primary and mature secondary lowland forest, also mid-altitude, lower montane and occasionally montane forest and associated grasslands. From sea level to ca. 2000 m (Mt Kupe) on mainland (Wild *et al.* 2005) but not reported over 1000 m on Mt Cameroon, the highest peak in Drill range (Gadsby & Jenkins 1992). From sea level to at least 1400 m on Bioko I., but reported by hunters to occur to 1500 m (Butynski & Koster 1994, González-Kirchner & Sainz de la Maza 1996, T. Butynski pers. obs.). Most groups occur at lower altitudes between 0 and 600 m, but may favour higher, more difficult terrain in response to hunting pressure in accessible lowland areas. Within Drill range annual rainfall records include 2690 mm (mean for 1953–63) at Bakundu and 8570 mm at Idenau, Cameroon (Gartlan & Struhsaker 1972); 2790 mm and 3030 mm (means for 2000–05) at Calabar and Afi Mountain, Nigeria, respectively (records from Drill Rehabilitation & Breeding Center, DRBC); ca. 4000 mm on Pico Basile to >10,000 mm on extreme S Bioko I. (Butynski & Koster 1994).

Abundance In 1986, Butynski & Koster (1994) conducted 373 km of primate census on Bioko I. and encountered Drills (seen or heard) at the rate of 0.02 groups/km. In 1990 González-Kirchner (1990) conducted 212 km of primate census on Bioko and encountered Drills at the rate of 0.03 groups/km. Also in 1990, Schaaf *et al.* (1990) conducted 92 km of primate census within the Gran Caldera Volcánica de Luba, SW Bioko, and encountered Drills at the rate of 0.09 groups/km. In 1992, Maté & Colell (1995) conducted 100 km of primate census on SE Bioko and encountered Drills at the rate of 0.02 groups/km. Encounter rate of 0.05 groups/km in 2008 along 44 km of transect in the Gran Caldera de Luba, and 0.08 groups/km in 2009 along 48 km of transect and 0.06 groups/km in 2010 along 50 km of transect at Badja North, SW Bioko (T. Butynski, G. Hearn, M. Kelly & J. Owens pers. obs.). The Gran Caldera de Luba and Badja North are remote sites where hunting is relatively uncommon and where there are no other anthropogenic impacts. As such, the encounter rates at these two sites are likely close to what is expected for an undisturbed population of Drills. Based on field surveys at many sites on Bioko, and on bushmeat market surveys, T. Butynski,

G. Hearn & W. Morra (pers. obs.) estimate the total Drill population on Bioko at 3000–4000 animals.

Drills were once abundant in Korup N. P. (Struhsaker 1972), but are today less common. At one site in north Korup N. P., Drills were encountered at a rate of 0.016 groups/km in 1990 (Edwards 1992). Waltert *et al.* (2002) reported group encounters of 0.01/km at a site ca. 5 km away (in the Korup Support Zone) a decade later. In 2000 Steiner (2001) encountered only one group of Drills during 152 km of census in north Korup N. P. and in the Korup Support Zone (0.007 groups/km). In 2006, however, Astaras *et al.* (2008) encountered 0.015 Drill groups/km during 1346 km of surveys in southern Korup N. P. They estimated density at 1.7 ind/km² within their 63 km² study area and, on this basis, extrapolated the number of drills in Korup N. P. at roughly 1130. About 2500–3000 Drills occur in the Korup region (Astaras 2009).

At the Ebo Forest research site at the eastern edge of the species' range, Drills are seen regularly (B. Morgan pers. comm.). Widespread and relatively common in the Ndokbou Forest (>1000 km²) and Ebo Forest (1400 km²) in the Yabassi region, Cameroon (Dowsett-Lemaire & Dowsett 2001). Within other remaining habitats, such as Takamanda F. R. and Mone F. R., Mt Cameroon, Banyang Mbo Wildlife Sanctuary, Bakossi, Nkwende Hills, Ejagham F. R. (Forbosh *et al.* 2007), Rumpi Hills F. R., Cameroon, and Cross River N. P., Nigeria, Drills are present but infrequently encountered. In five months of foot surveys in Banyang Mbo Wildlife Sanctuary, Drills were heard twice but not seen (Greengrass & Maisels 2007). In 735 km of surveys in the western Oban Hills of Cross River N. P. and adjoining community forest, Birch & Tooze (2006) had five encounters with Drills. While Drills persist across much of their original range where habitat remains, numbers are not evenly distributed. Gadsby & Jenkins (1998) estimated the total number of Drills in Nigeria and Cameroon at 3000–6000 animals.

Adaptations Diurnal and semi-terrestrial. In SW Cameroon, Drills spend more than 50% of time foraging, resting and travelling on or near the ground (Gartlan & Struhsaker 1972). They are agile climbers, younger and lighter animals in particular being capable of making long leaps between outer tree branches (D. Schaaf pers. obs.). Drills ascend trees before dusk to sleep at heights from 8 m to the tree crowns (Astaras 2009, E. Gadsby pers. obs.). They habitually flee from danger on the ground unless pursued by Dogs (Gadsby 1990, Astaras 2009). On Bioko, typically flee into deep, steep-sided canyons where people and Dogs cannot pursue (T. Butynski pers. obs.). They are swift runners, although no estimate of speed is known; also able to swim. The sternal gland of *Mandrillus* spp. is unique among primates (Hill 1970). Drills scent-mark by rubbing this gland against objects such as branches, stones and even food. The Drills' black muzzle serves to make several expressive behaviours appear more conspicuous and species-specific, notably yawns that display canines (associated with mild threats, uncertainty or tension), a mild form of 'lip-smacking' (observed during mutual grooming, and by ♂♂ during copulation; E. Gadsby pers. obs.) and a 'smile' in which the corners of mouth are pulled back to expose the teeth while the head is wagged from side to side (associated with greeting, during play and also seen when ♂♂ court ♀♀).

Foraging and Food Omnivorous. Diet little known. Drills forage in groups, mainly on the ground. About 74% of sightings by Gartlan

& Struhsaker (1972) of feeding Drills in SW Cameroon were on the forest floor. Almost all encounters during daylight hours (except at dusk or dawn at sleeping sites) were of groups foraging on the ground, with only a few individuals at heights of 1–5 m. Feeding groups climb trees to seek shelter during heavy rain (C. Astaras pers. comm.). Gartlan & Struhsaker (1972) found Drills eating fruits of *Musanga cecropioides*, *Oncocalamus wrightianus*, two *Cola* spp. and possibly *Pycnanthus angolensis*. Snails (*Pseudoachatina* and *Lignus* spp.) also eaten. Drill faeces sometimes contained orthopteran (crickets and their allies) and coleopteran (beetles) exoskeletons. Based on analysis of faecal samples in Korup N. P., Astaras (2009) found that fruit and seeds comprised >72% of diet by volume, with pronounced seasonal variations. Fruit and seeds of *M. cecropioides*, *Scottellia klaineana* and *Morinda morindoides*, fruit pulp of *Irvingia gabonensis* and seeds of *Oncoba glauca*, *Pentadesma butyracea* and *Treculia obovoidea* eaten. *Irvingia gabonensis* present in 96% of faecal samples in May and often accounted for the bulk of a sample, but entirely absent in the previous three months (study period Feb–Jun 2006). *Musanga cecropioides* eaten throughout the study period, but occurred at higher rate in 75% of samples in Mar. Further observations in the 2007 rainy season (C. Astaras pers. comm.) identified fruits of eight *Cola* spp., ten *Diospyros* spp., five *Landolphia* spp. and five *Strychnos* spp. as main sources of food during the major fruiting season (Jul–Sep). Leafy material consisted mainly of grass blades, less often leaves of trees and forbs. Fungi (mushrooms) in small amounts in 5% of samples. Insect remains occurred in 70% of samples and consisted mainly of ants, termites and orthopterans. While diet probably consists mainly of fruits and seeds, it is varied and also includes nuts, leaves, flowers, pith, roots, tubers, corms, bark, fungi, invertebrates, eggs (including bird, reptile and snail), small vertebrates (e.g. amphibians and fish) and possibly small to medium-sized mammals (Schaaf *et al.* 1990, E. Gadsby pers. obs.). Semi-captive Drills at DRBC eat frogs, lizards, snakes, snails and birds, and kill, but do not eat, small mammals including genets *Genetta* sp. Skillfully catch and eat flying insects by snatching them out of the air (E. Gadsby pers. obs.). See also Astaras & Waltert (2010).

On Bioko I., Drills eat giant land snails (*Achatina* sp.) (Butynski & Koster 1994), freshwater crabs, ripe fruits of *Xylopia aethiopica* (T. Butynski pers. obs.), *Hunteria umbellata* (Q. Luke pers. comm.), and Oil Palm *Elaeis guineensis*, Coconuts *Cocos nucifera* (Schaaf *et al.* 1990, González-Kirchner & Sainz de la Maza 1996) and termites (Schaaf *et al.* 1990). They dig up and eat marine turtle eggs on the southern beaches (Butynski & Koster 1989). González-Kirchner & Sainz de la Maza (1996) estimate the following for the diet, based on four stomach samples: 58% fruit, 25% insects, 16% other plant foods (e.g. leaves, stems, pith), 1% other invertebrates. Hunters on Bioko I. imitate distress calls of Ogilby's Duiker *Cephalophus ogilbyi* and Blue Duiker *Philantomba monticola* to lure Drills within shotgun range, suggesting that Drills may kill and eat large prey (Schaaf *et al.* 1990, Butynski & Koster 1994, González-Kirchner & Sainz de la Maza 1996). Under other circumstances, Drills and duikers forage peacefully in close proximity (C. Astaras & D. Schaaf pers. obs.).

Foraging includes sifting through leaves and detritus on the ground, digging, turning over stones and wood, breaking open rotten wood and climbing trees for fruit and other foods. Readily enter shallow water to cross streams and forage for aquatic foods such as crabs, turning over small and large stones in the process.

There are no data on the size of Drill home-ranges. Ukizintambara (2006) reports Mandrill *Mandrillus sphinx* home-ranges in Gabon of

100 km², and Drill home-ranges on the mainland may be of similar size. Home-ranges of at least some groups on Bioko are unlikely to be greater than 30 km² (T. Butynski pers. obs.).

Social and Reproductive Behaviour Highly social. Group size variable, with ratio of fully adult ♂♂ to other group members estimated at 1 : 20 (Gartlan 1970). Astaras (2009) reported groups of 25–77 in Korup N. P. (mean 43.3, S.D. = 18.4, n = 8), with multiple large ♂♂ in some of the larger groups. Group size averaged 23.3 individuals (9–55, n = 12) in SW Cameroon, where groups larger than about 20 contained adult ♂♂ in ratio of less than 1 : 20 (Struhsaker 1969). Gartlan (1970) estimated average group size in SW Cameroon at 63.5 (14–179, n = 11). Gadsby (1990) reported mean group size of 28 (5–50, n = 58) based on hunter interviews in Nigeria. Group size estimates collected over 32 years (1970–2002) in Bakossiland, Cameroon, range 5–400 (mean 93.1, n = 105; Wild *et al.* 2005). Wild *et al.* (2005) found no correlation between group size and seasonality, habitat type, or altitude. Abernethy *et al.* (2002) suggest that, in absence of total counts, Mandrill groups may be underestimated by as much as 40%; Drill groups may be similarly underestimated. Groups larger than about 20 individuals may be aggregations of two or more ‘one-male-units’. Larger aggregations (or ‘super-groups’ or ‘hordes’) may form when smaller units congregate. Super-groups are reported as increasingly rare as Drill populations decline (Gadsby 1990).

On Bioko I. groups range in size from 2 to 20 individuals (González-Kirchner & Sainz de la Maza 1996). Hunters indicate that group size is usually around 20 animals, rarely 25, and that only one adult ♂ is present (González-Kirchner 1990, Butynski & Koster 1994). Super-groups never reported for Bioko.

Solitary animals are always adult ♂♂. Of 15 ‘reliable’ Drill counts in Bakundu F. R., only two (13%) were of solitary adult ♂♂ (Gartlan 1970). In Korup N. P. only 2 of 33 visual encounters (6%) were of solitary adult ♂♂ (Astaras 2009). Solitary ♂♂ may be more common on Bioko than on the mainland. Of 11 encounters with Drills by González-Kirchner (1990), four (36%) were solitary ♂♂. González-Kirchner & Sainz de la Maza (1996) reported that 29% of encounters on Bioko I. were with solitary ♂♂. Of solitary ♂♂, 83% were on the ground and 17% in trees. In another study on Bioko, four of 12 encounters (33%) with Drills were with probable solitary individuals (Butynski & Koster 1994, T. Butynski pers. obs.).

There is no indication that Drills are territorial. In some areas they may be semi-nomadic seasonally, based on hunter reports that they are not permanent residents of a given forest area but appear at regular times of the year (Gadsby 1990). On the western edge of the Oban Hills, researchers recorded Drills only in rainy season months (D. Birch pers. comm.). In Korup N. P., Astaras (2009) found Drills in the study area year-round.

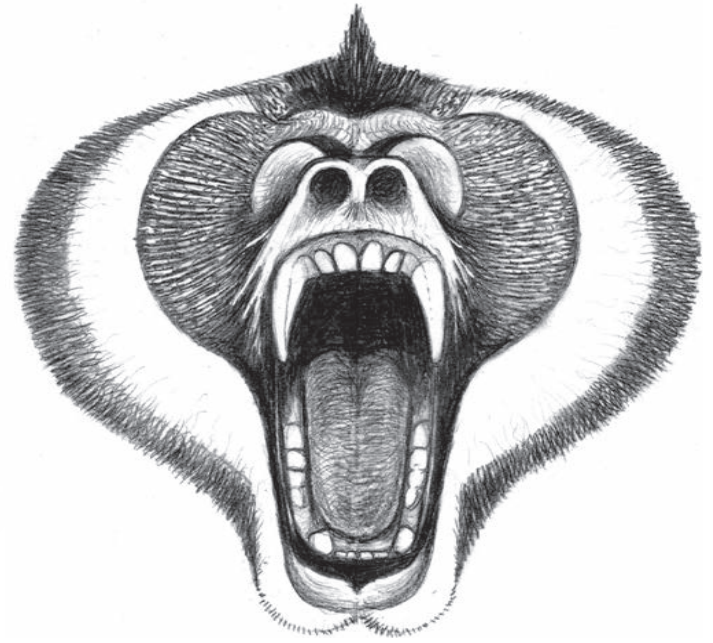
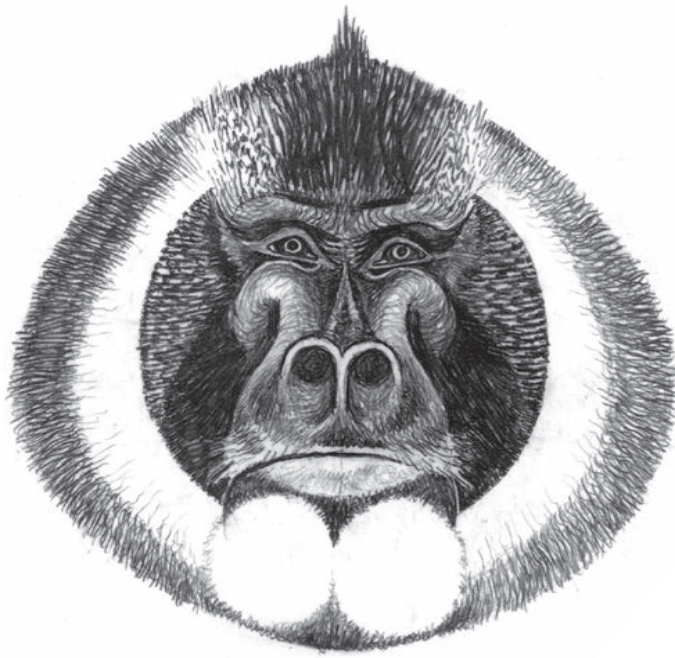
Gartlan & Struhsaker (1972) found associations of Drills and other primate species infrequent and transient, more so than polyspecific associations among some *Cercopithecus* spp. They reported three associations in SW Cameroon (Idenau and Bakundu) involving Drills and Putty-nosed Monkeys *Cercopithecus nictitans*, Red-eared Monkeys *Cercopithecus erythrotis*, Crowned Monkeys *Cercopithecus pogonias* and Mona Monkeys *Cercopithecus mona*. In Korup N. P., Drills showed highest association with Red-capped Mangabeys *Cercocebus torquatus*, being present in 10% of all mangabey encounters, but *C. nictitans*

was present in 39% of all drill encounters (Astaras 2009). Drills also associated with all other diurnal primates in Korup (Preuss’s Red Colobus *Procolobus preussi*, Putty-nosed Monkeys, Red-eared Monkeys, Crowned Monkeys and Mona Monkeys) except Robust Chimpanzees *Pan troglodytes*, but these associations were often transient. Monkeys in association with Drills on 50% of 44 encounters (Astaras *et al.* 2011). Among hunter groups interviewed in Nigeria, 59% (n = 67; Gadsby 1990) reported that Drills associate with other primates at fruiting sites, with Drills foraging on fruit dropped by guenons. Some of these also indicated Drills forage on the ground with Red-capped Mangabeys. Of groups interviewed, 3% said Drills associate similarly with Robust Chimpanzees. E. Gadsby (pers. obs.) notes that Mona Monkeys pass through Drill enclosures at DRBC, and feed in trees with Drills.

Associations between Drills and other species of monkeys on Bioko I. are uncommon. González-Kirchner & Sainz de la Maza (1996) observed Drills in association with other primates three times over an 18-month period; once with Black Colobus *Colobus satanas*, once with Crowned Monkeys and once with Red-eared Monkeys. Of 12 encounters by T. Butynski (pers. obs.) with Drills on Bioko, only twice (17%) were the Drills close to another species of monkey; <50 m from a group of Crowned Monkeys and <35 m from a group of Black Colobus.

Gartlan (1970) described Drill vocalizations heard in Bakundu F. R. ‘Alarm barks’ (or ‘pant-threats’) given when immediate danger is detected. This is a two-note, ‘staccato bark’, with the second note higher than the first. ‘Crowing’ contact calls given when individuals or groups are separated and seeking to reunite, and mutually by young and their mothers when separated. Deep, ‘two phase grunts’ or ‘roars’ (called ‘type A’ by Gartlan) given only by adult ♂♂ to mobilize groups, and maintain contact during travel and foraging. Lower intensity ‘two-phase huffing grunt’ (Gartlan’s ‘type B’) is a series of rapid or slowly modulated grunts or pants given by adult ♂♂. In multimale groups at DRBC the two-phase huffing grunt can be heard for hours when two or more adult ♂♂ sit in close proximity to one another (E. Gadsby pers. obs.). Wood (2007) described ‘directed screech,’ which is high-pitched and continuous, most often given by adult ♀♀ or juveniles, and directed toward another individual. By screeching and glancing toward other group members, the ‘aggrieved’ individual draws attention to the ‘transgressor’, toward whom aggression may then be directed by the group. The ‘directed screech’ (Wood 2007) and ‘yell’ described by Feistner (1989) for Mandrills are likely to be the same. Females of all ages ‘coo’ with lips pursed to form a ‘placating face’, as do infants seeking or receiving comfort. All sexes and ages make a sharp version of the staccato grunt, which is repeated continuously to intimidate or signal aggressive intent (E. Gadsby pers. obs.).

Adult ♂♂ grind their teeth at times of extreme agitation, typically when they cannot gain access to a rival (Feistner 1989, E. Gadsby pers. obs.). During altercations, adult ♂♂ may perform a ‘tooth-gnashing’ visual and auditory display, during which the upper canines grind against the anterior premolars, sharpening the canines (Every 1970, Wood 2007). Some of the calls described above (e.g. the crow) are probably unique to *Mandrillus* spp. Despite a rich vocal repertoire, Drills do not have a characteristic adult ♂ ‘loud-call’ as do most cercopithecids. The crow is probably the loudest and most far-reaching. The crow can be heard to >500 m, depending on terrain (C. Astaras pers. comm.).



Facial geometry of Drill *Mandrillus leucophaeus* adult male.

Behaviour of Drills in the wild is not well documented. Semi-captive Drills of both sexes, immature as well as adult, but especially adult ♂♂, scent-mark by rubbing the sternal gland against branches and tree trunks. Novel objects, like sticks, stones and food items, may also be marked. Usually an object is picked up, sniffed and dragged down under the chin and across the centre of the chest one or more times. This activity, seen frequently at DRBC, may be accompanied by salivation (Hill 1970, K. Wood pers. comm.). Adult ♂♂ scent-mark trees by rubbing the chest in upward motion against the object one or more times; more than one individual may mark the same spot (K. Wood pers. comm.). In the wild, scent-marking may aid in orientation, prevent groups from meeting and aid in reunion when animals are dispersed. Scent-marking is not thought to demarcate territory (Jouventin 1975), except in a short-term, localized way, as when two or more ♂♂ meet.

Although subadult ♂♂ may act as sentinels, there is no evidence that adult or subadult ♂♂ defend the group against predators; indeed, they are often the first to flee (Struhsaker 1969, Gartlan 1970). Dominant adult ♂♂ may initiate group movement but do not lead; instead, they usually stay in the middle or rear of the group when on the move (Gadsby 1990). Gartlan (1970) observed herding of group members, enforcement of group cohesion (by subadult and adult ♂♂) and initiation of group movement by adult ♂♂. He concluded that there are relatively high rates of aggression among Drills. However, in semi-captivity at DRBC, affiliative behaviours are more frequent than aggressive behaviours for all group members. Aggression rates by ♀♀ and ♂♂ are equal, but adult ♂♂ are more likely to exhibit aggression toward other adult or subadult ♂♂, often in proximity to an oestrous ♀. Females most often initiate aggression with other ♀♀ (Wood 2007). Herding was never seen at DRBC in 770 h of observation; this, in contrast to Gartlan's (1970) observations, may be due to the wild animals' perception of an observer as a threat, or may be a behavioural deficit occasioned by semi-captivity and the constant proximity of humans.

Aggression is expressed in several ways both by ♂♂ and ♀♀: 'head bobbing', staring at opponent and jerking head forward and down; 'threat rush', a rapid quadrupedal charge ending without physical contact; 'threat jerk', head and upper trunk suddenly thrust forward, eyes wide open, medial crest raised, and lips generally compressed and pushed slightly forward; and 'branch-shaking', jumping onto a branch and shaking it sharply up and down several times (Gartlan 1970). Subadult and adult ♂♂ yawn to display canines as a mild threat, or to show uncertainty or tension.

Affiliative behaviour includes a mild form of 'lip-smacking', observed during mutual grooming, and sometimes exhibited by ♂♂ during copulation (E. Gadsby pers. obs.). Almost any group member may groom another, but the dominant ♂ performs the least grooming and is only groomed by adult ♀♀ (K. Wood pers. comm.). Females at DRBC are more likely to groom related ♀♀ than unrelated ♀♀ and ♂♂ (Wood 2007). High-ranking ♀♀ may monopolize grooming opportunities with high-ranking ♂♂ (K. Wood pers. comm.). The 'smile' involves pulling corners of mouth back to expose canines and premolars, while the head may be moved slowly from side to side; it is thought to function as a greeting and to signal amicability. Use of the smile as affiliative behaviour is unique to *Mandrillus* spp. in that higher-ranking animals may display it to lower-ranking individuals, and vice versa. Infants and juveniles often 'smile' when initiating play bouts, as do ♂♂ courting oestrous ♀♀.

The following description of courtship and mating is based on observations of semi-captive animals at DRBC (where large social groups of Drills live in 0.5–7.0 ha enclosures of native forest habitat), and may not be typical of Drills in the wild. Drill ♀♀ in oestrus exhibit prominent sexual swellings. The dominant ♂ attempts to monitor all swollen ♀♀ in the group, while other ♂♂ may attempt to mate opportunistically, especially with lower-ranking or younger ♀♀. Dominant ♂♂ show preference for high-ranking and mature ♀♀ when several ♀♀ are swollen

simultaneously. A high-ranking ♀ may also attempt to follow and maintain proximity to the dominant ♂, thereby excluding other ♀♀ access. Courtship involves ♂ following ♀ with maximal swelling, sometimes for several days (K. Wood pers. comm.). Target ♀ frequently monopolizes courting male's time by leading him in extended pursuit until eventually allowing him to mount. Female may stand or crouch while ♂ grasps her ankles with his feet, or she may kneel while ♂ stands on her calves, placing hands on her hips during intromission. Male may occasionally take scruff of female's neck in his teeth. During mating, ♀ frequently glances back over her shoulder at ♂, who may lip-smack. *Mandrillus* spp. are single-mount ejaculators (Caldecott *et al.* 1996). See also Marty *et al.* (2009).

Reproduction and Population Structure Except as noted, information on reproduction is based on data gathered during 1994–2005 from $n = 197$ live births involving 56 ♀♀ at DRBC (Wood 2007). Gestation range 161–197 days, mean gestation 176 days ($n = 125$). Seymour (1998) found mean gestation of 176 days for the five years 1993–97. During 2000–05, 72% of births occurred during May–Sep with nearly half of all births occurring in Jun and Jul, showing a strong correlation to peak rainfall months. Only 7% of all births occurred during Dec–Feb, the driest months. Birth peak in wild populations is believed to be the same as that seen in DRBC animals, as evidenced by estimated age of incoming wild-born infants (E. Gadsby pers. obs.).

Males are capable of reproduction at five years, but believed to be suppressed by dominant animals. Females exhibit first perineal (sexual) swelling at 2.7 years (1.6–4.6, $n = 47$) and first birth at 4.5 years (3.1–7.4, $n = 56$). The mean cycle length for ♀♀ is 33 days ($n = 124$ cycles; Seymour 1998). Birth-weight 400–650 g (E. Gadsby pers. obs.). One infant is born at a time. Only one set of twins (0.4%) among >220 births at DRBC. Inter-birth interval variable (mean = 473 days, 209–991 days, $n = 140$). Inter-birth interval significantly shorter after an infant death (Wood 2007). Many ♀♀ reproduce annually. As breeding is seasonal at DRBC, infants are born into ready-made peer groups (Wood 2007). Drill mothers do not actively wean their young; as infants become less dependent on their mothers they still nurse opportunistically until the next offspring is born. Juveniles spend most of their time in playgroups. With the onset of puberty at three years ♀♀ begin to break away from playgroups and join adult society. While sexually mature ♂♂ do not reach their full size, including expression of secondary sexual characteristics until 8–10 years. No observations reported on social structure or reproductive parameters of wild Drills. At DRBC, family members, particularly ♀♀, maintain lifelong affiliations. There is one dominant ♂, and other adult ♂♂ are either group-associated or solitary. Group-associated ♂♂ interact with other group members, but may be aggressively pursued by the dominant ♂ when attempting to mate. Solitary ♂♂ appear to avoid group contact, leaving an area when a group approaches (Wood 2007).

DRBC ♂♂ show signs of aging by 14 years and sometimes as early as 11 years, and typically die of 'old age' without specific pathology at 16–19 years (E. Gadsby pers. obs.). Probably die earlier in the wild. Mortality of wild-born ♂♂ in all age classes at DRBC is significantly higher than for ♀♀. At 20 years, oldest ♀ at DRBC continues to

cycle and bear young. Longevity record in captivity is 28 years for ♂♂ and 37 years for ♀♀ (Jones 1962, Knieriem & Cox 2002).

Predators, Parasites and Diseases Few data. Leopards *Panthera pardus* are probably predators on the mainland. Leopards absent from Bioko. Central African Rock Pythons *Python sebae* are probably a predator both on the mainland and on Bioko. Humans are the major predator of the Drill, both on the mainland and on Bioko (see Conservation below). Parasites found in wild Drill faeces from Afi Mountain, Nigeria are: *Balantidium coli*, *Blastocystis hominis*, *Endolimax nana*, *Entamoeba chattoni*, *E. coli*, *E. hartmanni*, *E. histolytica dispar*, *Enteromonas hominis*, hookworm sp., *Iodamoeba buetschlii* and *Trichomonas* sp. (J. Lewis pers. comm.). Drills have their own simian immunodeficiency virus (SIVdrl) (Clewley *et al.* 1998) found asymptotically in about 20% of incoming wild Drills at DRBC. Other species-specific viruses isolated from wild-born Drills at DRBC are cytomegalovirus (DrCMV) and foamy virus (SFV-drl) (Blewett *et al.* 2003).

Conservation IUCN Category (2012): Endangered. CITES (2012): Appendix I.

The Drill is the African primate with highest conservation priority (Oates 1996a). Populations reduced throughout small historic range and eliminated from much of range due to commercial bushmeat hunting and habitat loss (Wolfheim 1983, Lee *et al.* 1988, Gadsby 1990, Oates 1996a). In the early 1980s commercial hunting for bushmeat became the greatest threat for the Drill. Both on the mainland (Gadsby *et al.* 1994) and on Bioko I. (Butynski & Koster 1994, Hearn *et al.* 2006), Drill is a preferred bushmeat and hunting is widespread and often intense. Drills are hunted at all sites with shotguns and sometimes with dogs. Dogs hold a group at bay in trees while one or more hunters massacre the animals in the group (Gadsby *et al.* 1994, Waltert *et al.* 2002); without dogs, hunters are unlikely to kill more than two or three Drills during an encounter. In Korup hunters claim to kill from 2 to 25 Drills during these encounters, with a mean of 7.2 taken (Steiner *et al.* 2003). In many areas commercial hunters work from semi-permanent camps in the forest, periodically carrying out head-loads of smoked or fresh meat to traders who transport it to urban markets. As a result of widespread and intensive hunting, Drill super-groups have rarely been seen since the mid-1980s in Nigeria but still occurred, albeit at lower frequency, or with smaller-sized super-groups, in Cameroon (Gadsby & Jenkins 1998, Wild *et al.* 2005). According to Gadsby *et al.* (1994: 443): 'The relentless persecution reduces group size, lowers density, increasingly isolates groups of Drills, and may also be affecting behavioural and ecological strategies. It is becoming apparent that the formation of super-groups, which may play a crucial role in transfer of individuals, and thus genetic material, is occurring with decreasing frequency.'

In Nigeria, >60% of remaining Drill habitat lies within Cross River N. P. (3440 km² in two discontinuous divisions). In Cameroon, Korup N. P. (1259 km²) supports Drills and has a 17 km common boundary with Cross River N. P. On Bioko I. Drills occur both in the Pico Basile N. P. (330 km²) and in the Gran Caldera and Southern Highlands Scientific Reserve (510 km²). In none of these 'protected areas', however, is protection effectively enforced, and Drill subpopulations in all areas are probably in decline (Gadsby *et al.* 1994, Waltert *et al.* 2002, Steiner *et al.* 2003, Hearn *et al.* 2006). There is meaningful protection for Drills in Afi Mountain Wildlife Sanctuary,

a small (ca. 100 km²) out-lying habitat at the north-west edge of Drill range (see below). However, the global population of Drills may be losing viability as subpopulations become smaller and increasingly isolated by habitat fragmentation (Gadsby & Jenkins 1998). Habitat loss and hunting continue to drive population decline. With reduced and scattered subpopulations, large aggregations of Drills (hordes or super-groups) that may facilitate both the exploitation of seasonally abundant fruit and the transfer of genetic material are increasingly rare. See also Ting *et al.* (2012).

On Bioko I., Drills are sympatric with four other threatened species of primate (IUCN 2010); Red-eared Monkey (Vulnerable), Preuss's Monkey *Allochrocebus preussi* (Endangered), Pennant's Red Colobus *Procolobus pennantii* (Critically Endangered) and Black Colobus (Vulnerable). In addition, seven of Bioko's 11 species of primate are listed as 'Endangered' at the subspecies level (Butynski & Koster 1994, Hearn *et al.* 2006, IUCN 2010). Six subspecies of primate are endemic to Bioko. No place in Africa, perhaps no place in the world, has so many threatened endemic taxa of primate in such a small area (2017 km²). None the less, hunting of all seven of Bioko's monkey species for the commercial bushmeat trade continues unabated, driving all species closer to extinction on the island (Fa *et al.* 1993, Colell *et al.* 1994, Hearn *et al.* 2006).

Drill group encounter rates during primate census on Bioko declined ca. 33% during the 20 years from 1986 to 2006 (Hearn *et al.* 2006). Bushmeat surveys were conducted at the Malabo bushmeat market for 5–6 days/week from Oct 1997–Sep 2007. During this period, 2366 Drill carcasses were tallied. The total number is certainly greater as the market surveyor was not present all day every day. Island-wide questionnaire surveys were used to assess the percentage of Drill carcasses brought to this market; results indicated that ca. 60% of the Drills killed on Bioko are sold at the Malabo bushmeat market. If so, the total number of Drills killed on Bioko by hunters during this period is estimated at ca. 3940 (W. Morra & G. Hearn pers. comm.). In 1998, 226 Drills were counted at the Malabo bushmeat market during 283 days of survey. In 2006, 544 Drills were counted at the same market during 304 days of survey. Of these, 243 (45%) were adult ♂♂, 198 (36%) were adult ♀♀, 96 (18%) were immature and 7 (1%) had no age/sex data recorded (W. Morra & G. Hearn pers. comm.). If 544 Drills is 60% of the number killed, then roughly 900 Drills were killed by hunters on Bioko in 2006.

Continued rapid decline in Drill distribution and abundance on Bioko indicates that this level of exploitation is far from sustainable. The mean price paid per adult ♂ Drill at the Malabo bushmeat market changed from ca. US\$31 in 1997 to ca. US\$142 in 2007, a more than four-fold increase (Reid *et al.* 2005, W. Morra & G. Hearn pers. comm.). Less than 0.1% of the people of Bioko hunt monkeys. Monkey hunting accounts for <0.002% of Equatorial Guinea's gross domestic product (Reid *et al.* 2005, W. Morra pers. comm.). Monkey meat fulfils <1% of the minimum protein requirements of the urban population, and costs twice as much as beef or chicken (W. Morra pers. comm., T. Butynski pers. obs.). As summarized by W. Morra in Reid *et al.* (2005: 14): 'The primates of Bioko are on their way to extinction, driven by market forces. The decline in supply, coupled with inelastic demand as well as rising income and population, represents a recipe for an ecological catastrophe. And yet, the economic, employment and nutritional gains brought by

monkey hunting are negligible. In other words, Equatorial Guinea risks losing unique national assets and receiving almost no economic gain in return.' On Bioko there is ample primary and secondary forest for all 11 species of primate. Shotgun hunting is the only significant threat, accounting for 99% of monkey kills (Reid *et al.* 2005). As such, the primary conservation action required to conserve Bioko's monkeys is a complete ban on shotgun hunting (Hearn *et al.* 2006).

Critical sites for long-term conservation of the Drill on Bioko are Pico Basile N. P. and the Gran Caldera and Southern Highlands Scientific Reserve.

On the mainland, Drills are sympatric with six other threatened species of primate (IUCN 2010); Preuss's Red Colobus (Critically Endangered), Red-capped Mangabey (Vulnerable), Preuss's Monkey (Endangered), Red-eared Monkey (Vulnerable), Western Gorilla *Gorilla gorilla* (Critically Endangered) and Robust Chimpanzee (Endangered). As such, efforts to conserve the Drill will benefit all six of these species. In Nigeria critical sites for the long-term conservation of these six threatened species are the two divisions of the Cross River N. P., Okwangwo (640 km²) and Oban (2800 km², the largest protected area of Drill habitat), the Afi Mountain Wildlife Sanctuary (ca. 100 km²) and Mbe Mountains community forest (85 km²). Korup N. P. is currently the only Drill habitat in Cameroon where hunting is technically banned; the Banyang Mbo Wildlife Sanctuary (667 km²) allows limited hunting. Proposed protected areas in Cameroon include Takamanda N. P. (675 km²), Mount Cameroon N. P. (646 km²), Bakossi N. P. (ca. 800 km²) and Ebo N. P. (ca. 1100 km²). Legal creation of these protected areas is important for long-term survival of the species, but all new areas, as well as existing protected areas, require tremendous resources and commitment to sustain meaningful protection. Additionally, preserving and restoring habitat corridors to maintain larger protected landscapes will address further fragmentation of subpopulations. Key habitat blocks include: (1) the proposed Takamanda N. P. contiguous with Mone F. R. in Cameroon, Okwangwo Division and Mbe Mts in Nigeria; (2) Banyang Mbo Wildlife Sanctuary and the proposed Bakossi N. P., including Mt Kupé and Mt Manengouba; (3) the largest area and core of Drill habitat, the Oban Division (Nigeria) contiguous with Korup N. P. and its support zone, Ejagham F. R., Rumpi Hills F. R., Nkwende Hills and Nta Ali F. R., all in Cameroon (transboundary cooperation will be required); and (4) the ca. 12 km long forest corridor that connects Pico Basile N. P. and the Gran Caldera and Southern Highlands Scientific Reserve on Bioko. At present this corridor is under threat from agriculture, settlement and road construction, and is heavily hunted (T. Butynski pers. obs.).

In 2007, there were only 67 Drills in European, American and Japanese zoos; this managed population is descended from just six founders (A. Knieriem pers. comm.). At the DRBC, Nigeria, in 2009, there are 302 Drills in seven reproductive groups (wild born, F1, F2, F3) with 54 founders and 22 potential founders. At the Limbe Wildlife Centre, Cameroon, a breeding group of 59 is maintained. Breeding loans from these centres will be required to sustain a viable zoo population into the future. As of 2009, DRBC is planning release of a Drill group in the Afi Mountain Wildlife Sanctuary to reinforce the wild Drill population there (Gadsby 2002, 2006). Drills may be monitored with satellite telemetry. If methods prove successful, additional groups will be released to restock other habitats where Drills are now rare (if adequate protection is realized in those areas).

Measurements*Mandrillus leucophaeus**M. l. leucophaeus*

HB (♂ ♂): 720, 830 mm, n = 2

HB (♀ ♀): 455, 500 mm, n = 2

T (♂ ♂): 108 (86–125) mm, n = 10

T (♀ ♀): 75 (50–94) mm, n = 11

HF (♂ ♂): 211 (196–239) mm, n = 10

HF (♀ ♀): 177 (152–195) mm, n = 12

E (♂ ♂): 45, 47 mm, n = 2

E (♀ ♀): 41, 45 mm, n = 2

WT (♂ ♂): 32.9 (19.8–45.0) kg, n = 12

WT (♀ ♀): 11.6 (7.2–20.5) kg, n = 13

From wild-born Drills at DRBC (E. Gadsby pers. obs.)

HB (♂ ♂): 754 (580–1080) mm, n = 8

T (♂ ♂): 99 (81–126) mm, n = 7

HF (♂ ♂): 202 (158–220) mm, n = 7

E (♂ ♂): 45 (41–50) mm, n = 4

WT (♂ ♂): 20 kg, n = 1

GLS (♂ ♂): 211 (197–235) mm, n = 14

GLS (♀ ♀): 144 (135–157) mm, n = 12

GWS (♂ ♂): 125 (115–133) mm, n = 15

GWS (♀ ♀): 87 (82–95) mm, n = 13

Upper tooththrow (♂ ♂): 52 (50–56 mm), n = 15

Upper tooththrow (♀ ♀): 46 (43–52) mm, n = 10

Various localities; specimens at BMNH, USNM, AMNH, PCM

Body measurements and weights (Hilzheimer 1906, Malbrant & Maclatchy 1949, Hill 1970, C. P. Groves pers. comm.)

Skull measurements (Hill 1970)

GLS (♂ ♂): 213 (192–231) mm, n = 35

GWS (♂ ♂): 123 (120–130) mm, n = 5

Braincase breadth (♂ ♂): 93 (84–102) mm, n = 25

Upper tooththrow (♂ ♂): 53 (54–56) mm, n = 14

Various localities (C. P. Groves 2001, pers. comm.). There is probably some duplication of measurements here with Hill (1970; see above).

GLS (♂ ♂): 208 mm, S.D. = 9.1, n = 18

GLS (♀ ♀): 150 mm, S.D. = 9.4, n = 7

Various localities in Cameroon (Elton & Morgan 2006)

Mandrillus l. poensis

HB (♂ ♂): 668 (600–740) mm, n = 28

HB (♀ ♀): 538 (470–620) mm, n = 41

T (♂ ♂): 85 (65–100) mm, n = 31

T (♀ ♀): 63 (40–90) mm, n = 40

HF (♂ ♂): 182 (160–200) mm, n = 30

HF (♀ ♀): 149 (140–165) mm, n = 38

E (♂ ♂): 37 (30–44) mm, n = 30

E (♀ ♀): 32 (28–41) mm, n = 41

WT (♂ ♂): 20.0 (14.5–27.0) kg, n = 26

WT (♀ ♀): 8.5 (6.5–12.0) kg, n = 39

Upper canine (♂ ♂): 36 (28–40) mm, n = 26

Upper canine (♀ ♀): 7 (4–16) mm, n = 30

Lower canine (♂ ♂): 22 (18–28) mm, n = 30

Lower canine (♀ ♀): 6 (3–11) mm, n = 30

GLS (♂ ♂): 195 (186–207) mm, n = 8

GWS (♂ ♂): 124 (114–135) mm, n = 6

Braincase breadth (♂ ♂): 86 (78–94) mm, n = 8

Upper tooththrow (♂ ♂): 49 (45–50) mm, n = 6

Bioko I., Equatorial Guinea. Body and canine measurements (Butynski *et al.* 2009)

Skull measurements (C. P. Groves 2001, pers. comm., T. Butynski pers. obs.)

GLS (♂ ♂): 196 (186–207) mm, n = 4

GLS (♀): 131 mm, n = 1

GWS (♂ ♂): 127 (117–135) mm, n = 5

GWS (♀): 76 mm, n = 1

Upper tooththrow (♂ ♂): 50 (49–52) mm, n = 5

Bioko I., Equatorial Guinea (Hill 1970, Eisentraut 1973). There is probably some duplication of measurements here with Groves (2001; see above).

Key References Astaras 2009; Astaras *et al.* 2011; Butynski & Koster 1994; Gadsby & Jenkins 1998; Gartlan 1970; González-Kirchner & Sainz de la Maza 1996; Oates 2011; Wood 2007.

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GENUS *Lophocebus***Baboon-mangabeys (Grey-cheeked Mangabeys, Black Mangabeys)***Lophocebus* Palmer, 1903. Science, n.s. 17: 873.

Formerly lumped within *Cercocebus*, the species *albigena* and *aterrimus* have been recognized as distinct from other mangabeys since Barnicot & Hewett-Emmett (1972) showed that they were closer to *Papio* than to *Cercocebus* species. This affinity confirmed by Cronin & Sarich (1976) and by Groves (1978), who revived the generic name *Lophocebus*. Molecular studies (Goodman *et al.* 1998, Disotell 2000) further support this assessment. The vernacular name for *Lophocebus*, ‘baboon-mangabeys’, recognizes the relatively close phylogenetic relationship between *Papio* and *Lophocebus*. Molecular

study puts the time of divergence between *Mandrillus/Cercocebus* and *Papio/Lophocebus* at 6.7 mya (late Miocene) and between *Papio* and *Lophocebus* at 4.1 mya (mid-Pliocene; Perelman *et al.* 2011).

In 2003 and 2004, two small and isolated populations of similar mangabeys were discovered in SC Tanzania. On the basis of visual observations, vocalizations and photographs alone, they were allocated to *Lophocebus* as *L. kipunji* and given the vernacular ‘Kipunji’ (Jones *et al.* 2005). In 2006, with a juvenile specimen to hand and a molecular study, this monkey was allocated a new genus, *Rungwecebus*



Uganda Grey-cheeked Mangabey *Lophocebus ugandae* showing cheek-pouches.

(Davenport *et al.* 2006). That Kipunji does not belong in *Lophocebus* is supported by more recent molecular findings (Zinner *et al.* 2009a).

Lophocebus is distinct in the following respects: scapula long and narrow, deltoid plane on humerus narrow, brachialis flange on humerus narrow, supinator crest restricted, elbow joint broad, ilium constricted at base, lateral lip of patellar groove prominent, tibial shaft compressed, premolars not enlarged. In all these features, *Lophocebus* differs from *Cercocebus* and from *Mandrillus*, and closely resembles *Papio* and *Theropithecus*, to which it is closely related according to molecular data (see above). In addition, *Lophocebus* differs from *Cercocebus* in the following external features: eyelids not pale, a primitive feature among Old World monkeys; hairs solid toned with no medulla, a unique feature of the genus; crown hair raised, often crested, another unique feature among Cercopithecinae; tail long, flexible, another primitive feature but emphasized in this genus, to the extent that it has been referred to as 'semi-prehensile', though this is not entirely accurate, although tails are often looped over branches in an idiosyncratic way. These mangabeys sit sprawled, their limbs spread-eagled, giving them a sort of untidy, 'loose-limbed' appearance. All taxa within *Lophocebus* are arboreal, forest-dependent and confined to equatorial Africa.

Chromosome 10 is of standard papionin type, whereas the banding pattern is modified in *Cercocebus*. Unlike in *Cercocebus* there is no heterochromatic region on chromosome 12. *Lophocebus* is not as widespread as *Cercocebus*, as they do not occur west of the Cross R. in Nigeria, barely reach NW Tanzania, and are absent from Kenya. They are, however, common in the forests of the Congo Basin and SW Uganda.

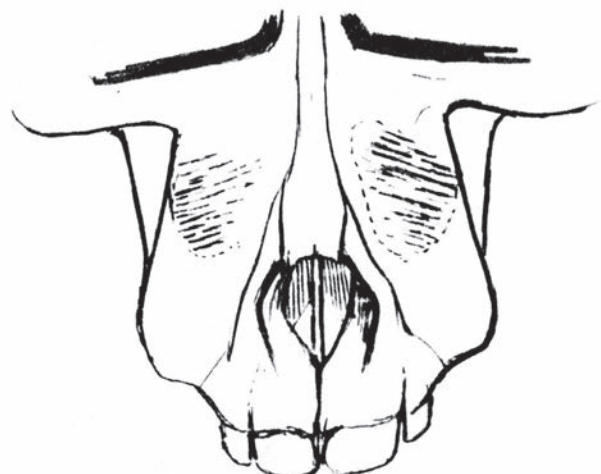
Traditionally, two species recognized: *Lophocebus albigena*, from east, north and west of the Congo–Lualaba River System, and *L. aterritus* from south of the Grand Cuvette. Groves (1978), operating on an extreme interpretation of the Biological Species Concept, united these two into one species, citing certain features suggesting gene-flow across the Lualaba R. Later, however, he not only separated them again but raised a third taxon, *L. opdenboschi*, to species rank

(Groves 2001). Most recently the same author divides *L. albigena* into four species: Western Grey-cheeked Mangabey *L. albigena* (coastal and riverine forests of the west–central African region), Osman Hill's Grey-cheeked Mangabey *L. osmani* (plateau forests of Cameroon, west to the Cross R.), Johnston's Grey-cheeked Mangabey *L. johnstoni* (forests of N and NE DR Congo, Rwanda, Burundi and Semliki Forest, extreme W Uganda) and Uganda Grey-cheeked Mangabey *L. ugandae* (confined to the forests of SW Uganda and the shores of L. Victoria, including Minziro Forest in extreme NW Tanzania) (Groves 2007a). Here, as almost nothing is known about *L. johnstoni* or *L. albigena*, and little about *L. osmani* (all long-term field studies have been on *L. ugandae*), we continue to treat these four species under the heading of the earliest-described of them, *L. albigena*. Similarly, while recognizing that the Southern Black Mangabey *L. opdenboschi* is as different from the Northern Black Mangabey *L. aterritus* as the latter is from the *L. (albigena)* Group, both are treated under *L. aterritus*, about which little is known in the wild.

Brief characterizations of the six species/forms are as follows:

- 1 pelage long, loose, with a paler mane (= cape = mantle) on shoulders; cheek-whiskers long, thin, pale; a short, partially upright tuft or pair of tufts on crown;
- 2 *albigena*: mane light grey; underside brown; cheeks creamy-white;
- 3 *osmani*: mane red-tinged brown; underside yellowish; cheeks bright greyish-white or golden-white; no long crown-tufts;
- 4 *johnstoni*: mane dark brown; underside dark brown; cheeks light greyish-brown;
- 5 *ugandae*: resembles *johnstoni* but much smaller, with relatively large teeth and jaws; no mane; cheek-whiskers thick, not pale; crown-tuft tidy, not 'scruffy';
- 6 *aterimus*: pelage short, coarse; cheek-whiskers long, swept back with a slight outward curve, grey; crown-tuft tall, upright, thin, coconut-like;
- 7 *opdenboschi*: pelage long, lax; cheek-whiskers short, black; crown-tuft broad, pyramidal, lying back.

Colin P. Groves & Thomas M. Butynski



Uganda Grey-cheeked Mangabey *Lophocebus ugandae* muzzle from above showing 'crepe' textured area between orbits and canines.

Lophocebus albigena (also *L. osmani*, *L. johnstoni*, *L. ugandae*) GREY-CHEEKED MANGABEY

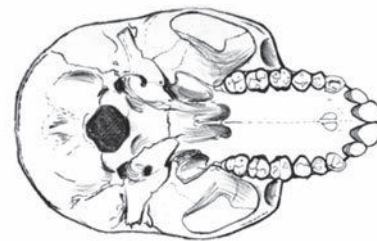
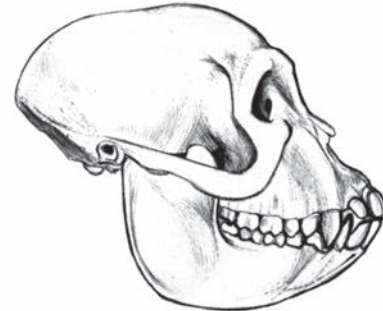
Fr. Mangabé à joues grises; Ger. Grauwangenmangabe

Lophocebus albigena (Gray, 1850). Proc. Zool. Soc. Lond. 1850: 77. Mayombe, DR Congo.Western Grey-cheeked Mangabey *Lophocebus albigena*.

Taxonomy Monotypic species. Originally *Presbytis albigena*. Formerly included in *Cercocebus*. Considered a distinct genus (*Lophocebus*) by Groves (1978). Number of subspecies is debated. Groves (2001) suggested three *albigena* subspecies: *L. a. albigena*, *L. a. johnstoni* and *L. a. osmani*. Subsequently, Groves (2007a) elevated all three to species and added a fourth, *L. ugandae*. Kingdon (1997) recognizes *L. albigena zenkeri*. Grubb *et al.* (2003) and Oates (2011) consider all subspecific distinctions to be uncertain. Gautier-Hion *et al.* (1999) do not recognize the Black Mangabey *Lophocebus aterrimus* as specifically distinct from *L. albigena*.

Separation among taxa is based mostly on similarities in shape and colour of the mane (= cape = mantle), colour of the ventrum and cheeks, and shape of the crown-tuft(s) (Gautier-Hion *et al.* 1999, Groves 2001). There are also well-marked, consistent, craniometric differences that, according to Groves (2007a), enable them to be distinguished at the specific level. For example, *L. osmani* is extremely sexually dimorphic in size (♀♀ have smaller skulls than ♀♀ of other taxa, while ♂♂ have larger skulls but relatively smaller teeth), whereas *L. ugandae* is distinguished by a smaller skull, reduced sexual dimorphism and relatively large masticatory apparatus. Groves (2007a) places these four species in the '*Lophocebus (albigena) Group*'. This is the taxonomy adopted here. *Lophocebus ugandae* is relatively well-studied in the field, and there is some information for *L. albigena*. *Lophocebus osmani* and *L. johnstoni* remain poorly known. Therefore, for convenience, this profile treats these four taxa together as the *Lophocebus (albigena) Group* with most of the information presented here coming from field research on *L. ugandae*.

Nuclear DNA sequences indicate that *Lophocebus* forms a clade with *Papio* and perhaps *Theropithecus*, and is less closely related

Lateral and palatal views of skull of Uganda Grey-cheeked Mangabey *Lophocebus ugandae* adult male.

to terrestrial mangabeys; in particular, gamma-globulin intron sequences suggest that *Lophocebus* diverged from *Cercocebus* ca. 5 mya (early Pliocene), but from *Papio* and *Theropithecus* 4 mya (mid-Pliocene; Disotell 1994, Harris 2000, Page & Goodman 2001). The diphyletic origin of mangabeys is further supported by cranial and postcranial skeletal features (Nakatsukasa 1996, Fleagle & McGraw 1999). Synonyms: see Geographic Variation. Chromosome number: $2n = 42$ (Romagno 2001).

Description Lanky, blackish, medium-sized, arboreal monkeys. One of the largest arboreal cercopithecines. Sexes similar in colour but adult ♀♀ smaller than adult ♂♂. In *L. ugandae*, adult ♀♀ weigh ca. 70% as much as adult ♂♂. Eyelids black. Pelage long, loose, blackish-brown. Hair may form a short, partially upright tuft on crown or pair of tufts above eyebrows. Mane of longer, paler pelage over shoulders (light grey, greyish-brown, yellowish-brown or rusty-brown depending on species). Mane more prominent in ♂, continuous with thin, pale cheek-whiskers (Groves 2001). Tail long, often held in a distinctive arch over the back. Skin is bare over the ischial callosities. Callosities are pronounced, 'C'-shaped and continuous in ♂♂, but broken at the middle in ♀♀ to form two comma-shaped protrusions. Face, palms, soles and perianal area pink in newborns, turning to grey and eventually black by age nine months (Deputte 1992).

Geographic Variation The species of the *Lophocebus (albigena) Group*, according to Groves (2007a), are:

***L. albigena* Western Grey-cheeked Mangabey** (synonyms: *weynsi*, *zenkeri*). Most of western central Africa, west of the Congo R., including all of Congo, Gabon, mainland Equatorial Guinea (i.e. Rio Muni) and coastal S Cameroon. Mane light grey, sometimes with faint straw tones.

***L. osmani* Groves, 1978: Osman Hill's Grey-cheeked Mangabey.** Batouri District, Cameroon, west to Cross R. into SE Nigeria. Mane rusty-brown.

***L. johnstoni* Lydekker, 1990: Johnston's Grey-cheeked Mangabey** (synonyms: *ituricus*, *jamrachi*, *mawambicus*). Burundi, Rwanda, N and NE DR Congo (north of Congo R. and east of Lualaba R.), and Semliki Forest in far W Uganda. Mane usually dark brown, but sometimes pale whitish-grey or chocolate.

***L. ugandae* Matshiei, 1913: Uganda Grey-cheeked Mangabey.** SW and C Uganda and extreme NW Tanzania in Minziro F. R. Mane short, contrastingly yellowish-brown or greyish-brown; skull small.

Similar Species

Cercocebus agilis. Broadly sympatric with *L. albigena* and *L. johnstoni*. Semi-terrestrial. Pelage brownish-grey, short, fine and agouti-banded. Eyelids pale grey.

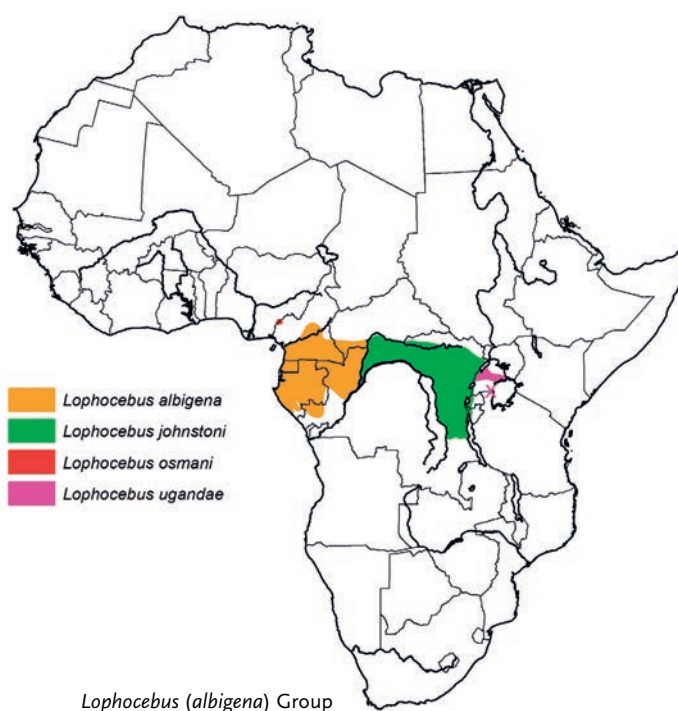
Lophocebus aterrimus. Allopatric with *L. albigena* along Congo/Lualaba R., and with *L. johnstoni* along lower Congo R. On right bank. Black; cheek-whiskers brown and greyish-brown; crest conical.

Distribution Endemic to equatorial Africa. Rainforest BZ. Ranges from Cross R., SE Nigeria, through lowland rainforest of S Cameroon, Equatorial Guinea and Gabon, east to Central African Republic, DR Congo and Congo north of the Congo/Lualaba R. Occurs in East Africa in forest patches through SW Uganda to the Nile R. and into extreme NW Tanzania.

Habitat Grey-cheeked mangabeys inhabit low and medium altitude tropical rainforest. In drier areas they are limited to swamp forest and the immediate environs of water-courses (Kingdon 1971). Almost strictly arboreal, they use the middle and high strata of the forest, including emergent trees. In secondary forests density is low. In forests with mosaics of habitat types they are more commonly found where tree density is high, as in closed canopy swamp and tall forest. Rarely seen foraging on open grasslands and open swamp adjacent to closed canopy forest (W. Olupot pers. obs.). Grey-cheeked mangabeys tend to occur at low density where sympatric with swamp-adapted Red-capped Mangabey *Cercocebus torquatus* (Cashner 1972) or Agile Mangabey *Cercocebus agilis* (Quris 1976). Found from ca. 1600 in Uganda to ca. 2350 m in Nyungwe N. P., Rwanda, and Kahuzi-Biega N. P., DR Congo (Kingdon 1971, Jones *et al.* 2005).

Abundance In Kibale N. P., Uganda, there are 14 ind/km² (Olupot *et al.* 1994) and 0.87–2.41 groups/km² (Chapman *et al.* 2000). Chalmers (1968a) reported 133 ind/km² in forest patches surrounded by recent cultivation in Uganda. In Gabon, L. J. T. White (1992) found 10.0 ± 7.7 ind/km² and 0.2–1.1 groups/km². Cashner (1972) reported 22.1 ± 3.5 ind/km² in Equatorial Guinea.

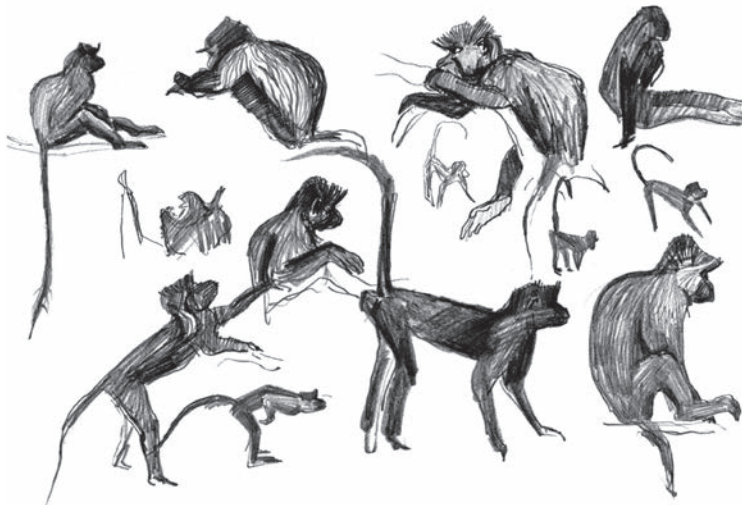
Adaptations Diurnal and arboreal. Like all cercopithecine species, Grey-cheeked Mangabeys have cheek-pouches in which they store



food when feeding rapidly or on hard seeds. Tail mildly prehensile, a feature most visible in young infants, which wrap their tails around those of their mothers when they are clinging. Like several other forest primates, Grey-cheeked Mangabey ♂♂ possess extralaryngeal air sacs that serve as resonators during the production of the species-typical, stereotyped ♂ loud-call that can be heard from 500–1200 m (Gautier 1971, Waser 1977b). These air sacs are thought to make possible the low pitch of these calls, which allow them to travel long distances with little distortion through the forest canopy. Grey-cheeked Mangabeys have better low frequency hearing than humans (Brown 1989a). Powerful jaws, arms and hands make it possible for them to open and obtain seeds from large, hard fruits (e.g. *Monodora myristica*), and to tear apart dead wood in search of invertebrates. Other African primates of this size (e.g. guenons) do not have this capacity.

Food and Foraging Omnivorous. Grey-cheeked Mangabeys in Kibale forage throughout the day, with peaks at 08:00–09:00h and 14:00–15:00h. Feed on a wide variety of items. Fruit is the most important item in the diet. Feeding on fruit, including pulp, arils and seeds, takes up 58–80% of the feeding time (Waser 1977a, Ham 1994, Poulsen *et al.* 2001, Brugière *et al.* 2002, Shah 2003). Seeds are taken from dehiscent pods, wind-dispersed fruit and immature succulent fruit. Fruits are taken ripe or unripe, depending on the plant species and availability. In Kibale feeding on fruits of *Ficus* spp. comprises a large proportion (16%) of feeding observations. When opening an unripe, insect-infected fig, Grey-cheeked Mangabeys eat the grubs, some seeds and pulp. Other commonly eaten fruits include ripe *Celtis durandii*, *Celtis africana*, *Diospyros abyssinica*, *Uvariopsis congensis*, *Phoenix reclinata* and *Maesopsis eminii*.

May use calls of frugivorous primates and birds, particularly Black-and-white-casqued Hornbills *Bycanistes subcylindricus*, to locate fruit (Olupot *et al.* 1998). Long-term spatial memory suggested to improve foraging efficiency (Janmaat & Chancellor 2010). Fruit sources strongly influence movements. Over a few days group



Uganda Grey-cheeked Mangabey *Lophocebus ugandae*.

movements centre on large fruit patches. After their depletion, the group typically abandons the area for a richer patch. In central Africa seed eating seems to be more common in forests dominated by Caesalpinaceae, which contribute up to 58% of the plant diet (Brugière *et al.* 2002). In Cameroon important food species include *Erythrophloeum suaveolens* and *Enantia chlorantha* (Poulsen *et al.* 2001). In Gabon a total of 75 species of fruit are taken, with seeds of *Pterocarpus soyauxii* being the most selected (Ham 1994).

At all study sites, second to fruit feeding is invertebrate foraging, which takes up 12–31% of the feeding time. Invertebrate foraging includes splitting dead twigs, tearing dead bark, epiphyte masses and liana tangles and searching for and eating objects found there (Waser 1977a). In Gabon 33% of insects are taken from leaves and 17% from flowers; caterpillars and ants comprise 75% of insect-eating (Ham 1994). Leaves (mostly young), flowers and other food items, account for 4–13%, 0–5% and 0–4%, respectively, of feeding time in Kibale, and 4%, 2% and 0.5%, respectively, in Gabon. In Kibale favourite sources of leaves are *Premna angolensis* and *Millettia dura*; in Gabon, *Cryptosepalum staudtii* and *Millettia* sp. Flowers are mostly taken from *M. dura*, *Erythrina* spp., *Symphonia globulifera* and *Monodora myristica* at Kibale and from *Pterocarpus soyauxii* and *Pentaclethra macrophylla* in Gabon. Prominent in the list of ‘other’ items are live bark and pith. Eggs and small vertebrates, including snakes, are infrequently taken (Waser 1977a).

In East Africa home-ranges are 13 ha (Chalmers 1968a) to 410 ha (Waser 1977a), but probably average ca. 250 ha. A home-range of 215 ha was used by one group of 18–23 individuals for one year in Gabon (Ham 1994). Home-range overlap, like home-range size, depends on group density with less overlap in higher density conditions.

Social and Reproductive Behaviour Social. Not territorial. Lives in groups containing several adult ♂♂ and adult ♀♀ and young of various ages. Most groups consist of 10–20 ind (5–30). Small groups may contain only one adult ♂. Group sizes average 18.9 ± 2.3 individuals in Gabon (L. J. T. White 1992). In Kibale weekly counts of six groups over 218 weeks gave an average count of 16.0 ± 2.4 individuals with 3.1 ± 1.2 adult ♂♂, 0.6 ± 0.4 subadult ♂♂, 6.2 ± 0.8 adult ♀♀, 3.6 ± 1.1 juveniles and 2.5 ± 1.3 infants (W. Olupot pers. obs.).

Frequently forms polyspecific associations with other monkeys, rarely with Robust Chimpanzees *Pan troglodytes*. In Gabon the most frequent association is with Crowned Monkeys *Cercopithecus pogonias*; in Uganda, with Red-tail Monkeys *C. ascanius*. These associations may include young of different species playing together and grooming between different species. Grey-cheeked Mangabeyes are highly vocal. Their calls include a variety of ‘grunts’ used in the context of contact, ‘staccato barks’ used in alarm situations, and the adult ♂♂ ‘whoop-gobbles’ loud call (Chalmers 1968b) used for inter-group spacing and coordinating group movements (Waser 1977b, Olupot *et al.* 1998). Adult ♀♀ have a call similar to the whoop-gobble of the adult ♂♂ but this call is rarely given (R. Kaserengenyu & C. Kaganzi pers. comm.). Grey-cheeked Mangabey groups usually avoid one another, but occasionally groups fuse. While groups are mixed, some level of aggression may occur among members of different groups, usually involving adult ♂♂ and adult ♀♀. Large groups can fission temporarily or permanently (Janmaat *et al.* 2009). Stable dominance hierarchy among ♀♀ (Chancellor & Isbell 2009). Infant carrying by ♀♀ other than mothers occurs. Adult ♂♂ also sometimes carry infants, especially when the group is disturbed. Intergroup transfer primarily by adult ♂♂ (Olupot & Waser 2005, Chancellor *et al.* 2011) though it is possible that ♀♀ also transfer between groups (W. Olupot pers. obs.). Mortality rate for transferring ♂♂ is higher than for ♂♂ in groups (Olupot & Waser 2001a).

Reproduction and Population Structure Breeding and birth occur throughout the year. There is no obvious relationship between the timing of breeding or births and rainfall, food availability or food quality. In captivity ♂♂ begin to exceed ♀♀ in weight at 3–4 years (Deputte 1992). In Kibale ♂♂ reach maturity at ca. 7.5 kg at 6–7 years (Olupot 2000b). Testes descend and canines emerge at 4–5 years of age (Deputte 1992). In captivity ♀♀ exhibit their first sexual swelling at 3–4 years of age at a weight of ca. 5 kg, after which their growth rate slows. Cycles (average of 31 days) are initially long and irregular, suggesting a period of adolescent infertility (Deputte 1992). In Kibale the ratio of adult ♂♂ to adult ♀♀ is 1 : 2; adult to young ratio is 1 : 1.4. Birth rate is 0.4 per adult ♀/year (W. Olupot pers. obs.). Gestation is 175 days (Deputte 1991). One infant is born at a time. No cases of twinning reported. In captivity infants weigh ca. 425 g at birth (Ross 1991).

Number of adult ♂♂ in a group is strongly related to the number of oestrous ♀♀ (Olupot & Waser 2001b). A ♀ in oestrus develops a sexual swelling at the genitalia. Most mating occurs at the peak of the swelling (Wallis 1983). Mating is promiscuous. Complete copulation between a ♂ Ashy Red Colobus Monkey *Procolobus rufomitratu* *tephrosceles* and cycling ♀ Grey-cheeked Mangabeyes observed at Kibale on at least four occasions (T. Struhsaker & T. Butynski pers. comm., R. Kaserengenyu pers. comm.).

One ♂ usually dominates matings, but the ♀♀ also mate with other ♂♂, including old juveniles (Arlet *et al.* 2008). Male–female interactions often resemble mate guarding or consortships in baboons *Papio* spp. Each ♂ attempts to maintain close spatial association with the ♀ and tries to prevent other ♂♂ from getting close to her. Exclusive consortships of one ♂ with a ♀ occasionally continue over an entire oestrous period. As in baboons, there are sometimes high levels of aggressive competition for the ♀ and several ♂♂ mate during the oestrous cycle. Mating is followed by post-copulatory grunts by the ♀.



Uganda Grey-cheeked Mangabey *Lophocebus ugandae* showing suborbital indentations.

In captivity, longevity of at least 32 years, 8 months recorded (Jones 1982).

Predators, Parasites and Diseases African Crowned Eagles *Stephanoaetus coronatus* and Robust Chimpanzees are suspected to be the main non-human predators. Solitary ♂♂ are believed to be particularly vulnerable to attacks by *S. coronatus*. Robust Chimpanzees observed to kill an infant Grey-cheeked Mangabey in Kibale (R. Kaserengenyu pers. comm.). *Stephanoaetus coronatus* observed to kill a subadult ♂ in Central African Republic (N. Shah pers. comm.). Circumstances surrounding the death of several radiotracked ♂♂ in Kibale strongly suggest predation by *S. coronatus* (Olupot & Waser 2001a). Male responses to *S. coronatus* attacks are rank-dependent and elevate faecal cortisol (Arlet & Isbell 2009). Grey-cheeked Mangabey bones found under *S. coronatus* nests (Mitani *et al.* 2001) in Kibale and in Leopard *Panthera pardus* scats in Gabon (Henschel *et al.* 2005, 2011).

Conservation IUCN Category (2012): Least Concern as *L. albigena*. *L. johnstoni*, *L. osmani* and *L. ugandae* not assessed. CITES (2012): Appendix II.

Grey-cheeked Mangabeys are sensitive to heavy logging (Skorupa 1988, Kambale Saambili 1998, Olupot 2000a) and forest clearing for agriculture and settlement. In central and West Africa they are also threatened by the bushmeat trade. No records of crop-raiding recorded anywhere but in the Lwamunda Forest, Uganda (Chalmers 1968a).

Measurements

Lophocebus ugandae

HB (♂♂): 520 (470–600) mm, n = 31

T (♂♂): 810 (570–890) mm, n = 31

HF (♂♂): 170 (150–180) mm, n = 31

WT (♂♂): 8.7 (7.5–11.0) kg, n = 31

Kibale Forest, Uganda (Olupot 2000a, b)

Lophocebus johnstoni

HB (♂♂): 580 (540–620) mm, n = 16

HB (♀♀): 510 (440–640) mm, n = 15

T (♂♂): 890 (820–940) mm, n = 16

T (♀♀): 820 (740–900) mm, n = 15

WT (♂): 8.2 kg, n = 1

WT (♂): 6.1 kg, n = 1

From several sites in Zaire (Allen, 1925. Added to this sample are one ♂ and one ♀ from Ituri Forest, Zaire, housed at PCM; C. P. Groves pers. comm.). Sample may include one or more immature individuals.

Lophocebus albigena

WT (♂♂): 9.0 kg, n = 5

WT (♀♀): 6.4 kg, n = 6

Gabon (Gautier-Hion & Gautier 1976)

HB (♂♂): 630 (570–750) mm, n = 9

HB (♀♀): 550 (540–560) mm, n = 4

T (♂♂): 900 (750–1010) mm, n = 9

T (♀♀): 830 (750–880) mm, n = 4

WT (♂♂): 9.2 (8.5–10.0) kg, n = 5

WT (♀♀): 6.0 (6.0–6.0) kg, n = 2

Bipindi region, SW Cameroon, and Odzala and Mambili Districts, Congo. Specimens at PCM and MNHN (C. P. Groves pers. comm.).

Lophocebus osmani

HB (♂): 610 mm, n = 1

T (♂): 920 mm, n = 1

Batouri District, Cameroon. Specimen at PCM (C. Groves pers. comm.).

Key References Brugière *et al.* 2002; Chalmers 1968b; Oates 2011; Olupot & Waser 2001a, b; Poulsen *et al.* 2001; Waser 1977a.

William Olupot & Peter M. Waser



Uganda Grey-cheeked Mangabey *Lophocebus ugandae*.

Lophocebus aterrimus (also *L. opdenboschi*) **BLACK MANGABEY**

Fr. Mangabé noir; Ger. Schopfmangabe

Lophocebus aterrimus (Oudemans, 1890). Der Zoologische Garten 31: 267. Stanley Falls, DR Congo.Northern Black Mangabey *Lophocebus aterrimus* adult male.

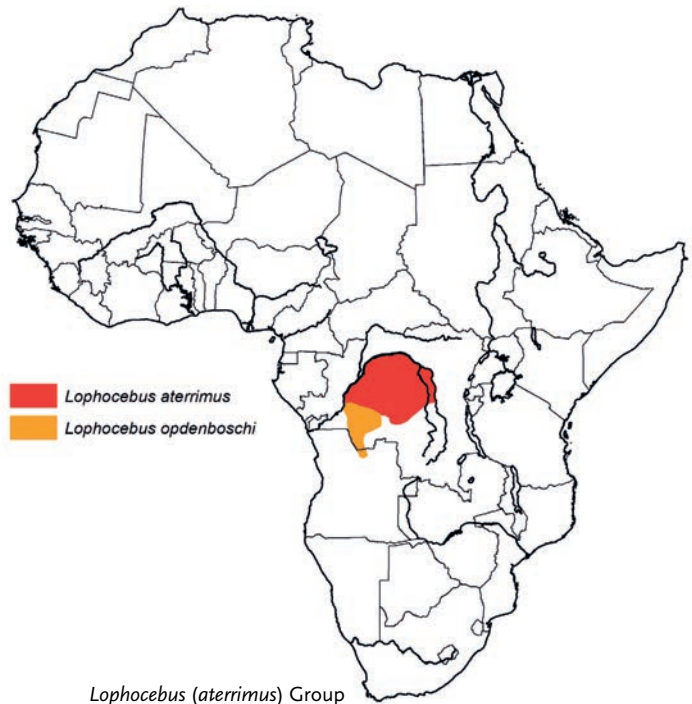
Taxonomy Monotypic species. Described as a full species (Schouteden 1944b), then reduced to a subspecies of the Grey-cheeked Mangabey *Lophocebus albigena* (Schouteden 1948, Groves 1978, Horn 1987a). Re-evaluated as a full species with two subspecies *L. a. aterrimus* and *L. a. opdenboschi* (Kingdon 1997) and this taxonomy was adopted by Grubb *et al.* (2003). Groves (2001, 2007a) has since argued for full species designation for both *aterrimus* and *opdenboschi*, the taxonomy adopted here. *Lophocebus aterrimus* is relatively poorly known, and *L. opdenboschi* is even less studied in the field. Therefore, for convenience, this profile treats these two species together as the ‘*Lophocebus* (*aterrimus*) Group’ with almost all of the information presented here coming from field research on *L. aterrimus*. Synonyms: see Geographic Variation. Chromosome number: $2n = 42$ (Dutrillaux *et al.* 1979).

Description Slender, medium-size, black, arboreal monkeys. Sexes alike in colour. Weight of adult ♀ ca. 70% that of adult ♂. Entirely glossy black fur except for the long curled cheek-whiskers. Albinistic and leucistic individuals not uncommon (Groves 1978, Eppley *et al.* 2010). No eyebrow tufts. Upstanding crest in the centre of the crown (up to 80 mm long). Long sparse fur, up to 150–200 mm on the shoulders forming a mane (= mantle = cape). Long tail and long limbs. Females have red sexual swellings. Total or partial albinism is frequent in *L. aterrimus* (Schouteden 1948, Horn 1987a). Young similar in colour to adults.

Geographic Variation The species of the *Lophocebus* (*aterrimus*) Group, according to Groves (2001, 2007a), are:

***L. aterrimus* Northern Black Mangabey** (synonyms: *coelognathus*, *congicus*, *hamlyni*, *opdenboschi*, *rothschildi*). C Congo Basin, between left bank of Lualaba R. to ca. 4°S in east and to right bank of Kasai R. in west. Cheek-whiskers brown and greyish-brown; crest conical (Schouteden 1944b).

***L. opdenboschi* Schouteden, 1944: Southern Black Mangabey.** W Congo Basin (south of Kasai R.) and NE Angola to ca. 17°05' E, 09°S (Schouteden 1948, Machado 1969, Gautier-Hion *et al.* 1999). Cheek-whiskers black; crest ridged (Schouteden 1944b).

*Lophocebus* (*aterrimus*) Group**Similar Species**

Lophocebus albigena. Allopatric with *L. aterrimus* along Congo/Lualaba R. On right bank. Mane light grey. Ventrums brown. Cheeks creamy white. Crown hair long and scruffy, often forming two small tufts above brows.

Lophocebus johnstoni. Allopatric with *L. aterrimus* along lower Congo R. On right bank. Mane (= mantle = cape) and ventrum dark brown. Cheeks greyish-brown.

Distribution Endemic to Congo Basin. Rainforest BZ. Forested areas of Congo Basin south of the Congo R to NE Angola. See Geographic Variation.

Habitat Moist forest. Data only available for *L. a. aterrimus* studied in the L. Tumba region (Horn 1987b), in the Lomako Forest (McGraw 1994) and in Salonga N. P. (Gautier-Hion & Maisels 1994, Gautier-Hion pers. obs.). Mostly inhabits primary rainforest; frequently in swamp forests at Salonga (but not at Lomako); avoids secondary forest. Known altitudinal range ca. 100–400 m. Annual rainfall 1700 mm–>2100 mm (Ergo & de Halleux 1979).

Abundance The most abundant primate at Lomako with 73 ind/km² and a biomass of 585 kg/km² (McGraw 1994). A comparable density (69 ind/km²) deduced from one group's home-range at Tumba L. (Horn 1987b). Common in the Salonga N. P.

Adaptations Diurnal and arboreal. In the absence of colour markings, even on the face, body postures exhibiting the black silhouettes of

the monkey should be the most important longer-range visual signals. Gives facial grimaces at close quarters. The rich vocal repertoire of *L. aterrimus* may offset a narrower range of visual communication (Kingdon 1997). Inflation of large vocal sacs allows adult ♂♂ to produce a loud 'whoop-gobble' call that can be heard to at least 500 m.

Foraging and Food Omnivorous. Forages extensively in the middle and upper canopy. Often forages in subgroups (Horn 1987b, Gautier-Hion pers. obs.). Home-ranges of two groups were 48 ha and 70 ha with range overlaps with other groups of *L. aterrimus* of 60% and 75%, respectively. When licking nectar from flowers in the canopy along a river bank, one group of ten animals often divided into three subgroups separated by up to 400 m. Adult ♂♂ sometimes forage alone (Gautier-Hion & Maisels 1994). Diet at L. Tumba includes fruits (57%), seeds (30%), flowers (4%), immature leaves (3%) and insects (2%) (Horn 1987b). Thirty-three plant species used at Salonga N. P. where the diet is dominated by arils (32%) and seeds (30%) and includes a small amount of fruit pulp (4%). Flowers (including nectar of *Daniellia pynaertii*; Caesalpiniaceae) comprise 18% of the diet, and leaves 16% (Gautier-Hion & Maisels 1994, A. Gautier-Hion & F. Maisels pers. obs.). At this site most animal prey (insect larvae and ants) are found by searching under bark. Bark and palm shoots also consumed. Strong seasonal dietary variations reflect food availability. During a year-round study, the diet was successively dominated by nectar and leaves (monthly maxima of 50% and 40%, respectively, in Feb), then by arils (mainly from Annonaceae and Myristicaceae with monthly maximum of 73% in May), finally by seeds (mainly from legumes with monthly maximum of 65% in Sep; Gautier-Hion pers. obs.).

Social and Reproductive Behaviour Social. Multile, multi-female groups, with a mean of 10–11 members (Lomako, McGraw 1994; Salonga, Gautier-Hion pers. obs.) numbering up to 19 individuals (Horn 1987b). Two groups, both of 19 individuals, each included three adult ♂♂ and five adult ♀♀. Subgroups and single adult ♂♂ occur. Single adult ♂♂ of a group may visit oestrous ♀♀ in neighbouring groups, but rejoin their own group by nightfall. No territorial defence observed (Horn 1987b). Courtship and mating behaviour, as well as development of the young has not been studied. *Lophocebus aterrimus* frequently engages in polyspecific association (ca. 80% of the time at Salonga, 59% at Lomako), mainly with Wolf's Monkey *Cercopithecus wolffi* (70–90% of bi-specific groups), and with *C. wolffi* and Red-tailed

Monkey *Cercopithecus ascanius* (80% of tri-specific groups). At Salonga *L. aterrimus* occasionally found with Red Colobus *Procolobus rufomitratus* and Angola Colobus *Colobus angolensis* in the presence of *C. wolffi*. The vocal repertoire of *L. aterrimus* is very similar to that of *L. albigena*: includes the 'whoop-gobble' call of adult ♂♂, which serves inter-group spacing and intra-group rallying, and the 'karaou' call that is given by adult and subadult ♂♂ and adult and subadult ♀♀ during alarming situations. A variety of grunts are exchanged at short inter-individual distances (Gautier-Hion pers. obs.).

Reproduction and Population Structure This is one of Africa's least studied monkeys. Few data available on life history parameters or on population structure. Probably very similar to *L. albigena* and *L. johnstoni*. Sexual swellings in adult ♀♀. Ratio ♂ : ♀ about 1 : 1.5.

Predators, Parasites and Diseases No data. Like other monkeys, *L. aterrimus* responds with warning calls to presence of African Crowned Eagles *Stephanoaetus coronatus*.

Conservation IUCN Category (2012): Near Threatened. Near Threatened for *L. a. aterrimus*. Data Deficient for *L. a. opdenboschi*. CITES (2012): Appendix II.

Contemporary status insufficiently known. Salonga N. P. appears to be the most important area for long-term conservation of *L. aterrimus*. Both species are too poorly known to make recommendations for their long-term conservation.

Measurements

Lophocebus aterrimus

HB (♀): 530 mm, n = 1

T (♀): 750 mm, n = 1

Unknown origin (Napier 1981)

WT (♂): 7.9 kg, n = 1

WT (♀♀): 5.6 (4.5–6.7) kg, n = 4

DR Congo (Colyn 1994)

Key References Groves 1978, 2007a; Horn 1987a, b; McGraw 1994; Schouteden 1944b.

Annie Gautier-Hion

GENUS *Rungwecebus*

Kipunji

Rungwecebus Davenport, Stanley, Sargis, De Luca, Mpunga, Machaga & Olson, 2006. Science 312: 1379.

Rungwecebus is a monotypic genus endemic to two areas of forest in SC Tanzania, the Southern Highlands and the Udzungwa Mts (Davenport 2005a, Jones *et al.* 2005, Davenport *et al.* 2006, 2008). The main characteristics are given in the profile for the Kipunji *Rungwecebus kipunji*. Initially described as belonging to the mangabey genus *Lophocebus* (Jones *et al.* 2005), molecular phylogenetic analyses demonstrate that *R. kipunji* is closer to *Papio* than to *Lophocebus*, *Theropithecus*, *Cercocebus* or *Mandrillus*. Morphological data revealed distinct differences from *Papio*, thus necessitating the description of

a new genus, *Rungwecebus* (Davenport *et al.* 2006). The validity of *Rungwecebus* was questioned (Ehardt & Butynski 2006b, C. P. Groves pers. comm. to von Buol 2006), but evidence from additional molecular markers support Kipunji's current taxonomic status (Olson *et al.* 2008). Zinner *et al.* (2009a) accepted that Kipunji does not belong within *Lophocebus*, but, based on an analysis of mitochondrial sequences from the individual studied by Davenport *et al.* (2006), raised the question of whether *Rungwecebus* is a sister taxon to, or a member of, *Papio*. Morphometric analyses of a subadult



Kipunji *Rungwecebus kipunji* adult.

skull, however, show that whilst possibly more similar to *Lophocebus* than to *Papio* (Gilbert *et al.* 2011), *Rungwecebus* is morphologically distinct from both (Singleton 2009). Burrell *et al.* (2009) suggest that *Rungwecebus* originated by hybridization between Yellow Baboon *Papio cynocephalus* ♀♀ and *Lophocebus* sp. ♂♂. More recently, Roberts *et al.* (2010) provided the first DNA sequences of *Rungwecebus* from Ndundulu, as well as two additional sequences from Mt Rungwe-Kitulo. These data result in consistent topologies with respect to the unique placement of *Rungwecebus* and also demonstrate, as originally suggested by Olson *et al.* (2008), that local introgression by *Papio* ♀♀ only in Rungwe-Kitulo, and not hybrid origin, explains mitochondrial DNA variation in *R. kipunji*.

Rungwecebus differs from *Lophocebus* in having a light to medium greyish-brown pelage, an off-white centre of ventrum and distal half of tail, and crown with long, broad, erect crest of hair. *Rungwecebus* usually holds its tail curved up and backward, but rarely vertical or arched forward. *Rungwecebus* gives a distinctive 'honk-bark' when conspecific groups meet (Jones *et al.* 2005) and when threatened. The 'honk-bark' bears some structural similarity to the *Papio* 'roar-grunt'. *Rungwecebus* does not emit the 'whoop-gobble' loud-call characteristic of *Lophocebus* and *Cercocebus*. *Rungwecebus* differs from *Papio*, *Theropithecus* and *Mandrillus* in lacking the long rostrum and deep mandibular fossae characteristic of these genera. *Rungwecebus* possesses deep suborbital fossae on the maxillae similar to *Lophocebus* and *Cercocebus*, but these are distinct from the deep maxillary fossae present on the rostrum of *Papio*, *Theropithecus* and *Mandrillus*. *Rungwecebus* is much smaller in body size and far more arboreal than *Papio*, *Theropithecus* and *Mandrillus* (Davenport *et al.* 2006).

Discovery and description of this new genus challenges some assumptions about papionine evolution. For example, the molecular data demonstrate that *Rungwecebus* evolved from a *Papio*-like ancestor (Davenport *et al.* 2006), thus casting doubt on the assumption that baboons became more successful by becoming less arboreal. Indeed, it would seem that successful terrestrial primates may have given rise to arboreal species. *Rungwecebus* implies support for the theory posed by Kingdon (1971) that African arboreal monkeys evolved from larger, less arboreal ancestors that resembled baboons. Alternatively

Rungwecebus might represent a stabilized hybrid between *Papio* and a now extinct ancestral *Lophocebus* (C. J. Jolly pers. comm.).

Another important question raised by the discovery of *Rungwecebus* centres on how the suborbital fossa is interpreted. In this respect, the superficial similarity with *Lophocebus* influenced the initial allocation of *kipunji* to the latter genus. It was subsequently revealed that the Kipunji's molecular profile is sufficiently different from *Lophocebus* to merit its separation as a new genus. Instead, *Rungwecebus* has proved to be genetically close to *Papio*, implying that suborbital fossae may simply be evolutionary artefacts deriving from phylogenetic reduction and retraction of mandibles under crania. If this is so, it raises the interesting possibility that extended muzzles in the separate ancestors of *Lophocebus*, *Cercocebus* and *Rungwecebus* shrank and migrated backwards, independently, in the three lineages. In each case J. Kingdon (pers. comm.) suggests derivation from long-faced, mainly terrestrial ancestors. He suggests that during favourable climatic periods in seasonal, non-forest habitats these terrestrial ancestors evolved an ecological strategy that was 'expansive' and relied on large groups ranging far and wide over varied landscapes (much as baboons do today). This is consistent with the evolution of multimale social systems where large, long-muzzled ♂♂ effectively diminish risk from both predation and competition.

The cercopithecine (guenon) radiation demonstrates that an intensive use of arboreal resources by a suite of smaller-bodied monkeys in smaller, more localized groups is generally easier to sustain in forests, where food is relatively scarce on the ground and smaller bodies are better suited to exploit varied vegetation, fruit and invertebrates in the canopy. Kingdon therefore argues that wherever and whenever climatic changes (and/or competitors) diminished the resources available to large groups of terrestrial foragers, their large ♂♂ and heavy, large muzzles became redundant as their expansive strategy ceases to be viable. During the climatic fluctuations of the early Pliocene (5 mya), diverse and widely scattered populations of large-muzzled papionines presumably faced this situation many times. Kingdon suggests that rapid selection for diminished muzzles might help explain the independent evolution of this feature in three lineages, with the evolution of *R. kipunji*, as a sister-group to *Papio*, presumably the most recent.

Great interest is also attached to the biogeography of *Rungwecebus*. The two localities in which *Rungwecebus* has been found can, with confidence, be described as vestiges of a formerly more extensive range. What cannot be determined at present is how wide-ranging this genus once was, nor when its distribution was more or most extensive. None the less, the occurrence of *Rungwecebus* east of a major biogeographic divide (the Somali-Kalahari Arid Corridor) suggests that *Rungwecebus* might have been essentially a south-eastern genus. Benefit (1999) shows that the fossil record makes a southern African origin for *Papio* (and probably most other long-faced papionines) likely. This is consistent also with the biogeography of other restricted-range faunal taxa with an epicentre in the Southern Highlands and a northern limit in the Udzungwas (Davenport 2004, 2005b). J. Kingdon (pers. comm.) agrees that the restriction of *Rungwecebus* to S Tanzania is consistent with isolation of an early *Papio* or *Papio*-like population in this formerly well-forested region. The vulnerability of *Rungwecebus* may therefore be partly connected with widespread deforestation but its precarious hold on existence might be influenced by its evolution before the arrival of arboreal *Cercopithecus* monkeys from western central Africa.

Tim R. B. Davenport

***Rungwecebus kipunji* KIPUNJI**

Fr. Kipunji; Ger. Kipunji

Rungwecebus kipunji (Ehardt, Butynski, Jones & Davenport, 2005). In: Jones, Ehardt, Butynski, Davenport, Mpunga, Machaga & De Luca. 2005. Science 308: 1162. Rungwe-Livingstone (09° 07' –09° 11' S; 33° 40' –33° 55' E), Southern Highlands, SW Tanzania.

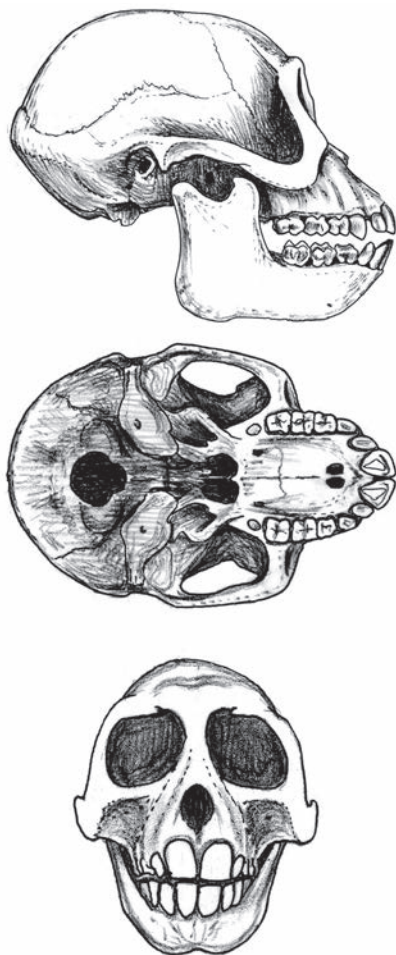


Kipunji *Rungwecebus kipunji* adult.

Taxonomy Monotypic species. Originally allocated to *Lophocebus* (Jones *et al.* 2005) based on the non-contrasting black eyelids and arboreal nature, but later placed in a new monotypic genus *Rungwecebus* (Davenport *et al.* 2006) on the basis of molecular and morphological data acquired from a voucher specimen. The genus to which the Kipunji belongs has been questioned (Ehardt & Butynski 2006b, C. P. Groves pers. comm. to von Buol 2006, Zinner *et al.* 2009a) but additional molecular evidence and morphometric analysis supports the phylogenetic position and taxonomic status of *Rungwecebus* (Olson *et al.* 2008, Burrell *et al.* 2009, Singleton, 2009, Roberts *et al.* 2010, Gilbert *et al.* 2011). Synonyms: none. Chromosome number: not known.

Description A mostly brown, medium-sized, long-tailed, arboreal monkey. Sexes similar in colour. Little sexual dimorphism;

adult ♀♀ estimated to be 90–95% the weight of adult ♂♂. No adult body weights available but estimates range 8–16 kg (T. Davenport pers. obs.). Facial skin, including eyelids, black. Muzzle bare, relatively elongated, black. Suborbital fossa pronounced. Eyes brown. Cheek-whiskers long, extending laterally and curving downward. Crown with prominent, long, broad, erect crest of dark greyish-brown hair. Shoulder mane (= mantle = cape) of adult ♂♂ variable in colour and length; typically of long, straight, cinnamon-brown hairs. Dorsum light to medium greyish-brown over distal half. Tail dusky-brown over proximal half and off-white with interspersed darker hairs over distal half. Tail pelage smooth, not shaggy or lax. Tail longer than HB. Forelimbs dark greyish-brown. Upper hindlimbs dark rufous-brown. Lower hindlimbs cinnamon. Hands and feet black. Ventrums off-white. Patch on upper chest that



Lateral, palatal and frontal views of skull of Kipunji *Rungwecebus kipunji* juvenile.

is close to cinnamon. Individual hairs long and straight, without banding or speckling (Davenport *et al.* 2006). Ischial callosities pink; fused in ♂ and unfused in ♀. Tail carried loosely and parallel to, or below, the plane of the back, curving downward to the level of the feet during locomotion. Tail not held arched over the back when standing, nor held vertically, except as a semi-prehensile support (Jones *et al.* 2005, Davenport *et al.* 2006). Infants less hirsute with a reddish tinge to pelage.

Geographic Variation Two isolated populations known, but no subspecies described. Ventrum off-white and sharply demarcated from the brown of rest of body in some Ndundulu Forest animals, but lighter and not sharply demarcated in Rungwe–Kitulo animals. Ndundulu animals seem less vocal than Rungwe–Kitulo counterparts.

Similar Species None that is sympatric or parapatric.

Distribution Afromontane–Afroalpine BZ. Endemic to S Tanzania; known only from two populations separated by ca. 350 km of largely non-forested land. One (fragmented) population occurs at 1750–2450 m in 12.4 km² of Rungwe–Kitulo Forest in the Southern Highlands of SW Tanzania (09° 07′–09° 11′ S, 33° 40′–33° 55′ E; Davenport *et al.* 2008). The Rungwe–Kitulo Forest includes Mt



Rungwecebus kipunji

Rungwe F. R. (150 km²) and Livingstone Forest (191 km²), which lies within Kitulo N. P. (412 km²) (Davenport & Bytebier 2004, Davenport *et al.* 2008). Mt Rungwe F. R. and Livingstone Forest are connected by the Bujingijila Corridor, a narrow (<2 km wide) swathe of degraded and encroached-upon forest. *Rungwecebus kipunji* inhabits the wetter forest of south Mt Rungwe and isolated groups are scattered in the north and south of Livingstone Forest (Davenport 2005a, 2006b, Jones *et al.* 2005, Davenport *et al.* 2006, 2008). Area of occupancy in Mt Rungwe and Livingstone Forest is 6.72 and 4.08 km², respectively. Extent of occurrence in Mt Rungwe and Livingstone is 8.15 and 4.25 km², respectively. Anecdotal evidence from interviews points to the historic presence of *R. kipunji* in other Southern Highland forests, though this is unconfirmed, and recent extensive searches have found no new subpopulations in other forests (Davenport *et al.* 2008).

The other population of *R. kipunji* ranges 1300–1750 m in altitude in the Vikongwa Valley, Ndundulu Forest (07° 40′–07° 51′ S, 35° 10′–36° 50′ E; ca. 180 km of closed forest), in the Kilombero Nature Reserve in the Udzungwa Mts, S Tanzania (Jones *et al.* 2005). The area of occupancy of *R. kipunji* in the Ndundulu Forest is 1.98 km² and the extent of occurrence 5.28 km² (Davenport *et al.* 2008). Research to date in Ndundulu Forest, and the lack of independent knowledge of the species among local villagers, indicate that *R. kipunji* is absent from large parts of this forest (Jones 2006, Davenport *et al.* 2008).

Habitat Habitat ranges from degraded montane and upper montane forest from 1350–2450 m in Rungwe–Kitulo, to pristine submontane forest from 1300–1750 m in Ndundulu (Davenport *et al.* 2006, 2008, 2010). In Rungwe–Kitulo the canopy is often broken and at 10–30 m with emergents to 35 m. *Rungwecebus kipunji* prefers steep-sided gullies and valley edges, and is often found near streams (T. Davenport, N. Mpunga & S. Machaga pers. obs.). Ridges and open areas are usually avoided. The most common trees in

Rungwe–Kitulo include *Agauria salicifolia*, *Allophylus chaunostachys*, *Aphloia theiformis*, *Bersama abyssinica*, *Casearia battiscombei*, *Cassipourea gummiflua*, *Cassipourea malosana*, *Chrysophyllum gorungosanum*, *Clausena anisata*, *Cornus volkensii*, *Diospyros whyteana*, *Ekebergia capensis*, *Ficalhoa laurifolia*, *Ficus sur*, *Ficus thonningii*, *Garcinia buehneri*, *Hagenia abyssinica*, *Macaranga capensis*, *Macaranga kilimandscharica*, *Maesa lanceolata*, *Maytenus acuminata*, *Neoboutonia macrocalyx*, *Nuxia congata*, *Olinia rochetiana*, *Peddiea fischeri*, *Syzygium guineense*, *Tabernaemontana angolensis*, *Trichocladus ellipticus*. The numbers of *Albizia gummifera*, *C. battiscombei*, *Entandrophragma* sp., *M. kilimandscharica*, *Ocotea usambarensis*, *Olea capensis*, *Parinari excelsa*, *Podocarpus latifolius* and *Prunus africana* have all been greatly reduced by logging (Lovett 1986, McKone & Walzem 1994, Davenport 2005b, 2006a). Thick undergrowth is typical, with the tree fern *Cyathea manniana*, wild banana *Ensete ventricosum* and large stands of bamboo *Sinarundinaria alpina* common in the south and south-east of Mt Rungwe and in the north-west of Livingstone (T. Davenport pers. obs.). *Rungwecebus kipunji* rarely frequents the bamboo, and leaves the forest only to raid nearby crops (see below), especially in Feb–Apr (T. Davenport, N. Mpunga & S. Machaga pers. obs.). In areas inhabited by *R. kipunji*, annual rainfall ca. 1850–2500 mm (T. Davenport pers. obs.). Mean annual rainfall from 1968–2008 was 2133 mm. Wet season is Nov–May and dry (colder) season is Jun–Oct (Davenport *et al.* 2010).

In Ndundulu, the primary *P. excelsa*-dominant forest is undisturbed and the canopy is unbroken, reaching a height of 40–50 m with emergents to 60 m (Jones 2006). Other trees (and shrubs) present include *B. abyssinica*, *C. gummiflua*, *Cola stelecantha*, *Craterospermum longipedunculatum*, *Dicranolepis usambarica*, *Ixora scheffleri*, *Myrianthus* sp., *Oxyanthus speciosus*, *Polyscias fulva*, *Psychotria* sp., *Strombosia scheffleri*, *Strychnos* sp., *Tarenna pavettoides*, *Tarenna quadrangularis*, *Uvariopsis* sp., *Vitex amaniensis* and *Zanthoxylum gillettii* (Ehardt & Butynski 2006b).

Abundance Following 2864 h of surveys, 772 h of simultaneous multi-group observational monitoring events and 209 group counts, the total *R. kipunji* population is estimated to be 1117 animals in 38 groups. Of these, 1042 individuals are estimated to occur in Rungwe–Kitulo in 34 groups, and 75 individuals in Ndundulu in four groups. Initial density estimates are 83.9 ind/km² in Rungwe–Kitulo, and 14.2 ind/km² in Ndundulu, with the total species density, excluding home-range overlaps, being 63.1 ind/km² (Davenport *et al.* 2008).

Adaptations Diurnal and arboreal, mainly >10 m above the ground, although occasional feeding on the ground observed in both populations. Moves to ground to cross degraded forest patches and to avoid intra-group conflict and predators (Davenport *et al.* 2006). Tolerant of low temperatures; temperatures in parts of Rungwe–Kitulo can drop to –3 °C during Jun–Aug. Sleep high (usually >30 m) in branches of trees such as *B. abyssinica*, *H. abyssinica*, *M. lanceolata* and *S. guineense*. Typically rests in the middle of the day for 30–60 min. Most active 08:00–11:30h and 15:00–18:00h (T. Davenport, N. Mpunga, D. De Luca & S. Machaga pers. obs.). Able to open large, hard fruits and break dead wood in search of grubs.

Foraging and Food Omnivorous. Groups in Rungwe–Kitulo travel a mean of 1.29 km/day (S.E. = 0.15, 0.99–1.71, n = 235

days) (De Luca *et al.* 2009) and group members usually remain within 300 m of each other, except when disturbed (T. Davenport, D. De Luca, N. Mpunga, S. Machaga & C. Bracebridge pers. obs.). Using fixed kernel density, estimation calculated using the ‘reference’ method as a smoothing parameter, mean home-range size of *R. kipunji* in Mt Rungwe is 3.06 km² (S.E. = 0.67, 1.16–4.30, n = 4 groups) (De Luca *et al.* 2009).

During 9498 h of observation of 34 groups in the Southern Highlands, 122 food plants were recorded from 60 families (64 tree species, 30 herbs, 9 climbers, 7 shrubs, 6 liana, 3 grasses and 3 ferns). Diet comprised mature leaves (22%), unripe fruits (14%), ripe fruits (13%), young leaves (12%), bark (11%), stalks (9%), flowers (9%), pith (7%), insects (2%) and seed pods, rhizomes, shoots, tubers, epiphytes, ground herbs, climbers, moss, fungi and lichen (2%). Soil eaten on two occasions. Raids maize, bean, pea, sweet potato and banana fields, and granaries if close to the forest edge. Most frequently eaten plant was *M. capensis*. Other commonly eaten plants were *Ilex mitis*, *Psydrax parviflora*, *C. gorungosanum*, *B. abyssinica*, *Myrianthus holstii*, *Tabernaemontana stapfiana*, *Landolphia buehneri*, *Ureia hypselodendron*, *T. pavettoides*, *C. gummiflua*, *Allophylus abyssinicus*, *P. excelsa*, *Entandrophragma excelsum*, *F. thonningii*, *P. fulva* and *Multidentia crassa*. *Kipunji* appears to be more folivorous during the dry season and more frugivorous during the wet season (Davenport *et al.* 2010, Bracebridge *et al.* 2012). Most foraging occurs in early morning and late afternoon (Davenport *et al.* 2006).

Social and Reproductive Behaviour Social. Not territorial (De Luca *et al.* 2009). Groups comprise several adult ♂♂ and several adult ♀♀. Size estimates for Rungwe–Kitulo groups 25–39 ind/group (mean 30.6, S.E. = 0.62, n = 34) and in Ndundulu from 15 to 25 ind/group (mean 18.8, S.E. = 2.39, n = 4). For *R. kipunji* as a whole, groups number 15–39 animals (mean 29.4, S.E. = 0.85, n = 38; Davenport *et al.* 2008). In 34 groups closely observed in Rungwe–Kitulo, there was a maximum of two clinging infants/group (Davenport *et al.* 2008). There is no evidence that solitary animals occur (Davenport *et al.* 2006). In Rungwe–Kitulo groups form polyspecific associations with Peter’s Angola Colobus *Colobus angolensis palliatus* and Sykes’s Monkey *Cercopithecus mitis*, especially early in the morning and late in the afternoon, and the three species often sleep in neighbouring trees (Davenport *et al.* 2006). *Rungwecebus kipunji* groups at Ndundulu form polyspecific associations with *C. a. palliatus*, *C. mitis* and Udzungwa Red Colobus *Procolobus gordonorum* (Davenport *et al.* 2005, 2006).

Four copulations observed in Rungwe–Kitulo in late Sep. One pair moved ca. 200 m from the main group, copulated twice in 10 min and again after a further 45 min. No ♀ post-copulatory vocalizations heard. Copulation lasted 3–7 sec (T. Davenport, N. Mpunga & S. Machaga pers. obs.). Infants carried beneath ♀. Instances of ‘kidnapping’ observed in Ndundulu accompanied by loud screams, a chase and one animal falling to the ground (T. Davenport & T. Jones pers. obs.) and in Mt Rungwe (C. Bracebridge pers. comm.). Grooming observed most often in early afternoons. Oestrous ♀♀ often groomed by young ♂♂, though female–female, female–male, and adult–juvenile grooming also observed (T. Davenport, T. Jones, N. Mpunga, C. Bracebridge & R. Starkey pers. obs.).

Inter-group territorial displays occur where ranges overlap. Disputes often highly vocal in Rungwe–Kitulo, usually involving

adult ♂♂, but sometimes ♀♀ and juveniles also calling. No inter-group physical contact observed in over 772 h of direct observation (Davenport *et al.* 2008).

In the Rungwe–Kitulo population adult ♂♂ emit a distinctive, loud, low-pitched ‘honk-bark’, most evident when conspecific groups meet, and when threatened or disturbed (Jones *et al.* 2005). Adult ♀♀ also give this call but less often than adult ♂♂ (T. Davenport pers. obs.). Honk-barks can be heard by the human ear to 1 km and are used as a group-spacing mechanism. Honk-barks given throughout the day but most often in early morning and late afternoon. A call similar to the honk-bark has been heard at Ndundulu but this remains unanalysed (T. Jones pers. comm.). The characteristic ‘whoop-gobble’ of *Lophocebus* and *Cercocebus* mangabeys (Waser 1977b) is not known in *R. kipunji*. The honk-bark is qualitatively and quantifiably different from the whoop-gobble (Jones *et al.* 2005) and exhibits some structural congruence to the ‘roar-grunt’ of *Papio* (Davenport *et al.* 2006). At least six other call types have been identified (T. Davenport, C. Bracebridge & T. Jones pers. obs.). Contact ‘grunts’ given. High-pitched, sharp ‘chirrup’ given in alarm at African Crowned Eagles *Stephanoaetus coronatus*. ‘Screams’ given during intra-group agonistic encounters (Davenport *et al.* 2005). ‘Chutters’ emitted within groups when foraging. High-pitched ‘squeals’ also given (Davenport *et al.* 2005, Ehardt & Butynski 2006b).

Reproduction and Population Structure Genital swelling in oestrous ♀♀. Singletons born ($n = >38$). Twins not observed. No evidence of a birth season, with infants born throughout the year (T. Davenport & N. Mpunga pers. obs.).

Predators, Parasites and Diseases Main predators are African Crowned Eagles and humans (Davenport 2005a). On seeing an eagle, adult *R. kipunji* emit a series of alarm ‘chirrup’ (N. Mpunga & T. Davenport pers. obs.) that can last up to 15 min (Ehardt & Butynski 2006b). On hearing an eagle, individuals drop into thick vegetation and the entire group is silent. When the eagle has passed, the *R. kipunji* emit a few low ‘grunts’, although they do not move immediately, on one occasion remaining still for a further 14 min. Hunted by humans but primarily as retribution for crop-raiding and as a by-catch when hunting *C. mitis*. No longer targeted for meat as was once the case (Davenport *et al.* 2006). *Rungwecebus kipunji* emits one or several loud, sharp, alarm ‘chirrup’ on seeing a human (T. Davenport & T. Jones pers. obs.) and there is an accompanying vigorous head shake directed towards the threat (Davenport 2005a). One or two subadults often act as sentinels, watching the threat and diverting it by lagging behind as the main group escapes. Sentinels can become separated from the group by >500 m in such instances (T. Davenport, N. Mpunga & S. Machaga pers. obs.). Leopards *Panthera pardus* also eat primates in the Southern Highlands (D. De Luca & N. Mpunga pers. comm.) and probably take *R. kipunji* in both Rungwe–Kitulo and Ndundulu.

Conservation IUCN Category (2012): Critically Endangered. CITES (2012): Appendix II.

Known world population fragmented and comprised of ca. 1117 individuals over an area of ca. 20 km² (Davenport *et al.* 2008). *Rungwecebus kipunji* is among Africa’s most threatened animals (Davenport *et al.* 2008, Davenport 2009) and one of the world’s 25

most threatened primates (Ehardt *et al.* 2007, Davenport *et al.* 2009). The threats to *R. kipunji* are considerable. The Rungwe–Kitulo forests are severely degraded; logging, charcoal-making, illegal hunting and unmanaged resource extraction are common (Davenport 2003, 2005b, 2006a, Machaga *et al.* 2005). The narrow Bujingijila Corridor linking Mt Rungwe to Livingstone Forest, and the corridors joining the northern and southern sections of Livingstone, are encroached by farmers and degraded (Davenport 2005b). Without immediate conservation intervention these forests will be fragmented, resulting in isolated *R. kipunji* subpopulations some of which are unlikely to be viable over the long-term (Davenport *et al.* 2008). Protecting these corridors is of the highest priority for the conservation of this genus/species (Bracebridge *et al.* 2011, De Jong & Butynski 2012). *Rungwecebus kipunji* is hunted by local people, especially on farms. The more disturbed the forest is, the more this happens (Davenport *et al.* 2006). Mount Rungwe, while nominally a Forest Reserve, remains largely unmanaged and unprotected, although it was upgraded to Nature Reserve status in June 2009 (T. Davenport pers. obs.). The smaller Livingstone Forest population is within Kitulo N. P. but swift and effective conservation action is needed in both areas.

Although Ndundulu Forest is in excellent condition, and largely undisturbed, *R. kipunji* is present in very low numbers. The reasons for this are unclear and whether this population is viable in the long-term is debatable (Davenport & Jones 2005, Davenport *et al.* 2008). It is hoped that the gazettelement in August 2007 of Kilombero Nature Reserve incorporating Matundu, Iyondo and West Kilombero Scarp Forest Reserves, will serve to further protect *R. kipunji* in Ndundulu. The forests of the Southern Highlands and of the Udzungwas Mts are rich in endemic and threatened taxa of plants and animals (Rodgers & Homewood 1982, Fjeldså & Lovett 1997, Davenport 2002, 2003, 2004, 2005b, 2009, Burgess *et al.* 2004a, 2007, Davenport & Bytebier 2004, Rovero & De Luca 2007). Within the Udzungwa Mts, the Ndundulu Forest is especially important for the long-term survival not only of *R. kipunji* but also of several taxa that are either endemic to the Udzungwas, or to the Udzungwas and one or more nearby montane forests. These include the ‘Endangered’ Udzungwa Forest-partridge *Xenoperdix udzungwensis* (a monotypic genus endemic to the region), the ‘Vulnerable’ Rufous-winged Sunbird *Nectarina rufipennis*, the ‘Vulnerable’ Udzungwa Red Colobus, the recently discovered Phillips’s Congo Shrew *Congosorex phillipsorum* (Stanley *et al.* 2005) and Grey-faced Giant Sengi *Rhynchocyon udzungwensis* (Rovero *et al.* 2008). Ndundulu is the only known site in Tanzania for the Cassin’s Hawk-eagle *Spizaetus africanus* (Jones 2007). As the largest, most charismatic and rarest of these species, *R. kipunji* is now serving as a ‘flagship’ genus/species for the enhanced conservation of the biodiversity both of the Udzungwa Mts and the Southern Highlands (Davenport *et al.* 2005, Davenport 2006b, Jones 2006, von Buol 2006).

The presence of *R. kipunji* in both sites further supports the notion that the Southern Highlands are zoologically more aligned to the Eastern Arc Mts than has usually been thought (Davenport 2004, 2005b, Carleton & Stanley 2005, Davenport & Jones 2005, Davenport *et al.* 2006) and that both regions remain refugia for relict populations of ancient lineages whose closest relatives are geographically very distant (Fjeldså & Lovett 1997, Davenport 2004, Stanley *et al.* 2005).

Measurements

Rungwecebus kipunji

No adult body measurements available. HB of adult ♂ estimated at 850–900 mm. WT of adult ♂ estimated at 10–16 kg (Jones *et al.* 2005). Measurements of one subadult ♂: HB 370 mm; T 499 mm; HF 128 mm; E 35 mm; WT ca. 4.0 kg; GLS 96 mm; GWS 66 mm (Davenport *et al.* 2006).

Key References Davenport 2005a; Davenport *et al.* 2005, 2006, 2008, 2009; Davenport & Jones, 2008; Ehardt & Butynski 2006b; Jones *et al.* 2005.

Tim R. B. Davenport & Thomas M. Butynski

GENUS *Papio*

Baboons

Papio Erxleben, 1777. Systema Regni Animalis, 1, Mammalia, 15.



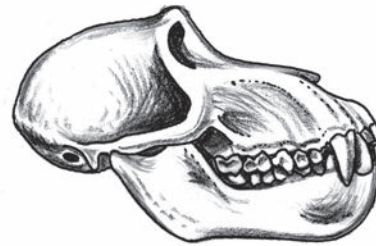
Olive Baboon *Papio anubis* adult male.

Papio is a polytypic genus endemic to sub-Saharan Africa and Arabia. This account follows Groves (2001, 2005c) and Grubb *et al.* (2003) in recognizing five extant species of *Papio*: Hamadryas Baboon *Papio hamadryas*, Yellow Baboon *Papio cynocephalus*, Chacma Baboon *Papio ursinus*, Olive Baboon *Papio anubis* and Guinea Baboon *Papio papio*. Collectively, their non-overlapping but often contiguous ranges occupy most of Africa south of the Sahara (from sea level to >3300 m), in any habitat, from evergreen forest to semi-desert, that affords food, a night refuge on rock faces or in tall trees, and surface water. *Papio* baboons are, however, notably absent from western central African rainforest areas occupied by Mandrills *Mandrillus sphinx* or Drills *Mandrillus leucophaeus*, and from the central Congo Basin.

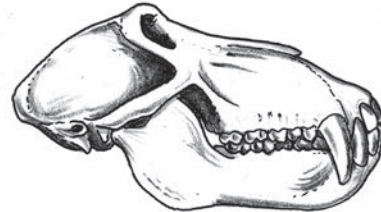
Papio exhibits the distinctive features of cercopithecine and papionin monkeys (e.g. buccal pouches, dental traits). They are distinguished from their closest relatives, the other African papionins (*Mandrillus*, Kipunji *Rungwecebus kipunji*, drill-mangabeys *Cercocebus* spp. and, especially, Geladas *Theropithecus gelada* and baboon-mangabeys *Lophocebus* spp.) by the following combination of features, some of which are probably ancestral for the African papionin clade: size large (adult ♂ >14 kg, >20 kg in most populations); muzzle prominent, defined by marked concavity of the ante-orbital

profile, but lacking prominent, longitudinal bosses; suborbital fossa moderate or absent; tail subequal to head and body, neither long and muscular nor extremely reduced; molar teeth not unusually high-crowned or complex; ♀ periovulatory swelling anogenital. Details of postcranial structure show distinct but not extreme adaptations to terrestrial digitigrade posture and locomotion.

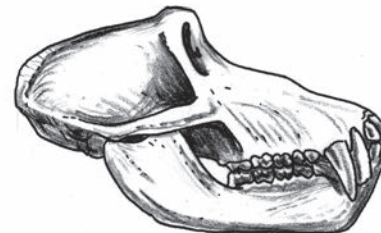
Papio spp. are justly renowned for their ecological eclecticism and adaptability, reflected in their present-day wide geographical range



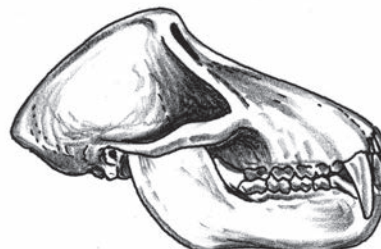
Hamadryas Baboon
Papio hamadryas



Olive Baboon *Papio anubis*



Yellow Baboon
Papio cynocephalus



Chacma Baboon *Papio ursinus*

Skulls of four baboon *Papio* species.

and habitat diversity. The ecological diversity of the genus makes it especially amenable to studies of the interaction between habitat and behaviour – especially social behaviour (e.g. Hill & Dunbar 2002). Most inter-population differences in physique and physiology, however, are not obviously related to ecological adaptation. The one major exception is *P. hamadryas*, whose social system, and correlated features of pelage, development and physiology, can be seen as adapted to the semi-arid environments.

Genetic and palaeontological information suggest that the last common ancestor of the extant *Papio* clade lived in southern Africa ca. 2 mya (Delson 1988, Wildman *et al.* 2004, Burrell *et al.* 2009, Zinner *et al.* 2009b). Baboons seem to have spread rapidly from this base during the Pleistocene, presumably diversifying as their range was dissected by climatically driven changes in habitat distribution. Until the late Pleistocene, however, *Papio* is far rarer in the fossil record than its close relative *Theropithecus*, which is now reduced to a single, relict species. As the species accounts indicate, some populations of *Papio* have been studied in depth for more than 30 years, but these studies divulge but a small fraction of the variation within this ecologically diverse genus. The natural history and behaviour of other populations, including the widespread and distinct Kinda Baboon (regarded here as a subspecies of the Yellow Baboon *P. c. kindae*, but see Zinner *et al.* 2011), remain largely undocumented.

Though the main outlines of intra-generic diversity of *Papio* are relatively clear, the taxonomy of *Papio* is disputed, largely because of conflicting species definitions. Diagnosable geographical 'forms' within the genus have parapatric ranges, and most, perhaps all, interbreed at their boundaries, forming hybrid zones (Jolly 1993, Kingdon 1997). Thus, they might be distinguished as full (phylogenetic) species, or regarded as subspecies of a single, polytypic (biological) species (*Papio hamadryas*) (Jolly 1993, Sarmiento 1998a, b, Groves 2001, Frost *et al.*

2003). The five-species solution, adopted here, is a practical compromise that groups forms of generally similar external appearance. Another configuration, less defensible but commonly adopted (e.g. Smuts *et al.* 1987), separates *P. hamadryas* ('the Desert Baboon') as a distinct species, but groups all others ('the Savanna Baboons') as subspecies of a single species, *P. cynocephalus*. The latter taxon, however, appears not to be monophyletic, and the implication of an ecological and behavioural dichotomy is overly simplistic and even misleading. Regardless of the taxonomy used to express it, diversity within the genus *Papio* includes features hinting at a complex evolutionary history. *Papio papio*, for example, exhibits physical and behavioural traits (Jolly & Phillips-Conroy 2006) that ally it most closely with the *P. hamadryas*, from which it is currently separated by at least 5500 km of *P. anubis* range. Genetic information suggests a history that includes deep genetic introgression between species ('mitochondrial capture'), and possibly the formation of species by hybridization (Wildman *et al.* 2004, Burrell 2009, Zinner *et al.* 2009a, b, Keller *et al.* 2010, Zinner *et al.* 2011).

The species (and subspecies) within the genus *Papio* are identified primarily by the colour and texture of the pelage (Hill 1970, Jolly 1993, Rowe 1996, Kingdon 1997, Groves 2001). Besides overall colour, important diagnostic features are the extent of development, if any, of a mane (= cape = mantle) of waved hair over the forequarters, or of a fringe of long, straight hairs on the trunk and nape; the extent to which pelage of the cheeks contrasts in colour and/or length with that of the crown; the presence/absence of contrastingly lighter ventral pelage; and the facial profile, especially the projection of the nose. All these diagnostic features are most fully developed in adult ♂♂.

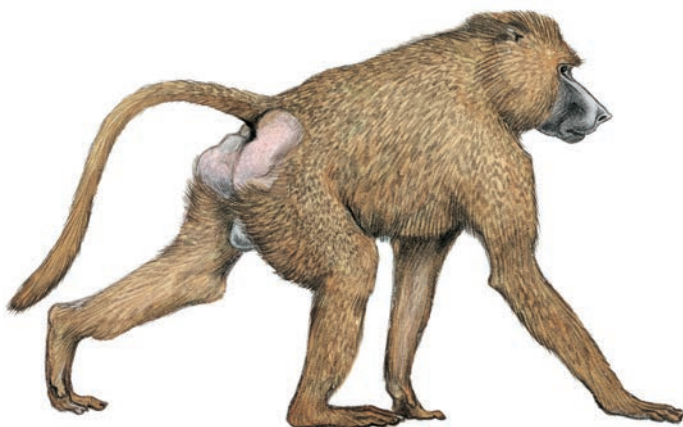
Clifford J. Jolly

Papio papio GUINEA BABOON

Fr. Babouin de Guinée; Ger. Guinea-Pavian

Papio papio (Desmarest, 1820). Encyclopédie Méthodique, Mammalogie 1: 69. 'Coast of Guinea'.

Taxonomy Monotypic species. Individuals of appearance intermediate between *Papio papio* and Olive Baboon *Papio anubis*



Guinea Baboon *Papio papio* adult male.

occur in Mali (Pollock in Sharman 1981) but little is known about this hybrid zone (Sarmiento 1998a). See molecular information in Zinner *et al.* (2011). Synonyms: *olivaceus*, *rubescens*, *sphinx*. Chromosome number: 2n = 42 (Romagno 2001).

Description Medium sized, uniformly grizzled reddish-brown baboon. Female like ♂, but smaller, with barely half the body weight of the ♂. Face dark pinkish-purple. Male with distinct mane (= cape = mane) on shoulders. Tail arched; not 'kinked' or 'broken'. Perineum varies from bluish-grey to mottled. Female has largest oestrous swelling of any monkey. Pelage changes from black to brown, skin from pink to black, by seven months of age. Whitish individuals (albinos?) occur (Dupuy & Gaillard 1970, A. Galat-Luong pers. obs.).

Geographic Variation None recorded.

Similar Species

Papio anubis. Closely adjoining and probably parapatric range in Mali and perhaps Guinea. Said to be sympatric in Sierra Leone (T. S.

Jones in Booth 1958b). Larger, with darker, greyish-brown pelage; mane of adult ♂ less pronounced; tail 'broken'.

Distribution Endemic to West Africa. Sudan Savanna and Northern Rainforest–Savanna Mosaic BZs. Atlantic coast eastwards to ca. 12°W, ca. 11–18°N.

Historical Distribution Booth (1958b) set the historic northern limit in Mauritania, whereas Dupuy (1971) set the north-western limit at St Louis and Podor, Senegal. One ecological limit is the absence of broad-leaved trees and the dominance of *Acacia nilotica* (A. Galat-Luong pers. obs.). Northern limit has moved south due to decreasing rainfall (Verschuren 1982). Some fragmented populations may still occur in Casamance, Senegal (13°05'N, 16°20'W; Galat-Luong *et al.* 2006). Tahiri-Zagret (1976) noted that the Edinburgh Zoo, UK, received two *P. papio* from Ghana and speculated about the presence of the two species in Côte d'Ivoire. There are, however, no confirmed records for Ghana and G. Galat & A. Galat-Luong (pers. obs.) only found *P. anubis* in Côte d'Ivoire during nine years of fieldwork.

Current Distribution S Mauritania south-east through Senegal, Gambia, Mali, Guinea-Bissau, Guinea into Sierra Leone; an area of >200,000 km². Range of reintroduced individuals in Saloum, Senegal, is expanding (G. Galat & A. Galat-Luong pers. obs.).

Habitat In all types of savannas. Preferred habitats include Sudanese shrubby wooded savannas and sub-Guinean mosaic woodlands (400–1200 mm annual rainfall). In Niokolo Koba N. P., Senegal, a representative area of the preferred habitat, time spent in scrub about 40%, in open woodland 29%, in forest 21%, in grass 6%, in bush 4% and in gallery forest <1% (Sharman 1981). Of 506 group encounters in this area, 49% were in shrubby savanna, 35% in tree savanna, 8% in bamboo, 4% in open grassland, 2% in Ronier Palm *Borassus aethiopium* areas and 2% in forest (G. Galat & A. Galat-Luong pers. obs.). Also found in Sahelian steppe (200–400 mm annual rainfall) and, in the southern part of its distribution, in secondary high forest (1200–1400 mm annual rainfall). Will enter mangrove swamps (Galat-Luong *et al.* 2006). Not found in Sahelian acacia forests. Guinea Baboons present at altitudes from 0 to >1000 m (Fouta Djallon, Guinea) and over the temperature range ca. 20–50°C. In Niokolo Koba N. P. they sleep in tall trees, including *Ceiba pentandra* (85% of the sleeping trees, n = 52), *Cola cordifolia*, *Erythrophleum suaveolens*, *Azelia africana* (Sharman 1981), *Anogeissus leiocarpus*, *Antiaris africana* (Ndiaye 1983) and *B. aethiopium*, near stream beds or on branches overhanging rivers (Sharman 1981, Adie *et al.* 1997). The same sleeping sites are often used (92 of 133 observation nights; Anderson & McGrew 1984). Daytime sleeping sites are located in the shadow of large trees, thickets, cliffs and caves (A. Galat-Luong pers. obs.). Guinea Baboons require surface water and typically drink at least once per day.

Abundance In Niokolo Koba N. P., Sharman (1981) estimated 5.5–8.7 ind/km² (n = 2 groups), Verschuren (1982), Galat *et al.* (1998a, b) 6.3 ind/km² in 1990–93 (n = 305 group encounters), and 7.3 ind/km² in 1994–98 (n = 237 group encounters), while the densities of the ungulates were decreasing. In this National Park, density near water was higher, up to 19 ind/km² (n = 365 group



encounters; Lavocat 1997). In Upper Niger N. P., Guinea, Touré *et al.* (1997) estimated 46 ind/km². Verschuren (1982) estimated 100,000 Guinea Baboons for an 8000 km² area (12.5 ind/km²) in Senegal that included Niokolo Koba N. P. He rejected estimations of 200,000–300,000 baboons made for this same area in 1977.

Adaptations Diurnal and semi-terrestrial. In Senegal, although water is still available at the end of the dry season in river beds, Guinea Baboons (and Robust Chimpanzees *Pan troglodytes*) dig holes in sand near stagnant, putrid water. Thus, they drink sand-filtered water, cleaned of pathogenic microbes (Galat-Luong & Galat 2000).

Foraging and Food Omnivorous. In Niokolo Koba N. P., Guinea Baboons spend 24% of time feeding and 37% of time moving (Sharman 1981). Locomotion and feeding peaks occur 09:00–11:30h and 15:30–18:00h (Boese 1973). Water pool use showed two peaks, 07:00–10:00h and 16:00–18:00h (Galat *et al.* 1997, Lavocat 1997). Moving also occurs during two periods, 08:00–09:00h and 16:00–17:00h (Galat *et al.* 1997). In Niokolo Koba N. P. they feed on fruits (60% of feeding records), mainly of *Adamsonia digitata*, *Saba senegalensis*, *Lannea acida*, *Vitex madiensis*, *Spondias mombin* and *B. aethiopicus*. Also eaten are the shoots of *Oxytenanthera abyssinica*, seeds (17% of *B. aethiopicus* and *Combretum* spp.), various parts of *C. pentandra*, as well as buds, flowers, new leaves, roots, fungi, invertebrates, eggs and small vertebrates (n = 2024 feeding records, 58 food species; Sharman 1981). Other foods include the fruits of *Mangifera indica*, *Parkia biglobosa*, *Borassus flabellifer*, *Parinari macrophylla* and *Bombax costatum* (Ndiaye 1983), and the flowers of *Mitragyna inermis* and leaves of *Andropogon* sp. (Lavocat 1997). Feed on floating water plants while wading in the Gambia R. (A. Galat-Luong pers. obs.).

Guinea Baboons open termitariums of *Cubitermes* sp., roll over laterite boulders (Fady 1972, Sharman 1981, A. Galat-Luong pers.

obs.), and follow fire in order to catch invertebrates and small vertebrates to eat (Ndiaye 1983, A. Galat-Luong pers. obs.). They 'fish' for oysters *Etheria* sp. (Ndiaye 1983); also feed on grasshoppers and Agama Lizards *Agama agama*; occasionally hunt Scrub Hares *Lepus saxatilis*, Bushbucks *Tragelaphus scriptus* and Red-flanked Duikers *Cephalophus rufilatus* (McGrew *et al.* 1978, Sharman 1981). Guinea Baboons enter mangrove swamps to feed on Fiddler Crabs *Uca tangeri* (A. Galat-Luong pers. obs.), raid crops, steal stored grain in villages and food left out at field camps. Local people say Guinea Baboons feed on the rumen and the intestines of recently dead cattle. They dig in the ground to reach salt (A. Galat-Luong pers. obs.). Day range is 4–13 km (mean 8, $n = 49$; Sharman 1981). Home-ranges of two neighbouring groups were 19 km² and 43 km², with 9 km² overlap (Sharman 1981).

Social and Reproductive Behaviour Social. In Niokolo Koba N. P., Guinea Baboons show a multi-level group structure (Galat-Luong *et al.* 2006). First-level social unit is a 'one-male unit' (OMU) (Stammbach 1987), which is probably a matrilineal kin group (Sharman 1981). The OMU is best seen during feeding, foraging and sleeping periods. While moving, OMUs are led by an adult ♂. While resting, a subadult ♂ assumes vigilance (Boese 1973).

OMUs (Boese 1973) join with larger subgroups (second-level subgroups) to form a 'troop' before they begin to move or while sleeping at night (A. Galat-Luong pers. obs.). Multimale troops (Dunbar & Nathan 1972, Boese 1975) move in long columns (Bert *et al.* 1967a, b, Boese 1973) where the OMU (Boese 1973) and the second-level subgroups are still identifiable (A. Galat-Luong pers. obs.). Juveniles occasionally move from one OMU to another within these larger subgroups. At night the second-level subgroups sleep separately (Anderson & McGrew 1984) or together (Dunbar 1972). Several troops may join forming sleeping aggregations (Sharman 1981). In Niokolo Koba N. P. mean size of troops varies with climatic conditions between years (Boese *et al.* 1982). Mean number of instantaneously visible individuals in groups changes: 14 in 1990, 15 in 1991, 10 in 1992, 6 in 1993, 9 in 1994, 8 in 1995, 11 in 1998 ($n = 539$ group encounters, same transects, Feb.) (G. Galat & A. Galat-Luong pers. obs.). Size of troops declines in the dry season (50–90 individuals, $n = 2$ troops) and increases during the wet season (135–250 individuals, $n = 2$ troops; Sharman 1981). Mean number of visible individuals in groups also varies with time of day: 8 at 07:00h, 12 at 08:00–11:00h, 15 at 17:00h, 8 at 18:00h ($n = 96$ group encounters; G. Galat & A. Galat-Luong pers. obs.).

In Niokolo Koba N. P. mean sizes of the different categories of groups are:

First-level social unit: mean ca. 8 individuals (1 adult ♂, 3–4 adult ♀ and their young; Dekeyser 1956); 10 individuals (3–23, $n = 30$, 1 adult ♂, 3 adult ♀, 1 subadult ♂, 3 juveniles and 3 infants; Boese 1973).

Second-level moving and day rest subgroups: mean 19 individuals (5–65, $n = 45$; Galat-Luong *et al.* 2006), second-level sleeping subgroups median 20–24 individuals (8–65, $n = 92$; Anderson & McGrew 1984).

Third-level troops: mean 64 individuals (10–200, $n = 10$; Boese 1973); 193 individuals (135–250, $n = 2$; median = 55 individuals, $n = 16$;

Sharman 1981); 91 individuals (13–223, $n = 19$; Boese *et al.* 1982); 100 individuals (63–122, $n = 3$; Galat *et al.* 1998a, b); 62 individuals (22–249, $n = 111$; Galat-Luong *et al.* 2006).

To the south-east outside the Niokolo Koba N. P. group size is 72 individuals (24–200, $n = 14$; Galat-Luong *et al.* 2006); to the west (Saloum), 51 individuals (30–80, $n = 7$; A. Galat-Luong pers. obs.). In Upper Niger N. P. the distribution of group size was: 1–20 individuals, 20%; 21–50, 27%; 51–100, 47%; >100, 7% ($n = 871$ individuals; Touré *et al.* 1997). Sleeping aggregations number up to 630 individuals (Sharman 1981).

Separate behaviours described total 35: seven friendly, five agonistic, six sexual, six subgroup-specific, 11 mother–infant relations (Boese 1973). 'Noisy branch shaking', for example in Ronier Palms, and 'prancing' are frequent during agonistic displays. 'Kick press', recorded in captivity, has not been seen in the wild (Boese 1973). Spacing behaviour described (Boese 1973); territorial behaviour not observed. Guinea Baboons spend 19% of their time in social activities and 21% resting (Sharman 1981). Inter-subgroup herding (Galat-Luong *et al.* 2006) and intra-subgroup sexual herding occur (Boese 1973). Young are carried ventrally for up to four months and then in the jockey position (Boese 1973). Young are cared for by mother, sisters and aunts. Infant care and carrying by adult ♂♂ occurs (Boese 1973). One mother carried her dead newborn for three days (A. Galat-Luong pers. obs.). Few vocalizations are described. Boese (1973) and Byrne (1981) postulate an inter-group spacing role to the adult male's loud two-syllable 'wahoo' bark. Muffled grunt-like vocalization given by ♀♀ in 39% of the copulations, but is not specific to copulation only (Boese 1973).

Green Monkeys *Chlorocebus sabaeus* chase Guinea Baboons from trees and water pools. Guinea Baboons and Robust Chimpanzees avoid each other (A. Galat-Luong pers. obs.).

Reproduction and Population Structure First oestrous cycle at 3.5–4.5 years. First large perineal swelling at 4.5 years (Boese 1973). Mean age at sexual maturity for ♀♀ is 3 years 8 months, and first pregnancy at 4 years, 3 months (Gauthier 1994). Length of gestation is 26 weeks (Rowell 1967). A birth peak during Jan–Mar at Niokolo Koba (Dunbar 1974). Male to ♀ ratio 1 : 1.4 (1 : 1 and 1 : 1.5, $n = 2$ groups; Boese 1973). Group composition: 23% adult ♂♂, 32% adult ♀♀, 45–47% immatures (Boese 1973, Sharman 1981). Longevity >23 years of age for two wild-born ♀♀ living in the Parc Zoologique de Paris (MNHN).

Predators, Parasites and Diseases Humans, Leopards *Panthera pardus* (one Leopard for one troop of baboons; Verschuren 1982), Central African Rock Pythons *Python sebae*, Spotted Hyaenas *Crocuta crocuta* and African Wild Dogs *Lycaon pictus* are the main predators. Attacks observed by Nile Crocodiles *Crocodylus niloticus*, Leopards (five dead baboons found at a sleeping site after a nocturnal attack; Ndiaye 1983) and Spotted Hyena (three hyenas chasing a group of 80 baboons fleeing and climbing vertical cliffs; A. Galat-Luong pers. obs.). Since 1994, attacks by Lions *Panthera leo* have increased in Niokolo Koba N. P. due to reduced numbers of large ungulates (A. Galat-Luong pers. obs.). Side-striped Jackals *Canis adustus*, Caracals *Felis caracal*, Servals *Felis serval* and large eagles, like the Martial Eagle *Polemaetus bellicosus*, perhaps prey on young.

Walker & Spooner (1960) noted *Histoplasma* infections. Identified intestinal parasites and the percentage of animals infected are: Niokolo Koba – 98%: *Entamoeba coli* (30%), Nematoda (68%), Strongylidae (33%), *Strongyloides stercoralis* (22%), *Trichuris trichura* (30%), *Ascaris lumbricoides* (21%) (n = 63; Pourrut *et al.* 1997). Assirick, Senegal – Nematoda: *Strongyloides* sp. (26%), *Necator* sp. (38%), *Physaloptera* sp. (31%), *Trichuris* sp. (28%), *Streptophargus* sp. (23%), Trematoda *Schistosoma mansoni* (23%), *Stringoidea* sp. (44%); Protozoa: *Balantidium coli* (72%), *E. coli* (87%), *Iodamoeba butschilli* (38%) (n = 39; McGrew *et al.* 1989a). See Howells *et al.* (2010) for infection rates at Fongoli, Senegal. Susceptible to malaria, filariasis, tuberculosis; healthy carriers of amari virus. Particularly susceptible to epilepsy, thus, sleep and encephaloelectrophysiology has been studied in the wild (Bert *et al.* 1967a, b, Bert 1971, Balzamo *et al.* 1975, 1982). No simian immunodeficiency virus detected (n = 484; Durand *et al.* 1990).

Conservation IUCN Category (2012): Near Threatened. CITES (2012): Appendix II.

Habitat degradation and loss due to expanding agriculture and livestock grazing have led to significant population declines outside the national parks (Galat *et al.* 2000). Hunted for meat and to stop crop-raiding. Mean number traded per year (1989–93) was 131 (118 from Senegal) (Butynski 1996). Guinea Baboons still common in large protected areas in Senegal, Mali and Guinea.

Measurements

Papio papio

HB: 687 mm, n = 1

T: 560 mm, n = 1

No locality provided (BMNH; Napier 1981)

HB (♂♂): 600, 620 mm, n = 2

WT (♂♂): 25, 27 kg, n = 2

WT (♀♀): 14 (7–21) kg, n = 21

Born and raised in captivity (MNHN)

HB (♂♂): 642 (407–780) mm, n = 13

HB (♀): 530 mm, n = 1

T (♂♂): 555 (360–650) mm, n = 13

T (♀): 500 mm, n = 1

HF (♂♂): 190 (140–213) mm, n = 13

HF (♀): 160 mm, n = 1

E (♂♂): 49 (43–56) mm, n = 13

E (♀): 46 mm, n = 1

♂♂ from Kudang, Gambia; Passe de Soufa, Mauritania; Tambacounda, Senegal.

♀ from Kudang, Gambia (USNM; compiled by E. E. Sarmiento pers. comm.)

Key References Boese 1973; Galat-Luong *et al.* 2006; Oates 2011; Sharman 1981; Zinner *et al.* 2011.

Anh Galat-Luong & Gérard Galat

Papio hamadryas HAMADRYAS BABOON (SACRED BABOON)

Fr. Babouin Hamadryas; Ger. Mantelpavian

Papio hamadryas (Linnaeus, 1758). Systema Naturae, 10th edn, 1: 27. Egypt.

Taxonomy Monotypic species. Mitochondrial evidence suggests that populations of Hamadryas in the Arabian peninsula have been separated from those in the Horn of Africa for at least 37,000 years. The time of separation is estimated at 37,000–74,000 years ago by Wildman *et al.* (2004) and at 85,000–119,000 years ago by Winney *et al.* (2004). Synonyms: *aegyptiaca*, *arabicus*, *brockmani*, *chaeropithecus*, *cynamoligus*, *nedjo*, *wagleri*. Chromosome number 2n = 42 (www.snprc.org/baboon/baboonGenomics.html, Romagno 2001).

Description Distinguished from other *Papio* spp. by lighter pelage, lighter and redder faces, and large greyish-white mane (= mantle = cape) on adult ♂. Face skin and ears pink to reddish-grey to dark greyish-black. Muzzle prognathic. Perineum pink in both ♂♂ and ♀♀, tail medium-length and held in gentle arch. Sexes differ in colour of pelage. Adult ♀♀ about 59% of the weight of adult ♂♂. Adult ♂: pelage light greyish-brown to greyish-white with short hair on crown of head, forelimbs below elbows, hindlimbs, posterior torso and tail. Mane large, formed by long, thick hair on shoulders, anterior torso, cheeks and sides of head, ranging from dark greyish-brown to silvery grey to off-white. Large, prominent areas of bare skin, usually bright pink, lateral to ischial callosities and extending to sides of buttocks. Ischial callosities not separated. Tail has tuft at tip. Adult ♀: more



Hamadryas Baboon *Papio hamadryas* adult male.

uniform in colour, golden brown, no mane, smaller body size and smaller area of paracallosal skin. Paracallosal skin pale to bright pink depending on reproductive state (colour of face immediately around eyes may also vary from grey to pink depending on reproductive state). Ischial callosities separated. Tail lacks tuft at tip. Infant pelage black until 6–12 months of age, when it turns brown.

Geographic Variation No consistent morphological differences among regional populations. Among Horn of Africa populations, pelage and skin are darker in colour in more western parts of range (near areas of hybridization with Anubis Baboon *Papio anubis*) and lighter (with whiter mane in adult ♂♂) in eastern parts of range (Kummer 1968, Kummer *et al.* 1985, Jolly 1993). African and Arabian populations distinguished by mitochondrial haplotypes (Wildman *et al.* 2004).

Similar Species

Papio anubis. Parapatric or narrowly sympatric above ca. 500 m on eastern edge of range in Ethiopia and Eritrea. Sympatric at Debre Libanos (ca. 2000 m; C. Jolly pers. comm.). Olive-brown to olive-grey pelage. Mane short to medium and same colour as rest of pelage. Face purple-black. Perineum black. Tail kinked (i.e. 'broken').

Theropithecus gelada. Sympatric in highlands of N Ethiopia above 1700 m, but usually above 2400 m. Dark to light brown pelage. Face skin dark brown to black. Less prognathic. Mane of adult ♂ brown instead of grey as in Hamadryas. Mane extends to below elbows. Patch of naked pink skin on upper chest in both sexes.

Distribution Endemic to arid zone of Horn of Africa and SW Arabian Peninsula. Sudan Savanna and Afromontane–Afroalpine BZs. Throughout N, C and E Ethiopia. Also in NE Sudan, Eritrea, Djibouti, N Somalia, SW Saudi Arabia and SW Yemen. It is not clear how Hamadryas originally dispersed to the Arabian Peninsula, nor whether they speciated from other *Papio* spp. on the Arabian Peninsula or in the Horn of Africa. Mitochondrial data suggest two Pleistocene invasions

of Arabia by African Hamadryas, one in the early late Pleistocene and again sometime between 37,000 and 119,000 years ago (Wildman *et al.* 2004, Winney *et al.* 2004), though Kummer (1995) regards such a lengthy separation to be unlikely. Hamadryas distribution meets that of *P. anubis*, with which they hybridize (Phillips-Conroy *et al.* 1991, 1992), in Awash N. P. and elsewhere in Ethiopia and in Eritrea.

Habitat Usually in arid semi-desert dominated by *Acacia* spp. trees and shrubs, *Grewia* spp. and *Dobera glabra* (Kummer 1968), but also occur where annual rainfall is >900 mm (Zinner *et al.* 2001a). Found from sea level up to 3300 m in the Simien Mts, NC Ethiopia (Crook & Aldrich-Blake 1968, Yalden *et al.* 1996) and up to 3000 m in Eritrea (Zinner *et al.* 2001a); also in highland regions of SW Saudi Arabia and Yemen (Biquand *et al.* 1992, Al-Safadi 1994). Important components of the habitat are permanent sources of drinking water and vertical rock faces on which to sleep.

Abundance Population density ranges from 1.8 ind/km² in the Erer Gota region of Ethiopia (Kummer 1968) to 23.9 ind/km² in the Durfo region of Eritrea (Zinner *et al.* 2001a).

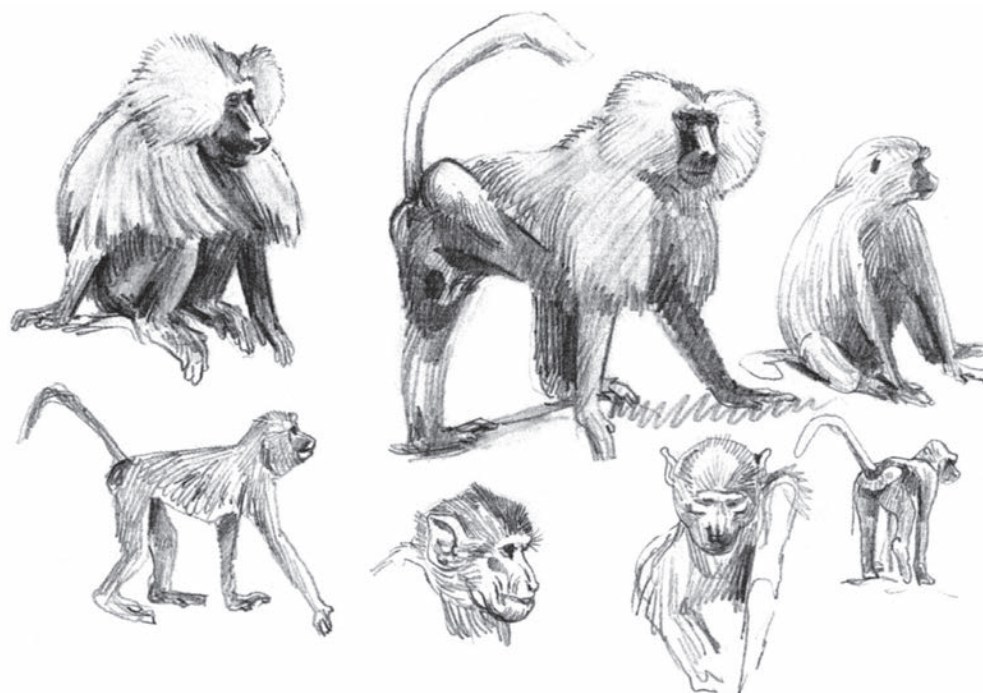
Adaptations Diurnal and terrestrial. Well adapted to dry habitats and widely dispersed, scarce resources. Hamadryas sleep on cliffs throughout range and in Doum Palms *Hyphaene thebaica* at one location where cliffs are not available (Schreier & Swedell 2008). Compared with Olive Baboons, Yellow Baboons *Papio cynocephalus*, Rhesus Macaques *Macaca mulatta* and humans, Hamadryas are able to maintain their blood plasma volume when dehydrated by reducing evaporative water loss and urine flow and thus appear to be physiologically better-adapted to water scarcity (Zurovsky & Shkolnik 1993).

Foraging and Food Omnivorous. Larger home-ranges and longer daily travel distances than most other *Papio* spp. (Sigg & Stolba 1981, Sigg 1986, Swedell 2002b, Schreier 2010). Home-range size for two well-studied bands in Ethiopia was 28 km² (Sigg & Stolba 1981) and 38 km² (Schreier 2009); but 9 km² for a commensal population in Saudi Arabia (Boug *et al.* 1994). No territorial behaviour occurs other than occasional inter-band aggression over access to sleeping sites. Hamadryas travel up to 19 km/day, leaving sleeping cliffs in early to mid-morning and returning (to the same or a different sleeping cliff) before dusk (Kummer 1968). Mean daily travel distance 6.5–13.2 km at three sites in C Ethiopia (Kummer 1968, Nagel 1973, Sigg & Stolba 1981, Swedell 2002b, 2006, Schreier 2010). Approximately 57% of daytime spent travelling and foraging, and 43% resting and grooming (Schreier 2009).

Relies mainly on plant foods. Common food items include flowers, leaves and seeds of *Acacia* spp. trees and shrubs, *Grewia* spp. berries, and grasses such as *Cyperus rotundus* and *Seddera bagshawei* (Kummer 1968, Al-Safadi 1994, Swedell *et al.* 2008, Schreier 2010). They feed opportunistically on insects, small mammals such as Abyssinian Hares *Lepus habessinicus*, agricultural crops and refuse from yards or garbage dumps. Foods that constitute a sizable portion of diet in limited parts of their range include the fruits of *H. thebaica* in the Awash region of C Ethiopia (Swedell *et al.* 2008) and the fruit and young shoots of Prickly Pear *Opuntia* spp. in Ethiopia (Kummer 1968) and Eritrea (Zinner *et al.* 2001a). The latter may be an important source of water, as its water content is over 96% (Zinner *et al.* 2001a). Diet



Papio hamadryas



varies seasonally, with flowers and young leaves constituting a greater portion of the diet during the long rains of Jul–Aug (Schreier 2010). There are no reported sex differences in foraging behaviour or diet.

Social and Reproductive Behaviour Social, with a complex, multi-level social structure. Smallest stable social unit is the one-male unit (OMU), comprising one adult ‘leader’ ♂, 1–9 ♀♀, dependent offspring and sometimes one or more ‘follower’ ♂♂. Cohesion of OMUs maintained by aggressive herding of the leader ♂, who threatens and bites ♀♀ to condition them to stay near him (Swedell & Schreier 2009). Several OMUs comprise a ‘band’ (the social unit analogous to the ‘group’ or ‘troop’ of other papionins) whose members coordinate their movements. Size of bands varies from about 30 to over 400 individuals. Bands are larger in areas of greater food abundance: 150–400 individuals (mean 192, $n = 3$; Schreier & Swedell 2012) at Filoha, Ethiopia, where range includes Doum Palm forests, vs. 30–95 at Erer Gota, Ethiopia (Kummer 1968: 30–90; Sigg & Stolba 1981: 62–95; Abegglen 1984: 52–90). Also within bands are ‘solitary’ ♂♂ who, along with older juvenile ♂♂, move freely within the band and interact mainly with other solitary ♂♂ and juveniles (Pines *et al.* 2011). Two or more bands sharing a common sleeping site comprise a ‘troop’, a temporary aggregation that does not function as a consistent social group (Kummer 1968). Abegglen (1984) and Schreier & Swedell (2007, 2009) observed a fourth level of social organization, the ‘clan’: a subset of a band composed of several OMUs whose ♂ leaders share affiliative relationships and may be related. Unlike other baboons, Hamadryas are more ‘male-bonded’ than ‘female-bonded’. Social relationships among ♂♂ may take the form of grooming (among solitary ♂♂) or ritualized ‘notifications’ (among leader ♂♂ or between leaders and followers) whereby one ♂ approaches, looks at, presents his buttocks to and quickly leaves another ♂. In general, Hamadryas social organization is based largely on competition among ♂♂ over exclusive access to and control of ♀♀, but ♀ choice and relationships among ♀♀ appear to play a role as well (Kummer 1968, Bachmann & Kummer 1980,

Abegglen 1984, Colmenares 1992, Colmenares *et al.* 1994, Swedell 2002a, 2006, Pines & Swedell 2011, Pines *et al.* 2011).

Current evidence suggests composition of Hamadryas bands is quite stable over time compared with other baboons (Sigg *et al.* 1982, Swedell *et al.* 2011). Males at least occasionally disperse among bands, probably to gain reproductive access to ♀♀ (Phillips-Conroy *et al.* 1991, 1992), and ♀♀ are forcibly transferred among OMUs, clans and (less often) bands by leader ♂♂ during takeovers (Kummer 1968, Sigg *et al.* 1982, Abegglen 1984, Swedell 2000, Swedell & Schreier 2009, Swedell *et al.* 2011). Genetic data from Eritrean and Saudi Arabian populations support a pattern of transfer among bands mainly by ♀♀ (Hapke *et al.* 2001, Hammond *et al.* 2006), while microsatellite data from an Ethiopian population suggest high levels of relatedness among all individuals in a band, suggesting relatively little gene flow overall (Woolley-Barker 1999, Swedell & Woolley-Barker 2001).

Copulations occur almost exclusively between ♀♀ and their leader ♂♂. Subadult follower and solitary ♂♂ occasionally gain sexual access to ♀♀, but fully adult non-leader ♂♂ rarely copulate and appear to be waiting for future reproductive opportunities (Kummer 1995, Swedell 2006, Swedell & Saunders 2006, Pines *et al.* 2011). Copulations occur, on average, about once an hour for oestrous ♀♀. Most copulations involve multiple mounts, averaging 7.5 thrusts per mount (1–14, $n = 66$), five minutes between mounts (1–17, $n = 8$), and one ejaculation per four mounts (Swedell 2006). Juveniles remain in natal OMU until 2–3 years of age, by which point ♂♂ spend most of their time in play groups and ♀♀ have been incorporated into another OMU. Infants and juveniles sometimes carried by adult and subadult ♂♂ in addition to their mothers (Kummer 1968, Swedell 2006).

Vocalizations are similar to other *Papio* spp. ‘Grunts’ given during affiliative interactions and at onset of group movement. ‘Alarm barks’ emitted in response to predators. ‘Contact barks’ given when ♀♀ or juveniles lose contact with other group members. ‘Wahoo barks’ given by adult ♂♂ during inter-band encounters, aggressive interactions,

♀ herding, and loss of contact with group. 'Kecks' or 'staccato-coughs' (♀ ♀ only) and 'screams' (all age and sex classes) given during agonistic interactions and in response to aggression or threat. 'Copulation calls' given by some ♀ ♀ during and/or after copulation (Swedell 2006, Swedell & Saunders 2006, J. Saunders pers. comm.).

Reproduction and Population Structure Female ovarian cycles average 39 days in the wild (31–52, $n = 17$; Swedell 2006) and 42 days in captivity (33–49, $n = 9$; D. Zinner pers. comm.). Like other baboons, Hamadryas ♀ ♀ undergo pronounced swelling of the perineal region (medial to the ischial callosities) during the periovulatory period. Sexual swelling generally coincides with behavioural oestrus (Caljan *et al.* 1987, Swedell 2006). Reproductive synchrony occurs in some wild populations (Kummer & Kurt 1963, Kummer 1968) but not others (Swedell 2006), and occurs in captivity (Schwibbe *et al.* 1992, Zinner *et al.* 1994). Gestation averages 26 weeks (24.4–27.3, $n = 52$; Kaumanns *et al.* 1989); singleton births are the norm. Twins not reported. Birth weight ca. 900 g ($n = 1$; D. Zinner pers. comm.). Interval between births of surviving infants ranges 18–28 months (mean 22, $n = 12$) at Erer Gota (Sigg *et al.* 1982), though this interval may be shorter (mean 19 months, 15.5–21.5, $n = 3$) in richer habitats (Swedell 2006). In general, no birth seasonality occurs, though Kummer (1968) observed two birth peaks over one year at Erer Gota (however, the timing of these peaks varied among groups in the same area). In the wild, adolescent ♀ ♀ undergo their first oestrous cycles at about four years of age (mean 4.3, $n = 13$) and first birth at about six years of age (mean 6.1, 5.5–7.0, $n = 8$), at which point they have reached adult size (Sigg *et al.* 1982). Female reproductive maturation occurs more than a year earlier in captivity (Caljan *et al.* 1987, Kaumanns *et al.* 1989). Adolescent ♂ ♂ reach the size of an adult ♀ at about five years of age, at which point the testes have descended but the mane has not yet developed. By ten years of age, ♂ ♂ have attained adult body size and have a full mane (Sigg *et al.* 1982). Although ♀ ♀ give birth to their first surviving infant by six years of age, ♂ ♂ in the wild probably do not reproduce until they are at least nine years of age (Sigg *et al.* 1982).

The sex ratio within bands is 1.1–2.4 adult and subadult ♀ ♀ per adult and subadult ♂. There are 1.1–1.6 adults and subadults per infant or juvenile (Kummer 1968, Kummer *et al.* 1985, Zinner *et al.* 2001b, Swedell 2006). Birth rates in captivity average 0.6 infants/♀/year, with a peak in ♀ fertility at 9–14 years of age and a sharp reduction in fertility (to zero) after 20 years of age (Caljan *et al.* 1987, Chalyan *et al.* 1994). Infant survival to one year of age is 82% at Erer Gota (Sigg *et al.* 1982) and 87% at Filoha (Swedell pers. obs.). These survival rates are higher than those of many other *Papio* spp. populations, suggesting that the OMU social structure may provide better protection for Hamadryas infants compared with other baboons (Sigg *et al.* 1982). Longevity in the wild is not known, but most Hamadryas in captivity live to an age of about 20 years and few survive beyond 30 years (Lapin *et al.* 1979).

Predators, Parasites and Diseases Potential predators include Lions *Panthera leo*, Leopards *Panthera pardus*, Cheetahs *Acinonyx jubatus*, Spotted Hyenas *Crocuta crocuta*, Striped Hyenas *Hyaena hyaena*, Black-backed Jackals *Canis mesomelas*, Nile Crocodiles *Crocodylus niloticus* and Verreaux's Eagles *Aquila verreauxii*. Over a period of 20 months near

Awash, Lions and Spotted Hyenas (and baboon alarm calls) were heard frequently near the sleeping cliffs at night and snake bites were a suspected cause of at least two deaths (Swedell 2006). In the same region a group of 180 Hamadryas, upon encountering three Spotted Hyenas at dawn at their sleeping cliff, ran faster and farther from the cliff than they had ever been observed to do before, suggesting that Spotted Hyenas are indeed a threat (Swedell 2006). At Erer Gota two Leopards, fresh blood and two dead ♀ Hamadryas were observed at dawn at the base of a sleeping cliff, and body parts of one of the Hamadryas were found in a tree, presumably put there by a Leopard (Kummer 1995). In Eritrea, Verreaux's Eagles observed interacting with Hamadryas in a manner highly suggestive of hunting behaviour, and the Hamadryas responded by giving alarm calls, seeking protective cover and, in the case of adult ♂ ♂, threatening the birds (Zinner & Peláez 1999). Hamadryas are also threatened by farmers and their dogs in Eritrea, but adult ♂ ♂ can successfully repel dogs (Zinner *et al.* 2000). Overall, the vertical cliffs used as sleeping sites (ranging from 10 to over 50 m in height) presumably afford Hamadryas adequate protection against nocturnal terrestrial predators, and Hamadryas do not, in general, appear to be at great risk from predation.

Intestinal parasites such as *Giardia* spp., *Entamoeba* spp., *Balantidium coli*, *Hymenolepis nana*, *Schistosoma mansoni*, *Ascaris* sp., *Enterobius* sp., *Trichuris* sp. and hookworm found in wild and commensal populations in Saudi Arabia (Nasher 1988, Ghandour *et al.* 1995), though few, if any, parasites found in Ethiopian populations. Prevalence of parasites appears to vary depending on proximity to human habitation (Ghandour *et al.* 1995). It is not known what other diseases occur in wild populations of Hamadryas.

Conservation IUCN Category (2012): Least Concern. CITES (2012): Appendix II.

Not greatly threatened by the nomadic pastoralists with whom they share most of their range, but by the extension of agriculture into dry river valleys via irrigation (D. Zinner pers. comm.). Not hunted for food, but sometimes shot for skins, for their callosities (which are used in traditional medicine in some parts of Eritrea), or as a result of crop-raiding (Wolfheim 1983, Biquand *et al.* 1992, Zinner *et al.* 2001c). In Eritrea young are used as pets (Zinner *et al.* 2001c). Main threat overall is loss of habitat to agriculture and human settlement.

Measurements

Papio hamadryas

HB (♂): 750 mm, $n = 1$

T (♂ ♂): 565 (460–660) mm, $n = 37$

T (♀ ♀): 480 (460–500) mm, $n = 3$

HF (♂ ♂): 210 (190–220) mm, $n = 34$

HF (♀ ♀): 180 (170–190) mm, $n = 2$

WT (♂ ♂): 17 (13–24) kg, $n = 41$

WT (♀ ♀): 10 (7–13) kg, $n = 39$

Central Ethiopia (Phillips-Conroy & Jolly 1981, C. J. Jolly & J. E. Phillips-Conroy pers. comm.)

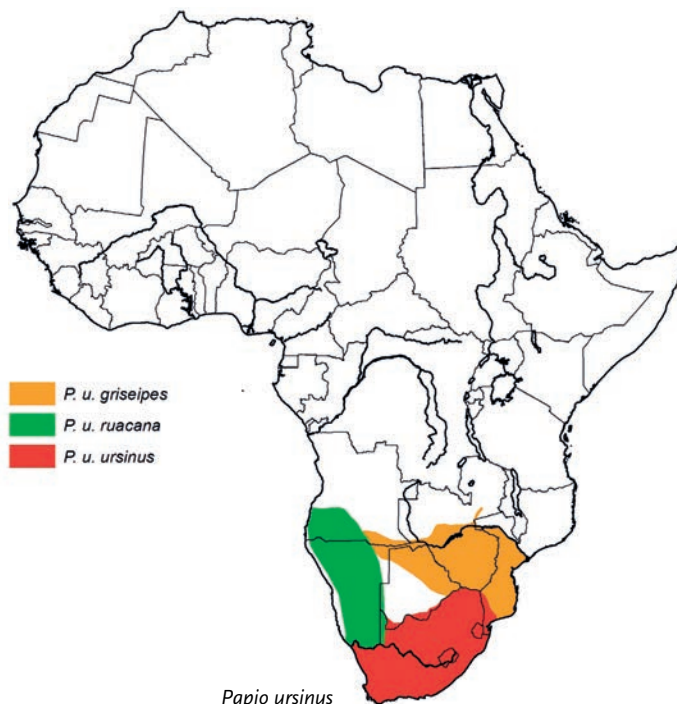
HB: Napier (1981)

Key References Abegglen 1984; Kummer 1968, 1995; Swedell 2006.

Larissa Swedell

Papio ursinus CHACMA BABOON

Fr. Chacma; Ger. Bärenpavian

Papio ursinus (Kerr, 1792). Animal Kingdom, p. 63. Western Cape Province, Cape of Good Hope, South Africa.Chacma Baboon *Papio ursinus* adult male.*Papio ursinus*

Taxonomy Polytypic species. Treated as a subspecies in a monotypic genus by some authorities (e.g. Skinner & Chimimba 2005). Groves (2001, 2005) recognizes three subspecies within *P. ursinus*. Grubb *et al.* (2003) recognize two subspecies. The taxonomy of Groves (2001, 2005) is followed here. For recent molecular findings, see Sithaldeen *et al.* (2009), Keller *et al.* (2010) and Zinner *et al.* (2011). Synonyms: *capensis*, *chacamensis*, *chobiensis*, *comatus*, *griseipes*, *ngamiensis*, *nigripes*, *occidentalis*, *orientalis*, *porcaria*, *ruacana*, *sphingiola*, *transvaalensis*. Chromosome number: $2n = 42$ (Romagno 2001).

Description Large, robust baboon with ventrum and sides of muzzle noticeably paler than dorsum, and tail 'broken' near base. Adult ♀♀ like adult ♂♂, but much smaller; body weight of adult ♀♀ half that of adult ♂♂. Pelage coarse, blackish, dark brown, or dark yellowish-grey (*griseipes*) above, paler below. Male mane (= cape = mantle) relatively thin, often with back-curling hairs on nape of neck. Skin of face, extremities and around the ischial callosities grey or black. Muzzle long, robust, usually more downwardly-flexed than in other baboons. Nostrils do not protrude beyond plane of upper lip or snout. Tail 'broken': proximal one-third of tail held up, distal two-thirds hangs down at sharp angle.

Geographic Variation Little is known of these subspecies, so the following should be treated as preliminary (Hill 1970, Groves 2001).

P. u. ursinus Southern Chacma. Widespread across S Botswana and South Africa. Black or charcoal grey in western and south-western part of range, but lightens to grey and brown towards the east (although still with dark extremities). Face, hands, feet and tail black.

P. u. griseipes Grey-footed Chacma. SW Zambia, Zimbabwe, N Botswana, Mozambique (south of Zambezi R.) and NE South Africa. Pelage fawn. Hands, feet and tail grey rather than blackish.

P. u. ruacana North-western Chacma. SW Angola and Namibia. Small. Feet black. Crown and back blackish, tending to contrast with lighter flanks and limbs.

Similar Species

Papio cynocephalus. Sympatric or parapatric at southern extreme of range. Smaller with yellow-brown dorsum and off-white ventrum.

Distribution Endemic to southern Africa. Zambezi Woodland, South-West Arid, Highveld, and South-West Cape BZs. Widespread throughout the Southern African Subregion south of Zambezi R. to SW Angola and SW Zambia, southwards through much of Namibia, Zimbabwe and South Africa to the Cape.

Habitat *Papio ursinus* is an adaptable, semi-terrestrial generalist that occurs in most habitats, including desert, savanna grassland and woodland, montane grassland and Cape Fynbos. Limited by the availability of water and safe sleeping sites (tall trees or cliff faces). Occurs from sea level to at least 3000 m where there is often snow and temperatures below freezing (Hall 1966).

Abundance Population density varies substantially among habitats: 1.4 baboons/km² in montane grassland (Whiten *et al.* 1987); 3.2/km² in savanna grassland (Anderson 1981); 5.3/km² in desert oases (Hamilton *et al.* 1976); and 24.0/km² in savanna woodland (Hamilton *et al.* 1976).

Adaptations Diurnal and semi-terrestrial. There is substantial variation in body mass among sites, especially for adult ♂♂ (mean adult ♂ weight 23–31 kg, mean adult ♀ weight 14–16 kg, across 11 sites). This variation related to local patterns of rainfall and temperature; body size tends to be larger in wetter, cooler

habitats, presumably reflecting higher habitat quality (Barrett & Henzi 1997). High temperatures can also cause thermal stress. In response, *P. ursinus* is able to tolerate substantial fluctuation in core body temperature – as much as 5.3 °C – and undertake behavioural actions such as ‘sandbathing’ (Brain & Mitchell 1999). Adaptations shared with other *Papio* spp. include cheek pouches. In *P. ursinus* these are used primarily to accumulate food rapidly when faced with competition from other group members, e.g. when food is limited and when foraging in the centre of the group (Hayes *et al.* 1992).

Foraging and Food Omnivorous. Forage during daylight hours and frequently cover substantial distances over the course of the day, e.g. 4.1 km across a home-range of 14.5 km² (Whiten *et al.* 1987). Travelling and feeding occupy about 30% and 38% of daylight hours, respectively, while the remaining hours are spent resting and grooming (Hill 1999a). Habitats are selected in order to both maximize food intake rates and minimize predation risk. Food-rich habitats avoided if high risk, in favour of safer habitats where food is less abundant (Cowlshaw 1997a). As such, foraging preferentially takes place close to refuges, such as large trees and cliffs, to reduce the risk of predation (Cowlshaw 1997b). Vigilant to predators (Cowlshaw 1998). Foraging ♀♀ adopt similar patterns of anti-predator vigilance across populations (Hill & Cowlshaw 2002).

As in all baboons, diet of *P. ursinus* is diverse and highly flexible. Diet typically includes fruits and pods (including seeds), flowers, leaves and subterranean items (e.g. roots and corms). The predominant foods are usually fruits/pods (Hill 1999a). However, the relative importance of the different dietary constituents varies both among sites and seasons. Animals are also included in the diet; most commonly insects (Hamilton *et al.* 1978), but on occasions tortoises, birds, mammals and fish (Hamilton & Busse 1982, Hamilton & Tilson 1985, Hill 1999b).

Although the diet of *P. ursinus* is broad, it is also selective. Individuals preferentially select foods high in protein and lipid, and avoid foods high in fibre, phenolics and alkaloids (Whiten *et al.* 1991). A comparison between low-altitude and high-altitude montane groups found that individuals in both groups obtained the same nutrient yields despite a high degree of seasonality and different foraging substrates (Byrne *et al.* 1993). During periods of food shortage, adults switch to less-preferred foods, and juveniles learn of these by observation of the adults (Hamilton 1986). Prefer to drink daily, but can go without drinking for 11 days (Brain 1991) or longer (Brain & Mitchell 1999).

Social and Reproductive Behaviour Social. Live in stable social groups, or ‘troops’, of about 22–79 individuals (Henzi *et al.* 1999). The adult sex ratio within these groups is variable, although always female-biased; e.g. 0.15–0.81 ♂♂ per ♀♀ (Henzi *et al.* 1999). Within groups ♀♀ tend to be philopatric whereas ♂♂ disperse to other groups at adulthood, although there are exceptions in both cases (Hamilton & Bulger 1990, Henzi *et al.* 2000b).

Following immigration into new groups and/or the acquisition of high social rank (see below), ♂♂ often attempt to kill infants in the group. This behaviour benefits the ♂ since it leads to the resumption of oestrous cycling by previously lactating ♀♀, thereby

maximizing his own opportunities to father offspring (Palombit *et al.* 2000). In response, ♀♀ often mate with many ♂♂ to confuse paternity (thus reducing the likelihood that any one ♂ will subsequently attempt infanticide), a strategy that may be assisted through both sexual swellings and copulation calls (O’Connell & Cowlshaw 1994). In addition, following conception, ♀♀ often develop and maintain ‘friendships’ with particular ♂♂ with whom they have mated. These ♂ friends help protect the infants, for example by carrying them out of danger (Anderson 1992, Palombit *et al.* 1997, Weingrill 2000).

Competition for limited, but monopolizable, resources within groups leads to the development of dominance hierarchies in which high-ranking individuals benefit most. Amongst ♂♂, dominant individuals monopolize ♀♀ when they are most likely to conceive (through mate-guarding ‘consortships’), and thus achieve the highest mating success (Bulger 1993, Weingrill *et al.* 2000). Amongst ♀♀, dominant individuals may obtain more food, potentially leading to higher birth rates (Bulger & Hamilton 1987). They also occupy positions of greater safety from predators, potentially leading to higher survival rates (Ron *et al.* 1996). In addition, dominant ♀♀ can experience higher infant survival rates (Bulger & Hamilton 1987), possibly as a result of their ability to monopolize access to ♂ friends (Palombit *et al.* 2001). The strength of such rank effects are variable among sites depending upon the local availability of limited resources.

Individuals may elicit tolerance and support from others during competition through grooming them. Grooming can be viewed as a ‘commodity’ that is valuable in itself (it is associated with the release of endorphins into the bloodstream and plays a role in ectoparasite removal), and group members can exchange this commodity for either reciprocal grooming or for tolerance at, and thus access to, limited resources (Barrett *et al.* 1999, 2002). Active coalitionary support, in contrast, appears to be rare in *P. ursinus*, regardless of grooming relationships (Silk *et al.* 1999). Grooming is often, but not always, directed towards kin and high-ranking individuals (Seyfarth 1976, Barrett *et al.* 1999, Silk *et al.* 1999), and typically reflects social bonds between individuals. Social bonds tend to be strongest between ♀♀, although strong bonds also occur between ♂♂ and ♀♀ (including ‘friendships’; see above) (Henzi *et al.* 2000a). Females spend about 12% of their day grooming (Hill 1999a), during which time they strive to groom all other ♀♀ in the group. However, when there is insufficient time to groom everyone, ♀♀ focus on their key social partners (Henzi *et al.* 1997b, Silk *et al.* 1999). Bonds between social partners are also mediated through vocalizations. ‘Soft grunts’ are used by dominant individuals to reassure subordinate animals and to reconcile combatants after fights (Cheney *et al.* 1995, Silk *et al.* 1996).

Even when not socializing, group members tend to stay close to one another. Adults are usually within 5 m of at least one other adult, and rarely more than 25 m away. This probably reflects a response to predation risk (these distances are greater where predators are absent), although spatial proximity within groups appears to be most strongly influenced by ♂ defence of infants (Cowlshaw 1999). When social partners lose sight of one another, loud ‘contact’ barks are used to maintain contact (Cheney *et al.* 1996). Males, similarly, use loud two-syllable ‘wahoo’ calls when they become separated from the group. However, ♂ ‘wahoos’ are primarily used as alarm

calls or as vocal signals of stamina and competitive ability (Fischer *et al.* 2002, Kitchen *et al.* 2003).

Not territorial. Encounters between groups can be infrequent, e.g. once every five days (Cowlshaw 1995). On occasion, groups attempt to monopolize valuable ecological resources (Hamilton *et al.* 1976), but more commonly resource-defence is absent and groups encounters are relatively peaceful (Cowlshaw 1995). Males primarily use inter-group encounters to assess potential mating opportunities in neighbouring groups. The ensuing mate-guarding behaviour by resident ♂♂ leads to aggressive chasing, or 'herding', of ♀♀ away from the approaching group (Cheney & Seyfarth 1977, Henzi *et al.* 1998, Kitchen *et al.* 2004).

Reproduction and Population Structure Gestation averages 187 days (173–193, $n = 14$). Newborn weighs 600–800 g and has black pelage and pink skin (Gilbert & Gillman 1951). Adult ♀♀ give birth to a single infant. Inter-birth interval is 20–38 months (Hill *et al.* 2000). Although births occur throughout the year, birth peaks reported both in the Drakensburg Mts, South Africa, and Okavango Delta, Botswana. These birth peaks most likely reflect improved conception rates following periods of high food abundance (Lycett *et al.* 1999, Cheney *et al.* 2004). At De Hoop, South Africa, infants begin weaning at about 4–5 months, although suckling can continue until 12–13 months (Barrett & Henzi 2000). High maternal dominance rank can increase growth rates in infant and juvenile ♀♀, but the same effect is not seen in ♂ offspring (Johnson 2003).

Population structure is primarily determined by group size (and thus the number of discrete units that comprise the population). Minimum group size is determined by predation risk and the minimal requirements for safety, whereas maximum group size is determined by food abundance and the time available to maintain grooming relationships with other group members. As groups grow in size there is no corresponding increase in time available for grooming additional group members. In fact, the time available for grooming can even decline, due to the demands of foraging time, since feeding competition can intensify as groups grow. Hence ♀♀ find it increasingly difficult to sustain all of their grooming relationships and begin to focus only on their key social partners. As a result, the social coherence of the group is weakened and large groups eventually fission (Henzi *et al.* 1997a, b).

Predators, Parasites and Diseases Leopards *Panthera pardus* are the most important predator of *P. ursinus*. Other predators include Lions *Panthera leo*, Brown Hyenas *Hyaena brunnea*, Spotted Hyena *Crocuta crocuta*, Nile Crocodiles *Crocodylus niloticus* and Southern African Rock Pythons *Python natalensis* (Cowlshaw 1994, Cheney *et al.* 2004). Verreaux's Eagles *Aquila verreauxii* will attack *P. ursinus* to defend their nests, but do not appear to prey on them (Gargett 1990). Adult *P. ursinus* ♂♂, who are least vulnerable to predation (due to their size and ferocity), will often take an active role in group defence against predators – occupying the most dangerous position in the group during travel (Rhine & Tilson 1987) and often retaliating against predators following attack (Cowlshaw 1994).

Papio ursinus is vulnerable to a variety of parasites and pathogens. Patterns of infection with gastrointestinal parasites, primarily

protozoans and helminths, vary both with altitude and habitat (Appleton & Henzi 1993, Appleton & Brain 1995). Ectoparasites are relatively rare, although one case of heavy tick infestation has been recorded (Brain & Bohrmann 1992). In this case, the ticks (genus *Rhipicephalus*) appeared to be directly or indirectly responsible for over half of all infant deaths. An epidemic disease (possibly bacterial yersiniosis, or an unknown haemorrhagic/enteric viral infection) also recorded (Barrett & Henzi 1998). The disease killed 85% of members in one group, and 32% of members in a second group, before heavy rains appeared to terminate the epidemic. Males appeared to be particularly vulnerable to this infection (and facilitated its transmission between the groups).

Patterns of mortality in *P. ursinus* are complex. In the Okavango Delta mortality is highest among infants, and can largely be attributed to infanticide. In contrast, the lower mortality rates seen among juveniles and young adults are driven primarily by predation. Mortality from both sources shows a seasonal peak that occurs when groups are more dispersed and travel along more predictable routes (Cheney *et al.* 2004). The relationship between social rank and mortality is variable across populations. Predation can affect all ♀♀ equally (Cheney *et al.* 2004), or low-ranking ♀♀ in particular (Ron *et al.* 1996). Similarly, infanticide may be most severe among high-ranking and low-ranking ♀♀ (Cheney *et al.* 2004), or infant mortality may be highest among low-ranking ♀♀ (Bulger & Hamilton 1987). Infant mortality can also increase in larger groups (Bulger & Hamilton 1987). As well as infanticide and predation, *P. ursinus* also suffers mortality from disease (see above) and wounds sustained during fights (Brain 1992). In addition, a food and water shortage in a Namib Desert oasis led to widespread mortality from starvation. In this case, adult ♀♀, juveniles and infants were more susceptible to starvation than adult ♂♂ (Hamilton 1985).

Conservation IUCN Category (2012): Least Concern. CITES (2012): Appendix II.

The widespread geographic range of *P. ursinus*, together with its ability to survive over a wide range of habitats and to live commensally with people, should ensure its long-term survival. However, *P. ursinus* can experience local persecution as a result of crop-raiding and livestock predation. In addition, *P. ursinus* is subject to trophy hunting and live-trapping for biomedical research, although analyses of the known legal trade in the early 1990s suggested that its impact on wild populations is minimal (Butynski 1996).

Measurements

Papio ursinus ursinus

HB (♂): 720 (670–755) mm, $n = 5$
 HB (♀): 613 (550–681) mm, $n = 15$
 T (♂): 566 (530–605) mm, $n = 5$
 T (♀): 471 (415–515) mm, $n = 15$
 HF (♂): 209 (197–220) mm, $n = 5$
 HF (♀): 176 (170–184) mm, $n = 15$
 E (♂): 59 (55–63) mm, $n = 5$
 E (♀): 48 (45–54) mm, $n = 15$
 WT (♂): 28.3 (26.6–30.0) kg, $n = 5$
 WT (♀): 15.1 (11.1–18.3) kg, $n = 15$
 Tsaobis, Namibia (G. Cowlshaw pers. obs.).

Papio ursinus (probably *ursinus* and *griseipes* combined)

TL (♂♂): 1450 (1320–1570) mm, n = 9

TL (♀♀): 1190 (1080–1160) mm, n = 5

T (♂♂): 725 (598–840) mm, n = 9

T (♀♀): 585 (556–610) mm, n = 5

HF (♂♂): 223 (217–236) mm, n = 9

HF (♀♀): 184 (176–194) mm, n = 5

E (♂♂): 58 (54–65) mm, n = 8

E (♀♀): 50 (44–52) mm, n = 5

WT (♂♂): 31.8 (27.2–43.5) kg, n = 9

WT (♀♀): 15.4 (14.6–17.2) kg, n = 5

Botswana (Smithers 1971). See Skinner & Chimimba (2005) for more WT data.

Key References Barret *et al.* 1999; Bulger 1993; Cheney *et al.* 2004; Cowlishaw 1997a; Henzi *et al.* 1997b; Whiten *et al.* 1991.

Guy Cowlishaw

Papio cynocephalus YELLOW BABOON

Fr. Babouin cynocéphale; Ger. Gelber Pavian

Papio cynocephalus (Linnaeus, 1766). Systema Naturae, 12th edn, 1: 38. Inland from Mombasa, Kenya.



Yellow Baboon *Papio cynocephalus* adult male.

Taxonomy Polytypic species. The Yellow Baboon presently retains its own species designation, *Papio cynocephalus*, with three subspecies – Central *cynocephalus*, Ibean *ibeanus* and Kinda *kindae* (Grubb *et al.* 2003). Some researchers suggest separating baboons into two species, *Papio hamadryas* for the Hamadryas or Sacred Baboon, and *P. cynocephalus* for the Savanna Baboons (Groves 2001). Under this construct, the Yellow Baboon would be a subspecies of Savanna Baboon. Alternatively, Jolly (1993) suggests lumping all baboons under one species, *P. hamadryas*, which would result in at least five subspecies. Synonyms: *antiquorum*, *babouin*, *basiliscus*, *flavidus*, *ibeanus*, *jubilaeus*, *kindae*, *langheldi*, *ochraceus*, *pruinusos*, *?rhodesiae*, *ruhei*, *streptus*, *sublutea*, *thoth*, *?variegata*. Chromosome number 2n = 42 (Romagno 2001).

Description Slender baboon with dorsum light brown to yellowish-brown to pale reddish-brown, contrasting with whitish ventrum. Sexes alike in colour of pelage. Adult ♂♂ weigh about twice as much as adult ♀♀. Adult ♂: skull not flattened behind the supraorbital ridge. Head appears pointed when viewed from the front, sometimes with a crest. Forehead not parallel with the angle of the muzzle (Alberts & Altmann 2001). Muzzle predominantly bare, greyish to black, often with varying amounts of sparse and patchy white pelage. Nostrils set back from the lips. Mane (= cape = mantle) absent or greatly reduced relative to other *Papio* spp. Dorsum, tail and outer limbs range from light brown to yellowish-brown to pale reddish-brown. Ventrums,

inner limbs and cheeks lighter, almost white, and pelage more sparse. Pelage long, especially on sides. Skin grey to black on primarily bare hands and paracallosities, but paracallosities of Kinda can be rosy-pink both on adult ♂♂ and adult ♀♀ (Y. de Jong & T. Butynski pers. comm.). Skin on rest of body, in densely pelaged areas, and in armpits and crotch, ranges from grey to pinkish or almost white, often in a splotchy pattern. Tail tends to be tapered with a sharp bend or hook between a proximal ascending portion and descending, distal one; tail shape is highly individually variable, however, and is useful in individual recognition. Angle of tail becomes more vertical during ontogeny (Hausfater 1977). Scrotum grey. Paracallosal skin fused.

Adult ♀: paracallosal skin split vertically. Nipples pinkish and button-like until ♀ has nursed an infant. Nipples of multiparous ♀♀ are dark, and the two nipples tend to differ considerably in length and often in colouration.

Immatures: infants of Central and Ibean, but not Kinda, have a black natal coat that is characteristic of all other baboon species. According to Groves (2001), Kinda newborns are unique among baboons in that the coat is reddish, not black. Kinda newborns at Mahale N. P., Tanzania, at the north-east corner of the range for this subspecies, have whitish pelage, pink muzzle and ears, but older infants have a reddish-brown coat. Infants in transition between these two pelage colours are pale yellowish-orange (Y. de Jong & T. Butynski pers. comm.). Between 6 and 12 months of age pelage gradually changes to the species-typical coat. Muzzle, ears, ischial callosities, paracallosities and scrotum are pink, and the ischial callosities are split in both sexes. Between 7 and 15 months of age, skin colour, except for scrotum, changes to the grey of adults and the paracallosities of ♂♂ fuse (Altmann *et al.* 1981). Body mass growth is approximately 5 g/day for both sexes through 3–4 years of age, after which ♂♂ experience an adolescent growth spurt (Altmann & Alberts 2005).

Geographic Variation

P. c. cynocephalus Central or Typical Yellow Baboon. South coast of Kenya southwards through most of Tanzania, Malawi, east of the Luangwa R. in Zambia and into N Mozambique. Straight, soft, silky pelage. Mane absent (Jolly 1993, Groves 2001, Zinner *et al.* 2009b). New-born with black pelage.

P. c. ibeanus Ibean Yellow Baboon. Central and S Somalia, SE Ethiopia, and E and SC Kenya. Hill (1970) indicates that *P. c. ibeanus* meets *P. c. cynocephalus* at the Galana-Sabaki R. Wavier and coarser pelage.

Trace of a mane. More like the Olive Baboon *Papio anubis* and Guinea Baboon *Papio papio* (Jolly 1993, Groves 2001, Zinner *et al.* 2009b). Newborn with black pelage.

P. c. kindae Kinda Yellow Baboon. From Cunene R. in S Angola north to the Congo R., then eastward across southern DR Congo to SW L. Tanganyika and C and N Zambia (south to Zambezi R.) (Jolly 1993, Groves 2001, Zinner *et al.* 2009b). Probably also up west side of L. Tanganyika (Mahale Mts) to Malagarasi R. (T. Butynski & Y. de Jong pers. comm.). Straight, soft, silky pelage. Mane absent. Bare skin around eyes pink. Body size is unusually small (Hill 1970, Jolly 1993, Groves 2001). Adults of both sexes can have rosy-pink callosities. Newborn with whitish pelage at Mahale Mts (Y. de Jong & T. Butynski pers. comm.).

Numerous photographs of the three subspecies of *P. cynocephalus* at many sites in Kenya and Tanzania are available at: www.wildsolutions.nl

Similar Species

Papio anubis. Sympatric or parapatric in W Somalia, SE Ethiopia, C and S Kenya, N Tanzania and south-east DR Congo. More robust. Grizzled, olive-brown dorsum. Mane thick over neck and shoulders. Top of head appears flat when viewed from the front. Tail appears 'broken'. Nose not 'upturned'.

Papio ursinus. Sympatric or parapatric in S Angola, SW Zambia and NW Mozambique. More robust. Grey, dark brown, to blackish dorsum.

Distribution Endemic to tropical Africa, mostly south of the equator. Southern Rainforest–Savanna Mosaic, Somalia–Maasai Bushland, Zambezian Woodland and Coastal Forest Mosaic BZs. Widely distributed in south-central and East Africa. Ranges from Angola through south DR Congo to E Kenya, SE Ethiopia and C Somalia through much of Tanzania, Malawi, most of Zambia to the Zambezi R. Valley and into N Mozambique. Whereas Yellow Baboons and Olive Baboons both inhabit the central latitudes of Africa, and their distributions overlap in a number of hybrid zones (Maples & McKern 1967, Jolly 1993, Alberts & Altmann 2001, Zinner *et al.* 2009b), Yellow Baboons typically inhabit low-altitude woodlands and savannas. Their distribution may be correlated more with vegetation than geography (Jolly 1993).

Two areas of Yellow–Olive hybridization are known. One runs through Amboseli N. P., SC Kenya, and the surrounding area, extending north and south of the Amboseli Basin. Genetic models and previous surveys suggest that the hybrid zone is relatively narrow and historically stable through this region, with Olive Baboons to the west of Amboseli and Yellow Baboons to the east (Charpentier *et al.* 2012; see also Maples & McKern 1967, Altmann & Altmann 1970, Samuels & Altmann 1986, Alberts & Altmann 2001).

A second, broad, clinal hybrid zone occurs between the Laikipia Plateau in C Kenya and the Lower Tana R./Indian Ocean. This cline appears to start just to the north-east, east and south-east of Mt Kenya and covers an upper altitudinal range of from roughly 1000 m asl at Mwea National Reserve (to the south of Mt Kenya) to roughly 600 m asl at Meru N. P. (to the north of Mt Kenya). The zone then continues south-eastwards towards the lower Tana R. to at least 30 m asl, perhaps to the Indian Ocean. Baboons in this >200 km wide region are intermediate and cannot be readily allocated to either Olive or Yellow Baboons. As one moves south-eastwards towards the



Papio cynocephalus

Kenya coast, however, the baboons become increasingly Yellow-like in their phenotypes (T. Butynski & Y. de Jong pers. comm.).

A potential Yellow Baboon–Chacma Baboon *Papio ursinus* hybrid zone exists in the Zambezi R. Valley. Some confusion exists as to whether Central or Kinda are in areas of Zambia. In the Zambezi R. Valley the Yellow Baboon range is thought to be only north of the Zambezi R., whereas the predominantly southern range of the Grey-footed Chacma Baboon *P. u. griseipes* extends north of the Zambezi R. as well, perhaps creating a hybrid zone there.

Habitat Primarily in open and woodland savanna. Associated with miombo (*Brachystegia* spp.) woodland over much of the range. In East Africa, Fever Trees *Acacia xanthophloea* and Tortilis Trees *Acacia tortilis* are used as sources of food and shelter. Yellow Baboons use woodland groves for sleeping at night, as well as for sources of shade during hot days. A water source within a day's walk appears to be necessary (Altmann & Altmann 1970). Distribution between wet and dry season lengths varies across the range. Most parts of the range experience one long wet season and one dry season. However, the Amboseli area usually experiences two wet and two dry seasons: one long and one short (Altmann *et al.* 2002). Mean annual rainfall over the range of the Yellow Baboon varies from ca. 320 mm (e.g. Garissa on the Tana R., EC Kenya) to ca. 1200 mm (e.g. Mombasa, SE Kenya; T. Butynski pers. comm.). Mean annual rainfall at two of the main Yellow Baboon study sites is as follows: 348 mm in Amboseli N. P. (over 25 years; Altmann *et al.* 2002); 842 mm in Mikumi N. P., SC Tanzania (over 20 years; Norton *et al.* 1987). Yellow baboons range in altitude from sea level to at least 1800 m (Mahale Mts, WC Tanzania; Kano 1971, T. Butynski & Y. de Jong pers. comm.) and to at least 1900 m in the Udzungwa Mts, SC Tanzania (Rovero *et al.* 2009). Altitude is ca. 1100 m at Amboseli and 450–740 m at Mikumi.

Abundance Abundant in parts of their range, with densities of 10–60 ind/ km² (Wolfheim 1983). Population density in the

Amboseli Basin decreased from 73 to 4 baboons/km² during the 1960s (Altmann *et al.* 1985). Density in the mid-1980s was 1.2 baboons/km² (Samuels & Altmann 1991). Almost two decades later, the density remains similar, although the distribution of groups shifted within the Basin, primarily to the south and west.

Adaptations Diurnal and semi-terrestrial. Behaviour and movement are adjusted to the thermal environment and microhabitats encountered (Stelzner 1988). Sitting position is adjusted relative to wind (Stelzner & Hausfater 1986). Behaviours include huddling for warmth, particularly by mothers with infants, and by young juveniles with each other, and resting on tree limbs or under trees for shade during the day. In Ruaha N. P., Tanzania, sun avoidance behaviour is regulated by temperature in the dry season and by humidity in the wet season (Pochron 2000). Other adaptations are those characteristic of the genus, with Yellow Baboons perhaps exhibiting *Papio*'s ecological and social adaptability to the greatest extent among the species.

Foraging and Food Omnivorous. Yellow Baboons forage throughout the day. Movement patterns are influenced by season and the availability of food. Completely wild-foraging groups spend ca. 70–75% of their time foraging (feeding + walking), and travel as much as 8–10 km/day, whereas groups that exploit garbage dumps reduce their foraging time to ca. 35–40% and travel 2–4 km/day (Muruthi *et al.* 1991, Altmann *et al.* 1993). Less time is spent feeding during the wet seasons and in years of high rainfall (Bronikowski & Altmann 1996, Alberts *et al.* 2005). These differences in foraging time are more pronounced for wild-foraging groups than for those that exploit garbage dumps. Yellow Baboons appear to be obligate drinkers: they drink almost daily and their home-ranges tend to include a water source within a half-day's journey (Altmann 1998). Yellow Baboons are not territorial, but have overlapping home-ranges of approximately 24 km² (for a group of about 40 animals).

Yellow Baboons have a highly diverse diet that incorporates a wide variety of plant and animal species. At the same time, they are extremely selective, as is evident in their differential use of plant parts of high nutritive value and their avoidance of toxic ones (Altmann 1998). Yellow Baboons incorporate new foods as they become available, whether through season or habitat change (Alberts *et al.* 2005). In Mikumi N. P., 85 plant foods are eaten (Norton *et al.* 1987) compared with 277 foods (plant & animal) for Amboseli (Altmann 1998). Foods available or utilized differ seasonally and, to a lesser extent, from year to year. Consequently, the duration, timing of study, and criteria for 'splitting' or 'lumping' food types influences the number of foods reported in the diet.

The numerous foods that Yellow Baboons consume include all or parts of various species of trees (particularly *Acacia* spp.), grasses, sedges and bushes, as well as animal matter, including insects (e.g. grasshoppers, beetles and larvae), and meat of several species of mammals. In Amboseli these include Cape Hare *Lepus capensis*, Thomson's Gazelle *Eudorcas thomsonii* and Grant's Gazelle *Nanger (granti) granti* and, more rarely, Impala *Aepyceros melampus*, Vervet Monkey *Chlorocebus pygerythrus*, Northern Lesser Galago *Galago senegalensis*, birds, reptiles and bird and reptile eggs. The inclusion of meat in the diet is largely opportunistic. Vertebrate prey are caught by juveniles and adults of both sexes, but consumption of larger prey is primarily restricted to adult baboons, particularly adult ♂♂.

Human refuse piles near settlements and tourist lodges are also exploited (Muruthi *et al.* 1991). Availability of these food sources results in less energy expenditure, more rapid juvenile growth, earlier physical maturation, more frequent reproduction, higher infant survival and adults that are larger and obese (Altmann *et al.* 1993, Altmann & Alberts 2005).

Social and Reproductive Behaviour Social. Yellow Baboons typically live in multimale, multifemale groups ranging in size from 18 to 100 individuals. The number of adult ♂♂ in a group is correlated with the number of adult ♀♀. Males tend to leave groups with few reproductive opportunities and join ones with many (Alberts & Altmann 1995a). Single-male groups also exist in Amboseli. These relatively ephemeral single-male groups occasionally join a multimale group; more commonly, additional ♂♂ join and thereby create a multimale group. Groups in Amboseli sometimes fission at approximately 60–70 individuals for wild-foraging groups and at larger sizes for groups with high food availability, but there is no simple relationship between group size and fission.

Females remain in their natal group for life; exceptions occur when a female's natal group fissions or fuses with another group. Females form a linear dominance hierarchy that tends to be stable among matrilineal and across generations. Maternal rank acquisition determines a young female's rank, even in the absence of her mother. Specifically, older juvenile ♀♀ usually attain a rank immediately below their mother, but above their older sisters. The daughters of the family matriarch are therefore ranked in inverse age-order. All long-lived ♀♀ that have adult daughters and that are not members of the top-ranking family lose rank to their adult daughters (Combes & Altmann 2001). Daughters of high-ranking ♀♀ reach maturity earlier and conceive their first offspring earlier than those of low-ranking ♀♀ (Altmann *et al.* 1988), particularly when groups are large.

Males are the dispersing sex. Natal dispersal occurs at ca. 8.5 years of age (6.8–13.4), although recent evidence suggests that Olive ♂♂ and hybrid Yellow–Olive ♂♂ in the Amboseli area disperse earlier than Yellow ♂♂ (Alberts & Altmann 1995b, 2001). Secondary dispersal is common. Group tenure averages 24 months in non-natal groups. Male maturation is also affected by mother's dominance rank. Sons of high-ranking ♀♀ physically mature earlier, as indicated by testicular enlargement, and attain adult dominance rank earlier than sons of low-ranking ♀♀ (Alberts & Altmann 1995b). Males form a linear hierarchy, but one that is much less stable than that of ♀♀ (Hausfater 1975). Fighting ability and age influence a male's rank. Male dominance rank predicts mating success. Mating success and offspring production are coincident with the time a ♂ is high-ranking in a non-natal group (Alberts *et al.* 2006).

Females have prominent oestrous swellings that are closely related to reproductive condition. When the ♀ is in oestrus, ♂♂ and ♀♀ form close associations, called 'consortships'. This form of mate-guarding is characterized by a ♂ following and mating exclusively with the oestrous ♀ for periods ranging from hours to several days (Rasmussen 1985). Fertilization is most likely to occur within the five days prior to the deturgescence of the sexual skin (Hendrickx & Kraemer 1969). Oestrogen levels are highest during this period, and consortships are most likely then, particularly with the highest-ranking ♂ (Gesquiere *et al.* 2007). Males, especially middle- and

lower-ranking ones, sometimes form coalitions in order to take over a consortship. These ♂♂ are usually older and past their prime, and have been resident in the group for a relatively long time (Noë 1992). Approximately half of the ♂♂ in Amboseli commence reproducing (i.e. begin consorting) in their natal group. Maternal siblings are usually strongly avoided as consort partners. Although consortships between paternal siblings do occur, these consort pairs exhibit lower levels of cohesion and sexual behaviour than do non-kin pairs (Alberts 1999).

Aggressive behaviours include lunging, staring, displaying the canines, and/or raising the eyebrows to show the white skin of the eyelids. Submissive gestures include cowering (of the whole body or part of the body), baring teeth while pulling back lips (in a grimace), screaming and raising the tail. Noisy and obvious fights between animals sometimes occur. More common, particularly among ♀♀, are the more subtle threats, displacements and responses to eyebrow-raising. Infant deaths from infanticide or kidnapping occur rarely (J. Altmann & S. Alberts pers. obs.).

Affiliative behaviours include reaching out a hand, huddling, grooming and remaining in close proximity. Grooming is common, and easily identifiable by the groomer's active brushing and searching of another's fur (sometimes removing dead skin flakes and ectoparasites) and by the relaxed posture of the individual being groomed. Adult and juvenile ♀♀ are the most common age/sex classes to engage in grooming. They groom each other, their infants and adult ♂♂. New mothers are particular targets of grooming behaviour by other ♀♀ in the group. Adult ♂♂ groom ♀♀, primarily during consortship. Female infants become more reciprocal groomers with their mothers than ♂ offspring and at a younger age. Females tend to disproportionately groom and stay near certain individuals within their social group; these 'friends' are most commonly, but not exclusively, their close maternal and paternal kin (Smith *et al.* 2003, Silk *et al.* 2006).

Infant Yellow Baboons ride ventrally on their mothers for the first few months and then gradually transition to predominantly ride dorsally or 'jockey' style by eight months. Contact is maintained primarily by the mother during the first month or two; as the infants age, however, they become more responsible for maintaining proximity to or finding their mothers (Altmann 1980). Infants and juveniles of both sexes spend considerable time playing with each other. By four years of age, play behaviour of the two sexes differentiates, and play groups tend to become single-sex; ♂♂ spend more time playing, and the play of ♂♂ becomes more rough (Pereira & Altmann 1985).

The behavioural repertoire includes at least ten vocalizations, including contact calls, 'grunts' and 'screams'. Grunts are given during foraging and may facilitate affiliative interactions and close spatial proximity. 'Lip-smacking' (a rapid movement of the tongue between the lips) is also an affiliative vocalization. Screams occur during agonistic interactions. Alarm calls and contact 'barks' also occur. Both sexes produce almost all of the vocalizations. Males produce a loud bark, a 'wahoo', more frequently than ♀♀ and in more varied contexts, including alarms and aggressive displays. Females produce individually identifiable copulation calls that vary in form over the menstrual cycle (Semple 2001). Specifically, calls are longer and contain more units during matings with higher-ranking ♂♂ (Semple *et al.* 2002). Infants produce a 'coo' distress call that is



Yellow Baboon *Papio cynocephalus* adult male.

virtually never given by adults. This rather mournful-seeming call is usually produced while the infant is crouching, and the call sometimes alternates with higher intensity screeches and 'ikks' (aka 'geckers').

Reproduction and Population Structure Polygynandrous. A single infant is born after a gestation of ca. 180 days. Twinning is rare (twice in 700 births in Amboseli; in one case the twins were stillborn, in the other one infant died after ten days and the other survived). Infants weigh ca. 850 g at birth (Ross 1991). Yellow Baboons are not seasonal breeders; both conceptions and births occur at appreciable frequencies year-round. However, under harsh conditions, such as drought, reproduction is more likely to fail at each stage – cycling, conception and foetal survival (Beehner *et al.* 2006). Weaning is completed between 12 and 18 months of age. Nutritional intake of ♀♀ during their weaning period predicts their lifetime reproductive success (Altmann 1991).

Males reach full adulthood at ca. 7–8 years of age. Although testicular enlargement, which is indicative of sperm production, occurs at a median age of 5.7 years (5.0–6.2, $n = 32$), the transition from subadulthood to adulthood occurs when ♂♂ enter the adult ♂ dominance hierarchy. At this time ♂♂ are large and strong enough to win fights with other adults. Median age of attainment of first adult dominance rank is 7.4 years (6.7–8.4). Adult ♂♂ then quickly rise in rank when young, but usually maintain high-ranking tenure for less than a year; eight months on average in Amboseli (Alberts *et al.* 2003; see Hamilton & Bulger 1990 and Packer *et al.* 2000 for similar patterns in Chacma and Olive Baboons, respectively). Attainment of adult dominance rank always precedes first consortship. Median age of first consortship is 7.9 years (7.4–8.5). High-ranking ♂♂ essentially monopolize consortships and, therefore, infant paternity during their tenure. As a result, age cohorts sometimes represent paternal sibships, although considerable variation exists in the extent to which this is true.

Females mature, as indicated by first sexual swelling, at ca. 4.5 years (Rhine *et al.* 2000, including a table comparing ♂ life-history milestones for Mikumi and Amboseli). Median cycle length is 39 days, including adolescent and immediate postpartum cycles that

are often longer than others (Gesquiere *et al.* 2007). Daughters of high-ranking mothers reach menarche and first conception earlier than those of low-ranking ♀♀. Following a period of adolescent sub-fertility, a ♀ first gives birth at ca. 6.5 years (Rhine *et al.* 2000). Pregnancy is marked by pink colouration around the edge of the callosities, on the paracallosal skin and sometimes by pink under the eyes in late pregnancy. Pregnancy is usually characterized by an absence of sexual swelling. Inter-birth intervals average two years in wild-feeding groups, and as little as one year during times of food abundance or in garbage-feeding groups. If the infant dies, ♀♀ resume cycling within one month of the death and conceive within one or two cycles (Altmann *et al.* 1988). If the infant survives, the mother experiences a postpartum amenorrhoea of 10–12 months and experiences three or four cycles before conceiving.

Sex ratio at birth is 1 : 1. Adult sex ratio is female-biased. In Amboseli wild-feeding groups have, on average, 1.6 adult ♀♀ per adult ♂, and groups with some garbage feeding have 2.5 adult ♀♀ per adult ♂; approximately half the population consists of sexually mature animals (0.61–1.35; Samuels & Altmann 1991). Infant mortality is approximately 30% within the first two years of life (Alberts & Altmann 2003). This is in addition to about 14% of pregnancies resulting in miscarriage (Altmann *et al.* 1988, Beehner *et al.* 2006). After the first two years of life, mortality rates are low until late adulthood. Median adult life-span is approximately 12 years in the wild. Maximum known life-span of wild Yellow Baboons is 27 years (Alberts & Altmann 2003). In captivity they can live into their early 30s (Bronikowski *et al.* 2002).

Predators, Parasites and Diseases Known predators of Yellow Baboons include Leopards *Panthera pardus*, Lions *Panthera leo*, Spotted Hyenas *Crocuta crocuta* and Nile Crocodiles *Crocodylus niloticus*. Robust Chimpanzees *Pan troglodytes* communally kill and eat immature Yellow Baboons in Mahale Mountains N. P. (Wrangham & Van Zinnicq Bergmann-Riss 1990, Nishie 2004). Potential predators include Cheetahs *Acinonyx jubatus*, jackals, raptors and pythons. Black-backed Jackal *Canis mesomelas* and raptor predation attempts have been observed on juvenile Yellow Baboons only (Altmann & Altmann 1970). Leopards appear to be particularly adept predators of baboons due to their nocturnal hunting and ability to climb trees, but Spotted Hyenas or Lions may be the predominant predator in some locales or years, depending on abundance. Humans occasionally kill Yellow Baboons as pests.

Starting >30 years ago (Kalter 1973), parasite screening of blood or faeces has occasionally been conducted for laboratory and field populations of various baboon species (see the recent, ongoing public database at www.mammalparasite.org). None the less, prevalence, incidence, temporal changes within populations and extent of pathogenesis remain largely unknown for virtually all parasites and baboon populations. This gap may soon be redressed as a recent surge of interest in primate disease has already resulted in one book (Nunn & Altizer 2006). The malaria-like parasite *Hepatozoon simiae* occurs in Yellow Baboons (Phillips-Conroy *et al.* 1988, Tung *et al.* 2009). In Amboseli screening for gastrointestinal parasites has been conducted several times and most recently reported in Hahn *et al.* (2003). Coxsackie virus type B2, a paralytic disease, has been found in wild populations, including Amboseli (Kalter 1973). SIV has been reported in two Yellow Baboons in

Mikumi N. P. (Kodama *et al.* 1989). In a serum viral screening (M. Isahakia pers. comm.) no SIV was found in approximately 80 animals in the Amboseli area.

Specific causes of death may differ by location and over time even in the same population as predator presence, disease presence and environmental factors change. More than half of the deaths in the Amboseli population are probably due to predation.

Conservation IUCN Category (2012): Least Concern. CITES (2012): Appendix II.

Although the Yellow Baboon is not currently threatened, the effects of human encroachment on numbers remain unclear. The baboons' tendency for crop-raiding and foraging in areas of human habitation has caused them to be treated as vermin in many areas, creating a situation that might lead, in the short-term, to local extinction, and in the long-term to more broad endangerment. However, their prevalence in non-farmland areas in Kenya and Tanzania reduces their vulnerability to human–animal conflict.

Habitat changes may also influence population size, density and ranging patterns. Although the cause(s) of decline in the baboon population in Amboseli in the 1960s is unknown, the dependence of Yellow Baboons on woodland savanna, and the degradation of this habitat in the Amboseli area, has caused local changes in range and range use in the decades since then. The woodland loss in Amboseli since the 1970s is associated with temperature increases in the area as a result of global climate change (Altmann *et al.* 2002).

Measurements

Papio cynocephalus

HB (♂♂): 730 (620–840) mm, n = 6
 HB (♀♀): 620 (550–680) mm, n = 4
 T (♂♂): 600 (450–660) mm, n = 6
 T (♀♀): 500 (380–560) mm, n = 4
 WT (♂♂): 24.9 (22.8–28.3) kg, n = 3
 WT (♀♀): 13.6 kg, n = 1
 BMNH, various locations (Napier 1981)

WT (♂♂): 25.8 kg, n = 20

WT (♀♀): 11.9 kg, n = 18

Wild-foraging individuals at Amboseli N. P., Kenya; see source for body measurements for garbage-feeding individuals (Altmann *et al.* 1993)

WT (♂♂): 24.7 (21.6–29.4) kg, n = 33

WT (♀♀): 13.0 (10.5–16.1) kg, n = 43

Wild-foraging individuals at Amboseli N. P., Kenya (2006–08; S. Alberts & J. Altmann pers. obs.)

WT (♂♂): 22.6 (18.6–27.7) kg, n = 35

WT (♀♀): 12.1 (9.1–16.8) kg, n = 35

Wild-foraging individuals at Mikumi N. P., Tanzania (J. Rogers pers. comm.)

Key References Altmann 1980, 1998; Amboseli Baboon Project website: www.princeton.edu/~baboon; Rhine *et al.* 2000.

Jeanne Altmann, Stephanie L. Combes & Susan C. Alberts

Papio anubis OLIVE BABOON (ANUBIS BABOON)

Fr. Babouin Doguera; Ger. Anubispavian

Papio anubis (Lesson, 1827). Manuel de Mammalogie ou Histoire Naturelle des Mammifères, p. 27. Upper Nile.Olive Baboon *Papio anubis* adult male.

Taxonomy Monotypic species. The ‘tangle’ characterizing baboon taxonomy (Groves 2001: 237) has generated at least three classifications for ‘Olive Baboon’: (1) a species, closely allied to Yellow Baboon *Papio cynocephalus*, Guinea Baboon *Papio papio* and Chacma Baboon *Papio ursinus*; or (2) a subspecies of a single species (*P. cynocephalus*) uniting these four forms under the common name ‘Savanna Baboon’; or (3) part of a ‘superspecies’ comprising these four taxa plus the Hamadryas Baboon *Papio hamadryas* (Sarmiento 1998a, b). Mitochondrial data argue compellingly against the second of these taxonomies and underscore the close phylogenetic relationship of Olive Baboons and Yellow Baboons (Newman *et al.* 2004, Zinner *et al.* 2009a, b). Four to seven geographic variants (subspecies) of Olive Baboon have been recognized (Hill 1967, 2000, Napier & Napier 1967). Currently, however, no subspecies are recognized (Groves 2001, 2005c, Grubb *et al.* 2003). Synonyms: *doguera*, *furax*, *graueri*, *heuglini*, *lestes*, *lydekkeri*, *neumanni*, *nigeriae*, *niloticus*, *olivaceus*, *silvestris*, *tessellatum*, *tibestianus*, *vigilis*, *weneri*, *yokoensis*. Chromosome number: $2n = 42$ (Romagno 2001).

Description Large, semi-terrestrial, diurnal monkey. Nares frequently projecting beyond nose (cf. ‘upturned’ nose of Yellow Baboon). Top of head appears flat when viewed from the front. Face naked, dark grey to black, framed by prominent ruffs of hair at cheeks. Ears large, though usually obscured by surrounding pelage. Pelage coarse, varying from dark grey to olive-brown, sometimes grading into olive- or light brown (khaki or grey). Dorsum and ventrum similarly coloured. Pelage of hands and/or feet black in

some populations. Tail well-furred, sometimes bent at acute angle midway (due to fused tail vertebrae), appearing as if ‘broken’. Ischial callosities variable shades of grey. Adult ♂♂ much larger than adult ♀♀ and with heavy, but not large, mane (= cape = mantle). Adult ♀♀ are about 54% the weight of adult ♂♂. Canines of adult ♂♂ long and pointed (worn down or broken in older individuals). Adult ♀ with much less well developed mane and smaller canines than ♂. Fertile ♀♀ undergo monthly cycles of conspicuous swelling of the pink/red perineal sexual skin. Paracallosal skin pink during pregnancy. Infants have black natal coat, pink face and paracallosal region; skin typically changed to black by 10–12 months of age, though maturational change in pelage colouration is more variable. Numerous photographs of *P. anubis* at many sites in Kenya and Tanzania are available at: www.wildsolutions.nl

Geographic Variation Four to eight geographic variants differentiated as subspecies (Hill 1967, Napier & Napier 1967) or even species (Elliot 1913b). Nevertheless, in spite of geographic variation in coat colour, the distribution of black pelage on hands and feet, and cranium size, Jolly (1993: 7) emphasizes how ‘remarkably similar’ Olive Baboons are across their entire distribution. Based on cranial measurements, the forms found in Uganda and DR Congo appear largest, while the smallest are Saharan isolates and populations in Tanzania and Ethiopia where distribution adjoins that of the Yellow Baboon and Hamadryas Baboon, respectively (Jolly 1993). One commonly cited form, the so-called ‘Heuglin’s Baboon’ of S Sudan and SW Ethiopia, is of unclear status: its wavy hair and mane are shared in common with other Olive Baboons, but its lighter colour and pale cheeks and undersides are distinctly different (Sarmiento 1998a).

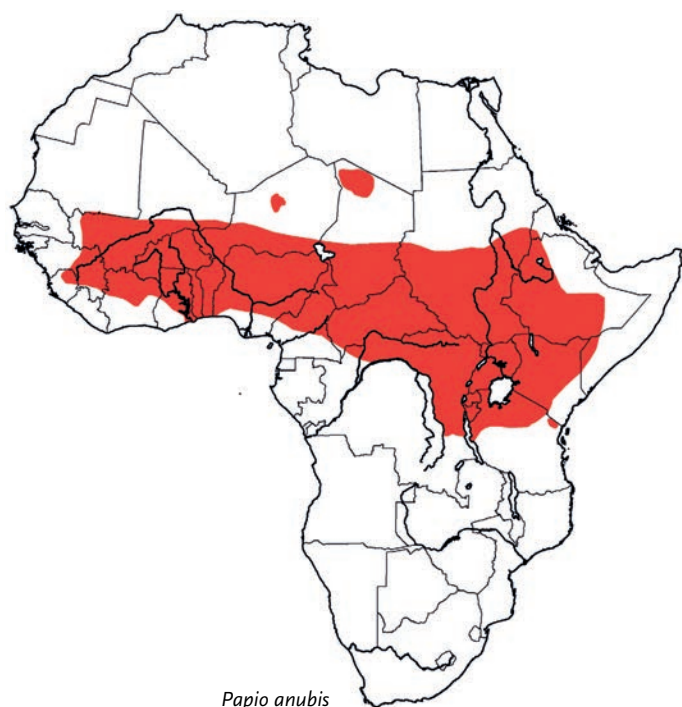
Similar Species

Papio cynocephalus. Sympatric or parapatric in SE Ethiopia, W Somalia, C and S Kenya, N Tanzania and south-east DR Congo. More gracile (slender). Mane of ♂♂ generally absent or much less developed. Dorsum light brown to yellowish-brown. Tail not ‘broken’. Nose ‘upturned’ (see above). Head appears pointed when viewed from the front.

Papio papio. Closely adjoining and probably parapatric in Mali and perhaps Guinea. Said to be sympatric in Sierra Leone (T. S. Jones in Booth 1958b). Smaller, with lighter, uniformly grizzled reddish-brown pelage; mane of adult ♂ more pronounced; tail arched.

Papio hamadryas. Sympatric or parapatric from above ca. 500 m on western edge of range in Ethiopia and Eritrea. Body smaller. Facial skin bright pink to red. Cheek tufts long, laterally projecting and silvery. Tail gently arched at distal end. Mane of adult ♂♂ generally much more prominent (to elbows) and silvery, contrasting with back. Male anogenital area is reddish.

Theropithecus gelada. Sympatric in highlands of N Ethiopia. Altitudinal overlap from ca. 2300–3800 m. Less prognathic. Mane extends to below elbows. Tail not ‘broken’. Patch of naked pink skin on upper chest in both sexes.

*Papio anubis*

Distribution Endemic to tropical Africa, mostly north of the equator. Sudan Savanna, Guinea Savanna, Northern Rainforest–Savanna Mosaic, Eastern Rainforest–Savanna Mosaic, Afromontane–Afroalpine, and Somalia–Masai Bushland BZs. Distribution more extensive than any other baboon; in fact, most African primates generally (only 3 of 64 species have larger latitudinal range; Cowlishaw & Hacker 1997). Straddles circumtropical Africa from Mauritania to N Cameroon eastward to C Ethiopia and SW lowlands of Eritrea, southwards through East Africa as far as SE DR Congo, Burundi and NC Tanzania (Wolfheim 1983). Southern-most population in Tanzania is probably at Mt Hanang ($4^{\circ}28'S$, $35^{\circ}24'E$, 2050 m asl; T. Butynski & Y. de Jong pers. comm.). Isolated populations occupy Tibesti Plateau ($20^{\circ}N$, $16^{\circ}E$) and Air Massif in Saharan Chad. In the wild a broad hybrid zone with Yellow Baboon runs along a north-east/south-west line from at least Meru N. P. in the north, through Tsavo East N. P. to the south-west Amboseli Basin, Kenya, to L. Manyara N. P., Tanzania (Alberts & Altmann 2001, Y. de Jong & T. Butynski pers. comm.). Hybridizes with Hamadryas Baboon in Ethiopia (Nagel 1973), SC Eritrea (Zinner *et al.* 2001c, 2009b), and Somalia (J. Beehner pers. comm.). In one stable hybrid zone along a 20 km stretch of the Awash Valley, C Ethiopia, admixture is maintained by movements of ♂♂ of both parental species, as well as of hybrid stock, among 8–12 groups (Phillips-Conroy *et al.* 1992). Hybridizes with Geladas *Theropithecus gelada* in Ethiopia (Dunbar & Dunbar 1974c, Jolly *et al.* 1997). Hybridization is suspected, though unsubstantiated, where distributions of Olive Baboons and Guinea Baboons presumably abut in Mali (Groves 2001).

Habitat As befitting its wide geographic range, *P. anubis* occupies an enormous variety of vegetation and climatic conditions from lowlands to high mountains. Found near sea level in Ghana (Depew 1983, L. Depew & I. Gordon pers. comm.) and probably also Togo, Bénin and SW Nigeria (Wolfheim 1983, Sarmiento 1998a). Occurs at 500–3300 m in Ethiopia (Yalden *et al.* 1977). Sighted at 3850 m on

Mt Orobó, Ethiopia, which is about 500 m above the treeline (Bolton 1973). Lowest altitude reported for East Africa (where the Yellow Baboon occupies the lower regions) is at 540 m in Meru N. P., C Kenya (Y. de Jong & T. Butynski pers. comm.). Highest altitudes reported for East Africa are 2500 m in the Echuya F. R., SW Uganda (E. E. Sarmiento pers. comm.), 2300 m in the Bwindi Impenetrable N. P., SW Uganda, 2370 m at Nyahururu (Thompson's Fall), C Kenya, and 2550 m at Empakai Crater in the Ngorongoro Conservation Area, NC Tanzania (Y. de Jong & T. Butynski pers. comm.).

Typically an open-country species, and thus common in Sudan and Sahel savannas, grassland, woodlands and rocky hill habitats. Individuals in some populations, however, spend up to 50–60% of their activity period in forest (Rowell 1966); mixed forest-mosaic and mid-altitude and montane forest (e.g. W Uganda, NE DR Congo), and high-altitude bamboo *Arundinaria alpina* forest (DR Congo). When in closed-canopy moist forest, *P. anubis* is seldom found more than 2 km into the forest. *Papio anubis* is nowhere known to live entirely within closed-canopy moist forest (T. Butynski pers. comm.). In the dry montane forest of the Mathews Range, C Kenya, *P. anubis* is common and appears to spend almost all of the time deep within forest, although there is some use of the limited 'open habitats' (cliffs, tallus slopes, burnt sites). Here it is important to note that all other cercopithecines are absent except for De Brazza's Monkey *Cercopithecus neglectus* (which is uncommon here). As such, this might be a case of 'competitive release', perhaps especially in the absence of Sykes's Monkey *Cercopithecus mitis* (De Jong & Butynski 2010a). Also inhabits semi-desert steppe and arid thorn scrub with gallery forest (Ethiopia) (Aldrich-Blake *et al.* 1971, Dunbar & Dunbar 1974b), though may be limited to river beds and gallery forests in these habitats (Zinner *et al.* 2001c). Makes use of mangrove forest in Kenya (T. Butynski & Y. de Jong pers. comm.) and in Ghana (L. Depew & I. Gordon pers. comm.) but does not appear to be able to live solely in this habitat. Habitat selection is limited primarily by availability of water and secure sleeping sites. These baboons require regular access to water, and moisture from subterranean plant parts is important in dry seasons.

Where studied, *P. anubis* inhabits areas with mean annual rainfall of 2022 mm in E Nigeria (Gashaka-Gumti N. P., Higham *et al.* 2009), 1400–1500 mm in SW Uganda (Bwindi Impenetrable N. P., Butynski 1985; Budongo F. R., Plumptre 1996; Kibale N. P., Struhsaker 1997), to 570 mm in Ethiopian semi-desert (J. Beehner pers. comm.), and ca. 300–900 mm in W Eritrea (Zinner *et al.* 2001c), with intervening values elsewhere, such as 710–756 mm in the Eastern Rift Valley, Kenya (Harding 1976) and 550 mm on the Laikipia Plateau, Kenya (Barton *et al.* 1996). Must have access to communally used sleeping refuges providing safety from predators: either large trees (e.g. Fever Trees *Acacia xanthophloea* in gallery forests [R. Palombit pers. obs.], Oil Palms *Elaeis guineensis* along L. Victoria [A. Matsumoto-Oda pers. comm.]) or steep cliff faces or rocky inselbergs ('koppies') [DeVore & Hall 1965]).

Abundance Considered 'abundant or common' in at least eight countries (Wolfheim 1983). Population density varies from 4 ind/km² in arid savanna–woodland habitats (DeVore & Hall 1965), 11–14 ind/km² in moist forests in W and SW Uganda (Rowell 1966, Butynski 1985, Plumptre & Reynolds 1994), to 30–35 ind/km² in moist forests in W Tanzania (Ransom 1981) and WC Uganda (Struhsaker 1997).

Adaptations Diurnal and semi-terrestrial. Primary adaptation is extreme adaptability and flexibility to conditions, as exemplified by ability to exploit foods of many kinds. Digitigrady (body weight borne on volar surfaces of fingers) represents morphological adaptation for increased efficiency of terrestrial locomotion (Whitehead 1993), convergent in kind with ungulate specialization. ‘Sunbathing’ at the sleep tree or sleep cliff in early morning is common (R. Palombit pers. obs.). Ambient temperature affects activity budgets (Dunbar 1994) and social behaviour, such as ventro-ventral contact and huddling of mothers with infants, which are negatively correlated with temperature (Brent *et al.* 2003).

Foraging and Food Omnivorous. Feeding occurs throughout daylight hours. Of the daily activity budget, feeding variably accounts for 20% (Ghana; Depew 1983), 26% (Tanzania; Ransom 1981), 31% (Ethiopia; Nagel 1973), 31% (Nigeria; Warren 2003), 40% (Kenya; Barton 1989), 41% (Côte d’Ivoire; Kunz & Linsenmair 2008b) and 51% (Kenya; Harding 1976). Diet shifts continually with season and even time of day, allowing exploitation of a range of items as they become available in space and time. Time spent feeding does not vary significantly across seasons, however (Bercovitch 1983). Diets do not differ qualitatively between the sexes, but ♀♀ spend significantly more time feeding than do ♂♂ (except when engaged in sexual consortships) (Bercovitch 1983).

Ecological adaptability of *P. anubis* is exemplified by a dietary diversity so pronounced that early researchers remarked it would be easier to list foods *not* eaten, than to attempt a complete inventory. Tallies of plant species eaten vary from 22+ (Rowell 1966), 45+ (Barton *et al.* 1993), 62+ (Ransom 1981), 84 (Kunz & Linsenmair 2008b), 94+ (DeVore & Hall 1965), to 111 (Warren 2003). Plants constitute the majority of diet, up to 98% in Kenya (DeVore & Hall 1965) and Côte d’Ivoire (Kunz & Linsenmair 2008b). Digging up rhizomes – as well as other forms of underground storage parts in plants (e.g. bulbs, tubers, corms) – represents a principal ecological adaptation made possible by baboons’ combination of prehensile hands and committed terrestriality. Underground storage parts account for up to 16% of the plant diet (Barton *et al.* 1993). Grass (e.g. *Paspalum conjugatum*) is a principal food for Olive Baboons in savanna/woodlands, but also for ‘forest dwelling’ Olive Baboons, which forage extensively in nearby grass plains (Rowell 1966). Diverse grass parts are utilized: young meristems growing in moist soil, seeds (filtered by pulling distal ends of intact stems through the mouth [R. Palombit pers. obs.]) and nutrient- and water-rich subterranean rhizomes.

Ripe and unripe fruits eaten, particularly in forests where preference is for fleshy fruits, such as figs *Ficus* spp. (DeVore & Hall 1965, Barton *et al.* 1993). In more arid regions they eat less pulpy fruits of trees and bushes/shrubs (e.g. *Carissa edulis*, *Scutia myrtina* [R. Palombit pers. obs.] and *Parkia biglobosa* [Kunz & Linsenmair 2007]). Olive Baboons are likely dispersal agents for numerous plants (e.g. *Securinega virosa*, *Azadirachta indica*, *Nauclea latifolia*, *Lannea acida*, *Diospyros mespiliformis*, *Tapura fischeri*, *Oxyanthus racemosus* [Lieberman *et al.* 1979, Kunz & Linsenmair 2008a]). Seeds are also eaten, particularly of drier fruits (e.g. *Acacia tortilis*, *Acacia drepanolobium* [R. Palombit pers. obs.]). Partially digested seeds are harvested from the fresh faeces of herbivores (e.g. Impala *Aepyceros melampus*, African Buffalo *Syncerus caffer*, Savanna Elephant *Loxodonta africana*). Flowers are eaten seasonally (e.g. *A. xanthophloea*, *A. drepanolobium*, *Cullumia squarrosa*

[DeVore & Hall 1965]). Along waterways Olive Baboons eat aquatic plants (e.g. *Trifolium* sp. and roots/storage parts of Nymphaeaceae [R. Palombit pers. obs.]). Numerous species among the herbaceous ground cover provide food in the form of fruits, seeds, flowers and, occasionally, young leaves. Fungal mycorrhiza and fruiting sporophores are exploited (R. Palombit pers. obs.); discovery of large mushrooms excites as much feeding competition as predatory capture of meat (see below). Gum is an important dietary supplement in drier habitats (e.g. *A. drepanolobium*-dominated woodland in C Kenya). Adult Olive Baboons access tree cambium by peeling bark off or, more often, by snapping saplings (requiring strength more often possessed by adult ♂♂). *Papio anubis* is a human commensal in some locales, feeding in garbage dumps near towns, small settlements and tourist lodges (Kemnitz *et al.* 2002). They also exploit foods introduced by humans (e.g. the base stem of prickly pear cactus *Opuntia vulgaris* [R. Palombit pers. obs.]) and plants domesticated for agriculture, see below).

Insects are eaten consistently but opportunistically, usually via random discovery of individuals (particularly orthopterans and lepidopterans) in grass or underbrush, or small numbers of ants and termites exposed as searching baboons systematically overturn rocks (DeVore & Hall 1965, Rowell 1966). Olive Baboons of Laikipia Plateau, C Kenya, regularly eat harvest ants (*Crematogaster* spp., *Camponotus* spp., *Tetraponera* spp.) residing symbiotically inside galls of *A. drepanolobium* (R. Palombit pers. obs.). Also eaten are temporarily superabundant insects, e.g. termite alates during nuptial flights and infestations of army worm caterpillars (DeVore & Hall 1965). Other invertebrates taken include scorpions and snails (terrestrial and aquatic) (DeVore & Hall 1965, Rowell 1966). Although the Olive Baboon’s catholic diet is unambiguously vegetarian, meat constitutes a potentially important protein supplement. In two populations occupying different habitats, a successful predation event was observed every 22 h (Harding 1973) and 30 h (Rowell 1966). As with plant foods, a great variety of vertebrate prey are eaten, including fish, frogs, lizards, crocodile eggs, terrapins, birds (caught on the ground or occasionally on the wing, e.g. guineafowl *Agelastes* spp., Yellow-necked Spurrow *Francolinus leucoscepus*, nightjars, quail, plover), birds’ eggs, various rodents (mice, ground squirrels, tree squirrels), bats, Cape Hares *Lepus capensis*, Vervet Monkeys *Chlorocebus pygerythrus*, small antelopes (e.g. Guenther’s Dik-dik *Madoqua guentheri*), Oribi *Ourebia ourebi*, Thomson’s Gazelle *Eudorcas thomsonii* and Grant’s Gazelles *Nanger (granti) granti*, and the young only of larger ungulates (Impala, Bushbuck *Tragelaphus scriptus*, Hartbeest *Alcephalus buselaphus*) (Rowell 1966, Kingdon 1971, Harding 1973, Brashares & Arcese 2002). Of these animals, hares, mice and small antelopes are the most common prey. The ecological relationship with prey such as Impalas, Bushbucks and Vervet Monkeys is curious, since Olive Baboons also associate with these animals without causing alarm (see below). Carrion is exceptional as a food.

Prey is located by (literally) stumbling upon it, and captured by seizing it and immediately commencing eating (usually while the prey is still alive). Behaviour reminiscent of more deliberate ‘hunting’ also occurs. Careful and apparently purposeful scanning of vegetation, flushing of prey, and pursuit precede some instances of successful captures, suggesting organized predatory behaviour (Harding 1973). Olive Baboons hunt individually, however, not cooperatively. Juveniles, as well as adults, are able to capture small prey (e.g. mice and small birds), which is eaten quickly in a gulp or two; larger prey (the size of an adult hare and above) requires a long processing time

and are most often captured by adult ♂♂ (Harding 1975). Capture of large prey arouses social tension as well as overt aggression, as the carcass makes its way 'up the hierarchy', being surrendered to progressively higher-ranking ♂♂ arriving at the scene of the kill (R. Palombit pers. obs.). Direct food sharing (cf. Robust Chimpanzees *Pan troglodytes*) has not been observed, although adult ♂♂ tolerate the proximity of certain individuals (particularly fertile ♀♀), which will snatch scraps of meat from the ground. An interesting, but as yet unsubstantiated, proposition is that variation in predatory behaviour reflects the action of cultural transmission, generating contrasting 'traditions' of meat-eating (Strum 1975).

Polyspecific associations are relatively rare, but Olive Baboons associate with Impalas, Bushbucks, Plains Zebras *Equus quagga* and Vervet Monkeys in apparent mutualism. Ungulates and Olive Baboons beneficially attend to each other's alarm calls (DeVore & Hall 1965), while young Vervets and Olive Baboons sometimes play with one another (Kingdon 1971).

Social and Reproductive Behaviour Social. Olive Baboon groups vary from 12 to as many as 130 individuals. Average group size is reported as 87.5 individuals (S.D. = 20.4, $n = 4$) in C Kenya (Berger 1972b), 65 individuals (S.D. = 34, $n = 7$) in Kenya (Harding 1976), 30 individuals (S.D. = 24.8, $n = 6$) in Ethiopia (Brett *et al.* 1982), 32 individuals (S.D. = 12.8, $n = 8$) in Tanzania (Ransom 1981), 30 individuals in Ghana (Depew 1983), 20.7 individuals (S.D. = 5.1, $n = 22$) in Nigeria (Higham *et al.* 2009), and 15 individuals ($n = 8$) in Côte d'Ivoire (Kunz & Linsenmair 2008b). Socioeconomic sex ratio of adult ♀♀ per adult ♂♂ varies from 1.65 (Tanzania; Ransom 1981), 2.02 (Kenya; Barton 1989), 2.22 (Ghana; Depew 1983), 2.5 (Kenya; DeVore & Hall 1965) to 3.83 (Kenya; Harding 1976). Greater preponderance of adult ♀♀ arises more through sex differences in maturation rates rather than differential mortality. Immature individuals typically outnumber adult ♀♀ 2 : 1.

Males typically disperse from natal groups at 6–9 years of age, although emigrations at ages as young as four years occur (Packer 1979a). Given the rarity of sightings of solitary individuals, they apparently soon enter another group rather than live alone for prolonged periods. Females are philopatric, remaining in their natal groups their entire lives (with rare exceptions). This sex difference generates the matrilineal structure of Olive Baboon groups: related ♀♀ affiliate with one another and compete with other sets of ♀♀ relatives. Male and ♀ relationships are organized into dominance hierarchies that are maintained by a rich repertoire of vocal, visual and tactile communicative displays (e.g. the subordinate 'grimace' facial expression), and by occasional aggression. Females usually acquire dominance status via 'youngest daughter ascendancy', in which a maturing ♀ assumes a rank position immediately below her mother and above her older sisters (as well as all of the ♀♀ ranking below her mother) regardless of body size (Hall & DeVore 1965, Ransom 1981, Strum 1987). Female hierarchies are typically linear and highly stable, changing little over lifetimes.

Male social relationships are also generally organized around dominance status, but in contrast to ♀♀ hierarchies are more variable, dynamic and even obscure at times (Packer 1979b, Harding 1980, Ransom 1981, Strum 1982, Sapolsky 1993). Male hierarchies are not always linear, e.g. when individual alliances generate 'clusters' of ♂♂ that collectively dominate one another (Hall & DeVore 1965). Males also experience substantial changes in rank during

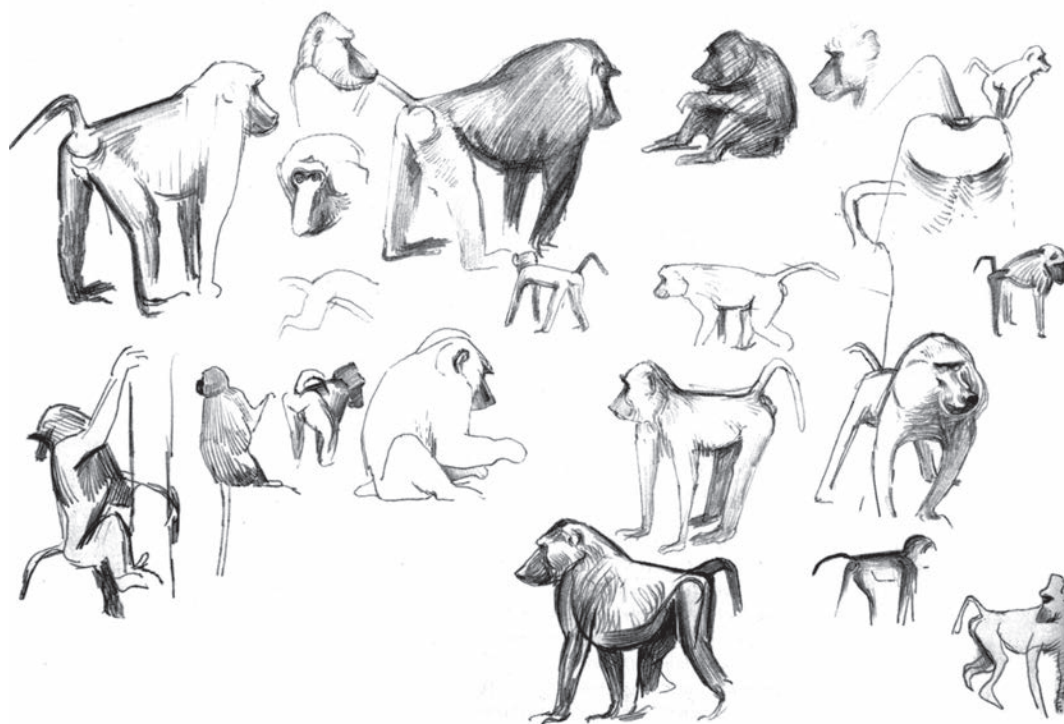
their lives. This is partly because immigration of new male(s) may temporarily destabilize the hierarchy (Sapolsky 1993), and partly because coalitionary behaviour undermines the stability of dominance relationships. Thus, ♂ rank is apparently influenced by body and canine size, and physical stamina, but also by social skill in forming and maintaining coalitions. In addition to their unambiguous competitive basis, social relationships among ♂♂ also show conspicuous affiliative components, which are likely related to maintenance of these alliances (Harding 1980, Smuts & Watanabe 1990).

Olive Baboons are polygynous. Adult ♀♀ can copulate at any time, but proceptivity and receptivity generally track the monthly menstrual cycle (Hall & DeVore 1965, Ransom 1981, Bercovitch 1991). Adult ♂ sexual interest depends largely on the condition of the female's sexual skin, which is generally correlated to ovulatory status (Wildt *et al.* 1977, Higham 2008a, b, Daspre *et al.* 2009). Males closely follow and groom fertile ♀♀ while the sexual skin increases gradually in size, but cease this 'sexual consortship' after the rapid 'deflation' of the skin 2–3 days following ovulation (Bercovitch 1986). Females 'present' hindquarters to ♂♂ to solicit close examination of the sexual swelling and/or copulation. Copulation rarely involves conspicuous vocalizations (Bercovitch 1991). There is debated evidence that ♀♀ of greater reproductive quality (i.e. earlier menarche or greater offspring survival) have consistently longer swellings (Domb & Pagel 2001, Zinner *et al.* 2002a). This suggests an intriguing, but unsubstantiated, potential for ♂♂ to use visible variation in females' swellings to discriminate among potential mates and to mediate mating competition with rival ♂♂.

Male Olive Baboons compete intensely with one another to maintain sexual consortships – and thus copulatory access – with swollen fertile ♀♀, especially maximally swollen ♀♀. The strong sexual dimorphism of the species is a likely consequence of this competition.

Dominant ♂♂ are generally more successful than subordinate rivals in obtaining periovulatory matings, but coalitionary confrontations by multiple ♂♂ may override an individual's dominance advantage (Bercovitch 1988). Typically, two or more 'follower' ♂♂ tag along behind a consort pair for hours or even days (Danish & Palombit 2008), and then cooperatively displace a (sometimes higher-ranking) ♂ from his consortship through threats and/or aggression; one of the coalitionary challengers then becomes the new consort of the ♀ (Hall & DeVore 1965, Ransom 1981, Strum 1987, R. Palombit pers. obs.). This behaviour was originally interpreted as an example of reciprocal altruism, in which unrelated ♂ allies presumably take turns obtaining the mating opportunities achieved through successive coalitionary episodes (Packer 1977). Unambiguous symmetry of benefits has not been substantiated by subsequent research, however (Noë & Sluijter 1995). Middle-ranking ♂♂ are more likely than high- or low-ranking ♂♂ to develop the affiliative bonds that engender successful coalitionary cooperation. Newly immigrant ♂♂ are disproportionately the targets of such coalitions. Although most conspicuous in the reproductive context, ♂ coalitions also occur during disputes over meat, defence of infants, general aggression and for no obvious reason (Smuts 1985). Stable alliances between ♂♂ can obscure dominance relationships by altering the rank of a ♂ in the presence of his ally. Thus, a positive correlation between non-natal adult ♂ rank and mating success has been documented in some studies (Packer 1979a, b), but not in others (Bercovitch 1986). Variation in male–male aggressiveness and affiliation is also attributed to cultural transmission of contrasting social 'traditions' (Sapolsky & Share 2004, Sapolsky 2006).

Olive Baboons
Papio anubis.



Lactating ♀♀ (and sometimes pregnant ♀♀) associate conspicuously with a particular adult ♂ or two (Smuts 1985, R. Palombit pers. obs.). These cohesive 'friendships' may beneficially promote ♂ protection of ♀♀ and/or their dependent infants from harassment from other (higher-ranking) ♀♀ and especially ♂♂. This has been substantiated by playback experiments, which show that ♂♂ respond significantly more strongly to the distress vocalizations of their ♀♀ friends than control ♀♀ of similar rank and reproductive status (Lemasson *et al.* 2008). Furthermore, cortisol levels in lactating ♀♀ suggest that ♂ friends buffer ♀♀ from harassment-induced stress (Shur 2008). In particular, the hormonal data suggest that lactating ♀♀ are susceptible to stress from harassment by adult ♂♂ (rather than higher-ranking ♀♀), and that friendships with ♂♂ may ameliorate this stress. Mating patterns suggest that these ♂ associates are often, but not always, the fathers of the infants of their ♀ 'friends'. In cases where a ♂ is not the father of his ♀ friend's infant, Smuts (1985) hypothesized that he will be preferentially selected by the mother as sire of her next infant. Genetic data are currently unavailable to test these alternatives directly. Higher-ranking ♀♀ generally achieve greater lifetime reproductive success than lower-ranking rivals, due to earlier menarche, faster reproductive rate (e.g. inter-birth intervals up to six months shorter), or greater offspring survivorship (Smuts & Nicolson 1989, Packer *et al.* 1995, Garcia *et al.* 2006). Compared to subordinates, however, dominant ♀♀ experience higher rates of spontaneous abortion and miscarriage (Packer *et al.* 1995), though the explanation that this results from higher circulating levels of androgens is questioned (Altmann *et al.* 1995). In any event, any greater difficulties in completing pregnancies do not override other reproductive advantages of high rank, which derive primarily from priority of access to resources via supplanting of subordinate rivals from food sources. Thus, ♀♀ at the top of the hierarchy may obtain food at rates 30% higher than those at the bottom (Barton & Whiten 1993). In addition to these nutritional issues, rank-related reproductive rates may be influenced by psychosocial stress (Rowell 1970a, Bercovitch

& Strum 1993) and access to ♂♂ as protective associates (Smuts 1985). Agonistic interaction accounts for a larger proportion of the activity budget of ♀♀ than of ♂♂ (Bercovitch 1983). Coalitions among related ♀♀ do occur, but usually less frequently than among ♂♂ (Johnson 1987, Barton *et al.* 1996). Reconciliation behaviour following conflicts occurs among all age/sex classes, but is more common among ♀ kin (Castles & Whiten 1998).

The Olive Baboon has a rich and diverse vocal repertoire that has not been rigorously studied since Hall & DeVore's (1965) initial description (see also Ransom 1981). The loud bi-phasic 'wahoo' is arguably the most conspicuous call, audible up to 3.0 km, given primarily by adult ♂♂, and elicited by intense male-male aggression (intra- and inter-group), encounters with predators, or spontaneously (in sleep trees usually). This vocalization, however, occurs far less frequently than the more common barks, growls, grunts, screams and coughs that mediate intra-group social interactions in, currently, unclear ways.

There is great variation in mean home-range size; 4–5 km² in moist forest or semi-forest habitats (Rowell 1966, Ransom 1981); 0.4–1.7 km² (Kunz & Linsenmair 2008b), 1.5 km² (Warren 2003), 19.7 km² (Harding 1976), 31.0 km² (Smuts 1985) and 43.6 km² (Barton *et al.* 1992) in drier savanna/woodlands; 4.3 km² (Aldrich-Blake *et al.* 1971) and 0.9 km² (Dunbar & Dunbar 1974b) in arid thorn scrub. Mean daily distance travelled is 2.4–6.0 km in savannas (Harding 1976, Barton *et al.* 1992, Kunz & Linsenmair 2008b), 2.4 km in forests (Rowell 1966) and 1.2 km in arid Ethiopia (Dunbar & Dunbar 1974b). In savanna/woodland habitats day range increases as resources become seasonally scarcer, suggesting a time-minimizing (rather than energy-maximizing) foraging strategy (Barton *et al.* 1992). Access to waterholes particularly influences ranging in dry season. Groups are not territorial. Home-ranges overlap extensively. Inter-group interactions are frequently peaceful, after which one group (often the smaller) moves off (DeVore & Hall 1965). Chases may occur, but these are often adult ♂♂ herding ♀♀ of their own group away from the other group. Individuals from neighbouring

groups sometimes commingle completely, but tensions run high and intense fighting can suddenly break out, involving numerous individuals of both sexes; in one episode in Kenya multiple ♂♂ and ♀♀ mobbed a subadult ♂ from another group, fatally wounding him (R. Palombit pers. obs.).

Reproduction and Population Structure Onset of puberty in ♂♂ (i.e. testicular enlargement) occurs at 5–6 years of age (Packer 1979a) when ♂♂ are ca. 7–8 kg (Jolly & Phillips-Conroy 2003). Testes, body size and mane length attain maximal adult proportions at around the same time (Strum 1991, Jolly & Phillips-Conroy 2003), which has been reported at 6.5–7.5 years (Packer 1979a) and 9–10 years of age (Glassman *et al.* 1984, Strum 1991). Canine eruption occurs at about eight years (Strum 1991). Females reach sexual maturity (i.e. commence monthly menstrual cycling) at ca. 4.5–5 years, pass through a period of adolescent sterility and give birth for the first time at ca. 6–7 years (Packer 1979a, Scott 1984, Bercovitch & Strum 1993, Williams-Blangero & Blangero, 1995). Mean inter-birth interval (in months) ranges from 22.2 (Packer 1979b), 23.5 (Kenyatta 1995), 25.2 (S.E. = 1.2, n = 13; Smuts & Nicolson 1989), 29.9 (Higham *et al.* 2009), 30.3 (Depew 1983). Inter-birth intervals are much shorter for ♀♀ that obtain additional food through captive provisioning (mean = 15.0 months, S.D. = 0.70, n = 21; Garcia *et al.* 2006) or crop-raiding (16.5 months) (Higham *et al.* 2009). Breeding occurs throughout the year (Bercovitch & Harding 1993). In some (not all) populations a peak in births occurs at the onset of rains (e.g. in Oct–Dec in Kenya), just before food supplies also peak (DeVore & Hall 1965). Single young are born after a gestation of 180–185 days (154–185 days; Packer 1979a, Smuts & Nicolson 1989, Garcia *et al.* 2006). Weight at birth in captivity is 980 g for ♂♂ (670–1220 g, n = 77) and 920 g for ♀♀ (700–1400 g, n = 66; Coelho 1985). Twins not reported.

Direct care of infants (e.g. nursing, carrying) is predominantly by mothers, although mothers' ♀ kin and ♂ 'friends' (see above) may interact affiliatively with infants at high rates. Weaning is gradual and difficult to demarcate, but is generally complete by 300 days (Packer 1979a) to 420 days of age (Nicolson 1982). Adolescents of both sexes experience a growth spurt, which is delayed and more intense in ♂♂ (Glassman *et al.* 1984). Mean inter-birth intervals are 22–26 months for Tanzanian and Kenyan populations (Packer 1979a, Smuts & Nicolson 1989, Kenya 1995), and 30 months for a Ghanaian population (Depew 1983). If infants die, mothers resume cycling within 1–3 months and are shortly, thereafter, pregnant again (Collins *et al.* 1984, Smuts & Nicolson 1989). Infant mortality is 57% among primiparous mothers, 16% in multiparous ♀♀ (Nicolson & Smuts 1989), and is due primarily to disease, predation and nutritional/energetic stress. Infanticide by ♂♂ is widespread but uncommon (accounting for <5% of infant mortality), with the possible exception of the Gombe Stream N. P. population, Tanzania (where it apparently accounts for 10–25% of infant mortality; Palombit 2003). The patterning of infanticide suggests it is unlikely to constitute a ♂ reproductive strategy. Maximum longevity is 48 years in captivity (Kingdon 1971), though considerably less in the wild (ca. 20 years; Bronikowski *et al.* 2002).

Predators, Parasites and Diseases The primary non-human predator of the Olive Baboon is the Leopard *Panthera pardus*, which

usually (but not always) attack at night (preferentially targeting adult ♂♂). Hunting success of Leopards is significantly reduced by communal mobbing by multiple adult and subadult ♂♂ (and occasionally adult ♀♀) (Cowlshaw 1994). This aggressive and raucous defence may result in death to the Leopard, but ♂♂ sometimes immediately and hastily retreat from a Leopard, abandoning even adult ♀♀ and infants in their wake. The reasons for such contrasting ♂ responses to Leopard encounters are unknown. In one case, mobbing generated a foraging benefit, when a Leopard attacked by ♂♂ baboons fled, yielding a freshly killed Impala (Cavallo 1990). Other predators are Lions *Panthera leo*, Spotted Hyenas *Crocuta crocuta*, Nile Crocodiles *Crocodylus niloticus* and Pythons *Python* spp. Robust Chimpanzees communally prey on immature Olive Baboons (e.g. Gombe N. P.; Wrangham & Van Zinnicq Bergmann-Riss 1990). Medium-sized carnivores, such as Cheetahs *Acinonyx jubatus* and African Wild Dogs *Lycaon pictus*, are unlikely predators, but potentially dangerous (given the defensive antagonism they occasionally elicit from Olive Baboons). Raptors are unlikely predators, but there is one report of Olive Baboon remains in the nest of an Africa Crowned Eagle *Stephanoaetus coronatus* (Mitani *et al.* 2001). Even the diets of known predators, including Leopards, typically emphasize other, less pugnacious prey (such as small ungulates) (Bailey 1993). A study in Côte d'Ivoire reported the relative frequency of Olive Baboon prey remains in Lion and Leopard scats as only 2% (Bodendorfer *et al.* 2006). Thus, although the Leopard, Lion and, locally, Robust Chimpanzee are serious predators, the Olive Baboon is not their primary prey. In terms of demographic impact, the most serious predator is humans, which probably kill tens of thousands of Olive Baboons each year through trapping, poisoning and hunting.

The Olive Baboon is vulnerable to infectious diseases such as tuberculosis (bovine and human), non-tuberculosis *Mycobacterium*, yaws *Treponema pertenu* and simian immunodeficiency virus (SIV) (Wallis & Lee 1999, J. Mwenda pers. comm.). Herpes B *Herpes simiae* has not been found in wild populations (Kingdon 1971). Olive Baboons living near settlements may be indirectly infected by humans (Wallis & Lee 1999), and humans by Olive Baboons (Legesse & Erko 2004). Olive Baboons are capable of hosting a wide variety of internal parasites (Toft 1986, Strum *et al.* 1989, Wallis & Lee 1999, Hope *et al.* 2004, Legesse & Erko 2004, Ocaido *et al.* 2004). Susceptible to protozoans, such as *Cryptosporidium*, *Endolimax nana*, *Entamoeba coli*, *Entamoeba histolytica*, *Enteromonas hominis*, *Giardia* as well as the malarial *Plasmodium gonderi* (although monkeys can theoretically act as vectors for malarial transmission to people in the presence of *Anopheles* mosquitoes, *P. gonderi* is not among the four *Plasmodium* species commonly responsible for malaria in human populations). Olive Baboons typically host a complement of metazoan endoparasites, particularly nematodes. *Trichuris*, *Strongyloides*, *Oesophagostomum* and *Ternidens* appear to be relatively common, though not necessarily in all populations. Also known is the nematode *Enterobius*, trematode fluke *Schistosoma mansoni*, tapeworms (*Diphylobothrium*, *Hymenolepis*, *Spirometra*, *Multiceps*), roundworms (*Ascaris*), hookworms (*Ancylostoma*, *Necator*), filarial worms (*Loa*) and cestode tapeworms (*Diphylobothrium*, *Spirometra*, *Anoplocephala*, *Dipylidium*). Cestodes (e.g. *Echinococcus*, *Mesocestoides*), whose primary hosts are other mammals (e.g. canids) or birds, may also occur in Olive Baboons. Ectoparasites include fleas (*Tunga*), lice (*Anoplura*), ticks (*Ixodidae*) and mites (*Proscorptidae*).

Natural infestation rates are poorly understood, partly because clinical symptoms are mild or absent in unstressed or otherwise healthy

individuals, but recent study of three populations reveals variation in gastrointestinal infection. Among Olive Baboons in C Kenya, *Strongyloides* and the pinworm *Enterobius* were found in 76% and 12% of samples, respectively ($n = 42$; Hahn *et al.* 2003). In a population in moist forest in Uganda 79% exhibited *Ascaris* infection, 37% *Strongyloides*, 16% *Trichuris* and 42% *Ternidens*. Protozoans in 140 samples were represented as follows: 32% *Cryptosporidium*, 58% *Giardia* and 99% *Eimeria* (Hope *et al.* 2004). In Ethiopia infection rates by the most common intestinal parasites were: 83% *E. coli*, 37% *Strongyloides*, 27% *Trichuris* and 20% *S. mansoni* ($n = 59$; Legesse & Erko 2004). Although infectious diseases and endoparasites are suggested to limit Olive Baboon demography (Rowell 1966) as well as geographic expansion of the species into equatorial rainforests (Kingdon 1971), direct empirical evidence is lacking. Nevertheless, the potential influence of parasites on demography is indicated by observed associations between: (1) age (and possibly dominance rank) of Olive Baboons and *Strongyloides* load, and (2) *Trichuris* egg output and ♀ reproductive status (Müller-Graf *et al.* 1996). Parasites also influence individual behaviour. Besides the servicing of intra-group social relationships, social grooming removes most ectoparasites from body areas inaccessible by self-grooming. Additionally, Olive Baboons' periodic change in sleeping sites may reduce potentially infectious contact with accumulations of faeces containing the eggs of endoparasites.

Conservation IUCN Category (2012): Least Concern. CITES (2012): Appendix II.

Considered an agricultural pest throughout its range – particularly to inadequately guarded farms near forest edges – and therefore officially classified as ‘vermin’ (African Convention) (Paterson 1999). Responsible for much of the animal-induced damage to African crops (up to 70% in some W Uganda localities), especially maize and cassava, as well as tuber crops ignored by other primates (Naughton-Treves *et al.* 1998, Hill 2000). Thus it rivals – and in some areas surpasses – the crop damage caused by Bushpigs *Potamochoerus larvatus* and Bush Elephants. Although recent studies suggest that patrolling and informed placement of farms reduce crop-raiding by Olive Baboons (Hill 2000), previous control measures have typically emphasized vigorous campaigns of extermination. The consequent killing of tens of thousands annually poses the most serious conservation threat, followed by habitat conversion (particularly near forests), and some continued trapping for biomedical research. Nevertheless, the Olive

Baboon remains abundant throughout much of its range. Long-term demographic trends remain unclear, however, in light of intensifying agricultural conflict with humans, habitat loss and local extinctions.

Measurements

Papio anubis

T (♂♂): 568 (S.D. = 32) mm, $n = 142$

T (♂♂): 479 (S.D. = 35) mm, $n = 95$

HF (♂♂): 217 (S.D. = 93) mm, $n = 157$

HF (♀♀): 185 (S.D. = 81) mm, $n = 91$

WT (♂♂): 22.8 (15.5–29.4) kg, $n = 185$

WT (♀♀): 12.3 (8.9–18.1) kg, $n = 112$

Awash, C Ethiopia (Jolly *et al.* 1997, C. J. Jolly & J. E. Phillips-Conroy pers. comm.)

HB (♂♂): 770 (622–838) mm, $n = 130$

HB (♀♀): 665 (609–731) mm, $n = 173$

T (♂♂): 508 (381–603) mm, $n = 130$

T (♀♀): 432 (318–533) mm, $n = 173$

HF (♂♂): 203 (178–229) mm, $n = 130$

HF (♀♀): 175 (152–190) mm, $n = 173$

WT (♂♂): 21.1 (7.9–29.5) kg, $n = 177$

WT (♀♀): 12.2 (6.3–16.8) kg, $n = 237$

Laikipia Plateau, C Kenya (Berger 1972a)

WT (♂♂): 24.4 (21.2–29.0) kg, $n = 11$

WT (♀♀): 12.8 (9.8–15.2) kg, $n = 30$

Gilgil, SW Kenya (Smuts 1985)

WT (♂♂): 22.8 (19.3–26.8) kg, $n = 10$

WT (♀♀): 12.3 (9.5–16.1) kg, $n = 39$

Nairobi N. P., SC Kenya (DeVore in Popp 1983)

WT (♂♂): 27.1 (21.8–32.0) kg, $n = 54$

WT (♀♀): 14.0 (10.9–18.0) kg, $n = 23$

Masai Mara National Reserve, SW Kenya (Popp 1983)

Key References DeVore & Hall 1965; Kunz & Linsenmair 2008b; Ransom 1981; Smuts 1985; Strum 1987.

Ryne A. Palombit

GENUS *Theropithecus*

Gelada

Theropithecus I. Geoffroy, 1843. Arch. Mus. Hist. Nat. Paris 2: 576.

The genus is monospecific in the extant fauna with the one species, Gelada *Theropithecus gelada*, restricted to the Central Ethiopian Plateau. Includes at least two extinct lineages, well documented by fossils of Pliocene and Pleistocene age (ca. 4 mya to ca. 125,000 years ago), in Africa (throughout), India, the Middle East and S Europe.

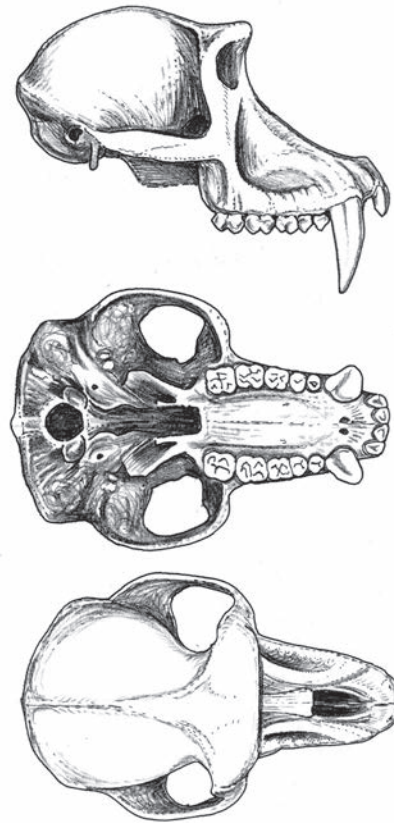
Theropithecus is closest phylogenetically to *Lophocebus* and *Papio*. Last common ancestor between *Theropithecus* and *Papio* at 4.5–3.2 mya (Perelman *et al.* 2011, Roos *et al.* 2011). Distinguished from *Lophocebus* by larger size and postcranial features associated with

terrestrial adaptation. Distinguished from *Papio* by relatively shorter hindlimbs, abbreviated index finger (giving a precise thumb–finger grip) and, especially, relatively large, high-crowned and complex molar teeth, all adaptations to feeding on small, tough, herbaceous vegetation while seated on the ground. Earliest representatives have *Papio*-like cranial shape; later ones show a progressively deepening face, with a high, vertical ascending ramus of the mandible.

Clifford J. Jolly

Theropithecus gelada **GELADA (GELADA BABOON)**

Fr. Gelada; Ger. Dschelada

Theropithecus gelada (Rüppell, 1835). Neue Wirbelt. Fauna Abyssin. Gehörig. Säugeth., p. 5. Semien (Simien), Ethiopia.Gelada *Theropithecus gelada* adult male.Lateral, palatal and dorsal views of skull of Gelada *Theropithecus gelada* adult male.

Taxonomy Polytypic species. Only extant member of genus *Theropithecus*. Two subspecies recognized: *T. g. gelada* and *T. g. obscurus* (de Beaux 1925, Yalden *et al.* 1977, Kingdon 1997, Groves 2001, 2005c, Grubb *et al.* 2003), although this distinction may not be warranted (Crook 1966, Mori & Belay 1990, Gippoliti 2010, C. Hunter pers. comm.). There appears to be no barrier between the Northern Gelada *T. g. gelada* and the Southern Gelada *T. g. obscurus* (both of which are found to the west of the Rift Valley). As such, there may be a phenotypic cline here (but see Gippoliti 2010). A third subspecies, *T. g. senex*, is described from a single specimen and not widely recognized (Gippoliti 2010). In 1990 a very isolated population of Geladas was discovered east of the Rift Valley (Wabi Shebeli Gorge, Arsi region). This population is comprised of individuals that are smaller and of lighter pelage than the more geographically proximate *T. g. obscurus*, resembling the more geographically distant *T. g. gelada* (Mori & Belay 1990, 1991). The taxonomic status of the Gelada's of the Arsi region remains to be determined but recent molecular evidence indicates that this population is distinct from Geladas west of the Rift Valley (having diverged 1.17 mya; range 0.7–1.2) leading to the suggestion that they represent a distinct subspecies (Belay & Mori 2006). Geographic variation within *T. gelada* remains poorly documented and the taxonomy is in need of validation. Gippoliti (2010) provides a detailed review of the history of the taxonomy of *T. gelada*, and points out errors and misunderstandings therein. Here we follow the taxonomy of de Beaux (1925). Synonyms: *obscurus*, *ruppelli*, *senex*. Chromosome number: $2n = 42$ (Chiarelli 1962b).

Description A large-bodied, terrestrial quadruped similar in size and appearance to *Papio* spp. Highly sexually dimorphic; weight of adult ♀♀ about 60% that of adult ♂♂. Muzzle prognathic (but

less so than *Papio*) and rounded with suborbital maxillary hollows. Nose upturned. Skin black except whitish or pale pink eyelids and red skin patch on chest and neck shaped like an hour-glass. Pelage of dorsum pale brown to near black with gold, red and grey tones; darker around hands and feet. Redness of chest patch highly variable depending on age (Bergman & Beehner 2008), reproductive stage, recent activity, or social position (Bergman *et al.* 2009). Black ischial callosities on buttocks with two black smooth pads below callosities produce a 'four-leaf clover' pattern. Tail medium-length (shorter than *Papio*) with tuft at tip.

Adult ♂: mane (= mantle = cape) of long, thick golden hair on shoulders, anterior torso and head. Fur around face and chest patch often greyish. Canines long (mean 43 mm, 39–49mm, $n = 13$; Washburn & Ciochon 1974). Adult ♀: more uniform in pelage colour, no mane. Chest/neck patch pale pink surrounded by vesicles that swell to indicate the periovulatory period (vesicles also present on inner thighs and paracallosal skin). Female chest patch brighter red when in oestrus or pregnant. Infants: skin light, pelage black for first five months.

Geographic Variation

T. g. gelada Northern Gelada. West side of Rift Valley north of the deep gorges of the Belagaz R. and upper Tacazze R. in Begemdir

and Tigre Provinces (Yalden *et al.* 1977, Gippoliti 2010). Mane pale brown to chocolate. Circumpectoral pelage iron grey, not extensive.

T. g. obscurus Southern Gelada. West side of Rift Valley south of the deep gorges of the Belagaz R. and upper Tacazze R. in Wolle Province and northern half of Shoa Province (Yalden *et al.* 1977, Gippoliti 2010). Mane dark chocolate to near black. Circumpectoral pelage pure white, extensive, going to inner side of upper arms. Note that Groves (2001) and Grubb *et al.* (2003) are incorrect in stating that *T. g. obscurus* occurs east of the Rift Valley.

T. g. ssp. nov. Eastern Gelada. East of the Rift Valley in the Wabi Shebeli Gorge, Arsi region (Mori & Belay 1990). Smaller. Mane pale brown.

Similar Species

Papio spp. more uniformly coloured, lack chest patches and pads below ischial callosities, ♂♂ having only one 'joined' callosity. Hamadryas Baboon *Papio hamadryas* and Olive Baboon *Papio anubis* both found in Ethiopia, but they are rare above 2000 m whereas Gelada are rare below 2400 m (Yalden *et al.* 1996).

Papio hamadryas. Sympatric. Altitudinal overlap from ca. 1700 to 3300 m. Males and ♀♀ have lighter pelage and red skin on face and rear. Male's mane more grey/white.

Papio anubis. Sympatric. Altitudinal overlap from ca. 1700 to 3850 m. Sympatric at Debre Libanos (ca. 2000 m; C. J. Jolly pers. comm.). Small or moderate mane. Pelage darker, agouti. Tail longer with sharp bend ('broken') at base and no tuft.

Distribution Endemic to the mountains of Ethiopia. Afro-montane–Afroalpine BZ. Main population confined to high, afroalpine, grassland escarpments near deep gorges in the Central Ethiopian Plateau. To the west of the Rift Valley, Geladas occur (or once occurred) as far to the north-east as Mt Azbi (near Adigrat; 13° 87' N, 39° 74' E (Gippoliti 2010). Today, known west of the Rift Valley from Begemdir and Tigre Provinces in the north (ca. 13° N) through Wolle Province and northern half of Shoa Province south to 09° 29' N in the Muger R. Valley (9–14° N, 37–40° E; Yalden *et al.* 1977, 1996, D. Yalden pers. comm.). Western limit at Ambo Mineral Springs, ca. 24 km west of L. Tana (12° 00' N, 36° 40' E; Gippoliti 2010). Not today known from west or north of Blue Nile Gorge, which transects the Plateau. An isolated population lives in the Arsi Region, east of the Rift Valley (7° 30' N, 40° E; Mori & Belay 1990, 1991).

Habitat Restricted to high montane grasslands of Ethiopian Plateau (Jolly 1967, Pickford 1993). Found along grassland steppes near steep escarpment edges that provide refuge from predators and sleeping sites. Nutritional content of grasses eaten is sensitive to ambient temperature (Dunbar 1998). Availability of grasses restricts Gelada habitat to a typical altitudinal range of 2400–4200 m, but known from 1700–4600 m (Yalden *et al.* 1977, 1996, Iwamoto 1993, Hunter 2001). Water resources, mainly streams and ponds, plentiful. Mean annual precipitation ranges 1300–1500 mm in north to ca. 1100 mm in south (Kebede 1964, Dunbar 1998). Mean daily temperature ranges 7–10 °C in the north to ca. 16 °C in the south (Iwamoto & Dunbar 1983). Daily temperature range is large (~25 °C), commonly below freezing at night, suggesting



Gelada *Theropithecus gelada* adult male showing lip-flip.

high energetic demands of thermoregulation (Dunbar 1984). Gelada found in association with afroalpine vegetation dominated by montane grasses (mainly *Festuca* spp.), herbs (e.g. *Thymus* spp., *Trifolium* spp. and *Geranium arabicum*), Giant Heath *Erica arborea*, St John's Wort *Hypericum revolutum* and patches of Giant Lobelia (*Lobelia rhynchopetalum*) (Dunbar 1978).

Abundance Densities west of the Rift Valley range from 15–73 ind/km². Patchily distributed corresponding to areas of grassland near sleeping cliffs. Within patches, estimated densities of 147/km²



Theropithecus gelada

of available grass cover (Iwamoto & Dunbar 1983). In the 1970s total population west of the Rift Valley estimated at ca. 500,000 (Dunbar 1993a). Thought to be much lower at present. Population estimate for the only protected population area in which Gelada occur (in and around Simien Mountains N. P.) is ca. 4300 individuals (Beehner *et al.* 2007). Size of the population east of the Rift Valley (i.e. the Arsi population) is not known but appears to be extremely small.

Adaptations Diurnal and terrestrial. Activity budgets comprise moving 10–20%, resting 1–20%, social 10–30% and feeding 50–70% (Kawai & Iwamoto 1979, Hunter 2001). Geladas spend more time foraging than other herbivorous primates. Must feed more because of energy requirements for thermoregulation and to counterbalance low nutrient content of grass (Dunbar 1984). Physiological stress for Geladas highest at colder temperatures (either during colder months or at higher altitudes; Beehner & McCann 2008). They have specializations for grass foraging including: (1) ‘scooting’ locomotion, hindquarters on ground and foraging with both hands; (2) extra pad below ischial callosity allowing hindquarters to slide on ground while foraging; (3) first finger and thumb shortened and highly opposable, for grasping blades of grass. Probably related to frequent ‘scooting’ posture that obscures the rear, red chest patch signals reproductive state just as do perineal sexual swellings in *Papio* ♀♀. Function of patch in ♂♂ is unknown but thought to vary with level of strenuous activity (e.g. aggression) and social status (Dunbar & Dunbar 1974b, Dunbar 1984, Bergman *et al.* 2009).

Foraging and Food Graminivorous. Only graminivorous primate. Geladas forage primarily in a seated position while gathering blades of grass simultaneously with both hands. They carry grass sheaves to the mouth, remain in a seated position, move (scoot) ca. 0.5 m and renew grass-picking in next feeding bout. For subterranean food items, Geladas dig up items using both hands as hoes to scrape out ground, also in a seated position (Crook & Aldrich-Blake 1968, Iwamoto 1979). Feeding composed of picking 86% and digging 14% (Iwamoto 1979). They feed primarily on high-protein, monocotyledon grasses (mainly *Danthonia subulata*, *Festuca* spp. and *Agrostis* spp.) at altitudes above 1700 m (Dunbar 1977, Iwamoto 1979). Diet consists of ca. 90% grass, with addition of underground corms during the dry season (Iwamoto 1979, Hunter 2001). Geladas are non-ruminants. They digest a high cellulose diet chiefly by bulk feeding and thorough mastication of food (Dunbar & Bose 1991) with larger molars than *Papio* spp. (Teaford 1993). Day range ca. 1.5 km (0.7–3.2, $n = 55$), home-range ca. 7.2 km² (6.1–8.2, $n = 2$). Geladas feed throughout the day, although morning hours are preferentially spent on social activity (Kawai & Iwamoto 1979).

Social and Reproductive Behaviour Highly social. Complex, multi-level social structure, superficially similar to Hamadryas Baboons (Snyder-Mackler *et al.* 2012). The basic component of a Gelada group is a one-male unit (OMU): one breeding ♂, 1–12 adult ♀♀, dependent offspring and sometimes a follower male(s) (Mori 1979b, Kawai *et al.* 1983, Dunbar 1986). Other adult ♂♂ form all-male groups of 2–15 ♂♂ (Dunbar 1993b). OMUs and all-



Gelada *Theropithecus gelada* adult female showing sexual swellings and pectoral vesicles.

male groups that share a common home-range are called a ‘band’. Bands range from 30–250 individuals (Kawai *et al.* 1983, C. Hunter pers. comm.). OMUs from two or more bands that forage together form a ‘herd’. Herds may comprise as many as 1200 individuals; these are among the largest wild-foraging primate groups. No territorial behaviour. Before puberty, juvenile ♂♂ leave natal unit and join all-male groups (Dunbar & Dunbar 1975b). They remain in all-male groups for 2–4 years, then try to acquire access to reproductive ♀♀. There are two strategies: (1) take over existing OMU by ousting incumbent leader ♂ or, less commonly, (2) join unit as subordinate follower ♂ to acquire peripheral and/or juvenile ♀♀ (Dunbar 1993b). Male dominance hierarchy in all-male groups. Chasing displays between ♂♂ common, actual fighting rare. Males in all-male groups frequently harass OMU ♂♂ in attempt to take control of unit (Mori 1979c). Copulations only between OMU ♀♀ and incumbent leader ♂ (Mori 1979b).

Adult ♀♀ constitute core of Gelada society. Females remain in natal OMU for life and are close relatives (le Roux *et al.* 2011). Female dominance hierarchy within units (Mori 1979a, le Roux *et al.* 2011). High-ranking ♀♀ reproduce at a faster rate (Dunbar & Dunbar 1977, Dunbar 1980a, but see le Roux *et al.* 2011). Cohesion of OMUs maintained through ♀ bonds (Dunbar & Dunbar 1975b, le Roux *et al.* 2011). OMU ♀ bonds persist beyond tenure of one leader ♂ (le Roux *et al.* 2011). Females can join together, attack leader ♂ and evict him from the unit (Dunbar & Dunbar 1975b).

Geladas have one of the largest vocal repertoires in the Papionini (Gustison *et al.* 2012) with 22–30 distinct vocalizations (Kawai 1979), including 11 contact calls and 11 aggressive-defensive calls (Aich *et al.* 1990). The large number of contact vocalizations is thought to be related to their large, complex social system (Kawai 1979). Some vocalizations are unique to animals of various social status (e.g. emitted only by highest-ranking OMU ♀) (Aich *et al.* 1990).



Geladas *Theropithecus gelada*.

Reproduction and Population Structure Female reproductive condition signalled by swelling of vesicles around chest patch. Menstrual cycle 30.7 days (28–34, $n = 10$; Dunbar & Dunbar 1974d, Harvey & Clutton-Brock 1985). Median age at menarche 56.4 months (41–78, $n = 40$). Median age at first birth 68.8 months (57.8–81.0, $n = 13$; J. Beehner pers. obs.). Pregnancy indicated by reddening of chest patch by mid-gestation (Dunbar & Dunbar 1974d). Gestation 183 days (175–195, $n = 16$; Roberts *et al.* 2012). Weaning 517 days (163–736, $n = 17$; J. Beehner pers. obs.). Approximately 1–3 cycles per conception (Dunbar & Dunbar 1974d). Single offspring born per ♀ every 29 months (14–50, $n = 51$; J. Beehner pers. obs.). One possible case of twinning observed (J. Beehner pers. obs.). Birth-weight 464 g (Harvey & Clutton-Brock 1985). Birth sex ratio equal ($n = 134$; Ohsawa 1979, Dunbar 1980a). Adult ♂ to ♀ sex ratio 1:2.3–1:3.0 ($n = 2308$; Dunbar 1980a, Beehner *et al.* 2007). Adult sex ratio favours ♀♀ because of faster maturation and lower mortality (Dunbar 1984). Reproduction occurs throughout year with moderate birth peaks in Jun–Jul and Nov–Dec. Survivorship estimated to be 91% to 18 months of age and 88% to four years of age. Life expectancy at birth is 12.3 years for ♂♂ and 13.8 years for ♀♀ (Dunbar 1984). Live to at least 20.8 years in captivity (Jones 1982). Occasional mortality from intra-specific fighting (J. Beehner pers. obs.). Several reports of infanticide by adult ♂♂ (Moos *et al.* 1985, Mori *et al.* 1997, 2003), usually in the months following unit takeovers. Infanticide in Geladas appears to be part of the ♂ reproductive strategy (Beehner & Bergman 2008). See also Roberts *et al.* (2012).

Predators, Parasites and Diseases Primary predators are Leopards *Panthera pardus* and Spotted Hyaenas *Crocuta crocuta* (Dunbar 1984). Juveniles jump and look nervously at any large bird, suggesting that large raptors are also predators. Geladas killed by humans and domestic dogs. Some mortality caused by parasitic tapeworm, *Multiceps* sp. (Ohsawa 1979). Main cause of mortality probably respiratory and other infections contracted during periods of rain and subzero temperatures (Dunbar 1984, Ohsawa & Dunbar 1984).

Conservation IUCN Category (2012): Least Concern. Vulnerable as *T. g. gelada* and Least Concern as *T. g. obscurus*. CITES (2012): Appendix II.

In a review of the taxonomy and geographic range of Gelada, Gippoliti (2010) concluded that the diversity within Gelada may be grossly underestimated and that, as such, more research on the variability within Gelada is urgently required. Gippoliti (2010)

identifies priority regions for taxonomic research and conservation action.

It should be noted that the latest IUCN assessment of degree of threat for the Gelada is based on rough estimates made during the 1970s. More recent surveys indicate that the estimates of the 1970s were much too high. For example, the population of the Simien Mountains was estimated at 10,000 during the 1970s whereas a recent survey yielded an estimate of 4300 (Beehner *et al.* 2007). Numbers probably in decline due to restricted range and loss of specialized habitat. Geladas face intense competition from expanding human populations and their livestock. Geladas are hunted for ceremonial use of skins, killed for crop-raiding, and sold locally as pets. The only 'protected area' in which Geladas occur is the Simien Mountains N. P. (and World Heritage Site) but the protection here is poor (Beehner *et al.* 2007). Priority actions for the long-term conservation of this genus/species should be to enhance protection of the Simien Mountains N. P. (*T. g. gelada*), the Menz Highlands (*T. g. obscurus*) and the Arsi region (*T. g. ssp. nov.*). It is uncertain, however, how enhanced protection for these three sites might be achieved. Strengthening traditional local protection for the Guassa might help restore the conservation values of the Menz Highlands, otherwise an effectively managed national park seems necessary. The Arsi population may need protection within a national park in order to improve long-term prospects for survival. The taxonomic status of the Arsi population needs to be assessed (Belay & Mori 2006). A survey to determine the size and distribution of the Arsi population is a priority, as is an assessment of its IUCN/SSC Red List degree of threat status (since this is likely to be assessed as a Critically Endangered subspecies).

Measurements

Theropithecus gelada

HB (♂♂): 720 (690–740) mm, $n = 2$

HB (♀♀): 580 (500–650) mm, $n = 2$

T (♂♂): 480 (460–500) mm, $n = 2$

T (♀♀): 460 (320–640) mm, $n = 5$

HF (♀♀): 156 (154–157) mm, $n = 3$

E (♀♀): 41 (37–50) mm, $n = 3$

WT (♂♂): 19.0 (16.5–20.5) kg, $n = 5$

WT (♀♀): 11.7 (8.3–13.8) kg, $n = 8$

Various localities. HB, T, HF, E (Napier & Napier 1967, Hill 1970). WT (Dechow 1983).

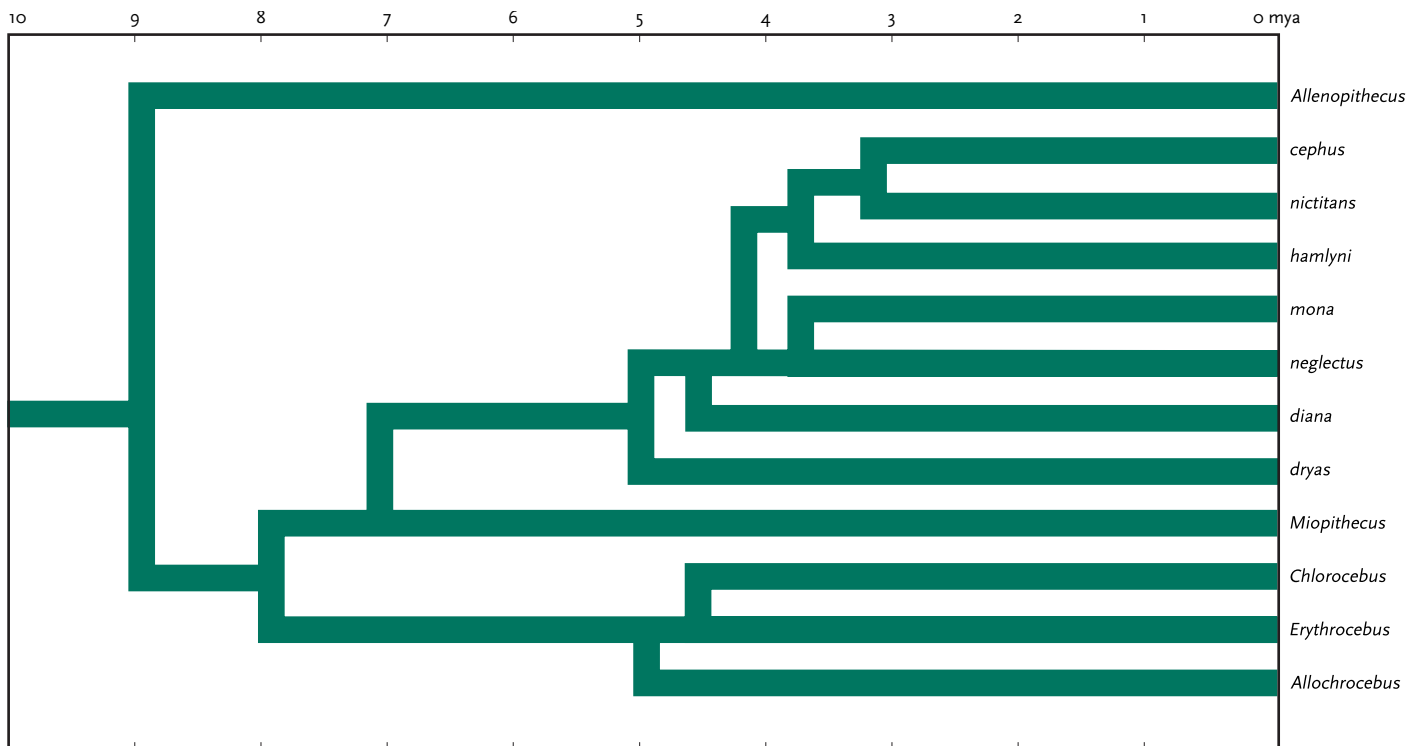
Key References. Dunbar 1984; Dunbar & Dunbar 1975b; Gippoliti 2010; Jablonski 1993; Kawai 1979; le Roux *et al.* 2011.

Thore J. Bergman & Jacinta C. Beehner

Tribe CERCOPITHECINI

Cercopithecins: Guenons (Allen's Swamp Monkey, Talapoin Monkeys, Patas Monkey, Savanna Monkeys, Mountain Monkeys, Arboreal Guenons)

Gray, 1821. London Medical Repository 15: 296–310.



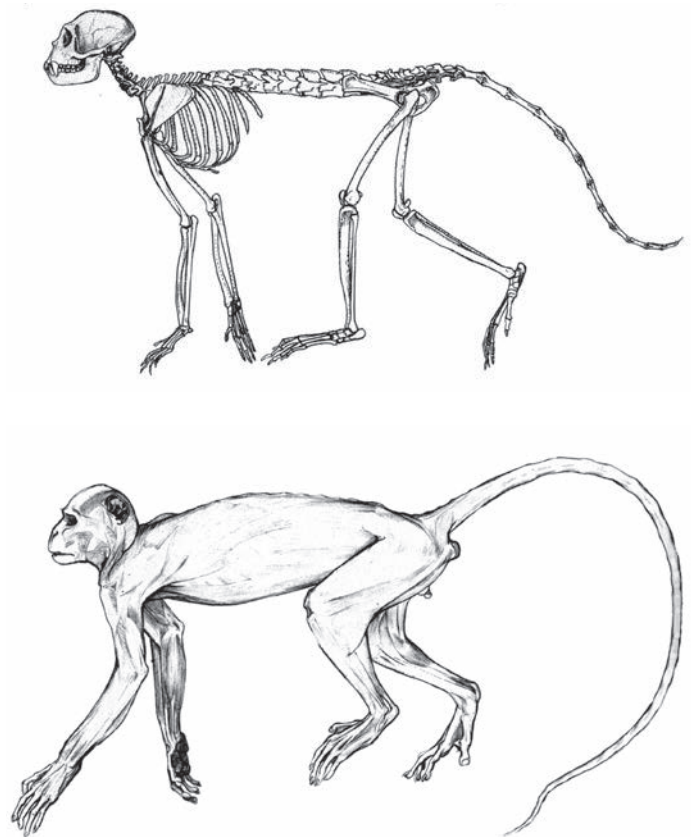
ABOVE: Tentative phylogenetic tree for the guenons Cercopithecini (partly after Tosi *et al.* 2005 and Moulin *et al.* 2008)

RIGHT: L'Hoest's Monkey *Allochrocebus lhoesti* skeleton.

BOTTOM RIGHT: De Brazza's Monkey *Cercopithecus neglectus* myology.

The Cercopithecini are, for the most part, generalized, long-tailed, medium-sized monkeys. For the purposes of this work, this tribe comprises six genera: *Allenopithecus*, *Miopithecus*, *Erythrocebus*, *Chlorocebus*, *Allochrocebus* and *Cercopithecus*. All are generally described as 'guenons' and, in the past, have occasionally been lumped in the single genus *Cercopithecus* (Verheyen 1962). These six genera are currently considered to embrace 33 species, making this quite the most speciose of all African primate taxonomic groups. Their ecological success seems to be based on extremely fast and well-coordinated movement in the trees, optimized body sizes for each species-specific substrate and, probably, physiological resistances to a variety of equatorial pathogens and parasites. The divide between Cercopithecini and Papionini is not clear-cut, with two genera, *Miopithecus* and *Allenopithecus*, showing a mosaic of features that make them difficult to allocate with any certainty; but they have non-papionine chromosome counts and are generally regarded as being stem guenon lineages that retain many conservative features in spite of being quite specialized in other respects.

Although there is little doubt that *Allenopithecus* and *Miopithecus* belong to the Cercopithecini, there has been some discussion about this because both have a mix of cercopithecine and papionine features. Like many papionins, but unlike other cercopithecins, both exhibit periodic

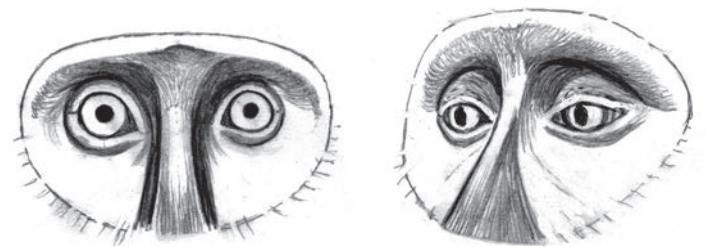




sexual swellings in the ♀. *Allenopithecus* has molar flare (the buccal and lingual walls of the molars are convex, so that the cusp tips appear somewhat drawn together), which is characteristic of most Papionini; and in the ♂ the ischial callosities fuse across the midline as in all genera of Papionini except for *Macaca*. On the other hand, *Allenopithecus* and *Miopithecus* both lack the maxillary fossae and the M_3 hypoconulids seen in (most) Papionini, and in this they resemble the other Cercopithecini. They appear to have a similar range of facial gestures as the Papionini, whereas the other Cercopithecini make less use of facial signals and appear to have less mobile faces. In the past this difference was taken to imply less developed social systems in the latter, more developed in the former. In fact it seems more likely to have a connection with some fundamental differences in mechanisms for social cohesion that might, in turn, be mediated by opposite facial signals. Dominant animals among arboreal species are less able to coerce conspecifics than species living mainly on the ground because escapes are easier and close approaches depend more upon conciliation than upon coercion (Marler 1965, Kingdon 2007). If cohesion among arboreal monkey species has forced group members to *avoid* sending aggressive or ambiguous signals to one another there could have been active selection for the suppression of emphatic facial signals such as those typical of terrestrial monkey species. These differences in visual communication deserve further study. All Papionini have diploid chromosome numbers $2n = 42$, whereas the numbers are higher than this in all Cercopithecini.

Schematic illustration of coloured visual signals transmitted by several species of guenons (Cercopithecini).

Top, left to right: Putty-nosed Monkey *Cercopithecus nictitans*. Diana Monkey *Cercopithecus diana*. Red-eared Monkey *Cercopithecus erythrotis*. Crowned Monkey *Cercopithecus pogonias*. Wolf's Monkey *Cercopithecus wolfi*. Middle, left to right: De Brazza's Monkey *Cercopithecus neglectus*. Diana Monkey *Cercopithecus diana*. De Brazza's Monkey *Cercopithecus neglectus*. Diana Monkey *Cercopithecus diana*. Bottom, left to right: Owl-faced Monkey *Cercopithecus hamlyni*. De Brazza's Monkey *Cercopithecus neglectus*. L'Hoest's Monkey *Allochrocebus lhoesti*. De Brazza's Monkey *Cercopithecus neglectus*.

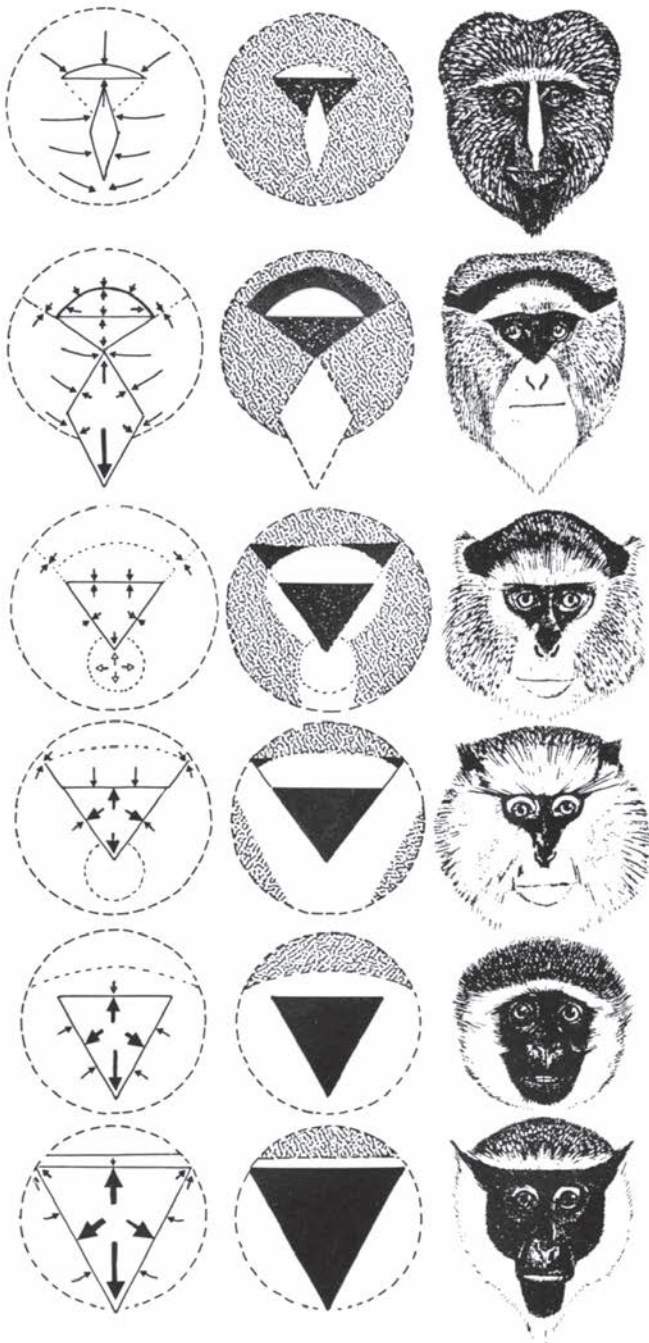


Eye-contact (aggressive/centrifugal) and eye-eversion (submissive/centripetal) in a guenon.



LEFT: Potentially expressive movements of the head and features of a guenon.

BELOW LEFT: Schematic diagram of tonal distribution on the faces of six guenons illustrating how 'flag' or 'visual target' designs can be enlarged or diminished, sometimes masking or compromising facial expressions. *Cercopithecus lowei* has least differentiated pattern. Arrows on disks suggest intensification of tonal contrast or extension of tonal area. Top to bottom: Owl-faced Monkey *Cercopithecus hamlyni*; De Brazza's Monkey *Cercopithecus neglectus*; Lowe's Monkey *Cercopithecus lowei*; Campbell's Monkey *Cercopithecus campbelli*; Vervet Monkey *Chlorocebus pygerythrus*; Diana Monkey *Cercopithecus diana*.



The majority of guenons are restricted to the equatorial forest belt but a small number of species, belonging to three groups, range more widely; the Savanna Monkeys Group *Chlorocebus* (*aethiops*) range throughout the more wooded parts of sub-Saharan Africa, the Patas *Erythrocebus patas* is primarily a Sahelian species, and the Gentle Monkeys Subgroup *Cercopithecus* (*mitis/albogularis*) have an extensive coastal, riverine and montane range, mostly through the south-eastern quarter of Africa.

Cercopithecini can be diagnosed and distinguished from most other Old World monkeys by possession of only four cusps on their third lower molars; but see Groves (1978) and Napier (1981) for discussion of the difficulties of making a clear-cut diagnosis. Cercopithecini vary in their chromosome count more than any other group of primates, with numbers ranging from 48 to 72. According to Dutrillaux *et al.* (1988b) and Ruvolo (1988) this genetic diversity is due to unusually frequent translocations and inversions.

Behavioural differences between guenons and papionins are subtle, but Rowell (1988) has noted some distinguishing traits, notably greater reliance on species-specific visual and vocal signals in guenons, and more emphatic gestural signals in papionins. Male guenons are generally intolerant of other conspecific adult ♂♂ and both sexes tend to defend territories in which ♂ tenure is often more ephemeral than in the hierarchical multimale societies that preponderate among papionins.

The evolutionary history of this tribe of primates has confounded the expectations of many early scientists. For example, in conformity with the widespread assumption that arboreal primates were definitively more 'primitive', Schwarz (1928b) regarded most of the very varied assemblage of *Cercopithecus* as deriving from the most arboreal forms. Subsequent molecular and morphological studies have shown that this pattern is actually an inversion with the most arboreal species being the most recently evolved (Verheyen 1962, Thorington & Groves 1970, Dutrillaux *et al.* 1980, 1988b, Ruvolo 1988, Purvis 1995). Dutrillaux *et al.* (1980) showed that there was a basal split in the earliest Cercopithecini into one branch that retained semi-terrestrial ancestral traits and a second branch that became more arboreal, culminating in two separate lineages of small, wholly arboreal monkeys; Mona Monkeys Group *Cercopithecus* (*mona*) and Cephus Monkeys Group *Cercopithecus* (*cephus*) (Dutrillaux *et al.* 1988b, Tosi *et al.* 2005; figure p. 245). Some of the roots of this counter-intuitive progression lie in the peculiar climatic history of Africa, which has often tended to favour non-forest and semi-arboreal organisms, as outlined in earlier profiles.

GENUS *Allenopithecus*

Allen's Swamp Monkey

Allenopithecus Lang, 1923. Amer. Mus. Novit. 87: 1.

A monotypic genus embracing Allen's Swamp Monkey *Allenopithecus nigroviridis*. Shares some resemblances with cercopithecins and with *Miopithecus* in particular, but also shares several conditions with the Papionini, notably fused ischial callosities in adult ♂♂, flared molars and periodic sexual swellings in ♀♀ (Groves 2001). Heavy build, short limbs, very broad hands and feet, leaf-shaped ears and shortish tail are also somewhat macaque-like. These features imply the selective retention of some conservative features combined with some specialized adaptation to the deep seasonal flooding of the riverine and swamp forests in which this species lives.

T. Harrison (pers. comm.), like Groves (2001) and others, considers papionin-like features of *A. nigroviridis* to be symplesiomorphies of Cercopithecidae with no implication of a close phylogenetic relationship. There is no fossil record for this genus.

Allenopithecus has a lower chromosome count than most Cercopithecini ($2n = 48$; other guenons range from 54 to 72 while all Papionini have 42). Early treatments sometimes placed this species within *Cercopithecus* (Pocock 1906), often as a subgenus

(Verheyen 1962). Molecular research (Tosi *et al.* 2005, Perelman *et al.* 2011) indicates that *Miopithecus* represents the surviving lineage closest to *Allenopithecus* (none the less they diverged 9.3–8.2 mya [late Miocene]). The same authors estimated an 11.5 (10.2–12.8) mya (mid-Miocene) separation between ancestral *Allenopithecus* and ancestral *Macaca*, thus confirming earlier studies that allied *Allenopithecus* with the Cercopithecini. Ruvolo (1988) positioned *Allenopithecus* as the first branch to separate out at the base of the cercopithecine tree. Instead, Dutrillaux *et al.* (1980, 1988b), in early comparisons of chromosome banding patterns, placed *Allenopithecus* below a deep bifurcation, close to the more arboreal branch of cercopithecins that became the genus *Cercopithecus*. The phylogeny adopted in this work broadly follows the arrangement supported by Tosi *et al.* (2005) and Perelman *et al.* (2011). See figure p. 245.

For other characteristics of this genus, see the species profile.

Colin P. Groves & Jonathan Kingdon

Allenopithecus nigroviridis ALLEN'S SWAMP MONKEY

Fr. Singe des marais; Ger. Sumpfmeeerkatze

Allenopithecus nigroviridis (Pocock, 1907). Proc. Zool. Soc. Lond. 1907: 739. Upper Congo R., DR Congo.Allen's Swamp Monkey *Allenopithecus nigroviridis* adult male.

Taxonomy Monotypic species. Originally described by Pocock as *Cercopithecus nigroviridis*. Separated from *Cercopithecus* by Thorington & Groves (1970). *Allenopithecus* first described as a genus by Lang (1923). Some morphological features more similar to those of macaques *Macaca*, drill mangabeys *Cercocebus* and baboon mangabeys *Lophocebus* than to guenons: ear shape (pointed), tooth shape (flare molars) and skull shape (more prominent and oblique than in

Cercopithecus; Verheyen 1962). These characters, as well as results from blood proteins analysis (Ruvolo 1988), chromosomal analysis ($2n = 48$; Dutrillaux *et al.* 1988b), vocal repertoires (Gautier 1988) and molecular studies, converge in suggesting that the Swamp Monkey is near the root of the cercopithecine tribe (Verheyen 1962). Synonyms: none. Chromosome number: $2n = 48$ (Dutrillaux *et al.* 1988b).

Description Medium size, stocky, khaki-coloured monkey, sexes similar in colour. Pronounced sexual dimorphism in body size and weight. Muzzle dark grey. Facial disc grizzled with long, dense fur on cheeks. Black lines around cheeks. Cheek hair bushy, directed backwards. Supraciliary band with stiff black hairs. Throat light grey. Upperparts and outer sides of limbs and tail are khaki-coloured. Limbs short. Tail shortish, only a little longer than HB (90–107%). Underparts dirty-white to grey. Both sexes have sexual skin. Adult ♂ especially stocky. Scrotum large, pale blue. Orange-red perineal patch of bare skin between the root of the tail and the dorsal margin of the callosities. Adult ♀ has more extensive sexual skin, which undergoes cyclical turgescence (Hill 1966). Pelage of newborn resembles that of adult but coat paler, more yellowish-brown. Crown markedly paler, covered with long, fine, silky, almost white hairs. Natal coat replaced at around ten weeks (Pournelle 1962).

Geographic Variation None recorded.

Similar Species None.

*Allenopithecus nigroviridis*

Distribution Endemic to central Africa: DR Congo and Congo. Presence in SE Cameroon and NE Angola requires confirmation. Rainforest BZ. Mainly linked to the left bank tributaries of the Congo R., between Lomami R. and Kasai R. Malbrant & Mclatchy (1949) reported Swamp Monkey from the right bank of Congo R. between Likouala R. and near the mouth of Sangha R. On islands in the Sangha R. close to Bomassa (N Congo) at border with Cameroon. One group seen on Ndoki R., 25 km north-east from Bomassa. Thus Swamp Monkey occurs at least to 01° 13' N; 16° 31' E in NW Congo. Probably limited in the north by Ubangui R. and its tributary Uélé R. In south could be present to Kwango R. Known limits of distribution: 03° N–06° 30' S; 16° 31'–26–27° E (Gautier 1985, Maisels *et al.* 2006b).

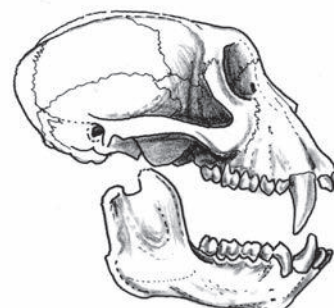
Habitat Riparian forests along rivers, lakes or islands, especially where hydromorphic soils are present: periodically inundated forests, swamp forests, low vegetation types such as dense thickets of *Pandanus*, impenetrable thickets of herbaceous vegetation (Zingiberaceae, Marantaceae, Araceae) and stands of palms (*Calamus*, *Ancistrophyllum*, *Eremospatha*) that occur in swampy areas, especially along small rivers (Gautier 1985). Altitudinal range from about 100 m to at least 350 m. Annual rainfall 1700–2100 mm (Ergo & de Halleux 1979).

Abundance Abundant in the Salonga N. P. (DR Congo), reaching 100 monkeys/km² (deduced from the sizes of three groups and their home-ranges; A. Gautier-Hion pers. obs.). Not observed in dry upland areas of Lomako Forest. Fairly common in the swamp forest bordering the Lomako River System (W. S. McGraw pers. comm.). Considering that suitable hydromorphic biotopes probably cover more than a quarter of the surface area on the left bank of the Congo R., and that the human population density there is low, Swamp Monkey populations are probably numerous and not yet threatened.

Allen's Swamp Monkey *Allenopithecus nigroviridis* adult male.

Adaptations Diurnal and semi-terrestrial. Incipient sacculated stomach suggests some capacities to digest plant material (Hill 1966). Large vocal sacs used for production of loud-calls by adult ♂ (Gautier 1988). Cutaneous glandular area on chest of adult ♂ (Hill 1966) used for scent-marking trunks and branches (Loireau & Gautier-Hion 1988). Along river edges Swamp Monkeys travel through the thickest vegetation at low levels, using stilted roots of *Pandanus* trees and walking across suspended soil and debris retained by the web of roots; where necessary they wade into the water or swim. Where the substrate is clear or unflooded they either walk across the ground with a quadrupedal stance like baboons *Papio* or they gallop. Swamp Monkeys in trees <10% of time. When in trees, usually <5 m high. Climbing into tall trees primarily relates to feeding. At night groups prefer to sleep in trees that overhang rivers. Swamp Monkeys are good swimmers, spontaneously plunging into the water, especially when alarmed. During the day and on terra firma, they flee on the ground (Gautier 1985, Gautier-Hion *et al.* 1999).

Foraging and Food Omnivorous. Fruits, seeds, arils, stems, piths of herbaceous plants, cotyledons of young seedlings, stems of palm seedlings, young leaves, leaf petioles, flowers, nectar and mushrooms are eaten. Animal prey, including flying insects, spiders, caterpillars, small fishes, crustaceans and snails, account for about 20% of the diet. Earthworms are probably eaten. Swamp Monkeys

Lateral view of skull of Allen's Swamp Monkey *Allenopithecus nigroviridis* adult male.

forage in groups or subgroups. Plant food taken from trees, shrubs and herbs near the ground level. They forage mainly on the ground, picking up fallen mature and immature dry fruit and seeds that have fallen from tall trees. Succulent ripe fruits are, however, mainly harvested directly from trees. Among the most conspicuous of the foraging activities are the uprooting of numerous young palm saplings (20–30 cm high) and digging. In freshly drained areas Swamp Monkeys regularly sift the litter, scratching or digging holes to a few centimetres depth to expose animal prey, probably earthworms. Up to 35 monkeys seen digging simultaneously. Intensive seasonal feeding on nectar of *Daniellia pynaertii* (Caesalpinaceae) flowers (Gautier-Hion & Maisels 1994). In inundated areas covered by herbaceous plants or *Pandanus* shrubs they spend long periods diving and surfacing, presumably in search of aquatic prey. Also wade rivers and actively fish with one hand (Gautier-Hion *et al.* 1999).



Allen's Swamp Monkey *Allenopithecus nigroviridis* adult male.

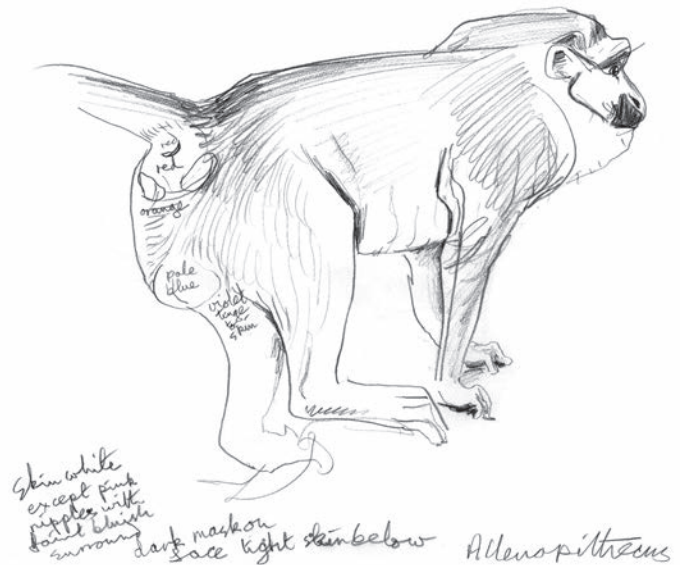
Social and Reproductive Behaviour Social. At Salonga N. P. the size of groups ranged from 23 to 57 individuals (mean 35, $n = 26$). One group of at least 85 individuals was counted early in the morning close to their sleeping site, suggesting that subgroups may forage independently during the day. Groups are multimale but the ratio of adult ♂♂ to adult ♀♀ is low; only four adult ♂♂ in a group of 32 individuals. During progression, large adult ♂♂ may be grouped together at the front of the group. Solitary adult ♂♂ occasionally observed (Gautier-Hion *et al.* 1999, A. Gautier-Hion pers. obs.). At Lomako only groups of four individuals ($n = 3$) were seen (McGraw 1994).

The shape of home-ranges (50–70 ha; $n = 3$) is determined by river banks and their hydromorphic habitat. No overlaps among home-ranges yet detected, nor have any territorial interactions been observed (A. Gautier-Hion pers. obs.). There are no data on courtship, mating behaviour, or parent–young interactions. Swamp Monkeys found in polyspecific associations in about 30% of 56 cases. These associations included one to four species; Wolf's Monkey *Cercopithecus wolffi*, Red-tailed Monkey *Cercopithecus ascanius*, Black Mangabey *Lophocebus aterrimus*, Red Colobus *Procolobus badius tholloni* and Angola Colobus *Colobus angolensis*. Bi-specific groups were the commonest (38%), followed by tri-specific (27%) and quadri-specific (30%) groups. Wolf's Monkey was present in 75% of cases. The presence of Swamp

Monkeys in polyspecific associations is of short duration. No mixing between Swamp Monkeys and De Brazza's Monkey *Cercopithecus neglectus* observed (A. Gautier-Hion pers. obs.).

Vocal repertoire of the Swamp Monkey is consistent with its having branched off a common cercopithecine ancestral stock. Cohesion-contact 'grunts' and warning 'chirps' are very similar to those of Putty-nosed Monkeys *Cercopithecus nictitans*; loud-calls of adult ♂♂ recall the 'gobble' of mangabeys; the copulation 'quaver' given by ♀♀ recalls that of ♀♀ red colobus *Procolobus*. Finally, the metallic components of its chirps recall those of talapoin *Miopithecus* (Gautier 1988). When arriving at their sleeping sites, Swamp Monkeys, like talapoin, utter a chorus of calls that include most of their repertoire, including the isolation calls of young, alarms, 'screams' and cohesion calls, all punctuated by the gobbles of adult ♂♂. During and after copulation, adult ♀♀ give specific calls that are frequently heard but are easily mistaken for those of adult ♀♀ Tshuapa Red Colobus *Procolobus rufomitatus tholloni*.

In the field, only one olfactory marking episode observed; an adult ♂ embraced a trunk at 6 m above the ground while rubbing it up and down with his throat and chest (A. Gautier-Hion pers. obs.). In captivity marking is typically provoked in adult ♂♂ by the introduction of new supports into the enclosure; ♂♂ rub the new supports with their muzzle, throat and chest and occasionally stop to scratch the chest or lick the marked area. Females show no marking behaviour but they do sniff marked areas.



Allen's Swamp Monkey *Allenopithecus nigroviridis* adult male.

Reproduction and Population Structure Adult ♀♀ have regular sexual swellings. Gestation lasts about 5½ months. In the wild, ♀♀ with young infants observed in Feb–Apr while copulation calls heard mainly during Jul–Aug (A. Gautier-Hion pers. obs.). This suggests a seasonal pattern of reproduction similar to that found in guenons, where the mating period coincides with the main dry season and birth period with the short dry season (Butynski 1988). Females give birth to one young. Birth weight 221 g. Ratio of adult ♂♂ to adult ♀♀ in groups is about 1 : 8. Population structure, longevity, birth and mortality rates are unknown for wild populations. Live to at least 23 years in captivity (Jones 1982).

Predators, Parasites and Diseases No predation events observed. Close to villages (where Swamp Monkeys feed on nuts of Oil Palms *Elaeis guineensis*) they are sometimes captured in traps. Like other guenons, Swamp Monkeys utter loud alarm calls towards raptors. Carnivores and snakes are likely predators as well. As with *Miopithecus*, locating their sleeping sites close to river banks constitutes an effective anti-predator strategy. Nothing known concerning diseases and parasites.

Conservation IUCN Category (2012): Least Concern. CITES (2012): Appendix II.

The Swamp Monkey's preference for hydromorphic habitats provides some protection against predators (including hunters) and habitat destruction (including loggers). However, Swamp Monkeys are prone to hunting and trapping. Since 1981 extensive logging concessions have been granted in the Congo Basin.

Measurements

Allenopithecus nigroviridis

HB (♂ ♂): 475 (455–510) mm, n = 3

HB (♀ ♀): 330, 410 mm, n = 2

T (♂ ♂): 508 (499–525) mm, n = 3

T (♀ ♀): 355, 400 mm, n = 2

HF (♂ ♂): 135, 135 mm, n = 2

HF (♀ ♀): 111 mm, n = 1

E: (♂): 42 mm, n = 1

E: (♀): 33 mm, n = 1

WT (♂): 6.2 kg, n = 1

WT (♀ ♀): 3.2, 3.4 kg, n = 2

DR Congo (Hill 1966, J.-P. Gautier pers. comm.)

Key References Gautier 1985; Gautier-Hion *et al.* 1999; Hill 1966.

Annie Gautier-Hion

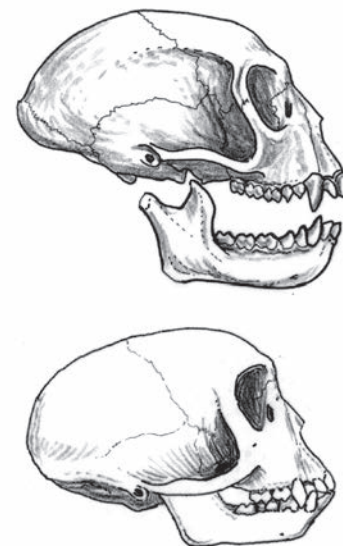
GENUS *Miopithecus* Talapoin Monkeys

Miopithecus I. Geoffroy, 1842. C. R. Acad. Sci. Paris 15: 720.

This genus includes two species, the Southern Talapoin *Miopithecus talapoin* and Northern Talapoin *Miopithecus ogouensis*. *Miopithecus talapoin* occurs in lowland forest south of the Congo R. from the Angolan coast and Kwango R. Valley east to the Kasai R. (Thompson 2001). *Miopithecus ogouensis* occurs in lowland forest north of the Congo R. throughout much of the Ogooué R. Basin as far north as the Sanaga R. There are no fossils closely related to this genus.

The chromosome count for *Miopithecus* is $2n = 54$, which is the same as for Patas *Erythrocebus patas* (it is striking how infant Patas resemble enlarged, longer-limbed versions of young *M. talapoin*). The phylogenetic position of this lineage of highly distinctive and diminutive monkeys has recently been revised. There is strong statistical support for the view that *Miopithecus* evolved after the common ancestor of the terrestrial cercopithecins (Xing *et al.* 2007). This conclusion, based upon SINE insertions, is surprising because *Miopithecus* shares many features with *Allenopithecus*, while the other three genera of semi-terrestrial guenons (*Erythrocebus*, *Chlorocebus*, *Allochrocebus*) share more of their external characteristics with the arboreal guenons (*Cercopithecus*) than they do with either *Miopithecus* or *Allenopithecus*. However, it should be noted that putatively the most primitive member of the arboreal *Cercopithecus* radiation, Dryad Monkey *Cercopithecus dryas*, is also a diminutive monkey, supporting the concept that the *Cercopithecus* lineage started as small-bodied animals.

Another recent molecular study (which retains *Miopithecus* closer to *Allenopithecus*) estimates that *Miopithecus* diverged from *Erythrocebus* >8 mya (late Miocene) and from *Allenopithecus* 9.3 mya (Tosi *et al.* 2004). See also Perelman *et al.* 2011. In several respects (body-size, large social groups and preference for riverine understorey vegetation, not to mention its greenish pelage and strictly seasonal breeding), *Miopithecus* shows convergent characteristics with the South American squirrel monkeys *Saimiri* spp.



Lateral view of skull of Northern Talapoin Monkey *Miopithecus ogouensis* adult male compared with that of Patas Monkey *Erythrocebus patas* juvenile.

Miopithecus can be diagnosed by small size and associated paedomorphic features (especially the small facial skeleton compared to the large braincase), the reduced hypoconulid on the third lower molar, the female's periodic sexual swellings, and the highly developed facial gestures, in which it resembles the Papionini (in most Cercopithecini facial gestures have been replaced by whole-head movements that emphasize species-specific colour patterns). Body proportions appear to differ between the two species of *Miopithecus* but detailed comparative studies have yet to be made. For all specific characters, see species profiles.

Jonathan Kingdon & Colin P. Groves

Miopithecus talapoin SOUTHERN TALAPOIN MONKEY (ANGOLAN TALAPOIN MONKEY)

Fr. Talapoin du sud; Ger. Südliche Zwergmeerkatze

Miopithecus talapoin (Schreber, 1774). Die Säugethiere 1: 101, 186, pl. 17. Angola.Southern Talapoin Monkey *Miopithecus talapoin* adult male.Southern Talapoin Monkey *Miopithecus talapoin* adult male.

Taxonomy Monotypic species. Disputed taxonomy. Originally named *Simia talapoin* Schreber, 1774, then included in the genus *Cercopithecus* (Erxleben 1777), then raised to the genus *Miopithecus* (I. Geoffroy, 1842). On the basis of craniological studies, considered a subgenus of *Cercopithecus* (Verheyen 1962). Type specimen of unknown origin but (wrongly) thought by Pocock (1907) to be from Gabon or Cameroon. He then described a new subspecies from Angola, *M. t. ansorgei* (Pocock, 1907). Machado (1969), examining 15 live or dead specimens from Angola, showed that the type specimen corresponded to monkeys found on the left bank of the Congo R. and not from Gabon or Cameroon. *Miopithecus t. ansorgei* was then subsumed in *M. talapoin*. The northern form is now named *Miopithecus ogouensis* Kingdon, 1997. The subspecies *pilettei* Lönnberg, 1919 from Mt Rwenzori, E DR Congo, is likely due to a deception or false provenance (Gautier-Hion *et al.* 1999). Synonyms: *ansorgei*, *capillatus*, *melarhinus*, *niger*, *pileatus*, *pilettei*, *vlesschouwersi*. Chromosome number: unknown.

Description Small, grizzled, yellowish-olive monkey. Africa's second smallest monkey. Sexes similar in colour. Adult ♂ larger than adult ♀. Lips and subocular areas ochre-pink. Cheeks and chin white. Facial mask bare, black. Ears large, bare, black. Head and back grizzled yellowish-olive. Outer limbs pallid chrome-yellow. Tail grizzled brown above and yellowish-grey below. Underparts and inner surfaces of limbs white. Females: pink sexual swellings. Scrotum pale blue (Machado 1969, Kingdon 1997).

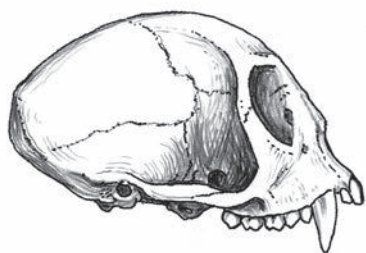
Geographic Variation None recorded.

Similar Species

Miopithecus ogouensis Northern Talapoin. North of Congo R. Allopatric. Slightly smaller; pelage shorter; ears relatively small; bare skin of face and ears pinkish; outer limbs golden-yellow; underside yellowish to greyish-white not contrasting sharply with sides.

Distribution Endemic to N Angola and SW DR Congo south (left bank) of lower Congo R. Rainforest BZ. Present in SW DR Congo (from 04°S) and coastal regions of N Angola (up to 12°30'S; Machado 1969), extending to the eastern limit of the floodplain especially along tributaries of the Kwango R. in the Kasai R. watershed (about 18°E; Gautier-Hion *et al.* 1999). Recently discovered on right bank of Kasai R. at Mimia (02°29'S, 20°E, Thompson 2001). This discovery brings the range of *M. talapoin* close to that of Allen's Swamp Monkey *Allenopithecus nigroviridis*.

*Miopithecus talapoin*



Lateral view of skull of Southern Talapoin Monkey *Miopithecus talapoin* adult male.

Habitat Not well known. Likely a riverine species (as *M. ogouensis*) living in dense vegetation and colonizing old plantations (Machado 1969).

Remarks One of Africa's least known monkeys. Ecology and behaviour not studied but likely similar to *M. ogouensis*. Kingdon (1997) suggests that *M. talapoin* could have more terrestrial habits than *M. ogouensis*, as a result of longer dry seasons and less extensive flooding due to cooler and drier climate.

Conservation IUCN Category (2012): Least Concern. CITES (2012): Appendix II.

Measurements

Miopithecus talapoin

HB (♂ ♂): 342 (322–400) mm, n = 5

T (♂ ♂) 471 (450–525) mm, n = 5

N Angola (Machado 1969)

Key References Machado 1969; Thompson 2001.

Annie Gautier-Hion

Miopithecus ogouensis NORTHERN TALAPOIN MONKEY (GABON TALAPOIN MONKEY)

Fr. Talapoin du nord; Ger. Nördliche Zwergmeerkatze

Miopithecus ogouensis Kingdon, 1997. The Kingdon Field Guide to African Mammals, p. 55. West Gabon.



Northern Talapoin Monkey *Miopithecus ogouensis* adult female.



Northern Talapoin Monkey *Miopithecus ogouensis* adult female.

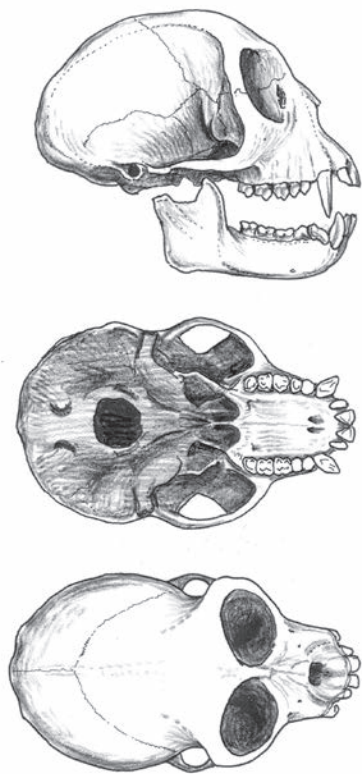
Taxonomy Monotypic species. There has been much confusion concerning the taxonomy of the northern and southern forms of talapoin monkeys. Machado (1969) found that the description for the type form *Miopithecus talapoin*, commonly called 'Gabon Talapoin', was based on a specimen from south of the Congo R. not from north of the Congo R. He convincingly argued that there were two species of talapoins but provided no formal description or name for the northern species. His claim that there were two species was subsequently supported by research on cellular and endogenous viral sequences that also suggested the existence of subspecies (Van der Kuyl *et al.* 2000). The brief description and name for the Northern Talapoin, *Miopithecus ogouensis*, put forth by Kingdon (1997, p. 55) as 'A *nomen nudum* ... in anticipation of a formal description' was accepted (Groves 2001, Grubb *et al.* 2003). It is important to note that, as a result of these recent taxonomic changes, most of the published data on talapoin monkeys are based upon observations of *M. ogouensis*, not on *M. talapoin* as stated. Synonyms: none. Chromosome number: 2n = 54 (Dutrillaux *et al.* 1988b).

Description Smallest Old World monkey. Sexes similar in colour. Adult ♀ weighs about 82% as much as adult ♂. Head large. Lips and eyelids yellowish-pink. Nose and 'sideburns' slightly darker than face. Cheek-stripes black. Face and ears naked and flesh-coloured. Crown and dorsal pelage speckled, varying from yellowish-olive to olive-brown. Ears and preauricular tufts small. Pelage short. Limbs thin. Outer surface of limbs, hands and feet yellowish to golden-yellow. Inner surfaces of limbs and ventral surface vary from yellowish to greyish-white, not contrasting sharply with sides. Sides of tail greyish, ventral and dorsal surfaces yellowish, darker at tip. Underside of tail base yellowish. Adult ♀ ♀ with pink sexual swellings. Scrotum large, pale blue. Young similar in colour to adults.

Geographic Variation None recorded.

Similar Species

Miopithecus talapoin Southern Talapoin. South of Congo R. Allopatric. Slightly larger; pelage longer; ears relatively large; bare skin of the



Lateral, palatal and dorsal views of skull of Northern Talapoin Monkey
Miopithecus ogouensis adult male.

face and ears black; outer limbs pallid chrome-yellow; underside white or whitish contrasting sharply with sides (Kingdon 1997, Groves 2001).

Distribution Endemic to central Africa. Rainforest BZ. Coastal watersheds of S Cameroon, W Congo, Equatorial Guinea (Rio Muni), Gabon and Angola (Cabinda). From the Atlantic coast eastward to the upper reaches of the north-west tributaries of the Congo R. (e.g. Alima R., Likouala R., Sangha R., Dja R.). Northern limit is at ca. 06° N in Mbam et Djerem N. P., C Cameroon (Maisels *et al.* 2006a). Southern limit is in Cabinda at ca. 05° 40' S. Not found in the region south of the loop of the Ogooué R. (Lopé Reserve, Forêt des Abeilles, Mt Doudou area) (Gautier-Hion *et al.* 1999). Reported, but not confirmed, in gallery forest in Central African Republic at ca. 08° N (Blancou 1958, J. L. Tello pers. comm.). Known limits of distribution: 06° N–05° 40' S; 08° 36'–16° E (Maisels *et al.* 2006a).

Habitat Riverine forest, flooded forest, swamp, secondary forest and old plantations. Favours dense undergrowth of lianas and small shrubs; avoids primary forest with open undergrowth. Not known to occur farther than 500 m from a water-course with suitable night sleeping sites. Such water-courses must be at least 10 m wide and deep enough to allow the monkeys to dive and swim (Gautier-Hion 1971a). Altitudinal range is from sea level to at least 400 m. Annual rainfall 1600 mm to >2800 mm.

Abundance Night censuses by boat along banks of Ivindo R., NE Gabon, yielded a minimum of 0.16 groups/km (n = 50 km), and a density of ca. 30–40 ind/km². Mean density based on home-ranges of three commensal groups was 90 ind/km² (Gautier-Hion 1971a).



Miopithecus ogouensis

Adaptations Diurnal and arboreal. Vertical thin-stems specialist able to leap vertically between thin supports. Spends most of the day in low vegetation, sometimes near the ground. Individuals (mainly juveniles) may gallop on the ground over short distances when obliged to cross open areas. Sometime stands up on hindlegs and tail tip in a 'tripod' posture (Gautier-Hion 1971a, b). Good swimmer with head submerged. Dives into water when disturbed at the sleeping site. Immatures play together in water. A 3–4-month-old hand-reared baby spontaneously plunged into a water bucket (Gautier-Hion & Gautier 1971). In NE Gabon one group swam every evening and morning to and from its sleeping site on a small island 20 m from the mainland (J.-P. Gautier pers. comm.). Each group regularly uses the same sleeping site (80% of time for nine groups, n = 343 nights). Sleeping sites always located near a river. Subgroups of up to four individuals sleep huddled together in trees, palms or lianas overhanging rivers (Gautier-Hion 1971a).

Foraging and Food Frugivorous-insectivorous. Northern Talapoins forage in a group. They are agile and lively monkeys; daily movements average 2300 m (1500–2950, n = 120 days, three groups) with two peaks, one in early morning (mean 400 m/h) and one at 16:00–17:00h (350 m/h). Home-range size averages 120 ha (110–140, n = 3 groups), of which at least 50% is seasonally flooded forest. They forage for fruit mostly during early morning and late afternoon, and for insects at all times of day. Arthropods comprise up to 80% of stomach contents (mean 35% of diet). Favoured mobile prey are Orthoptera (ca. 50% of prey), and moths and butterflies. Also eat caterpillars, spider cocoons and ants. Fruit and seeds account for ca. 58% of overall diet, and ca. 90% of the plant portion of the diet. Leaves and buds make up ca.

6% of the diet. About 70% of the food is taken from flooded forest, and at least 13% taken from lianas. Groups close to human settlements feed heavily on cassava tubers taken from cassava soaking sites, especially when fruit is in short supply (i.e. when fruit accounts for <45% of the diet). Also raids crops of maize and cucumbers (Gautier-Hion 1971a).

Social and Reproductive Behaviour Social. Multimale groups of 34–115 individuals (NE Gabon). Largest groups are those living close to human settlements (mean 66 animals, $n = 4$ vs. mean 37 animals, $n = 6$ for 'wild' groups). No clear evidence of territorial behaviour (Gautier-Hion 1971a). One group of 70 animals observed in Cameroon (Rowell 1973). During daily travels adult ♂♂ are grouped at the front of the group with a few moving at the back; pregnant and lactating ♀♀ with their infants tend to be grouped on their own; juveniles follow in subgroups of up to ten individuals mixed with some adults and subadults. During day resting (11:00–14:00h) adult ♀♀ with infants and juveniles stay at the centre of the group. Adult ♂♂ and oldest subadults stay at the periphery. In the evening, juveniles go back to their mothers (Gautier-Hion 1970). During one breeding period, Rowell (1973) observed an almost complete segregation of the adults by sex. She also recorded 'baby sitting' of juveniles by adult ♂♂. During one month in the mating season, Rowell & Dixon (1975) found that adult ♂♂ travel more with adult ♀♀, and that ♀♀ leave their infants (about six months old at this period) with juveniles. Only ♀♀ observed to carry young. Mothers push away attempts from other ♀♀ to carry their babies (Gautier-Hion 1971b).

During the night three main types of subgroups are formed: female-offspring subgroups, either pregnant ♀♀ with 1–2 juveniles (1–2 years of age) or lactating ♀♀ with infants plus 1–2 juveniles; immature subgroups (juveniles and/or subadults 2–4 years of age); lone adult ♂♂ or sometimes pairs of adult ♂♂. Immature subgroups and lone adult ♂♂ tend to sleep in higher strata than female-offspring subgroups (Gautier-Hion 1970, 1971a). Northern Talapoin are occasionally found in polyspecific associations with other arboreal cercopithecines, most often Moustached Monkeys *Cercopithecus cephus*. There is, however, no consistent tendency to form such associations (Gautier & Gautier-Hion 1969).

Highly graded vocal repertoire that includes 11 basic call types within which there are 31 different sounds. Some calls are very high pitched. A specific call is given during copulation by one or both partners. Harassing calls also given by immatures towards mounting or copulating animals (Gautier 1974). Low pitched 'cohesion calls' by adult ♀♀ and immatures precede and accompany oriented group movements (Gautier 1974). The frequency of the cohesion call increases as the likelihood of loss of contact among individuals in the group increases. Adult ♂♂ give a deeper cohesion call than adult ♀♀. The cohesion call is given in long series by a single adult ♂ during oriented group movements or during a change of route. Adult ♀♀ and immatures also give the cohesion call after any strong disturbance (Gautier 1974).

Reproduction and Population Structure Males reach full adult size at about six years. Females give birth for the first time at about four years ($n = 4$; Gautier-Hion & Gautier 1976). Northern Talapoin are highly seasonal breeders. Mating takes place during the

long dry season (Jun–Aug); births during the short dry season (Jan–Feb; Gautier-Hion 1968, 1971a; Rowell 1973). In a given group all ♀♀ (up to 27) may give birth in less than a two-month period (Dec–Jan; Gautier-Hion 1970). Most ♀♀ breed every year. At the peak of sexual activity sexual skin surrounds the callosities and the anus (Gautier-Hion 1968). Copulation is preceded by a display during which the ♂ and the ♀ follow each other in a *chassé-croisé*: partners look at one another, the ♀ presents to ♂, ♂ sniffs the female's genitalia; partners wait for each other, groom and make mutual hand contact. These displays observed both in wild and in captivity and may last >30 minutes. Captive ♀♀ copulate up to nine times per day with the same ♂ (Gautier-Hion 1971b). Adult ♂ sexual behaviour is dependent upon rank (Scruton & Herbert 1970, Gautier-Hion 1971b). Mode cycle duration in captive ♀♀ is 31 days ($n = 43$; Rowell 1977) and mean cycle duration is 33 days (Scruton & Herbert 1970). Gestation is 158–166 days ($n = 6$; Rowell 1977). At birth the infant weighs ca. 180 g ($n = 2$), which is about a fifth of the female's weight. Head of the newborn infant almost as large as its body. Twins not observed (Gautier-Hion 1971b). A captive ♀ died when 25 years old and a captive ♂ at 19 years (A. Gautier-Hion pers. obs.).

In one group of 115 individuals in NE Gabon, the adult sex-ratio was 13 ♂♂ to 27 ♀♀ (1 : 2). Adults constitute about 35% of group members. At the end of the birth season the group included 27 newborns, 16 juveniles one year old, 21 juveniles two years old and 11 subadults (Gautier-Hion 1971a).

Predators, Parasites and Diseases Since Northern Talapoin are small (1–2 kg), they are potential prey for numerous carnivores, raptors and snakes. African Golden Cats *Profelis aurata* observed several times at dusk close to a group arriving at its sleeping site, inducing alarm calls by monkeys. In the dense low strata typically used by Northern Talapoin, their small size and homochromatic colour make them difficult to see. In addition, the consistent location of their sleeping sites over rivers constitutes an effective anti-predator strategy. Female-offspring subgroups sleep closer to the water than other subgroups, sometimes less than 3–4 m above the water (Gautier-Hion 1971a). No data available on parasites or disease.

Conservation IUCN Category (2012): Least Concern. CITES (2012): Appendix II.

The Northern Talapoin remains widespread and abundant. In the 1960s cassava eating by Northern Talapoin was widespread. In NE Gabon every village had 'its' Northern Talapoin group, which regularly slept in trees and lianas overhanging the place where villagers washed themselves each evening. In so doing, Northern Talapoin probably gained protection from predators deterred by human presence, and stayed close to cassava soaking sites located close to settlements. Northern Talapoin in NE Gabon were not fearful of people in the 1960s because hunters did not waste a cartridge for such a small prey. Trapping campaigns were undertaken only when crop-raiding became excessive. They were not at all afraid of women and just hid in the close-by foliage when they arrived to collect the cassava (Gautier-Hion 1971b). The situation has since changed; with increasing scarcity of game from over-hunting Northern Talapoin are now hunted. In 1982 the main commensal groups studied between 1965 and 1968 were no longer present close to the villages (J.-P. Gautier pers. comm.).

Measurements*Miopithecus ogouensis*

HB (♂ ♂): 324 (260–360) mm, n = 6

HB (♀ ♀): 278 (230–310) mm, n = 8

T (♂ ♂): 411 (315–450) mm, n = 6

T (♀ ♀): 370 (340–390) mm, n = 8

HF: n. d.

E: n. d.

WT (♂ ♂): 1.38 (1.00–1.72) kg, n = 10

WT (♀ ♀): 1.13 (0.99–1.22) kg, n = 11

NE Gabon (Gautier-Hion *et al.* 1999, A. Gautier-Hion pers. obs.)

HB (♂ ♂): 338 (320–350) mm, n = 5

HB (♀ ♀): 335, 340 mm, n = 2

T (♂ ♂): 408 (375–449) mm, n = 5

T (♀ ♀): 337, 380 mm, n = 2

Various localities (BMNH; Napier 1981)

Key References Gautier-Hion 1970, 1971a; Oates 2011; Rowell 1973; Rowell & Dixon 1975.**Annie Gautier-Hion****GENUS *Erythrocebus*****Patas Monkey***Erythrocebus* Trouessart, 1897. Catalogus Mammalium tam Viventium quam Fossilium 1: 19.Patas Monkey *Erythrocebus patas* adult male.

Erythrocebus is a monotypic genus. The single species, the Patas Monkey *E. patas*, is so distinctive, both in its appearance (lanky, greyhound-like proportions; overall red colour with white underside;

small moustache) and in its habitat (open grasslands and woodlands), that it has almost invariably been awarded generic status separate from *Cercopithecus*. None the less, both morphological (Groves 1989, Sargis *et al.* 2008) and molecular evidence now indicate its close affiliation with savanna monkeys *Chlorocebus* and mountain monkeys *Allochocebus* (Dutrillaux *et al.* 1988a, b, Tosi *et al.* 2004, Tosi 2008). There is no evidence for *Erythrocebus* ever occurring south of its present limits in N Tanzania (De Jong *et al.* 2009). Chromosome number $2n = 54$ (Romagno 2001).

Erythrocebus shares with *Chlorocebus* a number of derived cranial features: the orbits in lateral view do not slope forward inferiorly; the tympanic tube has a V-shaped lower margin (seen only in juveniles in *Cercopithecus*); and the orbits are angular instead of oval. At the same time, the two genera lack derived conditions of *Cercopithecus* (shape of the nasal aperture and nasal bones, and conditions of the upper incisors). As shown by Gebo & Sargis (1994), *Erythrocebus* shares the extreme adaptations to terrestriality of *Allochocebus* (as listed under that genus).

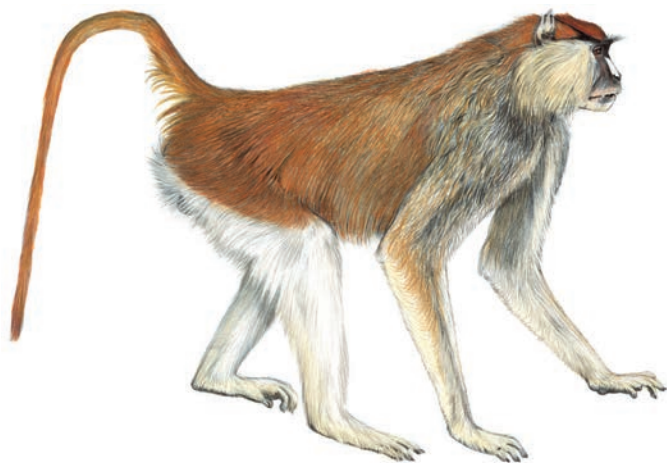
Like other members of the Cercopithecini, *Erythrocebus* lacks molar flare and a hypoconulid on the third lower molar, and the ♀ does not develop prominent sexual swellings. Ischial callosities small and well separated in both sexes. Skull of the ♂ distinctive, with a long, narrow but protuberant muzzle. Hands and feet show more resemblances with *Chlorocebus* than with any other guenons (Kingdon 1988a).

Current molecular evidence suggests that *Erythrocebus* diverged from the cercopithecine tree during the Messinian (5.3–4.5 mya), an exceptionally dry period that probably led to the early evolution of Saharan endemics (Purvis 1995, Perelman *et al.* 2011). Such an origin is consistent with restriction of *Erythrocebus* to the southern margins of the Sahara/Sahelian belt, although it seems unlikely that the ancestral *Erythrocebus* was as extremely adapted to drought and open landscapes as is the extant *E. patas*. Kingdon (1971) suggests that the later emergence of *Chlorocebus* might have served to displace *Erythrocebus* from more mesic habitats (e.g. woodlands) out into the drier margins of its range, with concomitant adaptations.

Colin P. Groves & Jonathan Kingdon

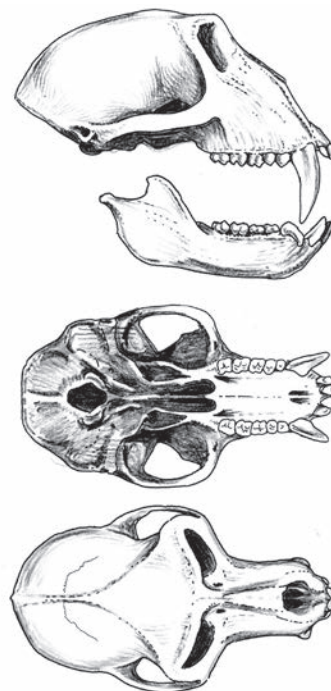
Erythrocebus patas PATAS MONKEY (HUSSAR MONKEY, NISNAS)

Fr. Patas; Ger. Husarenaffe

Erythrocebus patas (Schreber, 1775). Die Säugethiere 1: 98. Senegal.Patas Monkey *Erythrocebus patas* adult male.

Taxonomy Polytypic species. Three subspecies recognized here, in contrast to Kingdon (1997), who recognized four (*E. p. patas*, *E. p. pyrrhonotus*, *E. p. baumstarki* and *E. p. villiersi*), Dorst & Dandelot (1969), who recognized two (*E. p. patas* and *E. p. pyrrhonotus*) and Groves (2001, 2005c, Grubb *et al.* 2003), who recognized none. The decisions to recognize no subspecies were assisted by documented changes in females' facial colouration with changes in reproductive condition (Loy 1974, Palmer *et al.* 1981). Loy (1974) reported that the animals in his captive colony originated from Ethiopia. Following Napier (1981), Groves (2001, 2005c) suggested that these changes could account for some of the variation that had been previously attributed to subspecific variation. Loy later found, however, that the animals originated from Nigeria (Goldman & Loy 1997, J. Loy pers. comm.). In a ten-year study of Patas in Kenya, Isbell *et al.* (2009) found that although pelage colour of individual ♀♀ may vary from light orange to orange-red over time, facial colouration does not change with reproductive status and nose colouration remains white once ♀♀ reach adulthood. These differences in facial colouration suggest that Patas in West Africa (*E. p. patas*) and Patas in most of East Africa (*E. p. pyrrhonotus*) are distinct subspecies. The Tanzanian population (*E. p. baumstarki*) is apparently isolated (De Jong *et al.* 2009), a condition that would facilitate the evolution of subspecific differences. The facial colouration of adult ♂♂ is different from all other populations, noticeably lacking a white moustache and white nose. This population is thus also considered a subspecies. The Aïr Massif, C Niger, population, has been assigned to the subspecies *villiersi*. This isolated population is said to differ from *E. p. patas* only in body size, a characteristic that is also heavily influenced by environmental conditions. In the absence of other differences, particularly facial colouration, we do not here recognize *villiersi* as a subspecies of *E. patas*.

The year that Schreber described and named Patas is variously given as '1774' (Dandelot 1974, Napier 1981, Groves 2001, Grubb *et al.* 2003) or '1775' (Hall 1966, Groves 2005c). Examination of this publication indicates that the correct year is '1775'.

Lateral, palatal and dorsal views of skull of Patas Monkey *Erythrocebus patas* adult male.

Synonyms: *albigenus*, *albo-fasciatus*, *albosignatus*, *baumstarki*, *circumcinctus*, *formosus*, *kerstingi*, *langheldi*, *nigro-fasciatus*, *poliomystax*, *poliophaeus*, *pyrrhonotus*, *rubra*, *rufa*, *sannio*, *villiersi*, *whitei*, *zechi*. Chromosome number: $2n = 54$ (Baylet & Grattepanche 1964).

Description Medium-sized, long-legged, terrestrial monkey with reddish-brown crown, back and flanks, and cream or white below. Deep-chested but torso slender and limbs longer than those of other primates of similar size. Adult ♂: chest and front of neck cream or white. Scrotum turquoise or aquamarine blue. Anus red. Proximal one-third of tail carried arched behind the body while walking. Adult ♀: weighs about half as much as adult ♂ and with less contrast in colour. Tail less arched. Infant: face pink, pelage dark brown or black when born, changing to adult ♀ colouration by three months. Scrotum changes from grey to blue at ca. three years of age. Photographs of *E. patas* from several countries available at: www.wildsolutions.nl

Geographic Variation Three subspecies recognized:

E. p. patas Western Patas Monkey. Senegal to Chad. Adult ♂: chin white; muzzle pinkish, grey or black; nose black; cheeks grey or white, ruffed with long hairs; 'moustache' white; ear tips white. Neck, back and flanks fawn with long hairs. Chest and ventrum beige. Shoulders with cape-like pelage, red hair mixed with grey and black. Lower legs and feet white. Adult ♀: similar to adult ♂ but legs and feet cream to orange-red. During pregnancy facial

*Erythrocebus patas*

skin becomes lighter, facial hair, especially on nose, turns white, and black temporal and superciliary lines disappear (Loy 1974).

E. p. pyrrhonotus Eastern Patas Monkey. Sudan to W Ethiopia, N DR Congo, N Uganda and localized areas of W and C Kenya (De Jong *et al.* 2008). Adult ♂: muzzle black; nose white; black 'mask' around eyes continuing as black superciliary line above the eyes onto forehead and crown; cheeks white, separated from dark reddish-brown forehead and crown by black temporal lines to black ears; 'moustache' white; ear tips white. Back and flanks reddish-brown. Shoulders mixed red, brown and black. Legs white. Pelage longer than *E. p. patas*. Adult ♀: similar to adult ♂ but muzzle lighter and legs creamy. No facial colouration changes during pregnancy. Shoulders, back and flanks orange or orange-red to red but individuals variable over time. Shoulder pelage ca. 5 cm long but not cape-like.

E. p. baumstarki Southern Patas Monkey. NC Tanzania (De Jong *et al.* 2009). Adult ♂: face black; 'moustache' and nose black; black temporal lines contrast with white pelage below and above; ear tips black. Legs greyish. Adult ♀: similar to adult ♂ but lighter coloured.

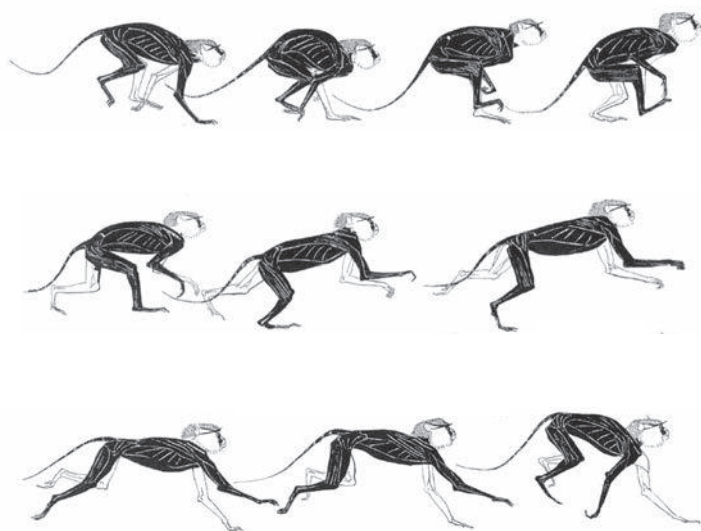
Similar Species None.

Distribution Endemic to tropical Africa. Sahel Savanna, Sudan Savanna, Guinea Savanna and Somalia–Masai Bushland BZs. Widespread in grassland and woodland savanna below the Sahara Desert and above the tropical forest belt. Western limit is Dakar-Yoff, NW Senegal (17° 29' W; A. Galat-Luong & G. Galat pers. comm.). From NW Senegal through Sudan to W Ethiopia to N DR Congo, N Uganda, W, C and S Kenya and NC Tanzania. Distribution discontinuous in the east. In Kenya, Patas occur in Turkana, West-Pokot, Busia, Baringo, Laikipia, Nyeri, Makueni and Taita Taveta Districts. Historic geographic range in Kenya ca. 88,800 km². Current geographic range in Kenya ca. 48,200 km² (04° 00' N–03° 00' S;

34° 06'–38° 27' E; De Jong *et al.* 2008). In Tanzania, on west and south-west sides of Mt Kilimanjaro, with an isolated population in western Serengeti, near the Grumeti R. Historic geographic range in Tanzania ca. 30,800 km² (01° 28'–04° 02' S; 33° 36'–37° 37' E). Current geographic range in Tanzania ca. 20,700 km² (01° 28'–04° 02' S; 33° 36'–37° 25' E; De Jong *et al.* 2009). Another isolated population on Air Massif, Niger (Wolfheim 1983, Kingdon 1997, Groves 2001). Reaching 17° N, Patas (on the Air Massif, Niger), together with the Green Monkey *Chlorocebus sabaeus* in Senegal and Tantalus *Chlorocebus tantalus* in Mali, probably has the northern-most range of any species of guenon in West Africa at this time.

Habitat Grasslands, savannas and savanna-woodlands. In West Africa, Patas occur in Guinean and Sahelian savanna-woodlands. Patas enter bamboo *Oxytenanthera abyssinica* in SE Senegal (A. Galat-Luong & G. Galat pers. comm.). In Kala Maloue N. P., Cameroon, they occur in habitats dominated by *Acacia seyal*, *Acacia nilotica* and *Balanites aegyptiaca*, and in grasslands dominated by *Zornia glochidata* and *Panicum* spp. where mean annual rainfall is ca. 500 mm and there is one wet season (May–Sep). Mean monthly temperature ranges from 23 °C in Jan to 34 °C in May (Nakagawa 1999). In Murchison Falls N. P., NW Uganda, Patas are present in *Acacia sieberiana*, *Tamarindus indica* and *Combretum aculeatum* woodland where the mean annual rainfall is ca. 1000 mm (Hall 1965). In Kenya and NC Tanzania Patas may be limited now to areas with poorly drained and seasonally waterlogged vertisolic ('black cotton') soils. In such areas Whistling Thorn *Acacia drepanolobium* is the dominant tree, and *Pennisetum mezianum*, *Pennisetum stramineum* spp. and *Themeda triandra* are the predominant grasses (Taiti 1992, Young *et al.* 1997). In Tanzania, mean annual rainfall over the range of Patas is 250–1050 mm (De Jong *et al.* 2009), and in Kenya this is 270–1435 mm (De Jong *et al.* 2008). On the Laikipia Plateau, C Kenya, Patas occur where the mean annual rainfall is ca. 500–800 mm (Young *et al.* 1998; De Jong *et al.* 2008; Isbell *et al.* 2009). Here rainfall is trimodal, with two distinct wet seasons (Apr–Jun and Oct–Nov) and a transitional wet/dry season (Jun–Aug; Isbell *et al.* 2009). Annual mean monthly minimum and maximum temperatures in Laikipia, during 1993–2002, were 9° and 32 °C, respectively, with the widest mean monthly differential (20 °C) occurring in the dry season months of Feb–Mar (L. A. Isbell pers. obs.). Altitudinal limits are from sea level at Saloum Delta N. P., Senegal (where Patas enter mangrove; Labouze *et al.* 1996), to 300 m in SE Senegal (A. Galat-Luong & G. Galat pers. comm.) to 2000 m at Kekohey (north of L. Naivasha, Kenya), to 2030 m at Ol Pejeta Conservancy on the Laikipia Plateau, to 2050 m in West Pokot, W Kenya (De Jong *et al.* 2008). Patas drink daily when possible, and they appear to be restricted within drier habitats to those having a year-round supply of water (De Jong *et al.* 2008, 2009).

Abundance Little is known about the current abundance of Patas. They are apparently more abundant in the west of their geographic range than in the east (S. Gartlan pers. comm.). In SE Senegal, Patas are the most frequently sighted mammal outside national parks (J. Pruetz pers. comm.). As of 2000, there were ca. 300 Patas on the Laikipia Plateau, the region in Kenya where they are most abundant (Isbell & Chism 2007). The density is 0.2–1.5 ind/km² where groups are found (Chism & Rowell 1988, Isbell & Chism



Patas Monkey *Erythrocebus patas* running (analysis from film and dissection).

2007). In Murchison Falls N. P. density was 0.03 ind/km² in the 1960s (Hall 1965).

Adaptations Diurnal and largely terrestrial. Although similar to *Cercopithecus* spp. in many ways, Patas differ by having longer forearms and legs (Hurov 1987, Strasser 1992), longer tarsal bones (Strasser 1992), shorter metatarsal bones (Gartlan 1974, Matsubayashi *et al.* 1978), and hindfoot digitigrady (Meldrum 1991), all of which increase stride length (Hildebrand 1982). Their unique morphology is viewed as an adaptation for high-speed terrestrial locomotion primarily for escaping predators and/or for efficient travel, either for long-distance daily travel while foraging for small and scattered foods, or for exploiting waterholes or high densities of foods that are widely separated (Hall 1965, Chism & Rowell 1988, Isbell 1998, Isbell *et al.* 1998a, b, 1999b, Nakagawa 1999). At Segera, on the Laikipia Plateau, Patas spend 25% of their time moving, more than half of which (14%) is spent feeding and foraging while walking. The time that Patas spend acquiring food while walking is nearly four times greater than in the sympatric Vervet *Chlorocebus pygerythrus*. Feeding while not moving accounts for an additional 22% of their time (Isbell *et al.* 1998a).

In East Africa, where Patas sleep in small *A. drepanolobium* (mean height 2.6 m, 0.5–6.0 m; Enstam & Isbell 2002), groups seldom sleep in the same area on successive nights (Hall 1965, Chism & Rowell 1988), and group members typically sleep individually in separate trees except for mothers and their dependent offspring (Chism & Rowell 1988). In West Africa, where Patas have access to larger sleeping trees (mean height 7.8 m, 4–12 m; Nakagawa 1999), co-sleeping is more common (Nakagawa 1992).

Foraging and Food Omnivorous. In East Africa, Patas are strongly associated with *A. drepanolobium* from which they obtain gum (37% of their diet at Segera) and arthropods (30–40%) – dietary staples available year-round (Isbell 1998, Isbell & Young 2007). The majority of their arthropod diet comes from ants (adults, larvae and eggs) of the genus *Crematogaster*, which live in the swollen thorns of *A. drepanolobium*. Adult ants aggressively defend their colonies, swarming rapidly and biting when they detect disturbances.

Largely because of the ants' defensive behaviour, Patas typically bite open and feed on the contents of only one or two swollen thorns per tree before moving on. Patas have been described as feeding at a steady walk (Hall 1965), scanning for arthropods in the grass, and for gum and arthropods on trees as they walk. At Segera they also feed on flowers (7%), fruits and seeds (10%), leaves (2%) and vertebrates such as geckos and birds' eggs and nestlings (1%) (Isbell 1998). In addition to *A. drepanolobium*, they feed on *Acacia xanthophloea*, *A. seyal*, *Lycium europeum*, *Sarcostema viminale*, *Lippia javanica*, *Cucumis aculeata*, *Commelina* spp., *Hibiscus* sp., *Plectranthus* sp. and *Termitomyces* sp. (Chism & Rowell 1988, Isbell 1998). In areas where *Opuntia* cactus has been introduced, Patas readily eat the succulent leaves (Chism & Rowell 1988). The wet season diet of Patas in Kala Maloue N. P. includes flowers (65%), arthropods (12%), gums (7%), leaves (6%), stems (5%) and fruits (5%) taken mainly from *A. sieberiana*, *A. seyal*, *B. aegyptiaca*, *Cassia* sp., *Abelmoschus* sp., *Commelina* sp. and *Ipomoea* sp. (Nakagawa 1989).

Only minor differences exist in the diet of individuals of different age/sex classes. At Segera the diet of infants is more similar to that of the resident ♂ whereas the diet of juveniles is more similar to that of adult ♀♀. The resident adult ♂ and infants ate gum most often (44% and 38%, respectively), followed by swollen thorns (36% and 31%, respectively). Adult ♀♀ and juveniles ate swollen thorns most often (41% and 39%, respectively), followed by gum (34% and 36%, respectively). Flowers were the third most numerous food type for all age/sex classes (7–16%). Seeds were the fourth most numerous food type for the resident adult ♂ and infants (4% and 8%, respectively), whereas free-living arthropods were the fourth most numerous food type for adult ♀♀ and juveniles (5% for each) (Isbell 1998).

Patas are affected by the distribution and abundance of water (Nakagawa *et al.* 2003, De Jong *et al.* 2008, 2009). In Laikipia they benefit from cattle ranches that have established water troughs and tanks from which they drink daily, especially during the dry season (Chism & Rowell 1988, Isbell & Chism 2007). During the dry season, these monkeys are relatively easily found because they are often near such water sources, but when there are puddles of rainwater on the ground during the wet season, they become much more difficult to find in their large home-ranges. In West Africa aggression observed between groups at waterholes (Struhsaker & Gartlan 1970). In Kala Maloue N. P., Patas drink daily from waterholes during the dry season, and preferentially use areas where such waterholes occur (Nakagawa 1999). A large decline in population size there was attributed to a three-year drought (Nakagawa *et al.* 2003). In Niokolo-Koba N. P., Senegal (J. Pruetz pers. comm.) and in NC Tanzania (De Jong *et al.* 2009) they drink at streams in riverine forests.

Patas begin moving out of their sleeping trees around 07:30h (Chism & Rowell 1988, Nakagawa 1989). They feed and forage while moving at a rate of ca. 320 m/h until around 11:30h (Chism *et al.* 1983, Nakagawa 1989) or around 13:30h (Hall 1965), when there is usually a rest period of about two hours. Following the rest period they resume feeding, foraging and moving. At Segera inactivity (resting, sleeping, standing still) accounts for about 40% of adult time, while self-grooming and social grooming account for about 14% of adult time (Isbell *et al.* 1998a). Patas travel fastest in the late afternoon (435 m/h), just before settling into their sleeping trees (Chism *et al.* 1983).

Daily travel distance for a group with a mean of 45 members was extrapolated to 3188 m based on straight-line distances of the group during 30-minute periods ($n = 133$ days; Isbell *et al.* 1999b, Enstam & Isbell 2007). At Mutara, also on the Laikipia Plateau, mean daily travel distance for a group of 16–23 was 3830 m (1380–5880 m, $n = 61$ days) and, for a group of 47–54, 4420 m (2380–7500 m, $n = 55$ days; Chism & Rowell 1988). In Kala Maloue N. P. the mean daily travel distance for a group of 8–14 ranged from 4350 m in the early dry season ($n = 10$ days) to 6200 m in the mid-dry season ($n = 10$ days; Nakagawa 1999). Patas travel extraordinarily long distances for their body size, but daily travel distance does not increase significantly with group size, suggesting that these monkeys move more in rank formation than in file formation (Altmann 1974).

Home-range size does increase with group size, however. In Laikipia, home-ranges, systematically mapped over 1.0–1.5 years, were 23.4 km² for a group of 16–23 individuals, 28.5 km² for a group of 20–51, and 32 km² for a group of 47–54 (Chism & Rowell 1988, Enstam & Isbell 2004). Actual home-ranges may be larger. The home-range of the group of 20–51 was ca. 40 km² based on sightings of the group in several places >2 km from areas that had been mapped (Enstam & Isbell 2004). In Murchison Falls N. P. one group of 31 had a home-range of ca. 52 km² (Hall 1965). Though Kingdon (1971) mentioned that home-ranges may be as large as 80 km², this has not been confirmed. None the less, Patas have the largest home-ranges for their body size of any primate (Clutton-Brock & Harvey 1977, Chism & Rowell 1988, Isbell *et al.* 1998a).

Social and Reproductive Behaviour Social. Patas live in single-male, multifemale groups for most of the year. Group sizes in West Africa and East Africa are similar. In Waza N. P., Cameroon, groups had 7–34 members. Group compositions ranged from 1–2 adult ♂♂, 3–17 adult ♀♀, 0–7 juveniles and 0–7 infants ($n = > 5$; Struhsaker & Gartlan 1970). In Murchison Falls N. P. groups had 5–31 members. Group compositions ranged from 0–1 adult ♂, 2–18 adult ♀♀, 2–14 juveniles and 0–10 infants ($n = 8$; Hall 1965). In Laikipia groups had 13–56 members. Group compositions ranged from 0–1 adult ♂, 1–19 adult ♀♀, 5–22 juveniles and 0–16 infants ($n = 10$; Chism & Rowell 1988).

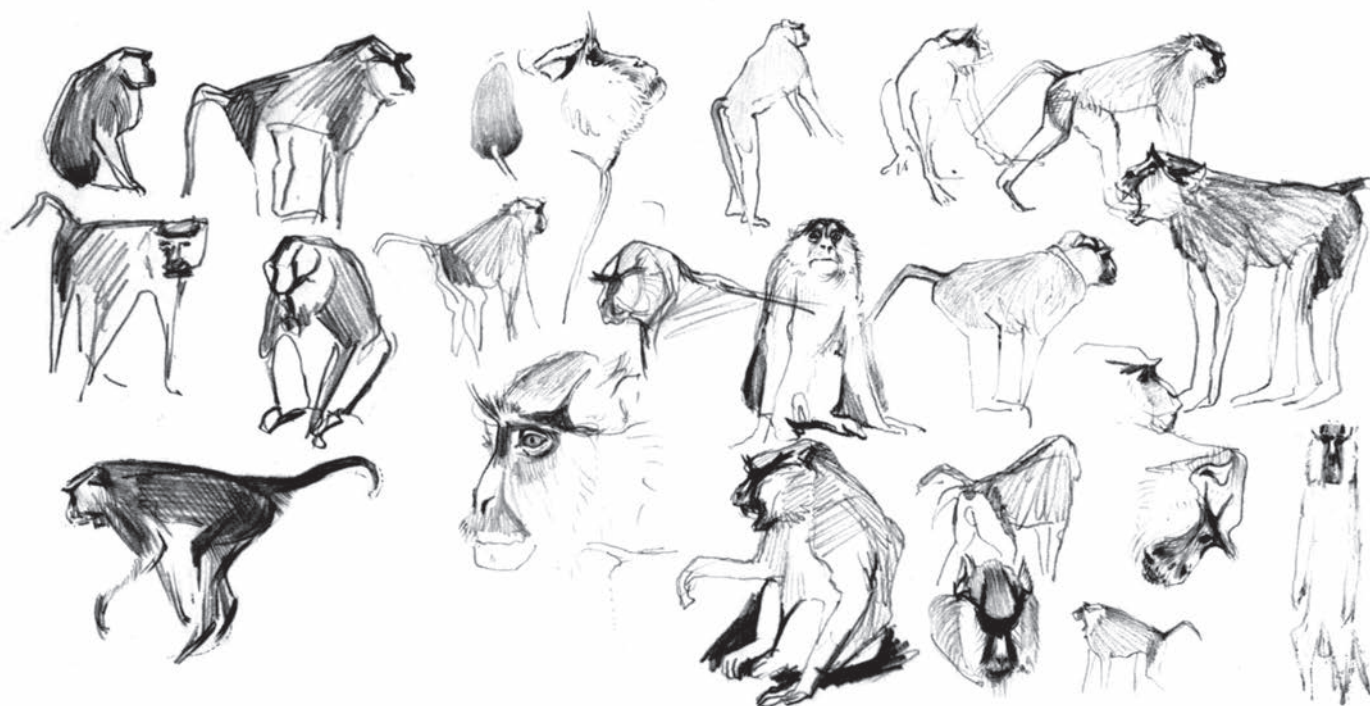
The size of a group can fluctuate widely over time. At Segera a group observed for ten years increased from 28 to 51 individuals in the first six years, then declined to seven over the next four years (Isbell *et al.* 2009). In Kala Maloue N. P. a group fluctuated between 26 and 45 over 13.5 years, decreasing from 45 to 16 over the first 2.5 years, increasing to 37 during the following 7.5 years, and decreasing again to 26 in the final 3.5 years (Nakagawa *et al.* 2003). Group composition can also change dramatically over the short term as a result of seasonal births. Birth sex ratios are unknown because immature Patas are difficult to sex visually unless observed as newborns at close proximity. The next opportunity to sex immatures occurs at ca. two years of age when ♀♀ develop a pink vulva.

Females typically remain in their natal groups throughout life. Groups are not territorial but are intolerant of other groups. Interactions between groups are aggressive, with adult ♀♀ and immatures of one group often running at high speed for prolonged distances (up to 3 km) as they chase the other group away (Chism *et al.* 1984, Chism 1999b). Resident ♂♂ are seldom involved in inter-

group encounters except during the breeding season (Struhsaker & Gartlan 1970, Chism & Rowell 1988, Chism 1999b). Physical contact is rare during inter-group encounters. The frequency of inter-group encounters varies depending on the extent of home-range overlap. At Mutara groups shared 44–58% of their home-range with other groups (Chism & Rowell 1988) and 72 inter-group encounters were observed in two years. At Segera, ca. 20 km from Mutara, only 5–10% of the home-range of one group was used by other groups and only 11 inter-group encounters were observed in ten years (L. A. Isbell pers. obs.). Segera differed from Mutara by (1) having fewer artificial water sources, (2) a greater tolerance by ranch management for Olive Baboons *Papio anubis* (and thus a higher density of this potential competitor for water) and (3) a near absence of *Opuntia* (an introduced cactus that was abundant, highly clumped and a main food resource for Patas at Mutara [Chism & Rowell 1988, J. Chism pers. comm., L. A. Isbell pers. obs.]). In Murchison Falls N. P. home-range overlap is minimal (Hall 1965). In Kala Maloue N. P. home-range overlap is extensive, with 80% of the home-range of one group being used by at least one of three other groups (Nakagawa 1999).

Within groups, adult ♀♀ often have poorly defined dominance hierarchies, particularly over short periods. This is because many dyads interact agonistically so rarely that relative positions in the dominance hierarchy are unclear (Isbell & Pruettz 1998). At Segera adult ♀♀ were, on average, 13.5 m from their three nearest neighbours, perhaps too far apart for agonistic interactions to be frequent. Large inter-individual distances have been suggested as a strategy by Patas to minimize detection by predators (Hall 1965), but they also correspond closely to the spatial distribution of food (Isbell & Enstam 2002). Dominance hierarchies are more obvious in captivity and in other situations, e.g. where foods are larger and thus more usurpable, or perhaps when there is demographic instability (Isbell & Pruettz 1998, Isbell 2008, N. Nakagawa pers. comm.). Dominance hierarchies may also be unstable over time, partly resulting from challenges to older ♀♀ from younger, maturing ♀♀ (Isbell & Pruettz 1998, Chism 1999a). Adult ♀♀ and immatures display by bouncing off vertical surfaces such as trunks of trees and fenceposts. Affinitive interactions among group members are mainly expressed as allogrooming, but coalitions are sometimes formed against others, including the resident ♂ (Nakagawa 1992, Muroyama 1994, L. A. Isbell pers. obs.). Females rarely groom the resident ♂ (Chism & Rowell 1988, Nakagawa 1992).

Males disperse from their natal groups as juveniles before their testes descend (by ca. three years of age) (Hall 1965, Chism *et al.* 1984, Nakagawa *et al.* 2003, Rogers & Chism 2009, L. A. Isbell pers. obs.). Males do not face increased aggression from the resident ♂ and are not evicted, but may leave to forestall more intense aggression in the future (Rogers & Chism 2009). At Segera, of two ♂♂ that left and later returned to their natal group, one was killed by the resident ♂ and the other returned only after the resident male's disappearance (L. A. Isbell pers. obs.). This suggests that maturing ♂♂ may prefer their natal group (particularly at low group densities) but stay away because of the high potential cost of intra-sexual aggression (L. A. Isbell pers. obs.). Extragroup ♂♂ range solitarily or in small associations with other ♂♂ and may converge upon groups of ♀♀ and the sole resident adult ♂ during the breeding season (Chism *et al.* 1984, Chism & Rowell 1986, Harding & Olson 1986, Ohsawa *et al.* 1993, Chism & Rogers 1997, Carlson & Isbell 2001). At Segera, over a seven-year period, 14 ♂♂ joined the group for at least ten



Patas Monkey *Erythrocebus patas* adult male.

days; all but two joined the group during the breeding season. Mean tenure length was 5.9 months (0.7–12.4; Enstam *et al.* 2002). One of the 14 ♂♂ later achieved tenure of 2.6 years (L. A. Isbell pers. obs.). At Mutara, where the population density was higher, 16 ♂♂ became resident in two groups during a two-year period; the longest tenure length was nine months (Chism & Rowell 1986). Multimale influxes and high rates of ♂ replacement occur more often with higher densities of Patas ♂♂ (Chism & Rogers 1997, Carlson & Isbell 2001).

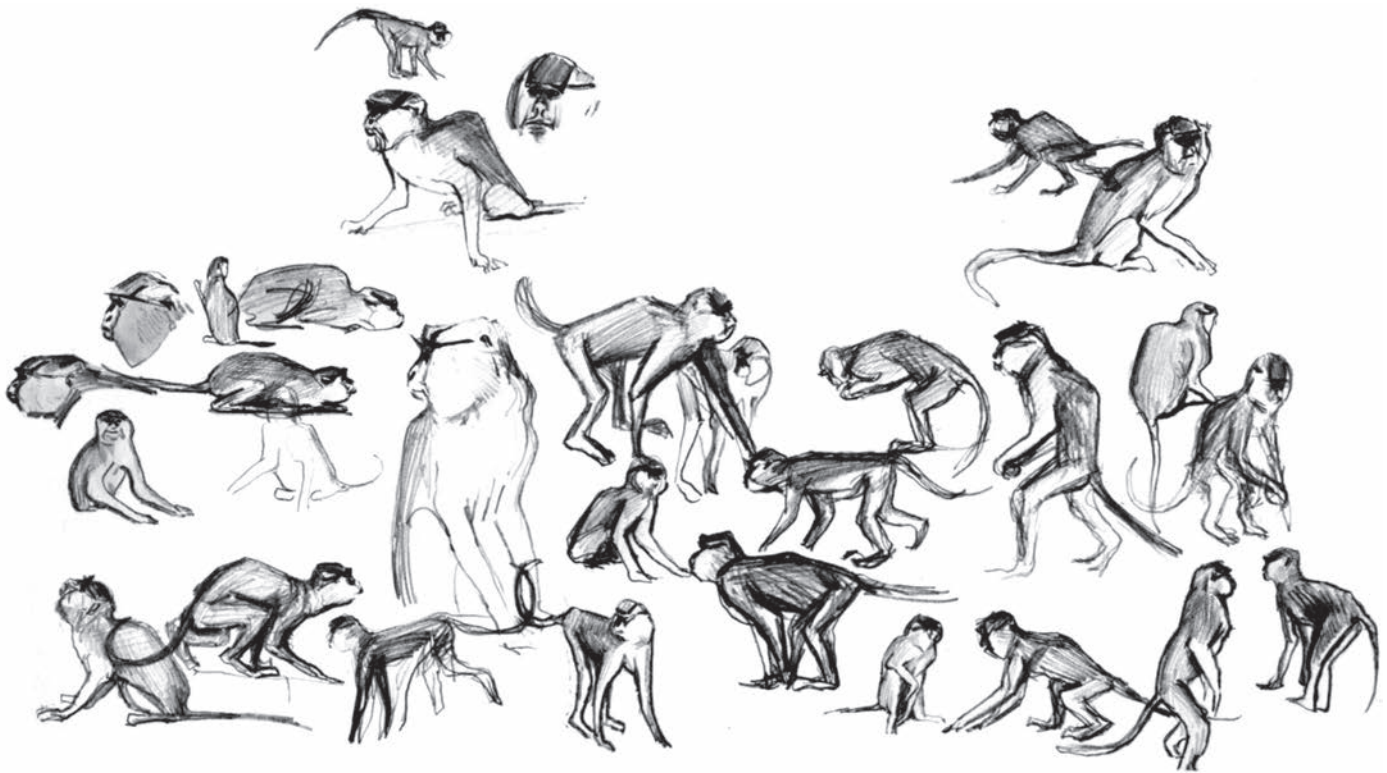
Adult ♂♂ are intolerant of each other in the presence of adult ♀♀ and their offspring (Hall 1965). The resident adult ♂ frequently sits at the top of the taller trees and scans into the distance (Hall 1965, Harding & Olson 1986). When he detects another adult ♂, he yawns, exposing his canine teeth, and ‘barks’ or ‘bark-grunts’ before chasing the intruder (Hall 1965, L. A. Isbell pers. obs.). Yawning is also done in other tense situations, such as during habituation to human presence and the close approach by a human after habituation. Other displays include branch-shaking and vertical bouncing. Resident ♂♂ are socially peripheral, interacting with other group members only when grooming, mating, excluding others from preferred resources (♀♀, food, water and space), or being threatened by coalitions of ♀♀.

At 2.5 years of age ♀♀ begin to solicit adult ♂♂, particularly during the breeding season. They have no sexual swellings; signs of oestrus are limited to behavioural changes. Females solicit the ♂ by running past him with the tail curled up and stopping abruptly in a crouched position in front of him. Sometimes they accompany this by puffing out their cheeks and drooling (Chism *et al.* 1984). Matings are often aborted as a result of harassment by immatures and sometimes by adults of either sex (Loy & Loy 1977, Zucker & Kaplan 1981, Carlson & Isbell 2001). Males are single-mount ejaculators (Loy 1975).

Although there is a distinct breeding season, ♀♀ also solicit matings from ♂♂ outside the breeding season and even during

pregnancy (Rowell & Hartwell 1978, Enstam *et al.* 2002). Such out-of-season solicitations increase in frequency during a change in the social environment, e.g. when a new ♂ becomes resident with the ♀♀ or after a ♀ has lost her infant as a result of infanticide (Rowell & Hartwell 1978, Enstam *et al.* 2002). Infanticide has been inferred only once in Patas (at Seger, out of 85 births); its rarity appears to be a function of the willingness of ♀♀ to solicit matings from multiple ♂♂, and of the replacement of resident ♂♂ during the breeding season (Enstam *et al.* 2002, Isbell *et al.* 2009). A ♂ that becomes resident with the group of ♀♀ during the breeding season may be a sire of the next cohort of infants (Ohsawa *et al.* 1993, Enstam *et al.* 2002).

Patas do not interact with most other animals in their environments, the exceptions being potential predators, their own prey, and Olive Baboons and Temminck’s Red Colobus *Procolobus badius temminckii*. Patas groups sometimes travel and play with Temminck’s Red Colobus groups in Saloum Delta N. P. (Galat-Luong & Galat 2005). Their main responses to potential predators involve vocalizations (alarm calls), active pursuit and avoidance. Adult ♀♀ and immatures give at least three different alarm calls to mammalian predators: (1) a ‘chirp’ or ‘nyow’, a high-pitched, staccato call, in response to the presence of Olive Baboons, Domestic Dogs *Canis familiaris* and Lions *Panthera leo*; (2) a loud ‘chutter’, which is softer than the chirp, given to Black-backed Jackals *Canis mesomelas* and Domestic Dogs; and (3) a ‘cough’ call, which is softer than the loud chutter and given when a Black-backed Jackal or African Wild Cat *Felis sylvestris* is close to, or within, the group (Enstam & Isbell 2002). The adult ♂ Patas’ equivalent to the females’ chirp is a two-note ‘bark-grunt’ (probably the ‘whoo-wherr’ vocalization of Hall [1965]) and is acoustically similar to the bark-grunt given when the resident ♂ detects another adult ♂ Patas. If Patas are in trees when they detect mammalian predators, they leave the trees. If they are already on the ground, they remain on the ground. Depending



Patas Monkey *Erythrocebus patas* adult female.

on the type of predator and the circumstances, they may run away quickly (Olive Baboons, African Wild Dogs *Lycaon pictus* and domestic dogs), chase the predator (Black-backed Jackals and African Wild Cats), or collectively mob it (Leopards *Panthera pardus*) (Hall 1965, Chism & Rowell 1988, Enstam & Isbell 2002). Patas also give 'soft chutters' to snakes. While chattering, they gather around the snake, stand bipedally and stare at it. Adult ♀♀ give 'gecker' vocalizations to raptors and sometimes chase them (Olson & Chism 1981, Enstam & Isbell 2002). Patas raid birds' nests and eat nestlings and eggs, largely ignoring mobbing attacks by the victims' parents. Patas seem perturbed enough as they feed on biting ants and their brood that they do not deplete trees of their ants but move to other trees to feed on ants that have not yet been disturbed (Isbell 1998).

Vocalizations given toward mammalian and avian potential predators are audible to humans outside the group. In contrast, vocalizations directed toward other group members are typically difficult to hear unless the observer is nearby. 'Moo' calls are the most frequent vocalizations, and are given in a variety of situations. 'Moos' are given by infants that are separated from their mothers, by ♀♀ as they approach and interact with mothers and their neonates, by ♀♀ that encounter another group, and by all age/sex classes when the rest period is over and the group begins to move again (Chism 1986, Nakagawa 1992, 1998, L. A. Isbell pers. obs.). Immatures squeal when they are at risk of physical attack by another group member. Immatures and adult ♀♀ frequently chatter, or gecker, and less frequently scream during agonistic interactions (Loy *et al.* 1993, L. A. Isbell pers. obs.).

Reproduction and Population Structure Beginning at three years of age, ♀♀ give birth to one infant every ca. 11.8 months at

Mutara ($n = 31$ inter-birth intervals; Chism *et al.* 1984, Chism & Rowell 1986), every 12.9 months at Segera ($n = 29$; Isbell *et al.* 2009) and every 14.4 months in Kala Maloue N. P. ($n = 33$; Nakagawa *et al.* 2003). At Segera an average of 79% of all adult ♀♀ in one group reproduced each year ($n = 9$ years). In the first five years, during a period of population increase, the mean reproductive rate was 92% per year (Isbell *et al.* 2009). Mean gestation length in captivity is 23.8 weeks ($n = 142$; Sly *et al.* 1983). Birth-weight is ca. 504 g (Harvey *et al.* 1987). Births are seasonal but variable across study sites. At Mutara births occur primarily in Dec–Feb (Chism *et al.* 1983). At Segera the birth season starts one month later (Enstam *et al.* 2002). In Kala Maloue N. P. births usually occur in Jan–Feb (Muroyama 1994, Nakagawa 1999, Nakagawa *et al.* 2003). In Waza N. P. births occur in Nov–Jan (Struhsaker & Gartlan 1970). In Niokolo-Kobu N. P. births occur in Jan–Mar (J. Pruett pers. comm.). Regardless of the locality or the months in which births occur, the birth season of Patas is invariably within the dry season (Butynski 1988). Females usually give birth during the day (Chism *et al.* 1983).

When infants are born, other ♀♀ are attracted to them and attempt to take them from their mothers. Though 'allomothering' does not obviously harm infants most of the time, infants protest at being taken and mothers attempt to retrieve them (Chism 1986, 2000), suggesting that allomothering is selfish rather than mutualistic, and might be better called 'kidnapping'. Of 85 infants born over nine years at Segera, allomothering/kidnapping resulted in the deaths of four infants, all of which were born the year following the worst year of reproduction during the study, when only 27% of adult ♀♀ reproduced. In all other years 67–100% of adult ♀♀ reproduced (Isbell *et al.* 2009). Infants from other groups are sometimes kidnapped during inter-group encounters (Nakagawa 1995, Chism



Patas Monkey *Erythrocebus patas* adult male.

1999b). When infants are two months old they spend ca. 25% of their time out of physical contact with their mothers. By the time they are three months old, weaning begins, and infants spend 45% of their time out of contact with their mothers. By four months, infants rarely sleep with their mothers during the day. By seven months, mothers no longer carry infants except in emergencies (Chism 1978, 1986). Infants orphaned at six months can survive (Isbell *et al.* 2009).

In captivity, Patas can live to about 24 years of age (Nowak 1999). Life-span in the wild appears to be considerably shorter. At Segera mean infant mortality during the first year was 30% over nine years. During a five-year period of population increase, mean infant mortality was 15%. In the following four years, as the population declined, infant mortality increased to 48% per year. Of 85 infants born during the study, 22 (26%) died in their first year (Isbell *et al.* 2009). The oldest ♀♀ were estimated to have lived at least nine years. Of the 11 adult ♀♀ that were parous when the study began, the minimum average age at death was 6.2 years. Of the 24 adult ♀♀ born during the 10-year study and surviving long enough to reproduce, 22 died. The mean age at death for those ♀♀ was 4.7 years. Mean annual mortality for adult ♀♀ was 33%. During the five years of population increase, mean annual adult ♀ mortality was 28%, and during the four years of population decline, it increased to 47% (Isbell *et al.* 2009). At Kala Maloue N. P. mean annual adult ♀ mortality was 22% ($n = 32$), and the oldest ♀ lived to about 17 years (Nakagawa *et al.* 2003). With rapid maturity, short inter-birth intervals and early age at death, Patas have the life-history traits of r-selected species.

Predators, Parasites and Diseases Little is known about the impact of predators on Patas. Black-backed Jackals and Domestic Dogs *Canis familiaris* are their only confirmed predators (Chism & Rowell 1988, L. A. Isbell pers. obs.). Puff Adders *Bitis arietans* observed to kill but not eat infant Patas (Chism *et al.* 1984). Overnight disappearances of monkeys coupled with Leopard tracks in their sleeping areas strongly implicate Leopards (Chism & Rowell 1988,

L. A. Isbell pers. obs.). Other potential predators include Lions, Spotted Hyenas *Crocuta crocuta*, African Wild Dogs, Olive Baboons, Robust Chimpanzees *Pan troglodytes* (in West Africa only) and Martial Eagles *Polemaetus bellicosus* (Chism *et al.* 1983, Enstam & Isbell 2002, J. Pruetz pers. comm.). Servals *Felis serval*, Caracals *Felis caracal* and African Wild Cats are potential predators of infant Patas. Immatures give alarm calls to Tawny Eagle *Aquila rapax*, African White-backed Vulture *Gyps africanus* and Eastern Chanting Goshawk *Melierax poliopterus*, which are probably not potential predators of Patas (L. A. Isbell pers. obs.). At Segera, while in tall trees, Patas spend up to 50% of their time scanning the environment (compared to 36% in short trees, $n = 12$ individuals). Their more frequent alarm-calling in tall trees suggests that they are scanning for predators (Enstam & Isbell 2004). Patas also disperse widely at their sleeping sites and rarely sleep in the same area on consecutive nights. These behaviours probably minimize detection by Leopards (Hall 1965, Chism *et al.* 1983, Chism & Rowell 1988, Nakagawa 1989).

Little is known about diseases in Patas. McGrew *et al.* (1989b) found five genera of intestinal nematode (*Stongyloides*, *Necator*, *Physaloptera*, *Streptopharagus*, *Trichuris*) and two genera of protozoa (*Entamoeba*, *Iodamoeba*) in a Senegalese population. Patas also harbour simian immunodeficiency virus (SIV) (Galat-Luong *et al.* 1994a). After particularly heavy El Niño-caused rains in Kenya in 1997, five of 14 adult ♀♀ in one group became ill, which was manifested by weakened and stiffened hindlimbs, weight loss, lethargy, apparent confusion and, in some individuals, cataracts and bleeding in the eyes (Isbell *et al.* 2009). Despite being hindered in their movements, none was immediately taken by a predator and all were able to keep up with the group until just before they disappeared and were presumed dead. Although most died within four months, one survived for >1 year with the symptoms. All failed to reproduce after they developed the symptoms.

Conservation IUCN Category (2012): Least Concern. CITES (2012): Appendix II.

Erythrocebus p. patas of West Africa is widespread and relatively common, although surveys have not been conducted for >25 years. Their range may even be expanding as Sahelian habitats spread southwards. Increased interaction with humans may, however, be reducing their numbers (S. Gartlan pers. comm.). In Kenya, the geographic range of Patas has declined from ca. 88,800 km² (prior to 1995), to roughly 48,200 km² in 2008 (ca. 54% of the known historic range). In addition, the populations of Patas in Kenya have become increasingly fragmented and isolated (De Jong *et al.* 2008). Patas are declining in Kenya partly as a result of conversion and fragmentation of habitat into small-scale agricultural use and the removal of trees, particularly *A. drepanolobium*, for charcoal manufacture (Chism & Rowell 1988, Isbell & Chism 2007). A survey of Trans-Nzoia, Uasin Gishu, Baringo and Laikipia Districts in 2001 located Patas only in the latter two districts (K. Ngece & L. A. Isbell pers. obs.). Their presence in Machakos, Busia, West Pokot and Nyeri Districts was confirmed during a survey in 2003–04 (De Jong *et al.* 2008). The status of Patas in Uganda is unknown but populations are presumed to be declining as expanding human populations move into habitats once considered marginal for agriculture. In Tanzania they appear to be in rapid decline with a population in 2008 estimated at 150–900 individuals living over an area of ca. 20,700 km². The range of the

Patas in Tanzania is estimated to have declined by ca. 33% between 1995 and 2008. All three of the populations of Patas in Tanzania have become smaller and increasingly isolated (De Jong *et al.* 2009).

Measurements

Erythrocebus patas

HB (♂♂): 623 (606–640) mm, n = 3

HB (♀): 490 mm, n = 1

T (♂♂): 621 (430–724) mm, n = 3

T (♀): 510 mm, n = 1

HF (♂): 162 mm, n = 1

HF (♀): 130 mm, n = 1

E (♂): 43 mm, n = 1

E (♀): 40 mm, n = 1

WT (♂): 7.0 kg, n = 1

Locality not stated (Napier 1981)

HF and E: BMNH (P. Grubb pers. comm.)

E. p. patas

HB (♂♂): 700 (630–750) mm, n = 4

T (♂♂): 688 (630–720) mm, n = 4

HF (♂♂): 165, 172 mm, n = 2

WT (♂♂): 12.4 (5.4–18.0) kg, n = 9

WT (♀♀): 6.5 (5.4–8.0) kg, n = 14

Linear measurements: various localities (Hill 1966)

WT: Fathala Forest, Senegal (Galat-Luong *et al.* 1996)

E. p. pyrrhonotus

HB (♂♂): 626 (575–670) mm, n = 4

T (♂♂): 680 (620–740) mm, n = 3

T (♀♀): 547 mm, n = 1

HF (♂♂): 156 (140–175) mm, n = 4

HF (♀♀): 167 mm, n = 1

Various localities (Hill 1966)

Key References Chism & Rowell 1988; Chism *et al.* 1984; Hall 1965; Isbell & Chism 2007; Isbell *et al.* 2009; Nakagawa 1999; Oates 2011.

Lynne A. Isbell

GENUS *Chlorocebus*

Savanna Monkeys

Chlorocebus Gray, 1870. Catalogue of Monkeys, Lemurs and Fruit-eating Bats in the Collections of the British Museum, p. 26.

With the exception of Gray (1870) and Groves (1989, 2001), the six major populations of the Savanna Monkeys Group *Chlorocebus* (*aethiops*) have previously been treated as *Cercopithecus* and the various forms have often been lumped under a single species, *Cercopithecus aethiops*. The six forms that are provisionally recognized in this work are Grivet *Chlorocebus aethiops*, Tantalus *Chlorocebus tantalus*, Green Monkey (Callithrix) *Chlorocebus sabaeus*, Vervet *Chlorocebus pygerythrus*, Malbrouck *Chlorocebus cynosuros* and Djam-Djam (or Bale Monkey) *Chlorocebus djamdjamensis*. The need for a comprehensive genetic study of the *Chlorocebus* radiation and the provisional nature of all previous taxonomic arrangements, including ours, can be illustrated by the difficulties surrounding *C. cynosuros*. This taxon was based upon a type specimen collected from north of the mouth of the Congo R. Because this gigantic river is one of the major natural barriers in Africa and the savanna monkeys south the Congo R. are broadly similar to the small population north of the Congo R., it is reasonable to suppose that the northern population derives from an early introduction by humans. Implicit in this situation is the likelihood that *cynosuros* from north of the Congo R., like any other isolated population deriving from a very small number of ancestors, will show genetic founder-effects.

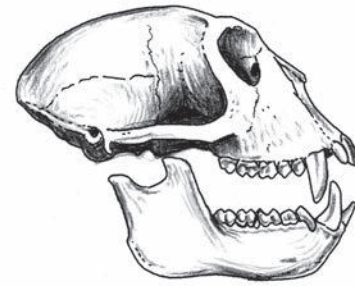
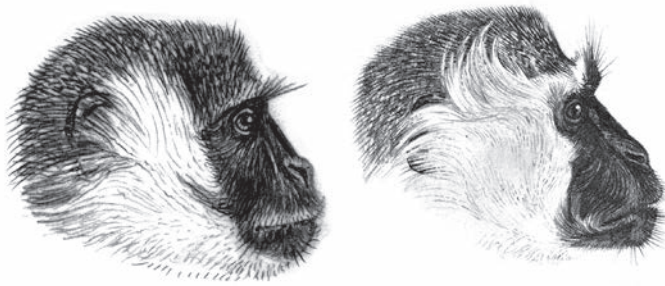
Although many individuals from Angola share characteristics of the *cynosuros* type there is considerable variation among animals from south of the Congo R. and this variability increases to the east. E. E. Sarmiento (pers. comm. and *C. cynosuros* profile) was unable to find consistent differences between supposed *pygerythrus* and *cynosuros* from either side of L. Malawi. Only a thorough molecular study is likely to resolve the many questions raised and this



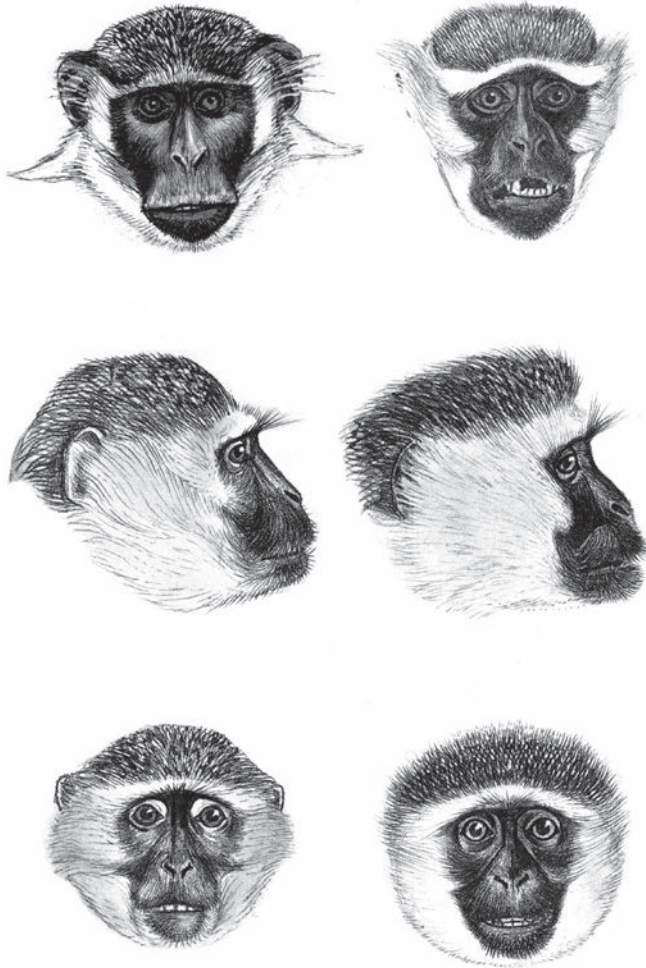
Green Monkey *Chlorocebus sabaeus* adult male.

qualification extends to most areas where regional populations of savanna monkeys meet.

Savanna monkeys are semi-terrestrial, grey, greenish or brownish monkeys with black faces surrounded by white facial ruffs. They range throughout sub-Saharan Africa outside true forest and desert and are particularly successful in acacia woodlands and riverine galleries.



Lateral view of skull of Tantalus Monkey *Chlorocebus tantalus* adult male.



Four savanna monkey *Chlorocebus* species (adult males).

Top left: Green Monkey *Chlorocebus sebaeus*.

Top right: Tantalus Monkey *Chlorocebus tantalus*.

Bottom left: Malbrouck Monkey *Chlorocebus cynosuros*.

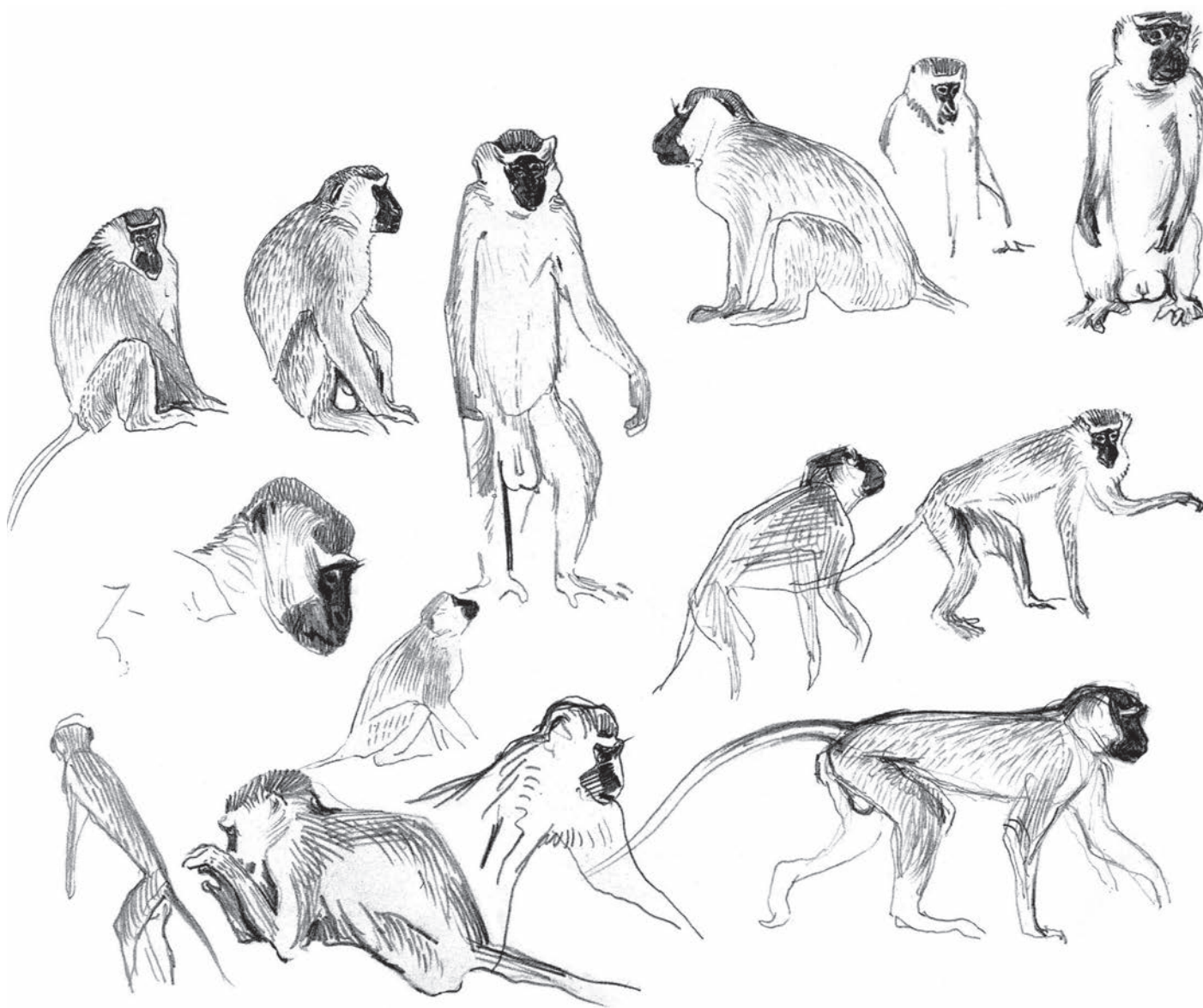
Bottom right: Vervet Monkey *Chlorocebus pygerythrus*.

Chlorocebus has no known fossil record but is a well-established group with closest affinities with two very different monkey genera, the Patas *Erythrocebus* and the mountain monkeys *Allochrocebus* (*preussi*) Group. These three genera represent the less arboreal bifurcation of the Cercopithecini (see figure, p. 245).

Chlorocebus is treated here as a full genus partly as a move towards less subjective taxonomies. While we have not yet adopted the criteria proposed by Goodman *et al.* (1998) in their entirety we have consciously

taken into account the 'age of divergence' criteria that were put forward in their paper. With the refinement of molecular clocks and calibration against fossils, contemporary scientists are, at last, providing some convincing phylogenetic trees and with them some basis for more objective ranking. This has been particularly relevant to the taxonomy of the Cercopithecini, which has always been an exceptionally large, diverse and opaque group in terms of understanding inter-relationships. The molecular phylogenetic trees assembled by Tosi *et al.* (2005) and Tosi (2008) show that the savanna monkeys, the Patas and the mountain monkeys cluster closely, a conclusion that is in accord with all genetic studies since Dutrillaux's pioneering work in the 1970s and 1980s, as well as with studies based on the postcranial skeleton (Gebo & Sargis 1994, Sargis *et al.* 2008). As a result of these findings it is illogical to call Patas '*Erythrocebus*' while retaining *Cercopithecus* for its two sibling groups. Divergence of the common ancestor of *Erythrocebus*, *Chlorocebus* and *Allochrocebus* from *Cercopithecus* (*sensu nova*) is estimated at 8 mya (late Miocene) (Tosi *et al.* 2005, Perelman *et al.* 2011), a divergence that is possibly older than that of *Miopithecus* (which is no longer disputed to be a full genus). According to Tosi *et al.* (2005) and Roos *et al.* (2011), *Erythrocebus*, *Chlorocebus* and *Allochrocebus* diverged from one another 5–6 mya (late Miocene), an age that justifies generic status for all three groups (Goodman *et al.* 1998).

Not surprisingly, the excision of savanna monkeys from *Cercopithecus* has not met with universal acceptance and we are grateful to L. Isbell & K. Jaffe (pers. comm.) for expressing some arguments contrary to our current views. They write: 'Groves (1989, 2001) places the Vervet in a separate genus, referring to it as *Chlorocebus pygerythrus*, with five subspecies. Although Patas *Erythrocebus patas* share these same morphological characteristics with Vervets, he dismisses the alternative of including both Vervets and Patas in the same genus because they share relatively few derived traits and it would mean that Patas would become *Chlorocebus*, which has priority over *Erythrocebus* by 27 years. However, based on molecular data that separate the more terrestrial from the more arboreal species within the Cercopithecini, Tosi *et al.* (2002) recommend that Vervets and Patas be placed together in the genus *Chlorocebus* to recognize their shared terrestriality. Also using molecular data, Tosi *et al.* (2003, 2004) agree with Groves (1989, 2001), placing Vervets in their own genus. We do not concur with these authors. We recommend that both Vervets and Patas be included in the genus *Cercopithecus* for the following reasons: (1) molecular data do not eliminate that alternative; (2) shared morphological characteristics do not always reveal true phylogenetic relationships and unique morphological characteristics do not always reveal the absence of phylogenetic relationships; (3) it is no more difficult to change the generic name for Patas than to change the generic name for Vervets



Tantalus Monkey *Chlorocebus tantalus* adult male.

since each alternative requires one traditional name to be changed; (4) terrestriality is a matter of degree rather than a discrete category among the Cercopithecini (McGraw 2002, see also below); (5) in addition to Vervets and Patas, the “terrestrial” clade includes one and possibly two species still in the genus *Cercopithecus* (L’Hoest’s Monkey *C. lhoesti* and the Sun-tailed Monkey *C. solatus*) (Tosi *et al.* 2004, 2005, Xing *et al.* 2007); (6) differences in diets and in foraging, ranging and social behaviour are slight between Vervets and Patas and *Cercopithecus* spp. and the differences are no greater than those within the genus *Cercopithecus* (Enstam & Isbell 2007); and (7) Vervets have hybridized with both Patas and Zanzibar Sykes’s Monkeys *Cercopithecus mitis albobularis* in captivity (Matsubayashi *et al.* 1978, Erhart *et al.* 2005).’

Some of the arguments put forward above articulate views that before the genetic revolution were not far from our own!

Djam-Djam, as a highly localized Ethiopian highland bamboo forest endemic, is the only member of the *C. (aethiops)* Group that does not range widely through savanna and woodland. We think this form might represent the relict of an early *Chlorocebus* stock

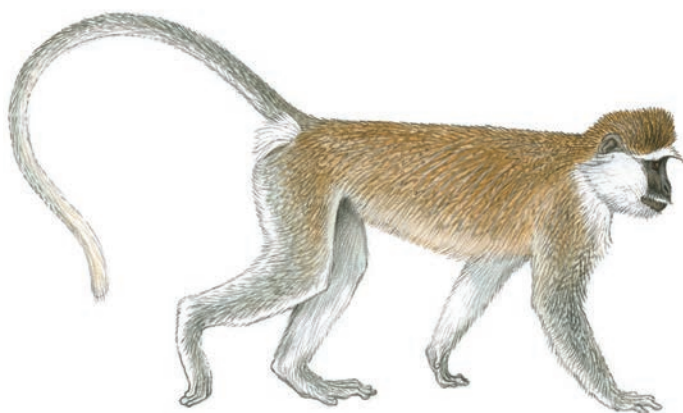
that, having adapted to the cool, dry conditions of a botanically impoverished montane Ethiopia, has resisted, so far, being replaced by later savanna monkey populations because of its adaptations to the special demands posed by bamboo forests. It seems possible that intermediate types from other parts of the Ethiopian massif represent the product of past genetic mixture outside Djam-Djam’s current refuge in the bamboo forests of S Ethiopia.

Chlorocebus shares with *Erythrocebus* a number of derived cranial features: the orbits in lateral view do not slope forward inferiorly; the tympanic tube has a V-shaped lower margin (seen only in juveniles in *Cercopithecus*); and the orbits are angular instead of oval. At the same time, the two genera lack derived conditions of *Cercopithecus* (shape of the nasal aperture and nasal bones, and conditions of the upper incisors). As shown by Gebo & Sargis (1994), *Chlorocebus* lacks the extreme terrestrial adaptations of the postcranial skeleton shared by *Erythrocebus* and *Allochrocebus*.

Colin P. Groves & Jonathan Kingdon

Chlorocebus aethiops GRIVET MONKEY

Fr. Grivet; Ger. Äthiopische Grünmeerkatze

Chlorocebus aethiops (Linnaeus, 1758). Systema Naturae, 10th edn, 1: 28. Sennaar, Blue Nile, Sudan.Grivet Monkey *Chlorocebus aethiops* adult male.

Taxonomy Polytypic species. The savanna monkey of NE Africa, the Grivet, has frequently been treated as a subspecies of the polytypic species or superspecies *Cercopithecus (aethiops)* (Schwarz 1926, Kingdon 1971, Thorington & Groves 1971, Napier 1981, Groves 1989, 1993, Grubb *et al.* 2003). Following Dandelot (1959, 1974), however, most of the recent taxonomies treat the Grivet as a full species (Hill 1966, Yalden *et al.* 1977, 1996, Lernould 1988, Kingdon 1997, Groves 2001, 2005c). Groves (1989, 1993, 2001, 2005c) returned the savanna monkeys to the genus *Chlorocebus* and treated some of the subspecies as full species, including the Grivet *Chlorocebus aethiops*. This taxonomy is supported by Tosi *et al.* (2003) and is the one followed here. The allocation of regional populations to full species has faced widespread criticism. For example, relatively modest differences in blood proteins between *C. aethiops* and Green Monkey *Chlorocebus sabaeus* suggest that subspecific ranking could be appropriately retained in this instance (Lucotte *et al.* 1982). This would ally all *Chlorocebus* (or at least the three boreal populations, *aethiops*, *tantalus* and *sabaeus*) under a common specific name. Such issues can only be resolved by further study, particularly at the molecular level.

Although regional types such as *C. aethiops* are well differentiated over much of their ranges, the existence of morphs or subpopulations that show mixed or intermediate characteristics on the edges of geographic ranges has reinforced objections to elevation of the types within *Chlorocebus* to species status. *Chlorocebus aethiops* is no exception (Yalden *et al.* 1977, Napier 1981, Lernould 1988). For example, the animals from the Omo R. region of extreme SW Ethiopia ('*zavattarii*' types) suggest admixture with Vervet *Chlorocebus pygerythrus*, as do those ca. 60 km south of Bale Mountains N. P. (T. Butynski pers. obs.). On the other hand, *Chlorocebus* living around the shores of the low-lying Rift Valley Lakes Abaya and Ch'amo of C Ethiopia are unequivocally *C. p. arenarius* and show no admixture with *C. aethiops*. In the western highlands of Ethiopia darker variants (*C. a. matschiei*) possibly represent adaptation to higher, wetter habitats or, alternatively, admixture with Djam-Djam *Chlorocebus djamdjamensis* (Kingdon 1997). Apparent hybrids between *C.*

aethiops and *C. djamdjamensis* reported but no sites of sympatry are known (Mekonnen *et al.* 2012, J.-M. Lernould pers. comm.). Here we follow the taxonomy of Kingdon (1997) in recognizing two subspecies; *C. a. aethiops* and *C. a. matschiei*.

Synonyms: *cailliaudi*, *cano-viridis*, *?cinereo-viridis*, *engytithia*, *griseo-viridis*, *griseus*, *matschiei*, *subviridis*, *toldti*, *weidholzi*, *zavattarii*. Dandelot & Prévost (1972), Dandelot (1974), Hill (1966) and Grubb *et al.* (2003) consider *ellenbecki* and *hilgerti* to be synonyms of *C. aethiops* but here and elsewhere (Groves 2001, 2005c) they are treated as synonyms of *C. pygerythrus*. Chromosome number: $2n = 60$ (Dutrillaux *et al.* 1988b).

Description Long-tailed, medium-sized, semi-terrestrial, savanna monkey with white hairs on upper lip and white tail tip. Sexes similar in colour but adult ♀ smaller than adult ♂. Adult ♀ weighs about 67% as much as adult ♂. Lips and chin with white hairs (i.e. white moustache). Face black. Cheek whiskers pure white, long, prominent, contrasting sharply with crown, concealing the ears. Brow band narrow, white, confluent with whiskers. Crown and back grizzled and variable in colour; pale olive-fawn, greyish-green, dark fawn or russet. Crown darker than back. Limbs mouse-grey. Hands and feet pale grey with brownish tinge. Underside and inner limbs white to pale grey. Tail base with white tuft below and to either side. Tail greyish above, white below. Distal 15–20% of tail pure white to creamy white. Scrotum sky blue (Hill 1966, Dandelot 1974, Napier 1981). Infant born with dark, brownish-grey fur and pink face and ears, but acquires similar colouring to the adult at an early age.

Geographic Variation

C. a. aethiops Common Grivet Monkey. East of White Nile R., Sudan, through C and N Ethiopia, S and C Eritrea into Djibouti. Back grizzled olive-fawn or greyish-green, sometimes with reddish tint (e.g. at Awash N. P., C Ethiopia; C. J. Jolly & J. E. Phillips-Conroy pers. comm.).

C. a. matschiei Matschie's Grivet Monkey. Endemic to SW Ethiopia within and west of Rift Valley (Kaffa and Djimma Districts; Dandelot 1974). Back colour variable, grizzled dark fawn to russet. Toes dark brown. Longer fur around face.

Similar Species

Chlorocebus tantalus. Probably allopatric along eastern edge of range, separated from *C. aethiops* by the White Nile R. Ghana east of the White Volta R. to Ubangi R. then C and S Sudan, N Uganda and NW Kenya. Lips and chin without white hairs. Brow band more sinuous, constricted in centre, separated from whiskers by line of black hairs at outer corner of eye. Whiskers long, stiff, yellowish, sometimes speckled, tips curled upwards, contrasting sharply with crown and concealing the ears. Hands and feet pale grey. Tail base with white tuft below and to either side. Tail tip creamy white. Scrotum sky blue sometimes surrounded by orange-hued hairs (Dandelot 1974, Napier 1981).

*Chlorocebus aethiops*

Chlorocebus djamdjamensis. Parapatric on the Bali Massif, SC Ethiopia.

Only in bamboo forest above 2400 m. Temples black. Brow-band absent or narrow. Tail short. No white tufts at base of tail.

Chlorocebus pygerythrus. Probably narrowly sympatric along northern edge of range where *C. pygerythrus* x *C. aethiops* hybrids occur. S Somalia, S Ethiopia, E and SW Uganda, through Kenya south through South Africa. Lips and chin without white hairs. Brow band broad, confluent with whiskers. Whiskers short, pure white, not concealing the ears. Hands and feet dark grey to black. Tail base lacks white tufts. Patch of red hairs beneath base of tail (i.e. red subcaudal patch) and around anus in adult ♂. Tail tip dark grey to black. Scrotum turquoise blue.

Distribution Endemic to NE Africa. Sudan Savanna, Somalia-Masai Bushland, and Afromontane–Afroalpine BZs. Historically as far north as NE Sudan, east of Nile R. to at least 19° 30' N; 33° E along the Nile R. Whether *C. aethiops* occurs this far north along the Nile R. today is doubtful as there has been much loss of forest along the Nile R. At this time the northern limit along the Nile R. is probably south of 15° N (i.e. Khartoum; Kock 1969). None the less, this is probably the northern-most point for any guenon in Africa. Apparently no records for Egypt. South in Sudan to at least 05° 10' N; 31° 46' E at Mongalla, SE Sudan (Dandelot 1974). From the Nile R. of E Sudan eastward through SW, C and N Ethiopia, and S, C and N Eritrea (Yalden *et al.* 1977, 1996, Zinner *et al.* 2001c, 2002b, D. Zinner pers. comm., T. Butynski pers. obs.) to the Goda Mts and Mabla Mts, N of the Gulf of Tadjoura, C Djibouti (11° 46' N; 42° 40' E; Künzel *et al.* 2000). This is apparently also the southern limit along the Red Sea coast. Northern limit in Eritrea (based on records from the mid-1800s) is on the NW border with Sudan at the confluence of the Barka R. and Anseba R. (ca. 17° N; 37° 24' E; Yalden *et al.* 1977, Zinner *et al.* 2001c, D. Zinner pers. comm.). In 2003, observed by D. Zinner (pers. comm.) at Dawit Berhane (west of Nakfa near the confluence of the Zara R. and Anseba R.; 16° 38' N;

37° 50' E). This is the northern-most (recently documented) point for any guenon in eastern or central Africa. Among guenons, only the Patas *Erythrocebus patas*, Tantalus *Chlorocebus tantalus* and Green Monkey *Chlorocebus sabaeus* might range as far north (ca. 17°) as *C. aethiops*. North-eastern limit in Eritrea appears to be in the region of Semanawi Bahiri in EC Eritrea (15° 46' N; 38° 28'; Butynski 1995a). Hall (1966) gives northern limit along the Red Sea coast as Tokar (18° 25' N; 37° 45' E (but this needs validation). Southern limit in Ethiopia is unclear as there is confusion with the northern limit for *C. p. hilgerti* that is at least partly caused by apparent *C. p. hilgerti* x *C. a. aethiops* hybrids (Dandelot 1959, Dandelot & Prévost 1972, Yalden *et al.* 1977, Lernould 1988, T. Butynski pers. obs.). South-western limit in Ethiopia (on the border with Sudan) appears to be near Kantiere (06° 31' N; 35° 01' E), possible to the Omo R. (Groves 2001). In C Ethiopia *C. aethiops* and *C. pygerythrus* meet in the Rift Valley between L. Shala and L. Zwai (Groves 2001) as well as at L. Abaya (Dandelot & Prévost 1972, Lernould 1988). *Chlorocebus aethiops* present ca. 50 km west of L. Shala, near Hosa'ina (07° 33' N; 37° 51' E; Q. Luke pers. comm.). About 20 km south of Mena (ca. 06° 05' N; 39° 40' E, 1400 m), which is on the east side of the Rift Valley about 60 km south of Bale Mountains N. P., 'hybrids' are present. These monkeys have the black hands, feet and tail tip of *C. pygerythrus* and the white caudal tuft of *C. aethiops*. About 30 km to the south-west of here, on the Genalé R. (06° 00' N; 39° 42' E, 1100 m), 'good' *C. pygerythrus* are present (T. Butynski pers. obs.). South-eastern limit for *C. aethiops* in Ethiopia appears to be in the vicinity of Härer (09° 14' N; 42° 15' E; Yalden *et al.* 1977). No records found for *C. aethiops* in Somalia. T. Butynski (pers. obs.) now strongly suspects that further research will find that there is a broad '*C. aethiops*–*C. pygerythrus* clinal zone' across S Ethiopia from about Kantiere in the west then south-eastwards through L. Shala, L. Zwai and L. Abaya to Härer with monkeys gradually appearing more *C. pygerythrus*-like (and less *C. aethiops*-like) north to south through this clinal zone.

Habitat Savannas, woodlands, riverine forests, deciduous forest, montane forest and cultivation mosaics, always close to permanent sources of drinking water and to large trees for sleeping (Yalden *et al.* 1977, Zinner *et al.* 2001c, 2002b). Prefer woodland/riverine forest/grassland margins but often feeds in open areas. Lives in forest where other species of guenon are absent, such as 5 km into the Semanawi Bahiri Forest of EC Eritrea (Butynski 1995a). Also use pure stands of eucalyptus *Eucalyptus* spp. and Prickly Pear Cactus *Opuntia* sp. (Zinner *et al.* 2001c, 2002b). Present from <200–>3000 m in Ethiopia (Yalden *et al.* 1977, 1996), but records >2500 m are few (Mekonnen *et al.* 2012). From ca. 750–2600 m in Eritrea (Zinner *et al.* 2001c, 2002b). Mean annual rainfall over the range of *C. aethiops* in Eritrea is 350–1000 mm (Zinner *et al.* 2001c) but the lower limit is probably close to 300 mm for those *C. aethiops* living in riverine forest along the Setit/Tacazze R. (Eritrea's only permanent river) and the larger seasonal rivers. In Ethiopia, *C. aethiops* present where mean annual rainfall is >2000 mm (Dunbar & Dunbar 1974b). Mean annual rainfall near Awash N. P. (08° 30' N, 39° 40' E) is 551 mm (313–839, n = 34 years). Here most rain falls during Jul–Aug (C. J. Jolly & J. E. Phillips-Conroy pers. comm.).

Most of what we know about the ecology and behaviour of *C. aethiops* comes from 58 h of observations during five months of

field work in the Bole Valley, WC Ethiopia (09° 25' N; 38° 00' E), during 1971 and 1972 (Dunbar & Dunbar 1974b). The Bole Valley is 1700 m at the river bed. There is one wet season (May–Oct) and one dry season (Nov–Apr). Mean annual rainfall ca. 2000 mm. Daytime temperatures are generally around 35 °C. Dominant trees are *Ficus* spp., *Syzygium guineense*, *Bridelia micrantha*, *Podocarpus gracilior* and *Albizia* spp.

Chlorocebus aethiops must drink at least every other day, depending on the amount of moisture in the diet. Drinking water in Eritrea is mostly found in valleys where water collects in rocky crevices after rains and where underground springs feed waterholes that are either naturally occurring or dug by Savanna Elephant *Loxodonta africana*, Common Warthog *Phacochoerus africanus*, Olive Baboon *Papio anubis*, Hamadryas Baboon *Papio hamadryas* or people. For *C. aethiops* in Eritrea, the median distance between sleeping sites and the nearest site with a high potential for permanent surface water was 459 m (14–3348, $n = 46$); 64% of *C. aethiops* were <1500 m from permanent surface water and only 2% were >3000 m from permanent surface water (Zinner *et al.* 2001c, 2002b).

Abundance Density of *C. aethiops* in the Bole Valley estimated at 73 ind/km² and biomass estimated at 207 kg/km² (Dunbar & Dunbar 1974b). *C. aethiops* is the most widespread and most commonly encountered monkey in Ethiopia (Dunbar & Dunbar 1974b, Yalden *et al.* 1977). Overall, densities of *C. aethiops* seem to resemble those of many *C. pygerythrus* populations in East Africa (i.e. <1–9 ind/km² with localized densities much higher at 10–>100 ind/km² (Wolfheim 1983, Cheney 1987).

Adaptations Semi-terrestrial, diurnal, and opportunistic. Follow riverine vegetation strips always keeping close to trees or shrubs, foraging both on the ground and in trees and shrubs. Commensal with humans at many sites, sometime living next to settlements and within agricultural sites (T. Butynski pers. obs.). In Eritrea, the median distance from *C. aethiops* sleeping sites to the nearest human settlement was 2858 m (58–24,609, $n = 46$), and to the nearest agricultural area this was 297 m (0–8402, $n = 46$); 32% of records <1000 m from the nearest village and 37% of records <500 m from the nearest agriculture (Zinner *et al.* 2001c, 2002b).

Chlorocebus aethiops rests in shade during the heat of the day, probably thereby avoiding heat-stress, water-stress and predators. Depends on concealment in dense vegetation when threatened by large eagles. Colouring well suited to concealment when motionless but when moving the black face in a white setting, and the tip of the tail and the white tuft at the base of the tail, are conspicuous, perhaps especially to conspecifics. When walking directly away from an observer, the laterally extended pure white whiskers and the pure white tuft at the base of the tail are roughly in line with one another and ‘flash’ as the animal moves (T. Butynski pers. obs.).

Unlike Tantalus *Chlorocebus tantalus* to the west and *C. pygerythrus* to the south, *C. aethiops* in Ethiopia and Eritrea makes use of closed forest. It seems highly likely that this is a case of ‘competitive release’ from the more forest-adapted *Cercopithecus* spp., perhaps particularly the widespread Gentle Monkey *Cercopithecus mitis*. At most sites where *C. tantalus* or *C. pygerythrus* occur in the vicinity of closed forest there is at least one species of *Cercopithecus* present (usually *C. mitis*). At none of these sites does *Chlorocebus* enter the

closed forest (indeed, *Chlorocebus* appears to avoid even the forest edge). While *Chlorocebus* and *Cercopithecus* live side-by-side at many sites over the range of *Chlorocebus*, they seldom, if ever, share the same sites or form polyspecific associations (Enstam & Isbell 2007, De Jong & Butynski 2009). It is, therefore, significant that over that part of the range of *Chlorocebus* where (1) there is access to closed forest, and (2) *Cercopithecus* is absent, *Chlorocebus* (i.e. *C. aethiops*) is found living deep within (at least some) closed forests (e.g. 5 km within Semanawi Bahiri Forest, E. Eritrea; T. Butynski pers. obs.). Not all closed forests, however, harbour *C. aethiops*. For example, *C. aethiops* appears to be absent from the Herenna Forest on the southern slope of Bale Mountains N. P., down-slope from, and well south of, *C. djamdjamensis* (T. Butynski pers. obs.). It may be that altitude and/or levels of rainfall determine whether *C. aethiops* will occupy a particular closed forest with, perhaps, the wetter forests at the higher altitudes being unsuitable.

Foraging and Food Omnivorous. In the Bole Valley, mean home-range size was 24.5 ha (19.5–29.4, $n = 2$) and mean day range was 700 m (600–800, $n = 4$ days). During the daylight hours, *C. aethiops* spent ca. 27% of the time feeding. Amount of time spent feeding tended to increase gradually through the day with most feeding taking place in the afternoon. Peaks in movement occurred in the early morning and early afternoon. They slept in trees and spent 57% of the daylight time in trees ($n = 1545$ scans; Dunbar & Dunbar 1974b).

In Bole Valley, food ($n = 352$ items) obtained from creepers (0.9%), shrubs (2.8%), grasses (3.7%), bushes (4.1%), herbs (33.5%) and trees (56.0%). Items eaten were bark (5.7%), insects (7.4%), flowers (17.6%), leaves (18.7%) and fruits/seeds (50.6%). Most frequently eaten items were fruits of *Maytenus undata* (18.7% of diet), fruits of *Ficus* spp. (17.3%), leaves and flowers of *Trifolium ruepellianum* (14.8%) and fruits of *S. guineense* (5.7%). *Chlorocebus aethiops* took 28.2% of 326 food items from the ground and 63.9% from trees (Dunbar & Dunbar 1974b). In Awash N. P., *C. aethiops* eat winged termites, fruits of *Celtis* sp., *Ficus sycamorus*, *Acacia tortilis*, *Acacia brevispica* and *Zizyphus* sp., and flowers of *Acacia tortilis* (C. J. Jolly & J. E. Phillips-Conroy pers. comm.). In Eritrea, fruits of figs *Ficus* spp. and the fruits and young shoots of *Opuntia* sp. (an exotic species that is both common and widespread) are frequent foods of *C. aethiops*. *Opuntia* has water content of ca. 96%, making it an important source of water during the long dry season. *Chlorocebus aethiops* is a crop pest at many sites, eating bananas, citrus and other crops (Zinner *et al.* 2001c, 2002b).

The above, and anecdotal information, suggests that the foraging behaviour and diet of *C. aethiops* resembles that of other *Chlorocebus* spp., but whereas gum is a major component of the diet of *C. pygerythrus* at some sites (up to 37%; Enstam & Isbell 2007), the eating of gum has not been reported for *C. aethiops*. Groups forage together, with ♂♂ and ♀♀ mixed with young of various ages. Foraging is restricted to a limited range. Judging from studies of other savanna monkeys the extent of home-ranges is likely to vary between ca. 10 ha. to ca. 100 ha. Solitary foragers are exceptional. Although *Chlorocebus* spp. are generally viewed as semi-terrestrial, *C. aethiops* might be considered an arboreal species when in closed forest. For example, R. I. M. Dunbar (pers. comm.) seldom observed *C. aethiops* on the ground in the dense gallery forest of the Bole Valley.

Social and Reproductive Behaviour Social. Live in multi-male/multifemale groups (L. Fairbanks, L. Swedell, R. I. M. Dunbar pers. comm.). Mean size of four groups in the Bole Valley estimated to be 19 individuals ($n = 4$ groups), with the largest group comprised of 29 individuals (Dunbar & Dunbar 1974b). In Awash N. P., estimated group size ranges from 10 to 35 individuals and most groups are multimale. Solitary adult ♂♂ are present (C. J. Jolly & J. E. Phillips-Conroy pers. comm.). In Eritrea, Zinner *et al.* (2002b) assessed the size of *C. aethiops* groups at 22 sites and obtained a mean of 9.1 ind/group (S.D. = 4.5, 3–22, $n = 22$). They also observed a solitary adult ♂, and an adult ♂ with a subadult ♂ that were 5–10 km from the nearest group (Zinner *et al.* 2002b). At Awash N. P. there are adult and subadult ♂♂ that are spatially peripheral to, but associated with, social groups (L. Fairbanks pers. comm.).

Not reported to be sympatric with other species of guenons. In the Bole Valley, *C. aethiops* are sympatric with Guereza *Colobus guereza*, Gelada Baboon *Theropithecus gelada* and *P. anubis*. *Chlorocebus aethiops* not observed in polyspecific association with *T. gelada*, and in association with *P. anubis* only 7% of the time ($n = 340$ observations; Dunbar & Dunbar 1974b). It should be noted, however, that the ‘Vervets generally reacted nervously when in association with Anubis Baboons, and would often withdraw if the *anubis* moved into the trees they were in.’ (Dunbar & Dunbar 1974b, p. 53). Sympatric with *C. guereza* and *P. anubis* in Awash N. P. but appear to avoid *P. anubis* even though they exploit the same arboreal resources (C. J. Jolly & J. E. Phillips-Conroy pers. comm.).

There are few data on the social and reproductive behaviour of *C. aethiops*. L. Fairbanks (pers. comm.), who studied *C. aethiops* in Awash N. P., *C. pygerythrus* in Amboseli N. P., Kenya, and an introduced population of *C. sabaes* on St Kitts I., West Indies, found that these three species are behaviourally indistinguishable. She observed infant care-taking by non-mothers, adult ♀ coalitions against adult ♂♂, and male–male competition among *C. aethiops* in Awash N. P.

Size of *C. aethiops* groups in Eritrea may average smaller than *C. pygerythrus* groups in Kenya (which average roughly 20 ind/group). As such, *C. aethiops* groups probably comprise at least twice as many adult ♀♀ as adult ♂♂, and young animals and infants outnumber adults. Males habitually forsake their natal groups while ♀♀ are much more sedentary. Cheney (1983) emphasized how the sexes in *C. pygerythrus* tend to have separate hierarchies enforced by ♂ aggression and a close association between dominant ♂♂ and equally high-ranking ♀♀ whose hierarchy depends upon matrilineal histories. There is no information for *C. aethiops* on the extent to which home-ranges of neighbouring groups overlap. Behaviour indicating inter-group hostility, led by the group’s adult ♀♀, has frequently been observed (C. J. Jolly pers. com.) and strongly suggests that *C. aethiops*, like the other *Chlorocebus* (Cheney 1987), is territorial.

The vocal repertoire of *C. aethiops* has not been studied, but the warning ‘chirps’ of immatures and adult ♀♀ and the loud ‘aarr’ call of the adult ♂♂ in SW and E Eritrea, and in S and C Ethiopia, sound like those of *C. pygerythrus* (T. Butynski, C. J. Jolly & J. E. Phillips-Conroy pers. obs.).

Reproduction and Population Structure Reproduction not studied. However, based on what we know concerning the relationship between birth seasons, breeding seasons and the timing of annual rainfall at other sites where *Chlorocebus* spp. occur (Butynski 1988),

some predictions can be made. For *C. aethiops* in the Bole Valley, where there is one wet season (May–Oct), one dry season (Nov–April) and a mean annual rainfall of 2000 mm, it is expected that there is an annual peak in births during Jan–Apr, that most mating occurs during Sep–Dec, and that food is most abundant during Aug–Nov. If reproductive parameters from other *Chlorocebus* spp. (Butynski 1988, Cheney *et al.* 1988, Enstam & Isbell 2007) are applied to *C. aethiops*, mean inter-birth interval is 1.2–1.7 years, gestation is ca 5.4 months, and age at weaning is 9–18 months. Else *et al.* (1986) found that *C. pygerythrus* in captivity has a 32.5 day ovulatory cycle. Extrapolating from other *Chlorocebus* spp., ♀ and ♂ *C. aethiops* reach sexual maturity at ca. 4 years and 5 years, respectively, and ♀♀ first give birth at ca. 5 years.

The only information on birth seasonality in *C. aethiops* comes from Awash N. P., which is ca. 250 km east of Bole Valley. Here many adult ♀♀ carry infants less than two months old during the main wet season (Jun–Aug), but only semi-independent infants observed during the dry season (Jan–Feb) (C. J. Jolly pers. comm.). Live to at least 24 years in captivity (Flower 1931).

Predators, Parasites and Diseases *Chlorocebus aethiops* has been captured and exported for thousands of years, as is attested by Cretan, Minoan and Egyptian murals. Humans, and their Domestic Dogs *Canis familiaris* (which, in the highlands of Eritrea, sometimes run in packs; D. Zinner pers. comm.), are therefore likely to have been the major predators for a long time. The African Crowned Eagle *Stephanoaetus coronatus* and Leopard *Panthera pardus* are probably the most frequent non-human predators of *C. aethiops* as they are important predators for most species of guenons (Enstam & Isbell 2007). Some of the other likely predators are Verreaux’s Eagle *Aquila verreauxii*, Martial Eagle *Polemaetus bellicosus*, Lion *Panthera leo*, Cheetah *Acinonyx jubatus*, Striped Hyaena *Hyaena hyaena*, Spotted Hyaena *Crocuta crocuta*, jackals *Canis* spp., Hamadryas Baboon, Olive Baboon, Central African Rock Python *Python sebae* and Nile Crocodile *Crocodylus niloticus*. The populations of most of these predators have, however, declined greatly over the range of *C. aethiops* during the past century (Yalden *et al.* 1996, Department of Environment 1999, Zinner *et al.* 2001c, 2002b).

The disease profile for *C. aethiops* is likely to prove to be as extensive and significant as for other *Chlorocebus*. Natural populations in Ethiopia harbour endemic simian immunodeficiency virus (SIV), without obvious ill effects (Phillips-Conroy *et al.* 1994). Juveniles and infants are rarely SIV-positive, so maternal transmission is evidently rare, but almost all animals become positive with the initiation of sexual contact. All sexually mature ♀♀ and most mature ♂♂ are therefore SIV positive, for an overall rate of about 50% (Jolly *et al.* 1996).

Conservation IUCN Category (2012): Least Concern. CITES (2012): Appendix II.

Persecuted as a crop pest (Dunbar & Dunbar 1974b, Yalden *et al.* 1977, Zinner *et al.* 2001c). Captured and exported in the past for medical research. Even as long ago as 1969, *C. aethiops* was being extirpated from many sites due to loss of habitat (Kock 1969). In Eritrea, forest cover declined from 30% of the land area in 1900 to <3% in 1990 (EAE 1995). There can be no doubt this loss of food trees and of sleeping trees has resulted in a concomitant decline of Eritrea’s population of *C. aethiops* and of other forest-

and woodland-dependent species. Already, almost 50% of the larger species of mammal historically present in Eritrea have been extirpated (DoE 1999). As noted by Zinner *et al.* (2002b, p. 157) for Eritrea, 'The ongoing reduction of riverine woodland, the expansion of agricultural activities through irrigation projects and an increasing human population, particularly by resettlement programmes for refugees from Ethiopia and Sudan, intensify the conflict between Grivets and humans.' None the less, *C. aethiops* remains Eritrea and Ethiopia's (and probably north-east Africa's) most widespread and common monkey (Dunbar & Dunbar 1974b, Yalden *et al.* 1977, Zinner *et al.* 2001c, 2002b). *Chlorocebus aethiops* is present in five of Ethiopia's nine national parks (Yalden *et al.* 1996) and Eritrea is planning a protected areas system that will support populations of *C. aethiops* (EAE 1995).

Measurements

Chlorocebus aethiops

HB (♂): 480 mm, n = 1

T (♂): 645 mm, n = 1

HF (♂): 135 mm, n = 1

E (♂): 31 mm, n = 1

WT (♂♂): 4.2 (2.6–5.4; S.D. = 0.57) kg, n = 64

WT (♀♀): 2.8 (1.4–3.6; S.D. = 0.38) kg, n = 70

GLS (♂♂): 98 (965–103), n = 6

GLS (♀♀): 85, n = 1

GWS (♂♂): 65 (62–68), n = 6

GWS (♀♀): 55, n = 1

Linear measurements from 'NE Africa' (Hill 1966)

WT: Awash N. P., C Ethiopia (J. E. Phillips-Conroy & C. J. Jolly pers. comm.)

Key References Dunbar & Dunbar 1974b; Hill 1966; Yalden *et al.* 1977.

Thomas M. Butynski & Jonathan Kingdon

Chlorocebus tantalus TANTALUS MONKEY

Fr. Tantale; Ger. Tantalus-Grünmeerkatze

Chlorocebus tantalus (Ogilby, 1841). Proc. Zool. Soc. Lond. 1841: 33. Locality not known.



Tantalus Monkey *Chlorocebus tantalus* young male.

Taxonomy Polytypic species. Schwarz (1926) and Grubb *et al.* (2003) considered Tantalus to be a subspecies of *Cercopithecus aethiops*. Dandelot (1959) raised Tantalus to species status and this is supported by Kingdon (1997) and Groves (2001, 2005c). Groves (1989) resurrected the generic name *Chlorocebus* for the Savanna Monkeys Group *C. (aethiops)*. Here we follow Kingdon (1997) and Groves (2001) in recognizing three subspecies for *C. tantalus*. Synonyms: *alexandri*, *beniana*, *graueri*, *griseistictus*, *itimbiensis*, *passargei*, *pousarguei*, *viridis*. Chromosome number $2n = 60$ (Chu & Giles 1957).

Description Medium-sized, long-tailed, black-faced, semi-terrestrial monkey. Adult ♂ like adult ♀ in colour but larger. Brow-

band wide, sinuous, of white or yellowish hairs above intensely black face. Brow hairs sometimes speckled at the tips. Black tuft between eyes. Brow-band sometimes separated from the whiskers by a black line at the outer corner of the eyes. Long white hairs on temple sweep upwards in older individuals. Cheek-hair sweeps backwards, separating above the ear, which is covered in mature animals. Crown and back grizzled gold to greenish. Ventrums white. Limbs and tail grey. Tuft of long whitish hairs to either side of base of tail. Tip of tail whitish. Perineal skin pink, sometimes with light covering of orange hairs. Penis red. Scrotum sky-blue surrounded by tuft of orange hairs. Tantalus is the largest of the *Chlorocebus* spp. (Kingdon 1997).

Geographic Variation

C. t. tantalus Common Tantalus Monkey. Ghana east of White Volta R. east to S Chad and Ubangi R. Back olive-green.

C. t. budgetti Budgett's Tantalus Monkey. S Chad and Ubangi R. through S Sudan east to Nile R. NE DR Congo, N Uganda and Kenya west of L. Turkana. Back more olive-brown, whiskers more yellowish with more extensive speckling. Feet and tail tip darker.

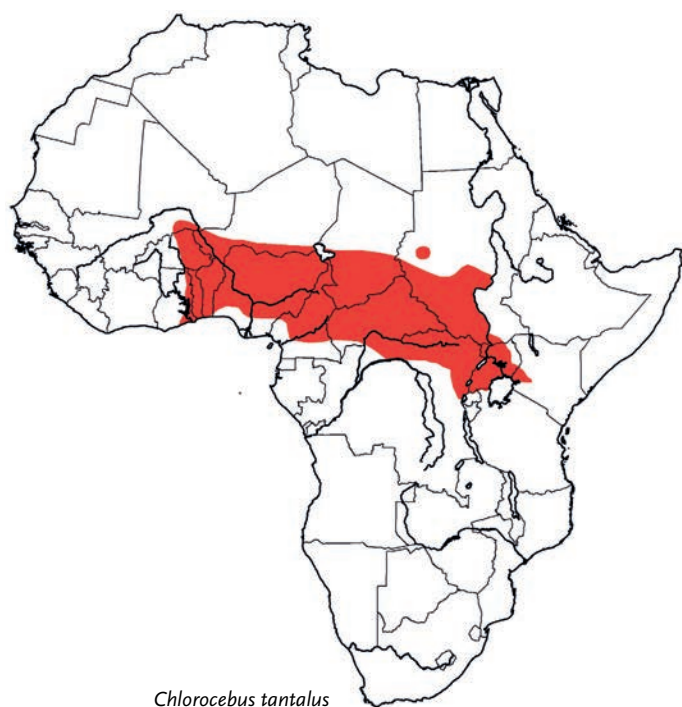
C. t. marrensis Jebel Marra Tantalus Monkey. On Jebel Marra Plateau, CW Sudan. Isolated by desert. Like *C. t. tantalus*, but colour tends to be lighter olive-fawn (Kingdon 1997, Groves 2001).

Similar Species

Chlorocebus sabaeus. Gambia to west of Volta R., Ghana. No white brow-band. Tail tip golden yellow. No tuft of whitish hairs at base of tail. Scrotum pale blue.

Chlorocebus aethiops. East of Nile R. and south of Khartoum, S Sudan through S Eritrea, C and N Ethiopia into Djibouti. Brow-band narrow, white, confluent with whiskers. Moustache white.

Chlorocebus pygerythrus. S Somalia, S Ethiopia, E Uganda and Kenya south through South Africa. Brow-band broad, white, confluent

*Chlorocebus tantalus*

with short whiskers. Hands and feet dark grey to black. Underside of base of tail of adult ♂ with patch of red hairs. No tuft of whitish hairs at base of tail. Tail tip dark brown to black. Scrotum turquoise blue, surrounded by white hairs.

Distribution Endemic to Africa, mostly north of the Equator. Sahel Savanna, Sudan Savanna and Guinea Savanna BZs. Mali, Burkina Faso and Ghana east of the White Volta R. eastward to north of Ubangi R. through S Sudan to Nile R., NE DR Congo, N Uganda into NW Kenya west of L. Turkana. Northern limit poorly known, but probably to ca. 17°N in Mali, making this one of the guenons with the northern-most distribution (T. Butynski pers. comm.). Around the boundaries of its distribution, zones of hybridization with other *Chlorocebus* spp. occur, often over a wide band. *Chlorocebus t. tantalus* interbreeds with the Green Monkey *Chlorocebus sabaeus* in Ghana west of the White Volta R. (Bole); *C. t. budgetti* with the Vervet *Chlorocebus pygerythrus hilgerti* in Kenya west of L. Turkana and with *C. p. rufoviridis* in SW Uganda east of L. Edward and L. Kivu, and north and west of L. Victoria (Kingdon 1971, 1997).

Habitat *Tantalus* occupies a variety of habitats, including savanna woodland, gallery forest, swamp forest and forest edge. Prefers riverine vegetation for access to water and sleeping trees. Mean annual rainfall of three habitats used by *C. tantalus* in Cameroon are: 3580 mm in forest edge at Bakossi (04°53'N); 1450 mm in Guinea savanna at Benoue N. P. (08°06'N); 650 mm in Sahel savanna at Kala Maloue N. P. (12°09'N) (Kavanagh 1981). Occurs from sea level in West Africa (Grubb *et al.* 1998) to at least 1600 m in Nigeria (Agmen *et al.* 2009) and to at least 1500 m in Uganda (T. Butynski pers. comm.).

Abundance Group density in Kainji Lake N. P., Nigeria, was 0.22 ind/km² in the Oli R. Valley and 0.05 ind/km² away from the

Valley in 1971–72. Given that the average group size is ten animals, the total population in Kainji Lake N. P. (3675 km²) was estimated to be ca. 2600 animals (Child 1974 in Wolfheim 1983). Despite its overall abundance, populations have been decreasing in some areas. In Sudan, for example, the northern boundary of distribution has retreated from 19°N to 15°N in the last 100 years because of tree-cutting along the Nile R. for firewood (Butler 1966). In Cameroon, on the other hand, populations are probably increasing because felling of rainforest provides *Tantalus* with suitable habitats such as secondary savanna and fallow land (S. Gartlan pers. comm. in Wolfheim 1983).

Adaptations Diurnal and semi-terrestrial. Generalized omnivorous diet and semi-terrestriality enable *Tantalus* to live in arid and/or open habitats. *Tantalus* invade recently cultivated fields in rainforest at Bakossi, Cameroon, while the indigenous Mona Monkey *Cercopithecus mona* seems less adept at exploiting changed habitats (Kavanagh 1980). *Tantalus* take long rests in large shaded trees at mid-day to avoid heat stress and terrestrial predators. As soon as they notice canids, such as Common Jackals *Canis aureus* and Domestic Dogs *Canis familiaris*, *Tantalus* climb to safety in nearby trees and emit loud alarm calls. It is believed that *Tantalus* at Bakossi keep silent in response to the presence of dogs accompanied by human hunters. *Tantalus* emit a 'quiet call' for intra-specific contact or to serve as a low-intensity alarm call. This call is hardly ever uttered by *Tantalus* in habitats where hunting pressure by humans is rare or absent (Kavanagh 1980).

Foraging and Food Omnivorous. *Tantalus* descend from sleeping trees in dense woodland or gallery forest early in the morning and begin feeding. They range extensively into savanna grassland when moving between wooded areas, but never feed there for long periods of time. After resting for 2–3 of the hottest hours of the day in large shade trees, they resume feeding and then go back to a wooded area to sleep. Mean home-range size was 55 ha (n = 5 groups), ranging from 12 ha at Bokossi to 103 ha at Benoue. Daily distance moved by groups varied with habitat and/or season: 0.7–3.7 km at Benoue (n = 1 group, 20 days) and 0.5–2.5 km at Kala Maloue (n = 2 groups, 20 days) (Kavanagh 1981, Nakagawa 1999). At both sites, about 30% of foraging was on the ground and 90% of foraging was <10 m above the ground (n = 1 group, 475 h for Benoue; n = 1 group, 512 h for Kala Maloue; Kavanagh 1978).

Generalist omnivores, feeding on plant parts and animals (mostly invertebrates but also, infrequently, reptiles and birds). *Tantalus* feed on a larger number of food items of lower quality (poorer in protein and energy, richer in fibre) than do sympatric Patas *Erythrocebus patas* in Kala Maloue (Nakagawa 2003). Sources of protein include flowers (9% of diet), leaves (9%) and invertebrates (6%), while sources of energy are fruits (56%) and lipid-rich seeds (17%) (n = 37 different kinds of foods). Among the more frequent items eaten are the flowers of *Kigelia africana* and *Tamarindus indica*, leaves of *Panicum* sp. and *Indigofera* sp., fruits of *Celtis integrifolia*, *Diospyros mespiliformis* and *Morela senegalensis*, and seeds of *K. africana* (Nakagawa 2000b). Adult ♀♀ choose protein-rich foods (i.e. invertebrates, leaves and flowers) while adult ♂♂ select foods that contain less protein but more energy (e.g. fruits; Nakagawa 2000b). Disperses seeds of forest edge species into grasslands (Agmen *et al.* 2009).



Tantalus Monkey *Chlorocebus tantalus* subadult male.

Social and Reproductive Behaviour Social. Tantalus form stable multimale heterosexual groups. Solitary adult ♂♂ also occur. Group size and composition reported from three sites in Cameroon (Kavanagh 1981, Nakagawa 1999). Mean group size is 29 animals (11–76, $n = 5$), including 1–10 adult ♂♂ and 3–18 adult ♀♀. There are 0.5–1.0 ♂♂ per ♀. In two populations, group adult ♂♂ observed in territorial defence, emitting loud vocalizations at high vantage points and rushing towards the intruding group. In another population agonistic interactions were rarely observed during group encounters, and consequently 18% of the home-range was shared with neighbouring groups (Kavanagh 1981).

Both ♂♂ and ♀♀ in a group form a lineal dominance hierarchy (Nakagawa 2008). Young ♀♀ and adult ♀♀, regardless of kin-relatedness to the infants, frequently display allomothering behaviours such as touching, holding, nuzzling, grooming and sometimes carrying young.

Reproduction and Population Structure A single infant is born. Twins not reported. Kavanagh (1983) found inter-population differences in birth seasons in Cameroon. Births take place during Oct–Nov at the end of wet season in Bakossi; during Jan–Feb during the mid-dry season in Buffle Noir, and during Jul–Aug in the wet season in Kala Maloue. No consistent relationship between rainfall seasonality and birth frequency has been found. However, in Kala Maloue, with the least amount of annual rainfall (650 mm), the birth season corresponds not only to a period of high rainfall but to a period of a high percentage of fruit in the diet, although the relationship between overall food availability and birth frequency is unknown. In Kala Maloue sympatric Patas have their mating season in the wet season and their birth season during Jan–Feb at the middle of the dry season. The latter corresponds with the mating season of Tantalus. To evaluate the optimality of species-specific birth seasons, Nakagawa (2000a) estimated the daily intake of available energy and gross protein, and the energy expenditure of both Tantalus and Patas

between their respective birth and mating seasons. The monkeys obtained a larger amount of available energy and gross protein in the birth season than in the mating season. No significant seasonal differences were found in their energy expenditure. Thus, births appear to be timed to the season in which the monkeys can obtain the most surplus energy and protein. Tantalus ♀♀ experience first birth at 4–5 years of age ($n = 3$) in Kala Maloue. Four out of six inter-birth intervals were one year and the remaining two were two years (mean 16 months) (N. Nakagawa pers. obs.).

Predators, Parasites and Diseases There is little information on predation of Tantalus. A one-year-old juvenile caught by a Common Jackal in Kala Maloue (N. Nakagawa pers. obs.). Side-striped Jackal *Canis adustus*, African Wild Dog *Lycaon pictus*, Spotted Hyaena *Crocuta crocuta*, Leopard *Panthera pardus* and Serval *Felis serval* are potential predators in Cameroon (Kavanagh 1980, 1983). Almost nothing is known concerning disease in Tantalus. Species-specific simian immunodeficiency virus (SIV) and simian T-cell leukaemia virus present in feral Tantalus, although infected monkeys demonstrate no external evidence of these diseases (Hirsch *et al.* 1993b, Saksena *et al.* 1993).

Conservation IUCN Category (2012): Least Concern. CITES (2012): Appendix II.

While unsustainable firewood-collection in savanna regions eventually diminishes Tantalus populations, felling of rainforest is likely to favour increases in population. Further surveys needed to determine the conservation status of Tantalus living in various habitats across the species' extensive range.

Measurements

Chlorocebus tantalus

HB (♂♂): 515 (380–830) mm, $n = 10$

HB (♀♀): 415 (385–440) mm, $n = 6$

T (♂♂): 697 (575–1140) mm, $n = 10$

T (♀♀): 571 (555–600) mm, $n = 6$

HF (♂♂): 138 (90–152) mm, $n = 10$

HF (♀♀): 129 (125–135) mm, $n = 6$

E (♂♂): 38 (32–42) mm, $n = 6$

E (♀♀): 40 (40–40) mm, $n = 6$

WT (♂): 2.9 kg, $n = 1$

WT (♀): 2.7 kg, $n = 1$

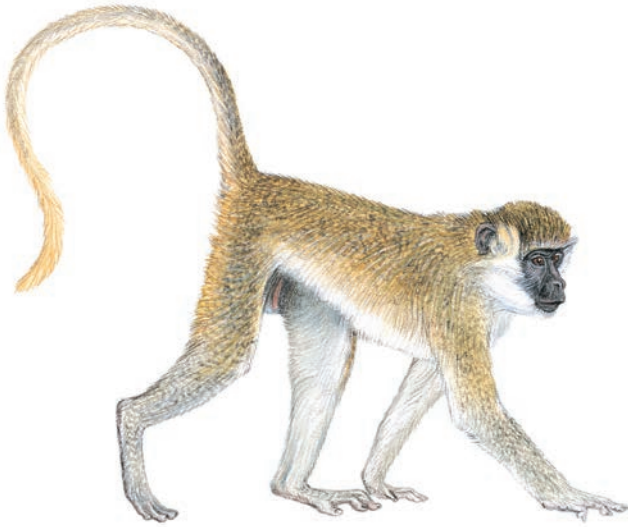
Various localities. Linear measurements: ♂♂ compiled from three subspecies (Elliot 1913c, Hill 1966); ♀♀ *C. t. budgetti* (Hill 1966) WT: ♂ *C. t. tantalus* (Hill 1966); ♀ *C. t. tantalus* (H. Ohsawa, M. Inoue-Murayama & O. Takenaka pers. comm.)

Key References Dandelot 1959; Groves 2001; Kavanagh 1980; Nakagawa 1999, 2000b; Oates 2011.

Naofumi Nakagawa

Chlorocebus sabaeus GREEN MONKEY (*CALLITHRIX*)

Fr. Singe vert; Ger. Westliche Grünmeerkatze

Chlorocebus sabaeus (Linnaeus, 1766). Systema Naturae, 12th edn, 1: 38. Cape Verde Is.Green Monkey *Chlorocebus sabaeus* adult male.*Chlorocebus sabaeus*

Taxonomy Monotypic species. Member of the Savanna Monkeys Group *Chlorocebus* (*aethiops*). Although the differentiation of blood proteins and electrophoretic distances between *Chlorocebus sabaeus* and the related Grivet *Chlorocebus aethiops* are moderate and could support arguments for subspecies or intermediate ranking (Lucotte *et al.* 1982), full species status is now accepted by most authorities (Lernould 1988, Kingdon 1997, Groves 2001, 2005c). Hybridization with *Erythrocebus patas* in the wild (Galat 1998) and with *Macaca mulatta* in captivity (Zuckerman in Hill 1966). Synonyms: *callitrichus*, *chrysurus*, *wernerii*. Chromosome number: $2n = 60$ (Sineo *et al.* 1986, Dutrillaux *et al.* 1988b).

Description Medium-sized, long-legged, long-tailed, semi-terrestrial, olive-green monkey. Chest deep, waist slim. Adult ♀ like adult ♂ but smaller, weighing about 70% as much. Face black. Whiskers whitish to yellowish. Temporal 'cowlick' that is directed upwards in front of ears. Brow-band greyish (not white) indistinct or absent. Dorsum and upper limbs and base of tail grizzled olive-green (hairs speckled green, yellow and black). Hands and feet pale grey. Underparts whitish. Tail shortish, tip fawn to golden yellow in adults and grey in immatures. Anus red in adult ♂. Scrotum yellow to green except blue for dominant ♂♂. Newborn with face pale pink. Dorsal pelage black.

Geographic Variation There is a slight north to south gradient with regard to sexual dimorphism (♂♂ larger in north) and colour of dorsum, which is yellower in the north (Galat *et al.* 2011). Some local populations/groups have distinctive characteristics. Namely, nasal ridge may be more or less white-haired and face exhibits variable patterns of depigmented spots; conspicuousness of the brow-band varies; throat and front of chest ranges from whitish to orange (A. Galat-Luong pers. obs.).

Similar Species

Chlorocebus tantalus. Eastward of Nakambe/Volta R. in Burkina Faso and Ghana. Smaller. Cheek-hair long and yellowish with short black tips. White 'facial ring' broken by black line from eyes to temples. Brow-band distinct, white. Dorsum gold to greenish. Base of tail with white tuft of hairs to either side. Tail tip whitish. Perineum sometimes with orange hairs.

Distribution Endemic to W Africa. Sahel Savanna, Guinea Savanna and Northern Rainforest–Savanna Mosaic BZs.

Current Distribution Atlantic coast of Senegal, Gambia, Guinea-Bissau, Guinea and Sierra Leone eastwards to the Nakambe/Volta R. in Burkina Faso and Ghana. Western limit is Dakar, Senegal (17° 28' W; A. Galat-Luong & G. Galat pers. obs.). Northern limit is at ca. 17° N in Mauritania and Mali. Area of occurrence is ca. 1,000,000 km². Most northern populations are now relics. Reaching 17° N, the Green Monkey, together with the Tantalus *Chlorocebus tantalus* in Mali, the Patas *Erythrocebus patas* on the Air Massif, Niger, and the Grivet in Eritrea, probably has the northern-most range of any species of guenon at this time. Southern limit of the primary range is at ca. 05° 50' N both in Côte d'Ivoire (A. Galat-Luong & G. Galat pers. obs.) and Ghana. There are, however, isolated outliers in mangrove and associated secondary forest in Côte d'Ivoire at Ebrié Laguna near Jacqueline (05° 10' ; 04° 30' W; Galat 1983) and on Elouamin I., Iles Ehotilé N. P. (05° 09' N; 03° 18' W; Gonedélé Bi *et al.* 2009). Introduced to Cape Verde Is. and the West Indies (Barbados, Nevis and St Kitts).

Historical Distribution Geographic range not greatly reduced, but some populations living near or in cities have disappeared (e.g. a population lived in Dakar until 1998; G. Galat & A. Galat-Luong pers. obs.). One of the last monkeys to disappear as a result of human-caused habitat modifications.

Habitat Prefers Sudanian–sub-Guinean woodlands, gallery forests and wooded savannas. Mean annual rainfall over geographic range varies from 200–1200 mm. Green Monkeys stay in sight of trees. They prefer to sleep in trees at the fringe of wooded areas (or near water) with a good look-out over open land (A. Galat-Luong pers. obs.). They spend about half of the time in forest or arboreal savanna, one-third in shrubby savanna and little time in grasslands (G. Galat & A. Galat-Luong pers. obs.). Water generally available within 5–10 km. Groups use unique sleeping sites (i.e. preferentially chosen groves of trees) in the north. Sometimes two groups sleep at the same site (Galat 1983). In the south of their range a group can use several sleeping sites (Galat & Galat-Luong 1976). Do not use the same site twice in areas where hunted (Galat 1983).

Marginal habitats include Sahelian acacia forests (*Acacia nilotica*, *Acacia radiana*, *Acacia seyal*, *Acacia senegal*, *Acacia albidia*). Plant diversity may be low: no more than 43 plant species (including small herbs) recorded from one group's home-range (Galat 1983). May spend 80% of time (and three days consecutively) in mangrove swamps (*Rhizophora* sp., *Avicennia nitida*; Galat & Galat-Luong 1976). The time spent in trees depends on habitat structure, ranging from 28% (Senegal R. Valley, Senegal) to 72% (Saloum, Senegal) (Galat & Galat-Luong 1976). In the Senegal R. Valley, adults significantly more often recorded on the ground than young ($n = 5398$), and adult ♂♂ more often on the ground than adult ♀♀ ($n = 2732$). Spent 15% of time on vertical trunks, 50% on horizontal boughs, 17% on branches and 18% on twigs ($n = 3773$) (Galat 1983). Adults significantly more often recorded on larger branches than young ($n = 2733$), and adult ♂♂ more often than adult ♀♀ ($n = 994$). Altitude ranges from 0 to ca. 1000 m. Maximum temperature ranges from ca. 20 to 57°C. Minimum 1°C.

Abundance Densities are 1.6–1.7 ind/km² in Niokolo Koba N. P., Senegal (Galat *et al.* 1998) and 1.4 ind/km² maximum density in Comoé N. P., Côte d'Ivoire (Geerling & Bokdam 1973). Highest densities for Green Monkeys occur in refuges close to areas where raiding crops is habitual (maximum density of 7 ind/km² at Fathala, Senegal). Density inside home-ranges 10–112 ind/km²: 18–28 ind. in 1.78 km² at Assirick, Senegal (Harrison 1983a), 15 ind. in 15 ha at Bandia, Senegal (Galat 1983), and 174 ind. in 1.56 km² at Ndioum Wallo, Senegal (Galat 1983).

Adaptations Diurnal and semi-terrestrial. Opportunistic. Green Monkeys adapt to uncommon environments (e.g. mangrove swamps; Galat & Galat-Luong 1976, Gippoliti & Dell'Omo 1996) and foods. They swim (up to 100 m with an infant under the belly; Galat 1989), and play and dive in the sea at high tide (A. Galat-Luong pers. obs.). Use unique techniques to hunt Nile Grass Rats *Arvicantis niloticus* (Galat 1983), Laughing Doves *Streptopelia senegalensis* (Galat 1989) and Fiddler Crabs *Uca tangeri* (Galat & Galat-Luong 1976). Can live without water for six months, but not in arid areas. During the hotter hours and when food is scarce they take long rests in the shade for up to six hours per day (Galat 1983).

Foraging and Food Opportunistic omnivores. Green Monkeys feed in the morning and late in the afternoon. Subgroup foraging occurs (Galat 1983). Home-range size in Senegal 15–178 ha (Galat & Galat-Luong 1976, Galat 1983, Harrison 1983b) depending on habitat quality. Day range 0.5–2 km (Harrison 1983a, G. Galat pers. obs.) to 4–8 km (G. Galat pers. obs.). They can travel up to 2 km in 45 minutes (Galat 1983). Green Monkeys are generalists, feeding on fruits (24–50%, annual means), leaves (28–50%), seeds (13%), flowers (3–13%), buds, young twigs, stems, thorns, bark, gum (11–15%), fungi, and also bird faeces, termitarium earth, invertebrates (5–50%) and vertebrates, including eggs, young birds, sparrows, lizards and small mammals (Galat & Galat-Luong 1977, 1978b, McGrew *et al.* 1978, Galat 1983, Harrison 1983a). Important food plant species in Senegal are *Parinari* spp., *Ficus* spp., *Ziziphus mauritiana*, *Ziziphus mucronata*, *Icacina senegalensis*, *Acacia siberiana*, *Acacia nilotica*, *Adansonia digitata*, *Aphania senegalensis*, *Rhizophora* sp., *Nymphaea* sp. (Galat & Galat-Luong 1976, 1977, Galat 1983), *Pterocarpus erinaceus*, *Pseudospondias microcarpa* and *Nauclea latifolia* (Harrison 1982). In poor environments a single plant group or species can make up most of the diet (leaves of grasses up to 63% in wet season, all parts of *A. nilotica* up to 44%; Galat & Galat-Luong 1978a). During periods of scarcity, rodents can constitute, by time spent feeding, 47% (one 125 g Nile Grass Rat for three monkeys) and Laughing Doves 28% of the animal prey (Galat *et al.* 2011). Green Monkeys prey occasionally on adult Red-billed Hornbills *Tockus erythrorhynchus* (attacks on African Grey Hornbills *Tockus nasutus* fail; A. Galat-Luong pers. obs.) and young Scrub Hares *Lepus saxatilis* (Galat & Galat-Luong 1977, 1978a). Mobbing from Abyssinian Rollers *Coracias abyssinicus* and gulls *Larus* sp. is frequent at Senegal R. Valley (Galat 1983). In mangrove swamps, Fiddler Crabs can represent >50 g of fresh meat per animal per day (G. Galat pers. obs.). Crop raiding and food stealing occur (Galat 1983). Feeding takes 8–32% of time, locomotion 17–48% and resting 23–64% (Dunbar 1974, Galat & Galat-Luong 1976, Harrison 1983a). There are significant seasonal differences in how time is spent (Galat 1983, Harrison 1984, 1985).

Social and Reproductive Behaviour Social. Green Monkey groups are multimale/multifemale. Adult ♂♂ emigrate, sometimes into adjacent groups (Galat 1983). Mean sizes of groups in Senegal are: north, 52 ind. (15–174, $n = 11$ groups; Galat & Galat-Luong 1977, Galat 1983), 19 (5–35, $n = 5$; A. Galat-Luong pers. obs.); north-east, 16 ($n = 1$; Galat 1983); west (Dakar), 12 (8–18, $n = 3$; Galat 1983, A. Galat-Luong pers. obs.); west (Saloum), 34 (24–45, $n = 13$; A. Galat-Luong pers. obs.); south-west, 10 ($n = 1$; Galat 1983); south-east, 12 (8–16, $n = 5$; Dunbar 1974), 19 ($n = 12$; Harrison 1983b), 27 (10–40, $n = 7$, A. Galat-Luong pers. obs.). In Guinea, group size was: 1 ind. (31%), 2–10 (43.3%), 11–20 (20.9%), >21 (4.5%) ($n = 454$ individuals; Touré *et al.* 1997), and in Côte d'Ivoire mean group size was 6 ind. (4–9, $n = 3$; Galat & Galat-Luong 1980). There are two levels of organization in the larger groups, which can fragment into subgroups of up to 15 individuals (Galat 1983).

Social behaviour occupies 7–13% of time (Dunbar 1974, Galat & Galat-Luong 1976). In rich environments (annual rainfall >500 mm), home-ranges (and groups) are small, just large enough to include most of the plant diversity of the area (Galat 1989). Territorial behaviour is common if food is available (Galat & Galat-Luong 1976, 1977, 1978b, Harrison 1982, 1983b). Dominant ♂♂ give

territorial displays from high vantage points every morning at dawn and sometimes in the evening at twilight. Display includes powerful jumps, exhaled/inhaled barking and exhibition of the white belly, red penis and blue scrotum (Galat & Galat-Luong 1976). Territorial boundaries may remain unchanged for 25 years (G. Galat pers. obs.). Territorial behaviour is absent if resources are scarce, patchy and unpredictable (Galat & Galat-Luong 1978b). For example, in the Senegal R. valley, four groups, totalling >200 individuals, observed feeding together on *Z. mauritiana* without exhibiting agonistic behaviour, and several groups observed queuing for access to a single *Ptilostigma thonningii* (Galat 1989). However, artificial provisioning can induce territorial behaviour (Galat 1983). One group may dominate another (Galat 1983). 'Nurseries' can comprise infants from several groups (Galat 1983). In large (northern) groups, at the beginning of the wet season, adult ♂♂ may herd several pregnant ♀♀ and control subgroups made up of 12–15 individuals (Galat 1983). Herding is rare in the southern populations (Harrison 1983b).

Copulation is most often seen at dawn in the cool season (Galat 1983). Young are carried under the belly and are taken care of by their mother, sisters, aunts and sometimes adult ♂♂. More than 60 gestures and 30 vocalizations given, including chest-to-chest rubbing (Galat 1975, 1983). Alarm vocalizations distinguish predator categories (aerial or terrestrial) and degree of threat. Comparison of these behaviours with those described by McGuire (1974) on St Kitts indicates that they are almost identical, and that there was no genetic drift on St Kitts in these behaviours in spite of three centuries of isolation. Differences in some behaviours described for Vervet *Chlorocebus pygerythrus* (Struhsaker 1967a, b) are considerable (Galat 1975). Only 4% of adult ♂♂ Green Monkeys have a blue scrotum (Galat 1983), and they lack the strongly contrasted anal characters of the Vervet; Green Monkeys have a pale pink perianal ring (instead of intense red) and lack the white 'moustache' beneath the anus. As such, the 'red-white-and-blue' dominance display (Struhsaker 1967a, b) of the adult ♂♂ Vervet is replaced in the adult ♂♂ Green Monkey by a 'lateral display' whereby the ♂ presents his lateral profile and 'enlarges' himself by raising the tail over the back. Experiments with young ♂ Green Monkeys (Lucotte *et al.* 1982) demonstrated that they are able to display like *C. pygerythrus*, but that, for lack of reinforcement by effective visual stimuli, they do not give this display when adult. Vocalization structures are similar to *C. pygerythrus* but context (meaning) slightly differs (G. Galat & A. Galat-Luong pers. obs.).

In Saloum, Green Monkeys in association with Patas on 27% of encounters, with Temminck's Red Colobus *Procolobus badius temminckii* on 18%, and with both Patas and Temminck's Red Colobus on 3% (n = 78 encounters; Pourrut *et al.* 1996). In Gambia (at Pirang), Green Monkeys in association with Temminck's Red Colobus on eight of ten encounters (Galat-Luong 1988). Such associations appear to enable Temminck's Red Colobus to follow Green Monkeys into mangrove swamps (Galat-Luong & Galat 2005), and enable Green Monkeys to exploit the margins of the high forest. In Burkina Faso, seen sharing sleeping trees with White-naped Mangabeys *Cercocebus lunulatus* (Galat & Galat-Luong 2006b) and the same (secure) swamp area with Olive Baboons *Papio anubis* (A. Galat-Luong pers. obs.). Bushbuck *Tragelaphus scriptus* (Galat-Luong, 2006) and Lord Derby's Eland *Taurotragus derbianus derbianus* (A. Galat-Luong & G. Galat pers. obs.) also associate with Green Monkeys. Play is varied and may be inter-specific, including with Northern Lesser Galagos *Galago*

senegalensis, Patas, Temminck's Red Colobus, grass snakes and birds (Galat 1983, 1989, A. Galat-Luong pers. obs.).

Reproduction and Population Structure Birth seasons vary geographically: Feb–Mar (Saloum; A. Galat-Luong pers. obs.), Mar–Apr (Niokolo Koba; Dunbar 1974, Harrison 1983a), Dec–Jan and Jun–Jul (Senegal R. Valley; Bourlière *et al.* 1976). In the Senegal R. Valley ♀♀ can give birth twice a year, at seven-month intervals (Bourlière *et al.* 1976, Galat & Galat-Luong 1977). In Niokolo Koba one adult ♀ was observed to suckle two infants simultaneously (A. Galat-Luong pers. obs.). Male : female sex ratio varies from 1 : 1 to 1 : 3.5. Adult : immature ratio varies from 1 : 0.4 to 1 : 1.2 (Galat & Galat-Luong 1976, 1977). Galat-Luong (1994) estimated longevity in the wild at 27 years, a value close to the 30-year record for captives (Jones 1962, Baulu 1988). If climatic conditions and subsequent food availability change drastically, reproductive success may be 100% in one year and then near zero the following year (n = 3 groups; Galat & Galat-Luong 1977).

Predators, Parasites and Diseases Humans, Leopards *Panthera pardus*, Central African Rock Pythons *Python sebae* (attack of pregnant ♀ observed by A. Galat-Luong), Spotted Hyenas *Crocuta crocuta* and African Wild Dogs *Lycaon pictus* are the main predators. Striped Jackals *Canis adustus*, Caracals *Felis caracal*, Servals *Felis serval*, Domestic Dogs *Canis familiaris* and large eagles probably prey on young. Green Monkeys recognize individually the dogs that herd sheep and have a different flight distance for each dog (that seems to depend on how much of a threat each dog is). For example old, rheumatic dogs evoke flight at <5 m, whereas faster, more dangerous dogs evoke alarm calls and flight at >100 m (A. Galat-Luong pers. obs.). Brewer (1978), under semi-captive and reintroduction conditions, recorded the Robust Chimpanzee *Pan troglodytes* as a predator. Pruetz & Bertolani (2007) saw a wild Robust Chimpanzee feeding on a Green Monkey. Excessive dry periods can cause blindness due to vitamin A deficiencies, high adult mortality, and increased rates of stillbirths and miscarriages (Galat & Galat-Luong 1977). Penile and scrotum necrosis also occurs (A. Galat-Luong pers. obs.).

Identified intestinal parasites include Nematoda *Strongyloides* sp. (69% of faecal samples), *Necator* sp. (6%), *Physaloptera* sp. (6%); Protozoa *Entamoeba coli* (75%), *Iodamoeba butschlii* (25%) (Assirick, n = 16 faecal samples; McGrew *et al.* 1989b). *Entamoeba coli* (49%), Nematoda (32%), *Strongylidae* (20%), *Strongyloides stercoralis* (11%), *Trichuris trichura* (3%), *Ascaris lumbricoides* (9%) (n = 94 faecal samples from various sites in Senegal; Pourrut *et al.* 1997). Nematode infection in Green Monkeys is lower where *A. nilotica* is a staple food. *Acacia nilotica* is used by the local people against intestinal parasites, but the low rainfall in those areas also thwarts nematode development (overall infestation W, N and SE Senegal was 79%, n = 94 faecal samples; Pourrut *et al.* 1997).

Green Monkeys are healthy carriers of the simian immunodeficiency virus (SIV), which is similar to human immunodeficiency virus (HIV), and thus are used as biomedical models. Prevalence is 46% in wild populations in Senegal (n = 352; Galat & Galat-Luong 1997). Prevalence is higher in adults (51–81%) than in immatures (20%), indicating sexual transmission (Galat-Luong *et al.* 1994b, 1995), and implying other possible infection routes such as bites (Galat & Galat-Luong 1997). Comparing these values with those for Patas

(6% of the population, 10% for adults, 4% for immatures), Galat-Luong *et al.* (1994b) showed the importance of differing strategies in the choice of sexual partners for the transmission of SIV (multiple partners among Green Monkeys and single-male groups among Patas). Transmission of Green Monkey's SIVagm to Patas in the wild occurs (Bibollet-Ruche *et al.* 1996, Galat-Luong *et al.* 1996). Infection with SIV or STLV-I (Simian T-cell Lymphotropic Virus) increases the risk for a second retroviral infection (Durand *et al.* 1995).

Conservation IUCN Category (2012): Least Concern. CITES (2012): Appendix II.

Only some populations are threatened, such as at Île à Morfil, Senegal, where an 85% reduction of the *A. nilotica* forest resulted in the disappearance of 83% of the Green Monkeys. Here the number of ♀ ♀ per ♂ dropped from 3.0 in 1975 and 2.5 in 1976 (wet season data) to 1.4 in 1988 as a result of increased mortality among adult ♀ ♀. Likewise, the number of young per adult, which was 0.96 in 1975 and 0.76 in 1976, declined to 0.67 in 1988 (Galat-Luong & Galat 1994).

Measurements

Chlorocebus sabaeus

HB (♂ ♂): 540 (470–650) mm, n = 7

HB (♀ ♀): 420, 460 mm, n = 2

T: n. d.

HF: n. d.

E: n. d.

WT (♂ ♂): 6.3 (4.7–7.5) kg, n = 17

WT (♀ ♀): 4.4 (3.4–5.9) kg, n = 20

Body measurements: HB: Senegal and Côte d'Ivoire (A. Galat-Luong pers. obs.)

WT: Senegal (Galat-Luong *et al.* 1996)

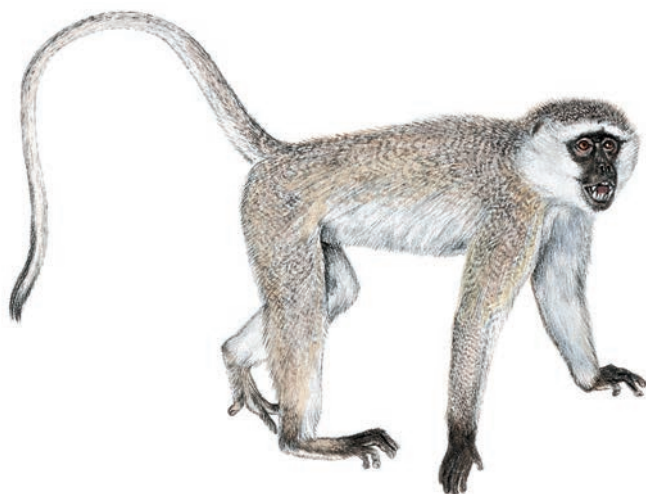
Key References Galat 1983; Galat & Galat-Luong 1976, 1977; Harrison 1982; Oates 2011.

Gérard Galat & Anh Galat-Luong

Chlorocebus pygerythrus VERVET MONKEY

Fr. Vervet; Ger. Südliche Grünmeerkatze

Chlorocebus pygerythrus (F. Cuvier, 1821). Histoire Naturelle Mammifères, pl. 139, pt. 24: 2. 'Africa'.



Vervet Monkey *Chlorocebus pygerythrus* adult male.

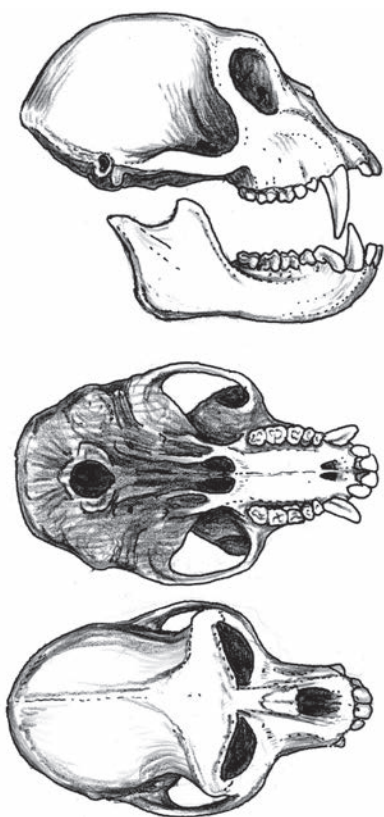
Taxonomy Polytypic species. Dorst & Dandelot (1969), Kingdon (1971), Haltenorth & Diller (1977), Napier (1981) and Grubb *et al.* (2003) considered the Vervet to be a subspecies (*Cercopithecus aethiops pygerythrus*) within the *C. (aethiops)* Group. Hill (1966), Dandelot (1974) and Kingdon (1997) treated *C. pygerythrus* as a distinct species with 13, 14 and 6 subspecies, respectively. Groves (2001, 2005c) also viewed the Vervet as a full species (with five subspecies), but places this taxon within the genus *Chlorocebus*. Here we adopt the taxonomy of Groves (2001, 2005c), but with reservations over the use of the genus name '*Chlorocebus*' as we believe current evidence supports '*Cercopithecus*' as the more appropriate genus for the *C. (aethiops)* Group (see our comments in the *Chlorocebus* genus profile). Only cases of hybridization in the wild are of one Zanzibar Sykes's

Monkey *Cercopithecus mitis albogularis* × *C. pygerythrus* hybrid at Diani, SE Kenya, and of one Kolb's White-collared Monkey *Cercopithecus mitis kolbi* at Nairobi, SC Kenya (De Jong & Butynski 2010b). Synonyms: *arenaria*, *callida*, *centralis*, *?circumcinctus*, *cloetei*, *contigua*, *ellenbecki*, *erythropysga*, *excubitor*, *flavidus*, *rubellus*, *rufoniger*, *rufoviridis*, *glaucus*, *helvescens*, *hilgerti*, *johnstoni*, *lalandii*, *luteus*, *marjoriae*, *nesiotes*, *ngamiensis*, *pembae*, *pusillus*, *silaceus*, *tumbili*, *voeltzkowi*, *whytei*. Chromosome number: 2n = 60 (Sineo *et al.* 1986).

Description Medium-sized, semi-terrestrial, long-tailed monkey with grizzled light brown, greyish-brown, tawny, olive-brown, olive-green or brownish-yellow dorsum and sides. Adult ♀ weighs about 70% as much as adult ♂. Adult ♂ and adult ♀ similar except for colouration over anogenital region. Face black with white cheek-whiskers and brow forming ring around face. Eyes and ears black. Ventrums white or off-white. Limbs greyish-brown to grey outside, white inside. Feet and hands black. Tail light to dark brown dorsally, light brown ventrally, with tip dark brown to black. Ischial callosities grey. Adult ♂: scrotum turquoise blue surrounded by white hairs. Adult ♂ with patch of red hairs under base of tail, perianal skin and penis red, perineal stripe white. Adult ♀: perineum pink, clitoris red, vulvar area blue, no perineal stripe. Infants: face pink, pelage black or dark brown. By the third month, the face is black, the brow white and the cheek-hairs obvious. By six months, the back has acquired adult colouration (Struhsaker 1971b). Photographs of *C. pygerythrus* from many sites in Kenya and Tanzania available at: www.wildsolutions.nl

Geographic Variation Five subspecies recognized:

C. p. excubitor Manda Vervet Monkey. Manda I. and Patta I., north coast of Kenya. Pale brownish-yellow; smaller than *C. p. hilgerti*.



Lateral, palatal and dorsal views of skull of Vervet Monkey *Chlorocebus pygerythrus* adult male.

- C. p. hilgerti* Hilgert's Vervet Monkey. E Uganda through Kenya to S Ethiopia east of the Rift Valley, S Somalia and N Tanzania. Similar to *C. p. excubitor* but larger.
- C. p. nesiotis* Pemba Vervet Monkey. Pemba I. and Mafia I., Tanzania. Brownish-fawn; whiskers long, speckled; ventrum often reddish; smaller than *C. p. rufoviridis*.
- C. p. pygerythrus* Southern Vervet Monkey. South of Zambesi R. in Botswana, Zimbabwe, Mozambique and South Africa. Grey or olive-green; greyer in west, greener in east.
- C. p. rufoviridis* Reddish-green Vervet Monkey. S Uganda west of L. Victoria, through Tanzania, south to Zambesi R. east of Luangwa R., Zambia. Similar to *C. p. nesiotis* but larger.

Similar Species

- Chlorocebus aethiops*. East of White Nile R. and south of Khartoum, Sudan, to C Eritrea, C Ethiopia into Djibouti. Hybridizes with *C. p. hilgerti* at Omo R., Ethiopia. Cheek-hair long and fluffy; face often with white moustache; back yellower; feet and hands pale grey; base of tail with tufts of white hair to either side; tail tip whitish; scrotum sky blue.
- Chlorocebus djamdjamensis*. Parapatric on the Bali Massif, SC Ethiopia. Only in bamboo forest above 2400 m. Temples black. Brow-band absent or narrow. Thin white moustache. Tail short. No red patch under base of tail in adult ♂.
- Chlorocebus tantalus*. Nigeria to S Sudan, N and C Uganda and NW Kenya. Hybridizes with *C. p. rufoviridis* along northern and western shores of L. Victoria, Uganda. Cheek-hair long and yellow with short black tips; white facial ring broken by black line from eyes



Chlorocebus pygerythrus

to temples; white above eyes more sinuous than rounded; back and crown gold to greenish; base of tail with tufts of white hair to either side; tail tip whitish; perineal area orange; scrotum sometimes with light covering of orange hairs.

Chlorocebus cynosuroides. Distribution relative to *C. pygerythrus* is unclear. Through S DR Congo and Angola to N Namibia, eastward to west of Luangwa R. and southwards to north of Zambezi R., Zambia, and L. Kariba, Zimbabwe. Face pinkish, blotched. Dorsum olive-buff to olive-grey. Bare skin of palms and soles pinkish. Ischial callosities rose-pink. Scrotum slate blue to violet.

Distribution Endemic to eastern and southern Africa. Somalia—Masai Bushland, Zambezian Woodland, Coastal Forest Mosaic, South-West Arid and Highveld BZs. Occurs in S Somalia, S Ethiopia, E and S Uganda, Kenya (including Manda I.), Tanzania (including Pemba I., Zanzibar I., Mafia I.), Malawi, Zambia, Mozambique, N and E Botswana and South Africa. See Geographic Variation.

Habitat Primarily along water-courses, swamps, lakeshores, and the coast of the Indian Ocean in savanna-woodlands. In Amboseli N. P., S Kenya, until the 1990s when groves of *Acacia xanthophloea* declined, Vervets live in habitats dominated by *A. xanthophloea* near water and *Acacia tortilis* away from water. On the Laikipia Plateau, C Kenya, Vervets feed and sleep along rivers dominated by *A. xanthophloea*, and also feed in non-riverine habitat dominated by *Acacia drepanolobium* (Isbell *et al.* 1998b). In Samburu-Isiolo National Reserves, Kenya, Vervet habitats along the Ewaso Nyiro R. are dominated by *Acacia elatior*, *Hyphaene coriacea* and *A. tortilis* farther away from the river (Whitten 1983, 1988). On Lolui I., L. Victoria, Uganda, Vervets live in areas dominated by *Alchornea cordifolia* and *Antiaris schweinfurthii* (Hall & Gartlan 1965, Gartlan & Brain 1968). At Windy Ridge Game Park, Natal Province, South Africa, they are found in mixed *Acacia* woodland (Baldellou & Henzi 1992). In the Karkloof area of Natal, Vervets live in mature montane forest

edged with Black Wattle *Acacia mearnsii* commercial plantations and cultivated crops, e.g. yams *Dioscorea* sp. (Bruerton *et al.* 1991). Near L. Sibayi, KwaZulu Province, South Africa, they live in strips of dune forest that include *Celtis africana*, *Acacia karroo* and *Acacia kraussiana* (Van der Zee & Skinner 1977). In Ndumu G. R., NE South Africa, Vervets live along the Usutu R. and Pongola R. where *A. xanthophloea* and *Ficus sycomorus* dominate. Some groups here range mainly in habitats dominated by thickets of *Acacia burkei*, *Acacia nigrescens* and *Dicrostachys cinerea* (De Moor & Steffens 1972). Along the Milk R., Klein Karoo Region of Western Cape Province, South Africa, Vervets are found with *A. karroo*, *Rhus lancea* and *Schinus molle* (McDougall 2011).

Mean annual rainfall in eastern Africa ranges from 330 mm (Amboseli) to 1524 mm (Lolui I.), but tends to be low. At four Vervet sites in Kenya, annual rainfall ranges from ca. 200–400 mm (Kimana), 350–400 mm (Samburu), 400–600 mm (Mosirot) and >600 mm (Naivasha) (Whitten & Turner 2004). Annual rainfall in southern Africa is more extreme. In Klein Karoo, mean annual rainfall is 300 mm (McDougall *et al.* 2010), but near Windy Ridge, just nine months spanning 1987–88 (excluding Jul–Sep 1988) yielded 9920 mm (490 mm in Dec 1987 to 2000 mm in Mar 1988) (Baldellou & Adan 1998). Rainfall patterns are variable, with two distinct wet seasons (Nov–Dec and Mar–Apr) in Amboseli (Cheney *et al.* 1988), two wet seasons (Apr–Jun and Oct–Nov) at Segera (Isbell *et al.* 2009), and year-round rainfall on Lolui I. (Gartlan 1969). At Ndumu there is one wet season (Nov–Apr; De Moor & Steffens 1972). Minimum and maximum daily temperatures are ca. 9 and ca. 32 °C, respectively, in Amboseli (Struhsaker 1967c). Annual mean monthly minimum and maximum temperatures from Jan 1993 to Feb 2002 were 11.3 and 29.6 °C, respectively, at Segera (L. A. Isbell pers. obs.). Near Windy Ridge, mean monthly minimum temperatures for Oct 1987 to Jun 1988 ranged from 13.3 °C in Jun to 22.6 °C in Mar, while mean monthly maximum temperatures ranged from 21.9 °C in Jun to 29.3 °C in Feb (Baldellou & Adan 1998). Altitudinal limits are from sea level in coastal areas (e.g. coastal East Africa) to >2000 m at Naivasha (Whitten & Turner 2004; T. Butynski & Y. de Jong pers. comm.), to >2000 m at Mt Hanang, N Tanzania (Y. de Jong & T. Butynski pers. comm.), to 1900 m in the Udzungwa Mts, SC Tanzania (Rovero *et al.* 2009).

Abundance Widespread but patchy and prone to local extinction. Densities 9–>104 ind/km². In Amboseli the density of Vervets in the Kitirua/Ol Lengia area declined from 79–104/km² in 1977 to 29–56/km² in 1983, continuing a decline that began in the early 1970s (Struhsaker 1973, 1976, Cheney *et al.* 1988). By 1988, six groups became so small that they joined other groups (Hauser *et al.* 1986, Isbell *et al.* 1991). This population decline is attributed to a die-off of *A. xanthophloea*, exacerbated by a period of heavy predation (Cheney *et al.* 1988, Isbell 1990). Vervet densities on Segera also declined, from 80/km² in 1992 to 9/km² by 2002 (L. A. Isbell pers. obs.). This decline is attributed to poor recruitment of ♀♀ and heavy predation (Isbell & Enstam 2002, Isbell *et al.* 2009). The density of Vervets on Lolui I. is ca. 50–88/km² (Hall & Gartlan 1965, Gartlan & Brain 1968) and in Samburu, 39/km² along the river and 1.6/km² in the Reserve as a whole (Whitten 1982). At Burman Bush Nature Reserve, South Africa, where Vervets are provisioned by humans, the density is 59–89/km² (Henzi & Lucas 1980).

Adaptations Diurnal and semi-terrestrial. Compared to the sympatric, more arboreal, Gentle Monkeys *Cercopithecus mitis*, Vervets possess more traits associated with terrestrial locomotion, i.e. shorter trunk length relative to body weight, shorter humerus relative to the femur, and higher brachial (i.e. longer forearm relative to arm) and crural (i.e. longer crus relative to thigh) indices (Anapol *et al.* 2005). Vervets also have traits that are associated with arboreal locomotion, including wider humeral and talar heads, a shorter tibia, a longer ischium and a longer tail than expected of terrestrial primates (Taylor 1976, Rodman 1979, Anapol *et al.* 2005). In Amboseli, Vervets spend equal amounts of daytime on the ground and in trees overall but there is considerable variation among groups (Cheney & Seyfarth 1990, L. A. Isbell pers. obs.). Similarly, at Segera, one group of Vervets spent more time on the ground than another (L. A. Isbell pers. obs.). At Segera, when Vervets are not in *A. xanthophloea*, ca. 60% of their time is spent on the ground (Enstam & Isbell 2002). Vervets at Segera climb nearly four times as often as sympatric Patas *Erythrocebus patas*, reflecting their greater use of tall trees, but they do not leap more often (Isbell *et al.* 1998a). At Naivasha, where Vervets are terrestrial only 20% of the time, leaping constitutes 10% of their locomotion (McGraw 2002). At Ngezi Forest, some groups of Vervets live well within the forest where they are strictly arboreal. No other guenon is present on Pemba I. That Vervets live within forest at Ngezi, and are arboreal, is probably attributable to ‘competitive release’ (T. Butynski & Y. de Jong pers. comm.).

Foraging and Food Omnivorous. Vervets forage both arboreally and terrestrially, typically beginning the day by feeding within their sleeping trees. By mid-morning they descend to forage on shrubs and herbaceous plants. After a mid-day rest, Vervets continue foraging, either on the ground or in trees, until dusk when they climb back into sleeping trees. At Segera seven adult ♀♀ in one group maintained a mean 6.6 m from their nearest neighbour. This is close to the mean of 6.1 m between feeding sites (Isbell & Enstam 2002). In Amboseli, individuals in six groups spent 30–40% of their time feeding and 15–20% of their time moving (Isbell & Young 1993b). Two groups with mean group sizes of 17.2 and 16.4 in Amboseli travelled a mean 950 m and 1440 m/day, respectively (135–2558, n = 114 days; Struhsaker 1967c). Daily travel distances of two groups at Segera were 1025 m (n = 44 days) for a group averaging eight members and 1632 m (n = 144 days) for a group averaging 27 members (based on straight-line distances of the groups during 30-minute periods; Isbell *et al.* 1999b, Enstam & Isbell 2007). Larger groups and groups in poorer habitats travel farther per day than smaller groups and groups in higher-quality habitats (Struhsaker 1967c, Isbell *et al.* 1999b).

Vervets use hand-to-mouth movements to eat leaves, flowers, fruits, seeds and arthropods, but apply the mouth directly to scrape gum off trees. They rely heavily on *Acacia* spp. In Amboseli, flowers, gums, leaves and pods of *A. xanthophloea* and *A. tortilis* account for ca. 50% of total time spent feeding (Lee & Hauser 1998). At Segera, *A. drepanolobium* and *A. xanthophloea* account for ca. 35% and ca. 22% of the diet, respectively (Pruetz & Isbell 2000). In Samburu, *A. tortilis* and *A. elatior* account for >60% of total time spent feeding (Whitten 1988). Other important food species are the woody shrubs *Azima tetracantha* and *Salvadora persica*, the herbs *Abutilon mauritanium* and *Lycium europaeum*, and the grasses *Pennisetum mezianum*, *Cynodon*

dactylon and *Cynodon plectostachyus* in Amboseli (Struhsaker 1967c, Lee & Hauser 1998), *Acacia gerrardii*, *Acacia seyal*, *Commelina* spp., *L. europaeum* and *Euclea divinorum* at Segera (Pruetz & Isbell 2000), and *H. coriacea*, *Boerhavia erecta*, *Abutilon hirtum*, *F. sycamorus* and *Aphania senegalensis* in Samburu (Whitten 1983).

With the exception of gums, which are available year-round, foods are eaten as they come into season. Flowers are preferred over other foods in Amboseli and Samburu. In Amboseli, *A. tortilis* flowers are most abundant in Jan–Mar, Oct–Dec (Wrangham & Waterman 1981, Isbell 1995, Lee & Hauser 1998). In Samburu Vervets spend 43% of their feeding time eating flowers (Whitten 1988). At Segera, which has no *A. tortilis*, gums are eaten more frequently (37%) than flowers (8%). Other foods eaten at Segera are fruits (10%), seeds and grasses (8% each), and leaves and swollen thorns (2% each). Small, unidentified items account for 23% of the diet; most of these are probably arthropods (L. A. Isbell pers. comm.), e.g. termites, beetles, moths, butterflies, grasshoppers, spiders and army worms *Spodoptera exempta*. Though percentages are not available for the diet of Vervets in the southern part of their range, foods of Vervets in the dune forests near L. Sibayi include floral parts of *C. africana*, fruits of *Mimosa affra*, *Ziziphus mucronata*, *Sideroxylon inerme*, *Ficus natalensis*, *Grewia* sp. and *Cucumis* sp., seeds of *A. karroo*, *A. kraussiana* and *Albizia adiantifolia*, and leaves of *C. africana*, *A. karroo*, *A. kraussiana*, *Vepris undulata* and *A. adiantifolia* (Van der Zee & Skinner 1977). Although omnivorous, Vervets in southern Africa eat leaves less often than Samango Monkeys *Cercopithecus mitis labiatus* and have gastrointestinal tracts that are less specialized for digesting foliage (Bruerton *et al.* 1991). Vervets sometimes eat the eggs and young of birds (Struhsaker 1967c, Skinner & Skinner 1974, Lee & Hauser 1998), and they drink regularly when water is available (Wrangham 1981). In Amboseli, Vervets visited waterholes, on average, about once every two days, and drank most often in the early afternoon ($n = 53$ in 1677 h) (Struhsaker 1967c). At Segera, Vervets are no longer able to drink throughout the year because irrigation practices upstream have caused the Mutara R. to dry up entirely from Mar–Jul in recent years, e.g. 1999 and 2000 (L. A. Isbell pers. obs.). Young Vervets acquire adult food habits as they mature. During their first two months infants feed asynchronously with their mothers. At three months, infants begin to feed synchronously with their mothers on the same food items (Hauser 1993). Adult ♂♂ and adult ♀♀ eat the same foods (L. A. Isbell pers. obs.).

Vervets live in home-ranges of 5–103 ha ($n = 27$) (Struhsaker 1967d, De Moor & Steffens 1972, Whitten 1982, Cheney & Seyfarth 1987, Isbell *et al.* 1990, 2002, Lee & Hauser 1998). Large group size, low density of food trees and absence of neighbouring groups all increase home-range size (Struhsaker 1967d, De Moor & Steffens 1972, Isbell *et al.* 1990, L. A. Isbell pers. obs.). Vervets use all parts of their home-range throughout the year, and invariably defend the boundaries of their home-ranges against incursions by neighbouring groups (Struhsaker 1967d, Gartlan & Brain 1968, De Moor & Steffens 1972, Cheney 1981, L. A. Isbell pers. obs.). Home-range overlap in Amboseli was 11–33% in 1963–64, 26–42% in 1977–80 and 4–57% in 1986–88 ($n = 15$) (Cheney 1987, Isbell *et al.* 1990). The wider range of overlap in the latter time period occurred because some neighbouring groups ceased to exist and larger groups expanded into the home-ranges of smaller groups.

Vervets prefer to sleep in trees that are tall and large. In Amboseli, Vervets prefer *A. xanthophloea* over *A. tortilis* (Struhsaker 1967c), and prefer groves rather than isolated trees (Struhsaker 1967c, L. A. Isbell pers. obs.). The same few sleeping sites are repeatedly used (De Moor & Steffens 1972, L. A. Isbell pers. obs.). Small groups often share the same sleeping tree. Larger groups may split into subgroups and spread out to sleep within a small number of trees. Individuals typically sleep on the highest branches and as far along the distal ends of branches as will bear their weight (Andelman *et al.* 1985, L. A. Isbell pers. obs.).

Social and Reproductive Behaviour Social. Vervets live in cohesive groups of 2–10 adult ♀♀ and their offspring, usually accompanied by multiple adult ♂♂ (Struhsaker 1967c, Whitten 1983, Young & Isbell 1994, Whitten & Turner 2004). In Amboseli, maximum group size declined over 30 years from 53 ($n = 4$) to 4 ($n = 2$) (Struhsaker 1967b, Cheney & Seyfarth 1987, L. A. Isbell pers. obs.). At Segera group sizes declined over ten years in two groups from 10 and 30 to one group of 9 (Isbell *et al.* 2009). On Lolui I., group sizes ranged from 6 to 21 ($n = 46$) (Gartlan & Brain 1968). In Samburu group sizes were 37 and 40 ($n = 2$) (Whitten 1983). In Mosi-Oa-Tunya N. P., Zambia, group sizes ranged from 23 to 47 ($n = 4$) (Tembo 1994). At Burman Bush Nature Reserve, where groups are provisioned by tourists, three groups ranged in size from 8 to 37 (Henzi & Lucas 1980). At Windy Ridge one group had a maximum of 23 individuals (Baldellou & Henzi 1992). At Nduma, South Africa, two groups comprised ca. 22 and 37 members (De Moor & Steffens 1972). Along the Milk R., two groups had 48 and 69 members (McDougall *et al.* 2011).

Females remain in their natal groups throughout life, except under unusual circumstances, e.g. group fusions. Males disperse from their natal groups around sexual maturity (ca. 5–6 years). Most dispersing natal ♂♂ do not become solitary but immediately join adjacent groups (Henzi & Lucas 1980, Cheney & Seyfarth 1983, Isbell *et al.* 2002). In Amboseli, over a five-year period, 22 of 23 (96%) natal ♂♂ in three groups dispersed to adjacent groups (Cheney & Seyfarth 1983). At Segera, over a ten-year period, five of six (83%) ♂♂ in two groups joined neighbouring groups and stayed an average of 16 months (Isbell *et al.* 2002). Males also disperse with siblings and join groups that former groupmates previously joined (Cheney & Seyfarth 1983, Isbell *et al.* 2002). The tendency of Vervets to live along narrow strips near rivers limits the number of adjacent groups to two in most areas. When this is coupled with the high risk of mortality that Vervets face while moving into unfamiliar areas (Isbell *et al.* 1990, 1993), dispersal options become more limited and, thus, likely result in shorter dispersal distances and greater relatedness among Vervet ♂♂ than among ♂♂ of other species of primates. Limited dispersal options may contribute to the social system of Vervets, which is unusual among the Cercopithecini in having a permanent multimale presence in most areas (Isbell *et al.* 2002). Vervets do form single-male multifemale groups in some areas, e.g. along L. Naivasha and in the dune forests near L. Sibayi (Van der Zee & Skinner 1977, Whitten & Turner 2004, T. R. Turner pers. comm.). Solitary ♂♂ must exist in such places but they have not been reported.

Adult ♂♂ and adult ♀♀ both have easily detectable, linear dominance hierarchies (Struhsaker 1967d, Whitten 1983, Isbell &

Pruetz 1998). Males assert their dominance over subordinate ♂♂ with vocalizations and displays, e.g. the red-white-and-blue display, in which the dominant ♂ holds his tail high while walking back and forth or circling the subordinate ♂, thereby exposing his red perianus, blue scrotum and white stripe of fur that connects the scrotum and perianus (Struhsaker 1967b). Female hierarchies are more stable than those of ♂♂, with daughters occupying ranks near their mothers (Cheney 1983, Lee 1983b). The female dominance hierarchy also influences grooming and coalitionary support during agonistic interactions (Seyfarth 1980).

Young Vervets begin interacting with group members other than their mothers within the first week of life, often through play with other immatures. Time spent playing increases during the first three months of life (Lee 1984), more so in ♂♂ than ♀♀ (Lee 1983c). Males become more socially peripheral as they mature, whereas ♀♀ remain active in social life, maintaining grooming bonds and handling infants of other ♀♀ (Lee 1983a). It is not always apparent that infant handlers are helpers. In most cases infants are handled gently when they are taken from the mother (Lee 1983a); rarely, infants are mistreated (e.g. bitten). Mothers continue to carry their infants for up to one year, but the frequency tapers off after one month (Struhsaker 1971b, Lee 1984). In their first three months infants are carried for 30–100% of the time mothers are moving. By the time infants are four months old they are carried only 1–20% of the time (Whitten 1982).

Vervets produce at least 33 acoustically distinct vocalizations (e.g. 'squeals', 'screams', 'grunts', 'chutters', 'wrrs', 'waas' and 'aarrs') (Struhsaker 1967a). Some (e.g. grunts and 'loud aarr' calls) convey information about the identities of group members and members of other groups (Cheney & Seyfarth 1980, 1982a, b, 1990). Vervets also give different alarm calls to mammalian predators, raptors, snakes and humans (Struhsaker 1967a, Seyfarth *et al.* 1980b). Alarms to Leopards *Panthera pardus* of adult and subadult ♂♂ differ from those of adult ♀♀ and juveniles (Struhsaker 1967a, Seyfarth *et al.* 1980b, Enstam & Isbell 2002). Because Vervets give alarm calls to some species but not others, they effectively categorize species into predators and non-predators. Adults are the most selective, and give alarm calls to their most dangerous predators (Seyfarth *et al.* 1980a). Though infants are able to distinguish between general classes of predators, they are more likely to direct alarm calls at inappropriate stimuli (Seyfarth & Cheney 1980).

Vervets respond differently to different alarm calls (Struhsaker 1967a, Seyfarth *et al.* 1980b). They respond to 'eagle alarms' primarily by looking up and to 'snake alarms' by looking down and approaching the snake (Struhsaker 1967a, Seyfarth *et al.* 1980b, Cheney & Seyfarth 1990, Enstam & Isbell 2002). In areas with tall trees, Vervets respond to 'leopard alarms' primarily by climbing or remaining in trees. In areas with shorter trees, Vervets respond by descending trees, running away and scanning while bipedal (Enstam & Isbell 2002). Vervets also attend to alarm calls of other animals, e.g. Superb Starling *Lamprolornis superbus*, Helmeted Guineafowl *Numida meleagris*, Crowned Lapwing *Vanellus coronatus*, Impala *Aepyceros melampus*, Plains Zebra *Equus quagga*, Common Warthog *Phacochoerus africanus* and Yellow Baboon *Papio cynocephalus* (Struhsaker 1967c, Cheney & Seyfarth 1990). They are mobbed by birds, e.g. Lilac-breasted Roller *Coracias caudata*, Fork-tailed Drongo *Dicrurus adsimilis*, Northern White-crowned



Vervet Monkey *Chlorocebus pygerythrus* adult female.

Shrike *Eurocephalus rueppelli* and Hildebrandt's Starling *Lamprolornis hildebrandti* (Struhsaker 1967c).

Vervet groups do not form polyspecific associations with other primate species, though occasionally they are found in proximity to baboons *Papio* spp., Sykes's Monkeys, Patas and Northern Lesser Galagos *Galago senegalensis*. One exception appears to occur in Ngezi Forest, where preliminary observations suggest that the Zanzibar Red Colobus *Procolobus kirkii* (an introduced species) is frequently, if not almost always, in association with Vervets (T. Butynski & Y. de Jong pers. comm.). Vervets react variably to Yellow Baboons, Olive Baboons *Papio anubis* and Patas, sometimes moving away and other times ignoring them. Juvenile Vervets sometimes play with juvenile Yellow Baboons and Patas (Struhsaker 1967c, L. A. Isbell pers. obs.). Individual Vervets may temporarily, at least, join groups of Yellow Baboons or Patas (Struhsaker 1967c, Enstam & Isbell 2007, L. A. Isbell pers. obs.).

Vervets have no elaborate courtship behaviour. Males and ♀♀ do not form consortships (Andelman 1987). Males are single-mount ejaculators (Struhsaker 1967b) and matings are brief. Female Vervets do not have obvious indicators of reproductive state, other than a willingness to copulate more during some months of the year than others. None the less, ♂♂ initiate copulations most frequently around the period of conception (Andelman 1987), suggesting that ♀♀ provide some cue(s). Vaginal secretions perhaps indicate reproductive state. Males frequently sniff the perineum of ♀♀, and may obtain information about reproductive state in this way. Chest-rubbing (i.e. apparent scent-marking) occurs but perhaps not in all populations (Gartlan & Brain 1968, De Jong & Butynski 2010b, Freeman *et al.* 2012).

Reproduction and Population Structure Vervets are seasonal breeders. In Amboseli ♀♀ copulate from Apr–Oct, but conceptions occur about two months after the onset of mating. Females normally conceive on the first ovulatory cycle of the year (Andelman 1987). Most births (87%) occur in Oct–Dec ($n = 75$; Cheney *et al.* 1988). In Samburu copulations occur in Mar–Jun ($n = 22$); most births (88%) occur in Nov–Dec ($n = 16$; Whitten 1983). Timing of matings and births in Amboseli and Samburu associated with seasonal abundance of flowers, especially those of

Acacia spp. (Whitten 1983, Butynski 1988). At Segera, copulations observed in all months except Jan, Mar and Apr, but most often in Jun–Oct (L. A. Isbell pers. obs.). Over a ten-year period, 30 of 40 births (75%) that could be assigned to a particular month occurred in Jan–Mar. The percentage of births that occurred outside these peak birth months was nearly double (25%) that of Amboseli (13%) (Cheney *et al.* 1988, L. A. Isbell pers. obs.). Segera's less distinct birth seasonality may be related to its less seasonal rainfall (Butynski 1988). Females also copulate during pregnancy (Gartlan 1969, Andelman 1987). Mean length of gestation in captivity is 163.2 days \pm 6.2 S.D. ($n = 38$) (Johnson *et al.* 1973). In the wild, gestation length for one ♀, based on hormonal analyses of urine, was 156–161 days (Andelman *et al.* 1985).

Females give birth to one infant every 1–2 years, depending largely on habitat quality and the survival of preceding infants. In Amboseli, mean inter-birth intervals for ♀♀ in three groups ranged from 13.8 to 21.3 months, with the longer inter-birth interval occurring in a group without access to permanent water (Cheney *et al.* 1988). At birth, infants weigh 300–400 g (Smithers 1971, Nowak 1999). Weaning begins at around three months and is complete by around 18 months, or earlier if the mother reproduces the next year (Whitten 1983). Infants orphaned at six months can survive. The earliest age at first reproduction is ca. 3.5 years (Isbell *et al.* 2009). In Amboseli mean age at first reproduction was earlier (4.4 years) in a group with better access to food and water than in two groups with poorer access (5.1 and 5.7 years) (Cheney *et al.* 1988). At Segera, where water is no longer always available year-round, the mean age at first reproduction was 5.1 years (3.5–6.1) for the three ♀♀ born during the ten-year study that survived long enough to reproduce. The youngest ♀ to reproduce gave birth unusually during the mating season after an extraordinarily wet El Niño event. This female's two subsequent births were also six months off the peak birth season and well into the mating season (L. A. Isbell pers. obs.).

During the mating season ♀♀ mate with multiple ♂♂. High-ranking ♂♂ do not monopolize matings during the most probable week of conception. Females refuse most attempts by ♂♂ to copulate (Andelman 1987). Males can commit infanticide, but incidence appears to vary with habitat structure, costs of dispersal, and corresponding degree of relatedness between immigrants and members of the groups they join. Where Vervets are restricted to linear home-ranges along rivers (e.g. Segera), high costs of dispersal limit movement to one of two adjacent groups and increases genetic relatedness between immigrants and the groups they join. In such groups infanticide is rare, if it occurs at all. In nine years of observation no attempts at infanticide were observed at Segera (Isbell *et al.* 2002). In areas with more dispersal options (e.g. a greater number of adjacent groups in Amboseli), genetic relatedness between immigrants and members of non-natal groups declines, and infanticide is more common. In Amboseli, where each group shared home-range boundaries with up to five other groups, three infants were victims of immigrating ♂♂, at a rate of 0.03 infanticides/100 immigration events (Isbell *et al.* 2002). No data are available for Vervets at Naivasha where genetic relatedness between immigrant ♂♂ and non-natal groups must be lower because groups are limited to only one adult ♂. The rate of infanticide in Green Monkeys *Chlorocebus sabaeus* living in single-male groups in Barbados is 4.5/100 immigration events (Horrocks & Baulu 1988, Isbell *et al.*

2002). Infanticide is normally attributed to intense male–male competition for reproductive success, but there is no *a priori* reason to expect competition to be less intense in multimale groups unless ♂♂ are more closely related to each other.

Sex ratios at birth are biased toward ♂♂. In Amboseli the birth sex ratio of 41 (56%) ♂♂ and 32 (44%) ♀♀ was 1 : 0.8 (Cheney *et al.* 1988). Of 50 unambiguously sexed infants at Segera the birth sex ratio of 31 (62%) ♂♂ and 19 (38%) ♀♀ was 1 : 0.6 (L. A. Isbell pers. obs.). This is not an artefact of easier identification of ♂♂ in the first weeks of life; in fact, ♀♀ were initially sexed incorrectly more often than ♂♂. The sex ratio becomes more biased toward ♀♀ in adulthood. In Amboseli the adult sex ratio per group varied from 1 : 0.8 to 1 : 7.0 ($n = 3$) over five years (Melnick & Pearl 1987, Cheney *et al.* 1988). In Samburu the mean adult sex ratio for two groups was 1 : 1.0 (Melnick & Pearl 1987). On Lolui I. the adult sex ratio was 1 : 1.4 (Hall & Gartlan 1965). At Segera the mean monthly adult sex ratio of two groups was 1 : 1.2 ($n = 101$ months) and 1 : 1.5 ($n = 73$ months) (L. A. Isbell pers. obs.).

At Segera mean annual birth rate was 0.62 offspring/adult ♀ over ten years. Mean annual infant mortality rate for two groups over ten years was 48%; mean annual adult ♀♀ mortality rate over 11 years was 15% (Isbell *et al.* 2009). In Amboseli, 57% of individuals died during their first year, on average. Vervets can live to about 30 years in captivity (Nowak 1999) and to at least 18 years in the wild (Cheney & Seyfarth 1990).

Predators, Parasites and Diseases Predation accounted for at least 69% of all Vervet deaths and only 27% of ♀♀ survived to adulthood in Amboseli (Cheney *et al.* 1988). Such high losses to predators may account for the large percentage of time (30–40%) Vervets devote to scanning the environment ($n = 54$ individuals in six groups) (Isbell & Young 1993a). Similarly, at Segera, at least 7 of 15 adult ♀♀ (47%) died of suspected or confirmed predation (Isbell & Enstam 2002, Isbell *et al.* 2009). Only 16% (3/19) ♀♀ born during the study survived to adulthood (Isbell *et al.* 2009).

Confirmed predators of Vervets include Leopards, African Crowned Eagles *Stephanoaetus coronatus*, Martial Eagles *Polemaetus bellicosus*, Central African Rock Pythons *Python sebae*, Yellow Baboons and Domestic Dogs *Canis familiaris* (Struhsaker 1967c, Cheney *et al.* 1988, Baldellou & Henzi 1992, Isbell & Enstam 2002, T. Butynski pers. comm.). Potential predators include Lions *Panthera leo*, Spotted Hyenas *Crocuta crocuta*, Cheetahs *Acinonyx jubatus* and Black-backed Jackals *Canis mesomelas*, based on alarm calls or greater vigilance of Vervets toward those animals. Though large enough to attack Vervets, African Hawk-eagles *Hieraaetus spilogaster*, Black-chested Snake Eagles *Circaetus pectoralis*, Tawny Eagles *Aquila rapax* and Giant Eagle-owls *Bubo lacteus* are not likely predators, based on their dietary preferences and the indifference of Vervets to those animals. Egyptian Cobras *Naja haje*, Black Mambas *Dendroaspis polylepis* and Puff Adders *Bitis arietans* are not predators but Vervets give alarm calls to them (Struhsaker 1967a, L. A. Isbell pers. obs.) and bites can, undoubtedly, be fatal. Estimated annual predation rates range from 6% in Samburu to 15% in Amboseli (Cheney & Wrangham 1987, Cheney *et al.* 1988). Predation rates occasionally spike. In Amboseli the estimated predation rate was at least 45% in 1987, largely from a brief period of intense predation by Leopards (Isbell 1990). Similarly, brief but intense Leopard

predation over a seven-month period at Segera resulted in the loss of 21 of 28 (75%) study animals (Isbell & Enstam 2002, Isbell *et al.* 2009). Predators depress Vervet populations periodically, even to the extent of decimating local populations. Evidence from carcasses, scratch marks on tree trunks and footprints indicates that Leopard predation often occurs at night while Vervets are in their sleeping trees, and that multiple Vervets can be killed in one night, especially when ♀ Leopards hunt with cubs (Isbell *et al.* 2009). Leopard predation is less likely to occur when humans are nearby (Isbell & Young 1993a).

Vervets sometimes develop an unidentified seasonal malady. In Amboseli, in at least two consecutive years during Nov–Jan, 16 of 51 (34%) adults and subadults, and four of 22 (18%) juveniles, lost hair on their abdomens, knees, elbows and/or inner thighs, and developed hyperpigmentation of the exposed skin. Males also developed scrotal hyperpigmentation (Isbell 1995). Hair loss occurs more rarely at Segera, in May–Jun (L. A. Isbell pers. obs.). In no case has this disease progressed to scrotal bleeding or bursting as observed in Amboseli (Struhsaker 1967c). At Segera, infants may have been more susceptible than adults to respiratory illnesses. Those that died within their first year (n = 17, excluding those dying of predation and after losing the mother) were, on average, born in significantly wetter months (mean 45 mm rainfall) than infants that survived their first year (mean 24 mm rainfall, n = 24) (Isbell *et al.* 2009).

Vervets harbour a variety of viruses, protozoa, bacteria and helminths. Viruses include HTLV-like STLV-1, Papillomavirus SA-12, Spumavirus Simian Foamy Virus, Lentivirus SIV agm, Alphavirus-SFV Complex Chikungunya and Polyomavirus SAV-12. Protozoa include *Babesia macaci* and *Babesia pitheci*. Bacteria include *Salmonella* sp., *Shigella* sp., *Borrelia harveyi*, *Chlamydia* sp., *Leptospira* sp. and *Rickettsia cornorii*. Helminths include *Schistosoma matthei*, *Schistosoma mansoni*, *Cercopithifilaria vervezi*, *Dirofilaria aethiops* and *Enterobius bipapillatus* (Nunn & Altizer 2005). Vervets are implicated, along with Olive Baboons, in Kenya's first recorded outbreak of Yellow Fever among humans in 1992–93 in the Kerio Valley (Reiter *et al.* 1998). The effects of parasites and diseases on Vervet populations are unknown.

Conservation IUCN Category (2012): Least Concern. CITES (2012): Appendix II.

Though Vervets are geographically widespread and can tolerate a wide range of habitats, they are none the less patchily distributed. In the two areas where Vervets were studied for at least ten years (Amboseli and Segera), the Vervet populations suffered severe declines (Cheney *et al.* 1988, Isbell *et al.* 2009). More limited surveys at Kasoje in the Mahale Mts, Tanzania (Uehara & Ihobe 1998) and L. Naivasha (L. A. Isbell pers. obs.) also suggest local declines. In the

latter case the decline is likely the result of human encroachment and habitat destruction along the lake shore. Though it is difficult to determine overall population trends from a few studies of this widespread species, reported declines, combined with the absence of studies reporting increases in numbers of Vervets, suggest that Vervet populations are declining, particularly where habitat change (e.g. tree die-offs, river water depletion and human encroachment) is occurring. The tendency for Vervets to live in small, isolated populations probably makes them particularly susceptible to local extinction. Detailed surveys of the extent of isolation are needed throughout their range.

Measurements

Chlorocebus pygerythrus pygerythrus

HB (♂ ♂): 490 mm, n = 30

HB (♀ ♀): 446 mm, n = 30

T (♂ ♂): 652 (600–750) mm, n = 30

T (♀ ♀): 575 (485–653) mm, n = 30

HF (♂ ♂): 144 (133–170) mm, n = 30

HF (♀ ♀): 125 (115–137) mm, n = 30

E (♂ ♂): 38 (31–42) mm, n = 30

E (♀ ♀): 35 (30–40) mm, n = 30

WT (♂ ♂): 5.5 (3.9–8.0) kg, n = 29

WT (♀ ♀): 4.1 (3.4–5.3) kg, n = 30

N Botswana (Smithers 1971). Range for HB not given.

C. p. hilgerti

HB (♂ ♂): 492 (430–570) mm, n = 4

HB (♀ ♀): 451 (420–515) mm, n = 4

T (♂ ♂): 646 mm, n = 47

T (♀ ♀): 548 mm, n = 61

HF (♂ ♂): 140 mm, n = 35

HF (♀ ♀): 120 mm, n = 48

E (♂ ♂): 27, 33 mm, n = 2

E (♀ ♀): 30 (25–33) mm, n = 4

WT (♂ ♂): 4.2 kg, n = 48

WT (♀ ♀): 2.7 kg, n = 61

Various localities

T, HF, WT: Samburu, Mosiro and Kimana (Anapol *et al.* 2005); range not given.

HB and E: compiled by T. Butynski from Heller (1913) and Hill (1966)

Key References Cheney & Seyfarth 1990; Gartlan 1969; Isbell *et al.* 2002, 2009; Struhsaker 1967b, c.

Lynne A. Isbell & Karin L. Enstam Jaffe

Chlorocebus cynosuros MALBROUCK MONKEY

Fr. Malbrouck; Ger. Malbrouck-Grünmeerkatze

Chlorocebus cynosuros (Scopoli, 1786). *Deliciae Faunae et Florae Insubricae* 1: 44, pl. 19. No locality, but fixed at Banana, right bank lower Congo R., DR Congo, by Schwarz (1926).



Malbrouck Monkey *Chlorocebus cynosuros* adult male.

Taxonomy Monotypic species. Classically considered as a subspecies of the *Cercopithecus (aethiops)* Group or Superspecies (Schwarz 1926, Hill 1966, Thorington & Groves 1971, Dandelot 1974, Napier 1981, Lervold 1988). A recent revision by Groves (2001) elevated and reassigned the savanna monkeys to *Chlorocebus* and gave species status to most of the subspecies, including *C. cynosuros*. Unfortunately, a planned alpha taxonomy of the group was left uncompleted (Grubb *et al.* 2003). Given the extensive overlap of characters used to distinguish the different types (i.e. species and subspecies; Napier 1981), neither the specific validity of *C. cynosuros* nor the varieties contained within the species of *Chlorocebus* are certain. Grades imperceptibly into the Vervet *Chlorocebus pygerythrus* at the north-eastern, eastern and south-eastern ends of distribution (Schwarz 1926, Smithers 1971, Ansell 1978, Napier 1981, E. E. Sarmiento pers. obs). No obvious biogeographic barrier exists between *C. pygerythrus* and *C. cynosuros*.

Classification of *C. cynosuros* is therefore problematic (Ansell 1978) and little agreement exists as to whether some varieties are subspecies of *C. pygerythrus* or synonyms of either species (Ellerman *et al.* 1953, Hill 1966, Dandelot 1974, Ansell, 1978). The last author considered all animals in Zambia (except those east of the upper Zambezi R. in extreme SW Zambia) to be *C. cynosuros*, but there is no proven continuity between the W Angolan animals and those in Zambia.

In regard to species, if a cline is geographically narrow with relatively few animals participating in the clinal interzone then, in the here and now, the populations at either end can be regarded as true species (species can be defined only in narrow time horizons). On the other hand, if the cline is geographically wide with more animals in the interzone than exist at either end of the cline, then, in the here and now, the entire population can more realistically be treated as a single species. In the past it may have been different and in the future it will

no doubt differ yet again, but in the present the status of populations, especially within this section of the *Chlorocebus* complex, remains uncertain. We need to recognize that many blanks in knowledge will need to be filled in before the decision as to what is or what is not a species can be asserted with any confidence. In this case most of the data for making such a decision are in Angola waiting to be tapped. For the sake of both simplicity and convenience, *C. cynosuros* is tentatively treated here as a monotypic species, although given its extensive range it probably contains more than one variety.

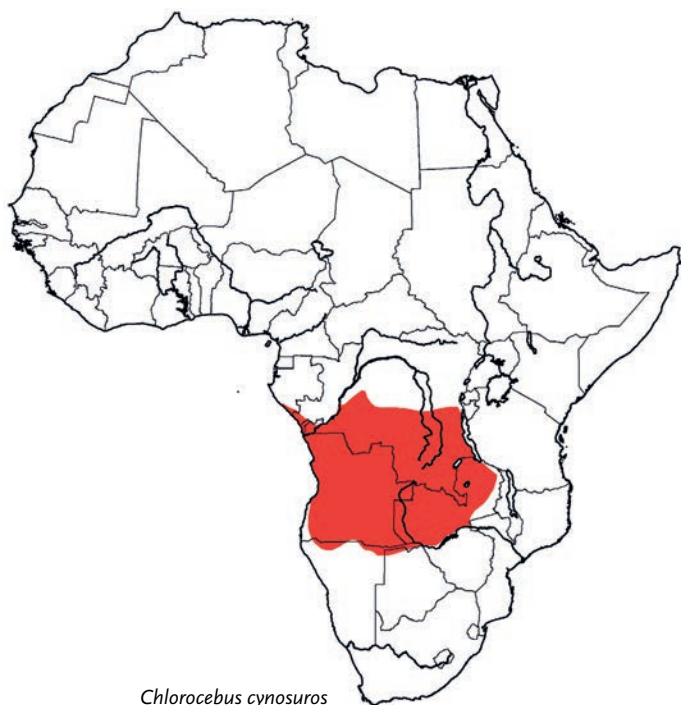
It is a little suspicious that *C. cynosuros* occurs on both sides of the lower Congo R., supposedly with animals from both sides being indistinguishable (Schwarz 1926). Given that this river is a formidable biogeographic barrier for so many primate species, human transportation of these animals as pets must be considered as a distinct probability (Van der Kuyl *et al.* 1996). In yet another complication, the type of *C. cynosuros* may not have come from Banana, on the right bank of the Congo R. The type locality was fixed as such because *cynosuros* is supposedly similar to *weynsi* from Banana (Matschie 1912).

This has resulted in a highly atypical distribution that further confounds our efforts to classify *cynosuros* to species or subspecies. To complicate matters still further, many *C. cynosuros* diagnostic characters (i.e. facial skin, ischial callosity and genital colour) can only be clearly documented in living animals and not in the museum specimens that most taxonomies are based on (Dandelot 1959).

Note that the species name applied to the Malbrouck is misspelled '*cynosurus*' in some taxonomic works. The name that Scopoli (1786) provides is '*cynosuros*'.

Synonyms: *cynosurus*, *katangensis*, *lukonzolwae*, *tholloni*, *weynsi*. Chromosome number: $2n = 60$? All savanna monkeys karyotyped from East, West and southern Africa show a diploid number of 60 chromosomes (Dutrillaux *et al.* 1988b). Although the chromosome number for *C. cynosuros* is unknown, the chances are it shares this number with other *Chlorocebus* species.

Description Medium-sized, semi-terrestrial, olive-buff monkey with flesh-coloured facial skin, often splotched and darker on nose and ears. Sexes similar in appearance but adult ♀ smaller, being ca. 70% weight of adult ♂. Lips and chin with short white hairs. Frontal (brow) band white with some interspersed black hairs delimited below by a thin line of long stiff black hairs. Cheek-whiskers short, white, sweep backwards and upwards but not covering ears. Whiskers progressively darken around temple blending in colour with hair on crown. Ears naked, brown and lack tufts. Jowls and throat largely white. Dorsum of head, neck and body covered in yellow-tipped black-banded grey hairs, producing a dark olive-buff with varying brown to yellow highlights. Ventrums and inner limbs light grey to dirty white. Outer limbs, hands and feet with white-tipped grey hairs that produce a grey wash. Tail dorsum mottled grey and black. Dorsum of tail tip dark grey to black with a greater proportion of



Chlorocebus cynosuros

fully black hairs than remainder of tail. Tail underside light grey to dirty white with reddish tuft of hair at base. Ischial callosities flesh-coloured or pallid pink. Scrotum described as slate-blue (Elliot 1913b), lapis lazuli blue (Dandelot 1974) or violet (Schwarz 1926), presumably contrasting with the turquoise blue of other *Chlorocebus* spp. Exposed skin (i.e. facial, plantar, palmar, genital) is pink. Newborn infants have soft dark-brown pelage. Infants with complete milk dentition already show adult colour pattern.

Geographic Variation Newborn infants in Angola with light grey pelage while those in Zambia have dark brown pelage. Otherwise, *C. cynosuros* requires study to determine if patterns in geographic variation exist (see Taxonomy).

Similar Species To the east, *C. pygerythrus rufoviridis* in Malawi and Tete Province, Mozambique, are in all respects indistinguishable from animals in Zambia that Ansell (1978) classified as *C. cynosuros*. As such, there is disagreement as to where *C. cynosuros* ends and *C. pygerythrus* begins, and to which of the two species synonyms should be referred (Ellerman *et al.* 1953, Hill 1966, Dandelot 1974, Ansell, 1978, Groves 2001). *C. pygerythrus* has black skin on face, palms and soles, grey ischial callosities, and turquoise blue scrotum.

Distribution Endemic to Africa south of Equator, north of Tropic of Capricorn, west of Luangwa R., and north of Zambezi R. Southern Rainforest-Savanna Mosaic and Zambezian Woodland BZs. Distribution poorly known but believed to occur across Africa west of the Rift Valleys between the Congo Basin forests, DR Congo, in the north, and Zambezi R., Zambia, and lower Cunene R., Angola, in south. In north-west (ca. 12° E) in savannas and at the edge of grasslands as far north as Banana, just north of Congo R. (i.e. right bank) at 06° S. Eastwards, right bank of Congo R., reaches Brazzaville at 04° 15' S (Matschie 1912, E. E. Sarmiento pers. obs.). In central Africa, reaches northwards slightly past 02° S on eastern

and western shores of L. Mai-Ndombe (L. Leopold in Schouteden 1944a). Northern extent probably limited by Lukeka R. at ca. 06° S. Eastern limit supposedly L. Tanganyika (ca. 30° W) and the Malawi Highlands (ca. 33° W) but, as discussed above, species allocations are far from secure in this region. Unlikely to extend north-eastwards into Tanzania between L. Tanganyika and Malawi. Animals from close to border in Mbeya and Sumbawanga Districts, Tanzania, are unequivocally of *C. pygerythrus* appearance (see Swynnerton & Hayman 1951 and colour plate illustrating *C. pygerythrus*). Eastwards towards W Malawi and Tete Province Mozambique, *C. cynosuros* and *C. p. rufoviridis* are more or less indistinguishable (Schwarz 1926, Ansell & Dowsett 1988). Authors differ as to which biogeographic barriers separate the two species (Hill 1966, Dandelot 1974, Ansell 1978, Groves 2001). Southern limit appears to be the Zambezi R. and L. Kariba (Ansell 1978) at 16–18° S, although this is not certain (Hill 1966). Towards the west, along the Cunene R., Okavango R. and Caprivi Strip, *C. cynosuros* supposedly comes into contact with *C. p. helveticus* (Smithers 1971). Here the aridity of the Etosha Plains and the Kalahari Desert prevent southward movement of *C. cynosuros*.

Within its geographic range, *C. cynosuros* absent from Lukulu and Zambezi Districts of W Zambia and from montane areas (Ansell 1978). Poorly known from Angola, especially the eastern half (from where no museum specimens have been collected). In summary, the distribution of *C. cynosuros* extends deep into S DR Congo, Angola, Zambia and depending on authors or diagnosis, into W Malawi, W Mozambique, N Botswana, N Namibia and N Zimbabwe.

Habitat Woodlands and riparian forests running through savanna, grassland and scrub. Always close to year-round water sources. Usually at sites that lack other guenon competitors. Appears to prefer edge, utilizing trees or large shrubs for sleeping and shelter, and more open areas for foraging. A large part of the geographic range includes miombo woodlands (*Brachystegia* spp., *Julbernardia* spp. and *Isoblerina* spp.) and mopane woodlands (*Colophospermum mopane*) between 500–1000 m. Also in areas from near sea level (4 m) at mouth of Congo R. to 1400–1600 m on Angolan Plateau, NE Zambia. To 1850 m in Upemba N. P., DR Congo. If the savanna monkey on the Nyika Plateau, Malawi, is *C. cynosuros* (Ansell 1978), then this species occurs to at least 1950 m. Mean annual rainfall in *C. cynosuros* habitat varies from 1750 mm near the equator to ca. 450 mm along the Namibia–Angola border. Over most of the range there is one long dry season with little or no rain during Jun–Sep. Temperatures are generally between 18 and 24° C year-round and even at the highest altitudes never dip below freezing, reaching lows of only 5° C.

Abundance No data on population density. Avoidance of montane areas and affinity for water-courses suggests that *C. cynosuros* is much less common in the hilly country west of L. Tanganyika than in Katanga, DR Congo (Frechkop 1954) or on the plains of Zambia. Absence of *C. cynosuros* museum specimens from N and E Angola (Seabra 1908, Hill & Carter 1941, Machado 1969) probably reflects their relatively low abundance in these regions. *C. cynosuros* avoids areas with other (competing) guenons and may show high density in human-modified environments that provide sleeping sites, water and food, especially cultivated areas.

Adaptations Diurnal and semi-terrestrial. An opportunistic forager capable of moving long distances on the ground in search of food and water. Uses trees and shrubs as sleeping sites and for protection, but most food gathering is linked to ground movement. On the whole, adaptations and life-style, including a markedly varied diet, allow for exploitation of undependable and widely varying food sources in areas with long dry seasons and seasonal flooding.

Foraging and Food Omnivorous. Diet not systematically studied. Information presented here is based largely on the author's observation in Zambia and Angola, including reports by local people and the examination of stomach contents from museum specimens. Preferentially a frugivore, *C. cynosuros* eats the fruit of the Sugar Plum *Uapaca kirkiana*, Buffalo-thorn *Ziziphus mucronata*, African Ebony (or Monkey-guava) *Diospyros mespiliformes*, Marula Plum *Sclerocarya birrea* and various figs *Ficus* spp. Shoots and stems of *Euphorbia* spp. and gum, seeds and seed pods of *Acacia* spp. also eaten. Commonly raids maize, sorghum and fruit orchards, although typically much less destructive than baboons *Papio* spp. Stomach contents in museum specimens usually show fruit and some vegetative material, and sometimes a high proportion of locusts and termites. Consumption of small vertebrates, eggs and tubers have not been verified for *C. cynosuros*, although this is likely.

Chlorocebus cynosuros, like other savanna monkeys, is diurnal and forages in large multimale/multifemale groups. Smallest groups include one adult ♂, one adult ♀ and immatures, or can be composed solely of ♂♂. Movement between food sources is generally on the ground. Feeding begins at daybreak with movement of animals towards food sources and ends at sunset with movement to sleeping sites. Reported to move nearly 18 km overnight (Brain 1965).

Social and Reproductive Behaviour Social. No systematic studies conducted on *C. cynosuros*. Social and reproductive behaviour expected to be similar to other members of the *C. (aethiops)* Group. *Chlorocebus cynosuros* is territorial and has a flexible social system. Territories are defended by all members of the group except the youngest individuals. Inter-group interactions may be friendly with temporary merging of groups, or antagonistic ending in fights. Uses vocalizations, facial expressions and body postures to communicate. 'Splaylegged' displays exhibiting adult ♂ genitals warn ♂ members of encroaching groups. Alarm calls warn group members of predators. Grooming, agonistic behaviours and social play are all part of this species' intra-group interactions (E. E. Sarmiento pers. obs.).

Reproduction and Population Structure Little studied. Not clear if *C. cynosuros*, like other *Chlorocebus* spp., is a seasonal breeder, museum records indicate most offspring are born Aug–Oct in the middle of the dry season (Frechkop 1954, E. E. Sarmiento pers. obs.). Given a 5.5 month gestation (Eley *et al.* 1989b), most conceptions occur in Mar–Apr at the end of the rainy season. One infant is born, weighing ca. 400 g ($n = 2$). All ♀♀ in the group may partake in the care of each other's infants (E. E. Sarmiento pers. obs.).



Malbrouck Monkey *Chlorocebus cynosuros* adult male.

Predators, Parasites and Diseases Hunted in Angola and Zambia as a pest and often eaten when captured. Infants and young juveniles often kept as pets. Humans, Yellow Baboons *Papio cynocephalus kindae* and Domestic Dogs *Canis familiaris* are documented predators of *C. cynosuros*. Lions *Panthera leo*, Leopards *Panthera pardus*, Cheetahs *Acinonyx jubatus*, Servals *Felis serval*, Caracals *Lynx caracal*, Brown Hyenas *Hyaena brunnea*, Spotted Hyenas *Crocuta crocuta*, Black-backed Jackals *Canis mesomelas*, Martial Eagles *Polemaetus bellicosus*, African Crowned Eagles *Stephanoaetus coronatus*, pythons *Python* spp. and Nile Crocodiles *Crocodylus niloticus* likely prey on *C. cynosuros*.

Conservation IUCN Category (2012): Least Concern. CITES (2012): Appendix II.

A crop pest in some areas. *Chlorocebus cynosuros* populations probably increasing and expanding along with human cultivation, the related increase in water availability and the reduction of competing guenon species.

Measurements

Chlorocebus cynosuros

HB ♂♂: 496 ± 60.7 (342–697) mm, $n = 81$

HB ♀♀: 440 ± 35.8 (379–540) mm, $n = 92$

T ♂♂: 643 ± 59.1 (440–785) mm, $n = 82$

T ♀♀: 570 ± 44.9 (460–742) mm, $n = 94$

HF ♂♂: 141 ± 12.1 (89–178) mm, $n = 85$

HF ♀♀: 125 ± 11.8 (95–183) mm, $n = 94$

E ♂♂: 36 ± 4.8 (25–46) mm, $n = 83$

E ♀♀: 34 ± 3.4 mm, 20–40 mm, $n = 91$

WT ♂♂: 5.4 ± 0.87 (5.4–7.4) kg, $n = 80$

WT ♀♀: 3.7 ± 0.68 (2.0–5.1) kg, $n = 88$

Various localities. Field-collected animals in AMNH, USNM, MCZ, RMCA, NMZB, TM, AM

Key References Brain 1965; Hill 1966; Schwarz 1926.

Esteban E. Sarmiento

Chlorocebus djamdjamensis DJAM-DJAM MONKEY (BALE MONKEY)

Fr. Cercopithèque du Balé; Ger. Bale-Grünmeerkatze

Chlorocebus djamdjamensis (Neumann, 1902). Sitzb. Ges. Naturf. Fr. Berlin, p. 51. Bamboo forest at 3300 m near Abera, east of L. Abaya, Ethiopia.



Djam-djam Monkey *Chlorocebus djamdjamensis* adult male.

Taxonomy Monotypic species. Member of the Savanna Monkeys Group *Chlorocebus (aethiops)*. Djam-djam was initially given the status of a species by Neumann (1902) based on one study skin and an incomplete description. This designation was accepted by Pocock (1907) and Elliot (1913b). Subsequently, however, this taxon was variously treated as a synonym of Matschie's Grivet *Chlorocebus aethiops matschiei*, Ellenbeck's Vervet *Chlorocebus pygerythrus ellenbecki* and Hilgert's Vervet *Chlorocebus pygerythrus hilgerti* (Schwarz 1926, de Beaux 1943, Dandelot 1959, Hill 1966, Yalden *et al.* 1977, Groves 2001, Grubb *et al.* 2003), all three subspecies of which were also described by Neumann (1902) at the time he described *C. djamdjamensis*.

On the basis of seven additional specimens from three new localities, Dandelot & Prévost (1972) redescribed *djamdjamensis* and resurrected *C. a. djamdjamensis*. This taxonomy was widely accepted (e.g. Lernoùld 1988). Yalden *et al.* (1996) and Kingdon (1997) independently resurrected *djamdjamensis* to species rank. This taxonomy was followed by Groves (2001, 2005c), but not by Grubb *et al.* (2003). Although *C. djamdjamensis* has phenotypic characters of *C. aethiops*, it is distinctly different (Dandelot & Prévost 1972, Yalden *et al.* 1996, Kingdon 1997, Groves 2001, J.-M. Lernoùld pers. comm., T. Butynski pers. obs.). Photographs of *C. djamdjamensis* are presented in Dandelot & Prévost (1972), Carpaneto & Gippoliti (1994), Rowe (1996) and Yalden *et al.* (1996). Kingdon (1997: 62) suggests that, since *C. djamdjamensis* is so distinctive, 'it seems likely that it is the montane relict of an older regional population belonging to the earliest dispersal of savanna monkeys'.

Synonyms: none. Chromosome number: $2n = 60$? Chromosome number not known, but diploid number likely 60 as for all other *Chlorocebus* spp. for which the karyotype has been studied (Dutrillaux *et al.* 1988b, Romagno 2001).

Description Medium-sized, short-tailed, grizzled-brown, semi-terrestrial monkey of bamboo forest on the Bale Massif, SC Ethiopia. Adult ♂ like adult ♀ but larger. Pelage long and woolly. Face below

eyes covered with short black hairs. Brow and broad (temple) band from eyes to ears, black. Brow sometimes with faint white line. Cheek-whiskers short, dense and white. Moustache white, narrow, variable, from well-defined to diffuse and nearly absent. Beard short, bushy, white. Ears black and exposed. Sides of neck and throat to chest white. Neck and shoulder pelage long and thick, almost forming a mane. Crown, shoulders, back and front of thighs with long, thick, grizzled dark brown to yellowish-brown pelage. Upper half of arms, and upper half of legs, brown to dark grey. Lower limbs greyish. Hands and feet dark grey or blackish-brown. Ventrums white, creamy-white, or off-white sometimes mixed with grey on chest. Upper tail dark grey to blackish-brown. Underside of tail pale grey. Base of tail with inconspicuous red-brown tufts at base (Kingdon 1997). Tail tip black with tuft nearly absent. Tail held out straight behind body when moving. Tail noticeably short, being much shorter than HB (Pocock 1907). This is also the observation in the field (T. Butynski pers. obs.) and of a live captive individual (J.-M. Lernoùld pers. comm.), but three adult ♀♀ obtained from the north-west extreme of the geographic range have tails that are slightly longer than HB (see Measurements; Dandelot & Prévost 1972). Relative to HB, *C. djamdjamensis* may have the shortest tail of any guenon. Scrotum blue.

Geographic Variation None recorded.

Similar Species Not reported to be sympatric with any other guenon, including *Chlorocebus* spp.

Chlorocebus aethiops. Parapatric to the north-west and west. Temples and brow-band white. Whiskers long and sickle-shaped. Distinct white moustache. Tail long, tipped white. White tuft under and to sides of base of tail.

Chlorocebus pygerythrus. Parapatric to the north-east, east and south (J.-M. Lernoùld pers. comm.). Temples and brow-band white. No white moustache. Tail long. Red patch under base of tail in adult ♂♂.

Distribution Endemic to the bamboo zone of the Bale Massif and other areas in the Southern Ethiopian Highlands, SC Ethiopia. The Bale Massif covers an area of ca. 5550 km². Afro-montane–Afroalpine BZ. Known from eight localities, but about 60% of the potential range has never been surveyed (Mekonnen *et al.* 2010b). The known extremes of the range are as follows: east (Odobullu): 06° 52' N, 40° 10' E; south and south-west (Abera): 06° 27' N, 38° 28' E; west (Wando = Wendo = Wondo = Uondo): 06° 37' N, 38° 24' E; north (ca. 25 km south-east of Goba): 06° 57' N, 40° 10' E; A. Mekonnen pers. comm.) Distance across the range from west to east is ca. 210 km. Distance across the range from north to south is ca. 55 km. Extent of occurrence ca. 8000 km². Since much of this area lacks bamboo, *C. djamdjamensis* probably occupies but a small portion of this 8000 km² area.

*Chlorocebus djamdjamensis*

Habitat Bamboo forest with scattered large trees on the Bale Massif. About 21% (15 km²) of the Odobullu Forest (71 km², 06° 50' – 06° 56' N; 40° 07' – 40° 12' E, 2250–3020 m) is Mountain Bamboo *Sinarundinaria alpina* forest. Of 43 encounters with groups of *C. djamdjamensis* in Odobullu Forest, all were within bamboo forest (Mekonnen *et al.* 2010b). The larger species of trees here include *Hagenia abyssinica*, *Dombeya torrida*, *Schefflera volkensii*, *Schefflera abyssinica* and *Manilkara butugi* (A. Mekonnen pers. comm.). Species richness for plants >2 m tall in the home-ranges of two study groups here was poor, comprising *S. alpina*, 13 tree species, 1 shrub, 5 liana, 1 epiphyte and 2 herbs within the vegetation quadrats. *Sinarundinaria alpina* accounted for 90% of the total stems (Mekonnen *et al.* 2010a).

At another site where *C. djamdjamensis* is present, Katcha (2400 m in Harenna Forest on the south slope of the Bale Massif), the dominant plant is 7–10 m tall *S. alpina*. The most common large trees here are *S. abyssinica* and *H. abyssinica*. Also present: Giant St John's Wort *Hypericum revolutum*, Croton *Croton macrostachyus*, Red Stinkwood *Prunus africana*, Pillar Wood *Cassipourea malosana*, *Lepidotrichilia volkensii*, *Erica* spp., *D. torrida*, *Galiniera saxifraga*, *Rhamnus prinoides*, *Maytenus* sp. and *Lobelia* sp. The ground cover in open areas is dense and includes *Rubus* sp., *Discopodium penninervium*, *Urera hypselodendron*, *Impatiens* spp., *Plectranthus* spp. and *Bothriocline* sp. There is an extremely heavy cover of moss, ferns and other epiphytes on the larger trees, especially on *S. abyssinica* (Carpaneto & Gippoliti 1994, T. Butynski pers. obs.). In Harenna Forest, as in Odobullu Forest, *C. djamdjamensis* confined to areas of tall (6–10 m) bamboo, often where there are scattered, large, trees (e.g. *S. abyssinica*, *H. abyssinica*, *D. torrida*). Here, *C. djamdjamensis* present from 2200–3400 m (Wakjira *et al.* 2011). *Chlorocebus djamdjamensis* not known to occur anywhere below 2200 m as bamboo is short (<6 m) or absent below this altitude. Known upper altitudinal limit is 3400 m as this is the upper limit of the treeline (Mekonnen

et al. 2012). Mean annual rainfall limits over the range of *C. djamdjamensis* ca. 1300–1800 mm. Wet season is Mar–Oct and dry season is Nov–Feb. During much of the wet season the Bale Massif is covered by a thick fog (Mekonnen *et al.* 2010b, A. Mekonnen pers. comm.).

Guerezas *Colobus guereza* are common in Harenna Forest and in Odobullu Forest. Olive Baboons *Papio anubis* are also present here along the roads and in the vicinity of agriculture (Carpaneto & Gippoliti 1994, A. Mekonnen pers. comm., T. Butynski pers. obs.). No other non-human primates are present.

Abundance Harenna Forest appears to be one of two strongholds for *C. djamdjamensis* (Hillman 1986). None the less, *C. djamdjamensis* is uncommon here. Two observers, working alone, each encountered *C. djamdjamensis* but once during 2.5 days of field surveys in 2003 (Q. Luke & T. Butynski pers. obs.). In Harenna Forest, based on 79 km of foot surveys, there are roughly 1437 (S.E. = 1315) *C. djamdjamensis* (ca 9.6 ind/km² [S.E. = 8.8] in ca. 149 km² of suitable habitat; Wakjira *et al.* 2011). Mekonnen *et al.* (2010b) conducted 280 km of foot surveys in Odobullu Forest, of which 76.8 km were in bamboo forest. Whereas they encountered no groups of *C. djamdjamensis* in grassland, bushland, forest and tree-dominated habitats, they encountered 43 groups within bamboo forest (0.58 groups/km ± 0.08). Within bamboo forest there were ca. 7.0 groups/km² and ca. 132 ind/km². The estimated total number of *C. djamdjamensis* in Odobullu Forest is 1700–2000.

Adaptations Diurnal and arboreal. Whereas the other five species of savanna monkeys are generalists, *C. djamdjamensis* is a bamboo forest specialist (Mekonnen *et al.* 2010a). As noted by T. Butynski (pers. obs.), where one or more *Cercopithecus* spp. are present, *Chlorocebus* do not enter the forest and barely even make use of the forest edge (e.g. along the lower Tana R., Kenya, where *C. p. hilgerti* is present in woodlands and Pousargues's White-collared Monkey *Cercopithecus mitis albitorquatus* is confined to gallery forest). However, *Chlorocebus* is found well within forest in the absence of any species of *Cercopithecus* (e.g. the Pemba Island Vervet *Chlorocebus pygerythrus nesiotes* on Pemba I., Tanzania, and Common Grivet *Chlorocebus aethiops aethiops* in Eritrea). Utilization of forest habitats by *Chlorocebus* in the absence of *Cercopithecus* appears to be a good example of 'competitive release'. T. Butynski (pers. obs.) is of the opinion that *C. djamdjamensis* in the highlands of Ethiopia represents another such case of competitive release where, in the absence of *Cercopithecus* (perhaps especially the Gentle Monkey *Cercopithecus mitis*), a *Chlorocebus* sp. has been able to adapt to at least the more open, lower stature, forest habitat that the mix of large bamboo and trees offers.

Data from the study of two groups of *C. djamdjamensis* in Odobullu Forest yielded the following diurnal activity budget over an 8-month period: feeding (66%), moving (14%), resting (11%), social (7%), other behaviours (2%) (n = 11,393 scans; Mekonnen *et al.* 2010a).

Unlike other *Chlorocebus* spp., *C. djamdjamensis* rarely comes to the ground. *Chlorocebus djamdjamensis* moves into large trees during periods of rain and to sleep at night (A. Mekonnen pers. comm.). This is an alert, cryptic and relatively quiet monkey that is difficult to detect and observe in its typical bamboo forest habitat.

Foraging and Food Omnivorous ('bambooivore'). T. Butynski (pers. obs.) encountered one group at Kacha (2400 m). The members of this group were foraging in thick bamboo (with a dense herbaceous ground cover) at ca. 4 m above the ground. They were breaking down newly sprouted ca. 4 m tall bamboo and eating the pith from the top ca. 1.5 m. At Kacha it is fairly common to find small piles of young bamboo leaves and pith. These piles, which represent *C. djamdjamensis* feeding sites, appear identical to the piles that Golden Monkeys *Cercopithecus mitis kandti* make while feeding on bamboo shoots in the Virunga Mts, SW Uganda.

The diet of two *C. djamdjamensis* groups at Odobullu Forest comprised young leaves (80%), fruits (10%), flowers (3%), animals (2%), shoots (2%), stems (1%), mature leaves (1%) and roots (1%) (n = 7223 items). Only 11 plant species were eaten, with the top five accounting for 94% of the diet. *Sinarundinaria alpina*, provided 77% of the food items, with 95% of these being young leaves. Other important food plants were *Psychotria orohila* (11% of food items) and *D. torrida* (3%; Mekonnen *et al.* 2010a). Foraging for young leaves of bamboo occurred to a height of 8 m, while the highest food items (flowers of *D. torrida* and leaves of *U. hypselodendron*) were up to 25 m (A. Mekonnen pers. comm.). See Wakjira *et al.* (2011) for a preliminary list of foods eaten in Harenna Forest.

The two focal groups at Odobullu Forest had home-ranges (during 8 months of study) of 12.3 ha and 18.1 ha. These groups were adjacent to one another but exhibited only 3–4% home-range overlap. Mean daily distance moved was 898 m (724–1207, n = 13 days) and 956 m (759–1288, n = 25 days; Mekonnen *et al.* 2010a).

Social and Reproductive Behaviour Social. One group at Kacha was comprised of at least two young juveniles, three juveniles and three adult ♀♀ (T. Butynski pers. obs.). At this same site, a group of about nine individuals was observed in 1986 (Yalden *et al.* 1996). In one study in Odobullu Forest, group size counts during surveys ranged from 13 to 41 (mean 19.1 ± 5.43 , n = 41; Mekonnen *et al.* 2010a, b). However, two research groups at this site comprised 46–50 and 55–60 individuals. In another study, group size counts during surveys ranged from 9–29 (mean 19.5 ± 4.5 , n = 37; Mekonnen *et al.* 2012). Solitary individuals occur. Most groups have at least two adult ♂♂. One group had no fewer than three adult ♂♂ (A. Mekonnen pers. comm.). Vocalizations include warning 'chirps', long 'screeches' and 'wavering growls'. All three of these vocalizations sound similar to those given by *C. pygerythrus* and *C. mitis* (T. Butynski pers. obs.). A. Mekonnen (pers. comm.) believes that the vocal repertoire of *C. djamdjamensis* does not differ from that of *C. aethiops*. *C. djamdjamensis* and *C. guereza* form polyspecific associations in areas where large trees are present within bamboo (Carpeneto & Gippoliti 1994, Mekonnen *et al.* 2012). Such associations are, however, uncommon (A. Mekonnen pers. comm.).

Reproduction and Population Structure Not studied. Apparently only one infant born at a time. Twins not observed (A. Mekonnen pers. comm.).

Predators, Parasites and Diseases No observations of predation or disease. Both African Crowned Eagles *Stephanoaetus coronatus* and Leopards *Panthera pardus* are present over the range of *C.*



Frontal portrait of Djam-Djam Monkey *Chlorocebus djamdjamensis* adult male.

djamdjamensis. They are probably the two most important predators of this species.

Conservation IUCN Category (2012): Vulnerable. CITES (2012): Appendix II.

Chlorocebus djamdjamensis lives in a region of great biogeographic importance where many other species of plants and animals are also threatened. Most notable among these are the two 'Endangered' flagship species of the Bale Massif; Mountain Nyala *Tragelaphus buxtoni* and Ethiopian Wolf *Canis simensis*. The main threat to *C. djamdjamensis* in Odobullu Forest is habitat loss and degradation as a result of the collection of bamboo for local consumption (Mekonnen *et al.* 2010a, b, 2012). Harenna Forest, although within the Bale Mountains N. P., is under threat from an expanding human population, fire, agriculture, including livestock grazing, and the taking of forest products such as bamboo, lumber, fuelwood and charcoal (Oates 1996a, Wakjira *et al.* 2011, T. Butynski & A. Atickem pers. obs.). More than 8000 households (ca. 55,000 people) are located within the Bale Mountains N. P. (Flintan 2005). The human population in this region is growing at the rapid rate of 3.1% per year (WWF 2001).

Hybridization may be a threat as forest clearance for agriculture at the lower levels of montane forest presumably brings *C. aethiops* and *C. pygerythrus* closer to the range of *C. djamdjamensis* (Kingdon 1997). Apparent hybrids recently reported at three sites (Mekonnen *et al.* 2012, J.-M. Lernoould pers. comm.). Another result of the loss of habitat and proximity of people is that crop raiding by *C. djamdjamensis* is now common, with *C. djamdjamensis* being hunted at many sites (Mekonnen *et al.* 2012).

The African Buffalo *Syncerus caffer* and the Savanna Elephant *Loxodonta africana* have been extirpated from the Bale Massif. The loss of the two largest herbivores must have had a significant impact

on the ecology of this ecosystem, perhaps resulting in a far more closed bamboo forest and fewer and smaller short-grass glades. The impact on *C. djamdjamensis* is likely to have been significant, but remains unknown. Haremma Forest, with the adjacent Forest Priority Areas, encompasses an area of >4000 km², making this the second largest forest in Ethiopia (Williams 2002). Top priorities for the conservation of *C. djamdjamensis* are (1) to survey this region to determine the distribution and abundance of *C. djamdjamensis* and (2) to provide improved management and protection to those areas where this species occurs, especially Haremma Forest and Odobullu Forest.

Measurements

Chlorocebus djamdjamensis

HB (♀ ♀): 442 (430–455) mm, n = 3

T (♀ ♀): 488 (470–505) mm, n = 3

HF (♀ ♀): 121 (117–125) mm, n = 3

E (♀ ♀): 32 (30–33) mm, n = 3

WT (♀ ♀): 3.4 (3.0–3.6) kg, n = 3

GLS (♀ ♀): 91 (87–96) mm, n = 3

GWS (♀ ♀): 63 (61–65) mm, n = 3

Two specimens from 18 km west-south-west of Koffolé and one from the road between Koffolé and Goba (Dandelot & Prévost 1972)

Key References Dandelot & Prévost 1972; Mekonnen *et al.* 2010a, b, 2012; Yalden *et al.* 1996.

Thomas M. Butynski, Anagaw Atickem & Yvonne A. de Jong

GENUS *Allochrocebus*

Mountain Monkeys

Allochrocebus Elliot, 1913. Review of the Primates 1: xl, 2: 296.



L'Hoest's Monkey *Allochrocebus lhoesti*
adult male.



Preuss's Monkey *Allochrocebus preussi*
adult male.

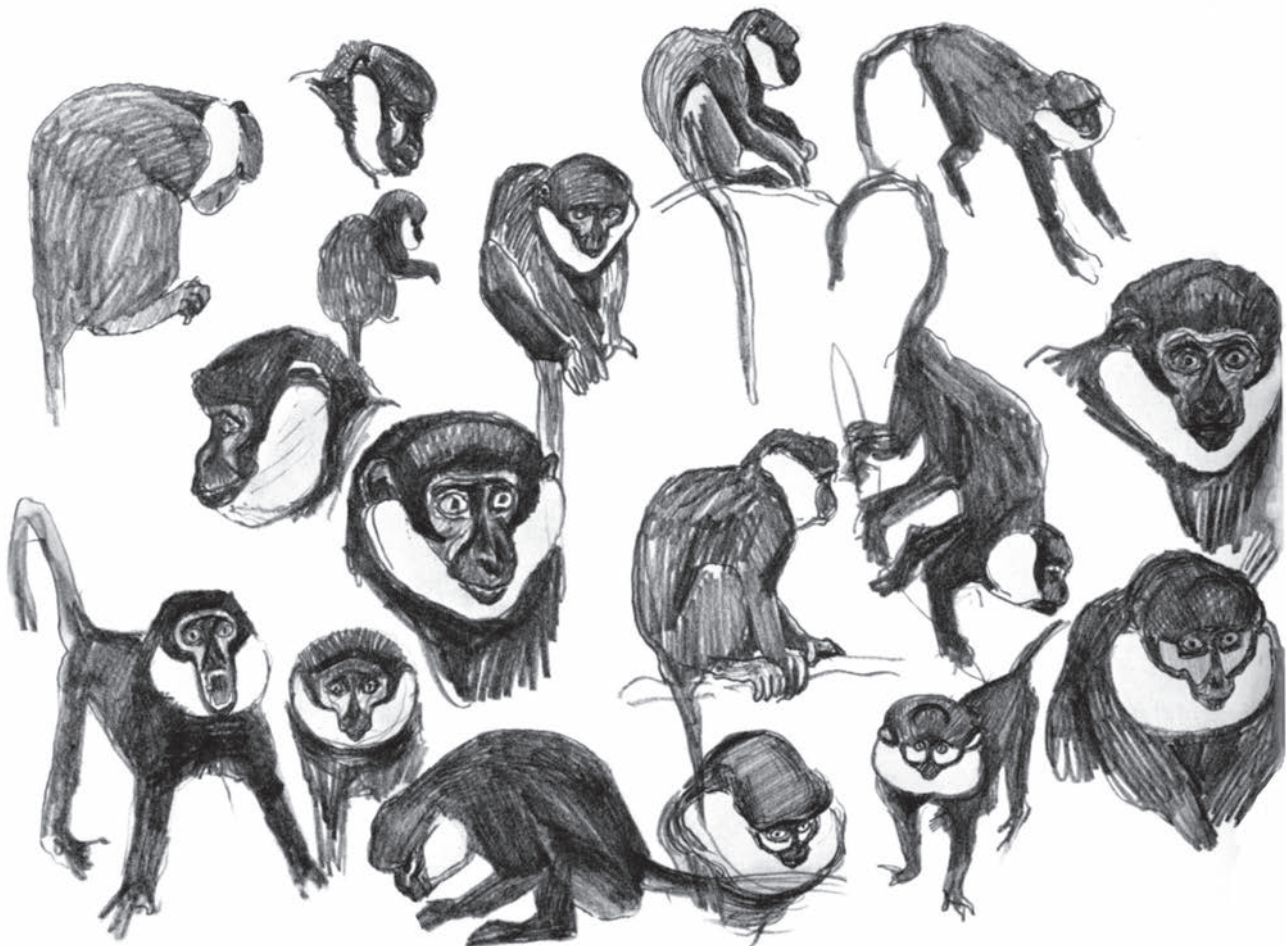


Sun-tailed Monkey *Allochrocebus solatus*
adult male.

Polytypic genus endemic to equatorial Africa. The *Allochrocebus* (*preussi*) Group embraces three species; Preuss's Monkey *Allochrocebus preussi*, L'Hoest's Monkey *A. lhoesti* and Sun-tailed Monkey *A. solatus*. Although allocation of *A. lhoesti* to the subgenus *Allochrocebus* dates back to 1913 (Elliot 1913b), the profiles presented here represent one of the first of contemporary works to return formal recognition for the distinctness of this group. Until recently this group had usually been placed in *Cercopithecus*. Indeed, Gautier *et al.* (2002), while acknowledging that the three species cluster with savanna monkeys *Chlorocebus* and the Patas *Erythrocebus patas*, still consider that the three species in the *A. (preussi)* Group possess sufficient characters to keep them in the genus *Cercopithecus* (J.-P. Gautier pers. comm.). Our reasons for taking *Allenopithecus*, *Miopithecus*, *Erythrocebus*, *Chlorocebus* and *Allochrocebus* out of *Cercopithecus* are founded upon robust, molecular studies that are discussed in other genus profiles. The affinities of *Allochrocebus* are revealed by molecular analysis (Dutrillaux *et al.* 1980, 1982a, 1988a,

b, Muleris *et al.* 1986, Purvis 1995, Disotell 2000, Disotell & Raaum 2002, Tosi *et al.* 2005, Xing *et al.* 2007, Tosi 2008, Perelman *et al.* 2011, Hart *et al.* 2012) as well as analysis of vocalizations (Gautier 1988, Gautier *et al.* 2002), biogeography and behaviour (Kaplin & Moermond 2000, Kaplin 2001), and comparison of the morphology of hands and feet (Kingdon 1988a) and of the postcranial skeleton (Gebo & Sargis 1994, Sargis *et al.* 2008). All these studies concur in associating members of the *A. (preussi)* Group with *Erythrocebus* and *Chlorocebus*. Dutrillaux, Muleris and their colleagues showed that the ancestor of these three groups branched away to form a radiation that was quite distinct from all the arboreal guenons as well as being earlier. Gautier (1988) showed that vocalizations allied *A. preussi* more closely with *Chlorocebus* than with *A. lhoesti* and *A. solatus*, which clustered more closely with one another.

The skull of *Allochrocebus* is similar to *Cercopithecus* and *Erythrocebus*, but the postcranial skeleton strongly differs from *Cercopithecus*.



L'Hoest's Monkey *Allochocebus lhoesti*.

Allochocebus has a shorter supraspinatus fossa of the scapula, narrower head of the humerus with more proximally extended greater and lesser tuberosities, reduced deltopectoral crest, flatter capitulum, smaller trochlea, smaller radial facet on the ulna, narrower patella facet, narrower medial condyle of the femur, taller and narrower head of the talus, narrower tuber calcanei and longer cuboid (Gebo & Sargis 1994, Sargis *et al.* 2008). These provide more stable limb joints with less mobility, as befits a terrestrial life-style, and resemble *Erythrocebus* more than *Chlorocebus*. Kingdon (1988a) noted the exceptionally long, narrow feet of *A. lhoesti*, *Erythrocebus* and *Chlorocebus*, but both of the latter have much shorter toes, and neither have the robust first digit of *A. lhoesti*. The shallow calcaneo-cuboid facet of *A. lhoesti* resembles that of *E. patas*, suggestive of terrestrial traits, while the astragalo-calcaneal facet approximates more closely to that of the Grivet *Chlorocebus aethiops*. A relatively short and lightly built calcaneum suggests that the lever-arm of the Achilles tendon is less developed in *A. lhoesti* than in the more consistently cursorial *Chlorocebus* and *Erythrocebus* (Kingdon 1988a).

Although it was noted that *A. lhoesti* spend much of their time on the ground, and that the leaves of various herbs, shrubs and trees were common foods (Kingdon 1971), it took the detailed studies of Kaplin & Moermond (2000) and Tashiro (2006) to reveal that terrestrial forest herbs comprise as much as 78% of the diet in undisturbed forest habitats, especially those on steep terrain. Kaplin (2001) argues that reliance on terrestrial forest herbs may be the limiting factor in their distribution and the link with broken terrain is also suggestive.

The *A. (preussi)* Group has been associated with many *Cercopithecus* species, including Gentle Monkey *C. mitis* (Pocock 1907, Eisentraut 1973, Ruvolo 1988), Owl-faced Monkey *C. hamlyni* (Schwarz 1928b, Allen 1939, Ruvolo 1988), Groves 1989), Putty-nosed Monkey *C. nictitans*, Red-bellied Monkey *C. erythrogaster* (Groves 1989, Kingdon 1971), Diana Monkey *C. diana* and De Brazza's Monkey *C. neglectus* (Dandelot 1974), as well as with talapoin *Miopithecus* spp. (Disotell & Raaum 2002). Ruvolo (1988) followed earlier precedents in allying the *A. (preussi)* Group with *C. mitis* but she also suggested an affinity with *C. hamlyni*. Most of these authors partly based their association of the *A. (preussi)* Group with arboreal forest species on resemblances in colour and pattern. This similarity is, in fact, greater than with their actual sister-species among savanna monkeys and Patas.

According to Tosi *et al.* (2005) and Perelman *et al.* (2011), the common ancestors of *Allochocebus*, *Chlorocebus* and *Erythrocebus* branched off from the other guenons ca. 8 mya (late Miocene) and could not, of course, have been as specialized as any of the surviving species. Tosi (2008) estimates that *A. solatus* separated from the ancestral stock at 2.1 mya, and that *A. preussi* and *A. lhoesti* bifurcated at ca. 0.5 mya (but see Page *et al.* 1999) when a montane forest dispersal corridor is posited to have connected the highlands of east central and west central Africa. This mini-radiation seems to have involved *Allochocebus* adapting to denser, more heavily forested areas of the equatorial forest belt while *Chlorocebus* and *Erythrocebus* specialized in the drier, more open ends of the climatic and ecological spectrum both to the south and to the north of the Equator.

Allochocebus are long-legged, dark, strongly patterned monkeys with minimal sexual dimorphism in colour but substantial differences in body size between adult ♂♂ and adult ♀♀; adult ♀♀ weigh about 60% as much as adult ♂♂ (T. Butynski pers. comm.). Males have particularly large canines, set in robust, narrow, elongated muzzles. The oval nose-pad in *A. lhoesti* is covered in a deep black plush. The facial skin of the ♂ is purple. The naked, sky-blue testicles strongly contrast against the dark black fur of the buttocks. The limbs have subtle anatomical modifications that render the relatively unspecialized hands and feet particularly flexible at wrist and ankle. The three species in the *A. (preussi)* Group can be distinguished from one another by the colour of the tail and by the distribution of white on the face and throat.

Until the discovery of *A. solatus* in lowland forest in Gabon in 1984 (and named in 1988), the two other species were popularly known as 'mountain monkeys' because of the predominantly montane distribution of *A. lhoesti* and *A. preussi*. It should be noted, however, that *A. preussi* descends to ca. 900 m (i.e. lower montane forest, on Bioko I., Equatorial Guinea) but T. Butynski (pers. comm.) suggests that this is a case of 'competitive-release' as no other medium-sized semi-terrestrial primate occurs on Bioko. It now seems likely that *Allochocebus* is less of a montane genus than a semi-relictual array of semi-terrestrial monkeys that are adapted to living mainly off terrestrial herbs (Kaplin 2001) in well-drained, but densely vegetated forest, perhaps during cooler climatic periods of the past. Most other medium-sized, forest-living, semi-terrestrial primates, such as the drill-mangabeys *Cercocebus* spp., Allen's Swamp Monkey *Allenopithecus nigroviridis*, *C. hamlyni* and *C. neglectus* tend to prefer swampy and riverine areas in warm, wet lowland forests. This probably left a niche for *Allochocebus*, not only in the cool, wet, montane forests, but also in the deeply-cut, mainly well-drained areas south of the Ogooué R., Gabon, where *A. solatus* occurs.

For semi-terrestrial animals a likely advantage of living in swamp-forest is decreased vulnerability to predation and, perhaps, reduced

competition. If this is so, it can be predicted that *Allochocebus* spp. suffer higher levels of predation from Leopards *Panthera pardus* and Golden Cats *Profelis aurata* (and possibly greater competition from other ground-feeders) than the swamp-dwellers. It is certain that they suffer more than other monkeys from trapping by humans (J.-P. Gautier & T. Butynski pers. comm.). Susceptibility to predators is probably mitigated by exceptional alertness, quietness, fast pace (over the ground, and even through heavily obstructed undergrowth), and an ability to take to the trees.

Extrapolating from *C. lhoesti* (the best known of the three species), *Allochocebus* spp. live in tightly knit groups of a single adult ♂ and one or more adult ♀♀ and their offspring. These apparently range widely through well-defined and routinely travelled home-ranges. Confrontations between groups of *A. lhoesti* involve all members. Adult ♂♂ make frequent threats and forward rushes, then posture with chin thrust forward and tail raised, frequently turning to display lateral, rear and frontal views. The adult male's brilliant blue testicles against a jet black rear end make for a highly conspicuous display. These confrontations are usually followed by a sudden and silent withdrawal (Kingdon 1997). Their otherwise low-key types of communication imply that individuals can easily get isolated or lost and this would encourage tight social formations.

The limited distribution of *Allochocebus* spp. could be explained by a reluctance to move across more open habitats, even an inability to cross river barriers. For whatever reasons, a limited geographic range suggests that they are poor dispersers. Dependence on continuity of experience possibly makes it difficult for *Allochocebus* species to regain lost ground after major disturbance or local extirpation. This poses special problems for their conservation in the face of extensive agricultural expansion into their habitats (Kingdon 1997).

Jonathan Kingdon & Colin P. Groves

Allochocebus preussi PREUSS'S MONKEY

Fr. Cercopithèque de Preuss; Ger. Westliche Vollbartmeerkatze

Allochocebus preussi (Matschie, 1898). Sitzb. Ges. Naturf. Fr. Berlin, p. 76. Victoria, Cameroon.



Preuss's Monkey
Allochocebus preussi
adult male.

Taxonomy Polytypic species. Preuss's Monkey *Allochocebus preussi* is a member of the *Allochocebus (preussi)* Group (Grubb *et al.* 2003) or the *Allochocebus (lhoesti)* Group (Gautier *et al.* 2002, Groves 2005c). Until recently, often considered a subspecies of L'Hoest's Monkey *Allochocebus lhoesti* (Rahm 1970, Thorington & Groves 1970, Dandelot 1974), but now widely regarded as a full species that differs considerably from *A. lhoesti* (Tappen 1960, Hill 1966, Napier & Napier 1967, Napier 1981, Harrison 1988b, Kingdon 1997, Gautier-Hion *et al.* 1999, Groves 2001, 2005c, Butynski 2002b, Gautier *et al.* 2002, Grubb *et al.* 2003, Tosi 2008). Synonyms: *crossi*, *insularis*. Chromosome number: $2n = 60$ (Groves 2001).

Description Medium-sized, semi-terrestrial monkey with white throat, grizzled grey cheeks, chestnut-red back and rump, and blue scrotum. Distal ca. 15% of the tail sharply curved towards the underside of the tail. Adult ♀ like adult ♂ in colouration but smaller, being ca. 65% as heavy. Cheeks, crown, nape, shoulders and upper arms blackish, grizzled-grey. Throat and front of neck white.

Iris amber. Nose and ridge of muzzle black. Sides of muzzle greyish. Ears slaty, hidden by hair of crown. Flanks grey with buff banding. Back with large, chestnut-red patch, beginning narrowly between shoulders and becoming increasingly broad over rump. Forearms black. Outside of thighs black and/or speckled grey. Wrists, hands, shanks, ankles and feet black. Callosities brownish-black. Ventrums dark grey. Scrotum skin is blue. Tail chestnut-red on dorsal surface for proximal 10–20%, then dark grey above and light grey below, then black over distal 25–35%. As for *A. lhoesti* and Sun-tailed Monkey *Allochrocebus solatus*, when moving (either on ground or in trees), tail stretched-out behind the body and curved gradually downwards with distal ca. 15% curved sharply downwards. When standing, tail often held vertical or over back with distal ca. 15% pointing backwards. When tail is dangling (e.g. when sitting in a tree), the tip curves distinctly forwards. *Allochrocebus* spp. are the only African monkeys to carry the tail in this manner. Infant with mostly yellowish-brown hairs tipped blackish. Skin of face, ears, hands and feet pale pink. Young juvenile with yellowish-brown pelage that is longer and more shaggy/fluffy than infant. Skin of face pinkish. Skin of hands and feet blackish. Hair of chin, throat and upper chest whitish with distinct yellow-gold tinge. Chestnut on dorsum less extensive than for adult. Almost no chestnut on tail. Tip of tail blackish (T. Butynski pers. obs.).

Geographic Variation

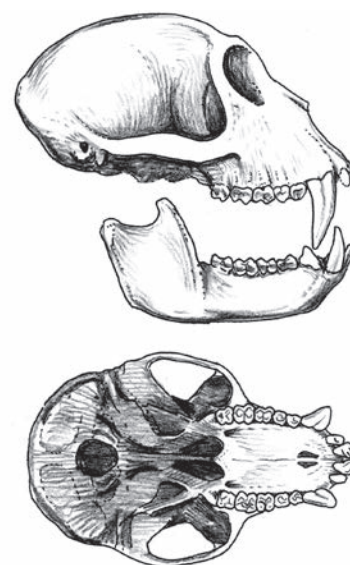
A. p. preussi Mainland Preuss's Monkey. Cameroon–Nigeria border region. Larger (see Measurements). Dorsal saddle brighter chestnut. Limbs black with grizzle-grey on front of hindlimbs. Chestnut covering ca. 20% of dorsal surface of tail. Tail lighter grey (Eisentraut 1973).

A. p. insularis Bioko Preuss's Monkey. Bioko I., Equatorial Guinea. Smaller, HB and T ca. 80–85% as long as for *A. p. preussi* (see Measurements). Dorsal saddle duller chestnut. Limbs grizzled-grey. Chestnut covering ca. 10% of dorsal surface of tail. Tail darker grey (Eisentraut 1973, T. Butynski pers. obs.).

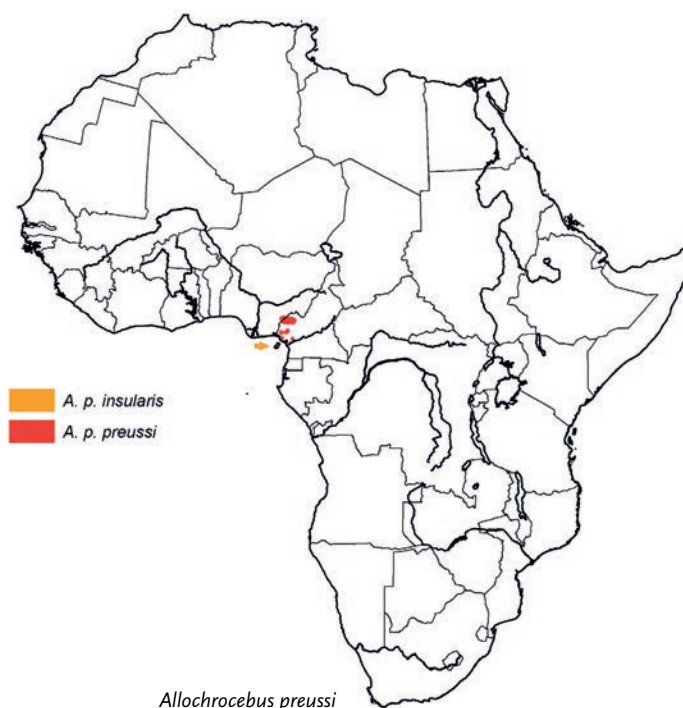
Similar Species None within geographic range.

Distribution Endemic to SE Nigeria, W Cameroon and Bioko I. Rainforest BZ; *A. p. preussi* in highlands of SE Nigeria–W Cameroon border region from Cross R. drainage (Cross River Highlands and Obudu Plateau) south to south side of Mt Cameroon and Sanaga R. Present in Bamboutos Mts, Mt Oku, Mt Kupé, Rumpi Hills, Oban Hills F. R., Bamenda Highlands, Takamanda Reserve, Boshi-Okwangwo and Mt Cameroon (including Etinde F. R.) (Wolfheim 1983, Oates *et al.* 2004). Northern limit ca. 07° N (Tappen 1960). Western limit ca. 08° E (Booth 1958b). In Cameroon found in an area of less than 120 km × 120 km (14,400 km²; Gartlan 1973). *A. p. preussi* on Bioko I. in Pico Basilé N. P. (330 km²) and Gran Caldera and Southern Highlands Scientific Reserve (510 km²) (Butynski & Koster 1994, Hearn *et al.* 2006).

Habitat Moist forest. Both on the mainland and on Bioko I., occurs in primary and secondary lowland, submontane and montane forest, but attains highest densities in montane forest. Also in isolated forest patches in montane grasslands. From 100–3000 m on the mainland, but primarily above 1000 m (Gartlan & Struhsaker 1972, Gartlan 1973, Beeson *et al.* 1996). From ca. 450–2800 m on Bioko



Lateral and palatal views of skull of Preuss's Monkey *Allochrocebus preussi* adult male.



I., but uncommon below 900 m (Butynski & Koster 1994, Hearn *et al.* 2006). Mean annual rainfall ca. 2000–9000 mm. Lives in some of the wettest sites in Africa.

Abundance No estimates of numbers for *A. p. preussi*, but the most common guenon in montane forest on Mt Kilum in the early 1990s (Beeson *et al.* 1996). *Allochrocebus p. insularis* at low densities over much of its range. Encounter rate during an island-wide primate census on Bioko I. in 1986 was 0.03 groups/km (373 km of census), but this survey underestimated density as it included sites below 450 m where *A. p. insularis* probably does not occur due to unsuitable habitat (Butynski & Koster 1994). In 2008, encounter rate of 0.09 groups/km along 44 km of transect in Gran Caldera

de Luba, and 0.14 groups/km on south slope of Pico Basilé along 49 km of census. Highest rate of encounter during censuses on south Pico Basilé in 2008 was 3 groups/km (T. Butynski, G. Hearn & J. Owens pers. obs.). Both the Gran Caldera de Luba and the south slope of Pico Basilé are remote and receive relatively low levels of hunting. Also, there has been little to no anthropogenic impact on the habitats at these sites. As such, these encounter rates are likely close to what is expected for undisturbed populations of *A. p. insularis*. In 1986, *A. p. insularis* may have been the most common monkey on Pico Basilé (Butynski & Koster 1994), but numbers have probably declined considerably since as a result of commercial hunting over the more assessable parts of this mountain. Number of *A. p. insularis* unlikely to be >1000. This may be the rarest species of monkey on Bioko I. (Hearn *et al.* 2006).

Adaptations Diurnal and semi-terrestrial. Spends much time foraging on the ground and within a few metres of the ground, but also climbs well and is often seen in trees. Runs on the ground when fleeing from people (Struhsaker 1969, Gautier-Hion 1988). May be more arboreal on Bioko I. than on the mainland. Preliminary observations of groups in the most remote areas (where hunters do not go) suggest that *A. p. preussi* travels and forages primarily above ground. Where hunted on Bioko I., and where the tree canopy is continuous, they flee through the trees, not on the ground (T. Butynski pers. obs.). More active during the first few hours after dawn and last few hours before dusk than during the middle part of the day.

Foraging and Food Omnivorous. An opportunistic feeder on the mainland (Struhsaker 1969). Studied for 15 months at Mt Kilum, Cameroon, where diet comprised 52% seed/fruit, 26% tree shoot, 14% herb, 4% pith, 1% tree leaf, 1% flower (n = 1284). Invertebrates comprised only 1% of the diet. Shoots, herbs and pith comprised 44% of the diet, which is far more than for most species of guenons. The invertebrate component of the diet is far less than for most guenons. Thirty-one items from 18 plant species were eaten. Small aquatic animals (possibly frogs and crabs) caught from streams were eaten in the middle of the dry seasons (Beeson *et al.* 1996). On Bioko I., eat ripe fruits of *Ficus sur* (J. Owens pers. comm.) and *Tiliacora funifera*, flowers of Giant St John's Wort *Hypericum revolutum*, and search foliage and moss for invertebrates (T. Butynski pers. obs.).

Social and Reproductive Behaviour Social. *A. p. preussi* groups on Mt Cameroon range in size from 2 to 9, with a mean of 5.6 individuals (n = 10; Struhsaker 1969). Group size is considerably smaller than for most other forest-living species of guenon. Groups typically include one adult ♂ and one or more adult ♀♀ and their offspring. Solitary individuals occur but seem to be uncommon. On Mt Kilum the largest group observed had 19 individuals and groups of >10 were often encountered. Here, groups often have more than one adult ♂. Ratio of adult ♂♂ to adult ♀♀ was ca. 1:3. Solitary (single) adult ♂♂ often observed but never solitary adult ♀♀ (Beeson *et al.* 1996). There are few data on group size on Bioko I. Hunters claim *A. p. insularis* live in groups of 4–5 individuals but most groups probably considerably larger than this (Butynski & Koster 1994). J. Owens (pers. comm.) obtained a complete count of one group in a remote area where hunters do not go. This group

comprised seven individuals (one adult ♂, one subadult ♂, two adult ♀♀, two juveniles and one infant). A second group in this area comprised at least six individuals. The impression is that most groups comprise 5–10 individuals (T. Butynski pers. obs.).

A relatively quiet monkey (Gautier-Hion 1988, Gautier *et al.* 2002, T. Butynski pers. obs.). Adult *A. p. preussi* ♂ gives loud, two-part, booming 'oop-uuh' (or 'oop-weur') calls in the late afternoon (17:50–18:40h; Struhsaker 1969, 1970, Gautier *et al.* 2002). Dowsett-Lemaire & Dowsett (2001) refer to this as the 'ouou-owe' dusk call. This call is 'contagious' in that several adult ♂♂ give the oop-uuh call once the first adult ♂ gives this call. Struhsaker (1969) heard as many as five adult ♂♂ give this call within a 1.5 minute period, and Gautier *et al.* (2002) report up to ten adult ♂♂ responding to each other. The function of the oop-uuh call is not known, but its contagious effect and marked diurnal periodicity implies that it provides information about the number and distribution of adult ♂♂ and, therefore, aids in group spacing (Struhsaker 1969, Gautier *et al.* 2002). It is important to note that neither *A. lhoesti* nor the Sun-tailed Monkey *Allochrocebus solatus* has a loud call, and that the structure of the oop-uuh call differs from the loud calls of all other cercopithecines or colobines (Gautier 1988, Gautier *et al.* 2002). The strong periodicity of this call and the large number of adult ♂♂ that participate is unique, at least among African primates. Interestingly, the oop-uuh call is not known for *A. p. insularis* on Bioko I. (even in areas where this subspecies is most common at a density of 3 groups/km of transect; T. Butynski pers. obs.).

Other calls of *A. p. preussi* are warning/alarm 'chirps', which are given by adult ♀♀, subadults and juveniles, and unity/alarm/warning 'hacks' and 'hack-trains', which are given by adult ♂♂. *Allochrocebus p. preussi* not heard to give contact 'trills' (Struhsaker 1969, 1970, Gautier 1988, Gautier *et al.* 2002, T. Butynski pers. obs.). One call given by *A. p. insularis* (probably adult ♀♀), but that has not been reported for any other species of guenon, is the 'purr' (T. Butynski pers. obs.). The purr appears to be a cohesion/contact call and may represent a much modified 'grunt' (i.e. 'type 2 quavered call' of Gautier *et al.* 2002).

Allochrocebus p. preussi forms polyspecific associations with other monkeys, including Mona Monkeys *Cercopithecus mona*, Putty-nosed Monkeys *Cercopithecus nictitans*, Red-eared Monkeys *Cercopithecus erythrotis*, Crowned Monkeys *Cercopithecus pogonias* and Red-capped Mangabey *Cercocebus torquatus*. In Cameroon, 7% of *A. p. preussi* groups encountered were in polyspecific associations (n = 27; Gartlan & Struhsaker 1972, Struhsaker 1981a, Gautier-Hion 1988).

Allochrocebus p. insularis not often in polyspecific association, but this may be because (1) few other monkey species occur at the higher altitudes, and (2) these other species are usually at low densities. Observed in association only with *C. erythrotis*. When *A. p. insularis* adult ♂ gives hacks, adult ♂♂ in *C. erythrotis* groups (to >100 m away) may give hacks in response (T. Butynski pers. obs.).

Adult ♂♂ give the 'blue balls and tail display' in a manner that appears to be identical to that *A. lhoesti* and *A. solatus* (Gautier *et al.* 2002). During this ritualized visual (threat/dominance) display, the ♂ stands on all four legs and faces the opponent. He then, in one continuous movement, turns 180° while raising the tail high over his back. He then stops and displays his blue testicles for ca. 2–4 seconds while facing away from the opponent. On Bioko I., a ♂ may give this

display towards a human observer several times in a matter of a few minutes (T. Butynski pers. obs.). *Allochrocebus p. preussi* may be unique among cercopithecines in possessing both a loud call and a highly ritualized visual display.

Reproduction and Population Structure No information available. Live to at least 19 years and 4 months of age in captivity (Jones 1962).

Predators, Parasites and Diseases No information available. Two of the primary predators of monkeys on mainland Africa, Leopards *Pantherus pardus* and African Crowned Eagles *Stephanoaetus coronatus* are absent from Bioko I. (Struhsaker 2000a, T. Butynski pers. obs.). Humans are the main predator for *A. preussi* both on the mainland and on Bioko I.

Conservation IUCN Category (2012): Endangered as *A. preussi*, *A. p. preussi* and *A. p. insularis*. CITES (2012): Appendix II.

Main threats are habitat loss and fragmentation due to logging and clearance for agriculture, and commercial hunting. Amount of habitat available to *A. p. preussi* has been greatly reduced (Wolfheim 1983, Oates 1996a, Lee *et al.* 1988). Significant populations thought to exist in Nigeria in the Oban Hills F. R. and in the mountains near Obudu (Oates 1986). Still locally common in Ndokbou Forest (>1000 km²) and Ebo Forest (1400 km²), W Cameroon, but hunting is a major threat here and some populations have apparently been extirpated (Dowsett-Lemaire & Dowsett 2001). Surveys needed to better assess abundance, distribution and conservation status, especially in the Oban Hills, Mamfe-Obudu area on the Cameroon–Nigeria border, Etinde Reserve on Mt Cameroon, and Ndokbou Forest and Ebo Forest. All populations should be strictly protected, in particular Okwangwo Division of Cross River N. P., Afi River F. R. and Obudu Plateau, Nigeria, and Takamanda F. R., Mone River F. R., Etinde Reserve and forests of Bakossiland, Mt Kube and Mt Oku (= Mt Kilum), Ndokbou Forest and Ebo Forest, Cameroon (Oates 1996a, Butynski 2002a). Six threatened primate species are sympatric with *A. p. preussi* (IUCN 2012); Drill (Endangered), Preuss's Red Colobus (Critically Endangered), Red-capped Mangabey (Vulnerable), Red-eared Monkey (Vulnerable), Western Gorilla *Gorilla gorilla* (Critically Endangered) and Robust Chimpanzee (Endangered). These species, and hundreds of others, would benefit from conservation actions focused on *A. p. preussi*.

The number of *A. p. insularis* killed by hunters each year has increased from roughly 50 in 1998–2000 to ca. 300 in 2005, when the price paid per adult was ca. US\$31 (Hearn *et al.* 2006). In October 2007 a Presidential Decree banning the hunting and possession of primates in Equatorial Guinea (including Bioko I.) was signed. For a few months after the signing of the Decree the killing of monkeys on Bioko was reduced by >95%. The Decree was, however, never effectively enforced and by early 2009 the number of monkeys killed on Bioko was back to pre-October 2007 levels. Conservation priorities include surveys of Pico Basilé N. P. and much improved management and protection of Pico Basilé N. P. and of the Gran Caldera and Southern Highlands Scientific Reserve (Butynski 2002a). Effective protection of these two areas would provide for the long-term survival, not only of *A. p. insularis*, but also of the six other species of monkeys on Bioko I., four of which are threatened at the

species level and all of which are threatened at the subspecies level (IUCN 2009, Butynski *et al.* 2009).

Measurements

Allochrocebus preussi

A. p. preussi

HB (♂ ♂): 575 (550–605) mm, n = 5

HB (♀ ♀): 498 (450–530) mm, n = 10

T (♂ ♂): 678 (640–690) mm, n = 5

T (♀ ♀): 565 (490–616) mm, n = 10

HF (♂ ♂): n.d.

HF (♀ ♀): 129mm, n = 1

E (♂ ♂): n.d.

E (♀ ♀): 28mm, n = 1

W Cameroon (Hill 1953, Eisentraut 1973, Napier 1981). No body weights for this subspecies.

A. p. insularis

HB (♂ ♂): 484 (420–540) mm, n = 23

HB (♀ ♀): 403 (370–440) mm, n = 40

T (♂ ♂): 553 (500–600) mm, n = 23

T (♀ ♀): 477 (410–560) mm, n = 42

HF (♂ ♂): 140 (130–150) mm, n = 24

HF (♀ ♀): 123 (110–145) mm, n = 42

E (♂ ♂): 31 (28–35) mm, n = 23

E (♀ ♀): 29 (24–35) mm, n = 43

WT (♂ ♂): 5.5 (4.7–6.5) kg, n = 24

WT (♀ ♀): 3.5 (2.9–4.7) kg, n = 42

Upper canine (♂ ♂): 17 (13–22) mm, n = 23

Upper canine (♀ ♀): 11 (6–16) mm, n = 39

Lower canine (♂ ♂): 12 (10–14) mm, n = 24

Lower canine (♀ ♀): 7 (3–12) mm, n = 41

Bioko I., Equatorial Guinea (Butynski *et al.* 2009)

Key References Beeson *et al.* 1996; Butynski & Koster 1994; Eisentraut 1973; Gautier *et al.* 2002; Hill 1966; Lee *et al.* 1988; Oates 2011; Wolfheim 1983.

Thomas M. Butynski



Bright and contrasting skin pigments under the fur of an adult male L'Hoest's Monkey *Allochrocebus lhoesti*.

Allochocebus lhoesti L'HOEST'S MONKEY

Fr. Cercopithèque de L'Hoest; Ger. Östliche Vollbartmeerkatze

Allochocebus lhoesti (Sclater, 1899). Proc. Zool. Soc. Lond. 1898: 586 [1899].

Restricted to Tschopo R. (Tschepo R.), near Stanleyville, 'Congoland' (DR Congo) by Pocock (1907).

L'Hoest's Monkey *Allochocebus lhoesti* adult male.

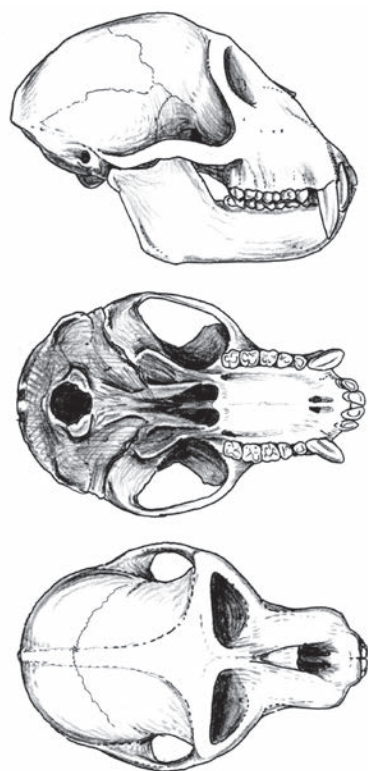
Taxonomy Monotypic species. Most easterly distributed member of the *Allochocebus* (*preussi*) Group. Following Groves (2001), treated here as a monotypic species, although given the allopatry of the three main *Allochocebus* types (Preuss's Monkey *A. preussi*, L'Hoest's Monkey *A. lhoesti* and Sun-tailed Monkey *A. solatus*), their specific status is subjective and unresolved. Resolution would entail showing that the differences among *Allochocebus* species are as great as those that separate other guenon species (but see Gautier *et al.* 2002). Dutrillaux *et al.* (1988a, b) found the same chromosome number in *A. lhoesti* and *A. solatus* but noted differences in the banding patterns of chromosomes 11 and 17. *Allochocebus lhoesti* has classically been considered a species of *Cercopithecus*, the nominate subspecies of *C. lhoesti* (Allen 1939, Hill 1966, Thorington & Groves 1970, Dandelot 1974), and grouped with Owl-faced Monkey *Cercopithecus hamlyni* (Schwarz 1928b, Allen 1939, Groves 1989). Other authors have grouped L'Hoest's Monkey with savanna monkeys *Chlorocebus* spp. (Pocock 1907), Gentle Monkey *Cercopithecus*

mitis (Matschie 1898, Sclater 1898, Pocock 1907, Elliot 1913b, Eisentraut 1973, Ruvolo 1988), Putty-nosed Monkey *Cercopithecus nictitans* and Red-bellied Monkey *Cercopithecus erythrogaster* (Pocock 1907, Kingdon 1971, Groves 1989), Diana Monkey *Cercopithecus diana* and De Brazza's Monkey *Cercopithecus neglectus* (Dandelot 1974).

Elevation of Elliot's (1913b) subgenus to a genus gives specific status to all three known types (Groves 2001), but unnaturally separates them from *C. hamlyni* and from the other semi-terrestrial guenons all of which appear to share a special relationship with *Allochocebus*. Blood protein analyses by Ruvolo (1988) support classic taxonomies that show *Allochocebus* is uniquely related to *C. hamlyni*. If this relationship is true, recognition of *Allochocebus* would require either elevating *C. hamlyni* to its own genus or transferring it to *Allochocebus*. Further complicating matters, morphology (Kingdon 1988a, Gebo & Sargis 1994, Sargis *et al.* 2008), chromosome banding (Dutrillaux *et al.* 1988a, b) and recent DNA analyses (Tosi *et al.* 2003, Xing *et al.* 2007, Tosi 2008, Hart *et al.* 2012) all show that *Allochocebus* shares a unique relationship with *Chlorocebus* and *Erythrocebus* not shared by the more arboreal guenons. Considering that *Cercopithecus* encompasses a greater variety of types than *Chlorocebus*, it could be argued that *Allochocebus* is more properly a subgenus of *Chlorocebus*. Since most arboreal guenons, regardless of their diversity, have been placed in *Cercopithecus*, it is inconsistent to place all the main types of terrestrial (or semi-terrestrial) guenons into separate genera. To maintain taxonomic consistency, recognition of *Allochocebus* appears to merit a general reworking of guenon taxonomy. Affinities between *A. lhoesti* and *A. solatus* in vocal communication systems, but significant differences of both to *A. preussi*, further suggest that a three-species classification of *Allochocebus* is far from clear-cut (Gautier *et al.* 2002).

Synonyms: *rutschuricus*, *thomasi*. Chromosome number: $2n = 60$ (Romagno 2001, Moulin *et al.* 2008).

Description Medium-sized, semi-terrestrial, long-tailed monkey with a well-developed white beard (enveloping the throat, jowls and sides of neck), which contrasts with the dark head, body and limbs. Sexes similar in colouration but average adult ♀ weight is ca. 57% that of adult ♂. Snout long. Snout, nose, chin and upper and lower lips covered in black to dark-brown hairs. Sides of eye orbits outlined by long white-banded black hairs, producing a grey colour bordering on the white beard below and the white-ticked black cap above. In some highland populations (i.e. Bwindi Impenetrable N. P., SW Uganda and Nyungwe N. P., SW Rwanda) short white hairs cover infraorbital area flanking nose and snout, resulting in light grey to white patches below each eye. Brow with sizeable bony torus. Crown and cap black, individual hairs variably exhibiting narrow white bands. White-banded black hairs just above the brow may produce a narrow frontal band. White beard hairs long, thick, directed upwards and backwards but fail to fully cover the mainly bare ear. White of throat continues downwards, tapering to a narrow white patch over the breastbone.



Lateral, palatal and dorsal views of skull of L'Hoest's Monkey *Allochrocebus lhoesti* adult male.

Remainder of body underside is black to dark brown. Back of neck and shoulders with white-ticked black hairs. Body dorsum with a chestnut-coloured 'saddle' extending from between shoulder blades to hips and downwards to flanks. Saddle composed of dark brown hairs with three orange bands that produce green highlights. At saddle periphery, the orange bands whiten, resulting in grey along flanks and over dorsal root of tail. Limbs, and dorsum of hands and feet jet black. Tail, both above and below, covered with black and white hairs that produce a grizzled grey colour. Tail black over distal 25% of underside, proximal ca. 15% of dorsum and distal ca. 20% of dorsum. Tail tip with modest tuft. Female and ♂ genitalia and perianal region marked by tuft of white hairs. Scrotum skin turquoise blue (similar to *Chlorocebus* spp., *C. hamlyni* and *Lesula Cercopithecus lomamiensis*). Newborns have uniformly brown pelage. Adult colour pattern develops by the time the deciduous dentition is fully erupted. When moving, tail carried in a downwards curve that bends upwards then downwards near the tip. Young wrap the tail around supports and each other showing prehensile tendencies (Dandelot 1974).

Geographic variation Differences in facial markings and altitudes at which different populations occur might further separate *A. lhoesti* populations into subspecies (Lonnberg 1919).

Similar Species None within geographic range.

Distribution Endemic to Burundi, E DR Congo, W Rwanda and SW Uganda. Afromontane–Afroalpine, and Rainforest BZs. In moist forest between the right banks of the Congo and Lualaba Rivers, and the forest flanking the eastern border of the Western Rift Valley. Northern, eastern and southern limits roughly coincide with



Allochrocebus lhoesti

the break-up of the forest in this region. Western-most extent (at nearly 25°E) limited by left bank of the Lindi R., whose arching course forms the western half of the northern boundary for *A. lhoesti*. In the east, however, found north of the upper Lindi and Aruwimi Rivers, in the Nepoko, Epulu and Ituri River valleys, reaching as far north as 02° 30' N. Eastward, *A. lhoesti* crosses the Western Rift as far east as 30° 30' E. Southwards, in Burundi, found to 30° 18' E, well east of L. Tanganyika and the Ruzizi R. Southern boundary is south of the Elila R., reaching roughly 04° S in the vicinity of Lualaba town, DR Congo (Colyn 1988). Geographic range ca. 474,000 km² (accounting for hilly terrain).

Habitat *Allochrocebus lhoesti* inhabits savanna woodlands, and bamboo, montane, mid-altitude, riverine, lowland gallery and mono-dominant (*Gilbertiodendron*) forests (Rahm & Christiaensen 1963, Hill 1966, Butynski 1985, Hart *et al.* 1986). Commonly ranges into disturbed land, i.e. lava fields, landslides on steep slopes and cultivated land (Hoier 1955, Rahm & Christiaensen 1963, Kaplin 2001, E. E. Sarmiento pers. obs.). Inhabits a wide altitudinal range from ca. 400 m (in forests flanking the Tshopo R. near Kisangani, DR Congo), to ca. 2700 m in bamboo and montane forests in the Western Rift mountains (Rahm & Christiaensen 1963, Butynski 1984, 1985, Kaplin & Moermond 2000, J. Hart pers. comm., museum records). Found at all altitudes (1160–2600 m), including bamboo forest, in Bwindi Impenetrable N. P. and (formerly) near Kisenyi, W Rwanda. Apparently absent from all other bamboo forests within its geographic range.

In Nyungwe N. P. 18% of one group's annual home-range comprised landslide slopes (Kaplin 2001). Although no *A. lhoesti* have been recorded at altitudes above 2700 m, it is possible that those inhabiting the Rwenzori Mts and Virunga Mts, on occasion, reach the ericaceous vegetation zone at 3000 m. Throughout its range mean annual rainfall is above 1400 mm and may be in excess of 3000 mm on mountain slopes facing L. Kivu. Mean annual temperatures at the

lowest (ca. 400 m) and highest altitudes (2700 m) at which *A. lhoesti* is found are roughly 26 °C and 8 °C, respectively. Only rarely, at the highest altitudes (>2500 m), may temperatures fall below freezing. Over that part of the geographic range close to the Equator there are two dry seasons, each roughly two months in duration. One progressively shortens and the other lengthens with distance from the Equator to form a single dry season that is about three months long at the limit of *A. lhoesti*'s southern extent.

Abundance In all areas where *A. lhoesti* have been studied they are more abundant along roads, in disturbed areas, and at the edge of forests than in the (less disturbed) forest interior (Rahm & Christiaensen 1963, Butynski 1985, Kaplin 2001, Plumptre *et al.* 2002), and seem to tolerate a high level of human disturbance. Occur at low density over most of their geographic range (i.e. forests below 1200 m), with so few sightings that accurate density calculations are not possible (Hart *et al.* 1986, Hall *et al.* 2003). *Allochrocebus lhoesti* are much more common in the montane forests of the Western Rift. In Nyungwe N. P. they are most abundant in open canopy forest and burned habitats (2180–2690 m), have low abundance (three- to eight-fold less) in closed canopy forest at lower altitudes in the north-western sector (1500–2150 m), and are absent or have undetectably low abundance in bamboo forest and in higher altitude closed canopy forest (2260–2450 m; Plumptre *et al.* 2002). In contrast, *A. lhoesti* are most abundant in the bamboo zone at Bwindi Impenetrable N. P. (>2300 m). Here density over the 115 km² used is ca. 10 ind/ km² (Butynski 1984, 1985). At ca. 4 ind/km² at Ngogo, Kibale N. P., SW Uganda (Mitani *et al.* 2001), and ca. 0.4 ind/km² in Ituri, DR Congo (Thomas 1991).

Adaptations Diurnal and semi-terrestrial. The ability of *A. lhoesti* to exploit food both in trees and on the ground enables it to inhabit forests with two or more other species of (competing) guenons. The ability to exploit herbaceous vegetation and tolerance to a wide altitudinal range enables it to live in disturbed and rapidly changing environments (i.e. burned forests, volcanic slopes) within or adjacent to forests that are not available to other forest-living guenons. This ability may be further enhanced by a small ♀ : ♂ body-size ratio, which optimizes habitat-carrying capacity for producing the next generation, allowing for quick expansion into disturbed habitats. The colobine-like molars, with relatively high cusps and wide occlusal surfaces, are advantageous for processing foliage, including terrestrial herbs on which it heavily depends (Hill 1966, Kaplin 2002). The stark black and white coat may serve as warning colouration that is linked to the terrestrial life-style. Kingdon (1971) interpreted their relatively quiet vocal repertoire and tendency to climb repeatedly onto vantage points as adaptations to the risks involved in ground-dwelling.

Foraging and Food Omnivorous. Most of what is known of the diet and foraging behaviour of *A. lhoesti* comes from animals living at altitudes above 1500 m, while practically nothing is known from lower altitudes. Leaves, seeds, fruit, flowers (including fern sporangium), insects, pith, bark, lichen, mushrooms and tree gum are all part of a varied diet (Rahm & Christiaensen 1963, Kaplin 2001, Tashiro 2006, Tolo *et al.* 2007). They raid bean, maize, rice, papaya, oil palm *Elaeis guineensis*, cassava *Manihot* and banana



L'Hoest's Monkey *Allochrocebus lhoesti* adult male.

plantations (Rahm & Christiaensen 1963, Carpaneto & Germi 1989, E. E. Sarmiento pers. obs.). Vertebrate consumption not reported. Diet varies greatly from area to area. In Kalinzu F. R., SW Uganda, they spend as much as 66% of feeding time on insects (Tashiro 2006). By contrast, in Nyungwe N. P., only 9% of feeding time is spent on insects, with most feeding time spent on terrestrial herbs (35%), fruits (24%) and seeds (17%). A sizeable percentage of time feeding on fruits (26%) and seeds (23%) is spent in canopy trees and colonizing trees, respectively (Kaplin & Moermond 2000). Fruits and seeds are more often eaten in early morning and afternoon, and insects (mostly gathered from tree leaves) throughout the day (Kaplin 2001). Fruits and insects are more frequently eaten during the dry season (accounting for 42% and 24% of feeding time, respectively). Fruit and insect feeding is positively correlated and inversely related to time spent eating seeds (Kaplin & Moermond 2000). *Macaranga* *Macaranga capensis* and *Beilschmiedia* sp. are the major source of seeds and fruits, comprising 23% and 10% of feeding time, respectively (Kaplin & Moermond 2000). In Bwindi Impenetrable N. P., *A. lhoesti* commonly feed on bamboo *Sinarundinaria alpina* shoots (E. E. Sarmiento pers. obs.). To the west of L. Kivu, *A. lhoesti* eat fruits of *Aframomum* sp. and seeds of *Eugenia* sp. (Rahm & Christiaensen 1963). In Bwindi Impenetrable N. P. they eat the gum and pods of the Australian Black Wattle *Acacia mearnsii* (Kingdon 1971, T. Butynski pers. comm.).

In Nyungwe N. P., at 2100–2700 m, a group of 29 *A. lhoesti* had a mean monthly home-range of ca. 44 ha, and an annual home-range of ca 117 ha. This group travelled an annual mean daily distance of 2029 m, with Aug (a dry month) averaging the highest (2439 m) and

Apr (a wet month) the lowest (1626 m; Kaplin 2001). Travelled less per day when seeds were a major food and travelled most when fruit was a major food. Feeding and moving made up most of the daily activity. Although 62% of daily activity and 66% of feeding occurred in trees, 53% of travel occurred on the ground. This group spent as much time feeding on the ground (16% of diurnal activity) as in the canopy of the highest trees. When in disturbed habitats, they spent 90% of feeding time eating herbaceous vegetation. Nevertheless, 59% of herbs eaten came from undisturbed forest. They used trees next to feeding sites to sleep in at night, but spent >25% of their diurnal rest time and nearly 40% of their social time on the ground (Kaplin & Moermond 2000, Kaplin 2001).

Social and Reproductive Behaviour Social. Solitary animals commonly seen venturing into open habitats or sitting along dirt roads or paths (Rahm & Christiaensen 1963, E. E. Sarmiento pers. obs.). Groups usually comprised of one adult ♂, numerous adult ♀♀ and immature animals. Rarely, a group contains more than one adult ♂. Adult ♂ tends to stay peripheral to the group and take up the rear when the group moves or is alarmed (Kingdon 1971, E. E. Sarmiento pers. obs.). In Kibale N. P., mean group size was ca. 17 animals (S.D. 8.0, $n = 25$; T. Butynski pers. comm.). At Ngogo, Kibale N. P., mean group size was ca. 18 animals and density was 0.24 groups/km² (Mitani *et al.* 2001). Groups of 5–8 animals in forest to the west of L. Kivu (Rahm & Christiaensen 1963). In Ituri Forest only solitary animals or groups of three or less were encountered (Thomas 1991). Groups as large as 29 at Nyungwe N. P. are not uncommon (Kaplin 2001). As in most guenons, it is likely that ♀♀ stay with groups they are born into, but ♂♂ transfer to another group when sexually mature. The latter seems to be supported by presence of solitary ♂♂ in areas of high *A. lhoesti* density (E. E. Sarmiento pers. obs.).

Polyspecific associations during feeding with other mammals occur, but are not common. At Bwindi N. P., they feed with Doggett's Silver Monkey *Cercopithecus mitis doggetti*, Schmidt's Red-tailed Monkey *Cercopithecus ascanius schmidtii*, Western Guereza *Colobus guereza occidentalis*, Black-fronted Duiker *Cephalophus nigrifrons* and Crested Guinea fowl *Guttera pucherani* (E. E. Sarmiento & T. Butynski pers. obs.). In Nyungwe N. P., *A. lhoesti* feeds with *C. m. doggetti* (Kaplin 2001). In Maramagambo Forest, SW Uganda, a three-species group (*A. lhoesti*, *C. a. schmidtii* and *C. guereza*) seen feeding in a single tree (Kingdon 1971). In Kalinzu F. R. observed on cultivated land feeding with Olive Baboons *Papio anubis* and, when fruit was abundant, fed in trees with Stuhlmann's Blue Monkeys *Cercopithecus mitis stuhlmanni* and *C. a. schmidtii* (E. E. Sarmiento pers. obs.).

Vocal communication is not as varied as in other guenons; warning calls consist of a single 'chirp' and there is no contact call or a loud rallying call from adult ♂♂ (Gautier 1988, Gautier *et al.* 2002). Although scent-marking by *A. lhoesti* may occur, as it does in at least some other semi-terrestrial guenons (e.g. *C. hamlyni*, *C. neglectus*, *Chlorocebus* spp. and Allen's Swamp Monkey *Allenopithecus nigroviridis*; De Jong & Butynski 2010b), it has yet to be reported (Gautier *et al.* 2002).

Reproduction and Population Structure There is little information on *A. lhoesti* reproduction in the wild. There are no data on ovulatory cycle length or gestation length, but these, as in



L'Hoest's Monkey *Allochrocebus lhoesti* adult male in alert lateral posture.

most other guenons, are likely to last 30–32 days and 140–187 days, respectively (Hill 1966). When ready to copulate, ♀♀ present their backside to the ♂. Females do not show external signs of ovulation. During a period of 13 years of research in Kibale N. P., all 46 observations of clinging infants were during Oct–Apr with a peak in Dec–Feb (Butynski 1988). December–Feb is in the longer of the two dry seasons when fruit and invertebrates are relatively abundant. Infant specimens collected in different months show similar dental ages, indicating year-round births over its geographic range (E. E. Sarmiento pers. obs.).

Predators, Parasites and Diseases *Allochrocebus lhoesti* is not commonly hunted. Mbuti pygmies (Bataka) have taboos against eating the flesh, but use the skin for arrow quivers and ceremonial hats (Carpaneto & Germe 1989). In Uganda, Bakonjo and Bakiga use the skin for shoulder-bags (Haddow 1952, Kingdon 1971, E. E. Sarmiento pers. obs.). Due to their terrestrial nature, *A. lhoesti* are sometimes caught in snares set for antelopes and pigs. At Kahuzi-Biega N. P., Robust Chimpanzees *Pan troglodytes* prey on *A. lhoesti* (Basabose & Yamagiwa 1997). In Kibale N. P., an African Crowned Eagle *Stephanoaetus coronatus* observed on the carcass of a freshly killed adult ♂ *A. lhoesti* (T. Butynski pers. com.). Because *A. lhoesti* uses forest upper storey less frequently than most other guenons and their density in trees when feeding is low, they are relatively rare prey of *S. coronatus* (Mitani *et al.* 2001). Nevertheless, juvenile and infant reluctance to feed on fruit high in trees in Kalinzu F. R. is attributed to *S. coronatus* presence (Tolo *et al.* 2007). One study in Ituri Forest found that *A. lhoesti* accounted for 8% of the prey items in the diet of Leopards *Panthera pardus* (Hart *et al.* 1996). Natives report African Golden Cats *Profelis aurata* and pythons *Python* spp. as predators of *A. lhoesti* in NE DR Congo (Carpaneto & Germe 1989).

At the high altitudes of the Western Rift from which *A. lhoesti* is best known, there are few insect vectors for disease transmission, so that most of the diseases attacking other guenons at lower altitudes are not found in *A. lhoesti* (Haddow 1952). Nevertheless, *A. lhoesti* carries simian immunodeficiency virus (Hirsch *et al.* 1999, Beer *et al.* 2000). The stomach of an *A. lhoesti* from Kibale N. P. contained the nematode *Trichuris trichura* (Allen & Loveridge 1942) and faeces contained eggs of *T. trichura*, *Oesophagostomum* sp. and *Strongyloides fuelleborni* (Gillespie *et al.* 2004). Life-span not documented but may be in excess of 30 years for captives (Weigl 2005).

Conservation IUCN Category (2012): Vulnerable. CITES (2012): Appendix II.

Allochrocebus lhoesti thrives in markedly disturbed areas within or adjacent to forests, with most individuals living outside protected areas. Given its habitat preferences, *A. lhoesti* is not immediately threatened and may actually benefit from human disturbance to habitats. The relatively small geographic range (ca. 474,000 km², accounting for hilly terrain), when compared to that of baboons *Papio* spp. and savanna monkeys, and its apparent inability to exploit extensively human-altered areas as effectively as these monkeys poses a threat to its survival.

Among sites important for the long-term conservation of *A. lhoesti* are Kibale N. P., Bwindi-Impenetrable N. P., Kalinzu F. R., Kasyoha-Kitomi F. R., and Maramagambo F. R. in Uganda, Nyungwe N. P. in Rwanda, Kabira N. P. in Burundi, and Kahuzi-Biega N. P., Itombwe Mts, Maiko N. P. and Okapi Faunal Reserve in DR Congo. Much more research is needed on the ecology and behaviour of this poorly known species, particular in mid-altitude and lowland forest.

Measurements

Allochrocebus lhoesti

HB (♂♂): 553 ± 29.28 (510–585) mm, n = 5

HB (♀♀): 487 ± 50.99 (425–600) mm, n = 8

T (♂♂): 715 ± 24.23 (695–755) mm, n = 5

T (♀♀): 568 ± 68.24 (480–670) mm, n = 8

HF (♂♂): 161 ± 23.42 (134–189) mm, n = 5

HF (♀♀): 136 ± 11.78 (120–160) mm, n = 8

E (♂): 42 mm, n = 1

E (♀): 30 mm, n = 1

WT (♂♂): 6.1 ± 1.37 (3.2–8.5) kg, n = 20

WT (♀♀): 3.5 ± 0.76 (1.6–5.2) kg, n = 51

Linear measurements from specimen labels at MCZ, AMNH, RMCA and Basel Museum of Natural History. Specimens from various localities in Rwanda, Uganda and DR Congo.

WT from various localities in DR Congo (RMCA, Colyn 1994)

Key References Gautier *et al.* 2002; Hill 1966; Kaplin 2001; Kaplin & Moermond 2000; Kingdon 1971; Rahm & Christiaensen 1963; Tashiro 2006; Tolo *et al.* 2007.

Esteban E. Sarmiento

Allochrocebus solatus SUN-TAILED MONKEY

Fr. Cercopithèque à queue de soleil; Ger. Sonnenschwanzmeerkatze

Allochrocebus solatus (Harrison, 1988). J. Zool. Lond. 215: 562. Forêt des Abeilles, Bali R., 00° 14' S, 12° 15' E, SE of Booué, C Gabon.



Sun-tailed Monkey *Allochrocebus solatus* adult male.

Taxonomy Monotypic species. *Allochrocebus solatus* belongs to the *Allochrocebus (preussi)* Group. Molecular evidence suggests that *A. solatus* is the oldest member of the *A. (preussi)* Group, from which

A. preussi and *A. lhoesti* split ca. 0.5 mya (Tosi 2008). In common with many other scientists (e.g. Groves 2001, 2005c, Grubb *et al.* 2003), the authors of this profile have reservations about the genus *Allochrocebus*, preferring to retain *solatus* in *Cercopithecus*. The Editors' reasons for instituting this significant taxonomic change are given in the generic profile. *Allochrocebus solatus* has the same chromosome number as *A. preussi* and *A. lhoesti*, but differs in the banding of chromosomes 11 and 17. This helps to validate their full species status (Dutrillaux, *et al.* 1988a, b). Synonyms: none. Chromosome number: 2n = 60.

Description Medium-sized, semi-terrestrial monkey with pale grey cheeks and throat, chestnut-orange back, and yellowish-orange tail tip. Adult ♀ similar adult ♂ but smaller (weighing ca. 60% as much as the adult ♂), colouring less bright, and pelage pattern exhibiting less contrast (Harrison 1988a). Muzzle, periorbital skin, ears and forehead black. In adult ♂, cheeks with speckled pale grey hairs that begin below the periorbital skin at mid-eye and reach the upper chest to form a pale grey throat-ruff. The pale grey throat-ruff poorly developed in adult ♀. Dorsum and flanks speckled chestnut-orange. Chest and belly greyish-black. Legs and feet black. Proximal ca. 20% of tail speckled blackish-grey becoming progressively lighter grey up to about two-thirds the length of tail. Distal about 45% of tail yellowish-orange. Scrotum bright blue. Pelage colouring and contrasts less developed in young. Neonate yellowish-brown, i.e. very different from adults (Gautier *et al.* 2002).

Geographic Variation None recorded.



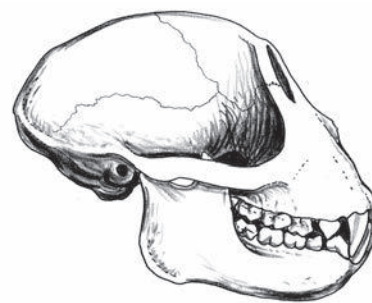
Allochrocebus solatus

Similar Species None.

Distribution Endemic to forests of C Gabon. Rainforest BZ. Total geographic range is 11,000–12,000 km² encompassing Forêt des Abeilles. West of the Offoué R., within Lopé N. P., but not to the west of 11° 30' E. Known northern and eastern limits are the Ogooué R., 00° 03' S and 12° 33' E, respectively. Southern limit unclear, apparently to foothills of the Massif du Chaillu. Confirmed at 01° 24' S, but probably present as far south as 01° 35' S. Reports to the north of the Ogooué R. (in particular the Mokékou Mts, ca. 00° 10' N, 11° 40' E) and close to the border with Congo unconfirmed (Harrison 1988a, Gautier *et al.* 1992, White & Mackanga 1995, Brugière *et al.* 1998, Coad *et al.* 2010, Motsch *et al.* 2011).

Habitat Evergreen primary and secondary rainforests (Harrison 1988a, Gautier *et al.* 1992). Altitudinal range from 140 m (along Ogooué R.) to 980 m (Iboundji Mts). Seems to prefer mid-altitudinal zones (400 m) and densely overgrown gullies along the banks of water-courses (Gautier *et al.* 1992, Brugière *et al.* 1998). Lives in degraded vegetation close to villages (occasionally raiding crops) and in heavily-logged forests. Here the dense undergrowth provides relatively abundant food and protection against predators (Gautier *et al.* 1992). Mean annual rainfall from 1500 mm (north Lopé) to 2400 mm (Massif du Chaillu).

Abundance Suspected to be abundant throughout its range (according to opportunistic observations and hunter reports) except in the mountainous parts in the south and west (Gautier *et al.* 1992). Density estimates available for the Makandé Field Research Station (MFRS; 00° 40' S, 11° 54' E), Forêt des Abeilles, and in southern part of Lopé N. P. At Makandé *A. solatus* had the highest density (25 ind/km²) and highest biomass (73 kg/km²) among the seven species that made up the Cercopithecidae community (Brugière *et al.* 2002).



Lateral view of skull of Sun-tailed Monkey *Allochrocebus solatus* adult male.

In southern Lopé N. P., near the south-western limit for *A. solatus*, density is only ca. 10% that at Makandé (Brugière 2005).

Adaptations Diurnal and semi-terrestrial. Because of its semi-terrestrial habits, *A. solatus* has a specific anti-predator strategy based on crypticity (Gautier 1998). In contrast to arboreal species, few sounds are exchanged during foraging: cohesion calls possess weak intensity and are atonal in structure. Because the group can be totally silent while on the move, individuals risk losing contact with one another and isolation (lost) calls are more frequent than in arboreal species, being given even by adults. No loud-calls for spacing and rallying are produced. The most frequent calls are given under conditions that imply a warning function: loud 'barks' by adult ♂♂ and high-pitched 'chirps' by adult ♀♀ and immatures, followed by silent flight on the ground. In contrast with arboreal species, *A. solatus* was in polyspecific associations in only 14% of 224 encounters; 6% were proximity associations, while 8% were true mixed group associations. Mixed groups appeared only under conditions where no danger could be anticipated, presumably because large groups increase the risk of detection by predators. As for most semi-terrestrial primates, there is considerable size dimorphism between adult ♂♂ and adult ♀♀. This is attributed to the defensive role that ♂♂ play in an environment where predators are more numerous and less visible than in the trees. At the Centre International de Recherche Médicale de Franceville (CIRMF), Franceville, Gabon, the daily activity pattern of one semi-free-ranging group of 13 individuals in a 0.5 ha enclosure has two peaks: one soon after dawn and the other from mid-afternoon until nightfall, when the group retires to sleep in trees; there is a period of low activity and rest during the middle of the day (Peignot *et al.* 1999).

Foraging and Food Omnivorous. During daylight hours, *A. solatus* at CIRMF spent 86% of time on the ground and 89% below 2 m (Peignot *et al.* 1999). Food is mainly found on the ground and in the undergrowth. Foraging begins early in the morning (as soon as the group climbs down from the sleeping trees), there is a slight decrease in foraging activity at mid-day, and increases again during the afternoon. Mean daily travel distance at Makandé (two radio-collared groups) was 1–2 km (n = 139 days). Home-ranges 150–300 ha (n = 2 groups). At dusk the group climbs into trees at a new sleeping site. Composition of the annual diet of *A. solatus* at CIRMF was invertebrates 27.5%, grasses 27.5%, fruits 19.5%, mushrooms 6.7%, flowers 5.8%, seeds 5.8%, pith 4.2%, leaves 3.3% (Peignot *et al.* 1999). As with *A. lhoesti*, *A. solatus* exhibits predatory behaviours.

A young individual (initially hand-raised and then living free at MFRS until 28 months old) regularly ate invertebrates, birds' eggs and small birds. He displayed hunting behaviours (on the ground as well as in the trees), stalking reptiles, small galagos, larger birds (Guinea fowls, touracos) and even a Blue Duiker *Philantomba monticola* (Fleury & Gautier 1998).

Social and Reproductive Behaviour Social. Of 247 encounters with *A. solatus* at MFRS, 21% were with solitary individuals, of which 17% were adult ♂♂ and 4% were not sexed. Mean group size was 18 individuals (9–25, $n = 5$). Two exceptional counts of 40 and 46 individuals in a single group suggest possible fusion of two or more social groups. Sex ratio is close to one adult ♂ per five adult ♀♀. A group of 16 individuals comprised 1 adult ♂, 5 adult ♀♀ and their offspring, 1 subadult, 2 juveniles and 2 infants. Overlap of home-ranges of two radio-tagged groups was 15%. At CIRMF, one-male organization observed with prolonged ♂ tenure and expulsion of maturing ♂♂ to the periphery of the enclosure. Only dominant ♀♀ gave birth (17 births over 11 years). As only one ♂ sired offspring during his period of tenure, a decrease of fitness among the animals in this colony was observed (Charpentier *et al.* 2005a, Charpentier *et al.* 2008). Territorial behaviour is not supported by stereotyped vocal displays (as in sympatric arboreal monkey species) but territorial conflicts do occur, with aggressive interactions (including chases) between adult ♂♂.

Reproduction and Population Structure Length of gestation and age at weaning are not known. At CIRMF the birth season coincided with the two annual wet seasons (8 births out of 11; four in Oct–Dec and four in Mar–May). Mean interval between births was 18 months (Peignot *et al.* 1999, 2002). Mean birth-weight is 380 g ($n = 4$). One young born at a time (twins not reported). Captive ♂♂ sexually mature at 5–7 years. Captive ♀♀ sexually mature at about four years.

Predators, Parasites and Diseases Leopards *Panthera pardus*, African Golden Cats *Profelis aurata* and African Crowned Eagles *Stephanoaetus coronatus* are presumed predators. At Makande a subadult ♂ found dead with two small holes on the neck revealing the bite of an unidentified snake. Vigorous vertical jumps, displayed by captive and semi-captive *A. solatus* facing live snakes or snake models, suggests that this is one way to escape from snakes. A young ♂ caught in the wild was infected under the skin with three larvae of the fly *Cordylobia anthropophaga*. A new and specific simian immunodeficiency virus (SIVsun) identified from a wild-born 12-year-old captive ♂ (Beer *et al.* 1999, Liégeois *et al.* 2011). This monkey appeared healthy.

Conservation IUCN Category (2012): Vulnerable. CITES (2012): Appendix II.

Until the 1990s the entire geographic range of *A. solatus* was virtually uninhabited by people, but within the last 20 years virtually all of the forests within the range have been logged (except forests in the southern part of Lopé N. P.). *Allochrocebus solatus* does well in logged forest, as the resultant dense undergrowth provides relatively abundant food. Where logging has occurred, however, there is a dense network of roads. As a result, commercial bushmeat hunting has increased dramatically in the Forêt des Abeilles. This will be the main threat for *A. solatus* for years to come. Hunters report that *A. solatus* is difficult to hunt as a result of its cryptic behaviour, but non-selective ground snares (usually set for duikers *Cephalophus* spp. and *P. monticola*) represent a particularly acute threat for this semi-terrestrial species.

About 10–20% of the geographic range of *A. solatus* lies within the southern part of the Lopé N. P. (4910 km²) but this includes those parts of the species' geographic range where density is at its lowest. Proposed conservation actions include the control of commercial hunting, the creation of a protected area in the Forêt des Abeilles (i.e. a part of their geographic range that exhibits high density), and minimization of human settlement in the Forêt des Abeilles (Gautier 1989b, Brugière & Gautier 1999). The CIRMF Colony of breeding *A. solatus* was founded in 1986 with four individuals; by 2012 this colony numbered 15 individuals (P. Motsch pers. comm.). Reintroduction into the wild of a young ♂ taken from hunters was successfully carried out at MFRS (Fleury & Gautier 1998).

Measurements

Allochrocebus solatus

HB (♂♂): 530 (460–580) mm, $n = 7$

HB (♀♀): 480 (450–540) mm, $n = 8$

T (♂♂): 680 (590–760) mm, $n = 7$

T (♀♀): 600 (560–680) mm, $n = 9$

HF (♂♂): 160 (150–160) mm, $n = 6$

HF (♀♀): 140 (130–140) mm, $n = 6$

E (♂♂): 46 (40–50) mm, $n = 4$

E (♀♀): 45 (40–50) mm, $n = 5$

WT (♂♂): 6.9 (5.8–8.7) kg, $n = 6$

WT (♀♀): 4.0 (3.7–4.3) kg, $n = 7$

Forêt des Abeilles, Gabon (Harrison 1988a, Gautier *et al.* 1992)

Key References Brugière & Gautier 1999; Dutrillaux *et al.* 1988a; Gautier *et al.* 1992; Harrison 1988a; Peignot *et al.* 1999, 2002.

Jean-Pierre Gautier & David Brugière

GENUS *Cercopithecus*

Arboreal Guenons

Cercopithecus Linnaeus, 1758. *Systema Naturae*, 10th edn, 1:26.

| | | |
|--|-------------------------|--------|
| <i>Cercopithecus dryas</i> (1 species) | Dryad Monkey | p. 306 |
| <i>Cercopithecus (diana)</i> (2 species) | Diana Monkeys Group | p. 309 |
| <i>Cercopithecus neglectus</i> (1 species) | De Brazza's Monkey | p. 315 |
| <i>Cercopithecus (mona)</i> (6 species) | Mona Monkeys Group | p. 319 |
| <i>Cercopithecus (hamlyni)</i> (2 species) | Owl-faced Monkeys Group | p. 339 |
| <i>Cercopithecus (nictitans)</i> (2 species) | Nictitans Monkeys Group | p. 344 |
| <i>Cercopithecus (cephus)</i> (6 species) | Cephus Monkeys Group | p. 363 |

Cercopithecus, as presented here, consists of 20 species of long-tailed, arboreal monkeys commonly referred to as the 'arboreal guenons'. Compared to most other Cercopithecidae they are slender and medium-sized. They have short faces and the skull is particularly short-muzzled in both sexes of the smaller arboreal species but more prominent in the adult ♂ of the Diana Monkeys Group *C. (diana)*, De Brazza's Monkey *C. neglectus*, Owl-faced Monkeys Group *C. (hamlyni)* and Nictitans Monkeys Group *C. (nictitans)*. Ischial callosities consist of two prominent pads that are separate and attached to the posterior extremities of the pelvis. Females lack the catamenial swellings typical of Papionini. They have agouti coats, often with bright colour contrasts on the face and/or limbs. Dentally, M_3 lacks a hypoconulid and M_2 and M_3 have no mesostylids. Molars without the flares that typify papionins and Allen's Swamp Monkey *Allenopithecus nigroviridis*. For detailed morphological diagnosis see Hill (1966).

In the present volume the genus *Cercopithecus* is more restricted than in any previous work. The rationale for this taxonomic contraction derives, in large part, from molecular work that has been unambiguous in separating the 'terrestrial' guenon lineages from the 'arboreal' ones (Dutrillaux *et al.* 1978, 1980, 1988a, b, Purvis 1995, Tosi *et al.* 2005, Tosi 2008, Perelman *et al.* 2011). Some recent molecular studies have gone still farther, suggesting that the talapoin *Miopithecus* lineage, a genus formerly associated with *Allenopithecus*, evolved after the 'terrestrial' Cercopithecini and clusters with *Cercopithecus* (Xing *et al.* 2007, Perelman *et al.* 2011). This finding serves to isolate the arboreal guenons still farther from their former congeners. Moulin *et al.* (2008), however, question this view, instead associating *Miopithecus* with *Erythrocebus* and allies.

Consistent with these studies, Groves (2000a) recognized that the savanna monkeys, formerly the *Cercopithecus (aethiops)* Group, should be treated as a distinct genus *Chlorocebus*, as should their sister-groups, the open-country Patas Monkey *Erythrocebus patas*, and now, given their known genetic affinity, the forest-dwelling Mountain Monkeys Group *Allochocebus (preussi)* (formerly the *Cercopithecus (preussi)* Group). All were previously lumped under *Cercopithecus*.

In this newly restricted sense, *Cercopithecus* embraces 20 species belonging to seven 'Groups' (sometimes also referred to as 'species-groups' or 'superspecies'), namely: the Dryad Monkey Group *Cercopithecus dryas* (1 sp.); Diana Monkeys Group *C. (diana)* (2 spp.); De Brazza's Monkey Group *C. neglectus* (1 sp.); Mona Monkeys Group *C. (mona)* (6 spp.); Owl-faced Monkeys Group *C. (hamlyni)* (2 spp.); Nictitans Monkeys Group *C. (nictitans)* (2 spp.); Cephus Monkeys Group *C. (cephus)* (6 spp.). These are, for the most part, medium-sized, long-tailed, arboreal forest monkeys. They include some of the

most colourful of all primates and their highly geometric signals are correlated with increased specialization in the visual communication channel of the species or group concerned (Kingdon 1980, 1988b, 2007; and illustration on p. 304).

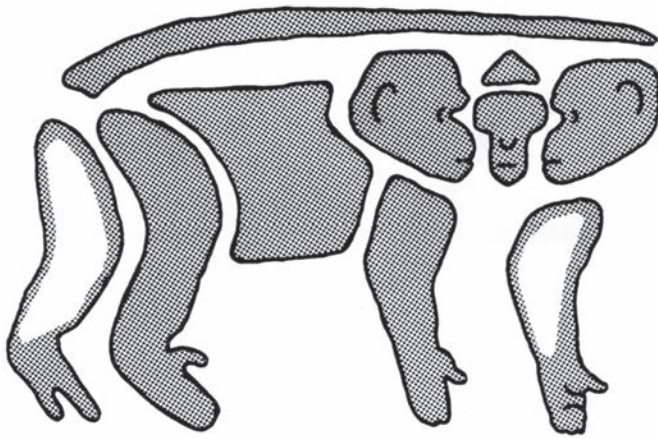
The radiation of *Cercopithecus* has exercised many scientists, including Schwarz (1928b), Verheyen (1962), Hill (1966), Thorington & Groves (1970), Kingdon (1971, 1990, 1997), Dutrillaux *et al.* (1978, 1980, 1982, 1988b), Muleris *et al.* (1986), Ruvolo (1988), Groves (1989, 1993, 2000b, 2001, 2005c), Purvis (1995), Disotell & Raam (2002, 2005), Tosi *et al.* (2002, 2005), Grubb *et al.* (2003), Xing *et al.* (2007), Moulin *et al.* (2008), Tosi (2008) and Oates (2011). Schwarz's (1928b) assumption that the most arboreal species were the most conservative was generally accepted for more than 40 years, but Kingdon (1971, 1980) presented arguments that the smallest, most arboreal species were actually the most highly evolved and derived. The latter view has since been confirmed by molecular scientists (Dutrillaux *et al.* 1978, 1980, 1988b, Purvis 1995, Xing *et al.* 2007), but the assumption that the Cercopithecini had 'arboreal' origins is still made (Tosi *et al.* 2004). In fact, as discussed under Cercopithecinae, the ancestral condition for all Cercopithecini was probably semi-terrestrial, with the smaller-bodied types having a general tendency to be more arboreal.

Chromosome numbers range from 58 to 72 (Dutrillaux *et al.* 1988b, Romagno 2001).

Understanding the detailed relationships among species has been complicated by some genetic features unique to *Cercopithecus*. It would seem that the ancestral *Cercopithecus* had many polymorphic genetic elements and these remained during and after speciation; such elements seem to have become randomly fixed in some lineages or lost in others (Xing *et al.* 2007). Furthermore, hybridization in the wild occurs between species (Detwiler *et al.* 2005) and even between genera (De Jong & Butynski 2010b), further complicating the genetic heritage of species. This means that some taxa that are easily identified on external appearances may have hidden hybrid ancestry in some, many, possibly all members of a given population. That this can make for startling inconsistencies between external appearances and molecular profiles is demonstrated by Moulin *et al.* (2008) associating *C. hamlyni* with *C. (mona) pogonias*!

Molecular clocks suggest that ancestors of the seven major lineages all evolved during the late Miocene and Pliocene (6.2–2.2 mya; Tosi *et al.* 2005, Perelman *et al.* 2011). This rapid speciation into distinct ecological and dietary niches can be partly explained by the extreme climatic fluctuations that took place over this time. Periods of intense aridity would have fragmented populations along a latitudinal axis, isolating those in the far west ('Upper Guinea') from those in central West Africa (the 'Cameroon/Gaboon Centre of Endemism') and those in east-central Africa ('Central Refuge' or 'Haute Zaire'), and each of these regional forest refugia have been further subdivided. Furthermore, the Congo R. is one of the major biogeographic dividing lines in Africa, with populations readily differentiating north and south of the river.





OPPOSITE AND ABOVE: Two dimensional schematic charts of adult males of eight guenon species.

These charts 'map' the colour and pattern on the inner surface and the outer surface of the limbs, and of the head-on facial plate. Note the concentration of signals at the genital pole in the more terrestrial species (Owl-faced Monkey *Cercopithecus hamlyni* and Tantalus Monkey *Chlorocebus tantalus*), and at the facial pole in the more arboreal species (Moustached Monkey *Cercopithecus cephus* and Crowned Monkey *Cercopithecus pogonias*).

From top to bottom, left to right:

Putty-nosed Monkey *Cercopithecus nictitans*. Moustached Monkey *Cercopithecus cephus*.

Lowe's Monkey *Cercopithecus lowei*. Crowned Monkey *Cercopithecus pogonias*. De Brazza's Monkey *Cercopithecus neglectus*. Diana Monkey *Cercopithecus diana*.

Owl-faced Monkey *Cercopithecus hamlyni*. Tantalus Monkey *Chlorocebus tantalus*.

Taking the present distribution of species as a guide, Kingdon (1990) outlined a possible geographic scenario for the early emergence of four major *Cercopithecus* lineages during periods of forest fragmentation. In their studies of chromosomes, Dutrillaux *et al.* (1980, 1982, 1988b) were the first to reveal that the genus *Cercopithecus* (as used in this work) represents the more arboreal side of a primary bifurcation of the Cercopithecini. Dutrillaux's team was unable to secure material from the extremely localized and little-known *C. dryas* but this species can be tentatively extrapolated as a specialized relict close to the stem of this fecund radiation. The suggestion, based on genetic evidence, that *Miopithecus* might be closer to *Cercopithecus* than to *Allenopithecus* (Xing *et al.* 2007, Perelman *et al.* 2011), adds a new possibility to the little-known beginnings of arboreal guenon evolution: body-size. *Miopithecus*, at about 1.2 kg, is very small, while *C. dryas*, estimated at ca. 2.5 kg, is larger but is still a relatively small monkey. In coat pattern *C. dryas* has a close resemblance to 3–6 kg *C. (diana)*. According to Dutrillaux's team, *C. (diana)* (which were once locally successful, mainly canopy inhabitants of mature West African high forest) derive from a basal lineage of *Cercopithecus (sensu novo)*. Most molecular, morphological and behavioural studies agree that the other species subdivide into two distinct clusters, with *C. (mona) / C. neglectus* closest to *C. (diana)* and *C. (nictitans) / C. (cephus)* somewhat farther removed. *Cercopithecus hamlyni* occupies a rather ambiguous position in between the two, showing affinity with *C. neglectus*, *C. (nictitans)* and *C. (mona)* (see figure p. 245). While it has long been clear that the *mona/neglectus* complex antecedes the *nictitans/cephus* radiations,

a basal position for *C. (mona) campbelli* has been proposed by Moulin *et al.* (2008). This important conclusion is discussed further in the *C. (mona)* profile. Likewise, the *nictitans/cephus* radiation poses special taxonomic problems because (*cephus*) appears to nest within the putatively older (*nictitans*) group. It is therefore possible that *C. (nictitans)*, as described in this work, might eventually merit further subdivision.

A temporal framework for the *Cercopithecus* radiation was first offered by Purvis (1995) on the basis of molecular clock computations. This suggested that divergence of *Cercopithecus* from the other, less arboreal, cercopithecine genera took place just before or during the end of the Miocene Messinian, a period when tropical lowland forests would have been of minimal extent and scattered along an equatorial axis. A more recent estimate (Tosi *et al.* 2005; and figure p. 245), implies an earlier divergence between terrestrial and arboreal cercopithecines but agrees with Purvis in dating the main radiation of *Cercopithecus* between about 4.6 and 3 mya (early to mid-Pliocene). Perelman *et al.* (2011) place the start of the *Cercopithecus* radiation at 7–6 mya (late Miocene).

Central and West African equatorial forests have been the geographical focus for this radiation, and, if *C. dryas* represents the oldest form, it seems significant that it should occupy the centre of *Cercopithecus* range, a small area east of a former Pliocene lake, L. Congo (Beadle 1974). This understory, riverside species is now adapted to a uniquely local niche, and it seems likely that the survival of its lineage through the climatic vicissitudes of the later Pliocene and Pliocene was facilitated by the unusual ecological continuity of plant communities growing close to ground-water swamps and riverine forests in the central Congo Basin. The much larger and less specialized *C. neglectus* occupies a comparable habitat but over an extensive but patchy range, from the Atlantic to Ethiopia and Kenya (but this species evolved substantially later).

One influence that makes reconstructing the *Cercopithecus* radiation difficult is the relatively short period during which the founders of today's main lineages are thought to have diverged. Five lineages, *diana*, *neglectus*, *mona*, *hamlyni* and *nictitans/cephus*, all emerged from a common ancestral stock between 4.2 and 3.2 mya (mid-Pliocene). What is especially interesting is the timing of the emergence of the two most speciose lineages, *C. (mona)* and *C. (cephus)*. According to Tosi *et al.* (2005), ancestral *C. (mona)* diverged from *C. (diana)* and *C. neglectus* between 4.1 and 3.9 mya whereas the divergence of *C. (cephus)* from *C. (nictitans)* was about 1.3 million years later; when forests were particularly fragmented. Yet the fact that the location of tropical Africa's forest refuges corresponds well with the distribution of *C. (mona)* and *C. (cephus)* populations implies that their periodic fragmentation tended to follow the same general pattern over several, probably many, climatic fluctuations. Although fragmentary fossils have been allocated to *Cercopithecus*, none provides any guide to the evolution of modern species. None the less, their restriction to the African Plio-Pleistocene confirms their late and exclusively African provenance.

The species can generally be easily distinguished on the basis of body size and pelage patterns. Detailed diagnoses are presented in the species profiles.

Jonathan Kingdon & Colin P. Groves

Cercopithecus dryas DRYAD MONKEY (SALONGO MONKEY)

Fr. Cercopithèque Dryade; Ger. Dryadmeerkatze

Cercopithecus dryas Schwarz, 1932. Rev. Zool. Bot. Afr. 21: 251. Ikela Zone, Yapatsi, DR Congo.Dryad Monkey *Cercopithecus dryas* adult male.

Taxonomy Monotypic species. *Cercopithecus dryas* first described from a juvenile ♂ specimen thought to have been collected at Lomela (02° 20' S, 23° 12' E), but the type locality now in serious doubt (Schouteden 1946, Thys van den Audenaerde 1977, Colyn 1988, Sarmiento 2000). About 45 years after *C. dryas* was described, Thys van den Audenaerde (1977) described the Salongo Monkey *Cercopithecus salongo* from the incomplete skin of an adult specimen obtained in 1977 by T. Kano in Wamba Forest, near Wamba Village, Zone de Djolu, DR Congo (Kuroda *et al.* 1985, Sarmiento 2000, Groves 2001). The coordinates for the type locality of *C. salongo* are given as 00° 01' N–00° 01' S, 22° 31–33' E. In 1977 and 1978 the intact skins of a ♂ and ♀ were obtained near Wamba. These are described in detail in Kuroda *et al.* (1985). Wamba Village is ca. 255 km north-north-east of Lomela. Colyn *et al.* (1991) concluded that Thys van den Audenaerde had not described a new species of monkey, but rather the adult form of *C. dryas*. This conclusion has been generally accepted (Kingdon 1997, Groves 2001, 2005c, Grubb *et al.* 2003). Sarmiento (2000), however, questions the synonymy of *C. dryas* and *C. salongo*, arguing that they should be treated as separate species pending more data. S. Kuroda (pers. comm.) also questions the synonymy of *C. dryas* and *C. salongo*, pointing out that G. Idani photographed a juvenile Salongo Monkey with the same colour pattern as the adult, including the black-tipped tail – not the colour pattern of the juvenile described by Schwarz (1932) (see below).

Resolution of whether *C. dryas* and *C. salongo* represent one species or two species/subspecies is of high priority for those concerned with the taxonomy and conservation of Africa's primates.

Schwarz (1932), Napier (1981) and Lernoould (1988) consider *C. dryas* to be a central African representative of the Diana Monkeys Group *Cercopithecus (diana)* of West Africa. Similarly, Thys van den Audenaerde (1977) judged *C. salongo* to also be most similar to *C. (diana)*. Kingdon (1997) suggests that *C. dryas* might be a relict species sharing ancient affinities with *C. (diana)* and De Brazza's Monkey *Cercopithecus neglectus* in spite of differing from both in its small size. Kuroda *et al.* (1985) and Hurley & Lokasola (2007), however, found the ecology and behaviour of *C. dryas* to differ considerably from that of *C. (diana)* (see below). The dramatic juvenile to adult pelage colour change pattern (assuming *C. salongo* is a synonym of *C. dryas*), as well as the small upper lateral incisors, both suggest affinity with *C. neglectus* (Groves 1989, 2001). The triangular shape of the face, pattern of colour on the face and at base of the tail, and light blue scrotum, all recall the savanna monkeys *Chlorocebus* spp. (T. Butynski pers. obs.).

Hill (1966) placed *dryas* as a subspecies of Diana Monkey *Cercopithecus diana diana*. Thorington & Groves (1970), however, retained *dryas* as a separate species. Groves (quoted in Thys van den Audenaerde 1977: 1007) initially considered *C. dryas* to be most closely related to the Grivet *Chlorocebus aethiops*, but on the evidence of a photograph of an adult skull in Kuroda *et al.* (1985), stated the following (Groves 1989: 139):

'The figure of the skull makes it clear that it is indeed a *Cercopithecus*, not a *Chlorocebus*, with its oval orbits, nasals apparently not pointed, and so on; and nasals seem short and somewhat triangular, which would ally it to *C. cephus*, but its exceptionally small I² would place it near *C. neglectus*. On the other hand the interorbital pillar is not constricted unlike in *C. neglectus*; the premaxilla seems to be narrow, unlike in the *C. (mitis)*, (*preussi*), and (*hamlyni*) Groups; and the internasal suture is closed in the figured skull. The species is small in size, perhaps the smallest of the genus, and with very little sexual dimorphism.'

Of the skull of the holotype of *C. dryas*, a juvenile that he examined directly, Groves (1989: 140) wrote:

'The inferior mandibular border is not curved in the *C. diana* fashion ... There are a few features recalling *Chlorocebus*, such as the less-oval shape of the orbits than *Cercopithecus*, but at its immature age it is difficult to tell whether this is a true resemblance or only apparent. It does not have the V-shaped auditory tube, unlike *Chlorocebus*.'

Most recently, Groves (2000a: 96) wrote:

'It [*C. dryas*] is a thoroughly distinct species, not part of any of the well-known species-groups of the genus [*Cercopithecus*]. It appears to lack the character states of the *Chlorocebus/Erythrocebus* group, and to



Dryad Monkey *Cercopithecus dryas*.

possess those of true *Cercopithecus*: orbit not oval, upper incisors do not form a single unified bite surface, nasals not pointed at tips, small supraorbital torus.'

While there is no doubt that *C. dryas* is a member of *Cercopithecus*, it appears to be a very divergent species, possibly the sister to all other *Cercopithecus* spp. (Groves 2000a). Grubb (2006) points out that 'Dryad' is the accepted spelling for the vernacular of this species. Synonyms: *salongo*. Chromosome number: $2n$ = not known.

Description Small forest monkey with black face and jet black all around lower limbs, white around face, and white on chest and ventrum. Smallest *Cercopithecus* spp. Detailed descriptions provided by Thys van den Audenaerde (1977) and Koruda *et al.* (1985). Adult ♂ like adult ♀ but slightly larger with short, projecting, beard on chin. Face black, triangular. Temples with elongated, whitish horizontal tufts. Brow-band white. Cheeks, temples, sides of head, chin, beard, throat, front of shoulders, insides of upper arms and legs, ventrum, back of the thighs, and buttocks white or creamy-white. White of temples separated from brow-band by a posteriorly directed bare black line. Crown, back, sides, front of thighs and upper arms greyish-brown or dark olive-grey speckled with chestnut. The hairs here are grey over the basal half with the distal half alternating black and orange-brown rings. This mixing creates a general greyish-chestnut colour, which is much darker on crown than elsewhere. Lower limbs, including hands and feet, jet black all around. Tail of medium length, dirty white, with large black spot (i.e. inverted V) below at base and narrow grey line along



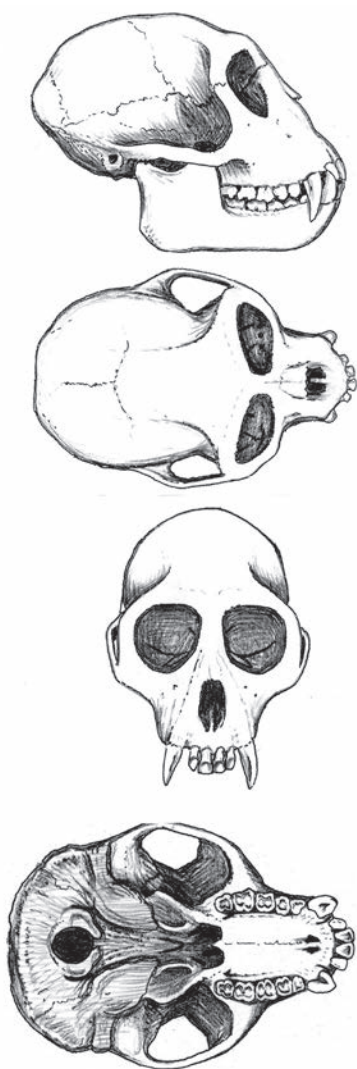
Cercopithecus dryas

upper surface. Distal ca. 10 cm of tail black with relatively long hairs. Scrotum light blue. White parts of the body sharply demarcated and strongly contrasting with black parts of the body, especially the white around the face, and on the chest and buttocks. See photos in Koruda *et al.* (1985: 327). In juvenile: brow-band, area around face, throat and ear tufts white; crown and dorsum greenish-gold with yellow ticking and rufous highlights; limbs duller than back, whitish medially (no black); dorsum of hands and feet dirty grey; ventrum mouse-grey; tail black at the base and rufous-green distally (Schwarz 1932, Napier 1981, Kuroda *et al.* 1985, Kingdon 1997, Groves 2001).

Geographic Variation None recorded.

Similar Species None within geographic range.

Distribution Endemic to one or a few small areas in DR Congo. Rainforest BZ. Distribution poorly-known. Although the provenance of the type *C. dryas* is given as Lomela (02° 20' S, 23° 12' E), it may be Yapatsi (01° 33' S, 23° 13' E) – or somewhere else (Thys van den Audenaerde 1977, Colyn 1988, Sarmiento 2000). Primate surveys in the Lomela area have failed to locate *C. dryas* (Hurley & Lokasola 2007). Only known from Kokolopori Forest, between right (north) bank of Maringa-Luo R. and left (south-west) bank of the Lopor R., Wamba region (Hurley & Lokasola 2007). There are, however, unconfirmed reports of *C. dryas* on the left bank of the Maringa-Luo R. (S. Koruda pers. comm.). Primate surveys have recently been conducted over a large region around Wamba, including the left bank of the Maringa-Luo R. and the right bank of the Lopor R. and *C. dryas* has not been encountered. While more intensive surveys may yield new populations of *C. dryas*, it now appears that *C. dryas* is a species with a very limited, fragmented, geographic range. Thus far, four, apparently isolated, populations of *C. dryas* have been located in the eastern part of Kokolopori Forest. Together, these four populations



Lateral, dorsal, frontal and palatal views of skull of Dryad Monkey *Cercopithecus dryas* adult male.

cover an area of ca. 500 km². The extent of occurrence is estimated at 3000 km² (Hurley & Lokasola 2007).

Habitat Main habitat is undergrowth (thicket) in secondary lowland moist forest, but also in swamp forest and old plantation (Kuroda *et al.* 1985). Primary forest is not used; indeed, primary forest may serve as a barrier among populations of *C. dryas* (Hurley & Lokasola 2007). J. Hart (pers. comm.) suggests that *C. dryas* is limited to small pockets of relatively high productivity in an otherwise oligotrophic region. The result is a localized and patchy distribution, not only for *C. dryas*, but also for humans, Gracile Chimpanzees (Bonobos) *Pan paniscus*, Tshuapa Red Colobus *Procolobus rufomitratus tholloni*, and probably numerous other species. Altitude ca. 380 m asl. Mean annual rainfall ca. 1900 mm.

Abundance Poorly known. Population density low in the Wamba region, but not considered rare (Kuroda *et al.* 1985). Recent surveys lead Hurley & Lokasola (2007) to suggest that the world population for *C. dryas* may be <200 individuals. Although S. Kuroda (pers. comm.) agrees that *C. dryas* is rare, he believes that the number remaining is >200 individuals. In 2006 he conducted one survey

along 1.5 km of transect through abandoned plantation to the south-west of Wamba. During this survey he encountered six groups of *C. dryas*. Although the visibility along the transect was poor, the number of individuals observed in these groups ranged from two to ten.

Adaptations Diurnal and arboreal. Highly secretive and cryptic in dense vegetation, usually close to the ground. Sometimes forages on the ground. When on the ground and threatened or surprised, moves quickly upward into dense undergrowth/thicket. Not observed in the middle canopy or upper canopy (S. Kuroda pers. comm.). Relatively large temporal muscles and large jaws. Dentition unusual in that the upper incisors are splayed, narrow and small (Kuroda *et al.* 1985, Kingdon 1997). Although the adaptive significance of these characters is not known, S. Kuroda (pers. comm.) suggests that the large jaw may be an adaptation for chewing foods that are more fibrous than are typically eaten by other *Cercopithecus* spp., especially food items from plant species in the families Zingiberaceae and Marantaceae.

Foraging and Food Omnivorous. Forages mostly in the lower stratum of secondary forest but also frequently on the ground. Diet poorly-known. Feeds on fruits supplemented with young leaves and shoots (Kuroda *et al.* 1985). S. Kuroda (pers. comm.) reports *C. dryas* feeding on the tips of shoots of arrowroot *Megaphrynium macrostachum* (Marantaceae), *Haumania liebrechtsiana* (Marantaceae), *Sarcophrynium schweinfurthii* (Caesalpinaceae) and ginger *Aframomum* spp. (Zingiberaceae), and the fruits of *Calancoma welwitschii* (Achariaceae). Dryas Monkeys appear to be most active early in the morning and late in the afternoon, becoming much more difficult to locate after ca. 10:00h (S. Kuroda pers. comm.). Preliminary studies on four groups indicate home-range areas of 2.8–7.0 ha (Hurley & Lokasola 2007).

Social and Reproductive Behaviour Social. According to Kuroda *et al.* (1985), group size is typically 2–15 individuals, but groups of up to 30 individuals occur. The four groups under study at Kokolopori comprise 15–31 individuals (Hurley & Lokasola 2007). Dryas Monkeys are polygynous, with one adult ♂ per group, occasionally with extra-group ♂♂. Solitary adult ♂♂ occur (Kuroda *et al.* 1985). Calls and vocal behaviour not yet described other than a ‘chirp’ alarm call that is given only once or a few times before group members flee. No loud-call described. Local people say that *C. dryas* does not have a loud-call (S. Kuroda pers. comm.). Forms polyspecific associations with other species of primates (Kuroda *et al.* 1985), including Red-tailed Monkey *Cercopithecus ascanius* (S. Kuroda pers. comm.).

Reproduction and Population Structure No information available.

Predators, Parasites and Diseases Humans appear to be the primary predator for *C. dryas*. Probable predators are African Crowned Eagles *Stephanoetus coronatus*, Leopards *Panthera pardus*, African Golden Cats *Profelis aurata* and Central African Rock Pythons *Python sebae*. No information on diseases and parasites.

Conservation IUCN Category (2012): Critically Endangered. CITES (2012): Appendix II.

The emerging picture from current field research is that *C. dryas* may be Africa's most threatened species of primate. The two main threats to *C. dryas* are hunting for the commercial bushmeat trade and loss of habitat to agriculture (Hurley & Lokasola 2007). While conducting research on *P. paniscus* at Wamba during the 1980s, S. Kuroda (pers. comm.) found *C. dryas* in most areas with secondary forest thicket. By 2006 this was no longer the case as *C. dryas* in the Wamba area now appears to be largely restricted to areas of old plantation. S. Kuroda (pers. comm.) has observed a general decline of the larger mammal fauna in this area as a result of hunting for bushmeat.

Cercopithecus dryas is one of the least studied species of primate in Africa. Priorities for the conservation of *C. dryas* are: (1) a study of age-related pelage change to determine whether *C. salongo* is the same as *C. dryas*; (2) additional surveys to better understand distribution, abundance and conservation status; (3) long-term research on habituated groups to determine ecology, behaviour and habitat requirements; (4) molecular research to assess taxonomic status; and (5) the rapid establishment of a well-managed, well-funded, protected area that encompasses the entire known geographic range of this species (Butynski 2002a, Grubb *et al.* 2003). The entire known geographic range for *C. dryas* falls within the

new, community-based Kokolopori Bonobo Reserve (ca. 4875 km²). Effective management of this Reserve is not only important to the conservation of *P. paniscus* in this region, it is critical to the survival of *C. dryas*. There is no captive population for *C. dryas*.

Measurements

Cercopithecus dryas

HB (♀): 380 mm, n = 1

T (♀): 500 mm, n = 1

HF: n. d.

E: n. d.

WT (♂): 3.0 kg, n = 1

WT (♀): 2.2 kg, n = 1

Young adult ♂ and fully adult ♀ from Kokolopori Forest, DR Congo (Kuroda *et al.* 1985)

Key References Colyn *et al.* 1991; Hurley & Lokasola 2007; Kuroda *et al.* 1985; Sarmiento 2000; Thys van den Audenaerde 1977.

Thomas M. Butynski

Cercopithecus (diana) GROUP Diana Monkeys Group

Cercopithecus diana (Linnaeus, 1758). Systema Naturae, 10th edn, 1: 26. Liberia.

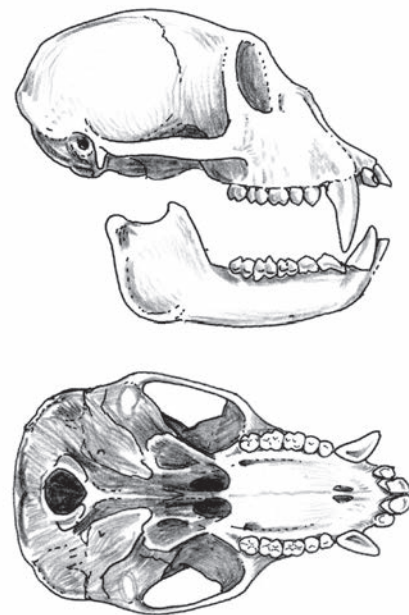
The *Cercopithecus (diana)* Group embraces two species, the Diana Monkey *Cercopithecus diana* and the Roloway Monkey *Cercopithecus roloway*. Apart from Schreber (1774), who described and named the Roloway Monkey and Elliot (1913b), the Diana monkeys have been treated as subspecies of a single species. Here we follow Groves (2001), who emphasized that the differences between the two forms are absolutely clear-cut and that they stand as distinct species.

Both species are dark grey with white banding and a deep maroon lumbar saddle; most of underside black, except for the chest, throat and inner arms, which are white, sharply separated from the black of the underside; inner surfaces of legs are either red or yellow; characteristic white stripe across the haunch; facial skin jet black; prominent, narrow beard on the chin; and pale brow-band, shaped like a crescent moon (hence the species is named after Diana, the Roman moon goddess). The two species are separated by the shape and colour of the beard and brow-band, colour of the buttocks and inner surfaces of the thighs, and the number of agouti-bands on the hairs.

Cercopithecus diana ranges from Sierra Leone to the Sassandra R., Côte d'Ivoire; *C. roloway* originally ranged from the Sassandra R., Côte d'Ivoire, to the Pra R., Ghana, but is now close to extinction.

Both species are almost entirely arboreal and dependent on a continuous canopy. They show a strong preference for high canopy, primary rainforest but are also found in mature secondary, riverine and semi-deciduous forests and galleries. These are fast, highly vocal, conspicuous monkeys. Their foraging strategy seems to be that of coarse-grain foragers, moving rapidly over a relatively large range and relying upon good shared communication, rapid reaction times and fast escapes to mitigate predation.

Colin P. Groves & Jonathan Kingdon



Lateral and palatal views of skull of Diana Monkey *Cercopithecus diana* adult male.

Cercopithecus diana **DIANA MONKEY**

Fr. Diane (Capitaine); Ger. Diana-Meerkatze

Cercopithecus diana (Linnaeus, 1758). Systema Naturae, 10th edn, 1: 26. Liberia.Diana Monkey *Cercopithecus diana* adult male.*Cercopithecus diana*

Taxonomy Monotypic species. *Cercopithecus diana* has long been regarded as one species with two subspecies, the Diana Monkey *C. diana* and the Roloway Monkey *C. roloway* (e.g. Kuhn 1967, Napier 1981, Oates 1988b, 2011), but Groves (2001, 2005c) treats *diana* and *roloway* as distinct species within the *Cercopithecus (diana)* Group (or Superspecies). Grubb *et al.* (2003) revert to the traditional two-subspecies taxonomy. Synonyms: *faunus*, *ignita*. Chromosome number: $2n = 58$ (Dutrillaux *et al.* 1988b).

Description A brightly coloured, long-limbed, long-tailed, arboreal monkey, with beard, white chest and white thigh stripe. Adult ♀ like adult ♂ in colouration but smaller, weighing about 75% as much. Face black. Brow-band white, not prominent. Throat, cheeks, chest and inner arms white. Beard square, ca. 20 mm long, blackish at base and white at tip. Ears tufted. Shoulders, anterior part of back, sides, outer arms and ventrum black or dark grey. Posterior part of back with a chestnut 'saddle'. Inner thigh russet-orange. Outer thigh black with white femoral (thigh) stripe. Feet and tail black. Neonate with head, shoulders, back, sides, ventrum, feet and tail dark grey. Chest white. Adult colouration develops within 12 months of birth.

Geographic Variation None recorded.

Similar Species Unlikely to be confused with any sympatric species.

Cercopithecus roloway. Allopatric (east of Sassandra R., Côte d'Ivoire; Oates 1988b). Beard much longer (80–100 mm), pointed, all white; ear-tufts absent; inner thighs creamy white or yellow; brow-band white, greater lateral extent, more prominent.

Distribution Endemic to Guinea, Sierra Leone, Liberia and Côte d'Ivoire. Rainforest BZ. Restricted to lowland rainforest from W Guinea eastwards through Sierra Leone and Liberia to Sassandra R., Côte d'Ivoire (the boundary with *C. roloway*; Oates 1988b, Grubb *et al.* 1998). Tappen (1960) noted the western limits of the range as 13°N, 17°W in Gambia, but this record is probably spurious. Most westerly recent record is from Kounounkan Forest, Forécariak Province, W Guinea, at about 12°30'W (Barnett *et al.* 1994).

Habitat Appears to prefer relatively undisturbed high moist forest but seen occasionally in regenerating farmbrush (Oates 1988b, Hill 1991, Fimbel 1994b). Mean annual rainfall at Diana Monkey study sites ranges from 1700 mm (Taï N. P., Côte d'Ivoire; McGraw & Zuberbühler 2007) to 2708 mm (Tiwai I., Sierra Leone; Oates & Whitesides 1990). This species occurs from just above sea level in S Sierra Leone to at least 1300 m in the Loma Mts, Sierra Leone.

Abundance Diana Monkeys were common at Tiwai I. (30–43 ind/km²; Whitesides *et al.* 1988), but their numbers were decimated during the 1991–2002 civil conflict (Stephan 2008). Common in Taï N. P.; of 70 ind/km² (calculated from group densities and mean group size cited in Holenweg *et al.* 1996), 48.2 ind/km² (Zuberbühler & Jenny 2002) and, for 2006–08, 1.45 groups/km², 16.9 ind/km², and total population of 97,000 (N'Goran *et al.* 2012). Density in Sapo N. P., Liberia, in 1988–89, was 11 ind/km² (calculated from group density and mean group size; Agoramoorthy 1989). Density in Gola Forest, Sierra Leone, ca. 71 ind/km² (Klop *et al.* 2008).



Diana Monkey *Cercopithecus diana* adult male.

Adaptations Diurnal and arboreal. Long limbs, narrow hands and feet, and long tail enable Diana Monkeys to travel and forage in all forest strata using a range of differently sized supports. Whilst not restricted to a particular forest stratum, and sometimes moving on the ground, they spend most of their time in the higher strata (Whitesides 1991, McGraw 1998a, McGraw & Sciulli 2011). Buzzard (2006b) found that this species spends 2% of its time on the ground, 18% at 0–5 m, 43% at 5–20 m and 38% in the canopy (i.e. >20 m). They are terminal branch feeders, adopting a range of postures to access foods, including the ‘stand/forelimb suspend’ posture and occasionally suspending themselves by both hindlimbs. They use the tail for additional support, curling it round tree branches and trunks (McGraw 1998c). Activity budget varies across studies. At Tiwai I., activity budget was: foraging and feeding 35%, travelling 25%, resting 21%, vigilance (scanning) 8%, social behaviour 6% (Hill, 1991), but Whitesides (1991) observed higher rates of foraging & feeding (48%) and substantially lower levels of resting (1%). At Tã, activity budget was: feeding 33%, travelling 28%, foraging 28%, resting 9% and social behaviour 1% (McGraw 1996).

Foraging and Food Omnivorous. Diana Monkeys feed mainly on fruits and arthropods. Most arthropod feeding occurs in the tops of emergent trees. Foraging and prey capture techniques suggest most prey is slow-moving or stationary. Animals search through leaves turning them over to inspect the underside, removing food items with fingers and occasionally lips. They scan the crowns of flowering emergent trees, making a sudden grabbing action with one and sometimes both hands. At Tã, dietary overlap is greater between Diana Monkey and Campbell’s Monkey *Cercopithecus campbelli* than between Diana Monkey and Lesser Spot-nosed Monkey *Cercopithecus petaurista*. Inter-specific feeding competition is reduced partly through occupation of different vertical strata (Buzzard 2006b).

Leaves, flowers and seeds are eaten to a lesser extent (Hill 1991, Whitesides 1991, Eckardt & Zuberbühler 2004). They occasionally raid bird nests for eggs or nestlings (Hill 1991), and eat foam nests

of the tree frog *Chiromantis rufescens* (Rödel *et al.* 2002). Like other guenons they exhibit dietary flexibility. A greater proportion of leaves and flowers, and less fruit, is eaten at Tiwai I. than at Tã (Galat & Galat-Luong 1985, Whitesides 1991, Wachter *et al.* 1997), possibly reflecting differences in food availability between sites. Ripe fleshy fruits are eaten when available, e.g. *Landolphia hirsuta* and *Uapaca guineensis* (Hill 1991). Fleshy arils encasing *Pycnanthus angolensis* seeds are also eaten at Tiwai I., as is fluid from the unripe pods of *Funtumia africana* and *Holarrhena floribunda* (Hill 1991, Whitesides 1991). Also eat fallen fruits (Buzzard 2006b).

Social and Reproductive Behaviour Social. Diana Monkeys live in groups of 15–30 individuals. Groups comprise 1–2 adult ♂♂ and 6–13 adult ♀♀ and young (Hill 1991, 1994, Whitesides 1991, Buzzard 2006b, Wolters & Zuberbühler 2003). Solitary adult ♂♂ observed travelling and feeding within group home-ranges at Tiwai I. (Oates & Whitesides 1990, Hill 1991). Adult ♀♀ and young groom each other regularly; the adult ♂ is rarely seen allogrooming but is groomed by adult ♀♀ (Hill 1991, Buzzard & Eckardt 2007). Few agonistic interactions seen among members of the same group at Tiwai, though some displacements over preferred food resources observed (C. M. Hill pers. obs.). Home-range sizes at Tã of 93 ha ($n = 1$; Galat & Galat-Luong 1985), 67 ha ($n = 1$; Holenweg *et al.* 1996) and 59 ha ($n = 2$; Buzzard & Eckardt 2007) are greater than those reported for Tiwai by Hill (1991) (Group W: 40 ha; Group E: 37 ha) and by Whitesides (1991) (Group W: 42 ha; Group E: 29 ha). Neighbouring groups’ ranges overlap by 16–29% at Tiwai (Hill 1991) and by 65–67% at Tã (Buzzard & Eckardt 2007). Diana Monkeys are active animals and travel extensively. Mean day range length at Tiwai (1668 m/day) differs between groups and across seasons (730–3125 m/day, $n = 103.5$ days, $n = 2$ groups). Mean day range significantly longer during the dry season (Hill 1991, Whitesides 1991). Conversely, at Tã, longest day ranges occur during the main wet season ($1,274 \pm 351$ m, $n = 8$ days, $n = 1$ group) and shortest day ranges occur during the main dry season (965 ± 368 m, $n = 8$ days, $n = 1$ group; Buzzard 2006c). Mean day range at Tã, 1215–1240 m/day ($n = 56$ days, $n = 1$ group), is comparable with Tiwai figures (Holenweg *et al.* 1996). At Tiwai group spread is typically >100 m and sometimes in excess of 200 m (Oates & Whitesides 1990); at Tã group spread is typically ca. 70 m (R. Noë, unpublished data, cited in Zuberbühler 2000c). This difference between the two sites may be a reflection of the much higher predation risk at Tã than Tiwai. Home-range use is strongly influenced by fruit availability and interactions with neighbouring conspecifics. Animals at Tiwai spend more time in boundary/overlap regions during the breeding season, a time when there is increased inter-group calling behaviour (Hill 1991).

Diana Monkeys defend exclusive territories against conspecifics. Inter-group encounters were rare at Tiwai but when groups met only adult ♀♀ and immature animals were seen chasing, threatening, biting and pulling members of the intruder group. Adult ♂♂ remained at the top of emergents, giving loud-calls and displaying by bouncing, stiff-legged, through the canopy, and producing additional noise by breaking twigs and small branches. Inter-group calling bouts were common; ♀♀ give ‘chatter-screams’ that incite the adult ♂ to give loud-calls (Hill 1994).

Several matings observed at Tiwai; the adult ♂ approached the adult ♀ and mounted her briefly. Infants are carried ventrally by the

mother. They are carried occasionally by immature animals during play (C. M. Hill pers. obs.).

Diana Monkeys have a rich repertoire of vocalizations comprising contact calls, alarm calls and inter-group calls. Contact calls are given almost exclusively by adult ♀♀ and immature animals, and comprise a range of whistles and trills, given during most group activities. All members of group give alarm calls. Research at Tāi indicates adult ♂♂ and adult ♀♀ give different, sex-specific alarm calls that convey information about the predator type (Zuberbühler *et al.* 1997, 1999). Animals modify their calling behaviour to avoid detection by specific predators, using calling and mobbing behaviour to warn off African Crowned Eagles *Stephanoaetus coronatus* and Leopards *Panthera pardus* (Zuberbühler 2000a, Bshary 2001). Male and ♀ Diana Monkeys also use calls to advertise territorial possession. Adult ♀♀ initiate inter-group calling bouts; the adult ♂ gives his loud-call after group ♀♀ have given several 'chatter-screams' (a short, quiet vocalization that is difficult to locate the source of) (Hill 1994). Males also use loud-calls to engage in male–male competition in the form of inter-male calling bouts (Hill 1991). Diana Monkeys respond to alarm calls of sympatric species (Oates & Whitesides 1990). Their response to alarm calls of Campbell's Monkeys suggest they understand the semantic context in which Campbell's Monkey alarm calls are given (Zuberbühler 2000b).

Diana Monkeys spend much of their time in association with other primate species. This is thought to be an anti-predator strategy (Oates & Whitesides 1990, Whitesides 1991). At Tiwai, Olive Colobus *Procolobus verus* groups are in permanent association with Diana Monkey groups; these associations are maintained by the Olive Colobus (Oates & Whitesides 1990). At Tāi, Diana Monkeys associate with Olive Colobus (Galat & Galat-Luong 1985), Campbell's Monkeys (Zuberbühler 2000b), Lesser Spot-nosed Monkeys (Buzzard 2010) and Western Red Colobus (Noë & Bshary 1997). Diana Monkeys were not observed in association with Western Red Colobus at Tiwai; this difference between the two sites may reflect the greater predation pressure at Tāi as compared with Tiwai (Holenweg *et al.* 1996).

Reproduction and Population Structure There are few data from wild populations on reproductive parameters. Diana Monkeys do not have sexual swellings. Average gestation in captivity is 180 days (Stevenson 1993). Diana Monkeys are seasonal breeders, giving birth to singletons. At Tiwai new infants observed from late Dec to early Feb (Hill 1991) and Jan–Apr (Whitesides 1989); at Tāi births reported from Oct–Jan (Uster & Zuberbühler 2001). Captives in UK show some seasonality with 50% of births during Mar–Jun ($n = 634$; G. Catlow pers. comm.). Birth season in the wild coincides with the early dry season, a period of relatively high abundance of flowers, fruits and seeds; thus the diet contains a high proportion of fruits and seeds during late gestation and early lactation, as in other guenon species (Butynski 1988, Hill 1991).

Birth-weights for wild Diana Monkeys not available. Mean birth weight for two captives is 475 g (R. D. Martin, A. McLarnon & R. Rudder pers. comm.). Mean inter-birth interval for captives is 590 days ($n = 150$; G. Catlow pers. comm.); average inter-birth intervals may be longer in wild populations if food quality and availability influences ♀ reproduction. Estimates from wild observations

suggest weaning is complete by ca. 12 months (C. M. Hill pers. obs.). Mean age at first reproduction in captivity is 87 months (ca. 24–147, $n = 167$) for ♀♀ and 105 months (ca. 105–185, $n = 143$) for ♂♂ (G. Catlow pers. comm.) Live to >25 years in captivity.

Using census data, group size and structure data from Tiwai ($n = 2$ groups), and taking into account solitary ♂♂, population sex ratios (adult ♂♂ : adult ♀♀) are ca. 1 : 3.0–3.5/km² and adults to immatures ratios are ca. 1 : 1.3–1.4/km².

Predators, Parasites and Diseases Humans have been, and continue to be, the most important predators of Diana Monkeys (Bshary 2001, Koné & Refisch 2007, McGraw 2007b). Robust Chimpanzees *Pan troglodytes*, Leopards *Panthera pardus* and African Crowned Eagles are also predators of Diana Monkeys (Hoppe-Dominik 1984, Boesch & Boesch 1989, Zuberbühler & Jenny 2002, 2007, Shultz & Thomsett 2007, Oates 2011).

Conservation IUCN Category (2012): Vulnerable. CITES (2012): Appendix I.

Populations affected by habitat loss through agricultural expansion and intensive commercial logging, and by hunting for bushmeat. In Gola F. R., Sierra Leone, Davies (1987) found the highest Diana Monkey densities where there was light hunting pressure, whereas none was encountered where hunting pressure was intense (Mahoi Forest, Gola East Forest). Where hunting pressure was light, he encountered Diana Monkeys at similar frequencies in selectively logged and unlogged forest. In a 1989–90 survey in Liberia, just before that country's civil war, Dunn (1991) found that Diana Monkeys were the third most vulnerable primate to hunting pressure, following Western Red Colobus and King Colobus *Colobus polykomos*. See also N'Goran *et al.* (2012). Important sites for the long-term survival of Diana Monkey are Tiwai Island Wildlife Sanctuary, the proposed Gola Forest N. P., the proposed Loma Mountains N. P., Sapo N. P. and Tāi N. P.

Measurements

Cercopithecus diana

HB (♂♂): 525, 615 mm ($n = 2$)

HB (♀♀): 440, 450 mm ($n = 2$)

TL (♂♂): 820, 901 mm ($n = 2$)

TL (♀♀): 700, 725 mm ($n = 2$)

HF: n. d.

E: n. d.

WT (♂♂): 5.2 (4.0–6.3) kg, $n = 4$

WT (♀♀): 3.9 (2.9–4.9) kg, $n = 11$

Linear measurements: locality not given (Napier 1981)

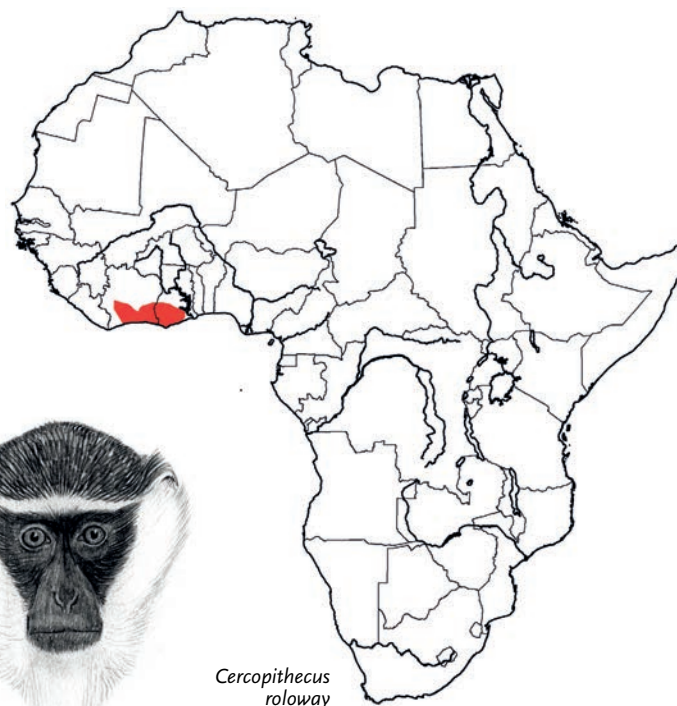
WT: three ♂♂ and ten ♀♀ from Liberia in collection of H.-J. Kuhn, Göttingen, Germany, one ♂ from near Tiwai, Sierra Leone, weighed by J. F. Oates in Kambama (Oates & Whitesides 1990), and one ♀ from Côte d'Ivoire in USNM.

Key References Buzzard 2006b, c; Hill 1991; McGraw & Zuberbühler 2007; Oates 2011; Oates & Whitesides 1990; Whitesides 1991).

Catherine M. Hill & John F. Oates

Cercopithecus roloway ROLOWAY MONKEY

Fr. Diane roloway (Palatine); Ger. Roloway-Meerkatze

Cercopithecus roloway (Schreber, 1774). Die Säugethiere 1: 186. 'Guinea' (= West Africa in general).*Cercopithecus roloway*ABOVE AND RIGHT: Roloway Monkey *Cercopithecus roloway* adult male.

Taxonomy Monotypic species. Recognized by some (e.g. Elliot 1913b, Groves 2001, 2005c) as a distinct species, but more often given subspecific status with the Diana Monkey *Cercopithecus diana* (e.g. Hill 1966, Napier 1981, Oates 1988b, 2011, Kingdon 1997, Grubb *et al.* 1998, 2003). Here the Roloway Monkey is treated as a full species within the *Cercopithecus (diana)* Group (or Superspecies). Colour of inner thighs white to pale yellow or orange in Ghana to rusty red at the Sassandra R., Côte d'Ivoire, making the Sassandra population identical to *C. diana* in this character (Oates 1988b), but beard length and colour, and brow-band width and colour distinguish the two species (Schreber 1774, Erxleben 1777, Allemand 1799, Schlegel 1876, Jentink 1898, Pocock 1907, Elliot 1913b, Booth 1956a, b, Groves 2001, 2005c). Synonyms: *palatinus*. Chromosomes: $2n = 58$ (Napier 1981, Dutrillaux *et al.* 1988b).

Description An elegant monkey, long-limbed and long-tailed, with richly coloured and complex markings, including pure white beard, chest and thigh stripe. Adult ♀ like adult ♂ in colouration but smaller. Face black, framed by broad white diadem and long (80–100 mm) all-white pointed or forked beard. Sides of throat, chest to nipples, and inner arms pure white. Crown black, shading into dark

grey on nape and sides. Ears lack tufts. Shoulders dark grey grading into a deep mahogany 'saddle' that widens over the rump and extends onto the base of the tail. Hairs of dorsum usually with more than four pairs of alternating light and dark bands (Groves 2001). White stripe on thigh extending from underside of tail and curving along outer thigh to knee, separating dark grey dorsal pelage from black pelage of outer thigh and lower leg. Ventrums, hands and feet black. Inner thighs and perineum cream to apricot in Ghana to rusty-red at the Sassandra R. Tail black, >130% length of HB. Pattern of natal pelage like adult but with paler colours.

Geographic Variation None recorded except as noted above.

Similar Species Unlikely to be confused with any sympatric species.

Cercopithecus diana. Allopatric (west of Sassandra R., Côte d'Ivoire; Oates 1988b). Brow-band a narrow white or cream crescent; not prominent. Beard short (ca. 20 mm), square, blackish at chin, white distally. Ears tufted. Hairs with four pairs only of alternating light and dark bands (Groves 2001). Inner thighs and perineum bright red-bay.

Distribution Endemic to Côte d'Ivoire and Ghana. Rainforest BZ. From Sassandra R., Côte d'Ivoire, north and east to Goaso in the Brong-Ahafo Region and east to Pra R., Ghana (Oates 1988b, Grubb *et al.* 1998, Oates *et al.* 2000a), but reported farther east in Kakum N. P., Ghana (P. Symonds pers. comm.).

Habitat Confined to wet evergreen, moist evergreen, moist semi-deciduous primary forest (Hall & Swaine 1981) and old secondary forest (Booth 1956b). In Bia N. P., Ghana, Roloway Monkeys are near sea level. Annual rainfall here 1441 mm in 1976 and 938 mm in 1977 (S. Curtin pers. obs.).

Abundance At low population densities throughout geographic range. Nowhere abundant at this time. About 8 ind/km² in Bia N. P., during 1976–77 (Curtin 2002).

Adaptations Diurnal and arboreal. Body slender, long limbs and long tail, long narrow hands and feet. An agile inhabitant of the middle and upper strata of mature rainforest. Exploits small, unstable terminal branches of emergent trees for insects, despite relatively large body size for a guenon. Bright coat colours and conspicuous markings may be related to social communication and associated with emphatic postures and displays (Kingdon 1997).

Foraging and Food Omnivorous. Diet largely ripe fruits and invertebrates. Eats significant proportion of seeds and, in the wet season, young leaves and flowers. Diet of one Roloway Monkey group in Bia N. P. over a nine-month period consisted of 31% mature fruit pulp, 25% invertebrates, 22% seeds of mature fruit, 7% new leaves and leaf buds, 6% flower buds and flowers, and 9% other (n = 3224 feeding scores). Pulp of mature fruit and invertebrates, especially small immobile insects in the terminal branches of *Piptadeniastrum africanum*, are the two most important food categories both in dry and wet seasons; seeds of mature fruit, especially the oil-rich seeds of *Pycnanthus angolensis*, is the third leading category in the dry season, replaced by new leaves and flowers in the wet season. They ate plant parts from >130 species of trees, climbers and epiphytes and took invertebrate prey (caterpillars, moths, ants, scale insects, beetles, grasshoppers, millipedes, spiders) from leaf, twig and bark surfaces of an additional 22 tree species (Curtin 2002).

One bisexual group in Bia N. P. comprised 15 animals and had a home-range of 189 ha.

Group members dispersed during foraging, often spread >100 m. Day ranges in the dry season averaged 2280 m (997–3038 m, n = 25 days), in the wet season 1505 m (939–2382 m, n = 25 days). Roloway Monkeys frequently forage in association with White-thighed Colobus *Colobus vellerosus*, especially in the wet season (May–Jul), the period of greater insect abundance (average daily association time: 4.63 h). They actively initiate and maintain these associations and apparently use the colobus to dislodge insects as they forage beneath, or to flush insects from arboreal pathways as they follow close behind (Curtin 2002).

Social and Reproductive Behaviour Social. A typical social group (n = 3 groups) contains 15–20 animals including only one adult ♂, although a second adult ♂ may be tolerated by the resident ♂ during non-breeding months (Nov–Jan). Groups are territorial and maintain spacing by long-calls that can be heard by the human ear to >1.5 km. Occasional incursions made by solitary extra-group ♂♂ are repelled by the resident ♂. No all-male groups observed. One territory 189 ha. Only the resident adult ♂ forms consortships and performs serial mounts and intromissions, although a subadult ♂ may steal single mounts with intromission. Roloway Monkeys form transient inter-specific associations with groups of *C. vellerosus*,

Lesser Spot-nosed Monkeys *Cercopithecus petaurista* and Lowe's Monkey *Cercopithecus lowei* (Curtin 2002).

Reproduction and Population Structure Births recorded at Bia N. P. in late Nov–early Dec (2) and in Mar (1). Copulations recorded Feb–Jul, peaking in Jul (n = 12; no observations Aug–Oct). Sex ratio: 4 ♂♂ to 7 ♀♀ (includes extra-group ♂♂). Adult to young ratio: 9 : 7 (Curtin 2002). Lives to at least 30.7 years in captivity (Jones 1962).

Predators, Parasites and Diseases Probably the same predators as for *C. diana*. Humans are the Roloway Monkey's most significant predator. African Crowned Eagles *Stephanoaetus coronatus* prey on other monkeys in Bia N. P. (Martin 1991) and presumably also prey on Roloway Monkeys. Diseases unknown.

Conservation IUCN Category (2012): Endangered (as *C. diana roloway*). CITES (2012): Appendix I as *C. diana roloway*.

Currently listed among the 25 most threatened primate taxa in the world (McGraw & Oates 2009). Together with the White-naped Mangabey *Cercocebus lunulatus* and Miss Waldron's Red Colobus *Procolobus badius waldroni*, the Roloway Monkey is among the three most threatened monkeys of the Upper Guinea Forest Block (Oates 1996a). Severely impacted throughout its geographic range by habitat loss due to logging, clearing of forest for subsistence farming and oil palm plantations, and by hunting for the bushmeat trade (Asibey 1978, Lee *et al.* 1988, Oates 1996a, 1999, McGraw 1998d, Oates *et al.* 2000a). Roloway Monkeys are especially vulnerable because their high canopy habits and long-carrying territorial calls advertise their presence to hunters. Highest priority should be given to protection of Krokosua Hills (L. Magnuson pers. comm.), Ankasa Reserve and Nini-Suhien N. P. in Ghana (Oates 1996a), and to the Tanoé Forest in Côte d'Ivoire (Koné & Akpatou 2005, McGraw & Oates 2009, Gondelé Bi *et al.* 2012).

Measurements

Cercopithecus roloway

HB (♂): 636 mm, n = 1

T (♂): 839 mm, n = 1

Locality of collection not known (Schlegel 1876)

HB: 512 mm, n = 1

T: 755 mm, n = 1

HF: 135 mm, n = 1

Sex and locality of collection not stated (Elliot 1913b)

HB (♀): 422 mm, n = 1

T (♀): 515 mm, n = 1

HF (♀): 118 mm, n = 1

E (♀): 29 mm, n = 1

WT (♀): 2.3 kg, n = 1

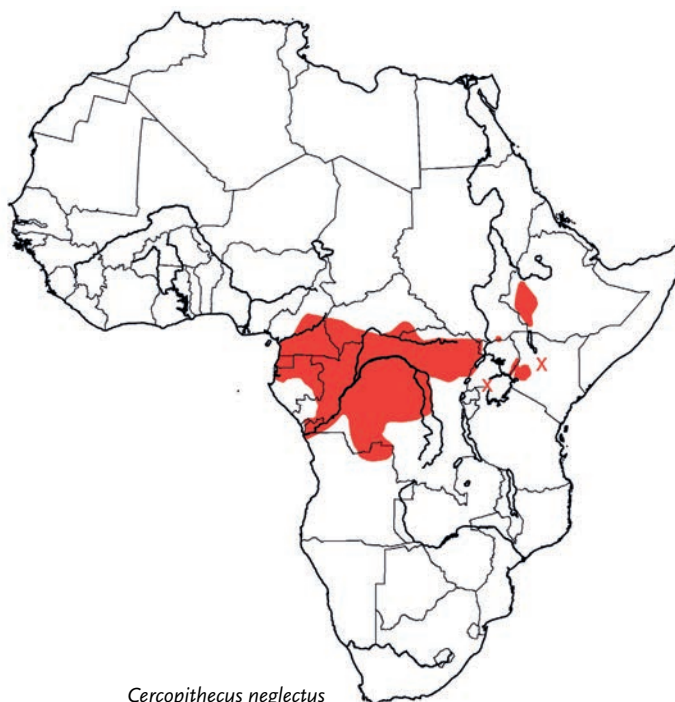
Captive at Chester Zoo, UK (Hill 1966)

Key References Curtin 2002; Grubb *et al.* 1998; Hill 1966; Kingdon 1997; Martin 1991; Oates 2011.

Sheila H. Curtin

Cercopithecus neglectus DE BRAZZA'S MONKEY

Fr. Cercopithèque de Brazza; Ger. Brazza-Meerkatze

Cercopithecus neglectus Schlegel, 1876. Mus. Hist. Nat. Pays-Bas. Simiae, p. 70. 'White Nile', SE Sudan.De Brazza's Monkey *Cercopithecus neglectus* adult male.*Cercopithecus neglectus*

Taxonomy Monotypic species. Age variation in pelage of a juvenile *Cercopithecus neglectus* specimen led Pocock (1908) to erroneously name *Cercopithecus ezrae*. Phylogenies inferred from blood proteins (Ruvolo 1988), chromosomes (Dutrillaux *et al.* 1988b) and vocal repertoires (Gautier 1988) agree in placing De Brazza's Monkey in the *Cercopithecus* (*mona*)–(*diana*) cluster. The geometry of colours and white beard resemble Diana Monkey *Cercopithecus diana* and Roloway Monkey *Cercopithecus roloway* (Pocock 1908). Phylogenies drawn from genetic analyses do not differentiate *C. neglectus* from the arboreal cercopithecines and its exact phylogenetic position remains unresolved (Disotell 1996). Synonyms: *brazzae*, *brazziformis*, *ezrae*, *uellensis*. Chromosome number: $2n = 62$ (Dutrillaux *et al.* 1988b).

Description Robust, semi-terrestrial, long-tailed monkey with rufous brow, long white beard and white thigh stripe. Strongly patterned monkey with dense pelage. Adults of both sexes similar in colour, but ♂ almost twice as heavy as ♀. Muzzle, throat and long 'beard' white. Diadem bright rufous topped by a black stripe. Black mask surrounds eyes. Cheek-whiskers, back and flanks greyish-olive speckled with black. Forearms, hands, feet, belly and tail black. Inner thighs and buttocks dazzling white. White stripe down leg. Tail slightly longer than HB (ca. 120%) but relatively shorter than in arboreal guenons. Scrotum of adult ♂ bright blue (Hill 1966). Perineum of adult ♀ pink. Newborn infants entirely yellowish with pink face, hands and feet. Infantile pelage retained up to 4–5 months. Adult pelage takes about four years to develop (Kirkevoold & Crockett 1987, A. Gautier-Hion pers. obs.). In between, fur gradually becomes speckled and turns brownish-grey; ventrum and tail become greyish. Bare skin on face becomes black; long white hairs grow on chin. At about two years, white beard becomes distinct, limbs and tail turn black, inner thighs and rump turn white and frontal diadem becomes more rufous. Upper black coronal bar appears at around four years.

Geographic Variation Some in eastern Africa have all-black forearms but this is not a common trait.

Similar Species Unlikely to be confused with any other monkey but juveniles may be difficult to identify on their own.

Distribution Endemic to equatorial Africa. Rainforest, Northern Rainforest-Savanna Mosaic, Eastern Rainforest-Savanna Mosaic, and Afromontane–Afroalpine BZs. From E Cameroon, Equatorial Guinea (Rio Muni), N Gabon and NE Angola eastwards through the Congo Basin to S Sudan, SW Ethiopia and C Kenya. Western limit is the Atlantic coast. North-western limit is Mbam & Djerem N. P., Cameroon, just north of the Sanaga R. (Maisels *et al.* 2007a). Northern limit is in gallery forests in N Central African Republic (08° 30' N; Fay 1988). Southern limit is 10° S in NE Angola. North-eastern limit is 07° 26' N, 35° 20' E in SW Ethiopia (Brown & Urban 1969). Eastern limit is in the Mathews Range F. R., C Kenya (01° 11' N, 37° 22' E; Mwenja 2007, De Jong & Butynski 2010a). The Mathews Range population, discovered in 2000 (Douglas-Dufresne 2005), is the only population east of the Eastern Rift Valley. Absent from western main Atlantic basins (except in Equatorial Guinea; Malbrant & Maclatchy 1949, Gautier-Hion *et al.* 1999). Found through most of Congo Basin except south of the Maiko R.

Historic Distribution: In East Africa, De Brazza's Monkeys were probably more regularly distributed in riverine forests in the past than at present. Noting the likelihood of some form of inter-specific intolerance limiting De Brazza's Monkeys in multi-species communities, Kingdon (1971) hypothesized that the species formerly 'must have

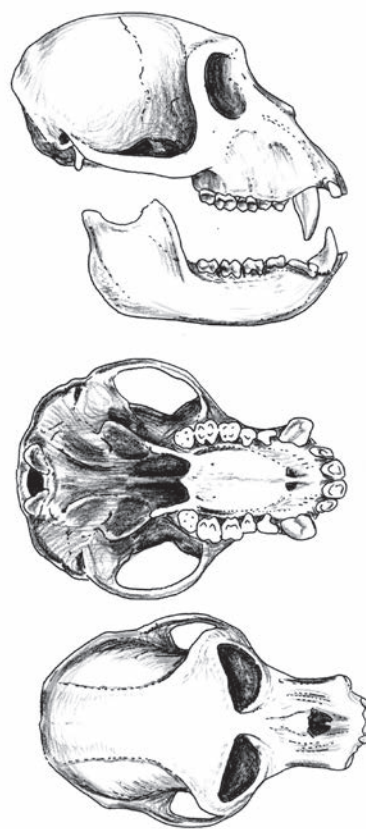
been very numerous to maintain a degree of gene-flow capable of sustaining the present homogeneity of the species over so vast an area of central and East Africa'. He also noted that De Brazza's Monkey is not limited to swamp forest throughout its range, being found in East Africa (where there are few other *Cercopithecus* species) in closed forests, in bamboo and along water-courses of dry montane forest. He suggests that, within eastern Africa, De Brazza's Monkey 'almost certainly ranged through all forest types in the past', an opinion that probably needs some qualification.

De Jong & Butynski (2010a) note that in central Africa, where primate communities in forests are typically comprised of at least four cercopithecine species, De Brazza's Monkey is an animal of lowland swamps and riverine forests (i.e. habitats with few cercopithecine species). In E Uganda and W Kenya, in the eastern part of the range, there are but one or two cercopithecine species in the forests and here De Brazza's Monkey appears to be less strongly associated with water and also occupies mid-altitude and dry montane forest (e.g. Mt Elgon to 2100 m; Kingdon 1971). At the eastern extreme of the range (Mathews Range), where there is no other forest cercopithecine species, De Brazza's Monkey is found >2 km from water and to an altitude of at least 2200 m in dry montane forest. These observations suggest that competition with other cercopithecine species (perhaps particularly Gentle Monkey *Cercopithecus mitis*) is a major factor in not only determining whether De Brazza's Monkey occurs, but also the habitats and altitudinal range occupied by this species. De Jong & Butynski (2010a) point out that the only site east of the Eastern Rift Valley where De Brazza's Monkey occurs (i.e. Mathews Range) is one of the few forested sites east of the Eastern Rift Valley in Kenya where *C. mitis* is absent.

Habitat Riverine species that inhabits periodically flooded forests, swamps, riverine forests and gallery forests. Found from 100 m up to 2200 m (Mathews Range; Mwenja 2007). Mean annual rainfall varies across the range from 700 to 4000 mm. In East Africa, De Brazza's Monkey occurs in forest pockets amidst expanding farmlands; occasionally found in secondary forests, *Acacia* woodlands and crops (Brennan 1985). Avoids primary forest with open understorey. In Central African Republic, Congo and DR Congo, group home-ranges always border or include a river (Gautier & Gautier-Hion 1969, Gautier-Hion & Gautier 1978, A. Gautier-Hion pers. obs.).

In undisturbed forest blocks in central Africa, De Brazza's Monkey depends on water-courses and is seldom observed farther than 300–400 m from a river and always selects dense undergrowth. Of 24 groups encountered in the Mathews Range during one study, all were <200 m from water except for one group that was ca. 1000 m from water (Mwenja 2007). However, of three groups encountered in the Mathews Range during another study, two groups were >2 km from a perennial stream (De Jong & Butynski 2010a).

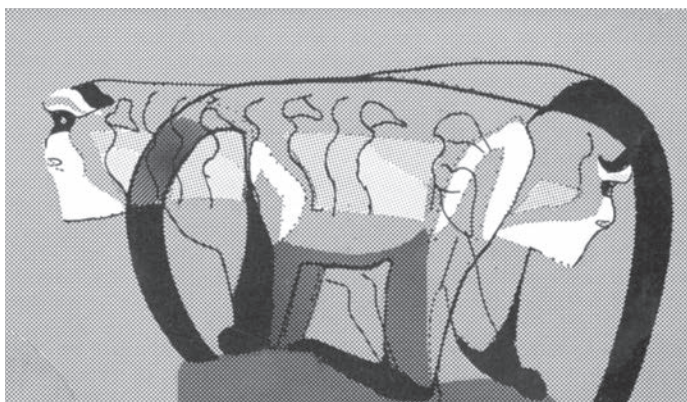
Abundance In large forest blocks densities vary from 0.2 ind/ha (Central African Republic; Brugière *et al.* 2005b) to 0.3–0.6 ind/ha (NE Gabon; Quris 1976, Gautier-Hion & Gautier 1978). Among forest islands in E Uganda and W Kenya, density varies from 0.2 to 2.6 ind/ha (Brennan 1985, Wahome *et al.* 1993, Decker 1995). At low density in the Mathews Range, with only three groups encountered along 62 km of transect (62 h) in forest (0.05 groups/km, 0.05 groups/h; De Jong & Butynski 2010a).



Lateral, palatal and dorsal views of skull of De Brazza's Monkey *Cercopithecus neglectus* adult male.

Adaptations Diurnal and semi-terrestrial. De Brazza's Monkey terrestriality increases with increasing density of ground cover and thickness of undergrowth (Quris 1976, Gautier-Hion & Gautier 1978, Wahome *et al.* 1993). De Brazza's Monkeys spend >20% of daylight hours on the ground and >50% under 5 m in dense understorey vegetation. In areas with open understorey they move at a height of <5 m height for only 20% of time, and on the ground for <10% of time. Adult ♂♂ more terrestrial than adult ♀♀ and young. De Brazza's Monkeys sleep at night in crowns of high trees located on or close to rivers (Gautier-Hion & Gautier 1978).

De Brazza's Monkey has the broadest and most robust foot of any guenon, resembling that of Allen's Swamp Monkey *Allenopithecus nigroviridis*, but more arboreally than terrestrially adapted (Kingdon 1988a). Postcranial skeleton is similar to those of arboreal monkeys (Gebo & Sargis 1994). Excellent swimmers, De Brazza's Monkeys cross rivers >300 m wide, plunge into water to avoid predators, and can swim under water. Young De Brazza's Monkeys play together in water (Gautier-Hion & Gautier 1971). Scent-marking of branches and trunks includes serial rubbing that involves muzzle, throat and chest, with or without rubbing and licking palms of the hands. Sternal region has specialized cutaneous glandular area (Loireau & Gautier-Hion 1988). In captives, scent-marking occurs in all age and sex classes except infants less than one year old. Adult marking bouts are more frequent and last longer than those of juveniles. Most marking sequences provoke responses from other group members, especially inducing over-marking. 'Freezing' posture also characterizes the De Brazza's Monkey and



Schematic diagram (from film) of De Brazza's Monkey *Cercopithecus neglectus* adult male during one 'sweep' of his loud call display. Superimposed outlines of head and beard indicate positions (from right to left) during this 2.2 second traverse.

occurs in all age/sex-classes. When 'frozen' the monkey keeps still and remains curled up with head lowered so that white beard and rump are hidden. Freezing can last for at least 5 h (Gautier-Hion & Gautier 1978). This species lacks an alarm call in its repertoire (Gautier & Gautier-Hion 1977). 'Boom' calls of adult ♂♂ involve large vocal sacs in the throat that are inflated then deflated during booms (Gautier 1971).

De Brazza's Monkey is remarkable for its anti-predator behaviour. Monkeys respond to potential predators either by freezing or dropping into the undergrowth before fleeing silently. Adult ♂♂ may drop violently to the ground; the sound seems to act as a signal for congeners, which freeze. Harassing behaviour is mostly restricted to adult ♂♂, which may face off a predator (e.g. African Crowned Eagle *Stephanoaetus coronatus* or humans) at which time they utter impressive aggressive barks.

Foraging and Food Omnivorous. Forages mainly in trees. Contrary to strictly arboreal guenons, De Brazza's Monkeys handle food carefully and avoid wasting fruit. Both in Gabon and W Kenya, foraging for fruit is intensive and only a few fruiting sites are visited per day. For example, in Gabon a fruiting Apocynaceae liana was exploited on 14 days out of 20 consecutive observation days until most of the fruit was consumed (Gautier-Hion & Gautier 1978). In W Kenya one group used two neighbouring *Manilkara butugi* trees every day for two weeks (Chism & Cords 1998). Group home-ranges are small: 4–10 ha ($n = 16$ groups) in Gabon and 4–6 ha ($n = 3$ groups) in W Kenya. At both sites home-ranges of neighbouring groups overlap. Daily movements are short: mean 530 m (250–1010 m, $n = 24$ days) in Gabon and range is 330–1000 m in W Kenya. In Gabon 75% of the diet is comprised of fruit/seeds (from at least 27 species), 10% leaves, 5% mushrooms (genus *Mycera* and genus *Termitomyces*) and 5% animal prey (Gautier-Hion & Gautier 1978). In W Kenya diet comprised of 45% fruit/seeds (from 17 plant species), 30% leaves, 10% invertebrates and 2% mushrooms (Wahome *et al.* 1993). At both sites animal prey were mostly sedentary or slow moving insects (caterpillars, ants, cocoons, resting moths and termites). In East Africa, De Brazza's Monkeys raid crops (Maize *Zea mays*, green cotton *Gossypium* sp. bolls, avocados *Persea aguacate*, Guavas *Psidium guajava*; Mugambi *et al.* 1997, Chism & Cords 1998).

Social and Reproductive Behaviour Social. Most group counts give similar mean values. In NE Gabon the mean group size was 3.7 animals (2–6, $n = 16$ groups; Gautier & Gautier-Hion 1969, Quris 1976, Gautier-Hion & Gautier 1978); in W Kenya 3.8 ($n = 14$; Brennan 1985) and 3.7 (2–6, $n = 19$; Decker 1995); and in E Uganda 3.6 (2–6, $n = 16$) excluding four larger groups of 10, 12, 15 and 22 animals (Decker 1995). Groups in the Mathews Range numbered 2–18 ($n = 24$; Mwenja 2007). Three large groups of 11, 13 and 16 individuals in a small population in Kisere Forest, W Kenya (Wahome *et al.* 1993). Large groups, occurring in isolated small forests in East Africa (Kingdon [1971] noted groups of up to 35 individuals in E Uganda), could reflect sex differences in predation pressure (Kingdon 1997), aggregations of individuals within diminished forest patches (Decker 1995), or the difficulty facing animals who try to disperse from their natal groups because of insufficient or diminished suitable habitat (Chism & Cords 1998). Solitary animals, mainly adult ♂♂, observed at all sites. Three solitary adult ♂♂ present in a population of 38 monkeys in W Kenya (Wahome *et al.* 1993). One all-male group may have occurred in Kisere Forest but sexing of individuals was uncertain (Chism & Cords 1998). Groups are either families that include one adult ♂ and one adult ♀ and their offspring, or consist of small polygynous groups with one ♂ and up to four adult ♀♀ (Quris 1976, Gautier-Hion & Gautier 1978, Wahome *et al.* 1993). However, at least one multimale group observed in Uganda (Decker 1995).

Inter-group encounters are not aggressive but are accompanied by an increase in arousal and cohesion calls. The adult ♂ emits 'boom' calls that rally adult ♀♀ and regulate inter-group spacing (Gautier & Gautier-Hion 1977, Gautier-Hion & Gautier 1978). In captivity, courtship and mating are discrete events. In captivity, adult ♂ avoids his own offspring and rejects advances by the offspring after about two months of age, increasing rejections with time. Adult ♂ may play with an infant on rare occasions until it is seven months old, but between 11 and 18 months contacts between father and infant are neither positive nor aggressive (A. Gautier-Hion pers. obs.).

De Brazza's Monkeys in NE Gabon rarely occur in polyspecific associations (Gautier & Gautier-Hion 1969, Quris 1976). Aggressive chases of members of groups of sympatric arboreal monkeys, including Putty-nosed Monkeys *Cercopithecus nictitans*, Crowned Monkeys *Cercopithecus pogonias* and Moustached Monkeys *Cercopithecus cephus*, as well as against solitary adult ♂♂, observed several times (Gautier-Hion & Gautier 1978). Similarly, in East Africa Gentle Monkeys *Cercopithecus mitis* and Red-tail Monkeys *Cercopithecus ascanius* avoid De Brazza's Monkeys, which react aggressively towards them (Kingdon 1971, Wahome *et al.* 1993). In contrast, Guereza *Colobus guereza* may intermix peacefully with De Brazza's Monkeys in feeding trees (Wahome *et al.* 1993, Decker 1995, Mugambi *et al.* 1997). Observed feeding in the same trees with Guereza and Vervets *Chlorocebus pygerythrus* in Mathews Range (Mwenja 2007). Behavioural differences among semi-terrestrial De Brazza's Monkeys and arboreal guenons (shy and elusive nature vs. more extrovert nature) that appear both in foraging strategies (intensive vs. extensive) and in anti-predator strategies (freezing vs. fleeing) could explain inter-specific antipathy (Gautier-Hion & Gautier 1978).

The vocal repertoire of De Brazza's Monkey includes seven main call types. The vocal repertoire is distinguished by discrete non-



De Brazza's Monkey *Cercopithecus neglectus*.

graded calls, by non-quavered cohesion calls, by a copulatory call in adult ♀♀, and by the absence of high-pitched warning calls. Three calls (including 'booms', 'barks' and 'roars') are specific to adult ♂♂ (Gautier & Gautier-Hion 1977, Gautier 1988).

Reproduction and Population Structure In captivity the onset of puberty in ♂♂ occurs at about six years and is accompanied by an increase in body weight. Duration of oestrous cycles not known. No external signs indicate oestrous periods. The age of first parturition is 4–5 years (exceptionally 3.5 years). Gestation lasts 5.5 months (Gautier-Hion & Gautier 1976). The single offspring weighs ca. 350 g. In the wild (Gabon), births occur from Nov to Apr with a peak in Jan–Feb during the minor dry season when fruit availability is maximum ($n = 10$; Gautier-Hion 1968, Gautier-Hion & Gautier 1978). Similarly, in W Kenya, three births were observed in Jan–Feb dry season (Wahome *et al.* 1993). The adult ♂♂ : adult ♀♀ ratio varies from 1 : 1 to 1 : 3. De Brazza's Monkeys have lived to 31 years (♀) and 20 years (♂) in captivity (A. Gautier-Hion pers. obs.). This ♀ reproduced nine times between the age of five and 15 years, with a mean birth interval of 16 months (7–28 months). The two shortest intervals occurred after stillbirths.

Predators, Parasites and Diseases No predation event observed in the wild. Like other guenons, De Brazza's Monkeys react to African Crowned Eagles, large reptiles and humans.

Conservation IUCN Category (2012): Least Concern. CITES (2012): Appendix II.

In the main forest block of central Africa, De Brazza's Monkey is probably not threatened. This species is not hunted systematically for bushmeat because it is so cryptic and, as such, is rarely seen for sale. The future of De Brazza's Monkey is more uncertain in East Africa where its habitat is under severe threat from human encroachment (cultivation, logging, firewood collection, cattle grazing) and the animals are victims of human harassment, including trapping and hunting by dogs (Mugambi *et al.* 1997, Chism & Cords 1998, Mwenja 2007). Said to be common in SW Ethiopia, near Godare (Brown & Urban 1969) but present status in Ethiopia not known (but likely that populations are now threatened by habitat loss). In Kenya, said to be plentiful on some slopes of Mt Elgon in 1954 (Hill 1966), but this is no longer the case. The population in the Mathews Range, estimated at 200–300 individuals, is probably the largest population in Kenya (Mwenja 2007). Brennan (1985) only found the species in a

few isolated small forest patches in W Kenya in Trans-Nzoia District (including Saiwa N. P., Mt Elgon, and Cherangani Hills). Since then the status of the species has deteriorated still further; recent deforestation was observed at 7 out of 15 sites visited; traps and snares were found on four sites and hunting with dogs was also recorded (Decker 1995). Small populations still present on Mt Elgon and in Cherangani Hills (Mugambi *et al.* 1997). Also present in Kisere Forest, 2 km north of Kakamega Forest with no evidence of its presence in the main block of Kakamega Forest (Chism & Cords 1998, M. Cords pers. comm.). Inhabits isolated forest patches in nearby Tororo District, E Uganda, where a 1984 census found 124 individuals at 13 small sites. De Brazza's Monkey now in danger of becoming locally extinct (Decker 1995) in E Uganda and W Kenya. Animals isolated amidst expanding farmlands (where populations number only 2–7) cannot successfully move to new sites, nor are these populations genetically viable (Brennan 1985, Decker 1995). Elsewhere in Uganda, De Brazza's Monkey is known from Semliki Forest, Sango Bay and Mt Kadam (Kingdon 1971), but current status at these sites is not known.

Measurements

Cercopithecus neglectus
HB (♂ ♂): 550 mm, n = 26
HB (♀ ♀): 450 mm, n = 19
T (♂ ♂): 695 mm, n = 26

T (♀ ♀): 555 mm, n = 19
HF (♂ ♂): 552 mm, n = 5
HF (♀ ♀): 384 mm, n = 3
E (♂ ♂): 40 mm, n = 1
WT (♂ ♂): 6.4 (4.8–8.0) kg, n = 8
WT (♀ ♀): 3.6 (2.5–4.9) kg, n = 71
Gabon and DR Congo. HB, T and WT (Gautier-Hion *et al.* 1999).
HF and E (A. Gautier-Hion pers. obs). Ranges not available for HB, T, HF, E.

HB (♂ ♂): 560 (484–595) mm, n = 13
HB (♀ ♀): 464 (394–543) mm, n = 11
T (♂ ♂): 691 (591–784) mm, n = 13
T (♀ ♀): 530 (470–574) mm, n = 11
HF: n. d.
E: n. d.
WT (♂ ♂): 7.8, 8.2 kg, n = 2
WT (♀ ♀): 4.1, 4.8 kg, n = 2
Localities not given (Napier 1981)

Key References Decker 1995; Gautier-Hion & Gautier 1978; Gautier-Hion *et al.* 1999; Wahome *et al.* 1993; Wenja 2007.

Annie Gautier-Hion

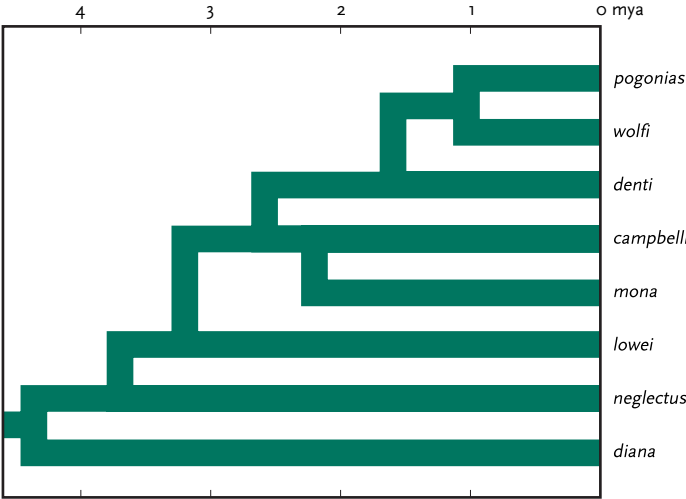
Cercopithecus (mona) GROUP
Mona Monkeys Group

Cercopithecus mona (Schreber, 1774). Die Säugethiere 1: 103. 'Guinea'.

| | | |
|---------------------------------------|-------------------|--------|
| <i>Cercopithecus (mona) mona</i> | Mona Monkey | p. 322 |
| <i>Cercopithecus (mona) lowei</i> | Lowe's Monkey | p. 325 |
| <i>Cercopithecus (mona) campbelli</i> | Campbell's Monkey | p. 328 |
| <i>Cercopithecus (mona) denti</i> | Dent's Monkey | p. 330 |
| <i>Cercopithecus (mona) wolfi</i> | Wolf's Monkey | p. 333 |
| <i>Cercopithecus (mona) pogonias</i> | Crowned Monkey | p. 335 |

We describe six species in the distinctive *Cercopithecus (mona)* Group. All are small, wholly arboreal, fast-moving monkeys: Mona Monkey *Cercopithecus (mona) mona*, Campbell's Monkey *Cercopithecus (mona) campbelli*, Lowe's Monkey *Cercopithecus (mona) lowei*, Dent's Monkey *Cercopithecus (mona) denti*, Wolf's Monkey *Cercopithecus (mona) wolfi* and Crowned Monkey *Cercopithecus (mona) pogonias*. All have grizzled dorsal pelage, crown with black temples between conspicuous ears, dark bluish masks around the eyes, pink muzzles and prominent brow-patches. Forelimbs black on their outer aspect. Forelimbs and hindlimbs white or orange on their inner sides. Hands and feet black. Outer surface of hindlimbs vary in colouring among species and races. Long tails have black tips but tend to be bicoloured in their middle section. Hands are compact with, relatively, the shortest digits among guenons. These proportions appear to be adapted for the capture of small, active invertebrates and rapid traverse over small branches. Chromosome number 2n = 66, 68 or 72 (Dutrillaux *et al.* 1988b).

Differing chromosome numbers and disparate affinities with other guenons demonstrate that this morphologically conservative

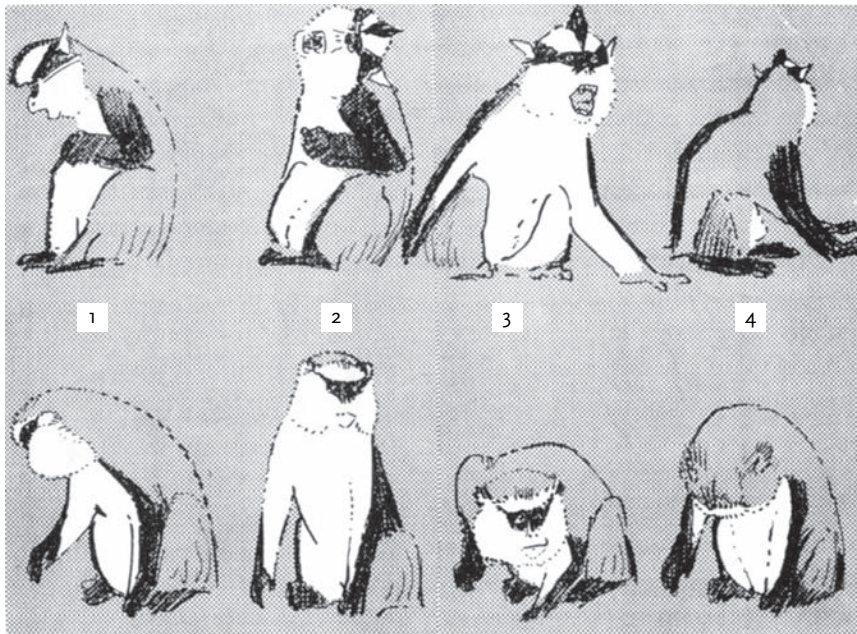


Tentative phylogenetic tree for the Mona Monkeys Group *Cercopithecus (mona)* (modified from Tosi *et al.* 2005).

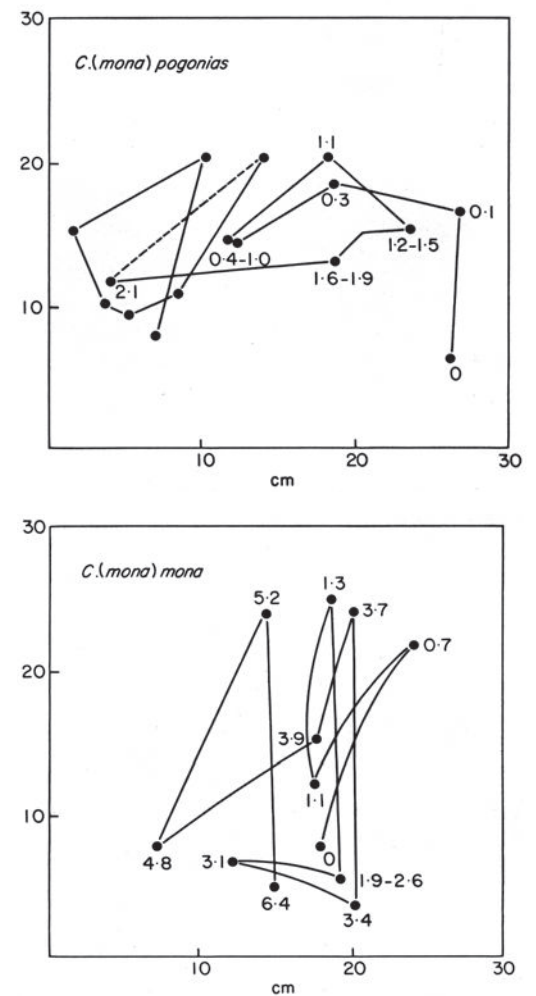
lineage has some poorly understood and puzzling relationships both within and outside the group. Nevertheless, we retain *C. (mona)* as a discrete group because it is an immediately recognizable entity.

Cercopithecus (m.) pogonias and *C. (m.) wolfi* are the most similar and derived in both morphology and chromosomes; *C. (m.) lowei*, *C. (m.) campbelli* and *C. (m.) denti* are the least derived. At the molecular level, *campbelli* differs most from other members of the *C. (mona)*

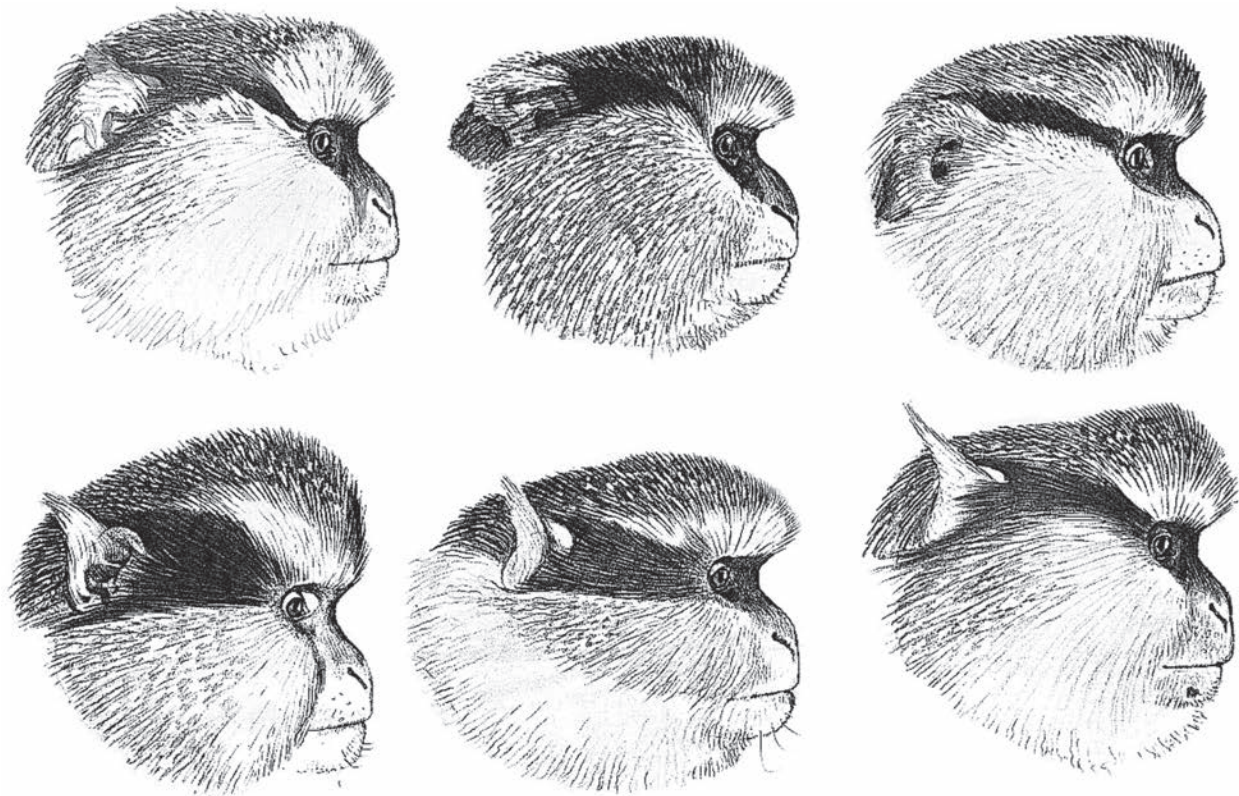
Analysis (from film) of Crowned Monkey *Cercopithecus pogonias* adult male threat behaviour sequences (top) compared with Mona Monkey *Cercopithecus mona* adult male (bottom). Both sequences (left to right) show: (1) 'cut-off' phase; (2) advertisement phase; (3) threat/vocalization phase; (4) 'cut-off' phase.



BELOW: Comparison of sonograms of adult male loud calls of Crowned Monkey *Cercopithecus pogonias* (left) and Wolf's Monkey *Cercopithecus wolfi* (right). Note species-specific modification of common sonic structure and pelage patterns.



ABOVE: Comparison of time and motion records from threat displays by (above) *C. (mona) pogonias* (below) *C. (mona) mona*. Note lateral signal design and greater lateral amplitude in the former.



The six species in the Mona Monkeys Group *Cercopithecus (mona)*.

Top, left to right: Campbell's Monkey *Cercopithecus campbelli*. Lowe's Monkey *Cercopithecus lowei*. Mona Monkey *Cercopithecus mona*. Bottom, left to right: Crowned Monkey *Cercopithecus pogonias*. Wolf's Monkey *Cercopithecus wolfi*. Dent's Monkey *Cercopithecus denti*.

Group that have been studied (Dutrillaux *et al.* 1988b, Moulin *et al.* 2008). The Dutrillaux and Moulin teams have determined that *C. (m.) pogonias* and *C. (m.) wolfi* have 72 chromosomes and a supposedly exclusive affinity with *C. hamlyni*, whereas *C. (m.) campbelli* has 66 chromosomes – the same as species in the Cephus Group *Cercopithecus (cephus)*. The chromosomes of *C. (m.) lowei* and *C. (m.) denti* have yet to be studied but *C. (m.) lowei* is likely to be the most conservative member of the *C. (mona)* Group. There are two interpretations for 66 chromosomes in *C. (m.) campbelli*. One is that hybridization has taken place, perhaps during a relatively recent period when the size of populations had greatly contracted. The other possibility is that *C. (m.) campbelli* has a much older basal position in the *C. (cephus)* radiation (and, by implication, also *C. (nictitans)*).

Using X-chromosome molecular analysis, Tosi *et al.* (2005) confirmed that *wolfi* and *pogonias* were the most recently evolved species while *mona* derived from an earlier branch. This study estimated that the *mona* radiation took place ca. 3.5 (2.9–4.1) mya (mid-Pliocene) subsequent to the emergence of the Diana Monkeys *Cercopithecus (diana)* and De Brazza's Monkey *Cercopithecus neglectus* lineages. This, and their restriction to well-developed equatorial forests, suggests that *C. (mona)* evolved within an established and diverse primate community to fill a relatively narrow niche, and were/are strongly constrained by the competition of other primates and, perhaps, birds.

The *C. (mona)* Group resembles the larger, semi-terrestrial *C. neglectus* in their longitudinally striped limbs, brow-patches, bright pattern contrasts and some aspects of their vocal repertoire (Gautier 1988).

Molecular studies also suggest that *C. neglectus* is their closest relative among guenons (Dutrillaux *et al.* 1988b, Disotell & Raam 2002, Tosi *et al.* 2004, Perelman *et al.* 2011). All members of this group are fast, omnivorous monkeys, living predominantly in the canopy. In response to predators they are adept at hiding and 'freezing' in patches of dense vegetation. Social structure consists of multifemale groups, usually with a single adult ♂. Group numbers average about 14 (8–25).

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Dent's Monkey *Cercopithecus denti*.

Cercopithecus mona **MONA MONKEY**

Fr. Mone; Ger. Mona-Meerkatze

Cercopithecus mona (Schreber, 1774). Die Säugethiere 1: 103. 'Guinea'.Mona Monkey *Cercopithecus mona* adult male.*Cercopithecus mona*

Taxonomy Monotypic species. Formerly grouped as one species with other members of the *Cercopithecus (mona)* Group (or Superspecies). Now widely accepted as a distinct species (Kingdon 1997, Groves 2001, 2005c, Grubb *et al.* 2003, Oates 2011) due to differences in vocalizations with Campbell's Monkey *Cercopithecus campbelli* and Crowned Monkey *Cercopithecus pogonias* (Struhsaker 1970, 1981a) and sympatry with Lowe's Monkey *Cercopithecus lowei* and *C. pogonias*; however, some hybridization with both species occurs (Booth 1955, Struhsaker 1970). Common name 'Mona Monkey' often assigned to other members of the *C. (mona)* Group causing confusion. 'Mona Monkey' should refer only to *C. mona*. Synonyms: *monacha*, *monella*. Chromosome number: $2n = 68$ (Romagno 2001).

Description Medium-sized arboreal monkey with bright white underparts and bright white oval spot ('hip disc') on either side of base of tail. Sexes similar in colouration, but adult ♀ smaller, being ca. 60% as heavy as adult ♂. Skin above nostrils and around eyes dark greyish-blue. Head round. Muzzle short. Skin below nostrils light pink with sparse white hairs. Cheek pelage long, white to yellowish-white to light yellowish-grey. 'Mask' stripe black, extending from eyes to ears. Brow white or pale yellow. Crown flat, grizzled yellow and black. Ear tufts short and rounded. Dorsum reddish-brown agouti. Hands and outer forelimbs glossy black. Feet and outer hindlimbs glossy dark greyish-black. Throat, chest, belly, inside of limbs bright white. Sharp contrast between black and white surfaces of forelimbs and hindlimbs. Rump near base of either side of tail with bright white oval spots. Tail long (about 40% longer than HB), dark greyish-black, blackish towards tip. Young similar in colour to adults. Newborns blackish to black.

Geographic Variation None recorded.

Similar Species

Cercopithecus lowei. Just east of Cavally R., Côte d'Ivoire, to just east of Volta R., Ghana. Lacks white spot on either side of base of tail.
Cercopithecus pogonias. East of Cross R., Nigeria, to just north of Sanaga R., Cameroon. Lacks white spot on either side of base of tail; crown raised into a black crest.

Distribution Endemic to West Africa. Rainforest BZ. In forests from just west of Volta R., Ghana, eastwards through Togo, Bénin and Nigeria, to just south of Sanaga R., Cameroon (Booth 1955, 1956b, Struhsaker 1970, Oates 1988b). Introduced 150–500 years ago to Gulf of Guinea islands of São Tomé and Príncipe (Glenn *et al.* 1999b) and 150–300 years ago to Caribbean island of Grenada (Glenn 1998). Grenada population derived from São Tomé population (Horsburgh *et al.* 2002).

Habitat Secondary and primary moist forest, mangrove swamp, seasonal dry forest and riverine forest from sea level to 1700 m (Dunn 1993). In Cameroon occurs in mangrove swamp, secondary moist forest and forest edges more often than primary moist forest (Struhsaker 1969, Howard 1977, Whitesides 1981, Glenn *et al.* 1999a). Mean annual rainfall 800 mm to >8000 mm.

Abundance Populations locally reduced or eliminated in some areas in Nigeria and Cameroon due to overhunting by humans (M. E. Glenn & K. J. Bensen pers. obs.). Average of 0.04–0.09 groups

sighted/km and second most often sighted primate in Korup N. P., Cameroon (Linder & Oates 2011). Average of 0.22 groups sighted/km (4.5 groups/km^2) and most commonly sighted primate in Okomu N. P., SW Nigeria (Akinsorotan *et al.* 2011). Formerly common but now uncommon to rare in Ghana due to overhunting by humans (J. Mason pers. comm.). Common in Lama Forest Noyau Central, Bénin, despite hunting pressure (Matsuda Goodwin 2007). Average 15 ind/km^2 in the Douala Edea Reserve, Cameroon (Whitesides 1981), 49 ind/km^2 in E Nigeria (Dunn 1993) and $30\text{--}49 \text{ ind/km}^2$ in the Lama Forest Noyau Central (Matsuda Goodwin 2007). Common in introduced island range; estimated to be >6000 on São Tomé (19 ind/km^2), >1000 on Príncipe (21 ind/km^2) (Glenn *et al.* 1999b) and >2000 on Grenada (42 ind/km^2) (Glenn 1998).

Adaptations Diurnal and arboreal. Primarily arboreal but descends to ground for short periods. Spends 30% ($n = 1995$ scans) time on ground in seasonal dry forest (Matsuda Goodwin 2007). Regularly swims in rivers and mangrove estuaries (Howard 1977, Z. Tooze pers. comm.). Considered ecological generalists because of use of diverse forest types, varied diet and successful introduction to non-African forest habitats. Rapid quadrupedal locomotion facilitated by equal forelimb and hindlimb proportion. Extremely long tail used for balance.

Foraging and Food Omnivorous. Mona Monkeys forage in groups or in polyspecific associations. Home-range ca. 25–100 ha ($n = 4$) in SW Cameroon (Howard 1977). Often entire group forages in one fruiting tree where individuals rapidly pick ripe fruits, placing them into their cheek-pouches for consumption later. Unripe fruit dropped. Animals often investigate holes in trees and tree bark crevices, and scan leaves and twigs, for arthropods. They pounce upon arthropods moving in the open. They are most active during early morning and late afternoon, but forage at all times of the day (Howard 1977, Glenn 1996, Matsuda Goodwin 2007). The introduced population on Grenada uses primary forest more when fruit abundance there is high (Glenn 1996).

Mona Monkeys primarily eat fruit and arthropods, but also regularly eat other foods, including leaves, leaf piths, flowers, nectaries, lizards and birds' eggs and nestlings (Howard 1977, Glenn 1996). In mangrove swamp they also eat crabs, snails and perhaps fish (Gartlan & Struhsaker 1972, Glenn *et al.* 1999a, Z. Tooze pers. comm.). In seasonal dry forest in Bénin, Mona Monkeys eat fruits (42%), seeds (22%), leaves (13%), flowers (12%), insects (10%), others (1%) ($n = 566$ items); they eat more ripe fruits in the wet season and more unripe fruits, nectar, flowers and soft seeds in the dry season (Matsuda Goodwin 2007). Mona Monkeys regularly raid a wide variety of crops along the forest edge, such as banana *Musa* spp., Mango *Mangifera indica*, Cocoa *Theobroma cacao*, Breadfruit *Artocarpus altilis*, Oil Palm *Elaeis guineensis* and Maize *Zea mays* (Howard 1977, Glenn 1996, Glenn *et al.* 1999a, b.)

Social and Reproductive Behaviour Social. Two types of social groups occur. 'Bisexual groups' ranged in size from three to 40 individuals and comprised of one or more adult ♂♂, juveniles, subadults and several adult ♀♀ with their infants (Struhsaker 1969, Gartlan 1973, Glenn 1997, Matsuda Goodwin 2007). At Mungo Reserve, Cameroon, three groups averaged 20 animals,



Lateral view of skull of Mona Monkey *Cercopithecus mona* adult male.

with three adult ♂♂, 12 adult ♀♀ and the remaining animals subadults and juveniles (Howard 1977). In Bénin, groups averaged 13 animals (2–35, $n = 64$ groups), containing one or more adult ♂♂ (Matsuda Goodwin 2007). 'All-male groups' contain only adult and subadult ♂♂ and range in size from two to five individuals (Glenn 1997, Matsuda Goodwin 2007). On Grenada individually identifiable all-male groups averaged 2.4 animals (S.D. = 0.6, $n = 33$) with the same animals together for a few days to >2 years (Glenn *et al.* 2002). This is the only *Cercopithecus* species known to regularly form long-term all-male groups. Bisexual groups are territorial. Physical agonistic encounters between bisexual groups occur infrequently (Howard 1977). All-male groups appear to avoid agonistic encounters with bisexual groups but encounters occasionally occur. Males in all-male groups occasionally vocalize and/or visually threaten (head-bob) towards other all-male groups when in close proximity (M. E. Glenn, K. J. Bensen & R. Matsuda Goodwin pers. obs.).

Mona Monkeys observed in polyspecific associations during 95% ($n = 166$; Howard 1977) and 94% ($n = 173$; Struhsaker 1981a) of encounters. Observed in association with Crowned Monkeys, Putty-nosed Monkeys *Cercopithecus nictitans*, Red-eared Monkeys *Cercopithecus erythrotis*, Sclater's Monkeys *Cercopithecus sclateri* and White-throated Monkeys *Cercopithecus erythrogaster* (Gartlan & Struhsaker 1972, Howard 1977, Oates 1985). Polyspecific associations possibly provide anti-predator and/or foraging benefits (e.g. Gautier-Hion *et al.* 1983, Mitani 1991, Struhsaker 2000a).

In bisexual groups on Grenada usually only one adult ♂ gives the deep 'double boom' loud-call. This call is usually given twice in succession (range 1–5 times) followed by a long series of rapid 'hack' calls. These calls are given during alarm situations and/or as a territorial warning (Struhsaker 1970, Howard 1977, Glenn 1996). In seasonal dry forest in Bénin, 1–4 adult ♂♂ in the same bisexual group will give double booms and hacks, sometimes in succession. Some ♂♂ in these groups show affiliative behaviour (Matsuda Goodwin 2007). Other members of bisexual groups give 'high hack' calls when alarmed. Females occasionally give extremely high-pitched 'chirps' when alarmed. When foraging, a soft, high, one-note 'ooo' or 'squeak' contact call given by all group members. Infants 'scream' when abandoned (Struhsaker 1970, Glenn 1996). Members of all-male groups rarely vocalize except when giving contact calls or when encountering another all-male group (M. E. Glenn & K. J. Bensen pers. obs.). Possibly give predator-specific alarm calls (Howard 1977). Flee silently and give alarm vocalizations when encountering humans in areas where monkey hunting is



Mona Monkey *Cercopithecus mona* adult male.

common. Bisexual group members react to vocalizations of other primate species (Gartlan & Struhsaker 1972, Howard 1977). All individuals, both of bisexual and all-male groups, communicate threats by exaggerated head and upper body movements that alternately show and hide either white chest and belly or black eye-stripes (Struhsaker 1969, Howard 1977, Kingdon 1980, M. E. Glenn & K. J. Bensen pers. obs.). Agitated subadult and adult ♂♂ shake branches, and open mouths showing large canine teeth. Juveniles are the most curious and are often found on the periphery of the group. Juveniles are usually first to give alarm calls and last to depart from a perceived threat (M. E. Glenn & K. J. Bensen pers. obs.). On Grenada only ♂♂ in bisexual groups known to mate (Glenn 1996). In Cameroon multiple ♂♂ in same bisexual group mate (Howard 1977). The ♂ and ♀ emit unique 'rapid grunting' and 'warbling' vocalizations during copulation (Struhsaker 1970, Howard 1977, Glenn *et al.* 2002). Subadult ♂♂ in all-male groups and juveniles in bisexual groups in Grenada regularly mount each other without vocalizing (Glenn 1997). Only ♀♀ observed to carry young (M. E. Glenn, K.J. Bensen & R. Matsuda Goodwin pers. obs.). Young regularly play with each other and with young of other primate species (Howard 1977).

Reproduction and Population Structure Oestrous cycle, age at first reproduction, time to weaning and birth interval are unknown in the wild. Oestrous period occurs every six months in captive ♀♀ in Nigeria (Z. Tooze pers. comm.). Gestation length for one captive was between 128 and 187 days (median 158 days) (Takeshita 1962). Black newborns observed in Mar–Aug in Cameroon (Howard 1977). In Bénin one newborn observed in Mar (Matsuda Goodwin 2007). The introduced population on Grenada has no breeding seasonality (Glenn 1996). In Cameroon copulations observed throughout the year, but peaked in Sep–Oct (Howard 1997). Copulation calls heard most frequently from Sep–Mar during major dry season in seasonal dry forest in Bénin (Matsuda Goodwin 2007). Females give birth to one young; twins never observed in the wild. Age at first reproduction in captivity 3.2 years (Kappeler & Pereira 2003). Weight at birth in captivity ca. 284 g (Ross 1991).

Ratio of adult ♂♂ to adult ♀♀ in bisexual groups ranges from 1 : 5.5 to 1 : 8.8 (n = 3 groups). Ratio of adults to immatures ranges from 1.3 : 1 to 2.6 : 1 (n = 3 groups) (Howard 1977). Longevity, birth rates and mortality rates unknown for wild populations. Lives to 22 years in captivity (Ross 1991).

Predators, Parasites and Diseases Humans are the primary predator of the Mona Monkey throughout its range. The only observed wild predator is the African Crowned Eagle *Stephanoaetus coronatus* (Howard 1977, M. E. Glenn & K. J. Bensen pers. obs.). Other predators likely include Robust Chimpanzees *Pan troglodytes*, Leopards *Panthera pardus*, African Golden Cats *Profelis aurata* and large arboreal snakes. No details known about diseases. Nigerian populations tested positive for Yellow Fever neutralizing antibodies (Monath & Kemp 1973). The introduced Grenada population tested negative for simian immunodeficiency virus (S. Morse pers. comm.).

Conservation IUCN Category (2012): Least Concern. CITES (2012): Appendix II.

Populations are decreasing in parts of the range and the species has been extirpated from some sites due to habitat loss and over-hunting for the commercial bushmeat trade (M. E. Glenn & K. J. Bensen pers. obs.). Potentially more resilient to human hunting than most other monkeys (Linder & Oates 2011).

Measurements

Cercopithecus mona

HB (♂♂): 545 (410–631) mm, n = 8

HB (♀♀): 419 (375–457) mm, n = 7

T (♂♂): 767 (635–879) mm, n = 8

T (♀♀): 587 (533–655) mm, n = 7

HF (♂♂): 137 mm, n = 1*

HF (♀♀): n. d.

E (♂♂): 34 mm, n = 1*

E (♀♀): n. d.

WT (♂♂): 4.6 kg, n = 1*

WT (♀♀): 2.7–4.0 kg**

Various localities in Africa (Napier 1981)

*Hill (1966)

**Booth (1960); sample size not given

HB (♂♂): 473 (435–515) mm, n = 13

HB (♀♀): 381 (341–422) mm, n = 7

T (♂♂): 670 (570–730) mm, n = 13

T (♀♀): 563 (524–620) mm, n = 7

HF (♂♂): 134 (127–143) mm, n = 13

HF (♀♀): 114 (105–128) mm, n = 7

E: n. d.

WT (♂♂): 4.7 (3.2–5.7) kg, n = 13

WT (♀♀): 2.8 (2.1–4.3) kg, n = 7

Introduced population, Grenada, E Caribbean (Glenn & Bensen 1998)

Key References Glenn 1996; Howard 1977; Matsuda Goodwin 2007; Oates 2011; Struhsaker 1969, 1970.

Mary E. Glenn, Keith J. Bensen & Reiko Matsuda Goodwin

Cercopithecus lowei **LOWE'S MONKEY**

Fr. Mone de Lowe; Ger. Lowe-Meerkatze

Cercopithecus lowei Thomas, 1923. Ann. Mag. Nat. Hist., ser. 9, 11: 608. Bandama, Côte d'Ivoire.Lowe's Monkey *Cercopithecus lowei* adult male.*Cercopithecus lowei*

Taxonomy Monotypic species (Groves 2001, 2005c, Kingdon 2001). Often grouped with Campbell's Monkey *Cercopithecus campbelli* as one species (Booth 1955, Hill 1966, Dandelot 1974, Napier 1981, Lernould 1988, Grubb *et al.* 2003, Oates 2011). Intermediate forms with Campbell's Monkey near Guiglo, between the Cavally R. and Sassandra R., Côte d'Ivoire (Booth 1956b, Oates 1988b). Member of the *Cercopithecus (mona)* Group (or Superspecies) with *C. campbelli*, Mona Monkey *C. mona*, Dent's Monkey *C. denti*, Crowned Monkey *C. pogonias* and Wolf's Monkey *C. wolffi*. Synonyms: none. Chromosome number: not known.

Description Medium sized, arboreal monkey with yellow brow, rectangular cheek-ruffs and white ventrum. Adult ♀ approximately two-thirds the weight of adult ♂. Sexes similar in colour. Skin above nostrils and around eyes dark bluish-grey. Head round. Muzzle short. Skin below nostrils light pink with sparse white hairs. Cheeks light greyish-white to yellowish-white. Shape of cheek-ruffs long, broad, rectangular. 'Mask' (temporal) stripe broad, black, extending from eyes to ears. Brow yellow. Crown flat, grizzled dark yellow and black. Ear tufts grizzled light yellowish-white, short and rounded. Throat, chest, belly and inner limbs white. Dorsum reddish-brown agouti. Feet, hands and outer forelimbs black. Outer hindlimbs dark greyish-black. Sharp contrast between inner and outer limbs. Tail long, yellowish-grey to greyish-black near tip. Infant with pink face and pelage more greyish and less contrasted than adult; like adult at three months.

Geographic Variation No significant variation recorded.

Similar Species

Cercopithecus campbelli. Senegal to Cavally R. on Liberia–Côte d'Ivoire border. Sympatric between Sassandra R. and Nzo R. (G. Galat & A. Galat-Luong pers. obs.). Cheek-ruffs rounded. Brow white. Temporal stripe narrow. Belly and lower forelimbs brownish-tawny grizzle.

Distribution Endemic to West Africa. Rainforest BZ. Historically widespread in forest from Sassandra-Nzo R., Côte d'Ivoire, to Volta R., Ghana. Current distribution like historic distribution but more limited at ca. 300,000 km². Eastern-most record between Sassandra R. and Nzo R. at 06° 34' 30"N, 07° 07' 00"W in Forêt classée de Duékoué, Côte d'Ivoire (G. Galat & A. Galat-Luong pers. obs.). Distribution now more patchy than given by Lernould (1988) but less patchy than given by Oates (1988b) or Kingdon (2001). Distribution reduced due to hunting and habitat loss but still fairly widespread (McGraw 1998d).

Habitat Primary forest, secondary forest, forest outliers, gallery forests and mangrove swamps (Jones 1950). Marginal habitats include isolated forest blocks (e.g. Boabeng-Fiema Monkey Sanctuary, Ghana) that are considered sacred by some people (Fargey 1991). Present where mean annual rainfall is 1200–2500 mm.

Abundance One of the most common forest-dwelling monkeys in West Africa due to its ability to exploit degraded forest (McGraw 1998d). Relatively common near villages. Found in 13 of 19 protected forests surveyed in Ghana and Côte d'Ivoire (Oates *et al.* 2000a). Biomass was 363 kg/km² in a sacred protected forest in Ghana (Fargey 1991). One group of 5–6 individuals in degraded forest at Adiopodoume, Côte d'Ivoire, had a home-range of 14 ha (Galat-Luong & Galat 1979).

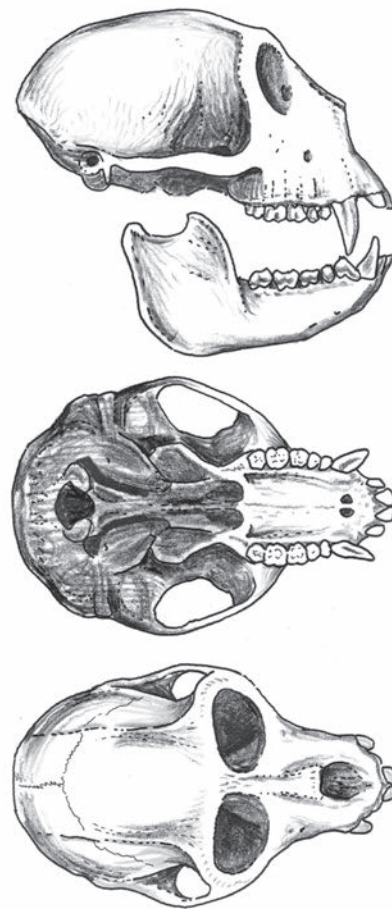
Adaptations Diurnal and arboreal. Does well in secondary forest and mangrove swamps. One of the arboreal monkeys best able to

survive outside primary forest. A. Galat-Luong (pers. obs.) found that at Adiopodoume, in degraded forest (without high emergent trees), Lowe's Monkeys are 68% of time in canopy, 30% in lower strata, 2% on ground ($n = 2811$), and spend 66% of time sitting and 30% in quadrupedal position ($n = 2793$). Spend 72% of time on branches, 25% on twigs, 2% on horizontal boughs, rarely on vertical trunks ($n = 2735$). Lowe's Monkeys sleep in tall trees with large spherical canopy (A. Galat-Luong pers. obs.). They frequently travel on the ground (W. S. McGraw pers. obs.).

Foraging and Food Primarily frugivorous. Home-ranges of two groups at Adiopodoume were 9 ha and 14 ha (A. Galat-Luong & G. Galat pers. obs.). At Boabeng-Fiema, home-range averaged 8.6 ha (S.D. = 3.6, $n = 13$ groups; Fargey 1991). In Ghana, Jeffrey (1974) noted that the fruit of *Musanga cercropiodes* was much favoured. At Adiopodoume, species eaten by Lowe's Monkeys include *Elaeis guineensis* and *Ficus exasperata* (fruit), *Ipomoea involucre* (flowers), grasshoppers and larvae in dead wood (Bourlière *et al.* 1969). They frequently feed on liana fruits. Feeding and locomotion (partially provisioned group in disturbed habitat) account for 6% and 15% of time, respectively ($n = 2841$) (A. Galat-Luong pers. obs.). Lowe's Monkeys obtain drinking water from deep tree-holes by dipping and then licking their hands (Bourlière *et al.* 1970, A. Galat-Luong pers. obs.). They also drink from freshwater springs flowing into salt water lagoons (A. Galat-Luong pers. obs.). Lowe's Monkeys can be a major pest of farms (Jeffrey 1974) and raid crops near villages (mangos, bananas, oil palm nuts; A. Galat-Luong pers. obs.).

Social and Reproductive Behaviour Social. At Adiopodoume, one group varied in size from 9 to 16 individuals (Bourlière *et al.* 1970), and declined to six individuals (Galat-Luong & Galat 1979). Average of 16.6 ind/group (S.D. = 3.8, $n = 13$) at Boabeng-Fiema (Fargey 1991). Groups at Boabeng-Fiema included one adult ♂, several adult ♀♀ and immatures. Non-sex-differentiated group structure averaged 4.9 (S.D. = 1.2) adults, 5.8 (S.D. = 1.5) subadults, 3.4 (S.D. = 1.0) juveniles and 2.5 (S.D. = 1.1) infants ($n = 13$; Fargey 1991). Subadult and young mature ♂♂ emigrate becoming solitary or forming new groups with emigrating ♀♀ (Bourlière *et al.* 1969, Hunkeler *et al.* 1972, A. Galat-Luong pers. obs.). Herding occurs (Galat-Luong & Galat 1979). Fission of groups occurs as subadult ♂♂ become 4–5 years old, following Dec–Feb births, significantly modifying group structure (Hunkeler *et al.* 1972). Galat-Luong & Galat (1979) observed the adult ♂ of one group take over leadership of a neighbouring group that comprised no adult ♂ but one subadult ♂. The adult ♀♀ of the neighbouring group, some carrying young, had severe conflicts with the new adult ♂. Four infants died during the conflicts, suggesting infanticides by the new adult ♂. The adult ♂ went back to his former group but returned to the neighbouring group during each of the following four years to copulate with the adult ♀♀ in the neighbouring group during the mating season.

Territorial behaviour is conspicuous: jumping, chest-thrusting, swaying side-to-side, penile display (Galat-Luong & Galat 1979). First inter-group distancing loud-calls made at five years of age, one year after testicles drop. At dusk the adult ♂ climbs an emergent tree and emits two 'booms', separated by ca. 4 sec. This low frequency sound (80 Hz) can be heard >1 km away. About 10 sec later he



Lateral, palatal and dorsal views of skull of Lowe's Monkey *Cercopithecus lowei* adult male.

emits a series of about ten noisy 'barks' (containing higher frequency sounds) that provide directional information. The intensity of barks is in a decrescendo, adding distance information. Neighbouring ♂♂ emit responses. Duets are performed with Lesser Spot-nosed Monkeys *Cercopithecus petaurista*. Similar barks are also emitted after a disturbance. Barks were once heard emitted in response to an ultra-light motorized airplane (the group then kept quiet for five hours) (A. Galat-Luong & G. Galat pers. obs.). All individuals emit a pure tone, non-quavered, cohesion-contact 'o-mii' call during which low and high pitches merge. As ♂♂ become four years old, and the testicles drop, this call becomes a low-pitched, still pure tone, 'mao' call (A. Galat-Luong & G. Galat pers. obs.). High-pitched warning calls (e.g. 'chirps') are not given. Adult ♀♀ give a protruded mouth, rhythmic, copulation request and copulation call (A. Galat-Luong & G. Galat pers. obs.). Other vocalizations include a loud sneeze alarm call and a nasal 'ooeeoo' contact call (Kingdon 2001).

Adult ♂ solicits mounting by putting his hand on the rump of the ♀. She puts her tail on her back permitting him to mount, or sits to refuse. Young ♀♀ accept courtship of extraneous ♂♂ more readily than do older ♀♀ (Galat-Luong & Galat 1979). Allocare of young infants by adult and immature ♀♀ is common (Bourlière *et al.* 1970), while rare by immature ♂♂ (one individual in five; Hunkeler *et al.* 1972, A. Galat-Luong pers. obs.).

Social and resting behaviours account for 8% and 70% of time, respectively (partially provisioned group) (A. Galat-Luong pers.

obs.). Cohesion of group important: mean distance of the nearest individual is 3 m at dawn (ca. 06:00h), increases gradually to 6 m at 09:00h, is 5 m until 14:00h, increases to 7 m at 16:00h, and decreases gradually to 4 m at dusk (ca. 18:45h) ($n = 2818$). The nearest neighbour is a ♀ 72% of the time ($n = 2499$); an adult 40% of the time and an infant 25% of the time ($n = 2862$) (A. Galat-Luong pers. obs.). Lowe's Monkeys display various play behaviours (Galat 1983), including chasing of ants (*Oecophylla longinidis*), frogs, Gambian Sun Squirrels *Heliosciurus gambianus*, doves, Black Kites *Milvus migrans* and African Pied Hornbill *Tockus fasciatus* (Bourlière *et al.* 1970, Hunkeler *et al.* 1972). Lowe's Monkeys associate with other monkey species, especially *C. petaurista*, and are frequently followed by White Crested Hornbills *Tropicranus albocristatus* (Bourlière *et al.* 1969, A. Galat-Luong pers. obs.).

Reproduction and Population Structure Oestrous cycle, birth-weight, time to weaning, and age at first reproduction unknown. After 25 weeks' gestation singletons are born ($n = 18$; Bourlière *et al.* 1969, A. Galat-Luong pers. obs.); twins are not reported. At Adiopodoume one adult ♀ gave birth to one infant per year for four years (i.e. birth interval ca. one year) from two different ♂♂ (A. Galat-Luong & G. Galat pers. obs.). Most matings occurred after the long rains and during the coolest part of the year (Jun–Sep). Birth peak in Dec–Jan at end of short rains and beginning of main dry season. Sex ratio ♂ : ♀ 1 : 2.0 to 1 : 1.5; adult to immature ratio 1 : 1.4 to 1 : 4.3 ($n = 1$ group; Bourlière *et al.* 1970). Longevity >28 years in the wild (A. Galat-Luong pers. obs.).

Predators, Parasites and Diseases Humans, and probably also Leopards *Panthera pardus*, African Crowned Eagles *Stephanoatus coronatus* and Robust Chimpanzees *Pan troglodytes* are the main predators. Harass mambas *Dendroaspis* sp. (as if they were potential predators) with sneezes, loud-calls (barks) and branch-shaking until the mambas fall (A. Galat-Luong & G. Galat pers. obs.). Lowe's Monkeys play a major role in the transmission of Yellow Fever to humans because they: (1) have a high proportion of immature animals in the population; (2) are adapted to second growth forest; (3) inhabit lower forest strata; and (4) readily live near villages (Galat-Luong & Galat 1979, Galat & Galat-Luong 1982, 1997).

Conservation IUCN Category (2012): Least Concern (as *C. campbelli lowei*). CITES (2012): Appendix II.

Lowe's Monkeys are threatened when forest patches are reduced and fragmented, but survive if they are sufficiently connected (Mühlenberg *et al.* 1990). Benefits from the protection of sacred forests (Galat & Galat-Luong 1997).

Measurements

Cercopithecus lowei

HB (♂♂): 480 (400–550) mm, $n = 3$

T (♂♂): 600 (510–770) mm, $n = 3$

HF (♂♂): 130, 150 mm, $n = 2$

E (♂♂): 28, 31 mm, $n = 2$

WT (♂♂): 4.3 (3.5–5.5) kg, $n = 3$

Various localities (Hill 1966, A. Galat-Luong pers. obs.)

HB (♂♂): 500 (420–550) mm, $n = 11$

HB (♀♀): 400 (360–430) mm, $n = 5$

T (♂♂): 720 (490–850) mm, $n = 11$

T (♀♀): 640 (580–680) mm, $n = 5$

WT (♂♂): 4.3 (3.9–4.6) kg, $n = 5$

WT (♀♀): 2.2, 2.2 kg, $n = 2$

Various localities. These values are a combination of *C. lowei* and *C. campbelli* measurements (Napier 1981)

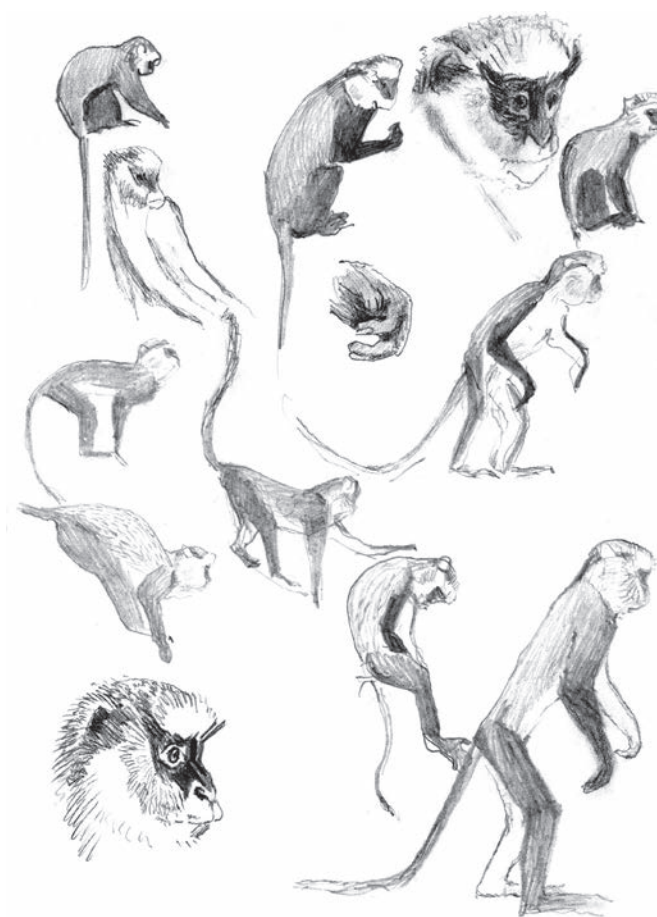
WT (♂♂): 3.9 (3.2–4.6) kg, $n = 11$

WT (♀♀): 2.6 (1.8–5.0) kg, $n = 14$

Various localities (Delson *et al.* 2000)

Key References Bourlière *et al.* 1970; Galat-Luong & Galat 1979; McGraw 1998a, c.

Anh Galat-Luong, Gérard Galat, Mary E. Glenn & W. Scott McGraw



Lowe's Monkey *Cercopithecus lowei*.

Cercopithecus campbelli CAMPBELL'S MONKEY

Fr. Mone de Campbell; Ger. Campbell-Meerkatze

Cercopithecus campbelli Waterhouse, 1838. Proc. Zool. Soc. Lond. 1838: 61. Sierra Leone.Campbell's Monkey *Cercopithecus campbelli* adult male.*Cercopithecus campbelli*

Taxonomy Monotypic species (Groves 2001, 2005c, Kingdon 2001). Often grouped with Lowe's Monkey *Cercopithecus lowei* as one species (Booth 1955, Hill 1966, Dandelot 1974, Napier 1981, Lernoould 1988, Oates 1988b, 2011, Grubb *et al.* 2003). Intermediate forms with Lowe's Monkey near Guiglo, between Cavally R. and Sassandra R., Côte d'Ivoire (Booth 1956b, Oates 1988b, 2011). Member of the *Cercopithecus (mona)* Group (or Superspecies) with Mona Monkey *C. mona*, Dent's Monkey *C. denti*, Crowned Monkey *C. pogonias* and Wolf's Monkey *C. wolffi*. Synonyms: *burnettii*, *monella*, *?temminckii*. Chromosome number: $2n = 66$ (Dutrillaux *et al.* 1988b).

Description Medium-sized, arboreal monkey with white brow, rounded cheek-ruffs, and brownish-tawny belly and lower limbs. Adult ♀ approximately two-thirds size of adult ♂. Sexes similar in colour. Skin below nostrils light pink with sparse white hairs. Skin above nostrils and around eyes dark bluish to greyish-black. Head round. Muzzle short. Cheeks pale greyish-white to yellowish-white, with long, broad, circular shape. 'Mask' (temporal) stripe narrow, black, extending from eyes to ears. Brow whitish. Crown flat, grizzled dark yellow and black. Ear tufts grizzled light yellowish-white, short and rounded. Dorsum reddish-brown agouti. Outer limbs and rump dark grey. Inner limbs and belly brownish-tawny grizzle. Tail long, grey in middle to greyish-black near tip. Infant with pink face and pelage more greyish and less contrasted than adult; like adult at three months.

Geographic Variation No significant variation recorded.

Similar Species

Cercopithecus lowei. Cavally R. (Groves 2001) or Sassandra-Nzo R. (Galat 1983), Côte d'Ivoire to Volta R., Ghana. Sympatric between Sassandra R. and Nzo R. (G. Galat & A. Galat-Luong pers. obs.). Cheeks rectangular. Brow yellow. Belly and lower inner forelimbs white.

Distribution Endemic to West Africa. Rainforest BZ. Gambia to Côte d'Ivoire, west of Sassandra–Nzo R. over an area of ca. 100,000 km². Distribution more patchy than drawn by Lernoould (1988) but less patchy than drawn by Oates (1988b) and Kingdon (2001). Historically, distributed throughout primary and secondary forest zone from Gambia to Sassandra–Nzo R.

Habitat Primary and secondary forests, forest outliers and gallery forests. Marginal habitats include isolated forests and gallery forests in wooded savanna, mangrove swamps and forests that people consider sacred (Jones 1950, Galat & Galat-Luong 1997). Annual rainfall 1200–2500 mm. Altitude ranges from 0 m (mangrove swamps) to 900 m at Mt Nimba, Guinea (Galat-Luong & Galat 1990), and to 1400 m at Fouta Djallon, Guinea (A. Galat-Luong pers. obs.).

Abundance The most common and widespread monkey in Sierra Leone (Jones 1950, Grubb *et al.* 1998). Represents 15% of the groups ($n = 427$ groups encountered) and 10% of the individuals

($n = 7455$ individuals encountered) in Tai Forest, Côte d'Ivoire. Based on these data and on the estimations of Bourlière (1985), Oates *et al.* (1990) calculated ca. 2.5–3.5 groups/km² and a biomass of 82–94 kg/km² for Tiwai, Sierra Leone. For 2006–08 in Tai N. P., 0.92 groups/km², 5.3 ind/km², and total population of 29,700 (N'Goran *et al.* 2012).

Adaptations Diurnal and arboreal. Adapts readily to young secondary forest and mangrove swamps. Particularly good swimmer in Sierra Leone (Grubb *et al.* 1998). One of the arboreal monkeys best able to survive near villages. In undisturbed forest (Tai) spends 15% of time on the ground, 79% in understorey and 5% in main canopy (Galat & Galat-Luong 1985, $n = 633$; McGraw 1998a). Fimbel (1994a) observed higher terrestriality (33%) in disturbed habitats, including abandoned farms. Frequently drops to the ground for long-distance travel in primary forest (McGraw 1998a). Predominantly quadrupedal (80%) with moderate amounts of climbing (14%) and leaping (5%) (McGraw 1996, 1998a, b, c, 2000); 71% of time sitting, 22% standing (McGraw 1998c). Uses large boughs (15–32%), branches (44–48%), twigs (20–28%) and other supports (<1–16%) (Galat & Galat-Luong 1985, McGraw 1998b, c). Sleeping sites include tall trees with large, spherical canopy (Galat 1983).

Foraging and Food Omnivorous. Campbell's Monkey is a slow, cautious forager. In Tai mean day range 1.2 km (1.0–1.5 km, $n = 85$ days; Buzzard 2006c) and home-range 40 ha ($n = 1$) (Galat & Galat-Luong 1985). Feeding (23–36%) and foraging (35–46%) are the principal maintenance activities, while resting and social activities take, respectively, 20–26% and 3–5% of time (Galat 1983, Galat & Galat-Luong 1997, McGraw 1998a, 2000). Diet comprises fruit 46–78%, invertebrates 15–33%, foliage 0–8%, flowers 0–1% and other 7–9% (data collected over 14 months; Galat & Galat-Luong 1985, Buzzard 2006b). Species eaten include *Ficus* spp., *Parinari excelsa*, *Dialium guineense*, *Mangifera indica*, *Parkia biglobosa* (Harding 1984a) and *Pseudospondias microcarpa* (D. Starin pers. comm.). Eat wild and cultivated fruits, seeds, cocoa, coffee, insects and grubs, small amphibians and lizards. In mangrove swamps eats mangrove leaves, germinating hanging seeds of *Rhizophora* sp., crabs, shrimps and mud skippers (Grubb *et al.* 1998).

Social and Reproductive Behaviour Social. Groups are one-adult male harems. Mean group size = 7.7 individuals (1–24, $n = 23$) at Kilimi, Sierra Leone (Harding 1984b), 11.4 (5–33, $n = 9$) at Tai (Galat & Galat-Luong 1985), 5–25 (Grubb *et al.* 1998) and 14 ($n = 1$) in Sierra Leone (Oates *et al.* 1990). Territorial behaviour is conspicuous. At dawn and dusk the adult ♂ climbs an emergent tree and emits two 'booms', separated by ca. 4 sec, the time necessary to inflate its vocal sac. This low frequency sound (80 Hz) can be heard for up to 1 km. After ca. 10 sec (the time necessary for other adult ♂♂ to also climb emergent trees), a series of up to ten noisy barks is emitted, including higher frequency vocalizations that give directional information. The intensity of these barks is in decrescendo, adding distance information. Speed of barks is related to context and caller identity (Lemasson *et al.* 2010). Concatenated sequences, affixations and ♀♀ alarm calls are linked to specific external events (Ouattara *et al.* 2009a, b, c). Pure tone, non-quavered, cohesion-contact calls are given; a low ('oo') and high-pitched whistle ('mii') merge ('o-mii').

No high-pitched warning calls (e.g. 'chirps') are emitted (G. Galat & A. Galat-Luong pers. obs.). Also see McGraw & Zuberbühler (2008).

The adult ♂ solicits mounting by putting his hand on the rump of the ♀. She puts her tail upon her back, permitting the mount.

In Sierra Leone, Campbell's Monkeys associated with one or more other monkey species in 37% of encounters ($n = 52$; Whitesides 1989, Oates & Whitesides 1990), and in 76% of encounters at Tai ($n = 63$; Galat & Galat-Luong 1985). At Tai they associate with Diana Monkeys *Cercopithecus diana* (44% of encounters during censuses), Putty-nosed Monkeys *Cercopithecus nictitans* (<1%), Lesser Spot-nosed Monkeys *Cercopithecus petaurista* (50%), Sooty Mangabeys *Cercocebus atys* (23%), Western Red Colobus *Procolobus badius* (31%), Olive Colobus *Procolobus verus* (28%) and King Colobus *Colobus polykomos* (12%). Campbell's Monkeys synchronize movements with *C. diana* and *C. petaurista* (Galat & Galat-Luong 1985) and engage in polyspecific territorial conflicts that are led by *C. diana*. During these conflicts, the species emit loud-calls in the following order: *C. diana*, Campbell's Monkey and *C. petaurista*, variously followed by *P. badius*, *P. verus* and *C. polykomos* (Galat 1983). Adult ♂♂ are the first to emit inter-group distancing loud-calls thus initiating the inter-location process of the other monkey species while choosing sleeping trees for the night. Long loud-call duets are performed with *C. petaurista*, with which home-range overlaps extensively (85%) (Galat & Galat-Luong 1985). One solitary subadult ♂ in Gambia associated with *P. badius* (Starin 1991). Blue Duikers *Philantomba monticola* follow below Campbell's Monkey groups (A. Galat-Luong pers. obs.). See also Buzzard (2010).

In Tai inter-specific interactions involving Campbell's Monkeys include displacement by *C. diana* and *P. badius*, play fighting with *P. badius*, grooming solicitation with *P. badius*, and grooming by *P. badius* and *P. verus* (Galat-Luong 1979, McGraw 2000, W. S. McGraw pers. obs.). D. Starin (pers. comm.) observed grooming by *P. badius* and a tentative mounting of an adult ♀♀ Green Monkey *Chlorocebus sabaeus*. Campbell's Monkey group members are often positioned closer to other cercopithecoid species than to conspecifics (A. Galat-Luong & G. Galat pers. obs.).

Reproduction and Population Structure Gestation is 25 weeks; singletons born; twins not reported. Birth peak Dec–Jan. At Tai ♂ : ♀ ratio ranges from 1 : 1.0 to 1 : 1.9 ($n = 7$ groups) and adult to immature ratio is 1 : 1 ($n = 11$). One solitary adult ♂ observed (Galat & Galat-Luong 1985). Maximum longevity in captivity 33 years (Jones 1982).

Predators, Parasites and Diseases Campbell's Monkeys are preyed upon by humans (McGraw 2007b), Leopards *Panthera pardus* (Hoppe-Dominik 1984, Zuberbühler & Jenny 2002, 2007), Robust Chimpanzees *Pan troglodytes* (Alp 1993, Alp & Kitchener 1993) and African Crowned Eagles *Stephanoaetus coronatus* (Schultz 2001, Schultz & Thomsett 2007). A young Campbell's Monkey survived a *S. coronatus* attack by fleeing on the ground and, just prior to the attack, crouching and hiding in the grass (Galat 1983). Campbell's Monkeys emit predator-specific alarm calls for *S. coronatus* and *P. pardus* (Zuberbühler 2000b, McGraw & Zuberbühler 2008).

Campbell's Monkey plays a major role in the transmission of Yellow Fever to humans because it is adapted to second growth forest, inhabits lower forest strata and readily lives near villages (Galat & Galat-Luong 1997).

Conservation IUCN Category (2012): Least Concern. CITES (2012): Appendix II.

The destruction of the rainforest and its replacement with farms, farm bush and secondary forest, with its congenial habitat and more abundant food supply, suits Campbell's Monkey and has led to its increase. Campbell's Monkey is now limited only by hunting, particularly in the south-east. They are a serious pest of crops, being particularly damaging to both swamp and upland rice, which is pulled up and the juicy ends of the central leaves eaten, and later also the grain. Also a pest of Cocoa *Theobroma cacao* (Grubb *et al.* 1998). The species is threatened or eliminated when forest patches are reduced or where it is over-hunted by humans, particularly in Gambia (Starin 1989). Probably extirpated from Gambia in the 1980s (E. D. Starin pers. comm. to T. Butynski). Campbell's Monkey is protected in sacred woods (Galat & Galat-Luong 1997) and survives in forest islands if they are sufficiently connected.

Measurements

Cercopithecus campbelli

HB (♂ ♂): 500 (420–550) mm, n = 11

HB (♀ ♀): 400 (360–430) mm, n = 5

T (♂ ♂): 720 (490–850) mm, n = 11

T (♀ ♀): 640 (580–680) mm, n = 5

HF: n. d.

E: n. d.

Various localities. These values are a combination of *C. lowei* and *C. campbelli* measurements (Napier 1981)

WT (♂ ♂): 4.8 (3.2–5.5) kg, n = 24

WT (♀ ♀): 2.6 (2.0–4.5) kg, n = 22

Various localities (MNHN, Oates *et al.* 1990, J.-L. Berthier pers. comm.)

Key References Galat 1983; Galat & Galat-Luong 1985; McGraw 1998c, 2000; Oates 2011.

Gérard Galat, Anh Galat-Luong, Mary E. Glenn & W. Scott McGraw

Cercopithecus denti DENT'S MONKEY

Fr. Mone de Dent; Ger. Dent-Meerkatze

Cercopithecus denti Thomas, 1907. Abstr. Proc. Zool. Soc. Lond. (1907) 38: 1. Ituri Forest between Mawambi and Avakubi, DR Congo.



Dent's Monkey *Cercopithecus denti* adult female.

Taxonomy Monotypic species. The most easterly distributed type of the *C. (mona)* Group or Superspecies (Schwarz 1928c, Booth 1955). This taxon is provisionally treated here as a monotypic species, although the taxonomic classification remains unresolved. While many have placed *denti* in its own species (Pocock 1907, Thomas 1907, Matschie 1912, Lonnberg 1919, Booth, 1955, Hill 1966, Thorington & Groves 1970, Napier 1981, Groves 2001, 2005c), others treated *denti* as a subspecies of Mona Monkey *Cercopithecus mona* (Schwarz 1928c, Allen 1939), Wolf's Monkey *Cercopithecus wolffi* (Colyn 1988, Lernoold 1988, Gautier-Hion *et al.* 1999), or more recently Crowned Monkey *Cercopithecus pogonias* (Thomas 1991, Grubb *et al.* 2003, Detwiler 2010). Because the range of *C. denti* must overlap or abut that of Gray's Crowned Monkey *Cercopithecus pogonias grayi* in forests north

of the Congo R., DR Congo, objective proof that *denti* is a species, as opposed to a subspecies, depends in part on what occurs at this contact zone. The specific status of *C. denti* would be further clarified by resolving the status of what some may argue is its closest relative, the Lomami River Wolf's Monkey *Cercopithecus wolffi elegans* (Lonnberg 1919, Schwarz 1928c, Booth 1955, Gautier-Hion *et al.* 1999, Grubb *et al.* 2003). In forests between the Lomami R. and Lualaba R. DR Congo, *C. elegans* may come into contact with *C. wolffi*, but nothing is known of this contact zone. Finding at this contact zone that *C. elegans* is specifically distinct from *C. wolffi* would suggest that *C. denti* (the closest relative of *C. elegans*) is also specifically distinct from *C. wolffi*. Nevertheless, there still would be the question as to whether *C. elegans* is more properly referred to as a subspecies of *C. denti* or belongs in its own species, *C. elegans*. If *C. denti* is recognized as specific, the various nested relationships and large number of types (11) within the *C. (mona)* Group (Schwarz 1928c, Booth 1955) indicate this group should be elevated to a generic rank, for which *Mona* (Reichenbach 1862) is available. Synonyms: *liebrechtsi*. Chromosome number: $2n = 68$ (Dutrillaux *et al.* 1988b).

Description Medium-sized, arboreal monkey with cream to white undersides that reach high up on flanks and are sharply demarcated from burnt-amber coloured back. Colouration same in both sexes. Average adult ♀ weight is about two-thirds that of average adult ♂. Bare facial skin around deeply sunk eyes is slate-blue. Frontal band off-white, indistinct, varies in presence and development (Lonnberg 1919, Allen 1925). Black hair tuft from outer corner of brow extends back to just above ear to form a high, variably fading, black temporal band. Upper and lower lips covered in short white hairs. Cheeks and jowls covered in buff hairs, some with

single black bands resulting variably in a light grey to grey tint. Ears with long, curved, off-white to straw-yellow hair tuft. Crown and nape olive-grey, speckled by hairs with off-white bands producing yellow highlights. Speckling continuous onto upper back, shoulders and arms. On back, from base of tail to shoulders, colour grades to burnt-umber. This colour is produced by grey-based hairs with three to four black and dark orange (sienna) alternating bands. Dorsum of forelimbs from elbow down to hand black. Outside of hindlimbs brown, lighter than back with speckling producing orange highlights. Foot dorsum black. Cream-white of undersides extends to chin and throughout inner-side of limbs where it is sharply demarcated from the colour of the outside limbs. Burnt-umber of back continues onto tail dorsum gradually grading into grizzled grey ca. 25% of the way down. Proximal ca. 25% of tail underside cream to light yellow, well demarcated from dorsal colour, but distally colour grades into light grey without clear demarcation from dorsum. Distal ca. 20–33% of tail gradually grades into black all around ending in a slight tuft. Scrotum pale greyish-blue. Palmar and plantar skin is black. As noted by Allen (1925), *C. denti* shows relatively little variation in coat colouration when compared to other guenon species. An infant with only an erupting first milk molar and first incisor had adult colour pattern. Hair, however, is much softer and shorter than in adult and undersides of body and inner-sides of limb are nearly bare, exposing golden skin (Allen 1925).

Geographic Variation There is no reported variation linked to geographic distribution that would relate to population or subspecific differences (Allen 1925, Napier 1981, Groves 2001, 2005c).

Similar Species

Cercopithecus wolffi elegans. Eastern Congo Basin between upper reaches of Lomami R. and Lualaba R. White brow-band extends back over temples to just above the ears, adpressed hair below temples, and sharp colour division between light grey thighs and dark greyish-brown of small of the back (Booth 1955, Napier 1981).

Cercopithecus pogonias grayi. West of 22° E between Congo R. and Ubangi R. Rump dark brown or black; tail black throughout dorsal extent; outer hindlimbs tan-grey to iron-grey; underparts light yellow to yellow grading into dark yellow flanks and chestnut-brown back without a sharp colour demarcation; sagittal crest of erect black hairs running back from the brow and flanked on either side by an oval patch of off-white hairs medial to wide black temporal bands.

Distribution Endemic to E DR Congo, Burundi, Rwanda and SW Uganda. Rainforest BZ. In forest block between Western (Albertine) Rift Highlands and right bank of Congo R. and Lualaba R. Distribution poorly known north of Congo R., but collected as far north at 03° 30' N (just south of Uele R.), and as far east as 30° 45' E (in headwaters of Kibali R. and Ituri R. in highlands west of L. Albert). Blancou's (1935) often cited (Malbrant 1952, Booth 1955, Napier, 1985, Lernoould 1988, Groves 2001, 2005c) claim of *C. denti* extending to forests north of the Ubangi R. (06° 40' N) near M'brés, Central African Republic, is based on a misidentification of *C. p. grayi* that was later corrected by Blancou (1958, cited in Lernoould 1988).

Along right bank of Congo R. the westward extent seems to be limited by the lower Itimbiri R. (Lernoould 1988), but, farther



Cercopithecus denti

north, collected on both sides of the Itimbiri R. Western extent past 24° E not known. Considering *C. p. grayi* has been collected just east of 22° E in forest between Ubangi R. and Congo R. (Schouteden 1944a, Booth 1955), and ranges as far east as 25° E to between Uele R. and Mbomu R. (E. E. Sarmiento pers. obs.), the intervening area is likely a zone of parapatry, sympatry or hybridization (Booth 1955). Records north of the Uele R., shown in Schouteden's (1944a), Booth's (1955) and Dandelot's (1965) maps, have not been verified on the basis of museum specimens, locality reports or field observations. Given that eastwards the Uele R. and its tributaries (Bomakandi R. and Kibale R.) are porous barriers, the north-eastern extent of *C. denti* is unknown. *Cercopithecus denti* may occur north of the Uele R. and its tributaries (Dandelot 1965), but has never been collected here, north of the Mbomu R. or in Sudan (Kock 1969), where forest fragmentation becomes extensive. Throughout most of its eastern extent *C. denti* is found west of the Western Rift lakes, only occurring east of the lakes along their interconnecting rivers (i.e. Semliki R. and Ruzizi R.); enters SW Uganda crossing the Semliki R. to reach Bwamba Forest at just over 30° E; enters W Rwanda north of L. Kivu to reach Kisenyi at 29° 15' E; and crosses the Ruzizi R. to enter S Rwanda (Nyungwe N. P.) and N Burundi (Ruzizi Plain) at ca. 29° 15' E. Southern limit for *C. denti* is Kabambare at roughly 04° 42' S. This is south of the Luama R. and coincides with the break-up of equatorial forest. No recent records for Virunga N. P., highlands west of L. Edward (Frechkop 1938, 1943, Hoier 1955, Curry-Lindhal 1956, Verschuren 1972) or region around L. Kivu (Rahm & Christiaensen 1963, E. E. Sarmiento pers. obs.), although there are early museum records for these localities.

Habitat Inhabits riverine, lowland and secondary forests and, less commonly, lower montane forest, at altitudes between 400 m and 1900 m (Haddow 1952, Rahm 1966, Thomas 1991, E. E. Sarmiento pers. obs. in DR Congo and SW Uganda). Report of an adult ♀ *C. denti* and its supposed hybrid offspring in a group of Doggett's Silver

Monkeys *Cercopithecus mitis doggetti* at 2500 m in Nyungwe N. P. (B. Kaplin pers. obs. in Detwiler *et al.* 2005) has not been verified. This report is 600 m higher than otherwise observed for *C. denti*.

In Semliki N. P., SW Uganda, and Ituri Forest, DR Congo, *C. denti* more often in secondary forest and forest interior than on periphery (Haddow 1952, Thomas 1991). In SW Uganda, marginally ranges into swamp forest and *Cynometra* forest (J. Kingdon pers. obs.). Usually found close to water or in forests where floods create sites with secondary growth. Mean annual rainfall is >1400 mm and may be >3000 mm in the highlands west of L. Albert where *C. denti* reaches maximum altitude. Mean annual temperature at the lowest (ca. 400 m) and highest (1900 m) altitudes is roughly 25 °C and 15 °C, respectively. Nowhere in the range do temperatures drop below freezing. Close to the Equator there are two dry seasons, each roughly two months in duration. One dry season progressively shortens and the other lengthens with distance from the Equator so that at those latitudes farthest from the Equator *C. denti* may endure a three-month dry period with little rain.

Abundance Common all along right banks of Congo R. and Lualaba R. from the Congo–Itimbiri confluence to 03°S (Colyn 1988). In Ituri Forest, common in the southern and central sectors, which have a wealth of rivers (Biena, Epulu, Ituri, Lindi, Nepoko and Semliki) creating gaps for secondary forest growth within mast-fruiting, monodominant (*Gilbertiodendron*) forests (Hart *et al.* 1986, Thomas 1991). Uncommon in northern Ituri with fewer rivers (Nepoko and Ituri) and mixed forests dominated by *Brachystegia laurentii* and *Cynometra alexandri* (Hart *et al.* 1986). In secondary forests within Ituri, *C. denti* most abundant in year-round fruiting stands of Umbrella Tree (African Corkwood) *Musanga cecropioides* (Thomas 1991). In central and northern Ituri, transect censusing estimated 23.1 ind/km² and group density of 2.4/km² (Thomas 1991). Common in forests between L. Kivu and Lualaba R. (Rahm 1966). Transect censusing within the Lowland Sector of Kahuzi-Biega N. P. yielded estimates of 12.6 ind/km² and 1.3 groups/km² in the KB1 Sector, and 17.3 ind/km² and 1.8 groups/km² in the KB2 Sector (Hall *et al.* 2003).

Adaptations Diurnal and arboreal. *Cercopithecus denti*'s ability to associate in groups with other monkeys, maximize food availability and minimize competition may be the most important adaptations, and all likely linked to its rich vocal repertoire. Unfortunately, the corresponding anatomy, physiology and behaviour underlying these adaptations is unknown. The relatively small body size enables *C. denti* to exploit food on peripheral branches and facilitates movement up trees and through the canopy.

Foraging and Food A frugivore–folivore supplementing diet with invertebrates. Diet of *C. denti* not studied in detail. Stomach of one animal collected in Bwamba Forest comprised almost entirely of leaves and shoots (Haddow *et al.* 1947). Stomachs from animals collected in lowland forests east of L. Kivu close to Irangi contained 'Mutakala' fruit and tree gum (Rahm 1966). Mbuti pygmies report that *C. denti* eats Maize *Zea mays*, Oil Palm fruits *Elaeis guineensis*, banana *Musa* sp., Papaya *Carica papaya* and pumpkin *Cucurbita* sp. (Carpaneto & Germi 1989). This species is likely to consume fruits, young leaves and shoots, seeds, insects and gum in order of decreasing proportion in the diet.

Nectar, mushrooms and vertebrates probably form a small part of the diet. As for other guenons, proportions of items in the diet are likely to change with season and availability, with seed consumption inversely related to insect and fruit consumption. Considering the diet of other *C. (mona)* Group members, the frequent association of *C. denti* with Schmidt's Red-tail Monkeys *Cercopithecus ascanius schmidtii*, and their similarities in body size, *C. denti* is likely to include less fruit and more leaves and seeds in their diet than *C. ascanius*. Haddow (1952) notes *C. denti* has two feeding periods during the day, one in early morning and a much longer one in afternoon to evening.

Cercopithecus denti usually occupies the higher levels of the understorey and lower levels of the canopy, but sometimes feeds in the highest part of the canopy. They occasionally move on the ground (Haddow *et al.* 1951), probably in search of food. Natives claim that *C. denti* never comes to ground to feed on salt or other minerals (Carpaneto & Germi 1989, E. E. Sarmiento pers. obs.) and they report that *C. denti* has the ability to swim (E. E. Sarmiento pers. obs.). Nothing is known of daily travel distance or of home-range. Given its body size and group size, a mean daily travel distance of 1.0–1.5 km is expected.

Social and Reproductive Behaviour Social. Group composition has yet to be studied in detail but *C. denti* groups appear to consist of a single adult ♂, with two or more ♀♀ and their offspring. All-male groups probably exist but have yet to be verified. Mean group size in Kahuzi-Biega N. P. was 9.8 individuals (Hall *et al.* 2003) and in Ituri Forest was 9.6 individuals (7–21, n = 52 groups; Thomas 1991). Kingdon (1971) observed a group of 12 individuals in Bwamba Forest and noted that *C. denti* groups disperse into subgroups of twos and threes when pursued by hunters.

Cercopithecus denti often feeds in company of *C. ascanius* and Grey-cheeked Mangabey *Lophocebus albigena* (Haddow 1952, Rahm 1966, E. E. Sarmiento pers. obs. in Semliki N. P.). In Semliki N.P. also seen with Guereza *Colobus guereza*. Mbuti pygmies in NE DR Congo report that *C. denti* also forms associations with Stuhlmann's Blue Monkeys *Cercopithecus mitis stuhlmanni*, Eastern Red Colobus *Procolobus rufomitratus* and *C. guereza* (Carpaneto & Germi 1989).

In Nyungwe N. P., *C. denti* reported to hybridize with *C. m. doggetti* and *C. a. schmidtii* (Detwiler *et al.* 2005, Detwiler & Gray 2006, Detwiler 2010). The hybrids resided with a *C. m. doggetti* group and an Angola Colobus *Colobus angolensis* group, respectively. Photographs of the alleged *C. denti* × *C. a. schmidtii* hybrid depict an animal that strongly resembles a *C. a. schmidtii* × *C. m. doggetti* hybrid. This, together with the absence of any obvious hybrids among hundreds of *C. denti* museum specimens (Allen 1925, E. E. Sarmiento pers. obs.), questions the existence of *C. denti* hybrids in Nyungwe N. P.

Cercopithecus denti has a large (but unstudied) vocal repertoire that includes 'chirps', 'screams', 'coos' and 'booms' (E. E. Sarmiento pers. obs. in Semliki N. P.). Boom calls, uttered only by adult ♂♂, probably serve to space-out neighbouring groups and rally group members, especially after disturbances (J. Kingdon pers. obs.).

Reproduction and Population Structure Nothing known of *C. denti* reproduction or population structure in the wild. Ovulatory cycle length and gestation length, as in most other guenons, are likely 30–32 days and 140–187 days, respectively (Hill 1966). Females show no external signs of ovulation. Museum records of infants of

the same dental age occur throughout the year (E. E. Sarmiento pers. obs.), indicating there is no exclusive breeding season. As for other guenons, an annual birth peak for *C. denti* is likely (Butynski 1988).

Predators, Parasites and Diseases Ugandan and Congolese natives do not commonly hunt *C. denti* (E. E. Sarmiento pers. obs.). Mbuti pygmies have taboos against adults of child-bearing age or participants in circumcision rites eating the flesh of *C. denti* (Carpaneto & Germe 1989). *Cercopithecus denti* not known to be used for utilitarian or ornamental purposes. As such, hunting by humans does not appear to pose a serious threat. *Cercopithecus denti* is a relatively rare prey of Leopards *Panthera pardus* (Hayward *et al.* 2006). Although its body size is probably within the optimal prey size for African Golden Cats *Profelis aurata*, Mbuti pygmies claim it climbs too fast to be this cat's prey (Carpaneto & Germe 1989). A propensity to feed high in trees makes *C. denti* a likely predator for African Crowned Eagles *Stephanoaetus coronatus*, but its constant association with other vigilant monkeys probably greatly reduces this threat. Its occasional forays into water may make it susceptible to attacks by Nile Crocodiles *Crocodilus niloticus*, especially in Semliki N. P. and Ituri Forest, where *C. niloticus* are numerous. Mbuti pygmies also claim *C. denti* is prey to pythons *Python* sp. (Carpaneto & Germe 1989).

Cercopithecus denti in SW Uganda carries Yellow Fever, Semliki Forest Virus and Bwamba Fever Virus (Haddow 1952). Early reports that *C. denti* carries simian immunodeficiency virus (SIV) were based on analyses of other *C. (mona)* Group members. More recent studies verify that *C. denti* carries a unique SIV strain (Dazza *et al.* 2005). This species harbours the liver parasite *Hepaticystes kochi* (Haddow 1952).

Conservation IUCN Category (2012): Least Concern (as *C. p. denti*). CITES (2012): Appendix II.

Cercopithecus denti has been extirpated from Kisenyi as a result of clearing of forests. Its survival on the Ruzizi Plain is far from certain and no doubt precarious. In Bwamba Forest numbers are said to be declining (Kingdon 1971). Dependent on forests within an area of occurrence of roughly 564,000 km² (correcting for hilly terrain). Rapidly growing human populations over much of the range of *C. denti* will continue to reduce the abundance and geographic range of this species.

Measurements

Cercopithecus denti

TL (♂ ♂): 1275 ± 95.7 (1050–1430) mm, n = 22

TL (♀ ♀): 1087 ± 84.4 (915–1215) mm, n = 14

Trunk length (♂ ♂): 467 ± 35.93 (380–515) mm, n = 22

Trunk length (♀ ♀): 414 ± 44.16 (320–475) mm, n = 14

T (♂ ♂): 808 ± 72.39 (650–960) mm, n = 22

T (♀ ♀): 673 ± 72.31 (530–770) mm, n = 14

HF (♂ ♂): 149 ± 9.79 (125–177) mm, n = 22

HF (♀ ♀): 142 ± 7.44 (115–142) mm, n = 14

E (♂ ♂): 36 ± 2.11 (32–39) mm, n = 12

E (♀ ♀): 35 ± 2.30 (31–38) mm, n = 14

WT (♂ ♂): 4.2 ± 0.572 (3.6–5.0) kg, n = 4

WT (♀ ♀): 2.8 ± 0.340 (2.0–3.7) kg, n = 36

Linear measurements from various localities (AMNH).

WT from various localities (Colyn 1994)

Key References Carpaneto & Germe 1989; Hill 1966; Rahm 1966; Thomas 1991.

Esteban E. Sarmiento & Jonathan Kingdon

Cercopithecus wolffi WOLF'S MONKEY

Fr. Mone de Wolf; Ger. Wolf-Meerkatze

Cercopithecus wolffi Meyer, 1891. Notes Leyden Museum 13: 63. 'Central West Africa'.



Congo Basin Wolf's Monkey *Cercopithecus wolffi wolffi* adult.

Taxonomy Polytypic species in the *Cercopithecus (mona)* Group (or Superspecies). Considered by some authorities as a subspecies of Crown Monkey *C. pogonias* or as conspecific with Dent's Monkey *C. denti* (Dorst & Dandelot 1970, Gautier-Hion *et al.* 1999, Grubb *et al.* 2003). Here we follow Groves (2001, 2005c) in recognizing three subspecies: Congo Basin Wolf's Monkey *C. w. wolffi*, Lomami River Wolf's Monkey *C. w. elegans*, and Fire-bellied Wolf's Monkey *C. w. pyrogaster*. Synonyms: *elegans*, *pyrogaster*. Chromosome number: 2n = 72 (Dutrillaux *et al.* 1988b).

Description A round-headed, short-muzzled, long-tailed, arboreal monkey with a black facial mask, long ear-tufts, and light dorsal stripe. Adult ♀ like adult ♂ in colouration but smaller, weighing ca. 75% as much as adult ♂. There is considerable variation in pelage colour among the three subspecies (see Geographic Variation). Facial skin above nostrils dark blue. Eyelids flesh-coloured. Muzzle below nostrils flesh-coloured with sparse white hairs. Pelage of nasal region and around eyes black, fine and short, forming a facial 'mask'. Black pelage of upper cheeks shorter and



Congo Basin Wolf's Monkey *Cercopithecus wolfi wolfi* adult.

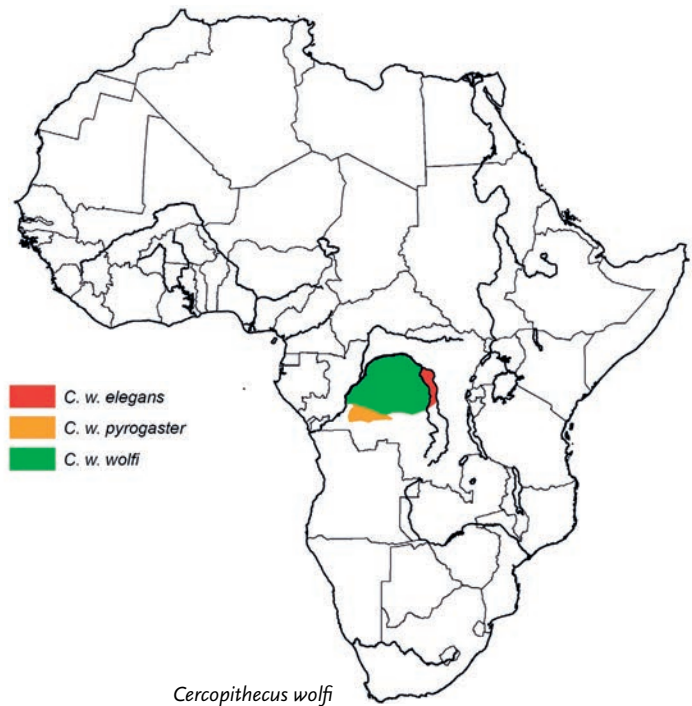
thinner than pelage on lower cheeks, which is pale agouti. Brow diadem extends to ears. Ears with long (up to 35 mm) tufts tapering to a point. Crown flat, not raised into a crest or bouffant. Upper body pelage dense, agouti grizzled, with paler, broad, dorsal midline stripe. Underside and inner limbs white or pale. Outer forearms black. Hindlimbs sharply differentiated in colour. Hands (relative to other guenons) slight, short and broad with stubby third and fourth fingers of similar length. First digit (thumb) relatively long. Feet relatively small and short with long, strong first digits ('big toes'). Feet and outer surfaces of forearms and hands blackish or black, glossy. Tail dorsum blackish or black. Tail ventrum off-white to grey near base, more uniform and paler in mid-section, and blackish or black distally with black terminal tuft. Young similar in colour to adults (Gautier-Hion *et al.* 1999).

Geographic Variation

- C. w. wolfi* Congo Basin Wolf's Monkey. Central Congo Basin between Congo R. and Kasai R. Diadem broad, off-white; facial 'mask' narrow; lower cheeks yellow speckled with black; ear-tufts orange to red; back slate-grey; dorsal midline stripe olive; lateral stripes broad, orange; ventral and inner limb surfaces white or yellow; thighs and lower hindlimbs tawny orange or reddish.
- C. w. elegans* Lomami River Wolf's Monkey. Eastern Congo Basin between upper reaches of Lomani R. and Lualaba R. Diadem of medium width, white; facial 'mask' broad; ear-tufts grey or white; lower cheeks whitish; back dark greyish-brown; dorsal midline stripe greyish-ochre; no lateral stripes; ventral and inner limb surfaces white; thighs and lower hindlimbs light grey with greenish freckle. Morphology somewhat intermediate between *C. wolfi* and *C. denti*.
- C. w. pyrogaster* Fire-bellied Wolf's Monkey. Southern Congo Basin south of Kasai R. to ca. 07° S and west to Kwango R. Diadem narrow, buff; ear-tufts reddish; facial 'mask' broad; lower cheeks orange; back dark greyish-brown to black; dorsal midline stripe chestnut; lateral stripes narrow, reddish; ventral and inner limb surfaces yellowish-orange to red; thighs and lower hindlimbs orangish-red to rusty red.

Similar Species

Cercopithecus ascanius. Throughout range of *C. wolfi*. Tail mostly reddish. Nose-spot white, black or russet.



Distribution Endemic to Congo Basin, DR Congo. Rainforest BZ. In most forests on the left bank of the Lualaba/Congo R. south to about 07° S. Present at Lokutu (01° 09' N, 23° 37' E) on the Congo R., which must be close to, or at, the northern extreme of the range (Butynski & Sanderson 2007). Kwango R. is probably western limit (Colyn 1988, Gautier-Hion *et al.* 1999).

Habitat Lowland rainforests. Rainforest BZ. Details available only for *C. w. wolfi* (McGraw 1994 at Lomako; F. Maisels & A. Gautier-Hion pers. obs. at Salonga). Occurs both in terra firma and in flooded areas. More common in primary forest than in swamp forests. Rarely observed in secondary forests. At Lomako most often in the mid-canopy of primary forest (usually 20–40 m above ground); in swamp forests tends to frequent lower levels. In flooded forests in Salonga mostly in upper and middle canopy; also in emergent trees. Altitude range ca. 100–400 m. Mean annual rainfall 1700–2100 mm.

Abundance Mean of 44 ind/km² and biomass of 168 kg/km² at Lomako (McGraw 1994). At Salonga the population studied within an area of ca. 2.5 km² included five groups that totalled about 75 individuals. This yields a population density of ca. 30 ind/km² (A. Gautier-Hion pers. obs.).

Adaptations Diurnal and arboreal. Never observed on the ground. Like other species of the *C. (mona)* Group, adult ♂ *C. wolfi* gives loud 'boom' calls that help maintain intra-group cohesion and spacing among neighbouring units (Gautier 1988). The 'boom' can be heard by the human ear to ca. 300 m. The typical ♂ display is a stiff-legged raised-rump posture. Ritualized head-flagging resembles that found in some other guenons (Kingdon 1997).

Foraging and Food Omnivorous. Diet of fruit, leaves, flowers and invertebrates. At Salonga the annual plant diet in a flooded forest dominated by Caesalpiniaceae (ca. 40% of trees) was composed

of ca. 30% arils, 20–25% seeds, 30% leaves, 11–15% flowers and only 5% fleshy fruit. Nectar of *Daniellia* flowers (Caesalpiniaceae) constituted a major resource during the period of fruit scarcity. Leaves and flowers mostly taken from Caesalpiniaceae. Seeds mainly came from Caesalpiniaceae, Mimosaceae and Olacaceae, and arils from Myristicaceae and Annonaceae (F. Maisels & A. Gautier-Hion pers. obs.). Mean size of five group home-ranges was ca. 60 ha (50–70). Home-ranges did not overlap.

Social and Reproductive Behaviour Social. Groups contain only one adult ♂ that gives loud ‘booms’; other adult ♂♂ can be present. Solitary individuals not observed. At Lomako mean group size is 10.1 individuals (n = 37 groups). At Salonga mean group size is 16 individuals (13–25, n = 5). Both at Lomako and Salonga *C. wolffi* observed in polyspecific groups in >80% of encounters. Mixed groups include either one species (57% of encounters), two species (37%) or three species (6%; McGraw 1994). At both sites, such associations include Grey-cheeked Mangabey *Lophocebus aterrimus* in >80% of encounters. This pattern is similar to *C. pogonias*, which most frequently associates with *L. albigena*. *Cercopithecus wolffi* also often associates with *C. ascanius* (50% of encounters). Less often, mixed groups include Angola Colobus *Colobus angolensis* (Lomako and Salonga) and/or Tshuapa Red Colobus *Procolobus rufomitatus tholloni* (Salonga).

Reproduction and Population Structure No field data available. It is likely that life history characteristics are similar to those of *C. pogonias*. Two captive-born ♀♀ gave birth for the first time when five years old. Then they reproduced at one to three year intervals with a mean of about two years (n = 11 births; T. Petit pers. comm.).

Predators, Parasites and Diseases Little is known about predation or disease in *C. wolffi*. African Crowned Eagle *Stephanoaetus coronatus*, Central African Rock Python *Python sebae*, African Golden Cat *Profelis aurata* are likely predators.

Conservation IUCN Category (2012): Least concern as *C. p. wolffi*. CITES (2012): Appendix II.

Habitat loss and hunting for the bushmeat trade are the two primary threats. *Cercopithecus wolffi* is an alert and fast-moving species, characteristics that make it relatively difficult to hunt. This, together with a small body size, probably makes *C. wolffi* one of the least attractive targets in the diurnal primate community (Butynski & Sanderson 2007).

Measurements

Cercopithecus wolffi

HB (♂♂): 485 (445–511) mm, n = 3

T (♂♂): 779 (695–822) mm, n = 3

HF: n. d.

E: n. d.

WT (♂♂): 3.9 (2.6–5.0) kg, n = 17

WT (♀♀): 2.9 (1.8–3.7) kg, n = 120

Body measurements: locality not stated (Napier 1981)

WT: DR Congo (Gautier-Hion *et al.* 1999)

Key References Maisels & Gautier-Hion 1994; McGraw 1994.

Annie Gautier-Hion

Cercopithecus pogonias CROWNED MONKEY

Fr. Cercopithèque couronné; Ger. Kronenmeerkatze

Cercopithecus pogonias Bennett, 1833. Proc. Zool. Soc. Lond. 1833: 67. Fernando Po (=Bioko I.), Equatorial Guinea.



Taxonomy Polytypic species in the *Cercopithecus (mona)* Group (or Superspecies). Some authorities include *wolffi* as a subspecies within *C. pogonias* (e.g. Grubb *et al.* 2003). Based on analyses of chromosomes (Dutrillaux *et al.* 1988b), proteins (Ruvolo 1988) and vocalizations (Gautier 1988) the two species are, indeed, phylogenetically close together. This profile follows Groves (2001, 2005c) in recognizing the subspecies: Golden-bellied Crowned Monkey *C. p. pogonias*, Black-footed Crowned Monkey *C. p. nigripes* and Gray's Crowned Monkey *C. p. grayi*. A fourth subspecies, Schwarz's Crowned Monkey *C. p. schwarzianus* from Mayumbe, DR Congo, was put in synonymy by Napier (1981) but is recognized by Groves (2001, 2005c). This profile follows Grubb *et al.* (2003) in leaving poorly-known *C. p. schwarzianus* in synonymy. Synonyms: *erxlebeni*, *grayi*, *nigripes*, *pallidus*, *petronellae*, *schwarzi*, *schwarzianus*. Chromosome number: 2n = 72 (Dutrillaux *et al.* 1988b).

Crowned Monkey *Cercopithecus pogonias* adult male.



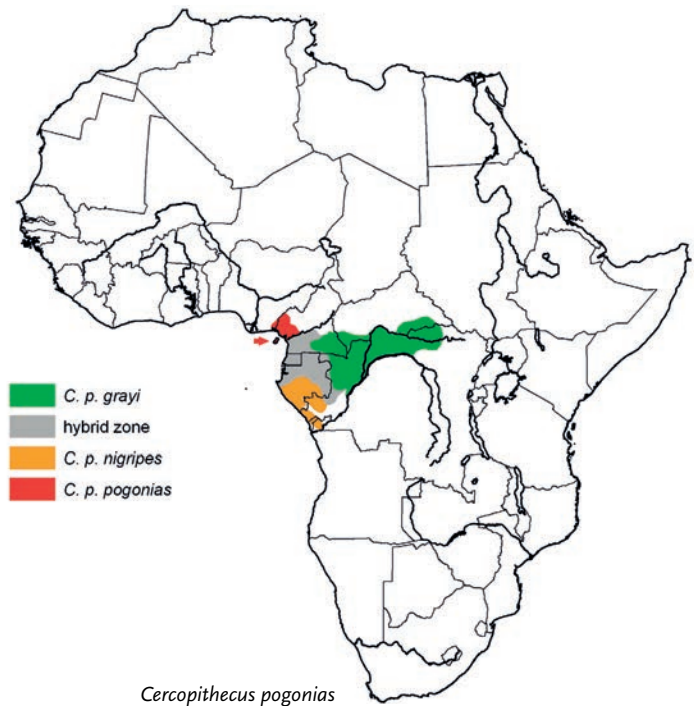
Gray's Crowned Monkey *Cercopithecus pogonias grayi* adult male.

Description Arboreal, long-tailed, medium-sized monkey with three broad black stripes on crown and prominent ear-tufts. Sexes similar in colour but adult ♀ smaller, weighing ca. 65–75% as much as adult ♂. Facial skin bluish or grey with pinkish eyelids and muzzle. Broad black central crest on crown and broad black stripes on temples separated by white or yellow patches. Ear-tufts prominent and pointed, orange-yellow or whitish. Black or grey ridge down middle of back. 'Saddle' on lower back black or dark red. Sides grizzled khaki to grey-olive. Outer arms black or blackish. Outer parts of lower hindlimbs yellowish or buffy-grey. Underside and inner sides of limbs whitish, yellow or orange. Toes black. Tail dorsum black, at least distally; tail ventrum pale yellowish-grey to orange.

Geographic Variation

C. p. pogonias Golden-bellied Crowned Monkey. Bioko I. (former Fernando Po), Equatorial Guinea, and the adjacent mainland between Cross R., Nigeria and Sanaga R., Cameroon. On Bioko I., limited to the southern ca. 25% of the island and to the lower southern slope of Pico Basilé (Butynski & Koster 1994, Hearn *et al.* 2006). Gautier-Hion *et al.* (1999) believe it possible that the Cameroon form may be an undescribed subspecies. Crown and nape dark grey with yellowish speckling; has least brightly coloured crest. Cheeks yellowish, lightly speckled with agouti near ear. Ear-tufts orange to red. Saddle black, sharply defined with variably tinted agouti on flanks. Underside and inner sides of limbs yellow to orange. On Bioko, underside of adult ♂♂ is darker orange than in adult ♀♀ (T. Butynski pers. comm.). Outer lower hindlimbs yellowish-agouti. Hands and feet black. Black on outer surfaces of forelimbs extends up to elbow or higher. Tail as above.

C. p. nigripes Black-footed Crowned Monkey. Endemic to Gabon from south of Ogooué R. southwards to perhaps the Kouilou R. (Gautier-Hion *et al.* 1999). Crown and nape dark grey with yellowish speckling; has strongly contrasting crest but frontal part of crest pale with central crown dark only on distal part. Cheeks



yellowish, lightly speckled with agouti. Ear-tufts yellow or orange. Saddle black, sharply defined with variably tinted agouti on flanks. Underside and inner sides of limbs orange. Outer lower hindlimbs buffy-grey agouti. Hands and feet black. Tail dorsum orange.

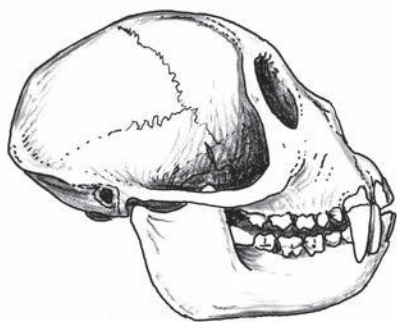
C. p. grayi Gray's Crowned Monkey. Sangha Basin of SE Cameroon, S Central African Republic and Congo, eastward to north of Itimbiri R., NC DR Congo, southwards to north bank of Congo R. to Cabinda (Gautier-Hion *et al.* 1999). Crown and nape dark chestnut-red with yellowish speckling; well-defined crest with dark central stripe extending onto brow. Cheeks yellowish, lightly and partially speckled with agouti. Ear-tufts whitish or pale yellow. Saddle dark red blending with orange-tinted agouti on flanks. Underside and inner sides of limbs orange to yellow. Outer lower hindlimbs and feet buffy-grey agouti. Only toes of feet black. Tail dorsum yellowish-grey.

A large zone of hybridization between the three subspecies may exist in the Atlantic coastal basin between Sanaga R. and Ivindo R., along the upstream tributaries of the Congo R. (see map p. 37 in Gautier-Hion *et al.* 1999).

Similar Species No sympatric monkeys are likely to be confused with this species.

Distribution Rainforest BZ. Endemic to western central Africa from Cross R. south to Congo R. On Bioko I., otherwise limited by the Atlantic Ocean on the west and extending eastwards to north bank of Itimbiri R. (Gautier-Hion *et al.* 1999). See details of distribution in Geographic Variation.

Habitat Preferentially inhabits mature lowland rainforests with tall trees and clear understorey. Also in inundated forests and old secondary forests. Avoids young secondary forests with dense understorey (Gautier-Hion *et al.* 1983, Butynski & Koster 1994).



Lateral view of skull of Crowned Monkey *Cercopithecus pogonias* adult male.

Rarely encountered in gallery forests and never seen in small forest fragments that extend into savanna (Tutin *et al.* 1997b). Not reported to be crop-raider. Altitude range is from sea level to 1200 m (south Bioko I.; Butynski & Koster 1994). Mean annual rainfall ranges from 1500 mm on the mainland to 10,000 mm on south Bioko I.

Abundance Biomass is 9–11 kg/km² in C Gabon (Forêt des Abeilles and Lopé Reserve; White 1994, Brugière *et al.* 2002), 60 kg/km² in NE Gabon, and 115 kg/km² in Ngotto Forest, Central African Republic (Gautier-Hion & Gautier 1974, Gautier-Hion 1996). Density is 4–48 ind/km². Minimal density occurs at the forest-savanna ecotone (Tutin *et al.* 1997b). In Ngotto Forest *C. pogonias* has the lowest density and biomass of the arboreal guenons. Encounter rates of 0.04 groups/km of transect on Bioko I. during an island-wide survey in 1986 (373 km of census; Butynski & Koster 1994). Encounter rate of 0.34 groups/km in 2008 along 44 km of transect in the Gran Caldera de Luba, and 0.56 groups/km in 2009 along 48 km of transect and 0.52 groups/km in 2010 along 50 km of transect at Badja North, south-west Bioko (T. Butynski, G. Hearn, M. Kelly & J. Owens pers. comm.). The Gran Caldera de Luba and Badja North are remote sites where hunting is relatively uncommon and where there are no other anthropogenic impacts. As such, the encounter rates at these two sites are likely close to what is expected for an undisturbed population of *C. pogonias*.

Of 108 groups of monkeys encountered on Bioko during the island-wide survey in 1986, 15 (14%) were *C. pogonias* (Butynski & Koster 1994). During a 2008 survey in the Gran Caldera de Luba, south-west Bioko, *C. pogonias* accounted for 24% of the 62 groups of monkeys (six species) encountered. At Badja North, south-west Bioko, 26% of 105 groups encountered in 2009, and 29% of 91 groups encountered in 2010 were *C. pogonias* (T. Butynski, G. Hearn, M. Kelly & J. Owens pers. comm.).

Adaptations Diurnal and arboreal. Agile and highly vocal monkey with a wide repertoire of graded calls. Like many African cercopithecines, adult ♂♂ and ♀♀ possess laryngeal sacs. Male sacs are twice as large as those of ♀♀ and among the most developed of the arboreal guenons. When inflated, they act as resonators and amplifiers, especially for the adult ♂ 'boom' call (Gautier 1971). The boom can be heard to a distance of >200 m (T. Butynski pers. comm.). An 'arched' posture, accompanied by 'pouting', is common in receptive ♀♀. Tail-twining postures are common in resting groups (Gautier & Gautier-Hion 1977). They also perform a ritualized head display (Kingdon 1997).

Foraging and Food Omnivorous. Fruit and seeds dominate the diet (60–87% depending on the site). Relative amount of seeds, taken from immature fleshy fruit, dry pods or fruit with wind dispersed seeds, varies from 3% (NE Gabon; Gautier-Hion 1980) to 50% in a forest dominated by Leguminosae (Forêt des Abeilles; Brugière *et al.* 2002). At both sites, arils may account for up to 50% of fleshy pulp ingested. Leaves and flowers make up about 15–17% of diets. In NE Gabon, 67 fruit species in the diet; mostly from tall trees and lianas belonging to three families: Annonaceae, Apocynaceae and Euphorbiaceae. Throughout the year, fruit of the liana *Cissus dinklagei* (Vitaceae) was the most consumed item. During the period of fruit scarcity, arils of Myristicaceae (*Coelocaryon* and *Pycnanthus*) are the staple plant food (the same was observed at Lopé Reserve; Tutin *et al.* 1997a). At Forêt des Abeilles, seeds and leaves of Caesalpiniaceae contribute 52% to the annual plant diet and Burseraceae contribute 12%. During the period of fruit scarcity, pulp and seeds of drupes of several species of *Dialium* may account for 75% of monthly feeding scores. However, the fruiting of these species is irregular from year to year, so they cannot be considered a true keystone resource. Animal prey makes up 6–16% of the diet of *C. pogonias* and includes mainly orthoptera and caterpillars, and to a lesser extent ants, cocoons, spiders, insect larvae, moths and butterflies. Compared to sympatric Putty-nosed Monkey *Cercopithecus nictitans* and Moustached Monkey *Cercopithecus cephus*, *C. pogonias* has the least seasonal variation in diet and the least dietary difference between ♀♀ and ♂♂ (Gautier-Hion 1980).

Cercopithecus pogonias forage in groups or in polyspecific associations. Home-range size varies from 55 to 148 ha depending partly on whether alone or in a polyspecific association. Monospecific *C. pogonias* groups rarely occur and they have the smallest home-ranges. One group of 18 individuals (followed for 900 h) associated all the time with a *C. nictitans* group of 20 individuals and ranged over 148 ha. When both groups associated with a *C. cephus* group of 15 individuals (42% of the time), home-range declined to 119 ha; home-range size appears to depend on which species are involved, not on the size of the association. Mean day range of *C. pogonias* monospecific groups estimated at 1600 m. Mean day range of *C. pogonias* when associated with *C. nictitans* was 1825 m and increased to 1980 m when *C. cephus* was present (Gautier-Hion & Gautier 1974, Gautier-Hion *et al.* 1983). *Cercopithecus pogonias* strongly favour upper strata (20–25 m with >50% of observations over 20 m); descending occasionally to <10 m (10% of observations). Never observed on the ground (Gautier-Hion & Gautier 1974).

Social and Reproductive Behaviour Social. Mean group size varies from 8 to 20 with a mean of 12.6 individuals at Lopé Reserve (White 1994), 14 at Makandé, Gabon (Brugière 1998) and 16 at Ngotto Forest and Odzala N. P. (Gautier-Hion 1996). Groups only contain one adult ♂ capable of giving the 'boom' calls. This call serves to rallying group members and in spacing groups (Gautier & Gautier-Hion 1977, T. Butynski pers. comm.). This suggests that *C. pogonias* live in one-male groups. Additional adult ♂♂ may, however, be present in some groups as indicated by their loud 'barks' that accompany the boom sequences of the group adult ♂ (A. Gautier-Hion pers. obs.).

On Bioko I. the group adult ♂ typically gives 'booms' in series of twos (43% of the time) or threes (51%), but sometimes once

(4%) or four times (2%) ($n = 51$ series). The interval between booms given in a series is usually 5–7 sec (range 4–9). When a series of three booms is given, the time interval between the first and second booms is ca. 1–2 sec shorter than between the second and third booms. Adult ♀♀, subadults, and probably juveniles, give soft ‘honk’ and (louder) ‘myaow’ contact calls. Myaows can be heard to >200 m. Adult ♀♀, by giving a chorus of ‘strained honks’, are able to elicit booms from the group’s adult ♂♂. This is reminiscent of when adult ♀♀ Gentle Monkeys *Cercopithecus mitis* give a chorus of ‘strained grunts’ that elicits a single boom from the adult ♂♂. On Bioko, adult ♂♂ frequently give loud, sharp two or three syllable hacks (‘padunk’ and ‘padunkaka’). These calls vary greatly in volume and often grade into ‘hack-trains’ (similar to the ‘ka-trains’ of adult ♂♂ *C. mitis*). Hacks can be heard to >200 m and are given in the context of alarm/warning. Adult ♂♂ Red-eared Monkey *Cercopithecus erythrotis* sometimes give ‘hacks’ (which are shorter than those of *C. pogonias*) in response to the hack call of *C. pogonias*. Calls similar to the ‘trill’, ‘grunt’ and ‘chirp’ of the sympatric *C. erythrotis* and other species in the *C. (cephus)* Group are not given by *C. pogonias* (T. Butynski pers. comm.).

No all-male groups observed. Solitary adult ♂♂ are less frequent than in other arboreal guenons, partly because they associate easily with groups of other species. Group cohesion is maintained by the modulated ‘myaow’ exchanged among adult ♀♀ and immature animals. Territorial conflicts occur. When two groups come in contact, adult ♂♂ exchange aggressive ‘hacks’ until they space out again after which one ♂ in each group gives boom calls. No overlap between home-ranges described. Infants carried only by the mother (Gautier-Hion & Gautier 1976).

Cercopithecus pogonias is rarely in monospecific groups: 0–15% of encounters in Central African Republic (Fay 1988, Gautier-Hion 1996), less than 5% both at Lopé Reserve (Ham 1994) and Forêt des Abeilles (A. Gautier-Hion pers. obs.) and 20% in NE Gabon. Occurs most often in bi-specific groups with *C. nictitans* or Grey-cheeked Mangabey *Lophocebus albigena*, and in tri-specific groups with *C. nictitans* and/or *C. cephus*, and/or *L. albigena*. Bi-specific groups with *C. cephus* are rare, the latter species being found with *C. pogonias* in the presence of at least a third species. Both at Lopé Reserve and Forêt des Abeilles, the association between *C. pogonias* and *L. albigena* accounted for at least 55% of all observed associations. Some groups may include up to six species (Gautier & Gautier-Hion 1969). Contrary to bi- or tri-specific groups, which may be stable over years (Gautier-Hion *et al.* 1983), associations including more than four species are temporary. Lone *C. pogonias* adult ♂♂ may associate with *L. albigena* groups (Ham 1994) or with Black Colobus *Colobus satanas* groups (Fleury & Gautier-Hion 1997). A lone *C. pogonias* was regularly observed within a group of *C. satanas* for three years. *Cercopithecus pogonias* is particularly adept at catching the more mobile of insects that have been flushed by other species, one benefit that they apparently obtain by associating with other primates. This species, which is often high in the canopy, is more alert to aerial predators than other monkeys, and the first to give alarm calls (Gautier & Gautier-Hion 1983). Male *C. pogonias* are the first to give loud-calls, thereby providing a vocal control in the formation and disbanding of mixed groups. This also serves to coordinate movements and spacing among groups, suggesting a supraspecific organization in which *C. pogonias* plays a leading role.

When the association includes *L. albigena*, this species may lead the mixed group (Ham 1994). On Bioko I., *C. pogonias* forms associations with *C. nictitans*, *C. erythrotis* and Pennant’s Red Colobus *Procolobus pennantii* (Butynski & Koster 1994, T. Butynski pers. comm.).

Cercopithecus pogonias has a graded vocal repertoire that is comprised of at least nine calls (see above in this section). Low-pitched cohesion calls and high-pitched contact calls are both non-quavered. These two call types may be associated or even merged. High-pitched warning calls are given by ♀♀ and immatures (Gautier 1988).

Reproduction and Population Structure Like the majority of guenons, *C. pogonias* has a mating season centred on the main dry season (Jul–Aug) and a birth season centred on the short dry season (Dec–Feb; Butynski 1988). Gestation ca. 5.5 months. The single newborn weighs ca. 300 g. In captive animals the onset of ♂ puberty occurs at about six years following a large increase in body weight. However, social maturity and especially a male’s ability to give boom calls depend not only on age but both may be inhibited by the presence of a calling leader ♂ within the captive group. In ♀♀ sexual maturity is reached around four years (Gautier-Hion & Gautier 1976). Ratio of ♂♂ to ♀♀ is 1 : 2.8, and adults to immatures 1 : 1.5 ($n = 11$; Maisels 1995).

Predators, Parasites and Diseases Crowned Monkeys are highly vigilant towards the African Crowned Eagle *Stephanoaetus coronatus* (observed to kill a juvenile ♀ in Ngotto Forest; A. Gautier-Hion pers. obs.). Upon sensing a predator, adult ♂♂ often stay in the tree canopy and bark. Warning calls by ♀♀ follow. Then ♀♀ and immatures may plunge into the understorey. Other likely predators are Leopards *Panthera pardus* (Henschel *et al.* 2005) and large snakes. Humans are the primary predator throughout the range.

Conservation IUCN Category (2012): Least Concern as a species, but *C. p. pogonias* is Vulnerable. CITES (2012): Appendix II. Like other arboreal monkeys, *C. pogonias* is vulnerable to hunting by humans for the commercial bushmeat trade over much of its range. Despite their vigilance, *C. pogonias* constituted ca. 15% of 397 arboreal guenons and mangabeys killed for bushmeat in Cameroon (P. Auzel pers. comm.). On Bioko I. (2017 km²), during 2005, about 320 *C. p. pogonias* carcasses were brought to the main bushmeat market in Malabo. Hunting with shotguns is the only threat to *C. p. pogonias* on Bioko, but this activity may extirpate this species from the island. The total number of *C. p. pogonias* killed on Bioko I. during 2005 for the bushmeat trade was ca. 720. The price paid per carcass in 2005 was ca. US\$27. It is unlikely that there were >5000 *C. p. pogonias* on Bioko I. in 2005 (Hearn *et al.* 2006). Forest clearance also threatens this species, which prefers tall primary forest. Protection of the population in the Gran Caldera & Southern Highlands Scientific Reserve (510 km²) on south Bioko is critical to the long-term conservation of this monkey on Bioko (Hearn *et al.* 2006).

Measurements

Cercopithecus pogonias

Cercopithecus pogonias (subsp. ?)

HB (♂♂): 540 (520–550) mm, $n = 5$

HB (♀♀): 440 (440–480) mm, $n = 5$

T (♂♂): 820 (750–870) mm, $n = 5$

T (♀ ♀): 724 (710–740) mm, n = 5

Localities not given (Napier 1981)

Cercopithecus p. nigripes

WT (♂ ♂): 4.4 (3.3–4.5) kg, n = 6

WT (♀ ♀): 2.9 (2.4–3.2) kg, n = 10

Makokou area, NE Gabon (Gautier-Hion *et al.* 1999)

Cercopithecus p. pogonias

HB (♂ ♂): 407 (370–480) mm, n = 46

HB (♀ ♀): 372 (340–410) mm, n = 40

T (♂ ♂): 624 (560–730) mm, n = 47

T (♀ ♀): 557 (480–610) mm, n = 42

HF (♂ ♂): 124 (118–140) mm, n = 47

HF (♀ ♀): 114 (110–120) mm, n = 41

E (♂ ♂): 27 (22–30) mm, n = 47

E (♀ ♀): 26 (22–30) mm, n = 41

WT (♂ ♂): 3.7 (3.0–5.1) kg, n = 45

WT (♀ ♀): 2.8 (2.2–3.8) kg, n = 39

Upper canine (♂ ♂): 14 (10–20) mm, n = 48

Upper canine (♀ ♀): 10 (7–14) mm, n = 32

Lower canine (♂ ♂): 10 (6–13) mm, n = 48

Lower canine (♀ ♀): 7 (4–12) mm, n = 33

Bioko I., Equatorial Guinea (Butynski *et al.* 2009)

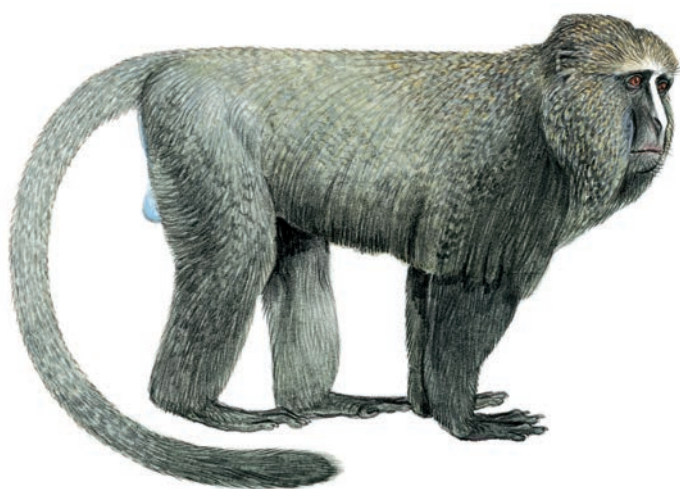
Key References Gautier & Gautier-Hion 1983; Gautier-Hion 1980; Gautier-Hion *et al.* 1983; Tutin *et al.* 1997b.

Annie Gautier-Hion

***Cercopithecus hamlyni* OWL-FACED MONKEY (HAMLYN'S MONKEY)**

Fr. Cercopithèque à tête de hibou; Ger. Eulenkopfmeerkatze

Cercopithecus hamlyni Pocock, 1907. Ann. Mag. Nat. Hist. ser. 7, 20: 521. Ituri Forest, DR Congo.



Owl-faced Monkey *Cercopithecus hamlyni* adult male.

Taxonomy Polytypic species. Two subspecies recognized by Colyn & Rahm (1987), Kingdon (1997), Gautier-Hion *et al.* (1999), Groves (2001, 2005c) and Grubb *et al.* (2003): the nominate lowland form *C. h. hamlyni* and a montane subspecies *C. h. kahuziensis* (Colyn & Rahm 1987). *Cercopithecus h. kahuziensis* described from one juvenile and two subadult specimens collected in 1959, and reputedly restricted to a small area of bamboo forest in the Kahuzi-Biega N. P., DR Congo. Field studies over the past two decades in Kahuzi-Biega N. P., however, cast doubt on the validity of *C. h. kahuziensis*. All *C. hamlyni* observed on primate surveys in the Kahuzi-Biega N. P., in areas within the reported range of *C. h. kahuziensis* (Colyn & Rahm 1987), had prominent white nose-stripes, the primary diagnostic character for *C. h. hamlyni*; no individuals without white nose-stripes were observed (J. Hall, J. Hart, P. Kaleme & B. Finch pers. obs.). Similarly, during eight encounters with three groups at 2100–2400 m in Kahuzi-Biega N. P., Maruhashi *et al.* (1989) found that all adults had white nose-stripes,

while in some of the younger individuals the white nose-stripe was not clear. On the other hand, the white nose-stripe is variably present and often reduced in lowland populations of *C. hamlyni* in the Ituri Forest and South Kivu (Itebero and Shabunda regions, DR Congo; J. Hart, J. Mwanga & P. Kaleme pers. obs.). Described on the basis of three immature animals, and on characters that are variably present in immature *C. h. hamlyni*, it is not clear that *C. h. kahuziensis* is a valid subspecies. While we are doubtful of the validity of *C. h. kahuziensis*, we provisionally accept this subspecies – pending further study.

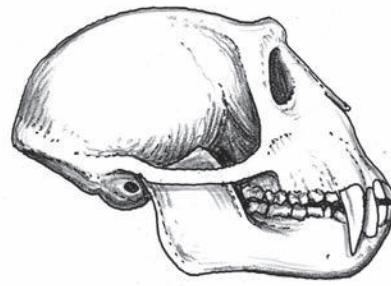
Rahm (1970) speculated that highland forms have longer tails than lowland forms, and may be separated on this basis, but makes no mention of the nose-stripe or other features. In addition to the lack of a white nasal stripe, *C. h. kahuziensis* may have a darker face and a reduced diadem (photo in Rahm & Christiaensen 1963: 24). Concerning relative tail length and variation in the colour of the dorsum, Colyn (1988: 115) says:

Rahm (1970) emphasizes the difference in relative length of head-body and tail existing between the mountain forest (Kivu Ridge) and the lowland forest populations. This character, however, has no taxonomic importance, as similar differences were found in a single population around Kisangani, DR Congo; the same applies to the differences in mantle colour, which range from greenish to dull yellow-buff, some times tinged with orange.

Cercopithecus hamlyni is most closely related to the recently discovered Lesula *C. lomamiensis* (Hart *et al.* 2012; see this volume p. 17). Otherwise, not closely related to any other species, as borne out by the unique structure of the skull (Raven & Hill 1942, Hill 1966). Blood protein analyses (Ruvolo 1988) place *C. hamlyni* close to L'Hoest's Monkey *Allochrocebus lhoesti*, as do similarities in palatine bone shape, coat colour and texture, external nose hair distribution, molar cusp relief, and genital colour and morphology (Schwarz 1928b, Groves 2000a, E. E. Sarmiento pers. obs.), but their karyotypes differ (2n = 64 for *C. hamlyni* and 2n = 60 for *A. lhoesti*; Romagno

2001) and molecular data do not support a close relationship (Hart *et al.* 2012). Similarities between De Brazza's Monkey *Cercopithecus neglectus* and *C. hamlyni* in most of their (relatively few) vocalizations (Gautier 1988), ritualized scent-marking behaviours (Loireau & Gautier-Hion 1988), and natal coat colour and age-related changes in coat colour (Hill 1966), suggest that *C. neglectus* is relatively close to *C. hamlyni*. These similarities, however, are probably all characteristic of the primitive Cercopithecini condition and do not reflect a uniquely shared relationship between the two. They more likely reflect conservative evolution in these two lineages since their divergence from the ancestral Cercopithecini stock. Synonyms: *aurora*, *kahuziensis*. Chromosome number: $2n = 64$ (Romagno 2001, Moulin *et al.* 2008).

Description Medium-sized, semi-terrestrial, stocky, large-headed, grizzled olive-grey monkey, with conspicuous white nose-stripe in nominate race. Sexes alike in colour but adult ♀ ca. 64% as heavy as adult ♂. Muzzle relatively heavy and prolonged with contrasting white stripe running along midline from crown, down nose to upper lip. De-pigmented pink skin underlying white hair stripe continues onto glabrous portions of upper and lower lip midline giving the appearance that the stripe crosses mouth. White-stripe absent in *C. h. kahuziensis* and variably absent in juveniles and adult *C. h. hamlyni*. Face skin dark brown in *C. h. hamlyni*, covered with tiny dark brown hairs interspersed with white hairs on upper and lower lip. Face entirely black in *C. h. kahuziensis*, except for interspersed white hairs in orbits around eyes and on chin. Neck, throat, chin and cheeks of *C. h. hamlyni* with black tipped, tan hairs banded pale yellow. This results in an olive hue that progressively lightens from crown to throat. Wider white or pale yellow bands on the hairs of the crown result in a pale yellow or white diadem that, together with the nose-stripe, forms a characteristic 'T' that demarcates the face. Brow of *C. h. kahuziensis* indistinct (no diadem), not demarcated from cheeks or crown. Wide white or pale yellow bands on hair surrounding face result in a lighter olive hue than is typical of *C. h. hamlyni*. Iris brown or brick red. Crown hairs long, soft and continuous with bushy cheek whiskers extending to ears to form a smooth, compact, 'hood' over crown, cheeks and throat, completely hiding the ears. Hood gives animals a distinctive, large-headed, 'owl-like' appearance. Ears largely bare with no tuft. Nape and upper back greyer than crown; hairs silver at base usually with three alternating pale yellow and black bands ending in a white tip ($n = 19$; E. E. Sarmiento pers. obs.). Lower back, flanks and rump hairs may have as many as four to five alternating bands (Hill 1966, Groves 2001, E. E. Sarmiento pers. obs.). Dorsum and flanks yellowish-grey or olive-grey, becoming paler towards base of tail. Variably darker yellow or orange banding on hairs of dorsum may produce a yellow or orange tinged mantle. Dorsum of *C. h. kahuziensis* with a more olive-green hue than typical of *C. h. hamlyni*. Outer thigh has white tipped grey/brown hairs with a single wide black band and narrow yellow band, producing a darker grey hue than on dorsum. Upper limbs, hands, inner thighs, legs and feet black or dark brown. Proximal two-thirds of tail with silver-green hue produced by white-tipped black or dark grey hairs with no banding. Distal third of tail black with slight tuft at tip. Tail slightly longer than HB. Ventrums, black or dark brown. Pelage of ventrum not as thick as on dorsum. Callosities blackish-brown. Scrotum, perineum and lower abdomen of ♂ a striking aquamarine or malachite green.



Lateral view of skull of Owl-faced Monkey *Cercopithecus hamlyni* adult male.

Newborn lacks facial pattern and is uniformly light yellowish-brown with a paler (fawn) face (photo in Hill 1966: 513). Young juvenile (four months of age) differs both from infant and adult by having brighter colours and more golden-yellow on the face, throat, sides of neck and upper chest; medium yellow over the lower back, limbs, hands and feet. Tail mostly greenish-yellow proximally and greyish-black distally (Hill 1966). Juveniles that are half adult size, and that are still carried by mothers, have adult markings and pelage colour (see photos in Schouteden 1944a: 50–51). M1 erupts when juvenile about half adult size.

Geographic Variation

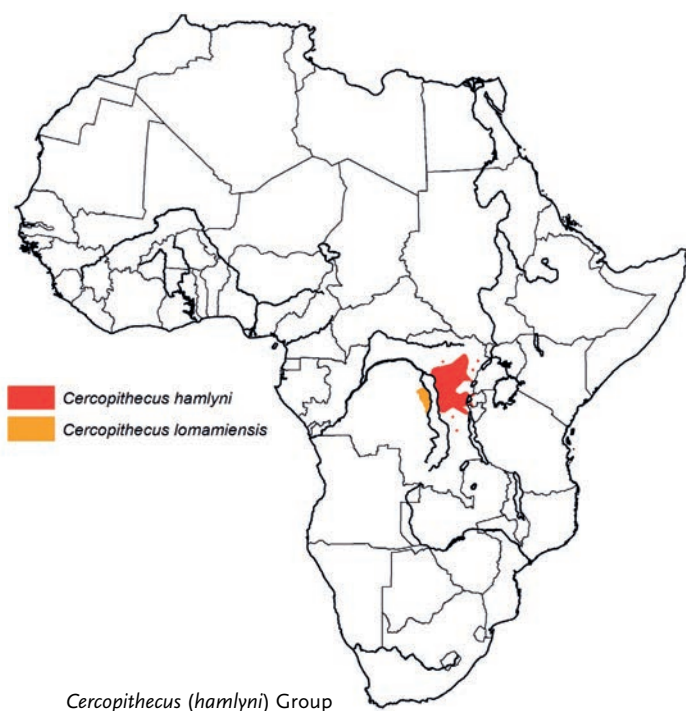
C. h. hamlyni Nose-stripe Owl-faced Monkey. Found over entire range of *C. hamlyni*, including the Bamboo *Sinarundinaria alpina* zone (2000–3000 m) of Mt Kahuzi (Maruhashi *et al.* 1989). Nose with white stripe from between eyes to mouth. Diadem white.

C. h. kahuziensis Mt Kahuzi Owl-faced Monkey. Only known from the bamboo zone and the marshy zone below the bamboo zone (2000–3000 m) on Mt Kahuzi, DR Congo. Type from the vicinity of Musisi Swamp (02° 18' S, 28° 42' E) between Mt Kahuzi and Mt Biega (Colyn & Rahm 1987). The montane portion of Kahuzi-Biega N. P. is at 02° 04'–02° 37' S, 28° 36'–28° 46' E; 2000–3308 m). No white vertical stripe on face.

Similar Species None that is parapatric or sympatric. Similar *C. lomamiensis* is separated from *C. hamlyni* by two major rivers, the Lualaba R. and the Lomami R. (Hart *et al.* 2012). See map on p. 341 and illustration on p. 344.

Distribution Endemic to CE DR Congo and W Rwanda. Rainforest BZ. Geographic range not well known, but range east of Congo R. similar to that of *A. lhoesti*. Present in the Lindi River Basin in the north-west, Nepoko R. in the Okapi Faunal Reserve in the north (J. Hart pers. obs.), southward through Ituri Forest and along right bank of Lualaba R. to at least 50 km south of confluence with the Elila R. (A. Vosper & J. Hart pers. obs.). Eastward to the Albertine (Western) Rift Valley to within ca. 70 km south of L. Albert in the north and to the north end of L. Tanganyika in the south. Several isolated, outlying populations in extreme E DR Congo and in W Rwanda. Extent of occurrence roughly 193,000 km², but area of occupancy much less than this (Y. de Jong & T. Butynski pers. obs.).

The following are the known range limits for *C. hamlyni* (Schouteden 1944a, Rahm 1965, 1970, Colyn 1988, Dowsett & Dowsett-Lemaire 1990, J. Hart pers. obs.). All sites are in DR Congo unless otherwise indicated. *Western limit*: ca. 25° 10' E to north of Congo R. near



Kisangani, and to ca. 24° 14' E to south along Lualaba R. *Northern limit*: ca. 02° 24' N, just south of Nepoko R. *North-eastern and eastern limit*: ca. 01° 57' N, 30° 01' E at Mongbwalu (Kilo Mines). Limit of contiguous moist forest and great lakes of Albertine Rift Valley are the apparent barriers to the north-east and east. Recently recorded for Semliki Forest in the Virunga N. P. (Nixon & Lusenge 2008). *Southern limit*: ca. 05° 20' S at Butondo (ca. 80 km north of Nyunzu). Limit of moist forest and/or the Lukuga R. the apparent barriers. Butondo (05° 20' S, 27° 52' E) and Nyombe (03° 53' S, 27° 25' E) are both isolated forests far south of the main distribution for *C. hamlyni*. At least one specimen collected at each of these two sites. *South-western limit*: ca. 03° 05' S, 25° 58' E, about 16 km south of Kindu. *South-eastern limit*: ca. 02° 47' S, 29° 27' E in Nyungwe N. P., SW Rwanda.

Important, but isolated, populations present in upland sector of Kahuzi-Biega N. P. (Hall *et al.* 2003), Mt Tshiaberimu in the Virunga N. P. (Sarmiento & Butynski 1997), and Nyungwe N. P. (ca. 02° 36'–02° 48' S, 29° 12'–29° 29' E; Dowsett & Dowsett-Lemaire 1990, Ntare *et al.* 2006, Easton *et al.* 2011, N. Barakabuye, A. Vedder & A. Plumptre pers. comm.). The south-eastern limit is in Nyungwe N. P. at 02° 47' S, 29° 29' E. Although there are no reports of *C. hamlyni* in Burundi, this species may well occur there in the bamboo zone of the Kibira N. P., which is contiguous with the bamboo zone at Nchili in Nyungwe N. P. where *C. hamlyni* is present (A. Vedder, N. Barakabuye & B. Kaplin pers. comm.).

Rahm (1970) says *C. hamlyni* present in 'bamboo forest near Kabale (Uganda)'. His locality map indicates that what he is referring to is the Echuya F. R., a now isolated bamboo forest centred on 01° 17' S, 29° 49' E. This is apparently the only reference for *C. hamlyni* in Uganda. Rahm (1970) does not indicate the basis for this locality record. There is no museum specimen from any site in Uganda (E. Sarmiento & T. Butynski pers. obs.). While Echuya F. R. (34 km², 2270–2570 m) appears to be suitable habitat for *C. hamlyni* (as was once much of extreme SW Uganda), *C. hamlyni* is almost certainly not present there today (T. Butynski

& E. E. Sarmiento pers. obs.). If this is a valid record, *C. hamlyni* has been extirpated from Uganda.

Locations where museum specimens were collected, but where the species is now apparently extirpated, include the Virunga Mts and several sites in NW Rwanda (e.g. Gishwati Forest and Gisenyi Bamboo Forest; A. Plumptre pers. comm.). All sites were greatly reduced in size during the twentieth century. The most recent record for *C. hamlyni* in this region is for Gishwati Forest in 1989 (J. Ray pers. comm.).

Habitat In lowland, montane and bamboo forest (J. Hart, J. Hall & P. Kaleme pers. obs.). The lowest altitude record is 450 m (east of Kisangani). The nominate race occurs in various types of evergreen forest, from ca. 450 m (Yamagiwa *et al.* 1989, Hall *et al.* 2003) in lowland forest and older secondary forest through submontane, montane and bamboo forest to ca. 3000 m. The highest sites are Nyungwe Forest N. P., Kahuzi-Biega N. P. and Mt Tshiaberimu (Rahm & Christeaensen, 1963, Rahm 1965, 1966, Dowsett & Dowsett-Lemaire 1990, Sarmiento & Butynski 1997). In Nyungwe N. P. (970 km²) *C. hamlyni* restricted to 2260–2570 m within bamboo forest (Dowsett & Dowsett-Lemaire 1990, A. Vedder pers. comm., N. Ntare pers. comm.), even though there is a large area of montane forest here. There is an extraordinary record of a mummified head found in 1927 at ca. 4500 m on Mt Karisimbi, Virunga Mts, Rwanda–DR Congo border (Raven & Hill 1942). This is the only record for the Virunga Mts. Whether this animal was a 'wanderer' that reached this altitude on its own accord, or whether the head was carried there by another species (e.g. White-necked Raven *Corvus albicollis*) is a matter for speculation. In Ituri Forest (ca. 740–1100 m) and in relatively low altitude forests in Kivu District (down to 600 m), *C. hamlyni* is present in the extensive monodominant stands of *Gilbertiodendron dewevrei*, as well as in mixed canopy moist forests (Hart & Bengana 1996, Hall *et al.* 2003). *Cercopithecus hamlyni* appears to be restricted to terra firma forests. Except for the museum specimen that represents the southernmost location (at Butondo), there is no evidence that *C. hamlyni* ranges into the forest savanna mosaic. *Cercopithecus h. kahuziensis* reported only from the bamboo zone and marshy zone below the bamboo zone (2000–3000 m) on Mt Kahuzi. Mean annual rainfall over the geographic range of *C. hamlyni* ca. 1200–2500 mm (perhaps 3000 mm at 3000 m asl at Kahuzi-Biega N. P.; Inogwabini *et al.* 2000). Night-time temperature sometimes <0°C at the highest altitudes where *C. hamlyni* occurs.

Abundance A shy, cryptic, quiet species and, therefore, difficult to detect or observe. Absent or rare over large areas of its geographic range, while locally abundant in other areas, in particular, Kahuzi-Biega N. P., Irangi, Masisi and Kasese, DR Congo (Yamagiwa *et al.* 1989, Hall *et al.* 2003), and in central Ituri Forest (Hart & Bengana 1996). J. P. Chapin & H. Lang, who collected >400 primate specimens from Kisangani through the Ituri Forest from 1909–1915, never encountered a live *C. hamlyni*, although they did purchase dead specimens (Allen 1925). Density in central Ituri Forest estimated at 0.1 ind/km² (Thomas 1991). Based on frequency of dawn call, *C. hamlyni* is widespread and common in the Okapi Faunal Reserve, where the dawn call was heard at least once during 40% of 115, 30-minute 'dawn call point counts'. *Cercopithecus hamlyni* especially prevalent in monodominant *Gilbertiodendron* forests in the Epulu area, central Ituri Forest (J. Hart pers. obs.).

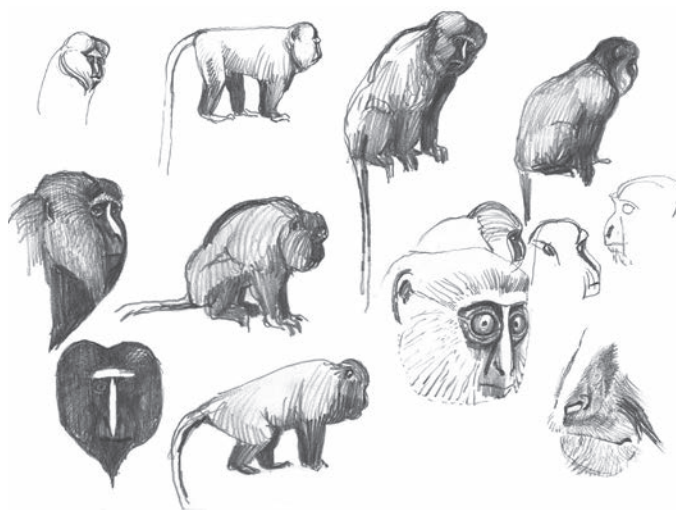
Widely distributed and common in Kahuzi-Biega N. P. and the adjoining Kasese region between the Lowa R. and Oku R. Hall *et al.* (2003) provide the following estimates for *C. hamlyni* in the KB1 Lowland Sector (700–800 m) of Kahuzi-Biega N. P.: 2.5 groups/km², 6.7 ind/km², 18.4 kg/km² and the following estimates for the KB2 Lowland Sector: 2.0 groups/km², 5.3 ind/km² and 14.7 kg/km². In the Mountain Sector (2000–3308 m) of Kahuzi-Biega N. P., *C. hamlyni* is also widespread and common, with the ‘boom’ call being heard by primate survey teams on about half of the days, a rate similar to that heard in the lowland sectors (Inogwabini *et al.* 2000). Encountered rate 0.08 groups/km in Nyungwe N. P. (Easton *et al.* 2011).

Adaptations Semi-terrestrial and diurnal. The impression is that *C. hamlyni* spends more time on the ground than any other forest guenon (J. Hart pers. obs.). Although *C. hamlyni* uses all forest strata, a preliminary study in Nyungwe N. P. found that, during the daytime, *C. hamlyni* spends ca. 61% of time on the ground; ca. 81% of play, 68% of feeding, 64% of travel, 43% of grooming and 47% of resting occurs on ground. About 18% of time spent both at 0–2 m and 2–12 m above ground, with only 3% of time >12 m above ground (N. Ntare pers. comm.). When threatened, *C. hamlyni* often flees quietly on the ground rather than climbs. Initial reports (e.g. Allen 1925) that *C. hamlyni* is nocturnal are not supported by field observations (Rahm 1970, J. Hart & J. Hall pers. obs.). The brilliant aquamarine scrotum and perineum of the adult ♂♂ is typical of other semi-terrestrial guenons (i.e. *C. neglectus*, the Mountain Monkeys Group *Allochrocebus (preussi)*, the Savanna Monkeys Group *Chlorocebus (aethiops)* and Patas Monkey *Erythrocebus patas*).

Cercopithecus hamlyni has a distinctive odour, readily detected when the animals are nearby. Male and ♀ captives mark their surroundings by rubbing with their chests (Kingdon 1997, D. Messenger pers. comm.), on which there are scent-producing sternal (apocrine) glands. The only other guenons for which ritualized olfactory marking has been observed are *C. neglectus*, Green Monkey *Chlorocebus sabaenus*, Vervet *Chlorocebus pygerythrus*, Allen’s Swamp Monkey *Allenopithecus nigroviridis*, and a free-living *C. pygerythrus* × Sykes’s Monkey *Cercopithecus mitis* hybrid (De Jong & Butynski 2010b). All four of these species (and the hybrid) are semi-terrestrial. The ritualized olfactory marking in *C. neglectus* is believed to be related to that species’ low development of visual and vocal signalling, small group size, cryptic behaviour and small home-range size (Gartlan & Brain 1968, Gautier & Gautier-Hion 1977, Gautier-Hion & Gautier 1978, Loireau & Gautier-Hion 1988). Like *C. neglectus*, *C. hamlyni* is a highly cryptic species with a relatively limited vocal repertoire (Gautier 1988) and small group size. This suggests that *C. hamlyni* will also be found to have a small visual signal repertoire and small home-ranges relative to other *Cercopithecus* spp. as well as to *Allochrocebus* spp.

With more colobine-like molars than any other guenon (Hill 1966), *C. hamlyni* is probably less dependent on fruits than other guenons. As such, *C. hamlyni* is expected to do well in monodominant forests (e.g. bamboo forest and *Gilbertiodendron* forests) where the year-round availability of fruit is relatively low and where, concomitantly, competing species (e.g. Stuhlmann’s Blue Monkey *Cercopithecus mitis stuhlmanni* and *A. lhoesti*) are absent or at low densities.

Kingdon (1997: 78) notes that: ‘The hands of owl-faced monkeys are unique among guenons in the elongation of the phalanges. This is the opposite of a terrestrial trait and, combined with a relatively



Visual suppression of facial expression in the Owl-faced Monkey *Cercopithecus hamlyni*.

strong thumb, suggest a powerful grip (as would be needed for climbing slippery bamboo stalks).’

Foraging and Food Poorly known. Probably omnivorous. Forages mainly on the ground, often in dense bamboo and herbaceous vegetation (Dowsett & Dowsett-Lemaire 1990, J. Hart & J. Hall pers. obs.). Bamboo *Sinarundinaria alpina* shoots (leaves) and fruits of *Syzygium guineense* in stomach of an individual from Mt Kahuzi (Rahm & Christiaensen 1963). Local people at Mt Tshiaberimu state that *C. hamlyni* feeds largely on fungi and bamboo, and cleanly breaks off young bamboo shoots from the stem base to feed on them. In contrast *C. m. stuhlmanni* tease apart shoots with hands separating individual leaves from the shoots (E. E. Sarmiento pers. obs.). Removal of individual blades from bamboo shoots also observed for Doggett’s Blue Monkey *Cercopithecus mitis doggetti* in Nyungwe N. P. (N. Ntare pers. comm.). Main foods during one brief study in Kahuzi-Biega N. P. were the fruits of *Macaranga kilimandscharica* and *Maesa lanceolata* (Maruhashi *et al.* 1989). Eats fruits of Maranthaceae (Rahm 1966). Raids crops (e.g. Maize), but this is not common (Mwanza *et al.* 1989).

In Nyungwe N. P., at least 17 species of plants eaten (Ntare *et al.* 2006). Items eaten include, piths, stems, leaves, shoots, sheaths, flowers, roots, insects, mushrooms and lichens. During the dry season, *Triumfetta cordifolia* and *Anisoparum humberti* consumed. In October, diet dominated by young bamboo shoots; a highly seasonal food only available during the wet season. Diet comprised 36% stems, 36% pith, 10% leaves, and 7% bamboo shoots – which is yet another source of leaves (Ntare *et al.* 2006). This is a unique diet for an African monkey, with fruit comprising a minor part of the diet. Fruits of *M. kilimandscharica*, *S. guineense* and *Rubus pinatus* eaten (N. Ntare pers. comm.). Fruits are relatively uncommon in bamboo forest. *Cercopithecus hamlyni* living in mid-altitude and montane forest probably eat much more fruit than those living in bamboo forest. In the lowland and mid-altitude monodominant primary forests, however, periods of low fruit availability are prevalent and fruit availability at these times may not be that different from the situation in bamboo forests.

In the Epulu area *C. hamlyni* feeds on the ground on fallen seeds of *Erythroleum suaveolens* and on the sprouting seeds of *G. dewevrei*.

Stomach contents of two animals in the Ituri Forest during a period of low fruit availability only contained fungi. Mbuti pygmies here report that *C. hamlyni* joins Blue Duikers *Phlantomba monticola* and other duikers *Cephalophus* spp. in foraging on the ground under feeding groups of arboreal primates. Observed accompanying Olive Baboons *Papio anubis* and Robust Chimpanzees *Pan troglodytes* in south Ituri Forest (J. Hart pers. obs.). An adult *C. hamlyni* ♂ seen chasing a *C. m. doggetti* ♀ out of a fruiting *Maesa* tree (Maruhashi *et al.* 1989).

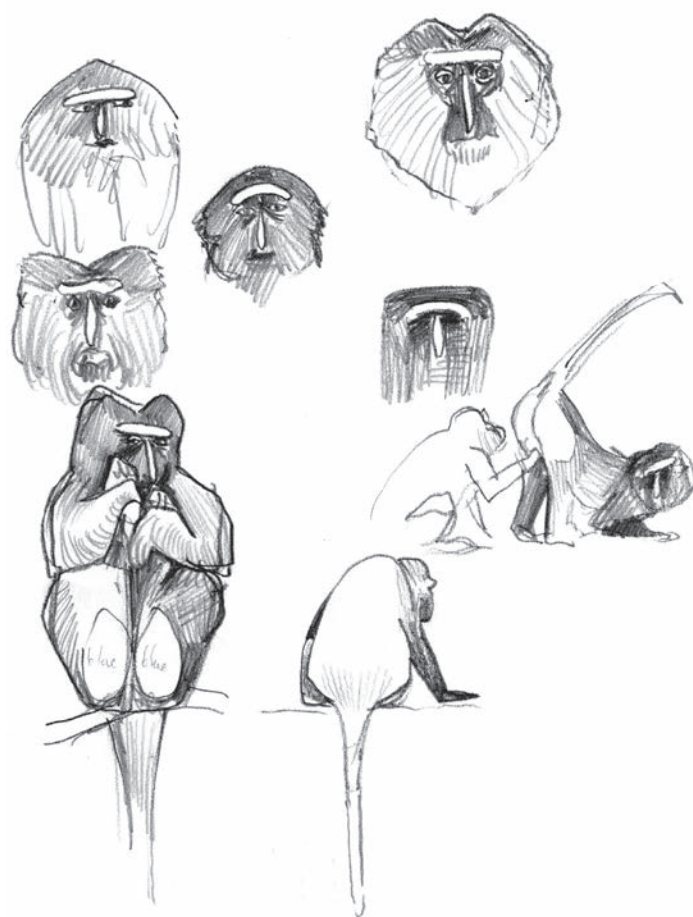
Social and Reproductive Behaviour Social. Groups described as small (Dowsett & Dowsett-Lemaire 1990), not exceeding ten individuals (Rahm 1970, Gautier-Hion *et al.* 1999). Usually encountered in groups of 2–4 individuals, but larger groups also occur (J. Hart & J. Hall pers. obs.). Fourteen observations on the Terrain Scientifique de Lenda (an area of no hunting, 10 km south-east of Epulu), where group size was determined with certainty, included three single animals (twice adult ♂♂, once sex not determined), five groups of two animals (♂ and ♀, or sex unknown), two groups of three, two groups of four, one group of six (including two adult ♂♂ and two ♀♀ with young), and one exceptional group of 30–35, including multiple adult ♂♂, which was accompanied by one White-bellied Duiker *Cephalophus leucogaster* (J. Hart pers. obs.).

Mean minimum group size for three groups encountered during censuses in the lowland sector of Kahuzi-Biega N. P. was 2.7 individuals (Hall *et al.* 2003). During eight encounters with three groups at 2100–2400 m in Kahuzi Biega N. P., Maruhashi *et al.* (1989) judged all three groups to be comprised of at least five individuals, including one adult ♂. *Cercopithecus hamlyni* was in association with *C. m. doggetti* during three of seven group encounters. Solitary adult *C. hamlyni* ♂♂ present here.

One study group in Nyungwe N.P. comprised 24 individuals, including two adult ♂♂. The two adult ♂♂ fought when they met, suggesting that the study occurred during a period when a satellite ♂ was attempting to usurp the harem ♂. *C. hamlyni* and *C. m. doggetti* form polyspecific associations in Nyungwe N. P. (N. Ntare pers. comm.). Ranger-Based Monitoring Patrols in Nyungwe N. P. recorded an average of 5.3 individuals/encounter ($n = 78$ groups), but this method is likely to underestimate group size (Easton *et al.* 2011).

Vocalizations include the ‘boom’ loud-call and ‘uh-uh-uh’ or ‘tyo-tyo-tyo’ alarm call of the adult ♂. The boom may be given once, or more than once, with a brief pause in between. Other calls include the ‘pitiak’ alarm call, and the ‘moan’ or ‘oooh-oooh’ contact call (Gautier 1988, Gautier-Hion *et al.* 1999, N. Ntare pers. comm.). A distinctive ‘barking’ call (‘krot, krot, kro-krot ...’) described from Nyungwe Forest N. P. (Dowsett & Dowsett-Lemaire 1990). The loud, high-pitched warning ‘chirps’ of most guenons is given by infant *C. hamlyni* but is not part of the vocal repertoire of older animals (Kingdon 1997).

In the Ituri Forest and Kahuzi–Biega lowlands, the distinctive descending boom call is usually uttered for a brief period before dawn. Hall *et al.* (2003) and Hart & Bengana (1996) used the boom call to determine the presence and relative abundance of *C. hamlyni* on wide-ranging surveys. However, if the boom call is not known, the presence of this species can easily be overlooked.



Diverse modelling of hair on the crowns of Owl-faced Monkeys *Cercopithecus hamlyni*.

Cercopithecus hamlyni is often described as being a discrete and quiet monkey that is relatively difficult to detect and observe. When encountered by humans it usually remains quiet, retreating on the ground without giving warning calls (N. Ntare pers. comm., J. Hart & J. Hall pers. obs.).

Reproduction and Population Structure Females carrying infants recorded in Ituri Forest in Feb, May and Aug. Birth season in western portion of range (i.e. Kisangani and Kindu) is Jul–Nov based on the size of embryos in 13 collected specimens. As such, births occur during the single annual dry season (Jun–Aug) and well into the subsequent wettest period of the year (Gevaerts 1992). Records from Singapore Zoo show a gestation of 5–6 months. Twins not reported. No birth weights available, but one 3-day-old ♂ infant at Edinburgh Zoo weighed 320 g (G. Catlow pers. comm.). The European Endangered Species Breeding Program (EEP) Studbook indicates the following for *C. hamlyni* in captivity: gestation = 180 days; youngest ♀ at first birth = 2.25 years; oldest ♀ to give birth = 24 years. Captive ♂ lived to >23 years and captive ♀ lived to >28 years.

Predators, Parasites and Diseases Four *C. hamlyni* captured in net drives on the Terrain Scientifique de Lenda were equipped with radio collars. Within 45 days all had been killed: one by an African Crowned Eagle *Stephanoaetus coronatus*, and three by Leopards *Panthera pardus*. The four animals were caught over three

days during a food shortage and unusual drought. They were readily detected as they moved through dry forest litter, and appeared to be in weakened condition, making them relatively easy to capture. Hairs of *C. hamlyni* found in two (0.9%) of 222 Leopard scats in Ituri Forest (Hart, J. A. *et al.* 1996). Although no *C. hamlyni* hairs were found in 60 African Golden Cat *Profelis aurata* scats examined during this study, *P. aurata* is a likely predator of *C. hamlyni*. Robust Chimpanzees and African Rock Pythons *Python sebae* are probable predators. The most important predator for *C. hamlyni* is almost certain humans. The semi-terrestrial habit of *C. hamlyni* makes this species especially susceptible to snares and hunters with dogs. They are more frequently caught in snares set for duikers than any other primate species in the Ituri Forest (J. Hart pers. obs.). No information on diseases and parasites.

Conservation IUCN Category (2012): Vulnerable. CITES (2012): Category II.

Probably extirpated from Uganda (depending on validity of Rahm's (1970) record), and restricted in Rwanda to the bamboo zone in Nyungwe N. P. (Easton *et al.* 2011, R. Dowsett, A. Vedder & A. Plumptre pers. comm.). The population on Mt Tshiaberimu must be very small and, as such, may not be viable. Most important threats are habitat degradation (including the harvesting of bamboo), loss and fragmentation of forest as a result of agricultural expansion, as well as hunting for bushmeat (Mwanza *et al.* 1989, Inogwabini *et al.* 2000, Easton *et al.* 2011). Protected areas important for the long-term survival of *C. hamlyni* include Okapi Faunal Reserve, Maiko N. P., Kahuzi-Biega N. P. and Nyungwe N. P.

Cercopithecus hamlyni is a survivor of a unique primate lineage. None the less, it remains one of Africa's least studied species of primate. A long-term, detailed, study of the ecology, behaviour and habitat requirements of *C. hamlyni* would not only be exceedingly interesting and help fill a major gap in African primatology, it would also contribute valuable information towards the conservation of this species.

Measurements

Cercopithecus hamlyni

HB (♂ ♂): 540 (510–550) mm, n = 3

HB (♀ ♀): 460 (430–480) mm, n = 3

T (♂ ♂): 570 (500–630) mm, n = 3

T (♀ ♀): 530 (490–560) mm, n = 3

HF (♂): 148 mm, n = 1

HF (♀ ♀): 133 (120–145) mm, n = 3

E (♂): 44 mm, n = 1

E (♀ ♀): 29 (28–30) mm, n = 3

WT (♂ ♂): 5.5 (4.4–7.3) kg, n = 14

WT (♀ ♀): 3.6 (2.6–4.5) kg, n = 18

GWS (♂ ♂): 110, 112 mm, n = 2

GWS (♂ ♂): 74, 74 mm, n = 2

Various localities (Hill 1966, Rahm 1966, Gevaerts 1992, Gautier-Hion *et al.* 1999, P. Kaleme pers. comm., E. Gilissen & W. Wendelen pers. comm., J. Hart pers. obs.)

Key References Easton *et al.* 2011; Gautier-Hion *et al.* 1999; Hall *et al.* 2003; Hill 1966; Rahm 1970; Raven & Hill 1942.

**John A. Hart, Thomas M. Butynski, Esteban E. Sarmiento
& Yvonne A. de Jong**



Lesula *Cercopithecus lomamiensis* adult male.

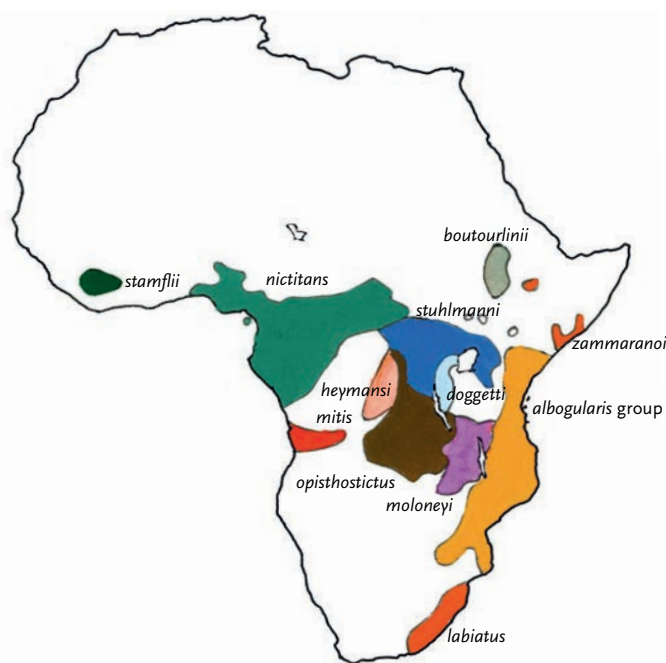
Cercopithecus (nictitans) GROUP

Nictitans Monkeys Group

Cercopithecus nictitans (Linnaeus, 1766). Systema Naturae, 12th edn, 1: 40. Benito R., Rio Muni, Equatorial Guinea.

The name *Cercopithecus nictitans* has two different taxonomic expressions. One restricts the name to a single species, the Putty-nosed Monkey. The other, much more complex expression, *Cercopithecus (nictitans)*, refers to a more inclusive taxon, a species-group (or superspecies) that ranges from West Africa to Zanzibar I., and from SW Ethiopia to the southern tip of South Africa. In this appellation, the *C. (nictitans)* Group, described in 1766, includes both the Putty-nosed Monkey *Cercopithecus (nictitans)* Subgroup and the Gentle Monkey *Cercopithecus (mitis/albogularis)* Subgroup (first described in 1822 and 1831, respectively) (Grubb *et al.* 2003).

While 52 forms have been named within the *C. (nictitans)* Group, we provisionally recognize 21 forms here. It has been a matter of convention and convenience that the western *C. nictitans* has been profiled separately from the rest of the *C. (nictitans)* Group in this and many other works. Three species are frequently recognized: *C. (n.) nictitans*, Blue Monkey *C. (n.) mitis* and Sykes's Monkey *C. (n.) albogularis*. The boundaries between taxonomic subgroups and sections of all monkeys of the *C. (nictitans)* Group remain poorly understood (Grubb *et al.* 2003). There is the strong likelihood that at least a third/fourth species, *C. (n.) opisthostictus*, should be distinguished as it, like *C. (n.) nictitans*, has a chromosome count of $2n = 70$, whereas all of the other forms



Schematic distribution of populations in the *Cercopithecus (nictitans)* Group.

in the *C. (nictitans)* Group that have so far been assayed have $2n = 72$ chromosomes (Dutrillaux *et al.* 1980). In addition, *opisthostictus* may be sympatric with *moloneyi* (Ansell 1958, O. Burnham pers. comm., T. Davenport pers. comm.).

Some outlying and geographically separate forms in the *C. (nictitans)* Group appear to share certain conservative traits. This implies a complex history of population expansions and contractions out of and back into climatically determined enclaves. Recent molecular studies hint at just such complications, reinforcing the recognition that *nictitans* and *albogularis* belong to the same complex and are closely related in spite of coming from opposite sides of Africa (Tosi *et al.* 2005). The latter authors' use of X chromosomes as an indicator of affinity has also confirmed the relationship of *albogularis* with *mitis*. The phylogenetic tree offered here attempts to sketch out one possible sequence of events whereby seven regional clusters might have evolved, but until detailed genetic profiles become available, any phylogenetic tree must be regarded as tentative and provisional. Taking Tosi *et al.*'s (2005) study of X chromosomes and their associated molecular clock as a guide, this tree supposes the initial spread of a large, relatively unspecialized ancestor across those parts of Africa that were webbed at that time by a network of riverine forests. Molecular clocks are consistent in positioning this spread during a warm spell that preceded the cold, arid period of 3.2–2.8 mya (mid-Pliocene). This prolonged dry period would have fragmented forests and with them early *C. (nictitans)* populations. The main fracture-lines between forest blocks would have fragmented this lineage, much as they did many other forest lineages (see map of biogeographical sub-regions in Volume I, Chapter 6). Regional subpopulations would have emerged in far Upper Guinea, on both sides of the northern Congo Basin and, divided by the Congo R., on both sides of the southern Congo Basin. Forests watered by moist Indian Ocean winds would have sustained a separate population along the eastern African littoral but these too would have fragmented. Climate has fluctuated many times over the

past 2.8 million years and it is currently impossible to correlate the emergence of specific contemporary populations with particular past climatic events. However, differences among contemporary members of the *C. (nictitans)* Group encourage the identification of seven 'deep' lineages. These are consistent with geography and with the forest refugia listed above.

On the eastern side of the south Congo Basin *opisthostictus* is the most likely candidate for direct descent from the founding lineage. It may be that *opisthostictus* still lives in the vicinity of, or in a part of, the region in which the ancestors of the *C. (nictitans)* Group emerged. It has already been pointed out that, with the exception of *C. (n.) nictitans*, *opisthostictus* has a smaller number of chromosomes than other members of the *C. (nictitans)* Group ($2n = 70$ instead of $2n = 72$; Dutrillaux *et al.* 1982a). (*Cercopithecus (n.) heymansii*, which most resembles *C. (n.) opisthostictus*, possibly shares the same count.) *Cercopithecus (n.) heymansii* occupies what looks like a relict range, sandwiched between two major rivers, with the implication that it belongs to a group that was formerly more widespread. When more is known about primate populations in the Congo Basin the two forms may actually be shown to represent a clinal continuum.

Assuming that their primary spread reached the farthestmost parts of their present range it seems significant that geographically isolated populations from the extreme west, north-east and south of the range of the *C. (nictitans)* Group should show striking similarities. Thus *C. (n.) n. stamflii*, from West Africa, *C. (n.) albogularis labiatus* from South Africa, *C. (n.) albogularis zammaranoi* from the Juba R., Somalia, and *C. (n.) m. boutourlinii* from SW Ethiopia all have white throats and upper chests, dark olive backs, intensely black arms graduating to dark agouti grey on upper shoulders, and dark grey agouti legs. Some further resemblances between these four populations and *opisthostictus* and *heymansii* are best explained by retention of conservative genotypes shared by the most isolated populations in their common ancestor's once extensive range. In spite of their likely genetic heritage, these outliers are commonly assigned to three different species. The isolation of *C. (n.) n. stamflii* in the west is enough to explain its differentiation from the Eastern Putty-nosed Monkey *C. (n.) n. nictitans*. On the face of it, the latter should descend from the same *nictitans* ancestor, yet its close resemblance to *C. (n.) m. stuhlmanni* suggests many complications, including the possibility that the latter genotype has mixed with that of *nictitans* long after their parental stocks diverged. Should this turn out to be so, *C. (n.) n. nictitans* would represent a stabilized hybrid, or even, in places, a hybrid swarm.

Late genetic crossing might also help explain mixed characteristics in *boutourlinii*, which combine many *opisthostictus*-like features with some of those of its nearest neighbour, *stuhlmanni*. Should *boutourlinii* be allied with *stuhlmanni* (as it now is) or are there any ways in which its likely links to an older heritage could find expression? Some of the ancestors of *boutourlinii* were probably shared with those of *zammaranoi* at the time of their first entry into north-east Africa. Yet today there are decisive differences in body size, habitat and geographic range. Both forms have continued to evolve adaptations to their localities. Their current taxonomic allocations are certainly artificial and are likely to be changed in the future.

The penetration of geographic extremities includes an altitudinal dimension and it is possible that descent from an earlier *nictitans* may be exemplified in the mountains of the Western Rift Valley by *doggetti*,



Some monkeys in the Nictitans Monkeys Group *Cercopithecus (nictitans)* radiation.

Top row, left to right: Eastern Putty-nosed Monkey *Cercopithecus nictitans nictitans*. Angola Pluto Monkey *Cercopithecus mitis mitis*. Moloney's Monkey *Cercopithecus mitis moloneyi*. Stuhlmann's Blue Monkey *Cercopithecus mitis stuhlmanni*. Kolb's Monkey *Cercopithecus mitis kolbi*.

Bottom row, left to right: Martin's Putty-nosed Monkey *Cercopithecus nictitans martini*. Lomami River Monkey *Cercopithecus mitis heymsi*. Rump-spotted Monkey *Cercopithecus mitis opisthictus*. Doggett's Silver Monkey *Cercopithecus mitis doggetti*. Tanzania Sykes's Monkey *Cercopithecus mitis monoides*.

kandti and, farther south, by *moloneyi*. The isolation of such distinctive types on cool upland suggests that past global glacials encouraged the spread of an appropriately adapted morpho-type and that subsequent climatic changes led to regional differentiation. Thus, *doggetti*, *kandti*, *moloneyi* and possibly another outlying and isolated population, *C. (n.) m. mitis* (which occurs south of the Congo R. mouth both in upland and low-lying areas of N Angola), might all have a common ancestry and have been connected across the temperate southern African highlands. The exceptionally successful *stuhlmanni* is predominantly a lowland form but probably represents a late derivative from the same stock as *doggetti*. Thus there appear to be multiple temporal levels in a slow-growing evolutionary radiation that may well have been strung out over some 3 million years.

These are but a few of the phylogenetic questions. As such, it is not surprising that current taxonomic allocations are confused, contradictory, and sometimes arbitrary. Since the *C. (nictitans)* Group represents one of the most promising exemplars of 'evolution in action', these monkeys beg much more study. In the interests of provoking further study of these ecologically and evolutionarily significant monkeys, we list and map the ranges of identifiable regional populations and allocate them, provisionally, to seven regional 'clusters' (Kingdon 1997) that have also been called 'sub-groups' and 'sections' (Grubb 2001, Grubb *et al.* 2003). We have used established names to tentatively rank each of these clusters and while these imply that each could be regarded as a species in its own right we regard formal recognition at the species level as premature, pending deeper molecular studies. We believe our restraint might help move the study of these interesting monkeys towards a less superficial and more eco-biogeographic and evolutionarily based treatment. The 22 forms listed here are generally recognized as morphologically and geographically distinct. All of the seven proposed clusters embrace more than one subspecies.

Cluster I: *Cercopithecus opisthictus* Cluster

C. (n.) opisthictus. A highly distinctive form with a different chromosome count from all others in the *C. (nictitans)* Group

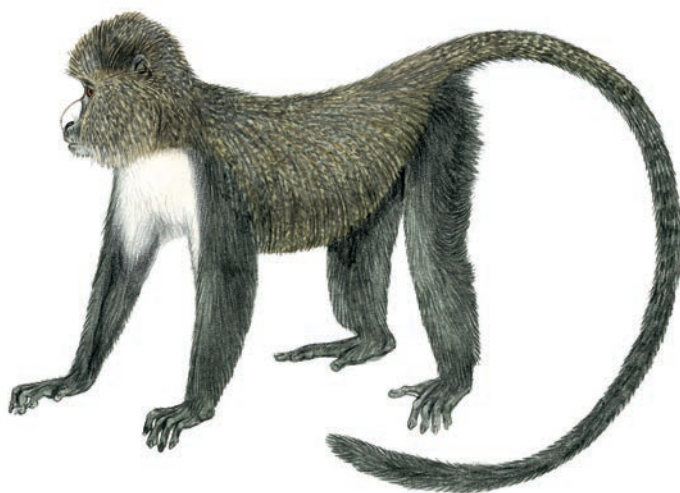
except for *C. (n.) nictitans* ($2n = 70$ instead of $2n = 72$, Dutrillaux *et al.* 1982a). Appears to be sympatric without interbreeding in a narrow region of overlap with *C. (n.) moloneyi* (see below). The dense, light olive to steel-grey agouti pelage of the dorsum is exceptionally soft, resembling that of Owl-faced Monkey *Cercopithecus hamlyni* and De Brazza's Monkey *Cercopithecus neglectus* in colour and texture. Cheek-fur particularly long, hiding the ears and drooping down towards the shoulders. Muzzle, chin and throat off-white. Diadem upwardly arched, 'sculpted' and poorly defined in colour, but paler than rest of the crown (which matches colour of dorsum). Arms and underside black. Hindlimbs a darker shade of agouti than dorsum. Muzzle longish in adult ♂.

C. (n.) o. opisthictus Rump-spotted Monkey. Crown relatively monochromatic agouti. Throat off-white. Face pale. Inhabits forest mosaics, especially ground-water swamp forests, within the moister miombo woodlands of the south-eastern Congo Basin and upper Zambezi Basin to western littoral of L. Tanganyika. In low-lying forests along the southern eastern littoral of L. Tanganyika (T. Davenport pers. comm.). Kasai R. possibly forming western boundary with L. Tanganyika and Muchinga Uplands defining much of eastern limit.

C. (n.) o. heymsi Lomami River Monkey. Similar to *C. (n.) o. opisthictus* but black band across temples and nape and diadem near-white, narrow. Face black. White on throat less extensive. Crown, neck and shoulders blue-grey. Ventrums lighter than back. Between Lualaba R. and Lomami R., E DR Congo. Some authors allocate *heymsi* to other clusters (Colyn & Verheyen 1987b, Lawes *et al.* this volume).

Colyn & Verheyen (1987) suggest that *heymsi* and *opisthictus* hybridize near Lusambo, DR Congo, but it is also plausible that there is (or has recently been) a more or less continuous cline between the two forms.

The singular distribution pattern of the *opisthictus* Cluster implies a formerly more extensive range. If so, displacement to the east could have been due to expansion by *C. m. stuhlmanni*. To the



Martin's Putty-nosed Monkey *Cercopithecus nictitans martini* adult male.

west, competition from what are now rare forms of the *C. (nictitans)* Group seems unlikely. However, species that are rare today need not have been rare in the past. Furthermore, if the *opisthictus* Cluster represents an early form of (*nictitans*), then displacement by subsequent descendant populations is plausible. With regard to understanding the dynamics of speciation/sub-speciation in the *C. (nictitans)* Group, it is important to document details of the relationships of *C. (n.) opisthictus* with *C. (n.) m. stuhlmanni* and *C. (n.) m. doggetti* to the north-east and with some form of *C. (n.) mitis* (possibly *C. (n.) m. maesi*) to the west.

Cluster II: *Cercopithecus nictitans* Cluster

- C. (n.) nictitans*. Most strikingly distinguished by its white 'putty nose'. Back pelage greyish-olive or kaki-olive agouti and relatively coarse (compared with *opisthictus*). Arrangement of cheek-fur differs between subspecies. Arms black. Hindlimbs a darker shade of agouti than dorsum. Muzzle medium length in adult ♂. *Cercopithecus (n.) nictitans* has a lower number of chromosomes ($2n = 70$) than all other members of the *C. (nictitans)* Group ($2n = 72$) with the exception of *opisthictus* ($2n = 70$). Based on protein analyses, the *C. nictitans* Cluster, the four *C. (n.) mitis*-like clusters (i.e. *mitis*, *doggetti*, *moloneyi* and *stuhlmanni* Clusters) and the *C. (n.) albobularis* Cluster are phylogenetically extremely close. In the eastern parts of the range of *C. (n.) nictitans* the possibility of long-term hybridization, even replacement of earlier *stuhlmanni* populations, should be borne in mind.
- C. (n.) n. nictitans* Eastern Putty-nosed Monkey. Back, head and underside warm, greyish-olive. Laterally bunched fur on cheeks. Chest black. Some features of this form may have been influenced by hybridization, possibly on a broad scale, with *stuhlmanni*. Sanaga R. and Cameroon Highlands eastwards to Congo R. and Itimbiri R. (DR Congo), and southwards to Congo R.
- C. (n.) n. martini* Martin's Putty-nosed Monkey. Khaki-olive back and head. Throat off-white. Chest and abdomen dusky grey. Restricted to Bioko I., Equatorial Guinea.
- C. (n.) n. stampflii* Stampfli's Putty-nosed Monkey. Khaki-olive back and head. Cheek-fur downwardly deflected giving face a narrower appearance. Throat, chest, inner surfaces of upper arms and underside with variable amounts of white, cream or light grey.

Sanaga R. and Cameroon Highlands, disjointedly, westwards to far western Upper Guinea. Probably the most conservative form within this cluster. Synonyms: *insolitus*, *ludio*.

Cluster III: *Cercopithecus mitis* Cluster

- C. (n.) mitis*. Back dark grizzled agouti. Crown with paler diadem. Chin pale. Cheek-whiskers broad. Muzzle longish in adult ♂. Populations appear to be relictual.
- C. (n.) m. mitis* Angola Pluto Monkey. Diadem very pale. Muzzle with short, white hairs. Crown, neck and limbs black. Dorsal and ventral pelage dark grey to black. Synonyms: *diadematus*, *dilophus*, *leucampyx*, *pluto*, *nigrigenis*. W Angola.
- C. (n.) m. maesi* Kutu Pluto Monkey. The validity of this apparently rare form has been challenged and the provenance (Kutu, near the centre of the Congo Basin) of the holotype questioned (Colyn & Verheyen 1987, Groves 2001), but Schouteden (1947) allocated several specimens from west of Lomami R. and south of Congo R. to this subspecies. Whatever taxonomic designation is eventually arrived at, it is clear that *C. (n.) mitis* is of sporadic occurrence through the Congo Basin south of the Congo R. and west of the Lomami R. The occurrence of the *C. (n.) mitis* form in this region needs further study. It should be noted that this heavily forested region is well separated from both *C. (n.) mitis* and *C. (n.) stuhlmanni* (the two forms *maesi* has been commonly allied with). Schouteden's descriptions imply most resemblance with *C. (n.) m. mitis* but with a narrower brow-band, a black temporal streak and fine agouti cheek-fur tones that graduate from paler near the face to darker on the margins.

Cluster IV: *Cercopithecus doggetti* Cluster

- C. (n.) doggetti*. Back grizzled grey or golden. Crown black with sharply defined diadems. Cheek-whiskers high, well-developed. Muzzle of adult ♂ long. Isolated populations associated with Western Rift Valley of DR Congo, Uganda, Rwanda, Burundi and Tanzania.
- C. (n.) d. doggetti* Doggett's Silver Monkey. Back grizzled varying from ash-grey to tawny-grey. Arms, hands and feet intense shiny black. Legs dark grey with some agouti on upper thighs. Occurs in both upland and lower-lying forests from western shore of L. Victoria westwards to Bwindi Impenetrable N. P. southwards to northern shore of L. Tanganyika. Synonym: *sibatoi*.
- C. (n.) d. kandti* Golden Monkey. Cape and base of tail red or orange. Cheeks and diadem with 'golden' tints. Crown, arms and tail black. The amount of red varies individually with some individuals scarcely distinguishable from *doggetti*. Inhabits montane and bamboo forests on Virunga Mts (where Uganda, Rwanda and DR Congo meet). Synonym: *insignis*.
- C. (n.) d. schoutedeni* Schouteden's Silver Monkey. An island isolate possibly deriving from hybridization between *doggetti* and *kandti* or an example of founder-effect. Idjwi and Shushu Is. in L. Kivu and western Virunga Mts, DR Congo. Diadem very pale agouti. Crown, neck and forelimbs black. Back pale olive-grey. Underside lighter.

Cluster V: *Cercopithecus moloneyi* Cluster

- C. (n.) moloneyi*. Until the ambiguous affinities of these monkeys have been clarified we treat them, provisionally, as a distinct cluster.



ABOVE: Pousargues's Monkey *Cercopithecus mitis albatorquatus* adult male.
 ABOVE LEFT: Moloney's Monkey *Cercopithecus mitis moloneyi* adult female.
 BELOW LEFT: Stuhlmann's Blue Monkey *Cercopithecus mitis stuhlmanni* adult male.

distinguished by red ear-tufts and by red and white hairs under tail. Restricted to Vipya/Nyika plateau and Mt Waller, Malawi.

Cluster VI: *Cercopithecus stuhlmanni* Cluster

C. (n.) stuhlmanni Cheek-whiskers broad. Cheek-whiskers, back, sides and base of tail deep slate-blue agouti. Diadem paler. Crown and arms black. Legs dark blueish-grey agouti. Muzzle relatively short in adult ♂. Expansive range in E and NE DR Congo and East Africa. Possibly into Ethiopia.

C. (n.) s. stuhlmanni Stuhlmann's Blue Monkey. As above. From east of Itimbiri R. and north of Congo/Lualaba R., DR Congo to Eastern Rift Valley, north of L. Victoria, SW Kenya. Also isolated massifs in N and W Uganda and SE Sudan. Includes *neumanni*, *carruthersi*, *mauae*, *elgonis* (*elgonis* is a particularly dark form from the montane forests of Mt Elgon).

C. (n.) s. boutourlinii Boutourlini's Blue Monkey. Crown grizzled (not black). Diadem undifferentiated from crown. Dorsum with greenish or yellowish tinge. Dandelot & Prévost (1972) emphasize similarity with *opisthostictus*. Genetically, might be allied to a hypothetical class of 'relictual populations on the extremities', so the possibility of *stuhlmanni* and an earlier relict type meeting and hybridizing in Ethiopia should be borne in mind. SW Ethiopia from L. Turkana northwards to L. Tana, along west side of Eastern Rift Valley. Synonym: *omensis*.

Cluster VII: *Cercopithecus albogularis* Cluster

C. (n.) albogularis. Back grizzled and mostly relatively light in colour. Cap and diadem grizzled, not clearly differentiated from one another. Diadem peaked, long and pointed in centre. Boundary between white or off-white chin/chest fur and grizzled cheek-fur highly variable. Tail mainly black. Muzzle medium length in adult ♂.

This cluster is distributed from S Somalia to Eastern Cape Province, South Africa, along the littoral and up most (perhaps all) Indian Ocean major river basins. It could be argued that the dark, apparently conservative populations at the northern (*C. (n.) a. zammaranoi*) and southern (*C. (n.) a. labiatus*) extremities of this range should be excised from this cluster. Were these two populations to be excluded, a more

This cluster has been variously associated with *doggetti* (Kingdon 1971), *albogularis* (Groves 2001) and *mitis* (Kingdon 1997). A flat 'cap' and light diadem are conspicuous features and, for all higher-altitude populations, a dark mahogany 'saddle'. Muzzle of adult ♂ medium length. Restricted to montane areas to north and west of L. Malawi. On the extreme western edges of range may be sympatric with *C. (n.) opisthostictus* without interbreeding (Ansell 1958, O. Burnham pers. comm., T. Davenport pers. comm.). This separation appears to be facilitated by *opisthostictus* inhabiting swamp or lower-altitude forests while *moloneyi* occupies montane forests or narrow riverine strips descending from higher altitudes. May form a phenotypic cline with *C. (n.) albogularis monoides* in the Udzungwa Mts, SC Tanzania (T. Butynski pers. comm.).

C. (n.) m. moloneyi Moloney's Monkey. Cheek-fur broad, grizzled. Throat pale grey. Dorsum with mahogany saddle. Sides and thighs light grey. Individuals from lower altitudes may have olive dorsum: whether this is due to admixture with *C. (n.) albogularis monoides* is not known. Arms, hands and feet black. Ventrums of tail sometimes reddish. Widely distributed in the Southern Highlands of Tanzania, from the north shore of L. Malawi westwards along riverine forests draining the Lavusi/Muchinga Highlands and the Luangwa R., Zambia.

C. (n.) m. francescae Red-eared White-collared Monkey. Often subsumed as a synonym of *moloneyi* but regarded as a distinct montane isolate by Ansell (1960). Resembles *moloneyi* but darker overall and



Pousargues's Monkey *Cercopithecus mitis albоторquatus*.

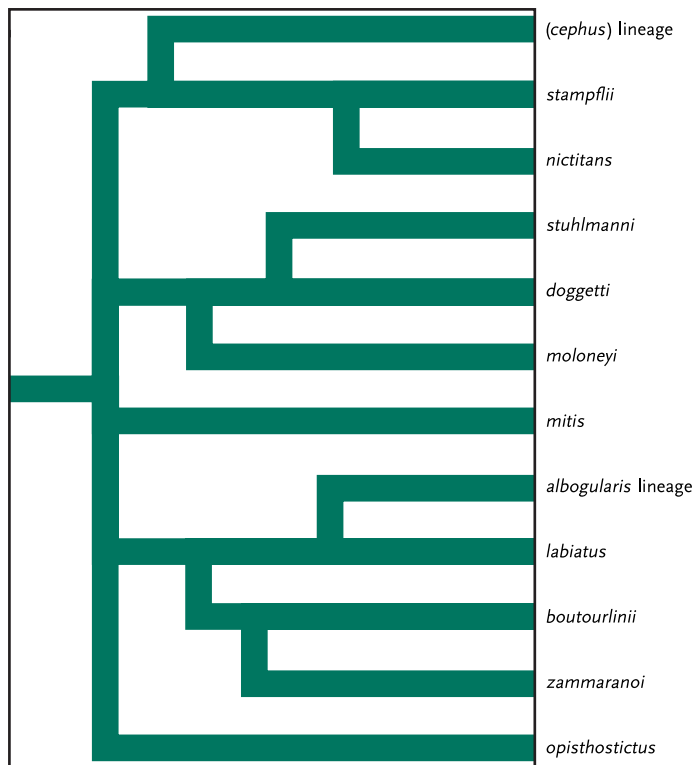
restricted *albogularis* Cluster might turn out to represent a self-contained radiation centred on the tropical Indian Ocean littoral, but embracing most of the major river basins between the Zambezi R. and the Tana R.

- C. (n.) a. albogularis* Zanzibar Sykes's Monkey. Ear-tufts small, white. Neck collar narrow, white. Back pale khaki agouti graduating to darker reddish-yellow on rump. Head and shoulders agouti grey. Distributed along the Indian Ocean coast and inland between the Galana/Sabaki River Basin and the Ruvu River Basin. Also Mt Kilimanjaro, Mt Meru, Taita Hills and Zanzibar (Nguja) I. After observing monkeys in the field at many sites within and at the extremes of the range of *C. (n.) a. albogularis*, De Jong & Butynski (2009) conclude that there is gradual but considerable phenotypic variation along north–south and west–east clines. For example, monkeys at the extremes of the range (e.g. at Gedi, EC Kenya, and west of Mt Kilimanjaro, NCTanzania) differ greatly in appearance from those on Zanzibar I., the type locality for *C. (n.) a. albogularis*. Multiple photographs of several of these subspecies are available at: www.wildsolutions.nl Synonym: *kibonotensis*.
- C. (n.) a. kolbi* Kolb's Monkey. Neck collar broad, nearly encircles the neck, and pure white, contrasting strongly with narrow brown agouti cheeks and jet black arms. Crown brown agouti, sometimes nearly black. Ear-tufts long, prominent, white. Back varies from khaki to deep brown or mahogany-red. Legs variable shades of grey. *Cercopithecus (n.) a. kolbi* forms a west–east cline with *C. (n.) a. albоторquatus* down the east side of the Kenya Highlands then down the Tana R. to the Indian Ocean (De Jong & Butynski 2009). Found in forests in the Kenya Highlands east of the Rift Valley (mainly Aberdares Range and Mt Kenya). *Cercopithecus (n.) a. kolbi* may also be the form in the Chuyulu Hills, SC Kenya. Synonyms: *hindei*, *nubilus*.
- C. (n.) a. albоторquatus* Pousargues's Monkey. Back and sides pale agouti yellow ochre. Upper cheek-patches narrow. Legs and shoulders dove-grey. Arms black. Conspicuous and extensive white ear-tufts and collar. Found on the lower Tana R., Tana Delta and north along the coast, perhaps as far as the Caanoole R., SE Somalia. Also Pate I. It is presumably *albоторquatus* that is on Lamu I. and Manda I., Kenya (De Jong & Butynski 2009). Along the course of the Tana R., *albоторquatus* graduates with *kolbi* on

the Aberdares Range and Mt Kenya. In contrast, there are sharp differences between *albоторquatus* and *C. (n.) a. zammaranoi*, the two being separated by ca. 100 km of unsuitable habitat along the dry littoral of S Somalia. Synonyms: *phylax*, *rufotinctus*.

- C. (n.) a. monoides* Tanzania Sykes's Monkey. Crown, cheeks, neck and shoulders yellowish-olive. Rump reddish-brown. Underside grey. Otherwise similar to *albogularis* (and only marginally separable taxonomically). Occurs on coastal littoral from Rufiji Basin southwards to the Rovuma Basin. Also Mafia I. Synonym: *rufilatus*.
- C. (n.) a. erythrarchus* Stairs's Monkey. Similar to *monoides* but with variable infusions of yellow (non-agouti) colouring on back, crown, cheeks, ear-tufts and root of tail (where red fur may surround ischial callosities). Underside off-white to grey. Inhabits Indian Ocean littoral (including Bazaruto I.) and Mozambique interior from Mualo Basin south to Limpopo Basin and Manica Highlands. Synonyms: *mossambicus*, *nyasae*, *schwarzi*, *stairsi*, *stevensoni*.
- C. (n.) a. zammaranoi* Zammarano's Monkey. The smallest of all forms in the *C. (nictitans)* Group. Once given the Italian vernacular name of *scimmia nera* (black monkey) (Funaioli 1957, 1971), this is a dark form (in spite of coming from the arid S Somali coastal/riverine region) (de Beaux 1923, 1937, Zammarano 1930, Patrizi 1935). Resembles *C. (n.) a. labiatus* and *C. (n.) n. martini* in white throat and chest, dark olive back, intensely black arms graduating to dark agouti grey on upper shoulders, and dark grey agouti legs. *Cercopithecus (n.) a. zammaranoi* differs in lacking black on head, the crown being grizzled dark olive graduating at the temples to dark grey on the cheeks. Diadem not differentiated in colour from the crown but is prominently peaked. Nape paler grey. Ears protrude only slightly and are without tufts (unlike its nearest neighbour, the pale, white bibbed, white ear-tufted *C. (n.) a. albоторquatus*, to which it is not closely related) (Funaioli & Simonetta 1966, Varty 1988, Gippoliti 2003).
- C. (n.) a. labiatus* Samango Monkey. Like *C. (n.) a. zammaranoi* this is a dark form but significantly larger. *Cercopithecus (n.) a. labiatus* shows some resemblances with *C. (n.) o. heymansi*. The similarities might be superficial or convergent but are more likely to signify the retention of a conservative genotype at the extremities of the range of the *C. (nictitans)* Group. Cheek-whiskers dark olive agouti, long and downwardly deflected. Diadem prominent, strongly peaked and sometimes contrasts strongly with black crown. Back dark grey agouti tinged with yellow. Arms black. Legs grey. Found from Eastern Cape Province to the Pongola R. Valley. Synonym: *samango*. Like *zammaranoi* and *boutourlinii*, this form may require re-allocation once its genotype has been examined and compared with those of other members of the *C. (nictitans)* Group.

Of all the true forest guenons, *C. (nictitans)* spp. and ssp. are the only ones with sufficient ecological plasticity to sustain a wide distribution in southern and eastern Africa. Showing a striking adaptability to both altitude and latitude, they range up into cool montane habitats and south into temperate South African forests. The secret of their success in peripheral forests appears to derive from a physiological ability to fall back on leaves as a staple during periods when fruit and invertebrates are lacking or in short supply. These relatively large, mainly arboreal monkeys are therefore relatively generalized compared to other arboreal forest guenons (which specialize in fruit and/or invertebrates, leaving leaf-eating



Tentative phylogenetic tree for the Nictitans Monkeys Group *Cercopithecus (nictitans)* (J. Kingdon reconstruction).

to appropriately adapted colobines). Within the crowded primate communities of the equatorial forests *C. (nictitans)* are frequently rare, even absent, and it would seem to be competition from other guenons (and perhaps colobines) that constrains, or excludes them from some areas. Outside the main forest block this susceptibility to competition may not include the mangabeys (*Cercocebus* and *Lophocebus*), with which they co-exist over parts of their range. Indeed, under conditions of food stress it is the mangabeys that may be too specialized to compete with *C. (nictitans)*. The relatively large body-size of *C. (nictitans)* must operate as a constraint under some climatic and ecological states, as well as in some competitive contexts. Thus it may be significant that one population, *zammaranoi*, isolated in botanically impoverished gallery forests in Somalia in the absence of other forest monkeys, is relatively small. The same trend was probably followed in far western Africa, resulting in the emergence of a dwarfed lineage ancestral to the *Cercopithecus (cephus)* lineage. For this initially restricted population small size opened new opportunities that are discussed in the *C. (cephus)* Group profile. With regard to their conservation, although the *C. (nictitans)* Group, taken as a whole, is common and widespread, several forms, notably *mitis*, *zammaranoi*, *stampflii*, *francescae*, *kandti* and *labiatus*, are rare and localized. All forms deserve to be studied and conserved as representatives of one of the most complex and interesting of all pan-tropical primate radiations.

Jonathan Kingdon

Cercopithecus nictitans PUTTY-NOSED MONKEY (GREATER SPOT-NOSED MONKEY)

Fr. Pain à cacheter; Ger. Große Weißnasemeerkatze

Cercopithecus nictitans (Linnaeus, 1766). Systema Naturae, 12th edn, 1: 40. Benito R., Rio Muni, Equatorial Guinea.

Taxonomy Polytypic species that is treated here as a species within the *Cercopithecus (nictitans)* Group or Superspecies (see previous profile). This profile follows Dandelot (1971), Groves (2001, 2005c)

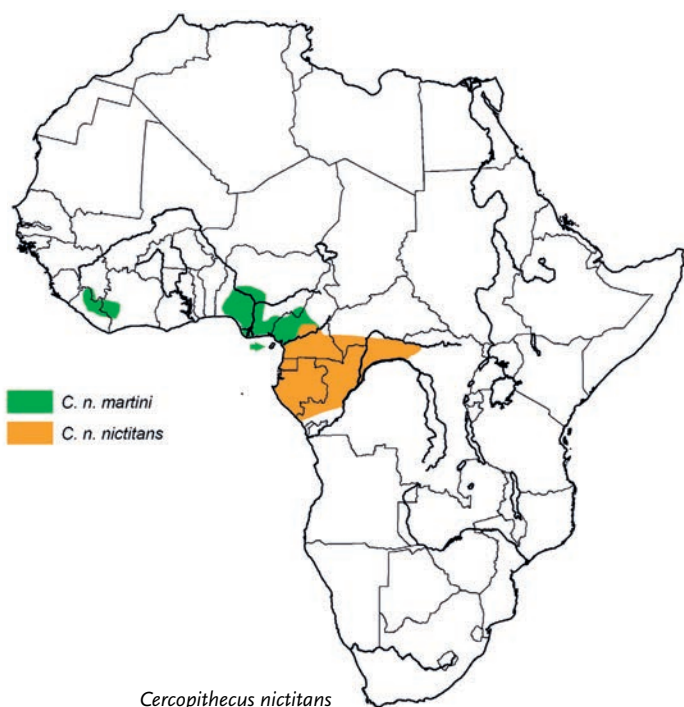


Eastern Putty-nosed Monkey *Cercopithecus nictitans nictitans*.

and Grubb *et al.* (2003) in recognizing two subspecies, Eastern Putty-nosed Monkey *C. n. nictitans* and Martin's Putty-nosed Monkey *C. n. martini*. While the validity of *C. n. stampflii* is in question, this subspecies is recognized by several authorities, as well as in the *C. (nictitans)* Group profile presented above. Oates (1988b, 2011) and Grubb *et al.* (2000) recognize an additional two subspecies; *C. n. ludio* and *C. n. insolitus*.

Cercopithecus nictitans has fewer chromosomes ($2n = 70$) than most members of the *C. (nictitans)* Group ($2n = 72$), although the Rump-spotted Monkey *Cercopithecus mitis opisthostictus* also has $2n = 70$ chromosomes (Moulin *et al.* 2008). Based on protein analyses, *C. nictitans* and forms in the *Cercopithecus mitis/albugularis* Subgroup are phylogenetically extremely close (Dutrillaux *et al.* 1988b, Ruvolo 1988). They also possess similar vocal repertoires (Gautier 1988). Thorington & Groves (1970) suggested they should be considered as conspecific, a conclusion that was later retracted (Groves 2001, 2005c). Synonyms: *insolitus*, *laglaizei*, *ludio*, *martini*, *stampflii*, *sticticeps*. Chromosome number: $2n = 70$ (Dutrillaux *et al.* 1988b, Ruvolo 1988, Moulin *et al.* 2008).

Description A moderately large, long-tailed monkey with a white nose spot on a grizzled greyish-olive or khaki-olive face. Sexes alike in colour but adult ♀ smaller, weighing ca. 60% as much as adult ♂ in the nominant subspecies and ca. 80% as much as adult



♂ in *C. (n.) n. martini* on Bioko I. (Butynski *et al.* 2009). Nose with white oval spot. Whiskers, diadem, crown, shoulders, back, legs and basal part of tail dark greyish-olive or khaki-olive due to ringed (grizzled) hairs. Arms, hands, feet, belly and distal part of tail black. Young similar in colour to adults but white nose spot not present at birth.

Geographic Variation

C. n. nictitans Eastern Putty-nosed Monkey. Occurs mainly south of Sanaga R., Cameroon, southwards through Equatorial Guinea (Rio Muni), Gabon and Cabinda (Angola) to Congo R. and eastwards across Central African Republic and Congo into DR Congo to north of Congo R. and west of Itimbiri R. (Oates 1988b, Gautier-Hion *et al.* 1999, Grubb *et al.* 2000). The Sanaga R. is not, however, a clear-cut barrier as at least one population occurs north of Sanaga R. Overall dark greyish-olive with broad, largely blackish crown and rounded face. Underside as dark as upperside. Chest black.

C. n. martini (including *stampflii*) Martin's Putty-nosed Monkey. Disjunct distribution; N Liberia and SW Côte d'Ivoire and then in S Nigeria and SW Cameroon to Sanaga R. (Oates 1988b, 2011, Grubb *et al.* 2000). Also Bioko I., Equatorial Guinea, where it appears to be limited to the lower southern slope of Pico Basilé and to the remote and extremely wet southern ca. 25% of the island (Butynski & Koster 1994). Overall, khaki-olive (lighter than *C. n. nictitans*). Crown with black, narrow sides. Whiskers downward deflected giving face a narrower appearance. Throat and inner surfaces of upper arms white or off-white. Underside dusky grey.

Similar Species

Cercopithecus mitis stuhlmanni. Mainly allopatric. Bluer and lacks distinctive white nose spot. Kingdon (1980), however, points out that spot-nosed individuals resembling *C. m. stuhlmanni* are described from places as far apart as Gabon (Pocock 1907) and Ubangi, DR Congo (Elliot 1909a). He suggests that relict

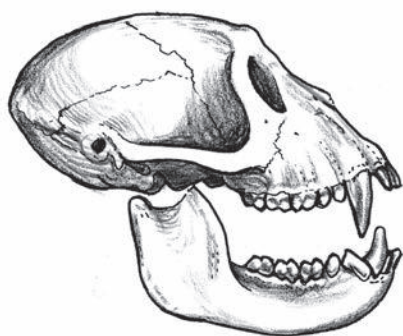
populations of *stuhlmanni* might be in a late process of being absorbed genetically by *C. n. nictitans*.

Cercopithecus petaurista. Sympatric with *C. n. stampflii*. Body smaller and coat lighter. Ventrums white. White stripe on lateral sides of face.

Distribution Endemic to West Africa and western central Africa. Rainforest BZ. See details for distribution in Geographic Variation. Northern limit in central Africa is at ca. 08° 20' N in Central African Republic to ca. 05° S in Congo. Absent from the left (south) bank of Congo R. (Schouteden 1947, Colyn 1988, Oates 1988b, 2011, Gautier-Hion *et al.* 1999).

Habitat Lowland and medium-altitude forests. Typically lives in primary forest with tall trees, but also in riverine and old secondary forests. In relict patches of high forests within forest-savanna mosaics (Oates 1988b for West Africa). In gallery forests and patches of forest in Central African Republic (Fay 1988) and Gabon (Tutin *et al.* 1997b). Prefers middle and upper strata of the canopy, at similar height to Crowned Monkey *Cercopithecus pogonias*. Spends 56% of time above 20 m and only 3% below 10 m. Rarely observed on the ground (Gautier-Hion & Gautier 1974) except to cross savanna between forest patches/forest galleries and continuous forest (C. Tutin pers. comm.). On Bioko I. observed only in pristine forest and in slightly degraded primary forest, not in secondary forest (T. Butynski pers. comm.). From sea level to >1000 m on the mainland. From 0–900 m on Bioko I. where it appears to have the most limited altitude range of any of the seven species of primates (Butynski & Koster 1994). Annual rainfall from ca. 1500 mm to ca. >4000 mm on the mainland and from ca. 4000–10,000 mm on Bioko I.

Abundance Biomass for *C. n. nictitans* in primary forests ranges from ca. 40 kg/km² in the Forêt des Abeilles, C Gabon (Brugière 1988), to ca. 480 kg/km² at Odzala N. P., Congo (Bermejo 1999). At most sites the greatest biomass is in mature forest. At Odzala N. P., biomass varies from 41 kg/km² in forest patches, 60 kg/km² in riverine forests, 90 kg/km² in secondary forests to 480 kg/km² in mature forest (adapted from Bermejo 1999). In Lopé Reserve, C Gabon, biomass is lower in the continuous forests (Marantaceae forests with dense undergrowth) than in gallery forests and forest patches of the neighbouring savanna (81 kg/km² vs. 135 kg/km²; Tutin *et al.* 1997a, b). In gallery forests of St Floris N. P., Central African Republic, the biomass is less than 10 kg/km² (Fay 1988). At most sites, in both mainland mature forest and riverine forest, *C. n. nictitans* is more abundant than its congeners *C. pogonias* and Moustached Monkey *Cercopithecus cephus*. In secondary forest its density is generally lower than that of *C. cephus*. On the mainland, in northern Korup N. P., W. Cameroon, the density of *C. n. martini* ca. 1.1–1.5 groups/km² and biomass at 51 kg/km² (A. Edwards quoted by J. Oates pers. comm.). Another study in Korup N. P., conducted in 2004–05, found 0.08–0.37 groups/km² (Linder & Oates 2011). Uncommon in Okomu N. P., SW Nigeria, where Akinsorotan *et al.* (2011) sighted only 0.02 groups/km. In Liberia and Côte d'Ivoire, *C. n. nictitans* is usually rare and occurs only in the drier, more deciduous forest north of the main evergreen forest (H.-J. Kuhn quoted by J. Oates pers. comm.). This might be influenced by competition with Diana Monkey *Cercopithecus diana* (Oates 1988b).



Lateral view of skull of Eastern Putty-nosed Monkey *Cercopithecus nictitans* adult male.

Perhaps the rarest primate on Bioko I. Encounter rate of 0.01 groups/km of transect during an island-wide survey in 1986 (373 km of census; Butynski & Koster 1994). Encounter rate of 0.02 groups/km in 2008 along 49 km of transect the south slope of Pico Basilé, and 0.06 groups/km in 2009 along 48 km of transect and no groups encountered in 2010 along 50 km of transect at Badja North, SW Bioko (T. Butynski, G. Hearn, M. Kelly & J. Owens pers. comm.). The south slope of Pico Basilé and Badja North are remote sites where hunting is relatively uncommon and where there are no other anthropogenic impacts. As such, the encounter rates at these two sites are likely close to what is expected for an undisturbed population of *C. nictitans* living near the upper altitude range for the species (i.e. 500–900 m). In contrast, at Arihá, SE Bioko, an area in which there is a moderate level of hunting for primates but that is at the lower altitude range for *C. nictitans*, Maté & Colell (1995) encountered 0.10 groups/km in 1992 along 100 km of transect. They estimated 0.05 groups/km² and ca. 0.3 ind/km² at Arihá.

Adaptations Diurnal and arboreal. As a species, *C. nictitans* is a successful monkey, able to colonize different habitats and to come to the ground occasionally to cross open areas. This generalist species has two adaptive advantages: highly developed arboreal skills and the ability to eat leaves and insects during periods when fruit is scarce. The large white spot on the nose provides a distinctive cue for species recognition. The main function of the white nose spot seems to be to serve as a visual distraction from the eyes. The nose-spot becomes especially conspicuous during 'head flagging', which Kingdon (1988b, 2007) considers part of 'cut-off' behaviour. This behaviour has resulted in the French name of 'hocheur' (i.e. 'head shaker') for this species. However, this name is confusing because the behaviour also occurs in other guenons and, in DR Congo, the Red-tailed Monkey *Cercopithecus ascanius* is also named 'hocheur'. Like other cercopithecines, *C. nictitans* possesses large cheek-pouches. These are used to store large amounts of fruit before moving to ingest the fruit in a place more sheltered from predators and while foraging for more nutritious insects. Adult ♂♂ have large air sacs used for producing loud-calls that are highly specific to the *C. nictitans* Group (Gautier 1971).

Foraging and Food Omnivorous. In Makokou area, NE Gabon, annual diet of *C. nictitans* dominated by fruit and seeds (70%), followed by leaves (17%) and animal matter (10%; Gautier-Hion 1980). Great seasonal variations in diet occur with an inverse relationship between

fruit and leaf intake. Adult ♂♂ are more frugivorous than adult ♀♀, especially when fruit is abundant, while the ingestion of leaves by adult ♀♀ is twice that of adult ♂♂. Seventy-one plant species identified in the diet, mainly taken from Annonaceae, Apocynaceae, Burseraceae and Euphorbiaceae. Females eat more animal matter. Sedentary prey forms the great majority of captures (>90%), caterpillars and ants being the most common prey. In Forêt des Abeilles, the annual plant diet comprised 36% fruit (including 11% arils), 57% seeds and 11% leaves. Seeds and leaves of Caesalpiniaceae comprised 46% of the diet (Brugière *et al.* 2002). At Lopé Reserve, diet of *C. nictitans* in a continuous forest differed from that in neighbouring forest fragments by more fruit eating (59% vs. 44%) and seed eating (11% vs. 4%) and by less insect eating (3% vs. 24%; Tutin *et al.* 1997a, b). Forages in groups or in polyspecific associations. Most active in early morning and late afternoon. Home-range size ca. 55–100 ha; daily range ca. 1500 m (Gautier-Hion 1988).

Social and Reproductive Behaviour Social. Bisexual groups contain only one adult ♂ who gives 'pyow' calls, especially at dawn and dusk (Gautier & Gautier-Hion 1977). These loud-calls help to maintain space between groups and rally group members. When two groups are close to each other, 'pyow' calls are accompanied by loud aggressive 'barks'. Territorial conflicts occur. Mean group size varies from 11 individuals at Forêt des Abeilles (8–19, $n = 35$; Brugière *et al.* 2002), to 14.6 individuals at Odzala N. P. (5–27, $n = 61$; Maisels 1995), to 18 individuals at Ngotto Forest, Central African Republic (15–20, $n = 6$; Gautier-Hion 1996). In large groups the number of adult ♀♀ may reach 11. Solitary adult ♂♂ are frequent (up to 28% of encounters during a census).

Cercopithecus n. nictitans is in polyspecific associations with one or more arboreal monkey species 50% of the time on average (30–87% of the time, depending on site). The lowest incidence is at Odzala N. P., which harbours the highest density of *C. n. nictitans*; suggesting that not all groups can find partners with which to associate. The species that associate most frequently with *C. n. nictitans* are *C. cephus* (45% of cases), *C. cephus* + *C. pogonias* (32%), and *C. pogonias* (16%). On Bioko I., *C. n. martini* in association with *C. pogonias*, Red-eared Monkey *Cercopithecus erythrotis*, Black Colobus *Colobus satanas* and Pennant's Red Colobus *Procolobus pennantii* (Butynski & Koster 1994, T. Butynski pers. comm.).

In tri-specific associations that include *C. pogonias* + *C. cephus*, the adult ♂ *C. n. nictitans* generally gives his 'pyow' calls after the 'boom' calls of the adult ♂ *C. pogonias*. This is true for the call sequences given ritually at dawn, during which the adult ♂ *nictitans* called after the adult ♂ *pogonias* in 77% of cases, as well as when the mixed group faced an avian predator (adult ♂ *nictitans* called first in 11% of cases) or a climbing predator (adult ♂ *nictitans* called first in 8% of cases). These figures suggest reduced vigilance by the adult ♂ *nictitans*. The adult ♂ *nictitans* called first mostly after violent, loud, perturbations such as a tree fall or a rumble of thunder (Gautier & Gautier-Hion 1983, Gautier-Hion *et al.* 1983). When in polyspecific association, the adult ♂ *nictitans* may actively pursue African Crowned Eagles *Stephanoaetus coronatus* even when the eagles' attack was on a monkey of another species (Gautier-Hion & Tutin 1988).

Cercopithecus n. nictitans in Gabon gives the boom call. The boom of *C. nictitans* is weaker and lower-pitched (112 Hz) than the boom of De Brazza's Monkey *Cercopithecus neglectus* or Crowned Monkey

Cercopithecus pogonias (150 Hz). In this regard, the boom of *C. n. nictitans* is similar to that of the Gentle Monkey *Cercopithecus mitis* (Gautier 1973, J.-P. Gautier pers. comm.). A particularly interesting question is, does *C. nictitans* give the boom over its entire geographic range? The opinion of T. Butynski (pers. comm.) is that *C. n. martini* on Bioko does not give the boom, or else gives this call so infrequently that it has not, as yet, been detected by researchers. *Cercopithecus n. martini* is a common monkey in Korup N. P., but J. Linder has not heard this species give the boom there, nor has J. Oates heard this call from *C. n. martini* in the Cross R. forests of Nigeria. Struhsaker (1970) makes no mention of the boom call for *C. n. martini* in Cameroon. In Gashaka Gumti N. P., NE Nigeria, *C. n. martini* does give the boom, but much less frequently relative to Campbell's Monkey *Cercopithecus campbelli* (K. Arnold pers. comm.).

Reproduction and Population Structure *Cercopithecus nictitans* reproduces seasonally in synchrony with other cercopithecines (Gautier-Hion 1968, Butynski 1988). Mating takes place in the main dry season (most often Jul–Aug) and births peak around the short dry season (Dec–Feb). Sexual maturity is reached around six years for ♂♂ and four years for ♀♀. Gestation length is about 5.5 months (Gautier-Hion & Gautier 1976). The single infant weighs about 350 g (Gautier-Hion 1968). Structure of 36 groups in Odzala N. P. averaged 8% adult ♂♂, 35% adult ♀♀, 20% subadults, 24% juveniles and 14% infants (Maisels 1995). Solitaries account for about 9% of a population in C Gabon (Brugière *et al.* 2002).

Predators, Parasites and Diseases Leopard *Panthera pardus* is a predator of *C. nictitans* (Henschel *et al.* 2005, 2011). Humans are the most frequent predators of *C. nictitans* on Bioko I. where *S. coronatus*, Leopards and Golden Cats *Profelus aurata* are absent (Struhsaker 2000a, T. Butynski pers. comm.). No information on diseases and parasites.

Conservation IUCN Category (2012): *C. nictitans* is Least Concern, whereas *C. n. martini* is Vulnerable. CITES (2012): Appendix II.

Among arboreal monkeys, *C. nictitans* may be the most tolerant of heavy hunting pressure, but near villages, this species is often decimated by hunting (Linder & Oates 2011). There remain large, dense populations in several places. There is particular concern for *C. n. martini* (including *stampflii*) as this subspecies has a relatively small, highly fragmented range and is heavily hunted both on the mainland (Oates *et al.* 2004) and on Bioko I. (Hearn *et al.* 2006). On Bioko I.

(2017 km²), hunting with shotguns is the only threat to *C. n. martini*. The price paid per carcass in 2005 was ca. US\$31. This is possibly the least common monkey on Bioko I. and is unlikely to number >1000 individuals (Hearn *et al.* 2006). Forest clearance also threatens this species, which prefers primary lowland forest. Protection of the population in the Gran Caldera & Southern Highlands Scientific Reserve (510 km²) is critical to the long-term conservation of this monkey on Bioko (Hearn *et al.* 2006).

Measurements

Cercopithecus nictitans

Cercopithecus n. nictitans

HB (♂♂): 550 mm, n = 9

HB (♀♀): 435 mm, n = 3

T (♂♂): 910 mm, n = 9

T (♀♀): 765 mm, n = 3

HF: n. d.

E: n. d.

WT (♂♂): 6.7 (3.5–9.8) kg, n = 56

WT (♀♀): 4.1 (2.7–6.1) kg, n = 48

Makokou area, NE Gabon (Gautier-Hion *et al.* 1999); ranges not available for linear measurements

Cercopithecus n. martini

HB (♂♂): 485 (420–570) mm, n = 14

HB (♀♀): 439 (400–500) mm, n = 20

T (♂♂): 740 (700–790) mm, n = 13

T (♀♀): 648 (558–700) mm, n = 19

HF (♂♂): 139 (130–150) mm, n = 14

HF (♀♀): 125 (112–132) mm, n = 18

E (♂♂): 30 (28–35) mm, n = 15

E (♀♀): 29 (26–32) mm, n = 20

WT (♂♂): 5.1 (4.0–6.0) kg, n = 14

WT (♀♀): 4.1 (3.0–5.6) kg, n = 20

Upper canine (♂♂): 16 (12–20) mm, n = 13

Upper canine (♀♀): 9 (6–12) mm, n = 16

Lower canine (♂♂): 11 (10–12) mm, n = 13

Lower canine (♀♀): 6 (4–10) mm, n = 18

Bioko I., Equatorial Guinea (Butynski *et al.* 2009)

Key References Gautier-Hion 1980; Gautier-Hion *et al.* 1983; Oates 1988b, 2011; Tutin *et al.* 1997b.

Annie Gautier-Hion



Adult female Putty-nosed Monkey
Cercopithecus nictitans presenting
genitalia during oestrus.

Cercopithecus mitis GENTLE MONKEY (DIADEMED MONKEY, BLUE MONKEY, SYKES'S MONKEY)

Fr. Cercopithèque à diadème; Ger. Diademmeerkatze

Cercopithecus mitis Wolf, 1822. Abbild. Beschreib. Merkw. Naturgesch. Gegenstandes 2: 145. Angola (holotype a menagerie animal and not in existence).



Golden Monkey *Cercopithecus mitis kandti* adult male.

Taxonomy Polytypic species. Several classifications place *Cercopithecus mitis* and *Cercopithecus nictitans* in the *Cercopithecus* (*nictitans*) Group or Superspecies (Hill 1966, Dandelot 1974, Lernould 1988, Kingdon 1997, Grubb *et al.* 2003). See *Cercopithecus* (*nictitans*) Group profile. This classification is supported by DNA analysis (Van der Kuyl *et al.* 1995, Tosi *et al.* 2005), vocalizations (Gautier 1989a), facial pattern (Kingdon 1980, 1988b, 1997), proteins (Ruvolo 1988), chromosomes (Sineo 1990), and external morphology and distribution patterns (Hill 1966). A recent molecular study recognizes *C. nictitans*, *C. mitis* and *C. albogularis* as a single genetic entity (Tosi *et al.* 2005). This profile deals with the Gentle Monkeys *C. mitis/albogularis* Subgroup of the *C. (nictitans)* Group.

Highly polytypic species (Kuhn 1967, Rahm 1970, Groves 1993) within which Grubb *et al.* (2003) recognize 16 subspecies. Two species, Blue Monkey *C. mitis* and Sykes's Monkey *C. albogularis*, have been widely recognized (Hill 1966, Dandelot 1974, Napier 1981, Lernould 1988). Groves (2001) recognizes four species in the *C. mitis/albogularis* Subgroup; *C. mitis*, *C. albogularis*, Silver Monkey *C. doggetti* and Golden Monkey *C. kandti*. The great variability in this taxon and its disputed taxonomy is indicated by the use of non-traditional nomenclature in previous classifications including

'subspecies-groups' (Napier 1981), 'clusters' (Kingdon 1997), 'sections' (Grubb 2001, Grubb *et al.* 2003), 'species-groups' and 'species-subgroups' (Grubb *et al.* 2003).

In the *C. (nictitans)* Group profile presented above, Kingdon presents a taxonomy that recognizes 18 forms of Gentle Monkeys in six 'clusters'. Here we recognize 17 subspecies in five sections in two clusters. The difference is that Kingdon recognizes *maesi*. Both of these taxonomies are similar to Grubb *et al.* (2003) except that Grubb *et al.* (2003) do not recognize *maesi* or *zammarnoi*. The five sections put forth here follow Grubb *et al.* (2003).

Hybridization between Red-tailed Monkey *Cercopithecus ascanius* and *C. mitis* occurs in East Africa at several sites (Aldrich-Blake 1968, Struhsaker *et al.* 1988, Detwiler 2002, Detwiler *et al.* 2005). There are also three instances of a inter-generic hybridization between *C. mitis* and Vervet *Chlorocebus pygerythrus* in Kenya (De Jong & Butynski 2010b). Several authors report intra-specific hybridization in *C. mitis*. Individuals showing intermediate pelage patterns reported by Rahm (1970), Colyn (1988, 1991) and Twinomugisha *et al.* (2003) – *C. m. doggetti* × *C. m. kandti*, *C. m. stuhlmanni* × *C. m. schoutedeni*, *C. m. opisthostictus* × *C. m. stuhlmanni*, *C. m. heymansi* × *C. m. opisthostictus*, *C. m. stuhlmanni* × *C. m. kandti* and *C. m. doggetti* × *C. m. stuhlmanni*. Booth (1968) noted a hybrid swarm (*C. m. stuhlmanni* × *C. m. albogularis*) in the Ngorongoro–L. Manyara area of N Tanzania.

Synonyms: *albogularis*, *albotorquatus*, *beirensis*, *boutourlinii*, *carruthersi*, *chimango*, *diadematus*, *dilophos*, *doggetti*, *elgonis*, *erythrarchus*, *francescae*, *heymansi*, *hindei*, *insignis*, *kanti*, *kibonotensis*, *kima*, *kolbi*, *labiatus*, *leucampyx*, *maesi*, *maritima*, *mauae*, *moloneyi*, *monoides*, *mossambicus*, *neumanni*, *nigrigenis*, *nubilis*, *nyasae*, *omensis*, *opisthostictus*, *otoleucus*, *phylax*, *pluto*, *princeps*, *rufilatus*, *rufotinctus*, *samango*, *schoutedeni*, *schubotzi*, *schwarzi*, *sibatoi*, *stairsi*, *stevensoni*, *stuhlmanni*, *zammarnoi* (Groves 2001, 2005c, Grubb *et al.* 2003).

Chromosome number in *C. mitis* (including *C. albogularis*): 2n = 72 (Chiarelli 1962b, 1968a, b, Bender & Chu 1963, Sineo 1990, Hirai *et al.* 2000, Moulin *et al.* 2008). Dutrillaux *et al.* (1980) report 2n = 70 for a captive hybrid *C. m. opisthostictus* × *C. m. stuhlmanni* and a *C. m. opisthostictus* ♀.

Description A moderately large, long-tailed arboreal monkey. Face dark with backward- and downward-directed whiskers and often with oval-shaped cheeks giving face a round appearance. Lacks a beard. Forelimbs, hands, feet and distal half of tail black or blackish. Saddle and shoulders variously coloured from dark grey to grey suffused with green, yellow or orange. Shoulder/saddle hair can be long, giving appearance of a mantle. Ventrums black or grey to white. Sexes alike in colouration but adult ♀ smaller than adult ♂, weighing ca. 60% as much. Adult ♂ has a more prognathous jaw and larger canines than adult ♀. Newborns black/brown, without grizzled pelage; sometimes with faint diadem.

General descriptions of this species are here divided into two clusters: one of eight subspecies found north and west of the Eastern

Rift Valley, and one of nine subspecies found east and south of the Eastern Rift Valley.

Northern and Western Cluster: West of the Eastern Rift Valley in SW Ethiopia, S Sudan, Uganda, W Kenya, DR Congo, Zambia and Angola, includes subspecies *boutourlinii*, *doggetti*, *heymansi*, *kandti*, *mitis*, *opisthostictus*, *schoutedeni* and *stuhlmanni*. Pale brow-band (diadem) contrasting in colour with dark crown, except in *opisthostictus*; cheeks rounded, speckled; chin pale; ear-tufts white. Crown and neck dark grey or black. Back dark, usually grey or greenish, except in *kandti*; black band across shoulders.

Southern and Eastern Cluster: East of the Eastern Rift Valley from SE Somalia to the Eastern Cape Province in South Africa, includes subspecies *albogularis*, *albotorquatus*, *erythrarchus*, *francescae*, *kolbi*, *labiatus*, *moloneyi*, *monoides* and *zammaranoi*. Diadem not distinct; ear-tufts white, buff, or red; brow hairs long, speckled, stiff and projecting forward; chin and cheeks white; throat-patch pale and forms partial neck collar in northern forms. Back grey, yellowish-grey, or dark olive, in some shows gradual increase in yellow or red from the shoulders to back of rump; shoulders same colour as crown and without black band. Ventrums light. Undersurface of tail base with orange, red or brown hairs, except in *labiatus*. Photographs of several of these subspecies are available at: www.wildsolutions.nl

Geographic Variation

South and East

Cercopithecus mitis albogularis Section:

- C. m. zammaranoi* Zammarano's Monkey. S Somalia, along course of Jubba R. and Shabeelle R. Small size; back, shoulders and rump olive-green; ventrum ashy-grey; no rufous tint on inner thighs or lumbar region; limbs dark, almost black; white collar reduced compared with nearby *albotorquatus*.
- C. m. albotorquatus* Pousargues's Monkey. Extreme S Somalia, Pate I., and middle and lower course of Tana R., Kenya. Diadem and crown dark olive; throat and (near complete) neck collar white. Back and shoulders dark olive; rump olive, yellowish, or reddish-brown; inner thighs may also be reddish-brown. Ventrums ashy-grey or cream. See De Jong & Butynski (2011) for details. Synonyms: *phylax*, *rufotinctus*.
- C. m. kolbi* Kolb's Monkey. Kenya Highlands east of the Rift Valley. Ear-tufts long, white; collar broad, white, and nearly complete. Back russet, slightly darker than *albogularis*. Ventrums dark. Synonyms: *hindei*, *nubilus*.
- C. m. albogularis* Zanzibar Sykes's Monkey. SE Kenya, Zanzibar I., Mt Kilimanjaro, Mt Meru, NE Tanzania. Head and shoulders grey; ear-tufts small and white; throat white; collar narrow. Rump reddish-yellow. Synonym: *kibonotensis*.
- C. m. monoides* Tanzania Sykes's Monkey. Coastal Tanzania, Mafia I., NE Mozambique. Throat-patch variable in size; crown, cheeks, neck and shoulders yellowish-olive. Back reddish-brown. Ventrums dark slate-grey. Synonym: *rufilatus*.
- C. m. francescae* Red-eared White-collared Monkey. West of L. Malawi, Malawi. Collar short and grey; ear-tufts red. Shoulders dark grey. Back brownish-grey. Ventrums dark grey.
- C. m. moloneyi* Moloney's Monkey. SW Tanzania to northern shore of L. Malawi, Zambia east of Luangwa R., N Malawi. Throat-patch cream. Back with dark red saddle. Sides and thighs light grey. Ventral surface of tail reddish.

C. m. erythrarchus Stairs's Monkey or Samango Monkey. N South Africa (Limpopo Province, N KwaZulu–Natal Province), Mozambique (incl. Bazaruto I.), NE Zimbabwe. Ear-tufts yellowish-white. Back light grey to olive-green, especially on saddle, grizzled. Ventrums whitish or pale grey. Ischial callosities with yellow, orange or red hairs. Tail black. Synonyms: *beirensis*, *mossambicus*, *nyasae*, *schwarzi*, *stairsi*, *stevensoni*.

C. m. labiatus Samango Monkey. Eastern Cape Province to KwaZulu–Natal midlands and southern Mpumalanga Province, South Africa. Crown almost black. Back dark-grey, darkest of all subspecies in the *albogularis* Section. Ventrums pale ashy grey. Tail with dark dorsal band, buff laterally and ventrally; base of tail with no red. Synonym: *samango*.

North and West

Cercopithecus mitis heymansi Section:

- C. m. heymansi* Lomami River Monkey. Between Lualaba R. and Lomami R., DR Congo. Face black; diadem white and narrow; crown, neck and shoulders blue-grey. Ventrums lighter than dorsum.

Cercopithecus mitis mitis Section:

- C. m. opisthostictus* Rump-spotted Monkey. S DR Congo, N Zambia, N Zimbabwe, E Angola. Lips, chin, throat white; diadem grey, speckled; crown like back. Back uniformly olive to light grey; shoulders, neck and ventrum black. Hindlimbs dark but not black.
- C. m. mitis* Angola Pluto Monkey. Coastal Angola. Diadem whitish and conspicuous; nose, lips, chin with short, white hairs; crown, neck, shoulders and hindlimbs black. Back and ventrum dark grey to black. Synonyms: *diadematus*, *dilophos*, *leucampyx*, *nigrigenis*, *pluto*.

Cercopithecus mitis boutourlinii Section:

- C. m. boutourlinii* Boutourlini's Blue Monkey. SW Ethiopia. Diadem not differentiated from crown; lips, chin and throat white. Back dark green or yellowish-grey. Shoulders black with grey speckling. Hindlimbs and ventrum black. Synonym: *omensis*.

Cercopithecus mitis stuhlmanni Section:

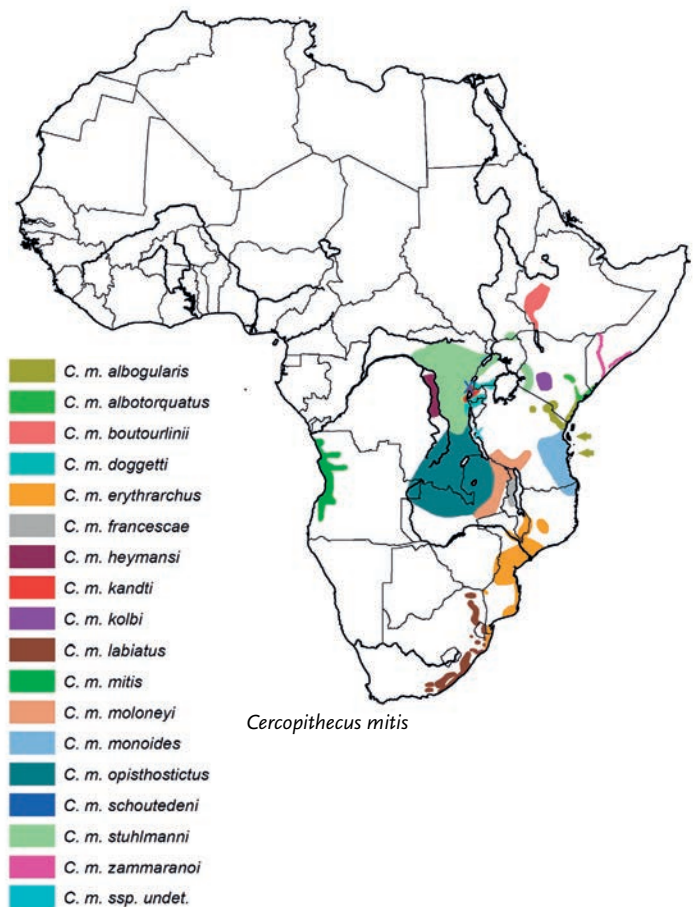
- C. m. stuhlmanni* Stuhlmann's Blue Monkey. NE DR Congo, Uganda, W Kenya, SE Sudan. Chin and throat white; diadem grey; crown and neck black. Back steel blue-grey, but sometimes faintly greenish. Ventrums lighter than dorsum. Synonyms: *carruthersi*, *elgonis*, *maesi*, *mauae*, *neumanni*, *otoleucus*, *princeps*.
- C. m. schoutedeni* Schouteden's Silver Monkey. Idjwi I. in L. Kivu and western Virunga Mts, E DR Congo. Diadem white and speckled; crown and neck black. Back pale olive-grey. Ventrums lighter than dorsum.
- C. m. doggetti* Doggett's Silver Monkey. Burundi, Rwanda, SW Uganda, NW Tanzania, E DR Congo. Crown and neck black, contrasting sharply with diadem. Back light grey-brown. Hindlimbs blackish-grey. Synonym: *sibatoi*.
- C. m. kandti* Golden Monkey. E DR Congo near L. Kivu, Virunga Mts and Nyungwe N. P., SW Rwanda. Diadem dark yellowish-grey; crown and nape black. Back large amount of red or orange, amount of red individually variable; shoulder band narrow. Ventrums rust or orange. Synonym: *insignis*.

Similar Species

Cercopithecus nictitans. Western central Africa and West Africa. Parapatric and, perhaps, narrowly sympatric at eastern edge of geographic range. Nose with large white spot.

Distribution Endemic to Africa south of the Sahara. Rainforest, Afromontane–Afroalpine, Somalia–Masai Bushland, Zambezian Woodland, and Coastal Forest Mosaic BZs. Widespread in all forest types in central, East and southern Africa. Nominal subspecies in extra-limital populations in W Angola. Occurs south of ca. 11°N on the Ethiopian Plateau (*C. m. boutourlinii*; Napier 1981), in SE Sudan (*C. m. stuhlmanni*; Butler 1966), SE Somalia (*C. m. zammaranoi*; Gippoliti 2003), S Somalia and NE Kenya, including Pate I. (*C. m. albotoxatus*; Lernould 1988). *Cercopithecus m. stuhlmanni* east of Congo R. and to west of Eastern Rift Valley in Kenya. *Cercopithecus m. stuhlmanni* common on right bank of Congo/Lualaba River, from Itimbiri R. confluence to ca. 05°S (Colyn 1991). Range of *C. m. heymsi* is known with certainty only from northern part of forest between Lualaba R. and Lomami R. (E DR Congo; Colyn 1988). *Cercopithecus m. opisthostictus* in E Angola along the High Zambezi (Machado & Crawford-Cabral 1999). *Cercopithecus m. stuhlmanni* and *C. m. opisthostictus* in contact and may hybridize north of Lukuga R., E DR Congo (Colyn 1991). *Cercopithecus m. kandti* is restricted to Virunga Mts of SW Uganda, NW Rwanda and E DR Congo (Aveling 1984, Twinomugisha 2000), and possibly Nyungwe N. P., E Rwanda (A. Plumtre & B. Kaplin pers. comm.). Distribution of *C. m. schoutedeni* limited to Idjwi I. in L. Kivu (DR Congo) and small area to north (Lernould 1988). *Cercopithecus m. kolbi* confined to Kenya Highlands (Kingdon 1971, De Jong & Butynski 2009). *Cercopithecus m. monoides* in E Tanzania to the coast and bounded in the north by the Pangani R. and by *C. m. albogularis* whose range extends into SE Kenya (Lernould 1988, De Jong & Butynski 2009). *Cercopithecus m. albogularis* also on Unguja I. (formally Zanzibar). *Cercopithecus m. moloneyi* in vicinity of L. Rukwa, southern L. Tanganyika and NE Zambia (Lernould 1988). In Malawi *C. m. francescae* replaces *C. m. moloneyi* in north from Chombe Mt and is replaced by *C. m. erythrarchus* south of Ntchisi Mt (Ansell & Dowsett 1988). Exact boundary between coastal distributions of *C. m. monoides* and *C. m. erythrarchus* in N Mozambique unknown (Lernould 1988). *Cercopithecus m. erythrarchus* extends down eastern seaboard of southern Africa, including the eastern highlands of Zimbabwe, but not south of Umfolozi R. Remnant population of *C. m. erythrarchus* on Bazaruto I., S Mozambique (Downs & Wirminghaus 1997). Both *C. m. erythrarchus* and *C. m. labiatus* found in South Africa, but latter subspecies confined to higher-altitude forests and coastal forests of afromontane origin to ca. 33°S, Eastern Cape Province (Lawes 1990a).

Habitat In all types of evergreen forest from primary and secondary lowland rainforest, riverine, swamp, gallery, coastal, through montane forest, including bamboo zone, and up to 3800 m on Rwenzori Mts, Uganda (A. Plumtre pers. comm.). Prefers primary forest, but also in secondary forest, logged forest and thicket (Chapman *et al.* 2000, Fashing *et al.* 2012). More tolerant of poor habitat quality than most guenons, accounting for wide African distribution and use of diverse forest types (Lawes 1990a, Thomas 1991). Only forest guenon with an extensive range outside lowland rainforest. Occupies three broad forest types, many subspecies occurring in at least two: (1) afromontane (*stuhlmanni*, *schoutedeni*, *boutourlinii*, *doggetti*, *kandti*, *kolbi*, *francescae*,



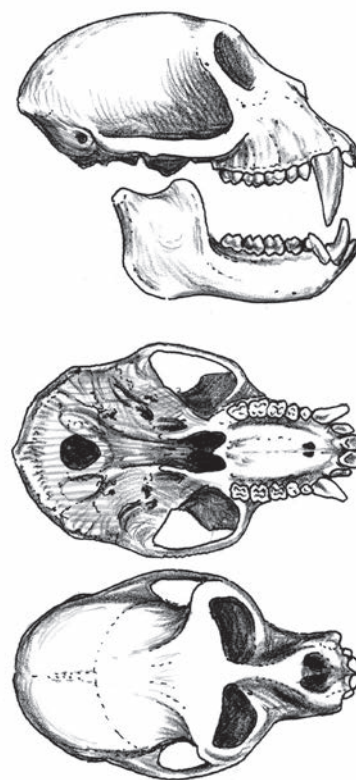
albogularis, *labiatus*); (2) central lowland forests (*stuhlmanni*, *doggetti*, *maesi*, *heymsi*, *opisthostictus*, *moloneyi*, *albogularis*, *mitis*); and (3) Indian Ocean coastal lowland and riparian forests (*zammaranoi*, *albotoxatus*, *albogularis*, *monoides*, *erythrarchus*) (Stott 1960, Butler 1966, Kingdon 1971, Bolton 1973, Colyn 1988, Gippoliti 2003, De Jong & Butynski 2009). *Cercopithecus m. stuhlmanni* is a denizen of larger lowland and montane forests. *Cercopithecus m. kolbi* occupies montane forests of the Kenya Highlands and ventures into pine (*Pinus* spp.) plantations adjacent to forest (De Vos & Omar 1971, Maganga & Wright 1991); it shares this behaviour with *C. m. francescae* and *C. m. labiatus* (Von dem Bussche & Van der Zee 1985, Beeson 1987). *Cercopithecus m. kandti* inhabits montane forests of the Virunga Mts, including the bamboo zone (Aveling 1984). *Cercopithecus m. doggetti* uses mature montane forests, bamboo forest, and papyrus swamps in marshy lowlands, but is more common in moist valley and riverine forest (*Macaranga* spp.) (Kaplin 2001). *Cercopithecus m. albotoxatus* in riparian forest patches along the middle and lower Tana R. and in coastal forests north of the Tana Delta (Butynski & Mwangi 1994). Subspecies in coastal lowland forest use coastal thicket where it is adjacent to high forest. *Cercopithecus m. erythrarchus* in a variety of forest types from coastal lowland forest and thicket, to riverine, swamp, deciduous dry and coastal dune forest on the mainland (Lawes 1992), and in low-quality swamp forest and mixed woodland on Bazaruto I. (Downs & Wirminghaus 1997). *Cercopithecus m. labiatus* in afromontane forests only (Lawes 1990a).

Abundance A shy and sometimes difficult species to observe, but nevertheless common throughout the geographic range. Can be a pest around lodges, human habitation and gardens (Chapman *et al.*

1998). Occurs at moderate density – 0.7 ind/ha (0.05–2.0) or 4.3 groups/km² (0.4–9.0) – over most of its range (Aldrich-Blake 1970, Moreno-Black & Maples 1977, Rudran 1978b, Schlichte 1978, Scorer 1980, Rodgers & Homewood 1982, Van der Zee & Viljoen 1984, Butynski 1990, Lawes *et al.* 1990, Thomas 1991, Cordeiro 1992, Kaplin & Moermond 1998, Kaplin 2001). At 1.2 ind/ha in gallery forest along the Tana R., Kenya (Butynski & Mwangi 1994). At greatest density in montane forests of East and central Africa (1.2–2.2 ind/ha; De Vos & Omar 1971, Beeson 1987, Cords 1987b, Fashing & Cords 2000, Twinomugisha 2000, Cords & Chowdhury 2010), and coastal forests of S Mozambique and Maputaland (>2.0 ind/ha; KwaZulu–Natal; Lawes 1992). At these localities *C. mitis* is usually the only resident guenon species. Low-density populations (<0.3 ind/ha) inhabit deciduous dry sand forests and riverine forests in southern Africa (Lawes 1992). Low-density populations (<0.2 ind/ha) also found in secondary forest in the Ituri Forest (DR Congo) (Thomas 1991). Abundance varies within the same forest over space and time. For example, in Kibale N. P., Uganda, there is more than a ten-fold difference in density between the Kanyawara population (0.65 ind/ha) and the Ngogo population (0.05 ind/ha; Butynski 1990). Abundance may be reduced by forest disturbance, at least partly because of effect on food supply. Abundance data lacking for populations in Ethiopia, along most of the eastern seaboard and for mountains of E Tanzania.

Adaptations Flexible dietary and habitat preferences make *C. mitis* a versatile and widely distributed species. Occasionally comes to the ground, but shares adaptations for arboreal life with other strictly arboreal primates – grasping hands, long tail for balance, and relatively short stocky forelimbs and long slender hindlimbs for jumping and bracing movement in forest canopy. An adult ♂ *C. m. stuhlmanni* at Governors' Camp, Mara, S Kenya, frequently swam ('dog paddled') ca. 25 m across the Mara R. (D. Richards pers. comm. to T. Butynski). Similarly, an adult *C. m. albitorquatus* seen swimming a ca. 35 m-wide channel in the Tana Delta, Kenya (Q. Luke pers. comm. to T. Butynski).

Can ferment foods in both the foregut and hindgut allowing considerable dietary flexibility. Possesses large caecum and colon in hindgut (Bruerton & Perrin 1988, 1991). Haustrum-like sacculations in caecum provide microhabitats for numerous symbiotic bacteria (Bruerton *et al.* 1991). Food can be directed into caecum via muscular valve (Bruerton & Perrin 1988) or allowed to pass by into colon. Slowed passage rate of food in caecum allows microbial fermentation, which facilitates digestion of fibrous foods like leaves (Bruerton & Perrin 1988, Bruerton *et al.* 1991). Foregut (stomach) digestion of fruits and hindgut (caecum and colon) fermentation of leaves allow a broad diet. No other cercopithecoid monkey, with possible exception of Allen's Swamp Monkey *Allenopithecus nigroviridis*, which shows signs of incipient sacculization of the stomach (Hill 1966), has similar gut adaptations. Capacity for folivory is one reason *C. mitis* copes better in secondary and/or logged forest than other guenon species (Rudran 1978a, Struhsaker 1978a, Thomas 1991). Like other Cercopithecidae, *C. mitis* uses cheek pouches for temporarily storing food, especially fruits. Activity is related to ambient temperature. Sunning behaviour common when cold – early mornings, after rainstorms and at higher altitudes. Less active when it is warmer, leading to a diurnal activity cycle with periods of rest most common at midday, especially on sunny, hot, days. Populations that include



Lateral, palatal and dorsal views of skull of Samango Monkey *Cercopithecus mitis labiatus*.

much low-quality food in the diet spend more time resting, probably to facilitate caecal fermentation of food (Lawes & Piper 1992).

Vocalizations, especially low frequency booms by adult ♂♂, involve large bilobed laryngeal air sacs that develop at puberty. This species is more sensitive than humans to both low (125–250 Hz) and high (8–16 kHz) frequencies, which correspond with some of their vocalizations (Brown & Waser 1984).

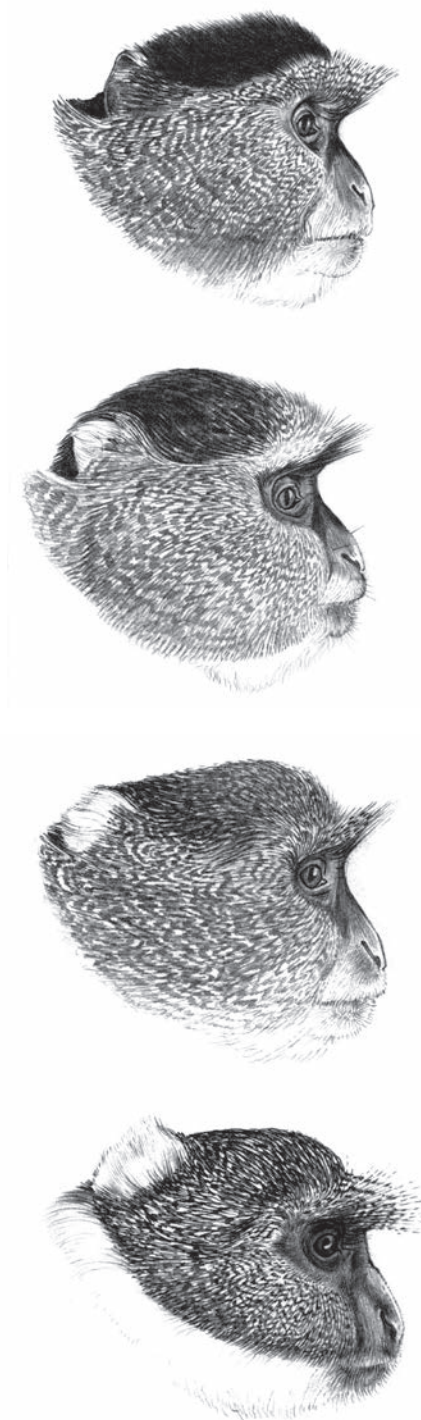
Foraging and Food Omnivore. Feeds primarily on fruit (ca. 40% of diet) (Cords 1987b, Butynski 1990, Lawes 1991) but much time spent foraging for invertebrates. Has most general diet of the guenons; includes fruit, leaves, flowers, stems, galls, bark, gum, fungi, invertebrates and occasionally small vertebrates (Butynski 1982c). Prefers ripe over unripe fruit and fleshy fruits over seeds (Lawes 1991, Kaplin & Moermond 1998, Kaplin *et al.* 1998). Targets fruit rich in sugars. Favours fig (*Ficus*) trees and follows seasonal fruit availability and distribution in the home-range. Includes more leaf material in diet than most guenon species (15–52%) (Cords 1987b), particularly during periods of fruit shortage, or where there are low densities of fruiting tree species (Beeson 1987, Lawes 1991, Twinomugisha 2000). *Cercopithecus m. francescae* (Zomba Plateau, Malawi) can survive on little or no fruit for months by eating leaves (52% of diet) (Beeson 1989). In Virunga Mts *C. m. kandti* subsists on bamboo *Sinarundinaria alpina* shoots, young culms and young leaves, combining this with fruits from tree species common in the bamboo zone (Twinomugisha 2000). Prefers young leaves and new shoots to mature leaves, as well as leaves low in fibre and high in protein (Lawes 1991). Although a large number of plant species may be included in the annual diet (from 57 at Cape Vidal, South Africa, to 104 at Kakamega, Kenya), on average 64% (44–94%) of monthly plant diet

derives from as few as five plant species or ten species-specific food items (Rudran 1978a, Cords 1986, Lawes 1991). Overlap in use of specific food items between consecutive months is ca. 40% on average (Rudran 1978a, Cords 1986, Beeson 1989, Lawes 1991), but may be as low as 25% (Lawes 1991) and as much as 99% between months (Beeson 1989). Adult ♂♂ include more fruit (ca. 60%) in their diet than ♀♀ (ca. 47%) or subadults (ca. 34–59%). Females and subadults have similar diets although subadults may eat fewer leaves and more insects (Rudran 1978b, Cords 1986, Lawes 1990b).

Insects and other animal prey provide a more readily digestible source of protein than leaves. Insects can form a large part of the diet (30–45%; Butynski 1990) but mostly comprise 5–20% of the diet (Rudran 1978b, Schlichte 1978, Beeson 1987, Cords 1987b, Lawes 1991, Beeson *et al.* 1996, Kaplin & Moermond 1998, Kaplin *et al.* 1998, Kaplin 2001). Populations that eat large amounts of insects often eat proportionally less leaves and vice versa (Beeson 1987, Kaplin *et al.* 1998, Twinomugisha 2000). In seasonal forests, such as those in southern Africa, insects are less abundant during winter (May–August); here *C. mitis* includes slightly more leaves and flowers in the diet than most other populations (Lawes 1991). Capable of catching and eating other animal prey and occasionally known to eat birds' eggs (Wahome *et al.* 1988), birds (Rudran 1978b, Cordeiro 1994), reptiles (small snakes and lizards, Wahome *et al.* 1988), small mammals such as bats (M. Cords pers. obs.), rodents (Wahome *et al.* 1988), squirrels (Mizuno *et al.* 1976, M. Cords pers. obs.) and even galagos (Butynski 1982a). Meat-eating is coincident with periods when fruit and young leaves are scarce (Butynski 1982a, Wahome *et al.* 1988). 'Wadging', the intermixing and chewing of leaves with meat, is reported for *C. mitis*, the only primate other than the Robust Chimpanzee *Pan troglodytes* that is known to do this (Butynski 1982a). As for other species of guenons, there is no evidence of cooperative hunting tactics, or meat-sharing behaviour, and vertebrate prey are opportunistically gathered (Butynski 1982c).

Feeding is usually concentrated in early morning, mid- to late-morning and the last hours of the day (Lawes & Piper 1992). The inbetween periods are spent resting and on social activities such as grooming. Group movements are coordinated and begin with directed movements of a few individuals, usually adult ♀♀, who are followed by the rest of the group. Group members may occupy several trees while feeding. Day range length is ca. 500–1900 m and averages 1100 m/day (Aldrich-Blake 1970, Rudran 1978a, Schlichte 1978, Beeson 1987, Cords 1987b, Butynski 1990, Lawes 1990b). A relatively small area (ca. 25%) of the home-range is used on any day, and consecutive daily ranges are often mutually exclusive (Rudran 1978b, Schlichte 1978, Cords 1987b, Butynski 1990, Lawes 1990b). Some *C. mitis* populations show a tendency to split into smaller satellite groups of 4–5 individuals during daily movement (Aldrich-Blake 1970, McMahon 1977, Moreno-Black & Maples 1977, Van der Zee & Viljoen 1984). This behaviour may be especially common for larger groups (M. Cords pers. obs.).

Foraging behaviour differs among sites and between seasons, depending on food availability. *Cercopithecus mitis* move more systematically about their home-range when fruit is scarce, ranging widely over a period of days, and selecting the most nutritious items from a broader spectrum of lower-quality foods such as mature leaves (Schlichte 1978, Scorer 1980, Beeson 1989). They may also travel longer distances to reach pockets of food outside their usual range (Omar & de Vos 1970, Schlichte 1978, Scorer 1980), such as young pine trees (from which they eat the cambium; Von dem Bussche & Van



Four subspecies of Gentle Monkeys *Cercopithecus mitis*.

Top to bottom: Doggett's Silver Monkey Cercopithecus mitis doggetti.

Moloney's Monkey Cercopithecus mitis moloneyi. Tanzanian Sykes's Monkey Cercopithecus mitis monoides. Kolb's Monkey Cercopithecus mitis kolbi.

der Zee 1985, Beeson 1987), flowering Black Wattle *Acacia mearnsii* plantations, or isolated fig trees. When fruit availability is low, but not critically so, they range less widely, have a clumped pattern of range use, use all available foods and have a diverse diet (Rudran 1978a, Butynski 1990, Lawes *et al.* 1990). If fruit is abundant they range widely, returning to favoured food species on consecutive days and/or sleep nearby to feed in a favoured tree in the morning. They are

fairly selective of items and have a less diverse diet than when fruit is less available (Rudran 1978b, Cords 1987b, Butynski 1990, Lawes *et al.* 1990). Where there is a marked seasonal difference in food availability (e.g. L. Kivu, DR Congo – *C. m. maesi*, Schlichte 1978; Zomba Plateau, Malawi – *C. m. francescae*, Beeson 1989) they range less widely when food is most abundant and day-range area decreases.

Social and Reproductive Behaviour Adult ♀♀ and young in permanent groups whose members are typically dispersed <100 m in daylight hours. Large groups may spread 200–300 m. At night individuals huddle in subgroups of 2–4, and groups are more cohesive. Typically, one resident ♂ accompanies each group, though influxes of ♂♂ occur regularly during the breeding season in some populations (Henzi & Lawes 1987), with individual ♂♂ shadowing or joining groups for periods of several hours to several months (Cords 2000c). Non-resident adult ♂♂ may be solitary, or form loose all-male associations (2–12 members) with flexible membership, especially in dense populations (Cords 2000c, Macleod 2000). Females are strictly philopatric (Cords & Chowdhury 2010). Subadult ♂♂ invariably transfer from natal group, but emigration is not closely tied to aggression from the resident ♂ (Ekernas & Cords 2007).

Group size is typically 10–25 individuals (mean 18, 3–65; Butynski 1990, Lawes 1992, M. Cords pers. obs.). Groups typically ca. 40% (31–75%) adult ♀♀ and 55% (21–69%) immatures. Adult to young ratio in heterosexual groups highly variable (range 0.33–2.60, median 0.82 across six populations). Group fission occurs when groups become larger than population norm. Resulting sister-groups divide original range, and develop antagonistic relations within one month after the fission (Cords & Rowell 1986). Group ♀♀ observed to cooperate to kill an unfamiliar adult *C. mitis* ♀ that entered their territory (Payne *et al.* 2003b).

Except for play, which occurs almost exclusively among immatures, most amicable interactions involve adult ♀♀. Allogrooming is the most frequent, occurring on average once per two hours, and accounting for 5–10% of daylight hours (Lawes & Piper 1992, Cords 2000a, Payne *et al.* 2003a). Adult ♀♀ do not groom all group members, nor do they groom their 'grooming partners' equitably (Cords 2000a, Payne *et al.* 2003b). Mothers groom their own offspring more often than they groom other juveniles (Cords 2000b). Adult ♀♀ frequently groom each other reciprocally. Group ♂ groomed more than he grooms in return. In some, but not all, populations grooming distributions among ♀♀ are rank-related, although grooming is not necessarily exchanged for feeding tolerance (Payne *et al.* 2003a, but see Cords 2000a). Nose-to-mouth sniffs, brief touches and coalition formation are rarer forms of amicable behaviour among ♀♀ and immatures. Direct amicable interactions (grooming, mounting) among adult ♂♂ are rare, especially in the proximity of ♀♀.

Aggressive behaviour includes chases, slaps, grappling fights, bites and threats such as head-bobbing, glaring, bounding displays in branches, and growling. Submissive behaviour includes flight, cowering, presenting the hindquarters and vocalizations like geckering, trilling and screaming. Aggression is rare among adult ♀♀, occurring once per 2.2 hours on average in a group (Cords 2000a, Payne *et al.* 2003a). Half of agonistic encounters involve aggressive behaviours; most of the remaining cases are approach–retreat interactions, with some spontaneous submission. Most within-group aggression is associated with fruit feeding (Rudran 1978b, Payne 1999, Cords

2000a, Pazol & Cords 2005). Adult ♀♀ can be arranged in shallow but stable dominance hierarchies but the advantages of high rank remain obscure (Pazol & Cords 2005). Aggression among ♂♂ is especially common during the mating season. Chases, ambushes and fights occur especially often during multimale influxes; resident ♂♂ usually prevail against visitors in such interactions.

In most populations, groups are territorial in the sense of defending a specific area (typical home-range about 15–25 ha, range 8–253 ha), even though range overlap with neighbouring groups may be extensive (98%) in high-density populations (Lawes & Henzi 1995), or minimal (<1%) in low-density populations (Butynski 1990). Boundary disputes involve mainly ♀♀ and may last up to an hour, with opposing phalanxes advancing and retreating with aggressive growls and chirps; physical fights are rare. Adult ♂♂ typically watch and vocalize (boom), and are seldom involved in aggression outside the mating season. Juvenile ♂♂ may take these opportunities to play with peers in other groups. Aggressive inter-group encounters often end with a frenzy of intra-group grooming (Cords 2002a, Payne *et al.* 2003a).

Both ♂♂ and ♀♀ may solicit copulations. Males head-flag ♀♀. Females head-flag, present and pucker to ♂♂. Persistent following is typical of courtship. Males may threaten ♀♀ who follow too persistently. Copulations may involve multiple mounts, especially when harassed by juveniles (mostly ♂♂). Older juvenile ♂♂ often shadow group's resident ♂. Ejaculatory pause is more likely if ♀♀ initiate the copulation (Cords *et al.* 1986).

Vocal repertoire includes at least ten calls (Marler 1973, Gautier 1988, Brown 1989b, Grant 1992). Only adult ♂♂ give loud-calls, including resonant 'booms' (100–150 Hz, 88 db at 2 m). 'Booms' given in response to various sources of disturbance (other ♂♂, other groups, falling branches and trees, thunder claps), also in response to prolonged (particularly loud and strained) adult ♀♀ grunts and immature trills, and sometimes for no discernible reason. Usually only one boom is given, but one group adult ♂ in Kibale N. P. typically gave a series of two booms separated by ca. 5 sec (T. Butynski pers. comm.). Only adult ♂♂ give sharp hacking 'pyows' (125–400 Hz, 100 db at 2 m). Pyows are usually given in a staccato sequence typically with 3–7 'pyows' spaced 6–10 seconds apart (Brown 1989b, Grant 1992), given as intra-group rallying call and during inter-group encounters; and 'ka'-train (a 1–5 sec series of 5–10 low frequency, resounding 'ka's, sometimes beginning with a single 'pyow'), given most often in alarm to raptors. The 'ka' and 'pyow' calls are occasionally given singly. While all three loud-calls carry over several hundred metres, only 'ka'-trains and 'pyows' are easy to locate. 'Pyows' can be heard by the human ear to at least 1 km. 'Pyow's, and possibly booms, are individually distinctive (Butynski *et al.* 1992, M. Cords pers. obs.). Adult ♂♂ also emit distinctive nasal screams when losing a fight against another ♂ ('waa!' call of Marler 1973). Females and juveniles give a harsh, rapid 'ah-ah' or a bird-like chirp or click when alarmed by predators or aroused at members of other groups, 'growl' as a threat to conspecifics, and 'gecker' to indicate submission to group mates. In *C. m. stuhlmanni* 'trills' also indicate submission, and may grade into 'screams' (M. Cords pers. obs.). Subadults and adult ♀♀ emit 'grunts', as contact calls (Marler 1973). In *C. m. labiatus/erythrarchus*, trills and grunts both appear to function as contact calls, with grunts less frequent and more likely to occur in times of tension (M. Lawes pers. obs.).

Relations with sympatric primate species vary from wary avoidance (of baboons *Papio* spp. and Robust Chimpanzees), to

occasional association (with Guerezas *Colobus guereza*, Eastern Gorillas *Gorilla beringei*, drill-mangabeys *Cercocebus* spp., baboon-mangabeys *Lophocebus* spp., red colobus monkeys *Procolobus* spp., savanna monkeys *Chlorocebus* spp., De Brazza's Monkey *Cercopithecus neglectus* and L'Hoest's Monkeys *Allochrocebus lhoesti*) (T. Butynski pers. comm.) to long-lasting (up to 12 h), coordinated association (with Red-tailed Monkeys *Cercopithecus ascanius*; Cords 1987b). Most inter-specific aggressive interactions involve only a few individuals, with outcomes determined by relative body size. Associations with *C. ascanius* involve entire groups of each species. Some associations appear random, while others result in improved protection from predation and more efficient foraging for shared foods (Cords 1987b). In associated groups, *C. ascanius* ♂♂ interpose 'hacks' (also termed 'pops') between *C. mitis* 'pyows'. Direct behavioural interaction includes mostly aggression, but juveniles also play. Some associations involve an adult ♂ from one species joining a heterosexual group of the other. Such ♂♂ often solicit grooming from heterospecific ♀♀, and in several populations are known to breed with them, producing fertile hybrids (Detwiler 2002, 2010, De Jong & Butynski 2010b). *Cercopithecus mitis* respond to alarm calls of non-primate vertebrates, such as antelopes, squirrels and birds.

Reproduction and Population Structure In captivity, mean ovarian cycle is 32 days (18–50 days, five ♀♀, $n = 59$ cycles; Else *et al.* 1985) and median is 30 days (19–57 days, six ♀♀, $n = 72$ cycles; Rowell 1970b). Females usually conceive on first cycle of season, although oestrogen titres and sexual behaviour may be elevated beforehand. Menses is difficult to detect; length averages 5.3 days in captivity (Else *et al.* 1985). Sexual receptivity is not closely tied to ovulation. Oestrus lasts 1–28 days ($n = 58$ periods; Pazol 2003). Gestation is ca. 176 days (95% C. L. = 162 and 190 days, $n = 21$) for wild *C. m. stuhlmanni* ♀♀.

Births occur seasonally from Nov to Mar, although in well-studied equatorial populations births recorded in all months (Butynski 1988). In Kakamega Forest, births occur during all months, but there is a peak during the 3-month period of Jan–Mar (dry season) when 64% of the births occurred. Only 9% of the births occurred during the 5-month period of Jun–Oct (wet season, $n = 347$; Cords & Chowdhury 2010). Late gestation and early lactation correspond with periods of fruit and invertebrate availability. About one-third to half of ♀♀ in a group give birth each year. Inter-birth intervals are typically 24–54 months if the first infant survives, and 14–20 months if the first infant dies (Cords & Rowell 1987, Butynski 1990). Mean inter-birth interval 27.9 months (7.2–81.9, $n = 256$ intervals; Cords & Chowdhury 2010). Occasional twins are born, but both may not survive (M. Cords pers. obs.). Newborns weigh ca. 400 g (Omar & De Vos 1971). Sex ratio at birth 1 : 1, but for breeding adults is biased toward ♀♀. Infant mortality (first 12 months) is typically 18–25% (Butynski 1990, M. Cords pers. obs.), although individual groups may show values three times greater if infanticide is common. In Kakamega Forest, 72% of infants survived to 1 year ($n = 341$; Cords & Chowdhury 2010).

Young infants are carried almost constantly by their mothers for the first two weeks but juvenile or subadult ♀ babysitters may carry infants only 2–3 days old. Contact time between mother and infant drops to 50% at 6–10 weeks, and to <10% by 15–22 weeks. Infants swallow first food from fifth week (Foerster & Cords 2002). Suckling can continue for up to 2.5 years (Macleod 2000). Males have a growth spurt at 6–8

years (Rowell & Richards 1979), at which time they leave the natal group (Ekernas & Cords 2007). Females reach adult size around 6.5 years; mean age at first birth is 7.2 years (4.6–10.8, $n = 66$; M. Cords pers. obs.). In Kakamega Forest, youngest ♀ to give birth was 4.6 years and oldest was ca. 26 years. Many ♀♀ in wild live to 20 years, and some live to >32.5 years (Cords & Chowdhury 2010).

Males compete for mates by taking over groups as sole resident, sneaking copulations when non-resident, or joining a group temporarily during a breeding season multimale influx (Henzi & Lawes 1987, 1988, Cords 1988). Influxes are more likely in populations where ratio of ♂♂ to groups in the population is high and when oestrus is synchronous among group ♀♀ (Henzi & Lawes 1988, Cords 2002b). During influxes, ♂♂ may solicit ♀♀ from the edge of the group with head-flagging and jumping displays; ♀♀ may leave their group for several hours to accompany an influx ♂. Males often show scars and missing or stiff digits from fights during the breeding season. Wounds may sometimes be severe and fatal. Adult ♂♂ probably experience higher age-specific mortality rates than adult ♀♀ (Macleod *et al.* 2002).

Resident ♂ tenure varies from a few months to six years (Butynski 1990, Cords 2002b). New resident ♂♂ are sometimes infanticidal (Butynski 1982b, Macleod *et al.* 2002, Cords & Chowdhury 2010, Cords & Fuller 2010). Infanticide may be thwarted by ♀ counter-aggression. Females show situation-dependent oestrus in response to presence of unfamiliar ♂♂, and may mate before the start of ovulatory cycles associated with the mating season, and even while pregnant (Pazol *et al.* 2002, Pazol 2003). Females return quickly to oestrus after death of an infant, but may not be fertile. Females appear to prefer some ♂♂ to others, and actively pursue them; they can deter unwanted ♂ suitors by sitting down. Oestrous periods are longer during ♂ influxes than when only one ♂ is resident.

Predators, Parasites and Diseases Confirmed predators include Afrian Crowned Eagles *Stephanoaetus coronatus* (van Jaarsveld 1984, Cordeiro 1992, Mitani *et al.* 2001, M. Macleod & H. Payne pers. comm.), Gaboon Vipers *Bitis gabonica* (Foerster 2008), Domestic Dogs *Canis familiaris* (T. Butynski pers. comm.), Golden Cat *Profelis aurata* (J. Rowing in Boy 2003) and Robust Chimpanzees (Hosaka *et al.* 2001). Humans kill *C. mitis* for meat, skins and to protect food and forestry crops (Wolfheim 1983). In undisturbed populations, *S. coronatus* appears to be the most important predator. Predation by Leopards *Panthera pardus* and Golden Cats *Profelis aurata* is likely, and predation by Central African Rock Pythons *Python sebae* and Black Mambas *Dendroapsis polylepis* has been suggested (Foerster 2008). *Cercopithecus mitis* gives alarm calls in responses to various species that resemble their confirmed and suspected predators, but which are unlikely to be dangerous, such as mongooses, medium-large birds that soar (small raptors, hornbills, turacos), African Palm Civets *Nandinia binotata* and Lord Derby's Anomalure *Anomalurus derbianus*. They also respond with alarm to various snakes, such as cobras, mambas and adders, which are potentially dangerous.

Various parasitic infections, confirmed in wild populations, including lice, ticks, gastrointestinal flukes, nematodes (Allen & Lawrence 1936, Else *et al.* 1982, T. Gillespie pers. comm.), protozoa (Freeland 1981, Appleton *et al.* 1994) and a simian immunodeficiency virus (Hirsch *et al.* 1993a). Captive *C. mitis* suffer from hypertension and a condition like human pre-eclampsia (blood poisoning during



Doggett's Silver Monkey *Cercopithecus mitis doggetti*.

pregnancy) (Benirschke & Kaufmann 2000). Infection from wounds is a cause of death, especially for adult ♂♂ who fight over ♀♀.

Conservation IUCN Category (2012): *C. mitis* is Least Concern. The threatened subspecies are *C. m. albоторquatus* (Vulnerable), *C. m. boutourlinii* (Vulnerable), *C. m. kandti* (Endangered), *C. m. labiatus* (Vulnerable), *C. m. schoutedeni* (Critically Endangered) and *C. m. zammaronoi* (Critically Endangered). Both *C. m. francescae* and *C. m. mitis* are Data Deficient. CITES (2012): Appendix II.

Greatest threat is destruction and fragmentation of forest habitat for agriculture. Many larger forests inhabited by *C. mitis* have been extensively logged and are secondary forest. Although this species

tolerates low quality and disturbed habitat better than most monkeys, it nevertheless is at lower densities in these habitats (Skorupa 1986, Johns & Skorupa 1987, Thomas 1991, Lawes 1992, Chapman *et al.* 2000). In spite of wide geographical range, *C. mitis* shows poor local colonizing ability in response to forest fragmentation and seldom occupies small (<50 ha) forest patches (Lawes *et al.* 2000, Chapman *et al.* 2003). Dietary flexibility may allow *C. mitis* to persist in disturbed patches longer than most primates, resulting in reluctance to move and increased vulnerability to local extirpation (Lawes 2002). Given a limited capacity for rescuing isolated populations (Cowlshaw & Dunbar 2000), the rate at which forests are destroyed and fragmented will ultimately determine the status and persistence of *C. mitis*. In some

highly fragmented forest archipelagos (e.g. afromontane forests of KwaZulu–Natal) *mitis* exists as relict non-equilibrium metapopulations in gradual, and probably irreversible, decline (Lawes *et al.* 2000).

Measurements

Cercopithecus mitis

C. m. zammaranoi

HB (♂ ♂): 390, 435 mm, n = 2
T (♂ ♂): 575, 640 mm, n = 2
GLS (♂ ♂): 96 (95–96) mm, n = 3
GWS (♂ ♂): 68 (66–69) mm, n = 3
SE Somalia (de Beaux 1923, 1937, Gippoliti 2003)

C. m. albotorquatus

HB (♂ ♂): 577 (510–620) mm, n = 3
T (♂ ♂): 768 (750–790) mm, n = 3
GLS (♂ ♂): 106, 106 mm, n = 2
GWS (♂ ♂): 70, 70 mm, n = 2
S Somalia (de Beaux 1923, 1937, Gippoliti 2003)

C. m. albogularis

HB (♂ ♂): 521 (463–602) mm, n = 12
HB (♀ ♀): 437 (369–593) mm, n = 22
T (♂ ♂): 795 (690–940) mm, n = 12
T (♀ ♀): 689 (626–798) mm, n = 22
HF (♂ ♂): 149 (92–172) mm, n = 12
HF (♀ ♀): 134 (122–145) mm, n = 22
E (♂ ♂): 44 (33–49) mm, n = 8
E (♀ ♀): 43 (34–50) mm, n = 21
WT (♂ ♂): 5.7 (4.2–7.8) kg, n = 6
WT (♀ ♀): 3.6 (2.3–4.3) kg, n = 15
Kenya, Tanzania (specimens in AMNH)

C. m. erythrarchus

HB (♂ ♂): 555 (445–650) mm, n = 13
HB (♀ ♀): 492 (444–550) mm, n = 10
T (♂ ♂): 726 (601–866) mm, n = 15
T (♀ ♀): 671 (572–850) mm, n = 12
HF (♂ ♂): 154 (140–178) mm, n = 10
HF (♀ ♀): 141 (130–160) mm, n = 11
E (♂ ♂): 39 (35–40) mm, n = 7
E (♀ ♀): 37 (34–43) mm, n = 11
WT (♂ ♂): 6.9 (2.7–10.0) kg, n = 24
WT (♀ ♀): 3.8 (2.6–6.0) kg, n = 38
GLS (♂ ♂): 117 (113–122) mm, n = 5
GLS (♀ ♀): 104 (95–110) mm, n = 3
GWS (♂ ♂): 78 (76–81) mm, n = 5
GWS (♀ ♀): 68 (64–69) mm, n = 3
Malawi (specimens in AMNH), South Africa (Roberts 1931, 1951, Rautenbach 1982, Skinner & Smithers 1990, Taylor 1998, M. Lawes pers. obs.), Mozambique (Pocock 1907), Zimbabwe (Delson *et al.* 2000), throughout range (Hill 1966)

C. m. stuhlmanni

HB (♂ ♂): 532 (410–625) mm, n = 24
HB (♀ ♀): 464 (315–520) mm, n = 18
T (♂ ♂): 961 (820–1090) mm, n = 24

T (♀ ♀): 822 (687–1020) mm, n = 18
HF (♂ ♂): 165 (145–183) mm, n = 24
HF (♀ ♀): 142 (133–154) mm, n = 18
E (♂ ♂): 45 (42–48) mm, n = 24
E (♀ ♀): 41 (35–45) mm, n = 18
GLS (♂ ♂): 110 (101–118) mm, n = 28
GLS (♀ ♀): 98 (93–103) mm, n = 18
GWS (♂ ♂): 72 (66–79) mm, n = 28
GWS (♀ ♀): 66 (61–68) mm, n = 18
DR Congo (Allen 1925), Uganda (specimens in AMNH)

WT (♂ ♂): 5.8 (3.6–7.8) kg, n = 41
WT (♀ ♀): 3.9 (2.2–5.2) kg, n = 94
DR Congo (Colyn 1994)

WT (♂ ♂): 6.8 (3.6–9.5) kg, n = 9
WT (♀ ♀): 4.2 (2.2–5.4) kg, n = 9
W Kenya, Uganda (Delson *et al.* 2000)

GLS (♂ ♂): 109 (102–115) mm, n = 19
GWS (♂ ♂): 74 (69–80) mm, n = 19
Kisangani, C DR Congo (Colyn 1991)

GLS (♂ ♂): 111 (104–119) mm, n = 19
GWS (♂ ♂): 74 (71–79) mm, n = 19
Akengé/Niapu, DR Congo (Colyn 1991)

GLS (♂ ♂): 115 (108–124) mm, n = 18
GWS (♂ ♂): 79 (74–86) mm, n = 18
Semliki Region, E DR Congo (Colyn 1991)

GLS (♂ ♂): 117 (110–124) mm, n = 15
GWS (♂ ♂): 78 (70–83) mm, n = 15
Kivu, E DR Congo (Colyn 1991)

GLS (♂ ♂): 118 (112–123) mm, n = 9
Zygomatic width (♂ ♂): 81 (75–86) mm, n = 9
Mt Elgon, W Kenya (Colyn 1991)

Note: In his study, Colyn (1991) concluded that skulls from *C. m. stuhlmanni* adult ♂ ♂ could be divided into two groups based on size. Those from the river forests of Kisangani (n = 19) and Akengé/Niapu (n = 19) were smaller than those from the Western Rift Valley regions of Semliki (n = 18) and Kivu (n = 15). In addition, based on skull size, he concluded that *C. m. elgonis* should be recognized as a subspecies.

C. m. mitis

GLS (♂ ♂): 115 (110–120) mm, n = 7
GLS (♀ ♀): 98, 99 mm, n = 2
GWS (♂ ♂): 76 (70–76) mm, n = 6
GWS (♀ ♀): 61, 62 mm, n = 2
Angola (Machado & Crawford-Cabal 1999)

Key References Butynski 1990; Cords 1987b; Cords & Chowdhury 2010; Lawes 1992, 2002; Pazol *et al.* 2002; Rudran 1978b.

Michael J. Lawes, Marina Cords & Cathi Lehn

Cercopithecus (cephus) GROUP

Cephus Monkeys Group

Cercopithecus cephus (Linnaeus, 1758). Systema Naturae, 10th edn, 1: 27. Africa.

| | | |
|---|--------------------------|--------|
| <i>Cercopithecus (cephus) cephus</i> | Moustached Monkey | p. 366 |
| <i>Cercopithecus (cephus) sclateri</i> | Sclater's Monkey | p. 369 |
| <i>Cercopithecus (cephus) erythrotis</i> | Red-eared Monkey | p. 371 |
| <i>Cercopithecus (cephus) ascanius</i> | Red-tailed Monkey | p. 375 |
| <i>Cercopithecus (cephus) petaurista</i> | Lesser Spot-nosed Monkey | p. 381 |
| <i>Cercopithecus (cephus) erythrogaster</i> | White-throated Monkey | p. 384 |



Some taxa of the Cephus Monkeys Group *Cercopithecus (cephus)*.

Top row, left to right:

Eastern Lesser Spot-nosed Monkey *Cercopithecus petaurista petaurista*.

White-throated Monkey *Cercopithecus erythrogaster*.

Second row, left to right:

Western Spot-nosed Monkey *Cercopithecus petaurista buettikoferi*.

Schmidt's Red-tailed Monkey *Cercopithecus ascanius schmidtii*.

Third row, left to right:

Sclater's Monkey *Cercopithecus sclateri*. Congo Basin Red-tailed Monkey *Cercopithecus ascanius whitesidei*.

Fourth row, left to right:

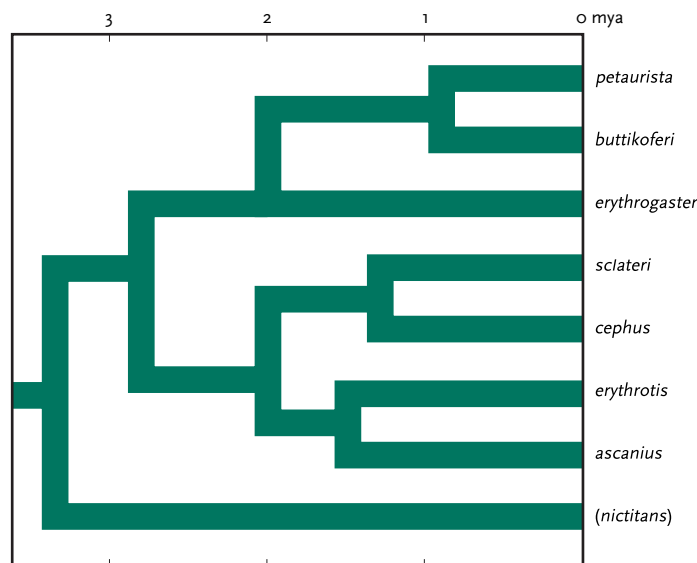
Red-eared Monkey *Cercopithecus erythrotis*.

Black-nosed Red-tailed Monkey *Cercopithecus ascanius atrinasus*.

Bottom row, left to right:

Moustached Monkey *Cercopithecus cephus*.

Generalized guenon *Cercopithecus* sp.



Tentative phylogenetic tree for Cephus Monkeys Group *Cercopithecus (cephus)* (partly after Tosi *et al.* 2005).

The *Cercopithecus (cephus)* Group (or Superspecies) of small, arboreal African monkeys is the largest, most diverse and colourful of all African forest monkeys. This group embraces six species: the Moustached Monkey *Cercopithecus (cephus) cephus*, Sclater's Monkey *Cercopithecus (cephus) sclateri*, Red-eared Monkey *Cercopithecus (cephus) erythrotis*, Red-tailed Monkey *Cercopithecus (cephus) ascanius*, Lesser Spot-nosed Monkey *Cercopithecus (cephus) petaurista* and the Red-bellied Monkey *Cercopithecus (cephus) erythrogaster*. Taken as a whole, these rather small monkeys (3–5 kg) are confined to the main forest blocks where they exhibit similar behaviour and occupy a consistent niche within diverse primate communities. They range over the entire equatorial belt excepting the isolated eastern forests of the Indian Ocean coast and forests of the Eastern Arc Mountains of Kenya and Tanzania.

All species in the *C. (cephus)* Group are arboreal, with grizzled brownish backs and crowns and long tails that are either red or longitudinally bicoloured. In spite of their extraordinarily diverse and colourful face patterns, molecular studies confirm the close relationship of species and position them as possibly the most recently evolved of all guenon lineages (Ledbetter 1981, Muleris *et al.* 1986, Dutrillaux *et al.* 1988b, Ruvoilo 1988, Disotell & Raaum 2002, Moulin *et al.* 2008). Purvis (1995) indicates that *C. (cephus)* may have diverged from a *C. mitis*-like lineage at about the time of the first Glacial, 3–2.5 mya. This probably has a bearing on the high degree of face-pattern differentiation between broadly allopatric populations because glacial periods would have fragmented forests and the monkey populations inhabiting them (see below).

The recent discovery that Campbell's Monkey *Cercopithecus (mona) campbelli* has the same number of chromosomes (66) as members of the *C. (cephus)* Group has important implications for understanding evolution of the *C. (cephus)* Group. That the *C. (mona)* Group evolved



Distribution in the Central Forest Block of some taxa of the Cephus Monkeys Group *Cercopithecus (cephus)*.

Top, left to right: Sclater's Monkey *Cercopithecus sclateri*. Red-eared Monkey *Cercopithecus erythrotis*. Unnamed monkey that may be a variant of the Congo Basin Red-tailed Monkey *Cercopithecus ascanius whitesidei*.

Middle, left to right: Moustached Monkey *Cercopithecus cephus*. Centre: Congo Basin Red-tailed Monkey *Cercopithecus ascanius whitesidei*. Schmidt's Red-tailed Monkey *Cercopithecus ascanius schmidt*.

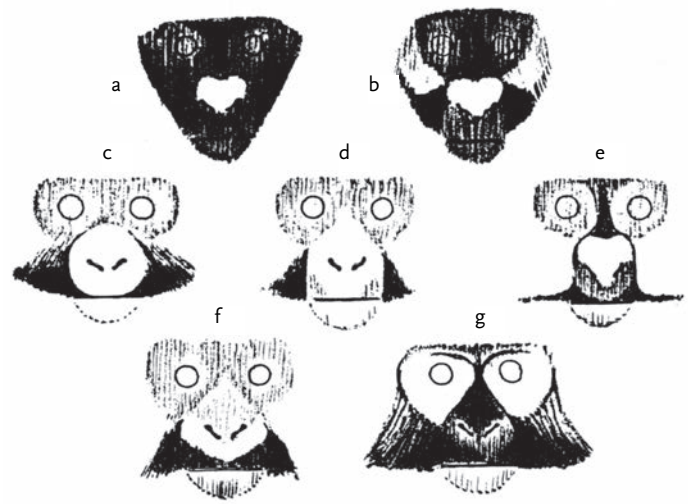
Bottom, left to right: Black-nosed Red-tailed Monkey *Cercopithecus ascanius atrinasus*. Black-cheeked Red-tailed Monkey *Cercopithecus ascanius ascanius*. Katanga Red-tailed Monkey *Cercopithecus ascanius katangae*.

before *C. (mona) campbelli* suggests that *campbelli* is the most basal member of the *C. (cephus)* Group (Moulin *et al.* 2008). Alternatively, *C. (m.) campbelli* might have acquired its current molecular profile through recent hybridization. Which explanation is correct remains to be determined.

In the field the *C. (cephus)* monkeys are readily recognized by their staccato, chirping alarm calls and alert, active demeanour: they have a faster metabolism and are active for more hours per day than many other guenon species (Struhsaker & Leland 1979). Comparing *C. (c.) ascanius* with Gentle Monkeys *Cercopithecus (nictitans) mitis*, the same study also demonstrated a five-fold increase in the time the former spent scanning their surroundings, suggesting that members of the *C. (cephus)* Group are more visually oriented than other guenons. They typically inhabit lowland and medium-altitude forests with high temperatures and well-distributed rainfall, and forage at all but the lowest levels of the forest. Marked differences in population density correlate with the presence or absence of other species, notably members of the *C. (mona)* Group and talapoin *Miopithecus* spp., with which there are substantial overlaps in habitat and diet. Thus *C. (c.) ascanius* in Uganda can reach densities of 140–175/km² while *C. (c.) cephus* in multi-species communities in Gabon live at less than one-third that density (Quris 1976, Struhsaker & Leland 1979, Gautier-Hion 1980, 1988, Sheppard 2000).

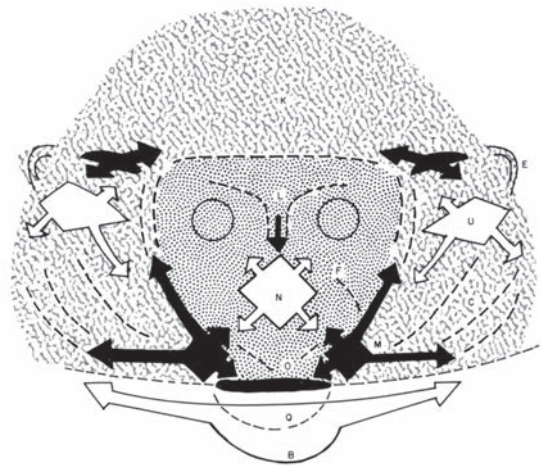
Feeding mainly on small, whole fruits and seeds, they also catch and consume arthropods, up to 20% in some samples (Struhsaker 1978a, Cords 1986, Gautier-Hion 1988). Relatively small body size allows *C. (cephus)* monkeys to forage on finer branches than larger species and their exceptional agility permits capture of active insects.

Groups of *C. (cephus)* monkeys generally number 10–40 individuals, usually attended by one adult ♂. They resemble the



Tonal contrasts on facial masks of some taxa of the Cephus Monkeys Group *Cercopithecus (cephus)*:

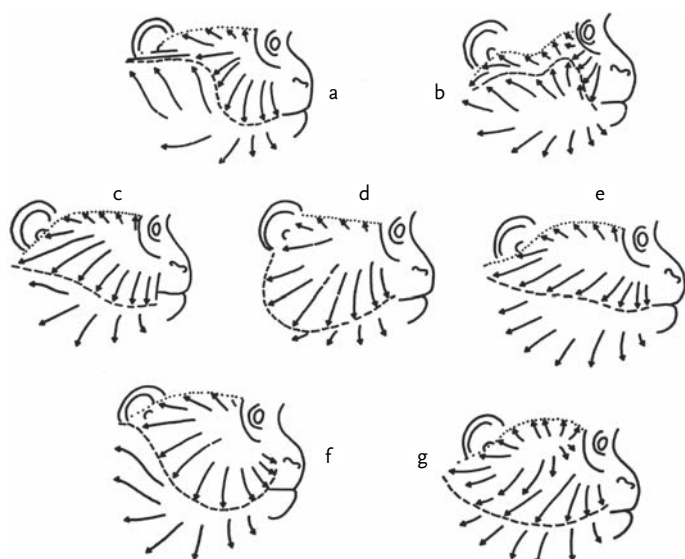
- (a) Eastern Lesser Spot-nosed Monkey *Cercopithecus petaurista petaurista*.
- (b) Western Lesser Spot-nosed Monkey *Cercopithecus petaurista buettikoferi*.
- (c) Red-eared Monkey *Cercopithecus erythrotis*.
- (d) Sclater's Monkey *Cercopithecus sclateri*.
- (e) Schmidt's Red-tailed Monkey *Cercopithecus ascanius schmidt*.
- (f) Moustached Monkey *Cercopithecus cephus*.
- (g) Black-nosed Red-tailed Monkey *Cercopithecus ascanius atrinasus*.



Facial zones, with light and dark foci, of species in the Cephus Monkeys Group *Cercopithecus (cephus)*.

members of the larger-bodied *C. (nictitans)* Group in many aspects of their morphology and behaviour and, in several respects, appear to be a juvenilized (neotenous), more recently evolved, branch of, or even within, the same lineage; for example, the adult males' loud-calls are similar but the smaller vocal apparatus of *C. (cephus)* cannot generate the volume or depth of *C. (nictitans)* calls (Gautier 1988).

Members of the *C. (cephus)* Group have unusually numerous short-wave cones in their eyes (Mollon 1989). This indicates relatively high sensitivity to colour and space perception. This helps confirm their greater use of and reliance on visual signals, a variation in colour sensitivity that is also found in South American primates (Mollon *et*

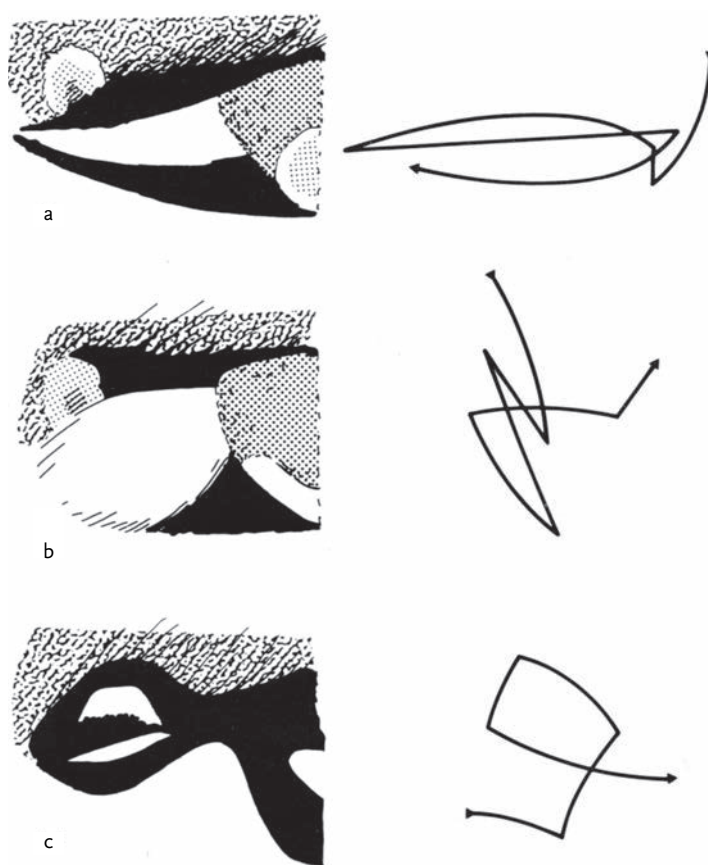


Cheek-hair arrangement on facial masks of some taxa of the Cephus Monkeys Group *Cercopithecus (cephus)*:

- (a) Sclater's Monkey *Cercopithecus sclateri*.
- (b) Western Lesser Spot-nosed Monkey *Cercopithecus petaurista buettikoferi*.
- (c) Generalized guenon *Cercopithecus* sp.
- (d) Moustached Monkey *Cercopithecus cephus*.
- (e) Red-eared Monkey *Cercopithecus erythrotis*.
- (f) Schmidt's Red-tailed Monkey *Cercopithecus ascanius schmidt*.
- (g) Black-nosed Red-tailed Monkey *Cercopithecus ascanius atrinasus*.

al. 1984, Sumner & Mollon 2003). The faces of *C. (cephus)* monkeys are of special interest because colour and pattern differences within the *C. (cephus)* radiation are exceptionally diverse and can differ from species to species as much as, or more than, the face patterns of more distantly related African monkeys. The biogeographic implication is that ancestral *C. (cephus)* monkey populations became fragmented, presumably due to cooling and drying during the first (and presumably subsequent) ice ages. If isolation coincided with early phases of facial pattern formation, minor discrepancies in visual appearance might have become progressively elaborated into major differences in pattern. Other features of their biology show no comparable divergence among species.

Cercopithecus (cephus) monkey face patterns tend to emphasize cheeks or noses and exhibit a geometry of design comparable with that of birds (Hill & McGraw 2006; figures pp. 363–5). The patterns are associated with species-specific head 'flagging' or signalling behaviour and one particular movement, a gesture of active 'eye-avoidance', appears to have driven the evolution of face patterns in *C. (cephus)* monkeys (Kingdon 1980, 1988b, 1997, 2007). Eye-avoidance gestures function during the contact, greeting, appeasement and courtship gestures of many primates. Indeed, for many mammals the gesture of avoiding eye-contact appears to be of great social utility and functional significance (Chance 1962, Kleiman & Eisenberg 1973). The eye-contact avoidance gesture serves to inform a conspecific viewer that, unlike a 'starrer', the head-avert is not socially threatening (Kingdon 1982, 1988b) and thus helps mediate the 'fission–fusion' systems typical of most higher primate societies (Marler 1961, 1968). In the case of



Schematic rendering of tonal contrasts on the sides of the head in three species of the Cephus Monkeys Group *Cercopithecus (cephus)* and charts of the head's traverse during ritualized head-flagging:

- (a) Red-eared Monkey *Cercopithecus erythrotis*.
- (b) Cephus Monkey *Cercopithecus cephus*.
- (c) Lesser Spot-nosed Monkey *Cercopithecus petaurista*.

C. (cephus), members of a group tend to forage quite independently in large, dispersed formations and the need for a conciliatory signal becomes particularly acute for ♂♂ that are seeking oestrous partners amongst the scattered and independent ♀♀. Reassuring gestures are also likely to operate when dispersed group members hastily come together to repel conspecifics from their territory or gather in sleeping trees for the night. *Cercopithecus (cephus)* monkey head movements, and the facial 'flags' that advertise them, appear to have evolved to translate subtle head movement and short-range facial expression into bolder, long-range signals.

The facial patterns of *C. (cephus)* have evolved, step by step, from progressive elaboration of small tonal differences in hair and skin. The diagrams on page 364 illustrate how visually diverse patterns have been built out of relatively minor expansions and contractions of light and dark foci. These face patterns remain the principal means of identifying species and subspecies within the *C. (cephus)* Group.

Jonathan Kingdon

Cercopithecus cephus MOUSTACHED MONKEY

Fr. Moustac; Ger. Blaumaulmeerkatze

Cercopithecus cephus (Linnaeus, 1758). Systema Naturae, 10th edn, 1: 27. Africa.Red-tailed Moustached Monkey *Cercopithecus cephus cephus* adult male.*Cercopithecus cephus***Geographic Variation**

- C. c. cephus* Red-tailed Moustached Monkey. Cameroon, Equatorial Guinea (Rio Muni), Congo and Gabon to right bank of Ogooué R. Skin of nose bluish-grey. Distal ca. 75% of tail bright orange-red.
- C. c. cephodes* Grey-tailed Moustached Monkey. Gabon on the left bank of the Ogooué R. Skin of nose bluish-grey. Distal ca. 75% of tail dark brown dorsally and greyish ventrally, darkening towards tip.
- C. c. ngottoensis* White-nosed Moustached Monkey. SW Central African Republic and NE Congo between Sangha R. and Lobaye R. Skin of nose white. Distal ca. 75% of tail orange-red.

Taxonomy Polytypic species. The nominal species within the *C. (cephus)* Group or Superspecies. Three subspecies are recognized (Groves 2001, 2005c, Grubb *et al.* 2003, Oates 2011); Red-tailed Moustached Monkey *C. c. cephus*, Grey-tailed Moustached Monkey *C. c. cephodes* and White-nosed Moustached Monkey *C. c. ngottoensis*. Synonyms: *buccalis*, *cephodes*, *gabonensis*, *inobservatus*, *ngottoensis*, *pulcher*. Chromosome number: $2n = 66$ (Dutrillaux *et al.* 1988b, Moulin *et al.* 2008).

Description Medium-sized monkey with long tail and brightly coloured face pattern, including white 'moustache'. Sexes similar in colour but adult ♀ weighs ca. 70% as much as adult ♂. Facial skin bright blue with bold white chevron ('moustache') below nose; black between chevron and upper lip. Cheek-ruffs yellow. Temples black. Crown and back reddish-brown agouti graduating into dark grey on outer surfaces of lower limbs. Throat, chest, belly and inner surfaces of limbs pale grey. Tail colour varies with subspecies (see Geographic Variation). Blue colour of the face poorly developed in newborn infants.

Similar Species Parapatric species in the *C. (cephus)* Group are similar in size and body colouring but all have highly distinctive face patterns.

Cercopithecus erythrotis. Sympatric with *C. c. cephus* over small area on left bank of Sanaga R. No white moustache. Nose and ears red.

Distribution Endemic to western central Africa. Throughout the forest block (05°N to 05°S) limited by Sanaga R. in north-west, Atlantic Ocean in west, Congo–Ubangi R. in east and Congo R. in south. See Geographic Variation.

Habitat Secondary and primary forests, riverine forest, gallery forest and thicket from sea level to at least 900 m (Gautier-Hion *et al.* 1981, Tutin *et al.* 1997b). Habitat preferences related in part to fruit availability and to anti-predator strategies (Gautier-Hion *et al.* 1981). Forests with dense undergrowth, encumbered by lianas and tangles



Blue and white pigmented skin on Red-tailed Moustached Monkey *Cercopithecus cephus cephus* face. Under the fur, the skin is all blue except for a white 'moustache', lips and upper eyelids (right).



preferred, especially during the day resting period. Forests with open understorey preferred at night. Annual rainfall 1400 mm to >4000 mm.

Abundance Often common. Number of individuals/km² varies from three to ten (C Gabon), 26 (Dja Reserve, Cameroon), 31 (Monte Alén N. P., Equatorial Guinea), 53 (Odzala N. P., Congo) and 66 (Ngotto Forest, Central African Republic; Brugière 1988). Abundant in some natural forest fragments; 30.2 ind/km² (Tutin 1999). Lowest densities occur in primary forests with open understorey. Densities low in riverine forests.

Adaptations Diurnal and arboreal. Mainly found in low and middle forest strata. Found at less than 15 m high in forest about 60% of time and at less than 10 m 30% of time. Immatures come to the ground for short periods to forage for insects or to play, especially during the hot hours of the day (Gautier-Hion *et al.* 1981, Quris *et al.* 1981). Alert monkey that is more visually oriented than species of the Nictitans Group *Cercopithecus (nictitans)*. This visual bias may be linked with greater use of visual signals. Striking facial patterns correlated with head-flagging displays (Kingdon 1980, 1988b, 1997, 2007). Vocal sacs smaller than for other guenons. As a result, calls specific to adult ♂♂ are not loud (Gautier 1974). Vocal repertoire includes about 28 sounds belonging to nine basic call types (Gautier 1978). Prone to form polyspecific associations, especially with Putty-nosed Monkeys *Cercopithecus nictitans*, with which *C. cephus* shares similar cohesion calls and alarm calls.

Foraging and Food Omnivorous. Fruit, seeds, leaves and animal matter constitute diet. Fruit pulp from about 100 plant species can make up to 80% of diet. Fruit of preferred species have brightly coloured pulp rich in water and sugar or possess arils high in protein and fatty acid. Invertebrates contribute 13% of ♂ diet and 25% of ♀ diet (Gautier-Hion 1980, Sourd & Gautier-Hion 1986). Time spent feeding on insects varies from 24% in adult ♂♂ and 38% in adult ♀♀ to 50% in immatures (Quris *et al.* 1981). Females capture more mobile prey (e.g. Orthoptera) than ♂♂ (more caterpillars and spiders). Seasonal variations in diet greater for ♂♂ than for ♀♀.

During the season of fruit scarcity, ♀♀ maintain the same amount of fruit in their diet whereas ♂♂ eat less fruit and more leaves (Gautier-Hion 1980). In natural forest fragments, home-range size can be <10 ha. Here diet is similarly dominated by fruit but shows strong month-to-month variations and, when fruit is scarce, large quantities of insects are eaten (Tutin 1999). Forages in groups. Most fruit-feeding occurs in high strata (mean 19 m) in early morning and late afternoon. Forages for insects in lower dense forest strata (mean 11 m; Quris *et al.* 1981), mostly in the middle of the day. Groups range on average 1.2 km/day. Territories 35–90 ha (Gautier-Hion *et al.* 1981). Monkeys use their cheek-pouches to collect fruit quickly in tree canopies before seeking safer locations in densest vegetation to eat.

Social and Reproductive Behaviour Social. Group size is 5–22 individuals; mean among sites = 6.4 ind/group (n = 10 in Lopé Reserve, Gabon, Ham 1994), 9.6 (n = 14 in Lopé Reserve, White 1994), 9.3 (n = 17 in Odzala N. P., Maisels 1995); 15 (n = 4 in Ngotto Forest, A. Gautier-Hion pers. obs.); 11.5 (n = 5 in NE Gabon, Gautier-Hion & Gautier 1976, Gautier-Hion *et al.* 1981). Only bisexual groups occur, with one adult ♂, several adult ♀♀ and immatures of both sexes. During the mating period, solitary ♂♂ may live at periphery of bisexual groups and copulate with ♀♀ (A. Gautier-Hion pers. obs.). Bisexual groups are territorial. Inter-group encounters may lead to violent fighting by adult ♀♀ and subadults while adult ♂♂ sit high in trees, barking (Gautier-Hion *et al.* 1999). *Cercopithecus cephus* in polyspecific associations during 38% of encounters in Odzala N. P., 53% in Ddja Reserve, 56% in Lopé Reserve, 76% in Monte Alén N. P., 83% in Ngotto Forest (Gautier-Hion 1996) and 88% in NE Gabon (Gautier-Hion 1968). Bi-specific associations with *C. nictitans*, tri-specific associations with *C. nictitans* and *C. pogonias*, and quadri-specific associations with *C. nictitans*, *C. pogonias* and Grey-cheeked Mangabeys *Lophocebus albigena* are most common. In these associations, *C. cephus* benefits from more efficient location of fruit (and thus a more diversified fruit diet) and from collective defence against predators (Gautier-Hion *et al.* 1983). Male *C. pogonias* give alarm call to aerial predators and *C. cephus* ♀♀ and immatures give alarm calls to terrestrial predators. In addition, the

heaviest ♂♂ of *C. nictitans* and *L. albigena* sometimes actively attack African Crowned Eagles *Stephanoetus coronatus* (Gautier & Gautier-Hion 1983, Gautier-Hion & Tutin 1988).

In *C. cephus* groups, only the adult ♂ gives the 'mpack' loud-call. This call helps to bring territorial conflicts or alarm situations to an end. In polyspecific associations, loud-calls of other species appear to stimulate vocal activity in *C. cephus* ♂♂. This species rarely initiates group movements. During alarm situations, the adult ♂ will also give 'hack' calls whereas ♀♀ and immatures give high-pitched 'chirps'. When moving or foraging, ♀♀ and immatures give soft, low-pitched 'grunts' (Gautier 1978, Gautier & Gautier-Hion 1983).

Reproduction and Population Structure Life history parameters poorly known in the wild. In Gabon, births occur from Dec to Mar (n = 10; Gautier-Hion 1968). In captivity, sexual maturity of ♂♂ occurs at about six years; accompanied by an increase in body weight. Sexual maturity of ♀♀ at about four years (Gautier-Hion & Gautier 1976). No obvious sexual swelling. Menses sometimes visible. Oestrous periods signalled by characteristic posture, including buttock presentation, erected tail and pout face. Gestation lasts ca. 165 days. A single young is born. Birth-weight 320 g (n = 1 ♂; A. Gautier-Hion pers. obs.). Estimates from wild specimens ca. 260–320 g (n = 10; Gautier-Hion 1968). In captivity a still-living ♂ is 33 years old and a still-living ♀ is 28 years. This ♀ reproduced nine times with a mean inter-birth interval of 19.2 months (11–33). First baby was stillborn. Last baby born when mother was 20 years of age (A. Gautier-Hion pers. obs.). Ratio ♂ : ♀ is 1 : 2.8 and ratio adults to immatures 1 : 2.13 (n = 17 groups with a mean size of 9 individuals; Maisels 1995). Ratio ♂ : ♀ 1 : 4.8 and adults to immatures 1 : 2 in one group of 15 individuals (Quris *et al.* 1981).

Predators, Parasites and Diseases Main predators are humans and *S. coronatus*. Leopard *Pantherus pardus* is a known predator (Henschel *et al.* 2005, 2011). Other predators likely include large snakes. The secretiveness of *C. cephus* and their association with large groups of Northern Talapoin Monkeys *Miopithecus ogouensis* helps them survive near villages. No information on parasites or diseases.

Conservation IUCN Category (2012): Least Concern. *C. c. ngottoensis* is Data Deficient. CITES (2012): Appendix II.

Populations locally reduced due to hunting by humans. Censuses conducted at five-year intervals in Ngotto Forest indicate that, following hunting, *C. cephus* density decreased by a factor of 2.5 (D. Brugière pers. comm.).

Measurements

Cercopithecus cephus

HB (♂♂): 480 mm, n = 4

HB (♀♀): 440 mm, n = 7

T (♂♂): 800 mm, n = 4

T (♀♀): 700 mm, n = 7

HF: n. d.

E: n. d.

WT (♂♂): 4.1 (2.6–5.2) kg, n = 29

WT (♀♀): 2.8 (1.8–3.8) kg, n = 30

Gabon (Gautier-Hion *et al.* 1999)

Ranges for linear measurements not available

HB (♂♂): 552 (510–600) mm, n = 8

T (♂♂): 804 (700–850) mm, n = 8

WT (♂♂): 4.5 (3.6–5.5) kg, n = 7

Gabon (Malbrant & Mclatchy 1949)

HB (♂): 580 mm, n = 1

HB (♀♀): 487 (475–495) mm, n = 3

T (♂): 780 mm, n = 1

T (♀♀): 693 (670–720) mm, n = 3

Unknown origin (Napier 1981)

Key References Gautier-Hion 1980; Gautier-Hion *et al.* 1981, 1999; Tutin 1999.

Annie Gautier-Hion

Cercopithecus sclateri SCLATER'S MONKEY

Fr. Cercopithèque de Sclater; Ger. Sclater-Meerkatze

Cercopithecus sclateri Pocock, 1904. Abstr. Proc. Zool. Soc. Lond. (1904) (5): 18. Type locality not known (see below).Sclater's Monkey *Cercopithecus sclateri* adult male.

Taxonomy Monotypic species. Member of *Cercopithecus* (*cephus*) Group, or Superspecies. Although Pocock (1904) gave an accurate description of a distinctly new form of monkey based on a single specimen, when Schwarz (1928b) published his revision of the genus *Cercopithecus*, the type skin was still the only specimen available. Schwarz argued that it represented a specimen of the Red-eared Monkey *Cercopithecus erythrotis*, in which the black pigment is reduced, and he synonymized *sclateri* with what he called *Cercopithecus cephus erythrotis*.

Hayman (quoted in Sanderson 1940: 649–651) reported on a second specimen received by the British Museum in 1935, collected in Okigwi Division, Nigeria. This specimen was identical to the type and convinced Hayman that *sclateri* was a distinct and well-defined taxon, which he treated as a subspecies of *C. erythrotis*.

Hill (1966) also recognized *sclateri* as a subspecies of *C. erythrotis*, and included a specimen from Obubra, E Nigeria, in the taxon. He noted, however, that this specimen had a brick-red nose and red ear-tufts, and that it 'possibly pertains to (*erythrotis*) *camerunensis*'. He mistakenly stated that Obubra lies west of the Cross R., when in fact it is located on the river's east bank; therefore the Obubra specimen (with no collection or specimen number) seems most likely to have been an example of the Cameroon Red-eared Monkey *C. erythrotis camerunensis*. Kingdon (1980) considered *sclateri* sufficiently distinct from *erythrotis* to be regarded as a species rather than a subspecies.

Type specimen (that died in the London Zoological Gardens) said to have come from 'Benin' (Pocock 1904). This must refer to Benin in present-day Nigeria, since, as of 1904, the former Dahomey had yet to be renamed 'Benin'. Groves (2001, 2005c) gives the type locality as 'Benin City', but this is unlikely to be correct as Benin City is west of the Niger R. It is much more likely that the type was obtained in Benin City or the surrounding region, but originated east of the Niger R. (Oates & Anadu 1989). No wild population of *C. sclateri* is known west of the Niger R., where the Red-bellied Monkey *Cercopithecus erythrogaster* occurs. Synonyms: none. Chromosome number: not known.

Description Small, long-tailed guenon, similar in bodily proportions to other members of the *C. (cephus)* Group. Sexes alike except adult ♀ smaller. In captivity, adult ♀ weighs ca. 70% as much as adult ♂. Upper nose creamy-white to varying shades of yellow-orange, forming a distinctive triangular 'nose spot'. Skin of muzzle, including tip of nose, pale pink. Cheek-tufts lemon-yellow. Diadem gold-flecked; gold-flecking results from hairs banded alternately with black and gold. Crown bordered posteriorly with a black band, which is broadest behind the ears. Ears fringed with white hairs. Throat white, but no distinctive, dense 'ruff' as in *C. erythrogaster*. Back, flanks, outer limbs and dorsal proximal surface of tail have 'agouti' appearance (i.e. hairs grey at base, banded yellow and black towards tip). Belly grey, speckled with agouti. Undersurface of proximal half of tail rust-red. Distal half of tail typically greyish-white with charcoal tip, although there is considerable variation in this feature. Pelage colour and pattern of juvenile same as that of adult. Newborn lacks facial hair, but colouration over rest of body resembles that of adult.

Geographic Variation Intra-population variation in pelage, especially nose colour and extent of red on tail, but no obvious geographical pattern of variation.

Similar Species

Cercopithecus erythrogaster. SE Togo, S Bénin and SW Nigeria. In Nigeria west and west-north-west of *C. sclateri*, with small area of sympatry. Hybridization on eastern edge of Niger Delta in Bayelsa State. No nose-spot, no white on ears, no red on tail.

Cercopithecus erythrotis. S and E Nigeria, Cameroon coast and Bioko I., Equatorial Guinea; *C. sclateri* occurs to west of lower Cross R. and *C. erythrotis* to east, with no good evidence of sympatry. Nose-spot and ears red, tail mostly red.

Distribution Endemic to SE Nigeria. Rainforest BZ. Restricted to forests between Niger R. and Cross R., SE Nigeria. Extent of occurrence: ca. 28,500 km² (Baker & Olubode 2008). Occurrence confirmed close to left bank of Niger R. at 05° 39' N, 06° 39' E and close to right bank of Cross R. at 05° 22' N, 08° 04' E (Oates & Anadu 1989, Oates *et al.* 1992), as well as coastal freshwater swamp forest (Gadsby 1989, Tooze 1996b), freshwater swamp forest located just inland from coastal mangroves (Powell 1995, Tooze 1996a, Baker & Olubode 2008) and north-east as far as 06° 16' N, 08° 11' E, in gallery forest in derived savanna zone (Baker & Olubode 2008). Many of the inhabited forests are small fragments within a largely agricultural landscape.

Kingdon (1980) not only shows the location of the 'Benin' specimen (see Taxonomy), but also indicates the locations of two hybrid specimens from near the Cross R.; one of these is placed near Obubra and is probably Hill's (1966) specimen of *C. erythrotis camerunensis* and thus likely not a hybrid. Powell (1995) and Baker (2005) report an area of sympatry between *C. erythrogaster* and *C.*

sclateri on the eastern edge of the Niger Delta, east-north-east of Yenagoa in Bayelsa State (ca. 04° 54–59' N, 06° 20–25' E). In 1999 the Centre for Education, Research and Conservation of Primates and Nature (CERCOPAN) in Calabar, Nigeria, held two captives that originated from this area; they have features intermediate between *C. sclateri* and *C. erythrogaster*, presumably resulting from hybridization.

Current distribution of *C. sclateri* probably similar to its historical distribution, but populations are today highly fragmented as a result of widespread replacement of natural forest by farms, plantations and human settlements.

Habitat Lowland moist forest, including seasonally flooded swamp forest on eastern edge of Niger Delta and fringing forests along waterways. Predominantly in low-lying areas (<400 m asl). Mean annual rainfall within the species' range varies from ca. 1500 mm in the north to >3000 mm in the south. Mean annual temperatures range from 22 °C to 38 °C. Within this area there is typically one dry season, from Nov or Dec through Mar. At inland locations in E Nigeria, between Niger R. and Cross R., most of the natural forest has been replaced by farmland; here a few relict populations of *C. sclateri* survive in gallery forest, farm bush, forest fragments, and isolated tree groves where local human communities regard this monkey as sacred (Oates *et al.* 1992, Baker & Olubode 2008).

Abundance Though now rare or absent across much of its presumed original range because of regional habitat loss, this species is still relatively common in several locations. In one survey (n = 24 forest sites) *C. sclateri* was one of the two most frequently encountered primates (0.18 detections/km walked) (Baker & Olubode 2008). In a site where the species is considered sacred (Lagwa, Imo State) the population in 2005 was ca. 124 individuals in 15 groups (Baker *et al.* 2009). In another sacred site (Akpugoeze, Enugu State) a 2006 population estimate was 193 individuals in 20 groups (Baker *et al.* 2009). This is similar to a 1994 estimate for this population of 199 individuals in 12 groups (Tooze 1994). In Edumanom F. R., Bayelsa State, model-weighted occupancy yielded 3.7 groups/km² (95% C.I. yielded 1.4–7.7 groups/km²), or 3.1 groups/km² after adjusting for groups that straddled sample-plot boundaries (Baker *et al.* 2011).

Adaptations Diurnal and arboreal. Like other members of the *C. (cephus)* Group *C. sclateri* is a small, agile monkey. Often uses mid- to low-canopy levels; mean height = 11.5 m (S.D. = 5.1, range 6–21, n = 14 sightings); mean height of trees in which sightings occurred = 15.4 m (S.D. = 4.6, range 10–22) (Baker & Olubode 2008). Behaviour and ecology of *C. sclateri* have not been the subjects of an extended field study.

Foraging and Food Omnivorous. Not systematically studied. Diet, home-range size and foraging behaviour probably similar to other members of the *C. (cephus)* Group. Diet likely comprised mostly of fruits, insects and young foliage. In villages where *C. sclateri* is considered sacred, these monkeys feed largely on plants cultivated by humans, such as Cassava *Manihot esculenta*, Papaya *Carica papaya*, Maize *Zea mays*, Banana and Plantain *Musa* spp., Mango *Mangifera indica* and Oil Palm *Elaeis guineensis*.



Cercopithecus sclateri

Social and Reproductive Behaviour Social. In Lagwa, Imo State, mean group size ca. 8.3 individuals (S.D. = 3.3, range 4–14, n = 15 groups), with dependent infants comprising 12% of population; in Akpugoeze, Enugu State, mean group size ca. 9.7 (S.D. = 4.2, range 4–19, n = 20 groups), with infants making up 8% (Baker *et al.* 2009). Tooze (1994) found a mean group size in Akpugoeze of 16.6 individuals (8–28, n = 12 groups), with infants comprising ca. 17%. Adult ♂ loud-calls usually come from only one location in a group, suggesting that one-male groups are the norm. Alarm call a rapidly repeating, nasal, high-pitched 'squeak'. Adult ♂ loud-call a low-pitched, rapidly repeating, nasal, snort-like vocalization. There is no information on reproductive behaviour.

Reproduction and Population Structure No information, but probably similar to other members of the *C. (cephus)* Group.

Predators, Parasites and Diseases No detailed information available, but humans are currently the most important predator of *C. sclateri*. African Crowned Eagles *Stephanoetus coronatus* prey on other members of the *C. (cephus)* Group elsewhere, but *S. coronatus* now extirpated across all or most of the range of *C. sclateri*. No information on diseases and parasites.

Conservation IUCN Category (2012): Vulnerable. CITES (2012): Appendix II.

Most remaining populations are not only hunted, but also occur in a highly fragmented pattern due to habitat destruction. Survival of *C. sclateri* likely related to its small size, adaptability and cryptic nature; such factors allow these monkeys to persist in small areas of degraded habitat and make them difficult to hunt. This species also provides lower return-on-investment for shotgun hunters (Baker & Olubode 2008). The largest contiguous forests holding populations of *C. sclateri* (and thus perhaps the largest remaining populations of the species) are the 310 km² Stubbs Creek F. R., Akwa Ibom

State, which, in the early 1990s, contained ca. 80 km² of relatively undisturbed swamp forest (Gadsby 1989, Oates 1990, Tooze 1995), and the 87 km² Edumanom F. R. and 90 km² Upper Orashi F. R. in the E Niger Delta. These reserves offer no protection against hunting and little to no protection against logging. In the villages of Akpugoeze and Lagwa, where *C. sclateri* is held as sacred, there is a traditional ban on the hunting of this species. However, these beliefs are likely eroding, and the habitat available to the monkeys is already small and declining (Oates *et al.* 1992, Tooze 1994, Baker *et al.* 2009). Conservation-awareness efforts were initiated in both Lagwa and Akpugoeze in 2006. Surveys conducted in Akpugoeze in 1989, 1994, 2004 and 2006 indicate that the *C. sclateri* population has remained stable at ca. 200 monkeys (population estimates, respectively: 180–225, 199, 187 and 193) (Baker *et al.* 2009).

Measurements

Cercopithecus sclateri

HB (♂ ♂): 373, 375 mm, n = 2

HB (♀ ♀): 326, 341 mm, n = 2

T (♂ ♂): 820, 849 mm, n = 2

T (♀ ♀): 673 (616–762) mm, n = 3

HF: n. d.

E: n. d.

WT (♂ ♂): 5.0, 5.5 kg, n = 2

WT (♀ ♀): 3.8 (3.1–4.6) kg, n = 3

Captives at CERCOPAN, Calabar, Nigeria

Key References Baker & Olubode 2008; Baker *et al.* 2009; Oates 2011; Oates & Anadu 1989; Oates *et al.* 1992; Tooze 1995.

John F. Oates & Lynne R. Baker

Cercopithecus erythrotis RED-EARED MONKEY (RED-NOSED MONKEY)

Fr. Moustac à oreilles rouges; Ger. Rotohrmeerkatze

Cercopithecus erythrotis Waterhouse, 1838. Proc. Zool. Soc. Lond. 1838: 59. Fernando Po (=Bioko I.), Equatorial Guinea.

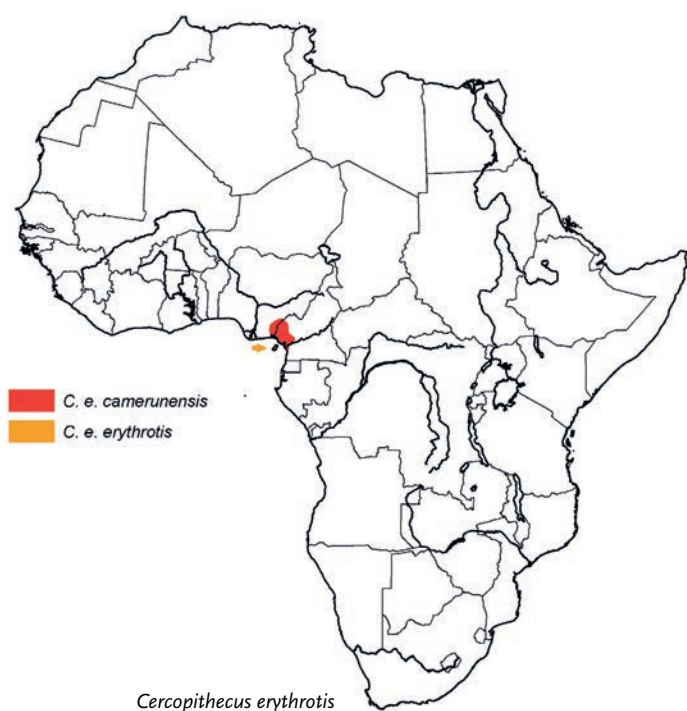


Red-eared Monkey *Cercopithecus erythrotis* adult male.

Taxonomy Polytypic species within the *Cercopithecus (cephus)* Group (or Superspecies). The more recent taxonomic history is summarized by Grubb *et al.* (2003). Although Waterhouse (1838) and Schwarz (1928b) considered *C. erythrotis* as most closely related to the Moustached Monkey *Cercopithecus cephus*, Hill (1966) regarded the Red-tailed Monkey *Cercopithecus ascanius* as the closest relative. Struhsaker (1969, 1970) and Gartlan & Struhsaker (1972) considered *C. cephus* to be conspecific with *C. erythrotis* based on their identical vocal repertoires, the frequent occurrence of intermediate forms on the left bank of Sanaga R., and strong similarities in their ecology and behaviour.

Sclater's Monkey *Cercopithecus sclateri*, once considered a subspecies of *C. erythrotis* (e.g. Dandelot 1974, Napier 1981, Wolfheim 1983, Lee *et al.* 1988, Lernoould 1988), now widely recognized as a full species (Kingdon 1980, Oates 1996a, Grubb *et al.* 2000). We follow Kingdon (1997), Groves (2001, 2005c), Grubb *et al.* (2003) and Oates (2011) in recognizing two subspecies for *C. erythrotis*. Synonyms: *camerunensis*. Chromosome number: 2n = 66 (Muleris *et al.* 1985, Dutrillaux *et al.* 1988b).

Description Medium-sized, long-tailed monkey with red nose, ears and tail. Sexes alike but adult ♀ smaller, being about 84% the weight of adult ♂. Facial skin purplish. Eyelids and region around mouth and front of nose with pink skin. Nose-spot triangular and red. Ears prominent, bright rusty-red with well-developed red tufts. Cheeks white to pale cream or bright yellow (depending on subspecies), tapered to a point below the ear. Brow, temples and region between cheeks and throat black, contrasting strongly with the cheeks. Chin, throat, ventrum and inner legs with off-white to medium-grey hair and showing pale lilac skin. Crown, nape, shoulders, back, flanks and upper limbs dark grey to almost black, grizzled yellowish. Hairs of dorsum grey at base with three pairs of alternating red and black bands (Groves 2001). Lower outer limbs dark grey to blackish, not grizzled. Hands and feet blackish. Distal edge of rump, perineal region and scrotum bright red. Tail mostly



bright red above but 25–30% of proximal upper side is colour of back and distal ca. 30 mm is blackish. Tail with faint, thin, dorsal stripe along entire length except at base and tip.

Young infants duller than adult and with less defined patterning but soon acquire adult pattern. Young juveniles have full adult pattern but lack ear-tufts and have chin and throat pure white (Hill 1966). One ca. three-month-old *C. e. erythrotis* with finer, more fuzzy pelage than adult, and with cheeks, brow and dorsum much more heavily grizzled light yellow than adult (T. Butynski pers. obs.).

Geographic Variation

C. e. erythrotis Bioko Red-eared Monkey: Bioko I., Equatorial Guinea. Smaller body (HB adult ♂ <500 mm, see Measurements). Overall tints appreciably darker. Cheeks white to pale yellow.

C. e. camerunensis Cameroon Red-eared Monkey. Extreme SE Nigeria and SW Cameroon. Larger body (HB adult ♂ >500 mm, see Measurements). Overall tints appreciably lighter. Cheeks bright yellow.

Similar Species

Cercopithecus sclateri. SE Nigeria west of lower Cross R. Parapatric, perhaps sympatric in vicinity of Cross R. Nose and ears with little or no red. Tail mostly off-white.

Cercopithecus cephus. Sympatric over small area on left bank of Sanaga R. Moustache white. Nose and ears not red.

Distribution Endemic to Bioko I., extreme SE Nigeria and SW Cameroon. Rainforest and Afromontane–Afroalpine BZs. Over most of Bioko I., being absent only from areas with a high human population density (Butynski & Koster 1994, González-Kirchner 1996). On mainland from north of upper course of Cross R., SE Nigeria (05° 22' N, 08° 04' E and 06° 11' N, 08° 04' E), southwards to just south of Sanaga R., SW Cameroon (03° 32' N, 09° 37' E and 05° 12' N, 13° 31' E). Present south of Sanaga R. (near Tinaso;

03° 37' N, 09° 57' E) where it interbreeds with *C. cephus* (Struhsaker 1970).

Habitat Moist forest. On mainland in primary and secondary riverine, lowland, mid-altitude and montane forest as well as seasonally flooded swamp forest. Prefers immature forest (Struhsaker 1969, Gartlan & Struhsaker 1972, Lee *et al.* 1988). Habitats at two sites in SW Cameroon are described in detail by Gartlan & Struhsaker (1972). Occurs from near sea level to >900 m. Mean annual rainfall over the range is from ca. 1400 to >8600 mm.

On Bioko I., *C. erythrotis* occurs in forest from sea level to 2600 m, then to the top of Pico Basilé (the highest point on Bioko at 3011 m) where present in the subalpine zone (which is dominated by grass *Festuca* sp., and by the shrubs *Hypericum revolutum* and *Erica mannii*; Butynski & Koster 1994, T. Butynski pers. obs.). Preferred habitat on Bioko is primary lowland forest, a vegetation type that covers about 39% (795 km²) of the island (González-Kirchner 1996). Present where mean annual rainfall ranges from ca. 2000 mm on the north coast to >10,000 mm (perhaps 14,000 mm) on the SW coast (which may be the wettest site in Africa). The wet season is Apr–Oct and the dry season is Nov–Mar. Temperatures range from ca. 34 °C on the coast to probably near freezing on top of Pico Basilé.

Abundance In Lombé part of Douala-Edéa Reserve, Cameroon, density was 2–3 groups/km² during the mid-1970s (D. McKey cited in Lee *et al.* 1988). In Korup N. P., W Cameroon, one study estimated 0.3 groups/km² (Edwards 1992), while a second study, in 2004–05, based on 320 km of foot transect, estimated 0.05–0.34 groups/km² (Linder & Oates 2011). Still widespread and, apparently, fairly common in the Yabassi region north of the Sanaga R., SW Cameroon (Dowsett-Lemaire & Dowsett 2001). For four primate communities in Cameroon, *C. erythrotis* groups accounted for 8–21% of 304 groups encountered (Gartlan & Struhsaker 1972).

Of seven species of monkeys on Bioko I., the most common and widespread is *C. erythrotis*. Of 108 groups of monkeys encountered during an island-wide survey in 1986, 48 (44%) were *C. erythrotis* (Butynski & Koster 1994). During a 2008 survey in the Gran Caldera de Luba, SW Bioko, *C. erythrotis* accounted for 40% of 62 groups of monkeys (six species) encountered. On the south slope of Pico Basilé, 60% of the 35 groups encountered during a 2008 survey were *C. erythrotis*. At Badja North, south-west Bioko, 33% of 105 groups encountered in 2009, and 32% of 91 groups encountered in 2010, were *C. erythrotis* (T. Butynski, G. Hearn, M. Kelly & J. Owens pers. obs.).

In 1986 *C. erythrotis* on Bioko was encountered at the rate of 0.13 groups/km during the island-wide survey that involved 373 km of foot census, much of which was through heavily hunted areas (Butynski & Koster 1994). Other encounter rates on Bioko are as follows: 0.57 groups/km in 2008 along 44 km of transect in Gran Caldera de Luba; 0.43 groups/km in 2008 along 49 km of transect on south slope of Pico Basilé; and 0.72 groups/km in 2009 along 48 km of transect and 0.58 groups/km in 2010 along 50 km of transect at Badja North (T. Butynski, G. Hearn, M. Kelly & J. Owens pers. obs.). These last-mentioned three sites are remote and receive relatively low levels of hunting. Also, there has been little to no anthropogenic impact on the habitats at these sites. As such, these encounter rates are likely close to what can be expected for undisturbed populations of *C. erythrotis*.

In 1992 in the Arihá area on the coast of SE Bioko, *C. erythrotis* was encountered at a rate of 0.14 groups/km during 100 km of foot survey. Density here was estimated at 0.26–0.39 ind/km². Here *C. erythrotis* was the third most common monkey (behind Crowned Monkey *Cercopithecus pogonias* and Putty-nosed Monkey *Cercopithecus nictitans*) (Maté & Colell 1995).

Adaptations Diurnal and arboreal. As with other *C. (cephus)* Group species, *C. erythrotis* is a very visually alert monkey. Its short-range visual signals include rapid head-shaking. The horizontal orientation of facial stripes, and the vivid red ears and nose, serve to make the rapid shaking of the head highly conspicuous. Likewise, there are repetitive behaviour patterns to suggest that postures and movements of the bright red tail provide information about dominance ranking (Kingdon 1980, 1997, 2007). The likely function of these signals is discussed on pages 364–5. Species-specific behaviour of *C. erythrotis* has yet to be studied in detail but preliminary observations indicate that it resembles that of other *C. (cephus)* Group species in its more obvious features (Struhsaker 1970, Gartlan & Struhsaker 1972, T. Butynski pers. obs.).

In Cameroon, groups of *C. erythrotis* are frequently in polyspecific association with *C. nictitans* and *C. pogonias*, and sometimes also associates with Mona Monkeys *Cercopithecus mona* and Preuss's Monkey *Allochrocebus preussi*. At Idenau in polyspecific association during 96% of group encounters ($n = 27$), and at Southern Bakundu Reserve in polyspecific association during 78% of group encounters ($n = 222$) (Gartlan & Struhsaker 1972). The possible predation and foraging advantages for the formation and maintenance of polyspecific associations among groups of primates of different species has been much discussed (e.g. Gartlan & Struhsaker 1972, Gautier-Hion 1988, Struhsaker 2000a) and will not be reviewed here.

On Bioko groups of *C. erythrotis* form polyspecific associations with Pennant's Red Colobus *Procolobus pennantii*, Black Colobus *Colobus satanas*, *C. pogonias*, *C. nictitans* and *A. preussi* (T. Butynski pers. obs.). During a 1986 survey, *C. erythrotis* groups were in polyspecific association on six (15%) of 41 encounters but much of this survey was conducted in heavily hunted areas where primate densities were low and where, in some cases, *C. erythrotis* was the only monkey species present (Butynski & Koster 1994). A 1992 study of an undisturbed community of primates on SW Bioko found *C. erythrotis* groups ($n = 16$) to be in polyspecific association on 50% of encounters (Struhsaker 2000a). During a 2008 study of the high density, but somewhat hunted, primate community within the Gran Caldera de Luba, only two (8%) of the 25 groups of *C. erythrotis* encountered were in polyspecific association (T. Butynski, G. Hearn & J. Owens pers. obs.).

On Bioko the two primary natural predators of forest monkeys are absent, namely the Leopard *Panthera pardus* and African Crowned Eagle *Stephanoaetus coronatus*. This might account for the low incidence of polyspecific association for *C. erythrotis* on Bioko relative to the mainland. In areas where human hunters are also largely absent, *C. erythrotis* is frequently seen on the ground (Butynski & Koster 1994, Struhsaker 2000a).

The range of habitats and altitudes occupied by *C. erythrotis* on Bioko is far greater than on the mainland. The reasons for this remain unknown. A study of the great ecological plasticity shown by this species on Bioko could shed considerable light on the environmental



Red-eared Monkey *Cercopithecus erythrotis* adult male.



Typical head-flagging sequence in Red-eared Monkey *Cercopithecus erythrotis* adult male (2.1 seconds duration).

conditions that restrict the distribution and abundance of *C. erythrotis*, as well as illuminate the dynamics of ecological partitioning among *Cercopithecus* spp. in general.

Foraging and Food Omnivorous. Foraging behaviour and diet yet to be systematically studied. In Cameroon *C. erythrotis* fairly frequently seen on the ground but generally a species of the lower strata of the forest. Travels and feeds at lower heights than *C. pogonias* or *C. nictitans*, with 50% of feeding below 15 m (Gartlan & Struhsaker 1972). A list of 15 species of plants eaten by *C. erythrotis* at Southern Bakundu F. R. is provided by Gartlan & Struhsaker (1972). Fruits are, by far, the most frequently recorded plant part eaten. On Bioko found on the ground during 5% of encounters during surveys, at 1–10 m above the ground during 42% of encounters, at 10–20 m during 33% of encounters, at 20–30 m during 13% of encounters, and >40 m (in emergents) during 7% of encounters ($n = 153$; González-Kirchner 1996). A study on the coast of SE Bioko found *C. erythrotis* at 10–20 m above the ground during ca. 72% of encounters (Maté & Colell 1995). On Bioko feeds near villages on bananas *Musa* sp., Cocoa *Theobroma cacao* and Oil Palm *Elaeis guineensis* fruits (Butynski & Koster 1994, González-Kirchner 1996). Wild fruits eaten include *Antidesma laciniatum*, *Allanblackia montecola*, *Antrocaryon klaineianum*, *Sterculia tragacantha* and *Ficus sur* (K. Nowak, E. Good & T. Butynski pers. obs.). Also feeds on flowers of *A. montecola*, *Psychotria* sp. and *H. revolutum*. Much of the time spent foraging involves searching for invertebrates, especially within dry, curled, leaves (T. Butynski pers. obs.).

Social and Reproductive Behaviour Social. In Cameroon group size ranges from ca. 4 to >29 animals ($n = 4$, Struhsaker 1969). S. Gartlan (pers. comm. to Wolfheim 1983) reported group size as 30–35 animals. Few group size data available for Bioko; Maté & Colell (1995) give group size at 8–12 animals (but no sample size provided). T. Butynski (pers. obs.) has the impression that most groups comprise 10–20 animals. Both in Cameroon and on Bioko there is no indication that groups have more than one adult ♂ (Struhsaker 1969, T. Butynski pers. obs.).

Solitary ♂ ♂ common, at least at some sites. Of 48 encounters with *C. erythrotis* on Bioko in 1986, seven (15%) were thought to be with solitary ♂ ♂ (Butynski & Koster 1994). Similarly, of 20 encounters with *C. erythrotis* on Bioko in 1992, four (20%) were believed to be with solitaires. Of 20 encounters with *C. erythrotis* in Korup N. P., two (10%) were believed to be with solitaires (Struhsaker 2000a). Preliminary observations on the social behaviour of *C. erythrotis* in Cameroon are presented in Struhsaker (1969) and in Gartlan & Struhsaker (1972).

The vocal repertoire of *C. erythrotis* includes 'screams', 'screeches', 'growls', 'chirps', 'twitters', 'grunts', 'trills', 'chutters' and 'hacks' (Struhsaker 1970, Gautier 1988, T. Butynski pers. obs.). Chirps, twitters, grunts, trills and chutters given only by adult ♀ ♀ and immatures. Chirps and twitters are given primarily in situations of alarm, such as towards a human observer or other potential predator (e.g. African Crowned Eagle). Grunts facilitate group cohesion. Chutters given during intra- and inter-group agonistic encounters. The hack is the loudest call and is given by adult ♂ ♂ and, perhaps, large subadult ♂ ♂. None the less, this call can not be heard much beyond 100 m and is, therefore, not nearly as loud as the loud-calls of most other *Cercopithecus* spp. Hacks are generally given at the rate of ca. 1/sec, but to 2/sec when the ♂ is especially excited. Hacks often grade into a series of hack-trains and sharp, soft, 'aints', in a manner similar to Gentle Monkey *Cercopithecus mitis* (T. Butynski pers. obs.). Hacks are typically given in alarm situations and often immediately after the (louder) hacks of *C. nictitans*, *C. pogonias* or *C. mona*, but rarely precedes them (Struhsaker 1970, T. Butynski pers. obs.). Also given after *C. pogonias* booms. The hack sounds distinctly different from the 'pop' of *C. ascanius* and not nearly as loud. Overall, *C. erythrotis* is notably less vocal than other *Cercopithecus* spp. (Dowsett-Lemaire & Dowsett 2001, T. Butynski pers. obs.). Struhsaker (1970) suggests that *C. erythrotis* may not be territorial. If so, this may be related to the absence of a far-carrying loud-call in this species.

Reproduction and Population Structure No information available from the wild. Probably similar to other members of the *C. (cephus)* Group. Captive ♀ ♀ indicate oestrus to adult ♂ ♂ through an arched back and tail-up presentation of the genitalia while at the same time puckering their lips (J. Kingdon pers. obs.).

Predators, Parasites and Diseases Few data available on predation. Humans are, by far, the most important predator, both on Bioko and on the mainland. Probable main natural predators on the mainland are African Crowned Eagles, Leopards, African Golden Cats *Profelis aurata*, Robust Chimpanzees *Pan troglodytes*, Central African Rock Pythons *Python sebae* and Nile Crocodiles *Crocodylus niloticus*. African Crowned Eagles are likely the most significant natural predator of *C. erythrotis* on the mainland (Struhsaker 2000a).

Except for *P. sebae*, all of these natural predators are absent from Bioko. Drill *Mandrillus leucophaeus*, which are present over much of the range of *C. erythrotis*, may kill and eat small monkeys but there are, as yet, no records for this. No data available on parasites and diseases. *Cercopithecus erythrotis* lives to at least 14.2 years in captivity (Jones 1962). No information on diseases and parasites.

Conservation IUCN Category (2012): Vulnerable. CITES (2012): Appendix II.

Hunting for the commercial bushmeat trade, and habitat degradation, loss and fragmentation, are the main threats, both on Bioko (Butynski & Koster 1994, Hearn *et al.* 2006) and in Nigeria and Cameroon (Wolfheim 1983, Lee *et al.* 1988, Bowen-Jones & Pendry 1999, Waltert *et al.* 2002, Oates *et al.* 2004, Linder & Oates 2011). Most of the historic range is now highly fragmented and degraded within an anthropogenic landscape in which it is likely that almost all remaining populations are hunted. The survival of *C. erythrotis* is, however, assisted by the animal's small size, cryptic behaviour, ability to survive in small forests near agriculture and human settlement, and considerable ecological and behavioural plasticity. On Bioko, this species is better able to survive sustained hunting than any of the other species in the primate communities in which it occurs (Koster & Butynski 1994, González-Kirchner 1996).

On Bioko fairly abundant in the Gran Caldera & Southern Highlands Scientific Reserve (510 km²) and Pico Basilé N. P. (330 km²). Neither area is, however, effectively managed and, as such, all primates are heavily hunted. In 2005 the number of *C. erythrotis* carcasses counted at the Malabo Bushmeat Market was ca. 1750. The total number killed by bushmeat hunters on Bioko during 2005 is estimated to be ca. 4000. The average price paid in 2006 in the Malabo Bushmeat Market for an adult *C. erythrotis* was ca. US\$ 29. The number of *C. erythrotis* on Bioko in 2006 was estimated at 20,000 individuals, down roughly 35% since 1986 (Hearn *et al.* 2006).

In Nigeria found in Cross River N. P., Mbe Mountains, and Afi River F. R. In Cameroon present within South Bakundu Reserve, Douala-Edéa Reserve, Korup N. P. and, apparently, also the Makombé Forest (ca. 600 km²), Ndokbou Forest (>1000 km²) and Ebo Forest (ca. 1400 km²) in the Yabassi area (Dowsett-Lemaire & Dowsett 2001). Probably also present in the following forests: Obudu, Takamanda, Ejagham, Mone Mta Ali, Banyang-Mbo, Rumpi Hills, Mokoku, Bambuko, Mouyaka, Dibombe, Mababe, Mungo and Bakala.

Priority actions for the long-term conservation of this species are to (1) stop the hunting of this species for the bushmeat trade and (2) conduct surveys to better determine the current distribution and abundance of this species, particularly in the Yabassi area.

Measurements

Cercopithecus erythrotis

C. e. erythrotis

HB (♂ ♂): 420 (390–500) mm, $n = 66$

HB (♀ ♀): 384 (360–430) mm, $n = 64$

T (♂ ♂): 609 (490–730) mm, $n = 67$

T (♀ ♀): 553 (460–660) mm, $n = 62$

HF (♂ ♂): 124 (112–144) mm, $n = 67$

HF (♀ ♀): 114 (105–130) mm, $n = 64$

E (♂ ♂): 28 (24–31) mm, $n = 67$

E (♀ ♀): 27 (22–32) mm, n = 64
 WT (♂ ♂): 3.7 (3.0–5.6) kg, n = 64
 WT (♀ ♀): 3.1 (2.4–5.4) kg, n = 64
 Upper canine (♂ ♂): 14 (12–18) mm, n = 65
 Upper canine (♀ ♀): 10 (6–14) mm, n = 59
 Lower canine (♂ ♂): 9 (7–12) mm, n = 64
 Lower canine (♀ ♀): 7 (5–11) mm, n = 59
 GLS (♂ ♂): 91 (89–94) mm, n = 4*
 GLS (♀ ♀): 87 (85–90) mm, n = 4*
 GWS (♂ ♂): 59 (58–60) mm, n = 4*
 GWS (♀ ♀): 56 (53–59) mm, n = 4*
 Bioko I. (Butynski *et al.* 2009)
 *Hill (1966), Eisentraut (1973)

C. e. camerunensis

HB (♂ ♂): 524 (490–549) mm, n = 4
 HB (♀ ♀): 435 mm, n = 1
 T (♂ ♂): 729 (690–770) mm, n = 4

T (♀ ♀): 620 mm, n = 1
 HF (♂ ♂): 135 (132–137) mm, n = 4
 HF (♀ ♀): 122 mm, n = 1
 E (♂ ♂): 28 (24–30) mm, n = 4
 E (♀ ♀): 33 mm, n = 1
 WT (♂ ♂): 4.2, 4.2 kg, n = 2
 WT (♀ ♀): 3.5 kg, n = 1
 GLS (♂ ♂): 101 (93–113) mm, n = 8
 GLS (♀ ♀): 93 (86–97) mm, n = 7
 GWS (♂ ♂): 67 (63–73) mm, n = 8
 GWS (♀ ♀): 61 (58–65) mm, n = 7
 Various localities (Hill 1966, Eisentraut 1973)

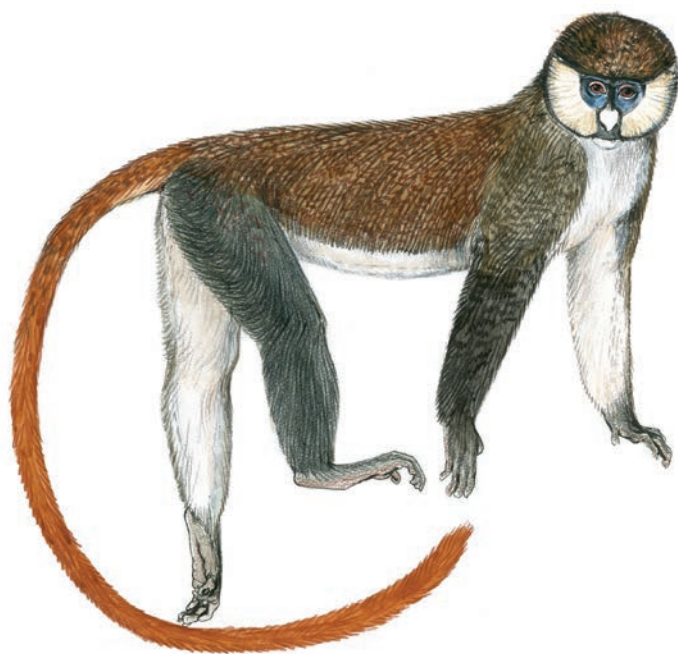
Key References Butynski & Koster 1994; Gartlan & Struhsaker 1972; González-Kirchner 1996; Oates 2011; Struhsaker 2000.

Thomas M. Butynski & Jonathan Kingdon

Cercopithecus ascanius **RED-TAILED MONKEY**

Fr. Ascagne; Ger. Kongo-Weißnasenmeerkatze

Cercopithecus ascanius (Audebert, 1799). Histoire Naturelle des Singes et des Makis 4(2): 13. Lower Congo R., NW Angola.



Red-tailed Monkey *Cercopithecus ascanius*.

Taxonomy Polytypic species within the *Cercopithecus* (*cephus*) Group (or Superspecies). Encompasses five distinct geographic types with an unresolved taxonomy. Lacking detailed information about their distributional boundaries, it is unknown if the various types intergrade, are parapatric or sympatric. Some types, therefore, could be distinct species, especially the Schmidt's Red-Tailed Monkey *Cercopithecus ascanius schmidtii* (Sarmiento *et al.* 2001), but without taxonomic resolution all types are referred here, for practical reasons, to five subspecies (Kingdon 1997, Gautier-

Hion *et al.* 1999, Groves 2001, 2005c, Grubb *et al.* 2003): *C. a. ascanius*, *C. a. atrinatus*, *C. a. katangae*, *C. a. schmidtii*, *C. a. whitesidei*. Synonyms: *atrinatus*, *cirrhorhinus*, *enkamer*, *histrio*, *ituriensis*, *kaimosae*, *kassaiensis*, *katangae*, *melanogenys*, *montanus*, *mpangae*, *omissus*, *orientalis*, *pelorhinus*, *picturatus*, *rutschuricus*, *sassae*, *schmidtii*, *whitesidei*. Many synonyms lack locality data and thus have no subspecific resolution. Chromosome number: 2n = 66 (Chiarelli *et al.* 1979a, Moulin *et al.* 1985, Dutrillaux *et al.* 1988b).

Description Medium-sized, arboreal, long-tailed monkey with heart-shaped, white, yellow, orange or black nose-spot and partially red or orange-red tail, depending on subspecies. Sexes identical in colour of pelage, but adult ♂ has bluer skin on face and on loins than adult ♀. Weight of average adult ♀ ca. 75–80% that of average adult ♂. Adult ♂ has proportionately larger canines. Most subspecies have temporal rosette (hair whorl), variably coloured sub-ocular patch and fronto-temporal band, and black band on cheek and lower jaw. Bare facial skin, blue or purple, less commonly brown/black. Ear helix can have tuft of orange-red or white hairs. Undersurface of throat, body, limbs and proximal tail white, cream or light grey. Dorsum of head, body, limbs and proximal tail agouti; individual hairs translucent, light grey or light brown at base grading into black distally. Distal black half of each hair has one to four orange, straw-yellow or cream bands. According to number, width, spacing and colour of bands dorsum takes on an olive-brown hue, with yellow and red highlights on head and body, respectively. Outer hindlimbs usually lighter in colour than outer forelimbs. Hands and feet, including digits, covered dorsally by black to dark brown hairs, variably single-banded. Distal two-thirds of tail ventrum red or orange hairs. Tail tip usually black dorsally, but ventrally, orange banding of black hairs can produce red highlights. Pedal hairs longer than manual ones, and latter can be sparse on middle and distal phalanges. Exposed skin

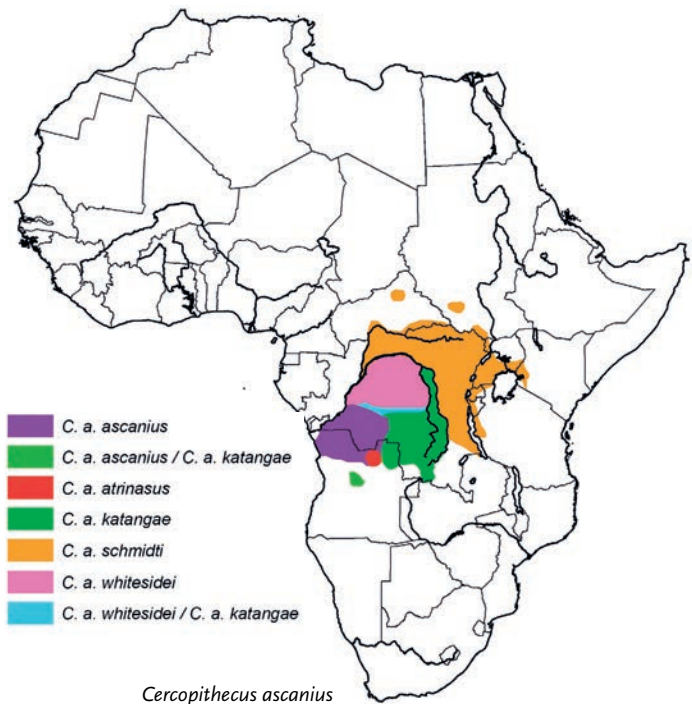
and ischial callosities brown to black. Scrotal skin varying shades of blue. Tail long (ca. 167% of HB). Upper-limb length (humerus + radius) averages 79% of lower-limb length (femur + tibia). Third finger longest, followed by fourth, second and fifth finger. Third and fourth toe sub-equal in length and considerably longer than sub-equal second and fifth toes. Natal pelage soft, woolly, greyish-brown. Nose-spot faint. No red in tail. Palm and sole skin pink. Facial skin much lighter blue than in adult. Adult colour pattern appears as early as three weeks (Haddow 1952), and is fully developed by time first deciduous molars erupt.

Geographic Variation Five subspecies currently recognized (Kingdon 1997, Gautier-Hion *et al.* 1999, Groves 2001, 2005c, Grubb *et al.* 2003). Range limits roughly coinciding with major rivers.

C. a. ascanius Black-cheeked Red-tailed Monkey. South of lower Congo R. and Kasai R., DR Congo, below 500 m. West of Kwilu (Cuilo) R., DR Congo. Eastern and southern extent poorly known. At ca. 15° E and ca. 08° S, but may reach west (left) bank of Kwilu (Cuilo) R., Angola, ca. 19° E where it intergrades with *C. a. atrinasus*. Reports of *C. ascanius* west of upper Kwango (Cuango) R. possibly place these monkeys as far as 11° S (Machado 1969). Cheek-whiskers black. Nose-spot white. Temporal whorl cream. Fronto-temporal band broad and black. Shoulders black. Tail dorsum maroon-red over distal ca. 66–75%. Tail ventrum orange-red over distal ca. 75%. Ears with long, bushy red hairs between helix and anti-helix. Shoulder colour distinguishes *C. a. ascanius* from all other subspecies except *C. a. atrinasus*. Synonyms: *melanogenys*, *picturatus*.

C. a. atrinasus Black-nosed Red-tailed Monkey. In small area (ca. 2500 km²) in extreme north-west Lunda District, Angola, around Wamba R. and Lué R. Fully within *C. a. ascanius* distribution (Machado 1969). Although Zova (08°07' S, 18°04' E, 850 m), the type locality, is near DR Congo border (Machado 1969), this subspecies not reported from DR Congo. Nose-spot and chin black. Upper lip dark brown. Distinct subocular patch absent. Otherwise, resembles *C. a. ascanius* (Machado 1965, 1969). Black nose spot distinguishes *C. a. atrinasus* from all other subspecies. Synonyms: none.

C. a. katangae Katanga Red-tailed Monkey. Mainly south of Equator between Kasai R. and Lualaba R., DR Congo, at 500–1300 m. North of Equator between Lualaba R. and Lomami R., DR Congo, reaching juncture of these rivers at 00°28' N. In west, northern limit is fork of Sankuru R. and Kasai R. Centrally, northern limit is between Sankuru R. and Lomami R. (Machado 1969) around headwaters of Lukenie R. in area of transition with *C. a. whitesidei*. In Angola crosses upper Kasai R. as far west as right bank of upper Kwilu (Cuilo) R. where supposedly mixes with *C. a. atrinasus* (Machado 1969). Local people report *C. a. katangae* at 11° S across central and E Angola and as far west as upper Cuanza R. (Machado 1969), but these might be *C. a. ascanius*. At ca. 11°14' S in NW Mwinilunga District, N Zambia (Ansell 1978). Black fronto-temporal band deficient. Subocular patch and temporal whorl present. Black band on cheek and lower jaw tapering posteriorly. Facial skin dark blue to purple. Tail dorsum dark brown to black. Absence of red on tail dorsum distinguishes *C. a. katangae* from all other subspecies. Synonyms: none.



C. a. schmidtii Schmidt's Red-tailed Monkey. Widest geographic and altitudinal distribution (400–2500 m) of the five subspecies. North of Congo R., east of lower Ubangi R. and Lualaba R., and mainly west of east flank of Western (Albertine) Rift Valley. In small patches of isolated habitat between L. Kyoga and northern shore of L. Victoria. East to Mau Forest, Kenya, reaching west flank of Eastern (Gregory) Rift Valley. In Uganda northern limit is Victorian Nile. West of Western Rift Valley north of Uele R., and Mbomu R. to ca. 06° N in S Sudan and 08°10' N in Central African Republic (Kock 1969, Fay 1988). South along either side of L. Tanganyika reaching Mt Wansisi on the east at ca. 06°45' S (Kano 1971) and Marungu Mts on west at ca. 08° S (Matschie 1893). No information from areas west of Marungu Mts regarding possible overlap with *C. a. katangae*. Cheek-whiskers white. Temporal whorl and subocular patch absent. Ear-tufts usually white but may be orange or red. Tail ventrum grey on proximal one-third. Any one of these characters distinguishes *C. a. schmidtii* from all other subspecies. White proximal tail ventrum in animals from north bank of Congo R. suggests admixture with *C. a. whitesidei*. Synonyms: *enkamer*, *ituriensis*, *kaimosae*, *montanus*, *mpangae*, *orientalis*, *rutschuricus*, *sassae*.

C. a. whitesidei Congo Basin Red-tailed Monkey. Mainly south and east of Congo R. and west of Lomami R., DR Congo, below 500 m. Lukenie R. is southern boundary, but monkeys fitting this description known south of Lukenie R. grading into *C. a. katangae* and *C. a. ascanius*. Yellow (not orange) nose-spot in animals from between Lomami R. and Lualaba R. could indicate transition zone with *C. a. katangae* (Colyn 1988). Monkeys with white tail ventrum from right bank of Congo R. suggest it crosses the Congo R. and interbreeds with *C. a. schmidtii*. Resembles *C. a. katangae*, but distinguishable from all other subspecies by chestnut-red middle third of tail dorsum, and yellow, orange or red nose-spot. Synonyms: *cirrhohinus*, *kassaicus*, *omissus*, *pelorhinus*.

Similar Species Allopatric species belonging to the *Cercopithecus* (*cephus*) Group are similar in size and body colouring but all have a highly distinctive face colour pattern. Sympatric monkeys of the *Cercopithecus* (*mona*) Group, notably Dent's Monkey *Cercopithecus denti* and Wolf's Monkey *Cercopithecus wolffi*, are similar in size but are unlikely to be confused with this species.

Distribution Endemic to forests of tropical Africa. Rainforest, and Afromontane–Afroalpine BZs. East of lower Congo R. and lower Ubangi R. North of Ubangi R. above bend. Northern, eastern and southern limits marked by absence of moist forests, long dry season and decreased rainfall. From N Angola, DR Congo and Central African Republic eastwards to W Kenya and NW Tanzania. Claimed distribution west of Sangha R., Cameroon, and NE border of Congo probably based on misidentifications (Colyn 1999). Absence from forest block between Sangha R. and Ubangi R. (Colyn 1999), and from mangrove and swamp forests circumscribing Congo R. Delta, linked to presence of Moustached Monkey *Cercopithecus cephus*. Reported *C. ascanius* × *C. cephus* hybrids over large areas of Sangha–Ubangi Forest (Colyn 1994) apparently misidentifications (Colyn 1999). See Geographic Distribution for details of distributions of the subspecies.

Habitat Mostly occupies wet (>1300 mm mean annual rainfall) lowland, swamp, gallery, lakeshore, mid-altitude and montane forests from 0 to 2500 m asl, including forest islands, degraded forest and secondary forest. Ranges into *Brachystegia* woodland (eastern shore L. Tanganyika), undifferentiated woodlands, exotic plantations (e.g. Blue Gum *Eucalyptus* spp.), and dryer forest (1100–1300 mm mean annual rainfall) adjoining moist forest habitat. Inhabits small forest patches devoid of other monkeys. Absent from the interior of primary forests where secondary vegetation is uncommon (Schouteden 1944a). Spends most time in lower and middle forest strata (10–20 m), but occasionally seen on ground (Haddow 1952, Gathua 2000a).

Abundance *Cercopithecus a. schmidtii* in East Africa is often most abundant at forest edge and in secondary forest, unless disturbance is extreme. Density ca. 8–184 ind/km² (1.0–13.3 groups/km²) (Cords 1987b, Plumptre & Reynolds 1994, Fashing & Cords 2000, Mitani *et al.* 2001, Fashing *et al.* 2012). Within the same forest, density can vary three-fold across distances of <20 km. Effects of logging disturbance are not consistent across forests. In Budongo F. R., Uganda, density higher in heavily logged (46–60 ind/km²) than in unlogged (8–19 ind/km²) forest (Plumptre & Reynolds 1994, Sheppard 2000). In Kibale N. P., Uganda, highest group densities in lightly logged forest (4.8–11.5 groups/km²), intermediate densities in unlogged forests (3.8–5.6 groups/km²), and lowest densities in heavily logged forests (1.0–2.5 groups/km²; Chapman & Lambert 2000). Variation in density across forests with similar disturbance histories is also considerable. For example, densities in unlogged forests range from 8.3 ind/km² (Budongo F. R.; Plumptre & Reynolds 1994) to 162 ind/km² (Kibale N. P.; Mitani *et al.* 2001).

Adaptations Diurnal and arboreal. Main diurnal activities are foraging and feeding (26–69%), resting (9–59%), moving (5–40%), and various social behaviours (1–8%) (Struhsaker 1980, Cords



Congo Basin Red-tailed Monkey *Cercopithecus ascanius whitesidei* variant morph.

1987b, Jones & Bush 1988, Kirathe 1996, Worch 2002). Locomotion involves mainly climbing and quadrupedal walking, running and leaping on supports 6–25 cm in circumference (Gebo & Chapman 1995). Activity peaks in early morning and late afternoon.

Like all cercopithecines, *C. ascanius* possesses highly innervated, glandular cheek-pouches that probably aid in food processing and digestion. Cheek-pouches serve to reduce feeding competition and predation risk (Lambert 2004). As for other guenons, slow gut passage rates probably facilitate digestion of high fibre diets and detoxify plant secondary compounds, permitting dietary flexibility (Lambert 2002). Small body size allows exploitation of tree periphery, with movement between trees, and foraging in parts of trees where sympatric primates are less agile and/or unable to secure stable supports (E. E. Sarmiento pers. obs.).

Foraging and Food Frugivore-insectivore. Information on foraging and food comes almost entirely from studies of *C. a. schmidtii* in W Kenya and SW Uganda. Daily travel distance 1–2 km and averages ca. 1.5 km, enabling daily coverage of a large portion of home-range (Cords 1987b, Struhsaker & Leland 1988, Gathua 2000a). Group home-ranges 15–67 ha (Mizuno *et al.* 1976, Struhsaker & Leland 1988, Gathua 2000a).

Feeding peaks in early morning and later afternoon, undeterred by rain. Some group members forage or feed at all times of day. Fruit-feeding most common in early morning and late afternoon, leaf-feeding most common at midday. Invertebrate-feeding most common from 08:00–16:00h, and relatively rare later in day (Cords 1987b). Most invertebrate prey (60–65%) collected from foliage (Struhsaker 1978a, Cords 1987b). Search methods include careful turning and unrolling of leaves, with most prey captured directly by mouth, and less commonly by hand. Faster capture techniques allow *C. ascanius* to feed on more mobile prey than sympatric Blue Monkeys *Cercopithecus mitis stuhlmanni*.

Major diet items are fruit (35–61%), invertebrates (mainly insects; 14–31%) and young leaves (7–33%) from trees and lianas (Cords 1987b, Chapman & Chapman 2000, Gathua 2000a). Figs

Ficus spp. are a major fruit class. Prefer ripe to unripe fruit, and leaves with high protein:fibre ratios (Dominy & Lucas 2001). Eats unripe fruit when ripe fruit unavailable (Conklin-Brittain *et al.* 1998). Large seeds are spat out (Lambert & Garber 1998). Will feed on cotyledons and herbs from ground (Gathua 2000a). Flowers, nectar, mature leaves, stems, gum, bark, fungi and shed snake skin make up remainder of known diet. One report of successful hunting of African Green Pigeons *Tieron calva* (Furuichi 2006). Raids Banana *Musa* spp., Mango *Mangifera indica*, Guava *Psidium guajava* and Maize *Zea mays* crops (Naughton-Treves *et al.* 1998). One ♀ observed to drink own urine (Lambert 2000).

In Kakamega Forest, Kenya, *C. ascanius* feeds on up to 98 wild plant species/year, but depends on relatively few plants at any one time. Top ten plant species provide 68–97% of monthly plant-based diet, with *Heinsenia diervilleoides*, *Ficus exasperata*, *Strychnos usambarensis* and *Trilepisium madagascariense* among most important sources across multiple months (Cords 1984b, Gathua 2000a). Proportions of major food items comprising diet can vary from month to month by factors as great as 2.3 for fruits, 3.7 for leaves and 5.0 for invertebrate prey (Cords 1986, Gathua 2000a). When fruit consumption is low, *C. ascanius* feeds primarily on invertebrates, young leaves, flowers or seeds (Cords 1987b, Gathua 2000a). In Kakamega Forest and Kibale N. P., major food items often not consumed in proportion to relative abundance (Gathua 2000a, Chapman *et al.* 2002).

Adult ♂♂ eat more fruit but fewer leaves and invertebrates than adult ♀♀. Juveniles eat more fruit but fewer insects and leaves than adults (Cords 1986). Infants ingest solid food at ca. 2 months (Haddow 1952). They suckle frequently during their first six months and may still suckle occasionally at 1.5 years (M. Cords pers. obs.). Yearlings acquire most of their own food.

Social and Reproductive Behaviour Social. Information on social behaviour comes almost entirely from *C. a. schmidtii* studied in W Kenya and SW Uganda. Typical group size is 25–35 members (3–50; Cords 1987b, Struhsaker 1988, Gathua 2000a), but groups of 10–15 also exist where density is low (Fay 1988, McGraw 1994, Sheppard 2000, Detwiler 2010). Large groups (>50 animals) will fission, with resultant groups dividing original home-range (Struhsaker & Leland 1988, Windfelder & Lwanga 2002). Crop-raiding parties of up to 200 members (Haddow 1952) probably include several groups. Groups usually include one adult resident ♂. Adult ♀♀ make up, on average, 36% of group, and immatures the remaining 60%. During annual mating season, up to six adult ♂♂ per month can join group. Groups in which four adult ♂♂ resided simultaneously for >1 year have been reported (Central African Republic; Galat-Luong 1975). Males leave natal groups as subadults (>4 years old), and can spend >3 years away from groups containing *C. ascanius* ♀♀ (Struhsaker & Pope 1991), living either alone or in loose ephemeral associations. Females remain in natal groups for life.

Intra-group amicable behaviours are more frequent than aggressive behaviours and include grooming and sitting in contact. Grooming bouts in which adult ♂♂ receive grooming from other group members, and adult ♀♀ groom each other, occur disproportionately often (Struhsaker & Leland 1979). Play-wrestling and chasing are most common among young animals. Aggressive behaviour includes shaking of head and forequarters, stare-threats, aggressive growls, chases and contact fights with slapping and biting.



Schmidt's Red-tailed Monkey *Cercopithecus ascanius schmidtii*.

Most agonistic interactions comprise two individuals. Overlap of group home-ranges is 0–64%. Groups defend territorial boundaries with aggressive inter-group encounters once every 3–6 days, and more frequently after group fissions (Cords 1987b, Struhsaker & Leland 1988, Windfelder & Lwanga 2002). Females involved much more than ♂♂ in inter-group aggression. Occasionally adjacent groups do not interact, or they supplant one another without obvious aggression.

Pre-copulatory behaviour includes persistent following by either partner, head-flagging by ♂♂ and lip-puckering by ♀♀. Copulations often involve multiple mounts with intromission and thrusting before final mount ending in a coital pause, possibly associated with ejaculation. Vaginal semen plugs often visible after copulation. Juveniles frequently harass copulating partners and sometimes disrupt copulation. Males gain reproductive access to ♀♀ in several ways. Some ♂♂ take over groups aggressively to become sole residents. Resident ♂♂ occasionally copulate with ♀♀ from neighbouring groups. Non-resident ♂♂ sometimes join a heterosexual group for a few days to several months during the mating season. Often several ♂♂ join a group at once, resulting in a multimale influx. Influx ♂♂ usually confine their visits to just one heterosexual group in a given year (Jones & Bush 1988, Struhsaker 1988). During influx, fights between ♂♂ are frequent, and can lead to severe wounds. Initially ♀♀ respond to incoming ♂♂ with varying degrees of aggression and tolerance, but often mate with multiple ♂♂ (up to five) in a given oestrous period. Influx ♂♂ copulate less frequently than the resident ♂ (Cords 1984a, Struhsaker 1988). Only ♂♂ with full adult body size seen to copulate. Within a month after group takeover, the sole resident ♂ sometimes kills (and eats) young infants. Loss of the suckling infant probably hastens the mother's return to oestrus and increases the infanticidal male's chance of siring offspring (Leland *et al.* 1984). Group members resist infanticide with counter-aggression



Schmidt's Red-tailed Monkey *Cercopithecus ascanius schmidtii* subadult male.

(Struhsaker 1977). Newborns are highly attractive to older group members, especially adult ♀♀ and juveniles. Group members often nuzzle and handle infants but seldom remove them from their mother before 1–2 months of age. Attractiveness to group members diminishes as natal pelage disappears, although juveniles carry and cuddle older infants. Adult ♂♂ seldom interact directly with infants. Infants older than six months are seldom carried (Struhsaker & Pope 1991, Gathua 2000a).

At least eight vocalizations recognized (Marler 1973, Struhsaker 1977, Gautier 1988). Adult ♂♂ give three loud-calls. Short cough-like 'hack' or 'pop' often given during group disturbances, repeated rapidly when group is alarmed, often interposed between 'pyows' of sympatric *C. mitis* ♂♂. 'Ka', a low-pitched (1.15–1.39 kHz) call given singly or in rapid sequence of 2–7 calls (average 4.1, $n = 12$, 'ka-train'; Marler 1973), is usually a response to large raptors (Cords 1987b). Prolonged 'waa' nasal scream sometimes given during male–male fights (Struhsaker 1977, Cords 1984b). Female and juvenile calls lower in volume than those of adult ♂♂. 'Phrased grunts' given during and preceding active periods (feeding, moving). Shrill, bird-like 'chirps' often given repeatedly when alarmed by a predator or during territorial encounters. Searing, high-pitched 'trills' (3.93 kHz mean top frequency, range 2.6–5.0, $n = 14$; Marler 1973) given as submission signals and as vocal exchange when caller is alert but not moving quickly. During aggressive encounters, adult ♀♀ and juveniles often threaten each other with growls, and scream shrilly if attacked. *Cercopithecus mitis* have a similar vocal repertoire but *C. ascanius* calls generally lower in volume and higher-pitched.

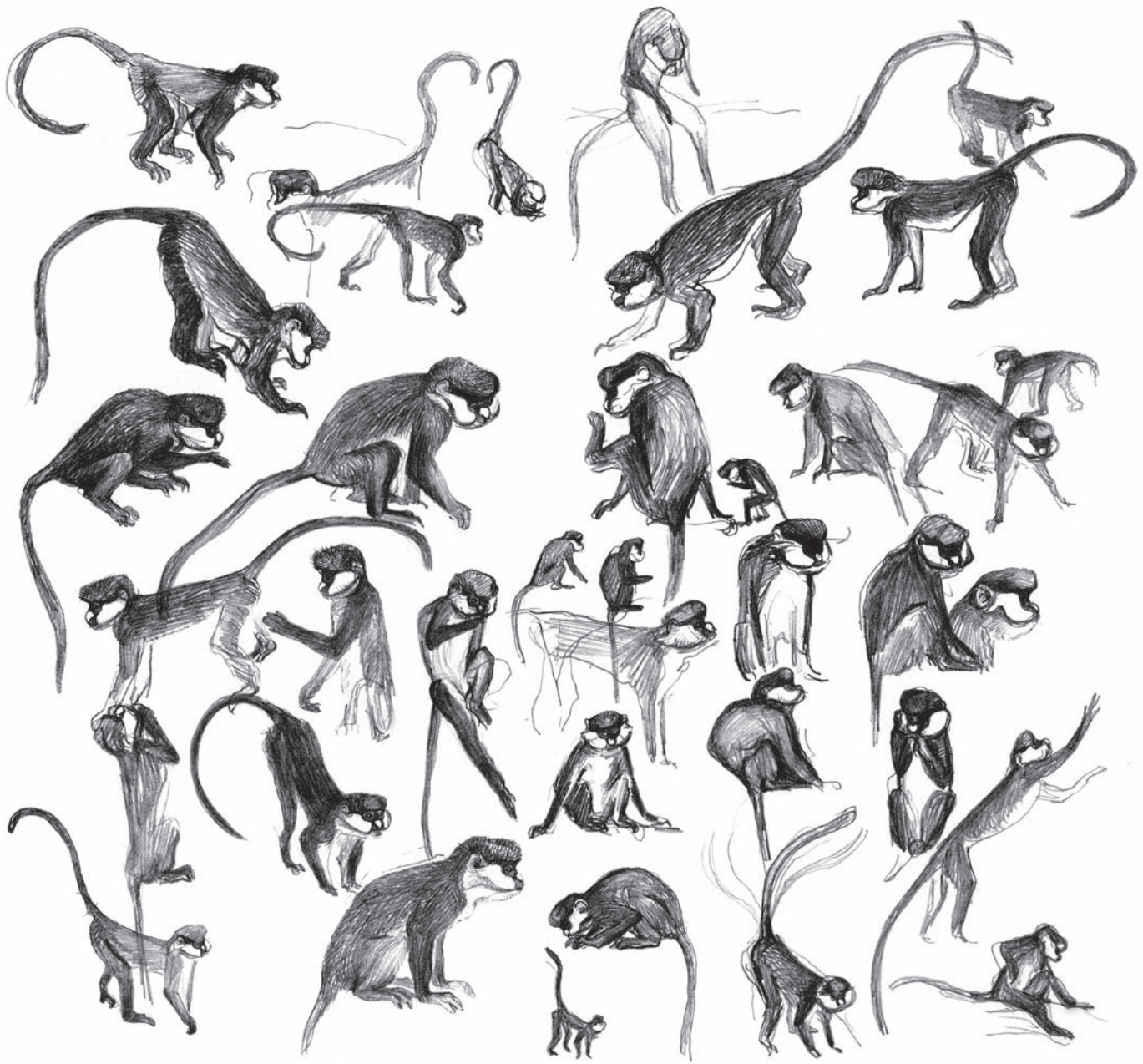
Cercopithecus ascanius often forms mixed-species associations with individuals or groups of other guenon species, and with Guerezas *Colobus guereza*, Ashy Red Colobus *Procolobus rufomitratus tephrosceles* and Grey-cheeked Mangabeys *Lophocebus albigena* (Cords 1987b, Chapman & Chapman 2000, Teelen 2007). In East Africa they avoid De Brazza's Monkeys *Cercopithecus neglectus* and Robust Chimpanzees

Pan troglodytes (Struhsaker 1981a, Wahome *et al.* 1993). Solitary *C. a. whitesidei* sometimes travel with Gracile Chimpanzees (Bonobos) *Pan paniscus* (Maté *et al.* 1996). Associations reduce predation risk and facilitate finding food (Struhsaker 1981a, Cords 1987b). Behavioural interactions with association partners most often involve aggression but also include play and grooming (Struhsaker 1981a, Cords 1987b, Gathua 2000b). Because of relatively small body size, *C. ascanius* usually loses inter-specific aggressive confrontations with sympatric primates. *Cercopithecus ascanius* responds to alarm calls from sympatric monkeys, birds (e.g. Crested Guinea Fowls *Guttera pucherani*, Black-and-white-casqued Hornbills *Bycanistes subcylindricus*, Great Blue Turacos *Corythaeola cristata*) and duikers (e.g. Blue Duiker *Philantomba monticola*, Peter's Duiker *Cephalophus callipygus*) (Struhsaker 1981a, T. Butynski pers. comm., M. Cords pers. obs.). Duikers and *G. pucherani* occasionally move beneath *C. ascanius* groups to eat dropped fruits (Struhsaker 1981a).

Cercopithecus a. schmidtii hybridizes with *C. mitis* in three forests in Uganda and one in Tanzania. Hybrids with *C. m. stuhlmanni* rare in Budongo F. R., Itwara F. R. and Kibale N. P., where only 2–10 hybrids were identified. Hybrids with Doggett's Monkey *C. m. doggetti* much more common in Gombe Stream N. P. (18% of all individuals in groups including *C. m. doggetti* or *C. ascanius*). As deduced from physical appearance and ♀ hybrid maternity, hybrids are fertile, backcross with either parental species, and reside in groups of either parental type. In Kibale N. P., hybrids known to reside only in *C. a. schmidtii* groups (Struhsaker *et al.* 1988). At Budongo F. R. and Gombe Stream N. P., hybrids are in groups of either parental species as well as in mixed-species groups (Aldrich-Blake 1968, Detwiler 2002, Detwiler *et al.* 2005, E. Sarmiento pers. obs.). Genetic studies documenting ♂ hybrid paternity are wanting.

Reproduction and Population Structure Females are in oestrus (accept and/or solicit copulation) for, on average, 6.9 days (1–28, $n = 10$ periods). Most ♀♀ solicit copulations more than once during an annual mating season of up to nine months, with ca. 11–60 day intervals of non-acceptance. Mating appears not to be closely tied to ovulation, and ♀♀ sometimes mate when pregnant (Cords 1984a). No external signs of ovulation or menses observed. Gestation length not known. Mean weight of *C. a. katangae* newborns is 257 g (245–265, $n = 3$) (E. E. Sarmiento pers. obs.). Births most common during 2–6 month period corresponding with end of wet season and subsequent dry season (Nov–Feb) for *C. a. schmidtii* in East Africa (Cords 1984a, Butynski 1988), and end of dry season and subsequent wet season (Apr–Nov) for a compiled sample of *C. a. schmidtii*, *C. a. katangae* and *C. a. whitesidei* from around Bondo (03° 29' N, 23° 24' E), Kisangani (00° 19' N, 25° 19' E) and Kindu (02° 33' S, 25° 33' E), DR Congo (Gevaerts 1992). Peak birth periods correspond with high fruit and arthropod abundance in East Africa (Butynski 1988). Degree of birth seasonality can differ from group to group within a single forest, or annually for populations as a whole (Struhsaker 1997).

In Kakamega Forest, ♀♀ are usually >4 years old when they first give birth (M. Cords pers. obs.), and are only known to give birth to one offspring. Inter-birth intervals average 54 months (49–60, $n = 3$) when previous infant survives >12 months, and 25 months (12–50, $n = 3$) when previous infant dies <2 months after birth (Cords & Rowell 1987). Birth rates vary from group to group within a forest



Schmidt's Red-tailed Monkey *Cercopithecus ascanius schmidtii*.

(0.36–0.74 births/adult ♀/year), with higher birth rates in groups with more stable adult ♂ membership (Kibale N. P.; Struhsaker & Leland 1988). In Kakamega Forest 70–85% of newborns survive to one year of age (Cords 1984a, Cords & Rowell 1987). Assuming a 1 : 1 sex ratio at birth, only ca. 19% of ♂♂ and ca. 60% of ♀♀ live to adulthood. Adult ♀♀ outnumber adult ♂♂ 3 : 1 (Kibale N. P.; Struhsaker & Pope 1991).

Predators, Parasites and Diseases Predators include African Crowned Eagles *Stephanoaetus coronatus* (Mitani *et al.* 2001), Leopards *Panthera pardus* (Kingdon 1984) and Robust Chimpanzees (Nishida *et al.* 1979). In Ituri Forest, DR Congo, ca. 4% of the prey items in Leopard scat were *C. ascanius* (Hart, J.A. *et al.* 1996). Humans also kill *C. ascanius* for food, fur, or as vermin. In response to predators and to species physically resembling predators, *C. ascanius* usually gives

alarm calls and plummets into denser vegetation. Groups known to mob cats (Struhsaker 1981a) and adult ♂♂ rush *S. coronatus* (Leland & Struhsaker 1993).

Osteoarthritis, hypertension, and kidney, heart, spleen, liver and alimentary tract diseases in natural populations (Haddow 1952). Parasitic and commensal infections include nematodes (*Enterobius* sp., *Oesophagostomum* sp., *Streptopharagus* sp., *Strongyloides fulleborni*, *Trichuris* sp.), a Dicrocoeliid liver fluke, tapeworm (*Bertiella* sp.) and protozoans (*Chilomastix mesnili*, *Cryptosporidium* sp., *Entamoeba coli*, *Entamoeba histolitica*, *Entamoeba hartmanni*, *Iodamoeba butschlii*, *Giardia lamblia*, *Hepatozoon* [*Plasmodium*] *kochi*); Haddow 1952, Gillespie *et al.* 2004, Salzer *et al.* 2007, Kooriyama *et al.* 2010). Viral infections include Yellow Fever (Haddow 1952). Simian immunodeficiency virus, tumours and yeast (*Cryptococcus*) infections in captives (Verschoor *et al.* 2004, Cooper *et al.* 2005, Bronson & Mankowski 2006).

Conservation IUCN Category (2012): Least Concern. *Cercopithecus a. atrinatus* is Data Deficient. CITES (2012): Appendix II.

IUCN conservation category is based on supposition that all types belong to one species and this is probably not the case. Population numbers of *C. a. ascanius* and *C. a. atrinatus* are unknown and likely to be low. Taxonomic resolution, therefore, is of utmost importance to the conservation of *C. ascanius*. Threatened most by habitat degradation, agricultural encroachment and forest exploitation. Heavy logging reduces population densities for decades (Chapman *et al.* 2000). Suffers from retaliatory hunting by farmers because of crop-raiding and, in DR Congo, from commercial hunting. *Cercopithecus ascanius* is alert and fast-moving, characteristics that make it relatively difficult to hunt. This, together with a small body size, probably makes *C. ascanius* one of the least attractive African primates to hunt (Butynski & Sanderson 2007).

Measurements

Cercopithecus ascanius

Cercopithecus a. ascanius

HB (♂ ♂): 497 (445–545) mm, n = 3

HB (♀): 470 mm, n = 1

T (♂ ♂): 825 (775–900) mm, n = 3

T (♀): 650 mm, n = 1

HF (♂ ♂): 152 (145–157) mm, n = 3

HF (♀): 125 mm, n = 1

Angola (Sarmiento *et al.* 2001)

Cercopithecus a. katangae

HB (♂ ♂): 494 (470–510) mm, n = 3

HB (♀): 430 mm, n = 1

T (♂ ♂): 799 (750–830) mm, n = 3

T (♀): 630 mm, n = 1

HF (♂ ♂): 145 (144–145) mm, n = 3

HF (♀): 121 mm, n = 1

WT (♂ ♂): 3.7 (2.2–4.9) kg, n = 32

WT (♀ ♀): 3.0 (1.8–4.0) kg, n = 155

DR Congo. Lengths from Sarmiento *et al.* (2001) and E. E. Sarmiento (pers. obs.). WT from Colyn (1994).

Cercopithecus a. schmidt

HB (♂ ♂): 475 (430–515) mm, n = 38

HB (♀ ♀): 408 (340–485) mm, n = 37

T (♂ ♂): 795 (600–920) mm, n = 38

T (♀ ♀): 670 (540–790) mm, n = 37

HF (♂ ♂): 142 (135–155) mm, n = 38

HF (♀ ♀): 124 (110–140) mm, n = 37

WT (♂ ♂): 3.7 (3.0–4.8) kg, n = 32

WT (♀ ♀): 2.8 (2.1–3.8) kg, n = 55

Lengths from Uganda (Haddow 1952). WT from Zaire (Colyn 1994).

Cercopithecus a. whitesidei

HB (♂): 535 mm, n = 1

HB (♀): 443 mm, n = 1

T (♂): 785 mm, n = 1

T (♀): 767 mm, n = 1

HF (♂): 144 mm, n = 1

HF (♀): 135 mm, n = 1

Zaire (E. E. Sarmiento pers. obs.)

Key References Cords 1987b; Gautier-Hion *et al.* 1999; Haddow 1952; Hill 1966; Sarmiento *et al.* 2001; Struhsaker 1988; Struhsaker & Leland 1979.

Marina Cords & Esteban E. Sarmiento

Cercopithecus petaurista LESSER SPOT-NOSED MONKEY

Fr. Pétauriste; Ger. Kleine Weißnasenmeerkatze

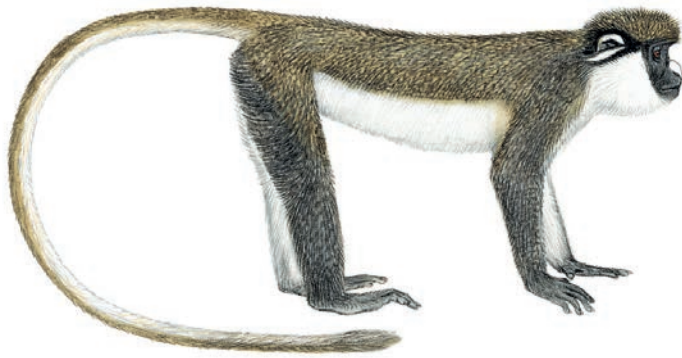
Cercopithecus petaurista (Schreber, 1774). Die Säugethiere 1: 97, 185. 'Guinea'.



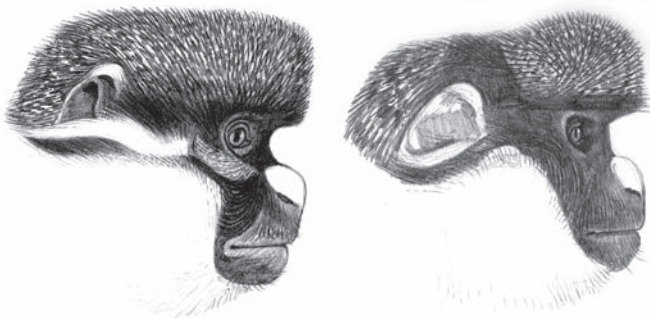
Eastern Lesser Spot-nosed Monkey *Cercopithecus petaurista petaurista*.

Taxonomy Polytypic species (Napier 1981, Kingdon 1997, Groves 2001, 2005c, Grubb *et al.* 2003, Oates 2011). Member of the *Cercopithecus (cephus)* Group or Superspecies. Originally described by Schreber as *Simias petaurista* from a type locality listed simply as 'Guinea'. No type specimen available. As noted by Hill (1966) and Oates (1988b), Schwarz (1928b) wrongly regarded members of this species as subspecies of Putty-nosed Monkey *Cercopithecus nictitans*. Synonyms: *albinasus*, *buettikoferi*, *fantiensis*, *pygrius*. Chromosome number: 2n = 66 (Dutrillaux 1988b, Romagno 2001).

Description Small, long-tailed, arboreal monkey with white nose. Sexes similar in colour. Adult ♀ weighs ca. 66% as much as adult ♂ (Oates *et al.* 1990). Face black with white stripe extending from temple laterally and inferior to the ear. Superior ridge of pinna has white tuft. Crown, back, thigh, arm and tail are predominately olive-green or khaki. Mid to lower back reddish in some forms. Individual hairs flecked with black and yellow, particularly on crown above orbits. On the limbs the khaki coat graduates to grey distally.



Eastern Lesser Spot-nosed Monkey *Cercopithecus petaurista petaurista*.



Left: Western Lesser Spot-nosed Monkey *Cercopithecus petaurista buettikoferi*.
Right: Eastern Lesser Spot-nosed Monkey *Cercopithecus petaurista petaurista* adult male.

towards hands and feet. Ventral surfaces of throat, chest, limbs and tail are white or cream. Infant has colour and pattern of adult.

Geographic Variation

C. p. petaurista Eastern Lesser Spot-nosed Monkey. From Sassandra R., Côte d'Ivoire, to W Togo. Margins around orbit completely black.

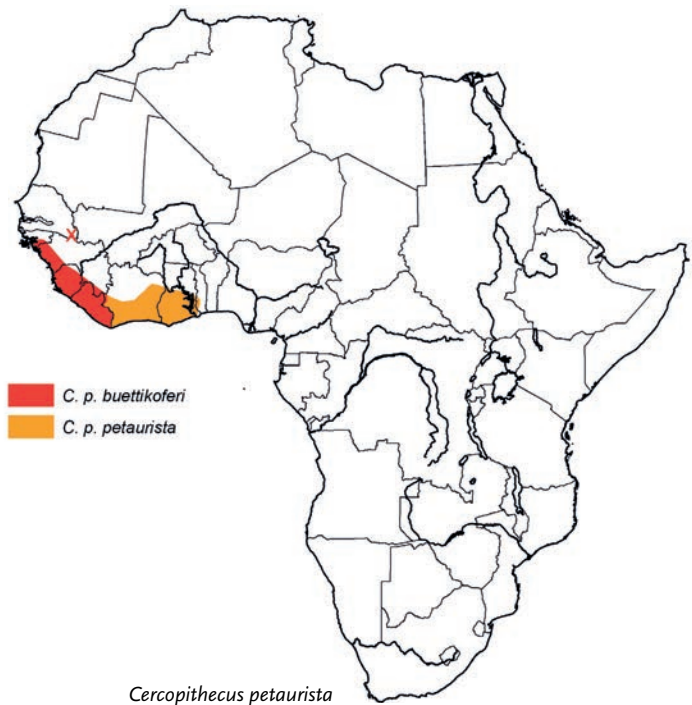
C. p. buettikoferi Western Lesser Spot-nosed Monkey. From Sassandra R. to Guinea (possibly). Margins around infero-lateral orbital rim khaki-coloured.

Subspecies range demarcation debated. Napier (1981) states that Sassandra R. approximates the subspecies boundary. Oates (1988b) states that the boundary is the Cavally R. on the Liberia–Côte d'Ivoire border. The ranges of *buettikoferi* and *petaurista* overlap between the Cavally R. and Nzo R., where intermediate individuals (e.g. BMNH 1956.309) have been collected (Oates 1988b, Groves 2001). Specimens reported from the Guinea-Bissau archipelago (Monard 1938, Frade 1949) may be from introduced populations.

Similar Species

Cercopithecus nictitans stampflii. Sympatric. Body larger and coat darker. Ventrums black. No white stripe on lateral sides of face.

Cercopithecus erythrogaster. Allopatric. Ventrums varies from grey to red. No white stripe on lateral sides of face. White spot on nose absent in some forms.

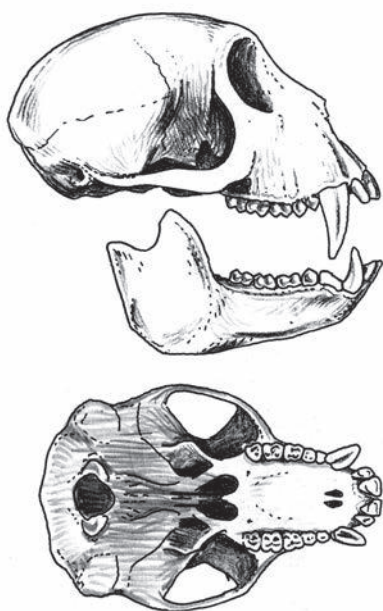


Cercopithecus petaurista

Distribution Endemic to West Africa. Rainforest BZ. Common and widespread in most forest types from Sierra Leone to W Togo. Presence of mainland populations north-west of Sierra Leone is unclear (Oates 1988b). Groves (2005c) states that Gambia is this species' western limit, though Starin (1989) does not cite it among the five cercopithecids in this country. Dupuy (1972) reports E. Brewer's sighting of *C. nictitans* in Casamance, Senegal, near the Gambia border, but these might be *C. petaurista*. He also reports that *C. nictitans* (perhaps *C. petaurista*) is known from Guinea-Bissau and Guinea. Surveys in Kounounkan Forest, Guinea (Barnett *et al.* 1994), failed to locate *C. petaurista*. Gippoliti & Dell'Omo (2003) report *C. petaurista* in Guinea Bissau. First record of *C. p. petaurista* in Tambacounda region, SE Senegal, reported in 2005 (Pruetz *et al.* 2010). See Geographic Variation.

Habitat Primary forest is preferred habitat but populations abundant in disturbed (secondary) forest throughout range (Coe 1975, Harding 1984a, Sayer & Green 1984, Barnett & Prangley 1997, Grubb *et al.* 1998, McGraw *et al.* 1998b, McCullough 2004, Gonedélé Bi *et al.* 2006). In thick stands of palms in Guinea-Bissau. Occurs between 500 and 800 m asl on Mt Nimba. A frequent crop-raider (Mackenzie 1952), *C. petaurista* thrives in abandoned farm clearings and young successional forest (Fimbel 1994b); adaptable to multiple habitat types.

Abundance Surveys in Sierra Leone, Côte d'Ivoire and Ghana (Oates 1988b, McGraw *et al.* 1998b, Gonedélé Bi *et al.* 2006) suggest that *C. petaurista* is one of the most abundant forest monkeys in West Africa due to its ability to exploit areas of secondary growth. On Tiwai I., Sierra Leone, densities are 3.3–4.0 groups/km² or 46–56 individuals/km² (Oates *et al.* 1990). At Taï N. P., Côte d'Ivoire, in protected primary forest, *C. petaurista* ranks second in number of group encounters ($n = 427$) and fourth in number of individual encounters ($n = 7455$) out of seven species (Galat & Galat-Luong 1985). Density here is 21 ind/km² (Buzzard 2006c).



Lateral and palatal views of skull of Lesser Spot-nosed Monkey *Cercopithecus petaurista* adult male.

Adaptations Diurnal and arboreal. Generalized skeleton typical of tree-dwelling guenons (Gebo & Sargis 1994). Cryptic, cautious monkey that prefers the forest understorey and areas of dense, secondary growth. In undisturbed forest, spends >75% of time in understorey; rarely ascends to top of high canopy trees (Galat & Galat-Luong 1985, McGraw 2000). Locomotion tends to be slow, cautious and deliberate, which accords well with its overall cryptic life-style (McGraw & Zuberbühler 2007). Predominantly quadrupedal (71%) with moderate amounts of climbing (19%) and leaping (10%) ($n = 512$; McGraw 2000). Inter-membral index of 81 (Fleagle 1999). As is typical of forest guenons, *C. petaurista* spends the majority of time in trees during all activities. In primary forest, uses large boughs (10–29%), branches (including lianas) (49–55%) and twigs (24–39%) (Galat & Galat-Luong 1985, $n = 1199$; McGraw 2000), with almost no differences between young and adults nor between adult ♂♂ and adult ♀♀ (Galat 1983). Like all cercopithecines, uses cheek-pouches to store food while foraging (Buzzard 2006a). When cheek-pouches are expanded, white throat region becomes prominent, resembling a snowball. Activity budget of one group at Tai Forest is feeding (38%), resting (32%), social (4%), travelling (7%) and foraging (18%) (McGraw 2000). An able swimmer, with young occasionally playing in rivers and streams.

Foraging and Food Omnivorous. Foraging is generally slow and cautious. Small body size allows individuals of all ages to easily acquire food from terminal branches and twigs as well as from larger supports (Galat & Galat-Luong 1985). Feeding (38%) and foraging (18%) comprise largest portion of activity budget ($n = 2042$, McGraw 2000). Diet varies seasonally (Galat & Galat-Luong 1985, Buzzard 2006b). Annual diet at Tai is comprised of leaves 40%, fruit 34%, 12% insects, flowers 6%, and other 8% (Buzzard 2006a, b, $n = 924$). Foliage and fruit from lianas are especially important (Buzzard 2006a). Key food items in primary forest include *Saccoglottis gabonensis*, *Dialium aubrevillei* and *Memecylon lateriflorum*

(Buzzard 2006b). At Tai, *C. petaurista* forages in more dispersed groups than sympatric Campbell's Monkey *Cercopithecus campbelli* and Diana Monkey *Cercopithecus diana* (McGraw 2000, McGraw & Zuberbühler 2007). Two groups at Tai had an average daily travel distance of 1051 m (S.D. 263, $n = 77$ days; Buzzard 2006c). Home-ranges at Tai were ca. 41–69 ha (Galat & Galat-Luong 1985, $n = 1$; Buzzard 2006b, c, $n = 2$). Home-ranges overlapped 64% those of neighbouring groups (Buzzard & Eckardt 2007). At Dezidougou, Côte d'Ivoire (80 km east of Bouake), G. Galat & A. Galat-Luong (pers. obs.) radio-tracked a group that moved through 94 ha of cultivated fields and young secondary growths.

Social and Reproductive Behaviour Social. At Tai, groups average 10.5–11.3 individuals (4–24, $n = 25$ groups) and usually contain one adult ♂, several breeding ♀♀ and their offspring (Galat & Galat-Luong 1985, Buzzard & Eckardt 2007). One group, after a ♂ take-over, contained two adult ♂♂ for five months of a 17 month study (Buzzard & Eckardt 2007). One group at Tiwai I. comprised 14 animals (Oates *et al.* 1990). The core of the group consists of related ♀♀; ♂♂ disperse from their natal groups. One solitary adult ♂ observed (Galat & Galat-Luong 1985). During movement young cling to their mother's ventrum until about six months of age. Individual members make frequent, soft, 'wurring' contact calls to maintain group cohesion. Adult ♂♂ produce loud-calls resembling a 'hiccup-growl', often in duets with *C. campbelli* (McGraw & Zuberbühler 2007, 2008). Adult ♂ loud-call is most similar to that of Red-bellied Monkey *Cercopithecus erythrogaster* (Gautier 1988). Non-resident adult ♂♂ may move alone or with groups of Olive Colobus *Procolobus verus* or Western Red Colobus *Procolobus badius*.

At Tai, inter-group encounters are four times more common among *C. petaurista* groups than among *C. campbelli* groups. During encounters, members typically ignore each other and aggressive interactions are rare. Aggressive encounters usually occur at feeding sites; adult ♂♂ take active roles including giving loud-calls and head bobs directed at the other group (Buzzard & Eckardt 2007). Agonistic interactions with *C. campbelli* and *C. diana* are frequent (McGraw & Zuberbühler 2007). *Cercopithecus petaurista* occasionally groom *P. verus* and *P. badius*, as well as by other *Cercopithecus* spp. Form polyspecific associations with all other monkeys especially *C. campbelli*, *C. diana* and *P. verus* (Galat & Galat-Luong 1985, Buzzard & Eckardt 2007, McGraw & Zuberbühler 2007, 2008, Buzzard 2010).

Reproduction and Population Structure Poorly known. No visible changes in sexual skin of ♀♀ are apparent. Gestation period is seven months. Single births are the norm. Preliminary evidence indicates that births occur year round. A captive ♀ lived to 29 years (Hill 1966).

Predators, Parasites and Diseases Frequently preyed upon by African Crowned Eagles *Stephanoetus coronatus* (Shultz *et al.* 2004, McGraw *et al.* 2006, Shultz & Thomsett 2007). Occasionally eaten by Robust Chimpanzees *Pan troglodytes* (Boesch & Boesch-Achermann 2000) and Leopards *Panthera pardus* (Hoppe-Dominik 1984, Zuberbühler & Jenny 2002, 2007). Easily and often hunted by humans. Infants and juveniles are frequently kept by villagers (McGraw *et al.* 1998b, McGraw 2007b). As *C. petaurista* are still found in sacred forests and other forests near villages. As healthy

carriers, they play a major role in Yellow Fever outbreaks in the forest–savanna contact area (Galat & Galat-Luong 1997). During a Yellow Fever outbreak in Côte d'Ivoire, a survey of primates found 64% had antiamaril antibodies, 30% of which with high titre ($n = 24$ monkeys; Lhuillier *et al.* 1982). No simian immunodeficiency virus detected (Bibollet-Ruche *et al.* 2004, Apetrei *et al.* 2005).

Conservation IUCN Category (2012): Least Concern. CITES (2012): Appendix II.

This is probably the most common monkey in West Africa, although its numbers are undoubtedly decreasing owing to habitat loss and hunting for the bushmeat trade.

Measurements

Cercopithecus petaurista

HB (♂ ♂): 492 (440–527) mm, $n = 10$

HB (♀ ♀): 411 (290–493) mm, $n = 9$

T (♂ ♂): 712 (523–787) mm, $n = 10$

T (♀ ♀): 649 (556–690) mm, $n = 9$

HF (♂ ♂): n. d.

HF (♀ ♀): 121 mm, $n = 1$

E (♀ ♀): 35 mm, $n = 1$

WT (♂ ♂): 4.4 (3.9–5.0) kg, $n = 13$

WT (♀ ♀): 2.9 (2.3–3.8) kg, $n = 7$

Various localities. HB & T (Napier 1981), HF & E (Hill 1966), WT (Oates *et al.* 1990)

Key References Buzzard 2006a, b, c; Galat & Galat-Luong 1985; McGraw 2000; McGraw & Zuberbühler 2007; Oates 2011; Oates *et al.* 1990.

W. Scott McGraw, Anh Galat-Luong & Gérard Galat

Cercopithecus erythrogaster WHITE-THROATED MONKEY (RED-BELLIED MONKEY)

Fr. Cercopithèque à ventre rouge; Ger. Rotbauchmeerkatze

Cercopithecus erythrogaster Gray, 1866. Proc. Zool. Soc. Lond. 1866: 169. 'West Africa'.

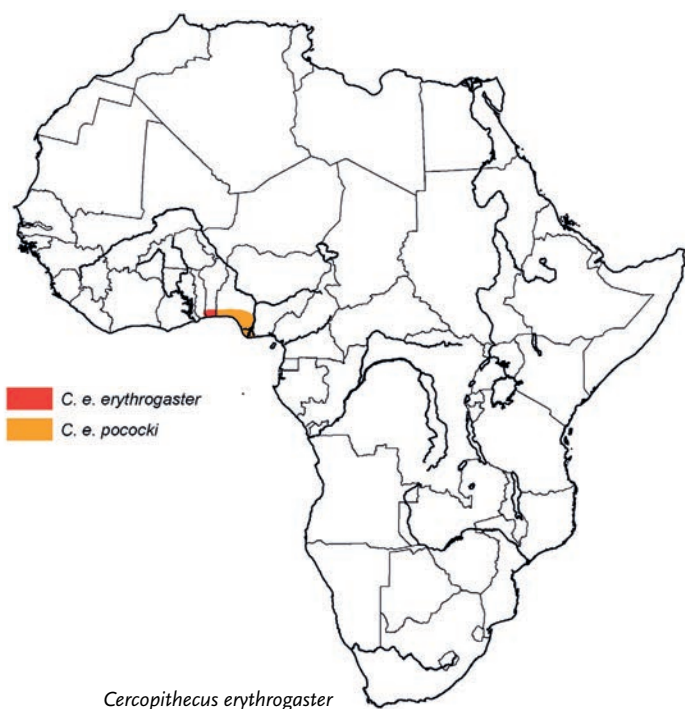


Red-bellied Monkey *Cercopithecus erythrogaster erythrogaster* adult male.

Taxonomy Polytypic species. Member of the *Cercopithecus* (*cephus*) Group or Superspecies (Kingdon 1980, Groves 2001, 2005c, Grubb *et al.* 2003, Oates 2011). Hill (1966) followed Booth (1956a) in placing *C. erythrogaster* in the *Cercopithecus* (*petaurista*) Superspecies; Booth excluded Moustached Monkey *Cercopithecus cephus* and Red-eared Monkey *Cercopithecus erythrotis* from this species, but Hill excluded only *C. cephus*. Most authorities now recognize the affinities of all these forms, of which *C. cephus* was the first-named.

Schwarz (1928b) listed *erythrogaster* as a subspecies of the Putty-nosed Monkey *Cercopithecus nictitans*, and he later (Schwarz 1954) argued that *Cercopithecus signatus* is a synonym of *C. erythrogaster*. However, *C. erythrogaster* and *C. nictitans* are broadly sympatric in W Nigeria and are clearly separate species. Oates (1985) notes that the three museum specimens assigned to *signatus* are very different from *erythrogaster* and may be hybrids between *C. nictitans* and some member of the *C. cephus* group. Two subspecies of *C. erythrogaster* are recognized, Red-bellied Monkey *C. e. erythrogaster* and Nigeria White-throated Monkey *C. e. pococki* (Grubb *et al.* 2003, Groves 2005c, Oates 2011). Synonyms: none. Chromosome number: $2n = 66$ (Moulin *et al.* 2008).

Description Small, long-tailed monkey with prominent white ruff on front and sides of neck and gold-flecked diadem. Sexes alike but adult ♀ smaller than adult ♂. Cheek-tufts of light yellow-and-black banded hairs. Diadem distinct; gold-flecked, edged black, the result of 2–3 mm long golden-yellow bands about 5 mm below the tip of black hairs. Throat with prominent white ruff extending onto sides of neck. Back, flanks, outer proximal limbs and dorsal proximal surface of tail reddish-brown with olive tinge. Lateral surfaces of forearms black or dark brown. Ventrums bright rust-red or brownish-grey, depending on the subspecies. Tail with pale greyish-white ventral surface and dark tip. Viewed in the dense forest understorey, this monkey appears dark, with only the white throat, gold crown patch and light tail undersurface standing out. Infant pelage like adult but paler and less well demarcated (P. Neuenchwander & J.-M. Lernoould pers. comm.).



Geographic Variation

C. e. erythrogaster Red-bellied Monkey. S Bénin and far eastern edge of Togo. Ventrums bright rust-red.

C. e. pococki White-throated Monkey. SW Nigeria and Niger Delta. Ventrums brownish-grey, sometimes with slight reddish tinge. Although the name 'pococki' was used on the label of the holotype in the British Museum (Natural History) by J. G. Dollman, and referred to by Napier (1981), it was not validated until 1999 (Grubb *et al.* 1999).

Similar Species

Cercopithecus petaurista. Not sympatric with *C. erythrogaster*, but present to the west from Senegal to W Togo. Nose-spot, ears, stripe below the ears and belly white.

Cercopithecus sclateri. Possibly sympatric with *C. e. pococki* in east. SE Nigeria, between Niger R. and Cross R. Nose-spot and ears white. Muzzle pinkish. Ventral surface of proximal part of tail red.

Distribution Endemic to E Togo, S Bénin and S Nigeria. Rainforest BZ. Restricted to dry and, particularly, moist forest. In Togo restricted to the Togodo Faunal Reserve (310 km²) adjacent to the Bénin border. In Bénin in Lama Forest (a forest relict in the Dahomey Gap), in Lokoli Forest, in several small forest patches in the lower Ouémé R. Valley (most of which are sacred groves), along Okpara R. and Mono R., and possibly at Banon (08° 29' N) (Oates 1996b, Sinsin *et al.* 2002a, Campbell *et al.* 2008b, Nobimè *et al.* 2009, 2011). In Nigeria on both sides of Niger R., from near Ijebu-Ode in the west to Orashi R. at eastern edge of Niger Delta in east (Oates 1985, Powell 1995). On west bank of Orashi R., in vicinity of Upper Orashi F. R., there may be a hybrid zone between *C. e. pococki* and *C. sclateri* (see *C. sclateri* profile).

Current distribution of *C. e. pococki* in Nigeria is probably similar to historical distribution, but populations are today greatly fragmented due to forest destruction for agriculture. Distribution of

C. e. erythrogaster in Bénin and Togo is much smaller than its presumed historical distribution, with area of occurrence in Bénin in 2000 estimated at 24% of its extent in 1950 (Sinsin *et al.* 2002b).

Habitat Lowland moist and dry semi-deciduous forest, gallery forest and (in the Niger Delta and Ouémé R. Valley) seasonally flooded swamp and marsh forest (Oates 1985, Sinsin *et al.* 2002b, Nobimè *et al.* 2009). *Cercopithecus e. erythrogaster* can also survive in small patches of secondary vegetation in a fragmented landscape (Hanon 2001, Campbell 2005). Annual rainfall within the species' range is from ca. 1100 mm in S Bénin (where there are two dry seasons) to >2500 mm in the Niger Delta (where only Nov–Feb are relatively dry). *Cercopithecus erythrogaster* typically frequents the lower levels of the forest canopy, and dense tangled growth in canopy gaps and along rivers. Altitudinal range ca. 0–400 m.

Abundance Common in suitable habitat when hunting pressure is low. The second most frequently encountered monkey in Okomu N. P., SW Nigeria, where, in 1994 there were >30 ind/km² (Robinson 1994). In Okomu N. P., in 2008–09, 0.11 groups/km (2.7 group/km²; Akinsorotan *et al.* 2011). In Lama Forest, ca. 10.4 ind/km² in 'dense' (= mature) forest and 7.5 ind/km² in disturbed forest (Goodwin 2006). Throughout its range, however, *C. erythrogaster* is now generally rare due to intense commercial hunting. There are >3400 *C. erythrogaster* in the core of Okomu N. P. (the former Wildlife Sanctuary) (Robinson 1994), while estimates for the Lama Forest are 300–800 individuals (Kassa 2001, Campbell 2005, Goodwin 2006).

Adaptations Diurnal and arboreal. Like other members of the *C. (cephus)* Group, this small, highly arboreal monkey is an agile quadruped, walking, running and climbing quietly through the forest on small and medium-sized supports. *Cercopithecus erythrogaster* appears to have high aural and visual acuity. Will quickly drop out of sight on detecting approaching humans, and creep away silently through the lower canopy (Robinson 1994).

Foraging and Food Omnivorous. Foraging and feeding behaviour of *C. erythrogaster* have not been the subject of systematic study. In a few sightings of undisturbed wild animals in Nigeria, they forage (as a group) in a dispersed fashion, carefully searching for such food items as small fruits and insects (Oates 1985). In Lama Forest, fruit (especially *Mimusops andongensis* and *Diospyros mespiliformis*) is the predominant food item, while groups living in sacred groves raid farm crops (Sinsin *et al.* 2002b). Often in close association with other monkeys, especially Mona Monkey *Cercopithecus mona*; in 127 sightings of *C. erythrogaster* in Lama Forest, in association with *C. mona* on 50% of occasions (Goodwin 2006).

Social and Reproductive Behaviour Lives in social groups, but group size not accurately measured; no groups yet habituated to humans, and the species is cryptic in its behaviour. In Nigeria most groups probably range in size from 5 to 20; average group size may be <10 at Okomu (Mason 1940, Oates 1985, Robinson 1994). In S Bénin group size estimated to average five individuals, with a range of 2–12 (Campbell 2005). Adult ♂♂ have a distinctive low frequency, guttural, 'croaking' (or 'growling') loud-call, similar to that of Lesser Spot-nosed



White-throated Monkey *Cercopithecus erythrogaster*.

Monkey *Cercopithecus petaurista* (Oates 1985). In Lama Forest these calls commonly follow the loud-calls of ♂ *C. mona* (Goodwin 2006). Loud-calls usually come from only one location in a group, suggesting that one-male groups are the norm. Solitary adult ♂♂ occasionally seen. No details of reproductive behaviour available, but *C. erythrogaster* likely resembles other members of the *C. (cephus)* Group.

Reproduction and Population Structure No information.

Predators, Parasites and Diseases No information available, but humans are the most important predator at the present time. African Crowned Eagle *Stephanoaetus coronatus* prey on other members of the *C. (cephus)* Group elsewhere, but they are now rare within the range of *C. erythrogaster*.

Conservation IUCN Category (2012): Vulnerable. Endangered as *C. e. erythrogaster* and Vulnerable as *C. e. pococki*. CITES (2012): Appendix II.

Due to habitat destruction and modification, remaining populations occur in a fragmented pattern, and almost all are hunted. The largest remaining population of *C. e. erythrogaster* is probably in Lama Forest (163 km²), Bénin, whose 'Noyau Central' (48 km², of which 19 km² is natural forest) is managed by the Office National du Bois; some smaller populations in Bénin receive protection through their occurrence in sacred groves. The largest population of *C. e. pococki* is in the central part of the Okomu F. R., Edo State, Nigeria, which became a Wildlife Sanctuary in 1985 and a National Park in 1999 (the

original size of Okomu F. R. was 1200 km², but much of this area is now plantations and farms; the National Park covers ca. 181 km²). *Cercopithecus e. pococki* also occurs in Omo F. R., Ogun State, Nigeria, where a protected area is planned. The largest area of continuous forest remaining within the range of *C. erythrogaster* is in the Niger Delta; this forest contains no protected area and has been everywhere modified by logging, but hunting pressure is lower there than in other parts of S Nigeria.

Measurements

Cercopithecus erythrogaster

HB (♂): 457 mm, n = 1

HB (♀ ♀): 429 (381–457) mm, n = 3

T (♂): 864 mm, n = 1

T (♀ ♀): 640 (584–700) mm, n = 3

HF: n. d.

E: n. d.

WT (♀): 2.4 kg, n = 1

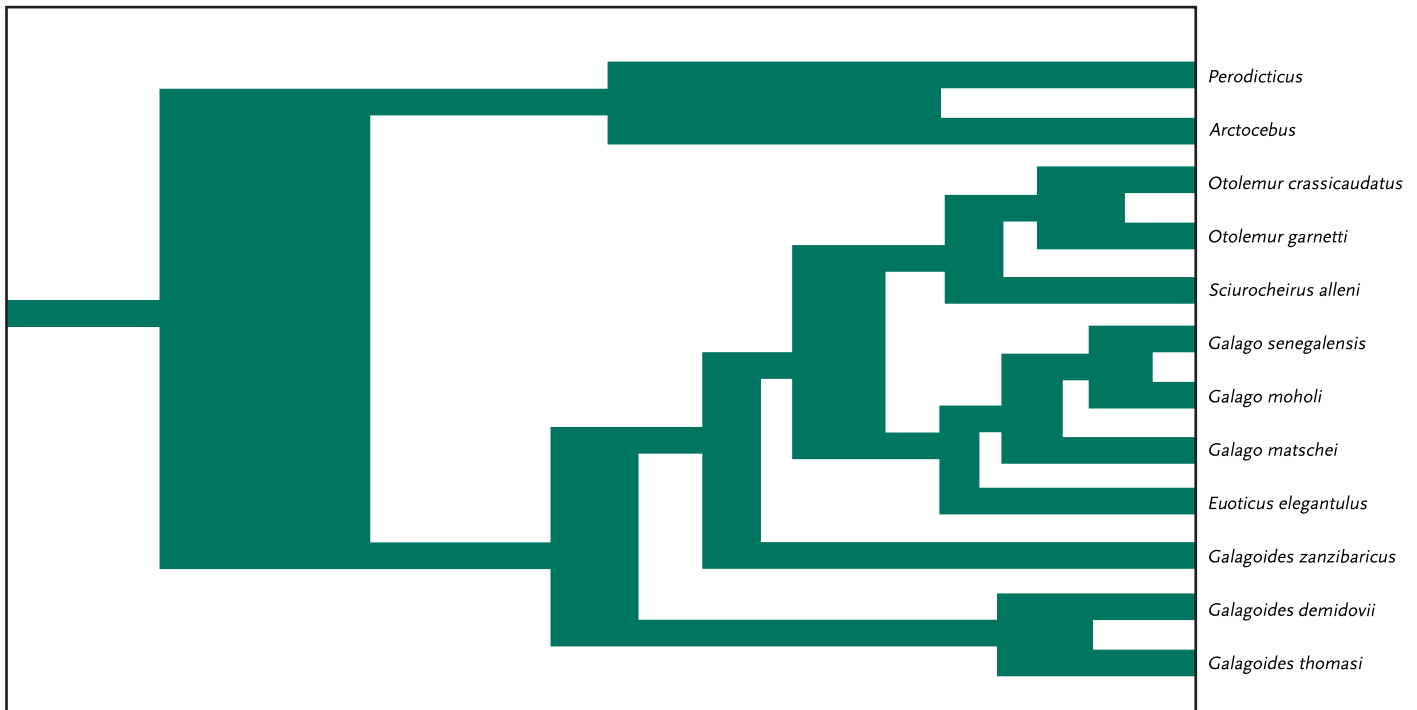
Lengths from BMNH (Napier 1981). WT from Okomu, Nigeria (Oates 1985). See Nobimè *et al.* (2011).

Key References Grubb *et al.* 1999; Nobimè *et al.* 2009, 2011; Oates 1985, 2011; Sinsin *et al.* 2002b.

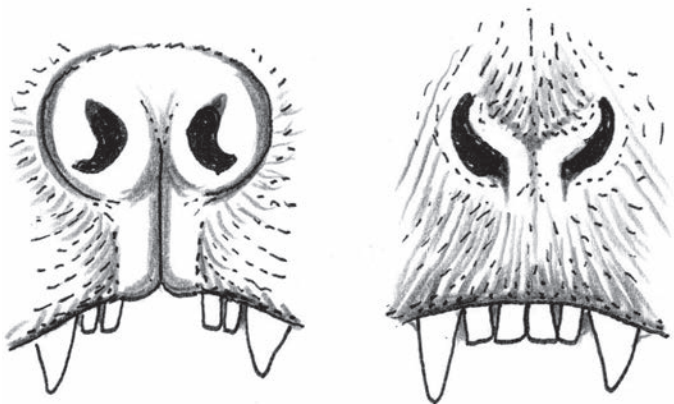
John F. Oates

Suborder STREPSIRRHINI – Strepsirrhines: Lemurs, Lorises, Pottos, Galagos

Strepsirrhini É Geoffroy, 1812. Ann. Mus. Hist. Nat. Paris 19: 156.



Tentative phylogenetic tree for the African lorisoids Lorisoidea (after Masters *et al.* 2007).



Nasal structure in (left) Strepsirrhines and (right) Haplorhines (after Martin 1990).

The Strepsirrhini are arboreal primates with typically monkey-like hands and woolly coats but most have pointed, scent-sensitive noses. Their unfortunate name means ‘twist-nosed’ while their popular vernacular name, ‘prosimian’, meaning ‘monkey-forerunner’, has the misleading implication of animals frozen in a time-warp. In reality they are distinctive and successful members of many modern ecological communities.

Commonly grouped under the appellation of Prosimii (Simpson 1945), the reasons for abandoning this name have been discussed in the profile for order Primates. We, in common with most contemporary workers, use É. Geoffroy’s (1812b) ‘Strepsirrhini’ to embrace all the lemurs, lorises, pottos and galagos. Strepsirrhini is generally thought also to embrace the fossil families Adapidae, Notharctidae and Sivaladapidae. When fossil adapids are excluded, the remaining extant strepsirrhines are sometimes described as ‘Lemuriloriformes’ (Groves 2001), but for the purposes of any classification of living primates, this taxon can be taken as synonymous with Strepsirrhini.

Phylogenies based on molecular clocks come up with different dates for divergence of strepsirrhines from anthropoid primates during the Cretaceous, from as early as 90 mya (Douady & Douzery 2003, Bininda-Emonds *et al.* 2007), to 87 mya (Perelman *et al.* 2011), to 80 mya (Arnason *et al.* 1998), while phylogenies based on a sparse fossil record suggest divergence well after the Cretaceous–Tertiary Boundary (‘K–T Boundary’), 65 mya; Gingerich & Uhen 1994, Wible *et al.* 2007). Substantial differentiation among fossil primates by the Paleocene make the later dates less plausible but both the time and place for strepsirrhine origins remain uncertain.

There are two major groups of African strepsirrhines (or ‘lemuriforms’). Groves (1989) allocated them both to the family Lorisidae, with the potto and allies in the subfamily Lorisinae and galagos in the subfamily Galaginae. He subsequently (Groves 2001) upgraded Galagonidae to familial rank, separating the African members of the Loridae into the subfamily Perodicticinae while



Potto *Perodicticus potto* infant showing very supple vertebral column and exceptionally flexible limbs.

Lorinae embraced all the Asiatic lorises. We here follow this change in ranking, although in line with Opinion 1995 of the International Commission on Zoological Nomenclature (2002), we revert to the names Lorisidae, Lorisinae, Galagidae and Galaginae. The change in ranking reflected new molecular discoveries that imply that some of the detailed resemblances between African and Asiatic Lorisidae are essentially convergent. Exactly how the Perodicticinae relate to the Asian lorises and when there was an inter-continental exchange still remains uncertain and controversial.

The galagos are arboreal walkers and leapers with long tails, elongated hindlegs and relatively large ears. The potto group are arboreal clingers and climbers with short tails, limbs of equal length and relatively short ears. Both groups are wholly nocturnal, have round heads, pointed muzzles, forward-facing eyes, a moist nose and a cleft, 'tied' upper lip. They are distinct from other primates in the structure of their placenta, retina, inner ear, blood circulation and digestion. All species have modified lower incisors, which form a fur comb (in some species the incisors also form a sharp chisel). In this respect modern strepsirrhines differ from all early fossil 'prosimians', none of which show modified lower incisors. Hands, feet and nails have been modified in various minor ways but all have a spatulate, fur-grooming claw on the second digit of the foot. These specializations, known to be very ancient within living lineages, serve to keep the woolly fur in good condition. Prosimian fur is important not only as a typical mammalian insulator but also as an indicator of sexual, social and individual status through its role as a scent-dispenser for a variety of secretions produced by glands, excreta, skin and hair

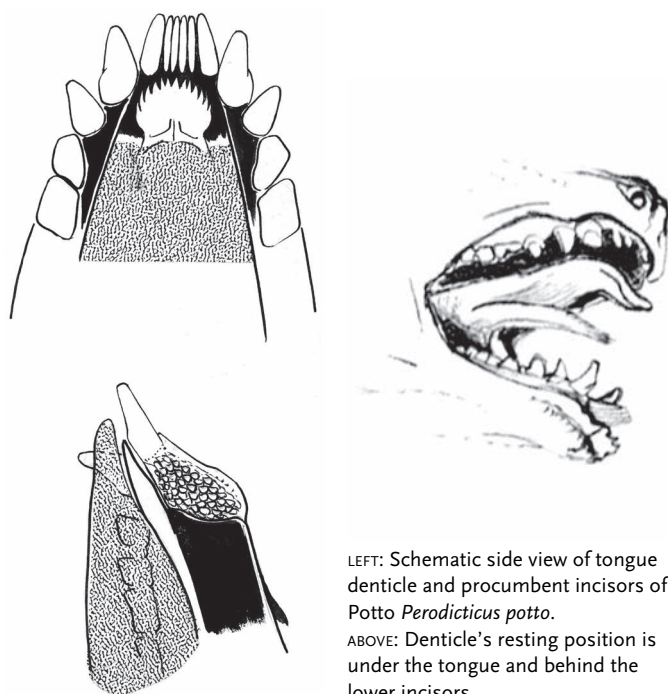


Strepsirrhine hand and foot (exemplified by Spectacled Lesser Galago *Galago matschiei*).

follicles. Scent plays a major, but incompletely understood, part in their social and territorial behaviour. The periodic activity and localized occurrence of some of these odours have been investigated with interesting implications for intra-specific sexual and social communication. For example, Yasuda *et al.* (1961) found hair follicles rich in glycogen and phosphorylase but physiological activity was intermittent. Likewise, Montagna & Yun (1962) found phosphatase activity was strongly acidic on the face and feet of pottos while other parts of the body were alkaline.

Moulting of the fur occurs in most, probably all, lemuriforms and is linked with reproductive cycles and nutritional status. Moulting, skin glands and other scents, and modifications to the front teeth in the lower jaw, the sub-lingual denticle and grooming claw are all physiological and anatomical adaptations that owe their development to natural selection for a set of sensory and communicative behaviours unique to modern prosimians. Those behaviours are inseparable from many of the features that we use to define and describe the Strepsirrhini.

In general, nocturnal primates are less sensitive to colour, some having monochromatic vision, others being dichromatic (greens



LEFT: Schematic side view of tongue denticle and procumbent incisors of *Potto Perodicticus potto*.

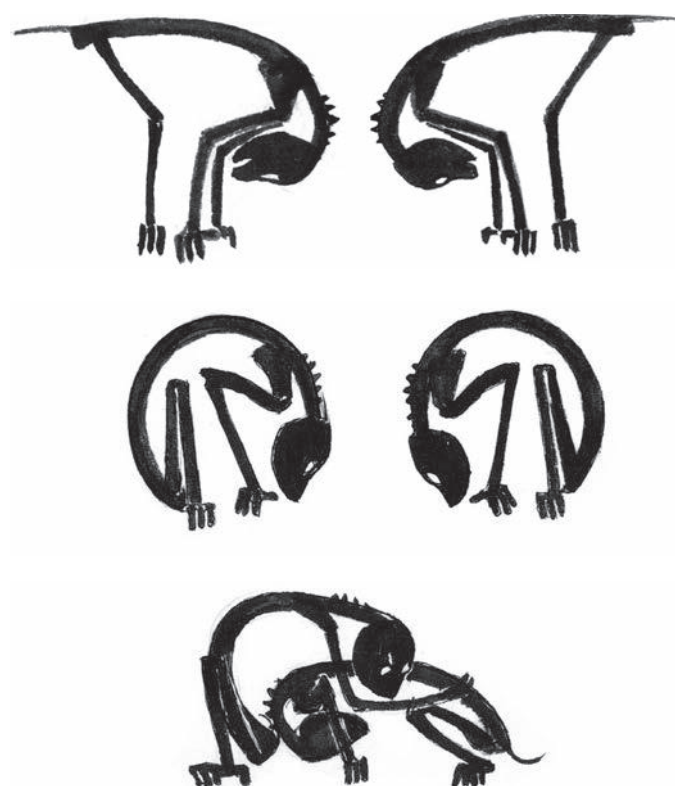
ABOVE: Denticle's resting position is under the tongue and behind the lower incisors.

and blues), but have greater sensitivity (are better able to see under minimal natural lighting).

The African and Madagascan branches of Strepsirrhini are estimated (by molecular clocks) to have diverged 60 mya (Pennisi (2007) or 68.7 mya (Perelman *et al.* 2011) in the mid-Palaeocene. Living African strepsirrhines show many resemblances with Asian and Malagasy forms and detailed research on which traits are convergent and which are inherited commonalities remains an ongoing task. For example, African dwarf galagos *Galagoides* show many close similarities with the Malagasy mouse lemurs *Microcebus*, while African squirrel galagos *Sciurocheirus* resemble Malagasy sportive lemurs *Lepilemur*. Galagos and lemurs even show some resemblances with totally unrelated marsupials in Australia and South/Central America. Such detailed convergences are relevant to the very subtle differences among some African galago species and help explain the large number of cryptic species revealed in recent years. These resemblances also suggest that the generalized body-form typical of the earliest arboreal mammals has remained under tight constraints in small, nocturnal species, so that phylogenetically distant taxa can look superficially very similar.

In the profiles that follow, limb proportions, body measurements and subtle differences in minor anatomical structures have been examined in exceptional detail because these otherwise generalized arboreal climbers and jumpers have been modified to perform various, still further specialized functions.

Fruit and animal foods are combined in different ratios by all lemuriforms (Chivers *et al.* 1975). Few rely heavily on fruits and this may be due to competition, not only from diurnal birds and mammals but also from fruit bats, which are better adapted to seeking out all major sources of ripe fruits. Many lemuriforms eat tree exudates (gums) to a greater or lesser extent. These not only serve as a 'filler', permitting them to survive long periods of food shortage, but may also provide scarce nutrients. Some species appear to possess a special capacity to digest this low energy food (Smith



Diagrams of main socio-sexual interaction between Pottos *Perodicticus potto*.

Both sexes have richly innervated and super-sensitive neuchal spines, skin and genitalia in these chemically complex areas.

Above: Two ♂♂ (occasionally ♀♀) butt neck/shoulders.

Middle: Individuals confront passively. Potential for aggression or closer contact.

Below: 'Hugging' in which genitalia and associated glands are stimulated by neuchal spines: behaviours and morphology that are still a challenge to science.

& Montgomery 1959, Caton *et al.* 2000). Buffered by gums, many lemuriforms are well-adapted gleaners of marginal resources (both fruit and animal) in the face of much competition. Predation, mainly by diurnal and nocturnal raptors and arboreal carnivores, appears to be a major constraint on the ecological success of all prosimians.

Of special interest is apparent competitive exclusion between the Potto *Perodicticus potto* and the two greater galagos, Large-eared Greater Galago *Otolemur crassicaudatus* and Small-eared Greater Galago *Otolemur garnettii* (Butynski & De Jong 2007). The Potto is mainly an equatorial rainforest animal, while the two greater galagos occupy a wider range of forests and woodland habitats in eastern and southern Africa. This pattern broadly coincides with the centre-west/south-east divide discussed in Volume I, Chapter 6, pp. 79–84. In spite of these ecological and biogeographic differences there seems to be substantial coincidence in habitat and habits, and detailed comparative studies have yet to be made. Although primarily an equatorial forest group, a few galago species have adapted to acacia, commiphora and other dry-country bushlands and woodlands, including some in semi-temperate, southern latitudes. Their dependence on forests, woodlands and bush lands for food and shelter seems to have precluded them from crossing the desertic barriers that confine them to Africa. Thus, there are no extant lemuriforms on the Arabian Peninsula.

Jonathan Kingdon & Colin P. Groves

Infraorder LORISIFORMES – Lorisiforms: Lorises, Pottos, Galagos

Lorisiformes Gregory, 1915. Bull. Geol. Soc. Amer. 26: 436.

Lorisiformes, one of three infraorders within the Strepsirrhini, embraces 18 (described and named) species of galagos, family Galagidae, and ten or more lorises, family Lorisidae. Galagos are exclusively African, while the lorises includes at least seven Asiatic species. The divergence between African and Madagascan strepsirrhines is thought to be during the mid-Palaeocene, 60–70 mya (Pennisi 2007, Perelman *et al.* 2011).

The main characteristics of the Strepsirrhini are the shape of the external nose and the possession of a so-called ‘toilet-claw’ on the second digit of the foot, as described under suborder Strepsirrhini; also, in two of the three infraorders (Lemuriformes and Lorisiformes), but not in the third (Chiromyiformes), the possession of a dental comb, consisting of the lower incisors and canines. Lorisiformes are distinguished by the structure of the bony ear region; the tympanic ring is not enclosed in the auditory bulla as in the other two infraorders, but is at its mouth, while the bulla itself is divided into anterior and posterior chambers.

Asian lorises are distinguished from the African genera by a number of skull features, notably the more tubular orbits and the more marked prolongation of the tympanic ring into a tube. In Africa and in Asia there is a ‘fat genus’ (*Perodicticus*, *Nycticebus*) and a ‘thin genus’ (*Arctocebus*, *Loris*). The relative sizes and build of these two morphs involve dietary differences (the fat ones are more frugivorous, the thin ones more insectivorous), and aspects of the structure of the teeth converge accordingly. Characteristics separating loris and lemur groups were first listed by Gregory (1915) and Weber (1928) but Charles-Dominique & Martin (1970) noted that the course of the carotid artery and form of the orbit in lorises was shared with the Malagasy dwarf and mouse lemurs (Gheirogaleidae), raising issues about the monophyly of the Malagasy lemurs.

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Superfamily LORISOIDEA – Lorisoids: Lorises, Pottos, Galagos

Lorisoidea Gray, 1821. London Medical Repository 15: 298.

There are two families of Lorisoidea in Africa: Lorisidae (containing *Perodicticus* and *Arctocebus*) and Galagidae (containing *Otolemur*, *Sciurocheirus*, *Galago*, *Euoticus* and *Galagoidea*). Groves (2001) placed these non-Malagasy strepsirrhines in their own infraorder, Loriformes (which, since Opinion 1995 was issued, must become Lorisiformes). In this volume the next highest rank (superfamily) is here recognized, which (again following Opinion 1995) is to be called Lorisoidea. The Lorisoidea differ from the Malagasy superfamilies Lemuroidea and Daubentonioidea primarily in the structure of the auditory bulla. In the Malagasy strepsirrhines the bulla is a simple globular structure, so large that it extends lateral to the tympanic ring, which is consequently incorporated into it. In the Lorisoidea, on the other hand, the bulla is smaller, with the tympanic ring at its mouth and forming a short

tube; and behind the bulla, the mastoid region and the bone medial to the bulla are noticeably inflated. The internal carotid system does not pass through the bulla; in this, the Lorisoidea are convergent with one of the Malagasy families (Cheirogaleidae), and in addition there is an arterial rete. Of the two families, the Galagidae are confined to Africa, whereas the Lorisidae have Asian representatives as well (although very different from the African genera). The Galagidae have hindlimbs that are much longer than the front limbs, large ears that project noticeably from the head, and long tails (>130 mm). The Lorisidae have limbs subequal in length, small ears that are mostly hidden by fur, and short tails (<130 mm).

Colin P. Groves

Family LORISIDAE
LORISIDS: LORISES, POTTO, ANGWANTIBOS

Lorisidae Gray, 1821. London Medical Repository 15: 298.

| | | |
|----------------------------------|-----------------------------|--------|
| <i>Perodicticus</i> (1? species) | Potto | p. 393 |
| <i>Arctocebus</i> (2 species) | Angwantibos (Golden Pottos) | p. 399 |

The African Lorisidae (subfamily Perodicticinae) embraces two established genera: *Perodicticus* for the Potto (which may eventually be shown to include more than one species) and *Arctocebus* for two accepted species of angwantibo. A third genus, *Pseudopotto*, has been proposed on the basis of skeletal remains of only two captive specimens. Opinions are sharply divided on its recognition, with Sarmiento (1998c) regarding the specimens as aberrant Pottos, while others (Bearder 1998, Groves 1998) regard the characteristics, as described, as being sufficiently distinctive to merit provisional recognition, while others (e.g. Grubb *et al.* 2003) regard recognition as premature, the course adopted here.

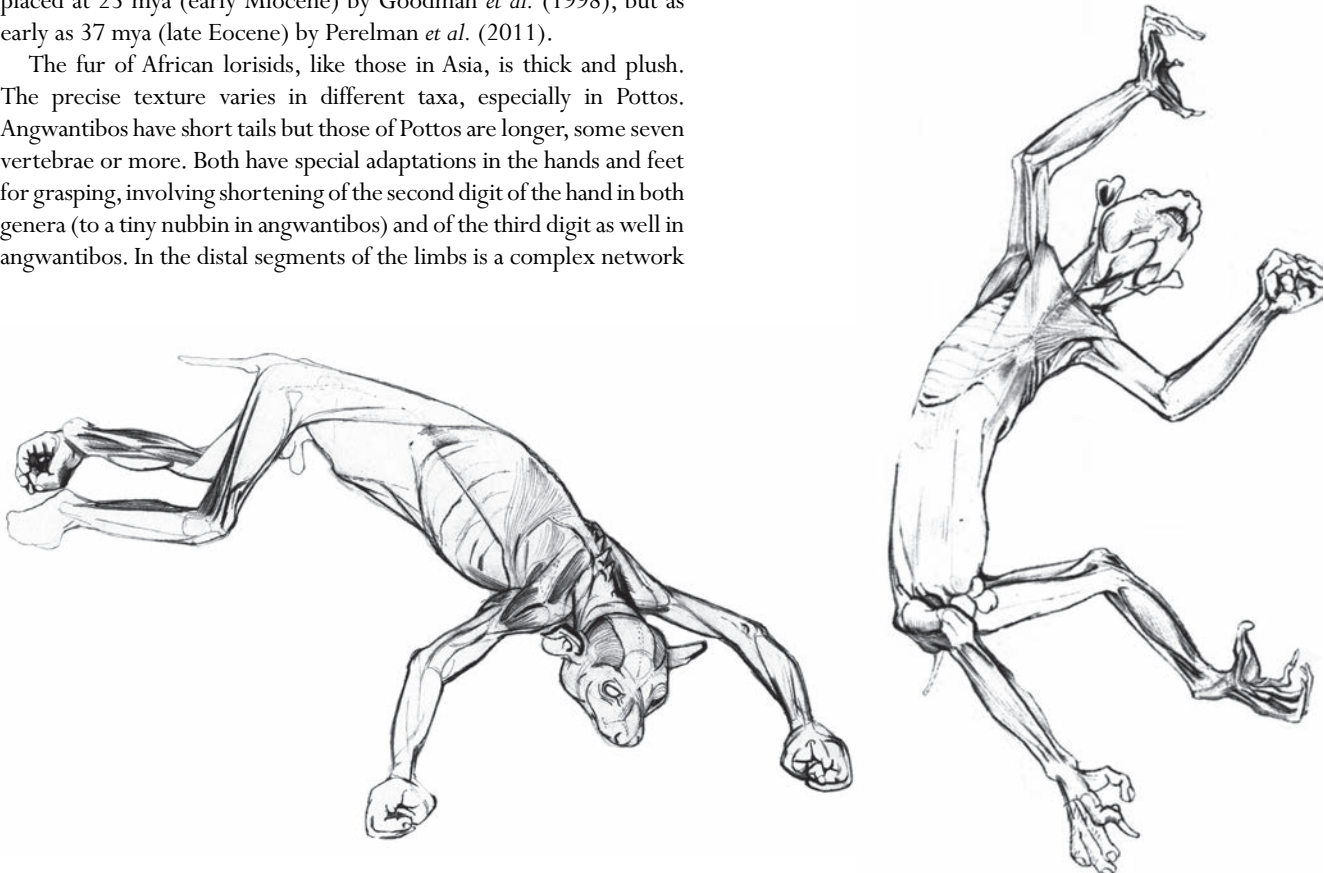
The African Lorisidae are restricted to the rainforest belt. Pottos occur throughout the zone, whereas angwantibos are restricted to west-central African region, between the Niger R. and Congo R., the region to which the primate genera *Sciurocheirus*, *Euoticus* and *Mandrillus* are likewise restricted. The diversity of African lorisids is about equivalent to that of those in Asia (subfamily Lorinae); reconsiderations of the taxonomy in both continents is gradually yielding evidence of more species than have customarily been recognized. The Lorisidae split to Perodicticinae and Lorisinae was placed at 23 mya (early Miocene) by Goodman *et al.* (1998), but as early as 37 mya (late Eocene) by Perelman *et al.* (2011).

The fur of African lorisids, like those in Asia, is thick and plush. The precise texture varies in different taxa, especially in Pottos. Angwantibos have short tails but those of Pottos are longer, some seven vertebrae or more. Both have special adaptations in the hands and feet for grasping, involving shortening of the second digit of the hand in both genera (to a tiny nubbin in angwantibos) and of the third digit as well in angwantibos. In the distal segments of the limbs is a complex network

of blood vessels called *rete mirabile*, in which exchange of arterial and venous blood enables the extremities to grip tightly on branches for long periods without fatigue. Indeed, the name ‘Potto’ derives from a Ghanaian name ‘Aposo’, which means ‘tenacious’ (Smeenck *et al.* 2006). Lorisids are enabled in this way to keep hold of branches and remain completely still, or move very slowly, or more quickly but with a gliding motion, which enables them to escape detection by potential predators and by animal prey alike. This contrasts markedly with the leaping and running of galagos.

Molecular data agree with anatomical data that phylogenetic relationships in the Lorisidae separate the two African genera in one clade from the two Asian genera in another. Thus, the evolution of a fat and a thin genus has proceeded independently on each continent. We follow Groves (2001, 2005c) and Grubb *et al.* (2003) in recognizing the following: Calabar Angwantibo *Arctocebus calabarensis*, Golden Angwantibo *Arctocebus aureus* and Potto *Perodicticus potto*. We think it highly likely that there are more than one species in *Perodicticus* (Oates 2011) and we defer judgement on the validity of *Pseudopotto martini*. The peculiarities of each genus are described in the appropriate profile.

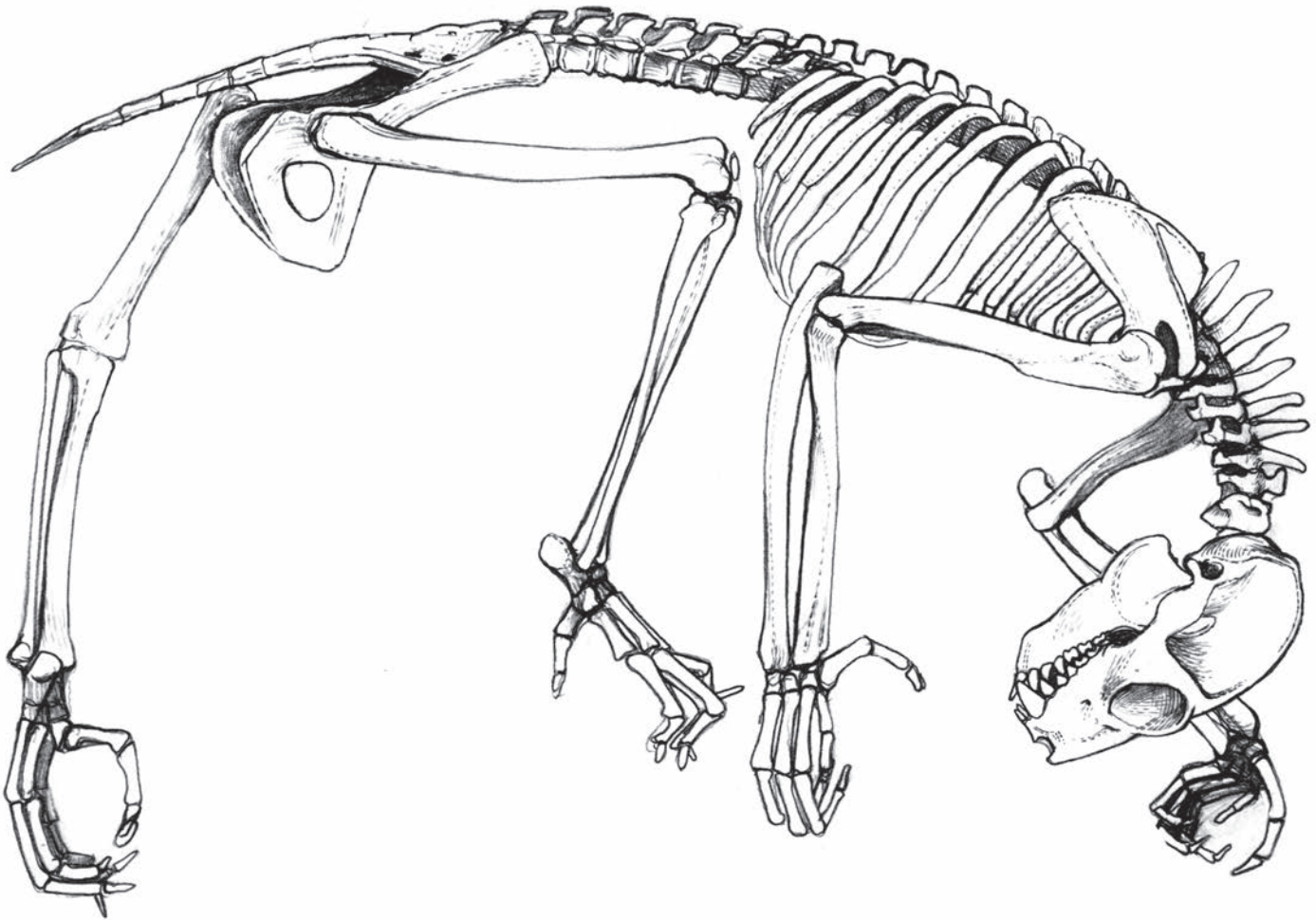
Colin P. Groves & Thomas M. Butynski



Myology of Potto *Perodicticus potto*.

Subfamily PERODICTICINAE – African Lorises: Potto, Angwantibos (Golden Pottos)

Perodicticinae Gray, 1870. Catalogue of Monkeys, Lemurs and Fruit-eating Bats in the Collections of the British Museum, pp. 69, 93.



Potto *Perodicticus potto*.

Subfamily endemic to the moist forests of tropical Africa from Guinea (perhaps Guinea-Bissau) eastwards to C Kenya (Hill 1953, Wolfheim 1983, Jenkins 1987, Oates 1996a). Two genera (*Perodicticus* and *Arctocebus*) and three species recognized by most authorities (Groves 1993, Oates 1996a, Kingdon 1997, Grubb *et al.* 2003). In addition, Groves (1998, 2001, 2005c) provisionally recognizes the monotypic genus *Pseudopotto* and the Martin's False Potto *Pseudopotto martini* (Schwartz 1996). Molecular data indicate that the *Perodicticus*–*Arctocebus* split occurred during the early Miocene, about 20 mya (Perelman *et al.* 2011). Members of the Perodicticinae are characterized within Lorisidae by the absence of an index finger (*Arctocebus*) or by an index finger that is but a stump (*Perodicticus* and *Pseudopotto*).

Tooth formula $I^{2/2}, C^{1/1}, P^{3/3}, M^{3/3} = 36$. Three pairs of nipples (two axial, two pectoral, two abdominal (Hill 1953).

The holotype for the controversial *P. martini* is a partial skull and 'essentially' complete skeleton of an adult ♀ that lived in the Zurich Zoo and which is said to have originated in 'Equatorial Africa'. The only other specimen attributed to *P. martini* (Schwartz 1996) is represented

by a juvenile/subadult skull without a fully erupted dentition from Cameroon (exact locality unknown). The skeletal differences that Schwartz (1996) attributes to *Pseudopotto* are summarized by Groves (1998), Leon (2000) and Sarmiento (1998c). Sarmiento (1998c) examined the non-metric characters for *Pseudopotto* and found them to be prevalent in *Perodicticus* specimens obtained from localities well outside Cameroon. He concluded (p. 45) that, 'Schwartz (1996) does not present convincing data that merit the erection of a new genus or even a new species. All of the data that could be tested indicate that *Pseudopotto* does not differ in any significant manner from *P. potto*.' Grubb *et al.* (2003) also rejected *Pseudopotto* based on current evidence. Despite searches in the forests of Cameroon, no *Pseudopotto* have been located (E. Pimley pers. comm.). This work follows Groves (1993), Oates (1996a, 2011), Kingdon (1997) and Grubb *et al.* (2003) in recognizing but two genera (*Perodicticus* and *Arctocebus*) within Perodicticinae.

Thomas M. Butynski

GENUS *Perodicticus*

Potto

Perodicticus Bennett, 1831. Proc. Zool. Soc. Lond. 1830: 109 [1831].

Genus presumed to be monotypic. Endemic to tropical Africa in moist forest from Guinea (perhaps Guinea-Bissau) eastwards to C Kenya (Hill 1953, Jenkins 1987, Wolfheim 1983, Groves 1993, 2001, 2005c, Oates 1996a, 2011, Kingdon 1997, Butynski & De Jong 2007). There may be more than one species within *Perodicticus* as there is considerable morphological variation among the four to six 'subspecies' (Elliot 1913a, Schwarz 1931b, Hill 1953, Jenkins 1987, Schwartz & Beutel 1995, Groves 2001, Grubb *et al.* 2003, Stump 2005, Butynski & De Jong 2007). Indeed, Oates (2011) recognizes three species. Genus readily distinguished from the one other genus in Perodicticinae (i.e. *Arctocebus*) by a premaxillary that is not elongated, by larger size (HB 290–410 mm vs. <270 mm for *Arctocebus*; T 37–130 mm vs. <15 mm for *Arctocebus*; WT 600–1900 g vs. <325 g for *Arctocebus*), by the presence of a tail and an (intact) third digit, and by long spinous processes ('nuchal' or 'apophyseal' spines) on 3–6 thoracic and cervical vertebrae capped by tubercles that project above the level of the muscles (Elliot 1913a, Schwarz 1931b, Hill 1953, Jenkins 1987, Kingdon 1997). Other characteristics of *Perodicticus* given in the *P. potto* profile.

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Position of nuchal spines on a Potto *Perodicticus potto* in defensive position.

Perodicticus potto POTTO

Fr. Potto; Ger. Potto

Perodicticus potto (Müller, 1776). In Linnaeus, Vollstrand Natursyst. Suppl., p. 12. Elmina, Gold Coast [Ghana].

Taxonomy Polytypic species. Following Schwarz (1931b), Jenkins (1987), Groves (2001, 2005c) and Grubb *et al.* (2003), one species of Potto is recognized here. Schwarz & Beutel (1995), Groves (2001), Grubb *et al.* (2003) and Stump (2005) suggest that there may be several species here, particularly within *P. p. edwardsi* (Butynski & De Jong 2007). Indeed, recent mitochondrial DNA data indicate that *potto*, *edwardsi* and *ibeanus* might deserve species designation (C. Roos pers. comm.). This is supported by marked differences in body size and skull morphology (Stump 2005, Ravosa 2007). Although Hill (1953), Napier & Napier (1967) and Petter & Petter-Rousseaux (1979) recognize five subspecies, Schwarz (1931b) recognizes four subspecies. More recent taxonomies (Jenkins 1987, Groves 2001, Grubb *et al.* 2003) recognize three subspecies: *potto*, *edwardsi* and *ibeanus*. Oates (2011) treats these as full species. Recently, an additional subspecies has been described, *stockleyi*. Synonyms: *arrhenii*, *batesi*, *bosmannii*, *edwardsi*, *faustus*, *geoffroyi*, *guineensis*, *ibeanus*, *ju-ju*, *nebulosus*, *stockleyi*. Chromosome number: $2n = 62$ (Bender & Chu 1963).



Potto *Perodicticus potto*.



Potto *Perodicticus potto* adult male.

Description Largest loriscid (1.1–1.6 kg). Slow-moving, hunched, quadrupedal climber with thick, woolly pelage. Sexes similar in size and colour. Head round. Muzzle short, robust, overhanging shallow lower jaw. Eyes protuberant, golden-brown. Ears thickened, small, rounded, naked. Nape with thick skin under dense fur (that often has patch of dense, long vibrissae). Body and limbs long and slender, but this not obvious due to the thick fur and typical hunched posture. Pelage of dorsum and outer limbs ranging from blackish to grey to brownish to cinnamon, depending on subspecies. Chin, ventrum and inside of limbs pale grey. Hands and feet with opposable spatulate thumbs and flat nails, except for second digit of hindfoot, which has a grooming claw. Index finger reduced to rudimentary knob. Large scrotum of adult ♂♂ and vulval labia of adult ♀♀ are globular with chequered surface colouring. Long spinal processes on cervical vertebrae 3–9 project above the muscles and are capped by horny tubercles. Pottos born with a white pelage and blue eyes; pelage becomes greyer with age (Cowgill 1969).

Geographic Variation

P. p. edwardsi Central Potto. Western central Africa. Lower Niger R., Nigeria, south-east to Congo R. and Ubangi R., Central African Republic, to south of Congo R., DR Congo, where limit is unknown. Largest subspecies (ca. 1200 g). Dorsum grey or cinnamon-brown to mahogany-brown. Tail relatively short. Skull length: mean 65.8 mm (63.1–68.0, $n = 44$; Schwarz 1931b). Large teeth: upper tooththrow (C–M³): mean 22.9 mm (21.7–24.3, $n = 44$; Schwarz 1931b). P₃ usually higher than P₄ (Groves 2001). A smaller form of *P. p. edwardsi* is found in the Congo Basin (formerly termed *P. p. faustus* (Schwarz 1931b, Jenkins 1987). Synonyms: *batesi*, *faustus*.

P. p. ibeanus Eastern Potto. Central Africa and East Africa. East and south of the Ubangi R., and north and east of Congo R., DR Congo, eastward through Burundi, Rwanda and Uganda to at least the Kakamega-Nandi Forest region, W Kenya. Extent of occurrence estimated at roughly 850,000 km² (Butynski & De Jong 2007). Intermediate in size (ca. 1000 g). Dorsum with tripartite colour pattern; head and forelimbs light brown, shoulders blackish, hindquarters grey to reddish-brown. Dorsum exceptionally thick,

long and woolly. Skull length: mean 63.9 mm (60.0–66.7, $n = 34$; Schwarz 1931b). Small teeth, with upper tooththrow (C–M³): mean 20.8 mm (19.2–22.5, $n = 34$; Schwarz 1931b). P₃ higher than P₄ (Groves 2001). Synonyms: *arrhenii*, *nebulosus*.

P. p. potto Western Potto. West Africa, S Senegal east to Niger R., Nigeria (Grubb *et al.*, Oates 2011). Smallest form (ca. 800 g). Dorsum reddish-brown with dark spinal stripe. Tail relatively long. Skull length: mean 61.4 mm (60.5–63.3, $n = 6$; Schwarz 1931b). Small teeth, with upper tooththrow (C–M³): mean 20.0 mm (18.1–21.3, $n = 6$; Schwarz 1931b). P₃ lower than P₄ (Groves 2001). A larger form (previously termed *P. p. ju-ju*) occurs between Volta R. and Niger R. (Schwarz 1931b, Jenkins 1987, Oates 2011, E. Pimley pers. obs.). Synonyms: *bosmannii*, *geoffroyi*, *guineensis*, *ju-ju*.

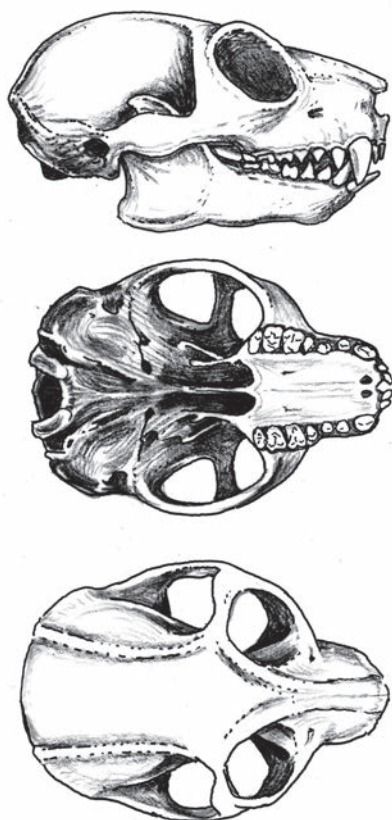
P. p. stockleyi Mount Kenya Potto. Known only from one specimen obtained on Mt Kenya, C Kenya. About 210 km from the nearest known other population of *P. potto*. Dorsum cinnamon to dark russet with short (ca. 14 mm) hairs. Vibrissae on dorsum short (ca. 14 mm). Second digit of hand relatively long (6 mm). Tail relatively long (>96 mm; >31% of head+body length; Butynski & De Jong 2007). Synonyms: none.

Similar Species

Arctocebus aureus. Sympatric with *P. p. edwardsi*. South of Sanaga R., Cameroon, south to Congo R., Congo. Much smaller (150–250 g) than Potto. Second digit of hand absent and third digit greatly reduced.

Arctocebus calabarensis. Sympatric with *P. p. potto*. Between Niger R., Nigeria, and Sanaga R., Cameroon. Much smaller (270–325 g) than Potto. Second digit of hand absent and third digit greatly reduced.

Distribution Endemic to Equatorial Africa. Rainforest and Afromontane–Afroalpine BZs. Upper Guinea to about 00°18' N, 37°19' E in C Kenya, south to at least 08° S in DR Congo. There are reports of Pottos for Gambia, Senegal and Guinea-Bissau, but these need confirmation (Hill 1953, Jewell & Oates 1969b; McGrew *et al.* 1978, Petter & Petter-Rousseaux 1979, Wolfheim 1983, Jenkins

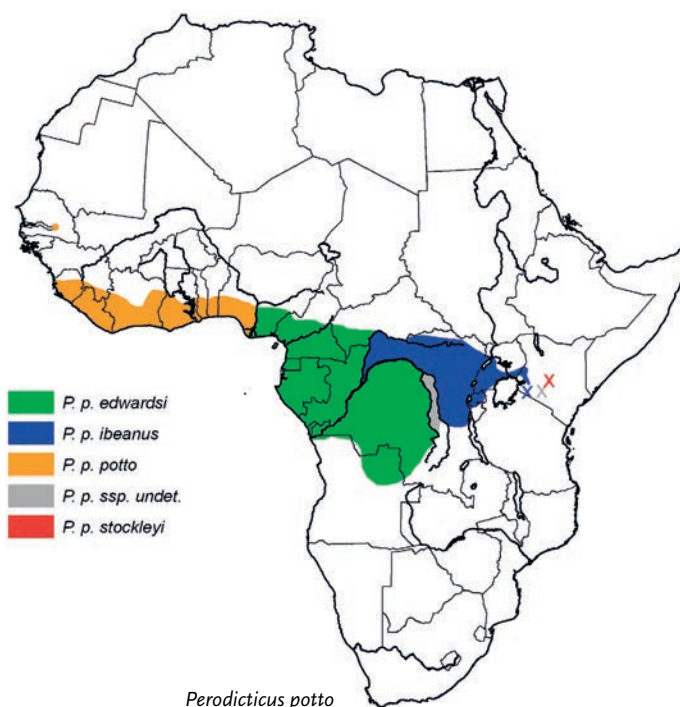


Lateral, palatal and dorsal views of skull of Potto *Perodicticus potto* adult male.

1987, Groves 2001, Grubb *et al.* 2003). See 'Geographic Variation'.

Habitat Swamp, lowland, mid-altitude, montane and riverine forest, coastal scrub, woodland and plantation from 0 to >30 m above ground. Most common in secondary, colonizing forest, flooded primary forest, riverine forest and forest edge (Kingdon 1971, Charles-Dominique 1977, Wolfheim 1983, Oates 1984, Pimley 2002). In Cameroon, most frequently (47% of 8334 observations) at 6–10 m with 32% of observations at 11–15 m (Pimley 2002). Prefers canopy at 5–30 m in C Gabon (Charles-Dominique 1977). *Perodicticus p. edwardsi* occurs from near sea level to at least 1500 m in SW Cameroon (E. Pimley pers. obs.). *Perodicticus p. ibeanus* occurs from 600 to 2300 m (Butynski & De Jong 2007). Mean annual rainfall over the geographic range of *P. p. ibeanus* ranges from ca. 1300 mm to 2000 mm (Butynski & De Jong 2007). For the species as a whole, the approximate limits for rainfall and temperature are 1000–5000 mm and 22–34 °C, respectively (Times Atlas 1975).

Abundance Density averages 8–10 ind/km² (up to 28 in flooded forest) at Makokou, C Gabon (Charles-Dominique 1977). Highest densities occur in flooded primary and riverine forest. Density 4.7 ind/km² in mixed secondary forest and farm bush on Mt Kupé, SW Cameroon (n = 13) (Pimley 2002). In Kibale N. P., SW Uganda, Weisenseel *et al.* (1993) estimate 1.8 ind/km² in selectively logged forest and 17.7 ind/km² in unlogged forest. In contrast, Off (2003), also in Kibale N. P., never encountered Potto in unlogged forest but obtained an estimate of 11.7 ind/km² in logged forest. Encounter rates for several other sites presented in Butynski & De Jong (2007).



Perodicticus potto

Adaptations Nocturnal and arboreal. Reflective tapetum in eye facilitates night vision. Basal metabolic rate (36–40 kcal/day/kg^{0.75}), approximately half that expected for a mammal of this body size (Pollock 1986). Potto has larger brain size than predicted from low metabolic rate. Spines of cervical vertebrae, together with the compact mass of muscle and thick skin of shoulder and neck, form a protective 'scapular shield'. The Potto faces the predator, grips a branch with hands and feet, and tucks the head into the chest to present the scapular shield, accompanied by long touch-sensitive guard hairs. Swinging backwards or sideways from this position, the Potto makes threat 'grunts'. The animal also thrusts forward in attempts to dislodge the predator. A highly agitated Potto will suddenly lunge at a predator by uncoiling the back and striking out with an open mouth or butting with the scapular shield (Charles-Dominique 1977, E. Pimley pers. obs.).

The low vertebral spines of the thorax may increase flexibility, facilitating the Potto's characteristic lateral spinal movement (Kingdon 1971). Such movements enable Pottos to bridge gaps in the canopy and search for fruit clusters while remaining suspended in one spot. Pottos sleep in dense foliage and do not build nests. They use tree-holes in Uganda (Bearder *et al.* 2003). The powerful grip of the Potto, and its ability to remain motionless and silent for long periods, are facilitated by a multi-branched arterial and venous system in the limbs (Suckling *et al.* 1969). Charles-Dominique (1977) found that a 1 kg Potto could support 15 times its body weight suspended underneath it.

Foraging and Food Omnivorous. Pottos forage mainly in the canopy, but also at lower levels and on the ground. Foraging occurs intermittently throughout the night from ca. 1 h after sunset to ca. 1 h before sunrise (E. Pimley pers. obs.). Pottos in C Gabon only became active under full night-time conditions (<20 lux) (Charles-Dominique 1977). In SW Cameroon, Potto ♂♂ travel (i.e. horizontal + vertical travel) an average of 2811 m/night (1330–



OPPOSITE: Potto *Perodicticus potto*.

6440, $n = 6$ animals), while ♀♀ travel an average 707 m/night (951–3290 m, $n = 4$ animals) (Pimley 2002).

Pottos eat ripe fruit and nectaries of banana trees (*Musa* spp.). The Potto peels the flower petals from nectaries to consume nectar and resident insects, while holding the remaining flower in both hands. Pottos frequently move along branches and trunks with their noses and body close to the substrate, sometimes licking up ants or other small invertebrates from the bark (Pimley 2002). This enables effective location of ants, slow-moving invertebrates and gum (Oates 1984). Pottos occasionally forage among Oil Palms *Elaeis guineensis*, presumably for beetles and their larvae (Pimley 2002). Pottos use their teeth and pointed, cornified, tongue, to extract giant West African Land Snails *Achatina achatina* from their shells. For the smaller snails (<8 cm), they hold the shell in one hand, and for the larger shells (>8 cm) both hands are used. Pottos catch moths opportunistically by sitting silently and motionless until a moth flies within arm's reach. The Potto follows the movement of the moth with its eyes, rapidly extends its arm to catch the moth in one hand, and feeds on the moth while it is firmly grasped in one hand (Pimley 2002).

In Uganda, 19 stomachs obtained over seven months held ca. 60% gum and ca. 30% insects. Here it appears gum is the main food during drier periods, and insects and fruit the main foods during wetter periods (Kingdon 1971). In C Gabon, stomach contents yielded 65% fruits, 21% gum and 10% insects (mostly ants) ($n = 41$) (Charles-Dominique 1977). Pottos eat insects that other primates find unpalatable, especially ants, which make up 65% of the invertebrate portion of the diet in C Gabon (Charles-Dominique 1977). Pottos eat the ripe fruits of a large number of plant species, including *Musanga cercopioides*, *Pseudospondias microcarpa*, *Cola longifolia*, *Saphradaceae allophylus*, *Musa* spp., *Peasea americana*, *Psidium guajava*, *Ficus* spp., *Parkia* sp., *Avoun* sp., *Uapaca* sp., *Myrianthus* sp., *Tabernaemontana* sp. and *Parinari* sp. Leaves of *Urera* sp. and gum of *Albizia* sp. and *Sterculia* sp. are eaten. They also eat moss, lichen, fungi, beetles, beetle larvae, caterpillars, locusts, grasshoppers, spiders, millipedes, centipedes, slugs, frogs, birds' eggs, small birds and young bats (Kingdon 1971, Charles-Dominique 1977, Oates 1984, Pimley 2002).

Social and Reproductive Behaviour Non-gregarious. Pottos in C Gabon spend 96% of the time alone and 4% of the time with conspecifics (<20 m apart, $n = 105$; Charles-Dominique 1977). In SW Cameroon, Pottos are within 20 m of conspecifics during 22% of observations ($n = 8334$; Pimley *et al.* 2005b). There is evidence of complex social networks among individuals constituting a dispersed form of social organization. Pottos in C Gabon sleep alone except for mothers with infants (Charles-Dominique 1977). By contrast, in SW Cameroon certain ♂♂ and ♀♀ 'pairs' were together 29% of the time ($n = 8334$ observations) and slept within 20 m of each other 26% of the time ($n = 43$). On one occasion a ♂ and ♀ were observed waking at the same site (Pimley *et al.* 2005b). Members of these 'pairs' were not observed in contact with other Pottos of the opposite sex. They have higher levels of association with each other than with other conspecifics. The only affiliative and sexual behaviour observed between members of the opposite sex was within these 'pairs'. Overlap of home-ranges between 'pairs' is not only spatial, as with neighbouring (unpaired) Pottos, but also temporal, with animals

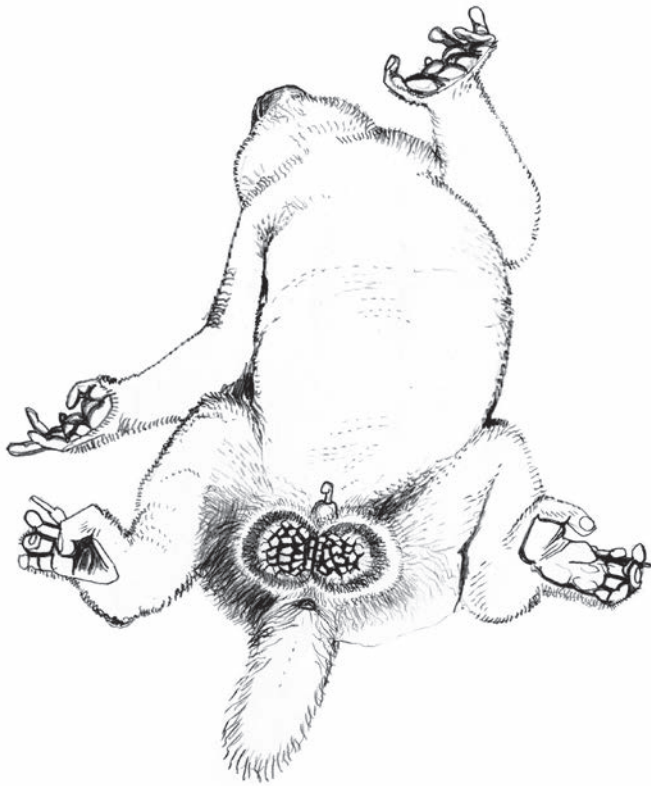
overlapping each other's ranges at the same time. Interactions within the sexes are lower than between paired ♂♂ and ♀♀. Adult ♂ spend marginally more time within 20 m of a ♂ (1.5% of 8334 observations) than adult ♀♀ spend with other ♀♀ (0% of 8334 observations) (Pimley 2002).

In the montane forests of SW Cameroon, Pottos have a dispersed unimale–unifemale social system, where the ♂ and ♀ of a 'pair' forage alone but show affiliative interactions throughout the year, although not necessarily on a daily basis. This fact, the lack of sexual dimorphism, and the relatively small testes, imply a monogamous mating system in SW Cameroon (Pimley 2002, Pimley *et al.* 2005b). However, in the lowland forest of C Gabon, Pottos have a dispersed unimale–multifemale social system, where the ♂ patrols the home-ranges of one to three ♀♀ (Charles-Dominique 1977). Matriarchies are absent. Charles-Dominique (1977) assumed that Pottos have a polygynous mating system in C Gabon. Differences in the social arrangement of the Potto in C Gabon and SW Cameroon (both *P. p. edwardsi*) are most likely due to ecological differences between the two study sites.

In C Gabon, home-ranges of ♀♀ (mean 7.5 ha, 6–9, $n = 5$) are much smaller than of ♂♂ (mean 17.8 ha, 9–40, $n = 5$) (Charles-Dominique 1977). Home-ranges of ♂♂ and ♀♀ in SW Cameroon are of similar size (mean 31.5 ha, 13.1–44.1, $n = 4$ for ♀♀ and ♂♂ mean 30.6 ha, 19.1–34.2, $n = 6$; Pimley *et al.* 2005a). Home-ranges of one or two ♀♀ and their infant overlapped the territory of one ♂ in C Gabon (Charles-Dominique 1977), while in SW Cameroon the range of one ♂ overlapped extensively the range of one ♀ (mean overlap 68%, $n = 10$ home-ranges; Pimley 2002). Adults are sedentary, except for young ♂♂ at puberty, who have a dispersal stage (Charles-Dominique 1977). These ♂♂ are sexually mature, with testes similar in size to older, sedentary, ♂♂, but their body weight is less. Young adult ♀♀ remain in or near their natal home-ranges.

Much communication is by olfactory cues (urine marking and genital gland secretions) (Kingdon 1971, Charles-Dominique 1977, Pimley 2002). The Potto's method of moving close to branches with the nose down enables scent-marks of conspecifics to be easily located. This also allows for the marking of substrates while moving (Oates 1984). Vocal exchanges are limited (no alarm calls or loud-calls). Screams sometimes given when handled. Pottos in captivity with conspecifics make a high-pitched 'whistle' that seems to serve as a spacing mechanism when other Pottos come too near (E. Pimley pers. obs.). Cowgill *et al.* (1989) frequently observed cooperative behaviour (food-sharing, food-saving, paternal behaviour) among Pottos in captivity. This led them to suggest that such behaviours are part of the natural behavioural repertoire.

Direct scent-marking occurs between same-sex and different-sex pairs during allogrooming (Manley 1974, Charles-Dominique 1977, Pimley 2002). A ♂ scratches his scrotum with his hands, and transfers the secretion to the dorsal pelage of the ♀. Males and ♀♀ pass over the backs of their partner, transferring genital secretions. Scent-marking by the ♂ may inform conspecifics that the ♀ is associated with that ♂, thereby giving him preferential access to her (Gosling 1982). A ♂ updates his scent-marks during regular visits to a ♀. This might inform other ♂♂ of his physical condition and of his 'ownership' of the ♀. Such means of assessment avoid the costs of exerting dominance by threats or overt aggression (Gosling 1982).



Elaborated skin around scrotum of Potto *Perodicticus potto*.

Pimley (2002) observed copulations between Pottos in SW Cameroon. The ♂ and ♀ sit on a branch next to each other for several minutes and then sniff and groom each other's head and neck. The hands are then placed on the shoulder of the other Potto and each side of the face is sniffed and licked alternately for a few minutes. The ♂ then sniffs and licks the female's genitalia, and the ♀ sniffs and licks his genitalia. They then adopt a dorsal-ventral mating position, usually with the ♀ suspended from the underside of a branch and the ♂ suspended under the ♀. One incidence of mating on top of a branch was observed, with the ♂ on the female's back. Copulations last an average of 2.4 min (1–4, $n = 7$). After mating, the pair sit together grooming their own genitalia. The ♂ and ♀ remain within 20 m of each other for an average of 1.9 h (0.8–5.0 h, $n = 7$). Parturition occurs on a branch. Infant carried clinging to mother's ventrum until 3–4 months of age. After 3–8 days the infant is 'parked' among branches and lianas while the mother forages. She retrieves the infant before dawn when both infant and mother utter high-pitched 'tisc' contact calls. By 3–4 months the young Potto is constantly with its mother, either riding on her back or walking just behind (Charles-Dominique 1977).

Interactions between Pottos and other species are rarely observed in the wild (E. Pimley pers. obs.). In C Gabon, Pottos avoid competition with other frugivorous prosimians, such as Cross River Squirrel Galago *Sciurocheirus alleni cameronensis*, by utilizing the canopy to a greater extent (Pimley 2002). Pottos will displace fruit

bats feeding on the ripe fruits of the Umbrella Tree *M. cercopioides* while Two-spotted Palm Civets *Nandinia binotata* have feeding priority over Pottos (E. Pimley pers. obs.).

Reproduction and Population Structure In C Gabon, births ($n = 17$) occur Aug–Jan, inclusive (Charles-Dominique 1977). In contrast, Pottos in SW Cameroon appear not to have a birth season ($n = 4$) (Pimley 2002). Captive Pottos exhibited no seasonal oestrus (Cowgill *et al.* 1989). Oestrous cycle in captivity average 38 days (21–48, $n = 2$; Manley 1966). Gestation averages 197 days (194–205, $n = 5$) in captivity (Cowgill *et al.* 1989) and 193 days in the wild (Charles-Dominique 1977). Postpartum anoestrus of 1 month in SW Cameroon ($n = 1$; Pimley 2002). Inter-birth interval in C Gabon is 12–13 months (Charles-Dominique 1977). Single infant is born in wild populations ($n = 17$; Charles-Dominique 1977), although one case of twins in captivity (Cowgill 1974). Birth-weight for wild Pottos: mean 52 g ($n =$ not specified; Charles-Dominique 1977). Birth-weight for captive Pottos: mean 35 g (30–42, $n = 4$; Cowgill 1969). Weaned at 120–180 days (Charles-Dominique 1977).

In C Gabon offspring independent at 6–8 months ($n = 1$), although still living in the mother's home-range (Charles-Dominique 1977). Males leave mother's home-range at six months. Adult dentition complete by six months, adult body weight attained at 8–14 months, and full sexual maturity reached by 18 months (Charles-Dominique 1977). Sex ratio at birth 1 : 1 in free-ranging juvenile Pottos (Charles-Dominique 1977). Adult sex ratio female-biased in C Gabon, 1 : 1.9 ($n = 23$; Charles-Dominique 1977), but male-biased in SW Cameroon, 1 : 0.6 ($n = 11$; Pimley 2002). Pottos live 26 years in captivity (Bearder & Pitts 1987, Cowgill *et al.* 1989). Wild Pottos in C Gabon live to at least nine years ($n = 2$; Charles-Dominique 1977).

Predators, Parasites and Diseases Poorly known. Predators include Leopard *Panthera pardus* (Hoppe-Dominik 1984), Robust Chimpanzee *Pan troglodytes* (McGrew *et al.* 1978) and Two-spotted Palm Civet *Nandinia binotata* (Nekaris *et al.* 2007). Strong evidence for predation by Black-legged Mongoose *Bdeogale nigripes* (Charles-Dominique 1977). Monkeys (*Cercopithecus* spp., *Mandrillus* spp.), African Golden Cats *Profelis aurata*, Domestic Dogs, large owls *Bubo* spp. and large snakes are among the potential predators. Parasites include trypanosomes *Trypanosoma brucei gambiense* and filarial worms *Loa loa*, but no pathological symptoms observed (Pimley 2002).

Conservation IUCN Category (2012): Least Concern. *P. p. stockleyi* is Data Deficient. CITES (2012): Appendix II.

Widespread in secondary and primary forests, and in severely disturbed forest near human habitation. Main threat is habitat loss due to clear-cutting and intensive agriculture. Eaten by humans in West Africa and central Africa. Extirpated from large parts of its range (Wolfheim 1983). *P. p. stockleyi* only known from one specimen. Preliminary surveys of Mt Kenya and the Aberdares Range have failed to locate additional individuals. Additional surveys are needed in order to determine the distribution and abundance of this subspecies (Butynski & De Jong 2007).

Measurements*Perodicticus potto**P. p. edwardsi*

HB: 327 (305–370) mm, n = 33

T: 50 (37–70) mm, n = 33

WT: 1100 (850–1600) g, n = 33

Makokou, C Gabon (Charles-Dominique 1977); sexes combined

T (♂): 120 mm, n = 1

T (♀): 130 mm, n = 1

WT (♂♂): 1502 (938–1795) g, n = 7

WT (♀♀): 1572 (1407–1858) g, n = 4

Mt Kupé, SW Cameroon (E. Pimley 2002)

P. p. ibeanus

HB (♂♂): 349 (339–360) mm, n = 5

HB (♀♀): 326 (296–366) mm, n = 4

T (♂♂): 63 (60–68) mm, n = 5

T (♀♀): 62 (43–95) mm, n = 4

HF (♂♂): 72 (68–78) mm, n = 5

HF (♀♀): 69 (62–77) mm, n = 4

E (♂♂): 27 (25–29) mm, n = 4

E (♀♀): 26 (24–28) mm, n = 4

WT (♀♀): 847, 875 g, n = 2

Compiled from Thomas (1910; n = 1), Hollister (1924; n = 5) and specimens at NMK (n = 3) by Butynski & De Jong (2007). All specimens from the Kakamega/Kaimosi area, SW Kenya

HB: 309 (295–350) mm, n = 4

T: 78 (70–90) mm, n = 4

HF: 57 (50–65) mm, n = 4

E: 24 (20–25) mm, n = 4

WT: 823 (600–1170) g, n = 3

Eastern DR Congo. Compiled from Rahm (1966) by Butynski & De Jong (2007); sexes combined

P. p. stockleyi

HB ♀: 302 mm, n = 1

T: ♀: ~108 mm, n = 1

Mt Kenya, C Kenya (Butynski & De Jong 2007)

Key References Butynski & De Jong 2007; Charles-Dominique 1977; Jenkins 1987; Kingdon 1971; Oates 1984, 2011; Pimley 2002; Pimley *et al.* 2005a, b.**Elizabeth R. Pimley & Simon K. Bearder****GENUS *Arctocebus*****Angwantibos (Golden Pottos)***Arctocebus* Gray, 1863. Proc. Zool. Soc. Lond. 1863: 150.

The angwantibos, *Arctocebus*, comprise two allopatric species: Calabar Angwantibo *A. calabarensis* and Golden Angwantibo *A. aureus*. Both are confined to forest in the Bight of Biafra, between the Niger R. and Congo R. They are typically confined to areas of dense, liana-rich, undergrowth in primary, secondary and coastal forests that receive high rainfall.

Angwantibos are small, relatively short-limbed and slow-moving, woolly-coated nocturnal primates with short ears, moderately large eyes, narrow pointed muzzles and vestigial (short) tails. The wrists are extremely narrow. Both the third digit and, especially, the second digit of the hand are greatly reduced, specializations in which they resemble *Perodicticus* but even more extreme. There is a grooming claw on the somewhat shortened second digit of the foot. Olfaction appears to be of exceptional importance to both species.

Although bearing some general resemblance with the more robust, longer-tailed Potto *Perodicticus potto*, Angwantibos are much smaller (<325 g to the Potto's >800 g) and have the merest vestiges of a tail (<15 mm vs. >40 mm for Potto). Angwantibos have a more gracile skull with slender zygomatic arches, a more slender rostrum, and a longer, more pointed premaxilla; P⁴ is more molariform, there is a paraconid shelf on P₄, the lower molars have buccal cingulids and M³ is relatively large.

Although De Winton (1902) described *A. aureus* as a new species, Schwarz (1931b) treated this genus as monotypic, despite accurately listing many of the numerous craniodental differences between

them. General recognition of the existence of two species came later (Maier 1980). Following Schwarz (1931b), Jenkins (1987) and C. P. Groves (pers. obs.), the two species may be diagnosed as follows:

Arctocebus calabarensis. Between Niger R., Nigeria, and Sanaga R., Cameroon. Slightly larger, nasals relatively longer, width across orbits less than that across zygomata, premaxillary elongation not extreme, nasal aperture wider than high. Upper incisors relatively robust, with only a narrow gap between them, P² and P₃ crowns somewhat elongated, no buccal cingulum on upper cheekteeth. Dorsum pale tan brown, or buff, often with yellowish or orange tinge. Ventrums whitish or light grey.

Arctocebus aureus. South of Sanaga R., Cameroon, south to Congo R., Congo. Slightly smaller, nasals shorter, orbital rims expanded so that width across orbits is about equal to that across zygomata, greater elongation of premaxilla, nasal aperture higher than wide. Upper incisors tiny, only half the height of canines, with a wide gap between them, P² and P₃ not raised above occlusal plane of other cheekteeth, buccal cingulum present. Dorsum reddish-gold or russet. Ventrums cream, grey or reddish-buff.

The boundary between the two species is probably the Sanaga R., *A. calabarensis* to the north and north-west and *A. aureus* to the south.

Colin P. Groves & Jonathan Kingdon

Arctocebus calabarensis CALABAR ANGWANTIBO (NORTHERN GOLDEN POTTO)

Fr. Potto de Calabar; Ger. Gewöhnlicher Bärenmaki

Arctocebus calabarensis (J. A. Smith, 1860). Proc. Roy. Phys. Soc. Edinburgh 2: 177. Old Calabar, Nigeria.Calabar Angwantibo *Arctocebus calabarensis* adult.*Arctocebus calabarensis*

Taxonomy Monotypic species. Formerly considered one species with two subspecies: Calabar Angwantibo *A. c. calabarensis* and Golden Angwantibo *A. c. aureus*. 'Angwantibo' is the name of this primate in the Ibibio language (Nigeria). Synonyms: none. Chromosome number: $2n = 52$ (Stanyon *et al.* 1992).

Description Small, woolly, slow-moving climber with vestigial tail and pale tan-brown to yellowish-brown dorsal pelage. Sexes alike in size and colour. Muzzle pointed, projecting beyond the lower jaw. Nasal aperture wider than high. Eyes large. Circumocular pattern absent. Ears small, rounded, narrow and naked. Dorsal pelage pale tan-brown, orange-brown, buff or yellowish-brown. Dorsal guard hairs with brown or golden tips. Ventral pelage white, light grey or buff. Tail tip without dark hairs. Second digit of hand absent and third digit greatly reduced. Incisors about two-thirds canine height, with narrow diastema between them. Cheekteeth without buccal cingulum. Biorbital width less than bizygomatic. Nasals ca. 30% of skull length (Schwarz 1931b, Sanderson 1940, Hill 1953, Jenkins 1987, Kingdon 1997, Groves 2001). Infants woollier and more muted in colouring but otherwise resemble adults.

Geographic Variation None recorded.

Similar Species

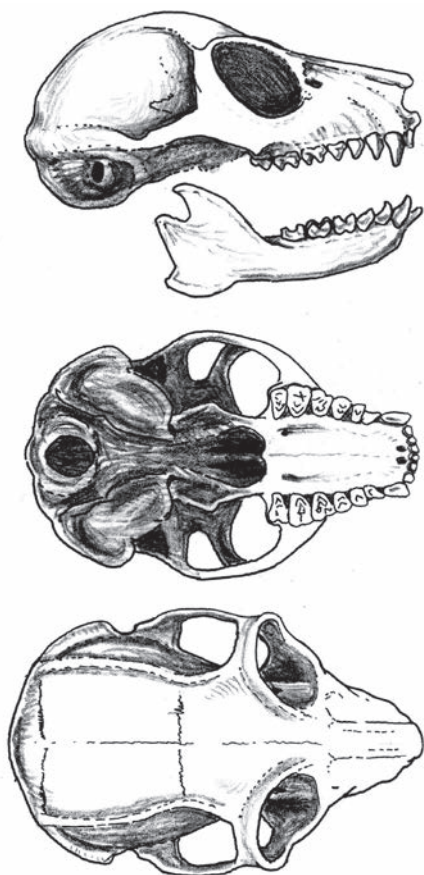
Arctocebus aureus. Parapatric. South of Sanaga R., Cameroon. Smaller (<270 g). Nasal aperture higher than wide. Dorsal pelage reddish-gold or russet. Tail tip with dark, stiff hairs. Incisors pin-shaped, half canine height, with wide gap between them (Schwarz 1931b, Hill 1953, Jenkins, 1987, Groves 2001).

Perodicticus potto. Sympatric. Appreciably larger (>600 g) with shorter muzzle and longer tail (>40 mm). Third digit present on hands. Neuchal area has long, black vibrissae and spinal processes of cervical vertebrae project above muscles.

Distribution Endemic to West Africa and western central Africa. Rainforest BZ. North to Benue R. and west to Niger R. in S Nigeria, and south to Sanaga R., SW Cameroon. Distribution patchy (Oates & Jewell 1967, Hill & Meester 1977).

Habitat Low to medium-altitude evergreen forest and sub-montane forest. In Nigeria most commonly encountered below 3 m in dense undergrowth of young secondary forest and forest edge where lianas and vines are abundant. Also in forest patches in the derived savanna zone (Jewell & Oates 1969b). In old, closed forest at Korup, Cameroon, below 5 m at forest edge and in tree-fall zones (Bearder & Honess 1992). Known from sea level to 400 m, in a region where mean daily temperature ranges from ca. 25–29 °C, depending on time of year. Across the species' range, mean annual rainfall ranges from 1500 to 4000 mm; in the wettest part of this area, near the coast, there is a Dec–Feb dry season (<50 mm rainfall/month); farther north, however, the dry season may begin in Nov and extend through Mar.

Abundance Can be common in the forest-farm bush-derived savanna mosaic of SE Nigeria, where it was encountered on 27 occasions during 48 night-walks each of 800 m (0.70 encounters/km; Jewell & Oates 1969b). At most other locations, difficult to locate and only infrequently observed.



Lateral, palatal and dorsal views of skull of Calabar Angwantibo *Arctocebus calabarensis* adult.

Adaptations Nocturnal and arboreal. Cryptic, usually moves in a slow, gliding fashion on small branches, twigs and climbers, but can move more rapidly during social interactions or if threatened. Will travel on the ground (Jewell & Oates 1969b, Bearder & Honess 1992). When threatened, can adopt a defence posture in which the back is hunched and head is withdrawn between the arms. Often rocks up and down in this position with its mouth open. If a predator attempts to touch the animal it will be bitten as the *A. calabarensis* lunges with its head beneath the arm-pit (Jewell & Oates 1969b).

Arctocebus calabarensis has poor eyesight and relies mainly on olfaction and hearing for food location and communication. They sleep by day in an upright position in dense vegetation where protected from sun, wind, rain and predators. Although Sanderson (1940) claimed that they sleep suspended from horizontal branches, this was never observed in captive animals in Nigeria.

Foraging and Food Insectivorous. Forages mostly in the undergrowth for invertebrates and fruit. Soft-bodied insects and grubs are preferred (Sanderson 1940). Recently captured *A. calabarensis* in Nigeria ate orthopterans, mantids, beetles and snails (Jewell & Oates 1969b). Based on what is known of the diet of *Arctocebus aureus* (Charles-Dominique 1977), it is likely that caterpillars are also an important part of the diet of *A. calabarensis*.

Social and Reproductive Behaviour Solitary. Not very vocal, relying mainly on scent-marking for communication. Vocal repertoire



Myology of Calabar Angwantibo *Arctocebus calabarensis*.

not studied, but when threatened produces 'hissing' calls (J. Oates pers. obs.). Use a high-pitched 'clicking' call for contact. Adult ♂ ♂ fight if placed together in captivity (Jewell & Oates 1969b). Young carried clinging to the fur or 'parked' while the mother forages. Previous offspring probably rejected on the birth of the next, since ♀ ♀ not observed with more than one young (Jewell & Oates 1969a).

Reproduction and Population Structure Births occur throughout the year in SE Nigeria. Births most common Jan–Apr (mid-dry season to early wet season). The following data on reproduction derive from a study of captives. In two cases, gestation estimated to be 131 and 132 days. Litter-size is one. Birth-weight of one captive was 37 g. Weaned at ca. 3.5 months. Minimum inter-birth interval ca. 4.5 months. Two young can be produced in one year. Sexual maturity at ca. 9–10 months. Oestrous cycle 36–45 days (Jewell & Oates 1969a). Few data available on population sex ratio, but of 13 young brought to Nsukka Zoo, seven were ♂ ♂ and seven were ♀ ♀; of 12 adults brought to the Zoo, two were ♂ ♂ and ten were ♀ ♀ (Jewell & Oates 1969a). Live in captivity to at least 13 years of age (Jones 1982).

Predators, Parasites and Diseases No information, but potential predators include genets *Genetta* spp., Two-spotted Palm Civet *Nandinia binotata*, Central African Linsang *Poiana richardsoni*, cats, monkeys, large owls *Bubo* spp. and large snakes.

Conservation IUCN Category (2012): Least Concern. CITES (2012): Appendix II. Occurs in a limited geographical area, but in the 1960s *A. calabarensis* flourished in a mosaic landscape in Nigeria that had a high human population density. Despite their small body size they are captured for human consumption in Nigeria (Jewell & Oates 1969b).

Measurements*Arctocebus calabarensis*

HB(♂♂): 236 (220–251) mm, n = 6

HB(♀♀): 231, 263 mm, n = 2

T(♂♂): 8, 8 mm, n = 2

T(♀♀): n. d.

HF(♂♂): 39 (36–43) mm, n = 6

HF(♀♀): 36, 36 mm, n = 2

E(♂♂): 25 (24–26) mm, n = 6

E(♀♀): 24, 26 mm, n = 2

WT(♂♂): 315, 320 g, n = 2

WT(♀♀): 298 (270–325) g, n = 9

Length measurements: Cameroon and Nigeria (Sanderson 1940)

WT: SE Nigeria (Jewell & Oates 1969a)

Key References Jewell & Oates 1969a, b; Oates 2011.**John F. Oates & Lesley Ambrose*****Arctocebus aureus* GOLDEN ANGWANTIBO (SOUTHERN GOLDEN POTTO)**

Fr. Angwantibo doré; Ger. Goldener Bärenmaki

Arctocebus aureus De Winton, 1902. Ann. Mag. Nat. Hist., ser. 7, 9: 48. 80 km up Benito R., Rio Muni, Equatorial Guinea.Golden Angwantibo *Arctocebus aureus*.*Arctocebus aureus*

darker. Ears small, rounded and naked. Dorsum reddish-gold or russet. Guard hairs on back, shoulders and haunches fine with light, crinkled tips that give a frosted appearance. Limbs slender and of about equal length. Ventral pelage cream, greyish or reddish-buff. Tail very short with dark, stiff hairs on tip. Second digit of hand absent and third digit greatly reduced. Incisors pin-shaped, half canine height, with wide gap between them. Juvenile darker than adult (Schwarz 1931b, Hill 1953, Jenkins 1987, Schwartz & Beutel 1995, Kingdon 1997).

Taxonomy Monotypic species. Originally considered a subspecies of Calabar Angwantibo *Arctocebus calabarensis*. Sanderson (1940) thought this taxon should be a distinct species and described as such by Maier (1980). Synonym: *ruficeps*. Chromosome number: not known.

Description Small, woolly, slow-moving climber with hunched body, vestigial tail and reddish-gold or russet dorsum. Sexes alike in size and colour. Nose pointed, projecting beyond lower jaw. Nostrils sculpted. Nasal aperture higher than wide. Circumocular pelage

Geographic Variation None recorded.

Similar Species

Arctocebus calabarensis. Parapatric at Sanaga R. SE Nigeria and SW Cameroon north of Sanaga R. Larger (>270 g). Dorsum pale tan-brown, yellowish-brown, buff or fawn. Tail lacks dark hairs. Nasal aperture wider than high. Incisors about two-thirds of canine height, with narrow diastema between them (Schwarz 1931b, Hill 1953, Jenkins 1987, Kingdon 1997, Groves 2001).

Perodicticus potto edwardsi. Sympatric. Much larger (>600 g) with shorter muzzle and longer tail (>40 mm). Third digit of hand present. Neuchal area has long, black vibrissae and spinal processes of cervical vertebrae project above muscles.

Distribution Rainforest BZ. Endemic to western central Africa. Cameroon south of Sanaga R., through Equatorial Guinea (Rio Muni), Gabon and Congo, south to Congo R. Eastwards through Congo to at least Congo R. and Ubangui R. Reported present in W DR Congo to 20° E, but this needs confirmation. Widespread but patchy distribution (Wolfheim 1983).

Habitat Low to medium altitude moist primary and secondary forest. Prefers old tree-fall zones rich in young lianas and where regenerating vegetation is dense (Charles-Dominique 1977).

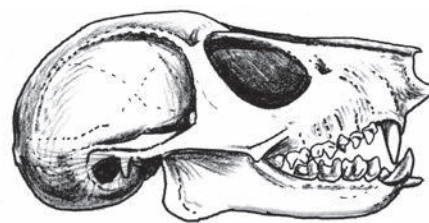
Abundance Rare to abundant. In C Gabon, 2 ind/km² in forest, but average density about 7 ind/km² in patches of more suitable habitat. Highest density reported is 18 ind/km² (Charles-Dominique 1971, 1974, 1977).

Adaptations Nocturnal and arboreal. Minimizes energy expenditure. *Arctocebus aureus* moves slowly, relying on crypsis, but when disturbed moves quickly to nearest clump of dense vegetation. Adopts a defence posture when threatened. Standing on widely spaced, rigid, fully extended limbs, the head is tucked on the chest with the open mouth beneath an arm-pit. The dark hairs on the tail are raised to form a circle around a pale zone formed by the tail tuft, thus making this the only conspicuous area of the body. A predator touching the tail or hindquarters is bitten by the sharp canines as the animal quickly lunges with its head beneath the arm-pit. If grasped when off the ground, it rolls into a ball and remains attached to a branch. Sometimes drop to the ground when disturbed (Charles-Dominique 1977).

Eyesight is poor but sense of smell good. Relies on scent-marking. Large vertical branches not used since hands and feet adapted only to close around stems <6 cm diameter. Sleeps in dense tangles of vegetation where protected from sun, wind, rain and predators (Charles-Dominique 1977, Kingdon 1997).

Foraging and Food Insectivorous. Usually in the undergrowth at <5 m, but occasionally to 15 m. Often moves to the ground to feed. Hunts in undergrowth, where prey are located primarily by scent. In C Gabon, 85% of diet is insects, 14% is fruit and 1% is wood fibre. Most common prey are caterpillars (65%) and beetles (20%). Also eats crickets, flies and ants (Charles-Dominique 1974, 1977). Smaller prey captured with the hands and transferred directly to the mouth, while larger prey are first held down and killed by biting. Will hold a caterpillar in its mouth by the head while wiping its hands along the caterpillar's body for up to 20 seconds to remove irritating hairs (Charles-Dominique 1977). One captive in S Gabon refused fruit but accepted all insect species offered. These insects were caught with rapid movements of the hands (L. Ambrose pers. obs.).

Social and Reproductive Behaviour Solitary. In C Gabon, *A. aureus* forages alone 98% of the time and in pairs 2% of the time. Animals sleep singly except for mother with infant. Employs 'deferred communication' by means of urine-marking and secretions from



Lateral view of skull of Golden Angwantibo *Arctocebus aureus* adult.

genital glands. This enables the ♂ to detect the approach of oestrus in the ♀. Parturition takes place on a branch. Neonate clings to the fur of the mother's abdomen. From 3 to 8 days after birth, foraging mothers 'park' their infants under a branch. Infants carried dorsally when older. Adult male's range overlaps ranges of several ♀♀ (Charles-Dominique 1977). Rarely vocalizes. Vocalizations are a 'tsic' for mother-infant contact, a deep two-phase 'groan' (inhalation, exhalation) for threat, and a 'wheet' for distress (Charles-Dominique 1977).

Reproduction and Population Structure In C Gabon births occur throughout the year, with the fewest Jun–Aug (dry season). Litter-size is one. Twins not reported. Inter-birth interval is 4–5 months. Mating follows birth without a break (Charles-Dominique 1977). Females can breed more than once a year, allowing a rapid rate of increase suited to exploiting temporary tree-fall zones (Charles-Dominique 1966). In captivity, gestation is 131–136 days (Manley 1967). Birth-weight is 24–30 g. Young are weaned at 100–130 days. Adult weight attained at 8–9 months. Sexual maturity reached at about 9–10 months. Sex ratio at birth, and among adults, is 1 : 1 (Charles-Dominique 1977). Longevity not known.

Predators, Parasites and Diseases No information, but probable predators include genets *Genetta* spp., Two-spotted Palm Civet *Nandinia binotata*, Central African Linsang *Poiana richardsoni*, cats, owls *Bubo* spp. and large snakes.

Conservation IUCN Category (2012): Least Concern. CITES (2012): Appendix II.

Has a fairly restricted range with patchy distribution and is not found at high densities. Too cryptic to be at risk from hunting by humans. Main threat is habitat loss.

Measurements

Arctocebus aureus

HB: 244 (230–260) mm, n = 30

T: 15 mm, n = 30 *

HF: n. d.

E: n. d.

WT: 210 (150–270) g, n = 30

Makokou, C Gabon (Charles-Dominique 1977); sexes combined

*Range not given.

HB: 242 (230–263) mm, n = 9

Various localities (Jenkins 1987); sexes combined.

Key References Charles-Dominique 1974, 1977.

Lesley Ambrose

Family GALAGIDAE
GALAGIDS: GALAGOS (BUSHBABIES)

Galagidae Gray, 1825. Annals of Philosophy, n. s. 10: 338.

| | | |
|----------------------------------|-----------------------|--------|
| <i>Otolemur</i> (2 species) | Greater Galagos | p. 407 |
| <i>Sciurocheirus</i> (3 species) | Squirrel Galagos | p. 417 |
| <i>Galago</i> (4 species) | Lesser Galagos | p. 424 |
| <i>Euoticus</i> (2 species) | Needle-clawed Galagos | p. 441 |
| <i>Galagoides</i> (7 species) | Dwarf Galagos | p. 446 |



Southern Lesser Galago *Galago moholi*.

Polygeneric family found throughout sub-Saharan Africa, except for the south-west and extreme south, inhabiting bushlands and woodlands in S and NE Africa as well as tropical and sub-tropical forests. Recently five genera and 24 species have been recognized (Grubb *et al.* 2003, Nekaris & Bearder 2011), five of which had yet to be formally described and named. The taxonomy presented here is more conservative, recognizing 18 species, while acknowledging that several species likely await discovery.

Jenkins (1987) and Kingdon (1997) characterize the galagos (also known as ‘bushbabies’) as long-tailed, woolly, nocturnal and mainly arboreal primates with long hindlegs and elongated bases to the feet (tarsi). The head is rounded, with forward-facing eyes and large, naked ears that retract into compact, folded structures. The moist nose is at the end of a pointed muzzle. The neck is very flexible. The brain case is broader than in Lorisidae and there is no sagittal crest. The orbits are farther apart and less upwardly inclined than in Lorisidae. The bullae are strongly inflated. The mandible has a slender horizontal ramus. The upper incisors are peg-like and subequal in size with a conspicuous central gap; in the upper dentition, the posterior premolar is molariform and the molars have prominent cusps and well-developed talons. Lower incisors and canines are modified to form a comb-like structure. A toothed pseudo-tongue, which serves as a specialized ‘comb’ cleaner, is situated between the tongue and the floor of the mouth.

The limbs are modified for leaping and grasping: the hands are long and prehensile; the thumb is pseudo-opposable; the phalanges are very elongated relative to the metacarpals; the tarsal region is elongated and the first toe (hallux) widely divergent. The palms of

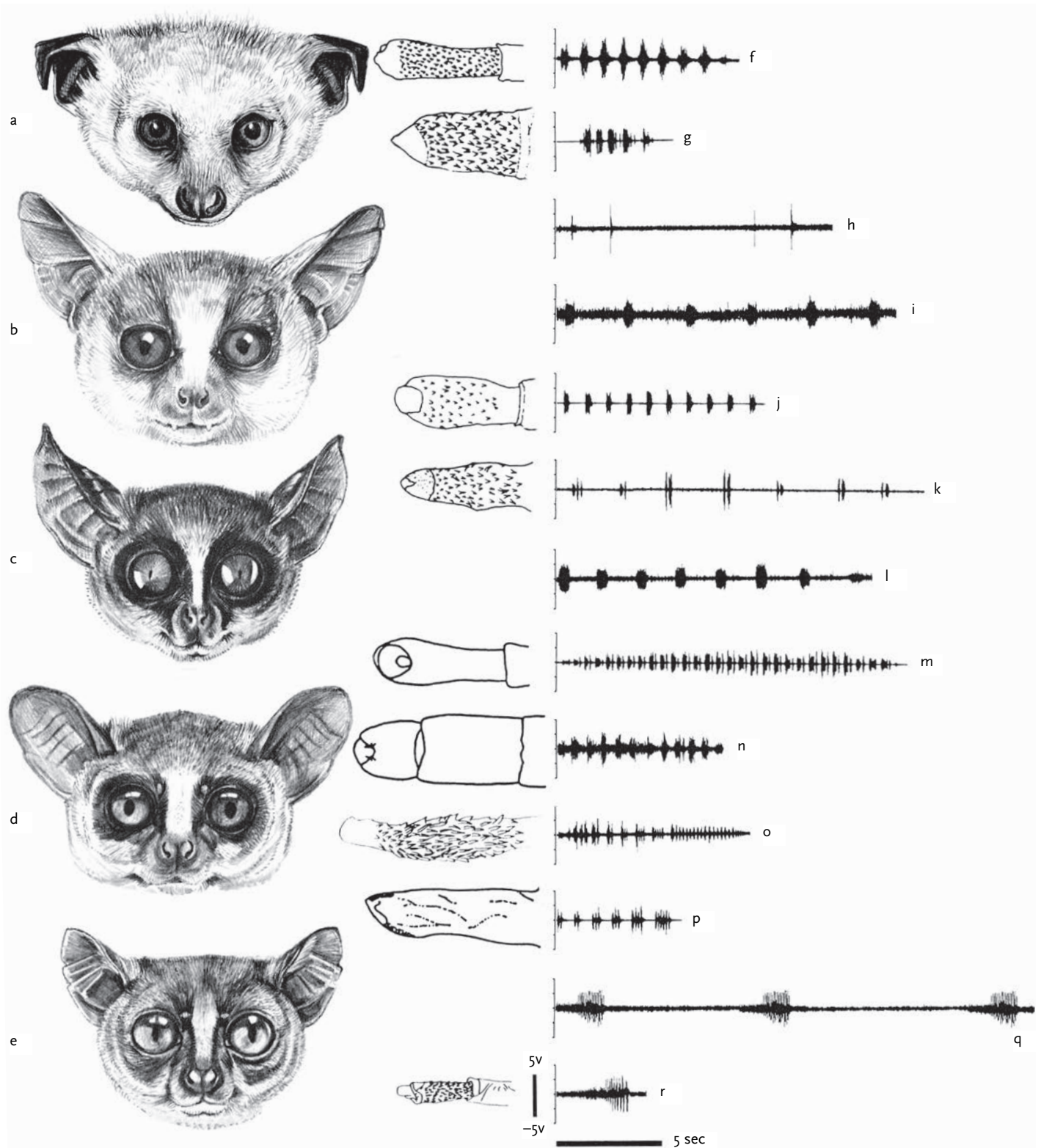


Myology of Small-eared Greater Galago *Otolemur garnettii*.

the hand and soles of the feet have six prominent pads with spatulate, padded tips and conspicuous friction ridges. Inter-ramal (chin) vibrissae are absent but other sets of facial vibrissae are present and carpal vibrissae are found in some species. The nipples are variably arranged in pairs of two or three. The glans penis is elongated and covered with spines; the os penis is simple with the tip often protruding as a knob. The clitoris is long and narrow in the limited sample of species that have been studied. Head + body length range 100–400 mm. Adult body mass ranges 60–2000 g.

The baby-like cries of the largest species, Large-eared Greater Galago *Otolemur crassicaudatus*, have given the galagos their popular name, but each species has a distinctive repertoire of 10 to 25 calls (a ‘vocal profile’) that is species-specific. Many species are best identified by such vocalizations because they play a crucial role in attracting the opposite sex, and they are more noticeably different than relative body sizes or colours.

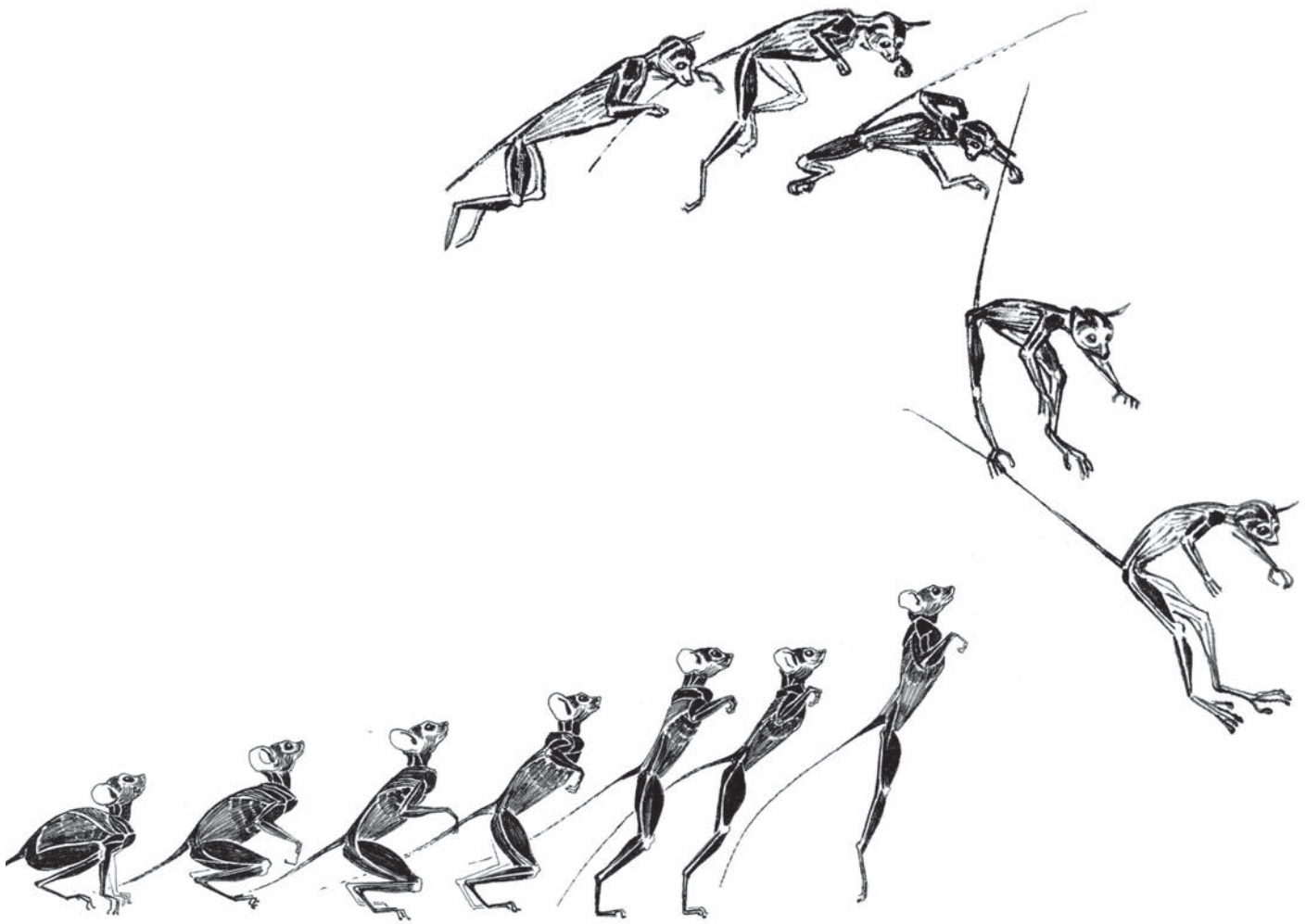
Galagos eat various combinations of insects, gum and fruit. Up to four species can be found sympatrically, avoiding dietary overlap, or exploiting different areas or heights, within the shared habitat. All species generally forage singly, but some appear to synchronize their movements with companions through calling,



Faces, penile shapes and oscillograms of the loud call for some galagos Galagidae (courtesy of S. Bearder, M. J. Anderson & P. Honess).

Faces: (a) Large-eared Greater Galago *Otolemur crassicaudatus*. (b) Southern Lesser Galago *Galago moholi*. (c) Spectacled Lesser Galago *Galago matschiei*. (d) Zanzibar Dwarf Galago *Galagoides zanzibaricus*. (e) Thomas's Dwarf Galago *Galagoides thomasi*.

Penile shapes and oscillograms: (f) Large-eared Greater Galago *Otolemur crassicaudatus*. (g) Small-eared Greater Galago *Otolemur garnettii*. (h) Northern Needle-clawed Galago *Euoticus pallidus*. (i) Bioko Squirrel Galago *Sciurocheirus alleni alleni*. (j) Northern Lesser Galago *Galago senegalensis*. (k) Southern Lesser Galago *Galago moholi*. (l) Spectacled Lesser Galago *Galago matschiei*. (m) Rondo Dwarf Galago *Galagoides rondoensis*. (n) Matundu Dwarf Galago *Galagoides zanzibaricus udzungwensis*. (o) Kenya Coast Dwarf Galago *Galagoides cocos*. (p) Mozambique Dwarf Galago *Galagoides granti*. (q) Thomas's Dwarf Galago *Galagoides thomasi*. (r) Demidoff's Dwarf Galago *Galagoides demidovii*.



Leaping sequences (from film) for Large-eared Greater Galago *Otolemur crassicaudatus* (top) and Northern Lesser Galago *Galago senegalensis* (from Kingdon 1971).

and in *O. crassicaudatus*, up to three juveniles move as a group with the mother when they feed on fruit, but move alone when only insects and gum are available. Territories are advertised by loud-calls and by laying down scent. Scent rubbing behaviour varies considerably, but all, except the needle-clawed galagos *Euoticus* spp., 'urine-wash'. Urine is voided onto the cupped hand, which is then rubbed onto the sole of one foot. This sequence is generally repeated on the other foot, and ensures that the hands and feet are permanently sticky, improving their grip. Urine-washing onto conspecifics observed in a few cases and direct deposit of urine onto specific areas of substrate ('rhythmic micturition') also occurs. Scent glands are common around the mouth, in the midline of the chest and in the ano-genital region.

Social networks are found in all species studied to date. Social bonds are maintained by regularly meeting others at night, with bouts of mutual sniffing, allogrooming and play, or by huddling together during the day. Adult ♀♀ usually maintain territories that exclude strange ♀♀ but may include adult daughters. The territories of the oldest ♂♂ are generally larger and centred over those of more than one matriarchal group. Males move away from the natal sites at puberty and establish new, large home-ranges. Subordinate ♂♂ avoid conflict with dominant ♂♂ by moving away or hiding when approached.

Galagos usually sleep alone, but sleeping groups of up to eight individuals occur. They sleep by day in a hidden retreat (tree-hole or vegetation tangle) and some species construct leafy nests, particularly when they have infants. Oestrus is usually restricted to a few days and is often synchronized within populations. Tropical species tend to give birth to a single young once a year, while in drier, more seasonal habitats, galagos can give birth to twins twice a year, coinciding with the wettest months. In some species, infants are carried between safe retreats by the mother grasping, in her mouth, a fold of skin on the infant's flanks. In some species of needle-clawed galagos *Euoticus*, greater galagos *Otolemur* and lesser galagos *Galago* the infants may also cling to the mother's fur. In the cold austral winters a dense underfur and the ability to digest gum allows survival even when other food sources are frozen solid. No species are known to exhibit torpor, unlike some lemurs.

Galago locomotion includes vertical clinging and leaping, with the legs brought forward on landing, but this is less common than landing hands first, or quadrupedal running and walking. Gaits employed vary with the demands of the wide range of habitats occupied by the galagos. A similar variety of specializations applies to the special senses. For example, species moving in different heights within forest have eye-shine of different colours (pink, red, yellow or orange) and their ears vary in shape, size and position.

Molecular data indicate that galagos have been a distinctively African lineage for ca. 40 million years (mid-Eocene). Teeth of a putative early galago (*Saharagalago*), dated at >34 mya, were found at a late Eocene site in the Fayum Depression in Egypt (Seiffert *et al.* 2003, 2005b). The phylogenetic relationships among loriforms remain ambiguous despite several attempts to resolve them with molecular, morphological and behavioural evidence. Adaptive radiation within the Galagidae is considerable – even within the same genus. Two genera (*Euoticus* and the squirrel galagos *Sciurocheirus*) are restricted to the moist forests of the Congo Basin and Gulf of Guinea, one (the dwarf galagos *Galagoides*) occurs across tropical Africa from the forests of West Africa and central Africa to the coastal forests along the east coast, and two (*Otolemur* and *Galago*) have representatives in tropical forests as well as in sub-tropical woodlands and bushlands. It remains unclear whether tropical forest forms colonized the sub-tropical regions, or the other way round. Molecular findings place the *Otolemur*–*Galago* split at 15.4 mya (mid-Miocene; Perelman *et al.* 2011).

Taxonomic controversies have been considerable, undoubtedly because of the highly cryptic characteristics of museum specimens and the difficulties of studying galagos in the wild. Hill (1953: 211), for example, notes: ‘The classification of the Galagidae is a vexed question. There is no doubt that 5 main types or groups of galagos at present exist in Africa, but whether each of these is to be regarded as a nominal species or whether they should be treated as genera or sub-genera is difficult to decide.’ The groups in question are:

- 1 the large forms of the *crassicaudatus* type;
- 2 medium-sized forms, long-fingered, *alleni* type;
- 3 small forms typified by *senegalensis* type;

- 4 small forms with specialized, needle-pointed nails typified by *elegantulus* type;
- 5 very small, mouse-like animals typified by *demidovii* type.

The taxonomy of the group has come full circle, largely returning to the treatment proposed by Gray (1863) who was followed, on the basis of cranial and dental peculiarities, by Mivart (1864). The number of species recognized by most authors has risen from six in 1967 to >20 in 2009, mainly on the basis of their species-specific vocal profiles and correlated distinctions in penile morphology. The rate at which new species have been recognized over the past two decades suggests that several more species have yet to be uncovered (Bearder 1999). This volume presents profiles for 18 species of galagos within five genera:

- 1 *Otolemur* for the largest galagos
- 2 *Sciurocheirus* for the long-fingered, forest understorey galagos
- 3 *Galago* for the small leaping, long hind-limbed galagos
- 4 *Euoticus* for the needle-clawed, gum-eating, forest galagos
- 5 *Galagoides* for the dwarf, ‘running’, forest galagos.

No profile is presented here for the recently resurrected, and little known, Malawi Dwarf Galago *Galagoides nyasae* (Grubb *et al.* 2003, Nekaris & Bearder 2011).

The genus *Galagoides* is the least consistent in terms of morphology, ecology and behaviour, representing a ‘wastebasket’ genus for the smallest galagos that may be separated further when more is known about their adaptations and genetics.

Simon K. Bearder & Judith Masters

GENUS *Otolemur* Greater Galagos

Otolemur Coquerel, 1859. Revue Zoologique, Paris 11: 458.



Mwera Greater Galago *Otolemur* sp. nov.? adult male.

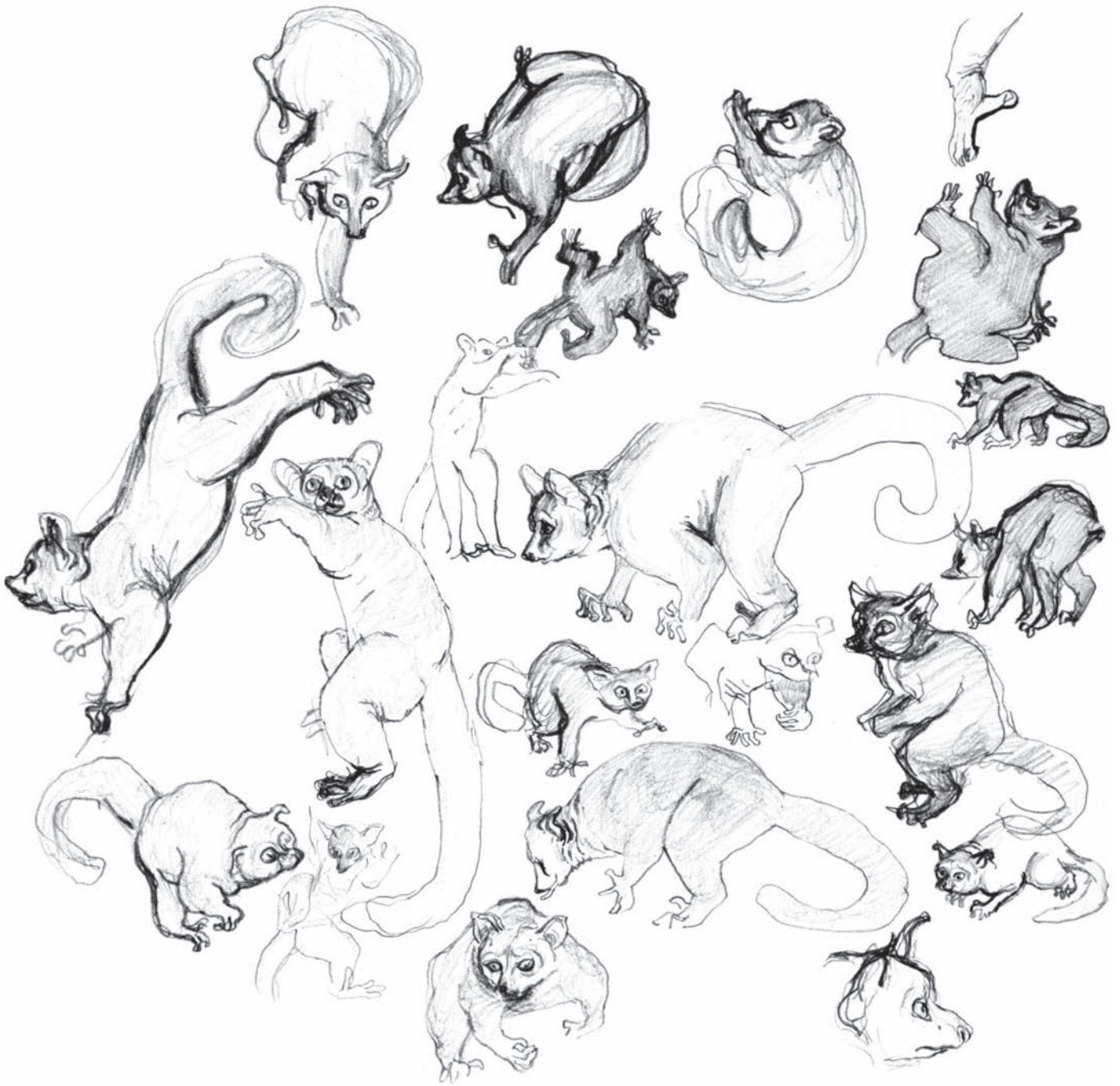
Otolemur is a polytypic genus endemic to the woodlands and forests of the southern half of Africa. There are two currently-recognized and named species; Small-eared Greater Galago *O. garnettii* and Large-eared Greater Galago *O. crassicaudatus* (Olson 1979). A third species, Miombo Silver Greater Galago *O. monteiri*, is sometimes recognized

(Groves 2001, 2005c, Grubb *et al.* 2003, Nekaris & Bearder 2011). This volume follows Olson (1979) and Jenkins (1987) in recognizing two species. *Otolemur garnettii* and *O. crassicaudatus* can be distinguished based on a number of characters, including body size and vocal profile.

Distributed throughout most of eastern and south-eastern Africa from coastal S Somalia in the north to KwaZulu–Natal in SE South Africa. From Angola eastwards through Tanzania. Northern distribution limited by the forests of the Congo Basin and deserts of N Kenya and S Somalia. In southern Africa, *Otolemur* does not penetrate the peripheral habitats of the Namib Desert, Kalahari Desert or High Veld of South Africa (Olson 1979, Nash *et al.* 1989, Kingdon 1971, 1997, Groves 2001).

A thorough review of the systematic history of the genus *Otolemur* is provided by Olson (1979). He describes this genus as part of his detailed morphological study of >4000 specimens. His diagnosis (p. 328) for dentally mature individuals is as follows:

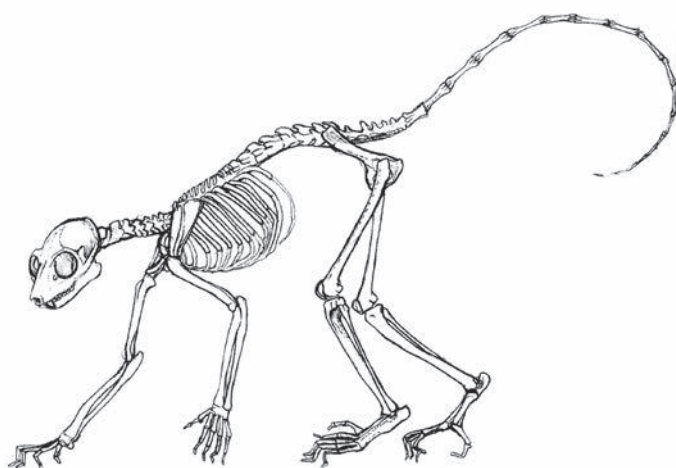
‘Head plus body length greater than 23 cm, hind foot greater than 8 cm, body weight over 500 grams, cranial length greater than 5.5 cm, length of upper pre-molar-molar series greater than 1.85 cm



Small-eared Greater Galago *Otolemur garnettii*.

and length of lower pre-molar-molar series greater than 1.65 cm. Cranial features associated with masticatory musculature well developed: marked postorbital constriction, robust zygomatic arches, deep maxillary root of zygomatic bone, relatively long zygomatic arch posterior to postorbital process, large lateral pterygoid plates, coronoid and angular processes of the mandible robust. Foramen magnum directed posteriorly, minimum basicranial flexion, fissure between orbital and temporal fossae large, palatine canals tiny, large triangular area of the horizontal plate of the palatine bones posterior to M3. Lingual margins of maxillary tooth rows parallel or only

slightly divergent posteriorly. Muzzle large and robust, broad not pointed. Molars and P4/4 with low rounded cusps, crowns lacking prominent crests. Diploid number 62. Glans penis clavate, gradually incrassate from base to truncated tip, the tip obliquely inclined from its superior surface downwards. Extraocular recti muscles inserted around equator of eyeball. Pronograde quadruped. Lateral surfaces of limbs more or less the same colour as dorsal body pelage. Dark circumocular rings and light coloured interocular stripe absent. Skin between palmar and plantar pads granular. Caecum unsacculate and rather small'.



Large-eared Greater Galago *Otolemur crassicaudatus*.

Olson (1979) provides a detailed description of the genus and a comprehensive list of features that distinguish *Otolemur* from each of the other genera within the Galagidae, of which the most obvious is their larger body size. Other characteristics that he describes include an intermembral index of 65–70; digital formulae $IV > III > V > II > I$; pedal digit II with toilet-claw; tarsal elongation not as pronounced as in most other galagos; overall colouration of limbs similar to body, lacking bright golden or yellowish colours; tail long and bushy; ventral and dorsal body pelage of different colours except in melanistic individuals; large areas of glandular skin frequently present in scrotal, pectoral and submental regions of mature adults. Male external genitalia with long and slightly curved penis, which gradually thickens towards the tip, glans penis covered with either unidentate or tridentate spines, urethral opening situated in triangular depression below projecting baculum, tip of baculum and urethra surrounded by wrinkled collar; ♀ external genitalia with long thick clitoris, large labia with fine lamellae that converge towards the vagina.

Dentition: $I^{2/2}$, $C^{1/1}$, $P^{3/3}$, $M^{3/3}$; deciduous dentition $i^{3/3}$, $c^{1/1}$, $m^{3/3}$; molariform teeth of both jaws with low rounded cusps and not exhibiting prominent crests between cusps. Postcranial skeleton rather generalized except for elongation of hindlimb, and the calcaneus and navicular elements of the tarsus.

Simon K. Bearder

Otolemur crassicaudatus LARGE-EARED GREATER GALAGO (THICK-TAILED GREATER GALAGO / BUSHBABY)

Fr. Galago à queue touffue; Ger. Großohr-Riesengalago

Otolemur crassicaudatus (É. Geoffroy, 1812). Ann. Mus. Hist. Nat. Paris 19: 166. Quelimane, Mozambique.



Large-eared Greater Galago *Otolemur crassicaudatus* adult male.

Taxonomy Polytypic species. Olson (1979) focused on the genus *Otolemur* and his classification, based on measurements from 4949 galago specimens (including all type specimens) from museums and private collections in Europe, Africa and North America, is used here. This species was referred to as *Galago*

crassicaudatus in most classifications prior to 1979, with *garnettii* as a subspecies (Hill 1953, Napier & Napier 1967, Groves 1974, Petter & Petter Rousseaux 1979). Recognition of two species belonging to the genus *Otolemur* (*O. crassicaudatus* and Small-eared Greater Galago *O. garnettii*) was established by Olson and substantiated by Jenkins (1987), Clark (1988), Zimmermann (1990), Masters (1991) and DelPero *et al.* (2000). Each species has a distinctive vocal profile (Bearder *et al.* 1995) with no obvious vocal differences among the subspecies. Olson (1979) recognizes three subspecies, *O. c. crassicaudatus*, *O. c. monteiroi* and *O. c. argentatus*, whereas Kingdon (1997) recognizes *argentatus* as a species, and Groves (2001, 2005c), Grubb *et al.* (2003) and Nekaris & Bearder (2011) recognize *monteiroi* as a species. This volume follows the taxonomy of Olson (1979).

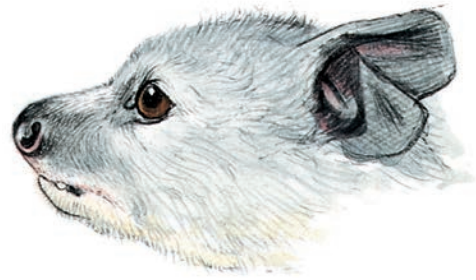
Honess (1996b), Kingdon (1997), Groves (2001), Grubb *et al.* (2003) and Nekaris & Bearder (2011) recognize a 'dwarf' form of Large-eared Greater Galago (Mwera Greater Galago *Otolemur* sp. nov.?) based on a population of extremely small individuals (<500 g) in SE Tanzania. The calls and appearance of the Mwera Greater Galago could not be distinguished from typical *O. crassicaudatus* (Honess 1996b). These animals are considerably smaller than *O. garnettii*, which share the same fruit trees in the village of Tandangongoro. Dwarfism may be the result of character displacement, since much larger individuals of *O. crassicaudatus* are found a few kilometres away, where *O. garnettii* is absent. Synonyms: *argentatus*, *badius*,

*Otolemur crassicaudatus*

kirkii, *lestradei*, *lonnbergi*, *monteiri*, *umbrosus*, *zuluensis*. Chromosome number: $2n = 62$ (de Boer 1973a, b, Stanyon *et al.* 2002).

Description Large galago with big ears and thickly-furred tail; strongly associated with miombo woodland. The largest galago, but wide variation among adults (550–2000 g). Head dominated by large ears and large robust muzzle. Eyes relatively small. Face markings indistinct or absent. No difference in colour between sexes but adult ♂ significantly heavier than adult ♀, weighing ca. 1500 g vs. 1250 g (Harcourt 1980, 1986b, Masters 1988). Pelage colour highly variable in both sexes, with dorsum ranging from silver-grey to dark brown. Melanistic individuals present in Kenya, Tanzania and E DR Congo, living side by side with individuals that are light silver (almost white). Some individuals are entirely black, or have white on the underside. Outsides of limbs and face typically same colour as body but ventrum is variable in colour and the bushy tail may be lighter or have a black tip. Males have particularly large, light-coloured bare patches of glandular tissue on their chest (Clark 1978a, 1982a, b). Hindlimbs slightly longer than forelimbs but quadrupedalism is the norm; unable to land feet first when leaping (Bearder 1974, Olson 1979, Crompton 1983, 1984, Nash *et al.* 1989). Nails convex and lack lateral points. The newborn is covered with uniform greyish fur. Photographs of *O. crassicaudatus* in Kenya and Tanzania available at: www.wildsolutions.nl

Geographic Variation There is considerable disagreement about subspecies (Hill 1953, Olson 1979, Jenkins 1987, Kingdon 1997, Groves 2001, 2005c Grubb *et al.* 2003, Nekaris & Bearder 2011). Olson's extensive museum studies provide a solid foundation for further research, including studies of genetics, vocalizations and behaviour. In addition to the subspecies noted below, Olson examined 250 individuals that he considered to be hybrids between *O. c. crassicaudatus* and the Miombo Silver Galago *O. c. monteiri* in a wide region from the southern end of L. Malawi, through Zimbabwe and C Mozambique to the confluence of the Bube R. and Limpopo R.

Large-eared Greater Galago *Otolemur crassicaudatus* adult female.

Jenkins (1987) indicates that these animals, together with specimens from S Tanzania, may constitute a separate subspecies for which the earliest name would be *O. c. kirkii*.

O. c. crassicaudatus South African Thick-tailed Galago (99 specimens examined by Olson). In eastern coastal areas south of Limpopo R. South along the KwaZulu–Natal coast, South Africa, to Durban and inland to Pietersberg and Potgeitersrus (Constantino 2001). Only found in riverine or dune forest (Olson 1979). Relatively large HB, tail relatively short (only slightly longer than HB and usually <400 mm). Ears relatively small (60–65 mm). Pelage brown to dark brown, rarely reddish-brown. Tail colour of body but tip sometimes black or dark brown. Melanistic individuals are not known.

O. c. monteiri Miombo Silver Galago (374 specimens examined by Olson). Occurs over a vast area broadly corresponding to *Brachystegia* ('miombo') woodland/savanna between 10 and 15°S. Also in montane and riverine forest. From Angola through Zambia, Zimbabwe, Malawi through Mozambique. Southern limits poorly known. Also in SE DR Congo, Rwanda, Burundi and Tanzania (Olson 1979). In Tanzania, at L. Rukwa, Mahale Mountains N. P. on east shore of L. Tanganyika, Tabora, Dar es Salaam, Mt Kilimanjaro, Mt Meru and Sadaani N. P. In SE Kenya, south of Mombasa (A. Perkin, Y. De Jong & T. Butynski pers. comm.). *Otolemur c. monteiri* similar to *O. c. crassicaudatus* in overall biometrical features but differs significantly in having larger ears (65–70 mm) and a tail (>400 mm) that is notably longer than the body. Dorsum is typically silver or light grey, sometimes with slight brownish wash. Tail almost always lighter in colour than the body and rarely has a blackish tip (Y. de Jong & T. Butynski pers. comm.). Melanistic individuals and populations occur throughout the range. Olson (1979) notes a deviation from the typical pelage pattern in a series of eight specimens from atypical habitat in the Kahemba District, SE DR Congo, which tempted him to designate a new taxon, but he considered that the sample size was too small.

O. c. argentatus Northern Silver Galago (23 specimens examined by Olson). Largest and morphologically most distinctive subspecies. Tanzania and Kenya around the east and south-east shore of L. Victoria, where geographically isolated from other subspecies. In Loita Hills, SC Kenya (Butynski & De Jong 2012). Possibly in NE Rwanda. Characterized by absolutely larger size (HB averages 350 mm and head length 77 mm compared with 320 mm and 70 mm for *O. c. monteiri*) and relatively small ears (55–60 mm). Pelage almost indistinguishable from *O. c. monteiri*, although brownish wash absent except on top of head. Melanistic and silver individuals occur throughout the range and melanism probably more common than in *O. c. monteiri*.



Melanistic Northern Silver Galago *Otolemur crassicaudatus argentatus* adult male.

Similar Species

Otolemur garnettii. Narrowly sympatric or parapatric on coast of East Africa from Mombassa (e.g. Kaya Teleza) to N Mozambique, and from Usambara Mts to Ngorongoro Crater (Nash *et al.* 1989). Sympatric in Loita Hills (Butynski & De Jong 2012). Separated ecologically, preferring wetter parts of shared sites, although they may be seen together in the same tree. About 70% as large as *O. crassicaudatus*. Superficial similarities in appearance mask more subtle contrasts. *Otolemur garnettii* is more agile and able to land feet first when leaping; relatively small ears; nails with concave distal ends and lateral points for gripping branches; single as opposed to multiple births; a longer gestation period; different penile morphology and shape of the baculum (Eaton *et al.* 1973, Olson 1979, Dixson 1995, 1998, Anderson 1998, 2000); a different call repertoire, particularly the loudest calls that are used to attract companions and repel rivals (Bearder *et al.* 1995). Fur carriage of infants not confirmed. Melanistic forms not reported (Nash *et al.* 1989). Confusion between these two species makes the earlier literature difficult to interpret.

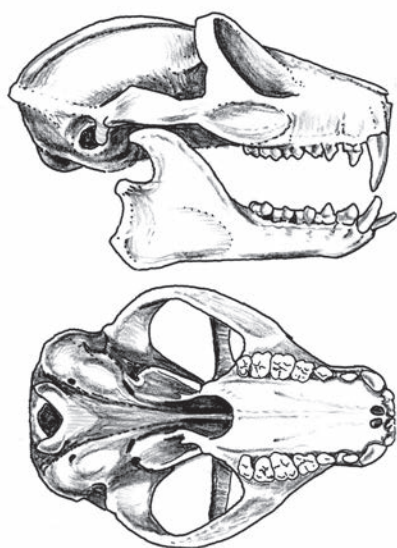
Distribution In Somalia-Masai Bushland, Coastal Forest Mosaic, Zambezian Woodland, Southern Rainforest-Savanna Mosaic, Highveld, and Afroalpine BZs. Endemic to Africa south and east of the Congo Basin. Northern distribution in Angola and DR Congo restricted by Congo Basin forest. In NW Tanzania, immediately south of border with Uganda, *O. crassicaudatus* in riverine vegetation bordering moist forest occupied by Thomas's Dwarf Galago *Galagoides thomasi* and Demidoff's Dwarf Galago *Galagoides demidovii*. Distribution restricted by the drier savannas and bushlands of S Kenya and Tanzania. Extends from S Kenya through Tanzania, Malawi, Zambia, E Zimbabwe, E Botswana, E South Africa, and Swaziland to Zululand, south of Durban (Olson 1979, Skinner & Smithers 1990). See Geographic Variation for distributions of subspecies. Kingdon (1971) notes that northern limit of *O. crassicaudatus* corresponds with the southern range of Potto *Perodicticus potto*. Major rivers not a serious barrier to dispersal.

Habitat Found in areas with well-defined seasons. Open woodland and savanna occupied in northern parts of range, especially miombo woodlands. Mainly associated with forests, thickets and well-developed woodland of higher rainfall areas farther south. Over southern part of range, restricted by dry and less densely wooded vegetation of desert margins and savannas. Requires dense shelter to hide during the day but penetrates far into dry regions where there is riverine vegetation (e.g. W Zimbabwe and in Northern Province and Mpumalanga, South Africa). Distribution coincides with availability of tree gum. Eucalyptus *Eucalyptus* spp., pine *Pinus* spp. and Black Wattle *Acacia mearnsii* plantations can be used for sleeping. Occupies urban and peri-urban gardens where there are sufficient fruit trees for food. Occurs from sea level to >1800 m in E Zimbabwe (Skinner & Smithers 1990, Kingdon 1997), and to 2000 m in Udzungwa Mts, SC Tanzania (Rovero *et al.* 2009).

Abundance Locally common. No systematic density estimates exist as detailed studies have been made only in narrow tracts of riverine vegetation as opposed to uniform forest cover. Bearder (1974) studied a ♀ and three infants with a home-range of approximately 7 ha where they were occasionally joined by a ♂. On the east shore of L. Tanganyika, in Mahale Mountains N. P., Tanzania, in old secondary forest (dominated by abandoned Oil Palm *Elaeis guineensis*, Guava *Psidium guajava* and Mango *Mangifera indica*) density of *O. c. monteiri* >50 ind/km² at forest/beach ecotone, but much less than this in the forest interior (T. Butynski & Y. de Jong pers. comm.).

Adaptations Nocturnal and arboreal. Hindlimbs slightly longer than forelimbs but quadrupedalism is the norm; unable to land feet first when leaping (Bearder 1974, Olson 1979, Crompton 1983, 1984, Nash *et al.* 1989). Least agile of the galagos, generally walking or running along the top of broad, horizontal supports, or on the ground (sometimes over 100 m). Able to leap 3 m between trees and hop along the ground bipedally if distressed. Frog-like, quadrupedal hopping on the ground appears unique to *O. crassicaudatus*. Ability to maintain a grip when hanging upside-down beneath a wide horizontal branch to reach gum is remarkable (Bearder & Doyle 1974a, Crompton 1983). Most common sleeping site is dense tangles of creepers and branches at a height of 5–12 m above ground. At one site in Mahale N. P. some sleep among the dense fronds at the top of >10 m high Oil Palms (T. Butynski & Y. de Jong pers. comm.). Adult ♀♀ make nests when they have infants – inaccessible leafy platforms, depressed in the middle with foliage above for shelter (Bearder & Doyle 1974a). Individuals have more than one sleeping site and are not known to move away from a sleeping site during the day (Bearder & Doyle 1974a). Caves and roof spaces in human dwellings also used as shelters. Chest glands produce three major volatile compounds, which are different from those of *O. garnettii* (Katsir & Crewe 1980, Clark 1988).

Foraging and Food Omnivorous. Diet comprised of invertebrates, fruit and gum. Individuals follow regular pathways to reach well-known sources of gum or fruiting trees (Bearder & Doyle 1974a). Usually forages alone when searching for small sources of gum and insects (Clark 1985), but move as a group where large fruit trees are common (Bearder 1974). In South Africa, trees that



Lateral and palatal views of skull of Large-eared Greater Galago *Otolemur crassicaudatus* adult male.

produce abundant gum from established wounds (usually Sweet Thorn *Acacia karoo*) are visited regularly, particularly during the cold, dry winter (Harcourt 1986b, Nash & Weisenseel 2000). In NE South Africa, diet includes 33% fruit, 62% gum and 5% invertebrates where fleshy fruit is readily available (Bearder 1974) but 41% gum and 59% invertebrates where fruit is absent (Clark 1985). Flowers, seeds, nectar and millipedes also consumed (Coe & Isaac 1965, Crompton 1984, Clark 1985, Harcourt 1986b). Feed on hard-shelled and woody, dried fruits in South Africa (Masters *et al.* 1988), and arthropods from the orders Coleoptera, Orthoptera, Hymenoptera, Odonata, Chilopoda and Isoptera. Millipedes (Diplopoda) taken during the summer months (Harcourt 1986b). Termites, *Macrotermes* sp., eaten in Malawi (Happold & Happold 1992). Fish captured from a basin and eaten in captivity (Welker 1976). Many reports of birds being captured in the wild and their brains eaten. This, however, is probably a local tradition as it appears to be absent from some populations (Bearder 1974). Water is obtained from the diet or by licking dew.

Social and Reproductive Behaviour Dispersed groups. Most gregarious of all galagos, probably related to large body size and diet. Where fruit is abundant, the young stay with the mother during the long period of immaturity (15 months) and they frequently move with her as a cohesive group. If an individual becomes separated from the group, it, unlike any other galago, gives a 'buzz' call until reunited (Bearder 2007). Cohesive groups not formed where food sources are scattered in small clumps (Clark 1985, Bearder 1987). Grouping also occurs at sleeping sites during the day when a mother and up to three offspring may be joined by an adult ♂.

Adult ♀♀ occupy separate territories, which they share with their offspring of one or more generations. The sex ratio at birth appears to be biased towards ♂♂. This has been interpreted as an adaptation to reducing competition for food resources (gum) that are shared among related ♀♀. Males on the other hand tend to disperse (Clark 1978b). Male ranges are larger and overlap those of ♀♀. Adult ♀♀ occupy adjacent territories that are visited by up

to six adult ♂♂. Young adult ♂♂ have less frequent access to the ♀♀ but all age/sex classes engage in amicable social interactions, especially grooming, with the exception of territorial ♂♂, which never come together. Juveniles engage in object play, locomotor play and social play, including group play between a mother, two juveniles and an adult ♂ (Bearder 1974).

Females may have mating access to up to six ♂♂ during their oestrus (3–5 days) once each year, indicating a polygynandrous (multimale/multifemale) mating system (Clark 1985). Oestrus periods are synchronized within populations during two weeks during winter (Jun/Jul). Prolonged copulation is common (up to 45 minutes) and has been interpreted as a form of mate-guarding (Dixson 1995). At parturition, ♀♀ may become unusually aggressive to cage-mates (including previous offspring) and mothers cease to join their usual sleeping partners (Bearder & Doyle 1974a, Bearder 1987).

Communication involves a wide range of auditory, visual, tactile and olfactory signals, including 18 structurally distinct calls (Bearder 1974, Clark 1978a, 1988, Petter & Charles-Dominique 1979, Masters 1991, Bearder 2007). The loud child-like cries, audible at 300 m, are the origin of the name 'bushbaby'. Raucous whistles, yaps and cackles of alarm are also given. Conspicuous scent-marking behaviours include cheek-rubbing, chest-gland-rubbing, ano-genital rubbing, rhythmic urination, urine-washing of the hands and feet, and foot-rubbing, which is peculiar to *Otolemur* (Welker 1973, Clark 1982a, b, 1988). An individual will rub the roughened area of the sole of one foot against a branch and then the other, making a distinctive scraping noise (Bearder & Doyle 1974a). Foot-rubbing is done mainly by adult ♂♂ and may accompany urine-washing, rhythmic urination and chest-gland-marking when disturbed in social situations or in the presence of a predator (Bearder 1974, Hager 2001). Chest-gland-marking by adult ♂♂ in captivity is testosterone-dependent (Bullard 1984).

Reproduction and Population Structure Gestation is 132.8 ± 2.6 days ($n = 3$) in the wild (Bearder 1974). Of 20 pregnancies in captivity, six (30%) resulted in singletons and 14 (70%) multiple births, two of which were triplets and 12 twins (Masters *et al.* 1988). In South Africa there is a single birth season during Nov which coincides with the start of the rains (Bearder & Doyle 1974a). In E Zimbabwe (Smithers & Wilson 1979) and Zambia (Ansell 1960) births occur in Aug/Sep. No defined birth season observed in captivity. Infants born in nests, which, at other times, are used as resting places. Just before giving birth the ♀ relines the nest with fresh green leaves and twigs. At birth the neonate weighs ca. 40 g, the eyes are open. Neonate can crawl within 30 min of birth. At first the mother carries each infant, one at a time, in her mouth, holding it by a fold of skin on the flanks or by the back. After about eight days up to three infants may cling to their mother's back. At about three days infants vocalize by giving 'squeaks', and at nine days emit 'clicks' and 'crackles'. In the wild the young travel with the mother after about 25 days of age, either following her or being carried (Bearder 1974). Lactation lasts around ten weeks (Bearder 1974). Mother–infant cannibalism can occur in captivity after the death of an infant (Tartabini 1991). Young move independently after 17 weeks. Maximum longevity in captivity is about 15 years (Doyle 1979).

Predators, Parasites and Diseases Robust Chimpanzee *Pan troglodytes* is a predator of *O. c. monteiroi* (Uehara 1997). Other predators include Leopards *Panthera pardus*, large owls *Bubo* spp., large snakes and genets *Genetta* spp. (Crompton 1984). A wide variety of parasites and pathogens reported for prosimians in captivity although they have few health problems in captivity (Kohn & Haines 1982, Benirschke *et al.* 1985).

Conservation IUCN Category (2012): Least Concern. CITES (2012): Appendix II.

The conservation status of *O. c. argentatus* is of considerable concern as most of the habitat of this isolated subspecies has been destroyed by human activities (N. S. Svoboda & D. Roberts pers. obs.). The population identified by Olson (1979) in the Kahemba District, SE DR Congo (see Geographic Variation), is in particular need of study.

Measurements

Otolemur crassicaudatus

HB: 313 (255–400) mm, n = 360

T: 410 (300–550) mm, n = 357

HF: 93 (70–108) mm, n = 340

E: 62 (48–72) mm, n = 344

WT: 1131 (567–1814) mm, n = 157

Data from numerous museums. All subspecies represented in this sample (Olson & Nash 2002); sexes combined

O. c. crassicaudatus

TL (♂♂): 712 (630–785) mm, n = 16

TL (♀♀): 588 (501–715) mm, n = 5

T (♂♂): 383 (350–440) mm, n = 16

T (♀♀): 319 (285–388) mm, n = 5

HF (♂♂): 93 (84–101) mm, n = 15

HF (♀♀): 83 (80–88) mm, n = 5

E (♂♂): 61 (54–65) mm, n = 15

E (♀♀): 55 (49–63) mm, n = 4

WT (♂♂): 1270 (550–1650) g, n = 9

WT (♀♀): 740, 740 g, n = 2

Former Transvaal, South Africa (Rautenbach 1982)

O. c. crassicaudatus

TL (♂♂): 681 (640–710) mm, n = 10

TL (♀♀): 619 (590–637) mm, n = 3

T (♂♂): 359 (280–430) mm, n = 10

T (♀♀): 325 (300–345) mm, n = 3

KwaZulu–Natal, South Africa (Taylor 1998)

O. c. monteiroi

TL (♂♂): 739 (685–798) mm, n = 23

TL (♀♀): 727 (685–780) mm, n = 12

T (♂♂): 416 (360–450) mm, n = 23

T (♀♀): 407 (355–450) mm, n = 12

HF (♂♂): 96 (90–101) mm, n = 23

HF (♀♀): 91 (84–100) mm, n = 13

E (♂♂): 60 (54–65) mm, n = 23

E (♀♀): 59 (53–65) mm, n = 13

WT (♂♂): 1220 (940–1640) g, n = 24

WT (♀♀): 1130 (990–1460) g, n = 13

Zimbabwe (Smithers & Wilson 1979)

Key References Bearder & Doyle 1974a; Clark 1985; Harcourt 1980; Masters 1985; Olson 1979.

Simon K. Bearder & Nadine S. Svoboda

Otolemur garnettii SMALL-EARED GREATER GALAGO (GARNETT'S GALAGO / BUSHBABY)

Fr. Galago de Garnett; Ger. Kleinohr-Risengalago

Otolemur garnettii (Ogilby, 1838). Proc. Zool. Soc. Lond. 1838: 6. Zanzibar I., Tanzania (designated by Thomas 1917).



Small-eared Greater Galago *Otolemur garnettii*.

Taxonomy Polytypic species. Originally called *Otolicnus garnettii* by Ogilby (1838), with no provenance given to the type specimen; the type locality was designated by Thomas (1917: 48) to be Zanzibar I. (now Unguja I.). Since then, numerous synonyms for both the generic and specific name have been used (for details see Olson 1979). Until recently, this taxon considered a subspecies of *Otolemur* (also called *Galago*) *crassicaudatus* (e.g. Hill 1953, Petter & Petter-Rousseaux 1979). This taxon now generally accepted to be a full species (Olson 1979, Harcourt 1984, Jenkins 1987, Masters 1988, Nash *et al.* 1989, Groves 2001, 2005c, Grubb *et al.* 2003, Nekaris & Bearder 2011). Following Groves (2001, 2005c) and Grubb *et al.* (2003), four subspecies are recognized. Chromosome number: 2n = 62 (Masters 1986, Jenkins 1987, Groves 2001). Synonyms: *agisymbanus*, *hindei*, *hindsii*, *kikuyuensis*, *lasiotis*, *panganiensis*.

Description Relatively large galago (size of small domestic cat) with long bushy tail. Second largest galago. Occurs in forests.

Sexes alike, but ♂ slightly heavier than ♀. Head colour varies with colour of dorsum (see below), but may have a whitish face (A. Perkin & T. Butynski pers. obs.) Muzzle blunt and dog-like. Forehead sometimes with darker vertical furrow. Eye-rings not obvious. Ears small relative to size of head and to other galagos. Dorsum varies from reddish-brown to greyish-brown to silvery (Olson 1979, Nash *et al.* 1989), sometimes with a greenish tinge (Groves 2001). Ventrums vary from creamy-white to buff-brown. Tail colour highly variable even within same population (Harcourt 1984). Generally proximal half, or more, of tail is same colour as dorsum, with distal half, or less, varying from black, dark brown to white. Chin, throat and ventrum generally same colour as distal part of tail (Y. de Jong & T. Butynski pers. comm.). Nails are convex. Penile spines usually tridentate, with some bidentate. Baculum elongated, extending beyond glans penis (Dixson 1989, 1995). Photographs of *O. garnettii* from Kenya and Tanzania available at: www.wildsolutions.nl

Geographic Variation

- O. g. garnettii* Zanzibar Small-eared Galago. Zanzibar I., Pemba I. and Mafia I. Dorsum rich reddish-brown. Ventrums yellow, slightly greenish toned. Tail almost black over distal half (Jenkins 1987, Groves 2001).
- O. g. panganiensis* Pangani Small-eared Galago. Loita Hills and at Tavetta, extreme SC Kenya, Tanzania from Tanga, Mt Kilimanjaro, Mt Meru and L. Manyara to south (right) bank of Ruvuma R., extreme N Mozambique (Olson 1979). Dorsum greyish-brown, sometimes with yellow wash. Lacking greenish tones. Ventrums grey-white. Tail usually brown or dark brown over distal quarter (Jenkins 1987, Groves 2001), but sometimes whitish at tip (e.g. Usa R., Mt Meru; Y. de Jong & T. Butynski pers. comm.).
- O. g. lasiotis* White-tailed Small-eared Galago. Juba R., Somalia, south along Kenya and Tanzania coasts to Tanga. Inland to Taita Hills and Kibwezi, Kenya (Jenkins 1987, Groves 2001). Dorsum greyish, greyish-brown or silvery. At Diani, extreme SE Kenya, dorsum varies from dark brown to pale brown. Individuals at Watamu-Gedi, central coast of Kenya, are exceptionally variable in colour (Olson 1979, De Jong & Butynski 2009). Ventrums greyish-white; always paler than dorsum. Distal half or less of tail highly variable, ranging from black, dark brown to white, even at the same locality (Harcourt 1984, De Jong & Butynski 2009).
- O. g. kikuyensis* Kikuyu Small-eared Galago. Kenya Highlands, east of the Eastern Rift Valley; Nairobi, Ngong, Masinga, Aberdares and Mt Kenya. Dorsum grey, often iron grey, with a tinge of green. Muzzle, eye-rings, ears, hands and feet blackish. Ventrums yellow-white. Tail very full, light brown, often nearly black over distal quarter, but sometimes with whitish tip (Groves 2001, De Jong & Butynski 2009).

Similar Species

Otolemur crassicaudatus. Narrowly sympatric or parapatric on the coast of East Africa from Mombasa (e.g. Kaya Teleza; A. Perkin pers. obs.), SE Kenya, to N Mozambique. Sympatric in Loita Hills, SC Kenya (Butynski & De Jong 2012). Also sympatric in Tanzania from Usambara Mts to Ngorongoro Crater (Nash *et al.* 1989). Larger with mean weight of adult ♂ ca. 1250 vs. 900 g for *O. garnettii*. Ears larger, and larger relative to the head (ca. 60



Small-eared Greater Galago *Otolemur garnettii* adult male.

vs. 46 mm). Pelage greyer. Loud 'trailing call' (or 'cry') distinctive (Nash *et al.* 1989, Bearder *et al.* 1995). Confusion between these two species makes the earlier literature difficult to interpret.

Distribution Endemic to eastern Africa. Somalia–Masai Bushland and Coastal Forest Mosaic BZs. In coastal and riverine forests from Jubba R., Somalia, south to N Mozambique. Northernmost record is in the Mathews Range, C Kenya (01° 15' N, 37° 18' E, 1414 m; De Jong & Butynski 2010a). On Manda, Pemba, Zanzibar and Mafia Is. Inland in forests of Kenya Highlands east of Eastern Rift Valley, Tsavo, Taita Hills, Chyulu Hills, Mt Kasigau, Mt Kilimanjaro, Mt Meru, L. Manyara and most Eastern Arc Mts (Olson 1997, De Jong & Butynski 2009, A. Perkin pers. obs.). Only known site in Southern Highlands is Milo Forest (Honess 1996b, A. Perkin & T. Davenport pers. obs.). Although the map in Nash *et al.* (1989) shows *O. garnettii* in the Udzungwa Mts, SC Tanzania, there is not yet evidence of this (Honess 1996b, Butynski *et al.* 1998, Perkin 2001) except for Mbatwa riverine forest in north Udzungwa Mountains N. P. (Rovero *et al.* 2009). Olson (1979) indicates that *O. garnettii panganiensis* occurs just south of the Ruvuma R. in extreme N Mozambique, and that it may occur farther south. See Geographic Variation.

Habitat In forested and forest-agriculture mosaic from sea level to 2000 m, rarely higher; in Tanzania to 2400 m on Mt Kilimanjaro (Grimshaw *et al.* 1995) and in Kenya to 2290 m on Aberdares Range (M. Dodds pers. comm. to Y. de Jong). Mean annual rainfall over geographic range ca. 600–1500 mm (Olson 1979, Y. de Jong & T. Butynski pers. comm.). Gedi and Diani coastal forests, Kenya, are lowland, dry forest on coral rag (Moomaw 1960). These forests are multistratal, often with a thick understorey, a canopy at 15–20 m, mostly of *Combretum schumannii*, and emergents to 25 m (Harcourt & Nash 1986b). In submontane and montane forests of Mt Kenya, Aberdares Range, Mt Meru, Mt Hanang and Eastern Arc Mts, *O. garnettii* is most common at forest edges and in secondary vegetation (A. Perkin, Y. de Jong & T. Butynski pers. obs.).



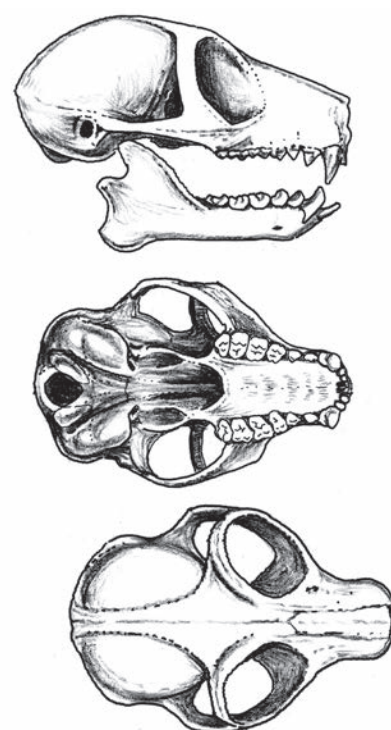
Otolemur garnettii

Abundance In Diani and Gedi Forests, Kenya, ca. 31–38 ind/km² (Nash & Harcourt 1986). Brief foot and/or vehicle surveys of >20 sites in Kenya and Tanzania yielded encounter rates of 1–5 ind/h, with highest rates in Kenya at Tana River Primate National Reserve, Meru F. R., Ngaia F. R. and Diani (De Jong & Butynski 2009), and in Tanzania at Ngezi-Vumawimbi Nature F. R. (NW Pemba I.), Zanzibar I., Arusha, Zaraningi Forest (in Sadaani N. P.) and L. Manyara (Y. de Jong & T. Butynski pers. comm.).

Adaptations Nocturnal and arboreal. Day spent sleeping in tangled vegetation in tall bushes or trees. Not known to use tree-holes. Loud ‘trailing call’ given by both sexes to announce their presence to conspecifics; most other calls are associated with alarm situations (Harcourt 1984, Bearder *et al.* 1995). Predator and prey detection and localization are associated with well-developed visual and hearing systems. Olfactory communication is important: urine-washing and chest- and foot-rubbing. Glands on chest and abdomen produce an oily, yellowish apocrine secretion (Kingdon 1997). Both sexes have spiky patches on soles of the hindfeet, which are used to rub a substrate and generate sound (Hager 2001).

Locomotion in *O. garnettii* is quadrupedal; when leaping it usually lands hindfeet first, or on all four feet (like *O. crassicaudatus*) (Harcourt 1984); bipedal hopping when on the ground (Harcourt 1984, Harcourt & Nash 1986b). On Mt Kilimanjaro, shows a preference for horizontal supports in mature trees; 51% of 420 observations on horizontal supports and 42% of 527 observations at >10 m in canopy (Svoboda 1999).

Foraging and Food Omnivorous. Forages mostly in trees, rarely on ground. About half of the time spent above 5 m (Harcourt & Nash 1986b). Mostly forages alone, though several animals may congregate in fruiting trees (Nash & Harcourt 1986, A. Perkin pers. obs). Faecal samples indicate that diet at Diani is ca. 50% animal matter and 50% fruit. Fruits eaten include *Ficus* spp., *Grewia* sp.,



Lateral, palatal and dorsal views of skull of Small-eared Greater Galago *Otolemur garnettii* adult male.

Lannea stuhlmanni and *Vitex strickeri* (Harcourt 1984, Harcourt & Nash 1986b). Stomach samples indicate that 50% of diet is of animal matter and 50% is fruits and seeds (Masters *et al.* 1988). Invertebrates make up the majority of animal matter, mostly beetles, orthopterans and centipedes. Spiders, ants, caterpillars, millipedes, heteropterans, snails and termites also eaten. Observed feeding actively on invertebrates disturbed by swarming army ants (= safari ants = driver ants) *Dorylus* sp. (T. Butynski & Y. de Jong pers. comm.). Birds taken on occasion and probably include, at Diani, Kenya Crested Guinea Fowl *Guttera pucherani* (Harcourt & Nash 1986b). Also forages in farmland, taking Bananas *Musa* sp., Breadfruit *Artocarpus altilis*, Mangos *Mangifera indica*, Papaw *Carica papaya* and other fruit crops, plus Coconut Palm *Cocos nucifera* sap, which is tapped by local people for the manufacture of ‘palm wine’ (Masters *et al.* 1988, A. Perkin pers. obs.).

Social and Reproductive Behaviour Solitary. Mean home-range size at Gedi and Diani, calculated from trapping, radio-tracking and sleeping site data is 12.0 ha (10.8–13.0, n = 4) for adult ♀♀ and 17.1 ha (16.6–17.8, n = 3) for adult ♂♂. Home-ranges of resident adult ♂♂ overlap slightly or not at all, though they overlap ranges of younger ♂♂. Transient ♂♂ move through the home-ranges of resident ♂♂ and ♀♀. Same-age ♀♀ also tend to have non-overlapping home-ranges, though they can share home-ranges with others, which are probably relatives. At Gedi both sexes travel, on average, 1.6 km/night; at Diani one radio-collared adult ♂ travelled, on average, farther than the one radio-collared adult ♀, 3 km and 1.8 km, respectively. Adults spend most of the night alone and, usually, sleep alone as well, though grooming and play between individuals occurs. The apparently less social behaviour of this species, compared with *O. crassicaudatus*, may be due to fewer infants

being born (*O. crassicaudatus* frequently has twins or triplets and many of the interactions seen are between adults and youngsters), or to differences in diet (Nash & Harcourt 1986).

Otolemur garnettii has an extensive vocal repertoire, with 12 spectrographically different call types used by adults of both sexes (Harcourt 1984, Zimmermann 1990, Bearder *et al.* 1995, Honess 1996b, Becker *et al.* 2002). The loud 'trailing call' starts with two lower frequency introductory units followed by 5–8 units, which are repeated and trail away. Alarm calls – 'squawks', 'chatters' and 'cackles' – given frequently, are mostly repetitive and are generally not replied to. Low frequency 'growls' given in a state of anxiety. Other calls recorded in captivity are the low frequency 'flutter/hum' and 'short growls', high frequency 'infant clicks', and high frequency adult ♂ 'clicks' and 'spits' (Becker *et al.* 2002).

Little is known about the mating system of *O. garnettii*. Dixon (1998) suggests *O. garnettii* has a 'dispersed' multimale-multifemale mating system inferred from social organization, copulatory patterns and mating activity in captivity, as well as complex penile morphology and large testes. Non-receptive ♀♀ avoid ♂♂. Males initiate copulations with receptive ♀♀. Copulations are lengthy with intromission lasting 13–260 min; this may be related to mate-guarding (Dixon 1998). In the wild it is thought that olfactory cues play an important role in signalling the sexual condition of the ♀ and in attracting mates in the nocturnal non-gregarious society of *O. garnettii* (Dixon 1998).

Reproduction and Population Structure Not well known. It appears that in the Kenyan coastal forests, infants are born Aug–Nov with ♀♀ giving birth once per year (Nash 1983, Harcourt 1984). Of 95 pregnancies in captivity, 91 (96%) yielded singletons, while four (4%) yielded twins (Izard & Simons 1986). Mothers transport infants in their mouths and 'park' them when foraging. In captivity, ovarian cycle is 39–59 days (mean 44), oestrus 7–24 days (mean 12.4), and there is a restrictive phase of receptivity of 2–10 days (mean 5.8) with a peak of 1–2 days (Eaton *et al.* 1973). Eaglen & Simons (1980) give gestation in captivity as 119–138 days.

Predators, Parasites and Diseases Predators probably include large snakes, genets *Genetta* spp., Two-spotted Palm Civets *Nandinia binotata*, large owls *Bubo* spp. and monkeys. When a potential predator is located, *O. garnettii* mobs the predator while emitting a series of loud 'squawks' that can go on for >40 minutes (Honess 1996b, A. Perkin pers. obs.). Other conspecifics generally do not join in this behaviour but may gather round. Prey avoidance strategies enabled by excellent hearing, smell and vision combined with rapid arboreal locomotion skills and cryptic colouration. Will move around during the day when disturbed by humans (A. Perkin pers. obs.).

Conservation IUCN Category (2012): Least Concern. CITES (2012): Appendix II. The discontinuous distribution and small size of many of the forests in which *O. garnettii* occurs makes this species vulnerable to clearing for agriculture, logging, settlement and tourism. This is especially the case along the coast and on Zanzibar I. In many areas, killed as a presumed agricultural pest and a symbol of bad luck. Hunted for meat in several localities, such as in the Makonde tribal area, SW Tanzania. There is small-scale collecting for the pet trade (Perkin 1998, A. Perkin pers. obs.).

Measurements

Otolemur garnettii

HB: 266 (230–338) mm, n = 368

T: 364 (308–440) mm, n = 363

HF: 91 (80–103) mm, n = 359

E: 45 (34–55) mm, n = 356

WT: 767 (550–1040) g, n = 269

Data from numerous museums. All subspecies represented in this sample (Olson & Nash 2002). Sexes combined

O. g. lasiotis

HB (both sexes): 278 (260–294) mm, n = 7*

T (both sexes): 360 (330–410) mm, n = 14**

WT (♂♂): 846 (690–1060) g, n = 14

WT (♀♀): 805 (604–985) g, n = 11

Gedi and Diani, Kenya (Nash & Harcourt 1986)

*Gedi; **Diani

O. g. lasiotis

HB (♂♂): 295 (270–350) mm, n = 4

HB (♀♀): 284 (280–291) mm, n = 3

T (♂♂): 340 (330–350) mm, n = 4

T (♀♀): 319 (314–323) mm, n = 3

HF (♂♂): 90 (85–94) mm, n = 4

HF (♀♀): 84 (82–88) mm, n = 3

E (♂♂): 47 (43–54) mm, n = 4

E (♀♀): 46 (45–47) mm, n = 3

WT (♂♂): 916 (820–990) g, n = 4

WT (♀♀): 755 (650–815) g, n = 3

Taita Hills, Kenya (Perkin *et al.* 2002)

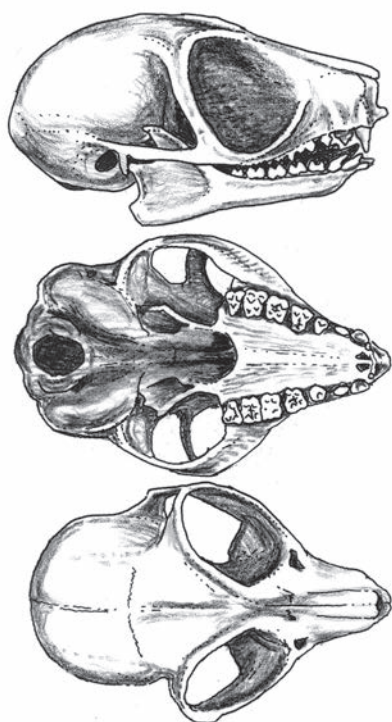
Key References Harcourt 1984; Harcourt & Nash 1986b; Nash & Harcourt 1986; Olson 1979.

Caroline S. Harcourt & Andrew W. Perkin

GENUS *Sciurocheirus*

Squirrel Galagos

Sciurocheirus Gray, 1873. Proc. Zool. Soc. Lond. 1872: 857 [1873].



Lateral, palatal and dorsal views of skull of Bioko Squirrel Galago *Sciurocheirus alleni alleni* adult.

Squirrel galagos or the 'Allen's Galago Group' have generally been treated as *Galago* by most recent authors, although Gray (1873) erected a separate genus, *Sciurocheirus* (squirrel galagos) for *S. alleni*. Masters *et al.* (1994) and Crovella *et al.* (1994) have, on the basis of genetic similarities, allied this species with the greater galagos *Otolemur* spp. Bayes (1998) found considerable genetic differences between *Otolemur* and *Sciurocheirus*, implying an ancient separation. He placed this divergence at ca. 37 mya (mid-Eocene). *Sciurocheirus* spp. differ considerably from *Galago* spp. in skull shape (Hill 1953), anatomy of the foot (Jouffroy & Gunther 1985) and vocal repertoire, including the loud call (Ambrose 2003). Taxonomic placement of the squirrel galagos has been a recurrent problem. Jouffroy & Gunther (1985) showed that, in their locomotor anatomy and in their behaviour, the squirrel galagos stood well apart from all other galagos. Bearder *et al.* (1995) categorized the *alleni* Group within the *Galago senegalensis/moholi* and *matschiei* Group. Groves (1989, 2001) recorded

his misgivings in placing these distinctive animals in *Galago* but could find no clear affinity with any other group of galagos. In their most recent molecular study Masters *et al.* (2007) contend that the closest genetic affinities of these galagos are with *Otolemur*, not *Galago*. This discovery is currently the focus for various re-appraisals of both genera, in the hope of a better diagnosis of their common ancestry and a more refined appreciation of galago evolution.

Groves (2001, 2005c) designated three allopatric forms as full species: Allen's Squirrel Galago *Galago alleni*, Cross River Squirrel Galago *G. cameronensis* and Gabon Squirrel Galago *G. gabonensis*. Ambrose (2003) and Grubb *et al.* (2003) follow Gray (1873) in placing the squirrel galagos in the genus *Sciurocheirus*. Ambrose (2003) considers the loud call repertoires of *alleni* and *cameronensis* to be identical, thereby invalidating the specific distinction for *cameronensis*. There is, however, a significant difference in body weight, with *alleni* being about one-third heavier than *cameronensis*. On this basis, Ambrose (2003) retained *cameronensis* as a subspecies of *S. alleni*. A third species of *Sciurocheirus*, with a distinct vocal repertoire, facial markings and pelage colouration, was discovered in 1993 in the Makandé region, C Gabon, and is formally described and named here for the first time.

Sciurocheirus is a genus of medium-sized forest galagos with a distinct preference for feeding on or close to the floor in forests between the Niger R. and Congo R. These are greyish-brown galagos with russet tinges on the limbs. The pointed muzzle has a pale median stripe and the reddish eyes are set within well-defined mask-patches. Nipples = 2 + 2 + 2 = 6.

Sciurocheirus bound from one vertical support to another, clinging and leaping like a tree-frog. They land hands first, unlike other galagos, which land feet first or with all limbs simultaneously.

Given that their closest genetic relationship appears to be with *Otolemur* (Masters *et al.* 2007), there is the implication that their common ancestor had a wider ecological and geographic range than either descendant lineage. Furthermore, their current occupation of a restricted ecological niche in a restricted geographic region suggests contraction from a wider range of habitats and behaviours. The co-existence and probable competition of five other lorisooids might have influenced just such a contraction and refinement of niche. There are interesting implications for 'use of space' by these galagos, for understanding their preferred foraging zones and the physical structure of their micro-environment.

Colin P. Groves & Jonathan Kingdon

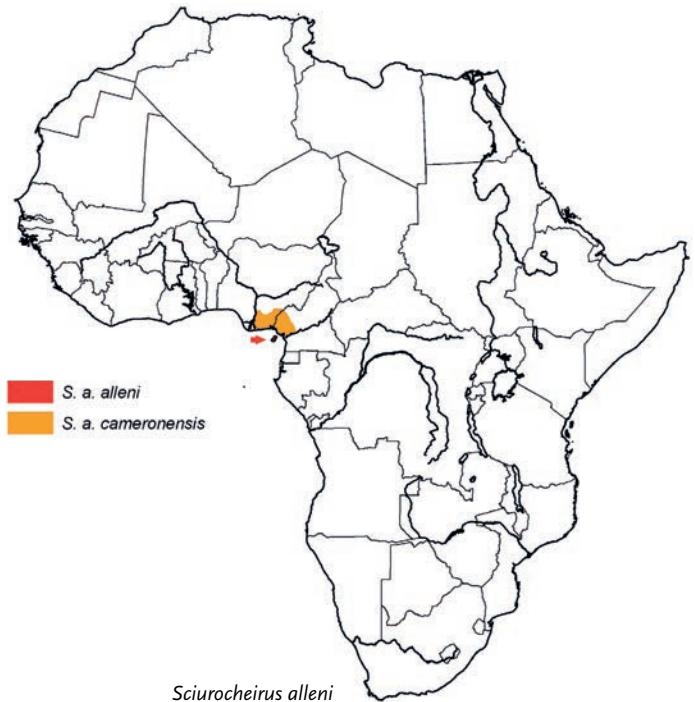
Sciurocheirus alleni ALLEN'S SQUIRREL GALAGO

Fr. Galago d'Allen; Ger. Allen-Buschwaldgalago

Sciurocheirus alleni (Waterhouse, 1838). Proc. Zool. Soc. Lond. 1837: 87 [1838]. Fernando Po (= Bioko I.) Equatorial Guinea.Bioko Squirrel Galago *Sciurocheirus alleni alleni*.

Taxonomy Polytypic species. Gray (1873) placed this species in a new genus, *Sciurocheirus* (squirrel galagos), but most recent authors (Jenkins 1987, Kingdon 1997, Groves 2001, 2005c) have kept *alleni* with the lesser galagos *Galago*. This species is, however, distinct from *Galago* in a number of characters, including the proportions of the skull (Hill 1953) and foot (Jouffroy & Gunther 1985). The vocalizations are also distinct from all other galagos (Ambrose 2003). Recent genetic studies place *alleni* in a clade with the greater galagos *Otolemur* spp. (Crovella *et al.* 1994, Masters *et al.* 1994, 2007). According to Bayes (1998), there is considerable genetic divergence between the squirrel galagos and the greater galagos, emphasizing their taxonomic distinctiveness; based on this evidence, *Sciurocheirus* has now been re-adopted as a full genus (Grubb *et al.* 2003, Nekaris & Bearder 2011). In recent taxonomies three subspecies were recognized, but *S. a. gabonensis* has now been reinstated to full species (Ambrose 1999, 2003) and is now widely recognized (Groves 2001, 2005c, Grubb *et al.* 2003, Nekaris & Bearder 2011). Synonym: *cameronensis*. Chromosome number: $2n = 40$ (Dutrillaux *et al.* 1982b).

Description Medium-sized galago of forests, vocalizing long 'whistles' either as single units, or in phrases of one to six descending units (Ambrose & Perkin 2000, Ambrose 2003). Sexes similar in colouration but ♂♂ probably slightly larger. Snout prominent with pale grey nose-stripe, which forms a broader patch on the forehead.



Cheeks, chin, throat, ventrum and inside of legs whitish to pale grey. Broad black eye-rings make a dark face-mask. Eyes chocolate-brown, large and rounded. Ears bare, black, front and back. Base of ears sometimes ringed with pale grey. Dorsum brown, grizzled dark greyish-brown or grey. Shoulders, flanks, and front and outside of limbs medium to bright rust. Hands and feet greyish-black. Breast-stripe red, about 4 mm wide, in some individuals. Tail evenly bushy, longer than (ca. 120%) HB length, dark grey to black, sometimes with whitish tip (T. Butynski pers. comm.). Old infant/young juvenile/old juvenile all have colour of adult (A. Croce & T. Butynski pers. comm.).

Geographic Variation

S. a. alleni Bioko Squirrel Galago. Bioko I. Larger (WT 300–455 g) than *S. a. cameronensis*. Long 'whistles' nearly always given in descending phrases (Ambrose & Perkin 2000, Ambrose 2003).

S. a. cameronensis Cross River Squirrel Galago. South-east Nigeria and SW Cameroon. Smaller (WT 220–355 g) than *S. a. alleni*. Long 'whistles' most commonly given as single units (Ambrose & Perkin 2000, Ambrose 2003). Variation exists in pelage colour. Some individuals on Mt Kupé, SW Cameroon, have a pale grey tail, which gets progressively paler distally. About 25% of individuals on Mt Cameroon, W Cameroon, have brown dorsum and tail, little or no rust on limbs and flanks, and no obvious eye-rings (Ambrose 1999).

Similar Species

Sciurocheirus gabonensis. Allopatric. South of Sanaga R. S Cameroon south to N Gabon. Colouration similar in Cameroon but redder in Gabon. Tail dark charcoal grey or black, sometimes distal ca.

3 cm is white. Readily distinguished by the contact and alarm call; short, rapid 'whistles' in phrases of 1–10 units (Ambrose 2003).

Distribution Endemic to western central Africa. Rainforest BZ. In forests on Bioko I., Equatorial Guinea, and between Niger R., SE Nigeria and Sanaga R., C Cameroon. *Sciurocheirus a. alleni* widespread on Bioko I. *Sciurocheirus a. cameronensis* in SE Nigeria at Elele and Oban Group Forest Reserves; in S Nigeria at Itu, Tombia, Wilberforce I. and Gbanraun (Bayelsa State); in SW Nigeria in Okomu Forest; in SW Cameroon at Korup Mundemba, Korup Nguti, L. Barombi (Mbo near Kumba), Mt Cameroon and Mt Kupé (Jewell & Oates 1969b, Eisentraut 1973, Bearder & Honess 1992, Butynski & Koster 1994, Ambrose & Perkin 2000, Ambrose 2003, E. Pimley pers. obs.).

Habitat High rainfall lowland, mid-altitude and montane forest. Prefers open understorey in primary forest and old secondary forest. Occurs in plantations and farms on Bioko I. and in Cameroon, but these visited primarily for foraging (Ambrose 2003, T. Butynski pers. comm.). In secondary forest at Elele, Nigeria (Oates & Jewell 1967), and in isolated trees and forest patches in grassland at Moka, Bioko I. (Jewell & Oates 1969b, T. Butynski pers. comm.). In degraded forest fragments around Itu and in Niger Delta swamp forest, S Nigeria (E. Pimley pers. obs.). Occurs from sea level to at least 2250 m on Bioko I. (Butynski & Koster 1994), and up to at least 2000 m in SW Cameroon (Ambrose 1999). Mean annual rainfall over the geographic distribution of *S. alleni* ranges ca. 2000–10,000 mm (T. Butynski pers. comm.). There are two 'dry' seasons on Bioko I.; Dec–Feb when mean monthly rainfall is <100 mm) and Jul–Aug when mean monthly rainfall is <500 mm).

Abundance Common in suitable habitat. At particularly high densities in montane forest; i.e. 14 ind/km² in secondary forest on Mt Kupé (Pimley 2002). During night censuses at Moka, Bioko I., encountered at the rate of 1.8 ind/h (n = 34 encounters; Ambrose & Perkin 2000), and 1.2 ind/h and 1.2 ind/km (n = 59 encounters; Croce 2009). Nocturnal surveys at other sites on Bioko I. typically yield encounter rates of 1–2 ind/h and 1–2 ind/km of night transect (T. Butynski pers. comm.).

Adaptations Nocturnal and arboreal but often comes to the ground to forage. Elongated hindlimbs and long tail for vertical clinging and leaping. Able to move rapidly by leaping several metres between vertical supports (\pm 10 cm diameter). Lands forelimbs first, then 'swivels' around the support and launches off with hindlimbs, often at 1–2 m above the ground. Usually forages close to the ground, but sometimes up to 15 m above ground; in SW Cameroon, 47% of observations at 0–2 m and 81% of observations <5 m (n = 152; Ambrose 1999). On Bioko I., at 0–2 m above ground during 47% of encounters, 2–5 m 29%, 5–10 m 24% (n = 34). Not observed >10 m above the ground (Ambrose & Perkin 2000). Another study on Bioko I. encountered *S. alleni* at mean height of 5.9 m (0–15 m, n = 30, Croce 2009). Hollow trees and lianas are preferred sleeping sites (Bearder *et al.* 2003). Liana tangles favoured for resting and 'parking' young.

The greater part of the range of *S. alleni* is in forests sustained by heavy rainfall deriving from the nearby Atlantic. It is probable

that the ecology, behaviour, reproduction and other physiological adaptations of *S. alleni* are finely attuned to this unusual and localized climate and that, as such, this species differs from its congeners in many subtle respects.

Foraging and Food Frugivorous, insectivorous. Mostly forages on, or close to, the forest floor where it feeds on fallen fruit and hunts for invertebrates. Arthropods grabbed with the hands. Fruit usually bitten first before being held in the hands. Often sits above swarming ants to catch invertebrates disturbed by driver ants *Dorylus* sp. (Ambrose 2003, T. Butynski pers. comm.). Stomachs of specimens in Nigeria contained fruit, insects and molluscs (Jewell & Oates 1969b). One stomach on Bioko I. held beetles and bones of small mammal (T. Butynski pers. comm.). Observed catching and eating a small bird at night on Bioko I. (A. Croce pers. comm.). Frequently observed in banana trees *Musa* sp. where the ripest fruits are selected. Eat ripe fruits of *Rothmannia* sp., False Nutmeg *Pycnanthus angolensis* in Cameroon (Pimley 2002) and Cape Fig *Ficus sur* and *Psychotria* sp. on Bioko I. (T. Butynski & A. Croce pers. comm.). In SW Cameroon, *S. a. cameronensis* ♂♂ travel (i.e. horizontal + vertical travel) an average of 2043 m/night (1825–2261, n = 2 animals), while ♀♀ travel an average 961 m/night (612–1825, n = 6 animals) (Pimley 2002).

Social and Reproductive Behaviour Solitary foragers, but two or three individuals sometimes travel together. In Cameroon, home-ranges are 2.84 ha (2.09–3.58) for two ♂♂ and 1.97 ha (0.60–3.37) for six ♀♀ (Pimley *et al.* 2005a). Groups of between two and seven ♀♀ associated with one central adult ♂. Copulations with outside ♂♂ probably also occur. Some adult ♀♀ sleep together in the same tree-hole on a regular basis. An adult ♂ and adult ♀ recorded sleeping within 10 m of each other. Sleeping partners associate with each other during nocturnal activity and overlap each other's ranges at similar times. Adult ♂ and adult ♀ interactions less frequent. No ♂–♂ interactions observed. Adult ♂ ranges do not overlap. Maturing ♀♀ commonly remain in the home-range area of their mother and can continue to share a sleeping site (Pimley 2002). One mating recorded where copulation was preceded by urine-marking of substrates by both partners. Male mounts ♀ in dorsoventral position and copulatory lock lasts about one hour (Pimley 2002). Mother carries infant by mouth for up to 45 days (S. K. Bearder pers. comm.).

Contact maintained by exchange of 'whistles'. Harsh, low frequency 'croak' used for long-distance contact. Long 'whistles', either as single units, or in phrases of one to six descending units, are characteristic of this species. Variations on this call are used for contact, spacing, cohesion and mild alarm. 'Whistles' that rise and fall in frequency two or three times, and which are interspersed with 'qwocks', are given in the context of high alarm (Ambrose & Perkin 2000, Ambrose 2003).

Reproduction and Population Structure Births probably occur throughout the year. Oestrous and pregnant ♀♀ trapped at various times of the year in Cameroon (Pimley 2002). Infants, juveniles and lactating ♀♀ seen on Mt Kupé in Mar and Apr and parked juveniles in Korup in early Apr. Pregnant and lactating ♀♀ observed on Bioko I. in Mar and Oct (Ambrose 2003, T. Butynski

pers. comm.). Sanderson (1940) recorded pregnant ♀♀ in Cameroon in Dec, Jan, May, Jun and Jul. Adult ♂:adult ♀ ratio in Cameroon is 1 : 2.7 (Pimley 2002).

Predators, Parasites and Diseases Uncertain, but main predators probably include various large owls *Bubo* spp., large snakes, genets *Genetta* spp., Two-spotted Palm Civets *Nandinia binotata*, domestic cats and dogs. Fraser's Eagle-owl *Bubo poensis* occurs throughout the range of *S. a. alleni*. The strong and prolonged alarm calls given by *S. a. alleni* in response to the presence of *B. poensis* suggests that this large forest owl is a major predator (T. Butynski pers. comm.). Analysis of blood samples in Cameroon reveal malaria parasites *Plasmodium falciparum* in *S. a. cameronensis* in Cameroon but no pathological symptoms observed (Pimley 2002). Small numbers sold in the bushmeat market in Malabo, Bioko I.; these are likely caught as a by-catch in traps set for larger species (T. Butynski pers. comm.).

Conservation IUCN Category (2012): Least Concern. Endangered as *S. a. alleni*. CITES (2012): Appendix II.

Locally abundant and more secure in montane forest, although this forest is reduced and fragmented. *Sciurocheirus a. alleni*, endemic to Bioko I. (2017 km²), has a distribution of <1700 km² (T. Butynski pers. comm.). Logging and creation of commercial plantations are responsible for habitat loss in SW Cameroon and SE Nigeria.

Measurements

Sciurocheirus alleni

S. a. alleni

HB (♂♂): 238 (230–248) mm, n = 4

HB (♀♀): 209 (200–218) mm, n = 3

T (♂♂): 266 (254–274) mm, n = 4

T (♀♀): 280 (260–295) mm, n = 3

HF (♂♂): 81 (74–86) mm, n = 4

HF (♀♀): 80 (75–87) mm, n = 3

E (♂♂): 36 (35–37) mm, n = 4

E (♀♀): 43 (30–47) mm, n = 3

GLS (♀♀): 55 (54–56) mm, n = 3

GWS (♀♀): 36 (34–37) mm, n = 3

WT (♂♂): 403 (381–430) g, n = 4

WT (♀♀): 350 g, n = 1

Moka, Bioko I., Equatorial Guinea (T. Butynski & A. Croce pers. comm.)

S. a. alleni

HB: 233 (220–251) mm, n = 5

T: 275 (238–289) mm, n = 5

HF: 75 (64–83) mm, n = 5

E: 36 (28–47) mm, n = 5

WT: 432 (395–455) g, n = 5

Moka, Bioko I., Equatorial Guinea (Ambrose 1999, 2003). Sexes combined



Bioko Squirrel Galago *Sciurocheirus alleni alleni*.

S. a. alleni

HB: 200–280 mm, n = 11

T: 225–295 mm, n = 11

HF: 70–76 mm, n = 6

E: 32–45 mm, n = 11

WT: 300–410 g, n = 9

Bioko I., Equatorial Guinea (Groves 2001). Means not provided.

Sexes combined

S. a. cameronensis

HB: 222 (211–226) mm, n = 4

T: 263 (248–298) mm, n = 4

HF: 72 (65–78) mm, n = 4

E: 30 (27–35) mm, n = 4

WT: 276 (220–355) g, n = 18

Linear measurements from SW Cameroon (Ambrose 1999). WT from Mt Kupé, Cameroon, n = 16; Mt Cameroon, Cameroon, n = 1; Elele, Nigeria, n = 1 (Ambrose 1999, 2003, Jewell & Oates 1969a). Sexes combined

S. a. cameronensis

HB: 165–192 mm, n = 12

T: 222–282 mm, n = 12

HF: 58–75 mm, n = 12

E: 31–38 mm, n = 12

Various localities (Groves 2001). Means and WT not provided. Sexes combined

Key References Ambrose 2003, Ambrose & Perkin 2000; Jenkins 1987; Jewell & Oates 1969b; Oates 2011; Pimley *et al.* 2005a.

Lesley Ambrose & Elizabeth R. Pimley

Sciurocheirus makandensis sp. nov. MAKANDÉ SQUIRREL GALAGO

Fr. Galago écureuil de la Makandé; Ger. Makandé-Buschwaldgalago



Makandé Squirrel Galago *Sciurocheirus makandensis* adult.

Taxonomy Monotypic species. This is a new, previously unnamed, form discovered by L. Ambrose in 1993. Described (but not formally named) as a new species by Ambrose (1999, 2003). Recognized as a full species by Grubb *et al.* (2003) and Nekaris & Bearder (2007, 2011). Compared to other *Sciurocheirus* spp., *Sciurocheirus makandensis* has a distinct vocal repertoire, facial markings and pelage colouration. Synonyms: none. Chromosome number 2n: not known.

Holotype Adult ♂ in photograph in Figure 8b in Ambrose (2003).

An adult ♂ *Sciurocheirus makandensis* is also depicted in Figure 3.1E of Nekaris & Bearder (2007) and in Figure 4.2E of Nekaris & Bearder (2011).

Type locality Makandé, Forêt des Abeilles, SE Gabon, south of Ogooué R. Makandé is at 00° 40' 39" S, 11° 54' 35" E.

Diagnosis Unique loud-call repertoire and loud-call profiles, as detailed in Ambrose (1999, 2003). The alarm unit-whistle is particularly diagnostic; in phrases of 1–5 units with a strong emphasis on the first unit which comprises two audible sub-units. Black eye-rings broader than in other *Sciurocheirus* spp. Black extends from eye-rings down sides of nose and borders a pale grey nose-stripe. Overall a more reddish galago than other *Sciurocheirus* spp.



Sciurocheirus makandensis

Measurements No specimens available for measurement.

Etymology The species name 'makandensis' acknowledges the site of the holotype, Makandé, Forêt des Abeilles, SE Gabon.

Description Medium-sized, forest galago that gives short, fairly rapid 'whistles' in phrases of one to five units with a strong emphasis on the first unit. Sexes similar in colour and pattern of pelage. Eye-rings broad and black with the black extending down the sides of the nose and bordering the pale grey nose-stripe. Crown and facial area russet. Ears exceptionally large, black at base and dark grey distally. Cheeks, chin, throat, chest, belly and insides of the legs greyish-white. Russet colour can suffuse the entire ventrum in mature individuals giving the impression of a reddish rather than greyish galago. Back slate-grey. Pronounced rust colouration on flanks, and on front and outside of limbs. Dorsum of hands and feet russet. Tail typically dark slate-grey proximally and black over distal two-thirds, although this colouration varies with age (Ambrose 1999, 2003).

Geographic Variation Known only from a small area, the Forêt des Abeilles. No systematic variation observed.

Similar Species

Sciurocheirus gabonensis. Allopatric, perhaps parapatric. North of Ogooué R., N Gabon. Contact and alarm call: short, rapid 'whistles' in phrases of 1–10 units. Dorsum mid-grey to reddish-brown in Gabon part of range. Tail dark charcoal-grey or black, sometimes distal ca. 3 cm is white (Ambrose 1999, 2003).

Distribution Endemic to C Gabon. Rainforest BZ. Distribution poorly known. Only identified in Forêt des Abeilles, C Gabon, south of Ogooué R. Might be endemic to this forest or might extend into the adjacent Lopé Reserve, other areas of C Gabon, or even into Congo.

Habitat Forêt des Abeilles is medium altitude (200–700 m) forest of the Guinea-Congolaise type. Mainly primary, closed canopy forest on hilly ground. There are some small, selectively logged areas. Dominant tree families are Caesalpiniaceae (Leguminosae) and Burseraceae (Gesnot 1994). Mean annual rainfall ca. 1750 mm. Two wet seasons (Oct–Dec, Mar–May). Occupies the lower forest strata. Ninety-seven per cent of 37 observations <5 m above ground

Abundance At low densities. More often heard than seen.

Adaptations Nocturnal and arboreal but often forages on the ground. *Sciurocheirus makandensis* has not been studied. Adaptations probably similar to Allen's Squirrel Galago *Sciurocheirus alleni*. It is possible, although perhaps remotely, that the localized occurrence of a strongly erythristic form of *Sciurocheirus* might be influenced by the chemistry of local soils or foods. In this context, it should be noted that a form of Beecroft's Anomalure *Anomalurus beecrofti fulgens* has rufous colouring over much of its body and that this form is also locally distributed in Gabon.

Foraging and Food Omnivorous. Feeds on fruit, including fallen fruit, and invertebrates. Sometimes sits on a horizontal branch just above ants that are carrying invertebrate prey. It seems that the galagos, like many forest-floor birds, benefit both by seizing food items from the ants and by catching invertebrates disturbed by the swarming ants.

Social and Reproductive Behaviour Solitary foragers but up to four individuals sometimes move together through the forest. Animals seen together at dusk suggests that sleeping sites are shared. Use contact vocalizations to maintain regular social contact with familiar animals when dispersed. No information on reproductive behaviour. Harsh, low frequency 'croaks' used for long distance

contact. The characteristic (diagnostic) calls of *S. makandensis*, used in the context of contact and alarm, are short 'whistles' in phrases of one to five units with a strong emphasis on the first unit. These calls are frequently interspersed with 'growls'.

Reproduction and Population Structure Not studied. Immature individuals observed in Aug and Dec.

Predators, Parasites and Diseases No information. Probably predators include large owls *Bubo* spp., large snakes, genets *Genetta* spp., Two-spotted Palm Civet *Nandinia binotata*, Central African Linsang *Poiana richardsoni* and African Golden Cat *Profelis aurata*. One *S. makandensis* became very alarmed at the presence of a *N. binotata*. No information on parasites and diseases.

Conservation IUCN Category (2012): Not assessed. CITES (2012): Appendix II.

If endemic to Forêt des Abeilles, then *S. makandensis* will probably be assessed as Vulnerable; having a low and probably declining population, and a geographic range of <20,000 km². It should be noted that some other species of mammal are known only from the Forêt des Abeilles/Lopé Reserve region, including Duchailu's Rope Squirrel *Funisciurus duchailui* (Brugière *et al.* 2005a) and *A. solatus* (Harrison 1988b). Therefore, the effective protection of these two forests will do much to ensure the long-term conservation of these three species – and many others in this species-rich region. *S. makandensis* is not hunted by humans. Research is needed to determine the conservation status of *S. makandensis* as well as to obtain information on its ecology and behaviour.

Measurements

Sciurocheirus makandensis

None available.

Key References Ambrose 1999, 2003.

Lesley Ambrose

Sciurocheirus gabonensis GABON SQUIRREL GALAGO

Fr. Galago écreuil du Gabon; Ger. Gabun-Buschwaldgalago

Sciurocheirus gabonensis (Gray, 1863). Proc. Zool. Soc. Lond. 1863: 146. Gabon.

Taxonomy Monotypic species. Gray (1863) described this galago as a distinct species but most subsequent authors have regarded it as synonymous with *Galago alleni* (Hill 1953, Jenkins 1987). Described as a subspecies of *G. alleni* by Groves (1989) and Kingdon (1997), this taxon has since been re-elevated to full species (Ambrose 1999) and widely accepted (Groves 2001, 2005c, Grubb *et al.* 2003, Nekaris & Bearder 2007, 2011). Synonym: *batesi*. Chromosome number: not known.

Description Medium-sized galago with short, rapid 'whistles' in phrases of 1–10 units (Ambrose 2003). Sexes similar in colouring and size. Pale nose-stripe extends as a broader patch on the forehead. Cheeks, chin, throat and ventrum pale grey. Eye-rings black. Ears

large and rounded, dark brown to black. Dorsum variable among populations, from mid-grey to reddish-brown. Forelimbs, hindlimbs and flanks rust. Pelage redder in Gabon. Tail evenly bushy, charcoal-grey to black, occasionally distal ca. 3 cm is white.

Geographic Variation None recorded.

Similar Species

Sciurocheirus alleni cameronensis Cross River Squirrel Galago. Allopatric at Sanaga R., Cameroon. Distinguished by their calls. Various long, drawn-out 'whistles' given either as single units or in descending phrases of up to six units (Ambrose 1999, 2003, Ambrose & Perkin 2000).



Gabon Squirrel Galago *Sciurocheirus gabonensis* adult.

Sciurocheirus makandensis Makandé Squirrel Galago. Allopatric south of Ogooué R., C Gabon. Holotype from Fôret des Abeilles, C Gabon. Dorsum dark slate-grey. Ventrums and flanks often with extensive russet. Tail slate-grey at base with distal two-thirds black. Calls fairly rapid 'whistles' in phrases of one to five units, with a strong emphasis on first unit (Ambrose 1999, 2003).

Distribution Rainforest BZ. Endemic to western central Africa. In forest between the Sanaga R. and Ogooué R. from S Cameroon, through Rio Muni (Equatorial Guinea), to N Gabon. Distribution into S Gabon uncertain. Eastern extent probably bounded by the Congo R. and Ubangui R., Congo (Nash *et al.* 1989). Likely present in Congo and Central African Republic but no records as yet. In S Cameroon in Lobéké Reserve, Dja Reserve and Ebom (near Kribi) and in C Gabon at Makokou (Ambrose 2003). Also near Evinayong, Rio Muni (Jewell & Oates 1969b).

Habitat Low to medium altitude forest (up to 800 m). Deciduous, semi-deciduous and littoral forest in Cameroon and evergreen forest in Gabon. Prefers the understorey of primary forest but also in secondary forest and cultivated areas.

Mean annual rainfall 1600 mm at Dja Reserve (Laclavère 1980), 1650 mm at Lobéké Reserve (Fimbel & Fimbel 1996) and ca. 1700 mm at Makokou (Charles-Dominique 1977).

Abundance Occurs at low densities in most forests. Present at 15–20 ind/km² at Makokou, C Gabon (Charles-Dominique 1977).



Sciurocheirus gabonensis

Adaptations Nocturnal and arboreal. See Charles-Dominique (1977).

Foraging and Food Omnivorous. Forages on, or close to, the forest floor. In C Gabon an analysis of stomach contents ($n = 12$) revealed a diet of 73% fruit and 25% animal prey. Prey species included: beetles (25%), snails (15%), moths (15%), frogs (8%), ants (8%) and spiders (8%). Termites, centipedes and caterpillars also taken (Charles-Dominique 1977). Contents of one stomach in Rio Muni contained a large number of termites (Jewell & Oates 1969b).

Social and Reproductive Behaviour Solitary foragers but social, maintaining vocal contact with dispersed animals. Females have home-ranges of ca. 10 ha, the size being related to food availability. Males have larger home-ranges (30–50 ha) that overlap those of several ♀♀ and are determined by the locations of the ♀♀. In C Gabon, the range of one ♂ overlapped the ranges of at least eight ♀♀, and he could visit several ♀♀ in a night. Once a ♀ comes into oestrus, the ♂ remains with her exclusively for some days. Females are sedentary; ♂♂ disperse at puberty. Infrequent agonistic behaviour occur between ♂♂. Tree hollows are used as nesting sites. Two to three ♀♀ can sleep together with their offspring. Males always sleep separately. Substrates marked by urine-washing and genital secretions (Charles-Dominique 1977). As for other *Sciurocheirus* spp., a low frequency 'croak' is used for long-distance contact. Short, rapid 'whistles' in phrases of 1–10 units, used in the contexts of contact and alarm, are characteristic of *S. gabonensis* (Ambrose 2003).

Reproduction and Population Structure On the basis of limited data from C Gabon, births occur throughout the year with a slight peak in Jan (dry season). Gestation is 133 days; birth-weight 24 g. Usually a single infant is born, but occasional twin births occur. Infants carried in the mother's mouth from three to seven days after birth and are 'parked' close to the foraging mother. Mothers

and infants spend the day in a tree nest-hole. Adult body-weight is reached at 6–8 months of age and sexual maturity attained at 8–10 months (Charles-Dominique 1977). Birth ♂ : ♀ ratio 1 : 1, but adult ratio 1 : 4. This might be due to intense competition among ♂♂. Males travel greater distances and, therefore, may be at greater risk of predation (Charles-Dominique 1977).

Predators, Parasites and Diseases Uncertain. Large snakes, Two-spotted Palm Civet *Nandinia binotata*, Central African Linsang *Poiana richardsoni* and large owls (perhaps especially Frasher's Eagle-owl *Bubo poensis*) probably prey on *S. gabonensis*. Likely vulnerable to terrestrial carnivores such as Leopard *Panthera pardus*, African Golden Cats *Profelis aurata*, African Civet *Civettictis civetta* and genets *Genetta* spp., as *S. gabonensis* frequently forages in the undergrowth. Potential predators are harassed by following and uttering intense alarm calls. Unless they have been surprised, adult *S. gabonensis* can easily leap away, but infants are vulnerable. Parked infants remain immobile in situations of extreme danger. Only if the branch is shaken will they release their hold and drop to the ground uttering a distress call (Charles-Dominique 1977). No information on parasites and diseases.

Conservation IUCN Category (2012): Least Concern. CITES (2012): Appendix II.

Has a broad range over an almost contiguous forest block in S Cameroon, Congo, Rio Muni and N Gabon. Generally occurs at low densities. There is habitat degradation and destruction in some areas. Not hunted by humans.

Measurements

Sciurocheirus gabonensis

HB: 200 (185–205) mm, n = 17

T: 255 (230–280) mm, n = 17

HF: 70 (65–75) mm, n = 5*

E: 37 (33–41) mm, n = 5*

WT: 260 (188–340) g, n = 17

Makokou, C Gabon (Charles-Dominique 1977)

*N Gabon and Rio Muni, Equatorial Guinea (BMNH). Sexes combined.

Key References Ambrose 2003; Charles-Dominique 1977.

Lesley Ambrose

GENUS *Galago*

Lesser Galagos

Galago É. Geoffroy, 1796. Mag. Encyclop. 1: 49.

The 'lesser galagos', genus *Galago*, as used in this volume, currently comprises four species of short-faced, gum-eating galagos that live mainly outside the main forest block, or, in the case of the Spectacled Lesser Galago *G. matschiei*, in some restricted forest areas in eastern central Africa.

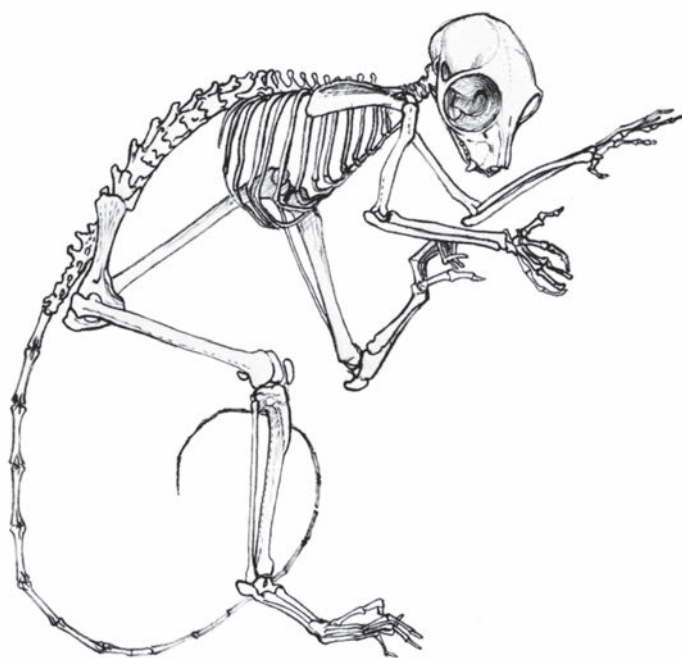
Species within *Galago* are of medium size with a grey or brownish back, round head, large eyes, dark eye-mask, short muzzle, pale nose-stripe, and tails that are not densely furred. They utter short

phrases or single cries that have a regular rhythm repeated many times. Volume depends upon the level of excitement in the caller. All are agile bounders, landing feet first.

Separation of the 'dwarf galagos' *Galagoides* from *Galago* is still controversial; Groves (2001, 2005c) retained all the small species (here provisionally classified as *Galagoides*) within a much enlarged treatment of *Galago*. This approach was supported by cladistic analysis of mainly morphological traits but Groves acknowledged



Southern Lesser Galago *Galago moholi*.



Southern Lesser Galago *Galago moholi*.

the difficulty of separating convergence and parallelism in a group of primates with exacting demands on their specialized anatomy. In the meantime, molecular studies by DelPero *et al.* (2000), Roos *et al.* (2004), Stiner & Turmelle (2003) and Masters *et al.* (2007) reveal complex phylogenetic trees that are consistent in finding *Galago* (in the restricted sense used here) the most recently evolved branch, well separated from the small galagos, which derive from older, more conservative stock (see figure p. 387). Vocal repertoires also support this separation (Bearder *et al.* 1995). We, therefore, join Olson (1979), Nash *et al.* (1989), Bearder *et al.* (1995), Kingdon (1997), Grubb *et al.* (2003), Masters *et al.* (2007) and Nekaris & Bearder (2011) in recognizing both *Galago* and *Galagoides*.

Masters *et al.* (2007) conclude that the non-forest species are the most derived in this group while the genetic profile of *G. matschiei*

puts it in an intermediate position between the dry-country *Galago* spp. and the forest-dwelling Needle-clawed Galagos *Euoticus* spp. *Galago matschiei* might, therefore, represent an approximation of the common ancestry of both genera and its inclusion in *Galago* could be semi-arbitrary because it also shares traits, such as enlarged orbits and pointed nails, with *Euoticus*.

The three non-forest species in *Galago* inhabit the entire woodland, treed savanna and dense bushland zones of tropical Africa; Northern Lesser Galago *G. senegalensis* and Somali Lesser Galago *G. gallarum* mainly north of the Equator on a centre–west axis, and South Lesser Galago *G. moholi* south of the Equator on a longitudinal south–east axis. They are commonest in woodlands dominated by *Acacia*, *Brachystegia*, *Isoberrlinia* and *Commiphora*, at lower densities, *Mopane* and *Colophospermum*. Gum and insects are the main foods. Other animal foods and fruits are more marginal but can be important locally and seasonally. Where tree hollows are present they are used for shelter but tree forks and branch tangles are more generally available. Where neither hollows nor trunks are available, *Galago* spp. may make a leaf shelter or take over an old bird's nest as a day-time retreat. Fires represent a major hazard, mainly because they expose the galagos to hawks and other predators as they flee.

Recruitment rates are high, with ♀♀ commonly bearing one or two young twice a year. Home-ranges in ♀♀ and ♂♂ overlap. Scent-marking with urine, genital rubbing and saliva-dribbling is most intense around sleeping sites but is maintained at favourite posts scattered around the home-range. Gestation is about 130 days and the young develop fast, moving out of the nest at two weeks and becoming independent at about two months.

The most striking adaptation of the lesser galagos is the extraordinary speed when jumping or running during escape or while hunting active prey. They have the physiological ability to extract nutrients and energy from the gums, which buffer them over seasonal droughts.

Jonathan Kingdon

Galago senegalensis NORTHERN LESSER GALAGO (SENEGAL LESSER GALAGO, SENEGAL LESSER BUSHBABY)

Fr. Galago du Sénégal; Ger. Senegal-Galago

Galago senegalensis É. Geoffroy, 1796. *Mag. Encyclop.* 1: 38. Senegal.

Taxonomy Polytypic species. Originally, only the species *Galago senegalensis* was recognized (Schwarz 1931a). Seven species have since been split from this taxon: Southern Lesser Galago *Galago moholi*, Somali Lesser Galago *Galago gallarum*, Spectacled Lesser Galago *Galago matschiei*, Zanzibar Dwarf Galago *Galagoides zanzibaricus*, Mozambique Dwarf Galago *Galagoides granti*, Malawi Dwarf Galago *Galagoides nyasae* and Kenya Coast Dwarf Galago *Galagoides cocos*, based on differences in vocalizations, genetics and morphology of the body, cranium, penis and hand pads (e.g. Zimmermann *et al.* 1988, Nash *et al.* 1989, Zimmermann 1990, Bearder 1999, Anderson *et al.* 2000, DelPero *et al.* 2000, Masters & Bragg 2000, Groves 2001, 2005c, Anderson, M. J. 1999, 2001, Grubb *et al.* 2003, Nekaris & Bearder 2011). All species can be distinguished by their

species-specific advertisement call. It may well be that additional cryptic species will be recognized from within *G. senegalensis* as this remains a widespread taxon with considerable variation (Masters & Bragg 2000). Here we follow Groves (2001, 2005c) in recognizing four subspecies. Synonyms: *acaciarum*, *albipes*, *braccatus*, *calago*, *camerounensis*, *dunni*, *galago*, *geoffroyi*, *pupulus*, *sennariensis*, *sotikae*, *teng*. Chromosome number: 2n = 36, 37, or 38 (Ying & Butler 1971, De Boer 1973a, b, Romagno 2001).

Description Medium-sized, long-limbed galago with long, short-haired tail. Low pitched 'woo' (or 'honk') advertisement (loud) call distinctive. Sexes similar in colour. In the wild, adult ♀♀ weigh ca. 89% as much as adult ♂♂ (Nash *et al.* 1989). Dorsum

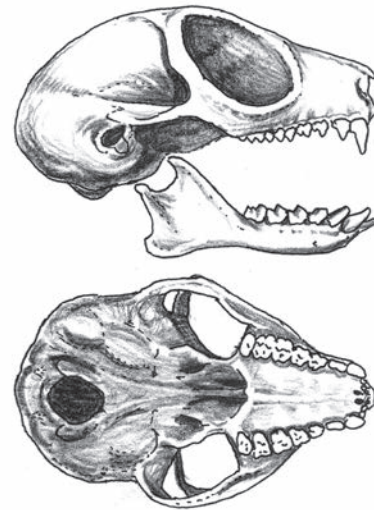


Northern Lesser Galago *Galago senegalensis* adult.

of head, neck, forelimbs and forefeet grey or brownish-grey. Eye-rings dark, complete. Inter-ocular stripe white. Ears greyish or flesh-coloured. Ventrums pale yellowish-white. Outer surface of hindlimbs and hindfeet pale to bright yellow. Tail grey to brown. Penile spines (Anderson 2000) and hand (volar) pads (Anderson 1999) diagnostic. Young similar to adult in colour. *Galago senegalensis* 'woo' call is distinctive as it is the lowest-pitched of all lesser galago advertisement calls. Photographs of *G. senegalensis* from many sites in Kenya and Tanzania available at: www.wildsolutions.nl

Geographic Variation Subspecies difficult to distinguish based on published data (Schwarz 1931a, Hill 1953, Kingdon 1997, Groves 2001, Grubb *et al.* 2003). Clear diagnosis requires sophisticated phylogeographic study taking into account vocalizations, behaviour, morphology and genetics. Ranges and sample sizes for the data on means presented in this section are given under Measurements.

G. s. senegalensis Senegal Lesser Galago. Senegal and Gambia, east across the White Nile to Karamoja, Uganda, to Mt Elgon, Kenya. Limited in south by forest belt and in north by Sahara. HB short



Lateral and palatal views of skull of Northern Lesser Galago *Galago senegalensis* adult.

(mean 164 mm). Ears medium (mean 40 mm). Lower parts of hindlimbs pale yellow. Tail grey, brown distally.

G. s. braccatus Kenya Lesser Galago. Highlands of C and S Kenya and N Tanzania east of Eastern Rift Valley to Indian Ocean. South through the Tsavo region to the Pangani R and Mt Meru. Northern limit undetermined. HB short (mean 164 mm). Ears medium (mean 38 mm). Front of limbs bright yellow or russet. Tail brown.

G. s. dunni Ethiopia Lesser Galago. Ethiopian Plateau, Ogaden and Somalia. Limits of range unknown. Limit coincident in east and south with that of *G. gallarum*, and in west with *G. s. senegalensis*. HB longest (mean 188 mm). Ears shortest (mean 35 mm). Hindlimbs pale yellow. Tail grey, brown distally.

G. s. sotikae Uganda Lesser Galago. Ankole, Uganda, to south of L. Victoria (Mwanza), Tanzania, to Telek R., Kenya. Recently observed in Grumeti G. R. (in western Serengeti), in L. Manyara N. P., near Dodoma, and in Mikumi N. P., Tanzania. As such, T. Butynski & Y. de Jong (pers. obs.) suspect that the southern limit is to at least Rufiji R., SC Tanzania. HB medium-long (mean 180 mm). Ears longest (mean 43 mm). Dorsum more brownish-grey than other subspecies. Hindlimbs without yellow wash. Tail grey-brown, browner distally.

Similar Species

Galago gallarum. L. Turkana, NW Kenya, east to Shebeyli R. of Ethiopia and Somalia, south-east to Tana R., Kenya. Back brownish-buff with pinkish tinge. Narrow dark brown eye-rings often incomplete laterally. Face and throat whitish. Tail mostly black. Ears black, short (mean 35 mm). Hindfoot short (mean 62 mm). Distinctive 'quack' loud-call (Butynski & De Jong 2004).

Galago matschiei. Lualaba R., DR Congo, east to E Uganda. Forest species. Dark brown. Eye-rings black and large. Nails keeled and pointed. Distinctive 'churr' call (= 'woo' = 'honk') higher-pitched and of longer duration.

Galago moholi. Northern limit is south end L. Victoria and C Tanzania. Very similar to *G. senegalensis*. Averages slightly smaller but much overlap in body measurements: HB mean 150 mm (n = 826) vs. 165 mm (n = 508) for *G. senegalensis*; T mean 228 mm (n = 824) vs. 255 mm (n = 498) for *G. senegalensis*;

HF mean 59 mm ($n = 812$) vs. 67 mm ($n = 498$) for *G. senegalensis*; WT mean 158 g ($n = 477$) vs. 206 g ($n = 388$) for *G. senegalensis* (Olson & Nash 2002). Thus, body size alone cannot be used to distinguish *G. moholi* from *G. senegalensis*. Inter-ocular stripe off-white. Hindlimbs less yellow or without yellow. Distinctive 'bark' loud-call mostly of 2–4 units, higher-pitched and shorter-duration than 'woo'.

Distribution Endemic to tropical Africa. Guinea Savanna, Sudan Savanna, Somalia–Masai, Afromontane–Afroalpine, and Zambezan BZs. Over most of its range *G. senegalensis* is the only small galago in savanna, thorn scrub and woodland. Limits of distribution poorly known. See Geographic Variation. Broad distribution across Africa from Senegal (ca. 16° N) to Gulf of Aden (ca. 15° N) in area between Sahara and coastal forest in west, and Congo Basin forests on the south. Present in suitable habitat over much of East Africa (Nash *et al.* 1989) south to at least L. Rukwa and Udzungwa Mts (Rovero *et al.* 2009).

Habitat Savanna, thorn scrub, open woodland and riverine woodland over most of its range, but also in closed forest east of L. Victoria (the most densely forested part of its range) (Nash *et al.* 1989, Svensson & Bearder 2012). Altitude and rainfall limits poorly documented; ca. 350–1200 mm annual rainfall. In Kenya known from near sea level to at least 2400 m (Mau F. R.) (T. Butynski pers. obs.). Closely associated with various *Acacia* spp. In *Terminalia* and *Combretum* bushland, and *Isoberlina* and *Julbernardia* woodland (Kingdon 1971, 1997). Not found in areas of long grass, perhaps due to fire (Haddow & Ellice 1964).

Abundance Locally common. Densities in moist Whistling Thorn *Acacia drepanolobium* and Fever Tree *Acacia xanthophloea* woodland in Laikipia, C Kenya, can be >20 ind/ha. Densities are usually much lower than this, however, with far fewer than 1 ind/ha in the drier, more scrubby habitats, and at the highest altitudes in closed canopy montane forest (T. Butynski pers. obs.). For example, surveys in riverine woodland and bush habitats in Laikipia yielded densities of 0.4–2.4 ind/ha, with highest density in *A. xanthophloea* woodland and lowest density in *Acacia etbaica* bushland (Off *et al.* 2008). At Mutara Ranch, Laikipia, another site dominated by *A. xanthophloea* and *A. drepanolobium*, present at ca. 1.5 ind/ha (Nash & Whitten 1989).

Adaptations Nocturnal and arboreal. Locomotor pattern involves leaps between supports and resting, usually with the body in a relatively vertical position (similar to *G. moholi* [Crompton 1984] and *G. gallarum* [Butynski & De Jong 2004]). Bipedal hopping when on the ground. In Laikipia, found at a mean height of 7.4 m (S.D. 6.6, $n = 185$ encounters); on ground 1% of time and <10 m high 59% (Off *et al.* 2008). Based on gut transit time and other indicators, gut adaptations for digestion of acacia gums has been suggested (Nash 1989). Predator and prey detection, and localization in a three-dimensional dark world, associated with well-developed visual and hearing systems. As determined by conditioned responses, the smallest determinable difference in visual depth corresponds to an angle of 42° , and visual acuity is $04^{\circ}28'$ of arc. This is greater than in rats, cats or Megachiroptera, but less than in diurnal anthropoid primates (Treff 1967). Ears highly mobile and



can move independently of each other. Hearing, as determined by the classically conditioned suppression of licking, 250–64,000 Hz. This is much broader than in anthropoid primates, which have high frequency limits falling between 17,600 and 49,500 Hz (Heffner *et al.* 1969, Heffner 2004).

In Karamoja, Uganda, *G. senegalensis* inhabits tree-holes, often 1–2 m above ground, especially in hollow rotten branches leading upwards from a hole. Also inhabits unoccupied man-made beehives (hollowed out sections of trees hung 5–10 m above the ground). Leaf nests rarely constructed in N Karamoja, but common on Tanzania coast where thicket habitat contains few large trees (Haddow & Ellice 1964). In *A. drepanolobium* scrubland in Laikipia, leaf nests 3–4 m above ground in trees with the densest foliage (e.g. *Scutia myrtina*, *Maerua triphylla*). Leaves for nest construction carried in the mouth. Nest a loose bundle of leaves among dense foliage of thin branches. Construction takes about 30 min. Also, nests in hollow boles and branches of short, stout trees (e.g. *M. triphylla*). One entrance hole only 35 cm above ground (T. Butynski & J. Kalina pers. obs.). Also in Laikipia, found sleeping in dense *Grewia* spp. shrubs (Nash & Whitten 1989) and in dense *Acacia mellifera* shrubs (Off *et al.* 2008). Uses wooden nest boxes placed for birds. One ♀ with young used abandoned nest, 7 m above ground, of White-bellied Go-away-birds *Corythaixoides leucogaster* (J. K. Waithaka, J. Kalina & T. Butynski pers. obs.). Nest at Naivasha in dead hollow limb (73 cm circumference) 5 m above ground. Diameter of entrance hole 5 cm (T. Butynski & Y de Jong pers. obs.). See Svensson & Bearder (2012) for data from The Gambia.

Foraging and Food Omnivorous. Active all night on the Equator in Laikipia, from dusk (ca. 18:45h) to just prior to dawn (ca. 05:30h). Moves at least 600 m/night (J. K. Waithaka pers. comm.), suggesting a home-range of at least 4 ha, probably much larger at some sites (T. Butynski & J. Kalina pers. obs.). In a brief study, animals foraged in trees and on the ground, and covered open

spaces of up to 50 m (by bipedal hopping) to move between foraging sites (Nash & Whitten 1989). No detailed study of the diet, but diet appears similar to that of *G. moholi* (Bearder & Doyle 1974a, Bearder & Martin 1980). Stomach contents of wild animals in Kenya held a variety of insects and some vegetable matter (Haddow & Ellice 1964). Coleoptera and Lepidoptera (caterpillars) made up the bulk of stomach contents ($n = 103$). Spiders and scorpions also found. Captures winged termites (alates) on the ground. Fruits of Desert Date *Balanites aegyptiaca*, Tamarind *Tamarindus* sp. and *Sclerocarya* sp. eaten (Kingdon 1971). *Acacia drepanolobium* and *A. xanthophloea* gum eaten in Kenya, probably extensively, at least during the dry season (Nash & Whitten 1989, J. K. Waithaka, J. Kalina & T. Butynski pers. obs.). Other acacia gums are probably used in other localities. Eats nectar from Baobab *Adansonia digitata* and other flowers, and may be a pollinator (Root 1973). See Svensson & Bearder (2012) for data from The Gambia.

Social and Reproductive Behaviour Solitary or in small groups. In Laikipia, of 123 encounters, 81% solitary, 16% pairs, 3% groups of three (Off *et al.* 2008). In Uganda, nesting groups of 1–6 animals (including immatures) usually found with either one or no ♂ (Haddow & Ellice 1964). One bird nest box in Laikipia was occupied by three animals (T. Magor & T. Elliot pers. comm.). Usually forage alone but sometimes in groups of up to three. In captivity courting ♂♂ chase ♀♀. Copulation durations range from a few seconds to ten minutes. A pair may mate repeatedly for the 24–48 h the ♀ is receptive (L. T. Nash & E. Zimmermann pers. obs.). Partner preferences during the juvenile period suggest, as in other galagos, that ♂♂ disperse from the natal range more often than ♀♀ (Nash 1993).

Most secondary references to the behaviour of *G. senegalensis* refer to studies of *G. moholi* in South Africa (e.g. Bearder & Doyle 1974a, Bearder 1987, Pullen *et al.* 2000). *Galago moholi* ♂♂ and ♀♀ form overlapping territories. Females may be intolerant of other adult ♀♀ in their ranges. Males appear more tolerant of other ♂♂, provided one ♂ is smaller and/or submissive. Although it is possible to place unrelated, same-sex adults of *G. senegalensis* in the same captive social group, aggression is most likely between same-sexed adults, and the most stable captive groups are formed from the descendants of a single pair (Nash 1993, E. Zimmermann pers. obs.). In an experiment that examined the effects of subject sex, intruder sex and mate presence/absence on behaviour, ♀♀ were more interested in ♀ intruders and did not alter their behaviour toward an intruder in the presence of their mate (Glick 1993). In contrast, ♂♂ were more interested in ♀ intruders when the mate was absent, but in ♂ intruders when the mate was present (possible mate-guarding). Females seemed more concerned with a resource competitor, whether or not the ♂ they lived with was present during the test. In captivity aggressive behaviours consist of chasing, grappling and biting that can lead to severe wounding. Such behaviour can be persistent once initiated. Submissive animals flee, often to the floor, and will vocalize when grappling or bitten. Multiharmonic screams, with variable frequency and temporal patterns, are given under such circumstances (L. T. Nash & E. Zimmermann pers. obs.).

In Laikipia, ♀♀ with young nest away from conspecifics (J. K. Waithaka pers. comm.). In captivity, reproduction often improves by separating the mother and neonate from other animals (L. T.

Nash pers. obs.). Successful reproduction in captive animals also occurred in a family group consisting of a breeding ♂, two breeding ♀♀ (mother and daughter) and four offspring ♂♂, of which two were sexually mature (E. Zimmermann pers. obs.). Sometimes in a group where mother and adult daughter have infants at the same time, the grandmother may nurse the grandchild, suggesting that cooperative breeding may occur (Kessler & Nash 2010). In contrast, at parturition ♀♀ may become unusually aggressive to cage mates (including previous offspring). This may correspond to the habit in the Large-eared Greater Galago *Otolemur crassicaudatus* and *G. moholi* of the mother ceasing to join her usual sleeping partners around the time of parturition (Sauer & Sauer 1963, Bearder & Doyle 1974a, Bearder 1987).

Galago senegalensis has an extensive vocal repertoire, with 18 spectrographically different call types used by adults of both sexes. This indicates the importance of the acoustic domain for social communication (Zimmermann 1985, 1989, Zimmermann *et al.* 1988). Short, high frequency ‘zek’ and ultrasonic calls by infants separated from their mothers alert the mother and lead to her sudden vocal and phonotactic responses (Zimmermann 1981). High frequency and ultrasonic calls might have evolved as an anti-predator strategy, since raptors are insensitive to this frequency range. During ontogeny these calls develop gradually into the low frequency species-specific contact or loud-calls. Loud-calls used in contact and alarm situations are the most prominent calls of the species’ repertoire (Zimmermann 1985, Bearder *et al.* 1995, Anderson *et al.* 2000, Svensson & Bearder 2012). Inter-specific differences in fundamental frequency and phonological syntax are important for distinguishing *G. senegalensis* and *G. moholi*. *Galago senegalensis* also uses urine-marking extensively, which may both enhance grip and leave chemical signals for conspecifics. Captive ♂♂ react differently to the urine of ♂♂, non-oestrous ♀♀ and oestrous ♀♀ (R. Carpetis pers. comm., L. T. Nash pers. obs.).

Infants carried in mother’s mouth, not clinging to her body. Mother ‘parks’ infant on a limb for the night and collects infant prior to dawn (Bearder *et al.* 2003). The same ‘parking places’ used repeatedly (J. K. Waithaka pers. comm.).

Reproduction and Population Structure Based on embryos of collected animals, two birth seasons/year in Sudan (10–12°N) ($n = 36$) and in N Karamoja, N Uganda (04°N) ($n = 66$) (Haddow & Ellice 1964, Butler 1967). In Karamoja this corresponds with births in Feb–Mar (late dry season) and Jun–Jul (peak wet season), while in Sudan birth peaks are probably in Mar (end dry season) and Dec (mid-dry season). As in *G. moholi* (Izard & Simons 1987), birth seasonality is lost under constant photoperiod in captivity (L. T. Nash pers. obs.). Also, no birth seasonality observed in captivity under the changing photoperiod of the northern hemisphere (in S Germany) with unrestricted food (E. Zimmermann pers. obs.). This suggests that seasonal reproduction is induced either by changing temperatures, or by a combination of changing temperatures and food availability.

Singletons are usual and twinning uncommon in *G. s. braccatus* and *G. s. senegalensis* (Haddow & Ellice 1964, Butler 1967, Izard & Nash 1988, Zimmermann 1989). Captive *G. senegalensis* may undergo long periods of anoestrous, during which the vagina remains sealed. Gestation averages 141 days \pm 2 days in both of two samples, one

from a captive colony of *G. s. braccatus* (n = 12) and one from a captive colony of *G. s. senegalensis* (n = 23) (Izard & Nash 1988, Zimmermann 1989). Compared to *G. moholi*, *G. senegalensis* has a longer gestation period (ca. 114%) and only occasional twinning (8% of litters vs. 41%) (n = 62 for *G. senegalensis*, n = 103 for *G. moholi*). These are major criteria separating the two taxa at the species level (Izard & Nash 1988).

Mean birth-weight of singletons is 19 ± 2.6 g (n = 40). A fertile postpartum oestrus can occur in both the wild and in captivity, leading to the co-occurrence of pregnancy and lactation (Haddow & Ellice 1964, L. T. Nash & E. Zimmermann pers. obs.). Captive ♀♀ reach sexual maturity (first vaginal opening) at 372 days (S.D. = 112, n = 12). This might be altered by birth seasonality in the wild. Males in captivity reach sexual maturity at about 455–540 days (n = 12). Inter-birth intervals in captivity are highly variable, ranging from one gestation period (ca. 141 days) to several years (due to periods of anoestrus). Weaning occurred at 10–14 weeks across two colonies (n = 33) (Zimmermann 1989, Nash 2003).

It is unclear whether the birth sex ratio is skewed toward ♂♂ as strongly as in some other galagos. About 58% of the *G. s. braccatus* born in a captive colony were ♂♂ (n = 46) (L. T. Nash pers. obs.), whereas in another captive colony there was no sex bias (n = 23) (E. Zimmermann pers. obs.). Limited field data suggest the adult sex ratio is not skewed toward ♂♂ (Masters *et al.* 1993). Longevity in captivity is >13 years (L. T. Nash & E. Zimmermann pers. obs.).

Predators, Parasites and Diseases Robust Chimpanzees *Pan troglodytes* preyed on galagos that were likely *G. senegalensis* (McGrew *et al.* 1978, O'Malley 2010) and capture *G. senegalensis* using spear-like tools (Pruetz & Bertolani 2007). In Kenya, L. T. Nash (pers. obs.) saw a *G. senegalensis* give a 'startle' response when foraging on the ground, possibly in response to a nearby, low-perched owl. As with other species of galagos, large raptors, large snakes, genets *Genetta* spp. and diurnal primates are likely predators.

Diseases poorly known. *Galago senegalensis* implicated as a reservoir of Yellow Fever virus as it can circulate the virus and develop antibodies without showing clinical signs of the disease (Haddow & Ellice 1964).

Conservation IUCN Category (2012): Least Concern. CITES (2012): Appendix II.

All four subspecies are widespread and able to survive in woodlands and bushlands that have been somewhat degraded by human activities.

Measurements

Galago senegalensis

HB: 165 (132–210) mm, n = 508
T: 255 (195–303) mm, n = 498
HF: 67 (52–78) mm, n = 498
E: 40 (21–57) mm, n = 483
WT: 206 (112–300) g, n = 388



Northern Lesser Galago *Galago senegalensis*.

GLS: 43 (S.D. ± 1.5) mm, n = 212

From many sites represented in many museum collections (Nash *et al.* 1989, Olson & Nash 2002), except GLS from Masters & Bragg (2000). Sexes combined. Captive adult *G. s. braccatus*, but not neonates, are sexually dimorphic in weight. Captive adults considerably heavier than wild adults. Captive ♂♂ = $360 \text{ g} \pm 72$ S.D. (n = 9); captive ♀♀ = $266 \text{ g} \pm 47$ S.D. (n = 10) (Izard & Nash 1988). Wild ♂♂ mean ca. 225 g and wild ♀♀ mean ca. 200 g (ranges and sample sizes not available; Nash *et al.* 1989).

G. s. senegalensis

HB: 164 mm, n = 55

E: 40 mm, n = 55

GSL: 44 mm, n = 21

Various sites. Sexes combined. Groves (2001)

G. s. braccatus

HB: 164 mm, n = 10

E: 38 mm, n = 10

GSL: 44 mm, n = 9

Various sites. Sexes combined. Groves (2001)

G. s. sotikae

HB: 180 mm, n = 1

E: 43 mm, n = 1

GSL: 48 mm, n = 4

Groves (2001)

G. s. dunni

HB: 188 mm, n = 5

E: 35 mm, n = 5

GSL: 46 mm, n = 4

Various sites. Sexes combined. Groves (2001)

Key References Masters & Bragg 2000; Nash 1993; Nash *et al.* 1989; Oates 2011; Off *et al.* 2008; Zimmermann 1981, 1990.

Leanne T. Nash, Elke Zimmermann & Thomas M. Butynski

Galago moholi SOUTHERN LESSER GALAGO (SOUTH AFRICAN LESSER GALAGO)

Fr. Galago Moholi; Ger. Moholi-Galago

Galago moholi A. Smith, 1836. Rept. Exped. Exploring Central Africa, 1834: 42 [1836]. Marico R.—Limpopo R. confluence, Limpopo, West Transvaal, South Africa.

Southern Lesser Galago *Galago moholi* adult.

Taxonomy Polytypic species. Formerly regarded as a subspecies of the Northern Lesser Galago *Galago senegalensis* (Groves 1974, Olson 1979). Although remarkably similar in appearance to *G. senegalensis*, there are marked differences in their biology. Despite being housed together, no *moholi* × *senegalensis* hybrids reported. Separated from *G. senegalensis* by Zimmermann *et al.* (1988), Jenkins (1987), Groves (1989) and Nash *et al.* (1989). Two subspecies recognized by Smithers (1971), Ansell (1978), Olson (1979), Meester *et al.* (1986), Skinner & Smithers 1990 and Grubb *et al.* (2003); Moholi Lesser Galago *G. m. moholi* and Namibia Lesser Galago *G. m. bradfieldi*. Synonyms: *australis*, *bradfieldi*, *conspicillatus*, *intontoi*, *mossambicus*, *tumbolensis*. Chromosome number: $2n = 38$ (Ying & Butler 1971).

Description Medium-sized galago with greyish-brown dorsum. Flanks, feet, hands and inner limbs yellowish. Advertisement call a distinctive sharp, tonal, 'bark'. Adult ♀♀ like adult ♂♂ but slightly smaller, weighing ca. 90% as much. Head broad. Muzzle short. Eyes large, orange. Eye-rings black, diamond-shaped. Nose-stripe pale off-white. Ears grey, large. Dorsum buffy or greyish-brown. Ventrums white, sometimes suffused with yellow. Hands have long spatulate fingers but nails not pointed. Tail long, darker than rest of pelage, but not very bushy. Differences in hand pad shape and size, and penile morphology between *G. moholi* and *G. senegalensis* distinguishes these two species (Anderson 1999, 2000, Anderson *et al.* 2000). Young are of similar colouration to adults.

Geographic Variation Subspecies occupy two sub-regions but geographic limits of both are poorly known. The two subspecies do not appear to differ noticeably in their body measurements

(Smithers 1971, Jenkins 1987, Groves 2001). As such, at this time, subspecific designation is based on pelage colouration. A review of the information available on body size and colouration of these two debated taxa suggest an extensive hybrid zone or cline between them (T. Butynski pers. comm.). Adjacent populations in NE South Africa diverge considerably in average body weights (♂♂ 210 g and 195 g, ♀♀ 185 g and 165 g, respectively), suggesting the importance of highly local influences (Nash *et al.* 1989).

G. m. moholi Moholi Lesser Galago. Occupies eastern part of species' range. From S Tanzania southward through E Zambia, Mozambique, Zimbabwe, E Botswana to Limpopo Province, NE South Africa. Outer limbs, feet and hands greyish-brown or light brown with yellow tinge. Sides of ventrum suffused with yellow.

G. m. bradfieldi Namibia Lesser Galago. Occupies western part of species' range. From N Namibia and SC Angola eastward through S DR Congo to W Zambia and Magadigadi Pans, N Botswana. Outer limbs, feet and hands pale grey with little or no yellow tinge. Sides of ventrum white with faint yellow wash (Sauer & Sauer 1963, Smithers 1971).

Similar Species

Galago senegalensis. In same habitat as *G. moholi* in Tanzania but not known to be sympatric. Probably parapatric in Tanzania from L. Victoria south to Rufiji R. Very similar to *G. moholi*. Slightly larger but much overlap in body measurements: HB mean 165 mm ($n = 508$) vs. 150 mm ($n = 826$) for *G. moholi*; T mean 255 mm ($n = 498$) vs. 228 mm ($n = 824$) for *G. moholi*; HF mean 67 mm ($n = 498$) vs. 59 mm ($n = 812$) for *G. moholi*; WT mean 206 g ($n = 388$) vs. 158 g ($n = 477$) for *G. moholi* (Olson & Nash 2002).

Thus, body size alone cannot be used to distinguish *G. senegalensis* from *G. moholi*. Inter-ocular stripe broader, shorter, much whiter. Eye-rings always round. Hindlimbs bright yellow. Distinctive low pitched, single-unit 'woo' (or 'honk') loud-call monotonously repeated many times (Zimmermann *et al.* 1988). Hand pad and penile morphology diagnostic (Anderson 1999, 2000, Anderson *et al.* 2000).

Galagoides granti. Eastern Africa coastline from Rufiji R. south to Limpopo R. and westward inland to S Malawi, extreme E Zimbabwe and W Tanzania (Butynski *et al.* 2006). Parapatric in Mozambique and Zimbabwe (Masters & Bragg 2000). In denser, more moist, vegetation types. Similar in size. Ears broad, black behind. Dorsum buffy-brown with pinkish tinge. Tail bushy, wider over distal ca. 80%, darker than dorsum with distal ca. 10–60% blackish-brown. Distinctive 'incremental' loud-call (Butynski *et al.* 2006).

Galagoides zanzibaricus udzungwensis. NE Tanzania along coastal plain south to Rufiji R. and inland to Udzungwa Mts of SC Tanzania. Similar in size but ears average shorter; seldom longer than 33 mm. Dorsum buffy-brown. Tail sparsely furred (tail bone visible), hairs relatively coarse/wiry, and distal ca. 25% slightly darker brown or dusky. Distinctive 'single-unit rolling' loud call (Butynski *et al.* 2006).

Distribution Endemic to Africa south of S Tanzania. Zambezan Woodland, Kalahari Desert and Coastal Forest Mosaic BZs. From NW Namibia and SC Angola eastward through S DR Congo to SE Tanzania, Mozambique and NE South Africa (Smithers 1971, Skinner & Smithers 1990). Presence in Rwanda and Burundi needs confirmation (Oates 1996, De Jong & Butynski 2012). See Geographic Variation.

Habitat Semi-arid habitats; open woodland, open savanna, bush, forest fringe. Present in association with *Acacia* spp., from which gum, the primary component of the diet, is obtained. Less common in *Baikiaea* and miombo *Brachystegia* associations, as well as mopane *Colophospermum* and mixed associations of *Burkea*–*Terminalia*, *Terminalia*–*Acacia*, and *Terminalia*–*Combretum* (Skinner & Smithers 1990). Able to live in close association with humans, occupying gardens and using buildings as sleeping places. Found from sea level to 1500 m (Soutpansberg, South Africa; Bearder 1974). Habitat is drought-prone with very unpredictable rainfall (mean annual rainfall 599–1463 mm; Bearder & Doyle 1974a).

Abundance Common in prime habitat. Density in NE South Africa 13.5 ind/km² (Pullen 2000) in uniform and contiguous vegetation where animals are distributed fairly evenly. At Balovale, Zambia, >50 ind/km² (Lumsden & Masters 2001). Abundance highest where vegetation is more contiguous since *G. moholi* is restricted to woody vegetation for food and nests. Land clearing is a major factor affecting distribution since *G. moholi* are unable to move across large gaps that lack woody vegetation.

Adaptations Nocturnal and arboreal. A robust galago able to withstand a wide range of temperature variation from 4 °C to 38 °C (Pullen 2000). Onset and cessation of activity usually triggered by critical levels of light at dusk and dawn. *Galago moholi* have a number

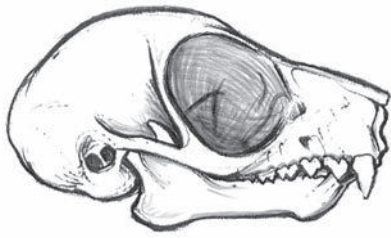


Galago moholi

of behavioural and physical characteristics that are highly specialized and suited to their nocturnal life-style. The limbs are long and powerful, particularly the hindlegs, and the spatulate hands and feet allow the animal to leap securely up to 5 m from tree to tree, even on dark nights. The long tail acts as a rudder to balance the jump. The longest leaps are accompanied by raising the arms sharply on either side of the head. Walking and climbing used to negotiate highly thorny trees. Frequently crosses between trees on the ground using rapid bipedal hopping.

The fur is cryptically coloured to blend in with the vegetation and thick enough to provide both insulation and scent dispersal. A thick under-fur develops before winter and is moulted in spring. No evidence of torpor despite freezing mid-winter temperatures (Mzilikazi *et al.* 2006). Glands on the chest and scrotum are often rubbed on the substrate to mark a location. 'Urine-washing' of the hands and feet serves both to mark the substrate and improve grip (see below). Indirect chemical signals allow conspecifics to assess each other at a distance. The solitary nature of *G. moholi* is thought to be a strategy to reduce predation and competition for food.

Eyesight is particularly well adapted to a nocturnal life with the benefit of a reflective tapetum in the eye to re-reflect available ambient light. The pupils narrow to a vertical slit during the day and the animals can move around without difficulty, even in bright sunlight, if disturbed or hungry. They sleep alone or in small groups during the day in nests, tree holes, or on branches and forks in trees. Nests are usually in particularly thorny and dense acacia trees and are made by using fresh leaves and small twigs from broad-leaved trees (e.g. *Rhus*, *Grewia*). These are shaped into a platform, which can support up to eight animals (Bearder 1969). At Balovale, nest holes found at heights of 1–13 m above ground with most between 3 and 8 m. About 20% of nests found were occupied. Of the inhabitants of 122 nest holes, 34% were single ♂♂, 29% single ♀♀, 15% ♂/♀ pairs. Nest had from 1–3 ♂♂ and 1–3 ♀♀. Mean group size in nests was 1.6 animals (Lumsden & Masters 2001). In particularly



Lateral view of skull of Southern Lesser Galago *Galago moholi* adult.

cold weather, *G. moholi* nest in more sunny positions and are more likely to share nests.

Gut specialized for digestion of gum (Caton *et al.* 2000). Free water not required. Procumbent lower incisors and canines form a well-developed tooth-comb or scraper, which is used to prise gum from the surface of trees, and during lengthy mutual or self-grooming sessions. Tooth comb kept clean by a serrated sub-lingula. Like all species of galago, *G. moholi* has a unique loud-call and penile morphology.

Foraging and Food Omnivorous/gummivorous. No fruit is consumed in the wild; invertebrates 52%, gums 48% (Bearder & Martin 1979, 1980). Gums, produced by trees (mostly *Acacia* spp.) in response to wood-boring insects and other damage, are composed of long-chain polysaccharides that can be digested by microorganisms in the specialized caecum, providing both energy and essential minerals (Bearder & Martin 1980). The most productive gum-producing trees are Sweet Thorn *Acacia karoo* and Umbrella Thorn *Acacia tortilis*. Feeding on gums increases during the cold, dry winter (May–Aug) when insect availability declines, or ceases (Charles-Dominique & Bearder 1979, Crompton 1984). In winter they move more directly from one gum tree to another, often along the ground. In the warm, wet summer (Nov–Feb), when they tend to feed more on insects, they travel mostly through the trees (Harcourt 1986b).

Feeding activity is at a maximum just after sunset, after which they rest and feed sporadically until sunrise. In the wet season *G. moholi* spends up to 2 h 15 min each night catching insects (Bearder 1969). The large eyes and highly mobile ears are used to pinpoint insects, and the excellent sense of smell helps to locate sources of gum. On the coldest nights the gum becomes frozen solid. On these occasions the animals cease their activity and return to their sleeping up to 4 h before dawn (Bearder & Martin 1980). Moths, grasshoppers and beetle larvae are favoured when plentiful in NE South Africa during the summer months (Nov–Feb), but the staple food is acacia gum, which is licked or eaten in small pieces. *Galago moholi* is able to live in a wide range of habitats, probably due in large part to the ability to use gum as a refuge food. *Galago moholi* always forages alone and when feeding will always include certain favourite trees. In winter (May–Aug) in NE South Africa, when the grass is dry and short, this species forages in grass for short periods (Pullen 2000). *Galago moholi* tends to use familiar pathways and to rigorously mark routes. The average nightly distance travelled is 2.0 km, moving through an average of 500 trees each night ($n = 57$, Bearder & Martin 1979).

Social and Reproductive Behaviour Though primarily non-gregarious, *G. moholi* shows much social association both during the

night and during the day (Bearder 1987). They spend up to 30% of the night within 50 m of conspecifics. In NE South Africa, home-ranges of adult ♂♂ (mean 7.2 ha, 3.8–13.2, $n = 9$) are larger than those of adult ♀♀ (mean 4.6 ha, 0.14–10.2, $n = 4$; Pullen 2000). Male home-ranges have considerable overlap both with ♂♂ (50%) and ♀♀ (38%), but ♀♀ do not share any of their home-range with ♀♀ other than their related offspring. Adult ♂♂ are not territorial. This reflects the social system, where adult ♀♀ are ‘dispersed’ in the environment, with adult ♂♂ being unable to defend an area containing sufficient ♀♀. Adult ♂♂ home-ranges may double in size in the mating season (Bearder & Doyle 1974a, Pullen 2000), as they search over wider areas for oestrous ♀♀. *Galago moholi* has a dispersed mating system where ♀♀ mate with more than one ♂ (Pullen 2000). The penile morphology of *G. moholi* fits well with the hypothesis that adaptation of complex penile morphologies are positively correlated with complexity of the mating system (Dixson 1989).

When individuals meet they may avoid each other or social interactions follow a predictable pattern depending on age, sex and familiarity. Interactions are generally brief (but can last several hours) and involve chasing, grooming and naso-nasal and naso-genital sniffing. Subordinates invariably retreat, usually descending to the ground, and give various anxiety and alarm calls. Dominant individuals remain silent. Friendly contact includes play, grappling, chasing and vigorous alternate grooming. Same sex adult strangers are highly aggressive and serious fights can occur (Bearder & Doyle 1974b). Adult ♀♀ rarely come into contact with one another unless related, while adult ♂♂ often interact with both sexes. During the day, adult ♂♂ sleep alone ca. 70% of the time, while adult ♀♀ sleep alone ca. 44% of the time (Pullen 2000). Adult ♂♂ often sleep with adult ♀♀ except during the birth season in Oct. During the mating season, dominant ♂♂ show a three-fold increase in nest-sharing with adult ♀♀. Infants share a nest with their mothers but are regularly carried one at a time in the mouth between nest sites or ‘parked’. Two ♀♀ and their infants may share the same nest but they only carry their own infants. Mothers spend only ca. 33% of the night with their infants, grooming and nursing. Infants make ‘click’ and ‘crackle’ vocalizations when distressed. At four weeks old they sometimes follow their mother and make independent forays but remain alone for most of the night until joined at dawn by their mother (Bearder 1969).

Adult ♀♀ are philopatric. Subadult ♂♂ disperse into new areas to avoid intrasexual competition and inbreeding. Originally the mating system was thought to be polygynous (Bearder & Martin 1979), however, ♀♀ can mate with up to four ♂♂ (Pullen 2000). The mating season in NE South Africa peaks in the middle of May (cold, dry season). During the short oestrus (up to three days), ♂♂ will mate with as many ♀♀ as possible. Just prior to the mating season ♂♂ show significant growth in body weight and testicular size (Pullen *et al.* 2000), a feature common in multimale mating systems that involve sperm competition. Due to intense competition for mates, copulation can be prolonged (up to 50 min). This is probably a mate-guarding tactic by ♂♂ (Dixson 1998). Genetic studies of paternity indicate twins may be fathered by two different ♂♂ (Pullen 2000).

Chemical communication is well developed. Glands on chin, chest and ano-genital region are often rubbed on the substrate

to mark a location, with bouts of mutual sniffing during social encounters (Bearder & Doyle 1974b). Oestrus is signalled by vaginal secretions (Lipschitz 1997). Marking is also carried out by urine washing using hands and feet to deposit urine, enhancing communication at a distance and moistening the hands and feet to promote grip (Harcourt 1981). Loud calls are made by both sexes, irrespective of the mating season. The vocal repertoire is sophisticated, including 19 calls, both continuous and discrete, that can be mixed into complex sequences, as well as two infant-specific calls (Bearder 2007). Most calls are associated with various levels of anxiety or alarm when disturbed; for example by conspecifics or potential predators. Calling may continue for >1 h, such as when mobbing a potential predator, and this sometimes attracts other galagos, which join in with calling. The mixture of different calls, and their loudness and speed of repetition, varies in relation to the intensity of the threat. Other calls are used to attract companions and maintain contact with infants. Companions and rivals are also recognized visually, probably by means of distinctive facial markings (Bearder *et al.* 2006). Apart from acacia rats *Thallomys* spp., there are no non-predator arboreal nocturnal animals with which *G. moholi* are known to interact.

Reproduction and Population Structure *Galago moholi* has two birth seasons. The primary one occurs in late Sep during the hot, wet season, when food is plentiful. Females sometimes enter a postpartum oestrus resulting in a second birth season in early Feb. So restricted is the primary birth season that in NE South Africa, during two consecutive years, three ♀♀ entered oestrus only one day later than the year before (Pullen 2000). Gestation in captivity is 121–124 days (Doyle *et al.* 1971), but wild ♀♀ appear to have a longer gestation of 125–130 days (n = 6; Pullen 2000). Females usually give birth to twins (85%, n = 6) though it is common for primiparous ♀♀ to give birth to singletons (Doyle *et al.* 1967). In the wild, five-day-old infants weigh ca. 12 g (n = 4) but weight gain is rapid and at ten days infants can weigh 33 g (n = 6; Pullen 2000). During the birth season ♀♀ nest alone and preferably use tree-holes as these offer greater protection than platform nests to their growing infants. Infants leave the nest for the first time at ten days and are weaned at 11 weeks (Doyle 1979). Females reach maturity at 200 days and ♂♂ at 326 days (Doyle 1979). Juvenile mortality rates are high. In captivity, Izard & Simons (1987) record a juvenile mortality rate of 51% while in the wild a rate of 55% was recorded (Pullen 2000). In NE South Africa, adult ♂♂ outnumber adult ♀♀ (1.8 : 1; n = 11; Pullen 2000; 2.6 : 1; n = 24; Bearder & Martin 1979). Male-biased sex ratio appears to be common in prosimians and is thought to occur due to a male-biased sex ratio at birth (Clark 1985, Debyser 1995, Watson *et al.* 1996). A high replacement rate of adult ♂♂ is found in the wild. This is common in most non-gregarious prosimians with ♀ philopatry. Live to at least 14 years in captivity (S. K. Bearder pers. obs.).

Predators, Parasites and Diseases Small carnivores, large owls and large snakes are probably the major predators (Charles-Dominique & Bearder 1979). Spotted Eagle-owls *Bubo africanus* observed feeding on *G. moholi*. White-throated Monitor Lizards *Varanus albigularis albigularis* also implicated in predation (Pullen 2000). Common Genets *Genetta genetta* often observed stalking *G.*

moholi and, judging by the intense alarm calls given by *G. moholi*, this is a predator to be taken seriously. Nightly travel distance and size of the area traversed are inversely related to the level of ambient light. *Galago moholi* generally retreat to a dense patch of trees when there is no moon, probably in relation to the risk of predation (Bearder *et al.* 2002). Parasites and diseases not studied but ear ticks and body lice are common.

Conservation IUCN Category (2012): Least Concern. CITES (2012): Appendix II.

Still common at many sites but widespread destruction, degradation and fragmentation of habitats means declining distribution and abundance. They are frequently taken from the wild and sold as pets, but their nocturnal activity and habit of urinating on their hands and feet do not make them ideal pets.

Measurements

Galago moholi

G. m. moholi + *G. m. bradfieldi*

HB: 150 (88–205) mm, n = 826

T: 228 (113–279) mm, n = 824

HF: 59 (37–78) mm, n = 812

E: 39 (23–50) mm, n = 807

WT: 158 (95–244) g, n = 477

From many sites represented in many museum collections (Olson & Nash 2002). Sexes combined.

G. m. moholi + *G. m. bradfieldi*

TL (♂♂): 370 (304–409) mm, n = 48

TL (♀♀): 363 (326–395) mm, n = 42

T (♂♂): 227 (206–258) mm, n = 45

T (♀♀): 223 (200–245) mm, n = 37

HF (♂♂): 57 (51–62) mm, n = 48

HF (♀♀): 56 (51–62) mm, n = 43

E (♂♂): 38 (32–41) mm, n = 44

E (♀♀): 35 (31–41) mm, n = 41

WT (♂♂): 155 (125–190) g, n = 33

WT (♀♀): 151 (132–177) g, n = 30

E Botswana and western Okavango, Botswana (Smithers 1971)

G. m. moholi

TL: 372 (327–400) mm, n = 6

T: 226 (201–246) mm, n = 6

HF: 59 (56–62) mm, n = 6

E: 40 (38–42) mm, n = 6

WT: 147 (102–161) g, n = 6

Gaborone and Sequane, SE Botswana (Smithers 1971). Sexes combined.

G. m. moholi

TL: 374 (334–409) mm, n = 9

T: 232 (218–258) mm, n = 8

HF: 55 (50–63) mm, n = 7

E: 36 (30–38) mm, n = 8

WT: 142 (114–172) g, n = 7

Tati Concession, Eastern Bamangwato, EC Botswana (Smithers 1971). Sexes combined.

G. m. moholi

TL (♂♂): 381 (330–420) mm, n = 51

TL (♀♀): 375 (350–400) mm, n = 8

T (♂♂): 221 (186–246) mm, n = 51

T (♀♀): 226 (190–227) mm, n = 8

HF (♂♂): 59 (50–66) mm, n = 51

HF (♀♀): 58 (50–63) mm, n = 7

E (♂♂): 38 (30–46) mm, n = 51

E (♀♀): 37 (35–39) mm, n = 8

WT (♂♂): 177 (145–212) g, n = 28

WT (♀♀): 155 (126–176) g, n = 4

Transvaal, NE South Africa (Rautenbach 1978)

G. m. moholi

TL: 379 (330–425) mm, n = 31

T: 225 (205–263) mm, n = 30

HF: 57 (52–63) mm, n = 32

E: 38 (34–42) mm, n = 32

WT: 153 (125–188) g, n = 18

South Africa (Roberts 1951). Sexes combined.

G. m. moholi

WT (♂♂): 205 (180–230) g, n = 19

WT (♀♀): 185 (155–210) g, n = 15

Limpopo Province, NE South Africa (Pullen 2000).

Key References Bearder 1969, 1987; Bearder & Martin 1979; Pullen 2000; Skinner & Smithers 1990; Smithers 1971.

Samantha Pullen & Simon K. Bearder

Galago gallarum SOMALI LESSER GALAGO (SOMALI BUSHBABY)

Fr. Galago de Somalie; Ger. Somali-Galago

Galago gallarum Thomas, 1901. Ann. Mag. Nat. Hist., ser. 7, 8: 27. Webi Dau (Dawa R.), Boran County, Ethiopia.



Somali Lesser Galago *Galago gallarum*.

Taxonomy Monotypic species. Named and first recognized as a species by Thomas (1901) but then subsumed as a subspecies of the Northern Lesser Galago *Galago senegalensis*. Elevated back to full species status by Olson, T.R. (1979, 1986). This taxonomy now widely supported (Nash *et al.* 1989, Bearder *et al.* 1995, Kingdon 1997, Masters & Bragg 2000, Groves 2001, 2005c, Grubb *et al.* 2003, Nekaris & Bearder 2011). Synonyms: none. Chromosome number: not known.

Description Medium-sized galago with whitish face and throat, and contrasting dark brown eye-rings, and black ears and tail. Loud advertisement 'quack' call distinctive. Sexes alike in colour and pattern of pelage. No data available on sexual dimorphism, but ♂♂ probably

slightly (10–20%) heavier than ♀♀ as in other *Galago* spp. (Izard & Nash 1988, Harcourt & Bearder 1989). Head broad. Muzzle short, blackish over distal half. Nose black, slightly up-turned at tip. Chin with light pink skin. Face, throat, chest and belly off-white, with greyish tint on belly. Inter-ocular stripe off-white, broad. Eye-rings dark brown, narrow, sometimes incomplete laterally. Black 'tear line' from inner corner of eyes down sides of muzzle. Eyelids greyish. Eyes large, orange-brown. Reflected eye-shine is bright orange. Ears bare, shiny black skin on front and dull black skin on back. Dorsal pelage short (not woolly), variable, from light sandy brown to buff to fulvous, lighter on head. Dorsal hairs dark grey over basal half, buff near middle followed by whitish subterminal band and blackish tip. Shoulders buff or light rufous. Outer forelimbs and hands buff to sandy-brown. Hips, outer hindlimbs and feet yellowish-buff. Digits blackish. Tail mostly black but dark brown or reddish towards base. Hand (volar) pads distinctive (Anderson 1999). Young similar to adult in colour. Photographs of *G. gallarum* in Kenya available at: www.wildsolutions.nl

Geographic Variation None recorded. In the field, animals in N Kenya appear more rufous on shoulders and flanks than those on the southern fringe of the range in Kenya.

Similar Species

Galago senegalensis. Sympatric with *G. gallarum* on northern and southern fringes of *G. gallarum* range (Olson, T.R. 1986, Nash *et al.* 1989, Butynski & De Jong 2004, D. Olson pers. comm.) and probably also along much of the western and north-eastern fringe. Loud 'woo' (or 'honk') advertisement call distinctive. Dorsum grey or brownish-grey. Ears brown or greyish on back and pinkish or flesh-coloured inside. Tail grey to brown. Generally in wetter habitats than *G. gallarum* (e.g. woodland, forest).

Galagoides cocos. Probably slightly sympatric or parapatric along the south-eastern (coastal) fringe of range of *G. gallarum* in Kenya and



Galago gallarum

Somalia. Smaller. Loud incremental advertisement call distinctive. Dorsum and outer limbs dark brown. Ears dusky behind and pinkish inside (Butynski *et al.* 2006). In wetter habitats than *G. gallarum* (e.g. coastal and riverine forest).

In the field under lamplight, *G. senegalensis* and *G. cocos* do not have a dark brown or black muzzle, eye-rings, ears, or tail that contrast sharply against a whitish face and pale (sandy and buff) body as for *G. gallarum*. Best single phenotypic museum character is the colour of the ears; black in *G. gallarum* and not black in *G. senegalensis* or *G. cocos*.

Distribution Somalia-Masai Bushland BZ. Endemic to the semi-arid thorn scrub and thorn scrub/woodland of E Kenya, Somalia and S Ethiopia where, in most places, it is the only small galago present. Distribution limits poorly known. Western limits uncertain, but may be present to at least east shore of L. Turkana, Kenya (Groves 2001, 2005c). Not known west of Eastern Rift Valley. From Eastern Rift Valley and southern base of Abyssinian Plateau, Ethiopia, east to NE Somalia, south-west to coastal strip of Somalia and NE Kenya, to lower Tana R. (Butynski & De Jong 2004, Butynski *et al.* 2006, De Jong & Butynski 2011). Known southern limit is 01° 34' 24" S; 40° 07' 07" E, 180 m asl (Perkin & Butynski 2003).

Habitat In drier habitats than other galagos. Prefers relatively dense *Acacia*–*Commiphora* deciduous bushland and thicket, and small trees (2–15 m). Here, most of the bushes and trees have thorns or spines, and many produce gum. The ground vegetation (grass and herbs) varies from dense to absent. Soils well drained, rocky or sandy – not loamy. Absent from open woodland and open bushland where the mean distance between bushes or trees is greater than ca. 3 m, and where fewer than about four woody species are present. At pristine sites in Meru N. P. (425–600 m), Kenya, where *G. gallarum* is present, the following woody species are common: Hook-thorn

Acacia mellifera, Umbrella Thorn *Acacia tortilis*, *Commiphora holtziana*, *Commiphora samharensis*, *Terminalia orbicularis*, *Terminalia spinosa*, *Boscia Boscia coriacea*, *Dobera glabra*, Doum Palm *Hyphaene compressa* and *Euphorbia bussei*. The area is especially rich in *Commiphora* spp., but *A. tortilis* is the dominant and tallest tree (ca. 15 m) in many places. Present at low density in 'bushy woodland' at some sites (e.g. Drake-Brockman 1910, De Jong & Butynski 2010a) but use of this habitat type seems uncommon. The one bushy woodland site found to date in Kenya (base of Mathews Range, C Kenya) borders a small swamp and *Acacia*–*Commiphora* bushland. This site is dominated by large *Newtonia Newtonia hildebrandtii*, *Melia volkensii* and *Acacia* spp.

Galago gallarum present (and sometimes common) in severely degraded habitats that are used intensively by people and livestock. For example, common in *A. mellifera*-dominant bushland and thicket where the following other woody species are present: Egyptian Thorn *Acacia nilotica*, False Umbrella Thorn *Acacia reficiens*, *B. coriacea* and Sickie Bush *Dichrostachys cinerea*. The tallest trees in such habitats are often <7 m.

Rainfall and altitude limits poorly documented: ca. 200–750 mm annual rainfall. Altitude in Kenya, from ca. 4 m (Kiunga, extreme north coast) to 1250 m (base of Mathews Range), and in Somalia from 5 m (at Jamaame) to 1200 m (at Odweina) (Butynski & De Jong 2004, De Jong & T. Butynski 2010a, 2011).

Abundance Locally common, but absent from large areas of unsuitable habitat within the species' geographic range. Over much of the range the density is probably less than 1 ind/ha but densities are much higher than this at some sites. For example, in Meru N. P. some sites hold > 4 ind/ha, while in N Kenya one site (near Moyale) supported an estimated >5 ind/ha (Butynski & De Jong 2004).

Adaptations Nocturnal and arboreal. In drier, 'thornier' habitats than any other galago, or any other African primate. Does not require 'free-water'. Can move rapidly through the thorniest of vegetation (e.g. *Acacia* spp., *D. cinerea*, *T. spinosa*). The ears and hindfeet of *G. gallarum* are shorter than those of the similar-sized *G. senegalensis*. These may be adaptations for moving through very thorny/spiny vegetation. When on bushes and trees, moves quadrupedally, head first much like a tree squirrel – even when moving vertically downwards. Adults make horizontal leaps of >2.5 m between branches. Because bushes and trees are often more than a few metres apart, adults frequently come to the ground to hop bipedally to the next bush or tree. Adults jump from >1.3 m to the ground, make a series of 2 m long hops, and then leap >1 m up into a bush or tree. Vision, sense of smell and hearing appear to be well developed. Ears highly mobile and often moved independently of each other.

Most habitats in which *G. gallarum* occurs have few or no trees large enough to provide holes big enough for *G. gallarum* to enter. Probably most often sleeps in the open on branches within a barrier of dense thorns or spines. No nest building observed but sometimes sleeps in bird or rodent 'grass ball' nests amongst dense thorns. Only one case of use of tree-holes observed to date; two individuals observed at dusk in a large, old, *N. hildebrandtii* in which there were numerous holes.

Probably receives a high level of protection against predators both by the camouflage afforded by its pelage and by the extremely dense, thorny/spiny, vegetation. This species is particularly cautious prior

to coming to the ground, suggesting that it is most vulnerable to predators while on the ground.

Foraging and Food Omnivorous. Diet little known. When active, *G. gallarum* spends most of the time foraging in bushes and trees. Forages at all heights from ground to near the top of the tallest trees (ca. 20 m), but mostly at 1–5 m. Also forages for invertebrates on the ground under cover of dense bushes or herbs. Will pounce on large (>4 cm long) invertebrates on the ground from height of >1 m. Gum frequently eaten, but most of the time foraging is spent intensively searching for invertebrates. Some fruit probably eaten when (seasonally) available. Expected to eat the eggs and nestlings of small birds, as well as the neonates of small arboreal mammals. This might prove be the galago with the highest portion of animal matter in the diet.

Social and Reproductive Behaviour Non-gregarious, usually alone or in pairs. Social behaviour poorly known but probably similar to other *Galago* spp. Largest number seen together (i.e. within 5 m) is three. Species-specific loud (advertisement) call is a ‘quack’ that is probably used in the context of long-distance spacing and territoriality. The human ear can hear the ‘quack’ at >300 m. Where densities are relatively high (>4 ind/ha) there may be a ‘dawn chorus’ of ‘quack’ calls with 4–5 animals calling over an area of 2 ha for ca. 10 min. ‘Dusk chorus’ not heard but ‘quacks’ often given during first five hours after dusk. Incidence of ‘quack’ calls appears to be directly related to population density. Other calls include ‘yaps’, ‘chitters’, ‘pings’ and ‘woos’ (Butynski & De Jong 2004, De Jong & Butynski 2004).

Scent-marks by rubbing chin and hands against branches. Mutual grooming between mother and large juvenile occurs. Large juvenile seen clinging to fur of ventrum of mother and carried. Carrying young on the fur is not known for any other *Galago* spp., and is only known for four other species of galagos (Bearder 1999, Bearder *et al.* 2003). Young ‘parked’ at night for long periods in a single clump of several trees while mother forages to at least 50 m away.

Reproduction and Population Structure Poorly known. Rate of reproduction unknown but probably two pregnancies per year as for other *Galago* spp. (Izard & Nash 1988, Zimmermann 1989). Since *G. senegalensis* and *G. gallarum* have similar body weights, it is likely that these two species are similar in terms of gestation length (139–146 days), litter-size (one), birth-weight (15–23 g), age at weaning (10–14 weeks), age at sexual maturity (15 months) and oestrus length (1–3 days) (data for *G. senegalensis*; Zimmermann 1989). Given the considerable seasonality of the region over which *G. gallarum* lives, reproductive activities are expected to be highly seasonal, with lactation and weaning coinciding with periods of maximum food availability (Nash 1983, Butynski 1988). In the region occupied by

G. gallarum, the periods of maximum food availability are likely to be during the Apr–Jun and Nov–Dec wet seasons. If so, births might peak in Feb–Mar and Sep–Oct. Twice in Sep 2003, Butynski & De Jong (2004) observed adult ♀♀ with single large juveniles that were probably weaned. This suggests both that a single infant is (usually) born and that at least some births occur around Mar.

Predators, Parasites and Diseases Unknown. There are many potential predators, including large snakes, large owls *Bubo* spp., Golden Jackals *Canis aureus*, Black-backed Jackals *Canis mesomelas*, mongooses *Herpestes* spp., genetids *Genetta* spp., Wildcats *Felis sylvestris*, Servals *Felis serval* and Caracals *Felis caracal*.

Conservation IUCN Category (2012): Least Concern. CITES (2012): Appendix II.

Common at some sites and widespread. Occurs in semi-arid areas that are of little value for crop production. Persists over large areas where the habitat has been severely degraded through human use and overgrazing by domestic livestock. Present in some protected areas in Kenya, including Meru N. P. and Shaba National Reserve. The long-term survival of this species appears secure.

Measurements

Galago gallarum

HB: 167 (130–200) mm, n = 25

T: 252 (205–293) mm, n = 25

HF: 62 (57–75) mm, n = 25

E: 35 (30–40) mm, n = 27

WT: n. d.

GLS: 42.5 (40.2–45.5) mm, n = 12

Body measurements: numerous museums (Olson & Nash 2002).

Skull measurements: BMNH (Schwarz 1931a). Sexes combined.

HB (♂♂): 178 (154–196) mm, n = 8

HB (♀♀): 168 (145–181) mm, n = 9

T (♂♂): 259 (245–274) mm, n = 8

T (♀♀): 246 (227–271) mm, n = 9

HF (♂♂): 67 (64–70) mm, n = 6

HF (♀♀): 63 (60–71) mm, n = 9

E (♂♂): 35 (28–38) mm, n = 7

E (♀♀): 34 (32–37) mm, n = 4

WT: n. d.

GLS: 42.8 ± 2.2 (40.2–45.5) mm, n = 5

Body measurements (J. Masters pers. comm. in Butynski & De Jong 2004). GLS is for ♂♂ and ♀♀ combined (Masters & Bragg 2000).

Key References Butynski & De Jong 2004.

Thomas M. Butynski & Yvonne A. de Jong

Galago matschiei SPECTACLED LESSER GALAGO (EASTERN NEEDLE-CLAWED GALAGO)

Fr. Galago mignon sombre; Ger. Brillengalago

Galago matschiei Lorenz, 1917. Ann. K. K. Naturhist. Hofmus, Wien 31: 237. Moera, Ituri R., DR Congo.Spectacled Lesser Galago *Galago matschiei* adult.

Taxonomy Monotypic species. Schwarz (1931a), unaware that Lorenz (1917) had already named this taxon, described it as a subspecies of the Senegal Galago *Galago senegalensis inustus*. Hayman (1937) noticed the unique keeled nails of *inustus* and raised this taxon to specific rank as *Galago inustus*. Hill (1953) included *inustus* in *Euoticus* and this was followed by most authors. Walker (1974) and Groves (1974) concluded that *inustus* was likely a forest derivative of *G. senegalensis* but, none the less, deserving of specific status. As pointed out by Olson (1979), the senior name is '*matschiei*'. Thus, current authorities use the name '*Galago matschiei*' (e.g. Bearder *et al.* 1995, Kingdon 1997, Groves 2001, 2005c, Grubb *et al.* 2003, Masters *et al.* 2007). Prior to Olson (1979), the type specimen for *matschiei* had been considered a junior synonym of Thomas's Dwarf Galago *Galagoides thomasi* (Jenkins 1987, Nash *et al.* 1989).

Those morphological (Olson 1979, Masters & Brothers 2002), vocal (Zimmermann 1990) and molecular (Masters *et al.* 2007) phylogenetic analyses that consider *G. matschiei*, all firmly place *G. matschiei* within the genus *Galago*. The most current morphological-molecular analysis (Masters *et al.* 2007) suggests that *G. matschiei* may be the most unique of the species within *Galago*, even more so than the Southern Needle-clawed Galago *Euoticus elegantulus*. This suggests that *G. matschiei* is a relict species within the *Galago* *Euoticus* clade. Synonym: *inustus*. Chromosome number: not known.

Description Medium-sized (ca. 210 g), dark-brown, forest-living galago with black ears and large eyes surrounded by brownish-black eye-rings. Adult ♀ like adult ♂ in pattern and colouration of pelage. Eyes and orbits large, surrounded by broad, well-demarcated, orbital rings ('face-mask') and bordered by a well-defined ridge, especially at the brows. Iris amber. Nose-stripe broad, white, extending onto forehead. Ears variable, either all black or black-tipped (Ambrose 2006). Sides of face, sides of neck, throat, ventrum and insides of legs pale grey. In the pattern of the face and the colour of the ears, *G. matschiei* most resembles the Somali Lesser Galago *Galago gallarum*. Dorsum and upper limbs dark 'burnt' brown or dark grey-brown. Shoulders brown with yellow tinge. Tail dark grey, sometimes grey-brown, darker distally. Tail evenly furred, not bushy or only moderately bushy, often held coiled when sitting and sometimes also when running (Ambrose 2006). Nails of hands and feet (except on pollex, hallux and second pedal digit), over the distal two-thirds of their length, have a slightly raised, central, longitudinal ridge or keel, and end in a sharp, projecting, point. Thus, the nails are similar to those of the needle-clawed galagos *Euoticus* spp., but not so strongly keeled (Hayman 1937, Hill 1953). Infants have full adult colouration (Ambrose 2006). The penile structure for *G. matschiei* is species-specific, being very different from that of all other species of galagos (Anderson 1998, 2000). Eye-shine is orange, but a much stronger orange in the west (e.g. Bwindi Impenetrable N. P. and Kibale N. P., SW Uganda) than in the east (e.g. Mabira, Mpanga and Zika Forest Reserves). At Bwindi Impenetrable N. P. the eye-shine is so bright that it leaves orange traces when the animals move their heads (Ambrose 2006, T. Butynski pers. obs.).

Geographic Variation None recorded except for the following one adult ♂ specimen captured (but not collected) on 20 April 1996 in bamboo at 2330 m on the Itombwe Massif, E DR Congo (03° 52' S, 28° 52' E) by T. Butynski. This site represents about a 130 km range extension to the south for *G. matschiei*. This specimen was identified as a *G. matschiei* based on its body measurements and keeled, pointed, nails. The specimen (photograph in Omari *et al.* 1999: 311) differs from typical *G. matschiei* as follows: face-mask pattern distinct (Bearder *et al.* 2003), with blackish-brown stripe from the inner corner of each eye down along the side of the muzzle to the mouth. Crown and dorsum light rusty-brown becoming lighter and more buff on the sides. Forelimbs and hindlimbs buff-brown. Tops of hands and feet lightly furred buffy-grey. Tail dark dusky brown all over, fuller towards tip. Chest buff, greyer towards midline. Ventrum greyish becoming buff towards the sides.

Similar Species

Galago senegalensis. Probably narrowly sympatric, especially in SC Uganda (e.g. Mpanga F. R.; Nash *et al.* 1989, Ambrose 2006). Dorsum greyer. In woodlands and on edge of dense, moist forest. Flanks distinctly yellow or yellowish-buff. Nails not keeled or pointed. Gives 'woo' (or 'honk' loud call).



Spectacled Lesser Galago *Galago matschiei*.

Galagoides demidovii. Sympatric. Much smaller (Jenkins 1987, Olson & Nash 2002). HB: mean 129 mm (73–155, $n = 200$). Tail: mean 179 mm (110–215, $n = 199$). WT: mean 70 g (44–97, $n = 49$). GLS: mean 37 mm (35–41, $n = 59$). Nails not keeled or pointed. Face-mask not obvious or well-demarcated. Gives 'crescendo' and 'buzz' calls.

Galagoides thomasi. Sympatric. Much smaller (Olson & Nash 2002). HB: mean 146 mm (123–166, $n = 47$). Tail: mean 195 mm (150–233, $n = 46$). WT: mean 99 g (55–149, $n = 29$). GLS: <40 mm (Groves 2001). Nails not keeled or pointed. Face-mask not obvious or well-demarcated. Gives 'crescendo' and 'buzz' calls.

Distribution Endemic to the Albertine Rift region and S Uganda. Rainforest and Afromontane–Afroalpine BZs. Northern limit Djugu Hills, DR Congo (ca. 01.92°N, 30.50°E; Schwarz 1931a), west side of L. Albert. Southwards down western flank of Albertine Rift to south end of Itombwe Massif (03° 52' S, 28° 52' E; Omari *et al.* 1999). Western range lies along the western flank of Albertine Rift (to ca. 90 km west of L. Kivu and 130 km west of L. Edward). Farthest locality west is ca. 28° 06' E (Rahm 1965). Eastern limit is Mabira F. R. (00° 29' N, 33° 00' E; Ambrose 2006) on left bank of Nile R. and north shore of L. Victoria, Uganda. On east flank of Albertine Rift from Bwamba (at the north end of the Rwenzori Mts) and Kibale

*Galago matschiei*

N. P., SW Uganda (not Budongo F. R.; Ambrose 2006) southwards to Kibira N. P., NW Burundi (02° 44' S, 29° 12' E; Masters *et al.* 2007). There may be a ca. 200 km gap in distribution between Albertine Rift population at Kibale N. P. and Mpanga F. R./Mabira F. R. population to east as there are no records from this region and suitable habitat may be lacking. Ambrose surveyed South Busoga F. R. and Mt Elgon, Uganda, east of the Nile R., but did not find *G. matschiei* at either site. Specimens reported to be *G. matschiei* from Mt Moroto (02° 32' N, 34° 46' E) on the Uganda/Kenya border ca. 300 km north-east of Mabira F. R. and on the right bank of the Nile R. (Nash *et al.* 1989). Otherwise, there are no specimen or site records for *G. matschiei* east of the Nile R. The extent of occurrence for *G. matschiei* is roughly 79,000 km². The area of occupancy remains unknown but is certainly very much less than this.

Interestingly, *G. matschiei*, Demidoff's Dwarf Galago *Galagoides demidovii* and Thomas's Dwarf Galago *Galagoides thomasi* are not confirmed to occur to the east of the Nile R. in the moist forests of eastern Uganda, Kenya or Ethiopia. In Kenya and Ethiopia, at least, *G. senegalensis* is the smallest galago of moist forest – occurring at low densities at least on the edges of montane forest (e.g. Mau F. R., Kenya, and Herenna Forest, Ethiopia; T. Butynski pers. obs.). In Uganda and DR Congo, *G. senegalensis* is not known to be a member of the moist forest community of galagos (T. Butynski pers. obs.) except on the north-west side of L. Victoria where *G. senegalensis* is parapatric, if not sympatric, with *G. matschiei*, *G. demidovii* and *G. thomasi* (Ambrose 2002).

Habitat Restricted to primary and secondary mid-altitude, montane and bamboo forest. Uses vegetation at all heights, moving freely between the canopy and thick tangles at lower levels (Kingdon 1997, Ambrose 2006, T. Butynski pers. obs.). Altitudinal limits ca. 670–2500 m (Vincent 1972, Dowsett & Dowsett-Lemaire 1990). The lowest known altitude is on the Kirimia R., Bwamba (00° 52' N, 30° 05' E; R. Dowsett & F. Dowsett-Lemaire pers. comm.). Mean annual rainfall over geographic range ca. 1500–2500 mm.

Spectacled Lesser Galago *Galago matschiei* showing details of hands and feet.

Abundance Ambrose (2002, 2006) recorded the following encounter and loud-call rates for *G. matschiei* for seven sites across Uganda from the left bank of the Nile R. to near the border with DR Congo (range 0.08–1.71 ind/h; 0.00–0.57 calls/h):

Mabira F. R., SC Uganda: 0.33 ind/h (n = 15) and 0.02 calls/h (n = 2).

Zika Forest, SC Uganda: 1.14 ind/h (n = 4). No calls heard.

Mpanga F. R., SC Uganda: 0.36 ind/h (n = 11). No calls heard.

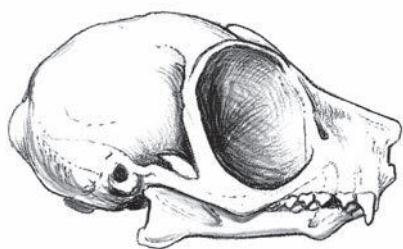
Buhoma, Bwindi N. P., SW Uganda: 0.37 ind/h (n = 19) and 0.02 calls/h (n = 1).

Kanyanchu, Kibale N. P., SW Uganda: 1.71 ind/h (n = 39) and 0.57 calls/h (n = 14). At highest density on forest edge in gum-producing *Albizia* sp. trees.

Echuya F. R., SW Uganda: 0.10 ind/h (n = 2). No calls heard.

Maramagambo F. R., SW Uganda: 0.08 ind/h (n = 1). No calls heard.

Adaptations Nocturnal and arboreal. The pointed, keeled nails of *G. matschiei* are thought to be an adaptation for more effective use of vertical supports (Cartmill 1974, Off & Gebo 2005). The exceptionally well developed face-mask probably aids in species recognition as well as in contact and spacing among conspecifics. Kingdon (1971), comparing the skull of *G. matschiei* with that of *G. moholi*, illustrated the enlarged, strongly ridged orbits of the former and noted that the mandibular ramus is shallow and splayed so that it intrudes less into the orbital cavity, a development that he judged an accommodation to the enlarged, forward-looking eyes of this species. Sleeps and seeks refuge predominantly in holes in trees



Lateral view of skull of Spectacled Lesser Galago *Galago matschiei* adult.

(Ambrose 2006, Bearder *et al.* 2003). Building of nests out of leaves and twigs not reported, but as for all other *Galago* spp., it is likely that *G. matschiei* does, at least occasionally, engage in nest-building.

Foraging and Food Omnivorous. Frequency of locomotor and postural behaviours studied in Kibale N. P. (Off & Gebo 2005). The most frequent locomotor behaviours for *G. matschiei* are leaps (31%) and bipedal hops (25%). Arboreal quadrupedalism (13%) is relatively infrequent. Leaping, bipedal hopping, and vertical clinging and leaping, comprise 75% of the locomotor behaviours ($n = 368$). The most common postures are vertical clinging (57%) and standing (32%) ($n = 44$).

In Kibale N. P., *G. matschiei* most often uses small (<5 cm circumference) supports (74%), followed by medium-sized (>5 cm to <25 cm) supports (25%). Large supports (>25 cm) used less than 1% of the time ($n = 527$). Oblique supports most frequently used (51%), followed by vertical ($>60^\circ$) supports (27%) and horizontal ($<30^\circ$) supports (22%) ($n = 543$). *Galago matschiei* spends more time in the mid-canopy (54%) than in the lower canopy (33%) or upper canopy (13%) ($n = 484$; Off & Gebo 2005).

In Kibale N. P., at first encounter, *G. matschiei* were on peripheral branches of the tree (86%, $n = 6$) and on central supports only once (14%, $n = 1$; Weisenseel *et al.* 1993). In Mabira F. R. uses all strata of the forest from 1 to 12 m, with 45% of the sightings at 2.5–4.5 m ($n = 11$). At Buhoma, Bwindi N. P., in near primary forest, 43% at 0–7 m, 19% at 7.5–14.5 m and 38% >15 m ($n = 21$). At Kanyanchu, Kibale N. P., 21% at 0–7 m, 43% at 7.5–14.5 m and 36% >15 m ($n = 23$; Ambrose 2002).

Diet poorly known, but insects (e.g. moths, caterpillars, beetles), fruits, flowers and gums eaten (Rahm 1966, Kingdon 1997, Ambrose 2006). Gum appears to be a dry-season food as Kingdon (1971) recorded insects only during the Nov rains while fruit and resins were the only foods in the Feb dry season in spite of *G. thomasi* feeding on insects only in the same forests during the same month. In Jul (later in the wet season) Kingdon found a *G. matschiei* feeding equally on fruit, resin, caterpillars and small beetles. Rahm (1966) recorded insects as the diet of a specimen collected in Sep.

Social and Reproductive Behaviour Largely solitary, but aggregations not uncommon. The loud, advertising call of *G. matschiei* is the 'churr' (= 'bark' = 'woo'), which is a single unit call repeated at regular, frequent intervals – often numerous times during a calling bout. The 'churr' may facilitate mate recognition, inter-individual cohesion, spacing of strangers and maintenance of territories. Other calls include the 'staccato-yap', 'grunt-yap' and 'screech-yap' alarm calls. Details and oscillograms of some of these calls are presented in Zimmermann

(1990), Bearder *et al.* (1995) and Ambrose (2000, 2006). Does not give 'crescendo' or 'buzz' calls (Bearder *et al.* 1995).

Mothers use their mouths to carry their infant. They also 'park' their infants, leaving them on branches outside their nest-holes while foraging (Ambrose 2006, Bearder *et al.* 2003). In Kibale N. P., Off & Gebo (2005) observed up to 11 individuals emerge on any given night from high in the canopy of a *Celtis durandii* tree. They then followed a predictable route each night off deeper into the forest.

Reproduction and Population Structure Few data but there may be a breeding peak in Nov–Dec (Kingdon 1971).

Predators, Parasites and Diseases No information. Probable predators, especially of young in nests, are genets *Genetta* spp., Two-spotted Palm Civets *Nandinia binotata*, monkeys (*Cercopithecus*, *Allochrocebus*, *Papio* spp.), Robust Chimpanzees *Pan troglodytes* and large, tree-living snakes. Fraser's Eagle-Owl *Bubo poensis* is broadly sympatric with *G. matschiei*. Small galagos give long bouts of loud alarm calls when they detect the presence of *B. poensis* (T. Butynski pers. comm.). It is likely that *B. poensis* is a major predator of all species of small galago within its extensive geographic range – including *G. matschiei*.

Conservation IUCN Category (2012): Least Concern. CITES (2012): Appendix II.

The mid-altitude, montane and bamboo forests that provide habitat for *G. matschiei* are on some of the best soils in Africa for growing crops. In addition, rainfall is reliable and human disease is relatively low in these areas. As such, a large proportion of former habitat for *G. matschiei* has been destroyed, especially over the past 100 years. The habitat that remains is often surrounded by a high human population density (>300 people/km²) and, as such, is becoming increasingly encroached upon in many places, degraded and fragmented. While viable populations of *G. matschiei* probably exist in over a dozen forests (e.g. Kibale N. P., Bwindi Impenetrable N. P., Kahuzi-Biega N. P. and Nyungwe N. P.), these populations are now isolated from one another with no chance for inter-breeding.

Measurements

Galago matschiei

HB: 166 (147–184) mm, $n = 6$

T: 255 (240–279) mm, $n = 6$

HF: 68 (63–70) mm, $n = 7$

E: 39 (37–42) mm, $n = 7$

WT: 210 (196–225) g, $n = 6$

Various localities (Nash *et al.* 1989, Olson & Nash 2002); sexes combined

HB (♂): 175 mm, $n = 1$

T (♂): 235 mm, $n = 1$

HF (♂): 65 mm, $n = 1$

E (♂): 37 mm, $n = 1$

WT (♂): 200 g, $n = 1$

Itombwe Massif, DR Congo (T. Butynski pers. obs.)

HB: 187 (170–200) mm, $n = 7$

T: 223 (195–250) mm, $n = 7$

HF: 67 (64–68) mm, n = 3

E: 39 (39–40) mm, n = 4

WT (♂): 220 g, n = 1

Various localities (Schouteden 1944a, Rahm 1966, Jenkins 1987, Masters & Bragg 2000, Groves 2001). Some of the specimens included in this sample may also be represented in the sample presented above for Nash *et al.* (1989) and Olson & Nash (2002). Sexes combined.

GLS: 43.2 (42.2–43.7) mm, n = 10

Various localities (Schwarz 1931a); sexes combined

GLS: 43.8 (S.D. = 1.4 mm), n = 14

Various localities (Masters & Bragg 2000); sexes combined

GLS: 43.4, 44.4 mm, n = 2

GWS: 22.9, 23.7 mm, n = 2

Various localities (Jenkins 1987); sexes combined

Key References Ambrose 2006; Kingdon 1971; Off & Gebo 2005.

Thomas M. Butynski & Yvonne A. de Jong

GENUS *Euoticus* Needle-clawed Galagos

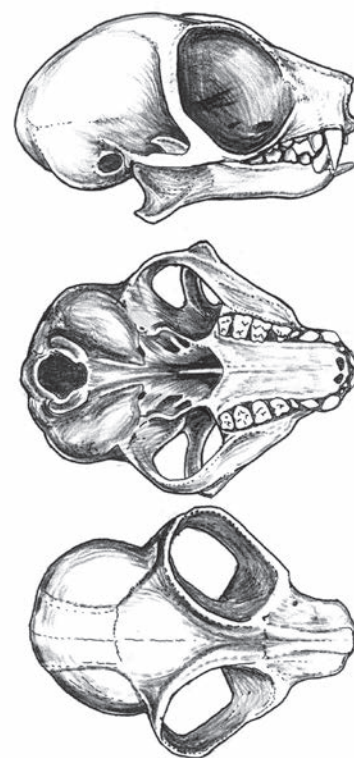
Euoticus Gray, 1863. Proc. Zool. Soc. Lond. 1863: 140.

There are two, allopatric, species of needle-clawed galagos: Southern Needle-clawed Galago *Euoticus elegantulus* and Northern Needle-clawed Galago *Euoticus pallidus*, with a restricted range in the Bight of Bénin, between the Niger and Congo Rivers. These gum-eating galagos inhabit both primary and secondary forests where they show preference for travelling in the canopy. Within the Biafran region their local distribution seems to be determined by the abundance of their preferred food plants, notably *Albizia*, *Newtonia* and *Entada* spp.

These are long-limbed, woolly, arboreal galagos with a short, blunt muzzle and large, pale orange eyes. There are prominent rims surrounding the eyes, a feature that derives from reinforced bony margins around the orbits. Hands and feet are large in proportion to the body. Keels on the nails of the hands and feet end in sharp points. These are adaptations to securing a firm, spread-eagled attachment to the larger branches and trunks that provide their main diet, gums. The gut shows specializations that are not found in other galagos and are thought to be linked with their dietary specialization in tree exudates (Hill 1953). The dental ‘comb’ is very procumbent and made up of greatly elongated lower incisors that have sharp blades on their outer edges; second premolars also exhibit elongation and ‘blading’. These elaborations suggest some ability to enlarge ready-made wounds in bark, but are insufficiently robust to initiate direct wounding of well-barked trees or lianas. Since several important food trees have a wide distribution in Africa, the restricted distribution of these galagos may well be governed by the presence of bark-wounding animals that make gum flow in sufficient and reliable quantities to satisfy the galago’s year-round requirements. Anomalures, cicadas and bark-boring beetles are likely to be major sources of bark-wounding.

This is the only group of galagos in which the nipples have been reduced to one pair. Bearder *et al.* (1995) showed that *Euoticus* used distinctive, loud ‘clicking’ calls that are brief and irregular. They also make characteristic ‘screeches’, ‘yaps’ and a bird-like ‘kwee’. These calls are unlike the calls of any other galago species or genus, further reinforcing the general recognition of these as a very distinctive type of galago.

The taxonomic history of this genus is long, complex and still controversial. Leconte first described *E. elegantulus* as ‘*Microcebus*



Lateral, palatal and dorsal views of skull of Southern Needle-clawed Galago *Euoticus elegantulus* adult.

elegantulus’ in 1857, mistakenly conflating this West African galago with the Madagascan mouse-lemurs. Gray (1863) coined the name *Euoticus* and Schwarz (1931a) regarded this as the only genus distinct from *Galago*. Comparing the detailed anatomy of *elegantulus* and the Spectacled Lesser Galago *Galago matschiei* (then generally called *inustus*), Kingdon (1971) regarded the latter as intermediate between the *Galago senegalensis/moholi* Group and *Euoticus*. He suggested that all the needle-clawed species might have originated with a return to forest-dwelling by a population of savanna galagos during past humid periods (positing that gum-eating might have evolved in savannas first

as a means of buffering seasonal shortages). This phylogenetic change of habitat was seen as driven by the exploitation of a previously under-utilized, gum-eating niche within the equatorial forests. Haltenorth & Diller (1977) treated *Euoticus* as a subgenus of *Galago* and went so far as to characterize *matschiei* (synonym *inustus*) as an eastern form 'Östlicher Kielnagelgalago' of the western 'Westlicher Kielnagelgalago' *G. elegantulus*.

More recently the prominent orbits, point-keeled nails and gummivorous diet of *G. matschiei* have tended to be dismissed as convergent attributes without taxonomic significance. A molecular study by Masters *et al.* (2007) has rekindled this debate by showing that *Euoticus* and *senegalensis/moholi* cluster with *matschiei* (*inustus*) in a genetic grouping that is separate from all other galagos. These authors place *matschiei* and *elegantulus* in more basal positions than the savanna species, implying that contemporary *senegalensis/moholi* are the more derived. Stiner & Turmelle (2003) also provide data in support of *Euoticus* as the most basal radiation within Galagidae and as an exclusive genus.

While it is obvious that *senegalensis/moholi* have made the deepest excursions into dry, strongly seasonal (mainly acacia) woodlands, it is equally obvious that *elegantulus/pallidus* and *matschiei* both show substantially greater anatomical and, perhaps, physiological specialization than the savanna species. It is therefore likely that a common ancestor for the entire cluster was a relatively generalized, gum-eating galago and that all three lineages have elaborated different permutations of specialization in ecology, diet and anatomy.

The taxonomic status of *matschiei* within the cluster remains problematic. It can be treated (as Haltenorth & Diller did in 1977), as an eastern form of *Euoticus*, or (the course provisionally followed here) included in *Galago* while acknowledging its likely, but distant, affinities with *Euoticus*.

In the field the two acknowledged species of *Euoticus* can be identified by peculiar colouring, a fast, running gait along branches, and short, blunt muzzles. The two species are distinct, but have traditionally been regarded as subspecies of a single species. Their colour, skulls and teeth readily distinguish them:

E. elegantulus: bright foxy red above, contrasting strongly with the grey-white underside. Nasal bones become wider anteriorly. Upper central incisors with only a narrow gap between them; P² very strongly elongated and caniniform; P₂ simple, with at most a small talonid; M₃ five-cusped. Occurs south of the Sanaga R.

E. pallidus: pale reddish, buffy or reddish-grey, much greyer on arms, shoulders, neck and tail; dorsal stripe dark grey-brown; face light buff; underside yellowish-white or greyish-white, with comparatively little contrast to upper side. Nasal bones become wider posteriorly. Upper central incisors with wide gap between them; P² and P₂ less specialized, the latter with a strong talonid; upper first and second molars with prominent mesostyle; M₃ four-cusped. Occurs north and north-west of the Sanaga R. and on Bioko I.

There is considerable variation, apparently geographic, within *E. elegantulus*. Animals from the Belinga District, NE Gabon, are smaller than those from the coast, and those from inland regions of Congo are noticeably dark. Many individuals have a white tail-tip. *Euoticus pallidus* is always small in size, and does not have a white tail-tip. Compared to *E. p. talboti* on the mainland, *E. p. pallidus* is darker and greyer, dorsal stripe and underside are greyish, and black eye-rings extend onto the nose so that the white inter-orbital stripe does not extend so far towards the forehead. Underside of *E. p. talboti* is yellowish-white.

Jonathan Kingdon & Colin P. Groves

Euoticus elegantulus SOUTHERN NEEDLE-CLAWED GALAGO (ELEGANT GALAGO)

Fr. Galago mignon du sud; Ger. Südlicher Kielnagelgalago

Euoticus elegantulus (Le Conte, 1857). Proc. Acad. Nat. Sci. Phila. 9: 10. Ndjola, Ogooué R., Gabon.

Taxonomy Monotypic species. Originally placed by Leconte (1857) in genus *Galago*, Gray (1863) considered this species to belong in subgenus *Euoticus*. Schwarz (1931a) and Hill (1953) considered that this represented a distinct genus. Subsequent authors have disagreed. Two subspecies formerly described: *G. e. elegantulus* (Leconte 1857) and *G. e. pallidus* (Gray 1863). Groves (1989) elevated these to full species and placed them in the genus *Euoticus*. Recent genetic analysis places the needle-clawed galagos in a clade with the lesser galagos but separated from them by a considerable genetic distance (Bayes 1998), which supports their taxonomic distinctiveness. Synonyms: *apicalis*, *tonsor*. Chromosome number: not known.

Description Medium-sized galago with a bright orange dorsum and pale, silvery-grey ventrum. Adult ♀ like adult ♂ in pattern and colouration of pelage. Orange of dorsum can be darker on the shoulders and upper dorsum and sometimes extends part way across the chest forming an incomplete collar. Pale grey of the ventrum extends onto flanks under the fore- and hindlimbs creating a 'saddle'.



Southern Needle-clawed Galago *Euoticus elegantulus*.



Southern Needle-clawed Galago *Euoticus elegantulus* adult.

Ears narrow and comparatively small. Eyes large and oval. Snout relatively blunt for a galago. Pale grey nose-stripe in some individuals. Eye-rings indistinct. Tail long and evenly bushy. Tail colour appears to vary with age. In most adults the base of tail is same colour as dorsum, with the last two-thirds dark grey except for white over the distal 2–3 cm. Juveniles have entirely dark grey tails with a few white hairs at tip.

Geographic Variation One population in S Cameroon without white-tipped tail. Population in the Forêt des Abeilles, south of Ogooué R., S Gabon, has grey dorsum and exhibits regional variation in calls (Ambrose 1999).

Similar Species

Euoticus pallidus. Parapatric or allopatric at Sanaga R. North of Sanaga R. in SW Cameroon. Also in SE Nigeria and on Bioko I. In most populations dorsum is orange-brown or cinnamon with a darker dorsal stripe. Can be distinguished by harsh, long drawn-out screeches.

Distribution Endemic to western central Africa. Rainforest BZ. In forests south of the Sanaga R. in SW Cameroon, Equatorial Guinea (Rio Muni), Gabon, Congo and SW Central African Republic. Range thought to extend to Congo R. and Ubangui R., DR Congo (Nash *et al.* 1989). In Ebom, near Kribi, Dja Reserve and Lobéké Reserve, S. Cameroon, and Makokou, Lopé Reserve and Forêt des Abeilles C Gabon (Ambrose 1999). Four specimens from extreme SW Central African Republic indicate presence east of Sangha R. (Stiner & Turmelle 2003).

Habitat Low- to medium-altitude forest. Primary and secondary forest, including littoral, evergreen, semi-deciduous and deciduous forest. Present from near sea level to at least 700 m (J. Oates pers. comm.). Mean annual rainfall at some sites is 1600–1800 mm



Euoticus elegantulus

(Laclavère 1980, Wilkes 1990, Fimbel & Fimbel 1996). Occupies the canopy strata; at 15–30 ca. 72% of the time ($n = 155$ observations). Not observed below 4 m. Favours Umbrella Tree *Musanga cecropioides* on edge of forest and along roads (Ambrose 1999). In Rio Muni, in shade trees in coffee plantations; often Mimosaceae, presumably because of gums (J. Oates pers. obs.).

Abundance Locally common, but with a patchy distribution related to suitable food trees. Population density estimated at 15–20/km² at Makokou (Charles-Dominique 1977).

Adaptations Nocturnal and arboreal. Claw-like nails enable active movement on broad and smooth supports. Moves freely on tree trunks, runs along branches and is able to make leaps of up to 5 m to a neighbouring tree with some loss of height, or to free fall with outstretched limbs for about 8 m. Toilet-claw and toothcomb used for grooming. Young carried in mother's mouth. Juveniles parked in tree forks, often as low as 5 m, and only ascend if approached (Ambrose 1999).

Foraging and Food Gummivore. Feeds heavily on gum from a limited number of tree and liana species. At Makokou, 80% of gum eaten from one species of liane, *Entada gigas*. The search for gums is the principal activity and an individual will follow the same itinerary each night, visiting each site in sequence at regular times. Gums can be found by smell at 20–30 cm. Tiny droplets are licked or scooped with the toothcomb (Charles-Dominique 1977). Also eat invertebrates such as cicadas, which are caught with the hands (Ambrose 1999). Insects found in stomachs of specimens in Rio Muni (Jewell & Oates 1969b). Fruit occasionally eaten.

Social and Reproductive Behaviour Solitary forager but maintains vocal contact with familiar animals. Gathering call at dawn. Sleeps communally, up to seven individuals may sleep tightly

packed together in the vegetation. Individuals use several sleeping sites but usually within an area of <1 ha (Charles-Dominique 1977). One call-type is common both to *E. elegantulus* and *E. pallidus*: high-pitched single units often repeated in long sequences ('t'ya'). The characteristic call of this species comprises a pattern of relatively low frequency yaps interspersed with rapid, slightly ascending sequences or rattles (Ambrose 1999).

Reproduction and Population Structure Breeding thought to occur throughout the year. Four 'parked' juveniles observed in Dja Reserve in March (Ambrose 1999). Adult weight reached at 8–10 months of age. Almost equal proportion of ♂♂ to ♀♀ at Makokou (Charles-Dominique 1977).

Parasites, Predators and Diseases Predation not reported. Predators probably include pythons *Python* spp. and small arboreal predators such as the Two-spotted Palm Civet *Nandinia binotata* and Central African Linsang *Poiana richardsoni* (Charles-Dominique 1977). No information on diseases.

Conservation IUCN Category (2012): Least Concern. CITES (2012): Appendix II.

Occupies a large area of relatively undisturbed, contiguous forest. Affected by logging in some regions. Occurs at high densities at some sites.

Measurements

Euoticus elegantulus

HB: 200 (182–210) mm, n = 39

T: 290 (280–310) mm, n = 39

HF: 64 (62–67) mm, n = 3

E: 30 (29–32) mm, n = 3

WT: 300 (270–360) g, n = 39

HB, T, WT: Makokou, C Gabon (Charles-Dominique 1977); sexes combined

HF, E: Gabon and Rio Muni (BMNH)

Key References Ambrose 1999; Charles-Dominique 1977.

Lesley Ambrose

Euoticus pallidus NORTHERN NEEDLE-CLAWED GALAGO (PALLID GALAGO)

Fr. Galago mignon du nord; Ger. Nördlicher Kielnagelgalago

Euoticus pallidus (Gray, 1863). Proc. Zool. Soc. Lond. 1863: 140. Fernando Po (= Bioko I.), Equatorial Guinea.



Northern Needle-clawed Galago *Euoticus pallidus* adult.

Taxonomy Polytypic species. Formerly described as a subspecies of the Elegant Galago *Euoticus elegantulus*, elevated to full species by Groves (1989). Two subspecies are now recognized (Ambrose 1999, Grubb *et al.* 2003). Synonym: *talboti*. Chromosome number: not known.

Description Medium-sized galago with a cinnamon or orange-brown to grey dorsum and pale grey ventrum. Adult ♀ like adult ♂ in pattern and colouration of pelage. Pale grey extends up the sides of the face and onto the flanks by the shoulders and thighs in a saddle-shape. Thin but well-defined brown dorsal stripe in some individuals. This runs from the shoulder blades at least two-thirds of the way down the spine. Eye-rings black. Ears grey. Snout, feet and hands are pink. Tail long and bushy, same colour at base as the dorsum and grading distally to grey.

Geographic Variation

E. p. pallidus Bioko Needle-clawed Galago. Bioko I. Considerably larger than mainland form. Dorsum grey.

E. p. talboti Nigeria Needle-clawed Galago. SW Cameroon and SE Nigeria. Considerably smaller than Bioko I. form. Dorsum cinnamon.

Similar Species

Euoticus elegantulus. Allopatric. South of Sanaga R. in SW Cameroon. In Equatorial Guinea, Gabon, Congo and extreme SW Central African Republic. Most populations have orange dorsum with white tail-tip. Distinguishing call a slightly ascending rapid sequence or 'rattle' interspersed with 'yaps'.

Distribution Endemic to SE Nigeria, SW Cameroon and Bioko I. Rainforest BZ. In forest between lower Niger R. and Sanaga R., SE

Nigeria and SW Cameroon, and on Bioko I., Equatorial Guinea. In SE Nigeria at Elele and Mamu F. R., in SW Cameroon at Korup N. P., Mt Kupé and Mt Cameroon (Malbrant & Maclatchy 1949, Oates & Jewell 1967, Eisentraut 1973, Bearder & Honess 1992, Ambrose 1999, T. Butynski pers. comm.).

Habitat Primary and secondary lowland and montane moist forest. In Nigeria also in riverine swamp forest and tree plantations. On Bioko I., occurs from sea level to ca. 1600 m and where mean annual rainfall ranges 4000–10,000 mm (T. Butynski pers. comm.). On mainland, occurs from near sea level to at least 2000 m where mean annual rainfall is 1500–10,000 mm. On Mt Kupe and Mt Cameroon, SW Cameroon, 1000–2000 m, not on lower slopes. Over the wettest part of the range (i.e. coast of mainland and on Bioko I.) the dry season is Dec–Feb (<50 mm rainfall/month), whereas farther north the dry season is Nov–Mar.

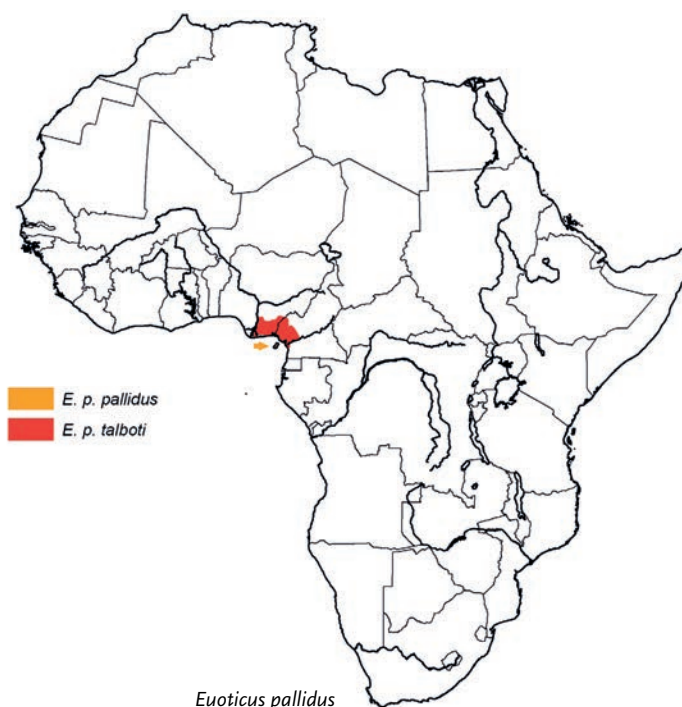
Abundance Uncommon in most locations; rarely encountered. Distribution probably patchy and relates to suitable gum-producing tree species. Uncommon on Bioko I. but regularly observed at specific sites (T. Butynski pers. comm.). At Moka, Bioko I., encountered at the rate of 0.2 ind/h (n = 12; Ambrose & Perkin 2000), 0.3 ind/h (Schlossman 2006), and 0.4 ind/h and 0.3 ind/km (n = 16; Croce (2009)). At most sites on the mainland, Ambrose (1999) recorded ca. 0.2 ind/h (n = 49), but 0.9 ind/h and 1.9 ind/km (n = 96) on Mt Kupé. Encounter rates of 1.4 ind/km (n = 232) in Korup N. P. (Bearder & Honess 1992) and 0.6 ind/km (n = 13) in Mamu F. R. (Jewell & Oates 1969b).

Foraging and Food Gummivore. Forages most often in the canopy; 61% of 63 observations >15 m (Ambrose 1999) but also descends into understorey. At Moka, 100% of 12 encounters with *E. pallidus* were above 5 m, and 83% were above 10 m (Ambrose & Perkin 2000). A second study at Moka yielded a mean height of 9.5 m (5–15 m, n = 10; Croce 2009). Feeds on tree gums that are scooped with the toothcomb and invertebrates that are grabbed with the hands. Sometimes hangs bipedally when catching insects.

Adaptations Moves actively on broad supports and can grip smooth surfaces with claw-like nails. Often descends trunks head first. Makes horizontal leaps between adjoining trees and drops vertically with outstretched limbs, sometimes re-ascending and repeating this behaviour a number of times when agitated. Hollow trees can be used for sleeping sites. Mother carries young in her mouth.

Social and Reproductive Behaviour Solitary forager but sleeps communally. Gives specific gathering call at dawn. Up to four individuals located together at dusk in Cameroon, but 86% (n = 80) of observations were of lone animals. No information on reproductive behaviour. One call-type is common both to *E. elegantulus* and *E. pallidus*: high-pitched single units often repeated in long sequences ('t'ya'). Long, harsh screeches are characteristic of this species.

Reproduction and Population Structure Thought to breed throughout the year. Sanderson (1940) collected pregnant ♀♀ in



Jan, May, Jun and Nov from Cameroon and E Nigeria. Jewell & Oates (1969a) collected a pregnant ♀ in Nov at Mamu, Nigeria. No information on population structure.

Predators, Parasites and Diseases Not studied. One record of Central African Linsang *Poiana richardsoni* killing and eating infant *E. pallidus* on Bioko I. (A. Croce pers. comm.).

Conservation IUCN Category (2012): Least Concern. Endangered as *E. p. pallidus*. CITES (2012): Appendix II.

Fragmented distribution in most habitats and occurs at low densities. Not hunted. Primary threat is habitat loss.

Measurements

Euoticus pallidus

E. p. talboti

HB (♂♂): 179 (170–185) mm, n = 5

HB (♀♀): 192 (176–205) mm, n = 3

T (♂♂): 272 (153–325) mm, n = 5

T (♀♀): 301 (289–320) mm, n = 3

HF (♂♂): 63 (60–66) mm, n = 4*

HF (♀♀): 46, 66 mm, n = 2

E (♂♂): 33 (30–36) mm, n = 4*

E (♀♀): 29, 31 mm, n = 2

WT: (♂) 279 g, n = 1

WT: (♀♀) 232, 250 g, n = 2

Body measurements: Nigeria and Cameroon (BMNH), Elele and Mamu, Nigeria (J. Oates pers. obs.); *Nigeria and Cameroon (BMNH)

WT: E Nigeria (Jewell & Oates 1969a)

E. p. pallidus

HB: 186, 250 mm, n = 2

T: 305, 345 mm, n = 2

HF: 69 mm, n = 1*

E: 32, 35 mm, n = 2

WT: n. d.

East coast of Bioko I. (Eisentraut 1973)

*Bioko I. (BMNH)

Key References Ambrose 1999; Jewell & Oates 1969a, b; Oates 2011.**Lesley Ambrose & John F. Oates****GENUS *Galagoides*****Dwarf Galagos***Galagoides* A. Smith, 1833. South African Quarterly Journal (1) pt 1: 32.Demidoff's Dwarf Galago *Galagoides demidovii* adult.

This genus must presently be considered as a wastebasket category for the smallest galagos that do not fit into any other genus but for which there are as yet insufficient data to assign them to a separate taxon. On the basis of an extensive cladistic analysis, Groves (2001) considered it unsafe to use this genus and assigned species to *Galago* instead. Extensive convergence or parallelism in animals of similar body size and habitats can easily be mistaken for a close phylogenetic relationship (Masters *et al.* 1994, Masters & Brothers 2002). Indications that further separation will be required come from new molecular evidence (e.g. DelPero *et al.* 2000, Stiner & Turmelle 2003, Roos *et al.* 2004, Masters *et al.* 2007) and comparisons of vocal repertoires (see below).

Grubb *et al.* (2003: 1309) give the following account:

[Osman] Hill (1953) emphasized the distinctiveness of *Galagoides* at a time when it was thought to be monotypic. Other species have since been allocated to the genus. *Galagoides zanzibaricus* was removed from Schwarz's (1931) *Galago senegalensis*, *sensu lato*, while *Galagoides granti*, *G. cocos* and *G. nyasae* were in turn detached from *G. zanzibaricus*. Three

more species have been described since Schwarz's (1931) review, or are waiting to be named. The genus includes small forest species with body mass below 200 g, and with shorter limbs and lighter build than *Galago sensu stricto*. They also differ from *Galago* in characters of the skull and teeth (Groves 1989). Buzz calls are present and calls used to attract companions and repel rivals comprise complex phrases. In contrast, *Galago* spp. do not give buzz calls and their recognition calls are repetitive in bouts of variable length (Bearder *et al.* 1995). Mitochondrial genes show that the percentage sequence divergence in an rRNA gene between *Galago senegalensis* and *Galagoides demidovii* is greater than that between *Galago senegalensis* and *Otolemur*, so *Galagoides* might be a sister taxon of a group including *Galago* and *Otolemur* (Bayes 1998). More information is needed to establish that *Galagoides* is a monophyletic taxon.

Since this was written, more detailed work on DNA sequence analysis shows large genetic distances between a clade linking the two small galagos that are ubiquitous throughout the forests of West and central Africa (Demidoff's Dwarf Galago *Galagoides demidovii* and Thomas's Dwarf Galago *G. thomasi*) and the remaining taxa, including Mozambique Dwarf Galago *G. granti* (DelPero *et al.* 2000, Masters *et al.* 2007), causing these authors to suggest that a new generic diagnosis is required. Similarly, comparative studies of penile morphology among five species of *Galagoides* from the Eastern Arc Mts and coastal forests of Tanzania and Kenya (Perkin 2007) show that the Mountain Dwarf Galago *G. orinus* and Rondo Dwarf Galago *G. rondoensis* diverge considerably from the other species and are probably phylogenetically distinct. These conclusions conform only partially with divergence in vocal repertoires (Bearder *et al.* 1995, Honess 1996b), which divides current members of the genus *Galagoides* into four groups based on broad characteristics of the loud-calls used to attract companions and repel rivals: (1) *G. demidovii* and *G. thomasi* give highly distinctive 'crescendo' calls; (2) *G. cocos* and *G. granti* have unique 'incremental' calls; (3) *G. zanzibaricus* and *G. rondoensis* have 'rolling' calls; and (4) *G. orinus* gives 'scaling' calls.

Paul E. Honess & Simon K. Bearder

Galagoides zanzibaricus ZANZIBAR DWARF GALAGO

Fr. Galago de Zanzibar; Ger. Sansibar-Galago

Galagoides zanzibaricus (Matschie, 1893). Sitzb. Ges. Naturf. Fr. Berlin, p. 111. Yambiani, Zanzibar, Tanzania.Zanzibar Dwarf Galago
Galagoides zanzibaricus
zanzibaricus adult.Matundu Dwarf Galago
Galagoides zanzibaricus
udzungwensis adult.

Taxonomy Polytypic species. Taxonomy unresolved. Previously regarded as a subspecies of *Galago senegalensis* (Schwarz 1931a), the specific name was revived by Kingdon (1971). Moved from genus *Galago* to genus *Galagoides* by Olson (1979) and, subsequently, three species split off: Mozambique Dwarf Galago *Galagoides granti*, Malawi Dwarf Galago *Galagoides nyasae*, and Kenya Coast Dwarf Galago *Galagoides cocos* (Honess 1996b, Groves 2001, Grubb *et al.* 2003), based on differences in vocalizations, and in body, penile and hand morphology (Bearder *et al.* 1995, Honess 1996b, Anderson 2000, Groves 2001, Butynski *et al.* 2006, Perkin 2007). Two subspecies recognized: Zanzibar Dwarf Galago *G. zanzibaricus zanzibaricus* and Matundu Dwarf Galago *G. z. udzungwensis* (Honess 1996b, Honess & Bearder 1996, Butynski *et al.* 2006). Note that *udzungwensis* originally given full species status and that the authority for this name is 'Honess 1996', not 'Honess 1997' as stated in Honess & Bearder (1996), Groves (2001) and in Grubb *et al.* (2003). Synonym: *udzungwensis*. Chromosome number: $2n = 36$ (Ying & Butler 1971, De Boer 1973a, b).

Description Small, buffy-grey to greyish-brown galago, with distinctive 'single-unit rolling' advertisement call (Honess 1996b, Butynski *et al.* 2006). Sexes alike in colour and pattern of pelage. Nose-stripe white to cream, broad, from base of rhinarium to just posterior to eyes. Dark patch on either side of muzzle not prominent. Cheeks and chin pale yellow to yellowish-buff. Throat yellow wash to orange-buff. Eye-rings indistinct or absent. Ears relatively erect, short, not notably pigmented. Dorsum rufous cinnamon to greyish-brown and buffy-grey. Tail of uniform thickness with relatively sparse hairs (can see skin). Distal ca. 25–35% of tail darker. Ventrums cream to yellowish-buff (Honess 1996b, Butynski *et al.* 2006). Immatures

like adults but with creamy-white throat. Penis is mostly spine covered and cylindrical in shape but expands greatly laterally in the mid-portion where spines are robust and pinnate. The baculum protrudes notably from the glans penis. Immature animals similar in shape but lacking spines (Honess 1996b, Perkin 2007).

Geographic Variation

G. z. zanzibaricus Zanzibar Dwarf Galago. Endemic to Zanzibar I and perhaps Mafia I. Throat washed with yellow. Ventrums pale yellow. Dorsum cinnamon. Tail with at least some rufous (Butynski *et al.* 2006). Baculum does not protrude beyond end of glans. Penile lappets absent. Penis has spines of uniform type (Honess 1996b, Anderson 2000).

G. z. udzungwensis Matundu Dwarf Galago. Endemic to several lowland forests on mainland of Tanzania. Throat orange-buff. Dorsum greyish-brown or buffy-brown. Tail lacks rufous. Ventrums yellowish-buff (Honess 1996b, Butynski *et al.* 2006). Baculum protrudes beyond end of glans. Penile lappets present. Penis lacks spines (Honess 1996b, Anderson 2000).

Similar Species

Galagoides cocos. Possibly slightly sympatric or parapatric with *G. z. udzungwensis* at north end of *G. z. udzungwensis* range. 'Incremental' advertisement call distinctive. Eye-rings prominent. Nose-stripe white, well defined. Patch on either side of muzzle dark and prominent. Ventrums greyish-white. Penis with robust, pinnate spines all along shaft. Baculum does not protrude beyond end of penis. Inside of ears darkens towards the tips. HB slightly longer (mean 157 mm, $n = 43$; range 145–170 mm, $n = 56$; Harcourt & Nash 1986a, Groves 2001, Butynski *et al.* 2006).

Galagoides granti. Probably parapatric with *G. z. udzungwensis* north of Rufiji/Kilombero River System and *G. granti* to south (Honess 1996b, Butynski *et al.* 2006). 'Incremental' advertisement call distinctive. Inside of the ears darkens towards tip and blackish behind. Tail relatively bushy with blackish-brown tip. Forefeet white on lateral surface. Penis thin and pointed, wider dorso-ventrally than laterally. Baculum does not protrude beyond penis tip (Honess 1996b, Anderson 2000, Perkin 2007). Slightly larger, especially the ears (mean 37 mm, $n = [3]17$; range 35–41 mm, $n = [3]22$); (Honess & Bearder 1996, Groves 2001, Butynski *et al.* 2006).

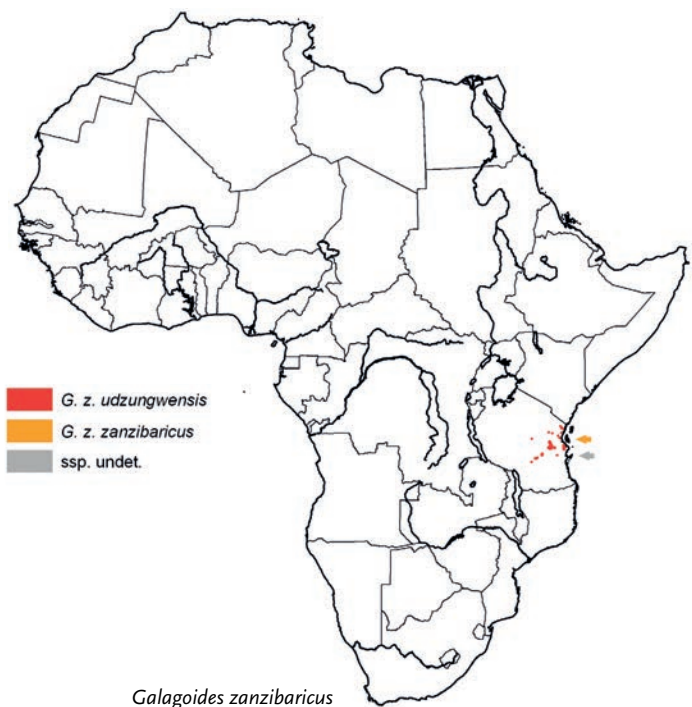
Galagoides orinus. Montane forest species that is sympatric with *G. z. udzungwensis* at 600–900 m. Double or triple unit scaling advertisement call distinctive (Honess 1996b, Perkin 2000b, 2001). Dorsum dark brown. Penis conical, tapering from the tip, with robust pinnate spines at the base (Perkin 2007). About one-third smaller (HB mean 132 mm, 125–138, $n = 4$; WT mean 90 g, 74–98, $n = 3$; Honess & Bearder 1996, Groves 2001, Perkin 2000b, 2004).

Galagoides rondoensis. Coastal forest species. Sympatric in Zareninge F. R., Pugu/Kazimzumbwi Forest Reserves and Pande G. R. on coastal Tanzania (Perkin 2004). Dorsum rich brown. Ventrums creamy-white. Double unit rolling advertisement call distinctive. Tail reddish-orange to greyish-brown, sparsely-haired with unique 'bottle brush' shape, often held in a curled up position when resting (Honess 1996b, Honess & Bearder 1996). Penis thin and flute shaped at distal end, spineless apart from two clusters of robust and pinnate spines beneath tip (Perkin 2007). Much smaller: HB mean 131 mm, 123–137, $n = 7$; WT mean 69 g, 60–73, $n = 7$ (all data from ♂♂).

Distribution Endemic to lowland forests of Tanzania. Somalia-Masai Bushland and Coastal Forest Mosaic BZs. *Galagoides z. zanzibaricus* endemic to Zanzibar I and probably Mafia I. (subspecies pending identification). Absent from Pemba I. *Galagoides z. udzungwensis* endemic to Eastern Arc Mts and coastal forests of mainland Tanzania; from South Pare Mts and East Usambara Mts south to the Rufiji R. and west to the Udzungwa Mts at Kihansi (Honess 1996b, Honess & Bearder 1996, Butynski *et al.* 1998, 2006, Rovero *et al.* 2009).

Habitat *Galagoides z. zanzibaricus* lives in a variety of habitats on Zanzibar I. including bush, low forest, ground-water forest, coconut groves and coral rag thicket (Lumsden & Masters 2001). No part of Zanzibar I. is above 120 m. Mean annual rainfall is ca. 1300 mm (Lumsden & Masters 2001). *Galagoides z. udzungwensis* is found in pristine and degraded, lowland forest from sea-level to 1070 m (Butynski *et al.* 2006). Not found in plantation forest (Honess 1996b, Butynski *et al.* 1998). Common in areas of thick secondary growth and tangles of vines, which may represent sleeping or resting sites and/or areas rich in invertebrate food. At sites where mean annual rainfall is 900–1400 mm in coastal forests (Burgess & Clarke 2000) and to 1700 mm in Kimboza F. R. (Uluguru Mts). Temperatures range 19–27°C (Lovett 1992, Honess 1996b), with temperature extreme of 39°C on Zanzibar (Burgess & Clarke 2000).

Abundance *Galagoides z. zanzibaricus* is widespread on eastern and southern parts of Unguja I. (Zanzibar) where suitable habitat remains. Recent surveys estimate >200 ind/km² (Butynski *et al.* 2006). Densities of *G. z. udzungwensis* highly variable. Common in the lowland Udzungwa Mts where 10.0 animals/h were encountered



Lateral view of skull of Zanzibar Dwarf Galago *Galagoides zanzibaricus* *zanzibaricus* adult.

($n = 29$ h). In contrast, 3.7 animals/h were encountered ($n = 10$ h) in the small (405 ha) Kimboza F. R., and 0.3 and 0.4 animals/h in lowland forest at two sites at Kihansi F. R. ($n = 15$ h and $n = 12$ h). In the Udzungwa Mts, during the 'dusk chorus', up to 20 ind/ha (>500 ind/km²) heard calling at some sites compared to <100 ind/km² at other sites (Butynski *et al.* 1998, 2006).

Adaptations Nocturnal and arboreal. Never observed on the ground (Honess 1996b). Usually forages within 10 m of the ground (up to 49% of observations under 5 m; mean 6.5 m, $n = 159$) and on branches that are 0.5–5 cm in diameter (mean 2.5 cm, $n = 26$) (Honess 1996b). Uses quadrupedal walking and running when moving along the tops of horizontal branches and leaping between more vertical stems and between trees. Observed climbing downwards head first, hanging under branches, and standing on the hindlegs (Honess 1996b). Nests, often two animals together, in tree holes and in tangles of dense vegetation (Honess 1996b, Lumsden & Masters 2001). Nests in tree holes 4–8 m high ($n = 5$) (A. Perkin pers. obs.) and probably dependent on tree-hole availability. Green leaves in nests show teeth marks at the base and some are transported from trees other than the nest tree. Two individuals seen making about ten trips each to collect fresh leaves to line tree hole 8 m up (A. Perkin pers. obs.). Coconut palm *Cocos nucifera* fibre and parts of ferns also found in nests (Lumsden & Masters 2001).



Zanzibar Dwarf Galago *Galagoides zanzibaricus zanzibaricus*.

Foraging and Food Omnivorous. Little information. Diet of fruit and invertebrates, with preference in captivity for invertebrates. Fruits include those of *Trichilia emetica* and *Vitex* sp. Observed to hang upside down to feed on ants on a vine below and taking insects in the leaf litter driven out by army ant columns (A. Perkin pers. obs.). Major feeding bouts are shortly after emergence at dusk, around midnight, and shortly before dawn. Not observed to eat gum in the wild. In captivity will take crickets, grasshoppers and moths; the wings are discarded. Insect prey is ambushed but may be taken with the hands if in flight (P. Honess pers. obs.).

Social and Reproductive Behaviour Predominantly solitary foragers; only 11 of 141 (8%) observations were of pairs. Groups larger than two not observed (Honess 1996b). 'Urine wash' and then rub the sternal gland on a branch (Honess 1996b). Vocal advertisement call is a 'single unit rolling call' often used as a 'gathering call'; it is most commonly given at dusk on emergence before first feeding and before dawn for reassembly of sleeping groups (Honess 1996b, Bearder *et al.* 2003). The single unit rolling call, composed of trilled units that increase then decrease in intensity, is highly variable in length (mean 14.1 units per call (1–46, $n = 2122$) (Honess 1996b). This call is given more frequently than other calls in the vocal repertoire (>90% of calls recorded; Honess 1996b). Other calls, primarily reflecting differing levels of alarm, include the 'buzz', 'rapid whistle', 'descending shriek', 'screech', 'screech-grunt' and 'yap', which may be graded in intensity or given in combination, making a total repertoire of at least 25 loud-calls (Honess, 1996b). Young are parked whilst the mother forages and are carried by mouth (A. Perkin pers. obs.).

Reproduction and Population Structure One or two infants produced. One *G. z. udzungwensis* ♀ caught in Sep 1994 aborted twins the same day, which were subsequently cannibalized (Honess 1996b). Among a sample of adult *G. z. zanzibaricus* on Zanzibar, the ♂ : ♀ ratio was 8 : 22 (Masters *et al.* 1993). Observations of pairs of *G. z. udzungwensis* in tree-hole nests (Honess 1996b) suggest a social system (similar to that of *G. cocos*) of a dispersed monogamy with one adult ♂ in close association with one or two adult ♀♀ (Harcourt & Nash 1986a, Bearder 1987, Harcourt & Bearder 1989). However, Lumsden & Masters (2001) report nest-sharing by up to five *G. z. zanzibaricus* (two adult ♂♂, one subadult ♂, one adult ♀, one subadult ♀).

Predators, Parasites and Diseases No data, but likely to be killed by snakes, owls and mammalian carnivores (e.g. Two-spotted Palm Civet *Nandinia binotata* and genets *Genetta* spp.). No information on parasites or diseases.

Conservation IUCN Category (2012): Least Concern. Endangered as *G. z. zanzibaricus*. CITES (2012): Appendix II.

Major threats are habitat degradation and loss. *Galagoides z. zanzibaricus* mainly confined to S and E Unguja I., Zanzibar (1660 km²), where the most significant areas of habitat remain in Jozani-Chwaka Bay N. P. (3 km²) (Burgess & Clarke 2000). *Galagoides z. udzungwensis* present in several relatively large Forest Reserves and receives most protection in the Udzungwa Mountains N. P., Sadaani N. P. and Amani Nature Reserve.

Measurements

Galagoides zanzibaricus

G. z. zanzibaricus

HB: 143 (125–150) mm, $n = 11$

T: 214 (198–235) mm, $n = 11$

HF: 56 (51–59) mm, $n = 11$

E: 32 (31–35) mm, $n = 11$

WT: 127 (104–172) g, $n = 10$

GLS: 42 mm, $n = 8$

Museum specimens from Zanzibar I. (Butynski *et al.* 2006); sexes combined

G. z. udzungwensis

HB: 162 (139–180) mm, $n = 17$

T: 222 (202–270) mm, $n = 17$

HF: 58 (50–70) mm, $n = 17$

E: 31 (25–37) mm, $n = 17$

WT: 145 (118–195) g, $n = 6$

GLS: 42 mm, $n = 1$

GWS: 27 mm, $n = 1$

Live specimens from Matundu F. R. (Honess 1996b, Honess & Bearder 1996), Pugu F. R., Pande G. R. (A. Perkin pers. obs.); museum specimens from Kissarawe, Bagilo (Uluguru Mts), Amboni (Tanga) (Butynski *et al.* 2006). Sexes combined

Key References Butynski *et al.* 2006; Groves 2001; Grubb *et al.* 2003; Honess 1996b; Honess & Bearder 1996.

Paul E. Honess, Andrew W. Perkin & Thomas M. Butynski

Galagoides rondoensis RONDO DWARF GALAGO

Fr. Galago de Rondo; Ger. Rondo-Galago

Galagoides rondoensis Honess, 1996. Soc. Biol. Hum. Affairs 61(1): 9. Rondo F. R., 10° 07' S, 39° 23' E, Rondo Plateau, Lindi District, Tanzania.

Rondo Dwarf Galago *Galagoides rondoensis* adult.*Galagoides rondoensis*

Taxonomy Monotypic species. First collected from sites in SE Tanzania (near Newala, Makonde Plateau, in 1953, and Rondo Plateau in 1955) and provisionally identified as Demidoff's Dwarf Galago '*Galago demidovii*' and later '*Galago demidovii orinus*' (Honess 1996b, Lumsden & Masters 2001). First recognized and described as a species, based on differences in vocalizations and morphology, by Honess (1996b) and the formal species description published by Honess (1996a). Note that the authority for the name *Galagoides rondoensis* is 'Honess 1996', not 'Honess 1997' as stated in Honess & Bearder (1996), Groves (2001) and Grubb *et al.* (2003). Subspecies not known. Synonyms: *demidoff*, *demidovii*. Chromosome number: not known.

Description One of Africa's two smallest primates. Little or no sexual dimorphism but pelage colour varies according to the maturity of individuals (see below). Muzzle long and slender, with a narrow, pale nose-stripe extending to the forehead. Area on muzzle between nose-stripe and cheek sparsely haired, with yellowish skin pigmentation in young animals and dark brown in mature animals (A. Perkin pers. obs.). Crown and forehead reddish-brown (in young animals) to dark brown (in mature animals). Ears mostly slate-grey, with yellow pigmentation on the auricular opening and edges. Yellow pigmentation of ears, lips and chin especially marked in young animals. Eye-rings absent (Honess 1996b) or thin and dark. Dorsum rich brown extending onto thighs and forelimbs. Ventral pelage creamy white with some yellow staining on the chest in some individuals.

Tail reddish-orange in immature animals and greyish-brown in mature animals. Sparsely haired until tip where hair is longer, giving

a 'bottle brush' shape unique to *G. rondoensis*. Mature animals have thicker hair on tail than immature animals. Tail often held in a curled-up position when resting (Honess 1996b, Honess & Bearder 1996, Perkin 2003). Penis conical and diagnostic in shape, broadening towards distal end (Honess 1996b, Anderson 2000). In mature ♂♂, where the distal end of penis enlarges, there is a diagnostic small semi-concentric patch of 'robust single pointed spines' (1–2 mm) situated just behind the tip (spine terminology after Dixson 1995 and see Anderson 2000). Rest of penis lacks spines in northern populations but heavy spines at base in southern populations (A. Perkin pers. obs.). In immature ♂♂, or possibly non-breeding ♂♂, spines greatly reduced or not present (A. Perkin pers. obs.). The species-specific advertising call, a double unit 'rolling' call, is diagnostic (Honess 1996b, Honess & Bearder 1996).

Geographic Variation No subspecies described but there are differences in call structure and penile morphology between southern nominate population and northern populations (A. Perkin pers. obs.). Limited data (see Measurements) suggest that *G. rondoensis* of the nominate population is smaller than animals of northern populations.

Similar Species

Galagoides zanzibarcus udzungwensis. Sympatric in Zareninge F. R., Pugu/Kazimzumbwi F. R. and Pande G. R. on coastal Tanzania. Larger by ca. 100–150%, greyish-brown dorsum, broad nose-stripe, tail not bushy, tail hairs wiry, penile spine patterns and species-specific advertisement call, the single unit 'rolling' call, diagnostic (Honess 1996b, Honess & Bearder 1996, Bearder 1999, Perkin 2003).

Galagoides granti. Sympatric in Rondo F. R., Litipo F. R. and Ziwani F. R., coastal Tanzania. Larger by ca. 100–150%, dorsum brown, tail not bushy, ears large and blackish. Penile spine patterns diagnostic, as is species-specific ‘incremental’ advertising call (Honess 1996b, Honess & Bearder 1996, Perkin 2003).

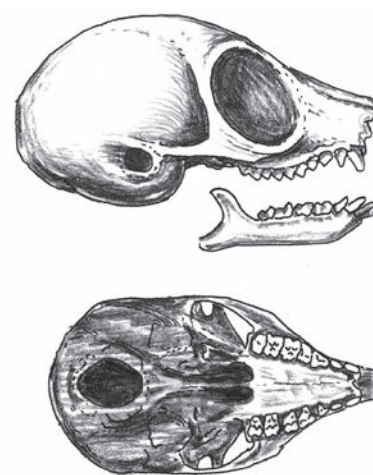
Distribution Coastal Forest Mosaic BZ. Endemic to and discretely distributed in six small moist forests in coastal Tanzania: Zarenige F. R. (06°05′ S, 38°23′ E) (Perkin 2000a), Pande G. R. (06°25′ S, 39°03′ E), Pugu/Kazimzumbwi F. R. (06°32′ S, 39°03′ E) (Perkin 2003, 2004), Rondo F. R. (10°06′ S, 39°06′ E), Litipo F. R. (10°01′ S, 39°17′ E) and Ziwani F. R. (10°13′ S, 39°09′ E) (Honess 1996b, Honess & Bearder 1996).

Habitat Occurs in East African coastal dry forest and mist-fed forest, and East African coastal scrub forest within the East African Zanzibar–Inhambane coastal forest belt *sensu* Clarke & Sorensen (2000). Found only in forest patches between 100 and 900 m asl that are wetter than the surrounding habitats (mean annual rainfall 936–1110 mm). Often associated with liana tangles around tree-falls.

Abundance Sight and trap data indicate *G. rondoensis* is locally common but has a highly variable distribution within and among forests. In Pande G. R. densities estimated at 3–6 ind/ha (Perkin 2003). Four individuals trapped in one night in Pugu F. R. in a 0.5 ha plot (Perkin 2004). Encounter rates (number of animals seen or heard per survey hour) range 3–10 animals/h in Pande G. R. and Pugu/Kazimzumbwi F. R. (Perkin 2003, 2004), and 3.9 ind/h in Rondo F. R. (Honess 1996b).

Adaptations Nocturnal and arboreal. Nests for daytime sleeping are in thick liana tangles normally 10–30 m above the ground. Three animals seen to occupy a flat leafy nest only 5 m off the ground in Rondo F. R. After leaving the nest at dusk most time is spent in the forest understorey (less than 3 m off the ground) (Honess 1996b). Locomotion is mainly vertical, clinging to thin stems (less than 5 cm diameter) and leaping. Seen hindleg-hopping on ground to cross small gaps, including single-lane tracks (<3 m), quadrupedal running on horizontal supports and running head-down down tree trunks. Jumps down to pounce on prey in leaf litter before jumping back immediately to a vertical support. Tail often held tightly curled up at rest but unfurled during locomotion. Utilizes a combination of hearing, sight and olfactory senses to locate prey, communicate with conspecifics and to detect potential predators. Will mob potential predators with intense bouts of alarm-calling.

Foraging and Food Omnivorous. Individuals mostly forage alone, leaping quickly from stem to stem to find food items. Insects make up a large proportion of the diet, with proportionately less fruit and gum than taken by larger galagos. When active, spends much time feeding in the understorey and leaf litter layer (Honess 1996b, Bearder *et al.* 2003, Perkin 2003). Often jumps to the ground to take invertebrates, particularly insects fleeing army ant columns. In Pugu/Kazimzumbwi F. R. up to four individuals seen together feeding next to an ant column, sometimes with Zanzibar Dwarf Galago *Galagoides zanzibaricus* (A. Perkin pers. obs.). Stomach analysis of three individuals in Rondo F. R. revealed remains of an unidentified



Lateral and palatal views of skull of Rondo Dwarf Galago *Galagoides rondoensis* adult.

red fruit (Lumsden & Masters 2001). In Pugu/Kazimzumbwi F. R. nectar and flowers are eaten. Entered traps baited with bananas and palm wine and often eat much of the banana.

Social and Reproductive Behaviour The limited data available suggest *G. rondoensis* is solitary or associates in small groups. Three individuals seen nesting together and up to four in loose groups when foraging. In Rondo F. R. 16% of observations were of two or more animals together, while 84% were alone ($n = 118$ animals; Honess 1996b). At night *G. rondoensis* mostly uses lower strata of the forest. In Rondo F. R. mean height 3 m ($n = 156$ animals; Honess 1996b). Three young seen sharing a day nest with a Mozambique Dwarf Galago *Galagoides granti* (Lumsden & Masters 2001).

Galagoides rondoensis has an extensive vocal repertoire with at least four discrete loud-calls. These are often mixed together to form other call structures depending on the context. In Rondo F. R. 70% of calls analysed were alarm calls with only 22% species-specific advertisement calls ($n = 647$; Honess 1996b). The species-specific advertisement call is used to advertise presence and for group reassembly in the morning (Honess & Bearder 1996, Bearder *et al.* 2003, Perkin 2003, 2004).

Infants carried in mother's mouth, not clinging to her body. Mother 'parks' infant during the night but duration of parking not known (Bearder *et al.* 2003, A. Porter pers. comm.).

Reproduction and Population Structure Based on ♀♀ trapped in Pugu F. R.: antenatal body weight = 93 g ($n = 3$), postnatal lactating weight 66.5 g ($n = 2$). Trapping data suggest reproduction is seasonally bimodal. Birth periods in mid-Apr and end of Dec in Pugu/Kazimzumbwi F. R. (Perkin 2004) and Jul–Aug in Rondo F. R. This coincides with the 'short' wet season (Nov–Dec) and the 'long' wet season (Mar–May).

Predators, Parasites and Diseases Uncertain, but owls, genets *Genetta* spp., Two-spotted Palm Civets *Nandinia binotata* and snakes are likely predators. Genets and snakes invoke intense episodes of alarm calling. Alarm calls by one individual can last >40 min, whilst conspecifics situated close by remain silent until the threat has gone (A. Perkin pers. obs.). Alarm calls comprise rapid high frequency phrases of 'rapid whistles' and/or 'shivering twitters' several seconds apart linked

with ‘yaps’ (Honess 1996b). Such calls also given in presence of *G. granti*, which is known to hunt vertebrates (S. K. Bearder pers. comm.).

Unidentified yellow mites occasionally on edges of ears of mature adults in Pugu F. R. (A. Perkin pers. obs.) and orange mites on head of one individual from Rondo F. R. (Honess 1996b).

Conservation IUCN Category (2012): Critically Endangered. CITES (2012): Appendix II.

Currently listed as among the 25 most threatened primate taxa in the world (Honess *et al.* 2009). Main threat is habitat loss. Known distribution 92.6 km² of coastal forest (Pande G. R. 2.4 km², Rondo F. R. 25 km², Ziواني F. R. 7.7 km², Pugu/Kazimzumbwi F. R. 33.5 km², Litipo F. R. 4 km² and Zareninge F. R. 20 km²) (Burgess & Clarke 2000, Perkin 2004). All sites require improved management. Further surveys in potential habitat areas and research on variation among populations are priorities.

Measurements

Galagoides rondoensis

Data for two populations are presented owing to intra-population variation in vocalization and body measurements.

HB: 107 mm, n = 7

T: 184 mm, n = 8

HF: 50 mm, n = 8

E: 28 mm, n = 7

WT: 60 g, n = 5

Rondo F. R., SE Tanzania (wild and museum labels) (Honess 1996b). Ranges not provided. Sexes combined.

HB (♂♂): 131 (123–137) mm, n = 7

T (♂♂): 168 (174–177) mm, n = 7

HF (♂♂): 46 (40–46) mm, n = 7

E (♂♂): 28 (29–30) mm, n = 7

WT (♂♂): 69 (60–73) g, n = 7

Pugu/Kazimzumbi F. R. and Pande G. R., central coastal Tanzania (Perkin 2003, 2004). Pande G. R. is only 10 km from Pugu/Kazimzumbi F. R., thus data lumped.

GLS: 35 mm, n = 3

Localities not given (Groves 2001)

Key References Bearder *et al.* 2003; Honess 1996b; Honess & Bearder 1996.

Andrew W. Perkin & Paul E. Honess

Galagoides orinus MOUNTAIN DWARF GALAGO

Fr. Galago uriner; Ger. Berggalago

Galagoides orinus (Lawrence & Washburn, 1936). Occas. Pap. Boston Soc. Nat. Hist. 8: 259. Bagilo, Uluguru Mts, C Tanzania.



Mountain Dwarf Galago *Galagoides orinus* adult.

Taxonomy Monotypic species. Originally described as *Galago demidovii orinus*. Recognized as a full species by Honess (1996b) and Honess & Bearder (1996) based on differences in vocalizations and morphology, and subsequently accepted by Kingdon (1997), Groves (2001) and Grubb *et al.* (2003).

Description A small, dark galago with a long-haired tail. No sexual dimorphism apparent; sexes alike in colour and pattern of pelage. Muzzle slender and slightly up-turned. Nose-stripe conspicuously white, contrasting with dark brown on either side. Eye-rings thin and dark. Ears with yellow pigmentation on anterior and outer edges; posterior dark brown. Yellow pigmentation decreases with age. Chin and neck yellowish-white. Crown, dorsum, forelimbs, thighs and flanks dark brown. Ventrums, inner-forelimbs and inner-hindlimbs creamy white. Dark yellow staining sometimes visible on chest due to glandular secretions. Lower forelimbs and lower hindlimbs yellowish-brown. Tail morphology is variable, with tails of wild-caught animals long but not densely haired, giving a bushy appearance, but Lawrence & Washburn 1936 describe tail as ‘noticeably short-haired’. Colour varies from completely reddish-brown to brown over proximal two-thirds and black over distal one-third. Penis is slightly cone-shaped, widening towards the distal end. Baculum protrudes from the end. Small, simple, spines cover the distal half and ca. 14 robust, single, pointed spines cover the proximal half, mostly on the ventral side (Perkin 2007) (spine terminology after Dixson 1995; see Anderson 2000). Species-specific advertisement call (double or triple unit scaling call), and alarm call ‘yaps’ and ‘descending



screeches' diagnostic (Honest 1996b, Perkin *et al.* 2002). Synonyms: none. Chromosome number: not known.

Geographic Variation Poorly known. Data suggest variation in vocalizations among populations in Tanzania (Udzungwa Mts, Uluguru Mts, Rubeho Mts, East Usambara Mts, Mt Rungwe) and N Malawi (Misuku Hills) (Perkin *et al.* 2002, Bearder & Karlsson 2009).

Similar Species

Galagoides zanzibaricus udzungwensis. In coastal, lowland and sub-montane forest from sea level to ca. 1070 m (Butynski *et al.* 1998). Narrowly sympatric with *G. orinus* from ca. 600–900 m at Mkungwe F. R. in the Uluguru Mts, but generally parapatric with *G. orinus* occurring at higher altitudes. About 50% larger. Overall pelage greyish-brown. Tail shorter, more thickly haired and held straight. Species-specific advertisement call a single unit 'rolling call' (Honest 1996b, Perkin *et al.* 2002). Penile morphology different (Perkin 2007).

The *Galagoides* sp. from the montane forests of the Taita Hills, SE Kenya, is similar in pelage and morphology but the species-specific advertisement call differs. Dorsal pelage cinnamon-brown with orange-brown tinge on shoulders and thighs. Tail tip appears to be bushier. It remains to be determined whether this is *G. orinus* or another taxon (Perkin *et al.* 2002).

Distribution Afromontane–Afroalpine BZ. Endemic to the montane and mid-altitude forests of most of the Eastern Arc Mts, Tanzania, southwards to Mt Rungwe in SC Tanzania, and Misuku Hills in N Malawi (Allen & Loveridge 1927, Lawrence & Washburn 1936, Honest 1996b, Butynski *et al.* 1998, Perkin 2000b, 2001, Daggart *et al.* 2006, Bearder & Karlsson 2009). Perhaps in Taita Hills, SE Kenya (Perkin *et al.* 2002).

Habitat Lives in sub-montane and montane moist forests as well as giant heather *Erica* sp. forest at the limit of the tree zone (Honest 1996b, Butynski *et al.* 1998, Perkin 2000b, 2001, 2004). It appears that disturbed forest, such as tree-fall zones, is preferred, especially areas of thick vine tangles (Perkin 2001). The canopy, mid- and understorey are utilized. Altitude range 600–2600 m (Butynski *et al.* 1998, Rovero *et al.* 2009). Mean annual rainfall 1000–>2000 mm per year (Lovett & Wasser 1993).

Abundance Abundance appears to be variable but measuring is difficult since *G. orinus* spends much time in the canopy, which probably reduces detection rates. In undisturbed forest Perkin (2001) in the Uluguru Mts, and Honest (1996b) in the East Usambara Mts report encounter rates of 2.7 animals/h ($n = 30$) and 1.2 animals/h ($n = 34$), respectively. In disturbed forest Perkin (2001) in the Uluguru Mts and Honest (1996b) in the East Usambara Mts report encounter rates of 4.5 animals/h ($n = 74$) and 4.7 animals/h ($n = 14$), respectively. Low encounter rates were also noted in the less disturbed sub-montane and montane forests of the Udzungwa (Butynski *et al.* 1998) and Rubeho Mountains (Perkin 2004). It is suspected that *G. orinus* occurs at a low density throughout much of its range (Butynski *et al.* 1998).

Adaptations Nocturnal and arboreal. Tree-holes and nests used for sleeping. One nest in the East Usambara Mts, which held three *G. orinus*, was round (ca. 30 cm diameter), and constructed of leaves and twigs 15 m up in a clump of lianas (Bearder *et al.* 2003). Locomotion mainly vertical clinging and leaping. Quadrupedal running on horizontal supports and running head first down tree trunks. Will hop to the ground but quickly returns to vertical stems. Utilizes all forest strata. Fast-moving; capable of jumps of >5 m. Utilizes a combination of hearing, sight and olfactory senses to locate prey, communicate with conspecifics and detect predators. Will mob potential predators with intense bouts of alarm calling.

Foraging and Food Omnivorous. Eats moths, cockroaches, nectar of wild bananas *Ensete edule* and gum from the liana *Toddalia asiatica*. Forages in trees and occasionally in leaf litter. Takes baits of banana and peanut butter (Perkin *et al.* 2002, Perkin 2004). In captivity accepted geckos (A. Perkin pers. obs.).

Social and Reproductive Behaviour Individuals move out of the sleeping site together at dusk but soon start to forage solitarily while maintaining contact by calling. Soon after leaving the sleeping site there is a bout of advertisement calling. There is a second calling peak at dawn (Perkin 2004). Sleeping group size ranges from 1 to 9 animals (mean 4.3, $n = 6$; Perkin 2000b, 2001, Bearder & Karlsson 2009). One tree nest hole held one mature ♂, one immature ♂, one mature ♀ and one immature ♀ (A. Perkin pers. obs.).

Reproduction and Population Structure Little known. Like other members of the genus *Galagoides*, *G. orinus* probably mouth carries infants and 'parks' them while foraging (Bearder *et al.* 2003). Reproductive parameters probably similar to those of other small, montane forest *Galagoides* spp. (e.g. Demidoff's Dwarf Galago *G. demidovii* and Thomas's Dwarf Galago *G. thomasi*).

Predators, Parasites and Diseases Unknown, but Usambara Eagle-owls *Bubo vosseleri*, genets *Genetta* spp., Two-spotted Palm Civets *Nandinia binotata*, Gentle (Sykes's) Monkeys *Cercopithecus mitis* and large snakes are likely predators. Usambara Eagle-owls, genets, African Wood Owls *Strix woodfordii* and humans may provoke intense episodes of alarm calling. Alarm calls by one individual can last for >1 hour, whilst conspecifics situated close by remain silent until the threat has gone (A. Perkin & T. Butynski pers. obs.). Of the 3–4 alarm calls known for *G. orinus* the 'yaps' and 'descending screeches' are given in situations of extreme threat from predators (Honess 1996b, Perkin 2004).

Conservation IUCN Category (2012): Near Threatened. CITES (2012): Appendix II.

Under the IUCN (2012) Degree of Threat criteria, and based on current data, *G. orinus* could be categorized as Endangered (category B,1,a,b,i,ii,iii). Conservation dependent on habitat preservation. Main threats are habitat clearance for agriculture, collection of building poles and pit-sawing. Research is required to confirm the range of this species. There is preliminary evidence of inter-population variation that may have taxonomic and conservation implications (Perkin *et al.* 2002).

Measurements

Galagoides orinus

HB: 132 (125–138) mm, n = 4

T: 180 (169–199) mm, n = 4

HF: 46 (43–48) mm, n = 4

E: 30 (25–32) mm, n = 4

WT: 90 (74–98) g, n = 3

One specimen each from Udzungwa Mts (New Dabaga F. R.), Kilanze Kitungulu Forest and Uluguru Mts (Bagilo, Mkungwe) (Lawrence & Washburn 1936, A Perkin pers. obs.). Sexes combined.

GLS: 39 mm, n = 1

Locality not stated (Groves 2001)

Key References Butynski *et al.* 1998; Honess & Bearder 1996; Lawrence & Washburn 1936; Perkin *et al.* 2002.

Andrew W. Perkin, Paul E. Honess & Thomas M. Butynski

Galagoides granti MOZAMBIQUE DWARF GALAGO (GRANT'S DWARF GALAGO)

Fr. Galago du Mozambique; Ger. Mosambik-Galago

Galagoides granti (Thomas & Wroughton, 1907). Proc. Zool. Soc. Lond. 1907: 286. Coguno, Inhambane District, S Mozambique.



Mozambique Dwarf Galago *Galagoides granti* adult.

Taxonomy Monotypic species. Originally described as a full species *Galago granti* and accepted by Elliot (1913a). Subsequently, classified as *Galago senegalensis granti* (Schwarz 1931a) then, following subdivision of *G. senegalensis* and recognition of Zanzibar Dwarf Galago *G. zanzibaricus* by Kingdon (1971), classified as a southern subspecies of Zanzibar Dwarf Galago *Galago zanzibaricus granti* (Jenkins 1987) or *Galagoides zanzibaricus granti* (Olson 1979, Meester *et al.* 1986, Nash *et al.* 1989, Skinner & Smithers 1990). Placed in its current genus and confirmed at full species status by Honess (1996a, b) based on species-specific advertisement calls, and penile and hair morphology (see also Anderson, M.J. 2000, 2001, Butynski *et al.* 2006). Synonym: *mertensi*. Chromosome number: not known.

Description A small galago with a long, bushy tail and notably long, rounded, blackish ears. Gives a distinctive 'incremental call' as its vocal advertisement. This call begins quietly, increases and then decreases in volume composed of 1–17 units (mean 5.8, n = 211), each made up of an increasing number of sub-units (Honess 1996a, b). Sexes alike in colour and pattern of pelage. Forehead greyer than top of head. Pale band on the top of the snout from forehead to nostrils (inter-ocular stripe). Eye-rings black and conspicuous. Ears relatively long (>37 mm), broad, blackish behind. Dorsal surface of head, neck, back and hindlimbs drab-brown, tipped buffy-brown with slight pinkish tint. Hairs ca. 12 mm. Outside of the forelimbs drab-brown fading to white on the forefeet. Ventrums and inner surface of legs cream-buff; in some specimens upperparts of the limbs have a yellowish tinge. Ventral hairs with basal three-fifths slate-grey. Tail long and bushy, wider over distal ca. 80%, hairs dense, with hairs c. 15 mm long, soft. Tail darker

than dorsum with distal ca. 10–60% blackish-brown. Some with tail tipped white. No information available on sexual dimorphism in body size or colouration. Penis cylindrical with spines in mature ♂♂ concentrated in the mid-region. Baculum does not protrude beyond the glans (Honess 1996b, Anderson 2000, Perkin 2007).

Geographic Variation Current data suggest this species is largely consistent across its described range (Butynski *et al.* 2006). The exclusion of specimens from Newala (6) and the Uluguru Mts (3) from his analysis of *G. granti* from Mozambique suggests that Groves (2001) was not confident of their identity. However, whilst those from Newala are *G. granti* (Lumsden & Masters 2001) specimens of a similar size from the Uluguru Mts are most likely Matundu Dwarf Galago *G. z. udzungwensis* (Honess 1996b, Perkin, 2000b).

A recent field study of populations identified in Malawi as Malawi Dwarf Galago *Galagoides nyasae* (Elliot 1907) and the nearby Mount Thyolo Dwarf Galago, *Galagoides* sp. nov. 2 (Groves 2001, Grubb *et al.* 2003), suggests that they are most likely *G. granti*, based on appearance, calling patterns and habitat use (Wallace 2006). However, a population studied at Kalwe, near Nkata Bay on the western shore of L. Malawi (*Galagoides* sp. nov. 1) is more distinctive in both appearance and vocalizations and merits further study (Courtenay & Bearder 1989, Bearder & Karlsson 2009).

Similar Species Kenya Coast Dwarf Galago *Galagoides cocos*, *G. zanzibaricus* and *G. granti* replace each other from north to south in the evergreen forests of the coastal strip of eastern Africa from N Kenya (perhaps S Somalia) to extreme S Mozambique and extreme E Zimbabwe. *G. cocos* is the northern species, *G. zanzibaricus* the central species and *G. granti* the southern species (Butynski *et al.* 2006). *Galagoides granti* is parapatric with Southern Lesser Galago *Galago moholi* in Mozambique and sympatric with Rondo Dwarf Galago *Galagoides rondoensis* in STanzania.

Galagoides zanzibaricus udzungwensis. Parapatric. In Tanzania south to Kihansi and Rufiji/Kilombero River System. Ears shorter (seldom longer than 33 mm) and dusky behind. Hair of dorsum ca. 9 mm. Tail hairs of even length over tail, sparse, ca. 11 mm, wiry. Proximal ca. 75% of tail same colour as dorsum (i.e. buffy-brown); distal ca. 25% slightly darker brown or dusky. ‘Single unit rolling call’ (Honess 1996b, Butynski *et al.* 2006).

Galago moholi. Sympatric or parapatric. In savanna woodland. Pelage greyer. Tail thinner and more uniform coloured. Muzzle long (palate length: >17 mm versus <15 mm for *G. granti*; Thomas & Wroughton 1907). Two to four unit ‘bark’ advertisement call (Bearder *et al.* 1995).

Galagoides rondoensis. Sympatric in SETanzania. Small (ca. 60–70 g). Tail curled ‘bottle-brush’. ‘Double unit rolling call’ (Honess 1996a).

Distribution Endemic to Tanzania, Malawi, Zimbabwe and Mozambique. Zambeian Woodland and Coastal Forest Mosaic BZs. From Kilombero-Rufiji R., SE Tanzania, west to Udzungwa Mts and Mahale Mts (D. Moyer pers. comm.), south to the Limpopo R., S Mozambique and inland to S Malawi and extreme E Zimbabwe (Smithers & Lobão Tello 1976, Smithers 1983, Jenkins 1987, Honess 1996b, Kingdon 1997, Perkin 2000b, Butynski *et al.* 2006, Bearder & Karlsson 2009).



Galagoides granti

Habitat Inhabits natural, lowland evergreen and semi-evergreen forest, dry coastal forest, thicket and scrub (Thomas & Wroughton 1907, Smithers & Tello 1976, Honess 1996b, Lumsden & Masters 2001), as well as mist-fed evergreen forest on Rondo Plateau and dry semi-evergreen thicket on the Makonde Plateau, E Tanzania (Honess 1996b). An isolated population exists in Nambiga F. R., E Tanzania (08° 21' S, 36° 18' E), in ground-water-dependent lowland evergreen forest (Honess 1996b, Perkin 2000a). Evergreen forest (e.g. on Rondo Plateau) is uncommon throughout the range but coastal thicket is more widespread. Also in forest-cultivation.

Mean annual rainfall: 950 mm (Newala, Tanzania: Lumsden & Masters 2001) to 1100 mm (Rondo Plateau; Eriksen *et al.* 1994, Burgess & Clarke 2000). Temperature: 22–28 °C (Newala; Lumsden & Masters 2001), 11–32 °C (Rondo Plateau; Clarke 1995). Altitude: from near sea level (Ziwani) to 870 m (Rondo F. R.) (Honess 1996b, Honess & Bearder 1996) to, rarely, 1600 m (Lulanda; A. Perkin pers. comm.). In Mozambique up to 360 m (Smithers 1983).

Abundance Well distributed in evergreen and semi-evergreen forest and thicket of coastal areas of its range. Optimal habitat remains unclear. Encounters per hour for five sites were 3.8 (Rondo), 4.5 (Mtopwa), 4.5 (Noto), 4.9 (Namatimbili) and 1.2 (Lulanda) (Honess 1996, Rovero *et al.* 2009).

Adaptations Nocturnal and arboreal. An agile jumper, leaping between vertical supports, also uses quadrupedal climbing and walking or scurrying. Large independently mobile ears used in prey location. Observed urine-washing (Mtopwa: Honess 1996b). Choice of daytime sleeping sites likely to vary depending on availability. At Rondo F. R. and in type locality, tree-holes used (Thomas & Wroughton 1907, Honess 1996b, Bearder *et al.* 2003), which may be as high as 5.5 m. At Newala, associated with green, leafy nests (ca. 35 cm diameter) at ca. 3 m from the ground and possibly those made of liana fibre, leaves and twigs. Nests shared with as many as five conspecifics of mixed sex (Honess



Mozambique Dwarf Galago *Galagoides granti*.

1996b, Lumsden & Masters 2001), other galago species (*G. rondoensis*; Lumsden & Masters 2001), and even phased sharing with diurnal squirrels – indicating scarcity of nest-holes (Rondo; Honess 1996b).

Foraging and Food Omnivorous. *Galagoides granti* prefers denser parts of the understorey at 6–20 m. At Rondo, takes insects and fruits (Honess 1996b). Specimens collected at Newala had stomachs containing fruit, flower and insect remains (Lumsden & Masters 2001). In E Zimbabwe they were a persistent nuisance when small birds were being netted in the forest in the early evening, as several individuals congregated at the mist-nets to chew the heads off netted birds (Smithers 1983). Seen feeding, in a head-down position, on gum from a tree.

Social and Reproductive Behaviour Non-gregarious, except at sleeping sites. Up to six individuals may be in close proximity, but >90% of observations at night ($n = 130$) are solitary animals (Honess 1996b). The incremental call accounts for 78% of loud calls ($n = 773$). This call is often answered by conspecifics and is most frequently given in the first two hours after sunset and last two hours before sunrise; corresponding with emergence from, and gathering for, sleeping. A wide range of different calls are given, alone and in mixed sequences, indicating the importance of vocal communication (Honess 1996b). These include primary alarm calls such as the ‘buzz’ (‘single drawn out, fading unit’), ‘sweep-screech’ (‘single unit resembles a shorter, more intense buzz’), ‘screech’ (‘harsh, intense single unit, often given in a series’), ‘descending screech’ (‘series of screeches descending in volume and intensity’), ‘yap’ (‘short, dog-like, single unit, often given in series’) and ‘screech-grunt’ (‘as screech but followed by a quiet grunt that is often only audible at close range’) (Honess 1996b).

Reproduction and Population Structure Female with two foetuses recorded in Dec in southern Africa. Likely that young are

born during the warm wet summer months (Nov–Feb). Whether ♀♀ produce more than one litter per year is not known.

Predators, Parasites and Diseases Predators unknown but probably include larger snakes, owls, genets *Genetta* spp. and Two-spotted Palm Civets *Nandinia binotata*. Sometimes eaten by humans (Thomas & Wroughton 1907). Trombiculids recorded on the ear tragus (W. H. R. Lumsden in litt.). Thought, along with other galagos in East Africa, to act as an intermediate host for Yellow Fever (Haddow & Ellis 1964).

Conservation IUCN Category (2012): Least Concern. CITES (2012): Appendix II.

Higher population densities in mildly disturbed habitats and agriculture mosaics suggests no imminent extinction threat, locally or regionally. Remains vulnerable to extensive habitat reduction to meet fuel and agricultural demands of expanding human populations.

Measurements

Galagoides granti

HB: 153 (140–160) mm, $n = 12$

T: 230 (216–237) mm, $n = 12$

HF: 58 (54–63) mm, $n = 12$

E: 38 (36–43) mm, $n = 12$

Coguno and Tambarara, Mozambique. Specimens obtained by C. H. B. Grant during the Rudd Expedition and housed at BMNH. Coguno is the type locality for *G. granti* (Butynski *et al.* 2006). Sexes combined.

HB: 162 mm, $n = 10$

T: 232 (214–254) mm, $n = 10$

HF: 62 (59–63) mm, $n = 10$

E: 40 (38–41) mm, $n = 9$

WT: 165 (139–178) g, $n = 6$

Extreme E Zimbabwe (Smithers & Wilson 1979); sexes combined

HB: 164 (154–181) mm, $n = 3$

T: 214 (208–222) mm, $n = 3$

HF: 58 (58–59) mm, $n = 3$

E: 37, 38 mm, $n = 2$

WT: 136 (110–160) g, $n = 3$

Combined measurements for two ♂♂ and one ♀. Tanzania: Kichi Hills F. R. ($n = 2$) and Lulunda, Udzungwa Mts ($n = 1$) (A. Perkin pers. obs.)

GLS: 42 mm, $n = 17$

Localities not stated (Groves 2001); sexes combined

Key References Butynski *et al.* 2006; Courtenay & Bearder 1989; Honess 1996b; Perkin 2000b; Lumsden & Masters 2001.

Paul E. Honess, Simon K. Bearder & Thomas M. Butynski

Galagoides cocos KENYA COAST DWARF GALAGO (DIANI DWARF GALAGO)

Fr. Galago de Diani; Ger. Diani-Galago

Galagoides cocos (Heller, 1912). Smith. Misc. Col. 60: 1. Mazeras, Kenya.Kenya Coast Dwarf Galago *Galagoides cocos*.*Galagoides cocos*

45° angle from the vertical plane rather than upright. Dorsum buffy-brown. Chin, chest and ventrum greyish-white, but strong yellow or orange wash may be present due to plant stains obtained while scent-rubbing (De Jong & Butynski 2011). Tail same colour as dorsum with distal one-third dark buffy-brown in some. Penis with pinnate, robust spines over most of length. Penis enlarges slightly in middle (where largest spines are located) before tapering off to the tip. Glans penis does not protrude from baculum (Perkin 2007). Immatures like adults, but white nose-stripe often incomplete towards rhinarium and penile spines absent or small.

Taxonomy Monotypic species. The Kenya Coast Dwarf Galago was originally named *Galago moholi cocos*, then elevated to *Galago cocos*, then, for many years, considered a subspecies or synonym of the Zanzibar Dwarf Galago *Galago zanzibaricus*. On the basis of its distinct loud advertising call, penile morphology and facial markings, *G. cocos* recently revived as a species (Grubb *et al.* 2003, Butynski *et al.* 2006, Perkin 2007). As such, most literature dealing with the ecology and behaviour of the Kenya Coast Dwarf Galago prior to 2003 is under the name '*Galago zanzibaricus*' (e.g. Harcourt 1986a, Harcourt & Nash 1986a, b, Nash *et al.* 1989, Bearder *et al.* 1995). Synonyms: none. Chromosome number: not known.

Description Small, brown galago with distinctive 'incremental' advertising call. Sexes similar in size and colour. Muzzle long, pointed, with broad white streak continuing well above eyes. Eye-rings prominent, formed by dark skin that continues down sides of muzzle to form 'tear' marks at the base of the muzzle. Ears large, held ca.

Geographic Variation None recorded.

Similar Species

Galagoides zanzibaricus udzungwensis. Probably sympatric, or at least parapatric, in northern part of range in NE Tanzania (Butynski *et al.* 2006). Single unit 'rolling' advertising call distinctive (Bearder *et al.* 1995). Nose-stripe greyish-white, less well defined. Patch on either side of muzzle less dark and prominent. Ears more erect, shorter. Tail short, evenly haired. In coastal and lowland forests of E Tanzania (Butynski *et al.* 2006).

Galago senegalensis. Marginally sympatric (e.g. lower Tana R.). Larger (ca. 200 g). Loud 'woo' (or 'honk') advertising call distinctive. Dorsum grey or brownish-grey. Tail grey to brown, bushier towards distal end. In woodland and acacia bushland (Butynski & De Jong 2004, Butynski *et al.* 2006, De Jong & Butynski 2011).

Galago gallarum. Probably marginally sympatric in southern part of range. Larger (ca. 200 g). 'Trumpeting quack' advertising call

distinctive. Ears black front and back. Tail grey proximally, dark brown and longer haired distally. In *Acacia–Commiphora* bushland (Butynski & De Jong 2004, Butynski *et al.* 2006).

Distribution Endemic to coastal strip of Kenya and NE Tanzania. Perhaps in SE Somalia. Northern limit perhaps Juba R. or Shabeelle R., south coast of Somalia. Confirmed northern, eastern and inland limits presented in De Jong & Butynski (2011). Southwards through coastal Kenya, to Mgambo F. R. and Kilulu Hill F. R., extreme NE Tanzania. Largely confined to the coastal strip and gallery forests (e.g. those of the lower Tana R.) from 0 to 210 m, but there is one record for Nairobi at ca. 1850 m (Butynski *et al.* 2006), but this requires confirmation.

Habitat Dry, mixed, coastal forests and thickets, and flood-plain forests. Coastal Forest Mosaic BZ. Where *G. cocos* has been most studied (i.e. at Gedi and Diani Forests, Kenya) there is a fairly thick understorey, commonly including *Lecaniodiscus fraxinifolius*, *Fagara chalybea* and *Meyna tetraphylla* at Gede, and *Diospyros abyssinica*, *Grewia goetzeana*, *Lantana camara* and *Zizyphus mucronata* at Diani. Canopy in both areas at 15–20 m, dominated by *Combretum schumannii*, while others, including *Ficus* spp. and *Tamarindus indica*, are also common. Emergents reach to 25 m (e.g. *Adansonia digitata*, *Sterculia appendiculata* and *Lannea stuhlmannii*). Rainfall bimodal, with long rains Apr–Jun and short rains in Oct–Nov. Mean annual rainfall ca. 1040 mm (Harcourt & Nash 1986b). In acacia woodland where *G. senegalensis* is absent, such as north-east of Bodhei on the north coast of Kenya (De Jong & Butynski 2011).

Abundance Variable, about 170–180 ind/km² at Gedi and Diani, but at much lower densities at some sites (Harcourt & Nash 1986a).

Adaptations Nocturnal and arboreal. Spends day in tree hollows either alone or, more often, in groups of one adult ♂, one or two ♀♀ and their offspring (Harcourt & Nash 1986a, Bearder *et al.* 2003). Sleeping site use varies. In Diani a ♂ watched at dusk used 29 sites (n = 82), while one in Gedi used only seven sites (n = 96). Sleeping in groups may help thermoregulation in this small species, though temperatures do not drop below ca. 24 °C during the day. This is probably also a predator avoidance strategy (Harcourt & Nash 1986a, b). Insect prey is located by hearing and vision. Communication is through calling and, probably, olfaction.

Foraging and Food Omnivorous. Forages only at night, most frequently alone, and usually <5 m of the ground. Occasionally comes to the ground. Forages while moving on small branches (<5 cm diameter). Moves quadrupedally both in trees and on the ground. Jumps between supports, landing front feet first or quadrupedally. Mean distance travelled per night similar between ♀♀ (1708 m) and ♂♂ (1769 m) (Harcourt & Nash 1986b). Uses mouth and hands to catch insects. Based on analysis of faecal samples (n = 258), diet is ca. 70% invertebrates and ca. 30% fruit. Fruits eaten include *L. stuhlmanni*, *Monanthotaxis fornicata*, *Uvaria acuminata*, *Grewia* spp., *Phyllanthus* sp. and *Ficus* spp. The most frequently eaten invertebrates are beetles, orthopterans and centipedes, while spiders, ants, termites, caterpillars, millipedes and true bugs are also eaten (Harcourt & Nash 1986b). Passerine feathers found in a

faecal sample in Diani suggest that small birds are sometimes eaten (Harcourt 1984). Not observed eating gum naturally in the wild (Harcourt & Bearder 1989), but will eat gum when provisioned (Nash 1989).

Social and Reproductive Behaviour Social. Unlike other galagos studied to date, adult ♂♂ consistently sleep with the same one or two adult ♀♀ and their offspring. Night-time ranges of adult ♂♂ closely coincide with ranges of those adult ♀♀ with which they sleep. Home-ranges of adult ♂♂ overlap slightly (see Figure 1 in Harcourt & Nash 1986a) with those of neighbouring ♂♂. When adult ♂ leaves his territory (which happens rarely), increased calling and chases occur (Harcourt & Nash 1986a). At Gedi there is some indication that two classes of adult ♂♂ exist (dominants and subordinates) in the population as has been reported for Southern Lesser Galago *Galago moholi* (Bearder & Martin 1979). Same-age ♀♀ usually occupy almost exclusive home-ranges, but in some cases there is considerable overlap of ranges of two ♀♀. Females with overlapping ranges regularly sleep together and are probably related. Mean home-range size is 3.4 ha (1.8–5.1, n = 6) for adult ♂♂ and 1.9 ha (1.3–2.6, n = 8) for adult ♀♀. Young ♀♀ generally remain in their natal range, while ♂♂ disperse (Harcourt & Nash 1986a). Females leave their sleeping groups and sleep alone just before they give birth and for a few weeks afterwards (Harcourt 1986a). Infant carried in mother's mouth and 'parked' on a branch while she forages.

'Incremental' advertising call often, but not always, starts with a series of high-pitched, rapidly uttered, 'chirrup' followed by units arranged in phrases that are high in frequency and amplitude, and gradually become lower in amplitude. The number of units within each phrase typically increases 'incrementally'; often, phrases with same number of units are repeated. This call has a fundamental frequency of 0.8–1.2 kHz, with harmonic spectra visible up to the tenth or eleventh harmonic at 9.3 kHz, frequency range 0.65–11.15 kHz, range of unit frequency modulation 0.68–10.37 kHz (Courtney & Bearder 1989, Bearder *et al.* 1995, Butynski *et al.* 2006).

There is a peak of calling at the beginning and end of the night (Nash 1986, Butynski *et al.* 2006), and no sex difference in the rate of calling (Harcourt 1984). About half the calls are given in answer to a call or are answered (Harcourt 1984). A common alarm call is the 'buzz and rapid chatter'. This consists of an explosive buzz unit followed by a descending, rapid series of 15–20 units. Another alarm call, 'yaps and chirrups', consists of a series of high-pitched 'yap' units about a second or less apart interspersed with a rapid series of 'chirrup' units. *Galagoides cocos* gives contact calls at night to maintain cohesion between sleeping partners and has a morning reassembly call (Bearder *et al.* 2003).

Reproduction and Population Structure Females can give birth twice a year, with infants produced in Feb–Mar and late Aug–Oct (n = 10 at Diani) (Harcourt 1986a, Nash 1983). One ♂, born in captivity to an injured wild ♀, weighed 16.5 g at birth (Harcourt 1984, 1986a). Singletons are the rule, with occasional twins. Of 12 offspring with identified mothers at Diani, one ♀ may have had twins, giving the occurrence of multiple births as 9% (Harcourt 1986a). Infants move around independently at <1 month of age and are probably able to survive without the mother by 2 months of age

(Harcourt 1984). Females probably have their first offspring at ca. 12 months of age (Nash 1983, Harcourt & Nash 1986a). Gestation 120 days (Gucwinska & Gucwinska 1968). No data available on longevity.

Predators, Parasites and Diseases It is likely that genets *Genetta* spp., snakes, large owls *Bubo* spp. and monkeys *Cercopithecus* spp. prey on *G. cocos*, but there is no direct evidence of predation. *Galagoides cocos* gives alarm calls at genets, Puff Adders *Bitis arietans* (L. T. Nash pers. comm.) and snake skins (T. Butynski pers. comm.). No information on diseases and parasites.

Conservation IUCN Category (2012): Least Concern. CITES (2012): Appendix II.

Given the use of tangled undergrowth and its predominantly insectivorous diet, *G. cocos* does well in secondary vegetation and in areas of mixed cultivation where there are large trees (e.g. Coconut Palm *Cocos nucifera*, Mango *Mangifera indica* and Cashew Nut *Anacardium occi*) in which suitable sleeping sites can be found. Much of the forest on the coast of East Africa has been removed or greatly disturbed by logging, farming and tourism, but *G. cocos* continues to survive in such habitats – sometimes at high densities.

Measurements

Galagoides cocos

HB: 158 (142–183) mm, n = 46

T: 212 (182–230) mm, n = 38

HF: 54 (40–60) mm, n = 56

E: 31 (23–40) mm, n = 39

WT (♂♂): 150 (135–167) g, n = 36

WT (♀♀): 138 (117–172) g, n = 42

Butynski *et al.* (2006) compiled from specimens obtained at Gedi and Diani (n = 35), Mazeras (n = 8) and Arabuko-Sokoke F. R. (n = 2), Kenya, and East Usambara Mts, Tanzania (n = 1) by Hollister (1924), Harcourt & Nash (1986a) and A. Perkin (pers. obs.). No significant difference in linear body measurements for adult ♂♂ and ♀♀. As such, sexes combined. WT of adult ♂♂ and adult (non-pregnant) ♀♀ significantly different. As such, WT presented by sex (Harcourt Nash 1986a, C. S. Harcourt pers. obs., L. T. Nash pers. comm.).

GLS: 42 mm, n = 13

Several localities (Groves 2001); sexes combined

Key References Butynski *et al.* 2006; Harcourt 1984, 1986a; Harcourt & Bearder 1989; Harcourt & Nash 1986a, b.

Caroline S. Harcourt & Andrew W. Perkin

Galagoides demidovii DEMIDOFF'S DWARF GALAGO

Fr. Galago de Demidoff; Ger. Demidoff-Galago

Galagoides demidovii (G. Fischer, 1808). Comm. Soc. Phy. Med. Mosq. 1(1): 57. Senegal.



Demidoff's Dwarf Galago *Galagoides demidovii* adult.

Taxonomy Polytypic species. Often referred to as 'demidoff' (e.g. Jenkins 1987, Kingdon 1997, Groves 2001, 2005c). Grubb *et al.* (2003) argue for 'demidovii', maintaining that 'demidoff' is 'unavailable'. First placed in genus *Galago* (Fischer 1806, 1808), but Smith (1833) placed the smaller galagos in *Galagoides*. Schwarz (1931a) and some subsequent authors (Jenkins 1987, Groves 2001, 2005c) retained *Galago*, but Hill (1953), Bearder *et al.* (1995), Grubb *et al.* (2003), Masters *et al.* (2007), Oates (2011), De Jong & Butynski (2012) and others recognize *Galagoides*. Of the seven subspecies recognized by Hill (1953), two have been elevated to full species: Thomas's Dwarf Galago *Galagoides thomasi* (Elliot 1907, Olson 1979, Kingdon 1997, Groves 2001, 2005c, Grubb *et al.* 2003) and Mountain Dwarf Galago *Galagoides orinus* (Lawrence & Washburn 1936, Honess & Bearder 1996, Groves 2001, 2005c, Grubb *et al.* 2003). Five subspecies (*anomurus*, *demidovii*, *murinus*, *phasma*, *poensis*) were named based principally on pelage coloration (an often unreliable character trait in galagos) and their geographic range. Major synonyms: *anomurus*, *demidoff*, *medius*, *murinus*, *peli*, *phasma*, *poensis*, *pusillus*. Chromosome number: uncertain. Chromosome number may vary with site; 2n = 44 (Makokou, C. Gabon) and = 58 (Nigeria, Togo). This has led to the suggestion that there are at least two species within what is now referred to as *G. demidovii* (Stanyon *et al.* 1992, Groves 2001). Another possible, if not likely, explanation is that one or more of the specimens sampled was a *G. thomasi*.

Description Small, mouse-sized galago. One of Africa's two smallest primates. Phenotypic diversity high within and among populations. Adult ♀ like adult ♂, but probably slightly smaller. Limited data suggest that adult ♀ weights ca. 92% as much as adult ♂. Nose upturned with prominent white stripe. Eye-rings faint and variable. Ears relatively short. Dorsum medium to dark or reddish-brown, sometimes with greyish tones. Ventrums whitish, cream or yellowish. Tail not bushy, varies in colour: brown, reddish, dark grey or black. Species-specific loud (advertisement) call a distinctive long crescendo, which increases in volume, speed and pitch and given but once or twice per bout (Ambrose 1999).

Geographic Variation Poorly known (Hill 1953, Hill & Meester 1977, Jenkins 1987, Groves 2001). No consistent descriptions with diagnostic characters exist of subspecies. There is huge within-population variation in pelage colour and body size. Until the required detailed studies of vocalizations, behaviour, morphology and genetics are undertaken, the 'subspecies' listed here (Kingdon 1997) must be regarded as tentative and provisional (Grubb *et al.* 2003).

G. d. demidovii. Senegal to Niger R.

G. d. murinus. Niger R. to Congo R.

G. d. poensis. Endemic to Bioko I.

G. d. anomurus. Right bank of Congo R into Uganda.

G. d. phasma. Congo Basin, left bank of Congo R.

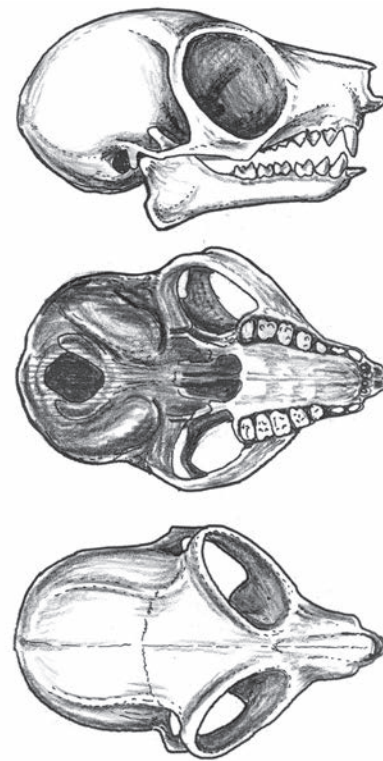
Similar Species

Galagoides thomasi. Broadly sympatric. Usually >5 m or more above the ground, often in the forest canopy. Runs and leaps on medium and large branches whereas *G. demidovii* scurries. Much more common in primary and old secondary forest. Crescendo call shorter and usually given at least three times per bout. Longer nose, longer ears (24 mm vs. 20 mm for *G. demidovii*). Pelage paler, longer and looser, with less contrast between dorsum and ventrum.

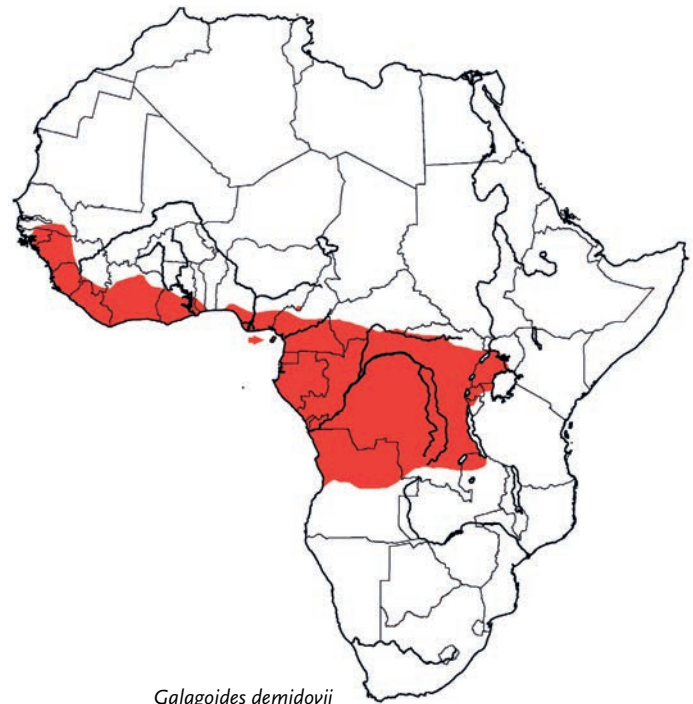
Galago matschiei. Sympatric in Uganda, probably also in E DR Congo. Much larger (200 g). Face mask well-demarcated. Ventrums pale grey. Tail dark grey. Ears more prominent. Nails keeled and pointed. Lacks 'crescendo' and 'buzz' loud calls. 'Churr' loud call repeated in sequences.

Distribution Rainforest and Afromontane–Afroalpine BZs. Endemic to the tropical forests of Africa from S Senegal southwards to Cameroon, Bioko I. and Rio Muni (Equatorial Guinea), Gabon, DR Congo and Angola, eastwards to L. Tanganyika, E DR Congo, Minziro Forest on west edge of L. Victoria, NW Tanzania, and Nile R., SE Uganda (Jenkins 1987, Nash *et al.* 1989, Kingdon 1997, Groves 2001, Ambrose 1999, 2006, Perkin & Bearder 2004).

Habitat Broad range of forest types, including evergreen, deciduous, semi-deciduous, littoral, gallery, marsh and riverine. Found along river banks, tree-fall zones, logged forest, roadsides and cultivated areas. Appears to prefer lowland secondary forest (Ambrose 1999). Present from sea level to >2000 m on Bioko I. (T. Butynski pers. obs.) and to >2000 m on Itombwe Massif, E DR Congo (Omari *et al.* 1999). Occupies fine-branch niche (± 1 cm diameter) in low, dense, secondary growth (Ambrose 1999). On Bioko I., at Moka, present within pure stands of Elephant Grass *Pennisetum purpureum*,



Lateral, palatal and dorsal views of skull of Demidoff's Dwarf Galago *Galagoides demidovii* adult.



Galagoides demidovii

>10 m from edge of montane forest at 1400 m, and sometimes common in mix of *P. purpureum*, Bracken Fern *Pteridium aquilinum*, *Harungana madagascariensis*, *Trema orientalis* and *Macaranga occidentalis* (T. Butynski pers. obs.). Of 18 encounters with *G. demidovii* at Moka, 39% in Elephant Grass, 33% in Bracken Fern, 28% in secondary forest and none in primary forest (Croce 2009). On Bioko I., present where mean annual rainfall is 2000–10,000 mm (T. Butynski pers.

obs.). At Makokou, C. Gabon (500 m asl), mean annual rainfall ca. 1700 mm, monthly mean minimum temperature is ca. 21–24 °C and monthly mean maximum temperature is ca. 26–30 °C (Charles-Dominique 1977). *Galagoides demidovii* present at 400 m asl on north bank of Congo R. at Lokutu, NC DR Congo, where mean annual temperature ca. 25 °C, no monthly mean temperature <18 °C, and annual rainfall is 1400–2200 mm (Butynski & McCullough 2007).

Abundance Often common in heavily disturbed habitats and on edge of forest. At Moka, Bioko I., *G. demidovii* encountered at 0.4 ind/h (Ambrose & Perkin 2000). Another study at Moka encountered 0.6 ind/h and 0.6 ind/km (Croce 2009). Other encounter rates are 1.3 ind/h in Taï N. P., Côte d'Ivoire; 0.2 ind/h on Mt Cameroon (Ambrose 1999); 1.6 ind/h in Korup N. P., Cameroon (Bearder & Honess 1992); 0.9 ind/h in Okomu N. P., Nigeria (Bearder & Oates 2009b). Ambrose (2002, 2006) obtained the following encounter and crescendo loud-call rates for *G. demidovii* from three sites across Uganda:

Mabira F. R., SC Uganda: 0.57 ind/h and 0.26 calls/h.

Mpanga F. R., SC Uganda: 0.16 ind/h. No calls heard.

Buhoma, Bwindi N. P., extreme SW Uganda: 0.33 ind/h and 0.20 calls/h.

Adaptations Nocturnal and arboreal. Rapid, darting (i.e. scurrying) movements on fine to medium-sized branches (± 1 cm diameter), usually below 5 m in dense secondary growth. Initiates leaps with hindlimbs, lands with forelimbs. Oval-shaped, ca. 25 cm diameter nests of leaves or bark constructed for breeding, especially in the wet season (Bearder & Honess 1992, Bearder *et al.* 2003). Nests placed <5 m above ground in very dense vegetation. Not known to use nest holes. Mother carries young in her mouth.

Foraging and Food Omnivorous. Insects chased and grabbed with one or both hands. Able to hang bipedally when foraging or feeding. Fruit picked by mouth or hand. At Makokou, diet mainly invertebrates (mainly beetles, moths and caterpillars) with some fruit, gum, leaves and buds (Charles-Dominique 1977). At Moka, often on the ground or <0.5 m above the ground, especially when foraging in Bracken Fern and Elephant Grass (T. Butynski pers. obs.). At Moka, mean height above ground 1.5 m (0–4 m, n = 18; Croce 2009), although forages to >12 m (Ambrose & Perkin 2000).

Social and Reproductive Behaviour Non-gregarious. Females have overlapping home-ranges of 0.8 ha in Gabon. Home-range of dominant ♂♂ vary 0.5–2.7 ha, usually overlap with several ♀♀. Smaller ♂♂ tolerated within range of dominant ♂ while peripheral ♂♂ occupy marginal ranges. Males leave natal area at puberty. Sleeps in groups of 2–10, huddled in dense vegetation or aggregates of leaf nests. Nest occupants usually ♀♀ with offspring, occasionally adult ♂ present (Charles-Dominique 1977). Loud (advertisement) call; long 'crescendos', which increase in volume, speed and pitch, given once or twice per bout. Used as contact, spacing and gathering call. 'Chips' produced in short phrases in the

context of mild alarm. Explosive 'buzz' for contact avoidance. 'Chips' that speed and slow are given when highly alarmed (Ambrose 1999).

Reproduction and Population Structure Females give birth once a year, usually to singleton, occasionally twins. Gestation 110–114 days. Weaned at two months, sexually mature at six months. Primary breeding season varies by region. Births C Gabon throughout the year, birth peak Jan–Apr, when fruit and insects are most abundant (Charles-Dominique 1977). Birth peaks DR Congo Sep–Oct and Jan–Feb (Vincent 1969). Infants and juveniles observed in S Cameroon in Jun, in S Gabon in Jul (Ambrose 1999). Longevity >12 years in captivity (Charles-Dominique 1977).

Predators, Parasites and Diseases Poorly known, however, likely large owls *Bubo* spp., genets *Genetta* spp., linsangs *Poiana* spp., mongooses, Two-spotted Palm Civets *Nandinia binotata* and snakes. Blood parasites in Cameroon include malarial *Plasmodium falciparum*, filarial worm *Mansonella perstans* and *Leishmania major*, although no pathological symptoms observed (E. Pimley pers. comm.).

Conservation IUCN Category (2012): Least Concern. CITES (2012): Appendix II.

Widespread across West and central Africa and patchily common. Thrives in disturbed forests and able to occupy areas affected by human activity (Charles-Dominique 1977, Ambrose 2006). If *G. d. poensis* is a valid subspecies, and endemic to Bioko I., then its extent of occurrence is <1500 km² (T. Butynski pers. obs.).

Measurements

Galagoides demidovii

HB (♂♂): 159 (140–169) mm, n = 6

HB (♀♀): 150 (143–155) mm, n = 3

T (♂♂): 175 (160–185) mm, n = 6

T (♀♀): 165 (157–175) mm, n = 3

HF (♂♂): 44 (40–48) mm, n = 6

HF (♀♀): 45 (42–48) mm, n = 3

E (♂♂): 21 (17–24) mm, n = 6

E (♀♀): 15 (12–18) mm, n = 3

WT (♂♂): 60 (52–72) g, n = 17

WT (♀♀): 55 (45–68) g, n = 16

Centre International Recherche Medicale de France (CIRMF), Franceville, Gabon (Ambrose 1999)

HB: 129 (73–155) mm, n = 200

T: 179 (110–215) mm, n = 199

HF: 46 (35–60) mm, n = 191

E: 24 (14–35) mm, n = 180

WT: 70 (44–97) g, n = 49

Numerous locations (Olson & Nash 2002); sexes combined

Key References Ambrose 1999, 2006; Charles-Dominique 1977; Hill 1953; Jenkins 1987; Oates 2011; Vincent 1969.

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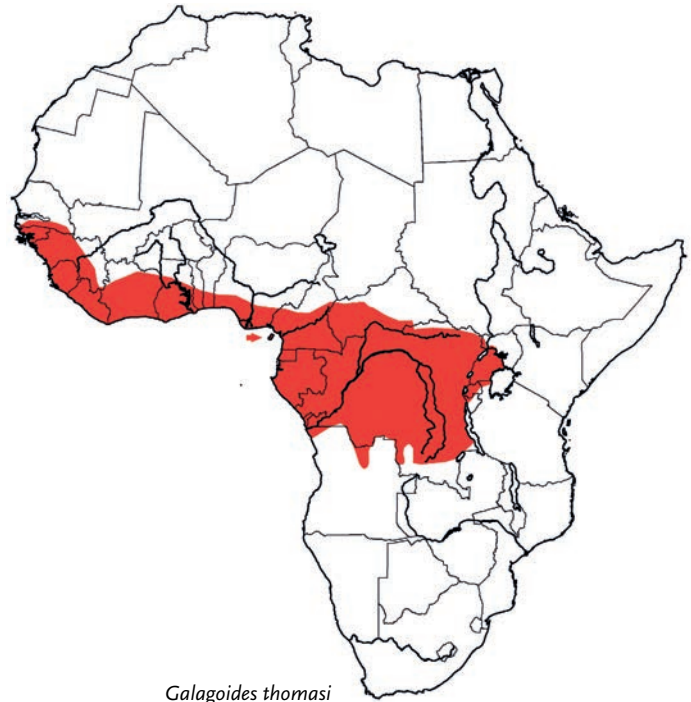
Galagoides thomasi THOMAS'S DWARF GALAGO

Fr. Galago de Thomas; Ger. Thomas-Galago

Galagoides thomasi (Elliot, 1907). Ann. Mag. Nat. Hist., ser. 7, 20: 189. Beni, DR Congo.Thomas's Dwarf Galago *Galagoides thomasi* adult.

Taxonomy Monotypic species. Elliot (1907) described Thomas's Dwarf Galago as a species, but subsequently this taxon regarded as a subspecies of Demidoff's Dwarf Galago *Galagoides demidovii*. Hill (1953) remarked that *G. d. thomasi* was a distinctive subspecies due to its larger body size and longer, looser fur. Olson (1979) resurrected *thomasi* to full species based on its morphology and sympatry with *G. demidovii*. Synonyms: none. Chromosome number: not known. Chromosome research on some specimens identified as *G. demidovii* may have, in fact, been on *G. thomasi*. This might account for the discrepancy in chromosome (2n) numbers (i.e. 44 vs. 58) reported for *G. demidovii* (Stanyon *et al.* 1992, Romagno 2001).

Description Small (ca. 100 g) galago usually found between 12–20 m in forest canopy. Diagnostic short 'crescendo' loud-call that rapidly increases in speed and pitch, usually repeated at least three times and often in sequences lasting several minutes. Muzzle comparatively long, often with a pale nose-stripe. Sexes similar in colour and pattern of pelage. Eye-rings variable; in some populations fine and indistinct, in others broad, forming a dark mask. Pale nose-stripe not sharply demarcated from the dark forehead and muzzle (as in *G. demidovii*). Dorsum dark to light brown. Ventrums slightly lighter

*Galagoides thomasi*

brown than dorsum in many populations. Pelage colour, however, strongly influenced by moult, being more ashy just before moult and darker just after. Outer limbs, hands and feet similar to dorsum. Tail long, not bushy, same colour as dorsum or slightly darker brown. Pelage overall darker, longer and looser than *G. demidovii*.

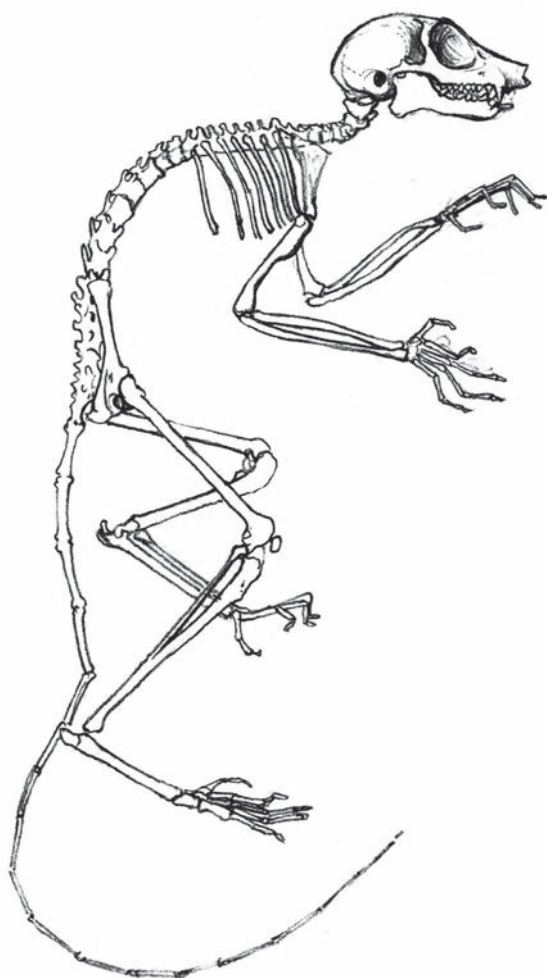
Geographic Variation Exceptionally uniform phenotypically, behaviourally and vocally. This is as expected for a relatively abundant species with an apparently continuous gene-pool. Ventrums orange in Cameroon, yellowish in DR Congo.

Similar Species

Galagoides demidovii. Broadly sympatric. Prefers undergrowth <5 m, often in secondary growth and on forest edge. Scurries on fine branches (usually <1 cm diameter). 'Crescendo' call longer and usually given but once or twice per bout. Nose pointed and upturned. Ventrums white, cream or yellow. Pelage darker, shorter and less loose, with more contrast in colour between dorsum and ventrum. Penile morphology diagnostic (Wickings *et al.* 1998).

Galago matschiei. Sympatric in Uganda, and probably also in DR Congo. Much larger (200 g). Face mask well-demarcated. Ventrums pale grey. Tail dark grey. Ears more prominent. Nails keeled and pointed. Lacks 'crescendo' and 'buzz' loud calls. 'Churr' loud call repeated in sequences.

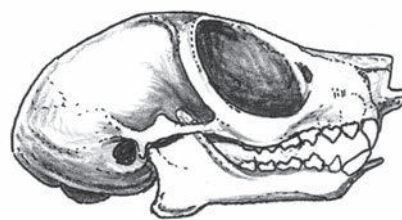
Distribution Endemic to central Africa and West Africa. Rainforest and Afromontane–Afroalpine BZs. Distribution limits uncertain, but most likely through West Africa from Nigeria to



Thomas's Dwarf Galago *Galagoides thomasi*.

at least Côte d'Ivoire (Ambrose 1999), and perhaps as far west as Senegal (Burnham & Navaza-Leon 1998). Bioko I., Equatorial Guinea (Ambrose & Perkin 2000). From Cameroon and Gabon, southwards to N Angola and N Zambia, eastwards to L. Tanganyika, E DR Congo, Minziro Forest on west edge of L. Victoria, NW Tanzania, and Nile R., SE Uganda (Nash *et al.* 1989, Kingdon 1997, Ambrose 1999, 2006, Perkin & Bearder 2004).

Habitat Primary and secondary lowland to montane forest: evergreen, deciduous, semi-deciduous, littoral, gallery, marsh and riverine forests. Occupies plantations and farms. Prefers primary montane forest but can occur anywhere where sufficient trees remain. *Galagoides thomasi* at Moka, Bioko I., appears to differ from *G. demidovii* in that it has yet to be found in Bracken Fern *Pteridium aquilinum* or Elephant Grass *Pennisetum purpureum* (T. Butynski pers. obs.). Lower altitudinal limit poorly known, but to at least 400 m at Makokou (Charles-Dominique 1977, Ambrose 1999). Occurs >2000 m on Mt Cameroon, W Cameroon (Ambrose 1999), Pico Basile N. P., Bioko I. (T. Butynski pers. obs.) and Itombwe Massif, E DR Congo (Omari *et al.* 1999). To >2350 m in Bwindi Impenetrable N. P., SW Uganda (T. Butynski pers. obs.), and to >2690 m on Mt Tshiaberimu, E DR Congo (Sarmiento & Butynski 1997). Mean annual rainfall over geographic range from ca. 1500 to >4000 mm (T. Butynski pers. obs.).



Lateral view of skull of Thomas's Dwarf Galago *Galagoides thomasi* adult.

Abundance Locally common but patchy in distribution. Reaches highest density in montane forest and old (tall) secondary forest. Density estimates absent. At Moka, Bioko I., encountered at rate of 0.2 animals/h ($n = 9$; Ambrose & Perkin 2000). Another study at Moka encountered 0.3 animals/h and 0.3 animals/km of transect ($n = 13$; Croce 2009). Other encounter rates are 1.9 ind/km in Korup N. P., Cameroon (Bearder & Honess 1992) and 3.0 ind/h in Okomu N. P., Nigeria (Bearder & Oates 2009b).

Ambrose (2002, 2006) recorded the following encounter and crescendo loud-call rates for *G. thomasi* for seven sites across Uganda from the left bank of the Nile R. to near the border with DR Congo (range 0.10–2.00 ind/h; 0.00–1.33 calls/h):

Mabira F. R., SC Uganda: 0.42 ind/h ($n = 19$) and 0.13 calls/h ($n = 6$).

Mpanga F. R., SC Uganda: 0.46 ind/h ($n = 14$) and 0.23 calls/h ($n = 7$).

Rubongo, Murchison Falls N. P., CW Uganda: 2.00 ind/h ($n = 5$) and 0.80 calls/h ($n = 2$).

Pabidi, Budongo F. R., CW Uganda: 2.00 ind/h ($n = 3$) and 1.33 calls/h ($n = 2$).

Buhoma, Bwindi N. P., extreme SW Uganda: 0.10 ind/h ($n = 5$). No calls heard.

Kanyanchu, Kibale N. P., SW Uganda: 0.66 ind/h ($n = 15$) and 0.53 calls/h ($n = 12$).

Echuya F. R., extreme SW Uganda: 0.10 ind/h ($n = 2$) and 0.05 calls/h ($n = 1$).

Adaptations Nocturnal and arboreal. In Kibale N. P., SW Uganda, *G. thomasi* emphasizes fast and slow arboreal quadrupedalism (35%) and leaping (23%) in its locomotor repertoire ($n = 263$). Vertical clinging accounts for 54% of postures ($n = 37$). Small (<5 cm circumference) supports used 76% of time ($n = 308$). Oblique supports used 49% of time, horizontal supports 28% and vertical supports 24% ($n = 251$; Off & Gebo 2005). Can make rapid movements, mainly when agitated, and will frequently ascend and descend, leaping up to 1.8 m between supports (Ambrose 1999). Like other galagos, urine-washes and marks its surroundings with anogenital and other glandular secretions. Fluctuating intensities of yellow skin secretions from the bare face, ears, hands, feet and heels have been tentatively correlated with sexual activity (Kingdon 1997). Commonly sleeps in self-made nests in Uganda. Occasionally occupies natural crevices or tree holes, which they line with fresh leaves (J. Kingdon pers. comm.).

Foraging and Food Omnivorous. Diet in Uganda contained insects (78%), gum or resin (18%), and fruit and seeds (4%). Insects



Thomas's Dwarf Galago *Galagoides thomasi*.

most frequently eaten are *Coleoptera*, *Orthoptera* and *Hymenoptera*, however there is evidence of seasonal changes in diet (Kingdon 1971). *Galagoides thomasi* fed almost exclusively on caterpillars, which were abundant during Mar–Apr. Crickets were the principal food in Dec. Forages by running rapidly and leaping on medium-size and large branches with its back legs doubled up beneath the belly (Kingdon 1971, Oates 2011). Insects caught by a pounce and rapid grab with both hands. Able to hang bipedally when catching or eating food. Where sympatric with *G. demidovii*, usually >10 m above ground and often >20 m (Ambrose 1999, Bearder & Oates 2009a, b). At Moka, mean height during one study was 10.4 m (4–18, $n = 11$; Croce 2009) and in another study all nine animals encountered were >5 m (Ambrose & Perkin 2000). Expected to use lower strata more often where *G. demidovii* is absent, such as in Kibale N. P.; lower canopy 28% of observations, mid-canopy 63% and upper canopy 9% ($n = 250$; Off & Gebo 2005).

Social and Reproductive Behaviour Mainly solitary while foraging but maintains occasional vocal contact with conspecifics; 79% alone, 16% two individuals, 2% three individuals, 2% four individuals, 1% five individuals ($n = 142$; Ambrose 1999). Kingdon (1971, 1997) characterized this as a social species ordered into ‘clans’ of up to 12 animals in which only gravid ♀♀ separate out from their group in order to give birth in a ‘singleton nest’. Sleeps communally, with up to five individuals gathering at dawn in Cameroon (Ambrose 1999, Bearder *et al.* 2003). In Uganda, social groups of 8–12 animals occur. Even or near-even adult sex ratios and may represent adult ♂♂–♀♀ pairs supplemented by recent offspring. Adults, especially older ♂♂, frequently have wounds on face and ears. Aggression and appeasement might be partially mediated by olfactory cues emanating from skin secretions, glands and excreta. Sleeps in dense vegetation, but leaf nests are the norm in Uganda (Kingdon 1971). These nests are made at various levels in the forest strata and are either augmented with new leaves or made afresh each day. Nests made in the wet season are often lodged in tree forks, larger, and used longer compared to dry season nests (Kingdon 1997). In Kibale N. P., Uganda, nests sometimes constructed inside old nests of Robust Chimpanzees *Pan troglodytes* (Llorente *et al.* 2003).

Vocal repertoire distinct. Contact calls are short ‘crescendos’, which rapidly increase in speed and pitch, usually repeated at least three times in quick succession and often occur in sequences lasting several minutes. ‘Trills’ are associated with conspecifics meeting at dawn and can be characterized as assembly calls. Rapid, loud ‘chips’ are given in the context of mild alarm, usually in long sequences for about 30 min (Ambrose 1999). High intensity alarm calls include rapid ‘chips’ in discrete phrases. Rapid and rhythmical ‘chips’ are produced, often interspersed with ‘grunts’ and ‘buzzes’ (Ambrose 1999). Lives >10 years in captivity (Kingdon 1971).

Reproduction and Population Structure Kingdon (1971) reports a poorly defined mating peak in Uganda during Aug, and a discernible birth peak (five records) in Dec–Feb (the driest time of year). These are, however, extrapolated births and adult ♀♀ were never recorded pregnant or nursing. Nine records of subadult animals Feb–Mar support the likelihood of a birth peak Dec–Jan in Uganda. J. Kingdon (pers. comm.) observed mothers carrying infants both in their mouth (sometimes while making long jumps) and by clinging to



Thomas's Dwarf Galago *Galagoides thomasi* adult.

the mother's ventrum. At two weeks the infant is active and at three weeks makes short jumps (J. Kingdon pers. comm.). At this time infants are able to feed while hanging upside down from a branch, run along branches using four limbs, and defend themselves with open-mouth threats and bites. At four weeks the juvenile transfers urine to the hindfeet after catching it in the hands and ambitious leaps are made (Kingdon 1971). Young weaned by six weeks but continue to request and grab food from mother. J. Kingdon (pers. comm.) never saw captive mothers actively feed their young. At nine weeks the young are independent and approximately adult in size; ♀♀ fiercely repel their young at this age (Kingdon 1971). Charles-Dominique (1972) noted that the infant-to-mother relocation call transmutes into the dawn adult call that aids regrouping. Although the study in which his observations were made did not discriminate between *G. thomasi* and *G. demidovii*, it is likely that this detail concerns *G. thomasi*.

Gestation ca. 110 days (Blackwell 1969, possibly referring to what was then regarded as *G. d. thomasi*). There is an interest in the reproductive physiology of *G. thomasi* since Hill (1953) reported that the zygote uniquely implanted deep in the mucous lining of the uterus. Birth weight estimated ca. 25 g, head–body length 75 mm and tail length 90 mm (J. Kingdon pers. comm.). Birth-weights likely to depend on single or twin birth. Single young are about as frequent as twins. Sex ratios appear to be relatively consistent at 1 : 1, both at birth and among adults.

Predators, Parasites and Diseases Poorly known, however, likely to be consistent with *G. demidovii*. Genets *Genetta* spp., Two-spotted Palm Civets *Nandinia binotata*, linsangs *Poiana* spp., forest hawks and large owls *Bubo* spp. are potential predators. Small galagos preyed upon by Blue Monkeys *Cercopithecus mitis stuhlmanni* (Butynski 1982a) and Black-and-white Casqued Hornbills *Ceratogymna subcylindricus* (Kalina 1988) in Kibale Forest, SW Uganda, are probably of this species. Fraser's Eagle-owl *Bubo poensis* is broadly sympatric with both *G. thomasi* and *G. demidovii*. When *B. poensis* is detected, *G. thomasi* give long bouts of loud alarm calls (T. Butynski pers. obs.). It is likely that *B. poensis* is a major predator both of *G. thomasi* and *G. demidovii*. Because *G. thomasi* respond to the alarm calls of other galagos, as well as to their own alarm calls, there is a strong implication that this small, solitary forager is vulnerable to predation (Ambrose 1999).

Galagos, thought to be *G. thomasi*, have natural resistance to Yellow Fever virus (Bugher 1951, Simpson 1965). This discovery was of considerable medical significance because Yellow Fever is a ‘canopy



Thomas's Dwarf Galago *Galagoides thomasi* adult.

disease' that is extremely dangerous to humans, especially those living close to the forest edge. Canopy mosquito vectors probably have the opportunity to transmit this virus from galagos and monkeys to humans.

Conservation IUCN Category (2012): Least Concern. CITES (2012): Appendix II.

One of the most widely distributed and adaptable of all galagos.

Measurements

Galagoides thomasi

HB (♀): 174 mm, n = 1

T (♀): 165 mm, n = 1

HF (♀): 49 mm, n = 1

E (♀): 21 mm, n = 1

WT (♂♂): 82 (74–88) g, n = 6

WT (♀♀): 75 (60–85) g, n = 6

Centre Internationale Recherche Medicales de France (CIRMF), Franceville, Gabon (Ambrose 1999)

HB: 146 (123–166) mm, n = 47

T: 195 (150–223) mm, n = 46

HF: 52 (39–58) mm, n = 46

E: 29 (23–33) mm, n = 46

WT: 99 (55–149) g, n = 99

Numerous locations (Olson & Nash 2002); sexes combined

Key References Ambrose 1999, 2006; Kingdon (1971); Oates 2011; Off & Gebo 2005.

Lesley Ambrose & Thomas M. Butynski

Glossary

abbrev. = abbreviation

adj. = adjective

cf. = *confer*, compare with; as opposed to

Lat. = Latin

pl. = plural

q.v. = *quod vide*, 'which see' (used after a word or term that appears elsewhere in the glossary)

adult: physically and reproductively mature individual.

afroalpine: habitats and/or vegetation occurring above the treeline on African mountains. Includes montane grassland, heathlands and wetlands.

afromontane: mountainous regions in Africa, e.g. afromontane forests and afromontane grasslands.

agouti: even mixture of pale- and dark-tipped hairs on the pelage, creating a grizzled, speckled or 'pepper and salt' appearance. Hairs with a specific sequence of alternating pale and dark bands creating a grizzled appearance.

Albertine Rift Valley: *see* Rift Valley (*q.v.*).

allele: alternative form of a gene. A diploid organism carries two alleles (which may be same or different) for each gene locus. At any one locus, there may be several possible alleles (although only two are present in a single organism).

allogrooming: reciprocal cleaning of the pelage.

allopatry (*adj.* **allopatric**): situation where populations of the same or different species have non-overlapping geographic ranges; refers also to populations of the same, or different, species that are geographically separated. *cf.* sympatry (*q.v.*); syntopy (*q.v.*).

anterior: of, or towards the front end of an animal.

anthropophilic: loving or thriving with humans; inhabiting domiciles; thriving in habitats substantially modified by humans (e.g. towns, farmlands).

arboreal: living mainly above the ground in trees and shrubs. *cf.* terrestrial (*q.v.*).

association: grouping of two or more species that travel and/or feed together.

auditory bulla (*pl.* **bullae**): bony structure encapsulating the middle and inner ear, situated on the ventral surface of the skull. Often greatly inflated. Sometimes referred to as tympanic bulla.

autosome: any chromosome other than the sex chromosomes.

baculum (*pl.* **bacula**, *adj.* **bacular**): os penis, or penis bone, which supports the penis in some mammals.

bicuspid: having two points or cusps (particularly of teeth).

bifid: divided by a shallow notch.

biomass: sum of the weights of the organisms in a particular area.

bipedal: body supported by the two hindlimbs; movement not using the forelimbs.

braincase (= **cranium**): that part of the skull housing the brain; the part of the skull posterior to the front line of the orbits.

buccal: cheek side of a tooth.

bushmeat: meat for human consumption derived from wild animals.

bushveld: savanna vegetation type characterized by a grassy ground layer and a moderately dense upper layer of shrubs and scattered trees.

BZ: (*abbrev.*) Biotic Zone.

C or **c**: (*abbrev.*) canine tooth; upper case denotes adult dentition, lower case denotes deciduous dentition (milk teeth). *See also* canine.

c.u.: (*Lat.* *cum unguis* = with nail) measurement of the hindfoot when length of the nail on the claw is included in the measurement. Usually hindfoot is measured without the claw because claws may be broken or worn. When length of claw is included, it is conventional to record as 'HF c.u.'. *cf.* s.u. (*q.v.*).

canine: tooth posterior to the incisors and anterior to the premolars that is usually elongated and pointed.

canopy: upper forest level, which receives the most sunlight. May be continuous or have gaps or taller emergent trees.

carnivore: animal that primarily eats flesh of other animals.

carrying capacity: maximum population size that can be sustained by the available resources in the environment.

caudal: tail; toward the tail.

cecum: saclike appendage between the small and large intestines.

central Africa: Cameroon (south of the Sanaga R.), Central African Republic (but only south of ca. 7° N), Equatorial Guinea, Gabon, DR Congo (except SE). Mainly rainforest habitats and rainforest–savanna mosaics.

cf. (in general usage): compare or compare with. In the context of descriptions, implies a difference or contrast: e.g. 'In *T. niveiventer*, ventral pelage white (cf. *T. thersites* in which the ventral pelage is dark brown).'

cf. (in taxonomy): precedes the specific name if there is uncertainty in the assignment.

cheekteeth: premolar (*q.v.*) and molar (*q.v.*) teeth combined.

cheek-pouches: pair of deep pouches extending from the cheeks into the neck skin. Used for temporary storage of food.

chromosome: one of the thread-like bodies within the nucleus of a cell, that carries the genes (genetic material) in linear order; each chromosome is composed of one long molecule of DNA (and two long molecules at cell division). Chromosomes occur in pairs (one from each parent) and are visible as rod-like bodies in cells that are dividing. The total number of chromosomes in a cell is expressed as the diploid number (2n).

cingulum (*pl.* **cingula**): ridge around the base of the crown of a tooth.

circumgenital: around the genitalia.

circumocular ring: ring around the eye.

clade: branch of a phylogenetic tree containing the set of all organisms descended from a common ancestor.

cladistic (analysis): methodology that provides a classification in which organisms are grouped in terms of the time when they had a common ancestor.

cline (*adj.* **clinal**): in context of geographic variation, a gradual

and sequential change of a character(s) without a significant break such as would justify division into subspecies or species.

comparatively: used in the context of describing the size of one character compared with the size of the same character in a different species. Sizes described as small, medium or large (if range is divided into three) or very small, small, medium, large, very large (if range is divided into five). *cf.* relatively (*q.v.*).

competitive exclusion: principle that two species cannot indefinitely occupy the same ecological niche.

condylar process: process at the posterior upper corner of the mandible, which forms the lower hinge of the jaw articulation; fits into the glenoid fossa of the skull.

condyle: rounded process on a bone, that articulates with a socket-like concavity in another bone.

congeneric: belonging to the same genus.

conspecific: belonging to the same species.

convergence: evolution of similar characteristics in unrelated animals as a result of adaptation to similar environmental conditions or for similar function.

coprophagy: eating of faeces.

copulatory plug: plug formed in the vagina of the female after copulation; formed from seminal fluids of the male. Prevents or reduces the chance of sperm from another male(s) entering the female reproductive tract if the female copulates again soon after copulation with the first male.

core area: part of the home-range that is used most intensively.

coronoid process: angular pointed process on the upper margin of the mandible, situated anteriorly to the condylar process (*q.v.*); does not participate in the jaw articulation.

corridor: broad and more or less continuous connection between adjacent land masses or habitat types that allows for dispersal of organisms between adjacent areas.

craniodental: skull and teeth.

cranium: that part of the skull housing the brain. Also called braincase.

crepuscular: at, of, twilight, when light intensity is higher than at night but lower than during the day. *cf.* diurnal (*q.v.*); nocturnal (*q.v.*).

crown: (1) top of head; (2) exposed part of a tooth (visible above gum), especially the grinding surface.

cryptic: hidden, inconspicuous, difficult to detect. Usually referring to external colouration and markings, but also behaviour.

cursorial: adapted for running.

cusp (*adj.* **cuspidate**): prominence or sharp point, such as on the occlusal surface of some teeth.

Dahomey Gap: geographic region where savanna extends southwards to the West African coast in E Ghana, Togo, Benin (formerly Dahomey) and extreme SW Nigeria. The presence of savanna forms a break (or gap) in the extensive Rainforest Biotic Zone, that extends along the West Africa coast from Sierra Leone to Cameroon. The Dahomey Gap is an important biogeographical barrier separating the faunas to the east and west of the Gap.

day-range: distance travelled during 1 day.

dental formula: simple numerical method of denoting the number of incisor (I), canine (C), premolar (P) and molar (M) teeth on one side of the upper jaw and lower jaw, and the total number of teeth. For example, the dental formula of a primitive mammal

is $I^{3/3}, C^{1/1}, P^{4/4}, M^{3/3} = 44$, which means there are three incisors, one canine, four premolars and three molars on each side of the upper jaw and also the lower jaw, making a total of 44 teeth. The formula may also be expressed in the form $^{3143}/_{3143} = 44$. Each incisor, premolar and molar is numbered according to its position in the tooth row; superscript numbers indicate upper jaw, subscript numbers indicate lower jaw (mandible), e.g. P^4 (upper fourth premolar), M_2 (lower second molar).

diagnostic: distinguishing characteristic, e.g. diagnostic features of a group of organisms.

dichromatism: condition in which members of a species show one of only two distinct colours or colour-patterns.

digit: any finger or toe.

diphyly: derivation of a taxon from two separate lines of descent. *cf.* monophyly (*q.v.*).

diploid number (2n): total number of chromosomes (including sex chromosomes) in a somatic cell of an organism.

disjunct: distinctly separate or discontinuous ranges in which one or more populations are separated from other populations by sufficient distance to prevent gene flow between them.

dispersal: one-way movement or spreading of organisms from the natal area to new areas.

display: relatively conspicuous pattern of behaviour that conveys specific information to others, usually to members of the same species; can involve visual and/or vocal elements, as in threat, courtship or greeting. A behaviour pattern that has been modified (ritualized) by evolution to transmit information by a sender to a receiver.

distal: end of any structure farthest away from the mid-line of the body or farthest from the point of attachment. *cf.* proximal (*q.v.*).

diurnal: at, active in, daytime; when light intensity is high. *cf.* crepuscular (*q.v.*); nocturnal (*q.v.*).

DNA: (*abbrev.*) deoxyribonucleic acid; the very large self-replicating molecule that carries the genetic information of a chromosome; each molecule is composed of two complementary chains of DNA.

dorsal: back or upper surface (opposite of ventral).

dorsoventral (dorsoventrally): from dorsal to ventral surface; from back to belly of an animal.

dorsum: dorsal surface of an animal.

E: length of external (outer) ear (= pinna), measured from tip of ear to the posterior point of the ear conch). Length and shape usually affected by preservation.

East Africa: Kenya, Uganda, Rwanda, Burundi and Tanzania.

eastern Africa: SE Sudan, Ethiopia, Eritrea, Djibouti, Somalia, Kenya, Uganda, Rwanda, Burundi, Tanzania, Malawi (but only south of L. Malawi and east of the Shire R. Valley) and Mozambique (but only east of Malawi and north of the Zambezi R.).

ecological niche: overall pattern of resource use by a species due to its adaptations for exploiting different resources and occupying different habitats. Role of a species in an ecological community.

ecotone: habitat created by the juxtaposition of distinctly different habitats, such as a zone of transition between woodland and grassland.

emergent trees: trees that are above the canopy.

emigration: departure of an individual from a group to live alone or join another group (usually at adulthood).

- endemic:** restricted to, peculiar to, or prevailing in, a specified country or region.
- Eocene:** geological epoch (within the Tertiary period), 38–55 mya.
- epizootic:** pertaining to disease that spreads rapidly through an animal population.
- equatorial:** geographic region bordering the equator.
- extant:** living at the present time. *cf.* extinct.
- extirpation:** extermination of a population or taxon from a given area.
- exudate:** substance that flows from the vascular system of a plant (e.g. gum, sap, resin).
- eye-ring:** ring of coloured fur around the eye.
- F. R.:** (*abbrev.*) Forest Reserve.
- family:** taxonomic division subordinate to an order and superior to a genus.
- fission-fusion social system:** social system in which individuals regularly leave for foraging (often in subgroups) but from time to time join together in larger groups.
- flank:** side of the body of a mammal.
- folivore** (*adj.* **folivorous**): animal that primarily eats leaves.
- foramen** (*pl.* **foramina**): aperture (which is usually small, round or elliptical) in a bone, or between bones, for the passage of a nerve, blood vessel or muscle.
- foramen magnum:** large opening at the posterior end of the skull through which the spinal cord passes.
- forest island:** *see* relict forest.
- frugivore** (*adj.* **frugivorous**): animal that primarily eats fruit.
- fundamental number (FN):** ambiguous term sometimes defined as (1) the total number of chromosomal arms in the full chromosomal complement of an organism (i.e. including the sex chromosomes), or (2) the total number of chromosomal arms found in the autosomal chromosomes only (i.e. excluding the sex chromosomes). When only the autosomal chromosomes are included, some authors (but not all) use aFN instead of FN to avoid ambiguity.
- G. R.:** (*abbrev.*) Game Reserve.
- gallery forest:** type of forest outlier (in a savanna region) found in narrow sheltered valleys and ravines on hillsides, where soils are moist enough, and conditions humid enough, to support rainforest trees (Rosevear 1953).
- genotype:** genetical term to describe the genetic constitution of an individual inherited from its parents. *cf.* phenotype (*q.v.*).
- genus** (*pl.* **genera**): taxonomic division superior to species and subordinate to family.
- geographical range:** area over which a population or taxon is distributed.
- gestation:** development of embryo/foetus, which takes place in the uterus; the period during which this development takes place. The gestation period is defined as the interval between conception and parturition (birth). Strictly speaking, the gestation period is not the interval between copulation (mating) and parturition (birth), although many authors take it to be this interval.
- glans penis:** bulbous tip of the penis.
- GLS:** greatest length of skull, measured from anterior end of incisor teeth or nasal bone (whichever is most anterior) to the posterior end of the skull (occiput, occipital condyles or auditory bullae, whichever is most posterior).
- gracile:** relatively slender, delicately or lightly built. *cf.* robust.
- graminivore = granivore** (*adj.* **graminivorous = grani-vorous**): an animal that primarily eats grains and seeds.
- gregarious:** living together in groups, flocks, herds. *cf.* solitary.
- Gregorian Rift Valley:** *see* Rift Valley.
- guard hair:** long thin bristle-like hairs, mainly on the back and flanks, that project beyond the soft hairs of the pelage; when present, conspicuous but never as numerous as soft hairs; probably tactile in function.
- gumivore** (*adj.* **gumivorous**): animal that primarily eats plant exudates (e.g. gum, sap, resin).
- GWS:** greatest width of skull *See also* zygomatic arch.
- hallux:** first digit of the hindlimb; the big toe.
- HB:** length of head and body, from tip of nose/snout to base of tail.
- HF:** length of hindfoot (measured from the 'ankle bone' to the tip of the longest digit; usually measured without including the claw. *See also* c.u.; s.u.).
- herbivore** (*adj.* **herbivorous**): animal that eats plants.
- high forest:** rainforest that has matured, stabilized and reached the climax stage of succession.
- highveld:** high plateaux characteristic of inland southern Africa, dominated by grasses.
- Holocene:** epoch of the Quaternary period (*q.v.*) following the Pleistocene epoch (*q.v.*), present time to ca.11,000 years ago. Sometimes referred to as the 'Recent' epoch.
- holotype:** single specimen designated or indicated as 'the type' by the author at the time of publication of the original description of a new species or subspecies. The holotype illustrates the definitive characters of that new species or subspecies. Also called 'type' (as in 'type specimen' and 'type locality').
- home-range:** area (expressed in square metres, hectares, or square kilometres) routinely used by an animal for its day-to-day activities and requirements, and which contains the resources required for survival and reproduction. Within the home-range there may be a 'core area' or 'centre of activity', that is utilized more frequently than other parts (e.g. 80% or 90% of known time-based observations). *cf.* territory (*q.v.*).
- homoplasy:** similarity between different organisms or taxa resulting from evolution along similar lines (e.g. convergent evolution) rather than descent from a common ancestor.
- hybrid:** offspring of parents of different species.
- I or i:** (*abbrev.*) incisor (*q.v.*) tooth; upper case denotes adult dentition, lower case denotes deciduous dentition (milk teeth). *See also* incisor.
- I. (pl. Is.):** (*abbrev.*) Island.
- immigration:** movement of new individuals into a population.
- inbreeding:** mating among closely related individuals.
- incertae sedis:** (*Lat.*) taxon of uncertain status and that may be taxonomically invalid.
- incisor:** tooth rooted in the premaxillary bone (most anterior bone of upper jaw) and in an equivalent position in the mandibular bone (lower jaw); always anterior to the canine teeth, if present. The number and form of the incisor teeth varies in different species.
- infanticide:** deliberate killing of infants.
- infraorbital foramen** (*pl.* **foramina**): foramen that connects the orbit (eye-socket) with the rostrum (premaxilla and maxilla bones); outer surface often expanded to form zygomatic plate (*q.v.*); foramen contains the masseter medialis muscle.

- inguinal:** groin.
- inner:** nearest to mid-line of body, e.g. inner incisor, inner margin of ear.
- insectivore** (*adj.* **insectivorous**): animal that primarily eats insects.
- inselberg:** isolated rocky hill; term used mainly in western Africa. *See also* *jebel*; *kopje*.
- insular:** isolated from others of the same type (as on an island).
- inter-aural:** between the ears.
- inter-group:** between or among groups.
- inter-ocular stripe:** stripe that runs vertically between the eyes.
- inter-orbit/inter-orbital constriction:** narrowest part of the skull between the orbits when viewed dorsally at the level of the frontal bones.
- inter-specific:** between species.
- intra-group:** within a group.
- intra-specific:** within one species; among members of the same species.
- invertebrate:** animal without a backbone (e.g. insects, spiders, worms, crustaceans).
- ischial callosities:** pads of tough, fatty, horny skin attached to the flattened parts of the ischium of all Old World monkeys.
- ischium:** one of the three bones of the pelvis.
- jebel:** isolated rocky hill in savanna and arid habitats; term used mainly in northern Africa. *See also* *inselberg*; *kopje*.
- juvenile:** individual between infancy and sexual maturity.
- Kaokoveld:** area of sandstone and lava hills of the Namib Desert (Biotic Zone 11b) in NW Namibia, inland from the Skeleton Coast.
- Karoo:** southern African term for grassy dwarf shrubland on the semi-arid central plateau of the western half of South Africa at altitudes of 500–2000 m.
- karyological:** nucleus and chromosomes.
- karyotype:** chromosomes in the cell of an animal.
- kopje:** rocky hill with boulders, rock crevices and sparse vegetation; term used mainly in southern Africa. *See also* *inselberg*; *jebel*.
- labial:** lips; situated near the lips; on the outer side of the teeth within the mouth. *cf.* *lingual* (*q.v.*).
- labially:** in the direction of the lips. *cf.* *lingually* (*q.v.*).
- lachrymal bone:** small bone in skull situated at the upper anterior margin of the orbit, near the lachrymal (tear) gland.
- lactation:** secretion of milk for nourishing the young after birth.
- lambdoid crest (= supraoccipital crest):** crest or ridge of bone running transversely across back of the skull at the junction of the dorsal (parietal) and posterior (occipital) bones of the braincase.
- lambdoid suture:** line at the junction of the occipital and parietal bones of the skull. May be clearly defined in juveniles or obscured by complete fusion in adults, or by the formation of a lambdoid crest.
- lateral:** located away from the mid-line, at or toward the sides.
- lectotype:** specimen chosen from syntypes (*q.v.*) to stand as ‘the type’ of a species or subspecies when no holotype (*q.v.*) was designated by the author who described the new species or subspecies.
- liana (= liane):** climbing woody plant (woody vine).
- limiting factor:** principle that the growth or functioning of an organism is limited when any essential factor (or resource) is lacking or in short supply, regardless of the quantity available of any other factor (or resource). The principle may also be applied to the proliferation and/or distribution of a population or species.
- lingual:** pertaining to the tongue; situated near the tongue; on the inner (tongue) side of the mouth. *cf.* *labial* (*q.v.*).
- lingually:** in the direction of the tongue. *cf.* *labially* (*q.v.*).
- longitudinal:** lengthwise; running in a head to tail direction. *cf.* *transverse* (*q.v.*).
- lowveld:** savanna at lower altitudes below the Great Escarpment of South Africa, with vegetation consisting of a grassy lower layer and a woody upper layer of shrubs and/or trees, at either high density (woodland) or intermediate density (bushveld, *q.v.*).
- M:** (*abbrev.*) molar tooth. *See also* *molars*.
- Maghreb:** *see* north-west Africa.
- mandible:** lower jaw.
- mandibular ramus:** one of the two branches (sides) of the mandible (*q.v.*); the two rami are joined at the mandibular symphysis.
- mastoid:** bone on the posterior ventral part of the skull, immediately behind the auditory meatus (auditory opening).
- matrilineal:** kinship or descent through female lines.
- maxilla** (*pl.* **maxillae**): one of the pair of bones in the skull that forms that part of each upper jaw in which the canine (*q.v.*) (if present) and cheekteeth (premolars and molars) (*q.v.*) are rooted.
- maxillary:** pertaining to the maxilla (*q.v.*).
- maxillary process:** projection of bone from the maxilla, which forms the anterior portion of the zygomatic arch (*q.v.*); usually oriented vertically to the anterior–posterior line of the skull.
- meatus:** passage or channel; the opening of a passage.
- medial:** situated in the middle.
- melanistic:** having an abnormally large amount of black or dark pigment in pelage and skin.
- metabolic water:** water produced by oxidative processes within the body; an important source of water for arid-adapted mammals when free (drinking) water and water within the food is in short supply or unavailable.
- metacarpals:** long bones of the hand, situated between the carpal bones of the wrist and the proximal phalanges of the fingers.
- metatarsals:** long bones of the foot, situated between the tarsal bones of the ankle and the most proximal phalanges of the toes.
- mid-dorsal stripe (or line):** in primates, a stripe of differentially coloured fur that runs along the ridge of the back.
- migration:** movements of species that travel, predictably and more-or-less directly, from one habitat to another (and back again), along predetermined routes, in response to seasonal changes in climate, food supply or any other resource. *cf.* *localized movements* (*q.v.*); *nomadic movements* (*q.v.*).
- milk teeth:** teeth (usually simple) occurring in newborn mammals, or appearing soon after birth, and preceding the permanent teeth of the adult animal. Also called deciduous teeth.
- Miocene:** geological epoch (within the Tertiary period), ca. 5–23 mya.
- miombo:** vernacular name applied to trees in the genus *Brachystegia*; a type of savanna woodland in the Zambezian region where *Brachystegia* spp. are the commonest trees or one of the commonest trees.
- mitochondrial DNA:** small amount of DNA contained within the mitochondria of a cell.

- molar**: grinding tooth; the most posterior teeth of the cheekteeth in adult mammals. Not preceded by deciduous (milk) teeth.
- molariform**: having approximately the form of a molar tooth.
- monogamy** (*adj.* **monogamous**): mating system in which one male mates with one female. Neither sex has the opportunity of monopolizing additional members of the opposite sex. Fitness often maximized through shared parental care (Emlen & Oring 1977). *cf.* polygyny (*q.v.*).
- monophyletic**: describes a taxonomic group descended from a common ancestor that was itself a member of that taxonomic group, and including *all* the descendants of that ancestor (Groves 2001). *cf.* paraphyletic (*q.v.*); polyphyletic (*q.v.*).
- monophyly**: derivation of taxa from a common ancestor. *cf.* diphily (*q.v.*), polyphyly (*q.v.*).
- monotocous**: normally having only one young per litter (twinning, if it occurs, is very rare and abnormal). *cf.* polytocous (*q.v.*).
- monotypy** (*adj.* **monotypic**): describes a taxon containing only one intermediately subordinate taxonomic unit, e.g. a monotypic family contains only one genus; a monotypic genus contains only one species. *cf.* polytypy (*q.v.*).
- montane**: mountain habitats.
- mopane**: vernacular name applied to the tree *Colophospermum mopane*; a type of savanna woodland in the Zambezi region in which *C. mopane* is the commonest species of tree.
- multimale group**: group of animals in which several males and several females are reproductively active.
- Mt.** (*abbrev.*) Mount.
- mtDNA**: (*abbrev.*) mitochondrial DNA (*q.v.*).
- Mts.** (*abbrev.*) Mountains.
- muzzle**: snout; the nose and jaws of a mammal.
- mya.** (*abbrev.*) million years ago.
- n. d.**: (*abbrev.*) no data.
- N. P.** (*abbrev.*) National Park.
- natal group**: group into which an individual is born.
- neonate**: newly born animal.
- neoparatype**: any specimen described at the same time as the neotype (*q.v.*).
- neotype**: specimen selected as the type in cases where the primary types are definitely known to be lost or destroyed.
- niche**: *see* 'ecological niche'.
- nipple**: external opening of a mammary gland. Nipple number and position vary according to the taxon, but are generally consistent within a species. Nipples arranged in pairs, one of the pair on each side of the body.
- nocturnal**: active mainly during the night. *cf.* crepuscular (*q.v.*); diurnal (*q.v.*).
- nomadic movements**: irregular and unpredictable movements, from one locality to another, made by species living in unpredictable habitats. *cf.* localized movements (*q.v.*); migration (*q.v.*).
- nomen dubium**: when the available evidence is not sufficient to permit the identification of a species, its name is considered to be a *nomen dubium* and, therefore, not available for taxonomic purposes.
- nomen nudum**: name that is not valid because, when it was originally published, the organism to which it referred was not adequately described, defined or sketched. The name is, therefore, invalid because it is impossible to associate it indisputably with any specific organism.
- nominate subspecies**: subspecies that bears the name of the species to which it belongs (e.g. *Cercopithecus mitis mitis*), only brought into existence by the creation of one or more other subspecies in the same species (e.g. *Cercopithecus mitis kolbi*).
- North Africa**: those parts of Mauritania, Morocco, Algeria, Tunisia, Libya and Egypt that are north of the Sahara Desert.
- north-central Africa**: Southern Chad and southern Sudan, west of the Nile R. and south of the Sahara Desert. Mainly savanna habitats.
- north-west Africa**: (= **Mahgreb**) those parts of Mauritania, Morocco, Algeria and Tunisia that are north of the Sahara Desert.
- nulliparous**: not having given birth.
- occiput**: posterior part of the skull, above the foramen magnum (*q.v.*).
- occlusal**: pertaining to the biting surface of a tooth.
- Oligocene**: geological epoch (within the Tertiary period), ca. 23–38 mya.
- omnivore** (*adj.* **omnivorous**): animal that eats a wide range of foods, including both animal and plant material.
- one-male group**: group containing several reproductively active females but only one reproductively active male.
- orbit**: bony cavity (eye-socket) in which the eye is situated.
- order**: taxonomic division subordinate to class and superior to family.
- oestrus**: period during which a female mammal will permit copulation.
- outer**: farthest from the mid-line of the body.
- P** or **p.** (*abbrev.*) premolar tooth; upper case denotes adult dentition, lower case denotes deciduous dentition (milk teeth). *See also* premolar.
- Palaearctic**: zoogeographic region comprising Europe, North Africa and Asia (except for southern portion of the Arabian Peninsula and tropical and sub-tropical regions of the Oriental Region).
- Palaeocene**: geological epoch (within the Tertiary period), 55–65 mya.
- palate**: roof of the mouth. The anterior part (hard palate) comprises the bony palate (formed by the premaxillae, maxillae and palatine bones), and a covering mucous membrane. The posterior part (soft palate) is composed only of muscular tissue covered by a mucous membrane.
- parapatry** (*adj.* **parapatric**): situation where two or more species have geographic ranges that are contiguous but do not overlap. This abutting may be along a line of habitat discontinuity, ecotone, or altitudinal/climatic contour, but may also arise from competitive exclusion of one (or both) by the other.
- paraphyletic**: describes a taxon containing units that have evolved from a single ancestral taxon but which do not contain all of the descendants of the most recent common ancestor.
- paratype**: specimen collected at the same time and place as the holotype (*q.v.*) and designated by the original authority as such. There may be one or more paratypes.
- parietal**: one of the pair of bones forming the vault of the braincase, situated between the frontal and the occipital bones.
- parous**: having given birth.

- parturition:** process of giving birth.
- pectoral:** pertaining to or situated on the chest.
- pelage:** hairy, woolly or furry covering of the body in mammals. The pelage variously consists of hairs, guard hairs and underfur according to the species.
- perineal swelling:** inflation with fluid of the tissue between anus and vulva, signalling onset of oestrus and, at its fullest, ovulation.
- phenotype:** visible characters of an individual resulting from the interaction between the genotype (*q.v.*) and the environment.
- philopatry:** tendency to remain in or consistently return to the place where one was born.
- phylogenetics:** pertaining to the line of descent of a taxon; a method of classification that attempts to show the evolutionary relatedness of organisms.
- phylogeny** (*adj.* **phylogenetic**): evolutionary history and line of descent of a species or higher taxonomic unit.
- pinna** (*pl.* **pinnae**): external (outer) ear.
- plantar:** of the sole of the foot.
- Pleistocene:** geological epoch (within the Quaternary period), ca. 10,000 to 1.7 million years ago.
- Pliocene:** geological epoch (within the Tertiary period), ca. 2–5 mya.
- polygamous:** mating system in which both males and females mate with multiple members of the opposite sex.
- polygynous:** mating system in which males mate with more than one female and females typically provide most of the parental care.
- polymorphism** (*adj.* **polymorphic**): existence, within a species or population, of individuals having different forms (colour, size, shape, etc.).
- polyphyletic:** describes a taxon derived from two or more ancestral sources; not of a single, immediate line of descent (Mayr *et al.* 1953). *cf.* monophyletic (*q.v.*).
- polyphyly:** derivation of a taxon from two or more ancestral sources. *cf.* monophyly (*q.v.*).
- polytypy** (*adj.* **polytypic**): taxon that has several taxa in the next lower taxonomic category, e.g. a polytypic family contains two or more genera, a polytypic genus has two or more species. *cf.* monotypy (*q.v.*).
- population:** all the individuals that comprise a single interbreeding group.
- posterior:** of or towards the rear of an animal.
- postorbital:** behind (posterior) to the orbit.
- premaxilla:** one of a pair of bones at the anterior end of the skull that bears the incisor teeth.
- premolar:** tooth situated immediately anterior to the molar teeth; usually preceded in time by deciduous (milk) tooth.
- preorbital:** anterior to the eye.
- primary forest:** mature, undisturbed, forest.
- primitive feature:** behavioural or morphological feature that is characteristic of a species and its ancestors.
- prognathism:** prominence of the snout.
- promiscuity:** mating system in which each male mates with several females and each female mates with several males.
- proximal:** nearest to the body or to the mid-line of the body; nearest to the point of attachment. *cf.* distal (*q.v.*).
- pterygoid:** one of a pair of cranial bones forming part of the roof of the mouth.
- quadrupedal:** body supported by four limbs; movement using all four limbs.
- Quaternary:** geological period, present time to ca. 2 mya, comprising two epochs: Pleistocene (*q.v.*) and Holocene (Recent) (*q.v.*).
- R.:** (*abbrev.*) River.
- race:** *see* subspecies.
- ramus:** one half (left or right) of the lower jaw or mandible.
- relict forest:** forest that persists where local conditions are favourable after the disappearance of forest from the surrounding area as a result of climate change or human activity. Relict forests include those at the base of inselbergs that are watered by rainwater running off the inselberg, and forests growing in graveyards and sacred sites that are protected. Sometimes known as forest islands.
- relict population:** one that persists where local conditions are favourable after the extirpation of the species from at least part of its former range.
- resident:** living within a definite, limited range, as opposed to being migratory or nomadic.
- Rift Valley:** deep valley extending from the Red Sea through Ethiopia and East Africa to Malawi; formed ca. 12 mya by subsidence of the valley floor and uplifting of the edges to form mountains and highlands. Four parts: (1) Ethiopian Rift Valley dividing the Ethiopian Plateau into two parts; (2) Albertine Rift Valley (= Western Rift Valley) in Uganda, E DR Congo and W Tanzania; (3) Gregorian Rift Valley (= Eastern Rift Valley) in N Kenya, C Kenya and N Tanzania; (4) Malawian Rift Valley – the extension of the Albertine Rift Valley in Malawi.
- riparian:** habitat along the banks of a waterway.
- riverine forest:** forest growing along the banks of a river or stream where conditions are moister than in the surrounding area.
- robust:** relatively heavily and strongly built. *cf.* gracile.
- s.u.:** (*Lat. sans unguis* = without claw) sometimes added as a suffix to the hindfoot measurement to emphasize that HF has been measured without the claw. However, since this is the standard method of measurement, most authors write ‘HF’, not ‘HF s.u.’. *cf.* c.u. (*q.v.*).
- sagittal crest:** longitudinal crest of raised bone on the mid-dorsal line of the cranium.
- saltatorial:** jumping or leaping on the two hindlimbs.
- scent gland:** odour-producing gland.
- scent-mark:** olfactory message communicated by rubbing glandular secretions or leaving urine or faeces at a specific site.
- scrotum:** external sac containing the testes and epididymides in male mammals.
- secondary compounds:** poisons produced by plants that deter animals from eating them.
- secondary forest:** forest characterized by immature stages of the succession cycle.
- sedentary:** occupying a relatively small home-range.
- sensu lato:** in a broad sense.
- sensu stricto:** in a restricted sense.
- septum:** dividing wall separating two cavities.
- sex ratio:** number of males to the number of females, usually expressed as a proportion to one male, e.g. 1 : 1 (equal numbers of males and females), 1 : 0.5 (= twice as many males as females), 1 : 2 (= twice as many females as males).

- sexual dimorphism:** observable (phenotypic) difference(s) (e.g. in colour, size or form) between the males and females of a species or higher taxon.
- sibling species:** true species, that are reproductively isolated and do not interbreed but are difficult to separate solely on basis of morphological characters.
- side-stripe:** longitudinal stripe(s) of contrasting colour on each flank, usually from shoulder to rump or upper part of hindlimbs.
- singleton:** neonate that is born singly as opposed to being one of a larger litter.
- sister species:** species that are thought to have arisen from a single dichotomous splitting event.
- solitary:** unsocial; not living in a social group. *cf.* gregarious.
- south-central Africa:** Angola, SE DR Congo, Zambia and Malawi (but only west of L. Malawi and the Shire R. Valley).
- southern Africa:** south of the Cunene R. and Zambezi R., i.e. Namibia, Botswana, Zimbabwe, southern Mozambique and South Africa (after Smithers 1983).
- species:** populations(s) of closely related and similar organisms, that are capable of interbreeding freely with one another, and cannot or typically do not interbreed with members of other species.
- species-group (= superspecies):** two or more closely related species.
- species-specific:** characters that distinguish a species (e.g. shape, colour, markings, habits).
- sternal:** chest region near the sternum (breastbone).
- sub, sub-:** prefix meaning under, signifying beneath or ventral to (as in anatomical features) or south of (as in sub-Saharan); less than (as in subsonic); not quite, nearly, almost, somewhat (as in subequal, subtriangular). In taxonomy, indicates a group just below the status of the taxa immediately following it (e.g. a genus may contain two or more subgenera).
- subadult:** individual between sexual maturity and full adulthood; not yet fully adult physically and/or socially.
- subauricular:** below the ear.
- subcaudal:** below the tail.
- subspecies (= race):** geographically localized and isolated subdivision of a species, which differs genetically, morphologically and taxonomically from other subdivisions of the species.
- subterminal:** just below the end or tip.
- suckling:** act of a mother giving milk directly from her breast (mammary glands) to her young. Mothers suckle; their young suck.
- supraoccipital crest:** ridge of bone, oriented transversely across the back of the skull, at the junction of the parietal and/or supraoccipital bones and the occipital bone. Sometimes referred to as the lambdoid crest.
- supraorbital:** above (dorsal to) the orbit.
- supraorbital ridge:** ridge of bone along upper rim of orbit (eye-socket); can be well developed, low or absent.
- sympatry** (*adj.* **sympatric**): the situation where populations of two or more different species have overlapping geographic ranges; refers also to populations of two or more species whose geographic ranges are partly or wholly overlapping. They may or may not interact. *cf.* allopatry (*q.v.*); syntopy (*q.v.*).
- synonym:** one or more different names for the same taxonomic unit. A synonym may be a 'senior synonym' (the oldest name), or a 'junior synonym' (a more recent name), that is no longer considered as valid. May be used to refer to all names that have been associated, at some time in the past, with the taxonomic unit as currently understood.
- syntopy** (*adj.* **syntopic**): describes the situation where two or more species use the same or similar habitats and activity times. They may or may not interact. *cf.* allopatry (*q.v.*); sympatry (*q.v.*).
- syntype:** any specimen, or one of a series of specimens, used to designate a species when a holotype (*q.v.*) and paratype(s) (*q.v.*) have either not been selected, or have been lost or destroyed.
- systematics:** the science of arranging organisms in a way that reflects their evolutionary relationships; such relationships may be expressed as a phylogeny (*q.v.*). Often defined (somewhat incorrectly) as a synonym of taxonomy (*q.v.*).
- T:** length of tail, measured from anterior of the first caudal vertebra to the posterior end of the last caudal vertebra (excludes tufts, bristles, etc. at tip of tail).
- tapetum:** layer of the eye (of some animals) that enhances night vision.
- taxon** (*pl.* **taxa**): any defined unit (e.g. family, genus, species, subspecies) in the classification of organisms.
- taxonomy:** science of biological nomenclature; the study of the rules, principles and practice of naming and classifying species and other taxa. Sometimes considered as an integral part (and near synonym) of systematics (*q.v.*).
- terra firma forest:** lowland forest that is not seasonally flooded.
- terrestrial:** living primarily on the ground. *cf.* arboreal (*q.v.*).
- territory:** area defended by an individual against certain other members of the species, usually by overt aggression or advertisement; territory is marked by the urine, faeces or glandular secretions of the territory's owner. *cf.* home-range.
- Tertiary:** geological period, 2–65 mya, comprising five epochs: Palaeocene, Eocene, Oligocene, Miocene and Pliocene (*q.v.*); followed by the Quaternary period (*q.v.*).
- testes:** male gonads, or testicles, in which spermatozoa are formed and in which the male hormone is produced.
- TL:** total length from tip of snout to the distal end of the tail bone (excludes tufts, bristles, etc. at tip of tail). Equivalent to the head and body length plus tail length added together. *See also* HB and T.
- topotype:** any specimen from the type locality (*q.v.*), i.e. the same locality as that from which the holotype (*q.v.*) was taken.
- topotypical:** pertaining to the type locality (e.g. a topotypical population is one found at the type locality).
- transverse:** in a direction across the body from side to side. *cf.* longitudinal (*q.v.*).
- Tropical:** geographical region between tropic of Cancer (23.5° N) and tropic of Capricorn (23.5° S).
- tympanic bulla** (*pl.* **tympanic bullae**): one of a pair of usually rounded bony capsules, on underside of skull (one on each side), housing structures of the middle and inner ear in many mammals. Also called auditory bulla (*q.v.*).
- type description:** original description of a species; the original description of the holotype (and paratype[s] if included).
- type locality:** locality from which a holotype (*q.v.*), lectotype or neotype was collected. Also called topotypical locality.
- type series:** holotype and all specimens collected at the same place and time and used, together with the holotype, to describe a new species.

type species: usually the species that was the first to be described under the name of a new genus. Not all genera had a designated type species when they were first created; in such cases, other rules determine which species will be the type species.

type specimen: *see* holotype.

underfur: dense and often woolly layer of the pelage, situated close to the skin and below the soft hairs and guard hairs.

understorey: part of a forest that lies below the canopy.

vagrant: individual that has been found well outside the normal geographic range of its species.

veld: Afrikaans word, used mainly by southern African biologists, to refer to a wide variety of grassland vegetation types typically used for grazing. *See also* bushveld, highveld, lowveld.

ventral: underside or lower surface (opposite of dorsal).

vertebra (*pl.* **vertebrae**): any of the bones that make up the backbone.

vibrissa (*pl.* **vibrissae**): long stiff hairs on the face, especially around nostrils and lips; often associated with the perception of tactile sensation; 'whiskers'.

vlei: southern African term for a marsh or swamp, either permanent or seasonal.

wadi: desert valley, usually dry at the surface except after heavy rainfall.

West Africa: ca. south of 18°N from Senegal to the Sanaga R. in Cameroon, and Bioko I. (Equatorial Guinea) (Rosevear 1965).

WT: weight (mass) of an individual.

zygomatic arch: one of a pair of cheekbones, formed of the maxillary process anteriorly, jugal bone medially and squamosal bone posteriorly. Ranges from massive, broad, widely flared and bony, to frail, slender and cartilaginous. When present, provides protection to the eyes and orbits. Also called zygoma.

zygomatic width (ZW): greatest width between the outer aspect of one zygomatic arch to the equivalent position on the opposite zygomatic arch. *See also* GWS.

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MAMMALS OF AFRICA

VOLUME III
RODENTS, HARES AND RABBITS

EDITED BY DAVID HAPPOLD

B L O O M S B U R Y

MAMMALS OF AFRICA

VOLUME III

RODENTS, HARES AND RABBITS



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MAMMALS OF AFRICA

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RODENTS, HARES AND RABBITS

EDITED BY DAVID C. D. HAPPOLD



COLOUR AND PENCIL ILLUSTRATIONS BY JONATHAN KINGDON
PEN AND INK ILLUSTRATIONS BY MEREDITH HAPPOLD

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| GENUS <i>Desmodillus</i> Cape Short-tailed Gerbil – J. A. J. Nel | 266 | <i>Gerbillus gerbillus</i> Lesser Egyptian Gerbil (Small Egyptian Gerbil) – L. Granjon | 308 |
| <i>Desmodillus auricularis</i> Cape Short-tailed Gerbil (Namaqua Gerbil) – J. A. J. Nel | 267 | <i>Gerbillus harwoodi</i> Harwood's Gerbil – D. C. D. Happold | 309 |
| GENUS <i>Gerbilliscus</i> Gerbils – L. Granjon & E. R. Dempster | 268 | <i>Gerbillus henleyi</i> Henley's Gerbil – L. Granjon | 310 |
| <i>Gerbilliscus afra</i> Cape Gerbil – E. R. Dempster | 270 | <i>Gerbillus hesperinus</i> Moroccan Gerbil – D. C. D. Happold | 311 |
| <i>Gerbilliscus boehmi</i> Boehm's Gerbil – D. C. D. Happold | 272 | <i>Gerbillus hoogstraali</i> Hoogstraal's Gerbil – D. C. D. Happold | 312 |
| <i>Gerbilliscus brantsii</i> Highveld Gerbil – E. R. Dempster | 273 | <i>Gerbillus juliani</i> Julian's Gerbil – D. C. D. Happold | 313 |
| <i>Gerbilliscus gambianus</i> Gambian Gerbil – J.-M. Duplantier & L. Granjon | 274 | <i>Gerbillus latastei</i> Lataste's Gerbil – D. C. D. Happold | 314 |
| <i>Gerbilliscus guineae</i> Guinea Gerbil – L. Granjon & J.-M. Duplantier | 276 | <i>Gerbillus lowei</i> Lowe's Gerbil – D. C. D. Happold | 315 |
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| <i>Gerbilliscus leucogaster</i> Bushveld Gerbil – E. R. Dempster | 279 | <i>Gerbillus nancillus</i> Sudan Gerbil – L. Granjon | 318 |
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| | | <i>Gerbillus pyramidum</i> Greater Egyptian Gerbil – L. Granjon | 325 |
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| | | <i>Gerbillus somalicus</i> Somalian Gerbil – D. C. D. Happold | 330 |
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| | | <i>Gerbillus tarabuli</i> Tarabul's Gerbil (Libyan Gerbil) – L. Granjon | 331 |
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| | | <i>Meriones crassus</i> Sundevall's Jird (Silky Jird) – E. Fichet-Calvet | 335 |
| | | <i>Meriones libycus</i> Libyan Jird – E. Fichet-Calvet | 336 |

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C. T. Chimimba, A. V. Linzey & M. H. Kesner | 374 |
| <i>Microdillus peeli</i> Peel's Pygmy Gerbil (Somali Pygmy
Gerbil) – D. C. D. Happold | 340 | <i>Aethomys stannarius</i> West African Veld Rat (West African
Aethomys) – A. V. Linzey, C. T. Chimimba &
M. H. Kesner | 375 |
| GENUS <i>Pachyuromys</i> Fat-tailed Jird – D. C. D. Happold | 341 | <i>Aethomys thomasi</i> Thomas's Veld Rat (Thomas's Aethomys)
– C. T. Chimimba, A. V. Linzey & M. H. Kesner | 376 |
| <i>Pachyuromys duprasi</i> Fat-tailed Jird – D. C. D. Happold | 341 | GENUS <i>Apodemus</i> Field Mice – C. Denys | 377 |
| GENUS <i>Psammomys</i> Sand Rats – E. Fichet-Calvet | 343 | <i>Apodemus sylvaticus</i> Long-tailed Field Mouse (Wood
Mouse) – C. Denys | 378 |
| <i>Psammomys obesus</i> Fat Sand Rat – E. Fichet-Calvet | 344 | GENUS <i>Arvicanthis</i> Grass Rats – L. Granjon & J.-F. Ducroz | 379 |
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E. Fichet-Calvet | 346 | <i>Arvicanthis abyssinicus</i> Ethiopian Grass Rat (Abyssinian
Grass Rat) – Afework Bekele | 381 |
| GENUS <i>Sekeetamys</i> Bushy-tailed Jird – C. Denys | 347 | <i>Arvicanthis ansorgei</i> Ansorge's Grass Rat (Sudanian
Arvicanthis) – L. Granjon & J.-F. Ducroz | 382 |
| <i>Sekeetamys calurus</i> Bushy-tailed Jird – C. Denys | 347 | <i>Arvicanthis blicki</i> Blick's Grass Rat – Afework Bekele | 383 |
| GENUS <i>Taterillus</i> Taterils (Gerbils) – L. Granjon & G. Dobigny | 349 | <i>Arvicanthis nairobae</i> Nairobi Grass Rat – S. Takata | 384 |
| <i>Taterillus arenarius</i> Sand Tateril (Robbins's Tateril) –
L. Granjon & G. Dobigny | 350 | <i>Arvicanthis neumanni</i> Neumann's Grass Rat (Somali Grass
Rat) – Afework Bekele | 386 |
| <i>Taterillus congicus</i> Congo Tateril – L. Granjon & G. Dobigny | 351 | <i>Arvicanthis niloticus</i> Nile Grass Rat (Unstriped Grass Rat) –
L. Granjon, Afework Bekele & J.-F. Ducroz | 387 |
| <i>Taterillus emini</i> Emin's Tateril – L. Granjon & G. Dobigny | 352 | <i>Arvicanthis rufinus</i> Rufous Grass Rat (Guinean Grass Rat)
– L. Granjon & J.-F. Ducroz | 388 |
| <i>Taterillus gracilis</i> Slender Tateril (Gracile Tateril) –
L. Granjon & G. Dobigny | 353 | GENUS <i>Colomys</i> African Water Rat – F. Dieterlen | 389 |
| <i>Taterillus lacustris</i> Lake Chad Tateril – L. Granjon &
G. Dobigny | 354 | <i>Colomys goslingi</i> African Water Rat (Velvet Mouse, African
Wading Rat) – F. Dieterlen | 390 |
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L. Granjon & G. Dobigny | 356 | <i>Dasyomys foxi</i> Fox's Shaggy Rat – M. D. Carleton | 394 |
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| <i>Leimacomys buettneri</i> Büttner's Forest Mouse (Büttner's
Togo Mouse) – F. Dieterlen | 359 | <i>Dasyomys rufulus</i> Rufous Shaggy Rat – J.-M. Duplantier | 399 |
| SUBFAMILY MURINAE Rats and Mice – G. G. Musser &
M. D. Carleton | 361 | GENUS <i>Dephomys</i> Defua Rat – D. C. D. Happold | 400 |
| GENUS <i>Aethomys</i> Veld Rats – C. T. Chimimba,
A. V. Linzey & M. H. Kesner | 362 | <i>Dephomys defua</i> Defua Rat – D. C. D. Happold | 400 |
| <i>Aethomys bocagei</i> Bocage's Veld Rat (Bocage's Aethomys) –
C. T. Chimimba, A. V. Linzey & M. H. Kesner | 364 | GENUS <i>Desmomys</i> Scrub Rats – D. C. D. Happold | 402 |
| <i>Aethomys chrysophilus</i> Red Veld Rat (Red Aethomys) –
A. V. Linzey, M. H. Kesner & C. T. Chimimba | 365 | <i>Desmomys harringtoni</i> Harrington's Scrub Rat
(Harrington's Desmomys) – Afework Bekele | 402 |
| <i>Aethomys granti</i> Grant's Veld Rat (Grant's Aethomys) –
C. T. Chimimba, A. V. Linzey & M. H. Kesner | 367 | <i>Desmomys yaldeni</i> Yalden's Scrub Rat (Yalden's Desmomys)
– D. W. Yalden | 403 |
| <i>Aethomys hindei</i> Hinde's Veld Rat (Hinde's Aethomys) –
A. V. Linzey, C. T. Chimimba & M. H. Kesner | 368 | GENUS <i>Grammomys</i> Thicket Rats – F. Dieterlen | 404 |
| <i>Aethomys ineptus</i> Tete Veld Rat (Tete Aethomys) –
A. V. Linzey, M. H. Kesner & C. T. Chimimba | 369 | <i>Grammomys aridulus</i> Jebel Marra Thicket Rat (Arid
Woodland Grammomys) – F. Dieterlen | 406 |
| <i>Aethomys kaiseri</i> Kaiser's Veld Rat (Kaiser's Aethomys) –
A. V. Linzey, C. T. Chimimba & M. H. Kesner | 370 | <i>Grammomys buntingi</i> Bunting's Thicket Rat (Bunting's
Grammomys) – D. C. D. Happold | 407 |
| <i>Aethomys namaquensis</i> Namaqua Veld Rat (Namaqua
Aethomys) – M. H. Kesner, A. V. Linzey & C. T. Chimimba | 371 | <i>Grammomys caniceps</i> Grey-headed Thicket Rat (Grey-
headed Grammomys) – R. Hutterer | 408 |
| | | <i>Grammomys cometes</i> Mozambique Thicket Rat
(Mozambique Grammomys) – F. Dieterlen | 409 |

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| <i>Grammomys dolichurus</i> Woodland Thicket Rat (Common Grammomys) – D. C. D. Happold | 410 | GENUS <i>Lemniscomys</i> Grass Mice – M. D. Carleton | 441 |
| <i>Grammomys dryas</i> Albertine Rift Thicket Rat (Albertine Rift Grammomys) – S. O. Bober & J. C. Kerbis Peterhans | 411 | <i>Lemniscomys barbarus</i> Barbary Grass Mouse (Barbary Lemniscomys) – D. C. D. Happold | 443 |
| <i>Grammomys gigas</i> Giant Thicket Rat (Mount Kenya Grammomys) – F. Dieterlen | 412 | <i>Lemniscomys bellieri</i> Bellier's Grass Mouse (Bellier's Lemniscomys) – E. Van der Straeten | 444 |
| <i>Grammomys ibeanus</i> East African Thicket Rat (East African Grammomys) – F. Dieterlen | 413 | <i>Lemniscomys griselda</i> Griselda's Grass Mouse (Griselda's Lemniscomys) – A. Monadjem | 445 |
| <i>Grammomys kuru</i> Shining Thicket Rat (Eastern Rainforest Grammomys) – D. C. D. Happold | 414 | <i>Lemniscomys hoogstraali</i> Hoogstraal's Grass Mouse (Hoogstraal's Lemniscomys) – F. Dieterlen | 446 |
| <i>Grammomys macmillani</i> Macmillan's Thicket Rat (Macmillan's Grammomys) – F. Dieterlen | 416 | <i>Lemniscomys linulus</i> Senegal Grass Mouse (Senegal Lemniscomys) – E. Van der Straeten | 447 |
| <i>Grammomys minnae</i> Ethiopian Thicket Rat (Ethiopian Grammomys) – D. W. Yalden | 417 | <i>Lemniscomys macculus</i> Buffoon Grass Mouse (Buffoon Lemniscomys) – F. Dieterlen | 448 |
| GENUS <i>Heimyscus</i> African Smoky Mouse – J. C. Ray & J. R. Malcolm | 418 | <i>Lemniscomys mittendorfi</i> Mittendorf's Grass Mouse (Mittendorf's Lemniscomys) – E. Van der Straeten | 449 |
| <i>Heimyscus fumosus</i> African Smoky Mouse – J. C. Ray & J. R. Malcolm | 418 | <i>Lemniscomys rosalia</i> Single-striped Grass Mouse (Single-striped Lemniscomys) – A. Monadjem | 449 |
| GENUS <i>Hybomys</i> Forest Mice – M. D. Carleton | 420 | <i>Lemniscomys roseveari</i> Rosevear's Grass Mouse (Rosevear's Lemniscomys) – E. Van der Straeten | 451 |
| <i>Hybomys badius</i> Cameroon Forest Mouse (Cameroon Highland Hybomys) – R. Hutterer | 422 | <i>Lemniscomys striatus</i> Striated Grass Mouse (Striated Lemniscomys) – D. C. D. Happold | 452 |
| <i>Hybomys basillii</i> Basilio's Forest Mouse (Bioko Hybomys) – R. Hutterer | 423 | <i>Lemniscomys zebra</i> Zebra Grass Mouse (Heuglin's Lemniscomys) – D. C. D. Happold & F. Dieterlen | 454 |
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| <i>Hylomyscus aeta</i> Beaded Wood Mouse (Beaded Hylomyscus) – J. C. Ray & J. R. Malcolm | 430 | <i>Mastomys awashensis</i> Awash Multimammate Mouse (Awash Mastomys) – L. A. Lavrenchenko & H. Leirs | 462 |
| <i>Hylomyscus alleni</i> Allen's Wood Mouse (Allen's Hylomyscus) – J. C. Ray | 431 | <i>Mastomys coucha</i> Southern African Multimammate Mouse (Southern African Mastomys) – H. Leirs | 463 |
| <i>Hylomyscus baeri</i> Baer's Wood Mouse (Baer's Hylomyscus) – D. C. D. Happold | 433 | <i>Mastomys erythroleucus</i> Guinea Multimammate Mouse (Reddish-white Mastomys) – H. Leirs | 464 |
| <i>Hylomyscus carillus</i> Angolan Wood Mouse (Angolan Hylomyscus) – D. C. D. Happold | 433 | <i>Mastomys huberti</i> Hubert's Multimammate Mouse (Hubert's Mastomys) – H. Leirs | 465 |
| <i>Hylomyscus denniae</i> Montane Wood Mouse (Montane Hylomyscus) – F. Dieterlen | 434 | <i>Mastomys kollmannspergeri</i> Kollmannsperger's Multimammate Mouse (Kollmannsperger's Mastomys) – H. Leirs | 467 |
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| <i>Hylomyscus parvus</i> Lesser Wood Mouse (Lesser Hylomyscus) – J.-M. Duplantier | 437 | <i>Mastomys pernanus</i> Dwarf Multimammate Mouse (Dwarf Mastomys) – H. Leirs | 470 |
| <i>Hylomyscus stella</i> Stella Wood Mouse (Stella Hylomyscus) – F. Dieterlen | 438 | <i>Mastomys shortridgei</i> Shortridge's Multimammate Mouse (Shortridge's Mastomys) – H. Leirs | 471 |
| GENUS <i>Lamottemys</i> Mount Oku Rat – R. Hutterer | 439 | GENUS <i>Muriculus</i> Ethiopian Striped Mouse – D. W. Yalden | 472 |
| <i>Lamottemys okuensis</i> Mount Oku Rat (Mount Oku Lamottemys) – R. Hutterer | 440 | <i>Muriculus imberbis</i> Ethiopian Striped Mouse – D. W. Yalden | 472 |
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| <i>Mus callewaerti</i> Callewaert's Pygmy Mouse – D. C. D. Happold | 478 | <i>Pelomys fallax</i> East African Creek Rat (East African Pelomys) – F. Dieterlen | 515 |
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| <i>Mus haussa</i> Hausa Pygmy Mouse – F. Petter | 480 | <i>Pelomys isseli</i> Ssesse Islands Creek Rat (Lake Victoria Pelomys) – F. Dieterlen | 518 |
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| <i>Mus mahomet</i> Mahomet Pygmy Mouse – D. W. Yalden | 482 | GENUS <i>Praomys</i> Soft-furred Mice – D. C. D. Happold | 519 |
| <i>Mus mattheyi</i> Matthey's Pygmy Mouse – F. Petter | 483 | <i>Praomys daltoni</i> Dalton's Soft-furred Mouse (Dalton's Praomys) – L. Granjon | 522 |
| <i>Mus minutoides</i> Tiny Pygmy Mouse – A. Monadjem | 484 | <i>Praomys degraaffi</i> De Graaff's Soft-furred Mouse (De Graaff's Praomys) – J. C. Kerbis Peterhans & S. O. Bober | 523 |
| <i>Mus musculoides</i> West African Pygmy Mouse – D. C. D. Happold | 486 | <i>Praomys delectorum</i> Delicate Soft-furred Mouse (East African Praomys) – D. C. D. Happold | 524 |
| <i>Mus musculus</i> House Mouse – D. C. D. Happold | 487 | <i>Praomys derooi</i> De Roo's Soft-furred Mouse (De Roo's Praomys) – L. Granjon | 526 |
| <i>Mus neavei</i> Neave's Pygmy Mouse – F. Petter | 489 | <i>Praomys hartwigi</i> Hartwig's Soft-furred Mouse (Hartwig's Praomys) – R. Hutterer | 527 |
| <i>Mus orangiae</i> Orange Pygmy Mouse – A. Monadjem | 490 | <i>Praomys jacksoni</i> Jackson's Soft-furred Mouse (Jackson's Praomys) – F. Dieterlen | 527 |
| <i>Mus oubanguii</i> Oubangui Pygmy Mouse – F. Petter | 491 | <i>Praomys lukolelae</i> Lukolela Soft-furred Mouse (Lukolela Praomys) – D. C. D. Happold | 529 |
| <i>Mus setulosus</i> Peters's Pygmy Mouse – D. C. D. Happold | 492 | <i>Praomys minor</i> Least Soft-furred Mouse (Least Praomys) – E. Van der Straeten | 530 |
| <i>Mus setzeri</i> Setzer's Pygmy Mouse – A. Monadjem | 493 | <i>Praomys misonnei</i> Misonne's Soft-furred Mouse (Misonne's Praomys) – F. Dieterlen | 531 |
| <i>Mus sorella</i> Sorella Pygmy Mouse (Thomas's Pygmy Mouse) – F. Petter | 494 | <i>Praomys morio</i> Cameroon Soft-furred Mouse (Cameroon Praomys) – D. C. D. Happold | 532 |
| <i>Mus spretus</i> Algerian Mouse (Western Mediterranean Mouse) – D. C. D. Happold | 495 | <i>Praomys mutoni</i> Riverine Soft-furred Mouse (Masako Soft-furred Mouse, Riverine Praomys) – E. Van der Straeten | 533 |
| <i>Mus tenellus</i> Delicate Pygmy Mouse – F. Petter | 496 | <i>Praomys obscurus</i> Obscure Soft-furred Mouse (Gotel Mountain Praomys) – R. Hutterer | 534 |
| <i>Mus triton</i> Grey-bellied Pygmy Mouse – F. Dieterlen & D. C. D. Happold | 497 | <i>Praomys petteri</i> Petter's Soft-furred Mouse (Petter's Praomys) – E. Van der Straeten | 535 |
| GENUS <i>Mylomys</i> Mill Rats (Three-toed Grass Rats) – F. Dieterlen | 499 | <i>Praomys rostratus</i> West African Soft-furred Mouse (West African Praomys) – E. Van der Straeten | 536 |
| <i>Mylomys dybowskii</i> Dybowski's Mill Rat (Dybowski's Three-toed Grass Rat, Common Mylomys) – F. Dieterlen | 500 | <i>Praomys tullbergi</i> Tullberg's Soft-furred Mouse (Tullberg's Praomys) – D. C. D. Happold | 537 |
| <i>Mylomys rex</i> King Mill Rat (Ethiopian Three-toed Grass Rat, Ethiopian Mylomys) – D. W. Yalden | 501 | <i>Praomys verschureni</i> Verschuren's Soft-furred Mouse (Verschuren's Praomys) – F. Dieterlen | 538 |
| GENUS <i>Myomyscus</i> Meadow Mice – D. C. D. Happold | 502 | GENUS <i>Rattus</i> Rats – D. C. D. Happold | 539 |
| <i>Myomyscus angolensis</i> Angolan Meadow Mouse (Angolan Myomyscus) – H. Leirs | 503 | <i>Rattus norvegicus</i> Brown Rat (Norway Rat) – D. C. D. Happold | 540 |
| <i>Myomyscus brockmani</i> Brockman's Meadow Mouse (Smoky Meadow Mouse, Brockman's Myomyscus) – D. C. D. Happold | 504 | <i>Rattus rattus</i> Black Rat – D. C. D. Happold | 541 |
| <i>Myomyscus verreauxii</i> Verreaux's Meadow Mouse (White-footed Mouse) – D. C. D. Happold | 505 | GENUS <i>Rhabdomys</i> Four-striped Grass Mouse – D. C. D. Happold | 544 |
| GENUS <i>Nesokia</i> Bandicoot Rats – D. C. D. Happold | 506 | <i>Rhabdomys pumilio</i> Four-striped Grass Mouse – D. C. D. Happold | 545 |
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ABOVE LEFT: Jan Kalina.

ABOVE: From left to right: Jonathan Kingdon, Thomas Butynski, Meredith Happold, David Happold and Andrew Richford.
LEFT: Jonathan Kingdon (left) and Michael Hoffmann.

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D. C. D. Happold

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Mammals of Africa: *An Introduction and Guide*

David Happold, Michael Hoffmann, Thomas Butynski and Jonathan Kingdon

Mammals of Africa is a series of six volumes that describes, in detail, every extant species of African land mammal that was recognized at the time the profiles were written (Table 1). This is the first time that such an extensive coverage has been attempted; all previous books and field guides have either been regional in coverage, or have described a selection of mammal species – usually the larger species. These volumes demonstrate the diversity of Africa's mammals, summarize what is known about the distribution, ecology, behaviour and conservation status of each species, and serves as a guide to identification.

Africa has changed greatly in recent decades because of increases in human populations, exploitation of natural resources, agricultural development and urban expansion. Throughout the continent, extensive areas of forest have been destroyed and much of the forest that remains is degraded and fragmented. Savanna habitats have been altered by felling of trees and development for agriculture. Many of the drier areas are threatened with desertification. As a result, the abundance and geographic ranges of many species of mammals have declined – some marginally, some catastrophically, some to extinction. Hence, it seems appropriate that our knowledge of each

species is recorded now, on a pan-African basis, because the next few decades will see even more human-induced changes. How such changes will affect each mammalian species is uncertain, but this series of volumes will act as a baseline for assessing future change.

The study of African mammals has taken several stages. During the era of European exploration and colonization, the scientific study of African mammals was largely descriptive. Specimens that were sent to museums were described and named. As more specimens became available, and from different parts of the Continent, there was increasing interest in distribution and abundance, and in the ecological and behavioural attributes of species and communities. At first, it was the largest and most easily observed species that were the focus of most studies, but as new methodologies and equipment became available, the smaller, seldom seen, secretive species became better known. Many species were studied because of their suspected role in diseases of humans and livestock, and because they were proven or potential 'pests' in agricultural systems. During the past decade or so, there has been greater emphasis on the karyotypic and molecular/genetic characters of species. These studies have produced a wealth of information, especially during the past 40 years or so. These volumes are not only a distillation of the huge literature that now exists on African mammals, but also of much previously unpublished information.

There is a huge discrepancy among species in the amount of information available. Some species have been studied extensively for many years, especially the so-called 'game species', some species of primates, and a few species that are widespread and/or easily observed. In contrast, other species are known only by one or a few specimens, and almost nothing is known about them. Likewise, some areas and countries have been well studied, while other areas and countries have been neglected. During the preparation of these volumes, the editors have often been surprised by the wealth of information about some species when little was anticipated, and by the paucity of information about others, some of which were assumed to be 'well known'. In addition to presenting information that is based on sound scientific evidence, the aims of these volumes are to point out where there are gaps in knowledge and to correct inaccurate information that has become embedded in the literature. For most taxa, the detail provided in the species profiles allows accurate identification.

Mammals of Africa comprises six volumes (Table 2). The volumes consist mainly of species profiles – each profile being a detailed

Table 1. The mammals of Africa.

| Order | Number of families | Number of genera | Number of species |
|-----------------|--------------------|------------------|-------------------------|
| Hyracoidea | 1 | 3 | 5 |
| Proboscidea | 1 | 1 | 2 |
| Sirenia | 2 | 2 | 2 |
| Afrosoricida | 2 | 11 | 24 |
| Macroscelidea | 1 | 4 | 15 |
| Tubulidentata | 1 | 1 | 1 |
| Primates | 4 | 25 | 93 |
| Rodentia | 15 | 98 | 395 ^a |
| Lagomorpha | 1 | 5 | 13 |
| Erinaceomorpha | 1 | 3 | 6 |
| Soricomorpha | 1 | 9 | 150 |
| Chiroptera | 9 | 49 | 224 |
| Carnivora | 9 | 38 | 83 |
| Pholidota | 1 | 3 | 4 |
| Perissodactyla | 2 | 3 | 6 |
| Cetartiodactyla | 6 | 41 | 93 |
| 16 | 57 | 296 | 1116^b |

^aIncluding five introduced species. ^bSpecies profiles in *Mammals of Africa*.

Table 2. The six volumes of *Mammals of Africa*.

| Volume | Contents | Number of species | Editors |
|--------|--|-------------------|--|
| I | Introductory chapters. Afrotheria (Hyraxes, Elephants, Dugong, Manatee, Otter-shrews, Golden-moles, Sengis and Aardvark) | 49 | Jonathan Kingdon, David C. D. Happold, Michael Hoffmann, Thomas M. Butynski, Meredith Happold and Jan Kalina |
| II | Primates | 93 | Thomas M. Butynski, Jonathan Kingdon and Jan Kalina |
| III | Rodents, Hares and Rabbits | 408 | David C. D. Happold |
| IV | Hedgehogs, Shrews and Bats | 380 | Meredith Happold and David C. D. Happold |
| V | Carnivores, Pangolins, Equids and Rhinoceroses | 93 | Jonathan Kingdon and Michael Hoffmann |
| VI | Pigs, Hippopotamuses, Chevrotain, Giraffes, Deer and Bovids | 93 | Jonathan Kingdon and Michael Hoffmann |

account of the species. They have been edited by six editors who distributed their work according to the orders with which they were most familiar. Each editor chose authors who had extensive knowledge of the species (or higher taxon) and, preferably, had experience with the species in the field. Each volume follows the same general format with respect to arrangement, subheadings and contents. Because *Mammals of Africa* has contributions from 356 authors (each with a different background and speciality), and because each volume was edited by one or more editors (each with a different perspective), it has not been possible or even desirable to ensure exact consistency throughout. Species profiles are not intended to be exhaustive literature reviews, partly for reasons of space. None the less, they are written and edited to be as comprehensive as possible, and to lead the reader to the most important literature for each species. Inevitably, not all information available could be accommodated for the better-known species, and so such profiles are a précis of available knowledge. Extensive references in the text alert the reader to more detailed information.

In addition to the species profiles, there are profiles for the higher taxa (genera, families, orders, etc.). Thus, there is a profile for each order, for each family within the order, for each genus within the family, and for each species within the genus. For some orders there are additional taxonomic levels, for example, tribes (e.g. in Bovidae), subgenera (e.g. in *Procolobus*) and species-groups, or 'superspecies' (e.g. in *Cercopithecus*). The taxonomy used in these volumes mostly follows that presented in the third edition of *Mammal Species of the World: A Geographic and Taxonomic Reference* (Wilson & Reeder 2005), although authors have employed alternative taxonomies when there were good reasons for doing so. Volume I differs from the other volumes in that it contains a number of introductory chapters about Africa and its environment, and about African mammals in general.

The continent of Africa

For the purposes of this work, 'Africa' is defined as the continent of Africa (bounded by the Mediterranean Sea, the Atlantic Ocean, the Indian Ocean, the Red Sea and the Suez Canal) and the islands on the continental shelf, which, at some time in their history, have been joined to the African continent. The largest of the 'continental islands' are Zanzibar (Unguja), Mafia and Bioko (Fernando Po). All 'oceanic islands', e.g. São Tomé, Príncipe, Annobón (Pagulu), Madagascar, Comoros, Seychelles, Mauritius, Socotra, Canaries, Madeira and Cape Verde are excluded, with the exception of Pemba, which is included because of its close proximity (ca. 50 km) to the mainland.

The names of the countries of Africa are taken from the *Times Atlas* (2005). The Republic of Congo is referred to as 'Congo' and the Democratic Republic of Congo (former Zaire) as 'DR Congo'. Smaller geographical or administrative areas within countries are rarely referred to except for Provinces in South Africa, which are used extensively in the literature. Maps showing the political boundaries of Africa (Figure 1a), the Province of South Africa (Figure 1b) and the physical features of Africa with the major rivers and lakes (Figure 1c) are provided, as well as a list of the 47 countries including their previous names that are used in the older literature on African mammals (Table 3).

Africa is the second largest continent in the world (after Asia), but it differs from other continents (except Australia and Antarctica) in being essentially an island. At various times in the past, Africa has been joined to other continents – a situation that has had a strong influence on the fauna and flora of the continent. Africa is a vast continent (29,000,000 km², 11,200,000 mi²) that straddles the Equator, with about two-thirds of its area in the northern hemisphere and one-third in the southern hemisphere. As a result, Africa has many varied climates (with seasons in each hemisphere being six months out of phase), many habitats (including deserts, savannas, woodlands, swamps, rivers, lakes, moist forests, monsoon forests, mountains and glaciers), and altitudes ranging from 155 m (509 ft) below sea level at L. Assal, Djibouti, in the Danakil (Afar) Depression, to 5895 m (19,341 ft) on Mt Kilimanjaro, Tanzania. Africa is comprised of 47 countries, some of which are very large (e.g. Sudan [2,506,000 km²; 967,000 mi²], Algeria [2,382,000 km², 920,000 mi²] and Democratic Republic of Congo [2,345,000 km², 905,000 mi²]), and others that are relatively small (e.g. Djibouti [23,200 km², 9,000 mi²], Swaziland [17,400 km², 6,700 mi²] and The Gambia [11,300 km², 4,400 mi²]). The human population density of each country also varies greatly, from about 346/km² in Rwanda to only about 2.5/km² in Namibia. With its great size and varied habitats, Africa supports a high biodiversity, including a large number of species of mammals. Likewise, most countries have a high diversity of mammals (especially when compared with temperate countries).

Africa may also be divided into biotic zones (Figure 2). A biotic zone is defined as an area within which there is a similar environment (primarily rainfall and temperature) and vegetation, and which differs in these respects from other biotic zones. Thirteen biotic zones are recognized, two of which may be divided into smaller categories. The biotic zones in which each species of mammal has been recorded are listed in each profile for several reasons. They indicate the environmental conditions in which the species lives and they provide data with which the geographic distribution can



Figure 1. (a) Political map of Africa; (b) provinces of South Africa; (c) altitudes and major rivers of Africa. South Sudan and Somaliland are not identified as separate countries in the text.

Table 3. The countries of Africa: names, areas and human population density.

| Country name | Area
(km ²) '000 | Area
(miles ²) '000 | Human population
'000 (2006) | People per km ² |
|--|---------------------------------|------------------------------------|---------------------------------|----------------------------|
| Algeria | 2,382 | 920.0 | 33,500 | 14.1 |
| Angola (includes Cabinda) | 1,247 | 481.0 | 15,800 | 12.7 |
| Benin * [Dahomey] | 113 | 43.0 | 8,700 | 77.0 |
| Botswana [Bechuanaland] | 582 | 225.0 | 1,800 | 3.1 |
| Burkina Faso * [Upper Volta; Burkina] | 274 | 106.0 | 13,600 | 49.6 |
| Burundi [part of Ruanda-Urundi (= part of Belgian Congo)] | 27.8 | 10.7 | 7,800 | 280.5 |
| Cameroon [includes former French Cameroon, German Cameroon and part of Eastern Nigeria] | 475 | 184.0 | 17,300 | 36.2 |
| Central African Republic # | 623 | 241.0 | 4,300 | 6.9 |
| Chad [Tchad] | 1,284 | 496.0 | 10,000 | 5.8 |
| Congo [Republic of Congo] | 342 | 132.0 | 3,700 | 10.8 |
| Côte d'Ivoire * [Ivory Coast] | 322 | 125.0 | 19,700 | 61.2 |
| Democratic Republic of Congo [Belgian Congo; Congo (Kinshasa); Zaire] | 2,345 | 905.0 | 62,700 | 26.7 |
| Djibouti [French Somaliland] | 23.2 | 9.0 | 800 | 34.5 |
| Egypt | 1,001 | 387.0 | 75,400 | 75.3 |
| Equatorial Guinea # (includes Rio Muni [Spanish Guinea] and Bioko I. [Fernando Po]) | 28.1 | 10.8 | 500 | 17.8 |
| Eritrea (formerly part of Ethiopia) | 94 | 36.0 | 4,600 | 48.9 |
| Ethiopia [Abyssinia] | 1,128 | 436.0 | 74,800 | 66.3 |
| Gabon # | 268 | 103.0 | 1,400 | 5.2 |
| The Gambia | 11.3 | 4.4 | 1,500 | 132.7 |
| Ghana [Gold Coast] | 239 | 92.0 | 22,600 | 94.6 |
| Guinea * | 246 | 95.0 | 9,800 | 39.8 |
| Guinea-Bissau [Portuguese Guinea] | 36 | 13.9 | 1,400 | 38.9 |
| Kenya | 580 | 224.0 | 34,700 | 59.8 |
| Lesotho [Basutoland] | 30.4 | 11.7 | 1,800 | 59.2 |
| Liberia | 111 | 43.0 | 3,400 | 30.6 |
| Libya | 1,760 | 679.0 | 5,900 | 3.6 |
| Malawi [Nyasaland] | 118 | 46.0 | 12,800 | 108.5 |
| Mali * | 1,240 | 479.0 | 13,900 | 11.2 |
| Mauritania * | 1,030 | 412.0 | 3,200 | 3.1 |
| Morocco [includes former Spanish Morocco and French Morocco]; (now also includes Western Sahara = former Spanish Sahara) | 447 | 172.0 | 32,100 | 71.8 |
| Mozambique [Portuguese East Africa] | 802 | 309.0 | 19,900 | 24.8 |
| Namibia [South-west Africa] | 825 | 318.0 | 2,100 | 2.5 |
| Niger * | 1,267 | 489.0 | 14,400 | 11.3 |
| Nigeria | 924 | 357.0 | 134,500 | 145.6 |
| Rwanda [part of Ruanda-Urundi (= part of Belgian Congo)] | 26.3 | 10.2 | 9,100 | 346.0 |
| Senegal * | 197 | 76.0 | 11,900 | 60.4 |
| Sierra Leone | 71.7 | 27.7 | 5,700 | 79.5 |
| Somalia [‡] [British Somaliland and Italian Somaliland; Somali Republic] | 638 | 246.0 | 8,900 | 13.9 |
| South Africa | 1,220 | 471.0 | 47,300 | 38.7 |
| Sudan [§] [Anglo-Egyptian Sudan] | 2,506 | 967.0 | 41,200 | 16.4 |
| Swaziland | 17.4 | 6.7 | 1,100 | 63.2 |
| Tanzania [German East Africa; Tanganyika] (now includes Zanzibar I., Mafia I. and Pemba I.) | 945 | 365.0 | 37,900 | 40.1 |
| Togo [Togoland] | 56.8 | 21.9 | 6,300 | 110.9 |
| Tunisia | 164 | 63.0 | 10,100 | 61.6 |
| Uganda | 236 | 91.0 | 27,700 | 117.4 |
| Zambia [Northern Rhodesia] | 753 | 291.0 | 11,900 | 15.8 |
| Zimbabwe [Southern Rhodesia] | 391 | 151.0 | 13,100 | 33.5 |
| Totals/mean density | 29,448 | 11,383 | 902,600 | 56.8 |

Former names are listed in chronological order in square brackets, with the oldest name listed first. Obsolete names are listed because much of the older literature refers to past colonial entities. * = formerly part of French West Africa. # = formerly part of French Equatorial Africa. § At the time of going to press, the country of Sudan had been divided into two: the Republic of Sudan in the north, and the Republic of South Sudan in the south. ‡ The former British Somaliland is now a self-declared state under the name of the Republic of Somaliland, but remains internationally unrecognized.



Figure 2. The biotic zones of Africa.

be explained and predicted. Furthermore, the number of biotic zones exploited by a species indicates its level of habitat tolerance and the extent to which it is vulnerable to loss of a particular type of habitat. The Rainforest Biotic Zone (Figure 3) and the South-West Arid Biotic Zone are divided into regions and sub-regions that reflect the different biogeographical distributions of species, each region/sub-region having a community of mammals and other animals that is different to any other. Details of the Biotic Zones of Africa, and the regions and sub-regions of the Rainforest Biotic Zone and the South-West Arid Biotic Zone, are given in Volume I of *Mammals of Africa*.

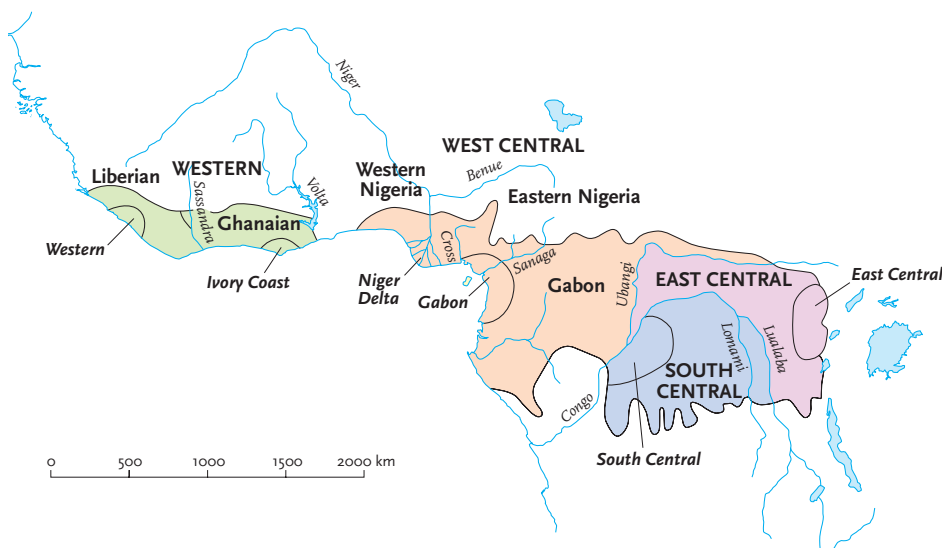


Figure 3. The Rainforest Biotic Zone showing the regions, sub-regions and refugia. Regions are indicated in capital letters and colours: Western region – green; West Central region – brown; East Central region – purple; South Central region – blue. Sub-regions are indicated in lower case letters. Refugia are indicated in lower case italics (after Happold 1996 and references therein; see also Happold & Lock, Volume I, *Mammals of Africa*).

The rodents, hares and rabbits of Africa

This volume, Volume III, is devoted to the orders Rodentia and Lagomorpha. The order Rodentia contains more species (395 spp.) than any other order of African mammals and comprises about 36% of African mammals; in contrast, the order Lagomorpha contains relatively few species (13 spp.). These two orders, together with two orders (Afrosoricida and Macroscelidea) in Volume I and three orders (Erinaceomorpha, Soricomorpha and Chiroptera) in Volume IV, constitute the ‘small mammals of Africa’ and collectively comprise 74.1% (827 of 1116) of all African mammalian species. Many of these small species have not been studied in detail because of their rarity and small geographic ranges. However, some of the more common and widespread species are quite well known, especially with respect to their importance within their communities and because of their importance as ‘bushmeat’ and as hosts for diseases of humans and livestock.

The profiles for Volume III were submitted to the editor between 2001 and 2005. It has not been possible to revise profiles since then except for a few details such as the completion of citations for papers previously given as ‘in press’, alterations (if necessary) to the category of threat in the conservation section of species profiles, and where there have been changes in taxonomy and distribution. An Appendix has been added listing new taxa of African rodents described during the period 2005–2010 and which have not been profiled in this volume.

Species profiles

Information about each species is given under a series of subheadings. The amount of information under each of these subheadings varies greatly between species; where no information is available, this is recorded as ‘No information available’ or words to this effect. The sequence of subheadings and other information is as follows:

Scientific name (genus and species) The currently accepted name of the species.

Vernacular Names English, French and German names are given, as available. The first given English name is the preferred vernacular name for the species; alternative names are given in parentheses for some species. Wilson & Cole (2000) list proposed vernacular names for all the world's mammals; most of these names were also given in the third edition of *Mammal Species of the World* (Wilson & Reeder 2005). Although these works have been consulted, the names used have not always been adopted in *Mammals of Africa*. In Volume III, French names were either provided by authors, or taken from Gunther (2002); most of the German names were provided by Anke Hoffman.

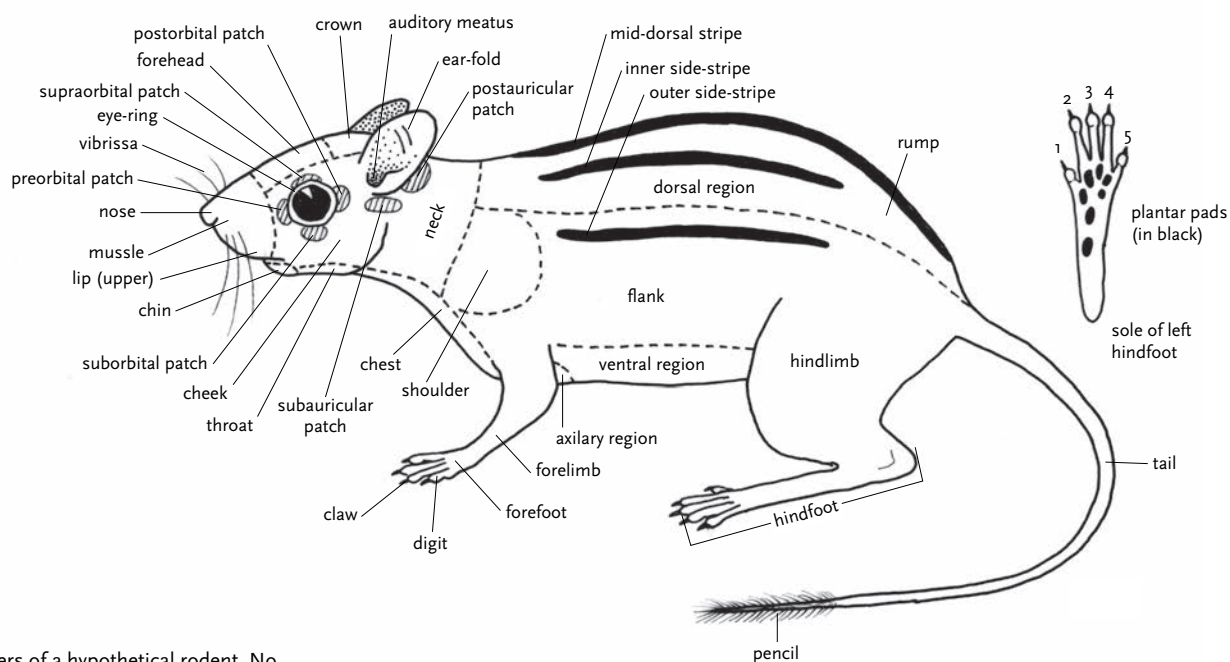
Scientific Citation This provides the full scientific name of the species, i.e. genus name, species name, authority name and date of authority. Parentheses around the authority's name and date indicate that the species was originally named in a different genus to the one it is placed in now. The scientific name is followed by the publication in which the species was described, and the type locality (i.e. where the type specimen [or type series] was obtained). Most of this information is taken from Wilson & Reeder (2005).

Taxonomy This section contains information about previous scientific names of the species, and problems and controversies (if any) associated with its nomenclature and relationships with other species. For some species, there is considerable information about these topics; for others, there may be nothing. Synonyms are listed in alphabetical order (without the taxonomic authority for each unless essential for clarity) and the number of subspecies (if any) is presented; most of this information is taken from Wilson & Reeder (2005). The chromosome number is given if available, and in some cases this is followed by other information relevant to the chromosomes. In late 2006, a revised edition of the *Atlas of Mammalian Chromosomes* was published (O'Brien *et al.* 2006), but it has not been possible to incorporate the findings of that important work here.

Description This section, together with the illustrations and relevant tables, provides sufficient information to identify the species as well as describing characters that are relevant to the habits and lifestyle of the species. The section begins with a brief overall description of the species, including an indication of size. This is followed by a detailed description of the external characters of the species – head (and parts of the head), dorsal pelage, legs, feet, ventral pelage, and tail (in this order), as well as any special characteristics unique to the species. For some species, diagnostic characteristics of the skull are given. The characters described in this section are common to all subspecies (if any) of the species (see also Geographic Variation). It was not possible – or desirable – to describe the same suite of characters for every species. Instead, an appropriate selection was made for each family and/or genus, and therefore the same suite of characters is described for all members of the relevant taxon. Consequently the descriptions of related species are comparable and compatible. Characters that are diagnostic to the genus are not necessarily repeated in a species profile; hence higher taxa profiles should also be consulted. The number and arrangement of nipples in adult females is noted wherever this feature varies between the taxa being discussed (see Glossary). The Tables allow easy comparison between taxa within a genus or family.

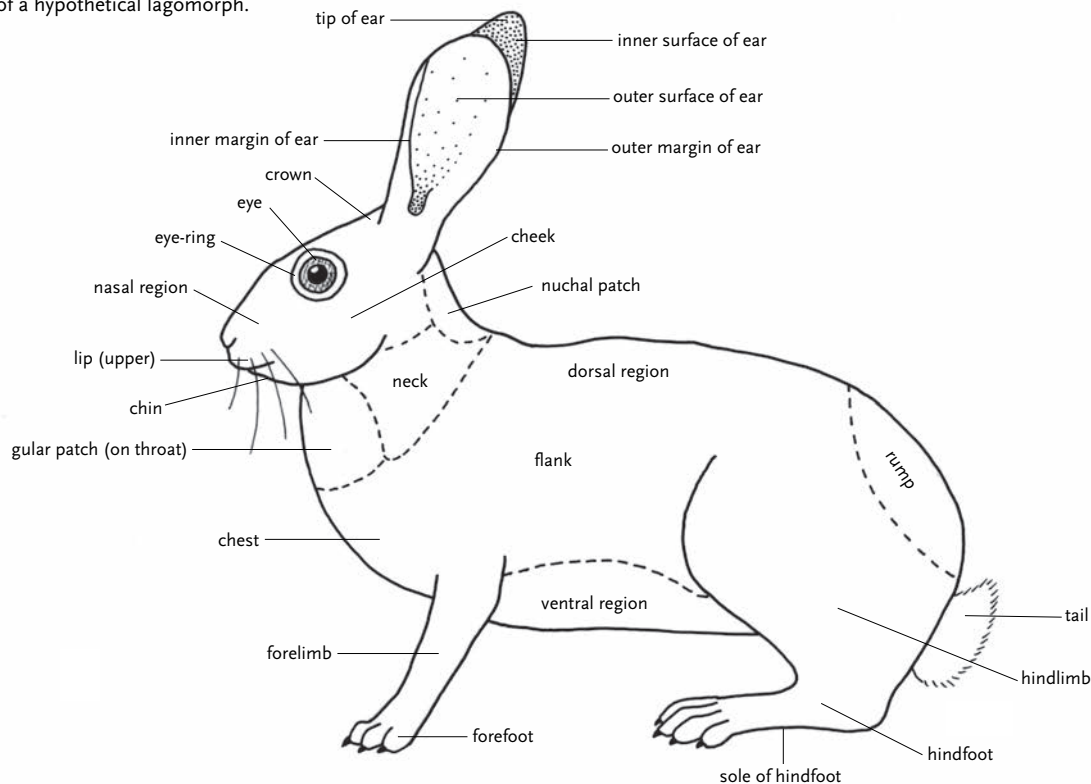
Geographic Variation Variation within the species may be of two sorts: (a) clinal variation without subspecies, or (b) subspecific variation. If (a), there is a description of the character(s) that alter clinally across the geographic range of the species. If (b), each of the subspecies is listed with its geographic range and the characters that distinguish it from other subspecies of the species.

Similar Species Species that are sympatric or parapatric with the species under consideration, and with which it may be confused, are listed along with diagnostic characteristics (additionally, readers may



External characters of a hypothetical rodent. No species has this particular combination of characters.

External characters of a hypothetical lagomorph.



refer to profiles of the similar species in question). In some instances, similar species that are allopatric in distribution are also included.

Distribution The first sentence, 'Endemic to Africa', if given, indicates that this is an African species and does not occur in the wild on any other continent; if a species also occurs outside Africa (and hence is not endemic), this is noted at the end of this section. The next sentence gives the Biotic Zone (or Zones) in which the species has been recorded because this information indicates the sorts of environments exploited by that species, its tolerance of different environmental conditions, and the extent to which it is likely to be threatened by habitat change. Also, it is the basis for predictions of its distribution outside the currently known limits. Finally, the countries (or parts of countries) where the species has been recorded are listed; sometimes other data (such as altitudinal range and habitat) are also included. As a general rule, descriptions of the geographic range for species with very restricted distributions are more precise in terms of information given (including, for example, geographic coordinates) than for more widespread species, where a more generalized statement is adequate. A distribution map (see below) augments the information given here.

Habitat This section provides a description of the habitat, or range of habitats, where the species lives. Details of plant communities, plant species, vegetation structure, soil type and/or structure and water availability, etc. (if available) are also recorded. Other information may include average annual rainfall, altitudinal limits and seasonal variations in habitat characteristics.

Abundance This section attempts to indicate the comparative abundance of the species in its habitat. For many species, quantitative data are unavailable but the species can be assessed as 'abundant',

'common', 'uncommon', 'rare', 'rarely seen but frequently heard', 'rarely collected' etc. For some species, abundance may be expressed as estimates of density (e.g. number/ha or number/km²), or relative abundance within the community (e.g. 'comprised 40% of small mammals captured', 'the second most numerous species'). For the better-known or rare species, actual numbers of individuals for the species may be given. Other information may include seasonal changes in density, frequency of observations, or the relative abundance of specimens in collections.

Adaptations This section describes morphological, physiological and behavioural characteristics that show how the species uniquely interacts with its environment, with conspecifics, and with other animals. This section may also describe species-specific adaptations for feeding, locomotion, burrowing, domiciles, mechanisms for orientation, production of sound, sensory mechanisms and activity patterns. In some instances, comparison with related or convergent species allows the unique adaptations of the species under discussion to be detailed or emphasized.

Foraging and Food The first sentence briefly describes the diet of the species (e.g. insectivorous, carnivorous, granivorous, etc.). This may be followed by the methods of collecting food (foraging), size of home-range and daily distance moved, and descriptions of feeding behaviour. The diet, if well-known, is then described in one or more of the following ways: a list of the taxa of animals or plants consumed, a quantitative measure based on direct observations, or by a qualitative or quantitative analysis of the stomach contents or faeces.

Social and Reproductive Behaviour Topics in this section may include social organizations (e.g. solitary, social, or colonial), group

size and composition; agonistic and amicable behaviour, territoriality and home-range (including quantitative data), courtship and mating, parental behaviour, and parent–young interactions, cooperative breeding, social vocalizations, and interactions with other species (mammals, birds, etc.).

Reproduction and Population Structure This section begins with an assessment of reproductive strategy (if known) and the times/seasons of the year when individuals are reproductively active (pregnancy and lactation in females, active spermatogenesis in males). Other information may include length of gestation, times/seasons of births, including peaks of births, litter-size, birth-weight and size, spacing of litters, growth and time to weaning, maturity, longevity, and mortality rates. Reproductive chronologies, if known, give data for both individuals and local populations. Reproductive strategies, if known, are described with respect to locality, food availability and population density. Population structure (sex ratio, adult/young ratio, abundance of different cohorts in the population at different times of the year) may be described, and related to seasonal variations in reproduction and environmental variables.

Predators, Parasites and Diseases The known predators, known parasites (usually ectoparasites only) and some diseases are listed. Additional information is given if the species is a host to diseases that affect humans and domestic stock, and if it is utilized as food for humans ('bushmeat').

Remarks This subheading subsumes five of the above subheadings (Adaptations, Foraging and Food, Social and Reproductive Behaviour, Reproduction and Population Structure, and Predators, Parasites and Diseases) in those instances where there is little or no information available.

Conservation The conservation status of the species (i.e. its IUCN Category) is taken from the 'Red List of Threatened Species' prepared by the International Union for Conservation of Nature (IUCN). The IUCN Red List Categories follow the definitions given in the *IUCN Red List Categories and Criteria Version 3.1* (see www.iucnredlist.org) and are listed in Table 4. For those species that are classified as threatened (i.e. 'Vulnerable', 'Endangered' and 'Critically Endangered'), readers may obtain detailed reasons (the criteria) for the classification on the IUCN Red List website. The status of some species has been changed in recent years because of improved knowledge, changes in taxonomy, or the impact of threatening processes or conservation action; detailed reasons for the present status, and past status, are given on the IUCN Red List website. If a species is listed on an Appendix I or Appendix II under CITES (Convention on International Trade in Endangered Species; www.cites.org), this is also indicated. For some species, additional information is provided, such as presence in protected areas, major threats, and current or recommended conservation measures.

Measurements A series of morphological measurements is provided. For each species there is a standard set of measurements. The abbreviation and definition for each measurement is given in the Glossary. A measurement is cited as the mean value (with minimum value to maximum value in parentheses) and sample size. For some, the standard deviation (mean \pm 1 S.D.) is given instead of the range. For most measurements, data for males and females are combined but where there is sexual dimorphism, measurements for males and females are given separately. Where possible, measurements also detail the location(s) where the specimens were obtained, and the source of the data. Sources are either cited publications, or specimens in museums, or unpublished information from authors or others. The acronyms for museums where specimens were examined

Table 4. Definitions for the IUCN Red List categories (from IUCN – Red List Categories, Version 3.1).

| Category | Description |
|-----------------------------------|--|
| Extinct (EX) | A taxon is Extinct when there is no reasonable doubt that the last individual has died. A taxon is presumed Extinct when exhaustive surveys in known and/or expected habitat, at appropriate times (diurnal, seasonal, annual), throughout its historic range have failed to record an individual. Surveys should be over a time frame appropriate to the taxon's life-cycles and life form. |
| Extinct in the Wild (EW) | A taxon is Extinct in the Wild when it is known only to survive in cultivation, in captivity or as a naturalized population (or populations) well outside the past range. A taxon is presumed Extinct in the Wild when exhaustive surveys in known and/or expected habitat, at appropriate times (diurnal, seasonal, annual), throughout its historic range have failed to record an individual. Surveys should be over a time frame appropriate to the taxon's life-cycle and life-form. |
| Critically Endangered (CR) | A taxon is Critically Endangered when the best available evidence indicates that it meets any of the criteria A to E for Critically Endangered, and it is therefore considered to be facing an extremely high risk of extinction in the wild. |
| Endangered (EN) | A taxon is Endangered when the best available evidence indicates that it meets any of the criteria A to E for Endangered, and it is therefore considered to be facing a very high risk of extinction in the wild. |
| Vulnerable (VU) | A taxon is Vulnerable when the best available evidence indicates that it meets any of the criteria A to E for Vulnerable, and it is therefore considered to be facing a high risk of extinction in the wild. |
| Near Threatened (NT) | A taxon is Near Threatened when it has been evaluated against the criteria but does not qualify for Critically Endangered, Endangered or Vulnerable now, but is close to qualifying for (or is likely to qualify for) a threatened category in the near future. |
| Least Concern (LC) | A taxon is Least Concern when it has been evaluated against the criteria and does not qualify for the Critically Endangered, Endangered, Vulnerable or Near Threatened categories. Widespread and abundant taxa are included in this category. |
| Data Deficient (DD) | A taxon is Data Deficient when there is inadequate information to make a direct, or indirect, assessment of its risk of extinction based on its distribution and/or population status. Data Deficient is not a category of threat. Listing of taxa in this category indicates that more information is required and acknowledges the possibility that future research will show that a threatened classification is appropriate. |
| Not Evaluated (NE) | A taxon is Not Evaluated when it has not yet been evaluated against the criteria. |

and measured are given in Table 5. Most museum records have been provided by the author of the profile; others – when an author did not have the measurements or did not have the opportunity to visit museums – were provided by the editor.

Key References A select list of references, which provides more general information on the species. Each reference is given in full in the Bibliography.

Author The name of the author, or authors, is given at the end of each profile. All profiles should be cited using the author name(s).

Tables For selected taxa (mainly families and genera) tables provide details of the main characteristics of these taxa and can be used as an aid to identification. The tables were prepared by the editor.

Higher taxon profiles

The profiles for orders, families and genera are less structured than for the species. Each profile usually begins with a listing of the taxa in the next lower taxon; for example, each family profile lists the genera in that family. An exception to this arrangement is where a

Table 5. Acronyms for museum and private collections.

| Acronym | Museum name |
|---------|---|
| ACBG | Museo di Anatomia Comparata, Università di Roma ‘La Sapienza’, Rome, Italy. |
| AM | Amatole Museum, King William’s Town, South Africa [formerly Kaffrarian Museum]. |
| AMNH | American Museum of Natural History, New York, USA. |
| BMNH | Natural History Museum, London, UK [formerly British Museum (Natural History)]. |
| CM | Carnegie Museum of Natural History, Pittsburgh, USA. |
| DM | Durban Natural Science Museum, Durban, South Africa. |
| FMNH | Field Museum of Natural History, Chicago, USA. |
| HC | Happold Collection, Canberra, Australia (private collection). |
| HZM | Harrison Zoological Museum, Sevenoaks, Kent, UK. |
| IRSN | Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium. |
| LACM | Los Angeles County Museum, Los Angeles, USA. |
| MM | McGregor Museum, Kimberley, South Africa. |
| MNHN | Museum National d’Histoire Naturelle, Paris, France. |
| MZUF | Museo Zoologico de ‘la Specola’, Università di Firenze, Italy. |
| NMK | National Museums of Kenya, Nairobi, Kenya. |
| NMN | National Museum of Namibia, Windhoek, Namibia. |
| NMW | Naturhistorisches Museum, Wien (Vienna), Austria. |
| RMCA | Royal Museum for Central Africa, Tervuren, Belgium. |
| SAM | South African Museum, Cape Town, South Africa. |
| SMF | Senckenberg Museum, Frankfurt, Germany. |
| SMNS | Staatliches Museum für Naturkunde, Stuttgart, Germany. |
| TM | Transvaal Museum, Pretoria, South Africa. |
| USNM | United States National Museum of Natural History, Smithsonian Institution, Washington, USA. |
| ZFMK | Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany. |
| ZMMU | Zoological Museum, Moscow University, Moscow, Russia. |

taxon has only one lower taxon. Higher taxa profiles provide the characteristics common to all members of that taxon. Some of these characteristics may not be repeated in lower taxon profiles (unless essential for identification) so readers are encouraged to consult also the next higher taxon profile, e.g. the species profile for *Lophuromys sikapusi* should be consulted in association with the genus *Lophuromys* profile.

Distribution maps

Each species profile, with very few exceptions, contains a pan-African map showing the geographic range of the species. Most maps were provided by the author of the profile and were compiled from literature records and museum specimens; some maps were provided by the editor(s) when it was not possible for the author to do so. Each map shows the boundaries of the 47 countries of Africa, some of the major rivers (Nile, Niger–Benue, Congo [with the tributaries Ubangi, Lualaba and Lomani], Zambezi and Orange), and Lakes Chad, Tana, Turkana (formerly Rudolf), Albert, Edward, Victoria, Kyoga, Kivu, Tanganyika, Malawi, Mweru, Bangwuela and Kariba. The map projection is ‘Transverse Mercator, with the following parameters: False Easting: 0; False Northing: 0; Central Meridian: 20; Linear Unit: metre; Datum: Clarke 1866’.

The geographic distribution of a species is indicated as:

- red shading = current range(s). When presented, different colour shading denotes subspecies.
- × = isolated locations considered to be separate from the main geographic range(s). Some locations indicated by × may include two or more closely spaced locations.
- ? = locality of uncertain validity; relevant information usually in text.
- red arrow = present on the island indicated by the arrow.

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Order RODENTIA – Rodents

Rodentia Bowdich, 1821.

| | | |
|---------------------------------------|--|--------|
| Sciuridae (10 genera, 37 species)* | Squirrels | p. 38 |
| Gliridae (2 genera, 16 species) | Dormice | p. 102 |
| Dipodidae (2 genera, 3 species) | Jerboas | p. 135 |
| Spalacidae (2 genera, 3 species) | Mole-rats, African Root-rats | p. 143 |
| Nesomyidae (12 genera, 34 species) | Pouched Rats and Mice, Swamp Mouse, Climbing Mice, Large-eared Mice, Fat Mice, White-tailed Rat, Rock Mice | p. 153 |
| Cricetidae (2 genera, 2 species) | Voles, Maned Rat | p. 210 |
| Muridae (50 genera, 264 species)** | Gerbils and Jirds, Old World Rats and Mice, Vlei Rats | p. 216 |
| Anomaluridae (3 genera, 7 species) | Anomalures | p. 602 |
| Pedetidae (1 genus, 2 species) | Springhares | p. 618 |
| Ctenodactylidae (4 genera, 5 species) | Gundis | p. 628 |
| Bathyergidae (5 genera, 15 species) | Mole-rats | p. 641 |
| Hystriidae (2 genera, 3 species) | Porcupines | p. 671 |
| Petromuridae (1 genus, 1 species) | Noki (Dassie Rat) | p. 680 |
| Thryonomyidae (1 genus, 2 species) | Cane Rats | p. 685 |
| Myocastoridae (1 genus, 1 species)† | Coypu | p. 691 |

* Including *Sciurus carolinensis* introduced recently into South Africa.

** Including *Mus musculus*, *Rattus norvegicus* and *Rattus rattus* introduced in recent historical times.

† Introduced recently into Kenya.

Distribution and diversity

Rodentia is the largest order of Mammalia, encompassing 2,277 of 5,422 living mammal species or approximately 42% of worldwide mammalian biodiversity (Wilson & Reeder 2005); of these 2,277 rodent species, 395 species (in 15 families and 98 genera) occur in Africa (see above and Table 1). Rodents are indigenous to every continent except Antarctica and inhabit most small to large land-bridge and oceanic islands (originally absent from Iceland, New Zealand and some oceanic and high Arctic islands). The order's global presence has become nearly ubiquitous as certain commensal species (see subfamily Murinae profile) have expanded their ranges in concert with human peregrinations during the Holocene. Large islands, island archipelagos and those continents with a geologic history of periodic isolation, have afforded ideal geographic settings for *in situ* radiations of major clades of Rodentia. Nowhere, with the arguable exception of South America, is this cladogenetic exuberance of the order so spectacularly showcased as in Africa, where 14 of the 33 recognized rodent families (*sensu* Wilson & Reeder 2005) are indigenous; a 15th family, Myocastoridae, has been introduced into Africa (Table 6). Seven of these 15 families are endemic to the continent (Table 6); at the generic and specific levels, the extent of endemism is substantially greater and highlights the contribution of African landscapes to the phylogenetic diversification of these rodent families (Table 1). Most non-endemic genera and species involve North African taxa that range into the nearby Arabian Peninsula and

Table 6. The 15 families of recent African Rodentia, with the number of constituent genera and species. Percentage endemism is based on the geographic limits of the African continent as defined for this volume and on the taxa recognized herein.

| Family | Endemic | No. of genera | No. of endemic genera | No. of species | No. of endemic species |
|-----------------|------------------|---------------|-----------------------|----------------|------------------------|
| Sciuridae | No | 10 | 9 | 37 | 36 |
| Gliridae | No | 2 | 1 | 16 | 16 |
| Dipodidae | No | 2 | 0 | 3 | 1 |
| Spalacidae | No | 2 | 1 | 3 | 2 |
| Nesomyidae | Yes ^a | 12 | 12 | 34 | 34 |
| Cricetidae | No | 2 | 1 | 2 | 2 |
| Muridae | No | 50 | 41 | 264 | 250 |
| Anomaluridae | Yes | 3 | 3 | 7 | 7 |
| Pedetidae | Yes | 1 | 1 | 2 | 2 |
| Ctenodactylidae | Yes | 4 | 4 | 5 | 5 |
| Bathyergidae | Yes | 5 | 5 | 15 | 15 |
| Hystriidae | No | 2 | 0 | 3 | 2 |
| Petromuridae | Yes | 1 | 1 | 1 | 1 |
| Thryonomyidae | Yes | 1 | 1 | 2 | 2 |
| Myocastoridae | No ^b | 1 | 0 | 1 | 0 |
| Totals | 15 | 98 | 80 | 395 | 375 |
| % endemics | 47% | | 82% | | 94.9% |

^a Excluding the Malagasy subfamily Nesomyinae. ^b Introduced family.

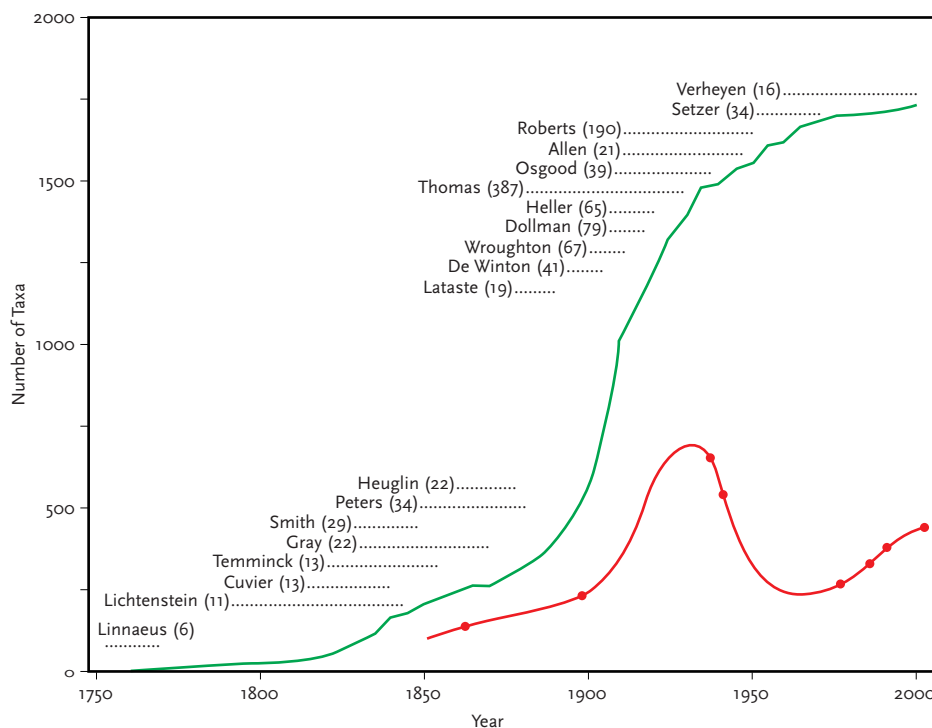


Figure 4. The number of taxa of African rodents. Green line: cumulative number of species-group taxa (species and subspecies) described from Linnaeus (ca. 1750) to the year 2003 (total = 1729); principal authors and the span of their scientific contributions (dotted lines) are indicated, with the number of African taxa they described in parentheses. Red line: number of species considered scientifically valid (line fitted visually); red dots indicate species numbers recognised by Murray (1866), Trouessart (1897–98), Allen (1939), Ellerman (1940–41), Corbet & Hill (1980, 1991), Wilson & Reeder (1993, 2005). (From original by M. D. Carleton.)

Middle East; generic and specific endemism is nearly 100% within sub-Saharan zones, where taxa tend to be more narrowly restricted in distribution and limited to distinct sub-regions (e.g. Coe & Skinner 1993, Happold 1996).

The magnitude of species endemism within Africa, albeit nearly 95% (Table 6), surely remains an underestimate, for the number of rodent species considered to be valid has continued to increase in the last quarter-century (Figure 4). Knowledge of the diversity of African rodents initially grew slowly in the post-Linnaean discovery phase (ca. 1800–1860s). However, an exceptionally fertile period of natural history exploration and taxonomic description commenced in the late 1800s, during which the subspecies emerged as a standard rank to formally identify intra-specific variation. Oldfield Thomas of the British Museum of Natural History was a prodigious worker and influential systematist throughout this eruptive phase of taxonomic description (ca. 1880–1930s). By the conclusion of this era, more than 600 species of African rodents were recognized (Allen 1939). During the middle 1900s (ca. 1940–1970s), the number of species considered to be valid dipped to less than 300 (Corbet & Hill 1980), a decrease driven by widespread acceptance of the biological species concept and its taxonomic application as intergrading geographic races (subspecies). New subspecies continued to be named at a high rate, and many species described during the preceding eruptive phase were cursorily demoted to subspecies. The last subspecies of African Rodentia were named in 1983. The revived appreciation of greater species richness, as witnessed in the past two decades, has been impelled by new field discoveries, by reinvigorated museum-based revision and by improved methodologies for evaluating and taxonomically interpreting inter-population differences, be they morphological, chromosomal, or molecular. Thus, the approximately 400 species covered herein are a tenuous summary of an animated study in progress, whose outcome over the next 10–15 years is likely to stabilize the number of African rodents at about 500 species (Figure 4).

Coupled with its species richness, the Rodentia is remarkable for its morphological diversity, and essentially every ecological, behavioural, trophic and locomotory adaptive theme that has evolved within the order is represented among the African taxa (see familial and generic accounts).

Morphological definition and incisor function

Notwithstanding the protean morphological variety exhibited by rodents, the order is well defined in combination by several derived characters or functionally related character complexes. The upper and lower jaws each bear a single pair of enlarged and ever-growing chisel-like incisors that ontogenetically represent retained deciduous second incisors ($i^{2/2}$ – Luckett 1985); the incisor enamel is mainly limited to the anterior surface and is two-layered, the inner layer of which is composed of hydroxyapatite crystal prisms arranged in characteristic decussating patterns (Martin 1993, 1999). The dentition consists of a maximum of 22 teeth (incisors $1/1$, canines $0/0$, premolars $2/1$, molars $3/3$) as documented in the earliest of fossil species currently recognized as rodents. The upper and lower molars are quadritubercular, the uppers possessing a longitudinal enamel connection (mure) between the protocone and hypocone and the lowers lacking a paraconid (Meng *et al.* 2003, Marivaux *et al.* 2004). The glenoid fossa is elongate, lacking pre- and postglenoid processes, and enables the free anterior–posterior excursion of the mandible into effective occlusion for gnawing (incisors) or chewing (cheekteeth). A conspicuous diastema is present between the anterior incisors and posterior cheekteeth due to loss of the first and last incisors, canines and anterior premolars; the upper diastema is significantly longer than the lower. With formation of a diastema, fur-covered labial infoldings occur behind the incisors to partially segregate gnawing from chewing activity. The masticatory muscles

are complexly subdivided, the masseteric series being massive in size and volume relative to the temporalis; a discrete superficial masseter is always present. In primitive rodents, all masseter muscles originate from the zygomatic arch, and the infraorbital foramen is small, serving as passage only for nerves and blood vessels (protrogomorphous). In derived rodents, different masseteric bundles extend anteriorly either onto an expansive zygomatic plate (sciurumorphous), through a greatly enlarged infraorbital foramen onto the lateral rostrum (hystricomorphous), or onto both in combination (myomorphous). The latter three zygomaseteric morphologies are represented among living African Rodentia (Figure 5) and have figured prominently as characters in its subordinal classification (see below). The auditory bulla is composed entirely of the ectotympanic bone. The literature on rodent morphology is extensive: see Tullberg (1899), Ellerman (1940) and Carleton (1984) for additional morphological characterization of Rodentia; see Hartenberger (1985), Luckett (1985), Luckett & Hartenberger (1993), Landry (1999) and Meng *et al.* (2003) for phylogenetic commentary on the preceding traits and others as ordinal synapomorphies, particularly as compared with Lagomorpha.

The enlarged incisor teeth, reduced to a single pair each at the front of the upper and lower jaws, represent a key evolutionary innovation (*sensu* Brooks & McLennan 1991) that plausibly fostered the remarkable success of the order, which typically constitutes the most species-rich clade of Mammalia found in the fossil record since its initial radiation in the early to middle Eocene (40–55 mya). That success owes much to the intrinsic biomechanical properties of the continually erupting incisors and their consequent effectiveness as a multipurpose tool. The differential hardness of the enamel and dentine, together with microstructural specializations of the enamel layers, allow formation of an acute edge. Hydroxyapatite crystal prisms of the inner enamel layer are arranged in intricately interwoven patterns (pauciserial in early rodents, multiserial and uniserial in derived lineages – Martin 1993); these further reinforce the working bevel of the incisors and inhibit propagation of cracks along the relatively brittle and thin enamel sheath during conditions of intense activity and when strong forces are concentrated on the narrow tips (von Koenigswald 1985, Martin 1993). Ultimately, the keen sharpness and chisel shape of the incisors are achieved by deliberate honing motions of the lower incisors upon the upper incisors, not as a coincidental result of wear (von Koenigswald 1985, Druzinsky 1995). Indeed, some researchers consider the chisel shape of the rodent lower incisor and its intentional maintenance as a cardinal morphological-behavioural synapomorphy of the order (Landry 1999, Meng *et al.* 2003).

The adaptive role of the incisors is usually described as ‘gnawing’, but that term inadequately captures the range and multiplicity of their uses. Biting and cutting, piercing and stabbing, holding and seizing, tearing and slicing, gouging and scraping (digging), chipping and prising, interdental sharpening and chattering, gathering and carrying of foodstuffs or nesting material, carrying of young by parents and teat-clinging by neonates, are other functions observed within species and across the order (Lawrence 1941, Landry 1970, Offermans & DeVree 1990, Druzinsky 1995, van der Merwe & Botha 1998). Most of the functions of the incisors involve feeding and food habits and reflect the diverse trophic niches and dietary flexibility that are hallmarks of Rodentia (Landry 1970); other functions relate to aspects of communication, behaviour, ecology and reproduction. The exceptional mobility of the mandible, so integral to a rodent’s

livelihood, was evolutionarily realized through extensive reorientation of the jaw muscles and concomitant remodelling of the head skeleton. Although these adaptations originally appeared to protrude the mandible for incisor occlusion and to strengthen incisal cutting (Meng *et al.* 2003), they coincidentally preadapted the masticatory apparatus for subsequent evolution of molar hypsodonty, planar occlusal surfaces and propalinal chewing suited to triturating high-fibre plant material, notably grasses (Landry 1999, Mess *et al.* 2001). Expanding reliance upon herbivorous resources has characterized several rodent lineages that independently radiated in concert with the development of open environments in the Oligocene and proliferation of grasslands in the Miocene (Jacobs *et al.* 1999, Mess *et al.* 2001).

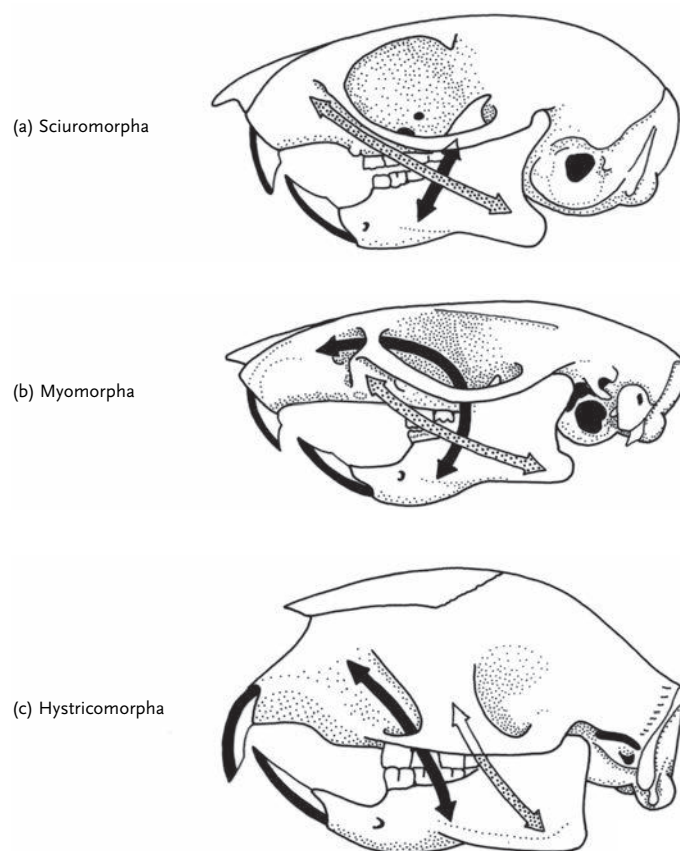


Figure 5. Orientation of jaw musculature in the three suborders of African Rodentia. Stippled arrow = masseter lateralis muscle (= middle masseter). Black arrow = masseter medialis muscle (= deep masseter). Clear arrow = muscle attached to inner surface of zygomatic arch.

(a) Sciuromorpha: masseter lateralis originates on outer side of skull in front of orbit (zygomatic plate) and inserts on posterior part of mandible, and masseter medialis originates on the inner surface of the zygomatic arch and inserts on the middle part of the mandible. Infraorbital foramen is very small; no part of the masseter muscle passes through the foramen.
(b) Myomorpha: masseter lateralis is similar to that of Sciuromorpha but the masseter medialis has pushed up through the orbit and through the enlarged infraorbital foramen so its origin is on the rostrum.
(c) Hystricomorpha: masseter lateralis retains the primitive position originating on the inner surface of the zygomatic arch and inserts on the mandible, and the masseter medialis has its origin more anteriorly on the mandible and passes through the enlarged infraorbital foramen and inserts on the rostrum. Other jaw muscles (superficial masseter muscle and temporalis muscles), which are similar in all suborders, are not shown. The area of muscle attachment to the underlying bone is more extensive than the arrows indicate (after Romer 1966).

Phylogeny and classification

Such morphological traits have long encouraged the view that living rodents are derived from a common ancestor, as conveyed in numerous classifications of Rodentia from Brandt (1855) to Landry (1999). Taxonomically broad, cladistic studies of morphological characters have sustained the historical view of Rodentia as a monophyletic group (Novacek 1985, Novacek & Wyss 1986, Luckett & Hartenberger 1993, Shoshani & McKenna 1998, Meng *et al.* 2003). Although some early gene-sequencing studies implied, or concluded, that hystricognath rodents (*Cavia* and relatives) represent a separate mammalian order and that Rodentia as conventionally classified is polyphyletic (Graur *et al.* 1991, 1992, D'Erchia *et al.* 1996), the ensuing wave of molecular research, based on wider sampling of taxa (particularly the in-group Rodentia) and genes, has decisively solidified the case for rodent monophyly (Huchon *et al.* 1999, 2002, Robinson-Rechavi *et al.* 2000, Adkins *et al.* 2001, 2003, Debry & Sagel 2001, Lin *et al.* 2002, Armine-Madsen *et al.* 2003, Debry 2003, Waddell & Shelley 2003, Reyes *et al.* 2004).

Recognition of major lines of descent within Rodentia and their formal classification, usually at the rank of suborders, historically has provoked more contention than the question of monophyly of the order.

The two prevalent classificatory schemes stem from Brandt (1855) and Tullberg (1899): Brandt's tri-subordinal division emphasized zygomaseteric morphology (sciuromorphy, hystricomorphy and myomorphy); and Tullberg's dual subordinal arrangement integrated mandibular conformation (sciurognathy versus hystricognathy) with zygomaseteric criteria (Table 7). Subsequently, most systematists have adopted or elaborated either Brandt's (Alston 1876, Simpson 1945, Wood 1965) or Tullberg's subordinal taxonomies (Ellerman 1940, Chaline & Mein 1979, Landry 1999). Other classifications have recognized anywhere from five to 16 major phyletic divisions within Rodentia, whether or not called a suborder *per se* (Thomas 1897, Miller & Gidley 1918, Wood 1955, Thaler 1966, Hartenberger 1985, 1998, McKenna & Bell 1997, Carleton & Musser 2005). In spite of these classificatory disagreements at the level of suborder, certain phyletic affinities among the 33 recognized families have consistently emerged based on morphological and gene-sequencing evidence published over the past decade. Although ranks between family and order are not considered in this volume, the following four kinship-groups are apparent among the 14 rodent families that occur in Africa. Morphological characters, evidence for monophyly, and fossil history of individual families are covered in the respective family introduction.

Table 7. Taxonomic placement and presumed higher-level relationships among 14 African families as interpreted in past influential classifications of Rodentia.^a

| Alston (1876) | Tullberg (1899) | Simpson (1945) | McKenna & Bell (1997) |
|--|---|---|---|
| Sciuromorpha
Sciuridae
Anomaluridae | Sciurognathi
Sciuromorphi
Sciuridae | Sciuromorpha
Sciuridae
Sciuromorpha <i>i.s.</i>
Anomaluroidea
Anomaluridae
Pedetidae | Sciuromorpha
Sciuridae |
| Myomorpha
Gliridae
Dipodidae
[Pedetidae]
Spalacidae
[Bathyergidae]
Muridae
[Cricetidae]
[Nesomyidae] | Myomorphi
Myoidea
Gliridae
Dipodidae
Spalacidae
Nesomyidae
Cricetidae
Muridae
Anomaluroidea
Anomaluridae
Pedetidae
Ctenodactyloidea
Ctenodactylidae | Myomorpha
Gliroidea
Gliridae
Dipodoidea
Dipodidae
Muroidea
Spalacidae
Cricetidae
[Nesomyidae]
Muridae | Myomorpha
Myodonta
Dipodidae
Muridae
[Spalacidae]
[Cricetidae]
[Nesomyidae]
Gliromorpha
Gliridae
Anomaluromorpha
Anomaluridae
Pedetidae
Sciuravida
Ctenodactylidae |
| Hystricomorpha
Hystricidae
Octodontidae ^b
[Ctenodactylidae]
[Petromuridae]
[Thryonomyidae] | Hystricognathi
Hystricomorphi
Hystricidae
Petromuridae
Thryonomyidae
Bathyergomorphi
Bathyergidae | Hystricomorpha
Hystricidae
Petromuridae
Thryonomyidae
Hystricomorpha <i>i.s.</i>
Bathyergidae
Suborder <i>i.s.</i>
Ctenodactylidae | Hystricognatha
Hystricidae
Petromuridae
Thryonomyidae
Bathyergidae |

i.s. = *incertae sedis*.

^aThose African families in brackets were not specifically recognized in a given classification, but their genera belong to the family listed above.

^bIn early classifications, such as Alston (1876) and Thomas (1897), *Petromus*, *Thryonomys* and the ctenodactylid genera were grouped with the Octodontidae of South America. Subsequent research, beginning with Tullberg (1899), has indicated that these African families constitute distinct families endemic to Africa and that they are only distantly related to the octodont rodents of South America.

(1) *Sciuridae + Gliridae (= Sciuriomorpha)*

Sciurid rodents possess a sciurognathus mandible and sciuriomorphous masseteric condition and have composed the core of Brandt's (1855) Sciuriomorpha, as reflected in classifications generated from the late 1800s to the present (e.g. Alston 1876, Thomas 1897, Simpson 1945, McKenna & Bell 1997). Union of Sciuridae with Gliridae (dormice) in an expanded clade, however, recently has garnered additional evidence. The zygomaseteric structure of extant glirids (excepting African *Graphiurus*) was widely interpreted as myomorphous, and so influenced systematists to associate dormice with Myomorpha (Alston 1876, Thomas 1897, Ellerman 1940, Chaline & Mein 1979, Wahlert *et al.* 1993). However, the 'myomorphy' observed in most living dormice is now understood to be convergent to the zygomaseteric configuration in Myomorpha proper and has been termed 'pseudomyomorphy' (Vianey-Liaud 1985, Maier *et al.* 2002). The deep and rich fossil record of Gliridae implies their derivation in the very early Eocene from protrogomorphous ischyromyids (Vianey-Liaud 1985, 1994, Hartenberger 1994, 1998), the same fossil group also known to be ancestral to Sciuridae (and North American Aplodontidae). In agreement with the palaeontological interpretation, analyses of both mitochondrial and nuclear genes disclose Gliridae as sister-group to Sciuridae or to a sciurid-aplodontid clade (Kramarov *et al.* 1999, Huchon *et al.* 1999, 2002, Adkins *et al.* 2001, 2003, Debry & Sagel 2001, Montgelard *et al.* 2002, Reyes *et al.* 2004).

(2) *Dipodoidea [Dipodidae] + Muroidea [Spalacidae–Nesomyidae–Cricetidae–Muridae] (= Myomorpha)*

Common ancestry of the Dipodoidea and Muroidea has long been recognized, notably as first depicted by Tullberg (1899). Their close phyletic union has been sustained by substantial palaeontological data (Wilson 1949, Emry 1981, Walsh 1997, Emry *et al.* 1998) and morphological systems, such as molar occlusal patterns and loss of the lower fourth premolar (Flynn *et al.* 1985, Marivaux *et al.* 2004), cephalic arterial plans (Bugge 1985) and foetal membrane traits (Luckett 1985). Although extant dipodoids (hystricomorphous) and muroids (myomorphous) differ in their zygomaseteric construction, extinct cricetids of the late Eocene and early Oligocene possessed a hystricomorphous infraorbital condition (Flynn *et al.* 1985, Vianey-Liaud 1985); fossils with intermediate zygomaseteric structures, along with plausible myological transformations (Klingener 1964), endorse the derivation of myomorphy from an hystricomorphous ancestor. Such a conclusion is further implicit in molecular studies of broad taxonomic scope (Nedbal *et al.* 1996, Adkins *et al.* 2001, 2003, Debry & Sagel 2001, Michaux *et al.* 2001, Jansa & Weksler 2004). Schaub (1958) formally identified the cognate relationship of Dipodoidea and Muroidea as the infraorder Myodonta, within the suborder Myomorpha, a classification also recognized by McKenna & Bell (1997).

(3) *Anomaluridae + Pedetidae (= Anomaluromorpha)*

Scaly-tailed squirrels (*Anomaluridae*) and springhares (*Pedetidae*) are characterized by a hystricomorphous skull and sciurognathus mandible, an unusual combination of traits that has confused their clear-cut assignment to the traditional suborders. Some systematists have treated one or both families as *incertae sedis* within Rodentia (e.g. Simpson 1945, Wood 1965, Chaline & Mein 1979, Hartenberger

1998). Others have arranged the two groups in the same superfamily or suborder (Winge 1887, Tullberg 1899, McKenna & Bell 1997), and this kinship has drawn support based on arterial patterns (Bugge 1974b, George 1981c), middle ear anatomy (Lavocat & Parent 1985, Meng 1990) and mitochondrial genes (Montgelard *et al.* 2001, 2002). Some investigators dispute any special relationship between *Anomaluridae* and *Pedetidae* (e.g. Jaeger 1988a, Hartenberger 1998, Landry 1999), especially given fundamental microstructural differences in their incisor enamel (Martin 1993, 1995). These authors would independently derive *Anomaluridae* from certain Eocene families (Martin 1993, Hartenberger 1998) or ally it as a sister-group with *Sciuridae* (Landry 1999), and tentatively affiliate *Pedetidae* with the *Ctenodactylidae*–*Hystricognathi* clade (George 1985b, Martin 1995, Landry 1999). The phylogenetic issues surrounding *Anomaluridae* and *Pedetidae* and their suprafamilial classification continue to invite resolution.

(4) *Ctenodactylidae + Hystricognathi [Bathyergidae, Hystricidae, Petromuridae, Thryonomyidae] (= Hystricomorpha)*

The African gundis, *Ctenodactylidae*, represent another group whose phylogenetic placement has perplexed systematists. The family was early placed in *Hystricomorpha* (Alston 1876, Thomas 1897), but later arranged within *Sciurognathi* (Ellerman 1940, Chaline & Mein 1979), isolated (among living families) in its own suborder, *Sciuravida* (McKenna & Bell 1997), or left as a suborder or infraorder *incertae sedis* (Simpson 1945, Wood 1955, 1965). A jointly impressive body of research supports association of ctenodactylids with *Hystricomorpha sensu lato*. Such corroborative studies broadly draw upon morphology, both individual character systems and multicharacter cladistic analyses (Landry 1957, 1999, Bugge 1985, George 1985b, Lavocat & Parent 1985, Meng 1990, Martin 1994, 1995, Bryant & McKenna 1995), palaeontology (Flynn *et al.* 1986, Marivaux *et al.* 2002, 2004, Marivaux & Welcomme 2003) and DNA sequences (Huchon *et al.* 2000, 2002, Adkins *et al.* 2001, 2003, Huchon & Douzery 2001, Montgelard *et al.* 2002, Jenkins *et al.* 2005). Since Tullberg's (1899) seminal monograph, the four African families that possess hystricomorphous jaw musculature and a hystricognathus mandible (*Bathyergidae*, *Hystricidae*, *Petromuridae*, *Thryonomyidae*) have been viewed as closely related to one another and to those in the New World. Subsequent research has ratified his arrangement in the broad sense (see summaries in Luckett & Hartenberger 1985, Landry 1999, Jenkins *et al.* 2005). Whether the Palaeotropical families (*Phiomorpha sensu* Lavocat 1971) and Neotropical families (*Caviomorpha sensu* Wood & Patterson 1959) represent monophyletic radiations within *Hystricognathi* remains uncertain, although some recent investigations support such an interpretation (Nedbal *et al.* 1994, Huchon & Douzery 2001, Marivaux *et al.* 2004).

Rodents have long been accepted as most closely related to hares and rabbits. The two groups were initially arranged as the suborders *Simplicidentata* (rodents) and *Duplicidentata* (hares and rabbits) in the order Rodentia or Glires (e.g. Alston 1876, Thomas 1897, Gregory 1910) and later placed in separate orders, Rodentia and Lagomorpha, within the cohort Glires (Gidley 1912, Simpson 1945, Landry 1999). Surprisingly, a persuasive palaeontological foundation for their cognate relationship did not emerge until the late 1900s (Li *et al.* 1987, Li & Ting 1993, Dashzeveg *et al.* 1998). With increased knowledge of these extinct groups (*Mimotonidae*, *Eurymylidae* and others), relationships

among basal Glires and their classification have become correspondingly complex (see Meng *et al.* 2003). Notwithstanding the phylogenetic intricacies involving extinct gliriform mammals, common ancestry of the orders Lagomorpha and Rodentia among living mammals is decisively sustained in modern phylogenetic studies (for morphological evidence, see Novacek & Wyss 1986, Novacek *et al.* 1988, Lockett & Hartenberger 1993, Shoshani & McKenna 1998, Martin 1999, Meng & Wyss 2001, Meng *et al.* 2003; for molecular evidence, see Eizirik *et al.* 2001, Murphy *et al.* 2001, Huchon *et al.* 2002, Lin *et al.* 2002, Armine-Madsen *et al.* 2003, Waddell & Shelley 2003). The clade Rodentia–Lagomorpha is distantly related to Primates, Dermoptera (colugos) and Scandentia (tree shrews), a phyletic association of five orders now recognized as the superorder Euarchontoglires (Murphy *et al.* 2001, Scally *et al.* 2001, Huchon *et al.* 2002, Lin *et al.* 2002, Helgen 2003, Waddell & Shelley 2003, Reyes *et al.* 2004).

Geologic age and continental areas of origin

The oldest rodents represent several ischyromyid genera (Sciuromorpha) from the late Palaeocene of North America, and these or related forms are documented in the early Eocene of Asia and Europe (McKenna & Bell 1997, Hartenberger 1998). The explosive diversification of Rodentia into principal lineages (suborders) occurred during the early to middle Eocene, and examples of most modern families are encountered by the middle to late Oligocene (Wood 1959, Hartenberger 1996, 1998). In Africa, the earliest rodents so far recorded appear in the early Eocene, including forms (Zegdomyidae) considered to be ancestral to living Anomaluridae (Vianey-Liaud *et al.* 1994), and in the late Eocene–early Oligocene, including forms (Phiomyidae) related to African Hystricognathi, in particular Thryonomyidae (Wood 1968, Lavocat 1978, Jaeger *et al.* 1985). These Eocene and Oligocene records originate from sites in the Sahara and along the Mediterranean rim of North-West Africa. The first geologic appearances of most African rodent families, including the largest groups (Sciuridae, Gliridae, Nesomyidae, Muridae, Bathyergidae), date from the middle to late Miocene, the majority as recorded from sub-Saharan countries (Table 8). Based on the oldest fossils so far discovered and their cladistically basal stature within Glires or Rodentia, Asia is presently accepted as the continental area of origin for the order (Bryant & McKenna 1995, Dawson & Beard 1996, Hartenberger 1996, Beard 1998, Meng & Wyss 2001).

African rodent groups are generally thought to be derived from southern Asian progenitors, some time during the middle to late Miocene, and they presumably reached Africa by immigration through the Arabian Peninsula into East Africa and along the Mediterranean into North Africa. The timing and direction of faunal interchange are based on intercontinental comparisons of earliest fossil dates (Lavocat 1978, Jacobs 1985, Wang 1994, Winkler 1994, Flynn & Jacobs 1999) and on cladistic biogeography as inferred from phylogenetic studies (Huchon & Douzery 2001, Mercer & Roth 2003). Such a biogeographic origin and dispersion chronology convincingly account for certain families that occur in the Sahara and North Africa. For example, the ctenodactylids persist as relicts from a much older but now extinct radiation in Asia (Flynn *et al.* 1986, Wang 1994, Dashzeveg & Meng 1998), and the few African dipodids

Table 8. Earliest geologic occurrence of extant families and subfamilies of African Rodentia.

| Family/Subfamily | Epoch |
|---------------------------------------|---|
| Sciuridae ¹ | E. Miocene (<i>Vulcaniscirus</i> , Kenya) |
| Gliridae ² | M.–L. Miocene (<i>Graphiurus</i> , South Africa; <i>Microdryomys</i> , Morocco; <i>Otaviglis</i> , Namibia) |
| Dipodidae ³ | M. Miocene (<i>Protalactaga</i> , Morocco) |
| Spalacidae ⁴
Spalacinae | Recent (<i>Spalax</i> , Libya) |
| Tachyoryctinae? | L. Miocene (<i>Nakalimys</i> , Kenya) |
| Subfamily? | M.–L. Miocene (<i>Harasibomys</i> , Namibia; <i>Pronakalimys</i> , Kenya) |
| Nesomyidae ⁵ | E. Miocene? (<i>Protarsomys</i> , Kenya) |
| Cricetomyinae | L. Miocene (<i>Saccostomus</i> , Ethiopia, Namibia) |
| Dendromurinae | M.–L. Miocene (<i>Dendromus</i> , Ethiopia, Namibia; <i>Mabokomys</i> , Kenya; <i>Ternania</i> , Kenya) |
| Mystromyinae | E. Pliocene (<i>Mystromys</i> , South Africa) |
| Petromyscinae | L. Miocene (<i>Harimyscus</i> , Namibia) |
| Cricetidae ⁶ | M. Miocene (<i>Democricetodon</i> , Kenya) |
| Arvicolinae | M. Pleistocene (<i>Microtus</i> , Libya) |
| Lophiomyinae | L. Miocene (<i>Lophiomyis</i> , Morocco) |
| Muridae ⁷
Deomyinae | L. Miocene (<i>Preacomys</i> , Ethiopia, Namibia) |
| Gerbillinae | M.–L. Miocene (<i>Mioharimys</i> , Namibia; <i>Myocricetodon</i> , Kenya, Morocco; <i>Protatera</i> , Morocco) |
| Murinae | M.–L. Miocene (<i>Aethomys</i> , Namibia; <i>Leakeymys</i> , Kenya; <i>Paraethomys</i> , Algeria; <i>Saidomys</i> , Kenya) |
| Otomyinae | L. Miocene (<i>Euryotomys</i> , South Africa) |
| Anomaluridae ⁸ | L. Eocene (<i>Nementchamys</i> , Algeria) |
| Pedetidae ⁹ | E. Miocene (<i>Megapedetes</i> , Kenya; <i>Parapedetes</i> , Namibia) |
| Ctenodactylidae ¹⁰ | M. Miocene (<i>Africanomys</i> , Morocco, Tunisia) |
| Bathyergidae ¹¹ | E. Miocene (<i>Proheliophobius</i> , Kenya) |
| Hystricidae ¹² | L. Miocene (<i>Hystrix</i> , Kenya) |
| Petromuridae ¹³ | E. Pleistocene (<i>Petromus</i> , South Africa) |
| Thryonomyidae ¹⁴ | L. Eocene–E. Oligocene (<i>Guadeamus</i> , Egypt; <i>Paraphiomys</i> , Egypt) |

Epoch: E. = Early; M. = Middle; L. = Late.

References: ¹Lavocat 1973. ²Lavocat 1978, Denys 1990b, Mein *et al.* 2000a. ³Jaeger 1977b. ⁴Flynn & Sabatier 1984, Tong & Jaeger 1993, Mein *et al.* 2000a. ⁵Lavocat 1973, Denys 1991, Tong & Jaeger 1993, Winkler 1998, Mein *et al.* 2000b, 2004, Geraads 2001. ⁶Tong & Jaeger 1993, McKenna & Bell 1997, Geraads 1998. ⁷Jaeger 1977b, Tong & Jaeger 1993, Sènégas & Avery 1998, Mein *et al.* 2000b, 2004, Winkler 2001. ⁸Jaeger *et al.* 1985, Vianey-Liaud *et al.* 1994. ⁹Lavocat, 1978. ¹⁰Robinson & Black 1973, Jaeger 1977b, Winkler 1994. ¹¹Winkler, 2001. ¹²Lavocat 1973. ¹³Lavocat 1978. ¹⁴Wood 1968, Lavocat 1978.

(3 spp.) represent outliers of the core diversity of Dipodidae, both as fossils and extant species, in Asia (Klingener 1984, Wang & Dawson 1994, Wang & Qiu 2000). Other taxa plausibly represent much younger (Pliocene–Pleistocene) incursions to North Africa, presumably following a circum-Mediterranean route (Cricetidae [Arvicolinae], Spalacidae [Spalacinae], Gliridae [*Eliomys*]).

The timing and direction of continental exchange are not so clear-cut for many groups whose distribution and diversity are centred in sub-Saharan Africa, although the conventional explanation emphasizes migration from Asia into Africa (Jacobs 1985, Winkler 1994, Flynn

& Jacobs 1999). For example, all African sciurids belong to an extensive radiation (Xerinae: Xerini and Protoxerini) that is notably abundant in sub-Saharan biomes (Mercer & Roth 2003, Steppan *et al.* 2004); Holarctic ground squirrels and chipmunks constitute a derived clade (Marmotini) within this subfamily. The other extant genus of African Gliridae, *Graphiurus*, is modestly speciose within sub-Saharan forests and woodlands and is the sole member of a distinctive subfamily (Graphiurinae) that represents the earliest phyletic branch within the family (Wahlert *et al.* 1993, Montgelard *et al.* 2003), which also occurs in Europe and Asia (Hartenberger 1994). A related graphiurine (*Otaviglis*) has been recently described from the late Miocene of Namibia, and *Graphiurus* itself is recorded from the latest Miocene of South Africa (Table 8); according to molecular estimates, differentiation of the graphiurine lineage dates to 40–50 mya (Montgelard *et al.* 2003). Living members of Nesomyidae are similarly known only from the sub-Saharan region (some fossil Dendromurinae documented from North Africa and Arabian Peninsula – see subfamily profile), and the several subfamilies compose a clade separate from, perhaps basal to, the radiation of Cricetidae and Muridae (Michaux *et al.* 2001, Jansa & Weksler 2004). The Miocene diversity of the family, including earliest records of extant genera, has been revealed by significant studies published since the middle 1990s (Table 8). Three of the five subfamilies of Muridae (Deomyinae, Leimacomomyinae, Otomyinae) are concentrated within the sub-Saharan region (*Acomys*, a deomyine, also occurs in North Africa and the Middle East). The murid subfamily Gerbillinae has a broader distribution throughout Africa and into the Middle East and central Asia, but early-branching clades of Gerbillinae (Ammodillini, Taterillini) predominantly lie within the sub-Saharan region (Pavlinov *et al.* 1990). The Murinae, too, has an extensive distribution within Africa, across Eurasia and into Indomalaya and Australia; generic and specific endemism within sub-Saharan biomes is pronounced and includes a few large, well-defined clades (Watts & Baverstock 1995a, Ducroz *et al.* 2001, Lecompte *et al.* 2002b). A molecular-clock estimate places the divergence between Deomyinae, Gerbillinae and Murinae in the early Miocene (Michaux *et al.* 2001). Bathyergidae (African mole-rats) is another family endemic to the sub-Saharan region and contains five strongly differentiated genera (Honeycutt *et al.* 1991). Molecular studies divulge startlingly older dates for phyletic divergence among bathyergids (middle Eocene, ca. 40 mya – Huchon & Douzery 2001) than presently reflected in palaeontological data (Table 8) and point to an autochthonous East African origin of the family (Faulkes *et al.* 2004).

Although Asia, or to a lesser extent Europe, seems the probable source-area for Africa's ancient (Eocene) rodent stocks, the foregoing examples implicate the continent as an important secondary centre for the origin (Oligocene–early Miocene) of major groups. The substantial taxonomic differentiation at the generic, subfamily and family levels, Miocene appearances of extant genera, and deep cladistic patterns all indicate a longer phase of phylogenetic differentiation of Rodentia within sub-Saharan Africa than can be presently documented by the fossil record. The rarity (early Miocene) or absence (Oligocene) of critical-aged, productive fossil sites within the region offers, at best, a precarious foundation to argue continental origins and intercontinental exchanges for many African rodent families. Palaeontological investigation continues, of course, and it is instructive that some of the more exciting discoveries of

earlier appearances have emerged from contributions of the past decade. Future phylogeographic studies that include ample species sampling of genera, subfamilies and families with both African and Asian geographic ranges (e.g. Hystricidae, Spalacidae, Muridae [Gerbillinae, Murinae]) would measurably improve our understanding of continental origin and directions of faunal interchange.

Biology

The immense variation in the biological characteristics of African rodents reflects the large number of species, their evolutionary diversity, and the very varied environments where they are found. This section provides a necessarily brief overview of the diversity of some aspects of the biology of the order. More detailed information may be found in each genus and species profile. General reviews are given in Delany & Happold (1979), Delany (1972, 1986) and Happold (2001); and the role of rodents in African ecosystems is discussed by Dieterlen (1989) and Happold (1996) for rainforests, Happold (1984) for deserts, and Happold (1983) for savannas. The amount of biological information on African rodents varies greatly depending on the species; for some, nothing is known because of their rarity and limited geographical distribution; for many, a limited number of observations are available; and for only a few species (those which are widespread, unusual, or of economic importance) there is substantial information. In spite of the impressive diversity of the order, few species are biologically well understood, and even the best-known species are not so well known as many of Africa's iconic large mammals that belong to far less speciose orders (Proboscidea, Primates, Carnivora, Perissodactyla and Ruminantia).

African rodents vary greatly in size; the majority weigh 20–80 g, but the smallest weighs only 3 g (*Mus haussa*), and the largest weigh ca. 3.25 kg (*Pedetes* spp.) and ca. 20 kg (*Hystrix* spp.). Most African rodents are typically 'mouse-like' or 'rat-like' but there are many that are very different; for example, jerboas (*Allactaga*, *Jaculus*) and springhares (*Pedetes*) have extremely long hindlimbs and jump like kangaroos; anomalures (*Anomalurus*, *Idiurus*) have large wing-like membranes so they can glide from tree to tree; and mole-rats (*Bathyergus*, *Georchychus*, *Heliophobius*) have blunt muzzles, cylindrical bodies, large short spatulate forelimbs, rudimentary (or non-existent) eyes, and huge incisor teeth (for excavating burrows). Because of the large number of species representing families of distant evolutionary origins, there are some interesting examples of ecological and morphological convergence: species of Dipodidae and Pedetidae are bipedal and saltatorial; species of Bathyergidae and Spalacidae are permanently subterranean; species of Muridae, Gliridae and Sciuridae all include some species that are arboreal; and species of Dipodidae and Gerbillinae have the ability to produce very concentrated urine and hence can live in very dry habitats devoid of free water. Likewise, convergence in form and biology occurs in distantly related taxa that inhabit similar but well separated habitats; for example the following genera occur, respectively, in the Sahara Arid BZ and the South-West Arid BZ: *Gerbillus* spp. and *Gerbillurus* spp., *Atlantoxerus* and *Xerus* spp., *Ctenodactylus* spp. and *Petromus typica*, and *Acomys* spp. and *Petromyscus* spp. The rich morphological variety exhibited by African rodents presupposes the remarkable diversity recorded in their life histories, habits and ecological niches.

Rodents are found throughout the African continent, in every biotic zone, and in almost every habitat from the driest of deserts to the wettest of rainforests. Most species are terrestrial, living on the surface of the ground; many of them rest in burrows or under rocks when inactive. Other species may be described as scansorial because they also clamber about in low vegetation close to the ground. Arboreal species (several genera of squirrels, *Graphiurus*, *Grammomys*, *Thallomys*) spend all (or most) of their time in large shrubs and trees, and rarely descend to the ground. Some small species are adapted for climbing on tall grasses (*Dendromys*, *Dendroprionomys*, *Prionomys*) and have opposable fingers and prehensile tails for holding on to slender grass stems. A number of genera (*Bathyergus*, *Georchychus*, *Heliophobius*, *Heterocephalus*) are subterranean and live permanently underground. Only a few species typically live in wet swampy habitats and are capable of swimming; such forms (*Deomys ferrugineus*, *Colomys goslingi* and *Malacomys* spp.) are characterized by relatively long limbs and large hindfeet. Most species are very habitat-specific, being found in only one or two habitats. In contrast, a few species (e.g. *Mastomys natalensis*, *Cricetomys gambianus*, *Thryonomys swinderianus*, *Hystrix* spp.) are widespread and habitat generalists.

The geographical range of many species is relatively well known from museum specimens and trapping records (see maps in each species profile). However, such geographical ranges do not provide any indication of the abundance of a species within its range. Abundance may be expressed either as the numbers of individuals captured using a standardized trapping method, or as a proportion (usually expressed as a percentage) that a species contributes to the community in which it lives, or as the density of individuals/unit area (such as the number of individuals of a species per hectare, or the total number of individuals of all species per hectare). Such measures may vary greatly between habitats and locations, and according to the time of year. Typical examples of proportional representation are: individuals of *Dasyms rufulus* comprise 14.6% of the community of trappable small mammals at Mount Nimba (Guinea), 9.2% in the savannas at Bolo (Côte d'Ivoire) and 7.5% in the savannas at Lamto (Côte d'Ivoire). *Dephomys defua* contributes 10% in four different rainforests in Ghana, *Heimyscus fumosus* contributes 4.6–20.5% (mean 11.5%) and forms the second or third commonest species of nine syntopic species in Gabon, and *Praomys daltoni* comprises 0–78% (mean 50%) at 11 localities in Nigeria. Density is a particularly useful measure of abundance because it provides actual numbers; for example, the density of *Hybomys univittatus* in forests of the Central African Republic was 3.02/ha (in lightly logged forest) and 4.14/ha (in heavily logged forest) (Malcolm & Ray 2000); the density of *Lophuromys flavopunctatus* in DR Congo varied from 9.8/ha (in savannas) to 19.6/ha (in dry seasonal swamps) (Misonne 1963); and the density of *Aethomys namaquensis* in different countries ranged from 2/ha in succulent Karoo, South Africa, to 5.4/ha in Namibia, 4–13/ha in Mozambique and 5.2–27.3/ha in Zimbabwe. Density also varies seasonally; e.g. the density of *Arvicanthis abyssinicus* in Ethiopia was 65–75/ha during the wet season and 130–250/ha during the dry season (Müller 1977), and in *Praomys tullbergi* in Nigerian rainforest, density ranged between 9.5/ha and 27.9/ha according to season over a period of three years (Happold 1977). Seasonal fluctuations in numbers tend to be smallest in species that live in rainforest, and largest in species that live in conditions where rainfall is low and unpredictable. Inter-annual fluctuations are typically rather large in dry localities; e.g. densities of *Taterillus*

pygargus in the sahel savanna of Senegal varied from 0/ha after the drought of 1972 to 180/ha after the good wet season of 1975 (Poulet 1978). For just a few species, live-trapping of individual animals over a long period of time has provided detailed information on population dynamics, home-ranges, movements and longevity (e.g. *Praomys tullbergi*, *Acomys spinosissimus*, *Mastomys natalensis*). Such relatively well-known species are the exception among African rodents. Many more have been rarely encountered and have very restricted geographical ranges, and hence very little is known about the biology of such species. Whether this 'rarity' is real or due to inappropriate methods of study is uncertain; whatever the reason, obtaining information on such species provides a challenge for ecologists in the future. The examples given above refer only to single species; other measures concern all the species that comprise a community; these include 'species richness' (= the number of species in the community) and density (= the total number of individuals of all species known to be alive [KTBA]) in the community. These community measures are especially useful when assessing trophic interactions between species, the overall impact of the community on its environment, and the interactions between different species in the community, especially in respect of reproductive strategy and seasonal changes in demography. For example, the species richness in a rainforest in SW Gabon was 11 species of rodents (plus ten species of shrews) (Nicolas & Colyn 2003; Nicolas *et al.* 2005). In a similar rainforest in Nigeria, species richness was seven species of rodents (and two species of shrews) and density, which varied according to season, was 14.3–25/ha (Happold 1977). (Equivalent data on numbers are unavailable for Gabon.) Similar variations are recorded in savanna habitats: in *Brachystegia* savanna in Malawi, species richness was seven species of rodents (and one species of sengi [Macroselidae]) and density was 3–21/ha according to season (Happold & Happold 1991); equivalent data for thornbush savanna in Malawi was seven species of rodents (and one species of shrew) and 1–33/ha (Happold & Happold 1990). In *Brachystegia* savanna in Zimbabwe, species richness was seven species of rodents (and one species of shrew) and density was 2–10/ha (Linzey & Kesner 1997a). Habitat has a very strong influence on community structure; for example, species richness and density of small rodents during one year in Zimbabwe varied greatly in five neighbouring habitats as follows: riverine grasslands – 7 spp. 1–36/ha; miombo woodland – 7 spp., 2–10/ha; mopane woodland – 5 spp., 1.6–19/ha; talus – 4 spp., 8–25/ha; and thicket – 0.8–2/ha (Linzey & Kesner 1997a) (see also below). The reasons for such variation between habitats are uncertain and need further investigation; but the fact that such variations do occur implies differing levels of resources, differing levels of exploitation by rodents of these resources, and differing numbers and diversity of rodent predators in each habitat.

Rodents show a wide range of reproductive methods and reproductive strategies. The strategy of any particular species is determined partly by its phylogeny, but also by the environment and location. Species vary greatly in their fecundity: squirrels, anomalurids and *Pedetes* have only 1–2 young per litter; many species have 3–6 young per litter; some have up to 10/litter; and the most fecund species (e.g. *Mastomys natalensis*, *Heterocephalus glaber*) may have as many as ca. 20/litter. Litter-size within a species may vary geographically, seasonally and in relation to the size/weight of the female; for example in *Saccostomus campestris* mean embryo number varies from 4.8 (South Africa) to 7 (Botswana) (see profile for

references); in *Gerbilliscus nigricaudus* mean litter size is 4.2 in the dry season and 5.5 in the wet season (Neal 1982); and in *Acomys spinosissimus* mean litter-size is 2.9 for smaller females and 3.6 for larger females (Hanney 1965). Pregnancy and lactation is adaptively timed to ensure a high survival rate for the young. Because small rodents have relatively short gestations (ca. 25–40 days), they can be very responsive to changes in climate. Hence the start of the wet season (in tropical climates), or the end of 'winter' (in temperate Africa) initiates the reproductive process, and the young are born and weaned while the favourable conditions last. Within this reproductive period, many species show a 'peak' of reproductive activity (as measured by the percentage of adult females that are pregnant). In *Beamys hindoi*, for example, pregnancy rate ranged from 20% to 60% during the nine months of reproductive activity (Fitzgibbon *et al.* 1995), and in *Hylomyscus denniae* in E DR Congo, pregnancy rate ranged from 80% (dry season/early wet season) to 9% (wet season) and then to 47% (late wet season/early dry season) (F. Dieterlen unpubl.). Larger rodents, with longer gestations (e.g. 100–120 days in *Atherurus africanus*, 112 days in *Hystrix cristata*, ca. 80 days in *Pedetes capensis*) are unable to respond so quickly to changing environmental conditions. Because of the short gestation of many species of small rodents, a female may have several litters during the time when conditions are favourable for reproduction. A strategy that includes short gestation, rapid growth of young to independence and a postpartum oestrus (so the female is able to conceive again immediately after parturition) is especially important to species where favourable conditions are short-lived and/or unpredictable. A corollary of small size is a short life-span (often only a few months) and hence it is necessary for small rodents to attain sexual maturity rapidly, to have large litters, and to produce several litters in quick succession in order to maximize their lifetime reproductive success. For *Acomys wilsoni* in Kenya (mean embryo number: 2.2), estimates suggest 7.9 litters/female/year and an annual production of 17.4 young/female/year (Neal 1983).

Population structure within a species is a consequence of the characteristics of its reproduction and environment quality. Again, there are few long-term studies that document the changing structure of rodent populations. In *Praomys tullbergi*, a rainforest species that reproduces in most months of the year (with two peaks of reproductive activity) and has comparatively small litters, the population structure remains more or less constant throughout the year; young, subadults and adults are represented in all months (with the ratio of each changing slightly month by month) (Happold 1977). In contrast, the savanna-dwelling *Mastomys natalensis* reproduces only during the wet season and early dry season and has comparatively large litters; the population consists mostly of subadults at the end of the dry season, mostly adults and many young during the wet season and early dry season, and mostly subadults again (after most of the reproductive adults have died) in the mid- and late dry season. These examples (which probably represent the two extremes of population structure) also illustrate another aspect of demography in small rodents: species that occupy relatively constant and predictable environments throughout the year experience only small population fluctuations (e.g. the maximum number of *Praomys tullbergi* in Nigerian rainforest is only 2–3 times the minimum number; Happold 1977); whereas those in environments that are less predictable and have large seasonal variations in climate and resources exhibit larger fluctuations (e.g. the maximum number of *Mastomys natalensis* in

thornbush savanna is up to 33 times the minimum population size; Happold & Happold 1991).

Because most species of rodents are small, only a limited volume of food can be ingested, and hence that food needs to be highly nutritious. The majority of species of African rodents feed on plants, and may be broadly categorized as herbivores (those feeding on grasses, leaves and/or herbs), granivores (seeds, nuts) or frugivores (fruit and flowers). Others are omnivores, feeding on plants and animals (usually arthropods), and a very few are wholly insectivores. For those species that have been investigated, the diet tends to be rather precise; preferred food items (i.e. those that are most nutritious in relation to their bulk) are selected, and most species alter their diet seasonally. For example, squirrels are primarily granivorous and frugivorous, although some species (e.g. *Funisciurus lemniscatus*, *F. pyrropus*, *Myosciurus pumilio*) are omnivorous because they also eat significant amounts of insects (mainly termites). Most glirids are omnivorous. Most species of Muridae are herbivorous or omnivorous, feeding on a variety of grasses, herbs, seeds and fruits; many are opportunistic and although basically herbivorous, will include a small amount of arthropod food in their diet when other foods are unavailable during some seasons of the year. A few species are wholly herbivorous (*Arvicanthis* spp., *Otomys* spp., *Ctenodactylus* spp.). Others are consistently omnivorous, with a high percentage of arthropods and worms in their diet (e.g. *Acomys* spp., *Lophuromys* spp., *Uranomys ruddi*, *Heimyscus fumatus*, *Hybomys* spp., *Malacomys* spp.). Only a few species are known to be wholly insectivorous (*Deomys ferrugineus*, *Colomys goslingi*). Subterranean species (species of Bathyergidae and Spalacidae) feed on a variety of underground corms, bulbs, tubers, fibrous roots and rhizomes. Perhaps because of their tropical and sub-tropical distributions, it is unusual for African rodents to store food, although there are some exceptions: some squirrels collect nuts, which are placed in caches; *Beamys hindoi*, *Cricetomys* spp. and *Saccostomus* spp. carry seeds in their cheek pouches and store them in their burrows for later consumption; and some subterranean species store geophytes. The foregoing generalizations on food habits underscore the necessity of thorough, year-round, trophic studies of African rodents, especially for species in the families Nesomyidae and Muridae.

The behaviour of African rodents has not been studied as extensively as that for the larger mammals. Their small size, nocturnal activity and lack of visibility make it very difficult to pursue behavioural studies on rodents (and other small mammals). However, there are several notable studies on diurnal species that are easily visible during the daytime (see, for examples, profiles on several species of Sciuridae, *Rhabdomys pumilio*, *Thallomys* spp., *Pedetes capensis*, *Ctenodactylus gundi*, *Thryonomys* spp. and *Hystrix* spp.). Additional studies (which provide information on sociality, agonistic behaviour, nesting behaviour and maternal behaviour) have been made on several species in captivity. Although most species tend to be asocial and/or solitary except for times during reproductive activity, some species form loose aggregations and social groups (e.g. squirrels, gundis, porcupines). All species of rodents that have been studied show many forms of intra- and inter-specific communication; these include vocal (e.g. calls, squeaks, whistles), visual (e.g. amicable or aggressive displays, postures, tail-flicking, etc.), non-vocal auditory (foot-drumming, tooth-chattering) and olfactory (scent-marking) signals. Territoriality is well-developed in some species and territories are maintained by visual and olfactory signals, and also (in some species) by fighting and chasing. Maternal behaviour has been well-studied (usually in

captivity) in some species; most mothers are solitary when raising their young but there are interesting exceptions such as some species of *Acomys* (Muridae: Deomyinae) in which there is social care of the young by the several mothers. One of the most studied species, *Heterocephalus glaber* (Bathyergidae), has a social system resembling that of eusocial insects. Within any family, there may be some species that are asocial and territorial, and others that are highly social (see, e.g. Bathyergidae, Sciuridae, Muridae: Otomyinae).

Rodents play an important role in ecological processes in Africa due to the many species present, their collectively widespread distributions and the sometimes large population numbers within particular habitats. Because the vast majority of species are herbivores and granivores, they assume a major role in recycling nutrients. Granivorous species transport seeds away from the parent plant and bury them, thus increasing seed dispersal. By their normal activities, rodents change the environment in which they live – a process known as ‘ecological engineering’; familiar examples include burrowing whereby the soil profile is altered and new soil is brought to the surface where it can act as ‘seed-beds’ for plants; defecating at regular latrines, which provides small areas of increased nutrients which promotes plant growth; and feeding on grasses and herbs, which promotes plant growth (in the same way as do larger herbivorous mammals). Although the influence of one individual rodent may seem trivial (compared with that of a mega-herbivore), the very large numbers of rodents in many ecosystems mean that their total influence is not inconsiderable. The only quantitative data available showed that in the tall grass plains of the Serengeti (where there are many large herbivores), small mammals utilized 69 kg/ha (= 1.2% of the total) of the annual grass biomass compared with 1122 kg/ha (=18.8% of the total) for the large mammals (Sinclair

1975). At times, rodents may be detrimental to human endeavours; some species (e.g. *Mastomys* spp., *Gerbillus* spp.) destroy seeds and crops in agricultural fields, and also feed on stored grains in houses and granaries. The role of rodents in African savanna and rainforest ecosystems has been reviewed by Happold (1983, 1996).

Rodents are important prey for many small and medium-sized carnivores such as mongooses, genet, civets, small canids, small felids, owls (especially *Tyto alba* and *T. capensis*), hawks and snakes (see entries under ‘Predators, Parasites and Diseases’ in each species profile). For example, Giant Root-rats *Tachyoryctes macrocephalus* form 47% and *Lophuromys melanonyx* form 40% of the food of Ethiopian Wolves *Canis simensis* (Sillero-Zubiri & Gottelli 1995); at least 14 species of rodents form nearly 30% of the prey of seven species of small carnivores in the rainforests of the Central African Republic (the other significant prey was shrews, arthropods and herpetofauna) (Ray 1998); and small rodents formed almost all of the food of African Grass-owls *Tyto capensis* on Zomba Plateau, Malawi, where four species (*Otomys angoniensis*, *Dasymys incomtus*, *Pelomys fallax* and *Dendromus nyikae*) comprised the majority of the prey (Happold & Happold 1986). Humans are also important predators of some species such as *Cricetomys emini*, *C. gambianus* and *Thryonomys* spp. Some species of rodents are responsible directly (or indirectly through parasites that they carry) for the transmission of diseases of humans; well-known examples are some species of *Gerbillus* (formerly *Tatera*) and *Gerbillus* (plague), *Meriones* spp. and *Psammomys obesus* (leishmaniasis), *Rattus rattus* and *R. norvegicus* (plague) and *Mastomys erythroleucus* and *M. natalensis* (Lassa fever and other diseases). Control measures may be necessary when population numbers of these species become too large close to human environments.

Table 9. African families of the order Rodentia.

| Family | Length of tail ^a | Tail ^b | Pelage texture | Cheekteeth | Jaw musculature ^c | HB (typical size or range) (mm) ^d | Ecology and form |
|-----------------|-----------------------------|-------------------|--------------------|--|------------------------------|--|--|
| Anomaluridae | L | H | Soft | ⁴ / ₄ | Hy | 63–75, 280–380 | Arboreal; patagia present (except in <i>Zenkerella</i>) |
| Gliridae | L | H | Soft | ⁴ / ₄ | Hy, My | mostly 60–100 | Arboreal; patagia absent |
| Petromuridae | L | H | Soft | ⁴ / ₄ | Hy | 140–220 | Terrestrial, rupicolous |
| Sciuridae | L | H | Soft | ⁴ / ₄ , ⁵ / ₄ | Sc | 110–126, 180–240 | Arboreal; patagia absent; one species 60–70 mm |
| Dipodidae | L | T | Soft | ³ / ₃ | Hy | 98–118, 137–160 | Terrestrial; elongated hindlimbs |
| Pedetidae | L | T | Soft | ³ / ₃ | Hy | 350–430 | Terrestrial, elongated hindlimbs |
| Nesomyidae | L | P | Soft | ³ / ₃ | My | 50–63, 270–300 | Terrestrial, some scansorial |
| Cricetidae | L | P | Soft | ³ / ₃ | My | 100–124, 180–300 | Terrestrial |
| Muridae | L (some S) | P | Soft (some coarse) | ³ / ₃ | My | 44–52, 135–190 | Terrestrial, some scansorial, some rupicolous |
| Ctenodactylidae | S | H | Soft | ³ / ₃ (⁴ / ₄) | Hy | 125–230 | Terrestrial, rupicolous |
| Bathyergidae | S | P | Soft | ⁴ / ₄ (up to ⁶ / ₆) | Hy | 90–190 | Subterranean |
| Hystriidae | S | P | Spines | ⁴ / ₄ | Hy | 650–850 | Terrestrial |
| Thryonomidae | S | P | Coarse | ⁴ / ₄ | Hy | 400–790 | Terrestrial |
| Myocastoridae | S | P | Coarse | ⁴ / ₄ | Hy | 470–570 | Aquatic; terrestrial |
| Spalacidae | S or A | P or NA | Soft | ³ / ₃ | My | 160–200, 225–315 | Subterranean |

^a S = tail short <50% of HB; L = tail longer >50% of HB; A = tail absent (or not visible externally).

^b P = naked or with small bristles; H = covered with long hairs; T = well-developed tuft of hair at tip; NA = not applicable.

^c Hy = hystricomorphous; My = myomorphous; Sc = sciuriomorphous.

^d Approximate and typical sizes. Where there is wide variation within a family, the smallest and largest species are indicated.

Systematic arrangement of Rodentia in *Mammals of Africa*

The 15 families of African rodents (14 indigenous and the introduced Myocastoridae) are treated in accordance with the phylogenetic relationships reviewed above and as presented by Carleton & Musser (2005) in the Third Edition of *Mammal Species of the World* (Wilson & Reeder 2005). The families, in the sequence given in this volume (Table 6, see also Table 9), are Sciuridae, Gliridae, Dipodidae, Spalacidae, Nesomyidae, Cricetidae, Muridae, Anomaluridae, Pedetidae, Ctenodactylidae, Bathyergidae, Hystricidae, Petromuridae, Thryonomyidae and Myocastoridae. Four families (Spalacidae, Nesomyidae, Cricetidae, Muridae) are further divided into subfamilies, which are arranged alphabetically, as are the genera within each subfamily and the species within each genus.

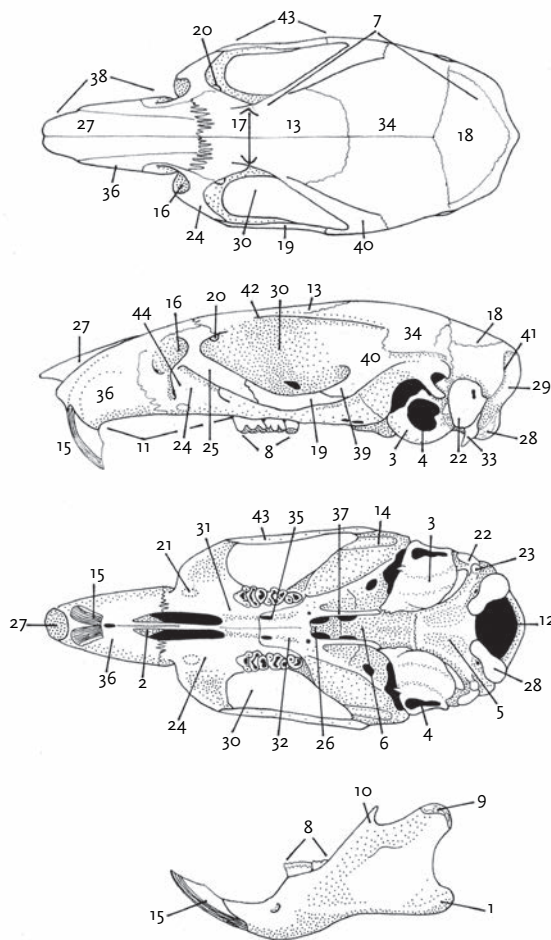


Figure 6. The bones and terminology of the skull of a 'typical' murine rodent (*Praomys tullbergi*). 1 Angular process, 2 Anterior palatal foramen, 3 Auditory bulla, 4 Auditory meatus, 5 Basisphenoid, 6 Basisphenoid, 7 Braincase, 8 Cheekteeth (molar row), 9 Condylar process, 10 Coronoid process, 11 Diastema, 12 Foramen magnum, 13 Frontal, 14 Glenoid fossa, 15 Incisor, 16 Infraorbital foramen, 17 Interorbital constriction, 18 Interparietal, 19 Jugal, 20 Lachrymal, 21 Masseteric knob, 22 Mastoid, 23 Mastoid process, 24 Maxilla, 25 Maxillary process (zygomatic arch), 26 Mesopterygoid fossa, 27 Nasal, 28 Occipital condyle, 29 Occipital, 30 Orbit, 31 Palate, 32 Palatine, 33 Paraoccipital process, 34 Parietal, 35 Posterior palatal foramen, 36 Premaxilla, 37 Pterygoid process, 38 Rostrum, 39 Squamosal process (zygomatic arch), 40 Squamosal, 41 Supraoccipital crest (if present), 42 Supraorbital ridge (if present), 43 Zygomatic arch (Zygoma), 44 Zygomatic plate.

Size categories

In the Descriptions, an indication of the size of each species is recorded comparatively to other species in the family. The size categories, based on mean head and body length (HB), are:

| Family | Size categories (mean head and body length) |
|---|---|
| Dipodidae, Spalacidae, Nesomyidae, Cricetidae, Muridae, Pedetidae, Ctenodactylidae, Hystricidae, Petromuridae, Thryonomyidae, Myocastoridae | Very small: 50–84 mm
Small: 85–119 mm
Medium-sized: 120–154 mm
Large: 155–189 mm
Very large: 190–350 mm
Extremely large: >350 mm |
| Gliridae | Small: 70–99 mm
Medium: 100–129 mm
Large: 130–159 mm |
| Sciuridae, Anomaluridae | Very small: 70–119 mm
Small: 120–169 mm
Medium sized: 170–219 mm
Large: 220–269 mm
Very large: 270–421 mm |
| Bathyergidae | Small: <100 mm
Medium-sized: 101–200 mm
Large: >200 mm |

The length of the tail, expressed as a percentage of the length of HB, is described as very short (<30%), short (30–77%), long (78–110%), very long (111–160%) or extremely long (>161%). The names of the bones of the skull are shown in Figure 6, and the nomenclature of the cusps on the cheekteeth of a murine rodent are shown in Figure 7.

Michael D. Carleton & D. C. D. Happold

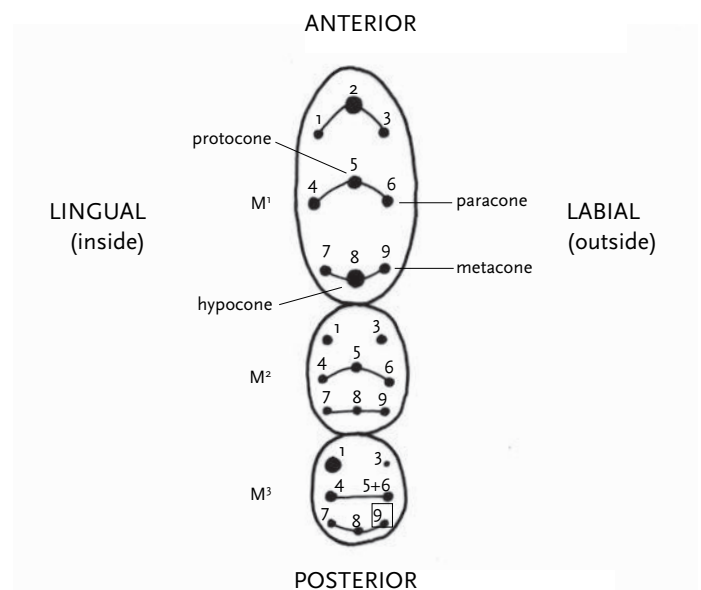


Figure 7. A schematic view of the upper left cheek teeth (M^1 , M^2 , M^3) of a murine rodent showing the nomenclature of the cusps. Cusps labelled as 1, 2, etc. (= t_1 , t_2 , etc.). Inner (lingual) side on left, outer (labial) side on right. Cusps = black dots. Lines = lophs or ridges joining cusps. t_2 on M^2 and M^3 never or rarely present. t_3 of M^3 very small or absent. t_5 and t_6 of M^3 usually joined. Wear on occlusal surface (with age and use) obliterates the cusp pattern.

Family SCIURIDAE

SQUIRRELS

Sciuridae Fischer de Waldheim, 1817. *Adversaria zoologica*, p. 408.

| | | |
|---|--------------------------|-------|
| <i>Allosciurus</i> (1 species) | Slender-tailed Squirrel | p. 40 |
| <i>Atlantoxerus</i> (1 species) | Barbary Ground Squirrel | p. 42 |
| <i>Epixerus</i> (1 species) | Splendid-tailed Squirrel | p. 44 |
| <i>Funisciurus</i> (10 species) | Rope Squirrels | p. 46 |
| <i>Heliosciurus</i> (6 species) | Sun Squirrels | p. 61 |
| <i>Myosciurus</i> (1 species) | Pygmy Squirrel | p. 70 |
| <i>Paraxerus</i> (11 species) | Bush Squirrels | p. 72 |
| <i>Protoxerus</i> (1 species) | Giant Squirrel | p. 89 |
| <i>Sciurus</i> (1 species) (introduced) | Grey Squirrel | p. 92 |
| <i>Xerus</i> (4 species) | Ground Squirrels | p. 93 |

The Sciuridae is a polygeneric family of rodents distributed throughout most of the Americas, Eurasia and Africa, in habitats ranging from alpine to tropical and from desert to rainforest. There are 51 genera and 277 species in the family (Thorington & Hoffmann 2005). The Sciuridae is divided into five subfamilies, with all African squirrels included within the subfamily Xerinae, which also includes all the North American and northern Eurasian ground squirrels. The squirrels are a very successful group, widespread on all continents except Australia and Antarctica. The present fauna of South America includes three genera and 19 species, North America has eight genera and 83 species, Europe has four genera and six species, and Asia has 22 genera and 92 species. Africa has ten genera and 37 species of squirrels, including the introduced Grey Squirrel *Sciurus carolinensis* (subfamily Sciurinae), in South Africa. The anomalures (or scaly-tailed flying squirrels) of Africa belong to a different family of rodents, the Anomaluridae.

Squirrels are small to large rodents, usually with a long well-haired tail and a relatively short rostrum. Some species are rather plain with a uniform reddish or brownish colouration, others are very colourful. Most squirrels have long tails, with long lateral hairs and shorter dorsal and ventral hairs; the tail may be slender or bushy and in some species has noticeable rings or bands of colour along its length. Longitudinal lateral side-stripes are common among terrestrial squirrels and some genera of arboreal squirrels. There are four digits on the forefoot (Digit 1 small or vestigial) and five long digits on the hindfoot. The skull is sciuro-morphous, with the anterior deep masseter muscle originating on the zygomatic plate and (except in *Paraxerus* and *Funisciurus*; Thorington & Darrow 1996) the lateral surface of the rostrum. No part of the masseter muscle passes through the infraorbital foramen. Postorbital process present. Supraorbital ridge with small foramen (or notch) at anterior end in some genera. The masseteric tubercle, a bony knob-like projection on the maxilla bone anterior to the cheekteeth, is present in some genera and a useful diagnostic character. Dental formula is $I \frac{1}{1}, C \frac{0}{0}, P \frac{1}{1} \text{ or } \frac{2}{1}, M \frac{3}{3} = 20 \text{ or } 22$. There are four upper cheekteeth (one premolar (= P^4) and three molars) in *Epixerus*, most *Heliosciurus*, *Myosciurus* and *Protoxerus*, and five upper cheekteeth (two premolars (P^3 , which is often very small, and P^4) and three molars in *Allosciurus*, *Atlantoxerus*, *Funisciurus*, *Paraxerus* and *Xerus*. Size categories of species in the family (based on mean head and body length) are given in the order Rodentia profile.

Squirrels are terrestrial and arboreal, and one group of arboreal squirrels (the non-African Pteromyini) consists of species that are also able to glide. Most terrestrial species live in underground burrows, and

most arboreal squirrels make nests in tree hollows or on tree branches. Many squirrels feed extensively on hard seeds, but diets vary greatly from soft fruit or leaves to fungi, insects or other animal matter. Many non-African species of squirrels (e.g. Marmots, Chipmunks) hibernate, some for seven months each year. A few species aestivate during the hottest months of the year. Dwarfism has evolved independently three or four times in different groups of arboreal squirrels, in Africa, Asia and South America (Mercer & Roth 2003, Thorington *et al.* 1997). On all three continents, these diminutive squirrels have evolved a form of foraging known as bark-gleaning. The African Pygmy Squirrel *Myosciurus* is one of the smallest species, averaging 16 g in weight. The largest terrestrial squirrels are the Marmots *Marmota*, some of which may reach 9 kg. In contrast, the largest African ground squirrels, *Xerus*, do not exceed 1 kg. The largest tree squirrels are the Oriental Giant Squirrels *Ratufa*, with some individuals exceeding 2 kg. The largest African tree squirrels, *Protoxerus*, average 700 g. Most squirrels are solitary, with each individual having its own home-range. Some species are territorial. Colonial community structure and complex social behaviour occur in a number of terrestrial squirrels, especially the Prairie Dogs *Cynomys*, Marmots *Marmota* and Ground Squirrels *Spermophilus* of North America. Some African Ground Squirrels are also colonial (*Atlantoxerus*, *Xerus inauris* and *Xerus princeps*) but most African arboreal squirrels are not, and are seen singly, in pairs, or in small groups.

Squirrels exhibit a variety of reproductive strategies, with average litter-sizes ranging from slightly more than one to more than nine. The largest litter-sizes are found among the North American ground squirrels, which have only a single litter per year; e.g. in *Spermophilus*, the average litter-size ranges from 3.3 to 9.3, and in *Marmota* from 3.4 to 4.2 (Heaney 1984). The largest of these may defer breeding until two or three years of age and produce litters every other year. North American tree squirrels have smaller litter-sizes (averaging 1.9–4.5 young), and commonly have more than one litter per year. In contrast, African Ground Squirrels have 2–4 young/litter (Moore 1961), and African tree squirrels have only 1–2 young/litter (Emmons 1979a). African tree squirrels are born at a more advanced stage of development and are ready to leave the nest at an earlier age than North American tree squirrels: e.g. the *Paraxerus* leave at 3–4 weeks of age, and young of *Tamiasciurus* and *Sciurus* at 5–9 weeks (Ferron 1984). Emmons (1979a) attributes this to a greater risk of nest predation in the African tropics.

The earliest fossil squirrel is *Douglassia* of the late Eocene of North America (Emry & Thorington 1982). Squirrels (*Palaeosciurus*) appear in the European fauna in the early Oligocene (Vianey-Liaud 1974), immediately after the time known as the ‘grande coupure’, when many Asian species entered the European fauna. The African Ground Squirrels are first known from *Heteroxerus* in the late Oligocene of Europe. The genus *Getuloxerus*, perhaps synonymous with *Atlantoxerus* (the extant Barbary Ground Squirrel), is found in Spain and North Africa in the late Miocene (Black 1972a). Squirrels are first found in sub-Saharan Africa in the Miocene (Lavocat 1973). *Volcanisciurus* of the early Miocene is not referable to any modern tribe. *Kubwaxerus* of the upper Miocene is closely related to the extant genera *Epixerus* and *Protoxerus* and is the earliest known member of the Protoxerini

Table 10. Genera in the family Sciuridae.

| Genera | Posterior end of bony palate | Masseteric tubercle | Side-stripe on each flank | Mean HB* (mm) | Number of cheekteeth (upper/lower jaw) | Mean GLS* (mm) | Notes |
|------------------------------|--|---------------------|------------------------------------|---------------|--|----------------|---|
| <i>Allosciurus</i> (1 sp.) | In line with posterior end of M ³ | Small | None | 240 | ⁵ / ₄ | 59 | Terrestrial/arboreal. West African rainforests (Liberia/Sierra Leone to Ghana) |
| <i>Atlantoxerus</i> (1 sp.) | Considerably posterior to M ³ | Prominent | 1 (+ single mid-dorsal stripe) | 194 | ⁵ / ₄ | 46 | Terrestrial. NW Africa |
| <i>Epixerus</i> (1 sp.) | Posterior to M ³ | Not prominent | None | 284 | ⁴ / ₄ | 69 | Terrestrial and arboreal. Rainforests of West and central Africa |
| <i>Funisciurus</i> (9 spp.) | Approximately in line with posterior end of M ³ | Not prominent | 1 (sometimes obscure) ^a | 152–211 | ⁵ / ₄ | 38.8–52.7 | Arboreal and tangles. Rainforests of West and central Africa; some spp. extend to relict forests in savanna |
| <i>Heliosciurus</i> (6 spp.) | Approximately in line with posterior end of M ³ | Prominent | None | 196–237 | ⁴ / ₄ ^b | 42.7–54.2 | Arboreal. Widespread. Rainforest and savanna of sub-Saharan Africa |
| <i>Myosciurus</i> (1 sp.) | Approximately in line with posterior end of M ³ | Absent | None | 66 | ⁴ / ₄ | 21.3 | Arboreal. Rainforests SE Nigeria to Gabon |
| <i>Paraxerus</i> (11 spp.) | Approximately in line with posterior end of M ³ | Prominent | None, 1 or 2 ^c | 102–230 | ⁵ / ₄ | 30.6–55.6 | Rainforest and tangles, woodland savanna. West, central and East Africa |
| <i>Protoxerus</i> (1 sp.) | Approximately in line with posterior end of M ³ | Not prominent | None | 297 | ⁵ / ₄ or ⁴ / ₄ | 67.8 | Arboreal. Rainforest of West and central Africa |
| <i>Xerus</i> (4 spp.) | Considerably posterior to M ³ | Prominent | 1 ^d | 212–259 | ⁵ / ₄ | 50.7–60.8 | Terrestrial. Savanna and semi-arid; sub-Saharan Africa |

* Where range of values given, smaller value refers to smallest species in genus and larger value to largest species in genus.

^a Except *F. isabella*, with two black stripes on each flank. ^b Except *H. ruwenzorii* – ⁵/₄ with small P³ present. ^c Plus single mid-dorsal stripe in two species with two stripes on each flank (*P. boehmi*, *P. alexandri*). ^d Except *X. rutilus*.

(Cifelli *et al.* 1986). It is also the largest known African squirrel and is estimated to have weighed 1.4 kg. It had the thickest incisors of any known squirrel and probably, like *Epixerus*, subsisted on very thick nuts. *Paraxerus* from the Pliocene of East Africa is the earliest known of the *Paraxerus*–*Funisciurus* group of squirrels.

Because of recent molecular studies (Mercer & Roth 2003, Steppan *et al.* 2004), the family Sciuridae is now divided into five subfamilies (Thorington & Hoffmann 2005); only one of these – the Xerinae – is represented in Africa. Within this subfamily there are three tribes: the Xerini, the Protoxerini and the Marmotini, the first two tribes containing all the African squirrels. The Xerini includes the two genera of African Ground Squirrels, *Xerus* and *Atlantoxerus*. The Protoxerini includes seven genera: the Sun Squirrels *Heliosciurus*, the African Giant Squirrel *Protoxerus*, the Slender-tailed Squirrel *Allosciurus*, the Splendid-tailed Squirrel *Epixerus*, the African Bush Squirrels *Paraxerus*, the Rope Squirrels *Funisciurus* and the African Pygmy Squirrel *Myosciurus*. These tribal assignments, and the presence of Xerini in the fossil record of Europe, suggest that the Xerini invaded Africa from Eurasia. The Protoxerini are endemic to Africa and may have evolved there from an unidentified ancestor. The nine genera of endemic African squirrels (Table 10) are listed here alphabetically by genus; additionally there is a tenth genus, *Sciurus*, which has been introduced into South Africa.

Allosciurus: Large unstriped arboreal squirrel of West Africa, with long slender non-bushy tail. Skull: rostrum curved down anteriorly,

supraorbital notch present, cheekteeth ⁵/₄.

Atlantoxerus: Ground Squirrel of North Africa. Three pale longitudinal stripes on back. Skull: bony palate extends well behind third molar, cheekteeth ⁵/₄, masseteric tubercles prominent. (1 sp.)

Epixerus: Large unstriped, terrestrial rainforest squirrel. Bushy tail with ventral V-shaped black and white pattern. Skull: bony palate ends in line with posterior end of third molar, cheekteeth ⁴/₄, masseteric tubercles not prominent, skull sutures still prominent in adult between parietal bones and surrounding interparietal bone. (1 sp.)

Funisciurus: Mostly small forest squirrels, often with a side-stripe on each side of body. Skull: bony palate ends in line with posterior end of third molar, cheekteeth ⁵/₄, cheekteeth flat-crowned, fossa for origin of anterior deep masseter muscle does not extend onto the rostrum. (10 spp.)

Heliosciurus: Medium to large arboreal forest squirrels of sub-Saharan Africa. Skull: bony palate ends in line with posterior end of third molar, cheekteeth ⁴/₄, third premolar absent in all but one species. Prominent masseteric tubercles, fossa for origin of anterior deep masseter muscle extends onto the rostrum. (6 spp.)

Myosciurus: Pygmy tree squirrel. Length of head and body less than 7.5 cm. Skull: bony palate ends in line with posterior end of third molar, cheekteeth ⁴/₄, skull length less than 25 mm, body mass less than 20 g. (1 sp.)

Paraxerus: Diverse group of forest and bush squirrels, some species with side-stripes, some without side-stripes. Skull: bony palate

ends in line with posterior end of third molar, cheekteeth $5/4$, fossa for origin of anterior deep masseter muscle does not extend onto the rostrum, mandibular cheekteeth cuspidate, upper cheekteeth flat-crowned. (11 spp.)

Protoxerus: One of the largest arboreal forest squirrels of sub-Saharan Africa. Tail not bushy. Skull: bony palate ends in line with posterior end of third molar, cheekteeth $4/4$, masseteric tubercles not prominent, fossa for origin of anterior deep masseter muscle extends onto the rostrum, skull sutures fused in adult between parietal bones and surrounding interparietal bone. (1 sp.)

Sciurus: Exotic species found only in parts of South Africa. No stripes on back. Skull: bony palate extends well behind third molar; cheekteeth $5/4$, masseteric tubercles not prominent, fossa for origin of anterior deep masseter muscle does not extend onto the rostrum. (1 sp.)

Xerus: Ground squirrels of sub-Saharan Africa. Bristly fur; most species have a white side-stripe on each side of body. Skull: bony palate extends well behind third molar, cheekteeth $5/4$, masseteric tubercles prominent. (4 spp.)

Richard W. Thorington, Jr

GENUS *Allosciurus* Slender-tailed Squirrel

Allosciurus Conisbee, 1953. *A list of Names proposed for Genera and Subgenera of Recent Mammals*: 6.

Monotypic genus. A large squirrel confined to the Rainforest BZ (Western Region). The characters of the genus include comparatively large size (mean HB 240 mm), back and flanks without longitudinal side-stripes, and long slender hairy tail (mean 298 mm), which is longer than HB (cf. *Protoxerus*). Females have four pairs of nipples; presence of baculum in ♂ not known. The skull is characterized by the curved-down rostrum (in lateral view), supraorbital notch (on supra-orbital ridge at lateral side of frontal bone) open above the orbit (not a foramen), infraorbital foramina large and oval, masseteric knob small, five upper cheekteeth and auditory bullae well developed, extending ventrally well below the line of the cheekteeth.

The single species, *Allosciurus aubinnii*, is frequently considered as belonging to *Protoxerus*, but its many unique features indicate that it should be placed in its own genus (see Thomas 1909a, Ellerman 1940, 1941, Rosevear 1969, Grubb *et al.* 1998; *contra* Moore 1959, Amtmann 1966, Thorington & Hoffmann 2005). *Allosciurus* differs from *Protoxerus* and *Epixerus* (and from *Heliosciurus* where indicated) in a number of important ways: (1) skull with unusual shape, relatively high, strongly convex in nasofrontal region with down-curved rostrum (cf. not down-curved in *Protoxerus*, *Epixerus* and *Heliosciurus*); (2) cheekteeth always $5/4$

(cf. $4/4$ in *Heliosciurus*, though $5/4$ in *Heliosciurus ruwenzorii* and rarely in some *Epixerus* specimens); (3) skull length <60 mm (cf. >65 mm); (4) supraorbital notch present (cf. closed to form supraorbital foramen – and in *Heliosciurus*) (Figure 8); (5) no sharp boundary between hair of flanks and underparts (cf. sharp boundary between hairs of flanks and relatively hairless underparts); (6) tail dark-coloured, with long black tips to hairs (cf. tail marked with dark and pale bands – and in *Heliosciurus*); (7) colouration dark (cf. relieved by light speckling and/or reddish tones – and in *Heliosciurus*).

Allosciurus forms a monophyletic clade with *Heliosciurus*, *Protoxerus* and *Epixerus* (Moore 1959).

Peter Grubb



Allosciurus aubinnii.

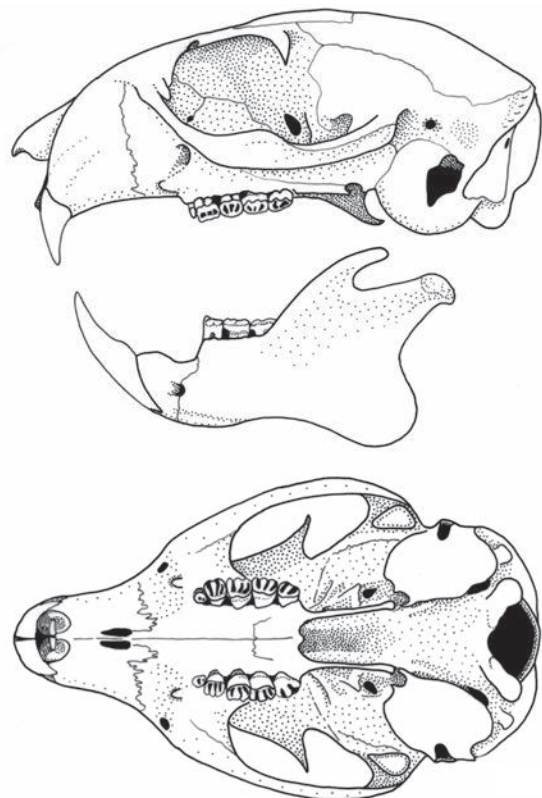


Figure 8. Skull and mandible of *Allosciurus aubinnii* (BMNH 45-331).

***Allosciurus aubinnii* SLENDER-TAILED SQUIRREL (AUBINN'S SQUIRREL)**

Fr. Écureuil d'Aubinn; Ger. Dünnschwanzhörnchen

Allosciurus aubinnii (Gray, 1873). Ann. Mag. Nat. Hist., ser. 4, 12: 65. Fanti, Ashanti Province, Ghana.

Taxonomy Originally described in the genus *Myrsilus*. Rosevear (1969) considers there to be sufficiently important differences in the skull and pelage for this species to be placed in its own genus, *Allosciurus*, separate from *Protoxerus*. Grubb *et al.* (1998) also place the species in *Allosciurus* (see genus profile). In contrast to *Protoxerus*, *Allosciurus* has no trace of red or rufous in the pelage, the tail lacks any white rings or banding, and the rostrum is down-curved. Hoffmann *et al.* (1993) and Thorington & Hoffman (2005) retain the species in the genus *Protoxerus*, but invoke *Allosciurus* as a subgenus. Synonyms: *salae*. Two subspecies. Chromosome number: not known.

Description Large dark slender squirrel without any other special colouring or marking. Dorsal pelage, head and limbs, dark brown to brownish-black, slightly speckled with yellow or buff; hairs brownish-black with 2–3 narrow, pale yellow bands. Ventral pelage similar but paler than dorsal pelage. When viewed from side, head has rounded profile due to down-curved rostrum. Ears short and rounded with dense hairs on outer surface. Tail long (ca. 125% of HB); slender and not bushy; black with intermixture of yellow or buff towards tip; hairs long (ca. 35 mm), mostly black at base, and with wide pale bands towards tip. Skull heavily built but less so than in *P. stangeri* and *Epixerus ebii*; rostrum down-curved, supraorbital ridge with open notch; cheekteeth $5/4$; posterior end of bony palate in line with posterior end of upper M^3 ; masseteric tubercle not prominent (see also genus profile). Nipples: 1 + 1 + 1 + 1 = 8.

Geographic Variation

P. a. aubinnii: Ghana, Côte d'Ivoire. Pelage as described above.

P. a. salae: Liberia (and probably Sierra Leone – Grubb *et al.* 1998).

Very dark form; hairs along mid-dorsal line without bands; hairs of tail without bands except at tip.

Similar Species

Epixerus ebii. Pelage contains rufous colouration; tail long and bushy, flecked with white.

Protoxerus stangeri. Grizzled white pelage on head and chest; large bushy tail liberally flecked with white.

Distribution Endemic to Africa. Rainforest BZ (Western Region). Recorded from Sierra Leone (near the Liberian border), Liberia, Côte d'Ivoire and Ghana.

Habitat Moist primary rainforests, often associated with *Raphia* palms (G. S. Cansdale in Rosevear 1969). Maybe partly a ground-living squirrel (G. S. Cansdale in Grubb *et al.* 1998).



Allosciurus aubinnii

Abundance Usually rare or uncommon, but may be as common as *P. stangeri* in some moist mature rainforests (Booth 1960).

Remarks One stomach contained the husks of *Raphia* palms (G. S. Cansdale in Rosevear 1969). Probably solitary.

Conservation IUCN Category: Data Deficient.

Measurements

Allosciurus aubinnii

HB: 240 (230–250) mm

T: 298 (270–310) mm

HF: 58 (55–61) mm

E: 20 (18–21) mm

WT: n. d.

GLS: 59.3 (59–60) mm

GWS: n. d.

P^3-M^3 : 11.1 (10.8–11.4) mm

Ghana (for *P. a. aubinnii*) (Rosevear 1969)

Sample size not given

Key References Grubb *et al.* 1998; Rosevear 1969.

Chad E. Schennum & Richard W. Thorington, Jr

GENUS *Atlantoxerus*

Barbary Ground Squirrel

Atlantoxerus Forsyth Major, 1893. Proc. Zool. Soc. Lond. 1893: 139. Type species: *Sciurus getulus* Linnaeus, 1758.

The genus *Atlantoxerus* was originally a subgenus of *Xerus*, and later raised to full generic rank by Thomas (1909c). Closely related to *Xerus*, it presently comprises only one species, which occurs in NW Africa, originally described as *Sciurus getulus*. The single species in the genus mainly inhabits rocky areas in semi-arid and arid regions where they rely on natural shelters or self-dug burrows to escape the extremes of climate. Placed in the Tribe Xerini (together with *Xerus*, the only other genus of ground squirrels).

Barbary Ground Squirrels are medium-large squirrels with a striking bushy tail, relatively large eyes and small ears (without hair brush). The head tends to be blunt and round, with powerful muscles. The nostrils are narrow and naked, and can be closed by the tip of the muzzle. In contrast to other Palearctic ground squirrels, the skull is not angular, has a strong sagittal crest, and the palate extends posteriorly to the cheekteeth. The hindfeet have naked soles and slender digits. The claws, adapted to digging, are long and only slightly curved. Most features are similar to those of the genus *Xerus*, but the fur is not as bristly, although it is short and stiff. Dental formula: $I^{1/1/}, C^{0/0}, P^{2/1}, M^{3/3} = 22$. The skull is characterized by two upper premolars (P^3 is minute, sometimes absent) on each side of the upper jaw, each upper incisor frequently has traces of a groove, and molar surfaces are slightly concave with transversal ridges (M^1 and M^2 are lacking mesostyle, lower molars without anteroconid), palate long (ca. 62% of GLS) with the posterior end of bony palate well posterior to M^3 (as in *Xerus* and unlike other sciurids); masseteric tubercle very prominent (Figure 9). The baculum is long and narrow, ends in a spatulate enlargement with a small crest above and a larger one, bent to the left, below (Cabrera 1932).



Atlantoxerus getulus.

The genus *Atlantoxerus* was first identified with certainty from the early Miocene of China (Li & Qiu 1980, Qiu *et al.* 1999) and middle Miocene of Arabia (Sen & Thomas 1979). Later, it differentiated and spread quickly over southern Europe (Spain; Pelaez-Campomanes 2001), North Africa (Morocco; Lavocat 1961) and eastern Asia (China; Wu 1988). In the upper Miocene, at least four species are known from Spain (De Bruijn & Mein 1968), France (Aguilar *et al.* 1995), Algeria (Ameur 1988), Morocco (Geraads 1998) and Rhodes (De Bruijn *et al.* 1970). In Morocco, several specimens related to *A. getulus* have been reported from the lower and middle Pleistocene (Jaeger 1975, Michel 1990). However, the origin of *A. getulus* (the only extant species of the genus) remains unknown; it does not seem to be a descendant of any known extinct species of the genus that were present in the Maghreb at earlier periods. Jaeger (1977a) suggested a close relationship with the Spanish fossil-form *A. androveri* (De Bruijn & Mein 1968). Additional fossils from the Pliocene are needed to clarify the evolution of the genus, as well as genetical studies on the tribe Xerini to elucidate the relationships of the various genera.

Stéphane Aulagnier

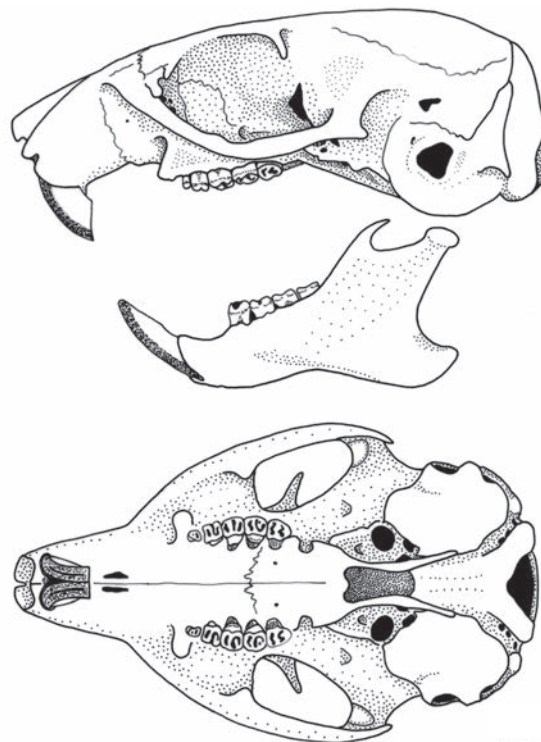


Figure 9. Skull and mandible of *Atlantoxerus getulus* (BMNH 22.5.30.20).

Atlantoxerus getulus BARBARY GROUND SQUIRREL

Fr. Ecureuil fouisseur de Barbarie; Ger. Nordafrikanischer Erdhörnchen (Atlashörnchen)

Atlantoxerus getulus (Linnaeus, 1758). Syst. Nat., 10th edn., 1: 64. 'in Africa'. Restricted by Thomas (1911) to 'Barbary', and by Cabrera (1932) to Agadir, Morocco.

Taxonomy Originally described in the genus *Sciurus*. Synonyms: *praetextus*, *trivittatus*. Subspecies: none. Chromosome number: $2n = 38$, $aFN = 68$.

Description Medium-sized ground-dwelling squirrel with a short pale greyish-brown dorsal pelage and three pale stripes along the body. Pelage short (ca. 3–5 mm) and slightly coarse. Dorsal pelage greyish-brown; hairs pale brown or pale buff terminally, sometimes with black tip. Long black guard hairs, especially on mid-back and rump. Single white side-stripe on each flank from behind shoulders to mid-rump (not to base of tail), bordered on each side by darker background colouration. Single less obvious pale stripe on mid-dorsal line, shorter in length than white side-stripes on flanks. Elongated patch of whitish hair on lower flank between limbs. Ventral pelage sparse; hairs white, sometimes grey at base. Head is rounded and similar in colour to back. Ears small, eyes with narrow pale eye-ring. Limbs moderately long, similar in colour to body. Forefoot with four long digits, each with sharp claw; Digit 1 reduced to small tubercle without claw. Hindfoot with five digits; Digit 1 short; all with long curved claws. Tail of moderate length (ca. 80% of HB), hairs long (ca. 25–30 mm), creamy-white with two wide black bands equidistant along length of hair giving a black–white banded pattern; tip white. Young differ from adults by having longer and smoother pelage. Skull: cheekteeth $5/4$; P^3 very small and peg-like, sometimes absent; posterior end of bony palate well posterior to M^3 ; masseteric tubercle prominent. Nipples: $1 + 1 + 1 + 1 = 8$.

Geographic Variation None recorded.

Similar Species

Xerus erythropus. Dorsal pelage brown, harsh, marked with a single short stripe on each side; muzzle longer with a projecting nose; distribution overlaps only in the Souss plain (Morocco) (Blanc & Petter 1959).

Distribution Endemic to NW Africa. Mediterranean Coastal BZ. Recorded in Morocco and a small area of NW Algeria (Ksours Mts); known from the coastal zone up to 4165 m, mainly in the Middle and Grand Atlas south to Agadir, the Anti-Atlas, and the northern edge of the western Sahara south to Sequiat el Hamra. Introduced (extraliminally) to Fuenteventura (Canary Is.) in 1965.

Habitat Stony regions and open habitats, from mountain slopes to desert. Common in open country with scattered trees and bushes of Juniper *Juniperus* spp., Thuya *Tetraclinis articulata* and Argan *Argania spinosa*, but avoiding areas devoid of vegetation and forests. Also present in various agricultural habitats, favouring stone walls, which provide refuge. Not recorded in irrigated fields.

Abundance Abundant on the lower slopes and valleys. Very common up to 2000 m in the Grand Atlas; but then becoming less



Atlantoxerus getulus

common with increasing altitude. Population numbers also decrease dramatically in the eastern part of the range. Maybe locally numerous in some desert habitats. Fluctuations of population numbers are suspected; for example, they were very numerous in 1952 and rare in 1971 in the same region (Saint Girons 1974).

Adaptations Diurnal and terrestrial. Exhibits two periods of activity: in the morning from 07:00h to 11:00h with a peak of activity at about 09:00h, and in the afternoon from 14:00h to 18:00h with a peak at 15:00h. Optimal temperature for activity is 24 °C. The activity rhythm observed in the Toubkal massif was similar to that at Ademine forest and Jbel Bani at lower altitudes (Petter & Saint Girons 1965). Shelters in burrows during the night and during the heat of the day. Burrows are excavated under rocks, or among stones in screes that have been consolidated by vegetation. Requires permanent water in the southern part of its distribution. At high altitudes, daily activity is reduced greatly during winter, even in the absence of snow cover. True hibernation has not been recorded.

Foraging and Food Mainly herbivorous, sometimes omnivorous. Forages on acorns, nuts and seeds, including those of Argan, but also fruits of wild olive-trees *Oliva europaea*, Juniper and Thuya (Cabrera 1932), and fruits and seeds of Pistachio trees *Pistacia atlantica*. The diet may also include grasses and roots (Carpentier 1932), and also domestic crops, where fallen seeds and stems are eaten (Brosset 1960). Occasionally feeds on insects (Cabrera 1932), and on rubbish in small villages.

Social and Reproductive Behaviour The simplest family unit is composed of a single ♀ with her young. Two ♀♀ with their litters may share a common shelter, at least when the young are able to move around the shelter independently. Pairs of ♀♀ are common before the reproductive season, and sharing of a common natal nest is suspected. These family units may form loose colonies. More complex social groups, including at least three lactating ♀♀ with their young and an adult ♂ have been observed (Gouat & Yahyaoui 2001). Group composition differs greatly (especially during the reproductive season), even between sites that are geographically close together. During the mating period ♂♂ usually stand on a prominent site during the day and call for ♀♀. Several ♂♂ can court one ♀, chasing each other. Records of matings are very rare, and matings are suspected to occur in burrows.

Reproduction and Population Structure Reproductive season varies geographically. Females pregnant in E Morocco in April (Brosset 1960), by which time young have already been born in Saharan Atlas (Cabrera 1932) and young have been weaned in Western Sahara (Valverde 1957). At higher altitudes (Middle Atlas, Grand Atlas, Anti-Atlas), young born in July. Two litters/year may be possible in the Tazenakht region (Anti-Atlas). Litter-size: up to four; in Canary Is., litters of up to nine have been recorded. Young weigh 6–9.5 g at birth, and they leave the burrow when 5–6 weeks old. Captive animals have lived for five years.

Predators, Parasites and Diseases Main predators are diurnal raptors (occasionally owls), and also foxes and genets. Many parasites have been collected (Dollfus 1953, Hastriter & Tipton 1975); the louse *Neohematopinus pectinifer* is reported to carry spirochetes, causing relapsing fever in humans (Blanc *et al.* 1933).

Conservation IUCN Category: Least Concern. Widespread within its range, and not threatened.

Measurements

Atlantoxerus getulus

HB: 194 (165–230) mm, n = 18

T: 158 (90–190) mm, n = 18

HF: 46.5 (41–52) mm, n = 18

E: 15.5 (12–18) mm, n = 16

WT: 250 g, n = 1

GLS: 45.9 (38.4–50.0) mm, n = 13

GWS: 27.9 (23.6–30.8) mm, n = 13

P⁴–M³: 8.8 (7.2–9.7) mm, n = 12

Morocco (MNHN)

Key References Gouat & Yahyaoui 2001; Petter & Saint Girons 1965; Saint Girons 1953, 1974.

Stéphane Aulagnier, Patrick Gouat & Michel Thévenot

GENUS *Epixerus* Western Palm Squirrel

Epixerus Thomas, 1909. *Ann. Mag. Nat. Hist.*, ser. 8, 3: 472. Type species: *Sciurus wilsoni* Du Chaillu, 1860 (= *Sciurus ebii* Temminck, 1853).

Epixerus contains a single species distributed in the Rainforest BZ of West and Equatorial Africa. The genus is distinguished by its large size, long hindfoot (usually over 55 mm) and tapered bushy tail with strongly banded hairs that produce a splendid pattern of chevrons when spread and viewed from below. Skull characteristics are large size (>65 mm), palate extends well posteriorly to the posterior end of M³, ratio of palatal length to interorbital breadth is 56.0% to 65% (Amtmann 1966), masseteric tubercle absent or not prominent, and supraorbital ridge has a foramen (Figure 10). Dental formula: I¹/₁, C⁰/₀, P¹/₁, M³/₃ = 20. Additional characters are given in the species profile.

The number of species in the genus is debatable. Two species are sometimes recognized (e.g. Verheyen 1959, Hoffman *et al.* 1993): *E. wilsoni* (du Chaillu, 1860), with a subspecies *E. w. mayumbicus*, and *E. ebii* (Temminck 1853), with two subspecies *E. e. ebii* and *E. e. jonesi*. Kuhn (1964) revised the genus and, on the basis of a large geographic sample, recognized a single species, *E. ebii* (see also Amtmann 1966, Thorington & Hoffman 2005). Here, a single species, *E. ebii*, is recognized.

Louise H. Emmons

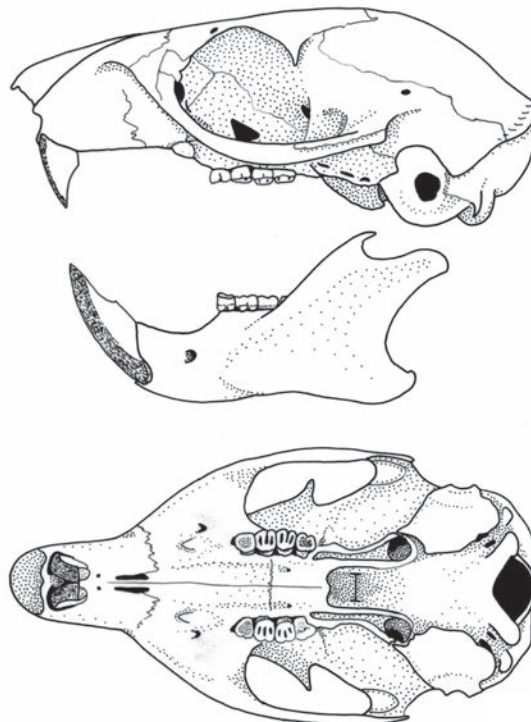


Figure 10. Skull and mandible of *Epixerus ebii* (BMNH 98.3.19.12).

Epixerus ebii WESTERN PALM SQUIRREL

Fr. Écureuil des palmier; Ger. Westliches Palmenhörnchen

Epixerus ebii (Temminck, 1853). Esquisses zoologiques sur la côte de Guinée, p. 129. 'Les grandes forêts de la Guinée'. Ghana.

Taxonomy Originally described in the genus *Sciurus* (see also genus profile). The form *wilsoni* was formerly considered as a distinct species (e.g. by Perret & Aellen 1956, Verheyen 1959 and Rosevear 1969), but is here considered as a subspecies. Synonyms: *jonesi*, *mayumbicus*, *wilsoni*. Subspecies: three. Chromosome number: not known.

Description Very large, reddish, slender-bodied squirrel with long legs and long, bushy, grey-frosted tail. Pelage short. Dorsal pelage dull brownish-red, finely grizzled with yellow and black. No side-stripes on flanks. Ventral pelage sparse with some whitish hairs on chest; yellow ventral skin sharply delineated from lateral pelage. Head large and broad, with large eyes; ears relatively large, naked, extending above crown. Bulging cheeks (due to large highly developed masseter muscles). Limbs and feet long and slender, similar in colour to dorsal pelage. Tail long (ca. 95% of HB), bushy, tapered at tip, frosted grey, with indistinct alternating bands of blackish and pale grey. Alternating bands of red, black and grey on the tail hairs create a pattern of chevrons on the underside of the tail when hairs are spread and viewed from below (not normally visible in the field). Tail carried horizontally, straight out behind the body, or hanging, not curled up against back. Skull: cheekteeth $4/4$; posterior end of bony palate posterior to M^3 ; masseteric tubercle not prominent. Nipples: $1 + 1 + 1 + 1 = 8$; one specimen with five pairs = 10 was reported in Liberia (Kuhn 1964).

Geographic Variation

E. e. jonesi: Liberia and Sierra Leone. Head and dorsal pelage rufous.

E. e. ebii: Ghana and Côte d'Ivoire. Head rufous, dorsal pelage browner.

*Epixerus ebii**Epixerus ebii*.

E. e. wilsoni: Cameroon, Gabon, Equatorial Guinea and Congo. Head and dorsal pelage reddish-brown.

Similar Species

Protoxerus stangeri. Larger, greyer, with stout body, long back, short robust legs; head grizzled grey; short ears that do not extend above crown; arboreal.

Distribution Endemic to Africa. Rainforest BZ (Western and West Central Regions). Recorded from Liberia and Sierra Leone to Ghana; S Cameroon, Gabon, Equatorial Guinea and Congo.

Habitat Evergreen rainforests. Undergrowth in forest, including *Raphia* palms. In Sierra Leone, recorded from montane forest at 1020 m (Grubb *et al.* 1998).

Abundance Rare in collections and rarely seen; but in Gabon it is more common than usually supposed. Its terrestrial habits, extreme wariness and tendency to escape silently on the ground at the slightest disturbance, allow it to exist undetected by Western naturalists (who often mistake it for a Forest Giant Squirrel *Protoxerus stangeri*). None the less, local peoples who hunt game with nets know this species well and have specific names for it. The very short activity period (see below) may contribute to the perceived rareness of these squirrels.

Adaptations Diurnal. A cursorial, fast-running terrestrial species with elongated, slender limbs and feet, and a slender lower abdomen;

sometimes assumes a digitigrade posture with forelimbs bearing weight only on the tips of the digits. The masseter muscles are highly developed and the incisors are robust, consistent with a diet of kernels from hard nuts. A prominent glandular pocket in the inside corner of the lips may be used in scent marking (Emmons 1975, 1980).

Western Palm Squirrels make dens in tree hollows and favour those hollows with small entrances (mean height: 8.1 m [1.5–20 m]; $n = 12$ den sites; Emmons 1975). The nest itself is undescribed. They leave the nest at dawn; in Gabon they have a short activity period (mean 7.69 h) and return to the nest in the late afternoon or well before dusk (mean entry time 14:50h; range: 12:30–17:03h, $n = 16$; Emmons 1980). Climbing to the nest is their only arboreal activity.

Foraging and Food Feeds terrestrially on fallen seeds and fruit, especially on thick-walled nuts (98% dry mass, $n = 4$ stomach contents; Emmons 1980). A few insects are also consumed. To feed on nuts it jumps up from the ground onto a low feeding perch (0.5–1.5 m), probably to scan for predators while deafened by gnawing. In Gabon, feeds mostly on nuts of *Panda oleosa*, a large, elephant-dispersed fruit. The presence of this squirrel in an area can be readily ascertained by the presence of large middens of shells from opened *Panda* nuts beneath low perches: the seeds are extracted by either splitting along the lines of dehiscence (old nuts) or by the extraordinary feat of ‘sawing’ nuts in half across the middle (fresh nuts). No other animal opens *Panda* nuts by this method. Western Palm Squirrels hoard *Panda* nuts by burying them in the ground at distances of 15–20 m or more from the parent tree (Emmons 1975), thereby assisting the dispersal of the seeds.

Social and Reproductive Behaviour In 50 observations, squirrels were solitary 80% of the time and seen with 1–3 others in the remainder of sightings (Emmons 1980). Two adults feeding under the same *Panda* tree tolerated each other and showed no aggression. Two adult ♂♂ followed by radio-tracking in Gabon had home-ranges of 21.1 ha and 21.7 ha, and a single subadult ♀ had a home-range of 13.9 ha. Movement is rapid: ♂♂ travel at a mean rate of 115 m/h and ♀♀ at 144 m/h (means of all hours when active). The social organization is unknown, but in one apparent ‘mating chase’ several calling ♂♂ pursued a presumably oestrus ♀ (Emmons 1980).

Vocalizations are described in detail in Emmons (1978). The low intensity alarm call consists of soft, short (about 400 ms), rapid, machinegun-like bursts of chattering of the incisor teeth. High intensity alarm is indicated by a staccatto series of short, broad-frequency pulses. When alarmed, a squirrel may climb to a low vantage point on a horizontal or vertical support, with the long bushy tail hanging straight downward. At the start of each high intensity alarm call, the base of the tail is wagged rapidly and vigorously from side to side a few times, the tail-tip following passively, whipping loosely back and forth below the body. Squirrels calling from the ground hold the tail horizontally, with no wagging display.

Reproduction and Population Structure The only published litter-size is 2 ($n = 1$, Emmons 1979a).

Predators, Parasites and Diseases Sometimes captured by local people in hunting nets.

Conservation IUCN Category: Least Concern. Likely to be threatened only by loss of mature rainforest. Home-ranges are large so that the density of squirrels is always relatively low.

Measurements

Epixerus ebii

HB: 284 (275–300) mm, $n = 7$

T: 272 (250–310) mm, $n = 5$

HF: 68 (65–70) mm, $n = 5$

E: 20–21 mm, $n = ?$ *

WT: 594 (540–650) g, $n = 7$

GLS: 69.4 (68.6–69.8) mm, $n = 4$

GWS: 36.9 (35.9–37.7) mm, $n = 3$

P⁴–M³: 10.8 (10.3–11.2) mm, $n = 7$

Gabon (Emmons 1975, L. Emmons unpubl.)

*Rosevear 1969

Key References Emmons 1975, 1978, 1980; Kuhn 1964.

Louise H. Emmons

GENUS *Funisciurus*

Rope Squirrels

Funisciurus Trouessart, 1880. Le Naturaliste 2 (37): 293. Type species: *Sciurus isabella* Gray, 1862.

A genus of small- to medium-sized squirrels with ten species endemic to the Rainforest BZ and parts of the adjacent Rainforest–Savanna Mosaics (Table 11). The greatest diversity is in west-central Africa, with five species in Cameroon. Most species are arboreal; some species live in the canopy in natural rainforest, and others live in tangled vegetation close to the ground and in secondary growth. A few species enter plantations and gardens. The vernacular name ‘Rope Squirrel’ refers to the ability of these squirrels to clamber and climb on rope-sized branches and lianas. An alternative vernacular name ‘African Striped Squirrel’ refers to the lateral side-stripe(s) on each flank.

The genus is characterized by relatively small size (mean HB usually 130–200 mm), long well-haired tail slightly shorter than the head and body, and (in most species) a longitudinal side-stripe along each flank. The species of the genus are the smallest of African squirrels, except for the single species of *Myosciurus* (HB 61–74 mm). The head is small, with small ears held close to the skull; the limbs are short, and the long tail is covered with long hairs that are held erect to give a bushy appearance. The tail is commonly held upwards and backwards, close to the back with the tip curling away from the shoulders; it is constantly flicked backwards and forwards as a means of



Funisciurus squirrels.

communication and when the squirrel is agitated. Females have either two pairs of nipples (most species) or four pairs (*F. leucogenys*). Rope Squirrels produce a range of vocal noises, including clicks, squeaks and chatters.

The skull is characterized by the dental formula $I \frac{1}{1}, C \frac{0}{0}, P \frac{2}{1}, M \frac{3}{3} = 22$; orange ungrooved incisors, five (not four) cheekteeth in

each upper ramus (cf. *Heliosciurus*); small masseteric tubercle; fossa for origin of anterior deep masseter muscle does not extend onto the rostrum; supraorbital foramen absent; and the posterior end of the bony palate is approximately in line with the posterior end of M^3 (in this latter respect it is similar to several other genera of squirrels but different from *Atlantoxerus*, *Xerus* and *Epixerus* where it

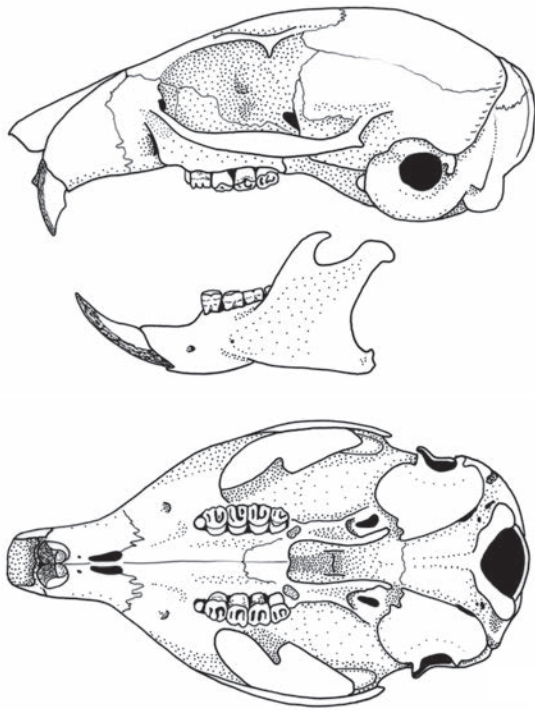


Figure 11. Skull and mandible of *Funisciurus anerythrus* (BMNH o.2.5.33).

is posterior to M^3). Cusps of cheekteeth are worn down early in life, leaving flattened surfaces (not concave with prominent ridges as in *Heliosciurus*) (Figure 11).

The genus exhibits considerable diversity in morphology, especially in colour and in the form of the lateral side-stripe. Species in the genus range from small black-striped squirrels to somewhat larger squirrels with successive reduction of the stripes on each side. The gradual reduction in number and size of the side-stripes is illustrated in the following sequence: (a) *F. isabella*, *F. lemniscatus* (smaller species; two black stripes); (b) *F. congicus* (smaller species; stripe pattern slightly modified to a blackish-brown side-stripe bordered by a cream stripe); (c) *F. bayonii*, *F. substriatus* (relatively small species; stripes reduced to a pale lateral side-stripe); (d) *F. pyrrhopus*, *F. anerythrus* (larger species, reddish pigment in many subspecies; pale side-stripe, often rather obscure); (e) *F. leucogenys* (largest; stripes reduced to line of whitish spots); and (f) *F. carruthersi* (relatively large, no side-stripe). See Rosevear (1969) for a full discussion of the genus.

The genus is placed in the subfamily Xerinae and tribe Protoxerini (which also includes all the other African sciurids except *Atlantoxerus* and *Xerus* – the Ground Squirrels – which are placed in the tribe Xerini) (Thorington & Hoffman 2005).

Species in the genus are distinguished by colour, number and character of the lateral side-stripes, colouration of body and limbs, and body and skull size (Table 11).

Peter Grubb

Table 11. Species in the genus *Funisciurus*. Arranged in order of increasing number of side-stripes on each flank.

| Species | Side-stripes on each flank | Red colouration on pelage | General colouration | HB mean (mm) | HF mean (mm) | GLS mean (mm) | Notes |
|-----------------------|--|---------------------------|----------------------------|------------------|----------------|---------------|--|
| <i>F. carruthersi</i> | Absent | None | Olive-green | 203 | 48 | 48 | Montane forests, Rwenzori region |
| <i>F. anerythrus</i> | One, pale | None | Brown | 182 | 44 | 47 | Rainforests, Nigeria to W Uganda |
| <i>F. bayonii</i> | One, pale, usually indistinct | None | Dull olive, speckled black | ca. 180 | 42 | 42 | NE Angola, SW DR Congo south of Kasai and Congo rivers. Rare |
| <i>F. congicus</i> | One, wide white bordered ventrally by brownish-black | None | Yellowish-brown | 160 | 40 | 33 | Rainforests of DR Congo (south of river), Angola, Namibia |
| <i>F. substriatus</i> | One, pale white bordered ventrally by dark stripe | None | Greenish-yellow | ca. 172 | 43 | 44 | Guinea and Sudan Savanna, Burkina to Benin |
| <i>F. pyrrhopus</i> | One, white | Forelimbs and hindlimbs | Grey-black | 211 | 46 | 52 | Rainforests, Senegal to DR Congo and Rwanda |
| <i>F. leucogenys</i> | One, whitish-yellow broken into spots | Head and cheeks | Grey-brown | 209 | 51 | 51 | Rainforests, Ghana to Central African Republic |
| <i>F. isabella</i> | Two, black, separated by buffy-brown | None | Grizzled brown | 158 ♂♂
152 ♀♀ | 35–36 | 41 | Rainforests of central Africa |
| <i>F. lemniscatus</i> | Two, black separated by yellow | None | Brown | 164 ♂♂
160 ♀♀ | 36 ♂♂
35 ♀♀ | 43 | Rainforests of central Africa |
| <i>F. duchailui</i> | Two, black | None | Olive-brown | 197 | 45 | 42 | Gabon |

***Funisciurus anerythrus* THOMAS'S ROPE SQUIRREL (REDLESS TREE SQUIRREL)**

Fr. Funisciure de Thomas; Ger. Rotloses Baumhörnchen

Funisciurus anerythrus (Thomas, 1890). Proc. Zool. Soc. Lond. 1890: 447, pl. 40. Buguera, south of Lake Albert, Uganda.

Taxonomy Originally described as a subspecies of *Sciurus pyrrhopus* in 1890 and later raised to specific rank. There has been great confusion about the taxonomic placement of the named subspecific forms of *F. anerythrus* and *F. pyrrhopus*; several subspecies have ping-ponged back and forth between the two species. In Gabon, where the local forms of the two species are sympatric, they are unequivocally distinguished by their physical characters and their entirely distinctive calls, as well as by major ecological differences in habitat, diet and nest sites (Emmons 1975, 1980). These distinctions, described below, should be considered when assigning West African forms to one of these two species. Synonyms: *bandarum*, *mystax*, *niapu*, *ochrogaster*, *raptorum*. Subspecies: four. Chromosome number: $2n = 38$, $FN = 62$ (Benin, Civitelli *et al.* 1996).

Description Medium-sized plain brown squirrel with a pale side-stripe from shoulder to rump. Dorsal pelage grizzled brown flecked with buff; hairs banded. Single pale buff side-stripe from shoulder to hindquarters, bordered below with dark brown. Ventral pelage thickly haired, dull grey to white or orange. Head similar to dorsal pelage. Eye bordered above and below with pale buff line. Ears small. Fore- and hindlimbs dull buff; digits with well-developed claws. Tail medium (ca. 85% of HB – relatively short for a squirrel), hairs long, banded reddish at base, black distally, white at tip. Tail appears reddish medially when viewed from below, and from above it is dark with white frosting. Tail carried curled up against back when squirrel is at rest; often held high, with the base vertical and tip curled backward when squirrel is moving. Skull: cheekteeth $5/4$; posterior end of bony palate in line with posterior end of M^3 ; masseteric tubercle not prominent (and often barely visible). Nipples: $0 + 0 + 2 + 2 = 4$.

Geographic Variation Four subspecies were recognized by Amtmann (1966):

F. a. anerythrus: W Uganda and DR Congo south to Mt Kabobo. Dorsal pelage reddish-brown, ventral pelage ochraceous.

F. a. bandarum: Central African Republic. Dorsal pelage buff-tinged, ventral pelage pale grey to orange.

F. a. mystax: S Cameroon to Gabon. Dorsal pelage warm brown, ventral pelage orange.

F. a. raptorum: SW Nigeria. Dorsal pelage grey-tinged, ventral pelage whitish.

Amtmann (1966) placed far western forms (e.g. *mandingo*; Sierra Leone), previously attributed to this species, in *F. pyrrhopus*.

Similar Species

Funisciurus pyrrhopus. Larger (HB: 190–230 mm); longer nose; limbs bright to dull reddish; ventral pelage white.

Distribution Endemic to Africa. Rainforest BZ (West Central, East Central and South Central Regions) and surrounding forest–savanna mosaics. Recorded from Benin, Nigeria, Cameroon,

*Funisciurus anerythrus*

Equatorial Guinea, S Central African Republic, Gabon, DR Congo and Congo.

Habitat Permanently or seasonally flooded waterside habitats of swamps, gallery forests, seasonally flooded riversides, and islands in rivers. Especially abundant in *Raphia* palm swamps. In Gabon, it is not found in terra firma forest even where this abuts directly on riversides (Emmons 1975, 1980). In Nigeria, prefers lower strata of secondary forest and tangled vegetation where there is a dense growth of shrubs and creepers; may also be seen climbing in medium-sized trees and oil palms (Happold 1977).

Abundance Common in suitable habitats, where it can reach higher densities than does any other species of African tree squirrel.

Adaptations Diurnal and scansorial. Forages on the ground and at all levels within the low-canopy of seasonally flooded forests (mean height: 3.8 m [1–13 m], $n = 20$). Builds round nests (20–24 cm diameter) of leaves lined with fibres. In habitats dominated by *Raphia* palms, the outer shell of the nest is often built with palm leaflets. The nests are exposed, but partially hidden in dense clumps of vegetation in the branches of trees or on the rachis of palm leaves. Most nests are built in vegetation that overhangs water (Emmons 1975).

Foraging and Food Omnivorous. Feeds on fruits and seeds (77% dry mass of stomach contents in Gabon, $n = 15$), arthropods (20%) and minor amounts of green plant tissues and mushrooms. In *Raphia* palm swamps, these squirrels feed intensively on the orange pericarp

of *Raphia* fruits, and they can be seen feeding and climbing around in the crowns of palms. They temporarily cache these palm nuts by wedging them into above-ground crevices. The arthropod portion of the diet is dominated by ants (92% occurrence) and termites (58% occurrence), but many other taxa are also eaten (Emmons 1980).

Social and Reproductive Behaviour These squirrels often live in dense populations, and in Gabon were seen with other conspecifics 50% of the time ($n = 431$ observations). Individuals travelling in pairs (28% of observations) followed each other closely, groomed each other, and rested in contact. Up to six individuals were seen feeding at the same fruit tree. A captive heterosexual pair shared a nest box and showed contact behaviour, but competed aggressively for food (Emmons 1980). The social organization is unknown, but the above observations are consistent with monogamous pair formation.

Vocalizations are common (see Emmons 1978 for details). The low intensity alarm call consists of frequency-modulated chucks emitted in groups of 1–6, but usually singly (45% of 166 call bouts). The high intensity call is an astonishing sound unlike that of any other species: a long series of stereotyped groups of 2–4 rhythmic pulses followed by 1–2 long, low frequency whistles (dada dada dadada . . . dadaweeeeeeou). Only the final whistles can be heard at a distance. During a low intensity alarm call, the tail is jerked sharply downward from its resting position against the back, then slowly returns up to its normal posture. As the tail is flicked down, the hindfeet are simultaneously stamped on the substrate, followed by stamping of the forefeet as the tail is raised.

Reproduction and Population Structure Embryo number: 1.2 (1–2, $n = 77$ litters; Rahm 1970) in E DR Congo, and 1.5

(1–2, $n = 6$; Dubost 1968, Emmons 1979a) in Gabon. In E DR Congo, pregnancies occur in all months of the year, with the highest pregnancy rate at the end of the dry season and beginning of the wet season (Aug–Oct) (Rahm 1970).

Predators, Parasites and Diseases These squirrels have been implicated as hosts for the monkeypox virus (Jezek & Fenner 1988).

Conservation IUCN Category: Least Concern.

Its widespread distribution and commonness in many habitats would suggest that the appropriate category is Least Concern.

Measurements

Funisciurus anerythrurus

HB: 182 (167–198) mm, $n = 19$

T: 159 (150–170) mm, $n = 16$

HF: 43.8 (42–46) mm, $n = 11$

E: 16 (15–16) mm $n = ?$ *

WT: 219 (190–240) g, $n = 14$

GLS: 47.6 (46.1–49.0) mm, $n = 3$

GWS: 26.2 (25.7–27.1) mm, $n = 3$

P³–M³: 8.7 (8.5–8.9) mm, $n = 4$

Gabon (Emmons 1975, L. Emmons unpubl.)

*Rosevear 1969

Key References Emmons 1978, 1979a, 1980; Rahm 1970.

Louise H. Emmons

Funisciurus bayonii LUNDA ROPE SQUIRREL

Fr. Funisciure de Bocage; Ger. Bocages Baumhörnchen

Funisciurus bayonii (Bocage, 1890). Jornal de Sciencias Mathematicas Physicas e Naturaes da Academia de Lisboa, ser. 2, 2: 3. '... du Duque de Bragança'. N Angola (exact locality not known).

Taxonomy Originally described in the genus *Sciurus*, but reallocated on the basis of skull characters to *Funisciurus* by Hayman (1951). Synonyms: none. Chromosome number: not known.

Description Small to medium-sized dark squirrel with indistinct white side-stripe. Dorsal pelage uniformly dull olive, speckled with black. Indistinct side-stripe from shoulder to rump, buff to whitish-buff. Ventral pelage grey tinged with buff. Upper surface of head, fore- and hindlimbs similar to dorsal pelage. Pale eye-ring. Tail long (ca. 100% of HB), grizzled, black and ochre without obvious rings, darker than body. Skull: short muzzled, resembling *F. congicus* in this respect; postorbital processes well developed; nasals broad; cheekteeth 5/4; posterior end of bony palate in line with posterior end of M³; masseteric tubercle not prominent. Nipples: not known.

Geographic Variation None recorded.

Similar Species

F. congicus. Paler, also with side-stripe; probably not sympatric.



Funisciurus bayonii

Distribution Endemic to Africa. Zambezian Woodland BZ. Recorded from NE Angola and SW DR Congo south of Kasai and Congo rivers.

Habitat Uncertain. According to Amtmann (1966), who based his conclusions on a vegetation map of the species range, the habitat is probably moist forest at low to medium elevations; and forest–savanna mosaic, woodland and savannas in south-western parts of the range (principally on Kalahari Sand).

Abundance No information. Known only by a few specimens.

Remarks Apparently no other information.

Conservation IUCN Category: Data Deficient.

Measurements

Funisciurus bayonii

HB: 167, 190 mm, n = 2

T: 178, 170 mm, n = 2

HF: 42, 41 mm, n = 2

E: n. d.

WT: n. d.

GLS: 42 (41–44) mm, n = 5

GWS: 24.7 (24–26) mm, n = 5

P³–M³: 7.7 (7.5–7.8) mm, n = 5

Angola (Hayman 1951)

Key References Amtmann 1975; Hayman 1951.

Richard W. Thorington, Jr, Lindsay A. Pappas &
Chad E. Schennum

Funisciurus carruthersi CARRUTHERS'S ROPE SQUIRREL (CARRUTHERS'S MOUNTAIN SQUIRREL)

Fr. *Funisciure de montagne*; Ger. Carruthers Baumhörnchen (Bergstreifenhörnchen)

Funisciurus carruthersi Thomas, 1906. Ann. Mag. Nat. Hist., ser. 7, 18: 140. 'Rwenzori East, 6500 ft' (= 1900 m), Uganda.

Taxonomy *Funisciurus carruthersi* appears to straddle a taxonomic boundary in sharing characteristics of both the Rope Squirrels *Funisciurus* and Bush Squirrels of the *Paraxerus lucifer/byatti* complex. In common with *Funisciurus* spp., adults have flat-crowned upper and lower cheekteeth. By contrast, the colouring, body size and ecological habits of *F. carruthersi* appear to ally it more closely with *Paraxerus*. Hopefully, molecular studies will help shed some light on an ambiguous taxonomic situation. Synonyms: *birungensis*, *chrysippus*, *tanganyikae*. Subspecies: three. Chromosome number: not known.

Description Medium to large soft-furred olive-green squirrel with grey ventral pelage. Dorsal pelage grizzled olive-green and black, darker on mid-dorsal line; hairs long and soft, dark grey or black at base, yellowish-buff or olive-green subterminal band, and black tip. Long black guard hairs, especially on mid-dorsal line. Flanks paler, with fewer black-tipped hairs, and without side-stripes. Ventral pelage from throat to tail grey or greyish-white; hairs medium-grey at base, white or greyish-white at tip. Scrotum olive-green, as flanks. Head and cheeks similar to dorsal pelage. Conspicuous creamy-yellow eye-ring. Ears small, pigmented, with sparse short hairs, and with sharply angled leading edge (so overall shape intermediate between the rather rectangular ear of *Funisciurus* and more rounded ears of *Paraxerus*). Forelimbs with four digits; hindlimbs with five digits (Digit 1 reduced); all digits have a strong sharp claw. Colour of pelage of limbs fades to brown before the moult. Tail long (ca. 100% of HB), ochre and black, with inconspicuous bands along length; hairs long, ochre at base, with black subterminal band and ochre at tip. Skull: cheekteeth ⁵/₄; posterior end of bony palate in line with posterior end of M³; masseteric tubercle not prominent. Nipples: 1 + 2 = 6.

Geographic Variation Amtmann (1966) lists the following subspecies:



Funisciurus carruthersi

F. c. carruthersi: Rwenzori Mts.

F. c. birungensis (including *chrysippus*): Mountains of SE Uganda, E DR Congo, Rwanda and NW Burundi.

F. c. tanganyikae: Mountains around north end of L. Tanganyika.

Similar Species

Heliosciurus ruwenzori. Similar size; dorsal pelage grey, ventral pelage white; tail with grey and white bands.

Heliosciurus rufobrachium. Similar size; pelage of limbs reddish or rufous; tail with conspicuous black and white bands.

Distribution Endemic to Africa. Afromontane–Afroalpine BZ. Recorded from the montane forests of the Rwenzori Mts and Albertine Rift Valley mountains in E DR Congo, Uganda, Rwanda and Burundi (Thorington & Hoffman 2005). Altitude range: 1500–2800 m.

Habitat Montane forests, especially in stands of *Prunus* (*Pygeum*) *africanum*, a common tree species in the region and, at the upper reaches of its altitudinal range, in forests of *Hagenia abyssinica*. Prefers areas of forest with a broken canopy where trees are smothered in climbers, and undergrowth is densely tangled. Does not adapt well to cultivated areas. In E DR Congo most observations were close to rivers (Rahm & Christiaensen 1963).

Abundance Uncertain. Apparently common in all *Prunus africanum* stands throughout their range. Supposedly less common in higher reaches of montane forest. Abundance is difficult to assess because these squirrels are very shy and inhabit dense vegetation.

Adaptations Diurnal and arboreal. Carruthers's Mountain Squirrels are unusual among squirrels at higher altitudes in becoming active shortly after dawn as well as in the evening. They are less conspicuous than Sun Squirrels *Heliosciurus* living in the same habitat. The drab-coloured tail, in particular, which is commonly carried over the back, is less conspicuous, even when waved about. This suggests that the principal function of tail flicking is dispersion of scent from the anal glands. There may therefore be a bias in this species towards communication by olfactory rather than by visual signals. Their olive-green colouring provides well-matched camouflage on leafy branches and on the mossy, lichened trunks and branches of trees. Their colouring and noteworthy shyness may reflect greater vulnerability than Sun Squirrels to the abundant buzzards, hawks and hawk-eagles found in montane habitats.

Foraging and Food Primarily frugivorous. Foraging occurs at all levels, even, rarely, on the ground. Recorded as feeding on the fruits of *Bridelia* spp., *Alchornea* spp., *Carapa grandifolia* and *Strombosia scheffleri* and the fruits of an unnamed gourd (Rahm & Christiaensen 1963). Traces of insects have been found in stomachs but very fine

mastication has prevented accurate identification of plant foods (Kingdon 1974).

Social and Reproductive Behaviour Usually seen singly, occasionally in pairs. They have been heard to make a rasping, quacking cry, possibly an advertising or contact call, but its significance has not yet been determined. Reported to make large nests of plant material in liana tangles; these are lined with finely shredded bark torn from a local shrub (Kingdon 1974).

Reproduction and Population Structure Very little information. There is a single record of a lactating ♀ from SW Uganda in May (Kingdon 1974). An absence of records of juveniles suggests young remain well concealed.

Predators, Parasites and Diseases Likely predators are hawk-eagles *Hieraaetus africanus* and *H. dubius*, eagles, buzzards and, more rarely perhaps, genets and Golden Cats *Profelis aurata* (Kingdon 1974).

Conservation IUCN Category: Least Concern. Previously considered as Vulnerable.

Measurements

Funisciurus carruthersi

HB: 203 (187–236) mm, n = 7

T: 201 (180–231) mm, n = 6

HF: 48 (46–50) mm, n = 7

E: 19 (17–20) mm, n = 7

WT: 222 (200–280) g, n = 4

GLS: 48.7 (46.4–50.2) mm, n = 7

GWS: 28.0 (25.5–29.0) mm, n = 7

P³–M³: 8.55 (8.2–9.0) mm, n = 7

Body measurements: Uganda, DR Congo (BMNH)

Weight: Rahm & Christiaensen 1963

Key References Kingdon 1974; Rahm & Christiaensen 1963.

Jonathan Kingdon

Funisciurus congicus CONGO ROPE SQUIRREL (STRIPED TREE SQUIRREL)

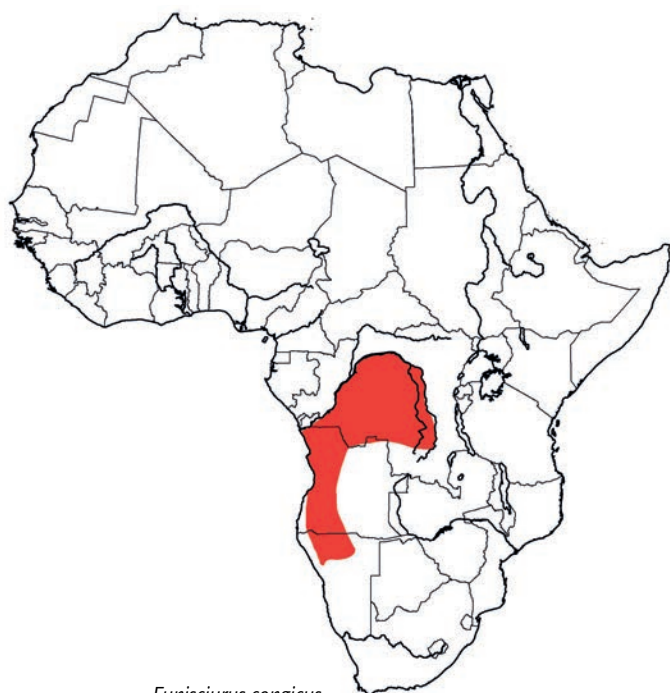
Fr. Funisciure du Congo (Funisciure de Kuhl); Ger. Kongo Baumhörnchen

Funisciurus congicus (Kuhl, 1820). Beiträge zur Zoologie und vergleichenden Anatomie 2: 66. 'Congo'; no specific locality given, probably Angola (Hill & Carter 1941).

Taxonomy Originally described in the genus *Sciurus*. Seven subspecies have been described, but Amtmann (1975) considered them invalid because geographic variation in size and colouration is highly correlated with temperature and rainfall (Amtmann 1966). *Funisciurus poolii* included in this species by Amtmann (1975). Synonyms: *damarensis*, *flavinus*, *interior*, *oenone*, *olivellus*, *poolii*, *praetextus*. Subspecies: none. Chromosome number: not known.

Description Small brown squirrel with long wide side-stripes. Pelage short and soft. Dorsal pelage grizzled yellowish-brown; hairs

black at base, yellowish-brown terminally, some with black tip. Each flank with wide white or cream side-stripe from shoulder to rump, and narrow pronounced brownish-black stripe below the white stripe. Ventral pelage white. Crown of head brown, cheeks and throat white. White stripes above and below eye, forming incomplete eye-ring; stripes buff or pale ochre on specimens from northern Angola. Ears with white, buff, or pale ochre hairs on outer margins. Outer surface of limbs buff, inner surface white. Tail long (ca. 105% of HB), thin and bushy, black and buff above, pure white below; hairs black at base with alternating bands of buff and black, buff tip above,



Funisciurus congicus

white below. At rest, tail held along surface of back, with terminal quarter curled over posteriorly. Skull: cheekteeth $5/4$; posterior end of bony palate in line with posterior end of M^3 ; masseteric tubercle not prominent. Nipples: $0 + 0 + 1 + 1 = 4$.

Geographic Variation Pelage varies geographically. Individuals from drier regions have paler colouration; those from more humid areas (e.g. C DR Congo) tend to be dark brownish-black.

Similar Species

F. bayonii. Slightly larger; uniformly dull olive, speckled with black; side-stripe indistinct.

Other *Funisciurus* spp. Darker, often with rufous and rusty colouration.

Paraxerus cepapi. Slightly larger (HB♂: 145–203 mm); pelage grey, yellowish-brown or brown; without side-stripe.

Distribution Endemic to Africa. Rainforest BZ (South Central Region), western parts of Southern Rainforest–Savanna Mosaic, and Zambezian Woodland BZ. Widely but patchily distributed in DR Congo (south of Congo R.), W Angola and NW Namibia.

Habitat Coastal palm groves, mopane woodland and tall forest trees, especially along watercourses and on granite outcrops. Requires denser vegetation than *Paraxerus cepapi*, with which it is sympatric in parts of the geographic range.

Abundance Common. In optimal habitat in Namibia, densities may reach 12–18 animals/ha (Viljoen 1978).

Adaptations Diurnal, arboreal and terrestrial. In Namibia, these squirrels emerge from their nests soon after dawn (from 07:05h to 08:15h, depending on whether the day is clear or overcast) and return to their nests in early evening (18:00–18:50h), well before

sunset. On cool mornings they are especially active, probably in order to generate body heat. During hot days they bask in the sun, and may also hold the white underside of the tail over the back to prevent over-heating. These squirrels are very agile and move easily and quickly, jumping from branch to branch. Observations ($n = 210$) indicate that they prefer habitats on or near the ground: 39% on ground, 42% in subcanopy (<2.5 m) and only 18% in the canopy (>2.5 m above ground) (Viljoen 1978). If disturbed on the ground they immediately flee into the trees. Nests are made in the forks of branches and are constructed of twigs, leaves and grass; sometimes nests are in the holes of trees. When running, the tail is held over the back in the form of a question mark (Viljoen 1978).

Foraging and Food Omnivorous. Foraging takes place on the ground (39% of the time) and in the subcanopy, mostly in trees up to 2.5 m high. The diet includes seeds, fruits, stems and shoots, especially of *Colophospermum mopane*, Velvet Commiphora *Commiphora mollis*, *Grewia bicolor* and other trees. One individual was observed feeding on Mopane Caterpillars *Gonimbrasia belina*. Hard foods may be buried for eating later (Viljoen 1978, Smithers 1983).

Social and Reproductive Behaviour Congo Rope Squirrels are social animals, and live in small groups of up to four individuals. Individuals in the group keep in contact by a series of bird-like high-pitched chirps, and by sight. Individual recognition is by the use of scent, and bonding within the group is maintained by scent and by mutual grooming. The alarm call, in response to a raptor, is a series of high-pitched whistles, which causes other individuals to ‘freeze’ instantly. When a ground predator is spotted, the squirrels emit bird-like chirps accompanied by flicking of the tail; a group may mob a predator by peering down at it while tail-flicking and chattering. Daily home-range of a group living in narrow riverine vegetation (20 m wide on either side of the river bank) is about 0.5 ha; one group moved 200 m on either side of the river during a day, a home-range of ca. 0.4 ha (Viljoen 1978, 1997).

Reproduction and Population Structure Juvenile specimens in museum collections are most common in Apr–Jun and Oct–Jan suggesting two birth seasons/year. Litter-size: 2 ($n = 8$; Viljoen 1978).

Predators, Parasites and Diseases Ectoparasites include two species of ticks (*Haemaphysalis* sp. and *Rhipicephalus* sp.) and one species of flea (*Libyastus vates*). Predators probably include snakes, mammalian carnivores and hawks.

Conservation IUCN Category: Least Concern.

Measurements

Funisciurus congicus

HB: 155.9 (142–168) mm, $n = 50$

T: 169.9 (153–190) mm, $n = 50$

HF: 40.2 (37–42) mm, $n = 50$

E: 16.7 (16–18) mm, $n = 50$

WT: 111 (108–113) g, $n = 63$

GLS: 38.8 (35.6–40.5) mm, $n = 14$

GWS: 22.0 (19.3–23.8) mm, $n = 14$

P³–M³: 6.7 (6.1–7.0) mm, n = 13

Body measurements: Namibia (Shortridge 1934)

Weight: throughout geographic range (Smithers 1983)

Skull measurements: Angola (BMNH)

Key References Amtmann 1975; Smithers 1983; Viljoen 1978, 1997.

Richard W. Thorington, Jr, Lindsay A. Pappas & Chad E. Schennum

Funisciurus duchaillui DU CHAILLU'S ROPE SQUIRREL

Fr. Funisciure de Duchailu; Ger. Duchailu Baumhörnchen

Funisciurus duchaillui Sanborn, 1953. Mammalia 17: 167. Poingi (01° 39' S, 11° 46' E), Gabon.

Taxonomy Described as a valid species from a single specimen; later placed as a synonym of *F. isabella* (Amtmann 1975, Hoffman *et al.* 1993, Thorington & Hoffman 2005). Reinstated as a full species, separable from *F. isabella*, on the basis of size and ecology by Brugièrè *et al.* (2005). Synonyms: none. Chromosome number: not known.

Description Medium-sized arboreal squirrel with four stripes on back. Dorsal pelage olive-brown. Two side-stripes on either side of mid-dorsal line; black from head to base of tail. Flanks grey to greyish-white; hairs with white tip. Ventral pelage grey; hairs with white tip. Head olive-brown. Limbs, fore- and hindfeet grey. Tail long (ca. 100% of HB), slender, with long hairs. When at rest, the tail is curled over the back and is frequently flicked. Skull: cheekteeth $5/4$. Nipples: not known.

Geographic Variation None recorded.

Similar Species

F. lemniscatus. Smaller (HB mean: 164 mm; GLS mean: 43.6 mm); ventral pelage white or buffy; two side-stripes on each flank from base of neck to rump; more widespread distribution.

F. isabella. Smaller (HB mean: 158 mm, GLS mean: 40.9 mm); ventral pelage grey, white at tip; two side-stripes on each flank from ears/head to rump/base of tail; more widespread distribution.

Distribution Endemic to Africa. Rainforest BZ (West Central region [Gabon subregion]). Recorded from C Gabon, south of the Ogooué R. and south to the Massif du Chaillu. Appears to be allopatric to *F. isabella*.

Habitat Rainforest, especially where trees of the families Cesalpiniaceae and Burseraceae are common.

Abundance Moderately common within its restricted range; comprised 29% of sightings (n = 95; Brugièrè *et al.* 2005), and was the commonest of eight species observed (the second most numerous species was *F. lemniscatus* [22% of observations]).

Remarks Usually seen singly or less frequently in pairs. Mostly observed in the lower storeys of the forest at 4–6 m above ground, but has been recorded in all storeys from ground level to >25 m (mean height: 10.2 m, median height: 6.0 m). When alarmed, escaped along branches or into higher levels of the forest, never along the ground (cf. *F. lemniscatus*) (Brugièrè *et al.* 2005). Observed eating fruits of *Xylopia aethiopica* and *Dialium* sp.



Funisciurus duchaillui

Conservation IUCN Category: Not Evaluated. Probably should be assessed as Data Deficient or Least Concern. Conserved within Lopé National Park, Gabon.

Measurements

Funisciurus duchaillui

HB: 197 ± 13 (185–212) mm, n = 4

T: 210 ± 20 (190–230) mm, n = 3

HF: 45 ± 5.7 (42–50) mm, n = 4

E: n. d.

WT: 200 ± 8.3 (180–220) g, n = 4

GLS: 47.2 ± 0.4 (46.9–48.3) mm, n = 3

GWS: 27.1 ± 1.0 (26.2–28.2) mm, n = 3

P³–M³: 7.8 ± 0.3 (7.5–8.2) mm, n = 3

Mean values ± 1 S.D.

Gabon (Brugièrè *et al.* 2005, D. Brugièrè unpubl.)

Key References Brugièrè *et al.* 2005; Sanborn 1953.

David Brugièrè

Funisciurus isabella LADY BURTON'S ROPE SQUIRREL

Fr. Funisciure d'Isabella (Funisciure de Gray); Ger. Lady Burtons Baumhörnchen

Funisciurus isabella (Gray, 1862). Proc. Zool. Soc. Lond. 1862: 180, pl. 24. Cameroon Mountain, Cameroon. 7000 ft (2130 m).

Taxonomy Originally described in the genus *Sciurus*. Named after the wife of Sir Richard Burton, the British Consul in Fernando Poo at the time (Rosevear 1969). Taxonomy is reviewed in Amtmann (1966) and Rosevear (1969). The form *duchailui*, placed as a synonym of *F. isabella* by Thorington & Hoffman (2005), is considered as a full species here (see above). Synonyms: *dubosti*. Subspecies: none. Chromosome number: not known.

Description Small brown squirrel with four black side-stripes. Dorsal pelage brown, slightly grizzled with buff; hairs black with buff tips. Two black side-stripes on each flank: inner side-stripe from between ears to base of tail; outer side-stripe from base of neck/shoulder to rump; buffy-brown pelage between all black dorsal side-stripes, but paler than on shoulders. Ventral pelage grey; hairs grey at base, white at tip. Tail long (ca. 100% of HB), slender, with long hairs, buff at base, black distally, with frosted buff tip. Skull: cheekteeth $5/4$; posterior end of bony palate in line with posterior end of M^3 ; masseteric tubercle not prominent. Males tend to be slightly larger than ♀♀. Nipples: $0 + 0 + 1 + 1 = 4$.

Geographic Variation None recorded.

Similar Species

F. lemniscatus. Inner black side-stripes do not extend onto neck; pelage between inner side-stripes is darker (dull brown) than between outer and inner side-stripes (pale yellow).

Distribution Endemic to Africa. Rainforest BZ (West Central Region). Recorded from S Cameroon, Equatorial Guinea (Rio Muni), Gabon, SW Central African Republic and NW Congo. Also Brazzaville, S Congo.

Habitat Lady Burton's Squirrels are found in dense, brushy or viny thickets within the Rainforest BZ. Preferred habitats include dense secondary growth alongside roads, abandoned gardens and plantations, and other habitats with closed vegetation below 5 m (Emmons 1975, 1980). They do not live in tall mature rainforest. In some parts of their range, they share this habitat with *F. lemniscatus*.

Abundance Common where habitat is optimal, but distribution is patchy.

Adaptations Diurnal and scansorial. Forage above the ground (90% of sightings), but generally stay below 10 m in dense thickets and vine tangles where often the most numerous species of squirrel (Emmons 1980). Nests found where there were many *F. isabella*, but no *F. lemniscatus*, closely resembled nests of *F. lemniscatus* in structure and placement (see *F. lemniscatus*). Bates (1905, cited in Rosevear 1969) stated that nests consist of a ball of dry leaves and fibres.



Funisciurus isabella

Foraging and Food Omnivorous. In Gabon, diet is fruits and seeds (81% of dry matter of stomach contents, $n = 14$), green plant tissue (9.2%) and arthropods (6%), with minor amounts of fungi. Arthropods consumed are chiefly ants (79% occurrence), termites (59% occurrence) and lepidopteran larvae (29%) (Emmons 1980).

Social and Reproductive Behaviour Usually seen alone or in pairs, occasionally in threes (69% alone, 21% pairs, 10% threes; $n = 29$ sightings). Two captive ♀♀ shared a nest box and groomed each other (Emmons 1980). There is no detailed information on social organization.

Lady Burton's Squirrels call readily and often (see Emmons 1978 for details). The low intensity alarm call is a series of chucks emitted singly (45% of 71 groups) or in groups of two (41%) to four. The unique high intensity alarm call is a series of linked, frequency-modulated pulses that form a long warbling sound. The most frequent number of warbles in a call is 7 (60% of 95 calls), followed by 5 (30%), but calls may consist of 2–10 warbles. Warbles alternate between shorter (about 160 ms) and longer (about 310 ms) pulses. Each series of warbles may be preceded by 1–14 stereotyped short warbles. Because of the density of their habitat, Lady Burton's Squirrels are more often heard than seen, and their presence is most easily determined by identifying their calls.

Reproduction and Population Structure Litter-size seems restricted to one ($n = 11$; Dubost 1968, Emmons 1979a).

Predators, Parasites and Diseases No information.

Conservation IUCN Category: Least Concern.
Previously considered as Near-Threatened.

Measurements

Funisciurus isabella

HB (♂ ♂): 158 (150–170) mm, n = 7
HB (♀ ♀): 152 (143–165) mm, n = 16
T (♂ ♂): 159 (150–180) mm, n = 6
T (♀ ♀): 163 (135–185) mm, n = 14
HF (♂ ♂): 35 (34–38) mm, n = 7
HF (♀ ♀): 36 (34–38) mm, n = 16

E: 14.5 (12–16) mm, n = ?*
WT (♂ ♂): 116 (97–140) g, n = 8
WT (♀ ♀): 104 (90–116) g, n = 10
GLS: 40.9 (39.6–41.9) mm, n = 3
GWS: 22.4, 22.4 mm, n = 2
P³–M³: 7.1 (6.7–7.7) mm, n = 5
Gabon (Emmons 1975, L. Emmons unpubl.)
*Rosevear 1969

Key References Emmons 1978, 1980.

Louise H. Emmons

Funisciurus lemniscatus RIBBONED ROPE SQUIRREL

Fr. Funisciure rayé; Ger. Streifiges Baumhörnchen

Funisciurus lemniscatus (Le Conte, 1857). Proc. Nat. Acad. Sci. Philadelphia 9:11. Equatorial Guinea (Rio Muni).

Taxonomy Originally described in the genus *Sciurus*. Taxonomy reviewed in Amtmann (1966) and Rosevear (1969). Synonyms: *mayumbicus*, *sharpei*. Subspecies: two. Chromosome number: not known.

Description Small brown squirrel, similar to *F. isabella*, with four black side-stripes on each flank. Dorsal pelage brown, hairs finely banded black and buffy. Two black side-stripes on each flank from base of neck to rump; inner side-stripes separated by dull brown (on mid-dorsal line); outer side-stripe separated from inner side-stripe by pale yellow pelage. Ventral pelage white or buffy. Tail long (ca. 80% of HB), bushy, with banded hairs, grizzled buff and black, with yellowish-buff below. Tail curled up over the back when the squirrel is at rest. Skull: cheekteeth $5/4$; posterior end of bony palate in line with posterior end of M³; masseteric tubercle not prominent. Nipples: 0 + 0 + 1 + 1 = 4.

Geographic Variation Two subspecies were recognized by Amtmann (1966) and Thorington & Hoffmann (2005):

F. l. lemniscatus: north of Ogoué R., Gabon. Ventral pelage white.

F. l. mayumbicus: south of the Ogoué R., Gabon. Ventral pelage buffy.

Similar Species

F. isabella. Slightly smaller (HB ♂ ♂: 158 [150–170] mm); two inner black side-stripes extend to between the ears; buffy-brown pelage between all black side-stripes. The alarm calls of this species and *F. lemniscatus* are distinctive.

Paraxerus alexandri and *P. boehmi*. Considerably smaller (mean HB 120 mm for *P. alexandri*, 102 mm for *P. boehmi*); tawny-orange or brown mid-dorsal stripe from shoulders to rump, bordered on each side by a black side-stripe and a yellow/cream side-stripe.

Distribution Endemic to Africa. Rainforest BZ (West Central Region [Gabon sub-region]). Recorded from Cameroon (S of Sanaga R.), Equatorial Guinea (Rio Muni), Gabon, Congo, SW Central African Republic, extreme SW DR Congo, and Angola (Cabinda).



Funisciurus lemniscatus

Habitat Lowland evergreen humid rainforests; rare in secondary or disturbed vegetation (where *F. isabella* is the common species).

Abundance Common in favourable habitats.

Adaptations Diurnal and scansorial. The feet are long and narrow, well suited for terrestrial travel. Ribboned Rope Squirrels forage chiefly on the ground (47% of 167 sightings) and in low vegetation below 5 m; they are rarely seen above 5 m (4% of sightings; Emmons 1975, 1980). They build round nests (mean diameter 21 cm) of single, large, dead leaves taken from the ground, and lined with a ball of fine plant fibres (about 11 cm diameter). Nests have 2–3 entrances. Five individuals followed by radio-tracking used 17 nests: 11 exposed in small treelets (mean height 3.8 m, range 2–10 m), three in hollows

of standing trees or lianas (mean height 1.9 m, range 1.5–2.2 m) and three in hollow logs that lay on the ground. Exposed leaf nests are placed in the top of saplings where branches divide, in the top of stumps, in free-hanging tangles of lianas, or against tree trunks where an epiphyte, liana or branch provides a support. If disturbed at night by noise or vibration while in an exposed nest, will jump out quickly and run to refuge in another nest nearby (Emmons 1975). Tree-cavity dens had small entrances just large enough to admit the squirrel, and were too small to hold normal-sized nests.

Radio-collared squirrels left their nests at dawn and returned in the late afternoon or at nightfall (mean return time 18:22h; range 16:16–18:49h, $n = 14$) and thus had a long mean daily activity period of 11.22 h (Emmons 1975, 1980).

Foraging and Food Omnivorous. Insects can be captured by extending the highly extensible tongue into confined spaces (as into a deep vial when in captivity) (L. Emmons unpubl.). In Gabon, feeds on fruits and seeds (59% of dry mass of stomach contents, $n = 15$) and arthropods (36%). Arthropods consumed are mainly termites (100% occurrence) and ants (60%). Sometimes large numbers of termites are consumed, contributing up to 100% of a stomach content, indicating opportunistic feeding behaviour (Emmons 1980).

Social and Reproductive Behaviour Ribboned Rope Squirrels were usually seen alone (59% of 222 sightings), but sometimes in pairs (21%), threes (11%) and fours (7%). They are commonly observed in pairs or small groups, which join in alarm calling or foraging together, with individuals spaced at least 1 m apart, but more often 5–20 m apart. A captive heterosexual pair did not share nest boxes, the dominant often attacking the subordinate and defending food and space. A ♂ and ♀, with overlapping home-ranges, that were followed by radio-tracking for eight days (Emmons 1975, 1980) stayed within the same 0.5 ha for two days, but spaced 15–40 m apart. Home-ranges (assessed by radio-tracking) were 0.94 ha (subadult ♀), 1.0 ha and 1.24 ha (two adult ♂♂) and 1.6 ha (one adult ♀). During activity, ♂♂ moved at a mean rate of 51 m/h ($n = 9$ days of activity), and ♀♀ at 43 m/h ($n = 20$ days of activity).

Ribboned Rope Squirrels call readily and often (details in Emmons 1978). The low intensity alarm call is a series of chucks given in groups of 1–8, but most often in triplets (36% of 61 groups). The high intensity call is a similar series of more prolonged and frequency-modulated chucks or chips, which are linked together in groups of 1–7, but usually in pairs (43% of 83 calls) or triplets (47%). The linked calls drop in frequency between successive calls, and are often preceded by single chucks. Low intensity alarm calling is associated with a downward tail-flick display like that described for *F. anerythrus*.

Reproduction and Population Structure Embryo number: 1.8 (1–3, $n = 4$; Emmons 1979a); 1.7 (1–2, $n = 10$; Dubost 1968).

Predators, Parasites and Diseases No information.

Conservation IUCN Category: Least Concern.

Measurements

Funisciurus lemniscatus

HB (♂♂): 164 (150–177) mm, $n = 13$

HB (♀♀): 160 (153–173) mm, $n = 10$

T (♂♂): 132 (115–145) mm, $n = 9$

T (♀♀): 135 (122–145) mm, $n = 9$

HF (♂♂): 38 (35–40) mm, $n = 13$

HF (♀♀): 38 (33–41) mm, $n = 11$

E: n. d.

WT (♂♂): 140 (123–158) g, $n = 12$

WT (♀♀): 141 (132–155) g, $n = 7$

GLS: 43.6 (42.1–43.9) mm, $n = 3$

GWS: 23.8 (22.9–24.6) mm, $n = 3$

P³–M³: 7.3 (6.9–7.7) mm, $n = 6$

Gabon (Emmons 1975, L. Emmons unpubl.)

Key References Emmons 1975, 1978, 1980.

Louise H. Emmons

Funisciurus leucogenys RED-CHEEKED ROPE SQUIRREL

Fr. Funisciure à oreilles noires; Ger. Orangenköpfiges Baumhörnchen

Funisciurus leucogenys (Waterhouse, 1842). Ann. Mag. Nat. Hist., ser. 1, 10: 202. Bioko I., Equatorial Guinea.

Taxonomy Originally described in the genus *Sciurus*. The species name, which means ‘white-cheeked’, is a misnomer; Waterhouse apparently intended the more appropriate name *erythrogeus* (‘red-cheeked’) (Rosevear 1969). Synonyms: *auriculatus*, *beatus*, *boydi*, *erythrogeus*, *oliviae*. Subspecies: none. Chromosome number: not known.

Description Medium-sized squirrel with grey-brown pelage, red cheeks and one side-stripe on each flank broken into spots. Pelage colour varies geographically (see below). Dorsal pelage soft-textured, dark grey-brown to brownish-black; yellow on shoulders. Single side-stripe on each flank, whitish-yellow, broken into spots. Ventral pelage white or pale orange-red. Head and cheeks bright

orange-red; black speckling on crown of head. Ears rounded, black on outer surface; dark postauricular patch often present. Thighs and forearms greyish. Hindfeet more strongly built than forefeet. Tail long (ca. 79% of HB), bushy, hairs long; black or brownish-black with white tips above, red below. Tail constantly erect and frequently carried curled over back. Skull: cheekteeth $5/4$; posterior end of bony palate in line with posterior end of M³; masseteric tubercle not prominent. Nipples: 2 + 2 = 8.

Geographic Variation Rosevear (1969) described four variations as subspecies; here considered as colour variants related to altitude and climate. (1) Ventral pelage white and side-stripe indistinctly broken into stripes (Bioko I.; *leucogenys*). (2) Ventral



pelage tinged with orange, side-stripe broken into spots, crown of head red, with obvious black patches behind ears, underside of tail brilliant red (Ghana, Togo, Nigeria and W Cameroon; *olivae*). (3) Ventral pelage tinged with orange, crown blackish-red, black patches behind ears; greyish-white 'frosted' mantle on shoulders (Upper Cameroon, Mt Cameroon; *auriculatus*). (4) Similar to *auriculatus*, but darker with buffy-grey mantle on shoulders (higher altitudes on Mt Cameroon and highlands; *boydi*).

Similar Species

F. anerythrus. Pelage drab; pale side-stripe not broken into spots; ventral pelage greyish; no dark postauricular patch; more common in secondary habitats.

F. pyrrhopus. Pale side-stripe not broken into spots, thighs and forearms bright red; no dark postauricular patch.

Distribution Endemic to Africa. Rainforest BZ (West Central Region, and extreme east of Western Region). Recorded from Ghana (east of Volta R.), Togo, Benin, Nigeria, Cameroon, Equatorial Guinea (Rio Muni) and Central African Republic (upper Sanga R.), Bioko I.

Habitat Lower strata in relatively undisturbed rainforest habitats and forest relics in rainforest–savanna mosaic (Sanderson 1940, Happold 1987). Of 19 individuals live-trapped in Dazing-Sangria, Central African Republic, eight were in unlogged mixed-species forest, eight in monodominant *Gilbertiodendron dewevrei* forest, two on skidder trails (i.e. trail used by a bulldozer to drag a log to the nearest road) and one on a secondary logging road (Ray 1996; J. C. Ray & J. R. Malcolm unpubl.).

Abundance No information.

Remarks Diurnal and arboreal (J. C. Ray & J. R. Malcolm unpubl.). During trapping at three heights in Dzanga-Sangha, Central African Republic, captured on ground and understorey (ca. 2 m), but not at 15 m (n = 9; Malcolm & Ray 2000; J. R. Malcolm unpubl.). Nests in holes entered either from tree hollow or from beneath vegetation or other suitable cover (Sanderson 1940). Vocalizations described as 'excited chattering with a staccato quality' (Rosevear 1969). Young born in simple nests lined with grass and leaves in holes among roots of trees. Pregnancies recorded in dry and early wet seasons (Dec, Feb and May) in Dzanga-Sangha. Embryo number: 1 (n = 3; J. C. Ray & J. R. Malcolm unpubl.).

Conservation IUCN Category: Data Deficient.

Deforestation and degradation of forests by logging and clearing constitute potential threats.

Measurements

Funisciurus leucogenys

HB: 209.3 (181–225) mm, n = 14

T: 165.7 (151–178) mm, n = 12

HF: 51.6 (49–54) mm, n = 14

E: 20.1 (18–21) mm, n = 14

WT: 237.3 (171–298) g, n = 12

GLS: 51.2 (48.0–52.9) mm, n = 11

GWS: 27.8 (25.7–29.0) mm, n = 11

P³–M³: 23.6 (21.7–24.7) mm, n = 11

Dzanga-Sangha, Central African Republic (J. C. Ray & J. R. Malcolm unpubl., USNM)

Key Reference Rosevear 1969.

Justina C. Ray

Funisciurus pyrrhopus FIRE-FOOTED ROPE SQUIRREL (RED-LEGGED ROPE SQUIRREL)

Fr. Funisciure à pattes rousses; Ger. Rotfüssiges Baumhörnchen

Funisciurus pyrrhopus (F. Cuvier, 1842). In: E. Geoffroy Saint-Hilaire and F. Cuvier, Histoire Naturelle des Mammifères, vii, No. 66. Tab. 4: 240. Gabon.

Taxonomy Originally described in the genus *Sciurus*. The type locality was described as 'et elle venoit de l'île Fernandopô, dans le gulfes de Guinée'. However, the species is not known from Fernando Poo (now Bioko I.) and since the animal was a pet, it probably came from the mainland (see Hoffman *et al.* 1993). Type locality is likely to be Gabon or Equatorial Africa (Rio Muni). Rosevear (1969)

refers to the species as *Funisciurus pyrrhopus* (with an 'h'), which is an unjustified emendation (Hoffmann *et al.* 1993). Taxonomy is reviewed in Amtmann (1966) and Rosevear (1969). Rosevear lists five subspecies, but does not include any forms east of the Sanaga R. in Cameroon, and Amtmann (1966) recognizes the nine subspecies given below. Some of the named forms (*leonis*, *mandingo*) were placed

in *F. anerythrus* by Rosevear (1969). The allocation and validity of named forms of *Funisciurus* squirrels is in need of revision. Synonyms: *akka*, *emini*, *erythropros*, *leonis*, *leucostigma*, *mandingo*, *nigrensis*, *niveatus*, *pembertoni*, *rubripes*, *talboti*, *victoriae*, *wintoni*. Subspecies: nine. Chromosome number: not known.

Description Beautiful, medium-sized, long-nosed squirrel with a dark back, pale side-stripe on each flank, and bright reddish limbs. Dorsal pelage grizzled greyish or blackish; hairs banded black with buff tip. Head below crown, muzzle, forelimbs below shoulders, and hindlimbs below hips brilliant rufous to dull rusty-red; hairs pure rufous or rusty-red. White or pale grey side-stripes. Ventral pelage pure white or off-white. Eyes ringed with buff. Ears pale behind. Tail long (ca. 80% of HB) and bushy; hairs banded, black at base, rufous distally, with white-frosted tip. When squirrel is at rest, tail is curled up over back; when moving, tail is carried with base vertical and tip curled backwards or horizontally straight behind body. Skull: cheekteeth $5/4$; posterior end of bony palate in line with posterior end of M^3 ; masseteric tubercle not prominent. Nipples: $0 + 0 + 1 + 1 = 4$.

Geographic Variation Highly variable, as attested by the large number of named forms (see also above). Amtmann (1966) recognizes nine subspecies:

- F. p. akka*: E Congo, Uganda. Sides and crown without red; limbs and muzzle dull red; underparts washed orange.
- F. p. leucostigma*: S. Ghana. Red parts of pelage duller and brownish-red; sides below side-stripes red; crown not red.
- F. p. leonis*: Liberia and Sierra Leone. Red parts of pelage deep rufous; sides red.
- F. p. mandingo*: Gambia. Dorsal pelage pale, straw-coloured sprinkled with black; limbs and ears orange.
- F. p. nigrensis*: Nigeria from Cross R. to Niger R. Head brownish.
- F. p. niveatus*: Côte d'Ivoire. Red parts orange-red rather than rusty.
- F. p. pembertoni*: N Angola. Greyish, with limbs red.
- F. p. pyrropus*: S Cameroon to Mayumbe forest, Congo. Brightly coloured.
- F. p. talboti*: Mt Cameroon and SE Nigeria. Red on flanks mixed with greenish-brown.

Similar Species

- F. anerythrus*. Smaller (HB: 167–198 mm); pelage brown without red or rufous on limbs; whooping birdlike alarm call.
- F. leucogenys*. Limbs greyish similar in colour to back; black postauricular patch.

Distribution Endemic to Africa. Widespread but disjunct in Rainforest BZ (Western, West Central and East Central Regions), and Rainforest–Savanna Mosaics. Recorded from NW Angola, Burundi, Cameroon, Congo, Côte d'Ivoire, Equatorial Guinea (Rio Muni), Gabon, Gambia, SW Ghana, W Guinea, Guinea-Bissau, Liberia, SE Nigeria, Rwanda, S Senegal, Sierra Leone, Uganda and DR Congo. Although sympatric with *F. anerythrus* in the east of its range (Nigeria eastwards), it is allopatric in the west of its range (from Ghana westwards (Grubb *et al.* 1998).

Habitat Tall evergreen forest and older secondary forests.



Funisciurus pyrropus

Abundance Common in suitable habitat.

Adaptations Diurnal and terrestrial. Fire-footed Rope Squirrels have long, narrow feet, suitable for terrestrial living. They forage on the ground and on fallen logs and brush below 1.5 m. Unlike other squirrels, they build nests on the ground and in burrows. Of 17 nest sites used by four individuals (found by radio-tracking), 14 were in underground burrows and three in hollow logs on the ground. Six burrows were of characteristic structure and were probably dug by the Fire-footed Rope Squirrels themselves. These were simple tubes, often constructed within a termite nest, with an entrance at each end and a central nest chamber (illustrated in Emmons 1975). The other burrows were probably excavated by other mammals, such as *Cricetomys emini* (1 den) and *Atherurus africanus* (1 den), and were likely to be used opportunistically by these squirrels. Radio-tracked individuals left their nest soon after daylight and returned to it at 15:18–18:52h ($n = 17$ times of return; Emmons 1980), and hence had a mean daily activity period of 9.86 h.

Foraging and Food Omnivorous. The long muzzle is probably associated with hunting insects in small crevices. In Gabon, feeds on fruit and seeds (83% of dry matter of stomach contents, $n = 12$) and insects (12%) (Emmons 1980). The insect portion of the diet consists chiefly of ants (100% occurrence) and termites (92% occurrence). These are consumed in large numbers – soldiers, workers, eggs and larvae together – suggesting that the squirrels find and raid ant and termite nests.

Social and Reproductive Behaviour Fire-footed Rope Squirrels appear to be mainly solitary: 80% of individuals ($n = 56$ sightings) were of single individuals, and 14% were in groups of two that were widely spaced and engaged in mobbing. In captivity, a heterosexual pair slept in different nest boxes and did not groom each other until they had been together many months. A 'mating chase',

when several ♂♂ pursued a ♀, has been observed (Emmons 1980). Home-ranges (assessed by radio-tracking) were 5.2 ha (one adult ♂), 1.0 ha (a lactating ♀) and 2.3 ha (a subadult ♀). Movements were slow, at a mean rate of 35 m/h for two ♀♀ and 61 m/h for two ♂♂ (Emmons 1975).

Vocalizations are frequent (Emmons 1978). The low intensity alarm is a loud single chuck, or more rarely, a double chuck. The high intensity alarm is distinctive and consists of a staccato, machine gun-like series of chucks, lasting about 20–40 seconds (tatatatatatatatata . . .). This call superficially resembles that of *Epixerus ebii*, and is unlike the calls of any sympatric *Funisciurus* species. The tail-flick display during low intensity alarm is similar to that described for *F. anerythrus*.

Reproduction and Population Structure Litter-size usually seems to be one (range 1–2), but there are few records (Emmons 1979a).

Predators, Parasites and Diseases No information.

Conservation IUCN Category: Least Concern.

Measurements

Funisciurus pyrropus

HB: 211 (190–230) mm, n = 11

T: 167 (153–180) mm, n = 9

HF: 46 (44–49) mm, n = 11

E: 18 (17–18) mm, n = ?*

WT: 283 (260–334) g, n = 9

GLS: 52.7 (50.4–56.7) mm, n = 5

GWS: 28.0 (26.5–29.8) mm, n = 5

P³–M³: 8.8 (8.1–9.2), n = 6

Gabon (Emmons 1975, L. Emmons unpubl.)

*Rosevear 1969

Key References Emmons 1975, 1978, 1980.

Louise H. Emmons

Funisciurus substriatus KINTAMPO ROPE SQUIRREL

Fr. Funisciure de Kintampo; Ger. Kintampo-Baumhörnchen (Togo Streifenhörnchen)

Funisciurus substriatus de Winton, 1899. Ann. Mag. Nat. Hist., ser. 7, 4: 357.

‘near Kintampo, Gold Coast hinterland, 800 feet (240 m)’ (= Kintampo, Ghana).

Taxonomy This form is usually listed as a valid species (Amtmann 1975; Hoffmann *et al.* 1993), but there is underlying doubt about species limits in *Funisciurus*. This species closely resembles *Funisciurus anerythrus*, a species originally described from W Uganda. It is not clear whether *Funisciurus substriatus*, distributed from E Ghana to Benin, is reproductively isolated from populations further east and south and which are here described as *Funisciurus anerythrus*. Synonyms: none. Chromosome number: not known.

Description Medium-sized plain-coloured squirrel with single faint pale stripe on each flank, very similar to *F. anerythrus*. Dorsal pelage greenish-yellow or ochre, heavily speckled with black; especially pale in Burkina. Single side-stripe on each flank, faint, whitish, bordered ventrally by darker stripe. Ventral pelage white, occasionally suffused with pale ochre; hairs dark grey at base. Fore- and hindlimbs similar to dorsal pelage. Tail long (ca. 100% of HB), similar but darker than back, with noticeable rings of black and buff; dorsal hairs black with short pale tips; lateral hairs with long pale buff tips, ventral hairs ochre. Skull: cheekteeth ⁵/₄; posterior end of bony palate in line with posterior end of M³; masseteric tubercle not prominent. Nipples: 0 + 0 + 1 + 1 = 4.

Geographic Variation None recorded.

Similar Species

F. anerythrus. Very similar in form and colour; distinguished mainly by distribution; ventral pelage does not show the ochre to orange colouration of populations of *Funisciurus anerythrus* to the east and south of Cameroon.



Funisciurus substriatus

Distribution Endemic to Africa. Guinea Savanna BZ and Northern Rainforest-Savanna Mosaic and some relict forests in Sudan Savanna BZ. Recorded from Burkina, E Ghana, Togo and Benin. Does not appear to extend eastwards into Nigeria (where replaced by *F. anerythrus*), or westwards to Côte d'Ivoire.

Habitat Woodland savanna and remnant forests; rocky habitats and along rivers in Burkina (specimen labels).

Abundance No information.

Remarks Apparently no other information available.

Conservation IUCN Category: Data Deficient.

Measurements

Funisciurus substriatus

TL: 326.3 (300–348) mm, n = 28

T: 154.7 (130–178) mm, n = 28

HF: 43.1 (40–45) mm, n = 33

E: 17.5 (13–19) mm, n = 33

WT: 142.5 (115–187) g, n = 28

GLS: 44.2 (42.5–45.3) mm, n = 10

GWS: 24.2 (23.4–24.6) mm, n = 8

P³–M³: 7.2 (6.9–7.5) mm, n = 10

Burkina, E Ghana, Togo, Benin (USNM)

Key References Amtmann 1975; Hoffman *et al.* 1993.

Richard W. Thorington, Jr & Chad E. Schennum

GENUS *Heliosciurus*

Sun Squirrels

Heliosciurus Trouessart, 1880. Le Naturaliste, 2nd year, 1: 292. Type species: *Sciurus gambianus* Ogilby, 1835.



Heliosciurus rufobrachium.

Heliosciurus comprises six species of small to large tree squirrels widely distributed in sub-Saharan Africa except for arid or treeless regions. There are representatives in rainforest and montane forest (three spp.) and in savanna habitats (three spp.). Two species are widespread while four have rather small ranges. The vernacular name 'Sun Squirrel' is a literal translation of the generic name, and refers to the habit of these squirrels of living at higher levels in the forest where they are more likely to encounter sunny habitats.

The genus is characterized by moderate size (HB: 170–270 mm, larger than *Myosciurus* and *Funisciurus*, but smaller than *Protoxerus* and *Epixerus*), slender build, and long tail, usually longer in length than HB. The pelage of the back and flanks is speckled and there is no lateral side-stripe (cf. *Funisciurus*). The head is relatively large, with small ears held close to the skull. The limbs are relatively long. The colouration of *Heliosciurus* squirrels is typically greyish or brownish, but one species has rufous or reddish limbs and shoulders (*H. rufobrachium*) and another has reddish-brown or rufous-brown body pelage (*H. mutabilis*). The tail is covered with long hairs, each alternately banded with dark and pale bands; the tail is extended

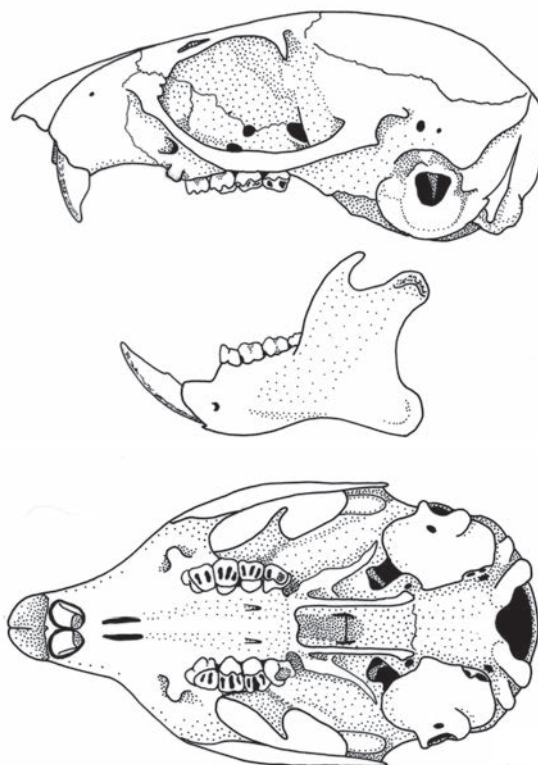


Figure 12. Skull and mandible of *Heliosciurus gambianus* (BMNH 62.346).

backwards in line with the body when the squirrel is running along branches, and hangs downwards when the squirrel is resting (cf. *Funisciurus*). Females have three pairs of nipples (not four as in *Allosciurus*, *Protoxerus* and *Epixerus*). Baculum absent.

The length of the skull is larger than that of *Myosciurus*, overlaps extensively with that of *Allosciurus*, *Paraxerus* and *Funisciurus*, but is smaller than in *Protoxerus* and *Epixerus*. The skull is characterized by orange ungrooved incisors (except *H. rufobrachium* – slightly grooved), fossa for the origin of anterior deep masseter muscle extending onto the rostrum, supraorbital notch which is closed on margin of orbit forming a foramen piercing the frontal bone, large sphenopalatine foramina, anterodorsal process of premaxilla, which

Table 12. Species in the genus *Heliosciurus*. Arranged according to amount of red colouration on the pelage.

| Species | Red colouration on pelage | Colour of ventral pelage | HB mean (range) (mm) | HF mean (range) (mm) | GLS mean (range) (mm) | Number of cheekteeth (upper/ lower) | Notes |
|------------------------|---|---|----------------------|----------------------|-----------------------|-------------------------------------|---|
| <i>H. gambianus</i> | None | White, cream or buff; sparse | 196 (180–230) | 44 (40–50) | 37 (45–51) | ⁴ / ₄ | Widespread savannas N and S of Rainforest BZ |
| <i>H. undulatus</i> | None | Whitish-grey to ochre | 233 | 56 | 32 | ⁴ / ₄ | Lowland and montane forests SE Kenya, NE Tanzania, Mafia and Zanzibar Is. |
| <i>H. punctatus</i> | None | Grey | ca. 390 (355–524) | 46 (37–50) | 47 (37–50) | ⁴ / ₄ | Rainforest and forest relicts, Liberia to Ghana |
| <i>H. ruwenzorii</i> | None | Creamy-buff, with white mid-ventral stripe | 240–260 | 54 | 51–52 | ⁵ / ₄ | Montane forests E DR Congo, Rwanda, Uganda, NW Burundi |
| <i>H. mutabilis</i> | Rufous cinnamon (new pelage) | Creamy-buff; sparse | 236 (217–269) | 53 (46–60) | 54 (52–56) | ⁴ / ₄ | Savannas of eastern Africa; eastern part of Zambesian Woodland BZ |
| <i>H. rufobrachium</i> | Shoulders and limbs rufous to reddish (very varied) | Brown, reddish, rufous, grizzled as dorsal pelage | ca. 230 (205–249) | 47–49 (40–56) | 53 (50–54) | ⁴ / ₄ | Widespread throughout Rainforest BZ and forest relicts |

risers to about level with anterolateral angle of nasal, prominent masseteric tubercle (unlike all other African tree squirrels), and the posterior end of bony palate is approximately in line with the posterior end of M³ (Figure 12). There are four cheekteeth in each ramus (⁴/₄), although *Heliosciurus ruwenzorii* (⁵/₄) has a very small additional tooth (P³). Dental formula: I ¹/₁, C ⁰/₀, P ¹/₁, M ³/₃ = 20 (except *H. ruwenzorii* – see above; cf. *Paraxerus*).

Two species are widespread (*H. gambianus*, *H. rufobrachium*) and four species have rather constricted ranges. All are arboreal. *Heliosciurus ruwenzorii* lives in montane forest, *H. rufobrachium* and *H. punctatus* in lowland rainforest, *H. undulatus* and *H. mutabilis* in forests and woodlands of East Africa, and *H. gambianus* lives primarily in savannas of West Africa. The species are mostly allopatric, but *H. punctatus* is entirely sympatric with *H. rufobrachium*, and the range of *H. gambianus* is parapatric with that of *H. rufobrachium* at least in West Africa, though the two species are ecologically segregated. These squirrels are mostly seen singly or in pairs. Sun Squirrels produce a large variety of vocal noises, which are mostly species-specific.

Heliosciurus forms a monophyletic clade with *Allosciurus*, *Protoxerus* and *Epixerus* (Moore 1959). There has been some disagreement concerning the allocation of subspecies to species. The taxa *brauni*, *coenosus*, *emissus* and *lualabae*, including the populations in the rainforest south of the Congo R., were allocated to *H. gambianus* by Amtmann (1975) but to *H. rufobrachium* by Thorington & Hoffmann (2005). *Heliosciurus ruwenzorii* was formerly placed in subgenus *Aethosciurus* (Ellerman 1940), whose type species (*poensis*) is now included in *Paraxerus*. The genus is placed in the subfamily Xerinae and tribe Protoxerini (which also includes all the other African sciurids except for *Atlantoxerus* and *Xerus* – the Ground Squirrels – which are placed in the tribe Xerini) (Thorington & Hoffmann 2005).

Species in the genus are distinguished by presence/absence of reddish colouration of the pelage, colour of ventral pelage, bushiness of the tail, body and skull size, and habitat (Table 12).

Peter Grubb

Heliosciurus gambianus GAMBIAN SUN SQUIRREL

Fr: Heliosciure de Gambie; Ger. Gambisches Sonnenhörnchen

Heliosciurus gambianus (Ogilby, 1835). *Proc. Zool. Soc. Lond.* 1835: 103. ‘brought from Gambia’, possibly near Fort St Mary, Gambia.

Taxonomy Originally described in the genus *Sciurus*. Geographic variation in pelage colour over an extensive range has led to the description of 20 forms of *H. gambianus* (Hoffman *et al.* 1993), many of which are synonyms. The rainforest representative, *H. punctatus*, originally regarded as a subspecies (e.g. Rosevear 1969), is now considered to be a separate species (Roth & Thorington 1982). Synonyms: *abassensis*, *albina*, *annularis*, *annulatus*, *bongensis*, *canaster*, *dysoni*, *elegans*, *hoogstraali*, *kaffensis*, *lateralis*, *limbatus*, *loandicus*, *madogae*, *multicolor*, *omensis*, *rhodesiae*, *senescens*, *simplex*. Subspecies: none. Chromosome number: not known.

Description Medium-sized arboreal greyish-brown squirrel with long banded tail, and mostly without any obvious bright colours or markings; considerable geographic variation in colour (see below). Pelage short, slightly coarse. [Description of form *gambianus*] Dorsal pelage and flanks grizzled pale brown or buff, flecked with black; dorsal hairs with alternating black and buff bands, usually with black tip. Ventral pelage sparse (so skin visible in parts), hairs longer than on dorsal pelage, pure white, cream or buff. Forehead and muzzle similar to dorsal pelage. Chin, throat, chest, as ventral pelage. Eyes large, dark. Ears small and rounded, covered with short hairs,



Heliosciurus gambianus.

situated close to head. Fore- and hindlimbs short, grizzled buff without any rufous colour (cf. *H. rufobrachium*). Forefeet with four digits (D1 vestigial), each with long claw; hindfeet with five digits, each with long claw. Tail long (ca. 110% of HB), buff with up to 15 black circular bands, some clearly defined, others obscure; hairs buff with 3–4 alternating black bands. Skull: cheekteeth $4/4$; posterior end of bony palate in line with posterior end of M^3 ; masseteric tubercle prominent. Nipples: $0 + 1 + 1 + 1 = 6$.

Geographic Variation Considerable geographic variation in pelage colour, although these differences in colour are not recognized as subspecific. For example:

H. g. gambianus: West Africa. See Description above.

H. g. dysoni: Ethiopia, S Sudan. Dark brown with bright rufous around genitalia, around base of tail and on undersurface of tail.

H. g. elegans: Uganda. Medium brown; hairs with wide whitish-cream bands provide a flecked pattern on pelage (rather than a grizzled pattern).

H. g. rhodesiae: Zambia. Greyish-cream; hairs longer and softer than in other forms. A larger and heavier form than those in East and West Africa.

Similar Species

H. rufobrachium. Larger (HB: 212–249 mm); limbs red; rainforest habitats; mostly allopatric.

H. mutabilis. Larger (HB: 217–269 mm); limbs brownish; savanna habitats; allopatric.

H. punctatus. Similar in size (HB: ca. 180–190 mm); pelage dark; rainforest and mosaic habitats; restricted to Rainforest BZ (Western Region).

Distribution Endemic to Africa. Guinea and Sahel Savanna BZs, Northern Rainforest–Savanna Mosaic, Southern Rainforest–Savanna Mosaic, and Zambezian Woodland BZ. Recorded from Senegal and Gambia eastwards across West and central Africa to S Sudan, Eritrea and Ethiopia; and from Angola, S DR Congo, N Zambia (west of the Muchinga escarpment) and extreme SW Tanzania (Ufipa Mts). Outlier populations (which appear to be isolated from the main geographic range) on Jebel Marra (W–C Sudan) and C Tanzania (Tabora).



Heliosciurus gambianus

Habitat Wooded savanna, especially where savanna trees are denser and taller than average because of better soil and access to water (Rosevear 1969). Preferred habitats include Guinea savanna of West Africa (Rosevear 1969), savanna woodlands and secondary forest in Uganda (Delany 1975), and *Brachystegia* woodland in Zambia (Ansell 1960). Also recorded from rather dry locations in E Uganda (e.g. Karamoja) and NW Kenya (e.g. Lodwar, west of L. Turkana). Along the margins of the Rainforest BZ, Gambian Sun Squirrels have moved into areas where forests have been replaced by palm plantations and other savanna-like habitats (Happold 1987). Here they may occur sympatrically with *H. rufobrachium* and *Paraxerus* spp. (Rosevear 1969).

Abundance Widely distributed and not uncommon in suitable habitats. Probably the most frequently seen of the tree-living savanna squirrels. In many localities, it is the only species of arboreal squirrel. Quantitative information on abundance not available.

Adaptations Arboreal and diurnal. Gambian Sun Squirrels are very agile, running along branches, and jumping from one tree to another where the canopies are close together. In more open woodlands, they descend to the ground to forage and to travel (usually with a short bounding gait) to adjacent trees. They are active only during the day, especially the early morning and late afternoon, and they rest at night in nests, lined with leaves, in holes of trees. Gambian Sun Squirrels are remarkably tolerant of a wide range of environmental conditions, from well-wooded moist savannas to dry semi-arid savannas. There is no detailed ecological and behavioural information on this widespread and common species.

Foraging and Food Mainly vegetarian, but also omnivorous. The diet includes fruits, nuts and insects, and occasionally eggs, geckos, lizards and nestlings are consumed (Ansell 1960, Delany 1975).

Social and Reproductive Behaviour Usually observed as single individuals, suggesting they are solitary. Vocalizations are important for communication and include high-pitched squeaks, various chattering and trilling notes, and a long ‘ker ... ker ... ker’ emitted when alarmed (Delany 1975).

Reproduction and Population Structure Embryo number: 5 ($n = 1$), 1 ($n = 1$) in Zambia (Ansell 1960). Young (about one-third grown) observed in Zambia in Sep and Oct. Young individuals in Karamoja (Uganda) in Feb (Kingdon 1974). Young born in nests in holes in trees; at birth young are almost naked and the eyes are closed.

Predators, Parasites and Diseases No detailed information, but likely to be preyed upon by diurnal birds of prey.

Conservation IUCN Category: Least Concern.

Unlikely to be threatened: a relatively common species with a very large geographic range.

Measurements

Heliosciurus gambianus gambianus

HB: 196.6 (180–230) mm, $n = 10$

T: 214.4 (189–240) mm, $n = 10$

HF: 44.5 (40–50) mm, $n = 9$

E: 15.3 (14–16) mm, $n = 9$

WT: 220 g, $n = 1$

GLS: 47.3 (44.9–51.0) mm, $n = 10$

GWS: 26.2 (24.4–27.6) mm, $n = 10$

P^4-M^3 : 8.4 (8.0–8.9) mm, $n = 10$

West Africa (BMNH)

The southern African form, *rhodesiae*, is slightly larger, e.g. HB: 211.1 (197–230) mm, T: 244.7 (222–268) mm.

Key References Happold 1978; Rosevear 1969.

D. C. D. Happold

Heliosciurus mutabilis MUTABLE SUN SQUIRREL

Fr. Heliosciure variable; Ger. Mutaibles Sonnenhörnchen

Heliosciurus mutabilis (Peters, 1852). Bericht Verhandl. K. Preuss. Akad. Wiss. Berlin 17: 273. ‘Africa orientalis, Boror, 17° Lat. Austr.’ (= Boror, 19 km NW of Quelimane, Mozambique).

Taxonomy Originally described in the genus *Sciurus*. The form *mutabilis*, originally described as a valid species, is considered either as a subspecies of *H. gambianus* (e.g. by Ellerman [1940] and Swynnerton & Hayman [1950]) or of *H. rufobrachium* (e.g. by Rosevear [1963], Smithers & Lobão Tello [1976], Ansell [1978], Smithers & Wilson [1979], and De Graaff [1981]). Grubb (1982) showed that *mutabilis* is a valid species clearly separable from *H. gambianus* and *H. rufobrachium*, a systematic opinion followed by Ansell & Dowsett (1988), Hoffman *et al.* (1993) and in this volume. Grubb (1982) lists five subspecies; Hoffman *et al.* (1993) and Thorington & Hoffman (2005) list these forms as ‘synonyms’ without distinction between synonyms and subspecies (see below). Synonyms: *beirae*, *chirindensis*, *shirensis*, *smithersi*, *vumbae*. Subspecies: five (but see below). Chromosome number: not known.

Description Large brown or rufous-brown squirrel, often with patches of contrasting colour on different parts of the body, which result in a scruffy unkempt appearance. Pelage long (15–20 mm on mid-back), slightly coarse. Dorsal pelage and flanks brown or rufous-brown, abundantly flecked with cream. Dorsal hairs with five bands: brown at base, two paler bands and a broad buff band in centre, and cream at tip. Ventral pelage sparse; hairs long, cream or buff. No side-stripe. Head, cheeks and limbs similar to dorsal pelage. Fore- and hindlimbs (outer and inner surfaces) grey or brown (not russet or red as in *H. rufobrachium*). Tail long (ca. 112% of HB), dark blackish-brown with up to ten obscure cream or buff bands. Tip of tail may be rufous or rich cinnamon (especially when pelage is old). Striking colour changes occur when moulting: newly moulted pelage is cinnamon, rufous or chestnut, and brightly coloured; as the pelage ages, it becomes brown or blackish-brown, and dull. In many

individuals moulting occurs in patches, so the dorsal pelage appears as a patchwork of brown, black, cinnamon and rufous, partly bright, partly dull – a pattern quite unlike that seen in any other species of squirrel. Hence pelage shows seasonal changes in colour and pattern, as well as geographical variation. Skull: cheekteeth $4/4$; posterior end of bony palate in line with posterior end of M^3 ; masseteric tubercle prominent. Nipples: $0 + 1 + 1 + 1 = 6$.

Geographic Variation Mutable Sun Squirrels show considerable variation in pelage colouration within populations (mainly due to moulting patterns – see above) and between populations. In Malawi, for example, the following variation is visible in a series of specimens: (a) crown of head and upper back black, mid-back and flanks bright cinnamon, tail rufous with paler bands; (b) dorsal pelage cinnamon, flecked with buff; (c) crown of head, dorsal pelage and tail dark rufous or chestnut brown, flanks cinnamon flecked with pale buff, tail without any discernible bands. In other parts of the range (e.g. E Zimbabwe) some individuals are almost black. The pelage of populations living in montane habitats is particularly long and intensely pigmented, and without cream flecking (P. Grubb unpubl.).

Grubb (1982) recognized five subspecies but suggested that much of the colour variation is clinal. Because variation within populations may obscure geographic variation, only the distribution of each of these taxa is provided:

H. m. shirensis: S and E Zambia, N Malawi, SW Tanzania. The most widespread form.

H. m. beirae: S Tanzania and coastal Mozambique.

H. m. chirindensis: highland regions of E Zimbabwe and adjacent Mozambique.



H. m. mutabilis: S Malawi and adjacent Mozambique.

H. m. vumbae: SE Zimbabwe and adjacent Mozambique.

Similar Species

Paraxerus cepapi. Smaller (HB: 145–203 mm); dorsal pelage dull grey or yellowish-brown; no side-stripe; cheekteeth $4/4$.

Paraxerus palliatus. Similar size (HB: 187–221 mm); brightly coloured with rufous or red on ventral ventrum, cheeks and/or tail; no side-stripe; cheekteeth $4/4$.

Paraxerus flavovittis. Smaller (HB: 165–176 mm); dorsal pelage rusty-brown or red-brown; white side-stripe bordered by lower black stripe; cheekteeth $4/4$.

Distribution Endemic to Africa. Eastern parts of Zambezan Woodland BZ and southern parts of Coastal Forest Mosaic BZ, including some highland regions. Recorded from S Tanzania, E Zambia, Malawi, E Zimbabwe, and S and C Mozambique. May occur in N Mozambique, but no definite records. Recorded from sea level to ca. 2100 m. In Tanzania, replaced by *H. undulatus* north of Rufigi R.

Habitat Very varied: montane forests, *Brachystegia* woodland savanna, especially where trees are dense, thickets, riparian forests and coastal forests. Sometimes occurs in mopane woodlands (Dowsett 1969).

Abundance Uncertain; may be quite common in suitable habitats.

Adaptations Arboreal and diurnal. Runs quickly and nimbly among denser branches and twigs, and in the canopy of trees. Nests in holes of trees.

Foraging and Food Mostly vegetarian. Feeds on wild fruits, berries, nuts, fresh green shoots and flowers; occasionally eats insects and eggs (Smithers 1966, Smithers & Wilson 1979).

Social and Reproductive Behaviour Normally observed as solitary individuals or in pairs. When alarmed, makes loud ‘clucking’ sounds and flicks tail, and sometimes lies flat along the length of a branch or hides in a tree hole (Smithers 1966, 1986a).

Reproduction and Population Structure Young born in ‘summer months’ in Zimbabwe. Litter-size: up to four (Smithers 1986a).

Predators, Parasites and Diseases No information.

Conservation IUCN Category: Least Concern.

Measurements

Heliosciurus mutabilis

HB: 236.3 (217–269) mm, n = 10

T: 265.0 (241–302) mm, n = 10

HF: 53.5 (46–60) mm, n = 10

E: 16.7 (13–19) mm, n = 10

WT: 380 g, n = 1

GLS: 54.2 (52.2–56.2) mm, n = 10

GWS: 32.0 (30.4–34.5) mm, n = 10

P⁴–M³: 10.3 (9.7–11.1) mm, n = 10

Malawi, Zambia, Tanzania (BMNH)

Key References Grubb 1982; De Graaff 1981.

D. C. D. Happold

Heliosciurus punctatus PUNCTATE SUN SQUIRREL (SMALL SUN SQUIRREL)

Fr. Heliosciure de forêt; Ger. Geflecktes Sonnenhörnchen (Kleine Sonnenhörnchen)

Heliosciurus punctatus (Temminck, 1853). Esquisses Zoologiques sur la Côte de Guinée, p. 138. ‘dans toutes les forêts de la Guinée’. Guinea coast, no exact locality given. Ingoldby (1927) suggested type locality as ‘Secondi and Bibiani, Gold Coast’, Ghana.

Taxonomy Originally described in the genus *Sciurus*. Considered as a subspecies of *H. gambianus* by Ingoldby (1927), Ellerman (1940), Rosevear (1969) and Amtmann (1975), but as a valid species by Allen (1939), Roth & Thorington (1982), Hoffman *et al.* (1993) and Grubb *et al.* (1998). Rosevear (1969) commented that *punctatus* was ‘obviously merely a form of *gambianus* darkened through residence

in the moister climate of the forest’. Included in *H. gambianus* by Kingdon (1997). Synonyms: *savannius*. Subspecies: two. Chromosome number: not known.

Description Medium-sized rather dark squirrel, with long ringed tail. Pelage long and soft. Dorsal pelage and flanks dark brown

grizzled with buff; hairs sepia at base, bands of dark and buff distally, with black tip. Ventral pelage greyish. Insides of thighs dark grey. Tail long (ca. 120% of HB), slender, banded with dark and pale rings; hairs dark with white tip; underside paler than the upperside. Skull: cheekteeth $4/4$; posterior end of bony palate in line with posterior end of M^3 ; masseteric tubercle prominent; comparatively larger braincase than in *H. gambianus*. Nipples: $0 + 1 + 1 + 1 = 6$.

Geographic Variation

H. p. punctatus: forest regions from Liberia to Volta R., Ghana. Darker coastal form.

H. p. savannius: savanna regions of Côte d'Ivoire. Paler inland form.

Similar Species

H. gambianus. Similar but with paler ventral pelage; smaller braincase; different distribution.

H. rufobrachium. Larger; reddish colouration on limbs.

Distribution Endemic to Africa. Rainforest BZ (Western Region) and Northern Rainforest–Savanna Mosaic. Recorded from Sierra Leone, E Liberia, S Côte d'Ivoire and S Ghana (west of the Volta R.).

Habitat Primary and secondary rainforest (including open areas), relict forests in Rainforest–Savanna Mosaic, and southern parts of the Guinea Savanna BZ.

Abundance No information.

Remarks Apparently no other information available.

Conservation IUCN Category: Data Deficient.

Measurements

Heliosciurus punctatus

TL (σ σ): 383.3 (355–412) mm, $n = 32$

TL (φ φ): 396.6 (365–524) mm, $n = 28$

T (σ σ): 201.8 (170–220) mm, $n = 32$



Heliosciurus punctatus

T (φ φ): 207.3 (112–230) mm, $n = 28$

HF: 45.9 (37–50) mm, $n = 60$

E: 15.9 (14–19) mm, $n = 59$

WT (σ σ): 166.2 (109–222) g, $n = 30$

WT (φ φ): 169.1 (114–256) g, $n = 27$

GLS: 47.2 (43.5–49.7) mm, $n = 14$

GWS: 25.2 (22.9–26.6) mm, $n = 12$

P^4-M^3 : 8.4 (8.0–8.8) mm, $n = 13$

Ghana, Côte d'Ivoire, Liberia (USNM)

Key References Rosevear 1969; Roth & Thorington 1982.

Richard W. Thorington, Jr & Chad E. Schennum

Heliosciurus rufobrachium RED-LEGGED SUN SQUIRREL

Fr. Héliosciure à pieds roux; Ger. Rotbeiniges Sonnenhörnchen

Heliosciurus rufobrachium (Waterhouse, 1842). Ann. Mag. Nat. Hist., ser. 1, 10: 202. Fernando Poo (= Bioko I., Equatorial Guinea).

Taxonomy Originally described in the genus *Sciurus*. Rosevear (1969) and Amtmann (1966) recognized two species from the *gambianus*-like group of Sun Squirrels: *H. gambianus* for small, pale-coloured squirrels from dry habitats, and *H. rufobrachium* for large, darker squirrels from wetter habitats. Subsequently Grubb (1982) allocated specimens of this species from S Tanzania, Malawi, Mozambique, Zambia and Zimbabwe to *H. mutabilis* (see species profile). Hoffman *et al.* (1993) list 26 synonyms, attesting to the large amount of variation within the species (see below, and Thorington & Hoffman 2005). Synonyms: *acticola*, *arthenii*, *aschantiensis*, *aubryi*, *benga*, *brauni*, *caurinus*, *coenosus*, *emissus*, *hardyi*, *isabellinus*, *keniae*, *leakyi*, *leonensis*, *libericus*, *lualabae*, *maculatus*, *medjanius*, *nyansae*, *obfuscatus*, *occidentalis*, *pasha*, *rubricatus*, *rufobrachius*, *semlikii*, *waterhousii*.

Subspecies: possibly 16. Chromosome number: not known.

Description Large dark brown to grey squirrel with red-tinged limbs and a slender faintly banded tail with pale yellow and blackish bands. Dorsal pelage dark brown, grey or rusty-red, grizzled with buff; hairs have 3–5 bands of dark brown and buff. Variation in the colour of bands produces the many local variations in overall pelage colour. Ventral pelage pale brown, whitish-brown, reddish or orange, grizzled as in dorsal pelage. Shoulders, limbs, inner surface of hindlimbs vary from bright rusty-red to grizzled brown or grey. Head smallish, slightly flattened. Ears short. Eyes large, often bordered by a pale eye-ring. Tail long (ca. 195% of HB), slender, faintly banded with paler bands; carried straight out behind or drooping downward

over a branch, not curled up against back. Skull: cheekteeth $4/4$; posterior end of bony palate in line with posterior end of M^3 ; masseteric tubercle prominent. Nipples: $1 + 0 + 1 + 1 = 6$.

Geographic Variation There is much geographical variation in colour, especially in the overall colour of the pelage, and in the colour and intensity of colour of the limbs. Of the 32 named forms, Amtmann (1966) synonymized several forms and listed 16 subspecies (four of them now included in *H. mutabilis*) without detail.

H. r. arrhenii: N Kivu, DR Congo.

H. r. aubryi: SW Central African Republic, Gabon, DR Congo between Tshuapa and Kasai rivers.

H. r. caurinus: Guinea-Bissau.

H. r. hardyi: Côte d'Ivoire.

H. r. isabellinus: E Nigeria to Togo.

H. r. keniae: western slope of Mt Kenya.

H. r. leonensis: Sierra Leone.

H. r. maculatus: Liberia.

H. r. medjanius: DR Congo.

H. r. nyansae: Nyando R. valley, Kenya, Tanzania west of L. Victoria.

H. r. obfuscatus: SE Nigeria, Mt Cameroon.

H. r. pasha: DR Congo.

H. r. rufobrachium: Bioko I.

H. r. semlikii: Semliki R., DR Congo.

Similar Species

H. mutabilis. Paler, less rufous on limbs; multi-coloured pelage during moult; allopatric to *H. rufobrachium*.

H. gambianus. Paler without any reddish colouration; mainly savanna habitats.

H. ruwenzorii. Broad, mid-ventral white stripe; restricted distribution only near Albertine Rift Valley.

Protoxerus stangeri. Much larger, with grizzled grey head, conspicuously bushy tail and sharply delineated almost naked yellow belly.

Distribution Endemic to Africa. Widespread in Rainforest BZ (Western, West Central and East Central Regions), Northern and Eastern Rainforest–Savanna Mosaics, and parts of Guinea Savanna BZ. Recorded from Benin, Burundi, Cameroon, Central African Republic, Congo, Côte d'Ivoire, Equatorial Guinea, Gambia, Ghana, Guinea, Guinea-Bissau, W Kenya, Liberia, Nigeria, Rwanda, Senegal, Sierra Leone, N Tanzania, Togo, Uganda, DR Congo, Bioko I.

Habitat Habitats with large trees in lowland evergreen moist rainforests, secondary forests, plantations and gardens in Rainforest BZ; forest outliers and some relict forests in savanna.

Abundance Common.

Adaptations Diurnal and arboreal. Red-legged Sun Squirrels live in the canopy and middle levels of the forest. They are morphologically adapted for arboreal life, with a long back, short limbs and short broad feet. Red-legged Sun Squirrels nest within tree hollows and prefer those with small entrances. Fifteen nest holes in Gabon were at a mean height of 8.8 m (range 1–20 m). Nests within the tree hollows are constructed of sprays of green leaves attached to their



Heliosciurus rufobrachium

twigs (Emmons 1975). In Gabon, Red-legged Sun Squirrels left their nests at dawn, but often returned well before dark (mean hours of activity 9.46 h); mean time of nest entry 15:55h; range 12:21–18:31h; $n = 13$).

Foraging and Food Omnivorous. In Gabon, feed on fruits and seeds (89% by dry mass of stomach contents), green vegetative parts of plants (6%) and arthropods (5%) ($n = 15$ stomachs). Although the nutritional return is evidently low, Red-legged Sun Squirrels spend much of their time hunting for arthropods (76% of 38 observations, Emmons 1980) by searching intently along branches and lianas, poking their nose into crevices and cavities, and rummaging around in epiphytes and suspended debris. Red-legged Sun Squirrels have a predatory, mongoose-like appearance, and they sometimes move with a slow, sneaking, weasel-like gait. In captivity they quickly captured and ate birds flying within their cages, killing them with bites to the head; and they readily ate bird's eggs as well as arthropods (Emmons 1975). Arthropods identified in the diet included ants, lepidopteran larvae, Coleoptera and others.

Social and Reproductive Behaviour Red-legged Sun Squirrels in the wild have been observed singly (60% of observations), in pairs (32%) and in threes (5%) ($n = 128$ sightings). In captivity they were gregarious and contact-loving: two adult ♂♂ and a ♀ always crammed themselves tightly together to sleep in the same nest box, and they frequently groomed each other and rested in physical contact, often draped over one another. They had a strict dominance hierarchy with respect to food. Wild pairs of undetermined sex were seen to forage, groom each other, play and rest together. Two radio-collared ♂♂ and two ♀♀ nested and travelled alone (Emmons 1975, 1980). The social organization is thus unclear, but bonded pairs seem likely.

Squirrels of this species are not highly vocal and are heard calling more rarely than are other species of squirrel (Emmons 1978). The

low intensity alarm call is a single- or double-pulsed chuck or bark, given in groups of 1–3, most often singly. The squirrel may call repeatedly for a few minutes. The distinctive high intensity alarm call sounds somewhat like the cooing of a dove. It has two parts: a low amplitude, descending frequency whine immediately followed by a short, rapid trill of low frequency pulses. During a calling bout, usually only one, or at most a few, calls are emitted at long intervals. Alarm chucks are emitted with a visual display similar to that of *Paraxerus poensis*. As the call is emitted, the tail is jerked upward in a stiff C shape, or with a somewhat circular sweep, and the feet are stamped on the substrate. If the squirrel is sitting with the tail hanging below, the tail may be jerked stiffly in random directions.

Reproduction and Population Structure Litter-size: 1–2, with more litters of one than of two (Rahm 1970). Pregnancy rate seems low; none of 11 adult ♀♀ collected in all seasons in Gabon was pregnant (L. Emmons & G. Dubost unpubl.).

Predators, Parasites and Diseases No information.

Conservation IUCN Category: Least Concern.

Measurements

Heliosciurus rufobrachium

HB (♂♂): 237.3 (212–249) mm, n = 12

HB (♀♀): 230.5 (205–241) mm, n = 8

T (♂♂): 248 (210–265) mm, n = 12

T (♀♀): 248 (230–260) mm, n = 8

HF (♂♂): 47 (45–56) mm, n = 12

HF (♀♀): 49 (40–55) mm, n = 8

E: n. d.

WT (♂♂): 356 (300–420) g, n = 12

WT (♀♀): 351 (290–387) g, n = 7

GLS: 52.8 (50.6–54.5) mm, n = 5

GWS: 30.8 (29.1–31.8) mm, n = 5

P⁴–M³: 9.9 (9.4–10.4) mm, n = 5

Gabon (Emmons 1975, L. Emmons unpubl.)

Key References Emmons 1978, 1980; Rosevear 1969.

Louise H. Emmons

Heliosciurus ruwenzorii RWENZORI SUN SQUIRREL

Fr. Héliosciure de Rwenzori; Ger. Ruwenzori Sonnenhörnchen

Heliosciurus ruwenzorii (Schwann, 1904). *Ann. Mag. Nat. Hist.*, ser. 7, 13: 71. Wimi Valley, Rwenzori, E DR Congo.

Taxonomy Originally described as *Sciurus rufobrachiatatus ruwenzorii*. Formerly included in the genus *Aethosciurus*, which is here included in *Paraxerus* following Moore (1959). Synonyms: *ituriensis*, *schoutedeni*, *vulcanius*. Subspecies: four. Chromosome number: not known.

Description Medium to large grey squirrel with broad white stripe running down the underside from the throat to the genitals; geographical variation in pelage colour (see below). Pelage thick and dense. Dorsal pelage and flanks medium grey, slightly grizzled. Ventral pelage (on either side of white stripe) creamy-buff to olivaceous. Hairs pure white in ventral stripe. Head and outer surface of limbs grey. Chin, throat and chest white. Tail long (ca. 110% of HB) and slender, markedly banded with alternating grey and white bands. Skull: cheekteeth $\frac{5}{4}$ (anterior premolar P³ small); posterior end of bony palate in line with posterior end of M³; masseteric tubercle prominent. Nipples: 0 + 1 + 1 + 1 = 6.

Geographic Variation

H. r. ituriensis: E DR Congo (mountains west of L. Albert near Djalasinda and Djugu). Darker ventrally, showing less contrast with the dorsal pelage than in *H. r. ruwenzorii*; tail blacker; dorsal surfaces of feet less brown.

H. r. ruwenzorii: W Uganda and E DR Congo (Rwenzori Mts, 1980–2590 m). See Description above.

H. r. schoutedeni: E DR Congo (mountains from west of L. Edward to west of L. Kivu, area around Kahuzi-Biega N. P.), NW Rwanda (Parc National des Volcans, as *vulcanius*), SW Uganda. Brown on feet and muzzle; ventral pelage beige on either side of the white stripe.



Heliosciurus ruwenzorii

H. r. vulcanius: NW of L. Tanganyika (Mt Kandashomwa, 2330 m, Itombwe area), NW Burundi (Kibira N. P.), SW Rwanda (Nyungwe N. P., usually above 2000 m). Dorsal pelage sooty-brown, finely speckled with pale buffy; ventral pelage washed with ochraceous on either side of white stripe; rufous on feet.

Similar Species

Heliosciurus spp. Third upper premolar absent; without white ventral stripe.

Distribution Endemic to Africa. Afromontane–Afroalpine BZ. Montane forests of E DR Congo, W Rwanda, W and SW Uganda and NW Burundi.

Habitat Montane and bamboo forests (1600–2700 m) (*H. r. ruwenzorii*); montane forests, gallery forests and forest edges and lightly wooded areas (*H. r. schoutedeni*, *H. r. vulcanius*), transitional and disturbed montane forests (*H. r. ituriensis*), cultivations (*H. r. vulcanius*).

Abundance Uncertain. Formerly common in the forests of Rwenzori Mts.

Adaptations Diurnal and arboreal. Lives mainly in lower vegetation rather than in the canopy. One nest was made of grass and leaves (Rahm & Christiaensen 1963). When travelling, the tail is held horizontally, in line with the body (Kingdon 1974). Vocalizations include a loud chattering call (Thomas & Wroughton 1910).

Foraging and Food Vegetarian and occasionally insectivorous. Near L. Kivu, at the edges of the forest, the diet includes the fruits of several species of trees – *Parinari holstii*, *Syzygium cordatum*, *Conopharyngia holsteii*, *Carapa* sp. and *Urera hypselodendron* – as well as the lichen *Usnea* (Rahm & Christiaensen 1963). In farmlands and plantations, feed on guavas, papaya, bananas and palm nuts. Stomachs contained fragments of leaves, stems and insects. Local people say that these squirrels store food (Rahm & Christiaensen 1963).

Social and Reproductive Behaviour Usually seen alone or in pairs (Rahm & Christiaensen 1963).

Reproduction and Population Structure Little information. One pregnant ♀ with three large young found in Mar (Rahm & Christiaensen 1963).

Predators, Parasites and Diseases No information.

Conservation IUCN Category: Least Concern.

Measurements

Heliosciurus ruwenzorii

HB: 217 (192–242) mm, n = 19

T: 240 (220–267) mm, n = 19

HF: 54.9 (51–58.5) mm, n = 18

E: 17.7 (15–20) mm, n = 15

WT: 286 (249–318) g, n = 8

GLS: 51.3 (48.8–54.4) mm, n = 24

GWS: 29.2 (27.5–30.4) mm, n = 23

P³–M³: 9.1 (8.3–10.1) mm, n = 25*

Throughout geographic range (AMNH, FMNH, LACM, MCZ, USNM)

*RMCA

Key References Kingdon 1974; Prigogine 1954; Rahm & Christiaensen 1963.

J. Kerbis Peterhans & Richard W. Thorington, Jr

Heliosciurus undulatus ZANJ SUN SQUIRREL

Fr. Héliosciure de Zanj; Ger. Zanj Sonnenhörnchen

Heliosciurus undulatus (True, 1892). Proc. U. S. Nat. Mus. 15: 465. 'Male. Mount Kilima-Njaro, 6000 feet (1800 m). Female. Kahé, south of Mount Kilima-Njaro'. Tanzania.

Taxonomy Originally described in the genus *Sciurus*. Considered a subspecies of *Heliosciurus rufobrachium* (e.g. Kingdon 1974) until separated from this species by Grubb (1982). Does not intergrade with the populations of *H. rufobrachium* to the south or west. The form *keniae*, included in this species by Kingdon (1974), is now retained in *H. rufobrachium* (Thorington & Hoffman 2005). Synonyms: *daucus*, *dolosus*, *marwitzi*, *shindi*. Subspecies: none (Grubb 1982). Chromosome number: not known.

Description Large tawny-grey squirrel with long ringed tail. Dorsal pelage grizzled tawny-grey; hairs banded black and orange, with white subterminal band. Ventral pelage whitish-grey to ochre. Face, nose and feet similar to dorsal pelage, but suffused with pale grey-ochre to orange-ochre. Tail long (ca. 120% of HB), slender, with 10–14 black bands alternating with pale bands, tail hairs ca. 40 mm. Pelage colour varies geographically (see below). Skull: cheekteeth ⁴/₄; posterior end of bony palate in line with posterior end of M³; masseteric tubercle prominent. Nipples: not known.

Geographic Variation Individuals from higher altitudes are darker and richer in colour; those from the north of the range are paler, and those from the south are duller and greyer (Grubb 1982).

Similar Species

H. ruwenzorii. White ventral stripe; Rwenzori and Albertine Rift Valley only.

H. rufobrachium. Reddish colouration of ventral pelage, and on limbs; different distribution.

H. mutabilis. Darker colour, with seasonal changes in pelage colour; different distribution.

Distribution Endemic to Africa. Somalia–Masai Bushland BZ (perhaps also northern parts of Coastal Forest Mosaic BZ). Recorded from SE Kenya and NE Tanzania, including Mafia and Zanzibar Is. Does not overlap with *H. rufobrachium* or with *H. mutabilis*. Occurs up to 1800 m on Mt Kilimanjaro.



Habitat No information.

Remarks Omnivorous. Fruits, seeds, palm dates, leaves, buds, with insects important seasonally (Kingdon 1997). Nests in hollow trees or branches.

Conservation IUCN Category: Data Deficient.

Measurements

Heliosciurus undulatus

HB: 233 ± 20.7 mm, n = 18

T: 281 ± 28.1 mm, n = 18

HF: 56.2 ± 3.2 mm, n = 17

E: 17.1 ± 2.1 mm, n = 16

WT: n. d.

GLS: 53.9 ± 1.4 mm, n = 16

GWS: 31.6 ± 0.8 mm, n = 18

P⁴-M³: n. d.

Throughout geographic range; mean \pm 1 S.D. (Grubb 1982)

Key References Grubb 1982; Kingdon 1974, 1997.

Chad E. Schennum & Richard W. Thorington, Jr

GENUS *Myosciurus* African Pygmy Squirrel

Myosciurus Thomas, 1909. Ann. Mag. Nat. Hist., ser. 8, 3: 474. Type species: *Sciurus minutus* Du Chaillu, 1860 (= *Sciurus pumilio* Le Conte, 1857).

Myosciurus is a monotypic genus, with restricted distribution in rainforests of Cameroon, Equatorial Guinea, Gabon and NW Congo. The most obvious character is the very small size ('not much bigger than a man's thumb' – Rosevear 1969) and the absence of any externally visible pollex (Digit 1 of forefoot). The skull is small, broad and rounded, with rounded orbits, semicircular zygomatic arch, large auditory bullae, and narrow rostrum (Figure 13). Masseteric tubercle absent. Dental formula is $I^{1/1}, C^{0/0}, P^{1/1}, M^{3/3} = 20$.



Myosciurus pumilio.

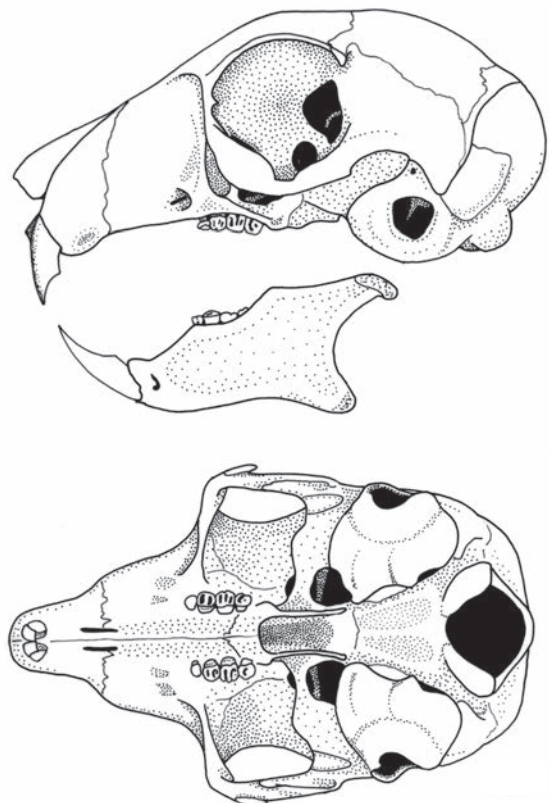


Figure 13 Skull and mandible of *Myosciurus pumilio* (BMNH 5.5.23.25).

Pygmy squirrels similar in size to the African *Myosciurus* are found in South America and the East Indies. The remarkable similarity between these forms is thought to be the result of convergent evolution, and does not to imply any close phylogenetic relationship

between them (Rosevear 1969). There is a single species, *Myosciurus pumilio*.

Louise H. Emmons

***Myosciurus pumilio* AFRICAN PYGMY SQUIRREL**

Fr. Écureuil pygmée; Ger. Afrikanischer Zwerghörnchen

Myosciurus pumilio (Le Conte, 1857). Proc. Acad. Nat. Sci. Philadelphia 9: 11. 'headwaters of the Ovenga River', Gabon.

Taxonomy Originally described in the genus *Sciurus* (Rosevear 1969). Synonyms: *minutulus*, *minutus*. Subspecies: none. Chromosome number: not known. See also Gharaibeh & Jones (1996).

Description Very small rufous-brown squirrel, about the size of a mouse. Pelage soft, of moderate length. Dorsal pelage rufous-brown, grizzled with buff; hairs dark grey or black at base, rufous-red or yellowish-red terminally. Ventral pelage pale brown. Head similar to dorsal pelage, with prominent pale buff eye-ring. Ears brown, with inner and outer margins bright pale buff. Fore- and hindfeet elongated and narrow; forefeet with no external evidence of a Digit 1, although the vestigial, much reduced bones persist within the wrist (Emmons 1979b). Tail moderate (ca. 86% of HB), slender, hairs rufous at base tipped with black above. Tail is held straight out behind the body, never over the back. Skull: incisors slightly proodont; cheekteeth $4/4$; posterior end of bony palate slightly posterior to M^3 ; masseteric tubercle absent. Nipples: $0 + 0 + 1 + 1 = 4$.

Geographic Variation None recorded.

Similar Species No other squirrel in Africa is as small as this species. The next largest squirrel is *Paraxerus alexandri* (HB: 102.5 [91–114] mm, T: 110.3 [93–126] mm).



Myosciurus pumilio

Distribution Endemic to Africa. Rainforest BZ (West Central Region, parts of Eastern Nigerian and Gabon sub-regions). Recorded from S Cameroon, NW Congo, Equatorial Guinea (Rio Muni and Bioko I.) and Gabon. There is no evidence that the species occurs in eastern Nigeria (see Happold 1987).

Habitat Restricted to evergreen moist rainforests and secondary forests. Uses all levels of the vegetation from near the ground to the canopy, but mostly uses 0–5 m (Emmons 1980).

Abundance Mostly rare, with a patchy distribution and small geographic range. May be fairly common in some localities.

Adaptations Diurnal and arboreal. The tiny body size is probably an adaptation to a specialized life-style of feeding on both the top and bottom surfaces of large tree trunks and branches. The elongated toes and the loss of Digit 1 on both fore- and hindfeet appear to be adaptations associated with a lizard-like locomotion, with the long limbs splayed sideways and the body flattened against the substrate, held by the hooked claws (Emmons 1979b). The nest is undescribed, but individuals have been seen entering tree holes.

Foraging and Food Omnivorous. African Pygmy Squirrels have a highly specialized foraging behaviour. They forage almost incessantly, moving rapidly over the surfaces of tree trunks and branches, pulling off small chips of bark, and holding them in the forepaws while something is scraped with the teeth from the bark surface before the chip is dropped. Three stomach contents included bark scrapings (30%), fruit (33%) and ants and termites (37%). The nutritive material sought from bark is unidentified, and it may be a bacterial or fungal film (Emmons 1979b, 1980). The Neotropical Pygmy Squirrel *Sciurillus pusillus* and Bornean Pygmy Squirrels *Exilisciurus exilis* and *E. whiteheadi* have virtually identical behaviour; they feed on a yellow material, probably fungus or bacteria growing on exudate, under the bark of particular species of living trees, especially certain legumes (Emmons & Feer 1997, L. Emmons unpubl.). In contrast, African Pygmy Squirrels forage on the surface of bark pulled from both dead and living trees. These squirrels, unlike many other squirrels, are not known to cache food.

Social and Reproductive Behaviour Pygmy Squirrels are apparently solitary: they are usually sighted alone (87%; $n = 45$ observations) and only rarely are two active on the same tree (13%). The simple alarm call is a low amplitude pipping sound consisting of widely spaced short (18 ms, $n = 14$) pulses, which are emitted repeatedly (mean interval between pulses 279 ms, $n = 12$) (Emmons

1978). The squirrel usually does not stop foraging when it calls. The tail is carried stiffly straight behind the body when the squirrel is calling and its base is twitched from side to side, while the tip stays more or less centred. Because these squirrels spend most of their time splayed against trunks (and only the dorsal surface is normally seen), the side-to-side tail movement is an effective display.

Reproduction and Population Structure Embryo number: 2 (n = 1; Emmons 1979a).

Predators, Parasites and Diseases No information.

Conservation IUCN Category: Least Concern. Previously considered as 'Vulnerable'.

Measurements

Myosciurus pumilio

HB: 66 (61–74) mm, n = 6

T: 56 (45–60) mm, n = 6

HF: 18.7 (18–20) mm, n = 6

E: 8 (7–8) mm, n = ?*

WT: 16.5 (12.4–20) g, n = 6

GLS: 21.3 (20.3–22.1) mm, n = 6

GWS: 13.5 (12.9–14.1) mm, n = 6

P⁴–M³: 2.8 (2.7–2.9) mm, n = 4

Gabon

Body measurements and weight: Emmons 1975, L. Emmons unpubl.

Skull measurements: BMNH

*Rosevear 1969

Key References Emmons 1979b, 1980.

Louise H. Emmons

GENUS *Paraxerus*

Bush Squirrels

Paraxerus Forsyth Major, 1893. Proc. Zool. Soc. Lond. 1893: 189. Type species: *Sciurus cepapi* A. Smith, 1836.



Paraxerus alexandri.

A genus of very small to medium-sized tree squirrels with 11 species widely distributed over much of Africa south of the Sahara, except for arid areas and savanna habitats north of the Rainforest BZ. All species are arboreal; most species live in rainforest or montane forests, but two live in wooded savanna habitats. The genus is best represented in eastern Africa, where nine species are recorded. Most species are geographically and/or ecologically separated.

The genus is characterized by very small to medium size (HB: 91–114 mm for the smallest to 145–203 mm for the largest species), and a long well-haired tail mostly longer than the head and body. Pelage markings and colouration show considerable variation. The muzzle is slightly elongated, and the ears are mostly relatively longer than in *Funisciurus* and *Heliosciurus* (as expressed by percentage of GLS). Depending on the species, there is no side-stripe, one side-stripe or two side-stripes, and the side-stripes are pale or dark. Females have three pairs of nipples (for those species in which the number has been recorded). The skull is similar to that of *Funisciurus*

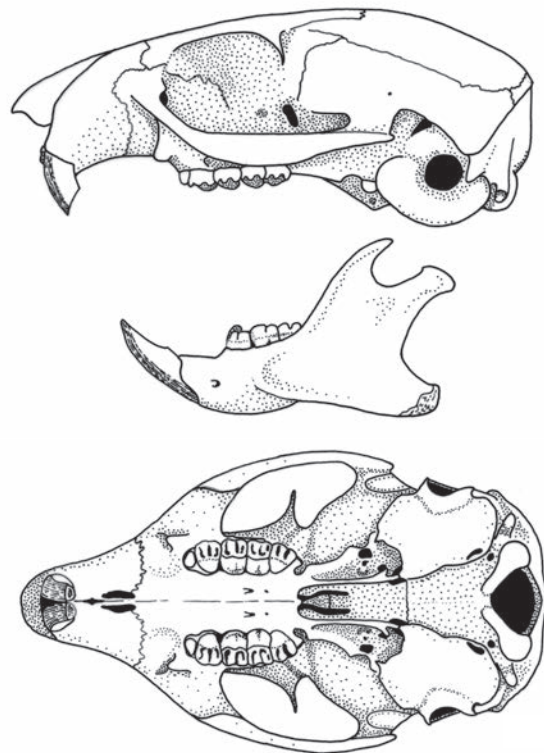


Figure 14. Skull and mandible of *Paraxerus cepapi* (HC 2172).

but without the specialized condition of the cheekteeth. There are five subhypsodont upper cheekteeth and four lower cheekteeth, all with prominent cusps; the posterior end of the bony palate is in line with the posterior end of M³; supraorbital foramen absent, and the masseteric tubercle is small and insignificant (Figure 14). Dental formula: I ¹/₁, C ⁰/₀, P ²/₁, M ³/₃ = 22 (cf. *Heliosciurus*).

Ecological characteristics of species in the genus also show considerable variation. Three species (*P. alexandri*, *P. boehmi*, *P. peoensis*) live in rainforest, four species (*P. cooperi*, *P. lucifer*, *P. vexillarius*, *P. vincenti*) live in montane forests, two species (*P. flavovittis*, *P. palliatus*) live in the coastal forests and neighbouring savannas of eastern Africa, and two species (*P. cepapi*, *P. ochraceus*) live in savanna woodlands. Likewise, diet and reproductive characteristics also

exhibit considerable variation. The ecology of most of these species is poorly known.

Paraxerus, *Funisciurus* and *Myosciurus* form a monophyletic clade. *Paraxerus* is related to *Funisciurus*, and the species of *Paraxerus* are more variable in ecology, size and in the number of transverse septae than *Funisciurus* species. From external appearance and habitat, Kingdon (1974) thought *F. carruthersi* was more like species of *Paraxerus* (*P.*



Courtship behaviour of *Paraxerus palliatus*.

1. one tail flagging approaches other
2. then grooms
3. alert
4. rests
5. resume grooming hindquarters and genitalia
6. leave off and then self groom side by side
7. resume grooming
8. sudden excitement; ♀ curls tail
9. ♂ mounts

Table 13. Species in the genus *Paraxerus*. Arranged in order of increasing number of side-stripes on each flank. (n. d. = no data).

| Species | Side-stripes on each flank | Red colouration on pelage | HB mean (mm) | HF mean (mm) | GLS mean (mm) | Notes |
|-----------------------|---|---|--------------------|-------------------|-------------------|---|
| <i>P. poensis</i> | None | None | 153 | 33 | 38 | Rainforests; Sierra Leone to Zaire; mostly greenish-olive |
| <i>P. cepapi</i> | None | None | 175 | 44 | 42 | Widespread Zambesian Woodland BZ; savanna and thickets |
| <i>P. cooperi</i> | None | Golden-rufous on thighs | 203 | 42 | 46 | Montane forest in Cameroon only |
| <i>P. lucifer</i> | None | Head and dorsal pelage bright rufous | 222 | 52 | 55 | Montane forests in Malawi and Tanzania; black patch on dorsum |
| <i>P. palliatus</i> | None | Cheeks, limbs and ventral pelage bright rufous | 187.7 ^a | 43.9 ^a | 45.3 ^a | Coastal regions S Somalia to South Africa |
| <i>P. vexillarius</i> | None | Limbs, feet and tip of tail rufous-orange | ca. 230 | ca. 50 | 53 | Montane habitats NE and C Tanzania |
| <i>P. vincenti</i> | None | Rich rufous on limbs, feet, ventral pelage and around eye | 212 | 46 | 50 | Namuli Mt, Mozambique only |
| <i>P. ochraceus</i> | None (or one, pale) | None | 155 | 40 | 41 | Savannas; SE Ethiopia to Tanzania |
| <i>P. alexandri</i> | One, black, bordered ventrally by creamy-yellow | None | 102 | 26 | 31 | Rainforest of NE DR Congo and W Uganda; edges of ears white; mid-dorsal colour tawny-brown |
| <i>P. flavovittis</i> | One, white, bordered ventrally by black | None | 172 | 39 | n. d. | SE Kenya to N Mozambique; savannas and forests |
| <i>P. boehmi</i> | Two, black, separated by yellow | None | 120 | 30 | 35 | Rainforest BZ (East Central Region) and relicts to N Zambia; edges of ears not white; mid-dorsal colour tawny-brown |

^a *P. palliatus bridgmani*; *P. p. ornatus* is ca. 20% larger in all measurements.

cooperi, *P. vexillarius*) than other species of *Funisciurus*, and considered *Paraxerus* to be a subgenus of *Funisciurus*. *Paraxerus* has in the past been confused with *Heliosciurus*. Ellerman (1940), for example, included *Heliosciurus ruwenzorii* and species of *Paraxerus* (*P. poensis*, *P. lucifer*, *P. vexillarius*) in a subgenus (*Aethosciurus*) of *Heliosciurus*. The skulls of the two genera (*Paraxerus* and *Heliosciurus*) are superficially similar but are distinguished by absence of the supraorbital foramen and small insignificant masseteric knob in *Paraxerus* (cf. supraorbital foramen present and large masseteric knob in *Heliosciurus*) and the form of the naso-premaxillary suture. *Paraxerus* can also be differentiated from *Heliosciurus* (Ellerman 1940) by the form of the zygomatic plate, which is shorter with the ridge stopping abruptly over the infraorbital foramen, and not approaching the superior border of the rostrum in *Paraxerus* (cf. zygomatic plate more strongly ridged, ridge

extending forward in *Heliosciurus*); and by the cheekteeth, which are usually more cuspidate in *Paraxerus*, especially in the lower tooth row, though *P. poensis* is conservative and resembles *Heliosciurus*.

Relationships of the genus have recently been re-assessed. Moore (1959) placed the genus in the tribe Funambulini (with non-African genera), whereas Thorington & Hoffmann (2005), on the basis of molecular studies by Mercer & Roth (2003) and Steppan *et al.* (2004), place it in the tribe Protoxerini with all the other African squirrels (except *Xerus* and *Atlantoxerus*).

Species in the genus are distinguished by size, presence/absence of side-stripes, presence/absence of reddish colouration of pelage, and habitat (Table 13).

Peter Grubb

Paraxerus alexandri ALEXANDER'S BUSH SQUIRREL

Fr. Écureuil de brousse d'Alexander; Ger. Alexander Buschhörnchen

Paraxerus alexandri (Thomas and Wroughton, 1907). Ann. Mag. Nat. Hist., ser. 7, 19: 376. Upper Welle, River Iri, Gudima, DR Congo.

Taxonomy Originally described in the genus *Funisciurus*. Referred to as *Tamiscus alexandri* by Rahm (1966, 1970). Synonyms: none. Chromosome number: not known.

Description Very small, snub-nosed, greenish-brown squirrel with white edges to ears and five long stripes on back and flanks. Dorsal pelage grizzled yellow, black and grey, giving appearance of greenish-brown at a distance; hairs dark grey at base, subterminal band yellow, usually with black tip. Some long pure black guard hairs. Wide tawny-orange mid-dorsal stripe from shoulders to mid-back bordered on each side by a thin black stripe and a thin creamy-yellow stripe. Ventral pelage similar but paler than dorsal pelage, often with irregular patches and streaks of yellow; hairs dark grey at base, yellow or buff at tip. Head similar in colour to dorsal pelage. Vibrissae long. White eye-ring around eye; not obvious in some individuals. Edges of ears finely covered with short white hairs. Limb extremities proportionally large compared with other small squirrels. Forelimbs greenish-brown; four slim long digits each with thin long sharp claw. Hindlimbs greenish-brown, with five digits, Digit 1 reduced; digits and claws similar to forelimbs. Tail long (ca. 100% of HB), well covered with short hairs, indistinctly marked with irregular brown and ochre bars, tapered towards tip. Seasonal changes in intensity of colouration (due to seasonal moulting or to fading?) have been noted: specimens collected between Nov and Feb were brighter than those in Apr, May and Sep. Skull: cheekteeth $5/4$; posterior end of bony palate in line with posterior end of M^3 ; masseteric tubercle not prominent. Nipples: $1 + 2 = 6$.

Geographic Variation None recorded.

Similar Species

P. boehmi. Slightly larger; tawny-orange mid-dorsal stripe from shoulders to rump, bordered on each side by two black stripes separated by a yellow or cream stripe; ears pigmented without white hairs; comparatively longer nose; relatively smaller fore- and hindfeet.



Paraxerus alexandri

Funisciurus lemniscatus. Slightly larger, longer-nosed squirrel of darker overall colour. Dull brown mid-dorsal stripe bordered on each side by two black stripes from base of neck to rump, the outer stripe separated from the inner stripe by a pale yellow stripe; longer, more strongly patterned tail.

Distribution Endemic to Africa. Rainforest BZ (East Central Region) and parts of Eastern Rainforest–Savanna Mosaic. Recorded from NE DR Congo and Uganda. Distribution extends (east to west) from the Victoria Nile to the Lualaba R., and (north to south) from the Mbomou R. to the Lukuga R., at altitudes of 500–1500 m.

Habitat Lowland rainforest with a preference for tall relatively mature forest. Apparently common in Ironwood *Cynometra alexandri* (Caesalpinaceae), a climax species that forms extensive, nearly monospecific stands in many parts of its geographic range. Sometimes occurs in abandoned plantations within the rainforest in E DR Congo (Rahm 1970).

Abundance Commonly seen in mature forests. Locally, populations may be dense. Rare or absent in young forests regenerating after felling.

Adaptations Arboreal and diurnal. Alexander's Bush Squirrels have a compact body, with relatively large hands and feet, sharp claws and thin relatively long digits enabling them to scuttle, spread-eagled, over the very extensive surfaces of large forest trees. There is some indication that they prefer smoother types of bark. They are commonly seen on the bare surfaces of boles and large branches of very large forest trees such as Ironwood, Mahogany, Khaya and Mututu *Klainedoxa*, and may be seen emerging from hollow branches. It is uncertain whether they build nests or live in holes in trees. They live at many levels of the forest, but more often on larger branches than other squirrels. The reduced nasal region suggests that they rely less upon scent than most other species of squirrels, and they appear to be able to find scent clues only at very close quarters. The incisors are relatively small, suggesting a poor ability to gnaw; this is consistent with a diet of micro-fauna and flora (see below).

Foraging and Food Omnivorous. Commonly seen moving in fits and starts over the surfaces of branches. Food appears to be found at many levels of the forest but apparently not normally in the leafy canopy. Movements are fast, and a foraging squirrel explores continuously, stopping only briefly to consume the food items it encounters. Alexander's Bush Squirrels mostly forage alone, perhaps because of the dispersed nature of their food supply. The diet includes small ants and other insects (about 50% in a small sample). The exact composition of plant matter (such as that retrieved from stomach contents) has yet to be determined. It is possible that lichens may be a significant part of their diet. Traces of tree resins have been recorded (Kingdon 1974; J. Kingdon unpubl.). The diet is more insectivorous than that of sympatric *Funisciurus pyrrhopus* (Rahm 1970).

Social and Reproductive Behaviour Commonly seen alone but not infrequently in pairs. Larger numbers have not been noted. Typically silent, but may be the originator of a sharp, rather bird-like twitter sometimes heard when Alexander's Bush Squirrels are nearby. The large, mobile and white-coloured ears suggest that ear movements might be significant during social interactions.

Reproduction and Population Structure In E DR Congo pregnant ♀♀ have been recorded in Mar, Apr, Jul and Sep (Rahm 1970). In Uganda, pregnant ♀♀ were taken in Sep and Nov and juveniles in Apr, Oct and Nov (Kingdon 1974). Embryo number: usually one, sometimes two (Rahm 1970). Testes of specimens collected in Uganda vary in size; whether fluctuating testis size follows a seasonal trend has yet to be determined.

Predators, Parasites and Diseases The most likely predators are accipiterine hawks but hornbills perhaps represent a hazard, especially for animals sheltering in crevices or nests. Snakes may also be predators occasionally. Ectoparasites have not been noted by collectors.

Conservation IUCN Category: Least Concern.

Previously considered as Near Threatened. The habitat is declining in area due to logging of forests.

Measurements

Paraxerus alexandri

HB: 102.5 (91–114) mm, n = 10

T: 110.3 (93–126) mm, n = 10

HF: 26.2 (23–28) mm, n = 10

E: 13.2 (12–14) mm, n = 9

WT: 46 (40–72) g, n = 9*

GLS: 30.6 (29.2–33.1) mm, n = 8

GWS: 17.9 (17.4–18.6) mm, n = 8

P³–M³: 5.2 (4.8–6.1) mm, n = 8

Measurements: Uganda and DR Congo (BMNH)

Weight: Rahm 1966

Key References Kingdon 1974; Rahm 1966, 1970.

Jonathan Kingdon

Paraxerus boehmi BOEHM'S BUSH SQUIRREL

Fr. Écureuil de brousse de Boehm; Ger. Boehms Buschhörnchen

Paraxerus boehmi (Reichenow, 1886). Zool. Anz. 9: 315. 'Marungu (Inner-Afrika)' (= Marungu, SE DR Congo).



Paraxerus boehmi.

Taxonomy Originally described in genus *Sciurus*. One form, provisionally treated here as a subspecies (*P. b. vulcanorum*, see below) has, with some justification, been regarded as a separate species by some authorities (e.g. Schouteden 1946, as *Tamiscus vulcanorum*). This interesting situation deserves further study in the field, supplemented by molecular work to determine whether more than one species is involved. Referred to as *Tamiscus emini* by Rahm (1966) and Rahm & Christiaensen (1963). Synonyms: *antoniae*, *emini*, *gazella*, *lunaris*, *tanganyikae*, *ugandae*, *vulcanorum*. Subspecies: four. Chromosome number: not known.

Description Small olive-coloured squirrel with five long stripes. Pelage varies geographically (see below). Dorsal pelage grizzled yellow, black and grey giving appearance of olive or greenish-brown at a distance. Wide mid-dorsal stripe, tawny-orange, from shoulders to rump, bordered on each flank by two black side-stripes separated by white or cream (giving the impression of an additional stripe). Ventral pelage paler than dorsal pelage. Head similar in colour to dorsal pelage with three pale longitudinal stripes (sometimes indistinct): one above and below each eye, and one across cheek. Ears small, rounded, deeply pigmented, and without white hairs. Fore- and hindlimbs greenish-brown; forelimb with four digits, each with thick claw; hindlimb with five digits each with sharp thick claw. Tail long (ca. 125% of HB), well covered with short hairs; mottled black and ochre and indistinctly barred; tapers towards tip. Skull: cheekteeth $5/4$; posterior end of bony palate in line with posterior end of M^3 ; masseteric tubercle not prominent. Nipples: not known.

Geographic Variation Pelage colour and pattern of stripes vary geographically. Lowland and upland forms meet and reportedly overlap in range at about 2000 m. Four subspecies are recognized:

- P. b. boehmi*: lowland forest west of Albertine Rift Valley. Pelage darker and sparse; white stripe conspicuous (see Description above).
- P. b. emini*: lowland forest east of Albertine Rift Valley. Pelage paler and sparse; white stripe conspicuous.
- P. b. gazellae*: lowland forest margins in S Sudan. Pelage paler, somewhat 'bleached', but otherwise resembles *P. b. boehmi*.
- P. b. vulcanorum*: montane forests of the Albertine Rift (Rwenzori Mts and the mountains between L. Edward and L. Tanganyika). Pelage darker olive/russet, dense and long; upper black side-stripe wide; lower black side-stripe narrow, white stripe (in between the black side-stripes) narrow and not conspicuous. This subspecies may be a distinct montane species (J. Kingdon unpubl.).

Similar Species

- P. alexandri*. Very small (smaller than *P. boehmi*); wide tawny-orange mid-dorsal stripe from shoulders to mid-back bordered on each side by thin black stripe and thin creamy-yellow stripe; vivid white ears; relatively larger fore- and hindfeet.
- Funisciurus lemniscatus*. Slightly larger, mainly terrestrial squirrel of darker overall colour. Dull brown mid-dorsal stripe (but redder than in *P. boehmi*) bordered on either flank by two black stripes from base of neck to rump, the outer stripes separated from inner stripes by pale yellow band; longer, more strongly patterned tail.

Distribution Endemic to Africa. Rainforest BZ (East Central Region). Recorded from E DR Congo, Uganda, S Sudan, NW Tanzania and N Zambia. The range of subspecies *P. b. vulcanorum* includes the montane forests of the Albertine Rift Valley. Records from W Kenya need confirmation. An outlier population is present in Bahr el Ghazal (at two localities west of Malek) in C Sudan (F. Dieterlen unpubl.).

Habitat Typically found in the undergrowth and lower storeys of rainforest, notably in thick tangles of lianas and sometimes on the ground. The montane form prefers disturbed areas with dense undergrowth. Although mainly a true rainforest species it has



Paraxerus boehmi

been recorded from wooded savanna in E DR Congo (Rahm & Christiaensen 1963), as well as on the edges of plantations and in tangles along roadsides (Rahm 1966).

Abundance Common in suitable habitats. The subspecies *P. b. vulcanorum* is especially common in montane areas.

Adaptations Arboreal and diurnal. Boehm's Bush Squirrels are well adapted to moving fast through dense tangles of vegetation by virtue of their tapered limbs and small hands and feet. They can travel in any direction over trunks and branches, even hanging upside-down to examine the underside of branches. The inner toe of the hindfoot is partially opposable, increasing the squirrel's ability to grip plant stems and twigs. The robust muzzle and incisor teeth are well suited to tearing bark, moss and lichen and, it seems, to catching, gnawing and carrying food items.

Boehm's Bush Squirrels make unusually large nests (which resemble the nests of birds) that are dense agglomerations of fine twigs and grasses with a chamber in the middle lined with finer materials, including strands of soft shredded bark. They are built in thick tangles 2–8 m from the ground (Rahm & Christiaensen 1963).

As with some other squirrels, the tail is likely to serve as a scent disperser for pheromones emanating from the anal glands. Sustained flicking of the tail is often accompanied by a bird-like chitter. This has been interpreted as an alarm but is just as likely to serve as a combined olfactory/auditory/visual set of signals directed at conspecifics.

Foraging and Food Frugivore and insectivore. Animals forage by travelling along branches, tearing moss, lichen and bark with their incisor teeth. However, unlike other species of squirrels, the forefeet seem to be less commonly used to hold food, which is usually seized by the mouth. Of 30 stomachs investigated in Uganda, seven contained insects alone (mainly ants but also caterpillars and beetles), ten contained a large proportion of insects, while eight

had traces of insects; 12 contained vegetable matter (including the fruits of *Rubus* and epiphytic mushrooms) and ten contained large quantities of tree resin (Kingdon 1974). In E DR Congo, stomach contents contained resins from *Albizzia* trees, and the remains of fruits, caterpillars, beetles and other insects (Rahm & Christiaensen 1963). Feeding on insects is unusual for squirrels.

Social and Reproductive Behaviour Normally solitary, but also observed in pairs and trios. Boehm's Bush Squirrels sometimes forage close to another individual for some time. They never aggregate, but the regularity of sightings suggests that they remain fairly evenly dispersed, and perhaps are more densely distributed in suitable habitats. Reproductive ♂♂ pursue ♀♀ relentlessly, and copulation has been seen even while hanging on a vertical trunk.

Reproduction and Population Structure In E DR Congo, where rainfall occurs in all months, Rahm (1970) recorded reproductively active and pregnant ♀♀ in all months of the year. The percentage of pregnant ♀♀ varied monthly from 10 to 35% (total n = 222 ♀♀ examined, range 8–41 ♀♀/month) with the highest percentages occurring towards the end of the dry season and the beginning of the wet season. Rahm (1970) commented that rainfall did not seem to exert a strong influence on the timing of reproduction. In Uganda, Kingdon (1974) provided confirmatory evidence, with records of pregnant ♀♀ in Jan, Jun, Nov and Dec (total n = 4), and lactating ♀♀ in Jan, May, Jun and Jul (total n = 5). Embryo number: 1 (90%) or 2 (10%) (n = 61 pregnant ♀♀; Rahm 1970). This pattern of reproduction indicates that the population contains young, subadult and adult individuals, and reproductively active and inactive individuals, in all months of the year.

Predators, Parasites and Diseases The most likely predators are accipiterine hawks (especially the Long-tailed Hawk), hornbills and snakes. They might also be vulnerable to nocturnal arboreal carnivores such as *Genetta* spp. and Palm Civet *Nandinia binotata*, especially while in their nests. They are host to a particular coccidial parasite, *Wenyonella parva* (Van den Berghe 1938).

Conservation IUCN Category: Least Concern.

Measurements

Paraxerus boehmi emini

HB: 120 (111–126) mm, n = 10

T: 152 (140–160) mm, n = 9

HF: 30.7 (28–34) mm, n = 9

E: 13 (11–14) mm, n = 10

WT (♂♂): 69 (48–80) g, n = 9

WT (non-pregnant ♀♀): 79 (72–83) g, n = 6

GLS: 34.9 (33.9–36.6) mm, n = 10

GWS: 19.5 (18.1–21.7) mm, n = 10

P³–M³: 5.8 (5.3–6.4) mm, n = 10

Measurements: Ituri Forest, DR Congo (BMNH)

Weight: near L. Kivu, E DR Congo (Rahm & Christiaensen 1963)

Mean HB measurements from E DR Congo (HB ♂♂: 135 [110–145] mm; ♀♀ 137 [129–145] mm; Rahm & Christiaensen 1963) are greater than those from Ituri

Key References Kingdon 1974; 1997, Rahm 1970; Rahm & Christiaensen 1963.

Jonathan Kingdon

Paraxerus cepapi SMITH'S BUSH SQUIRREL

Fr. Écureuil de brousse de Smith; Ger. Smiths Buschhörnchen

Paraxerus cepapi (A. Smith, 1836). Report on the Expedition and Exploration of Central Africa, p. 43.

Marico River, Rustenberg District, W Transvaal, South Africa.

Taxonomy Originally described in the genus *Sciurus*. Kingdon (1974) proposed that *Paraxerus cepapi* and *Paraxerus palliatus* hybridize in the wild and form hybrid populations; Viljoen (1989) disagreed, pointing out distinctive differences in behaviour and habitat use between the two species. Many subspecies have been described: Amtmann (1975) lists ten subspecies although recognizing that not all of them are valid, and Ansell & Dowsett (1988) subsequently synonymized *soccatus* with *yulei*. Synonyms: *cepate* (lapsus for *cepapi*), *bororensis*, *carpi*, *cepapoides*, *chobiensis*, *kalaharicus*, *maunensis*, *phalaena*, *quotus*, *sindi*, *soccatus*, *yulei*. Subspecies: nine. Chromosome number: not known.

Description Medium-sized yellowish-brown grizzled squirrel without any bright colours or markings. Dorsal pelage and flanks grey, yellowish-brown or brown; hairs annulated with alternating bands of yellow and black, usually with black tip. Ventral pelage dull white, tending to yellow or buff on the chest. No side-stripe. Head with indistinct upper and lower white eye-stripes; cheeks pale yellowish-brown. Limbs short, similar in colour to flanks; well-developed digits with sharp claws. Tail long (ca. 95% of HB), bushy, with long

hairs annulated with alternating bands of black and yellowish-brown. Pelage colour varies geographically. Skull: cheekteeth ⁵/₄; posterior end of bony palate in line with posterior end of M³; masseteric tubercle not prominent. Nipples: 0 + 1 + 1 + 1 = 6.

Geographic Variation Amtmann (1975) lists the following subspecies (see also above):

P. c. bororensis: Namabieda, Boror, north of the Zambezi R., Mozambique. Darker and more chestnut than *P. c. cepapoides*. Sides of body and lower part of hind legs greyer.

P. c. carpi: Junction of Messenguez and Zambezi rivers, Mozambique. Small size (HB: 158 mm; T: 150 mm). Paler than *P. c. cepapi*, with thighs and mid-line of underside of tail orange-yellow, feet whitish or whitish-yellow.

P. c. cepapi: Transvaal, S Botswana and S Zimbabwe. See Description.

P. c. cepapoides: Zimbiti, Beira, Mozambique. More rusty coloured than *P. c. cepapi*, with the upper parts of body and thighs having a more tawny hue.

- P. c. chobiensis*: N Botswana and N Namibia. Ventral pelage and toes whiter than in *P. c. cepapi*.
- P. c. phalaena*: Ovamboland, Namibia, and SW Angola. Dorsal pelage pale grey, with crown, shoulders, hips and legs also grey. Fore- and hindfeet pale buffy-white, paler than in *P. c. cepapi*.
- P. c. quotus*: SE Katanga and N Zambia. Darker colouring with no suffusion of colour on flanks.
- P. c. sindi*: Tete district, Zambezi R., Mozambique and S Malawi. Thighs and underside of mid-line of tail ochre. Ventral pelage white.
- P. c. yulei*: NE Zambia, N Malawi and W Tanzania. A large subspecies (type specimen HB: 205 mm). Dorsal colour pale coarsely grizzled tawny, greyer over the shoulders, sides paler greyish-tawny; ventral colour white, more greyish on the belly; fore- and hindfeet greyish-white to whitish-yellow.

Similar Species

- P. ochraceus*. Darker, with many white-tipped hairs in dorsal pelage; mostly in E Tanzania and Kenya (further north than *P. cepapi*).

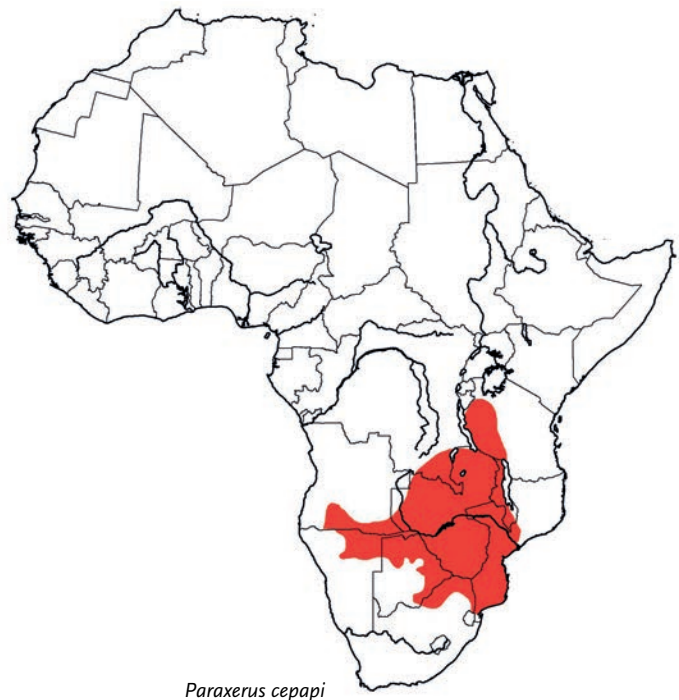
Distribution Endemic to Africa. Zambezian Woodland BZ. Recorded from S Angola, Zambia, SE DR Congo, Malawi, SW Tanzania, S Mozambique, N Namibia, N Botswana, Zimbabwe and South Africa (former Transvaal).

Habitat Mixed woodlands and thickets, especially in stony, hilly country, especially in *Colophospermum* (mopane), *Brachystegia* (miombo) and *Acacia* woodlands, and in riverine forests. These squirrels prefer areas where there are trees with suitable holes for nesting.

Abundance Widespread and fairly common. In sandveld habitat in South Africa, density was 2.08–2.58 individuals/ha (biomass of 449–557 g/ha) (Viljoen 1986).

Adaptations Diurnal and arboreal. Smith's Bush Squirrels avoid activity during the hottest times of the day. Winter mornings usually begin with basking and grooming in the sun. Both auto- and allogrooming are significant social behaviours (see below). They are very alert and can be quick on the ground and swift in the trees when danger is near. Although mainly arboreal, individuals will descend to the ground to forage for fallen fruits. They are very active, running quickly along branches and jumping from tree to tree. At night, squirrels retire to their holes, where they nest in territorial groups. While holes in trees are favourite nest sites, they will also nest in holes in the ground, in rocky crevices and in roofs of houses. Nests are lined with grass and leaves, and the squirrels frequently clean them out, possibly to reduce the number of parasites in the nest (Smithers 1983).

Foraging and Food Predominantly vegetarian; sometimes omnivorous. Bush Squirrels forage in the trees and on the ground, and suitable foods are held in the forefeet while eating. In South Africa (Viljoen 1977b) they feed opportunistically on a wide variety of seeds, berries, flowers, stems, leaves and gum, changing the diet according to the season. Seeds and gums of *Acacia*, and seeds and flowers of *Aloes* are favourite foods. Analysis of stomach contents showed that insects (mostly termites) formed about 30% of the diet on an annual basis (range 0–85%), and 79% of stomachs ($n = 49$) contained some insect material. Over a period of several



Paraxerus cepapi

months, more than 30 species of plants were utilized in the diet (Viljoen 1975). In East Africa, they are reported to feed on fruits of *Sclerocarya*, *Pterocarpus* and *Kigelia*, *Aloe* and *Euphorbia* leaves, as well as unspecified bulbs, nuts, seeds, insects and bird's eggs (Kingdon 1974). In gardens and plantations, they feed on mangoes and many other cultivated fruits (De Graaff 1981). Seeds are cached close to grass tufts and tree trunks, thus facilitating dispersal and germination of savanna trees (Viljoen 1997). Smith's Bush Squirrels drink water, both in the wild and in captivity, usually from holes in trees (Viljoen 1975). Smith's Bush Squirrels are a 'colonizing species' (Viljoen 1983a), living in vegetation that grows quickly and produces many fruits and seeds (in contrast to tall mature forest); hence a squirrel can find sufficient daily food in a small area (see above).

Social and Reproductive Behaviour Social and territorial. Average group size is five animals (rather large for squirrels), usually including one or two adults and several juveniles. Group size in South Africa varied seasonally, from an average of 2/group in Sep to 12/group in Nov when adults were accompanied by young, and in different years (Viljoen 1977a). Pairs and solitary animals are commonly seen. They are territorial, except during the mating season when strange squirrels are tolerated. Territory size in termitaria thickets is 0.3–1.26/ha, although within this area an individual or group may feed within only 150 m² (Viljoen 1986, 1997). Territory size varies with habitat, being smallest in termitaria thickets and larger in woodlands. Territorial behaviour includes vocalizations, chasing of strangers and scent marking. Scent marking is very common and can include mouth-wiping, urination and anal-dragging (Viljoen 1983b).

A dominance hierarchy was observed by Viljoen (1977a), especially with regards to feeding and access to food. In captivity, individuals are very aggressive towards each other; fighting results in many torn ears and sometimes an individual is killed. Dominance–subordination relationships are important in the social organization of these squirrels, and hence behaviour such as chasing, fighting, mutual

grooming and scent-marking play important roles in maintaining group bonds and territorial boundaries.

Vocal communications are well developed (Viljoen 1983b). Most vocalizations begin with a loud call (usually a 'click', 'rattle' or 'whistle') and continue with decreasing intensity and descending pitch. Different types of calls may be joined in succession, depending on the circumstances. Four calls have been described: (a) Whistle call – a high frequency call, with 6–7 notes emitted at about 1 sec intervals; rather similar to a bird call, indicating extreme alarm. (b) Rattle and clicks, a series of different calls indicating alarm and alertness, and also used in territorial defence. These complicated calls results in 'chir-chir-chir' alarm rattles and clearer 'click-click-click' calls, spread out over several seconds. (c) Murmurs – a low-pitched nasal sound emitted during courtship and mating by the male. Clicking noises are also emitted by both ♂ and ♀ during courtship, and by ♀ when communicating with young. (d) Grunting and growling – when disturbed at the nest.

Mating behaviour occurs in the morning. Mating chases are initiated by enthusiastic calls of ♀, a sound similar to the alarm rattle; ♂ also has a distinct mating call, and clicking and tail flicking are common in both sexes. Male allogrooms ♀ during mating, and they both autogroom afterwards (Viljoen 1977a).

Reproduction and Population Structure In Botswana, pregnant ♀♀ recorded in every month except May and Sep (n = 256 ♀, Smithers 1971); the number of pregnant or lactating ♀♀ was significantly lower during the cold dry months (4.5%) than during the warm wet months (51%). In South Africa, reproduction is seasonal and most young are born in Oct–Jan (Viljoen 1997). While one litter/year is most common, inter-birth interval in captive animals is 60–63 days (n = 4; Viljoen, 1977a). Gestation: 56–58 days (longer than for most squirrels). Litter-size: 2 (1–3), sample size not recorded. At birth, young are comparatively precocious. Eyes open by Day 7–8, young begin to climb out of the nest by Day 19, take solid food by Day 21 and are fully weaned by Day 29–42.

Sexual maturity by 6–10 months. Both parents groom their young. Subadults are usually evicted from the group when sexually mature. Infanticide has been observed occasionally by ♂♂ in a group, after which ♂♂ may try to mate with ♀♀ (De Villiers 1986).

Predators, Parasites and Diseases Predators probably include raptors, snakes and probably some carnivorous mammals. Ectoparasites include a species of chigger, two species of mites, seven species of ticks, four species of fleas and one species of sucking louse (details in De Graaff 1981). Blood parasites include several bacteria (transmitted by ticks), which are responsible for a variety of fevers. Viljoen (1977b) noted that all the squirrels she studied were heavily infected with the parasitic nematode *Syphacia paraxeri*.

Conservation IUCN Category: Least Concern.

Measurements

Paraxerus cepapi

HB: 175.5 (145–203) mm, n = 38

T: 169 (116–215) mm, n = 61*

HF c.u.: 43.0 (26–49) mm, n = 61

E: 19.0 (16–21) mm, n = 128

WT: 192.3 (76–265) g, n = 52

GLS: 44 (43–45) mm, n = 8

GWS: 26 (25–26) mm, n = 8

P³–M³: 7.4 (6.8–7.9) mm, n = 15

T, HF and WT: Transvaal, South Africa (Rautenbach 1978)

HB, E and P⁴–M³: throughout geographic range (USNM)

GLS and GWS: Botswana (Smithers 1971)

*♀♀ only

Key References De Graaff 1981; Smithers 1971; Viljoen 1975, 1977a, b, 1983a, b, 1997.

Lindsay A. Pappas & Richard W. Thorington, Jr

Paraxerus cooperi COOPER'S BUSH SQUIRREL (COOPER'S MOUNTAIN SQUIRREL)

Fr. Écureuil de brousse de Cooper; Ger. Cooper Buschhörnchen

Paraxerus cooperi Hayman, 1950. Ann. Mag. Nat. Hist., ser. 12, 3: 262. Kumba Division, Rumpi Hills, Cameroon.

Taxonomy Although originally described in the genus *Paraxerus*, Rosevear (1969) placed this species (together with *poensis*) in the genus *Aethosciurus* even though he admitted that the status of the genus was questionable. Eisentraut (1976) placed *cooperi* in a separate genus, *Montisciurus*, because it has many palatal ridges between the molars. Synonyms: none. Chromosome number: not known.

Description Medium-sized dark squirrel with pale golden-rufous thighs. Pelage very soft and long. Dorsal pelage blackish-brown speckled with creamy-buff, becoming more olive-green and golden on flanks; dorsal hairs dark grey or black at base, subterminal band bright buff or gold, with black tip. Ventral pelage medium grey at base, golden-yellow at tip. Head similar to dorsal pelage. Ears darkly pigmented, mostly naked, with yellow-tipped hairs on outer surface. Lips and cheeks golden. Forearms, upper surface of forefeet

and hindfeet rufous. Thighs deep rufous. Tail long (ca. 100% of HB), blackish golden-green above, without bands or rings, golden-yellow stripe (similar in colour to ventral pelage) below. Skull: cheekteeth 5/4; posterior end of bony palate in line with posterior end of M³; masseteric tubercle not prominent. Nipples: not known.

Geographic Variation None recorded.

Similar Species

P. poensis. Smaller (HB: 148–161 mm), lacks rufous colour on limbs and feet.

Distribution Endemic to Africa. Afromontane–Afroalpine BZ. Recorded only from forested montane regions of S Cameroon (Kupe Mts, Oku Mts, Rumpi Hills; Eisentraut 1973).

*Paraxerus cooperi*

Habitat Lower storeys of forest remnants in the Bamenda highlands at altitudes above 1400 m (Rosevear 1969).

Abundance No information. In the late 1960s, the species may have been far more abundant than previously thought (M. Eisentraut in Rosevear 1969).

Remarks One individual (the holotype) was feeding on the succulent flowers of the guttiferaceous tree *Pentadesma butyracea* and was noticeably fat. This record is the only direct evidence of squirrels feeding on flowers in W Africa (Rosevear 1969).

Conservation IUCN Category: Data Deficient.
Previously considered as Vulnerable.

Measurements

Paraxerus cooperi

HB: 203 (192–212) mm, n = 12

T: 179 (161–200) mm, n = 12

HF: 42 (41–45) mm, n = 12

E: 16 (15–17) mm, n = 12

WT: n. d.

GLS: 45.9 (44.4–46.6) mm, n = 12

GWS: 26.7 (26.2–27.3) mm, n = 12

P³–M³: 8.8 (8.3–9.0) mm, n = 12

Oku Mts, Cameroon; ♂♂ only (Eisentraut 1973)

Key Reference Rosevear 1969.

Richard W. Thorington, Jr & Chad E. Schennum

Paraxerus flavovittis STRIPED BUSH SQUIRREL

Fr. Écureuil de brousse rayé; Ger. Gestreiftes Buschhörnchen

Paraxerus flavovittis (Peters, 1852). Bericht Verhandl. K. Preuss. Akad. Wiss. Berlin 17: 274. 'Africa orientalis. Mossimboa, Quitangonha, a 11° ad 15° Lat. Aust'. Mocimboa, NE Mozambique.

Taxonomy Originally described in the genus *Sciurus*. Commonly spelled *flavivittis*, but this was an unjustified emendation by Peters (1852). Four subspecies usually recognized, but individual and seasonal variations suggest that *mossambicus* is a synonym of *flavovittis* (see Hinton 1920). Synonyms: *exgeanus*, *ibeanus*, *mossambicus*. Subspecies: three. Chromosome number: not known.

Description Medium-sized arboreal squirrel with a lateral whitish side-stripe. Pelage short and slightly coarse. Dorsal pelage rusty-brown or red-brown; hairs black with one or two wide rusty-brown bands, usually black at tip. White to yellowish side-stripe, 9–10 mm wide, bordered below by a darker stripe. Flanks (below dark side-stripe) olive-brown. Ochraceous hairs tint the forelimbs, and ochraceous colouration may extend across the shoulders forming a mantle, and even onto the crown and into the lumbar region. Ventral pelage white or off-white. Head similar to dorsal pelage, though usually not ochraceous. Cheek with two indistinct white bands, one above the eye and one below, from nasal region to base of ear. Fore- and hindfeet whitish. Tail long (ca. 97% of HB), bushy towards tip, with black and white rings at distal end. Pelage colour

varies seasonally or individually, and also during the moult. Skull: cheekteeth ⁵/₄; posterior end of bony palate in line with posterior end of M³; masseteric tubercle not prominent. Nipples: not known.

Geographic Variation

P.f. exgeanus: SE Tanzania. Side-stripe narrower (5 mm wide) and not as long as in *flavovittis*.

P.f. flavovittis: NE Mozambique (Mossimboa). See Description above.

P.f. ibeanus: NE Tanzania and SE Kenya. Side-stripe slightly broader than in *exgeanus*, but shorter; facial stripes faint.

Similar Species

Paraxerus spp. (other striped species). Mostly smaller in body size.

P. cepapi. No side-stripe.

P. ochraceus. No side-stripe.

Distribution Endemic to Africa. Coastal Forest Mosaic BZ and nearby regions of Zambezian Woodland BZ. Recorded from SE Kenya, E and SE Tanzania, SE Malawi and N Mozambique.



Habitat Savanna and forest, especially where there are *Uapaca* trees, and hardwood trees with holes (suitable for nesting). May also occur in cultivations.

Abundance Common and widespread between the Rufigi and Rovuma rivers in Tanzania. Particularly numerous where there are many old hardwood trees (Kingdon 1974).

Adaptations Diurnal and arboreal. These squirrels nest in the holes and hollows of hardwood trees, and sometimes nest in the roofs of houses (Kingdon 1974).

Foraging and Food Omnivorous. Forages on the ground and in the trees. Feeds on fruits, seeds, buds, leaves, roots and some animal matter. In farmland, eats millet and other grains (Kingdon 1974, 1997).

Social and Reproductive Behaviour Little information. Usually seen in pairs or as ♀ with her young (Kingdon 1974).

Reproduction and Population Structure Young and juveniles have been recorded in Mar, Apr, Jun and Sep (Kingdon 1974). Young are born in nests inside hollow trees; one nest was made of coconut fibres and grass (A. Loveridge in Kingdon 1974). Both pale and dark side-stripes are present in young when HB 90–100 mm (labels, BMNH).

Predators, Parasites and Diseases No information.

Conservation IUCN Category: Least Concern.
Previously considered as Least Concern.

Measurements

Paraxerus flavovittis

HB: 172.7 (165–176) mm, n = 6

T: 168.8 (160–175) mm, n = 4

HF: 39.2 (35–40) mm, n = 6

E: 16.6 (15–18) mm, n = 5

WT: n. d.

GLS: 40.1 (38.6–42.2) mm, n = 8

GWS: 22.5 (21.1–23.7) mm, n = 8

P³–M³: 4.7 (6.7–7.9) mm, n = 8

Body measurements: Lumbo, Mozambique (Hinton 1920)

Skull measurements: Tanzania (BMNH)

Key References Kingdon 1974, 1997.

Chad E. Schennum & Richard W. Thorington, Jr

Paraxerus lucifer BLACK-AND-RED BUSH SQUIRREL

Fr. Écureuil de brousse rouge et noir; Ger. Tanganjika-Buschhörnchen

Paraxerus lucifer (Thomas, 1897). Proc. Zool. Soc. Lond. 1897: 430. Kombe Forest, Misuku Mts, Malawi.

Taxonomy Originally described in the genus *Xerus* (*Paraxerus*). *Paraxerus lucifer* is closely related to three other species, *P. vincenti*, *P. palliatus* and *P. vexillarius*. Synonyms: none. Chromosome number: not known.

Description Large bright rufous squirrel, sometimes with blackish patch on back. Pelage long and dense. Dorsal pelage bright rufous or russet with large patch of rufous-black in centre of back; dorsal hairs dark grey on basal half, bright rufous on terminal half, with black tip; numerous long pure black guard hairs in centre of back. Flanks bright rufous; hairs pale grey on basal half, bright rufous on terminal half. Ventral pelage, throat and chest dove-grey; hairs dove-grey with silver or whitish tip. Crown of head, cheeks and chin similar to dorsal pelage. Forelimbs and hindlimbs very bright rufous. Tail moderately long (ca. 60% of HB), similar in colour to dorsal pelage; above hairs pale rufous

at base with subterminal black band and bright rufous tip; below hairs bright rufous without banding; tail bands very indistinct. Skull: cheekteeth ⁵/₄; posterior end of bony palate in line with posterior end of M³; masseteric tubercle not prominent. Nipples: 0 + 1 + 1 + 1 = 6.

Geographic Variation None recorded.

Similar Species

P. palliatus. Ventral pelage rufous.

P. vexillarius. Ventral pelage grey, limbs rufous, sometimes with orange tail tip; Kilimanjaro and Usambara Mts, Tanzania only.

P. vincenti. Ventral pelage and limbs rufous; Namuli Mountain, Mozambique only.

P. cepapi. Yellowish brown without any rufous colour; widespread.

P. flavovittis. Lateral whitish side-stripe.

Distribution Endemic to Africa. Afromontane–Afroalpine BZ. Recorded from montane habitats in N Malawi (Misuku Hills, Nyika Plateau), SW Tanzania (Poroto Mts, Nkuka Forest) (Ansell 1978, Ansell & Dowsett 1988). Not yet found in the Mafinga and Makutu Mts of NE Zambia where it might be expected to occur (Ansell 1978).

Habitat Restricted to montane forests in isolated montane regions that have a high annual rainfall (Kingdon 1974).

Abundance Maybe numerous in some habitats (Kingdon 1974).

Adaptations Diurnal and arboreal. Tend to be rather noisy, with a loud and distinctive call.

Foraging and Food Omnivorous. May forage on the ground. The diet includes vegetable matter, fruit, nuts, termites and ants (Kingdon 1974).

Social and Reproductive Behaviour No information.

Reproduction and Population Structure A single ♀ caught in Sep was both pregnant and lactating, indicating two litters in close succession. Of eight ♀♀ examined in Mar and Apr, none was reproductively active (Kingdon 1974).

Predators, Parasites and Diseases Ectoparasites reported: fleas of the genus *Libyastus* (Ansell & Ansell 1973).

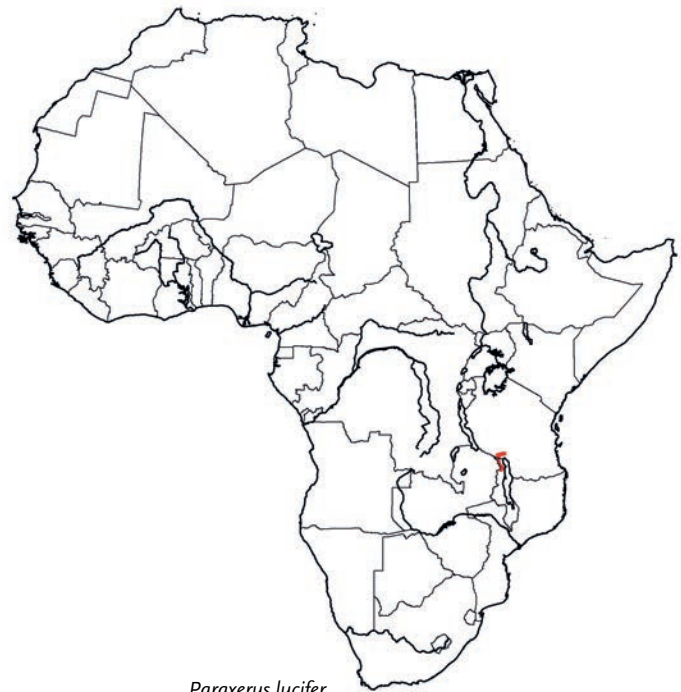
Conservation IUCN Category: Data Deficient.
Previously considered as Least Concern.

Measurements

Paraxerus lucifer

HB: 222 (201–241) mm, n = 10

T: 202 (186–218) mm, n = 10



Paraxerus lucifer

HF: 52.2 (48–55) mm, n = 13

E: 19.7 (15–22) mm, n = 12

WT: 496 (300–675*) g, n = 7

GLS: 55.6 (53.8–56.4) mm, n = 12

GWS: 31.2 (30.0–31.7) mm, n = 10

P³–M³: 9.3 (8.8–9.6) mm, n = 15

Nyika Plateau, Zambia (Ansell & Ansell 1973)

*Three individuals of 1.5 lb (= 675 g)

Key References Ansell 1978; Kingdon 1974, 1997.

Chad E. Schennum & Richard W. Thorington, Jr

Paraxerus ochraceus OCHRE BUSH SQUIRREL

Fr. Écureuil de brousse ocre; Ger. Ockerfarbiges Buschhörnchen

Paraxerus ochraceus (Huet, 1880). Nouvelles Archives, Museum d'Histoire Naturelle, Paris, ser. 2, 3: 54. 'Cette petite espèce provient de Bagamoyo, station de nos missionnaires, sur côte de Zanguebar ...' Bagamoyo (06° 25' S, 38° 54' E), Tanzania.

Taxonomy Placed in genus *Funisciurus* (subgenus *Paraxerus*) by Kingdon (1974). Synonyms: *affinis*, *animosus*, *aruscensis*, *augustus*, *capitis*, *electus*, *ganana*, *jacksoni*, *kahari*, *pauli*, *percivali*, *salutans*. Amtmann (1975) recognized eight subspecies, but two of them were considered provisional; Kingdon (1974) recognized the five subspecies listed below. Chromosome number: not known.

Description Small squirrel with dull yellowish-brown pelage and slightly ringed tail. Dorsal pelage pale yellow, ochre or dark olive, grizzled. Pelage colour varies geographically (see below). Pale side-stripe in some subspecies. Ventral pelage yellow to off-white, not grizzled. Fore- and hindfeet same as dorsal pelage. Dorsal surface of fore- and hindfeet ochraceous. Tail long (ca. 100% of HB), with black and pale irregular bars and patches; tail is mostly held horizontally

behind the body. Skull: cheekteeth $5/4$; posterior end of bony palate in line with posterior end of M³; masseteric tubercle not prominent. Nipples: 0 + 1 + 1 + 1 = 6.

Geographic Variation Five subspecies recognized by Kingdon (1974):

P. o. aruscensis: NE Tanzania and SE Kenya. Pelage colour richer than

P. o. ochraceus, with a yellow ventral pelage; without a side-stripe.

P. o. electus: W Kenya. Pale form with white ventral pelage, perhaps without a side-stripe.

P. o. ganana: S Ethiopia, NE Kenya and Tana River area. Small, pale, sandy-yellow coloured race, without a side-stripe.



Paraxerus ochraceus.

P. o. jacksoni: S Kenya and most mountain forests in Kenya. The largest subspecies, generally darker than others with a rather green colouring and sometimes a pale side-stripe near the shoulder.

P. o. ochraceus: Central and E Tanzania. A medium-sized subspecies; mostly sandy grizzled ochre, ventral pelage off-white; distinct side-stripe.

Similar Species

P. cepapi. Ventral pelage paler. Occurs further south, and probably is not sympatric with *P. ochraceus*.

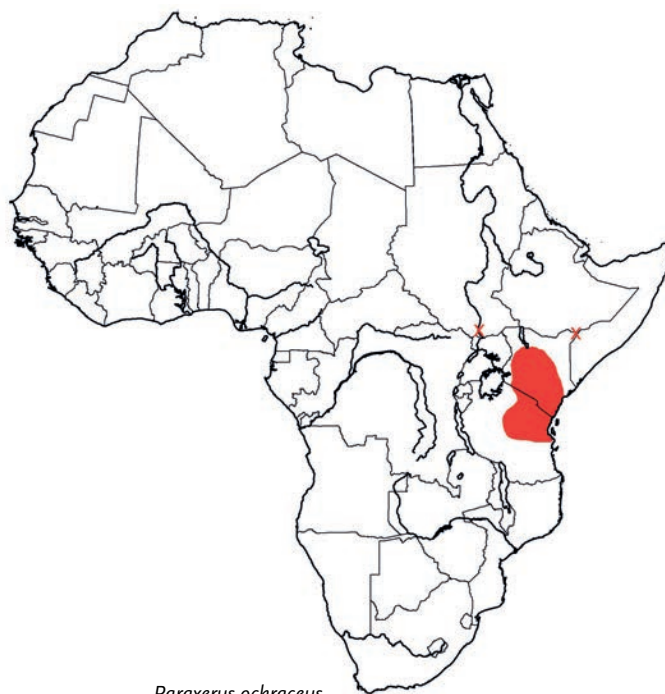
Distribution Endemic to Africa. Somalia–Masai Bushland BZ. Recorded from Kenya and N Tanzania. Outliers in Somalia (near to Kenya/Ethiopian border) and in S Sudan.

Habitat Tolerant of many habitats; recorded from diverse wooded savannas, riverine forests in semi-arid regions, and thickets from near sea level to at least 2000 m. Also recorded from plantations (coffee, *Grevillea*, *Eucaplytus*) and in suburban gardens (e.g. in Nairobi).

Abundance Very common in some localities.

Adaptations Diurnal and arboreal. Most activity is in the early morning and late afternoon, with a rest period at the hottest time of the day. Ochre Bush Squirrels are very active, running quickly along branches and between the ground and the tops of trees. Calls include a high-pitched metallic ‘Burr’, which is emitted when threatened, accompanied by flicking of the tail.

Foraging and Food Mostly vegetarian. Forages in the trees and on the ground. The diet includes fruits, seeds, buds, flowers, roots, bulbs, *Acacia* gum and occasionally animal matter (Kingdon 1997).



Paraxerus ochraceus

Social and Reproductive Behaviour Live in pairs or small groups. Courtship involves a lot of chasing, mutual grooming and arching of the tail over the body.

Reproduction and Population Structure Little information. Observations in Kenya suggest that reproduction occurs in most months of the year. Litter-size: 2–3. Two ♀♀ with young may nest together. Young emerge from nest when 3–4 weeks of age. A mother may carry young in her mouth at times (A. Root in Kingdon 1974).

Predators, Parasites and Diseases Buzzards, snakes and genets are likely predators.

Conservation IUCN Category: Least Concern.

Measurements

Paraxerus ochraceus

HB: (♂♂): 155.1 (123–190) mm, n = 30

HB: (♀♀): 163.5 (143–175) mm, n = 20

T: 162.5 (113–183) mm, n = 48

HF: 39.7 (34–45) mm, n = 52

E: 15.2 (10–27) mm, n = 45

WT: n. d.

GLS: 41.3 (40.0–42.1) mm, n = 9

GWS: 23.5 (22.0–24.5) mm, n = 10

P³–M³: 6.8 (6.5–7.2) mm, n = 11

Kenya (USNM)

Key References Kingdon 1974, 1997.

Richard W. Thorington, Jr & Chad E. Schennum

Paraxerus palliatus RED BUSH SQUIRREL

Fr. Écureuil de brousse à ventre roux; Ger. Rotbäuchiges Buschhörnchen

Paraxerus palliatus (Peters, 1852). Bericht Verhandl. K. Preuss. Akad. Wiss. Berlin 17: 273.

Mainland near Mocimboa do Ide, Mozambique I. 'Africa orientalis, Quintangonha, 15° Lat. Aust.'. Mozambique, near Mozambique I.

Taxonomy Originally described in the genus *Sciurus*. This species consists of a series of populations living in isolated forests. Kingdon (1974) suggested that some of the populations are hybrids between *Paraxerus cepapi* and *P. palliatus*, but Viljoen (1989) pointed out that this was unlikely because there are important differences between the species in behaviour and habitat. *Paraxerus palliatus* is closely related to three other species, *P. lucifer*, *P. vexillarius* and *P. vincenti*. The species exhibits considerable variation in pelage colour and pattern, such that Amtmann (1975) listed 11 subspecies but noted that this was probably an excessive number. Kingdon (1974) recognized three subspecies in the northern part of the range and Viljoen (1989) recognized four subspecies in southern Africa; all seven subspecies are recorded here. Body size and colouration seem to be influenced greatly by habitat, with larger darker squirrels in moist forest and smaller paler squirrels in dry forest (Viljoen 1989). The form *vincenti*, recognized as a valid species here, was classified as subspecies (*P. p. vincenti*) by Kingdon (1997). Synonyms: *auriventris*, *barawensis*, *bridgmani*, *freiei*, *lastii*, *ornatus*, *sponsus*, *suahelicus*, *swynnertoni*, *tanae*, *tongensis*. Subspecies: seven. Chromosome number: not known.

Description Medium to large arboreal squirrel with rufous or yellowish ventral pelage, variable geographically (see below, and Measurements). (Description for *P. p. palliatus*.) Dorsal pelage brownish, grizzled with buff. No side-stripes. Ventral pelage bright rufous. Crown of head grizzled brown, cheeks rufous. Fore- and hindlimbs, fore- and hindfeet rufous. Tail long (ca. 90% of HB), bushy, grizzled brown at base, bright rufous on terminal two-thirds. Individuals in drier climates are smaller (mean 210 g) than those in humid climates (mean 380 g). Skull: cheekteeth $5/4$; posterior end of bony palate in line with posterior end of M^3 ; masseteric tubercle not prominent. Nipples: 0 + 1 + 1 + 1 = 6.

Geographic Variation

- P. p. tanae* (including *barawensis*): S Somalia, E Kenya and N Tanzania (south to Pangani R.). Tail completely rufous-orange.
- P. p. freiei* (including *lastii*): Mafia and Zanzibar Is. Similar to coastal populations of *P. p. palliatus*, but with black feet.
- P. p. palliatus* (including *suahelicus*): E coastal Tanzania and N Mozambique. See Description above.
- P. p. swynnertoni*: Chirinda Forest, E Zimbabwe. Dorsal pelage grizzled black and buff; ventral pelage cinnamon-rufous. Face coloured like dorsal pelage, cheeks like ventral pelage. Colouration resembles *P. p. palliatus* and *P. p. ornatus*, but the different colouration of the face, fore- and hindfeet, and its smaller size, distinguishes it from these two.
- P. p. bridgmani* (including *auriventris* and *tongensis*): E coastal Mozambique (south of the Save R.). Dorsal pelage dark brown, grizzled; ventral pelage orange; generally paler and more 'yellowish' than other subspecies. (This may be a separate species – Amtmann 1975.)

*Paraxerus palliatus*

- P. p. sponsus*. Perhaps indistinguishable from *P. p. palliatus* with its brown dorsal pelage and bright rufous ventral pelage (see above), but geographically very close to *P. p. bridgmani*.
- P. p. ornatus*: South Africa (Ngoye Forest, Eshowe District, Zululand). Large; dorsal pelage dark brownish-black grizzled with buff; ventral pelage orange-rufous; tail dark brownish-black tinged with rufous.

Similar Species

- Paraxerus* spp. Without brightly coloured ventral pelage (i.e. not rufous, orange-rufous, yellowish).
- P. vincenti*. Similar in most respects, but restricted to Namuli Mountain, Mozambique.

Distribution Endemic to Africa. Coastal Forest Mosaic BZ of eastern Africa and some adjacent parts of the Zambezian Woodland BZ, especially extending inland along riverine forests and on some inland montane forests. Recorded from S Somalia, E Kenya, E Tanzania, Malawi, E Mozambique, E Zimbabwe and South Africa (KwaZulu–Natal), Mafia and Zanzibar Is. Some populations occur far inland along riverine forests (e.g. along the Tana and Ruaha Rivers; Kingdon 1974).

Habitat Dry to wet forests, preferring woodlands with shady thickets; dune forests and evergreen moist forests in Mozambique and South Africa. Montane populations up to about 2000 m (e.g. Mt Mlanje, Malawi).

Abundance Varies according to locality. In favoured habitats in South Africa, mean density was 4.32 squirrels/ha (*P. p. ornatus*) and 2.15 squirrels/ha (*P. p. bridgmani*) (Viljoen 1986). Biomass varies with locality: in Ngoye Forest (South Africa) was 1659 g/ha (maximum) and 595 g/ha in Mkwakwa Forest (Viljoen 1986).

Adaptations Diurnal and arboreal. Also spends a considerable amount of time on the ground, but the proportion of time spent foraging on the ground is uncertain. Nests in holes in baobabs and *Kigelia* trees.

Foraging and Food Omnivorous, feeding on seeds, fruits, nuts and invertebrates. Seems to prefer the seeds to the fleshy parts of the fruit. Viljoen (1983a) reported that captive squirrels ate raw liver and biltong. Drinks water when available, but does not appear to be dependent on it. Red Bush Squirrels are scatter hoarders of larger seeds, although they do not hoard large quantities of food as do squirrels of more temperate climates. They scratch under bark to get at insects, and Viljoen (1983a) reported that in captivity, they displayed hunting behaviour when stalking invertebrates.

Social and Reproductive Behaviour Although Red Bush Squirrels are quite common and diurnal, they are shy animals. Normally observed as solitary individuals or in pairs (Ansell & Dowsett 1988), although several squirrels may nest together in larger groups (mean 3.1 ± 1.2 ; Viljoen 1986). They nest in tree holes. Home-range varies according to habitat and sex: in evergreen moist forest, mean home-range (*P. p. palliatus*) was 3.18 ha ($\sigma^7 \sigma^7$) and 2.19 ha ($\sigma^7 \sigma^7$), and in coastal forest and thickets, mean home-range (*P. p. bridgmani*) was 4.17 ha ($\sigma^7 \sigma^7$) and 0.73 ha ($\sigma^7 \sigma^7$). Communication between animals is maintained by visual, auditory and olfactory signals. Viljoen (1983b) recorded lots of tail flicking and fluffing, especially in dense habitats. Vocalizations include an array of murmurs, hisses, growls, clicks, twitters and barks. Urine dribbling and anal dragging are also common. Males make murmuring vocalizations when chasing $\sigma^7 \sigma^7$. This may serve as a trigger to stimulate oestrus. Female builds nest in a tree hole lined with leaves. She keeps the nest very clean while young are being reared. When offspring are very young $\sigma^7 \sigma^7$ are extremely protective and respond aggressively toward intruders, including the male. Later, σ^7 , σ^7 and young form a family group. When young reach subadulthood (early winter in southern Africa), parents drive them away from the nest (Viljoen 1980).

Reproduction and Population Structure In the wild $\sigma^7 \sigma^7$ have 1–2 young/litter, and probably one litter/year. In captivity, multiple litters per year are possible. One lactating σ^7 recorded in March in S Kenya (Kingdon 1974). In southern Africa, young born during the warm wet season (Aug–Mar) (Smithers 1983). Gestation: 60–65 days. At birth, young weigh 13–14 g. Eyes open Day 7–10. Leave nest about Day 18. Weaned by Day 40 (Viljoen 1980).

Predators, Parasites and Diseases Uncertain, but it would be expected that snakes and arboreal mongooses would prey on young, and that hawks and raptors would be predators of adults.

Conservation IUCN Category: Least Concern.

Previously considered as Vulnerable.

Measurements

Paraxerus palliatus

HB (*P. p. ornatus*): 221.5 ± 9.2 mm, $n = 30$

HB (*P. p. bridgmani*): 187.7 ± 9.9 mm, $n = 11$

T (*P. p. ornatus*): 203.8 ± 8.6 mm, $n = 86$

T (*P. p. bridgmani*): 176.8 ± 9.1 mm, $n = 28$

HF (*P. p. ornatus*): 51.8 ± 1.7 mm, $n = 103$

HF (*P. p. bridgmani*): 43.9 ± 1.8 mm, $n = 36$

E (*P. p. ornatus*): 20.6 ± 1.4 mm, $n = 75$

E (*P. p. bridgmani*): 19.4 ± 1.5 mm, $n = 32$

WT (*P. p. ornatus*): 368.2 ± 22.4 g, $n = 104$

WT (*P. p. bridgmani*): 209.1 ± 19.2 g, $n = 60$

GLS (*P. p. ornatus*): 50.9 ± 1.6 mm, $n = 11$

GLS (*P. p. bridgmani*): 45.3 ± 0.8 mm, $n = 13$

GWS (*P. p. ornatus*): 29.4 ± 1.3 mm, $n = 11$

GWS (*P. p. bridgmani*): 26.3 ± 0.6 mm, $n = 13$

P³–M³: 9.6 (9.3–9.9) mm, $n = 9$

P. p. ornatus: Ngoye forest, South Africa (Viljoen 1989)

P. p. bridgmani: L. St Lucia, South Africa (Viljoen 1989)

P³–M³: Ngoye forest, South Africa (BMNH)

Measurements given as ± 1 S.D.

Key References Kingdon 1974; Smithers 1983; Viljoen 1983a, b, 1986, 1989.

Richard W. Thorington, Jr, Lindsay A. Pappas &
Chad E. Schennum

Paraxerus poensis GREEN BUSH SQUIRREL

Fr. Petit Écureuil de brousse; Ger. Grünes Buschhörnchen

Paraxerus poensis (A. Smith, 1834). South Afr. Quart. J., 2nd ser., 2: 128. Fernando Poo (= Bioko I., Equatorial Guinea).

Taxonomy Originally described in the genus *Sciurus*. The species has been placed, at different times, in the genera *Aethosciurus*, *Heliosciurus*, *Funisciurus* and *Paraxerus*. Thomas (1916a) placed *poensis* into a new genus, *Aethosciurus*, citing molar differences to separate it from *Heliosciurus* and *Funisciurus*. Hollister (1919) placed it in *Heliosciurus* because of dental similarity, as did Ellerman (1940), who noted the similarity to *Paraxerus*. Moore (1959) placed it in *Funisciurus*, noting some cranial similarities. Rosevear (1969)

restored it to *Aethosciurus*, stating that it possessed characters of both *Heliosciurus* and *Funisciurus* and could not be placed unambiguously in either. Amtmann (1966) allocated the species to *Paraxerus*, even though its teeth differ from those of some members of that genus. Here, following Hoffman *et al.* (1993) and Thorington & Hoffman (2005), it is placed in the genus *Paraxerus* (see also Rosevear 1969 for a review). Synonyms: *affinis*, *musculus*, *olivaceus*, *subviridescens*. Subspecies: none. Chromosome number: not known.



Description Small, greenish-olive squirrel with a slender tail. Pelage soft, thick and dense. Dorsal pelage dark grizzled golden-green; hairs black at base with greenish-yellow tips. No lateral side-stripe. Ventral pelage pale yellow, thickly furred; hairs grey at base with long yellow tip. Cheek with yellow above and below eye, bordering a darker stripe to base of ear. Fore- and hindlimbs dark golden-green. Tail long (ca. 105% of HB), slender, not bushy, slightly darker than dorsal pelage. Skull: cheekteeth $5/4$; posterior end of bony palate in line with posterior end of M^3 ; masseteric tubercle not prominent. Nipples: $1 + 0 + 1 + 1 = 6$.

Geographic Variation None recorded.

Similar Species

P. cooperi. Slightly larger (HB: 192–212 mm); rufous colour on fore- and hindlimbs; sympatric with *P. poensis* only in parts of Cameroon. *Myosciurus pumilio*. Much smaller, with inner and outer surface of ears white; sympatric with *M. pumilio* in west of range.

Distribution Endemic to Africa. Rainforest BZ except for eastern part of the East Central Region. Distributed in three disjunct populations: (a) from Sierra Leone to Ghana, (b) Cameroon, Equatorial Guinea (Rio Muni and Bioko I.), Gabon and Congo and (c) N DR Congo. *Paraxerus poensis* is the only small, greenish arboreal squirrel in its geographic range.

Habitat Lowland evergreen moist rainforests, secondary forest and tangles. Often seen in farmlands and plantations (Rosevear 1969).

Abundance Frequently seen.

Adaptations Diurnal and arboreal. Green Bush Squirrels are morphologically adapted for arboreal life, with short limbs and short, broad feet with strong, curved claws. Most observations

suggest they prefer vegetation above 5 m (Emmons 1980). Nests are undescribed; anecdotal reports suggest that Green Bush Squirrels build arboreal, exposed, leaf nests (Emmons 1979a) or nest in tree hollows (Rosevear 1969). In captivity, nest boxes were lined with finely teased fibres (Emmons 1975).

Foraging and Food Omnivorous. Forages arboreally. Six of 12 observations of foraging behaviour in the wild were of insect hunting by intense searching of stems, bark and arboreal crannies. In Gabon, the diet is mainly fruit and seeds (88% dry mass of stomach contents, $n = 8$) and arthropods (11%). The arthropods eaten are a miscellaneous mixture as might be expected from random searching (Emmons 1975, 1980). In captivity, Green Bush Squirrels were adept at capturing flying insects, which they pursued eagerly, and they opened and ate the eggs of small birds (Emmons 1975).

Social and Reproductive Behaviour Usually seen singly (68%, $n = 44$) or in pairs (18%) (Emmons 1980). The social organization is undescribed, but in captivity heterosexual pairs housed together showed extreme cohesion and many bonding behavioural characteristics (e.g. always sharing a nest box, grooming each other, resting in physical contact). After ♀ gave birth, ♂ continued to share the nest box and showed strong parental behaviour towards young when they emerged. Female showed no aggression towards ♂ at parturition or any other time (L. Emmons, unpubl.). These behaviours suggest that these squirrels live in monogamous pairs.

Vocalizations are described in detail in Emmons (1978). The single type of alarm call is a loud buzz composed of about 25 pulses emitted in a one-second burst; pulses are so close together that they are indistinguishable to the human ear. Calls are emitted singly, but can be repeated more than 100 times. The alarm call is always associated with a highly stereotyped visual display in which the squirrel sits, stands, or moves along a branch with the tail held out stiffly behind, its tip curved upward. While it emits a call, the squirrel freezes, then immediately jerks the tail sharply upward until its base is nearly vertical, maintaining a stiff C-shape. As the tail goes up, the hindfeet alone, or both fore- and hindfeet, are hopped or stamped, often moving the body slightly forward. The tail then relaxes to the horizontal and the display may be repeated (see also *Heliosciurus rufobrachium*).

Reproduction and Population Structure Litter-size: 1–2, with more litters of one than of two (Emmons 1979a).

Predators, Parasites and Diseases No information.

Conservation IUCN Category: Least Concern.

Measurements

Paraxerus poensis

HB: 153 (148–161) mm, $n = 5$

T: 160 (150–165) mm, $n = 5$

HF: 33 (30–35) mm, $n = 5$

E: 13 (11–15) mm, $n = ?^*$

WT: 104.5 (101–114) g, $n = 4$

GLS: 38.5 (37.7–39.1) mm, $n = 3$

GWS: 21.4, 21.7 mm, $n = 2$

P^3 – M^3 : 6.5 (6.3–6.9) mm, $n = 4$

Gabon (Emmons 1975, L. Emmons unpubl.)

*Rosevear 1969

Key References Emmons 1978, 1980; Rosevear 1969.

Louise H. Emmons

***Paraxerus vexillarius* SWYNNERTON'S BUSH SQUIRREL**

Fr. Écureuil de brousse de Kershaw; Ger. Lushoto-Buschhörnchen

Paraxerus vexillarius (Kershaw, 1923). Ann. Mag. Nat. Hist., ser. 9, 11: 591. Lushoto, Wilhelmsthal, Usambara, Tanzania.

Taxonomy Originally described in the genus *Funisciurus*. It is possible that the two forms, *vexillarius* and *byatti*, given here as subspecies, are valid species (e.g. as in Allen 1939 and Ellerman 1940). Amtmann (1975) regarded them as forms of *P. vexillarius* and also commented that they may be distinct species. Inexplicably, Kingdon (1974) treated *P. byatti* as a subspecies of *P. lucifer*. See Allen and Loveridge (1933). Synonyms: *byatti*, *laetus*. Subspecies: two. Chromosome number: not known.

Description Large squirrel with grizzled brownish dorsal pelage and sometimes with rufous-orange tip to tail. Dorsal pelage olive-green to brown, grizzled. Ventral pelage dove-grey. Limbs and feet rufous-orange. Tail long (ca. 85% of HB), brown and whitish rings at base, bright orange at tip; hairs at base banded black and white. Skull: cheekteeth $5/4$; posterior end of bony palate in line with posterior end of M^3 ; masseteric tubercle not prominent. Nipples: not known.

Geographic Variation

P. v. byatti: Mt Kilimanjaro, Tanzania. Very similar to *P. v. vexillarius*, but described as being more ochraceous-buff on the back and darker ventrally. This name is usually attributed to animals throughout the range of *P. vexillarius* lacking an orange tail tip, a condition found only among some individuals of the Usambara population, as suggested in the original description of *P. vexillarius*. Perhaps this subspecies should not be recognized.

P. v. vexillarius: Usambara, Uluguru and Uzungwa Mts, Tanzania. Dorsal pelage grizzled brown, greyer on the sides, and dull rufous on the flanks and outside of thighs; arms and shoulders dark rufous, fore- and hindfeet tawny-ochraceous. Tail coloured like back for proximal one-fifth of its length; distally more buff; hairs sometimes tipped more white. Rufous on nose, around mouth, and a broad streak running through the eye to the ear. This name is



Paraxerus vexillarius

usually attributed only to animals with an orange tail tip, but this is probably a local variation within the Usambara population of *P. vexillarius*, as noted by Kershaw (1923).

Similar Species

P. palliatus. Rufous or orange ventral pelage; more widespread distribution.

P. lucifer. Predominantly rufous with black dorsal patch; limited distribution in S Tanzania and N Malawi.



Paraxerus spp., pelage colours. Left to right: *P. cooperi*, *P. lucifer*, *P. palliatus*, *P. poensis* and *P. vexillarius*.

Distribution Endemic to Africa. Afromontane–Afroalpine BZ. Mountains of NE to S Tanzania (details as above).

Habitat Montane forest.

Abundance No information.

Remarks Arboreal. Feeds on fruits and seeds.

Conservation IUCN Category: Near Threatened.

Survival of this species is threatened because the montane forests of the Usambara Mts are being fragmented and are decreasing in area as a result of expanding agriculture.

Measurements

Paraxerus vexillarius

HB: 230 (190–264) mm, n = 4

T: 195 (180–210) mm, n = 4

HF: 49.7 (45–52) mm, n = 4

E: 18, 15 mm, n = 2

WT: n. d.

GLS: 54, 53 mm, n = 2

GWS: 33.6, 31 mm, n = 2

P³–M³: n. d.

Tanzania (*P. vexillarius* type specimen and *P. v. byatti* type specimen [Kershaw 1923]; USNM [2])

Key References Kingdon 1974, 1997.

Richard W. Thorington, Jr & Chad E. Schennum

Paraxerus vincenti VINCENT'S BUSH SQUIRREL (SELINDA MOUNTAIN SQUIRREL)

Fr. Écureuil de brousse de Vincent; Ger. Vincents Buschhörnchen

Paraxerus vincenti Hayman, 1950. Ann. Mag. Nat. Hist., ser. 12, 3: 263. Namuli Mountain, Mozambique. 5000 ft (= 1500 m).

Taxonomy Classified as a subspecies of *Paraxerus palliatus* by Kingdon (1994, 1997), but considered here to be a valid species because of its very limited distribution and its isolation from all subspecies of *P. palliatus*. *Paraxerus vincenti* is closely related to three other species, *P. lucifer*, *P. palliatus* and *P. vexillarius*. Synonyms: none. Chromosome number: not known.

Description Medium-sized squirrel very similar to *Paraxerus palliatus ornatus*. Dorsal pelage blackish, grizzled. Ventral pelage rich rufous. Crown of head and cheeks darkish-brown, rufous around eye and nasal region. Fore- and hindlimbs and upper surfaces of feet similar to dorsal pelage. Tail long (ca. 100% of HB), blackish-brown tipped with rufous; hairs black at base, rufous at tip. Skull: cheekteeth ⁵/₄; posterior end of bony palate in line with posterior end of M³; masseteric tubercle not prominent. Nipples: not known.

Geographic Variation None recorded.

Similar Species

Paraxerus spp. Ventral pelage less intense and less bright. Hayman (1950) noted that *P. palliatus* has 'brick-red' ventral pelage whereas in *P. vincenti* is rich rufous.

Distribution Endemic to Africa. Afromontane–Afroalpine BZ. Recorded only from Namuli Mountain, N Mozambique (15°21' S, 37°04' E).

Habitat Moist evergreen forests (Viljoen 1989).

Remarks Apparently no other information available.

Conservation IUCN Category: Endangered.



Paraxerus vincenti

Measurements

Paraxerus vincenti

HB: 212 ± 5.9 mm, n = 5

T: 209 ± 8.9 mm, n = 5

HF: 46.6 ± 2.0 mm, n = 5

E: 21.1 ± 0.6 mm, n = 5

WT: n. d.

GLS: 50.4 ± 0.4 mm, n = 5

GWS: 29.8 ± 0.3 mm, n = 5

P³–M³: n. d.

Mozambique (Viljoen 1989)

Measurements given as mean value \pm 1 S.D.

Key References Hayman 1950; Viljoen 1989.

Richard W. Thorington, Jr & Chad E. Schennum

GENUS *Protoxerus* Forest Giant Squirrel

Protoxerus Forsyth Major, 1893. Proc. Zool. Soc. Lond. 1893: 189. Type species: *Sciurus stangeri* Waterhouse, 1842.

Monotypic genus. A very large tree squirrel with a wide distribution in the Rainforest BZ and some adjacent rainforest relicts in the Rainforest–Savanna Mosaics. The single species *Protoxerus stangeri* lives in the upper storeys of rainforest, feeds primarily on nuts and fruits, and tends to be solitary.

The genus is characterized by very large size (HB 270–306 mm) and long tail, about the same length as the head and body. The pelage is longer and denser than in *Heliosciurus* spp., and the hairs have three or five bands, which result in a strongly speckled effect. Flanks without longitudinal stripes. The ventral surface is mostly hairless. The tail is long and bushy, and about as long as HB; each hair with 7–9 bands and white at the tip on the dorsal and lateral sides. Females have four pairs of nipples (as in *Epixerus*); ♂♂ have large baculum. The skull is characterized by large size (66–73 mm in length) and is larger than in any other African squirrel; four upper cheekteeth; supraorbital notch closed on margin of orbit forming a foramen piercing the frontal bone; posterior end of bony palate in line with posterior end of M^3 ; anterodorsal process of premaxilla rises to abut evenly with anterolateral angle of nasal; pronounced masseteric ridge; and masseteric tubercle absent or very small (Figure 15).

Protoxerus forms a monophyletic clade with *Heliosciurus*, *Allosciurus* and *Epixerus* (Moore 1959). *Protoxerus* resembles the related genera *Heliosciurus*, *Allosciurus* and *Epixerus* in relative length of tail; differs from *Heliosciurus* but agrees with *Epixerus* in having a small masseteric tubercle (absent in some individuals) and four pairs of nipples. *Protoxerus* also resembles *Epixerus* in speckled pelage of upperparts, contrasting sparse pelage of underparts and banded pattern of tail.

Some authors have allocated *Allosciurus* to *Protoxerus* as a synonym or subgenus (Moore 1959, Amtmann 1966, Thorington & Hoffman 2005), though in many features, *Protoxerus stangeri* is more similar to *Epixerus* than to *Allosciurus*. *Protoxerus* and *Allosciurus* have not been recorded to share derived character-states absent in other squirrels, so are not demonstrably sister-taxa. *Epixerus ebii* has sometimes been misidentified as *Protoxerus stangeri* but their skulls have been compared in considerable detail, and can be readily distinguished. For differences between *Protoxerus* and *Allosciurus*, see *Allosciurus* genus profile.

Peter Grubb



Protoxerus stangeri.

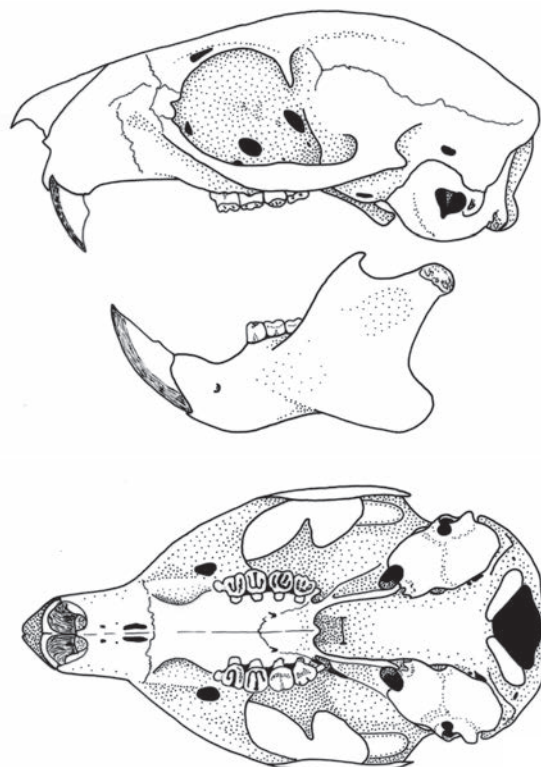


Figure 15. Skull and mandible of *Protoxerus stangeri* (RMCA 16124).

***Protoxerus stangeri* FOREST GIANT SQUIRREL (AFRICAN GIANT SQUIRREL)**

Fr. Écureuil géant de Stanger; Ger. Afrikanisches Riesenhörnchen

Protoxerus stangeri (Waterhouse, 1842). Proc. Zool. Soc. Lond. 1842: 127 (publ. 1943). Fernando Poo (= Bioko I., Equatorial Guinea).

Taxonomy Originally described in the genus *Sciurus*. This species shows considerable geographic variation, which has resulted in 19 named forms; 11 of these may be considered as subspecies (Amtmann 1975, Thorington & Hoffman 2005), although the validity of these subspecies is uncertain. Synonyms: *bea*, *calliurus*, *caniceps*, *centricola*, *cooperi*, *dissonus*, *eborivorus*, *kabobo*, *kwango*, *loandae*, *moerens*, *nigeriae*, *nordhoffi*, *notabilis*, *personatus*, *signatus*, *subalbidus*, *temmincki*, *torrentium*. Subspecies: 11. Chromosome number: not known.

Description Very large long-bodied squirrel with very long ringed tail; the largest African arboreal squirrel. Pelage short and stiff. Dorsal pelage medium brown, grizzled with yellow or buff; hairs banded, black at base, yellow or buff on terminal half, with black tip; some hairs have five alternating dark-pale bands. Ventral surface naked yellow skin; almost hairless. Head large and rounded with conspicuously large cheek muscles. Crown and nasal region of head similar to back except terminal half of hairs are white, giving a frosted appearance to the head. Cheeks thinly haired showing yellow skin below and behind eye; ears short, nearly naked, yellowish. Chest usually white. Limbs and feet short and robust. Tail long (ca. 100% of HB), extremely bushy, mostly black and white; hairs long with 7–9 bands of black and white, with white tips, which result in pale (but sometimes obscure) rings along the length of the tail; undersurface of tail varied, black and white, but not always forming rings. Tail carried straight out behind the body during locomotion, and hangs below body while squirrel is at rest; not normally curled against back. Skull and mandible large and heavily built; cheekteeth $4/4$; posterior end of bony palate in line with posterior end of M^3 ; supraorbital ridge with small foramen; pronounced masseteric ridge; masseteric tubercle inconspicuous or absent. Females slightly larger, on average, than males. Nipples: 1 + 1 + 1 + 1 = 8.

Geographic Variation Amtmann (1975) lists 11 subspecies, as follows, without comment:

- P. s. bea*: Kakamega Forest, Kenya.
- P. s. centricola*: between Congo and Oubangui rivers, DR Congo; forest relics in Uganda; Mt Kungwe, Tanzania; Equatoria District, S Sudan.
- P. s. eborivorus*: E Nigeria south to Ogooué R., Gabon, and east to Oubangui R., DR Congo.
- P. s. kabobo*: Montane forests of Mt Kabobo, E DR Congo.
- P. s. kwango*: near Kasonga Lunda, Bandundu Province, SW DR Congo.
- P. s. loandae*: N Angola.
- P. s. nigeriae*: between Volta R., Ghana and Niger R., Nigeria.
- P. s. personatus*: between Ogooué R., Gabon and Congo R., DR Congo.
- P. s. signatus*: between Congo R. and Kasai R., DR Congo.
- P. s. stangeri*: Bioko I.
- P. s. temmincki*: Sierra Leone to Volta R., Ghana.

*Protoxerus stangeri***Similar Species**

Epixerus ebii. Reddish head, slender body, long legs; ventral surface with yellow skin; mostly terrestrial.

Heliosciurus spp. Smaller, crown the same colour as back, tail slender, ventral surface well haired, without visible yellow skin; arboreal.

Distribution Endemic to Africa. Widely distributed in the Rainforest BZ and Rainforest–Savanna Mosaics from Sierra Leone to the Kavirondoro district of Kenya, and from N Angola to N Tanzania. Recorded from N Angola, Cameroon, Central African Republic, Congo, Côte d'Ivoire, Equatorial Guinea (Rio Muni and Bioko I.), Gabon, Ghana, W Kenya, Liberia, Nigeria, Sierra Leone, N Tanzania, Togo, Uganda and DR Congo.

Habitat Lowland evergreen rainforest and rainforest outliers, mostly at lower altitudes. Within this area, occupies many forest types including tall mature forests, secondary forests, plantations and gardens with trees.

Abundance Common. One of the most abundant and frequently seen species of rainforest squirrels.

Adaptations Diurnal and arboreal, living mostly in the forest canopy and upper vegetation levels (Emmons 1980) but descending to the ground occasionally (J. C. Ray & J. R. Malcolm unpubl.). The short limbs with short, broad palmar and plantar surfaces are suitable for running along large branches and up and down tree trunks

(Emmons 1980). The incisor teeth are robust, and the masseter muscles are massive, as befits its diet of hard nuts (see below). A prominent glandular pocket in the inside corner of the lips may be used in scent marking.

Forest Giant Squirrels nest in tree hollows and favour those with entrances just large enough for the squirrel to squeeze through (mean height 9.3 m; range: 4–17 m; $n = 7$). The nest within the hollow is constructed of twigs with sprays of attached green leaves (Emmons 1975). Animals leave their nests at dawn (range 06:00–06:08h); in Gabon they have a relatively long activity period (mean 10.46 h/day) and return to their nests in the late afternoon or well before dusk (mean entry time 16:33h; range: 15:25–17:55h, $n = 16$; Emmons 1980).

Foraging and Food Primarily vegetarian. In Gabon, feeds mainly on seeds extracted from fruits of trees and lianas, notably from the thick-walled nuts of *Panda oleosa*, *Coula edulis* and species of *Klaineodora*, *Irvingia*, *Elaeis* and many other species. The diet is supplemented by minor amounts of plant vegetative parts (9%) and insects (0.4%) (Emmons 1980). Many of the fruits whose seeds are eaten by Forest Giant Squirrels are primarily dispersed by elephants (Gautier-Hion *et al.* 1980). Ten of 60 observations of feeding in the wild were of insect-hunting behaviour (Emmons 1980), but wild-caught captive Forest Giant Squirrels had little predatory tendency and ignored both live and dead birds, and bird's eggs (Emmons 1975).

Social and Reproductive Behaviour Mostly asocial. Forest Giant Squirrels forage, travel and nest alone; 80% of sightings were of solitary animals, the remainder were either aggressive encounters or mothers followed by young. Individuals appear to avoid each other and can chase conspecifics out of fruiting trees. In captivity, squirrels housed together avoid each other, and there is a complete absence of contact, mutual grooming, chasing, or sharing of nest boxes. Apart from these notes, which suggest a solitary life-style, the social organization is undescribed. An apparent 'mating chase' in which several calling ♂ pursued a presumably oestrous ♀, was seen once by Emmons (1980). Two subadult ♀ (followed by radio tracking) had home-ranges of 3.2 and 5.0 ha (Emmons 1975).

Vocalizations most often heard in the wild are two types of alarm calls: the low intensity alarm consists of repeated soft to loud sniffs or sneezes, sometimes alternating with clicks of the incisors; and the unique, diagnostic, high intensity alarm call is a loud whinny composed

of a mean of 12 modulated pulses that drop in frequency about 300 Hz from beginning to the end of a call, with a mean call duration of 1.3 s. Calls are repeated at intervals of 5–20 s (Emmons 1978). Alarm calls in this species are not accompanied by displays of the tail other than erection of the tail hairs; however, when approaching a strange object, Forest Giant Squirrels may fluff out the tail, raise the base vertically over the back with the tip curled posteriorly downwards, and slowly wave it from side to side (Emmons 1978).

Reproduction and Population Structure There are few records; litter-size seems to be 1–2, with more litters of one than of two (Emmons 1979a). One juvenile (HB 172 mm) in Bwamba, Uganda, in Sep (label, BMNH).

Predators, Parasites and Diseases Preyed upon by eagles and other large raptors. Hunted for its meat where larger game is scarce.

Conservation IUCN Category: Least Concern.

Could be threatened by destruction and fragmentation of rainforest, and by hunting where terrestrial game species are rare.

Measurements

Protoxerus stangeri

HB (♂ ♂): 297 (270–306) mm, $n = 13$

HB (♀ ♀): 300 (294–305) mm, $n = 10$

T (♂ ♂): 271 (250–335) mm, $n = 11$

T (♀ ♀): 317 (300–340) mm, $n = 10$

HF (♂ ♂): 63.7 (61–67) mm, $n = 10$

HF (♀ ♀): 64.0 (60–67) mm, $n = 7$

E: 22 (18–25) mm, $n = ?$ *

WT (♂ ♂): 685 (536–769) g, $n = 13$

WT (♀ ♀): 701 (680–730) g, $n = 8$

GLS: 67.8 (65.9–70.0) mm, $n = 7$

GWS: 37.2 (34.5–38.7) mm, $n = 7$

P⁴–M³: 11.2 (10.5–11.6) mm, $n = 5$

Gabon (Emmons 1975, L. Emmons unpubl.)

*Rosevear 1969

Key References Emmons 1975, 1978, 1980.

Louise H. Emmons

GENUS *Sciurus*

Squirrels

Sciurus Linnaeus, 1758. Syst. Nat., 10th edn., 1: 63. Type species: *Sciurus vulgaris* Linnaeus, 1758.

The genus contains 28 species widely distributed in North America and South America with a few species in Europe, the Middle East, parts of Asia, and Japan. Since the genus is not indigenous to Africa, and is represented by only one introduced species in a limited area

of South Africa, details of genus are not given (see Thorington & Hoffman 2005 for further details). The single species in Africa is *Sciurus carolinensis*.

Sciurus carolinensis GREY SQUIRREL

Fr. Écureuil Gris; Ger. Grauhörnchen

Sciurus carolinensis Gmelin, 1788. In: Linnaeus, Syst. Nat., 13th edn, 1: 148. Carolina, USA.

Taxonomy This profile refers to the species in Africa only. For general information of the species extraliminally to Africa, see Koprowski (1994), Thorington & Hoffmann (2005) and Southern (1964). Chromosome number: $2n = 40$, $FN = 76$.

Description Very large grey squirrel with bushy tail. Hairs rather coarse. Dorsal pelage yellowish-brown or greyish-brown (summer) to silvery-grey (winter); hairs ca. 10 mm; scattered black guard hairs (ca. 15 mm). Often slightly darker (and/or browner) along mid-dorsal region. Ventral pelage paler, usually grey to greyish-white; hairs less dense; ca. 8 mm. Flanks sometimes with rufous streak at junction of dorsal and ventral pelages. Head similar in colour to dorsal pelage. Ears small, rounded; small white or yellow tuft on each ear tip (winter only). Limbs short but moderately long for a

squirrel; similar in colour to dorsal pelage, sometimes with rufous on upper surfaces; digits with well developed claws. Tail long (ca. 75% of HB), densely covered with long hair (typically 30–40 mm, but up to 45 mm); very large and bushy; yellowish-brown, with subterminal black band and white tip (which gives a ‘frosted’ appearance); tail hairs can be flattened or erected depending on mood. When animal is at rest, tail is held horizontally over back, with the tip pointing vertically upwards. Upper tooththrow with five cheekteeth (the anterior tooth being a very small peg-like P^3 , and sometimes absent) (Figure 16). Albino individuals may occur in some populations (Britain and South Africa). Nipples: $1 + 1 + 1 + 1 = 8$.

Geographic Variation None recorded in Africa.

Similar Species

Heliosciurus rufobrachium. Similar in size; pelage much redder; limbs rufous-red.

Distribution Introduced from North America (via Britain) in ca. 1890–1900 by Cecil Rhodes (at Groote Schuur Estate in Cape Town). Confined to a small area of SW Cape Province, South Africa (in the regions of Cape Town, Stellenbosch, Paarl, Elgin, Swellendam and Ceres). Details of the expansion of Grey Squirrels within South Africa are documented by Davis (1950), Millar (1980) and Lever (1985). Natural expansion of this range is unlikely because of the surrounding unsuitable habitat (e.g. fynbos); currently, the species occurs in suitable patches of habitat within an area of ca. 7000 km², and is confined to urban, agricultural and afforested environments (Long 2003). Extraliminally widespread as an indigenous species in the USA and Canada; introduced into Britain, Ireland and to parts of N Italy; also to parts of Victoria State, Australia (1880–1973, but now extinct) (Lever 1985, Long 2003). Map not given.

Habitat Woodlands with suitable food trees including oaks, selected species of pines, eucalypts, acacias etc. May also occur in fruit orchards if suitable woodlands are nearby. Does not occur in monocultures such as pine plantations, nor in indigenous forests.

Abundance No information; tends to be common in suitable habitats in natural distribution and where introduced successfully.

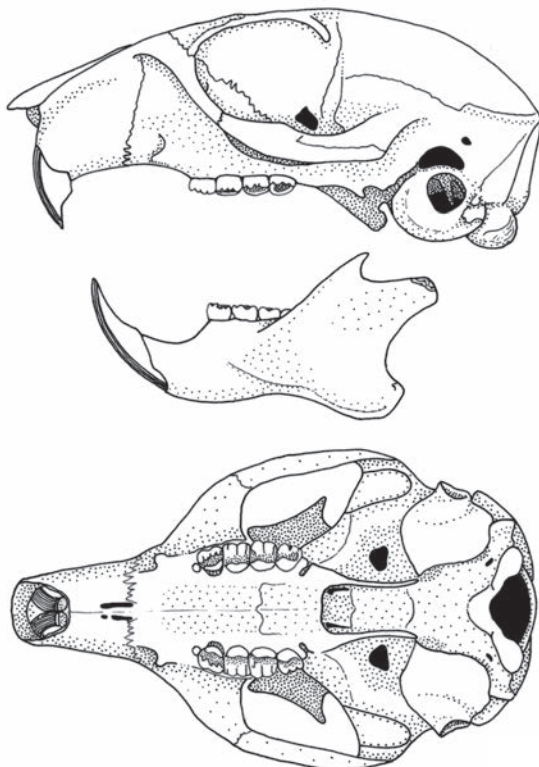


Figure 16. Skull and mandible of *Sciurus carolinensis* (BMNH 2004.96).

Adaptations Diurnal and arboreal, although may descend to the ground to feed and cross small open spaces. Builds spherical nests (dreys) of twigs, 30–60 cm diameter, amongst branches and twigs of trees; may sometimes live in natural cavities in trees. Activity outside nest varies seasonally and is influenced by temperature. In warmer months with longer days, activity is from after dawn until ca. 10:00h and after 16:00h until near dusk; in cooler months with shorter days, activity is mostly between 10:00h and 14:00h (Millar 1980 in Smithers 1983). In the northern hemisphere, Grey Squirrels enter torpor on cold days and do not leave the drey for several days at a time; whether torpor occurs in South African Grey Squirrels is not recorded.

Foraging and Food Herbivorous, mostly frugivorous. Foods in South Africa include acorns, pine nuts and other deciduous fruits. Occasionally omnivorous; feeding, in addition, on bird's eggs, fungi, pollen, insects, bark and leaves (Millar 1980 in Smithers 1983). The majority of the diet is provided by acorns and pine nuts, which together provide a balanced diet of carbohydrate, protein and fat (acorns: protein 4.9%, fat 5%, carbohydrate 84.5%; pine nuts: protein 31%, fat, 47.4%, carbohydrate 11%) (Millar 1980 in Smithers 1983).

Social and Reproductive Behaviour Usually solitary; may occur in small groups (mother and young). May rest in dreys in small groups (especially in cooler weather). Young are born in the dreys.

Reproduction and Population Structure In South Africa, mating occurs in Jul–Aug and in Nov–Dec; young are born in Aug–Nov (spring) and Dec–Feb (summer). Embryo number: 2.5 (1–4, mode 2 and 3). Litter-size tends to be smaller in spring (mean 2.2, $n = 11$) and

larger in summer (mean 2.6, $n = 16$) (Millar 1980 in Smithers 1983). General information from elsewhere: gestation 44 days; young weaned at ca. Week 7; breeding first occurs in second year of life when 11–16 months of age. Females sometimes have two litters per year.

Predators, Parasites and Diseases No information.

Conservation IUCN Category: Least Concern (in northern hemisphere).

Measurements

Sciurus carolinensis

TL: 498 (431–572) mm, $n = 250$

HB: (ca. 282 mm)*

T: 216 (115–269) mm, $n = 250$

HF: 60 (51–67) mm, $n = 179$

E: 25–33 mm**

WT: 579 (434–750) g, $n = 256$

GLS: 59.0 (54.6–62.9) mm, $n = 13$

GWS: 34.2 (32.8–36.1) mm, $n = 12†$

P^3-M^3 : 10.9 (10.1–11.4) mm, $n = 10†$

South Africa (Millar 1980 in Smithers 1983)

*Calculated mean (mean TL – mean T)

**North America; mean and sample size not given (Koprowski 1994)

†Southern England (BMNH); P^4-M^3 where P^3 is absent

Key References Koprowski 1994; Millar 1980; Smithers 1983.

D. C. D. Happold

GENUS *Xerus*

Ground Squirrels

Xerus Hemprich and Ehrenberg, 1833. Symb. Phys. Mamm., vol. 1, sig. Ee, pl. 9. Type species: *Sciurus (Xerus) brachyotus* Hemprich and Ehrenberg, 1832 (= *Sciurus rutilus* Cretzchmar, 1828).

The genus *Xerus* is endemic to Africa, and comprises four species distributed throughout the semi-arid regions of the continent. Placed in the Tribe Xerini (together with *Atlantoxerus*, the only other genus of ground squirrels). Typical habitats are semi-arid desert, grassland and lightly wooded savannas. Only one species, *Xerus princeps*, inhabits rocky, hilly ground.

The genus is distinguished by its bristly fur and small ear pinnae. Skull characteristics include cheekteeth $5/4$ although upper anterior premolar (P^3) very small and often absent in adults; palate long (ca. 62% of occipital-nasal length) with the posterior end of bony palate well posterior to M^3 (as in *Atlantoxerus* and unlike other sciurids); masseteric tubercle very prominent; lachrymal enlarged; jugal joining the lacrimal with a blunt truncation, supraorbital notch small (occasionally absent), posterior end of bony palate well posterior to M^3 , and masseteric tubercle prominent (Figure 17). Dental formula: $I^{1/1}$, $C^{0/0}$, $P^{2/1}$, $M^{3/3} = 22$ (but see also *Xerus erythropus*). There are two pairs of nipples, although *Xerus erythropus* has three pairs (Moore 1961).

Little is known about the biology and reproduction except for *Xerus inauris*. All four species are diurnal, terrestrial and semi-



Xerus erythropus.

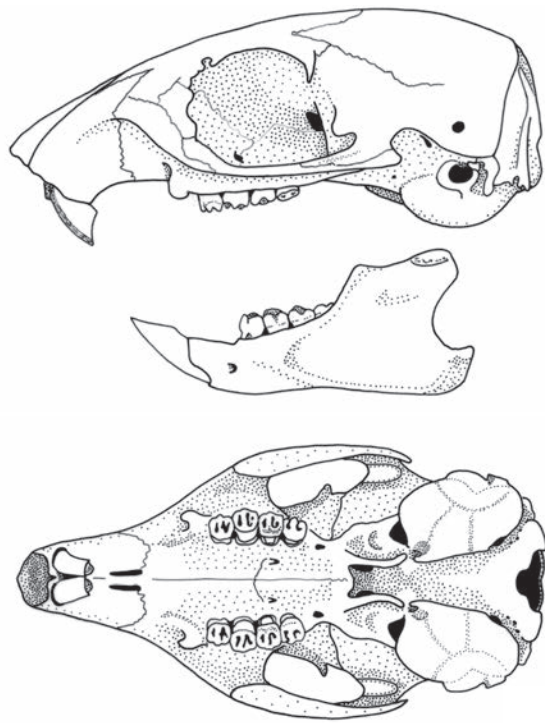


Figure 17. Skull and mandible of *Xerus erythropus* (BMNH 50.21). The first premolar is missing in this specimen.

fossorial. All, except for *X. inauris*, are asocial. Burrows are usually simple, with 2–6 openings. In *Xerus inauris*, groups of ♀♀ maintain complex burrows with multiple burrow openings (up to 60). All four species are mainly herbivorous, feeding on grasses, leaves, fruits and nuts. *Xerus inauris* and *X. rutilus* can breed throughout the year. Litter-size in the genus appears to range from 1 to 6 young/litter.

The genus *Xerus*, together with *Atlantoxerus* and the non-African *Spermophilopsis*, was first placed in the tribe Xerini by Simpson (1945). Nadler & Hoffman (1974) supported the classification of *Xerus rutilus* as a member of the tribe Xerini rather than in a subfamily of its own and subsequently others have supported this classification. The currently recognized species have been described under numerous names, resulting in a long list of synonyms. The genus was split into two subgenera, *Euxerus* and *Geosciurus*, by Simpson (1945). Moore (1959), following Pocock (1923), supported Simpson's classification; however, Moore suggests that *Euxerus* might deserve elevation to generic status. The genus is currently considered to contain three subgenera: *Euxerus* (*X. erythropus*), *Geosciurus* (*X. inauris*, *X. princeps*) and *Xerus* (*X. rutilus*) (Ellerman 1940, Moore 1959, Amtmann 1975, Thorington & Hoffman 2005).

The species are distinguished on the presence or absence of a lateral side-stripe, the number of dark bands on tail hairs, presence or absence of an extra premolar (P^3) in the skull, and the colour of the front incisors.

Jane M. Waterman

***Xerus erythropus* STRIPED GROUND SQUIRREL (AFRICAN GROUND SQUIRREL,
WEST AFRICAN GROUND SQUIRREL, GEOFFREY'S GROUND SQUIRREL)**

Fr. Écureuil fouisseur du Sahel; Ger. Gestreiftes Erdhörnchen

Xerus erythropus (E. Geoffroy, 1803). In: Cat. Mamm. Mus. Hist. Nat., Paris, p. 178. Unknown, but neotype given as Senegal.

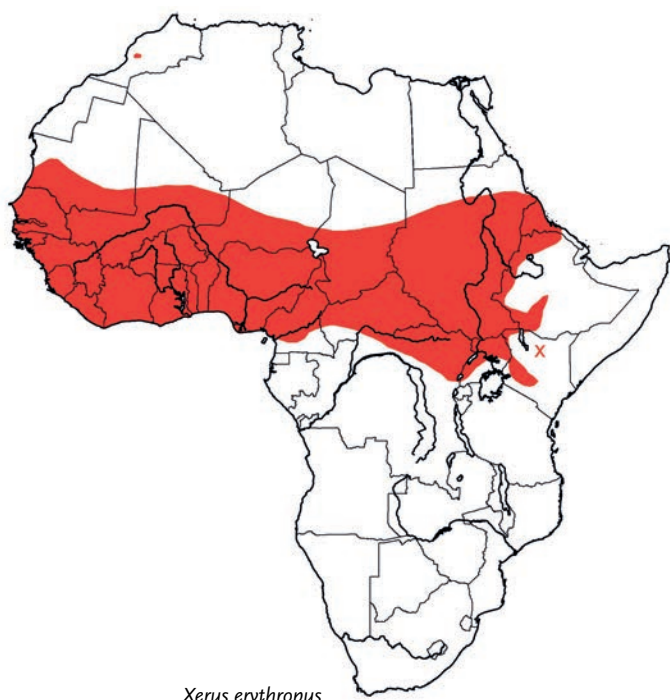
Taxonomy Originally described in the genus *Sciurus* and later placed in either the genus *Euxerus* or *Xerus*. *Euxerus* is now considered to be a subgenus by most authors. The species name was first cited as *erythropus* [sic] but the emended spelling is now accepted (see Grubb [2004] for a discussion of the specific name). For general account, see Herron & Waterman (2004). Synonyms: *agadius*, *albovittatus*, *chadensis*, *fulvior*, *lacustris*, *lessoni*, *leucoumbrinus*, *limitaneus*, *maestus*, *marabutis*, *microdon*, *prestigiator*. Subspecies: five. Chromosome number: $2n = 38$ (Dobigny *et al.* 2002b).

Description Large terrestrial squirrel with coarse pelage. Hairs sparse, especially on ventral surface; black skin underlying hairs easily visible. Dorsal pelage dark brown to pale cinnamon and sandy-yellow; hairs sandy coloured at base, sometimes with black or brown tip. Most geographical variation in colour is due to colour of hair tip (see below). Ventral pelage white or pale. Conspicuous white side-stripe on each flank. Head with narrow white stripes above and below the eyes. Ears small and rounded. Limbs and feet paler than dorsal pelage. Tail moderately long (ca. 80% of HB), dorsoventrally flattened, hairs long, with alternating black and white bands; hairs project vertically from tail to form large brush. Males slightly larger than females. Skull: cheekteeth $5/4$ (anterior upper premolar (P^3) may be shed in some

adults so cheekteeth $4/4$); posterior end of bony palate considerably posterior to M^3 ; masseteric tubercle prominent; outer surface of incisor teeth orange. Nipples: $0 + 0 + 1 + 2 = 6$.



Xerus erythropus.



Geographic Variation Many forms of *X. erythropus* have been recognized, all based on differences in pelage colour. Amtmann (1975) and Thorington & Hoffman (2005) recognized six subspecies, and Rosevear (1969) recognized five subspecies. Populations in high to moderate rainfall areas are dark rufous-brown or dark chocolate-brown, those in arid regions are pale oatmeal or sandy; all shades of pelage colour between these extremes are recorded from areas of intermediate rainfall. Six subspecies, of uncertain validity, are listed here.

- X. e. chadensis*: Lake Chad (N Nigeria, W Chad, N Cameroon) and W Sudan. Dorsal pelage buff to creamy-buff. Paler than other subspecies.
- X. e. erythropus*: mainly Sahel Savanna BZ, from Senegal to S Mauritania to NE Nigeria (and perhaps further east). Also SW Morocco. Dorsal pelage pale reddish-brown to sandy-yellow; some hairs on back have black tips.
- X. e. lacustris*: NE DR Congo and Uganda. The darkest brown subspecies. Rosevear (1969) suggests that this subspecies is the same as *X. e. maestus* (see Taxonomy).
- X. e. leucombrinus*: Sudan Savanna BZ from Senegal to Ethiopia, including NW Kenya. Dorsal pelage dark red-brown.
- X. e. limitaneus*: W Sudan. Dorsal pelage similar to *leucombrinus*, darker than *chadensis*. Said to be larger than *leucombrinus* and *chadensis*.
- X. e. microdon*: Rosevear (1969) suggests this subspecies ranges from Senegal to Kenya but Amtmann (1975) suggests it only occurs in SW Kenya. Dorsal pelage dark brown. Rosevear (1969) questions the validity of subspecific status for this form, suggesting that it is the same as *X. e. leucombrinus*.

Similar Species

X. rutilus. Smaller body size; side-stripe absent; lacks the extra premolar characteristic of *X. erythropus* (premolar is often shed in adult *X. erythropus*); marginally sympatric in parts of eastern Africa.

Atlantoxerus getulus. Smaller (HB: 165–230 mm; GLS: 38.4–50.0 mm); pelage soft and less coarse; side-stripe on each flank and single mid-dorsal stripe; usually five upper cheekteeth; sympatric in W Morocco, but more widespread in N Africa, including montane habitats, than *X. erythropus*.

Distribution Endemic to Africa. Widespread across sub-Saharan Africa in Sahel, Sudan and Guinea Savanna BZs, and Northern and Eastern Rainforest–Savanna Mosaics, from Senegal and Mauritania to E Sudan. Extends southwards into margins of Rainforest BZ where there is suitable habitat (see below). Small isolated population in W Morocco (near Agadir). Recorded from SW Morocco, S Mauritania, Senegal, Gambia, Guinea-Bissau, Guinea, Sierra Leone, Côte d'Ivoire, S Mali, Burkina, Ghana, Togo, Benin, SE Niger, Nigeria, N Cameroon, NE Congo, S Chad, Central African Republic, Sudan, NE DR Congo, Uganda, Rwanda, Eritrea, W Ethiopia (except montane regions) and W Kenya. Unconfirmed record in N Tanzania.

Habitat Open habitats in semi-desert, grassland savannas, woodland savannas and coastal scrub, and also in grassy clearings in the Rainforest–Savanna mosaic and the northern edge of the Rainforest BZ. Lives in rocky areas, tree root crevices, termite mounds and self-dug burrows.

Abundance Common. Densities not known.

Adaptations Diurnal and terrestrial. Burrows consist of a central chamber and about three entrance tunnels, and are simpler than those of *X. inauris*. During the heat of the day, Striped Ground Squirrels move into areas of shade or shelter in their burrows. They also press the ventral surface of the body on shaded or cool sand as a means of losing body heat (Ewer 1966, Linn & Key 1996).

Foraging and Food Herbivorous. Feeds mainly on leaves, flowers, roots, seeds, soft fruits, and nuts. The diet may also include insects (especially termites) and meat (Ewer 1966). Food in much of the habitat is patchy and unpredictable, and hence individuals tend to forage alone. Striped Ground Squirrels are scatter hoarders, burying food well away from the burrow entrances (Ewer 1966, 1968). In some regions they are regarded as a pest because of their consumption of maize (Key 1990).

Social and Reproductive Behaviour Asocial. Adults usually live singly or in small family groups. Interactions between individuals are usually brief – two individuals approach and touch nasal areas and then move on. Overt aggression is rare. Often during a meeting, one individual is submissive and the other dominant, but detailed information on these interactions is lacking (Linn & Key 1996).

In an area of periodic drought, when resources were very patchy, home-range size of three ♀♀ averaged 12.4 ha. In an area of higher rainfall, home-range of a single ♀ was 3.34 ha and for four ♂♂ was 9.43 ha. Individuals forage widely within the home-range and often do not return to the same sleeping burrow each night. Home-ranges overlap considerably between conspecifics and there is no evidence of territoriality. Very tolerant of conspecifics and even burrows are not defended from visitations by a succession of other individuals (Linn & Key 1996).

Nothing is known about mating behaviour, although mating chases have been noted (Linn & Key 1996). Young animals participate in

social play but this decreases as they reach maturity. Vocalizations are rare. Juveniles emit distress calls and individuals will give alarm calls while running toward the burrow if they are threatened. Scent marking by rubbing cheek glands on objects has been described as more common in ♀♀ than ♂♂ (Ewer 1966, 1968).

This species appears to be displacing *X. rutilus* in parts of Kenya, possibly because it is more aggressive and larger (Key 1990); however, O'Shea (1976) reported that the two species share burrows.

Reproduction and Population Structure Almost nothing is known about reproduction and growth. Probably breeds prior to one year of age (Ewer 1966). Litter-size: usually 4 (2–5). Eyes open ca. Day 26. First moult ca. Day 55. Eat solid food ca. Week 5 (Ewer 1966). May live up to six years in captivity (Kingdon 1974).

Predators, Parasites and Diseases Major predators include hawks, eagles, snakes (especially Puff Adder *Bitis arietans*), servals, wild cats and jackals (Kingdon 1974). Can harbour a number of diseases, including *Streptobacillus moniliformis*, which causes rat-bite fever (Linn & Key 1996), *Trypanosoma (Herpetosoma) xeri* (Marinkelle & Abdalla 1978) and many species of ticks.

Conservation IUCN Category: Least Concern.

Unlikely to be threatened because of widespread distribution and commonness.

Measurements

Xerus erythropus

HB (♂♂): 259 (160–390) mm, n = 45

HB (♀♀): 250 (193–430) mm, n = 48

T (♂♂): 200 (124–269) mm, n = 47

T (♀♀): 197 (138–226) mm, n = 48

HF (♂♂): 67 (51–75) mm, n = 48

HF (♀♀): 66 (47–75) mm, n = 48

E (♂♂): 16 (7–24) mm, n = 46

E (♀♀): 17 (7–19) mm, n = 45

WT (♂♂): 513 (346–750) g, n = 26

WT (♀♀): 429 (226–565) g, n = 30

GLS: 60.8 (57.4–65.7) mm, n = 127

GWS: 32.4 (30.7–34.5) mm, n = 17

P³–M³: 12.1 (10.9–13.5) mm, n = 17

Body measurements and weight: throughout geographic range (USNM)

Skull measurements: throughout geographic range (BMNH). In those specimens (7 of 17) that do not have the very small P³, the measurement is P⁴–M³

Key References Ewer 1966; Kingdon 1974; Linn & Key 1996; Rosevear 1969.

Jane M. Waterman

Xerus inauris CAPE GROUND SQUIRREL (SOUTH AFRICAN GROUND SQUIRREL)

Fr. Écureuil fousseur du Cap; Ger. Kaperdhörnchen

Xerus inauris (Zimmermann, 1780). Geogr. Gesch. Mensch. Vierf. Thiere 2: 344. 160 km north of Cape of Good Hope, South Africa.

Taxonomy Originally described in the genus *Sciurus*. Previously allocated to the genera *Sciurus*, *Myoxus*, *Geosciurus* and *Xerus*. Subgenus *Geosciurus*. *Xerus inauris* is considered to be a separate species from *X. princeps* based on minor chromosomal differences and morphological studies (Robinson *et al.* 1986, Herzig-Straschil *et al.* 1991). For a general account, see Skurski & Waterman (2005). Synonyms: *africanus*, *albovittatus*, *capensis*, *dschinshicus*, *gininianus*, *levaillantii*, *namaquensis*, *setosus*. Subspecies: none. Chromosome number: 2n = 38 (Robinson *et al.* 1986).

Description Large terrestrial squirrel with white side-stripes and very small ears (hence the name *inauris*). Hairs sparse and short; dark skin underlying hairs easily visible. Dorsal pelage pale cinnamon-brown; hairs sandy with small white tip; some longer hairs with black tip. Conspicuous white side-stripe from shoulders to hips. Ventral pelage off-white or pale yellowish-white. Eyes large, with dull white stripe above and below each eye, extending anteriorly to nostrils. Testes on ♂♂ large, approximately 19.8% of HB. Forelimbs short, sandy above, off-white below; forefoot with four digits, each with long dark claw. Hindlimbs sandy; hindfoot off-white above, naked below; five digits, each with long dark claw. Tail moderately long (ca. 85% of HB), dorsoventrally flattened; hairs long (ca. 50–60 mm), banded, each hair white with two black bands (short blackish-brown band near base, long black band near tip) and long white tip. Skull: cheekteeth ⁵/₄; posterior end of bony palate considerably posterior

to M³; masseteric tubercle prominent; outer surface of incisor teeth white. Nipples: 0 + 0 + 1 + 1 = 4.

Geographic Variation None recorded.

Similar Species

X. princeps. Incisor teeth orange; tail hairs white with three black bands; tail comparatively longer; marginally sympatric in W Namibia.

Distribution Endemic to Africa. Widespread in semi-arid regions of southern Africa. South-West Arid BZ (Kalahari Desert, Namib Desert and Karoo) and western part of Highveld BZ. Recorded from C South Africa, Botswana, W Lesotho and Namibia. Not recorded from coastal Namibia.

Habitat Open semi-arid regions where mean annual rainfall is 125–500 mm. Preferred habitat is hard ground with some scrub cover along the edges of pans, river beds and open sandy veld; also recorded from short grasslands, overgrazed areas and cultivated fields. In Namibia, areas with short annual grass (*Schmidtia kalahariensis*) are preferred, and areas with longer perennial grasses are avoided.

Abundance Common. In the Kalahari region of SE Namibia, density is 3–4/ha, with approximately 1.2 adult ♀♀/ha, 1.3 adult ♂♂/ha and 1.3 subadults/ha (Waterman 1995). In drought years,

*Xerus inauris*.

density declines significantly (Waterman & Fenton 2000). Probably live in higher densities in areas with higher rainfall, but no comparable data available.

Adaptations Diurnal and terrestrial. Cape Ground Squirrels dig their own complex burrows, which may be 60–80 cm deep, with 60 or more burrow openings within a cluster of burrows and more than one nest chamber in a burrow system (Herzig-Straschil 1978). When digging, the nostrils can be closed. During the heat of the day, the tail is orientated towards the direction of the sun while held up over the body, providing shade on the back and head. Cape Ground Squirrels also use their burrows as thermal retreats (Bennett *et al.* 1984). Their kidneys have a thick medulla, and urine concentrations are high. Hence squirrels can survive largely on metabolic water, without the need for free drinking water (Marsh *et al.* 1978).

Foraging and Food Primarily herbivorous, also omnivorous. The diet consists of leaves, sheaths and roots of grasses, as well as seeds, fruit and insects. Preferred foods in central South Africa include the grasses *Cynodon dactylon* and *Enneapogon brachystachyus*, while in SC Namibia and the Kalahari National Park their diet includes the grasses *Schmidtia kalahariensis* and *Eragrostis lehmanniana* (Herzig-Straschil 1978, Knight 1991, Waterman 1996). They will also feed on the berries of *Boscia albitrunca*, *Grewia flava* and the fruits of *Citrullus lanatus*. Insects consumed include termites, beetles, locusts and caterpillars. No evidence of food hoarding has been found when the contents of burrows were examined. They have been blamed for damage to maize crops in southern Africa, but Zumpt (1970) attributed the damage by squirrels as only 0.2–0.4%.

Social and Reproductive Behaviour Social. Females live in matrilineal groups of 1–4 adult ♀♀ and up to nine subadults of either sex (Herzig-Straschil 1978, Waterman 1995). Colonies can be as large as 30 individuals (Smithers 1971) and several groups of ♀♀

*Xerus inauris*

may inhabit a colony or cluster of burrows (Herzig-Straschil 1978). In Namibia, only a single group of ♀♀ inhabits a burrow area. Some studies have indicated that a dominance hierarchy exists amongst ♀♀ (Herzig-Straschil 1978, Knight 1991), but no such hierarchy was observed in a study in Namibia (Waterman 1995). Adult ♂♂ form permanent, non-aggressive groups of up to 19 individuals that live independently of groups of ♀♀ (Waterman 1995, 1997). On a daily basis, ♂♂ form temporary subgroups (4–5 individuals), the size and individual composition of which are constantly changing. While in these subgroups, ♂♂ forage, sleep and roam their home-range together.

Interactions between members of the same group of ♀♀ are primarily amicable, with frequent approaching, greeting and allogrooming. Agonistic interactions within a group are rare (Herzig-Straschil 1978, Waterman 1996). Juveniles interact as amicably with other members of the group as they do with their mothers. Interactions between different groups of ♀♀ are rare and usually agonistic. Agonistic interactions amongst ♂♂ in an all-male groups are also rare, and injury has never been observed. There is a linear dominance hierarchy in the group, which is correlated with age (Waterman 1995, 1997) and determined by non-aggressive displacements, rather than fighting. Interactions between different groups of ♂♂ have not been recorded.

Females in the same social group share sleeping burrows and home-ranges. Home-range area during a normal rainfall year was 4 ha; however during drought, ranges more than doubled in area (Waterman 1995, Waterman & Fenton 2000). There is some overlap of home-ranges of adjacent female social groups but no overlap of core areas between social groups. Females will defend core areas from neighbouring groups of ♀♀ (Herzig-Straschil 1978). Home-ranges of male groups encompass a number of female groups but are not defended against other male groups, and new ♂♂ are accepted into the band without aggression (Waterman 1995). Males forage and roam their home-range together in smaller subgroups, sleeping

together in vacant burrow clusters away from groups of ♀♀, and may join and leave a subgroup on a daily basis, resulting in continuous fission and fusion of subgroups (Waterman 1995, 1997). Average range size of radio-collared ♂♂ was 12.5 ha (Waterman 1995). Herzig-Straschil (1978) found smaller home-ranges for both ♂♂ and ♀♀ in a region with high rainfall. Herzig-Straschil (1978) described single ♂♂ associating with groups of ♀♀ for a few weeks during receptivity. Observations in Namibia and central South Africa suggest members of male subgroups travel together from one female group to another. Male subgroups sleep or stay in an occupied burrow area if a ♀ is coming into oestrus, otherwise they sleep in vacant burrow areas (Waterman 1995, 1997, unpubl.). The majority of ♂♂ from the male group will attempt to mate with the ♀ on her day of oestrus.

Oestrus and parturition were asynchronous within and between groups of ♀♀. The operational sex ratio on a day of oestrus (oestrus lasts about 3 h) averaged ten ♂♂ to a ♀. Mating occurs both above and below ground, and the most dominant ♂ usually has preferential access to the oestrous ♀. Both ♂♂ and ♀♀ mate promiscuously. The large size of the testes of ♂♂ suggests that sperm competition could be an important element of their mating system (Waterman 1998).

All members of the group (mother, other adult ♀♀ and subadult ♀♀ and subadult ♂♂) provide care of juveniles through allogrooming, play and possibly predator detection and deterrence (Waterman 1995, unpubl. data). Knight (1991) reported seeing communal nursing. There is no male parental care.

Cape Ground Squirrels have a number of vocalizations, including a high pitched alarm call that is given when the animal detects a potential threat. They will also respond to the alarm calls of other species, particularly Crowned Plovers and White-browed Sparrowweavers. Other vocalizations include an aggressive growl (used in encounters with conspecifics), a scream (used when released from a trap), a play call (used by young animals), nest-chirping (used in infants) and a protest squeak (Herzig-Straschil 1978). Adult ♂♂ and ♀♀ use secretions from the anal-genital region and the circumoral area for marking. Secretions are deposited by rubbing the body on the sand or by rubbing the snout on an object (Straschil 1975). Marking is most common on emergence from the burrow in the morning. Cape Ground Squirrels frequently share their burrow systems with Yellow Mongooses *Cynictis penicillata* and Suricates *Suricata suricatta*. The three species usually ignore each other and rarely interact (J. Waterman unpubl.).

Reproduction and Population Structure Reproduction occurs throughout the year, with peaks of mating in the dry winter months. Litter loss is high, with some 70% of all oestrus cycles failing to produce successful litters (Waterman 1996). Females can have 1–4 litters per year. Gestation: 7 weeks. Litter-size: 1–4. Body weight at 7 days: 23.5 g (Herzig-Straschil 1978). Mothers lactate for

7.5 weeks. Sex ratio of litters at emergence is 1 : 1. Sexual maturity: 8 months (♂), 10 months (♀). Female maturity is delayed within larger groups of ♀♀ (Waterman 2002).

Dispersal is male-biased. Males disperse at 8–10 months of age, whereas ♀♀ usually remain in their natal group. Adult sex ratio is 1 : 1 and the annual survival of ♂♂ is slightly higher than that of ♀♀ (78% vs. 70%). In captivity, individuals may live up to 13 years but the life-span in the wild is most likely to be 4–5 years. Survival of young to six months of age is negatively influenced by the number in the social group (Waterman 2002). During drought, the social structure remains intact; however, densities drop significantly and all reproductive activity ceases (Waterman & Fenton 2000).

Predators, Parasites and Diseases Major predators include hawks, eagles, snakes, wild cats and jackals. Individuals of a group may mob potential predators such as Cape Cobras *Naja nivea*, Puff Adders *Bitis arietans* and Monitor Lizards *Varanus exanthematicus* (Waterman 1996, unpubl.). Ectoparasites include many species of fleas, ticks and mites (De Graaff 1981). Endoparasites include various helminth worms. Some of these parasites are vectors of human diseases such as plague, enterobiasis, biliary fever, East Coast fever and tick-bite fever (De Graaff 1981 and references therein).

Conservation IUCN Category: Least Concern.

Measurements

Xerus inauris

HB (♂♂): 246 (195–293) mm, n = 88

HB (♀♀): 239 (181–300) mm, n = 134

T (♂♂): 209 (181–282) mm, n = 88

T (♀♀): 206 (160–255) mm, n = 134

HF (♂♂): 69 (63–75) mm, n = 72

HF (♀♀): 67 (45–74) mm, n = 114

E (♂♂): 12 (9–14) mm, n = 28

E (♀♀): 11 (12–14) mm, n = 49

WT (♂♂): 591 (312–822) g, n = 71

WT (♀♀): 565 (367–907) g, n = 84

GLS (♂♂): 56.7 (49.4–60.8) mm, n = 66

GLS (♀♀): 55.3 (43.9–59.5) mm, n = 108

GWS (♂♂): 34.0 (29–38.3) mm, n = 66

GWS (♀♀): 33.8 (26.5–37) mm, n = 106

P³–M³: 11.4 (10.0–12.6) mm, n = 157

Throughout geographic range (USNM, NMN, Waterman 1996, Herzig-Straschil *et al.* 1991)

Key References Skurski & Waterman 2005; Herzig-Straschil 1978; Smithers 1983; Waterman 1995, 1996, 2002.

Jane M. Waterman

***Xerus princeps* DAMARA GROUND SQUIRREL (MOUNTAIN GROUND SQUIRREL, KAOKOVELD GROUND SQUIRREL)**

Fr. Écureuil fouisseur du Damara; Ger. Damara-Erdhörnchen

Xerus princeps (Thomas, 1929). Proc. Zool. Soc., Lond. 1929: 106. Otjitundua, central Kaokoveld, N Namibia.*Xerus princeps*.

Taxonomy Originally described in the genus *Geosciurus*. Minor chromosomal and morphological differences of the skull support *Xerus princeps* as a separate species from *X. inauris* (Robinson *et al.* 1986, Herzig-Straschil *et al.* 1991). For general account, see Waterman & Herron (2004). Synonyms: none. Chromosome number: $2n = 38$ (Robinson *et al.* 1986).

Description Large terrestrial squirrel similar in appearance to *X. inauris*. Hairs sparse, coarse and short; dark skin underlying hairs easily visible. Dorsal pelage cinnamon-brown flecked with white; hairs sandy or dark brown at base, white at tip, which gives the species a more 'grizzled' appearance than *X. inauris*. Conspicuous white side-stripe from shoulders to hips. Ventral pelage white. Eyes large, with dull white stripe above and below each eye extending anteriorly to nostrils. Ears small. Tail long (ca. 99% of HB), dorsoventrally flattened; hairs long (ca. 70 mm), banded, each hair white with three black bands (two short blackish-brown bands near base, long black band near tip) and long white tip. Skull: cheekteeth $5/4$; posterior end of bony palate considerably posterior to M^3 ; masseteric tubercle prominent; outer surface of incisor teeth white or pale orange. Nipples: $0 + 0 + 1 + 1 = 4$.

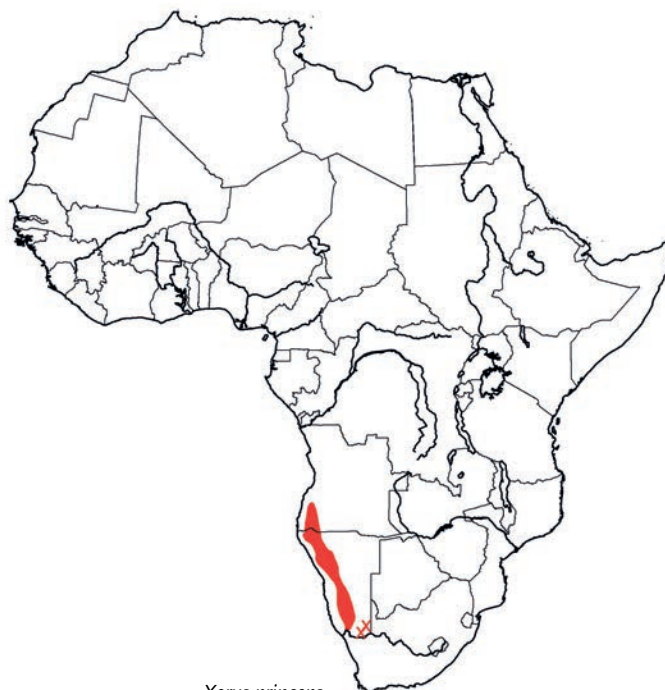
Geographic Variation None recorded.

Similar Species

X. inauris. Incisor teeth white; tail hairs white with two black bands; tail comparatively shorter; distribution more extensive; very social.

Distribution Endemic to Africa. South-West Arid BZ, mainly in the Namib Desert. Recorded from only the narrow band of the western escarpment that runs from SW Namibia north to SW Angola.

Habitat Rocky, hilly ground in arid areas where mean annual rainfall is ca. 125–250 mm (Herzig-Straschil & Herzig 1989). Also recorded on open plains, but prefers habitats with gravel and rocks in areas with single trees or sparse bush cover.

*Xerus princeps*

Abundance Herzig-Straschil & Herzig (1989) suggest that densities are very low. No detailed information.

Adaptations Diurnal and mainly terrestrial. Burrow systems are simple when compared to *X. inauris*, with only 2–5 openings and a single nest chamber (Herzig-Straschil & Herzig 1989). Burrow entrances are usually found under piles of rocks or boulders. Damara Ground Squirrels use the tail as a thermal shade (as described for *X. inauris*) and they are better adapted to survive high temperatures than *X. inauris* (Haim *et al.* 1987). The thermoneutral zone of *X. princeps* is 32–35 °C, and hyperthermy occurs at 35 °C (Haim *et al.* 1987). Salivation was observed at 38 °C. Thermal conductance was high (0.084 ± 0.005 ml O_2 /g/h/ °C), which results in high heat dissipation and water conservation. In comparison with *X. inauris*, the faeces of *X. princeps* are significantly drier ($14.21 \pm 4.2\%$ moisture content) (Haim *et al.* 1987).

Foraging and Food Mainly herbivorous. Feeds on the base of grass stems and roots. In mopane savanna, animals have been observed climbing mopane trees (*Colophospermum mopane*) to feed on plant lice (*Copaijera mopane*) and on mopane leaves (Herzig-Straschil & Herzig 1989).

Social and Reproductive Behaviour Solitary, or small family groups (mother and young) of 2–4 individuals (Haim *et al.* 1987, Herzig-Straschil & Herzig 1989). Adult ♂♂ are associated with some groups but otherwise live solitarily. No allogrooming, playing or other

cohesive behaviours have been documented during the short period of time they have been observed (Herzig-Straschil & Herzig 1989).

Reproduction and Population Structure Little information. Breeding most likely occurs during the winter months. Gestation: ca. 7 weeks. Litter-size: 1–3 (Herzig-Straschil & Herzig 1989).

Predators, Parasites and Diseases Nothing is known about potential predators. The only recorded ectoparasite is a flea (*Ctnocephalides connatus*) (De Graaff 1981).

Conservation IUCN Category: Least Concern.

The limited geographical range and comparative rarity of the species may be cause for concern in the future (Waterman & Herron 2004).

Measurements

Xerus princeps

HB (♂ ♂): 244 (230–280) mm, n = 15

HB (♀ ♀): 239 (235–290) mm, n = 13

T (♂ ♂): 241 (220–260) mm, n = 15

T (♀ ♀): 239 (205–282) mm, n = 13

HF (♂ ♂): 70 (65–75) mm, n = 15

HF (♀ ♀): 71 (68–73) mm, n = 13

E (♂ ♂): 13 (12.5–14) mm, n = 15

E (♀ ♀): 14 (13–15) mm, n = 13

WT (♂ ♂): 572, 716 g, n = 2

WT (♀ ♀): 610, 700 g, n = 2

GLS: 58.2 (54.6–61.4) mm, n = 22

GWS: 35.4 (33.4–37.1) mm, n = 22

P³–M³: 11.2 (10.3–11.9) mm, n = 22

Throughout geographic range

Body measurements and weight: NMN, Skinner & Smithers 1990

Skull measurements: Herzig-Straschil *et al.* 1991

Key References Herzig-Straschil & Herzig 1989; Skinner & Smithers 1990; Waterman & Herron 2004.

Jane M. Waterman

Xerus rutilus UNSTRIPED GROUND SQUIRREL (PALLID GROUND SQUIRREL)

Fr. Écureuil fousseur unicolore; Ger. Streifenloses Erdhörnchen

Xerus rutilus (Cretzschmar, 1828). In: Rüppell's Atlas Reise Nordl. Afr., Zool., Säugeth. p. 59. Eastern slope of Abyssinia, Ethiopia (probably Massawa, Eritrea – see Mertens 1925: 26).



Xerus rutilus.

Taxonomy Originally described in the genus *Sciurus*. Polytypic with up to eight subspecies (Amtmann 1975, O'Shea 1991). For a general account, see O'Shea (1991). Synonyms: *abessinicus*, *brachyotis*, *dabagala*, *dorsalis*, *fuscus*, *intensus*, *massaicus*, *rufifrons*, *saturatus*, *stephanicus*. Subspecies: eight (validity uncertain). Chromosome number: 2n = 38 (Nadler & Hoffmann 1974).

Description Medium-sized terrestrial squirrel with bristly coarse pelage and without side-stripe. Dorsal pelage pale tan to rich reddish-brown with variable amounts of pale and dark speckling; hairs short (ca. 5–6 mm), dark reddish-brown at base, with buff or black tip. Individuals in drier areas tend to be pale. No side-stripe (cf. all other species in genus). Ventral pelage whitish, and paler than dorsal pelage; hairs sparse. Head with conspicuous white or off-white eye-ring. Ear small. Upper surface of fore- and hindfeet white (reddish-brown in some individuals). Tail of moderate length (ca. 86% of HB); hairs long (ca. 40 mm), each hair banded, off-white at base, blackish-brown in middle, with reddish-brown (e.g. Tanzania) or white (e.g. Somalia) at tip. Skull: cheekteeth ⁴/₄; posterior end of bony palate considerably posterior to M³; masseteric tubercle prominent; outer surface of incisor teeth orange. Nipples: 0 + 0 + 1 + 1 = 4.

Geographic Variation The validity of the eight subspecies is dubious (Amtmann 1975). Differences in pelage colouration perhaps only reflect differences in soil colouration rather than taxonomic differences. Populations in drier areas tend to be paler.

X. r. rutilus: N Ethiopia and NE Sudan. Dorsal pelage reddish brown.

X. r. dabagala: Somalia and southern Ethiopia. Dorsal pelage dull to bright rufous or tawny.

X. r. intensus: Gerlogubi Wells; red sandy country of C Somalia. Hairs of crown and dorsal region tipped with white. Tail rufous at base above and white below.

X. r. stephanicus: L. Stephanie, Ethiopia. Dorsal pelage grizzled yellowish-grey.

X. r. rufifrons: Guaso Nyiro, N Kenya. Rufous marking on muzzle extends onto dorsal region of head.

X. r. saturatus: SE Kenya and NE Tanzania. Dorsal pelage with dark reddish tinge.

X. r. dorsalis: L. Baringo, Kenya. Dorsal pelage dark olive, speckled with yellow and white.

X. r. massaicus: Masai Reserve, Kenya. Rufous tinge on forehead, yellow on throat and underparts; skull appears to be larger than in other subspecies.

Similar Species

X. erythropus. Larger body size; side-stripe present; extra premolar (P³) present in some individuals; sympatric in some parts of geographic range.

Distribution Endemic to Africa. Somalia–Masai Bushland BZ. Recorded in NE Sudan, E and S Ethiopia, Djibouti, Eritrea, Somalia,



Xerus rutilus

Kenya, NE Uganda and NE Tanzania. The geographic range appears to be contracting in some areas of Kenya, possibly as a result of competition with the larger more aggressive *X. erythropus* (Key 1990).

Habitat Semi-arid dense thornbush interspersed with open grassland (O'Shea 1991). In South Turkana, Kenya, lives in alluvial flats and gullies and in thickets of *Salvadora persica* (Coe 1972).

Abundance Common. In South Turkana, Kenya, estimated densities may reach 848 individuals/km² or approximately 8.5 individuals/ha (Coe 1972).

Adaptations Diurnal and terrestrial. Burrows are often located at the base of bush stems or in termite mounds, and usually have 2–6 entrances. Unstriped Ground Squirrels may also shelter in the burrows of other mammals (including *X. erythropus* [O'Shea 1976]). In order to prevent overheating, the ventral surface of the body is pressed onto shaded or cool sand (Coe 1972).

Foraging and Food Herbivorous and omnivorous. Feeds on herbaceous plants including seeds, leaves, flowers, soft fruits and the large fruits of baobab trees, as well as insects (Coe 1972, O'Shea 1991). Greater than 50% of stomach contents were found to be small dry seeds and leaves (Coe 1972). Unstriped Ground Squirrels are scatter-hoarders, storing food in many caches (O'Shea 1976).

Social and Reproductive Behaviour Primarily a solitary species, although small family groups (mother and young), and ♂♂ living with one or two ♀♀ are also common (O'Shea 1976). Numbers of individuals sharing a burrow system can range from 1 to 6 (Coe 1972; O'Shea 1976). Individuals of different sexes tend to avoid each other; however, at feeding sites ♂♂ appeared to be dominant over ♀♀, as indicated by chases and displacements. Threat behaviour

includes lunges by the dominant individual, but biting and fighting have not been observed (O'Shea 1976). A number of vocalizations have been noted, including churring vocalizations used by ♀♀ and juveniles when approached by ♂♂, and a scolding chatter given by dominant individuals to subordinates (O'Shea 1976).

Home-ranges of ♂♂ (7 ha) are larger than those of ♀♀ (1.4 ha); home-ranges overlap considerably within and between the sexes. There is no evidence of territoriality but individuals with overlapping home-ranges appear to form a linear dominance hierarchy.

Males court ♀♀ by pilo-erecting the hairs of the tail, arching the tail over the head and approaching the ♀♀. Females usually move away, making quiet vocalizations, flicking the tail rapidly and slightly dragging the perineal region of the body on the ground. When ♂ approaches ♀, she takes a prostrate posture and rolls onto her side allowing ♂ to sniff her anogenital region. The ♂ then mounts the prostrate ♀ (O'Shea 1976). Young are born in burrows, which are usually located at the edge of a female's home-range. Three to four weeks after the juveniles emerge, ♀ returns to the centre of her home-range, away from the juveniles (O'Shea 1976).

Reproduction and Population Structure Almost nothing is known about reproduction and population dynamics. Breeding appears to occur throughout the year. Litter-size: one or two (Kingdon 1974, O'Shea 1991). All young eventually disperse from their natal area (O'Shea 1976). Sex ratio is probably 1 : 1 (Coe 1972). In captivity, a single ♂ has been documented to live for over six years (O'Shea 1991).

Predators, Parasites and Diseases No information on potential predators. Ectoparasites include a tick that is specific to the species (*Haemaphysalis calarata*), and a flea (*Synosternus somalicus*). One cestode (*Catenotaenia geosciuri*) also recorded (O'Shea 1991).

Conservation IUCN Category: Least Concern.

The species does not appear to be threatened at the present time.

Measurements

Xerus rutilus

HB (♂♂): 212 (161–230) mm, n = 6
 HB (♀♀): 215 (168–237) mm, n = 11
 T (♂♂): 185 (153–195) mm, n = 6
 T (♀♀): 185 (145–205) mm, n = 11
 HF (♂♂): 54 (50–60) mm, n = 6
 HF (♀♀): 54 (51–59) mm, n = 11
 E (♂♂): 14 (12–16) mm, n = 3
 E (♀♀): 14 (12–17) mm, n = 4
 WT (♂♂): 325 (135–440) g, n = 3
 WT (♀♀): 313 (155–420) g, n = 3
 GLS: 50.7 (47.1–53.7) mm, n = 17
 GWS: 29.4 (27.0–32.3) mm, n = 17
 P³–M³: 9.3 (8.7–10.0) mm, n = 17

Body measurements and weight: throughout geographic range (USNM)
 Skull measurements: Somaliland (BMNH)

Key References O'Shea 1976, 1991.

Jane M. Waterman

Family GLIRIDAE

DORMICE

Gliridae Muirhead, 1819. Glirini Muirhead, 1819: 433. Mazology [sic]. pp. 393–480, pls. 353–358, in *Edinburgh Encyclopedia*, Vol. 13 (D. Brewster, ed.).

| | | |
|--------------------------------|----------------|--------|
| <i>Eliomys</i> (2 species) | Garden Dormice | p. 104 |
| <i>Graphiurus</i> (14 species) | Dormice | p. 109 |

The nine genera and 28 living species of Gliridae (commonly known as dormice) are currently arranged in three subfamilies and occur in tropical and temperate forests, savannas, steppes and deserts in Africa and the Palaearctic region (Holden 2005). The name Myoxidae is the original name for this family, but the Commission on Zoological Nomenclature (see Holden 2005) has ruled that the name is invalid, and that Gliridae is the valid family name for dormice. The family is divided into three subfamilies: Glirinae, Leithiinae and Graphiurinae (Wahlert *et al.* 1993, Montgelard *et al.* 2003, Holden 2005). The Glirinae contain *Glis*, indigenous to Europe, N Turkey, Caucasus, N Iran and SW Turkestan; and *Glirulus*, endemic to the Japanese islands of Honshu, Dōgo, Shikoku and Kyushu. The Leithiinae contains the genera *Chaetocauda*, *Dryomys*, *Eliomys*, *Muscardinus*, *Myomimus* and *Selevinia*, and is distributed throughout Europe, the Middle East, C and W Asia; the geographic range of *Eliomys* also includes North Africa. The subfamily Graphiurinae contains only *Graphiurus*, and is endemic to sub-Saharan Africa. The family is represented in Africa by *Eliomys* (2 spp.) and *Graphiurus* (14 spp.).

Living glirids range in body size from small to moderately large (HB 60–190 mm) although the maximum HB for nine of the 16 African glirid species is ca. 100 mm. The tail (40–165 mm) is usually moderately long relative to body size, and well-covered with hair throughout its length (in a similar way to the tail of squirrels). Most species have thick, soft dorsal pelage, are predominantly arboreal and resemble small squirrels in body form. Two exceptions are

the non-African *Myomimus* and *Selevinia*, which are terrestrial and have thinly haired tails. Colour of dorsal pelage ranges from pale grey to dark brown. Many species have a narrow or broad dark stripe (eye-mask) extending from the muzzle to the ears; some species exhibit only a thin dark line (eye-ring) encircling the eyes. Colour of ventral pelage is usually grey or white. In several species, especially in *Graphiurus* and the non-African *Glis*, the chin, chest and sometimes forelimbs are discoloured in many individuals; this discolouration is often reddish-brown, but is sometimes pale yellow or yellowish-green (Channing 1984, Nowak 1999, M. E. Holden unpubl.). This discolouration may result from staining that occurs when the dormice ingest insects (such as earwigs) and certain fruits (Chapin [in Hatt 1940a], Rosevear 1969, Nowak 1999), or it may be genetically induced (Channing 1984, B. Kryštufek & R. M. Baxter pers. comm.). All species have rounded ears, large eyes and short fore- and hindlimbs. The forefeet have four digits, the hindfeet have five and the palmar and plantar surfaces are naked. Claws are short and sharp, and those of arboreal species are recurved. The skull is smooth, usually without postorbital processes or supraorbital and temporal ridging. The zygomatic arches are prominent, the anterior palatal foramina are generally short, their posterior margins usually anterior to or even with the front margins of the ventral maxillary zygomatic processes, and the bony palate is long. Auditory bullae are usually large, often appear inflated relative to skull size and are divided internally by bony septae. The infraorbital foramen is moderately tall, ovate and is penetrated by a portion of the anterior medial masseter. The zygomatic plate, from which originates part of the anterior lateral masseter, tilts upwards in all genera (modified or convergent

Table 14. Species in the family Gliridae. Arranged in order of increasing head and body length. (n. d. = no data.)

| Species | HB mean (range) (mm) | T mean (range) (mm) | GLS mean (range) (mm) | Upper toothrow length mean (range) (mm) ^a | Anterior palatal foramina length mean (range) (mm) | |
|----------------------------------|----------------------|---------------------|-----------------------|--|--|--|
| <i>Graphiurus johnstoni</i> | 74.3 (69–84) | 68.5 (65–75.5) | 23.6 (23.3–23.9) | 3.4 (3.3–3.5) | 2.7 (2.6–2.9) | |
| <i>Graphiurus kelleni</i> | 82.4 (75–92) | 68.3 (54–81) | 24.0 (23.1–24.5) | 2.9 (2.8–3.0) | 2.9 (2.6–3.2) | |
| <i>Graphiurus lorrainae</i> | 83.0 (72–93) | 65.7 (54–74) | 24.5 (22.7–26.1) | 3.1 (2.8–3.4) | 2.6 (2.0–3.0) | |
| <i>Graphiurus murinus</i> | 91.5 (81–103) | 76.6 (69–85) | 26.4 (25.2–28.8) | 3.1 (3.0–3.3) | 3.1 (2.7–3.7) | |
| <i>Graphiurus crassicaudatus</i> | 92.6 (83–98) | 59.4 (55–70) | 26.6 (25.2–27.8) | 3.8 (3.4–4.2) | 2.5 (2.3–2.8) | |
| <i>Graphiurus christyi</i> | 97.6 (86–107) | 79.8 (73–95) | 28.0 (26.7–29.7) | 3.2 (3.0–3.3) | 3.0 (2.4–3.3) | |
| <i>Graphiurus microtis</i> | 98.8 (75–115) | 75.2 (62–86) | 27.4 (25.5–29.1) | 3.0 (2.9–3.4) | 3.4 (3.0–3.8) | |
| <i>Graphiurus angolensis</i> | 98.8 (79–112) | 79.2 (70–96) | 28.2 (26.3–30.8) | 3.2 (2.9–3.5) | 3.4 (3.0–3.9) | |
| <i>Graphiurus surdus</i> | 99.0 (87–110) | 72.3 (65–82) | 27.6 (26.5–29.4) | 3.2 (2.9–3.5) | 2.8 (2.5–3.2) | |
| <i>Graphiurus platyops</i> | 107.1 (95–122) | 78.7 (65–98) | 30.4 (28.6–32) | 3.1 (2.8–3.5) | 3.2 (2.7–4.1) | |
| <i>Graphiurus rupicola</i> | 110 (105–119) | 104.2 (96–118) | 31.3 (30.5–32.3) | 3.4 (3.3–3.7) | 3.4 (3.1–3.6) | |
| <i>Eliomys munbyanus</i> | 117 (100–140) | 108 (96–118) | 33.6 (31.7–35.6) | 4.7 (n. d.) | 4.3 (4.0–4.9) | |
| <i>Eliomys melanurus</i> | 128 (111–144) | 122 (100–136) | 35.9 (34.2–37.0) | 5.3 (n. d.) | 4.3 (3.8–4.8) | |
| <i>Graphiurus ocellaris</i> | 134.3 (117–145) | 114.5 (103–150) | 35.8 (34.2–37.5) | 3.3 (3.0–3.5) | 3.5 (3.0–4.1) | |
| <i>Graphiurus nagtglasii</i> | 138.5 (120–155) | 105 (65–122) | 36.8 (34.9–39.1) | 5.1 (4.6–5.7) | 3.7 (2.9–4.3) | |
| <i>Graphiurus monardi</i> | 160 | 130 | 34.1 (32.5–36.6) | 3.9 (3.6–4.3) | 4.1 (3.8–4.7) | |

^a P⁴–M³

myomorphous configuration) except in *Graphiurus* where it is below the infraorbital foramen (modified hystricomorphous condition, except no separate infraorbital neurovascular foramen is present, which is a feature of true hystricomorphy). The zygomatic plate is narrow, and its anterior margin does not project forward beyond the dorsal maxillary zygomatic process, so no zygomatic notch is present. The mandible has laterally directed angular processes that are usually perforated. Dental formula: $I^{1/1}, C^{0/0}, P^{1/1}, M^{3/3} = 32$. Incisor tips form V-shaped cutting edges (forming a V-shaped notch from anterior view) in most species of *Graphiurus*, but straight cutting edges in species of *Eliomys* and other glirids. Premolars are absent in the non-African *Selevinia*, and markedly reduced in *Graphiurus* *ocularis*. Cheekteeth are low-crowned (brachydont), and their occlusal patterns are variations of four transverse lophs into which cusps are subsumed, forming a range of patterns defined by basins, transverse ridges and accessory crests. Glirids do not have a caecum, and lack a noticeable morphological boundary between large and small intestines. The arterial circulation to the brain is provided by the vertebral artery (the same pattern as in squirrels) rather than the internal carotid (the primitive condition). Females of all glirid species usually have four pairs of nipples (pectoral, brachial, and two inguinal) although some variation has been documented in the non-African *Glis* (Kryštufek 2004). These and other morphological attributes of glirids are described, illustrated and reviewed by Ellerman (1940), Klingener (1984), Bugge (1985), Wahlert *et al.* (1993), Holden (1996), Nowak (1999), Rossolimo *et al.* (2001), Potapova (2001) and Holden (2005).

Glirids are one of the oldest families of living rodents. Their fossils first appear in the early Eocene deposits (Daams & De Bruijn 1995, Daams 1999), suggesting a late Palaeocene-early Eocene origin (Hartenberger 1994, 1998). This is concordant with the most recent molecular dating estimate based upon combined markers (Huchon *et al.* 2002, Adkins *et al.* 2003, Montgelard *et al.* 2003). Most extant glirid genera were clearly differentiated and exhibited their greatest

species diversity by the early to middle Miocene (Hartenberger 1994, Daams & De Bruijn 1995, Daams 1999). The Graphiurinae are an exception; definite examples of *Graphiurus* are known only as far back as the Pliocene (Pocock 1976, Hendey 1981), although late Miocene graphiurines have been recorded from South Africa and Namibia (Denys 1990b, Mein *et al.* 2000b). The living Palearctic genera are relicts of a rich adaptive radiation of up to 15 genera.

Modern glirids (excluding species of *Graphiurus*) have been characterized as myomorphous, and several authors have included Gliridae within the suborder Myomorpha (Simpson 1945, Chaline & Mein 1979, Wahlert *et al.* 1993, McKenna & Bell 1997). Wahlert *et al.* (1993) placed them within Myomorpha based on derived cranial characters; their phylogenetic reconstruction indicated that the hystricomorphous-like *Graphiurus* is the most primitive extant glirid, and the myomorphy exhibited by all other extant glirids is convergent to that of true myomorphs. The terms 'pseudomyomorphy' (Vianey-Liaud 1985, Maier *et al.* 2002) or 'pseudosciuromorphy' (Landry 1999) have been employed to distinguish the zygomaseteric muscular arrangement found in glirids from that of muroids, and Maier *et al.* (2002) noted that pseudomyomorphy (the convergent myomorphous musculature of glirids) is one of the derived diagnostic characters of Gliridae.

The origin of glirids, and the evolutionary relationship between glirids and other rodent groups, are subjects of historical debate and controversy (Holden 2005). Glirids have alternately been placed in the rodent suborder Myomorpha (Simpson 1945, Wahlert *et al.* 1993 and references therein), in the infraorder Sciuirida (that also contains Sciuiridae; see Meng 1990, McKenna & Bell 1997) and in the suborder Sciuromorpha (in subfamily Microparamyinae; Vianey-Liaud 1994, Vianey-Liaud & Jaeger 1996). There is an overwhelming lack of support for inclusion of glirids in Myomorpha based upon recent morphological and molecular research (see Holden 2005, and references therein), and they are currently placed in the suborder Sciuromorpha (Carleton & Musser 2005). Most researchers

| | Auditory bullae length mean (range) (mm) | White tip to tail | Geographic distribution | Notes |
|--|--|---------------------|--|---|
| | 6.8 (6.6–7.1) | Yes | Malawi (limits uncertain) | Forest and woodland savanna habitats |
| | 7.8 (7.3–8.2) | Yes (faint in some) | West, eastern and south-central Africa | Woodland savanna habitats |
| | 7.2 (6.6–7.8) | No | West and central Africa | Rainforest habitats |
| | 7.1 (6.7–7.7) | No (faint in some) | Ethiopia to South Africa | Forest habitats |
| | 6.7 (6.5–6.9) | Yes | Liberia to Cameroon | Rainforest habitats; broad interorbital constriction; supraorbital ridge present. |
| | 7.4 (6.7–7.9) | No | N DR Congo, SW Cameroon | Rainforest habitats |
| | 8.1 (7.3–8.6) | Yes | Chad/Sudan to South Africa | Woodland savanna habitats |
| | 9.0 (8.3–9.7) | Yes | C and S Angola, Zambia | Woodland savanna habitats; commensal |
| | 7.3 (6.9–7.7) | No | Cameroon, Equatorial Guinea, Gabon, Congo | Rainforest habitats |
| | 8.4 (7.8–8.9) | Yes | Southern Africa, Zambia | Rocky habitats; skull flattened |
| | 9.4 (9.2–10.2) | Yes | Angola, Namibia, South Africa | Rocky habitats; skull flattened |
| | 10.2 (9.6–10.5) | Yes | Western Sahara/Morocco to Libya (coastal) | Forests, plantations, bushes, cultivations, rocky habitats |
| | 11.7 (11.2–12.2) | No (faint on some) | Libya, Egypt (coastal) | Trees, bushes, gardens, rocky habitats |
| | 9.8 (9.2–10.5) | Yes | South Africa | Rocky habitats; skull flattened |
| | 7.9 (7.4–8.4) | No | Sierra Leone to Central African Republic/Gabon | Rainforest habitats |
| | 10.3 (9.8–11.1) | Yes | NE Angola, S DR Congo, NW Zambia | Woodland savanna habitats |

currently agree with Wahlert *et al.* (1993) that the myomorphous-like zygomaseteric structure exhibited by most living glirid species is convergent with that of muroids, and most advocate glirid 'pseudomyomorphy' as being derived from a protrogomorphous ancestor.

Vianey-Liaud & Jaeger (1996) proposed that Gliridae are paraphyletic, hypothesizing that graphiurines and anomalurids are closely related and should possibly be placed in the same family because, in their view, both groups are descended from African Eocene zegdomyids. However, results from all other morphological inquiries, as well as molecular information, do not support this hypothesis, but rather support the monophyly of Gliridae (Meng 1990, Wahlert *et al.* 1993, Hartenberger 1994, 1998, Catzefflis *et al.* 1995, Daams & De Bruijn 1995, Hänni *et al.* 1995, Robinson *et al.* 1997, Suzuki *et al.* 1997, Debry & Sagel 2001, Montgelard *et al.* 2002, 2003). Results of molecular analyses by Bentz & Montgelard (1999) and Montgelard *et al.* (2002, 2003) explicitly refute paraphyly and phylogenetic alliance with anomalurids.

Ecological information on African dormice is rather sparse, and only a few species have been studied in a moderate amount of detail. Most species of dormice are primarily arboreal, and three species are mainly found in rocky habitats. The digits of the fore- and hindfeet grip small twigs and branches, and the long claws allow for climbing up slightly uneven surfaces such as rock faces, boulders, tree trunks and walls. Dormice live in many arboreal habitats, such as forests, scrublands, plantations, orchards and woodland savannas where there are suitable hollows and crevices for nesting (see also below). They have been recorded in holes of trees, woodpiles, human houses, thatched rondavels, gardens, kitchens and food stores, banana plantations, date palms, abandoned nests of weaver-birds and beehives. Rock-living species (such as *Eliomys* spp. and *G. ocellaris*) are found on limestone cliffs, in caves, under boulders and in rock crevices. In all these habitats, dormice build spherical nests of vegetation (shredded bark, leaves), which are lined with hair or wool; entrance holes for nests are hard to find, perhaps because it is important that dormice need to be totally surrounded by warm

nesting material to ensure adequate thermoregulation (see below). Dormice do not dig (or live in) burrows and hence are rarely trapped on the ground.

Most studies suggest that dormice are vegetarians or omnivores. Details on the diet vary according to species and location, but there are few detailed studies. Vegetable foods include nuts, seeds, berries, cocoa pods, oil palm nuts, paw-paw, bananas and other fruits. Animal foods include eggs and a wide variety of insects (e.g. grubs, moths and earwigs) and other invertebrates (millipedes). One species (*Eliomys munbyanus*) has been observed catching butterflies.

Dormice are mostly nocturnal, although there are a few records of daytime activity. When active, dormice are agile and swift, running swiftly along twigs and branches and up and over walls and rocks. However, activity is temperature dependent. In cooler weather, dormice become lethargic and torpid (hence the vernacular name 'dormouse' from the Latin *dormire* = to sleep). In those species that have been studied, Tb drops dramatically when Ta is low and/or when food is limited.

Social organizations, and how they may change during the year, are virtually unknown. Most species appear to be solitary except when mothers are with their young, and when a male associates with his mate and young. Some species (e.g. *Graphiurus ocellaris*, *G. platyops*, *G. kelleni*) are known to emit a variety of specific vocalizations and displays, which indicate, for example, agonistic behaviour and non-aggressive communication. Some species (e.g. *G. ocellaris*) may have territories, but nothing is known in this regard for most species. Reproductive behaviour is also poorly known: there are typically 2–3 young (maximum about six); reproduction in the temperate parts of Africa appears to be mainly during summer, but information from tropical Africa is too scanty to make any generalizations.

The two African genera are distinguished by the length of the rostrum, form of the zygomatic plate, zygomaseteric musculature arrangement, relative position of certain cranial foramina, dental morphology and facial colour pattern (Table 14).

Mary Ellen Holden

GENUS *Eliomys*

Garden Dormice

Eliomys Wagner, 1840. Gelehrte Anz. I. K. Bayer. Akad. Wiss., München 8 (37):297. (See Kryštufek & Kraft (1997) for clarification of the publication date for *Eliomys* Wagner [1839 or 1840]). Type species: *Eliomys melanurus* Wagner, 1840.

There are three living species in the genus *Eliomys*: *E. quercinus* is a European endemic that occurs from Western Europe east to the Urals, and on numerous Mediterranean islands; *E. melanurus* is distributed in southern Turkey, the Middle East (Sinai to Iraq) and eastern North Africa; and *E. munbyanus* is endemic to western North Africa (Holden 2005). The habitats of the two African species include desert scrub, rocky escarpments, limestone cliffs and cultivated areas.

The genus is characterized externally by a conspicuous striking facial colour pattern (dark, broad eye-mask that extends posteriorly under ears, and which contrasts with pale (white or cream) cheeks and postauricular patches), and by the contrasting colours of tail and tail tip. The skull is distinguished by a long and narrow rostrum, an upward tilted zygomatic plate in which the anterior margin extends

slightly anteriorly to the infraorbital foramen, pseudomyomorphous (convergent myomorphous) zygomaseteric musculature arrangement, position of certain cranial foramina, the presence of four clearly defined transverse lophs or ridges on cheekteeth, and differences in incisor enamel microstructure (Ellerman 1940, Wahlert *et al.* 1993, von Koenigswald 1993, 1995, Nowak 1999) (Figure 18).

All species of *Eliomys* are predominantly arboreal and partly terrestrial, and are nocturnal. They are agile climbers. The two species in Africa are omnivorous, and consume fruits, seeds, invertebrates and small vertebrates. Individuals of both species become torpid at low ambient temperatures.

The closest living relative of *Eliomys* is probably *Dryomys*, which is distributed in Europe, the Middle East and central Asia. This



Eliomys melanurus.

relationship is supported by cranial and dental characters (Wahlert *et al.* 1993, von Koenigswald 1993, 1995, Daams & De Bruijn 1995, Potapova 2001, Rossolimo *et al.* 2001), and by molecular data (Bentz & Montgelard 1999, Montgelard *et al.* 2003). The evolutionary history of *Eliomys* dates from the middle Miocene of Europe, and from the early Pliocene of western Asia and the Mediterranean region (Daams & De Bruijn 1995, Nadachowski & Daoud 1995). In Africa, it is known only from Pleistocene sediments in North Africa (Mein & Pickford 1992, McKenna & Bell 1997). *Eliomys* possibly reached Africa at least twice, once during the Messinian (6.7–5.2 mya) from Iberia, and later during the late Pleistocene from the eastern Mediterranean. Multiple colonizations may account for the lack of morphometric cohesion among certain populations of North African endemic *E. munbyanus*.

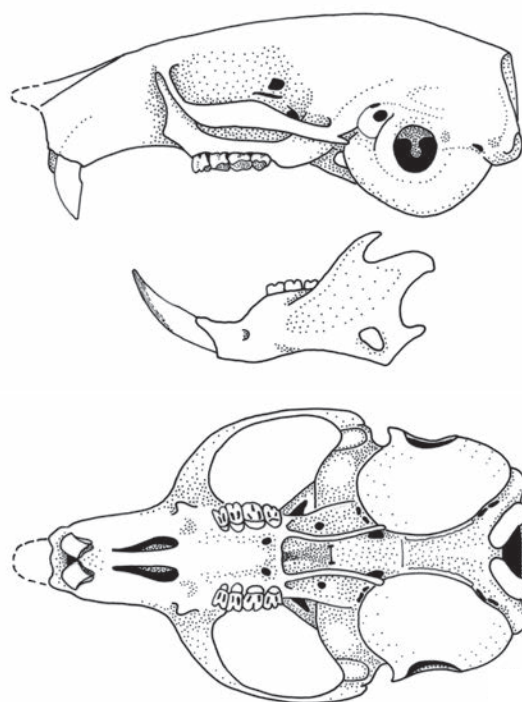


Figure 18. Skull and mandible of *Eliomys melanurus* (RMCA 91-090-M-45).

The two species are distinguished by body size, absolute lengths of ear and tail, degree of conspicuousness of postauricular patches, bushiness of tail, colour of the tail tip and by skull characters. The two species are mostly allopatric, although they are marginally parapatric in Libya.

Mary Ellen Holden

Eliomys melanurus LARGE-EARED GARDEN DORMOUSE

Fr. L  rot du Sud-Est Asiatique; Ger. Gro  hr L  ffelbilch

Eliomys melanurus (Wagner, 1840). Gelehrte Anz. I. K. Bayer. Akad. Wiss., M  nchen 8 (37): 299.

Sinai (restricted to vicinity of Mt Sinai by Nader *et al.* 1983), Egypt.

Taxonomy Originally described in genus *Myoxus*. *Eliomys melanurus* has historically been listed as a synonym of *E. quercinus* (Niethammer 1959, Corbet 1978), but more recently recognized by most researchers as a separate species (Ellerman & Morrison-Scott 1966, Niethammer 1987, Holden 1993, 2005, Filippucci *et al.* 1988b, c, Harrison & Bates 1991, Kry  tufek & Kraft 1997). The geographic distribution and taxonomy of *E. melanurus* remains unresolved (Holden 2005). Based on morphometric analyses, many authors (e.g. Kahmann & Thoms 1981, Niethammer 1987, Kry  tufek & Kraft 1997 and references therein) assign the western North African populations to *E. quercinus*, and the eastern North African and Middle Eastern populations to *E. melanurus*. Filippucci *et al.* (1988b, c), Filippucci & Kotsakis (1995) and Filippucci & Capanna (1996) analysed allozymic and karyological characters and identified all North African and Middle Eastern populations as *E. melanurus*. Holden (2005) agreed with Kry  tufek & Kraft (1997) that only eastern North African and Middle Eastern populations represent *E. melanurus*, but suggested (as

Delibes *et al.* 1980 did) that the western North African populations should be recognized as a separate species, *E. munbyanus*, and that it is probably closely related to *E. melanurus*. Synonyms: *cyrenaicus*. Subspecies: none. Chromosome number $2n = 48$ (Filippucci *et al.* 1988b, c, 1990, Zima *et al.* 1995).

Description Medium-sized dormouse. Dorsal pelage ranges from reddish- and yellowish-brown to yellowish-grey. Pelage soft, sometimes woolly, and moderately long (rump hairs 10–12 mm, guard hairs up to 17 mm). Ventral pelage white or cream slightly suffused with grey. Dorsal and ventral pelage colours clearly delineated. Head colour matches that of dorsal pelage; paler towards muzzle. Eyes large; dark eye-mask conspicuous. Cheeks cream or white, forming part of a pale lateral stripe that extends from cheeks to shoulders. Ears large, brown, oval-shaped. White or cream postauricular patches usually present, though sometimes inconspicuous. Hindfeet white. Tail long (ca 95% of HB), hairs

shorter at base (3–4 mm) and longer at tip (up to 23 mm); dorsally black, or black with faint white tip, except for reddish- and yellowish-brown (similar to back) at base; undersurface similar to uppersurface. Skull long (35.9 mm), angular and broad (20.9 mm), with moderately long rostrum (15.6 mm) and anterior palatal foramina (4.3 mm). Upper tooththrow (5.3 mm) relatively long. Auditory bullae long (11.7 mm) and inflated (mastoid breadth 17.3 mm) relative to skull length (measurements listed are mean values from Libya [Kahmann & Thoms 1981]). Nipples: 1 + 1 + 2 = 8.

Geographic Variation None recorded.

Similar Species (size comparisons refer to mean values only)

Eliomys munbyanus. Smaller average head and body length (117 mm). Tail (108 mm), hindfeet (25 mm) and ears (24 mm) shorter. Dorsal pelage similar, postauricular patches usually more conspicuous. Tail not bushy; black with conspicuous white at tip. Ventral tail colour uniformly pale grey or brownish-white from base to tip in some populations. Skull slightly shorter (33.6 mm) with shorter rostrum (14.7 mm). Upper tooththrow shorter (4.7 mm), and auditory bullae shorter (10.2 mm) and less inflated (mastoid breadth 16.8 mm) both absolutely and relatively (measurements listed are mean values from Morocco [Kahmann & Thoms 1981]). Not sympatric, although both species occur in Libya.

Distribution Mediterranean Coastal BZ and northern margins of Sahara Arid BZ. Recorded from Libya, eastwards from Barqah (Cyrenaica) and Egypt including the Sinai Peninsula (Holden 2005). Extraliminally known from the Middle East, Iraq and southern Turkey.

Habitat Coastal dunes and adjacent inland plateaux, Mediterranean scrubland, escarpments, steppe-deserts, rocky areas, mountains, gardens and human dwellings (Flower 1932, Wassif & Hoogstraal 1953, Ranck 1968, Osborn & Helmy 1980, Harrison & Bates 1991). Other

habitat records include limestone cliffs in coastal desert (Osborn & Helmy 1980), on upper slopes of a wadi near coastal escarpment under a large evergreen bush (Setzer 1957), in a small mountainside garden at 1700 m, near a spring in a garden, and in a Bedouin tent (Wassif & Hoogstraal 1953). In eastern North Africa, captured at elevations from sea level to 1700 m (Harrison & Bates 1991).

Abundance Little information. Probably uncommon in eastern North Africa, based on the low numbers of specimens obtained at individual localities, as well as collectors' notes (Setzer 1957, Ranck 1968). In Israel, trap success during one night in spring (Mar–May) was 11.7%; in other seasons at the same localities the animals were uncommon (Haim & Rubal 1995).

Adaptations Arboreal and terrestrial; nocturnal (Haim & Rubal 1995, Qumsiyeh 1996). Resting metabolic rate is relatively low. Daily energy expenditure is conserved by entering torpor even when T_a is as high as 25 °C (Haim & Rubal 1995). In the Negev Highlands, T_a ranges from above 30 °C to below 0 °C during the winter; dormice trapped in winter at ambient temperatures close to 0 °C were found in traps in torpor with a T_b of 12 °C; torpor can last up to several days (Haim & Rubal 1995).

Foraging and Food Omnivorous, predominantly insectivorous and carnivorous. Stomach contents have included insects and other invertebrates, and occasionally small mammals and other small vertebrates (Atallah 1978, Nader *et al.* 1983, Qumsiyeh 1996). These dormice readily enter live-traps (Osborn & Helmy 1980).

Social and Reproductive Behaviour Little information. Osborn and Helmy (1980) characterized wild caught animals as extremely wild and aggressive.

Reproduction and Population Structure Apparently solitary. Mean litter-size in captivity: 2.8 (Kahmann & Thoms 1981, Kahmann 1987); no information for wild individuals. Gestation: ca. 22 days (in captivity; Kahmann & Thoms 1981). In Israel, a pregnant ♀ was captured in Apr, and a lactating ♀ was captured in May (Kahmann 1981). Sex ratio 40% ♂♂, 60% ♀♀ (Egypt; Osborn & Helmy 1980).

Predators, Parasites and Diseases Ectoparasites include the siphonapteran fleas *Myoxopsylla laverani*, *Nesophyllus henleyi* and *Xenopsylla ramesis* (Hoogstraal & Traub 1965b, Krasnov *et al.* 1999). Mites (not identified) were collected from some individuals collected in Saudi Arabia (Nader *et al.* 1983). In Israel, skeletal remains were found in pellets of Barn Owls *Tyto alba*; in Syria, skeletal elements were identified in pellets of Barn Owls and Long-eared Owls *Asio otus* (Obuch 2001).

Conservation IUCN Category: Least Concern.

Measurements

Eliomys melanurus

HB: 128.0 (111–144) mm, n = 10

T: 122.0 (100–136) mm, n = 10

HF: 26.7 (26–27) mm, n = 10

E: 27 (26–29) mm, n = 10

WT: 51.8 (38.4–63.0) g, n = 16*



Eliomys melanurus

GLS: 35.9 (34.2–37.0) mm, n = 7

GWS: 20.9 (19.8–22.0) mm, n = 7

P⁴–M³: 5.3 mm, n = 8**

Libya (Kahmann & Thoms 1981)

*Western Mediterranean Coastal Desert, Egypt (Osborn & Helmy 1980)

**Mean value only

Key References Kahmann & Thoms 1981; Harrison & Bates 1991; Osborn & Helmy 1980; Ranck 1968.

Mary Ellen Holden

Eliomys munbyanus MAGHREB GARDEN DORMOUSE

Fr. L  rot Nord-africain; Ger. Nordafrikanischer L  ffelbilch

Eliomys munbyanus (Pomel 1856). Comptes Rendus de l'Academie des Sciences, Paris 42: 653. Region d'Oran (Province of Oran), Algeria.

Taxonomy Originally described in genus *Myoxus*. *Eliomys munbyanus* has historically been considered a synonym of *E. quercinus* (Niethammer 1959, Kry  tufek & Kraft 1997), although Filippucci *et al.* (1988a, b), Filippucci & Kotsakis (1995) and Filippucci & Capanna (1996) considered *munbyanus* to be synonymous with the Middle Eastern *E. melanurus*, an arrangement tentatively followed by Holden (1993). A few authors have suggested recognizing certain North African populations as a separate species, utilizing the names *E. munbyanus* (Delibes *et al.* 1980) or *E. tunetae* (Tranier & Petter 1978). Holden (2005) argues that recent morphometric analyses (Kry  tufek & Kraft 1997), considered together with karyologic and allozymic analyses (Delibes *et al.* 1980, Filippucci *et al.* 1988a, b, Filippucci & Kotsakis 1995, Filippucci & Capanna 1996), support the recognition of *E. munbyanus* as a separate species that is probably closely related to *E. melanurus*. The assignment of synonyms and geographic distributions are based primarily on the results of Kry  tufek & Kraft's (1997) morphological study. Additional genetic and karyological sampling of *E. munbyanus* and North African *E. melanurus* populations is needed. Only the Moroccan population of *E. munbyanus* has been sampled for allozyme variation, and karyological data have only been reported from Moroccan and Tunisian populations. The hypothesized distribution of *E. munbyanus* is concordant with that of other mammalian endemics of the Maghreb (see Carleton & Van der Straeten 1997). Synonyms: *denticulatus*, *lerotina*, *occidentalis*, *tunetae*. Subspecies: none. Chromosome number: 2n = 46 (Tranier & Petter 1978, Delibes *et al.* 1980, Moreno & Delibes 1982, Filippucci *et al.* 1988a, Zima *et al.* 1995).

Description Medium-sized dormouse. Dorsal pelage reddish- or yellowish-brown suffused with grey. Pelage soft, sometimes woolly and moderately long (rump hairs 10–11 mm, guard hairs up to 16 mm). Ventral pelage white slightly suffused with grey. Dorsal and ventral pelage colours clearly delineated. Head colour matches that of dorsal pelage; paler towards muzzle. Eyes large; dark eye-mask conspicuous. Cheeks cream or white, forming part of a pale lateral stripe that extends from cheeks to shoulders. Ears moderately large, brown, oval-shaped. White or reddish postauricular patches usually present. Hindfeet white. Tail long (ca. 92% of HB), tail hairs shorter at base (3–4 mm) and longer at tip (up to 19 mm); dorsally black with white at tip, except for reddish- and yellowish-brown (similar to back) at base; ventrally either uniformly pale grey or brownish-white, or pale grey or brownish-white at base with a black middle section and white tip. Skull moderately long (33.6 mm), angular and broad (19.5 mm), with moderately short rostrum (14.7 mm) but comparatively long anterior palatal foramina (4.3 mm). Upper

toothrow (4.7 mm) relatively short. Auditory bullae moderately long (10.2 mm) and moderately inflated (mastoid breadth 16.8 mm) relative to skull length (measurements listed are mean values from Morocco [Kahmann & Thoms 1981]). Nipples: 1 + 1 + 2 = 8.

Geographic Variation Ventral tail colour and pattern varies geographically. In Western Sahara and SW Morocco, the ventral tail colour is white or grey proximally, changing to solid black in the middle section, with a conspicuous white tip. The black region of the tail is sometimes fringed in white. Specimens collected from other regions of Morocco and Algeria have a totally greyish-white or white ventral tail colour (similar to European *E. quercinus*). Individuals from Tunisia and W Libya exhibit the same pattern as those from Western Sahara and SW Morocco (Kahmann & Thoms 1981). Tail length and body size also appear to vary among some populations. Populations from N Morocco have a longer tail length (tail length exceeds that of head and body) than surrounding populations (Moreno & Delibes 1982). This population also exhibits smaller body size (reflected in shorter HB and GLS lengths), and less inflated auditory bullae compared with populations from southern Morocco and Algeria (Cabrera 1932, Saint-Girons & Petter 1965, Moreno & Delibes 1982, Aulagnier & Th  venot 1986).

Similar Species (size comparisons refer to mean values only)

Eliomys melanurus. Larger average head and body length (128.0 mm). Tail (122.0 mm), hindfeet (26.7 mm) and ears (27.0 mm) longer. Dorsal pelage similar, postauricular patches usually less conspicuous. Tail bushy; distal dorsal colour uniformly black, or black with faint white tip. Ventral tail colour not paler, and does not vary significantly geographically. Skull slightly longer (35.9 mm) and longer rostrum (15.6 mm). Upper tooththrow longer (5.3 mm) and auditory bullae longer (11.7 mm) and more inflated (mastoid breadth 17.3 mm), both absolutely and relatively (measurements listed are mean values from Libya – see Measurements). Not sympatric, although both species occur in Libya.

Distribution Endemic to Africa. Mediterranean Coastal BZ. Recorded from Western Sahara, Morocco, Algeria, Tunisia and Libya (as far east as the Tar  bulus region of Tripolitania) (Holden 2005). One population in the Sahara Arid BZ in the Fezzan. Recorded from sea level up to 3800 m.

Habitat Captured in thick Mediterranean scrubland comprised of heath (*Arbutus*, *Calluna*, *Erica*), mock privet *Phillyrea*, pistachio

*Eliomys munbyanus*

Pistacia, myrtle *Myrtus*, Mediterranean fan palm *Chamaerops*; young cork oak *Quercus suber*; pine plantations (*Pinus halepensis*, *P. insignis*); mixed oak forests (*Quercus canariensis*, *Q. pyrenaica* and *Q. suber*); dry, overgrazed habitats with isolated *Acacia*, pistachio and Mediterranean fan palm (Saint-Girons & Petter 1965, Moreno & Delibes 1982); large oases and adjoining areas in or near date palms *Phoenix* and tamarisk *Tamarix* (Ranck 1968); potato fields (Khidas 1993); and occasionally in prickly pear cactus *Opuntia* (Kahmann & Thoms 1981). Other habitats include coastal dunes, montane cedar forests, montane boulder fields and cultivated areas (Ranck 1968, Kahmann & Thoms 1981, Moreno & Delibes 1982, Aulagnier & Thévenot 1986, Kowalski & Rzebik-Kowalska 1991). In the Fezzan, captures were in or adjacent to oases.

Abundance Uncommon (Ranck 1968, Moreno & Delibes 1982, Aulagnier & Thévenot 1986, Khidas 1993).

Adaptations Predominantly arboreal, partly terrestrial; nocturnal (Kahmann & Thoms 1981, Aulagnier & Thévenot 1986). Often enter torpor in winter in response to prolonged cooler ambient temperatures (Kahmann & Thoms 1981). In Libya, individuals were infrequently captured during the winter months when ambient temperatures at night often dropped below -1°C ; Ranck (1968) suggested that the seemingly low abundance might be explained by inactivity of torpid individuals. In Morocco, one individual was caught during a night during which the ambient temperature dropped below 0°C (Moreno & Delibes 1982). Nests have been found in many situations: in holes in trees (including tamarisk, olive, willow, poplar and several species of palm), in shrubs (small palms, and rarely prickly pear cactus), in rock crevices, caves and at the bases of large rocks, and in thatched roofs, alcoves, attics and conduits of huts (Ranck 1968, Kahmann & Thoms 1981). Materials used to construct nests include grass, barley stems, palm fibre, goat hair, sheep and possibly dromedary wool, and even flower clusters of *Acacia* (Pomel

1856, Ranck 1968, Kahman & Thoms 1981). Kahmann & Thoms (1981) stated that the primary physical requirement of a nest is to provide all-round body contact.

Foraging and Food Probably omnivorous, consuming fruit, insects, seeds and sometimes eggs. In Tunisia, reported to be a pest in fruit plantations (favouring pomegranate) and in vegetable gardens (legumes, paprika, eggplant); may also eat chicken eggs (Kahmann & Thoms 1981). Kahmann & Thoms (1981) attempted stomach analyses of 11 individuals from Cap Bon, Tunisia, but were unsuccessful. Remains of insects and land snails were found near nest entrances in rocky fields, and individuals were observed capturing butterflies by springing into the air with both forelimbs stretched out in front (Kahmann & Thoms 1981). Bait made from bread dipped in cooking oil (Morocco; Moreno & Delibes 1982) and moistened oatmeal (Libya; Ranck 1968) attracted these dormice.

Social and Reproductive Behaviour No information.

Reproduction and Population Structure Solitary. Reproductively active in spring and, at lower altitudes, autumn (Kahmann & Thoms 1981, Moreno & Delibes 1982). Litter-size: probably 4–6, although one pregnant ♀ contained eight embryos (Kahmann & Thoms 1981, Moreno & Delibes 1982). Young stay in the nest for approximately seven weeks (Kahmann & Thoms 1981). In N Morocco, lactating ♀♀ were captured in Nov (Moreno & Delibes 1982). In Tunisia, two pregnant ♀♀ were collected in Mar, and one pregnant ♀ was captured in Apr (Kahmann & Thoms 1981). In Tunisia, sex ratio was found to be male-biased, but this may reflect a sampling artefact due to seasonal differences in activity between sexes (Kahmann & Thoms 1981).

Predators, Parasites and Diseases Principal host for the hoplopleurid louse *Schizophthirus pleurophaeus* (Durden & Musser 1994). In Algeria, skeletal remains were identified in owl pellets (Kowalski & Rzebik-Kowalska 1991) and in the scat of a jackal (Khidas 1986).

Conservation IUCN Category: Least Concern.

Measurements

Eliomys munbyanus

HB: 117 (100–140) mm, n = 26

T: 108 (96–118) mm, n = 26

HF: 25 (22–27) mm, n = 26

E: 24 (20–27) mm, n = 26

WT: 52 (42–62) g, n = 14

GLS: 33.6 (31.7–35.6) mm, n = 8

GWS: 19.5 (18.6–20.1) mm, n = 8

P⁴–M³: 4.7 mm*

Morocco (Kahmann & Thoms 1981)

*Mean value only

Key References Kahmann & Thoms 1981; Kryštufek & Kraft 1997; Moreno & Delibes 1982; Niethammer 1959; Ranck 1968.

Mary Ellen Holden

GENUS *Graphiurus*

African Dormice

Graphiurus Smuts, 1832. Enumer. Mamm. Capensium, pp. 32–33. Type species: *Sciurus ocularis* Smith, 1829.



Graphiurus murinus.

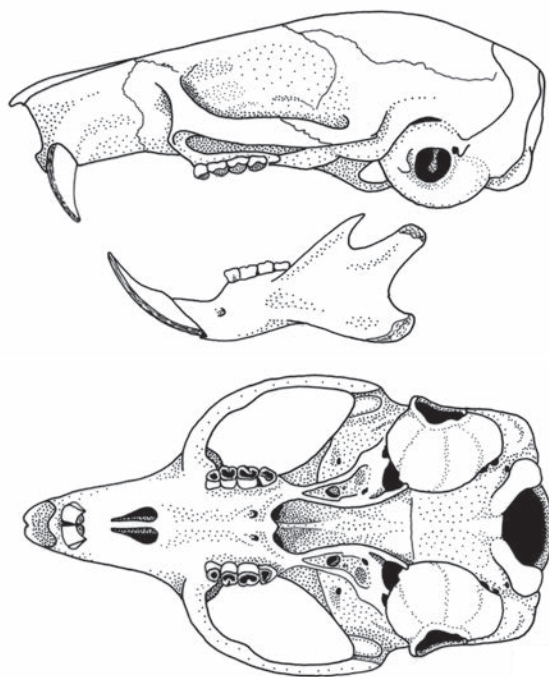


Figure 19. Skull and mandible of *Graphiurus nagtglasii* (RMCA RG 5556).

The 14 living species of the genus *Graphiurus* occur throughout sub-Saharan Africa in tropical lowland rainforest, montane evergreen and semi-deciduous forest, moist and arid savanna woodlands and grasslands, as well as the Nama- and succulent-Karoo biomes and fynbos in southern Africa. Treeless deserts, such as the Namib, are devoid of dormice, except near oases. Primary habitat requirements for African dormice are trees, woody vines, bushes and weathering granitic outcrops (kopjes) that provide shelter and nesting sites.

The genus is characterized externally by a generally plain-coloured face without obvious markings in most species (except *G. ocularis*), and the colour of the tail and tail tip. The skull is distinguished by a short, often broad rostrum, very narrow zygomatic plate that is situated entirely beneath the infraorbital foramen, modified hystricomorphous zygomatic muscle arrangement, differences in position of certain cranial foramina, V-shaped cutting edges of incisor tips (forming a V-shaped notch from anterior view) in most species, and indistinct, usually incomplete lophs or ridges on cheekteeth (Ellerman 1940, Wahlert *et al.* 1993, Nowak 1999) (Figure 19). Many closely related species of *Graphiurus* are difficult to distinguish, although a few species are easy to identify because of their unique prominent characters: *G. crassicaudatus* has a broad interorbital constriction and pronounced supraorbital ridging, and *G. nagtglasii* is the largest species and has a distichous tail. Species that typically dwell in rock crevices, such as *G. platyops* and *G. ocularis*, have a flattened cranium that is easily distinguished from the vaulted cranium found in all other species. *Graphiurus ocularis* is also easily identified by its striking facial colour pattern and its reduced, circular premolar.

In their morphology and habits, all sub-Saharan African dormice resemble small-bodied arboreal squirrels, and like these animals all species of *Graphiurus* are arboreal; even those using crevices in rocky habitats, such as kopjes, for nesting sites are excellent climbers. All species are nocturnal, although at least one species (*G. platyops*) has also been documented to be active at dawn (Wilson 1975), and another species (*G. angolensis*) was reportedly active during the day (field notes; specimen labels). Most species are omnivorous, and consume fruits, insects, seeds and nuts; *G. ocularis* is predominantly insectivorous (Channing 1984). Some species, such as *G. lorrainus* and *G. murinus*, enter torpor during periods of low ambient temperature and inadequate food supply (Lachiver & Petter 1969, Webb & Skinner 1996b).

Hartenberger (1994) considered many aspects of graphiurine morphology to be primitive, and speculated that the group has been in Africa since the Miocene; late Miocene graphiurines are recorded from Namibia (Mein *et al.* 2000b) and South Africa (Denys 1990b). Mein *et al.* (2000b) described the late Miocene *Otaviglis* from Namibia as the oldest known graphiurine (10–11 mya), possibly derived from the middle Miocene *Microdryomys* found in North Africa, and suggested it could be ancestral to *Graphiurus*. Molecular-clock calibrations derived from phylogenetic analyses of nuclear and mitochondrial gene sequences indicate that the adaptive radiation within *Graphiurus* occurred 8–10 mya, which pre-dates the oldest

fossil representative of the genus (early Pliocene, ca. 5 mya), but is consistent with the late Miocene graphiurine records (Montgelard *et al.* 2003). The time frame also brackets a period of low sea levels and extensive interchange of faunas between Europe and Africa. Following the colonization of Africa by a late Miocene ancestor, graphiurines underwent an adaptive radiation resulting in a modern fauna that is richer in species than those in all the other genera of dormice combined (Montgelard *et al.* 2003).

The taxonomic revision of extant *Graphiurus* by Genest-Villard (1978a) was based mostly on size grades and underestimated species diversity, particularly in *G. murinus* and closely related species. Subsequently, certain species were defined in reports covering different geographical regions (e.g. Robbins & Schlitter 1981, Ansell & Dowsett 1988, Holden 1996). Profiles of the 14 species in this volume are based on literature sources, examination of museum specimens and preliminary multivariate analyses of cranial and dental measurements (M. E. Holden unpubl.). It is likely that future studies that incorporate molecular data will show that some species recognized here actually contain two or more separate species.

Graphiurus has been divided into as many as four separate genera (e.g. Allen 1939, Holden 1996, Pavlinov & Potapova 2003): *Aethoglis*, containing the largest African dormouse *G. nagtglasii* (sometimes erroneously including *G. monardi*); *Graphiurus* comprising *G. ocellaris*, with its reduced, simple upper premolar; *Gliriscus* consisting of the rupicolous *G. platyops* and *G. rupicola*; and *Claviglis* the so-called

‘tree dormice’, to which the remaining species of *Graphiurus* were assigned. Two of these, *Graphiurus* and *Claviglis*, have often been retained as subgenera (e.g. Ellerman *et al.* 1953, Rosevear 1969). No published studies based upon a broad sample of species have addressed the validity of these subgeneric boundaries as used by past authorities, nor have they presented hypotheses of relationships among species. However, phylogenetic analyses of cranial and middle ear morphology by Pavlinov & Potapova (2003) identified three monophyletic groups (subgenera) within *Graphiurus*: *Aethoglis* (containing *G. nagtglasii*), *Claviglis* (containing *G. crassicaudatus*) and *Graphiurus* (containing all other *Graphiurus* species). Their study suggested that first *G. nagtglasii*, then *G. crassicaudatus*, diverged early in the evolution of African Dormice, and that the remaining taxa that they sampled (*angolensis*, *christyi*, *kelleni*, *lorraineus*, *murinus*, *ocellaris*, *parvus* and *surdus*) form a separate monophyletic group. Pavlinov & Potapova’s (2003) subgeneric arrangement is followed by Holden (2005). Here, the species are listed alphabetically.

The 14 species are distinguished externally by body size, length of tail, ear and hindfoot, degree of conspicuousness of eye-mask, and colour of the tail tip. The skulls are differentiated by the overall shape of the skull, the shape of the zygomatic arch, presence/absence of supraorbital ridges, length and relative inflation of auditory bullae, differences in toothrow measurements and relative size of the upper premolar, and several skull dimensions.

Mary Ellen Holden

Graphiurus angolensis ANGOLAN AFRICAN DORMOUSE

Fr. Graphiure d’Angola; Ger. Angolischer Bilch

Graphiurus angolensis de Winton, 1897). Ann. Mag. Nat. Hist., ser. 6, 20: 320. Caconda, Angola.

Taxonomy Originally described in the genus *Gliriscus*. Allen (1939) recognized *G. angolensis* as a species distinct from *G. platyops*, *G. rupicola* and *parvulus*. Ellerman *et al.* (1953) included *G. angolensis*, *G. rupicola* and *parvulus* as subspecies of *G. platyops*. Genest-Villard (1978a) placed *G. rupicola* as a subspecies of *G. platyops*, but synonymized *G. angolensis* and *parvulus* under *G. murinus*. Ansell (1974, 1978) recognized that the north-western Zambian population (identified by him as *G. platyops parvulus*) is morphologically and ecologically different from *G. platyops*. Holden (1993) provisionally listed populations from Angola, S DR Congo and NW Zambia under *G. platyops*. Populations in Angola and NW Zambia exhibit a distinctive skull morphology that is consistently separable from that of *G. platyops* and *G. rupicola* (M. E. Holden unpubl.). Ansell (1974, 1978) had correctly surmised that these populations are probably aligned with *G. microtis*. Here, following Allen (1939), *G. angolensis* is considered as a valid species and distinct from *G. platyops* and *G. rupicola*. The form *parvulus* (as described by Monard 1933) is probably a junior synonym of *G. angolensis* (Holden 2005). Synonyms: *dasilvai*, *parvulus*. Subspecies: none. Chromosome number: not known.

Description Small dormouse. Dorsal pelage dark brown, rufous, golden, or drab brown, with darkening of pelage towards the mid-line of head and back in some individuals. Dorsal pelage soft, sleek, thick and moderately long (rump hairs 8 mm, guard hairs up to 12 mm).

Ventral pelage white or cream slightly suffused with grey. Dorsal and ventral pelage colours clearly delineated. Head colour matches that of dorsal pelage, slightly paler towards muzzle. Eyes large; eye-mask conspicuous. Ears brown, large, rounded. Cheeks cream or white, forming part of a pale lateral stripe that extends from cheeks to shoulders. Cream postauricular patches usually present. Hindfeet white, or white with dark metatarsal streak. Tail moderately long (ca. 80% of HB), tail hairs shorter at base (5–10 mm) and longer at tip (up to 33 mm). Tail colour generally matches dorsal pelage. White hairs are mixed throughout tail; tip white. Skull long, robust and moderately broad (15.5 mm), with a relatively vaulted braincase (height of braincase 7.7 mm). The appearance of a vaulted braincase is augmented by the concave curvature of the braincase (lateral view) and large auditory bullae. Interorbital constriction moderately narrow (4.2 mm), anterior palatal foramina comparatively long (3.4 mm) and wide (2.1 mm), and auditory bullae long (9.0 mm) and inflated relative to skull length (mean values from Kabompo and Zambezi [formerly Balovale], Zambia; M. E. Holden unpubl.). Nipples: 1 + 1 + 2 = 8.

Geographic Variation Individuals from C Angola are notably darker and usually exhibit a dark metatarsal streak on the hindfeet, whereas individuals from S and C Angola (type locality of *parvulus*) and Zambia are drab or golden brown, usually with white hindfeet.

Ear pinnae shorter (on average) in Angolan specimens (13.5 mm) than in Zambian specimens (15.9 mm) (mean values from Ondjiva and Caconda, Angola, and from Kabompo and Zambezi [formerly Balovale], Zambia; M. E. Holden unpubl.).

Similar Species (size comparisons refer to mean values only)

Graphiurus microtis. Similar mean head and body length (98.8 mm).

Tail (mean 75.2 mm) and hindfeet (mean 16.9 mm) absolutely and relatively shorter. Dorsal pelage often similar in colour, but grey in some populations. Skull similar in length (27.4 mm), but slightly narrower (15.0 mm). Interorbital constriction (3.9 mm) slightly narrower. Anterior palatal foramina 3.4 mm long, 2.1 mm wide. Mean upper tooththrow length (3.0 mm) shorter, and mean upper premolar breadth (0.8 mm) narrower. Auditory bullae (8.1 mm) absolutely and relatively shorter and less inflated (measurements listed are mean values from Zimbabwe; M. E. Holden unpubl.). Parapatric in NW Zambia (Ansell 1978). *Graphiurus microtis* occurs in savannas throughout most of sub-Saharan Africa.

Graphiurus rupicola. Slightly larger head and body length (mean 110 mm). Tail (mean 104.2 mm) and hindfeet (mean 21.5 mm) absolutely and relatively longer. Dorsal pelage grey. Mean skull length slightly longer (31.3 mm). Interorbital constriction broader (5.0 mm) and palate longer (10.4 mm) both absolutely and relatively. Braincase absolutely more vaulted (8.0 mm), but flatter relative to skull length. Anterior palatal foramina 3.4 mm long, 2.3 mm wide. Upper tooththrow (3.4 mm) similar in absolute length, but shorter relative to skull length (measurements listed are mean values from Erongo, Karibib and Mt Brukkaros, Namibia; M. E. Holden unpubl.). Parapatric in Angolan highlands; also occurs in Namibia and NW South Africa.

Distribution Endemic to Africa. Zambezian Woodland BZ. Recorded only from C and S Angola and NW Zambia (Holden 2005).



Graphiurus angolensis

Habitat Little information. Woodland savanna. Most collecting localities in Angola are in or near wetter miombo woodland, and in wetter miombo woodland and Zambezian dry evergreen forest in Zambia. Individuals have also been captured in human dwellings.

Abundance Common in the Kabompo and Zambezi districts of Zambia (Ansell 1978). The species is probably common in the interior plateaux region of Angola (Bocage 1890, Hill & Carter 1941).

Adaptations Arboreal, probably nocturnal. (Most species of African Dormice are nocturnal.) Some individuals of this species were noted to be active during the day in C Angola (field notes; specimen labels). These dormice have most often been caught in trees; in Angola, they were also found in abandoned beehives (field notes; specimen labels). In Zambia, they have sometimes been captured in buildings; one ♀ with young was caught in the roof of an African hut, another solitary ♀ was caught among some planks in a carpenter's shop, and one ♂ was obtained in a store (Ansell 1978; specimen labels).

Foraging and Food Probably omnivorous. Little is known regarding the diet. An individual captured in Angola was recorded to have eaten tree grubs and the fruit of a 'parasitic growth on trees' (field note, Phipps-Bradley Angola Expedition). One individual was caught in a trap baited with meat (Chubb 1909).

Social and Reproductive Behaviour Little information. Lactating ♀♀ are often caught with young. One ♀ was recorded as being caught 'with four half-grown young, but apparently no longer lactating' (specimen label). Monard (1935) states that Angolan Dormice are aggressive.

Reproduction and Population Structure Litter-size: probably 3–5 (Ansell 1963; specimen labels). In Zambia, a ♀ captured in late Oct gave birth the following day to three young (Ansell 1963).

Predators, Parasites and Diseases No information.

Conservation IUCN Category: Data Deficient.

Measurements

Graphiurus angolensis

HB: 98.8 (79–112) mm, n = 49

T: 79.2 (70–96) mm, n = 45

HF: 18.4 (17–20) mm, n = 50

E: 15.9 (14.5–18) mm, n = 50

WT: n. d.

GLS: 28.2 (26.3–30.8) mm, n = 36

GWS: 15.5 (14.4–16.6) mm, n = 21

P⁴–M³: 3.2 (2.9–3.5) mm, n = 39

Kabompo and Zambezi, Zambia (M. E. Holden unpubl.)

Key References Ansell 1978; Hill & Carter 1941; Monard 1935.

Mary Ellen Holden

Graphiurus christyi CHRISTY'S AFRICAN DORMOUSE

Fr. Graphiure de Christy; Ger. Christys Bilch

Graphiurus christyi Dollman, 1914. Revue Zoologique Africaine 4 (1): 80. Mambaka, DR Congo.

Taxonomy Morphologically similar to some named forms currently synonymized under *G. murinus*, some of which occur in areas adjacent to this species, e.g. *vulcanicus* from the Virunga Mts. Other named forms synonymized under *G. murinus* that occur in adjacent areas are morphologically distinct, e.g. *soleatus*, from the Rwenzori Mts. Synonyms: none. Chromosome number: not known.

Description Small dormouse. Dorsal pelage medium brown, rufous-brown or rufous golden-brown. Dorsal pelage soft, silky and moderately thick (rump hairs 6–8 mm, guard hairs up to 11 mm). Ventral pelage grey washed with white. Dorsal and ventral pelage colours not clearly delineated. Head colour matches that of dorsal pelage. Eyes large; eye-mask usually conspicuous. Ears brown, large, rounded. Cheeks usually white. Postauricular patches not present. Hindfeet white with dark metatarsal streak. Tail moderately long (ca. 82% of HB), hairs shorter at base (3–5 mm) and longer at tip (up to 21 mm). Tail colour generally matches that of dorsal pelage and does not exhibit white tip. Skull medium length (28.0 mm), moderately narrow (15.1 mm) and moderately vaulted (height of braincase 8.1 mm). Interorbital constriction (4.7 mm) narrow. Supraorbital ridges present. Premaxilla and nasal bones often extend farther beyond the anterior face of the incisors than in similar species. Anterior palatal foramina moderately long (mean 3.0 mm) and wide (mean 2.2 mm), palate moderately long (8.5 mm), auditory bullae short (7.4 mm) and not inflated relative to skull length. Anterior chamber of auditory bullae markedly less inflated than posterior chambers in some individuals (measurements listed are mean values from DR Congo; M. E. Holden unpubl.). Nipples: 1 + 1 + 2 = 8.

Geographic Variation None recorded.

Similar Species (size comparisons refer to mean values only)

Graphiurus lorraineus. Smaller head and body length (mean 83 mm), ears shorter (mean 12.1 mm). Dorsal pelage usually more rufous. Skull (24.5 mm) shorter and anterior palatal foramina narrower (1.7 mm) relative to skull length. Nasals and premaxilla usually do not extend as far beyond incisors. Palate absolutely shorter (7.8 mm) but relatively similar. Anterior palatal foramina 2.7 mm long, 1.7 mm wide. Auditory bullae similar in length (7.2 mm), but longer relative to skull length (measurements listed are mean values from DR Congo; M. E. Holden unpubl.). Sympatric in SW Cameroon and NE DR Congo. Occurs in West and central Africa.

Graphiurus surdus. Similar mean head and body length (99.0 mm), ears shorter (mean 12.3 mm). Dorsal pelage usually greyish-brown, not rufous. Tail (mean 72 mm) absolutely and relatively shorter (ca. 73% of HB). Zygoma robust, and the anterior, superior margins are relatively straight when viewed from side (see Holden 1996). Palate longer (9.3 mm); anterior palatine foramina absolutely and relatively shorter (2.8 mm) and narrower (1.8 mm) (measurements listed are mean values from Cameroon, Equatorial Guinea and Gabon; Holden 1996). Not sympatric,

*Graphiurus christyi*

although both species have been collected in SW Cameroon and N DR Congo.

Graphiurus crassicaudatus. Smaller head and body length (mean 92.6 mm). Dorsal pelage rufous-brown, similar to some individuals of *G. christyi*. Skull shorter (26.6 mm). Breadth of skull (16.1 mm) and interorbital constriction (4.9 mm) markedly broader relative to skull length. Supraorbital ridges present. Anterior palatal foramina absolutely and relatively shorter (2.5 mm) and narrower (1.6 mm). Palate (9.4 mm) and upper toothrow (3.8 mm) absolutely and relatively longer (measurements listed are mean values from S Cameroon; M. E. Holden unpubl.). Not sympatric, though their distributions overlap in SW Cameroon; occurs in West and west-central Africa.

Distribution Endemic to Africa. Recorded from Rainforest BZ (mainly East Central Region) with one outlier in West Central Region. Recorded from NE DR Congo (many localities, all north of the Congo and Lualaba rivers) and SW Cameroon (one locality). A specimen from Inkongo, C DR Congo, identified as this species (Hatt 1940a) is, in fact, a specimen of *G. surdus* (Holden 1996).

Habitat Rainforest. According to Hatt (1940a), these dormice occur in high forest.

Abundance Little information and rarely encountered. The Lang–Chapin Congo Expedition collected 29 specimens at Medje, DR Congo, but caught only one specimen at each of the three other localities where they encountered this species. Robbins & Schlitter

(1981) obtained four individuals from Lolodorf, SW Cameroon, and Schlitter *et al.* (1985) collected eight individuals from Yalosemba, DR Congo.

Adaptations Arboreal and probably nocturnal. Nests in hollow trees (Hatt 1940a).

Foraging and Food Probably omnivorous, eating fruit, insects, seeds and nuts. Notes taken by the Lang–Chapin Congo Expedition indicated that the stomachs of four individuals contained ‘a whitish or somewhat greenish paste-like vegetable matter’ (Hatt 1940a).

Social and Reproductive Behaviour In DR Congo, five individuals were collected from a hollow tree that contained no nest: two ♂♂, two ♀♀ and one escaped (Hatt 1940a).

Reproduction and Population Structure Litter-size: probably 2–3 (Hatt 1940a). In DR Congo, a ♀ was found in Jan with two young (eyes closed); two additional young (eyes closed) were collected from a separate nest; and one pregnant ♀ contained three embryos (Hatt 1940a).

Predators, Parasites and Diseases Little information. Some specimens in museum collections have several louse exoskeletons attached to pelage and tail hairs

Conservation IUCN Category: Least Concern.

Measurements

Graphiurus christyi
 HB: 97.6 (86–107) mm, n = 27
 T: 79.8 (73–95) mm, n = 25
 HF: 18.0 (16–20) mm, n = 28
 E: 14.2 (12–17) mm, n = 27
 WT: 29.0 (25–33) g, n = 6
 GLS: 28.0 (26.7–29.7) mm, n = 23
 GWS: 15.1 (13.3–16.7) mm, n = 22
 P⁴–M³: 3.2 (3–3.3) mm, n = 29
 DR Congo (M. E. Holden unpubl.)

Key References Hatt 1940a; Holden 1996; Robbins & Schlitter 1981; Schlitter *et al.* 1985.

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Graphiurus crassicaudatus THICK-TAILED AFRICAN DORMOUSE

Fr. Graphiure à grosse queue; Ger. Dickschwanz-Bilch

Graphiurus crassicaudatus (Jentink, 1888). Notes from the Leyden Museum 10: 41–42. Hill Town, Du Queah River, Liberia.

Taxonomy Originally described in the genus *Claviglis*. Rosevear (1969) and Holden (1996) hypothesized that the morphological similarity between *G. crassicaudatus* and *G. nagtglasii* (formerly *G. hueti*) indicated a close phylogenetic relationship between the two species. In contrast, recent cladistic analysis of African dormice based on cranial and middle ear characters does not support this conclusion (Pavlinov & Potapova 1993, see also Holden 2005). Synonyms: *dorotheae* (see Allen 1939, Rosevear 1969). Subspecies: none. Chromosome number: not known.

Description Small dormouse. Dorsal pelage usually rufous-brown. Pelage soft and short (rump hairs 4–5 mm, guard hairs up to 10 mm). Ventral pelage grey washed with ochre, cream or white. Dorsal and ventral pelage colours clearly delineated. Head colour matches that of dorsal pelage; muzzle short. Eyes large; eye-mask conspicuous in some individuals. Ears brown, short and rounded. Postauricular patches usually not present. Hindfeet white, or white with a dark metatarsal streak. Tail short (ca. 65% of HB), hairs shorter at base (3–4 mm) and longer at tip (up to 27 mm). Tail colour generally matches that of dorsal pelage. A few white hairs are mixed throughout the tail, but tip is not white. Skull broad (16.1 mm), with vaulted braincase (height of braincase 7.9 mm) and conspicuously wide interorbital constriction (4.9 mm) with supraorbital ridges. Anterior chamber of auditory bullae usually markedly less inflated than posterior chambers. Zygomatic arches flare out at a 90 degree angle from the rostrum. Rostrum short and narrow, with short nasal bones (8.9 mm). Anterior palatal foramina comparatively short (mean 2.5 mm) and very narrow (mean 1.6 mm) relative to skull

length. Palate (9.4 mm) and upper toothrow (3.8 mm) relatively long (measurements listed are mean values from southern Cameroon; M. E. Holden unpubl.). Nipples: 1 + 1 + 2 = 8.

Geographic Variation None recorded.

Similar Species (size comparisons refer to mean values only)

Graphiurus lorraineus. Smaller head and body length (mean 83.0 mm). Dorsal pelage similar in colour. Skull shorter (24.5 mm) and narrower (13.8 mm), with much narrower interorbital constriction (4.3 mm) and without supraorbital ridges. Anterior palatal foramina 2.6 mm long, 1.7 mm wide. Palate (7.8 mm) and upper toothrow (3.1 mm) absolutely and relatively shorter, auditory bullae similar in length (7.2 mm), but relatively longer (measurements listed are mean values from DR Congo; M. E. Holden unpubl.). Sympatric at several localities in Liberia, Côte d’Ivoire and S Cameroon; occurs in West and central Africa.

Graphiurus surdus. Larger head and body length (mean 99.0 mm), with longer hindfeet (mean 20.8 mm). Dorsal pelage greyish-brown, with no rufous hue. Skull narrower (14.6 mm), with narrower interorbital constriction (4.5 mm) and without supraorbital ridges. Anterior palatal foramina 2.8 mm long, 1.8 mm wide. Upper toothrow (3.2 mm) absolutely and relatively shorter (measurements listed are mean values from Cameroon, Equatorial Guinea and Gabon; Holden 1996). Sympatric in SW Cameroon, also occurs in DR Congo.

Graphiurus christyi. Larger head and body length (mean 97.6 mm). Dorsal pelage sometimes similar in colour. Skull slightly longer



(28.0 mm). Breadth of skull (15.1 mm) and interorbital constriction (4.7 mm) narrower relative to skull length, and without supraorbital ridges. Anterior palatal foramina absolutely and relatively longer (3.0 mm) and wider (2.2 mm). Palate (8.5 mm) and upper toothrow (3.2 mm) absolutely and relatively shorter (measurements listed are mean values from DR Congo; M. E. Holden unpubl.). No records of sympatry, though geographic range overlaps in SW Cameroon; also occurs in DR Congo.

Distribution Endemic to Africa. Rainforest BZ (Western and West Central Regions) and Northern Rainforest–Savanna Mosaic. Recorded from Liberia and Guinea east to SW Cameroon (excluding Benin) and Bioko I. (see Rosevear 1969, Eisentraut 1973).

Habitat In or near primary and secondary rainforest.

Abundance Uncommon. The species is represented by a total of approximately 50 museum specimens, and it is considered rare or at least difficult to trap (Heim de Balsac 1967a, Robbins & Schlitter 1981, Happold 1987, Grubb *et al.* 1998).

Adaptations Arboreal. Individuals have been collected from hollow trees, on horizontal branches and vines, among bushes, among rocks

and in grass near houses (Sanderson 1940, Rosevear 1969, Robbins & Schlitter 1981; specimen labels), and even in a hole in a concrete culvert under railway tracks (Schlitter *et al.* 1985). In Nigeria, Sanderson (1940) found large, spherical nests a few feet above the ground in dense vegetation and, in Cameroon, he found five individuals living in a nest in a hollow tree. This nest was made of dead leaves, and lined with fibre from a species of nut that lay in large quantities on the surrounding ground. (Rosevear 1969 correctly noted that the specimens Sanderson (1940) identified as *Claviglis spurrelli* and *Claviglis haedulus* actually represent *G. crassicaudatus*.) Captive animals adapted the nests of weaver-birds for their use (Rosevear 1969).

Foraging and Food Probably omnivorous, consuming nuts (Rosevear 1969, Robbins & Schlitter 1981), insects (Rosevear 1969) and probably fruit.

Social and Reproductive Behaviour In Cameroon, Sanderson (1940) reported five adults in the same nest in a hollow tree. Two ♀♀ were caught, the other three escaped. This species bred readily in captivity (Rosevear 1969).

Reproduction and Population Structure No information.

Predators, Parasites and Diseases An ectoparasitic hoplopleurid louse, *Schizophthiris* sp., has been recorded on this species in Liberia (Kuhn & Ludwig 1965).

Conservation IUCN Category: Data Deficient.

Measurements

Graphiurus crassicaudatus

HB: 92.6 (83–98) mm, n = 11

T: 59.4 (55–70) mm, n = 9

HF: 17.7 (16–19) mm, n = 12

E: 13 (11–14) mm, n = 9

WT: 24.8 (20–29) g, n = 6

GLS: 26.6 (25.2–27.8) mm, n = 8

GWS: 16.1 (15.7–16.6) mm, n = 6

P⁴–M³: 3.8 (3.4–4.2) mm, n = 14

S Cameroon (M. E. Holden unpubl.)

Key References Holden 1996; Robbins & Schlitter 1981; Rosevear 1969.

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Graphiurus johnstoni JOHNSTON'S AFRICAN DORMOUSE

Fr. Graphiure de Johnston; Ger. Johnstons Bilch

Graphiurus johnstoni Thomas, 1898. Proc. Zool. Soc. Lond. 1897: 934. Zomba, Malawi.

Taxonomy Ansell & Dowsett (1988), Ansell (1989b), Happold & Happold (1989a) and Holden (1993) synonymized *johnstoni* under *G. kelleni*. Recent re-examination and comparisons of museum specimens (including all holotypes), and preliminary multivariate

analyses, indicate that *G. johnstoni* is a separate valid species (M. E. Holden unpubl.). Morphologically, it is closely related to *G. lorrainae* and distinct from *G. kelleni*. Here, *G. johnstoni* is retained as a valid species, pending further revision of the genus (see also Holden

2005). Few specimens exist that can be attributed to *G. johnstoni* with certainty. If future research indicates that *G. johnstoni* and *G. lorrainaeus* are conspecific, the latter would be a junior synonym of *G. johnstoni*; this would substantially modify and enlarge the geographic range of what is now considered *G. johnstoni*. Synonyms: none. Chromosome number: not known.

Description Small dormouse. Dorsal pelage reddish-brown. Dorsal pelage soft and short (rump hairs 5–6 mm, guard hairs up to 8–9 mm). Ventral pelage grey, moderately suffused with buff or cream. Dorsal and ventral pelage colours not clearly delineated. Head colour matches that of dorsal pelage. Eyes large; eye-mask inconspicuous. Ears brown, short and rounded. Cheeks cream or grey suffused with cream. Postauricular patches not present or inconspicuous. Hindfeet cream with dark metatarsal streak. Tail long (ca. 92% of HB), hairs shorter at base (2–3 mm) and longer at tip (up to 19 mm). Tail appears splayed because the hairs project laterally. Tail colour generally matches that of dorsal pelage and is uniform in colour, with sparse or no white hairs, and without white at tip. Skull short (23.6 mm), moderately vaulted (height of braincase 7.3 mm) and broad (13.9 mm) with relatively short rostrum (length of nasal bones 8.4 mm). Interorbital constriction broad (4.0 mm), tooththrow long (3.4 mm) and upper premolar wide (1.0 mm) relative to skull length. Anterior palatal foramina moderately long (2.7 mm) and moderately narrow (mean 1.7 mm) relative to skull length. Auditory bullae relatively short (6.8 mm) and moderately inflated. Nipples: 1 + 1 + 2 = 8.

Geographic Variation None recorded.

Similar Species (size comparisons refer to mean values only)

Graphiurus lorrainaeus. Larger head and body length (mean 83.0 mm). Ear (12.6 mm) slightly larger. Tail relatively shorter (65.7 mm) with similar colouration. Dorsal pelage colour similar. Skull slightly longer (24.5 mm). Rostrum relatively short as in *G. johnstoni*, but length of nasal bones absolutely longer (9.1 mm). Anterior palatal foramina 2.6 mm long, 1.7 mm wide. Upper tooththrow slightly shorter (3.1 mm) and upper premolar narrower (0.8 mm). Not sympatric; *G. lorrainaeus* occurs in West and central Africa.

Graphiurus microtis. Larger head and body length (98.8 mm). Tail relatively shorter (75.2 mm), usually with white hairs mixed throughout, and with conspicuous white tip. Dorsal pelage colour sometimes similar, but beige or grey in some populations. Skull longer (27.4 mm) and wider (15.0 mm), auditory bullae longer (8.1 mm) and more inflated. Interorbital constriction (3.9 mm) similar in breadth, but relatively narrower. Anterior palatal foramina absolutely and relatively longer (3.4 mm) and wider (2.1 mm). Tooth row shorter (3.0 mm) both absolutely and relative to skull length. Sympatric in Thyolo, Malawi, but probably not syntopic; widespread in savannas of eastern and central Africa.

Distribution Endemic to Africa. Zambezian Woodland BZ. Recorded only from S Malawi; limits of geographic range unknown.



Graphiurus johnstoni

Habitat Little information. Habitats on the Shire Highlands (ca. 900–1500 m) include sub-montane forests, miombo woodlands, farmlands, tobacco fields and secondary growth (Happold & Happold 1989a, b, 1997, 1998). Several specimens have been found in houses surrounded by ornamental gardens. Mean annual rainfall is ca. 1300 mm, with considerable annual variation.

Abundance No information. Rarely encountered.

Remarks Little information. Probably arboreal and nocturnal. Happold & Happold (1997) captured an individual in a farmhouse, indicating that this species may nest in human dwellings.

Conservation IUCN Category: Data Deficient.

Measurements

Graphiurus johnstoni

HB: 74.3 (69–84) mm, n = 3

T: 68.5 (65–75.5) mm, n = 3

HF: 16 (15–17) mm, n = 4

E: 11.8 (11–12) mm, n = 4

WT: n. d.

GLS: 23.3, 23.9 mm, n = 2

GWS: 13.6, 14.1 mm, n = 2

P⁴–M³: 3.4 (3.3–3.5) mm, n = 3

S Malawi (M. E. Holden unpubl.).

Key References Ansell 1989b; Ansell & Dowsett 1988; Happold & Happold 1989a, 1997.

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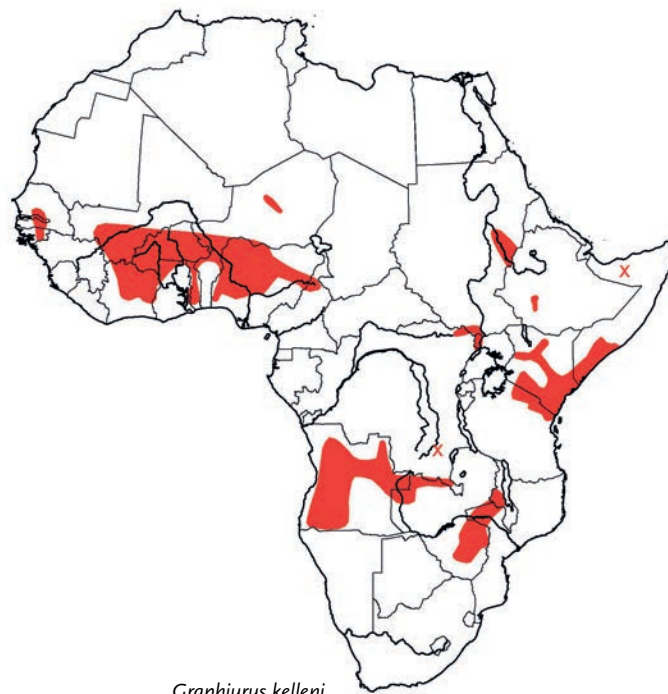
Graphiurus kelleni KELLEN'S AFRICAN DORMOUSE

Fr. Graphiure nain (Graphiure de Kellen); Ger. Kellens Bilch

Graphiurus kelleni (Reuvens, 1890). Notes from the Leyden Museum 13: 74. Reuvens originally listed Damaraland, Namibia, as the type locality; this was later emended to 'Damara-land', Mossamedes district, Angola (Hill and Carter 1941).

Taxonomy Originally described in genus *Eliomys*. Comparisons of museum specimens (including holotypes) and multivariate analyses of cranial morphology of *G. kelleni*, *G. parvus* and *G. olga* (M. E. Holden unpubl.) support the recognition of only one species (*G. kelleni*), and hence *olga* and *parvus*, previously considered as separate species (Holden 1993), are now placed as synonyms. These and other synonyms listed below have either been treated as separate species or included in species other than *G. kelleni* (see summary in Holden 1996, 2005). Ansell (1978) listed the species as *G. johnstoni* (recognized here as a separate valid species), but later (Ansell & Dowsett 1988, Ansell 1989b) referred to it as *G. kelleni*. The species requires taxonomic revision. Future studies will need to include larger samples, specimens from poorly collected localities and genetic data; such studies may well show that two or more separate species are contained within *G. kelleni*. No specimens of *G. kelleni* have been identified from South Africa (M. E. Holden unpubl.); however, some South African populations that are now placed in *G. murinus* are small in size. Future study and comparison of those populations may show that they are *G. kelleni* or an as yet undescribed species. Schlitter *et al.* (1985) discussed taxonomic problems and historical treatment of this species, and pointed out that *G. kelleni* is the oldest available scientific name. Synonyms: *ansorgei*, *brockmani*, *cuanzensis*, *dollmani*, *foxi*, *internus*, *nanus*, *olga*, *parvus*, *personatus*, *tasmani*. Subspecies: none. Chromosome number: $2n = 70$ (Dobigny *et al.* 2002b).

Description Small dormouse. Dorsal pelage various shades of brown, beige or grey, sometimes with golden or reddish hue, with darkening of pelage towards the mid-line of the head and back in some individuals. Dorsal pelage silky, sleek in some populations, thick in others (rump hairs 6–7 mm, guard hairs up to 11 mm). Ventral pelage usually white or cream, lightly or moderately suffused with grey. Dorsal and ventral pelage colours clearly delineated. Head colour usually matches that of dorsal pelage, sometimes paler towards muzzle. Eyes large; eye-mask conspicuous. Ears brown, medium or large, rounded. Cheeks cream or white, forming part of a pale lateral stripe that extends from cheeks to shoulders. Cream or white postauricular patches usually present. Hindfeet white, or white with dark metatarsal streak. Tail moderately long (ca. 82% of HB), tail hairs shorter at base (2–3 mm) and longer at tip (up to 20 mm). Tail appears splayed in some populations (particularly in Angola, Zimbabwe and Zambia) because hairs project laterally. Dorsal tail colour matches that of dorsal pelage, often laterally fringed with white hairs and with faint or conspicuous white at tip. Ventral tail colour usually paler than dorsal tail colour. Skull short (24.0 mm), moderately vaulted (height of braincase 7.0 mm) and moderately broad (13.5 mm), sometimes gracile. Interorbital constriction moderately narrow (4.0 mm), anterior palatal foramina relatively long (2.9 mm) and auditory bullae long (7.8 mm) and inflated relative to skull length (measurements listed are mean values from Zambezi [formerly Balovale], Zambia; M. E. Holden unpubl.). Nipples: $1 + 1 + 2 = 8$.

*Graphiurus kelleni*

Geographic Variation Certain populations of *G. kelleni* exhibit variations in the colour and texture of dorsal pelage and in skull morphology that are consistent within these populations; e.g. in Somalia, dorsal pelage is sleek and pale reddish-tan; in montane populations in Kenya, dorsal pelage is thick and medium golden-brown. Some skulls in certain populations are very delicately built, others are robust; some are comparatively flat, others moderately vaulted; some have long and inflated auditory bullae, others exhibit short and only moderately inflated auditory bullae relative to skull length. On the basis of predominantly small sample sizes, and inadequate sampling over the vast geographic range of this species, preliminary morphometric analyses support the recognition of just a single species without subspecies.

Similar Species (size comparisons refer to mean values only)

G. microtis. Larger head and body length (mean 98.8 mm); ears longer (mean 15.5 mm). Dorsal pelage colour sometimes similar. Tail usually has white hairs mixed throughout, and conspicuous white tip. Skull longer (27.4 mm) and broader (15.0 mm). Anterior palatal foramina 3.4 mm long, 2.1 mm wide. Breadth of interorbital constriction (3.9 mm) and length of upper toothrow (3.0 mm) absolutely similar so relatively smaller in *G. microtis*. Auditory bullae absolutely slightly longer (8.1 mm), or of similar length in some populations, but relatively shorter. Sympatric in savannas throughout much of sub-Saharan Africa.

G. murinus. Larger head and body length (mean 91.5 mm). Hindfeet (18.5 mm) longer, ears (13.3 mm) absolutely and relatively

shorter. Dorsal pelage colour sometimes similar. Skull longer (26.4 mm), more vaulted (height of braincase 8.1 mm) and broader (14.2 mm). Interorbital constriction slightly broader (4.5 mm) and upper toothrow slightly longer (3.1 mm). Anterior palatal foramina 3.1 mm long, 1.9 mm wide. Auditory bullae shorter (7.1 mm) and less inflated relative to skull length (measurements listed are mean values from Mt Kenya; M. E. Holden unpubl.). Generally not sympatric, although they have been captured in close proximity at several Kenyan localities. Occurs in forests throughout much of sub-Saharan Africa.

Distribution Endemic to Africa. Recorded from parts of Sahel Savanna, Sudan Savanna, Guinea Savanna and Somalia–Masai Bushland BZs; also Zambezian Woodland BZ as far south as Angola, Malawi, Zimbabwe and Mozambique at altitudes up to 1524 m (Holden, 2005). Not recorded from Namibia, Botswana and South Africa.

Habitat Woodland savanna, riverine woodland, rocky areas including caves, disturbed areas and human dwellings. Specimens have been captured in or near dom palms (*Hyphaene thebaica*), thorn trees (*Acacia* spp.) and in miombo (*Brachystegia*) trees. Also occurs on mountains in East Africa (up to at least 1524 m), in rocky areas, and in caves (Osgood 1910, Dollman 1912, Hollister 1919; specimen labels). Less commonly found in disturbed areas, such as woodpiles, corn fields and in human dwellings (de Winton 1896, Stanley *et al.* 2002; specimen labels).

Abundance Little information. Comprised 1.7% of muroid and glirid rodents captured in savanna at Foro, Côte d'Ivoire, and 3.5% of muroid and glirid rodents captured in Guinea savanna in C Côte d'Ivoire (Gautun *et al.* 1991). Specimen labels from most localities indicate that the species is uncommon, but very large series from certain localities (e.g. C Angola, NE Zambia) indicate that it is common in at least certain parts of its range. No estimates of population density.

Adaptations Arboreal and nocturnal. These dormice frequently nest in crevices under bark, or in holes in savanna trees. Two nest holes were 0.5 m and 1 m above ground (specimen labels), and one nest was made of leaves and grass (Hill 1941). Several individuals were caught in nests of weaver-birds on *Acacia* trees and in the mud nests of swallows under roofs of caves or on undersides of rocks (Hollister 1919; specimen labels). Reported to utilize abandoned spider (*Stegodyphs* sp.) nests (Roberts 1951; specimen label) and abandoned beehives (Hill 1941). A few individuals have been caught in wood piles, in roofs of African huts and in pantries (Lawrence & Loveridge 1953; specimen labels).

Foraging and Food Probably omnivorous. In Somalia, one individual was caught in a trap baited with fresh meat (specimen label).

Social and Reproductive Behaviour Little information. Males are apparently solitary. Lactating ♀♀ are often caught with young (specimen labels). Vocalizations of this dormouse have frequency components that range from ca. 1 kHz to well into the ultrasonic range above 20 kHz. Most vocalizations (termed 'kecker/shrieks' and recorded from both sexes) seem to occur during agonistic behaviour (Hutterer & Peters 2002). Vocalizations characterized as 'twitters' also recorded from both sexes in non-aggressive close-range situations.

Reproduction and Population Structure Litter-size: 2–4 (Hollister 1919, Hill 1941; specimen labels). Young individuals and lactating ♀♀ found in many months of the year throughout the range; however, paucity of information does not allow any conclusions on reproductive seasons or reproductive strategy. The scattered information includes: Senegal, young in Jul; one young in Aug (Côte d'Ivoire); young in Apr (Benin); pregnant ♀♀ in Nov (Hollister 1919) and Dec, and young in Nov and Apr (Kenya); lactating ♀♀ in Dec and young in Apr (Zimbabwe); lactating ♀♀ in Sep and Oct, and young in Jan (NW Zambia); and young in Oct (Angola) (specimen labels).

Predators, Parasites and Diseases Principal host for the hoplopleurid louse *Schizophthirus graphiuri* (Durden & Musser 1994, Pajot 2000).

Conservation IUCN Category: Least Concern.

Measurements

Graphiurus kelleni

HB: 82.4 (75–92) mm, n = 14

T: 68.3 (54–81) mm, n = 13

HF: 16.0 (15.3–16.5) mm, n = 14

E: 14.8 (14–16) mm, n = 14

WT: 19.1 (10.9–23.5) g, n = 8*

GLS: 24.0 (23.1–24.5) mm, n = 13

GWS: 13.5 (12.9–14.1) mm, n = 14

P⁴–M³: 2.9 (2.8–3.0) mm, n = 13

Body and skull measurements: Zambezi (Balovale), Zambia (M. E. Holden unpubl.)

*Zimbabwe (M. E. Holden unpubl.)

Key References Ansell 1989b; Holden 2005; Hollister 1919.

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Graphiurus lorrainaeus LORRAINE'S AFRICAN DORMOUSE

Fr. Graphiure de Lorrain; Ger. Lorraines Bilch

Graphiurus lorrainaeus Dollman, 1910. Ann. Mag. Nat. Hist., ser. 8, 5: 285. Molegbwe, south of the Setema Rapids, Welle (Uele) River, DR Congo.

Taxonomy The named form *lorrainaeus*, originally described as a valid species, has been considered historically as a subspecies or synonym of *G. murinus* (Rosevear 1969, Eisentraut 1973, Genest-Villard 1978a), or as a valid species (Hatt 1940a, Robbins & Schlitter 1981, Holden 1993, 1996, 2005). Populations that are here placed in *G. lorrainaeus* (*haedulus* from Cameroon, *spurrelli* from Ghana) have never been thoroughly analysed and compared to the population of *G. lorrainaeus* from E DR Congo (see Geographic Variation). Future studies may show that one or more populations of what now comprises *G. lorrainaeus* merits recognition as one or more separate valid species. A comparative study of museum specimens and preliminary multivariate analyses (M. E. Holden unpubl.) showed that *G. lorrainaeus* appears to represent a valid species distinct from but closely related to *G. johnstoni*. If future research indicates that the two species are conspecific, *G. lorrainaeus* would become a junior synonym of *G. johnstoni*. Synonyms: *haedulus*, *spurrelli*. Subspecies: none. Chromosome number: $2n = 70$ (an individual from Côte d'Ivoire identified as *G. murinus* (Tranier & Dosso 1979) but probably represents *G. lorrainaeus*).

Description Small dormouse. Dorsal pelage reddish-brown, occasionally sandy or golden-brown. Dorsal pelage soft and short (rump hairs 5–6 mm, guard hairs up to 9 mm). Ventral pelage dark grey washed with cream or ochre, or mostly cream. Dorsal and ventral pelage colours usually not clearly delineated. Head colour matches that of dorsal pelage. Eyes large; eye-mask conspicuous in some individuals. Ears brown, short and rounded. Cheeks dark grey washed with cream or ochre, or predominantly cream. Postauricular patches usually not present, but white postauricular patches exhibited by some individuals from Cameroon. Hindfeet usually white with dark metatarsal streak. Tail moderately long (ca. 79% of HB), tail hairs shorter at base (2–3 mm) and longer at tip (up to 21 mm). Tail appears splayed because the hairs project laterally. Tail colour generally matches that of dorsal pelage and is uniform in colour, with sparse or no white hairs, and usually without white tip. Tail may be shorter than normal due to injury, ending in a thick, brush-like tuft of hairs (white in colour). Skull short (24.5 mm), broad (13.8 mm) and moderately vaulted (height of braincase 7.2 mm). Interorbital constriction (4.3 mm) relatively broad. Anterior chamber of auditory bullae markedly less inflated than posterior chambers in some individuals. Rostrum relatively short with short nasal bones (9.1 mm). Anterior palatal foramina comparatively short (mean 2.6 mm) and narrow (mean 1.7 mm), interorbital constriction moderately broad (4.3 mm), palate moderately long (7.8 mm), upper tooththrow moderately long (3.1 mm) and auditory bullae long relative to skull length (measurements listed are mean values from DR Congo; M. E. Holden unpubl.). Nipples: $1 + 1 + 2 = 8$.

Geographic Variation The populations of *G. lorrainaeus* in E DR Congo (*lorrainaeus*) and in S Cameroon (*haedulus*) are smaller than those from Ghana (*spurrelli*). Montane populations in Cameroon (*haedulus*) exhibit morphological and ecological differences compared with *lorrainaeus* and *spurrelli* (see Habitat).

Similar Species (size comparisons refer to mean values only)

Graphiurus christyi. Larger head and body length (mean 97.6 mm), with longer hindfeet (mean 18.0 mm), and longer ears (mean 14.2 mm). Dorsal pelage usually golden-brown or greyish-brown. Skull (28.0 mm) longer, with elongate, higher rostrum and longer nasal bones (10.5 mm); nasal bones and premaxilla extend well beyond incisors from lateral and ventral view. Anterior palatal foramina 3.0 mm long, 2.2 mm wide. Palate absolutely and relatively longer (8.5 mm). Interorbital constriction absolutely broader (4.7 mm), but narrower relative to skull length. Upper tooththrow similar in absolute length (3.2 mm), but relatively shorter. Auditory bullae average slightly longer (7.4 mm), but are relatively shorter (measurements listed are mean values from DR Congo; M. E. Holden unpubl.). Sympatric in NE DR Congo and SW Cameroon. Occurs in NE DR Congo and SW Cameroon.

Graphiurus crassicaudatus. Larger head and body length (mean 92.6 mm). Dorsal pelage similar in colour. Skull longer (26.6 mm) and broader (16.1 mm) with absolutely and relatively broader interorbital constriction (4.9 mm). Anterior palatal foramina absolutely similar in length (2.5 mm) and breadth (1.6 mm), but relatively shorter and narrower. Auditory bullae shorter (6.7 mm) relative to skull length. Palate (9.4 mm) and upper tooththrow (3.8 mm) absolutely and relatively longer (measurements listed are mean values from S Cameroon; M. E. Holden unpubl.). Sympatric at several localities in Liberia, Côte d'Ivoire and SW Cameroon. Occurs in W and WC Africa.

Graphiurus surdus. Larger head and body length (mean 99.0 mm), hindfeet (mean 20.8 mm) longer but relatively similar. Ears similar in absolute length (12.3 mm), but relatively shorter. Dorsal pelage greyish-brown. Skull (27.6 mm) longer; interorbital constriction absolutely broader (4.5 mm), but narrower relative to skull length. Zygomatic arch straight in lateral view (figured in Holden 1996). Palate absolutely and relatively longer (9.3 mm). Anterior palatal foramina similar in length (2.8 mm) and breadth (1.8 mm). Upper tooththrow (3.2 mm) and auditory bullae (7.3 mm) similar in absolute length, but relatively shorter (measurements listed are mean values from Cameroon, Equatorial Guinea and Gabon; Holden 1996). Sympatric in SW Cameroon, Equatorial Guinea and DR Congo. Occurs in C Africa.

Graphiurus johnstoni. Smaller head and body length (mean 74.3 mm), ear (mean 11.8 mm) slightly smaller. Tail relatively longer (68.5 mm) with similar colouration. Dorsal pelage colour similar. Skull slightly shorter (23.6 mm). Rostrum relatively short as in *G. lorrainaeus*, but length of nasal bones absolutely shorter (8.4 mm). Anterior palatal foramina absolutely similar in length (2.7 mm) and breadth (1.7 mm), but relatively longer. Upper tooththrow slightly longer (3.4 mm) and upper premolar broader (1.0 mm). Not sympatric. Occurs in S Malawi.



Graphiurus lorrainaeus

Distribution Endemic to Africa. Rainforest, Guinea Savanna and northern part of Zambezan Woodland BZs, and Rainforest–Savanna Mosaics. Recorded from Guinea to Cameroon, Central African Republic, Congo, E DR Congo, NE Angola and N Zambia; also Bioko I. (see Holden 2005). Not recorded from Togo, Benin and Nigeria west of Niger R. Specimens recorded from Gambia, originally thought to be this species (Schlitter *et al.* 1985) are now considered as *G. kelleni* (Grubb *et al.* 1998, Holden 2005). The western distributional limit for this species is Sierra Leone (Holden 1993, Grubb *et al.* 1998); specimens identified as ‘*Graphiurus murinus*’ (presumably *spurrelli*) from wooded savanna in Senegal (Hubert *et al.* 1973) cannot be substantiated, and are not included here.

Habitat Gallery forests, forest margins, woodland savanna and disturbed areas (including banana, cocoa, palmyra (*Borassus*) and pawpaw farms, and occupied and abandoned buildings) (Hatt 1940a, Heim de Balsac 1967a, Rosevear 1969, Jeffrey 1973, Robbins & Schlitter 1981, Schlitter *et al.* 1985, Grubb *et al.* 1998). In Côte d’Ivoire, Dosso (1975a) noted that the plant *Microdesmis*, commonly found in secondary and disturbed forest, was associated with areas where *G. lorrainaeus* was caught. These dormice were never trapped in, and seemed to avoid, primary forest (Hatt 1940a, Jeffrey 1973). In Cameroon, Eisentraut (1963; and specimen labels) trapped individuals in montane forest at altitudes of 1700–2100 m, but these populations (identified as *haedulus*) may represent a different species (see discussion under Taxonomy).

Abundance Relatively common compared with other forest dormice such as *G. crassicaudatus* and *G. surdus* (Hatt 1940a, Heim de Balsac & Lamotte 1958, Heim de Balsac 1967a, Rosevear 1969, Gautun *et al.* 1986). Comprised 0.77% of muroid and glirid rodents captured at Lamto, Côte d’Ivoire (Dosso 1975a), although in a later survey at Lamto they comprised 7.6% of captures (Traore *et al.* 1980). At Foro, Côte d’Ivoire, comprised 2.1% of rodent captures (Traore *et al.* 1980).

Adaptations Arboreal, although some individuals seem to spend much time on the ground (Rosevear 1969). Nocturnal. Distribution seems to depend on the presence of suitable nesting sites, such as cavities in trees in gallery forest and isolated savanna trees near forest, even in disturbed areas (Verheyen & Verschuren 1966, Rosevear 1969). Many individuals have been caught in or near occupied or abandoned buildings (Verheyen & Verschuren 1966, Rosevear 1969, Jeffrey 1973, Robbins & Schlitter 1981; specimen labels). In C Africa, some individuals have been found nesting in rocky caves (Verheyen & Verschuren 1966). Others were found in abandoned nests of swallows (Hatt 1940a, Verheyen & Verschuren 1966). One such nest (Hatt 1940a) was occupied by an active nest of paper wasps, and the dormice had to crawl upside down on a nearly horizontal stone surface to enter it. Nests have also been found amongst epiphytic ferns (Verheyen & Verschuren 1966) and in a cocoa pod (Schouteden 1946). In Sierra Leone, individuals were caught in spherical nests constructed of pappus. Eisentraut (1963) caught specimens of montane populations in Cameroon in traps set 6–10 m high on large diagonal or horizontal branches near holes in trees; individuals were never trapped on the ground, another indication that this population may represent a different species.

These dormice enter torpor under certain conditions. Lachiver & Petter (1969) found that individuals from Central African Republic became lethargic when experiencing sudden shifts from high to low ambient temperature, or when deprived of food at low temperature. Eisentraut (1962) could not induce torpor in individuals from Cameroon.

Foraging and Food Probably omnivorous, consuming fruit, insects, seeds and nuts. In Liberia, Central African Republic and DR Congo, individuals have been caught in banana plantations, where they reportedly ate the fruit (Hatt 1940a, Chippaux & Pujol 1964, Coe 1975). They have also been caught in areas where palmyra (*Borassus*) (Heim de Balsac 1967a), pawpaw (Jeffrey 1973), *Microdesmis* (Dosso 1975a), cassava, cocoa, oil palm, plantains, *Raphia* and yams are common (specimen labels). The type specimen of *haedulus* was noted to have been ‘caught in bushes eating seeds of *Piper subpellatum*’, a species of pepper (specimen label). Four specimens were taken from a nest containing the remains of several hundred earwigs (Hatt 1940). Verheyen & Verschuren (1966) saw an individual running and jumping after termites, finally capturing them mostly in mid-air.

Social and Reproductive Behaviour Lactating ♀♀ are often caught with young. In DR Congo, one adult ♀ was nesting in an old double nest of a swallow with her three ‘well-grown young’ (Hatt 1940a), indicating that offspring may stay in the nest past weaning. An adult ♂, in captivity, was observed to be very lively and aggressive. It moved its tail up and down with the hairs spread wide, and when excited would chatter ‘gak gak’ repeated four or five times in succession. These dormice reportedly bite ‘furiously’ (H. Lang in Hatt 1940a).

Reproduction and Population Structure Litter-size: 2–7. Mostly 2–4 nestlings or embryos are reported (Hatt 1940a, Eisentraut 1963, Jeffrey 1973). In Côte d’Ivoire, Heim de Balsac (1967a) captured one ♀ with six naked young, and another with a litter of seven (months of capture not given). These two litters are the largest recorded for this species. In Ghana and Cameroon,

pregnant ♀♀ have been collected in Jan, Mar and Jul (Eisentraut 1963, Jeffrey 1973). In Ghana, a lactating ♀ with three placental scars was captured in Nov (Jeffrey 1973).

Predators, Parasites and Diseases Predators include snakes and owls. Remains have been found in the stomach of a green mamba *Dendraspis viridis* (Jeffrey 1973) and in the pellet of a Barn Owl *Tyto alba* (Heim de Balsac & Lamotte 1958).

Conservation IUCN Category: Least Concern.

Measurements

Graphiurus lorrainaeus

HB: 83.0 (72–93) mm, n = 19

T: 65.7 (54–74) mm, n = 16

HF: 16.5 (14–19) mm, n = 20

E: 12.6 (9–15) mm, n = 18

WT: 16.8 (12–24) g, n = 5

GLS: 24.5 (22.7–26.1) mm, n = 21

GWS: 13.8 (12.2–14.9) mm, n = 15

P⁴–M³: 3.1 (2.8–3.4) mm, n = 29

DR Congo (M. E. Holden unpubl.)

Key References Eisentraut 1963; Grubb *et al.* 1998; Hatt 1940a; Robbins & Schlitter 1981; Rosevear 1969.

Mary Ellen Holden

Graphiurus microtis NOACK'S AFRICAN DORMOUSE

Fr. Graphiure de Noack; Ger. Noack's Bilch

Graphiurus microtis (Noack, 1887). Zoologische Jahrbücher 2: 248. Qua Mpala, Marungu, DR Congo.

Taxonomy Originally described in genus *Eliomys*. The type specimen of *G. microtis* has been lost, but Noack's (1887) figure depicts a dormouse whose skull morphology agrees with specimens of *G. microtis* from regions near the type locality (Holden 2005). The taxon *microtis* has historically been listed as a synonym or valid subspecies of *G. murinus* (Allen 1939, Ellerman *et al.* 1953, Genest-Villard 1978a). Genest-Villard (1978a) separated what she considered to be the 'savanna subspecies' of *G. murinus* from the 'forest subspecies', and considered *G. m. microtis* to be one of several valid savanna subspecies. Ansell (1989a) agreed, but considered that the three savanna subspecies comprised a single valid species, *G. microtis*, on the basis of morphological and ecological differences, a position endorsed by Holden (1993, 2005).

Holden (1996) summarized the historical taxonomic arrangements of *G. murinus* and other species of *Graphiurus*. Many of the 76 specific and subspecific names proposed for African Dormice are synonyms of *G. murinus* or *G. microtis*. Because *G. microtis* is now recognized as a valid species (Ansell & Dowsett 1988, Ansell 1989a, Holden 1993, 2005), synonyms associated with it have traditionally been listed as synonyms of *G. murinus*. Holden (1993) did not separate the synonyms associated with *G. murinus* and *G. microtis*, but the taxonomy presented here results from further examination of specimens, data and multivariate analyses (M. E. Holden unpubl.). Historically, many authors have not recognized *G. microtis* as a valid species, and the data given in their papers are thus composite for both species; when such publications are cited here, only the sections relevant to *G. microtis* as outlined in this account are pertinent. The species requires taxonomic revision; significant geographic variation exists, and it is likely that two or more separate species are contained within *G. microtis*. Synonyms: *albolineata*, *butleri*, *etoschae*, *griselda*, *littoralis*, *marrensis*, *?orobinus*, *pretoriae*, *schneideri*, *smithii*, *streeteri*, *sudanensis*, *tzaneenensis*, *vandami*, *woosnami* (Holden 2005). Subspecies: none. Chromosome number: 2n = 46 (Transvaal, South Africa; D. N. MacFadyen pers. comm.; see species profile for *G. murinus* for discussion of karyotypes).

Description Small dormouse. Dorsal pelage various shades of brown, beige or grey, sometimes with golden or reddish hue, with

darkening towards the mid-line of head and back in some individuals. Dorsal pelage usually sleek, but moderately thick in some populations (rump hairs 6–8 mm, guard hairs up to 13 mm). Ventral pelage usually white or cream, slightly or moderately suffused with grey. Dorsal and ventral pelage colours clearly delineated. Head colour usually matches that of dorsal pelage, sometimes becoming paler towards muzzle. Eyes large; eye-mask conspicuous. Ears brown, medium or large, rounded. Cheeks cream or white, forming part of a pale lateral stripe that extends from cheeks to shoulders. Cream or white postauricular patches usually present. Hindfeet white, or white with dark metatarsal streak. Tail moderately long (ca. 76% of HB), hairs shorter at base (5–8 mm) and longer at tip (up to 26 mm). Tail colour generally matches that of dorsal pelage. White hairs are usually mixed throughout tail; tip white. Skull moderately long (27.4 mm) with slightly to moderately vaulted braincase (height of braincase 7.5 mm), and relatively long anterior palatal foramina (3.4 mm). Anterior palatal foramina moderately long (mean 3.4 mm) and wide (mean 2.1 mm). Interorbital constriction narrow (3.9 mm) and auditory bullae usually long (8.1 mm) and inflated relative to skull length. Nipples: 1 + 1 + 2 = 8.

Geographic Variation Certain populations of this dormouse exhibit variations in the colour of the dorsal pelage and in skull morphologies that are consistent within these populations; e.g. in C Botswana, dorsal pelage colour is ash-grey and skulls tend to be long and comparatively flat, with a narrow interorbital constriction. In nearby Namibia, dorsal pelage colour is also grey, but skulls are shorter and more vaulted, with a broader interorbital constriction. Other populations, e.g. certain populations in Uganda and Sudan, have sandy- to medium-brown dorsal pelage, a long and comparatively vaulted skull with long anterior palatal foramina, broad interorbital constriction, and greatly inflated auditory bullae. Differences like these are found throughout the range of *G. microtis*. Some populations have such distinctive morphologies that future studies may show that one or more of them is a separate valid species.

Similar Species (size comparisons refer to mean values only)

Graphiurus angolensis: Similar head and body length (mean 98.8 mm).

Tail (mean 79.2 mm) and hindfeet (mean 18.4 mm) absolutely and relatively longer. Dorsal pelage sometimes similar in colour. Skull similar in length (28.2 mm), but slightly broader (15.5 mm) and more vaulted (height of braincase 7.9 mm). Auditory bullae markedly longer (9.0 mm) and more inflated relative to skull length (measurements listed are mean values from Kabompo and Zambezi [formerly Balovale], Zambia; M. E. Holden unpubl.). Parapatric in NW Zambia (Ansell 1978). Occurs in Angola and NW Zambia.

Graphiurus johnstoni: Smaller head and body length (mean 74.3 mm).

Tail relatively longer (mean 68.5 mm). Dorsal pelage colour sometimes similar, tail colour usually uniform and without white tip. Skull shorter (23.6 mm) and narrower (13.9 mm). Interorbital constriction (4.0 mm) similar in breadth, but relatively broader. Anterior palatal foramina absolutely and relatively shorter. Upper tooththrow (3.4 mm) longer and auditory bullae (6.8 mm) shorter both absolutely and relative to skull length (measurements listed are mean values from S Malawi; M. E. Holden unpubl.). Sympatric in Thyolo, Malawi, but probably not syntopic. Currently known to occur only in S Malawi.

Graphiurus kelleni: Smaller head and body length (mean 82.4 mm); ears shorter (mean 14.8 mm). Dorsal pelage colour sometimes similar. Tail usually more uniform in colour, with inconspicuous white tip. Skull shorter (24.0 mm) and narrower (13.5 mm). Breadth of interorbital constriction (4.0 mm) and length of upper tooththrow (2.9 mm) absolutely similar, so relatively larger in *G. kelleni*. Auditory bullae somewhat shorter (7.8 mm) both absolutely and relative to skull length (measurements listed are mean values from Zambezi, Zambia; M. E. Holden unpubl.). Sympatric in savannas throughout much of sub-Saharan Africa.

Graphiurus murinus: Similar head and body length (mean 91.5 mm). Hindfeet (18.5 mm) longer, and ears (13.3 mm) shorter. Dorsal pelage colour sometimes similar. Postauricular patches inconspicuous or not present. Ventral pelage colour usually greyer and not clearly delineated from dorsal pelage. Hindfeet usually have dark metatarsal streak. Tail usually uniform in colour, white tip inconspicuous or absent. Skull similar in length (26.4 mm), but slightly narrower (14.2 mm) and more vaulted (height of braincase 8.1 mm). Anterior palatal foramina absolutely slightly shorter (3.1 mm), but relatively shorter. Interorbital constriction broader (4.5 mm), and auditory bullae shorter (7.1 mm) and less inflated relative to skull length (measurements listed are mean values from Mt Kenya; M. E. Holden unpubl.). Not sympatric. Occurs in forests throughout much of sub-Saharan Africa.

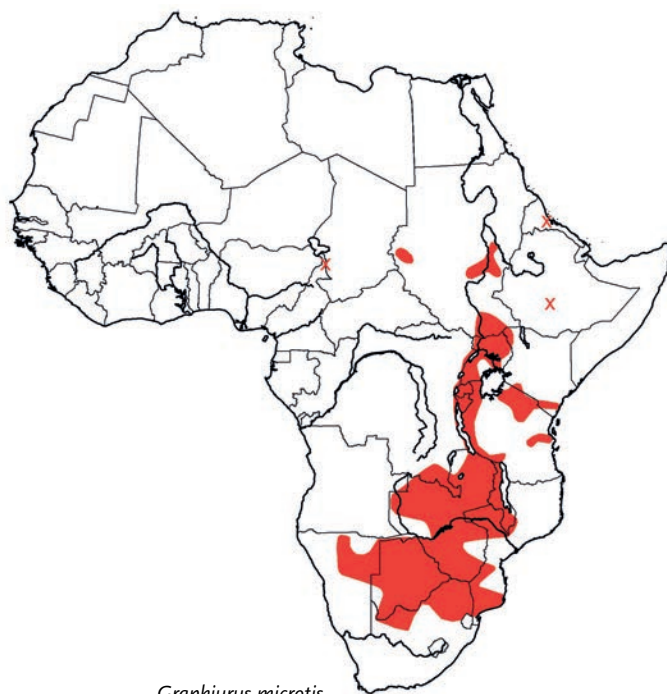
Graphiurus platyops: Larger head and body length (mean HB: 107.1). Tail (mean 78.7 mm) absolutely longer, but relatively shorter. Hindfeet (21.1 mm) longer, and ears (15.2 mm) shorter, both absolutely and relatively. Dorsal pelage grey to greyish-brown. Inconspicuous white postauricular patches sometimes present. Tail tip white. Skull longer (30.4 mm) and broader (17.1 mm). Height of braincase (7.8 mm) similar, so relatively flattened in *G. platyops*. Interorbital constriction (4.8 mm) absolutely and relatively broader. Anterior palatal foramina absolutely similar in length (3.2 mm), but relatively shorter. Upper tooththrow

(3.1 mm) and auditory bullae (8.4 mm) similar to slightly longer, so are relatively shorter (measurements listed are mean values from Zimbabwe and NE South Africa populations; M. E. Holden unpubl.). Generally sympatric throughout range of *G. platyops*, but seem to be segregated by habitat, and are probably not syntopic. Occurs in rocky habitats in eastern and south-eastern Africa.

Graphiurus rupicola: Slightly larger head and body length (mean 110 mm). Tail (104.2 mm). Hindfeet (21.5 mm) absolutely and relatively longer. Dorsal pelage colour sometimes similar in colour, especially in animals from Namibia. Small, cream supra-auricular patches and faint white postauricular patches present. Tail tip white. Skull markedly longer (31.3 mm) and most skull measurements are accordingly larger. Upper tooththrow (3.4 mm) absolutely longer, but relatively similar. Upper premolar (0.9 mm) absolutely slightly broader, but relatively narrower. Anterior palatal foramina absolutely similar in length (3.4 mm), but relatively shorter. Auditory bullae (9.5 mm) longer both absolutely and relative to skull length (measurements listed are mean values from Namibia; M. E. Holden unpubl.). Sympatric near Okahandja, Namibia. Occurs in rocky habitats in Angola, Namibia and NW South Africa.

Distribution Endemic to Africa. Widespread in Zambezan Woodland BZ, with extensions into parts of Eastern Rainforest–Savanna Mosaic, Guinea Savanna and Sudan Savanna BZs on the eastern side of the continent. Recorded from savannas in Chad, Sudan, Eritrea and Ethiopia south to Namibia and NE South Africa (Holden 2005). Late Quaternary fossils of *G. microtis* have been recorded from C Zambia (Avery 1996).

Habitat Woodland savanna, riverine woodland, rocky areas including caves, disturbed areas, and human dwellings. These dormice have been captured in or near aloes, willows, upaca trees



Graphiurus microtis

(*Upaca kirkiana*), thorn trees (*Acacia* sp.), camel thorn (*Acacia erioloba* (*giraffae*)), Zambeian teak or mukusi (*Baikiaea* sp.), mopane (*Colophospermum mopane*), leadwood (*Conbreum imberbe*), seringa (*Burkea* sp.), palm (*Hyphaene* sp.) and buffalo thorn (*Ziziphus mucronata*) (Shortridge 1934, Misonne 1965a, Misonne & Verschuren 1966, Smithers 1971, Wilson 1975, Smithers & Wilson 1979, Ansell & Dowsett 1988; specimen labels). They have been captured in tall grass near shrubs and trees, and in piles of debris deposited by high floods near seasonally dry rivers (Smithers 1983). Individuals have been observed on a vertical rock face at the entrance of a cave situated on a rocky hillside (Ansell 1974), and captured among rocks in or near caves (Roberts 1917, Misonne 1965a, Misonne & Verschuren 1966). Common also in disturbed areas, including buildings, fields, gardens and near rubbish dumps (Wilson 1975, Smithers & Lobão Tello 1976, Smithers & Wilson 1979, Ansell & Dowsett 1988, Taylor *et al.* 1994). When evaluating the range of microhabitats tolerated by these dormice, it is important to consider that more than one valid species is probably contained within *G. microtis* (see Taxonomy).

Abundance Common. Although published faunal surveys have not estimated population densities (due to the commonly mistaken inclusion of this species in *G. murinus*), the large number of museum specimens, and notes written on specimen labels, indicate that it is common throughout much of its range. In Malawi, Ansell & Dowsett (1988) found it to be the most frequently encountered dormouse, and stated that it is widely distributed.

Adaptations Primarily arboreal, partly terrestrial (Smithers & Wilson 1979, Smithers 1983). Nocturnal (Smithers 1971, 1983, Wilson 1975, Smithers & Wilson 1979). These dormice frequently nest in crevices under bark, or in holes in savanna trees (Shortridge 1934, Smithers & Lobão Tello 1976, Smithers 1983). The entrance to most nesting holes is circular, and is commonly situated 1–3 m above ground, although some have been found at heights of up to 6 m (Shortridge 1934; specimen labels). Nests are composed of soft plant material or grass, and sometimes feathers (Roberts 1951; specimen labels). They also nest in rocky habitats. One individual was observed at a cave entrance easily negotiating a vertical rock face (Ansell 1974), another was captured among rocks near a cave (Misonne 1965a). Several individuals nested in aloes in rocky terrain (Smithers & Lobão Tello 1976). They also utilize the nests of birds; one individual made its nest inside the nest of a swallow *Hirundo abyssinica* under a rock; the dormouse's nest contained feathers, wood debris, grass and scales from a snake (Misonne 1965a). Several adults and young have been found in nests of various species of weaver-birds (Roberts 1951). Nests may also be built in huts and houses, often in thatched roofs, sometimes in pantries or even in switch boxes of water pumps or transformers where they have caused short circuits in electrical supplies (Wilson 1975, Smithers & Lobão Tello 1976, Smithers 1983, specimen labels).

Foraging and Food Probably omnivorous, consuming fruit, insects, seeds, nuts and occasionally small vertebrates. Stomach contents have included dry outer skins of buffalo thorn fruit *Ziziphus mucronata*, seeds of *Acacia* sp., insects – including large moths, rose beetles, millipedes *Doratogonus flavifilis*, but not blister beetles nor Hemiptera (Misonne 1965a, Smithers 1971, 1983, Smithers & Wilson 1979, Pienaar *et al.* 1980). The stomach of one individual contained the remnants of a small bird (specimen label).

Social and Reproductive Behaviour Little information. Males are apparently solitary. Lactating ♀♀ are often caught with young.

Reproduction and Population Structure Litter-size: 3–7 (specimen labels). Most often 3–4 embryos or nestlings are reported (Ansell 1974, Wilson 1975, Smithers & Wilson 1979, Sheppe & Haas 1981, specimen labels). In Uganda, a pregnant ♀ was captured in Nov, and two lactating ♀♀ were captured in Aug. In Malawi, a pregnant ♀ was collected in Oct (Ansell 1974). In Botswana, a pregnant ♀ was obtained in Apr (Sheppe & Haas 1981). In Zimbabwe, pregnant ♀♀ have been collected in Feb, Apr, Jun, Nov and Dec (Wilson 1975, Smithers & Wilson 1979).

Predators, Parasites and Diseases One individual was found in the stomach of a mamba *Dendroaspis* sp. (specimen label). Close to 20 individuals were identified in owl pellets collected in Kruger N. P., South Africa (M. E. Holden unpubl.). These dormice are the type and a principal host for the trypanosome *Trypanosoma graphiuri* (Dekeyser 1955). They may host the same ectoparasites as *G. murinus* (see species profile).

Conservation IUCN Category: Least Concern.

Measurements

Graphiurus microtis

HB: 98.8 (75–115) mm, n = 33

T: 75.2 (62–86) mm, n = 28

HF: 16.9 (14–20) mm, n = 33

E: 15.5 (13–21) mm, n = 31

WT: 29.5 (17.6–42.5) g, n = 21

GLS: 27.4 (25.5–29.1) mm, n = 28

GWS: 15.0 (13.9–16.2) mm, n = 21

P⁴–M³: 3.0 (2.9–3.4) mm, n = 34

Zimbabwe (M. E. Holden unpubl.).

Key References Ansell & Dowsett 1988; Holden 2005; Misonne 1965a; Smithers 1983; Smithers & Lobão Tello 1976; Smithers & Wilson 1979.

Mary Ellen Holden

Graphiurus monardi MONARD'S AFRICAN DORMOUSE

Fr. Graphiure de Monard; Ger. Monards Bilch

Graphiurus monardi (St Leger, 1936). Ann. Mag. Nat. Hist., ser. 10, 17: 465. Kioko, 15 km above Dala, Tyihumbwe (Chiumbe) River, Angola. 1250 m (see Hill & Carter 1941).

Taxonomy Originally described in the genus *Claviglis*. Allen (1939) included *monardi* as a subspecies of *nagtglasii*, and Genest-Villard (1978a) followed this arrangement. Ellerman *et al.* (1953), Robbins & Schlitter (1981) and Holden (1993, 2005) agree that *monardi* has no close affinity with *G. nagtglasii*. Genest-Villard (1978a) included *schoutedeni* as a synonym of *G. platyops*, but Ansell (1989a) correctly arranged it as a synonym of *G. monardi*. Synonyms: *schoutedeni* (Ansell 1989a). Subspecies: none. Chromosome number: not known.

Description Large dormouse. Dorsal pelage yellowish-brown, darkening towards mid-line due to a higher density of guard hairs in that region. Dorsal pelage sleek and long (rump hairs 11–13 mm, guard hairs up to 17 mm), with many conspicuous dark brown guard hairs projecting beyond the fur. Ventral pelage cream, sometimes lightly suffused with grey. Dorsal and ventral pelage colours clearly delineated. Head colour matches that of dorsal pelage. Eyes large; eye-mask usually conspicuous. Ears brown, relatively small, rounded. Cheeks cream. Cream postauricular patches sometimes present. Hindfeet cream, sometimes with a thin, dark metatarsal streak. Tail moderately long (ca. 81% of HB), hairs shorter at base (6–9 mm) and longer at tip (up to 33 mm). Dorsal tail colour generally matches that of dorsal pelage, but ventral tail colour paler brown. Many white hairs are mixed throughout tail; tip white or cream. Skull long (34.1 mm) and vaulted (height of braincase 9.4 mm). Interorbital constriction narrow (mean 5.0 mm), anterior palatal foramina very long (4.1 mm) and wide (2.6 mm), and palate short (mean 10.7 mm) relative to skull length. Upper toothrow moderately broad as exhibited by medium breadth of upper premolar (mean 1.1 mm). Auditory bullae (mean 10.3 mm) absolutely and relatively long and inflated Nipples: 1 + 1 + 2 = 8.

Geographic Variation None recorded.

Similar Species (size comparisons refer to mean values only)

Graphiurus nagtglasii: This species is strikingly unlike *G. monardi*, but a comparison is given here due to previous inclusion of *monardi* in *G. nagtglasii*. Similar head and body length (mean 138.5 mm); most specimens of *G. monardi* have no data on head and body measurements, but based on specimen comparisons the size range of the two species is similar. Ear (mean 18.1 mm) and hindfoot (mean 26.5 mm) are absolutely and relatively longer. Dorsal pelage shorter and woolly, with inconspicuous guard hairs. Skull longer (mean 36.8 mm) with absolutely and relatively longer palate (mean 13.0 mm). Anterior palatal foramina shorter (3.7 mm) and narrower (2.3 mm) relative to skull length. Auditory bullae absolutely and relatively shorter (mean 7.9 mm) and much less inflated. Not sympatric. *Graphiurus nagtglasii* occurs in West Africa from Sierra Leone to Gabon.



Graphiurus monardi

Distribution Endemic to Africa. Zambezan Woodland BZ. Known from only seven localities in NE Angola, S DR Congo and NW Zambia.

Habitat Central African savanna. No specific habitat information has been recorded for this dormouse. All specimens, except one from Katanga (DR Congo), have been taken on plateaux in wetter Miombo woodland. St Leger (1936) gives anecdotal information obtained from Dr Monard that this dormouse occurs in forest, as well as in cultivated fields and houses. Another species, *G. angolensis*, is also found in this region, and is known to frequent vacant and occupied buildings. It is likely that some, if not all, of the reports of this species in cultivated fields and buildings are attributable to *G. angolensis*.

Abundance Little information. Only about a dozen museum specimens exist. Judging from the large numbers of specimens of dormice and other animals collected at some of the same localities, *G. monardi* appears to be rare.

Remarks Probably predominantly arboreal. Hayman (1963b) includes photographs of a live animal climbing on a branch.

Conservation IUCN Category: Data Deficient.

Measurements

Graphiurus monardi

HB: 160 mm, n = 1*

T: 130 mm, n = 1*
 HF: 21.9 (21.5–22) mm, n = 4
 E: 15.5 mm (estimated from two dry specimens)
 WT: n. d.
 GLS: 34.1 (32.5–36.6) mm, n = 6
 GWS: 19.7 (18.2–21.6) mm, n = 5
 P⁴–M³: 3.9 (3.6–4.3) mm, n = 9

NE Angola, S DR Congo and NW Zambia (M. E. Holden unpubl.)
 *St Leger (1936)

Key References Ellerman *et al.* 1953; Hayman 1963b; St Leger 1936.

Mary Ellen Holden

Graphiurus murinus FOREST AFRICAN DORMOUSE

Fr. Graphiure murin (Lérot de savanne); Ger. Busch-Bilch

Graphiurus murinus (Desmarest, 1822). Mammalogie. In: Encyclop. Méth., 2 (Suppl.): 542. Cape of Good Hope, South Africa.

Taxonomy Originally described in genus *Myoxus*. Many of the 76 scientific names proposed for African Dormice are synonyms of *G. murinus* (which usually inhabits forests) or *G. microtis* (which usually inhabits savannas) (see Holden 1996). Historically, many authors have not recognized *G. microtis* as a valid species, and the data given in their papers are thus composite for both species; when such publications are cited here, only the sections relevant to *G. murinus* as outlined in this account are pertinent. The species needs taxonomic revision, requiring comprehensive comparisons with *G. lorrainus*, *G. johnstoni*, *G. microtis* and *G. christyi* (Holden 2005). Significant morphological geographic variation exists, and it is likely that two or more separate species are contained within *G. murinus*. Because the definition of this species is so uncertain, information on abundance, distribution and biology may be applicable to other species, as yet undescribed. Synonyms: *alticola*, *cineraceus*, *cinerascens*, *collaris*, *erythrobrachus*, *griseus*, *isolatus*, *johnstoni* Heller, 1912 (not Thomas, 1898), *lalandianus*, *raptor*, *saturatus*, *selindensis*, *soleatus*, *?subrufus*, *vulcanicus*, *zuluensis*. Subspecies: none. Chromosome number: 2n = 46 (Natal, South Africa, D. N. MacFadyen pers. comm.; Hobbiton, South Africa, Kryštufek *et al.* 2004). Three different karyotypes were reported in the *G. murinus* species group in southern Africa (Dippenaar *et al.* 1983); however, *G. microtis* may have been included in this sample.

Description Small dormouse. Dorsal pelage various shades of golden- or greyish-brown, sometimes with reddish or coppery hue, with darkening of pelage towards the mid-line of head and back in some individuals. Dorsal pelage soft, silky, sometimes thick (rump hairs 7–8 mm, guard hairs up to 13 mm). Ventral pelage grey, lightly suffused with white or cream. Dorsal and ventral pelage colours usually not clearly delineated. Head colour matches that of dorsal pelage. Eyes large; eye-mask conspicuous in some populations. Ears brown, medium-sized, rounded. Cheeks cream or white. Postauricular patches usually not present. Hindfeet usually white with dark metatarsal streak. Tail moderately long (ca. 84% of HB), tail hairs shorter at base (2–4 mm) and longer at tip (up to 21 mm). Tail colour generally uniform, matching that of dorsal pelage. White hairs are sometimes mixed inconspicuously throughout tail in some populations, tip usually not white although some populations exhibit very faint white tip. Skull moderately long (26.4 mm) with moderately vaulted braincase (height of braincase 8.1 mm). Anterior palatal foramina of moderate length (3.1 mm) and width (1.9 mm); anterior portion often narrower anteriorly, resulting in tear-drop

shape. Palate moderately long (4.4 mm) and auditory bullae usually short (7.1 mm) and uninflated or moderately inflated relative to skull length. Nipples: 1 + 1 + 2 = 8.

Geographic Variation As with *G. microtis*, significant variation in external and skull morphology exists, and these differences are consistent within certain populations. Kryštufek *et al.* (2004) found that individuals from riverine forest near Grahamstown, South Africa, were significantly larger, and differed significantly in several cranial dimensions and proportions (weight, head and body, ear and length of PM⁴) than individuals from Afromontane forest at Hobbiton, South Africa (Kryštufek *et al.* 2004). Individuals from Ukinga Highlands, Tanzania, have smaller, broader skulls, with broader interorbital constriction and wider cheekteeth than individuals from nearby Uzungwa Mts and Rungwe Mts, Tanzania. Differences such as these are found throughout the range of *G. murinus*. Some populations have distinctive morphologies, and future studies may show that one (or more) of these populations is a separate species.

Similar Species (size comparisons refer to mean values only)

Graphiurus microtis. Similar head and body length (mean 98.8 mm). Hindfeet (mean 16.9 mm) shorter, ears (mean 15.5 mm) longer. Dorsal pelage colour similar to *G. murinus* in some populations. Postauricular patches often conspicuous. Ventral pelage colour usually paler and well delineated from dorsal pelage. Hindfeet usually white or cream. Tail usually with conspicuous white tip. Skull similar in length (27.4 mm), slightly broader (15.0 mm) and braincase less vaulted (height of braincase 7.5 mm). Anterior palatal foramina absolutely only slightly longer (3.4 mm), but relatively noticeably longer. Interorbital constriction narrower (3.9 mm) and auditory bullae longer (8.1 mm) and more inflated relative to skull length (measurements listed are mean values from Zimbabwe; M. E. Holden unpubl.). Not sympatric. Occurs in savannas throughout much of sub-Saharan Africa.

Graphiurus kelleni. Smaller head and body length (mean 82.4 mm). Hindfeet (mean 16.0 mm) shorter, ears (mean 14.8 mm) absolutely and relatively larger. Dorsal pelage colour similar to *G. murinus* in some populations. Skull shorter (24.0 mm), narrower (13.5 mm) and braincase less vaulted (height of braincase 7.0 mm). Anterior palatal foramina 2.9 mm long, 1.7 mm wide. Interorbital constriction slightly narrower (4.0 mm), and auditory bullae longer (7.8 mm) and much more inflated relative to skull length (measurements listed are mean values from Zambia; M.



Graphiurus murinus

E. Holden unpubl.). Generally not sympatric, although they have been captured in close proximity at several localities in Kenya. Occurs in savannas throughout much of sub-Saharan Africa.

Distribution Endemic to Africa. Afromontane–Afroalpine BZ in eastern and southern Africa, Highveld BZ, and Coastal Forest Mosaic BZ in southern part of range. Recorded from Ethiopia, Kenya, Uganda, Rwanda, Burundi (and possibly extreme NE DR Congo), Tanzania, N Malawi, Zimbabwe, South Africa, Swaziland and Lesotho (Holden 2005).

Habitat Primarily a forest species. Recorded mostly at altitudes of 1000–4100 m, and occasionally at sea level in coastal forests. Very adaptable and found in many types of forest (Afromontane, plateau, riverine, coastal). Less commonly recorded from montane grassland with rocks, giant groundsel, or trees. Rarely recorded from dry scrub or thicket. When evaluating the range of microhabitats tolerated by these dormice, it is important to consider that more than one valid species is probably contained within *G. murinus* (see Taxonomy). For example, at Grahamstown, South Africa, these dormice were trapped only in riverine forest and not in nearby dry thicket (B. Kryštufek pers. comm.), whereas at other South African localities individuals were captured in dry thicket and among rocks (Taylor 1998). It may be that individuals trapped in habitats other than forest are members of populations that will later be considered separate species.

Abundance Common in some regions, uncommon in others. In Giant's Castle Game Reserve, South Africa, relative abundance (as assessed by trap success) was 0.3% in grouped tree woodland, 0.8% in scrub, 3.8% in forest, 0.6% in temperate grassland boulder bed and 0.4% in temperate grassland (Rowe-Rowe & Meester 1982a). The species is fairly common and widespread in SE South Africa from Western Cape Province to Mpumalanga and Limpopo

Provinces, South Africa (Swanepoel 1988, Lynch 1983, 1989, Taylor 1998), but uncommon in Lesotho (Lynch 1994). Uncommon in four out of six montane forests in the Eastern Arc Mts, Tanzania (South Pare, West Usambara, East Usambara and Uluguru), and seemingly absent in two forests (Nguru and Udzungwa) (Stanley *et al.* 1998a, b); although Allen & Loveridge (1933) reported one individual from Udzungwa. At Chome Forest Reserve, Tanzania, comprised only 0.6% of small rodents (1 of 165) (Stanley *et al.* 1998a). Trap success (and assessment of abundance) is probably higher for traps set above ground than on the ground e.g. in Afromontane forest in South Africa, trap success was 2.3% above ground and 0.1% on the ground, and most individuals (94.5%) were captured in traps placed more than 0.5 m above ground (Kryštufek *et al.* 2004). Most published information derives from South African populations; more information is needed from populations throughout the range of the species to generally characterize its abundance.

Adaptations Primarily arboreal, partly terrestrial; some populations rupicolous. Frequently nests in holes and crevices in forest trees (Roberts 1951; specimen labels). Nests have also been found among epiphytic ferns and mosses of giant forest trees (Allen & Loveridge 1933), in beehives (Kingdon 1974), in swallows' nests, and less commonly, in human dwellings. Nests are often composed of strips of grass, bark and other material, which is finely shredded and formed into a round ball (Roberts 1951). A nest in NE South Africa was constructed of moss and lined with sheep's wool (specimen label). On Mt Kilimanjaro, Tanzania, a globular nest was composed of grass and slips of banana fronds, and lined with fine grass; it was about 13 cm in diameter, with a hole in its side, and was situated about 1.5 m above ground in a bush (specimen label).

Under certain conditions, will enter torpor (as do many species of glirids). If experimentally deprived of food at $T_a = 25^\circ\text{C}$, individuals initially decreased activity, but remained euthermic. At $T_a = 10^\circ\text{C}$, when deprived of food, the same individuals entered torpor with greater frequency during the day (Webb & Skinner 1996b). Cold temperatures (10°C) and simulated winter photoperiod (10 hours light, 14 hours dark) also induced torpor; these periods of torpor exceeded 24 hours, suggesting hibernation or deep torpor occurs under these conditions (Ellison & Skinner 1991).

The digestive system indicates a diet of mainly protein (see also below). Compared with 18 spp. of other rodents (mostly murids), the alimentary canal is short in relation to head and body length (3.7 times HB, cf. 4.8–5.6 for herbivores), the small intestine is relatively short and the large intestine is relatively long in relation to total hindgut length; the caecum is absent (the only species of those studied without a caecum) and there are no spiral folds in the large intestine (cf. all other 18 spp. except *Cryptomys hottentotus*). Most of these characters are primitive and indicative of a nutritious diet (Perrin & Curtis 1980).

Foraging and Food Omnivorous, predominantly insectivorous and carnivorous. Stomach contents have included insects and other invertebrates, seeds, leaves, stems, fruit and occasionally small vertebrates (Kingdon 1974, Perrin & Curtis 1980, Rowe-Rowe 1986, Wirminghaus & Perrin 1992, Taylor 1998; specimen labels). In KwaZulu–Natal, South Africa, most stomachs contained seeds, and all contained arthropods ($n = 11$; Rowe-Rowe 1986). In another study

in KwaZulu–Natal, South Africa, stomachs contained invertebrates (88.8%), fruits (11.04%), leaves and stems (0.16%), and flowers (0%); this population was thus predominantly insectivorous with more than 80% of the diet in any month comprising invertebrates ($n = 23$; Wirminghaus & Perrin 1992). One individual found in a beehive (Duff-MacKay 1965, quoted by Kingdon 1974) was extremely fat, and its stomach contained a brown sludge with white specks – presumably honey and wax.

Social and Reproductive Behaviour Little information. Lactating ♀♀ often caught with young. Allen & Loveridge (1933) observed subadult nestlings following an adult ♀ (up to eight individuals) as they climbed and leapt across tree branches. In two separate instances, adult ♀♀ were captured with two subadult ♂♂, indicating that offspring may stay in the nest past weaning (Allen & Loveridge 1933; specimen label).

Reproduction and Population Structure Litter-size: 1–5. Most often 3–4 embryos or nestlings are reported (Hollister 1919, Ansell 1974, De Graaff 1981; specimen labels). In Kenya, pregnant ♀♀ were collected in Sep and Nov (specimen labels). In Zambia, a pregnant ♀ was captured in Jul (Ansell 1974). In South Africa, ♀♀ exhibiting placental scars were captured in Feb, and pregnant ♀♀ were collected in Oct, Dec and Feb (Lynch 1989; specimen labels). Taylor (1998) suggests that this species may breed mostly during summer in KwaZulu–Natal, South Africa. No information on gestation and development of young. Sex ratio has been found to be female-biased in some southern African populations (De Graaff 1981, Smithers 1983).

Predators, Parasites and Diseases No information on predators. Most authors have included *G. microtis* as a synonym of

G. murinus, and therefore the ectoparasites listed here could have been collected from either species. Ectoparasites include three families of mites (Laelaptidae [1 sp.], Erynetidae [1 sp.] and Trombiculidae [8 spp.]), four families of fleas (Ceratomyzidae [1 sp.], Chimaeropsyllidae [1 sp.], Hystricopsyllidae [7 spp.] and Pulicidae [5 spp.]), and the rhipicephalid tick *Rhipicephalus simus* (De Graaff 1981). Type (and principal) host for the hoplopleurid louse *Schizophthirus graphiuri* (Durden & Musser 1994, Pajot 2000).

Conservation IUCN Category: Least Concern.

Further sampling is required to assess conservation status throughout geographic range; some historically recorded populations may be threatened or even extinct (e.g. the population in the Udzungwe Mts, Tanzania).

Measurements

Graphiurus murinus

HB: 91.5 (81–103) mm, $n = 21$

T: 76.6 (69–85) mm, $n = 19$

HF: 18.5 (16–20) mm, $n = 21$

E 13.3 (11.5–16) mm, $n = 7$

WT: 17 g, $n = 1$

GLS: 26.4 (25.2–28.8) mm, $n = 19$

GWS: 14.2 (13.2–15.9) mm, $n = 11$

P⁴–M³: 3.1 (3–3.3) mm, $n = 21$

Mt Kenya (1829–3353 m), Kenya (M. E. Holden unpubl.)

Key References Allen & Loveridge 1933; Kryštufek *et al.* 2004; Roberts 1951; Taylor 1998.

Mary Ellen Holden

Graphiurus nagtglasii NAGTGLAS'S AFRICAN DORMOUSE

Fr. Graphiure de Nagtglas (formerly Graphiure de Huet); Ger. Nagtglas Bilch

Graphiurus nagtglasii Jentink, 1888. Notes from the Leyden Museum 10: 38–41. Hill Town, Du Queah River, Liberia (restricted locality).

Taxonomy Most previous publications on dormice in West Africa have referred to this species as *G. hueti* (Huet's African Dormouse). Although originally described in genus *Graphiurus*, it was later placed in its own genus, *Aethoglis* (Allen 1936; see profile Genus *Graphiurus*). Grubb & Ansell (1996) recommended applying the name *G. nagtglasii* to the large West African dormouse, traditionally known as *G. hueti*, because of the dubious nature of the type locality of *G. hueti* given by de Rochebrune (1883), the lack of an available or likely holotype for *G. hueti*, and the existence of a holotype for *nagtglasii*. The animal used by de Rochebrune as a model to figure *G. hueti* is probably from Gabon, not Senegal (the type locality of *G. hueti*). Jentink (1888, and on his specimen labels) designated a series of five syntypes representing *G. nagtglasii* from Ghana and Liberia, and listed what are presumed to be the type localities as the Du Queah and Farmington rivers for the three Liberian specimens. As Rosevear (1969) noted, Jentink based his description on (and gave measurements for) an adult ♂ in alcohol that he considered typical of the species. Allen (1939) and Genest-

Villard (1978a) included *G. monardi* as a subspecies of *G. hueti* (now *G. nagtglasii*), but Ellerman *et al.* (1953), Ansell (1978), Robbins & Schlitter (1981) and Holden (1993, 2005) observed that *G. monardi* is clearly distinct from and probably not closely related to *G. nagtglasii*. Synonyms: *argenteus*, *hueti* (see Allen 1939, Grubb & Ansell 1996). Subspecies: none. Chromosome number: $2n = 40$ (Tranier & Dosso 1979).

Description Large dormouse. Dorsal pelage brown, greyish-brown, or rufous. Dorsal pelage soft, woolly, dense and short (rump hairs 5–7 mm, guard hairs up to 12 mm). Ventral pelage dark grey washed with ochre, cream or white. Dorsal and ventral pelage colours not clearly delineated. Head colour matches that of dorsal pelage. Eyes large; eye-mask usually conspicuous. Ears brown, medium-length, narrow and pointed. Cheeks greyish-white or ochraceous-white. Postauricular patches not present. Hindfeet brown, or white with dark metatarsal streak. Tail moderately long (ca. 76% of HB), tail hairs shorter at base (14–18 mm) and longer at tip (up

to 37 mm). Tail colour generally matches that of dorsal pelage, but has variegated frosted appearance. A few white hairs are occasionally mixed throughout tail; tip not white. Tail distichous underneath, and often nearly naked along mid-ventral line. Skull large, vaulted (height of braincase 10.2 mm) and somewhat broad (20.7 mm) relative to skull length. Anterior chamber of auditory bullae usually markedly less inflated than the posterior chambers. Interorbital constriction (5.5 mm) relatively narrow. Palate (13.0 mm) and upper toothrow (5.1 mm) relatively long, and wide as exhibited by breadth of upper premolar (1.5 mm). Anterior palatal foramina absolutely somewhat long (mean 3.7 mm) but relatively short. Auditory bullae short (7.9 mm) and uninflated relative to skull length (measurements listed are mean values from Ghana; M. E. Holden unpubl.). Nipples: $1 + 1 + 2 = 8$.

Geographic Variation None recorded.

Similar Species (size comparisons refer to mean values only)

Graphiurus monardi. This species is not at all similar to *G. nagtglasii*, but a comparison is given here due to previous inclusion of *G. monardi* in *G. nagtglasii*. Probably similar head and body length (mean 160 mm). (Only one adult specimen of *G. monardi* has information on head and body length associated with it; however, head and body length appears to be similar for other specimens.) Ear (15.5 mm) and hindfeet (21.9 mm) are shorter both absolutely and relative to skull length. Dorsal pelage long, straight and silky, with many conspicuous dark brown guard hairs. Skull shorter (34.1 mm) with absolutely and relatively shorter palate (10.7 mm). Anterior palatal foramina longer (4.1 mm), both absolutely and relative to skull length. Auditory bullae (10.3 mm) absolutely and relatively longer, and much more inflated (measurements listed are mean values from NE Angola, S DR Congo and NW Zambia populations; M. E. Holden unpubl.). Not sympatric. Occurs in S DR Congo, NE Angola and NW Zambia.



Graphiurus nagtglasii

Distribution Endemic to West Africa. Rainforest BZ (Western and West Central Regions) and Northern Rainforest–Savanna Mosaic. Recorded in or near rainforest from S Sierra Leone to Cameroon (excluding Benin), SW Central African Republic and Gabon. The southern distributional limit of this species is not known, as the Gabon specimen has no specific locality. Although de Rochebrune (1883) listed the type locality of *G. hueti* as Senegal, and reported it from neighbouring Gambia, the occurrence of the species has never been substantiated in these countries (Grubb & Ansell 1996).

Habitat Recorded in rainforest, secondary forest, abandoned farmlands, in cocoa plantations and other farms in forested areas (Rosevear 1969, Happold 1987, as *G. hueti* specimen labels). Most museum specimens were collected from hollow trees, one from an old hollow banana stem, and several from banana groves within cocoa plantations (Jeffrey 1973). They are often caught by farmers preparing new farms from secondary bush or forest (Jeffrey 1973). Several individuals were trapped on vines in secondary forest near hollow trees (Robbins & Schlitter 1981).

Abundance Rosevear (1969) stated that these dormice are fairly common and widespread throughout the West African rainforest. In Côte d'Ivoire, Heim de Balsac (1967a) found them to be fairly common in Lamto. In contrast, Dosso (1975a) did not trap this dormouse during his faunal study at Adiopodoumé, Côte d'Ivoire. Happold (1987) reported its occurrence in Nigeria as rare compared with *G. murinus* (the '*G. murinus*' of Happold (1987) is now known to represent *G. lorraineus*, *G. kelleni* and *G. crassicaudatus*). Based on numbers of specimens in museum collections from countries throughout its distribution, the abundance of this dormouse probably ranges from uncommon to common.

Adaptations Arboreal and probably nocturnal. According to Jeffrey (1973), these dormice climb well, but move slowly on the ground. Nests are often made in hollow trees, and one ♀ made a nest of dry banana fibres inside an old banana plant stem (specimen label). Eight ♀♀ with young trapped in banana groves made their nests of dry banana leaves. Happold (1987) states that these dormice curl up in their nests with the tail folded over the head during the day. Aside from one individual said by the collector, G. L. Bates, to have been 'shot with bow, coming out of hollow tree' (specimen label), all other specimens for which such information is available were taken while sleeping during the day.

Foraging and Food Probably omnivorous. In the wild, foods include cocoa pods, oil palm nuts, paw-paw, bananas and insects (Everard 1968, Happold 1987). Because these dormice are known to nest in hollow trees, and have been taken only among vines or in trees, they presumably do not forage on the ground.

Social and Reproductive Behaviour Apparently solitary, except for lactating ♀♀. Rosevear (1969) reported that this dormouse was less shy and not as easily scared as the smaller dormice occurring in West Africa.

Reproduction and Population Structure Litter-size: probably 2–3. In Liberia, Coe (1975) collected a parous adult in Apr.

In Ghana, G. S. Cansdale trapped several ♀♀ in Sep and Mar with three lactating young whose eyes were not yet opened (specimen labels). In W Ghana, Jeffrey (1973) found eight ♀♀, each nesting with two or three young in Sep, Oct and Nov. In Cameroon, an adult ♀ containing two embryos was found in Feb, and lactating ♀ was caught at the same locality in Apr (Robbins & Schlitter 1981). These very limited data suggest that most young are born during the wetter months of the year, but this needs confirmation.

Predators, Parasites and Diseases Heim de Balsac (1967a) and Jeffrey (1973) state that local people actively hunt *Nagtglas's* Dormice for their prized meat. This dormouse is the type and principal host for the hoplopleurid louse *Schizophthirus aethogliris* (Durden & Musser 1994, Pajot 2000).

Conservation IUCN Category: Least Concern.

Measurements

Graphiurus nagtglasii

HB: 138.5 (120–155) mm, n = 48

T: 105 (65–122) mm, n = 43

HF: 26.5 (20–30) mm, n = 46

E: 18.1 (15–22) mm, n = 44

WT: 73.1 (48–98) g, n = 18

GLS: 36.8 (34.9–39.1) mm, n = 35

GWS: 20.7 (18.3–22) mm, n = 39

P⁴–M³: 5.1 (4.6–5.7) mm, n = 48

Measurements: Ghana (M. E. Holden unpubl.)

Weight: Liberia, Côte d'Ivoire and Ghana (M. E. Holden unpubl.)

Key References Grubb & Ansell 1996; Grubb *et al.* 1998; Happold 1987; Robbins & Schlitter 1981; Rosevear 1969.

Mary Ellen Holden

Graphiurus ocularis SPECTACLED AFRICAN DORMOUSE (NAMTAP)

Fr. Graphiure du Cap; Ger. Brillen-Bilch

Graphiurus ocularis (Smith, 1829). Zool. J., 4: 439. Near Plettenberg Bay, Cape Province, South Africa.

Taxonomy Originally described in the genus *Sciurus*. In some regions of South Africa, the common name Namtap is used (see Channing 1987 for discussion of other common names applied to this species). Synonyms: *capensis*, *elegans*, *typicus* (see Allen 1939). Subspecies: none. Chromosome number: 2n = 46 (D. N. MacFadyen pers. comm.).

Description Large dormouse. Dorsal pelage medium silvery-grey. Dorsal pelage woolly, thick and moderately long (rump hairs 11–12 mm, guard hairs up to 16 mm). Ventral pelage dark grey washed with white. Dorsal and ventral pelage colours moderately delineated. Head silvery-grey, paler towards muzzle. Eyes large; eye-mask very conspicuous and broad, extending further posteriorly (to beneath the ear) than in other species of *Graphiurus*. Ears brown, moderately large, rounded. Cheeks white, forming part of a white sharply demarcated lateral stripe that extends from cheeks to shoulders. Conspicuous white supra-auricular patches. The combination of broader, more extensive face-mask, white cheeks, pale muzzle and larger, more conspicuous supra-auricular patches results in a striking black-and-white colour pattern on head and shoulders that allows for easy identification of this dormouse based on external characters alone. Hindfeet white and short (24.2 mm) relative to body size. Tail moderately long (ca. 85% of HB), tail hairs shorter at base (10–15 mm) and longer at tip (up to 35 mm). Dorsal tail colour generally matches that of dorsal pelage, but ventral tail colour solid brown-black medially, fringed with white laterally; tip white. Skull long (35.8 mm), moderately flattened (height of braincase 9.3 mm) and moderately broad (19.5 mm). Upper toothrow (3.3 mm) very short, upper premolar circular and very narrow (0.6 mm) both absolutely and relative to skull length; the reduced premolar allows for easy identification of skulls of this species. Anterior palatal foramina of moderate length (3.5 mm) and width (2.2 mm), but short and narrow relative to skull length.

Auditory bullae (9.8 mm) of medium length and only moderately inflated relative to skull length (measurements listed are mean values from Northern and Western Cape Provinces, South Africa; M. E. Holden unpubl.). Nipples: 1 + 1 + 2 = 8.

Geographic Variation None recorded.

Similar Species (size comparisons refer to mean values only)

Graphiurus rupicola. Smaller body length (mean 110 mm). The combination of paler grey dorsal pelage colour, darker muzzle, smaller and less conspicuous white supra-auricular patches and shorter eye-mask (terminating posterior to eye) results in a less striking facial colour pattern. Tail (104.2 mm), ear (17.3 mm) and hindfoot (21.5 mm) absolutely shorter, but relatively longer. Ventral tail colour similar to dorsal tail colour; not darker as in *G. ocularis*. Skull shorter (31.3 mm), interorbital constriction (5.0 mm) absolutely narrower, but relatively broader. Upper toothrow (3.4 mm) similar in absolute length, but longer relative to skull length. Upper premolar broader (0.9 mm) and oval-shaped. Anterior palatal foramina absolutely similar in length (3.4 mm) and breadth (2.3 mm), but relatively longer and broader. Auditory bullae (9.4 mm) absolutely shorter, but relatively longer and more inflated (mean values from Erongo, Karibib, and Mt Brukkaros, Namibia; M. E. Holden unpubl.). Parapatric in Little Namaqualand, Western Cape Province, South Africa. Also occurs in Namibia and Angola.

Distribution Endemic to Africa. South-West Arid (Karoo) and South-West Cape BZs. Recorded in Eastern Cape, Northern and Western Cape Provinces, South Africa. Altitudinal range from near sea level to 1585 m. Other historical distributional records outside the range given here are questionable (Holden 2005).



Graphiurus ocularis

Habitat Spectacled Dormice prefer rock piles, outcrops, crevices and stone kraals (Roberts 1951, Channing 1984, Fox *et al.* 1985, Skinner & Smithers 1990). They have also been captured in huts (Channing 1984) and within the hollow door of a farmhouse (De Graaff & Rautenbach 1983), and there is one report of an individual in a tree (Rautenbach 1982).

Abundance Uncommon. Population densities ranged from 1.8/ha to 3.1/ha on a 7.75 ha study site; densities vary according to the suitability of the habitats (Channing 1984). Smithers (1986a) and De Graaff & Rautenbach (1983) consider it rare.

Adaptations Predominantly rupicolous, also terrestrial. Nocturnal. The flattened cranium allows animals to move through narrow rock crevices. These dormice prefer to travel along rocks above ground level, even if the distance would be considerably shortened by taking a ground-level path (Channing 1997). Fox *et al.* (1985) suggest that these dormice are an early successional species after fire. They remain active throughout the year, but if there is a drop in temperature, and/or a scarcity of food, they can enter torpor for up to a month (Channing 1997, Perrin & Ridgard 1999). In captivity, they were unable to tolerate ambient temperatures greater than 35 °C (Perrin & Ridgard 1999).

Foraging and Food Predominantly insectivorous, occasionally carnivorous. Diet primarily insects and arthropods, although birds and lizards are also taken; probably no seasonal variation in diet (Channing 1984). In captivity, Spectacled Dormice consume

unnatural foods such as crackers, fruit, meat and honey, as well as dog food and rat pellets (Channing 1984, Perrin & Ridgard 1999).

Social and Reproductive Behaviour Spectacled Dormice emit vocalizations and exhibit intimidation displays during disturbance and aggression (Channing 1987, Van Hensbergen & Channing 1989). Fluorescent powder tracking suggests that individuals lay scent trails, and that ♂♂ and ♀♀ follow common routes (Channing 1984, Van Hensbergen & Channing 1989). Home-range (as assessed by harmonic range analysis) is 1.1–2.3/ha for ♀♀ and 2.1–3.8/ha for ♂♂ (Van Hensbergen & Channing 1989). There is some evidence that these dormice may be territorial because pairs remain together in the same area for up to 11 months.

Reproduction and Population Structure Reproductively active in spring and summer. Litter-size: 4–6. Litter interval: 6–8 weeks. Young stay in the nest for 5–6 weeks (Channing 1997). Social structure is primarily male–female pairs with their young of the year. Each pair (with young) occupies the most favourable habitats. Other individuals, including young after leaving their parents, occupy less favourable habitats. Average life-span is thought to be at least four years (Channing 1984).

Predators, Parasites and Diseases Ectoparasites include species of three families of fleas (Hystriopsyllidae, Listropsyllidae and Chimaeropsyllidae) and the tick *Rhipicephalus simus* (De Graaff 1981).

Conservation IUCN Category: Least Concern.

The categorization of this species should be changed to Near Threatened, or at least Data Deficient, due to its discontinuous distribution and poor representation in museum collections. Smithers (1986) categorized the species as rare.

Measurements

Graphiurus ocularis

HB: 134.3 (117–145) mm, n = 19

T: 114.5 (103–150) mm, n = 20

HF: 24.2 (20–26) mm, n = 25

E: 19.5 (15–25) mm, n = 24

WT: 78 (72–85) g, n = 4

GLS: 35.8 (34.2–37.5) mm, n = 20

GWS: 19.5 (18.3–20.9) mm, n = 15

P⁴–M³: 3.28 (3–3.5) mm, n = 24

Northern and Western Cape Provinces, South Africa (M. E. Holden unpubl.)

Key References Channing 1997; De Graaff 1981; Roberts 1951; Skinner & Smithers 1990.

Mary Ellen Holden

Graphiurus platyops FLAT-HEADED AFRICAN DORMOUSE

Fr. Graphuïre à tête plate; Ger. Flachkopf-Bilch

Graphiurus platyops Thomas, 1897. Ann. Mag. Nat. Hist., ser. 6, 19: 388. Enkeldorn, Mashonaland, S Zimbabwe.

Taxonomy Ellerman *et al.* (1953) synonymized *G. rupicola* from NW South Africa and Namibia, and *G. angolensis* (including *parvulus*) from Angola and NW Zambia within this species. Their arrangement was generally followed by Genest-Villard (1978a), though she placed the Angolan populations (*G. angolensis* and *parvulus*) as junior synonyms of *G. murinus*. Allen (1939) recognized *G. platyops*, *G. rupicola* and *G. angolensis*, as well as *parvulus* (listed here as a junior synonym of *G. angolensis*) as separate species. Roberts (1951) also treated *G. rupicola* and *G. platyops* as distinct species, a position followed by Holden (1993, 2005) based on comparisons of museum specimens. Following Ansell (1978), Holden (1993) provisionally listed *angolensis* and *parvulus* as synonyms of *G. platyops*, but analyses of museum specimens (M. E. Holden unpubl.) support recognition of the Angola and NW Zambia population as a separate valid species, *G. angolensis* (including *parvulus*). Synonyms: *eastwoodae*, *jordani* (see Holden [2005] regarding allocation of *albicaudatus*, a name that apparently was never published). Subspecies: none. Chromosome number: $2n = 46$ (D. N. MacFadyen pers. comm.).

Description Medium-sized dormouse. Dorsal pelage grey, brownish-grey or greyish-brown. Pelage sleek and moderately long (rump hairs 10 mm, guard hairs up to 13 mm). Ventral pelage white or cream suffused with grey. Dorsal and ventral pelage colours clearly delineated. Head colour matches that of dorsal pelage, paler towards muzzle. Eyes large; eye-mask conspicuous. Ears brown, moderately large, rounded. Cheeks white, forming part of a pale lateral stripe that extends from cheeks to shoulders. Faint white postauricular patches sometimes present. Hindfeet usually white, sometimes with dark metatarsal streak. Tail moderately short (ca. 71% HB), similar in colour to dorsal pelage, with many scattered white hairs; hairs shorter at base (5–7 mm) and longer at tip (up to 30 mm); tip white. Skull gracile, broad (17.1 mm) and flat (height of braincase 7.8 mm). In lateral profile, dorsal outline of skull from rostrum to occiput is practically horizontal. Interorbital constriction moderately broad (4.8 mm), anterior palatal foramina moderately long (3.2 mm), but somewhat short relative to skull length. Upper tooththrow relatively short (3.1 mm) and narrow as exhibited by narrow breadth of upper premolar (0.8 mm). Auditory bullae of medium length (8.4 mm) and only moderately inflated relative to skull length (measurements listed are mean values from Zimbabwe and NE South Africa; M. E. Holden unpubl.). Nipples: $1 + 1 + 2 = 8$.

Geographic Variation None recorded.

Similar Species (size comparisons refer to mean values only)

Graphiurus microtis. Smaller head and body length (mean 98.8 mm). Tail (75.2 mm) absolutely shorter, but relatively longer. Hindfeet (16.9 mm) shorter, and ears (15.5 mm) longer, both absolutely and relatively. Dorsal pelage greyish-brown to dark greyish-brown in populations sympatric with *G. platyops*. Skull shorter (27.4 mm), vaulted and relatively narrower (15.0 mm). Although

*Graphiurus platyops*

the height of braincase (7.5 mm) is absolutely shorter in *G. microtis*, in lateral view the braincase is markedly more vaulted and its dorsal outline convex. It is also relatively higher relative to skull length. Upper tooththrow (3.0 mm), anterior palatal foramina (3.4 mm) and auditory bullae (8.1 mm) similar to slightly shorter in length, so relatively longer. Anterior palatal foramina 3.4 mm long, 2.1 mm wide. Interorbital constriction (3.9 mm) absolutely and relatively narrower (measurements listed are mean values from Zimbabwe; M. E. Holden unpubl.). Generally sympatric throughout range of *G. platyops*, but seems to be segregated by habitat, and is probably not syntopic. *Graphiurus microtis* occurs in savannas throughout most of sub-Saharan Africa.

Distribution Endemic to Africa. Southern part of Zambezi Woodland BZ and northern part of Highveld BZ. Recorded from NE and S Zambia, Zimbabwe, S Malawi, E Botswana, S Mozambique and NE South Africa (Holden 2005). Previously thought to occur in C Botswana (De Graaff 1981); however, the museum specimen on which the record was based is *G. microtis* (Holden 2005).

Habitat Flat-headed African Dormice are most often trapped in crevices in rock kopjes, krantzies and under exfoliating granite (Roberts 1951, Smithers 1971, 1983, Wilson 1975). They have sometimes been found in association with dassies (*Heterohyrax* and *Procavia*) (Roberts 1951, Smithers & Lobão Tello 1976). Three individuals were trapped in caves in South Africa (specimen labels). On the Save R., Mozambique, individuals were collected in dry *Androstachys* sp. scrub thickets in a dry river bed (Smithers & Lobão

Tello 1976). In NE South Africa, one ♀ with three young was caught in a hollow tree branch (Roberts 1951). Rautenbach (1982) observed that this species generally occurs at altitudes higher than 609 m, and is not associated with mopane woodland.

Abundance Little information. Uncommon in E Zambia (Ansell 1978). There are only ca. 50 museum specimens of *G. platyops*, and usually only one or two individuals have been found at each locality, suggesting that even in suitable habitat, densities are not high.

Adaptations Predominantly rupicolous. The markedly flattened cranium allows movement of these animals through narrow rock crevices, where they are most commonly found. Most authors characterize this dormouse as being nocturnal (e.g. Smithers 1971), but five individuals trapped by Wilson (1975) in W Zimbabwe were taken between 06:00 and 09:00h, suggesting that at least some individuals are crepuscular or diurnal.

Foraging and Food Omnivorous. Stomach contents of individuals from Zimbabwe and Botswana contained remains of well-masticated small seeds, traces of green vegetable matter and the chitinous remains of insects, including moths (Smithers 1983). One animal was trapped using a portion of a rat carcass for bait (specimen label).

Social and Reproductive Behaviour Apparently solitary (Smithers 1983). Unbaited tunnel traps that have been entered by one individual seem to attract others, suggesting that, like Spectacled Dormice, these dormice use scent trails (Channing 1997). They are aggressive, flourishing and whipping their tails as a visual signal (Channing 1997). Vocalizations include a soft warning call, consisting of a number of short, low-pitched notes. An aggression call follows if the intruder does not leave. The aggression call consists of a series of brief spits, each consisting of a 0.1-second burst of high amplitude

white noise. The encounter escalates into a fight if the intruder remains (Channing 1997).

Reproduction and Population Structure Little information. In Zimbabwe, a pregnant ♀ carrying two full-term embryos was obtained in Feb (specimen label).

Predators, Parasites and Diseases Flat-headed African Dormice are hosts of the chimaeropsyllid flea *Chiaestopsylla nama*, which also occurs on other rupicolous rodents including *Aethomys namaquensis* and *Petromyscus collinus* (Haeselbarth *et al.* 1966, De Graaff 1981).

Conservation IUCN Category: Least Concern.

Little information is known regarding distribution and abundance; a more appropriate categorization would be Data Deficient.

Measurements

Graphiurus platyops

HB: 107.1 (95–122) mm, n = 18

T: 78.7 (65–98) mm, n = 15

HF: 21.1 (18–25) mm, n = 21

E: 15.2 (13–18) mm, n = 19

WT: 45.7 (30.4–52.8) g, n = 5

GLS: 30.4 (28.6–32) mm, n = 19

GWS: 17.1 (16.1–18.6) mm, n = 20

P⁴–M³: 3.1 (2.8–3.5) mm, n = 25

Zimbabwe and NE South Africa (M. E. Holden unpubl.)

Key References Ansell 1978; Channing 1997; De Graaff 1981; Roberts 1951; Smithers 1983.

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Graphiurus rupicola RUPICOLOUS AFRICAN DORMOUSE

Fr. Graphiure des rochers; Ger. Felsen-Bilch

Graphiurus rupicola (Thomas and Hinton, 1925). Proc. Zool. Soc. Lond. 1925: 232. Karibib, Namibia. 3842 ft (1170 m).

Taxonomy Originally described in the genus *Gliriscus*. Ellerman *et al.* (1953) and Genest-Villard (1978a) considered *rupicola* to be a subspecies of *G. platyops*. Roberts (1951) recognized the substantial morphological differences between *rupicola* and *platyops*, and listed *G. rupicola* as a separate species, an arrangement followed here. Synonyms: *australis*, *kaokoensis*, *montosus*. Subspecies: none. Chromosome number: not known.

Description Medium-sized dormouse. Dorsal pelage silvery-grey, drab grey or slate-grey. Dorsal pelage woolly, thick and moderately long (rump hairs 10–11 mm, guard hairs up to 17 mm). Ventral pelage white or cream lightly suffused with dark grey. Dorsal and ventral pelage colours clearly delineated. Head colour matches that of dorsal pelage, slightly paler towards muzzle. Eyes large; eye-mask conspicuous. Ears brown, large, oval-shaped. Cheeks cream or white, forming part of a pale lateral area that extends from cheeks to shoulders. Cream supra-auricular patches, and faint

postauricular patches present. Hindfeet white, or white with dark metatarsal streak. Tail long (ca. 95% HB), similar in colour to dorsal pelage, with many scattered white hairs; hairs shorter at base (9–12 mm) and longer at tip (up to 43 mm); white at tip. Skull long and moderately flattened (height of braincase 8.0 mm). Palate long (10.4 mm), upper premolar breadth (0.88 mm) somewhat narrow relative to skull length, interorbital constriction (5.0 mm) broad, anterior palatal foramina moderately long (3.4 [3.1–3.6] mm) and wide (mean 2.3 mm), auditory bullae long (9.4 mm) and inflated relative to skull length (measurements are mean values from Erongo, Karibib and Mt Brukkaros, Namibia; M. E. Holden unpubl.). Nipples: 1 + 1 + 2 = 8.

Geographic Variation None recorded.

Similar Species (size comparisons refer to mean values only) *Graphiurus angolensis*. Slightly smaller body length (mean 98.8 mm).

Tail (79.2 mm) and hindfeet (18.4 mm) are absolutely and relatively shorter. Dorsal pelage is drab or dark brown. Skull averages slightly shorter (28.2 mm). Although height of braincase (7.7 mm) is absolutely shorter in *G. angolensis*, in lateral view the braincase appears more vaulted and its dorsal outline is more convex. Interorbital constriction (4.2 mm) absolutely narrower and auditory bullae (8.9 mm) absolutely shorter but relatively longer. Upper premolar breadth (0.90 mm) absolutely similar but broader relative to skull length. Anterior palatal foramina absolutely similar in length (3.4 mm) but relatively longer (measurements listed are mean values from Kabompo and Zambezi [formerly Balovale], Zambia; M. E. Holden unpubl.). Parapatric in C Angolan highlands, occurs in Angola and NW Zambia.

Graphiurus microtis. Slightly smaller body length (mean 98.8 mm). Tail (75.2 mm) and hindfeet (16.9 mm) are absolutely and relatively shorter. Dorsal pelage sometimes similar in colour, especially in Namibia, Botswana and NE South Africa populations. Skull markedly shorter (27.4 mm). Palate (8.8 mm) shorter, interorbital constriction (3.9 mm) narrower, and auditory bullae (8.1 mm) shorter both absolutely and relatively. Upper tooththrow (3.0 mm) absolutely shorter, but relatively similar. Upper premolar breadth (0.85 mm) absolutely narrower, but broader relative to skull length. Anterior palatal foramina 3.4 mm long, 2.1 mm wide, similar in length, so relatively longer (measurements listed are mean values from Zimbabwe; M. E. Holden unpubl.). Sympatric near Okahandja, Namibia; occurs in savannas throughout sub-Saharan Africa.

Graphiurus ocularis. Larger body length (mean 134.3 mm). Tail (114.5 mm), ear (19.4 mm) and hindfeet (24.2 mm) are absolutely longer, but relatively shorter. Dorsal pelage darker grey with striking facial colour pattern. Dorsal tail darker than ventral tail colour. Skull (35.8 mm) longer. Palate (12.0 mm) absolutely longer, but relatively similar. Interorbital constriction (5.4 mm) absolutely broader, but relatively narrower. Auditory bullae

(9.8 mm) slightly longer and upper tooththrow (3.3 mm) similar, but both shorter relative to skull length. Anterior palatal foramina absolutely similar in length (3.5 mm) and breadth (2.2 mm), but relatively shorter. Upper premolar circular and greatly reduced in size (breadth 0.6 mm) (measurements listed are mean values from Northern and Western Cape Provinces, South Africa; M. E. Holden unpubl.). Parapatric in Little Namaqualand, Western Cape Province, South Africa; also occurs in Eastern and Northern Cape Provinces.

Distribution Endemic to Africa. South-West Arid BZ (with possible northern extension to Zambezian Woodland BZ in Angola). Occurs on central mountains and plateaux from Mt Soque, Angola, south to Port Nolloth and Eenriet in Little Namaqualand, South Africa (Holden 2005). The northern distributional limit for *G. rupicola* was previously thought to be Kamanjab, Namibia, but specimens from Mt Soque, Angola, are considered to represent this species (Holden 2005). A specimen from Dilolo, DR Congo, resembles *G. rupicola* in pelage characters, but resembles *G. monardi* in skull characters; at present the specimen cannot be allocated to either species (Holden 2005).

Habitat Rock crevices in rocky outcrops and kopjes, from altitudes of 400 m to at least 1586 m. Most specimens were caught in bushy Karoo–Namib shrubland or Karoo transition vegetation zones; two specimens from Mt Soque, Angola, were captured in ‘evergreen wood at mountain top’ (specimen label).

Abundance Little information. Roberts (1951) considered the species to be rare, an observation supported by the few specimens (ca. 20) in museums.

Remarks The moderately flattened skull enables animals to squeeze through narrow rock crevices. The very few habitat notes (Shortridge 1934, Roberts 1951; specimen labels) suggest that *G. rupicola* nests only in rock crevices. A ♀ obtained on Mt Brukkaros, Namibia, in Sep was pregnant (specimen label).

Conservation IUCN Category: Least Concern.

So little is known about the species that a classification of Data Deficient may be more appropriate.

Measurements

Graphiurus rupicola

HB: 110 (105–119) mm, n = 9

T: 104.2 (96–118) mm, n = 9

HF: 21.5 (21–22) mm, n = 8

E: 17.3 (16–20) mm, n = 9

WT: (subadult): 25 g, n = 1*

GLS: 31.3 (30.5–32.3) mm, n = 7

GWS: 17.2 (16.7–17.9) mm, n = 6

P⁴–M³: 3.4 (3.3–3.7) mm, n = 8

Erongo, Karibib and Mt Brukkaros, Namibia (M. E. Holden unpubl.)

*Pella Mission, south bank of the Orange River, South Africa (M. E. Holden unpubl.)

Key References Roberts 1951; Shortridge 1934.

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Graphiurus rupicola

Graphiurus surdus SHORT-EARED AFRICAN DORMOUSE

Fr. Graphiure sourd; Ger. Kurzohr-Bilch

Graphiurus surdus Dollman, 1912. Ann. Mag. Nat. Hist., ser. 8, 9: 314. Benito River, Rio Muni Province, Equatorial Guinea.

Taxonomy Although described and initially recognized as a species, *G. surdus* was later synonymized within a broadly defined *G. murinus* (Misonne 1974, Genest-Villard 1978a). Robbins & Schlitter (1981) and Holden (1996) provided morphological evidence for recognizing *G. surdus* as a valid species. Synonym: *schwabi*. Subspecies: none. Chromosome number: not known.

Description Small to medium-sized dormouse. Dorsal pelage greyish-brown. Dorsal pelage silky and moderately long (rump hairs 5–7 mm, guard hairs up to 11 mm). Ventral pelage dark grey washed with whitish-buff. Dorsal and ventral pelage colours not clearly delineated. Head colour matches that of dorsal pelage. Eyes large; eye-mask inconspicuous. Ears brown, short and rounded. Cheeks grey washed with white. Postauricular patches not present. Hindfeet cream or white with dark metatarsal streak. Tail moderately long (ca. 73% of HB), similar in colour to dorsal pelage, with many scattered white hairs resulting in a frosted appearance; hairs shorter at base (3–8 mm) and longer at tip (up to 20 mm); tip not white. Skull medium length (27.6 mm), moderately vaulted (height of braincase 8.1 mm), with narrow greatest width of skull (14.6 mm), and comparatively straight conformation of the zygomatic arch in lateral view (figured in Robbins & Schlitter 1981 and Holden 1996). Interorbital constriction (4.5 mm) narrow. Anterior chamber of auditory bullae markedly less inflated than posterior chambers in most individuals. Anterior palatal foramina relatively short (2.8 mm) and narrow (1.8 mm). Upper premolar narrow (0.8 mm), palate long (9.3 mm) and auditory bullae short (7.3 mm) and uninflated relative to skull length (measurements listed are mean values from Cameroon, Equatorial Guinea and Gabon; Holden 1996). Nipples: 1 + 1 + 2 = 8.

Geographic Variation None recorded.

Similar Species (size comparisons refer to mean values only)

Graphiurus christyi. Similar head and body length (mean 97.6 mm). Ears longer (14.2 mm). Dorsal pelage colour sometimes similar, but most individuals have a rufous hue. Eye-mask usually more distinct. Tail absolutely and relatively longer (ca. 83% of HB). Skull averages slightly shorter (97.8 mm). Palate shorter (8.5 mm) both absolutely and relative to skull length. Anterior palatal foramina absolutely similar in length (3.0 mm), but absolutely and relatively wider in breadth posteriorly (2.2 mm). Auditory bullae similar in length (7.4 mm) and relative inflation. (Measurements listed are mean values from DR Congo; M. E. Holden unpubl.). No sympatry recorded, though both species have been collected in SW Cameroon and N DR Congo (Holden 1996).

Graphiurus lorrainaeus. Smaller head and body length (mean 83 mm). Hindfeet (16.6 mm) shorter. Ears similar in size, but relatively larger. Dorsal pelage usually rufous, though sometimes brown. Anterior palatal foramina 2.6 mm long, 1.7 mm wide. Skull

(24.5 mm) much shorter, and palate absolutely and relatively shorter (7.8 mm). Similar average length of auditory bullae (7.1 mm) and breadth of upper premolar (0.8 mm), but bullae are longer and upper premolar is wider relative to skull length. Anterior palatal foramina absolutely similar in length (2.6 mm), but relatively somewhat longer (measurements listed are mean values from DR Congo; M. E. Holden unpubl.). Sympatric in SW Cameroon, Equatorial Guinea and DR Congo (Holden 1996).

Graphiurus crassicaudatus. Smaller head and body length (92.6 mm). Hindfeet (17.7 mm) and tail (59.4 mm) shorter. Dorsal pelage usually rufous-brown. Skull shorter (26.6 mm). Greatest width of skull (16.1 mm) and interorbital constriction (4.9 mm) markedly broader relative to skull length, supraorbital ridges present. Palate (9.4 mm) similar in length but relatively longer. Upper tooththrow (3.8 mm) absolutely and relatively longer (measurements listed are mean values from S Cameroon; M. E. Holden unpubl.). Sympatric in SW Cameroon; occurs in West and west-central Africa.

Distribution Endemic to Africa. Rainforest BZ (West Central Region [Gabon Subregion], and marginally East Central and South Central Regions). Recorded from two disjunct areas in central Africa: (1) S Cameroon south to Equatorial Guinea and Gabon; (2) NE Congo (Masako) and SC Congo (Inkongo). Of the 22 known specimens, 15 are from S Cameroon. Limits of geographic range unknown.

*Graphiurus surdus*

Habitat Probably occurs in primary rainforest; may also be found in secondary forest (specimen labels). These dormice have been trapped on the forest floor (W. Verheyen pers. comm.), and in forests with vines (Robbins & Schlitter 1981).

Abundance Little information. Most specimens are from localities that have been fairly well sampled. This suggests either low population densities, or that the species is trap-shy, or that traps have not been set in appropriate habitats.

Remarks Arboreal. One individual collected by G. L. Bates from Bitye, Cameroon was ‘smoked out of a hollow tree’ (specimen label). This suggests that, like *G. crassicaudatus*, *G. nagtglasii* and *G. lorraineus*, some individuals nest in hollow trees.

Conservation IUCN Category: Data Deficient.

Measurements

Graphiurus surdus

HB: 99.0 (87–110) mm, n = 8

T: 72.3 (65–82) mm, n = 6

HF: 20.8 (18–22) mm, n = 12

E: 12.3 (9–14) mm, n = 11

WT: 24.8 (18–34) g, n = 6

GLS: 27.6 (26.5–29.4) mm, n = 10

GWS: 14.6 (13.4–15.7) mm, n = 11

P⁴–M³: 3.2 (2.9–3.5) mm, n = 16

Cameroon, Equatorial Guinea, Gabon (Holden 1996)

Key References Holden 1996; Robbins & Schlitter 1981.

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Family DIPODIDAE

JERBOAS

Dipodidae Fischer de Waldheim, 1817. Mem. Soc. Imp. Nat., Moscow 5: 372.

| | | |
|------------------------------|------------------|--------|
| <i>Allactaga</i> (1 species) | Four-toed Jerboa | p. 136 |
| <i>Jaculus</i> (2 species) | Jerboas | p. 137 |

The Dipodidae contains 51 species arranged in six subfamilies and 16 genera (Holden & Musser 2005). The family is distributed throughout the Palaearctic region, the Middle East and North Africa in forests, grasslands and steppe, and in hot and cold deserts. Only two genera and three species of this widespread family occur in Africa.

The taxonomy of the family is controversial and uncertain. The family appears to be monophyletic (Holden & Musser 2005 and references therein) and to have diversified greatly in recent times. The family is divided into six subfamilies: Sicistinae (birch mice) with the single genus *Sicista*, Zapodinae (jumping mice) with *Zapus*, *Eozapus* and *Napeozapus*, Cardiocraniinae with *Cardiocranius*, *Salpingotus* and *Salpingotulus*, Euchoreutinae with *Euchoreutes*, Allactaginae with *Allactaga*, *Allactodipus* and *Pygeretmus*, and Dipodinae with *Dipus*, *Eremodipus*, *Jaculus*, *Paradipus* and *Stylodipus*. Only the Allactaginae and Dipodinae occur in Africa. The family as a whole is characterized by enlarged masseter muscles, which penetrate the infraorbital foramen (a character normally associated with hystricomorph rodents), an enlargement of the jugal to form a plate anterior to the orbit, which protects the eye, and the lack of a bony inflection on the angle of the mandible (which is characteristic of most murid rodents). Two of the subfamilies, the Sicistinae and Zapodinae, differ from the other four in many respects and some authorities place these subfamilies in a separate family, the Zapodidae; however, there is considerable overlap in characters between all the subfamilies and no clear dividing lines separating each subfamily. Because, on balance, Sicistinae and Zapodinae are similar to each other, with marked differences to the remaining subfamilies, the Dipodidae are here regarded as separate from the Zapodidae (Corbet & Hill 1986); this arrangement reduces the family Dipodidae to four subfamilies, 12 genera and 33 species. See Holden & Musser (2005) for further details.

The best-known characters of Dipodidae (as understood here) are large auditory bullae, non-cuspidate low-crowned cheekteeth, long hindlimbs (ca. 50–56% of HB in African species), reduction in the number of digits, elongation of the metatarsal bones and partial or total fusion of these bones to a form a single ‘cannon bone’, which supports the weight of the body, a flattened nasal region reminiscent of that of a pig, large (or very large) ears and large dark eyes. The neck is short and the vertebrae are small and fused in most species. The metatarsal bones and the phalanges of the hindfeet are very specialized and varied in structure. In *Cardiocranius* there are five hind digits (Digit 1 being the shortest) and the metatarsal bones are not fused; in *Salpingotus* Digits 1 and 5 are lost and the metatarsals are not fused; in *Allactaga* the metatarsals of Digits 2, 3 and 4 are fused (now called the ‘cannon bone’) and Digits 1 and 5 are very short and lie close and parallel to the cannon bone (in *A. tetradactyla*, Digit 1 on the inner side of the hindfoot is absent); and in *Jaculus* and *Dipus* the cannon bone is extremely elongated and Digits 1 and 5 are absent. In all species with a cannon bone, the three hind digits are well developed. In contrast to the hindlimbs,

the forelimbs are very short, have five digits and are rarely used for locomotion. The very long tail (ca. 140–170% of HB in African species) has a tuft of hairs at the tip and is used as a counterbalance during rapid running or hopping locomotion. When the long-legged species (*Jaculus*, *Dipus*, *Allactaga*) are resting on the hindlimbs, the end of the tail near the tip provides a tripod-like support. There are several modes of locomotion; the most typical is a fast bipedal jump using only the two hindlimbs (‘richochetal locomotion’). The skull is broad, and has an enlarged jugal plate, well-developed auditory bullae and laminate molars. The mandibles are weak without a bony inflection at the angle of the mandible, and perforations (fossae) on the angular process. Dental formula is: $I \frac{1}{1}, C \frac{0}{0}, P \frac{0}{0}, M \frac{3}{3} = 16$ (P is $\frac{0}{1}$ in some non-African species). Size categories of species in the family (based on mean head and body length) are given in the order Rodentia profile.

All species of the Dipodidae live in open, usually arid, habitats where vegetation is sparse. The climate where dipodids live is extremely varied: species that live the cold deserts of Asia hibernate for 6–7 months during the coldest season of the year, and some species (*Cardiocranius*, *Salpingotus*, *Pygeretmus*) store fat in their tails. Species living in hot deserts are lethargic, and exhibit less activity, during the coolest part of the year. During the day they rest in burrows, which may be up to 3 m underground and extend for many metres; when inside the burrow, some species block the entrance with a plug of sand. Individuals emerge at night to forage on the ground. Species with long legs hop and run over the substrate with great speed and agility. The diet is principally seeds, bulbs and grass stalks; some species may feed occasionally on insects. Species that live in arid habitats (e.g. *Jaculus* spp.) possess kidneys that have special anatomical features to minimize water loss. Little information is available on the social behaviour in dipodids; they are usually found singly or in small groups; during cold weather, several individuals often huddle together in a nest in the burrow. Reproduction is seasonal, litter-size is mostly 2–6, and ♀♀ of some species may have more than one litter each breeding season.

Fossil remains of dipodids are uncommon. Fossil jumping mice and jerboas are known from the Pliocene of Europe and from the Miocene and Pliocene of Asia. There are very few fossil remains of jerboas from Africa (Holden & Musser 2005).

In Africa, there are two subfamilies and two genera:

Allactaginae: five digits on hindfoot (four in *A. tetradactyla*), three metatarsals (Digits 2, 3 and 4) fused to form cannon bone, undersurface of hind digits with small hairs, three molars and one small premolar in each upper jaw; *Allactaga* (1 sp.).

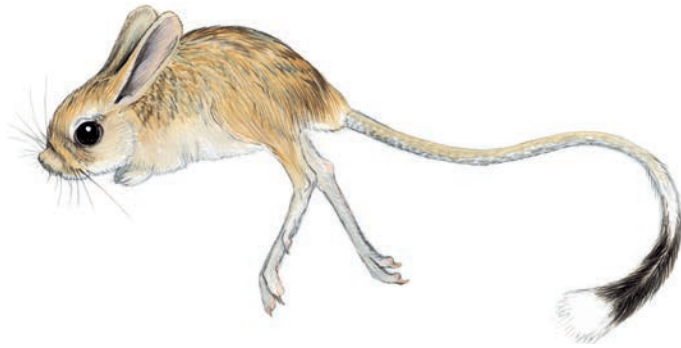
Dipodinae: three digits on hindfoot; three metatarsals (Digits 2, 3 and 4) fused to form cannon bone, undersurface of hind digits with abundant strong bristles, three cheekteeth without premolar in each upper jaw; *Jaculus* (2 spp.).

D. C. D. Happold

GENUS *Allactaga*

Jerboas

Allactaga F. Cuvier, 1836. Proc. Zool. Soc. Lond., 1836: 141 [1837]. Type species: *Mus jaculus* Pallas, 1778 (= *Dipus sibericus major* Kerr, 1792).



Allactaga tetradactyla.

Widespread genus with 11 species in 'cold deserts' from Iran and Afghanistan to Manchuria, and in 'hot deserts' of the Middle East and NE Africa (Holden 1993). Holden & Musser (2005) place *Allactaga* as the only genus in the subfamily Allactaginae.

The principal characters of the genus are: fusion of the metatarsal bones of Digits 2, 3 and 4 to form the 'cannon bone' (as in *Jaculus*). In most species, Digit 1 is short, although it is absent in *A. tetradactyla* (the only species of this genus in Africa). Digit 5 (outer digit) is short, ending half way along the length of the cannon bone. In general shape, *Allactaga* is reminiscent of *Jaculus*, except that the ears are much longer and often held upright from the head. Hindlimbs used for synchronized bipedal hopping, and for asynchronized bipedal trotting. Very long tail acts as counterbalance when hopping. Large eyes and ears. Pads of digits large and naked. The skull is characterized by a rudimentary premolar in each upper jaw (cf. *Jaculus*), perforations in the small angular process of the lower jaw, large auditory bullae but less developed than in *Jaculus*, well developed maxillary process, large orbit and wide zygoma (Figure 20). Baculum absent.

The single African species, *Allactaga tetradactyla*, is present only in Egypt and Libya.

D. C. D. Happold

Allactaga tetradactyla FOUR-TOED JERBOA

Fr. Gerboise tétradactyle; Ger. Vierzehen-Jerboa

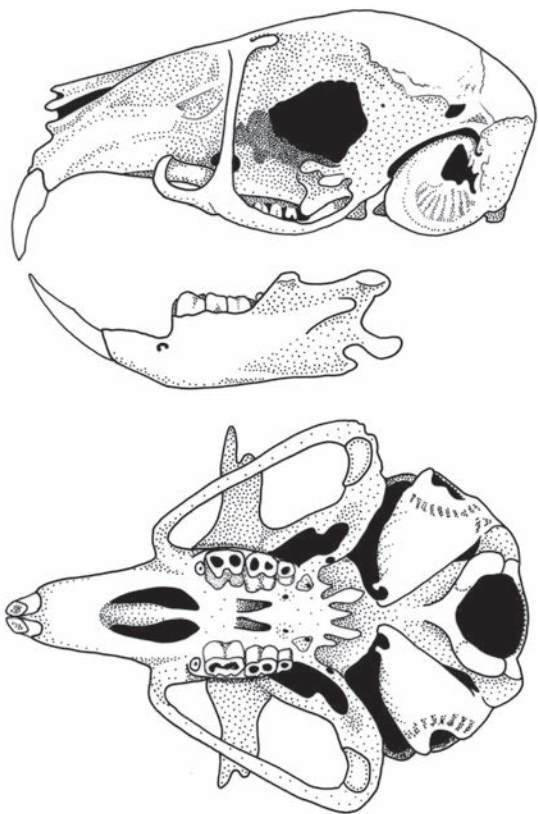


Figure 20. Skull and mandible of *Allactaga tetradactyla* (BMNH 14.3.6.1).

Allactaga tetradactyla (Lichtenstein, 1823). Verz. Doublet. Zool. Mus. Univ. Berlin, p. 2. 'Libyan Desert between Siwa and Alexandria' (= Egypt).

Taxonomy Originally described in the genus *Dipus*. Synonyms: *brucii*. Subspecies: none. Chromosome number: not known.

Description Small jerboa with large rounded head, extremely long hindlimbs, four toes on each hindfoot, and very long tufted tail. Dorsal pelage pale orange streaked with black, tending to grey on the flanks; hairs grey at base, orange on terminal half, sometimes with black tip. Ventral hairs pure white, without white colouration extending onto rump at base of tail. Head similar in colour to dorsal pelage. Eyes large. Ears long and darkly pigmented. Hindlimbs,

especially metatarsals, very long (ca. 51% of HB). Digits 2, 3 and 4 fused to form cannon bone; Digit 1 absent; Digit 5 short, ending with short claw visible about half way along outer surface of cannon bone (*contra* Kingdon 1997:191; inner digit [Digit 1] shown on right cannon bone is in error). Undersurface of cannon bone and base of toes with blackish hairs. Tail very long (ca. 150% of HB), with terminal tuft of black hairs, each hair black at base with white tip. Skull as in genus profile. Nipples: not known.

Geographic Variation None recorded.

*Allactaga tetradactyla*

Similar Species

Jaculus jaculus: Similar in general size, shorter ears (21 mm); three hind digits, Digits 1 and 5 absent.

Jaculus orientalis. Much larger (HB: 137–160 mm; HF: 71–78 mm); three hind digits, Digits 1 and 5 absent.

Distribution Endemic to Africa. Eastern part of Sahara Arid BZ. Regs and hamadas along the Mediterranean coast of Libya and Egypt west of the Nile Delta. Does not extend southwards into the Sahara Desert.

Habitat Salt marshes and valleys in coastal regions; further inland, recorded from clay deserts, especially near barley fields, and *Anabasis* shrublands (Osborn & Helmy 1980).

Abundance Rare and localized. Much less common than *J. orientalis*, which lives in similar habitats.

Remarks Terrestrial and nocturnal. Many of the adaptations of these jerboas are likely to be similar to those of the two species of *Jaculus*, but their rarity precludes detailed information. However, unlike *Jaculus* spp., Four-toed Jerboas appear to have a very limited ecological tolerance. Burrows are simple, 60–150 cm deep. Burrows are occupied only for brief periods; at other times unoccupied burrows of Greater Egyptian Jerboas are utilized (Hoogstraal 1963). Occasionally infested by the flea *Xenopsylla nubica*, and by four other species of fleas. Another flea species, *Hopkinsiopsylla occulta*, is species-specific to *A. tetradactyla*, and is mostly found in the nests and not on the host itself. Only 25 animals (of 200 examined) were infected by fleas (Hoogstraal & Traub 1965b).

Conservation IUCN Category: Vulnerable. This species is threatened with extinction because of its rarity, small geographical range and reclamation of its habitat for agriculture and development (Hoogstraal 1963).

Measurements

Allactaga tetradactyla

HB: 110 (102–119) mm, n = 19

T: 169 (154–180) mm, n = 17

HF: 56 (51–59) mm, n = 19

E: 41 (37–43) mm, n = 19

WT: 52 (48–56) g, n = 3

GLS: 28.9 (27.3–30.4) mm, n = 20

GWS: 20.9 (19.1–22.6) mm, n = 16

P⁴–M³: 5.9 (5.2–6.2) mm, n = 20

Auditory bulla: n. d.

Egypt (Osborn & Helmy 1980)

Key References Hoogstraal 1963; Osborn & Helmy 1980.

D. C. D. Happold

GENUS *Jaculus*

Jerboas

Jaculus Erxleben, 1777. Syst. Regni Anim. 1: 404. Type species: *Mus jaculus* Linnaeus, 1758.

Widespread genus with three species in arid habitats of North Africa and the Middle East, extending eastwards to western Pakistan and northwards to Turkmenistan and Uzbekistan (Holden 1993). The genus is placed in the subfamily Dipodinae, together with the non-Africa genera *Dipus* (1 sp.), *Eremodipus* (1 sp.), *Paradipus* (1 sp.) and *Stylodipus* (3 spp.). Two species of *Jaculus* occur in Africa.

The principal characters of the genus are elongated hindlimbs and fusion of the metatarsals of Digits 2, 3 and 4 to form a 'cannon bone' (as in *Allactaga*); Digits 1 and 5 absent. Hindlimbs used for synchronized bipedal hopping, and for asynchronized bipedal trotting. Very long tail acts as counterbalance when hopping. Eyes very large. Ears large, rounded at tip. Pads of digits small and covered with dense bristles. Lacks small premolar in upper jaw (cf.

Allactaga). Skull broad, auditory bullae greatly inflated and elongated (ca. 40% of GLS), zygoma absent (c.f. *Allactaga*), large orbit, and with perforations in small angular process of lower jaw (Figure 21). Baculum present.

Members of the genus are highly adapted for life in sandy arid habitats where the climate is alternately very hot during the day and cool or cold at night. They are nocturnal, and spend the day in deep burrows. The diet is seeds and dried grass. They are independent of free water, primarily because they have efficient kidneys that produce very concentrated urine.

Fossils of the genus are known from the late Miocene of Kazakhstan, late Pliocene of Morocco and Ethiopia, and Pliocene-Pleistocene of Kenya (details in Holden & Musser 2005).

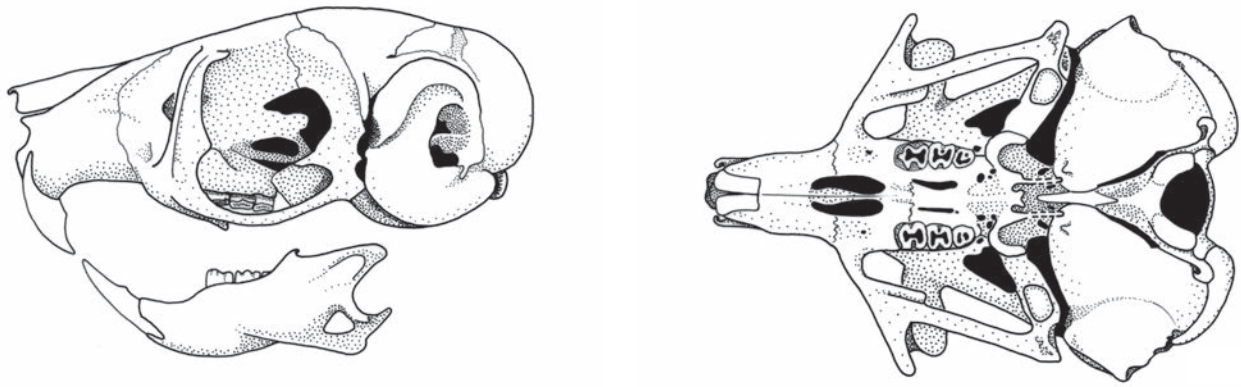


Figure 21. Skull and mandible of *Jaculus jaculus* (HC 504).

Two species are present in Africa: one widespread and common in North Africa; the other confined to the Mediterranean coastal zone. The species are distinguished by body size and geographical distribution.

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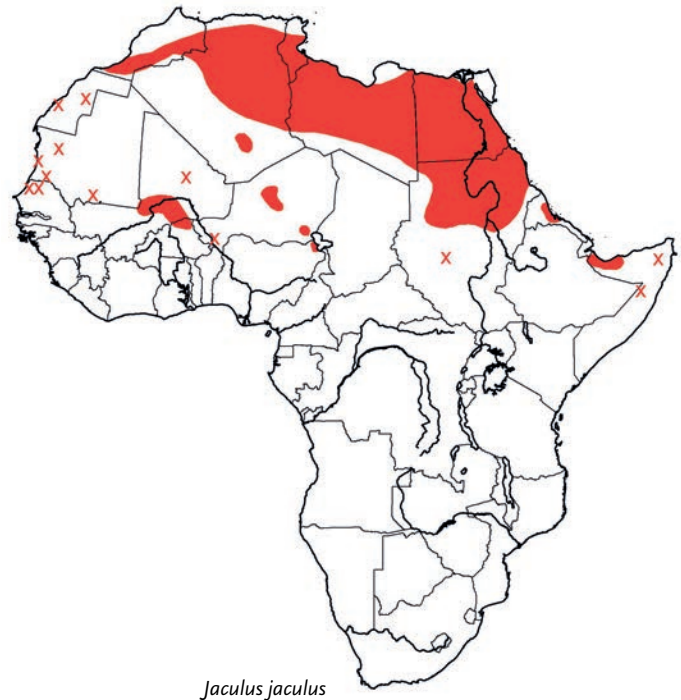
***Jaculus jaculus* LESSER EGYPTIAN JERBOA**

Fr. Petite Gerboise d’Egypte; Ger. Kleine Ägyptische Springmaus

Jaculus jaculus (Linnaeus, 1758). Syst. Nat., 10th edn, 1: 63. Giza Pyramids, Egypt.

Taxonomy Originally described in the genus *Mus*. About 19 subspecies (Misonne 1974) have been described throughout the extensive African range of the species. Individual countries may have several subspecies, e.g. Algeria five subspp. (Kowalski & Rzebik-Kowalska 1991), Egypt four subspp. (Osborn & Helmy 1980), Libya eight subspp. (Ranck 1968) and Sudan two subspp. (Setzer 1956). Some of these taxa were used as specific names in the past, but now all are regarded as synonyms (Holden & Musser 2005). *Jaculus deserti*, as recorded by Ranck (1968) in Libya, is a synonym of *J. jaculus* (Osborn & Helmy 1980; Musser & Carlton 1993). Synonyms (of *J. jaculus*): *airensis*, *arenaceus*, *butleri*, *centralis*, *collinsi*, *cufensis*, *favonicus*, *gordoni*, *microtis*, *sefrius*, *tripolitanicus*, *vulturinus*, *whitchurchi*; (of *J. deserti*): *favillus*, *fuscipes*, *rarus*, *schlüteri*, *vastus*. Subspecies: none (but see Geographic Variation). Chromosome number: $2n = 50$; $FN = 90$ (Senegal; Granjon *et al.* 1992); $2n = 48$ (Niger; Dobigny *et al.* 2002b).

Description Small pale-coloured jerboa with large rounded head, extremely long hindlimbs and very long tufted tail. Dorsal pelage long and silky, pale sandy-brown to sandy-rufous; hairs grey at base, sandy or brownish on terminal half, sometimes with black tip. Black-tipped hairs more numerous in individuals from moister habitats resulting in a streaked darker-coloured pelage. Ventral pelage pure white. White colouration extends dorsally onto rump forming white band at base of tail. Head similar in colour to back, broad and rounded, with small muzzle, many vibrissae, large eyes and large rounded ears. Hindlimbs, especially metatarsal bones, very long (ca. 56% of HB); three hind digits well covered on undersurface with whitish bristles. Forelimbs small, held close



Jaculus jaculus

under chin. Tail very long (ca. 170% of HB), basal two-thirds covered with short sandy-coloured hairs; terminal third with long hairs forming a large tuft, black on basal half, white on terminal half. Skull as in genus profile. Females tend to be heavier than ♂♂ (adult mean weights at Khartoum: ♀♀ [non-pregnant] 60 g; ♂♂ 49 g). Nipples 2 + 2 = 8.

Geographic Variation Colour of dorsal pelage (the basis for most subspecies descriptions) appears to be related to the colour of the soil or sand and the degree of aridity. Individuals from C Sahara are very pale sandy- or creamy-white (e.g. *airensis*), those from moister environments are sandy-brown to orange-brown with greater numbers of black-tipped hairs. Mean HB length varies with locality (and 'subspecies'): e.g. 105 mm (*butleri*, Khartoum); 110 mm (*jaculus*, Egypt); 111 mm (*flavillus*, Egypt).

Similar Species

J. orientalis. Larger (HB: 137–160 mm; HF: 71–78 mm); North African coastal regions only.

Allactaga tetradactyla. Similar in general size, ears longer (40 mm), four digits including short Digit 5 on outside of cannon bone; coastal regions Libya and Egypt only; rare.

Distribution Sahara Arid and Sahel Savanna BZs. Recorded from S Morocco, Mauritania and N Senegal in the west to Egypt and Sudan in the east. Not recorded in the coastal regions of Morocco north of the High Atlas and Saharan Atlas mountains of Morocco and Algeria. Isolated populations in coastal Eritrea, coastal Ethiopia and N Somalia. Perhaps occurs in Djibouti. There is some evidence that, since the 1970s, the distribution of jerboas has been moving progressively southwards within the Sahel Savanna BZ and into the Sudan Savanna BZ as a result of desertification of the savannas by humans. Also recorded from Israel, Iraq, Iran, Syria, Pakistan and Saudi Arabia.

Habitat Lesser Egyptian Jerboas live in a variety of open sparsely vegetated arid and semi-arid habitats, including loose sandhills and hillocks, sandy plains and wide sandy wadis. Also occur on flat solid substrates, such as coastal regions and higher altitude plateaux (up to ca. 1500 m), provided the sand or soil is suitable for burrowing. Also recorded near fields of barley, and in *Anabasis* steppe country, along the Mediterranean coast. Not found in rocky habitats or on jebels.

Their ability to live in many arid zone habitats and climates is one reason for their wide distribution.

Abundance In most habitats, Lesser Egyptian Jerboas are never abundant and distribution is patchy; tend to be rare over much of their geographic range especially where soil type is unsuitable, rainfall is very low and where food resources are limiting. Usually never abundant in Egypt (Osborn & Helmy 1980). Comparatively common in selected habitats near Khartoum (Happold 1967a, c, 1975a), and recorded as 'common on the meidan' in Somalia (specimens in BMNH, collected 1912). Where the three species of jerboas occur parapatrically, as in parts of Egypt, this species is rare (Hoogstraal & Traub 1965b).

Adaptations Nocturnal and terrestrial. Lesser Egyptian Jerboas emerge from burrows after dusk. They exhibit several methods of locomotion above ground (Figure 22) including walking on all four limbs when foraging for food, hopping bipedally and slowly when 'pottering', and hopping very quickly when escaping from danger. Occasionally they run with a fast bipedal trot (Happold 1967a). The tail is held out horizontally as a counterbalance when moving on the hindlimbs. They gain friction on the substrate from bristles on undersurface of the hindfeet. When disturbed or pursued, they hop extremely rapidly (up to ca. 30 km/h), often changing direction quickly and erratically. Mobility is necessary to find adequate food, and speed and manoeuvrability are essential to escape from predators in open environment. Lesser Egyptian Jerboas groom by licking their fur and by lying in a little concavity in the sand with the hindlimbs stretched out and rubbing the body backwards and forwards ('sand-bathing').

Lesser Egyptian Jerboas dig burrows in the sand using their teeth and forefeet to excavate the burrow, and push the excavated sand out of the burrow with the blunt flattened nose and muzzle (nostrils can be closed), and scatter it with the hindlimbs. Burrows are simple,

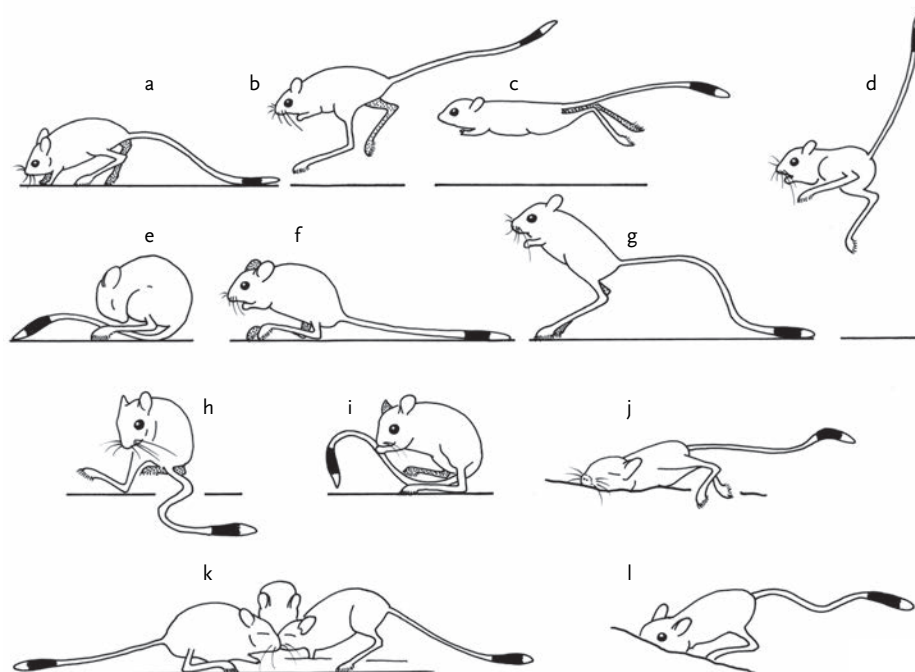


Figure 22. Behavioural characteristics of *Jaculus jaculus*.

- (a) movement on all fours;
- (b) medium speed;
- (c) fast speed;
- (d) high jump;
- (e) sleeping;
- (f) sitting submissive;
- (g) standing alert;
- (h) washing rump;
- (i) cleaning tail;
- (j) sandbathing;
- (k) social contact between three jerboas;
- (l) pushing sand with nose (after Happold 1967a).

usually with two entrances, and vary in depth according to season; at Khartoum, winter burrows are shallow (20–25 cm deep with almost horizontal passages, and in summer, burrows are deeper (70–75 cm) with steeply sloping passages (Ghobrial & Hodeib 1973). After an individual has entered its burrow, the entrance is plugged from the inside with sand so that the entrance is practically invisible. Small sleeping chamber at base of burrow is lined with grass. Temperature and relative humidity in the burrow is relatively constant (temperature 26–28 °C in cool season when air temperature is 5–27 °C, and 37 °C in hot season when air temperature is 28–46 °C; humidity 60–100%) and does not experience the temperature or humidity fluctuations of the sand surface.

Skull has enlarged zygomatic plates, which protect the orbits when anterior part of head is used for pushing sand. Auditory bulla is large (ca. 40% of GLS) and greatly inflated; it assists detection of vibrations in sand when animal is in the burrow, and airborne sounds when it is on the surface.

Lesser Egyptian Jerboas can obtain all their water from their food (but will lick dew and standing water when available), and possess many special anatomical and behavioural features for conserving water. The kidney produces only small amounts of extremely concentrated urine (4320 mMol/l), about double the maximum concentration produced by a white rat. In experimental conditions, without free water and feeding on barley, an individual lost ca. 30% of body weight after three weeks (Schmidt-Nielsen 1964). In this respect, these jerboas are not as well adapted to lack of water as some other species of desert rodents (e.g. some *Gerbillus* and *Meriones* spp.). Other ways to reduce water loss and energy loss include nocturnal activity, resting in relatively cool and moist burrows, sleeping curled in a ball to reduce water loss from the lungs, feeding on foods with high water content when available (moist vegetation, bulbs) and seasonal changes in activity (Happold 1967a). In cool weather, Lesser Egyptian Jerboas rest in their burrows curled into a tight ball, tucking the head close to the abdomen and covering the long hindlimbs with the body; activity above ground is greatly reduced. In hot weather, they rest with legs and tail stretched away from the body, and sometimes lick saliva on to the fur to increase heat loss.

Foraging and Food Foraging takes place only at night, when seeds and stems are collected from the substrate with short forelimbs. Lesser Egyptian Jerboas sit in a crouched position while eating, with the whole length of the cannon bone resting on the ground, and the food is held with the forelimbs. Near Khartoum (and presumably elsewhere) the diet consists of small seeds, dried desert grasses and roots, as well as bulbs and corms in the dry season. Sometimes the fleshy leaves of some succulent plants are also eaten. After rainfall, Lesser Egyptian Jerboas feed on newly germinated grass sprouts. Their weak jaws prevent them from feeding on large hard seeds. There is no evidence that these jerboas collect and store food (cf. *J. orientalis* and many species of *Gerbillus*).

Social and Reproductive Behaviour In the desert, Lesser Egyptian Jerboas are seen singly (or occasionally in pairs or trios). They show many of the behavioural characters of solitary species: agonistic behaviour (fighting, chasing) when confined with an unfamiliar individual; a tendency to nest alone and to have limited

interactions with other individuals. In an established group, members show tolerance towards each other. No information available on reproductive behaviour.

Reproduction and Population Structure Reproduction is seasonal. Near Khartoum, young individuals were found from Sep to Dec, and in Feb and Mar (1964–66); this suggests two periods of pregnancies, one in Jun and Jul during the annual ‘wet season’ (average 150 mm/year), and the second in Oct–Dec when monthly temperatures are declining and food is still relatively abundant (Happold 1967a). In other years (1970–72), reproduction was almost continuous with peaks in Sep–Nov and Dec–Feb (Ghobrial & Hodeib 1973). Reproduction is probably opportunistic, and dependent on availability of nutritive food (and hence rainfall). Gestation: 44–46 days. Litter-size/number of embryos (regardless of season): 3.4 (2–5, mode 3, $n = 18$; Happold 1967a). Mean litter-size at Khartoum varies according to season: 4.8 in Sep (end rains, food abundant), 3.0 in Dec (cool temperature, food less abundant) and 1.83 (Jun, hot temperatures, food scarce) (Ghobrial & Hodeib 1973). Young born naked; development is slow for a rodent of this size: hair develops by Day 22; eyes open Day 38. Hindfoot and auditory bullae develop rapidly, reaching adult size quicker than other structures. At birth, cannon bone formed of three separate metatarsal bones, each 9 mm in length; at Day 40, bones fused and 50 mm in length, but unable to support weight of body. Weight when first active above ground ca. 20 g (= 35% adult weight, age 50–60 days) (Happold 1970a).

The relative age of an individual can be estimated by the wear on the cheekteeth: youngest animals are Age-class 3 (least wear on molars) and oldest animals are age-class 17 (maximum wear) (Happold 1967a). At Khartoum, in Sep–Dec (1964–66), after the rains and the first breeding period, there were individuals of all age classes, suggesting three age-groups: (a) age-classes 3–8, weight <40 g, born previous Jun–Jul, age 3–6 months; (b) age-classes 5–10, wt >40 g, born previous Oct–Dec, age 9–12 months; and (c) age-classes 10–17, wt >40 g, age more than 12 months. By Jan–Mar, most of the individuals in age-group (a) had moved to age-group (b), and many of the oldest individuals in age-group (c) had disappeared from the population. (No detailed information for Apr–Aug.) Individuals of age-classes 14–17 may be 3–4 years of age. Only 25% of individuals attained an age-class of 10 or above (Happold 1967a).

Predators, Parasites and Diseases Remains of Lesser Egyptian Jerboas have been found in owl pellets in Algeria (Kowalski & Rzebik-Kowalska 1991) and they are likely to be preyed upon by owls in many parts of their geographic range. In Egypt, they are hosts to many species of fleas, the commonest being *Xenopsylla nubica*, *X. cheopis* and *Synosternus cleopatrae*; none is specific to *J. jaculus* and are found also on other small rodents. Infection rate is low; infested individuals typically host 3–4 fleas (Hoogstraal & Traub 1965b). The blood parasite *Hepatozoon balfouri* infected 41% of jerboas examined in Egypt ($n = 370$) as well as many other species of Egyptian small mammals (Hoogstraal 1961).

Conservation IUCN Category: Least Concern.

The wide distribution of Lesser Egyptian Jerboas, and the sparseness of humans in their habitats, suggest that they are not threatened.

Measurements

Jaculus jaculus jaculus

HB: 110 (98–118) mm, n = 78

T: 181 (160–203) mm, n = 76

HF: 62 (56–66) mm, n = 80

E: 21 (19–23) mm, n = 80

WT: 55 (45–73) g, n = 60

GLS: 31.3 (30.2–32.7) mm, n = 77

GWS: 22.6 (19.9–24.4) mm, n = 71

M¹–M³: 5.3 (4.8–5.6) mm, n = 77

Auditory bulla: 13.2 (12.8–13.5) mm, n = 10*

Egypt (Osborn & Helmy 1980)

*Sudan (*J. j. butleri*; BMNH)

Key References Happold 1967a, 1970a, 1975a; Osborn & Helmy 1980; Ghobrial & Hodeib 1973.

D. C. D. Happold

Jaculus orientalis GREATER EGYPTIAN JERBOA (ORIENTAL JERBOA)

Fr. Gerboise Orientale; Ger. Orientalische Springmaus

Jaculus orientalis Erxleben, 1777. Syst. Regn. Anim. 1: 404. 'In the mountains separating Egypt from Arabia' (= Egypt).

Taxonomy Several subspecies have been described (*orientalis*, *gerboa*, *mauritanus*) but none is recognized by Corbet (1978). This species was referred to (incorrectly) as *Dipus aegyptius* by Kirmiz (1962). The 'Desert Rats' of the North African campaign in World War II were named after this species. Synonyms: *bipes*, *gerboa*, *locusta*, *mauritanicus*. Subspecies: none. Chromosome number: not known.

Description Medium-sized jerboa with large rounded head, extremely long hindlimbs and very long tufted tail. Dorsal pelage brownish-orange, becoming paler on flanks; hairs grey at base, orange-brown on terminal half, sometimes with black tip. Ventral pelage pure white. Very similar in general characters to *J. jaculus*. Hindlimbs, especially metatarsal bones, very long (ca. 51% of HB); three hind digits well covered on undersurface with whitish bristles. Forelimbs short. Tail very long (ca. 146% of HB), ending with large tuft, black at base and white at tip. Nipples: not known.

Geographic Variation None recorded in Africa.

Similar Species

J. jaculus. Considerably smaller (e.g. HB: 98–118 mm; HF: 56–66 mm); widespread in desert habitats.

Allactaga tetradactyla. Considerably smaller but with longer ears (37–43 mm), four hind digits including short Digit 5 on outside of cannon bone; coastal regions Libya and Egypt only; rare.

Distribution Mediterranean Coastal BZ and coastal regions of Sahara Arid BZ in Libya and Egypt. Recorded from Morocco, Algeria and Tunisia, and the high plateaux of E Morocco and Algeria south to about 34°S, and in the regs and hamadas near the coast from W Libya to Egypt west of the Nile Delta. Prefers more humid environments to *J. jaculus* and does not extend southwards into the Sahara Desert. Also recorded from Sinai and S Israel. The geographical range overlaps with that of *J. jaculus* in a few areas of Algeria, Libya and Egypt.

Habitat Salt marshes with *Salicornia* bushes; limestone slopes covered by *Suada* bushes above the salt marshes; coastal dunes; gardens, meadows, olive growths and old barley fields covered with annual plants (Osborn & Helmy 1980). Compared with *J. jaculus*, these jerboas live in habitats that are less arid and have much more vegetation. Individuals found up to 1500 m on the High Atlas and Saharan Atlas mountains. Does not live in the sclerophyllous forests of Morocco, Algeria and Tunisia.

Abundance Very varied and dependent on food availability and character of the habitat. In Egypt, recorded as '1–50 jerboas per 0.8 km', and 'more or less common' on the desert slopes near the Mediterranean Sea from Egypt west of the Nile Delta to Libya and Algeria (Hoogstraal 1963). In Algeria, common on the high plateaux (Kowalski & Rzebik-Kowalska 1991).

Adaptations Terrestrial and nocturnal; similar in many ways to *J. jaculus* but confined to the Mediterranean coastal regions and hence less well adapted for desert environments. Greater Egyptian Jerboas have two main forms of locomotion: a bipedal hop with asynchronized foot support (rather like a gallop), and a bipedal trot, which is used for moving around and through bushes and shrubs (cf. *J. jaculus*) (Schröpfer *et al.* 1985).



Jaculus orientalis

Burrows usually 1–2 m in length, dug in hard ground, often on the slope of a hill (Kirmiz 1962). Burrow ends in a nest chamber lined with camel hair, shredded pieces of cloth or shredded vegetation. Some burrows have a food chamber (see below). Position of burrows changes seasonally: higher on hillsides during winter rains, and on lower ground close to fields in summer. When occupied, burrows are blocked with plugs of sand.

Water conservation has been measured by the percentage of body water that is 'turned over' in 24 h, and the volume and concentration of the urine. In cold conditions ($T_a = 8^\circ\text{C}$), water turnover (regardless of food) is ca. 10%/24 h, and in hot weather ($T_a = 32^\circ\text{C}$), it is reduced to 5%/24 h (when fed only on barley) and 9%/24 h (when fed on barley and 'salad'). Greater Egyptian Jerboas are able to produce small amounts of concentrated urine when required. For example, when fed on barley and 'salad', at $T_a = 8^\circ\text{C}$, urine production was 8.7 ml urine/24 h with an osmotic concentration of 714 mOsm/L, and at $T_a = 32^\circ\text{C}$ they produced 0.6 ml/24 h with an osmotic concentration of 2227 mOsm/L (Baddouri *et al.* 1985). In these respects, this species of jerboa is not as efficient at water conservation as *J. jaculus*.

In the winter, on parts of Mediterranean coast and high plateaux, air temperatures at night may be below freezing although the temperature in burrows is ca. 10°C . On the high plateaux of Morocco (1500 m), Greater Egyptian Jerboas taken from burrows in winter were immobile, breathing was spasmodic and body temperature was $10\text{--}11^\circ\text{C}$. On exposure to an air temperature of 17°C , shivering commenced and body temperature gradually increased to normal in ca. 4 h. Thus Greater Egyptian Jerboas show true hibernation, and are able to rewarm using endogenous mechanisms (El Hilali & Veillat 1975). They appear to be more tolerant of cold than Common Jerboas (Hooper & El Hilali 1972).

Foraging and Food Foraging is similar to that in Lesser Egyptian Jerboas but because of their large size, Greater Egyptian Jerboas are able to consume larger seeds. Food is mainly sprouting vegetation, plants, roots and barley grains (Kirmiz 1962). Various succulent shrubs such as *Salicornia* and *Suada* may be browsed by individuals inhabiting salt marshes (Osborn & Helmy 1980). Dates, barley and the seeds of several wild plants have been found in burrows.

Social and Reproductive Behaviour Sociable, and not usually encountered as solitary individuals (cf. *J. jaculus*) (Osborn & Helmy 1980). Parapatric (and perhaps syntopic) with *Allactaga tetradactyla* on the coasts of Libya and Egypt.

Reproduction and Population Structure Limited information. In Egypt, breeding occurs during winter (Nov–Feb) and summer, and less frequently during spring (Hoogstraal 1963). Births recorded in Feb, Apr and early Jul. Litter-size: 3, 4, 7 in Algeria (Kowalski & Rzebik-Kowalska 1991); 2, 3, 4, 5 (mode 3) in Egypt (Flower 1932).

Predators, Parasites and Diseases Remains found in owl pellets in Algeria (Kowalski & Rzebik-Kowalska 1991). In Egypt, a flea *Mesopsylla tuschkan* is found commonly in nests and on animals; nine other species of fleas have been recorded occasionally (Hoogstraal & Traub 1965b).

Conservation IUCN Category: Least Concern.

Measurements

Jaculus orientalis

HB: 148 (137–160) mm, $n = 31$

T: 224 (195–243) mm, $n = 31$

HF: 75 (71–78) mm, $n = 31$

E: 33 (28–35) mm, $n = 30$

WT: 134 (108–147) g, $n = 17$

GLS: 36.9 (36.2–38.0) mm, $n = 26$

GWS: 28.3 (27.1–30.0) mm, $n = 24$

$M^1\text{--}M^3$: 6.7 (6.2–7.4) mm, $n = 25$

Auditory bulla: 15.6 (15.2–16.7) mm, $n = 7^*$

Egypt (Osborn & Helmy 1980)

*Egypt (BMNH)

Key References Osborn & Helmy 1980; Kirmiz 1962.

D. C. D. Happold

Family SPALACIDAE

BLIND MOLE-RATS, AFRICAN ROOT-RATS, ZOKORS AND BAMBOO-RATS

Spalacidae Gray, 1821. London Med. Repos. 15: 303.

| | | |
|---------------------------------|----------------------|--------|
| <i>Spalax</i> (1 species) | Ehrenberg's Mole-rat | p. 145 |
| <i>Tachyoryctes</i> (2 species) | Root-rats | p. 148 |

This small family (six genera and 36 species) represents an old lineage of Muroidea whose extant members have acquired striking fossorial adaptations and evolved into predominantly subterranean niches. There are four subfamilies: Myospalacinae (Zokors), Rhizomyinae (Bamboo-rats), Spalacinae (Blind Mole-rats) and Tachyoryctinae (African Root-rats). The first two subfamilies are extralimital to Africa, myospalacines occurring in Siberian Russia and northern China, and rhizomyines in north-eastern India, southern China and the Malay Peninsula. The latter two subfamilies, the spalacines (one genus, one species) and tachyoryctines (one genus, two species), are geographically localized within Africa. The only African species of *Spalax* is found along the Mediterranean coastal region, and the two species of *Tachyoryctes* live in the highlands of Ethiopia and East Africa. Although each subfamily is readily diagnosed by unique traits (Carleton & Musser 1984), underground life in burrows has entailed the evolution of a suite of morphological, physiological, sensory and behavioural specializations common to subterranean forms in other rodent families and suborders (Nevo 1979, 1999, Nevo & Reig 1990, Lacey *et al.* 2000). General characters of Spalacidae include a cylindrical body shape with broad head and massive cervical musculature; very soft and fine pelage; small or vestigial pinnae and eyes; short or inconspicuous tail; short, stocky limbs and powerful appendicular musculature; enlarged claws, especially on the forelimbs; hypertrophy and procumbency of the lower incisors for chisel-tooth digging; and robust, hypsodont molars associated with their largely herbivorous diet of roots, bulbs and rhizomes (Carleton & Musser 1984, Stein 2000). Dental formula: $I^{1/1}$, $C^{0/0}$, $P^{0/0}$, $M^{3/3} = 16$ (Table 15).

Whether such phenotypic resemblance connotes phylogenetic relationship or evolutionary convergence, it has accounted for most of the differences in the classification of these rodents. Most taxonomic arrangements, implicitly or explicitly, reflect the view that the similar fossorial adaptations have evolved in parallel and have variously grouped the six genera within three or four separate subfamilies and in one to three families (see Topachevskii 1969, Carleton & Musser 1984 for reviews). In the prevalent classificatory treatment, Spalacidae and Rhizomyidae (including *Tachyoryctes*) have been retained as small outlying families separate from core Cricetidae and/or Muridae (e.g. Miller & Gidley 1918, Ellerman 1940, Simpson 1945, Pavlinov *et al.* 1995). Some palaeontologists have echoed a similar viewpoint and have considered that Spalacidae and Rhizomyidae (a non-African taxon) originated independently from different muroid stocks (Flynn *et al.* 1985).

As early as 1899, however, Tullberg interpreted their shared resemblance as phylogenetic relationship and placed *Myospalax*, *Spalax*, *Rhizomys* and *Tachyoryctes* in Spalacidae, separate from his Cricetidae and Muridae. Monophyletic union of these fossorial genera has earned substantial support from recent studies, including evidence from morphology of the cephalic arterial system (Bugge 1971, 1985) and repeatedly from phylogenetic reconstruction based on nuclear gene sequences (Robinson *et al.* 1997, Debry & Sagel 2001, Michaux *et al.* 2001, Jansa & Weksler 2004). These data collectively portray myospalacines, rhizomyines, spalacines and tachyoryctines as a clade (Spalacidae) that is a sister-group to representatives of all other muroid families so far investigated (Calomyscidae, Cricetidae, Muridae, Nesomyidae) and infer an early divergence (and possibly one of the earliest divergences) of Spalacidae within Muroidea from a middle or late Oligocene ancestral stock.

Table 15. Subterranean rodents in Africa.

| Family: genus | Number of upper cheekteeth | Upper cheektooth row | Upper incisor teeth | Infraorbital foramen | Eyes | Tail |
|---|---|----------------------|--|-------------------------------------|-------------------------|---|
| Spalacidae: <i>Spalax</i> | 3 (M^1 , M^2 , M^3) | Diverge anteriorly | Orthodont, ungrooved, not extrabuccal | Large, well developed | Absent (non-functional) | Absent externally |
| Spalacidae: <i>Tachyoryctes</i> | 3 (M^1 , M^2 , M^3) | Converge anteriorly | Pro-odont, ungrooved, slightly extrabuccal | Large, well developed | Very small | Short, visible externally (20–30% of HB); well haired |
| Bathyergidae: <i>Bathyergus</i> | 4 (P^4 , M^1 , M^2 , M^3) | Parallel | Pro-odont, grooved, strongly extrabuccal | Very small, round | Small | Short, visible externally (18–24% of HB); stiff bristles |
| Bathyergidae: <i>Heliophobius</i> | 6 (but usually 4 or 5; left side may differ from right) | Parallel | Pro-odont, grooved, strongly extrabuccal | Very small, round | Small | Very short, visible externally (9% of HB); stiff bristles |
| Bathyergidae: <i>Heterocephalus</i> | 3 (sometimes 2) | Parallel | Pro-odont, ungrooved, strongly extrabuccal | Very small, round | Very small | Moderately long (ca. 50% of HB); naked |
| Bathyergidae: all genera except <i>Heterocephalus</i> | 4 (P^4 , M^1 , M^2 , M^3) | Parallel | Pro-odont, ungrooved, strongly extrabuccal | Small, teardrop or elliptical shape | Small | Short, visible externally (7–18% of HB), stiff bristles |

Although Oligocene fossils are so far unknown, the documented fossil history of Spalacidae is suitably deep in time to be consistent with a middle to late Oligocene origin. The earliest indisputable records among the four subfamilies are early Miocene, around 19–20 mya in Asia Minor (*Debruijnina*, Spalacinae) and southern Asia (*Prokanisamys*, Rhizomyinae) (see Flynn 1990, Nevo 1999 and Cook *et al.* 2000 for palaeontological summaries). In Africa, the earliest occurrences of the family originate from middle to late Miocene strata of Kenya (as *Pronakalimys* and *Nakalimys*; Flynn & Sabatier 1984, Tong & Jaeger 1993) and the late Miocene of Namibia (as *Nakalimys* and *Harasibomys*; Mein *et al.* 2000a). Although dental contrasts between living spalacid genera are highly distinctive, it is noteworthy

that molar similarities among certain African Miocene forms render assignment to subfamily – whether rhizomyine, spalacine, or tachyoryctine – as indefinite (Mein *et al.* 2000a). Spalacids were more geographically widespread and taxonomically diverse during the late Miocene through Pliocene (see Flynn 1990, Ünay 1999, Cook *et al.* 2000), a comparison that reinforces the impression that the relatively few extant spalacids, so strongly differentiated from one another, are relicts from a much older muroid radiation.

Two subfamilies of Spalacidae occur in Africa: Spalacinae (1 genus, 1 species) and Tachyoryctinae (1 genus, 2 species).

Guy G. Musser & Michael D. Carleton

Subfamily SPALACINAE – Mole-rats

Spalacinae Gray, 1821. London Med. Repos. 15: 303.

The Spalacinae encompasses a single living genus, *Spalax*, whose range stretches from SE Europe and SW Asia around the Black and Caspian Seas, through Asia Minor and the near Middle East, to North Africa (see Nevo *et al.* 2001). The recent distribution broadly follows the hilly, uplifted region that corresponds to the ancient basin of the Mediterranean Sea and is generally concordant with that of known spalacine fossils (Ünay 1999). Conventionally, eight living species of *Spalax* are recognized (e.g. Topachevskii 1969, Musser & Carleton 1993), but this number may grossly underestimate the specific diversity (see later). Only a single species, *S. ehrenbergi*, occurs in Africa; its distribution is limited to the Mediterranean coastal region

of W Egypt and Libya (Lay & Nadler 1972). As currently understood, these North African populations are separated from those of *S. ehrenbergi* in the southern Levant by the Nile Delta and arid Sinai Desert (rainfall <100 mm).

The pronounced fossorial modifications exhibited by *Spalax* readily separate it from other African Muroidea, including *Tachyoryctes* (Tachyoryctinae, see below), the only other African representative of Spalacidae. The eyes, pinnae and tail are externally lacking in *Spalax*; bristly, facial hairs form stiff lateral keels and impart a wedge-like shape to the head; claws of fore- and hindfeet are enlarged; the occiput is slanted and the lambdoidal crest is shifted forward, forming a large occipital shield for insertion of cervical musculature; rear of glenoid fossa is enclosed by a bony wall that enlarges the occipital shield; the interparietal is undefined in adults; the jugal is short and thin; the infraorbital foramen is wide and ovoid, with the zygomatic plate narrow and nearly horizontal; mesopterygoid fossa U-shaped ending anteriorly in line with posterior end of third molars; roof of parapterygoid fossa open; upper incisors are orthodont and the lowers long and procumbent, the maxillary tooththrows parallel to one another; olecranon process for insertion of triceps brachii is elongate, about two-thirds the length of the main shaft of the ulna (Topachevskii 1969, Carleton & Musser 1984, Hildebrand 1985) (Figure 23). In contrast to *Tachyoryctes*, many traits of *Spalax* indicate that it is more highly specialized for subterranean living, differences that agree with its rare surface-foraging as compared with *Tachyoryctes*.

In view of its many autapomorphies, *Spalax* has been commonly classified in a family by itself (Ellerman 1940, Simpson 1945, Topachevskii 1969, Nevo 1999) or variously with other similarly adapted fossorial muroids, especially rhizomyines and tachyoryctines (Thomas 1897, Tullberg 1899). Recent phylogenetic evidence persuasively supports the latter relationship and cladistically arrays spalacines with such groups in a basal lineage (Spalacidae) of Muroidea (see family profile). Divergence times based on nuclear gene sequences estimate the separation of spalacines from other muroids as about 19 mya (Robinson *et al.* 1997, Michaux & Catzeflis 2000), an origin consistent with the antiquity of the earliest spalacines so far documented.

The oldest spalacine genera are recorded about 18–20 mya (*Debruijnina* and *Heramys* from the early Miocene of Turkey and Greece, respectively), and the speciose *Pliopspalax* is known from the middle

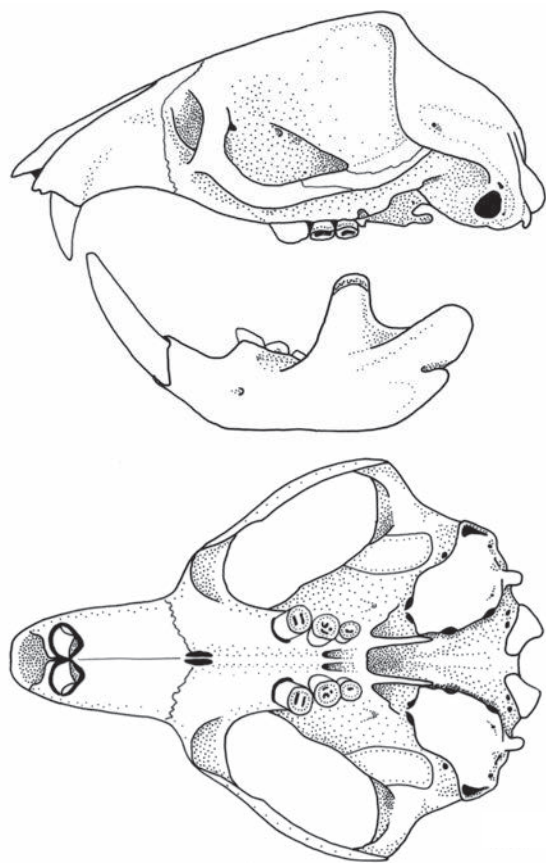


Figure 23. Skull and mandible of *Spalax ehrenbergi* (RMCA no number).

Miocene–Pliocene in Asia Minor and middle Miocene–early Pleistocene in Europe (see reviews by Ünay 1996, 1999, Kowalski 2001). Because fossorial adaptations already characterize Miocene *Pliospalax* (Sen 1977), spalacines are believed to have evolved into a fossorial and subterranean niche around 14–15 mya, much earlier than either tachyoryctines or rhizomyines (Flynn 1990). Living *Spalax* is a descendant of this once extremely diverse group, one thought to have originated and diversified in Anatolia (Ünay 1999). The genus itself appears in the early Pliocene of Europe and middle Pleistocene of SW Asia (Topachevsky *et al.* 1998, Ünay 1999, Kowalski 2001), and the *S. ehrenbergi* complex in Israel dates from at least 1.4 mya (Nevo 1995, Tchernov 1996). The North African segment of *S. ehrenbergi* was isolated relatively recently, separating from Levant populations only about 10,000 to 20,000 years ago (Lay & Nadler 1972, Nevo *et al.* 1992), perhaps coincident with the disjunction of *Microtus mustersi* in the same region.

The number of genera and species considered to be valid are subjects of continuing research. A single genus had been identified in most systematic accounts (e.g. Ellerman 1940, Ognev 1947) until Topachevskii (1969) recognized two genera, *Spalax* and *Microspalax* (= *Nannospalax*), based on subtle cranial and dental differences.

Although the dual generic arrangement gained acceptance in the late 1900s (e.g. Musser & Carleton 1993, Gromov & Erbaeva 1995, Mitchell-Jones *et al.* 1999), specialists on Blind Mole-rats continue to endorse only the single genus *Spalax* (Savic & Nevo 1990, Ünay 1996, 1999, Nevo *et al.* 2001), a taxonomy based more on expediency rather than firm understanding of supraspecific relationships. Based on morphological criteria, seven or eight living species have been usually recognized (Ognev 1947, Topachevskii 1969). None the less, the extraordinary variation in diploid and fundamental numbers ($2n = 38–62$, $FN = 72–124$) uncovered within *Spalax* has prompted some investigators to consider many of these morphological entities as superspecies, with the distinct chromosomal morphs representing as many as 30 to 50 biological species (Savic & Nevo 1990, Nevo *et al.* 1995). Populations in Egypt and Libya are members of the *S. ehrenbergi* superspecies (*sensu* Nevo 1991, Nevo *et al.* 2001). If these are treated as a separate species, as suggested by Nevo *et al.* (1992), then *aegyptiacus* is the name that should be applied to this North African segment of the *S. ehrenbergi* complex.

Guy G. Musser & Michael D. Carleton

GENUS *Spalax*

Mole-rats

Spalax Guldenstaedt, 1770. Nova Comm. Acad. Sci. Petropoli, ser. 14, 1: 410. Type species: *Spalax microphthalmus* Guldenstaedt, 1770.



Spalax ehrenbergi.

The genus *Spalax* contains eight species, of which only one is represented in Africa. The characters of the genus are given in the profile Subfamily Spalacinae (above) and the species profile (below). The single African species, *Spalax ehrenbergi*, was placed in the genus *Nannospalax* by Musser & Carleton (1993).

D. C. D. Happold

Spalax ehrenbergi MIDDLE EAST BLIND MOLE-RAT (EHRENBERG'S MOLE-RAT)

Fr. Spalax d'Ehrenberg; Ger. Ehrenberg-Blindmaus

Spalax ehrenbergi (Nehring, 1898). Sber. Ges. Naturf. Freunde Berlin 1897, p. 178. pl. 2. (publ 1898). Jaffa, Israel.

Taxonomy The Egyptian form described as *S. aegyptiacus* is now considered as junior synonym of *S. ehrenbergi*. Genetics, karyology, physiology, behaviour, adaptive radiation and evolution of the species has been extensively studied in Israel, although the definition and limits of the species are still uncertain (see Spalacinae). Considerable karyotypic variation: $2n$ may be 52, 54, 58 or 60, the highest $2n$ number being in populations from the most arid regions. Alternatively, according to Nevo (1991; details in Musser & Carleton 2005), 'ehrenbergi' in Israel may be considered as four parapatric species (*S.*

carmeli, *S. galili*, *S. golani*, *S. judaei*), each with different chromosome numbers and morphological traits (recent studies in Israel have referred to these four species as the '*S. ehrenbergi* superspecies'). African populations have the same number of chromosomes as those from arid regions of Israel, but can be distinguished by baculum morphology (Simson *et al.* 1993), cranial morphology (Ellerman & Morrison-Scott 1951) and molar variation (Butler *et al.* 1993). They may have evolved independently from populations in Israel (and the Middle East) as a result of long-term isolation imposed by the arid

conditions in the Sinai Desert (Nevo *et al.* 1992); if so, *S. aegyptiacus* is the correct name for the African populations (Musser & Carleton 2005). Synonyms: *aegyptiacus*. Subspecies: none. Chromosome number: $2n = 60$ (Egypt; Lay & Nadler 1972).

Description Large subterranean species with cylindrical shape and without visible tail. Pelage soft and silky, dense; hairs ca. 10 mm. Dorsal pelage greyish-brown with silvery sheen; hairs dark grey with pale brown or orange-brown at tip. Ventral pelage dark grey; hairs dark grey at base with or without pale brown or orange-brown tip. Head blunt and rounded; hairs pale, may be almost white, on anterior part of head. Eyes small and vestigial, permanently covered by skin. Rhinarium hairless, but with longer hairs on muzzle and upper lips. Incisors slightly extrabuccal. Ear pinnae reduced to small cartilaginous ring surrounding auditory meatus. Forelimbs short, same colour as body. Forefeet broad with five digits; Digit 1 shorter than Digits 2–5; short rounded claws. Hindfeet not broadened; five digits; Digits 1 and 5 short reaching only to base of Digits 2, 3 and 4. Tail very short, not visible externally. Skull: upper incisor teeth ungrooved; orthodont to slightly pro-odont; braincase triangular in shape; supraoccipital bone very large, slopes anteriorly so that lamboid crests are in line with end of zygomatic arches. On mandible, lower incisor teeth very long; well-developed alveolar and angular processes, in addition to the condylar process (Figure 23). See also profile Subfamily Spalacinae.

Geographic Variation In Libya, individuals on the Cyreniaca Plateau are smaller than those near the coast, perhaps because the soils of the plateau are harder and less sandy than those of the coast; hence burrowing is more difficult, and small size is advantageous (Ranck 1968). Pelage colour varies locally depending on soil colour (Nevo 1991).

Similar Species This is the only subterranean species in its geographic range, and the only species that has vestigial eyes. Body



shape bears resemblance to other subterranean rodents (e.g. *Tachyoryctes*, *Heliophobius*, *Cryptomys*, etc.) but all are allopatric to *S. ehrenbergi*.

Distribution Sahara Arid BZ. Recorded from coastal regions of Libya (Cyreniaca region) and Egypt (west of the Nile Delta). Not recorded further west, i.e. not recorded from Algeria (Kowalski & Rzebik-Kowalska 1991). Extralimittally present in Israel, Lebanon, Jordan, Syria and SW Turkey.

Habitat Soil quality and texture determine distribution. Preferred habitats in Egypt include deep sandy and loamy soils where *Asphodelus microcarpus* is the commonest plant, and fields of barley (Osborn & Helmy 1980). In Libya, recorded in fertile soils in valleys, on coastal plains and on the uplands of Cyreniaca Plateau (Ranck 1968). Prefers habitats where annual rainfall is 100–300 mm. Avoids areas where flooding may occur, rocky areas and areas of extreme aridity (annual rainfall <100 mm).

Abundance Populations are localized because of subterranean life-style and the difficulties of dispersal (see below). In optimal habitats in Israel, mean density was 3 individuals/1000 m² (range 0.6–6.1; Nevo 1982, in Heth 1991a). No information on abundance in Africa, although said to be widespread in coastal parts of Libya after rains (Ranck 1968). Probably less common in Africa than in some parts of the Middle East.

Adaptations Probably the most adapted of all rodents to subterranean life. Body shape is cylindrical, with wide blunt head, short powerful limbs and no tail. Unlike other subterranean rodents, the eye is atrophied and covered by a thick layer of skin (hence an external eye is not visible), and the orbits are filled with a gland, which produces secretions that are thought to reduce aggression during encounters with conspecifics (Shanas & Terkel 1995). Perception of light is very limited or non-existent. Burrows vary in length and depth: in Egypt, they are 30–40 m in length and ca. 45 cm below the surface (Osborn & Helmy 1980); in Israel, they are 20–40 cm below the surface and vary in length according to season, from 18.7 ± 4 m in the dry season to 39.1 ± 7.1 m in the wet season (Zuri & Terkel 1996). Typical burrows consist of a main tunnel, with multiple secondary tunnels, and two or more entrances. The large incisor teeth cut and scrape the soil during burrowing, the blunt head pushes and packs the soil within the burrow, and the fore- and hindlimbs push the loosened soil behind the body. Excavated soil is pushed into mounds on the surface; these are the most visible signs of Blind Mole-rats, and are especially visible when there is increased burrowing activity after rain. Burrows contain food-stores, toilets and nests; normally there are several nests, but only one is used at a time (Heth 1991a). Entrances to burrow are normally plugged with soil (Ranck 1968).

Although living underground (where daily variations in temperature are minimal, and it is dark all the time), Blind Mole-rats have peaks of locomotor activity from 08:00h to 11:30h during summer, and 11:00 to 19:00h during winter. It seems that brief light pulses perceived through the rudimentary eyes when pushing soil at the surface are an adequate stimulus to entrain a diurnal rhythm of activity (Goldman *et al.* 1997). Most burrowing activity occurs

during the wet season in winter and spring, and the least activity during the hot and dry summer (Osborn & Helmy 1980).

Ehrenberg's Mole-rats do not drink free water; rather they rely on water in the diet (see below).

Foraging and Food Herbivorous. Forages while digging 'feeding tunnels'; these usually form most of the burrow system. The main items in the diet are corms, bulbs, tubers, fibrous roots and rhizomes of those plant species that specialize in underground storage organs (Heth 1991a). Food items may be collected and hoarded in food stores. Analysis of 21 food stores in Israel showed many hundreds of items may be stored comprising at least 33 species of plants; these include the underground parts of geophytes (61%), perennial herbs (21%), annual herbs (15%) and dwarf shrubs (3%) (Heth *et al.* 1989). Blind Mole-rats are generalists feeders, utilizing many species of plants, probably because of the high energy requirements of burrowing and the low productivity of their subterranean environment (Nevo 1991). A further adaptation to low productivity is the relatively large caecum, with a spiral valve (as in rabbits) that doubles the absorptive surface area (Nevo 1991). Potatoes, carrots and onions are collected and eaten in cultivated areas.

Social and Reproductive Behaviour Solitary, aggressive and territorial. Normally only one individual inhabits each burrow system, where it lives for all its life (Heth 1991a). The burrow system is marked by deposits of urine and faeces. Blind Mole-rats use vibrations (produced by 'head drumming') to communicate with mole-rats in adjacent burrow systems (Zuri & Terkel 1996). Young disperse when ca. two months old; it burrows away laterally from the maternal burrow and, when ca. 4 m away, seals the burrow behind it and establishes its own territory (Rado *et al.* 1992). In dense populations, some young disperse above ground.

Reproduction and Population Structure In Israel, reproduction occurs during the cool winter season (Nov–Apr), but later at higher altitudes in Lebanon. Most births occur in Jan and Feb in Israel (Rado *et al.* 1992), but as late as Apr at higher

altitudes in Lebanon (Lewis *et al.* 1967). Gestation: 34 days. Litter-size: 2–3.

Predators, Parasites and Diseases Predation appears to be uncommon. Blind Mole-rats are preyed upon occasionally by Barn Owls *Tyto alba* in Israel. They formed 0.4% of the rodents and shrews in 1023 owl pellets from seven localities in Israel (Heth 1991b); all were juveniles or subadults, presumably caught above ground while dispersing. No fleas were found on these mole-rats, nor in their burrows, in Egypt ($n = \text{ca. } 100$ animals/burrows; Hoogstraal & Traub 1965b), possibly because the environment in burrows is too damp for fleas. *Ctenophthalmus levanticus* and a few other fleas have been found on these mole-rats in Lebanon (Lewis 1964, quoted by Hoogstraal & Traub 1965b).

Conservation IUCN Category: Data Deficient (throughout range; no separate assessment for Africa). In Israel, regarded as a pest in agricultural crops and tree plantations.

Measurements

Spalax ehrenbergi

TL: 189.0 (163–203) mm, $n = 7$

T: ca. 15–16 mm (not visible externally)

HF: 25.0 (23–26) mm, $n = 7$

E: 0 mm

WT: 107, 120 g, $n = 2^*$

GLS: 44.2 (42.5–46.5) mm, $n = 6$

GWS: 31.7 (29.5–33.8) mm, $n = 6$

M^1 – M^3 : 7.6 (7.4–7.7) mm, $n = 4$

Egypt (as *S. e. aegyptiacus*) (Osborn & Helmy 1980)

Males (except where indicated; ♀ ♀ slightly smaller)

* ♀ ♀ only

Key References Heth 1991a; Nevo 1991; Osborn & Helmy 1980; Ranck 1968.

D. C. D. Happold

Subfamily TACHYORYCTINAE – African Root-rats

Tachyoryctinae Miller and Gidley, 1918. J. Wash. Acad. Sci. 8: 437.

The Tachyoryctinae consists of a single living genus, *Tachyoryctes*, that is endemic to highlands of north-eastern Africa and whose greatest taxonomic diversity is centred on the highlands and mountains of Kenya. Considerable fossil evidence, however, indicates that the subfamily once extended into southern Asia, as far as northern India (summaries in Nevo 1999, Cook *et al.* 2000), and perhaps into south-western Africa, as far as Namibia (Mein *et al.* 2000a).

Although largely subterranean in habits, *Tachyoryctes* is not so fossorially specialized as *Spalax*. Eyes, pinnae and tail are small but clearly visible in *Tachyoryctes*; pelage of the head is unmodified, and the claws of the fore- and hindfeet are unremarkable in size. Skull characters include occiput nearly horizontal, occipital shield relatively small, rear of glenoid fossa open, interparietal reduced but distinct, jugal long and deep, infraorbital foramen round above and constricted below with the zygomatic plate much broader and more

vertical, mesopterygoid fossa V-shaped ending anteriorly between the third molars, and roof of parapterygoid fossa wholly osseous. The upper and lower incisors are procumbent and the maxillary toothrows are convergent anteriorly (Figure 24). The olecranon process for insertion of triceps brachii is elongate, about one-third of the length of the main shaft of the ulna (Carleton & Musser 1984, Hildebrand 1985).

Although *Spalax* occurs nearby in North Africa and the Middle East, *Tachyoryctes* is thought to be most closely related to the Bamboo Rats (*Cannomys* and *Rhizomys*: Rhizomyinae) of southern China and South-East Asia. Most systematists have thus classified *Tachyoryctes* with those Asian genera, usually as a distinctive subfamily of Rhizomyidae on the basis of differences in dentition, infraorbital canal and zygomatic plate (Miller & Gidley 1918, Chaline *et al.* 1977, Flynn 1990), or unsegregated within Rhizomyinae of Muridae *sensu lato* (Carleton &

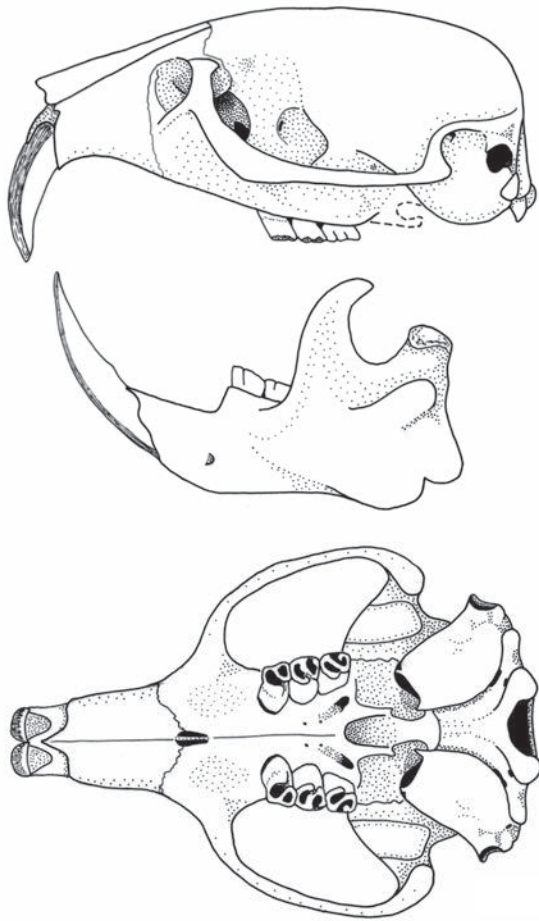


Figure 24. Skull and mandible of *Tachyoryctes splendens* (RMCA no number)

Musser 1984). Others, instead, have emphasized molar similarities between *Tachyoryctes* and the nesomyine *Brachyuromys* (Major 1897); classifications that reflect this interpretation of relationship have placed *Tachyoryctes* in its own subfamily within a broadly defined Muridae (Ellerman 1941) or Nesomyidae (Lavocat 1978). Palaeontological discoveries (Flynn 1982, 1990, Tong & Jaeger 1993) and phylogenetic evaluations of gene-sequence data (Michaux *et al.* 2001, Jansa & Weksler 2004) decisively reinforce close kinship of *Tachyoryctes* with Asian rhizomyines. The latter molecular studies

relate *Tachyoryctes* and *Rhizomys* as sister genera among those spalacids studied (also *Myospalax* and *Spalax*).

Tachyoryctines are documented by several extinct genera from the middle to late Miocene Siwalik faunas of Afghanistan, Pakistan and northern India (Black 1972b, Flynn 1982, 1990). As currently understood, tachyoryctines were more taxonomically diverse in those Miocene beds of south-western Asia than in comparably aged strata of Africa. In view of this past distribution and apparent cradle of early diversity, tachyoryctines are supposed to have originated in Asia and emigrated to Africa in one (>14 mya) or two stages, the last (ca. 5 mya) giving rise to *Tachyoryctes* (Flynn & Sabatier 1984, Flynn 1990, Tong & Jaeger 1993). The oldest record of *Tachyoryctes* proper is *T. pliocaenicus*, recorded from the late Pliocene (Hadar Formation) in Ethiopia (Sabatier 1978). Palaeontologists, however, are reluctant to definitely assign the earliest African forms – the middle Miocene *Pronakalimys* (Tong & Jaeger 1993) and late Miocene *Nakalimys* and *Harasibomys* (Flynn & Sabatier 1984, Mein *et al.* 2000a) – to subfamily, whether tachyoryctine or rhizomyine (Tong & Jaeger 1993) or even early spalacine (Mein *et al.* 2000). At this stage of understanding, the continental area of origin is equivocal. An alternative possibility, which merits consideration, is that the common ancestor of tachyoryctines and rhizomyines evolved in Africa, with subsequent dispersion (and cladogenesis) in Asia.

Morphological recognition of the genus is unproblematic, but how many of the 20 described forms of *Tachyoryctes* represent valid species remains unanswered. The number recognized has ranged from as many as 11–14 (Allen 1939, Ellerman 1941, Musser & Carleton 1993, 2005) to as few as two (Misonne 1974, Rahm 1980, Corbet & Hill 1991). Appreciation of the large morphological variation and acceptance of the polytypic species concept resulted in the abrupt reduction from 14 to two species in the latter 1900s. In view of the montane isolation among many tachyoryctine populations, and the re-emerging appreciation of diversity of other taxa distributed over East African Rift Mts, species recognition within *Tachyoryctes* should ultimately rest on some empirical framework instead of theoretical preconceptions. Until such evidence becomes available, the two conventional species, *T. macrocephalus* and *T. splendens*, are acknowledged here.

Guy G. Musser & Michael D. Carleton

GENUS *Tachyoryctes*

Root-rats

Tachyoryctes Rüppell, 1835. Neue Wirbelth. Fauna Abyssin. Gehörig., Säugeth: 35. Type species: *Bathyergus splendens* Rüppell, 1835.

The genus contains two species distributed in Ethiopia, Somalia, Kenya, Tanzania (Mt Kilimanjaro), Uganda, E DR Congo, Rwanda and Burundi. Found in a variety of habitats from forest to open grasslands at altitudes of above 1500 m (Ellerman 1940, Rahm 1980).

The body form is modified for subterranean existence: cylindrical head and body; short limbs; short tail (20–32% of HB); small ear pinnae closely applied to head; and small eyes. Pelage is thick and soft. Skull characters include conspicuously constricted frontals

(interorbital region); wide rostrum housing thick, orange, ungrooved incisors; long jugal bone almost reaching the lacrymal; narrow palate anteriorly, which broadens posteriorly with a prominent raised ridge running down the centre; and small anterior palatal foramina. Cheekteeth very hypsodont but rooted and with deep folds running across the teeth. Mandible with high recurved coronoid process and a prominent process (between condylar and angular) caused by the root of lower incisor (Ellerman 1940). See also profile subfamily Tachyoryctinae.



Tachyoryctes splendens.

African Root-rats are solitary aggressive animals living underground in a system of foraging burrows, where there is also a deep nest with associated toilet area, and a bolt-hole. They are exclusively herbivores, eating grasses, herbs and underground storage organs. Unlike the other subterranean rodents (Bathyergidae), root-rats forage both underground and on the surface. When foraging on the surface, root-rats keep their hindquarters in the hole, ready for rapid retreat, and hence foraging is limited to what can be reached

from the immediate vicinity of an open hole. They are chisel-tooth diggers but differ from the Bathyergidae in using one forelimb and the side of the face to push excavated soil onto the surface (Jarvis & Sale 1971). They also differ from the Bathyergidae in having better vision and small ear pinnae.

The number of species in the genus is uncertain; many species and a number of subspecies have been described but there is no clear consensus about the systematics of this genus. Musser & Carleton (1993, 2005) recognized 11 species, and Misonne (1974) and Corbet & Hill (1991) recognized only two (*T. splendens* and *T. macrocephalus*). Study of the 11 'species' from 53 locations throughout the range of the genus showed that most of the variation observed reflects adaptations to ecological conditions and hence there is no basis for the recognition of more than two species, *T. macrocephalus* and *T. splendens* (Beolchini & Corti 2004). Karyological and cytogenetic information is required to resolve these differences of opinion.

The two species are distinguished by size, width of the interorbital constriction, upper incisor width and geographic location.

J. U. M. Jarvis

Tachyoryctes macrocephalus GIANT ROOT-RAT (GIANT MOLE-RAT)

Fr. Rat-taupe géant d'Ethiopie; Ger. Riesen-Maulwurfsratte

Tachyoryctes macrocephalus (Rüppell, 1842). Mus. Senckenbergiana 3: 97, 115, pl. 8 fig 10 and pl. 10, fig 2. Shoa, Ethiopia.

Taxonomy Originally described in the genus *Rhizomys*. *Tachyoryctes macrocephalus* is clearly distinguished from its congener by its much larger size and different chromosome number. Synonyms: *hecki*. Subspecies: two. Chromosome number: $2n = 50$ (Aniskin *et al.* 1997b).

Description Very large, soft-furred root-rat (ca. 600 g) about three times the weight of *T. splendens*. Pelage soft, dense and long (up to 20 mm). Dorsal pelage pale brown; hairs dark grey at base, pale brown or buff at tip. Ventral pelage paler, silvery-grey to pale buff; hairs grey at base, pale buff at tip. Colour variable from silver to shades of orange. Head large; 1–3 dark brownish-black lines on crown of head (variable); dark spot on upper eyelid. Ears very small, held close to head, pigmented, with short hairs especially on outer margins. Limbs short. Fore- and hindfeet silvery-grey. Tail very short (ca. 20% of HB), thick at base with long hairs, tapering to tip with short hairs. Skull: interorbital width narrow (ca. 6–7 mm), large narrow extrabuccal incisors (size variable and useful for determining size, age and weight).

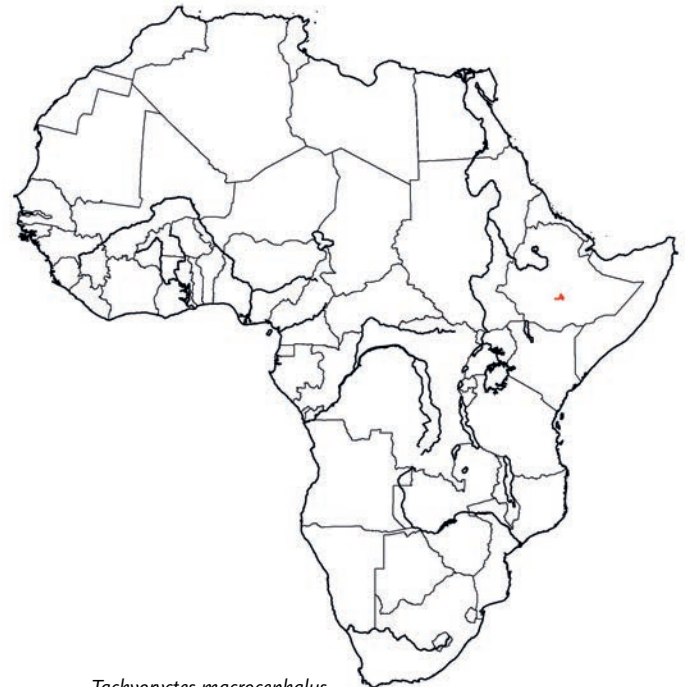
Geographic Variation

T. m. macrocephalus: N Ethiopia (only known from four specimens). Short anterior palatal foramina (ca. 5.0 [range 3.6–6.0] mm, $n = 4$); zygomatic plate angular.

T. m. hecki: Bale Mts, S Ethiopia. Longer anterior palatal foramina (ca. 8.5 [range 7.3–9.5], $n = 4$); zygomatic plate slopes down to the premaxillary–maxillary suture.

Similar Species

T. splendens. Smaller body size and weight (HB 159–215 mm, WT 140–315 g; wider interorbital width, absolutely and relatively (ca. 7 mm); more widespread in eastern Africa.



Tachyoryctes macrocephalus

Distribution Endemic to Africa. Afromontane–Afroalpine BZ. Confined to the high plateaux of Ethiopia, from 3000 to 4150 m. Known from Bale Mts east of the Rift Valley but apparently absent from nearby Arussi mountains. The type locality in N Ethiopia suggests that it occurs (or occurred) elsewhere, but the modern province of Shoa is nowhere high enough, and a locality in Wellu or Begemdir seems more probable (Yalden *et al.* 1976, Yalden & Largen 1992).

Habitat Highland grasslands and moorlands (Yalden 1988, Sillero-Zubiri *et al.* 1995a). In the Web Valley, Bale, most abundant in swamp shore grasslands, common in mixed herbaceous moorlands, but much scarcer in ericaceous scrub and rocky grasslands. Prefers soil depths over 50 cm (Sillero-Zubiri *et al.* 1995a). Often occurs with *Lophuromys melanonyx* and *Arvicanthis blicki*.

Abundance Common in its community, contributing to a tunnel-ridden landscape in which rodents, not plants, dominate the community (Yalden 1985, Miede & Miede 1994). Densities typically of 36/ha, but ranging from 90/ha in preferred habitats (Yalden 1975, Sillero-Zubiri *et al.* 1995a) to ca. 20/ha in less preferred habitats such as rocky grasslands and at lower altitude sites (Sillero-Zubiri *et al.* 1995a). Total rodent biomass in these communities may reach 26 kg/ha, of which this species contributes 50–60% (Sillero-Zubiri *et al.* 1995b).

Adaptations Subterranean and diurnal; activity begins around 08:00h and finishes by 16:00h; individuals visibly active at tunnel entrances for about ten bursts of activity totalling 60 min/day in the dry season, and slightly less in the wet season (Yalden 1975, Sillero-Zubiri *et al.* 1995a). Burrows are easily detected by mounds of earth on the surface; they are up to 90 m in length, with tunnels 12–15 cm in diameter below ground and 7.7 cm diameter at the entrance hole (Yalden 1975); burrows may cover an area of 360 m² (Shimelis Beyene 1986).

The eyes are placed high on the head (partly as a result of the narrow interorbital width), perhaps an adaptation for detecting predators in the open upland habitat (Yalden & Largen 1992). Root-rats make very rapid movements of the head upwards through earth mound (in order to detect potential danger), and then snatch grass and herbs near edge of mound; often accompanied by short squirrel-like squeaks (see also below). The large size (compared with other Ethiopian rodents), soft fur, diurnal habits and the habit of sealing the burrow system at night, are assumed to be responses to the low night-time temperatures at high altitude (Yalden 1975, Yalden & Largen 1992, Sillero-Zubiri *et al.* 1995a).

Foraging and Food Herbivorous. Feeds by opening a tunnel from below, gathering the available herbage within reach of the tunnel entrance while keeping the hindquarters inside the entrance. Each entrance hole is surrounded by bare ground to about 10 cm. When the food is depleted around one hole, the animal opens a new foraging hole, sealing the old one as it does so. Typically two holes are opened per animal/day, and these freshly used holes provide a good index of mole-rat density (Sillero-Zubiri *et al.* 1995a). Food is gathered in short bursts of 6–8 min at a time. The animal disappears below ground with each mouthful where (presumably) the food is consumed, thus minimizing exposure to predators. Principal foods are grasses and herbs, particularly *Festuca* and *Alchemilla*; roots and

tubers are not so important as for mole-rats (family, Bathyergidae) (Yalden 1975). Old nest material, food and faecal pellets are discarded periodically through a tunnel entrance resulting in ‘hay-piles’, another characteristic sign of this species.

Social and Reproductive Behaviour Little information. Appears to be solitary, and each animal occupies its own burrow system.

Reproduction and Population Structure Little information. Limited observations suggest ♀♀ produce only one young per litter. Juveniles weigh up to 300 g and form the majority of the prey of Ethiopian Wolves (see below); adults may increase in size throughout life, reaching a maximum of ca. 1000 g (Sillero-Zubiri *et al.* 1995a).

Predators, Parasites and Diseases Vulnerable to diurnal predators, especially Ethiopian Wolves (*Canis simensis*). Giant Root-rats contribute up to 47% by volume (69% by occurrence) of the diet of Ethiopian Wolves, and they are also preferred prey compared with other rodents in ‘cafeteria tests’ (Sillero-Zubiri & Gottelli 1995). Probably vulnerable to other diurnal predators, including raptors. Occasionally taken by owls (Yalden 1973).

Conservation IUCN Category: Endangered; formerly assessed as Vulnerable.

At present, sufficiently common and widespread, although the very limited range of the species is cause for concern. Giant Root-rats are very important to the dynamics of their ecosystem, and are an important food for the highly endangered Ethiopian Wolf (Miede & Miede 1994, Sillero-Zubiri *et al.* 1995a).

Measurements

Tachyoryctes macrocephalus

HB: 262 (224–313) mm, n = 10

T: 54 (40–65) mm, n = 10

HF: 35 (31–38) mm, n = 10

E: 13 (7–14) mm, n = 10

WT: 615 (330–930) g, n = 19

GLS: 64.1 (60.4–69.6) mm, n = 11

GWS: 43.8, 46.4 mm, n = 2

M¹–M³: 12.2 (10.8–13.2) mm, n = 17

Ethiopia

Body measurements and weight: Yalden 1975, Sillero-Zubiri *et al.* 1995b

Skull measurements: Yalden 1975

Key Reference Sillero-Zubiri *et al.* 1995a.

D.W.Yalden

Tachyoryctes splendens AFRICAN ROOT-RAT

Fr. Rat-taube de l'Est Africain; Ger. Afrikanische Maulwurfsratte (Afrikanischer Wurzelratte)

Tachyoryctes splendens (Rüppell, 1835). Neue Wirbelth. Fauna Abyssin. Gehörig., Säugeth. 1: 36. Gondar, Ethiopia.

Taxonomy Originally described in the genus *Bathyergus*. Here, *T. splendens* includes (as synonyms) 11 forms considered as valid species by Musser & Carleton (1993, 2005), i.e. *ankoliae*, *annectans*, *audax*, *daemon*, *ibeanus*, *naivashae*, *rex*, *ruandae*, *ruddi*, *spalacinus* and *storeyi*. Synonyms (of *T. splendens*; Musser & Carleton 1993, 2005): *canicaudus*, *cheesmani*, *gallarum*, *omensis*, *pontifex*, *somalicus*. Subspecies: none. Chromosome number: $2n = 48$ (Matthey 1956). See also profile Genus *Tachyoryctes*.

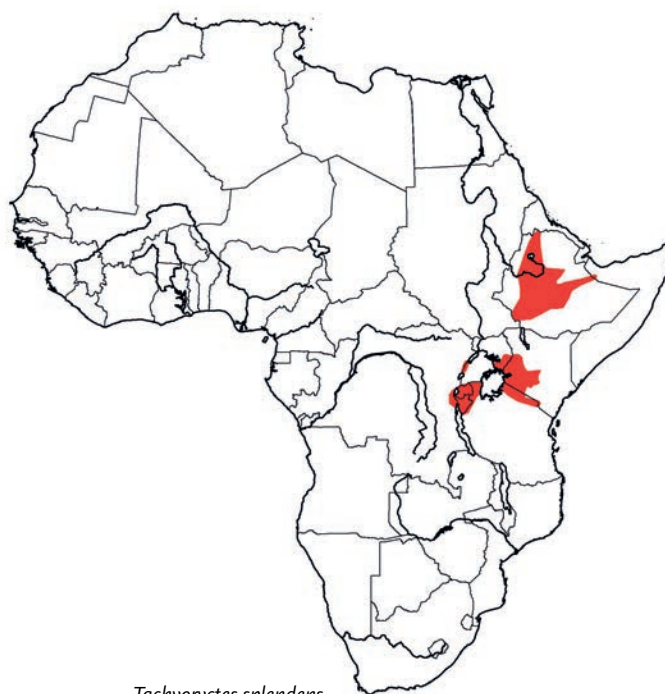
Description Very large subterranean rodent, solidly built with short limbs, and large orange incisors that are ungrooved, procumbent and extrabuccal. Pelage soft, thick and silky; hairs ca. 19 mm. Dorsal pelage ginger, cinnamon-brown or black (but variable) in adults, dark grey or black in juveniles. Ventral pelage paler, often tinged with buff. Patches of white pelage are common. Head similar in colour to dorsal pelage; lips have lateral folds. Well-developed vibrissae. Eyes small. Ears small, set close to head. Forelimbs short, with strong short claws; Digit 3 the longest digit; Digit 1 rudimentary. Hindfeet with five digits and short claws, Digit 2 the longest. Tail short (ca. 31% of HB), darkly pigmented above, well haired. Skull: rostrum thick, frontals constricted, occipital region prominent but not very high. Incisors large and wide (ca. 7 mm), pro-odont, and without grooves. Mandible with high recurved coronoid process and very prominent process between condylar and angular process (Figure 24). Males tend to be larger, weigh more and to be paler in colour than ♀♀. Nipples: $2 + 2 = 8$.

Geographic Variation Populations in different parts of the range differ in pelage colour, size and skull characteristics. This morphological variation can be explained by variations in soil characteristics (colour, hardness, structure) and the environment (rainfall, temperature, altitude, soil moisture). In any population, there is variation in (e.g.) pelage colour, shape of nasal bones, etc. (Ellerman 1940), which spans the variation of all described forms. Each of the 11 forms (listed as synonyms above) are allopatric and each occupies a very restricted distribution. (See also profile Genus *Tachyoryctes*.) The distribution of the various forms is as follows: *ankoliae*: SW Uganda; *annectans*: near lake Naivasha, Kenya; *audax*: Aberdare Range, Kenya; *daemon*: Mt Kilimanjaro, Mt Meru and district, N Tanzania; *ibeanus*: near Nairobi, Kenya; *naivashae*: L. Naivasha, Kenya; *rex*: Mt Kenya, Kenya; *ruandae*: mountains near L. Kivu (E DR Congo), Rwanda and Burundi, and possibly Rwenzori Mts, Uganda/E DR Congo; *ruddi*: Mt Elgon, Uganda/Kenya and Cherangani Hills, Kenya; *spalacinus*: between L. Naivasha and Mt Kenya, Kenya; *splendens*: most of Ethiopia and into NW Somalia; *storeyi*: L. Naivasha, Kenya.

Similar Species

T. macrocephalus. Much larger; Ethiopia only.

Heliophobius argenteocinereus. Similar size, white incisors (also extend beyond lips), no ear pinnae, very short tail.

*Tachyoryctes splendens*

Distribution Endemic to Africa. Afromontane–Afroalpine BZ and some adjacent areas. Recorded from highland areas in Ethiopia, NW Somalia, Kenya, Uganda, N Tanzania, Ruanda, Burundi and E DR Congo where annual rainfall is >510 mm. Occurs at altitudes above 1200 m, and reaches >4000 m in Kenya (Mt Kenya, Aberdare Ranges) and Tanzania (Mt Kilimanjaro).

Habitat Deep well-drained soils in savanna grasslands, open forests, afroalpine regions, agricultural fields and gardens.

Abundance Patchy and disjunct, but may be very common in suitable localities. Densities can be very high in cultivated land. Densities of 80 individuals/acre (= 200/ha) in a grassed area at Nairobi, Kenya (Jarvis 1973a), and of one individual/144 m² in E DR Congo (Rahm 1980) have been recorded. One field (100 m × 80 m) in E DR Congo contained 17 adult ♂♂, 16 adult ♀♀, nine juvenile ♂♂ and eight juvenile ♀♀ (Rahm 1980).

Adaptations Subterranean. African Root-rats live in a system of burrows 15–44 m long, comprised of foraging burrows 15–30 cm below ground, a slightly deeper nest chamber and a deeper bolt-hole ($n = 20$ burrow systems; Jarvis & Sale 1971, Rahm 1980). The nest chamber includes a sleeping area, a food store and a toilet area. The sleeping area, a hollow ball of grass and roots, lies close to the entrance of the nest chamber. The small food stores containing grass rhizomes, roots and geophytes are at the sides of the nest. The toilet area, behind the sleeping area, contains composting faeces and old nesting material, which generates heat. A rich invertebrate fauna, including

pseudoscorpions that feed on mites, is found in the nest chamber. African Root-rats dig by biting at the soil with their incisors. While digging, an animal will periodically turn round, and use one side of its head, and the foot of the same side, to hold the soil as it is pushed up a side branch leading to the surface. Once a mound has been completed, the side branch is thoroughly sealed. African Root-rats are diurnal, and active between 10:00h and 19:00h. Less than 25% of the 24-h day is spent out of the nest (Jarvis 1973b). They feel their way along the burrow by making small lateral movements of the head so the facial vibrissae brush the sides of the burrow. Unlike species of *Bathyergidae*, they rarely move backwards. They can rapidly turn around by curling on the side and walking round their almost stationary hindquarters.

Foraging and Food Herbivorous. The diet includes a wide variety of plants including grass rhizomes, stems and leaves, herbs, roots and storage organs of geophytes. African Root-rats may either dig up under a plant and pull the entire plant into the burrow, or forage around the periphery of an open hole. In this latter instance, they need to keep their eyes wide open and brace the hindfeet in the hole ready to effect a rapid retreat if alarmed. A foraging hole is plugged with a small and very characteristic heap of soil when foraging is complete (Jarvis & Sale 1971). Prior to eating small items of food, animals will grasp the food with the incisors and lightly brush the food with their cupped hands. Unless the item is very large, they walk forwards in the burrow while transporting food to the nest where it is eaten or stored. Stored bulbs and tubers are not disbudded when they sprout. African Root-rats do not drink water, obtaining their water requirements from their food.

Social and Reproductive Behaviour African Root-rats aggressively defend their burrow systems. They communicate seismically through the soil by tapping on the burrow floor with their upper incisors (Jarvis 1969a). Tapping consists of 3–10 taps, a pause and then a repeat of the sequence. Neighbouring animals will tap in response to each other's taps. When threatened, African Root-rats adopt an aggressive posture: the head is thrown back, jaws are agape and the feet are widely spaced and held stiff; the animal lunges forwards, snorting or squeaking and chattering its teeth. During aggressive encounters, or when alarmed, ♂♂ produce a strong musk-like odour from scent glands situated ventral to the eye and ear; ♀♀, in contrast, have very small glands. The position of the glands is clearly indicated by hairs that are stuck together by the secretions. The defensive posture is similar to the aggressive posture, but lacks vocalizations or tooth chattering. If completely submissive, an animal will lower its head and retreat (Jarvis 1969a).

Courtship is preceded by both animals tapping on the floor of their burrows. On meeting, ♂ emits a soft high-pitched twitter, the animals repeatedly lock incisors and ♀ will also squeak and gnash her teeth. Eventually ♀ turns, adopts the lordosis position, and ♂ mounts and bites her neck; during copulation, ♂ kneads flanks of ♀ with his hindfeet. Throughout copulation, which lasts 2–3 minutes, ♀ squeaks. Further copulations, which may continue at intervals for two days, are initiated by ♀. Between copulations, ♂ often rubs genital region on the floor, possibly marking the area with secretions from large bilobed preputial glands. The cellular structure of the two lobes is different: one produces a more oily secretion than the other and it is possible that they serve different functions. Unlike during the aggressive encounters, strong musk-odours are not produced during courtship (Jarvis 1969a).

Reproduction and Population Structure African Root-rats breed throughout the year, and are polyoestrous. Gestation: 46–49 days (Rahm 1969a). The ovary of pregnant ♀♀ contains accessory corpora lutea, and ♀♀ with full-term embryos have 2.5 corpora lutea per embryo. Foetal resorption occurs during pregnancy (Jarvis 1969b, Rahm 1980). Mating and a second pregnancy can occur during lactation. Litter-sizes are small: 1.65 (1–3) at Nairobi, 1.2 (1–3) at Nakuru, Kenya (Jarvis 1969b); 1.39 (1–4) at Kivu, E DR Congo (Rahm 1969a, 1980). At birth, young weigh 11–18 g (n = 14), are hairless and toothless. Fine hairs and small white incisors appear by Day 4. First solid foods eaten ca. Day 15–20. First leave nest Day 15–21. Eyes open Day 21–28. Digging and carrying food Day 24–30. Weaned ca. Day 35. Inter-sibling sparring begins at Day 37–60 and establishment of own burrow by Day 80. The vaginal closure membrane of young ♀♀ breaks down when 3 months old (Jarvis 1969a). Sex ratio at birth is parity (48.6%♂: 51.4% ♀, n = 3517), but biased towards ♀♀ in adults (58%, n = 9583) in E DR Congo (Rahm 1980). A similar bias towards ♀♀ occurred also in Kenya (Jarvis 1969a).

Predators, Parasites and Diseases Predators include Barn Owls (*Tyto alba*), diurnal birds of prey, small carnivores and snakes. These probably capture African Root-rats as they forage above ground in the vicinity of open holes. Ectoparasites include 15 species of fleas and 12 species of mites (Rahm 1980).

Conservation IUCN Category: Least Concern.

African Root-rats are considered agricultural pests in crops of cassava, sweet potato, peanuts, lucerne and maize. They also damage the roots of young trees and disfigure lawns and golf courses.

Measurements

Tachyoryctes splendens

HB (♂♂): 200 (170–215) mm, n = 50
 HB (♀♀): 189.5 (159–205) mm, n = 55
 T (♂♂): 62.7 (53–77) mm, n = 50
 T (♀♀): 60.4 (51–77) mm, n = 55
 HF (♂♂): 31.8 (28–35) mm, n = 50
 HF (♀♀): 30.3 (27–34) mm, n = 55
 E (♂♂): 11.3 (9–15) mm, n = 50
 E (♀♀): 10.5 (9–12) mm, n = 55
 WT (♂♂): 248 (180–305) g, n = 50
 WT (♀♀): 218 (140–315) g, n = 55
 GLS (♂♂): 45.9 mm, n = 20*
 GLS (♀♀): 43.6 mm, n = 20*
 GWS (♂♂): 33.2 mm, n = 20*
 GWS (♀♀): 32.1 mm, n = 20*
 M¹–M³ (♂♂): 8.6 mm, n = 20*†
 M¹–M³ (♀♀): 8.3 mm, n = 20*†

Body measurements and weights: Nairobi, Kenya (J. U. M. Jarvis unpubl.)

Skull measurements: E DR Congo (Rahm 1980)

*Mean only; minimum and maximum values not available

†Number of molar teeth variable – see genus profile

Key References Jarvis 1969a, b, 1973a, b; Jarvis & Sale 1971; Rahm 1980.

Family NESOMYIDAE

POUCHED RATS AND MICE, SWAMP MOUSE, CLIMBING MICE, LARGE-EARED MOUSE, FAT MICE, WHITE-TAILED RAT AND ROCK MICE

Nesomyidae Major, 1897. Proc. Zool. Soc. Lond. 1897: 718.

| | | |
|--------------------------------------|--|--------|
| Cricetomyinae (3 genera, 5 species) | Pouched Rats and Pouched Mice | p. 153 |
| <i>Beamys</i> (1 species) | Long-tailed Pouched Rats | p. 154 |
| <i>Cricetomys</i> (2 species) | Giant Pouched Rats | p. 157 |
| <i>Saccostomus</i> (2 species) | Pouched Mice | p. 161 |
| Delanymyinae (1 genus, 1 species) | Swamp Mouse | p. 165 |
| <i>Delanymys</i> (1 species) | Delany's Swamp Mouse | p. 166 |
| Dendromurinae (6 genera, 23 species) | Climbing Mice, Large-eared Mouse, Fat Mice | p. 168 |
| <i>Dendromus</i> (11 species) | African Climbing Mice | p. 169 |
| <i>Dendroprionomys</i> (1 species) | Velvet Climbing Mice | p. 184 |
| <i>Malacothrix</i> (1 species) | Long-eared Mouse | p. 186 |
| <i>Megadendromus</i> (1 species) | Bale Mouse | p. 188 |
| <i>Prionomys</i> (1 species) | Climbing Mouse | p. 189 |
| <i>Steatomys</i> (8 species) | Fat Mice | p. 191 |
| Mystromyinae (1 genus, 1 species) | White-tailed Rat | p. 201 |
| <i>Mystromys</i> (1 species) | White-tailed Rat | p. 201 |
| Petromyscinae (1 genus, 4 species) | Rock Mice | p. 203 |
| <i>Petromyscus</i> (4 species) | Rock Mice | p. 204 |

The family Nesomyidae encompasses several small groups of archaic muroid rodents whose living members are confined to sub-Saharan Africa (Cricetomyinae, Delanymyinae, Dendromurinae, Mystromyinae, Petromyscinae) and to Madagascar (Nesomyinae). In Africa, the family is represented by five subfamilies, 12 genera and 34 species. Each of the subfamilies is morphologically well characterized, but the family itself lacks clear diagnostic features in view of the immense heterogeneity embraced. Collectively, the five African subfamilies are highly diverse in size and morphology, habits, trophic niche and ecology (see subfamily and genus profiles).

Tullberg (1899) and later Chaline *et al.* (1977) recognized the Nesomyidae, but the content of the family was largely restricted to the indigenous Malagasy rodents as previously identified by Major (1897) at the rank of subfamily. Although differing in contents, the family composition observed here owes its conceptual roots to Lavocat (1973, 1978), who identified a number of small but morphologically well defined groups as relicts of a middle Tertiary (late Oligocene–Miocene) cricetodontine presence in Africa and

broadened the definition of Nesomyidae to embrace their diverse descendants (also see Carleton & Musser 1984). Prior to Lavocat's contributions, these archaic African muroids had been variously and inconsistently divided between Cricetidae and Muridae, or all were placed in an inclusive Muridae (see Carleton & Musser 1984, for classificatory review).

The family's expanded composition was initially based on tenuous dental links to middle Tertiary fossils, but results of molecular phylogenetic studies, although not wholly concordant, supply additional empirical support for Lavocat's view of Nesomyidae. These gene-sequence investigations associate Cricetomyinae, Dendromurinae, Mystromyinae and Nesomyinae as a monophyletic lineage (Nesomyidae) basal to other muroid taxa that represent Cricetidae and Muridae (DuBois *et al.* 1996, Jansa *et al.* 1999, Michaux & Catzeflis 2000, Michaux *et al.* 2001). Tong & Jaeger (1993), on the other hand, considered Lavocat's family to be a polyphyletic wastebasket that encompasses the remnants of early evolutionary branches leading to the major radiations of Cricetidae or Muridae. The evidence needed to settle these issues of relationship and classification will require greater emphasis on molecular and genetic characters and more extensive studies on morphology (rather than on dentition).

The antiquity of the five African subfamilies is substantiated by palaeontological information. Evolutionary origin of each has been linked, with varying degrees of confidence, to early Miocene to early Pliocene fossil genera, most of these known from sub-Saharan sites (see subfamily accounts). Only the Dendromurinae is firmly documented outside of sub-Saharan Africa in the middle Tertiary (e.g. Aguilar *et al.* 1984, De Bruijn 1999). The palaeontological argument for such phyletic connections remains sketchy and the hard evidence from critical middle Tertiary beds is scanty. Further discoveries from the Tertiary of Africa will help to clarify the validity of the family.

Compared with the African radiations of Gerbillinae and Murinae (Muridae), each of the subfamilies of Nesomyidae contains few genera and species: Cricetomyinae (3 genera, 5 species); Delanymyinae (1 genus, 1 species); Dendromurinae (6 genera, 23 species); Mystromyinae (1 genus, 1 species); and Petromyscinae (1 genus, 4 species).

Michael D. Carleton & Guy G. Musser

Subfamily CRICETOMYINAE – Pouched Rats and Pouched Mice

Cricetomyinae Roberts, 1951. Mammals South Africa, p. 434.

The three genera and five species comprising this subfamily are endemic to Africa, occurring in sub-Saharan savannas and in lowland and montane rainforest. Only one genus is found in West Africa (*Cricetomys*), but all three genera are represented in eastern and southern Africa (*Beamys*, *Cricetomys* and *Saccostomus*). Species in the

three genera are terrestrial and nocturnal, or predominantly so, consume seeds, fruits and bulbs, build relatively complex burrow systems, and hoard foods within those burrows for immediate or later consumption. The last habit is due, in part, to the possession of internal cheek pouches (a cardinal morphological trait of the

subfamily), which are used to carry food from the foraging area to the burrow. Capacious cheek pouches have also evolved within other lineages of Rodentia, namely Sciuridae (squirrels) and Geomyoidea (pocket gophers, kangaroo mice and rats), but in muroid rodents, such pouches characterize only this subfamily and the Palearctic hamsters (Cricetidae: Cricetini). Details of buccal histology, myology and innervation indicate that pouches were independently acquired by these muroid subfamilies (Ryan 1989). The infrequency of elastin fibres and absence of distensible folds in the pouch walls of cricetomyines suggest that they do not hoard foodstuffs or accumulate the vast underground larders to the extent documented for the cricetine hamsters.

Species in the subfamily are small (*Saccostomus*) to very large (*Cricetomys*) in size. They have a robust body, large head, comparatively short and stout limbs and very short (*Saccostomus*) or very long (*Beamys*, *Cricetomys*) tail. The cheek pouch retractor is derived from facial muscle, innervated by cranial nerve VII and originating from the anterior thoracic vertebrae (Ryan 1989). Hindfeet strongly built, broad across the metatarsus, with short toes that have inconspicuous ungual tufts; plantar surface naked with six pads, the thenar and hypothernar positioned distally and close to four interdigitals. The skull characters include strong construction, rostrum moderately long and interorbital region hourglass-shaped with edges squared to slightly beaded; zygomatic plate with slight dorsal notch, jugal forming a prominent element of the middle zygomatic arch; alisphenoid strut present; subsquamosal fenestra absent, postglenoid foramen present; tegmen tympani not overlapping squamosal (Carleton & Musser 1984). Molars cuspidate, uppers with three roots and lowers two; upper molars with accessory lingual conules positioned to form transverse laminae suggestive of a rudimentary triserial arrangement, lowers with labial conulids; longitudinal enamel connections between lamina absent (Petter 1966a, c). Upper incisors without grooves, lowers with inconspicuous parallel enamel striae (Pocock 1987). The cephalic arterial circulation lacks a supraorbital branch of stapedial artery (sphenofrontal foramen and squamosal-alisphenoid groove are absent), but the infraorbital branch is present (stapedial foramen and parapterygoid groove are present).

For so distinctive and closely related a group, African Pouched Rats and Mice were not formally acknowledged taxonomically until Roberts's (1951) classification of South African mammals. In the early systematic literature, the three genera were classified within

Murinae (e.g. Thomas 1897, Ellerman 1941, Simpson 1945), but subsequent systematic arrangements have followed Petter (1966a, c) in allying cricetomyines with cricetids (e.g. Misonne 1974, Rosevear 1969, Skinner & Smithers 1990). Molar occlusal configuration (Petter 1966a) and anatomy of internal cheek pouches (Ryan 1989) convincingly sustain the monophyly of the subfamily. Mitochondrial and nuclear DNA sequence data (Jansa *et al.* 1999, Michaux & Catzeflis 2000, Michaux *et al.* 2001) also support monophyly and indicate that Cricetomyinae is phylogenetically close to Dendromurinae and Mystromyinae, two other endemic African subfamilies. Indisputable fossil representatives are known from the late Miocene to Recent of eastern and southern Africa (Denys 1988, Senut *et al.* 1992, Avery 1995, 1996, Mein *et al.* 2004), and the autochthonous African origin of Cricetomyinae has been speculatively linked to Miocene Afrocricetodontinae, a phyletic connection that so far lacks persuasive demonstration (Chaline *et al.* 1977, Tong & Jaeger 1993).

Roberts (1951) segregated *Saccostomus*, as a lone member of Saccostomurinae, from other African pouched rats (Cricetomyinae), a division not recognized by later systematists (Petter 1966a, Ryan 1989); however, morphological traits and gene-sequence data link *Beamys* and *Cricetomys* as cognate relatives separate from *Saccostomus* (Carleton & Musser 1984, Corti *et al.* 2004).

Two tribes within the subfamily may be recognized: (1) Cricetomyini (*Beamys*, *Cricetomys*): tail longer than combined head and body; anterior palatal foramina short; bony palate relatively short, lacking posterolateral palatal pits; mesopterygoid fossa moderately long; alisphenoid bone possessing dorsal orbital flange; accessory foramen ovale present; ectotympanic bullae (part of auditory bullae) small; vertebral column with 13 thoracic and six lumbar vertebrae; entepicondylar foramen of humerus present; corpus of stomach densely papillated; (2) Saccostomurini (*Saccostomus*): tail conspicuously shorter than head and body; anterior palatal foramina long; bony palate long with prominent posterolateral palatal pits; mesopterygoid fossa short and wide; alisphenoid lacking dorsal flange; accessory foramen ovale absent; ectotympanic bullae moderately inflated; vertebral column with 12 thoracic and seven lumbar vertebrae; entepicondylar foramen absent; corpus smooth, lacking papillae.

The three genera and five species are listed alphabetically below.

Michael D. Carleton & Guy G. Musser

GENUS *Beamys*

Long-tailed Pouched Rat

Beamys Thomas, 1909. Ann. Mag. Nat. Hist., ser. 8, 4: 107. Type species: *Beamys hindei* Thomas, 1909.

The genus *Beamys* contains of one (or two) species confined to evergreen forests of eastern Africa. *Beamys* is probably close to the ancestral stock of the Cricetomyinae. Two of its features, its habitat and the presence of an ectoparasite *Hemimerus*, which also occurs on *Cricetomys*, are considered to be primitive characters. Many of the characters of *Beamys* such as cheek pouches, body shape, shape and colouration of tail, reduction of M³ and only two cusps on the lamina of M¹ are similar to those of *Cricetomys* (Hanney & Morris 1962,

Petter 1966c) (Figure 25). Musser & Carleton (2005) regard the two taxa, *hindei* and *major*, as separate species. An alternative arrangement is that there is a single species that shows a geographic cline in size – the smaller *hindei* in the northern part of range and the larger *major* in the southern part of range. Here, the genus is considered to have single species *Beamys hindei*. See also profile *Beamys hindei* below.

D. C. D. Happold

***Beamys hindei* LONG-TAILED POUCHED RAT**

Fr. Petit rat à abajoues; Ger. Langschwanz-Hamsterratte

Beamys hindei Thomas, 1909. Ann. Mag. Nat. Hist., ser. 8, 4: 108. Taveta, Coastal Province, Kenya.



Beamys hindei.

Taxonomy *Beamys hindei* was described in 1909 from an immature individual with a small hindfoot collected in S Kenya. Subsequently the species was shown to occur throughout E Tanzania. A second species (*B. major*), with a larger hindfoot, was described in 1914 from Malawi and is now known to occur also in E Zambia. Some authors (e.g. Misonne 1974, Musser & Carleton 1993, 2005) retain these two species, but others (e.g. Ansell & Ansell 1973, Fitzgibbon *et al.* 1995) consider *major* as a subspecies of *hindei*. Fitzgibbon *et al.* (1995) show that there is a trend for individuals from southerly latitudes to be slightly larger than those from northerly latitudes. Specimens of *major* from Malawi are only slightly larger than those from S Tanzania, as would be expected from the general trend of increasing size from north to south. Here, all populations from Kenya to Malawi are considered as belonging to a single species, *B. hindei*, which shows clinal variation in size; northern populations are referred to as *B. h. hindei* and southern populations as *B. h. major*. Synonyms: *major*. Subspecies: two. See also profile genus *Beamys*. Chromosome number: $2n = 52$ (Fitzgibbon *et al.* 1995).

Description Medium-sized rat, soft grey dorsally, white ventrally, and with thick whitish blotched tail. Dorsal pelage warm grey, sometimes with a russet tinge on rump and back; dorsal hairs medium grey with warm grey tips. Ventral pelage, chin, throat pure white. Pelage dense and soft. Face pointed, ears small and rounded; vibrissae long and black; eyes black, small. Some individuals have white blaze on forehead. Limbs short, fore- and hindfeet white. Forefeet with four digits; hindfeet five digits. Tail long (ca. 100% of HB), scaly, thick (especially at base), whitish often with irregular dark blotches. Dorsal pelage of juveniles pale grey. For most measurements, ♂♂ are larger on average than ♀♀.

Geographic Variation

B. h. hindei: northern part of range. On average, smaller in size.

B. h. major: southern part of range. On average, larger in size.

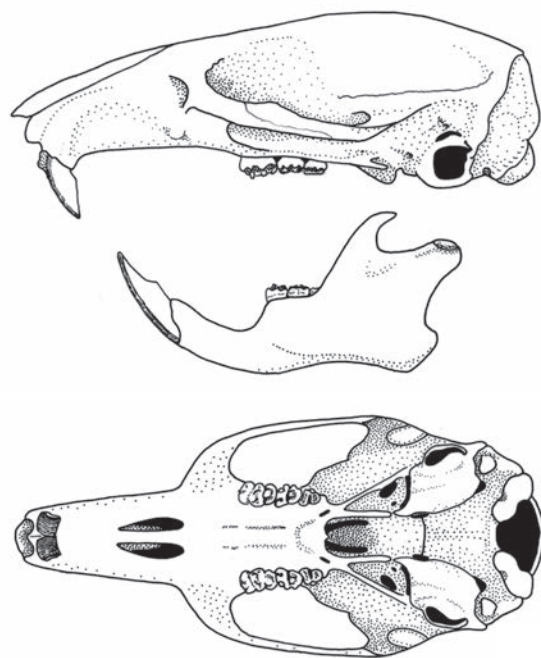


Figure 25. Skull and mandible of *Beamys hindei* (HC 2787).

Similar Species

Cricetomys gambianus. Much larger and heavier (mean HB: 326 mm); relatively long tail (ca. 85–130% [mean 107%] of HB); terrestrial, wider distribution.

Saccostomus campestris. Smaller (mean HB: ca. 114 mm), broader head; relatively short tail (ca. 44–50% of HB); terrestrial, wider distribution, not confined to forested habitats.

Distribution Endemic to Africa, Zambezan Woodland BZ and Coastal Forest Mosaic BZ. Recorded from coastal forests within about 100 km of coast from S Kenya to S Tanzania (*B. h. hindei*), and extreme SW Tanzania, Malawi (and perhaps parts of N Mozambique) and NE Zambia (*B. h. major*). Investigations in suitable habitats between the ranges of the two subspecies have failed to find any individuals (Fitzgibbon *et al.* 1995).

Habitat Evergreen or slightly deciduous forests preferably on sandy soils, and gallery forests associated with streams. At Arabuko-Sokoke, SE Kenya, these Pouched Rats also occur in *Afzelia* forest and, to a lesser extent, *Brachystegia* forest. Occasionally found on fallow land and cassava plantations (Kenya only).

Abundance Sparsely distributed; recorded from only a few localities but commoner than previously realized. In most localities, only one or two individuals have been found (perhaps because of trap-shyness). In a few optimal habitats, populations may be high, e.g. at Arabuko-Sokoke, where trees were close together and there



was dense vegetation below 4 m, density was 14–30 individuals/ha. Comparable abundance is known in at least one mixed dry forest in the northern East Usambara lowlands, but the species was surprisingly scarce 700 m higher in sub-montane habitats (N. Cordiero unpubl.).

Adaptations Nocturnal, scansorial. Although mainly terrestrial, can clamber about on twigs and small branches. When climbing, the tip of the prehensile tail is twisted around a twig, or it is held straight backwards as a counterbalance. During the day, individuals rest in a burrow. Most burrows have a straight vertical shaft with a nest chamber and latrine chamber. The nest is lined with fresh green leaves, which are changed regularly.

When foraging, seeds and other foods are collected and stored in the cheek pouches. The food is taken to the nest and disgorged. Pouched Rats store considerable quantities of food, which is eaten when conditions for foraging are poor (see below).

Pouched Rats are slow-moving and lethargic, spending a lot of time curled up in their nests. During cool weather, they may become dormant.

Foraging and Food Forage on the ground and in trees. Omnivorous, feeding primarily on seeds and fruits, and occasionally insects. Food is stored in the nest. One excavated nest (*B. h. major*) contained nearly 1400 seeds of several species (weight ca. 1200 g), which would have taken about 200 separate forays to collect (Hanney & Morris 1962).

Social and Reproductive Behaviour Usually solitary. In captivity, ♀♀ not in breeding condition attack ♂♂, biting them on hips, tail and scrotum. Receptive ♀♀ have been observed to perform a 'forwards and backwards' dance in a circular area in front of ♂, as well as biting him, prior to copulation (Hubbard 1970a).

Reproduction and Population Structure Times of reproduction depend on the locality. At Arabuko-Sokoke, reproduction occurs in most months of the year (Fitzgibbon *et al.* 1995). Lactating ♀♀ were present for nine months of the year (but not in Nov, Mar and Aug, the months of lowest rainfall); ♂♂ had scrotal testes in all months. However, only a proportion of all individuals were reproductively active in any month: 20–60% of ♀♀ were lactating during the nine months, and 50–90% of the ♂♂ were scrotal (except Sep – 25%). The highest percentage of breeding ♀♀ was in May at the height of the wet season. Females bred at least once per year. In Malawi, reproduction is seasonally polyoestrous; pregnant ♀♀ have been recorded Nov–May during the wet season and the beginning of the dry season (Hanney & Morris 1962); during the (cold and hot) dry season (Jun–Nov), testes of ♂♂ were abdominal.

Studies on captive animals (*B. h. hindei*) have provided detailed information on reproduction (Egoscue 1972): age at first conception: ca. 7–9 months. Gestation 22–23 days. Eyes of young open Day 21. Weaning Day 35–40. Minimum interval between births 62 days; no postpartum oestrus. Litter-size: 2.8 (1–5, mode 3, n = 39). In Malawi, litter-size: 4.6 ([n = 4] and 7 [n = 1]). Young born with pink-coloured skin and a fine down of grey hairs; wt 3.2 (2.1–4.3) g. Growth is rapid; at four weeks young are still suckling and weigh ca. 43 g (Hanney & Morris 1962). Longevity in captivity: 3–4 years.

At Arabuko-Sokoke, where breeding occurred throughout most of the year, there was a low but continuous recruitment of young individuals into the population. Numbers remained fairly constant throughout the year (14–30/ha) but with a peak in May and Jun due to recruitment of many young. There appears to be no seasonal change in weight.

Predators, Parasites and Diseases Remains of Pouched Rats have been found in owl pellets at Lunzu, Malawi (Hanney 1962), and one individual was found in the stomach of a Twig Snake (*Thelatornis capensis*) at Namakutwa, Tanzania (Fitzgibbon *et al.* 1995). In Malawi, nests of Pouched Rats may be infested with ectoparasitic earwigs (*Araeomerus morrissi*, formerly *Hemimerus morrissi* [Nakata & Maa 1974]) where it is assumed they feed on stored fruits, and less frequently on the skin of Pouched Rats (Popham 1984). One species of flea, *Xenopsylla microphthalmia*, has been recorded (Beaucornu & Kock 1996). (See also Genus *Cricetomys*.)

Conservation IUCN Category: Least Concern.

Populations are small and widely dispersed, and their forest habitats are being modified or reduced in area by human activities. (IUCN previously recognized *hindei* and *major* as full species; both were considered as Near Threatened.) Populations numbers are considered to be declining.

Measurements

Beamys hindei

HB (♂♂): 146 (135–158) mm, n = 5

HB (♀♀): 140 (115–164) mm, n = 10

T (♂♂): 135 (127–144) mm, n = 5

T (♀♀): 127 (112–145) mm, n = 10

HF (♂♂): 22 (21–24) mm, n = 5

T (♀♀): 21 (18–24) mm, n = 10

E (♂♂): 20 (18–22) mm, n = 5

E (♀♀): 20 (17–22) mm, n = 10

WT (♂♂): 69 (47–96) g, n = 5
 WT (♀♀): 67 (49–94) g, n = 10
 GLS (♂♂): 37.5 (35.7–39.1) mm, n = 5
 GLS (♀♀): 36.0 (32.6–39.0) mm, n = 10
 GWS (♂♂): 17.4 (16.0–18.7) mm, n = 5
 GWS (♀♀): 16.5 (14.7–18.2) mm, n = 10
 M¹–M³ (♂♂): 5.3 (5.2–5.4) mm, n = 5

M¹–M³ (♀♀): 5.1 (4.7–5.2) mm, n = 10
 Mnina, Tanzania (RMCA)

Key References Egoscue 1972; Fitzgibbon *et al.* 1995; Hanney & Morris 1962.

D. C. D. Happold

GENUS *Cricetomys* Giant Pouched Rats

Cricetomys Waterhouse, 1840. Proc. Zool. Soc. Lond. 1840: 2. Type species: *Cricetomys gambianus* Waterhouse, 1840.



Cricetomys gambianus.

The genus contains two to four species, and is distributed extensively throughout sub-Saharan Africa to about 27°S, including Zanzibar and Bioko Islands. The genus is represented in nearly all habitats from dry savanna to rainforest, and is often associated with human settlements.

Giant Pouched Rats are distinguished from most other African murids by their very large size, unscaled and bi-coloured tails (basal half dark, terminal half white), and ungrooved incisors (Figure 26). They have internally opening cheek pouches, a character shared with the other two genera in the subfamily Cricetomyinae (*Beamys* and *Saccostomus*).

The number of species in the genus is uncertain. Allen (1939) recognized six species, and Ellerman (1941) reduced these to subspecies of a single species, *C. gambianus*. Genest-Villard's (1967) revision provided evidence of two 'species', a predominantly savanna-dwelling species (*C. gambianus*) and a rainforest species (*C. emini*) (see Musser & Carleton 1993). These two species are recognized here. Musser & Carleton (2005) accept these two species for West Africa, but claim that Genest-Villard's character states and univariate analysis do not discriminate the southern African forms of the genus. These authors name the southern African forms of the genus as *C. ansorgei* and *C. kivuensis*. *Cricetomys ansorgei* (given as synonym of *C. gambianus* by Musser & Carleton 1993) is the savanna-living form, occurring in East Africa (including Zanzibar), westwards to Angola and southwards to South Africa. *Cricetomys kivuensis* (given as

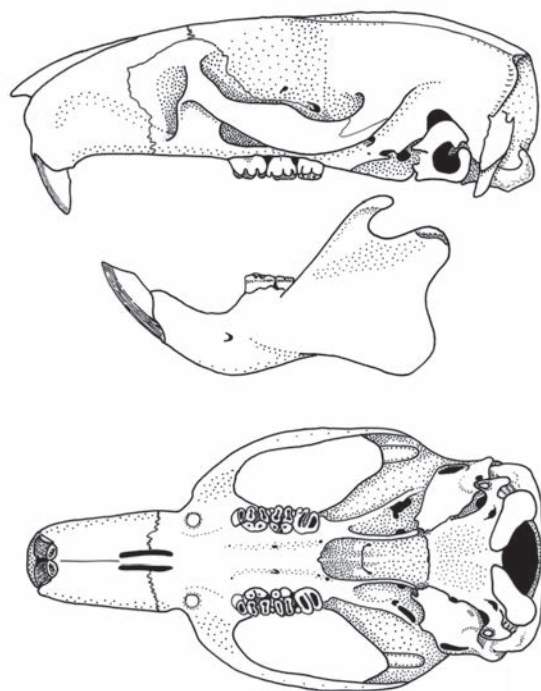


Figure 26. Skull and mandible of *Cricetomys gambianus* (HC no number).

synonym of *C. emini* by Musser & Carleton 1993) is a forest-living form, known from montane habitats of E DR Congo, S Uganda, Rwanda and Burundi.

The two species recognized here are: *Cricetomys emini*, which has soft, sleek dark brown pelage, a pointed face and is restricted to the Rainforest BZ; and *Cricetomys gambianus*, which has rather coarse greyish-brown pelage, a wide blunt face, and is restricted to savanna habitats and 'savanna-like' habitats around the margins of the Rainforest BZ.

Justina C. Ray & J.-M. Duplantier

***Cricetomys emini* EMIN'S GIANT POUCHED RAT (FOREST GIANT POUCHED RAT)**

Fr. Rat Géant d'Emin; Ger. Emins Riesenhamsterratte

Cricetomys emini Wroughton, 1910. Ann. Mag. Nat. Hist., ser. 8, 5: 269. Monbuttu, Gadda, DR Congo.

Taxonomy Synonyms: *dissimilis*, *dolichops*, *kivuensis*, *liberiae*, *luteus*, *poensis*, *proparator*, *sanctus*, *tephrus*. The form *kivuensis* is regarded as a valid species by Musser & Carleton (2005; see profile Genus *Cricetomys*). Grubb (2004) suggests that the correct specific name for this species may be *C. dissimilis* de Rochebrune, 1885 (see also Hatt 1940). Subspecies: none. Chromosome number: $2n = 80$, $aFN = 80$ (Codjia *et al.* 1994).

Description Largest of the African forest murid rodents; similar to *C. gambianus* but with slender body form. Pelage short, sleek and soft in texture. Dorsal pelage orange-brown to dark greyish-brown or brownish-black. Head and flanks generally paler in colour. Ventral pelage white; usually well delineated from colour of flanks. Guard hairs few in number but very long. Face narrow in appearance with large, pale, naked ears standing well above pelage. Whiskers numerous and long. Dark eye-ring absent. Limbs long and thin. Feet whitish, long and powerful, but with relatively short claws. Digit 5 of the forefoot rudimentary; Digit 5 of hindfoot reaches to about half the length of Digit 4. Tail very long (ca. 115% of HB), smooth without scales, dark on basal half, white on terminal half. Nipples: $2 + 2 = 8$.

Geographic Variation None recorded.

Similar Species

C. gambianus. More thick-set in body form, pelage rough, shaggy and longer; ventral pelage off-white, not clearly delineated from flanks; face broader with dark eye-ring; ear smaller, partly submerged in pelage; occurs in grasslands, woodlands and anthropogenic habitats in savannas, but sympatric with *C. emini* in some localities along edge of Rainforest BZ.

Distribution Endemic to Africa. Widespread in Rainforest BZ and Rainforest–Savanna Mosaics. Recorded from Sierra Leone to S Uganda, Rwanda, Burundi, DR Congo, NE Angola, Equatorial Guinea, Gabon and Congo, Bioko I. (Fa 2000).

Habitat Prefers 'high forest' as opposed to open savanna or commensal habitats (Rosevear 1969; Genest-Villard 1967). Within rainforest, demonstrates no marked preference for habitat type (Ray 1996). Also occurs in secondary forest along logging roads (Ray 1996, Malcolm & Ray 2000). In Dzanga-Sangha, Central African Republic, Forest Giant Rats were captured most often where the understorey was relatively open (Ray 1996).

Abundance Mean population density at three sites in central Africa is $134.0 \pm 16.9/\text{km}^2$ (Fa & Purvis 1997). Probably much more abundant than assessed by trapping (Dosso 1975b). Although only ten individuals were captured during 23,291 trap-nights in Taï Forest, Côte d'Ivoire, these Giant Rats were the species most often purchased from villagers or collected during night surveys on forest trails (Dosso 1975b).

*Cricetomys emini*

Adaptations Generally terrestrial, but able to climb and jump (Kingdon 1974). Captured frequently at height of 2 m in Dzanga-Sangha, Central African Republic, but significantly more abundant on the ground (Malcolm & Ray 2000). Nocturnal (Rahm 1967), but occasionally seen in daylight (Rosevear 1969). Shelters in underground burrows, either modified or self-constructed, among large tree roots, and in holes in rotten logs and fallen tree trunks (J. C. Ray unpubl., Sanderson 1940). Burrows are characterized by a 'complex system' of galleries with side branches and separate chambers for food storage, sleeping, or waste; there are several escape routes. Nests are lined with fresh leaves. Individuals constantly change burrows (Rosevear 1969). Well worn pathways are used regularly for travelling within the home-range (J. C. Ray unpubl., Sanderson 1940).

Foraging and Food Mainly vegetarian. Consumes wild and cultivated fruits (Rahm & Christiaensen 1963, Rosevear 1969). Snails also an important food-source (Rahm & Christiaensen 1963). Termites discovered in one stomach (Hatt 1940a). Detailed analysis of diet not available. Coprophagous.

Social and Reproductive Behaviour Solitary except when raising young. One individual to a burrow (Rosevear 1969). Produces call that is modulatory in nature, the function of which is unknown (Genest-Villard 1967).

Reproduction and Population Structure Lives up to 4.5 years in captivity. Gestation 42 days. Litter-size: 2–4 (Rosevear 1969).

Predators, Parasites and Diseases Humans are the most important predators. These Giant Rats are particularly common in local food markets throughout central and West Africa in those areas where ungulates and primates are rare (Fa 2000). Ranked the second commonest species at bushmeat markets on Bioko I., and eighth commonest species at markets in Rio Muni (Equatorial Guinea). Daily availability ranged from 0.43 carcasses (Rio Muni) to 5.3 (Bioko I.; Juste *et al.* 1995). Most common rodent in markets in Kisangani, DR Congo, representing 90% of 35,992 rodent carcasses (Colyn *et al.* 1987).

Remains are commonly found in the scats of mammalian carnivores, such as mongooses *Herpestes naso* and *Bdeogale nigripes*, genets *Genetta servalina*, African Civets *Civettictis civetta* and Golden Cats *Profelis aurata*, at a frequency of occurrence ranging from 3.3 to 11.8% (Ray & Sunquist 2001). Found in 4.9% (n = 150) of scats of Leopards *Panthera pardus* from Dzanga-Sangha, but in only 1.9% (n = 215) of scats from Taï Forest, Côte d'Ivoire (Hoppe-Dominik 1984). Absent in leopard scats (n = 222) from Ituri Forest, DR Congo, where leopards prey on larger species (Hart *et al.* 1996).

As for *C. gambianus*, ectoparasites include *Hemimerus* spp. The nematode *Capillaria hepatica* parasitizes the liver, and is known to have zoonotic potential, causing human hepatic capillariasis. A relatively high prevalence (27%) of this nematode has been recorded in wild-caught *C. emini* in DR Congo; because Giant Rats are frequently consumed by humans, this level of parasitism has important implications for public health (Malekani 1994).

Conservation IUCN Category: Least Concern.

Potential threats are overhunting close to human population centres where primates and ungulates have been depleted, and

where there has been deforestation. A well-known pest in cocoa farms where these rats climb the trunks of cocoa trees to feed on cocoa pods. In Sierra Leone, *C. emini* may be displaced by *C. gambianus* following removal of rainforest habitats (Grubb *et al.* 1998).

Measurements

Cricetomys emini

HB (♂ ♂): 336.4 (274–379) mm, n = 14

HB (♀ ♀): 328.2 (276–378) mm, n = 34

T (♂ ♂): 392.2 (339–426) mm, n = 13

T (♀ ♀): 386.5 (332–435) mm, n = 34

HF (♂ ♂): 66.8 (62–72) mm, n = 14

HF (♀ ♀): 65.8 (60–69) mm, n = 33

E (♂ ♂): 44.4 (39–51) mm, n = 14

E (♀ ♀): 45.1 (40–50) mm, n = 33

WT (♂ ♂): 935.5 (455–1300) g, n = 22

WT (♀ ♀): 902.7 (514–1200) g, n = 39

GLS (♂ ♂): 71.2 (62.6–74.8) mm, n = 10

GLS (♀ ♀): 71.9 (67–76) mm, n = 10

GWS (♂ ♂): 30.8 (28–32.7) mm, n = 9

GWS (♀ ♀): 31.4 (28.5–33) mm, n = 10

M¹–M³ (♂ ♂): 10.3 (9.5–10.8) mm, n = 10

M¹–M³ (♀ ♀): 10.6 (9.4–11) mm, n = 9

Dzanga-Sangha, Central African Republic (J. C. Ray & J. R. Malcolm unpubl.)

Key References Genest-Villard 1967; Rosevear 1969.

Justina C. Ray

Cricetomys gambianus GAMBIAN GIANT POUCHED RAT

Fr. Rat Géant de Gambie; Ger. Gambia-Riesenhamsterratte

Cricetomys gambianus Waterhouse, 1840. Proc. Zool. Soc. Lond., 1840: 2. River Gambia, Gambia.

Taxonomy Considered to include *C. emini* until the revision of Genest-Villard (1967) who clearly separated the two species and distinguished seven subspecies (currently synonyms) of *C. gambianus*. Synonyms: *adventor*, *ansorgei*, *buchanani*, *cosensi*, *cunctator*, *dichrurus*, *dissimilis*, *elgonis*, *enguvi*, *gambiensis* (spelling *lapsus*), *goliath*, *grahami*, *haageni*, *langi*, *microtis*, *oliviae*, *osgoodi*, *selindensis*, *servorum*, *vaughanjonessi*, *viator*. The form *ansorgei* is considered as a valid species by Musser & Carleton (2005; see profile Genus *Cricetomys*). Subspecies: none. Chromosome number: 2n = 78 (unknown origin, Matthey 1954), 2n = 80, aFN = 82 (Senegal; Granjon *et al.* 1992) and 2n = 82, aFN = 88 (Benin; Codjia *et al.* 1994).

Description The largest murid species in Africa (together with *C. emini*). Dorsal pelage coarse, rough and shaggy, ranging in colour from grey (savannas of West and central Africa to Uganda) to brown in the eastern and southern parts of the range. Flanks paler. Ventral pelage white to off-white, not clearly delineated from colour of flanks. Face broad with elongated muzzle; very long vibrissae. Eyes relatively small with dark eye-ring. Ears relatively large, lower part usually submerged in pelage. Limbs relatively short compared to

body size. Forefoot with a rudimentary thumb; hindfoot strong but with rather small claws. Tail long (85–130% [mean 107%] of HB), dark blackish-brown on proximal half, white on terminal half; smooth without scales and with short and sparse hairs on proximal end. Length of white tip varies regionally (31–68% [mean 50%] in Senegal [J.-M. Duplantier unpubl.]; 37–46% [mean 41%] for ♂ ♂, 31–45% [mean 38%] for ♀ ♀ on NTransvaal, South Africa [Smithers 1983]). Nipples: 2 + 2 = 8.

Geographic Variation Genest-Villard (1967) recorded seven subspecies (not recognized here):

C. gambianus: West and central Africa. Dorsal pelage predominantly grey; proximal part of tail very dark.

C. ansorgei: south of the Rainforest BZ. Dorsal pelage predominantly brown, more yellowish than *C. g. gambianus*; longer body length than *C. g. gambianus*. (Musser & Carleton [2005] recognize this form as a valid species, and give the five forms listed below as synonyms of *C. ansorgei*.)

C. microtis: Virunga Mts, DR Congo. The darkest and smallest form.

C. elgonis: Mt Elgon, Uganda/Kenya. Dark thick dorsal pelage and longer body length.

C. kenyensis: Mt Kenya; skull narrow.

C. enguvi: Taita hills and base of Mt Kilimanjaro (Kenya). Skull narrow and longer body length.

C. cosensi: Zanzibar. Very large anterior palatal foramina; narrowest skull and the longest body length.

Similar Species

C. emini. Slender body form; pelage shorter and softer, ventral pelage white, clearly delineated from flanks; face narrow without dark eye-ring; ears larger and standing above pelage, skull more elongated (Genest-Villard 1967); restricted to rainforest habitats.

Distribution Endemic to Africa. Widespread in Sudan and Guinea Savanna BZs, Zambezian Savanna BZ, Rainforest–Savanna Mosaics and marginally in southern part of Somalia–Masai BZ. Occasionally in Sahel Savanna BZ (see below). North of the Congo Basin recorded from Senegal and Guinea to Sudan, Uganda and Kenya; south of the Congo Basin recorded from Angola, S DR Congo, Zambia, Malawi, Tanzania, Mozambique and South Africa (KwaZulu–Natal and former Northern Transvaal Provinces) (Genest-Villard 1967, Smithers 1983). The distribution of *C. g. ansorgei* (see above) includes SE Kenya, Tanzania and all of the area from Angola to Mozambique and N South Africa. Zanzibar I.

Habitat Widespread in savanna habitats. Also recorded in human-modified habitats on edge of Rainforest BZ (Rosevear 1969, Happold 1987). In the Sahel Savanna BZ, found only in large cities. In the south-eastern part of its range, restricted to evergreen forests and moister habitats (Morris 1963, Skinner & Smithers 1990). Often commensal.

Abundance Generally considered as abundant throughout the range, but few quantitative data. Forty-five burrows found on a 5 ha

farmland in Nigeria (Ajayi 1975), 42 individuals taken from 0.5 ha garden in Zimbabwe (Smithers 1983).

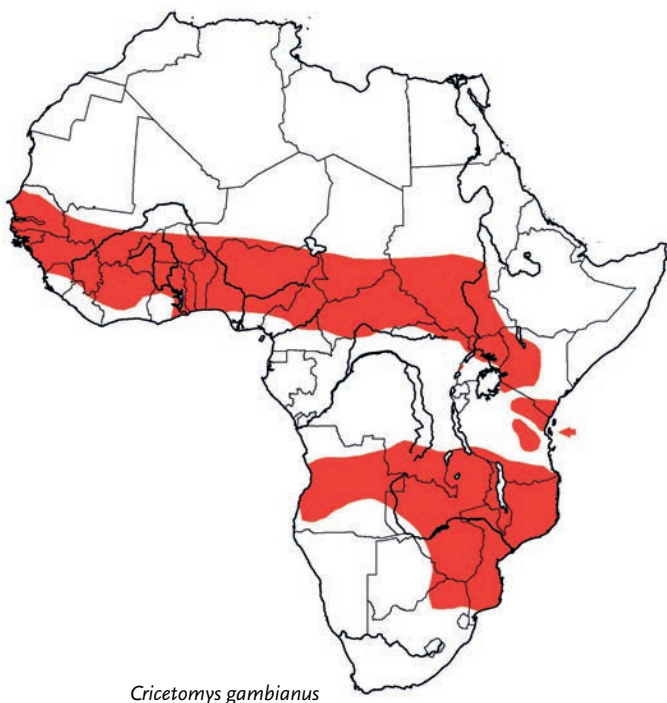
Adaptations Typically terrestrial, and predominantly nocturnal (Morris 1963, Ewer 1967). Giant Rats walk and run on all four legs, usually with the tail raised; they are good climbers and jumpers (Happold 1987). Nocturnal activity shows two peaks of activity, one at the beginning and one at the end of the night (Knight 1984). Burrows are often located in termite mounds or within the root system of large or dead trees (Morris 1963, Ajayi 1977), and range from 0.9 m to 2.9 m in length, with 50% less than 1.8 m (Ajayi 1977). A typical burrow has a large entrance leading to a nesting chamber composed of a nest, food store and sanitary area, and smaller additional burrows leading to small exit (escape) holes (Ajayi 1977). Burrows are excavated using the incisor teeth rather than claws (Morris 1963). May also live in rainwater drains and under houses.

Tooth-gnashing, inflation of cheek pouches (thus making the head appear larger than normal) and a 'puffing sound' are produced when threatened. Vocalizations for intra-specific communication include 'loud squeaks', 'high squeaks' and 'piping squeaks' (Ewer 1967).

Foraging and Food Omnivorous, but mainly vegetarian. The large cheek pouches are used to transport food (and nesting materials) to food stores in the nest (Ewer 1967). Food is frequently hoarded in nests: in Transvaal, South Africa, 8.7 kg of macadamia nuts were found in a single burrow (Knight 1984) and in Nigeria, 50% of stored food was palm fruits (Ajayi 1977). Diet of ♂♂ in S Nigeria (from stomach analysis, $n = 5$) was palm fruits (72%), seeds (12%), insects (7%) with some quantities of other fruits. Females consumed fewer palm fruits, but larger amounts of other fruits and vegetables. Diet varies according to location and food availability, and may include small quantities of animal matter (Iwuala *et al.* 1980). Most diets include adequate moisture but free water is drunk when necessary. Coprophagy appears to be a common habit (Ewer 1967).

Social and Reproductive Behaviour Generally considered to be solitary in the wild, but Happold (1987) mentions the presence of several individuals in the same burrow. In captivity, ♂♂ and ♀♀ can be kept together easily (Ewer 1967). Litter-mates may show aggressive behaviour toward each others (Ewer 1967). Home-ranges are 2.2–11 ha (mean ca. 5 ha; Skinner & Smithers 1990); home-ranges of ♂♂ larger than those of ♀♀. Detailed descriptions of complex courtship and mating behaviour, as well as parental–young interactions, in captivity are given by Ewer (1967).

Reproduction and Population Structure Pregnant ♀♀ and adults in breeding condition found all year round in Nigeria (Anizoba 1982). Young recorded between Sep and May in Malawi, suggesting that breeding takes place during the wet season (Morris 1963). Gestation: 27–42 days (Morris 1963, Ewer 1967, Ajayi 1975). Litter-size: 3 (1–5). Average weight at birth: 16–27 g, depending on litter-size; altricial; eyes closed, hairless. Silky covering of hair Day 10. First walking Day 16. First eating of solid food Day 18. Eyes open Day 20–24. Collects food in cheek pouches ca. Day 25, coprophagy Day 25 (Ewer 1967). Sexual maturity about 20 weeks for both sexes (Ajayi 1975).



Cricetomys gambianus

Predators, Parasites and Diseases Predators include the Steppe Eagle *Aquila rapax* and eagle-owls *Bubo capensis* and *Bubo lacteus* (De Graaff 1981). Highly appreciated by humans as bushmeat. In W Nigeria, ranked as the 2nd (22%) or 4th (8%) commonest species for sale as bushmeat (Martin 1983, Anadu *et al.* 1988) after small antelopes, Cane Rats and Brush-tailed Porcupines (Martin 1983). Ranked 20th of preferred wild animals as a source of food in N Cameroon (Njiforti 1996). Eaten frequently in East Usambara Mts as well as in other coastal and montane forests in E Tanzania (N. Cordeiro unpubl.).

Several species of *Hemimerus* ectoparasites (Insecta: Dermoptera; earwig family) are specific to *Cricetomys gambianus*, including *H. talpoides*, *H. prolixus*, *H. deceptor*, *H. bouvieri* (Ashford 1970, Popham 1984). *Hemimerus* is the only known parasitic member of this insect family (Happold 1987) and is found only on species of *Cricetomys* and *Beamys*. Other ectoparasites include a variety of ticks, mites and fleas; major intestinal parasites are tapeworms. Among human pathogens, *Babesia* and *Bartonella* bacteria have been identified in the blood (Dipeolu & Ajayi 1976); in West Africa, several viruses (including Bandia, Uganda S, Dugbe and Gabek-Forest) have been isolated from body organs of *C. gambianus* (Saluzzo *et al.* 1986).

Conservation IUCN Category: Least Concern.

Common and widespread species, and not threatened. Bred in captivity as a supply of 'bushmeat' (Ajayi 1975).

Measurements

Cricetomys gambianus

HB: 326 (273–407) mm, n = 66

T: 352 (277–423) mm, n = 58

HF: 62 (52–79) mm, n = 65

E: 37 (28–46) mm, n = 64

WT: 786 (500–1550) g, n = 65

GLS: 66.4 (58.8–70.5) mm, n = 34

GWS: 32.2 (28.7–34.5) mm, n = 35

M¹–M³: 10.3 (9.3–11.0) mm, n = 34

Senegal (J.-M. Duplantier unpubl.)

Key References De Graaff 1981; Ewer 1967; Genest-Villard 1967; Smithers 1983.

J.-M. Duplantier & L. Granjon

GENUS *Saccostomus*

Pouched Mice

Saccostomus Peters, 1846. Bericht Verhandl. K. Preuss. Akad. Wiss. Berlin, 11: 258. Type species: *Saccostomus campestris* Peters, 1846.



Saccostomus campestris.

The genus comprises two species widely distributed in savanna habitats in East and South Africa. Species in the genus are small-medium in size (and smaller than other members of the family), solidly built with broad heads, short limbs and short tails. Cheek pouches are well developed. The skull is characterized by long anterior palatal foramina and a long bony palate with prominent posterolateral palatal pits; the mesopterygoid fossa is short and wide, the alisphenoid lacks a dorsal flange, the accessory foramen ovale is absent, and the ectotympanic bullae are moderately inflated (Figure 27). These skull characteristics contrast with those of the other genera in the subfamily (*Cricetomys*, *Beamys*) and hence *Saccostomus* may be placed in a separate tribe, the Saccostomurini (see profile Subfamily Cricetomyinae).

Species in the genus are nocturnal and terrestrial, and live in burrows during the day. They are primarily granivorous; individuals collect seeds in their cheek pouches and deposit them in caches in burrows for later consumption. When food is abundant, they

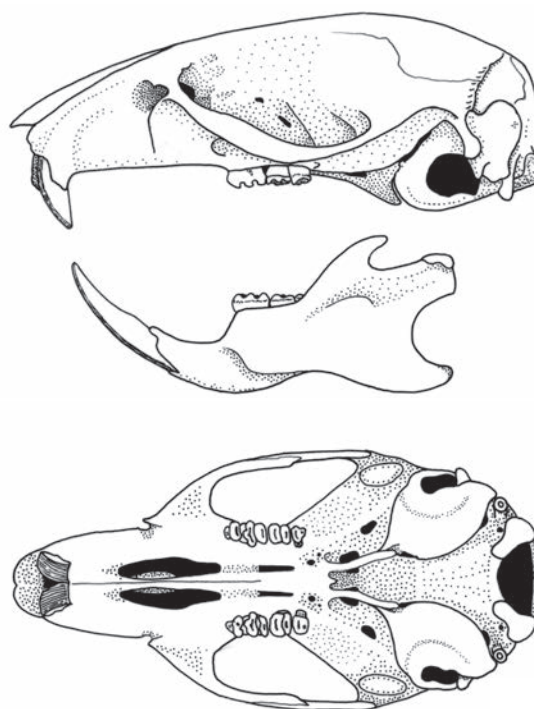


Figure 27. Skull and mandible of *Saccostomus campestris* (HC 2435).

accumulate fat and increase in weight; when food is scarce during cool and dry weather, they become inactive and torpid and survive, partly, on accumulated fat reserves. Litter-sizes are comparatively large, with up to ten young/litter.

Two species are recognized. One species, *S. campestris*, has a large variation in chromosome number and may represent more than one species. The significance of such variation is uncertain. The second species, *S. mearnsi* from East Africa, was until recently considered as a subspecies of the more widespread *S. campestris*.

The species are distinguished by colour of body pelage, body size, number of chromosomes and geographic distribution.

D. C. D. Happold

Saccostomus campestris CAPE POUCHED MOUSE (SOUTHERN AFRICAN POUCHED MOUSE)

Fr. Rat à abajoues du Cap; Ger. Kap-Hamsterratte

Saccostomus campestris Peters, 1846. Bericht Verhandl. K. Preuss. Akad. Wiss. Berlin 11: 58. Tete, Zambezi River, Mozambique.

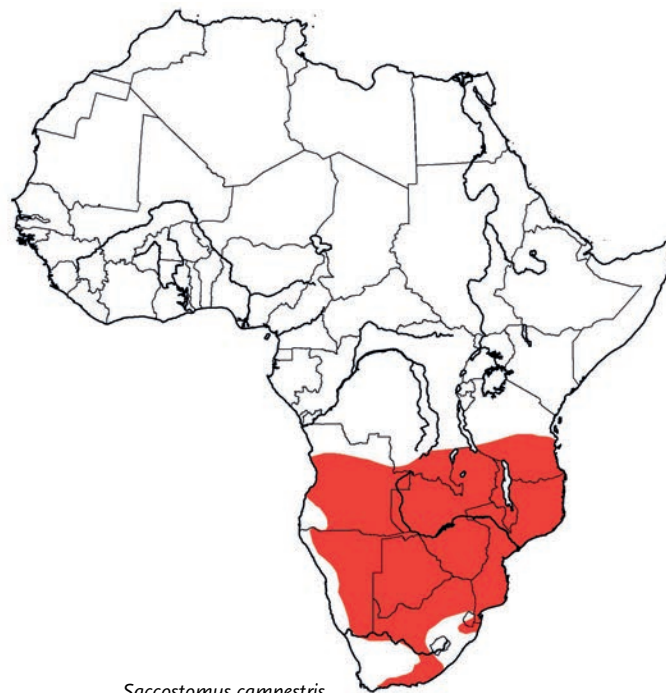
Taxonomy The species originally included *mearnsi* as a subspecies. The species, as currently defined, has considerable variation in chromosome numbers and in the structure of the chromosomes (Gordon & Rautenbach 1980, Gordon 1986). The variation is primarily geographic (see below), and more than one $2n$ number may occur in the same locality (Gordon 1986). There may be a complex of two or more species in southern Africa (Gordon 1986). Synonyms: *anderssoni*, *angolae*, *elegans*, *fuscus*, *hildae*, *lapidarius*, *limpopoensis*, *mashonae*, *pagei*, *streeteri*. Subspecies: none. Musser & Carleton (1993, 2005) suggest that *anderssoni* and *mashonae* deserve attention in respect of their relation to *campestris*. Chromosome number: $2n = 28$ to $2n = 50$, $FN = 46-62$ (details in Gordon 1986).

Description Small, stocky mouse with soft, thick coat and short tail. Pelage fine and dense. Dorsal pelage pale brownish-grey to grey with some black-tipped hairs along mid-dorsal line; hairs dark grey at base, medium grey or brownish-grey at tip. Colour of dorsal pelage varies geographically. Ventral pelage pure white. Colour of dorsal pelage clearly delineated from colour of ventral pelage. Chin, throat, lower cheek and base of muzzle white. Head broad, with rounded nose. Well-developed cheek pouches extend to near shoulders; very conspicuous when full of seeds. Ears short and rounded, held sideways from head. Fore- and hindlimbs white, short and stocky; four digits on forefeet, five digits on hindfeet. Tail short (ca. 44% of HB), without scales, dark above, white below, with sparse short bristles. Young animals are darker than adult animals. Body measurements of ♂♂ slightly larger on average than for ♀♀. Nipples: $3 + 2 = 10$.

Geographic Variation Sixteen chromosomal forms are recorded in southern Africa (Gordon 1986). There is a general decrease in $2n$ number from west (e.g. $2n = 46$ at the coast of KwaZulu-Natal Province, South Africa) to east (e.g. $2n = 30, 31, 32$ in W Namibia), but there are exceptions to this trend (e.g. $2n = 26-28$ in northern populations such as SE Angola and N Zimbabwe). In southern Africa, specimens from the drier western part of the range are paler in colour than those from the wetter eastern areas. Three colour forms – pale buffy-brown, blackish-grey and medium dark grey – recorded in Malawi; these may be partly associated with age (Hanney 1965).

Similar Species

S. mearnsi. HB on average larger; tail relatively longer; dorsal pelage dark grey to brownish-grey; ventral pelage dark grey, hairs sometimes with white tip (never pure white); East Africa; probably allopatric to *S. campestris* in C Tanzania (see also below).



Saccostomus campestris

Distribution Endemic to Africa. Zambezian Woodland and South-West Arid (Kalahari) BZs. Recorded from Angola, Zambia, Malawi, S Tanzania, Mozambique (mainly south of the Zambezi R.; records north of the river are sparse), SE DR Congo, C and N Namibia, Botswana, Zimbabwe and South Africa (SE Transvaal, C and N Free State, S KwaZulu-Natal, SW and E Cape Province). Not recorded from Lesotho (Lynch 1994). The northern boundary of the range of *S. campestris* in C Tanzania, where it adjoins the southern boundary of *S. mearnsi*, is uncertain.

Habitat Occurs in many types of woodland and grassland, and close to marshes. In Botswana, found in sandy regions, kopjes, open short grasslands, rocky kopjes, dry river beds, *Acacia* grasslands and mopane woodlands. In Malawi, found primarily in low altitude dry woodlands, but not on the high plateaux. In southern Africa, recorded in habitats where rainfall is 250 to over 1200 mm/annum, and from sea level to 1800 m. Sandy substrates with cover provided by bushes or open woodland are preferred habitat. In several parts of its range, burrows are dug in large abandoned termite mounds.

Abundance Widely distributed and locally common. Numbers fluctuate seasonally and individuals are rarely encountered during cool

dry weather. In South Africa, variations in density (0.31–1.70/ha) are related to the habitat, when the habitat was last burnt, and frequency of burning (Korn 1981). In *Acacia tortilis* savanna in north KwaZulu–Natal, densities varied from 0/ha to 3.8/ha, and in *Acacia nigrescens* savanna, from 0/ha to 1.8/ha (Swanepoel 1976). In thicket-clump savanna in Lengwe N. P., Malawi, mostly uncommon during the dry season (0–1/ha), but more abundant during and immediately after the wet season (up to 6/ha); during a ten-month period, they contributed 11% to the small mammal community, ranging from 0 to 1% in drier months and up to 28% in wetter months (Happold & Happold 1991).

Adaptations Terrestrial, scansorial and nocturnal. Excavates burrows in sandy soils or in termite mounds, or utilizes burrows made by springhares or Aardvarks. Burrows vary greatly in complexity and usually contain stores of seeds. When food is abundant, individuals store fat and put on weight. During the cool dry weather (or ‘winter’ in southern Africa), stored fat is metabolized and individuals lose weight; at this time, overall energy demands are reduced (Korn 1989), body temperature declines to 21–25 °C for 2–6 hours/day, there may be short bouts of daily torpor (Ellison & Skinner 1992), and overall activity is reduced. The stomach comprises a non-glandular forestomach and a distinctly differentiated glandular hindstomach; however, the relatively low density of bacteria in the forestomach suggests that bacteria do not contribute greatly to digestion and metabolism (Perrin & Kokkinn 1986).

Foraging and Food Predominantly granivorous. The diet includes a wide diversity of seeds. Seeds are gathered in the cheek pouches and taken to food caches in the burrow. The forefeet are used to help fill the cheek pouches. Seeds found in cheek pouches and in food caches include *Grewia monticola*, the umbrella thorn *Acacia tortilis*, sweet thorn *A. karroo*, scented thorn *A. nilotica*, camel thorn *Acacia erioloba*, nyala tree *Anthocercis zambesiaca*, red thorn *Acacia gerrardi*, *Combretum* spp., mopane *Colophospermum mopane*, sekelbos *Dicrostachys cinerea*, raisin bush *Grewia bicolor*, *G. flavescens*, *Burkea africana*, *Euclea crispa* and *Peltophorum africanum* (Smithers 1971, Swanepoel 1976, De Graaff 1981). Termites, grasshoppers and other insects are also eaten (De Graaff 1981). Kerley (1989) classified these Pouched Mice as ‘partially insectivorous granivores’ that forage widely from the burrows. The diet varies seasonally (Watson 1987): in Kruger National Park, during the dry season, it comprised 31% insects, 12% herbage and 57% seeds (n = 14), compared with 9% insects, 12% herbage and 79% seeds during the wet season.

Social and Reproductive Behaviour Solitary. Home-range in *Terminalia-Dichrostachys* grasslands of Kruger N. P., South Africa, is 1200 m² in control (unburnt) habitat and 1200–2800 m² in habitat burnt every three years (Korn 1981). Females in oestrus or pro-oestrus are aggressive and attack ♂♂ (Swanepoel 1976).

Reproduction and Population Structure Breeding and recruitment varies according to locality: Oct–Feb in KwaZulu–Natal (Swanepoel 1972), Oct–Apr in Transvaal (Rautenbach 1982), Jan–Apr in Botswana (Smithers 1971) and Feb–Apr in Zimbabwe (Smithers & Wilson 1979). These months are mostly during the warmer wetter months of the year. In Malawi, pregnant ♀♀ found in Apr/May (warm late wet season), Aug/Sep (cool dry season) and Dec/Jan (warm early wet season) (Hanney 1965). Litter-size also varies geographically, e.g. litter-size: 4.8 (2–8) in South Africa (Earl 1978); 7 (5–10) in Botswana (Smithers 1971); 6.7 (1–10, n = 7) in Zimbabwe (Smithers & Wilson 1979); and 5.1 (2–9, n = 10) in Malawi (Hanney 1965). Gestation: 20–21 days (Earl 1978). At birth, young fully furred, weight 2.8 g. Weaned Day 19–25 when 11 = 15 g. First litter Day 96 (Earl 1978). Females are spontaneous ovulators with a four-day cycle, without a postpartum oestrus (Westlin-Van Aarde 1988), and they exhibit a lactational anoestrus (Westlin-Van Aarde 1989). The energy demands of ♀♀ increase by 55% during pregnancy and by 110% during lactation (Perrin & Clarke 1987).

Predators, Parasites and Diseases Preyed on by Barn Owls *Tyto alba*, Grass Owls *T. capensis* and Giant Eagle-owls *Bubo lacteus*, and probably several small mammalian carnivores. They are hosts to a wide range of ectoparasites including 11 spp. of mites, 18 spp. of fleas and 4 spp. of ticks (details in De Graaff 1981). The nematode *Inermicapsifer madagascariensis* is a common endoparasite (details in De Graaff 1981).

Conservation IUCN Category: Least Concern.

Widely distributed and locally common, and not threatened in natural habitats.

Measurements

Saccostomus campestris

HB: 114 (83–145) mm, n = 21

T: 50 (32–83) mm, n = 21

HF: 21 (17–30) mm, n = 21

E: 14 (12–22) mm, n = 21

WT: 48.5 (33–68) g, n = 20

GLS: 30.7 (29.0–33.5) mm, n = 17

GWS: 15.0 (13.9–16.0) mm, n = 17

M¹–M³: 4.6 (4.0–4.9) mm, n = 17

Body measurements and weight: Botswana (Smithers 1971; ♂♂ only)

Skull measurements: Zambia, Malawi (BMNH)

Key References De Graaff 1981; Hanney 1965; Smithers 1983.

Mike Perrin

Saccostomus mearnsi MEARNS'S POUCHED MOUSE (EAST AFRICAN POUCHED MOUSE)

Fr. Rat à abajoues de Mearns; Ger. Mearns Hamsterratte

Saccostomus mearnsi Heller, 1910. *Smithson. Misc. Coll.* 54: 3. Changamwe, Coast Province, Kenya.

Taxonomy Morphological and chromosomal evidence indicate that *S. mearnsi* is distinct from *S. campestris* (Hubert 1978a, Gordon 1986). Synonyms: *cricetulus*, *isiolae*, *umbriventer*. Subspecies: none. Chromosome number: $2n = 40-42$ (Hubert 1978a), $FN = 40-42$.

Description Medium-sized, stocky mouse with soft, thick coat and short tail. Dorsal pelage pale to dark grey, dark brown or brownish-grey; hairs medium grey at base, grey or brownish-grey at tip. Flanks slightly paler. Ventral pelage grey (cf. *S. campestris*); some hairs tipped with white to give frosted appearance. Chin and base of muzzle whitish-grey. Head broad, with rounded nose and large eyes. Well-developed cheek pouches. Ears large and rounded, held sideways from head. Fore- and hindlimbs dark grey, short and stocky; four digits on forefoot, five digits on hindfoot. Tail short (ca. 50% of HB), thick at base, without scales, well covered with grey to brownish-grey hairs above, white below. Males often heavier than ♀♀. Nipples: probably $2 + 3 = 10$, as for *S. campestris*.

Geographic Variation None recorded.

Similar Species

S. campestris. Dorsal pelage medium grey; ventral pelage pure white; southern Africa as far north as C Tanzania.

Distribution Endemic to Africa. Somalia–Masai Bushland BZ, and marginally around the Afromontane–Afroalpine BZ of Kenya. Recorded from SW Ethiopia, S Somalia, E Uganda, Kenya and N Tanzania. The southern boundary of the range is uncertain; current records suggest that *S. mearnsi* and *S. campestris* are allopatric in Tanzania.

Habitat Savanna; details of habitat preferences are poorly known. In C Kenya, abundant in woodland savanna on poorly drained soils and in shrubby thickets along seasonal watercourses and on kopjes.

Abundance Comprised ca. 80% of a small mammal community in the Laikipia District of C Kenya (Keesing 1998a). Population numbers fluctuated from 45/ha following heavy rains to 6/ha after a prolonged drought, with a 5-year average of 20/ha. Mearns's Pouched Mice were twice as abundant in areas from which large mammals had been excluded (Keesing 2000), presumably because of increased availability of food. In the few other areas from where they have been reported, *S. mearnsi* is less abundant than at Laikipia.

Adaptations Terrestrial and nocturnal, and strikingly slow-moving. Capable of digging deep burrows in hard soil with their strong legs and toes. Adults continue to grow after attaining reproductive maturity at ca. 45 g; old ♂♂ weigh as much as 120 g. See also *S. campestris*.

Foraging and Food Omnivorous. Diet varies seasonally; in the wet season, forbs and browse (82%) form the majority of the diet

*Saccostomus mearnsi*

with smaller amounts of seeds (9%) and arthropods (7%); in the dry season, the diet contains more seeds (33%) and arthropods (22%) and lesser amounts of forbs and browse (43%) (Neal 1984a). Diet varies at different localities (Keesing 1998a, Metz & Keesing 2001). Pouched Mice clip and consume both forbs and tree seedlings and often leave small piles of harvested vegetation. In cafeteria trials and in the field, they show strong preferences for certain forbs (e.g. *Commelina* spp., *Monsonia angustifolia*) and for the seeds and seedlings of *Acacia* trees. Because of their consumption of seeds and seedlings, they may influence the recruitment of *Acacia* trees (Keesing 2000). They appear to compete with ungulates for some food resources, since the removal of ungulates results in rapid increases in their numbers (Keesing 1998b).

Social and Reproductive Behaviour Mostly solitary, living alone in burrows constructed in termite mounds, under shrubs and at the bases of trees. At high population densities, however, Pouched Mice live in close proximity, occasionally sharing burrow entrances and possibly entire burrow systems with conspecifics (Keesing 1998a). In encounters between pairs of same-sex individuals, both ♂♂ and ♀♀ exhibited a number of behaviours typical of more social rodents (e.g. vocalizations, allogrooming, appeasement). Based on data from long-term trapping records, ♀♀ appear to be territorial, while the home-ranges of ♂♂ are broadly overlapping and superimposed on those of ♀♀ (Keesing & Crawford 2001). Home-range of ♂♂: 0.21 ± 0.02 ha; home-range of ♀♀: 0.06 ± 0.01 ha.

Reproduction and Population Structure Reproduction is seasonal in C Kenya: almost all adult ♀♀ are in breeding condition

in Aug–Nov following the wet season (Apr–Jul), while only 10% are in breeding condition during the dry season (Jan–Mar). At least 85% of adult ♂♂ remain in breeding condition throughout the year. Litter-size: 3–5. Gestation, ontogeny and time to maturity unknown (but see *S. campestris*).

Predators, Parasites and Diseases Predators unknown. Reported to be hosts for juvenile stages of some *Rhipicephalus* ticks. However, larval ticks experimentally placed on mice were groomed off and never recovered, suggesting that these mice are poor hosts for juvenile ticks (F. Keesing unpubl.).

Conservation IUCN Category: Least Concern.

Measurements

Saccostomus mearnsi

HB: 137 (115–160) mm, n = 30

T: 69 (58–79) mm, n = 29
 HF: 21 (20–22) mm, n = 31
 E: 20 (19–23) mm, n = 29
 WT (♂♂): 79 (48–121) g, n = 121
 WT (♀♀): 62 (39–83) g, n = 97
 GLS (♂♂): 34.8 (33.0–37.1) mm, n = 3
 GLS (♀♀): 33.6 (30.4–36.3) mm, n = 5
 GWS (♂♂): 17.7 (16.9–19.1) mm, n = 4
 GWS (♀♀): 17.2 (16.0–17.8) mm, n = 5
 M¹–M³: 5.9 (5.5–6.1) mm, n = 8
 Laikipia District, Kenya (F. Keesing unpubl.)

Key References Hubert 1978a; Keesing 1998a, b; Metz & Keesing 2001.

F. Keesing

Subfamily DELANYMYINAE – Delany's Swamp Mouse

Delanymyinae Musser & Carleton, 2005. *In* Mammal Species of the World, 3rd Ed., p. 934.

The subfamily Delanymyinae contains only a single genus and species, *Delanymys brooksi*, endemic to Western Rift Mts in East Africa. This very small, gracile mouse possesses an exceptionally long and semi-prehensile tail and large hindfeet with slender toes. Such traits impressed Hayman (1962a), who described the species as convergently resembling Eurasian birch mice (*Sicista*, Dipodoidea); similar convergence in body form is also seen in the Sundaic and Sulawesi murine *Haeromys* (Musser 1990). Like these mice, *Delanymys* is an expert climber, adept at negotiating slim stems and branches and filling a semi-arboreal, granivorous niche.

Until recently, *Delanymys* had been grouped with *Petromyscus* in Petromyscinae, but the two genera differ in many essential features. In *Delanymys*, the tail is twice as long as the head and body and semi-prehensile (less than to moderately longer in *Petromyscus*), and the hindfoot is long and narrow (short and broad in *Petromyscus*). The cranium of *Delanymys* possesses a very short rostrum (long and slender in *Petromyscus*), narrow interorbital constriction (broad in *Petromyscus*), narrow zygomatic plate with a shallow dorsal notch (plate broad and notch deep in *Petromyscus*), and large subsquamosal foramen (closed in adult *Petromyscus*). Examples of *Delanymys* have a short bony palate, in contrast to the long palate that projects as a prominent shelf behind the third molars in *Petromyscus*. An alisphenoid strut is absent in *Delanymys* (present in *Petromyscus*), and the carotid circulation is fully derived, lacking supraorbital and infraorbital arteries and the accompanying squamosal-alisphenoid groove and sphenofrontal and stapedial foramina (partially derived in *Petromyscus*, which retains the infraorbital artery and a large stapedial foramen). The molars in both genera are brachydont and cuspidate, but those of *Delanymys* have anterolophids and mesolophids (all absent in *Petromyscus*), and its M³ is relatively large with an occlusal pattern that resembles M² (M³ very small in *Petromyscus*, with C-shaped occlusal pattern unlike M²) (Figure 28).

The unique morphology of *Delanymys*, especially characters of the molar dentition, has generated various interpretations of its phylogenetic placement. Hayman (1962) regarded *Delanymys*

as morphologically close to *Petromyscus* and considered both to be dendromurines, and Petter (1967) acknowledged this relationship by classifying *Delanymys* and *Petromyscus* in Petromyscinae, separate from Dendromurinae. Others have emphasized resemblances between *Delanymys* and *Mystromys* or have viewed *Delanymys* as a structural link between *Mystromys* and typical Dendromurinae (Lavocat 1964, Verheyen 1965a). These conflicting views hinge, in part, on disputes over the origin and homology of the lingual cusp on the upper molars of *Delanymys* and *Petromyscus*, believed to represent either the

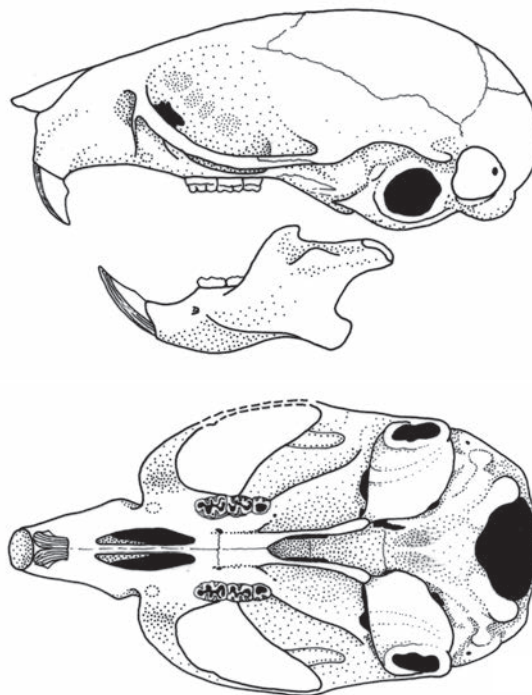


Figure 28. Skull and mandible of *Delanymys brooksi* (skull - RMCA 96-038-M-3386 with some detail from BMNH 61.1610; mandible after Verheyen (1965a); upper cheek teeth RMCA 96.038-M-3385).

protocone (Petter 1967) or a neomorphic acquisition comparable to those of dendromurines and certain Miocene fossils (Lavocat 1964, Jaeger 1977b). Aside from the questionable phylogenetic significance of these lingual cusps, *Delanymys* and *Petromyscus* share no other derived features that persuasively justify their joint membership in Petromyscinae as a natural group (Carleton & Musser 1984, Denys 1994a). Further, the dual retention of mesolophs(ids) and longitudinal enamel connections on its molars marks *Delanymys* as unique among living African Muroidea and suggests that it

represents a relictual descendant from a very early radiation of the superfamily within the continent. Musser & Carleton (2005) erected the subfamily Delanymyinae to contain the genus and urged further inquiry to illuminate its phylogenetic relationships.

Fossils of the Delanymyinae, represented as the extinct *Stenodontomys*, are known from the early Pliocene to the early Pleistocene of southern Africa (Pocock 1987, Senut *et al.* 1992, Denys 1994).

Guy G. Musser & Michael D. Carleton

GENUS *Delanymys* Delany's Swamp Mouse

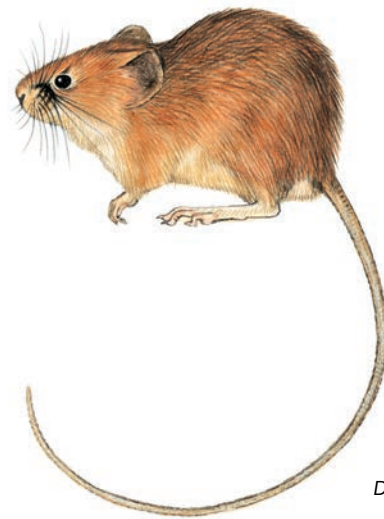
Delanymys Hayman, 1962. Rev. Zool. Bot. Afr. 65: 1–2. Type species: *Delanymys brooksi* Hayman, 1962.

Montotypic genus. In the description of the holotype, Hayman (1962) placed *Delanymys* in the subfamily Dendromurinae. An alternative view based on the 'longitudinal crest' in the molar row, is that it is closely related to *Mystromys* (subfamily Mystromyinae) (Lavocat 1964). Petter (1967) interpreted the molar structure of *Delanymys* as very similar to that of *Petromyscus* (both have an additional lingual cusp on M¹ and M², which is connected to other cusps by a longitudinal ridge); he placed both genera in the subfamily Petromyscinae, even though they are very different in other skull characters, external morphology, habits and distribution. The current opinion seems to be that *Delanymys* is far removed from the Dendromurinae, but whether the similarities to *Petromyscus* are phylogenetic or due to convergence is uncertain. Further details are given in the subfamily and species profiles.

Fritz Dieterlen

Delanymys brooksi DELANY'S SWAMP MOUSE

Fr. Souris palustre de Delany; Ger. Delanys Sumpfklettermaus



Delanymys brooksi.

Delanymys brooksi Hayman, 1962. Rev. Zool. Bot. Afr. 65: 1–2. Echuya (or Muchuya) Swamp, near Kanaba, Kigezi, SW Uganda.

Taxonomy See genus profile. Synonyms: none. Chromosome number: not known.

Description Very small climbing mouse with an extremely long tail and long hindfeet. Pelage long (8–10 mm). Dorsal pelage warm russet or rufous to hazel-brown; hairs dark slate-grey on basal two-thirds, russet or rufous on terminal one-third. Long black guard hairs (each with subterminal buff band) project well above pelage tending to give a generally darker colouration. Ventral pelage warm buff; hairs mostly ca. 7 mm, with tuft of long white hairs surrounding the urinogenital opening in both ♂♂ and ♀♀. Throat with longitudinal patch of pure white hairs. Eyes surrounded by short black hairs; black patch on nasal region between eyes and rhinarium. Lips with very long (20–25 mm) vibrissae. Ears relatively large, round, with well-developed ear folds, and long (5–7 mm) hairs in places. Upperparts of fore- and hindlimbs with dark hairs; inner surfaces with whitish hairs. Small tuft of white hairs on each wrist, thought to have a tactile function (Dieterlen 1969b). Fore- and hindfeet very small with long

digits and long curved claws (except for vestigial Digit 1 on forefoot, which has small nail); Digits 3 and 4 very long, Digits 2 and 5 long but shorter than 3 and 4. Tail extremely long (ca. 180% of HB), thin, almost hairless with small scales forming ring-like patterns. Males on average slightly smaller than ♀♀. Palatal ridges: three antemolar and four intermolar. Skull: rostrum very short, palate short, mesopterygoid fossa completely open anteriorly, zygomatic plate narrow; see also subfamily and genus profiles. Nipples: 2 + 2 = 8.

Geographic Variation None recorded.

Similar Species

Dendromus spp. Black mid-dorsal stripe in some species; tail long but mostly relatively shorter; more widespread distribution for most spp.

Distribution Endemic to Africa. Afromontane–Afroalpine BZ. Recorded from a small area bordering the Albertine Rift Valley in



Delanymys brooksi

SW Uganda, W Ruanda and E DR Congo (near L. Kivu). The most northern and eastern locality is Muchuya Swamp (01°15'–01°18' S; 29°47'–29°51' E), near Kanaba in Uganda where the type specimen was found in 1961 (Hayman 1962a). The southernmost record is Kitabi in Rwanda (02°34' S, 29°26' E; 2200 m). The geographic range may also include the area from the volcano region north of L. Kivu southwards to the Itombwe Mts north-west of L. Tanganyika.

Habitat Most individuals have been found in high altitude marshes, rich in plant species, at altitudes of 1700–1760 m. The typical habitat is swamp where sedge (*Cladium mariscus*) is standing in water, and the vegetation in the shallows is elephant grass (*Pennisetum*), *Hyparrhenia* grass and non-grassy plants such as *Abutilon*, *Rubus*, *Acanthus* and *Impatiens*. The medium height of such vegetation is 1.5–2.0 m. A few individuals have been found in non-marshy habitats such as dense grassy vegetation (Mt Gahinga [2700 m] and Mt Karisoke [3100 m]), and between ferns in a plantation of *Eucalyptus* at Kitabi (2200 m) (Van der Straeten & Verheyen 1983).

Abundance Using an enclosure and removal method, Delany's Swamp Mice comprised 6.2% of all small mammals ($n = 355$; >20 species) (Dieterlen 1967a, b). In non-marshy habitats, they are extremely rare (Dieterlen 1967a; Van der Straeten & Verheyen 1983) and it can be assumed that even in marshes they are not numerous, except in a few locations.

Adaptations Nocturnal and arboreal on grass stems. The fore- and hindfeet are extremely well adapted for climbing on the stems of grass and other low herbaceous plants in marshes and grasslands. The forefoot has a rudimentary Digit 1 (thumb), four relatively long fingers (Digits 2, 3, 4 and 5), five large plantar pads and numerous small but prominent tubercles on palm and fingers. When grasping, the proximal pads and the thumb form fit tightly against the flexible fingers. The fingers can be spread widely for climbing, and closed

tightly to prevent sliding down the plant. The hindfeet are unusually long (ca. 30% of HB) and have six plantar pads; Digits 2 to 5 are long, and Digit 1 is shorter but capable of being spread sideways. Digit 5 is especially long and strong, and is opposable. The long prehensile tail is used to provide balance when climbing, and the distal end can curl around stems to provide support. In these respects, the adaptations of the feet are very similar to those of *Dendromys* spp. The spreading ability of digits of the fore- and hindfeet is also very important when walking on the muddy ground.

Foraging and Food Vegetarian. Stomach contents ($n = 2$) contained only the whitish pulp of farinaceous seeds, probably from grasses, without any green material or animal remains. Captive animals preferred seeds, especially sorghum; water was permanently available and used not only for drinking but also for regular defecation (Dieterlen 1969b).

Social and Reproductive Behaviour Delany's Swamp Mice are gentle mice, and individuals of both sexes live peacefully together in captivity. In this respect, they differ from *Dendromys* spp., which tend to show aggressive behaviour.

Reproduction and Population Structure Embryo number: 3 ($n = 2 \text{ ♀} \text{ ♀}$); one ♀ found in a nest had four young. At birth, young are altricial. At Day 10, the eyes are closed, the incisors have not yet erupted and the short hazel-coloured pelage is brighter than in adults, WT = 2.5–2.7 g. Individuals in captivity did not reproduce.

Predators, Parasites and Diseases A dead individual found near the nest of an African Grass-owl *Tyto capensis* in E DR Congo suggests these owls may be potential predators (James Chapin, in Hayman 1963).

Conservation IUCN Category: Vulnerable. Schlitter (1989) classified the species as Rare, and hence of some conservation concern. The small geographical range has experienced considerable habitat destruction in recent years and has a very high human population density.

Measurements

Delanymys brooksi

HB: 56.8 (50–63) mm, $n = 24$

T: 104.1 (90–111) mm, $n = 22$

HF: 18.5 (17.0–20.5) mm, $n = 25$

E: 11.3 (10–13) mm, $n = 17$

WT: 5.8 (5.2–6.5) g, $n = 8$

GLS: 18.3 (17.3–19.0) mm, $n = 12$

GWS: 9.8 (9.5–10.1) mm, $n = 12$

M¹–M³: 2.5 (2.3–2.8) mm, $n = 15$

Throughout geographic range (Dieterlen 1969b; Hayman 1962a, b; Van der Straeten & Verheyen 1983; Verheyen 1965a)

Key References Dieterlen 1969b; Hayman 1962a, 1963a; Verheyen 1965a.

Fritz Dieterlen

Subfamily DENDROMURINAE – African Climbing Mice

Dendromurinae G. M. Allen, 1939. Bull. Mus. Comp. Zool., Harv. Coll. 83: 349.

The Dendromurinae encompasses a small muroid radiation (six genera and 24 species *sensu* Musser & Carleton 2005) whose living representatives are indigenous to sub-Saharan Africa. Although few in number, members of the six genera are highly diversified in their morphology, behaviour and ecology. *Dendromus* and *Megadendromus*, though occasionally active at ground level, are primarily adept climbers of slender grasses and shrubs where they forage and construct nests; accordingly, they are found in habitats where grasses and shrubby vegetation predominate (marshes, savannas, forest edges, alpine bamboo and heath zones). They are largely omnivorous, feeding upon seeds, berries and insects. In contrast, *Steatomys* is terrestrial, dwells primarily in savanna habitats, accumulates copious fat reserves during periods of abundant food and can aestivate in response to unfavourable environmental conditions. *Malacothrix*, endemic to the South-West Arid BZ, is terrestrial, granivorous and gerbil-like in certain aspects of its morphology and habits. *Dendroprionomys* and *Prionomys* are arboreal and insectivorous inhabitants of lowland evergreen rainforest. All are nocturnal.

Diagnostic features that unite so heterogeneous a group are few: first and second upper molars consist of bicuspid laminae, with a lingual accessory cusp adjacent to the middle lamina of M^1 and front lamina of M^2 . M^3 and M_3 are tiny and single-rooted. Each upper incisor has a single deep groove (except *Prionomys*). Other characters include: infraorbital foramen wide and ovoid; zygomatic plate narrow; dorsal notch indistinct or shallow; masseteric tubercle prominent; carotid circulatory pattern partially derived (sphenofrontal foramen and squamosal-alisphenoid groove absent, stapedial foramen spacious); postglenoid foramen large and subsquamosal fenestra present, middle lacerate foramen small; strut of alisphenoid bone present,

delineating an accessory foramen ovale; and tegmen tympani reduced, not contacting the squamosal (Petter 1966c, Dieterlen 1971, Carleton & Musser 1984) (Figure 29).

Dendromurines are small to very small in size, and the genera vary substantially in external characters. The pelage is short, soft and slightly woolly (*Dendromus*, *Megadendromus*), short and velvety (*Dendroprionomys*, *Prionomys*), or dense and silky (*Malacothrix*); a black, mid-dorsal stripe is well developed in *Megadendromus* and some *Dendromus*. Compared with body size, the ears are small (*Prionomys*), moderately large (*Dendromus*, *Megadendromus*) or exceptionally large (*Malacothrix*). Relative to the head and body, the tail may be longer (*Dendromus*, *Prionomys*), about equal to (*Megadendromus*) or conspicuously shorter (*Malacothrix*, *Steatomys*); and its surface naked to thinly haired and visibly scaly (*Dendromus*, *Megadendromus*, *Prionomys*) or moderately to thickly haired with caudal scales inconspicuous (*Malacothrix*, *Steatomys*). The forefoot may possess only three functional digits (Digits 2, 3 and 4; Digits 1 and 5 present but small and non-functional; *Dendromus*, *Megadendromus*), four digits (Digits 2, 3, 4 and 5; *Malacothrix*, *Steatomys*), or four plus a stubby but definitive Digit 1 (*Dendroprionomys*, *Prionomys*). *Malacothrix* has four digits on the hindfoot, the other genera have five digits (Figure 30). In certain dendromurines, the claw is replaced by a nail on Digit 1 of the hindfoot (*Dendromus*, *Dendroprionomys*, *Prionomys*) and on Digit 5 (some *Dendromus*, *Megadendromus*). Palmar and plantar surfaces are naked (*Dendromus*, *Megadendromus*, *Dendroprionomys*, *Prionomys*), hairy over the proximate third (*Steatomys*), or densely furred so that the plantar pads are obscured (*Malacothrix*).

The skull typically possesses a long and slender rostrum (most genera) or only moderately long and wide (*Steatomys*). The interorbital region is strongly constricted with smooth edges (*Dendromus*, *Malacothrix*, *Megadendromus*, *Steatomys*) or moderately wide with a weak postorbital ledge (*Dendroprionomys*, *Prionomys*). Anterior palatal foramina are slender and long, posterior margins reaching middle of first upper molars (*Dendromus*, *Malacothrix*, *Megadendromus*, *Steatomys*), or short and wide, the posterior margins set notably anterior to molar rows (*Dendroprionomys*, *Prionomys*). The auditory bulla is inflated in *Malacothrix* and *Steatomys* relative to other genera. Most genera have orthodont or opisthodont upper incisors, but in *Prionomys* the incisors

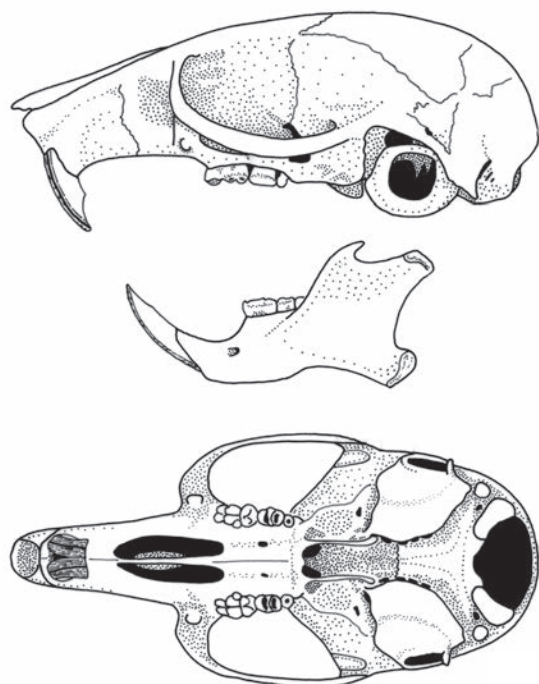


Figure 29. Skull and mandible of *Dendromus melanotis* (RMCA 38416).

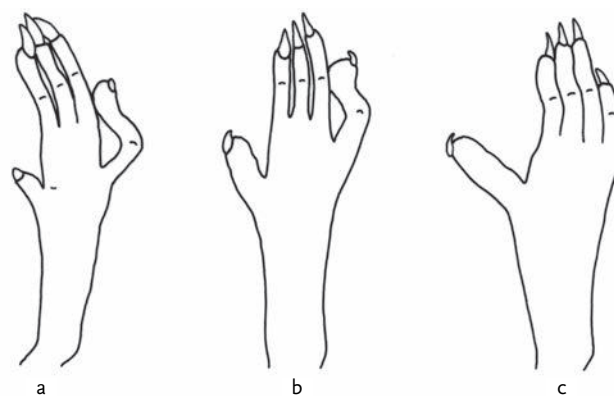


Figure 30. Right hindfoot of (a) *Dendromus* sp., (b) *Dendroprionomys rousseloti*, (c) *Prionomys batesi* to show relative sizes of Digit 1 and Digit 5 (after Petter 1966b). Hindfeet drawn to same length for each species.

are slightly pro-odont. The upper molar rows are parallel in most genera but divergent anteriorly in *Steatomys*; occlusal surfaces are cuspidate, or somewhat laminate in *Steatomys*; cusp rows of M^1 and M_1 lack longitudinal enamel crests in most genera, interconnecting longitudinal crests present in *Malacothrix*; posterior cingulum of M^1 and M^2 is small (*Dendroprionomys*, *Malacothrix*, *Prionomys*), laminar (*Steatomys*), large and oblong (*Dendromus*), or exceedingly large and forming an oblong cusp (*Megadendromus*).

In view of the variability and diversity of dendromurines, the employment of the taxon Dendromurinae in muroid classifications has suggested a 'waste-basket' for African taxa of highly specialized morphology and hence obscure relationships. The subfamily has been thought to include *Lophuromys* (Alston 1876), *Leimacomys* (Thomas 1897, and others), *Beamys* and *Saccostomus* (Allen 1939), *Petromyscus* (Ellerman 1941, Simpson 1945) and *Deomys* (Simpson 1945), genera that are now affiliated with four other muroid subfamilies (Cricetomyinae, Deomyinae, Leimacomyinae, Petromyscinae). While others have noted that Dendromurinae as arranged in former classifications is polyphyletic (e.g. Rosevear 1969, Carleton & Musser 1984), the cladistic analysis by Denys *et al.* (1995), based largely on dental traits, has convincingly demonstrated that the subfamily has a polyphyletic origin. However, strict interpretation of their study would exclude *Prionomys* and *Dendroprionomys* from the core dendromurines (*Dendromus*, *Malacothrix*, *Megadendromus*, *Steatomys*), a hypothesis that warrants continued testing in a broader systematic context.

As with the uncertainty surrounding its generic contents, Dendromurinae has been alternatively associated with murids (Miller & Gidley 1918, Simpson 1945) or cricetids (Allen 1939, Misonne 1974), and even ranked as a separate family (Chaline *et al.* 1977). In part, this vacillation hinges on the homology of the lingual accessory cusp (enterostyle) on the lamina of the upper molars,

whether a presumptive $t4$ corresponding to that in the murid triserial arrangement or a neomorphic acquisition evolved in parallel from a cricetid stock. Phylogenetic implications issuing from recent studies of morphology (Breed 1995, Denys *et al.* 1995) and DNA sequences (Verheyen *et al.* 1995, Michaux *et al.* 2001, Jansa & Weksler 2004) provide stronger vindication for the latter interpretation and support closer affinity of dendromurines to other archaic African muroids, here arranged in Nesomyidae, than to murids proper.

Although living species are today restricted to the sub-Saharan region, the subfamily was more widespread in the Tertiary. Fossils are known from the late Miocene of Africa's Mediterranean rim (Ameur 1984), the Iberian Peninsula (Aguilar *et al.* 1984) and the Arabian Peninsula (De Bruijn & Whybrow 1994, De Bruijn 1999). Certain extinct genera from the middle Miocene of North-West Africa, Pakistan and Thailand have been referred to Dendromurinae (e.g. Lindsay 1988, Mein & Ginsburg 1997), but their identification as such is disputed (e.g. Tong & Jaeger 1993, Wessels 1996). The earliest indisputable dendromurine thus far documented (*Ternania*) appears in the middle Miocene of Kenya, about 14 mya (Tong & Jaeger 1993). Representatives of *Dendromus* appear in the late Miocene of Ethiopia (Geraads 2001), and *Steatomys* is known from the late Miocene of Namibia (Senut *et al.* 1992). These genera, as well as *Malacothrix*, are commonly and widely recorded from the late Pliocene to the Quaternary in southern and eastern Africa (e.g. Jaeger 1979, Denys 1987a, b, 1994, Pocock 1987, Avery 1996, 1998).

Four of the six dendromurine genera are monospecific (*Dendroprionomys*, *Malacothrix*, *Megadendromus*, *Prionomys*), but *Dendromus* (ten species) and *Steatomys* (eight species) each contain several species and may prove to be even more diverse after further systematic study.

Guy G. Musser & Michael D. Carleton

GENUS *Dendromus* African Climbing Mice

Dendromus Smith, 1829. Zool. J. London, 4: 38. Type species: *Dendromus typus* Smith, 1829 (= *Mus mesomelas* Brants, 1827)

The genus *Dendromus* contains 11 or 12 species of small climbing mice distributed throughout sub-Saharan Africa. Most species occur in southern, central and East Africa; only one, with a very disjunct distribution, is recorded from West Africa. Three species have wide distributions; most have a small distribution, and others are restricted to one or more widely scattered locations. Typical habitats are long grasslands, bracken, dense scrub, grassy wetlands, and subalpine or alpine vegetation. In some regions, several species are sympatric (e.g. Kivu, E DR Congo; Dieterlen 1971).

Species in the genus are characterized by delicate build, small size, soft brown or reddish-brown pelage, long thin tail (100–160% of HB, depending on the species) and specialized feet. Several species have a black mid-dorsal stripe and one species (*D. lovati*) has three black stripes. The forefoot has only three well-developed digits (Digits 2, 3 and 4); Digit 1 is extremely reduced and Digit 5 is short. The hindfoot has five elongated digits; Digits 2, 3 and 4 are long and slender, Digit 1 is reduced but functional, and Digit 5 is long and semi-opposable and widely separated from other digits (Figure 30). Some species have a nail on Digit 5 of the hindfoot, rather than a claw. Skull characters



Skeleton of *Dendromus*.

include: small in size, delicate build, rostrum narrow, zygomatic plate narrow with the masseteric knob at lower corner of the plate, anterior palatal foramina extending to middle row of M^1 , supraorbital ridges absent and auditory bullae comparatively well developed. Upper incisors small, slightly opisthodont, each with single longitudinal groove. Cheekteeth small; M^2 about half size of M^1 ; M^3 very small; cusps biseral (two cusps in each row), with additional small lingual cusp on middle lamella of M^1 and (to a lesser extent) on M^2 .

Most species of *Dendromus* climb using the long digits of the forefeet and hindfeet. The opposable Digit 5 of the hindfeet (which can be

opposed to contact Digit 1) and the semiprehensile tail are especially important for climbing and balancing on twigs and grass stems. Some species tend to be more terrestrial than others. They feed primarily on seeds and are mostly nocturnal. Some species, kept in captivity, tend to rather aggressive to conspecifics and to other co-habiting species.

Systematically, *Dendromus* is one of the most difficult genera of African rodents. Rosevear (1969) records that over 50 forms have been given names, and that eight species have been recognized. Bohmann (1942) disposed of these forms in three 'Rassenkreisen', roughly equivalent to what are now considered as *D. mesomelas*, *D. melanotis*

Table 16. Species in the genus *Dendromus*, arranged alphabetically. (n. d. = no data.)

| Species | HB mean (range) (mm) | T mean (range) mm [% HB] | Colour of dorsal pelage | Colour of ventral pelage | Mid-dorsal stripe [width of stripe] | Claw/nail on Digit 5 of hindfoot | Notes |
|-----------------------|---------------------------|-------------------------------------|---|--|---|----------------------------------|--|
| <i>D. insignis</i> | 80.1 (68–96) | 97 (84–113) [120%] | Rich brown, reddish or buff | Buff-grey; grey at base | One. Back of head to rump [4 mm] | Claw (short) | Montane areas of eastern Africa. Chin/throat white. Pelage long and dense |
| <i>D. kahuziensis</i> | (77, 82) | (120, 132) [157%] | Dark brown, dusky | White; dark grey at base | One. Forehead to base of tail [8 mm] | Claw | Mt Kahuzi, E Zaire only. Chin, throat and chest white |
| <i>D. lovati</i> | 74 (57–95) | 73 (57–87) [100%] | Warm greyish-brown | Greyish; grey at base | Three. Middle stripe 40–50 mm long, rump to neck; outer stripes 25–30 mm long, rump to shoulders [n.d.] | Nail | Afroalpine, Ethiopia. Black stripe on head from between eyes to back of head |
| <i>D. melanotis</i> | 68 (56–81) ^a | 90 (76–108) ^a [120–130%] | Medium-brown to rufous-brown; flecked with grey | Greyish; grey at base | One. Shoulder to base of tail [3–4 mm] | Nail | Widespread in southern and eastern Africa. Common |
| <i>D. mesomelas</i> | 76 (69–80) ^a | 99 (91–105) ^a [130–140%] | Rufous-brown; woolly texture | Off-white; hairs dark at base with whitish tip | One. Shoulder to base of tail (absent in some) [variable] | Claw | Widespread in southern and eastern Africa. Common |
| <i>D. messorius</i> | 63.5 (60–68) | 88.6 (72–95) [140%] | Gingery-brown | Pure white | Absent (Occasionally faint brown in West Africa) | Claw | Mostly West Africa; often found in banana plants |
| <i>D. mystacalis</i> | 60.2 (55–65) ^a | 84.8 (75–95) [140–160%] | Bright rufous-brown | Pure white | One. Shoulder to base of tail [variable] | Claw | Widespread in southern and eastern Africa |
| <i>D. nyasae/kivu</i> | 74 (64–80) | 92 (84–105) [124%] | Rich brown | Silvery-white; grey at base | One. Neck to base of tail [2–3 mm] | Claw (short) | Albertine Rift Valley 1300–4200 m |
| <i>D. nyikae</i> | 66.8 (50–78) ^a | 86.4 (80–93) [130–160%] | Pale to dark cinnamon | Creamy-white; white at base (sometimes grey) | One. Shoulder to base of tail [variable] | Nail | Mostly eastern Africa; higher altitudes. White subauricular patch |
| <i>D. oreas</i> | 69.3 (60–74) | 95.3 (89–104) [135%] | Medium brown | Dark rufous to greyish-yellow; dark at base | One. Indistinct; mid-back to base of tail [3–4 mm] | Claw | Cameroon Mts only. White patches on chin, throat and chest |
| <i>D. vernayi</i> | 63.6 (60–66) | 82.0 (80–84) [130%] | Ochre- to cinnamon-brown; long and silky | Pinkish-buff to grey; grey at base | One [4.5 mm] | n. d. | Chitau, Angola. Rare. White patch on throat and axillary region |

^a Males only.

and *D. mystacalis*; but this reduction created additional problems. The genus as a whole possesses a very homogeneous morphology with respect to skull and dentition, but a great variability of pelage colour and pattern, so that classifying the species often depends on rather few details (Heim de Balsac & Lamotte 1958, Dieterlen 1971). Musser & Carleton (2005) recognize 12 species and list 44 synonyms for the whole genus. The distributional limits of many species are unresolved, and karyological information is unavailable for most species. The

genus is in need of further study and revision. Here, 11 species are recognized; the twelfth species of Musser & Carleton (2005), *D. leucostomus*, is placed as a synonym of *D. melanotis*.

The species are distinguished by body size, pelage colour, presence or absence and form of the mid-dorsal stripe, presence of nail or claw on Digit 5 of hindfoot, and distribution (Table 16).

Fritz Dieterlen

Dendromus insignis MONTANE AFRICAN CLIMBING MOUSE

Fr. Souris arboricole des montagnes; Ger. Gebirges-Klettermaus

Dendromus insignis (Thomas, 1903). Ann. Mag. Nat. Hist., ser. 7, 12: 341. Nandi, Kenya.

Taxonomy Originally described in the genus *Dendromys*. This species belongs to the *mesomelas* species-complex, although there is some doubt about which forms may be included within *insignis* (Thomas 1916b, Bohmann 1942, Ellerman *et al.* 1953). The holotype may be unrepresentative of the species as a whole, and its relationship to *mesomelas* is uncertain. According to Musser & Carleton (2005), most literature references to *D. mesomelas* in montane habitats north of the southern African sub-region prior to 1991 actually represent either *D. insignis* or *D. nyasae* (*kivu*), both of which may co-occur in the Albertine Rift Valley mountains. Synonyms: *abyssinicus*, *kilimandjari*, *percivali*. Subspecies: none. Chromosome number: not known (identity of Matthey's [1967, 1970] specimens is questionable).

Description Very small climbing mouse with broad mid-dorsal stripe; the largest species of *Dendromus*. Pelage long (8–9 mm) and dense; shows considerable individual variation (see below). Dorsal pelage rich brown tending to reddish or buff; hairs grey at base, brown at tip. Underfur dark grey, which may provide greyish tinge to pelage. Broad (ca. 4 mm) black mid-dorsal stripe from back of head to base of tail. Ventral pelage and flanks mainly buff or buffy-grey; hairs grey at base, buff at tip. Small area of chin and throat pure white. Indistinct black longitudinal stripe (ca. 10–20 mm in length) on head. Ears with short brown or black hairs. Hindfeet silver-grey. Hindfoot with five digits; Digit 1 short with nail, Digit 5 long with claw. Tail very long (ca. 120% of HB, but relatively short compared with other *Dendromus* spp.), dark brown above, much paler below with long silvery-grey hairs. Nipples: 2 + 2 = 8.

Geographic Variation Pelage variable: longer on individuals living above 2000 m; darker in colour in young and subadults than in adults; ventral colouration tends to be more variable than dorsal colour.

Similar Species

D. nyasae (*kivu*). HB on average slightly smaller (mean 73.4 mm); tail on average slightly shorter (mean 91.8 mm) but of similar relative length (ca. 124% of HB); mid-dorsal stripe 2–3 mm wide, from neck to base of tail; pelage not as dense.

D. mesomelas. HB on average smaller (mean 74–76 mm); tail on average longer (mean 99–103 mm) and relatively longer (130–140% of HB); narrower mid-dorsal stripe, sometimes absent; pelage woolly; larger geographic range.



Dendromus insignis

Distribution Endemic to Africa. Afromontane–Afroalpine BZ of eastern Africa. Recorded from the Rwenzori Mts (up to 4500 m; Misonne 1963, Verschuren *et al.* 1983); Virunga Range and Mitumba Mts west of L. Kivu (1700–3300 m; Dieterlen 1976a); Mt Kenya (2300–4300 m; Hollister 1919), Matthews Range, Mau Escarpment, Aberdare Range, Mt Kilimanjaro (3500–4700 m) and Uluguru Mts (Bohmann 1942, F. Dieterlen unpubl.). The total range of the species is uncertain because of the uncertain taxonomic status of some related forms and lack of material from large areas. Maybe sympatric with *D. nyasae* (*kivu*) at some localities in the mountains of the Albertine Rift Valley (Dieterlen 1971, 1976a, as *D. mesomelas* *kivu*).

Habitat In the cultivated regions near L. Kivu, DR Congo (1500–2000 m), lives with other species of *Dendromus* in open comparatively dry dense grassy areas (Dieterlen 1971) and, less frequently, in marshes and moist herbaceous vegetation. Also occurs in sparse bamboo and secondary forest above 2000 m, and in wet grass and

herbaceous vegetation in sub-alpine and alpine zones above 3000 m (Kingdon 1974, Dieterlen 1976a).

Abundance May be abundant at lower altitudes, but becomes progressively less common with increasing altitude.

Adaptations Probably nocturnal and diurnal. Although comparatively large and heavy (15 g) and often found on the ground, these mice are agile climbers. The opposable Digit 5 of hindfoot and the semi-prehensile tail are used to provide support when climbing. More terrestrial than many species of *Dendromus*. Because of its terrestrial habits, this species is trapped more often than other *Dendromus* spp. Most nests seem to be on the ground or in burrows.

Foraging and Food Omnivorous and/or insectivorous. Two stomachs contained remains of well-chewed seeds (including sorghum), reddish berries and arthropods (Dieterlen 1971, 1976a).

Social and Reproductive Behaviour No information, but it is presumed that individuals are mostly or entirely solitary.

Reproduction and Population Structure Near L. Kivu, most young born in the wet season between Sep and May. Gestation: not known (although probably similar to *D. nyasae* [kivu]). Embryo number: 4 (n = 3). Young extremely altricial at birth; postnatal development is slow. Sex ratio: 69 : 31% (ca. 7 : 3; n = 48). In most respects, reproduction and population structure appear to be similar to *D. nyasae* (kivu) (Dieterlen 1971).

Predators, Parasites and Diseases Small carnivores, birds and snakes are potential predators. Predatory ants are certainly a great danger for young in the nest during the first three weeks of life, especially when nests are on the ground or in burrows.

Conservation IUCN Category: Least Concern.

Measurements

Dendromus insignis

HB: 80.1 (68–96) mm, n = 34

T: 97.0 (84–113) mm, n = 34

HF: 22.3 (20.5–24) mm, n = 34

E: 15.7 (13–18) mm, n = 34

WT: 15.1 (9–27) g, n = 34

GLS: 24.1 (21.4–25.7) mm, n = 19

GWS: 12.1 (11.3–12.9) mm, n = 14

M¹–M³: 3.8 (3.7–4.1) mm, n = 22

West of L. Kivu, DR Congo (Dieterlen 1971, 1976a; F. Dieterlen unpubl.; SMNS, ZFMK)

Individuals from higher altitudes of Mt Kenya are slightly larger (e.g. mean HB: 85.4; mean T: 102.1)

Key References Bohmann 1942; Dieterlen 1971, 1976a; Musser & Carleton 1993.

Fritz Dieterlen

Dendromus kahuziensis KAHUZI AFRICAN CLIMBING MOUSE

Fr. Souris arboricole du Mont Kahuzi; Ger. Kahusi-Klettermaus

Dendromus kahuziensis Dieterlen, 1969. Z. Säugetierk. 34: 348–349. SSW slopes of Mount Kahuzi, Kivu, DR Congo. 2100 m.

Taxonomy Very distinct species of *Dendromus* with an extremely long tail, broad mid-dorsal stripe and long gracile rostrum. Systematic relationships unknown. Only two specimens known. Synonyms: none. Chromosome number: not known.

Description Small climbing mouse with a wide mid-dorsal stripe and very long tail; a comparatively large species of *Dendromus*. Dorsal pelage dusky dark-brown; hairs greyish-black with medium brown tip. Mid-dorsal blackish stripe from head (at level with the eyes) to base of tail; stripe broad (ca. 8 mm), broader than in other species of *Dendromus*. Flanks paler; hairs with pale brownish tip. Chin, throat and chest white; hairs dark grey at base. Head with pale brown on cheeks and behind ears. Eyes with black rings, which extend anteriorly on to nasal region. Ears with sparse short black and reddish hairs. Forefoot with three long digits; Digit 1 rudimentary, Digit 5 minute. Hindfoot with five digits; Digit 1 short without nail or claw, Digit 5 long and opposable with long claw. Tail very long (ca. 157% of HB), comparatively longer than in other *Dendromus* spp., with short dark bristles, darker above, paler below. Skull with long nasals and rostrum. Nipples: not known.

Geographic Variation None recorded.



Dendromus kahuziensis

Similar Species

- D. insignis*. HB similar; tail shorter (ca. 80 mm and ca. 120% of HB); mid-dorsal stripe broad (ca. 4 mm) from back of head to base of tail.
- D. nyasae* (kivu). HB slightly smaller; tail shorter (84–105 mm ca. 124% of HB); long mid-dorsal stripe (2–3 mm wide) from behind head to base of tail.
- D. mystacalis*. HB smaller; tail shorter (75–97 mm), but relatively long (140–160% of HB); mid-dorsal stripe from shoulders to base of tail.

Distribution Endemic to Africa. Afromontane–Afroalpine BZ. Recorded only from the montane forest on the SSW slopes of Mt Kahuzi, east of L. Kivu, DR Congo.

Habitat The only known habitat is a small deep valley, with a small stream in the bottom, covered with dense montane forest and bamboo *Arundinaria alpina* (Dieterlen 1969a). Other common plants include the trees *Polyscias fulva*, *Symphonia globulifera* and *Neobutonia macrocalyx*, and the ferns *Cyathea manniana* and *Marattia fraxinea*. The only species of *Dendromus* living in montane forest.

Adaptations The structure of the forefoot and hindfoot, and the long tail, suggest that these mice are good climbers, and probably spend most their time above the ground (as do species of *Dendromus* that live in grasslands). The two known specimens were caught in traps on the ground, so it seems that they sometimes descend to the ground, perhaps when foraging.

Foraging and Food One stomach contained homogeneous well-chewed vegetable material, probably composed of seeds and fruits; green vegetation and animal remains were not present.

Conservation IUCN Category: Critically Endangered.

The very small known geographic range, and presumably low population numbers, are cause for concern. Schlitter (1989) classified the species as ‘Rare’.

Measurements

Dendromus kahuziensis

HB: 82, 77 mm, n = 2

T: 132, 120 mm, n = 2

HF: 22, 21 mm, n = 2

E: 15, 14 mm, n = 2

WT: 12, 10 g, n = 2

GLS: 23.7, 23.4 mm, n = 2

GWS: 10.8, 11.0 mm, n = 2

M¹–M³: 3.5, 3.4 mm, n = 2

E DR Congo (Dieterlen 1969, 1976a)

Key References Dieterlen 1969a, 1976a.

Fritz Dieterlen

Dendromus lovati LOVAT’S AFRICAN CLIMBING MOUSE

Fr. Souris arboricole de Lovat (Souris arboricole des plateaux éthiopiens); Ger. Lovats Klettermaus

Dendromus lovati (de Winton, 1900). Proc. Zool. Soc. Lond. 1899: 986. (publ. 1900). Menagesha, Ethiopia. 2800 m.

Taxonomy Originally described in the genus *Dendromys*. A very distinctive species, sometimes placed in a subgenus *Chortomys* by itself. Synonyms: none. Chromosome number: 2n = 44 (Lavrenchenko *et al.* 1997).

Description Distinctive very small dendromurine, with three very obvious stripes over the rump (quite unlike any other species of *Dendromus*). Pelage dense and soft. Dorsal pelage warm greyish-brown, sometimes with a slight russet tinge; hairs dark grey at base, brown or buff at tip; some longer hairs with black tips. Three black longitudinal stripes on back, each widening anteriorly and highlighted by paler sandy edges; middle stripe (ca. 40–50 mm long, 8 mm wide on mid-back, tapering to 0–2 mm at base of tail) extends from neck to rump; two outer stripes (ca. 25–30 mm long, 5–6 mm on mid-back tapering to 0–2 mm at base of tail) extend from chest to rump. Middle stripe may be partially split lengthwise into a double median stripe. Ventral pelage greyish; hairs grey at base, off-white at tip. Head similar in colour to back with small longitudinal black stripe from back of head to between eyes. Ears sparsely furred, sandy, with patch of black hairs on lower part of inner surface and on anterior part of outer surface. Whitish subauricular spot. Fore- and hindfeet sandy-brown. Hindfoot with five digits; Digit 1 short with



Dendromus lovati

nail, Digit 5 with nail-like claw. Tail long (ca. 100% of HB) with short hairs, dark above, paler below; comparatively short for a species of *Dendromus*. Nipples: 2 + 1 = 6.

Geographic Variation None recorded.

Similar Species No other species of *Dendromus* has three longitudinal stripes on the back.

Distribution Endemic to Africa. Afromontane–Afroalpine BZ. Confined to the high plateaux of Ethiopia, from 2500 to 3900 m. Known from only about nine locations (Yalden *et al.* 1976, Yalden & Largen 1992, Sillero-Zubiri *et al.* 1995b).

Habitat Typically found in highland grasslands, but extending into the dry *Heliochrysum* heathland at 3900 m on Tullu Deemtu, Bale (Sillero-Zubiri *et al.* 1995a).

Abundance Uncommon, known only from about 30 specimens (Yalden *et al.* 1976, Yalden & Largen 1992). Recent collecting in Ethiopia (1968–98, $n = \text{ca. } 6300$ rodents) yielded only 23 individuals of this species (Müller 1977, Rupp 1980, Yalden 1988, Sillero-Zubiri *et al.* 1995a, Afework Bekele 1996a, Lavrenchenko *et al.* 1997, Nievergelt *et al.* 1998).

Adaptations Nocturnal and terrestrial. Compared with other *Dendromus*, this short-tailed species appears to have no climbing ability. Several specimens have been caught at night in open grassland, where they moved ‘in short hops’ (collector’s notes: R. E. Cheesman, BMNH). Individuals show no obvious adaptations to living in harsh high-altitude environments, leading Sillero-Zubiri *et al.* (1995a) to speculate that they might hibernate during the dry season (when, under clear skies, it is extremely cold at night). However, captures have been made throughout the year (author’s records, collectors’ notes).

Foraging and Food Unknown, but probably granivorous.

Social and Reproductive Behaviour Little known. Appears solitary, one individual was ‘dug out from nest in tuft of grass’ (collector’s notes: R. E. Drake-Brockman, BMNH)) and another was found in a nest beneath a boulder.

Reproduction and Population Structure A juvenile ♂ trapped in Dec and a parous ♀ in Jan in Bale, and a juvenile caught in Mar (label, BMNH), suggest that reproduction occurs in the dry season.

Predators, Parasites and Diseases No information.

Conservation IUCN Category: Least Concern.

The highland grassland (woina dega) habitat is threatened by continuing modification and destruction by humans and their livestock.

Measurements

Dendromus lovati

HB: 74 (57–95) mm, $n = 21$

T: 73 (57–87) mm, $n = 21$

HF: 18 (17–20) mm, $n = 17$

E: 16 (15–18) mm, $n = 16$

WT: 16.4 (11–23) g, $n = 11$

GLS: 19.4 (18.0–20.2) mm, $n = 6$

GWS: 10.5 (9.8–11.1) mm, $n = 4$

M^1 – M^3 : 3.3 (3.1–3.7) mm, $n = 9$

Ethiopia

Body measurements and weight: D. W. Yalden unpubl., Sillero-Zubiri *et al.* 1995

Skull measurements: D. W. Yalden unpubl.

Key References Müller 1977; Nievergelt *et al.* 1998; Sillero-Zubiri *et al.* 1995a; Yalden *et al.* 1976; Yalden & Largen 1992.

D. W. Yalden

Dendromus melanotis GREY AFRICAN CLIMBING MOUSE

Fr. Souris arboricole gris; Ger. Graue Klettermaus

Dendromus melanotis, Smith 1834. S. Afr. Quart. J. 2: 158. Near ‘Port Natal’ (= Durban), South Africa.

Taxonomy The taxonomic status of this species is uncertain, as manifested by karyotypic variability within the species and by the numerous synonyms currently recognized. The form *leucostomus* (known only from the type locality in Angola) is maintained as a synonym as in Musser & Carleton (1993) but raised to species status by Musser & Carleton (2005), following Hill & Carter (1941). Crawford-Cabral (1998) recorded that the dorsal pelage of *leucostomus* does not have a mid-dorsal stripe (cf. typical *D. melanotis*). Here, pending full taxonomic revision, *leucostomus* is retained as a synonym of *D. melanotis*. Synonyms: *arenarius*, *basuticus*, *capensis*, *chiversi*, *concinus*, *exoneratus*, *insignis* (Shortridge & Carter, 1938, not of Thomas, 1903), *leucostomus*, *nigrifrons*, *pallidus*, *pecilei*, *pretoriae*, *shortridgei*, *spectabilis*, *subtilis*, *thorntoni*, *vulturinus*. Subspecies: none. Chromosome number: $2n = 36$ (Matthey in Robbins & Baker 1978); $2n = 52$ (Dippenaar *et al.* 1983).

Description Very small slender mouse with soft woolly pelage and long slender tail. Dorsal pelage medium brown to rufous-brown, sometimes flecked with ashy-grey; hairs grey on basal two-thirds, pale brown on terminal third, some hairs with black tip. Dark stripe (usually 3–4 mm in width) extends along mid-dorsal line from between shoulders to base of tail. Ventral pelage white to greyish-white; hairs grey at base, off-white to pale grey at tip. Head with pointed muzzle and long vibrissae. Ears small and rounded, dark. Small white patch at base of ears. Limbs short. Forefeet with three long functional digits, Digits 1 and 5 greatly reduced but not absent. Hindfoot with five digits; Digit 1 short with nail, Digit 5 with nail (see also *D. nyikae*). Tail long (ca. 120–130% of HB), brownish above, paler below, sparsely haired. Nipples: 2 + 2 = 8.

Geographic Variation Pelage colour varies slightly throughout range. In the form *nigrifrons* (from e.g. Namibia, Kenya, Zambia), the mid-dorsal stripe extends to the forehead although usually indistinct between the ears and on the neck.

Similar Species

D. mystacalis. Similar in size and proportions; pelage rufous-brown; tail 140–160% of HB.

D. nyikae. Larger, head and body usually well over 70 mm; tail relatively longer (130–160% of HB).

D. mesomelas. On average larger, head and body generally well over 70 mm; tail relatively longer (130–140% of HB).

Distribution Endemic to Africa. Recorded in many biotic zones: Zambezian Woodland BZ, extending marginally into parts of Highveld and South-West Cape BZs of South Africa; Afromontane–Afroalpine BZ of Ethiopia; and (?) Guinea Savanna BZ of West Africa. Ranges widely from S and E South Africa through Botswana, E Namibia (Matson & Blood 1994), Zimbabwe, S Mozambique, Zambia, Malawi and S Angola (Crawford-Cabral 1998). Isolated populations in W Uganda (Wilson 1995), Tanzania and Kenya. Status in Ethiopia uncertain; distribution poorly known, and records may represent *D. mystacalis* (Yalden *et al.* 1976). In West Africa recorded at scattered localities in Nigeria, Benin, Liberia and Guinea (Happold 1987).

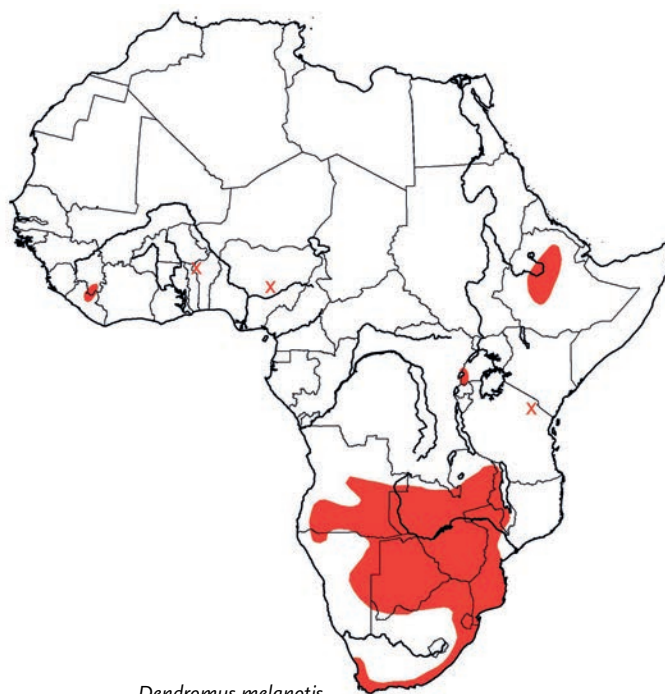
Habitat Inhabits a wide range of habitats. In southern Africa inhabits stands of tall *Hyparrhenia* grassland (Lynch 1994), short montane grassland (Rowe-Rowe & Meester 1982a, Taylor 1998), dry Kalahari scrub, fringes of rivers, dry *Baikiaea* woodland (Smithers 1971) and flood-plains (Sheppe & Haas 1981). May recolonize burnt grasslands within one month of fire (Rowe-Rowe & Meester 1981).

Abundance Relatively common. Third commonest species of small mammal in several different high-altitude grassland habitats in KwaZulu–Natal Province, South Africa (Rowe-Rowe & Meester 1982a). Detailed density estimates not available.

Adaptations Nocturnal. Limbs and tail modified for a semi-arboreal existence. Long, slender digits used to grip and climb thin stalks while long, prehensile tail provides balance. Weaves a grass nest with a single entrance, which is usually attached to grass stems or shrubs up to 1 m above the ground. Nest used only during the breeding season (Smithers 1971). May also use burrows up to 50 cm deep leading to a nest chamber with an emergency exit on the opposite side (De Graaff 1981).

Foraging and Food Predominantly granivorous. Frequency of occurrence of food types ($n = 14$ stomach contents) in sub-alpine grasslands of Drakensburg Mts, South Africa: seeds 100%, arthropods 24% and vegetable material 0% (Rowe-Rowe 1986).

Social and Reproductive Behaviour Poorly known. Thought to be predominantly solitary and territorial (Smithers 1971, Kingdon 1974). Known to fight ferociously with *D. mystacalis* in captivity. Parents reported to remain with offspring for some time after weaning.



Dendromus melanotis

Reproduction and Population Structure Little known. Breeding possibly confined to the wet season in southern Africa. Gravid ♀♀ with 2–8 embryos collected between Nov and Apr (Smithers 1971, Lynch 1994). In South Africa, juveniles captured at the end of the wet season during Apr and May (Rowe-Rowe & Meester 1982b).

Predators, Parasites and Diseases *Dendromus* spp. are difficult to distinguish in raptor pellets (Coetzee 1972), but remains have been found in the pellets of Barn Owls *Tyto alba* (Vernon 1972) and Black-shouldered Kites *Elanus caeruleus* (Mendelsohn 1982).

Conservation IUCN Category: Least Concern.

Measurements

Dendromus melanotis

HB (♂♂): 68 (56–81) mm, $n = 32$

HB (♀♀): 70 (60–86) mm, $n = 17$

T (♂♂): 90 (76–108) mm, $n = 26$

T (♀♀): 83 (71–113) mm, $n = 21$

HF (♂♂): 18 (16–21) mm, $n = 33$

HF (♀♀): 17 (16–20) mm, $n = 18$

E (♂♂): 14 (12–18) mm, $n = 30$

E (♀♀): 16 (13–19) mm, $n = 20$

WT (♂♂): 7.4 (6–10) g, $n = 11$

WT (♀♀): 7.0 (4–12) g, $n = 19$

GLS: 20.1 (19.8–21.0) mm, $n = 17$

GWS: 10.4 (10.0–11.2) mm, $n = 15$

M¹–M³: 3.0 (2.8–3.3) mm, $n = 22$

Body measurements and weights: throughout range (De Graaff 1981)

Skull measurements: Botswana, South Africa (Roberts 1951)

Key References Kingdon 1974; Rowe-Rowe & Meester 1982a.

A. Monadjem

Dendromus mesomelas BRANTS'S AFRICAN CLIMBING MOUSE

Fr. Souris arboricole noisette; Ger. Brants Klettermaus

Dendromus mesomelas (Brants, 1827). Het. Geslacht der Muizen, p. 122. Sunday's River, South Africa.

Taxonomy Originally described in the genus *Dendromys*. The name *mesomelas* refers to the large *Dendromus* of southern and central Africa (Musser & Carleton 1993) in which Digit 5 of the forefoot is absent. Some names formally included in *D. mesomelas* (see Misonne 1974) are now regarded as valid species (i.e. *D. insignis*, *D. nyasae*, *D. oreas* and *D. vernayi*). Synonyms: *ayres*, *major*, *pumilio*, *typicus*, *typus*. Subspecies: none. Chromosome number: not known.

Description Very small slender mouse with soft woolly pelage and very long slender tail. Dorsal pelage rufous-brown; hairs dark grey, rufous-brown to gingery-brown terminally. Dark mid-dorsal stripe of variable intensity from shoulders to base of tail; absent in some individuals. Ventral pelage off-white; hairs dark at base with whitish tip. Head with pointed nose and long vibrissae. Ears small and rounded. Limbs short. Forefeet with three long functional digits, Digit 1 greatly reduced and Digit 5 absent. Hindfoot with five digits; Digit 1 short with nail, Digit 5 long and opposable with claw. Tail very long (ca. 130–140% of HB), brownish above, paler below and sparsely haired. Nipples: 2 + 2 = 8.

Geographic Variation None recorded.

Similar Species

D. mystacalis. Smaller, HB less than 65 mm; ventral pelage white, hairs with white base. Tail 140–160% of HB.

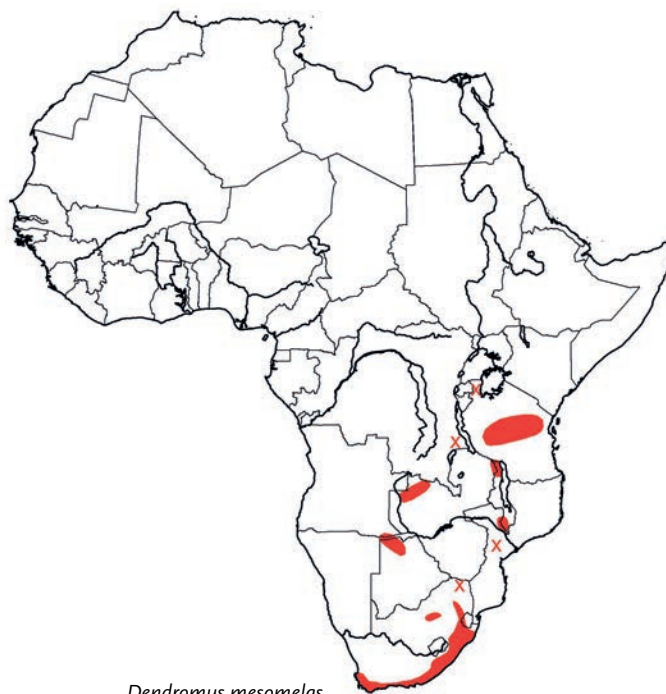
D. nyikae. Dorsal pelage pale to dark cinnamon suffused with grey; ventral pelage white, hairs with white base. Tail long (130–160% of HB).

D. melanotis. Smaller, HB usually less than 70 mm; dorsal pelage ashy-grey; ventral pelage greyish-white. Tail 120–130% of HB.

Distribution Endemic to Africa. Zambezian Woodland BZ, extending to southern part of Somalia–Masai Bushland BZ and to Coastal Forest Mosaic BZ (in South Africa). Distribution disjunct. Recorded in S and E South Africa, W Swaziland, N Botswana, Namibia (Caprivi Strip), Mozambique (Gorongosa Mt) (De Graaff 1981), NE and NW Zambia (Ansell 1978), S and N Malawi (Ansell & Dowsett 1988), SE DR Congo (Musser & Carleton 1993) and C Tanzania (Swynnerton & Hayman 1950).

Habitat Inhabits a wide range of grassland habitats mostly in temperate environments. In southern Africa also inhabits swamps and damp grasslands (Hanney 1965, Taylor 1998) as well as afromontane forest (Rowe-Rowe & Meester 1982, Monadjem 1998a). Prefers wet moist habitats and is absent from hot, low-lying river basins, arid savannas and miombo woodland.

Abundance Relatively common. No density estimates available, but relatively numerous in leaf-litter of afromontane forest in Swaziland (A. Monadjem unpubl.).

*Dendromus mesomelas*

Adaptations Mostly nocturnal, but may also be active during the day. Limbs and tail modified for a semi-arboreal existence. Long, slender digits used to grip and climb thin stalks while long, prehensile tail provides balance. Weaves a grass nest, which may be placed either above or below ground (Kingdon 1974). Also occupies nests of birds, e.g. *Ploceus* spp. (De Graaff 1981). Believed to be more terrestrial than other members of the genus (see also *D. lovati*).

Foraging and Food Predominantly granivorous. Proportional contribution of food types in stomach contents: 12% vegetable material, 87% seeds, 1% arthropods (n = 5, Swaziland; Monadjem 1997b). Elsewhere, in Botswana and South Africa, insects contribute a greater proportion of the diet (Smithers 1971, Rowe-Rowe 1986). Seasonal availability may limit the consumption of insects to the wet season.

Social and Reproductive Behaviour No information.

Reproduction and Population Structure Reproduction possibly confined to the wet season in southern Africa, but gravid ♀♀ have been collected in the dry season in Malawi (Hanney 1965). Embryo number: 2–6 (Hanney 1965, Taylor 1998).

Predators, Parasites and Diseases *Dendromus* spp. are difficult to distinguish in raptor pellets (Coetzee 1972), but remains have been found in the pellets of Barn Owls *Tyto alba* (Vernon 1972) and Black-shouldered Kites *Elanus caeruleus* (Mendelsohn 1982). Ectoparasites include the fleas *Ctenophthalmus verutus*, *C. cophurus*,

Dinopsyllus grypurus and *Nosopsyllus incisus*. May be susceptible to plague (De Graaff 1981).

Conservation IUCN Category: Least Concern.

Measurements

Dendromus mesomelas

HB (♂♂): 76 (69–80) mm, n = 5

HB (♀♀): 74 (67–85) mm, n = 7

T (♂♂): 99 (91–105) mm, n = 4

T (♀♀): 103 (94–109) mm, n = 7

HF (♂♂): 20 (19–21) mm, n = 4

HF (♀♀): 20 (18–22) mm, n = 7

E (♂♂): 18 (15–21) mm, n = 3

E (♀♀): 14 (12–17) mm, n = 7

WT (♂♂): 12.0 (11–13) g, n = 4

WT (♀♀): 10.6 (9–15) g, n = 5

GLS: 22.4 (20.8–24.7) mm, n = 9

GWS: 11.5 (10.7–12.5) mm, n = 9

M¹–M³: 3.3 (3.1–3.5) mm, n = 10

South Africa

Body measurements and weights: De Graaff 1981

Skull measurements: Roberts 1951

Key References De Graaff 1981; Hanney 1965.

A. Monadjem

Dendromus messorius BANANA AFRICAN CLIMBING MOUSE

Fr. Souris arboricole de bananier; Ger. Bananen-Klettermaus

Dendromus messorius (Thomas, 1903). Ann. Mag. Nat. Hist., ser. 7, 12: 340. Efulen, Cameroon.

Taxonomy Originally described in the genus *Dendromys*. Considered to be a synonym or subspecies of *D. mystacalis* (Rosevear 1969, Misonne 1974, Delany 1975 [referring to *ruddi*]) or as a valid species (Hatt 1940a, Verheyen & Verschuren 1966, Dieterlen 1971, Musser & Carleton 1993, 2005). Synonyms: *haymani*, *kumasi*, *ruddi*. Subspecies: none. Chromosome number: not known.

Description Very small slender climbing mouse with long tail and without mid-dorsal stripe. Dorsal pelage gingery-brown; hairs dark grey on basal three-quarters, gingery-brown on terminal one-quarter. Usually without mid-dorsal stripe (cf. some other *Dendromus* spp.); occasionally very faint brownish stripe is visible. Flanks paler than back. Ventral pelage pure white; clearly delineated from colour of flanks. Head similar colour to dorsal pelage. Ears comparatively large covered with short ginger hairs. Upper lips, lower lips, cheeks, throat and chest whitish. Long stiff black vibrissae on muzzle. Fore- and hindlimbs whitish. Forefoot with three functional digits (Digits 2, 3 and 4). Hindfoot with five digits; Digit 1 short with nail (or absent), Digit 5 long and opposable with claw. Tail very long (ca. 140% of HB), dark, with short blackish bristles. Skull: upper incisors opisthodont. Nipples: 2 + 2 = 8.

Geographic Variation Some individuals have a faint brownish stripe (e.g. *kumasi* from Ghana [Rosevear 1969]).

Similar Species

D. mystacalis. Similar size; well-developed dark mid-dorsal stripe; ventral pelage whitish; partially parapatric.

D. mesomelas. Larger; well-developed dark mid-dorsal stripe; ventral pelage off-white, hairs dark at base with whitish tip; partially parapatric.

Distribution Endemic to Africa. Rainforest BZ and Northern and Eastern Rainforest–Savanna Mosaics. Also Afroalpine BZ in Uganda and E DR Congo. Recorded from Ghana, Togo, Benin, E Nigeria (Umuahia only), Cameroon, DR Congo and Uganda. Distribution disjunct. Limits uncertain; may also occur in S



Dendromus messorius

Sudan and W Kenya (Musser & Carleton 2005). Recorded at 2000–3000 m on Mt Elgon (Clausnitzer & Kityo 2001, as *D. mystacalis ruddi*; see Musser & Carleton 2005).

Habitat Preferred habitat is banana plants in farmlands. Also found among sweet potatoes (Hatt 1940a), in holes in trees, in fissures, cracks and trunks of trees in gallery forest, and orange trees (Verheyen & Verschuren 1966). In Cameroon, recorded in long grass (Rosevear 1969).

Abundance May be common in some localities; in Garamba N. P., NE DR Congo, commoner than sympatric *Dendromus mesomelas* and *D. mystacalis* (Verheyen & Verschuren 1966).

Adaptations Nocturnal. At Medje, NE DR Congo, the nest of a ♀ with three young was ‘inserted between the bases of banana leaves, close to the stem, about eight feet from the ground. The nest was hardly visible being well concealed between the large bases of the closely growing banana leaves. Sliced up banana leaves were the only material used outside. On the underside larger pieces were utilised, but inside the leaves were so finely split that the material looked like fine grass’ (H. Lang in Hatt 1940a). This nest was about the size of a man’s fist, roundish in shape, with a single entrance. Two other nests, each occupied by a single ♂, were similar in construction. Nests also built in long grass, and a bush (type specimen) (Cameroon; Rosevear 1969).

Foraging and Food Vegetable material present in two stomachs (Hatt 1940a). Also feeds on fruits of *Sarcocephalus esculentus* (Verheyen & Verschuren 1966).

Social and Reproductive Behaviour Assumed to be solitary. The nests referred to above each occupied by a single adult animal.

Reproduction and Population Structure No information.

Predators, Parasites and Diseases No information.

Conservation IUCN Category: Least Concern. In Uganda, conserved in four National Parks (Mgahinga N. P., Bwindi Impenetrable N. P., Rwenzori N. P. and Semliki N. P. [Wilson 1995]).

Measurements

Dendromus messorius

HB: 63.5 (60–68) mm, n = 13

T: 88.6 (72–95) mm, n = 13

HF: 16.7 (15–19) mm, n = 13

E: 13.2 (11–14) mm, n = 13

WT: 8.8 (7.6–10.5) g, n = 10

GLS: 21.0 (20.2–21.6) mm, n = 7

GWS: 11.1 (10.5–11.6) mm, n = 7

M¹–M³: 3.2 (2.9–3.5) mm, n = 7

Uganda (BMNH)

Key References Hatt 1940a; Rosevear 1969; Verheyen & Verschuren 1966.

D. C. D. Happold

Dendromus mystacalis CHESTNUT AFRICAN CLIMBING MOUSE

Fr. Souris arboricole de Heuglin; Ger. Kastanienbraune Klettermaus

Dendromus mystacalis Heuglin, 1863. Nova Acta Acad. Caes. Leop.-Carol., Halle 30: 2, suppl. 5. Baeschlo region, Ethiopia.

Taxonomy A smaller version of *D. mesomelas* of southern Africa. Probably closely related to *D. mesomelas*, the two species forming a species-pair (Avery 1998; see also Musser & Carleton 2005). Synonyms: *acraeus*, *ansorgei*, *capitis*, *jamesoni*, *nairobae*, *ochropus*, *pallascens*, *pongolensis*, *uthmoelleri*, *whytei*. Subspecies: none. Chromosome number: 2n = 38 (Matthey in Robbins & Baker 1978).

Description Very small slender mouse with soft woolly pelage and very long slender tail. Dorsal pelage bright rufous-brown. Dark stripe on mid-dorsal line from shoulders to base of tail. Ventral pelage whitish, ventral hairs with white base. Head with pointed nose and long vibrissae. Ears small and rounded. Limbs short. Forefeet with three long functional digits, Digit 1 greatly reduced, Digit 5 absent. Hindfoot with five digits; Digit 1 short with nail, Digit 5 long and opposable with claw. Tail very long (ca. 140–160% of HB), brownish above, paler below, sparsely haired. Nipples: 2 + 2 = 8.

Geographic Variation None recorded.

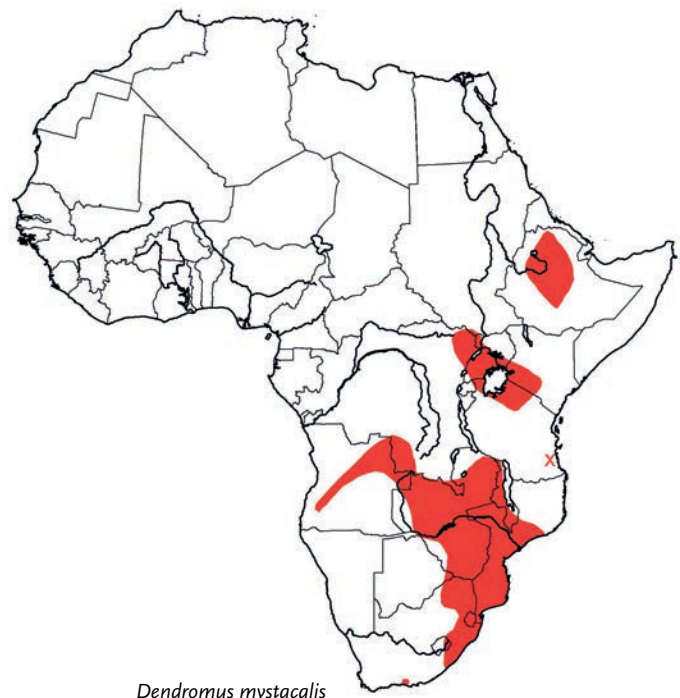
Similar Species

D. melanotis. On average larger; dorsal pelage ashy-grey; tail 140–160% of HB.

D. nyikae. On average larger; dorsal pelage pale to dark cinnamon; tail 130–160% of HB.

D. mesomelas. Larger; black mid-dorsal stripe sometimes absent; ventral hairs with dark base; tail 130–140% of HB.

D. messorius. Dorsal stripe absent. West Africa and central Africa only.



Dendromus mystacalis

Distribution Endemic to Africa. Zambezian Woodland BZ and parts of Eastern Rainforest–Savanna Mosaic and Afromontane–Afroalpine BZ in eastern Africa. Occurs widely from E South Africa northwards through Zimbabwe, Mozambique and Zambia. Ranges westwards in N Botswana and Angola. Isolated populations in E DR

Congo, Uganda, S Sudan, N Tanzania and S Kenya, and Ethiopia (Yalden *et al.* 1976).

Habitat Occupies a wide range of savanna habitats; presence of dense grass cover is essential. In Swaziland, high vegetation density in first 10 cm above ground appears to be a critical habitat feature (Monadjem 1997a). Tall stands of *Hyperthelia-Hyparrhenia* grassland are favoured, but also occurs in rank vegetation fringing wetlands, drainage lines and afro-montane forests. Predominantly a low-altitude species occurring below 2000 m (1200 m in southern Africa) generally preferring drier conditions than *D. nyasae (kivu)* (Dieterlen 1971). In Swaziland, associated with hilly landscapes (Monadjem 1999a).

Abundance Relatively common to abundant. Population densities not easy to determine because individuals do not regularly enter rodent traps. Densities of up to 19.8/ha reported from DR Congo (Misonne 1963) and 2.5/ha from Swaziland (A. Monadjem unpubl.).

Adaptations Nocturnal. Limbs and tail modified for a semi-arboreal existence. Long, slender digits used to grip and climb thin stalks while long, prehensile tail provides balance. Weaves a grass nest with multiple entrances, in which offspring are raised. Adults also use nest for resting. Nest usually located in tall grass about 1 m above ground (Monadjem 1998a) but may also be located higher up in gardens (Kingdon 1974). Known to utilize burrows and disused nests of weaver birds.

Foraging and Food Omnivorous. Diet (assessed by stomach contents): 44% vegetable material, 40% seeds, 16% arthropods (n = 6, Swaziland; Monadjem 1997b). Forages both on the ground and on tall, dense grass.

Social and Reproductive Behaviour In Swaziland, pairs were regularly trapped together in same rodent live-trap, suggesting that individuals often forage in pairs. Known to fight ferociously with *D. melanotis* in captivity.

Reproduction and Population Structure Breeding confined to the wet season with juvenile recruitment mostly Jan–Mar (Zimbabwe; Smithers & Wilson 1979). Embryo number: usually 3–4, but up to eight (Rautenbach 1982). In Swaziland, number of individuals trapped fluctuated seasonally; highest numbers in dry season between Jun–Oct (Monadjem & Perrin 2003). ‘Disappearance’ of these mice in the wet season was attributed to a change in foraging tactics rather than population fluctuations. In southern Africa, most grasses set seed in the late wet season, at which time individuals of this species probably take seeds from the grass stalks, rather than from the ground.

Predators, Parasites and Diseases *Dendromus* spp. are difficult to distinguish in raptor pellets (Coetzee 1972), but remains have been found in the pellets of Barn Owls *Tyto alba* (Vernon 1972) and Black-shouldered Kites *Elanus caeruleus* (Mendelsohn 1982).

Conservation IUCN Category: Least Concern.

Measurements

Dendromus mystacalis

HB (♂ ♂): 60.2 (55–65) mm, n = 6

HB (♀ ♀): 54.7 (47–62) mm, n = 3

T (♂ ♂): 84.8 (75–95) mm, n = 6

T (♀ ♀): 90.3 (82–97) mm, n = 3

HF (♂ ♂): 16.8 (15.9–17.6) mm, n = 6

HF (♀ ♀): 17.4 (16.4–19.5) mm, n = 3

E: 9.3 (7–12) mm, n = 3

WT (♂ ♂): 7.2 (5–10) g, n = 6

WT (♀ ♀): 8.7 (6–11) g, n = 3

GLS: 20.2 (18.7–21.6) mm, n = 16

GWS: 10.3 (9.4–10.8) mm, n = 16

M¹–M³: 3.1 (2.8–3.4) mm, n = 16

Body measurements and weights: Swaziland (Monadjem 1998a)

Skull measurements: South Africa (Roberts 1951)

Key References Dieterlen 1971; Monadjem & Perrin 2003.

A. Monadjem

Dendromus nyasae (kivu) KIVU AFRICAN CLIMBING MOUSE

Fr. Souris arboricole du Kivu.; Ger. Kivu-Klettermaus

Dendromus nyasae Thomas, 1916. Ann. Mag. Nat. Hist., ser. 8, 18: 241. Nyika Plateau, Malawi.

Dendromus kivu Thomas, 1916. Ann. Mag. Nat. Hist., ser. 8, 18: 242. Buhamba, Kivu region, DR Congo.

Taxonomy Thomas (1916b) described *kivu* as a subspecies of *D. insignis* and hence a member of the *mesomelas* species group, where it was also placed by Bohmann (1942). Musser & Carleton (1993) considered *kivu* to be a distinct species, morphologically similar to *D. mesomelas*. Referring to Osgood's (1936) two samples of *Dendromus* from Rwenzori, Musser & Carleton (1993) identified them as *D. lunaris* and *D. insignis*. *Dendromus lunaris* was found to be identical with (the pre-dated) *D. kivu*. The same sympatric combination – *D. kivu* and *D. insignis* – were found in two other series from the Kivu region. Dieterlen (1971, 1976a) recorded three species living sympatrically

in the region west of L. Kivu, and named them as *D. mesomelas kivu* (now *D. insignis*), *D. melanotis* (now *D. kivu*) and *D. mystacalis*. Musser & Carleton (2005) included *kivu* as a synonym of *nyasae*. This profile refers to what the present author considers as *D. kivu* from the Kivu region. The relationship between *kivu* and *nyasae* requires further investigation. Morphologically, *D. nyasae* seems to be most closely related to *D. vernayi* from Angola, *D. oreas* from the mountains of E Cameroon, and *D. insignis* from the mountains of East Africa (Musser & Carleton 2005). Synonyms: *hintoni*, *kivu*, *lunaris*. Subspecies: none. Chromosome number: not known.

Description Small climbing mouse (although one of the largest species of *Dendromus*) with a long mid-dorsal stripe and a long tail. Pelage colouration varies with age (see below). Adult dorsal pelage typically rich brown, tending to be darker on anterior part of body; hairs ash-grey at base, brown at tips. Pelage may appear greyish-brown when basal hair colour visible on surface. Dorsal stripe black, 2–3 mm wide from ca. 2 cm behind head to base of tail. Flanks yellowish-brown. Ventral pelage silvery-white; hairs grey at base, silvery-white at tip. Chin and throat with pure white patches. Eyes relatively large. Hindfoot with short hair, silver-grey, rarely with reddish tinge. Hindfoot with five digits; Digit 1 short, Digit 5 long and opposable with short claw. Tail very long (ca. 124% of HB), colour and hairiness very variable. Ventral pelage in young and subadults (when several weeks or months in age) may be whitish or greyish. Nipples: 2 + 2 = 8.

Geographic Variation None recorded.

Similar Species

- D. insignis*. HB on average slightly larger; tail slightly longer (mean 97 mm) but of similar relative length; mid-dorsal stripe broader (ca. 4 mm) from back of head to base of tail.
- D. mystacalis*. HB smaller; tail on average shorter (mean 84.8, 90.4 mm) but relatively longer (ca. 140–160% of HB); mid-dorsal stripe from shoulders to base of tail.

Distribution Endemic to Africa. Afromontane–Afroalpine BZ. Recorded from the western and eastern slopes of the Rwenzori Mts and the Kivu region of E DR Congo, from 1300–4200 m (see below). May be considered as an ‘Albertine Rift Valley’ endemic. Other East African montane forms, similar or identical to *D. kivu*, are known from Tanzania, Rwanda, Kenya, but their taxonomic status is uncertain. Musser & Carleton (2005) give the distribution (as *D. nyasae*) as follows: Western Rift Mts and Rwenzori Mts (E DR Congo, W Uganda), south

through E DR Congo to the Marungu Mts in SE DR Congo, Mbizi Mts in W Tanzania, Rungwe and Ukinga in SW Tanzania, Nyika Plateau in NE Zambia and N Malawi, and highlands in S Malawi; also through the Eastern Arc Mts in E Tanzania (Uzungwa Mts, Uluguru highlands, Ukaguru Mts, Nguru Mts and South Pare Mts).

Habitat Occurs over a wide range of habitats along the Albertine Rift Valley, and at altitudes of 1300–4200 m on the Rwenzori Mts (Verschuren *et al.* 1983) and 1600–2400 m to the west of L. Kivu (Dieterlen 1971, 1976a). All habitats are characterized by moist dense vegetation suitable for climbing. Favoured moist habitats at lower altitudes include grassy vegetation between cultivated fields, banana plantations and the edges of swamps. Above 2000 m occurs in sparse tree and/or bamboo forests and on the edges of swamps. At 4200 m (L. Marion, Rwenzori Mts), found in the afroalpine vegetation between immortelles (strawflowers) and alchemillas (Dieterlen 1976a, Verschuren *et al.* 1983).

Abundance In favoured habitats, e.g. at the edge of grassy thickets, populations may be abundant and comprise up to 10% of individuals in a community of 10–15 small mammal species (Dieterlen 1967a, b, 1971).

Adaptations Mostly nocturnal and arboreal. Agile climbers well adapted for life on stems and twigs. The large opposable Digit 5 of the hindfeet and the long semi-prehensile tail are used for holding onto small narrow stems. Ball-shaped nests, made of grass and leaves, are fastened between stalks and twigs some 30–80 cm above the ground (Dieterlen 1971).

Foraging and Food Omnivorous or insectivorous. Five stomachs contained a mixture of seeds and the remains of insects, and two other stomachs contained only insects (Dieterlen 1971, 1976a).

Social and Reproductive Behaviour No information, but it is presumed that individuals are mostly or entirely solitary.

Reproduction and Population Structure Near L. Kivu, reproduction occurs throughout most of the year. Most births have been recorded during the wet season (Sep–May) with a peak of reproductive activity in Jan–Mar (73% of the ♀♀ active, $n = 15$). In the dry season, only one (11%) out of nine ♀♀ was reproductively active (Dieterlen 1971). Gestation: probably 23–27 days. Mean litter-size: 4. Young are altricial at birth, unable to crawl, and the eyes and ears are closed. First hairs visible and dorsal stripe showing as pigmented skin Day 11. Incisors erupt Day 11. Molar teeth erupt Day 15–20. Eyes open, walking and climbing begins Day 22–24. Dark juvenile pelage complete (young much darker than adults) Day 24. Weaning begins Day 24. Young totally weaned and appearance like small adults (although HB not yet adult size) Day 35. Sex ratio: 69% : 31% (ca. 7 : 3; $n = 83$; Dieterlen 1967a, b, 1971; see also *D. insignis*).

Predators, Parasites and Diseases Small carnivores, birds and snakes are potential predators. The small intestine of one adult contained many parasitic worms, some 50 mm long.

Conservation IUCN Category: Least Concern.



Dendromus nyasae

Measurements

Dendromus nyasae (kivu)

HB: 73.8 (64–80) mm, n = 40

T: 91.8 (84–105) mm, n = 38

HF: 18.9 (17.0–21.5) mm, n = 40

E: 13.6 (11.0–15.5) mm, n = 40

WT: 10.5 (6.0–20.0) g, n = 40

GLS: 22.2 (20.7–23.2) mm, n = 32

GWS: 10.9 (10.1–11.5) mm, n = 16

M¹–M³: 3.4 (3.1–3.6) mm, n = 28

Lwiro and Kahuzi region, DR Congo (SMNS, Dieterlen 1971, 1976, F. Dieterlen unpubl.)

Key References Bohmann 1942; Dieterlen 1971, 1976a; Musser & Carleton 1993; Osgood 1936.

Fritz Dieterlen

Dendromus nyikae NYIKA AFRICAN CLIMBING MOUSE

Fr. Souris arboricole de Nyika; Ger. Nyika-Klettermaus

Dendromus nyikae Wroughton, 1909. Ann. Mag. Nat. Hist., ser. 8, 3: 248. Nyika Plateau, Malawi.

Taxonomy Closely related to *D. melanotis*. Sometimes placed (with *D. melanotis*) in the subgenus *Poemys*, which is characterized by the flattened nail on the Digit 5 of hindfoot (Crawford-Cabral 1998). *Dendromus nyikae angolensis* is considered to be a synonym of *D. pecilei* in Angola by Crawford-Cabral (1998) but *pecilei* is treated as a synonym of *D. melanotis* by Musser & Carleton (2005). Synonyms: *angolensis*, *bernardi*, *longicaudatus*. Subspecies: none. Chromosome number: not known.

Description A very small climbing mouse with a mid-dorsal thin black stripe, and very long tail. Dorsal pelage pale to dark cinnamon suffused with grey. Dorsal hairs short (6–7 mm), soft and dense; grey at base, cinnamon at tip. Black mid-dorsal stripe from shoulders to base of tail, sometimes rather inconspicuous and irregular; hairs of stripe grey with dark cinnamon or black tip. Ventral pelage usually pure creamy-white; hairs in some individuals medium grey at base, with small white tip. Throat and chest yellow or rufous in some individuals (?♂♂; ?glandular secretions). Head cinnamon, without black patch on crown. Small white subauricular patch. Ears rounded, conspicuous (standing out from side of head), brown with short brown hairs. Hindfoot with five digits; Digit 1 short with nail, Digit 5 very long and opposable with nail (see also *D. melanotis*). Tail long (ca. 130–160% HB), scaly with small pale bristles; longer hairs at tip. Nipples: not known.

Geographic Variation None recorded.

Similar Species

D. melanotis. Similar in size; well-defined wide dorsal stripe; flat nail on Digit 5 of hindfoot.

D. mystacalis. On average smaller; black dorsal stripe; ventral pelage pure white; small claw on Digit 5 of hindfoot.

D. mesomelas. On average larger HB, T and HF; dorsal stripe dark but variable; small claw on Digit 5 of hindfoot.

Distribution Endemic to Africa. Zambezian Woodland and Afromontane–Afroalpine BZs. Recorded from Angola, S DR Congo, Zambia, Zimbabwe, Malawi, SW Tanzania, Mozambique and N South Africa. A specimen of *D. melanotis nyikae* from Ukerewe I. in L. Victoria is, in fact, *D. mystacalis* (Musser & Carleton 2005).



Dendromus nyikae

Habitat Long grass in grassland savannas and plateaux, mostly at higher altitudes. May occur in grassland habitats within pine plantations. On Nyika Plateau, Malawi, some individuals found in unoccupied standard beehives (specimens; HZM). Does not enter forested habitats except very rarely.

Abundance Rather uncommon, although may be locally abundant. In Malawi, 'widespread but probably limited to upland areas' (Ansell & Dowsett 1988). Comprised 9.2% of grassland small rodents during a mark-capture study (n = 215) on Zomba Plateau, Malawi (1800 m) (Happold & Happold 1989c), but not present in tall *Hyparrhenia* and *Panicum* grasslands in Liwonde N. P., Malawi (500 m) (Happold & Happold 1990). In Malawi, numbers were highest where the montane grasslands were tall (i.e. 40–80 cm, depending on time of year and location), and lowest (or absent) where grasslands were short and after burning (Happold & Happold 1989c).

Adaptations Nyika Climbing Mice are adapted for climbing on thin tall grass stems. Their small size and grasping feet allow them to climb up and down grass stems from the flowerheads to ground level. When climbing, the hindfeet are held almost at right angles to the body. A grass stem is grasped by the forefeet as would a human hand, and the flexible Digits 1 and 5 of the hindfeet encircle the stem. The tail is stretched out from the rump at various angles to provide balance, or the tip is wound several times around a stem to provide an extra holding point. Locomotion is by swiftly climbing up and down stems, and reaching across gaps (equivalent to at least the length of head and body) to adjacent stems (D. C. D. Happold unpubl.). The burrow is a simple tunnel in the soil with a nest chamber lined with dead leaves (Hanney 1965).

Foraging and Food Seed-heads of grasses are obtained by climbing to the top of a stem, biting through part of the stem below the seed-head so that the head falls over but is still attached, and then nibbling at the seeds (D. C. D. Happold pers. obs.). Analysis of stomach contents (n = 6) revealed five with white vegetable material, one with grain husks and three with insects, including beetles (Hanney 1965).

Social and Reproductive Behaviour No information. Nyika Climbing Mice make a high-pitched squeal when disturbed.

Reproduction and Population Structure Pregnant ♀ in Nov (Malawi; Hanney 1965); lactating ♀ in Aug (S Tanzania; Kingdon 1974). Embryos: 4 (n = 1, Hanney 1965).

Predators, Parasites and Diseases Comprised 6% (n = 100 prey) and 30% (n = 46 prey) of prey numbers in the pellets of African Grass-owls *Tyto capensis* on Zomba Plateau, Malawi. When foraging on the tops of grass stems, they are probably easy prey for owls. Because of their small size, climbing mice comprised only 1% and 6% of prey biomass (Happold & Happold 1986).

Conservation IUCN Category: Least Concern.

Measurements

Dendromus nyikae

HB: 66.8 (50–78) mm, n = 24

T: 86.4 (80–93) mm, n = 21

HF: 16.7 (11–19) mm, n = 24

E: 14 (11–18) mm, n = 21

WT: 10.5 (11–18) g, n = 15

GLS: 21.8 (20.3–24.4) mm, n = 14

GWS: 11.1 (10.0–11.7) mm, n = 8

M¹–M³: 3.5 (3.2–3.6) mm, n = 8

Malawi (BMNH; D. C. D. Happold unpubl.)

Key References Hanney 1965; Happold & Happold 1986.

D. C. D. Happold

Dendromus oreas CAMEROON AFRICAN CLIMBING MOUSE

Fr. Souris arboricole du Cameroon; Ger. Kamerun-Klettermaus

Dendromus oreas Osgood, 1936. Field Mus. Nat. Hist., Zool. Ser. 20: 236.

South-west side of Mount Cameroon, Nigeria (now in Cameroon). 9000 ft (2740 m).

Taxonomy Described as a distinct species, but subsequently considered to be a synonym of *D. mesomelas* (Bohmann 1942, Rosevear 1969, Misonne 1974). Referred to as *D. mesomelas oreas* by Rosevear (1969). Musser & Carleton (1993, 2005) reinstated *oreas* as a valid species, and considered it to be related to *Dendromus lunaris* (now *D. nysae [kivu]*), and not to be a geographic outlier of *D. insignis*. Synonyms: none. Chromosome number: not known.

Description Very small climbing mouse with an indistinct mid-dorsal stripe and long tail. Dorsal pelage medium brown. Black mid-dorsal stripe from mid-back to base of tail, often rather indistinct. Ventral pelage varied, from dark rufous to pale greyish-yellow; hairs dark at base. White or cream patches on chin and throat, and around anus. Ears blackish-brown, with fine covering of blackish-tawny hairs; pale spot at base of outer margin of each ear, sometimes indistinct. Hindfoot with five digits; Digit 5 long and opposable with claw. Tail very long (ca. 135% of HB), dusky above, paler below. Nipples: not known.

Geographic Variation None recorded.

Similar Species

D. messorius. On average smaller; mid-dorsal stripe absent; usually occurs at lower altitudes; recorded from Cameroon (and many other countries) but not from mountainous habitats (see below).

Distribution Endemic to Africa. Afromontane–Afroalpine BZ; known only from Mt Cameroon (1700–4000 m), Mt Manenguba (1800–1900 m, ca. 120 km NE of Mt Cameroon) and Mt Kupé (ca. 80 km NE of Mt Cameroon, 850 m) in Cameroon (Eisentraut 1963, Rosevear 1969). Probably endemic to the mountains of W Cameroon. This is the only known species of *Dendromus* on the mountains of Cameroon.

Habitat Montane savannas above the montane forest zone, from ca. 1675 m to ca. 2900 m, on the ground amongst boulders of lava (Mt Cameroon). Also recorded on dry grassy and scrubby slopes (Mt Manenguba), and in plantations and farmlands (Mt Kupé). Has not been recorded in montane forest habitats at lower altitudes on these mountains.

Adaptations Mostly terrestrial, diurnal and nocturnal. Although well adapted for climbing, these mice spend most of their life on the ground and in their subterranean burrows.

Reproduction One ♀ with five embryos in late Nov (Eisentraut 1963).

Conservation IUCN Category: Vulnerable.

Geographic range is very limited and populations on each of the mountains are isolated.

Measurements

Dendromus oreas

HB: 69.3 (60–74) mm, n = 6

T: 95.3 (89–104) mm, n = 7

HF: 19.0 (18–20.5) mm, n = 7

E: 15.3 mm (13–19) mm, n = 6

WT: 11.1 (9–13) g, n = 5

GLS: 22.0 (21.6–22.5) mm, n = 4

GWS: 11.0 (10.9–11.3) mm, n = 4

M¹–M³: 3.5 (3.3–3.7) mm, n = 7

Cameroon (Osgood 1936, Eisentraut 1963, Rosevear 1969, F. Dieterlen unpubl.)



Dendromus oreas

Key References Eisentraut 1963; Rosevear 1969.

Fritz Dieterlen

Dendromus vernayi VERNAY'S AFRICAN CLIMBING MOUSE

Fr. Souris arboricole de Vernay; Ger. Vernays Klettermaus

Dendromus vernayi Hill and Carter, 1937. Amer. Mus. Novit. 913: 4. Chitau, Angola. 4930 ft (1500 m).

Taxonomy Described as a subspecies of *Dendromus mesomelas* (see also Misonne 1974). *Dendromus vernayi* is morphologically distinct from *D. nyasae* and *D. oreas*, and is probably phylogenetically more closely related to these species than to any other species of *Dendromus* (Musser & Carleton 2005). Synonyms: none. Chromosome number: not known.

Description Very small climbing mouse with dark mid-dorsal stripe. Pelage relatively long and silky. Dorsal pelage ochraceous and cinnamon-brown; hairs dark grey at base. Mid-dorsal stripe wide (ca. 4.5 mm). Ventral pelage varied, bright pinkish-buff or buffy-grey; hairs medium grey at base. Pure white patch on throat and in axillary region. Ears blackish on outer surface, short orange hairs on inner surface. Upper surface of fore- and hindfeet pinkish-buff. Hindfoot relatively long (>19 mm). (No information on digits of fore- and hindfoot.) Tail very long (ca. 130% of HB), dark above, paler below. Skull: rostrum heavier and shorter than in other species of *Dendromus*. Nipples: not known.

Geographic Variation None recorded.

Similar Species

D. melanotis. Body size slightly larger (mean HB: 68 mm); skull (GLS, GWS) slightly smaller; tail usually longer; hindfoot shorter (usually <19 mm); ventral pelage white to greyish-white; widespread distribution; probably sympatric.

D. mystacalis. Similar body size (although mean HB slightly smaller); ventral pelage white; tail usually longer (and relatively longer, 140–160% of HB); hindfoot on average shorter (usually <19 mm); ear smaller (mean 9.3 mm); M¹–M³ shorter; widespread distribution; probably sympatric.

D. nyikae. Body size on average slightly larger, but with shorter HF (mean 16.7 mm); ventral pelage creamy-white; tail on average longer and relatively longer (up to 160% of HB); widespread distribution; probably sympatric.

Distribution Endemic to Africa. Zambezan Woodland BZ. Known only from the type locality near Chitau (1500 m) in C Angola (Hill & Carter 1937, 1941, Crawford-Cabral 1998).

Habitat Not known.

Abundance Very rare. Known only from 14 specimens from the type locality.

Remarks No other ecological or biological information available. Three other species of *Dendromus* (*D. melanotis*, *D. mystacalis* and *D. nyikae*) also occur in C Angola.

Conservation IUCN Category: Data Deficient.

The geographic range is very small, and all known individuals are from a single population.

Measurements

Dendromus vernayi

HB: 63.6 (60–66) mm, n = 5

T: 82.0 (80–84) mm, n = 5

HF: 20.2 (19–22) mm, n = 5

E: 13.7 mm (13–14) mm, n = 3

WT: n. d.

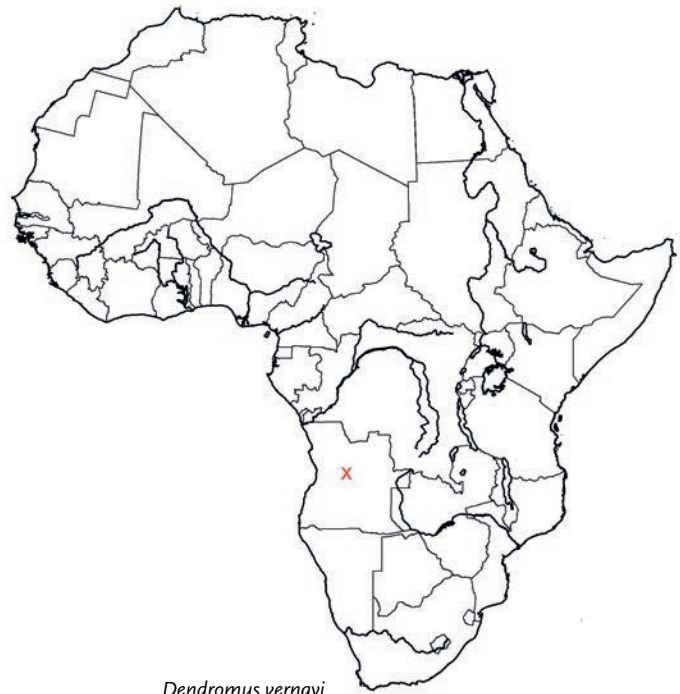
GLS: 21.4, 22.1 mm, n = 2

GWS: 11.2 (10.7–11.8) mm, n = 3

M¹–M³: 3.5 (3.4–3.7) mm, n = 4

Angola (Hill & Carter 1941, AMNH, F. Dieterlen unpubl.)

Key References Hill & Carter 1937, 1941; Musser & Carleton 2005.



Dendromus vernayi

Fritz Dieterlen

GENUS *Dendroprionomys* Velvet Climbing Mouse

Dendroprionomys F. Petter, 1966. Mammalia 30: 129. Type species: *Dendroprionomys rousseloti* F. Petter, 1966.

Dendroprionomys is a monotypic genus described in 1966 (Petter 1966b), and known only from Congo. The genus possesses a mixture of characters typical of the genera *Dendromus* and *Prionomys* (hence the name). The distinguishing characters of the genus are very small size, long tail relative to HB, feet modified for climbing, elongated Digit 1 of hindfoot (as in *Prionomys*) and opposable Digit 5 of hindfoot (as in *Dendromus*) (Figure 30). Skull characters include: upper incisors orthodont or slightly opisthodont, each with a longitudinal groove (as in *Dendromus*); elongated frontal-nasal region (cf. *Dendromus* and *Prionomys*); box-shaped braincase (as in *Prionomys*); crescent-shaped edges of inter-orbital constriction (as in *Prionomys*); anterior palatal foramina very short ending posteriorly at level of infraorbital foramen and far anterior to M¹ (as in *Prionomys*); and molar teeth



Dendroprionomys rousseloti.

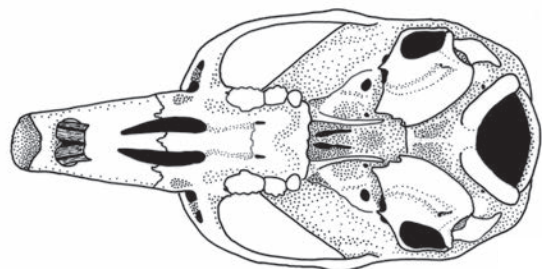
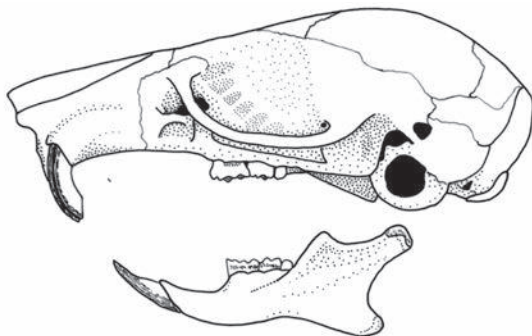


Figure 31. Skull and mandible of *Dendroprionomys rousseloti* (MNHN 1967/1368, with additional information from Petter 1966b).

with tall pointed cusps, two rows on upper molars and one row on lower molars (similar to *Prionomys* but much more developed) (Figure 31). The single species is *Dendroprionomys rousseloti*.

D. C. D. Happold

Dendroprionomys rousseloti VELVET CLIMBING MOUSE (CONGO TREE MOUSE)

Fr. Souris arboricole de Brazzaville; Ger. Samt-Klettermaus

Dendroprionomys rousseloti Petter, 1966. Mammalia 30: 129. Brazzaville, Congo.

Taxonomy The single species in the genus was described by Petter (1966b) on the basis of three specimens. Initially placed in the Dendromuridae (Chaline *et al.* 1977), the species is now placed in Nesomyidae (subfamily Dendromurinae) (Musser & Carleton 2005). Phylogenetic analysis of its dental pattern suggested that *Dendroprionomys* is closely related to *Prionomys* (Denys *et al.* 1995). Synonyms: none. Chromosome number: not known.

Description Very small mouse with very long tail (similar to *Dendromus* spp.). Pelage dense, short and soft, rather fluffy. Dorsal pelage medium-brown, tinged with russet especially on flanks; hairs grey at base with brown tips. Ventral pelage greyish-white; hairs grey on basal half, white on terminal half. Head similar in colour to dorsal pelage, with conspicuous brownish-black stripe from muzzle to (and around) eyes. Lips, chin and throat white. Long well-developed vibrissae. Ears long, darkly pigmented, seemingly naked but sparsely covered with extremely short dark hairs. Limbs short, white. Forefeet with four digits: Digit 1 absent, Digits 2, 3 and 4 long with short claws, Digit 5 short with (or without) very small claw. Hindfeet with five digits: Digit 1 short and stumpy with very small claw; Digits 2, 3, 4 and 5 long with claws; Digit 5 opposable (Figure 30). Tail very long and thin (ca. 140% of HB), brown, with scales arranged in rings, very short black bristles. Skull with globular-shaped braincase and narrow rostrum region, upper incisor teeth orthodont or slightly opisthodont, each with single groove; anterior palatal foramina not reaching level of M¹; small molar teeth with tall pointed cusps not linked in transverse chevrons but linked by longitudinal stephanodont crests. See also genus profile. Nipples: not known.

Geographic Variation None recorded.

Similar Species

Prionomys batesi. Pro-odont incisors without longitudinal groove; small ears; complete open longitudinal groove on upper molars; small Digit 5 of the hindfoot not opposable; Cameroon and Central African Republic.

Dendromus spp. Mid-dorsal stripe (in most species); Digit 1 on hindfoot very short; Digit 5 long and opposable.

Distribution Endemic to Africa. Rainforest BZ. Recorded only from the type locality in the Zoological Gardens at Brazzaville, SE Congo.

Habitat The Zoological Garden at Brazzaville is situated on a sand forest.



Dendroprionomys rousseloti

Abundance Extremely rare. Known from only eight specimens from the same locality, seven collected in 1948 and one in 1966.

Remarks The characters of the feet suggest an ability to climb on stems of grasses and herbs, and the long tail suggests that (like *Dendromus* spp.) it may be prehensile. The structure of the molar teeth suggest a partly insectivorous diet. The two lines of tall cusps on the lower molars fit into the grooves between the two lines of tall cusps on the upper molars (Petter 1966b), but to a lesser extent than in *Prionomys*.

Conservation IUCN Category: Data Deficient. Considered as 'Rare' by Schlitter (1989).

The very small geographic range and presumed rarity are cause for concern.

Measurements

Dendroprionomys rousseloti

HB: 77 mm, n = 1

T: 108 mm, n = 1

HF: 18 mm, n = 1

E: 16 mm, n = 1

WT: n. d.

GLS: 22.6–24.6 mm, n = 3*

GWS: 11.8 (11.5–12) mm, n = 3

M¹–M³: 3.36 (3.3–3.4) mm, n = 3

Brazzaville, Congo (MNHN, Petter 1966b)

*Mean not given

Key References Denys *et al.* 1995; Petter 1966b.

Christiane Denys

GENUS *Malacothrix*

Long-eared Mouse

Malacothrix Wagner, 1843. In: Schreber, Die Säugethiere, Suppl. 3: 496. Type species: *Otomys typicus* A. Smith, 1834.:



Malacothrix typica.

A monotypic genus occurring only in semi-arid habitats of southern Africa. Morphologically very distinctive compared with species of *Dendromus*, *Megadendromus* and *Steatomys* (Denys *et al.* 1995). The cheekteeth are small and delicate, similar to those of *Dendromus* and *Steatomys* spp., and extend far forward in the skull. Compared with these two genera, the palate is particularly broad (especially at the anterior end because the distance M¹–M¹ is greater than M³–M³), the comparatively robust zygomatic arches flair outwards to a greater extent, the rostrum is long and narrow, and the interorbital constriction is narrow (Figure 32). The single species is *Malacothrix typica*.

D. C. D. Happold

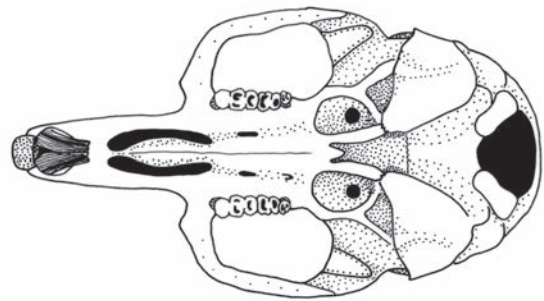
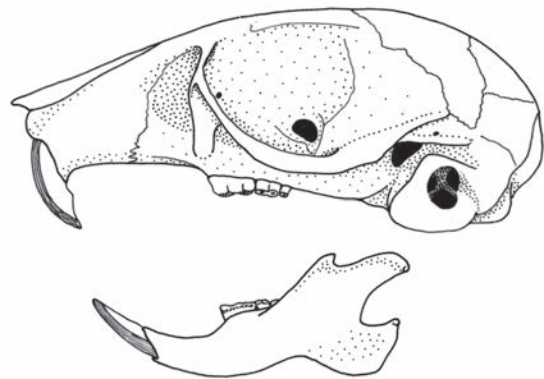


Figure 32. Skull and mandible of *Malacothrix typica* (BM 68.52). Details of the anterior cusps of upper M₁ are obscure in this specimen.

Malacothrix typica LONG-EARED MOUSE

Fr. Souris à grandes oreilles; Ger. Großohrmaus

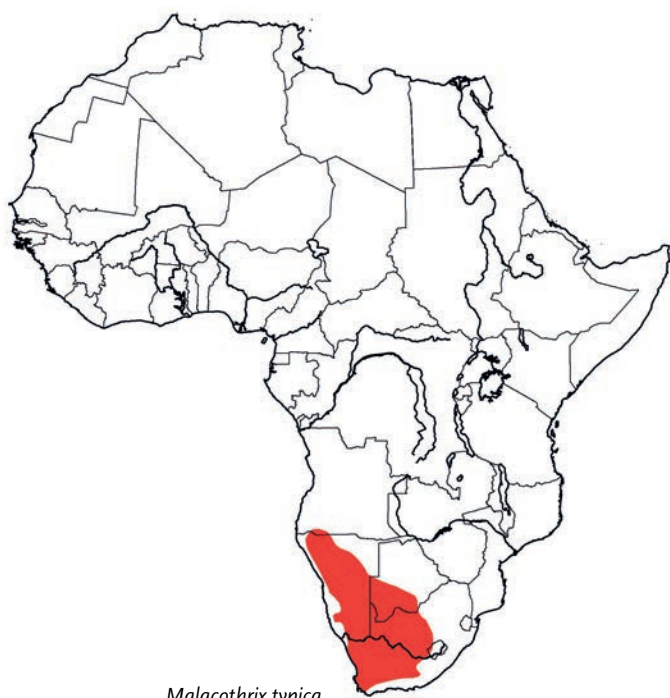
Malacothrix typica (A. Smith, 1834). S. Afr. Quart. J. 2: 148. Graaff Reinet District, Eastern Cape Province, South Africa.

Taxonomy Originally described in the genus *Otomys*. Synonyms: *damarensis*, *egeria*, *fryi*, *harveyi*, *kalaharicus*, *molopensis*. Subspecies: six have been described but they are of doubtful validity (Meester *et al.* 1986) and are not recognized here. Chromosome number: 2n = 38 (W. R. Harrison pers. comm.).

Description Very small mouse with large ears and short tail. Pelage soft and long (up to 8 mm). Dorsal pelage brindled creamy-grey, greyish-brown to reddish-buff; hairs dark grey at base with creamy-grey subterminal band and black tip. Black-tipped hairs result in darker patches and streaks on back to base of tail (very prominent), and on each rump. Flanks paler with fewer black-

tipped hairs. Ventral pelage pale grey to white. Head with large eyes. Ears very large, rounded at tip, naked and darkly pigmented; small patch of short creamy-yellow hairs at base of each ear. Lips and chin whitish. Limbs short and delicate. Forefoot with four digits. Hindfoot with four functional digits (Digits 2, 3, 4 and 5) (cf. *Dendromus* spp.). Tail short (ca. 45% of HB) and naked. Skull delicate; each upper incisor with groove on anterior face; M¹ relatively large (cf. M² and M³), wide palate and large curving zygomatic arches (see also profile Genus *Malacothrix*). Nipples: 2 + 2 = 8.

Geographic Variation Colour of pelage varies throughout range: dorsal pelage reddish-brown well streaked with black in



southern part of range in South Africa, pale buffy-brown in west in Namibia, and buffy-grey to reddish-buff in Botswana. Hairs of ventral pelage grey at base in eastern part of range, and pure white in the west (Smithers 1983).

Similar Species

Dendromys spp. Ears smaller; tail relatively longer (always longer than HB); dark mid-dorsal line, and without dark patches on back and rump; long prehensile tail; modified hindfoot with five digits (for climbing grass stems).

Steatomys spp. No mid-dorsal stripe or patches; hindfoot with five digits; ears shorter; body very fat at some times of year due to fat deposits under the skin and around other tissues.

Distribution Endemic to Africa. South-West Arid BZ and adjacent grasslands. Recorded from most of South Africa (except KwaZulu–Natal), Namibia, S Botswana and extreme SW Angola (De Graaff 1981).

Habitat Semi-arid grass savanna and succulent scrublands especially where substrate is hard and covered with pebbles, and where annual rainfall is 70–550 mm. In Botswana, and the Karoo of South Africa, lives near pans where there is a cover of karoo bushes. In the Kalahari Gemsbok N. P., lives on the flats and slopes of dry river banks, and on raised plateaux in the river bed but not on the duneveld nor in *Acacia* savanna (Nel & Rautenbach 1975). In the Karoo, also lives on rocky plains (J. Nel pers. comm.).

Abundance Uncommon or rare. Distribution records are scattered, and individuals are rarely caught in conventional traps but may be seen in the light of a spotlight. In the Kalahari Gemsbok N. P., where *Gerbillurus paeba* was the commonest small mammal (62% of captures), they formed only 0.35% of trappable small rodents (total $n = 1143$) (Nel & Rautenbach 1975).

Adaptations Terrestrial and nocturnal. The method of constructing a burrow is unusual: a burrow, 20–25 mm in diameter, is excavated deep into the soil. A nest chamber is built at the end of this burrow and the soil is pushed backwards to block the entrance. A new burrow is then excavated vertically to the surface ending in a tiny entrance hole. The soil from this new burrow is pushed back into the original burrow, which is now completely blocked. Nest chamber is lined with grass, and sometimes with feathers. In captivity, highest rate of activity is 19:00h to 04:00h. Well adapted for arid conditions: Tb is maintained at 37 °C even at low Ta, metabolic rate is low and 42% below predicted value, and conductance is low. When threatened, remains motionless (rather than running away); the blackish patches on the greyish-brown background probably provide cryptic camouflage (Knight & Skinner 1981).

Foraging and Food Herbivorous, primarily green vegetation and seeds (Smithers 1971). Individuals forage at least 100 m from the burrow entrance (Smithers 1971). In the Karoo, diet averaged 16% seeds, 72% herbage and 12% insects on a year-long basis ($n = 6$); this diet was very similar to three parapatric species – *Gerbillus paeba*, *Rhabdomys pumilio* and *Mus minutoides* (Kerley 1992). Competition between the four species was minimized because of differences in size and time of activity.

Social and Reproductive Behaviour Solitary and probably asocial (Nel 1975).

Reproduction and Population Structure In Botswana (Smithers 1971), young are born mainly during the warm wet months of the year (Aug–Mar); gestation: 22–26 days and litter-size (in captivity): 3.2 (2–6, $n = 10$). In South Africa (Knight & Skinner 1981), gestation: 23–25 days and litter-size: 4.0 (2–8, $n = 9$). At birth, young naked and blind; weight 1.1 g. Ear pinna free Day 6. External auditory meatus open Day 15. Weaned Day 32. Sexually active Day 70. Adult weight ca. Day 90. First litters for two ♀♀ at Day 102 and Day 120. Females have postpartum oestrus.

Predators, Parasites and Diseases Preyed upon by Barn Owls *Tyto alba* (Nel & Nolte 1965) and probably by smaller carnivores and snakes (De Graaff 1981). Several species of fleas (belonging to the families Pulicidae, Hystrichopsyllidae and Chimaeropsyllidae) have been recorded. The species is perhaps a reservoir for plague (De Graaff 1981).

Conservation IUCN Category: Least Concern.

Probably not threatened because of wide geographic range and because the preferred habitat is not utilized by humans.

Measurements

Malacothrix typica

HB: 77 (67–86) mm, $n = 36$

T: 34 (28–42) mm $n = 36$

HF: 18 (16–21) mm, $n = 36$

E: 19 (14–21) mm, $n = 36$

WT: 16 (12–23) g, $n = 4$

GLS: 24.6 (23.6–25.4) mm, $n = 8$

GWS 13.5 (11.8–14.0) mm, $n = 8$

M^1 – M^3 : 3.6 (3.5–3.8) mm, $n = 8$

Body measurements and weights: South Africa; ♂♂ only (De Graaff 1981)

Skull measurements: BMNH, HZM

Note: Figures given by Smithers (1981) suggest that ♂♂ (mean HB: 112 mm, mean WT: 16.4 g) are larger than ♀♀ (mean HB: 107,

mean WT: 10.4 g).

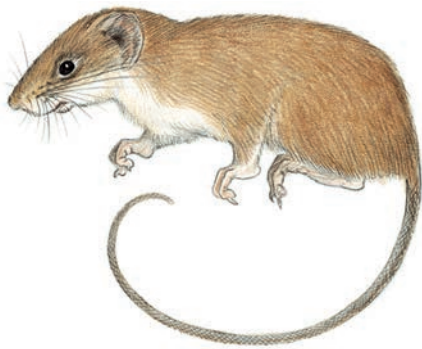
Key References De Graaff 1981; Knight & Skinner 1981; Smithers 1983.

D. C. D. Happold

GENUS *Megadendromus*

Bale Mouse

Megadendromus Dieterlen and Rupp, 1978. Z. Säugetierk. 43: 129. Type species: *Megadendromus nikolausi* Dieterlen and Rupp, 1978.



Megadendromus nikolausi.

Monospecific genus restricted to the highlands of Ethiopia. The genus is similar to *Dendromus* but is larger (mean HB: 117 mm, cf. mean HB: ca. 80 mm in the largest *Dendromus*) with a relatively short tail (ca. 80% of HB, cf. 100–160% in *Dendromus*), and with two lingual cusps on M^1 and on M^2 . *Megadendromus* is one of the core genera (with *Dendromus*) of the Dendromurinae (Musser & Carleton 2005), and is part of the clade that includes *Dendromus*, *Steatomys* and *Malacothrix* (Denys *et al.* 1995). Further details are given in the profile Subfamily Dendromurinae and species profiles. The single species is *Megadendromus nikolausi*.

D. W. Yalden

Megadendromus nikolausi BALE MOUSE (NIKOLAUS'S AFRICAN CLIMBING MOUSE, GIANT CLIMBING MOUSE)

Fr. Souris des montagnes Bale; Ger. Riesenklettermaus

Megadendromus nikolausi Dieterlen & Rupp, 1978. Z. Säugetierk. 43: 129. South of Goba, Bale Mts, Ethiopia.

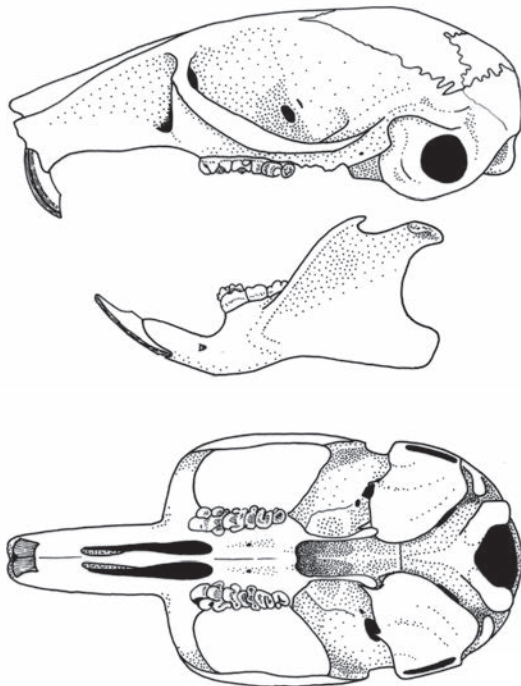


Figure 33. Skull and mandible of *Megadendromus nikolausi* (SMNS 23982, after original photograph by F. Dieterlen).

Taxonomy *Megadendromus* is a monospecific genus, distinguished by large size and dental characters from *Dendromus*. Synonyms: none. Chromosome number: not known.

Description Distinctive small dendromurine, with a strong mid-dorsal stripe, moderate size and tail somewhat shorter than HB. Pelage closely resembles *Dendromus melanotis*. Dorsal pelage deep brown with a strong mid-dorsal black stripe running from behind the ears to the base of the tail. Flanks slightly brighter than back. Ventral pelage greyish-brown, velvety in texture, slightly reddish on the front and sides of the chest. Fore- and hindfeet silvery-grey; forefoot with only three functional digits (as in *Dendromus*, cf. other genera in the subfamily); hindfoot with five digits, Digit 5 with nail (as in some *Dendromus* spp.). Ears lightly furred, brownish-grey. Very slight dark hair around the eyes, insufficient to produce a spectacled effect as in *D. melanotis*. Tail relatively long (ca. 80% of HB), rather thin; dark mid-dorsally due to dark bristles but greyish-white on sides and below. Apart from its larger size (cf. *Dendromus* spp.), the skull is also distinctive in having additional internal cusps on rows two and three of M^1 and M^2 (see Dieterlen & Rupp 1978) (Figure 33).

Geographic Variation None recorded.

Similar Species

Dendromus melanotis. Much smaller; tail 120% of HB.

Dendromus lovati. Much smaller, with three distinctive black stripes on back and rump.

Distribution Endemic to Africa. Afromontane–Afroalpine BZ. Confined to the high plateaux of SE Ethiopia, from 3000 to 3900 m. Known from only two localities, Dinshu in Bale and Mt Chilalo in Arssi (Dieterlen & Rupp 1978).

Habitat *Hagenia-Erica arborea* forest and *Erica arborea* scrub and forest (Dieterlen & Rupp 1978). Lives in same habitat as *Stenocephalemys griseicauda*, *Lophuromys flavopunctatus*, *Otomys typus* and *Dendromus melanotis*.

Abundance Rare, only 4 specimens known (Dieterlen & Rupp 1978, Demeter & Topál 1982). Collecting in Ethiopia during 1968–98 (n = ca. 6300 rodents) yielded no individuals of this species.

Remarks Presumably nocturnal. The large size and shorter tail of Bale Mice suggest that they may not be arboreal (cf. *Dendromus*). These characters may also be adaptations to the cold conditions at high altitudes. Presumably granivorous; detailed information not available. Some of the specimens came from owl pellets.

Conservation IUCN Category: Data Deficient.

Distribution is in an area where all woodland is being cleared very rapidly by the increasing human population. The species is undoubtedly threatened; the very limited range and rarity suggest it should be classified as Endangered. Schlitter (1989) listed it as rare.

Measurements

Megadendromus nikolausi

HB: 117 (98–129) mm, n = 4

T: 96 (86–106) mm, n = 4

HF: 26 (25–27) mm, n = 4



Megadendromus nikolausi

E: 23.5 (22–26) mm, n = 4

WT: 51 (40–66) g, n = 4

GLS: 29.4, 30.3 mm, n = 2

GWS: n. d.

M¹–M³: 5.8 (5.7–6.0) mm, n = 3

Ethiopia (Dieterlen & Rupp 1978, Demeter & Topál 1982)

Key References Demeter & Topál 1982; Dieterlen & Rupp 1978; Yalden & Largen 1992.

D.W.Yalden

GENUS *Prionomys* Bates's Climbing Mouse

Prionomys Dollman, 1910. Ann. Mag. Nat. Hist., ser. 8, 6: 226. Type species: *Prionomys batesi* Dollman, 1910.

Prionomys is a monotypic genus recorded only from rainforest habitats in Cameroon, Central African Republic and Congo. The genus is closely related to *Dendromus* and *Dendroprionomys* (Dollman 1910, Petter 1966b). The genus shares some characters with *Dendromus* and *Dendroprionomys* such as arboreal habit, small size and semi-prehensile tail. The forefoot has four functional digits (Digits 2, 3, 4 and 5) and a short stumpy non-functional Digit 1 (as in *Dendroprionomys*). The hindfoot has five digits; Digit 1 is opposable and Digit 5 is non-opposable (Figure 30) (cf. *Dendromus* and *Dendroprionomys*). The incisor teeth are pro-odont (cf. *Dendromus*, *Dendroprionomys*), and the cheekteeth have tall pointed cusps (as in *Dendroprionomys*). Additional details are given in the subfamily and species profiles. The single species is *Prionomys batesi*.

Christiane Denys



Prionomys batesi.

Prionomys batesi BATES'S CLIMBING MOUSE (DOLLMAN'S TREE MOUSE)

Fr. Souris arboricole de Bates; Ger. Bates Klettermaus

Prionomys batesi Dollman, 1910. Two new African mammals. Ann. Mag. Nat. Hist., ser. 8, 6: 226. Dja River, Bitye, Cameroon. 2000 ft (618 m).

Taxonomy Closely related to *Dendromus* and *Dendroprionomys* (see genus profiles). Synonyms: none. Chromosome number: not known.

Description Very small mouse with long tail. Pelage short, dense, soft and woolly. Dorsal pelage brownish-grey; hairs dark grey at base, brown at tips. Mid-dorsal stripe absent. Flanks pale grey; hairs dark grey at base, pale grey at tips. Ventral pelage pale grey, similar to flanks; hairs grey at base, paler at tips. Head similar in colour to dorsal pelage. Conspicuous brown eye-ring. Long stiff vibrissae. Ears moderate, darkly pigmented, with sparse brown hairs. Chin, throat and chest grey. Limbs short, with few short hairs. Forefoot with four digits: Digit 1 absent, Digits 2, 3, 4 and 5 thin, each with small pale claw. Large carpal tuberosity on 'hand'. Hindfoot with five digits: Digit 1 shorter than other digits, with 'nail-like' claw, Digits 2, 3, 4 and 5 long and thin, each with small claw; Digit 1 opposable (cf. Digit 5 opposable in *Dendromus* and *Dendroprionomys*) (Figure 30); three large callosities at base of digits on hindfoot. Tail long (ca. 122% of HB), brown, with scales arranged in rings; few (if any) small bristles. Skull: upper incisors pro-odont without longitudinal grooves, braincase globular-shaped, molar teeth with tall pointed cusps (Figure 34). Nipples: not known.

Geographic Variation None recorded.

Similar Species

Dendromus spp. Cheekteeth molariform; incisor teeth orthodont.

Dendroprionomys rousseloti. Cheekteeth with tall pointed cusps; incisor teeth orthodont.

Distribution Endemic to Africa. Rainforest BZ (West Central Region, Gabon Sub-region). Recorded from Cameroon, S Central African Republic and W Congo (Odzalla).

Habitat Rainforest, especially where there are small shrubs and lianas.

Abundance Uncertain; known only from a few specimens at five localities.

Adaptations Terrestrial and arboreal. Bates's African Climbing Mice climb on thin branches, twigs and lianas using the prehensile tail, long digits, callosity on the forefoot and opposable Digit 1 of hindfoot (in a similar way to *Dendromus* spp.). Burrows are made by digging in forest soil using the pro-odont upper and lower incisor teeth; each burrow is indicated by a little hillock of soil, ca. 30 cm diameter, without a visible entrance hole. The burrow contains a small nest chamber lined with dry leaves. Activity is entirely nocturnal: one individual emerged at 21:00h (three hours after nightfall) and climbed rapidly into nearby shrubs and lianas. Activity alternated between climbing (and foraging) in the forest and 15-minute 'rest' periods in the nest (F. Petter unpubl.). Bates's African Climbing Mice emit a strong odour, not unlike that of some species of shrews.

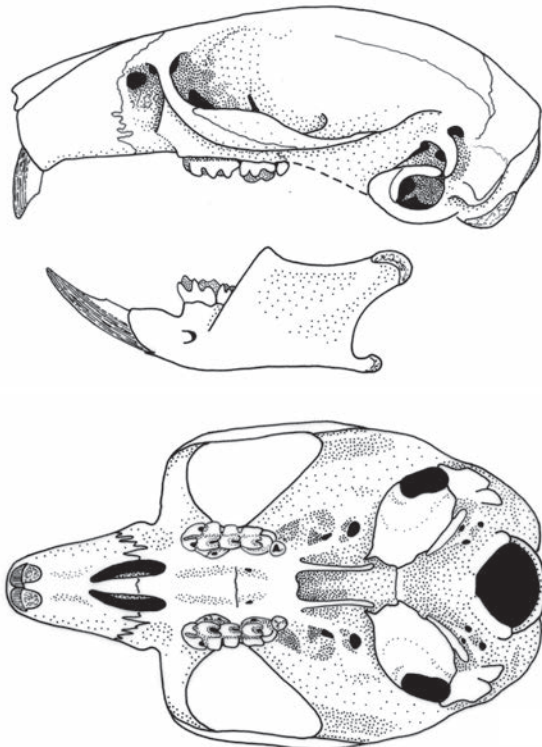


Figure 34. Skull and mandible of *Prionomys batesi* (BMNH 11.5.5.9, holotype).



Prionomys batesi

Foraging and Food Insectivorous. The diet consists (almost exclusively) of leaf-nesting ants, as well as spiders. The ants are captured with the tongue and crushed by the sectorial cusped cheekteeth. Large quantities of prey are consumed (F. Petter unpubl., Genest-Villard 1980).

Social and Reproductive Behaviour No information.

Reproduction and Population Structure Young are born in a nest chamber, lined with leaves, under the soil (see above).

Predators, Parasites and Diseases No information.

Conservation IUCN Category: Data Deficient.

Considered as Rare by Schlitter (1989). The very small geographic range and presumed rarity are cause for concern.

Measurements

Prionomys batesi

HB: 69 (54–78) mm, n = 11

T: 93.1 (67–103) mm, n = 10

HF: 14.9 (13–16) mm, n = 11

E: 10.3 (8–11) mm, n = 10

WT: n. d.

GLS: 24.4 (21.7–25.8) mm, n = 9

GWS: 13.9 (11.0–15.2) mm, n = 12

M¹–M³: 4.7 (4.3–5.0) mm, n = 9

Central African Republic (MNHN)

Key References Denys *et al.* 1995; Genest-Villard 1980; Petter 1966b.

Christiane Denys

GENUS *Steatomys*

Fat Mice

Steatomys Peters, 1846. Bericht Verhandl. K. Preuss. Akad. Wiss. Berlin 11: 258. Tete, Mozambique. Type species: *Steatomys pratensis* Peters, 1846.



Steatomys pratensis.

This exclusively African genus is widespread on the continent south of the Sahara and currently eight species are recognized. Four species are confined to West and sub-Saharan Africa, while the other four species occur in southern, central and East Africa. Species in the genus inhabit a variety of savanna habitats.

Species of the genus are small with soft shiny unpatterned dorsal pelage ranging in colour from pale grey-brown to brownish-buff. Ventral pelage is pure white. Tail is short, usually 50–60% of head-body length. Muzzle is pointed and ears are rounded. Limbs are short with white feet. Forefeet have four well-developed digits (Digit 1 absent), and hindfeet have five well-developed digits. All digits have long, sharp claws, which may be employed in the digging of burrows. Characteristics of the skull include orthodont incisors; each upper incisor with a single shallow groove on the outer face (usually paler in colour than the ungrooved part); zygomatic plate small and vertical (as in *Dendromys*) with a masseteric tubercle at lower anterior corner (also as in *Dendromys*); auditory bullae relatively large; palate wide, widest at level with upper M¹ and narrowest at level with upper M³; and ungrooved lower incisors. M¹ is the largest molar. M³ is greatly

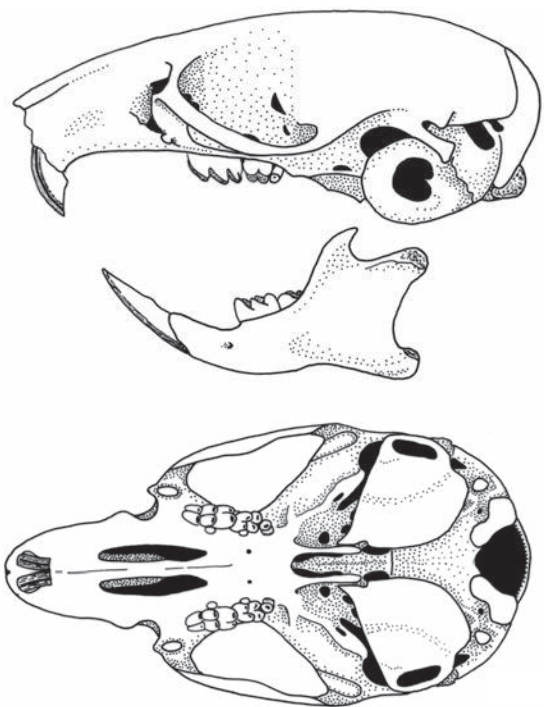


Figure 35. Skull and mandible of *Steatomys jacksoni* (HC 2797).

reduced (Figure 35). Species of this genus are readily identified by their rotund shape, short tail and grooved upper incisors.

A well-known character of all species in the genus is the ability to lay down substantial amounts of subcutaneous fat (hence the common name 'fat mouse'), a feature which allows them to enter torpor readily during cold conditions. Hibernation, however, does not occur, and individuals may be active throughout the year. All members of this genus are terrestrial and nocturnal. They construct their own burrows, which may be simple or relatively complex. Some

Table 17. Species in the genus *Steatomys*. Arranged in order of increasing head and body length. (n. d. = no data.)

| Species | HB mean (range) (mm) | GLS mean (range) (mm) | M ¹ –M ³ (mm) | Nipples | Notes |
|---------------------|--|-----------------------|-------------------------------------|----------------------------|--|
| <i>S. parvus</i> | 76 (64–84) | 22.6 (22–23) | 3.4 (3.3–3.5) | 2 + 2 = 8 | Botswana and Namibia, north to Zambia and Tanzania. Ethiopia |
| <i>S. cuppedius</i> | ca. 83 | 22.4 (21.3–23.9) | 3.8 (3.6–4.0) | 2 + 2 = 8 | Senegal to Nigeria |
| <i>S. krebsi</i> | 87.4 (78–95) [♂ ♂]
80.1 (77–86) [♀ ♀] | 24.4 (23.0–26.4) | 3.5 (3.2–3.8) | 2 + 2 = 8 | Southern Africa to Zambia |
| <i>S. pratensis</i> | 89.3 (75–102) [♂ ♂]
69.8(60–80) [♀ ♀] | 24.6 (22.9–26.0) | 3.9 (3.6–4.2) | 12–16, not always in pairs | Southern and eastern Africa |
| <i>S. jacksoni</i> | 101 (90–112+) | 25.0 (23.2–27.5) | 4.1 (3.8–4.5) | 2 + 4 = 12 | Ghana and Nigeria |
| <i>S. caurinus</i> | 104 (79–122) | 24.3 (19.5–27.3) | 4.1 (3.7–4.4) | >4 pairs | Senegal to Nigeria |
| <i>S. bocagei</i> | 119.1 (109–124) | 28.8 (27.5–29.8) | n. d. | 2 + 2 = 8 | Angola, SC DR Congo |
| <i>S. opimus</i> | 120 (115–125) | 26.9 (24.8–30.2) | 4.4 (4.3–4.7) | 2 + 3 = 10 | Cameroon to SW Sudan |

burrows have multiple entrances (some of which may be plugged) as well as a nest chamber. On account of their high fat content, fat mice are widely consumed by humans.

Historically, at least 18 species have been recognized (Musser & Carleton 2005). Coetzee (1977) provisionally acknowledged only three species. The taxonomic status of the genus is still unclear, as evidenced by the changing number of species. There is less controversy over the three West African species (revised by Swanepoel & Schlitter 1978), but the taxonomic status of the taxa in other parts

of Africa is unclear (see Coetzee 1977, Meester *et al.* 1986). Musser & Carleton (1993) recognized six species (*S. caurinus*, *S. cuppedius*, *S. jacksoni*, *S. krebsi*, *S. parvus*, *S. pratensis*), and more recently (2005) added *Steatomys bocagei* and *Steatomys opimus* (previously both synonyms of *S. pratensis*).

Species in the genus are distinguished by size, number of nipples and geographic distribution (Table 17).

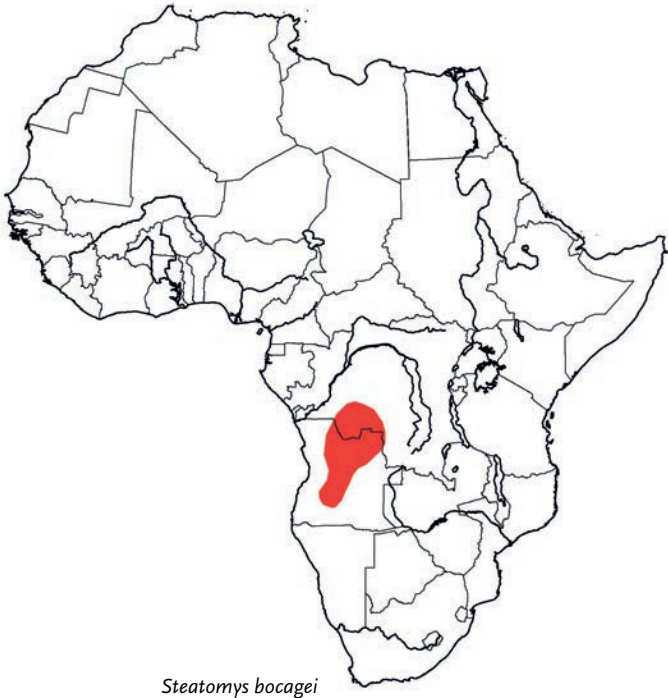
A. Monadjem

Steatomys bocagei **BOCAGE’S FAT MOUSE**
Fr. Souris adipeux de Bocage; Ger. Bocages Fettmaus

Steatomys bocagei Thomas, 1892. Ann. Mag. Nat. Hist., ser. 6, 10: 264. Caconda, Angola.

Taxonomy Referred to as *S. bocagei* by Hill & Carter (1941) and Ellerman *et al.* (1953), but considered to be a synonym of *S. pratensis* by Coetzee (1977) and Musser & Carleton (1993). However, the

presence of four pairs of nipples (Crawford-Cabral 1998) and the much larger size compared with *S. pratensis* warrants recognition of *bocagei* as a valid species (see Musser & Carleton 2005). Synonyms: *kasaicus*. Subspecies: none. Chromosome number: not known.



Description Small to medium-sized mouse, but one of the largest species of *Steatomys*. Dorsal pelage dull reddish-brown; hairs dark grey at base, brownish at tip. Ventral pelage pure white. Colour of ventral pelage well delineated from dorsal pelage. Muzzle, and area between eye and ear, cinnamon; lips white. Throat white. Ears short. Inner surfaces of limbs and feet white. Forefeet with four digits; Digit 1 absent, Digit 5 shorter than Digits 2, 3 and 4; claws long. Hindfeet short and broad with five digits; Digits 2, 3 and 4 much longer than Digits 1 and 5. Tail short (ca. 50% of HB), hairy, brown above, white below. Skull: large, with narrow interorbital region, and wide opisthodont upper incisors, each with single groove. Nipples: 2 + 2 = 8.

Geographic Variation None recorded.

Similar Species
S. pratensis. Smaller; tail bicoloured, brown above, pale below; nipples variable, but usually 10–14 nipples in 5–7 pairs; probably parapatric in east of range.

S. opimus. Similar size; dorsal pelage grey; tail dark brown above, white below; nipples 2 + 3 = 10; distribution Cameroon to SW Sudan.

Distribution Endemic to Africa. Zambezian Woodland BZ. Recorded from the Central Plateau of Angola (Crawford Cabral 1998) and eastward to SC DR Congo (Musser & Carleton 2005). Sympatric with *S. pratensis* in N Angola.

Habitat Grasslands in moist savannas and woodlands.

Abundance Common (Sanborn 1952, as *S. pratensis kasaicus*), although known from only a few localities.

Remarks Specimens very fat in the dry season (Sanborn 1952), suggesting a metabolism similar to that of other *Steatomys* spp. (see profiles Genus *Steatomys* and *S. opimus*). Digs its own burrow, and makes nest in burrow. After burning of the savanna, only ♀♀ captured (Sanborn 1952). Eaten by local people (Sanborn 1952) because of their high fat content.

Conservation IUCN Category: Least Concern.

Measurements

Steatomys bocagei

HB: 119.1 (109–124) mm, n = 8

T: 59.7 (52–72) mm, n = 8

HF: 19.1 (18–20) mm, n = 8

E: 16–19 mm, n = 3*

WT: n. d.

GLS: 28.8 (27.5–29.8) mm, n = 8

GWS: 13.7 (13.3–13.8) mm, n = 8

M¹–M³: 4.6–4.7 mm, n = 3*

Chitau, Angola (Hill & Carter 1941)

*Lunda District, Angola (Sanborn 1952; mean not recorded)

Key References Crawford Cabral 1998; Sanborn 1952.

D. C. D. Happold

Steatomys caurinus NORTH-WESTERN FAT MOUSE

Fr. Souris adipeux du Nord-Ouest; Ger. Nordwestlicher Fettmaus

Steatomys caurinus Thomas, 1912. Ann. Mag. Nat. Hist., ser. 9, 9: 271. Panyam, Nigeria. 4000 ft (1400 m).

Taxonomy Listed as a subspecies of *S. pratensis* by Coetzee (1977), but considered a valid species by Rosevear (1969) and Swanepoel & Schlitter (1978). Synonyms: *roseveari*. Subspecies: none. Chromosome number: 2n = 72 (Mali; B. Sicard & L. Granjon unpubl.).

Description Small mouse with coarse hairs and with short tail. Dorsal pelage medium-brown to reddish-brown, usually darker on mid-dorsal region; hairs grey at base, brown at tip. Flanks paler. Ventral pelage pure white, clearly delineated from colour of flanks. Nose pointed. Ears large and rounded, with longish hairs, especially on outer surface. Forefeet and hindfeet short, white. Tail short (ca. 38% of HB; range 16–54%), sparsely haired, brown above, white below. Individuals may be very fat at some periods of the year. Skull: interparietal bone small (length 3.5 mm or less). Nipples: number variable, always >8 (Coetzee 1977).

Geographic Variation None recorded.

Similar Species

S. cuppedius. Smaller size, pelage pale, hairs soft; tail relatively longer (51–57% of HB).

S. jacksoni. Same size as the largest *S. caurinus*, pelage dark brown, hairs soft; tail usually relatively longer (ca. 50% of HB); length of interparietal bone ca. 4.5 mm.

Distribution Endemic to Africa. Sudan and Guinea Savanna BZs. Recorded from Senegal, Mali, Burkina, N Côte d'Ivoire, N Ghana, Togo, Benin, NW Nigeria; eastern limits uncertain (Swanepoel & Schlitter 1978; B. Sicard & L. Granjon unpubl.).



Steatomys caurinus

Habitat Drier savannas on sandy soils, where vegetation cover is poor. Often found in traditionally cultivated fields and fallow lands.

Abundance Apparently uncommon, perhaps due to low trappability; specimens obtainable only through excavations of burrows. Infrequently found in pellets of Barn Owls *Tyto alba* in Senegal (L. Granjon, K. Ba & J.-M. Duplantier unpubl.).

Adaptations Nocturnal and terrestrial. Individuals accumulate fat during the wet season, which allows them to go into torpor and to be inactive during the dry season. In laboratory conditions, appears better adapted to dehydration than gerbils (Lacas *et al.* 2000).

Foraging and Food No information.

Social and Reproductive Behaviour Generally only one adult individual per burrow.

Reproduction and Population Structure Females with their young recorded in 11 burrows in Sep and Oct in S Mali; in each burrow, mean number of young 8.5 (range 5–12, $n = 11$) (B. Sicard & L. Granjon unpubl.).

Predators. Parasites and Diseases Found in pellets of Barn Owls *Tyto alba* in Senegal (Heim de Balsac 1965; Granjon, Bâ & Duplantier unpubl.).

Conservation IUCN Category: Least Concern.

Measurements

Steatomys caurinus

HB: 104.7 (79–122) mm, $n = 9$

T: 39.3 (18–51) mm, $n = 9$

HF: 16.5 (14.5–18) mm, $n = 9$

E: 15.9 (14–18) mm, $n = 9$

WT: 44.6 (16.5–101) g, $n = 9$

GLS: 24.3 (19.5–27.3) mm, $n = 8$

GWS: 12.9 (11.9–13.8) mm, $n = 9$

M^1 – M^3 : 3.9 (3.5–4.6) mm, $n = 9$

Senegal and Mali (B. Sicard & L. Granjon unpubl.)

Key References Coetzee 1977; Rosevear 1969; Swanepoel & Schlitter 1978.

B. Sicard & J.-M. Duplantier

Steatomys cuppedius DAINY FAT MOUSE

Fr. Souris adipeux gracile; Ger. Zierliche Fettmaus

Steatomys cuppedius Thomas and Hinton, 1920. Novit. Zool. 27: 318. Farniso near Kano, Nigeria. 1700 ft (518 m).

Taxonomy Although listed as a subspecies of *S. parvus* by Coetzee (1977), most authors (e.g. Rosevear 1969, Swanepoel & Schlitter 1978, Musser & Carleton 1993, 2005) consider *cuppedius* to be a valid species. Synonyms: none. Chromosome number: not known.

Description Small, delicate mouse with soft silky pelage and short white tail; the smallest of the West African species. Dorsal pelage pale, sandy to grey; hairs medium grey at base, sandy or grey at tip; darker on mid-dorsal line due to some black-tipped hairs. Ventral

pelage pure white. Nose pointed. Ears large and rounded. Nasal region, cheeks, lips and throat white. Forefeet and hindfeet white. Tail short (57% of HB, range: 51–67%), white, scantily covered with white hairs above and below. Nipples: $2 + 2 = 8$.

Geographic Variation None recorded.

Similar Species

S. caurinus. Larger size, pelage darker, hairs coarse; tail relatively short (mean 38% of HB).

Distribution Endemic to Africa. Sudan Savanna BZ. Recorded from several localities in Senegal, and also from N Nigeria and S Niger. Swanepoel & Schlitter (1978) expressed doubts about data concerning Senegal (Heim de Balsac 1965) but captures (in Mbour) and in owl pellets from various localities (L. Granjon, K. Ba & J.-M. Duplantier unpubl.) confirm the presence of the species in Senegal. May occur also in other parts of the Sudan Savanna BZ between these known localities. Records of this species from SE Ghana are now known to be *Uranomys ruddi* (see Grubb *et al.* 1998 for details).

Habitat In Senegal, trapped in sandy areas near gardens and near the coast. Seems to prefer drier habitats than *S. caurinus*.

Abundance Generally uncommon, but may be locally abundant: e.g. in Nigeria, 55 individuals caught within a week in a single locality (as *S. parvus*; Happold 1987), and in Senegal 12 individuals caught within two weeks on the same trap line. Comprised up to 30% of prey in pellets of Barn Owls *Tyto alba* in some localities in Senegal (L. Granjon, K. Ba & J.-M. Duplantier unpubl.).



Steatomys cuppedius

Adaptations Nocturnal and terrestrial. Individuals accumulate fat during the wet season, which allows them to go into torpor or to be inactive during the dry season.

Foraging and Food No information.

Social and Reproductive Behaviour Several individuals caught at the same place suggests the existence of colonies.

Reproduction and Population Structure No detailed information. Juveniles (HB: 58–62 mm) in Dec in N Nigeria (labels, BMNH). In Mbour (Senegal), sex-ratio in Aug was 10 ♂♂ : 2 ♀♀ for individuals caught at the same place within a few days.

Predators, Parasites and Diseases Preyed on by Barn Owls *Tyto alba* in Senegal (Heim de Balsac 1965; L. Granjon, K. Ba & J.-M. Duplantier unpubl.).

Conservation IUCN Category: Least Concern.

Measurements

Steatomys cuppedius

TL: 132.7 (120–143) mm, n = 6

T: 48.7 (46–54) mm, n = 6

HF: 16.0 (15–17) mm, n = 6

E: 13.7 (13–14) mm, n = 6

WT: 16.2 (13–22) g, n = 6

GLS: 22.4 (21.3–23.9) mm, n = 5

GWS: 11.8 (11.2–12.4) mm, n = 6

M¹–M³: 3.8 (3.6–4.0) mm, n = 10

N Nigeria (Swanepoel & Schlitter 1978)

Key References Rosevear 1969; Swanepoel & Schlitter 1978.

J.-M. Duplantier & B. Sicard

Steatomys jacksoni JACKSON'S FAT MOUSE

Fr. Souris adipeux de Jackson; Ger. Jacksons Fettmaus

Steatomys jacksoni Hayman, 1936. Proc. Zool. Soc. Lond. 1935: 930 (publ. 1936). Wenchi, Ghana.

Taxonomy Included in *S. caurinus* by Coetzee (1977) but retained as a distinct species by Swanepoel & Schlitter (1978) and Musser & Carleton (1993). The wide interparietal bone on the skull (compared with other species in the genus) is the diagnostic character for the species, but the significance of this character is uncertain. The validity of the species can not be assessed until additional specimens are available (Musser & Carleton 1993). Synonyms: none. Chromosome number: not known.

Description Small dark brown mouse, with a short tail and tendency to be fat (or very fat) at some seasons of the year. Pelage soft. Dorsal pelage dark brown; dorsal hairs dark slate-grey at base, medium-brown at tip. Ventral pelage pure white. Chin, throat, chest white. White postauricular spot, sometimes obscure. Fore- and hindlimbs and feet white. Forefoot with four well-developed digits. Tail short (ca. 50% of HB), bicoloured, dark above, whitish below. Skull with small cheekteeth (and M³ very small), palate not much prolonged posteriorly to cheekteeth, each upper incisor opisthodont with single groove and angled slightly outwards, and moderately well-developed auditory bullae; interparietal bone ca. 4.5 mm (cf. *S. caurinus*). Nipples: 2 + 4 = 12.

Geographic Variation None recorded.

Similar Species

S. caurinus. Dorsal pelage rufous-brown and paler; usually smaller, HB: 79–122 mm, HF: 14–18 mm, GLS: 19–27 mm; interparietal bone 3.0–3.5 mm; Guinea and Sudan Savanna BZs; may be parapatric with this species.

S. cuppedius. Dorsal pelage sandy-grey; smaller, HB: <90 mm, HF: 15–17, GLS: <24 mm; Sudan and Sahel Savanna BZs.

Mus musculoides. Dorsal pelage golden-brown to dark brown; much smaller (HB: 55–70 mm, HF: 12–14 mm, GLS: 18–20 mm);



Steatomys jacksoni

Guinea and Sudan Savanna BZs, and savanna habitats in Rainforest–Savanna Mosaics.

Distribution Endemic to Africa. Guinea Savanna BZ and Northern Rainforest–Savanna Mosaic. Recorded only from W Ghana and SW Nigeria. Two young animals from Wulehe, Togo perhaps represent this species (Rosevear 1969). The species was not recorded by Robbins & Van der Straeten (1996) in Togo and Benin, although another species of *Steatomys* (*S. caurinus*) was recorded.

Habitat At Olokomeji F. R., SW Nigeria, specimens were caught in tall grasslands with *Lophira lanceolata*, *Buterospermum paradoxum*, *Burkea africana* and *Daniella oliveri* trees; these grasslands were burned regularly in the early to mid-dry season (Anadu 1973). The holotype, from Wenchi, Ghana, was collected 'in open country, the completely destroyed edge of the high forest' (Rosevear 1969).

Abundance Very rare. Specimens are recorded only from one locality in Ghana and two localities in Nigeria (and possibly one locality in Togo). At Olokomeji, SW Nigeria, only eight individuals (Anadu 1979b) were captured on two study areas in two and half years, representing <0.01% of the small mammals ($n = 803$) (Anadu 1973); no other species of *Steatomys* was present.

Remarks Nocturnal and terrestrial. It seems likely that this species is similar to other species in the genus, i.e. digs extensive burrows, stores body fat when food is abundant and enters torpor when conditions are unfavourable. Anadu (1979b) recorded, that after capture, individuals curled up with their eyes closed and made a high pitched 'Kweee-kweee' vocalization – a response unlike that of any of the other sympatric small rodents.

Conservation IUCN Category: Data Deficient.

The rarity, fragmentation of populations, and lack of data make it very difficult to assess the category for this species.

Measurements

Steatomys jacksoni

HB: 101 (90–112) mm, $n = 3$

T: 51 (44–58) mm, $n = 3$

HF: 18.3 (18–19) mm, $n = 3$

E: 14.7 (14–16) mm, $n = 3$

WT: 25.3 (20–28) g, $n = 3$

GLS: 25.0 (23.2–27.5) mm, $n = 3$

GWS: 12.0 (11.6–12.3) mm, $n = 3$

M^1 – M^3 : 4.1 (3.8–4.5) mm, $n = 3$

Nigeria (Anadu 1979b)

The holotype, an old individual, was larger in some dimensions (HB: 120 mm, E: 18 mm, GLS: 28.9 mm, GWS [Zygomatic breadth]: 13.0 mm) than those given above (Rosevear 1969).

Key References Anadu 1979b; Rosevear 1969.

D. C. D. Happold

Steatomys krebsii KREBS'S FAT MOUSE

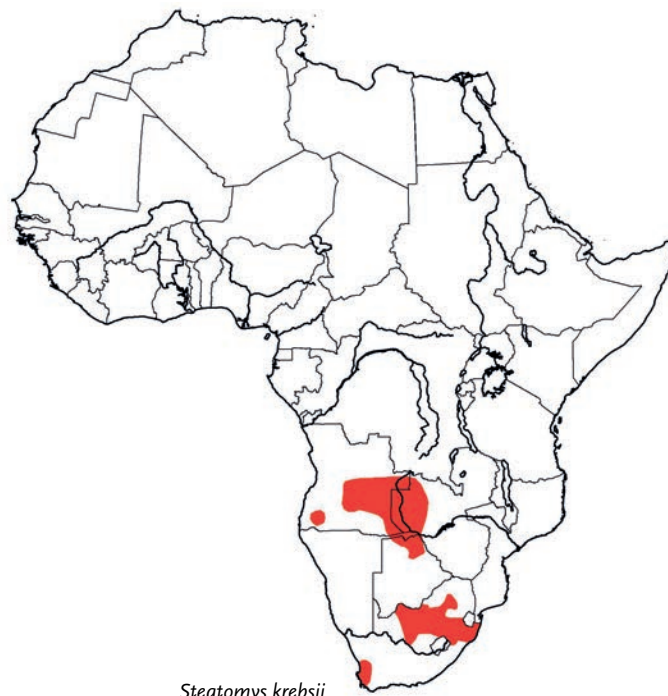
Fr. Souris adipeux de Krebs; Ger. Krebs Fettmaus

Steatomys krebsii Peters, 1852. Reise nach Mozambique, Säugethiere, p. 165. 'Kaffraria', South Africa.

Taxonomy Currently, only size and colour of tail separates *S. krebsii* from *S. parvus*, neither feature differing consistently between the two species. This has resulted in specimens from N KwaZulu–Natal Province, South Africa, having been assigned successively to one species or the other. Pending further investigation, they are considered here to belong to *S. krebsii* (Taylor 1998). Taxonomic relationships between the three or four disjunct populations need further study. Synonyms: *angolensis*, *bensoni*, *bradleyi*, *chiversi*, *mariae*, *orangiae*, *tongensis*, *transvaalensis*. Subspecies: none. Chromosome number: not known.

Description Small plump mouse with soft, shiny pelage. Dorsal pelage and flanks orange-buff to greyish-brown and dark brown; hairs with grey base, brown at tip; many black-tipped hairs, especially on upper part of back. Ventral pelage white; hairs pure white or grey at base with white tip. Head with pointed nose and long vibrissae. Ears small and rounded, brownish, with longish hairs on outer surface. Lower cheek, lips, chin and throat white. Limbs short. Feet white, each digit with long, sharp claw. Tail short (ca. 60% of HB), brownish above, white below. Nipples: $2 + 2 = 8$.

Geographic Variation Meester *et al.* (1986) recognized four subspecies in southern Africa, but the validity of subspecies is dubious. The form *pentonyx* (from Western Cape Province, South Africa) is distinguishable by white at base of ventral hairs. In South Africa, dorsal pelage orange-buff to pale brown; in Zambia, dorsal pelage brown to dark brown.



Steatomys krebsii

Similar Species

S. pratensis. On average slightly larger; nipples variable, but usually 10–14 nipples in 5–7 pairs.

S. parvus. On average smaller, tail white above and below; dorsal pelage pale buff in area of sympatry; nipples $2 + 2 = 8$.

Distribution Endemic to Africa. Zambezian Woodland, Highveld and South-West Cape BZs. Distribution disjunct. Recorded from three separate areas: (a) Angola, Botswana, W Zambia (Smithers 1971, Ansell 1978, Crawford-Cabral 1998), (b) Free State, Northwest and KwaZulu–Natal Provinces, South Africa, and (c) Western and Eastern Cape Provinces, South Africa (De Graaff 1981).

Habitat Tolerates a wide range of habitats on sandy to loamy soils. More moisture-tolerant than *S. pratensis* (Coetzee 1977).

Abundance Uncertain; poorly represented in museum collections.

Adaptations Terrestrial and nocturnal. Constructs burrows that tend to spiral downwards (De Graaff 1981).

Foraging and Food Probably granivorous (De Graaff 1981), although the stomach contents of a single specimen from South Africa consisted entirely of insect remains (Rautenbach & Nel 1980).

Social and Reproductive Behaviour Not communal (De Graaff 1981).

Reproduction and Population Structure Pregnant ♀ with five embryos (South Africa; Rautenbach *et al.*, 1981). Female with four young in Oct (Zambia; n = 2; labels BMNH).

Predators, Parasites and Diseases Populations may be infested sporadically with plague (De Graaff 1981).

Conservation IUCN Category: Least Concern.
Listed as ‘rare’ in KwaZulu–Natal (Taylor 1998).

Measurements

Steatomys krebsii

HB (♂ ♂): 87.4 (78–95) mm, n = 9

HB (♀ ♀): 80.1 (77–86) mm, n = 6

T (♂ ♂): 49.6 (45–55) mm, n = 9

T (♀ ♀): 48.0 (45–50) mm, n = 6

HF (♂ ♂): 17.8 (16–18) mm, n = 9

HF (♀ ♀): 17.2 (16–19) mm, n = 6

E (♂ ♂): 14.9 (14–18) mm, n = 9

E (♀ ♀): 14.4 (14–16) mm, n = 5

WT: 21.4 (17–26) g, n = 5

GLS: 24.4 (23.0–26.4) mm, n = 16

GWS: 12.2 (11.5–13.0) mm, n = 16

M¹–M³: 3.5 (3.2–3.8) mm, n = 16

South Africa

Body measurements and weight: South Africa (TM; P. J. Taylor unpubl.)

Skull measurements: Roberts (1951)

Key References De Graaff 1981; Smithers 1971.

A. Monadjem

Steatomys opimus POUSARGUES’S FAT MOUSE

Fr. Souris adipeux de Pousargues; Ger. Pousargues Fettmaus

Steatomys opimus Pousargues, 1894. Bull. Soc. Zool. de France, 19: 131. Balao, Central African Republic.

Taxonomy Considered to be either a valid species (Genest-Villard 1979, Musser & Carleton 2005) or a subspecies of *S. pratensis* (Coetzee 1977, Musser & Carleton 1993). Larger body size, larger on average skull size and reduced number of nipples compared with *S. pratensis*, supports specific status. Relationship with *S. bocagei* from Angola and S DR Congo (also larger than other species in the genus) warrants investigation. Synonyms: *gazellae*. Subspecies: none. Chromosome number: not known.

Description Small to medium-sized mouse, but one of the largest species of *Steatomys*. Often plump and rotund (due to extensive deposits of fat) with short limbs and tail. Pelage short and soft. Dorsal pelage and flanks grey or brown. Ventral pelage white. Head grey, throat white, lips white. Ears relatively long. Limbs short, grey; digits white with long white claws. Tail short (ca. 35% of HB), dark brown above, white below. Nipples: 2 + 3 = 10.

Geographic Variation None recorded.

Similar Species

S. bocagei. Similar size; dorsal pelage reddish-brown; tail ca 50% of HB; nipples 2 + 2 = 8; Angola and SW DR Congo.



Steatomys opimus

S. parvus. Smaller; dorsal pelage pale buff; tail white above and below; nipples 2 + 2 = 8; distribution to the east and south, may be parapatric in extreme east of range.

Distribution Endemic to Africa. Guinea Savanna BZ (western part) and Northern Rainforest–Savanna Mosaic; records disjunct. Recorded from Cameroon, S Central African Republic, N DR Congo and extreme SW Sudan (Musser & Carleton 2005).

Habitat Savanna habitats interspersed with forest relicts. Prefers sandy soils on valley slopes above riverine forest, with dense grasses (up to 4 m before burning) and termite mounds. In Central African Republic, densest populations found in savanna grasslands that are burned regularly and where there are small trees (especially *Hymenocardia acida* and *Amona senegalensis*) (Genest-Villard 1979).

Abundance Generally uncommon or rare; locally dense populations in favoured habitats.

Adaptations Terrestrial and nocturnal. Excavates complex burrow with entrance of 3–4 cm diameter. Spherical nesting cavity, 30–50 cm from entrance, filled with shredded interlaced grass leaves that completely fill the nesting chamber (10–15 cm diameter). Nest situated 7–15 cm below soil surface. Beyond nest, burrow spirals downwards in 1–3 complete spirals to a depth of 70–100 cm below soil surface; spiral may be open or filled with loose sand, and ends with small open ‘cul-de-sac’. Burrow length: 1.5–3 m. Temperature in nest during daytime is 27–30 °C when T_a is 22–36 °C. Preferred place for burrowing is in old termitaria and in the spill-heap of an aardvark burrow; these mice do not utilize the burrows of other rodents (Genest-Villard 1979). Individuals are often ‘blanketed by a layer of fat’ (Hatt 1940a) under the skin.

In captivity, activity outside the nest is restricted to about one hour in the evening (Petter 1966d); and in the wild, individuals seem to remain in their nests at all times during the cool season (perhaps a reason why they are rarely caught in traps). During activity (in captivity), T_b is 33–34.6 °C. When resting in the nest, T_b drops to 20–27 °C, roughly following T_a ; at these temperatures, the individual is lethargic and in a state of torpor (Petter 1966d). These mice (and perhaps all *Steatomys*) have evolved an unusual strategy for survival when the environment is dry and cool: low food intake (because the diet is rich in protein and fat – see below), storage of

fat in the tissues, an ability to lower body temperature (to reduce energy expenditure), low daily activity, and daily and seasonal torpor to minimize the use of energy.

Foraging and Food Primarily insectivorous. Contents of 23 (out of 25) stomachs (collected in Feb–Jul) were exclusively termites, with a few ants and some grains of sand. Termites provide a good source of fat (see above). May be granivorous at other times of year (Genest-Villard 1979).

Social and Reproductive Behaviour Most burrows contained a single individual; some contained a mother and 2–3 young or subadults.

Reproduction and Population Structure Reproduction probably during wet season (Jun–ca. Dec) in Central African Republic. Young (ca. 2 months old) caught in Feb, and subadults found at end of dry season. Litter-size: probably 3. Young unlikely to breed in the year of birth (Genest-Villard 1979).

Predators, Parasites and Diseases Because of their high fat content, they are collected for food by local people (Hatt 1940a).

Conservation IUCN Category: Least Concern.

Measurements

Steatomys opimus

HB: 120 (115–125) mm, $n = 5$

T: 60 (52–65) mm, $n = 5$

HF: 19 (18–20) mm, $n = 5$

E: 18 (17–20) mm, $n = 5$

WT: 30–50 g

GLS: 26.9 (24.8–30.2) mm, $n = 8$

GWS: 13.3 (12.8–14.5) mm, $n = 6$

M^1 – M^3 : 4.4 (4.3–4.7) mm, $n = 8$

Body measurements: Niangara, DR Congo (Hatt 1940a)

Weight: Central African Republic (Genest-Villard 1979), mean and sample size not given

Skull measurements: Faradje and Niangara, DR Congo (Hatt 1940a)

Key References Genest-Villard 1979; Hatt 1940a.

D. C. D. Happold

Steatomys parvus TINY FAT MOUSE

Fr. Petite souris adipeuse; Ger. Kleine Fettmaus

Steatomys parvus Rhoads, 1896. Proc. Acad. Nat. Sci. Philadelphia, p. 529. North shore of L. Rudolf (now L. Turkana), Ethiopia.

Taxonomy Formerly known as *Steatomys minutus*. The single Ethiopian record, given as *S. pratensis* (Yalden *et al.* 1976) was later re-identified as *S. parvus* (Yalden *et al.* 1996). The form *tongensis* from N KwaZulu–Natal Province, South Africa, has been allocated recently to *Steatomys krebsii* (Taylor 1998). Specimens recorded as *S. parvus* from N Nigeria (Happold 1987) are now considered to represent *S. cuppedius*. Taxonomic relationship between the geographically separated south-western and north-eastern populations needs to

be assessed. Synonyms: *aquilo*, *athi*, *kalaharicus*, *loveridgei*, *minutus*, *muanzae*, *swalius*, *thomasi*, *umbratus*. Subspecies: none. Chromosome number: not known.

Description Very small plump mouse with soft pelage. Dorsal pelage pale buff, with paler flanks; dorsal hairs with slaty base and rufous tip. Ventral pelage pure white to off-white. Head with pointed nose and long vibrissae. Upper lips, lower cheeks, throat and lower

shoulders white. Delineation between colour of flanks and ventral pelage more dorsal than in other species of genus. Ears small and rounded, brownish. Limbs short, feet pale. Forefeet with four well-developed digits. Hindfeet with five well-developed digits. All digits with long, sharp claws. Tail short (ca. 50% of HB), white above and below. Nipples: $2 + 2 = 8$.

Geographic Variation None recorded.

Similar Species

S. pratensis. Usually larger; tail bicoloured, brown above, pale below; nipples variable, but usually 10–14 nipples in 5–7 pairs.

S. krebsii. Usually on average larger; tail bicoloured, greyish-brown above, pale below; nipples $2 + 2 = 8$; occurs only south of ca. 10° S latitude.

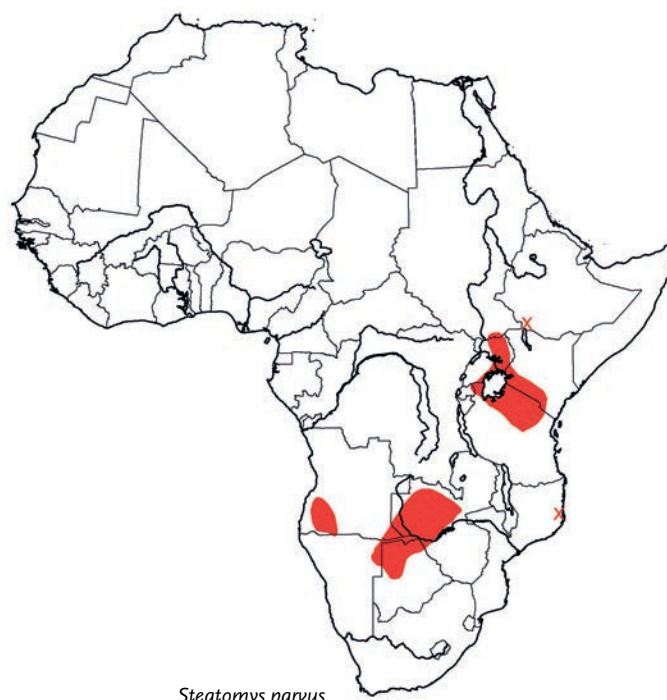
Distribution Endemic to Africa. Zambezan Woodland BZ and marginally Somalia–Masai Bushland BZ. Two, perhaps three, disjunct populations: (a) S Angola and N Namibia, (b) W Zambia and N Botswana, (c) N Tanzania through Kenya to Somalia (Funaioli & Simonetta 1966), S Ethiopia (Yalden *et al.* 1976) and east to Uganda (Wilson 1995).

Habitat Savanna on sandy soils. In Botswana, found in riverine flood-plains and woodlands, and in dry grassland with open scrub (Smithers 1971). Prefers drier habitats than *S. pratensis*. In Botswana, sympatric with *S. krebsii* and *S. pratensis* (Smithers 1971). Not recorded from moist woodlands, forests and montane grasslands.

Abundance Not known, but unlikely to occur at high densities.

Remarks Despite its wide distribution, little information available. Nocturnal and terrestrial. Excavates own burrow, which is used for nesting and food hoarding. Capable of accumulating large quantities of fat under the skin. A single lactating ♀ was collected in Nov in Botswana (Smithers 1971), suggesting that offspring are born in the wet season.

Conservation IUCN Category: Least Concern.



Steatomys parvus

Measurements

Steatomys parvus

HB: 76 (64–84) mm, $n = 5$

T: 40 (36–50) mm, $n = 5$

HF: 15 (14–16) mm, $n = 5$

E: 14 (13–14) mm, $n = 5$

WT: 13.3 (11.1–15.0) g, $n = 3$

GLS: 22.6 (22.0–23.0) mm, $n = 3$

GWS: 11.3, 12.0 mm, $n = 2$

M^1 – M^3 : 3.4 (3.3–3.5) mm, $n = 3$

Body measurements: South Africa (De Graaff 1981); ♂♂ only

Weights: Botswana (Smithers 1971); sexes unknown

Skull measurements: South Africa (Roberts 1951)

Key References De Graaff 1981; Smithers 1971, 1983.

A. Monadjem

Steatomys pratensis COMMON FAT MOUSE

Fr. Souris adipeux commune; Ger. Gemeine Fettmaus

Steatomys pratensis Peters, 1846. Bericht Verhandl. K. Preuss. Akad. Wiss. Berlin 11: 258. Tete, Mozambique.

Taxonomy The species *pratensis* is limited to the large *Steatomys* of southern, central and East Africa (Musser & Carleton 1993). Formerly, *caurinus* and *jacksoni* of West Africa were considered to be subspecies of *pratensis* (Coetzee 1977), but are now regarded as distinct species (Swanepoel & Schlitter 1978). The forms *opimus* and *bocagei* were also allocated as subspecies of *S. pratensis* (Coetzee 1977), but are now recognized as valid species (Genest-Villard 1979, Musser & Carleton 2005). Synonyms: *edulis*, *leucorhynchus*, *maunensis*, *natalensis*, *nyasae*. Subspecies: none. Chromosome number: $2n = 68$ (R. Matthey in Robbins & Baker 1978).

Description Small plump mouse with soft, shiny pelage. Dorsal pelage variable, rusty-brown, medium brown or dark brown; hairs slaty-grey at base, brown or black at tip. Flanks paler, tinged with rufous-brown. Ventral pelage pure white. Colour of ventral pelage clearly delineated from colour of flanks. Head with pointed nose and long vibrissae. Nose, chin and throat white. Ears small and rounded, brownish. Limbs short. Feet white, each digit with long sharp claw. Tail short (ca. 50% of HB) and thin, brownish above and paler below. Nipples variable, but usually 10–14 nipples in 5–7 pairs.

Geographic Variation None recorded.

Similar Species

S. parvus. Almost always smaller; tail white above and below; nipples $2 + 2 = 8$.

S. krebsii. On average smaller; tail bicoloured, greyish-brown above, pale below; nipples $2 + 2 = 8$.

Distribution Endemic to Africa. Zambezian Woodland BZ, and parts of Southern Rainforest–Savanna Mosaic and the South-West Arid BZ (Kalahari Desert). Recorded from NW Angola, Namibia, N Botswana, Zimbabwe, N South Africa, Swaziland, Mozambique, C Zambia, Malawi and STanzania. Due to past confusion with *Steatomys parvus*, distribution in East Africa is unclear. The record from owl pellets in EC Ethiopia (Demeter 1982, assessed as this species in Musser & Carleton 2005) needs verification, and is more likely to refer to *S. opimus* than *S. pratensis* (A. Monadjem unpubl.).

Habitat Grassland and woodland savannas, cultivated and fallow fields, and edges of rivers and swamps. Generally absent from forests and montane grasslands. Favours open savanna on sandy substrates, but in Swaziland may also occur on hard substrates. Appears to select recently burnt areas where there is new grass cover (Monadjem 1999b).

Abundance Relatively uncommon, but may be locally very abundant. Population densities rarely exceed 5/ha in Swaziland (A. Monadjem unpubl.).

Adaptations Nocturnal and terrestrial. Uses long claws to excavate a burrow, which is used for resting, nesting and food hoarding. Each burrow, usually up to 40 cm deep, may have more than one entrance; one burrow in southern Africa had four entrances leading to a nest chamber (De Graaff & Nel 1992). Fat mice are capable of accumulating large quantities of fat under the skin when food is abundant. Accumulated fat is used for metabolism in the dry and cold seasons. Adult ♂♂ achieve greatest body weights in wet

season (Monadjem 1999b), but remain fat throughout wet and dry seasons. In captivity, individuals readily enter torpor in cold conditions for variable durations, which are determined by the ambient temperature (Richardson & Perrin 1992), resulting in considerable saving of energy (Ellison 1995). Less active in the dry season.

Foraging and Food Predominantly granivorous. Eats mostly grass seeds, but also consumes vegetable material and insects.

Social and Reproductive Behaviour Usually solitary, but occasionally pairs occupy a burrow. In Swaziland, mean distance between successive monthly captures was 36.1 m, which suggests a rather sedentary existence (Monadjem 1999b).

Reproduction and Population Structure Reproduction occurs mainly in the wet season. Pregnant and lactating ♀♀ present mostly in Jan–Mar (southern Africa). Recruitment increases in late wet season (mostly Mar–May in Swaziland). Population numbers generally do not vary by more than a factor of two between seasons. Sex ratio does not deviate from parity (Monadjem 1999b).

Predators, Parasites and Diseases Remains collected from pellets of African Grass-owls *Tyto capensis*, Barn Owls *Tyto alba* and Black-shouldered Kites *Elanus caeruleus* (Vernon 1972, Mendelsohn 1982, Smart & Taylor 1990). Widely consumed by humans because of their high fat content. Ectoparasites include three species of mites, nine species of fleas and three species of ticks; some of these ectoparasites are implicated in the transmission of disease to humans and domesticated sheep (details in De Graaff 1981).

Conservation IUCN Category: Least Concern.

Widespread and common in places. Survives in agricultural landscapes and hence not likely to become threatened.

Measurements

Steatomys pratensis

HB (♂♂): 95 (83–105) mm, n = 25

HB (♀♀): 93 (82–106) mm, n = 27

T (♂♂): 44 (40–55) mm, n = 25

T (♀♀): 44 (40–51) mm, n = 25

HF (♂♂): 16 (15–19) mm, n = 29

HF (♀♀): 16 (14–18) mm, n = 26

E (♂♂): 15 (14–18) mm, n = 20

E (♀♀): 15 (14–18) mm, n = 22

WT (♂♂): 26.1 (22–30) g, n = 13

WT (♀♀): 39.7 (34–48) g, n = 9

GLS: 24.6 (22.9–26.0) mm, n = 15

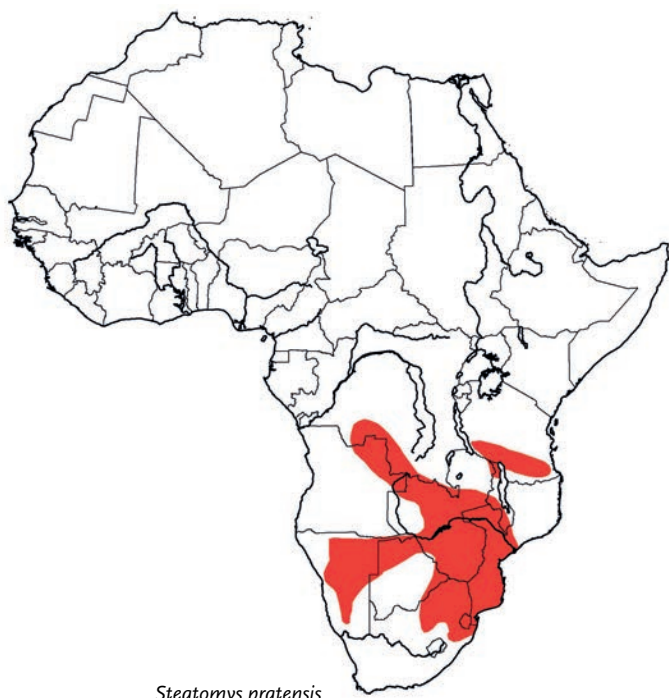
GWS: 12.2 (11.0–13.2) mm, n = 14

M¹–M³: 3.9 (3.6–4.2) mm, n = 19

Body measurements and weight: South Africa (De Graaff 1981)

Skull measurements: South Africa (Roberts 1951)

Key References De Graaff 1981; Ellison 1995; Monadjem 1999b; Richardson & Perrin 1992; Smithers 1983.



Steatomys pratensis

A. Monadjem

Subfamily MYSTROMYINAE – White-tailed Rat

Mystromyinae Vorontsov, 1966. Zool. Zh. 45: 437.

The single living genus and species, *Mystromys albicaudatus*, comprising this subfamily is confined to southern Africa, inhabiting the South-West Cape and Zambezian Woodland BZs. The thickset build, simple molars with biserial cusp arrangement, and short tail suggest similarity to the Palearctic hamsters (Cricetidae: Cricetinae) and inspired its less frequently used vernacular name, the Southern African Hamster. Indeed, the genus has been traditionally classified as a lone Afrotropical member of the otherwise Palearctic Cricetinae (Roberts 1951, Ellerman *et al.* 1953, Misonne 1974, De Graaff 1981, Pocock 1987, Skinner & Smithers 1990, Denys 1991). Such a restricted distribution, however, suggests that *Mystromys* is a relict of an older muroid radiation within Africa.

Vorontsov (1966) detailed numerous differences between *Mystromys* and the true hamsters and erected the subfamily Mystromyinae to underscore its morphological uniqueness and probable phylogenetic remoteness. Foremost among those contrasts are the lack of internal cheek pouches (present in Cricetinae), presence of parallel ridges on lower incisors (absent in Cricetinae), mammary glands with only four inguinal nipples (eight or more in Cricetinae), and possession of a hemiglandular stomach with densely papillated corpus (papillae absent in Cricetinae) (Vorontsov 1966, Maddock & Perrin 1983, Pocock 1987). Lavocat (1973, 1978) stressed the genealogical antiquity of *Mystromys*, noting its probable derivation from Miocene cricetodontine rodents, and recognized Mystromyinae as one group among several archaic African muroids within a broadly defined Nesomyidae (also see Carleton

& Musser 1984). The ancestral stock of *Mystromys* has been linked with *Democricetodon*, a cricetodontine from middle Miocene strata of Kenya (Tong & Jaeger 1993), or with *Mioharimys*, a myocricetodontine from the late Miocene of Namibia (Mein *et al.* 2000b).

Recent phylogenetic studies of nuclear and mitochondrial gene sequences reinforce Lavocat's perception of kinship, generally relating *Mystromys* to representatives of Malagasy Nesomyinae and African Cricetomyinae, Dendromurinae and Petromyscinae (Jansa *et al.* 1999, Michaux & Catzeffli 2000, Michaux *et al.* 2001). Analyses of the mitochondrial gene cytochrome *b* indicated *Petromyscus* as the nearest living relative of *Mystromys* (Jansa *et al.* 1999), a relationship supported by the unique development of an elongate medial spine on the ectotympanic bulla in both genera. Other interpretations of its phylogenetic affinity, whether with New World sigmodontine (Ellerman 1941) or gerbilline (Wessels 1996) rodents, find no support from these molecular studies or most morphological characters.

Extinct relatives of *Mystromys albicaudatus* include *M. pocockei* and *Proodontomys cookei*, both well represented by fossils from the Pliocene–Pleistocene australopithecine sites in South Africa (Pocock 1987, Denys 1991, Avery 1998). The distribution of *Mystromys* was once more widespread within the southern African sub-region, as indicated by the presence of mystromyines from the Pleistocene of Namibia (Senut *et al.* 1992).

Michael D. Carleton & Guy G. Musser

GENUS *Mystromys* African White-tailed Rat

Mystromys Wagner, 1841. Gelehrte Anz. I. K. Bayer. Akad. Wiss., München, 12 (54), col. 434.

Type species: *Mystromys albipes* Wagner, 1841 (= *Otomys albicaudatus* A. Smith, 1834).

A monotypic genus restricted to South Africa and Lesotho where it lives in savanna grasslands and fynbos habitats. Further details are given in the subfamily and species profiles. The single species is *Mystromys albicaudatus*.

D. C. D. Happold



Mystromys albicaudatus.

Mystromys albicaudatus AFRICAN WHITE-TAILED RAT (SOUTHERN AFRICAN HAMSTER)

Fr. Souris à queue blanche d'Afrique; Ger. Weißschwanzhamster

Mystromys albicaudatus (A. Smith, 1834). S. Afr. Quart. J., ser. 2, 2: 148: 1841, Illustrations of the Zoology of South Africa, Mammalia: pl. 33 and text. Albany District, Eastern Cape Province, South Africa.

Taxonomy Originally described in the genus *Otomys*. The relationships of this species are uncertain (see profile Subfamily Mystromyinae). Synonyms: *albipes*, *antiquus* (probably *nomen nudum*),

fumosus, *hauslichtneri*, *lanuginosa*. Subspecies: none. Chromosome number: not known.

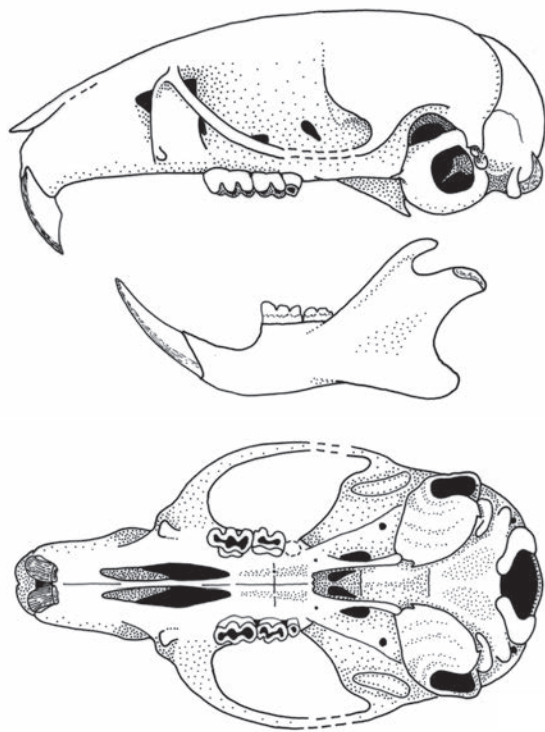


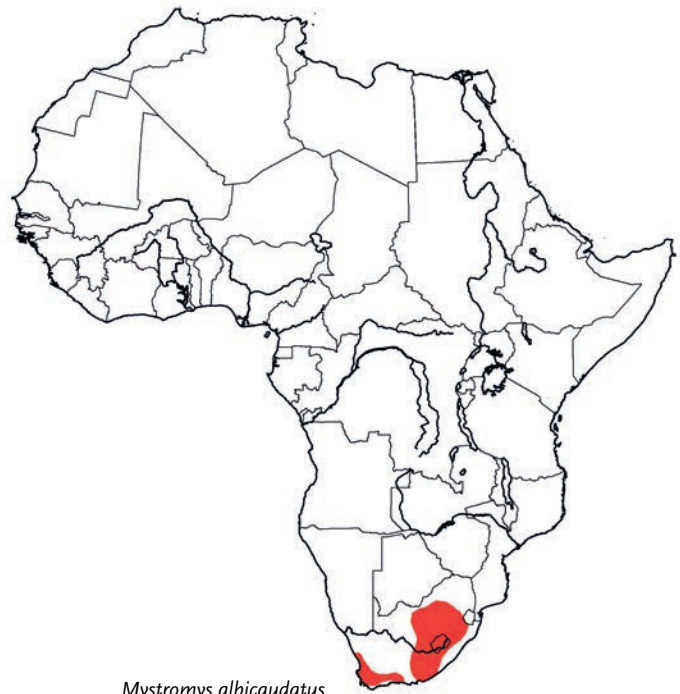
Figure 36. Skull and mandible of *Mystromys albicaudatus* (RMCA 34238).

Description Medium-sized to large, stocky rat with a soft, dense woolly pelage and short white tail. Dorsal pelage greyish-brown, slightly flecked with buff; hairs long (ca. 12 mm), dark grey at base, buff or black at tip. Ventral pelage greyish-white; hairs dark grey at base with off-white or cream tip. Head large and broad, mostly grey. Paler patches above eyes and at back of ears in some individuals. Side of face and upper lips pale grey or white, long vibrissae. Ears darkly pigmented, with dark brown and buff hairs. Fore- and hindlimbs short, off-white. Forefoot with four digits, and dense white hairs on upper surface; hindfoot with five digits, dense white hairs on upper and lateral surfaces; naked on plantar region. All digits with sharp claw. Tail short (ca. 35–40% of HB), unpigmented, with dense short white hairs above and below. Skull: incisors orthodont, zygomatic plate with vertical anterior margin, very long anterior palatal foramina, biserial cusps on molars (Figure 36); see also subfamily profile. Nipples: $0 + 2 = 4$.

Geographic Variation None recorded.

Similar Species No other species of similar weight within the geographic range has such a relatively short tail (ca. 35–40%).

Distribution Endemic to Africa. Highveld and South-West Cape BZs. Recorded in the eastern half of South Africa, south of 25° S (S Mpumalanga, Free State, KwaZulu–Natal and Eastern Cape Provinces) with a relict population in the fynbos of SW Western Cape Province. Also recorded from Lesotho (but not from Swaziland). Probably extended in the past throughout the southern savanna grasslands, heathlands and renosterveld of the SW Cape Province of South Africa. The record of *Mystromys* from Tanzania is incorrect (see Misonne 1974).



Mystromys albicaudatus

Habitat Grasslands, fynbos, montane grasslands, karoo, renosterveld and heathland habitats.

Abundance Uncertain, but probably uncommon or rare. Rarely encountered.

Adaptations Terrestrial and nocturnal. White-tailed Rats live in burrows or in cracks in the soil (De Graaff 1981). They possess a suite of unusual physiological characters: the bilocular hemiglandular stomach has a complex microflora and a ruminant-like digestion (Maddock & Perrin 1981) similar to that of the Gambian Giant Rat *Cricetomys gambianus* (Perrin & Kokkinn 1986); organic acids are produced by the catabolism of complex plant polysaccharides in the foregut and hindgut during digestion; food is fermented by bacteria in the hindgut; and metabolism and thermal regulation are typical of rodents adapted to a cold temperate habitat (Downs & Perrin 1995). The characters of the digestive system are assumed to enable White-tailed Rats to utilize plant foods containing chemical defences, which are unavailable as food to other species. The combination of high metabolic rate (higher than predicted for a mammal of this size), reduction of activity and foraging times in winter, and thermal insulation in burrows, are thought to reduce the necessity for torpor in winter. There is no evidence to suggest that White-tailed Rats enter torpor.

Foraging and Food No data available from wild populations. The special characters of the digestive system (see above) suggest an ability to digest a wide range of predominantly plant foods (Maddock 1981).

Social and Reproductive Behaviour No information.

Reproduction and Population Structure Likely to breed throughout the year in the wild (Roberts 1951) but confirmation

is required. Pregnant ♀♀ in the wild recorded in Jan, Jun and Jul. Gestation: 37 days. Litter-size in captivity: 2.9 (1–6). Embryo number: 3 and 4 (n = 2; Rautenbach 1982, Lynch 1983). Weight at birth 6.5 g. Eyes open Day 16–20. Weaned at about Day 38. Young cling to nipples until Day 19 (Hallett & Meester 1971). Minimum age of ♀♀ at first parturition is about six months; litter interval ca. 36 days. Breeds well in captivity.

Predators, Parasites and Diseases Predators include several species of owls (Davis 1959, Dean 1978a). Three species of mites and 12 species of fleas have been recorded (see De Graaff 1981). Susceptible to plague, which occurs sporadically in free-living populations (De Graaff 1981).

Conservation IUCN Category: Endangered. Listed as 'Vulnerable' in the South African Red Data Book (Smithers 1986b).

Habitat loss resulting from agriculture, habitat degradation and encroachment of the Karoo into grasslands are the main reasons for the decline in geographic distribution and populations numbers.

Measurements

Mystromys albicaudatus

HB (♂♂): 163 (139–184) mm, n = 12

HB (♀♀): 144 (105–147) mm, n = 16

T (♂♂): 58 (50–82) mm, n = 14

T (♀♀): 63 (53–97) mm, n = 16

HF (♂♂): 27 (24–30) mm, n = 14

HF (♀♀): 26 (24–28) mm, n = 16

E (♂♂): 26 (20–28) mm, n = 14

E (♀♀): 24 (20–27) mm, n = 16

WT (♂♂): 78, 113 g, n = 2

WT (♀♀): 75, 81 g, n = 2

GLS: 35.4 (34.2–36.9) mm, n = 7

GWS: 18.6 (17.6–19.2) mm, n = 7

M¹–M³: 5.9 (5.6–6.3) mm, n = 7

Body measurements and weights: South Africa (Rautenbach 1978)

Skull measurements: South Africa (TM)

Key References De Graaff 1981; Meester *et al.* 1986; Smithers 1986b.

Mike Perrin

Subfamily PETROMYSCINAE – Pygmy Rock Mice

Petromyscinae Roberts, 1951. Mammals of South Africa, p. 434.

This subfamily, consisting only of a single genus (*Petromyscus*) and four species, is endemic to Africa and confined to the South-West Arid BZ. Species of the subfamily live in dry regions where large boulders and rocky outcrops predominate; they are nocturnal, terrestrial and apparently omnivorous.

Rock Mice are small in size, with large pinnae, short limbs and long, soft and silky pelage. The moderately hairy tail is less than, equal to, or moderately longer than head and body depending upon the species. The hindfoot is short and broad, the toes relatively short with Digit 5 nearly as long as Digits 2–4. The cranium exhibits a long and slender rostrum, smooth and broad interorbital constriction, and wide and flat braincase devoid of temporal ridging; the jugal forms a large span of the zygomatic arch, and the zygomatic plate is wide with a deep dorsal notch (Figure 37). Anterior palatal foramina are narrow and long; bony palate wide and long, projecting behind the third molars as a prominent shelf; alisphenoid bone with well-developed dorsal flange and wide ventral strut; subsquamosal foramen closed in adults. The carotid circulatory pattern is partially derived, lacking a supraorbital artery (sphenofrontal foramen and squamosal-alisphenoid groove absent) but retaining the infraorbital (stapedial foramen large); ectotympanic bullae moderately inflated, with medial spine adnate to the basisphenoid. Entepicondylar foramen of humerus present. Stomach unilocular and hemiglandular. The molars are brachyodont and cuspidate, with uppers three-rooted and lowers two-rooted, and their cusps are longitudinally connected by short enamel crests. On M¹ and M² a large lingual cusp is adjacent to the protocone, coalescing with wear; anteroloph(id) and mesoloph(id) absent; discrete posteroloph absent on M¹ and M². M³ is very small, its occlusal pattern C-shaped and unlike that of M². The strongly opisthodont upper incisors have smooth enamel faces.

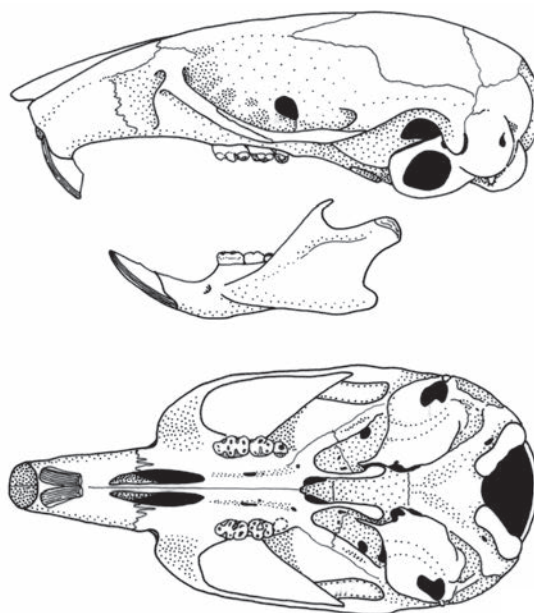


Figure 37. Skull and mandible of *Petromyscus collinus* (BMNH 25.1.2.154).

Petromyscus was initially considered an aberrant dendromurine because of the extra lingual cusp on its upper molars and the relatively small upper third molar (Allen 1939, Simpson 1945). Roberts (1951), however, diagnosed the subfamily Petromyscinae to stress the unique combination of traits exhibited by the genus and its relict distribution. Subsequent studies have generally reinforced Roberts's perception of phyletic isolation, although interpretations of the nearest generic relatives of *Petromyscus* have varied – whether

a distant kin of *Mystromys* (Ellerman 1941, Roberts 1951), an evolutionary link between *Mystromys* and dendromurines (Lavocat 1964, Petter 1966c), or a sister genus to *Delanymys* (Hayman 1962a, Petter 1967). As diagnostically contrasted above in the account of Delanymyinae, *Petromyscus* and *Delanymys* have little in common aside from the shared lingual molar cusps. Their union in the same subfamily, with the close phylogenetic affinity thereby implied, has been challenged (Carleton & Musser 1984, Denys 1994), and Musser & Carleton (2005) segregated each in its own subfamily. Close relationship of *Petromyscus* and *Mystromys*, on the other hand, has received support from phyletic interpretation of cytochrome *b* data

(Jansa *et al.* 1999), the two genera constituting a clade that is distantly removed from the single dendromurine sampled (*Steatomys*). The derivation of petromyscines has been linked with middle to late Miocene myocricetodontines, around 12–11 mya (Tong & Jaeger 1993, Mein *et al.* 2000b). In particular, Mein *et al.* (2000b) regarded *Harimyscus hoali*, of the late Miocene of Namibia, as the earliest known petromyscine. Namibia today encompasses the greater part of the distribution of three of the four extant species of *Petromyscus*.

Michael D. Carleton & Guy G. Musser

GENUS *Petromyscus*
Pygmy Rock Mice

Petromyscus Thomas, 1926. Ann. Mag. Nat. Hist., ser. 9, 17: 179. Type species: *Praomys collinus* Thomas and Hinton, 1925.



Petromyscus collinus.

The genus *Petromyscus* contains four species (Musser & Carlton 1993, 2005) distributed throughout the South-West Arid BZ (Davis 1962), and is the only genus in the subfamily. The characters of the genus are given in the profile of Subfamily Petromyscinae above. All species in the genus are restricted to rocky habitats where boulders and rocks provide shelter. The four species are distinguished by pelage colour, length of tail and ear, slight differences in skull characters, and geographic distribution (Table 18).

C. G. Coetzee

Table 18. Species in the genus *Petromyscus*. Arranged in increasing head and body length.

| Species | HB mean (range) (mm) | Tail mean (range) (mm) (% of HB) | Nipples | Dorsal pelage | Notes |
|------------------------|----------------------|----------------------------------|-----------|---------------------------|-------------------------------------|
| <i>P. monticularis</i> | 75.3 (63–93) | 73.3 (66–84) (98%) | 1 + 2 = 6 | Dark brown | Namibia, N South Africa |
| <i>P. barbouri</i> | 76 (71–79) | 82 (71–99) (108%) | 0 + 2 = 4 | Drab grey, speckled brown | NW South Africa |
| <i>P. collinus</i> | 79.8 (62–97) | 91 (67–114) (113%) | 1 + 2 = 6 | Buff-brown | SW Angola, Namibia, NW South Africa |
| <i>P. shortridgei</i> | 83.4 (65–98) | 87.4 (74–104) (104%) | 0 + 2 = 4 | Dark brown | S Angola, N Namibia |

Petromyscus barbouri BARBOUR’S PYGMY ROCK MOUSE (NAMAQUA PYGMY ROCK MOUSE)
Fr. Souris des rochers à queue courte; Ger. Barbours Felsenmaus

Petromyscus barbouri Shortridge and Carter, 1938. Ann. S. Afr. Mus. 32: 288. Kamiesberg, Witwater, Little Namaqualand, NW Cape Province, South Africa. 3500–3800 ft (1275–1385 m).

Taxonomy Considered to be a subspecies of *P. collinus* by Smithers (1983) and Meester *et al.* (1986); now recognized as a valid species (Musser & Carleton 1993, 2005). Synonyms: none. Chromosome number: not known.

Description Very small to small mouse, similar in general form to the House Mouse *Mus musculus*. Pelage fine, soft and silky. Dorsal pelage grizzled drab grey, speckled with pale brown. Ventral pelage drab grey. Head similar in colour to dorsal pelage. Juveniles drab

grey without speckled pale brown. Ears relatively large (ca. 83% of HF), darkly pigmented. Fore- and hindfeet relatively short, whitish. Tail long (ca. 108% of HB), bicoloured, drab grey above, white below with sparse bristles especially towards the tip, not forming a pencil or tuft. Nipples: 0 + 2 = 4.

Geographic Variation None recorded.

Similar Species

P. collinus. HB slightly larger; ear longer (mean 15 mm); tail length longer (mean 91 mm) and relatively longer, not bicoloured; longer skull length (mean 25 mm); relatively longer rostrum; sympatric and with much greater geographic range.

P. monticularis. HB similar (mean 75.3 mm); ear shorter (mean 11.6 mm); tail shorter (mean 73.5 mm) and relatively shorter, maybe bicoloured; ear shorter (mean 11.6 mm); allopatric or parapatric; restricted geographic range.

P. shortridgei. HB larger (mean 83.4 mm); ear longer (mean 15 mm); tail slightly longer (mean 87.4 mm), bicoloured; allopatric.

Distribution Endemic to Africa. South-West Arid BZ (Namib Desert and Karoo). Widely distributed in Namaqualand, South Africa (Shortridge & Carter 1938, Shortridge, 1942). In the lower Orange River basin of South Africa, distribution is sympatric or parapatric to that of *P. collinus* and *P. monticularis*.

Habitat Rocky outcrops and hills where there are succulent bushes and annual herbs during the winter rainfall season. Winters wet and cold, summers dry and hot.

Abundance Unknown; regarded as rare.

Remarks Nocturnal. Adapted to arid and semi-arid environment with moist, relatively cold and wet winters and warm, dry summers (Shortridge 1942). Mainly granivorous.

Conservation IUCN Category: Least Concern.

Parts of the range are protected in conservation areas (e.g. Goegab Nature Reserve near Springbok, and Namaqualand National Park). Goat farming could have a harmful and destructive effect on the habitat due to the grazing and browsing of goats amongst the rocks.



Petromyscus barbouri

Measurements*

Petromyscus barbouri

HB: 76 ± 7.3 (71–96) mm, n = 22

T: 82 ± 6.6 (71–99) mm, n = 22

HF (c.u.): 16.8 ± 1 (15–18) mm, n = 22

E: 14 ± 1.7 (13–22) mm, n = 22

WT: n. d.

GLS: 23 ± 1.06 (21.5–26.3) mm, n = 21

GWS: 11.7 ± 0.36 (11.1–12.6) mm, n = 21

M¹–M³: 3.6 ± 0.24 (3.2–4.1) mm, n = 21

Namaqualand, South Africa (C. G. Coetzee unpubl.)

*Mean \pm 1 S.D.

Key References Shortridge 1942; Shortridge & Carter 1938; Smithers 1983.

C. G. Coetzee

Petromyscus collinus PYGMY ROCK MOUSE

Fr. Souris de rochers pygmée; Ger. Zwerg Felsenmaus

Petromyscus collinus (Thomas and Hinton, 1925). Proc. Zool. Soc. Lond. 1925: 237. Karibib, Damaraland, Namibia. 1025 m.

Taxonomy Originally described in the genus *Praomys*. Allocated to the genus *Petromyscus* when that genus was proposed by Thomas in 1926. Synonyms: *bruchus*, *capensis*, *kaokoensis*, *kurzi*, *namibensis*, *rufus*, *variabilis*. Subspecies: none currently recognized but some of the forms listed as synonyms may prove to be valid subspecies. Chromosome number: 2n = 60 (T. Robinson and V. Rambau pers. comm.; Namibia).

Description Very small to small mouse. Pelage soft and silky. Dorsal pelage buff or brown (variable according to locality); hairs dark grey at base, buff or brown at tip. Juveniles dark grey. Ventral pelage white to pale grey; hairs grey at base, whitish at tip. Colours of dorsal and ventral pelage merge on flanks. Head similar in colour to dorsal pelage. Vibrissae long. Ears large (ca. 94% of HF) and rounded, pigmented, sparsely covered with short hairs of the same colour as head. Fore- and hindfeet short, dorsally covered with

short white hair, Digit 5 nearly as long as Digits 2–4. Tail relatively long (ca. 113% of HB), with rings of scales, darker above; may be bicoloured and paler below with sparse short whitish bristles. Skull characters as for genus. Nipples: $1 + 2 = 6$.

Geographic Variation No subspecies recognized but pelage varies in colour forming a cline from darker in the south-east to paler in the north-west.

Similar Species

- P. barbouri*. Slightly smaller body size; tail shorter (and relatively shorter); sympatric in southern part of range; more restricted geographical range.
- P. monticularis*. Smaller body size; dorsal pelage dark brown; tail shorter (and relatively shorter); ear shorter; mean GLS shorter; sympatric in southern part of range; restricted geographical range.
- P. shortridgei*. Larger body size; tail shorter (and relatively shorter); sympatric in central part of range.

Distribution Endemic to Africa. South-West Arid BZ (especially Namib Desert and parts of the Karoo). Recorded from Namibia, desert areas of SW Angola and the Orange River Valley and the central Karoo of South Africa. In Angola, known only west of the Chela Escarpment as far north as $13^{\circ}23'S$, and $13^{\circ}53'E$ (Crawford-Cabral 1998) and where the pro-Namib vegetation reaches the coast at Praia Madalena ($14^{\circ}37'S$, $12^{\circ}18'E$; C. G. Coetzee unpubl.). Widespread in W Namibia in the Namib and adjoining western mountainous regions, southwards to the Orange R. In South Africa, recorded throughout the central Karoo from the border with Namibia to about $33^{\circ}S$ and 19° – $22^{\circ}E$ (J. A. J. Nel unpubl., Stuart *et al.* 1987).

Habitat Arid and semi-arid habitats, especially in mountains and rocky areas where there are crevices amongst large boulders



and rock fringes. Mean annual rainfall 30–400 mm/annum. May also occur along canyons that support some vegetation, and where rainfall is even lower (ca. mean 15 mm/annum).

Abundance Generally rare. May be abundant at some localities, e.g. at Tumasberg, Namibia, where it comprised 65% of six species of small mammals (*Aethomys namaquensis* 21%, *Petromus typicus* 17%, *Elephantulus rupestris* 3%, *Gerbillus paebe* < 1%, *Mus minutoides* < 1%; $n = 239$; Withers 1979). Density on 6 ha study area during most of year was ca. 4–6/ha to 9.5/ha (Withers 1979).

Adaptations Nocturnal. Shelters during daytime in crevices under and amongst rocks and boulders. Emerges at dusk, most active until ca. 02:00h. Not active outside burrows during pre-dawn and early morning (Withers 1979). Broad feet adapted for climbing; limbs short (but capable of vertical jumps of 40 cm; C. G. Coetzee unpubl.). Individuals adjust their water requirements according to water availability. When free water is unavailable, they can survive on water in seeds and other windblown material without the need for drinking water. When water precipitates from fog, water turnover rates increase (Withers *et al.* 1980). Daily energy expenditure is low, and reduced Tb and torpor aid survival in cool weather. The combination of low reproductive potential, low annual mortality and ability to survive on a dry seed diet are advantageous for life in an arid environment. *Petromyscus* appears to be physiologically intermediate between *Petromus typicus* (well adapted) and *Aethomys namaquensis* (less well adapted) in its adaptations to an arid environment (Withers *et al.* 1980). Even so, *Petromyscus* is present in the more xeric regions of the Namib Desert where vegetation is sparse and confined to slight moist areas below or between rocks.

Foraging and Food Granivorous and omnivorous. Foraging for seeds occurs primarily close to the boulders and rocks that provide safety from predators rather than at the base of a kopje or further away (20 and 40 m) on the surrounding alluvial plain (Brown *et al.* 1998). The diet is primarily seeds, with some stems; insects form ca. 25% of stomach contents in the pro-Namib ($n = 16$; Withers 1979). This diet is comparable to that of sympatric *Aethomys namaquensis*, and unlike that of the larger, diurnal *Petromus typicus*, which feeds mainly on plant stems. An alternative source of food on kopjes (where the number of grasses and seeds is limited and hyraxes occur) is seeds deposited in the faecal pellets of hyraxes (which feed extensively away from the kopje), and insects, which themselves are feeding on the faecal pellets (Brown *et al.* 1998). Seeds accumulated amongst and below rocks form an important food source, especially on outcrops and in canyons in extreme xeric regions (C. G. Coetzee unpubl.).

Social and Reproductive Behaviour Solitary. Home-range ca. 0.27 ha (Withers 1979). Home-ranges of ♂♂ show little overlap, but may overlap with those of ♀♀. Home-ranges of ♀♀ often overlap. It is likely that ♂♂ defend their home-ranges against other ♂♂, but tolerate the presence of ♀♀ (Withers 1979). In captivity, fighting occurs between individuals of opposite sex, and ♀ does not tolerate the presence of ♂ (C. G. Coetzee unpubl.).

Reproduction and Population Structure Reproduction is seasonal and ♀♀ probably have 1–2 litters/year. Pregnant ♀♀ and

sexually active ♂♂ recorded Aug–Mar (C. G. Coetzee unpubl.; Namibia). At Tumasberg, Namibia, ♂♂ and ♀♀ become sexually active when fog precipitation begins (Oct–Mar, max Jan–Mar) (Withers 1983). Embryo number: 2.7 (1–6), n = 11 pregnancies (C. G. Coetzee unpubl.). Dempster & Perrin (1989) recorded an average of 2.8 young in eight litters born in captivity. Young are nipple-dragged by mother (Dempster & Perrin 1989). Sex ratio 1:1.27, n = 149 (C. G. Coetzee unpubl.); mean monthly survival 0.9; annual survival rate 0.36; life expectancy 6.6 months (Tumasberg, Namibia; Withers 1979).

Predators, Parasites and Diseases Predators include several species of mammals, owls and snakes (Mammals: *Felis lybica*, *Galerella sanguinea*, *G. pulverulenta*, *Canis mesomelas* and *Vulpes chama*. Owls: *Tyto alba*, *Otus leucotis*, *Glaucidium perlatus* and *Bubo africanus*. Snakes: *Python anchietae*, *Pseudopsis cana*, *Naja nigricollis*, *Naja haje*, *Bitis arietans*, *Bitis cornuta* and *B. caudalis*). Ectoparasites include two species of mites (*Laelaps brandbergensis*, *Androlaelaps zuluensis*) and one species of tick (*Haematophysalis leachii*). Five species of fleas (*Chistopsylla nama*, *Epirimia aganippes*, *Xenopsylla philoxera* [De Meillon *et al.* 1961], *Listropsylla agrippinae* and *Chistopsylla quadrisetis* [Stuart *et al.* 1987]). One species of endoparasite (nematode: *Acanthoxyuris shortridgei*) has been recorded (De Graaff 1981 and references therein).

Conservation IUCN Category: Least Concern.

Protected in several conservation areas such as Iona Park in Angola, Namibia and South Africa.

Measurements*

Petromyscus collinus

HB: 79.8 ± 7.97 (62–97) mm, n = 178

T: 91 ± 8.93 (67–114) mm, n = 171

HF (c.u.): 15.9 ± 1.37 (11–18) mm, n = 180

E: 15 ± 1.7 (11–17) mm, n = 177

WT: 100 ± 17.3 (80–129) g, n = 8

GLS: 25 ± 1.19 (21–27.9) mm, n = 162

GWS: 11.9 ± 0.53 (10.5–13.4) mm, n = 162

M¹–M³: 3.78 ± 0.24 (3.2–4.2) mm, n = 165

Angola, Namibia and South Africa (C. G. Coetzee unpubl.)

*Mean \pm 1 S.D.

Key References De Graaff 1981; Withers 1979, 1983.

C. G. Coetzee

Petromyscus monticularis BRUKKAROS PYGMY ROCK MOUSE (SHORT-EARED PYGMY ROCK MOUSE)

Fr. Souris des rochers des Monts Brukkaros; Ger. Brukkaros-Felsenmaus

Petromyscus monticularis (Thomas and Hinton, 1925). Proc. Zool. Soc. Lond. 1925: 238.

Small 'kopje' not far from Great Brukkaros Mt, near Berseba, S Namibia. 1100 m. (Type locality correction; Shortridge 1934.)

Taxonomy Originally described in the genus *Praomys*. Synonyms: none. Chromosome number: not known.

Description Very small to small mouse, the smallest species in the genus. Dorsal pelage dark brown; hairs dark grey on basal two-thirds, brown on terminal third. Flanks similar to dorsal pelage. Ventral pelage slate-grey without a clear delineation between dorsal and ventral colouration. Head similar in colour to dorsal pelage. Ear comparatively small (ca. 74% of HF; cf. other congeneric species 83% to 94%), darker than dorsal pelage. Hindfeet with five digits, Digit 5 nearly as long as Digit 2. Fore- and hindfeet whitish dorsally. Tail moderately long (ca. 98% of HB, but comparatively shorter than in other *Petromyscus*); slightly scaly, dark brown above, same colour or slightly paler below, sparsely covered with hairs. Nipples: 1 + 2 = 6.

Geographic Variation None recorded.

Similar Species (size comparisons refer to mean values only)

P. barbouri. Slightly larger body size, tail slightly longer, ears larger, diastema shorter in relation to upper molar tooththrow; probably parapatric in South Africa.

P. collinus. Slightly larger body size; dorsal pelage brown; tail longer (and relatively longer); ears larger (and relatively larger); sympatric throughout most of range; more extensive geographic range.

Aethomys namaquensis (young). Similar size (adults much larger); tail and hindfoot relatively longer.



Petromyscus monticularis

Mus indutus. Smaller body size; ventral pelage pure white, clearly delineated from dorsal pelage.

Distribution Endemic to Africa. South-West Arid BZ (mainly southern part of Namib Desert). Recorded only in Namibia and South Africa from the edge of the Namib Desert in the west (roughly between 25–26° S and 16–18° 30' E) south-eastwards into the arid Karoo to about 30° S and 21° E. Range extends upstream along the Orange R. catchment to below its junction with the Vaal R.

Habitat Rocky plains, mostly amongst small stones and rock rubble at the foot of rocky outcrops; does not live amongst large boulders on mountain slopes. Habitat is mostly Dwarf Shrub Savanna in Namibia (Giess 1971), and the Karoo in South Africa. Sympatric (and probably syntopic) with *P. collinus*.

Abundance Rare.

Remarks Mainly granivorous, and omnivorous. Stomach contents (n = 17) contained seeds (100% of stomachs), insects (53%) and plant remains (37%). In Feb, all individuals were adult: ♂♂ scrotal; ♀♀ not pregnant (Baker & Baker 1984). Grass seeds blowing in from the plains and accumulating amongst stones are an additional source of food, apart from the plants growing locally.

Conservation IUCN Category: Least Concern.

Habitat conservation is important for survival of the species. Habitat disturbance by domestic sheep and goats could be a problem, especially during periods of prolonged drought. Protected in the Fish River Canyon N. P. in Namibia, in the Augrabies N. P. in South Africa, and in private parks and conservation areas.

Measurements*

Petromyscus monticularis

HB: 75.3 ± 7.5 (63–93) mm, n = 27

T: 73.5 ± 5.2 (66–84) mm, n = 26

HF (c.u.): 15.6 ± 0.9 (13–17) mm, n = 28

E: 11.6 ± 1.1 (10–14) mm, n = 28

WT: n. d.

GLS: 22.6 ± 1.82 (19–26.2) mm, n = 28

GWS: 11.7 ± 0.5 (10.9–12.8) mm, n = 28

M¹–M³: 3.6 ± 0.26 (3.2–4.3) mm, n = 28

Namibia and South Africa (C. G. Coetzee unpubl.)

*Mean \pm 1 S.D.

Key Reference Shortridge 1934.

C. G. Coetzee

Petromyscus shortridgei SHORTRIDGE'S PYGMY ROCK MOUSE (KAOKOVELD PYGMY ROCK MOUSE)

Fr. Souris des rochers de Shortridge; Ger. Shortridges Felsenmaus

Petromyscus shortridgei Thomas, 1926. Proc. Zool. Soc. Lond. 1926: 306. Rua Cana Falls (= Cunene Falls), S Namibia. 877 m.

Taxonomy Originally described as a species by Thomas (1926), but considered to be a subspecies of *P. bruchus* (now a synonym of *P. collinus*) by Roberts (1951) or a subspecies of *P. collinus* (Ellerman *et al.* 1953, De Graaff 1981, Meester *et al.* 1986). Currently considered to be a valid species (Musser & Carleton 1993, 2005). Synonyms: none. Chromosome number: not known.

Description Very small to small mouse, although on average larger than other species in the genus. Pelage soft. Dorsal pelage dark brown, finely speckled with brownish-black; hairs dark grey on basal two-thirds, brown on terminal third. Ventral pelage greyish-white; hairs slate-grey at base, white at tip. Dorsal pelage in young and subadults greyish. Ears large (ca. 91% of HF), round. Fore- and hindfeet dorsally whitish. Hindfeet with five digits; Digit 1 reduced, Digit 5 nearly as long as Digit 2. Tail moderately long (ca. 104% of HB), bicoloured, dark brown above, cream below, bristles short. Nipples: 0 + 2 = 4 (sometimes ?1 + 2 = 6).

Geographic Variation None recorded.

Similar Species (size comparisons refer to mean values only)

P. collinus. Slightly larger; tail longer (and relatively longer); sympatric; larger geographical range (other *Petromyscus* spp. are allopatric to *P. shortridgei*).

Aethomys namaquensis (young). Similar size (adults much larger); tail and hindfoot relatively longer.



Petromyscus shortridgei

Mastomys coucha (subadult). Similar size (adults larger); dorsal pelage grey; Digit 5 of hindfoot not lengthened.

Distribution Endemic to South-West Arid BZ (northern part of the Kalahari Desert and Namib Desert) and adjoining parts of Zambezian Woodland BZ. Recorded from Angola and Namibia. In SW Angola, occurs in mountainous areas in semi-arid regions (Crawford-Cabral 1998), and in the Cunene River Valley below the Cunene Falls. In Namibia, occurs in the Kaokoveld north of ca. 22° S, and eastwards throughout the Karstveld towards the Otavi and Waterberg Mts.

Habitat Hilly mountainous country. Preferred habitat is rugged granitic mountainous areas (interspersed with dolomites and igneous complexes); here loose boulders are piled on top of each other, providing holes and crevices, and common trees are *Kirkia acuminata*, *Croton* spp. and *Commiphora* spp.

Abundance Generally rare, relatively more abundant than other rodents in extreme xeric areas, and in some localities may be the only species.

Remarks Nocturnal, solitary. Legs and feet short, well adapted for climbing and moving around boulders. Diet consists mainly of seeds but also insects, stems and leaves. Pregnant ♀♀ were collected during Feb, May and Aug–Nov. Embryo number: 2–4 (n = 16; Shortridge 1934, C. G. Coetzee unpubl.).

Conservation IUCN Category: Least Concern.

The habitat is currently not threatened because of the ruggedness of the terrain and low impact of human activities.

Measurements*

Petromyscus shortridgei

HB: 83.4 ± 7.5 (65–98) mm, n = 85

T: 87.4 ± 8.14 (74–104) mm, n = 81

HF (c.u.): 16.5 ± 1.4 (15–20) mm, n = 82

E: 15 ± 1.04 (13–18) mm, n = 82

WT: 18.9 ± 4.71 (12–31) g, n = 36

GLS: 25.7 ± 0.6 (24–28.8) mm, n = 58

GWS: 12.2 ± 0.43 (11–13.2) mm, n = 58

M¹–M³: 3.9 ± 0.24 (3.4–4.5) mm, n = 60

SW Angola and NW Namibia (C. G. Coetzee unpubl.)

*Mean \pm 1 S.D.

Key References Shortridge 1934; Skinner & Smithers 1990.

C. G. Coetzee

Family CRICETIDAE

HAMSTERS, VOLES AND NEW WORLD MICE AND RATS

Cricetidae Fischer de Waldheim, 1817. Mém. Soc. Imp. Nat., Moscow 5: 372.

| | | |
|-------------------------------|---------------|--------|
| <i>Microtus</i> (1 species) | Muster's Vole | p. 211 |
| <i>Lophiomyys</i> (1 species) | Maned Rat | p. 213 |

The family Cricetidae, embracing some 130 genera and over 670 species (Musser & Carleton 2005), represents one of the two dominant radiations of living muroid rodents. Species in the family are abundant in many terrestrial habitats in the New World (Neotominae and Sigmodontinae), Holarctic (Arvicolinae) and Palearctic (Cricetinae), but only two species with restricted distributions are present in Africa (one Arvicolinae in coastal regions of North Africa, and one Lophiomyinae in East Africa). Members of Arvicolinae and Lophiomyinae are so morphologically distinctive (see subfamily and species profiles below) that their separation is unmistakable, whether from one another or from any African species of Spalacidae, Nesomyidae or Muridae. Although possessing numerous derived traits, Arvicolinae and Lophiomyinae have molars whose cusps are arranged biserially and connected medially by longitudinal enamel crests, dental characters thought to be primitive for the family and indicative of their descent from some very distant common ancestor.

The recognition of a family Cricetidae, notably as distinct from a comparably speciose Muridae, has long and recurrent support in influential classifications of muroid rodents (e.g. Miller & Gidley 1918, Simpson 1945, Misonne 1974, Chaline *et al.* 1977, Reig 1984). The contents and rank of muroid groups apportioned among the two families have differed in detail (see summary in Carleton & Musser 1984); indeed, some authorities have recognized only a single, all-inclusive family Muridae that includes all those groups others have classified under Cricetidae (Thomas 1897, Ellerman 1941, Carleton & Musser 1984). Monophyly of the family, as understood here, finds general support in recent phylogenetic evaluations of gene-sequence data (Robinson *et al.* 1997, Dubois *et al.* 1999, Michaux & Catzeflis

2000, Michaux *et al.* 2001). This cladistic view of Cricetidae, in particular the inclusion of Lophiomyinae, requires extended phylogenetic investigation.

Within Africa, the Lophiomyinae is known from the late Miocene to Pleistocene in Morocco and Recent in East Africa (Aguilar & Michaux 1989–1990, Geraads 1998), and Arvicolinae from the middle Pleistocene to Recent in Mediterranean Africa (Jaeger 1988b). The fossil record of ‘cricetids’ in North America and Eurasia is more taxonomically diverse and geologically older (late Eocene to Recent; McKenna & Bell 1997), and several groups, e.g. cricetodontines, eucricetodontines, paracricetodontines and cricetomines, have been variously acknowledged as families separate from Cricetidae. In fact, certain African Miocene genera, such as *Afrocricetodon* and *Myocricetodon*, had been affiliated previously within a broadly defined Cricetodontinae in the family Cricetidae. The gist of current understanding, however, indicates that the latter genera, and their subsequently described relatives, have figured prominently in the evolutionary origin of other muroid assemblages concentrated in Africa (*Afrocricetodontinae* and *Nesomyidae*; *Myocricetodontinae* and *Gerbillinae*). The specifics of such ancestral-descendant connections, and their classificatory representation, are subject to dispute among palaeontologists, and new fossil discoveries from critical middle Tertiary beds continue to emerge and revise considerations of affinity. The reader is referred to Lavocat (1978), Tong & Jaeger (1993) and Mein *et al.* (2000b) for overviews of many of these extinct African groups.

In Africa, the family is represented by two subfamilies, Arvicolinae and Lophiomyinae, each with a single species. Size categories of species in the family (based on mean head and body length) are given in the order Rodentia profile.

Michael D. Carleton & Guy G. Musser

Subfamily ARVICOLINAE – Voles, Lemmings and Muskrats

Arvicolinae Gray, 1821. London Med. Repos. 15: 303.

This large Holarctic subfamily, numbering about 28 genera and 153 species worldwide (Musser & Carleton 2005), has only one representative (*Microtus mustersi*) in Africa. The members of this subfamily form an important component of ecological communities in temperate, boreal and arctic biomes throughout much of the northern hemisphere. In Asia and North America, a few species occupy montane tropical forests and sub-alpine parklands south of the Tropic of Cancer (22°S), whereas in Africa, the southern limit is about 30°N on the Mediterranean littoral of northern Libya. Climatic conditions along Africa’s Mediterranean littoral ameliorated periodically during the Pleistocene and Holocene, allowing voles to reach northern Africa from the Middle East. However, the present distribution of the subfamily in Africa is severely restricted by the arid environment of the Sahara Desert. Other voles, such as *Ellobius*, once occurred broadly over northern Africa during the middle to

late Pleistocene (Jaeger 1988a), extending as far west as Morocco; today, the nearest approach of this genus to Africa lies in eastern Turkey and north-western Iran.

Within the Arvicolinae, *M. mustersi* is a member of a highly derived genus, *Microtus* (63 species), and tribe, Arvicolini (ten genera), whose worldwide ranges are practically congruent with that of the subfamily. Monophyly of the genus is supported by chromosomal, allozymic and DNA studies (e.g. Chaline & Graf 1988, Zagorodnyuk 1990, Modi 1996, Conroy & Cook 2000). Many apomorphic morphological traits also characterize species of *Microtus* (see review by Carleton 1985): noteworthy are the possession of continuously growing (rootless) molars, cement in the re-entrant angles, increased number of molar prisms and subtle rearrangements of the enamel microstructure (Hinton 1926a, Guthrie 1971, Phillips & Oxberry 1972, von Koenigswald 1980). Such evolutionary

innovations, accompanied by architectural restructuring of the cranium and zygomatic musculature (Kesner 1980), served to enhance side-to-side chewing, comminution of abrasive foods such as siliceous forbs and grasses, and exploitation of a herbivorous niche, the trophic hallmark of the subfamily. *Microtus* is known from the late Pliocene to Recent (Repenning 1992, Chaline *et al.* 1999), but the major episode of specific radiation did not transpire until the middle

Pleistocene, about 1.3 mya (Conroy & Cook 2000). The geological range of Arvicolinae is early Pliocene to Recent in Eurasia and North America, and middle Pleistocene to Recent in Mediterranean Africa (Jaeger 1988, McKenna & Bell 1997).

Michael D. Carleton & Guy G. Musser

GENUS *Microtus*

Voles

Microtus Schrank, 1798. Fauna Boica 1: 72. Type species: *Microtus terrestris* Schrank, 1798 (= *Mus arvalis* Pallas, 1778).

The genus is widespread in the Palearctic region and is represented by only a single species (*Microtus mustersi*) in Africa. The characters of the genus are given in the profile Subfamily Arvicolinae and the species profile below.

D. C. D. Happold

Microtus mustersi MUSTERS'S VOLE

Fr. Campagnol de Musters; Ger. Musters Wühlmaus

Microtus mustersi Hinton, 1926. Merg, Cyrenaica, Libya. Ann. Mag. Nat. Hist., ser. 4, 18: 305.

Taxonomy The status of *mustersi* is debatable. Ranck (1968) considered *mustersi* as a species distinct from other species of *Microtus* in the Middle East, i.e. *M. philistinus*, *M. guentheri* and *M. irani*. In contrast, Musser & Carleton (1993) place *mustersi* as a synonym of *Microtus irani*, and Ellerman & Morrison-Scott (1951) and Musser & Carleton (2005) place it as a subspecies of *M. guentheri*. However, the Libyan population of *Microtus* is isolated from all other populations; the next nearest form (*philistinus* = *M. guentheri*) is in Israel about 1200 km to the east. Because of its isolation, as well as differences in skull morphology and colour from other members of the genus, *mustersi* is retained as a species here. Synonyms: none. Chromosome number: not known.

Description Small brown vole with soft pelage and short tail. Dorsal pelage medium-brown; dorsal hairs soft, dense and fairly short, dark grey with medium-brown tips. Pelage paler on flanks, merging into whitish-grey on ventral surface. Ventral hairs shorter than dorsal hairs, grey with creamy-white tips. Ears small and rounded, covered with short brown hairs, and partially covered by hairs on cheeks. Chin, throat and chest grey. Fore- and hindlimbs with creamy-white hairs. Tail very short (ca. 25% of HB) and thin, covered with short brown hairs above, white hairs below. Skull: incisors orthodont, ungrooved; zygomatic plate small and convex, not extending anteriorly to zygomatic arch; zygomatic arches smooth and wide; auditory bullae moderately inflated; cheekteeth with very characteristic 'zig-zag' pattern of enamel and dentine; M¹, M² and M³ almost of equal length, each with three labial outward-pointing cusps (Figure 38). Nipples: 2 + 2 = 8.

Geographic Variation None recorded.

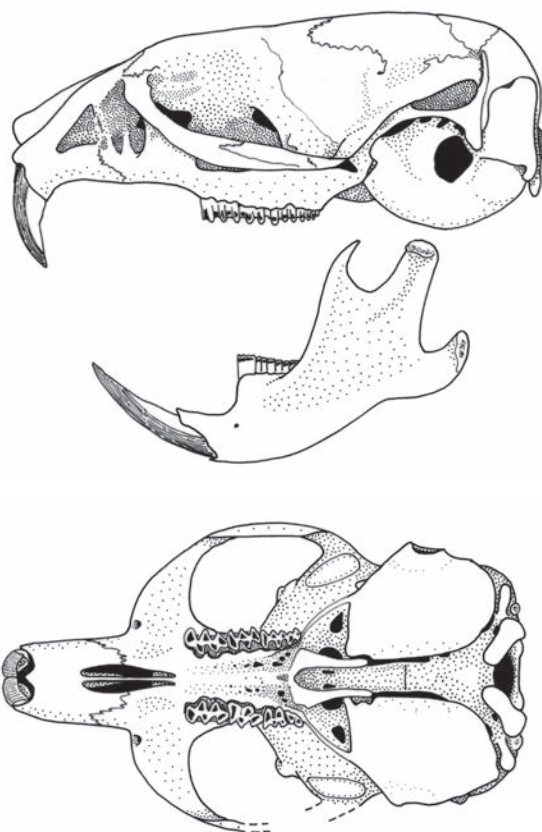


Figure 38. Skull and mandible of *Microtus mustersi* (BMNH 26.8.4.3).



Similar Species This is the only species of vole in Africa. Distinguished from other species of rodents in Libya by its shaggy pelage, small hairy ears and very short tail.

Distribution Endemic to Africa. Sahara Arid BZ. Recorded only on the Cyrenaica Plateau and coastal plains of N Libya. It seems likely that voles reached Cyreniaca from coastal Egypt (Ranck 1968), and that the present population is a relict from the time when the more boreal climates of the Pleistocene prevailed over North Africa. The Cyrenaica Plateau by virtue of its higher elevation has retained at least a vestige of these boreal elements, whereas the remainder of coastal Africa has become much drier and more sparsely vegetated and no longer contains habitats suitable for voles (Ranck 1968).

Habitat On the coastal plain, Musters's Voles live in dense cover of bush-like perennials, together with *Mus musculus* (*Mus spretus*), *Gerbillus campestris* and *Crocidura russula* (Ranck 1968), and rarely occur in tamarix, grass and sedge habitats (Ranck 1968). Also found in agricultural fields and areas where there is surface water in winter and spring. At higher elevations on the Cyrenaica Plateau, they live among large rocks and succulent vegetation (Hufnagl 1972).

Abundance 'Common' near the town of Merg (Hinton 1926b) where the type series was collected. In Lebanon, population numbers

of related species of voles fluctuate dramatically from year to year, and they may be serious agricultural pests when populations are high (Lewis *et al.* 1967, Atallah 1978).

Adaptations Voles (*Microtus* spp.) breed rapidly (see below) and hence their population numbers may increase very rapidly. Like voles in Europe, Musters's Voles dig burrows and make runs through dense vegetation. They appear to be active at most hours of the day and night.

Foraging and Food Herbivorous. Stalks of grasses are pulled into the burrows (J. L. Chaworth-Musters in Hinton 1926b).

Social and Reproductive Behaviour Live in groups in large burrows. Well-marked runways link burrow systems. There is some evidence that ♂♂ and ♀♀ live in different burrows during the breeding season (J. L. Chaworth-Musters in Hinton 1926b).

Reproduction and Population Structure No information. Related species in Lebanon are very prolific and breed throughout the year at lower altitudes; such ♀♀ produce an average of 8 embryos/litter ($n = 27$ ♀♀) and consequently when populations are increasing rapidly, they are comprised mainly of young animals (Atallah 1978).

Predators, Parasites and Diseases Preyed on by Barn Owls *Tyto alba* (specimens in SMF). Owls, hawks, foxes, mustelids and snakes prey on related species of voles in Israel (Qumsiyeh 1996).

Conservation IUCN Category: Least Concern (as *M. guentheri*). However, status of *M. mustersi* in Libya is poorly known; the populations are isolated and have a small geographic range.

Measurements

Microtus mustersi

HB: 117 (109–124) mm, $n = 5$

T: 22.8 (20–25) mm, $n = 5$

HF: 18 (12–18) mm, $n = 5$

E: 10.2 (10–11) mm, $n = 5$

WT: n. d.

GLS: 27.4 (27.2–27.7) mm, $n = 3$

GWS: 16.2 (15.8–16.5) mm, $n = 3$

M^1 – M^3 : 6.3 (6.2–6.4), $n = 3$

Cyrenaica, Libya (BMNH)

Key References Hinton 1926b; Hufnagl 1972; Ranck 1968.

D. C. D. Happold

Subfamily LOPHIOMYINAE – Maned Rat

Lophiomyinae Milne-Edwards, 1867. Arch. Mus. Hist. Nat. Paris. Memoires C, III: 81–116.

The geographic range of the single living genus and species comprising this subfamily is confined to eastern Africa. Within this region, the recorded distribution of *Lophiomyys imhausi* is disjunct and its altitudinal range is exceptionally broad, from sea level to over 3000 m; habitat

associations are correspondingly varied, including dry lowland woods and montane forest, rocky ravines and brush-covered banks (Hollister 1919, Kingdon 1974, Clausnitzer & Kityo 2001, Pearch *et al.* 2001). Eleventh-century archaeological records of the species from the

Judean Desert, Israel (Dor 1966) may represent human transport, and suppositions about a former natural range in Arabia (Kingdon 1991) are so far unsubstantiated (Kock & Künzel 1999). Abundant palaeontological evidence, however, documents the prehistorically wider occurrence of the subfamily in Africa, southern Europe and perhaps south-western Asia. The genus is known, as *Lophiomys maroccanus* or species indeterminate, from the late Miocene to Pleistocene of Morocco (Aguilar & Michaux 1989–1990, Geraads 1998). Further, *Protolophiomys* of the late Miocene in Spain (Aguilar & Thaler 1987) bears certain cranial and dental traits that warrant its membership in Lophiomyinae, while the subfamily allocation of *Microlophiomys*, described from isolated molars in late Miocene sediments in Ukraine (Topachevsky & Skorik 1984), remains open to question.

Lophiomys is very large in size and boldly coloured in black and white, such that its superficial appearance is non-muroid and even non-rodent. The colour patterning, exaggerated by an erectile dorsal crest flanked by the white-accented glandular tracts, suggests an aposematic function and has evoked comparisons with the zorilla, a small porcupine, opossum, or even the Malayan gymnure. While the strongly cuspidate molars of *Lophiomys* recall a large *Cricetus* (Cricetinae), the pebbled, dermal roofing of the skull is unique among the 1500 species of living Muroidea. Granulated extensions of the frontal, parietal, squamosal and jugal bones completely roof the temporal and much of the orbital fossae, perhaps functioning to deflect predatory attacks and protect the eyes, masticatory muscles and brain. Among the many other distinctive morphological traits of *Lophiomys* are the oval shape of the infraorbital foramen ('keyhole' shape in most muroids), absence of a horizontal plate of the parapterygoid fossa and accompanying foramen ovale accessorius (present in nearly all others), vertebral column with 16 thoracic and seven lumbar vertebrae (13 thoracic and six lumbar are typical), and the much reduced clavicles not contacting the scapulae and sternum (articulation with both elements is typical) (Tullberg 1899, Carleton & Musser 1984).

Lophiomys imhausi is apparently the only species among Muroidea whose stomach is highly compartmentalized. The stomach in most muroid species is single chambered, less commonly dual chambered in certain cricetids and murids (Vorontsov 1967, Carleton 1973, Perrin & Curtis 1980, Musser & Durden 2002). That of *Lophiomys*, however, contains five anatomically discrete sections that superficially resemble the sacculated configuration characteristic of ruminant artiodactyls (Vorontsov 1967). Studies of gastric histology, physiology and digestion would be extremely informative in relation to the animal's diet and ecological niche. By virtue of its large size and biomass, *Lophiomys* may be one of the few muroid rodents that can harbour a symbiotic microflora in the foregut and profit metabolically from gastric fermentation of cellulose. In contrast, hindgut fermentation (large intestine and caecum), in contrast to foregut (stomach) fermentation, is the nutritional process characteristic of muroid species.

The uniqueness and highly derived condition of such morphological adaptations are reflected in the taxonomic isolation of *Lophiomys imhausi*, typically classified as a monotypic family of Muroidea (Tullberg 1899, Ellerman, 1941) or subfamily of Cricetidae (Miller & Gidley 1918, Simpson, 1945, Chaline *et al.* 1977). Lavocat (1973, 1978), on the other hand, regarded *Lophiomys* as a derivative from the Miocene Afrocricetodontinae and arranged Lophiomyinae within a broadly defined Nesomyidae. The molars of extant *Lophiomys* are complex (Wahlert 1984), but occlusal patterns are less complicated in extinct forms and more closely resemble those of Miocene Cricetidae such as *Megacricetodon* and *Democricetodon*. The latter genus first appears in early Miocene sediments of Europe and has now been documented in the middle Miocene of East Africa, leading Tong & Jaeger (1993) to speculate that it represents the African ancestor of *Lophiomys*. Although Lophiomyinae is here associated within Cricetidae, the several interpretations of its relationship have yet to be rigorously investigated in a phylogenetic context.

Michael D. Carleton & Guy G. Musser

GENUS *Lophiomys*

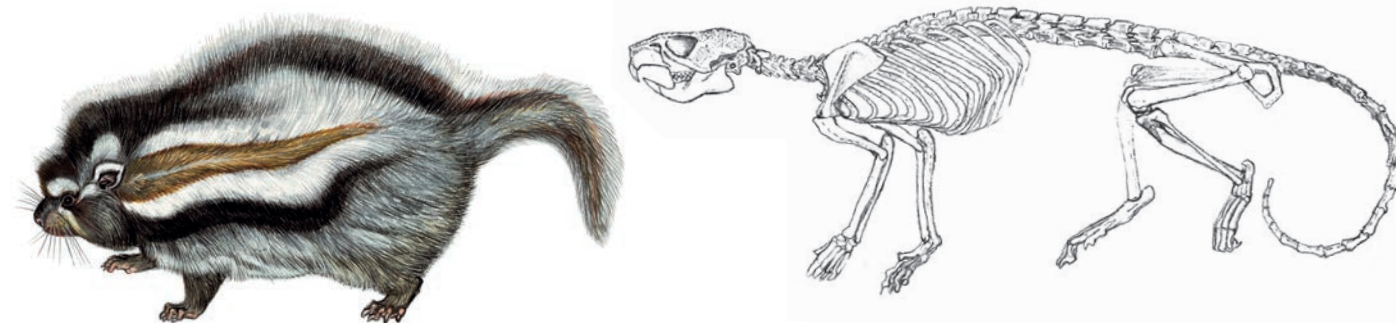
Maned Rat

Lophiomys Milne-Edwards, 1867. L'Institut, Paris 35: 46. Type species: *Lophiomys imhausi* Milne-Edwards, 1867.

Lophiomys is a monotypic genus distributed in eastern Africa. The characters of the genus are given in the subfamily and species profiles.

D. C. D. Happold

LEFT AND BELOW: *Lophiomys imhausi*.

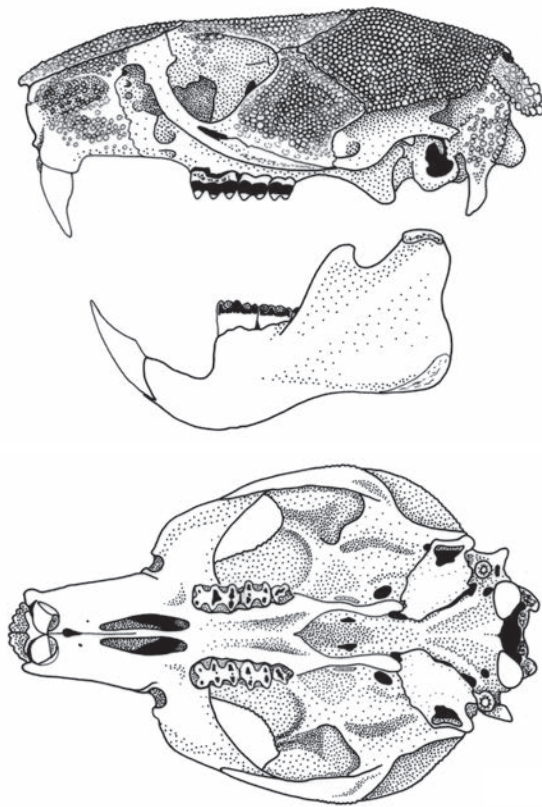


Lophiomyys imhausi MANED RAT (CRESTED RAT)

Fr. Rat à crinière; Ger. Mähnenratte

Lophiomyys imhausi Milne-Edwards, 1867. L'Institut, Paris 35: 36.

'Probably from the African coast opposite Aden, where it was purchased' (= Somalia).

Figure 39. Skull and mandible of *Lophiomyys imhausi* (BMNH 73.1756).*Lophiomyys imhausi*

Taxonomy Thomas (1910c) recognized four species of *Lophiomyys* in East Africa; all are now considered to represent a single species. Synonyms: *aethiopicus*, *bozasi*, *hinde*, *ibeanus*, *smithi*, *testudo*, *thomasi*. Subspecies: none. Chromosome number: not known.

Description Very large rat with thick shaggy black and white pelage and bushy tail. Dorsal pelage long and thick, mainly black, flecked with white. Guard hairs long and coarse (up to 65 mm in length); mostly black, some with white tip, some with white band near base. Underfur thick, shorter than guard hairs (ca. 30 mm), grey at base, white on terminal half; underfur mostly visible through guard hairs. Pelage when parted has four bands of colour: grey at base, then white, black and white. Long hairs on back, from top of head to base of tail, form thick white-tipped crest (or mane), which may be erected when animal is frightened. Flanks similar to dorsal pelage with longitudinal band of short brown or cinnamon hairs, broad anteriorly and becoming narrow posteriorly, from behind head to rump. Ventral pelage greyish; hairs 10–15 mm, pale grey to pale buff, with white tips. Head blackish-brown on muzzle, cheeks and around eyes (see also Geographic Variation). Ears smallish, rounded, with short blackish-brown hairs on surface and white hairs around outer margins. Fore- and hindlimbs black and shortish. Forefeet large; Digit 1 without claw, Digits 2–5 with well-developed claw. Hindfeet broad; Digits 1–5 with claw. Tail moderately long (80% of HB), well covered with long shaggy hair; hairs mostly black with white at tip. Skull is massive and strongly built; dorsal surface covered with small bony projections, which results in a 'pebbled' effect (Figure 39); see also subfamily profile, and below. Dental formula: $I\ 1/1, C\ 0/0, P\ 0/0, M\ 3/3 = 16$. Nipples: not known. See also subfamily profile.

Geographic Variation Considerable variation in the number of white-tipped hairs (and hence the 'whiteness' of the pelage). Individuals from Djibouti have a broad whitish line on the forehead, which extends backwards above each eye to base of each ear, and a white tip to the tail (Kock & Künzel 1999).

Similar Species No other rodent has such long shaggy black pelage and distinctive markings, nor a skull with a 'pebbled' structure on the dorsal surface. Rodents of similar size are: *Cricetomys gambianus*: short pelage, naked tail, black at base, white at tip, cheekteeth $3/3$. Squirrels: short pelage, long bushy tail, agile, arboreal (except *Xerus*), cheekteeth $4/4$.

Distribution Endemic to Africa. Somalia–Masai Bushland BZ and scattered localities in Afroalpine–Afroalpine BZ of eastern Africa. Recorded from E Sudan (Red Sea Hills), Eritrea, Ethiopia, Djibouti, Somalia, Kenya, Uganda (and W Tanzania) (Kock & Künzel 1999). Although the species is said to occur in Saudi Arabia (Kingdon 1991), its occurrence at the present time is unlikely (Harrison & Bates 1991, Kock & Künzel 1999).

Lophiomys imhausi.



Habitat Moist and montane forests in Kenya, but drier woodlands and rocky areas elsewhere. In Ethiopia, occurs from sea level to 3300 m.

Abundance Uncertain; rarely seen. Probably rare or uncommon.

Adaptations Nocturnal, semi-arboreal and slow-moving. At night, Maned Rats scramble over undergrowth and tree trunks, and climb trees. During day they hide in hollow tree trunks or in holes located on the edge of ravines or in bushy banks (Kingdon 1974). Aggressive; when an individual is disturbed or frightened, it hisses, growls, snorts or barks, and erects the crest of hairs on the back. The skull is unique amongst mammals: it is solidly built, the upper surface is strengthened with many small circular bony projections (0.3 mm across, and 0.3 mm between projections), and the parietal bones have lateral extensions that join with the zygomatic arch posterior to the orbit providing extra protection to the braincase.

Foraging and Food Herbivorous; feeds on leaves and tender shoots. The stomach has several compartments, and symbiotic fauna in the stomach are thought to assist in the digestion of food (see subfamily profile).

Social and Reproductive Behaviour Little information; usually seen singly.

Reproduction and Population Structure Litter-size: 1–3. Young slightly haired at birth. White markings and black stripes on

body visible by Day 9. Eyes open by Day 13. Hair sufficiently long that crest is erectile by Day 20. Mobile by Day 23. Weaned by Day 40 (Delany 1975).

Parasites, Predators and Diseases Ectoparasites include plague fleas (Kingdon 1974).

Conservation IUCN Category: Least Concern.

Conservation status is uncertain because individuals are rarely seen.

Measurements

Lophiomys imhausi

HB: 227 (180–305) mm, n = 7

T: 178 (145–205) mm, n = 6

HF: 48 (34–56) mm, n = 6

E: 28 (20–39) mm, n = 7

WT: 590–920 g*

GLS: 66.2 (65.3–67.3) mm, n = 4

GWS: 40.3 (39.2–40.9) mm, n = 3

M¹–M³: 13.2 (12.6–13.7) mm, n = 4

Kenya (NMK)

*Kingdon (1997); sample size not recorded

Key References Kingdon 1974; Kock & Künzel 1999.

D. C. D. Happold

Family MURIDAE
GERBILS, JIRDS, RATS AND MICE

Muridae Illiger, 1811. Abhandl. K. Akad. Wiss. Berlin for 1804–11, p. 46, 129.

| | | |
|-------------------------------------|---|--------|
| Deomyinae (4 genera, 30 species) | Spiny Mice, Link Rat and Brush-furred Rats and Mice | p. 217 |
| Gerbillinae (12 genera, 71 species) | Gerbils, Jirds | p. 260 |
| Leimacomyinae (1 genus, 1 species) | Buettner's Togo Mouse | p. 358 |
| Murinae (31 genera, 145 species) | Old World Rats and Mice | p. 361 |
| Otomyinae (2 genera, 17 species) | Vlei Rats | p. 571 |

The Muridae, the largest of the several families of Muroidea, is indigenous to the Old World, originally distributed throughout most of Eurasia, Africa (except Madagascar) and the Indo-Australian region. Currently, 150 genera and 730 species are recognized worldwide (Musser & Carleton 2005); of these, Africa contains five subfamilies, 50 genera and 264 species (as listed above; see also order profile). Certain commensal species of the subfamily Murinae opportunistically accompanied the Holocene meanderings of humans, spread far beyond their natural ranges, and now occur nearly worldwide. The family is abundantly represented throughout Africa, where two (Leimacomyinae, Otomyinae) of the five subfamilies are geographically restricted and where the others (Deomyinae, Gerbillinae, Murinae) are represented by taxonomically diverse, moderately to highly speciose radiations that are geographically widespread. All of Africa's biotic zones contain at least some members of the family, and species of Muridae typically comprise a substantial proportion of the numbers of individuals and biomass in most terrestrial small mammal communities. African murids range in size from about 5 g to 210 g, are mostly terrestrial and nocturnal, occupy numerous natural and anthropogenic habitats, and are well represented in herbivorous (many Murinae, Otomyinae), granivorous (Gerbillinae) and insectivorous and carnivorous trophic guilds (Deomyinae, Leimacomyinae, some Murinae).

The family has been conceived with a broad or narrow taxonomic meaning in the superfamily Muroidea. In the broad sense, Muridae was thought to contain most muroid groups, either excluding (Thomas 1897, Ellerman 1941) or including (McKenna & Bell 1997) the fossorially specialized Spalacidae and (non-African) Rhizomyidae. In the narrow sense, Muridae was separated from a comparably large and systematically diverse Cricetidae (and variously other families), in addition to the fossorial families (Tullberg 1899, Miller & Gidley 1918, Simpson 1945). Reduction or loss of longitudinal enamel crests on the molars (crests standardly found in Cricetinae) is a cardinal derived trait for postulating a sister-group relationship between Gerbillinae and Murinae (Flynn *et al.* 1985, Tong & Jaeger 1993), which together form the core of Muridae. The phyletic union of these and other subfamily members, as presented herein, draws convincing support from recent gene-sequencing studies, which collectively identify deomyines, gerbillines, murines and otomyines

(Leimacomyinae not yet sampled) as comprising a major lineage within Muroidea (Hänni *et al.* 1995, Robinson *et al.* 1997, Dubois *et al.* 1999, Martin *et al.* 2000, Michaux *et al.* 2001, Jansa & Weksler 2004). This large clade (Muridae) is hierarchically delineated from others that contain representative species of Spalacidae, Cricetidae and Nesomyidae (see family and subfamily profiles for additional discussion).

A consensus accepts *Antemus*, known from the middle Miocene of Pakistan, as the oldest-known murid, one believed to represent a stem member in the initial radiation of the family (Jacobs 1977, Flynn *et al.* 1985, Jacobs *et al.* 1990, Jacobs & Downs 1994, Freudenthal & Martín Suárez 1999). Earliest members of Muridae so far documented in Africa appear shortly thereafter in the late Miocene: *Preacomys* (Deomyinae) in Ethiopia (Geraads 2001), *Protatera* (Gerbillinae) in Morocco (Jaeger 1977b), *Paraethomys* and *Progonomys* (Murinae) in North Africa (Jaeger 1977b, Mein *et al.* 1993), *Karnimata* and *Saidomys* (Murinae) in Kenya (Winkler 2001) and *Euryotomys* (Otomyinae) in South Africa (Sénégal & Avery 1998). Myocricetodontines, a complex and widely distributed Neogene group (early Miocene–early Pliocene of Africa, Europe and southern Asia), are variously implicated in the origin of the two dominant murid subfamilies, Gerbillinae and Murinae (Tong 1989, Tong & Jaeger 1993, Lindsay 1994, Wessels 1996, 1999, Winkler 2002).

In view of this fossil record and palaeo-distribution, authors have routinely identified southern Asia as the evolutionary source of African Muridae (or specifically Murinae). Two or more immigrations in the middle Miocene to late Miocene–Pliocene are thought to account for the continent's present diversity and taxonomic composition (Jacobs 1985, Winkler 1994, 2002). Tong & Jaeger (1993), on the other hand, suggested an African origin of murids. Such speculations about evolutionary origin and intercontinental migration have a precarious foundation because new fossil sites in north-eastern Africa and the Arabian Peninsula continue to be discovered and the taxonomy of their rodent faunas still requires synthesis (Flynn & Jacobs 1999, Geraads 2001, Winkler 2001, 2002). In regard to the suggestion of Tong & Jaeger, it is instructive to note that two of the five murid subfamilies (Leimacomyinae, Otomyinae) are endemic to Africa, that the taxonomic diversity of two others (Deomyinae, Gerbillinae) is today strongly concentrated within the continent (and in the case of Gerbillinae, the earliest diverging clades are sub-Saharan), and that the fifth (Murinae) contains a large, possibly monophyletic group that radiated extensively within sub-Saharan biotopes. If Africa is not the area of origination of Muridae, its landscapes have none the less played a prominent role in the family's diversification.

Size categories of species in the family (based on mean head and body length) are given in the order Rodentia profile.

Michael D. Carleton & Guy G. Musser

Subfamily DEOMYINAE – Spiny Mice, Link Rat and Brush-furred Rats

Deomyinae Thomas, 1888. Proc. Zool. Soc. Lond. 1888: 132.

| | | |
|--------------------------------|--------------------|--------|
| <i>Acomys</i> (13 species) | Spiny Mice | p. 217 |
| <i>Deomys</i> (1 species) | Link Rat | p. 235 |
| <i>Lophuromys</i> (15 species) | Brush-furred Rats | p. 238 |
| <i>Uranomys</i> (1 species) | Brush-furred Mouse | p. 258 |

Deomyinae is a small subfamily that comprises only four genera (*Acomys*, *Deomys*, *Lophuromys* and *Uranomys*) and 30 species, whose specific and generic diversity is concentrated in sub-Saharan Africa. The genus *Acomys*, however, is also represented in North Africa, the Mediterranean islands of Cyprus and Crete, and the Middle East and Asia Minor. Deomyines are very small to medium in size, with hispid to spiny pelage, and each genus is highly distinctive in morphology. All species are terrestrial, mostly nocturnal, and primarily insectivorous, although some species of *Acomys* may consume substantial amounts of vegetable food.

The aggregation of these four genera into a distinctive murid subfamily appears anomalous when one considers their early classificatory history. In the case of *Acomys*, *Lophuromys* and *Uranomys*, systematists had noted their close relationship, especially similarities of pelage texture, palatal configuration and molar patterns, but continued to arrange them within the Murinae (Ellerman 1941, Misonne 1969a, Rosevear 1969), perhaps as an early offshoot based on retention of a discrete t3 on M³ (Denys & Michaux 1992, Denys *et al.* 1992). Monophyletic unity of these three genera has been sustained by subsequent morphological and molecular studies, and this evidence has prompted both a reconsideration of their antiquity relative to Murinae proper and possible kinship to Gerbillinae (Sarich 1985, Chevret *et al.* 1993b, Breed 1995, Hänni *et al.* 1995, Watts & Baverstock 1995a, Dubois *et al.* 1999).

In the case of *Deomys*, no special relationship to the above three genera, or even to Murinae, was appreciated. In fact, the genus was isolated in its own subfamily Deomyinae (Thomas 1888, Ellerman 1941) or reservedly grouped within a polyphyletic Dendromurinae (Rosevear 1969, Carleton & Musser 1984). A fresh perspective has emerged from recent sequence studies of mitochondrial and nuclear genes, which consistently support close relationship between *Deomys*

and *Acomys-Lophuromys-Uranomys*, in various combinations depending upon the study, and underscore the early divergence of the clade Deomyinae-Gerbillinae relative to Murinae (E. Verheyen *et al.* 1996, Michaux & Catzeflis 2000, Michaux *et al.* 2001, Chevret *et al.* 2001, Jansa & Weksler 2004). Cladistic analysis of morphological traits, primarily dental ones, has not disclosed a clade consisting of *Deomys* and *Acomys-Lophuromys-Uranomys* (Denys *et al.* 1995), but the synapomorphic value of their similar pelage has not been evaluated at the microscopic level (many muroids possess texturally stiffened cover hairs) and few soft-organ systems have been investigated.

The use of Acomyinae for this subfamily, as loosely adopted in the recent literature (e.g. Dubois *et al.* 1999, Michaux & Catzeflis 2000), constitutes a *nomen nudum* and is unavailable from these works. The valid family-group name for the clade intended to contain the genera *Acomys*, *Deomys*, *Lophuromys* and *Uranomys* properly dates to Thomas's (1888) Deomyes, which he clearly designated as a suprageneric rank coordinate to his Mures (modern Muridae) and Criceti (approximately equal to modern Cricetidae).

Of the four genera, only *Acomys* has a well-documented fossil history, known from early Pliocene and Pleistocene sites in eastern and southern Africa (Denys 1990a, Senut *et al.* 1992, Avery 1998). The subfamily itself certainly originated earlier, as indicated by the extinct genus *Preacomys*, described from the late Miocene in Ethiopia and considered a progenitor of *Acomys* (Geraads 2001). Molecular clock estimates place the divergence between Deomyinae, Gerbillinae and Murinae as early Miocene, around 18–21 mya (Michaux *et al.* 2001).

Two of the four deomyine genera (*Deomys* and *Uranomys*) are monotypic and the others are moderately speciose. The number of species of *Acomys* and *Lophuromys* is uncertain. Here, 13 species of *Acomys* and 15 species of *Lophuromys* are recognized, although Musser & Carleton (2005) recognized 15 species of African *Acomys* and 21 species of *Lophuromys*.

Michael D. Carleton & Guy G. Musser

GENUS *Acomys* Spiny Mice

Acomys I. Geoffroy, 1838. Ann. Sci. Nat. Zool. (Paris), ser. 2, 10: 126. Type species: *Mus cahirinus* É. Geoffroy, 1803.

The genus contains 13–15 species (see above) widely distributed in Africa, and four additional species extraliminally in the Middle East (Musser & Carleton 2005; see also below). In Africa, all species occur in arid and semi-arid habitats, or in dry savannas, where rainfall is sparse and seasonal and daytime temperatures may be high.

The distinguishing characters of the genus are small size (HB rarely more than 120 mm), dorsal pelage largely composed of spines (the only genus of small rodent to have spines; hence their common name of 'spiny mice'), tail with large scales and clothed with bristle-like hairs, hindfeet broad and rather short, digits not reduced, and

accessory tubercles in addition to the normal pads on the palms and soles. Skull has broad flattened braincase; very large interparietal bone; long anterior palatal foramina extending posteriorly to mid-M¹; and the anterior half of mesopterygoid fossa is closed by plate-like outgrowths from the palatines, the open parts of fossa thus reduced to a small triangular space (Figure 40).

Spiny mice inhabit deserts and other dry areas, where they live mostly in sheltering rocky habitats. They are opportunistic feeders, eating seeds, leaves, dry plants, invertebrates such as snails, insects and their larvae. All species living in arid habitats have well-developed

physiological and behavioural characters for water conservation, although they are not as 'desert-adapted' as many other arid zone small rodents (e.g. *Gerbillus*, *Jaculus*). The reproductive biology of species in the genus is unusual among murid rodents: in those species studied so far, the young are precocious when born, a fact to which several social traits of behaviour are associated such as midwifery, social care of the young and the social rank of mothers (Dieterlen 1961, 1962, 1963). Spiny mice are rarely preyed upon by owls, probably because the spines of the pelage are unpalatable.

The genus *Acomys* is very complex, and the systematics and relationships within the genus are far from clear. The first attempt at a systematic revision using morphological characters was made by Ellerman (1941), who established a 'subspinosus-group' with only *A. subspinosus*, and a 'cahirinus-group' with three sections comprising 15 species, plus several subspecies; additional forms could not be



Acomys cahirinus.

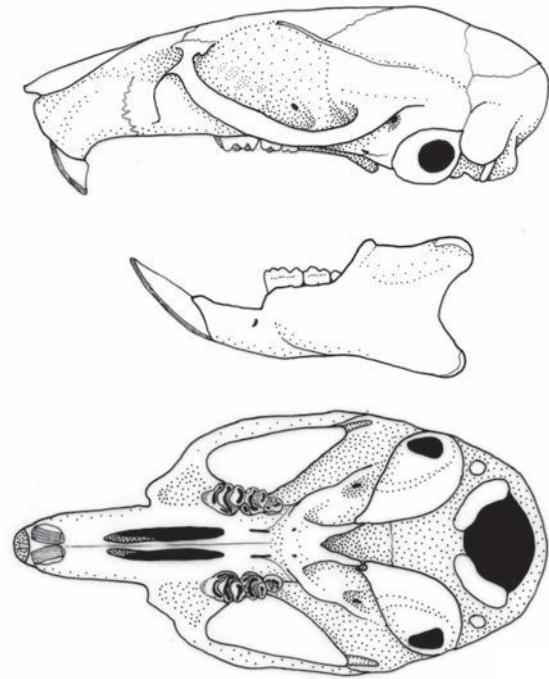


Figure 40. Skull and mandible of *Acomys johannis* (HC 1118).

Table 19. Species in the genus *Acomys*. Arranged in order of increasing size.

| Species | GLS mean (mm) | HB mean (mm) | T (% of HB) | Colour of ventral pelage | Geographic distribution | Chromosome number (FN) | Dorsal pelage |
|-------------------------|---------------|--------------|-------------|--------------------------------|--|------------------------|--|
| <i>A. spinosissimus</i> | <26 | <90 | 87% | Pure white | Tanzania to South Africa | 60 (68) | Dorsal pelage grey, fawn or russet-brown; soft spines |
| <i>A. subspinosus</i> | <26 | <90 | 95% | Pure white | South Africa | 60 (70) | Dorsal pelage rusty-brown, bristle-like |
| <i>A. percivali</i> | >26 | 90–99 | 76% | Pure white | S Sudan, Uganda, Kenya, SW Ethiopia | n. d. | Dorsal pelage grey; strong spines mid-back to base of tail |
| <i>A. ignitis</i> | >26 | 90–99 | 77% | Pure white | Kenya, Tanzania | 50 (66–68) | Dorsal pelage brownish-orange, bright reddish-orange on flanks; broad slatted spines on rump |
| <i>A. cinererus</i> | >26 | 90–99 | 90% | Pure white | Sudan, Djibouti, Ethiopia | 48 (58) | Dorsal pelage greyish-cinnamon |
| <i>A. wilsoni</i> | >26 | 90–99 | 87% | Pure white | Somalia–Masai BZ | 50 (n. d.) | Dorsal pelage bright cinnamon or chestnut |
| <i>A. kempi</i> | >26 | 90–99 | 94% | Pure white | S. Ethiopia, S Somalia, Kenya, NE Tanzania | n. d. | Dorsal pelage orange-buff, strong coarse spines mid-back to base of tail |
| <i>A. louisae</i> | >26 | 90–99 | 109% | Pure white | Somalia and Djibouti | n. d. | Dorsal pelage rufous, buff or greyish-brown; tail comparatively long (ca. 122% of HB) |
| <i>A. russatus</i> | >26 | >100 | 60% | White or greyish, grey at base | Egypt and Sinai | 66 (76) | Dorsal pelage golden-brown; soles of feet black; tail comparatively short (ca. 60% of HB) |
| <i>A. airensis</i> | >26 | >100 | 85% | Pure white | Mauretania, Mali, Niger | 40–46 (66) | Dorsal pelage orangey-grey |
| <i>A. johannis</i> | >26 | >100 | 90% | Pure white | West Africa (Sudan and Sahel BZs) | 66–68 (n. d.) | Dorsal pelage chocolate-brown to grey |
| <i>A. cahirinus</i> | > 26 | >100 | 92% | Pure white | NE Africa | 36–38 (68) | Dorsal pelage pale to dark brown, spines from shoulders to rump |
| <i>A. mullah</i> | >26 | >100 | 100% | Pure white | Ethiopia and Somalia | n. d. | Dorsal pelage slate-grey; tail comparatively long (ca. 100% of HB) |

allocated to any group due to lack of adequate material. Setzer (1975) produced a simple key which recognized five species (*A. cahirinus*, *A. dimidiatus*, *A. russatus*, *A. spinosissimus* and *A. subspinosus*) and 34 subspecies. A regional systematic revision of southern Africa was published by Dippenaar & Rautenbach (1986). Petter (1983) studied the pattern of molar teeth of the holotypes of *Acomys* spp. and, together with information from chromosome morphology (Matthey 1968), divided the genus into three groups, two of which belong to the subgenus *Acomys* and the third to a new subgenus *Peracomys* (*A. louisae*; Petter & Roche 1981) characterized by the presence of t7 on M¹ and M². Further insights into the complexities of the genus were highlighted by chromosomal reviews by Volobouev *et al.* (1991), Sokolov *et al.* (1993) and Kunze *et al.* (1999), and by biochemical and molecular analyses of species clusters by Janecek *et al.* (1991) and Barome *et al.* (2000). Denys *et al.* (1994) used chromosome and electrophoresis information, as well as morphological characters of the teeth and skull, and proposed a third subgenus, *Subacomys* (containing only *S. subspinosus*). Musser & Carleton (2005) commented that 'Regrettably, there is still no comprehensive taxonomic revision of the genus incorporating morphological as well as chromosomal and molecular data. Extant species are sorted into three subgenera (*Acomys*, *Peracomys* and *Subacomys*), but these grouping require reassessment by systematic revision' – a viewpoint that is maintained here.

Barome *et al.* (2001) presented two biogeographic hypotheses for the centre of origin of the genus and its dispersion. One suggests an origin in southern Africa and a northward dispersal along with subsequent evolution into species. The second suggests that East Africa is the centre – a hypothesis similar to that already made by Matthey (1968) – with dispersion and speciation in two directions, one northwards to the Mediterranean region and the other southwards to southern Africa. In both hypotheses, speciation could also have been caused by a progressive fragmentation resulting from the formation of the Rift Valley in its south-western part, and/or by the extension of tropical forest zones dividing the savanna regions into mosaics during climatic fluctuations, thus isolating the different species by vicariance.

Thirteen species (in Africa) are recognized here; in addition, Musser & Carleton (2005) recognized a further two species in Africa, *A. chudeaui* and *A. seurati*, which are here placed as synonyms of *A. cahirinus*. *Acomys dimidiatus* (perhaps also a subspecies of *A. cahirinus*) occurs in Sinai and further east and is not considered as an African species. The species are distinguished by size, pelage colour and texture, size, presence/absence of white spots on the head, number of palatal ridges, molar teeth characters and chromosome number (Table 19).

Fritz Dieterlen

Acomys airensis AÏR SPINY MOUSE (WESTERN SAHARAN SPINY MOUSE)

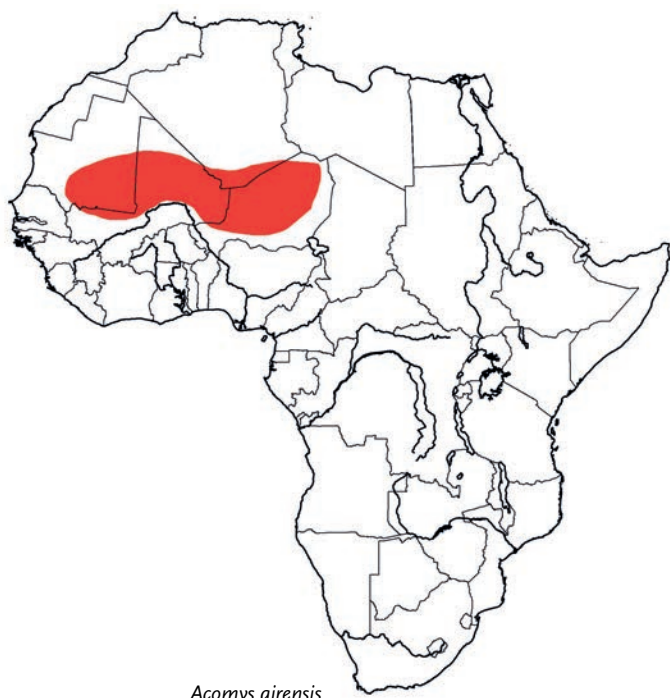
Fr. Souris épineuse de l'Aïr; Ger. Aïr-Stachelmaus

Acomys airensis Thomas and Hinton, 1921. Novit. Zool. 28: 8. Mount Baguezan, Asben (Aïr), Niger. 5200 ft (1580 m).

Taxonomy Musser & Carleton (1993) included *airensis* in *A. cahirinus*, but Volobouev *et al.* (1991, 1996a, b) clearly showed that chromosomal differences between these two forms (and between

them and *A. dimidiatus*) warrant a specific status for each. Molecular data show *A. airensis* to be the sister-group of a *A. cahirinus*/*A. minous*/*A. nesiotis*/*A. cilicicus* group within the '*cahirinus*–*dimidiatus*' complex (Barome *et al.* 2000). Conversely, the hypothesis that *A. chudeaui* from Morocco (karyotype described but not illustrated in Benazzou (1983) is conspecific with *A. airensis* can not be entirely ruled out. *Acomys chudeaui* would then be the correct name, predating *airensis*. Synonyms: none. Chromosome number: 2n = 40, 44 and 46 in Mali (Tranier *et al.* 1999, Dobigny *et al.* 2001b, L. Granjon and B. Sicard unpubl.), 2n = 40 in Mauritania (Bâ *et al.* 2001), 2n = 41 to 43 and 46 in Niger (Viegas-Péquignot *et al.* 1983, V. Volobouev & G. Dobigny unpubl.); all karyotypes have aFN = 66.

Description Small rodent with spiny dorsal hairs. Dorsal pelage orangey-grey, becoming paler on flanks; hairs whitish-grey at base, orangey subterminal band and grey at tip. Spiny hairs on the posterior half of the back, extending more towards the front in old individuals. Ventral pelage pure white, clearly delineated from colour of flanks. Head with pointed muzzle, small eyes and relatively large ears. Small white patch under eye more or less visible; white postauricular patch. Short hindfeet with short digits, Digit 1 being especially reduced in size. Tail moderately long (ca. 85–95% of HB). Skull remarkably flattened. Nipples: 1 + 2 = 6.



Acomys airensis

Geographic Variation Specimens from Air are smaller than those from Mali and Mauritania, with a relatively longer tail (see Measurements).

Similar Species

Acomys johannis. Pelage slightly to markedly darker; chromosome number: $2n = 66-68$; more southern distribution (right bank of Niger R.).

Distribution Endemic to Africa. Sahel Savanna BZ. Recorded from Mauritania, Mali on the left bank of Niger R. (with one exception; Tranier *et al.* 1999), and Niger. Would be also present in S Morocco if *chudeaui* is included in this species (but here included in *A. cahirinus*). The status of the specimens from S Algeria, with $2n = 38$ (referred to as *A. cahirinus* in Kowalski & Rzebik-Kowalska 1991), has to be ascertained.

Habitat Mostly found in rocky habitats, but also regularly in gardens and other human-related habitats, including huts (Bâ *et al.* 2001, Dobigny *et al.* 2001b, L. Granjon and B. Sicard unpubl.). One individual found in a completely sandy habitat of the inner delta of Niger R. (Tranier *et al.* 1999).

Abundance Probably locally abundant in favourable habitats, as suggested by relatively high trapping success in rocky habitats where found in Mauritania and Mali (K. Bâ and L. Granjon unpubl.).

Remarks Terrestrial and probably mainly nocturnal, although two specimens from Air were captured by day (labels, MNHN). May rest in rock cracks rather than in ground burrows. As in other *Acomys* species, the skin is very delicate and tears off the tail easily. In captivity, omnivorous and readily carnivorous. In S Mauritania,

pregnant ♀♀ were found in Aug (4 of 8) and Oct (2 of 5). Mean embryo number: 2.2 (range 2–3, $n = 9$; K. Bâ & L. Granjon unpubl.). Heavily preyed upon by Barn Owls *Tyto alba* on an inselberg in C Mali (near Niafunké; L. Granjon unpubl.).

Conservation IUCN Category: Least Concern.

Measurements

Acomys airensis

HB: 107.2 (94–115) mm, $n = 9$
T: 91.3 (78–103) mm, $n = 8$
HF: 16.8 (16–18) mm, $n = 9$
E: 17.2 (16–19) mm, $n = 9$
WT: 37.5 (25–55) g, $n = 31$
GLS: 28.0 (27–28.9) mm, $n = 5$
GWS: 12.2 (11.8–12.4) mm, $n = 5$
 M^1-M^3 : 4.1 (4–4.3) mm, $n = 5$
S Mauritania and W Mali (K. Bâ and L. Granjon unpubl.)

HB: 93.0 (90–95) mm, $n = 10$
T: 90.1 (80–105) mm, $n = 9$
HF: 17.3 (16–18) mm, $n = 11$
E: 15.0 (13–16.5) mm, $n = 11$
WT: n. d.
GLS: 27.6 (26–29.2) mm, $n = 9$
GWS: 11.8 (11.6–12.1) mm, $n = 10$
 M^1-M^3 : 4.0 (3.9–4.2) mm, $n = 11$
Air Massif, Niger (MNHN)

Key Reference Rosevear 1969; Nicolas *et al.* 2009.

Laurent Granjon & Khalilou Bâ

Acomys cahirinus CAIRO SPINY MOUSE (NORTHEAST AFRICAN SPINY MOUSE)

Fr. Souris épineuse du Caire; Ger. Kairo Stachelmaus

Acomys cahirinus (Geoffroy, 1803). Catalogue des Mammifères du Museum National d'Histoire Naturelle, p. 195. Cairo, Egypt.

Taxonomy Originally described in the genus *Mus*. The definition of *A. cahirinus* has been a subject of controversy, and several forms originally considered within 'cahirinus' are now recognized as separate species. *Acomys cahirinus*, as currently understood, is centred on NE Africa (with some forms in the Middle East) and can be distinguished from related forms by patterns of molar teeth (Denys *et al.* 1994), chromosome number (Volobouev *et al.* 1991, 1996a), and mitochondrial DNA cytochrome *b* sequences (Barome *et al.* 2000). Musser & Carleton (1993) listed 16 forms of *A. cahirinus* as synonyms, of which five are non-African. Currently, four of these African forms are regarded as separate species (*A. airensis*, *A. chudeaui*, *A. dimidiatus*, *A. seurati*) by Musser & Carleton (2005) and Denys *et al.* (1994). Here, *A. airensis* is given specific rank; in contrast, the other three forms are not given specific rank because, at the time of study, it was assumed that the correct name was 'A. cahirinus' and hence biological information collected for *A. cahirinus* may, in fact, be referable to one of these other forms. The 'cahirinus group' as a whole is in need of revision (Osborn & Helmy 1980, F.

Dieterlen unpubl.). Synonyms: *albigena*, *chudeaui*, *dimidiatus*, *helmyi*, *hunteri*, *megalodus*, *nubicus*, *sabryi*, *seurati*, *viator*. Subspecies: possibly five. Chromosome number: $2n = 36$, FN = 68 in Sinai/Egypt (Wahrman & Goitein 1972), Egypt (Togby *et al.* 1972, De Hondt *et al.* 1977) and Ethiopia (Sokolov *et al.* 1993). A different karyotype of *A. cahirinus* ($2n = 38$, FN = 68) (Wahrman & Zahavi 1953) in Israel and E Sinai hybridizes along a narrow strip of land of eastern Sinai with $2n = 36$, so producing $2n = 37$, FN = 68 (Wahrman & Goitein 1972).

Description Small mouse although large for the genus. Fine hairs on back of head and neck, stiff hairs on anterior part of back, spines (with longitudinal groove on upper surface) from shoulder to rump. Dorsal pelage pale to dark brown, or pale to dark cinnamon; colour varies geographically; hairs and spines white or pale grey at base, with cinnamon subterminal band, and black tip (mid-dorsal spines only). Ventral pelage pure white. Head similar in colour to dorsal pelage. Ears pigmented, covered with short whitish hairs.

White basal and postauricular patches. Eyes large, dark; conspicuous white suborbital spot. Limbs short. Feet white. Tail relatively long (90–100% of HB, depending on population), with scales, almost naked with scattered short bristles, brownish above, whitish below; tail often short or absent due to injury. Nipples: $1 + 2 = 6$.

Geographic Variation Following Osborn & Helmy (1980) five subspecies from Egypt and partly from Sudan are recognized provisionally: *A. c. cahirinus*, *A. c. helmyi*, *A. c. hunteri/nubicus*, *A. c. megalodus* and *A. c. viator*. Subspecifically, colour of dorsal pelage varies from dark brown (*hunteri*, *viator*) to pale brown (*helmyi*) to slate-grey (some *cahirinus*). *Acomys c. helmyi* is the largest subspecies (mean HB: 118 mm), and *A. c. cahirinus* from Bahariya Oasis is the smallest (mean HB: 98 mm) (Osborn & Helmy 1980). There are intergradations in colour, and overlap in measurements, between subspecies. Commensal individuals in the Nile Valley and Delta are often melanistic.

Similar Species

A. cineraceus. On average slightly smaller, tail shorter; geographic range further south in Sudan and Ethiopia.

Distribution Endemic to Africa. Sahara Arid and Sahel Savanna BZs and northern part of Somalia–Masai Bushland BZ. Recorded from most parts of Egypt including Sinai, Sudan (north of ca. 16°N), Eritrea, Djibouti and Ethiopia (five localities in the Rift Valley; Sokolov *et al.* 1993). Limits in C and S Sudan, and in Ethiopia uncertain. Less widely distributed in Libya (*viator*; Ranck 1968), Algeria (*seurati*; Kowalski & Rzebik-Kowalska 1991) and Morocco (*chudeaui*; Aulagnier & Thévenot 1986).

Habitat Rocky hillsides, cliffs, boulder-strewn canyons and other rocky habitats. May also occur in sandy desert habitats where there are date palms. Some populations live in human-made structures – houses, huts, tombs and temples – where holes and crevices provide

shelter. The five desert subspecies of Egypt and (partly) Sudan (Osborn & Helmy 1980) may also be found in settlements and local huts (Hoogstraal *et al.* 1957a). Altitude appears to have no effect on distribution as long as food is available (Hoogstraal *et al.* 1957b).

Abundance Common in suitable habitats. Numbers vary considerably between localities, and show some evidence of fluctuating annually (Osborn & Helmy 1980).

Adaptations In Egypt, activity is predominantly in the early morning and in the late afternoon (Osborn & Helmy 1980), although in N Sudan most activity occurs at night (Happold 1967c). On jebels (isolated rocky hills), live under boulders and in crevices of rocks where protected from heat and predators. Extremely agile, running quickly over and around rocks and boulders.

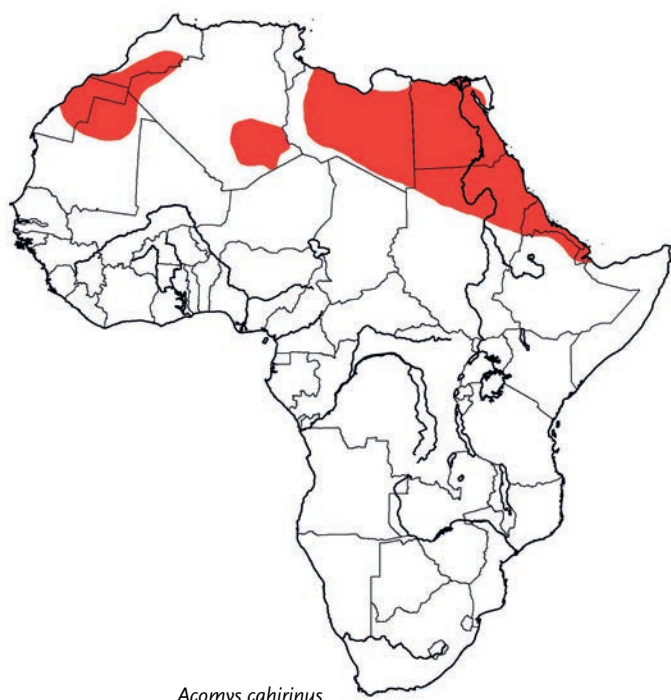
Foraging and Food Herbivorous and partly omnivorous. The diet is mainly seeds of herbs and grasses. Where plants are rare or lacking, Cairo Spiny Mice can forage on windblown plant remains trapped in crevices. In some areas, dates may be a staple food. Insects such as locusts, crickets, butterflies and moths are readily eaten and, on some occasions, desert snails (e.g. *Eremica desertorum*) are a preferred food. By eating desert snails, these spiny mice can compensate for high evaporative water loss (Shkolnik & Borut 1966, 1969). Unlike jerboas and jirds, they are unable to subsist for more than nine days without water-containing food. Licking dew from stones and plants could also provide some water.

A further kind of natural food may be undigested organic matter in the faeces of fruit bats (*Rousettus aegyptiacus*), which roost during the day in tombs of the Nile Valley (Maser 1966, Osborn & Helmy 1980). A strange source of food can be (or was) dried flesh and bone marrow of mummified humans in the tombs in Egypt (Osborn & Helmy 1980).

Social and Reproductive Behaviour Appears to live in social groups, mostly mothers and their offspring. Within a group there is a rank order, and individuals exhibit typical social behaviour such as mutual grooming. Females assist in birth and care of young (Dieterlen 1961, 1962, 1963). Similar behaviour is shown by *A. dimidiatus* and *A. minous* (a non-African species). See also profile Genus *Acomys*.

Reproduction and Population Structure Gestation: 38 days (range 36–40) in captive animals (Dieterlen 1961; as *A. c. dimidiatus*); 42 days (Bodenheimer 1949, see also Harrison & Bates 1991). Mean litter-size: 2.4 (range 1–5, $n = 123$; Dieterlen 1961). Young altricial at birth; maturity: 2–3 months.

Predators, Parasites and Diseases Generally, relatively rare in pellets of birds of prey. In middle Egypt, no remains of *Acomys* found in pellets of the Long-eared Owl (*Asio otus*) ($n = 590$; 91% of prey was *Mus musculus*; Handwerk 1990). In N Sudan (jebels north of Omdurman), pellets of the Desert Eagle-owl *Bubo ascalaphus* contained only six individuals of Cairo Spiny Mice (= 3.3% of prey items; $n = 182$); other prey items included *Gerbillus gerbillus* (ca. 26%), *Meriones crassus* (ca. 24%), *Gerbillus pyramidum* (ca. 19%), *Jaculus jaculus* (ca. 18%), *Desmodilliscus braueri* (ca. 8%) and *Arvicanthis niloticus* (ca. 1.2%) (F. Dieterlen unpubl.). In Egypt, *Parapulex*



Acomys cahirinus

chephrensis is the commonest species of flea found on *A. cahirinus*; other species include *Xenopsylla cheopis*, *Synosternus cleopatrae*, *Pulex irritans* and *Ctenocephalides felix* (Hoogstraal & Traub 1965b).

Acomys cahirinus is a possible reservoir for communicable arthropod-borne diseases (Hoogstraal *et al.* 1967). Of 92 serum samples from the Eastern Desert of Egypt, a relatively large percentage was positive for rickettsioses of humans: 34 contained *Rickettsia prowazekii*, responsible for epidemic louse-borne typhus; 5 were positive for *Rickettsia conorii*, responsible for tick-borne boutonneuse fever; and 11 for *Coxiella burnetii*, the mostly airborne causal organism of Q-fever.

Conservation IUCN Category: Least Concern.

A widespread, adaptable and common species.

Measurements

Acomys cahirinus cahirinus

HB: 111 (100–120) mm, n = 34

T: 102 (92–137) mm, n = 30

HF: 19.9 (18–21) mm, n = 27

E: 20.8 (18–24) mm, n = 35

WT: 40.8 (29.9–51.5) g, n = 20

GLS: 29.6 (27.6–31.4) mm, n = 34

GWS: 12.5 (11.5–13.4) mm, n = 36

M¹–M³: 4.4 (3.8–4.9) mm, n = 34

Nile Valley and Delta, Egypt (Osborn & Helmy 1980)

Key References Dieterlen 1961; Osborn & Helmy 1980.

Fritz Dieterlen

Acomys cineraceus GREY SPINY MOUSE (HEUGLIN'S SPINY MOUSE)

Fr. Souris épineuse de Heuglin; Ger. Heuglins Stachelmaus

Acomys cineraceus Heuglin & Fitzinger, 1866. Sitz. K. Akad. Wiss. Wien 54: 573.

Doka, eastern Sennaar, between the Atbara and Rahad rivers of Sudan.

Taxonomy Although originally described from Sudan as a valid species, often included within *A. cahirinus* (e.g. Setzer 1956, 1975, Happold 1969). Bates (1994, map) provisionally included the spiny mice from West Africa (Niger, Nigeria, Benin, Togo, Burkina) in *A. cineraceus*. Recent studies have clarified the status of these forms: the spiny mice of West Africa are now considered to represent *A. airensis* (Volobouev *et al.* 1991, 1996a), *A. johannis* and *Acomys* sp. 1 and *Acomys* sp. 2 (as yet undescribed) (Barome *et al.* 2000). *Acomys cineraceus* is now restricted to the spiny mice in parts of Sudan and W Ethiopia, and is karyotypically distinguished from other species in the genus (Kunze *et al.* 1999). Now considered as one of four species of *Acomys* occurring in Sudan (the others being *A. wilsoni*, *A. percivali* and *A. cahirinus*). Synonyms: *cinerascens* (a mis-spelling by Heuglin in 1877), *hawashensis*, *hystrella*, *intermedius*, *lowei*, *witherbyi*. Subspecies: none (but see Geographic Variation). Chromosome number: 2n = 48 or 50 (Ingessana Hills, Sudan); 2n = 50, FN = 59 (nine metacentrics) and 2n = 48, FN = 58 (ten metacentrics) (Kordofan, Sudan); 2n = 48 (Kunze *et al.* 1999).

Description Small spiny mouse with greyish-cinnamon pelage. Fine hairs on back of head and neck, and somewhat longer on anterior part of back. Dorsal pelage greyish or blackish-grey (see Geographic Variation); anterior part of back, flanks and sides of rump cinnamon. Ventral pelage pure white. Head with small whitish spots below each eye and behind each ear. Limbs and feet white or cream. Tail moderately long (ca. 90% of HB), upper surface darkish with short darkish bristles, below pale with whitish bristles. Nipples: 1 + 2 = 6.

Geographic Variation Three geographic forms recognizable in Sudan: (1) Dorsal pelage blackish-grey, flanks reddish-cinnamon, ventral pelage white (most parts of Blue Nile Province to east of southern Kordofan). (2) Dorsal pelage grey or greyish-black, flanks similar to dorsal pelage and without any reddish/cinnamon, ventral pelage white (E Sudan near to the Ethiopian border where annual



Acomys cineraceus

rainfall 700–1000 mm). (3) Similar to the above but colours are muted and only weakly contrasting (northern part of range, 13–15° N from Kassala to Darfur where annual rainfall 150–400 mm).

Similar Species

A. cahirinus. On average larger and tail longer; dorsal pelage pale to dark brown, or pale to dark cinnamon; distribution mostly further north, but may be parapatric in N Sudan.

A. percivali. On average smaller; dorsal pelage grey to greyish-brown, without any cinnamon or russet; distribution mostly further south in East Africa but may be parapatric in S Sudan.

A. wilsoni. Similar size; dorsal pelage bright cinnamon or chestnut; distribution further south in East Africa but may be parapatric in S Sudan.

Distribution Endemic to Africa. Recorded from Sudan, Ethiopia and Djibouti. In Sudan, known from south of ca. 17°N; widespread but localized in S, E and W Sudan, but less widespread in SW Sudan. Not recorded further west than W Sudan, e.g. not recorded in NE DR Congo (Garamba N. P., Verheyen & Verschuren 1966), nor in E Central African Republic (Petter & Genest 1970). Happold (1969) pointed out that the distribution of species of *Acomys*, as inhabitants of rocky regions and now mostly confined to jebels, expanded and contracted depending on climatic conditions during the past 15,000 years. They may have occurred in localities in parts of the present woodland savanna as well as on jebels, and many populations may have been continuously distributed.

Habitat *Acomys cineraceus* (and *A. cahirinus*) is the most typical rodent of the Sudanese rocky regions, especially on isolated rocky hills (jebels), mostly formed of granite and syenite, where boulders and crevices provide for shelter and for retaining grasses, seeds and moisture (Happold 1969). Not recorded in open arid sandy regions of N Sudan. These rocky islands project from the wide extensive plains, and are numerous in the provinces of Kassala, Blue Nile and Upper Nile in E Sudan, and also in the wooded savannas of S Sudan, mostly at low altitudes between 200 and 500 m. Also recorded from villages, huts in villages and other buildings in Upper Nile and Blue Nile Provinces. Further south, in C and S Sudan, found in fields, dry wooded savanna and at edges of swamps and grasslands (specimen labels) (F. Dieterlen unpubl.).

Abundance Probably similar in abundance to *A. cahirinus*. Often abundant in suitable habitats and the most numerous of small rodents. In N Sudan, comprised 80–94% of small mammals on four rocky jebels (n = 22–58/jebel; usually only 2–3 spp. on each jebel), and 0% on two other jebels (no small rodents present) (Happold 1969).

Adaptations Terrestrial and rupicolous; nocturnal and crepuscular. Colour of pelage is dependent on climate and environment (see Geographic Variation). Habitat restriction to jebels and other rocky habitats appears less pronounced in the acacia savannas of SE and S Sudan (e.g. Upper Nile and Equatoria Province) than in N Sudan. In S Sudan, occurs sympatrically with one of more of the following: *Acomys*

wilsoni, *A. percivali*, *Myomys fumatus*, *Aethomys hindei*, *Lemniscomys macculus*, *L. zebra* and *Mastomys* sp.

Foraging and Food Probably opportunistic and omnivorous. No detailed analysis of diet available, but probably varies seasonally and includes seeds of petrophilous plants, snails of several species, insects and their larvae, spiders and scorpions.

Social and Reproductive Behaviour No information.

Reproduction and Population Structure In N Sudan (Blue Nile and Khartoum Provinces), pregnant ♀♀ and many young animals in Nov and Dec; probably one breeding season/year 1–3 months after the rains (Happold 1966a). Further south (also Blue Nile Province), pregnant or lactating ♀♀ in Nov (n = 4) and in the wet season May and Jul (n = 7); probably two breeding seasons/year (F. Dieterlen unpubl.). In W Equatoria Province, S Sudan, almost 100% of adult ♀♀ were pregnant or lactating (n = 18) at the end of the wet season (Sep–Oct). Gestation: uncertain, probably 30–35 days. Mean embryo number: 2.53 (range 1–5; n = 30 pregnancies). Young precocial at birth with eyes open. Sexual maturity (♀♀ and ♂♂): ca. 2 months when body weight ca. 30 g. Adult ♂♂ have testes size of 10–13 mm at all times; no evident change in size during breeding season (F. Dieterlen unpubl.).

Predators, Parasites and Diseases See *A. cahirinus*.

Conservation IUCN Category: Least Concern.

Measurements

Acomys cineraceus

HB: 97.2 (89–116) mm, n = 30
T: 87.6 (72–121) mm, n = 23
HF: 17.2 (13–19) mm, n = 27
E: 15.3 (13–18) mm, n = 29
WT: 34.6 (26–61) g, n = 30
GLS: 27.6 (26.3–31.3) mm, n = 21
GWS: 13.0 (12.4–13.9) mm, n = 17
M¹–M³: 4.53 (4.1–5.4) mm, n = 21
Blue Nile Province, Sudan (SMNS)

Key Reference Happold 1969.

Fritz Dieterlen

Acomys ignitus FIERY SPINY MOUSE

Fr. Souris épineuse rougeâtre; Ger. Rote Stachelmaus

Acomys ignitus Dollman, 1910. Ann. Mag. Nat. Hist., ser. 8, 6: 229. Voi, Kenya.

Taxonomy Recognized as a valid species by Hollister (1919) and Ellerman (1941), and confirmed as such by recent studies on chromosomes (Matthey 1965), electrophoretic analyses (Janacek *et al.* 1991) and cytochrome *c* (Barome *et al.* 2000). Janacek *et al.* (1991) regard *A. ignitus* as closely related to *A. cahirinus*. The taxon

kempi, considered as a subspecies by Dollman (1914), Hollister (1919) and Ellerman (1941), has proved to be a valid species and its geographic range is well separated from that of *A. ignitus*. Synonyms: none. Chromosome number: 2n = 50; FN 66–68; with 16–18 meta- and submetacentric chromosomes (Matthey 1965).



Description A small 'handsome' species with bright reddish-orange flanks. Thin spinous hairs on head, shoulders, anterior part of back, and flanks; broad and flattened spines on rump and posterior part of back. Dorsal pelage brownish-orange, becoming bright reddish-orange ('fiery') on flanks; hairs slate-grey at base. Ventral pelage white, hairs rather spinous, pure white; sharply delineated from the reddish-orange flanks. Upper surface of hands and feet white. Tail relatively short (ca. 77% of HB), stout and comparatively coarse, silvery-grey, with black bristles above, white bristles below. For details of special characters of teeth, see Denys *et al.* (1994).

Geographic Variation None recorded.

Similar Species

A. kempi. Similar head and body size; dorsal pelage orange-buff with stiff spines on mid-back, flanks dull orange; tail longer (mean 93 mm) and relatively longer (ca. 95% of HB); sympatric but with more widespread distribution.

A. wilsoni. Similar head and body size; dorsal pelage bright cinnamon or chestnut; tail slightly longer (mean 84 mm) and slightly longer (ca. 90% of HB); often common and more widespread.

Distribution Endemic to Africa. Somalia–Masai Bushland BZ. Recorded from SE Kenya (22 known localities) and NE Tanzania (one locality – Usambara Mts) (Janecek *et al.* 1991, Bates 1994). In Kenya, found mostly in the region of Tsavo N. P. at altitudes between ca. 100 m and 800 m. In addition, there is a record from Somalia (Petter 1983), but without a locality (and hence not shown on map).

Habitat In Kenya, occurs mostly in rocky habitats in dry savanna and semi-desert in the region of Tsavo N. P. at altitudes between ca. 100 m and 800 m. Most of the known habitats are in the region of Tsavo N. P.

Abundance No information.

Remarks Apparently little information. Litter-size: 1.5 (1–2, n = 4; Hollister 1919).

Conservation IUCN Category: Least Concern. However, the small geographic range suggests it may be 'Near Threatened'.

Measurements

Acomys ignitus

HB: 92–114 mm

T: 70–85 mm

HF: 14.5–19 mm

E: 14.5–19 mm

WT: n. d.

GLS: 27.5–30.8 mm

GWS: 11.5–13.9 mm

M¹–M³: 4.1–4.5 mm

Kenya (Denys *et al.* 1994); no means or sample sizes given

Key References Dollman 1910; Hollister 1919.

Fritz Dieterlen

Acomys johannis JOHAN'S SPINY MOUSE

Fr. Souris épineuse de Johan; Ger. Johans Stachelmaus

Acomys johannis Thomas, 1912. Ann. Mag. Nat. Hist., ser. 8, 9: 272. Kabwir, Bauchi Plateau, Nigeria.

Taxonomy Previously included in *A. cineraceus* (Musser & Carleton 1993), but now considered to be a distinct species (Musser & Carleton 2005). Rosevear (1953) referred to this species as *A. johannis*; later (1969), he referred to *Acomys cahirinus johannis*, but also included specimens now considered to be *A. airensis*. Referred to as *A. cahirinus johannis* by Happold (1987). Barome *et al.* (2000) demonstrated the molecular proximity of specimens from Nigeria, Cameroon, Benin and Niger. '*Acomys* sp. 1' of Barome *et al.* (2000) from Burkina also considered here to be *A. johannis*. Synonyms: none.

Chromosome number: 2n = 66–68 (Volobouev *et al.* 1996b).

Description Small spiny mouse with brownish-grey pelage. Dorsal pelage chocolate-brown to grey, becoming paler on flanks; hairs brown to grey at base, with darker tip; spiny hairs on posterior half of the back, extending more anteriorly in old individuals. Ventral pelage entirely white; clearly delineated from flanks. Head with pointed muzzle, small eyes and relatively large ears. Hindfeet short with short digits, Digit 1 being especially reduced in size. Tail

moderately long (ca. 90% of HB), easily breakable, bicoloured (grey-brown above, white below) and naked (with the exception of very short hairs at tip). Nipples: $1 + 2 = 6$.

Geographic Variation Size and colour variation in Burkina, where brown individuals from S are significantly larger than grey and rufous individuals from C and N (Sicard & Tranier 1996).

Similar Species

A. airensis. Pelage slightly paler; chromosome number: $2n = 40-46$; more northern distribution (Mauritania, Mali and Niger [left bank of the Niger R]).

Distribution Endemic to Africa. Sudan Savanna and Sahel Savanna BZs. Recorded from Mali and Niger (right bank of Niger R.), Burkina, N Togo, Benin, Ghana, Nigeria, N Cameroon and Chad.

Habitat Found mainly in rocky habitats such as rock ledges, cliffs, small inselbergs and extensive rocky hills in Burkina (Sicard & Tranier 1996), Chad (Granjon *et al.* 2004), Mali (L. Granjon unpubl.) and Nigeria (Happold 1970b), but sometimes caught at some distance from rocks, in dense vegetation or near small water-courses, as in S Burkina (Sicard & Tranier 1996).

Abundance Locally abundant in favourable habitats, as suggested by relatively high trapping success in rocky habitats where it was found in Burkina (B. Sicard pers. comm.) and Chad (Granjon *et al.* 2004). Comprised 95% of small rodents on sandstone rocks in Yankari G. R., Nigeria ($n = 19$; Happold 1970b).

Remarks Terrestrial and nocturnal. Rests in rock cracks rather than ground burrows, and occasionally uses cracks in termitaria (Sicard & Tranier 1996). As for other *Acomys*, the skin is very delicate and the tail breaks easily. In captivity, omnivorous and readily carnivorous. Pregnant ♀♀ at end of dry season (Mar–Apr) in Yankari G. R., Nigeria; no data for other months. Mean embryo number: 1.4 (range 1–2, $n = 5$; Happold 1970b). One female with two embryos in Mali (L. Granjon unpubl.).

Conservation IUCN Category: Least Concern.



Acomys johannis

Measurements

Acomys johannis

HB: 105.4 (88–119) mm, $n = 75$

T: 97.4 (73–109) mm, $n = 57$

HF: 18.0 (16–20) mm, $n = 70$

E: 16.7 (14–19) mm, $n = 43$

WT: 36.6 (27–60) g, $n = 55$

GLS: 29.5 mm, $n = 33^*$

GWS: 13.8 mm, $n = 33^*$

M^1-M^3 : 4.5 mm, $n = 33^*$

Body measurements and weight: Burkina (MNHN)

Skull measurements: Burkina (Sicard & Tranier 1996)

*Ranges of values not given

Key References Happold 1970b; Sicard & Tranier 1996.

Laurent Granjon

Acomys kemp KEMP'S SPINY MOUSE

Fr. Souris épineuse de Kemp; Ger. Kems Stachelmaus

Acomys kemp Dollman, 1911. Ann. Mag. Nat. Hist., ser. 8, 8: 125. Chanler Falls, N Guaso Nyiro, Kenya.

Taxonomy Originally described as a species by Dollman (1911a), but later considered to be a subspecies of *A. ignitus* by the same author (Dollman 1914) (see also Hollister 1919 and Ellerman 1941). Treated as a subspecies of *A. cahirinus* by Setzer (1975), but reinstated as a species by Janeczek *et al.* (1991). Musser & Carleton (1993, 2005) also refer to *kemp* as a distinct species on the basis of morphological characters and distribution, and consider it to be an eastern segment of *A. cineraceus*. Synonyms: *montanus*, *pulchellus*. Subspecies: none. Chromosome number: not known.

Description Small spiny mouse with orange-grey pelage. Pelage stiff and coarse, spines (up to 10 mm) from mid-back to base of tail and on rump. Dorsal pelage orange-buff, darker on mid-dorsal line; not speckled; pale grey at base, orange-buff at tip. Flanks dull orange; hairs soft, whitish-grey at base, orange at tip. Ventral pelage pure white, colour sharply delineated from flanks. Head similar in colour to back. Cheeks orange-buff (as flanks); lips, chin, throat and chest white. White suborbital spot. White subauricular patch. Fore- and hindlimbs short. Feet white. Tail relatively long (ca. 94% of HB),

scaly, almost naked, brownish-grey above with black bristles, paler below with whitish bristles. Nipples: not known.

Geographic Variation None recorded.

Similar Species

A. ignitus. Similar size; dorsal pelage brownish-orange, with bright reddish-orange flanks; tail shorter (70–85 mm) and relatively shorter (ca 77%) than HB; low altitudes, SE Kenya and N Tanzania.

A. wilsoni. Similar head and body size; dorsal pelage bright cinnamon or chestnut; tail shorter (mean 84 mm) and relatively slightly shorter (ca. 85% of HB); often common.

Distribution Endemic to Africa. Somalia–Masai Bushland BZ. Recorded from S Ethiopia, S Somalia, Kenya and NE Tanzania. In Kenya, known only from 20 localities east of the Rift Valley between the Equator and ca. 03° 00' N, and from 37° 15' E to ca. 39° 00' E. In Ethiopia, known from three localities in S Sidamo Province, all east of the Rift Valley; northern limit ca. 06° 40' N. One record from NE Tanzania (Musser & Carleton 1993) and one record from S Somalia. Limits unknown; Gregorian Rift Valley appears to be western limit of distribution. Altitudinal range ca. 600–1800 m.

Habitat Rocky habitats in dry savanna and semi-desert.

Remarks Embryo numbers: 1 (n = 1), 2 (n = 1) (Hollister 1919). Apparently no other information available.

Conservation IUCN Category: Least Concern.

Measurements

Acomys kemp

HB: 99.2 (95–110) mm, n = 13

T: 93.0 (82–106) mm, n = 13



Acomys kemp

HF: 15.5 (15–16) mm, n = 13

E: n. d.

WT: n. d.

GLS: 25.4 (23.8–27.1) mm, n = 11

GWS: 13.2 (12.4–14.3) mm, n = 11

M¹–M³: 4.3 (4.0–4.6) mm, n = 11

Kenya (Dollman 1911a, Hollister 1919)

Key References Dollman 1911a; Hollister 1919.

Fritz Dieterlen

Acomys louisae LOUISE'S SPINY MOUSE

Fr. Souris épineuse de Louise; Ger. Louises Stechelmaus

Acomys louisae Thomas, 1896. Ann. Mag. Nat. Hist., ser. 6, 18: 269. Henweina Plain, 40 miles south of Berbera, Somalia.

Taxonomy The only representative of the subgenus *Peracomys*, characterized by the possession of a t7-cusp on M1 and/or M2 that is not present in the subgenus *Acomys* (Petter & Roche 1981). This character is found in *Acomys* from a large area in Somalia, Ethiopia, Kenya and N Tanzania and is probably evidence of an unrecognized species-complex (Petter 1983). Synonyms: *umbratus*. Subspecies: two. Chromosome number: not known.

Description Small and relatively long-tailed spiny mouse. Pelage spiny from shoulders to base of tail. Dorsal pelage rufous, buff or greyish-brown; hairs and spines dull brown, slightly darker at tip. Flanks similar to dorsum, stiff (not spiny), without any russet colour. Ventral pelage pure white, soft; colour clearly delineated from colour of flanks. Ears darkly pigmented, with scattered short whitish hairs on inner surface. Subauricular patch small (or absent). Pelage colour

varies geographically. Limbs and feet white. Tail relatively long (ca. 109% of HB), the relatively longest tail of any species in the genus, usually bicoloured, greyish-brown above, white below.

Geographic Variation

A. l. louisae: Henweina Plain, 40 miles S of Berbera. Dorsal pelage rich buff or ochre-buff; tail mostly all white.

A. l. umbratus: Wagar Mountain, Golis Mts, N Somalia. Dorsal pelage greyish-brown, paler on rump; tail bicoloured.

Similar Species

A. kemp. On average HB larger; T similar in length but relatively shorter than HB; dorsal pelage orange-buff.

A. mullah. HB larger; T on average slightly longer but relatively shorter than HB; dorsal pelage slate-grey.

A. wilsoni. HB similar in length; T shorter, and relatively shorter than HB; dorsal pelage pale brown, speckled.

Distribution Endemic to Africa. Somalia–Masai Bushland BZ. Recorded from N, NE and E Somalia, north of ca. 06°N (ten localities), and Djibouti. Probably extends to S Somalia; limits uncertain (D. Schlitter, pers. comm.).

Habitat Little information; recorded from coastal plains to ca. 1500 m (Petter & Roche 1981).

Abundance Presumably uncommon or rare; few records.

Remarks Apparently no other information available.

Conservation IUCN Category: Least Concern.

Measurements

Acomys louisae

HB: 95, 79 mm, n = 2

T: 104, 86 mm, n = 2

HF: 16, 16 mm, n = 2

E: 15, 12 mm, n = 2

WT: n. d.

GLS: 28.3 (27.3–29.3) mm, n = 3

GWS: 12.2 (12.0–12.5) mm, n = 3

M¹–M³: 4.3 (4.2–4.5) mm, n = 3

Somalia (Thomas 1923, De Beaux 1934)



Acomys louisae

Body measurements: holotype and paratype

Key References De Beaux 1934; Petter 1983; Petter & Roche 1981.

Fritz Dieterlen

Acomys mullah MULLAH SPINY MOUSE

Fr. Souris épineuse de Mullah; Ger. Mullah-Stachelmaus

Acomys mullah Thomas, 1904. Ann. Mag. Nat. Hist., ser. 7, 14: 103. Harar, Ethiopia.

Taxonomy Setzer (1975) treated *mullah* together with *brockmani* (Dollman 1911b) as subspecies of *A. dimidiatus*. Ellerman (1941) recognized *mullah* and *brockmani* as distinct species. Yalden *et al.* (1976) and Musser & Carleton (1993) included *mullah* as a synonym of *A. cahirinus*. Here, following Musser & Carleton (2005), *mullah* is retained as a valid species pending revision. Synonyms: *brockmani*. Subspecies: none. Chromosome number: not known.

Description Small greyish spiny mouse. Hairs spiny and long from shoulders to base of tail. Dorsal pelage slate-grey, becoming brownish on rump; spines off-white at base, pale brown or dark brown at tip. Flanks brownish. Ventral pelage soft, white; clearly delineated from colour of flanks. Head similar in colour to dorsal pelage. Ears large, pigmented with sparse covering of short blackish-brown hairs. Small white subauricular patch. Outer surface of forelimbs brownish. Fore- and hindfeet white. Tail relatively long (ca. 100% of HB), bicoloured, grey above, white below, with sparse covering of hairs. Skull very large, braincase broad and flat, ridges not very heavy; anterior palatal foramina very long reaching nearly to posterior end of M¹. Nipples: 0 + 2 = 4.



Acomys mullah

Geographic Variation The form *brockmani* differs from *mullah* (as above) in being slightly smaller; dorsal pelage pale yellow with rufous tint becoming darker on rump and less spiny; flanks slightly reddish, paler than in *mullah*; skull smaller with shorter anterior palatal foramina.

Similar Species

- A. louisae*. Smaller, dorsal pelage rufous, buff or greyish-brown; distribution possibly partly sympatric.
A. cahirinus. Dorsal pelage russet; on average smaller; more widespread in NE Africa.
A. percivali. Dorsal pelage dark brownish-grey; on average smaller; allopatric.

Distribution Endemic to Africa. Somalia–Masai Bushland BZ. Recorded from Ethiopia (type locality Harar) and Somalia (Upper Sheikh, Berbera, Bulhar); probably occurs in Eritrea and Djibouti. Limits unknown.

Habitat Specimens captured among rocks, on stony ground amongst crops; and in ‘bush country’ (R. S. Drake-Brockman, specimen labels; BMNH).

Abundance Very rare; only known from a few specimens from about four localities.

Remarks Nocturnal. Subadults (HB: 90–100 mm) recorded in Aug, Sep, Nov, Dec, Jan and Mar (BMNH).

Conservation IUCN Category: Least Concern.

Measurements

Acomys mullah

HB: 118 (106–134) mm, n = 7

T: 108 (95–117) mm, n = 7

HF: 16.9 (15–18) mm, n = 7

E: 17 (14–18) mm, n = 7

WT: n. d.

GLS: 28.8 (28.3–29.3) mm, n = 3

GWS: 13.6 (13.3–13.9) mm, n = 3

M¹–M³: 4.3 (4.1–4.7) mm, n = 3

Ethiopia and Somalia (BMNH)

Key Reference Petter 1983.

Fritz Dieterlen

Acomys percivali PERCIVAL'S SPINY MOUSE

Fr. Souris épineuse de Percival; Ger. Percivals Stachelmaus

Acomys percivali Dollman, 1911. Ann. Mag. Nat. Hist., ser. 8, 8: 126. Chanler Falls, Nyiro, Kenya.

Taxonomy Included as a synonym of *kemp*i and included within *A. cahirinus* by Setzer (1975), although most authors (e.g. Neal 1983, Petter 1983) consider *A. percivali* to be a valid species. Genetically closely related to *A. wilsoni* (Janacek *et al.* 1991). Synonyms: none. Chromosome number: not known.

Description Small grey spiny mouse. Pelage coarse and stiff with strong spines (ca. 10 mm) from mid-back to base of tail. Dorsal pelage grey to greyish-brown (mostly without any russet or reddish colouration as in other species of the genus); hairs/spines pale grey at base, darker grey at tip. Flanks grey, usually paler than dorsal pelage (occasionally with some cinnamon on flanks). Ventral pelage white, usually not stiff or spiny. Colour of ventral pelage clearly delineated from colour of flanks. Adult ♂♂ may have a patch of yellow, oily pelage from secretions of scent glands on centre of abdomen. Head similar in colour to dorsal pelage. Some individuals have small white suborbital spot. Ears large, darkly pigmented, sparsely covered with short small hairs. Subauricular and postauricular spots absent. Chin, throat and chest white. Hindlimbs and feet short; feet white above with strong claws. Tail short (ca. 76% of HB), almost naked but with scattered short bristles; grey above, whitish-grey below. Tail often absent or short due to injury. Nipples: not known.

Geographic Variation None recorded.



Acomys percivali

Similar Species

A. wilsoni. Similar head and body size; dorsal pelage bright cinnamon or chestnut; tail on average longer (mean 84 mm) and relatively longer (ca. 87% of HB); frequently syntopic; often common.

A. kempii. Similar head and body size; dorsal pelage orange-buff with stiff spines on mid-back, flanks dull orange; tail longer (mean 93 mm) and relatively longer (ca. 95% of HB); distribution restricted.

A. ignitus. Similar head and body size; dorsal pelage brownish-orange, with bright reddish-orange flanks; tail relatively and comparatively similar; restricted to low altitudes in SE Kenya and N Tanzania.

Distribution Endemic to Africa. Somalia–Masai Bushland BZ (part). Recorded from S Sudan (east of the White Nile), Uganda, Kenya and SW Ethiopia. Limits of distribution uncertain.

Habitat Kopjes and rocky habitats. The rodent fauna on kopjes in C Kenya is nearly always dominated by this species, sometimes to the near or total exclusion of all other species. On the exceedingly rare occasions when Percival's Spiny Mice are captured in other habitats, circumstances suggest they are almost certainly dispersing individuals.

Abundance Very common on kopjes, and often the most numerous species of small mammal, comprising 80–100% of total small rodents captured. Densities vary but are usually 100–300/ha (S. Takata unpubl.). Populations tend to be stable because these mice breed slowly and are long-lived. Even small kopjes may have stable populations. May be syntopic with *A. wilsoni* on some kopjes.

Adaptations Nocturnal and terrestrial. Percival's Spiny Mice are surprisingly good climbers on sloping, vertical and overhanging rocky walls. They are able to run and climb as readily as the agamid lizards that also live on the kopjes. At night, they run across open expanses of rock while foraging. They are also accomplished jumpers, and captives often leap half a metre into the air, somersaulting, and landing upside-down on the wire top of the enclosure. Their forelimbs are particularly dexterous, perhaps as a modification to help capturing insects. When threatened, Percival's Spiny Mice wedge themselves head-first into narrow cracks so that only the tail and spines protrude. Once the tail is pulled off, there is nothing left for predators to secure. The body is remarkably supple and, when wedged into a crevice, can be dorsoventrally flattened to the height of the skull.

Foraging and Food Omnivorous, but strongly insectivorous. Diet varies seasonally. In the dry season, diet comprises 60–95% arthropods and 5–10% stems, leaves or seeds; in the wet season 70–90% arthropods, 5–20% stems and leaves and 5–10% seeds; and in the intermediate season (between wet and dry) 45–50% arthropods, 10–25% stems and leaves and 35–40% seeds (Neal 1984a). The diet may also include gum exudates (Neal 1984b). Wild-caught captives in cafeteria-style feeding trials feed almost exclusively on insects (over 95% by weight) (S. Takata unpubl.). Percival's Spiny Mice are very adept at capturing large orthopterans, biting their legs off to immobilize them before eating (S. Takata unpubl.). When offered large flying moths, they will leap into the air to capture them. If given a choice of seeds, they prefer those of *Rhynchelytrum repens*, a kopje grass with relatively large seeds (S. Takata unpubl.). Preference for this seed is suggested also by the empty husks of seed heads of *R. repens* found on well-used paths through and under rocks on kopjes.

Social and Reproductive Behaviour Highly social. Spool-and-line tracking of individuals shows that on small and medium-sized

kopjes, each mouse uses the entire kopje with no obvious territoriality shown by either sex. In captivity, they are very social, sleeping together and grooming each other. In captivity, adults of both sexes groom and carry young animals; however, when densities are high, larger dominant mice, particularly ♀♀, become aggressive and may attack and kill younger individuals when they reach 1–2 months of age.

Reproduction and Population Structure Reproduction on a single kopje is highly synchronous, with all adult ♀♀ often giving birth within days of one another. However, there is little synchrony between nearby kopjes, and kopjes separated by only 1–2 km are completely out of synchrony. In Meru N. P., Kenya, pregnant ♀♀ were present throughout the year; the occurrence of pregnancy varied from ca. 45% to ca. 90%/month and was not closely associated with seasonal changes in rainfall (cf. syntopic *Gerbilliscus nigricaudus*) (Neal 1984a). Gestation: 34–35 days (S. Takata unpubl.). Mean litter-size: 1.85 (Neal 1983), 1.88 (S. Takata unpubl.). Weight of full-term embryos: 4–5 g (Neal 1983). At birth, young weigh 4–5.5 g (S. Takata unpubl.), and are precocious, fully haired with soft pelage, able to follow their mother and to feed on solid food. Spines erupt as young approach five weeks of age, and weigh 8–20 g. At this time, growth rates slow noticeably. Percival's Spiny Mice are long-lived: individuals marked as adults have been recaptured three years later on the same kopje. Dispersal seems to be rare as few marked animals (over a six-year period) have been found on other kopjes after disappearing from their natal kopjes (Kenya; S. Takata unpubl.).

Predators, Parasites and Diseases Remains have never been recovered from the faecal samples from over 300 small mammalian carnivores in C Kenya (S. Takata unpubl.). Remains have not been found in pellets of raptors, nor in snakes. Ectoparasite load is very low; the coarse spiny coat and social grooming probably facilitate removal of ticks and fleas.

Conservation IUCN Category: Least Concern.

Measurements

Acomys percivali

HB (♂♂): 96 (82–108) mm, n = 92

HB (♀♀): 98 (86–111) mm, n = 57

T (♂♂): 73 (44–92) mm, n = 70

T (♀♀): 76 (39–91) mm, n = 45

HF: 13 (9–15) mm, n = 18

E: 14 (11–15) mm, n = 17

WT (♂♂): 28 (18–38) g, n = 229

WT (♀♀): 33 (22–48) g, n = 244

GLS (♂♂): 27.1 (26.6–27.9) mm, n = 3

GLS (♀♀): 27.7 (27.5–28.2) mm, n = 3

GWS (♂♂): 13.4 (13.2–13.5) mm, n = 3

GWS (♀♀): 13.4 (13.2–13.5) mm, n = 3

M¹–M³: 4.2 (3.9–4.5) mm, n = 6

Laikipia District, Kenya (S. Takata unpubl.)

Tail length may include individuals that have partially lost the terminal part of the tail.

Key References Neal 1983, 1984a.

S. Takata

Acomys russatus GOLDEN SPINY MOUSE

Fr. Souris épineuse dorée; Ger. Goldstachelmaus

Acomys russatus (Wagner, 1840). Abhandlungen der Bayerischen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Klasse 3: 195 (pl. 3, fig. 2). Probably Nohel, Sinai, Egypt.

Taxonomy Originally described in the genus *Mus*. This species occupies an inter-generic distant position, the 'russatus section' of Ellerman (1941), a view confirmed by Denys *et al.* (1994) on the basis of karyology and dentition characters. The cusps t1 and t2 of M¹ are well fused transversely and arranged in a laminate pattern. A related form, *lewisi*, considered to be a separate species by Atallah (1967) and Qumsiyeh *et al.* (1986) on the basis of colour and the morphology of the baculum, is now considered to be a synonym or subspecies of *A. russatus* (see Osborn & Helmy 1980, Harrison & Bates 1991, Musser & Carleton 2005). This view is supported by studies on mitochondrial DNA cytochrome *b* sequences (Barome *et al.* 2000). Synonyms: *aegyptiacus*, *affinis*, *harrisoni*, *lewisi*. Subspecies: none. Chromosome number: 2n = 66, FN = 76 (Wahrman & Zahavi 1953).

Description Large golden-brown spiny mouse with relatively short tail. Well-developed spines on most parts of body, including on feet. Dorsal pelage pale golden-brown or reddish-orange, slightly darkening on rump; spines pale grey at base, with broad orange or yellowish subterminal band and black tip. Scattered long, fine, white hairs project beyond the spines on posterior half of back. Flanks yellowish-brown. Ventral pelage whitish or yellowish; hairs grey at base. Colour of dorsal and ventral pelage weakly delineated on flanks; strongly delineated on cheeks and side of neck. Head similar in colour to dorsal pelage. Eyes with conspicuous white suborbital patch. Ears black, relatively small, covered with short buffy hairs; subauricular and postauricular white patches. Fore- and hindlimbs

grey. Undersurface of feet black. Tail relatively short (ca. 60% of HB), black and scaly, with relatively long silvery bristles projecting between scales. Nipples: 1 + 2 = 6.

Geographic Variation The form *aegyptiacus* from the Eastern Desert differs from *russatus* by having a pale reddish-orange dorsal pelage and a shorter tail.

Similar Species

A. cahirinus. Dorsal pelage blackish or brownish (never golden-brown); tail longer and relatively longer (ca. 90–100% of HB).

Distribution Sahara Arid BZ. Recorded in Eastern Desert of Egypt between the Nile R. and the Red Sea (from ca. 26° N to ca. 30° N), and in Sinai. Extraliminally in Jordan, Israel, Saudi Arabia, N Yemen and Oman (Harrison & Bates 1991).

Habitat Boulder-strewn canyons, cliffs and rocky hillsides in arid environments. Occasionally may occur in gardens around habitations. Altitudinal range: below sea level (Dead Sea; Atallah 1970) to ca. 2285 m (Mt Sinai).

Abundance Rare and localized in Egypt (Osborn & Helmy 1980), especially when compared with syntopic *A. cahirinus*. In Middle East, appears to be common in some localities, e.g. densities of 14–46/ha (mean 28/ha) during spring and summer in Israel (Shargal *et al.* 2000).

Adaptations Terrestrial and rupicolous. Nocturnal and diurnal. Golden Spiny Mice tend to be diurnal and crepuscular when syntopic with *A. cahirinus* (Shkolnik 1971) and in cold weather (Haim & Borut 1975). Although most habitats are hot and arid, some populations survive on the summit of Mt Sinai (Jebel Musa; 2200 and 2285 m), where there is snow and a mean temperature of below 0 °C in winter (Jan–Mar). Adaptations to the cold environment include larger body size than individuals at lower altitudes, diurnal and crepuscular activity when daytime temperatures are warmer, maintenance of a stable Tb of 35–37 °C, and by not entering torpor or hibernation (Haim & Borut 1975).

Diurnal activity (an unusual feature of small mammals in arid environments) may result in potentially higher water loss. Golden Spiny Mice are able to utilize salty water and extract water from halophytic plants, and additional water is obtained by eating desert snails (Shkolnik & Borut 1969).

Golden Spiny Mice adapt to the presence of syntopic *A. cahirinus* in several ways that are assumed to reduce competition, e.g. diurnal activity rather than nocturnal activity and larger body size. In competitive situations, *A. russatus* is displaced by *A. cahirinus* despite being larger than *A. cahirinus* (Shargal *et al.* 2000).



Acomys russatus

Foraging and Food Omnivorous. The diet is mainly seeds of herbs and grasses; desert snails, insects and their larvae are also eaten. Unable to survive on a dry diet alone (Harrison & Bates 1991).

Social and Reproductive Behaviour In Israel, mean home-range was 533 m² for ♂♂ and 668 m² for ♀♀ (n = 12 for each species; Shargal *et al.* 2000). Females construct nests for their young – a character not recorded for any other species of spiny mice (Searight 1987). Competition for nesting sites is subject to fierce competition due to the harsh conditions under which *A. russatus* exists. Urine and oral secretions are used to mark the home area, especially nesting sites (Rozenfeld *et al.* 1994).

Reproduction and Population Structure In Egypt, pregnant ♀♀ recorded only in May and Jun (Osborn & Helmy 1980). In the Dead Sea area of Israel, reproductive activities restricted to four months in late spring and early summer (Apr–Jul) (Qumsiyeh 1996, Shargal *et al.* 2000). In captivity, reproduction occurs throughout the year (Searight 1987). Gestation: 44 days. Litter-size: 1–2 in young ♀♀, up to four in older ♀♀ (Harrison & Bates 1991). Young are precocial at birth. Females mature very early, at about Day 31.

Predators, Parasites and Diseases Ectoparasites include the fleas *Parapulex chephrensis*, *Nosopsyllus geneatus* and *N. henleyi* (Hoogstraal & Traub 1965b) and various lice (Johnson 1960). Infection rate with

fleas is low; and most of the 40 *A. russatus* examined at St Catharine's Monastery in Sinai (5000 ft) were not infected (Hoogstraal & Traub 1965b).

Conservation IUCN Category: Least Concern. Although rare or uncommon in Egypt, the species is widespread and not uncommon in other parts of its geographic range.

Measurements

Acomys russatus

HB: 109.2 (90–117) mm, n = 6

T: 64.4 (56–75) mm, n = 5

HF: 19.2 (19–20) mm, n = 6

E: 19.3 (16–20) mm, n = 6

WT: 37.0 (24.0–53.2) g, n = 3

GLS: 29.2 (27.8–31.1) mm, n = 5

GWS: 13.1 (12.4–13.6) mm, n = 4

M¹–M³: 5.2 (5.0–5.2) mm, n = 5

Eastern Desert, Egypt (Osborn & Helmy 1980)

Body measurements of individuals from Sinai are slightly larger

Key References Harrison & Bates 1991; Osborn & Helmy 1980.

Fritz Dieterlen

Acomys spinosissimus LEAST SPINY MOUSE (SOUTHERN SPINY MOUSE)

Fr. Souris épineuse petite; Ger. Kleine Stachelmaus

Acomys spinosissimus Peters, 1852. Reise nach Mossambique, Säugethier, p. 160. Buio and Tette (= Tete), Mozambique.

Taxonomy Differences in size and colour have confused the taxonomy of this species. *Acomys spinosissimus*, as understood here, is a valid species with regional variation in pelage colouration. Southern grey-coloured individuals were originally described as *A. selousi*, the northern richer russet-coloured individuals as *A. spinosissimus*, and individuals intermediate in colour as *A. transvaalensis* (Dippenaar & Rautenbach 1986, Janecek *et al.* 1991). Populations from all parts of the range are considered as monophyletic, and quite distinct from species found further south (*A. subspinosus*) and further north (e.g. *A. wilsoni*, *A. ignitus*, *A. cahirinus*) (Barome *et al.* 2000). Synonyms: *selousi*, *transvaalensis*. Subspecies: none. Chromosome number: 2n = 60, FN = 68 (South Africa; Dippenaar & Rautenbach 1986).

Description Small mouse with spiny hairs on the back and rump. Dorsal pelage grey or fawn to bright russet-brown, but variable (see below). Hairs on shoulders and flanks soft and brush-like; hairs on rump and back thickened to form soft spines, pointing posteriorly and slightly longer than other hairs; hairs pale grey, white at base, and tipped with grey, fawn or russet. Hairs on flanks softer and paler than on back. Some individuals have patch-like pattern of grey and russet dorsal pelage. Ventral pelage pure white, without spines. Head similar in colour to back; chin and throat white; white spot below each eye. Ears naked, rounded and moderate in size; eyes large, black, protruding. Fore- and hindfeet white dorsally, naked and unpigmented below. Tail relatively long (ca. 80–90% HB), grey

or russet above, white below, almost naked. Males are, on average, slightly larger than ♀♀. Nipples: 0 + 2 = 4.

During the moult, faded old hairs are replaced by brighter and darker new hairs. The junction between old and new hairs as the moult proceeds from the rump to the head is very clear cut.

Geographic Variation Southern parts of range (South Africa, W Zimbabwe), dorsal pelage slate-grey, or grey with a tinge of brown. Northern part of range (E Zimbabwe, Mozambique, Malawi), dorsal pelage fawn, apricot, or russet brown. In Zimbabwe, Smithers & Wilson (1979) recognized three subspecies, now synonyms: *A. s. spinosissimus* (reddish-brown, east of range), *A. s. selousi* (west of range, greyish) and *A. s. transvaalensis* (centre of range, intermediate in colour).

Similar Species

A. subspinosus. Similar size; Cape region of South Africa only.

A. wilsoni. On average larger; spines very stiff; dorsal pelage bright cinnamon; distribution further north in Tanzania and Kenya; may be parapatric in C Tanzania.

Distribution Endemic to Africa. Zambezi Woodland BZ. Recorded from Tanzania and W Zambia through SE DR Congo, Malawi, C Mozambique, Zimbabwe, W Botswana and South Africa (Northern and North-West Provinces). May also occur in N

*Acomys spinosissimus*

Mozambique, parts of C Zimbabwe (lack of records perhaps due to inadequate collecting) and NE Tanzania (habitats perhaps unsuitable).

Habitat Least Spiny Mice almost always associated with rocks and boulders in grassland habitats. Less often, found in dry deciduous thicket-bush. In a few localities, have been found in sandy soil near rivers (Smithers & Lobão Tello 1976). Do not normally occur in riverine grasslands nor in miombo and mopane woodlands where boulders are absent. They can survive in habitats that have long hot dry seasons when there is no drinking water, and where the grass is burned each year.

Abundance Abundance (as a % of the small rodent community) varies greatly according to locality and habitat. In Zimbabwe, comprised 7.9% in talus habitats (where they were the second most numerous species after *Aethomys namaquensis*) and 3.6% in thickets (Linzey & Kesner 1997b); in Mozambique, 24% in rocky grasslands near a stream (Gliwicz 1985); and in Malawi, 24% in thicket clump savanna at Lengwe N. P. (total $n = 222$) and 46% in rocky savanna at Liwonde N. P. (total $n = 106$) (Happold & Happold 1990, 1991). In Zimbabwe, annual minimum and maximum densities range from 0/ha (dry season) to 4.2/ha (wet season) (Linzey & Kesner 1997a); in Malawi, from 2/ha to 16/ha in Liwonde N. P., and 4/ha to 19/ha in Lengwe N. P. (Happold & Happold 1990, 1991).

Adaptations Nocturnal and terrestrial. During the day, Least Spiny Mice hide under, and in the crevices of, boulders and rocks. The simple nest is made of leaves and dry grass. Despite their short limbs, they are very agile, running and climbing over rocks quickly and easily. They do not burrow, except to forage (see below). At certain times of year, there may be many months when free water is not available and survival depends on water in their food; conservation of water is likely to be as efficient as for *A. cahirinus*.

Foraging and Food Insectivorous and granivorous. In Malawi, 93% ($n = 44$) of stomachs contained insect remains (mostly beetles, but also ants, tipulid larvae, cockroaches) and diplopods (centipedes), and 45% contained vegetable material (mostly roots) (Hanney 1965, as *A. cahirinus*). In Mozambique, the diet (assessed by stomach content analysis) was 60% insects and 40% starchy material (fruits, seeds, bulbs), with an increase in insects (to 75%) in the dry season (Gliwicz 1987). Middens of 'feeding waste' consisting of small shells and the discarded fragments of beetles, bugs, ants, termites and spiders (Vesey-Fitzgerald 1966) have been observed in sheltered crannies of rocks in Tanzania, suggesting that spiny mice catch their prey and then carry it to a safe place to eat it. In Malawi, 'feeding tunnels' lead to roots, which are eaten by spiny mice.

Social and Reproductive Behaviour In captivity, several individuals can be kept together, which suggests that they are social animals. On one occasion, two spiny mice were captured in the same live-trap; on release, they ran into separate holes 1.5 m apart (D. C. D. Happold unpubl.).

Reproduction and Population Structure Reproductive characters probably similar to those of *A. cahirinus*. In Malawi, reproduction is seasonal. Most pregnancies and births occur during the wet season (Dec–Apr), although some ♀♀ may give birth during the early dry season (May) (Hanney 1965; Happold & Happold 1990, 1991). Mean embryo number: 3.2 (range 2–5, mode 3 and 4, $n = 17$); however, number of embryos increases with size of mother: mean 2.9 for ♀♀ with HB = 80–97 mm ($n = 9$), and 3.6 for ♀♀ with HB >97 mm ($n = 7$). Largest, oldest ♀♀ produce nine young (= three litters) in a breeding season (Hanney 1965). Young are large and precocial at birth, and nipple-dragged by mother until Day 12; young weaned at Day 26.

In Malawi (Happold & Happold 1991), at end of the dry season (Sep–Oct), population numbers are small, mostly subadults plus a few old adults. At beginning of the wet season, subadults become adult, reproduction commences and the first young enter population. By end of the wet season and beginning of the dry season (Mar–Jun), all old adults have died, populations are mainly composed of young and subadults, and populations reach their peak (about ×3 minimum numbers). Longevity in the wild not more than 12 months.

Predators, Parasites and Diseases Rarely preyed upon by Barn Owls *Tyto alba* in Malawi (Hanney 1962). Ectoparasites include two species of fleas and one species of louse (Hanney 1965).

Conservation IUCN Category: Least Concern.

This widespread species is not threatened at present.

Measurements

Acomys spinosissimus

HB: 88 (79–97) mm, $n = 11$

T: 77 (67–90) mm, $n = 9$

HF: 16 (12–19) mm, $n = 11$

E: 14 (12–15) mm, $n = 10$

WT: 26 (20–31) g, $n = 22$

GLS: 25.7 (25.1–26.7) mm, $n = 10$

GWS: 12.7 (11.9–13.1) mm, $n = 10$

M¹–M³: 4.1 (3.7–4.6) mm, n = 9

Body and skull measurements: Malawi, Zambia, Mozambique (BMNH)
Weight: Malawi (D. C. D. Happold unpubl.)

Measurements given by De Graaff (1981) show that ♂♂ are, on average, slightly larger than ♀♀

Key References Dippenaar & Rautenbach 1986; Hanney 1965; Happold & Happold 1990, 1991; Linzey & Kesner 1997a, b.

D. C. D. Happold

Acomys subspinosus CAPE SPINY MOUSE

Fr. Souris épineuse du Cap; Ger. Kap-Stachelmaus

Acomys subspinosus (Waterhouse, 1838). Proc. Zool. Soc. Lond. 1837: 104. (publ 1838).

Cape of Good Hope, South Africa (= Table Mountain, Cape Town: Roberts 1951).

Taxonomy Originally described in genus *Mus*. The name *subspinosus* was originally used only for southern Cape population of *Acomys*; later some northern populations from southern Africa were also ascribed to *A. subspinosus* (Setzer 1975). Subsequent morphometric and karyotypic analyses confirm that *A. subspinosus* is restricted to the South-West Cape BZ, and that it is distinguished from *A. spinosissimus* in the north of southern Africa by its narrow teeth and reduced M³ (Dippenaar & Rautenbach 1986). Separation from other *Acomys* is indicated by phylogenetic analyses of mtDNA cytochrome *b* sequences (Barome *et al.* 2000). Synonyms: none. Chromosome number: 2n = 60, FN = 70 (Dippenaar & Rautenbach 1986).

Description Small spiny mouse with pale underparts, darker dorsal surface and distinctive bristle-like hairs. Dorsal pelage rust-brown to dark greyish-brown, flanks and outer surface of limbs paler. Ventral pelage and inside of limbs dirty white; hairs pure white. Clear delineation in colour between flanks and ventral pelage. Head narrow, with pointed nose, long vibrissae; sides of muzzle white. Medium-sized ears, light flesh colour on inner surface, dark brown on outer surface. Fore- and hindfeet white to dirty white above, yellowish-brown to brown below; five digits on each foot, Digit 5 on forefoot reduced to a small stump with a nail rather than a claw. Tail moderately long (ca. 95% of HB), stout, covered with short brown to dark greyish-brown bristles above, yellowish to whitish below. Skull with relatively broad, rounded braincase, and very short maxillary and mandibular toothrows; narrow teeth and reduced M³. Nipples: 1 + 2 = 6.

Geographic Variation None recorded.

Similar Species This species is the only species of *Acomys* in the South-West Cape BZ.

Distribution Endemic to Africa. South-West Cape BZ. Disjunct populations in S and SW of Western Cape Province, South Africa, from Citrusdal in the west to Knysna in the east, extending northwards into Namaqualand (Dippenaar & Rautenbach 1986). Present on the Cederberg Mts, Table Mountain, Swartberg, Outeniqua and Kammanassie Mts; and rocky slopes and ledges around Nieuwoudtville.

Habitat Rocky mountainous habitat, rocky slopes and ledges.

Abundance Varies from 0.9/ha to 13.7/ha in suitable habitat (Fleming & Nicolson 2002a).



Adaptations Nocturnal and terrestrial. Moves by quadrupedal running and walking. Physiological adaptations permit survival during cold temperate winter rainfall. At low ambient temperatures, Cape Spiny Mice utilize body reserves to generate heat, and are not homeothermic. Evaporative water loss is high, compromising survival in a water-scarce environment. Thermal conductance rises sharply above thermoneutral zone, indicating that the spiny pelage may facilitate heat loss at high ambient temperatures (Perrin & Downs 1994).

Foraging and Food Cape Spiny Mice feed almost exclusively on seeds (91–94%), as well as small amounts of green plant material and insects (Nel *et al.* 1980). Pollen from *Protea humiflora* comprised up to 80% of scats collected during winter months in a study conducted in Riviersonderend Mts. Cape Spiny Mice contribute significantly to pollination and seed-set in *P. humiflora* (Fleming & Nicolson 2002a).

Social and Reproductive Behaviour No information available.

Reproduction and Population Structure Juveniles and pregnant ♀♀ found throughout the year, with peaks in breeding in

some populations (Fleming & Nicolson 2002b). Breeding probably opportunistic, depending on resource availability. Gestation: >27 days. Mean litter-size: 3. Mean birth-weight: 3.3 g. Growth rate in first 28 days: 0.55 g/day. Young are altricial and do not nipple-cling. Hair visible Day 1–2, incisors erupt Day 7; eyes open Days 9–10 (Dempster *et al.* 1992).

Predators, Parasites and Diseases No information available.

Conservation IUCN Category: Least Concern.

Measurements

Acomys subspinosus

HB: 87.6 (73–102) mm, n = 69

T: 83.0 (65–89) mm, n = 69

HF: 17.1 (12–19) mm, n = 71

E: 12.5 (9–15) mm, n = 69

WT: 20.2 (13–26) g, n = 32

GLS: 25.1 (23.8–26.6) mm, n = 66

GWS: 11.1 (10.6–11.7) mm, n = 69

M¹–M³: 3.3 (3.0–3.6) mm, n = 73

Western Cape Province, South Africa (Dippenaar & Rautenbach 1986)

Key References Dempster *et al.* 1992; Dippenaar & Rautenbach 1986; Fleming & Nicolson 2002a; Perrin & Downs 1994.

Edith R. Dempster

Acomys wilsoni WILSON'S SPINY MOUSE

Fr. Souris épineuse de Wilson; Ger. Wilsons Stachelmaus

Acomys wilsoni Thomas, 1892. Ann. Mag. Nat. Hist., ser. 6, 10: 22. Mombasa, Kenya.

Taxonomy Formerly included in *A. subspinosus* (Setzer 1975). Genetically most closely related to *A. percivali* (Janacek *et al.* 1991). Synonyms: *ablutus*, *argillaceus*, *boronei*, *enid*, *nubilus*. Subspecies: none. Chromosome number: 2n = 50 (Matthey 1968).

Description Small chestnut or brownish spiny mouse. Pelage coarse and stiff with strong spines (ca. 5 mm) from mid-back to base of tail and on rump. Dorsal pelage bright cinnamon or chestnut to olive-brown, sometimes darker on mid-dorsal line, and with a 'speckled' appearance; hairs/spines pale grey at base with chestnut, cinnamon or brown terminal band, and black tip. Colour varies geographically (see below). Ventral pelage pure white. Colour of ventral pelage clearly delineated from colour of flanks. Head similar in colour to dorsal pelage. Small white suborbital spot. Ears pigmented (pale or dark), sparsely covered with small hairs. Subauricular and postauricular spots present in some individuals. Chin, throat and chest white. Limbs short. Fore- and hindfeet white. Tail relatively long (ca. 94% of HB), slightly scaly, almost naked but with scattered short bristles; pale brown or whitish above, white below. Tail often absent or short due to injury. Nipples: not known.

Geographic Variation Colour of dorsal pelage varies geographically: bright chestnut (N Kenya), brown speckled with buff (*argillaceus*; Sudan, N Kenya), or brownish-cinnamon and not speckled (Uganda).

Similar Species

A. percivali. Similar size; dorsal pelage grey; strong spines on mid-dorsal region; tail on average shorter (mean 73 mm) and relatively shorter (ca. 76% of HB); frequently syntopic; often very common.

A. kempi. Similar head and body size; dorsal pelage orange-buff, flanks dull orange; stiff spines on mid-back; tail on average longer (mean 93 mm) and relatively longer (ca. 94% of HB); distribution restricted.

A. ignitis. Similar head and body size; dorsal pelage brownish-orange, with bright reddish-orange flanks; tail probably shorter, and relatively shorter (77% of HB); restricted to low altitudes in SE Kenya and N Tanzania.

Distribution Endemic to Africa. Somalia–Masai Bushland BZ. Recorded from S Sudan, S Ethiopia, NE Uganda, S Somalia, Kenya and S to C Tanzania. Limits of distribution uncertain.

Habitat Rocky habitats, where coexist with *A. percivali* in C Kenya. Also found in grasslands where there is dense shrubby vegetation cover. Occasionally, individuals inhabit houses. In its choice of habitat, this species is more opportunistic than sympatric *A. percivali*.



Acomys wilsoni

Abundance Common in preferred habitats, although distribution is localized and patchy.

Adaptations Nocturnal, terrestrial and arboreal/scansorial. Excellent climbers on rocky outcrops and on trees. Similar in many respects to *A. percivali*.

Foraging and Food Omnivorous, mainly insectivorous. Diet varies seasonally. In the dry season, the diet comprises 60–95% arthropods and <5% stems and leaves and 5–40% seeds; in the wet season, 65–90% arthropods, 0–5% stems and leaves and 10–30% seeds; and in the intermediate seasons (between wet and dry) 35–55% arthropods, 0–15% stems and leaves and 45–50% seeds (Neal 1984a). In cafeteria-style feeding trials, wild-caught mice fed almost exclusively on insects (S. Takata unpubl.).

Social and Reproductive Behaviour Little information. In captivity, individuals are very tolerant of other adults of either sex and, unlike Percival's Spiny Mice, are not aggressive in captive colonies, even at high densities. Trapping in Kenya shows that adults have widely overlapping home-ranges; when caught in the same trap, two adults seem tolerant of one another.

Reproduction and Population Structure Breeding activity occurs throughout the year, with 60–100% of adult ♀♀ pregnant in all months except Mar (Neal 1983) and is similar to that of sympatric *A. percivali*. Wilson's Spiny Mice are prolific breeders, mainly because of continuous reproduction and the short interval between litters. Gestation: 4–6 weeks (S. Takata unpubl.). Mean interval between litters: 46.3 days (Neal 1983). Litter-size: 2 (no range recorded) (S. Takata unpubl.). Embryo number: 2.2 ± 0.09 ($n = 79$ pregnancies; Neal 1983); 1–3 ($n = 4$; Delany 1964a). Estimate of 7.9 litters/female/year and annual production of 17.4 young/female/year (Neal 1983). Larger older ♀♀ have larger litters (mean = 2.41) than smaller ♀♀ (mean = 1.97) (Neal 1983). At birth, young are precocious; weight = 3–4 g (wild-caught; Neal 1983); 5 g (in

captivity; S. Takata unpubl.). Weight at weaning 10 g, at puberty 10–13 g (♂♂) and 10–15 g (♀♀), adult size ca. 17 g.

There is little seasonal change in the structure of the population (as assessed by wear of molar teeth). Young, adult and old individuals are present in most months, with a reduction in the number of older animals in Jan–Jun (Neal 1983).

Predators, Parasites and Diseases Remains have not been found in faecal samples of mongooses and genets, even in areas where the mice are common. Like Percival's Spiny Mice, Wilson's Spiny Mice do not carry heavy loads of ectoparasites in the wild (S. Takata unpubl.).

Conservation IUCN Category: Least Concern.

Measurements

Acomys wilsoni

HB (♂♂): 99 (90–114) mm, $n = 25$

HB (♀♀): 96 (89–109) mm, $n = 18$

T (♂♂): 84 (65–97) mm, $n = 25$

T (♀♀): 87 (73–100) mm, $n = 18$

HF: 15 (15–16) mm, $n = 14$

E: 15 (14–16) mm, $n = 14$

WT (♂♂): 28 (22–39) g, $n = 92$

WT (♀♀): 33 (25–47) g, $n = 68$

GLS (♂♂): 28.6 (28.4–29.1) mm, $n = 5$

GLS (♀♀): 27.3 (26.2–29.4) mm, $n = 5$

GWS (♂♂): 13.7 (13.4–14.1) mm, $n = 5$

GWS (♀♀): 13.5 (12.8–13.6) mm, $n = 5$

M¹–M³: 4.3 (4.0–4.5) mm, $n = 10$

Laikipia District, Kenya (S. Takata unpubl.)

Key References Neal 1983, 1984a.

S. Takata

GENUS *Deomys*

Rusty Link Rat

Deomys Thomas, 1888. Proc. Zool. Soc. Lond. 1888: 130. Type species: *Deomys ferrugineus* Thomas, 1888.

Deomys is a monotypic genus restricted to the Rainforest BZ in the Congo Basin from S Cameroon to Uganda.

This genus is easily distinguished by a combination of diverse external characters, including its reddish coarse-textured pelage, long, pointed muzzle, large oval ears, pure white ventral pelage and musky shrew-like odour. Unique skull characters are the long tapered rostrum, sharply pointed and widely spaced cusps on the first two molars (somewhat reminiscent of the cusps on the molar teeth of a shrew), M¹ longer than M² + M³, M³ reduced, and the absence of zygomatic plates (Figure 41).

Although historically *Deomys* has been classified under the subfamily Dendromurinae, its morphological characters are not consistent

with that subfamily (see Rosevear 1969). More recently, genetical and molecular analyses consistently placed *Deomys* in the same clade as *Acomys*, *Lophuromys* and *Uranomys* (Musser & Carleton 2005 and references therein). However, dental characters are not those of these acomyine rodents (Denys *et al.* 1995) and sperm morphology is not that of the Dendromurinae nor the *Acomys/Uranomys* group (Breed 1995). The genus appears to be an isolated lineage, and is currently placed in the subfamily Deomyinae (see subfamily profile and Musser & Carleton 2005).

J. C. Ray & J. R. Malcolm



Deomys ferrugineus.

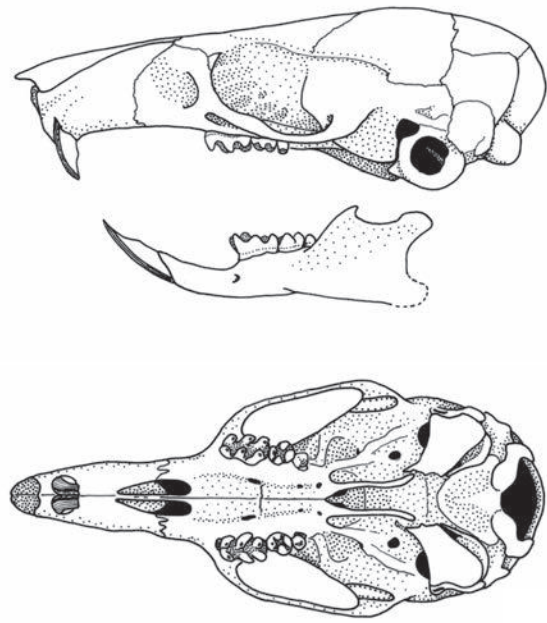


Figure 41. Skull and mandible of *Deomys ferrugineus* (BMNH 38.444).



Deomys ferrugineus.

Deomys ferrugineus RUSTY LINK RAT (CONGO FOREST RAT)

Fr. Rat à manteau roux; Ger. Deomys-Waldmaus

Deomys ferrugineus Thomas, 1888. Proc. Zool. Soc. Lond. 1888: 130. Lower Congo.

Taxonomy Synonyms: *christyi*, *poensis*, *vandenberghiei*. Subspecies: none. Chromosome number: not known.

Description Medium-sized rat with rich reddish-brown coarse-textured pelage and very long tail. Dorsal pelage reddish-brown; hairs pale white or silvery-grey at base, brown at tip. Hairs on mid-back and rump coarse and stiff, darker due to many black-tipped hairs. Ventral pelage pure white and sharply delineated from flanks. Head narrow with very long, pointed muzzle and long vibrissae. Large oval ears, appear naked but sparsely covered with very short hairs. Head similar in colour to back, with blackish band across muzzle in front of eyes. Nasal region and cheeks cinnamon. Chin, throat, chest and inner surface of hindlimbs white. Feet very long, covered in short white hairs and with five prominent subconical pads on soles. Hindfoot with five digits, Digits 2, 3 and 4 long; Digit 1 very short, Digit 5 short. Tail very long (ca. 140% HB), scaly, distinctly bicoloured (dark above and white below); covered with short bristles basally, with longer hairs terminally. Distinct, musky, shrew-like odour. Skull: elongated and flattish, long tapered rostrum, zygomatic plate absent; each upper incisor with groove close to inner edge; sharply pointed and widely spaced cusps on the first upper two molars, M^1 longer than $M^2 + M^3$; M^3 reduced. Nipples: $0 + 2 = 4$.

Geographic Variation Colour of dorsal pelage varies geographically, from reddish-brown (mainland Africa) to dark brown (Bioko I.; *poensis*).

Similar Species

Colomys goslingi. White ventral pelage woolly in texture; ears smaller and rounder; and Digit 5 on hindfoot longer.

Malacomys longipes. Dorsal pelage darker with velvet-like texture, ventral pelage whitish-grey and never pure white; ears rounder; hindfeet on average longer.

Distribution Endemic to Africa. Rainforest BZ (East Central Region and parts of West Central Region). Recorded from Cameroon Mountain and Benito R. (Rio Muni, Equatorial Guinea) to E DR Congo, W Uganda and Rwanda. Present on Bioko I. Not present in West Africa or in DR Congo south of the Congo R.

Habitat One of the few true African forest species (Rosevear 1969). Generally confined to deeper regions of virgin forest (Sanderson 1940), although Hatt (1940a) recorded it in more disturbed areas on forest edges and in farms. At Irangi, E DR Congo, all but two (of 35) individuals were captured in 'primary' forest on hills (Rahm 1972). Trapping over two-year period in logged forests of SW Central African Republic revealed that this species generally avoids disturbed habitats along logging roads. Preferred habitat (assessed by high abundance) was characterized by a low and sparse understorey, low density of saplings and closed canopy (Ray 1996, Malcolm & Ray 2000); and in NE Gabon, preferred habitat was in tree-fall gaps

*Deomys ferrugineus*

where there were particularly high amounts of fallen and dead woody debris (Duplantier 1989). Recorded at altitudes from near sea level to 6500 ft; may be particularly fond of montane forest above 1500 ft (Rosevear 1969). Delany (1975) and Kingdon (1974) reported a strong association with water in Uganda (as did Sanderson [1940] in Cameroon), but Ray (1996) captured few individuals close to streams in Central African Republic. Kingdon (1974) suggested that *Deomys* may fill the niche of the stream-dependent *Malacomys longipes* where that species is absent.

Abundance Represented 7% of total catch ($n = 3541$) at Irangi, DR Congo where 60–70% of specimens of *D. ferrugineus* were captured in primary forest habitats (Dieterlen 1985b). In SW Central African Republic comprised 11.1% of all captures ($n = 458$) from unlogged mixed-species forest, 3.7% from monodominant *Gilbertiodendron dewevrei* forest ($n = 406$), 1.1% along secondary logging roads ($n = 704$) and 0.5% along streams ($n = 200$) (Ray 1996). During six trapping sessions in undisturbed forest at Makokou, Gabon, relative abundance ranged from 1.3% to 12.6% (mean 11.1%, $n = 549$). Density at Makokou was 0.2–1.2 individuals/ha (Duplantier 1989).

Adaptations Nocturnal (Rahm 1967, Genest-Villard 1980, Kerbis Peterhans & Patterson 1995) and/or crepuscular (Sanderson 1940; Kingdon 1974). Narrow stilt-like hindfeet for wading in shallow water (Delany 1975; Kerbis Peterhans & Patterson 1995). Strictly terrestrial (Genest-Villard 1980, Malcolm & Ray 2000). Nests made of leaves and vegetable matter, located in holes at the base of trees (Rosevear 1969). Acutely cusped teeth adapted for

insectivorous diet (Rosevear 1969). The large infraorbital foramen, wedge-shaped cuspidation of the molar teeth, and the movements of the mandible so that different cusps can inter-digitate, are probably adaptations associated with the insectivorous diet (Lemire 1966).

Foraging and Food Predominantly insectivorous. Forages in leaf litter for ants, termites, grasshoppers, beetles, cockroaches, fly larvae, caterpillars, millipedes and centipedes (Rosevear 1969, Duplantier 1982). Of 15 stomachs collected by Rahm (1972), 11 (73.3%) contained insects only, two (13.3%) contained a mixture of insects and vegetable matter, and the remainder contained vegetable matter only. Nearly 100% of 29 stomachs from Makokou (Gabon) contained insects; remains of seeds, gastropods, earthworms, reptiles and rodents also present (Duplantier 1982). Hatt (1940a) also reported rodent flesh in one stomach from DR Congo. Insects were also the main component of the diet at Mbaiki (Central African Republic), although vegetable matter comprised 17–26% (Genest-Villard 1980). Living prey is pounced upon and attacked using the incisor teeth, then held down and torn apart (Kingdon 1974).

Social and Reproductive Behaviour Solitary or in pairs or with young; possibly territorial (Rosevear 1969, Delany 1975). In Makokou (Gabon), home-ranges of ♂♂ ($5467 \pm 160 \text{ m}^2$, $n = 3$) are significantly larger than for ♀♀ ($2533 \pm 874 \text{ m}^2$, $n = 6$). Maximum recapture distance for ♂♂ averaged 102.4 m ($n = 11$), and for ♀♀ 48.2 m ($n = 11$) (Duplantier 1982).

Reproduction and Population Structure Reproductively active for 95% of the year at Irangi, DR Congo – a situation seen in mainly insectivorous rodents whose main source of nutrition is abundant throughout the year (Dieterlen 1985a, 1986). Litter-size varies according to locality: 1.8 (1–2, $n = 25$; Dzanga-Sangha, Central African Republic; J. C. Ray & J. R. Malcolm unpubl.); 1.69 (1–4, $n = 67$; Irangi, DR Congo; Dieterlen 1985a); 3.0 (3–3, $n = 3$; Makokou, Gabon; Dubost 1968). The greatest proportion of ♀♀ were reproductively active during wet seasons in Dzanga-Sangha although the trend not as pronounced as for other species in the

same community (Ray 1996). Average body weights did not vary significantly between seasons or between two years (Ray 1996).

Predators, Parasites and Diseases Small carnivores from Dzanga-Sangha were found to prey selectively on this species, probably because all of them frequent the same micro-habitats while foraging for termites and other invertebrates (Ray 1998).

Conservation IUCN Category: Least Concern.

Close association with undisturbed forests, and general absence from secondary forests, means that deforestation and degradation of forests by logging and agricultural clearing are potential threats.

Measurements

Deomys ferrugineus

HB (♂♂): 131.0 (109–150) mm, $n = 46$

HB (♀♀): 131.2 (115–144) mm, $n = 42$

T (♂♂): 184.9 (170–198) mm, $n = 25$

T (♀♀): 186.1 (159–202) mm, $n = 21$

HF (♂♂): 35.9 (34–38) mm, $n = 47$

HF (♀♀): 35.5 (33–38) mm, $n = 42$

E (♂♂): 24.6 (23–27) mm, $n = 47$

E (♀♀): 24.5 (23–27) mm, $n = 42$

WT (♂♂): 54.0 (42–77) g, $n = 30$

WT (♀♀): 56.1 (40–68) g, $n = 5$

GLS (♂♂): 36.8 (34.4–38.2) mm, $n = 10$

GLS (♀♀): 36.6 (35.3–37.2) mm, $n = 10$

GWS (♂♂): 15.5 (13.9–16.7) mm, $n = 10$

GWS (♀♀): 15.3 (14.4–15.9) mm, $n = 10$

M¹–M³ (♂♂): 5.8 (5.6–6.4) mm, $n = 10$

M¹–M³ (♀♀): 5.8 (5.4–6.1) mm, $n = 10$

Dzanga Sangha, Central African Republic (J. C. Ray and J. R. Malcolm unpubl.; USNM)

Key References Kingdon 1974; Rosevear 1969.

Justina C. Ray & Jay R. Malcolm

GENUS *Lophuromys*

Brush-furred Rats

Lophuromys Peters, 1874. Monatsber. K. Preuss. Akad. Wiss. Berlin, p. 234.

Type species: *Lasiomys afer* Peters, 1866 (= *Mus sikapusi* Temminck, 1853).

The genus *Lophuromys* contains 15 species, widely distributed throughout tropical Africa. Preferred habitats of most species include moist grasslands, swamps and marshes, agricultural fields and abandoned farmlands provided there is dense cover and soft soil. They are rare in primary and secondary rainforest except where there are grassy patches. Distribution ranges from about 15°S to 15°N, and from near sea level to ca. 4500 m. Most species are endemic to isolated mountain regions; others (*L. flavopunctatus*, *L. sikapusi*, *L. nudicaudus*, *L. huttereri*) have larger geographic distributions.

Species within the genus have harsh to soft rufous, rusty or olive-coloured brush-like hairs, especially on the back and flanks (similar to those in the genus *Uranomys*, but not as thick or spiny as in *Acomys*).

The dorsal pelage may be 'speckled' (due to a scattering of pale-tipped hairs) or 'unspeckled'. They have small eyes, pointed muzzles, short limbs, long or short curved claws, and most species have a comparatively short hairless tail (which is often partially lost due to damage). The skull is rather slender, with small incisors, weak interorbital constriction and in most species the zygomatic plate is much reduced in width and cut away above (Figure 42).

They are exclusively terrestrial – most species are rather heavily built with short limbs, which makes climbing virtually impossible. Typically, locomotion is by running over the surface of the ground, and by pushing through and under litter and decaying vegetation; grass nests are constructed amongst litter and grass tussocks. They



Lophuromys flavopunctatus.

do not dig burrows. Activity is mostly diurnal and crepuscular. Brush-furred mice are omnivorous, and include a large proportion of insects and other invertebrates in the diet. Reproduction is seasonal, the young are rather precocial and litter-size is small (normally 1–3). A unique feature of the genus is the presence of a large gland on the undersurface of the stomach, which is associated with digestion, although its function is uncertain (Genest-Villard 1968, 1980; Dieterlen 1976b).

Ellerman (1941) and Misonne (1969a) considered *Lophuromys* as a ‘specialized and distinct offshoot’, an isolated group among the African Muridae, a view confirmed by Dieterlen (1976b), Denys & Michaux (1992) and W. Verheyen *et al.* (1996). Traditionally *Lophuromys* has been placed in the subfamily Murinae (e.g. Musser & Carleton 1993). However, non-morphological evidence (DNA/DNA hybridization experiments, mitochondrial RNA, amino-acid sequences, etc.) link *Lophuromys* with *Acomys*, *Uranomys* and *Deomys* in a monophyletic clade that is distinct from the Murinae. Here, following Musser & Carleton (2005), the genus is placed with these genera in the Deomyinae (see also profile Subfamily Deomyinae).

Despite its clear generic characters, the genus is considered to comprise three species-groups: (a) the ‘*sikapusi* species-group’, with short tail, short hindfoot and unspeckled pelage (*L. sikapusi* [including *ansorgei* and *angolensis*], *L. nudicaudus*, *L. hutcheri*, *L. roseveari*), (b) the ‘*flavopunctatus* species-group’, with short tail, short hindfoot and speckled pelage (*L. flavopunctatus*, *L. cinereus*, *L. brevicaudus*, *L. chrysopus*, *L. melanonyx*) or mainly unspeckled pelage (*L. dieterleni* and *L. eisentrauti*, as well as *L. rahmi*, which has slight speckling) and (c) the ‘*woosnami* species-group’ with long tail and long hindfoot and unspeckled pelage (*L. woosnami*, *L. luteogaster*, *L. medicaudatus*) (Dieterlen 1976b, Verheyen *et al.* 1986). An alternative arrangement

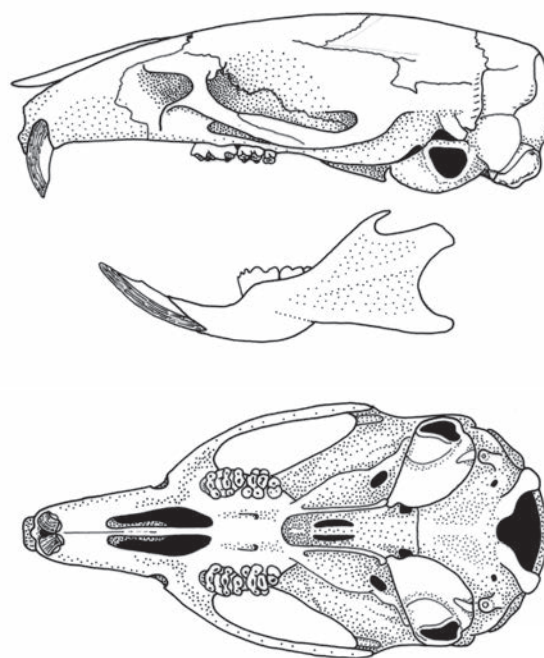


Figure 42. Skull and mandible of *Lophuromys sikapusi* (HC 1742).

(Dieterlen 1987) is division of the genus into two subgenera, *L. (Lophuromys)*, which represents all the short-tailed species (tail length 50–70% of HB) and *L. (Kivumys)*, which represents the three long-tailed species (tail length 85–105% of HB) of the ‘woosnami species-group’.

The taxonomy of the genus is controversial. Here, we profile 15 species (Table 20). In contrast, Musser & Carleton (2005) recognize 21 species including five that are treated here as synonyms. These are *L. zena* (Aberdare Range and Mt Kenya), *L. aquilus* (very widespread) and *L. brunneus* (S Ethiopia) which are treated here as synonyms of *L. flavopunctatus*; and *L. angolensis* (SW DR Congo) and *L. ansorgei* (eastern Africa) which are treated here as synonyms of *L. sikapusi*. Musser & Carleton (2005) also recognise two new species, *L. dudui* and *L. verhageni*, described on the basis of craniometric data and univariate analysis, by Verheyen *et al.* (2002). Musser & Carleton (2005) treat *L. cinereus* (profiled here as a valid species) as a synonym of *L. aquilus*.

The species can be distinguished by pelage colour and pattern, length of hindfoot, length of tail, cranial characters and by geographic location (Table 20).

Fritz Dieterlen

Table 20. Species in the genus *Lophuromys*. Arranged in order of species-group, and whether pelage is speckled or unspeckled.

| Species | Species-group ^a | Pelage speckled or unspeckled ^b | Tail ^c | Dorsal pelage | Ventral pelage | HB mean (range) (mm) | HF mean (range) (mm) | |
|----------------------------------|----------------------------|--|-------------------|---------------------------------|---------------------------------|----------------------|----------------------|--|
| <i>L. brevicaudus</i> | Fl | Sp | S | Grey, dull | Grey, cream | 114 (96–134) | 20.8 (19–22) | |
| <i>L. chrysopus</i> | Fl | Sp | S | Blackish-brown | Yellow to reddish | 114 (100–128) | 21.1 (19–23) | |
| <i>L. cinereus</i> | Fl | Sp | S | Brownish-grey | Pale grey | 122 (110–129) | 23.5 (20–24.5) | |
| <i>L. eisentrauti</i> | Fl | Sp | S | Reddish-brown | Pale reddish | 94 | 19 | |
| <i>L. flavopunctatus</i> | Fl | Sp | S | Reddish-brown to blackish-brown | Pale brown or cinnamon | 119 (98–144) | 21.3 (20–25) | |
| <i>L. melanonyx</i> | Fl | Sp | S | Grey-brown | Creamy-white | 145 (120–180) | 22.8 (19–26) | |
| <i>L. dieterleni</i> | Fl | Usp | S | Dark brown | Brownish | 123 (116–128) | 21.7 (20–24) | |
| <i>L. rahmi</i> | Fl | Usp | S | Dark reddish-brown | Bright reddish-orange | 102 (95–116) | 16.3 (13–18) | |
| <i>L. huttereri</i> ^d | Si | Usp | S | (Reddish-brown) | (Dark orange tinged with olive) | 93–114 | 18–20 | |
| <i>L. nudicaudus</i> | Si | Usp | S | Reddish-brown | Brilliant yellowish-red | 106.2 (89–119) | 18.6 (16–21) | |
| <i>L. roseveari</i> | Si | Usp | S | Reddish-brown | Reddish-brown | 127 (104–141) | 22.5 (20–25) | |
| <i>L. sikapusi</i> | Si | Usp | S | Rufous-rusty to blackish-brown | Pale rufous | 118 (110–130) | 22.2 (21–23) | |
| <i>L. luteogaster</i> | Wo | Usp | L | Olive-brown | Buff to pinkish-cinnamon | 102 (90–113) | 21 (19–22.5) | |
| <i>L. medicaudatus</i> | Wo | Usp | M | Dark olive-brown | Dark orange tinged with olive | 103 (92–112) | 20.8 (18–23) | |
| <i>L. woosnami</i> | Wo | Usp | L | Brown, tinged with olive-grey | Pale brown tinged reddish | 121 (111–135) | 26.5 (25–27) | |

^a Fl = *flavopunctatus* species-group (speckled pelage [most species], short tail, short hindfoot); Si = *sikapusi* species-group (unspeckled pelage, short tail, short hindfoot); Wo = *woosnami* species-group (unspeckled pelage, long tail, long hindfoot).

^b Sp = speckled pelage; Usp = unspeckled pelage.

^c S = short tail (50–70% of HB), M = medium tail (ca. 85% of HB), L = long tail (100–105% of HB).

^d External characteristics similar to *L. nudicaudus* (see profile).

Lophuromys brevicaudus SHORT-TAILED BRUSH-FURRED RAT

Fr. Souris hérissé à queue court; Ger. Kurzschwanz-Bürstenfellratte

Lophuromys brevicaudus Osgood, 1936. Zool. Ser. Field Mus. Nat. Hist. 20 (21): 241. Mt Albasso (= Mt Badda), Ethiopia.

Taxonomy Subgenus *Lophuromys*. Species-group: *flavopunctatus*. One of three Ethiopian endemic species of *Lophuromys*. Considered to be a synonym of *L. flavopunctatus* by Yalden *et al.* (1976). Allozyme, chromosomal and morphometric studies indicate that *L. brevicaudus* should be considered as a full species within the '*flavopunctatus* species-group' (Aniskin *et al.* 1997a, Lavrenchenko *et al.* 1997, 1998b). A very high level of genetic (allozyme) differentiation among populations from the Bale Mts is probably the result of isolation of local populations during Pleistocene glaciations (Lavrenchenko *et al.* 2000, Milishnikov *et al.* 2000). Synonyms: none. Chromosome number: 2n = 68 (the same as for *L. flavopunctatus sensu stricto*; Aniskin *et al.* 1997a, Lavrenchenko *et al.* 1997).

Description Small 'speckled' rat with relatively short tail. Dorsal pelage softer, shorter and generally duller than in other species of the *flavopunctatus* species-complex. Dorsal pelage dull grey; hairs grey at base with pale yellow subterminal band and black tip. Ventral pelage greyish, sometimes cream or yellowish; hairs dark grey at base, with

white tip (as in *L. melanonyx*). Underfur of dorsal and ventral pelage pale grey. Head dull grey, chin and throat grey with fewer white-tipped hairs than ventral pelage. Reddish-orange collar in some individuals, contrasting strongly with colour of chin and ventral region. Dorsal surface of forefeet blackish; dorsal surface of hindfeet grey with blackish central longitudinal band. Claws pale, longer than in other Ethiopian representatives of the '*flavopunctatus* species-group', especially on the forefeet. Tail short (ca. 50% of HB), grey, with scales and short black hairs above, whitish hairs below. Skull with unusually large auditory bullae medially close to each other. Nipples: 2 + 1 = 6.

Geographic Variation None recorded.

Similar Species

L. chrysopus. Tail relatively longer, greyish-rufous hindfoot with blackish toes; shorter claws; wider rostrum and skull base; more slender M¹ and more widely separated smaller auditory bullae.

| | Claw length and colour | Nipples | Notes |
|--|-----------------------------|------------------------|---|
| | Long, pale | 2 + 1 = 6 | Ethiopia only. 2n = 68 |
| | Short, pale | 2 + 1 = 6 | Ethiopia only. 2n = 54 |
| | Long, pale | 2 + 1 = 6 | Kivu Province, DR Congo; pelage grey |
| | n. d. | not known | W Cameroon only; small size |
| | Long, dark | 2 + 1 = 6
1 + 1 = 4 | Widespread. East and central Africa.
2n = 68 or 70 |
| | Long, black | 0 + 2 = 4 | Ethiopia only; largest sp. in genus. 2n = 60 |
| | n. d. | Not known | Mt Oku, Cameroon; pelage long |
| | Short-medium, pale or brown | Not known | E DR Congo and Rwanda; pelage rather harsh; small size |
| | Long, brown | Not known | C DR Congo. External characters similar to <i>L. nudicaudus</i> |
| | Long, brown | 2 + 1 = 6 | Central African rainforests; pelage very harsh; small size. 2n = 56 (polymorphic) |
| | Very long, brown | 2 + 1 = 6
1 + 1 = 4 | Mt Cameroon; pelage long |
| | Long, dark | 1 + 1 = 4 | Widespread in West and central Africa; pelage soft. 2n = 60 or 64 |
| | Short, pale | 2 + 1 = 6 | NE and E DR Congo; pelage harsh |
| | Short, pale | 2 + 1 = 6 | E DR Congo and Rwanda; montane; pelage harsh |
| | Short, pale | 1 + 1 = 4 | Mountains of Albertine Rift Valley; pelage soft; long HF. 2n = 42 |

L. flavopunctatus. On average larger and darker; relatively shorter claws, relatively smaller auditory bullae.

L. melanonyx. On average much larger and paler, black claws; tough skin (unusual in *Lophuromys*).

Distribution Endemic to Africa Afromontane–Afroalpine BZ of Ethiopia only. Confined to the western (Bonke) and eastern (Chilalo, Gedeb and Bale Mountains) high plateaux, from 2400 to 3750 m (Lavrenchenko *et al.* 1998b).

Habitat Afroalpine grasslands and *Erica* bush especially on mesa tops (Sillero-Zubiri *et al.* 1995a, Lavrenchenko *et al.* 1998b). Occurs also (in smaller numbers) in montane forest (Lavrenchenko *et al.* 1998b).

Abundance Numerous in suitable habitats; comprised 51% (n = 229 small mammals) trapped in the ericaceous zone of the Bale Mts (L. Lavrenchenko unpubl.).

Adaptations Diurnal and nocturnal; 50% of 80 captures occurred in the morning, 29% during the afternoon and 21% during the night in the Bale Mts (Sillero-Zubiri *et al.* 1995a). Long claws are presumed to be adaptations for burrowing. The relatively short tail might be an adaptation to the cold at high altitudes.

Foraging and Food Morphological studies show that the gastro-intestinal tract is intermediate in structure between that of *Aethomys* and *Mastomys* suggesting that the diet is mainly vegetable material (see also *L. chrysopus*). In this respect, this species differs



Lophuromys brevicaudus

from most other species of *Lophuromys*, which are insectivorous (L. Lavrenchenko unpubl.).

Social and Reproductive Behaviour Peaceful and un-aggressive. In captivity, neither ♂♂ nor ♀♀ demonstrate any

elements of agonistic behaviour towards conspecifics or parapatric *L. chrysopus*.

Reproduction and Population Structure Females collected in the Bale Mts during the late dry season and beginning of the wet season (Apr and May) were pregnant. Mean embryo number: 2.38 ± 0.18 (range 2–3; $n = 8$ pregnant ♀ ♀). Sex ratio close to unity.

Predators, Parasites and Diseases Little information. A few may be preyed upon by Abyssinian Long-eared Owls (*Asio abyssinicus*) (Yalden 1973). Not eaten by Simien Wolves (*Canis simensis*) (Sillero-Zubiri & Gottelli 1995).

Conservation IUCN Category: Near Threatened.

Abundant where found, but geographic range is very limited. Protected by the proposed Bale Mountains N. P.

Measurements

Lophuromys brevicaudus

HB: 114 (96–134) mm, $n = 87$

T: 59 (50–66) mm, $n = 60$

HF: 20.8 (19–22) mm, $n = 87$

E: 17 (15–19) mm, $n = 87$

WT: 43 (29–60) g, $n = 86$

GLS: 29.4 (28.0–31.0) mm, $n = 33$

GWS: 14.2 (13.6–15.2) mm, $n = 33$

M^1 – M^3 : 5.0 (4.7–5.5) mm, $n = 33$

Ethiopia (Lavrenchenko *et al.* 1998)

Key References Lavrenchenko 1998; Lavrenchenko *et al.* 2000; Milishnikov *et al.* 2000.

Leonid A. Lavrenchenko

Lophuromys chrysopus GOLDEN-FOOTED BRUSH-FURRED RAT (ETHIOPIAN FOREST BRUSH-FURRED RAT)

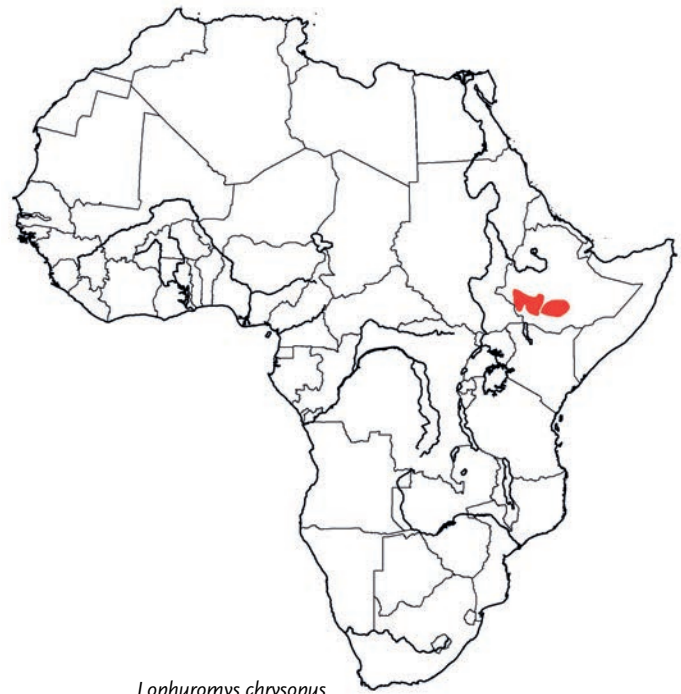
Fr. Souris hérissé à pieds d'or; Ger. Goldfüssige Bürstenfellratte

Lophuromys chrysopus Osgood, 1936. Zool. Ser. Field Mus. Nat. Hist. 20 (21): 242. Allata, Ethiopia.

Taxonomy Subgenus *Lophuromys*. Species-group: *flavopunctatus*. One of three endemic species of *Lophuromys* in Ethiopia. Considered as synonym of *L. flavopunctatus* (as *L. aquilus chrysopus*) by Yalden *et al.* (1976). Phylogenetic analyses (allozyme and RAPD) suggest that *chrysopus* is a rather recent and the most advanced derivative of the *flavopunctatus* species-group (Lavrenchenko *et al.* 2000, 2001), and separate from *L. flavopunctatus* and *L. brevicaudus*. Synonyms: none. Chromosome number: $2n = 54$ (Aniskin *et al.* 1997a, Lavrenchenko *et al.* 1997); a very high proportion of individuals (83%) in Beletta Forest possess supernumerary B chromosomes (2–6) (L. Lavrenchenko unpubl.).

Description Small 'speckled' rat with a relatively long tail. Pelage long (11–12 mm on mid-dorsal line), dense and slightly stiff. Dorsal pelage blackish-brown; hairs reddish-brown at base, black on distal half with pale yellow subterminal bands and black tip. Ventral pelage speckled, pinkish-cream to greyish-cream. Head similar in colour to dorsal pelage. Upper surface of forefeet blackish; upper surface of hindfeet greyish-rufous. Toes black. Claws pale, shorter, especially on forefeet, than in other Ethiopian representatives of this species-group. Tail relatively short (ca. 70% of HB), upper surface densely covered with grey or black scales and short black hairs; lower surface with pale grey scales and short dark grey hairs with white tips. Skull similar in size to *L. brevicaudus* but with wider rostrum and skull base, more slender M^1 and somewhat smaller and more widely separated auditory bullae. Nipples: $2 + 1 = 6$.

Geographic Variation Populations on either side of the Rift Valley differ in colour (Lavrenchenko *et al.* 1998). Dorsal hairs of individuals from west of the Rift Valley (Beletta Forest) are pale red on basal half, black on terminal half with pale tips, and ventral pelage is pale pink to reddish. Dorsal hairs of individuals from east of the Rift Valley (Hareenna Forest, Bale Mts) are bright red on basal half, black on terminal half with pale tips, and ventral pelage is yellow to pale orange.



Lophuromys chrysopus

Similar Species

L. brevicaudus. Shorter tail, grey hindfeet with black band, longer claws, larger auditory bullae.

L. flavopunctatus. On average larger size, relatively shorter tail, grey hindfeet with black band, longer claws (Lavrenchenko *et al.* 1998b).

L. melanonyx. On average much larger and paler, black claws: tough skin.

Distribution Endemic to Africa. Afromontane–Afroalpine BZ. Widespread in montane forests (1200 to 2760 m) of the Ethiopian Highlands on both sides of the Ethiopian Rift Valley.

Habitat Afromontane forests. Does not occur in afroalpine grasslands and *Erica* bush (cf. *L. brevicaudus*).

Abundance One of the commonest rodents in Ethiopian montane forests. Comprised 32% (n = 153 small rodents) caught in the Haremma Forest, and the second most numerous species after *Stenocephalemys albipes* (44%).

Adaptations Diurnal and nocturnal.

Foraging and Food Morphological studies show that the gastrointestinal tract is intermediate in structure between that of *Aethomys* and *Mastomys*, suggesting that the diet is mainly vegetable material. In this respect, this species (and *L. brevicaudus*) differs from most other species of *Lophuromys*, which are insectivorous (*L. Lavrenchenko* unpubl.).

Social and Reproductive Behaviour Peaceful and unaggressive. In captivity, neither ♂♂ nor ♀♀ demonstrated any elements of agonistic behaviour towards conspecifics or parapatric *L. brevicaudus*.

Reproduction and Population Structure Females collected in the Beletta Forest during the late dry season and the beginning of the wet season (Apr and May) were pregnant. Embryo number: 2.00 (n = 6 pregnant ♀♀). Sex ratio close to unity.

Predators, Parasites and Diseases No information.

Conservation IUCN Category: Least Concerned.

Destruction of montane forests will reduce the geographic range and population numbers of this forest rodent.

Measurements

Lophuromys chrysopus

HB: 114 (100–128) mm, n = 46

T: 79 (72–87) mm, n = 20

HF: 21.1 (19–23) mm, n = 46

E: 17.7 (16.5–20.0) mm, n = 46

WT: 43 (34–65) g, n = 45

GLS: 29.6 (28.2–31.3) mm, n = 53

GWS: 14.2 (12.5–15.7) mm, n = 53

M¹–M³: 4.9 (4.4–5.4) mm, n = 53

Ethiopia (*Lavrenchenko et al.* 1998b)

Key References *Lavrenchenko et al.* 1997, 1998b.

Leonid A. Lavrenchenko

Lophuromys cinereus GREY BRUSH-FURRED RAT

Fr. Souris hérissé gris; Ger. Graue Bürstenhaarmaus

Lophuromys cinereus Dieterlen & Gelmroth, 1974. Z. Säugetierk. 39: 338. Marais Mukaba, Parc National de Kahuzi-Biega, E DR Congo.

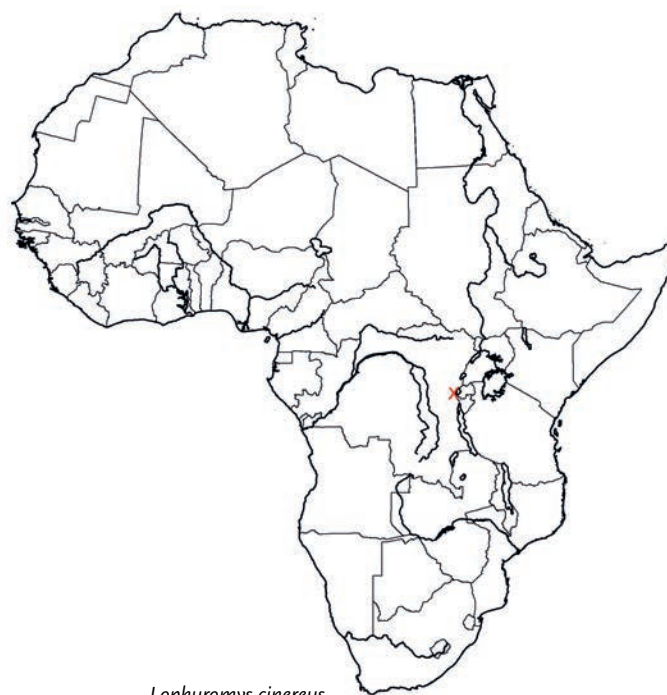
Taxonomy Subgenus *Lophuromys*. Species-group: *flavopunctatus*. Closely related to *L. flavopunctatus*. The status of this species is questionable (Dieterlen 1987) and it is not impossible that it is a grey-coloured mutant of *L. flavopunctatus*. Musser & Carleton (2005) considered *cinereus* to be a synonym of *L. aquilus*, a species treated here as a juvenile synonym of *L. flavopunctatus*. Synonyms: none. Chromosome number: not known.

Description Medium-sized grey unspeckled rat, with relatively short tail. Dorsal pelage harsh, generally brownish-grey; hairs grey at base, brownish-yellow distally, with blackish tip. Ventral pelage pale grey or soft brownish-grey. Large whitish spot on chest in some individuals. Naked parts of fore- and hindfeet blackish-grey. Tail short (ca. 57% of HB), darkly pigmented, short bristles black above, grey below. Skull large, similar to large individual of *L. flavopunctatus*. Nipples: 2 + 1 = 6.

Geographic Variation None recorded.

Similar Species Within the *flavopunctatus* species-group (see Table 20) and likely to be syntopic:

L. flavopunctatus. Pelage speckled; dorsal pelage reddish-brown; ventral pelage pale brown or cinnamon; claws dark.



Lophuromys cinereus

L. rahmi. Pelage unspckled; dorsal pelage reddish-brown; ventral pelage reddish-orange; claws pale or brown.

Distribution Endemic to Africa. Afromontane–Afroalpine BZ. Recorded only from near Mukaba in Kahuzi-Biega N. P., Kivu Province, E DR Congo (2275–2350 m). The collecting area covered less than 1 km². Probably an example of an Albertine Rift Valley endemic species.

Habitat Montane swamps of *Cyperus latifolius* (2275 m), and relatively dry short grasslands with *Hagenia abyssinica* and *Kotschy africana* trees.

Abundance Very rare; known only from four specimens from the type locality.

Remarks Very little is known about this species. Contents of four stomachs contained >50% arthropods and molluscs, the remainder being unidentified plant material (Dieterlen 1976b). One adult female had six placental scars, and another had one placental scar.

Conservation IUCN Category: Data Deficient.

Inadequate information to assess conservation status. As for other endemic species of the Albertine Rift Valley, limited geographic range and apparently small population numbers are cause for concern.

Measurements

Lophuromys cinereus

HB: 122 (110–129) mm, n = 3

T: 69.5 (65–74) mm, n = 3

HF: 23.5 (20–24.5) mm, n = 3

E: 19.1 (17–20.5) mm, n = 3

WT: 52 (45–56) g, n = 3

GLS: ca. 29.8 (28.0–31.0) mm, n = 3

GWS: 15.2 mm, n = 1

M¹–M³: 4.83 (4.8–4.9) mm, n = 3

E DR Congo (SMNS)

Key References Dieterlen 1976b, 1987; Dieterlen & Gelmroth 1974.

Fritz Dieterlen

Lophuromys dieterleni DIETERLEN'S BRUSH-FURRED RAT

Fr. Souris hérissée de Dieterlen; Ger. Dieterlens Bürstenhaarmaus

Lophuromys dieterleni Verheyen, Hulselmans, Colyn & Hutterer, 1997. Bull. Inst. Roy. Sci. Nat. Belgique, Biol. 67: 173.
Mount Oku, Bamenda-Banso Highlands, Cameroon. 2100 m.

Taxonomy Subgenus *Lophuromys*. Species-group: *flavopunctatus*. Eisentraut (1973) considered this form to be a montane subspecies of *L. sikapusi* because of its unspckled dorsal pelage. Verheyen *et al.* (1997) showed that, on the basis of craniology, it is a separate species, referable to the *flavopunctatus* species-group (which typically have a speckled pelage) and distinguishable from its geographically closest relative *L. eisentrauti*. Synonyms: none. Chromosome number: not known.

Description Unspckled medium-sized rat. Dorsal pelage soft, darkish-brown, similar to *L. sikapusi*; hairs ca. 11–12 mm. Ventral pelage brownish. Fore- and hindfeet pale brownish. Tail relatively short (ca. 61% of HB), dark brown above, paler below. Skull similar to *L. flavopunctatus*, broad in silhouette, rostrum rather short, clear ridge between t6 and t9 on M¹. Nipples: not known.

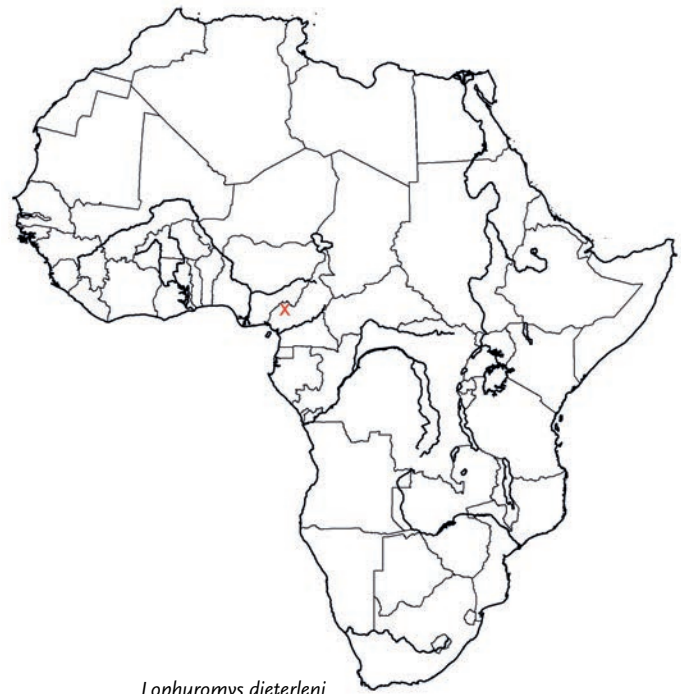
Geographic Variation None recorded.

Similar Species Four other species occur in the Cameroon–Nigeria area and are syntopic, sympatric, or narrowly sympatric:

L. eisentrauti. Pelage speckled; dorsal pelage reddish-brown; ventral pelage pale reddish; probably smaller size. W Cameroon.

L. roseveari. Pelage unspckled; dorsal and ventral pelages reddish-brown, and long; slightly larger on average; claws long and brown. Mt Cameroon.

L. sikapusi. Pelage unspckled; dorsal pelage rufous-rusty to blackish-brown; ventral pelage pale rufous; claws long and dark. Widespread distribution.



Lophuromys dieterleni

L. nudicaudus. Pelage unspckled and harsh; dorsal pelage reddish-brown; ventral pelage pale rufous; claws long and brown; on average smaller size. Central African rainforests.

Distribution Endemic to Africa. Recorded only from the edge of the crater lake on Mt Oku in the Bamenda highlands of Cameroon.

Habitat Montane forests on Mt Oku.

Remarks Apparently no other information available.

Conservation IUCN Category: Endangered.

The very limited geographic distribution, and the decline of forest cover on Mt Oku, suggest that the species should be given Critically Endangered status.

Measurements

Lophuromys dieterleni

HB: 123 (116–128) mm, n = 4

T: 75 (74–77) mm, n = 3

HF: 21.8 (20–24) mm, n = 4

E: 17.5 (17–18) mm, n = 4

WT: 61.3 (60–63) g, n = 4

GLS: 30.9, 31.0 mm, n = 2

GWS: 15.6 (15.3–16.1) mm, n = 5

M¹–M³: 4.9 (4.7–5.1) mm, n = 5

Mount Oku, Cameroon (ZFMK)

Key References Eisentraut 1968b, 1973; Verheyen *et al.* 1997.

Fritz Dieterlen

Lophuromys eisentrauti EISENTRAUT'S BRUSH-FURRED RAT

Fr. Souris hérissé de Eisentraut; Ger. Eisentrauts Bürstenhaarmaus

Lophuromys eisentrauti Dieterlen, 1979. Bonner Zoologische Beiträge 29: 296. Mt Lefo, Cameroon.

Taxonomy Subgenus *Lophuromys*. Species-group: *flavopunctatus*. A small *Lophuromys* similar to *L. sikapusi* (Dieterlen 1976b). Originally described as a subspecies of *L. sikapusi*, but elevated to a full species by Hutterer *et al.* (1992). Dieterlen (1976b) considered *eisentrauti* to be an 'unspckled' form, although on the basis of skull and molar characters Verheyen *et al.* (1997) placed it in the *flavopunctatus* species-group, i.e. with the 'speckled and short-tailed brush-furred' *Lophuromys*. Its closest relative may be *L. dieterleni*. Synonyms: none. Chromosome number: not known.

Description Smallest species of the genus (together with *L. rahmi* and *L. huttereri*). Pelage soft and unspckled, not very dense; hairs 9–10 mm. Dorsal pelage and flanks reddish-brown, ventral pelage pale reddish (similar to subadult *L. sikapusi*). Fore- and hindfeet reddish-brown. Tail relatively short (ca. 56% of HB), darkish above, paler below. Skull and rostrum short; braincase and interorbital constriction rather broad; zygomatic plate broad, front edge square (not rounded), pointing forward (not downwards). t3 on M² relatively large, t9 on M¹ and M² almost separate. Nipples: not known.

Geographic Variation None recorded.

Similar Species

L. dieterleni. Probably, on average, larger; tail longer; dorsal pelage darker; Mt Oku, Cameroon only.

L. roseveari. Larger; dorsal pelage darker; Mt Cameroon only.

L. sikapusi. Larger, tail longer; dorsal pelage darker; common and widespread.

Distribution Endemic to Africa. Afromontane–Afroalpine BZ. Recorded only from Mt Lefo (05° 50' N, 10° 20' E), Bafut-Ngamba Reserve, SE of Bamenda, W Cameroon, and probably endemic to the mountain. Map not given.

Habitat Montane cloud forest (at 1800–1900 m; about 700 m below the summit) where lichens, mosses, lycopods and tree ferns are common (Böhme 1975, Eisentraut 1975).

Abundance Very rare; known only by two subadult specimens from the type locality. Uncertain whether *L. eisentrauti* is the only *Lophuromys* on Mt Lefo, or whether it is syntopic with *L. sikapusi*.

Remarks Apparently no other information available.

Conservation IUCN Category: Endangered.

Very limited geographic distribution, and the decline of forest cover on Mt Lefo, suggest that the species should be given Critically Endangered status.

Measurements

Lophuromys eisentrauti

HB: 94 mm

T: 53 mm

HF: 19 mm

E: 14 mm

WT: n. d.

GLS: 26.8 mm

GWS: 13.2 mm

M¹–M³: 4.5 mm

Mt Lefo, Cameroon (Eisentraut 1975)

Holotype: ♂, probably subadult

Key References Dieterlen 1976b, 1979a; Hutterer *et al.* 1992.

Fritz Dieterlen

Lophuromys flavopunctatus **YELLOW-SPOTTED BRUSH-FURRED RAT (BUFF-SPOTTED BRUSH-FURRED RAT)**

Fr. Souris hérissé à tache jaune; Ger. Gelbgefleckte Bürstenhaarmaus

Lophuromys flavopunctatus, Thomas 1888. Proc. Zool. Soc. Lond. 1888.

Probably obtained at Ankober, Shoa, Ethiopia. (See also Thomas 1903, Proc. Zool. Soc. Lond. 1902: 314.)

Taxonomy Subgenus *Lophuromys*. Species-group: *flavopunctatus*. Previously regarded as a widespread and variable species with several forms or subspecies. The validity of the forms in Ethiopia is complex: two of them, *brevicaudus* and *chrysopus*, are now regarded as distinct species; *brunneus* may also be a valid species, and *simensis* and *zaphiri* are possibly subspecies of *L. flavopunctatus*. Verheyen *et al.* (2002) have revised *L. flavopunctatus* and consider that it can be separated into five species (see profile Genus *Lophuromys*). Synonyms: *aquilus*, *brunneus*, *giaquintoi*, *laticeps*, *majo*, *margarettae*, *rita*, *rubecula*, *simensis*, *zaphiri*, *zena*. Subspecies: none (see also below). Chromosome numbers vary according to locality: $2n = 70$, $FN = 86$ (*laticeps* from E DR Congo and Burundi [Matthey 1967, Dieterlen 1976b, Maddalena *et al.* 1989]); $2n = 68$, $FN = 82$ (*brunneus* from Ethiopia [Lavrenchenko *et al.* 1998b] and *L. flavopunctatus* from Ethiopia [Orlov *et al.* 1989]). Three populations of *laticeps* showed unusually high genetic variation in heterozygosity and polymorphic loci (Verheyen *et al.* 1986).

Description Small reddish-brown rat with thickset body, speckled pelage, short tail, short ears and short hindfeet with long claws. Pelage harsh and brush-like. Dorsal pelage blackish-brownish, brownish-reddish or tawny (depending on locality – see below); hairs reddish with yellow tinge at base, yellowish subterminal band and dark tip. Ventral pelage pale brown tinged with cinnamon; hairs dull brownish at base. In subadults, ventral pelage is more reddish than in adults. Head similar to dorsal pelage; eyes dark and rather small; ears darkly pigmented and naked. Fore- and hindfeet

brown or dark brown; claws long, mostly dark. Tail relatively short (ca. 50% of HB); dark and naked with scattered dark bristles above, dark with whitish bristles below. Nipples: $2 + 1 = 6$ or $1 + 1 = 4$. Considerable variation in size and colouration within populations and throughout geographic range.

Geographic Variation Variation in colour of pelage throughout range. Seven colour morphs previously regarded as subspecies: *margarettae*, *rubecula* and *zena* (Kenya); *aquilus* (Tanzania); *laticeps*, *major*, *rita* (DR Congo). None (except possibly *laticeps* from CE DR Congo, and *simensis* and *zaphiri* from Ethiopia) is now accepted as subspecies.

Similar Species The most widespread sympatric species is *L. sikapusi* (between and eastwards of the Congo and Ubangi rivers):

L. sikapusi. Similar size; pelage soft, unspeckled; dorsal pelage rufous/rusty; tail on average longer and relatively longer (mean 74 mm, 63% of HB); nipples: $1 + 1 = 4$; $2n = 60$ or 62 .

Many other species of *Lophuromys* occur within the geographic range of *L. flavopunctatus*; each has a very restricted range and is sympatric in only a very small area (see maps). In the Congo Basin, potentially sympatric (or syntopic) species are *L. cinereus*, *L. huttheri*, *L. luteogaster*, *L. medicaudatus*, *L. rahmi* and *L. woosmani*; in Ethiopia, potentially syntopic species are *L. melanonyx*, *L. brevicauda* and *L. chrysopus*.

Distribution Endemic to Africa. Rainforest BZ (primarily Eastern Central and South Central Regions), and afroalpine–Afroalpine and Zambezian Woodland BZs at selected places in eastern and central Africa. Widely distributed throughout DR Congo from the Congo Basin (300 m) up to 4500 m in the afroalpine zone of the Rwenzori and the Virunga Mts. Also recorded in W Uganda and S Sudan. Exceptionally may occur in a few areas receiving 800–1000 mm provided there are at least six wet months/year. Distribution patchy on forested mountains and plateaux, mostly above 1000 m where annual rainfall exceeds 1200 mm, in Uganda, Kenya, Tanzania, Malawi, N Zambia, NE Angola and N Mozambique. In Ethiopia, recorded on the plateaux on both sides of the Rift Valley.

Habitat Moist vegetation in a wide range of habitats and altitudes from lowland rainforest and forest tangles to montane grasslands and swamps (Misonne 1963, Delany & Neal 1966, Dieterlen 1976b, Happold & Happold 1989a, b). In drier areas, confined to habitats of permanent moisture such as montane and riverine forests and their adjacent belts of bush, grass and swamp (e.g. around L. Rukwa [Tanzania], in Ngorongoro crater and in the Rift Valley of Kenya).

Abundance A common species in suitable habitats, and often the most numerous species of small rodent in some communities. In

*Lophuromys flavopunctatus*

the highlands of Kivu, DR Congo (where sometimes there were as many as 16 spp. of small mammals), comprised on average 34% of captured small mammals in elephant-grass, 32% in bush and grassland habitats, 19% in secondary montane forest, 48% in bamboo forest with grassy cover, 44% in montane swamps and 53% in afroalpine heath (Dieterlen 1967c, 1976b). Similar levels of abundance have also been recorded in other regions, e.g. E DR Congo, Uganda, Malawi and Ethiopia (Misonne 1963, Hanney 1964, Delany 1971, 1972, Rupp 1980, Yalden 1988, Happold & Happold 1989c, Dudu 1991, Clausnitzer & Kityo 2001). In DR Congo, population densities vary according to habitat, ranging from 9.8 animals/ha in savanna to 19.6/ha in a dry seasonal swamp (Misonne 1963). Home-range in a montane grassland/tangle/forest habitat in Malawi was 3161 m² (1800–4500 m²) (Happold & Happold 1989c).

Adaptations Terrestrial, occasionally up to 1 m above ground. Locomotion by walking, running and scrambling over logs. When frightened or hunted by predators, the escape reaction is to hide rapidly in soil and under rotten vegetation. A ‘high jump’ is possible when an individual is frightened. In favoured habitats (moist soil, dense tangled vegetation), individuals develop a complex network of surface runways (Hanney 1964). Activity occurs during the day and night, but diurnal activity predominates when conditions are suitable. Individuals have a curious odour, quite unlike that of other mice (Woosnam in Thomas & Wroughton 1910). This strong odour, similar to that of shrews, appears to provide protection from predation by some terrestrial carnivores, but not from predatory birds (Dieterlen 1976b, Sillero-Zubiri *et al.* 1995a, Muhmenthaler 1999). The selective value of this character is obvious, but whether there is a relationship between the unattractive odour and the high numerical occurrence of individuals (and how this may effect the populations of other small mammals) is uncertain. Able to live in a very wide range of habitats and climates – and may be one of the most adaptable of small African murid rodents.

Foraging and Food Omnivorous. Foraging for arthropods and other foods occurs in the surface litter and in the upper layer of the soil. The long foreclaws are used for searching and scraping in litter, soil and rotting logs. Food intake is rapid. Individuals in captivity consume on average 3–4 g/day, and a near full-term pregnant female consumed 12 g/day (Delany 1971). In Malawi, the diet (based on percentage of stomachs in which any particular item of food was found) was 81% insects (beetles, larvae, ants, etc.), 39% earthworms, 11% seeds and 8% vertebrate remains (n = 117; Hanney 1964). In E DR Congo, most stomachs contained an equal amount of animal

food (insects, larvae, earthworms, snails) and vegetable food (seeds grains, tubers, but not green matter) (n = 50; Rahm 1972, Dieterlen 1976b). On Mt Elgon, Uganda (>3800 m, near summit), diet is snails, worms and Tipulidae larvae (V. Clausnitzer unpubl.). It appears that this species takes less animal food than most other species of the genus (Dieterlen 1976b) and that the respective portions of animal and plant foods depend on environment and season.

Social and Reproductive Behaviour Little information available. Many individuals in the wild have torn ears and mutilated tails suggesting agonistic behaviour. In captivity, individuals (especially ♂♂) fight and injure each other and deaths (with or without physical damage) are not uncommon. In captivity, individuals are very shy, hiding themselves in vegetation and nesting materials. They are able to utter a feeble cry (Hanney 1964; Delany 1972; Dieterlen 1976b; Muhmenthaler 1999).

Reproduction and Population Structure In most studies, reproduction occurs during the wet season. In Malawi, pregnancies were recorded during the late dry season, throughout the wet season, and at the beginning of the dry season (Oct–May), with the highest pregnancy rates in Nov–Mar (Hanney 1964; Happold & Happold 1989c). In Uganda, two peaks of pregnancy (Sep–Nov and Mar–Jun) coincided with the double peak of annual rainfall (Delany 1971, 1972). In Kivu, DR Congo, three populations living in different habitats and different rainfall regimes showed different patterns of reproductive activity (Table 21).

Reproduction shows considerable flexibility; shorter periods of reproduction are characterized by a lower pregnancy rate and larger litters, and longer periods of reproduction by a higher pregnancy rate and smaller litters. In Uganda, most pregnant ♀♀ are primiparous although a small number of older ♀♀ may be pregnant with their second to fifth litters (Delany 1971). In Uganda, some ♂♂ are fecund at all times of the year, with a higher fecundity rate when monthly rainfall is at its highest (Delany 1971). In Malawi, testis size in adult ♂♂ fluctuates during the year, being smallest in the dry season (when perhaps ♂♂ are not fecund) and largest in the wet season when the fecundity rate is also at its highest (Hanney 1964).

Litter-size varies depending on the environment (see above) and also on the size of the ♀. In Uganda, mean litter-size is 1.9 for ♀♀ of less than 40 g, 2.2 for ♀♀ of 40–49 g, and 2.3 for ♀♀ over 50 g (Delany 1971). In Malawi, litter-size is 2.4 (2–5); 51% of ♀♀ had 3 embryos and 25% had 2 embryos (total n = 43, Hanney 1964). Gestation: 30–31 days. At birth young are naked, with eyes and ears closed, but are rather large (6.5–9.5 g). Growth is rapid: thin

Table 21. Patterns of reproductive activity in populations of *Lophuromys flavopunctatus* living in different habitats with different rainfall regimes.

| Habitat and altitude | Rainfall (months) | Number of months of pregnancies | Pregnancy rate ^a | Litter-size mean (range) |
|-------------------------------|-------------------------|---------------------------------|-----------------------------|--------------------------|
| Cultivations, 1650–1850 m | 9 | 9 | 42% | 2.18 (1–4) |
| Montane forest, 2000–2300 m | 10 | 10 | 57% | 1.99 (1–4) |
| Lowland rainforest, 800–900 m | 9 (but mostly all year) | 12 | 87% | 1.83 (1–2) |

^aPregnancy rate = % of adult ♀♀ (40 g or more) which were pregnant, only during months when pregnancies recorded.

covering of dorsal hair by Day 3, and well covered with hairs by Day 3–6. Eyes open by Day 4–7. Walking by Day 5, and looking like a small adult by Day 9. Adult pelage by Day 30–35. Sexually mature by Day 50–70 when HB: 110–120 mm and weight ca. 45 g (Hanney 1964, Delany 1971, 1975, Dieterlen 1976b).

Sex ratio is fairly constant but varies according to time of year and locality. In Kivu, DR Congo, ♂♂ formed 53.5% of the population at the beginning of the breeding season. In different localities, ♂♂ comprised 51.0% to 55.9% of the population (Dieterlen 1976b, 1985a).

Young are born during many months of the year, and hence populations include young, subadults and adults (of various ages) in most months of the year. In Uganda (two wet seasons and two main periods of pregnancy), each of six age-classes are represented in each month with a tendency for larger numbers of younger animals in Oct–Jan and Apr–Jun (Delany 1971). In Malawi (one wet season and one period of pregnancy), the largest number of young (WT less than 40 g) occurs during and immediately after the wet season (Jan–Jun). These young are responsible for population numbers being at their highest at the time. Mortality of older individuals cause population numbers to be at their lowest in the late dry season (Sep–Dec) (Happold & Happold 1989c).

The large number of ♀♀ that have only one litter (compared with the small number that have two or more litters) suggests that there is high mortality and rapid turnover of the population (Delany 1971).

Predators, Parasites and Diseases The strong odour of this species makes them unattractive and unpalatable for some carnivores (see above). However, they are preyed upon by several diurnal and nocturnal birds such as eagles, herons (Misonne 1963) and Barn Owls *Tyto alba* (Rahm 1960b). Remains of *L. flavopunctatus* were not found in the pellets of African Grass-owls *Tyto capensis* in montane grasslands in Malawi, even though the species was common (Happold & Happold

1986). They are eaten by snakes of the genera *Naja*, *Dendroaspis* and *Bitis* (Allen & Loveridge 1942). Hanney (1964) reported that about 9% of individuals were diseased in Malawi; the percentage fluctuated throughout the year, being lowest during the cold dry season (3–7%) and highest (up to 15%) during the wet season. The most prevalent endoparasites were diphylobothriid larvae (Cestoda), which infested about 6% of individuals. Ectoparasites include five species of fleas (*Ctenophthalmus eximius*, *C. nyikensis*, *C. calceatus*, *Dinopsyllus* sp. and *Xiphiopsylla hyparetis*) (Hanney 1964).

Conservation IUCN Category: Least Concern.

This common and widely distributed species is not threatened at present, although clearance of suitable habitats will reduce numbers and limit the geographic range.

Measurements

Lophuromys flavopunctatus

HB: 119 (98–144) mm, n = 113

T: 63 (46–88) mm, n = 113

HF: 21.3 (20–25) mm, n = 113

E: 17.4 (13–20) mm, n = 113

WT: 52 (36–73) g, n = 102

GLS: 30.2 (26.8–31.3) mm, n = 56

GWS: 14.9 (12.9–15.9) mm, n = 56

M¹–M³: 4.8 (3.9–5.4) mm, n = 56

Body measurements and weight: throughout most of geographic range

Skull measurements: E DR Congo (Dieterlen 1976b, SMNS)

Key References Delany 1971; Dieterlen 1976b; Hanney 1964; Happold & Happold 1989c.

Fritz Dieterlen

Lophuromys huttereri HUTTERER'S BRUSH-FURRED RAT

Fr. Souris hérissé de Hutterer; Ger. Hutterers Bürstenhaarmaus

Lophuromys huttereri Verheyen, Colyn & Hulselmans 1996. Bull. Inst. Roy. Sci. Nat. Belgique, Biol. 66: 255.

Yaenoro, DR Congo (00° 12' N, 24° 47' E).

Taxonomy Subgenus *Lophuromys*. Species-group: *sikapusi*. An 'unspeckled' short-tailed *Lophuromys*, more closely related to *L. nudicaudus* than to the other representatives of the *sikapusi* species-group (W. Verheyen *et al.* 1996). The characteristics that distinguish this species from other *Lophuromys* are based mainly on the skull and teeth. Synonyms: none. Chromosome numbers: not known.

Description Similar in external characters to *L. nudicaudus*. Compared to *L. nudicaudus*, the skull has a wider and higher rostrum, the zygomatic plate is situated more anteriorly, and t3 on M² is nearly always totally absent. Can only be distinguished unambiguously from *L. nudicaudus* by discriminate analysis (see W. Verheyen *et al.* 1996).

Geographic Variation None recorded.

Similar Species

L. nudicaudus. Probably similar in size; rostrum narrower and lower; zygomatic plate narrow.

L. sikapusi. Zygomatic plate comparatively broad (mean 2.82 mm).

Distribution Endemic to Africa, Rainforest BZ (South Central Region). Recorded from between the Lualaba and Lomani rivers close to junction with the Congo R. (the type locality), and west of the Lomani R. to Ndele (00° 51' N, 21° 05' E); all localities on the left side of the Congo R. (cf. *L. nudicaudus*). The single specimen from Ndele seems to be closer to typical *L. nudicaudus* than to *L. huttereri*.

Habitat Rainforest.

Abundance Rare; known only from about three localities.

Remarks Apparently no other information available.

Conservation IUCN Category: Least Concern.

A rare and little-known species.

Measurements

Lophuromys huttereri

HB: 93–114 mm

T: 59–61 mm

HF: 18–20 mm

E: n. d.

WT: n. d.

GLS: 28.8 (28.0–29.9) mm

GWS: 14.4 (13.7–15.2) mm

M¹–M³: 4.4 (4.1–4.8) mm

Skull measurements: n = 7–10

DR Congo (W.Verheyen *et al.* 1996, BMNH, RUCA)

Key Reference W.Verheyen *et al.* 1996.

Fritz Dieterlen



Lophuromys huttereri

Lophuromys luteogaster BUFF-BELLIED BRUSH-FURRED RAT (HATT'S BRUSH-FURRED RAT)

Fr. Souris hérissée à ventre fauve; Ger. Gelbbauch Bürstenhaarmaus

Lophuromys luteogaster Hatt, 1934. Amer. Mus. Novitat. 708: 4. Medje, Ituri district, DR Congo.

Taxonomy Subgenus *Kivumys*. Species-group: *woosnami*. Synonyms: none. Chromosome number: not known.

Description Small unspeckled olive-brown rat with long tail, similar to *L. woosnami*. Pelage rather harsh. Dorsal pelage uniformly olive-brown and unspeckled, hairs reddish or yellowish at base. Ventral pelage pinkish-cinnamon to buff, hairs unicoloured. Dorsal colour merges to ventral colour on flanks. Head similar colour to dorsal pelage. Ears darkly pigmented with short greyish bristles. Forelimbs yellowish to reddish, hindlimbs pinkish-cinnamon, claws short, relatively weak, pale. Tail relatively long (ca. 100% of HB), dark above, pale below, except darkish tip. (The colour of dry skins in museums fades and loses its brightness when exposed to light). Skull: relatively long; M¹ relatively broad. Nipples: 2 + 1 = 6.

Geographic Variation None recorded.

Similar Species

L. woosnami. Similar colour; mostly larger in all body measurements; montane habitats of E DR Congo.

L. flavopunctatus. Dorsal pelage reddish-brown; on average larger HB and skull; tail shorter and relatively shorter; sympatric.

Distribution Endemic to Africa. Rainforest BZ (East Central Region). Recorded from only four localities in rainforest in NE and E DR Congo.



Lophuromys luteogaster

Habitat Lowland rainforests from 700 to 1100 m where dominant trees are either *Gilbertiodendron dewevrei* or *Julbernardia* and *Cynometra* (Hatt 1934, Dieterlen 1975, 1976b, Schlitter & Robbins 1977, Verschuren *et al.* 1983). Also occasionally in sub-montane forests of *Julbernardia* at about 1400 m (F. Dieterlen unpubl.). Of 26 records from

lowland rainforest, 11 were from primary forest, 14 from secondary forest and one from a cultivated area (Dieterlen 1975, 1976b).

Abundance Rare, comprising ca. 0.85% of terrestrial small mammals captured in the region of Irangi (DR Congo). Despite regular collecting during several years, almost 90% of captures ($n = 34$) were during the last three months of dry season and first three months of the wet season (Jun–Nov).

Remarks Terrestrial. Daily activity pattern not well known; mostly captured at night. Mostly insectivorous. Stomach analysis ($n = 9$) shows that the diet is mainly (90–100%) small grubs, caterpillars, small snails, small beetles and termites. Pregnancies recorded in Jun–Nov (no data at other times of year). During these months, pregnancy rate was high (11 out of 14). Embryo numbers: 2 ($n = 11$). Sex ratio 12 ♂♂ : 21 ♀♀. Sexually active ♂♂ had testes length of at least 6 mm.

Conservation IUCN Category: Least Concern.

Although a rare species, it is unlikely to be endangered because it lives in several habitats within the extensive rainforest.

Measurements

Lophuromys luteogaster

HB: 102 (90–113) mm, $n = 25$

T: 106 (90–117) mm, $n = 25$

HF: 21 (19–22.5) mm, $n = 25$

E: 17.5 (16.5–19) mm, $n = 25$

WT: 34 (28–41) g, $n = 25$

GLS: 28.8 (27.2–29.6) mm, $n = 12$

GWS: 13.2 (12.9–13.9) mm, $n = 12$

M¹–M³: 4.5 (4.2–4.9) mm, $n = 12$

E DR Congo (Dieterlen 1976b, SMNS)

Key References Dieterlen 1975, 1976b, 1987; Hatt 1934.

Fritz Dieterlen

Lophuromys medicaudatus MEDIUM-TAILED BRUSH-FURRED RAT (WESTERN RIFT BRUSH-FURRED RAT)

Fr. Souris hérissé a queue moyenne; Ger. Mittelschwänzige Bürstenhaarmaus

Lophuromys medicaudatus Dieterlen, 1975. Bonn. Zool. Beitr. 26: 295. Nyabutera near Lemera, Kivu, DR Congo.

Taxonomy Subgenus *Kivumys*. Species-group: *woosnami*. The only species of *Lophuromys* with a tail of 85% of HB. Closely related to *L. woosnami* and *L. luteogaster*. Synonyms: none. Chromosome number: not known. (Specimens named as *L. luteogaster* collected in the mountains west of L. Kivu by U. Rahm [Verheyen (1964c)], and one specimen from Nyungwe Forest, Rwanda [Elbl *et al.* 1966] are, in fact, *L. medicaudatus* [see Dieterlen 1975]).

Description Small beautiful rat with brightly coloured unspeckled pelage and medium tail length. Dorsal pelage and head uniform dark olive-brown, rather harsh; dorsal hairs paler at base, olive-brown at tip. Ventral pelage dark orange tinged with olive, colouration most intense on the chest; ventral hairs paler at base, olive at tip. Ears darkly pigmented, sparsely haired. Fore- and hindlimbs olive-brown. Tail long (ca. 85% of HB), darkish above, paler below. (The colour of dry skins in museums fades and loses its brightness when exposed to light.) Nipples: 2 + 1 = 6.

Geographic Variation None recorded.

Similar Species

L. woosnami. Larger, ventral pelage pale brown; tail longer (mean 123 mm, 105% of HB); sympatric and syntopic.

Distribution Endemic to Africa. Afromontane–Afroalpine BZ of the Albertine Rift Valley of E DR Congo and Rwanda around L. Kivu, at 1850–2500 m (Verheyen 1964c, Dieterlen 1975, 1976b, 1987, Verschuren *et al.* 1983). Specimens named as *L. luteogaster* collected in the mountains west of L. Kivu by U. Rahm (Verheyen 1964c), and one specimen from Nyungwe Forest, Rwanda (Elbl *et al.* 1966) are, in fact, *L. medicaudatus* (see Dieterlen 1975).



Lophuromys medicaudatus

Habitat Montane swamps of *Cyperus latifolius* and montane forests; syntopic with *L. flavopunctatus* and *L. woosnami*.

Abundance Rare; comprised 2.3% (9 specimens) of small mammals in montane swamps and 0.6% (17 specimens) in montane forests (Dieterlen 1975, 1976b).

Adaptations Terrestrial. There appear to be no special adaptations for locomotion in flooded swamp vegetation, but it is assumed that the ability to swim and climb must be essential for survival.

Foraging and Food Omnivorous. Stomach contents ($n = 11$) contained remains of many arthropods and some molluscs (70%, range 30–100%) as well as seeds and fruits.

Social and Reproductive Behaviour No information.

Reproduction and Population Structure Mean embryo numbers: 1.6 (range 1–2, mode 2, $n = 5$ ♀♀). Pregnant ♀♀ recorded in Feb, Apr and Jul. Testes length in mature ♂♂: 6–8 mm. Sex ratio 2 : 1 ($n = 30$).

Predators, Parasites and Diseases No information.

Conservation IUCN Category: Vulnerable.

This species is threatened because of its rarity and very restricted geographic range; in this respect it is similar to the other Albertine Rift endemics, e.g. *L. rahmi*, *L. woosnami* and *L. cinereus*.

Measurements

Lophuromys medicaudatus

HB: 103.2 (92–112) mm, $n = 27$

T: 87.2 (73–95) mm, $n = 27$

HF: 20.8 (18–23) mm, $n = 27$

E: 16.5 (15–19) mm, $n = 27$

WT: 35.4 (29–43) g, $n = 27$

GLS: 29.1 (27.7–30.2) mm, $n = 19$

GWS: 14.7 (14.1–15.6) mm, $n = 19$

M¹–M³: 4.1 (3.9–4.3) mm, $n = 19$

DR Congo (Dieterlen 1975, SMNS)

Key References Dieterlen 1975, 1976b, 1987.

Fritz Dieterlen

Lophuromys melanonyx BLACK-CLAWED BRUSH-FURRED RAT

Fr. Souris hérissé d’Ethiopie; Ger. Schwarzkralen-Bürstenhaarmaus

Lophuromys melanonyx Petter, 1972. Mammalia 36: 177. Dinshu, Bale, Ethiopia.

Taxonomy Subgenus *Lophuromys*. Species-group: *flavopunctatus*. One of three Ethiopian endemic species of *Lophuromys*. A distinctive species, larger than any other species of *Lophuromys*. Synonyms: none. Chromosome number: $2n = 60$ (Corti *et al.* 1995, Lavrenchenko *et al.* 1997).

Description Medium-sized to large speckled grey-brown rat with large ears; the largest species of *Lophuromys*. Dorsal pelage grey-brown, finely speckled with cream spots. Ventral pelage creamy-white. (Lacks the overall reddish-brown colouration of most of its congeners.) Ears prominent, grey, lightly furred with distinctive tuft of orange or cream at the base of ears. Feet whitish, with a grey wash dorsally, claws distinctively long and black. Tail short (ca. 43% of HB), dark above, whitish on the sides and below. Skull slightly larger than all congeners, with proportionately narrower interorbital region and strong zygomatic plate. Incisors strongly pro-odont (in contrast to moderately orthodont in all other *Lophuromys*). Skin tough (cf. fragile skin of other *Lophuromys* and *Acomys* spp.). Nipples: probably $0 + 2 = 4$.

Geographic Variation None recorded.

Similar Species

L. brevicaudus. On average much smaller size, pale claws; chromosome number $2n = 68$.

L. chrysopus and other species of the *flavopunctatus* species-group. Smaller, distinctive reddish colouration; chromosome number $2n = 54$ (*chrysopus*) or 68 (Lavrenchenko *et al.* 1997).

Distribution Endemic to Africa. Afromontane–Afroalpine BZ. Recorded only from Ethiopia at 3200–4300 m, commonly east of the Rift Valley in Bale, but rarely west of the Rift Valley (only from near



Debra Sina and Addis Ababa). Range perhaps more extensive, but not reported from Simien despite extensive surveys (e.g. by Müller 1977).

Habitat Afroalpine moorland, above the treeline (3500 m), ranging down to lower grasslands where open river valleys penetrate the woodland zones. Shares habitat with *Arvicanthis blicki*, *Tachyoryctes macrocephalus* and *Stenocephalemys albocaudata* and *Otomys typus* (Yalden 1988, Sillero-Zubiri *et al.* 1995a).

Abundance The most numerous of the small mammals trapped in the afroalpine habitat of Ethiopia. Comprised 33% of 3083 small mammals in Bale Mts. Population estimates, from live-trapping, suggested densities in different months of 102–658/ha in the grasslands of the Web Valley at 3450 m, and 118–601/ha at 3800–4050 m on the Sanetti Plateau (Sillero-Zubiri *et al.* 1995a). Biomass estimated, on the basis of actual captures, to be 4.9 kg/ha (annual range 3.9–6.6 kg/ha).

Adaptations Active only during daytime. Individuals emerge from their burrows around 08:00h, and the largest numbers of animals above ground occurs at 10:00–12:00h. Activity declines slowly towards 15:00h and sharply thereafter, and no animals are visible above ground after 18:00h (sunrise 06:00h; sunset 18:30h) (see also below). Trapping results reflect this activity: 07:00–12:30h (76%), 12:30–18:30h (23%), overnight (0.5%) (Sillero-Zubiri *et al.* 1995a). The long claws on the forefeet and pro-odont incisors are presumed to be adaptations for burrowing. Large size, relatively short tail and daytime activity might be adaptations to the cold at high altitudes.

Foraging and Food Limited data from stomach analysis suggest that the diet is primarily leaves of dicotyledonous herbs (93% occurrence), with smaller amounts of monocotyledonous leaf (2%), seeds (3%) and insects (2%) (Yalden & Lagen 1992). This diet differs from that of most other *Lophuromys*, which are largely insectivorous (Dieterlen 1976b), and from sympatric *Arvicanthis blicki*, which eats much monocotyledonous leaf (30%) as well as herbs.

Social and Reproductive Behaviour Lives in mixed colonies with *Arvicanthis blicki*; both species are diurnal, live in burrows and utter high-pitched alarm squeaks that warn of intruding predators (including humans). Because of the difficulty of distinguishing this species from *Arvicanthis blicki* in the field, observations (given above) refer to the mixed colonies.

Reproduction and Population Structure Pregnant and lactating ♀♀ found throughout the year. The occurrence of pregnancy is 80–100% at beginning of short wet season in Apr, falls to 40% in May (rainfall lower and variable), rises to 80–100% at the

beginning of the main wet season (Jun–Jul), declines to 40% in the wet season (Aug–Oct), and reaches its lowest level of ca. 20% during dry season (Nov–Mar). This pattern suggests at least two litters per year. Young mainly enter the trappable population in Oct–Feb, contributing ca. 15% of captures; apparent slowness of recruitment is puzzling; possibly due to slow growth or effects of high population density. Mean embryo number: 1.88 ± 0.38 ($n = 52$ pregnancies; Sillero-Zubiri *et al.* 1995a). Sex ratio close to unity.

Predators, Parasites and Diseases Important prey of Ethiopian Wolves in Bale, comprising 40% of 1307 prey occurrences in 689 scats and 15% by volume of prey (Sillero-Zubiri & Gottelli 1995); the third commonest prey after *Tachyoryctes macrocephalus* and *Arvicanthis blicki*. Probably also prey of diurnal raptors, but no detailed information available.

Conservation IUCN Category: Vulnerable.

Although abundant in suitable habitats, geographic range is very limited. Schlitter (1989) suggested it should be listed as rare.

Measurements

Lophuromys melanonyx

HB: 145.7 (120–180) mm, $n = 700$

T: 63.7 (30–99) mm, $n = 671$

HF: 22.8 (21–25) mm, $n = 234$

E: 22.1 (19–26) mm, $n = 235$

WT: 94.6 (60–142) g, $n = 717$

GLS: 33.1 (31.6–34.3) mm, $n = 9$

GWS: 16.7 (16.0–17.3) mm, $n = 10$

M¹–M³: 5.7 (5.4–6.0) mm, $n = 14$

Ethiopia

Body measurements and weight: Sillero-Zubiri *et al.* 1995b

Skull measurements: Petter 1972a

Key References Petter 1972a; Sillero-Zubiri 1995a; Yalden & Lagen 1992.

D. W. Yalden

Lophuromys nudicaudus FIRE-BELLIED BRUSH-FURRED RAT

Fr: Souris hérissé à ventre feu; Ger: Rotbauchige Bürstenhaarmaus

Lophuromys nudicaudus Heller, 1911. Smithson. Misc. Coll. 56 (17): 11. Efulen, Bula country, Cameroon.

Taxonomy Subgenus *Lophuromys*. Species-group: *sikapusi*. Closely related to *L. sikapusi* and *L. huttereri* (see W. Verheyen *et al.* 1996 for a review). Previously considered to be a subspecies of *L. sikapusi*, but now considered to be a valid species on the basis of skull and tooth characters (Rosevear 1969; Dieterlen 1976b, 1979a). The specific name (*nudicaudus* = naked tail) is misleading (Rosevear 1969). Synonyms: *afar*, *naso*, *nudicaudatus*, *parvulus*, *tullbergi*. Subspecies: two. Chromosome number: $2n = 56$, with considerable polymorphism (Verheyen & Van der Straeten 1980).

Description Small unspeckled species with harsh pelage, relatively short tail and relatively short hindfeet. Dorsal pelage dark

brown with reddish tinge, stiff and harsh; hairs paler at base. Ventral pelage bright rufous (especially in young animals) or yellowish-red. Overall colouration resembles that of young *L. sikapusi*. Head similar to dorsal pelage, throat and chest similar to ventral pelage. Fore- and hindlimbs brownish; claws long, usually pale or brown. Tail short (ca. 58% of HB) with black bristles, dark above, paler below. Skull: rostrum narrow; zygomatic plate narrow. Nipples: $2 + 1 = 6$ (W. Verheyen *et al.* 1996).

Geographic Variation The two subspecies are distinguished only by craniometric analysis (W. Verheyen *et al.* 1996).

L. n. nudicaudus: north and west of Congo R. to Sanaga R.
L. n. tullbergi: between Cross and Sanaga rivers, and on Bioko I.

Similar Species

L. sikapusi. Larger (HB: 136 (122–153) mm); sympatric.
L. huttermi. Probably similar in size and characters; rostrum wider and higher; zygomatic plate wide.

Distribution Endemic to Africa. Rainforest BZ (West Central Region), north and west of Congo and Ubangi rivers and westwards almost to Cross R. in Nigeria. Recorded from Congo, SW Central African Republic, Gabon, Equatorial Guinea (Rio Muni and Bioko I.), Cameroon and E Nigeria. Recorded also at one locality on the right bank of Aruwimi R. (DR Congo), and may extend westwards along Congo R. to its junction with Ubangi R.

Habitat Gaps and clearings within the rainforest and along logging roads (Rosevear 1969; Ray 1996; Malcolm & Ray 2000). Recorded from grassy and open habitats on the forest edge on Mt Cameroon (100–600 m) and Bioko I. (450–1200 m) (Eisentraut 1973). Does not occur in closed canopy rainforests.

Abundance Relatively rare, especially in disturbed forests. In SW Central African Republic, comprised 2.4% of small mammals (n = 704) along secondary logging roads (Ray 1996).

Remarks Terrestrial and diurnal (Rosevear 1969, Malcolm & Ray 2000). Stomach contents of two individuals consisted mainly of insects (80–100%) (Dieterlen 1976b). Solitary (Rosevear 1969). Number of embryos: 2, 5 (n = 2).

Conservation IUCN Category: Least Concern.
 Probably not threatened because of its large geographic range.

Measurements

Lophuromys nudicaudus
 HB: 106.2 (89–119) mm, n = 41



Lophuromys nudicaudus

T: 61.8 (47–74) mm, n = 33
 HF: 18.6 (16.3–21.0) mm, n = 44
 E: 14.6 (10–18) mm, n = 40
 WT: 39.5 (29–52) g, n = 23
 GLS: 27.9 (26.5–29.3) mm, n = 34
 GWS: 13.4 (12.2–14.2) mm, n = 43
 M¹–M³: 4.4 (3.9–5.0) mm, n = 47
 Throughout geographic range (W. Verheyen *et al.* 1996)

Key References Dieterlen 1976b, 1979a; W. Verheyen *et al.* 1996.

Fritz Dieterlen

Lophuromys rahmi RAHM'S BRUSH-FURRED RAT

Fr. Souris hérissé de Rahm; Ger. Rahms Bürstenhaarmaus

Lophuromys rahmi Verheyen, 1964. Rev. Zool. Bot. Afr. 69: 206. Bogamanda near Lemera, Kivu, DR Congo.

Taxonomy Subgenus *Lophuromys*. Species-group: *flavopunctatus*.
 Synonyms: none. Chromosome number: not known.

Description Small beautiful dark reddish unspeckled rat with short-tail, very short hindfeet and short rounded ears. Pelage rather harsh. Dorsal pelage dark reddish-brown, dorsal hairs pale reddish usually with dark tip. Some individuals may have pale tips to dorsal hairs to give slight speckling to pelage. Flanks paler than dorsal pelage. Ventral pelage bright reddish-orange in both young and adults; hairs paler at base. Head similar to dorsal pelage but duller. Ears short and rounded. Hindfeet very short. Tail short (ca. 51% of HB), darkish-brown above, paler below. Skull: short with rather broad interorbital constriction. Nipples: not known.

Geographic Variation None recorded.

Similar Species

L. cinereus. On average larger; dorsal pelage greyish-brown; very rare.
L. flavopunctatus. On average larger; dorsal pelage reddish-brown; widespread and common.
L. medicaudatus. Similar in size; tail relatively longer; pelage olive-brown; limited distribution, rare.
L. woosnami. On average larger; tail longer and relatively longer; dorsal pelage brown tinged with olive-grey; limited distribution, rare.

Distribution Endemic to Africa. Afromontane–Afroalpine BZ. Restricted to montane forests bordering Albertine Rift Valley of E

*Lophuromys rahmi*

DR Congo and Rwanda around L. Kivu at 1900–2500 m (Dieterlen 1976b, 1987, Verschuren *et al.* 1983). Also Bwindi Forest, SW Uganda (Kasangaki *et al.* 2003).

Habitat Dense primary montane forest especially in *Albizia gummifera*–*Carapa grandiflora*–*Parinari excelsa* forest. Also recorded in secondary forest with *Hagenia* and *Macaranga* trees, and in sparse bamboo stands (*Hagenia abyssinica*–*Sinarundinaria alpina*) with ground cover of grass (Dieterlen 1976b). May show a preference for habitats with small streams (Rahm 1967) although this preference is uncertain (Dieterlen 1976b, Verschuren *et al.* 1983).

Abundance Extremely rare, comprising less than 0.05% of terrestrial small mammals captured in montane forests and grasslands.

Remarks Terrestrial. Probably burrows amongst roots of trees. Mostly active during the night (Rahm 1967). Omnivorous, preferring insects (mostly larvae), small grubs, caterpillars, beetles, ants, etc. May also eat seeds. Forages on ground in leaf litter (Dieterlen 1976b). Embryo numbers: 2 ($n = 2$). Pregnant ♀♀ recorded in Feb and Jul. Adult size attained when HB >95 mm and weight >30 g. Males fecund when testes 5–10 mm. Sex ratio 16♂♂ : 5♀♀ (Dieterlen 1976b).

Conservation IUCN Category: Endangered.

This species is threatened because of its rarity and very restricted geographic range; in this respect it is similar to the other Albertine Rift endemics – *L. medicaudatus*, *L. woosnami* and *L. cinereus*. Schlitter (1989) classified the species as rare.

Measurements

Lophuromys rahmi

HB: 102 (95–116) mm, $n = 21$

T: 52.6 (48–56) mm, $n = 21$

HF: 16.3 (13–18) mm, $n = 21$

E: 12.5 (10–15) mm, $n = 21$

WT: 32.5 (30–45) g, $n = 21$

GLS: 25.3 (24.7–25.9) mm, $n = 14$

GWS: 14.1 (13.3–14.8) mm, $n = 11$

M¹–M³: 4.1 (3.8–4.4) mm, $n = 16$

DR Congo (Dieterlen 1976b; SMNS)

Key References Dieterlen 1976b, 1987; Verheyen 1964b; Verschuren *et al.* 1983.

Fritz Dieterlen

Lophuromys roseveari ROSEVEAR'S BRUSH-FURRED RAT (MOUNT CAMEROON BRUSH-FURRED RAT)

Fr. Souris hérissé de Rosevear; Ger. Rosevears Bürstenhaarmaus

Lophuromys roseveari Verheyen, Hulselmans, Colyn and Hutterer, 1997.

Bull. Inst. Roy. Sci. Nat. Belgique, Biol. 67: 167. Musake (slopes of Mount Cameroon), Cameroon. 1850–2200 m.

Taxonomy Subgenus *Lophuromys*. Species-group: *sikapusi*. Previously considered to be a montane race of *L. sikapusi* (Eisentraut 1963, 1973, Rosevear 1969, Dieterlen 1976b, 1979a) and now considered as a valid species (Verheyen *et al.* 1997). Morphologically and morphometrically similar to other species in the *sikapusi* species-group, but its status and systematic relationships need investigation (Verheyen *et al.* 1997, Musser & Carleton 2005). Synonyms: none. Chromosome number: not known.

Description Medium-sized reddish-brown unspeckled rat, with long dorsal hairs on rump and a short tail. Dorsal pelage reddish-brown; hairs reddish at base with reddish-brown tip. Hairs on rump long and dense (13–14 mm). Ventral pelage pale reddish-brown or dark cinnamon-brown. Head similar to dorsal pelage. Ears rather large.

Fore- and hindlimbs brown; claws very long, variable and brownish. Tail short (ca. 50% of HB), dark brown. Skull (compared to *L. sikapusi*): slender and fragile, with narrow choanae, more inclined borders of the zygomatic plates, supraorbital ridges and notch weakly developed, and zygomatic arches more slender; mandible relatively longer and with a more slender angular process (Verheyen *et al.* 1977). Nipples: 2 + 1 = 6, 1 + 1 = 4.

Geographic Variation None recorded.

Similar Species

L. sikapusi. Similar in size; ears on average shorter; dorsal pelage reddish-brown (probably paler); different skull characters (details in profile); widespread and common.



Lophuromys roseveari

Distribution Endemic to Africa. Afromontane–Afroalpine BZ. Mt Cameroon only. All specimens ($n = 44$) were collected from several localities on the slopes of Mt Cameroon at 1200–3000 m (Eisentraut 1963, 1973).

Habitat Montane forest, grasslands, forest fringes, small patches of woodland, gardens and plantations.

Remarks Apparently no other information available.

Conservation IUCN Category: Least Concern.

Distribution is restricted; changes in land use on the mountain may be cause of concern.

Measurements

Lophuromys roseveari

HB: 127.5 (104–141) mm, $n = 32$

T: 66.0 (50–78) mm, $n = 29$

HF: 22.5 (20–25) mm, $n = 32$

E: 18.5 (16–21) mm, $n = 28$

WT: 63.5 (49–88) g, $n = 24$

GLS: 31.3 (30.3–32.6) mm, $n = 15$

GWS: 14.7 (13.9–15.6) mm, $n = 21$

M^1 – M^3 : 4.8 (4.5–5.1) mm, $n = 36$

Mt Cameroon (Verheyen *et al.* 1997; BMNH, MNHN SMNS, ZFMK)

Key References Eisentraut 1963, 1973; Rosevear 1969; Verheyen *et al.* 1997.

Fritz Dieterlen

Lophuromys sikapusi RUSTY-BELLIED BRUSH-FURRED RAT

Fr. Souris hérissé de l'Ouest; Ger. Braunbauchige Bürstenhaarmaus

Lophuromys sikapusi (Temminck, 1853). Esquisses Zoologiques sur la côte de Guinée, p. 160. Dabocrom, Ghana.

Taxonomy Originally described in the genus *Mus*. Subgenus *Lophuromys*. Species-group: *sikapusi*. One form (*eisentrauti*) previously considered to be a synonym by Musser & Carleton (1993) now considered to be a valid species. Musser & Carleton (2005), following Verheyen *et al.* (2000), regard *ansorgei* (SW DR Congo near the mouth of the Congo R., Uganda, W Kenya, N Tanzania) and *angolensis* (SW DR Congo near the mouth of the Congo R. and NW Angola) as valid species; here they are retained within *L. sikapusi* pending further revision. Synonyms: *afer*, *ansorgei*, *angolensis*, *mantufeli*, *pyrrhus*, *tullbergi*. Subspecies: none. Chromosome number: $2n = 60$, FN = 66–70 (Côte d'Ivoire; Matthey 1958); $2n = 64$, FN = 76 (Mt Nimba, Guinea; Gautun *et al.* 1986).

Description Small unspeckled short-tailed rat. Pelage comparatively soft and less stiff than in other *Lophuromys*. Dorsal pelage rufous to rusty; blackish-brown in some populations. Ventral pelage pale rufous (most) or bright red (Côte d'Ivoire). Head pointed; eyes small, ears short. Limbs short. Fore- and hindfeet short, reddish-brown, with long dark curved claws. Digit 1 of forefoot much reduced. Tail short (ca. 64% of HB), dark with scaly rings and short dark bristles. Skull: zygomatic plate comparatively broad (2.82 [2.4–3.1 mm]). Nipples: $1 + 2 = 6$.

Geographic Variation Dorsal pelage is darkish-brown, and ventral pelage is also unusually dark, in *ansorgei* from W Kenya. Ventral pelage strikingly bright red in *pyrrhus* from N Uganda and S Sudan (Dieterlen 1987).

Similar Species

L. roseveari. Ear on average longer; dorsal pelage reddish-brown to blackish-brown; different skull characters (details in species profile); Mt Cameroon only, where may be sympatric.

L. flavopunctatus. Pelage harsh and brush-like, speckled; dorsal pelage blackish-brown; ventral pelage pale brown; tail on average shorter and relatively shorter; nipples $2 + 1 = 6$ or $1 + 1 = 4$; $2n = 68$ or 70.

Distribution Endemic to Africa. Rainforest BZ (Western, West Central and East Central Regions) and adjacent Rainforest–Savanna Mosaic. Recorded from Sierra Leone to Cameroon, southwards to Gabon, Equatorial Guinea, Congo, SW DR Congo and N Angola, and east to Central African Republic, N DR Congo (north of Congo R.), S Sudan, Uganda and W Kenya. In Tanzania, patchy distribution in some montane habitats (Dieterlen 1976b).

*Lophuromys sikapusi*

Habitat Dense moist grasslands, secondary growth, agricultural fields, abandoned farmlands, swamps and grassy plantations where there is abundant low cover. In primary and secondary rainforests, occurs only in grass and herbaceous patches (e.g. after a tree fall) and where grass and bushes grow in open areas. These habitats are preferred because they provide moist soil for digging, and abundant insects, throughout the year (see below). At Mt Nimba, Guinea, occurs up to 1600 m (Gautun *et al.* 1986). In Uganda, very common in heavily grassed bush country (Delany & Neal 1966).

Abundance Common and often numerous in preferred moist habitats, e.g. in S Nigeria comprised 46% of small rodents in swampy stream banks ($n = 43$, 7 spp.) and 13% in arable fields ($n = 138$, 8 spp.) (Funmilayo & Akande 1979a). Uncommon in primary rainforest, e.g. 2.9% of seven species of small rodents ($n = 482$) in a Nigerian rainforest, all individuals occurring in open herbaceous patches (Happold 1977). In Uganda, in grassland, comprised 14.5% of rodents ($n = 931$, 10 spp.) (Cheeseman & Delany 1979).

Adaptations Terrestrial, nocturnal and crepuscular (Cheeseman 1977). The long claws are used for scratching and digging soil while making tunnels through litter and long grass (Happold 1987). Nests of dry grass are constructed on or just under the surface. As in other species of the genus, the strong odour may be unattractive, and may reduce predation by some terrestrial carnivores but not by predatory birds (Dieterlen 1976b). Normally lives in moist rank dense habitats that are not burned; however, in grassland in Uganda, numbers declined after burning (Cheeseman & Delany 1979).

Foraging and Food Insectivorous and omnivorous. Forages by searching and digging in dead leaves or litter, where ants, termites, other small or large insects, millipedes, earthworms, molluscs and even carrion are devoured opportunistically. May also eat soft fallen fruits and small seeds of certain tree species. In Central African

Republic, the diet (as assessed by volume) varied according to season: in the dry season 60% insects (especially ants), 18% vegetable pulp and 22% miscellaneous (hairs, soil and myriopods etc.); and in the wet season, 46% insects (mainly ants and termites), 38% vegetable pulp, 5% seeds and 10% miscellaneous (hair, soil, etc.) (Genest-Villard 1980). In Uganda, ants and other insects comprised the major proportion of the food ($n = 37$ stomachs; Delany 1964). In S Nigeria, insects were found in 78% of stomachs, earthworms in 85% and plant material in 20% ($n = 61$ stomachs; Funmilayo & Akande 1979b). Similar diets are reported from DR Congo (Verheyen & Verschuren 1966), Rwanda (Misonne 1965a) and Côte d'Ivoire (Heim de Balsac & Aellen 1965).

Social and Reproductive Behaviour Probably solitary. Torn ears and mutilated tails are not uncommon, suggesting intra-specific aggression.

Reproduction and Population Structure Young ♀♀ become pregnant when 40 g (Happold 1987). In Uganda, a relatively high proportion of pregnant/lactating ♀♀ occurred in the wet seasons (Mar–Jun and Sep–Dec; $n = 183$; Delany & Neal 1969, Cheeseman & Delany 1979). In S Nigeria, pregnancies also recorded mainly in the wet season (Mar–Jun), with reduced pregnancy rates in the 'little dry season' (Jul–Aug) and in the 'long dry season' (Nov–Feb) (Happold 1974). Gestation: about 30 days (Genest-Villard 1968). Litter-size usually 2–3. Mean embryo numbers: 2.6 (range 1–3, $n = 8$) in Virunga Mts, DR Congo (Verschuren *et al.* 1983); 3.0 (range 2–5, $n = 13$) in S Nigeria (Happold 1974). At birth, young are precocial, weight ca. 8 g. Animals born in captivity weighed 35 g at three weeks of age (= 50% adult weight), and adult weight when 5–8 weeks (Genest-Villard 1968).

Predators, Parasites and Diseases In grasslands of Rwenzori N. P., Uganda, various species of predatory birds, carnivores (mongooses, genets, servals) and snakes were potential predators of small rodents (Cheeseman & Delany 1979).

Conservation IUCN Category: Least Concern.

A widely distributed and common species.

Measurements

Lophuromys sikapusi

HB: 118.5 (110–130) mm, $n = 10$

T: 74.2 (65–82) mm, $n = 10$

HF: 22.2 (21–23) mm, $n = 10$

E: 16.2 (15–17) mm, $n = 10$

WT: 62.7 (51–79) g, $n = 10$

GLS: 31.2 (29.8–32.6) mm, $n = 10$

GWS: 15.0 (14.4–15.9) mm, $n = 10$

M¹–M³: 5.0 (4.8–5.3) mm, $n = 10$

SW Nigeria (Happold 1974)

Key References Cheeseman & Delany 1979; Dieterlen 1976b; Genest-Villard 1968, 1980; Happold 1974, 1987.

Fritz Dieterlen

Lophuromys woosnami WOOSNAM'S BRUSH-FURRED RAT

Fr. Souris hérissé de Woosnam; Ger. Woosnams Bürstenhaarmaus

Lophuromys woosnami Thomas, 1906. Ann. Mag. Nat. Hist., ser. 7, 18: 146. Mubuku Valley Rwenzori East, Uganda; 6000 ft (1820 m).

Taxonomy Subgenus *Kivumys*. Species-group: *woosnami*. Synonyms: *prittiei*, undescribed (see below). Subspecies: two or three (Dieterlen 1976b). Chromosome number: $2n = 42$, $FN = 72$ (Dieterlen 1976b, Maddalena *et al.* 1989).

Description Medium-sized and slender-bodied rat with a long tail, long ears, long hindfeet and comparatively short claws. Pelage soft and conspicuously glossy; unspeckled. Dorsal pelage brown tinged with olive-grey; hairs reddish-brown at base. Ventral pelage pale brown tinged with reddish. In subadults, reddish colouration of dorsal and ventral pelage is brighter and more intense than in adults. Ears long, naked, rounded at tip. Fore- and hindfeet whitish with comparatively short claws. Hindfoot long (cf. other species in genus). Tail long (ca. 105% of HB), mostly naked with dark bristles, dark above, pale flesh-colour below. Nipples: $1 + 1 = 4$.

Geographic Variation

L. w. woosnami: Rwenzori Mts. HB: ca. 110 mm.

L. w. prittiei: highlands of Kigesi, Uganda; Virunga Mts in Uganda, Rwanda, DR Congo; Nyungwe Forest in Rwanda and Kibira Forest in Burundi. HB: ca. 115 mm.

L. w. undescr.: west of *L. Kivu*, DR Congo. HB: ca. 121 mm.

Similar Species

L. flavopunctatus. Dorsal pelage reddish-brown; E shorter; HF shorter; T much shorter.

Distribution Endemic to Africa. Afromontane–Afroalpine BZ in Uganda, Burundi, Rwanda and DR Congo. Recorded from the Albertine Rift Valley and bordering mountains from Rwenzori Mts in the north to the Itombwe massif (E DR Congo) and mountains of Burundi in the south. Distribution discontinuous, confined to forested mountains on both sides of the Rift Valley; 1800–3880 m.

Habitat Undergrowth in montane forests, cleared areas in forests, old and new bamboo forests, and amongst rocks in afroalpine vegetation (*Senecio*, *Lobelia*).

Abundance Common in suitable habitats and often the most numerous species of small rodents. Commonly syntopic with *L. flavopunctatus*. In many habitats in Kahuzi-Biega N. P., E DR Congo, one species of *Lophuromys* was considerably commoner than the other suggesting inter-specific competition. Percentage occurrence of *L. woosnami* and *L. flavopunctatus* in small mammal communities was, respectively, 25% and 19% in montane secondary forests, 42% and 6% in cleared montane primary forest, 13% and 4% in undisturbed montane primary forest, 56% and 8% in old bamboo, and 20% and 48% in young bamboo with grassy cover (Dieterlen 1976b).

Adaptations Terrestrial long-footed rat; runs with a 'jumping gallop' and good at climbing. This kind of locomotion, as well as the

*Lophuromys woosnami*

long legs, long tail and long ears suggests that these mice are very mobile and probably have a large home-range. Activity is mostly nocturnal (Rahm 1967, Delany 1972). Captive ♀♀ constructed simple nests of dry grass and leaves.

Foraging and Food Omnivorous. Stomach contents contained 40–50% arthropods (and some molluscs) and 50–60% vegetable material, seeds and bulbs (but not green matter) ($n = 15$; Dieterlen 1976b, Verschuren *et al.* 1983). Captive animals preferred meal worms, grasshoppers and dry insect larvae etc., but also ate sweet apples, peanuts and grains of sunflowers. Drinking water is essential.

Social and Reproductive Behaviour Captive animals are tame from the first day of captivity, showing no fear or panic even when handled for the first time. When in captivity for several months, adults and their young live together peacefully and without aggression towards one another. Individuals exhibit mutual grooming. Olfactory communication seems to be important. The typical odour, caused by sebaceous glands in the glossy pelage, probably has a socially stimulating effect (Dieterlen 1976b). Females exhibit 'midwifery' behaviour when a mother is giving birth; they try to get hold of the umbilical cord and, some moments later, to 'steal' and eat the placenta. Young are raised communally, several ♀♀ participating in the care of the young (Dieterlen 1976b); this behaviour is similar to that of *Acomys* spp. (Dieterlen 1962).

Reproduction and Population Structure In Kivu Province, DR Congo, reproduction is seasonal, occurring during the wet

season (Sep–Apr), with peaks in pregnancy rate (80–100%) in Oct–Dec and in Mar–Apr (Dieterlen 1976b). After a transition period in May, pregnancies not recorded during the dry season (Jun–Aug). Gestation: at least 32 days. At birth, young are precocial; postnatal development is rapid. Mean embryo numbers: 1.94 (1–3; mode 2 [84% of total]; $n = 96$). Females and ♂♂ became sexually active when 7–8 weeks old; at this age ♂♂ weigh 36–40 g (testes 10–12 mm). Adult ♂♂ weighing 50–60 g have permanently large testes of 20–25 mm. Sex ratio: 58% ♂♂: 42% ♀♀ ($n = 454$).

Predators, Parasites and Diseases No information.

Conservation IUCN Category: Least Concern.

The forests on the mountains of the Albertine Rift Valley, the only habitat of this species, are fragmented and declining in area. The future of the species depends on adequate protection of these forests.

Measurements

Lophuromys woosnami

HB: 121 (111–135) mm, $n = 20$

T: 123 (114–133) mm, $n = 20$

HF (c.u.): 26.5 (26–28) mm, $n = 20$

E: 22.9 (20–25) mm, $n = 20$

WT: 47 (38–64) g, $n = 20$

GLS: 31.5 (30.3–33.2) mm, $n = 20$

GWS: 14.4 (13.8–15.3) mm, $n = 20$

M¹–M³: 4.7 (4.4–4.9) mm, $n = 20$

DR Congo (Dieterlen 1976b, SMNS)

Key References Dieterlen 1976b, 1987; Kingdon 1974; Verschuren *et al.* 1983.

Fritz Dieterlen

GENUS *Uranomys*

Rudd's Brush-furred Mouse

Uranomys Dollman, 1909. Ann. Mag. Nat. Hist., ser. 8, 4: 551. Type species: *Uranomys ruddi* Dollman, 1909.



Uranomys ruddi.

A monotypic genus widespread in savannas of West and East Africa. The genus is characterized by small size, dorsal pelage composed of coarse brownish brush-like hairs, white ventral pelage and short tail. The skull has pro-odont incisors (except in one form), the palatine bones extend posteriorly to M³ and partly cover the mesopterygoid fossa, the small cheekteeth are similar to those of *Acomys* spp., and there is an enlarged process on the external aspect of the mandibular ramus (Figure 43). Further details are given in the species profile. The genus originally contained seven species (see synonyms below), but is now considered to contain only one species, *Uranomys ruddi*.

The genus is closely related to *Lophuromys* and *Acomys*, and (like these genera) is placed in the subfamily Deomyinae of the Muridae (Musser & Carleton 2005) rather than in the subfamily Murinae as in previous classifications (e.g. Musser & Carleton 1993). Other investigations (biochemical, molecular and karyological) confirm the monophyletic origin of *Uranomys*, *Lophuromys* and *Acomys*. Full details of these relationships are given in Musser & Carleton (2005, and references therein). The single species is *Uranomys ruddi*.

D. C. D. Happold

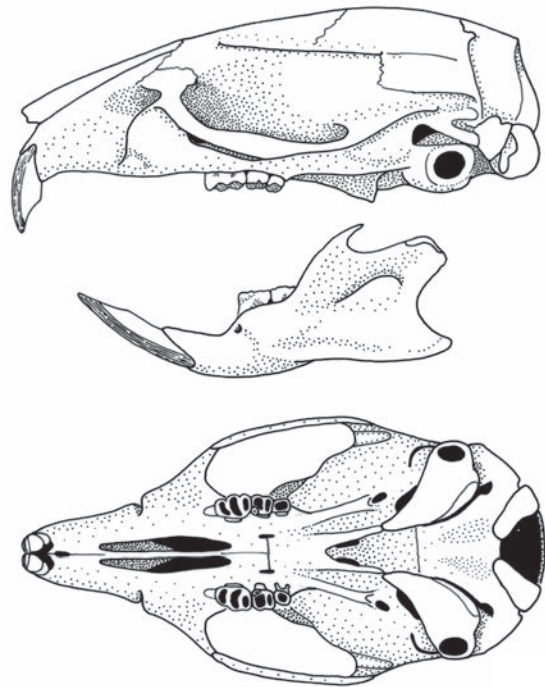


Figure 43. Skull and mandible of *Uranomys ruddi* (HC 1748).

Uranomys ruddi RUDD'S BRUSH-FURRED MOUSE

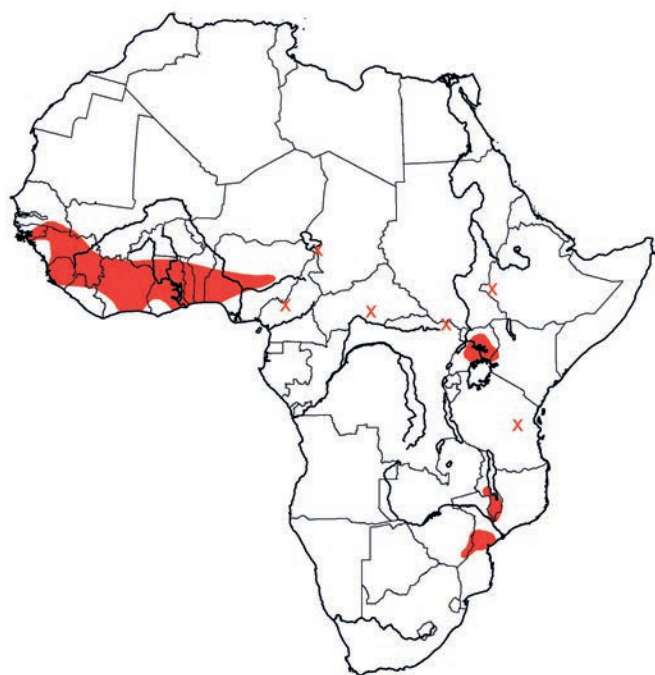
Fr. Souris de Rudd; Ger. Rudds Bürstenfellmaus

Uranomys ruddi Dollman, 1909. Ann. Mag. Nat. Hist., ser. 8, 4: 52. Kirui, Mount Elgon, Kenya. 6000 ft (1820 m).

Taxonomy Now considered as a single species with a very broad distribution (Verheyen 1964a; see also profile Genus *Uranomys*); however, variations in chromosome number perhaps indicate that more than one species is present. Synonyms: *acomyoides*, *foxi*, *oweni*, *shortridgei*, *tenebrosus*, *ugandae*, *woodi*. Subspecies: none. Chromosome number varies geographically: $2n = 50$ (Senegal), $2n = 58$ (Côte d'Ivoire), $2n = 52$ (Central African Republic).

Description Small mouse with small limbs, short tail and stiffened hairs on back and rump. Pelage short and stiff. Dorsal pelage grey to grey-brown, speckled with pale brown and black; hairs dark grey with pale brown tip, or with pale brown terminal band and black tip. Dorsal hairs stiffened as in an artist's brush, and not easily rubbed the wrong way. Dorsal hairs not spiny as in Spiny Mice (*Acomys* spp.). Ventral pelage dirty-white, sometimes tinged with pale cinnamon; colour of flanks merges gradually to colour of ventral pelage. Head rather slim and pointed, with small eyes and small ears. Chin, throat, chest and limbs white. Limbs short. Tail short (ca. 60% of HB), brownish, with scales and numerous very small black bristles. Skin thin and fragile; many individuals have damaged ears, and tail is frequently shortened or completely absent. Incisor teeth pro-odont (although occasionally opisthodont in some juveniles). See also genus profile. Nipples: $3 + 3 = 12$.

Geographic Variation The form *acomyoides* from Ghana has orthodont incisors (Ingoldby 1929 in Musser & Carleton 2005).



Uranomys ruddi

Similar Species

Acomys spp. Dorsal hairs spiny and thicker.

Mus minutoides/musculoides. Smaller, without stiffened hairs.

Distribution Endemic to Africa. Guinea Savanna BZ, Northern Rainforest–Savanna Mosaic, Eastern Rainforest–Savanna Mosaic, and parts of Zambezian Woodland BZ. In West Africa, recorded from Sierra Leone, Gambia, Guinea, Liberia, Côte d'Ivoire, Ghana, Togo, Benin and Nigeria. In central and eastern Africa, recorded in Uganda, Zimbabwe, Mozambique and Malawi. Isolated records in N Cameroon, Central African Republic, Chad, NE DR Congo, C Tanzania and W Ethiopia. May be more widespread than records indicate (see Abundance). Distribution disjunct.

Habitat Grasslands. The rarity of the species in most places, and its abundance in a few localities (see below), suggest that the preferred habitat has abundant grasses, few trees and moist soil, which provides moist or semi-swampy conditions. Also occurs in farmland (where soil is moist and friable) and oil palm plantations (where there are moist grasses and grass litter). One individual in Malawi was found 'in hole of Mole-rat on wooded hills', and others were found close to a river swamp where there were many ant and termite mounds (Hanney 1965).

Abundance Generally a rare species and seldom encountered. Not recorded from many savanna habitats and rare in others. However, is quite common at a few study sites, e.g. comprised 29% of small rodents in grass savanna at Lamto, Côte d'Ivoire ($n = 745$; Bellier 1968), 31% in farmland at Ibadan, Nigeria ($n = 710$; Happold 1974), 44% in grass swamp at Ibadan ($n = 86$; D. C. D. Happold unpubl.) and 55% in grass savanna at Dabou, Côte d'Ivoire ($n = 838$; Bellier 1968). Comprised 8% ($n = 1448$) in oil palm plantation in Côte d'Ivoire (Bellier 1968). Population numbers not adversely affected by burning of grasses at Ibadan, Nigeria, probably because of fossorial habits (D. C. D. Happold unpubl.).

Adaptations Nocturnal and crepuscular; terrestrial. Brush-furred Mice dig burrows, using their short strong feet. An excavated nest (in Côte d'Ivoire) about 15 cm below ground had a nest chamber 6–8 cm in diameter lined with fresh cut grass; another tunnel descending to about 30 cm below ground (Bellier 1968). Entrance holes were plugged. Brush-furred Mice seem to be partly fossorial; specimens in captivity burrowed under litter and grass when disturbed, and they blocked the entrances to their burrows and nestbox with soil which was sometimes glued together with fluid (? saliva) (D. C. D. Happold unpubl.). The pro-odont incisor teeth may be used for catching and holding insect prey, in a similar manner to shrews.

Foraging and Food Primarily insectivorous: the contents of two stomachs contained adult insect remains, dipteran larvae and ant pupae (Malawi; Hanney 1965). Vegetable foods include cassava

(manioc) and bulbs of savanna plants (Bellier 1968). Food has not been found in burrows.

Social and Reproductive Behaviour Little information. Burrows in Côte d'Ivoire were inhabited by two adults (Bellier 1968). In captivity several individuals live together amicably.

Reproduction and Population Structure In Côte d'Ivoire (Bellier 1968), pregnancies recorded in all months except Jan (early dry season) and juveniles in all months except Oct and Feb. Peak of reproductive activity in late wet season (Aug–Dec incl.). Seasonal variation in mean number of embryos: 4.3–5.7 (late wet season), 2.6–3.7 (dry season and early wet season) (Bellier 1968). Minimum weight at pregnancy: 22 g (Happold 1974). Sex ratio (live trapping) was 3 : 1 (Nigeria; D. C. D. Happold unpubl.).

Population structure unknown. At Ibadan, Nigeria, during a 5-month study, 72% of individuals were caught once and 18% were caught twice (n = 39 individuals), suggesting a rapid turnover of the population (D. C. D. Happold unpubl.).

Predators, Parasites and Diseases Preyed upon by Barn Owls *Tyto alba* (Rosevear 1969).

Conservation IUCN Category: Least Concern.

The widespread distribution suggests that the species is not threatened. However, its rarity (in most habitats) and loss of suitable habitat may be cause for concern.

Measurements

Uranomys ruddi
HB: 108 (101–119) mm, n = 15
T: 63 (55–68) mm, n = 15
HF: 17 (16–18) mm, n = 15
E: 13 (12–14) mm, n = 15
WT (♂♂): 37 (31–51) g, n = 5
WT (♀♀): 30 (22–31) g, n = 5
GLS: 25.1 (24.0–26.4) mm, n = 15
GWS: 12.3 (11.3–13.4) mm, n = 15
M¹–M³: 4.1 (3.8–4.3) mm, n = 15
Measurements: Côte d'Ivoire (MNHN)
Weight: Nigeria (Happold 1987)

Key References Bellier 1968; Happold 1974, 1987; Rosevear 1969; Verheyen 1964a.

D. C. D. Happold

Subfamily GERBILLINAE – Gerbils and Jirds

Gerbillinae Gray, 1825. Ann. Philos., n. s., 10: 342.

| | | |
|-----------------------------------|----------------------|--------|
| <i>Ammodillus</i> (1 species) | Ammodile | p. 262 |
| <i>Desmodilliscus</i> (1 species) | Dwarf Gerbil | p. 264 |
| <i>Desmodillus</i> (1 species) | Short-tailed Gerbil | p. 266 |
| <i>Gerbilliscus</i> (12 species)* | Gerbils | p. 268 |
| <i>Gerbillurus</i> (4 species) | Hairy-footed Gerbils | p. 287 |
| <i>Gerbillus</i> (36 species) | Gerbils | p. 295 |
| <i>Meriones</i> (3 species) | Jirds | p. 333 |
| <i>Microdillus</i> (1 species) | Pygmy Gerbil | p. 339 |
| <i>Pachyuromys</i> (1 species) | Fat-tailed Gerbil | p. 341 |
| <i>Psammomys</i> (2 species) | Sand Rats | p. 343 |
| <i>Sekeetamys</i> (1 species) | Bushy-tailed Jird | p. 347 |
| <i>Taterillus</i> (8 species) | Gerbils | p. 349 |

*Formerly *Tatera*

Members of this large subfamily, numbering 16 genera and about 101 species (Musser & Carleton 2005), occur throughout much of Africa and across the Palaearctic desert and steppe, from Asia Minor and the Middle East to southern Mongolia and northern China. In Africa, there are 12 genera and 71 species (see list above). Gerbils mostly live in arid and semi-arid environments, mostly in areas of sparse vegetation. Within Africa, they occur in many biotic zones except the Rainforest and Afroalpine BZs. Typical habitats include sandy and clay deserts, dunes and alluvium with meagre grass or brush cover, gravelly plains and semi-deserts, and a wide mixture of grasslands and woodlands from very dry and open to moderately moist. Certain forms, such as *Pachyuromys* and some *Gerbillus*, thrive in some of Africa's bleakest, seemingly inhospitable, habitats. In such environments, gerbils fill a terrestrial and largely granivorous niche

(the herbivorous *Psammomys* is a notable exception); most species are nocturnal and a few are diurnal (*Psammomys* and some *Meriones*).

Most gerbilline genera (12 of 16) contain species with distributions in Africa, and many are endemic to the continent (*Ammodillus*, *Desmodilliscus*, *Desmodillus*, *Gerbilliscus* [formerly *Tatera*], *Gerbillurus*, *Microdillus*, *Pachyuromys*, *Taterillus*). Three genera have distributions that include Africa and parts of the Middle East or Asia (*Gerbillus* [including *Dipodillus*], *Meriones*, *Psammomys*), and one of these has its greatest number of species within Africa (*Gerbillus* – 39 of 51 spp.). *Meriones* is the only genus that contains more species with ranges outside of the continent (13 of 17); the four species distributed entirely or partially in Africa occur only along the Mediterranean coast. *Psammomys*, too, has a predominantly North African distribution but also reaches to the near Middle East and Arabian Peninsula. Clearly, African environments have figured prominently in the evolutionary diversification of the subfamily, and the continent is considered by some to be its place of origin (e.g. Lay 1972). The present-day concentration of the early-branching clades of the Gerbillinae within the sub-Saharan region (namely Gerbillurina, Taterillina and Ammodillini (Pavlinov *et al.* 1990) is consistent with this biogeographic interpretation.

Most African gerbils are small to medium in body size, but extremes of very small (*Desmodilliscus*, some *Gerbillus*) and large (*Gerbilliscus*, *Psammomys*, some *Meriones*) are also represented. Body form ranges from stout and compact (*Pachyuromys*) to slender and gracile (*Gerbillus*, *Taterillus*). Counter-shading is generally pronounced, the dorsal pelage is pale sandy to saturated brown, and the ventral pelage is white. The expanded auditory bullae impart a relatively large and wide shape to the head. Pinnae are small, rounded and well furred in many species,

or larger, ovate and sparsely covered in some, especially the taterillines *Gerbillus* and *Taterillus*; conspicuous white to buffy postauricular patches occur in some (*Desmodilliscus*, *Pachyuromys*). The elongated metatarsal bones of the hindfoot reflect the running and semi-saltatory locomotion of most species, although none is strictly bipedal as in the dipodids *Allactaga* and *Jaculus*. The plantar surface is naked, moderately furred, or so densely furred as to obscure the plantar pads. The tail may be longer than, or about equal to the head and body, or notably shorter (as in *Desmodilliscus* and *Pachyuromys*); it is moderately to densely haired in most forms, with a terminal black pencil or tuft in some species (*Taterillus* and *Meriones*). A mid-ventral sebaceous gland is present in many species, and is especially well-developed in ♂♂. There are eight nipples (arranged as pectoral, post-axillary and two inguinal pairs) or six nipples (pectoral pair absent).

The head and postcranial skeleton exhibits diagnostic traits of the subfamily: supraorbital shelf present and well developed; zygomatic plate broad and dorsal notch deep; lacrimal enlarged, forming a conspicuous ledge over the anterior orbit; mesopterygoid fossa narrowly V-shaped and parapterygoid fossae compressed and cavernous; anterior palatal foramina and posterior palatine foramina extremely long and slit-like; optic foramen as large as sphenoidal fissure; stapedia foramen present, penetrating the wall of the tympanic bulla rather than the petrotympanic fissure; sphenofrontal foramen and accessory foramen ovale absent (except *Tatera*); angular process of mandible deflected laterally; auditory bullae inflated, both ectotympanic and mastoid chambers, and malleus of the perpendicular type; entepicondylar foramen present (except *Tatera*); scapula with third scapular fossa; vertebral column with 12 thoracic vertebrae and seven lumbar vertebrae (Lay 1972, Carleton 1980, Pavlinov 1980, Carleton & Musser 1984, Pavlinov *et al.* 1990). In all African species, the molars are rooted, anchored by accessory rootlets in most species, and their occlusal pattern is lophate, planar or prismatic; protoconulid present on M₁, distinct from or fused with anteroconid; M₃ greatly reduced and cylindriciform, the posterior lamina (hypoconid and entoconid) of M₃ absent; upper incisors with single groove (smooth in *Psammomys*) (Ellerman 1941, Rosevear 1969, Pavlinov 2001). Other notable characters of those Gerbillinae studied include: the glans penis is of the complex type; preputial glands are generally absent, remainder of accessory reproductive gland of ♂ is complete; the stomach is single-chambered and hemiglandular; and the stapedia artery lacks supraorbital and mandibular branches, the orbital blood supply instead is formed by the infraorbital branch (Arata 1964, Vorontsov 1967, Bugge 1970).

Morphology of the auditory bullae has figured prominently in the taxonomic and phylogenetic understanding of gerbilline rodents (Lay 1972, Pavlinov 1980, Pavlinov *et al.* 1990). Evolutionary increases in pneumatization of the mastoid portion are especially significant and have given rise to spectacular middle ear anatomies, such as those that characterize *Pachyuromys duprasi* and *Meriones crassus*. Enlargement of the middle ear chambers lessens impedance of air space behind the tympanic membrane and thereby enhances sensitivity to relatively low sound frequencies (Lay 1972, 1993, Webster & Webster 1984). These volumetric adaptations – coupled with modifications in the ossicular lever system, expanded surface area of the tympanic and accessory tympanic membranes, and acoustic specializations of the inner ear – constitute a clever predator-detection system for animals

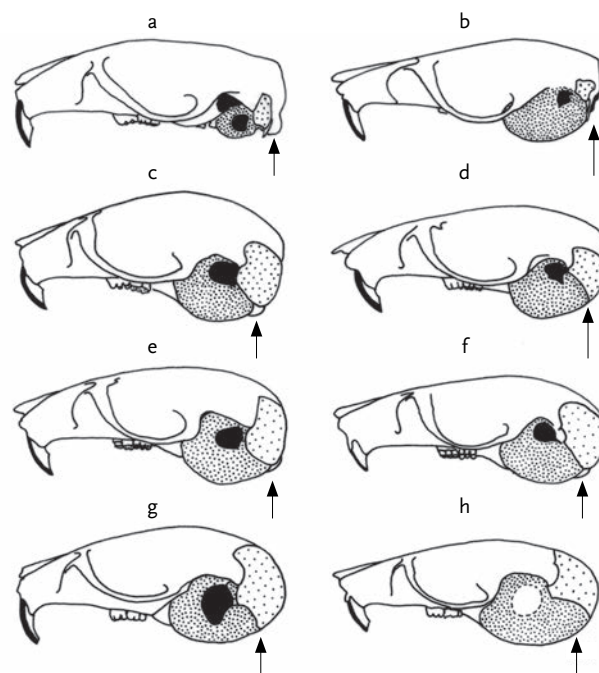


Figure 44. Structure of the auditory bulla in several genera of Gerbillinae to show relative and comparative sizes of tympanic bulla and mastoid. (a) *Arvicanthis niloticus* (Murinae) without any enlargement of auditory bulla, (b) *Gerbillus*, (c) *Microdillus*, (d) *Gerbillus*, (e) *Meriones*, (f) *Sekeetamys*, (g) *Desmodilliscus*, (h) *Pachyuromys*. Dark stipple = tympanic bulla. Light stipple = mastoid. Arrows indicate position of occipital condyles (not visible in lateral view). Variations between genera include size of tympanic bulla and mastoid (relatively and comparatively), size of bulla in relation to GLS, and position of posterior end of auditory bulla to the posterior end of the occipital condyles (see text for further details). Species within a genus may show slight variation to the generalized genus condition shown here. The condition in Dipodidae (*Allactaga*, *Jaculus*) is similar to that of *Desmodilliscus*. (Based on original illustration by D. C. D. Happold.)

living in open environments and must have contributed importantly to the ecological successes of the subfamily (Lay 1972). Indeed, the Gerbillinae contains more species indigenous to the great Saharo-Gobian realm of Africa and Asia than any other group of Rodentia (Petter 1961, Lay 1991, Shenbrot *et al.* 1999b). Parallel changes in middle ear anatomy characterize other rodent lineages that have radiated within desert and semi-arid biomes, in both North America (Heteromyidae) and Afro-Asia (Dipodidae) (Figure 44).

Although morphological evidence supporting the monophyly of Gerbillinae is substantial (Carleton & Musser 1984, Pavlinov *et al.* 1990), their phylogenetic stature as a subfamily of Muridae is a relatively recent apprehension, stemming from both palaeontological and molecular investigations. Gerbils were traditionally grouped with the Cricetidae in those classifications that maintained Muridae and Cricetidae as separate families (e.g. Miller & Gidley 1918, Simpson 1945, Misonne 1974), or accorded their own family status as Gerbillidae (Tullberg 1899, Chaline *et al.* 1977, Pavlinov *et al.* 1990). Phyletic interpretations of nuclear and mitochondrial DNA sequences, however, cladistically affiliate gerbillines with murines and deomyines (Martin *et al.* 2000, Michaux & Catzeflis 2000, Michaux *et al.*, 2001). Using molecular-clock estimates, Michaux *et al.* (2001) suggested that the divergence of Gerbillinae occurred during the early to middle Miocene, about 18 to 16 mya years ago.

Such divergence times are wholly reasonable in the context of the rich fossil history of gerbils. Their origin is convincingly linked to myocricetodontines, an extinct group known from the Miocene of both Africa and Asia and believed to represent the ancestral stock of the subfamily (Jaeger 1977b, Tong 1989, Lindsay 1994, Wessels 1996). Tong & Jaeger (1993) suggested that the Murinae were also derived from an early myocricetodontine, with the split between the two groups transpiring around 16 mya years ago. The oldest true gerbilline so far known from Africa is *Protatera*, from the late Miocene of Morocco (Jaeger 1977b); representatives of living genera appear in the late Pliocene and are commonplace in Pleistocene faunas (e.g. Lavocat 1978, Denys 1987a, 1989a, Senut *et al.* 1992, Avery 1998).

Generic interrelationships are relatively well understood, as set forth in the comprehensive monograph of Pavlinov *et al.* (1990, see also Pavlinov 2001), which serves as the basis for recognizing the following tribes (-ini) and subtribes (-ina) among African genera

(ranks as adapted by McKenna & Bell 1997). Here (in contrast to Musser & Carleton 2005), *Dipodillus* is considered as a synonym of *Gerbillus* (see *Gerbillus* profile) and hence 12 genera (Table 22) are recognized as follows:

- Taterillini: Gerbillurina (*Desmodillus*, *Gerbillurus*); Taterillina (*Gerbilliscus*, *Taterillus*).
- Ammodillini: (*Ammodillus*).
- Gerbillini: Desmodilliscina (*Desmodilliscus*); Gerbillina (*Gerbillus* [including *Dipodillus*], *Microdillus*); Pachyuromyina (*Pachyuromys*); Rhombomyina (*Meriones*, *Psammomys*, *Sekeetamys*).

The profiles for each genus, and for each species within each genus, are given alphabetically, not by their tribal and subtribal affiliations.

Michael D. Carleton & Guy G. Musser

GENUS *Ammodillus*
Ammodile

Ammodillus Thomas, 1904. Ann. Mag. Nat. Hist., ser. 7, 14: 102. Type species: *Gerbillus imbellis* de Winton, 1898.

Ammodillus is a monotypic genus found only in Somalia. It is very similar to *Gerbillus*, and distinguished from *Gerbillus* by special skull characters (especially the lack of a coronoid process on the mandible, and the posterior convergence of the upper cheekteeth). Characters

of the genus are given in the species account below. The only species is *Ammodillus imbellis*.

D. C. D. Happold

Table 22. Genera in the subfamily Gerbillinae. Arranged in order of increasing head and body length.

| Genera | HB
(mean or
range) (mm) | Tail
(% of HB) | Number of
cheekteeth | Bullae
(% of GLS) | Molar
form ^b | Position of posterior palatine
foramina | |
|--|-------------------------------|-------------------|-------------------------|----------------------|----------------------------|---|--|
| <i>Desmodilliscus</i> (1 sp.) | 55 | 75–80% | 3/2 | ca. 40% | Cuspidate | Mid M ² to anterior of M ¹ | |
| <i>Microdillus</i> (1 sp.) | 72 | 80% | 3/3 | 39% | Cuspidate | Mid M ² to front margin of M ¹ | |
| <i>Gerbillus</i> (36 spp.) | Mostly 80–129 ^a | 105–160% | 3/3 | 29–36% | Cuspidate | Posterior M ² to first row of cusps of M ¹ | |
| <i>Gerbillurus</i> (4 spp.) | 96–105 | 120–140% | 3/3 | ca. 30% | Cuspidate | Posterior M ² to mid M ¹ | |
| <i>Ammodillus</i> (1 sp.) | 99 | 145% | 3/3 | 33–37% | Cuspidate | Front margin to hind margin of M ² . Small | |
| <i>Pachyuromys</i> (1 sp.) | 108.3 (93–121) | 54% | 3/3 | 47% | Cuspidate
to laminate | Mid M ² to mid M ¹ | |
| <i>Desmodillus</i> (1 sp.) | 110 | 74–80% | 3/3 | 41% | Cuspidate | Posterior M ³ to mid M ¹ | |
| <i>Taterillus</i> (8 spp.) | 107–116 | 130–150% | 3/3 | 26–30% | Cuspidate
to laminate | Posterior M ² to front margin M ¹ | |
| <i>Sekeetamys</i> (1 sp.) | 118 | 120% | 3/3 | 33% | Prismatic | Mid M ² to mid M ¹ | |
| <i>Psammomys</i> (2 spp.) | 122–160 | 70–86% | 3/3 | 32% | Prismatic | Anterior M ² to posterior M ¹ (very short) ^d | |
| <i>Gerbilliscus</i> (12 spp.) ^c | 128–185 | 95–ca. 130% | 3/3 | 24–31% | Cuspidate | Posterior M ² to mid M ¹ | |
| <i>Meriones</i> (3 spp.) | 136 | 95–100% | 3/3 | 32–40% | Prismatic | Mid M ² to mid M ¹ | |

^a A few species of *Gerbillus* have a mean HB of less than 80 mm (*G. brockmani* 78 mm; *G. juliani* 63 mm; *G. henleyi* 65 mm; *G. nanus* 72 mm).

^b Cuspidate but often laminate in older animals, with transverse sets of cusps joining to form single transverse occlusal surface.

^c Formerly *Tatera*.

^d Shallow grooves may extend anteriorly to posterior end of anterior palatal foramina.

Ammodillus imbellis AMMODILE (WALO)

Fr. Ammodile; Ger. Walo

Ammodillus imbellis (de Winton, 1898). Ann. Mag. Nat. Hist., ser. 7, 1: 249. Goodar, Somalia.



Ammodillus imbellis.

Taxonomy Originally described in the genus *Gerbillus*, but later placed in a new genus, *Ammodillus* (see below). Synonyms: none. Chromosome number: 2n = 18 (Capanna & Merani 1981).

Description Small gerbil with a long tail ending in a brown pencil. Dorsal pelage reddish-fawn to brownish-yellow; hairs grey at base, with reddish fawn terminal band and black tip. Flanks paler and clearer. Ventral pelage white. Hairs of eyebrows, cheeks and upper surface

of forelimbs tipped with grey. White supraorbital and postauricular patches. Fore- and hindfeet white. Soles of hindfeet naked. Tail very long (ca. 145% of HB), dark above, paler below, slightly haired; brown hairs (8–10 mm long) on terminal one-third of upper surface form conspicuous pencil. Two skull characters are unique: the molar rows converge posteriorly (more so than in any other genus of the gerbils) and tend to be laminate rather than cuspidate, and there is no coronoid process on the mandible (Roche & Petter 1968, Funaioli 1971 in Nowak 1999). Incisors strongly opisthodont (Figure 45). Nipples: 1 + 2 = 6.

Geographic Variation None recorded.

Similar Species

Gerbillus brockmani. Smaller (HB: 71–84 mm).
G. somalicus. HF shorter (24–25 mm. Neither of these species has the skull characters of *Ammodillus* noted above.

Distribution Endemic to Africa. Somalia–Masai Bushland BZ. Recorded only from Somalia and E Ethiopia.

Habitat In S Somalia, found in coastal steppe (Capanna & Merani 1981). In E Ethiopia, found ‘in sandy soil close to wells’ at Gerlogobi (Thomas 1904a). Digs burrows in sandhills (near El Bur).

| | Pencil at tip of tail | Notes |
|--|--------------------------|---|
| | Absent | Sahel Savanna Zone; Mauritania to Chad |
| | Absent | Somalia |
| | Small to well-developed | Widespread in North, West and East Africa |
| | Absent to well-developed | South Africa, Namibia |
| | Well-developed | Somalia, Ethiopia |
| | Absent | North Africa |
| | Absent | South-West Arid BZ |
| | Well-developed | Widespread in savannas of West, central and East Africa north of Rainforest Zone |
| | Very well-developed | NE Africa |
| | Present | North Africa |
| | Absent to well-developed | Widespread in semi-arid and savanna habitats south of Sahara. Slight groove on each upper incisor |
| | Small | North Africa. Slight groove on each upper incisor |

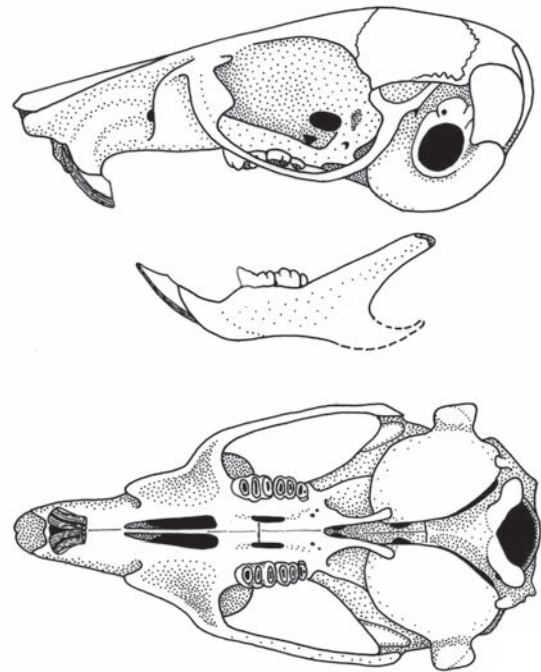


Figure 45. Skull and mandible of *Ammodillus imbellis* (MZUF M4940).

Abundance Very rare. Only known from a few specimens from seven localities.

Remarks The lack of a coronoid process on the mandible results in a weak bite (Nowak 1999); this suggests that *Ammodillus* can only eat soft foods. No information on diet. Found in small colonies on sandhills (A. Simonetta pers. comm.). Individuals are recorded to fight amongst themselves (Nowak 1999). One specimen was obtained from the stomach of a viper (*Bitis* sp.).

Conservation IUCN Category: Data Deficient.

Measurements

Ammodillus imbellis

HB: 99.3 (84–111) mm, n = 15

T: 145.1 (134–160) mm, n = 11

HF: 27.8 (26–29) mm, n = 15

E: 15.8 (14–18) mm, n = 12

WT: n. d.

GLS: 31.4 (30.1–32.7) mm, n = 12

GWS: 15.3 (14.7–16.5) mm, n = 12

M¹–M³: 4.4 (4.1–4.6) mm, n = 13

Auditory bulla: 10.5 mm, n = 1*

Somalia (Roche & Petter 1968)

*BMNH



Ammodillus imbellis

Key Reference Roche & Petter 1968.

D. C. D. Happold

GENUS *Desmodilliscus*

Brauer's Dwarf Gerbil

Desmodilliscus Wettstein, 1916. Anz. Akad. Wiss. Wien 53: 153. Type species: *Desmodilliscus braueri* Wettstein, 1916.

Desmodilliscus is a monotypic genus endemic to Africa, distributed throughout the Sahel Savanna BZ from Mauritania and Senegal to Sudan. The characters of the genus are those given below in the species account. The small overall size and the relatively short tail are the main external characters, but skull shape and reduction in the

number of cheekteeth (3/2) are unique among the Muroidea. Dental formula: I ¹/₁, C ⁰/₀, P ⁰/₀, M ³/₂ = 14.

L. Granjon

Desmodilliscus braueri BRAUER'S DWARF GERBIL (POUCHED GERBIL)

Fr. Gerbille naine de Brauer; Ger. Brauers Zwergrenmaus

Desmodilliscus braueri Wettstein, 1916. Anz. Akad. Wiss. Wien 53: 153. South of El Obeid, Sudan.

Taxonomy Setzer (1969) recognized three subspecies, but Rosevear (1969) and Hutterer & Dieterlen (1986) stated there was morphological homogeneity throughout its range. Synonyms: *buchanani*, *fuscus*. Subspecies: none. Setzer (1969) recognized three subspecies, but Rosevear (1969) and Hutterer & Dieterlen (1986) indicated that there is morphological homogeneity throughout the range and therefore no subspecies are recognized here. Chromosome number: 2n = 78, aFN = 104 (Senegal; Granjon *et al.* 1992).

Description Very small gerbil. Dorsal pelage sandy-grey; hairs blackish-grey at base, with sandy subterminal band and minute dark tip, giving a speckled and relatively dark effect. Hairs of the flanks white at base with sandy tip. Ventral pelage entirely white. Head relatively large with short ears, big eyes and white cheeks. White stripe above and behind the eyes, and white postauricular patch. Hindfeet slender; forefeet with a slight covering of short white hairs; soles of hindfeet naked. Tail short (ca. 65–75% of HB), covered with short hairs, but without any pencil. Skull: incisor teeth with curved



Desmodilliscus braueri.

front face, each with single deep groove situated laterally; very inflated tympanic bullae and mastoids that extend well posteriorly to the occipital condyles; palate broad; posterior palatal foramina very wide extending anteriorly to M¹ and to within about 1 mm of the anterior palatal foramina. Unique in possessing only two molars on the mandible (see genus profile above) (Figure 46). Nipples: 2 + 2 = 8.

Geographic Variation None recorded.

Similar Species No other species of gerbil has such a small head and body length (Table 22), and no other species of gerbil has only two cheekteeth in each ramus of the mandible.

Distribution Endemic to Africa. Sahel Savanna BZ. Widespread, most records being between 12°N and 18°N. Recorded from Mauritania and Senegal to Sudan, through Mali, Burkina, Niger, Nigeria, N Cameroon and possibly Chad (Heim de Balsac 1967b, Hutterer & Dieterlen 1986). Geographic range may be extending southwards, due to desertification (Duplantier *et al.* 1997).

Habitat Scrub savannas with sparse vegetation, especially on indurate sandy or sandy-clay soils, often with gravel. In Senegal, found in the northern *Acacia*-savanna, receiving an annual rainfall of 200–500 mm (Heim de Balsac 1967b, Poulet 1984).

Abundance Probably common to very abundant in suitable habitats (although difficult to catch in traps). Common in owl pellets in some localities of N Mali (Heim de Balsac 1967b). Dozens of these gerbils seen during a few hours of night driving in NW Mali in Nov 1999 (L. Granjon & B. Sicard unpubl.). Said to be much less abundant than syntopic *Taterillus* in N Senegal, with an estimate of 2–4 individuals/ha (at maximum) (Poulet 1984); in the same region, its abundance may vary inversely with that of other rodents, i.e. high during droughts and low after heavy rainfalls (Poulet 1978).

Adaptations Terrestrial and nocturnal. Lives in a small, shallow, but complex burrow with up to 13 entrances, possibly inhabited by groups of individuals (N Senegal; Poulet, 1984).

Foraging and Food No information.

Social and Reproductive Behaviour Most probably a social, or even colonial, species (Poulet 1984).

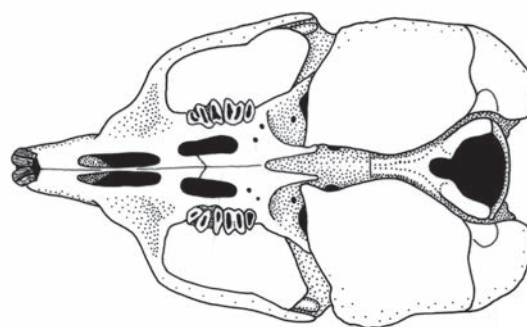
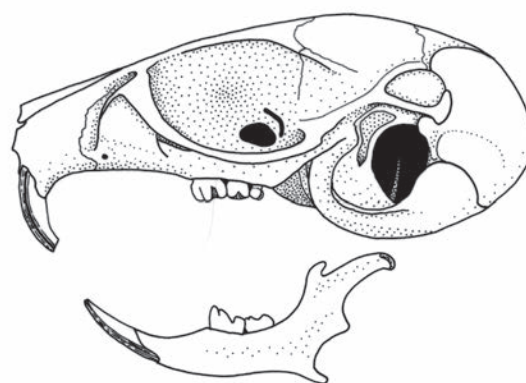
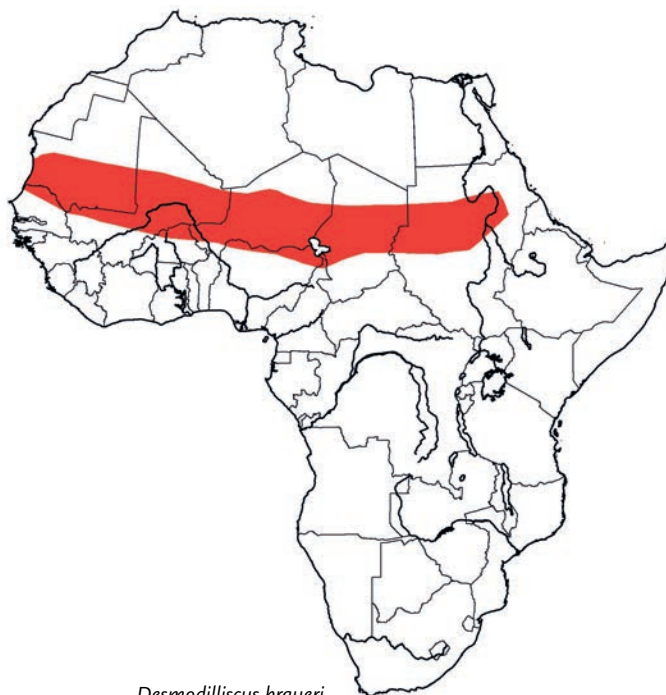


Figure 46. Skull and mandible of *Desmodilliscus braueri* (BMNH number not recorded).



Desmodilliscus braueri

Reproduction and Population Structure In captivity, reproduction observed only between Jun and Aug in Senegal (corresponding to the end of dry season and beginning of wet season). Gestation: 26 days. Litter-size: 2 and 3 (n = 8 litters). Weight at birth around 0.9 g. Weaned at 28 days, at a weight of 3–4 g (Poulet 1984).

Predators, Parasites and Diseases Locally preyed on extensively by Barn Owls *Tyto alba* (Heim de Balsac 1967b, Poulet 1984). Also preyed on by wild cats, foxes and snakes (e.g. *Eryx mulleri*; Poulet 1984).

Conservation IUCN Category: Least Concern.

Measurements

Desmodilliscus braueri

HB: 55.4 (41–74) mm, n = 29

T: 40.1 (33–49) mm, n = 29

HF: 14.1 (13.5–15) mm, n = 23

E: 8.6 (7–11) mm, n = 25

WT: 9.6 (6–14) g, n = 19

GLS: 22.1 (20.4–23.1) mm, n = 17

GWS: 12.8 (11.7–13.3) mm, n = 14

M¹–M³: 3.2 (2.9–3.4) mm, n = 18

Auditory bulla: 9.0, 9.9 mm, n = 2*

Burkina, Niger, Cameroon, Sudan (Hutterer & Dieterlen 1986)

*BMNH

Key References Hutterer & Dieterlen 1986; Poulet 1984.

L. Granjon

GENUS *Desmodillus* Cape Short-tailed Gerbil

Desmodillus Thomas and Schwann, 1904. Abstr. Proc. Zool. Soc. Lond. 1904 (2): 6. Type species: *Gerbillus auricularis* Smith, 1834.



Desmodillus auricularis.

Monotypic genus widespread in the South-West Arid BZ. The genus is characterized by small size (mean HB 110 mm), short tail (mean 84 mm and shorter than head and body) without any pencil or tuft, and short ears. Skull characters include very large tympanic bullae that extend posteriorly to the occiput, short zygomatic plate, long slender incisors each with a shallow groove. M¹ has three rows of cusps, M² has two rows of cusps, M³ has single cusp (Figure 47). The form of the bullae is quite different to that of *Gerbillus* and *Gerbilliscus* (formerly *Tatera*) (see Figure 44). Although larger than sympatric *Gerbillus*, it is smaller than *Gerbilliscus* (formerly *Tatera*) in southern Africa. Fossil forms have been found back to the Pleistocene

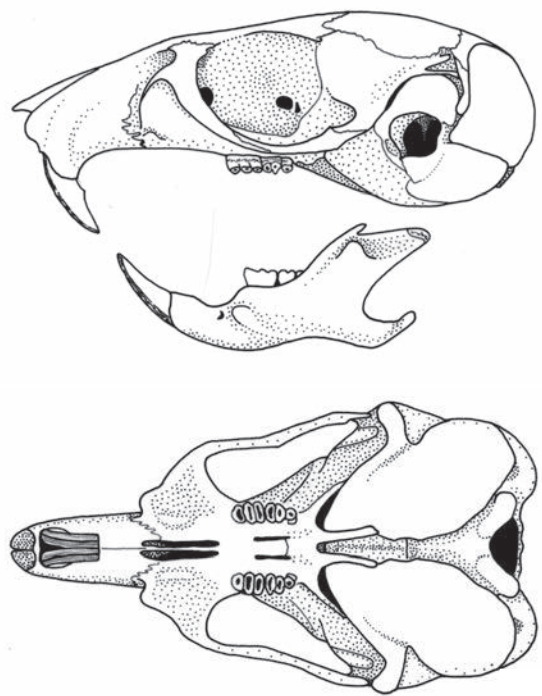


Figure 47. Skull and mandible of *Desmodillus auricularis* (BMNH 25.1.2.76).

in South Africa (Avery 1998) and Namibia (Senut *et al.* 1992, Musser & Carleton 2005). The single species is *Desmodillus auricularis*.

Jan A. J. Nel

Desmodillus auricularis CAPE SHORT-TAILED GERBIL (NAMAQUA GERBIL)

Fr. Gerbille à queue courte; Ger. Kurzschwanz-Rennmaus

Desmodillus auricularis (Smith, 1834). S. Afr. Quart. J., ser. 2, 2: 160. Kamiesberg, South Africa.

Taxonomy Originally described in the genus *Gerbillus*. Synonyms: *brevicaudatus*, *caffer*, *hoeschi*, *pudicus*, *robertsi*, *shortridgei*, *wolffi*. Subspecies: none. Chromosome number: $2n = 52$.

Description Small, stockily built gerbil with fine, soft, dense pelage. Dorsal pelage variable, ochrous-orange to tawny-brown; hairs slate-grey at base, ochrous-yellow in middle, with dark tip on some hairs. Ventral pelage, including chin and throat, pure white. Head large, with thickened nose, long black vibrissae and large eyes. Ears small, oval and flesh-coloured. Distinctive white postauricular patch; smaller less conspicuous supraorbital and suborbital patches. Fore- and hindlimbs short and thick, with short white hairs on upper surfaces of feet; four digits on forefeet, five on hindfeet; hindfeet with hairy soles. Tail of moderate length (ca. 75–80% of HB), same colour as dorsal pelage (with dark tip in darker coloured individuals); without pencil. Skull characterized by the greatly enlarged auditory bullae (ca. 41% of GLS, larger as percentage of GLS than in most other gerbillines). Nipples: $2 + 2 = 8$. Females weigh on average 20% less than ♂♂.

Geographic Variation None recorded.

Similar Species *Gerbillurus* spp. Smaller mean head and body length; tail longer (absolute and as percentage of HB length); pencil at end of tail (in some species); smaller bullae (ca. 30% of GLS).

Distribution Endemic to Africa. South-West Arid BZ (Kalahari and Namib Deserts, Karoo) and peripherally in the extreme south of the Zambezi Woodland and South-West Cape BZs. Widely distributed in Namibia (except NE), Botswana (except N and parts of E), arid parts of South Africa, and marginally in SW Angola. Recorded from near sea level to ca. 1600 m (extrapolated from distribution map in De Graaff 1981).

Habitat Favours calcareous ground, fine soils or consolidated sand (sometimes covered in pebbles) with a sparse cover of grass or low shrub. In the southern parts of the Kalahari and Little Namaqualand, more common in calcareous ground or outcrops and fringes of pans. Avoids dense grassland or thick scrub.

Abundance Common in suitable habitat. Comprises 4.95–5.5% of small mammals in SW Kalahari (Nel & Rautenbach 1975, J. A. J. Nel unpubl.), but with clear differences in abundance in different micro-habitats and at different times (Nel 1978). Large fluctuations in numbers rarely occur.

Adaptations Nocturnal and terrestrial. Locomotion is non-saltatorial. The greatly enlarged auditory bullae afford acute hearing and probably allow gliding owls to be located (Lay 1972). Burrows are extensive and complicated with 1–7 openings, blind alleys and storage chambers; they are 300–600 mm deep (sometimes deeper) and burrow diameter is ca. 53 mm (Nel 1967, Smithers 1971). At

*Desmodillus auricularis*

ambient temperatures of 11–30 °C, deep body temperature (T_b) can be kept nearly constant (varies by 0.5 °C in ♂♂, 0.1 °C in ♀♀) (Nel & Rautenbach 1977). Renal concentrating ability is very good (urine concentration up to 6.1 mOsmol/kg), and evaporative water loss at low relative humidity is very low (Christian 1978, 1979b, Buffenstein *et al.* 1985). These gerbils are independent of free water, and this allows breeding at times when other sympatric species are reproductively inactive (Christian 1979b). They can also store fat in the tail when conditions are good; hence some older individuals are very large, perhaps being in their second year.

Foraging and Food Omnivorous. Food includes seeds, annuals, seeds of wild melons, and insects. In winter, diet is mostly seeds and in summer it changes to insects and green leaves (in nearly equal amounts). Gerbils forage and feed up to 30 m from burrows. Food may be stored in burrows ('larder hoarding') and also other locations within the home-range ('scatter-hoarding').

Social and Reproductive Behaviour Asocial and solitary, although burrows can be close together and linked with pathways. In captivity, ♀♀ are dominant over ♂♂ and may kill and consume them, as well as other ♀♀. Males are tolerated by ♀♀, for a short period only, at times of copulation.

Reproduction and Population Structure Under favourable conditions, reproduction can occur throughout the year, but births are mostly during the hot wet season. Gestation: 21 days. Mean litter-size for ♀♀ caught in the wild: 2 ($n = 5$) in S Kalahari (Nel

& Stutterheim 1973) and 4 ($n = 19$) elsewhere (Keogh 1973). Mean weight of young at birth 1.84 g ($n = 10$) in the Kalahari and 4.4 g ($n = 19$) elsewhere. Nipple-clinging absent. Young naked and blind at birth. Ear pinnae free at Day 12. Eyes open Day 21. External auditory meatus open Day 23. Crawling starts Day 2; walking Day 15; grooming Day 24; digging and sand-bathing Day 30. Sucking ceases at Day 33 (Nel & Stutterheim 1973). In SW Kalahari, young enter the population towards the end of the wet season (Feb–Apr). Populations peak in mid-winter (Jun–Aug) and decline thereafter.

Predators, Parasites and Diseases Main predators include Barn Owls *Tyto alba*, Spotted Eagle-owls *Bubo africanus* and snakes (e.g. cobra, *Naja nivea*). Ectoparasites include 24 species of fleas (many involved in transmitting plague to man), mites and ticks (details in De Graaff 1981). Dwarf Gerbils are vectors of bubonic plague, and in the laboratory can become infected with listeriosis, louse typhus, murine or rat typhus and tick-bite fever (De Graaff 1981).

Conservation IUCN Category: Least Concern.

Measurements

Desmodillus auricularis

HB: 110.4 (86–129) mm, $n = 64$

T: 84.8 (70–98) mm, $n = 64$

HF (c.u): 25.3 (21–29) mm, $n = 62$

E: 11.6 (10–14) mm, $n = 62$

WT: 46.1 (29–82) g, $n = 71$

GLS: 35.7 (34.2–38.1) mm, $n = 10$

GWS: 19.7 (18.7–22.3) mm, $n = 10$

M¹–M³: 4.95 (4.6–5.6) mm, $n = 10$

Auditory bulla: 14.5 (13.1–15.5) mm, $n = 10$

Body measurements and weight: south-western Kalahari (J. A. J. Nel unpubl.)

Skull measurements: Namibia (C. G. Coetzee unpubl.)

Auditory bulla measurements: Namibia (BMNH)

The range of weights probably results from subadults being included, as sampling took place during all seasons

Key References De Graaff 1981; Nel 1978; Nel & Rautenbach 1975; Skinner & Smithers 1990.

Jan A. J. Nel

GENUS *Gerbilliscus*

Gerbils

Gerbilliscus Thomas, 1897. Proc. Zool. Soc. Lond. 1897: 433. Type species: *Tatera boehmi* (Noack, 1897).

The genus *Gerbilliscus* comprises 12 species, which are widely distributed in all sub-Saharan Africa with the exception of the Rainforest BZ, and they occupy a variety of habitats in both northern and southern savannas. *Gerbilliscus leucogaster*, *G. brantsii* and

G. validus are widespread and common in southern and eastern Africa; other species have less extensive distributions (*G. afra*, *G. gambiana*) and one species is very restricted (*G. phillipsi*).

Gerbilliscus, previously considered as a subgenus of *Tatera*, is now elevated to genus rank, to account for differences between true *Tatera* (represented by the sole Asian species *T. indica*) and the African species (Pavlinov *et al.* 1990, Pavlinov 2001, G. Musser pers. comm.). These differences are mainly in dental pattern and mastoid bone structure (more derived in *Gerbilliscus* than in *Tatera*), but also include humerus morphology and diploid number of chromosomes ($2n = 68$ in *Tatera*, $2n = 36$ to 52 in *Gerbilliscus*).

The species of *Gerbilliscus* are on average more powerfully built than species from the other genera of Gerbilline rodents; they generally have a darker pelage, although there is considerable geographic variation in colour of the dorsal pelage. Populations in arid to semi-arid habitats have paler colouration than populations in moister habitats. They have comparatively long hindfeet, and the soles are naked. The skull is robustly built, and the molar row is larger than in *Taterillus*. The auditory bullae are inflated anteriorly with a small posterior section, in contrast to *Gerbillurus* and *Desmodillus* in which the posterior section is also inflated. Posterior palatal foramina are short (no longer than 3 mm, and considerably shorter than in *Taterillus*), a feature considered diagnostic among the Gerbillinae by Davis (1975a) (Figure 48).

The species of *Gerbilliscus* are physiologically, morphologically and behaviourally adapted to living in dry environments. They are terrestrial and nocturnal, spending the daytime in burrows that can be complex and deep. They are predominantly granivorous, but may

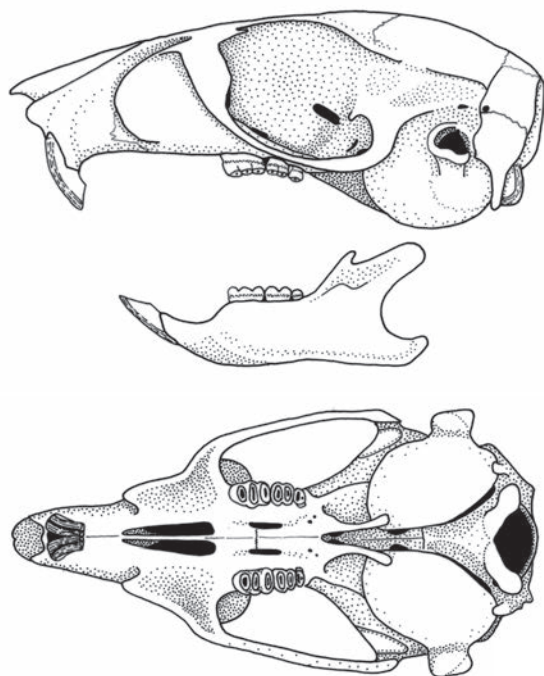


Figure 48. Skull and mandible of *Gerbilliscus kempi* (HC 1321).

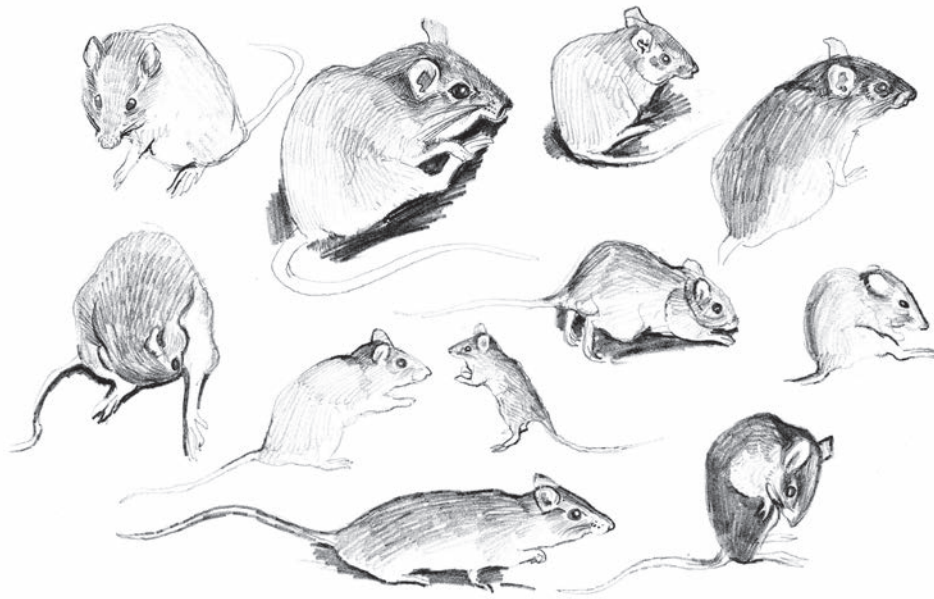
Table 23. Species in the genus *Gerbilliscus*. Arranged in order of increasing mean head and body length.

All measurements in mm. (n. d. = no data.)

| Species | Tail colour | HB mean (range) (mm) | T % of HB | GLS mean (range) (mm) | Upper incisor teeth | Chromosome number | Notes |
|-----------------------|---|----------------------|-----------|-----------------------|--|-------------------|---|
| <i>G. leucogaster</i> | Dark brown above, white below; dark pencil | 128.6 (89.0–155) | 115% | 37.3 (33.3–40.5) | Opisthodont; single groove | 2n = 40, FN = 66 | Eastern Africa; Tanzania to N South Africa |
| <i>G. brantsii</i> | Proximal half brown; distal half white above, white below | 134.6 (96.0–164) | 106% | 38.7 (35.6–42.2) | n. d. | 2n = 44, FN = 66 | Angola, Namibia, Zimbabwe |
| <i>G. afra</i> | Reddish-brown; evenly coloured throughout | 141.3 (124–157) | 110% | 39.1 (34.3–42.0) | Opisthodont; single groove | 2n = 44, FN = 66 | SW South Africa only |
| <i>G. phillipsi</i> | Pale orange-brown above, white below; some black hairs above towards terminal end; without pencil | 144.0 (143–145) | 130% | 38.9 (37.3–40.9) | Opisthodont; single groove | n. d. | N Kenya, Ethiopia |
| <i>G. guineae</i> | Dark above, white below; small black terminal tuft | 149.8 (128–178) | 110–140% | 36.2 (33.1–38.7) | Opisthodont; single groove | 2n = 50, FN = 64 | Senegal to Togo |
| <i>G. robustus</i> | Mostly brown above, usually pale or brown below; some individuals with black at tip or along most of length | 152.2 (120–190) | 115% | 41.9 (39.0–44.7) | Opisthodont; single well-defined groove | 2n = 40, FN = 70 | NE Africa |
| <i>G. inclusus</i> | Dark above, white below; occasionally with white tip | 156.0 (152–161) | 115% | 41.1 (36.7–44.3) | Opisthodont; deep single groove | n. d. | Tanzania, Mozambique, Zimbabwe |
| <i>G. kempfi</i> | Dark above, white below; small dark pencil | 158 (140–190) | 100% | 40.2 (38.7–41.6) | Opisthodont; single groove | 2n = 36 | Senegal to Cameroon |
| <i>G. boehmi</i> | Upper half/two-thirds dark brown, terminal half white; with pencil | 162.3 (139–179) | 130% | 43.5 (42.0–45.2) | Opisthodont; two faint grooves | n. d. | East-central Africa |
| <i>G. validus</i> | Brown above, pale below; without terminal pencil | 167 (135–195) | 95% | 41.7 (38.5–44.7) | Opisthodont; usually smooth without groove | n. d. | Angola, S and E DR Congo, Zambia, Tanzania, Uganda, Sudan and W Ethiopia. |
| <i>G. gambianus</i> | Dark above, orange-brown on sides, white below; without pencil | 168.2 (148–196) | 80–100% | 37.2 (34.0–40.7) | Opisthodont; single groove | 2n = 52, FN = 64 | Senegal, Mali, Niger, Chad |
| <i>G. nigricaudus</i> | Black above, black below; white hairs below near base of tail in some individuals | 185.8 (178–193) | 110% | 48.7 (47.0–50.5) | Opisthodont; single well-defined groove | n. d. | NE Africa |

eat a variety of food including insects, according to availability. They can be locally abundant and, in agricultural areas, may cause damage to crops. They are important vectors of fleas that carry plague.

The taxonomy of the genus is uncertain, because important intraspecific morphological variation masks the distinction between species. One species, *G. boehmi*, has been placed in the subgenus

Gerbilliscus gerbils.

Gerbilliscus on account of its double-grooved incisors and fringed, white-tipped tail; all the other African species are included in the subgenus *Taterona*. In the subgenus *Taterona*, the species have sometimes been distributed between an 'afra' and a 'robusta' group, the systematic status of which is questionable. *Gerbilliscus afra*, *G. brantsii* and *G. inclusus* are placed in the 'afra' group, and are distinguished from the 'robusta' group on the grounds of the quality of pelage, and morphological and craniological characters; however, there is some overlap between these subgeneric characters. Chromosomal and molecular data support the close relationship between *G. afra* and *G. brantsii*, but (on present evidence) do not support a monophyletic 'robusta' group.

Criteria used to distinguish between species include morphological and biometrical characters (colour, overall size, tail length, presence and size of terminal pencil on the tail, skull size and characters), as well as differences in karyotypes. Considerable geographic variation within species, and overlap in distinguishing characters between species makes precise identification difficult in some cases. Geographic locality aids identification, but two or more species of *Gerbilliscus* may occur sympatrically and syntopically in parts of the distribution range. Twelve species recognized: *G. afra*, *G. boehmi*, *G. brantsii*, *G. gambianus*, *G. guineae*, *G. inclusus*, *G. kempfi*, *G. leucogaster*, *G. nigricaudus*, *G. phillipsi*, *G. robusta* and *G. validus* (Table 23).

L. Granjon & Edith R. Dempster

Gerbilliscus afra CAPE GERBIL

Fr. Gerbille du Cap; Ger. Kap-Nacktsohlen-Rennmaus

Gerbilliscus afra (Gray, 1830). Spicilegia Zool. 2: 10. Cape of Good Hope, South Africa.

Taxonomy Originally described in the genus *Tatera* (see profile Genus *Gerbilliscus*). Synonyms: *africanus*, *caffer*, *gilli*, *schlegelii*. Subspecies: none. Chromosome number: $2n = 44$, $FN = 66$ (as *T. afra*); karyotype identical to that of *G. brantsii* (Qumsiyeh 1986).

Description Medium-sized gerbil with white underparts, darker dorsal surface and long tail. Dorsal pelage reddish-orange or pale buffy, faintly grizzled with dark brown; hairs dull lavender at base, reddish-orange or pale buff at tip. Hairs fairly long and broad, with chevron scale pattern. Flanks similar to dorsal pelage. Ventral pelage and inside of limbs white, with clear delineation between colour of flanks and ventral pelage. Head narrow, with pointed nose, long vibrissae, sides of muzzle white. Large eyes. Ears elongated, pale flesh colour inside, dark brown outside, rounded at tips. Outer surface of limbs reddish-orange; hindlimbs much longer than forelimbs; hindfeet elongated. Fore- and hindfeet white, five digits each, Digit 5 on forefeet reduced. Tail long (ca. 110% of HB),

covered with dense short hairs, same colour or slightly paler than dorsal pelage and coloured evenly to tip. Nipples: $2 + 2 = 8$, but considerable variation. Front face of each upper incisor with groove, lower incisors ungrooved; molar teeth broader and heavier than *G. leucogaster*. Auditory bullae not particularly enlarged. Males on average larger than ♀♀.

Geographic Variation None recorded.

Similar Species

G. brantsii. Ventral pelage white; tip of tail white; more widespread; allopatric.

G. leucogaster. Molar teeth narrower; auditory bullae not markedly inflated; allopatric.

Distribution Endemic to Africa. South-West Cape BZ. Recorded in Western and Northern Cape Provinces of South Africa, from

Nieuwoudtville in Northern Cape southwards to Cape Peninsula and eastwards coastally to Herold's Bay.

Habitat Confined to areas of loose, sandy soils or sandy alluvium. Common in cultivated lands.

Abundance Common in suitable habitats.

Adaptations Nocturnal and terrestrial. Moves by quadrupedal saltation. Excavates extensive burrows in sandy places. Numerous interconnecting tunnels end in a chamber containing nest of shredded vegetation.

Body temperature maintained at 34–36°C at Ta of 10–30°C, but susceptible to hyperthermia at Ta above 30°C. No significant drop in Tb at 5°C, indicating good tolerance of low temperatures. Water turnover rate higher than other species of southern African gerbils and probably associated with living in a mesic environment. Basal metabolic rate higher than average for gerbilline rodents, a condition that is probably related to the mesic environment, herbivory and tolerance of a relatively low ambient temperature (Duxbury & Perrin 1992).

Foraging and Food Herbivorous, and occasionally insectivorous. Cape Gerbils eat grass, bulbs, roots and seeds. Captive animals also eat insects.

Social and Reproductive Behaviour Social structure unknown. Adults rarely aggressive in laboratory encounters (Dempster *et al.* 1993). Copulation consists of series of mounts with and without intromission, culminating in intromission with ejaculation. No lock; copulatory plug deposited after ejaculation. Several bouts of mounting with and without ejaculation occur over about one hour.

Vocalizes audibly with calls of 1.6–5.3 kHz, with second to sixth harmonics. Ultrasonic whistles emitted in frequency range 20–34 kHz. Whistles are short (duration <225 msec) or long (duration >225 msec) (Dempster & Perrin 1994).

Reproduction and Population Structure In SW Cape Province, South Africa, ♀♀ have a breeding season of eight months (Aug to end Mar) followed by four months of anoestrus when there are no pregnancies and during which none of the young ♀♀ reach puberty (Measroch 1953). Males cease spermatogenesis and ♀♀ are anoestrus during the cool wet season. Breeding strategy is similar to other gerbil species: short gestation, large litter-size, altricial young, iteroparous. Embryo number: 4.0 (2–6). Litter-size: 4 (range 3–5). Mean weight at birth: 4.1 g. Growth rate in first 28 days: 0.8 g/day. Pups cling to nipples from 1 to 4 days old. Incisors erupt Day 10. Dorsal pelage visible Day 6–8. Eyes open Day 18–21. Weaned by Day 22–28. Females experience a postpartum oestrus (Dempster *et al.* 1992).

The population is mostly subadults Jan–Mar, mostly adults from Jul–Nov. Males and ♀♀ may survive to a second breeding season, with an estimated life-span of 12–17 months. During the breeding season, 60% of ♀♀ are pregnant. Females in the wild may have six to seven litters in one year (Measroch 1953). Testes in adult ♂♂ are unusually large, comprising over 8% of adult body weight (Allanson 1958).

Predators, Parasites and Diseases No information available on predators. Susceptible to infections of *Mycobacterium tuberculosis*, louse



Gerbilliscus afra

typhus caused by *Rickettsia prowazekii*, rat typhus caused by *R. typhi*, and tick-bite fever by *Rickettsia conorii*. Ectoparasites include mites of the families Laelaptidae (9 spp.), Myobiidae (1 sp.), Trombiculidae (2 spp.) and Listrophoridae (1 sp.); and fleas of the families Pulicidae (9 spp.), Hystricopsyllidae (1 sp.) and Chimaeropsyllidae (1 sp.). Like *G. brantsii*, afflicted by *Yersinia pestis*, which may lead to local outbreaks of bubonic plague (details in De Graaff 1981).

Conservation IUCN Category: Least Concern.

Although formerly listed in the South African Red Data Books, Smithers (1986b) recommended that it should be removed because it is not uncommon, adapts well to changing land use, and population numbers do not seem to have declined.

Measurements

Gerbilliscus afra

HB: 141.3 (124–157) mm, n = 44

T: 152.2 (133–175) mm, n = 44

HF: 37.5 (28–44) mm, n = 44

E: 24.5 (20–28) mm, n = 44

WT: 95.1 (78–113) g, n = 15

GLS: 39.1 (34.3–42.0) mm, n = 7

GWS: 19.9 (18.2–21.6) mm, n = 7

M¹–M³: 6.6 (6.2–7.0) mm, n = 5

Auditory bulla: 9.7 (9.2–10.3) mm, n = 5

Body measurements and weight: Western Cape (De Graaff 1981, as *Tatera afra*)

Skull measurements: Western Cape (P. J. Taylor unpubl.)

Key References Dempster & Perrin 1994; Dempster *et al.* 1992; Duxbury & Perrin 1992.

Edith R. Dempster

Gerbilliscus boehmi BOEHM'S GERBIL

Fr. Gerbille de Boehm; Ger. Boehms Nacktsohlen-Rennmaus

Gerbilliscus boehmi (Noack, 1887). Zool. Jahrb. Syst., 2: 241. Qua Mpala, Marungu, S DR Congo.

This locality has been stated to be in N Zambia (see Ansell 1978, Bates 1988).

Taxonomy Originally described in the genus *Tatera* (see profile Genus *Gerbilliscus*). Synonyms: *fallax*, *fraterculus*, *varia*. Subspecies: none. Chromosome number: not known.

Description Large dark-coloured gerbil with very long white-tipped tail. Dorsal pelage medium brown, flecked with black and ochre, darker on midline than on flanks; hairs medium grey at base, with black tip (mid-dorsally) or ochre tip (flanks). Ventral pelage white; sharp delineation between colour of flanks and ventral pelage. Hairs of cheeks and shoulders often tipped with cinnamon. Forehead and nasal region dark brownish-black. Eyes large. Ears large, rounded, with short black hairs. Chin, inner surface of limbs white. Soles of hindfeet naked and darkly pigmented. Tail very long (ca. 130% of HB), thin; proximal half or two-thirds with short hairs, dark above, white below; terminal half or third pure white above and below, often with small pencil of white hairs. Skull: large and deep; incisors orthodont, sometimes with two faint longitudinal grooves on each upper incisor tooth; cheekteeth broad, laminate and relatively long. Nipples: $2 + 1 = 6$ or $2 + 2 = 8$.

Geographic Variation None recorded.

Similar Species

Gerbilliscus leucogaster, *G. validus*, *G. robustus*, *G. nigricaudus*. All have shorter tails (actual and relative to HB) without white tip.

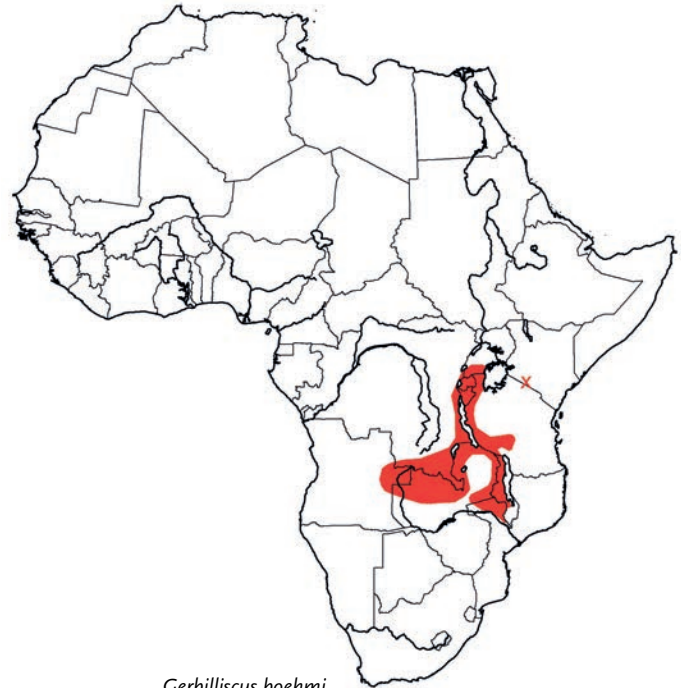
Distribution Endemic to Africa. Zambezian Woodland BZ, especially northern part. Widespread in savanna woodlands (mostly at 1000–2000 m) from SW Kenya and S Uganda to N Mozambique, Malawi, S DR Congo and W Zambia. Probably also present in Moxico Province of E Angola. Not known from east of L. Malawi or from the lowland areas of the Luangwa Valley in Zambia.

Habitat *Brachystegia* woodland, mostly at higher altitudes, where there is good cover of grass and herbaceous plants; also in grassy plains (Uganda) and 'bush' habitats. Prefers moister habitats (cf. *G. leucogaster*). Individuals found in old banana plantations (Misonne 1965a) and old millet fields (Kingdon 1974) in some parts of range.

Abundance Although widespread, mostly uncommon or rare. Reasons for rarity not known.

Adaptations Nocturnal. Burrows have one or two entrances and are not marked by a pile of excavated soil. Sometimes use burrows of other *Gerbilliscus* spp., or those of mole-rats (*Cryptomys* spp.) (Vesey-Fitzgerald 1966). Habitat and altitudinal range suggest that moderate climatic temperatures are required for survival.

Foraging and Food Omnivorous, primarily vegetable material and insects (Hanney 1965, Misonne 1965a).

*Gerbilliscus boehmi*

Social and Reproductive Behaviour Mostly unknown. May forage over a large area (Vesey-Fitzgerald 1966). In some localities, lives parapatrically with *G. validus* (Tanzania; Kingdon 1974), *G. leucogaster* (Malawi: Hanney 1965), and with *Lemniscomys* sp. and sengis (Kagera N. P., Rwanda; Misonne 1965a).

Reproduction and Population Structure Breeding recorded in early wet season (Nov) and end of wet season (May). Lactating ♀♀ in Nov (Zambia) and May (Malawi); pregnant ♀ in May (Rwanda). Embryo number: 5 ($n = 1$; Hanney 1965, Misonne 1965).

Predators, Parasites and Diseases Preyed upon by owls at several locations in Kagera N. P., Rwanda (Misonne 1965) and at Dedza, Malawi (Hanney 1965).

Conservation IUCN Category: Least Concern.

Measurements

Gerbilliscus boehmi

HB: 162.3 (139–179) mm, $n = 12$

T: 215.5 (190–234) mm, $n = 12$

HF: 40.8 (38–47) mm, $n = 11$

E: 24.3 (21–26) mm, $n = 12$

WT: 146 g, $n = 1$

GLS: 43.5 (42.0–45.2) mm, $n = 10$

GWS: 23.3 (22.0–24.3) mm, $n = 8$

M¹–M³ (alveolar): 7.4 (6.8–7.8) mm, $n = 15$

Auditory bulla: 12.9 (12.0–14.5) mm, $n = 14$
 Throughout geographic range (as *Tatera boehmi*; Bates 1988)
 Females only (limited data suggest that ♂♂ are slightly larger)

Key References Bates 1988; Vesey-Fitzgerald 1966.

D. C. D. Happold

Gerbilliscus brantsii HIGHVELD GERBIL

Fr. Gerbille du Veld; Ger. Brants Nacktsohlen-Rennmaus

Gerbilliscus brantsii (Smith, 1836). Rept. Exped. Exploring Central Africa, p. 43. Ladybrand, E Free State, South Africa. ‘Tops of hills near sources of Caledon River’ near Lesotho border (see Meester *et al.* 1986).

Taxonomy Originally described in the genus *Tatera* (see profile Genus *Gerbilliscus*). Synonyms: *breyeri*, *draco*, *griquae*, *humpatensis*, *joanae*, *maccalinus*, *maputa*, *miliaria*, *montanus*, *namaquensis*, *natalensis*, *perpallida*, *ruddi*, *tongensis*. Subspecies: three. Chromosome number: $2n = 44$, $FN = 66$ (as *Tatera brantsii*); karyotype identical to that of *G. afra* (Qumsiyeh 1986).

Description Medium-sized gerbil with darker dorsal surface, pale underparts and long tail. Dorsal pelage pale rufous-brown to pale reddish, with faint, uneven brown wash. Pelage soft and fluffy; hairs long and broad with narrow base and typical chevron pattern. Ventral pelage pure white to buffy-grey. Head narrow, with pointed nose and long vibrissae. Large eyes. Chin white. Ears elongated, dark brown, rounded at tips. Hindlimbs much longer than forelimbs, hindfeet long. Fore- and hindfeet pale, five digits each, Digit 5 on forefeet reduced. Tail long (ca. 106% of HB, shorter than HB in some individuals), similar in colour to dorsal pelage, or slightly darker for at least the proximal half; distal half white; white below. Auditory bullae well-developed. Nipples: $1 + 2 = 6$ or $2 + 2 = 8$.

Geographic Variation Dorsal pelage varies from pale in C Botswana, pale or distinctly reddish in south-western parts of distribution, to darker in south-east parts of distribution. Meester *et al.* (1986) recognize three subspecies:

- G. b. brantsii*: Lesotho, Eastern Cape and KwaZulu–Natal Provinces, South Africa and westwards to edge of Kalahari Desert. Buff-grey patches on chest; heavier molars.
- G. b. griquae*: Kalahari northwards to S Angola and W Zambia. Pure white ventral pelage; narrower molars; pale dorsal pelage.
- G. b. ruddi*: N KwaZulu–Natal Province, South Africa. Buff-grey ventral pelage; relatively long white-tipped tail; long hindfoot.

Similar Species

- G. leucogaster*. Brighter, sleeker fur; sharp line of delineation between flanks and ventral pelage; tail has distinct dark line on dorsal surface, never white-tipped.
- G. afra*. Ventral pelage pure white, tail evenly coloured to tip; confined to Western Cape Province, South Africa.

Distribution Endemic to Africa. South-West Arid and Highveld BZs, with marginal extension to southern Zambezan Woodland BZ. Recorded from S Angola, W Zambia, Botswana, E Namibia and South Africa. Limited distribution in N Zimbabwe and C Mozambique. Absent from extremely arid parts of W Namibia and W South Africa.



Gerbilliscus brantsii

Habitat Associated with sandy soils and sandy alluvium, with some cover of grass, scrub or open woodland. Also found in peaty soils around marshes and pans, sometimes using tunnels of mole-rats (*Cryptomys* spp.). Not normally found on heavy consolidated soils or very loose sandy soils.

Abundance Common. In N Transvaal Province, South Africa, Brant's Gerbils were the commonest species in the dry season (May–Jun): in ‘old field’, density was 16/ha and biomass was 1280 g/ha (ca. 80% of total numbers and biomass; $n = 5$ spp. of small terrestrial rodents) and in *Burkea* woodland, density was 12/ha and biomass was 960 g/ha (ca. 75% of total, $n = 6$ spp.) (Korn 1987). In southern African highlands, estimated density was 14.8/ha (Feb) and 27.1/ha (May) (De Moor 1969).

Adaptations Highveld Gerbils are strictly nocturnal with crepuscular peaks of activity. Move by quadrupedal saltation. They excavate complex burrows in loose, sandy soil. A burrow has many entrances, and tunnels (ca. 45–60 mm in diameter) that interconnect underground. Maximum depth of burrows about 20 cm; total length of burrow systems about 6 m. There is one nesting chamber, sealed with loose sand, in each burrow system.

Foraging and Food Highveld Gerbils eat mostly plants, including roots and green parts, with insects comprising about 5% of diet in southern Kalahari. More green than white plant material is eaten in hot season, depending on rainfall (Nel 1978). Gerbils may have significant effects on local vegetation: plant biomass, root biomass and vegetation height is significantly lower, and species diversity and evenness of plants significantly higher, near old colonies than in adjacent, undisturbed areas. Highveld Gerbils maintain high plant diversity in savanna habitats (Korn & Korn 1989). Gut morphology is simple and unspecialized suggesting a general opportunistic diet (Perrin & Curtis 1980).

Social and Reproductive Behaviour Colonial, with several individuals living in close proximity to others. Adults are rarely aggressive towards each other in laboratory encounters. If aggression does occur, both animals stand up on hindfeet, and strike at each other with their forepaws. Copulation consists of a series of mounts with and without intromission, culminating in intromission with ejaculation. No lock; copulatory plug deposited after ejaculation. Multiple copulations and ejaculations occur over about an hour.

Vocalizations include two kinds of ultrasonic whistles: short whistles of 17–27 kHz lasting about 157 msec, and long whistles of 17–31 kHz, lasting about 480 msec (Dempster & Perrin 1991b).

Reproduction and Population Structure Pregnant ♀♀ recorded throughout year, with peak of reproductive activity at onset of cool dry season (Gauteng Province, South Africa). Males show active spermatogenesis throughout year, with peak in warm wet season. Breeding strategy similar to that of other gerbils: short gestation, altricial young, iteroparous, but small litter-size. Gestation: 22 days. Embryo number: 2.8 (1–5). Mean litter-size: 2.8. Mean weight at birth: 4.6 g. Growth rate in first 28 days: 1.1 g/day. Pups cling to nipples from Day 1–4. Incisors erupt Day 6. Eyes open Day 16–20. Weaned by Day 28 (Scott 1979). Postpartum oestrus indicated by 40% of ♀♀ in the wild being both lactating and pregnant. Females may have five or six litters/year (Measroch 1953). Testes in adult ♂♂ are large, comprising ca. 5% of adult body weight (Allanson 1958; cf. *G. afra*).

Predators, Parasites and Diseases Preyed on by snakes, small mammalian carnivores, Barn Owls *Tyto alba* and African Grass-owls *Tyto capensis*. Wild populations sometimes afflicted by *Yersinia pestis*, leading to local outbreaks of bubonic plague. Susceptible to infection by *Pseudomonas pseudomallei*, *Listeria monocytogenes* and *Mycobacterium tuberculosis* in the laboratory. Endoparasites include the cestodes *Hymenolepis microcantha*, *H. taterae* and *Raillietina trapezoides*. Ectoparasites include 29 species of fleas and nine species of ticks (details in De Graaff 1981). Widely used as a laboratory animal for medical research.

Conservation IUCN Category: Least Concern.

Measurements

Gerbilliscus brantsii

HB: 134.6 (96–164) mm, n = 237*

T: 143.1 (103–186) mm, n = 237

HF: 35.0 (19–47) mm, n = 237

E: 21.5 (12–34) mm, n = 236

WT: 79.9 (25–126) g, n = 130

GLS: 38.7 (35.6–42.2) mm, n = 15

GWS: 21.6 (19.0–23.0) mm, n = 14

M¹–M³: 7.2 (6.7–7.9) mm, n = 15

Auditory bulla: 10.6 (9.6–11.7) mm, n = 13**

Body measurements and weight: Transvaal (Rautenbach 1978; recalculated – ♂♂ and ♀♀ combined; as *Tatera brantsii*)

Skull measurements: Drakensberg Mts, KwaZulu–Natal Province, South Africa (P. J. Taylor unpubl.)

*Recalculated; original data as total length

**P. J. Taylor unpubl.

Mean weight of ♂♂ in southern Kalahari is lower than in Transvaal: 64.9 g, n = 67 (Nel & Rautenbach 1975)

Key References Dempster & Perrin 1991b; Korn & Korn 1989; Measroch 1953.

Edith R. Dempster

Gerbilliscus gambianus GAMBIAN GERBIL

Fr. Gerbille de Gambie; Ger. Gambische Nacktsohlen-Rennmaus

Gerbilliscus gambianus (Thomas, 1910). Ann. Mag. Nat. Hist., ser. 8, 6: 428. Marakissa, Upper Gambia, Senegal.

Taxonomy Originally described in the genus *Tatera* (see profile Genus *Gerbilliscus*). Often considered to be a synonym of *G. kempi* (e.g. Rosevear 1969, Musser & Carleton 1993, 2005) or *G. validus kempi* (Bates 1988). Re-established as a distinct species by Hubert *et al.* (1973) following Matthey & Petter (1970). Distinguished by karyotype from other *Gerbilliscus*. Synonyms: *hopkinsoni*. (The form *hopkinsoni* was described later from the same region as *gambianus* [Gambia R], but this name was given improperly by various authors to specimens with 2n = 48, a karyotype never found in this region.) Subspecies: none. Chromosome number: 2n = 52, aFN = 64 (Matthey & Petter 1970; as *T. gambianus*).

Description Large robust gerbil. Dorsal pelage grey-brown; hairs dark grey at base, with wide brown or orange central zone, black at tip. Flanks paler; hairs without black tip. Ventral pelage white, clearly delineated from colour of flanks. Head rounded, similar in colour to flanks. Moderately pointed nose. Large eyes; moderately elongated ears. Chin, throat, chest and inner sides of limbs white. Hindfeet white above, dark below; forefeet entirely white. Tail moderately long (ca. 80–100% of HB), well haired, dark above, orange to brown on sides, white below, without any marked pencil of hairs at terminal end. Nipples: 2 + 2 = 8.

Geographic Variation None recorded.

Similar Species

G. kempi. Ear on average longer; chromosome number: $2n = 48$. More southern distribution; other species of this short-tailed group occur only in eastern and southern Africa.

G. guineae. Tail on average longer (110–140% of HB) with pencil. $2n = 50$. Similar distribution.

Distribution Endemic to Africa. Sahel Savanna and Sudan Savanna BZs of Senegal (Hubert *et al.* 1973) and Mali (B. Sicard & L. Granjon unpubl.). Recent captures in SE Niger (Kojimairi, 40 km south of Goudoumaria; Dobigny *et al.* 2002b) and at the southern edge of L. Chad (Granjon & Dobigny 2003) suggest a much larger range.

Habitat In Senegal, found in *Combretum* woodlands (where sympatric with *G. guineae*), but on soils that are more sandy. Also trapped in fallow lands and traditionally cultivated fields (Hubert 1977, Hubert *et al.* 1977). The only species of gerbil found on sandy and mangrove islands in the Saloum Delta, Senegal (Granjon & Duplantier 1989).

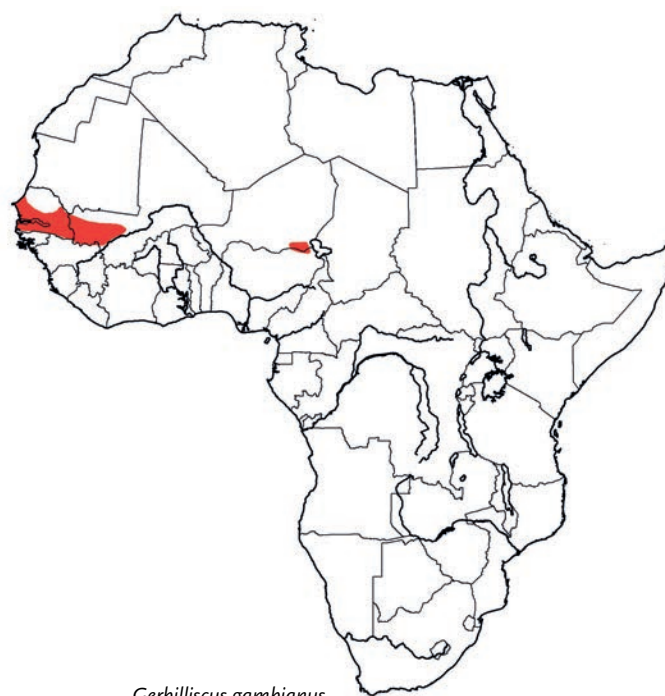
Abundance Very varied according to habitat. Density up to 15/ha in sahelo-sudanian woodland at Bandia, Senegal, where may represent up to 17% of the rodents in favourable habitats (Hubert 1977). In the Saloum Delta, abundance varied from 3.5 to 24 individuals/ha on a 2 ha study area during a two-year survey (Granjon *et al.* 1994). This species seems to show more pronounced variations in abundance than *G. guineae* in mainland Senegal.

Adaptations Terrestrial and nocturnal. Digs complex and moderately deep burrows (average 30 cm), with many entrances. Up to ten burrows can be found within the home-range of one individual (Hubert *et al.* 1977). Poor swimming abilities (Duplantier & Bâ 2001).

Foraging and Food Consumes seeds, but also large amounts of insects especially at the beginning of the dry season (Moro & Hubert 1983).

Social and Reproductive Behaviour Little information. Home-range 600–800 m². Mean successive recapture distance 12.5 m (max 21.5 m) during a period of 10–12 days; recapture distances smaller than for sympatric *G. guineae* in W Senegal. Considerable overlap in home-ranges between individuals of both sexes. Does not show agonistic or amicable behaviour towards other species (Hubert 1977).

Reproduction and Population Structure In W Senegal, pregnant ♀♀ recorded at end of wet season and first half of dry season (Sep–Feb) but no pregnancies recorded during second half of dry season and beginning of wet season (Mar–Aug). Gestation: 25 days. Litter-size: 2–6. Sexual maturity: 11–15 weeks (Hubert &



Gerbilliscus gambianus

Adam 1975). Monthly mortality rate up to 50% when population is decreasing (Hubert 1977).

Predators, Parasites and Diseases Remains found in pellets of Barn Owls *Tyto alba* from various localities in W Senegal (J.-M. Duplantier & L. Granjon unpubl.). Protozoan parasites include *Leishmania major* (Dedet *et al.* 1981) and *Borrelia crociduræ* (Trape *et al.* 1991). Arboviruses include Touré, Keuraliba, Gabek Forest and Koutango strains (Annual Reports of Pasteur Institute, Dakar).

Conservation IUCN Category: Least Concern.

Measurements

Gerbilliscus gambianus

HB: 168.2 (148–196) mm, $n = 24$

T: 149.2 (130–175) mm, $n = 24$

HF: 33.2 (31–35) mm, $n = 25$

E: 18 (17–20) mm, $n = 24$

WT: 94.1 (66–140) g, $n = 25$

GLS: 37.2 (34.0–40.7) mm, $n = 24$

GWS: 17.9 (16.0–19.6) mm, $n = 21$

M¹–M³: 5.9 (5.0–6.3) mm, $n = 24$

Auditory bulla: n. d.

Senegal (Diambour, Terres Neuves Region; MNHN)

Key References Hubert 1977; Hubert *et al.* 1977; Rosevear 1969.

J.-M. Duplantier & L. Granjon

Gerbilliscus guineae GUINEA GERBIL

Fr. Gerbille de Guinée; Ger. Guinea-Nacktschalen-Rennmaus

Gerbilliscus guineae (Thomas, 1910). Ann. Mag. Nat. Hist., ser. 8, 5: 351. Gunnal, Guinea-Bissau.

Taxonomy Originally described in the genus *Tatera* (see profile Genus *Gerbilliscus*). Referred by Davis (1975a) to *T. robusta* (now *Gerbilliscus robustus*), but generally considered as a valid species (Rosevear 1969, Bates 1985). Synonyms: *picta*. Subspecies: none. Chromosome number: $2n = 50$, $aFN = 64$ (Matthey & Petter 1970, as *T. guineae*).

Description Medium to large-sized robust rodent. Dorsal pelage grey-brown; hairs dark grey at base, brown to orange central zone, and usually with short black tip. Flanks and head paler; hairs mostly without black tip. Ventral pelage and inner sides of limbs white; ventral colour clearly delineated on lower flanks. Chin, throat and chest white. Head rounded with moderately pointed nose. Large eyes; relatively elongated ears. Hindfeet white above, dark below; forefeet entirely white. Tail relatively long (110–140% of HB), well haired, dark above, white below, with marked pencil of darkish hairs at terminal end. Nipples: $2 + 2 = 8$.

Geographic Variation None recorded.

Similar Species

G. kempi. Tail relatively shorter without terminal pencil; chromosome number: $2n = 48$; similar distribution.

G. gambianus. Tail relatively shorter without terminal pencil; $2n = 52$; overlapping distribution (in the northern part of the range of *G. guineae*).

Distribution Endemic to Africa. Sudan and Guinea Savanna BZs, and Northern Rainforest–Savanna Mosaic. Recorded from Senegal (Hubert *et al.* 1973), Guinea-Bissau and Guinea (Ziegler *et al.* 2002), Burkina (Matthey & Petter 1970), Sierra Leone (Grubb *et al.* 1998), Côte d'Ivoire (Gautun & Petter 1972), Ghana (Rosevear 1969) and Togo (Robbins & Van der Straeten 1996). Not recorded from Gambia (Grubb *et al.* 1998).

Habitat In Senegal, mostly found in *Combretum* woodlands on lateritic to clay, hydromorphous soils where there is a dense shrub layer and variable herbaceous cover (Hubert *et al.* 1977). Also trapped in cultivated areas (Senegal, Hubert *et al.* 1977; Mali, B. Sicard unpubl.) and on bare ironstone hills (Gambia; Rosevear 1969).

Abundance Little information. Uncommon in W Senegal. Density of ca. 4/ha in sahelio-sudanian woodland at Bandia, Senegal; comprised 7.7–21% of rodents in favourable habitats (Hubert 1977).

Adaptations Terrestrial and nocturnal. Digs relatively deep (average 50 cm) and moderately complex burrows in heavy soils. Entrances are hidden by heaps of excavated earth (Hubert *et al.* 1977).

Foraging and Food No information.

Social and Reproductive Behaviour Home-range 1400–

*Gerbilliscus guineae*

1500 m². Mean recapture distance 21 m (max 38 m during 10–12 days); larger than for sympatric *G. gambianus* in W. Senegal (Hubert 1977).

Reproduction and Population Structure In a monthly survey from Jun 1971 to Mar 1973 in W Senegal (Hubert 1977), pregnant ♀♀ were found mainly during the wet season (Aug–Oct), but reproduction continued until the middle of the dry season (Jan–Feb) in 1972. Embryo number: 4–5. Monthly mortality rate up to 30%, less variable than in *G. gambianus*.

Predators, Parasites and Diseases No information.

Conservation IUCN Category: Least Concern.

Measurements

Gerbilliscus guineae

HB: 149.8 (128–178) mm, $n = 35$

T: 175.3 (156–198) mm, $n = 32$

HF: 34.9 (32–37) mm, $n = 34$

E: 20.5 (19–22) mm, $n = 34$

WT: 73.7 (45–110) g, $n = 35$

GLS: 36.2 (33.1–38.7) mm, $n = 20$

GWS: 16.9 (15.4–18.4) mm, $n = 18$

M¹–M³: 5.7 (4.8–6.1) mm, $n = 20$

Senegal (Diambour, Terres Neuves Region; MNHN)

Key References Hubert 1977; Hubert *et al.* 1977; Rosevear 1969.

L. Granjon & J.-M. Duplantier

Gerbilliscus inclusus GORONGOZA GERBIL

Fr. Gerbille de Gorongoza; Ger. Gorongoza-Nacktschuh-Rennmaus

Gerbilliscus inclusus Thomas and Wroughton, 1908. Proc. Zool. Soc. Lond. 1908: 169. Tambarara, Mozambique.

Taxonomy Originally described in the genus *Tatera* (see profile Genus *Gerbilliscus*). Synonyms: *cosensi*, *pringlei*. Subspecies: three. The form *pringlei* was described as a valid species (Hubbard 1970b), treated as a subspecies here and by Davis (1975a), and as a synonym by Musser & Carleton (1993, 2005). Chromosome number: not known.

Description Large gerbil with dark dorsal pelage, long hindfeet and long tail. Dorsal pelage ochraceous-buff, washed with black; hairs dark slate, ringed with ochraceous and tipped with black. Flanks paler than dorsal pelage. Ventral pelage white from chin to tail tip. Colour varies geographically (see below). Head narrow, with pointed nose, long vibrissae, sides of muzzle darker than head. Large eyes with black mark under each eye. Ears pinkish, almost naked, relatively short. Hindlimbs longer than forelimbs, hindfeet elongated. Forefeet and hindfeet off-white, five digits each, Digit 5 on forefoot reduced. Tail long (ca. 115% of HB), dark above, white below, occasionally white-tipped. Upper incisors deeply grooved, lower incisors ungrooved. Nipples: 1 + 2 = 6 or 2 + 2 = 8.

Geographic Variation Meester *et al.* (1986) recognize three subspecies:

G. i. cosensi: N Mozambique and E Tanzania.

G. i. pringlei: Muheza, Tanzania (05° 10' S, 38° 47' E; Hubbard 1970b). Dorsal pelage black, ventral pelage and feet pure white; tail usually equal to or shorter than head and body length; only known from type locality.

*Gerbilliscus inclusus*

G. i. inclusus: E Zimbabwe and Mozambique south of Zambezi R. Dorsal pelage very dark (from forehead to base of tail); flanks dark ochraceous-buffy or reddish.

Similar Species

G. leucogaster. Smaller; paler in colour, texture of fur sleeker.

Distribution Endemic to Africa, Zambezan Woodland BZ and parts of Coastal Forest Mosaic BZ in Mozambique, E Zimbabwe and S Tanzania (east of L. Malawi). Perhaps occurs in localities between the currently known ranges.

Habitat Sandy ground or sandy alluvium, often on fringe areas between dry and riverine woodland, confined to areas with a mean annual rainfall of >800 mm. Often associated with agricultural lands and forest fringes, but not recorded within forests. The subspecies *G. i. pringlei* recorded in dense grassland with moist, sandy soil.

Abundance Not known.

Adaptations Nocturnal and terrestrial. Moves by quadrupedal saltation. Burrows of *G. i. pringlei* have an entrance tunnel, one or two chambers, one of which contains the nest, one or two side tunnels and an escape tunnel (which may be 2–2.5 m from the main burrow) (Hubbard 1970b). Food has not been found in burrows.

Foraging and Food Seeds, fruit and insects in captivity (as *G. i. pringlei*; Hubbard 1970b).

Social and Reproductive Behaviour Appear to have identical habits to Bushveld Gerbils (*G. leucogaster*), with which they occur sympatrically, although always in smaller numbers (Smithers 1983). Simple burrow systems indicate a more solitary social structure than Bushveld Gerbils; burrows normally occupied by a single animal or a ♀ with young. Copulation (in *G. i. pringlei*) consists of single mount with intromission and ejaculation. Animals footdrum by pattering the hindfeet alternately when alarmed (Hubbard 1970b).

Reproduction and Population Structure No information on seasonality of breeding. Gestation: 23–24 days. Litter-size: 2–3. Young not known to nipple-cling. Eyes open at Day 16–20.

Predators, Parasites and Diseases Little information. No fleas recorded on *T. i. pringlei*.

Conservation IUCN Category: Least Concern.

Measurements

Gerbilliscus inclusus

HB: 156.0 (152–161) mm, n = 13

T: 164.1 (135–191) mm, n = 13

HF: 41.2 (39–44) mm, n = 13
 E: 25 (21–29) mm, n = 13
 WT: 115.6 (99–154) g, n = 13
 GLS: 41.1 (36.7–44.3) mm, n = 4
 GWS: 21.2 (19.2–22.2) mm, n = 4
 M¹–M³: 6.9 (6.6–7.2) mm, n = 4
 Auditory bulla: 9.9 (8.9–10.7) mm, n = 4

Body measurements and weight: E Zimbabwe (recalculated from Smithers & Wilson 1979; as *Tatera inclusa*)
 Skull measurements: Mozambique (P. J. Taylor unpubl.)
T. i. pringlei: larger body size, with shorter tail, hindfoot and ears

Key References Hubbard 1970; Smithers 1983.

Edith R. Dempster

Gerbilliscus kemp KEMP'S GERBIL (NORTHERN SAVANNA GERBIL)

Fr. Gerbille de Kemp; Ger. Kems Nachtsohlen-Rennmaus

Gerbilliscus kemp (Wroughton, 1906). Ann. Mag. Nat. Hist., ser. 7, 17: 375. Aguleri, Nigeria.

Taxonomy Originally described in the genus *Tatera* (see profile Genus *Gerbilliscus*). Sometimes included within *Tatera valida* (now *Gerbilliscus validus*) (e.g. Davis 1975a, Happold 1987, Bates 1988), but more generally considered to be a valid species (Rosevear 1969, Grubb *et al.* 1998). Synonyms: *beniensis*, *benvenuta*, *dichrura*, *dundasi*, *flavipes*, *lucia*, *nigrita*, *ruwenzorii*, *smithi*, *soror*; *gambiana*, *giffardi*, *hopkinsoni*, *welmani*. All except the last four were included as synonyms under *Tatera valida* (= *Gerbilliscus validus*) by Musser & Carleton (1993). Subspecies: none. Chromosome number: 2n = 36 (Matthey & Petter 1980, in Robbins & Baker 1978).

Description Medium-sized robust rodent with shaggy hair and tail slightly longer than head and body. Dorsal pelage sandy-grey to sandy-orange; dorsal hairs sandy with dark grey at base and usually with black tip. Flanks similar to dorsal pelage, hairs usually without dark tips. Ventral pelage pure white. Dorsal and ventral colours clearly delineated. Chin, throat, chest and inner sides of limbs white. Eyes large, head rounded with moderately pointed nose. Tail long (ca. 100% of HB), sparsely haired, dark above, white below, with small pencil of darkish hairs (often lost in adults) at terminal end. Juvenile pelage sandy-grey, usually duller and less sandy than in adults. Males tend to be larger than ♀♀. Each upper incisor with single groove. Nipples: not known.

Geographic Variation Individuals at southern part of range (within, or close to, the Rainforest BZ) have greater density of black-tipped hairs and appear darker than northern individuals.

Similar Species

G. validus. On average larger (HB: 167 [135–195] mm, HF: 34.0 [30–39] mm, GLS: 41.7 [38.5–44.7] mm); tail lacks pencil at terminal end; auditory bullae larger; distribution mainly in eastern Africa.

G. guineae. Similar size. Hindfoot on average longer; tail on average longer and relatively longer with well-developed pencil; distribution Senegal to Ghana and Togo.

Taterillus gracilis. Much smaller and more slender; tail relatively longer (ca. 130% of HB) covered with short bristles and well-developed pencil at terminal end; syntopic and sympatric.

Distribution Endemic to Africa. Guinea Savanna BZ and Northern and Eastern Rainforest–Savanna Mosaics. Recorded from



Gerbilliscus kemp

Gambia and Sierra Leone to Nigeria, and probably to S Sudan and NW Kenya; may sometimes extend northwards into parts of Sudan Savanna BZ in the east of the range. Sometimes found in savanna-like habitats on edge of rainforest. Recorded from coastal grasslands of the Dahomey Gap in Ghana (Grubb *et al.* 1998), Togo and Benin (Robbins & Van der Straeten 1996). Extent of geographic range in central and eastern Africa uncertain (see also *G. validus*).

Habitat Savanna grasslands where there is good cover of grasses and/or dense shrubs, and where the soil is sandy and friable for digging burrows. Also occur wherever there are farmlands and plantations, such as maize and cassava fields, cocoa and oil palm plantations, and abandoned farmlands with thick grassy cover.

Abundance One of the commonest rodents in suitable savanna habitats where the rainfall is 1000–1500 mm/year and where the wet season lasts for 7–8 months (Apr–Nov). In the Rainforest–Savanna Mosaic of Nigeria (7–8°N), comprised less than 10% of small terrestrial rodents. Likewise on the grasslands of the Shai Hills

(Accra Plains, Ghana, ca. 6° N), formed about 10% of small rodents (n = 27) (Decher & Bahian 1999), and also ca. 10% (n = 3906 trappable small rodents; third commonest of 13 spp.) at Fro-Fro (7° 55' N), Côte d'Ivoire. Relative abundance increases from south to north, and near Kainji N. P., Nigeria (09° 50' N) comprised nearly 100% of small rodents (Happold 1975b). Density up to 46/ha (= ca. 4.6 kg/ha) in Kainji N. P., Nigeria.

Adaptations Nocturnal and terrestrial. Kemp's Gerbils live in burrows during the day and forage above ground at night. They have strong limbs and wide hindfeet for digging and burrowing, and large eyes and well-developed auditory bullae for good sensory perception.

Foraging and Food Granivorous, herbivorous and opportunistic. The diet is primarily seeds, but also leaves, shoots and roots. In the dry season, insects are eaten when succulent foods unavailable. Kemp's Gerbils also feed on crops and may cause damage in farmlands. They collect and store seeds in their burrows. Stored seeds probably provide food at beginning of the wet season when other seeds are scarce (D. C. D. Happold unpubl.).

Social and Reproductive Behaviour Mostly unknown. High density of individuals in suitable habitats suggests overlapping home-ranges. Several individuals may be kept together in captivity without any signs of aggressive behaviour.

Reproduction and Population Structure Pregnant ♀♀ recorded in late wet season (Dec) in S Nigeria. Juveniles (25–50 g) abundant in dry season (Dec–Mar) in Kainji N. P., Nigeria. In C Côte d'Ivoire (07° 55' N), adult ♀♀ were reproductively active in most

months of the year, and pregnant ♀♀ were recorded in Feb, Mar, Jun, Oct and Nov (Gautun 1975). The limited evidence suggests that pregnancies occur at the beginning and end of the wet season, and rarely during the main part of the wet season. Mean litter-size: 2.7 (n = 9) in Feb/Mar and 6.0 (n = 10) in Oct/Nov (Gautun 1975; no ranges given).

Predators, Parasites and Diseases No information.

Conservation IUCN Category: Least Concern.

A common and widespread species in suitable savanna habitats.

Measurements

Gerbilliscus kemp

HB: 158 (140–190) mm, n = 12

T: 156 (142–173) mm, n = 12

HF: 32.7 (27–36) mm, n = 12

E: 21.5 (17–26) mm, n = 12

WT: 97–105 g, n = 13

GLS: 40.2 (38.7–41.6) mm, n = 12

GWS: 20.4 (18.9–21.8) mm, n = 9

M¹–M³: 6.4 (6.2–6.6) mm, n = 12

Auditory bulla: 10.9 (10.5–11.3) mm, n = 12

Measurements: Nigeria (BMNH)

Weight: Nigeria (Happold 1987, as *Tatera valida*)

Key References Happold 1975b; Rosevear 1969.

D. C. D. Happold

Gerbilliscus leucogaster BUSHVELD GERBIL

Fr. Gerbille à ventre blanc; Ger. Weissbauch-Nacktsohlen-Rennmaus

Gerbilliscus leucogaster (Peters, 1852). Bericht Verhandl. K. Preuss. Akad. Wiss. Berlin, p. 274. Mesuril and Boror, Mozambique.

Taxonomy Originally described in the genus *Tatera* (see profile Genus *Gerbilliscus*). Synonyms: *angolae*, *bechuanae*, *beirae*, *beirensis*, *kaokoensis*, *limpopoensis*, *littoralis*, *lobengulae*, *mashonae*, *mitchelli*, *ndolae*, *nigrotibialis*, *nyasae*, *panja*, *pestis*, *pretoriae*, *salsa*, *schinzi*, *shirensis*, *stellae*, *tenuis*, *tzaneenensis*, *waterbergensis*, *zuluensis*. Subspecies: none. Previously, 17 of these forms from the southern African region were considered to be subspecies, but their distribution is contiguous and populations of these forms integrate evenly throughout their range. Chromosome number: 2n = 40, FN = 66 (Qumsiyeh, 1986).

Description Medium-sized gerbil with white underparts, darker dorsal surface and very long tail. Dorsal pelage reddish-brown to orange-buffy, depending on geographical area. Dorsal hairs slate-grey on basal two-thirds, changing to buffy-white, then pale rufous-buff at tip. Ventral pelage pure white from chin to tail tip. Head narrow, with pointed nose, long vibrissae, sides of muzzle white. Large eyes with white mark above and behind each eye. Ears elongated, dark brown, rounded at tips. Hindlimbs much longer than forelimbs, elongated hindfeet. Fore- and hindfeet pure white, five digits each, Digit 5 on forefoot reduced. Tail relatively long (ca. 115% of HB),

covered with dense short hairs, distinct brownish band down entire length on dorsal surface, white underneath, often darker terminal tuft. Anterior face of incisors grooved, lower incisors ungrooved. Auditory bullae well developed. Nipples: 2 + 2 = 8, but considerable variation.

Geographic Variation Dorsal pelage ranges from bright cinnamon-buff in west to reddish-brown in east.

Similar Species

G. brantsii. Pelage softer and fluffier; tail without distinct dark line, usually white at tip.

Distribution Endemic to Africa. Widely distributed in the Zambezi Woodland BZ, parts of the South-West Arid BZ (Kalahari Desert) and Highveld BZ. Northern limits uncertain, probably ca. 6° S. Widespread in Angola, S DR Congo, Zimbabwe, S Tanzania, Malawi, Mozambique, Namibia, Botswana and N South Africa. Southern limit in South Africa about 30° S, including the lowveld of Swaziland and NE KwaZulu–Natal Province.

Habitat Predominantly associated with open grasslands and wooded savannas on light sandy soils or sandy alluvium. Common on sandy plains along dry river courses in C Namib, in miombo woodland in Zimbabwe and woodland savanna in Malawi. Absent from areas of heavy red clay soils or soft sand. Generally restricted to areas with mean annual rainfall above 250 mm, although in Namibia occur in areas with mean annual rainfall less than 100 mm. Occur at altitudes of sea level to ca. 1600 m.

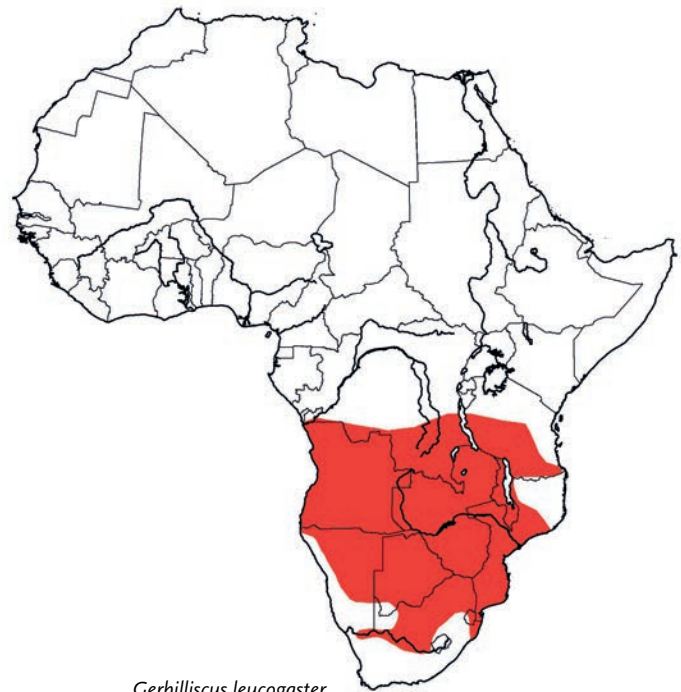
Abundance Abundance varies according to locality, vegetation and time of year. At Sengwa, Zimbabwe, number of individuals was 1.9–7.0/ha in *Brachystegia* woodland, 0.8–2.3/ha in thicket habitats and 0–1/ha in riverine grasslands (Linzey & Kesner 1997a). Percentage abundance was 70–90% (cool dry season) and ca. 86% (other seasons) in *Brachystegia* woodland (where it was always the most numerous species), 56–100% (cool dry season) and 67% (hot wet season) in thicket habitats, and 0% (most seasons) to 3% (cool dry season) in riverine grasslands. At Nylsvley, South Africa, percentage abundance varied during the dry season from 6% (in old fields, where it was the least common of the five species present) to 61% (in burnt *Acacia* woodland where it was the commonest of five species present) (Korn 1987). In Liwonde N. P., Malawi, comprised 18% of small terrestrial rodents ($n = 106$; 7 spp.) and was encountered only during the dry season (Happold & Happold 1990). The frequency of burning, and when burning occurs, has a considerable effect on the numbers of individuals and their percentage occurrence within the community of small mammals; in general formed higher proportions of the small mammal community in habitats that had been burnt at one or more times during the last three years than in unburnt control habitats (Korn 1981). De Graaff (1981) comments that ‘populations are subject to cyclic explosions in numbers’, but does not give quantitative data to support this statement.

Adaptations Nocturnal and terrestrial. Moves by quadrupedal saltation. Excavates burrows, which are about 40–45 mm in diameter, with the entrance at the base of small bushes or grass clumps. Burrows are complex with many entrances and tunnels that interconnect underground. Burrow systems include chambers lined with vegetable debris.

Bushveld Gerbils have many physiological characters concomitant with survival in hot, arid environments, although they are less arid-adapted than other gerbil species. Basal metabolic rate and evaporative water loss is lower than in mesic rodents, minimal wet thermal conductance is about the same as expected for body mass, resting body temperature below thermoneutrality is lower than in mesic rodents, and the thermoneutral zone is broader than in more xeric-adapted gerbil species (Downs & Perrin 1994, Webb & Skinner 1996a).

Foraging and Food Bushveld Gerbils eat insects, seeds and herbage. Individuals in N South Africa eat mostly insects and seeds during warm wet season, and lose weight in cool dry season when eating mostly herbage. No seasonal variation in diet in Zimbabwe.

Social and Reproductive Behaviour Social structure unknown, but burrows often clumped, and several individuals trapped from a single burrow system indicate a tolerant social structure. Adults rarely aggressive towards each other in laboratory encounters.



Gerbilliscus leucogaster

Copulation consists of series of mounts with and without intromission, culminating in intromission with ejaculation; there is no lock and a copulatory plug is deposited after ejaculation. Multiple copulations and ejaculations occur over about an hour. Vocalize audibly between 5.5 kHz and 4.8 kHz; ultrasonic whistles begin at 48 kHz, descending to a trill at about 30 kHz; short ultrasonic ‘peeps’ emitted at about 40 kHz and 63 kHz. Males perform a post-copulatory song, which consists of series of whistles beginning at about 50 kHz, descending to about 15 kHz, and lasts about one minute. Animals footdrum when alarmed. Hindfeet patter alternately in bursts of 6–10 beats (Dempster & Perrin 1994).

Reproduction and Population Structure Breeding occurs throughout the year, with peaks in Dec–Jan and Apr–May, associated with rainfall. Second breeding season in dry season reported in parts of Zimbabwe, elsewhere breeding ceases in cool dry season. Breeding strategy similar to other gerbil species: short gestation, large litter-size, altricial young, iteroparous (Perrin & Swanepoel 1987). Gestation: 28 days. Embryo number: 4.5 (2–9) over range of habitats. Mean litter-size: 5.0. Mean birth-weight: 3.6 g. Growth rate in first 32 days: 0.9 g/day. Young do not nipple-cling. Incisors erupt Day 5–6. Eyes open Day 16–21. Young weaned by Day 28. Annual reproductive capacity of ♀♀ is 28 young/year in mixed woodland habitat, and 12 young/year in miombo woodland habitat (Neal 1991). Testis mass of adult ♂♂: ca. 6% of total body weight, larger than most other rodent species. Testes of many ♂♂ regress during dry season. Sex ratio not significantly different from parity. Juveniles enter the population during the warm wet season, and population numbers decline in dry season; seasonal changes in population structure are variable.

Predators, Parasites and Diseases Recorded as a prey item of the Barn Owl *Tyto alba*. Susceptible to infection of the neurotropic strain of African horse sickness and *Listeria monocytogenes* under laboratory conditions. Recorded as a reservoir of the plague bacillus *Yersinia pestis*.

in South Africa and DR Congo. Fleas include 25 species in the families Hystrichopsyllidae, Chimaeropsyllidae and Pulicidae (details in De Graaff 1981). In East Africa, Bushveld Gerbils carry three species of fleas of their own: *Xenopsylla debilis*, *X. humilis* and *X. difficilis*.

Conservation IUCN Category: Least Concern.

Abundant throughout its geographic range.

Measurements

Gerbilliscus leucogaster

HB: 128.6 (89–155) mm, n = 1023

T: 148.5 (120–175) mm, n = 1024

HF: 33.5 (24–38) mm, n = 1068

E: 21.0 (18–26) mm, n = 1045

WT: 69.8 (32–114) g, n = 696

GLS: 37.3 (33.3–40.5) mm, n = 23

GWS: 19.0 (17.3–20.7) mm, n = 23

M¹–M³: 6.5 (5.6–7.9) mm, n = 23

Auditory bulla: 10.5 (9.7–11.1) mm, n = 18*

Body measurements and weight: Former Transvaal (Rautenbach 1978; as *Tatera leucogaster*)

Skull measurements: KwaZulu–Natal and Northern Cape Province, South Africa, and Namibia (P. J. Taylor unpubl.)

*A series from Angola (Crawford-Cabral 1988) had slightly smaller auditory bullae (10.3 [9.4–10.9] mm)

Key References Dempster & Perrin 1994; Neal 1991; Perrin & Swanepoel 1987; Webb & Skinner 1996a.

Edith R. Dempster

Gerbilliscus nigricaudus BLACK-TAILED GERBIL

Fr. Gerbille à queue noire; Ger. Schwarzschanz-Nacktschalen-Rennmaus

Gerbilliscus nigricaudus (Peters, 1878). Monatsber. K. Preuss. Akad. Wiss. Berlin 1879: 200. (publ. 1878). Ndi, Taita, Kenya.

Taxonomy Originally described in the genus *Tatera* (see profile Genus *Gerbilliscus*). This species, *G. robustus* and *G. validus* are closely related and sympatric in parts of their ranges. Although the all-black tail is the main character of *nigricaudus*, the tail of *G. robustus* is black (or partially black) in some parts of its range, especially in the northern part. The three species are difficult to differentiate with absolute certainty using external characters only; and some individuals ascribed to *nigricaudus* in the past are probably *G. robustus*. A combination of external measurements, colour and certain skull characters are necessary to separate these species from each other. Bates (1988) considered that *bayeri* (Mt Elgon and Karamoja) and *bodessae* (Ethiopia), both formerly considered to be subspecies of *G. nigricaudus*, are referable to *G. robustus*. Synonyms: *nyama*, *percivali*. Subspecies: two. Chromosome number: not known. The individuals referred to by Matthey (1969), for which he gave a chromosome number of 2n = 40, are considered to be *T. robusta* (now *Gerbilliscus robustus*) by Bates (1988).

Description Large brown gerbil with long black tail. Pelage long, soft and sleek. Dorsal pelage brown, suffused with black in some individuals; dorsal hairs pale grey at base, with ochre, brown or black at tip. Flanks paler; hairs white at base, pale ochre or sandy at tip. Ventral pelage white. Dorsal and ventral colours clearly delineated. Head and cheeks similar to dorsal pelage. Chin, chest, inner surfaces of limbs white. Hindfeet white; soles naked and darkly pigmented. Tail long (ca. 110% of HB), thickly covered with very dark brown or black bristles above and below; longer black hairs form small pencil at tip in some individuals; a few pale hairs may occur on undersurface, especially on distal third of tail; colours above and below merge laterally. Skull large; rostrum rounded and wide (cf. *G. robustus*); upper incisors opisthodont, each incisor with clearly defined single groove. Males larger than ♀♀ for most body and cranial measurements. Width of M¹ 2.4–2.5 mm. Nipples: not known.



Gerbilliscus nigricaudus

Geographic Variation Two subspecies are recognized (Bates 1988):

G. n. nigricaudus: NE Tanzania and S Kenya. Larger size; tail black above and below.

G. n. nyama (incl. *percivali*): N Kenya and Somalia. Smaller size; tail black above, with some pale hairs below, especially on distal third.

Similar Species

G. robustus. Smaller HB; tail brown, often with black at tip or on all of upper surface; often black/brown pencil at terminal end; no white tip to tail; skull on average smaller in all dimensions.

G. validus. HB on average smaller; tail brown, normally without any black, no white tip to tail, no pencil at terminal end; skull usually smaller.

G. boehmi. HB smaller; tail brown, usually longer (actual length and relative to HB), white at terminal end; skull usually smaller.

Distribution Endemic to Africa. Somalia–Masai Bushland BZ. Savanna woodlands and grasslands of C and N Kenya east of the Rift Valley, extreme NE Tanzania, S Somalia and S Ethiopia.

Habitat Savanna woodlands with bushy thickets and scattered *Acacia*, *Stercularia* and *Terminalia* trees; also open grassy plains dominated by *Chrysopogon*, *Sehima* and other grasses (Meru N. P., Kenya; Neal 1984b). Habitat shows seasonal changes in cover and productivity; rainfall is bimodal with two wet seasons per year.

Abundance Distribution patchy, although probably relatively common in suitable habitats.

Adaptations Nocturnal and terrestrial. Individuals exhibit rapid response to seasonal changes in food availability (caused by seasonal changes in rainfall, number of arthropods and plant growth), which, in turn, regulates reproductive cycle (see below).

Foraging and Food Omnivorous and opportunistic. Pronounced seasonal changes in diet. In the dry seasons (in Meru N. P., Kenya; Neal 1984b) arthropods (mainly insects) comprise the main proportion of the diet (ca. 90%), with smaller amounts of seeds (1–9%) and forbs (1–3%). In the wet seasons, the proportion of arthropods drops (50–70%), and the proportions of grasses and sedges (3–13%), forbs and browse (13–20%) and seeds (7–23%) increase. In the period after the wet season and before the dry season begins, when the grasses have set seed, the diet is mainly seeds (53–62%) and insects (30–35%) with hardly any grass or forbs (Neal 1984a). Gerbils utilize the foods that, at each season, are common and provide the best source of energy and protein. The diet was similar to that of parapatric *Acomys wilsoni* and *Gerbilliscus robustus* (as *Tatera robusta*), which suggests possible competition for food between these species (Neal 1984a).

Social and Reproductive Behaviour No information.

Reproduction and Population Structure Seasonal reproduction, with two periods of breeding each year, correlate with the bimodal pattern of rainfall. Reproductive activity (pregnancies, number of corpora lutea in ovaries) was maximum during each of the two wet seasons per year (Nov–Jan, Apr–May), declined during the

early dry seasons and ceased at the end of each dry season (Sep and Mar) (Meru N. P., Kenya; Neal 1982). Weight of testes greater during and immediately after wet season than during dry season; no evidence that ♂♂ sexually inactive at any time of year. Embryo number: 5.22 (1–8, n = 37 litters). Litter-size increases with increasing maternal weight, and mean litter-size (regardless of maternal size) is higher in wet season (5.5) than in early dry season (4.2). Pregnancy rate: up to 50% of adult ♀♀ pregnant during wet seasons. Females may have three litters/year, and a reproductive capacity of up to 24 young/year (Neal 1982). Young conceived and born during wet seasons are recruited into the trappable population in Jan–Feb and Jul–Aug; maturity is attained by beginning of following wet season. Young born in early dry seasons fail to contribute to the population (perhaps due to early mortality?).

Predators, Parasites and Diseases No information.

Conservation IUCN Category: Least Concern.

Measurements

*Gerbilliscus nigricaudus**

HB (♂♂): 185.8 (178–193) mm, n = 4

HB (♀♀): 164.0 (130–164) mm, n = 6

T (♂♂): 200.8 (190–208) mm, n = 4

T (♀♀): 187.2 (170–204) mm, n = 6

HF (♂♂): 40.5 (40–41) mm, n = 4

HF (♀♀): 37.3 (34–39) mm, n = 6

E (♂♂): 22.3 (20–24) mm, n = 3

E (♀♀): 21.8 (21–24) mm, n = 6

WT (♂♂): 132 (80–195) g**

WT (♀♀): 114 (80–161) g**

GLS (♂♂): 48.7 (47.0–50.5) mm, n = 3

GLS (♀♀): 45.3 (43.1–47.9) mm, n = 6

GWS (♂♂): 25.3 (24.2–26.1) mm, n = 4

GWS (♀♀): 22.6 (21.9–23.2) mm, n = 5

M¹–M³ (♂♂): 7.0 (6.7–7.3) mm, n = 3

M¹–M³ (♀♀): 6.9 (6.7–7.0) mm, n = 4

Auditory bulla (♂♂): 14.5 (13.6–15.1) mm, n = 4

Auditory bulla (♀♀): 13.3 (12.7–13.8) mm, n = 6

Measurements: Kenya (Bates 1988)

Weight: Kenya (Neal 1982)

*As *Tatera nigricauda nigricauda*

**No sample size

Key References Bates 1985, 1988; Neal 1982, 1984a.

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Gerbilliscus phillipsi PHILLIPS'S GERBIL

Fr. Gerbille de Phillips; Ger. Phillips Nacktsohlen-Rennmaus

Gerbilliscus phillipsi (de Winton, 1898). Ann. Mag. Nat. Hist., ser. 7, 1: 253. Hanka Dadi, Somalia.

Taxonomy Originally described in the genus *Tatera* (see profile Genus *Gerbilliscus*). Often considered to be a subspecies of *G. robustus*, but raised to specific level by Bates (1985, 1988) on the basis of size (see also Musser & Carleton 1993). Synonyms: *bodessana*, *umbrosa* and probably *miniscula* (see Bates 1988). Subspecies: none. Chromosome number: not known.

Description Medium-sized gerbil, similar to *G. robustus*. Smallest species of *Gerbilliscus* in eastern Africa. Dorsal pelage pale brown to orange-brown, darker on lower back and rump; hairs grey at base, with dull pale orange-brown subterminal band and (especially on rump) black tip. Flanks paler, with fewer black-tipped hairs. Ventral pelage pure white, clearly delineated from colour of flanks. Lips, cheeks, throat and chest pure white. Ears large, slightly pigmented. Forefeet white above; five digits; Digits 1 and 5 short. Hindfeet white above; soles with brown pigment; Digit 1 short, not reaching base of other digits; Digits 2, 3 and 4 long, Digit 5 shorter; all digits with short pointed claws. Tail long (ca. 128% of HB), bicoloured, pale orange-brown above, white below; some black hairs above towards terminal end but without pencil or tuft. Skull: smaller than that of *G. robustus* (as *T. robusta*; Bates 1988).

Geographic Variation Populations in Kenya have darker pelage than those further north in Ethiopia and Somalia (Bates 1985).

Similar Species

G. robustus. On average larger in body and skull measurements (HB: 152.2 [120–190] mm; GLS: 41.9 [39.0–44.7] mm; GWS: 21.1 [19.5–22.4] mm). Tail usually with pencil.

Distribution Endemic to Africa. Somalia–Masai Bushland BZ. Recorded from NC Kenya, Ethiopia (Rift Valley) and Somalia.

Habitat Dry arid savanna, and semi-desert. In the Omo Valley of Ethiopia (Hubert 1978b) populations (recorded as *Tatera nigricauda*) occur in the treeless grasslands and thickets where the soils are heavy and clay-like; these grasslands are seasonally flooded. On the lower slopes of the valley they live in very arid habitats of tuffs and recently eroded sediments, which support a sparse arid vegetation (e.g. *Euphorbia*, *Adenium*).

Abundance The species has been recorded at only nine localities (Bates 1988). In the Omo Valley, Ethiopia, comprised 21% of small trappable rodents in tree and shrub habitats near the river (total $n = 19$, 4 spp.), 20% in grasslands near the river (total $n = 53$, the second most numerous of 8 spp.) and 6% in the arid habitats (total $n = 30$; 6 spp.).

*Gerbilliscus phillipsi*

Remarks Only found in dry habitats, so evidently well adapted to high temperatures and a lack of free water. Recorded in the same habitat in the Omo Valley as *Acomys wilsoni*, *Saccostomus mearnsi* and *Mastomys erythroleucus* (in grasslands), and *Taterillus harringtoni*, *Arvicanthis somalicus*, *Gerbillus pusillus* and *Xerus rutilus* (in arid habitats) (Hubert 1978b).

Conservation IUCN Category: Least Concern.

Measurements

Gerbilliscus phillipsi

HB: 136.3 (116–145) mm, $n = 9$

T: 174.1 (162–185) mm, $n = 9$

HF: 34.0 (32–37) mm, $n = 10$

E: 19.2 (17–21) mm, $n = 9$

WT: n. d.

GLS: 38.4 (37.6–39.2) mm, $n = 9$

GWS: 17.8, 19.4 mm, $n = 2$

M^1 – M^3 : 5.9 (5.6–6.2) mm, $n = 9$

Auditory bulla: 11.8 (11.4–12.4) mm, $n = 9$

Throughout geographic range (Bates 1988, as *Tatera phillipsi*)

Females only; external measurements of ♂♂ are larger than for ♀♀

Key References Bates 1985, 1988.

D. C. D. Happold

***Gerbilliscus robustus* FRINGE-TAILED GERBIL**

Fr. Gerbille robuste; Ger. Fransenschwanz-Nacktsohlen-Rennmaus

Gerbilliscus robustus (Cretzschmar, 1826). In: Rüppell, Atlas Reise Nordl. Afrika, Zool. Säugeth. 1: 75. Ambukol, Sudan.

Taxonomy Originally described in the genus *Tatera* (see profile Genus *Gerbilliscus*). The species of *Gerbilliscus* in eastern Africa – *G. robustus*, *G. validus*, *G. nigricaudus* and *G. phillipsi* – are morphologically similar, and positive identification requires consideration of a number of characteristics (see Table 23). Colouration of tail and length of hindfoot are not good diagnostic characters by themselves. The similarity between this species and *G. nigricaudus* has resulted in some specimens of *G. robustus* being incorrectly identified as *G. nigricaudus* (e.g. Delany 1964a, Hubert 1978b). This species is closely related to *G. validus*, and the two may, in fact, represent a single polymorphic species (D. Kock pers. comm.). Synonyms: *bayeri*, *bodessae*, *iconica*, *loveridgei*, *macropus*, *mombasae*, *muansae*, *pothae*, *shoana*, *swathlingi*, *taylori*, *vicina*. Subspecies: none. Chromosome number: $2n = 40$, $FN = 70$ (Omo Valley, Ethiopia; Bates 1988 as *T. robusta*).

Description Large dark-coloured gerbil. Pelage long and soft. Dorsal pelage dark brown, flecked with black. Dorsal hairs (12–15 mm long) grey at base, with cinnamon, dark brown or black tip. Flanks paler, orange-brown, with fewer black-tipped hairs. Ventral pelage pure white. Dorsal and ventral colours clearly delineated. Head blackish-brown, with sandy-brown cheeks. Eyes large, sometimes with black eye-rings. Black vibrissae. Ears large, rounded and naked. Chin, throat, neck and chest pure white. Fore- and hindlimbs pale brown above, white below. Soles of hindfeet naked, darkly pigmented. Tail long (ca. 115% of HB), thickly covered with small short hairs; colour varied – brown with varying amounts of black to nearly all black, usually with pencil of hairs on terminal third; paler below; upper and lower colours usually clearly delineated (see details below). Skull: rostrum long and narrow; width of M^1 : 2.0 (2.0–2.4) mm (cf. *G. validus*; see Table 23). Sexes similar in size. Nipples: not known.

Geographic Variation Dorsal pelage varies in different parts of geographic range. Individuals from semi-arid areas of Sudan are paler than those from Kenya and Tanzania. Tail colour varies geographically. In southern part of range (Tanzania), brown above with some brownish-black or black hairs at terminal end or on terminal half; white, ochre or pale brown below; in northern part of range (Ethiopia), mostly or completely black above; ochre or brown below (and sometimes with black on the terminal third). Individuals intermediate between these extremes in central part of range. Individuals with dark tails appear very similar to *G. nigricaudus* although, in most individuals, the tail is not pure black above and below as in *G. nigricaudus* (Bates 1985). The large amount of variation in this species was responsible for each variant being described originally as a new species (see synonyms).

Similar Species

G. validus. Slightly larger on average; tail ca. 95% of HB, usually without any black colouration; width of M^1 usually >2.5 mm.

G. nigricaudus. Tail ca. 100% of HB, always black above and below; width of M^1 2.4–2.5 mm.

*Gerbilliscus robustus*

G. phillipsi. On average smaller size; tail ca. 130% of HB, orange-brown above; width of $M^1 <2.1$ mm.

Distribution Endemic to Africa. Widespread in Somalia–Masai Bushland BZ, and in eastern parts of Sahel Savanna and Sudan Savanna BZs. Recorded from Tanzania, Kenya, Somalia, Ethiopia (below 1700 m) and Sudan. Probably extends westwards to Chad (and perhaps Burkina – see Bates 1985; Musser & Carleton 1993, 2005).

Habitat Savanna grassland plains, *Acacia* bush, *Salvadora* thickets and grassy edges close to forest. In Ethiopia, lives in arid habitats at lower altitudes (below ca. 1600 m). In Serengeti, Tanzania, habitats on the higher levels of a catena are preferred to those at the base of a catena which are flooded during the wet season (Senzota 1984). In Sudan, found in semi-arid sandy soils with sparse vegetation. Tends to prefer loose soils suitable for burrowing.

Abundance Very varied. Recorded as ‘numerous’ in Serengeti, Tanzania (Misonne & Verschuren 1966). The number of burrows in Serengeti (Senzota 1984) suggests high populations in suitable habitats. In some habitats in Turkana, Kenya, recorded as the second most numerous species (after *Arvicanthis* sp.) with densities of up to 4860 individuals/km² (= 48 ind/ha) and biomass of 287 kg/km² (= 2870 g/ha) (Coe 1972). In Karamoja, Uganda (as *Tatera nigricauda*) formed 4% of trappable small rodents (total $n = 51$; Delany 1964a).

Adaptations Nocturnal and terrestrial. An adaptable species living in a wide range of savanna habitats. Constructs burrows with

multiple tunnels and entrances up to 60 cm below the surface; a single burrow system may cover an area of 3×2 m. Entrances are marked by spillheaps, which kill the grasses and herbs buried under the spillheap. In areas of high populations, spillheaps may cover 2% of the land area (Senzota 1984). Composition of diet suggests flexibility in feeding, and also that free water is not required when conditions are dry. Very high rainfall and flooding in low-lying habitats may result in mortality when burrows are flooded. Species that live syntopically with *G. robustus* in Ethiopia include *Mastomys erythroleucus*, *Saccostomus mearnsi* and *Acomys wilsoni* (in grassy riverine habitats with thickets) (Hubert 1978b), and *Arvicanthus niloticus*, *Acomys subspinosus*, *A. dimidiatus* and *Saccostomus mearnsi* in Kenya (Bates 1988).

Foraging and Food Omnivorous. On the Rojewero Plains, Kenya, the diet (expressed as mean % density of fragments in stomach contents, $n = 7$ stomachs) was 57% seeds, 29% arthropods, 12% grass and sedge, and 5% insects (Neal 1984a). In Turkana, Kenya (a drier habitat), diet was soft fruits 26%, seeds 26%, coarse plant material 21%, leaves and flowers 13% and insects 14% (Coe 1972). These gerbils probably forage opportunistically and the diet changes seasonally (as for other species of *Gerbilliscus*).

Social and Reproductive Behaviour No information.

Reproduction and Population Structure In Kenya, reproduction is seasonal, with two periods of reproduction each year (as for *G. nigricaudus*), and is correlated with the bimodal pattern of rainfall. Pregnancies (counts and inferred by lactation) recorded in Jul–Aug and Nov–Jan. Embryo number 4.69 (2–7, $n = 13$) (Neal 1982). In Turkana (Coe 1972), and no doubt elsewhere, reproduction is very responsive to seasonal and annual variations in rainfall and climate.

Predators, Parasites and Diseases Preyed on by Spotted Eagle-owls *Bubo africanus* in Awash N. P., Ethiopia (Demeter 1982). Analysis of owl pellets showed that these gerbils comprised the largest number of individual prey items (27%) and the greatest mass of the prey (62%) in the diet. Also preyed on by small carnivores such as jackals in Serengeti, Tanzania.

Conservation IUCN Category: Least Concern.

Considered to be a pest in some localities where it feeds on crops such as cassava and groundnuts (Senzota 1984).

Measurements

Gerbilliscus robustus

HB: 152.2 (120–190) mm, $n = 74$

T: 177.1 (125–215) mm, $n = 74$

HF: 35.3 (21–40) mm, $n = 81$

E: 20.9 (13–28) mm, $n = 81$

WT: 103 (80–152) g, $n = ?$

GLS: 41.9 (39.0–44.7) mm, $n = 67$

GWS: 21.1 (19.5–22.4) mm, $n = 65$

M^1 – M^3 : 6.6 (5.9–7.2) mm, $n = 83$

Auditory bulla: 12.5 (11.4–13.4) mm, $n = 74$

Measurements: throughout geographic range (Bates 1988)

Weight: throughout geographic range (Neal 1982, as *Tatera robusta*)

Males only; mean measurements for ♀♀ are similar to those for ♂♂

Key References Bates 1985, 1988; Neal 1982, 1984a.

D. C. D. Happold

Gerbilliscus validus SAVANNA GERBIL (SOUTHERN SAVANNA GERBIL)

Fr. Gerbille de savanne; Ger. Savannen-Nacktschuh-Rennmaus

Gerbilliscus validus (Bocage, 1890). J. Sci. Math. Phys. Nat. Lisboa 2 (5): 6. Caconda, Angola. (Locality restricted: see Hill & Carter 1941).

Taxonomy Originally described in the genus *Tatera* (see genus profile). The definition of this species is uncertain. Musser & Carleton (1993) limit *Tatera valida* (now *Gerbilliscus validus*) to eastern and central Africa; in contrast, Bates (1988) considered *kempi* to be a synonym of *validus* and hence extended the distribution of *validus* to the western edge of West Africa. Here, following Musser & Carleton (1993, 2005), *kempi* and *validus* are considered to be separate species. The status of populations in the central part of the northern savannas, where the two species meet, is uncertain because few specimens are available. This species is closely related to *G. robustus*, and the two taxa may, in fact, represent a single polymorphic species (D. Kock pers. comm.). Chromosome numbers vary in different regions of the *validus*–*kempi* geographic range, and it is uncertain whether these represent chromosome polymorphism in a single species or are indicative of separate species. Synonyms: *liodon*, *neavei*, *taborae*. Subspecies: possibly two. Chromosome number: not known.

Description Large dark gerbil with relatively short tail. Dorsal pelage dark brown; hairs dark grey, with buff or black tip. Flanks paler; hairs grey with buff or brown tip. Ventral pelage pure white. Dorsal and ventral colours clearly delineated. Fore- and hindlimbs white or buffy-white. Soles of hindfeet deeply pigmented and naked. Digits with long pointed claws. Tail of moderate length (ca. 95% of HB), thickly covered with short hairs, brown above, pale below; without black hairs and without terminal pencil (cf. other *Gerbilliscus* spp.). Skull: rostrum short and broad; width of M^1 : 2.5 (2.2–2.8) mm (cf. *G. robustus*; see Table 23). Males often slightly larger than ♀♀. Nipples: 1 + 2 = 6, 2 + 2 = 8.

Geographic Variation Many variations have been reported (originally as species, now considered synonyms). Individuals from northern semi-arid regions (e.g. Sudan) are paler than those from mesic areas (e.g. near L. Victoria). Bates (1988) refers to two subspecies (southern: *kempi*; northern: *valida*), based on the shape of the anterior lamina of the first lower molar tooth.

Similar Species

G. robustus. Tail ca. 115% of HB, often black on upper terminal half of tail, paler below, some individuals may have almost all-black tails; width of M^1 2.0–2.4 mm.

G. nigricaudus. GLS longer; tail ca. 100% of HB, always black above and below; width of M^1 2.4–2.5 mm.

G. phillipsi. GLS on average smaller; tail ca. 130% of HB, orange-brown above; width of M^1 <2.1 mm.

Distribution Endemic to Africa. Zambezi Woodland BZ, and northwards to eastern parts of Guinea Savanna and Sudan Savanna BZs. Recorded from Angola, S and E DR Congo, Zambia, Tanzania, Uganda, Sudan and W Ethiopia. The western limit in the savanna zones north of Rainforest BZ is uncertain (see above). Musser & Carleton (2005) do not include Sudan in the distribution of this species, preferring to allocate the Sudanese populations (and those to the west) to *G. kempi*.

Habitat In Tanzania, prefers well-drained sandy soils on the edges of valley grasslands above the flood-plain. Also found in sandy alluvium along rivers, and in abandoned cultivations (Vesey-Fitzgerald 1966). Recorded from upland grassland savannas in DR Congo. In Ethiopia, found only in the dry river valleys and gorges, not on the plateaux.

Abundance Recorded as ‘particularly abundant’ along the edge of flood-plain grasslands in the Rukwa Valley ‘where honey-combed warrens may extend for many miles along a belt facing the tree line’ (Vesey-Fitzgerald 1966). No information from elsewhere.

Adaptations Nocturnal and terrestrial. Like *G. robustus*, these gerbils dig complex burrow systems with multiple entrances. Burrows are 45–60 cm deep, with a chamber, and a steeply ascending

escape passage. A burrow system may cover an area of about 2.4×1.4 m. Often there are many burrows close together forming a warren. Runways on the surface lead from one burrow to another, and sometimes between warrens. During the day, gerbils shelter in the burrows. During the dry season, they can exist without access to free water. Sedentary, rarely leaving the safety of the warrens (Vesey-Fitzgerald 1966, Delany 1975).

Foraging and Food Omnivorous and herbivorous. In Tanzania (Vesey-Fitzgerald 1966, as *Tatera valida*), underground parts of grasses and sedges are the principal food. Feeding activity in the soil under the warrens kills the herbaceous vegetation so the soil on the surface becomes completely bare. Also feeds on blades of green grass in the wet season. One stomach of an individual in Uganda was full of insect remains (Delany 1964a).

Social and Reproductive Behaviour Lives in small groups.

Reproduction and Population Structure In Queen Elizabeth N. P., Uganda, two periods of reproduction each year during the wet seasons (mostly May–Jul and Sep–Dec) (Neal 1982). Embryo number: 3 ($n = 1$), 4 ($n = 4$) (Delany & Neal 1969, Delany 1975). Sexual maturity when 90–100 g. Reproductive capacity appears to be low: the interval between litters recorded as 109 days, and hence production of young is only 8.5 young/female/year (Neal 1982). The structure of the population (based on HB length) shows that there are adults and subadults during most months of the year, with young animals predominating in Jun–Aug and Dec–Feb.

Predators, Parasites and Diseases Preyed on by Servals *Felis serval*, Wild Cats *Felis libyca*, Puff Adders and House Snakes (Tanzania; Vesey-Fitzgerald 1966).

Conservation IUCN Category: Least Concern.

Measurements

Gerbilliscus validus

HB: 167 (135–195) mm, $n = 57$

T: 157.2 (115–186) mm, $n = 58$

HF: 34.0 (30–39) mm, $n = 58$

E: 21.8 (17–29) mm, $n = 57$

WT: 129 (90–160) g, $n = ?$

GLS: 41.7 (38.5–44.7) mm, $n = 65$

GWS: 21.1 (19.1–22.2) mm, $n = 47$

M^1 – M^3 : 7.1 (6.1–7.8) mm, $n = 70$

Auditory bulla: 12.9 (11.5–13.8) mm, $n = 68$

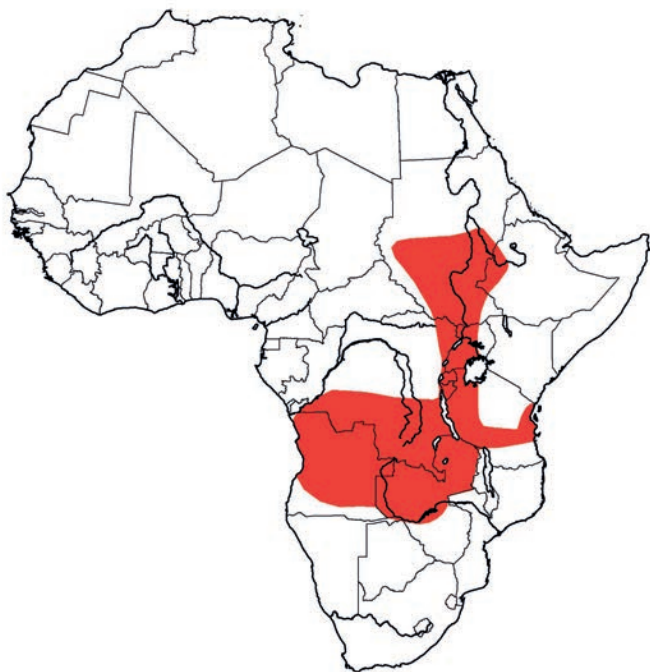
Measurements: throughout geographic range (Bates 1988, as *Tatera valida*)

Weight: Uganda (Neal 1982, as *Tatera valida*)

Males only; mean measurements for ♀♀ are slightly smaller than for ♂♂

Key References Bates 1988; Vesey-Fitzgerald 1966.

D. C. D. Happold



Gerbilliscus validus

GENUS *Gerbillurus*

Hairy-footed Gerbils

Gerbillurus Shortridge, 1942. Ann. S. Afr. Mus. 36 (1): 52. Type species: *Gerbillus vallinus* Thomas, 1918.



Gerbillurus vallinus.

The genus contains four species, which are restricted to the South-West Arid BZ and live in desert or semi-desert regions. The genus is characterized by small body size, long tail with variable terminal pencil, partially furred soles of the elongated hindfeet, large eyes and long rounded ears. Dorsal pelage varies from pale blonde to dark reddish-brown, with considerable geographic variation. Ventral pelage is always white (as in *Gerbillus*). The skull has inflated auditory bullae; molar teeth lack longitudinal crests connecting tooth cusps (cf. *Gerbillus*) (Figure 49).

The genus is the ecological equivalent of the genus *Gerbillus* of the arid regions of North Africa. *Gerbillurus* species move by quadrupedal saltation, and are capable of leaping up to four times their body length in a single hop. All species in the genus live in arid or semi-arid regions with scant vegetation. They dig their own simple burrows in sand or gravel, and each burrow contains a nest of shredded vegetation. Their diet varies according to the season; although mainly herbivorous, they eat seeds and insects at some times of the year. All species have good water-conserving abilities – concentrated urine, low faecal water loss and low water turnover. They avoid extreme daytime temperatures by remaining in their burrows where temperature and humidity are stable, and

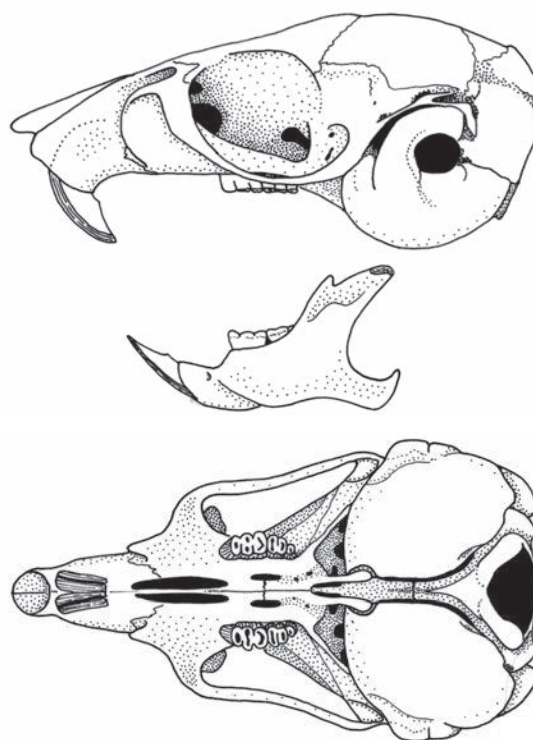


Figure 49. Skull and mandible of *Gerbillurus vallinus* (BMNH 25.1.2.85).

restricting activity to cooler nights. Sporadic population explosions have been reported in some species.

Gerbillurus was originally described as a subgenus of *Gerbillus*, but raised to generic rank by Shortridge (1942), a determination followed by Davis (1975a) and Musser & Carleton (1993, 2005). Molar enamel patterns indicate a closer relationship with *Gerbilliscus* (formerly *Tatera*) than with other gerbil groups. Chromosomal data support the close relationship between *Gerbillurus* and *Gerbilliscus*, with *Desmodillus* more distantly related (Qumsiyeh *et al.* 1991).

Table 24. Species in the genus *Gerbillurus*. Arranged in order of increasing mean head and body length.

| Species | HB
mean (range)
(mm) | T
mean (range)
(mm) [% of
HB] | Bulla length
mean (range)
(mm) | Tympanic
bulla
extends
posteriorly
to occiput | Posterior
palatine
foramina
mean (range)
(mm) | Chromosome
number | Notes |
|--------------------|----------------------------|--|--------------------------------------|---|---|----------------------|---|
| <i>G. paeba</i> | 96 (85–105) | 113 (102–125)
[120%] | <9 | No | >1.6 | 2n = 36,
FN = 68 | South-West Arid
BZ; widespread and
common |
| <i>G. tytonis</i> | 99 (90–108) | 126 (113–141)
[128%] | 9.8 (9.3–10.4) | Yes | 1.1 (0.6–1.6) | 2n = 36,
FN = 68 | SW Namibia; dunes of
Namib Desert |
| <i>G. vallinus</i> | 101 (96–110) | 138 (119–156)
[140%] | 10.6 (10–11) | Yes | 2.0 (1.4–2.5) | 2n = 60;
FN = 80 | West of South-West
Arid Zone; bare gravels |
| <i>G. setzeri</i> | 105 (104–118) | 127 (113–145)
[120%] | 11.4 (10.6–
12.4) | Yes | 2.3 (1.8–2.7) | 2n = 60;
FN = 76 | Namib Desert; gravel
plains |

The genus *Gerbillurus* may be divided into three subgenera: *Progerbillurus* (containing only *G. paeba*) characterized by small HB (mean 96.5 mm), small skull length (mean 28.6 mm) and small mean auditory bullae length (<9 mm); *Paratatera* (containing only *G. tytonis*) characterized by moderate HB (mean 99 mm), moderate skull length (mean 99 mm) and auditory bullae 9.3–10.1 mm; and *Gerbillurus* (*G. setzeri*, *G. vallisus*) characterized by the largest HB (means 101, 105 mm), largest skull length (29.9, 31.4 mm) and the longest auditory bullae (10.6–12.4 mm). These subgenera roughly correspond to the ‘*paeba* group’ (*G. paeba* only) and the ‘*vallisus* group’ (the other three species) of Schlitter (1973). Chromosomal data and habitat selection suggest that *G. paeba* and *G. tytonis* (both $2n = 36$,

$FN = 68$, preferring areas of loose sand) are closely related, while *G. setzeri* ($2n = 60$, $FN = 76$) and *G. vallisus* ($2n = 60$, $FN = 80$) form a second phylogenetic group, which are associated with gravel plains (Qumsiyeh *et al.* 1991).

The species may be distinguished on body size, relative length and form of tail, length of auditory bullae, length of posterior palatine foramina and chromosome number (Table 24). They are also distinguished by habitat, with *G. paeba* being far more widespread than the three specialist species.

Edith R. Dempster

Gerbillurus paeba PYGMY HAIRY-FOOTED GERBIL (PAEBA HAIRY-FOOTED GERBIL)

Fr. Gerbille pygmée à pieds velus; Ger. Paeba Zwergrennmaus

Gerbillurus paeba (A. Smith, 1836). Rept. Exped. Exploring Central Africa, app. p. 43.
‘Country beyond “Latakoo”; Vryburg, Northwest Province, South Africa’ (Roberts 1951).

Taxonomy Originally described in the genus *Gerbillus*. *Gerbillurus paeba* is the most widespread, generalized and primitive species of the genus, in contrast to the specialized desert species. Now assigned to *Gerbillurus*, subgenus *Progerbillurus* (see profile Genus *Gerbillurus*). Karyotypically similar to *G. tytonis*. Synonyms: *broomi*, *calidus*, *coombsi*, *exilis*, *infernus*, *kalaharicus*, *leucanthus*, *mulleri*, *oralis*, *swakopensis*, *swalius*, *tenuis*. Subspecies: five. Chromosome number: $2n = 36$, $FN = 68$ (Schlitter *et al.* 1984; Qumsiyeh 1986). Karyotypically similar to *G. tytonis*.

Description Small hairy-footed gerbil with white underparts, darker dorsal surface and long slightly tufted tail; the smallest species of the genus. Dorsal pelage varies with locality (see below) from reddish-orange to greyish-red or pale cinnamon-buff, with admixture of dark hairs. Colour of dorsal pelage matches colour of substrate. Ventral pelage pure white from chin to tail tip, extending to fore- and hindfeet and well up on to flanks. Head narrow, with pointed nose. Sides of muzzle white. Large deep reddish-brown eyes; small white supraorbital patch, not always discernible. Ears long and rounded, sparsely haired, paler colour than dorsal pelage, with darker margin. Hindlimbs much longer than forelimbs. Forefeet and hindfeet pure white, five digits each, fairly long claws; Digit 5 on forefeet reduced. Hindfeet elongated, soles of hindfeet furred except for a naked central line. Tail long (ca. 120% of HB), same colour as dorsal pelage above, white below; slightly tufted at tip. Skull: posterior palatal foramina >1.6 mm, auditory bullae slightly inflated posteriorly and laterally (8.91 [8.08–9.24] mm) but not extending posteriorly beyond occiput (cf. other spp. of genus). Nipples: $1 + 2 = 6$.

Geographic Variation

G. p. exilis: Alexandria dune field, Eastern Cape Province, South Africa. Larger than *G. p. paeba*; colour of dorsal pelage pale cinnamon-buff.

G. p. paeba: widely distributed throughout arid areas from SW Angola to Western Cape and Eastern Cape Provinces, South Africa. Size as described above; colour of dorsal pelage pale reddish-orange, but considerable variation.



Gerbillurus paeba

G. p. infernus: Skeleton Coast, Namibia.

G. p. coombsi: Soutpansberg, Limpopo Province, South Africa. Smaller than *G. p. paeba*.

G. p. mulleri: Cape Flats, Western Cape Province, South Africa. Larger than *G. p. paeba*, colour of dorsal pelage distinctive grey.

Similar Species

G. tytonis. Darker colour, larger size, longer hindfeet with splayed toes and distinctive fringe on digits, longer tail.

G. setzeri. Paler colour, larger size, distinct pencil at tip of tail.

G. vallisus. Darker colour, larger size, longer tail.

Distribution Endemic to Africa. South-West Arid and South-West Cape BZs. Recorded in SW Angola, Namibia, Botswana, W

Zimbabwe, W Mozambique and South Africa (Northern, Western and Eastern Cape Provinces). Substrate and vegetative cover are important habitat factors determining distribution. Isolated populations occur in the Alexandria dunefield of Eastern Cape Province, and relict patches of Kalahari sand in Limpopo Province, South Africa.

Habitat Arid or semi-arid environments with sandy soil or sandy alluvium, and with scant cover from grass, scrub, or occasionally light woodland. Absent from rocky areas and deep sand dunes of the Namib Desert (Griffin 1990) and consolidated soils in NE Botswana. Common in the Kalahari Desert in lightly vegetated dune slopes, calcrete river banks and pans with fine soil. Avoids areas of high plant diversity, and prefer more compact soil in inter-dune valleys than areas of deep sand in the eastern Namib Desert (Perrin *et al.* 1999a). *G. p. coombi* is restricted to sandy areas in Soutpansberg area of Limpopo (Rautenbach 1978), and *G. p. exilis* prefers dune valleys to dune crests in a coastal dunefield at Alexandria, Eastern Cape (Ascaray 1986).

Abundance Common throughout distribution range, and subject to massive fluctuations in population numbers. The most abundant rodent species in the Kalahari Desert, comprising 90% of the total rodent community in sand dune habitat and 54% in river bed habitat (Nel 1983). In the pro-Namib, density increases from near zero to 59/ha following good rains, and after experimental water provisioning and burning (Christian 1979a). Density of *G. p. paeba* varied from 1.0 to 7.7/ha in the eastern Namib Desert during 1984–85 (Perrin & Boyer 2000), while population density of *G. p. exilis* in Alexandria dunefields ranged from 0.7 to 3.3/ha (Ascaray *et al.* 1991).

Adaptations Terrestrial and nocturnal. Moves by quadrupedal saltation, and may leap up to 26 cm in one hop. Sandbathes frequently to maintain coat condition. *Gerbillurus p. paeba* in the Namib Desert excavate simple, unbranched burrows, with a single entrance leading to a blind-ending tube. Some burrows contain a wider nest area off the main tunnel. *Gerbillurus p. exilis* constructs complex, branched burrows, with entrance hidden in vegetation, never plugged with sand. Nests are cup-shaped, and constructed of shredded vegetation. Food caches containing seeds, leaves and insects are found in some tunnels. Burrow temperatures in Namib are stable at 22.9–24.4 °C at surface temperatures of 15.8–28.4 °C. Burrow humidity varies with weather conditions, being highest early morning and during fog or cloudy weather.

Avoids extreme aridity and temperature by nocturnal activity and fossorial habits rather than physiological adaptations. Preferred ambient temperature in laboratory trials (ca. 28 °C) slightly higher than mean burrow temperature in field. Body temperature is maintained at ca. 36–39 °C over range of ambient temperatures of 5–30 °C. Animals cannot survive ambient temperatures above 35 °C for more than one hour.

Energy is conserved by having a lower basal metabolic rate at thermoneutrality (32.3–35.1 °C) and slightly lower thermal conductance than expected for its body mass. Behavioural avoidance of high temperatures reduces the need for costly evaporative cooling mechanisms, thus conserving energy and water.

Renal function is efficient, but a diet of insects or succulent plant material is required to maintain water balance. Field water turnover

rate varies with environment from 85 ml/kg/day in the central Namib Desert to 232 ml/kg/day on the Namibian coast, both measurements taken in summer (Mar). Water turnover rate and urine osmolarity in captive animals varies with protein content and potential water yield of the diet. When deprived of water, a precipitate of allantoin contributes to reducing overall water output (Perrin *et al.* 1999a).

Foraging and Food Omnivorous and opportunistic; diet varies according to availability of suitable food. Principal foods of *G. p. exilis* are seeds of littoral marine plants, although arthropods are preferred in summer. The diet of *G. p. paeba* in the Karoo is, on average, 36.2% seeds, 46.8% foliage and 17.1% insects, with more seeds consumed in summer and autumn, more foliage in winter and more insects in spring (Kerley 1989). In the Kalahari, the diet of *G. p. paeba* was 76.4% white plant material, 23.6% green plant material and 0% insects in winter, changing to 39.3%, 43.8% and 16.8%, respectively, in summer (analysis of stomach contents; Nel 1978). In the E Namib Desert, *G. p. paeba* is mainly insectivorous and has little seasonal variation in diet (3.8% seeds, 40.6% green plant material, 52.9% arthropods and 3.0% unidentified material). Plant growth and production are affected by the foraging activities of *G. p. paeba* on the inter-dune plains of the eastern Namib, but impact is local and transient. Removal of green parts of plants may adversely affect plant growth, and seed predation may adversely affect plant species diversity (Perrin *et al.* 1992).

Social and Reproductive Behaviour *Gerbillurus p. paeba* is very active and aggressive in laboratory encounters. Simple burrow structures, and scattered nature of burrows, supports the view that *G. paeba* is solitary and intolerant of conspecifics. In staged laboratory encounters, *G. p. exilis* is less aggressive and active than *G. p. paeba*, with ♂♂ frequently seeking contact with conspecifics. Aggressive behaviour is expressed in the form of chasing, with occasional bouts of mutual 'boxing' rather than biting and kicking. May be displaced by *G. tytonis*, a more aggressive species, from favoured habitats where the two species are sympatric in the E Namib Desert.

Two of the subspecies, *G. p. paeba* and *G. p. exilis*, show no significant preference for odours of their own subspecies, and do not discriminate between potential mates of their own and a different subspecies in staged encounters. Acoustic communication occurs through footdrumming with the hindfeet, and ultrasonic whistles. In *G. p. paeba* and *G. p. exilis* ultrasonic whistles consist of strongly modulated whistles lasting about 78 msec, and broadband clicks with a duration of 21–22 msec. Main frequency range of whistles is 57–70 kHz, for *G. p. paeba* is 57–70 kHz, and 46–57 kHz for *G. p. exilis* (Perrin *et al.* 1999a).

Reproduction and Population Structure In Botswana, pregnant ♀♀ were recorded in all months of the year except Apr, May, Sep and Nov (sample sizes 7–61/month; n = 304 ♀♀); pregnancy rate in the months when pregnant ♀♀ were recorded was 8% to 28% (Smithers 1971). In E Namib Desert, reproductive activity was confined to mid- to late summer (Dec–Apr). Juvenile recruitment occurs during autumn and early winter (Feb–Jun) (Perrin & Boyer 2000). Increased population density follows summer rainfall in the Namib Desert (Christian 1979a, b), Kalahari Desert (Nel 1978) and in the Karoo (Kerley 1990).

Increased photoperiod stimulates reproduction in captivity. Oestrus cycle of *G. p. paeba* lasts 6–7 days, while that of *G. p. exilis* lasts 7–8 days in captivity. Litter-size: 3.7 (2–5, $n = 39$; wild-caught ♀♀, Botswana; Smithers 1971); 4.6 (1–6, $n = 7$; captive ♀♀; Perrin *et al.* 1999a); 3.7 (2–6, $n = 10$; *G. p. exilis*; captive ♀♀; Ascaray 1986). Gestation (*G. p. exilis*): 21 days. Females give birth in underground nests, and rarely leave the neonates during the first few days of life. Young altricial at birth; mean weight at birth 1.9 g ($n = 23$). Growth rate in first 21 days: 0.4 g/day. Incisors erupt at Day 12. Eyes open at Day 14–18. Weaning from Day 21 (Ascaray 1986, Perrin *et al.* 1999a). Young do not nipple-cling.

Predators, Parasites and Diseases Major predators in pro-Namib Desert and Alexandria dunefields are Spotted Eagle-owls *Bubo africanus* and Black-backed Jackals *Canis mesomelas*. Also taken by Large-spotted Genets *Genetta tigrina* in the Alexandria dunefields. Host to 11 species of fleas, two species of mites and one species of tick (details in De Graaff 1981), including some of economic importance.

Conservation IUCN Category: Least Concern.

Measurements

Gerbillurus paeba

HB: 96.5 (85–105) mm, $n = 40$

T: 113 (102–125) mm, $n = 40$

HF: 27 (26–29) mm, $n = 40$

E: 17 (16–19) mm, $n = 40$

WT: 25.4 (20–37) g, $n = 40$

GLS: 28.6 (27.1–30.0) mm, $n = 8$

GWS: 14.6 (14.0–15.0) mm, $n = 8$

M¹–M³: 4.0 (3.4–4.5) mm, $n = 8$

Body measurements and weight: SW Botswana (Smithers 1971)

Skull measurements: South Africa (TM)

Animals from E Namib Desert, Namibia, are generally smaller than those from Botswana, e.g. HB: 86.3 ± 6.3 mm, $n = 92$; T: 108.4 ± 8.9 mm, $n = 87$; HF: 28.1 ± 1.2 mm, $n = 92$; E: 12.6 ± 1.0 mm, $n = 92$; WT: 22.2 ± 0.3 g, $n = 178$ (mean \pm 1 S.E.; D. C. Boyer unpubl.)

Key References Ascaray 1986; Nel 1978; Perrin & Boyer 2000; Perrin *et al.* 1999a.

Mike Perrin & Edith R. Dempster

Gerbillurus setzeri SETZER'S HAIRY-FOOTED GERBIL

Fr. Gerbille pygmée de Setzer; Ger. Setzers Zwergrennmaus

Gerbillurus setzeri (Schlitter, 1973). Bull. S. California Acad. Sci. 72: 13. One mile east of the Namib Desert Research Station, Gobabeb, Namibia.

Taxonomy Originally described in the genus *Gerbillus* (subgenus *Gerbillurus*). Together with *G. vallinus*, assigned to the subgenus *Gerbillurus* (see profile Genus *Gerbillurus*). Synonyms: none. Chromosome number: $2n = 60$, FN = 76 (Schlitter *et al.* 1984, Qumsiyeh *et al.* 1991) Karyotypically similar to *G. vallinus*.

Description Small, robust pale-coloured gerbil, the largest of the species of *Gerbillurus*. Dorsal pelage pale sandy-brown (never reddish or rusty coloured); hairs pale slate-grey on basal half, pale sandy on terminal half. Flanks paler. Ventral pelage pure white. Colour of ventral pelage clearly delineated from dorsal pelage. Cheeks, chin and throat white. Large eyes with supraorbital white patch, which may be indistinct. Ears pale, unpigmented, sparsely covered with hairs that are same colour as on dorsum. Well-developed black and white vibrissae. Fore- and hindlimbs white. Forelimb with five digits; Digits 2–5 with claws, Digit 1 reduced without claw. Hindlimbs with five digits, each with claw and dense white hairs on undersurface of digit. Soles of hindfeet pale and hairy. Tail long (ca. 120% of HB), same colour as dorsal pelage above, white below, with well-developed grey pencil on distal one-third. Skull: auditory bullae inflated posteriorly and laterally (oblique length 10.6–12.4 mm (Schlitter 1973) extending posteriorly to occiput. Nipples: $1 + 2 = 6$.

Geographic Variation None recorded.

Similar Species

G. paeba. Similar colour where sympatric; on average smaller; tail without distinct pencil; $2n = 36$.

G. tytonis. Darker colour; on average smaller; slightly longer tail relative to body size; no distinct pencil, $2n = 36$.

G. vallinus. Darker colour; on average smaller; longer tail relative to body size.



Gerbillurus setzeri

Distribution Endemic to Africa. South-West Arid BZ (Namib Desert). Recorded from the Kuiseb R., Namibia, northwards to S Angola (Schlitter 1973).

Habitat Restricted to hot, dry gravel plains with shallow, semi-compacted soil lacking vegetation (Dempster *et al.* 1998). Occasionally disperse to adjacent sand dunes during periods of high population density (Schlitter 1973).

Abundance No detailed data on density, demography, or use of space. Trapping success in suitable habitat ranges from 4% in wet years to 0.1% in drought years. Occasionally, trap success is higher (9%) in selected habitats (Griffin 1990).

Adaptations Terrestrial and nocturnal. Moves by quadrupedal saltation. Excavates burrows in loose soil in dry river washes. Burrows are branched, with two or more entrances, average depth 281 mm and length about 2 m. Burrows contain stored food and nest of shredded vegetation, and provide a stable microenvironment when external conditions are extremely hot or cold.

Avoid extreme aridity and temperature by nocturnal activity and fossorial habits rather than physiological adaptations. Preferred ambient temperature in laboratory trials ca. 28°C, which is the mean burrow temperature in the field. Body temperature ranges from ca. 36°C to 38°C, with good thermoregulation below ambient temperature of 25°C. Reduces overheating above thermoneutral zone (32.2–34.8°C) by increasing dry thermal conductance, accompanied by small increase in oxygen consumption, thus avoiding evaporative water loss for cooling. Relatively large size and thick pelage facilitates thermal conductance and reduces the difference between total water loss and metabolic heat production. Above ambient temperature of 35°C, pulmocutaneous water loss increases sharply, while peripheral vasodilation and piloerection aid cooling. Animals cannot survive ambient temperatures above 35°C for more than one hour.

Low water turnover rate, low faecal water loss and high urinary concentrating ability enable indefinite survival in arid environments without free water. Urine osmolarity varies with diet in laboratory, being higher on a diet of arthropods or seeds without fresh vegetables than on a diet that includes fresh vegetables or water. Urine osmolarity in natural conditions is generally higher than in the laboratory. Urea concentration in urine varies with diet, being higher on seed diet than on arthropod diet. Urinary concentrating ability is the highest of all *Gerbillurus* species, enhanced by the conversion of urea to allantoin. Kidney structure is characterized by extremely long loops of Henle and a well-developed papilla renalis that extends into the ureter, thus promoting very efficient reabsorption of water from urine (Dempster *et al.* 1998).

Foraging and Food Omnivorous. Stomach contents of five individuals contained 50% arthropods, 40% plant material and 10% seeds (Perrin *et al.* 1992). Caches from burrows in C Namibia contained chewed vegetation and arthropod remains (Dempster *et al.* 1998).

Social and Reproductive Behaviour Less active than other *Gerbillurus* species, with little aggressive behaviour in staged laboratory encounters, indicative of a more tolerant social system than in other *Gerbillurus* species. Occasional aggressive bouts include chasing, interspersed with 'boxing', during which antagonists stand upright on toes of hindfeet, and rake each other with forepaws. Mating observed once only: a single mount with intromission, lock and single ejaculation. Copulatory plug deposited with ejaculate. Acoustic communication includes foot drumming with both hindfeet, and ultrasonic whistles at 39–49 kHz. Vocalizations are associated with sexual behaviour and contact-promoting behaviour (Dempster *et al.* 1998).

Reproduction and Population Structure Animals in breeding condition have been trapped throughout the year. Information available for one litter born in captivity. Gestation: 21 days. Litter-size: 3. Young altricial at birth; mean weight at birth: 2.3 g. Growth rate in first 23 days: 0.7 g/day. Eyes open Day 18. Young do not nipple-cling. Young vocalize at audible frequencies and also ultrasonically at 45–55 kHz (Dempster & Perrin 1991b).

Predators, Parasites and Diseases No information.

Conservation IUCN Category: Least Concern.

Measurements

Gerbillurus setzeri

HB: 105.6 (104–118) mm, n = 43

T: 127.4 (113–145) mm, n = 43

HF: 32.5 (30–35) mm, n = 44

E: 13.9 (12–16) mm, n = 43

WT: 36.7 (30–43) g, n = 17

GLS: 31.4 (29.5–32.6) mm, n = 23

GWS: 16.6 (15.7–17.4) mm, n = 29

M¹–M³: 4.3 (4.1–4.6) mm, n = 19

Auditory bulla: 10.6–12.4 mm

Namibia (Schlitter 1973)

Key References Dempster *et al.* 1998; Schlitter 1973.

Mike Perrin & Edith R. Dempster

Gerbillurus tytonis DUNE HAIRY-FOOTED GERBIL

Fr. Gerbille pygmée des dunes; Ger. Dünen-Zwergrennmaus

Gerbillurus tytonis (Bauer and Niethammer, 1960). Bonn. Zool. Beitr. 10: 236–261 (1959, publ. 1960). Sossusvlei, Namib Desert, Namibia.

Taxonomy Originally described as a subspecies of *Gerbillus vallinus*, but raised to specific rank (as *Gerbillus tytonis*) by Schlitter (1973); and then placed in the genus *Gerbillurus* by Davis (1975a) (see Meester *et al.* 1986). Now assigned to the subgenus *Paratatera* (see

profile genus *Gerbillurus*). Synonyms: none. Chromosome number: 2n = 36, FN = 68 (Schlitter *et al.* 1984, Qumsiyeh *et al.* 1991). Karyotypically similar to *G. paeba*.

Description Small hairy-footed gerbil with white underparts, darker dorsal surface and very long slightly tufted tail. Dorsal pelage rich reddish-brown; dorsal hairs dark at base, changing to reddish-brown distally. Ventral pelage white from chin to tail tip, extending to fore- and hindfeet and well up on to flanks. Sharp delineation between dorsal and ventral pelage colours. Head narrow, with pointed nose. Sides of muzzle white. Large eyes with small white supraorbital patch. Ears long and rounded, sparsely haired, paler than dorsal pelage, with narrow fringe of black pigmentation on lateral margin. Hindlimbs much longer than forelimbs. Fore- and hindfeet pure white, five digits each foot, Digit 5 on forefoot reduced. Hindfeet elongated with splayed digits; soles well furred, with distinctive fringe of hair along sides of each digit. Tail long (ca. 128% of HB), brown above, white below with variable pencil of greyish hairs at distal end. Skull: extremely short posterior palatal foramina (0.6–1.6 mm, $n = 57$); auditory bullae inflated (9.3–10.4 mm long) extending posteriorly to occiput. Nipples: $1 + 2 = 6$.

Geographic Variation None recorded.

Similar Species

G. paeba. Paler colour; narrower hindfeet without distinctive fringe on digits.

G. setzeri. Paler colour; on average larger; narrower hindfeet without distinctive fringe on digits.

G. vallinus. Darker colour; narrower hindfeet without distinctive fringe on digits.

Distribution Endemic to Africa. South-West Arid BZ (Namib Desert). Recorded only from coastal and inland dune systems of SW Namibia, from Swakopmund to Luderitz.

Habitat Restricted to hot, dry areas of shifting red sand-dunes of the Namib Desert where mean annual temperature exceeds 18 °C



Gerbillurus tytonis

and mean annual rainfall is less than 125 mm. Prefers zones within the dune system with comparatively high plant species richness (2–3 species), and avoids compact soils such as inter-dune valleys (Perrin & Boyer 1996). Digs burrows in sand stabilized by *Trianthema hereroensis* or *Stipagrostis sabulicola* and in islands of microhabitat formed by nara (*Acanthosicyos horrida*) (Hughes *et al.* 1994, Perrin *et al.* 1999b). In the dry Swakop river bed, prefers nara (*Acanthosicyos horrida*) habitat to adjacent grassland, where it occurs sympatrically with *Rhabdomys pumilio*.

Abundance The most abundant species of rodent occurring in the Namib Desert sand sea, and the only gerbil species permanently resident in this habitat. Population density varies from low in summer to high in autumn: 2–18.2/ha at Bushman's Circle, 0.3–6.3/ha at Far East and 0.8–7.8/ha at Nara Valley (Perrin & Boyer 2000).

Adaptations Terrestrial and nocturnal. Moves by quadrupedal saltation, leaping up to 41 cm in a single hop in open habitat. Sandbathes frequently to maintain coat condition. Burrows are branched or unbranched, having one or two entrances, with an average depth of 285 mm and about 1 m long. Burrows contain a nest of shredded vegetation and food caches.

Avoids extreme aridity and temperature by nocturnal activity and fossorial habits rather than physiological adaptations. Preferred ambient temperature in laboratory trials ca. 28 °C, slightly lower than mean burrow temperature (30 °C) in the field. Regulates body temperature at ca. 35–37 °C over range of ambient temperatures of 5–30 °C. Above ambient temperature of 35 °C, pulmocutaneous water loss increases sharply, while peripheral vasodilation and piloerection aid cooling. Animals cannot survive ambient temperatures above 35 °C for more than one hour. Energy is conserved by having lower basal metabolic rate at thermoneutrality (32.4–34.9 °C) and slightly lower thermal conductance than expected for body mass. Behavioural avoidance of high temperatures reduces the need for costly evaporative cooling mechanisms, thus conserving energy and water.

Field water turnover rate almost twice as high in summer as in winter, and is associated with change in diet. Urine osmolality varies with diet in laboratory, being higher on diets of arthropods or seeds without fresh vegetables than diets including fresh vegetables or drinking water. Urine osmolality in natural conditions is generally higher than laboratory measurements. Maintains body mass without access to succulent vegetation or drinking water, provided that diet includes arthropods; loses body mass on dry seeds alone.

Urea concentration in urine varies with diet, being higher on seed diet than on arthropod diet. Urine contains crystalline allantoin, which aids hyperosmotic urine production. Elongated papilla renalis extends into the ureter, promoting reabsorption of water from urine (Perrin *et al.* 1999b).

Foraging and Food Omnivorous and opportunistic. Diet contains more seeds in winter than in summer (0.2–33% in winter, 0–9.5% in summer), more green plant material in spring and summer than winter (28.8–57.7% in summer, 0.9–28% in winter), and more invertebrates in spring and summer than during other seasons (9.4–94% in summer, 23.5–75% in winter). Considerable variation exists between individuals, localities and seasons (Perrin *et al.* 1999b). In nara habitat, foraging activity decreases at periods of full moon and

decreases in the presence of competitors such as *Rhabdomys pumilio*. High predation risk in grassland habitat results in lower levels of foraging activity than in nara habitat (Hughes *et al.* 1994).

Social and Reproductive Behaviour The most aggressive and active of all *Gerbillurus* species. Dominance established in laboratory encounters by prolonged chasing rather than by contact fighting. Agonistic behaviour includes frequent bouts of mutual boxing, with both antagonists standing upright on toes of hindfeet. Males identify oestrous ♀♀ by chemosignals deposited on substrate during urination, defecation, sandbathing or walking. Mating observed twice: copulation characterized by lock lasting 20–26 sec and a single ejaculation. Copulatory plug deposited with ejaculate.

Acoustic communication includes footdrumming with both hindfeet and ultrasonic calls in the form of ‘stuttering’ (a series of clicks at 11–34 kHz) and strongly modulated whistles at 48–63 kHz. Vocalizations are associated with sexual and contact-promoting behaviour, and rarely accompany non-contact and agonistic behaviour. Ultrasonic vocalizations accompanied copulation in two observed copulations (Perrin *et al.* 1999b).

Reproduction and Population Structure Reproduction is seasonal, with peak recruitment during summer. Adult ♂♂ have scrotal testes throughout the year, whereas only 25–50% of adult ♀♀ are reproductively active during summer (Dec–May) and no ♀♀ are reproductively active during winter (May–Nov) (Perrin & Boyer 2000). Oestrous cycle lasts six days. Litter-size in captivity:

4.4 (2–6, *n* = 7 litters). Young altricial at birth; mean weight at birth: 1.9 g (*n* = 22). Growth rate in first 28 days: 0.4 g/day. Hair visible Day 10–13. Eyes open Day 22–24. Young do not nipple-cling (Perrin *et al.* 1999b).

Predators, Parasites and Diseases Major predators are Spotted Eagle-owls *Bubo africanus* and Black-backed Jackals *Canis mesomelas*.

Conservation IUCN Category: Least Concern.

Measurements

Gerbillurus tytonis

HB: 99.2 (90–108) mm, *n* = 55

T: 126.5 (113–141) mm, *n* = 55

HF: 33.4 (28–36) mm, *n* = 57

E: 13.0 (12–14) mm, *n* = 57

WT: 24.9 ± 0.3 g, *n* = 168

GLS: 29.3 (28.1–30.4) mm, *n* = 43

GWS: 15.6 (14.2–16.6) mm, *n* = 43

M¹–M³: 4.2 (4.0–4.5) mm, *n* = 50

Auditory bulla: 9.3–10.4 mm

Namib Desert (Schlitter 1973)

Key References Perrin *et al.* 1999b; Schlitter 1973.

Mike Perrin & Edith R. Dempster

Gerbillurus vallinus BRUSH-TAILED HAIRY-FOOTED GERBIL

Fr. Gerbille pygmée à queue touffue; Ger. Pinselschwanz-Zwergmaus

Gerbillurus vallinus (Thomas, 1918). Ann. Mag. Nat. Hist., ser. 9, 2: 148.

Tuin, near Kenhart, Hartebeest R., 29° S 21° E, Bushmanland, Northern Cape Province, South Africa.

Taxonomy Originally described in genus *Gerbillus*, and reallocated to *Gerbillurus* by Davis (1975a). Together with *G. setzeri*, assigned to subgenus *Gerbillurus* (see profile Genus *Gerbillurus*). Karyotypically similar to *G. setzeri*. Synonyms: *seeheimi*. Subspecies: two. Chromosome number: 2*n* = 60, FN = 80, with individual variation in the number of autosomal arms (Schlitter *et al.* 1984, Qumsiyeh *et al.* 1991). Karyotypically similar to *G. setzeri*.

Description Small hairy-footed gerbil with white underparts, dark dorsal surface and very long tail. Dorsal pelage, flanks and outer surface of limbs reddish-brown to dark greyish-brown. Ventral pelage white from chin to tip of tail, extending to forelimbs and feet. Head narrow, with pointed nose and long vibrissae. Sides of muzzle pale. Large eyes with variable off-white supraorbital patch, not always discernible. Ears long and rounded, paler than dorsal pelage; white patches in front of and behind ears, not always discernible. Hindlimbs much longer than forelimbs. Forefeet and hindfeet pure white, five digits each, Digit 5 on forefoot reduced. Hindfeet elongated; soles partially furred. Tail relatively long (ca. 140% of HB), covered with dense short hairs, with dark dorsal tail stripe at least halfway to end of tail; well-developed pencil, deep red to black. Skull: posterior palatal foramina comparatively

long (2.0 [1.4–2.5] mm); auditory bullae inflated posteriorly and laterally (oblique length 10–11 mm); bullae extends posteriorly beyond occiput. Nipples: 1 + 2 = 6.

Geographic Variation

G. v. vallinus: Northern Cape Province, South Africa; dorsal pelage dark reddish-brown; width across M³–M³ ca. 6.3 mm.

G. v. seeheimi: S Namibia; dorsal pelage grey; width across M³–M³ ca. 5.1 mm.

Similar Species

G. paeba. Similar colour where sympatric; on average smaller; tail shorter and relatively shorter without distinct pencil.

G. setzeri. Paler colour; larger size; tail shorter and relatively shorter without distinct pencil.

G. tytonis. Similar colour; slightly smaller; tail shorter but relatively longer without distinct pencil.

Distribution Endemic to Africa. South-West Arid BZ (Namib Desert, Karoo). Northern limit is around Solitaire, Namibia, extending southwards to Sutherland and eastwards to De Aar, Northern Cape Province, South Africa. Isolated population occurs



on Tsondeb River flood-plain, Namibia (Erasmus & Rautenbach 1984, Griffin 1990, B. H Erasmus unpubl.).

Habitat Restricted to areas of bare gravel, or shallow sand overlying gravels, with scant vegetation. In Northern Cape Province, burrows are constructed in mounds of loose soil around the base of bushes, particularly *Phaeoptilum spinosum* and *Rhigozum trichotomum* (Dempster *et al.* 1999).

Abundance Most abundant rodent species trapped in some areas at times, e.g. Brukaros–Berseba in Namibia. No numerical data available (Griffin 1990).

Adaptations Terrestrial and nocturnal. Moves by quadrupedal saltation. Sandbathes frequently to maintain coat condition. Excavates complex burrows; entrances 6–9 cm in diameter. Burrows contain insect remains, leaves and seeds, and a nest of shredded vegetation; and they provide a stable ambient temperature and relative humidity during the day.

Avoids extreme aridity and temperature by nocturnal activity and fossorial habits rather than physiological adaptations. Body temperature ranges from ca. 37°C to 38°C, with good thermoregulation below ambient temperature of 25°C. Reduces overheating above thermoneutral zone (33.1–35.0°C) by increasing dry thermal conductance, accompanied by a small increase in oxygen consumption, thus avoiding evaporative water loss for cooling. Relatively large size and thick pelage reduces thermal conductance at temperatures below 30°C; but above 30°C, dry thermal conductance and pulmocutaneous water loss increase sharply, thus facilitating cooling. Unable to survive ambient temperatures above 35°C for more than one hour.

Good ability to vary the concentration of the urine enables adjustment of the water turnover rate. This rate is also affected by variations in the protein content and potential water yield of the diet. Urine osmolarity is higher on diets that contain arthropods or seeds

without fresh vegetables than on diets that include fresh vegetables or drinking water; it is also higher on seed diets than arthropod diets. Body mass can be maintained without access to succulent vegetation or drinking water, provided that diet includes arthropods; body mass is lost on diet of dry seeds alone.

Urea concentration in urine varies with diet, being higher on a seed diet than on an arthropod diet, and higher on diets excluding water than on diets with access to drinking water. Urine contains more crystalline allantoin than in other *Gerbillurus* species, thereby conserving water. Urinary concentrating ability is facilitated by an elongated papilla renalis, which extends into the ureter (Dempster *et al.* 1999).

Foraging and Food Omnivorous. Remains of insect exoskeletons, monocotyledonous leaves and seeds reported in burrows at Kenhardt, Northern Cape Province, South Africa (Dempster *et al.* 1999).

Social and Reproductive Behaviour Gregarious, and less aggressive than other *Gerbillurus* species in staged encounters. Individuals tend to huddle together, sniff each other frequently and follow each other. Occasional aggressive bouts include chasing, interspersed with 'boxing', during which antagonists stand upright on toes of hindfeet and rake each other with forepaws. Females differentiate between conspecific and heterospecific ♂♂ by odours deposited on the substrate during urination, defecation, sandbathing or walking, while ♂♂ show no evidence of discrimination between odours of different species (Dempster & Perrin 1990). Acoustic communication occurs by footdrumming, when both hindfeet strike the ground alternately in short bursts of drumming, by modulated audible whistles at ca. 12 kHz, and by strongly modulated ultrasonic whistles at 22–40 kHz with a duration of 44 msec. Vocalizations are associated with sexual and huddling behaviour, and frequently follow sniffing and aggressive behaviour (Dempster *et al.* 1999).

Reproduction and Population Structure Proportion of pregnant and lactating ♀♀ in a population in Northern Cape Province was higher in summer than in winter (B. Erasmus & M. Linger unpubl.). Litter-size (in wild and captivity): 3 (1–5, n = 5 litters; Dempster & Perrin 1991a). Young altricial at birth, weight 2.0 g (n = 8). Growth rate 0.4 g/day for first 23 days after birth. Hair visible Day 4–6. Incisors erupt Day 11–12. Eyes open Day 16–20. Weaned at Day 23–28. Young vocalize at audible frequencies and also ultrasonically at 45–55 kHz. Young do not nipple-cling (Dempster & Perrin 1991a).

Predators, Parasites and Diseases No information.

Conservation IUCN Category: Least Concern.

Measurements

Gerbillurus vullinus

HB: 101 (96–110) mm, n = 26

T: 138.9 (119–156) mm, n = 26

HF: 31.2 (30–34) mm, n = 27

E: 14.4 (14–16) mm, n = 27

WT: 34.7 (30–43) g, n = 7

GLS: 29.9 (28.2–31.9) mm, n = 31

GWS: 15.7 (15.1–16.8) mm, n = 32

M¹–M³: 4.1 (3.7–4.5) mm, n = 33

Namibia and Northern Cape Province, South Africa (Schlitter 1973)
Weight: De Graaff 1981

Key References Dempster *et al.* 1999; Schlitter 1973.

Mike Perrin & Edith R. Dempster

GENUS *Gerbillus*

Gerbils

Gerbillus Desmarest, 1804. Tabl. Méth. Hist. Nat. In: Nouv. Dict. Hist. Nat. 24: 22.

Type species: *Gerbillus aegyptius* Desmarest, 1804 (= *Dipus gerbillus* Olivier, 1801).



Gerbillus gerbillus.

The genus *Gerbillus* is distributed in Sahara Arid, Sahel Savanna and Somalia–Masai BZs of Africa, and extraliminally throughout the Middle East to India. Gerbils are particularly abundant on sandy soils in arid and semi-arid habitats, but they may also be found on more clayey soils and even in rocky habitats. The number of species present in Africa is uncertain (see hereunder), but 35 species have been considered sufficiently well supported to be treated here.

Gerbillus species are small to very small rodents, characterized by a usually pale-coloured pelage, relatively large eyes and a tail longer (or much longer) than head and body, often with a terminal pencil or tuft of longer hairs. Depending on the species, soles of the hindfeet are naked, hairy, or intermediate (partially haired), whereas they are always naked in *Taterillus* and *Gerbillurus* (= *Tatera*). The skull is characterized by a variable but often important development of the auditory bullae and of the mastoid bones, which are visible when the skull is viewed from above (Figure 50). However, the mastoids do not project posteriorly to the same extent as in *Meriones*.

Gerbils are usually terrestrial and nocturnal, and actively dig burrows that can reach an impressive size (several metres when the various gallery lengths are added) and depth (up to 1 metre). They are predominantly granivorous, although a number of species also consume green vegetation and/or insects. Desert species show physiological and behavioural adaptations for water retention, such as lethargy or aestivation deep inside plugged burrows. Populations of some species may reach very high densities, and constitute a threat to agriculture in some regions (e.g. *G. nigeriae* in the Sahel Savanna BZ).

Taxonomically, *Gerbillus* is probably one of the most problematic genera of mammals. Species limits are not well-defined in a number of cases, due to the relatively great morphological homogeneity within

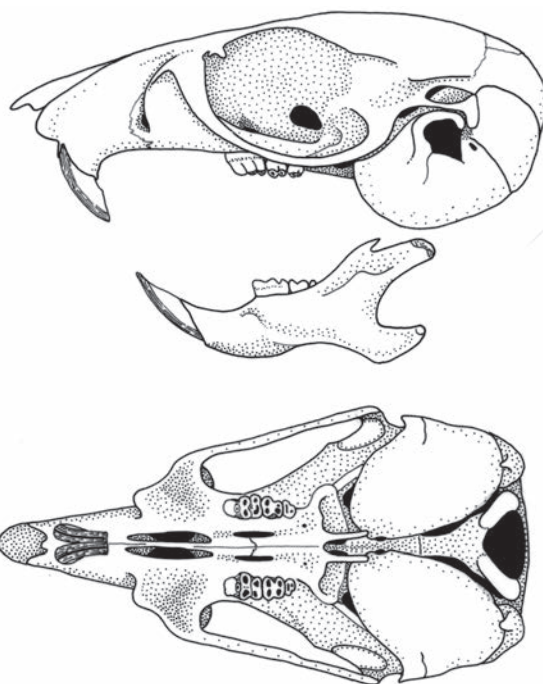


Figure 50. Skull and mandible of *Gerbillus pyramidum* (HC 291).

species groups. As a result, many forms considered as valid species by some authors may finally prove to be synonymous with other species, an option that we have adopted here for a small number of taxa considered as potentially valid species by Lay (1983) and Musser & Carleton (2005). Besides, we have decided to consider the following taxa as *incertae sedis*: *G. agag*, *G. burtoni*, *G. grobbeni*, *G. jamesi*, *G. muriculus*, *G. principulus*, *G. syrticus* and *G. vivax*. Opinions on these taxa have been highly variable, and many of them are known only from a very small number of individuals from the type locality. Moreover, virtually nothing is known of their biology. A careful re-examination of the taxonomic status of these taxa is needed before their possible species-specific attributes can be ascertained. Three recognized as species by Musser & Carleton (2005), namely *dongolanus*, *garamantis* and *mauritaniae*, are here regarded as synonyms.

Musser & Carleton (2005) decided to separate *Dipodillus* from *Gerbillus*, but they presented it, quoting Pavlinov, rather as a 'working hypothesis' than a definite arrangement, so we decided not to follow this decision here. Also, various subgeneric subdivisions have

Table 25. Species in the genus *Gerbillus*. Arranged by increasing mean head and body length. (n. d. = no data.)

| Species | HB mean (mm) | T mean (mm) [% of HB] | Pencil at tip of tail | Auditory bullae mean (mm) | Chromosome number | Subgenus ^a | Notes |
|------------------------|--------------|-----------------------|-----------------------|---------------------------|-------------------|-----------------------|---|
| <i>G. nancillus</i> | 61 | 84 [135%] | Thin | n. d. | 2n = 56 | G | Sudan, Mauritania, Niger and Mali |
| <i>G. juliani</i> | 63 | 96 [150%] | Well-developed | n. d. | n. d. | D | Somalia |
| <i>G. henleyi</i> | 65 | 87 [130%] | Small, thin | n. d. | 2n = 52 | G | Widespread Sahara Arid and Sahel Savanna BZs |
| <i>G. pusillus</i> | 71 | 110 [160%] | Conspicuous | 8.9 | 2n = 34 | G | Tanzania, Kenya, Ethiopia, Somalia and S Sudan |
| <i>G. nanus</i> | 73 | 112 [140–150%] | Well-developed | n. d. | 2n = 52 | G | Widespread western parts of Sahara Arid and Sahel Savanna BZs |
| <i>G. harwoodi</i> | 75 | 95 [126%] | Well-developed | 8.3 | n. d. | D | C Kenya and NC Tanzania |
| <i>G. percivali</i> | 75 | 110 [145%] | Thin | n. d. | n. d. | G | SE Kenya |
| <i>G. brockmani</i> | 78 | 110 [140%] | Small | 9.3 | n. d. | G | N Somalia |
| <i>G. mackilligini</i> | 78 | 120 [155%] | Conspicuous | 8.2 | n. d. | D | Egypt and NE Sudan |
| <i>G. amoenus</i> | 80 | 106 [130%] | Inconspicuous | 7.7 | 2n = 52 | D | Egypt and Libya |
| <i>G. simoni</i> | 81 | 86 [105%] | Absent | 7.0 | 2n = 60 | D | Morocco to Egypt (west of the Nile Delta) near to coast |
| <i>G. watersi</i> | 81 | 108 [135%] | Narrow | 9.1 | n. d. | G | NE Sudan |
| <i>G. bottai</i> | 86 | 106 [125%] | Small | 8.7 | n. d. | D | N Sudan (Khartoum) |
| <i>G. somalicus</i> | 86 | 117 [135%] | Well-developed | 9.5 | n. d. | D | N Somalia |
| <i>G. gerbillus</i> | 88 | 117 [130%] | Long | n. d. | 2n = 42, 43 | G | Widespread in Sahara Arid BZ |
| <i>G. dasyurus</i> | 90 | 127 [122–155%] | Well-developed | 8.0 | 2n = 60 | D | NE Egypt |
| <i>G. stigmonyx</i> | 90 | 102 [115%] | Well-developed | 9.1 | n. d. | D | Sudan (Khartoum) |
| <i>G. andersoni</i> | 92 | 124 [ca. 130%] | Inconspicuous | 8.5 | 2n = 40 | G | Tunisia to Egypt |
| <i>G. nigeriae</i> | 93 | 135 [145%] | Present | n. d. | 2n = 60–74 | G | Mauritania, Mali, Senegal, Burkina, Niger and Chad |
| <i>G. acticola</i> | 94 | 129 [140%] | Narrow | 11.1 | n. d. | G | N Somalia |
| <i>G. hoogstraali</i> | 96 | 114 [120%] | Small | 10.3 | 2n = 72 | G | Morocco |
| <i>G. occiduus</i> | 96 | 111 [115%] | Small | n. d. | 2n = 40 | G | Morocco |
| <i>G. pulvinatus</i> | 96 | 136 [140%] | Narrow | 10.6 | 2n = 62 | G | Ethiopia, Djibouti (? Somalia, N Kenya) |
| <i>G. rosalia</i> | 97 | 117 [120%] | Narrow | 10.4 | n. d. | G | C Sudan |
| <i>G. dunni</i> | 98 | 134 [137%] | Small | 9.8 | 2n = 74 | G | E Ethiopia, Eritrea and Somalia |
| <i>G. cosensi</i> | 100 | 125 [125%] | Narrow | 10.6 | n. d. | G | NW Kenya |
| <i>G. hesperinus</i> | 100 | 110 [ca. 115%] | Small | 7.8–8.7 | 2n = 58 | G | Morocco |
| <i>G. rupicola</i> | 100 | 139 [140%] | Well-developed | 7.8 | 2n = 52 | D | Mali |
| <i>G. campestris</i> | 103 | 133 [140%] | Well-developed | 7.6 | 2n = 56 | D | Widespread in Sahara Arid, Mediterranean Coastal and Sahel Savanna BZs. |
| <i>G. tarabuli</i> | 103 | 148 [145%] | Well-developed | n. d. | 2n = 40 | G | Widespread in Sahara Arid and Sahel Savanna BZs |
| <i>G. lowei</i> | 104 | 148 [140%] | Conspicuous | 9.3 | n. d. | D | W Sudan (Jebel Marra) |
| <i>G. perpallidus</i> | 107 | 137 [128%] | Small, white | 9.4 | 2n = 40 | G | N Egypt (west of Nile R.) |
| <i>G. latastei</i> | 110 | 128 [116%] | Narrow | 10.7 | 2n = 74 | G | Tunisia and W Libya |
| <i>G. maghrebi</i> | 112 | 107 [95%] | Present | 8.3 | n. d. | D | Morocco |
| <i>G. floweri</i> | 117 | 149 [120–130%] | Inconspicuous | 10.0 | n. d. | G | NE Egypt |
| <i>G. pyramidum</i> | 119 | 156 [125–145%] | Present, dark | 10.1 | 2n = 38 | G | Widespread in Sahara Arid and Sahel Savanna BZs |

^a G = *Gerbillus*, D = *Dipodillus*.

been proposed for the genus, but the criteria used have proved to be ambiguous, and it seems better not to recognize any subgeneric distinction in the present state of knowledge. To distinguish between species, morphological criteria such as body size, nature of the soles of the hindfeet (naked, hairy or intermediate), presence or absence of an accessory tympanum, relative size of the bullae, and molar morphology are of some help. However, as in many other genera of African rodents, the karyotype appears as an especially informative and unambiguous diagnostic, species-specific character in this genus. In future, the use of chromosomal techniques on samples from as many

localities as possible (including type localities) will undoubtedly help to clarify the content of this genus.

Here 36 species are recognized. Species are distinguished on size, relative length of tail, presence/absence of pencil at tip of tail, presence/absence of supraorbital and postauricular white patches, size of bullae and chromosome number (Table 25). The hairiness of the sole of hindfoot (often used to distinguish *Gerbillus* from *Dipodillus*) is useful in some situations.

Laurent Granjon

Gerbillus acticola BERBERA GERBIL

Fr. Gerbille de Berber; Ger. Berbera-Rennmaus

Gerbillus acticola Thomas, 1918. Ann. Mag. Nat. Hist., ser. 9, 2: 147. Berbera, Somalia.

Taxonomy Petter (1975a) refers to *acticola* as a subspecies of *G. pyramidum*. In contrast, Lay (1983) points out that the nearest populations of *G. pyramidum* are more than 1300 km away (and separated by many unsuitable habitats) and suggests *acticola* should be retained as a distinct species pending further studies. Synonyms: none. Chromosome number: not known.

Description Small gerbil. Dorsal pelage sandy-orange; dorsal hairs grey, with sandy-orange tips. Flanks slightly paler than back, hairs white with pale sandy-orange tips. Ventral pelage pure white, clearly delineated from colour on flanks. Crown of head sandy-orange, with white supraorbital white patch. Cheeks, throat, fore- and hindfeet white. Soles of feet naked. Tail long (ca. 140% HB), bicoloured; sandy-orange above, paler or white below. Longer brown and white hairs form narrow pencil at tip of tail. Auditory bullae large (ca. 37% of GLS).

Geographic Variation None recorded.

Similar Species

G. pyramidum. Similar in general size and colour; different geographic range.

Distribution Endemic to Africa. Somalia–Masai Bushland BZ. Only known from three localities, all in N Somalia (Berbera [type], Bulhar on the coast, and Buras at 3500 ft).

Habitat Field notes record ‘caught near wells’ and ‘caught on sandy plain’ on the coast near Bulhar.

Abundance Only a few specimens of this species have been collected (1910–30).

Remarks Juvenile and subadult individuals found in Apr–May and Nov–Dec.

Conservation IUCN Category: Data Deficient.



Gerbillus acticola

Measurements

Gerbillus acticola

HB: 94 (90–104) mm, n = 5

T: 129 (124–142) mm, n = 5

HF: 27 (26–29) mm, n = 5

E: 15 (15) mm, n = 5

WT: n. d.

GLS: 30.2 (28.3–31.6) mm, n = 5

GWS: 15.9 (15.5–16.3), n = 4

M¹–M³: 4.1 (4.0–4.2) mm, n = 5

Auditory bulla: 11.1 (10.8–11.4) mm, n = 5

Somalia (BMNH)

Key Reference Lay 1983.

D. C. D. Happold

***Gerbillus amoenus* CHARMING GERBIL (PLEASANT GERBIL)**

Fr. Gerbille charmant; Ger. Anmutige Rennmaus

Gerbillus amoenus (de Winton, 1902). Ann. Mag. Nat. Hist., ser. 7, 9: 46. Giza Province, Egypt.

Taxonomy Originally described in the genus *Dipodillus*. Historically the taxonomic status of *amoenus* has been uncertain, and it has been regarded as either a subspecies of, or synonymous with, *G. dasyurus*, *G. campestris* and *G. nanus* (Osborn & Helmy 1980). Following Wassif (1956), *amoenus* is considered a valid species by Osborn & Helmy (1980), Lay (1983) and Musser & Carleton (1993, 2005). Referred to as *Dipodillus amoenus* by Osborn & Helmy (1980). Synonyms: *vivax*. Subspecies: two. Chromosome number: $2n = 52$ (Lay 1983).

Description Small to very small brownish gerbil with large area of white on rump. Pelage short and soft. Dorsal pelage cinnamon to dark yellowish-brown; dorsal hairs grey at base, with yellowish subterminal band and usually with black tip. White on rump close to base of tail. Flanks yellowish; hairs white at base. Ventral pelage pure white. Head with conspicuous supraorbital and postauricular patches, and broad line of black-tipped hairs from base of eye to base of ear. Ears large, pigmented at tip. Chin, throat and chest white. Upper surface of limbs white. Soles of hindfeet naked, not pigmented. Tail long (ca. 130% of HB), bicoloured, cinnamon to dark yellowish-brown above, white below; brownish inconspicuous pencil on terminal one-quarter of tail. Nipples: not known.

Geographic Variation There appears to be little variation within the species in Egypt, but Ranck (1968) reports decreased size and reduction in the size of the auditory bulla from west to east in Libya. Mean external measurements are slightly larger in Libyan populations than in Egyptian populations (*amoenus*). Two subspecies have been described (see Ranck 1968, Osborn & Helmy 1980).

G. a. amoenus: Egypt. As above.

G. a. vivax: Libya. Paler in colour, larger in total length, and with larger pencil on tail.

Similar Species (size comparisons refer to mean values only)

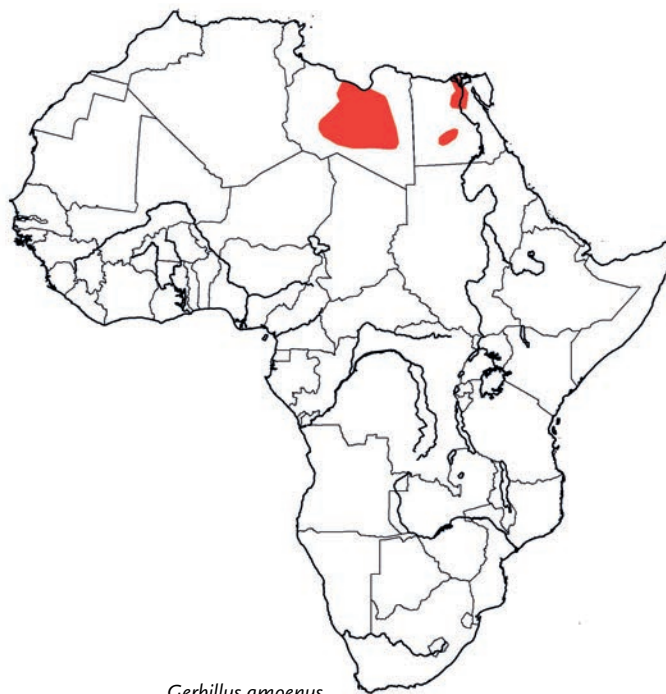
G. gerbillus. Smaller; white rump patch present; pencil of dark hairs on tail; chromosome number: $2n = 42$ (♀ ♀), $2n = 43$ (♂ ♂).

G. simoni. HB of similar size; white rump patch and white markings on head absent; tail shorter without pencil; chromosome number: $2n = 60$, FN = 68, 69.

G. campestris. Larger, pelage long and soft; supraorbital and postauricular patches inconspicuous or not present; white rump patch absent; tail with conspicuous pencil; chromosome number: $2n = 56$ and 58, FN = 68.

G. henleyi. Smaller; white rump patch prominent in specimens from Egypt, less so in specimens from West Africa; tail with thin pencil; chromosome number: $2n = 52$, aFN = 58–62.

Distribution Endemic to Africa. Sahara Arid BZ. Recorded from Egypt and Libya. In Egypt, recorded west of Nile Delta, in the Western Desert and in the southern part of Eastern Desert (Osborn & Helmy 1980). In Libya, occurs in many habitats throughout much

*Gerbillus amoenus*

of the country. The Egyptian and Libyan populations appear to be well separated from each other. Although Osborn & Helmy (1980) suggest that the species may possibly occur also in Tunisia, Algeria, Morocco and Mauritania, there are no records from these countries (Aulagnier & Thévenot 1986, Kowalski & Rzebik-Kowalska 1991, Musser & Carleton 1993, 2005).

Habitat Very varied: recorded in cultivated fields, on grassy canal banks, under tamarisk trees, under fallen fronds of date palms, in loose sand, in several types of semi-desert from regions with dense plant cover to barren hamadas, and in salt marshes. Has been found in tents set in semi-desert habitats. Avoids areas of permanent sand dunes (Ranck 1968, Osborn & Helmy 1980).

Abundance No detailed information; Ranck (1968) records that it is a common rodent in oases in Libya, and that it is usually less abundant than other species of sympatric gerbils.

Remarks Nocturnal and terrestrial. Burrows are simple and usually not deeper than ca. 25 cm (Ranck 1968), and often are excavated under bushes (e.g. under *Zilla spinosa* bushes in Egypt; Hoogstraal *et al.* 1957b). Sometimes individuals are found in the burrows of the larger *Psammomys* spp. Appears to be very tolerant of a wide range of environmental conditions. In Egypt, sympatric gerbils include *G. simoni*, *G. henleyi* and *G. campestris* in salt marshes, and *G. gerbillus* and *G. campestris* in sandy semi-desert areas (Osborn & Helmy 1980). A low incidence of infection with fleas has been recorded on 9 out of 40 individuals. Three species of fleas were

recorded: *Synosternus cleopatrae* (the commonest species), *Xenopsylla ramesis* (on individuals) and *Nosopsyllus henleyi* (in nests). All species of fleas have been recorded also on other species of gerbils (Hoogstraal & Traub 1965a).

Conservation IUCN Category: Data Deficient.

Measurements

Gerbillus amoenus

HB: 79.9 (73–96) mm, n = 17

T: 106.4 (99–116) mm, n = 17

HF: 22.6 (21–24) mm, n = 18

E: 12.2 (11–14) mm, n = 18

WT: 13.2 (11–17) g, n = 10

GLS: 25.2 (24.4–26.3) mm, n = 15

GWS: 13.4 (13.0–14.1) mm, n = 10

M¹–M³: 3.4 (3.2–3.7) mm, n = 18

Auditory bulla: 7.7 (7.3–8.2) mm, n = 19

Egypt (Osborn & Helmy 1980)

Key Reference Osborn & Helmy 1980.

D. C. D. Happold

Gerbillus andersoni ANDERSON'S GERBIL

Fr. Gerbille d'Anderson; Ger. Andersons Rennmaus

Gerbillus andersoni de Winton, 1902. Ann. Mag. Nat. Hist., ser. 7, 9: 45. Mandara, E Alexandria, Egypt.

Taxonomy The definition of this species is uncertain. In Egypt, Osborn & Helmy (1980) recognize three subspecies – *inflatus* in the coastal Western Desert, *andersoni* in the Nile Delta and *bonhotei* in northern Sinai. In contrast, Musser & Carleton (1993), following Lay (1983), regard *inflatus* and *bonhotei* as separate species. Ranck (1968) referred to *G. eatoni* and *G. inflatus* in Libya, and suggested that three closely related species occur along the North African coast: *G. eatoni* in the west (Libya and W Egypt), *G. andersoni* in the middle and *G. bonhotei* in the east. Musser & Carleton (1993, 2005) consider *eatoni* to be a synonym of *G. andersoni*. Here, *G. andersoni* is considered to include *inflatus* and *bonhotei* (following Osborn & Helmy 1980 and Musser & Carlton 2005), perhaps with subspecific status. Synonyms: *allenbyi*, *blanci*, *bonhotei*, *eatoni*, *inflatus*, *versicolor*. Subspecies: none recognized here. Chromosome number: 2n = 40, FN = 80 (Egypt; Lay *et al.* 1975).

Description Small gerbil. Dorsal pelage sandy-orange to orange-brown, lightly suffused with black along mid-dorsal line; dorsal hairs medium grey on basal half, orange-brown on terminal half; black tips on some hairs. Flanks paler than back; hairs white with orange tip. Ventral hairs pure white, clearly delineated from colour of flanks. Crown of head and nose similar to back. Inconspicuous supraorbital and postauricular white patches. Broad conspicuous band of dark-tipped hairs from nasal region, below eye to base of ear. Limbs and feet white. Soles of feet hairy and pigmented. Tail long (ca. 115–140% of HB), sparsely covered with short orange-brown hairs above, paler below; small rather inconspicuous pencil of brownish hairs at tip of tail. Nipples: not known.

Geographic Variation Six taxa have been named as subspecies but their value is dubious (see above): *bonhotei* (North Sinai and Jordan), *andersoni* (Nile Delta), *inflatus* (Western Desert of Egypt, eastern desert of Libya), *eatoni* (central coast of Libya), *versicolor* (central coast of Libya) and *blanci* (Tunis area). Differences include minor variations in pelage colouration (probably related to variation in sand and soil colour and moisture), overall size and extent of inflation of auditory bullae.



Gerbillus andersoni

Similar Species

G. campestris. Well-developed pencil on tail, naked soles.

G. gerbillus. Paler colour; large white rump patch, soles of feet not pigmented, conspicuous pencil on tail.

Distribution Sahara Arid BZ. Recorded from coastal regions of North Africa from about 16°E in Libya to about 34°E in North Sinai. An isolated population occurs in Tunisia in the region of Tunis (ca. 10°E). Apparent gaps in distribution along the coast may be due to inadequate surveys or lack of suitable habitat. Also recorded from Israel, Jordan and N Saudi Arabia (Harrison & Bates 1991).

Habitat Sandy habitats such as palm groves, cultivated and abandoned semi-desert, and vegetated sandy areas in oases. Also lives in coastal white sand dunes covered with *Atriplex* shrubs, in salt

marshes close to sedges, and in depressions containing sandy loam and *Artemisia* shrubs.

Abundance Common in the sandy areas of the Nile Delta and in the coastal parts of the Western Desert in Egypt (Hoogstraal 1963).

Adaptations Nocturnal and terrestrial. Rests in burrows during the day.

Foraging and Food Omnivorous; forages for food at night. On an annual basis, diet consists of 35% seeds (*Thymelaea* 25%, *Anabasis* 2%, *Cutandia* 1%), 19% leaves, 15% bulbs of iris, 8% other plants and 20% insects. Each of these items varies on a seasonal basis, e.g. in winter, during the wet season and when it is relatively cool, leaves form the major item of the diet (leaves 85%, seeds of *Thymelaea* 10%, insects 5%); during summer when hot and dry, the diet is more varied and includes a greater proportion of water-containing foods (insects 30%, bulbs 25%, leaves 10%, other plants 25% and seeds 10%) (Soliman & Wassif 1982). At other seasons, the mix of foods is somewhere between these extremes.

Social and Reproductive Behaviour Anderson's Gerbils live syntopically with several other species of small rodents including *G. gerbillus*, *G. perpallidus*, *G. amoenus*, *G. simoni*, *Meriones shawi*, *Psammomys obesus* (Osborn & Helmy 1980). Interactions between these species have not been studied.

Reproduction and Population Structure In Western Desert of Egypt (Wassif & Soliman 1980), ♀♀ are reproductively active in winter (Jan–Feb) and spring (Feb–May), with a peak in Jan–Mar. Males with scrotal testes (and max weight of testes) Nov–Jun with peak in Dec–Apr (>50% ♂♂ active). Reproduction strongly seasonal, with juveniles entering population in winter and spring (Feb–May/Jun). These individuals breed in following Jan–Mar (when ca. 8–12 months old) and form ca. 70% of breeding population; some older individuals (up to 30% of population) survive to breed during a second reproductive season (when ca. 18–24 months old).

Litter-size: 3.9 (3–7, $n = 10$). Some ♂♂ reproductively active at 5.5 months of age and weight 20 g, but most not until ca. 30 g.

In winter (Jan–Feb), at commencement of reproduction, population composed of two cohorts: adults (now 8–12 months) form 70–85% of population, and older adults (18–24 months) form 15–30% (see also above). During Mar–Aug, juveniles born in Jan–Apr form an increasing proportion of population, so by midsummer (Aug), population composed of 70% juveniles and 30% adults (now 13–18 months). During Aug–Dec, the proportion of juveniles gradually declines as these individuals become adults, and the adults who reproduced during the previous winter (now 18–20 months) form the older adult cohort.

Predators, Parasites and Diseases Six species of fleas have been recorded, the commonest being *Synosternus cleopatrae*, which is found also on many other species of gerbils (Hoogstraal & Traub 1965a).

Conservation IUCN Category: Not Evaluated.

Measurements

Gerbillus andersoni

HB: 92 (90–115) mm, $n = 26$

T: 124 (110–150) mm, $n = 26$

HF: 29 (27–32), $n = 27$

E: 16 (15–17), $n = 25$

WT: 30 (28–33) g, $n = 9$

GLS: 29.2 (27.7–31.0) mm, $n = 26$

GWS: 16.4 (14.9–17.6) mm, $n = 17$

M¹–M³ alveolar: 4.0 (3.6–4.8) mm, $n = 28$

Auditory bulla: 8.5 (7.8–9.1) mm, $n = 27$

Egypt (for *G. a. andersoni*; Osborn & Helmy 1980)

Key References Osborn & Helmy 1980; Soliman & Wassif 1982; Wassif & Soliman 1980.

D. C. D. Happold

Gerbillus bottai BOTTA'S GERBIL

Fr. Gerbille de Botta; Ger. Bottas Rennmaus

Gerbillus bottai Lataste, 1882. Le Naturaliste 4: 36. Sennar, Sudan.

Taxonomy The status of *bottai* is uncertain. Kock (1978a) regarded *G. bottai* to include *G. harwoodi* and *luteolus*, whereas Petter (1975a) kept *G. bottai* and *G. harwoodi* as valid species and placed *luteolus* within *G. campestris*. Lay (1983) and Musser & Carleton (1993) maintain *G. bottai* and *G. harwoodi* as valid species and place *luteolus* as a synonym of *G. stigmonyx* (= *Dipodillus stigmonyx* in Musser & Carleton 2005). It is of interest to note that *G. bottai* and *G. stigmonyx* are sympatric in the region between the Blue and White Nile rivers south of Khartoum, whereas *G. harwoodi* occurs only in Kenya, about 1200 km to the south in a completely different environment; this suggests that *G. harwoodi* should be regarded as a valid species distinct from *G. bottai* and *G. stigmonyx* (including *luteolus*). Musser & Carleton (2005) refer to this species as *Dipodillus bottai*. The taxa *bottai*, *stigmonyx* and *watersi*

may form a closely related species complex, and may even belong to the same species (F. Dieterlen, in litt.); all three are sympatric within an area of N Sudan bounded by 30–38°E and 20–28°N. Synonyms: none. Chromosome number: not known.

Description Small gerbil. Dorsal pelage sandy-brown, suffused with black especially on mid-dorsal line. Dorsal hairs rather short, dark grey at base, sandy-brown at terminal end, sometimes with black tip. Flanks paler than back, hairs white with orange-brown tips. Ventral pelage pure white. Nose and crown of head sandy-brown. Supraorbital and postauricular white patches. Ears orange-brown at base, black on tips. Chin and throat white. Limbs white. Soles of feet hairy or slightly hairy. Tail long (ca. 125% HB), slightly bicoloured;

short blackish-brown hairs above, paler below. Hairs at tip slightly longer forming ill-defined pencil.

Geographic Variation None recorded.

Similar Species (size comparisons refer to mean values only)

Three species are sympatric with *G. bottai*:

G. stigmonyx. Similar in general size; larger auditory bullae; rare.

G. watersi. Smaller HB and T; dorsal pelage pale orange clearly delineated on flanks from white ventral pelage; uncommon.

G. pyramidum. Larger HB; darker dorsal pelage; common.

Distribution Endemic to Africa. Sahel Savanna BZ. Known only from a small region between the White Nile and Blue Nile rivers south of Khartoum, Sudan.

Habitat Specimens have been found in fields of vegetables and cereals close to the Nile Valley near Khartoum (F. Dieterlen in litt.).

Abundance Rare. Known only from a few specimens at four or five localities.

Remarks Apparently no other information available.

Conservation IUCN Category: Data Deficient.

Measurements

Gerbillus bottai

HB: 86 (83–92) mm, n = 4

T: 106 (101–110) mm, n = 4

HF: 20 (19–21) mm, n = 4

E: 10.7 (10–11) mm, n = 4



Gerbillus bottai

WT: 23 (19–26) g, n = ?

GLS: 26.2 (25.4–27.0) mm, n = 4

GWS: 13.7 (13.4–14.0) mm, n = 3

M¹–M³: 3.6 (3.4–3.7) mm, n = 4

Auditory bulla: 8.7 (8.4–9.1) mm, n = 4

Jebel Moya, Sudan (SNHM)

Key Reference Kock 1978a.

D. C. D. Happold

Gerbillus brockmani BROCKMAN'S GERBIL

Fr. Gerbille de Brockman; Ger. Brockmans Rennmaus

Gerbillus brockmani (Thomas, 1910). Ann. Mag. Nat. Hist., ser. 8, 5: 420. Burao, 85 miles south of Berbera, Somalia.

Taxonomy Lay (1983) and Musser & Carleton (1993) regard *brockmani* as a valid species. Petter (1975a) considered *brockmani* to be a subspecies of *G. nanus* but this seems unlikely since the distribution of *G. nanus* is far removed from that of *brockmani*. Very similar to *G. somalicus* (considered as subspecies of *G. campestris* by Petter 1975a), which also occurs in N Somalia; a comparative study of the two species would be instructive. Synonyms: none. Chromosome number: not known.

Description Very small gerbil. Dorsal pelage sandy-orange to sandy-brown, long and soft. Dorsal hairs medium grey with subterminal orange band, some with black tip. Flanks paler. Ventral pelage pure white (one specimen has pale golden ventral pelage). Crown of head and nose sandy-brown. White supraorbital patch and inconspicuous white postauricular patch. Chin, cheeks and throat white. Upper surface of limbs and feet orange-brown. Soles of hindfeet naked. Tail long (ca. 140% of HB), with short sandy-brown

and black bristles. Longer hairs form small pencil on terminal one-third of tail. Cheekteeth very small; auditory bullae relatively large (ca. 37% of GLS).

Geographic Variation None recorded.

Similar Species

G. somalicus. On average slightly larger; larger M¹–M³.

Distribution Endemic to Africa. Somalia–Masai Bushland BZ. Only known from type locality, Burao, in N Somalia.

Habitat No information; type locality is in dry hilly country south of Berbera.

Abundance Presumably rare; only a few specimens are known.



Remarks Apparently no other information available.

Conservation IUCN Category: Data Deficient.

Measurements

Gerbillus brockmani

HB: 78 (71–84) mm, n = 4

T: 110 (106–117) mm, n = 4

HF: 21 (21–22) mm, n = 4

E: 12 (11–13) mm, n = 4

WT: n. d.

GLS: 25.4 (25.0–25.7) mm, n = 4

GWS: 13.5 (12.5–14.0) mm, n = 4

M¹–M³: 3.2 (3.1–3.4) mm, n = 4

Auditory bulla: 9.3 (9.2–9.6) mm, n = 3

Somalia (BMNH)

Key Reference Thomas 1910.

D. C. D. Happold

Gerbillus campestris NORTH AFRICAN GERBIL

Fr. Gerbille des champs; Ger. Nordafrikanische Rennmaus

Gerbillus campestris (Loche, 1867). Expl. Sci. Alg. Zool. Mamm., p. 106. Philipeville, Constantine Province, Algeria.

Taxonomy Originally described in the genus *Dipodillus*. The widespread distribution of this species has resulted in many forms being described either as species or subspecies. Lay (1983) lists 19 forms that have been regarded by various authors as synonyms of *campestris*. Of these, Lay (1983) and Musser & Carleton (1993) consider 13 to be synonyms (because of misidentification, incorrect taxonomy or very little data), and six as valid species pending further studies (*amoenus*, *jamesi*, *lowei*, *quadrimaculatus*, *somalicus*, *stigmonyx*). Here, four of these taxa are regarded as distinct species (*amoenus*, *lowei*, *somalicus*, *stigmonyx*), *jamesi* as *incertae sedis*, and *quadrimaculatus* as a synonym of *G. campestris*. All six taxa have very limited distributions and are known by only a few specimens. Some of the synonyms may, perhaps, be regarded as subspecies. Musser & Carleton (2005) refer to this species as *Dipodillus campestris*. Synonyms: *brunnescens*, *cinnamomeus*, *dodsoni*, *gerbii*, *haymani*, *hilda*, *minutus*, *patrizi*, *quadrimaculatus*, *riparius*, *rozsikae*, *somalicus*, *venustus*, *wassifi*. Subspecies: none; some of the synonyms may perhaps represent subspecies but none are recognized here. Chromosome number: 2n = 56 (specimens from Morocco, Algeria, Tunisia and Egypt; Lay *et al.* 1975); chromosomal polymorphism (2n = 56 and 58) from one locality in Morocco (Lay *et al.* 1975); 2n = 56, FN = 68 (Niger; Dobigny *et al.* 2002b).

Description Small orange-brown gerbil with long soft pelage and long tail with well-developed pencil. Hairs long and soft, more so than in other species of gerbils. Dorsal pelage cinnamon to orange-brown (with various shades of darkness). Dorsal hairs grey at base with sandy-brown or golden-brown terminal band, sometimes with black tip. Flanks paler than back. Ventral pelage

pure white, clearly delineated from flanks. Crown of head and nose similar to dorsal pelage, sometimes with longitudinal black stripe on nose. Supraorbital and postauricular patches inconspicuous or not present. Cheeks, chin and throat white. Limbs whitish. Feet whitish, sometimes suffused with golden-brown. Soles of hindfeet naked and darkly pigmented. Tail long (ca. 140% of HB), bicoloured, golden-brown above, well covered with small golden or blackish hairs, white below. Terminal half with well-developed pencil of long hairs.

Geographic Variation Dorsal pelage of individuals varies according to locality and substrate. Individuals from sandy areas are pale orange-brown suffused with grey; those from coastal regions are medium orange-brown, sometimes suffused with black. Individuals from rocky areas in the south (e.g. Sudan, as *G. c. venustus*; see Happold 1967b) are blackish golden-brown with most dorsal hairs tipped with black. Size and density of pencil varies geographically.

Similar Species

G. amoenus. Smaller in all mean measurements (although some overlap in ranges); head with conspicuous supraorbital and postauricular patches; broad line of black-tipped hairs from base of eye to base of ear; chromosome number: 2n = 52; Libya and Egypt.

G. andersoni. HB (mean 92 mm) and T (mean 124 mm) smaller, but with overlap in ranges; mean HF longer (29 mm); head with inconspicuous supraorbital and postauricular white patches; broad conspicuous line of dark-tipped hairs from nasal region, below eye to base of ear; chromosome number: 2n = 40, FN = 80; coastal regions of north-east Africa.

G. dasyurus. Smaller in all mean measurements (although some overlap in ranges); head with indistinct supraorbital and supraauricular patches; line of black-tipped hairs from base of eye to base of ear; chromosome number: $2n = 60$, $FN = 69/70$; NE Egypt, east of Nile R.

G. hoogstraali and *G. mahgrebi*. May be sympatric in Morocco.

Distribution Endemic to Africa. Sahara Arid, Mediterranean Coastal and Sahel Savanna BZs. Widespread in coastal regions from Morocco to Egypt, and southwards into the semi-deserts and deserts of Algeria, Libya and Egypt. Isolated populations in Mali (Adrar des Iforas), Niger (Air) (Dobigny *et al.* 2002b) and in rocky areas of Nile Valley and N Sudan (Happold 1967b).

Habitat These gerbils live in a variety of habitats. In Morocco, recorded in fields, coastal dunes, palm groves and amongst rocks (collectors' field notes). In Algeria, they have been found in fields, other open habitats and rocky hills (e.g. Hoggar), but not in forests or extensive sandy regions. In Libya, known from oases, mainly in mesic sedge habitats, tamarisk and acacia vegetation on edge of oases; also in cliffs, rocky outcrops and talus (Ranck 1968). In Egypt, recorded among limestone cliffs near the sea, temple ruins, vegetated rocky slopes, dunes, boulder habitats, palm groves and barley fields, and often found in mud and stone houses (Osborn & Helmy 1980). In general, these gerbils prefer habitats associated with rocks and vegetation rather than non-vegetated sand.

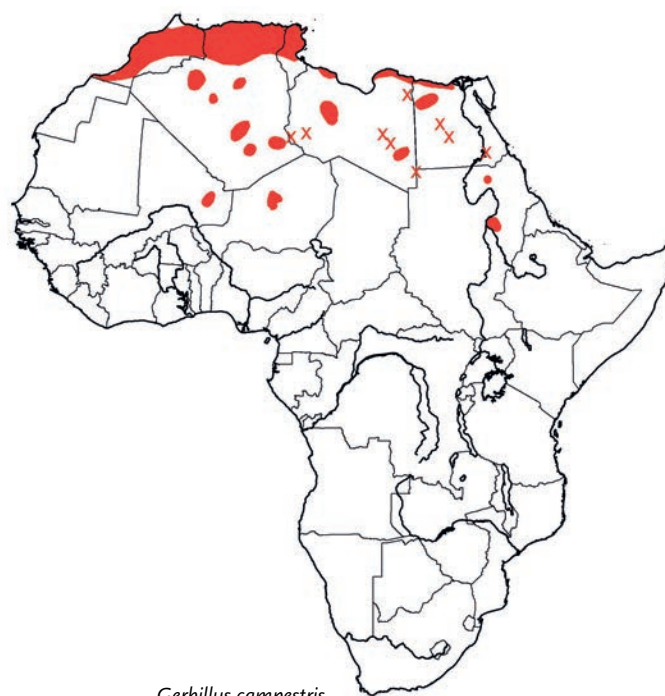
Abundance Considered 'the most widely distributed of all Libyan rodents' (Ranck 1968) and 'easily trapped in all habitats' in Egypt (Osborn & Helmy 1980). In N Sudan, considered uncommon and found only in two localities, both rocky jebels, where *Acomys cahirinus* was five times as numerous as *G. campestris* (Happold 1967b).

Adaptations Nocturnal and terrestrial. Digs burrows in sandy habitats; lives in crevices in rocky habitats.

Foraging and Food No information.

Social and Reproductive Behaviour In Egypt, occurs in sandy habitats with *G. gerbillus* and *G. andersoni*, amongst cliffs and rocky areas with *Acomys cahirinus* and *Eliomys melanurus*, and in salt marshes with *Psammomys obesus*, *G. amoenus*, *G. simoni* and *G. henleyi* (Osborn & Helmy 1980).

Reproduction and Population Structure Duration and timing of reproductive season varies according to locality and climate. Reproduction in coastal desert populations in Egypt occurs during winter rains (Nov–Apr), but inland populations may breed later (Osborn & Helmy 1980). In N Sudan, reproduction probably occurs in Sep–Nov, after the end of the short wet season when temperatures are declining. Lactating ♀♀ in Morocco in Aug. Litter-size: 5 (3–6, $n = 3$; Egypt).



Gerbillus campestris

Predators, Parasites and Diseases Remains of this species have been found in owl pellets throughout Algeria (Kowalski & Rzebik-Kowalska 1991). Four species of fleas have been found on individuals and in nests; infection rates at two localities in Egypt were 10% and 20% ($n = 30, 15$) (Hoogstraal & Traub 1965a).

Conservation IUCN Category: Least Concern.

This common widespread species is not threatened.

Measurements

Gerbillus campestris

HB: 103 (99–112) mm, $n = 59$

T: 133 (118–153) mm, $n = 51$

HF: 27 (25–29) mm, $n = 58$

E: 17 (15–20) mm, $n = 59$

WT: 29 (21–38) g, $n = 39$

GLS: 29.6 (27.9–31.9) mm, $n = 51$

GWS: 15.3 (14.0–17.1) mm, $n = 27$

M^1 – M^3 (alveolar): 4.1 (3.6–4.6) mm, $n = 54$

Auditory bulla: 7.6 (7.2–8.2) mm, $n = 45$

Western Desert, Egypt (*G. c. wassifi*) (Osborn & Helmy 1980)

Key References Lay 1983; Osborn & Helmy 1980.

D. C. D. Happold

Gerbillus cosensi COSENS'S GERBIL

Fr. Gerbille de Cosens; Ger. Cosens Rennmaus

Gerbillus cosensi Dollman, 1914. Abstr. Proc. Zool. Soc. Lond. 1914 (131): 25. Ngamatak, Turkwel Valley, Kenya.

Taxonomy Petter (1975a) considered *cosensi* to be a subspecies of *G. agag*, within the subgenus *Gerbillus*, with the suggestion that it could be a valid species. Lay (1983) and Musser & Carleton (1993) considered *cosensi* to be a valid species but Musser & Carleton (2005) treat *cosensi* as a synonym of *G. agag* (which is here regarded as *incertae sedis*). Synonyms: none. Chromosome number: not known.

Description Small pale gerbil. Dorsal pelage pale sandy-brown. Dorsal hairs grey at base with sandy-brown terminal band, black tip on some hairs in mid-dorsal line. Flanks paler. Ventral pelage pure white, poorly delineated from flanks. Crown of head and nose sandy-brown. Cheeks, chin and throat white. Supraorbital and postauricular white patches. Fore- and hindlimbs and feet white. Soles of hindfeet hairy. Tail long (ca. 125% of HB), slightly bicoloured, sandy above, white below; covered with short bristles; longer black and white hairs on terminal end form narrow pencil.

Geographic Variation None recorded.

Similar Species

G. harwoodi. Smaller in all measurements; dorsal pelage glossy, orange-brown to dark orange-brown; postorbital patch absent; postauricular patch present; hindfeet naked; tail with well-developed pencil; distribution disjunct in N Kenya.

Distribution Endemic to Africa. Somalia–Masai Bushland BZ. Known only from five localities in NW Kenya: Ngamatak (type locality), Kangatet, Lodwar, Lokori and Archer's Post.

Habitat Dry semi-arid country. Two specimens obtained in 'Sporobolus grass plains' at Archer's Post.

Abundance Rare; known only from a very few specimens.

Remarks 'Burrows in sand' (label, BMNH). 'Lives in sand dunes; covers entrance of hole in daytime' (collector's label; NMK).

Conservation IUCN Category: Data Deficient.

*Gerbillus cosensi***Measurements***Gerbillus cosensi*

HB: 100 (90–135) mm, n = 7

T: 125 (100–143) mm, n = 7

HF: 26 (25–30) mm, n = 7

E: 15 (13–20) mm, n = 7

WT: 30, 34 g, n = 2

GLS: 29.7 (29.6–29.8) mm, n = 3

GWS: 15.4 (14.7–16.0), n = 3

M¹–M³: 4.0 (4.0–4.1), n = 3

Auditory bulla: 10.6 (10.2–10.9) mm, n = 3

Northern Kenya (BMNH)

Key Reference Lay 1983.

D. C. D. Happold

Gerbillus dasyurus WAGNER'S GERBIL

Fr. Gerbille de Wagner; Ger. Wagners Rennmaus

Gerbillus dasyurus (Wagner, 1842). Arch. Naturgesch. 8: 20. Sinai, Egypt.

Taxonomy Originally described in the genus *Dipodillus*, and also placed in the genus *Dipodillus* by Musser & Carleton (2005). Synonyms (all extralimital to Africa): *dasyroides*, *gallagheri*, *leosollicitus*, *palmyrae*. Subspecies: none. Chromosome number: 2n = 60, FN = 69 and 70

(Egypt; other FN numbers in Middle East, see Wassif *et al.* 1969 in Harrison & Bates 1991).

Description Graceful small pale-coloured rodent with long well-haired tail. Pelage long and dense. Dorsal pelage sandy-buff, inconspicuously speckled with black; hairs grey at base, subterminal band sandy-buff, usually black at tip. Flanks paler with clear yellowish band on lower flanks (without blackish speckling). Dorsal pelage varies in colour geographically. Ventral pelage pure white. Head similar in colour to dorsal pelage. Line of black-tipped hairs from base of eye to base of ear. Supraorbital and supraauricular patches white, sometimes indistinct. Eyes large, dark. Ears greyish-fawn, with fringe of small white hairs. Chin, throat and chest white. Fore- and hindlimbs white. Soles of hindfeet darkly pigmented, naked. Tail long (122–155% of HB, % very variable), bicoloured, sandy-buff above, white below; well covered with short hairs at base, well-defined pencil on terminal half ending in small tuft. Skull: upper incisors each with single groove, auditory bullae inflated. Nipples: not known.

Geographic Variation Pelage colour varies according to substrate and environment (Harrison & Bates 1991). Individuals in Egypt are paler than some subspecies in the Middle East.

Similar Species

G. mackilligini. Very similar, HB on average shorter; tail long with well-developed pencil; larger auditory bullae; upper incisors grooved; SW Egypt and NE Sudan.

G. campestris. HB longer; tail with well-developed pencil; auditory bullae inflated; upper incisors grooved; in Egypt, only west of Nile R.

Sekeetamys calurus. HB longer; tail black, bushy with white tip; auditory bullae inflated; incisors ungrooved; Eastern Desert of Egypt and Sinai.

Distribution Sahara Arid BZ. Recorded in NE Egypt between the Nile R. and the Red Sea (between 29° N and 30° N), and in Sinai,



at 0–2000 m. Extralimittally in countries of the Arabian peninsula, Israel, Lebanon, Jordan, Iraq and Syria.

Habitat Crevices and rock shelves in sandstone and limestone cliffs, boulder-strewn wadis and in sandy areas beneath *Nitraria* bushes on coast (Sinai). Recorded in similar habitats in other countries, as well as in thorny thickets and salt flats. Syntopic with *Sekeetamys calurus*, *Acomys cahirinus*, *A. russatus* and *Eliomys quercinus* (Osborn & Helmy 1980).

Abundance No information for Egypt. In SW Saudi Arabia, population numbers varied at three study localities, and fluctuated by a magnitude of 2–3 during the course of a year. Minimum and maximum numbers were 5.19–13.92, 3.03–9.07 and 4.48–10.7 individuals/ha (Al-Khalili & Delany 1986). Very common in Israel (Qumsiyeh 1996).

Adaptations Nocturnal and terrestrial. Individuals in rocky habitats live in rock crevices and under boulders during the day. In sandy areas, they hide in burrows 15–20 cm below the surface, with the entrances plugged with sand.

Foraging and Food Herbivorous. In captivity, individuals feed on foliage of *Zygophyllum coccineum*, raw carrots and dry bread, but they do not eat insects (Osborn & Helmy 1980). In Saudi Arabia, feeds on seeds of annual herbs (Harrison & Bates 1991).

Social and Reproductive Behaviour Social. In captivity, individuals mark their territory by 'ceremonial digging', drumming with the hindfeet and by rubbing secretions from the mid-ventral gland on the substrate (Fiedler 1973). Usually only the ♀♀ look after the young.

Reproduction and Population Structure In Egypt, captive individuals bred from Oct–Jun; litter-size 2–6 (Flower 1932). In SW Saudi Arabia (Al-Khalili & Delany 1986), reproduction only during wettest period of year (Feb–May). Gestation: 24–26 days. Embryo number in wild: 5.12 (4–6, n = 27). Litter-size in captivity: 4.8 (3–6, mode 5 and 6, n = 6). At birth, mean weight = 1.68 g, young altricial, naked. Development comparatively slow: hair pigmentation visible Day 5; upper incisors erupt Day 15; ears open Day 19; eyes open Day 22; weaned Day 40; weight 14–15 g Day 70. Probably do not breed in year of birth. Ontogeny described in detail by Fiedler (1973).

Predators, Parasites and Diseases Ectoparasites include four species of fleas, *Xenopsylla dipodilli*, *X. nubica*, *X. conformis* and *Synosternus cleopatrae* (Egypt; Hoogstraal & Traub 1965a).

Conservation IUCN Category: Least Concern.

Measurements

Gerbillus dasyurus

HB: 90.0 (82–94) mm, n = 18

T: 126.8 (114–136) mm, n = 16

HF: 25.1 (24–27) mm, n = 19

E: 14.5 (14–16) mm, n = 19

WT: 22.8 (16–35) g, n = 15

GLS: 28.3 (27.2–29.5) mm, n = 18
 GWS: 14.8 (14.2–15.4) mm, n = 14
 M¹–M³ (alveolar): 4.0 (3.6–4.5) mm, n = 18
 Auditory bulla: 8.0 (7.5–8.6) mm, n = 19
 Eastern Desert, Egypt (Osborn & Helmy 1980)

Key References Fiedler 1973; Harrison & Bates 1991; Osborn & Helmy 1980.

D. C. D. Happold

Gerbillus dunni DUNN'S GERBIL

Fr. Gerbille de Dunn; Ger. Dunns Rennmaus

Gerbillus dunni Thomas, 1904. Ann. Mag. Nat. Hist., ser. 7, 14: 101. Gerlogobi, E Ethiopia. (Original description placed Gerlogobi in 'Somalia'.)

Taxonomy Petter (1975a), Lay (1983) and Musser & Carleton (1993) treat *dunni* as a valid species, but Cockrum (1977) considers it to be conspecific with *latastei*. Yalden *et al.* (1976) place *dunni* as a synonym of *G. pyramidum*. However, the geographic ranges of *latastei* and *pyramidum* are far from that of *dunni*. The type locality is in E Ethiopia, not in Somalia as recorded by Thomas. Synonyms: none. Chromosome number: 2n = 74 (Capanna & Merani 1981).

Description Small pale-coloured gerbil, with hairy soles and long tail. Dorsal pelage sandy-brown; hairs light grey at base, sandy-brown on terminal third, often with black tip. Hairs soft. Flanks paler, hairs white at base. Ventral pelage pure white, not sharply defined from flanks. Crown of head and nose similar to back, but darker and blacker. Chin and throat white. Supraorbital and postauricular patches inconspicuous or not present. Upper surfaces of hindlimbs sandy-fawn, inner surfaces white; feet white. Soles of hindfeet hairy (although maybe naked close to 'heel'). Tail long (ca. 137% of HB), grizzled sandy-brown above, white below; terminal pencil small and inconspicuous.

Geographic Variation None recorded.

Similar Species

G. pulvinatus. Similar in general size; soles hairy; auditory bullae larger.

G. pusillus. Smaller (HB: 65–77 mm, T: 110–115 mm); dorsal pelage darker; white ventral pelage sharply defined; soles naked.

Microdillus peeli. Smaller (HB: 66–82 mm); tail short (50–65 mm); soles naked.

Distribution Endemic to Africa. Somalia–Masai Bushland BZ. Known only from a few localities in E Ethiopia, Eritrea and Somalia. May occur in Djibouti (see Pearch *et al.* 2001).

Habitat Specimens have been obtained on the steppe and dry savanna habitats near the coast of Somalia (Capanna & Merani 1981).

Abundance Few specimens; rare or uncommon (?).

Remarks Juveniles found in Dec.

Conservation IUCN Category: Data Deficient.



Gerbillus dunni

Measurements

Gerbillus dunni

HB: 98 (93–102) mm, n = 4

T: 134 (130–143) mm, n = 5

HF: 30 (29–31) mm, n = 5

E: 14 (13–15), n = 5

WT: 39 (34–41) g, n = 3

GLS: 30.6 (30.3–30.8) mm, n = 5

GWS: 16.4 (16.2–16.6) mm, n = 5

M¹–M³: 4.1 (4.0–4.3) mm, n = 5

Auditory bulla: 9.9 (9.4–10.2) mm, n = 5
 Somalia (MNHN)

Key Reference Capanna & Merani 1981.

D. C. D. Happold

Gerbillus floweri FLOWER'S GERBIL

Fr. Gerbille de Flower; Ger. Flowers Rennmaus

Gerbillus floweri Thomas, 1919. Ann. Mag. Nat. Hist., ser. 9, 3: 559. Wadi Hareidin, 22.4 km south of Al Arish, Sinai, Egypt.

Taxonomy Considered by Lay (1983) as a potentially valid species, which may encompass at least part of the great chromosomal variability found near the type locality, with $2n$ ranging from 51 to 66 (near Gaza and in the Gaza strip; Wahrman & Gourewitz 1973). Retained here, as the name *G. floweri* has priority over *G. bonhotei* described from the same locality by Thomas (1919). Synonyms: none. Chromosome number: not known.

Description Small to medium-sized gerbil. Dorsal pelage pale cinnamon to tawny, with indistinct dorsal stripe; hairs grey at base, sandy-buff at tip. White patch on rump. Ventral pelage pure white. Prominent preorbital, postorbital and postauricular white spots. Nasal region white. Feet pure white. Soles of hindfeet hairy. Tail long (120–130% of HB), usually without brownish or blackish hairs dorsally and with a relatively inconspicuous fuscus pencil.

Geographic Variation None recorded in Africa.

Similar Species

G. pyramidum. Darker with more distinct dorsal stripe; mastoid portion of the auditory bullae less inflated; chromosome number: $2n = 38$; Egypt, Sudan and westwards to N Mali.

G. tarabuli. Smaller; chromosome number: $2n = 40$; only west of Libya.

G. gerbillus. Smaller; chromosome number: $2n = 42/43$; distributed throughout the whole Sahara.

Distribution Sahara Arid BZ. Recorded from Egypt in northern Sinai and the Eastern Desert; southern limit Wadi Wardan (Osborn & Helmy 1980). Extralimittally known from the Negev, and from the coastal plains of Israel and Palestine (Harrison & Bates 1991).

Habitat Palm groves, near cultivation, in wadis and sandy dunes (Osborn & Helmy 1980).

Abundance May live in dense populations in sand dunes of Sinai (Wahrman & Gourewitz 1973).

Remarks Nocturnal and terrestrial. Digs extensive burrows in loose sand, with small entrance holes plugged with sand (Wassif 1953, in Harrison & Bates 1991). Camel dung and seeds of *Citrullus colocynthis* found in burrows, and assumed to be part of the diet (Wassif 1953, in Harrison & Bates 1991).

*Gerbillus floweri*

Conservation IUCN Category: Least Concern.

Measurements

Gerbillus floweri

HB: 117.0 (112–123?) mm, $n = 21^*$

T: 149.1 (140–158) mm, $n = 21$

HF: 34.9 (33–36) mm, $n = 21$

E: 16.2 (15–17) mm, $n = 21$

WT: 54.1 (48.9–63) g, $n = 21$

GLS: 34 (32.6–35.4) mm, $n = 18$

GWS: 18.7 (18.1–19.4) mm, $n = 17$

M^1 – M^3 : 4.9 (4.8–5.1) mm, $n = 18$

Auditory bulla: 10.0 (9.5–10.5) mm, $n = 18$

Egypt (Osborn & Helmy 1980; as *Gerbillus pyramidum floweri*)

*Higher value erroneously given as 213 mm in Osborn & Helmy (1980)

Key References Harrison & Bates 1991; Osborn & Helmy 1980.

Laurent Granjon

Gerbillus gerbillus LESSER EGYPTIAN GERBIL (SMALL EGYPTIAN GERBIL)

Fr. Petite Gerbille des sables; Ger. Kleine Rennmaus

Gerbillus gerbillus (Olivier, 1801). Bull. Sci. Soc. Philom. Paris 2: 121. Giza Province, Egypt.

Taxonomy Originally described in the genus *Dipus*. Synonyms: *aegyptius*, *aeruginosus*, *asyutensis*, *discolor*, *foleyi*, *hirtipes*, *longicaudatus*, *psammophilous*, *sudanensis*. See Musser & Carleton (2005) for further comment. Subspecies: none. Chromosome number: $2n = 42$ (♀ ♀), $2n = 43$ (♂ ♂) (Qumsiyeh & Schlitter 1991).

Description Small gerbil. Dorsal pelage relatively long and soft, sandy in colour; hairs grey at base, yellowish to orange terminally or subterminally, with a minute dark tip in some individuals. White rump patch just above base of tail. Flanks paler, hairs with a white zone between grey base and sandy tip. Ventral pelage pure white, more or less well delineated from the flanks. Head with supraorbital and postauricular white patches. Ears relatively large and covered with short hairs. Eyes large. Fore- and hindfeet white; hindfeet long with narrow tarsus and long digits, covered with hairs of variable length, including some that may be very long. Tail long (ca. 130% of HB), bicoloured, sandy above and whitish below, with usually a long pencil of whitish to dark grey hairs. Mastoid portion of auditory bullae very inflated. Nipples: $2 + 2 = 8$.

Geographic Variation None recorded in Africa.

Similar Species

G. pyramidum. Larger on average; darker pelage; more robust hindfeet; chromosome number: $2n = 38$; present along the Nile Valley and in southern Sahara from Chad to Mali.

G. tarabuli. Larger on average; darker pelage; more robust hindfeet; chromosome number: $2n = 40$; widespread in desert to semi-desert regions of North Africa.

G. nigeriae. Similar size; usually darker; wider and less-hairy hindfeet; chromosome number: $2n = 62-74$; northern part of Sahel savannas from Mauritania to Chad.

Distribution Sahara Arid BZ. Widespread in desert and semi-desert regions of North Africa, from Mauritania to Egypt, south to N Mali, Niger and Chad. Extraliminally present in Sinai and S Israel (Harrison & Bates 1991).

Habitat In coastal Mauritania, found on shifting sand, either in dune or inter-dune habitats with sparse plant cover and, to a lesser extent, around temporary settlements of nomadic cattle pastoralists (Klein *et al.* 1975, Granjon *et al.* 1997a). In Egypt, found in dunes, sand patches in palm groves and cultivated areas, patches of windblown sand in wadis, and oases (Osborn & Helmy 1980). In Algeria, also found on shifting sand in dunes, oases or even wadis (Petter 1961, Kowalski & Rzebiak-Kowalska 1991). Shows strong preference for sandy habitats.

Abundance Common in suitable habitats. In coastal Mauritania, densities range from 0.2 to 4.8 individuals/ha during the course of the year (Klein *et al.* 1975); capture rates of 3.5–8 individuals/100

*Gerbillus gerbillus*

trap-nights recorded in favourable habitats in March 1995 (Granjon *et al.* 1997).

Adaptations Terrestrial and nocturnal. Burrows are 30–80 cm deep, and may be plugged with sand during the warm season (Osborn & Helmy 1980). Said to experience lethargy in the laboratory, an observation linked to its seasonal apparent disappearance from the field in Morocco (Saint Girons & Petter 1965). Homing behaviour was observed in ca. 50% of the individuals released 1000 m away from their burrows ($n = 40$) and 20% of those released 2000 m away ($n = 40$; Mermoud 1970).

Foraging and Food Predominantly granivorous at all seasons in Israel. Foods also include plant material (*Thynalea* sp., *Erodium* sp. and *Plantago* sp., especially in winter) and insects (especially in spring) (Bar *et al.* 1984).

Social and Reproductive Behaviour In Mauritania, home-range is large (diameter up to 100 m) and shifting (especially for ♂ ♂). Nocturnal movements potentially very important, associated with exploratory behaviour in search of food (Klein *et al.* 1975). Mean distance between successive captures was 10.7 m, and maximum distance between recaptures was 105 m, over a 4-day trapping period in March 1995 (Cosson *et al.* 1997).

Reproduction and Population Structure In NW Mauritania, reproduction is nearly continuous, with reduced rate in Jan and Feb. Mean monthly embryo number: 3.4–6.0 depending on time of year.

Maximal birth rates and minimal death rates recorded in the wet season with long daylength (Jul–Oct), followed by a major phase of population expansion in the cool dry season (Nov–Jan) (Klein *et al.* 1975). Reproductive activity said to be related to temperature and daylength, and fecundity to resource availability (Klein *et al.* 1975). In Egypt, reproduction from Jan–May; litter-size: 4.3 (3–6), $n = 7$; (Osborn & Helmy 1980).

Predators, Parasites and Diseases Predators include Sand Foxes *Vulpus pallida*, Barn Owls *Tyto alba* and *Cerastes* snakes (Klein *et al.* 1975, Granjon *et al.* 2002b). Ticks (*Hyalomma dromedarii* and *H. impeltatum*) and fleas (*Synosternus cleopatrae*) are often found on these gerbils; the fleas occasionally carry plague (Klein *et al.* 1975).

Conservation IUCN Category: Least Concern.

Measurements

Gerbillus gerbillus

HB: 88.2 (78–99) mm, $n = 74$

T: 117.1 (97–136) mm, $n = 74$

HF: 27.2 (25–30) mm, $n = 74$

E: 12.7 (11–14) mm, $n = 74$

WT: 21.9 (16–27) g, $n = 74$

GLS: 26.6 (25–28) mm, $n = 74$

GWS: 14.2 (12.9–15.6) mm, $n = 21$

M^1 – M^3 : 3.3 (3–3.6) mm, $n = 74$

Auditory bulla: n. d.

Nasri and Chami regions, NW Mauritania (recalculated from Klein *et al.* 1975); GWS: coastal Mauritania (MNHN)

Key References Klein *et al.* 1975; Osborn & Helmy 1980.

Laurent Granjon

Gerbillus harwoodi HARWOOD'S GERBIL

Fr. Gerbille de Harwood; Ger. Harwoods Rennmaus

Gerbillus harwoodi Thomas, 1901. Ann. Mag. Nat. Hist., ser. 7, 8: 275. L. Naivasha, Kenya.

Taxonomy Yalden *et al.* (1976) include *harwoodi* within *G. ruberrimus*; all other authors (Petter 1975a; Lay 1983; Musser & Carleton 1993) regard *harwoodi* as a valid species. The smaller size of *harwoodi*, its distinctive darker colouration and limited range in Kenya and Tanzania suggest that it is separable from other named forms. The form *luteus*, originally considered a full species, is probably a synonym of *harwoodi* (Petter 1975a, Musser & Carleton 1993). Referred to as *Dipodillus harwoodi* by Musser & Carleton (2005). Synonyms: *luteus*. Subspecies: none. Chromosome number: not known.

Description Very small gerbil, with orange-brown or sandy-brown back, and long tail. Dorsal pelage glossy, orange-brown to dark orange-brown; hairs dark grey at base, sandy-brown or orange-brown terminally, often with black tip. Flanks similar to back. Ventral pelage pure white, sharply delineated. Dorsal and ventral pelage long and soft. Head and nose similar to back; cheeks sandy-brown; postorbital patches absent. Postauricular patches present. Fore- and hindfeet white. Soles of hindfeet naked. Tail long (ca. 126% of HB), dark orange-brown above, paler below. Long dark hairs on terminal third form well-developed pencil. Nipples: not known.

Geographic Variation None recorded.

Similar Species

Gerbillus cosensi. Larger (HB: 90–135 mm, T: 100–143 mm); dorsal pelage pale sandy-brown; white of ventral pelage merges into colour of flanks; soles of hindfeet hairy.

G. percivali. Similar in size; dorsal pelage dark rusty-brown; white of ventral pelage clearly delineated from colour of flanks; hairs usually long and soft; soles of hindfeet naked; prefers drier environments.



Gerbillus harwoodi

G. pusillus. Similar in size and colour; white of ventral pelage clearly delineated from colour of flanks; hairs long and soft; soles of hindfeet naked; drier habitats of C and S Kenya.

Distribution Endemic to Africa. Somalia–Masai Bushland BZ and Afromontane–Afroalpine BZ. Limited distribution in the highlands and Rift Valley of C Kenya, as well as drier areas towards the coast (*harwoodi*), and N–C Tanzania (*luteus*).

Habitat Little information. Locality records suggest grasslands in *Acacia* savanna. Found on open plains to the west of L. Natron at night (specimen label, NMK).

Abundance 'Plentiful' (L. Naivasha in 1912 [specimen label BMNH]), but distribution evidently very restricted.

Remarks Nocturnal. Lives in deep burrows on grassy plains during daytime (collector's notes, NMK). Pregnant ♀ with four embryos in Jun at Nanyuki, Kenya (Southern & Hook 1963).

Conservation IUCN Category: Least Concern.

Measurements

Gerbillus harwoodi

HB: 75 (60–89) mm, n = 9

T: 95 (85–112) mm, n = 9

HF: 20.5 (19–25) mm, n = 9

E: 9.4 (9–10) mm, n = 9

WT: 14, 14 g, n = 2

GLS: 24.0 (22.9–25.3) mm, n = 7

GWS: 12.7 (12.2–13.3) mm, n = 5

M¹–M³: 3.7 (3.6–3.9) mm, n = 7

Auditory bulla: 8.4 (7.2–8.9) mm, n = 7

Kenya (BMNH)

Key Reference Lay 1983.

D. C. D. Happold

Gerbillus henleyi HENLEY'S GERBIL

Fr. Gerbille de Henley; Ger. Henleys Rennmaus

Gerbillus henleyi (de Winton, 1903). Novit. Zool. 10: 284. Zaghigh, Wadi Natron, Egypt.

Taxonomy Originally described in the genus *Dipodillus*. Synonyms: *jordani*, *makrami*, *mariae*. Subspecies: none. Chromosome number: 2n = 52, aFN = 58–62 (Volobouev *et al.* 1995).

Description Very small, delicate gerbil. Dorsal pelage sandy to ashy-beige, sometimes becoming more russet on the flanks; hairs brownish-grey at base, with subterminal band of sandy-buff, grey-black tip (some hairs with grey-black subterminal band and sandy-buff tip). White rump patch prominent in specimens from Egypt, less so in specimens from West Africa. Ventral pelage pure white, clearly delineated along the cheeks and flanks. Head with supraorbital and postauricular white (or pale) patches. Fore- and hindfeet white; hindfeet delicate and naked. Tail slender, long (ca. 130% of HB), with a thin pencil of more or less dark hairs. Nipples: 2 + 2 = 8.

Geographic Variation None recorded in Africa.

Similar Species

G. nanus. On average larger with a relatively longer tail; chromosome number: 2n = 52, aFN = 58–62; sympatric in western part of range.

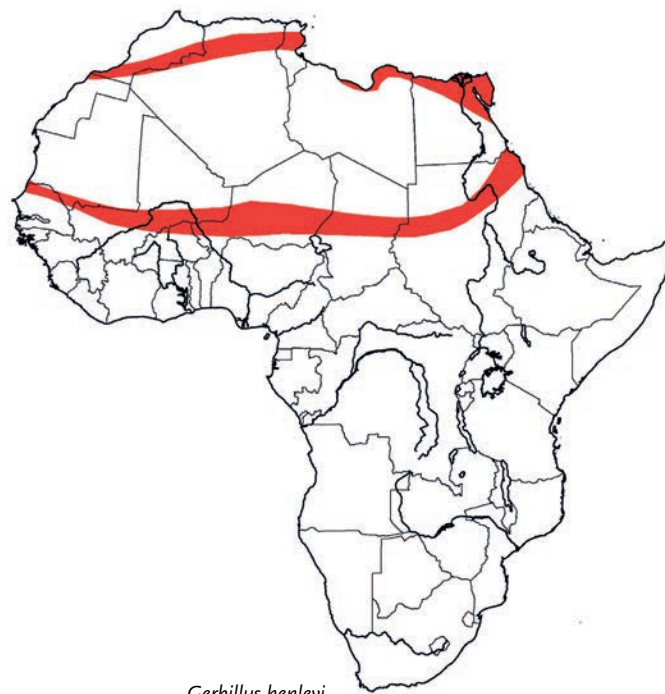
G. campestris. Larger; chromosome number: 2n = 56–58; sympatric in most of the range (except the SW part).

G. nigeriae. Larger, soles of hindfoot hairy; chromosome number: 2n = 62–74; sympatric south of Sahara.

G. gerbillus. Larger, soles of hindfoot hairy; chromosome number: 2n = 42–43; sympatric in most of the range.

G. nancillus. On average smaller; chromosome number: 2n = 56; sympatric south of Sahara.

Distribution Sahara Arid BZ (northern and southern fringes) and Sahel Savanna BZ. Widespread in desert to semi-desert regions of North Africa. Recorded from Morocco to Egypt, and from N Senegal westwards to Mali, Burkina, Niger, Chad and N Sudan (Musser &



Gerbillus henleyi

Carleton 1993, Dobigny *et al.* 2002b, L. Granjon unpubl.). Presence in N Burkina and N Senegal is interpreted as a possible southward extension of the range following desertification (Maddalena *et al.* 1988, Duplantier *et al.* 1991). Extraliminally present in the Arabian Peninsula and the Middle East.

Habitat Sandy areas, gravel plains, salt marshes, wadis and crop fields (review in Shenbrot *et al.* 1994). In C Negev (Israel), more abundant on gravel plains and in dry river beds on various substrates than in sandy habitats (Shenbrot *et al.* 1994).

Abundance Quantitative data lacking in Africa, but may prove to be locally more abundant than usually thought. Abundant in pellets of Barn Owls *Tyto alba* from the Senegal River Valley (L. Granjon unpubl.). Average densities ranged from 0.9 to 2.3 individuals/ha (range 0–5.5/ha) in four habitats in Israel (Shenbrot *et al.* 1994).

Adaptations Terrestrial and nocturnal. Burrows are shallow and narrow (Petter 1961, Harrison & Bates 1991). Moulting observed in early autumn (Sep–Oct) in Israel (Shenbrot *et al.* 1994).

Foraging and Food Mainly granivorous, but also herbivorous to some extent. In captivity, found to depend heavily on seeds, the husks of which are removed before eating to maximize energy intake. Individuals lost weight when provided only with fresh vegetation. Stems of *Atriplex halimus* and *Moricandia nitens* were preferred plants when offered a selection of green plants (Negev Desert, Israel; Khokhlova *et al.* 1995, Kam *et al.* 1997).

Social and Reproductive Behaviour Limited rates of recapture of individuals suggest regular changes of home-range in Israel (Shenbrot *et al.* 1994).

Reproduction and Population Structure In the Negev, reproductively active adults present from Feb to Oct. Young individuals present in population in low numbers (7–26%) in all months except Sep (76%) (Shenbrot *et al.* 1994). Embryo number: 3 (Jul; Senegal; K. Bâ unpubl.), 4 and 6 (Jun; Arabian Peninsula; Harrison & Bates 1991). Maximum recorded longevity of 241 days in the wild

(Shenbrot *et al.* 1994) and more than three years in captivity (Petter 1961).

Predators, Parasites and Diseases Predators include owls, especially the Barn Owl (Kowalski & Rzebik-Kowalska 1991). Represented only 3% of the prey of Barn Owls in N Senegal (Bâ *et al.* 2000). In Israel, infestation by non-specific species of fleas is low (Shenbrot *et al.* 1994).

Conservation IUCN Category: Least Concern.

Measurements

Gerbillus henleyi

HB: 64.9 (55–73) mm, n = 16

T: 86.7 (75–103) mm, n = 14

HF: 17.8 (17–20) mm, n = 16

E: 9.3 (8–11) mm, n = 15

WT: 10.6 (8–13.9) g, n = 9

GLS: 21.6 (20.5–22.3) mm, n = 11

GWS: 10.9 (10.6–11.6) mm, n = 13

M¹–M³: 2.9 (2.7–3.1) mm, n = 13

Auditory bulla: n. d.

Algeria, Tunisia, Senegal, Mali, Burkina, Niger and Chad (MNHN)

Key Reference Shenbrot *et al.* 1994.

Laurent Granjon

Gerbillus hesperinus MOROCCAN GERBIL

Fr. Gerbille de Maroc; Ger. Marokkanisch Rennmaus

Gerbillus hesperinus Cabrera, 1936. Bol. Real. Soc. Esp. Hist. Nat., p. 365. Mogador (= Essaouira), Morocco.

Taxonomy Lay (1975, 1983) and Musser & Carleton (1993, 2005) regard *hesperinus* as a valid species. In contrast, Petter (1975a) considered *G. hesperinus* to be a synonym of *G. pyramidum*. Synonyms: none. Chromosome number: 2n = 58, FN = 76 (Lay 1975) (cf. *G. pyramidum*).

Description Small gerbil with long soft pelage. Dorsal pelage dark sandy-brown, hairs dark grey at base with sandy-brown tips; flanks cinnamon. Ventral pelage pure white, clearly delineated from colour of flanks. Chin, throat, fore- and hindlimbs white. Soles of feet hairy. Tail long (ca. 115% of HB), cinnamon above, white below; longer hairs form slight pencil at terminal end.

Geographic Variation None recorded.

Similar Species In Morocco:

G. hoogstraali. Similar HB; longer ear; chromosome number: 2n = 72; very restricted distribution.

G. gerbillus. HB on average smaller; longer tail; white rump patch; GLS smaller; chromosome number: 2n = 42/42; widespread.

G. tarabuli. Similar HB; much longer tail; chromosome number: 2n = 40; widespread.



Gerbillus hesperinus

Distribution Endemic to Africa. Mediterranean Coastal BZ. Recorded only from near Essaouira on the coast of Morocco, north of the Middle Atlas mountains (Lay 1983).

Habitat Coastal sand dunes (Aulagnier & Thévenot 1986).

Abundance Probably rare; known only from a few specimens.

Remarks Apparently no other information available.

Conservation IUCN Category: Endangered.

The limited geographic distribution and fragmentation of sand dunes are cause for concern.

Measurements

Gerbillus hesperinus

HB: 90–114 mm

T: 98–120 mm

HF: 20–28 mm

E: 13–16 mm

WT: n. d.

GLS: 28–31 mm

GWS: 16.2 mm, n = 2*

M¹–M³: 3.9–4.3 mm

Auditory bulla: 7.8–8.7 mm

Morocco (Aulagnier & Thévenot 1986 [means and sample sizes not given])

* = Essaouira, Morocco (MNHN)

Key References Aulagnier & Thévenot 1986; Lay 1983.

D. C. D. Happold

Gerbillus hoogstraali HOOGSTRAAL'S GERBIL

Fr. Gerbille de Hoogstraal; Ger. Hoogstraals Rennmaus

Gerbillus hoogstraali Lay, 1975. Fieldiana Zool. 65: 90. 7 km south of Taroudannt, Morocco.

Taxonomy Distinguished from its closely related congeners by skull characters and karyology. This species is one of several allopatric species (*G. hesperinus*, *G. occidus*, *G. riggenbachi*), each of which has a very small geographic range on the coast of Morocco. Synonyms: none. Chromosome number: 2n = 72, FN = 80 (Lay 1975).

Description Small gerbil. Dorsal pelage sandy-brown; dorsal hairs medium grey with sandy-brown at tip, and sometimes with black terminal rings. Flanks paler than dorsal pelage and tending towards orange-brown. Ventral pelage pure white, clearly delineated from flanks. Head similar to dorsal pelage. Ears pale, with brownish band on outer margin. Slight ring of dark hairs around eye. Small postorbital spot in some individuals. White postauricular spot. Lower cheeks, chin, throat and chest white. Fore- and hindlimbs and feet with short dense white hairs. Soles of HF hairy. Tail long (ca. 120% of HB), bicoloured with short dense hairs; sandy-brown above, cream or white below; hairs longer and denser towards tip forming small pencil. Nipples: not known.

Geographic Variation None recorded.

Similar Species

G. campestris. Slightly larger; tail longer and relatively longer with well-developed pencil; soles of hindfoot naked; smaller auditory bullae; also occurs near Agadir.

Distribution Endemic to Africa. Mediterranean Coastal BZ. Recorded only in Morocco, from a few localities in the Sous Valley near Agadir and near Taroudannt. The distribution is restricted to the



Gerbillus hoogstraali

narrow Sous Valley, bordered by the High Atlas to the north and the Anti Atlas to the south.

Habitat Hard-packed sandy clay covered with fine red sand, alternating with low sand dunes. Vegetation sparse, mainly scattered thorny *Ziziphus* shrubs.

Abundance No information; known only from a few individuals. At the type locality, specimens were collected over an area of about 7 km by 7 km.

Remarks Terrestrial and nocturnal. Appears to be a typical arid-adapted gerbil. Burrow entrances are located at the bases of *Ziziphus* shrubs. One ♀ trapped in July contained six placental scars, and two subadults trapped at the same time, suggest that reproduction occurs during late spring and early summer (Apr–Jul). Duration of reproductive activity not known.

Conservation IUCN Category: Vulnerable.

The limited geographic distribution and fragmentation of sand dunes are cause for concern.

Measurements

Gerbillus hoogstraali

HB: 96 (90–100) mm, n = 3*

T: 113.8 (103–123) mm, n = 7

HF: 27.3 (26–28) mm, n = 7

E: 16.6 (16–17) mm, n = 7

WT: 22, 30 g, n = 2

GLS: 29.0 (27.8–29.8) mm, n = 3*

GWS: 15.5 (14.6–16.0) mm, n = 3*

M¹–M³: 3.8 (3.7–3.9) mm, n = 3*

Auditory bulla: 10.3 (9.8–10.6) mm, n = 3*

Morocco (Lay 1975; *SMNS)

Key Reference Lay 1975.

D. C. D. Happold

Gerbillus juliani JULIAN'S GERBIL

Fr. Gerbille de Julian; Ger. Julians Rennmaus

Gerbillus juliani (St Leger, 1935). Ann. Mag. Nat. Hist., ser. 10, 15: 669. Bulhar, Somalia.

Taxonomy Originally described in the genus *Dipodillus* and later placed in the genus *Monodia* by Roche & Petter (1968). Petter (1975a) allocated *juliani* to the genus *Gerbillus*, but regarded it as synonymous with *G. watersi* without supporting evidence. Musser & Carleton (1993), following Lay (1983), consider *G. juliani* as a valid species pending revision of the genus (a decision retained here), but Musser & Carleton (2005) place *juliani* as a synonym of *G. watersi*. Synonyms: none. Chromosome number: not known.

Description Very small gerbil. Dorsal pelage sandy-fawn; hairs steel-grey at base with sandy-fawn tips. Pelage on flanks brighter

than on back. Ventral pelage pure white. Head sandy-fawn; cheeks white, with thin sandy-fawn line below each eye. Supraorbital and postauricular white patches. Fore- and hindlimbs white, feet white. Tail very long (ca. 150% of HB), sandy-fawn above, white below, with pencil of long brown hairs at terminal end. Nipples: not known.

Geographic Variation None recorded.

Similar Species

G. brockmani. Larger (HB: 71–84 mm).

G. somalicus. Larger (HB: 82–90 mm).

Distribution Endemic to Africa. Somalia–Masai Bushland BZ. Recorded from only four localities in Somalia (Roche & Petter 1968); not recorded from arid regions in neighbouring Ethiopia.

Habitat Semi-arid habitats. One specimen from Bulhar ‘trapped on maritime plain near the town’. Other specimens captured in abandoned cultivation near the Webi Shabeelle river, in ‘bush’ and in ‘wooded steppe’ (Roche & Petter 1968).

Abundance ‘Must be rare, as it appears to be the only [specimens] I caught with numbers of *G. acticola* which was relatively common’ (R. E. Drake-Brockman, in St Leger 1935).

Remarks Little information. Presumably nocturnal, living in burrows during daytime. Apparently lives ‘alongside and fraternising with *G. acticola*’ (R. E. Drake-Brockman, in St Leger 1935).

Conservation IUCN Category: Least Concern.

Lack of specimens (especially in recent years) suggests that ‘Data Deficient’ is a more realistic assessment.



Gerbillus juliani

Measurements*Gerbillus juliani*

HB: 63.1 (53–70) mm, n = 9

T: 96.5 (85–110) mm, n = 6

HF: 20.0 (18–21) mm, n = 9

E: 8.9 (7–10) mm, n = 9

WT: n. d.

GLS: 23.3 (22.1–24.3) mm, n = 8

GWS: 11.9 (11.3–12.2) mm, n = 8

M¹–M³: 3.3 (3.0–3.5) mm, n = 11

Auditory bulla: n. d.

Somalia (Roche & Petter 1968)

Key References Lay 1983; St Leger 1935.

D. C. D. Happold

***Gerbillus latastei* LATASTE'S GERBIL**

Fr. Gerbille de Lataste; Ger. Latastes Rennmaus

Gerbillus latastei Thomas and Trouessart, 1903. Bull. Soc. Zool. France 28: 172. Kebili, Tunisia.

Taxonomy The definition of this hairy-footed gerbil species is controversial. Cockrum (1977) lists nine forms which he considers may be conspecific, five of which (*bonhotei*, *dunni*, *perpallidus*, *riggenbachi*, *rosalinda*) are considered as separate species by Lay (1983) pending revision. Ranck (1968) refers to *latastei* as a subspecies of *Gerbillus gerbillus*. Here, following Lay (1983) and Musser & Carleton (1993, 2005), *G. latastei* is considered as a valid species restricted to Tunisia and Libya. Synonyms: *aureus*, *favillus*, *nalutensis*. Subspecies: none. Chromosome number: 2n = 74, FN = 92–100 (as *aureus*; Jordan *et al.* 1974); specimens labelled *G. latastei* (in MNHN) have 2n = 74 and 75.

Description Small orange and white gerbil with long tail. Dorsal pelage bright orange; dorsal hairs grey at base with orange tip. Flanks whitish-orange; hairs white at base, orange at tip. Colour of flanks merges gradually into pure white of ventral pelage. Crown of head orange. Supraorbital, postorbital and postauricular white patches. Cheeks, nose, chin, throat, fore- and hindlimbs and feet white. Soles of hindfeet hairy. Tail long (ca. 116% of HB), sandy or sandy-orange above, sandy-orange or white below; darker hairs form narrow pencil at terminal end of tail.

Geographic Variation None recorded.

Similar Species

G. gerbillus. Smaller HB; shorter ear; white rump patch; chromosome number: 2n = 42/43; widespread.

G. tarabuli. Similar HB; longer tail; chromosome number: 2n = 40; widespread.

Distribution Endemic to Africa. Mediterranean Coastal BZ and Sahara Arid BZ. Recorded only from Tunisia and W Libya.

Habitat Slopes of sparsely vegetated hamadas, and on the margins of small wadis (Libya; Ranck 1968). In Tunisia, found in sand of dry river beds.

Abundance Probably rare or uncommon.

Remarks Apparently no other information available.

*Gerbillus latastei*

Conservation IUCN Category: Least Concern.

Measurements*Gerbillus latastei*

HB: 110 (100–120) mm, n = 7

T: 128 (120–135) mm, n = 7

HF: 30 (27–32) mm, n = 7

E: 15 (14–16) mm, n = 7

WT: n. d.

GLS: 30.4 (29.2–31.4) mm, n = 7

GWS: 16.8 (16.1–17.4) mm, n = 7

M¹–M³: 4.2 (3.9–4.5) mm, n = 7

Auditory bulla: 10.7 (9.9–11.2) mm, n = 7

Tunisia (MNHN)

Key References Cockrum 1977; Jordan *et al.* 1974; Ranck 1968.

D. C. D. Happold

***Gerbillus lowei* LOWE'S GERBIL**

Fr. Gerbille de Jebel Marra; Ger. Lowes Rennmaus

Gerbillus lowei (Thomas and Hinton, 1923). Proc. Zool. Soc. Lond. 1923: 261. Jebel Marra, Sudan. (Exact locality not recorded.)

Taxonomy Originally described in the genus *Dipodillus*. Regarded as a valid species by Lay (1983) and Musser & Carleton (1993). The limited geographical range, and isolation from other populations of *G. campestris*, suggest that *lowei* is not a subspecies of *G. campestris* as given by Petter (1975a). Thomas & Hinton (1923a), when describing the holotype as *Dipodillus lowei*, referred to it as 'a dark mountain form of the *D. campestris* group'. Musser & Carleton (2005) refer to this species as *Dipodillus lowei*. Synonyms: none. Chromosome number: not known.

Description Small, long-haired gerbil with long well-haired tail. Dorsal hairs 11–15 mm. Dorsal pelage dark brown; hairs dark grey at base, dark brown or chestnut at terminal end, often with black tip. Flanks paler, chestnut or cinnamon merging into pure white of ventral pelage. Crown of head and nose similar to dorsal pelage. Chin, throat white. Postorbital and postauricular white patches. Soles of hindfeet naked. Tail very long (ca. 140% of HB), dark brown above with short black-tipped hairs, paler below; terminal half or one-third with long soft dark hairs forming conspicuous pencil. Young animals paler than adults.

Geographic Variation None recorded.

Similar Species This species is the darkest of all gerbils and the only species of *Gerbillus* on Jebel Marra (see below).

Distribution Endemic to Africa. Afromontane–Afroalpine BZ. Recorded only from higher altitudes (2300–3000 m) of Jebel Marra, W Sudan. Not recorded from the dry Sahel Savanna BZ surrounding the jebel.

Habitat Lowe's Gerbils live only at the highest altitudes of Jebel Marra. They live under rocks of pumice where there is a dense cover of grasses and herbs, and among the crevices of pumice walls surrounding local vegetable gardens (Happold 1966b).

Abundance Distribution patchy; found only in selected habitats on Jebel Marra; in the single locality where most abundant, comprised 40% of rodents (total n = 15, 6 spp.; Happold 1966b).

Remarks Nocturnal and terrestrial; the very long hairs form a dense pelage, which provides insulation from the cold nights in 'winter' on Jebel Marra (minimum temperature near freezing). Diet is 'grass and flower seeds' (Lynes and Lowe, in Thomas & Hinton 1923a), as well as *Loranthus* seeds (Happold 1966b). Juveniles in several weight-classes in Nov, suggest prolonged breeding season during and after the wet season (Jul–Sep; 800 mm/year) (Happold

*Gerbillus lowei*

1966b). Small individuals (HB <85 mm) found in Nov, Dec, Mar and Apr (Lynes & Lowe specimens, BMNH).

Conservation IUCN Category: Data Deficient.

Lowe's Gerbils have a very restricted geographic range, and occur at only a few localities within their range.

Measurements*Gerbillus lowei*

HB: 104 (89–113) mm, n = 10

T: 148 (141–158) mm, n = 10

HF: 26 (25–27) mm, n = 10

E: 15 (14–16) mm, n = 10

WT: 36 (32–40) g, n = 3

GLS: 30.2 (28.5–31.1) mm, n = 10

GWS: 15.5 (14.6–16.4) mm, n = 8

M¹–M³: 4.3 (4.1–4.5) mm, n = 10

Auditory bulla: 9.3 (8.6–9.6) mm, n = 10

Jebel Marra, Sudan (BMNH)

Key References Happold 1966b; Thomas & Hinton 1923a.

D. C. D. Happold

Gerbillus mackilligini MACKILLIGIN'S GERBIL

Fr. Gerbille de Nubie; Ger. Mackilligins Rennmaus

Gerbillus mackilligini (Thomas, 1904). Ann. Mag. Nat. Hist., ser. 7, 14: 158. Wadi Alagai, Eastern desert of Nubia, Egypt.

Taxonomy In the type description, Thomas (1904b) referred to this species as 'a very pretty pencil-tailed gerbille' in the genus *Dipodillus*. Although some authors have placed this taxon in *G. nanus*, Osborn & Helmy (1980) show that *G. mackilligini* is a valid species. Referred to as *Dipodillus mackilligini* by Osborn & Helmy (1980) and Musser & Carleton (2005). The correct spelling of the specific name is *mackilligini*, not *mackillingini* as in Musser & Carleton (1993). Synonyms: none. Chromosome number: not known.

Description Small, darkish gerbil with a very long conspicuous pencil on tail. Pelage 9–10 mm on mid-back. Dorsal pelage sandy-brown suffused with black; hairs dark grey at base, sandy-brown at terminal end, some with black tip. Ventral pelage pure white, clearly delineated from colour on flanks. Crown of head and nose similar to back. Supraorbital, postorbital and postauricular white patches. Chin and throat white. Fore- and hindlimbs white. Soles of feet pigmented, naked. White rump patch absent. Tail long (ca. 155% of HB), dark brown with small short black hairs above, sandy-brown or white below; hairs (up to 20 mm in length at tip) form very conspicuous pencil on terminal half of tail, which extends beyond end of tail. Large auditory bullae. Nipples: not known.

Geographic Variation None recorded.

Similar Species

G. gerbillus. Dorsal pelage pale orange; slightly larger (HB: ca. 90 mm, T: ca. 120 mm); soles hairy; pencil small.

G. pyramidum. Dorsal pelage bright orange-cinnamon; larger (HB: ca. 120 mm, T: ca. 150 mm); soles hairy; pencil not conspicuous.

G. henleyi. Dorsal pelage pale sandy-orange; smaller (HB: ca. 66 mm, T: ca. 90 mm); soles naked; white rump patch conspicuous; pencil small.

G. amoenus. Dorsal pelage dark; similar size, but shorter tail (ca. 106 mm); soles naked; white rump patch conspicuous; pencil small.

Distribution Endemic to Africa. Sahara Arid BZ. Recorded from the Eastern Desert of Egypt and NE Sudan.

Habitat 'Grassy patches near water' and 'bush beside water in abandoned village' in Nubia (collector's field notes). Found in burrows in a grassy valley on Jebel Elba, near the Red Sea coast, at 2500 ft (Hoogstraal 1963).

Abundance Known from only a few localities and only a few specimens. Appears to be rare (Jebel Elba; Hoogstraal 1963).

Remarks Remains of this gerbil found in owl pellets at Jebel

*Gerbillus mackilligini*

Migif, some 300 km from the nearest known living populations. Because of the current dry local climate, and the virtual lack of vegetation nearby, these pellets may have been deposited hundreds of years ago (Goodman 1986). Four individuals examined in Egypt did not have any fleas (Hoogstraal & Traub 1965a).

Conservation IUCN Category: Least Concern.

Measurements

Gerbillus mackilligini

HB: 78 (72–86) mm, n = 6

T: 120 (99–138) mm, n = 6

HF: 24.2 (22–26) mm, n = 6

E: 12.9 (12–14) mm, n = 6

WT: n. d.

GLS: 26.9 (26.2–27.7) mm, n = 3

GWS: 13.3 (13.2–13.5) mm, n = 3

M¹–M³: 3.8 (3.5–4.0) mm, n = 4

Auditory bulla: 8.2 (8.0–8.3) mm, n = 3

Egypt (Osborn & Helmy 1980)

Key Reference Osborn & Helmy 1980.

D. C. D. Happold

***Gerbillus maghrebi* MAGHREB GERBIL**
Fr. Gerbille du Maghreb; Ger. Maghreb-Rennmaus

Gerbillus maghrebi Schlitter & Setzer, 1972. Proc. Biol. Soc. Washington 84: 387. 15 km WSW Taounate, Fes Prov., Morocco.

Taxonomy Placed in subgenus *Hendecapleura* by Lay (1975), and in genus *Dipodillus* by Musser & Carleton (2005). Synonyms: none. Chromosome number: unknown.

Description Small gerbil, although the largest of the North African short-tailed gerbils. Dorsal pelage pinkish-grey, purest on sides and flanks, strongly mixed with black becoming darker on forehead; hairs dark grey at base. Ventral pelage pale pinkish-buff. Head slightly darker than back. Lips pale. Colour of dorsal surface of fore- and hindfeet similar to ventral pelage. Soles of hindfeet naked. Tail long (ca. 95% of HB), slightly bicoloured, with terminal pencil. Skull large for the genus; maxilla-premaxilla junction anterior to the zygomatic plate; zygomatic arches rugged; upper toothrow relatively long; auditory bullae relatively small and well inflated ventrally. Mandible with high and large coronoid process, broad ramus and thick angular process, so that the sigmoid notch appears not to be very deep. Nipples: not known.

Geographic Variation None recorded.

Similar Species

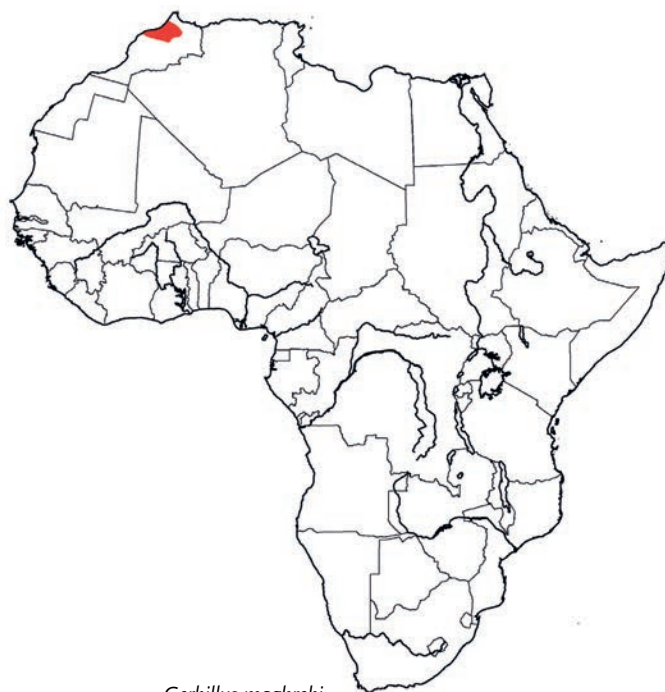
G. campestris. Only other gerbil in the distribution range of *G. maghrebi*; on average slightly smaller; tail longer, with pencil; can be distinguished by discriminant function analysis on skull and mandibular measurements (see Aulagnier *et al.* 1993). Maxilla-premaxilla junction concealed by the zygomatic plate.

Distribution Endemic to Africa. Mediterranean Coastal BZ. Recorded only in Morocco from south of the Rif Mts, the Prérif hills and the Saïss plain to Chaouia and even Jbilets (north of Marrakech); range limited to the east by the Middle Atlas Mts (Aulagnier *et al.* 1993).

Habitat Rock and clay terrains, especially on hills and slopes with natural herbaceous vegetation. Avoids sand dunes and river beds, and has not been found in large cultivated fields, nor in densely vegetated areas, forests and matorrals.

Abundance Common in the Fes region (Prérif and Saïss) where it is locally the only gerbil (the Algerian Mouse *Mus spretus* is the main species of rodent). Less abundant in most of the range where *G. campestris* is also present. Rare south of Casablanca.

Remarks Of three ♀♀ taken in May, one contained eight embryos (three in the right horn of the uterus) (Schlitter & Setzer 1972). Main predators are Barn Owls *Tyto alba* but other owls (particularly Tawny Owls *Strix aluco*) and diurnal raptors also prey on this gerbil. In the region of Fes, formed up to 14% of diet of Barn Owls.



Gerbillus maghrebi

Conservation IUCN Category: Least Concern.

The main threat is destruction of habitat following agricultural changes (e.g. regrowth of brushwood in fields and pastures).

Measurements

Gerbillus maghrebi

HB: 111.8 (106–119) mm, n = 6

T: 107.0 (102–111) mm, n = 6

HF: 26.9 (26–27) mm, n = 7

E: 18.2 (17–19) mm, n = 7

WT: 42.9 (34–58) g, n = 7

GLS: 31.3 (30.4–32.9) mm, n = 13

GWS: 16.7 (15.1–17.8) mm, n = 14

M¹–M³: 4.3 (3.9–4.5) mm, n = 40

Auditory bulla: 8.3 (7.9–8.6) mm, n = 7

Body measurements and auditory bulla: Morocco (Schlitter & Setzer 1972)

Skull measurements: Morocco (Aulagnier *et al.* 1993)

Key References Aulagnier *et al.* 1993; Lay 1975; Schlitter & Setzer 1972.

Stéphane Aulagnier

***Gerbillus nancillus* SUDAN GERBIL**

Fr. Gerbille du Soudan; Ger. Sudan Rennmaus

Gerbillus nancillus Thomas and Hinton, 1923. Proc. Zool. Soc. Lond. 1923: 260. 45' N El Fasher, Plains of Darfur, Sudan.

Taxonomy Synonyms: *mauritaniae* (following Tranier & Julien-Laferrière 1990). Subspecies: none. Chromosome number: $2n = 56$, aFN = 54 (Dobigny *et al.* 2002b).

Description Very small, delicate gerbil. Dorsal pelage sandy to orangish-brown; hairs grey at base, orange-brown terminally. Paler on flanks; hairs white at base. Ventral pelage pure white, well delineated from colour of flanks. Eye-ring and postauricular patch white. Fore- and hindfeet white. Soles of hindfoot partly naked behind, with short hairs at level of the metacarpal bones. Tail long (ca. 135% of HB), bicoloured, sandy-buff above, white below, with a thin pencil of terminal hairs. Nipples: not known.

Geographic Variation None recorded.

Similar Species

G. nanus. On average larger; naked hindfeet (or nearly so); $2n = 52$; western part of North Africa.

G. henleyi. On average slightly larger; naked hindfeet; $2n = 52$; circum-Saharan distribution.

Distribution Endemic to Africa. Sahel Savanna BZ. Distribution disjunct. Described from Sudan (Thomas & Hinton 1923a), and now known to occur also in Mauritania (as *mauritaniae*), Niger and Mali (Tranier & Julien-Laferrière 1990, Dobigny *et al.* 2002b).

Habitat Sandy to sandy-clay soils with *Cenchrus biflorus*; fallow land and millet fields in Mali and Niger (L. Granjon, G. Dobigny & A. Nomao unpubl.).

Abundance No information. Apparently difficult to catch in live-traps, so may be more abundant than suspected.

Remarks One ♀ with four embryos caught in Niger (Kollo) in Jun (G. Dobigny and A. Nomao unpubl.).

Conservation IUCN Category: Data Deficient.

*Gerbillus nancillus***Measurements***Gerbillus nancillus*HB: 61 (55–69) mm, $n = 12$ T: 83.9 (76–89) mm, $n = 10$ HF: 16.4 (15–18) mm, $n = 12$ E: 10.6 (10–11.5) mm, $n = 12$ WT: 8.4 (6.9–10.6) g, $n = 12$ GLS: 20.6 (19.2–21.8) mm, $n = 4$ GWS: 10.3 (10.2–10.4) mm, $n = 3$ M^1 – M^3 : 3.0 (2.9–3.1) mm, $n = 4$

Auditory bulla: n. d.

Mali and Niger (MNHN)

Key Reference Tranier & Julien-Laferrière 1990.

Laurent Granjon

***Gerbillus nanus* DWARF GERBIL (BALUCHISTAN GERBIL)**

Fr. Gerbille naine; Ger. Zwerg Rennmaus

Gerbillus nanus Blanford, 1875. Ann. Mag. Nat. Hist., ser. 4, 16: 312. Gedrosia, Pakistan.

Taxonomy Lay (1983) recorded that *G. nanus* shared a number of features with *G. amoenus* (similar karyotype, naked hindfeet and accessory tympanum) and that the two species are closely related. Given their distribution, they may even prove to be conspecific; if so, *G. amoenus* would be a junior synonym of *G. nanus*. Following Petter (1961),

Rosevear (1969) and Kowalski & Rzebik-Kowalska (1991), the form *garamantis* (found by Matthey [1954] to have $2n = 54$) is considered to be synonym of *G. nanus*. Synonyms: *arabium*, *garamantis*, *hilda*, *indus*, *lixa*, *mimulus*, *quadrimaculatus*, *setonbrownnei*. Subspecies: none. Chromosome number: $2n = 52$, aFN = 58–62 (Volobouev *et al.* 1995).

Description Very small gerbil. Dorsal pelage of variable colour, from sandy to relatively dark tawny-grey; hairs grey at base, sandy to tawny at tip. Flanks paler. Ventral pelage pure white, well delineated from flanks. Head with supraorbital and postauricular white patches. Cheeks similar in colour to flanks. Fore- and hindfeet white; hindfeet small, naked or nearly so. Tail very long (ca. 140–150% of HB), with a marked pencil of pale and dark grey hairs. Nipples: $2 + 2 = 8$.

Geographic Variation None recorded.

Similar Species

G. henleyi. Smaller on average; chromosome number: $2n = 52$, aFN = 58–62; circum-Saharan distribution.

G. nancillus. Smaller on average with a relatively smaller tail; chromosome number: $2n = 56$; northern Sahelian distribution from Mali to Sudan.

G. campestris. Larger; chromosome number: $2n = 56$ –58; all North Africa south to massifs of N Mali and Niger.

G. nigeriae. Larger on average; soles of hindfoot hairy; chromosome number: $2n = 62$ –74; northern Sahelian distribution from Mali to Chad.

G. gerbillus. Larger on average; soles of hindfoot hairy; chromosome number: $2n = 42/43$; distributed in all desert to semi-desert habitats of North Africa.

Distribution Sahara Arid and Sahel Savanna BZs. Widespread but only in western half of these BZs. Recorded from Mauritania to Tunisia south of the Atlas Mts, and south to N Mali, Niger and Chad (Lay 1983, Granjon *et al.* 1997a, Dobigny *et al.* 2002b, Granjon & Dobigny 2003 and unpubl.). Also present in the Arabian Peninsula and the Middle East to NW India.

Habitat Desert and semi-desert. Mostly found in parts of the desert with relatively deep soil and abundant vegetation, such as

wadis, oases, sebkhas edges and sandy-clay plains or basins (Petter 1961, Kowalski & Rzebik-Kowalska 1991, Granjon *et al.* 1997). In the N Sahel Savanna BZ, also common in millet fields, fallow lands, gardens and in the immediate vicinity of human dwellings (Dobigny *et al.* 2001a, b, Granjon & Dobigny 2003 and unpubl.).

Abundance Common in suitable habitats. In coastal Mauritania, capture rates of 4–6.5 individuals/100 trap-nights recorded in favourable habitats in Mar 1995 (Granjon *et al.* 1997a). It is the most numerous of gerbillids in the sandy bottom of wadis, and in oases in Algeria (Kowalski & Rzebik-Kowalska 1991). In a Saharan habitat of Morocco, 43 individuals were found on a 1 ha trapping grid (Zaïme & Pascal 1989).

Adaptations Terrestrial and nocturnal. In Algeria, uses the burrows of *Psammomys obesus* and *Meriones libycus*, as well as withdrawal cracks in dry clay soils (Petter 1961). A study of oxygen consumption and body temperature showed the species is well adapted to extreme arid areas, with a thermoneutral zone at $33 \pm 1^\circ\text{C}$ and an oxygen consumption at thermoneutrality of 50.6% of predicted value (Haim 1984).

Foraging and Food Granivorous and herbivorous. The diet is predominantly folivorous (mainly leaves of *Euphorbia calyptrata*) in the winter and spring (Feb–May), and predominantly granivorous (seeds of *Atriplex halimus* and *Salsola vermiculata*) in the summer months (Jun–Aug) (Sahara, Morocco; Zaïme & Gautier 1989).

Social and Reproductive Behaviour Found to be capable of very large movements (hundreds of metres each night) between the burrow and foraging areas in Algeria (Petter 1961). Trapping data in coastal Mauritania, showed that these gerbils display larger movements than coexisting *G. gerbillus*, *G. tarabuli* and *G. nigeriae*. Mean recapture distance 16.9 m (max 135 m) over a 4-day period (Cosson *et al.* 1997). Likewise, in Morocco, they display larger movements than coexisting *G. campestris* and *Meriones shawi*, where their mean recapture distance was 19.1 m (Zaïme & Pascal 1988).

Reproduction and Population Structure Embryo number: 2, 5 ($n = 2$; Arabia; Harrison & Bates 1991).

Predators, Parasites and Diseases Heavily preyed upon by Barn Owls *Tyto alba* in Israel (Pokines & Kerbis Peterhans 1997) as well as in Mauritania where it represented 45% of prey (Granjon *et al.* 2002b).

Conservation IUCN Category: Least Concern.

Measurements

Gerbillus nanus

HB: 72.8 (58–82) mm, $n = 25$

T: 111.9 (96–125) mm, $n = 74$

HF: 20.3 (19–22.5) mm, $n = 78$

E: 10.9 (10–12) mm, $n = 78$

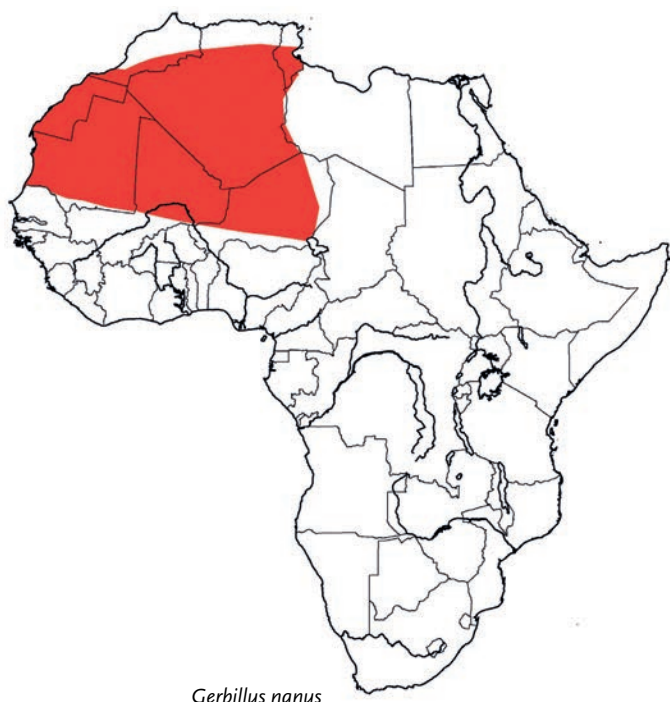
WT: 13.3 (9.5–18) g, $n = 76$

GLS: 22.3 (20.8–23.7) mm, $n = 11$

GWS: 13.0 (12.1–14.3) mm, $n = 11$

M^1 – M^3 : 3.3 (3.1–3.5) mm, $n = 12$

Auditory bulla: n. d.



Gerbillus nanus

W Mauritania (Granjon *et al.* 1999 and unpubl.; MNHN)
See Kowalski & Rzebik-Kowalska (1991) for Algerian specimens

Key References Kowalski & Rzebik-Kowalska 1991; Rosevear 1969.

Laurent Granjon

Gerbillus nigeriae NIGERIAN GERBIL

Fr. Gerbille du Nigeriae; Ger. Nigerianische Rennmaus

Gerbillus nigeriae Thomas and Hinton, 1920. Novit. Zool., 27: 317. Farniso near Kano, Nigeria.

Taxonomy Considered to be a synonym of *G. agag* (Petter 1975a, Kock 1978b), then as a distinct species (Tranier 1975, Lay 1983). Synonyms: none. Chromosome number: $2n = 60-74$; polymorphic due to multiple Robertsonian translocations and heterochromatin variations (Tranier 1975, Volobouev *et al.* 1988, Dobigny *et al.* 2002b).

Description Small gerbil. Dorsal pelage sandy to pale ochre-orange; hairs grey at base, with sandy to ochre-orange at terminal end. Ventral pelage pure white, usually well delineated from the flanks. Head with white preorbital, postorbital and postauricular patches. Fore- and hindfeet white; soles of hindfoot covered with hairs of variable length. Long powerful tail (ca. 145% of HB) with pencil of dark hairs. Nipples: $2 + 2 = 8$.

Geographic Variation None recorded.

Similar Species

G. pyramidum. Almost always larger; chromosome number: $2n = 38$; Mali to Egypt and Sudan.

G. tarabuli. On average slightly larger; chromosome number: $2n = 40$; only found west of Libya.

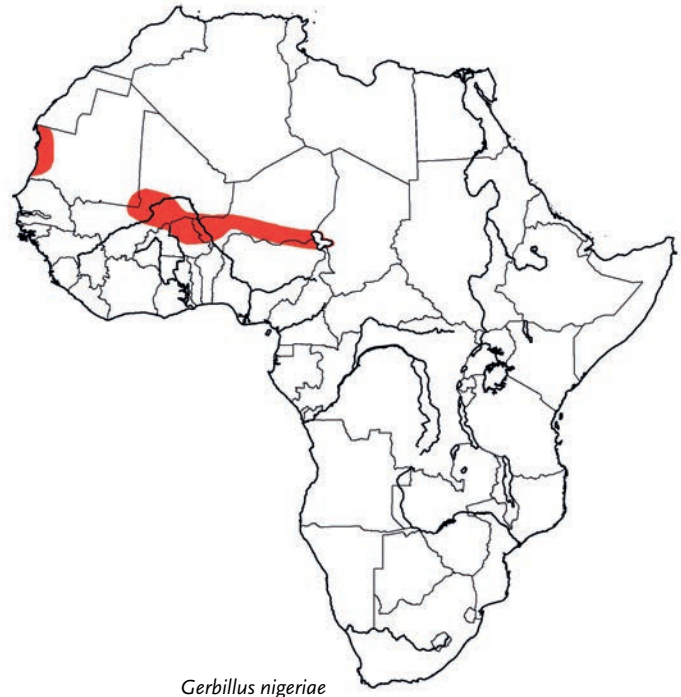
G. gerbillus. Similar size; soles of hindfoot more hairy; chromosome number: $2n = 42/43$; distributed throughout Sahara.

Distribution Endemic to Africa. Sahel Savanna BZ. Recorded from Mauritania, Mali, Burkina, Niger and Chad. Presence in these countries confirmed by chromosomal analysis (Granjon & Dobigny 2003).

Habitat Sandy areas (e.g. sand dunes, sandy veneers) and associated cultivated and fallow lands.

Abundance Large variations of abundance (0–ca. 150 ind/ha) recorded in natural habitats ('Oursi' dune, N Burkina; Sicard 1987) as well as in cultivated habitats ('Kolo' farm, Niger; Nomao & Gautun 2002). Annual cycles of abundance are biphasic (at 'Kolo') or monophasic (at 'Oursi').

Adaptations Terrestrial and nocturnal. In N Burkina, structure of burrows varies during different periods of the year: simple and superficial when individuals are dispersing; more complex, deep and filled with seeds during pre-aestivation and aestivation periods; and intermediate in characters during the breeding season (B. Sicard



Gerbillus nigeriae

pers. obs.). Efficient water conservation is indicated by extremely low values of body water turnover (ca. 12% of total body water per day) during aestivation (Sicard 1992). Dispersion occurs from Oct to mid-Jan when animals browse large areas in response to a decrease in water-rich resources. Pre-aestivation occurs from mid-Jan to Feb when animals collect and store seeds in the burrow. Aestivation occurs from Mar to May (during the dry-hot season; Sicard & Fuminier 1996; Sicard & Papillon 1996). Aestivation was not observed in Niger (Nomao & Gautun 2002).

Foraging and Food In N Burkina, diet is water-rich (seeds, arthropods and green vegetation) during the wet season and becomes water-poor (seeds only) during the dry hot season (Sicard 1992).

Social and Reproductive Behaviour Solitary and territorial. Home-ranges of ♂♂ overlap those of ♀♀ during the breeding period. Both home-range size and home-range shifts are minimal during aestivation, and are lower during the breeding season than during dispersion: home-range varies from $982 \pm 53 \text{ m}^2$ to $1581 \pm 101 \text{ m}^2$; home-range shift varies from $18 \pm 2 \text{ m}$ to $68 \pm 5 \text{ m}$. During pre-

aestivation, home-range size reaches a maximum ($2106 \pm 161 \text{ m}^2$) whereas home-range shift decreases near to zero (Sicard 1992).

Reproduction and Population Structure In N Burkina, maturation of the gonads occurs during aestivation and before the wet season begins (Apr–Jun). Mating and births are recorded during the wet season (Jun–Sep). Oestrus cycles occur throughout the year, but are shorter (5.1 ± 0.2 days, $n = 41$) between Jun and Sep than during the rest of the year (6.5 ± 0.2 days, $n = 27$) (Kyelem 1993). Male gonadotrophic activity and testis maturation start during aestivation (before the wet season) and stop after the wet season; e.g. plasma testosterone level is higher Apr–Sep ($1.57 \pm 0.15 \text{ ng/ml}$; $n = 37$) than during the rest of the year ($0.69 \pm 0.08 \text{ ng/ml}$; $n = 31$). Mean number of placental scars: 5.9 (range 3–7, $n = 21$). Litter-size: 3.4 (2–6, $n = 12$) (Sicard & Fuminier 1996).

Predators, Parasites and Diseases No information.

Conservation IUCN Category: Least Concern.

Measurements

Gerbillus nigeriae

HB: 92.6 (74–106) mm, $n = 70$

T: 135.5 (104–160) mm, $n = 59$

HF: 27.4 (23–31) mm, $n = 71$

E: 14.0 (11–16) mm, $n = 71$

WT: 26.2 (14–43) g, $n = 64$

GLS: 27.4 (23.8–30.6) mm, $n = 15$

GWS: 15.5 (13.2–15.6) mm, $n = 14$

M^1 – M^3 : 4.1 (3.6–4.5) mm, $n = 15$

Auditory bulla: n. d.

Mauritania (Colas *et al.* unpubl.); Burkina and Mali (B. Sicard & L. Granjon unpubl.)

Key References Sicard & Fuminier 1994; Volobouev *et al.* 1988.

B. Sicard

Gerbillus occiduus OCCIDENTAL GERBIL

Fr. Gerbille occidentale; Ger. Westliche Rennmaus

Gerbillus occiduus Lay, 1975. Fieldiana Zool. 65: 94. Aoreora, Morocco.

Taxonomy Synonyms: none. Chromosome number: $2n = 40$ (all metacentric chromosomes), FN = 76 (Lay 1975).

Description Small gerbil. Dorsal pelage intermediate between cinnamon and buffy-brown; hairs grey at base, with buffy-brown terminal band. Ventral pelage pure white. Colour of dorsal and ventral pelage clearly delineated. Head with prominent postauricular and supraorbital white patches, and narrow but distinct dark eye-

ring. Ear slightly pigmented on distal edge. Soles of hindfoot hairy. Tail long (ca. 115% of HB), with a very small terminal dark brown pencil. Nipples: not known.

Geographic Variation None recorded.

Similar Species

G. tarabuli. Larger; chromosome number: $2n = 40$; desert to semi-desert regions of North Africa, eastwards to Libya and Chad.

G. gerbillus. Similar size; chromosome number: $2n = 42/43$; desert to semi-desert habitats of North Africa.

G. hoogstraali. Similar size; ear on average larger; chromosome number: $2n = 72$; known only from the Souss Plain (between High Atlas and Anti Atlas Mts).

G. hesperinus. Similar size; hindfoot probably smaller; chromosome number: $2n = 58$; known only from near Essaouira on the coast of Morocco north of the Middle Atlas Mts.

Cranial and pelage characters also distinguish these species (see respective profiles, and Lay 1975). *Gerbillus hoogstraali*, *G. hesperinus* and *G. occiduus* are reported to have allopatric ranges (Lay 1975).

Distribution Endemic to Africa. Sahara Arid BZ. Known only from Morocco – from the type locality, 80 km WSW of Goulimine, Morocco, and further south on the coast in the vicinity of Tarfaya (Aulagnier & Thévenot 1986).

Habitat Type locality is an area of sparsely vegetated sand dunes (Lay 1975).

Abundance No information.



Gerbillus occiduus

Remarks Litter-size: 3.45 (1–5, $n = 11$ litters from two pairs). Six of 16 progeny of one ♀ were partial albinos (Lay 1975).

Conservation IUCN Category: Data Deficient. Only known from the type locality, so may be threatened because of small populations numbers and limited geographic distribution.

Measurements

Gerbillus occiduus

TL: 207.1 (202–213) mm, $n = 8$

T: 111 (103–119) mm, $n = 8$

HF: 29.1 (28–30) mm, $n = 8$

E: 13.9 (12–16) mm, $n = 8$

WT: n. d.

GLS: 30.7 mm, $n = 1$ (holotype)

GWS: n. d.

M^1 – M^3 : 3.5–4.3 mm*

Auditory bulla: n. d.

Morocco (Lay 1975)

*Aulagnier & Thévenot 1986

Additional skull measurements in Lay 1975

Key Reference Lay 1975.

Laurent Granjon

Gerbillus percivali PERCIVAL'S GERBIL

Fr. Gerbille de Percival; Ger. Percivals Rennmaus

Gerbillus percivali (Dollman, 1914). Ann. Mag. Nat. Hist., ser. 8, 14: 488. Voi, Kenya.

Taxonomy Originally described in the genus *Dipodillus*. Regarded as a valid species by Lay (1983), although included in *G. pusillus* by Petter (1975a). Occurs sympatrically with *G. pusillus* in Kenya. It is also sympatric with *G. harwoodi* in the southern part of its range, and resembles *G. harwoodi* very closely. The three taxa – *G. percivali*, *G. pusillus* and *G. harwoodi* – may form a closely related species complex, or even be a single species. Referred to as a valid species by Musser & Carleton (1993) but later (2005) as a synonym of *G. pusillus*. Synonyms: none. Chromosome number: not known.

Description Very small dark gerbil with a long tail. Dorsal pelage dark shiny rusty-brown; dorsal hairs medium grey at base, rusty-brown terminally. Dorsal pelage dense. Ventral pelage pure

white, clearly delineated from colour of dorsal pelage. Limbs and feet white. Tail long (ca. 145% of HB), brown above with small brown and black bristles, paler below; longer black hairs form thin pencil on terminal third of tail. Nipples: not known.

Geographic Variation None recorded.

Similar Species

G. harwoodi. Similar in size and colour; tail relatively shorter (ca. 126% of HB); recorded from highlands of Kenya only.

G. pusillus. Similar in size and colour; tail relatively longer (ca. 160% of HB); hairs long and soft; drier habitats of C and S Kenya.

Distribution Endemic to Africa. Somalia–Masai Bushland BZ. Known only from near Voi, SE Kenya.

Habitat 'Dry sandy plains' and 'trapped in long grass under thorn scrub' (collector's field note, at Maktou [BHNM]).

Abundance Rare; known only from a few specimens.

Remarks One ♀ contained three half-grown embryos in Aug.

Conservation IUCN Category: Data Deficient. Probably vulnerable because of small geographic range and apparent rarity.

Measurements

Gerbillus percivali

HB: 75 (73–78) mm, $n = 3$

T: 110 (106–113) mm, $n = 3$

HF: 19.5 (19–20) mm, $n = 3$

E: 10, 11 mm, $n = 2$

WT: 14 g, $n = 1$

GLS: n. d.

GWS: n. d.

M^1 – M^3 : n. d.



Gerbillus percivali

Auditory bulla: n. d.
Kenya (BMNH)

Key Reference Lay 1983.

D. C. D. Happold

Gerbillus perpallidus **PALE GERBIL**

Fr. Gerbille pâle; Ger. Helle Rennmaus

Gerbillus perpallidus Setzer, 1958. J. Egypt. Publ. Health Assoc. 33: 221. Bir Victoria, Egypt.

Taxonomy The taxonomy of this species is confused. Specimens now considered to represent this species were originally labelled as *G. tarabuli*, *G. andersoni* or *G. pyramidum*. May be closely related to *G. pyramidum*. Synonyms: none. Chromosome number: $2n = 40$, $FN = 76$ (Lay *et al.* 1975).

Description Small very pale gerbil with long soft pelage. Dorsal pelage pale sandy-orange to pinkish-cinnamon, without any darkening on the mid-dorsal line; dorsal hairs pale grey tipped with sandy-orange. Conspicuous white rump patch. Flanks pale sandy-white. Ventral pelage pure white. Crown of head and nose similar to back. Supraorbital, postorbital and postauricular white patches. Limbs and feet white. Sole of hindfoot hairy. Tail long (ca. 128% of HB), sandy above, white below, ending in small pencil of white hairs. Nipples: not known.

Geographic Variation None recorded.

Similar Species

G. pyramidum. Larger on average (HB: 109–135 mm) and heavier (WT: ca. 53 g); dorsal pelage orange-brown, darker on mid-line; chromosome number: $2n = 38$.

G. gerbillus. Smaller on average (HB: 77–104 mm) and lighter (WT: ca. 20 g); dorsal pelage orange; $2n = 42$ for ♀♀, chromosome number: $2n = 43$ for ♂♂.

G. andersoni. Slightly smaller on average (HB: 90–115 mm); dorsal pelage sandy-orange; chromosome number: $2n = 40$.

Distribution Endemic to Africa. Sahara Arid BZ. Recorded only from N Egypt, west of the Nile R.

Habitat Occurs in many habitats with very pale sand, either sandy wadis, coastal dunes or soft sand sheets. Near Wadi el Natroun, constructs burrows in the mud-sand beaches close to the lake where *Typha* rushes are growing (Osborn & Helmy 1980). Also occurs on barren slopes covered with ephemeral *Mesembryanthemum*.

Abundance Restricted, but not uncommon in suitable habitats.

Remarks Nocturnal, terrestrial. The very pale pelage, considerably paler than that of *G. pyramidum*, is very similar in colour to that of the pale sand where these gerbils live. Embryo number: 5 ($n = 1$; Apr). Three species of fleas have been collected on individuals and in nests (Hoogstraal & Traub 1965a).



Gerbillus perpallidus

Conservation IUCN Category: Least Concern.

Measurements

Gerbillus perpallidus

HB: 107 (95–117) mm, $n = 27$

T: 137 (128–150) mm, $n = 26$

HF: 33 (32–36) mm, $n = 21$

E: 16 (14–18) mm, $n = 21$

WT: 36 (26–48) g, $n = 20$

GLS: 32.3 (30.1–33.8) mm, $n = 27$

GWS: 17.4 (16.5–18.5) mm, $n = 25$

M^1 – M^3 : 4.8 (4.4–5.9) mm, $n = 33$

Auditory bulla: 9.4 (8.9–10.0) mm, $n = 28$

Egypt (Osborn & Helmy 1980)

Key Reference Osborn & Helmy 1980.

D. C. D. Happold

***Gerbillus pulvinatus* CUSHIONED GERBIL (RHOD'S GERBIL)**

Fr. Gerbille d'Éthiopie; Ger. Polster-Rennmaus

Gerbillus pulvinatus Rhoads, 1896. Proc. Acad. Nat. Sci. Philadelphia, p. 537. Rusia, L. Rudolf (= L. Turkana), Ethiopia.

Taxonomy Recognized as a valid species by Lay (1983) and by Musser & Carleton (1993, 2005). Petter (1975) and Yalden *et al.* (1996) included *bilensis* (known only from type locality: Bilen, Ethiopia) as a synonym although Lay (1983) recognized *bilensis* as a valid species. Yalden *et al.* (1976) included *pulvinatus* within *G. pyramidum*. Synonyms: *bilensis*. Subspecies: none. Chromosome number: $2n = 62$, $FN = 84$ (Hubert 1978c).

Description Small gerbil. Dorsal pelage sandy-brown, slightly darker on mid-dorsal line; dorsal hairs dark grey at base, sandy-brown at terminal end. Flanks paler, hairs white with pale sandy-brown tips. Ventral pelage pure white. Colour of ventral pelage merges with colour of flanks. Crown of head and nose similar to back; supraorbital and postorbital white patches. Postauricular white patch inconspicuous. Chin, throat, limbs and feet white. Soles of hindfeet partly hairy; toes with fringe of fine bristle-like hairs. Tail long (ca. 140% of HB), sandy-brown above, white below; darker longer hairs form narrow pencil towards tip. Nipples: not known.

Geographic Variation None recorded.

Similar Species

G. dunni. Similar HB and T; longer HF; $2n = 74$; mostly allopatric except in Djibouti.

G. pusillus. Smaller HB and T; shorter HF; $2n = 34$; mostly allopatric except near L. Turkana, Kenya.

Distribution Endemic to Africa. Somalia–Masai Bushland BZ. The form '*pulvinatus*' (including *bilensis* and *dunni*) is only known from Ethiopia and Djibouti but is likely to occur also in N Kenya and the drier regions of Somalia (Yalden *et al.* 1996).

Habitat In the Omo Valley, Ethiopia, these gerbils live in dry grassland savanna, sparsely covered with trees, and prefer sandy soils (Hubert 1978c). In Djibouti, recorded amongst sparse vegetation, and in areas of volcanic rock with bushes and trees (Pearch *et al.* 2001).

Abundance Few specimens are known. Probably rare and with a very local distribution.

Remarks Other species parapatric with these gerbils in the Omo Valley are *Taterillus harringtoni* (now a synonym of *T. emini*), *Acomys*

*Gerbillus pulvinatus*

wilsoni, *Arvicanthis somalicus* (now *A. neumanni*), *Gerbillus pusillus* and *Xerus rutilus* (Hubert 1978c).

Conservation IUCN Category: Least Concern.

Measurements

Gerbillus pulvinatus

HB: 96 (86–105) mm, $n = 10$

T: 136 (118–145) mm, $n = 10$

HF: 27 (25–28) mm, $n = 10$

E: 14.5 (10–16) mm, $n = 10$

WT: n. d.

GLS: 30.6 (30.1–31.7) mm, $n = 10$

GWS: 15.9 (15.2–16.6) mm, $n = 10$

M^1 – M^3 : 4.1 (3.9–4.3) mm, $n = 10$

Auditory bulla: 10.6 (10.2–10.9) mm, $n = 10$

Omo Valley, Ethiopia (MNHN)

Key References Hubert 1978c; Pearch *et al.* 2001.

D. C. D. Happold

***Gerbillus pusillus* LEAST GERBIL**

Fr. Petite gerbille de Peters; Ger. Winzige Rennmaus

Gerbillus pusillus Peters, 1878. Monatsber. K. Preuss. Akad. Wiss. Berlin 1879: 201 (publ. 1878). Ndi and Kitui, Kenya.

Taxonomy Lay (1983), Petter (1975) and Musser & Carleton (1993, 2005) regard *G. pusillus* as a valid species. However, Petter (1975) suggested that *percivali* (here regarded as valid species) and *ruberrimus* may be synonymous with *G. pusillus*. (See also *G. percivali*.) Synonyms: *diminutus*, *ruberrimus*. Subspecies: none. Chromosome number: $2n = 34$ (Somalia; Capanna & Merani 1981).

Description Very small gerbil. Pelage long and soft. Dorsal pelage bright dark cinnamon to dark rusty-brown, lightly washed with black. Dorsal hairs medium grey at base, rusty-brown terminally, sometimes with black tip. Flanks paler. Ventral pelage pure white. Colour of ventral pelage clearly delineated from colour of flanks. Crown of head and nose dark rusty-brown; inconspicuous postorbital white patch. Cheek, chin, throat, limbs and feet white. Soles of hindfeet naked. Tail long (ca. 160% of HB), rusty-brown or ginger above, paler below; longer russet-brown and black hairs form conspicuous pencil on terminal third of tail.

Geographic Variation None recorded.

Similar Species

G. harwoodi. HB slightly larger (mean 75 mm); T shorter (mean 95 mm) and relatively shorter (ca 126%); C and SE Kenya, NE Tanzania.

G. percivali. HB slightly larger (mean 75 mm), T similar length, but relatively shorter (ca. 145% of HB); HF slightly shorter (mean 19.5 mm); SE Kenya only.

Distribution Endemic to Africa. Somalia–Masai Bushland BZ. Recorded from scattered localities in Tanzania, Kenya, Ethiopia, Somalia and S Sudan.

Habitat Recorded in steppe habitats of coastal Somalia (Capanna & Merani 1981). In S Sudan, found in short grass on sandy soils (Dieterlen & Nikolaus 1985).

Abundance No information. Probably rare or uncommon; populations localized.

Remarks Subadults and juveniles in Jul (Somalia) and Aug (N Kenya). Remains found in owl pellets of Barn Owls *Tyto alba* in N Tanzania (SMF).

*Gerbillus pusillus*

Conservation IUCN Category: Least Concern.

Measurements

Gerbillus pusillus

HB: 70.6 (65–77) mm, $n = 3$

T: 110, 115 mm, $n = 2$

HF: 21 (?–?) mm, $n = 3$

E: 9 (?–?) mm, $n = 3$

WT: n. d.

GLS: 24.1 (23.5–24.5) mm, $n = 3$

GWS: 12.1, 12.3 mm, $n = 2$

M^1 – M^3 : 3.6 (3.5–3.7) mm, $n = 3$

Auditory bulla: 8.9 (8.1–8.3) mm, $n = 3$

Somalia (MNHN)

Key References Dieterlen & Nikolaus 1985; Capanna & Merani 1981.

D. C. D. Happold

***Gerbillus pyramidum* GREATER EGYPTIAN GERBIL**

Fr. Grande Gerbille d’Egypte; Ger. Grosse Ägyptische Rennmaus

Gerbillus pyramidum Geoffroy, 1803. Cat. Mamm. Mus. Natl Hist. Nat., Paris, p. 202. Giza Prov., Egypt.

Taxonomy The form *dongolanus* (known only from the type locality of Dongola, Sudan), here listed as a synonym, is recognized as a valid species by Musser & Carleton (1993, 2005). Setzer

& Ranck (1971) described *tibesti* from Chad as a subspecies of *G. pyramidum*; now placed as a synonym of *G. tarabuli* (Musser & Carleton 2005). Synonyms: *dongolanus*, *elbaensis*, *gedeedus*. Subspecies: none.

Chromosome number: $2n = 38$, all metacentric chromosomes, which excludes many forms from North Africa, West Africa and the Middle East that formerly have been referred to this species (Lay 1983, Granjon *et al.* 1999).

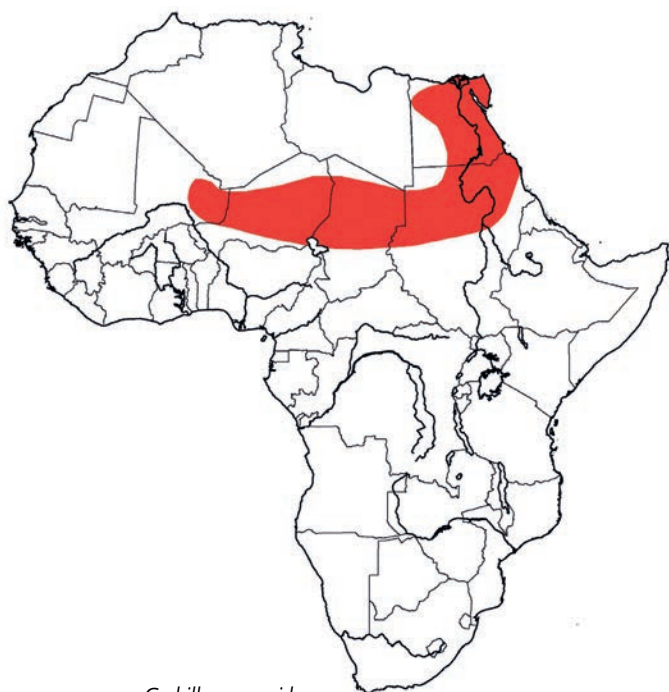
Description Small to medium-sized gerbil. Dorsal pelage medium/dark orange to brownish; hairs of variable length, grey at base, orange or brown at tip. Often darker along mid-dorsal region of back. Ventral pelage pure white. White rump patch of variable size, if present. Preorbital, postorbital and postauricular white marks, sometimes inconspicuous or absent. Fore- and hindfeet white; soles of hindfeet hairy. Tail long (125–145% of HB; cf. Osborn & Helmy 1980), with a more or less marked pencil of dark hairs. Nipples: $2 + 2 = 8$.

Geographic Variation None recorded.

Similar Species

- G. nigeriae*. Usually smaller; soles of hindfeet hairy; chromosome number: $2n = 62\text{--}74$; northern Sahelian distribution from Mali to Chad.
- G. gerbillus*. Smaller; soles of hindfeet hairy; chromosome number: $2n = 42/43$; distributed in all desert to semi-desert habitats of North Africa.
- G. tarabuli*. Usually smaller; soles of hindfeet hairy; chromosome number: $2n = 40$; desert to semi-desert regions of North Africa, eastwards to Libya and Chad.

Distribution Endemic to Africa. Sahara Arid and Sahel Savanna BZs. Widespread in the desert areas of Sudan and Egypt, especially along the Nile Delta and Valley, and in oases (Happold 1967c, Osborn & Helmy 1980, Tawil & Niethammer 1989). Also recorded from Chad, Niger, N Mali and possibly Mauritania (Dobigny *et al.* 2001a, b, 2002b; Granjon & Dobigny 2003).



Habitat In Egypt, found in a variety of sandy habitats such as palm groves, surroundings of cultivations, barren sand and gravel areas, coastal plains and dunes; often found in grassy areas with *Panicum turgidum*, or under *Acacia radiana* or *Tamarix* sp. trees (Osborn & Helmy 1980). In N Mali, Niger and Chad, lives in similar situations, as well as in storehouses and gardens (Dobigny *et al.* 2001a, Granjon & Dobigny 2003).

Abundance Few quantitative data. The commonest gerbil in the deserts of N Sudan (Happold 1967c); up to 14 individuals seen during 1-hour nocturnal drive censuses, but less abundant than coexisting *Jaculus jaculus* (Happold 1968).

Adaptations Terrestrial and nocturnal. Burrows are similar to those of *Gerbillus gerbillus* (Osborn & Helmy 1980) and to those of *Gerbillus tarabuli* excavated by Petter (1961) in Algeria. In Sudan, burrows are often on sandy mounds or ridges around trees or bushes (Happold 1967c). Moulting observed at most times of the year in wild individuals, and occurring between 40 and 120 days of age in captivity (Happold 1968). Vocalizations include squeaking and chattering noises in handled newborn young and high-pitched squeaks in frightened adults (Happold 1968).

Foraging and Food In Sudan, stores seeds and grasses during the wet season (Jun–Aug), which are eaten when food becomes scarce (Happold 1967c). In captivity, feeds on grass, sunflower seed, millet, soft maize and cucumber (Happold 1968).

Social and Reproductive Behaviour Tends to be colonial. Mating behaviour observed in captivity: copulation lasted for 1–3 seconds, and was repeated a number of times (Happold 1968).

Reproduction and Population Structure In N Sudan, reproduction recorded during the wet season and the following cool dry season (Jun–Feb). Young and subadults (WT: 40 g) in population during Jul–Mar. Gestation: ca. 22 days. Litter-size in captivity: usually 3 (2–5). At birth, young hairless and blind; WT: 2 g. Fine covering of hair by Day 8–10. Ears open Day 16–18. Eyes open Day 19–20. First eat solid food Day 22. Weaned by Day 25–30. Adult HB ca. Day 80–90. Adult weight Day 110–120. Longevity up to two years in captivity (Happold 1968).

Predators, Parasites and Diseases No data on predation. In Sudan, ectoparasites include ticks, fleas and lice (in Happold 1968). In Egypt, fleas found in burrows and on individuals include *Synosternus cleopatrae* (commonest species), *Synosternus pallidus*, *Xenopsylla cheopis*, *Stenoponia acmaea* and *Pulex irritans* (Hoogstraal & Traub 1965a).

Conservation IUCN Category: Least Concern.

Measurements

Gerbillus pyramidum

HB: 119.4 (102–135) mm, $n = 68$

T: 156.1 (128–180) mm, $n = 60$

HF: 35.0 (30–39) mm, $n = 70$

E: 17.6 (14–20) mm, $n = 69$

WT: 53.2 (37–67) g, n = 16
 GLS: 35.1 (32.5–38.1) mm, n = 67
 GWS: 18.7 (16.8–20.8) mm, n = 57
 M¹–M³: 4.9 (4.5–5.5) mm, n = 60
 Auditory bulla: 10.1 (9.2–11.5) mm, n = 73

Egypt (Osborn & Helmy 1980; recalculated from data on three subspecies – *G. p. pyramidum*, *G. p. gedeeus* and *G. p. elbaensis*)

Key References Happold 1968; Osborn & Helmy 1980.

Laurent Granjon

Gerbillus rosalia ROSALIND'S GERBIL (ROSALINDA GERBIL)

Fr. Gerbille de Rosalinde; Ger. Rosalindes Rennmaus

Gerbillus rosalia St Leger, 1929. Ann. Mag. Nat. Hist., ser. 10, 4: 295. Abu Zabad, 145 km SW El Obeid, Kordofan, Sudan.

Taxonomy The status of *rosalia* is uncertain because it is known only from the type locality and some nearby localities. Petter (1975a) suggested that *rosalia* may be a subspecies of *G. agag* (also known only from Sudan), although Setzer (1956) and Lay (1983) retain it as a valid species pending revision. In the original description, St Leger (1929) commented that *G. rosalia* was totally different from its 'near neighbours', *G. agag* and *G. pyramidum*. Synonyms: none. Chromosome number: not known.

Description Small dark gerbil. Dorsal pelage rich rusty-orange, darker on rump and on mid-dorsal line. Dorsal hairs grey at base with rusty-orange at terminal end; hairs on rump often with black tip. Flanks similar; hairs white at base with orange tips. Ventral pelage pure white. Colour of ventral pelage clearly delineated from colour of flanks. Crown of head and nose rusty-orange. Inconspicuous white postorbital patch. Cheeks, chin, throat, limbs and feet white. Soles of feet hairy. Tail long (ca. 120% of HB), covered with dense short hairs, orange-brown above, paler below; longer dark hairs at terminal end form narrow pencil. Nipples: not known.

Geographic Variation None recorded.

Similar Species Appears to be the only known species of *Gerbillus* in its area of distribution.

Distribution Endemic to Africa. Sudan Savanna BZ. Known from the region of Abu Zabad, SW of El Obeid, and a few other localities in C Sudan west of the White Nile (F. Dieterlen unpubl.; SMNS).

Habitat Grassy plains of Kordofan (St Leger 1929).

Abundance Known only from a few specimens.

Remarks Apparently no other information available.

Conservation IUCN Category: Least Concern.



Gerbillus rosalia

Measurements

Gerbillus rosalia

HB: 97 (87–106) mm, n = 11
 T: 117 (105–130) mm, n = 11
 HF: 25.3 (23–27) mm, n = 11
 E: 15.0 (13–16) mm, n = 11
 WT: 28.5 (20–35) g, n = 11
 GLS: 29.1 (27.5–31.6) mm, n = 20
 GWS: 15.3 (14.2–16.3) mm, n = 18
 M¹–M³: 4.0 (3.7–4.4) mm, n = 22
 Auditory bulla: 10.4 (9.6–11.2) mm, n = 16
 Sudan (SMNS, BMNH; G. Nikolaus and F. Dieterlen unpubl.)

Key Reference St Leger 1929.

D. C. D. Happold

Gerbillus rupicola **ROCK GERBIL**

Fr. Gerbille des rochers; Ger. Felsen-Rennmaus

Gerbillus rupicola Granjon, Aniskin, Volobouev and Sicard, 2002. J. Zool. Lond. 256: 183. Emnal'here, Mali.

Taxonomy Allocated to the genus *Dipodillus* by Musser & Carleton (2005). Synonyms: none. Chromosome number: $2n = 52$, $aFN = 68$.

Description Small gerbil. Dorsal pelage tawny-rufous; hairs grey at base. Ventral pelage white. Ventral colour well delineated from colour of flanks. Head with preorbital, supraorbital and postauricular white patches. Fore- and hindfeet white; soles of hindfoot naked. Tail very long (ca. 140% of HB), terminated by a marked pencil of dark hairs. Nipples: not known.

Geographic Variation None recorded.

Similar Species

G. campestris. Very similar externally; chromosome number: $2n = 56/58$; widespread. (See illustrations in Granjon *et al.* 2002b).

Distribution Endemic to Africa. Sahel Savanna BZ. As of 2003, known only from four individuals caught in two localities, 35 km apart.

Habitat Apparently associated with rocky habitats: the three specimens of the type series were caught on a rocky inselberg, the fourth one in fallen rocks at the foot of a cliff (J.-F. Cosson and E. Quesseveur pers. comm.).

Abundance No information.

Remarks Terrestrial and nocturnal. Apparently adapted to climb in rocky environments as does *Acomys* sp. with which it coexists (Granjon *et al.* 2002b).

Conservation IUCN Category: Data Deficient.

Measurements

Gerbillus rupicola

HB: 100.8 (95–106) mm, $n = 4$

T: 139 (136–142) mm, $n = 3$



Gerbillus rupicola

HF: 26.5 (26–27) mm, $n = 4$

E: 15.4 (14.5–16.5) mm, $n = 4$

WT: 35.5 (31–39) g, $n = 4$

GLS: 29.8 (29–30.6) mm, $n = 4$

GWS: 15.7 (15.4–15.9) mm, $n = 4$

M^1 – M^3 : 4.1 (4–4.2) mm, $n = 4$

Auditory bulla: 7.83 (7.8–7.9) mm, $n = 3$

Mali (MNHN)

Key Reference Granjon *et al.* 2002b.

Laurent Granjon

Gerbillus simoni **SIMON'S GERBIL**

Fr. Gerbille de Simon; Ger. Kleine Kurzschnanz-Rennmaus

Gerbillus simoni Lataste, 1881. Le Naturaliste 3: 499. Oued Magra, Algeria.

Taxonomy This species, known as *Dipodillus simoni* by some authors (Petter 1975a, Osborn & Helmy 1980, Musser & Carleton 2005), differs from all other gerbils by having a combination of unique characters – naked soles, tail similar in length to head and body, lack of pencil on tail, and special characters of the molar teeth (Petter 1959b, Schlitter & Setzer 1972; Cockrum *et al.* 1976). *Gerbillus simoni* has been described as 'a distinctive species' (Musser & Carleton

2005). Synonyms: *kaiseri*, *zakariai*. The status of *zakariai* is uncertain: considered as a synonym of *G. simoni* by Musser & Carleton (1993), but elevated to a species (*Dipodillus zakariai*) by Musser & Carleton (2005); *zakariai* is an insular taxon recorded only from the Kerkennah Is. (opposite the coastal city of Sfax, Tunisia) and related to *G. simoni* on the mainland. Subspecies: none. Chromosome number: $2n = 60$, $FN = 68, 69$ (Wassif *et al.* 1969, in Lay *et al.* 1975).

Description Very small gerbil with long soft fur and short tail; considered to be 'mouse-like'. Dorsal pelage pale brown to orange-brown; dorsal hairs dark or medium grey at base, with orange-brown subterminal band and black or orange tip. Flanks paler than back. Ventral pelage pure white. Colour of ventral pelage merges into colour of flanks. Crown of head and nose similar to back. Inconspicuous white supraorbital patch; conspicuous postorbital patch. Long vibrissae, some white, some black. Chin, throat, limbs and feet white. Soles of hindfeet naked. Tail relatively short (ca. 105% of HB, cf. other gerbils), covered with small brownish-orange bristles, upper and lower surfaces similar without pencil at terminal end; tail often thick (due to deposits of fat), especially at basal end. Nipples: not known.

Geographic Variation From west to east: increase in tail length, decrease in greatest width of skull and reduced inflation of auditory bullae (data from Algeria to Egypt: Osborn & Helmy 1980). There is also considerable variation in colour.

Similar Species No other species of gerbil has the unique characters listed above. Relative tail length of other species of *Gerbillus* is at least 120% of HB. Other species in the family Gerbillidae with short tails are larger and heavier (e.g. *Meriones* spp.: HB: 114–153 mm, WT: 54–112 g; *Pachyuromys* spp. HB: 93–121 mm, WT: 22–44 g; *Psammomys obesus* HB: 151–187 mm, WT: 116–205 g; data from Osborn & Helmy 1980).

Distribution Endemic to Africa. Mediterranean Coastal BZ and Sahara Arid BZ. Recorded from coastal regions from Morocco to Egypt (west of the Nile Delta). In Algeria, occurs in steppe habitats on the northern edge of the Hauts Plateaux but not in the coastal regions. A record in N Morocco needs verification.

Habitat Occurs in many habitats, especially where soils are loam or clay; e.g. 'Rich steppe country' and arable fields in Algeria; sparsely vegetated littoral desert and fallow fields in Tunisia; grassy valleys with lots of vegetation in Libya; and salt marshes, barley fields and vegetated slopes in Egypt.

Abundance 'Rather common' in vegetated salt marshes near the sea on the Egyptian coast (Hoogstraal 1963). In Libya, distribution is patchy; has not been found in many habitats that appear to be suitable (Ranck 1968).

Adaptations Nocturnal, terrestrial. Lives in burrows during daytime. Fat is stored in the tail during times of food abundance (in a similar manner to *Pachyuromys*); hence size of tail varies seasonally.

Foraging and Food No information.

Social and Reproductive Behaviour In Egypt, parapatric in salt marshes with *Gerbillus henleyi*, *G. amoenus*, *G. campestris* and two species



Gerbillus simoni

of jerboas, and in vegetated littoral desert with *G. andersoni*, *G. gerbillus*, three species of jerboas and *Meriones shawi* (Osborn & Helmy 1980).

Reproduction and Population Structure Embryo number: 4 (Tunisia, Oct; Harrison 1967) and 8 (Morocco, May; Schlitter & Setzer 1972). In captivity, gestation is 20 days and litter-size is 4–6; females enter oestrus 18–20 days after parturition (Lataste 1881 in Cockrum *et al.* 1976).

Predators. Parasites and Diseases No information.

Conservation IUCN Category: Least Concern.

Measurements

Gerbillus simoni

HB: 80.8 (72–89) mm, n = 26

T: 85.6 (72–96) mm, n = 25

HF: 21.0 (19–22) mm, n = 28

E: 12.2 (12–14) mm, n = 28

WT: 17.4 (12–22) g, n = 10

GLS: 25.2 (23.2–26.7) mm, n = 17

GWS: 13.6 (12.6–14.0) mm, n = 14

M¹–M³: 3.7 (3.2–4.0) mm, n = 24

Auditory bulla: 7.0 (6.7–7.4) mm, n = 19

Egypt (Osborn & Helmy 1980)

Key Reference Osborn & Helmy 1980.

D. C. D. Happold

Gerbillus somalicus SOMALIAN GERBIL

Fr. Gerbille de Somalie; Ger. Somalische Rennmaus

Gerbillus somalicus (Thomas, 1910). Ann. Mag. Nat. Hist., ser. 8, 5: 197. Upper Sheikh, Somalia.

Taxonomy Originally described in the genus *Dipodillus*. Petter (1975a) placed *somalicus* as a subspecies of *G. campestris*, but Lay (1983) recognized it as a valid species pending revision. In the original description, Thomas (1910b) placed *somalicus* as a species of *Dipodillus*, and suggested that it was allied to *G. stigmonyx*. Probably part of the *campestris* species complex. Musser & Carleton (2005) refer to this species as *Dipodillus somalicus*. Synonyms: none. Chromosome number: not known.

Description Small long-haired gerbil with a long tail. Pelage long and soft. Dorsal pelage dark sandy-brown or orange-brown; dorsal hairs medium grey at base, orange-brown at terminal end, often with black tip. Flanks paler and brighter. Ventral pelage pure white. Colour of ventral pelage merges into colour of flanks. Head, nose and cheeks similar to back. Postauricular white patch. Chin, throat, limbs and feet white. Soles of hindfeet naked. Tail long (ca. 135% of HB), sandy-orange covered with short sandy-orange and black bristles above, paler below; long blackish-brown hairs form well-developed pencil on terminal third of tail. Nipples: not known.

Geographic Variation None recorded.

Similar Species

G. atticola. Larger in all dimensions; known from Barras (1050 m) and from coastal locations in Somalia.

G. brockmani. Very similar, but on average smaller body measurements, and smaller M^1 – M^3 ; recorded only from type locality (Barao).

Distribution Endemic to Africa. Somalia–Masai Bushland BZ; recorded only from the highland area of N Somalia.

Habitat No information.

Abundance Known only from a few specimens; probably rare.

Remarks The long soft pelage is probably an adaptation to cool nights during ‘winter’ in the highlands (1200–1400 m).

Conservation IUCN Category: Data Deficient.

*Gerbillus somalicus***Measurements***Gerbillus somalicus*

HB: 86 (82–90) mm, n = 5

T: 117 (112–124) mm, n = 5

HF: 24.6 (24–25) mm, n = 5

E: 11.8 (11–12) mm, n = 5

WT: n. d.

GLS: 25.6 (24.6–26.5) mm, n = 3

GWS: 13.5 (13.3–13.7) mm, n = 3

 M^1 – M^3 : 3.8 (3.5–4.1) mm, n = 6

Auditory bulla: 9.5 (9.0–10.0) mm, n = 4

Upper Sheikh, Somalia (BMNH)

Key References Thomas 1910b; Lay 1983.

D. C. D. Happold

Gerbillus stigmonyx KHARTOUM GERBIL

Fr. Gerbille de Khartoum; Ger. Khartum-Rennmaus

Gerbillus stigmonyx (Heuglin, 1877). Reise in Nordost-Afrika 2: 78. Khartoum, Sudan.

Taxonomy Originally described in the genus *Dipodillus*. Petter (1975a) listed *G. stigmonyx* (and *luteolus*) as synonyms of *G. campestris*, but Lay (1983) retained *G. stigmonyx* as a valid species pending revision. *Gerbillus stigmonyx*, *G. watersi* and *G. bottai* may form a closely

related species complex, and even belong to the same species (F. Dieterlen in litt.); see *G. bottai*. Musser & Carleton (2005) refer to this species as *Dipodillus stigmonyx*. Synonyms: none. Chromosome number: not known.

Description Small gerbil with long tail. Dorsal pelage sandy-orange, darker along the mid-dorsal line. Dorsal hairs medium grey at base, sandy-orange at terminal end, often with black tip. Flanks paler; hairs white at base, orange terminally, without black tips. Ventral pelage pure white. Colour of ventral pelage clearly delineated from colour of flanks. Crown of head and nose similar to back; longitudinal stripe of blackish hairs on nose. Postorbital and postauricular white patches. Cheeks, chin, throat, limbs and feet white. Soles of hindfeet naked. Tail long (ca. 115% of HB), sandy-orange above and below, longer darker hairs form pencil on terminal third or quarter of tail. Nipples: not known.

Geographic Variation None recorded.

Similar Species

G. watersi. Similar, with overlap in most measurements; HB on average slightly smaller (mean 81.5 mm); tail relatively longer (ca. 135% of HB); distribution mostly further north.

G. bottai. Similar, with overlap in most measurements; auditory bullae usually smaller (mean 8.7 mm); known only from a small region between the White Nile and Blue Nile rivers, south of Khartoum.

G. pyramidum. Larger in all body and skull dimensions; perhaps parapatric in C Sudan.

Distribution Endemic to Africa. Sahel Savanna BZ. Known only from a small region along the White Nile from Khartoum to El Kowa, Sudan.

Habitat No information.

Abundance Rare. Known only from a few specimens from four localities.

Remarks Apparently no other information available.

Conservation IUCN Category: Data Deficient.



Gerbillus stigmonyx

Measurements

Gerbillus stigmonyx

HB: 90 (86–95) mm, n = 5

T: 102 (97–106) mm, n = 5

HF: 21 (20–23) mm, n = 5

E: 11 (8–13) mm, n = 5

WT: n. d.

GLS: 26.5 (25.9–26.9) mm, n = 6

GWS: 13.9 (13.6–14.3) mm, n = 6

M¹–M³: 3.6 (3.5–3.8) mm, n = 6

Auditory bulla: 9.1 (8.8–9.3) mm, n = 6

Sudan (BMNH)

Key Reference Lay 1983.

D. C. D. Happold

Gerbillus tarabuli TARABUL'S GERBIL (LIBYAN GERBIL)

Fr. Gerbille de Tarabul; Ger. Tarabuls Rennmaus

Gerbillus tarabuli Thomas, 1902. Proc. Zool. Soc. Lond. 1902: 5. Sebha, Libya.

Taxonomy Considered a valid species, distinct from *G. pyramidum*. Synonyms: *hamadensis*, *riggenbachi*, *tibesti*. Subspecies: none. Chromosome number: 2n = 40, aFN = 74 (Lay 1983, Granjon *et al.* 1999).

Description Small gerbil. Dorsal pelage sandy to light orange-brown; hairs grey at base on the back, white at base on flanks. Ventral pelage whitish to pure white, more or less well delineated from colour of flanks. Head with supraorbital and postauricular white patches. Fore- and hindfeet white; soles of hindfoot covered with

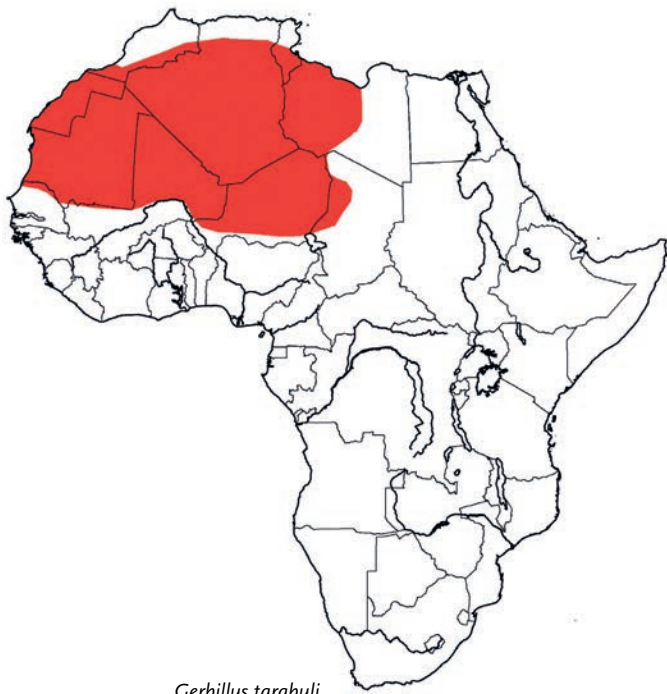
hairs of variable length. Tail very long (ca. 145% of HB), terminated by a marked pencil of usually dark hairs. Nipples: 2 + 2 = 8.

Geographic Variation None recorded.

Similar Species

G. nigeriae. Smaller on average; chromosome number: 2n = 62–74; northern Sahel Savanna BZ from Mali to Chad.

G. gerbillus. Smaller on average; chromosome number: 2n = 42/43; all desert to semi-desert habitats of North Africa.



G. pyramidum. Larger on average, with longer and more robust hindfoot; chromosome number: $2n = 38$; Nile Valley, and southern Sahara from Chad to Mali.

Distribution Endemic to Africa. Sahara Arid and Sahel Savanna BZs. Widespread in desert to semi-desert regions of North Africa, from Mauritania and Morocco to Libya, south to N Senegal, Mali, Niger and Chad (Granjon *et al.* 1999, Granjon & Dobigny 2003 and unpubl. data). Presence in N Senegal interpreted as a possible southwards extension of range following desertification (Duplantier *et al.* 1991).

Habitat Psammophile (sand-loving), but catholic in habitat choice, provided there is sand in the substrate (Petter 1961). In Mauritania, found in fixed dunes and sandy-clay plains (Klein *et al.* 1975, Granjon *et al.* 1997b), and associated with *Capparis-Panicum* vegetation in the Azzefal region (Klein *et al.* 1975). In Mali and Niger, occurs frequently in sand dunes where *Acacia* sp. or *Prosopis* sp. are present (L. Granjon & G. Dobigny unpubl.).

Abundance In coastal Mauritania, densities are 0.2–2 individuals/ha during the course of a year (Klein *et al.* 1975).

Capture rates of 3 to 5.3 individuals/100 trap-nights recorded in favourable habitats in March 1995 (Granjon *et al.* 1997b).

Adaptations Terrestrial and nocturnal. Burrow shallow (15–25 cm depth) but rather complex, and the entrances are plugged with sand during the day (Petter 1961). Homing behaviour was observed in nine (out of 13) individuals released 1000 m away from their burrows, and in two (out of 5) individuals released 2000 m away (Mermod 1970).

Foraging and Food No information.

Social and Reproductive Behaviour Less mobile than coexisting *G. nanus* and *G. gerbillus* in March 1995 in coastal Mauritania. Mean recapture distance 7.5 m (max 30 m) over a 4-day period (Cosson *et al.* 1997).

Reproduction and Population Structure In coastal Mauritania, main period of reproduction spans the whole of the wet season (Jul–Sep), from the end of hot dry season (Apr) to the following cool dry season (Nov); no reproductive activity observed in Jan–Feb. Embryo number: 3–6 (Klein *et al.* 1975).

Predators, Parasites and Diseases Occasionally preyed upon by Barn Owls *Tyto alba* in Mauritania (10 out of 210 prey items recorded; Granjon *et al.* 2002b).

Conservation IUCN Category: Least Concern.

Measurements

Gerbillus tarabuli

HB: 102.9 (89–112) mm, $n = 27$

T: 148.4 (134–163) mm, $n = 26$

HF: 29.2 (27–31) mm, $n = 27$

E: 14.6 (13–16) mm, $n = 19$

WT: 32.8 (19–42) g, $n = 21$

GLS: 30.7 (29.4–31.7) mm, $n = 26$

GWS: 16.6 (15.7–17.5) mm, $n = 27$

M^1 – M^3 : 3.9 (3.5–4.2) mm, $n = 27$

Auditory bulla: n. d.

Western Mauritania (Granjon *et al.* 1999, MNHN)

Key Reference Granjon *et al.* 1999.

Laurent Granjon

Gerbillus watersi WATERS'S GERBIL

Fr. Gerbille de Waters; Ger. Waters Rennmaus

Gerbillus watersi de Winton, 1901. Novit. Zool. 8: 399. Shendi, Sudan.

Taxonomy Setzer (1956), Petter (1975a) and Lay (1983) recognize *G. watersi* as a valid species. (Petter [1975a] – in error – also places *watersi* as a subspecies of *G. nanus*.) *Gerbillus watersi*, *G. bottai* and *G. stigmonyx* may form a closely related species complex, and may even belong to the same species (F. Dieterlen, in litt.);

(see species profile *G. bottai*). Musser & Carleton (2005) include *juliani* as a synonym, but Musser & Carleton (1993) and Lay (1983) retained *G. juliani* as a full species pending revision. Synonyms: none. Chromosome number: not known.

Description Small or very small pale gerbil with long tail. Dorsal pelage pale orange or sandy-orange, slightly darker along mid-dorsal line. Dorsal hairs grey at base, sandy-orange at terminal end, some with black tips. Flanks paler, hairs white at base with orange tips. Ventral pelage pure white. Colour of ventral pelage clearly delineated from colour of flanks. Crown of head and nose similar to back, darker on nose. Supraorbital and postauricular patches. Cheeks, chin, throat, limbs and feet white. Soles of hindfeet naked. Tail long (ca. 135% of HB), pale orange-brown above, well covered with short orange-brown hairs, white below; terminal half with longer dark hairs forming narrow pencil. See also Happold (1967c). Nipples: $2 + 2 = 8$ (specimen label, BMNH).

Geographic Variation None recorded.

Similar Species

G. pyramidum. Larger (HB: 110–110 mm, HF: 24–30 mm, WT: 39–51 g; Happold 1968): soles of hindfeet hairy; common.

G. stigmonyx: similar in size; very difficult to distinguish.

G. bottai. Similar in size; soles of hindfeet hairy or slightly hairy; very difficult to distinguish.

Distribution Endemic to Africa. Sahara Arid BZ/Sahel Savanna BZ. Recorded in NE Sudan, along the Nile Valley and on the Red Sea coast. Records of this species from Djibouti (Pearch *et al.* 2001) may represent *G. juliani*.

Habitat Near Khartoum, these gerbils live in sandy habitats with scattered trees and bushes.

Abundance Uncommon; found only in scattered localities. Much less common than *G. pyramidum*, which occurs in the same habitats.

Remarks Nocturnal, terrestrial. Lives in burrows during the daytime.

Conservation IUCN Category: Least Concern.



Gerbillus watersi

Measurements

Gerbillus watersi

HB: 81.5 (70–96) mm, $n = 11$

T: 108 (90–125) mm, $n = 11$

HF: 20.6 (18–23) mm, $n = 11$

E: 11.4 (10–13) mm, $n = 11$

WT: 17 (14–20) g, $n = 5$

GLS: 25.1 (24.2–25.9) mm, $n = 9$

GWS: 13.2 (12.5–13.7) mm, $n = 9$

M^1 – M^3 : 3.2 (3.0–3.7) mm, $n = 9$

Auditory bulla: 9.1 (7.8–9.5) mm, $n = 9$

Khartoum and Meroe, Sudan (BMNH)

Key References Happold 1967c; Setzer 1956.

D. C. D. Happold

GENUS *Meriones*

Jirds

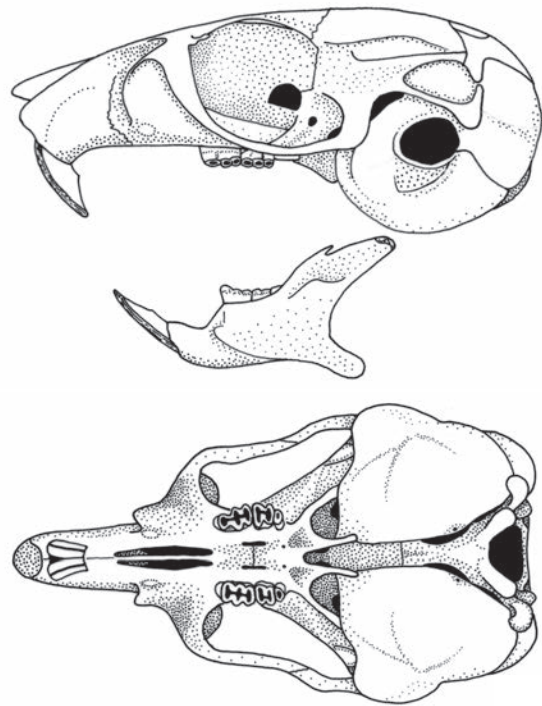
Meriones Illiger, 1811. Prodr. Syst. Mamm. Avium, p. 82. Type species: *Mus tamariscinus* Pallas, 1773.

The genus *Meriones* contains 16 species (Musser & Carleton 1993), which are widely distributed in North Africa, the Middle East, the Indian sub-continent, central Asia and China. Three or four species (see below) occur in Africa; all inhabit arid and semi-arid habitats of North Africa.

Species in the genus are large heavily built rat-like gerbils (commonly known as jirds). Dorsal pelage is sandy coloured, and the slender hairy tail is moderately long (usually ca. 75–100% of HB) with a black terminal pencil. Hindfeet slightly hairy. Skull is robust with well-developed supraorbital ridges and large inflated auditory bullae (Figure 51). Upper incisor teeth have a single

longitudinal groove. The cheekteeth are prismatic (successive rows are joined) and the laminae do not have cusps (at any stage of wear); they are similar in structure to those of *Sekeetamys* and (to a lesser extent) those of *Psammomys*. Dental formula: $I \frac{1}{1}, C \frac{0}{0}, P \frac{0}{0}, M \frac{3}{3} = 16$.

Species in the genus live in arid and semi-arid conditions, in a wide range of habitats including wadis, coastal areas, open plains and plateaux. They are nocturnal and diurnal (depending on the time of year). They feed on a wide variety of plants and seeds (but not saltbushes), have efficient water conservation and produce small quantities of concentrated urine (cf. *Psammomys*).

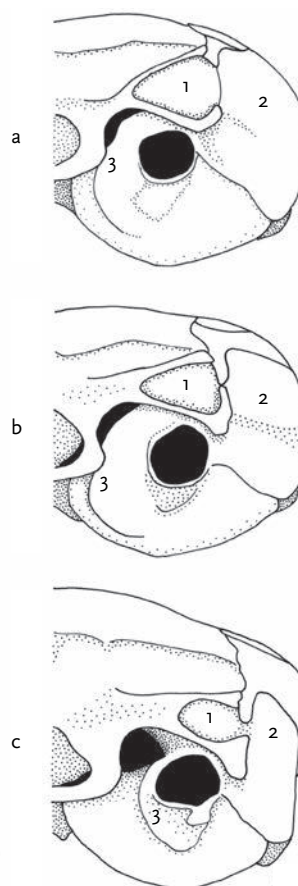
ABOVE: *Meriones crassus*.RIGHT: Figure 51. Skull and mandible of *Meriones libycus* (BMNH 8.7.12.17).**Table 26. Species in the genus *Meriones*. Arranged in alphabetical order.**

| Species | Length of tympanic bulla mean (range) (mm) | Suprameatus triangle | Tail | Claws | Inflation of mastoid bulla | Inflation of lip of auditory meatus | Accessory tympanum | Chromosome number |
|-------------------|--|--|-------------------------------------|-------|---|---|--------------------|-------------------|
| <i>M. crassus</i> | 15.5
(12.9–16.6) | Wide open; joins tympanic bulla | Conspicuous pencil at end of tail | Pale | Large; extends well posterior to paraoccipital process | Very conspicuous, touching zygomatic arch | Absent | 2n = 60, FN = 72 |
| <i>M. libycus</i> | 14.6
(13.2–15.7) | Closed; does not join to bulla | Conspicuous pencil at end of tail | Black | Moderate; extends slightly posterior to paraoccipital process | Conspicuous, touching or almost touching zygomatic arch | Present | 2n = 44, FN = 74 |
| <i>M. shawi</i> | 13.3
(12.4–14.2) | Partially open; narrow opening to tympanic bulla | Inconspicuous pencil at end of tail | Pale | Slight; does not extend posterior to paraoccipital process | Moderate, never touching zygomatic arch | Absent | 2n = 44, FN = 78 |

Table 27. Skull characters in the genera *Meriones*, *Psammomys*, *Sekeetamys* and *Pachyuromys*.

| Character | <i>Meriones</i> | <i>Psammomys</i> | <i>Sekeetamys</i> | <i>Pachyuromys</i> |
|------------------------------------|---|---|--|--|
| Supraorbital ridges | Well-developed | Well-developed | Well-developed | Slightly developed |
| Auditory bullae | Moderately inflated | Moderately inflated | Moderately inflated | Greatly inflated; posterior end well posterior to foramen magnum |
| Groove in each upper incisor tooth | Slight | None | Large | Slight |
| Form of cheekteeth | Prismatic | Slightly prismatic | Slightly prismatic | Prismatic |
| Anterior palatine foramina | Broad | Narrow | Narrow | Broad |
| Posterior palatine foramina | Mid M ¹ to mid M ² ; wide | Last lamina of M ¹ to first lamina of M ² ; very small and narrow | Mid M ¹ to posterior end of M ² ; wide | First lamina of M ¹ to mid M ² ; wide |
| Temporal and occipital ridges | None | Present | None | None |

RIGHT: Figure 52. Bulla region of three species of *Meriones* to show variation in opening of the suprameatus triangle to the mastoid, and position of meatus lip to the posterior edge of the zygomatic arch. (a) *M. crassus* (suprameatus triangle widely open, meatus lip touches zygomatic arch). (b) *M. libycus* (suprameatus triangle closed, meatus lip touches zygomatic arch). (c) *M. shawi* (suprameatus triangle slightly open, meatus lip does not touch zygomatic arch). 1 = suprameatal triangle, 2 = mastoid, 3 = meatus lip.



The number of African species in the genus is uncertain, and there is no recent review of the genus. Musser & Carleton (1993) recognize three species in Africa – *M. crassus*, *M. libycus* and *M. shawi*. The taxon *grandis*, formerly a subspecies of *M. shawi*, was raised to a full species by Musser & Carleton (2005), but is retained here as a subspecies of *M. shawi*. An additional species, *M. sacramenti*, occurs in NE Sinai (Egypt) and eastwards to Israel (Musser & Carleton 2005); it does not occur west of the Suez Canal and therefore is not considered as an African species (see Introduction: The Continent of Africa). For further information on this species, see Osborn & Helmy (1980) and Harrison & Bates (1991).

The three species of *Meriones* can be distinguished by numerous characters including head and body size, skull size, length of auditory bulla (Table 26), and the characteristics of the suprameatus triangle and meatus lip (Table 27, Figure 52). Other jirds (*Pachyuromys*, *Sekeetomys*) and sand rats (*Psammomys*) are superficially similar to *Meriones* but may be distinguished by several characteristics of the skull (Table 27).

E. Fichet-Calvet

Meriones crassus SUNDEVALL'S JIRD (SILKY JIRD)

Fr. Mérieone de Sundevall (Mérieone du désert); Ger. Sundevall Rennratte

Meriones crassus Sundevall, 1842. K. Svenska Vet. Akad., ser. 3, p. 233. Fount of Moses (Ain Musa), Sinai, Egypt.

Taxonomy Synonyms: *asyutensis*, *charon*, *ismahelis*, *longifrons*, *pallidus*, *pelerinus*, *perpallidus*, *swinhoi*, *tripolius*. Subspecies: none. Chromosome number: $2n = 60$, $FN = 70-74$ (Matthey 1957).

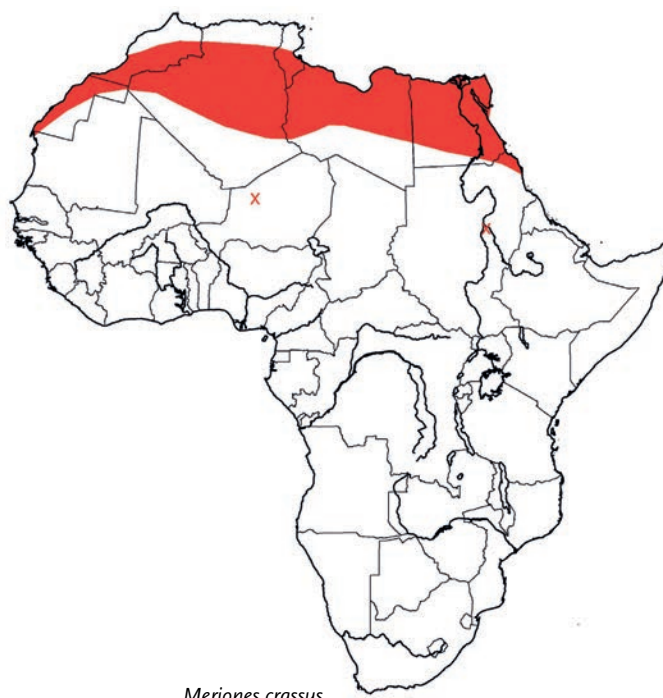
Description Medium-size jird. Pelage moderately long and soft. Dorsal pelage tawny or pale ochre; hairs grey at base, ochre or tawny at tip; grey of hair bases often shows on surface of pelage. Flanks paler. Ventral pelage greyish-white; hairs pale, grey at base, white at tip. Ears with small pale hairs, not pigmented. Conspicuous postauricular patch. Fore- and hindfeet white; soles partly hairy. Claws white. Tail long (ca. 100% of HB), well covered with hairs, grey at base, with small well-developed black terminal pencil. Skull: auditory bullae inflated (ca. 35–40% of GLS); narrow groove on each upper incisor; suprameatus triangle widely open, meatus lip touches zygomatic arch (Figure 52). Nipples: $2 + 2 = 8$.

Geographic Variation None recorded in Africa.

Similar Species (see also Figure 52)

M. libycus. Darker colour; smaller postauricular patch; black claws.

M. shawi. Similar colour; smaller postauricular patch; long line of clear colour on flanks.



Meriones crassus

Distribution Sahara Arid BZ (and occasionally Sahel Savanna BZ). Recorded from Mauritania and Morocco to Egypt (Petter 1961, Saint Girons & Petter 1965, Ranck 1968, Bernard 1969, Osborn & Helmy 1980, Aulagnier & Thévenot 1986, Kowalski & Rzebik-Kowalska 1991). Isolated records in Niger (Dobigny *et al.* 2002b), Mali (Heim de Balsac 1968) and N Sudan (Setzer 1956). Distribution is mostly south of the distribution of other *Meriones* spp. Extraliminally recorded from Israel to Afghanistan.

Habitat Arid habitats where vegetation is sparse. In Egypt, occurs in wadis with sparse cover of trees (mostly *Acacia* sp.), near date palms and rushes (but not in the Nile Delta), and in Algeria found in hamadas where few plants were growing. Also recorded in agricultural regions of S Tunisia (Bernard 1969). In the Negev Desert (Israel), animals move to new resource-rich habitats when previous habitats do not provide adequate food (Krasnov *et al.* 1996).

Abundance Common in suitable habitats. Densities range from 0.1/ha (Mar–Apr, Beni Abbes, Algeria; Petter 1961) to 11/ha (Koffler 1972).

Adaptations Nocturnal and terrestrial. Jirds are able to survive long periods of dry conditions feeding only on seeds and dry vegetation, but they require green vegetation for reproduction. Studies on water metabolism show a water influx that is higher in winter than in summer because of changes in diet (Degen *et al.* 1997). They excavate large complex burrow systems with many entrances in compact soil; a burrow may be used and altered by many generations of animals (Petter 1961).

Foraging and Food Granivorous and herbivorous. In Egypt, principal foods are fruits and seeds of *Colocynthis vulgaris*, *Anabasis articulata* and *Zilla* sp. (Osborn & Helmy 1980). In Israel, preferred green plants are *Atriplex halimus* and *Moricandia nitens* (Kam *et al.* 1997).

Social and Reproductive Behaviour Trapping results show that the maximum range length (RL, = distance between most distant captures of an individual) is large. In Algeria, mean RL for ♀♀ is 400 m and maximum is 960 m; for ♂♂, mean RL is 1500 m and maximum is 1870 m (Daly & Daly 1975a). Sometimes jirds may

move over even greater distances; for example, one ♂ returned to his burrow after being moved 6 km away (Petter 1961, 1968). Individuals are not socially tolerant, perhaps because they live in very arid habitats where resources are usually scarce (Daly & Daly 1975a). However, field and laboratory observations suggest that these jirds are sociable, but less so than *M. libycus*.

Reproduction and Population Structure In Egypt, ♀♀ are reproductively active in winter and early spring (Nov–Jun), and in Israel in Jan–Sep. Gestation: 18–22 days. Litter-size: 3.3 (1–5, n = 10). Young weaned: Day 17–23. Longevity: >18 months. Young form the highest percentage (50%) of the population in summer in Israel (Krasnov *et al.* 1996).

Predators, Parasites and Diseases Remains found in pellets of Eagle-owls *Bubo bubo* (0.1–1% occurrence) in S Morocco and Algeria (M. Thévenot pers. comm.). Recorded as a reservoir of the protozoan that causes zoonotic cutaneous leishmaniasis in humans in Egypt and Israel (Schlein *et al.* 1984) (see also *Psammomys obesus*).

Conservation IUCN Category: Least Concern.

Unlikely to be threatened because of large populations numbers and wide distribution.

Measurements

Meriones crassus

HB: 136 (114–153) mm, n = 47

T: 137 (105–158) mm, n = 40

HF: 34 (31–37) mm, n = 48

E: 19 (14–22) mm, n = 46

WT: 84 (65–109) g, n = 32

GLS: 39.1 (36.6–42.2) mm, n = 26

GWS: 21.2 (18.0–22.9) mm, n = 38

M¹–M³: 5.6 (4.8–6.4) mm, n = 45

Auditory bulla: 15.3 (12.9–16.6) mm, n = 39

Egypt (Osborn & Helmy, 1980)

Key References Petter 1961; Daly & Daly 1975a; Krasnov *et al.* 1996.

E. Fichet-Calvet

Meriones libycus LIBYAN JIRD

Fr. Mérieux à queue rougeâtre (Mérieux de Libye); Ger. Libysche Rennratte

Meriones libycus Lichtenstein, 1823. Verz. Doublet. Zool. Mus. Univ. Berlin, p. 5. Alexandria, Egypt.

Taxonomy Many forms (ca. 28) are considered as synonyms (Musser & Carleton 1993, 2005). Major synonyms (in Africa): *caudatus*, *gaetulus*, *guyonii*, *mariae*, *melanurus*, *renaultii*, *schousboeii*. Subspecies: none. Chromosome number: 2n = 44, FN = 74 (Nadler & Lay 1967).

Description Medium-sized jird. Dorsal pelage pale tawny-grey; hairs grey at base, tawny-grey at tip. Thin orange line on flank separates dorsal colour from ventral colour. Ventral pelage white; hairs pale grey at base, white on terminal half. Ears not pigmented, with sparse

whitish-fawn hairs. Small white postauricular patch. Fore- and hindfeet white, soles partly hairy. Claws black. Tail long (ca. 100% of HB), reddish at base, with conspicuous black terminal tuft (much larger than in *M. crassus*). Skull: auditory bullae inflated (33–39% of GLS); narrow groove on each upper incisor; suprameatus triangle slightly open, meatus lip does not touch zygomatic arch (Figure 52). Nipples: 2 + 2 = 8.

Geographic Variation None recorded in Africa.

Similar Species (see also Figure 52)

M. crassus. Paler colour, larger postauricular patch; white claws.

M. shawi. Paler colour, darker ears on the edges; white claws.

Distribution Sahara Arid BZ. Widely distributed from Morocco to Egypt. In Morocco, occurs on the Atlantic coast south to Agadir and south to Atlas Mts (Aulagnier & Thévenot 1986). In Algeria, recorded on southern edge of Atlas and Aures Mts, and in Hoggar and Tassili (Kowalski & Rzebik-Kowalska 1991). Present in S Tunisia (Bernard 1969). In Libya, occurs in the coastal desert and throughout the Fezzan (Ranck 1968, Vesmanis 1985), and in N Egypt confined to coastal regions west of the Nile Valley (Osborn & Helmy 1980). Isolated record in Mauritania. Extraliminally recorded from Israel to Afghanistan.

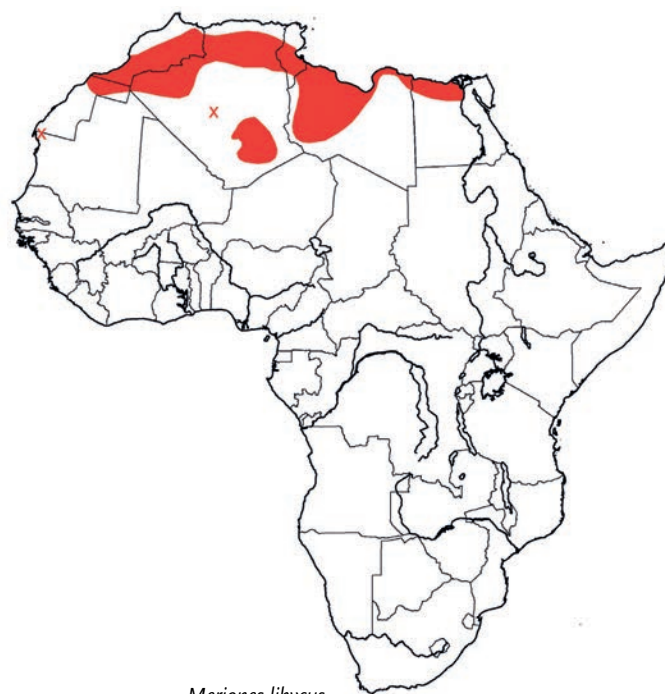
Habitat In Algeria, found in many habitats on clay or sandy substrates including sandy mounds, wadi borders, plateaux (= hamadas) with perennial vegetation and halophytic steppes (Petter 1961, Daly & Daly 1975a, Zaim & Pascal 1989). Libyan Jirds require more vegetation in their habitat than do Sundevall's Jirds (Daly & Daly 1975a). Commonly occurs in large burrows under jujube bushes (*Zizyphus lotus*).

Abundance Populations fluctuate seasonally, between high numbers in spring and low numbers in summer (Zaim & Gautier 1993). In June, jirds comprised 24% (16/67) of small mammals inhabiting halophytic steppe in Morocco (Zaim & Pascal 1989). In Algeria, Petter noted 1 ind/20 ha in hamada near Beni Abbes.

Adaptations Diurnal and nocturnal. Digs shallow burrows with numerous openings, which are not plugged with sand or earth (Osborn & Helmy 1980). Activity patterns vary seasonally; in Jan, Libyan Jirds are often seen from sunrise to 08:30h, and in the afternoon from 16:00h to sunset. In Mar, diurnal activity is rarer than in winter (Daly & Daly 1975a, Agren 1979). Capable of surviving long periods of drought by feeding on stored seeds. Efficient water conservation: metabolic water is obtained from food, and water loss is reduced to a minimum by production of concentrated urine. Urine osmotic pressure (2640 mOsmol/L) is similar to that of *P. obesus* (2775 mOsmol/L) whereas water turnover is lower (Bradshaw *et al.* 1976, Ben Chaouacha-Chekir *et al.* 1983). Compared to Shaw's Jirds, thyroid function in Libyan jirds is reduced with a low iodine intake (Ben Chaouacha-Chekir 1996).

Foraging and Food Granivorous and herbivorous; diet is mainly seeds and grasses (no details available). Eats many different plants and seeds but prefers cereal and fruit seeds. Also feeds on succulent plants such as *Colocynthis vulgaris* (Chenopodiaceae) and *Zizyphus lotus*. Seeds are stored in special chambers in burrows (Petter 1961, Bernard 1969).

Social and Reproductive Behaviour Trapping data show that the maximum range length (RL, = distance between most distant captures of an individual) is large although not as large as for *M. crassus*. Mean RL for ♀♀ is 111 m (Nov–Dec) to 140 m (Jan–Feb) and maximum is 2280 m (n = 16); for ♂, mean RL is 159 m (Nov–Dec) to 1420 m (Jan–Feb), and maximum is 2420 m (n = 13). Home-ranges of ♀♀ sometimes (but rarely) overlap; home-ranges



Meriones libycus

of ♂♂ overlap with those of several ♀♀. Females may remain in the same home-range for many months. Numerous agonistic interactions between ♀♀ suggest a high degree of territoriality. Home-ranges are marked by secretions from mid-ventral glands and during sand-bathing (Agren 1979). Libyan Jirds produce many vocalizations for communication in sexual, agonistic and mother–pup interactions (Daly & Daly 1975a). Alarm signals include vocalization, foot-thumping (Daly & Daly 1975a) and holding the tail upright (so the black tuft is very obvious) like a flag (Harrison & Bates 1991).

Reproduction and Population Structure Breeding occurs only in winter, with pregnancies from Nov to Feb. Gestation: ca. 25 days (or up to 35 days if mother is lactating). Litter-size: 3 (2–4, n = 4) (Egypt; Osborn & Helmy 1980). Maturity: 3 months. Juveniles present in Mar–Apr in Beni Abbes (Algeria; Daly & Daly 1975a).

Predators, Parasites and Diseases Many species of raptors (e.g. *Tyto alba*, *Bubo bubo*, *Asio otus*, *Strix aluco*) prey on Libyan Jirds. Remains have been found in pellets of Eagle-owls in Morocco and in Algeria (10–57% occurrence, M. Thévenot pers. comm.). Honey Badgers *Mellivora capensis* prey on jirds in Morocco (M. Cuzin pers. comm.). Recorded as a reservoir of the protozoan that causes zoonotic cutaneous leishmaniasis in humans in Tunisia, in Libya and in Iran (see also *Psammomys obesus*). Endoparasitic nematodes recorded in Tunisia.

Conservation IUCN Category: Least Concern.

Measurements

Meriones libycus

HB: 141.5 (123–155) mm, n = 53

T: 145.4 (115–157) mm, n = 44

HF: 35.1 (32–38) mm, n = 55

E: 19.6 (18–22) mm, n = 55

WT: 84.0 (65–109) g, n = 32

GLS: 38.6 (34.4–42.0) mm, n = 52
 GWS: 20.4 (18.9–22.3) mm, n = 42
 M¹–M³: 5.6 (5.1–6.8) mm, n = 52
 Auditory bulla: 14.6 (13.2–15.7) mm, n = 51
 Egypt (Osborn & Helmy 1980)

Key References Ben Chaouacha-Chekir *et al.* 1983; Ben Chaouacha-Chekir 1996; Daly & Daly 1975a; Petter 1961; Zaime & Pascal 1989.

E. Fichet-Calvet

Meriones shawi SHAW'S JIRD

Fr. Mérieone de Shaw; Ger. Grosse Wüstenrennmaus (Shaws Rennratte)

Meriones shawi (Duvernoy, 1842). Mem. Soc. d'Hist. Nat. Strasbourg 3: 22. Oran, Algeria.

Taxonomy Originally described in the genus *Gerbillus* by Duvernoy in 1842. Many forms (ca. 11) described as subspecies are now considered as synonyms (Musser & Carlton 1993, 2005). The relationship between *M. shawi* and *M. libycus* is uncertain (Musser & Carlton 1993). The form *grandis* may be synonymous with *shawi*, or it may be a separate species as suggested by Pavlinov (2000) on the basis of craniometric variation (see also Musser & Carleton [2005] who consider *M. grandis* to be distinct from *M. shawi*). However, fertile hybrids have been obtained by cross-breeding *M. shawi* and *M. grandis*, suggesting that these taxa are conspecific (F. Petter & J.-A. Rioux unpubl.). Synonyms: *albipes*, *auratus*, *auziensis*, *azizi*, *crassibulla*, *grandis*, *isis*, *laticeps*, *longiceps*, *richardii*, *savii*, *sellysii*, *trouessarti*. Subspecies: three. Chromosome number: 2n = 44, FN = 78.

Description Medium-sized or large brown jird. Dorsal pelage ochre to pale tawny; hairs medium grey on basal half, ochre or pale tawny on terminal half; guard hairs black. Pelage colour varies geographically (see below). Slightly paler on flanks. Ventral colour pure white clearly delineated from colour of dorsal pelage by thin pale orange line. Head similar to dorsal pelage. Throat slightly yellow. Ears darkly pigmented, with scattered short tawny hairs. Conspicuous postauricular patch. Fore- and hindfeet white. Soles of

hindfeet partly hairy. Claws white. Tail long (ca. 95% of HB), well covered with sandy-brown hairs; upper surface with some black hairs and well-developed black pencil on terminal third. Skull: auditory bullae inflated (32–34% of GLS); narrow groove on each upper incisor; suprameatus triangle slightly open, meatus lip does not touch zygomatic arch (Figure 52). Considerable variation in colour and size between subspecies (see below). Nipples: 2 + 2 = 8.

Geographic Variation

M. s. shawi: Morocco to Egypt on the Mediterranean coast, except on the Tangier peninsula. Intermediate in size, colour and weight (70–120 g) compared with *grandis* and *trouessarti* (see Description above).

M. s. grandis: Morocco to NW Tunisia (overlapping with *M. s. shawi*?). Large (see below) with dark pelage (Saint Girons & Petter 1965).

M. s. trouessarti: Morocco to Tunisia between the Atlas Mts and the Sahara Desert, including the Chat Jeered. Small, pale and less heavy (see below); the most desert-adapted of all jirds.

Similar Species (see also Figure 52)

M. libycus. Darker colour, larger black terminal tuft on tail.

Distribution Endemic to Africa. Mediterranean Coastal BZ and northern parts of Sahara Arid BZ. Recorded from Morocco (where it occurs locally in mountains up to 2800 m [M. Cuzin pers. comm.]), Algeria, Tunisia, Libya and Egypt. Southern limit defined by oases south to High Atlas (29° N) and Aures Mts.

Habitat Widespread in plains and mountains, except for rocky habitats. Present in cereal crops, orchards and halophytic steppes, often in sympatry with *M. libycus* and various species of gerbils (Zaime & Pascal 1989). In Tunisia, particularly common in mounds colonized by jujube bushes (*Zizyphus lotus*) or along the hedgerows planted with prickly pear trees (*Opuntia* sp.) under which rodents build their burrows. Lives in sandy and clayey soils.

Abundance Populations fluctuate according to seasons. High densities occur in spring (40–100 ind/ha) and low densities in late summer and autumn (10–20 ind/ha). On occasions, population numbers may attain >200 ind/ha causing damage to cereal and food crops, and becoming major pests in agricultural fields (Bernard 1969, Zaime & Gautier 1988).

Adaptations Nocturnal and partly diurnal. The most hydrophilic jird with a higher water turnover and a lower urine osmotic pressure



Meriones shawi

(2040 mOsmol/L) than *M. libycus*. Also requires a higher iodine intake than *M. libycus* to maintain thyroid function (Ben Chaouacha-Chekir 1996).

Foraging and Food Herbivorous and opportunistic, eating many different plants and seeds. Diet varies according to season and habitat. In Morocco, preferred plants are species of Gramineae (*Sorghum halepense* and *Stipa retorta*), Papilionaceae (*Medicago hispida*) and Compositae (*Calendula aegyptica*). Also eats *Salsola vermiculata* (Chenopodiaceae) in spring and autumn, and arthropods in Jul (Zaime & Gautier 1989). Seeds are stored in special caches in the burrows.

Social and Reproductive Behaviour Colonial. Range length (distance between most distant captures of an individual) varies according to season and sex. Range length in spring (May–Jun) is 40–50 m, and 10–20 m in autumn and winter (Sep–Feb). Range length of males (ca. 70 m) is larger than for females (ca. 30 m), especially in uncultivated areas where food availability is low (Zaime & Gautier 1988). Communication between individuals is by foot-drumming and vocalizations (Bridelance 1989).

Reproduction and Population Structure Pregnancies recorded during wet season in Morocco (Nov–May; Zaime & Gautier 1988) and during dry season in Tunisia (Mar–Sep; Bernard 1969). Gestation: 21 days. Litter-size: 5.0 (3–8, with a maximum [mean 6.2] in Mar). Weight at birth: 3.5–6 g.

Predators, Parasites and Diseases Predators include foxes (*Vulpes vulpes*) and owls (*Tyto alba*, *Asio otus*, *Strix aluco*, *Bubo bubo*). Remains found in pellets of eagle-owls, comprised 0.5–3.5% of prey in Morocco (M. Thévenot pers. comm.) and 29% in N Algeria (Boukhamza *et al.* 1994). Reservoir of protozoan *Leishmania major*, which causes zoonotic cutaneous leishmaniasis (WHO 1990) (see also *Psammomys obesus*). Endoparasites in Tunisia include nematodes (Bernard 1987).

Conservation IUCN Category: Least Concern.

Shaw's Jirds are considered as pests in cultivated areas. Control measures may be necessary when population numbers are high.

Measurements

Meriones shawi shawi

HB: 143 (128–160) mm, n = 31

T: 140 (122–155) mm, n = 25

HF: 35 (32–37) mm, n = 31

E: 19 (17–22) mm, n = 31

WT: 91 (70–120) g, n = 11

GLS: 38.8 (37.1–41.5) mm, n = 20

GWS: 22.2 (20.6–23.5) mm, n = 18

M¹–M³: 6.0 (5.6–6.3) mm, n = 22

Egypt (Osborn & Helmy 1980)

Meriones shawi grandis

HB: 167 (138–200) mm, n = 18

T: 159 (134–185) mm, n = 12

HF: 38 (33–40) mm, n = 18

E: 22 (19–24) mm, n = 17

WT: 242 (230–255) g, n = 3

GLS: 45.1 (39.9–50.4) mm, n = 18

GWS: 25.4 (22.3–28.6) mm, n = 17

M¹–M³: 6.2 (5.6–6.8) mm, n = 18

Morocco (MNHN)

Meriones shawi trouessarti

HB: 131 (115–150) mm, n = 19

T: 124 (112–146) mm, n = 19

HF: 31 (30–34) mm, n = 19

E: 16 (14–17) mm, n = 19

WT: 65 (45–86) g, n = 19

GLS: 35.7 (34.5–36.9) mm, n = 4

GWS: 19.7 (19.2–20.0) mm, n = 4

M¹–M³: 5.5 (5.5–5.6) mm, n = 4

Auditory bulla: 13.3 (12.4–14.2) mm, n = 15*

Tunisia, Sidi Bouzid (E. Calvet unpubl.)

*Egypt (Osborn & Helmy 1980)

Key References Zaime & Gautier 1988, 1989; Zaime & Pascal 1988.

E. Fichet-Calvet

GENUS *Microdillus*

Peel's Pygmy Gerbil

Microdillus Thomas, 1910. Ann. Mag. Nat. Hist., ser. 8, 5: 197. Type species: *Gerbillus peeli* de Winton, 1898.

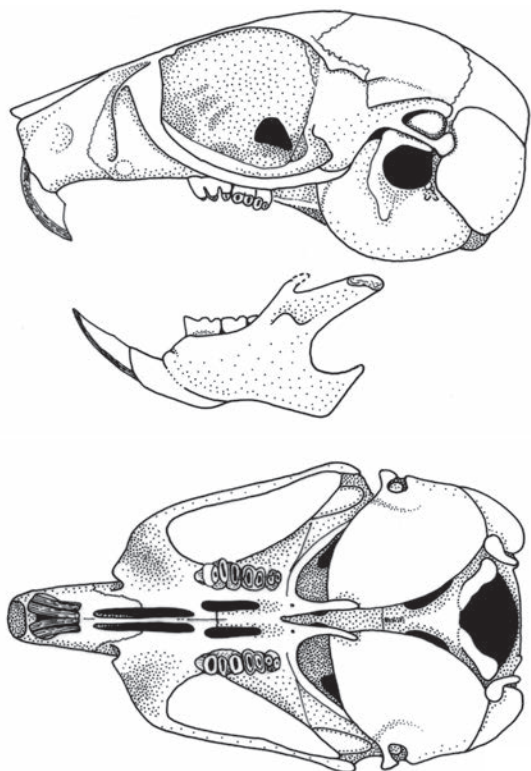
Small gerbil-like rodents, often considered as a subgenus of *Gerbillus* but now recognized as a full genus (Petter 1975a, Musser & Carleton 1993, 2005). The genus has many gerbil-like features, but is characterized by small size, short tail and short square skull, which is abnormally bowed with a strong convex cranial profile. Unlike

Gerbillus, the upper third molar has three or four cusps (Petter 1977a). There is only one species, *Microdillus peeli*.

D. C. D. Happold

Microdillus peeli PEEL'S PYGMY GERBIL (SOMALI PYGMY GERBIL)

Fr. Gerbille pygmée de Somalie; Ger. Peels Koboldrennmaus

Microdillus peeli (de Winton, 1898). Ann. Mag. Nat. Hist., ser. 7, 1: 250. Eyk, Somalia (see Roche & Petter [1968] for map).Figure 53. Skull and mandible of *Microdillus peeli* (BMNH 8.4.9.9).*Microdillus peeli*

Taxonomy Originally described in the genus *Gerbillus* (see genus profile). Synonyms: none. Chromosome number: not known.

Description Very small gerbil with long pelage and short tail. Dorsal pelage dull orange-brown; dorsal hairs grey at base, with orange-brown tips. Pelage long and shaggy, so that grey bases of hairs may show on surface of pelage. Flanks paler; hairs whitish-grey or white at base. Ventral pelage pure white. Crown of head similar to back. Large eyes. Nose, lower cheeks, chin and throat white. Conspicuous supraorbital and postauricular white patches. Limbs and feet white. Soles of feet naked. Tail short (ca. 80% of HB), rather thick, slightly scaly, covered with brown or blackish bristles; without terminal pencil. Skull short and square; upper incisors opisthodont; zygomatic arch curves deeply downwards to form a large orbit; zygomatic plate small with almost vertical anterior face; auditory bullae (tympanic bullae and mastoids) large (Figure 53). Nipples: not known.

Geographic Variation None recorded.

Similar Species In all other species of gerbils of similar size (except *Desmodillus braueri*) the tail is longer than HB (Table 22).

Distribution Endemic to Africa. Somalia–Masai Bushland BZ. Known only from three localities in N and C Somalia. Not recorded from similar habitats in Ethiopia.

Habitat In C Somalia, found in sandy habitats. Other individuals recorded from hilly country (1500 m) in N Somalia.

Abundance Probably rare; there are few records and populations are scattered.

Remarks The tail appears to be used for fat storage in the same way as in *Pachyuromys duprasi* and *Gerbillus simoni*. The long shaggy pelage is probably an adaptation to the cool nights in winter (as in *G. somalicus*). Most specimens were 'caught on track at night'.

Conservation IUCN Category: Least Concern. However, limited geographic range and probable rarity may be cause for concern.

Measurements*Microdillus peeli*

HB: 72.1 (66–80) mm, n = 12

T: 57.4 (50–65) mm, n = 12

HF: 17.8 (16–19) mm, n = 12

E: 11.4 (10–13) mm, n = 12

WT: n. d.

GLS: 24.4 (23.7–25.2) mm, n = 6

GWS: 14.5, n = 1

M¹–M³: 3.7 (3.6–3.9) mm, n = 6
 Auditory bulla: 9.5 (9.2–9.8) mm, n = 6
 Somalia (BMNH)

Key Reference Roche & Petter 1968.

D. C. D. Happold

GENUS *Pachyuromys*

Fat-tailed Jird

Pachyuromys Lataste, 1880. Le Naturaliste, 2 (40): 313. Type species: *Pachyuromys duprasi* Lataste, 1880.

A monotypic genus widespread in semi-arid regions of North Africa. The genus is characterized by hairy soles on the hindfeet, relatively short thickened tail without pencil and often club-shaped at terminal end, faint groove on each upper incisor, prismatic molars (but to a lesser extent than in *Psammomys*, *Meriones* and *Sekeetomys*), very

inflated auditory bullae and wide posterior palatal foramina from mid M¹ to mid M² (see also Table 27). Further details are given in the species profile. The single species is *Pachyuromys duprasi*.

D. C. D. Happold

Pachyuromys duprasi FAT-TAILED JIRD

Fr. Gerbille à queue grosse; Ger. Fettschwanzmaus

Pachyuromys duprasi Lataste, 1880. Le Naturaliste, 2 (40): 313. Laghouat, Algeria.

Taxonomy Synonyms: *faroulti*, *natronensis*. Subspecies: none. Chromosome number: 2n = 54 (Qumsiyeh & Schlitter 1991).

Description Small pale-coloured rodent with thick short naked tail. Pelage long, fine and soft with a rather shaggy appearance. Dorsal pelage beige, sandy or pale orange; hairs dark grey at base, beige or sandy subterminal band, sometimes with black tip. Dorsal hairs may lie irregularly so black tips form small lines across the body. Ventral hairs pure white. Head similar in colour to dorsal pelage. Eyes large, dark. Ears comparatively small, with sparse longish hairs; ears often partially obscured by pelage of head and neck. Muzzle, lips, chin and throat white. Fore- and hindlimbs small. Forefoot with four digits, each with small claw. Hindfeet with five digits, each with small claw. Feet and digits well covered with long white hairs. Tail short (ca. 54% of HB), thick and club-shaped, naked and without scales; terminal pencil absent; size of tail varies seasonally (see below). Skull with

single faint groove on each upper incisor, braincase broad, auditory bullae very inflated (ca. 47% of GLS) and extending posteriorly to occiput (see also genus profile) (Figure 54). Nipples: not known.

Geographic Variation None recorded.



Pachyuromys duprasi.

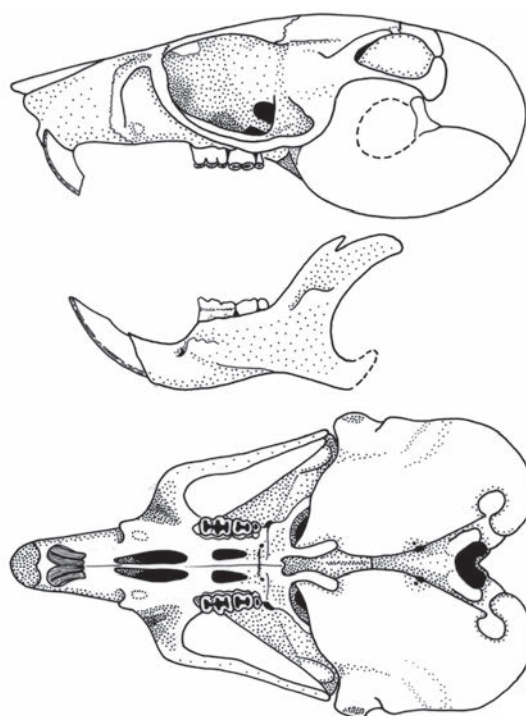
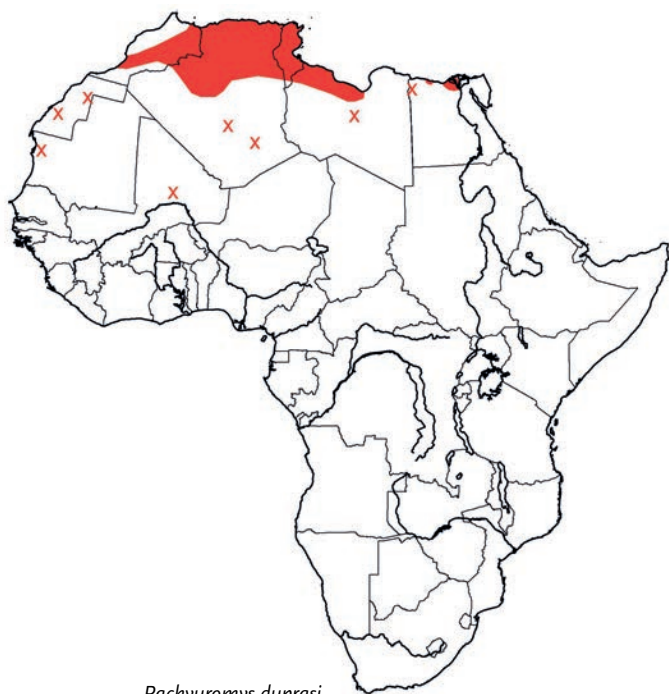


Figure 54. Skull and mandible of *Pachyuromys duprasi* (BMNH 4.11.3.118).

*Pachyuromys duprasi*

Similar Species

Meriones spp. Larger HB (mean >130 mm); tail long (mean >135 mm, at least 95% of HB) with black terminal pencil; upper incisor teeth each with distinct longitudinal groove; auditory bulla smaller (mean 14.6–15.3 mm, ca. 32–40% of GLS).

Psammomys spp. Larger HB (mean 122 mm or larger); tail moderately long (mean ca. 115 mm, ca. 75% of HB) with black terminal pencil; upper incisor teeth without longitudinal groove; auditory bulla smaller (mean 13.3 mm, ca. 32–39% of GLS).

Distribution Endemic to Africa. Sahara Arid BZ. Recorded from Mauritania, Morocco, Algeria, Tunisia, Libya and Egypt. Distribution is widespread but very localized in semi-arid areas south of the Atlas Mts in Morocco and Algeria, and south of the coastal plain in Libya and Egypt. In Algeria extends southwards to ca. 25°N (as evidenced by remains in owl pellets). One isolated record in N Mali (Heim de Balsac 1968).

Habitat Hamadas with coarse pebbles and large boulders where vegetation is sparse, and along the edges of shallow dry water-courses that bisect the hamadas (Libya: Ranck 1968; Algeria: Daly & Daly 1979). Vegetated 'sand sheets' among sparse vegetation, and rocky deserts (Egypt: Osborn & Helmy 1980).

Abundance Generally rarely encountered. Few specimens are obtained even where other species of rodents are common (Daly & Daly 1979). These jirds were more abundant than usual at Beni-Abbès, Algeria, when there were large numbers of crickets (Petter 1961) (see also below).

Adaptations Nocturnal and terrestrial. Movement is by walking and running, and not by bounding as in many other gerbils (Petter 1961). Fat-tailed Jirds construct large complex burrows, often on slopes, where the sand is dry and has been compacted by ephemeral

rainstorms. Burrows are extensive, with numerous entrances (up to 12), which descend almost vertically into the burrow. Burrows are mostly shallow (5–10 cm) and rarely deeper than ca. 30 cm (max depth ca. 100 cm), and contain a nest. Burrows may be used for storage of food (Petter 1961). Fat-tailed Jirds become active at dusk, and may forage considerable distances (up to 2 km) from their burrows (Mermod 1970). One of the unique features of this species is its short fat tail, which is used to store fat; the tail alters in size according to season and to the amount of stored fat. In captivity, they are capable of entering 'torpor' for several days when Tb is 32–35 °C (Petter 1961). The auditory bullae are greatly inflated and, as in many species of gerbils and jerboas, provide for very sensitive perception of sounds.

Foraging and Food Omnivorous; mostly herbivorous. Detailed information on diet not available. In Algeria, burrows contained fragments of fruits (*Colocynthis vulgaris* and *Hyoscyamus niger*) (Petter 1961), and in Egypt, Fat-tailed Jirds have been observed to feed on *Anabasis articulata* and *A. monosperma* (Osborn & Helmy 1980). In captivity, they feed on grains, chopped meat, cheese, lettuce and lucerne; the addition of food containing meat to the diet stimulated reproduction (Petter 1961). The suggestion that snails may be eaten (Setzer 1957) needs confirmation.

Social and Reproductive Behaviour No information.

Reproduction and Population Structure Gestation: ca. 21 days. Litter-size (in captivity): usually 3–5 (also 7 [n = 1], 9 [n = 1]). Births in captivity (Giza, Egypt) in Apr, May, Jul, Oct and Nov (Flower 1932). No data for wild populations, but likely to be opportunistic. Ears open Day 5–8, hair begins to grow Day 7–9; incisors erupt Day 11–15; eyes open Day 20–21; adult weight and body size ca. Week 10 (Petter 1961).

Predators, Parasites and Diseases Remains are common in owl pellets (Kowalski & Rzebiak-Kowalska 1991). One species of flea, *Xenopsylla nubica*, recorded in Algeria (Beaucornu & Kowalski 1985); seven species of fleas recorded on animals and in nests within burrows in Egypt: *Ctenocephalides felis*, *Synosternus cleopatrae*, *Xenopsylla conformis*, *X. ramesis*, *Stenopoma tripectinata*, *Nosopsyllus henleyi*, *Hopkinsipsylla oculata* (Hoogstraal & Traub 1965a). These fleas are also found on many other species of desert gerbils.

Conservation IUCN Category: Least Concern.

Although not common, the species has a widespread distribution and is unlikely to be threatened.

Measurements

Pachyuromys duprasi

HB: 108.3 (93–121) mm, n = 4

T: 58.2 (55–62) mm, n = 4

HF: 23.3 (22–24) mm, n = 4

E: 14.0 (12–16) mm, n = 4

WT: 36.5 (22–45) g, n = 3

GLS: 24.9 (32.4–36.5) mm, n = 4

GWS: 19.3 (17.5–20.2) mm, n = 4

M¹–M³: 5.2 (4.8–5.7) mm, n = 4
 Auditory bulla: 16.7 (15.6–17.6) mm, n = 10
 Egypt (Osborn & Helmy 1980)
 Auditory bulla: throughout geographic range (BMNH)

Key References Kowalski & Rzebik-Kowalska 1991; Osborn & Helmy 1980; Petter 1961.

D. C. D. Happold

GENUS *Psammomys*

Sand Rats

Psammomys Cretzschmar, 1828. In: Rüppell, Atlas Reise Nordl. Afr., Zool. Säugeth., p. 56. Type species: *Psammomys obesus* Cretzschmar, 1828.



Psammomys obesus.

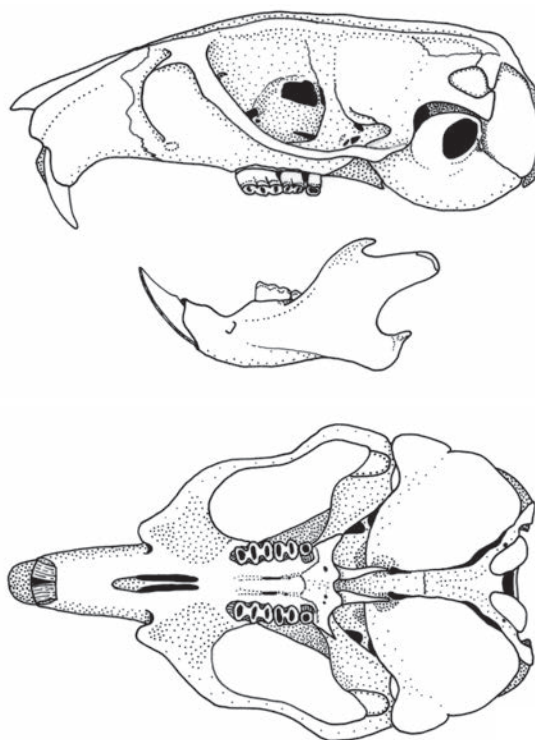


Figure 55. Skull and mandible of *Psammomys obesus* (BMNH 3.12.8.50).

The genus contains two species that live in semi-arid regions of N Africa, mostly north of the Sahara Desert. Habitats include salty lowlands, wadis and coastal deserts where saltbushes are prevalent.

Species in the genus are large heavily built rat-like gerbils. Dorsal pelage is sandy coloured, and the thick hairy tail is comparatively short (less than ca. 75% of HB) with a black terminal pencil. Hindfeet are broad and slightly hairy. The skull is robust, with well-developed supraorbital, temporal and occipital crests, large inflated auditory bullae (Figure 52), and narrow slit-like anterior and posterior palatal foramina. Upper incisors do not have a longitudinal groove (cf. *Meriones*); cheekteeth are similar in structure to those of *Meriones*. Cheekteeth do not have cusps (at any stage of wear) and the laminae are prismatic (as in *Meriones* and *Sekeetamys*) (Figure 55, see also Table 27).

Species in the genus are adapted for living in arid conditions. Their unique characters are diurnal activity and the production of large quantities of very concentrated urine. These characters are quite different to those of other arid-living small rodents and are associated with their ability to feed primarily on succulent saltbushes, rich in salt and water.

The genus *Psammomys* is placed in the subfamily Rhombomyini, which also includes the genera *Sekeetamys*, *Meriones* (and three other non-African genera [Pavlinov *et al.* 1990]). The number of species

in the genus is uncertain. Here, following Musser & Carleton (2005), two species are recognized – the larger *P. obesus* and smaller *P. vexillaris*. Several forms are considered now as synonyms of *P. obesus*, and *P. vexillaris* is also considered as a synonym of *P. obesus* by some authorities.

The two species of *Psammomys* are distinguished by body size, pelage colour and distribution.

E. Fichet-Calvet

Psammomys obesus FAT SAND RAT

Fr. Rat des sables obèse; Ger. Fette Sandratte

Psammomys obesus Cretzschmar, 1828. In: Rüppell, Atlas Reise Nordl. Afr., Zool. Säugeth., p. 58, pl. 22. Alexandria, Egypt.

Taxonomy Many forms have been described as species of *Psammomys*, including *algiricus* in Algeria, *tripolitanus* and *vexillaris* in Libya, *nicolli* and *obesus* in Egypt and *terraesantæ* in Palestine. All, except *vexillaris*, are now regarded as synonyms of *obesus* (Musser & Carleton 1993, 2005). The Fat Sand Rat is one of the best studied and most interesting of North African small rodents. Synonyms: *algiricus*, *dianae*, *elegans*, *nicolli*, *roudairi*, *terraesantæ*, *tripolitanus*. Subspecies: none. Chromosome number: $2n = 48$, $FN = 74-78$ (Qumsiyeh & Schlitter 1991).

Description Large heavily built sand rat with long pelage. Dorsal pelage ochre to tawny with long dark brown guard hairs; hairs dark grey at base, with orange or brown terminal band and black tip; width of bands varies geographically. Flanks and ventral pelage pale ochre. Massive head with large crown; vibrissae very long, pale or brown. Eyes large. Ears small and round, hairy, grey to ochre, set low on side of head. Small white postauricular patch. Fore- and hindlimbs short with buffy hairs on inner surface. Soles of hindfeet partly hairy; claws dark. Tail of moderate length (ca. 70% of HB), very hairy, ochre or brown with black terminal pencil. Skull: well-developed supraorbital ridges; auditory bullae inflated (ca. 32% of GLS); upper incisors smooth, without groove. Males tend to be larger than ♀♀. Nipples: $2 + 2 = 8$.

Geographic Variation None recorded.

Similar Species

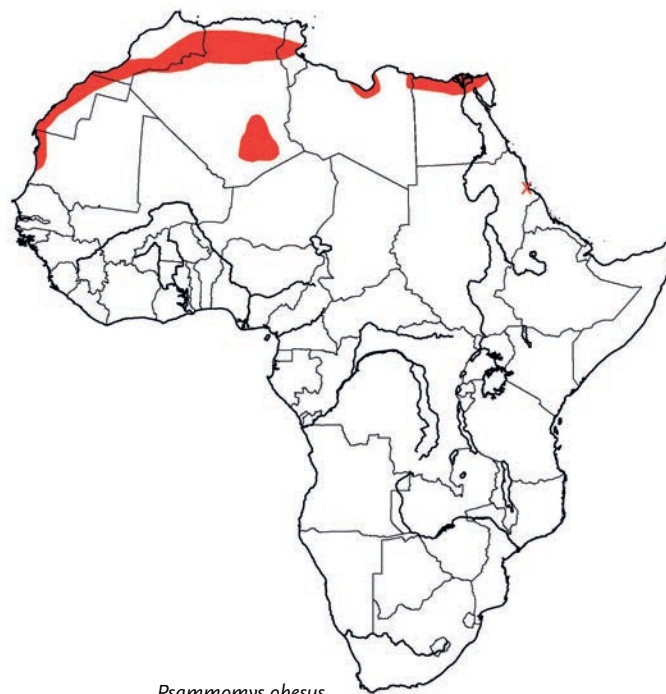
Psammomys vexillaris. On average smaller; pelage paler; ear smaller; E Algeria to W Libya only.

Meriones spp. Smaller (except for *M. shawi grandis*); dorsal pelage similar, but with white ventral pelage; ear on average larger; sympatric throughout most of geographic range.

Distribution Sahara Arid BZ. Widespread but disjunct distribution in salty lowlands, wadis and coastal deserts in Mauritania, Morocco, Algeria, Libya and Egypt where annual rainfall is 250–300 mm; also in southern part of the Haute Plateaux and Haggier Mts of Algeria. Outlier population on Red Sea coast of Sudan. Southern limit in the Sahara depends on the location of suitable habitats such as salt steppes near an oasis or a chott (= ancient lake). Extraliminally recorded from Syria, Jordan, Israel and parts of Arabian Peninsula.

Habitat Preferred habitats are succulent halophytic steppes (called *daya* in Egypt, and *sebkhet* in Tunisia) where the soil is moist, muddy and salty (salinity 9–30 g/L) (Petter 1961, Fichet-Calvet *et al.* 2000). The main plants in these habitats are saltbushes (*Arthrocnemum*, *Atriplex*, *Halocnemum*, *Salsola* and *Sueda*; family Chenopodiaceae), which are essential for the survival of these sand rats.

Abundance Generally common; populations fluctuate seasonally. Abundance in Tunisia ranged from 5 individuals/100 m of trap line

*Psammomys obesus*

(summer and early autumn) to 25/100 m (spring). In Morocco, densities (in Jul) of 42/ha have been recorded (Zaïme & Pascal 1988). Abundance also varies spatially in relation to flooding (in salt steppes). Multi-annual fluctuations have been recorded, but the causes are as yet unknown (Fichet-Calvet *et al.* 1999b, 2000).

Adaptations Fat Sand Rats live in an ecological niche utilized by no other species of rodent. They feed on the succulent leaves of saltbushes, which provide large amounts of water but are low in energy. The leaves of saltbushes contain salt (up to 12% by dry weight) as well as large quantities of water (up to 82%; Petter 1952). The kidneys are large and very efficient compared with those of other rodents, and are capable of producing a highly concentrated urine (salt concentration 2859 mmol/L, which is about four times as concentrated as seawater). Despite the high concentration of the urine, large quantities of urine have to be excreted each day (up to 25 ml/day) because of the high intake of water. This method of maintaining a positive water balance (and keeping cool in the desert during the daytime) is quite different to any other desert animal: it is a 'large water intake with large water loss' method, the large water loss being necessary because of the salty diet. This unusual method enables sand rats to exploit food that is inedible to other species, and to be diurnal when the ambient temperature is high (Ben Chaouacha-Chekir *et al.* 1983, Kam & Degen 1989).

Fat Sand Rats are diurnal and nocturnal. Activity above ground is usually 09:00h to 17:00h in winter, but confined to early morning and late afternoon in summer (Petter 1961, Ilan & Yom-Tov 1990). During the cooler months of the year, they bask in the sun.

Extensive complex burrows are excavated under bushes. Burrows are mostly less than 0.5 m deep but several metres in length, and have many entrances (usually 5–15 in Tunisia). A typical colony of Fat Sand Rats has a burrow under nearly every bush, with a maze of trails connecting burrows and food plants (Osborn & Helmy 1980). An actively used burrow can be recognized by fragments of saltbushes, faeces and urine marks at the entrance (Fichet-Calvet *et al.* 1999b). A chamber within the burrow may be used for faeces (Petter 1961). Burrows in salt marshes are abandoned in winter if flooded by water. An animal may use several burrows depending on climate and food resources, and lactating ♀♀ sometimes carry their offspring from one nest burrow to another.

Foraging and Food Herbivorous. Leaves and twigs of many species of saltbushes are the principal food. Fat Sand Rats forage 10–30 m around their burrows. They climb into low saltbushes and cut little branches, which they carry back to the main entrance of their burrows. The succulent leaves and twigs are eaten at the burrow entrance, where piles of discarded pieces are dropped onto the sand. Fragments of many species of plants are found in and near burrows: in Egypt, one burrow contained nine species of saltbush and another contained five species (Wassif 1953). Although food gathering does not take long, chewing and ingesting may take up to 4 h/day. Preferred plants vary depending on the locality, and include *Salsola vermiculata* (76.6% of the diet) in Morocco (Zaïme & Gautier 1989), *Suaeda mollis*, *Traganum nudatum* and *Salsola foetida* in Algeria (Daly & Daly 1973), *Suaeda fruticosa*, *Arthrocnemum glaucum* and *Salsola tetragona* in Tunisia (Fichet-Calvet *et al.* 2000) and *Suaeda monoïca*, *A. glaucum* and *Anabasis articulata* in Egypt (Wassif & Soliman 1979). Fat Sand Rats need to eat large quantities of food each day in order to provide adequate water for their metabolism (see above). Occupied burrows are positively correlated with the presence of green and vigorous Chenopod bushes (Daly & Daly 1974, Zaïme & Pascal 1989).

Social and Reproductive Behaviour Although Fat Sand Rats live in colonies, individuals tend to be solitary. Females have smaller range lengths (mean RL = 76 m) than ♂♂ (mean RL = 190 m). Only a small part of the range is used at a time: on a weekly basis, ♀♀ have a mean RL of 12 m and then move to an adjacent part of the range. Males have a mean weekly RL of 68 m; the range of a ♂ overlaps that of several ♀♀ so each ♀ is visited sequentially. Fat Sand Rats have to move (or ‘drift’) from one part of the range to another as they ‘eat out’ one patch of saltbushes and move on to another. Range lengths of juveniles when they are dispersing are larger than those of adults (e.g. juvenile ♂♂, mean 233 m; juvenile ♀♀, mean 208 m) (Daly & Daly 1975b).

Adult ♂♂ tend to be aggressive to juvenile ♂♂, chasing them from their home-range (Daly & Daly 1975b). Fat Sand Rats make sonic and ultrasonic squeals, associated sometimes with foot-drumming, when a conspecific is nearby. Predator warning squeals are brief, and produced close to the burrow (Bridelance 1989). Faeces and urine are used for marking the home-range (Fichet-Calvet *et al.* 1999b).

Reproduction and Population Structure Pregnancies occur during the cooler dry months of the year (Sep–Apr) with peaks of births in Oct and Feb (Tunisia: Fichet-Calvet *et al.* 1999a; Egypt:

Osborn & Helmy 1980). In years of low rainfall and low food availability, reproduction is restricted to Jan–Apr. Gestation: 24 days. Litter-size: 4.8 (2–8, n = 34; Fichet-Calvet *et al.* 1999a). Mean litter-size shows seasonal variation: 3.6 (n = 26) in Sep, and 6.0 (n = 18) in Jan–Mar. Weight at birth: 6–7 g. Weaned: Day 15. Adult size: Day 120. Sexual maturity: 3–6 months according to the season of birth. Longevity: 14–18 months (in field), 6 years (in captivity) (M. Kam unpubl.). Interval between litters: 35–44 days.

In Tunisia, age structure of population varies seasonally. In Sep (beginning of reproductive season), population is composed entirely of adult animals; these live and reproduce until the following Mar. Proportion of young increases from Oct to Mar (to max of 72% juveniles). In Mar, breeding population consists of two cohorts: a few old multiparous adults and some young primiparous young adults (born earlier in the season). Most of multiparous adults die at the end of breeding season (Daly & Daly 1975b, Amirat *et al.* 1977, Fichet-Calvet *et al.* 1999a).

Predators, Parasites and Diseases Predators include foxes (*Vulpes vulpes*), dogs, snakes (*Malpolon monspessulanus*) and raptors (*Buteo rufinus*, *Tyto alba*, *Bubo bubo*, *Strix aluco* and *Athene noctua*). Remains of Sand Rats have been found in pellets of Eurasian Eagle-owls *Bubo bubo* or Desert Eagle-owls *B. ascalaphus* (0.6–6% occurrence) in Morocco and Algeria (M. Thévenot pers. comm.). Occurrence in owl pellets is sometimes high (50%, S. Aulagnier pers. comm.). Fat Sand Rats are principal reservoir of a protozoa, *Leishmania major*, causing zoonotic cutaneous leishmaniasis in humans (WHO 1990). During the sylvatic plague cycle, the parasite circulates between the sand rats and sandflies living in the burrows. Bites of sandflies to humans cause cutaneous lesions. Population explosions of Fat Sand Rats increase the risk of transmission of this disease (70,000 cases in Tunisia from 1982 to 2000). Other parasites recorded from Sand Rats include bacteria (*Bartonella* spp., *Borrelia* spp.), Protozoa (*Babesia* spp.) and nematode and cestode worms. It is an important laboratory animal for studying disease such as diabetes.

Conservation IUCN Category: Least Concern.

Fat Sand Rats are common and widespread and not threatened. Control measures may be necessary when population numbers are high.

Measurements

Psammomys obesus

HB (♂♂): 161.4 (116–185) mm, n = 228

HB (♀♀): 156.9 (133–183) mm, n = 200

T (♂♂): 116.7 (88–140) mm, n = 219

T (♀♀): 115.6 (92–135) mm, n = 187

HF (♂♂): 34.5 (33–36) mm, n = 59

HF (♀♀): 34.0 (32–36) mm, n = 44

E (♂♂): 15.5 (14–17) mm, n = 41

E (♀♀): 14.9 (13–16) mm, n = 42

WT (♂♂): 157.6 (82–237) g, n = 229

WT (♀♀): 141.7 (83–220) g, n = 200

GLS (♂♂): 40.9 (36.9–43.0) mm, n = 40

GLS (♀♀): 40.4 (37.1–43.4) mm, n = 59

GWS (♂♂): 24.2 (21.4–26.2) mm, n = 40

GWS (♀♀): 23.4 (21.4–25.4) mm, n = 57

M¹–M³: 6.6 (6.0–7.4) mm, n = 100

Auditory bulla: 13.3 (12.3–14.4) mm, n = 73

Tunisia (40 km south of Sidi Bouzid; E. Calvet unpubl.)

Auditory bulla: Egypt (Osborn & Helmy 1980)

Key References Daly & Daly 1974, 1975b; Fichet-Calvet *et al.* 1999a, b, 2000; Petter 1961.

E. Fichet-Calvet

***Psammomys vexillaris* PALE SAND RAT (LESSER SAND RAT)**

Fr. Rat des sables pâle; Ger. Dünne Sandratte

Psammomys vexillaris Thomas, 1925. Ann. Mag. Nat. Hist., ser. 9, 16: 198. Bondjem, Libya.

Taxonomy Although *vexillaris* is sometimes considered synonymous with *obesus*, Ranck (1968) and Cockrum *et al.* (1977) consider, on the basis of skull morphology and chromosome numbers, that *vexillaris* is a valid species. Kowalski & Rzebik-Kowalska (1991) placed *vexillaris* as a synonym of *P. obesus* and therefore did not recognize this species in Algeria. Musser & Carleton (2005) recognize *P. vexillaris* pending revision of geographic variation in *P. obesus*. Synonyms: *edusa*. Subspecies: none. Chromosome number: 2n = 46, FN = 78.

Description Medium-sized gerbil, similar in form to *P. obesus* but smaller and paler. Dorsal pelage gold. Flanks and ventral pelage cream (or white). Ears small, hairy; postauricular patch absent. Fore- and hindlimbs short with white hairs on the inner surfaces. Soles of feet partly haired, claws dark. Tail long (ca. 86% of HB), hairy with a terminal pencil. Skull comparable to *P. obesus* but smaller; auditory bullae inflated (ca. 39% of GLS); upper incisors smooth, without groove. Nipples: not known.



Psammomys vexillaris

Geographic Variation None recorded.

Similar Species

Psammomys obesus. Usually larger, ventral pelage pale ochre; hindlimb buffy on inner surface; Mauritania and Morocco to Egypt and Sinai.

Meriones spp. Larger; dorsal pelage darker but with white ventral pelage; ear larger; sympatric throughout most of geographic range.

Distribution Endemic to Africa. Mediterranean Coastal and Sahara Arid BZs close to the Mediterranean Sea in E Algeria to W Libya. Recorded near Biskra, E Algeria (Thomas 1925); near Tozeur, Tunisia (Cockrum *et al.* 1977); and near Tripoli, Libya (Thomas 1925, Ranck 1968). Distribution of *P. vexillaris* is totally within the distribution of *P. obesus*.

Habitat Poorly known: alluvial soils on roadsides and hillocks (Ranck 1968). Inhabits sandier substrates than *P. obesus* (Cockrum *et al.* 1977).

Abundance Probably rare; known only from a few specimens.

Remarks Apparently no other information available.

Conservation IUCN Category: Data Deficient.

Measurements

Psammomys vexillaris

HB: 122 (115–130) mm, n = 7

T: 106 (80–120) mm, n = 7

HF: 31 (30–35) mm, n = 7

E: 11 (10–12) mm, n = 7

WT: n. d.

GLS: 34.8 (33.0–37.0) mm, n = 7

GWS: 21.5 (19.6–23.1) mm, n = 5

M¹–M³: 5.7 (5.2–5.9) mm, n = 7

Auditory bulla: n. d.

Nefta, Tunisia (MNHN)

Key References Cockrum *et al.* 1977; Kowalski & Rzebik-Kowalska 1991.

E. Fichet-Calvet

GENUS *Sekeetamys*

Bushy-tailed Jird

Sekeetamys Ellerman, 1947. Proc. Zool. Soc. Lond. 117: 271. Type species: *Gerbillus calurus* Thomas, 1892.

A monotypic genus distributed mainly in the Middle East with its western boundary in Egypt. The single species in the genus (*S. calurus*) occurs only in rocky habitats in semi-arid and arid environments. See species profile for further details.



Sekeetamys calurus.

The status of the genus is uncertain. Although the type for the genus was described as a *Gerbillus*, it was placed in a new genus, *Sekeetamys*, by Ellerman (1940). Other authorities have considered *calurus* as a species of *Gerbillus*, *Dipodillus* or *Meriones*. The genus is phylogenetically close to *Meriones* (Pavlinov *et al.* 1990) and also to *Microdillus* and *Gerbillus* (Tong 1989). The genus shows extensive chromosomal rearrangements, more so than in related genera, as well as special morphological features; on cytogenetic and allele evidence, it is closely related to *Psammomys* and *Meriones*, and less closely to *Desmodillus* (Qumsiyeh & Chesser 1988).

The distinguishing characters of the genus are the long very hairy tail, long narrow hindfeet, naked soles, large auditory bullae and narrow interorbital constriction. The teeth are intermediate between *Gerbillus* and *Meriones*. The single species is *Sekeetamys calurus*. See also Table 27.

Christiane Denys

Sekeetamys calurus BUSHY-TAILED JIRD

Fr. Gerbille à queue touffue; Ger. Bilchrennmaus

Sekeetamys calurus (Thomas, 1892). Ann. Mag. Nat. Hist., ser. 6, 9: 76. Tor, Sinai, Egypt.

Taxonomy Originally described in genus *Gerbillus*. Darker individuals from the Eastern Desert of Egypt described as a separate species, *S. mackrami* (Setzer 1961), are now recognized as a subspecies (Osborn & Helmy 1980). Synonyms: *mackrami*. Subspecies: two. Chromosome number: $2n = 38$, $aFN = 70$ (Qumsiyeh & Chesser 1988).

Description Medium-sized rodent with long bushy black tail, with white at tip. Pelage long (ca. 18–20 mm), soft, fine and dense. Dorsal pelage pale brownish-yellow to sandy-buff, speckled with black; hairs grey at base, with yellowish subterminal band and black tip. Flanks paler, with yellow or orange line from wrist to ankle. Ventral pelage pure white. Head similar in colour to back. Eyes large, dark. Ears large, darkly pigmented, rounded at tip, with sparse short hairs. Very long coarse vibrissae (up to 60 mm), mostly black, some white. Hindfeet long and narrow; upper surface with dense white hairs; soles naked. Tail very long (ca. 120% of HB), bushy throughout its length, densely covered with long black hairs, white at tip; tail is unlike that of any other species of gerbil. Skull: auditory bullae inflated, supraorbital and cranial ridges conspicuous, zygomatic arches compressed, rostrum long and narrow, interorbital constriction narrow, upper incisors opisthodont each with single longitudinal groove, molar teeth prismatic (Figure 56, see also Table 27). Nipples: $2 + 2 = 8$.

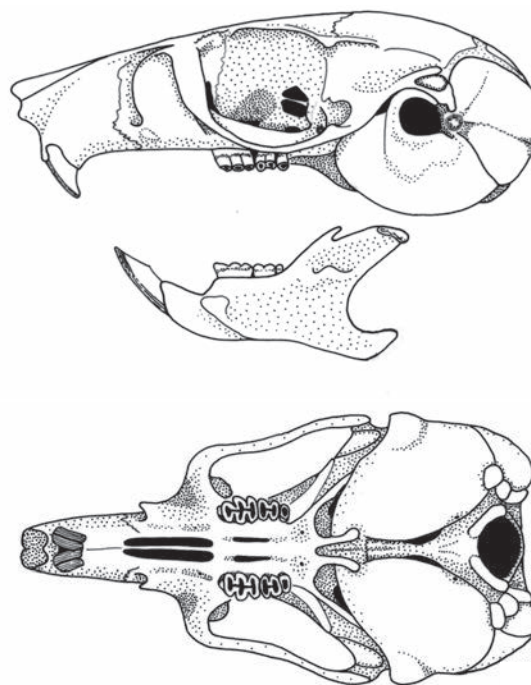


Figure 56. Skull and mandible of *Sekeetamys calurus* (BMNH 12.11.19.1).

Geographic Variation

S. c. calurus: Sinai Peninsula, Egypt. Paler dorsal pelage, sometimes with broad dark mid-dorsal stripe.

S. c. mackrami: Eastern Desert (between Nile R. and Red Sea coast), Egypt. Darker dorsal pelage with narrow dark mid-dorsal stripe.

Similar Species

Eliomys melanurus. Black bushy tail without white tip, black eye-ring and black stripe from back of eye to base of ear, auditory bullae only slightly inflated; mesic and semi-arid habitats.

Meriones spp. Sparsely haired pale tail with black pencil at tip, auditory bullae inflated but larger than in *Sekeetamys*; semi-arid and arid habitats.

Distribution Sahara Arid BZ. Recorded from Egypt (Eastern Desert and Sinai) and extreme NE Sudan. Extraliminally recorded from S Israel, Jordan and Saudi Arabia.

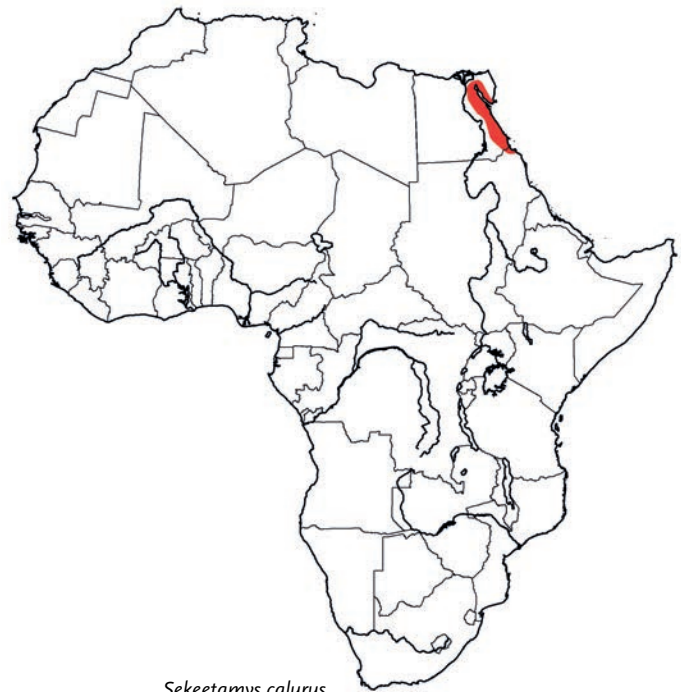
Habitat Rocky areas, sandstone cliffs, crevices in granite and amongst boulders in arid regions; also mountain regions in Sinai. Not recorded from sandy areas.

Abundance Uncertain; recorded as moderately abundant in Israel (Zahavi & Wahrman 1957). In Negev Highlands, Israel, density is 0.8–3.0 ind/ha; populations tend to be stable throughout the year (Shenbrot *et al.* 1999a).

Adaptations Nocturnal. Very agile; climbs rapidly on boulders and rock faces. During day rests in crevices of rocks and under boulders; does not dig burrows. At night, active for about 10.5 hours (Degan *et al.* 1986). During locomotion, the tail is held upright and curved forward in a squirrel-like fashion, and at times locomotion is bipedal. In Egypt, coexists with other rock-adapted species including *Eliomys quercinus*, *Acomys cahirinus*, *A. russatus* and *Gerbillus dasyurus* (Osborn & Helmy 1980).

Metabolic rate (as measured by oxygen consumption) is 31% (Degan *et al.* 1986) to 44% (Haim & Borut 1986) below predicted level at the thermoneutral zone ($T_a = 34\text{--}36^\circ\text{C}$) and variable depending on environmental conditions and temperature in different habitats. Food consumption is low (when compared with non-arid species of similar size). The dense pelage provides insulation against cold when active at night, yet thermal conductance is higher than expected (in spite of the dense pelage) enabling dissipation of body heat when T_a is high. Studies on water relations indicate that water flux was 99% of that predicted, and that *S. calurus* does not show any special adaptations for water conservation. The combination of a high proportion of insects in the diet, low food intake, relatively low metabolic rate and nocturnal activity (even though T_a is cold at night during some seasons) enables survival in an arid environment where resources are scarce (Degan *et al.* 1986, Haim & Borut 1986); this strategy for survival is quite different to that of granivorous desert rodents, which eat a low-water diet and exhibit many water-conservation abilities.

Foraging and Food Omnivorous. Detailed analysis of diet not available. Individuals trapped in crevices that contained parts of seeds and seed capsules, as well as bits of succulent plants. Insects



Sekeetamys calurus

probably supply 87% of food in wild-living individuals (Degan *et al.* 1986), although stomach contents of specimens (from Saudi Arabia) contained only green plant material (Nader 1974). Captive individuals ate cockroaches and crickets (Osborn & Helmy 1980).

Social and Reproductive Behaviour Mobility in ♂♂ greater than ♀♀. In ♂♂, mean distance between captures was 57 m (max 332 m); in ♀♀ 20 m (max 72 m). Adult ♂♂ have larger home-ranges (ca. 10–23 ha) than adult ♀♀ (0.7–0.8 ha) (Shenbrot *et al.* 1999a).

Reproduction and Population Structure Flower (1932) reported litters from captive animals every month of the year in Egypt except Sep. Litter-size (in captivity): 2.8 ($n = 47$ litters; max 6/litter [$n = 2$]). In the wild, period of reproduction appears to be limited and variable, and dependent on local conditions; longevity is probably high and reproductive success is low in natural conditions (Shenbrot *et al.* 1999a). Sex ratio of individuals captured in the Eastern Desert was 13 ♂♂ : 11 ♀♀ (Osborn & Helmy 1980).

Predators, Parasites and Diseases Preyed on by Eurasian Eagle-owls *Bubo bubo* at Gebel Migif, Egypt; remains of ten individuals found in pellets ($n = 45$ small mammals) (Goodman 1986). Four species of fleas recorded – *Xenopsylla nubica*, *X. dipodilli*, *X. conformus* and *Nesopsylla theodori* – from individuals near St Catharine's Monastery, Sinai, Egypt (Hoogstraal & Traub 1965a). Some of these species of fleas are also recorded from *Meriones crassus*.

Conservation IUCN Category: Least Concern.

Measurements

Sekeetamys calurus calurus

HB: 118.9 (98–128) mm, $n = 25$

T: 144.4 (131–164) mm, $n = 20$

HF: 33.1 (31–35) mm, $n = 25$

E: 21.4 (20–23) mm, n = 25
 WT: 41.4 (26.6–49.8) g, n = 17*
 GLS: 35.8 (34.5–37.4) mm, n = 20
 GWS: 18.2 (17.2–19.1) mm, n = 10
 M¹–M³: 5.2 (4.8–5.8) mm, n = 17
 Auditory bulla: 11.7 (11.0–12.7) mm, n = 25

Egypt (Osborn & Helmy 1980)

* = *S. c. makrami*

Key References Harrison & Bates 1991; Osborn & Helmy 1980.

Christiane Denys

GENUS *Taterillus*

Taterils (Gerbils)

Taterillus Thomas, 1910. Ann. Mag. Nat. Hist., ser. 8, 6: 222. Type species: *Gerbillus emini* Thomas, 1892.



Taterillus emini.

The genus *Taterillus* is endemic to Africa and contains eight species (Table 28). It has a widespread distribution, and occurs in the Sahel, Sudan and Guinea Savanna BZs from Mauritania to Somalia, from the Tilemsi Valley in N Mali to SW Nigeria, and from C Sudan to C Kenya. Typical habitats range from sandy dunes, thorny scrubs and woodland savannas, as well as fields, gardens and even human dwellings. Three species have fairly wide distributions (*T. gracilis* in West Africa, *T. congicus* in central Africa and *T. emini* in East Africa); the others mostly have very restricted distributions.

Species in the genus are small to medium-sized gerbils. Dorsal pelage is pale yellow to reddish-brown; ventral pelage, hands and feet are white. The head is characterized by a pointed muzzle, large eyes and elongated ears. The tail is longer than head and body, with soft hairs on its whole length, and a long terminal pencil of darker hairs. The hindfeet are long, naked and the soles are dark. The genus differs from *Gerbilliscus* (formerly *Tatera*) by overall smaller size, a more gracile appearance, elongated anterior palatal foramina, which end well forward of M¹, and longer slit-like posterior palatal foramina. It differs from *Gerbillus* by overall larger size, larger ears and longer and naked soles on the hindfeet; the skull is more robust with longer posterior palatal foramina and laminated molars without longitudinal crests connecting tooth cusps (Figure 57).

These gerbils are nocturnal and terrestrial. They dig burrows of various depth and complexity, and feed on seeds, stems, leaves and insects. They are often quite common, and sometimes subject to local

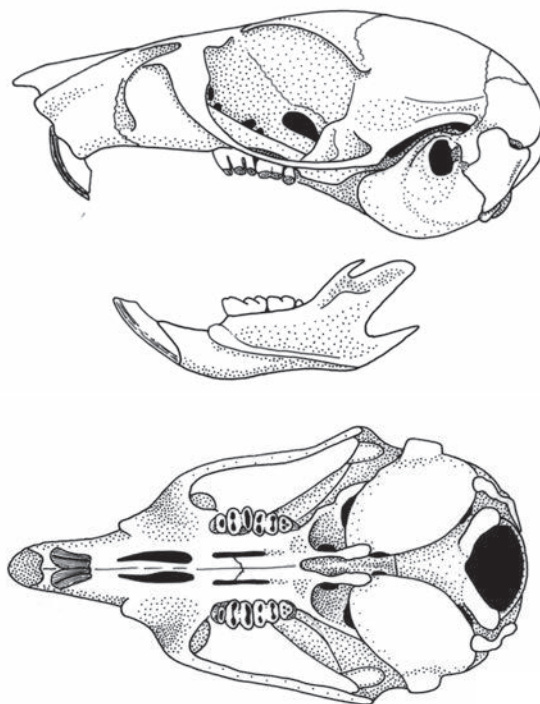


Figure 57. Skull and mandible of *Taterillus gracilis* (HC 1079).

population explosions that make them potential pests in agricultural fields. Cycles of abundance, as well as some eco-ethological and physiological attributes, are known for *T. gracilis* and *T. pygargus* in Senegal and for *T. petteri* in Burkina.

The taxonomy of the genus depends heavily on chromosomal information, as most species are very similar morphologically. Chromosome numbers are species-specific and vary from $2n = 14/15$ in *T. tranieri* to $2n = 54$ in *T. congicus*. One current problem concerns the characterization of *T. harringtoni* relative to *T. emini*: a karyotype of $2n = 44$ chromosomes has been attributed to both, and further studies are needed to clearly diagnose these two species; here, *harringtoni* is considered as a synonym of *T. emini*. Further cytotaxonomic investigations will undoubtedly lead to the discovery of new biological species, as suggested by the very complex chromosomal evolution of this group.

The genus can be divided in two distinct lineages as some species are characterized by a strong chromosomal synapomorphy, i.e. a double autosome–gonosome translocation. The males of one lineage (*T. arenarius*, *T. gracilis*, *T. petteri*, *T. pygargus*, *T. tranieri*) are

Table 28. Species in the genus *Taterillus*. Arranged in alphabetical order.

| Species | Chromosome number | Dorsal pelage | Notes |
|---------------------|------------------------------|---------------------------------|--|
| <i>T. arenarius</i> | 2n = 30 (♂ ♂), 2n = 31 (♀ ♀) | Pale sandy-yellow | Mauritania (Mali, Niger) |
| <i>T. congicus</i> | 2n = 54 | Chocolate-brown – reddish-brown | Central African Republic, Chad (Cameroon, Sudan, Uganda) |
| <i>T. emini</i> | 2n = 44 | Reddish-brown – orange | Sudan and Sahel BZs of eastern Africa, Somalia–Masai BZ |
| <i>T. gracilis</i> | 2n = 36 (♀ ♀), 2n = 37 (♂ ♂) | Reddish-yellow | Sudan and Sahel BZs of western Africa; widespread |
| <i>T. lacustris</i> | 2n = 28 (♀ ♀), 2n = 29 (♂ ♂) | Tawny | Area around L. Chad |
| <i>T. petteri</i> | 2n = 18 (♀ ♀), 2n = 19 (♂ ♂) | Pale orange – cinnamon | Sudan Savanna BZ (Burkina, Mali, Niger) |
| <i>T. pygargus</i> | 2n = 22 (♀ ♀), 2n = 23 (♂ ♂) | Yellow, reddish-brown | Sudan Savanna BZ (Senegal, Niger) |
| <i>T. tranieri</i> | 2n = 14 (♀ ♀), 2n = 15 (♂ ♂) | Buffy-brown | Sahel Savanna BZ (Mali) |

characterized by a set of three (X,Y1,Y2) sex chromosomes, whereas the males of the other lineage (*T. congicus*, *T. emini/harringtoni*, *T. lacustris*) are characterized by the classical XY sex chromosomes. (Females retain the usual XX sex chromosomes.) Again, the only non-ambiguous character to distinguish between species in the genus is the karyotype. Multivariate analyses of morphometric data have

been said to be of help, a result that was refuted by recent studies on karyotyped specimens.

The eight species are distinguished primarily on chromosome number but also on size and distribution (see also Table 28).

Laurent Granjon & Gauthier Dobigny

Taterillus arenarius SAND TATERIL (ROBBINS’S TATERIL)

Fr. Tâtérille des sables; Ger. Sahel-Rennmäuschen

Taterillus arenarius Robbins, 1974. Proc. Biol. Soc. Wash., 87: 399. Tiguent, Trarza Region, Mauritania.

Taxonomy Chromosome number distinguishes this species from its sibling species *T. gracilis*, *T. petteri*, *T. pygargus* and *T. tranieri* (Matthey 1969, Petter 1970, Volobouev & Granjon 1996, Dobigny *et al.* 2003). Synonyms: none. Chromosome number: 2n = 30 (♀ ♀), 2n = 31 (♂ ♂).

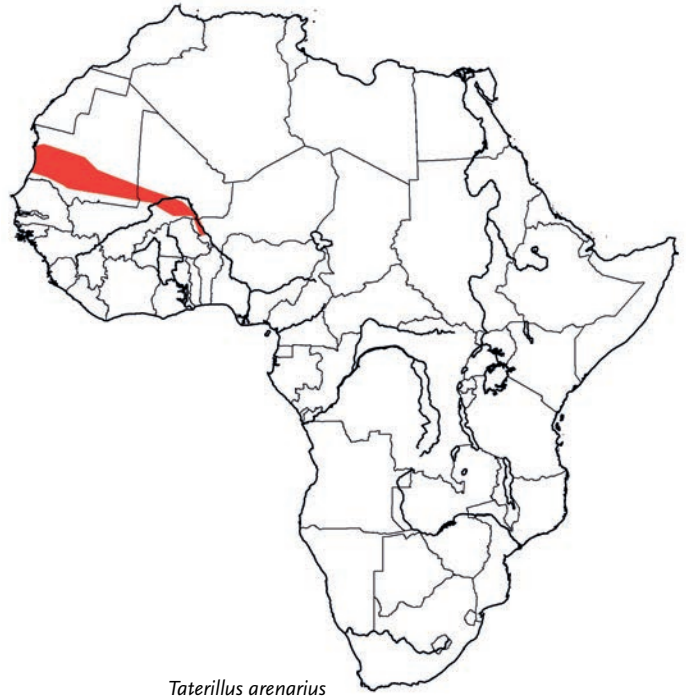
Description Medium-sized gerbil. Dorsal pelage pale sandy-yellow; hairs grey at base. Ventral pelage white, clearly delineated from dorsal pelage on flanks. Cheeks white, with white supraorbital and postorbital patches. Muzzle pointed, often with dark markings on upper part of nasal region. Large elongated ears. Large eyes. Fore- and hindfeet white. Hindfeet relatively long; soles dark and naked or nearly so; three median toes of similar length, Digit 1 short; rather long claws. Tail long (ca. 130–140% of HB) covered by short hairs, long terminal pencil of dark blackish-brown hairs. Nipples: 2 + 2 = 8.

Geographic Variation None recorded.

Similar Species

- T. gracilis*. Similar in morphology and size; chromosome number: 2n = 36/37; widely distributed in West Africa.
- T. petteri*. Similar in morphology and size; chromosome number: 2n = 18/19; Mali, Niger and Burkina mostly south of Niger R.
- T. pygargus*. Similar in morphology and size; chromosome number: 2n = 22/23; Senegal and Niger.
- T. tranieri*. Similar in morphology and size; chromosome number: 2n = 14/15; only in S Mauritania and W Mali.

Distribution Endemic to Africa. Sahel Savanna BZ. Presence confirmed (by chromosome number) only in Mauritania (Matthey 1969, Petter 1970, Volobouev & Granjon 1996). Recorded eastwards to Mali and Niger by Robbins (1974) on the basis of morphological



characters, but not yet confirmed by karyology (L. Granjon unpubl., Dobigny *et al.* 2002a).

Habitat Sandy-clay plains and inland dunes (Granjon *et al.* 1997b). Trapped in dry areas where average annual rainfall does not exceed 400 mm.

Abundance Densities probably low (Granjon *et al.* 1997b).

Remarks Found in pellets of Barn Owls *Tyto alba*; <3% of prey (Granjon *et al.* 2002b).

Conservation IUCN Category: Least Concern.

Measurements

Taterillus arenarius

HB: 113, 115 mm, n = 2

T: 156, 155 mm, n = 2

HF: 33, 33 mm, n = 2

E: 20, 20 mm, n = 2

WT: 20 g, n. d., n = 2

GLS: 33.6, 33.8 mm, n = 2

GWS: 17.0 mm, n. d., n = 2

M¹–M³: 4.8, 4.8 mm, n = 2

Auditory bulla: n. d.

Mauritania, MNHN

One ♂, one ♀ (karyotyped); for data on a larger sample of non-karyotyped individuals, see Robbins 1974

Key Reference Robbins 1974.

Laurent Granjon & Gauthier Dobigny

Taterillus congicus CONGO TATERIL

Fr. Tâtérille du Congo; Ger. Kongo-Rennmäuschen

Taterillus congicus Thomas, 1915. Ann. Mag. Nat. Hist., ser. 8, 16: 147. Poko, Upper Uele, DR Congo.

Taxonomy Synonyms: *clivus*. Subspecies: none. Chromosome number: 2n = 54 (Matthey & Petter 1970, Genest & Petter 1973, Tranier *et al.* 1973, G. Dobigny & L. Granjon unpubl.). Serum proteins also characterize this species (Tranier *et al.* 1973).

Description Medium-sized gerbil. Dorsal pelage chocolate- or reddish-brown to yellow; hairs grey at base. Ventral pelage white. Cheeks white; white supraorbital, postorbital and postauricular patches, more or less marked. Muzzle pointed. Ears large and elongated. Eyes large. Fore- and hindfeet white. Hindfeet long and narrow; soles dark and naked with narrow transverse band of white hairs behind the digits in some individuals; three median digits of hindfeet of similar length, Digit 1 shorter; rather long claws. Tail long (ca. 130–140% of HB), covered by short hairs, long terminal pencil of dark hairs. Nipples: 2 + 2 = 8.

Geographic Variation None recorded.

Similar Species

T. emini. Similar in morphology; chromosome number: 2n = 44; distributed from Somalia to Central African Republic.

T. lacustris. Similar in morphology; chromosome number: 2n = 29; restricted to L. Chad region.

Distribution Endemic to Africa. Widespread in parts of Sudan Savanna and Guinea Savanna BZs and parts of Northern Rainforest–Savanna Mosaic. Presence confirmed (by karyology) in Central African Republic and Chad (Matthey & Petter 1970, Genest & Petter 1973, Tranier *et al.* 1973, G. Dobigny & L. Granjon unpubl.) and N DR Congo (type locality). Presence suspected in Cameroon, Uganda and Sudan (Robbins 1977).

Habitat Thorn bush savannas in Sudan Savanna BZ, wooded savannas in Guinea Savanna BZ, and savanna islands in secondary rainforest habitats (Genest & Petter 1973). In SE Chad, found on sandy and sandy-clay soils with dense herbaceous cover and *Combretum* trees (C. Denys unpubl.).

Abundance Uncertain although locally common. Less common where syntopic with *Gerbilliscus* (= *Tatera*) spp. (ratio 1 *Taterillus* : 5 *Gerbilliscus*) in *Terminalia* savanna of S Central African Republic (Genest & Petter 1973).

Remarks Terrestrial and nocturnal. Digs burrows. Embryo number: 3 and 4 (n = 2); only 2 (of 30) ♀♀ were pregnant in Feb (Zakouma N. P., Chad; C. Denys unpubl.).

Conservation IUCN Category: Least Concern.

Measurements

Taterillus congicus

HB: 119.7 (86–174) mm, n = 59

T: 159.3 (130–195) mm, n = 39

HF: 33.1 (29.5–36) mm, n = 59



Taterillus congicus

E: 19.7 (16–23) mm, n = 59
 WT: 50.5 (23–77) g, n = 32
 GLS: 33.1 (30.2–34.7) mm, n = 18
 GWS: 17.5 mm (15.3–19.2), n = 14
 M¹–M³: 5.1 (4.8–5.4) mm, n = 18
 Auditory bulla: n. d.

Chad and Central African Republic (only karyotyped individuals, MNHN)

Key Reference Genest & Petter 1973.

Laurent Granjon & Gauthier Dobigny

Taterillus emini **EMIN'S TATERIL**

Fr. Tâtérille d'Emin; Ger. Emins Rennmäuschen

Taterillus emini (Thomas, 1892). Ann. Mag. Nat. Hist., ser. 6, 9: 78. Wadelai, Uganda.

Taxonomy Originally described in the genus *Gerbillus*. The relationship between this species and *harringtoni* is uncertain. A karyotype of $2n = 44$ chromosomes has been associated with *T. emini* (Matthey 1969, Robbins 1973), but also with *harringtoni* (Robbins 1977). The difference between these two species is mainly one of size (skull, bullae, incisors), a character that has proved to be of little help in species allocation. Here, *harringtoni* is considered as a junior synonym of *T. emini*. Synonyms (of *emini*): *anthonyi*, *butleri*, *gygas*; (of *harringtoni*): *illustris*, *kadugliensis*, *lorenzi*, *lowei*, *melanops*, *meneghetti*, *nubilus*, *osgoodi*, *perluteus*, *rufus*, *tenebricus*, *zammerani*. Subspecies: none. Chromosome number: $2n = 44$.

Description Medium-sized gerbil. Dorsal pelage reddish-brown to orange; hairs grey at base, with reddish-brown to orange tip. Ventral pelage white. Cheeks white, with white eye-ring and usually a white postauricular patch. Muzzle pointed. Ears large and elongated. Eyes large. Fore- and hindfeet white. Hindfeet long and narrow; soles darkly pigmented, naked except for a narrow transverse band of white hairs behind the digits in some individuals; three median digits of hindfeet of similar length, Digit 1 shorter, rather long claws. Tail long (140–150% of HB), with short hairs and long terminal pencil of slightly darker hairs. Nipples: $2 + 2 = 8$.

Geographic Variation None recorded.

Similar Species

T. congicus. Chromosome number: $2n = 54$; Central African Republic, S Chad and N DR Congo.

T. lacustris. Chromosome number: $2n = 29$; restricted to L. Chad region.

Distribution Endemic to Africa. Eastern parts of Sahel Savanna, Sudan Savanna and Guinea Savanna BZs, and Somalia–Masai Bushland BZ. Recorded from Somalia and Central African Republic (Genest & Petter 1973), Ethiopia (Matthey 1969) and Kenya (Robbins 1973). Karyotyped specimens recorded in Somalia to Central African Republic. Suspected to occur in Tanzania, N Uganda, NE DR Congo, Sudan and Chad (Robbins 1977), but no chromosomal data to confirm presence in these countries.

Habitat Uncertain. Collections from Somalia, Ethiopia and Central African Republic suggest an association with savanna habitats liable to flooding (Genest & Petter 1973).

Abundance No reliable information. Apparently much less abundant than *T. congicus* in Central African Republic (Genest & Petter 1973).

Remarks Probably terrestrial and nocturnal, as in other species of the genus; accurate information lacking.

Conservation IUCN Category: Least Concern.

Measurements

Taterillus emini

HB: 107.3 (105–110) mm, n = 3

T: 155 (150–160) mm, n = 3

HF: 31 (30–32) mm, n = 3

E: 18.7 (17–20) mm, n = 3

WT: n. d.

GLS: 30.1 (29.3–30.5) mm, n = 3

GWS: 17.1 (16.8–17.6) mm, n = 14

M¹–M³: 4.6 (4.3–4.8) mm, n = 3

Auditory bulla: n. d.

Somalia (n = 1), Central African Republic (n = 1), Ethiopia (n = 1);



Taterillus emini

MNHN; one ♂, two ♀ (karyotyped)

Key References Genest & Petter 1973; Robbins 1973.

Laurent Granjon & Gauthier Dobigny

Taterillus gracilis **SLENDER TATERIL (GRACILE TATERIL)**

Fr. Tâtérille gracile; Ger. Schlankes Rennmäuschen

Taterillus gracilis (Thomas, 1892). Ann. Mag. Nat. Hist., ser. 6, 9: 77. Gambia.

Taxonomy Originally described in the genus *Gerbillus*. Chromosome number (reviewed in Volobouev & Granjon 1996, Dobigny *et al.* 2003) and blood proteins (Tranier *et al.* 1973, Baron *et al.* 1974) distinguish this species from its sibling species *T. pygargus*, *T. arenarius* and *T. petteri*. Robertsonian polymorphism suspected (individuals with $2n = 36-39$, Matthey & Jotterand 1972, Dobigny *et al.* 2002a). Synonyms: *angelus*, *nigeriae*. Subspecies: none. Chromosome number: $2n = 36$ (♀ ♀), $2n = 37$ (♂ ♂).

Description Small- to medium-sized gerbil. Dorsal pelage yellow to reddish-brown; hairs grey at base with golden-yellow to orange-brown tip. Ventral pelage white, clearly delineated from dorsal pelage on flanks. Cheeks white; white supraorbital and postorbital patches. Muzzle pointed, often with dark blackish-brown markings on upper part of nasal region. Large elongated ears; large eyes. Fore- and hindfeet white. Hindfeet relatively long, soles dark and naked or nearly so; three median digits of similar length; Digit 1 short; rather long claws. Tail long (ca. 130–140% of HB), covered by short hairs, long terminal pencil of dark blackish-brown hairs. Nipples: $2 + 2 = 8$.

Geographic Variation None recorded.

Similar Species

T. arenarius. Similar in morphology and size; chromosome number: $2n = 30/31$; Mauritania only.

T. petteri. Similar in morphology and size; chromosome number: $2n = 18/19$; Mali, Niger and Burkina mostly south of Niger R.

T. pygargus. Similar in morphology and size; chromosome number: $2n = 22/23$; Senegal and Niger.

T. tranieri. Similar in morphology and size; chromosome number: $2n = 14/15$; only in S Mauritania and W Mali. Soil characteristics may help distinguish between sympatric *T. gracilis* and *T. pygargus* (Hubert *et al.* 1977).

Distribution Endemic to Africa. Widely distributed in Sahel Savanna and Sudan Savanna BZs. Presence confirmed (by karyology) in Senegal (N of Gambia R.), Burkina, Mali, SW Niger, N Côte d'Ivoire, N Ghana, N Benin and SW Nigeria (Matthey & Petter 1970, Matthey & Jotterand 1972, Robbins 1974, Robbins & Van der Straeten 1996, Capanna, Dobigny, Granjon, Sicard and Tranier unpubl.). Also present in the Gambia (type-locality) and Togo (Robbins & Van der Straeten 1996).

Habitat Woodland savanna and thorny scrub where average annual rainfall is over 400 mm. Found on soils relatively rich in clay,



Taterillus gracilis

which retain water, and often associated with plants of Combretaceae (Hubert 1977, Hubert *et al.* 1977, Sicard *et al.* 1988). Frequently common in fields and gardens.

Abundance Often common when environmental conditions are favourable, and potentially subject to local large fluctuations in population numbers. In Bandia, Senegal (Nov 1975 to Mar 1981), average density 5.1/ha, varying between 0.4/ha during drought and 44/ha during optimal conditions (Hubert 1982). In Nigeria, widespread but localized, and considerably less common than *Gerbillurus kempi* in most savanna habitats (Happold 1975b, 1987).

Adaptations Terrestrial and nocturnal. Digs rather vertical and deep (55 cm) burrows without ramifications (Hubert *et al.* 1977). During favourable conditions (wet season and beginning of dry season), stores body fat and has high water turnover (up to 210 ml/kg/day). During the hot dry season, utilizes body fat and has low water turnover (down to 110 ml/kg/day; Hubert & Demarne 1981, Sicard *et al.* 1988, Sicard & Papillon 1996).

Foraging and Food Omnivorous. Feeds primarily on seeds, stems and leaves, but also eats insects, especially in the dry season.

Consumes millet when available (Senegal; Hubert *et al.* 1981b, Moro & Hubert 1983).

Social and Reproductive Behaviour Short-term movements of 20–40 m, within home-ranges of 700 m² (♀ ♀) to 750 m² (♂ ♂). Home-ranges of ♂ ♂ and ♀ ♀ often overlap, while home-ranges of ♂ ♂ rarely overlap. Movements increase during the reproductive season (Senegal; Hubert 1977).

Reproduction and Population Structure In Senegal, reproductive season quite long, usually starting during the wet season and extending more or less into the dry season, depending on resource availability and population densities. Breeding ♀ ♀ recorded during 3–4 months of the year when environmental conditions are poor (e.g. 1976/1977) and up to 10 months when environmental conditions are good (e.g. 1978/1979; Hubert 1982, Moro & Hubert 1983). Gestation: ca. 30 days. Embryo number (natural conditions): 1–8. Litter-size (in captivity): 3–5 (Hubert & Adam 1975, Hubert 1982). Sexual maturity: 12 weeks. Longevity up to two years in the wild, up to four years in captivity (Hubert 1982). Mortality rate may reach 30% per month (Hubert 1977). Mortality rate is higher for cohorts born during the dry season than for cohorts born during the wet season (Hubert 1982).

Predators, Parasites and Diseases No information.

Conservation IUCN Category: Least Concern.

Probably not threatened due to widespread distribution, commonness and ability to live in cultivated areas.

Measurements

Taterillus gracilis

HB: 114.6 (96–130) mm, n = 39

T: 156.3 (135–176) mm, n = 23

HF: 30.4 (29–32.5) mm, n = 40

E: 19.3 (16–23) mm, n = 40

WT: 62.3 (45–81) g, n = 12

GLS: 31.9 (29.7–33.8) mm, n = 32

GWS: 17.8 (15.5–19.0) mm, n = 24

M¹–M³: 4.9 (4.6–5.2) mm, n = 32

Auditory bulla: n. d.

Senegal, Burkina, Mali, Côte d'Ivoire, Niger (MNHN, karyotyped individuals only)

Key References Hubert 1977, 1982; Matthey & Jotterand 1972.

Laurent Granjon & Gauthier Dobigny

Taterillus lacustris LAKE CHAD TATERIL

Fr. Tâtérille du Lac Chad; Ger. Tschadsee-Rennmäuschen

Taterillus lacustris (Thomas and Wroughton, 1907). Ann. Mag. Nat. Hist., ser. 7, 19: 370. L. Chad (Kaddai), Nigeria.

Taxonomy Originally described in the genus *Tatera*. Rosevear (1969) placed *lacustris* as a synonym of *T. gracilis*. Retained as a valid species by Petter (1975a), Robbins (1977) and Musser & Carleton (1993, 2005). Synonyms: none. Chromosome number: 2n = 28 (♀ ♀), 2n = 29 (♂ ♂) (Tranier *et al.* 1973, J.-M. Duplantier & K. Bâ unpubl.).

Description Small gerbil. Dorsal pelage tawny; hairs grey at base with orange to tawny-brown tip. Ventral pelage white, clearly delineated from dorsal pelage on flanks. Cheeks white; white supraorbital and postorbital patches. Muzzle pointed, often with dark blackish-brown markings on upper part of nasal region. Ears large and elongated. Eyes large. Fore- and hindfeet white. Hindfeet relatively long, soles dark and naked or nearly so; three median digits of similar length, Digit 1 short; rather long claws. Tail long (ca. 130–140% of HB), covered by short hairs, long terminal pencil of slightly darker brown hairs. Nipples: 2 + 2 = 8 (most probably).

Geographic Variation None recorded.

Similar Species

T. emini. Chromosome number: 2n = 44; on average slightly smaller; widely distributed to the east of L. Chad.

T. congicus. Chromosome number: 2n = 54; on average slightly larger in some measurements; distributed in S Chad, Central African Republic and N DR Congo.



Taterillus lacustris

Two other chromosomal forms, with chromosome number 2n = 22/23 and 2n = 24/25, have been described from the northern edge of L. Chad and undoubtedly correspond to new species (Dobigny *et al.* 2002a, Granjon & Dobigny 2003).

Distribution Endemic to Africa. Sahel Savanna and Sudan Savanna BZs near to L. Chad. Only known from NE Nigeria, and from N Cameroon just south of L. Chad.

Habitat Bushes, fallow lands and edges of fields in N Cameroon (J.-M. Duplantier & K. Bâ unpubl.).

Abundance No information.

Remarks Probably terrestrial and nocturnal. Some specimens in Nigeria were caught on the shores of L. Chad, which suggests that they may prefer a mesic habitat, or at least access to permanent water (Happold 1987).

Conservation IUCN Category: Least Concern.

The gradual drying of L. Chad during the latter years of the twentieth century may be a threat, especially if this species requires damp mesic conditions.

Measurements

Taterillus lacustris

HB: 116 (105–122) mm, n = 5

T: 151 (145–162) mm, n = 5

HF: 31.2 (30.5–32) mm, n = 4

E: 20 (16–22) mm, n = 5

WT: 45.7 (43–48) g, n = 3

GLS: 29.7, 34.2 mm, n = 2

GWS: ca. 19.7 mm, n = 1

M¹–M³: 5.2, 5.0 mm, n = 2

Auditory bulla: n. d.

Cameroon (MNHN; J.-M. Duplantier & K. Bâ unpubl.; karyotyped specimens only)

Key Reference Tranier *et al.* 1973.

Laurent Granjon & Gauthier Dobigny

Taterillus petteri PETTER'S TATERIL

Fr. Tâtérille de Petter; Ger. Petters Rennmäuschen

Taterillus petteri Gautun, Tranier and Sicard, 1985. Mammalia, 52: 188. Near Oursi Pond (14° 38' N–0° 26' W), Burkina. 330 m.

Taxonomy Belongs to a group of sibling species (*T. pygargus*, *T. arenarius* and *T. gracilis*) distinguishable by their karyotypes (Sicard *et al.* 1988, Volobouev & Granjon 1996). Synonyms: none. Chromosome number: 2n = 18 (♀ ♀), 2n = 19 (♂ ♂).

Description Small to medium-sized gerbil. Dorsal pelage pale orange to cinnamon; hairs grey at base. Ventral pelage white, clearly delineated from dorsal pelage on flanks. Lower part of cheeks white; white postauricular, supraorbital and postorbital patches. Large elongated ears; large eyes. Fore- and hindfeet white; hindfeet long with dark soles. Tail long (ca. 125% of HB), covered with short hairs, long terminal pencil of dark hairs. Nipples: 2 + 2 = 8.

Geographic Variation None recorded.

Similar Species

T. arenarius. Similar in morphology and size; chromosome number: 2n = 30/31; Mauritania only.

T. gracilis. Similar in morphology and size; chromosome number: 2n = 36/37; widely distributed in West Africa.

T. pygargus. Similar in morphology and size; chromosome number: 2n = 22/23; Senegal and Niger.

T. tranieri. Similar in morphology and size; chromosome number: 2n = 14/15; S Mauritania and W Mali.

Distribution Endemic to Africa. Sahel Savanna BZ. Presence confirmed by karyotype data only in Burkina, Niger and Mali, mostly on the right side of Niger R. (Sicard *et al.* 1988, B. Sicard unpubl.).

Habitat Sahel savanna where annual rainfall is 300–500 mm. Occupies sandy veneers, sandy cultivated lands and more rarely sand dunes.



Taterillus petteri

Abundance In N Burkina, more abundant on sandy veneers (0–50 ind/ha) than on sand dunes (0–20 ind/ha); seems not to be subject to local population explosions (Sicard 1987).

Adaptations Terrestrial and nocturnal. In N Burkina, burrows are simple and superficial during the dispersion period (dry cool season; Oct–Jan), more complex, deep and filled with seeds during the pre-aestivation and aestivation periods (cool to hot dry seasons; Jan–May), and intermediate in their characteristics during the

breeding period (wet season; Jun–Sep) (B. Sicard unpubl.). Body water turnover reaches maximal values during breeding period (30–48% of total body water/day), decreases during the dispersion period (ca. 25%) and is extremely low during aestivation (ca. 9%) (Sicard 1992). Due to particular physiological mechanisms, triggering of aestivation occurs prior to the dry and hot season (Sicard & Fuminier 1994), and triggering of reproduction occurs prior to the wet season (Sicard & Fuminier 1996).

Foraging and Food Diet is water-rich (seeds, arthropods and green vegetation) during the wet season and water-poor (seeds) during the dry hot season (Sicard 1987, 1992).

Social and Reproductive Behaviour In N Burkina, solitary and territorial; territories of ♂♂ overlap those of ♀♀ during the breeding season. Home-range varies seasonally: during the dispersion period it is $1875 \pm 168 \text{ m}^2$, increases to $2324 \pm 196 \text{ m}^2$ during the pre-aestivation period, decreases to a minimum during aestivation, and then increases again to $1234 \pm 196 \text{ m}^2$ during the breeding period. Several individuals have been observed to excavate burrows together (B. Sicard unpubl.).

Reproduction and Population Structure In N Burkina, ♀♀ have oestrous cycles throughout the year. Births occur in Jun–Sep. Embryonic scars: 5.4 (3–6), $n = 17$. Litter-size in Burkina: 3 (2–6, $n = 12$; Sicard & Fuminier 1996). One observation in Mali

indicates a litter-size of seven (B. Sicard & L. Granjon unpubl.). In males, endocrine testicular activity (plasma testosterone level) is higher between Apr and Sep ($1.71 \pm 0.22 \text{ ng/ml}$; $n = 15$) than during the rest of the year ($0.46 \pm 0.2 \text{ ng/ml}$; $n = 11$) (B. Sicard & M. Kyelem unpubl.).

Predators, Parasites and Diseases No information.

Conservation IUCN Category: Least Concern.

Measurements

Taterillus petteri

HB: 113.9 (101–135) mm, $n = 16$

T: 139.9 (100–166) mm, $n = 14$

HF: 29.9 (28–35.5) mm, $n = 16$

E: 18.8 (17–20) mm, $n = 16$

WT: 50.1 (30–62) g, $n = 16$

GLS: 31.1 (28.2–33.3) mm, $n = 11$

GWS: 17.5–17.9 mm, $n = 3$

M¹–M³: 4.8 (4.6–5.1) mm, $n = 11$

Auditory bulla: n. d.

Burkina and Mali (MNHN, karyotyped individuals only)

Key References Sicard *et al.* 1988; Sicard & Fuminier 1994.

Bruno Sicard

Taterillus pygargus SENEGAL TATERIL (CUVIER'S TATERIL)

Fr. Tâtérille de Cuvier; Ger. Senegal-Rennmäuschen

Taterillus pygargus (F. Cuvier, 1838). Trans. Zool. Soc. Lond. 2: 142. Saint Louis (?), Senegal.

Taxonomy Chromosome number (review in Volobouev & Granjon 1996, Dobigny *et al.* 2003) and blood proteins (Baron *et al.* 1974) distinguish this species from its sibling species *T. arenarius*, *T. gracilis*, *T. petteri* and *T. tranieri*. Synonyms: none. Chromosome number: $2n = 22$ (♀♀), $2n = 23$ (♂♂).

Description Small gerbil. Dorsal pelage yellow to reddish-brown; hairs grey at base with golden-yellow to orange tip. Ventral pelage white, clearly delineated from dorsal pelage on flanks. Cheeks white; white supraorbital and postorbital patches. Muzzle pointed, often with dark blackish-brown markings on upper part of nasal region. Large elongated ears. Large eyes. Fore- and hindfeet white. Hindfeet relatively long, soles dark and naked or nearly so, three median digits of similar length, Digit 1 short, rather long claws. Tail long (ca. 130–140% of HB), covered by short hairs, long terminal pencil of dark blackish-brown hairs. Nipples: $2 + 2 = 8$.

Geographic Variation None recorded.

Similar Species

T. arenarius. Similar in morphology and size; chromosome number: $2n = 30/31$; Mauritania only.

T. gracilis. Similar in morphology and size; chromosome number: $2n = 36/37$; widely distributed in West Africa. Presence on different soil types (see species profiles) may help distinguish between sympatric *T. gracilis* and *T. pygargus* (Hubert *et al.* 1977).
T. petteri. Similar in morphology and size; chromosome number: $2n = 18/19$; Mali, Niger and Burkina mostly south of Niger R.
T. tranieri. Similar in morphology and size; chromosome number: $2n = 14/15$; S Mauritania and W Mali.

Distribution Endemic to Africa. Sahel Savanna and Sudan Savanna BZs of West Africa. Presence confirmed (by karyology) only in Senegal (Matthey & Jotterand 1972) and Niger (Dobigny *et al.* 2002); said to occur in Mauritania by Robbins (1974) on the basis of morphological characters.

Habitat Bush savanna and thorny scrub where average annual rainfall is ca. 300–800 mm. Inhabits recent sand dunes and soils poor in clay content that drain easily. Found in habitats where *Gutierrezia* sp. and *Acacia albida* are common, as well as habitats dominated by plants of family Poaceae (Hubert *et al.* 1977, Poulet 1982). Also present in cultivated areas.

Abundance Often common when environmental conditions are favourable, and potentially subject to local population explosions. In



Taterillus pygargus

the Sahel Savanna BZ of Senegal (1970–1976), densities varied from 0/ha after the drought of 1972 to 180/ha after the good wet season of 1975 (Poulet 1978). Much more abundant than *T. gracilis* in N Senegal, and becoming less common further south (Poulet 1982).

Adaptations Terrestrial and nocturnal. Digs burrows in sandy soils at periods when soil is not too hard during a short period between the end of the rains and the beginning of the dry season. Burrows have several entrances and ramifications, are usually less than 35 cm deep, but may be deeper during the dry season to reach moister conditions (Hubert *et al.* 1977, Poulet 1982).

Foraging and Food Granivorous and insectivorous (Poulet 1982).

Social and Reproductive Behaviour Home-ranges of ♀♀ do not overlap, but home-ranges of ♂♂ may overlap with those of several other individuals, principally ♀♀. Home-range: 400–

700 m² for ♀♀; up to 1500 m² for ♂♂ corresponding to larger movements of ♂♂, especially during the breeding season. High rate of dispersal for juveniles, followed by settlement (as adults) as the reproductive season approaches. Individuals change burrows at end of the reproductive season, usually within established home-ranges (Fete Ole, Senegal, 1969–72; Poulet 1972a).

Reproduction and Population Structure In Senegal, the length of the reproductive season is variable: it starts in the second half of the wet season (usually Sep) and lasts for 2–8 months, depending on the amount of rainfall (Poulet 1978, 1982). Gestation: 26 days. Embryo number: generally 3–7 (in natural conditions; Poulet 1982). Litter-size (in captivity): 4–6. Weaning: Day 20–21. Sex ratio: 1 : 1 (Hubert & Adam 1975). Sexual maturity: Week 12 (♂♂), Week 8 (♀♀). Monthly mean mortality rate may reach 22% (Poulet 1972b).

Predators, Parasites and Diseases Reptiles (especially *Psammophis sibilans*, owls (especially *Tyto alba* and *Otus leucotis*) and carnivores (especially *Felis libyca*, *Vulpes pallida*, *Canis aureus* and *Genetta genetta*) are known predators (Poulet 1982).

Conservation IUCN Category: Least Concern.

Measurements

Taterillus pygargus

HB: 113.4 (102–120) mm, n = 24

T: 149.7 (140–165) mm, n = 21

HF: 31 (29–34) mm, n = 24

E: 19.1 (17–22) mm, n = 24

WT: 50.3 (31–79) g, n = 26

GLS: 31.7 (29.9–34.2) mm, n = 36

GWS: 17.7 (16.8–18.7), n = 14

M¹–M³: 4.7 (4.5–5.1) mm, n = 36

Auditory bulla: n. d.

Senegal (karyotyped individuals only; weight from captive-bred, non-karyotyped individuals; MNHN)

Key References Matthey & Jotterand 1972; Poulet 1972a, 1982.

Laurent Granjon & Gauthier Dobigny

Taterillus tranieri TRANIER'S TATERIL

Fr. Tâtérille de Tranier; Ger. Traniens Rennmäuschen

Taterillus tranieri Dobigny, Granjon, Aniskin, Bâ and Volobouev, 2003. Mammal. Biol. 68: 301. Dilly, Mali.

Taxonomy Chromosome number distinguishes this species from its sibling species *T. arenarius*, *T. gracilis*, *T. petteri* and *T. pygargus* (Volobouev & Granjon 1996, Dobigny *et al.* 2003). Only known from the type series (n = 4). Synonyms: none. Chromosome number: 2n = 14 (♀♀), 2n = 15 (♂♂).

Description Medium-sized gerbil. Dorsal pelage buffy-brown, with a slight greyish (specimens from Mali) to reddish-brown (specimens from Mauritania) tinge; hairs grey at base. Ventral pelage white. Cheeks white; white supraorbital and postorbital patches,

more or less marked. Muzzle pointed. Ears large and elongated. Eyes large. Fore- and hindfeet white. Hindfeet long, with soles dark and naked; three median digits of similar length, Digit 1 short; rather long claws. Tail long (at least 125% of HB), covered by short hairs; long terminal pencil of darker hairs. Nipples: 2 + 2 = 8.

Geographic Variation None recorded.

Similar Species Four species are similar in morphology and size: *T. arenarius*. Chromosome number: 2n = 30/31; Mauritania only.

T. gracilis. Chromosome number: $2n = 36/37$; widely distributed in West Africa.

T. petteri. Chromosome number: $2n = 18/19$; Mali, Niger and Burkina mostly south of Niger R.

T. pygargus. Chromosome number: $2n = 22/23$; Senegal and Niger.

Distribution Endemic to Africa. Sahel Savanna BZ. Only known from W Mali (Dilly, $15^{\circ}01'N$, $7^{\circ}40'W$) and S Mauritania (Chalkha, $16^{\circ}40'N$, $9^{\circ}18'W$).

Habitat Sandy-clay soil in a millet field surrounded by degraded savanna (Mali), and amongst thorny bushes in fallow land densely covered by grasses (Mauritania) (Dobigny *et al.* 2003).

Abundance No information.

Remarks Syntopic with *Gerbillus nigeriae* and *G. nancillus* (Dobigny *et al.* 2003) in Mali.

Conservation IUCN Category: Least Concern.

Measurements

Taterillus tranieri

HB: 123.5 (111–134) mm, $n = 4$

T: 160.5 (145–180) mm, $n = 4$

HF: 30.6 (30–31) mm, $n = 3$

E: 20.3 (19.5–20.5) mm, $n = 4$

WT: 46.8 (40–54) g, $n = 4$

GLS: 31.2 (30.2–32.5) mm, $n = 3$

GWS: 17.2 (16.9–17.7) mm, $n = 3$

M^1 – M^3 : 4.9 (4.8–5.1) mm, $n = 4$



Taterillus tranieri

Auditory bulla: n. d.

Mali and Mauritania; 2 ♂♂ and 2 ♀♀, karyotyped (Dobigny *et al.* 2003; MNHN)

Key Reference Dobigny *et al.* 2003.

Gauthier Dobigny & Laurent Granjon

Subfamily LEIMACOMYINAE – Büttner's Forest Mouse

Leimacomyinae Musser & Carleton, 2005. *In*: Mammal Species of the World, 3rd edn, p. 1246.

The subfamily is based on a single genus and species, *Leimacomys buettneri*, documented only from the 'high-forest belt' in Togo (Rosevear 1969; see also species profile). It has been unrecorded since the first two specimens were collected in 1890 and is believed extinct by some (see review in Grubb *et al.* 1998). Nothing is known of its habitat or habits, although it is thought to be insectivorous and presumably terrestrial (see species profile). The species may also occur in Ghana, since the type locality is close to the Ghana–Togo border (Grubb *et al.* 1998). Focused surveys of long duration, which emphasize techniques for collecting small insectivores, should be conducted in the forests of Togo and nearby Ghana to assess the status of this unique rodent.

Leimacomys is small, with small, densely haired pinnae and an extremely short naked tail. The wide and moderately long rostrum, slight supraorbital ridges and broad braincase contribute to the robustness of the skull (Rosevear 1969). The zygomatic arches are similarly stoutly constructed, with a broad zygomatic plate and pronounced dorsal notch. Other skull characters include: anterior palatal foramina narrow and long, extending posteriorly to the lingual root of first molars; bony palate wide and projecting well

behind third molars to form a prominent shelf; mesopterygoid fossa correspondingly short and wide; slender upper incisors pro-odont, with the anterior face possessing a shallow groove; and lower incisors very slender. The molars retain the primitive number of roots, and their occlusal surfaces are configured as simple laminae. The middle lamina on M^1 and anterior lamina on M^2 are composed of three cusps and appear chevron-shaped; cusps t1 and t7, longitudinal enamel crests and posterior cingulum are absent from upper molars; upper third molars are moderately reduced compared with second molars (Misonne 1966, Dieterlen 1976c, Denys 1993, Denys *et al.* 1995) (Figure 58).

Following Matschie (1893), most systematists have regarded *Leimacomys* as an atypical member of Dendromurinae (G. M. Allen 1939, Rosevear 1969, Carleton & Musser 1984). Among dendromurines, its molar topography exhibits strongest similarity to *Steatomys* (Misonne 1966, Dieterlen 1976c). In another interpretation, Ellerman (1941) tentatively associated the genus with Murinae, an opinion followed by Simpson (1945). As emphasized by Denys (1993), little of the external and cranial morphology of *Leimacomys*, except for the molar patterns, suggests affinity with dendromurines

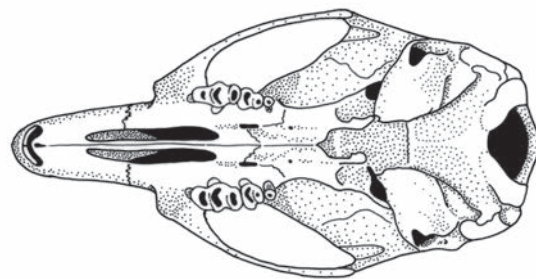
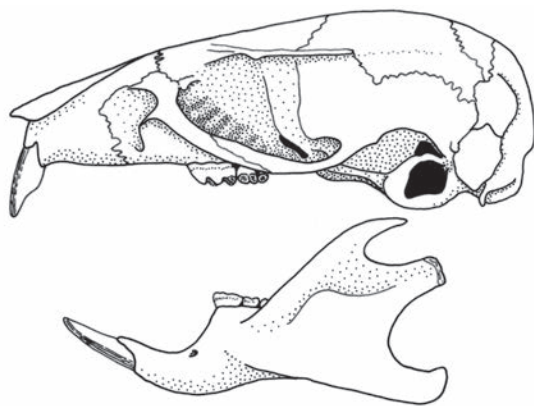


Figure 58. Skull and mandible of *Leimacomys buettneri* (after Misonne 1966 and Rosevear 1969).

proper. Instead, the conformation of the body and skull of *Leimacomys* resembles murine or deomyine rodents, and its cranial configuration is strikingly similar to the deomyine *Lophuromys*. Unlike murine and most deomyine rodents, however, the upper molars of *Leimacomys* lack a t1 cusp, a character common to those murid groups. Cladistic analysis, primarily using dental traits, has underscored the isolation of *Leimacomys* from dendromurines in the strict sense, and instead associated the genus in a lineage that also contains Gerbillinae and

Mystromyinae (Denys *et al.* 1995).

In view of its morphological and phylogenetic separation from dendromurines proper, Musser & Carleton (2005) placed *Leimacomys* in its own subfamily and provisionally consider it to be a cladistically primitive member of Muridae.

Guy G. Musser & Michael D. Carleton

GENUS *Leimacomys* Büttner's Forest Mouse

Leimacomys Matschie, 1893. Sber. Ges. Naturf. Freunde Berlin, p. 107. Type species: *Leimacomys buettneri* Matschie, 1893.



Leimacomys buettneri.

A monotypic genus known only from Togo in West Africa. This genus has had an interesting and controversial history (see details above). Musser & Carleton (2005) considered that *Leimacomys* is sufficiently different from the Dendromurinae to warrant placement in its own subfamily, Leimacomyinae, within the Muridae. *Leimacomys* could be the last existing element of a muroid lineage, isolated for a long time and endemic to the West African forest region. Rosevear (1969) provides a good discussion of the genus. Characteristics of the genus are given in the subfamily and species profiles. The single species in the genus is *Leimacomys buettneri*.

Fritz Dieterlen

Leimacomys buettneri BÜTTNER'S FOREST MOUSE (BÜTTNER'S TOGO MOUSE)

Fr. Souris sylvestre de Büttner; Ger. Büttners Togomaus

Leimacomys buettneri Matschie, 1893. Sber. Ges. Naturf. Freunde Berlin, p. 109. Bismarckburg, Togo (= near Yege, Togo). 710 m.

Taxonomy Only two specimens from the type locality are known, both collected in 1890 (see Rosevear 1969 and Dieterlen 1976c for comment). Both are preserved in alcohol: one is a flat skin and the other is a complete individual from which the skull and stomach have been extracted. Of the skulls, only one is extant and – due to mismatching – is composed of the mandible of one of the specimens (an old adult) and the cranium of the other (a young adult). From this, it is known that both specimens were adults. Dental characteristics suggest relationships to the Dendromurinae and not to the Murinae

(Misonne 1966). Because the species does not fit exactly into either of these subfamilies, Musser & Carleton (2005) place it by itself in a new subfamily, Leimacomyinae. Synonyms: none. Chromosome number: not known.

Description Small mouse with very short tail and pro-odont incisors. Dorsal pelage golden-brown; hairs grey at base, pale brown distally, with black tip; hairs up to 9.5 mm long. Paler on the flanks. Ventral pelage grey-brown. Ears with short hairs on outer and inner

sides. Forefeet with five digits; very long claws, except rudimentary Digit 1 of forefoot has a nail. The claws are relatively long, e.g. 2.1 mm on Digit 3 of forefoot, and 2.5 mm ($>10\%$ of HF) on Digit 3 of hindfoot; claws of hindfeet $>10\%$ of hindfoot. Tail short (ca. 30% of HB), mostly naked except for a few short bristles, tapering towards tip. Skull: incisors pro-odont, forming semicircle on cutting edge, single faint groove on anterior face of each incisor; interorbital constriction very conspicuous; slight supraorbital ridges; palate extends well posterior to the posterior end of cheekteeth (more so than in other murid rodents); M^1 and M^2 with lamina-like transverse rows; $t1$ on M^1 absent (Figure 58). The skull is similar in form to that of *Lophuromys* (due to convergence), although detailed structure suggests affinities to the Dendromurinae. (Description based on original description and on Rosevear 1969.)

Geographic Variation None recorded.

Similar Species

Steatomys spp. Similarly very short tail (ca. 50% of HB); four digits on forefoot; incisor teeth orthodont/opisthodont; zygomatic plate very small; zygomatic arches flared; palate short, not extending far behind the cheekteeth; tendency to become fat at certain times of year; widespread geographic distribution.

Distribution Endemic to Africa. Northern Rainforest–Savanna Mosaic. Recorded only from the type locality in Togo (see also below).

Habitat The type locality was described as in the ‘high forest belt’ (Rosevear 1969). However, the only known locality for this species is $08^{\circ}11'N$, $00^{\circ}41'E$, which is in the Rainforest–Savanna Mosaic where patches of riverine and relict forest alternate with grassland and woodland savanna. Rosevear also mentions that the generic name comes from the Greek *Lima* (garden or meadow) and *mys* (mouse), which suggests that the habitat may be dense grasslands close to riverine forest where the soil is moist and suitable for digging (see Remarks) – a habitat similar to that of *Lophuromys* spp.

Abundance Known only by the two type specimens.

Remarks Virtually nothing is known about this species. However, the morphology of the feet suggest that it is terrestrial and burrowing, and the very short tail suggests that it is not a climbing mouse like *Dendromus* spp. The single stomach was full of termites (Dieterlen 1976c). These limited observations suggest that it is an insectivore that probably gathers its prey by scratching in the soil and litter with its long claws – in much the same way as do *Lophuromys* spp.



Leimacomys buettneri

Conservation IUCN Category: Data Deficient.

Likely to be ‘Critically Endangered’ because of very limited range. No individuals of this species have been encountered since the type specimens were obtained more than 100 years ago. Two extensive surveys in Togo during the 1960s failed to find any evidence of this species, and none has been found in recent years. On this evidence, Schlitter (1989) considers it may be extinct.

Measurements

Leimacomys buettneri

HB: 118 mm

T: 37 mm

HF: 23 mm

E: 14 mm

WT: ca. 30 g

GLS: 30.3 mm

GWS: 15.6 mm

M^1 – M^3 : 4.9 mm

Bismarckburg, Togo

Body measurements: holotype (Matschie 1893)

Skull measurements: Dieterlen 1976c

Key References Denys 1993; Dieterlen 1976c; Rosevear 1969.

Fritz Dieterlen

Subfamily MURINAE – Rats and Mice

Murinae Illiger, 1811. Abhandl. K. Akad. Wiss. Berlin for 1804–11, p. 46, 129.

| | | |
|------------------------------------|-----------------------------------|--------|
| <i>Aethomys</i> (11 species) | Veld Rats | p. 362 |
| <i>Apodemus</i> (1 species) | Long-tailed Field Mouse | p. 377 |
| <i>Arvicanthis</i> (7 species) | Grass Rats | p. 379 |
| <i>Colomys</i> (1 species) | Water Rat | p. 389 |
| <i>Dasymys</i> (5 species) | Shaggy Rats | p. 392 |
| <i>Dephomys</i> (1 species) | Defua Rat | p. 400 |
| <i>Desmomys</i> (2 species) | Scrub Rat | p. 402 |
| <i>Grammomys</i> (11 species) | Thicket Rat | p. 404 |
| <i>Heimyscus</i> (1 species) | Smoky Mouse | p. 418 |
| <i>Hybomys</i> (6 species) | Forest Mice | p. 420 |
| <i>Hylomyscus</i> (8 species) | Wood Mice | p. 429 |
| <i>Lamottemys</i> (1 species) | Mount Oku Rat | p. 439 |
| <i>Lemniscomys</i> (11 species) | Grass Mice | p. 441 |
| <i>Malacomys</i> (3 species) | Swamp Rats | p. 455 |
| <i>Mastomys</i> (8 species) | Multimammate Mice | p. 460 |
| <i>Muriculus</i> (1 species) | Ethiopian Striped Mouse | p. 472 |
| <i>Mus</i> (20 species) | Mice, Pygmy Mice | p. 473 |
| <i>Mylomys</i> (2 species) | Mill Rats (Three-toed Grass Rats) | p. 499 |
| <i>Myomyscus</i> (3 species) * | Meadow Mice | p. 502 |
| <i>Nesokia</i> (1 species) | Short-tailed Bandicoot Rat | p. 506 |
| <i>Nilopegamys</i> (1 species) | Ethiopian Water Rat | p. 508 |
| <i>Oenomys</i> (2 species) | Rufous-nosed Rats | p. 509 |
| <i>Pelomys</i> (5 species) | Creek Rats | p. 513 |
| <i>Praomys</i> (16 species) | Soft-furred Mice | p. 519 |
| <i>Rattus</i> (2 species) | Rats | p. 539 |
| <i>Rhabdomys</i> (1 species) | Four-striped Grass Mouse | p. 544 |
| <i>Stenocephalemys</i> (4 species) | Ethiopian Rats | p. 547 |
| <i>Stochomys</i> (1 species) | Target Rat | p. 554 |
| <i>Thallomys</i> (4 species) | Acacia Rats (Tree Rats) | p. 556 |
| <i>Thamnomys</i> (3 species) | Thicket Rats | p. 563 |
| <i>Zelotomys</i> (2 species) | Broad-headed Mice | p. 567 |

*Formerly *Myomys*.

The Murinae forms the largest assemblage of species within either Muridae or the larger Muroidea and exhibits the most expansive geographic range. Totalling about 124 extant genera and 543 living species, the subfamily is indigenous to Eurasia, the Middle East, Arabian Peninsula, Indomalayan region, Japan, Ryukyu Islands, Philippine Islands, the numerous archipelagos stretching from the Sunda Shelf to the New Guinea and Australian region, and Africa (Musser & Carleton 2005). The subfamily is represented in Africa by 31 genera and 145 species. African endemics (27 genera, 139 species) comprise about 20% of all murine taxa. Most species of *Arvicanthis* and *Myomyscus* are also restricted to Africa, but a single species of each (*A. niloticus* and *M. yemeni*) is also found on the Arabian Peninsula. Of the 39 species of *Mus*, 17 (44%) are African endemics; some researchers view these sub-Saharan endemics, currently arranged as the subgenus *Nannomys*, as a separate evolutionary radiation that should be recognized as a genus. *Mus spretus* (subgenus *Mus*), native to the western Mediterranean region of south-western Europe, also occurs in the Maghreb of North Africa where, judged by late Pleistocene samples, it may have originated (Dobson 1998, 2000). Two genera, *Apodemus* and *Nesokia*, have large geographic

ranges outside of Africa and only marginal distributions on the continent. *Apodemus sylvaticus*, one of the 20 Palearctic species of *Apodemus*, reaches the Mediterranean fringe of North Africa (Kock & Felten 1980), which may represent an accidental introduction by humans followed by subsequent spread throughout Mediterranean coastal habitats (Dobson 1998, 2000, Michaux *et al.* 2002). *Nesokia indica*, indigenous to western Asia, the Middle East and the Arabian Peninsula, also occurs in north-eastern Egypt, and Pleistocene fossils from Egypt and northern Sudan point to a formerly broader African distribution (Osborn & Helmy 1980).

Three non-native murines – *Mus musculus*, *Rattus norvegicus* and *R. rattus* – have invaded parts of the continent, but have not been able to invade natural communities. They are mostly restricted to humanized environments such as cities, towns, villages and food stores. Although their initial evolution and original distribution are rooted in Eurasia, they are now found in many parts of the world and are members of a small cluster of murines (four genera and 14 species, possibly including *Apodemus sylvaticus*; see above) that have expanded their distributions far from their natural ranges through intentional or accidental processes associated with human migration and settlement (Musser & Carleton 2005). Also, the Indomalayan *Bandicota bengalensis* was introduced to Patta Island, Kenya, but whether a population became established is unknown (Corbet & Hill 1992). No other subfamily of Muroidea, or even Rodentia, has such a relatively large contingent of species whose present geographic distributions have been mediated by anthropogenic activities.

Living native African murines range in body size from small (e.g. most species of *Mus*) to large (e.g. some species of *Arvicanthis* and *Aethomys*). No endemic very large-bodied or giant murines are present. Variation in body form reflects terrestrial (e.g. *Arvicanthis*), scansorial (e.g. *Hylomyscus*), arboreal (e.g. *Thallomys*) and limnetic (e.g. *Colomys*) adaptations. Although some species may excavate burrows or shallow places to nest, none exhibits the morphological and physiological adaptations associated with muroids that are extremely fossorial (e.g. *Tachyoryctes* and *Spalax* in Spalacidae). Most African murines are nocturnal, some are diurnal; and they fill a variety of trophic niches, from omnivorous, herbivorous and granivorous to insectivorous and carnivorous. The bulk of endemic murine species occurs in the sub-Saharan biotic zones, inhabiting deserts, grasslands, savannas, rainforests and afro-montane forests. Only three genera of typically sub-Saharan murine rodents are represented in Africa north of the Sahara: *Lemniscomys barbarus* (a Maghreb endemic), *Mastomys erythroleucus* (primarily sub-Saharan with an isolated population in west-central Morocco) and *Arvicanthis niloticus* (also primarily sub-Saharan with populations in Egypt and Sudan; Musser & Carleton 2005).

The Murinae is characterized by a cohesive suite of morphological traits (Carleton & Musser 1984), but derived molar conditions form the cardinal basis for defining the subfamily. Two neomorphic cusps, the anterostyle (t1) and enterostyle (t4), are present on the lingual border of the upper first molar and form two chevron-shaped, transverse lamina; both upper and lower molars lack longitudinal enamel crests between lamina; and cusps on the lower molars are positioned opposite one another (Flynn *et al.* 1985, Jacobs *et al.* 1989,

Freudenthal & Martin Suárez 1999). Other derived cranial features include their modified carotid circulatory pattern (sphenofrontal foramen and squamosal-alisphenoid groove absent; stapedia foramen present) and a reduced tegmen tympani that does not contact the posterior squamosal (Bugge 1970, Carleton & Musser 1984 and unpubl.). The monophyly of Murinae is additionally supported by phylogenetic analyses of mitochondrial and nuclear genes (e.g. Verneau *et al.* 1997, 1998, Michaux *et al.* 2001, Debry 2003, Jansa & Weksler 2004), although the number of genera sampled to date is relatively few and in some studies includes only *Mus* and *Rattus*. Such studies identify Gerbillinae and Deomyinae as the closest relatives of Murinae (Martin *et al.* 2000, Michaux *et al.* 2001, Adkins *et al.* 2003, Jansa & Weksler 2004). The three subfamilies may have diverged from an ancestral muroid stock about 20.8–17.9 mya (early Miocene), an estimate derived from molecular-clock assumptions (Michaux *et al.* 2001). By late Miocene, but not earlier, representatives of each subfamily are recorded from African sediments (Jaeger 1977b, Mein *et al.* 1993, Geraads 2001, Winkler 2001).

While recognition of Murinae as a natural group is strongly supported, uncertainty over relationships among endemic African murines has produced two viewpoints to explain their diversity. Employing microcomplement fixation of albumin, Watts & Baverstock (1995a) identified an African murine clade separate from New Guinean, Australasian and South-East Asian evolutionary lineages, and suggested that living African murines represent ‘a period of rapid radiation from a single ancestor, beginning 8–10 mya and still continuing’. Mitochondrial and nuclear gene sequences have disclosed a large African murine clade (*Aethomys*, *Arvicanthis*, *Dasymys*, *Desmomyss*, *Grammomys*, *Hybomys*, *Lemniscomys*, *Mylomys*, *Pelomys* and *Rhabdomys*) that partly accords with the phylogenetic grouping identified by Watts and Baverstock (Ducroz *et al.* 2001). The alternate view, that living African

murines represent a paraphyletic assemblage, draws support from DNA/DNA hybridization (Chevret 1994) and from other gene-sequence analyses (Lecompte 2003, Jansa & Weksler 2004). In addition to an *Arvicanthis* clade (containing the same genera as given by Ducroz *et al.* 2001), Lecompte identified *Praomys* (*Colomys*, *Heimyscus*, *Hylomyscus*, *Mastomys*, *Myomyscus*, *Praomys*, *Stenocephalemys*, and *Zelotomys*), *Mus* (species in *Nannomys*) and *Malacomys* (containing only species of *Malacomys*) lineages, all three distantly isolated from the *Arvicanthis* clade and from each other.

The meagre number of Miocene taxa recovered from African sediments offer no resolution to whether the derivation of modern African murines is from a single ancestral group or from several ancestral groups, or to their origin as a result of one or more immigrations. Southern Asia is vaguely mentioned as the source area, with arrivals in Africa occurring in middle to late Miocene–Pliocene (Jacobs 1985, Winkler 1994, 2002). Late Miocene is the earliest documentation for *Progonomys* and *Paraethomys* in North Africa (Jaeger 1977b, Mein *et al.* 1993) and for *Karnimata* and *Saidomys* in Kenya (Winkler 2001). Murines from earlier Miocene strata are known only from northern Pakistan, including the middle Miocene *Antemus*, generally considered the earliest murine (Jacobs & Downs 1994, Freudenthal & Martin Suarez 1999). Fossils of living endemic African murines first appear in the Pliocene (Denys 1999, Winkler 2002). Although now largely confined to Africa, *Mastomys* and *Arvicanthis* are each extraliminally represented by a single species, now extinct, that lived in Israel during the Pleistocene (Tchernov 1968, 1996), and by an extinct Pliocene species on the Mediterranean island of Rhodes (De Bruijn *et al.* 1996).

The subfamily is currently represented in Africa by 31 genera.

Guy G. Musser & Michael D. Carleton

GENUS *Aethomys*

Veld Rats

Aethomys Thomas, 1915. Ann. Mag. Nat. Hist., ser. 8, 16: 477. Type species: *Epimys hindei* Thomas, 1902.

The genus *Aethomys* currently includes 11 species (Table 29), of which ten are endemic to East, central and southern Africa, and one species is endemic to West Africa (Musser & Carleton 1993, Chimimba 1998, Chimimba *et al.* 1999). An additional proposed species (*A.*



Aethomys kaiseri.

halleri) (see Denys & Tranier 1992) requires assessment. Species in the genus occur in a variety of savanna woodland and grassland habitats, preferring those that include shrubs or thick grass, hollow tree trunks and logs, creviced rocky areas, and/or termitaria. Some species may occur commensally with humans in agricultural areas. Although some are widely distributed (e.g. *A. chrysophilus*), others are restricted (e.g. *A. stannarius*, *A. silindensis*).

Veld Rats are generalized medium- to large-sized murid rodents. Species in the genus vary in body size, body proportions and pelage colour. The genus is most similar to *Rattus*, from which it differs in having molars that are clearly cuspidate and anterior palatal foramina that extend posteriorly to between the molars (Figure 59). Although generally considered ‘long-tailed’, tail length varies among species (ca. 70–150% of head and body length). Pelage is short, sleek or rough, and the dorsal pelage is often ‘sunburnt’ (hence the Greek-derived generic name: *eithos* = sunburnt; *mys* = mouse) in various shades of brown, grey, red and yellow. The hairs of the ventral pelage may be completely white, or grey at base with a white tip. Limbs are equal in size, the feet usually white above. Forefoot has four digits

Table 29. Species in the genus *Aethomys*. Arranged in order of increasing mean head and body length.
(n. d. = no data.)

| Species | HB mean (mm) | T mean (mm) [% of HB] | Dorsal pelage | GLS mean (mm) | Chromosome number | Width M' | Nipples | Notes |
|------------------------|------------------------|-----------------------------------|------------------------------------|---------------|-------------------|----------|------------|---|
| <i>A. granti</i> | 111 | 117 [97–113%] | Dull yellowish-brown to dark brown | 30.0 | 2n = 32 | n. d. | 3 + 2 = 10 | South Africa |
| <i>A. namaquensis</i> | 113 | 154 [140%] | Yellowish-brown; black tips | 31.3 | 2n = 24 | n. d. | 1 + 2 = 6 | Widespread in southern Africa |
| <i>A. chrysophilus</i> | 138 | 156 [120%] | Reddish-brown | 36.1 | 2n = 50 | <2.0 | 1 + 2 = 6 | Widespread. Kenya to South Africa |
| <i>A. nyikae</i> | 143 | 165 [95–115%] | Medium to dark brown; black tips | 35.1 | n. d. | 2.0–2.2 | 0 + 2 = 4 | NE Angola, S DR Congo, N Zambia, Malawi |
| <i>A. kaiseri</i> | 146 | 119 [95%] | Yellowish-brown | 36.4 | n. d. | >3.2 | 0 + 2 = 4 | East Africa to Zambia and Angola |
| <i>A. ineptus</i> | 147 | 162 [110%] | See <i>A. chrysophilus</i> | 35 | 2n = 44 | n. d. | n. d. | South Africa. Morphologically indistinguishable from <i>A. chrysophilus</i> |
| <i>A. stannarius</i> | 148 | 152 [110%] | Medium brown | 36.4 | n. d. | n. d. | 1 + 2 = 6 | N Nigeria and N Cameroon |
| <i>A. thomasi</i> | 150 | 124 [83%] | Grizzled rufous-brown | 26.0 | n. d. | ≥2.2 | n. d. | W and C Angola |
| <i>A. hindei</i> | 158 | 156 [70–110%] | Medium brown | 37.4 | 2n = 50 | <2.2 | n. d. | N Cameroon to East Africa |
| <i>A. bocagei</i> | 165 (♂ ♂)
143 (♀ ♀) | 189 (♂ ♂),
160 (♀ ♀)
[115%] | Pale brown | 40.9 | 2n = 50 | n. d. | 0 + 2 = 4 | W and C Angola, SW DR Congo |
| <i>A. silindensis</i> | 173 | 177 [92–114%] | Buffy-brown, black tips | 40.4 | n. d. | 2.2–2.3 | n. d. | E Zimbabwe |

(Digit 1 absent); hindfeet have five digits (Digits 1 and 5 are very small and do not reach to base of Digits 3, 4 and 5). The tail may appear naked, but has a sparse to moderate covering of short hairs. Females have four to six nipples.

Members of the genus are nocturnal and terrestrial, but some may be slightly arboreal. All species with known food habits are omnivorous, mostly feeding on grass, foliage, fruits and seeds, and occasionally on invertebrates. Nests are constructed from accumulations of grass, twigs and debris. Social behaviour is highly variable. Wild populations of some species may be composed of widely spaced, territorial pairs (e.g. *A. chrysophilus*), but others may include small groups nesting communally (e.g. *A. nyikae*). In some cases, confinement to limited habitat patches may give an erroneous impression of communal social behaviour. Population sizes are variable, especially in unpredictable environments. At high densities, some species may facilitate transmission of human diseases, as well as causing extensive damage to crops and stored grain.

Breeding patterns vary geographically, with some species breeding throughout the year, sometimes with summer peaks, while others show no evidence of breeding during colder, drier months (Skinner & Smithers 1990). Gestation: 21–31 days. Litter-size: 2–4. Females may have a postpartum oestrus. Nipple-clinging by young occurs in all species studied.

Although fossil remains are limited, records include *A. lavocati* and *A. deheinzeli* from the Pliocene and Pleistocene of East Africa, and *A. modernis* and *A. adamanticola* from Pliocene–late Pleistocene of South

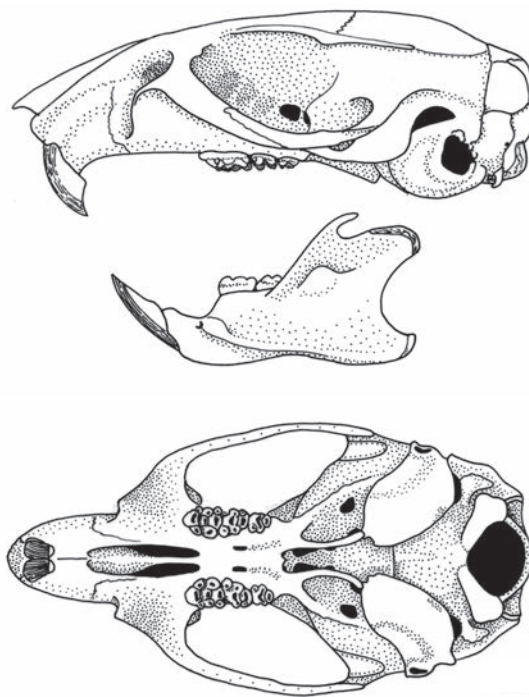


Figure 59. Skull and mandible of *Aethomys chrysophilus* (HC 2809).

Africa and the Pleistocene of Namibia (Wesselman 1984, Black & Krishtalka 1986, Denys 1990c). It is speculated that *A. adamanticola* may represent an advanced stage of an early Miocene lineage closely related to the genus *Dasymys*, but not ancestral to it. There is no indication of a close relationship between the East African and southern African fossil species, precluding speculation on the origin and time of divergence of the genus (Denys 1990c).

The taxonomic placement of *Aethomys* relative to other murid genera has a complex nomenclatural history as reflected by some currently recognized species within the genus that originally were ascribed to *Gerbillus*, *Praomys*, *Mus* and *Epimys* (De Graaff 1981). Particularly problematic is the relationship with *Rattus*. Thomas (1915a, b) for example, variously considered *Aethomys* as a subgenus of *Rattus* or as a full genus. Support for generic status is based on dental and karyological characters (Ellerman *et al.* 1953, Matthey 1964, Davis 1975b). Similarly, little is known about evolutionary relationships among the 11 currently recognized species of *Aethomys* (Musser & Carleton 1993, Chimimba 1998, Chimimba *et al.* 1999). No study has considered all these species simultaneously; previously postulated relationships were based largely on comparisons that were biogeographically restricted and involved only a few species (e.g. Musser & Carleton 1993). Other relationships have been inferred from previous taxonomic treatments (e.g. Ellerman 1941, Swynnerton & Hayman 1950, Rosevear 1969, Davis 1975b, Delany 1975, Ansell 1978, Hutterer & Joger 1982, Crawford-Cabral 1998, 1999).

The genus may be subdivided into two subgenera: *Micaelamys* (*A. granti* and *A. namaquensis*) and *Aethomys* (the remaining nine species). These subgenera exhibit distinct modes of karyotypic change and differences in gross sperm and bacular morphology (Visser & Robinson 1986, 1987). Other distinguishing characters include a more robust skull form with more prominent cranial sutures in members of the subgenus *Aethomys*, a well-developed anterior median cusp on the first upper molar in members of the subgenus *Micaelamys*, and differences in general body and cranial size. However, immunological (Watts & Baverstock 1995b) and molecular data (Ducroz *et al.* 2001, Castiglia *et al.* 2003, Russo 2003), as well as cladistic analyses of qualitative cranial data (Chimimba 2005) strongly suggest that the genus is paraphyletic and hence the taxonomic elevation of the currently recognized subgenera to full generic rank. This paraphyly and the differences outlined above led Skinner & Chimimba (2005) to recognize *Aethomys* and *Micaelamys* as two distinct genera.

The species of *Aethomys* are distinguished by differences in general body size, pelage colouration and texture, tail length relative to head and body length, molar cusp pattern and number of molar roots. Other distinguishing characters include haemoglobin protein electromorphs, DNA sequences, sperm and bacular morphology, chromosome number and number of nipples.

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Aethomys bocagei BOCAGE'S VELD RAT (BOCAGE'S AETHOMYS)

Fr. Rat des rochers de Bocage; Ger. Bocages Veld-Ratte

Aethomys bocagei (Thomas, 1904). Ann. Mag. Nat. Hist., ser. 7, 13: 416. Pungo Andongo, Angola.

Taxonomy Originally described as *Mus bocagei* but subsequently re-assigned to *Aethomys*. Regarded as a valid species by Hill & Carter (1941), Davis (1975b), Musser & Carleton (1993) and Crawford-Cabral (1998, 1999). Synonyms: none. Chromosome number: $2n = 50$ (Matthey 1963a).

Description Large rodent. Dorsal pelage generally pale brown, resulting from a mixture of blackish and clay hairs. Flanks grey. Ventral pelage white; hairs slate-grey at base, with white tip. Ears medium-sized, brown. Fore- and hindfeet with pure white upper surface. Tail very long (ca. 115% of HB), uniformly brown, coarsely scaled, naked with sparse fine hairs. Males usually larger than ♀♀. Nipples: $0 + 2 = 4$.

Geographic Variation None recorded.

Similar Species

- A. silindensis*. Similar in cranial, dental and external characters; molars moderately broad (M^1 : 2.2–2.3 mm); E Zimbabwe only.
- A. namaquensis*. Smaller (means HB: 113 mm, T: 154 mm, HF: 26 mm, but tail relatively longer (140% of HB); chromosome number: $2n = 24$; narrowly sympatric in southern part of range.
- A. thomasi*. Similar HB length (mean 150 mm); shorter tail (mean 125 mm, ca. 83% of HB); shorter HF (mean ca. 29 mm); narrowly sympatric in southern part of range.

Distribution Endemic to Africa. Zambezan Woodland BZ. Recorded only from W and C Angola and extreme SW DR Congo. Distribution limits unknown, but speculated to occur throughout NW Angola, and possibly W DR Congo and SW DR Congo (Hill & Carter 1941, Musser & Carleton 1993, Crawford-Cabral 1998, 1999).

Habitat Mostly associated with savanna interspersed with rainforest (Crawford-Cabral 1998). Type specimen was collected at 1200 m.

Abundance Uncertain, but probably common.

Remarks Apparently no other information available.

Conservation IUCN Category: Least Concern.

Status needs further evaluation.

Measurements

- Aethomys bocagei*
- HB (♂♂): 165 (150–174) mm, $n = 3$
 - HB (♀♀): 143 (137–147) mm, $n = 3$
 - T (♂♂): 180, 198 mm, $n = 2$
 - T (♀♀): 160 (155–165) mm, $n = 3$
 - HF (♂♂): 36 (34–37) mm, $n = 3$

HF (♀ ♀): 32 (32–37) mm, n = 3
 E (♂ ♂): 23, 23 mm, n = 2
 E (♀ ♀): 25 mm (25–25), n = 3
 WT: n. d.
 GLS: 40.9 (40.2–41.5) mm, n = 5
 GWS: 19.1 (18.6–19.4) mm, n = 4
 M¹–M³: 6.7 (6.2–7.0) mm, n = 4
 Angola
 Body measurements: Crawford-Cabral (1999)
 Skull measurements: holotype and Hill & Carter (1941)

Key References Crawford-Cabral 1998, 1999; Davis 1975b; Hill & Carter 1941.

**Christian T. Chimimba, Alicia V. Linzey
 & Michael H. Kesner**



Aethomys bocagei

Aethomys chrysophilus RED VELD RAT (RED AETHOMYS)

Fr. Rat des rochers roux; Ger. Rote Veld-Ratte

Aethomys chrysophilus (de Winton, 1897). Proc. Zool. Soc. Lond. 1896: 801 (publ. 1897). Mazoe, Mashonaland, Zimbabwe.

Taxonomy Originally described in the genus *Mus*. *Aethomys chrysophilus*, originally considered to be a single species, is now known to consist of two cytogenetically distinct sibling species, *A. chrysophilus* and *A. ineptus* (Chimimba *et al.* 1999). *Aethomys chrysophilus* (*sensu stricto*) is characterized by a karyotype of $2n = 50$ and sperm morphology typical of rodents (Gordon & Watson 1986, Breed *et al.* 1988). In contrast, *A. ineptus* has a karyotype of $2n = 44$ and a spatulate sperm structure (see *A. ineptus*). Because *A. chrysophilus* and *A. ineptus* cannot be distinguished externally, information included in this account is either based on positively identified specimens or on specimens whose identity can be inferred from their locality of collection (Linzey *et al.* 2003). Synonyms: *acticola*, *alticola*, *imago*, *singidae*, *voi*. Subspecies: none. Chromosome number: $2n = 50$.

Description Medium-sized robust rodent. Dorsal pelage reddish-brown mixed with black or brownish-black hairs. Variation in dorsal pelage due to concentration of dark hairs, leading to pelage being variously described as brown, orange-yellow, or cinnamon. Ventral pelage white; hairs white or white with grey base. Dorsal and ventral colouration sharply delineated. Upper surface of feet covered with white or pale yellow-orange hairs. Soles of hindfeet dusky. Tail longer than HB (ca. 120%), sparsely haired and coarsely scaled. Skull: mean 36.1 mm and relatively narrow, with greatest width <51% of greatest length; molars narrow ($M^1 < 2.0$ mm); incisors opisthodont. Nipples: $1 + 2 = 6$.

Geographic Variation Studies are needed to resolve significance of geographic variation within a newly defined geographic range that now excludes *A. ineptus*.

Similar Species

- A. ineptus*. May co-exist with *A. chrysophilus*, but there are no distinguishing external features.
- A. namaquensis*. Similar in appearance and frequently occurring in same habitats; adults generally smaller and more delicate (greatest length of skull <35 mm); tail relatively longer (135% of HB); hindfeet on average smaller.
- A. kaiseri*. Ventral pelage greyer; skull relatively wider (greatest width >55% of greatest length), molars wider ($M^1 > 3.2$ mm); incisors orthodont.
- A. nyikae*. Tail relatively shorter (95–115% of HB); molars wider ($M^1 2.0$ – 2.2 mm); incisors orthodont.

Distribution Endemic to Africa. Zambezi Woodland BZ, part of Sahara Arid BZ (Kalahari Desert) and southern part of Somalia–Masai Bushland BZ. Widespread in East, central and southern Africa. Recorded from SE Kenya southward and westward through Tanzania, Zambia, Angola, Malawi, Zimbabwe, N Mozambique and the Limpopo Valley of N South Africa to approximately 24° S (Linzey *et al.* 2003). Specimens from S Mozambique, N and E Botswana and N Namibia have not been positively identified. Ranges of *A. chrysophilus* and *A. ineptus* essentially parapatric, with the only area of significant overlap in the region west of Pretoria, South Africa. Known to co-occur only at one site (Limpopo Province, South Africa), although

*Aethomys chrysophilus*

co-occurrence likely at other sites in region of parapatry. Range in South Africa generally corresponds with distribution of mopane (*Colophospermum mopane*) and baobab (*Adansonia digitata*) trees.

Habitat A habitat generalist that occupies a variety of savanna-woodland habitats. Described as ubiquitous in many regions, but prefers abundant cover in the form of rocks, logs, thorn fences around agricultural plots, termitaria and/or heavy grass. Frequently found on kopjes in association with *A. namaquensis*, but appears to reach higher densities in habitats where *A. namaquensis* is absent.

Abundance Based on studies in Malawi, Zimbabwe, Mozambique and South Africa, generally occurs at low densities (<8/ha) (Gliwicz 1985, Happold & Happold 1990, Linzey & Kesner 1997a, b, A. Linzey and M. Kesner unpubl.). However, higher densities occur locally (A. Linzey & M. Kesner unpubl.).

Adaptations Nocturnal and terrestrial, but climbs trees occasionally. Excavates burrows under bushes, rocks, logs, or tree roots, or uses crevices in rocks or holes in termite mounds.

Foraging and Food Omnivorous, with average diet consisting of 25% insects, 40% seeds and 35% vegetation (Gliwicz 1987). Greater dependence on seeds in the dry season (10% insects, 75% seeds, 15% vegetation).

Social and Reproductive Behaviour Pairs widely spaced, with rarely more than two adults occupying a burrow or crevice (Choate

1972). In captivity, individuals aggressive toward conspecifics, but when groups are together for long periods, development of social ranking reduces overt aggression. Both sexes build nests in captivity, but females with young sometimes exclude males from the nest.

Reproduction and Population Structure Reproduction occurs throughout the year but most births recorded in late dry season and early wet season (Hanney 1965, Brooks 1972, Hubbard 1972, Gliwicz 1985, Happold & Happold 1990, Neal 1990). Gestation: minimally 26 days, but up to 31 days if female lactating. Litter-size: 3–4 (1–6). At birth, young altricial, weight ca. 4.5 g. Eyes open Day 10–14. Weaning Day 26–33. Nipple-clinging until ca. Week 3. Minimum age at sexual maturity in ♀♀ (in captivity): 82 days. Age classes defined by weights as follows: >63 g adult ♀, 31–63 g subadult ♀, <31 g juvenile ♀, >71 g adult ♂, 31–71 g subadult ♂, <31 g juvenile ♂ (Bowland & Perrin 1988).

Annual variation in population density, with higher numbers in Sep–Mar in Malawi (Happold & Happold 1990) and May–Aug in Zimbabwe (Linzey & Kesner 1997a). In late dry season, populations are composed of proportionally large numbers of subadult individuals probably born during the previous wet season. Turnover rate in natural populations high, with 50% chance of survival to one month, 30% to two months and 23% to three months. Interannual fluctuations in numbers associated with variations in annual precipitation.

Predators, Parasites and Diseases Parasites include lice, fleas, ticks, nematodes and tapeworms. Diseased livers observed in 10% of animals examined in Malawi (Hanney 1965). Known to be a carrier of plague.

Conservation IUCN Category: Least Concern.

Measurements

Aethomys chrysophilus

HB: 138 (108–164) mm, n = 39

T: 156 (126–202) mm, n = 39

HF: 31 (28–34) mm, n = 46

E: 20 (18–21) mm, n = 46

WT: 75 (40–114) g, n = 45

GLS: 36.1 (32.6–37.7) mm, n = 23

GWS: 14.9 (14.3–15.5) mm, n = 23

M¹–M³: 6.2 (5.7–6.6) mm, n = 12

Body measurements: various localities, Zimbabwe (CM)

Skull measurements: northern Limpopo Province, South Africa (TM)

Key References Chimimba *et al.* 1999; Happold & Happold 1990; Linzey & Kesner 1997a, b.

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***Aethomys granti* GRANT'S VELD RAT (GRANT'S AETHOMYS)**

Fr. Rat des rochers de Grant; Ger. Grants Veld-Ratte

Aethomys granti (Wroughton, 1908). Ann. Mag. Nat. Hist., ser. 8, 1: 257. Deelfontein, north of Richmond, Cape Province, South Africa.

Taxonomy Originally allocated to the genus *Mus* but subsequently variously placed in *Myomys* (= *Praomys*) (Allen 1939), *Mastomys* (Roberts 1951), *Rattus* (subgenus *Micaelamys*; Ellerman 1941) and *Aethomys* (subgenus *Micaelamys*; Davis 1975b, De Graaff 1981, Meester *et al.* 1986, Musser & Carleton 1993). Determined to be a valid species, based on qualitative and quantitative morphological data, by Chimimba (1998) and Chimimba *et al.* (1999). Following Chimimba (2005), Musser & Carleton (2005) refer *granti* to the genus *Micaelamys*. Synonyms: none. Chromosome number: $2n = 32$ (Matthey 1964, Misonne 1974, Visser & Robinson 1986).

Description Small yellowish-brown or dark brown rodent. Dorsal pelage dull yellowish-brown or dark brown, hairs brownish-grey at base, grey or greyish-white at tip. Ventral pelage pale grey or greyish-yellow; hairs grey at base and grey or greyish-white at tip. Hairs slender, shallowly grooved and characteristically covered with petal-shaped scales (Keogh 1985). Tail long (ca. 97–113% of HB), brownish-black or dark reddish-brown; reasonably well haired with dark-coloured bristles that are longer and denser at the tip (Chimimba 1998, Chimimba *et al.* 1999). Lower jaw with anterior and posterior borders of ascending ramus parallel to each other. Skull: incisors moderately opisthodont; anterior palatal foramina extends to the second root of the M^1 . Nipples: $3 + 2 = 10$.

Geographic Variation Skull size shows a south-westerly–north-easterly clinal pattern of variation, in which overall cranial size is negatively correlated with longitude, and positively correlated with latitude; thus, specimens with the smallest skulls are found in the south-west of the geographic range and the largest in the north-east of the geographic range (Chimimba *et al.* 1998).

Similar Species

A. namaquensis. Tail longer relative to head and body; pelage harsher; hairs broad and covered with cup-shaped scales; anterior palatal foramina extends to the first root of M^1 (Keogh 1985, Skinner & Smithers 1990); lower jaw with anterior and posterior borders of ascending ramus not parallel to each other (Chimimba 1998).

Distribution Endemic to Africa. South-West Arid BZ (Karoo) and northern fringes of South-West Cape BZ. Recorded in parts of Northern, Western and Eastern Cape Provinces of South Africa.

Habitat Prefers rocky terrain, where it may co-occur with *Aethomys namaquensis* (Skinner & Smithers 1990). Found in fynbos, succulent karoo and nama-karoo biomes (Mugo *et al.* 1995).

*Aethomys granti*

Abundance No information.

Remarks Apparently no other information available.

Conservation IUCN Category: Least Concern.

Measurements

Aethomys granti

HB: 111.8 (93–125) mm, $n = 55$

T: 116.8 (96–138) mm, $n = 55$

HF: 24.1 (22–26) mm, $n = 55$

E: 17.6 (16–20) mm, $n = 55$

WT: n. d.

GLS: 30.0 (28–32) mm, $n = 86$

GWS: 13.0 (12.4–13.8), $n = 86$

M^1 – M^3 : n. d.

South Africa (Chimimba *et al.* 1999)

Key References Chimimba 1998; Chimimba *et al.* 1999.

**Christian T. Chimimba, Alicia V. Linzey
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Aethomys hindei HINDE'S VELD RAT (HINDE'S AETHOMYS)

Fr. Rat des rochers de Hinde; Ger. Hinde's Veld-Ratte

Aethomys hindei (Thomas, 1902). Ann. Mag. Nat. Hist., ser. 7, 9: 218. Machakos, Kenya.

Taxonomy Originally described in the genus *Mus*. Originally considered a distinct species, but subsequently treated, in error, as a subspecies of *A. kaiseri* (e.g. Hollister 1919, Allen & Loveridge 1942, Swynnerton & Hayman 1951). Although noting that they were atypical, Hatt (1940a) assigned specimens of this species from NE Congo (= DR Congo) to *A. kaiseri medicatus*. Possibly *A. hindei* consists of a complex of species or subspecies (Denys & Tranier 1992). Synonyms: *alghazal*, *centralis*, *helleri*, *medicatus*, *norae*. Subspecies: none. Chromosome number: $2n = 50$ (Matthey 1963a).

Description Large rodent. Pelage soft and moderately long (mid-dorsal hairs ca. 10 mm). Dorsal pelage medium brown; hairs grey with brown tip; some longer hairs pure black, especially on mid-dorsal line. Flanks paler with few black hairs; hairs grey with pale brown tip. Ventral pelage greyish-white; hairs pale grey on basal half, whitish on terminal half. Head similar to dorsal pelage, without any special markings. Chin, throat and chest similar to ventral pelage. Limbs short; hindlimbs with scattered white hairs on upper surface. Tail moderately long (ca. 70–110% of HB, see also below); dark brown to black; ringed with many small scales; appears naked, but with many very small bristles. Skull: zygomatic width <55% skull length; molars narrow ($M^1 < 2.2$ mm); incisor teeth opisthodont; auditory bullae: 7.03 mm (cf. *A. stannarius*). Sexual dimorphism in weight noted in Uganda (♂♂ heavier; Okia 1976). Nipples: not known.

Geographic Variation Systematic studies are needed to resolve the significance of considerable geographic variation in morphological traits. Tail length is longer, and length relative to HB is greater, in populations from Cameroon (mean 156 mm, ca. 100% of HB) than in populations from Kenya (130 [128–132] mm, ca. 85% of HB), although HB length is very similar. Relative tail length varies on either side of Rift Valley: e.g. east of Rift Valley, tail length is <95% (70–95%) of HB; and west of Rift Valley, tail length is >95% (95–110%) of HB. Cranial and dental traits (e.g. ratio of zygomatic width to skull length, interorbital constriction width, auditory bullae length, length of M^1 – M^3 , and molar dimensions and features) also vary geographically (Denys & Tranier 1992).

Similar Species

A. kaiseri. Skull relatively wider (zygomatic width >55% of length); molar teeth broader ($M^1 > 3.2$ mm); incisors orthodont; west of Rift Valley, tail shorter (<95% of HB) but east of Rift Valley, tail same relative length.

Distribution Endemic to Africa. Eastern parts of Guinea Savanna BZ and Northern Rainforest–Savanna Mosaic and parts of Somalia–Masai Bushland BZ. Widespread. Recorded from N Cameroon eastwards to S Chad, N DR Congo, S Sudan and SW Ethiopia, Uganda, Kenya and N Tanzania. Southern limit uncertain.

*Aethomys hindei*

Habitat Rocky areas, in dense grass and bush cover, where annual rainfall averages 600–1500 mm (Misonne & Verschuren 1966, Delany 1972, Hubbard 1972, Okia 1976). Sometimes occurs in disturbed forest with thick undergrowth, overgrazed bush, or cultivated lands (Delany 1972, Okia 1976, Canova & Fasola 2000). Also recorded on lower slopes of mountainous areas (<2000 m) where farmland and grassland penetrate montane forest (Misonne 1963, Clausnitzer & Kityo 2001). Type specimen was collected at 1645 m.

Abundance Common in suitable habitats. In disturbed forest in S Uganda, populations (measured by minimum number known to be alive) are high from Jan–May (4.5–22.6/ha) and in August (13.6/ha), and generally low in the remaining months (0.0–9.1/ha) (Okia 1976). In coastal Kenya, density recorded as 6 individuals/ha in overgrazed bush. Populations in Uganda showed three- to four-fold multi-annual fluctuations, even though there were no obvious differences in quantity or distribution of rainfall (Okia 1976).

Adaptations Nocturnal and diurnal; terrestrial. In coastal Kenya, activity (as assessed by trapping records) equally divided between night and day (Canova & Fasola 2000). In Uganda, home-range varies from 30 to 1600 m² (Okia 1976).

Foraging and Food No information for wild-living individuals. In captivity, feeds on grains, fruits, nuts and vegetables (Hubbard 1972).

Social and Reproductive Behaviour Nipple-clinging of neonates is commonly observed (Allen & Loveridge 1942, Hubbard 1972). Females construct globular grass nests (Hubbard 1972).

Reproduction and Population Structure Reproduction probably occurs throughout the year; most pregnancies recorded during the wet season and most young animals caught in drier seasons (Hubbard 1972, Okia 1976). Gestation: 24–25 days. Mean litter-size: 2.0 (1–4, mode 1 and 2, $n = 18$ litters; Uganda; Okia 1976). At birth, young altricial. Development rapid, especially while attached to nipples. At birth, young lightly furred on back, heavily furred by Day 10. Eyes open Day 14. First leave nest Day 15. Adult size attained ca. Day 45 (Hubbard 1972). Sex ratio (field-caught adults) is ca. 1 : 1 (Okia 1976).

Predators, Parasites and Diseases No information.

Conservation IUCN Category: Least Concern.

Measurements

Aethomys hindei

HB: 158 (120–186) mm, $n = 33$

T: 156 (132–178) mm, $n = 32$

HF: 32 (29–34) mm, $n = 33$

E: 20 (18–22) mm, $n = 33$

WT (♂♂): 140–175 g, $n = 32^*$

WT (♀♀): 120–150 g, $n = 26^*$

GLS: 37.4 (33.5–41.1) mm, $n = 15$

GWS: 17.3 (15.5–19.9) mm, $n = 23$

M^1 – M^3 : 6.0 (5.2–6.3) mm, $n = 33$

Measurements: N Cameroon (Denys & Tranier 1992, CM)

Weights: Uganda (Okia 1976)

*No mean value recorded

Tail length in Cameroon is longer than in Kenya and Tanzania (see Geographic Variation)

Key References Denys & Tranier 1992; Hubbard 1972; Okia 1976.

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Aethomys ineptus TETEVELD RAT (TETE AETHOMYS)

Fr. Rat des rochers de Tete; Ger. Tete Veld-Ratte

Aethomys ineptus (Thomas and Wroughton, 1908). Proc. Zool. Soc. Lond. 1908: 546. Tette (= Tete), Zambezi River, Mozambique.

Taxonomy Originally described as *Mus chrysophilus ineptus*. *Aethomys ineptus* is morphologically indistinguishable from *A. chrysophilus* but is characterized by chromosome number of $2n = 44$ and spatulate sperm structure unique among murid rodents (Gordon & Watson 1986, Breed *et al.* 1988). Although a chromosome number of $2n = 44$ has been described from Côte d'Ivoire (Matthey 1958), it is now recognized that this material originated in South Africa (Chimimba 1998). Because *A. ineptus* and *A. chrysophilus* cannot be distinguished externally, information included in this account is either based on karyotypically identified specimens or is inferred from the geographic range (Linzey *et al.* 2003). Synonyms: none. Chromosome number: $2n = 44$.

Description See *A. chrysophilus*.

Geographic Variation None recorded.

Similar Species

A. chrysophilus. Externally indistinguishable from *A. ineptus*; chromosome number: $2n = 50$; may co-occur with *A. ineptus* in some parts of geographic range.

A. namaquensis. Similar in appearance; adults generally smaller and more delicate (greatest length of skull <35 mm); tail relatively longer (135% of HB); hindfeet on average smaller; frequently occurs in same habitats.

Distribution Endemic to Africa. Parts of Highveld BZ, and adjacent areas of Afromontane–Afroalpine and Zambezi Woodland BZs. Distribution is narrower than for *A. chrysophilus*, and possibly



Aethomys ineptus

confined to South Africa; there are no positively identified specimens from S Mozambique, Botswana and Namibia. In NC South Africa, occurs mostly above 1000 m, but occurs at lower elevations at more southern latitudes. Reaches southern limit in KwaZulu–Natal Province at about 30° S, but absent south and west of 23° S and 23° E. In Kruger National Park, the ranges of *A. chrysophilus* and *A. ineptus*

meet between Olifants and Satara, a region marked by transition from mopane shrubveld to open savanna (Linzey *et al.* 2003).

Habitat Grasslands, shrubs and rocks, where there is thick ground cover (Monadjem 1999a, A. Linzey & M. Kesner unpubl.). Appears to have same habitat preferences as *A. chrysophilus*.

Abundance Generally occurs at low to moderate densities (up to 18/ha; Miller 1994, Monadjem & Perrin 1998, Ferreira & Van Aarde 1999). However, higher local densities have been recorded, e.g. 37/ha near Pietermaritzburg (A. Linzey & M. Kesner unpubl.). Annual variation in population density, with higher numbers in the winter dry season, have been recorded in South Africa (1.01/ha in January to 3.24/ha in July; Korn 1981).

Remarks Nocturnal, with greater activity early in the night (Perrin 1981). In NE South Africa, reproduction is seasonal and confined to the wet summer months when nutritional supplies are abundant (Muteka *et al.* 2006c). However, follicular development and the presence of corpora lutea in ♀♀ outside the breeding season suggests that spontaneous ovulation may occur (Muteka *et al.* 2006a). Males have a significantly higher testicular mass and testicular volume, and the diameter of the seminiferous tubules is larger, when individuals are artificially subjected to a long daylength, suggesting reproduction is partially controlled by photoperiodicity (Muteka *et al.* 2006b).

Omnivorous; diet approximately 37–58% vegetation, 33–58% seeds and 0–8% insects (Miller 1994, Monadjem 1997b). Home-range: 1500–3000 m² (Korn 1981).

Conservation IUCN Category: Least Concern.

Measurements

Aethomys ineptus

HB: 147 (140–155) mm, n = 4*

T: 162 (144–170) mm, n = 4*

HF: 30 (26–32) mm, n = 4*

E: 20 (18–22) mm, n = 4*

WT: 82 (65–107) g, n = 15†

GLS: 35.0 (33.0–37.1) mm, n = 15†

GWS: 14.3 (13.7–14.3) mm, n = 15†

M¹–M³: 5.8 (5.5–6.3) mm, n = 15†

*KwaZulu–Natal Province, South Africa

†Gauteng Province, South Africa

Measurements from positively identified specimens only (TM; C. T. Chimimba unpubl.)

Key References Chimimba 1998; Linzey *et al.* 2003.

Alicia V. Linzey, Michael H. Kesner
& Christian T. Chimimba

Aethomys kaiseri KAISER'S VELD RAT (KAISER'S AETHOMYS)

Fr. Rat des rochers de Kaiser; Ger. Kaisers Veld-Ratte

Aethomys kaiseri (Noack, 1887). Zool. Jahrb. Syst. 2: 228. Mpala, Marungu, DR Congo.

Taxonomy Originally described in the genus *Epimys*. Currently considered a valid species by most taxonomic authorities. Previously considered to include the currently recognized and sympatric *A. hindei* as a subspecies (Hollister 1919, Swynnerton & Hayman 1951). Synonyms: *amalae*, *hintoni*, *manteufeli*, *pedester*, *turneri*, *vernayi*, *walambae*. Subspecies: none. Chromosome number: not known.

Description Medium-sized rodent with warm yellowish-brown pelage. Dorsal pelage yellowish-brown; hairs grey at base with ochre or brown tips; pure black hairs result in darker colour along mid-dorsal line. Flanks paler grading to yellowish-grey on lower flanks. Ventral pelage off-white; hairs grey on basal third. Head similar in colour to back; short black vibrissae. Ears darkly pigmented, with sparse dark brown hairs. Fore- and hindlimbs short, grey. Forefeet with four digits; hindfoot with five digits; all with claws. Tail moderately long (ca. 95% of HB), ringed with scales, with numerous very short bristles, brown above, pale below. Skull broad, with width >52% of length; molars broad (M¹ >3.2 mm); incisors opisthodont. Nipples: 0 + 2 = 4.

Geographic Variation Individuals from Uganda are larger in some body measurements than individuals from Zambia (see below). Geographical variation in relative tail length, e.g. tail 83% of HB in Zambia, and 94% of HB in Uganda (Delany & Neal 1966). The eastern-most population, isolated from the main geographic range

of the species, may be a separate subspecies, *A. k. vernayi* (Crawford-Cabral 1999). Analysis of intra-specific variation is required to evaluate the significance of regional morphological variation.

Similar Species

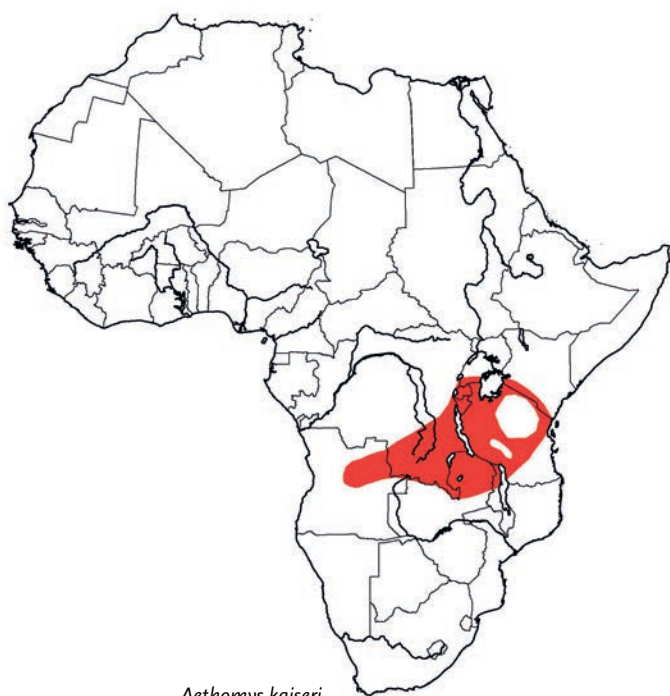
A. chrysophilus. Ventral pelage white with more grey; tail relatively longer (ca. 120% of HB); skull relatively narrower (zygomatic width <51% of length); molars narrower (M¹ <2.0 mm); incisors opisthodont.

A. nyikae. Tail relatively longer (95–115% of HB), more uniformly coloured; molars narrower (M¹ 2.0–2.2 mm); incisors orthodont.

A. hindei. Tail relatively longer west of Rift Valley (95–110% of HB), but not different east of Rift Valley; skull relatively narrower (zygomatic width <50% of length); molars narrower (M¹ <2.2 mm); incisors opisthodont.

Distribution Endemic to Africa. Northern part of Zambezi Woodland BZ extending marginally into surrounding areas. Recorded from SW Uganda, S Kenya, Tanzania, SE DR Congo, Malawi, Zambia and E Angola.

Habitat Savanna habitats with trees and shrubs (Delany 1964a, 1972, Delany & Neal 1966, Misonne & Verschuren 1966, Vesey-Fitzgerald 1966, Hubbard 1972, Cheeseman 1981). In Uganda, 93% of captures near shrubs in savanna. In Malawi, found in stream



valleys (where it co-existed with *A. chrysophilus*) (Hanney 1965), and also in woodlands where it inhabits anthills, montane forest edges at ca. 2120 m, and pine plantations (Ansell & Dowsett 1988).

Abundance Uncertain; appears to be less common than *A. chrysophilus*. Very rare in tropical grassland in Uganda (four individuals out of 349 rodents in 17 months; Cheeseman & Delany 1979).

Adaptations Terrestrial and nocturnal (Delany 1964a, Ansell & Dowsett 1988).

Foraging and Food Omnivorous, including both plant material and insects (n = 3, Hanney 1965).

Social and Reproductive Behaviour Females aggressive toward males after mating and while young are in the nest (Cheeseman 1981).

Reproduction and Population Structure Little known about reproduction in wild populations. In Uganda, pregnant ♀♀ in Oct, Nov, Jan and Apr; lactating ♀♀ in May, Jun and Nov, and several ♂♂ in reproductive condition in Jul (Southern & Hook 1963, Delany 1975). In Malawi, a ♀ collected in May was in reproductive condition and had produced at least two previous litters (Hanney 1965). Gestation: 26–28 days. Litter-size: 2.6 (1–4), n = 6 litters). Sex ratio at birth approximately 1:1. At birth, average WT = 6.1 g, ear pinnae usually unfolded and incisors erupted. Fully haired Day 3. Eyes open Day 8–10. Weaned Day 26. Average weight at weaning = 47.8 g. Young nipple-cling from birth to Day 12. A pair in captivity produced litters at intervals of 32, 40 and 37 days, indicating that mating does not always occur during postpartum oestrus (Cheeseman 1981).

Predators, Parasites and Diseases Little information. Known to harbour cutaneous *Leishmania*, which can be transmitted to humans (Githure *et al.* 1986).

Conservation IUCN Category: Least Concern.

Measurements

Aethomys kaiseri

HB: 146.5 (130–156) mm, n = 8
T: 119.7 (104–134) mm, n = 7
HF: 25.2 (24–27) mm, n = 7
E: 22.7 (22–26) mm, n = 8
WT: 95.5 (83–114) g, n = 6
GLS: 36.4 (34–38) mm, n = 9
GWS: 20.7 (19–26) mm, n = 8
M¹–M³: 6.8 (6–7) mm, n = 8
Zambia (Ansell & Ansell 1973)

HB: 158.9 (135–196) mm, n = 37
T: 149.2 (121–186) mm, n = 37
HF: 29.3 (26–33) mm, n = 36
E: 19.9 (16–23) mm, n = 30
WT: 98.0 (82–109) g, n = 17
Uganda (Delany & Neal 1966)

Key References Cheeseman 1981; Crawford-Cabral 1999.

Alicia V. Linzey, Christian T. Chimimba
& Michael H. Kesner

Aethomys namaquensis NAMAQUA VELD RAT (NAMAQUA AETHOMYS)

Fr. Rat du rochers du Namaqua; Ger. Namaqua Veld-Ratte

Aethomys namaquensis (A. Smith, 1834). S. Afr. Quart. J. 2: 160. Namaqualand, Cape of Good Hope, Cape Province, South Africa.

Taxonomy Originally described in the genus *Gerbillus*. A revision of *Aethomys* confirmed *A. namaquensis* as a valid species (Chimimba 1998). Following Chimimba (2005), Musser & Carleton (2005) refer *namaquensis* to the genus *Micaelamys*. Synonyms: *alborarius*, *arborarius*, *auricomis*, *avarillus*, *avunculus*, *calarius*, *capensis*, *centralis*, *drakensbergi*, *epupae*, *grahami*, *klaverensis*, *lechochloides*, *lechocla*, *longicaudatus*, *monticularis*, *namibensis*,

phippsi, *siccatus*, *waterbergensis* (Musser & Carleton 1993, 2005, Chimimba 2001). Subspecies: four. Chromosome number: 2n = 24.

Description Small to medium-sized rat with very long tail. Dorsal pelage yellowish-brown to reddish-brown grizzled with black that fades laterally; hairs black at base and yellowish-reddish at tip.

Ventral pelage white to pale grey or pale yellow-orange; hairs grey at the base (variable), white at tip. Pelage varies both geographically and individually. Feet white dorsally and dusky ventrally. Tail very long (ca. 140% of HB), sparsely haired, coarsely scaled and uniformly brownish-black. Anterior palatal foramina extend to first root of M^1 . Lower molar row with three cusps in the anterior row, a feature otherwise found only in *A. granti* within the genus. Nipples: $1 + 2 = 6$.

Geographic Variation Four subspecies are recognized and can be identified only by multivariate analysis of skull, dental characters and distribution (Chimimba 2001).

A. n. namaquensis: Succulent Karoo, Fynbos and the southern coastal Savanna/Grassland region of Northern Cape, Western Cape, Eastern Cape, KwaZulu–Natal and eastern Mpumalanga Provinces of South Africa.

A. n. lehocla: Nama–Karoo biome of southern Namibia, South Africa (North–West, SW Limpopo and NW Mpumalanga Provinces).

A. n. alborarius: Savanna biome of SW Angola, N Namibia, Botswana, Zimbabwe, Limpopo and W Mpumalanga Provinces of South Africa, and C Mozambique.

A. n. monticularis: Grassland biome of Free State, N Eastern Cape and SW Mpumalanga Province of South Africa, and Lesotho.

Similar Species

A. silindensis. Larger (mean HB: 174 mm); tail length similar to HB; rare, occurring only in eastern highlands of Zimbabwe.

A. granti. Tail length similar to HB; occurs only in S Cape Province of South Africa.

A. chrysophilus and *A. ineptus*. Ventral pelage greyer; chromosome number: $2n = 50$ (*A. chrysophilus*) and $2n = 44$ (*A. ineptus*). In *A. chrysophilus* and *A. ineptus*, the tail is thicker with coarser scaling, and the relative length of the tail is marginally shorter (ca. 120% of HB). However, there is considerable overlap in these characters

and distinguishing larger individuals of *A. namaquensis* from smaller individuals of *A. chrysophilus* and *A. ineptus* is problematic. The best differentiating characters for field identification are size (*A. chrysophilus* and *A. ineptus* ca. 25 g heavier), ratio of T to HB length (*A. chrysophilus* and *A. ineptus* tail shorter relative to HB), and hindfoot length (*A. chrysophilus* and *A. ineptus* on average larger) (M. Kesner & A. Linzey unpubl.).

Distribution Endemic to Africa. South–West Arid (Kalahari and Namib Deserts, Karoo), South–West Cape BZ and Highveld BZ. Widespread in southern Africa south of ca. 15°S from SW Angola to C Mozambique, including Botswana, Namibia, Zimbabwe, S. Zambia and South Africa. Not recorded in parts of S Mozambique nor from more arid areas of the central Kalahari, Karoo and Namib. Most northerly record is at higher altitudes on Mt Mulanje, Malawi (Ansell & Dowsett 1988, Happold & Happold 1992).

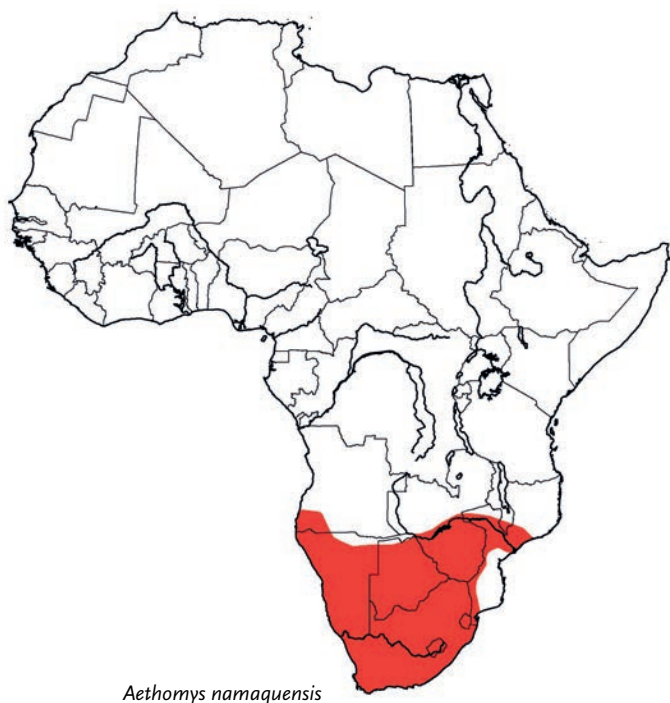
Habitat Savanna and semi-arid areas, often associated with rocky kopjes, outcrops or talus slopes dominated by medium-sized (10–20 cm) rocks. Also in adjacent non-rocky areas and occasionally in areas without rocks.

Abundance Common in suitable savannas, especially rocky habitats. Comprised 63–87% of the small mammal fauna in a talus slope habitat in W Zimbabwe (Linzey & Kesner 1997a) and the most common small mammal (38%) in rock-laden grassy slopes in N Mozambique (Gliwicz 1985). Density estimates vary geographically, seasonally and by habitat and include 2/ha (Succulent Karoo; Kerley & Erasmus 1992a), 5.4/ha (Namib; Withers 1979), 4–13/ha (Mozambique; Gliwicz 1985) and 5.2–27.3/ha (Zimbabwe; Linzey & Kesner 1997a). Biomass varies seasonally from 203 to 596 g/ha (Linzey & Kesner 1997b). Greatest numbers and biomass occurred in the early dry season of Zimbabwe and Mozambique.

Adaptations Terrestrial and semi-arboreal. Builds grass-stick nests in rock crevices and in upright or fallen hollow trees. In non-rocky habitats, grass-sticks are piled over the entrance to burrows under brush or other debris. Nocturnal, with slightly higher activity just after dusk and just before dawn. Well adapted to the large daily temperature fluctuations in rocky crevices or hollows of trees. Resting metabolic rate and thermal conductance is lower than expected, and hence individuals can exist for long periods without free water when on a low-fibre diet. However, Namaqua Rock Rats are restricted to more mesic parts of semi-arid habitats and are not as well-adapted to xeric conditions as gerbils (Buffenstein *et al.* 1985).

Foraging and Food Opportunistic. Diet is grass and foliage (60–90%), seeds (2–40%) and insects (0–8%) (Withers 1979, Gliwicz 1987, Kerley *et al.* 1990, Monadjem 1997b). The caecum is relatively large, a character found in other grass-eating herbivores (Perrin & Curtis 1980, Woodall & Mackie 1987).

Social and Reproductive Behaviour Reported as nesting singly, in pairs and small groups. For example, Choate (1972) found five nests with more than two adults, two nests with a pair, and one with a solitary individual. In captivity, adult σ σ are mutually



Aethomys namaquensis

intolerant and exhibited territorial behaviour (marking, aggression, etc.). Adult ♀♀ showed intolerance to other ♀♀. Aggression may lead to a more cooperative social structure once dominance relationships are established. In the Namib, residents had a clumped distribution while non-residents were randomly distributed (Withers 1979). Home-ranges of ♂♂ (n = 6) did not overlap with those of other ♂♂, and similarly for ♀♀ (n = 2), although there was overlap in the home-ranges of ♂♂ and ♀♀. Mean home-range: 3100 m². Withers (1979) documented a negative association between trap stations frequented by Namaqua Veld Rats and Western Rock Sengis (*Elephantulus rupestris*).

Laboratory observations suggest young are attached almost constantly to the nipples of their mother; however, ♀♀ are rarely trapped with young attached, suggesting ♀♀ do leave the young when foraging. Neal (1990 and citations therein) proposed that nipple-clinging might lessen predation in more exposed areas (rock crevices as opposed to burrows) if small litter-sizes allowed transport of the entire litter.

Reproduction and Population Structure In Mozambique, juveniles present from Jan to Apr (Gliwicz 1985) suggesting births from Dec to Mar–Apr. In Botswana, pregnant ♀♀ recorded in Sep–May, with probable peak of births in Mar and Apr (Smithers, 1983). In Zimbabwe, reproductive individuals recorded Sep–May with peak numbers toward the end of the wet season in Mar–Apr (M. Kesner & A. Linzey unpubl.). In South Africa, reproduction is seasonal and confined to the wet summer months when nutritional supplies are abundant (Muteka *et al.* 2006a). Males have a significantly higher testosterone concentration when artificially subjected to a long daylength, suggesting reproduction is partially controlled by photoperiodicity (Muteka *et al.* 2006b). Gestation: greater than 22 days. Litter-size is rather similar throughout geographic range: 3.3 (1–5, n = 43; Transvaal, Rautenbach 1982), 3.1 (2–7, n = 42; Botswana, Smithers 1983) and 3.4 (S.D. = 0.16, n = 53; Zimbabwe, Neal 1990). Birth-weight: 2.5 g. Young altricial. Nipple-cling to mother until Day 16–21. Growth rate 0.45 g/day. Eyes open Day 10–12. Weaned Day 21–26, when WT 10–15 g (Neal 1990).

Population structure in Mozambique varied during the year (Gliwicz 1985). In Oct, at the end of the dry season, populations consisted of 40% juveniles (molars not completely erupted) and 60% adults (molars fully erupted and worn). Reproduction commenced after Oct; by Jan (peak of the wet season), population structure was 15% juveniles, 30% subadults (molars erupted but unworn) and 55% adults. By Apr (beginning of the dry season), all juveniles had grown to subadults and population structure was 0% juveniles, 50% subadults and 50% adults. In Jul, population structure was 65% subadults and 35% adults. No data for Aug and Sep. Withers (1979)

found mean survival for four two-month periods was 0.57 (n = 27) in the Namib. In Zimbabwe, mean one-month survival over a 15-month study was 0.81 (SE = 0.05, n = 51) yielding an estimated two-month survival of 0.65 (M. Kesner & A. Linzey unpubl.).

In the Namib, Withers (1979) concluded that ♂♂ and ♀♀ occurred in equal proportions (n = 27). Preliminary data from other localities suggest either equality or a bias toward ♂♂: e.g. 1 ♂ : 1.19 ♀♀ (Limpopo Province, South Africa, n = 52), 1 ♂ : 0.65 ♀♀ (W Zimbabwe, n = 32) and 1 ♂ : 0.37 ♀♀ (North-West Province, South Africa, n = 35) (♂ : ♀ estimates adjusted for differential probability of capture: M. Kesner & A. Linzey unpubl.).

Predators, Parasites and Diseases Known to carry mites, ticks, fleas, various internal nematodes and cestodes. Reported to be a reservoir for Rift Valley fever virus but unlikely to be a major host. Gill *et al.* (1987) sampled throughout the Northern Cape and North-West Provinces of South Africa and found that Namaqua Rock Rats had the highest prevalence of plague antibody (3.5%, n = 170) of any small mammal in the study. They suggest Namaqua Rock Rats (with other murid rodents) may be as important as gerbils in maintaining the plague.

Conservation IUCN Category: Least Concern.

Measurements

Aethomys namaquensis

HB: 113 (80–147) mm, n = 2012

T: 154 (107–197) mm, n = 2012

HF: 26 (16–32) mm, n = 2012

E: 18 (11–24) mm, n = 2007

WT (♀♀): 48 (28–88) g, n = 166*

GLS: 31.3 (27.1–34.9) mm, n = 2730

GWS: n. d.

Breadth of braincase: 13.3 (11.9–14.7), n = 2730†

M¹–M³: 50 (33–80) mm, n = 134**

Southern Africa (Chimimba *et al.* 1999)

*C. T. Chimimba unpubl.

**Limpopo, Mpumalanga and eastern North West Provinces, South Africa (Rautenbach, 1982)

†Width at dorsal root of squamosals; if available, GWS would be slightly greater than breadth of braincase.

Key References Chimimba *et al.* 1999; Choate 1972; Linzey & Kesner 1997a; Neal 1990.

**Michael H. Kesner, Alicia V. Linzey
& Christian T. Chimimba**

Aethomys nyikae NYIKA VELD RAT (NYIKA AETHOMYS)

Fr. Rat des rochers de Nyika; Ger. Nyika Veld-Ratte

Aethomys nyikae (Thomas, 1897). Proc. Zool. Soc. Lond. 1897: 431. Nyika Plateau, Malawi.

Taxonomy Originally described in the genus *Mus*. Considered to be a synonym of *A. kaiseri* by Delany (1975) and a synonym of *A. chrysophilus* by Hanney (1965), but accepted as a valid species

by most authors (Ellerman *et al.* 1953, Davis 1975b, Ansell 1978, Musser & Carleton 1993). Synonyms: *dollmani*. Subspecies: none. Chromosome number: not known.

*Aethomys nyikae*

Description Medium-sized rodent. Pelage soft. Dorsal pelage medium to dark brown, tinged with rufous; hairs dark grey at base, with buff, rufous or black tip. Ventral pelage greyish-white (not pure white); hairs dark grey at base, off-white at tip. Head similar in colour to dorsal pelage. Ears darkly pigmented, sparsely covered with short buff or brown hairs. Chin and throat off-white. Upper surface of feet off-white. Tail long (95–115% of HB), ringed with scales, sparsely covered with short bristles, dark above, pale below. Skull: molars moderately broad (M^1 2.0–2.2 mm); incisors orthodont. Nipples: $0 + 2 = 4$.

Geographic Variation In Malawi, tail is slightly shorter than HB (95%); in Zambia, tail is longer than HB (115% of HB) (Davis 1975b).

Similar Species

A. chrysophilus. Dorsal pelage brighter and ventral pelage whiter; tail relatively longer (120% of HB); skull narrower; molars narrower ($M^1 < 2.0$ mm); incisors opisthodont.

A. kaiseri. Dorsal pelage pale brown; tail relatively shorter (70–95% of HB), pale below and with sparse hair; molars broader ($M^1 > 3.2$ mm).

Distribution Endemic to Africa, Zambezian Woodland BZ. Recorded from NE Angola, S DR Congo, N Zambia and Malawi. Limits of distribution uncertain (Musser & Carleton 1993, 2005; Crawford-Cabral 1998), although it is unlikely that the species occurs in southern Africa south of the Zambezi–Cunene rivers. Record from E Zimbabwe probably based on misidentification of a young *A. silindensis* (Chimimba *et al.* 1999).

Habitat Grasslands with bushes and trees, as well as cultivated areas (Hanney 1965). May frequent termite mounds in open woodland (Ansell 1960, De Graaff 1981). Also recorded from edge of montane forest in bracken or grass (Ansell & Ansell 1973) and along a river bank in alpine meadows with shrub patches (2200–2300 m; Chitaukali *et al.* 2001). Although mostly found at higher altitudes, has been reported to occur at 800 m (Mpemba) and 900 m (Likhubula) in S Malawi (Ansell & Dowsett 1988). Type specimen probably from lower slopes of Nyika Plateau in northern Malawi (Ansell & Ansell 1973, Ansell & Dowsett 1988).

Abundance Little information. In Malawi (Nyika Plateau), the original series included 15 *A. nyikae*, but only one *A. chrysophilus*.

Remarks Nocturnal and terrestrial. Perhaps communal or semi-communal (De Graaff 1981). Females with 2, 4 and 5 embryos reported from Zambia (Ansell 1960).

Conservation IUCN Category: Least Concern.

Measurements

Aethomys nyikae

HB: 143.4 (120–156) mm, $n = 12$

T: 165.8 (145–178) mm, $n = 12$

HF: 28.6 (28–29) mm, $n = 14$

E: 20.6 (20–21) mm, $n = 14$

WT: 90.2 (56–106) g, $n = 13$

GLS: 35.1 (34–38) mm, $n = 8$

GWS: 18.9 (18–20) mm, $n = 12$

M^1 – M^3 : 6.3 (6–7) mm, $n = 14$

Zambia (Ansell & Ansell 1973)

Key References Ansell & Ansell 1973; Hanney 1965.

Alicia V. Linzey, Christian T. Chimimba
& Michael H. Kesner

Aethomys silindensis SELINDA VELD RAT (SELINDA AETHOMYS)

Fr. Rat des rochers du Mont Selinda; Ger. Selinda Veld-Ratte

Aethomys silindensis Roberts, 1938. Ann. Transvaal Mus. 19: 245. Chirinda Forest, Mt Selinda, E Zimbabwe.

Taxonomy Ellerman *et al.* (1953) regarded *A. silindensis* as a subspecies of *A. chrysophilus*. Considered a valid species on the basis of large size and five-rooted M^1 (cf. small size and four-rooted M^1 in *A. chrysophilus*) (Meester *et al.* 1964, Davis 1975b), a viewpoint

supported by quantitative and qualitative analysis of morphological characters (Chimimba 1998, Chimimba *et al.* 1999). Differs from *A. chrysophilus* in cuticular scale pattern and groove characters of the hair (Keogh 1985). Synonyms: none. Chromosome number: not known.



Aethomys silindensis

Description Large robust rodent with brown dorsal pelage, yellowish-brown feet, and long scaly tail. The largest species of *Aethomys*. Dorsal pelage buffy-brown to dark brown; hairs brownish-grey at base and black at tip. Some black-tipped hairs also occur on head, neck and rump. Flanks paler. Ventral pelage pale grey or buffy-white. Upper lips, chin and throat buffy-white. Ears brown with thin covering of bright brown hairs. Feet bright yellowish-brown. Tail long (92–114% of HB), brownish above, paler below, with scales arranged in rings. Skull robust; pronounced supraorbital ridges, which extend posteriorly to junction with occipital crest; M^1 moderately broad (2.20–2.30 mm) with five roots; M^3 has large isolated anterior cusp. Nipples: not known.

Geographic Variation None recorded.

Similar Species

A. chrysophilus and *A. ineptus*. Similar in appearance, but smaller; molar teeth narrower ($M^1 < 2.0$ mm with four roots).

Distribution Endemic to Africa. Zambezian Woodland BZ. Known only from three localities in E Zimbabwe. Range may extend northwards along the escarpment in E Zimbabwe and into adjacent, ecologically similar areas of W Vila Pery District of Mozambique (Roberts 1951, Skinner & Smithers 1990).

Habitat Open areas with thick vegetation in valleys at ca. 700 m where rainfall is 1200–1400 mm/year. Not recorded from forest habitats. Also recorded in rocky areas with heavy vegetative cover (Smithers 1983).

Abundance Rare and restricted in distribution.

Remarks Apparently no other information available.

Conservation IUCN Category: Vulnerable.

Measurements

Aethomys silindensis

HB: 173.6 (155–200) mm, $n = 7$

T: 177.7 (166–194) mm, $n = 7$

HF: 33.6 (32–35) mm, $n = 8$

E: 22.6 (21–25) mm, $n = 8$

WT: n. d.

GLS: 40.4 (39–42) mm, $n = 6$

GWS: 16.2 (15.6–16.6) mm, $n = 6$

M^1 – M^3 : n. d.

Zimbabwe (Chimimba *et al.* 1999)

Key References Chimimba 1998; Chimimba *et al.* 1999; Keogh 1985; Smithers 1983.

Christian T. Chimimba, Alicia V. Linzey
& Michael H. Kesner

Aethomys stannarius WEST AFRICAN VELD RAT (WEST AFRICAN AETHOMYS)

Fr. Rat des rochers occidental; Ger. Zinn Veld-Ratte

Aethomys stannarius (Thomas, 1913). Ann. Mag. Nat. Hist., ser. 8, 11: 482. Kabwir, Bauchi Province, Nigeria.

Taxonomy Originally described in the genus *Epimys*. Considered to be a subspecies of *A. hindei* by Davis (1975b) and Happold (1987) but more usually considered to be a valid species (Ellerman 1941, Rosevear 1969, Hutterer & Joger 1982, Denys & Tranier 1992, Musser & Carleton 1993, 2005). See Rosevear (1969) for further details. Synonyms: none. Chromosome number: not known.

Description Medium-sized, relatively long-haired rodent with soft pelage. Description based on a single specimen (Rosevear 1969). Dorsal pelage medium-brown mixed with black and yellowish-brown

hairs. Longer 'sub-bristles' (14–15 mm) and blackish-brown 'guard hairs' (ca. 20 mm) extend beyond the pelage. Flanks greyish to pale brown. Ventral pelage white; hairs pure white or white with greyish-tan base. Colours of ventral pelage and flanks not clearly delineated. Ears with short hairs above and below. Feet densely covered with white hairs on upper surface. Tail long (ca. 110% of HB), scaly, with inconspicuous black hairs. Auditory bullae: 5.4, 6.9 mm, $n = 2$ (cf. *A. hindei*). Nipples: $1 + 2 = 6$.

Geographic Variation None recorded.

Similar Species

A. hindei. Mean values of HB and E larger, tail usually relatively shorter (95–110% of HB); auditory bullae longer (7.03 mm); distribution may overlap slightly in Cameroon.

Distribution Endemic to Africa. Guinea Savanna BZ. Recorded from N Nigeria (Happold 1987, as *A. hindei*) to N Cameroon (Mandara Mts; Eisentraut 1975).

Habitat Grassland, woodland savanna, bush, cultivated areas and forest edges where there is moderate to dense cover.

Abundance No information.

Remarks Apparently no other information available.

Conservation IUCN Category: Data Deficient.

Risk attributed to human-induced habitat loss and/or degradation. Area of geographic distribution very small and disjunct.

Measurements

Aethomys stannarius

HB: 148 (126–169) mm, n = 4

T: 152 (124–203) mm, n = 4

HF: 31 (28–33) mm, n = 4

E: 22 (20–24) mm, n = 4

WT: 92 (60–120) g, n = 3

GLS: 36.4 (34.4–39.8) mm, n = 6

GWS: 17.3 (16.3–19.0) mm, n = 6



Aethomys stannarius

M^1-M^3 : 6.4 (5.7–7.1) mm, n = 6

Nigeria and Cameroon (Rosevear 1969, Denys & Tranier 1992, CM)

Key References Rosevear 1969; Denys & Tranier 1992.

Alicia V. Linzey, Christian T. Chimimba
& Michael H. Kesner

Aethomys thomasi THOMAS'S VELD RAT (THOMAS'S AETHOMYS)

Fr. Rat des rochers de Thomas; Ger. Thomas Veld-Ratte

Aethomys thomasi (de Winton, 1897). Ann. Mag. Nat. Hist., ser. 6, 20: 327. Galanga, Angola.

Taxonomy Originally described in the genus *Mus*, but subsequently allocated to *Dasymys* by Allen (1939). Later *thomasi* was considered to be a subspecies of *Aethomys kaiseri* (Ellerman *et al.* 1953), but was re-instated as a full species by Crawford-Cabral (1999) and Musser & Carleton (1993, 2005). Difficult to distinguish from *vernayi* (now a subspecies of *A. kaiseri*) (Crawford-Cabral 1999). Synonyms: none. Chromosome number: not known.

Description Medium-sized rodent. Dorsal pelage uniformly grizzled rufous-brown. Ventral pelage greyish-white; hairs greyish-black at base, greyish-white at tip. Ears round, sparsely covered with short reddish-brown hairs. Limbs and feet short and stout; hindfeet with five plantar pads. Tail long (ca. 83% of HB), but relatively shorter than in other species in the genus, uniformly brown, with scales and evenly covered with short stiff hairs. Skull: upper molars moderately broad (M^1 : ≤ 2.2 mm); incisors opisthodont. Nipples: not known.

Geographic Variation None recorded.

Similar Species

A. kaiseri. Mean HB similar; T on average relatively longer; $M^1 > 3.2$ mm; perhaps partially sympatric in Angola.

A. bocagei. Mean HB larger ($\sigma \sigma$) or smaller ($\varphi \varphi$); T on average relatively longer; partially sympatric in Angola.

A. chrysophilus. Mean HB smaller; T on average relatively longer; $M^1 < 2.0$ mm; partially sympatric in Angola.

Distribution Endemic to Africa. Zambezan Woodland BZ. Recorded only from the plateaux of W and C Angola (Crawford-Cabral 1998). Probably parapatric with *A. kaiseri* in the highlands of C Angola (Crawford-Cabral 1999).

Habitat Uncertain. 'A large number of animals were collected on termitaria' (Crawford-Cabral 1999).

Abundance Probably rare (Crawford-Cabral 1999).

Remarks Half-grown specimens recorded in Feb, Mar, Aug and Dec; recently born young in Mar; 'appears that breeding is fairly continuous throughout the year' (Hill & Carter 1941).

Conservation IUCN Category: Least Concern.
Status needs further evaluation.

Measurements

Aethomys thomasi

HB (♂♂): 150 (142–162) mm, n = 6

HB (♀♀): 148 (140–158) mm, n = 4

T (♂♂): 124 (120–126) mm, n = 6

T (♀♀): 125 (112–135) mm, n = 5

HF (♂♂): 29 (27–31) mm, n = 6

HF (♀♀): 28 (25–30) mm, n = 4

E (♂♂): 22 (20–24) mm, n = 6

E (♀♀): 22 (20–25) mm, n = 5

WT: n. d.

GLS: 36.0 mm, n = 1

GWS: n. d.

M¹–M³: 6.5 mm, n = 1

External measurements: Angola (Crawford-Cabral 1999)

Skull measurements: Angola: type specimen



Aethomys thomasi

Key References Crawford-Cabral 1998, 1999; Hill & Carter 1941.

**Christian T. Chimimba, Alicia V. Linzey
& Michael H. Kesner**

GENUS *Apodemus*

Field Mice

Apodemus Kaup, 1829. Skizz. Entwickel.-Gesch. Nat. Syst. Europ. Thierwelt 1: 154. Type species: *Mus agrarius* Pallas, 1771.



Apodemus sylvaticus.

The genus comprises 21 species (Musser & Carleton 1993) distributed widely throughout the Palearctic region from Britain to China and Japan, and southwards to the Middle East, Nepal, Burma and N India. Member of the genus live, typically, in woods, hedgerows, field and gardens, and in other moist habitats. One species in the genus is represented in NW Africa (Morocco, Algeria, Tunisia) and is assumed to have reached Africa from Spain. None of the species in the genus that occur in Israel (and other countries of the Middle East) has reached Egypt or NW Africa. Further details are given in the species profile.

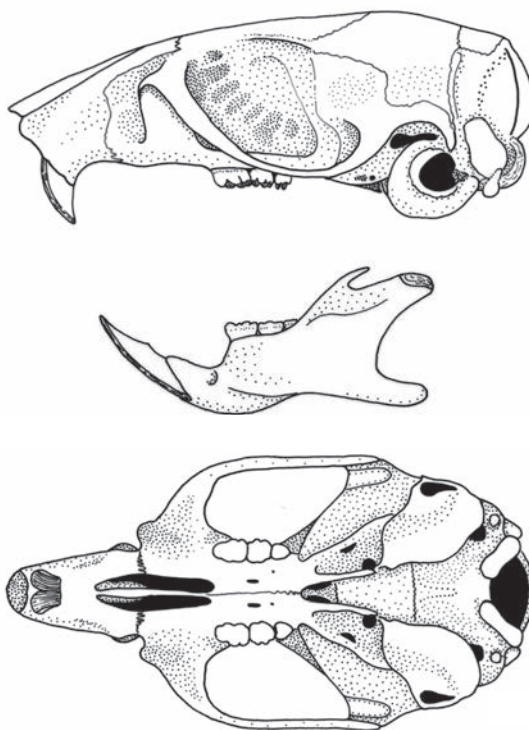


Figure 60. Skull and mandible of *Apodemus sylvaticus* (skull: MNHN 1957/538; mandible: BMNH 12.6.12.112). Details of the occlusal surface of the upper molar teeth are obscure and not included.

The characters of the genus are small size (HB: ca. 70–120 mm, WT: ca. 15–25 g), relatively long tail (usually about 100% of HB), soft pelage, brownish dorsal pelage and paler ventral pelage; narrow hindfeet with five digits, Digits 2, 3 and 4 long, Digits 1 and 5 shorter. Skull characters include rather broad braincase, long rostrum, wide anterior palatal foramina, narrow zygomatic arches, and absence of supraorbital ridges (Figure 69). Upper cheekteeth complex; M^1 larger than M^2 , M^2 larger than M^3 ; t_3 of M^1 well developed (Ellerman 1941).

The species in the genus are morphologically rather similar, and traditional morphometrics is often inadequate to distinguish between the species. Modern techniques, such as DNA sequencing of cytochrome *b* and 12S rRNA, provide better means for separating the species. There are numerous studies on the taxonomy and phylogeny of the genus in the Palearctic region (see Musser & Carleton 1993, 2005, for details and references).

The single species of the genus in Africa is *Apodemus sylvaticus*

Christiane Denys

Apodemus sylvaticus LONG-TAILED FIELD MOUSE (WOOD MOUSE)

Fr. Mulot sylvestre; Ger. Waldmaus

Apodemus sylvaticus (Linnaeus, 1758). Syst. Nat., 10th edn., 1: 62. Uppsala, Sweden.

Taxonomy Originally described in the genus *Mus*. Only information relevant to North Africa is given in this profile (see Musser & Carleton 2005 for further details of the species as a whole). The Wood Mouse in N Africa was originally described as *Mus algerus*. This specific name is no longer valid, and most authorities consider that the type specimen (now lost) was perhaps a representative of *sylvaticus*. The origins of *A. sylvaticus* in North Africa are uncertain. Either the species dispersed from Europe at the end of the last glaciation, or it was introduced through human activities. mtDNA studies show that populations of *A. sylvaticus* in N Africa are more closely related to populations in Spain, and much less related to populations from Sicily and the Balkans; human introduction from SW Europe across the Straits of Gibraltar in the early or middle Pleistocene (700,000 mya) is likely. Synonyms in Africa: *algerus*, *hayi*, *ifranensis*, *rufescens*. Subspecies: four were described from North Africa (see Saint Girons & Van Bree 1962 and Saint Girons 1972 for details) but none is now considered valid (Kock & Felten 1980, Kowalski &

Rzebik-Kowalska 1991). Analysis of many gene loci of North African specimens showed high genetic homogeneity between populations (Filippucci 1992), confirming that subspecific recognition is not warranted. Likewise, study of mtDNA restriction pattern fragments from 28 samples (several populations) throughout N Africa show that all are very homogeneous. Chromosome number: $2n = 48$, $FN = 48$ (Matsubara *et al.* 2004; non-African populations).

Description Small brownish mouse with large naked ears and bicoloured tail. Pelage soft and silky. Dorsal pelage rufous-brown or grey; hairs dark grey at base, brown at tips. Pelage darker on back and flanks due to numerous long black guard hairs on back and flanks. Colour of dorsal pelage varies geographically. Ventral pelage greyish-white; hairs dark grey on basal half, white on terminal half. Colours of dorsal and ventral pelage clearly delineated. Head similar in colour to dorsal pelage. Eyes dark, large. Ears large, darkly pigmented, round at tip, with small rufous or chestnut-brown hairs. Fore- and hindfeet white. Forefoot with four digits. Hindfoot with five digits; Digits 1 and 5 shorter than Digits 2, 3 and 4; all digits with claws. Tail long (ca. 107% of HB), with small scales arranged in rings, bicoloured, brown above, white below. Nipples: $1 + 2 = 6$.

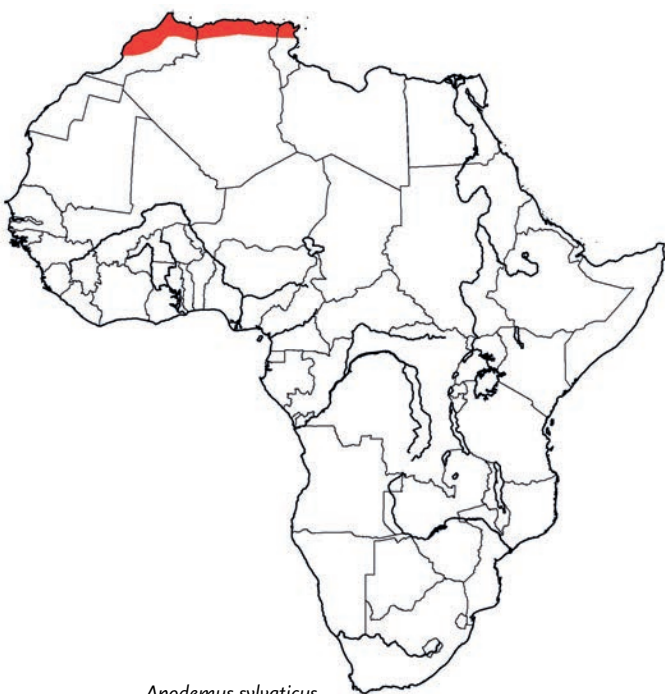
Geographic Variation Dorsal pelage varies: grey in summer and winter (Middle Atlas), grey in winter and brown in summer (coastal plains of Morocco); rufous-brown (drier habitats, High Atlas).

Similar Species

Mus spretus. Smaller in all body measurements; tail ca. 80% of HB; often syntopic in North Africa.

Distribution Mediterranean Coastal BZ. Recorded from coastal and mountainous regions of Morocco, Algeria and Tunisia. Primarily a Palearctic species, widespread in Europe and eastwards to China (see genus profile).

Habitat Shrubs on coastal sand dunes, dense forests of Middle and High Atlas Mts, pine forests and high mountain cedar forests (Aulagnier & Thévenot 1986, Kowalski & Rzebik-Kowalska 1991). Preferred habitats are where rocks and low vegetation are present (Khidas *et al.* 2002). May occur in meadows, but absent from open



Apodemus sylvaticus

and semi-arid habitats. Wood Mice avoid habitats altered by human activities, particularly agricultural areas (Khidas *et al.* 2002).

Abundance Common, especially in forested habitats. In N Algeria, Wood Mice comprised 12% of captured small mammals in mixed forest ($n = 43$, 4 spp.), 80% in *Quercus-Ilex-Olea* forests ($n = 10$, 2 spp.) and 100% in high mountain cedar forest ($n = 25$, 1 sp.) (Khidas 1993). Wood Mice tend to be less abundant in habitats where they co-exist with Algerian Mice (*Mus spretus*) (Khidas *et al.* 2002).

Adaptations Nocturnal and terrestrial. Construct burrows, often under rocks.

Foraging and Food Omnivorous, mainly seeds and fruits. The diet of Wood Mice in Algeria (assessed by analysis of stomach contents) includes seeds, acorns, fruits of *Myrtus communis* and *Ficus carica* (K. Khidas pers. comm.). In cultivated areas, leaves, stems and flowers comprise 19.5% of the diet. Arthropods comprise up to 25% of the diet. In Morocco, the diet is seeds, berries, insects, dry fruits and acorns; removal and storage of acorns is considered to assist in the regeneration of oak forests (Aulagnier & Thévenot 1986). On a yearly basis, seeds comprise 60–85% of the diet, and insects and green herbage each comprise 10% or less (Harich & Benazzou 1990).

Social and Reproductive Behaviour No information (for Africa).

Reproduction and Population Structure The timing of reproduction depends on locality. In the mountains of Morocco, reproduction occurs in the spring, summer and autumn, with peaks in spring (Mar–Apr) and autumn (Sep–Oct) (Saint Girons 1972), and ceases during the winter months (Oct–Mar). Similarly, in the mountains of Algeria (where there is snow during winter), reproduction is in spring and summer, as in Europe (Kowalski & Rzebik-Kowalska 1991). In contrast, on the hot coastal plains at lower altitudes, reproduction is limited to the cooler (winter) months of the year: in Morocco (near Rabat) from Sep to Apr, with peaks in

Nov–Dec and Feb (Harich & Benazzou 1990), and in Algeria (near Oran) pregnant ♀♀ were found only Oct–Mar (Kowalski 1985). Embryo number: 4.2 (3–6, mode 4, $n = 15$; Morocco; Harich & Benazzou 1990); 4.3 (3–5, Algeria; Kowalski 1985). Because of seasonality of reproduction, population numbers (at lower altitudes) increase from Dec to Apr, and decrease from Apr to Sep; individuals more than one year in age die during the summer months.

Predators, Parasites and Diseases Remains found occasionally in pellets of *Tyto alba* (Kowalski & Rzebik-Kowalska 1991) in Algeria. May also be preyed upon by jackals (Khidas 1988) and the owl *Athene noctua* (B. Baziz pers. comm.). Fleas found on Wood Mice in Algeria include *Typhloceras p. poppei*, *Rhadinopsylla masulana* and *Leptopsylla taschenbergi* (Beaucornu & Kowalski 1985).

Conservation IUCN Category: Least Concern.

Widespread and common, although geographic range in Africa is limited and category of threat unknown.

Measurements

Apodemus sylvaticus

TL: 193.3 (171–221) mm, $n = 145^*$

T: 100.5 (81–120) mm, $n = 145$

HF: 21.7 (19.5–24) mm, $n = 171$

E: 17.4 (14–19) mm, $n = 155$

WT: 25.7 (16–39) g, $n = 9$

GLS: 23.3 (21.4–25.1) mm, $n = 156$

GWS: 12.9 (11.4–13.8) mm, $n = 149$

M¹–M³: 4.1 (3.8–4.4) mm, $n = 171$

Algeria (Kowalski & Rzebik-Kowalska 1991)

*HB is typically 95–110 mm (BMNH).

Key References (Africa only) Aulagnier & Thévenot 1986; Harich & Benazzou 1990; Khidas *et al.* 2002; Kowalski & Rzebik-Kowalska 1991.

Christiane Denys

GENUS *Arvicanthis*

Grass Rats

Arvicanthis Lesson, 1842. Nouv. Tabl. Regn. Anim. Mammalifères, p. 147. Type species: *Lemmus niloticus* É. Geoffroy Saint-Hilaire, 1803.

The genus currently includes seven species, and is one of the most widespread and abundant of genera of African rodents (Table 30). Species of the genus are recorded from grassland to wooded savannas and moorlands of sub-Saharan Africa, in mesic habitats in semi-desert regions, and even from some massifs and wadis of the Sahara. The distribution extends from Senegal to Egypt, and southwards through eastern Africa to Zambia. In Ethiopia, the four species show altitudinal zonation: *A. niloticus* sea level to 2000 m, *A. neumanni* 400–1500 m, *A. abyssinicus* 2000–3400 m and *A. blicki* 2750–4100 m. Extralimital populations (of *A. niloticus*) can be found in coastal Yemen and Oman.

Arvicanthis are medium-sized murine rodents characterized by a distinctive harsh grizzled pelage. The genus is closely related to the genera *Desmomys*, *Lemniscomys*, *Mylomys*, *Pelomys* and *Rhabdomys*, but

recognizable by its mammary formula ($1 + 2 = 6$), short muzzle and a tail usually shorter than head and body. It can be distinguished from *Desmomys*, *Mylomys* and *Pelomys* by ungrooved upper incisors, and from *Lemniscomys* and *Rhabdomys* (both of which have very obvious stripes contrasting with the surrounding pelage) by the presence of a single, usually faint to nearly invisible, black mid-dorsal stripe. Unlike *Desmomys*, *Lemniscomys*, *Mylomys* and some *Pelomys*, Digit 5 on the forefoot is greatly reduced but still bears a claw. Skull characters include a widening of the median part of zygomatic arch, a wide zygomatic plate, a narrow interorbital constriction and strong supraorbital ridges (Figure 61). The presence of five roots at M¹, a particularly large M³ and pronounced dental lamination scheme also distinguish the genus from the previously mentioned ones.

Table 30. Species in the genus *Arvicanthis*. Arranged in order of increasing mean head and body length.
(n. d. = no data.)

| Species | HB mean (mm) | T mean (mm) [% of HB] | Dorsal pelage | GLS mean (mm) | Chromosome number | Notes |
|-----------------------|----------------------|---------------------------|---|------------------------|----------------------|---|
| <i>A. neumanni</i> | 97.8 | 93.0 [95%] | Brownish-orange; speckled cream | 27.6 | 2n = 62, FN = 66–67 | Ethiopia, Somalia, Kenya (dry, low altitudes) |
| <i>A. nairobae</i> | 139 | 101 [73%] | Chestnut-brown | 35.7 (♂ ♂), 32.4 (♀ ♀) | 2n = 62, aFN = 78 | Kenya and Tanzania, probably only east of Rift Valley (also ? S Ethiopia) |
| <i>A. abyssinicus</i> | 140.5 | 110.4 [80%] | Dark brown, boldly flecked | 32.0 | 2n = 62, FN = 68 | Ethiopia, mostly west of Rift Valley (2000–3400 m) |
| <i>A. rufinus</i> | 143.8 | 138.2 [96%] | Buffy-brown, flecked black | 33.6 | 2n = 62, aFN = 76 | Western West Africa, eastwards to Nigeria |
| <i>A. niloticus</i> | 150.8 | 129.7 [ca. 85%] | Buffy-brown, heavily speckled black and yellow | 32.9 | 2n = 62, aFN = 62–64 | Widespread. Nile Valley, Ethiopia (<i>dembeensis</i>), East Africa |
| <i>A. ansorgei</i> | 151 | 134 [90%] | Buffy-brown, heavily speckled | 33.4 | 2n = 62, aFN = 74–76 | Guinea-Bissau, Senegal, Mali, Burkina |
| <i>A. blicki</i> | 161 (♂ ♂), 158 (♀ ♀) | 100 (♂ ♂), 99 (♀ ♀) [62%] | Silvery-brown to greyish-brown, speckled silver/white | n. d. | 2n = 48, aFN = 64 | Ethiopia, east of Rift Valley (2750–4000 m) |

Arvicanthis rats are terrestrial, and often nest in very shallow burrows or directly under grasses on the ground surface. A significant part of their activity may be diurnal, and they often do well in the

immediate vicinity of humans (gardens, enclosures and irrigated farmlands), although rarely in houses. They are predominantly herbivorous. Population numbers may become very large when environmental conditions are favourable, and they may be potentially harmful to agriculture (especially *A. niloticus* in the Sahel Savanna BZ). They are also known as hosts of various viral, bacterial or protozoan diseases transmissible to humans.

Species within the genus were traditionally distinguished by pelage colour and body measurements, but identification is complicated by considerable inter-individual variability. Recent investigations using cytogenetic and molecular data have revealed the presence of at least three sibling species (*A. ansorgei*, *A. niloticus* and *A. rufinus*) in western and central Africa, where the single species *A. niloticus* was previously recognized. These studies have also shown that the diversity within the genus is organized in two well-differentiated clades that may have split around 4 mya: one clade contains *A. abyssinicus*, *A. blicki*, *A. neumanni* and *A. niloticus*, and the other *A. ansorgei*, *A. nairobae* and *A. rufinus*. Morphological, cytogenetic and molecular analyses have confirmed that the Ethiopian species *A. dembeensis* is synonymous with *A. niloticus*. The definition and distribution limits of several species (*A. ansorgei*, *A. nairobae*, *A. neumanni*, *A. rufinus*) require further investigation, and additional species may prove to be present, especially in central and eastern Africa.

The species are distinguished on karyology, size, pelage colouration (and amount of ‘speckling’) as well as on cytological and molecular characters.

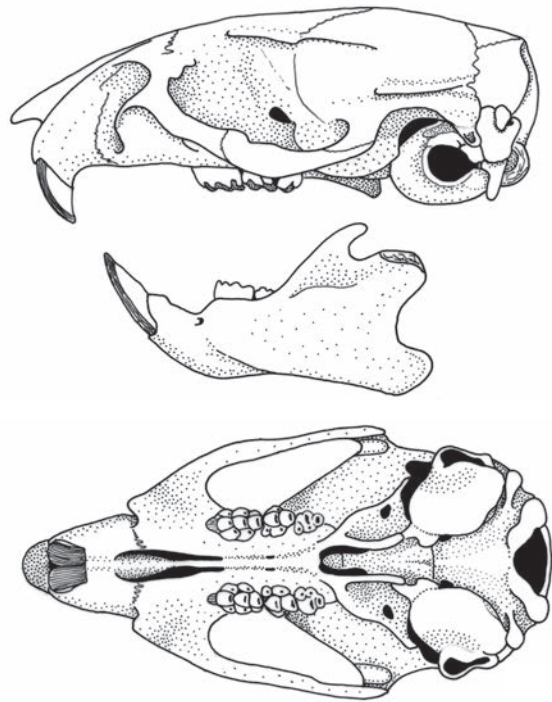


Figure 61. Skull and mandible of *Arvicanthis niloticus* (HC 62).

Laurent Granjon & Jean-François Ducroz

Arvicanthis abyssinicus ETHIOPIAN GRASS RAT (ABYSSINIAN GRASS RAT)

Fr. Rat roussard d'Abyssinie; Ger. Äthiopische Grasratte

Arvicanthis abyssinicus (Rüppell, 1842). Mus. Senckenberg. 3: 104. Entschetgab, Simien Mts, Ethiopia.

Taxonomy Originally described as *Mus abyssinicus*. Many geographic varieties of this species have been described in Ethiopia based upon variation in pelage colour and size (Afework Bekele *et al.* 1993). However, Rupp (1980), Demeter (1982) and Yalden *et al.* (1976) consider that *Arvicanthis* consists of series of sibling species/subspecies – *A. abyssinicus*, *A. blicki*, *A. somalicus* and *A. niloticus dembeensis*, which live in different habitats and at different altitudes. Each of these forms is considered to be a separate taxon here. Synonyms: *fluvicinctus*, *rufodorsalis*, *saturatus*. Subspecies: none. Chromosome number: $2n = 62$, $FN = 68$ (Capula *et al.* 1997).

Description Medium-sized dark rodent, intermediate in size between *A. somalicus* and *A. blicki*. Pelage slightly rough and coarse. Dorsal pelage brownish-black, boldly streaked with ochre or cream, especially on flanks; dorsal hairs 8–10 mm, black at base, ochre or cream or black at tip; black basal colouration clearly visible on surface of pelage. Pure black mid-dorsal stripe from neck to base of tail in some individuals. Ventral pelage greyish-ochre; hairs 3–4 mm, greyish-black at base, cream or white on terminal half. Head similar in colour to dorsal pelage. Ears rounded, pigmented brown or rufous, sparsely covered with short rufous hairs. Fore- and hindlimbs ochre-rufous above, almost naked below; claws pale. Tail long (ca. 80% of HB), bicoloured with small bristles, dark above, pale below; clearly ringed with small scales. Some 'albino' individuals with very pale creamy-cinnamon pelage recorded in Horogudru District, Wollega Province, Ethiopia (BMNH). Skull: ungrooved upper incisor teeth. Nipples: not known.

Geographic Variation None recorded.

Similar Species

A. blicki. On average larger; east of the Rift Valley in Ethiopia, mostly at higher altitudes (2750–4100 m); chromosome number: $2n = 48$, $FN = 64$.

A. neumanni. On average much smaller; lowlands of Ethiopia at lower altitude (400–1500 m); chromosome number: $2n = 62$, $FN = 66$ –67.

A. niloticus. On average slightly larger with longer tail (mean 139 mm); lowlands of Ethiopia at lower altitudes (0–2000 m), widespread in sub-Saharan Africa and East Africa; chromosome number: $2n = 62$; $aFN = 62$ –64.

Distribution Endemic to Africa. Afromontane–Afroalpine BZ. Widely distributed in the grasslands of the Ethiopian plateaux, mainly west of the Rift Valley and marginally to the east of the Rift Valley. Altitudinal range: 2000–3400 m (Rupp 1980).

Habitat Open grasslands usually at altitudes above 2000 m. In the Simien Mts, short grass steppe, rocky areas in short grass steppe, and *Carex* moorland along creeks are preferred habitats (Güttinger *et al.* 1998). Avoids heavily grazed areas as well as long grass–short grass mosaics. May occur in cereal fields at higher altitudes (Güttinger *et al.* 1998).

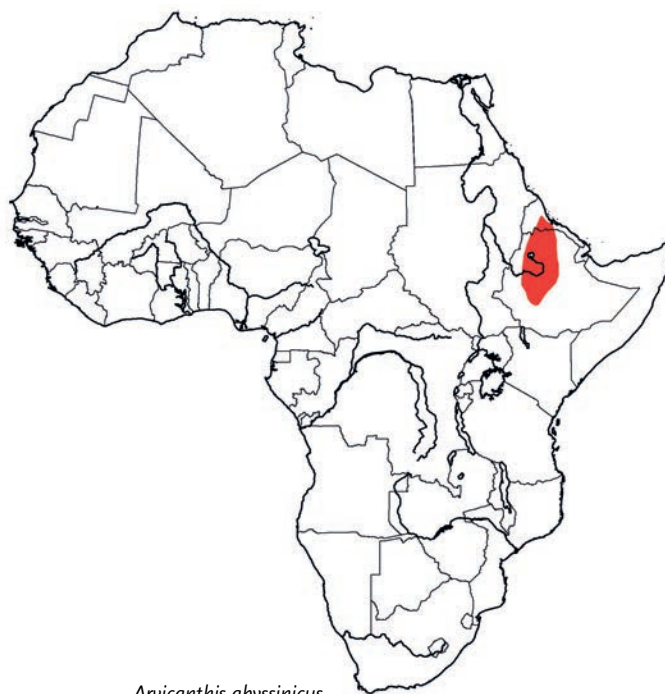
Abundance Abyssinian Grass Rats comprised 77% of the small rodents ($n = 57$) in the grasslands of the Simien Mountains (Müller 1977). Population numbers are highest in the late dry season (Jan–Mar) after many young have entered the population, and lowest in the wet season (May–Oct). Density varied from 65–75/ha (wet season) to 130–250/ha (dry season), and biomass varied from 4900–6800 g/ha (wet season) to 14,000–16,500 g/ha (dry season) (Müller 1977). Another study also found this species to be the commonest species in the Simien Mts (59 of 173; 6 spp. rodents, 1 sp. shrew) (Güttinger *et al.* 1998).

Adaptations Diurnal and terrestrial. The pelage is rather thin and animals may suffer from moist cold; hence activity is during the day and reproduction is limited to the dry season (when conditions are most favourable).

Foraging and Food No detailed information but presumed to be herbivorous.

Social and Reproductive Behaviour These grass rats have been observed entering their nests in groups, suggesting that they are gregarious. Home-range varied according to sex and season of the year: ♂♂ – 2750 m² (wet season), 1400 m² (dry season); ♀♀ – 950 m² (wet season), 600 m² (dry season) (Müller 1977). Grass rats live syntopically with *Stenocephalemys griseicauda*.

Reproduction and Population Structure In the Simien Mountains N. P., Ethiopia, reproduction occurs mainly in the first

*Arvicanthis abyssinicus*

half of the dry season (Oct–Dec) and ceases during the wet season (Mar–Sep) (Müller 1977). Young animals enter the population mostly in Nov–Jan. Litter-size: 5.6 (3–9, $n = 18$). Weight at birth: ca. 4 g (data from captive animals; Afework Bekele unpubl.).

Predators, Parasites and Diseases Birds of prey are frequently observed perching and catching individuals.

Conservation IUCN Category: Least Concern.

Deforestation of the highlands has expanded the range of the species by creating more open grounds. The species has become a pest of crops in fields and storage places.

Measurements

Arvicanthis abyssinicus

HB: 140.5 (132–160) mm, $n = 10$

T: 110.4 (101–142) mm, $n = 10$

HF: 26.4 (25–30) mm, $n = 10$

E: 17.6 (16–20) mm, $n = 10$

WT: 112.4 (90–130) g, $n = 10$

GLS: 32.0 (29.2–33.9) mm, $n = 10^*$

GWS: 17.4 (16.4–18.1) mm, $n = 10^*$

M^1 – M^3 : 7.0 (6.6–7.4) mm, $n = 10^*$

Entoto Mountains, Ethiopia (Afework Bekele, unpubl.)

*Ethiopia (several localities; BMNH)

Key References Afework Bekele *et al.* 1993; Capula *et al.* 1997; Müller 1977; Rupp 1980; Yalden *et al.* 1976.

Afework Bekele

Arvicanthis ansorgei ANSORGE'S GRASS RAT (SUDANIAN ARVICANTHIS)

Fr. Rat roussard soudanien; Ger. Ansorges Grasratte

Arvicanthis ansorgei Thomas, 1910. Ann. Mag. Nat. Hist., ser. 8, 5: 353. Gunnal, Guinea-Bissau.

Taxonomy Long considered as belonging to *A. niloticus* (Rosevear, 1969). Characteristics of the chromosomes distinguish this species from its sibling species *A. niloticus* and *A. rufinus* (Ducroz 1998; Fadda 1998; Volobouev *et al.* 2002). Synonyms: none. Chromosome number: $2n = 62$; aFN = 74–76.

Description Medium-sized, robustly built rat. Dorsal pelage usually buffy-brown heavily flecked with black and yellow; hairs dark brown at base with buff-yellowish subterminal zone and blackish tip. Rump and base of tail often suffused with pale red, especially in older individuals. Ventral pelage whitish to grey. Head blunt, short muzzle. Ears rounded and reddish. Digit 5 on forefeet considerably reduced but still functional; Digit 1 vestigial. Soles of hindfeet generally dark. Tail long (ca. 90% and usually shorter than HB), dark above, whitish or pale brown below. Skull: ungrooved upper incisor teeth. Nipples: $1 + 2 = 6$.

Geographic Variation None recorded.

Similar Species

A. niloticus. Chromosome number: $2n = 62$, aFN = 62–64; more northern distribution.

A. rufinus. Chromosome number: $2n = 62$, aFN = 70; more south-eastern distribution (Ducroz 1998, Fadda 1998, Volobouev *et al.* 2002).

Distribution Endemic to Africa. Sudan Savanna BZ of West Africa. Recorded from Guinea-Bissau (type locality) and Casamance (SW Senegal) across Mali to S Burkina (Ducroz 1998, Dobigny *et al.* 2002b). Southern and eastern limits of distribution insufficiently known. Sympatry with *A. niloticus* recorded in a vast area of central Mali (Sicard *et al.* 2004).

Habitat Sudan savannas and grasslands (annual rainfall 1000–2500 mm), except in the inner delta of the Niger R. in Mali where it occurs in more arid climatic conditions (Sicard *et al.* 2004). Also found in bushland, croplands, farms and villages, but rarely inside houses.

Abundance May be locally very abundant, as along the Niger R. south of Bamako (Sicard *et al.* 2004).

Adaptations Mainly diurnal, with activity peaks at dawn and dusk, reportedly less diurnal than *A. niloticus* (B. Sicard unpubl.).



Arvicanthis ansorgei

Builds nests of fine grass on the surface or in shallow burrows. Intensively uses runways radiating out from the nest through matted grass. More difficult to catch using live-traps than *A. niloticus* (L. Granjon & J.-F. Ducroz unpubl.).

Foraging and Food Probably mainly herbivorous.

Social and Reproductive Behaviour Gregarious species, sometimes found in colonies of several adult ♂♂ and ♀♀, with young (B. Sicard, unpubl.). Displays less aggressiveness than *A. niloticus* when handled, but apparently quite aggressive towards conspecifics in captivity (J.-M. Duplantier & L. Granjon unpubl.).

Reproduction and Population Structure Litter-size: 5.40 ± 0.28 ($n = 9$ pairs; S Senegal and Mali; Ducroz *et al.* 1997). Reproductive biology insufficiently known, but probably less prolific than *A. niloticus*.

Predators, Parasites and Diseases No information.

Conservation IUCN Category: Least Concern.

Measurements

Arvicanthis ansorgei

HB: 151.0 (128–182) mm, $n = 87$

T: 134.6 (102–169) mm, $n = 78$

HF: 33.0 (28–38) mm, $n = 87$

E: 19.6 (16–22) mm, $n = 87$

WT: 113.9 (70–219) g, $n = 87$

GLS: 33.4 (30.7–37.1) mm, $n = 12$

GWS: 17.7 (16.1–19.7) mm, $n = 11$

M^1 – M^3 : 6.9 (6.5–7.4) mm, $n = 12$

Senegal

Body measurements (karyotyped specimens): Mali (B. Sicard *et al.* unpubl.).

Skull measurements (karyotyped specimens): Burkina and Senegal (MNHN)

Key Reference Sicard *et al.* 2004.

Laurent Granjon & Jean-François Ducroz

Arvicanthis blicki BLICK'S GRASS RAT

Fr. Rat roussard d'Ethiopie; Ger. Blicks Grasratte

Arvicanthis blicki Frick, 1914. Ann. Carnegie Mus. 9: 20. Hora Mt base camp, Southern Chilalo Mts, Ethiopia. 2750 m.

Taxonomy Originally described as a subspecies of *A. abyssinicus*, but now considered to be a valid species. In morphology, ecology, geographic distribution and habits, *A. blicki* is a very distinctive species (Musser & Carleton 2005). More closely related to *A. abyssinicus* than to any other species of *Arvicanthis*. Synonyms: none. Chromosome number: $2n = 48$, $aFN = 64$ (Corti *et al.* 1996).



Description Large rodent, silvery-brown with faint dark mid-dorsal stripe; the largest species of *Arvicanthis* in Ethiopia. Dorsal pelage greyish-brown, strongly flecked with creamy-white or silvery-white; hairs 7–10 mm, greyish-black at base, with terminal band of pale ochre, creamy-white or silvery-white, and usually with dark russet or black tip. Thin black mid-dorsal stripe from neck to base of tail; sometimes obscure or absent. Flanks paler than dorsal pelage, due to absence of dark-tipped hairs. Ventral pelage paler than dorsal pelage; hairs rather sparse, ca. 5 mm; hairs pale brown at base, cream, buff or white at tip. Head similar to dorsal pelage; black vibrissae. Ears small, rounded, darkly pigmented, and well covered with short buff or cream hairs. Subauricular and postauricular white or cream spot (not rufous as in many *Arvicanthis* spp.). Limbs similar in colour to body. Forelimb with four digits, Digit 1 absent, Digit 5 reduced. Hindfoot with five digits, Digits 1 and 5 reduced. All digits with dense hairs above and dark claws. Tail short (ca. 62% of HB), dark above with dark bristles, paler below. Skull: ungrooved upper incisor teeth. Nipples: not known.

Geographic Variation None recorded.

Similar Species

A. abyssinicus. On average smaller (mean HB: 140 mm); mostly west of Rift Valley in Ethiopia at lower altitude (2000–3400 m); chromosome number $2n = 62$, $aFN = 68$.

A. neumanni. Much smaller (mean HB: 97 mm); lowlands at lower altitude (400–1500 m); chromosome number: $2n = 62$, $FN = 66$ –67.

A. niloticus. On average smaller (mean HB: 153 mm); lowlands at lower altitude (0–2000 m).

Distribution Endemic to Africa. Afromontane–Afroalpine BZ. Confined to plateaux of Ethiopia, east of Rift Valley, at high altitudes from 2750 to 4100 m (Yalden *et al.* 1976, Yalden & Lagen 1992). Probably occurs only in Chilalo and Bale Mts of Ethiopia.

Habitat Grasslands at medium and high altitudes. Also found in afroalpine habitats (3400–4200 m) characterized by short, sparse vegetation, heavy frosts and low rainfall (Sillero-Zubiri 1994).

Abundance Population numbers fluctuate seasonally, increase during the dry season (Nov–Jan) and fluctuate during the mid-wet season (Jun–Jul). Sillero-Zubiri *et al.* (1995a) recorded densities of 21/ha on the Sanetti Plateau in Bale Mountains N. P. (4050 m), and 53/ha in the Web Valley (3450 m).

Adaptations Diurnal and terrestrial. Trapping results showed that 80% of individuals (n = 584) were captured during the morning (assessed as 07:00–12:30h) and 20% during the afternoon (assessed as 12:30–18:30h). Observations showed few animals (this species and *Lophuromys melanonyx*) were above ground before about 09:00h or after about 15:30h (Sillero-Zubiri *et al.* 1995a). Lives in colonies in burrows, often in abandoned *Tachyoryctes macrocephalus* burrows.

Foraging and Food Herbivorous. The few records from afroalpine moorland (3900 m) show that the diet is mostly dicotyledonous leaves, as well as some monocotyledonous leaves (Yalden & Lagen 1992).

Social and Reproductive Behaviour Colonial, living in mixed colonies with *Lophuromys melanonyx*. When alarmed, emits a high-pitched whistle to provide warning of any potential danger (Yalden & Lagen 1992).

Reproduction and Population Structure Reproduction occurs throughout the year; with the greatest number of animals reproducing in the wet season (Apr–Oct) and the least number in the dry season (Nov–Mar). Pregnancies reach peaks (75%) in May and Sep, suggesting at least two litters/♀/year. Embryo number: 3.24 (range of means 2.31–4.17, n = 25; Sillero-Zubiri 1994). The proportion of juveniles in the population is highest (ca. 60%) at the beginning of the dry season (Nov/Dec), but declines throughout the

rest of the dry season and into wet season, to a minimum of 0% in Sep (Sillero-Zubiri *et al.* 1995a). Interestingly, the number of trappable juveniles does not increase markedly in Jul and Aug after the peak of pregnant ♀♀ in Jun, whereas it does increase markedly in Nov and Dec after the peak in Sep (Sillero-Zubiri *et al.* 1995a), suggesting better survival of juveniles in the dry season than in the wet season.

Predators, Parasites and Diseases Blick's Grass Rats are important prey for the Ethiopian Wolf *Canis simensis*; their remains occurred in 54% of predator scats and formed 27% of prey volume (n = 689 predator scats), and were the second most important prey species after the mole-rat *Tachyoryctes macrocephalus* (69% of predator scats). In 'cafeteria' tests, this species is much preferred as a source of food than are Black-clawed Brush-furred Rats *Lophuromys melanonyx* (40% occurrence) (Sillero-Zubiri & Gottelli, 1995).

Conservation IUCN Category: Near Threatened.

Since this species is an important source of food for the endangered Ethiopian Wolf, the survival of the wolf is partly dependent upon the presence of the species.

Measurements

Arvicanthis blicki

HB (♂♂): 161 (149–173) mm, n = 196

HB (♀♀): 158 (149–167) mm, n = 203

T (♂♂): 100 (92–108) mm, n = 193

T (♀♀): 99 (87–111) mm, n = 202

HF (♂♂): 30.8 (30–32) mm, n = 88

HF (♀♀): 30.0 (29–31) mm, n = 87

E (♂♂): 19.0 (17–21) mm, n = 87

E (♀♀): 19.2 (17–21) mm, n = 87

WT (♂♂): 128.0 (104–152) g, n = 198

WT (♀♀): 124.0 (106–142) g, n = 207

GLS: n. d.

GWS: n. d.

M¹–M³: n. d.

Bale Mts, Ethiopia (Sillero-Zubiri *et al.* 1995b)

Key References Corti *et al.* 1996; Sillero-Zubiri 1994; Sillero-Zubiri *et al.* 1995a; Yalden 1988; Yalden *et al.* 1976.

Afewerk Bekele

Arvicanthis nairobae NAIROBI GRASS RAT

Fr. Rat roussard du Kenya; Ger. Nairobi-Grasratte

Arvicanthis nairobae J. A. Allen, 1909. Bull. Amer. Mus. Nat. Hist. 26: 168. Nairobi, Kenya.

Taxonomy The name *nairobae* is the oldest name applicable to samples from east of the Rift Valley in Kenya and Tanzania. Closely related to *A. niloticus* from west of the Rift Valley, and to *A. neumanni*. Two species, *A. nairobae* and *A. neumanni*, are broadly sympatric, and their morphological and geographical relationships require investigation (Musser & Carleton 1993). Ducroz *et al.* (1998), however, have shown, by cytochrome *b* sequencing, that *A. nairobae*

is more closely related to a group of West and central African species (*A. ansorgei*, *A. rufinus*) than to East African species, a result confirmed by Castiglia *et al.* (2003) on karyological grounds. See Musser & Carleton (2005) for further comments. Synonyms: *chanleri*, *pallascens*, *praeceps*, *virescens*. Subspecies: none. Chromosome number: 2n = 62, aFN = 78.

Description Medium-sized grass rat. Dorsal pelage grizzled chestnut-brown. Ventral pelage tan and softer in texture than dorsal pelage. Ears small, held close to head and covered with short brown hairs. Tail short (ca. 73% of HB). Skull: ungrooved upper incisor teeth. Males on average larger than ♀♀.

Geographic Variation None recorded.

Distribution Endemic to Africa. Southern part of Somalia–Masai Bushland BZ, mostly in the highland areas of East Africa. The distribution is uncertain because of the similarity of the species with the Nile Grass Rat *A. niloticus*. Distribution is probably east of the Rift Valley from C Kenya to E and C Tanzania. May extend northwards into S Ethiopia.

Habitat Grasslands and savannas. Colonies of *A. nairobae* are usually found where there is thick woody cover with an understorey of grass, and occasionally in open grassland. Colonies can often be found under dead fallen trees, and especially in the walls of man-made bomas (livestock enclosures made from branches of *Acacia* trees and shrubs piled into fences). In both of these habitats, the exclusion of grazing by ungulates results in thick, tall grass, which supplies both food and cover.

Abundance May be extremely abundant in the walls of bomas, where they are the most numerous species of rodent, comprising 60–90% of rodents. Densities in walls of bomas may reach 100–200 rats/ha.

Adaptations Exclusively diurnal. Even during the hottest times of the year, individuals are fully active during the heat of the day. They do not climb well, but are extremely fast runners. Well-worn trails radiate out and branch for 10–15 m from the centre of the colony. Nairobi Grass Rats can be observed running within the walls of the boma and foraging for seed heads of grasses and leaves close to their trails.

Foraging and Food Little information, but probably similar to Nile Grass Rats (some publications on ‘Nile Rats’ may refer to this species). Probably granivorous and omnivorous, feeding primarily on seed heads and grass leaves. The diet of *Arvicanthis* sp. (possibly *A. nairobae*) in Meru N. P. (Kenya) was mostly grass, with smaller quantities of other plants and arthropods (Neal 1981).

Social and Reproductive Behaviour Very social, living in large colonies.

Reproduction and Population Structure Reproduction is seasonal. Pregnant ♀♀ are captured most often in the wet season (May–Jul) but litters are found occasionally at other times of year. A similar pattern of reproduction recorded for *Arvicanthis* sp. (possibly *A. nairobae*) in Meru N. P. (Neal 1981), where embryo number was 5.5 (2–12). Larger ♀♀ may have up to 27 placental scars (S. Takata unpubl.).



Arvicanthis nairobae

Predators, Parasites and Diseases Predators include snakes, mongooses and genets (which must capture them at dusk). One adult individual (possibly the mother) was seen chasing a snake (*Psammophis* sp.) that was carrying a young rat (approximately 10 days old) into a tree. Fleas (*Xenopsylla* sp.), mites and lice are recorded from wild Nairobi Grass Rats, although ectoparasite loads are generally lower than on other similar-sized species in the same area (S. Takata unpubl.).

Conservation IUCN Category: Least Concern.

Measurements

Arvicanthis nairobae

HB: 139 (118–167) mm, n = 246

T: 101 (94–129) mm, n = 246

HF: 26 (22–30) mm, n = 183

E: 17 (15–19) mm, n = 181

WT (♂♂): 91 (62–135) g, n = 141

WT (♀♀): 76 (51–124) g, n = 199

GLS (♂♂): 35.6, 35.8 mm, n = 2

GLS (♀♀): 32.4 (30.2–34.4) mm, n = 7

GWS (♂♂): 17.6, 18.3 mm, n = 2

GWS (♀♀): 16.9 (16.2–17.7) mm, n = 7

M¹–M³: 6.4 (6.2–6.8) mm, n = 9

Laikipia District, Kenya (S. Takata unpubl.)

Key Reference Neal 1981.

S. Takata

Arvicanthis neumanni NEUMANN'S GRASS RAT (SOMALI GRASS RAT)

Fr. Rat roussard de Neumann; Ger. Neumann-Rennmaus

Arvicanthis neumanni (Matschie, 1894). Sber. Ges. Naturf. Freunde Berlin 1894: 204. Barungi, Kondoa District, Central Tanzania.[*Arvicanthis somalicus* Thomas, 1903. Proc. Zool. Soc. Lond. 1902 (2): 312 [1903]. Shuk (= Sheik), Somalia.]

Taxonomy Formerly included in *A. niloticus* but now considered to be one of the four species of *Arvicanthis* in Ethiopia (Yalden *et al.* 1976, Rupp 1980, Demeter 1982, Demeter & Topal 1982, Corbet & Hill 1991). Musser & Carleton (1993) referred to this species as *A. somalicus* (with *neumanni* as a synonym), but in 2005 these authors referred to *A. neumanni* (with *somalicus* as a subspecies). Studies in Ethiopia (as cited here) refer to this species as *A. somalicus*. Whether there are one or two species within '*A. neumanni*' requires further investigation (see Fadda *et al.* 2001, Musser & Carleton 2005). The relationship of this species with *A. nairobiae* is unclear and requires investigation. Synonyms: *reptans*, *somalicus*. Subspecies: none. Chromosome number: $2n = 62$, $FN = 66-67$ (as *A. somalicus*; Awash N. P., Ethiopia; Baskevich & Lavrenchenko 2000).

Description Smallest and palest of the *Arvicanthis* spp. in East Africa. Dorsal pelage brownish-orange, speckled with cream, ochre or grey; hairs grey or black on basal half, ochre or rufous or grey on terminal half. Ventral pelage paler than dorsal pelage; hairs grey on basal half, white or cream on terminal half. Head similar in colour to dorsal pelage; black vibrissae. Ears small, rounded, with short ochre or rufous hairs. Fore- and hindfeet rufous or ochre above. Digits with pale claws. Tail long (ca. 95% of HB). Skull: ungrooved upper incisor teeth. Nipples: not known.

Geographic Variation None recorded.

Similar Species

- A. abyssinicus*. Larger (mean HB: 140 mm); Ethiopia west of Rift Valley at higher altitude (2000–3400 m); chromosome number $2n = 62$, $aFN = 68$.
A. blicki. Much larger (mean HB: 161 mm); Ethiopia east of the Rift Valley at higher altitudes (2750–4100 m); chromosome number: $2n = 48$, $FN = 64$.
A. niloticus. Larger (mean HB: 153 mm); chromosome number: $2n = 62$; $aFN = 62-64$.

Distribution Endemic to Africa. Somalia–Masai Bushland BZ. Occurs in dry low-altitude habitats in Ethiopia, Somalia and Kenya. In Ethiopia, occurs sympatrically with *A. niloticus* (as *A. dembeensis*) in the Awash N. P. and the lower Omo Valley of Ethiopia (Hubert 1978b).

Habitat Dry bushy and savanna regions from 400 to 1500 m. Frequents arid regions where the ground vegetation is scarce. At Metahara, occurs in sparse *Acacia* scrub where there is little herbaceous vegetation (Demeter 1982).

Abundance Very little information available. However, remains of this species are much more numerous (18:1) than those of

*Arvicanthis neumanni*

A. niloticus (as *A. dembeensis*) in owl pellets from Awash N. P., Ethiopia (Demeter 1982). At this locality, as evidenced by remains in owl pellets, it is one of the commonest small mammals in this region (18%)—cf. *Tatera robusta* (27%), *Crocidura fuscomurina* (14%), *Gerbillus pusillus* (10%), *Acomys cahirinus* (4%).

Remarks Semi-diurnal and terrestrial. Excavates burrows. Makes intricate runways under cover of *Acacia* trees, which are also used by *Acomys cahirinus*. In burnt areas, where there is absence of ground cover, these grass rats may be observed moving around in search of shelter and food. Details of diet unknown, but may feed on *Solanum* berries at some times of the year. Probably gregarious and colonial. An important prey of Spotted Eagle-owls *Bubo africanus* in Awash N. P. (Demeter 1982; see also above).

Conservation IUCN Category: Least Concern.

Measurements*Arvicanthis neumanni*HB: 97.8 (84–123) mm, $n = 14$ T: 93.0 (72–112) mm, $n = 14$ E: 13.4 (11–16) mm, $n = 14$ HF 23.8 (22–25) mm, $n = 14$ WT: 36.5 (26–74) g, $n = 14$ GLS: 27.6 (25.5–31.3) mm, $n = 14$ GWS: 14.1 (13.2–16.0) mm, $n = 14$

M^1-M^3 : 5.8 (5.6–6.2), $n = 14$

Ethiopia (Demeter & Topal 1982, as *A. somalicus*)

Key References Demeter 1982; Demeter & Topal 1982; Hubert 1978b; Rupp 1980; Yalden *et al.* 1976.

Afework Bekele

Arvicanthis niloticus NILE GRASS RAT (UNSTRIPED GRASS RAT)

Fr. Rat roussard du Nil (Rat du Nil); Ger. Nil-Grasratte

Arvicanthis niloticus (E. Geoffroy, 1803). Cat. Mamm. Mus. Nat. Hist. Nat., Paris, p. 186. Egypt.

Taxonomy Originally described in the genus *Arvicola*. Specimens from west of the Nile R. are genetically and morphometrically distinct, and could warrant subspecific status (*testicularis*) (Ducroz 1998, Fadda & Corti 1998). Populations in Ethiopia are sometimes referred to a separate species, *A. dembeensis* (e.g. Yalden *et al.* 1976, 1996), but *dembeensis* is here considered to be a synonym of *A. niloticus* (see Musser & Carleton 2005 for a full discussion on the taxonomy of this species). Synonyms: *centralis*, *centrosus*, *dembeensis*, *discolor*, *jebelae*, *kordofanensis*, *lacernatus*, *luctuosus*, *nubilans*, *major*, *mearnsi*, *minor*, *muansae*, *naso*, *ochropus*, *pelliceus*, *raffertyi*, *reichardi*, *rhodesiae*, *rossii*, *rubescens*, *solatus*, *tenebrosus*, *testicularis*, *variegatus*, *zaphiri*. Subspecies: none. Chromosome number: $2n = 62$, $aFN = 62-64$.

Description Medium-sized, robustly built rat. Dorsal pelage usually buffy-brown heavily flecked with black and yellow; specimens from sub-desert environments distinctly paler (Rosevear 1969); black mid-dorsal stripe absent or clearly visible; hairs dark brown at base with yellowish-buff subterminal zone and blackish tip. Rump often tinged with red or rufous, especially in older individuals. Ventral pelage whitish to grey. Head blunt, muzzle short. Ears rounded and

reddish. Digit 5 on forefoot considerably reduced but still functional; Digit 1 vestigial. Sole of hindfoot generally dark. Tail usually shorter than head and body (ca. 85%), dark above and whitish or pale brown below. Skull: ungrooved upper incisor teeth. Nipples: $1 + 2 = 6$.

Geographic Variation None recorded.

Similar Species

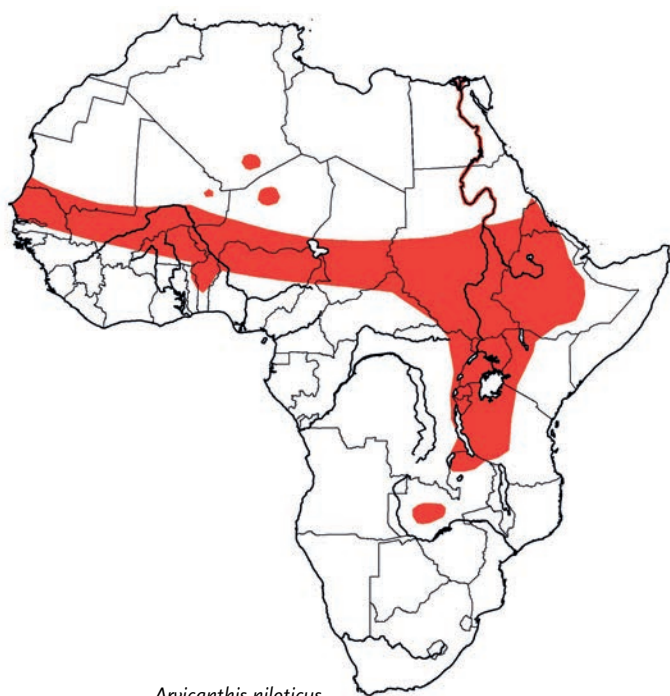
A. ansorgei (chromosome number: $2n = 62$, $aFN = 74-76$) and *A. rufinus* (chromosome number: $2n = 62$, $aFN = 70$) have more southern distributions (Ducroz 1998; Fadda 1998, Volobouev *et al.* 2002); West Africa only.

A. neumanni: (chromosome number: $2n = 62$, $FN = 66-67$) is much smaller, and restricted to the lowlands of Ethiopia. The other species in Ethiopia (*A. abyssinicus*, *A. blicki*) are confined to higher altitudes.

Distribution Endemic to Africa (but see also below). Sahel and Sudan Savanna BZs, Afroalpine–Afromontane BZ (partly) in Ethiopia, and southwards into parts of Eastern Rainforest–Savanna Mosaic and northern Zambezian Woodland BZ. Widespread in the Nile Valley (but not in the surrounding Sahara Arid BZ) from the Nile Delta in Egypt to the Great Lakes region (west of the Gregorian Rift Valley) in East Africa. In Ethiopia (as *dembeensis*), occurs in lowlands from sea level to ca. 2000 m. Also recorded from Saharan massifs (Adrar des Iforas, Aïr). Although mapped, presence in Benin, Zambia and W Tanzania uncertain. Sympatric with *A. ansorgei* in a vast area of central Mali (Sicard *et al.* 2004). An isolated population in SW Arabia.

Habitat Savannas and grasslands, often not far from water; recorded from arid steppes to moister grasslands where annual rainfall is 200–1200 mm. May occur in bushes and thickets. Common in croplands, farms and villages, but seldom found inside houses.

Abundance May be a dominant species in grasslands with good cover. Outbreaks can follow abnormally high rainfalls (e.g. density of 100/ha in Sahel Savanna BZ of Senegal in 1976 (Poulet & Poupon 1978). Densities of 600–800/ha have been recorded temporarily in rice fields of N Senegal (Poulet 1982), with a sharp decline in numbers in the dry season. Fluctuations in numbers tend to be greater (from 0 to 80/ha) in grassland habitats than in nearby maize fields (5–18/ha) in the Rift Valley of Ethiopia (Afework Bekele & Leirs 1997). When numerous, may be a pest in agricultural crops.



Arvicanthis niloticus

Adaptations Mainly diurnal (Duplantier & Granjon 1990). Builds nests of fine grass on the surface or in shallow burrows, and may use withdrawal cracks in drained clay soils (Poulet 1982). Intensively uses runways radiating out from the nest through matted grass. Can become arboreal (e.g. when feeding on the fruits of *Balanites aegyptiaca*) in the dry season when other resources are scarce (Poulet 1982).

Foraging and Food Primarily herbivorous; feeds on leaves, shoots and seeds of grasses, and cultivated crops. Small insects may comprise 20% of the diet in the wet season (Rabiu & Rose 1997).

Social and Reproductive Behaviour Gregarious, sometimes found in colonies of several adult ♂♂ and ♀♀ with young. Short-term movements from a few metres in dry rice fields to 20–40 m in sugarcane fields in N Senegal (Poulet 1982). Aggressive towards unfamiliar individuals of the same sex.

Reproduction and Population Structure The length and timing of the reproductive season varies by locality (Fisher 1991). Reproduction generally occurs at the end of, or after, the wet season. The length of the reproductive season is correlated with resource availability so that reproduction throughout the year is possible in favourable conditions. The proportion of reproductively active ♀♀ also varies by locality, e.g. in grasslands of Ethiopia at 1700 m (Afework Bekele & Leirs 1997), pregnant ♀♀ are present in all months of the year, but with a greater proportion of pregnant ♀♀ in the wet season than in the dry season. The range of variability in the number of months when reproduction occurs/year (and proportion of ♀♀ breeding on an annual basis) varies from 12 months/year (32%) at Mweya, Uganda, to ten months (43%) at Crater Track, Uganda (Neal 1981), nine months (52%) at Kitale, Kenya (Taylor & Green 1976), eight months (80%) at Rojwero, Kenya (Neal 1981), seven months (48%) at Kano, Nigeria (Rabiu & Fisher (1989) and five months (n. d.) in Senegal (Poulet & Poupon 1978). Although many variables affect when ♀♀ breed, there is a positive correlation between the number of months when ♀♀ breed and the number of 'humid' months (which in turn affects other environmental characters). A slightly different situation occurs at Khartoum, Sudan (where the number of humid months/year is very low) – pregnant ♀♀ and young occur in the irrigated fields close to Nile R. in most months of the year (Happold 1966a, Ghobrial & Hodeib 1982). Gestation: 21–23 days (Ghobrial & Hodeib 1982). Litter-size: 4.3

(2–10, n = 26; Ethiopia; Afework Bekele unpubl.) to 6.02 ± 7 (n = 56; Senegal; Ducroz *et al.* 1997). Mean litter-size also varies by habitat, e.g. 5.74 ± 2.65 in grasslands and 7.42 ± 2.63 in maize fields (Ethiopia; Afework Bekele & Leirs 1997). Sexual maturity: 2 months (Poulet 1982). Longevity in the wild is less than one year (Poulet 1982).

Predators, Parasites and Diseases Nocturnal and diurnal predators include mongooses, Barn Owls *Tyto alba*, Black-shouldered Kites *Elanus caeruleus*, Crested Hawk-eagles *Lophaelix occipitalis*, Lizard Buzzards *Kaupifalco monogrammicus* and snakes (*Naja* and *Pseustes* spp.) (Kingdon 1974, Bâ *et al.* 2000). Reported to be the reservoir of a fairly large number of diseases, including Rift Valley fever, leishmaniasis, borreliosis, intestinal schistosomiasis and bubonic plague (Gratz 1997). Many species of fleas found on animals, and in nests and burrows, in Egypt, including *Xenopsylla cheopis*, *Echidnophaga gallinacea*, *Synosternus cleopatrae*, *S. pallidus* and *Nosopsyllus londinensis* (Hoogstraal & Traub 1965b).

Conservation IUCN Category: Least Concern.

Agricultural expansion is likely to allow population numbers to increase and geographic range to expand. May be a pest in agricultural crops, and hence control measures may be necessary.

Measurements

Arvicanthis niloticus

HB: 150.8 (111–238) mm, n = 191

T: 129.7 (92–170) mm, n = 189

HF: 31.5 (23–38) mm, n = 188

E: 17.8 (12–24) mm, n = 179

WT: 110.8 (55–258) g, n = 44

GLS: 32.9 (27.9–39.1) mm, n = 190

GWS: 17.5 (14.8–21) mm, n = 191

M¹–M³: 6.9 (6.1–8.3) mm, n = 192

Burkina, Chad, Egypt, Ethiopia, Niger, Senegal, Sudan (J.-F. Ducroz *et al.* unpubl.; ACBG, MNHN, BMNH)

Key References Afework Bekele & Leirs 1997; Ducroz *et al.* 1997; Poulet 1982; Poulet & Poupon 1978; Rosevear 1969.

Laurent Granjon, Afework Bekele
& Jean-François Ducroz

Arvicanthis rufinus RUFIOUS GRASS RAT (GUINEAN GRASS RAT)

Fr. Rat roussard guinéen; Ger. Rote Grasratte

Arvicanthis rufinus (Temminck, 1853). Esquisses sur la côte de Guinée, p. 163. Given as Elmina, Ghana.

Taxonomy Originally described in the genus *Mus*. Long considered as belonging to *A. niloticus* (Rosevear 1969). However, chromosome number distinguishes this species from its sibling species *A. niloticus* and *A. ansorgei* (Civitelli *et al.* 1995, Ducroz 1998, Volobouev *et al.* 2002). Specimens from the Central African Republic with a similar aFN but reduced diploid number (2n = 56, 58; Matthey 1965, Volobouev *et al.* 1987) may belong to this species (Ducroz *et al.* 1998). Shows important genetic divergence from

species in eastern Africa, i.e. *A. niloticus* (as *A. dembeensis*), *A. abyssinicus* and *A. blicki* (Capula *et al.* 1997). Synonyms: *mordax*, *occidentalis*, *setosus*. Subspecies: none. Chromosome number: 2n = 62; aFN = 76 (Volobouev *et al.* 2002).

Description Medium-sized, robustly built rat. Dorsal pelage usually buffy-brown heavily flecked with black; hairs dark brown at base with yellowish to brown-red subterminal band and blackish tip.

Back and flanks tinged with pale red to deep reddish, especially on individuals from the Rainforest BZ (Rosevear 1969). Ventral pelage whitish to grey. Head blunt, short muzzle. Ears rounded and reddish. Digit 5 on forefeet considerably reduced but still functional; Digit 1 vestigial. Soles of hindfoot generally dark. Tail moderately long (ca. 96% and usually shorter than HB), dark above, whitish or pale brown below. Skull: ungrooved upper incisor teeth. Nipples: $1 + 2 = 6$.

Geographic Variation None recorded.

Similar Species

A. niloticus. Chromosome number: $2n = 62$, aFN = 62–64; more northern distribution.

A. ansorgei. Chromosome number: $2n = 62$, aFN = 74–76; more north-western distribution (Ducroz 1998, Fadda 1998, Volobouev *et al.* 2002).

Distribution Endemic to Africa. Guinea Savanna and Sudan Savanna BZs, and grassy clearings in Rainforest BZ of western West Africa. Distributional limits uncertain; suspected to occur from Sierra Leone (Fadda 1998) to Nigeria, and possibly to Central African Republic. Probably present in Togo and Ghana.

Habitat Grasslands and open clearings in Rainforest BZ (S Benin).

Abundance No information.

Remarks Nothing is recorded about the biology of this species, but it is presumed to be rather similar to that of *A. niloticus* (see above).

Conservation IUCN Category: Least Concern.

Measurements

Arvicanthis rufinus

HB: 143.8 (115–177) mm, $n = 13$



Arvicanthis rufinus

T: 138.2 (127–146) mm, $n = 4$

HF: 32.7 (29–38) mm, $n = 14$

E: 19.8 (16–24) mm, $n = 11$

WT: 103.3 (59–168) g, $n = 13$

GLS: 33.6 (30.0–38.5) mm, $n = 14$

GWS: 18.1 (16.8–20.6) mm, $n = 14$

M^1 – M^3 : 7.3 (7.0–7.9) mm, $n = 14$

Benin (ACBG)

Key References Happold 1987; Rosevear 1969.

Laurent Granjon & J.-F. Ducroz

GENUS *Colomys* African Water Rat

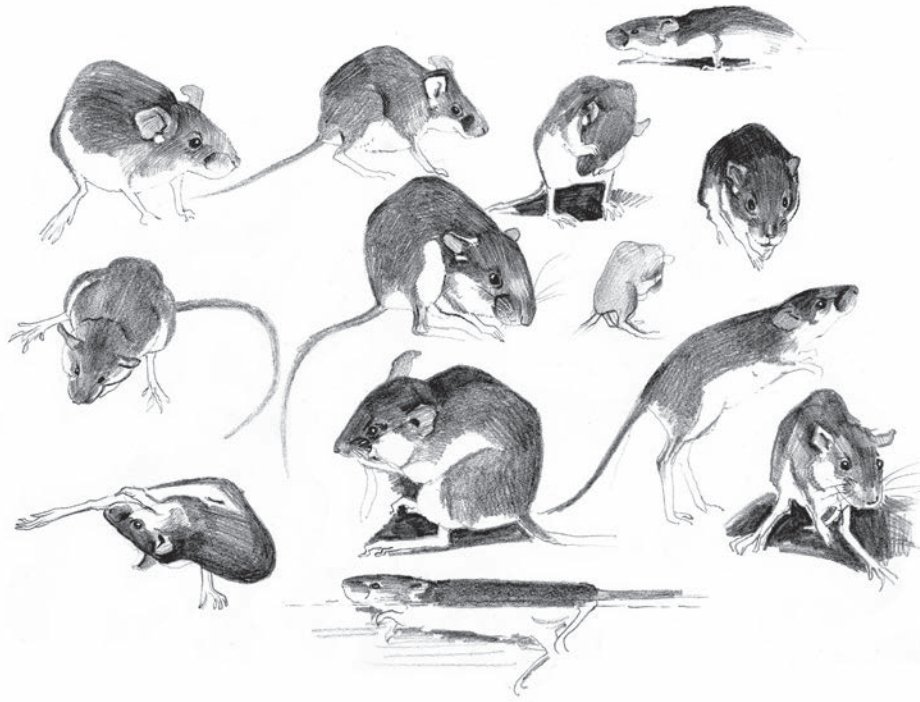
Colomys Thomas and Wroughton, 1907. Ann. Mag. Nat. Hist., ser. 7, 19: 379. Type species: *Colomys goslingi* Thomas and Wroughton, 1907.

A monotypic genus restricted to the rainforests of central Africa. The single species, *Colomys goslingi*, lives in or close to streams and has a similar life-style to species of *Deomys*, *Malacomys* and *Nilopegamys*. The genus is characterized by woolly pelage, long tail, long hindfeet, long vibrissae, pointed cusps on the cheekteeth and reduced M^3 . Further details are given in the species profile. *Colomys* appears to be closely related to *Zelotomys*; the genera are linked by similarities in cusps on the occlusal surfaces of the cheekteeth, mitochondrial DNA cytochrome *b* sequences and nuclear IRBP gene sequences. The molecular data place *Colomys* and *Zelotomys* with *Myomyscus verreauxii* in a monophyletic cluster, within a larger group composed of *Praomys*, *Mastomys*, *Hylomyscus*, *Heimyscus*, other *Myomyscus* and *Stenocephalemys* (details in Musser & Carleton 2005).



Colomys goslingi.

Fritz Dieterlen

Colomys goslingi.

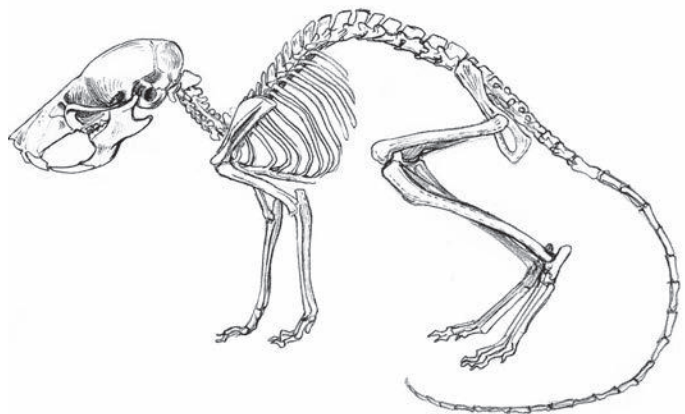
***Colomys goslingi* AFRICAN WATER RAT (VELVET MOUSE, AFRICAN WADING RAT)**

Fr. Rat aquatique d'Afrique; Ger. Afrikanische Waldbachmaus

Colomys goslingi Thomas & Wroughton, 1907. Ann. Mag. Nat. Hist., ser 7, 19: 380. Gambi, Uele River, DR Congo.

Taxonomy The single species of *Colomys* is widely recognized (Ellerman 1941, Misonne 1969a, Dieterlen 1983, Musser & Carleton 1993). More controversial is the status of *plumbeus*, which has been variously placed as a subspecies of *C. goslingi* (Hayman 1966, Misonne 1974, Dieterlen 1983, Musser & Carleton 1993) or as a full species in its own genus *Nilopegamys* (Kerbis Peterhans & Patterson 1995, Musser & Carleton 2005). Here, *plumbeus* is considered to be a full species (*N. plumbeus*). Another form, *eisentrauti* (here considered to be a subspecies of *C. goslingi*), may also be a valid species, as may be another form (as yet undescribed) from Liberia (R. Hutterer & F. Dieterlen in prep.). Synonyms: *bicolor*, *denti*, *eisentrauti*, *ruandensis*. Subspecies: five. Chromosome number: not known.

Description Medium-sized semi-aquatic rat with dense woolly pelage, white ventral pelage, long tail and very long hindfeet. Pelage dense soft and long; ca. 10 mm on back. Dorsal pelage dark russet-brown; hairs medium grey at base, brown at tip. Flanks slightly paler. Ventral pelage pure white; hairs dense, ca. 5 mm. Colour of ventral pelage clearly delineated from colour of flanks. Head similar in colour to dorsal pelage. Muzzle swollen, dark, with many long (up to 50mm) thick vibrissae. Lips thick, white. Ears relatively short, darkly pigmented, sparsely covered with russet hairs; small subauricular white spot. Chin, throat, lower cheeks, chest, fore- and hindlimbs white. Forefoot with four long digits, Digit 1 rudimentary with a minute nail; five palmar pads, soft and 'pulpy'. Hindfoot long (30–37% of HB), five digits, Digit 5 longer than Digit 4; 5–6 comparatively flat palmar pads. Tail very long (ca. 130% of HB), scaly, dark above with darkish bristles, paler or white below with white hairs; hairs



Skeleton of *Colomys goslingi*.

equally distributed, without lateral fringe but denser and longer towards tip; hairs 4–6 mm. Palatal ridges: $2 + 5 = 7$; the two antemolar ridges continuous, the five intermolar ridges medially interrupted. Skull elongated with relatively small GWS and dorsal-ventral height; cranium comparatively broad and rounded with comparatively large brain and a large foramen magnum; auditory bullae small; incisors large, orthodont; anterior palatal foramina extend posteriorly to at least anterior end of M^1 with expanded interpalatal septum; upper molars rather broad, M^3 remarkably reduced; cones of M^1 and M^2 relatively pointed and upright, resembling those of other (partly) insectivorous murids (Figure 62, see also below). Nipples: $1 + 1 + 2 = 8$.

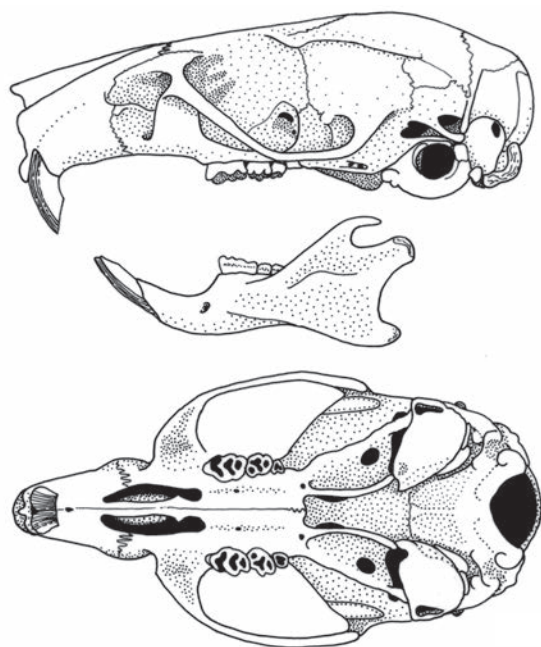


Figure 62. Skull and mandible of *Colomys goslingi* (BMNH 26.7.6.287).



Colomys goslingi

Geographic Variation Five subspecies have been described; the differences between them are slight and recognition of subspecies is of dubious validity.

- C. g. eisentrauti*: W Cameroon highlands. Large, long-tailed; dorsal pelage dark.
- C. g. bicolor*: Cameroon lowlands. Not as large or dark as *eisentrauti*.
- C. g. goslingi*: South of the Ubangi and Congo rivers. Description as above.
- C. g. ruandensis*: W Rwanda highlands. Smallest form of the genus.
- C. g. denti*: Highlands of Kenya, Uganda and S Sudan. Larger, longer-tailed, blackish-brown, due to many black-tipped hairs especially on back and rump.

Similar Species

- Nilopegamys plumbeus*. Large species, about the size of *Colomys goslingi eisentrauti*; Ethiopia only.
- Malacomys longipes*. Elongated and pointed head, larger ears; Rainforest BZ of central Africa.
- Deomys ferrugineus*. Elongated and pointed head, different in many details; Rainforest BZ of central Africa.

Distribution Endemic to Africa. Rainforest BZ and adjacent Forest–Savanna Mosaics. Distribution disjunct. Recorded from Cameroon, S DR Congo and NE Angola, NE DR Congo, Rwanda, Uganda (Mt Elgon), SW Kenya and S Sudan. Outlier localities in Liberia and NW Zambia. Distribution limits uncertain. Not recorded from Equatorial Guinea, Congo, or Central African Republic, nor in rainforests of West Africa, except Liberia.

Habitat Streams and waterways in primary and secondary rainforest, montane rainforest and gallery forests in savannas. Some individuals may live in non-forested savanna, but never far from the edge of the rainforest. On Mt Elgon, Uganda, two specimens were found in dense

montane forest at 2900 m and one specimen at 3200 m (above the upper altitudinal limit of forest) in a river bed adjacent to *Erica* heathland forest and *Lobelia* swamps. The lowest altitude recorded is about 400 m in the region of Kisangani, DR Congo. Generally records from below ca. 800 m are rare, and it appears that lowland forests are not favoured habitat.

Abundance Uncertain, but probably rare because of its specialized habitat requirements. Single specimens, or – in a few cases – pairs, have been recorded along 100–300 m of stream in montane forest glens. In montane habitats in E DR Congo, comprised 0.5% (n = 5871) of terrestrial small mammals (Dieterlen 1983) and 0.11% (n = 3645) in rainforest near Kisangani, DR Congo (Dudu 1991).

Adaptations Semi-aquatic and nocturnal. African Water Rats (together with *Nilopegamys plumbeus*) are probably the most aquatic-adapted of all African mice. They spend most of the time in or near water. They are buoyant, swimming very rapidly with powerful thrusts of the hindlegs (Kingdon 1974). The pelage is thick and dense (and probably water-repellent). Many of the characters of the species are associated with life in and close to water: the long limbs hold the body out of the water when paddling in shallow water, the hairs on the tail probably assist in better swimming and steering, the broad hindfoot provides effective power for propulsion when swimming, and the splayed digits and prominent palmar pads enable locomotion on soft mud.

An interesting character of *Colomys* is the relatively large brain compared with that of other similar-sized rodents, and the enlarged foramen magnum. Studies by Stephan & Dieterlen (1982) showed that estimated brain weight in relation to body weight was about 132% above expected, and comparatively heavier than in 17 other species of murid rodents. Likewise the area of the foramen magnum was about 127% greater than expected, and larger than in the other

murid rodents. Such enlargement in brain size is presumed to be associated with the complex behaviour patterns associated with an aquatic predatory life-style, as is seen also in *Potamogale* spp. (Potamogalinae: Tenrecidae) and *Malacomys* spp. (Rodentia: Muridae).

The muzzle is bulbous and swollen. The muzzle and thick upper lips have numerous thick dark vibrissae, which fan out around the mouth, and are assumed to be a very special adaptation for searching and detecting live animal food in the water (Kingdon 1974, Dieterlen 1983). When searching for food from the edge of the water, or while wading in water, the nose is held close to the water surface with the vibrissae spread out and dipped into the water. The muzzle has a highly developed sensory system, which is perceptive to the slightest vibrations (Stephan & Dieterlen 1982). Another adaptation, important for the mobility of the muzzle, is the remarkable long bony projection between the upper incisors, which is probably an insertion point for special muscles (Dieterlen 1983).

Foraging and Food Carnivorous. Observations of individuals in captivity show that they forage by actively hunting prey in the water and by filtering water through the vibrissae. They can capture tadpoles and small fish in complete darkness, probably by detecting small vibrations or water movement (Dieterlen & Statzner 1981). Aquatic invertebrates (which form the majority of the food – see below) are probably hunted in the same manner. A second method of obtaining prey is by sifting mud and debris in shallow water with the forelimbs; disturbed prey is detected by the muzzle and vibrissae, which are held just below the water surface (Kingdon 1974). A final method is by using the long vibrissae on the muzzle (which are spaced about 0.5 mm apart) as a net, which can filter food (such as the exuviae of insects) floating on or near the surface (Dieterlen & Statzner 1981). The vibrissae (and perhaps other tactile or sensory receptors on the muzzle) are clearly important in detecting and catching food, although their precise role in foraging is uncertain.

Stomach analysis (n = 15) shows that the diet is mainly benthic invertebrates, principally the larval stages of Trichoptera; other foods include larval and adult Coleoptera, larval Diptera, larval Plecoptera and larval Odonata (Dieterlen & Statzner 1981). The diet of each individual showed considerable variation, which suggests that feeding is opportunistic and dependent on location and availability; 85% of identified food items (n = 294) were aquatic in origin and

ca. 12% were of terrestrial origin. Occasionally snails, spiders and plant material were eaten.

Social and Reproductive Behaviour Trapping data suggests that they live singly or in pairs, well spaced out along the length of streams. No detailed information available.

Reproduction and Population Structure Most pregnant ♀♀ and young animals recorded in Sep–Mar/Apr in Kivu, E DR Congo (Dieterlen 1983). Embryo number: 2.09 (1–3, mode 2, n = 11). Females and ♂♂ become mature and sexually active when ca. 50 g. In adult ♂♂ testes length varied from 8 to 14 mm, possibly due to seasonal changes.

Predators, Parasites and Diseases Known predators include buzzards (Kingdon 1974) and African Grass-owls *Tyto capensis* (Ansell 1965). They also may be preyed upon by snakes and the Marsh Mongoose *Atilax paludinosus*, which may be common close to streams (Kingdon 1974).

Conservation IUCN Category: Least Concern.

Schlitter (1989) classified the species as ‘Rare’.

Measurements

Colomys goslingi

HB: 120 (105–135) mm

T: 159 (146–171) mm

HF: 37.2 (34–38.5) mm

E: 18.9 (16–21) mm

WT: 56 (46–73) g

GLS: 33.4 (31.8–34.7) mm

GWS: 15.8 (15.0–17.4) mm

M¹–M³: 5.3 (4.9–5.8) mm

n = 23–25

E DR Congo (F. Dieterlen, unpubl.)

Key References Dieterlen 1983; Dieterlen & Statzner 1981; Kingdon 1974.

Fritz Dieterlen

GENUS *Dasymys*

Shaggy Rats

Dasymys Peters, 1875. Monatsber. K. Preuss. Akad. Wiss. Berlin, p. 12. Type species: *Dasymys gueinzii* Peters, 1875 (= *Mus incommisus* Sundevall, 1847).

The genus *Dasymys* is endemic to Africa and is represented by five species intermittently distributed from Senegal to Ethiopia and southwards to the Cape region of South Africa. Shaggy Rats live in wetland environments, from sea level to 4000 m, where dense ground cover affords suitable habitat for runways and nests. Their distribution is accordingly patchy, and none of the species occurs in the Sahel Savanna, Somalia–Masai Bushland and South-West Arid BZs. Their semi-aquatic habits, and association with wetlands, account for the other common names applied to the species – Marsh Rats, Swamp Rats, or Water Rats.

Shaggy Rats are medium to large in size, and aptly named in view of the sometimes rumpled appearance imparted by their long, soft, lax pelage and dense underfur. The dorsal pelage is dull brown to greyish-brown and rather drab; the flanks often brighter, buffy-brown to silvery-grey; and the ventral pelage is pale whitish-buff. They have short, rounded ears, narrow hindfeet with short Digits 1 and 5, and relatively long tails (ca. 75–95% of HB).

The skull is distinguished by the following characters: robust with a greatly constricted interorbital constriction that is narrower than



Dasymys incomptus.

the rostrum; supraorbital edges reflected dorsally as a sharp bead that flattens and merges with temporal ridge. Rostrum moderate in length and width but deep. Zygomatic arches stout over anterior portion; zygomatic plate moderately wide, leading edge concave. Braincase elongate, temporal and lambdoidal ridging present but weakly defined. Anterior palatal foramina long (ca. 70–75% of diastema length), terminating posteriorly between the anterior roots of first molars. Toothrows close set and slightly convergent anteriorly, hard palate correspondingly compressed with low medial ridge. Parapterygoid fossae moderately recessed, and alisphenoid strut absent. Auditory bullae moderately sized. Molars stoutly proportioned and broad with M^3 as long as M^2 . Cusps heavy and blunt, individually defined in young animals but tending to unite transversely after moderate wear. Cusp $t3$ of M^1 small and weakly delineated from $t2$; $t3$ of M^2 usually absent, rudimentary if present; M_{1-2} without $t7$, $t9$ and posteroloph. Unlike *Otomys* spp., M^3 is not the longest molar tooth and the cheekteeth do not have multiple lamellae. Anteromedian and posterolabial conulids typically present on m_1 , anterolabial conulid well defined on m_2 ; posterolophid (postcingulum) absent on m_{1-2} . Molar root formula: $5-6/5, 4/4, 3/3$. Upper incisors broad and not grooved, opisthodont to nearly orthodont, enamel surface pale to deep orange (Figure 63).

The nearest generic relatives of *Dasymys* remain obscure. Ellerman (1941) viewed the genus as most closely related to *Arvicanthis*, and

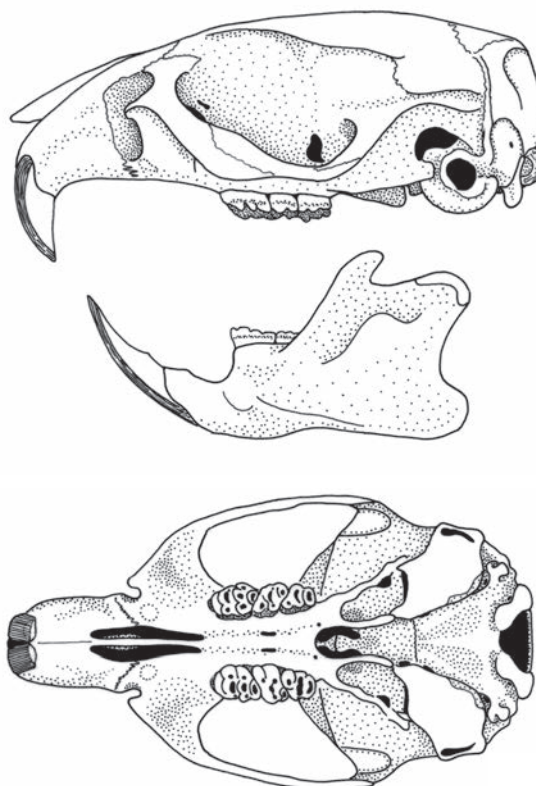


Figure 63. Skull and mandible of *Dasymys incomptus* (HC 2780, BMNH 52:1579).

Misonne (1969a) included *Dasymys* as a member of the *Arvicanthis* Division without further comment on its kinship. A close relationship between *Dasymys* and *Aethomys* has been suggested by Denys (1990c) based on dental similarities to a South African Pliocene fossil (*A. adamanticola*). In studies using albumin microcomplement fixation data (Watts & Baverstock 1995a) and mitochondrial DNA sequences (Ducroz *et al.* 2001), *Dasymys* is portrayed as cladistically strongly divergent from arvicanthines in the strict sense. Such a mixture of viewpoints invites further phylogenetic study that draws upon broader taxonomic sampling and other information sources.

No subgenera recognized. Several species had been acknowledged until Ellerman (1941) arranged most named forms as subspecies

Table 31. Species in the genus *Dasymys*. Arranged according to increasing mean head and body length.

| Species | HB mean (range) (mm) | T mean (range) (mm) [% of HB] | HF mean (range) (mm) | GLS mean (range) (mm) | Dorsal pelage | Notes |
|--------------------|----------------------|-------------------------------|----------------------|-----------------------|--------------------------------------|--|
| <i>D. rufulus</i> | 144.3 (130–170) | 145 (120–160) [100%] | 33.2 (30–35) | 35.5 (32.6–38.6) | Brown to greyish-brown, rufous tinge | Guinea BZ, Rainforest–Savanna Mosaic; widespread in West Africa ^a |
| <i>D. montanus</i> | 144 (132–156) | 102 (93–115) [70%] | 29.9 (28–31) | 31.8 (30.3–34.4) | Satiny dark brown | Afromontane–Afroalpine BZ (Rwenzori Mts area) |
| <i>D. foxi</i> | 157 (132–178) | 137 (121–155) [85%] | 33.6 (27–36) | 36.3 (33.1–39.3) | Buffy-brown | C Nigeria |
| <i>D. incomtus</i> | 165 (137–192) | 146 (119–160) [90%] | 33 (31–35) | 37.8 (34–41) | Dark grey to black | Central, East and southern Africa ^a |
| <i>D. nudipes</i> | 172 (152–205) | 168 (140–186) [95–98%] | 41.6 (39–45) | 39.6 (36.5–43.4) | Drab olive-brown | WC Angola, N Botswana, W Zambia |

^a Distribution uncertain; see text for further details.

of a highly variable *D. incommutus*. Recent regional studies have demonstrated that this view of lack of diversity is overly simplistic, resulting in the reinstatement of several species (Crawford-Cabral & Pacheco 1989; Carleton & Martinez 1991).

Criteria for species recognition have emphasized slight but consistent differences in external and cranial size, degree of molar robustness, relative length of tail, and occurrence of a sixth (hypothenar) plantar pad. The usefulness of karyotypic differences for specific identification requires further study but appears to be promising (see Gordon 1991, Volobouev *et al.* 2000). Species

allocation of populations in the Congo Basin is uncertain and requires further investigation (see *D. incommutus*, *D. rufulus*). Verheyen *et al.* (2003) described three new species based on craniometric and genetic data (*D. cabrali* [Caprivi Strip region, NE Namibia], *D. sua* [near Morogoro, Tanzania] and *D. ruandae* [Kinigi and district, Rwanda]), all of which are here included within the range of '*D. incommutus*'.

Five species (*D. foxi*, *D. incommutus*, *D. montanus*, *D. nudipes* and *D. rufulus*) are recognized here (Table 31).

Michael D. Carleton

Dasymys foxi Fox's SHAGGY RAT

Fr. Rat hirsute de Fox; Ger. Foxs Wollhaarratte

Dasymys foxi Thomas, 1912. Ann. Mag. Nat. Hist., ser. 8, 9: 685. Panyam, Nigeria. 4000 ft (1220 m).

Taxonomy Although described as a species (Thomas 1912a), *foxi* was later re-allocated as a race of a widely ranging *D. incommutus* by Ellerman (1941), whose classification was long observed in regional works (Rosevear 1969, Happold 1987). Based on morphometric evaluations, Carleton & Martinez (1991) considered *foxi* to be a species distinct from other West African *Dasymys*. Synonyms: none. Chromosome number: not known.

Description Large-sized rodent with long shaggy pelage; large for the genus but smaller than *D. nudipes*. Dorsal pelage warm buffy-brown; hairs plumbeous-grey on basal two-thirds, bright buff on distal third; guard hairs dusky-brown. Flanks grading to paler buffy-brown or greyish-brown. Ventral pelage pale to dark grey, usually with a creamy-buff wash; hairs plumbeous-grey at base, white at tip. Ears small and rounded, with medium brown hairs. Dorsal surface of fore- and hindfeet pale brown. Tail long (ca. 85% of HB), uniformly dark brown; caudal hairs short, exposing moderately

coarse scales. Six plantar pads on hindfoot, hypothenar pad small but normally present. Skull: stoutly built (GLS ca. 35–38 mm), broad across braincase and zygoma; molars robust. Upper incisors not grooved. Sexual dimorphism in cranial size not detected within a large population sample (Carleton & Martinez 1991). Nipples: 1 + 2 = 6.

Geographic Variation None recorded.

Similar Species

D. rufulus. Dorsal pelage having more reddish-brown tones; on average slightly smaller in most external and cranial dimensions; more broadly distributed in West Africa.

Distribution Endemic to Africa. Guinea Savanna BZ. As currently understood, restricted to the Jos Plateau, central Nigeria (Carleton & Martinez 1991).

Habitat Marshy area, with tall, dense grasses and sedges, bordering a stream on the Jos Plateau (an isolated elevated area of grasslands and rocks – see Happold 1987).

Abundance No information. Known only from the region of the type locality.

Remarks Very little is known about this species. Described as a 'water rat' and 'a great swimmer' by Reverend G. T. Fox, the collector of the type series (Thomas 1912a).

Conservation IUCN Category: Data Deficient.

Measurements

Dasymys foxi

HB: 157 (132–178) mm, n = 46

T: 137 (121–155) mm, n = 46

HF: 33.6 (27–36) mm, n = 46

E: 21.0 (19–23) mm, n = 49

WT: 118 (73–174) g, n = 49

GLS: 36.3 (33.1–39.3) mm, n = 43

GWS: 19.2 (18.1–20.1) mm, n = 43



Dasymys foxi

M¹–M³: 7.3 (6.8–7.7) mm, n = 43
Nigeria (Carleton & Martinez 1991)

Key References Carleton & Martinez 1991; Rosevear 1969.

Michael D. Carleton

Dasymys incommutus COMMON SHAGGY RAT

Fr. Rat hirsute Africain; Ger. Afrikanische Wollhaarratte

Dasymys incommutus (Sundervall, 1847). Ofv. K. Svenska Vet.-Akad. Forhandl, Stockholm 3: 120 (1846, publ. 1847) 'Caffraria prope portum Natal' (= Durban, South Africa).

Taxonomy Originally described in the genus *Mus*. Ellerman (1941) included all named forms of *Dasymys* within this species, either as subspecies or synonyms (see Genus profile). The current viewpoint is to regard the genus as a complex of several species (Musser & Carleton 1993, 2005). Rosevear (1969) recorded *D. incommutus* from West Africa, recognizing three subspecies: *rufulus* (now a valid species), *foxi* (now a valid species) and *longipilosus* (now a synonym of *D. rufulus*). Thus, on these criteria, *D. incommutus* is now restricted to forms found only in eastern, central and southern Africa. However, Mullin *et al.* (2002, 2004) restricted *D. incommutus* to populations in Zimbabwe and South Africa, and considered those in the Congo Basin, shown here (see map) as *D. incommutus*, to belong to a different species. On the basis of canonical analyses of skull shape, Mullin *et al.* (2004) suggested that populations from most of the northern range of *D. incommutus* represent part of the *D. rufulus* complex (see *D. rufulus* profile), that some populations in Zimbabwe, NE Botswana and N South Africa represent their new species *D. robertsi*, and that those in N Botswana represent another new species *D. shortridgei*. A further complexity regarding the definition and distribution of *D. incommutus* is provided by Verheyen *et al.* (2003) who referred confusingly to *bentleyi* in the Congo Basin, a taxon that may be considered either as a valid species, or as a subspecies of *D. incommutus*; these authors also described three new species (see Genus profile) whose distributions are within the geographic range of *D. incommutus* as mapped here. Synonyms: *bentleyi*, *capensis*. Subspecies: three. Chromosome number: not known.

Description Large shaggy rat, stoutly built with long tail. Pelage soft and shaggy, with distinct sheen; dorsal hairs 13–15 mm. Dorsal pelage dark grey to black; hairs dark grey at base, blackish-brown at tip. Ventral pelage dull grey; hairs pale grey at base, buffy-white at tip. Head broad, muzzle short. Vibrissae long. Eyes small. Ears broad and round, well-furred on inner surface. Fore- and hindfeet brown, almost hairless; claws long and white; typically six plantar pads. Tail long (ca. 90% of HB), heavily scaled, sparsely haired, dark above, pale below. Pelage of juveniles darker and woollier than adults. Skull with extreme interorbital constriction. Upper incisors not grooved. Nipples: 1 + 2 = 6.

Geographic Variation Three subspecies may be recognized (see Meester *et al.* 1986):

D. i. incommutus: E South Africa and possibly Mozambique. Dull buffy-brownish pelage; smaller than *D. i. capensis*.

D. i. bentleyae: N Angola and DR Congo. Smaller than *D. i. nudipes*.

D. i. capensis: SW South Africa. Dark pelage, pale yellow incisors, heavy mandible, short anterior palatal foramina; mandible oval shape between condyle and coronoid arch.

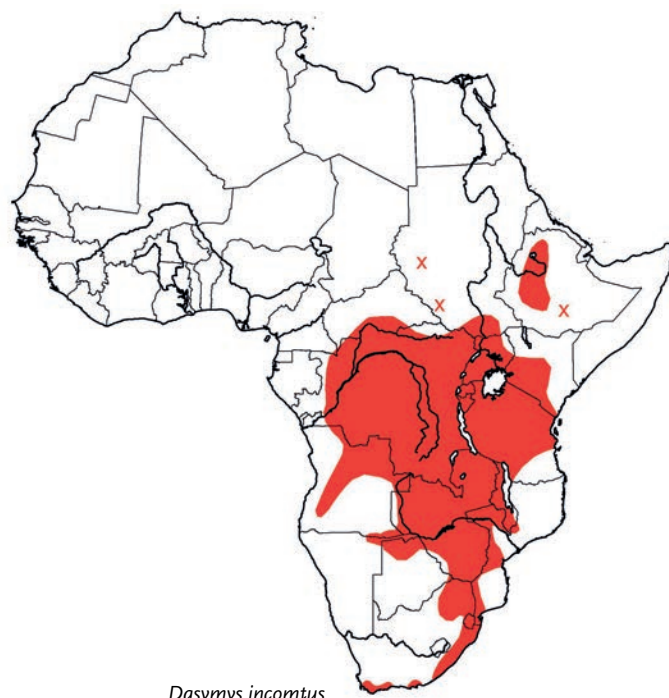
Similar Species

D. montanus. Pelage dark brown, tending to black dorsally; Rwenzori Mts, Uganda.

D. nudipes. Pelage olive-brown, blackish-brown dorsally; typically five plantar pads on hindfoot; on average larger body size and variation in configuration of interparietal bone; S Angola, N Botswana and W Zambia.

Otomys spp. Shorter tails (ca. 60% of HB); upper incisors with grooves.

Distribution Endemic to Africa. Widely distributed, but patchily (see Habitats) in Zambezian Woodland BZ and Rainforest BZ (East Central and South Central Regions), and marginally in southern part of Somalia–Masai BZ. Recorded in eastern, central and southern Africa, including S Sudan, Ethiopia, DR Congo, Uganda, Kenya,



Dasymys incommutus

Tanzania, Angola, Zambia, Malawi, Zimbabwe and South Africa (Musser & Carleton 1993).

Habitat Reed-beds, long grass close to water, semi-aquatic vegetation and marshes. Normally found close to water or damp vegetation, including drainage lines.

Abundance Despite their widespread distribution, African Shaggy Rats are rarely caught and are believed to occur at low densities (Smithers 1986b).

Adaptations Terrestrial and semi-aquatic. Shaggy Rats swim well and readily take to water; swimming is a 'dog-paddle' and is already developed before weaning (ca. Day 12; Pillay 2003). Predominantly crepuscular and diurnal (southern Africa; Smithers 1975). Nests of African Shaggy Rats in Malawi (Hanney 1965) were built 2–20 m from water; each nest consisted of two parts, an upper part on the surface of the ground and a lower part in a depression. Entrance to the nest was concealed in the depression, and led to well-defined runs. In two nests, the entrance led to an underground burrow that opened below water level. Nests are built of intricately woven grasses and other local materials.

Foraging and Food Predominantly herbivorous. The diet comprises a wide range of aquatic and semi-aquatic plants, although insect remains have been found in stomachs (Hanney 1965, Smithers 1975). In captivity, Shaggy Rats eat mealworms and a variety of fruit and vegetables.

Social and Reproductive Behaviour In captivity, both sexes are aggressive, suggesting a solitary life-style in the wild; ♀♀ tolerate unfamiliar ♂♂ only when they are in oestrus (Pillay 2003). The social organization and mating system are unknown.

Reproduction and Population Structure Seasons and months when reproduction occurs vary widely throughout geographic range. In Botswana and Zimbabwe, reproduction occurs during the warm wet season (Aug–Mar; Smithers 1975); a single pregnant and lactating ♀ was found in KwaZulu–Natal, South Africa in winter (Jun; Taylor 1998); and pregnant ♀♀ were recorded in the dry season in Malawi (Jun and Aug; Hanney 1965). Lactation recorded in Apr in Tanzania (Allen & Loveridge 1933). Females have spontaneous ovulation, and an oestrus cycle of 8 days (range 7–16;

Pillay 2003). Gestation (in captive population): ca. 29 days (Pillay 2003). Litter-size: 2–4 over geographic range (Allen & Loveridge 1933; Hanney 1965; Delany 1969; Kingdon 1974). Litter-size: 5 (2–9; South Africa; De Graaff 1981). At birth, young are altricial, weight ca. 8 g. Weaned ca. Day 24. Young nipple-cling until Day 30. Onset of sexual maturity in ♂♂ ca. Week 6, and first mating Week 8. First complete oestrus cycle and conception in ♀♀ ca. Week 18–19, suggesting that only ♀♀ born early in the breeding season are likely to reproduce in the season of their birth.

Predators, Parasites and Diseases Remains found in owl pellets (Hanney 1965, Happold & Happold 1986). Captured by humans for food in some parts of Malawi (D. C. D. Happold unpubl.). Ectoparasites include seven species of fleas, 28 species of mites and one species of tick; endoparasites include two species of platyhelminth worms (details in De Graaff 1981). Specimens in DR Congo have been found with large numbers of schistosome worms, which cause bilharzia in humans (Schwetz 1956).

Conservation IUCN Category: Least Concern.

Widespread with a wide geographic range. Shaggy Rats are associated with rivers and wetlands, and hence wetland destruction will reduce their geographical range and population numbers.

Measurements

Dasymys incommutus incommutus

HB: 165 (137–192) mm, n = 19

T: 146 (119–160) mm, n = 17

HF: 33 (31–35) mm, n = 9

E: 20 (15–24) mm, n = 12

WT: 158 (103–218) g, n = 13

GLS: 37.9 (34.3–41.6) mm, n = 17

GWS: 20.2 (19.1–21.2) mm, n = 17

M¹–M³: 7.5 (6.8–8.0) mm, n = 17

KwaZulu–Natal, South Africa (DM, Taylor 1998)

Body size varies according to locality, with no clear geographical pattern

Key References De Graaff 1981; Musser & Carleton 1993, 2005; Pillay 2003; Smithers 1975, 1983.

Neville Pillay

Dasymys montanus MONTANE SHAGGY RAT

Fr. Rat hirsute de montagne; Ger. Montane Wollhaarratte

Dasymys montanus Thomas, 1906. Ann. Mag. Nat. Hist., ser. 7, 18: 143. Mubuku Valley, Rwenzori East, Uganda. 12,500 ft (3810 m).

Taxonomy Like many other forms of *Dasymys*, Thomas's (1906) *montanus* was synonymized in Ellerman's (1941) broad polytypic treatment of *D. incommutus* and followed by later authors (e.g. Delany 1975). However, Thomas's original diagnosis was well founded (see Musser & Carleton 1993), because he also examined specimens of a larger *Dasymys* from the lower slopes of Rwenzori that he named (in the same paper) as *D. medius*, now considered to be a synonym of

D. incommutus. Whether *D. montanus* is limited to the Rwenzori Mts or occurs on other western Rift Valley mountains is uncertain. Synonyms: none. Chromosome number: not known.

Description Medium-sized, long-haired shaggy rat with a short tail. Pelage long and thick, texture very fine and soft. Dorsal pelage satiny dark brown, finely speckled with buff, more blackish

over mid-dorsum and slightly paler toward flanks; hairs dark grey at base, buff at tip. Ventral pelage slaty-grey. Ears short, heavily clothed with black hairs. Plantar pads six. Tail short (ca. 70% of HB), relatively the shortest in the genus, uniformly black. Skull small in most dimensions, about the size of *D. rufulus*, but zygomatic arches comparatively broad and auditory bullae large; interorbital ridges weakly developed. Upper incisors not grooved. Nipples: not known.

Geographic Variation None recorded.

Similar Species

D. incomtus. Similar in general appearance; on average larger in all body measurements and GLS; tail relatively longer (ca. 90% of HB); very widespread; although sympatric, probably not syntopic; occurs at lower altitudes.

Distribution Endemic to Africa. Afroalpine–Afroalpine BZ. So far known only from high altitudes (2600–4300 m) in the Rwenzori Mts of W Uganda and perhaps neighbouring DR Congo.

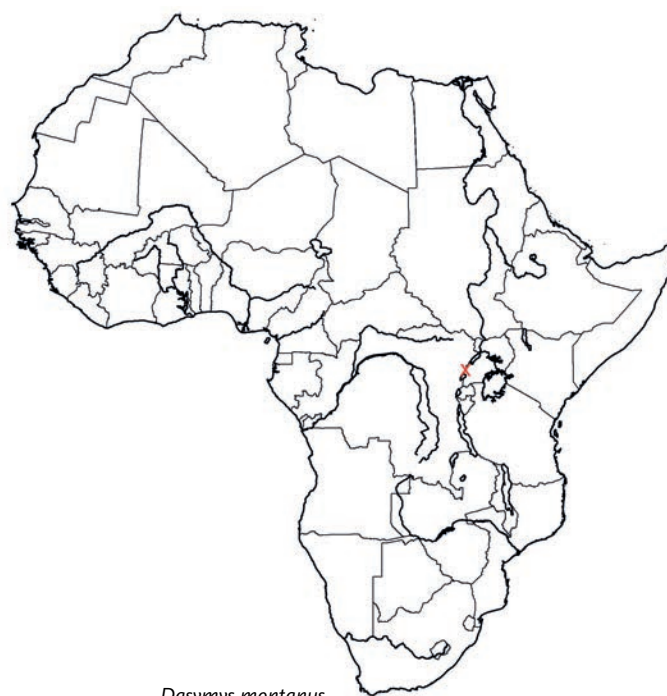
Habitat Afroalpine and subalpine habitats such as dense grassy slopes, fern-covered glades, sphagnum moss–lobelia bogs, and open moorland (Kerbis Peterhans *et al.* 1998; FMNH field notes).

Abundance Comprised 1–10% of small rodent captures (n = 69–175) at three localities (2700–3400 m) in Rwenzori Mountains N. P., Uganda; uncommonly captured compared to other syntopic species such as *Hylomyscus denniae* (32–51%) and *Lophuromys flavopunctatus* (25–43%) (Kerbis Peterhans *et al.* 1998). The highest percentage abundance was at the highest locality.

Remarks Trapping results suggest both diurnal and nocturnal activity (Kerbis Peterhans *et al.* 1998). Herbivorous; reported to feed on flower blossoms and succulent stems of new rushes (Thomas & Wroughton 1910). None of four ♀♀ taken in the wet season (Nov–Dec) or dry season (Apr–May) was visibly pregnant (Kerbis Peterhans *et al.* 1998).

Conservation IUCN Category: Endangered.

The species has a very small known geographic distribution, although the high altitude habitats where it occurs are relatively unaffected by human activities.



Dasymys montanus

Measurements

Dasymys montanus

HB: 144.6 (132–156) mm, n = 7

T: 102.6 (93–115) mm, n = 7

HF: 29.9 (28–31) mm, n = 7

E: 17.9 (17–19) mm, n = 7

WT: 84.9 (69–100) g, n = 7

GLS: 31.8 (30.3–33.4) mm, n = 4

GWS: 18.6 (18.1–19.5) mm, n = 4

M¹–M³: 6.9 (6.8–7.0) mm, n = 4

Uganda (FMNH, M. D. Carleton unpubl.)

Key References Kerbis Peterhans *et al.* 1998; Thomas 1906.

Michael D. Carleton

Dasymys nudipes ANGOLAN SHAGGY RAT

Fr. Rat hirsute d'Angola; Ger. Angolanische Wollhaarratte

Dasymys nudipes (Peters, 1870). Journ. Sci. Math. Phys. Nat., Lisboa, ser. 1, 3: 126. Huilla (= Huila), Angola.

Taxonomy Originally described in the genus *Mus*. Retained as a species as originally described until Ellerman (1941) reassigned *nudipes* as a subspecies of *D. incomtus*, a classification conventionally accepted throughout the mid-1900s (Ellerman *et al.* 1953, Misonne 1974; Honacki *et al.* 1982). However, based on morphological differences, the specific status of *nudipes* was restored by Crawford-Cabral (1983) and Crawford-Cabral & Pacheco (1989). The status and relationships of populations in SE Angola (Crawford-Cabral

1998), N Botswana (Smithers 1971) and SW Zambia (Ansell 1978), formerly assigned to *D. incomtus nudipes*, warrant re-evaluation. *Dasymys nudipes* may prove to be a species limited to the Angolan highlands (especially see Crawford-Cabral & Pacheco 1989). Synonyms: none. Chromosome number: not known.

Description Large shaggy rat, the largest in the genus. Dorsal pelage drab olive-brown, blackish-brown on middle dorsum,

sometimes iridescent; hairs dark plumbeous with short dull ochraceous tip; guard hairs blackish. Flanks with more buff than on back. Ventral pelage dull grey; hairs dark grey at base, dull white at tip. Ears darkly pigmented, short and hairy. Upper surface of hindfeet thinly furred, short brown hairs on tarsus-metatarsus and dull white on digits; typically five plantar pads on hindfoot, the lateral metatarsal pad (hypothenar) usually absent. Tail long (ca. 95–98% of HB), relatively the longest for the genus; uniformly dark brown to blackish, scale pattern moderately coarse, caudal hairs very short and indistinct. Skull and dentition robust (GLS: ca. 37–43 mm); rostrum relatively long; auditory bullae comparatively and relatively large. Cusp t3 of M^2 typically lacking. Upper incisors not grooved, anterior face burnt orange. Nipples: $1 + 2 = 6$.

Geographic Variation None recorded.

Similar Species

D. incomtus. On average smaller; HF shorter (ca. 30–35 mm); dorsal pelage with more reddish-brown; plantar pads typically six; tail shorter and relatively shorter; skull less robust (GLS: ca. 34–41 mm) and molar row shorter (M^1 – M^3 : <7.4 mm).

Distribution Endemic to Africa. Restricted areas of Zambezan Woodland BZ. Distribution, as currently understood, disjunct: (a) plateau of WC Angola; (b) the Okavango and Chobe river systems of SE Angola, Caprivi Strip and N Botswana, and W Zambia (Smithers 1971, Ansell 1978, Crawford-Cabral 1998). Possibly also occurs between these two areas.

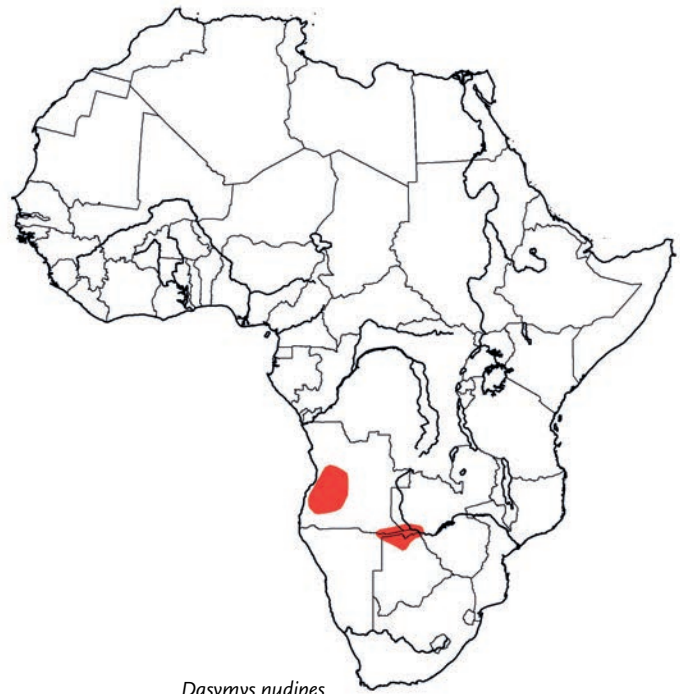
Habitat Reeds, sedges and semi-aquatic grasses bordering rivers and streams, swamps and marshland, especially where fallen leaves and other litter form a matted surface amongst dense wetland ground cover (Botswana; Smithers 1971).

Abundance No information.

Adaptations Terrestrial and semi-aquatic. Described as mainly nocturnal with limited diurnal activity. Constructs domed nests of cut grass and other vegetation, placed at ground level with a short refuge tunnel nearby (Botswana; Smithers 1971).

Foraging and Food Herbivorous and occasionally insectivorous. Feeds on fresh shoots and stems of reeds and semi-aquatic grasses, and other unidentifiable vegetable matter. Insect parts reported in some stomachs. Runways formed between nests and regular feeding areas are littered with fresh remains of severed reeds and grasses (Botswana; Smithers 1971).

Social and Reproductive Behaviour No information.



Dasymys nudipes

Reproduction and Population Structure Males with scrotal testes and lactating ♀♀ recorded in Aug and Nov (Angola; Hill & Carter 1941). Gravid ♀♀ and nestling young recorded in late dry to late wet season (Aug–Mar); litter-size: 5.3 (2–9, $n = 4$; Botswana; Smithers 1971).

Predators, Parasites and Diseases No information.

Conservation IUCN Category: Data Deficient.

Measurements

Dasymys nudipes

HB: 172 (152–205) mm, $n = 26$

T: 168 (140–186) mm, $n = 26$

HF: 41.6 (39–45) mm, $n = 26$

E: 22.4 (21–24), $n = 26$

WT: 128 (102–164) g, $n = 17$

GLS: 39.6 (36.5–43.4) mm, $n = 20$

GWS: 20.1 (18.4–21.6) mm, $n = 20$

M^1 – M^3 : 8.1 (7.8–8.4) mm, $n = 27$

Angola (AMNH, FMNH; M. D. Carleton unpubl.)

Weight: Botswana (Smithers 1971)

Key References Crawford-Cabral 1998; Smithers 1971.

Michael D. Carleton

Dasymys rufulus RUFIOUS SHAGGY RAT

Fr. Rat hirsute roux; Ger. Rote Wollhaarratte

Dasymys rufulus Miller, 1900. Proc. Washington Acad. Sci., 2: 639. Mount Coffee, Liberia.

Taxonomy Referred to as *D. incommutus rufulus* in previous studies (e.g. Rosevear 1969; Happold 1987). Following Carleton & Martinez (1991) and Musser & Carleton (2005), *rufulus* is considered here to be a valid species restricted to West Africa. Musser & Carleton (1993, 2005) recorded that the geographic range extends from Senegal to Cameroon and that the species of *Dasymys* in DR Congo and further east and south is *D. incommutus*. Previous studies suggested that *D. rufulus* is also the correct name for the populations of central and eastern Africa, formerly considered to be *D. incommutus* (Mullin *et al.* 2004). Moreover, morphometric evidence suggests that *D. rufulus* consists of five subgroups (possibly cryptic species) that replace one another geographically: (1) western West Africa (Senegal to SE Côte d'Ivoire); (2) eastern West Africa (SE Côte d'Ivoire to Nigeria and Chad); (3) central Africa (Cameroon, Congo, DR Congo); (4) central and East Africa (N Angola, Zambia, S Malawi, W Mozambique, Sudan); and (5) south central Africa (STanzania, N Malawi and Mozambique) (Mullin *et al.* 2004). Other techniques (e.g. DNA, chromosome analysis) should be used to further examine the relationship within *D. rufulus* with respect to these five subgroups. The subspecies, *D. i. longipilosus*, described from Mt Cameroon by Eisentraut (1963), is considered to be a valid species by Mullin *et al.* (2004) but a synonym of *D. rufulus* by Musser & Carleton (1993, 2005) and here. Synonyms: *longipilosus*. Subspecies: none. Chromosome number: $2n = 36-39$; $aFN = 44-50$ due to the presence of 0 to 3 B chromosomes (Volobouev *et al.* 2000).

Description Medium-sized stout rodent with soft dense shaggy pelage. Dorsal pelage brown to grey-brown with rufous tinge on mid-back, especially on rump; hairs dark grey with rufous tip. Underfur very fine and dense. Flanks brown, hairs with buff tip. Ventral pelage paler, hairs grey with dull white or whitish-buff tip. Colours of dorsal and ventral pelage merge on flanks. Head similar in colour to dorsal pelage; rufous tinge extends to tip of muzzle. Eyes dark, comparatively small. Ears small, rounded, densely covered with short rufous-brown hairs. Ears and eyes often hidden by hair. Limbs short. Forefoot with four digits; Digit 1 vestigial, Digit 5 short. Hindfoot with five digits; Digits 1 and 5 short, Digits 3, 4 and 5 long. Tail long (ca. 100% of HB), ringed with small scales, and with sparse very short dark bristles. Upper incisors not grooved. Nipples $1 + 2 = 6$.

Geographic Variation None recorded.

Similar Species (size comparisons refer to mean values only)

D. foxi. Larger in most body and cranial measurements; pelage buffy-brown or greyish-brown; restricted to Jos Plateau, Nigeria.

D. incommutus. Larger in most body and cranial measurements; pelage dark without reddish-brown or rufous tinge; southern and eastern Africa.

Distribution Endemic to Africa. Guinea Savanna BZ, Northern Rainforest–Savanna Mosaic, and Rainforest BZ of West Africa; may

*Dasymys rufulus*

extend into Sudan Savanna BZ in some regions. Recorded from S Senegal (south of Gambia), Guinea-Bissau, Guinea, Sierra Leone, Liberia, Côte d'Ivoire, Ghana, Togo, Benin, Nigeria and S Mali (Volobouev *et al.* 2000) and S Burkina (Gautun *et al.* 1985). One locality in Cameroon. Two isolated populations, north of the Gambia R. in Senegal (Duplantier *et al.* 1997). Following Mullin *et al.* (2002) and Mullin *et al.* (2004), the geographic range is far greater and includes parts of the Somalia–Masai and Zambezian Woodland BZ and the Southern Rainforest–Savanna Mosaic, and hence Congo, DR Congo, N Angola, Zambia, Malawi, W Mozambique, Sudan and Tanzania (see comments in genus and *D. incommutus* profiles).

Habitat Stream and river banks, marshy areas and swampy edges along rivers and lakes, wetter parts of flood-plains, young oil palm plantations, and rice fields.

Abundance Locally abundant in suitable habitats. Comprised 14.6% of the rodents trapped in grasslands at Mt Nimba (Guinea), 9.2% in savannas at Bolo and 7.5% in savannas at Lamto (Côte d'Ivoire), but only 0.5% in Adiopodoumé (Côte d'Ivoire) and 0.07% in Taï forest (Côte d'Ivoire) (Gautun *et al.* 1986). The most abundant rodent in young oil palm plantations in Côte d'Ivoire (trap success: 3.5–19.5% compared with 1–3% in nearby savannas), but uncommon in mature and old plantations (Bellier *et al.* 1964).

Adaptations Nocturnal (Duplantier & Granjon 1990). Very good swimmer (Duplantier & Bâ 2001). Occupies shallow burrows at the foot of grass tussocks (Coe 1975).

Foraging and Food Herbivorous. Feeds mainly on grasses and leaves (Coe 1975).

Social and Reproductive Behaviour No information.

Reproduction and Population Structure Gestation: 32 days (Gautun 1972). Mean embryo number: 3.22 ($n = 31$ ♀♀; Côte d'Ivoire; Bellier *et al.* 1964). In captivity, litter-size: 2.8 (2–3, $n = 8$; $n = 6$ in Côte d'Ivoire [Gautun 1972] and $n = 2$ in Senegal [J.-M. Duplantier unpubl.]).

Predators, Parasites and Diseases Remains found in pellets of Barn Owls *Tyto alba* in Guinea-Bissau (Heim de Balsac 1965) and Niayes region, Senegal (L. Granjon, K. Bâ and J.-M. Duplantier, unpubl.).

Conservation IUCN Category: Least Concern.

Measurements

Dasyms rufulus

HB: 144.3 (130–170) mm, $n = 44$

T: 145.1 (120–160) mm, $n = 43$

HF: 33.2 (30–35) mm, $n = 44$

E: 18.9 (17–21) mm, $n = 44$

WT: 78 (45–125) g, $n = 112$

GLS: 35.5 (32.6–38.6) mm, $n = 26$

GWS: 18.0 (16.6–19.5) mm, $n = 26$

M^1 – M^3 : 6.9 (6.3–7.3) mm, $n = 26$

Body and skull measurements: Guinea (MNHN)

Weight: Ghana, Liberia, Côte d'Ivoire (Carleton & Martinez 1991)

Key References Carleton & Martinez 1991; Rosevear 1969.

J.-M. Duplantier

GENUS *Dephomys*

Defua Rat

Dephomys Thomas, 1926. Ann. Mag. Nat. Hist., ser. 9, 17: 177. Type species: *Mus defua* Miller, 1900.



Dephomys defua.

A monotypic genus restricted to rainforest habitats in the Western Region of the Rainforest BZ. Although rather similar to *Stochomys* in external characters, its relationship to *Stochomys* is uncertain and is maybe more closely related to *Hybomys* (subgenus *Hybomys*) than to *Stochomys* (Musser & Carleton 2005). Appears to be the ecological equivalent to *Stochomys* in the rainforests of the Western Region (where *Stochomys* is not present). Distinguished from *Stochomys* by overall smaller size (smaller mean values, often non-overlapping measurements), thinner anterior palatal foramina, wider palate (relative to width of M^1) and smaller M^1 . Additional information is given in the species profile (see also Rosevear 1969). The single species is *Dephomys defua*.

D. C. D. Happold

Dephomys defua DEFUA RAT

Fr. Rat cible de Defua; Ger. Defua-Ratte

Dephomys defua (Miller, 1900). Proc. Washington Acad. Sci. 2: 635. Mt Coffee, Liberia.

Taxonomy Originally described in the genus *Mus*, and subsequently allocated to *Rattus* (Heim de Balsac & Bellier 1967), *Stochomys* (Misonne 1974) and *Dephomys* (Thomas 1926, Rosevear 1969, Van der Straeten 1984, Grubb *et al.* 1998). The subspecies *eburneae* from Côte d'Ivoire (Heim de Balsac & Bellier 1967) is considered (on the basis of canonical analysis) to be a valid species by Van der Straeten (1984) and Musser & Carleton (1993, 2005), but is considered here to be a subspecies of *D. defua*. Synonyms: *eburneae*. Subspecies: two. Chromosome number: $2n = 54$ (SW Côte d'Ivoire; *D. d. defua*?); $2n = 44$ ($n = 1$; Soubré, SW Côte d'Ivoire), $2n = 42$ (E Côte d'Ivoire; *D. d. eburneae*?) (Tranier & Dosso 1979). Variation in chromosome number in relation to distribution and taxonomic status requires investigation; Tranier &

Dosso (1979) suggest that different karyotypes may occur in different forest sub-regions – one to the west (i.e. Liberian Sub-region) and one to the east (i.e. Ghanaian Sub-region).

Description Medium-sized rat with very long tail similar to *Stochomys longicaudatus*. Pelage fairly long (ca. 10 mm) and coarse. Dorsal pelage brown to reddish-brown; hairs dark grey at base, reddish-brown at tip. Rump colour sometimes brighter (orangy-red) than mid-back. Long black guard hairs, often with pale tips, on rump. Ventral pelage whitish-grey; hairs dark grey at base, white or greyish-white at tip. Head long and pointed. Ears small, sparsely haired and rounded. Long dark vibrissae. Upper surfaces of fore- and

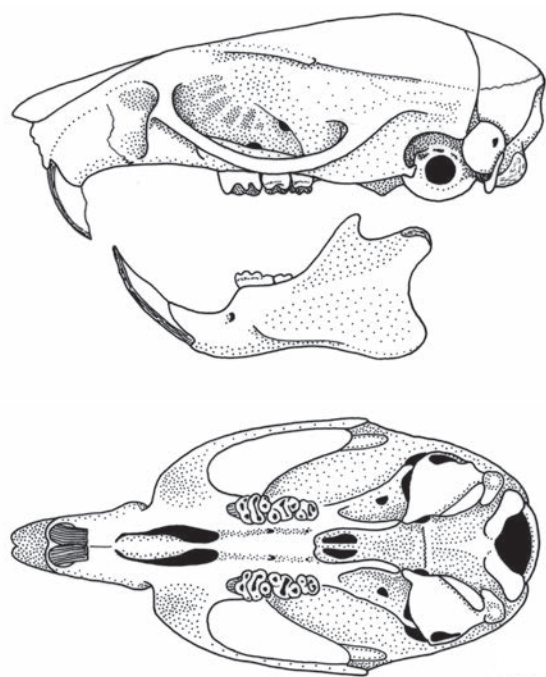


Figure 64. Skull and mandible of *Dephomys defua* (RMCA A2167).



Dephomys defua

hindfeet white or pale brown. Forefeet with four digits, each with small claw; Digit 1 absent. Hindfeet broad; five digits, Digits 1 and 5 shorter than Digits 2–4; each digit with small claw. Tail very long (ca. 154% of HB), dark, appears naked, but with rings of small scales and small bristles. Skull: incisors not grooved; supraorbital ridges well developed; auditory bullae small; anterior palatal foramina small and narrow, not reaching anterior end of M^1 ; width of palate at level of M^1 at least 1.5 times width of M^1 ; molar teeth rather weak; t_7 on M^1 absent; t_9 of M^1 present and moderately well developed; t_3 on M^2 very reduced and displaced (Figure 64). Nipples: $0 + 2 = 4$.

Geographic Variation Two subspecies, distinguishable mainly by canonical analysis (Van der Straeten 1984):

D. d. defua: recorded from Sierra Leone, Guinea (Mt Nimba) and Liberia.

Description as above; t_3 of M^1 present, but variable in structure.

D. d. eburneae: recorded in Côte d'Ivoire and Liberia. t_3 of M^1 reduced or absent; t_9 of M^1 reduced. Musser & Carleton (2005) regard this taxon as a valid species.

Similar Species

Stochomys longicaudatus. On average larger body measurements; similar externally, black guard hairs longer and more numerous, covering most of dorsal pelage; skull longer (mean GLS ca. 39 mm; mean M^1 – M^3 ca. 6.4 mm); t_9 on M^1 reduced to small displaced cusp; t_3 on M^2 very reduced and displaced; nipples $1 + 2 = 6$; allopatric (forest relics in Dahomey Gap and rainforests from Nigeria to E DR Congo). *Grammomys kuru*. Similar size; mainly arboreal; ventral pelage pure white; guard hairs not present; hindfoot narrower.

Distribution Endemic to Africa. Rainforest BZ (Western Region). Recorded from Sierra Leone, Guinea (Mt Nimba), Liberia, Côte d'Ivoire and Ghana.

Habitat Rainforest, swampy areas in rainforest, forest clearings and secondary growth. Also recorded in cocoa plantations (Jeffrey 1975) and oil palm plantations (Bellier 1964). On Mt Nimba, found in undisturbed forest, secondary scrub and grasslands (Coe 1975). Recorded very occasionally (2%, $n = 96$) in sacred groves (isolated patches of forest) in eastern region of Ghana (Decher 1997).

Abundance Rare or uncommon. At four rainforest sites in Ghana, comprised ca. 10% of small mammals ($n = 270$, 6 spp.; Cole 1975). In immature cocoa plantations, where *Praomys tullbergi* and *Lophuromys sikapusi* were the main species, only one individual was found ($n = 98$; 10 spp.), and in natural clearings in rainforest, only four were encountered ($n = 110$; 8 spp.) (Jeffrey 1977).

Remarks Nocturnal. May be partly arboreal. Diet is primarily vegetable material and some insects, and is similar to that of syntopic *Praomys tullbergi* and *Hylomyscus stella* (Cole 1975). Slugs and earthworms are not eaten (cf. *Malacomys* spp., Cole 1975). One pregnant ♀ in Ghana had two embryos (Jeffrey 1975; date not recorded), lactating ♀♀ were recorded in Taï N. P. (Côte d'Ivoire) in Feb (Lim & Van Coeverden de Groot 1997), and one ♀ was pregnant in Nov on Mt Nimba (Coe 1975).

Conservation IUCN Category: Least Concern.

Measurements

Dephomys defua

HB: 126.3 (109–137) mm, $n = 10$

T: 194.6 (176–210) mm, $n = 23$

HF: 26.5 (24–29) mm, $n = 26$

E: 17.1 (15–20) mm, $n = 26$

WT: 47 (41–53) g, $n = 8^*$

GLS: 33.6 (31.4–36.4) mm, $n = 26$

GWS: 16.0 (14.7–17.2) mm, n = 26

M¹–M³: 5.8 (5.5–6.4) mm, n = 26

Throughout geographic range (Van der Straeten 1984)

*Mt Nimba, Liberia (BMNH)

Key References Rosevear 1969; Cole 1975; Van der Straeten 1984.

D. C. D. Happold

GENUS *Desmomys*

Scrub Rats

Desmomys Thomas, 1910. Ann. Mag. Nat. Hist., ser. 8, 5: 284. Type species: *Pelomys harringtoni* Thomas, 1902.



Desmomys harringtoni.

The genus contains two species endemic to Ethiopia. Usually placed as a subgenus of *Pelomys* (e.g. Ellerman 1941, Misonne 1974) but cranial and body measurements are outside the normal range associated with *Pelomys* (Musser & Carleton 2005). The main diagnostic characters of the skull are a slight longitudinal ridge on outer surface of each upper incisor, ridge-like cusp t9 connecting central cusp t8 with labial cusp t6 on M¹ and M², ridge-like cusp t7 on M², well developed zygomatic plate, dome-shaped braincase, and heavily build mandibles (Figure 65). Semi-arboreal habit. The genus resembles *Myiomys* and *Pelomys* and is placed in the same lineage (based on mitochondrial DNA sequences) as *Arvicanthis*, *Lemniscomys*, *Rhabdomys*, *Pelomys*, *Myiomys* and *Arvicanthis* (Ducroz *et al.* 2001); and

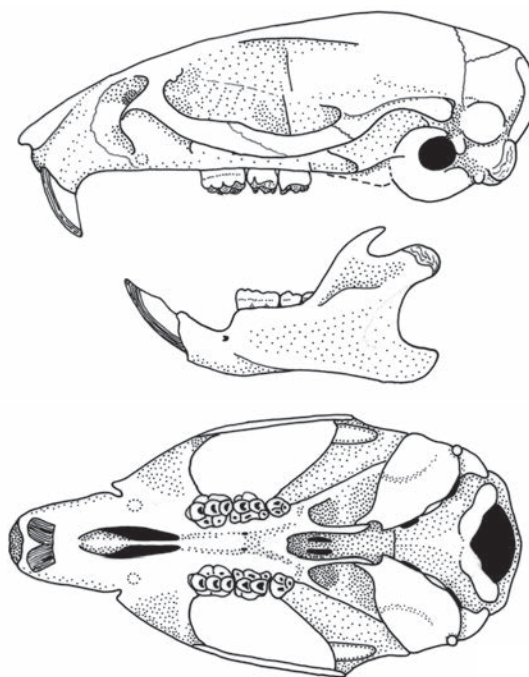


Figure 65. Skull and mandible of *Desmomys harringtoni* (BMNH 69.11.4.102 [skull], BMNH 70.752 [mandible]).

is more closely linked with *Rhabdomys* than with the other genera (see Musser & Carleton 2005). The species are distinguished by size, karyology and geographic distribution.

D. C. D Happold

Desmomys harringtoni HARRINGTON'S SCRUB RAT (HARRINGTON'S DESMOMYS)

Fr. Rat de Harrington; Ger. Harringtons Buschratte

Desmomys harringtoni (Thomas, 1902). Proc. Zool. Soc. Lond. 1902: 313. Katchisa, Shoa Province, Ethiopia. 2800 m.

Taxonomy Originally described in the genus *Pelomys*. The taxonomic name for this species has had a confused history (Dieterlen 1974, Yalden & Largen 1992). Although formerly placed in the genus *Pelomys* (e.g. Yalden *et al.* 1976), *harringtoni* is separated from *Pelomys* and allocated to the genus *Desmomys* (Musser & Carleton 1993, 2005, Yalden *et al.* 1996) on the basis of its distinctive tooth morphology (see Genus profile). The form *rex* (given as *Pelomys rex* in Yalden *et al.* 1976) is now considered as a synonym of *Myiomys dybowskii*. Synonyms: none. Chromosome number: 2n = 52; aFN = 72 (Capanna *et al.* 1996; see also *D. yaldeni*).

Description Medium-sized rodent, superficially similar to *Arvicanthis*. Pelage long (10–15 mm) and soft. Dorsal pelage blackish-brown, especially on mid-dorsal line; hairs dark grey at base, buff or yellowish at tip; some hairs longer, pure black; agouti pattern. Flanks paler, buff to pale cinnamon. Ventral pelage pure white or greyish-white, clearly delineated from colour of flanks by thin buff band; thin buff mid-ventral stripe on chest. Head similar in colour to dorsal pelage. Ears rounded, pigmented, with short buff hairs. Chin and throat greyish-white. Forelimbs with four digits; Digit 1 absent, Digit 5 reduced. Hindlimbs with five digits; Digits 1 and 5 reduced.

Tail long (ca. 95% of HB), bicoloured, dark above, pale below, ringed with scales, and short bristles. Skull: faint longitudinal ridge on each upper incisor; cheekteeth (M^1 – M^3) 6.2 (5.8–6.5) mm; width of palate (M^1 – M^1) 5.9–6.7 mm; and width of M^1 1.91–2.04 mm. Nipples: not known.

Geographic Variation None recorded.

Similar Species

D. yaldeni. Similar in appearance; on average HB slightly smaller; tail longer and relatively longer (ca. 115% of HB); on average shorter M^1 – M^3 (5.9–6.0 mm), narrower M^1 : (1.69–1.83 mm) and narrower palate (M^1 – M^1 : 5.2–5.4 mm); distribution very restricted.

Pelomys fallax. Groove on outer surface of each upper incisor; four functional digits on forefoot; widespread distribution.

Arvicanthis spp. No groove or ridge on outer surface of each upper incisor; four functional digits on forefoot; very widespread distribution.

Myiomys dybowskii. Groove on outer surface of each upper incisor; three functional toes on forefoot; widespread distribution.

Distribution Endemic to Africa. Afromontane–Afroalpine BZ. Widespread on the Ethiopian plateaux, primarily on the western side of the Ethiopian Rift Valley at altitudes between 1800 and 2800 m. In Menagesha State Forest, occurs at altitudes of 2200–3400 m (Afework Bekele 1996a).

Habitat ‘Bushy habitats’, disturbed open forest with *Kalanchoe* vegetation, amongst boulders and stony crevices in *Erica* scrub at higher altitudes, and marshes in W Ethiopia (Afework Bekele 1996a, Rupp 1980). Out of 45 specimens collected in Menagesha State Forest, three were in ‘bush’, eight in the open forest and 34 in the *Erica* scrub where boulders are common.

Abundance In bush habitats at Menagesha State Forest comprised 15.4% ($n = 293$; 9 spp.) of small rodents captured, and was the second most common species after *Myomys albipes*; in contrast, comprised only 2% of rodents captured in Juniper forest (Afework Bekele 1996a). In three suitable habitats in W Ethiopia formed 11–23% of rodents and was usually one of the most numerous rodent species (Rupp 1980). Generally a common species in suitable habitats.

Remarks Mostly nocturnal. Semi-arboreal and therefore unlikely to compete with the closely related terrestrial *Arvicanthis* where the two species are syntopic. Nests of woven grass built in bushes (label, BMNH). Six young in nest found in Dec (label, BMNH).



Desmomys harringtoni

Conservation IUCN Category: Least Concern.

Measurements

Desmomys harringtoni

HB: 136.3 (128–144) mm, $n = 21$

T: 128.3 (122–135) mm, $n = 21$

HF: 27.6 (27–29) mm, $n = 21$

E: 17.4 (17–18) mm, $n = 21$

WT: 64.9 (53–77) g, $n = 21$

GLS: 32.4 (30.8–34.9) mm, $n = 8$

GWS: 15.8 (15.1–16.6) mm, $n = 9$

M^1 – M^3 : 6.2 (5.8–6.5) mm, $n = 9$

Body measurements: Menagesha State Forest, Ethiopia (Afework Bekele unpubl.)

Skull measurements: Ethiopia (BMNH)

Key References Afework Bekele 1996a; Capanna *et al.* 1996; Rupp 1980; Yalden *et al.* 1976.

Afework Bekele

Desmomys yaldeni YALDEN'S SCRUB RAT (YALDEN'S DESMOMYS)

Fr. Rat de Yalden; Ger. Yaldens Buschratte

Desmomys yaldeni Lavrenchenko, 2003. Bonn. Zool. Beitr. 50: 320. Sheko Forest, Illubabor, Ethiopia. 1930 m.

Taxonomy With the exclusion of *Desmomys rex* (transferred by Musser & Carleton [1993] to *Myiomys*), *Desmomys* became a monotypic genus endemic to Ethiopia until Lavrenchenko (2003) reported the occurrence of this new species. *Desmomys yaldeni* is distinguished by its slightly smaller mean size, dark feet (ginger dorsally in *D.*

harringtoni), rather longer tail, more slight dentition and distinctive karyotype. Synonyms: none. Chromosome number: $2n = 52$, as in *D. harringtoni*, but with fewer bi-armed pairs (7 pairs, incl. sex chromosomes) and more acrocentric chromosomes (19 pairs) (cf. 12–13 bi-armed pairs and 13 acrocentrics in *D. harringtoni*).

*Desmomys yaldeni*

Description Slight, harsh-furred rat, very similar to *D. harringtoni* in appearance. Hairs ca. 11 mm. Dorsal pelage sandy-brown agouti dorsally; hairs grey at base with rufous subterminal band and black tip, giving the speckled (agouti) pattern. Ventral pelage greyish-white; grey at base, white at tip. Mid-ventral longitudinal straw-coloured band. Ears blackish, inner surfaces with short rufous hairs. Dorsal surface of forefeet blackish-rufous, fingers black, claws black. Hindfeet black dorsally. Tail very long (ca. 115% of HB), black above, yellow below, but hairs short so not producing a bicoloured tail (cf. *D. harringtoni*). Skull on average smaller than in *D. harringtoni*, though overlapping in most measurements. M^1 – M^3 (5.9–6.00 mm), breadth of M^1 (1.69–1.83 mm) and breadth across palate (M^1 – M^1 : 5.2–5.4 mm) significantly and distinctively smaller than for *D. harringtoni*. Nipples: not known.

Geographic Variation None recorded.

Similar Species

D. harringtoni. Similar in appearance; tail shorter and relatively shorter (ca. 95% of HB); on average longer M^1 – M^3 (6.0–7.0 mm), wider M^1 (1.91–2.04 mm) and wider palate (M^1 – M^1 : 5.9–6.7 mm); distribution more widespread.

Distribution Endemic to Africa. Afromontane–Afroalpine BZ. Only known from Illubabor Province, SW Ethiopia at 1800–1930 m.

Habitat Moist evergreen montane forest with abundant parasitic *Ficus* and an understorey of *Coffea arabica*. Syntopic species at type locality are *Dendromys melanotis*, *Lophuromys chrysopus*, *L. ?sikapus*, *Myomys albipes*, *Mus mahomet*, *Lemniscomys macculus* and *Otomys* sp. (Lavrenchenko 2003).

Abundance Only known from three specimens.

Remarks Longer tail suggests that this species is more arboreal than *D. harringtoni*, and shorter toothrow suggests the diet may be invertebrates and berries/fruits (Lavrenchenko 2003).

Conservation IUCN Category: Endangered.

Geographic range is limited and forest clearance is reducing the extent of suitable habitat.

Measurements

Desmomys yaldeni

HB: 117, 132 mm, n = 2

T: 141, 145 mm, n = 2

HF: 27, 29 mm, n = 2

E: 17.5, 18 mm, n = 2

WT: 45, 49 g, n = 2

CbL: 27.0, 28.8 mm, n = 2

GWS: 14.1, 15.4 mm, n = 2

M^1 – M^3 : 5.9 (5.9–6.1) mm, n = 3

Ethiopia (Lavrenchenko 2003)

Key Reference Lavrenchenko 2003.

D. W. Yalden

GENUS *Grammomys*

Thicket Rats

Grammomys Thomas, 1915. Ann. Mag. Nat. Hist., ser. 8, 16: 150. Type species: *Mus dolichurus* Smuts, 1832.

The genus *Grammomys* contains 11 species (Table 32), and has a wide geographical range in many rainforest and savanna habitats throughout sub-Saharan Africa. Four of these species (*G. cometes*, *G. dolichurus*, *G. ibeanus* and *G. kuru* [formerly *G. rutilans*]) have large geographical ranges; the remainder are rather localized. All species are arboreal or scansorial.

The genus is closely related to *Thamnomys* but is now considered as a valid genus although it shares many similarities with *Thamnomys* (see below). The characters of the genus are medium size, rather short and soft pelage, very long semi-prehensile tail (usually 120–160% of HB)

and relatively small hindfeet. The dorsal pelage is usually grey, brown or rufous without any patterning, and ventral pelage is pure white or cream. The t7 cusp (the postero-internal cusp) of M^1 and M^2 is never large and often reduced to a mere connecting ridge between t4 and t8 (a character which contrasts with that of *Thamnomys*). The ridge is inwardly projecting, giving a rounded shape to M^1 and M^2 on the lingual side. Together with the rounded shape of M^3 , the molars are easily distinguishable from the almost rectangular-shaped molars of *Thamnomys* spp., which have a quite large t7. In most species of *Grammomys*, t9 of M^1 and M^2 is well developed and t3 is mostly vestigial. The central row of

Table 32. Species in the genus *Grammomys*. Arranged in order of increasing mean head and body length.
(n. d. = no data.)

| Species | HB mean (mm) | T mean (mm) [% of HB] | Dorsal pelage | GLS mean (mm) | Chromosome number | M ¹ –M ³ | Notes |
|--------------------------------|------------------|------------------------------|---|-------------------------|-------------------|--------------------------------|--|
| <i>G. caniceps</i> | 97.4 | 150.7 [150%] | Grey, cinammon streaks, black flecks | 26.3 | 2n = 56, FN = 78 | 3.6 (3.6–3.8) | Coastal N Kenya and S Somalia |
| <i>G. macmillani</i> | 105 | 167 [ca. 160%] | Olive-brown to grey | 28.1 | 2n = 68–70 | 4.3 (4.1–4.5) | Eastern Africa; also Sierra Leone and Liberia. Limits uncertain |
| <i>G. buntingi</i> | 106 | 166 [157%] | Olive-grey to sandy-brown | 28.7 | 2n = 52, FN = 66 | 4.6 (4.6–4.7) | Sierra Leone to Côte d'Ivoire |
| <i>G. minnae</i> | 110 ^a | 173, 150 ^b [157%] | Greyish-brown; dark mask around eyes | 29.2, 29.5 ^b | 2n = 32, FN = 64 | 4.0, 4.3 ^b | Ethiopia (limited distribution) |
| <i>G. dryas</i> | 112 | 160 [160%] | Tawny-brown | 29.2 | n. d. | 4.36 (3.9–4.8) | Burundi, Rwanda, E DR Congo (higher altitudes, Albertine Rift Valley) |
| <i>G. cometes</i> ^c | 112–124 | 142–194 [120–160%] | Reddish-brown to buff | 31–33 | n. d. | ca. 4.5 | Southern Africa south of the Zambesi R. |
| <i>G. dolichurus</i> | 113 | 166 [150–180%] | Gingery-brown to cinnamon-brown | 28.9 | 2n = 52 | 4.3 (3.8–4.6) | Widespread. Eastern and southern Africa. Wooded savanna |
| <i>G. aridulus</i> | 113.7 | 184.7 [163%] | Reddish-brown to olive-brown | 29.9 | n. d. | 4.5 (4.1–4.9) | Jebel Marra, Sudan |
| <i>G. kuru</i> ^d | 114.3 | 182.5 [ca. 160%] | Greyish-brown, tinged with rufous-brown | 31.8 | 2n = 50 | 5.4 (5.1–5.7) | Widespread. SW Guinea to Cameroon and Central African Republic, south to DR Congo and Angola |
| <i>G. ibeanus</i> | 122 | 182 [ca. 150%] | Dull olive-brown | 32.0 | n. d. | 5.2 (4.9–5.5) | Eastern Africa – Uganda to Malawi; north of Zambesi R. |
| <i>G. gigas</i> ^e | 132 | 201 [ca. 150%] | Olive-grey | 35.5 | n. d. | 5.5 | Mt Kenya |

^a One specimen only.

^b Two specimens only.

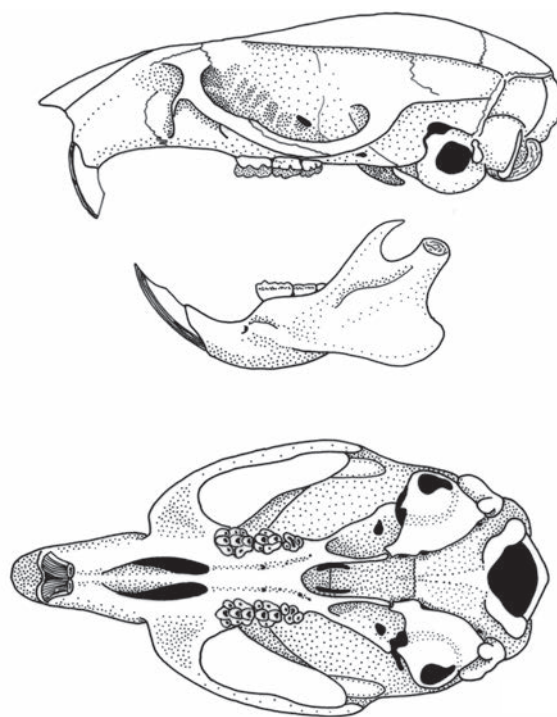
^c Range of measurements; means not available.

^d Formerly *G. rutilans*.

^e Known only from the holotype specimen.

cusps (t2–t5–t8) is markedly enlarged compared with the relatively smaller cusps of *Thamnomys*. The skull is comparatively short, the braincase appearing broad; supraorbital ridges are relatively weak or even absent, and the auditory bullae are small (Figure 66).

All species in the genus are arboreal, living in habitats where there are grasses, tangles, shrubs and trees for climbing. The long tail and semi-opposable digits of the hindfeet enable quick and efficient movement along small stems and twigs, and along larger branches. Thicket Rats are primarily nocturnal; in the daytime, they rest in nests of stems and leaves that are intertwined among the twigs of shrubs, and some may rest in hollows of trees. All species are vegetarian, feeding on a wide range of plants and fruits. Reproduction (for species that have been studied) is mostly seasonal; litter-sizes are small (usually 1–3 young/litter) compared with other rodents of



RIGHT: Figure 66. Skull and mandible of *Grammomys kuru* (HC 1263).

similar size – a character that may be related to continuous nipple-dragging by the mother, even when climbing and active outside the nest at night.

The genus *Grammomys* was split from *Thamnomys* by Thomas (1915) to accommodate those species in which t_7 on M^1 and M^2 was absent or reduced. Prior to Ellerman (1941), who accepted this arrangement, most studies referred to *Grammomys* as a subgenus of *Thamnomys* (see Rosevear 1969 for an historical review). In Ellerman's view, the major differences in cuspidation, and in the form of the feet, were

sufficiently important to warrant generic status to *Grammomys*, a view that is now widely accepted. The genus *Thamnomys* is now confined to three species (see that profile).

Eleven species are recognized here, although one species, *G. kuru* (= *G. rutilans*) may be a complex of two species. Species of the genus are distinguished by size, colour of pelage, size and details of skull characters and chromosome number.

Fritz Dieterlen

Grammomys aridulus JEBEL MARRA THICKET RAT (ARID WOODLAND GRAMMOMYS)

Fr. Souris sylvestre de Jebel Marra; Ger. Jebel Marra Buschmaus

Grammomys aridulus Thomas and Hinton, 1923. Proc. Zool. Soc. Lond. 1923: 268. Kulme, Wadi Aribo, Darfur, Sudan. 3300 ft (1005 m).

Taxonomy Originally described as 'a very well-marked species', later treated as a subspecies of *Grammomys macmillani* (Allen 1939, Ellerman 1941, Setzer 1956, Happold 1966b) or included in *Grammomys dolichurus* (Misonne 1974). Considered to be a valid species by Hutterer & Dieterlen (1984). Synonyms: none. Chromosome number: not known.

Description Small-sized *Grammomys*. Dorsal pelage pallid, reddish-brown to dull olive-brown, darker on mid-dorsal line. Flanks, rump and base of tail bright tawny. Ventral pelage creamy-white, contrasting with colour of flanks. Top of head and neck dull brownish-grey; cheeks grey. Ears bright ochraceous-tawny on outer and inner surfaces; small white patch at base of ears. Vibrissae very long, up to 39–47 mm. Fore- and hindlimbs and feet creamy-buff. Tail extremely long (ca. 163% of HB), darker above, paler below; terminal third with hairs, small brown pencil at tip. In juveniles, dorsal pelage dull brownish on rump, greyish on head. Nipples: 1 + 2 = 6.

Geographic Variation None recorded.

Similar Species The only species of *Grammomys* in its area of distribution. Species of *Grammomys* of similar size are:

G. dolichurus. Tail shorter and relatively shorter (mean 166 mm, ca. 150% of HB); dorsal pelage gingery-brown to cinnamon-brown; widespread in eastern Africa.

G. kuru. Tail of similar length and relative length; dorsal pelage greyish-brown; widespread in western Africa.

Distribution Endemic to Africa. Sahel Savanna BZ / Afroalpine BZ. Recorded only on Jebel Marra, Sudan, and probably endemic to the jebel. Recorded from four localities (Kulme, Gollol, Mortagello and Kelling) on the western side of the jebel at 1000–2000 m where annual rainfall is 800–1000 mm. Not recorded from drier semi-arid lowlands surrounding the jebel. This species has the northernmost geographic range of any species in the genus.

Habitat Trees, bushes, hedges in valleys. May occur close to human habitations. Vegetation in preferred habitat at 4000–6000 ft includes *Cordia abyssinica*, *Ficus* spp., *Euphorbia candelabrum*, *Hyparrhenia pseudocimbaria* and *Andropogon* spp. (Happold 1966b).

Abundance Rare. Known only from the type and a few specimens collected in 1965 (Happold 1966b) and 1983 (Dieterlen & Nikolaus 1985).

Remarks Arboreal, probably with similar adaptations to other species in the genus. One pregnant ♀ and two lactating ♀♀ in Jul (Dieterlen & Nikolaus 1985), and one subadult in Nov (Happold 1966b) suggest reproduction during wet season (May–Sep; 60% of annual rainfall in Jul–Aug; Wickens 1976). Embryo number: 1 (n = 1); litter-size: 4 (one ♀ with young, 3–4 weeks old).

Conservation IUCN Category: Data Deficient.

The very small area of distribution and rarity of the species are cause for concern.

Measurements

Grammomys aridulus

HB: 113.7 (110–116) mm, n = 3



Grammomys aridulus

T: 184.7 (181–188) mm, n = 3
 HF: 23.3 (23–24) mm, n = 3
 E: 18.0 (18) mm, n = 3
 WT: 43.3 (41–46) g, n = 3
 GLS: 29.9 (29.4–30.6) mm, n = 4
 GWS: 14.5 (14.2–14.9) mm, n = 4
 M¹–M³: 4.5 (4.1–4.9) mm, n = 4

Jebel Marra, Sudan (Dieterlen & Hutterer 1984, SMNS)

Key References Dieterlen & Nikolaus 1985; Happold 1966b; Hutterer & Dieterlen 1984.

Fritz Dieterlen

Grammomys buntingi BUNTING'S THICKET RAT (BUNTING'S GRAMMOMYS)

Fr. Souris sylvestre de Bunting; Ger. Buntings Buschmaus

Grammomys buntingi (Thomas, 1911). Ann. Mag. Nat. Hist., ser. 8, 7: 381. Gonyon, Basso, Liberia.

Taxonomy Originally described in the genus *Thamnomys*. Misonne (1974) included *buntingi* within *G. dolichurus* although other authors have regarded it as a valid species (e.g. Rosevear 1969, Petter & Tranier 1975, Musser & Carleton 1993, 2005). Synonyms: none. Chromosome number: 2n = 52, FN = 66 (Petter & Tranier 1975).

Description Small arboreal rat with extremely long tail. Dorsal pelage olive-grey to sandy-brown, becoming reddish-brown on rump; hairs dark grey at base, reddish-brown at tip. Flanks grey. Ventral pelage pure white. Colour of dorsal pelage delineated from ventral pelage by thin line of cream or buff. Ears comparatively small. Fore- and hindlimbs buffy-brown. Tail very long (ca. 157% of HB). Skull with t7 of M¹ poorly developed or absent. Nipples: not known.

Geographic Variation None recorded.

Similar Species

Grammomys kuru. On average larger in all body measurements; skull slightly larger and M¹–M³ longer (5.1–5.3 mm); chromosome number: 2n = 36; may be sympatric or parapatric in Côte d'Ivoire.

Distribution Endemic to Africa. Rainforest BZ (Western Region) and adjacent Northern Rainforest–Savanna Mosaic. Recorded from Sierra Leone, Liberia, Guinea and Côte d'Ivoire. Not recorded from Ghana or Gambia (Grubb *et al.* 1998).

Habitat Probably similar to *G. kuru* – secondary tangles on edge of rainforest (and gallery forests in Rainforest–Savanna Mosaic).

Abundance Uncertain, but probably 'rather rare' (Rosevear 1969). Only one individual was found at Foro-Foro, Côte d'Ivoire, in moist Guinea savanna (= 0.03% of all small rodents, n = 3906; Gautun 1975).

Remarks Very little is known about this species, but its biology is likely to be similar to *G. kuru* (= *G. rutilans*). The diet consists of seeds and leaves (T. S. Jones in Grubb *et al.* 1998).

Conservation IUCN Category: Data Deficient.



Grammomys buntingi

Measurements

Grammomys buntingi
 HB: 106 (102–108) mm, n = 4
 T: 166 (158–171) mm, n = 4
 HF: 23 (23–24) mm, n = 4
 E: 16 (15–16) mm, n = 4
 WT: n. d.
 GLS: 28.7 (28.0–29.3) mm, n = 4
 GWS: 13.5 (13.1–13.8) mm, n = 4
 M¹–M³: 4.6 (4.6–4.7) mm, n = 4
 Throughout geographic range (Rosevear 1969)

Key References Grubb *et al.* 1998; Rosevear 1969.

D. C. D. Happold

***Grammomys caniceps* GREY-HEADED THICKET RAT (GREY-HEADED GRAMMOMYS)**

Fr. Souris sylvestre du Kenya; Ger. Graukopf-Buschmaus

Grammomys caniceps Hutterer and Dieterlen, 1984. Stuttgarter Beitr. Naturk., ser. A, 374: 12. Malindi, Kenya.

Taxonomy Roche *et al.* (1984) referred to specimens of this species from Somalia as *G. dolichurus*. Synonyms: none. Chromosome number: $2n = 56$, $FN = 78$ (Hutterer & Dieterlen 1984; see also below).

Description Small climbing rat with very long tail. Dorsal pelage grey streaked with cinnamon-brown turning to bright cinnamon on rump; hairs mid-grey on basal two-thirds, bright cinnamon on terminal third. Scattered pure black hairs give blackish flecked appearance on back. Flanks paler with fewer black hairs. Ventral pelage pure white, clearly delineated from colour of flanks. Head similar in colour to dorsal pelage. Dark bar running from eye to base of whiskers. Upper lips, lower part of cheeks, chin and throat pure white. Comparatively short (30–34 mm) black vibrissae. Ears large, conspicuous, covered with short pale brown or pale cinnamon hairs. White postauricular spot extending dorsally onto back of head. Forelimbs white, short, with four well-developed digits (Digit 1 reduced to small tubercle without claw). Hindlimbs relatively short, white, with five digits. Tail very long (ca. 150% of HB), brown, scaly, appears almost naked but covered with very short brown bristles; white hairs at terminal end form small inconspicuous pencil. Nipples: $2 + 1 = 6$, or $1 + 1 = 4$.

Geographic Variation Roche *et al.* (1984) analysed the chromosomes of five specimens from Somalia and found a high degree of variation ($2n = 54$ to 61).

Similar Species

G. macmillani. On average larger in body and cranial measurements; dorsal pelage less grey.

G. cometes. On average larger in body and cranial measurements; different geographical distribution.

Distribution Endemic to Africa. Somalia–Masai Bushland BZ. Known only from Malindi, Kenya, and southern Somalia (Afgoi and Mogadiscio; Roche *et al.* 1984).

Habitat Probably dry coastal savanna. The holotype was found on a palm tree in a tourist area at Malindi. Roche *et al.* (1984) found animals in a nest on an *Acacia* tree.

Abundance No information. Appears to be uncommon.

Remarks Scansorial with a prehensile tail. Captive animals showed well-developed climbing behaviour. They were able to hang upside-down holding on with the hindfeet and curling the tail around a twig. Diet in the wild is unknown, but captive animals fed on seeds,

*Grammomys caniceps*

fruit and insect larvae. Bowl-like nests are constructed in *Acacia* trees (Roche *et al.* 1984). Captive-bred animals were tolerant towards other conspecifics and lived in groups of 5–10 animals in a single large cage; under these conditions they reproduced provided sufficient nest boxes and branches were provided (R. Hutterer unpubl.).

Conservation IUCN Category: Data Deficient.

Measurements

Grammomys caniceps

HB: 97.4 (86–105) mm, $n = 9$

T: 150.7 (147–155) mm, $n = 9$

HF: 21.1 (19–22) mm, $n = 9$

E: 16.0 (14–17), $n = 9$

WT: 28.4 (18–40) g, $n = 9$

GLS: 26.3 (25.8–27.8) mm, $n = 9$

GWS: 13.0 (12.5–13.5) mm, $n = 9$

M^1 – M^3 : 3.6 (3.6–3.8) mm, $n = 9$

Kenya, Somalia (Hutterer & Dieterlen 1984)

Key Reference Hutterer & Dieterlen 1984.

R. Hutterer

Grammomys cometes MOZAMBIQUE THICKET RAT (MOZAMBIQUE GRAMMOMYS)

Fr. Rat sylvestre de Mozambique; Ger. Mosambik-Buschmaus

Grammomys cometes Thomas & Wroughton, 1908. Proc. Zool. Soc. Lond. 1908: 549. Inhambane, Mozambique.

Taxonomy The taxonomic and geographic limits of this species are uncertain because of the morphological similarity between *G. cometes* and *G. ibeanus*. Misonne (1974) included *ibeanus* as a subspecies of *G. cometes*, as did Hutterer & Dieterlen (1984), with a geographic range from South Africa to S Sudan. Musser & Carleton (1993, 2005) restrict *G. cometes* to south of the Zambezi R., and consider all populations north of the river to be *G. ibeanus* (see that profile). The northern populations, between the Zambezi R. and Sudan, show considerable morphological variability and referring them all to *G. ibeanus* remains questionable (F. Dieterlen unpubl.). The form *silindensis* from S Zimbabwe, considered as a subspecies of *G. cometes* (e.g. Smithers 1983) is now considered a synonym. Synonyms: *silindensis*. Subspecies: none. Chromosome number: not known.

Description Small to medium-sized climbing rat with very long tail; the largest species (with *G. ibeanus*) in the genus. Pelage short and silky. Dorsal pelage reddish-brown to buff; hairs dark slate-grey on basal two-thirds, buff on terminal one-third; some hairs pure black. Ventral pelage pure white, clearly delineated from colour on flanks. Head similar in colour to dorsal pelage. Postauricular patch usually present. Fore- and hindfeet short, white; claws short. Tail very long (120–160% of HB), with a distinct terminal pencil. Skull: greatest length >31 mm; M¹–M³ long (4.5 mm); anterior palatal foramina long, extending posteriorly to level with t3 of M¹. Nipples: 0 + 2 = 4 or 1 + 2 = 6.

Geographic Variation None recorded.

*Grammomys cometes***Similar Species**

G. dolichurus. On average smaller; white postauricular patch absent; skull length <31 mm; easily confused with *G. cometes* in KwaZulu–Natal, South Africa.

G. ibeanus. Similar in size, north of the Zambezi R. only.

Distribution Endemic to Africa. South-eastern part of Zambezi Woodland BZ, and Coastal Forest Mosaic BZ of southern Africa. Recorded from Pirie Forest in Eastern Cape Province of South Africa north through KwaZulu–Natal and (former) Transvaal Provinces to E Zimbabwe and Mozambique south of the Zambezi R. (Musser & Carleton 1993). Following Musser & Carleton (1993, 2005), specimens from Malawi (De Graaff 1981, Ansell & Dowsett 1988) and further north formerly ascribed to this species are considered to be *G. ibeanus*.

Habitat Dense evergreen forests in South Africa (De Graaff 1981). In KwaZulu–Natal, found in mature *Podocarpus* forests and in montane forests; prefers denser, more well-developed forest than *G. dolichurus* (Taylor 1998). Recorded from forest fringes and thickets in Mozambique (Smithers & Lobão Tello 1976).

Abundance Uncertain, but appears to be rare or uncommon in collections. Much less common than sympatric *G. dolichurus*.

Remarks Arboreal and nocturnal. Probably similar to other species in the genus. Embryo number: 3 (n = 1; Ngome Forest, KwaZulu–Natal, South Africa; Taylor 1998).

Conservation IUCN Category: Least Concern.

Status recorded as 'Indeterminate' in South Africa (Smithers 1986b), and as 'Vulnerable' because of its dependence on evergreen forests (Schlitter 1989).

Measurements

Grammomys cometes

HB: 112–124 mm

T: 142–194 mm

HF: 23–25 mm

E: n. d.

WT: 52 g, n = 1*

GLS: 31–33.2 mm

GWS: n. d.

M¹–M³: ca. 4.5 mm

South Africa (De Graaff 1981; means and sample sizes not given)

*Taylor 1998

Key References De Graaff 1981; Hutterer & Dieterlen 1984; Musser & Carleton 1993.

Fritz Dieterlen

Grammomys dolichurus WOODLAND THICKET RAT (COMMON GRAMMOMYS)

Fr. Souris sylvestre commune; Ger. Wald-Buschmaus

Grammomys dolichurus (Smuts, 1832). Enumer. Mamm. Capensium, p. 28. Near Cape Town, South Africa.

Taxonomy Originally described in the genus *Mus*, but more recently allocated to *Thamnomys* (e.g. Hanney 1965; Smithers 1983) or *Grammomys* (e.g. Hutterer & Dieterlen 1984, Musser & Carlton 1993, Taylor 1998). Many names (including *surdaster*) are now synonyms; individuals in the north of the geographic range may be a separate species *G. surdaster* (Musser & Carlton 1993). Synonyms: *angolensis*, *arborarius*, *baliolus*, *discolor*, *elgonis*, *insignis*, *littoralis*, *polionops*, *surdaster*, *tongensis*. Subspecies: none. Chromosome number $2n = 52$, $FN = 66$ (Petter & Tranier 1975).

Description Small arboreal mouse, with dull gingery-brown dorsal pelage and an extremely long tufted tail. Dorsal pelage gingery-brown or cinnamon-brown suffused with grey and black. Dorsal hairs dark grey at base, gingery-brown on terminal third, often with back tip. Guard hairs, grey tipped with black. Ventral pelage usually pure white, clearly delineated from dorsal pelage, often with thin band of pale orange between dorsal and ventral pelage. Head gingery-brown; ears short and rounded, covered with short ginger hairs. Lacks postauricular white ear patch (cf. *G. cometes*). Chin and throat white. Feet white. Digit 1 of forefoot reduced to stump without claw. Hindfeet relatively short, Digit 5 long, adapted for grasping small twigs. Tail extremely long (ca. 150–180% HB), scaly, with short brown or black bristles; long black hairs form terminal pencil at tip. Nipples: $1 + 2 = 6$; $0 + 2 = 4$.

Geographic Variation None recorded.

Similar Species

G. cometes and *G. ibeanus*. On average larger; white subauricular patch.

G. macmillani. Usually slightly smaller; dorsal pelage olive-brown or reddish-brown; chromosome number: $2n = 68-76$.

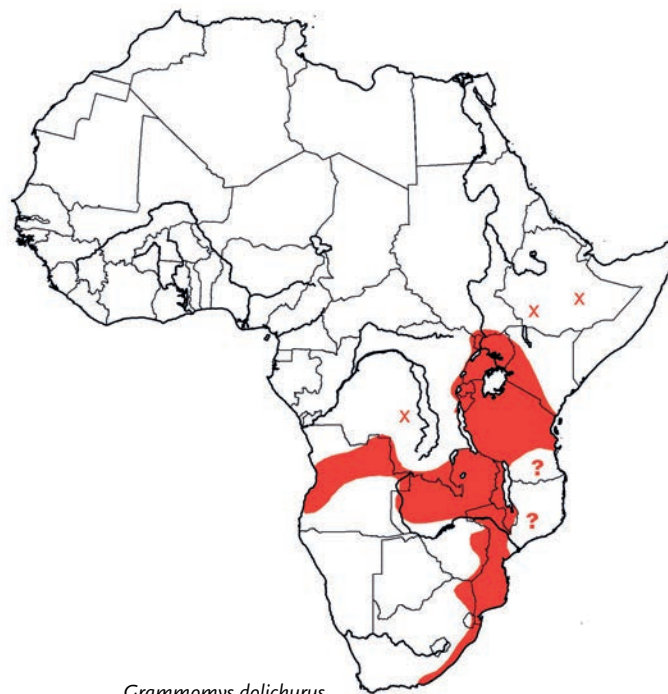
G. kuru. Rainforest BZ; similar in size but tail usually relatively longer; allopatric.

Hylomyscus spp. Smaller (HB: <90 mm, T: <130 mm, WT: <30 g).

Other species of *Grammomys* in eastern Africa (*G. caniceps*, *G. dryas*, *G. gigas*) have restricted ranges.

Distribution Endemic to Africa. Zambezan Woodland BZ, southern part of Somalia–Masai Bushland BZ, marginally in parts of Coastal Forest Mosaic BZ and marginally in lower parts of Afromontane–Afroalpine BZ of South Africa. Recorded from S Sudan through most of eastern Africa to the coastal region of eastern South Africa, and westwards to Angola. Widespread. Outlier populations in southern Ethiopia.

Habitat Woodland savannas and gallery forests within savanna. Recorded in many habitats where climbing is possible, including *Brachystegia* and *Acacia* woodlands, evergreen gallery forests, afromontane forests, shrubs, thickets, tall grasses and reeds.

*Grammomys dolichurus*

Abundance Although probably fairly abundant in suitable arboreal habitats, comprises only a small proportion of small mammals captured on the ground. For example, 0.2% in *Acacia* woodlands and 1.2–6% in plateau grasslands of Malawi (Hanney 1965); 1% in thicket habitats at Lengwe N. P., Malawi (Happold & Happold 1991); 1% in *Pennisetum* grassland and 'grassbush' of E DR Congo (Dieterlen 1967c); 3% in Majanga Forest, Uganda (Delany 1971); and 3.7% in afromontane forests of KwaZulu–Natal, South Africa (Wirminghaus & Perrin 1993). Density of ca. 1.1/ha in afromontane forest of South Africa (Wirminghaus & Perrin 1993).

Adaptations Nocturnal and arboreal; may be terrestrial where trees and bushes are sparse. Very agile, running along twigs and jumping from twig to twig. Adaptations for climbing include long Digit 5 on hindfoot, and extremely long tail for balance. The tail is sometimes wrapped around twigs and small branches but is not fully prehensile. Spherical nests with single entrance made of grasses and leaves, 20–30 cm in diameter, are built up to 4 m above ground, and lined with finely shredded grass. Other nests found in axils of banana leaves and pineapple plants. On occasion, Woodland Thicket Mice have been found in the abandoned nests of birds (barbets and weavers). Rapid development of young, especially early separation of the toes and development of the grasp reflex, are probably adaptations to arboreal life. In afromontane forests of South Africa, body fat varied by a factor of ca. 2.5 during the year (lowest in winter –18% mean minimum in winter; highest in summer –42% mean maximum). The annual fluctuation is lower than for terrestrial rodents in the same habitat, probably because Woodland Thicket Rats

have access to alternative foods (e.g. perched aerial insects and fruits) during winter (Wirminghaus & Perrin 1993).

Foraging and Food Predominantly vegetarian. Probably forages in trees and on the ground. In South Africa, average diet throughout the year was 47% fruit, 46% leaves and stems and 6% insects ($n = 11$); for most of year, diet was purely vegetarian and insects were consumed only in spring (Aug–Nov) (Wirminghaus & Perrin 1992). In Malawi (Hanney 1965), Woodland Thicket Mice are purely vegetarian with a preference for fruit and green bark. Captive individuals fed on cereals and fruit, but would not accept insects.

Social and Reproductive Behaviour Communal, several being found in a single nest. One record stated that they may be 'found in family parties, sometimes several families together' (Sweeney 1970, in Ansell & Dowsett 1988).

Reproduction and Population Structure Reproductive activity varies by locality and climate. In Malawi, pregnant or lactating ♀♀ in Feb, Mar and May (wet season) (Hanney 1965), and in Zimbabwe, pregnant ♀♀ in Jan and Sep (Smithers & Wilson 1979). In South Africa, ♀♀ in reproductive condition mainly in summer and autumn (Dec, Jan, Mar, May, Jul), and young in summer and autumn (Mar–Jul) (Wirminghaus & Perrin 1993). In Uganda, ♀♀ may give birth to young every 5–6 weeks (Delany 1975), suggesting more-or-less continuous reproduction in the tropics and smaller numbers of young/litter. Gestation ca. 24 days. Embryo number: 4.6 (3–6; Malawi; Hanney 1965); 2.8 (1–3; Uganda; Delany 1975). Young precocial at birth, covered with fine greyish hairs. Mean

weight at birth: 4.2 g. Mother nipple-drags young. Eyes open and young climb at Day 15. Growth and development rapid (Bland 1973; Panagis & Nel 1981). Adult size attained at ca. Day 40. Reproductive maturity attained when weight ca. 30 g and HB ca. 80–90 mm (Dieterlen 1967c).

Predators, Parasites and Diseases Domestic cats may prey on these mice in urban areas (e.g. Durban; Taylor 1998). Ectoparasites include 14 species of fleas, four species of mites and two species of ticks (details in De Graaff 1981).

Conservation IUCN Category: Least Concern.

Measurements

Grammomys dolichurus

HB: 113 (103–133) mm, $n = 28$

T: 166 (150–187) mm, $n = 27$

HF: 24 (21–26) mm, $n = 28$

E: 17 (15–20) mm, $n = 28$

WT: 40 (33–54) g, $n = 18$

GLS: 28.9 (28.2–31.4) mm, $n = 16$

GWS: 14.2 (13.0–15.5) mm, $n = 16$

M^1 – M^3 : 4.3 (3.9–4.7) mm, $n = 17$

S Sudan, E DR Congo, Tanzania (BMNH, SNHM)

Key References De Graaff 1981; Hanney 1965; Smithers 1983; Wirminghaus & Perrin 1992, 1993.

D. C. D. Happold

Grammomys dryas ALBERTINE RIFT THICKET RAT (ALBERTINE RIFT GRAMMOMYS)

Fr. Souris sylvestre du Rwenzori; Ger. Dryas-Buschmaus

Grammomys dryas (Thomas, 1907). Ann. Mag. Nat. Hist., ser. 7, 19: 123. Mubuku Valley, E Rwenzori, Uganda. 6000–7000 ft (1830–2130 m).

Taxonomy Originally described in the genus *Thamnomys*, an arrangement modified by Allen (1939) to *Thamnomys* (*Grammomys*) *dryas*. Placed in the genus *Grammomys* by Ellerman (1941), and as a synonym of *Grammomys dolichurus* by Misonne (1963, 1974) and Delany (1975). Referred to as *Thamnomys surdaster dryas* by Rahm & Christiaensen (1963), as *Thamnomys dolichurus dryas* by Rahm (1967), and as *Thamnomys surdaster* by Dieterlen (1967a, c). Maintained as a valid species by Musser & Carleton (1993, 2005). Synonyms: none. Chromosome number: not known.

Description Small to medium-sized rat, with very long tail (ca. 160% HB). Dorsal pelage tawny-brown, richer ochraceous on rump; head grey to greyish-brown. Flanks paler. Ventral pelage pure white. Colour of flanks and ventral pelage separated by thin line of buff. Upper surface of fore- and hindlimbs pale buff. Tail uniformly dark brown, with pencil at tip. Skull lightly built with delicate molars; auditory bullae small; anterior palatal foramina reaching to the level of the front of M^1 . Postero-internal cusp of first and second molars reduced to a narrow connecting ridge, often hardly perceptible. Nipples: $0 + 2 = 4$.

Geographic Variation Specimens from the type locality (Rwenzori Mts) are a brighter ochraceous colour compared with those from Kahuzi–Biega N. P. (DR Congo) and Kibira N. P. (Burundi). In Bwindi Impenetrable N. P., Uganda, two 'forms' may be recognized: (a) a higher elevation form (<2000 m), referred to here as *G. dryas*, with broader zygomatic plate, more inflated auditory bullae, and longer and higher skull; and (b) a mid-elevation form (1500–1700 m) that may represent a distinct taxon.

Similar Species In allied sympatric montane *Thamnomys* (i.e. *T. kempfi*, *T. venustus*), postero-internal cusp is well-developed, and M^1 – M^3 is >6 mm (cf. <5 mm in *Grammomys*). Ventral pelage of *Thamnomys* is grey at base.

Distribution Endemic to Africa. Afromontane–Afroalpine BZ. Endemic to the Albertine Rift Valley and surrounding hills of Uganda, Burundi, Rwanda and E DR Congo (including Idjwi I. in L. Kivu).

Habitat Exhibits a wide range of habitat preferences. In the L. Kivu region, prefers woodland savanna, banana plantations and sometimes shrubs and hedges around villages (Rahm 1967). Commonest in

*Grammomys dryas*

secondary growth with shrubs adjacent to swamps and in herbaceous savanna (at Tshiziri near L. Kivu, 1500 m). Not recorded in rainforest habitats where replaced by *G. rutilans* (now *G. kuru*) and *Thamnomys kemp* (Rahm 1967). Occurs in forested habitats as well as secondary growth in Kibira N. P. (Burundi, 1880–2390 m) and Bwindi Impenetrable N. P. (Uganda). In Mgahinga Gorilla N. P. (2700 m) prefers recolonizing shrubby habitats in *Hagenia* forest. Recorded at elevations between 1030 m (FMNH, Misonne 1963, Rahm 1967) and 2300 m (FMNH).

Abundance Abundance varies according to habitat and locality. Comprised 2.9% of small mammals (rodents and insectivores) and 2.4% of small rodents at five localities near L. Kivu, DR Congo (Rahm 1967), and was the 8th most common rodent species of 26 species captured ($n = 2340$ small mammals). Percentage abundance varied from 0% ($n = 300$ rodents) to 13% (3rd most abundant rodent; $n = 355$). In *Pennisetum* grasslands near L. Kivu, and in 'grass-bush habitats', formed 1% (and the least abundant) of all small

rodents (Dieterlen 1967a). In other locations, comprised 6% in Mgahinga Gorilla N. P., Uganda; 1% (mesic habitats, 500–1540 m) and 5.5% (forest habitats, 1500–2350 m) in Bwindi Impenetrable N. P., Uganda; and <1% (1220 m), 7% (2300 m) and 12% (2130 m) in Rwenzori Mts (DR Congo) (FMNH).

Remarks Nocturnal and arboreal, but often caught on ground. Vegetarian; stomach contents contained vegetable material and ground nuts (Rahm & Christiaensen 1966). Nests constructed of grasses and herbs found among shrubs and thickets (Rahm 1967). No well-defined breeding season; pregnancies recorded in Feb, Mar, Jul and Nov throughout geographic range. In Feb, one pregnant ♀ of one adult ♀ sampled (Bwindi Impenetrable N. P., Uganda); in Mar, one of two (Kibira N. P., Burundi), one of one (Bwindi Impenetrable N. P., Uganda) and none of three adult ♀♀ sampled (Mgahinga Gorilla N. P., Uganda). In Jul, six of 17 adult ♀♀ sampled (Lwiro, E DR Congo); and in Nov, one of one adult ♀ sampled (Kigezi G. R., Uganda). In Aug, two ♀♀ sampled in Kibira N. P., Rwanda, were not pregnant. No data for other months. Embryo number: 2.8 (1–3, mode 3, $n = 10$; Dieterlen 1967a, Rahm 1967, FMNH).

Conservation IUCN Category: Near Threatened.

Measurements

Grammomys dryas

HB: 112 (100–130) mm, $n = 36$

T: 160 (142–177) mm, $n = 36$

HF: 24.3 (22–28) mm, $n = 36$

E: 17.3 (15–21) mm, $n = 36$

WT (♂♂): 42.9 (33–59) g, $n = 35$

WT (♀♀): 38.5 (30–55) g, $n = 30$

GLS: 29.2 (27.2–31.8) mm, $n = 33$

GWS: 14.3 (13.0–15.5) mm, $n = 33$

M¹–M³: 4.4 (3.9–4.8) mm, $n = 37$

Burundi, DR Congo and Uganda (FMNH)

Key References Dieterlen 1967a; Rahm 1967; Rahm & Christiaensen 1963.

Sean O. Bober & Julian C. Kerbis Peterhans

Grammomys gigas GIANT THICKET RAT (MOUNT KENYA GRAMMOMYS)

Fr. Souris sylvestre du Mont Kenya; Ger. Grosse Buschmaus

Grammomys gigas Dollman, 1911. Ann. Mag. Nat. Hist., ser. 8, 7: 527. Solai, Mt Kenya, Kenya. 9000 ft (2740 m).

Taxonomy Known only by the holotype, an old ♂ with very worn molars. Recognized as a valid species by several authorities (Allen 1939, Ellerman 1941, Hutterer & Dieterlen 1984, Musser & Carleton 1993, 2005). Hollister (1919), without personal knowledge of the holotype, designated it as a synonym of *G. cometes*. The distinctly larger body and skull measurements suggest that *gigas* should be recognized as a separate species; however, it may be that it is simply a large individual of *G. ibleanus* (Musser & Carleton 2005). The external measurements of *G. gigas* are within the range recorded for *G. ibleanus*,

although the skull and teeth measurements are larger. Synonyms: none. Chromosome number: not known.

Description Medium-sized climbing mouse with very long tail; the largest species (with *G. ibleanus* and *G. cometes*) in the genus. Dorsal pelage 'olive-grey washed with tawny buff, the reddish tint increasing posteriorly on the rump becoming bright orange-red. Head, sides of face, neck and shoulders washed with yellowish buff. Flanks richly tinted with orange-buff and sharply marked off from



the white underparts' (Dollman 1911c). Ventral pelage white tinted with very pale pinkish-buff, the general colour appearing as almost white. Upper surfaces of fore- and hindfeet buff. Tail very long (ca. 152% of HB), covered with short hairs and with longer hairs forming slight pencil at tip. Skull very large and massive. Braincase much larger than in the allied species. Zygoma stout and heavy. Anterior palatal foramina very long. Auditory bullae large and slightly inflated. Molar teeth exceptionally large, the toothrow longer and broader than in *G. ibeanus* (Dollman 1911c). Nipples: not known.

Geographic Variation None recorded.

Similar Species (size comparisons refer to mean values only)

Grammomys ibeanus. Slightly smaller (see also above); sympatric.

G. cometes. Slightly smaller; south of Zambezi R. only.

G. dolichurus. Smaller; commoner; larger geographic range.

Distribution Endemic to Africa. Afromontane–Afroalpine BZ. Known only from the type locality on Mt Kenya. Dollmann (1911c) mentioned a further specimen from Kasituka, west of Mt Kenya.

Habitat No information; presumably similar to *G. ibeanus*.

Abundance Only known by the holotype collected in 1911.

Remarks Apparently no other information available.

Conservation IUCN Category: Endangered.

Measurements

Grammomys gigas

HB: 132 mm

T: 201 mm

HF: 26.5 mm

E: 19 mm

WT: n. d.

GLS: 35.5 mm

GWS: 16.9 mm

M¹–M³: 5.5 mm

Holotype

Kenya (BMNH)

Fritz Dieterlen

Grammomys ibeanus EAST AFRICAN THICKET RAT (EAST AFRICAN GRAMMOMYS)

Fr. Souris sylvestre d'Afrique Est; Ger. Ost Afrikanische Buschmaus

Grammomys ibeanus Osgood, 1910. Field Mus. Nat. Hist. Publ., Zool., ser. 10, 8. Molo, Kenya.

Taxonomy The populations of the *cometes*–*ibeanus* complex north of the Zambezi R. are considered to belong to *G. ibeanus* (following Musser & Carleton 1993, 2004). Considerable variation in morphological variation may indicate that *G. ibeanus*, as understood here, may contain more than one species, but it appears to be a different species from *G. cometes*. The form *insignis* from Mt Elgon, placed as a synonym of *G. dolichurus* by Musser & Carleton (1993), belongs to the *ibeanus*-complex (F. Dieterlen unpubl.). Morphological and distributional limits of *G. ibeanus* are unsatisfactory, particularly the extent of its distribution in Tanzania (Musser & Carleton 2005). Synonyms: *lutosus*, *insignis*. Subspecies: none. Chromosome number: not known.

Description Medium-sized climbing mouse with very long tail; the largest species (with *G. cometes* and *G. gigas*) in the genus. Dorsal pelage rather long and soft, dull olive-brown; hairs dark slate-grey, terminal one-third reddish-brown to dull olive-brown (see also

Geographical Variation). Flanks brownish-grey. Ventral pelage white or cream. Colour of dorsal pelage clearly delineated from ventral pelage, often by thin line of yellow. Ears comparatively large. White postauricular patch absent or present. Fore- and hindfeet with yellowish-red hairs; toes sometimes with silvery hairs. Tail very long (ca. 150% of HB), covered with short hairs and with longer hairs (up to 10 mm) forming slight pencil at tip. Nipples: 1 + 2 = 6.

Geographic Variation In most populations, dorsal pelage is dull olive-brown; in the form *insignis* from Mt Elgon, dorsal pelage is bright tawny-brown and flanks are buffy.

Similar Species (size comparisons refer to mean values only)

G. dolichurus. Smaller HB and T; M¹–M³ shorter (with no overlap in measurements); no postauricular patch; north of the Zambezi R.

G. cometes. Smaller HB and T; M¹–M³ shorter; no postauricular patch; south of the Zambezi R.

*Grammomys ibeanus*

Distribution Endemic to Africa. Zambezian Woodland and Somalia–Masai Bushland BZs, mostly at 2000–3000 m. Recorded from scattered localities in Uganda (Mt Elgon), S Sudan (Imatong Mts), Kenya (both sides of the Rift Valley), Tanzania (rim of Ngorongoro crater, region of L. Manyara, W Usambara Mts, and Mt Poroto), NE Zambia and Malawi. All localities are north of the Zambezi R. (cf. *G. cometes*).

Habitat Probably similar to *G. cometes*. Recorded from moist evergreen montane forests and thickets, edge of moist forest (rim of Ngorongoro crater, Tanzania), and dense vegetation with trees and thickets at 1900–2700 m (Imatong Mts, Sudan) (Dieterlen & Nikolaus 1985, F. Dieterlen unpubl.). On Mt Elgon, found in dense montane

forest, and on rock outcrops with bushes in afroalpine grasslands at 3200–3600 m (Clausnitzer & Kityo 2001, as *G. dolichurus*). The lowest altitude on Mt Elgon, Uganda, seems to be 2750 m, and on Laikipia Plateau, Kenya, ca. 1900 m (Dollman 1911d). In Malawi, recorded from montane forest, bracken, thick undergrowth and inside houses (Ansell & Dowsett 1988, as *G. cometes*) and on the Nyika Plateau (Chitaukali *et al.* 2001).

Abundance No information.

Remarks Arboreal and nocturnal. Embryo number: 3 ($n = 2$; Mt Gargues, Kenya; Hollister 1919). In S Sudan, in Apr (wet season), one lactating ♀ contained two embryos (F. Dieterlen unpubl.). In Malawi (as *G. cometes*), litter-size 2.9 (2–5, $n = 6$); reproduction mainly during the wet season from Nov–Apr (Hanney 1965).

Conservation IUCN Category: Least Concern.

Schlitter (1989) classified *G. cometes* (including *ibeanus*) as ‘Vulnerable’ because of its dependence on evergreen forests.

Measurements

Grammomys ibeanus

HB: 122 (105–140) mm, $n = 8$

T: 182 (160–202) mm, $n = 8$

HF: 25.9 (24–27) mm, $n = 8$

E: 20.5 (17–23) mm, $n = 8$

WT: 53 (35–65) g, $n = 7$

GLS: 32.0 (30.1–33.0) mm, $n = 6$

GWS: 15.5 (14.6–15.9) mm, $n = 5$

M¹–M³: 5.2 (4.9–5.5) mm, $n = 7$

Imatong Mts, S Sudan; Mt Elgon, Uganda (SMNS, Hutterer & Dieterlen 1984, Clausnitzer & Kityo 2001, F. Dieterlen unpubl.)

Key References Musser & Carleton 1993, 2005.

Fritz Dieterlen

Grammomys kuru SHINING THICKET RAT (EASTERN RAINFOREST GRAMMOMYS)

Fr. Souris sylvestre de forêt tropicale; Ger. Glanzbuschmaus

Grammomys kuru (Thomas and Wroughton, 1907). Ann. Mag. Nat. Hist., ser. 7, 19: 381. Angu, Uele River, Orientale, NE DR Congo.

Taxonomy Originally described in the genus *Thamnomys*. Referred to as *Thamnomys rutilans* (e.g. Rosevear 1969, Genest-Villard 1972, 1980, Happold 1974), or as *Thamnomys (Grammomys) rutilans* (Misonne 1974) in all publications prior to the present time. Currently allocated to the genus *Grammomys* (see Genus profile). The specific name *rutilans* is now known to be occupied by another species (the non-African *Mus rutilans*), and hence the next available specific name for this species is *kuru* (Musser & Carleton 2005). Not easily distinguished from *G. cometes* (Misonne 1974). Species limits uncertain. Musser & Carleton suggest ‘*G. kuru*’, as understood here, comprises two species: *G. poensis* occurring throughout West Africa from Guinea to Equatorial Guinea, Gabon and N Angola, and *G. kuru* occurring in Central African Republic, DR Congo and W Uganda. Status in Central African Republic, Congo and NW DR Congo uncertain.

Synonyms: *centralis*, *poensis*. Subspecies: none. Chromosome number: $2n = 50$ (as *rutilans*, probably refers to *kuru* from Congo; Matthey 1963a). Chromosome number of $2n = 36$ (*rutilans* in Côte d’Ivoire [Tranier & Dosso 1979] probably refers to *poensis* – see Musser & Carleton 2005).

Description Small arboreal rat with extremely long tail. Dorsal pelage greyish-brown often tinged with dark rufous or chestnut on mid-dorsal region; hairs dark grey at base, brown or dark rufous at tip. Black guard hairs sparsely scattered on mid-back. Flanks paler. Ventral pelage pure creamy-white tinged with orange. Colour of dorsal pelage clearly delineated from ventral pelage, with thin line of conspicuous cinnamon-orange, especially on chest. Head similar in colour to dorsal pelage; nasal regions slightly rufous. Black vibrissae.

Ears small, pigmented with short brown hairs. White subauricular patch absent. Forelimbs short, four digits with short claws; Digit 1 reduced to short pad. Hindlimbs short; hindfeet rather broad; five digits, Digit 1 somewhat elongated; Digit 5 elongated and semi-opposable; short claws. Tail extremely long (ca. 160% of HB), dark brown and scaly with short dark bristles; hairs slightly elongated at tip; tail semi-prehensile. Skull: rather elongated, with slight supraorbital ridges, short rostrum, $t7$ on M^1 well developed; upper incisors slightly opisthodont. Nipples: $0 + 2 = 4$.

Geographic Variation None recorded.

Similar Species

G. dolichurus. Ventral pelage pure white, white subauricular patch absent; woodland habitats of the southern savannas; may be sympatric in Uganda.

Hylomyscus spp. On average HB usually smaller; smaller hindfeet; often sympatric and syntopic; widespread in tangles and secondary forest.

Distribution Endemic to Africa. Rainforest BZ and forest relicts in Rainforest–Savanna Mosaics. Recorded from SW Guinea (Mt Nimba) and Côte d'Ivoire eastwards to Cameroon and Central African Republic; also from Equatorial Guinea, Gabon, DR Congo, W Uganda and N Angola, Bioko I. Not recorded from Liberia or Sierra Leone, although may occur in these countries.

Habitat Tangled vegetation in forest clearings and along roadsides, and in secondary forest. Also recorded, rarely, from cocoa and mature cocoa plantations (Jeffrey 1975), and in secondary bush surrounding farmlands. In Dzanga-Sangha, Central African Republic, occurred at similar frequencies in unlogged, logged and monodominant *Gilbertiodendron dewevrei* forests, with no captures in streamside habitats (Ray 1996); preferred micro-habitats were characterized by thick understorey vegetation characteristic of disturbed environments, such as treefall gaps.

Abundance Uncertain; mostly uncommon or rare, but abundance varies geographically. Rosevear (1969) recorded that the species is 'rare' at the western edge of the range (e.g. Côte d'Ivoire). Shining Thicket Rats comprised 7.8% of all small rodents obtained by local collectors trapping on and above ground level in a forest–savanna–farmland mosaic near Ibadan, Nigeria ($n = 584$; Happold 1974), and 5% of all rodents captured above ground level in Mayanga Forest, Uganda ($n = 345$; Delany 1971). They comprised only 1% ($n = 1747$ rodents) captured in terrestrial habitats in Dzanga-Sangha, Central African Republic (Ray 1996). The species was not recorded in primary rainforest when trapping was restricted to ground level only in Ghana (Cole 1975) and Nigeria (Happold 1977).

Adaptations Arboreal and nocturnal. Shining Thicket Rats are primarily arboreal, preferring tangled vegetation where twigs and small branches are less than ca. 25 mm in diameter. They are efficient climbers, using their long tail for balance and gripping small twigs and branches with the elongated semi-opposable Digit 5 of the hindfeet. In Uganda, they have been captured at heights up to ca. 3 m above ground (Delany 1971) but may ascend higher where the tangled vegetation is suitable. In Dzanga-Sangha, Central African Republic,



Grammomys kuru

they were more commonly captured at heights of 2 m and 15 m than on the ground (Malcolm & Ray 2000). Shining Thicket Rats descend to ground level to forage for fruits (see below). Nests are situated in dense vegetation, usually 2–3 m above ground level, and are made of shreds of liana, grasses and other vegetation, which is 'woven' into a hollow sphere (Genest-Villard 1972, D. C. D. Happold unpubl.). Shining Thicket Rats spend the day in their nests; at 21:45–22:00h (some five hours after nightfall) they leave the nest. For the rest of the night until ca. 05:00h they alternate between periods of activity outside and periods of inactivity in the nest (Genest-Villard 1972). Frequent returns to the nest may be associated with temperature control because the temperature in the nest is always warmer than that outside. When disturbed in its nest, a Shining Thicket Rat leaves quickly, descends to the ground and hides in a hole, an unusual escape behaviour for an arboreal species.

Foraging and Food Mainly frugivorous. Forages in tangled vegetation and on the ground (even though never, or rarely, captured on the ground). Perches on small branches while holding food with forefeet. At Mbaiki, Central African Republic, the diet in the wet season (as assessed by analysis of stomach contents) comprises 6% flowers and leaves, 0% seeds, 81% vegetable pulp (probably mostly fruits) and 12% insects; equivalent percentages in the dry season are 6%, 12%, 74% and 8% (Genest-Villard 1980). Shining Thicket Rats are the least insectivorous of 17 species of small mammals (except for *Stochomys longicaudatus*) investigated at Mbaiki. In the wild, they have been observed to feed on 19 spp. of fruits, with variations from month to month depending on which species are fruiting, and on the leaves of 27 spp. of small trees and lianas. In captivity, they ate 48 spp. of fruits (out of 52 spp. offered) (Genest-Villard 1980).

Social and Reproductive Behaviour At Mbaiki, Central African Republic, nests were spaced 30–50 m apart, with only one animal (or a mother with young) in each nest, suggesting a home-

range of 700–2000 m². There is some evidence that males may be territorial since they show agonistic behaviour when one male is confronted with another male (Genest-Villard 1972). In Central African Republic, Shining Thicket Rats share their arboreal niche with *Hylomyscus stella*, *Praomys* sp., *Oenomys hypoxanthus* and *Graphiurus* cf. *murinus*, and do not show agonistic behaviour towards individuals of these species.

Females nipple-drag their young for about 14 days after parturition, until a few days after the eyes of the young have opened. The young remain firmly attached to the mother's nipples, even when she is climbing about outside the nest. The incisors of newborn young are bifurcate at the tip enabling the young to attach very securely to the nipple until about Day 14 after birth.

Reproduction and Population Structure In SW Nigeria (Happold 1974), pregnant ♀♀ (n = 6) were recorded in Mar (end of dry season), Sep, Oct and Nov (end of wet season); during these months more adult ♀♀ were non-pregnant than pregnant. Young animals (less than 20 g, n = 9) were recorded from Apr–Sep (wet season). These limited data suggest a rather long period of reproduction throughout the wet season with only a proportion of adult ♀♀ breeding in any one month. Gestation: ca. 24 days. Litter-size: 1–3 (mode 2; Genest-Villard 1972); 2.1 (2–3, n = 7; Happold 1974). At birth, WT: 4–6 g, ears and eyes closed. Incisor teeth erupt and nipple-clinging begins Day 1. Fine hair on body Day 3. Eyes open Day 6–9. Pelage similar in colour to adult Day 14. Adult size ca. Week 13 (Genest-Villard 1972).

Predators, Parasites and Diseases In Dzanga-Sangha, Central African Republic, predators include the Long-nosed Mongoose

Herpestes naso and other small carnivores. Faecal analysis showed that Shining Thicket Rats comprised 6% of the small rodent prey of the mongoose (n = 86 small rodents, 6 spp.). Likewise they formed 6% of the small rodent prey of other small carnivores (n = 251 small rodents, 10 spp.) (Ray 1998). Shining Thicket Rats are hosts to several species of malarial parasites (*Plasmodium berghi*, *P. vinckei*), none of which are pathogenic to the rats or to humans; they have been used as 'model hosts' to study the biology of malarial parasites in general (Killick-Kendrick 1971).

Conservation IUCN Category: Least Concern.

Measurements

Grammomys kuru

HB: 114.3 (105–120) mm, n = 10

T: 182.5 (160–204) mm, n = 10

HF: 25.0 (21–30) mm, n = 10

E: 15.0 (14–16) mm, n = 10

WT: 52.6 (41–61) g, n = 10

GLS: 31.8 (31.2–33.5) mm, n = 10

GWS: 15.7 (14.7–16.8) mm, n = 10

M¹–M³: 5.4 (5.1–5.7) mm, n = 10

SW Nigeria (Happold 1974, as *Thamnomys rutilans*)

Males only; no significant difference between males and females

Key References Genest-Villard 1972, 1980; Happold 1974, 1987; Rosevear 1969.

D. C. D. Happold

Grammomys macmillani MACMILLAN'S THICKET RAT (MACMILLAN'S GRAMMOMYS)

Fr. Souris Sylvestre de Macmillan; Ger. Macmillans Buschmaus

Grammomys macmillani (Wroughton, 1907). Ann. Mag. Nat. Hist., ser. 7, 20: 504. Wouida, north of L. Rudolf (= L. Turkana), Ethiopia.

Taxonomy Originally described in the genus *Thamnomys*. Most subspecies are now considered to be synonyms, although one (*G. aridulus*) is now recognized as a valid species. *Grammomys macmillani*, as understood here, is on average smaller than *G. dolichurus*; the two species may be confused on external characters but are easily distinguished by different chromosome numbers. Synonyms: *callithrix*, *erythropygus*, *gazellae*, *oblitus*, *ochraceus*, *usambarae*, *vumbaensis*, *vumbensis*. Subspecies: none. Chromosome number: 2n = 68–76 (Petter & Tranier 1975, Civitelli *et al.* 1989).

Description Small arboreal mouse with very long tail; the smallest species of the genus. Dorsal pelage olive-brown or grey, bright rufous-brown on rump. Flanks paler. Small rusty subauricular tufts. Ventral pelage white or creamy-white. Colour of dorsal pelage clearly delineated from colour of flanks, usually by yellow or orange line. Colour of head similar to dorsal pelage. Limbs short. Tail very long (ca. 160% of HB), with short hairs, with slight pencil of longer hairs at tip. Skull: similar to other *Grammomys*, but with shorter greatest length and shorter M¹–M³. Nipples: 1 + 2 = 6.

Geographic Variation None recorded.

Similar Species

G. dolichurus. Similar in size; chromosome number: 2n = 52; partly sympatric.

Distribution Endemic to Africa. Guinea Savanna BZ and Northern Rainforest–Savanna Mosaic, extending southwards into southern regions of Somalia–Masai Bushland BZ. Recorded from S Sudan, Central African Republic, NE DR Congo, S Ethiopia, Kenya, Uganda and Tanzania (Hutterer & Dieterlen 1984). Also recorded from Sierra Leone (Grubb *et al.* 1998, Musser & Carleton 2005) and Liberia (Musser & Carleton 2005; but not by Kuhn 1966). Limits of distribution uncertain. In addition, Musser & Carleton (1993, 2005) include Malawi, Mozambique and E Zimbabwe, a statement pending revision (and not shown on map).

Habitat Forests, riverine forests, edges of forests, swamps with trees, and grasslands with trees and undergrowth. May also be found

*Grammomys macmillani*

in hollow trees, and in roofs of huts and houses. Most habitats in S Sudan have an annual rainfall of ca. 1000 mm.

Abundance No information.

Remarks Little information available. Arboreal and nocturnal. The diet is largely vegetable material.

Conservation IUCN Category: Least Concern.

Measurements

Grammomys macmillani

HB: 105 (95–120) mm

T: 167 (144–190) mm

HF: 24.0 (21–26) mm

E: 16.9 (14–20) mm

WT: 34 (27–45) g

GLS: 28.1 (26.0–29.0) mm

GWS: 13.8 (13.1–14.9) mm

M¹–M³: 4.3 (4.1–4.5) mm

n = 11–36

S Sudan (F. Dieterlen unpubl.)

Specimens from NE DR Congo and Uganda are slightly smaller in all measurements

Key Reference Hutterer & Dieterlen 1984.

Fritz Dieterlen

Grammomys minnae ETHIOPIAN THICKET RAT (ETHIOPIAN GRAMMOMYS)

Fr. Souris sylvestre d’Ethiopie; Ger. Minna-Buschmaus

Grammomys minnae Hutterer and Dieterlen, 1984. Stuttgarter Beitr. Naturk., Série A Biol. 374: 10. Bulcha Forest, S of Dilla, Sidamo Province, Ethiopia. ca. 1800 m.

Taxonomy Olert *et al.* (1978) described, without naming, a single specimen of a rodent from S Ethiopia that seemed somewhat intermediate between *Grammomys dolichurus* and *Thallomys paedulus*. This was subsequently nominated as the type of *G. minnae* in a review of the genus *Grammomys* (Hutterer & Dieterlen 1984). Synonyms: none. Chromosome number: 2n = 32, FN = 64 (Olert *et al.* 1978).

Description Small *Grammomys*, similar in size to *G. dolichurus* and *G. macmillani*. Dorsal pelage uniformly greyish-brown, except for a slight dark mask round the eyes (in adults). Ventral pelage creamy-white. Colour of dorsal pelage clearly delineated from ventral pelage. Hindfeet greyish-white. Tail very long (ca. 157% of HB), sparsely furred, hairs at tip slightly longer than at base forming a slight pencil. Nipples: not known.

Geographic Variation None recorded.

Similar Species

G. macmillani. Similar size; skull has wider interorbital region, shorter diastemma, wider and longer M¹ but smaller M³; chromosome number: 2n = 68–76; probably parapatric.

G. dolichurus. Similar size; chromosome number: 2n = 52, FN = 66; probably parapatric.

*Grammomys minnae*

Distribution Endemic to Africa, Somalia–Masai Bushland BZ. Recorded only from Ethiopia, at Bulcha Forest in the southern Rift Valley of Ethiopia and near Arba Minch at ca. 1800 m. Limits of distribution uncertain.

Habitat Gallery forest in bushy savanna (Hutterer & Dieterlen 1984).

Abundance Only known from the holotype and two others.

Remarks Nest built 10 m above the ground (H. Rupp in Hutterer & Dieterlen 1984).

Conservation IUCN Category: Vulnerable.

Measurements

Grammomys minnae

HB: 110 mm, n = 1

T: 173, 150 mm, n = 2

HF: 23 mm, n = 1

E: 18 mm, n = 1

WT: 36 g, n = 1

GLS: 29.2, 29.5 mm, n = 2

GWS: 14.2, 14.4 mm, n = 2

M¹–M³: 4.0, 4.3 mm, n = 2

Ethiopia (Hutterer & Dieterlen 1984)

Key References Hutterer & Dieterlen 1984; Olert *et al.* 1978; Yalden & Largen 1992.

D. W. Yalden

GENUS *Heimyscus* African Smoky Mouse

Heimyscus Misonne, 1969. Mus. Roy. Afrique Cent., Zool. 172: 125. Type species: *Hylomyscus fumosus* Brosset, Dubost, and Heim de Balsac, 1965.



Heimyscus fumosus.

Heimyscus is a monotypic genus restricted to Congo Basin in the Rainforest BZ. The characters of the genus are given in the species profile. *Heimyscus* bears close resemblance to *Hylomyscus*, the genus under which it was originally classified. External characters that distinguish this genus from *Hylomyscus* include longer thinner hindfeet, shorter Digits 1 and 5, smaller plantar tubercles and shorter tail. The molar teeth have pronounced cusps, more widely separated than in *Hylomyscus*. The affinities of the genus are uncertain. DNA/DNA hybridization studies indicate that *Heimyscus fumosus* is closer to *Hylomyscus stella* than to species of *Praomys*, *Myomyscus* (= *Myomys*) and *Mastomys* (Chevret *et al.* 1994), but mitochondrial cytochrome *b* analysis suggest that *Heimyscus* is divergent to *Hylomyscus* and more closely related to *Praomys* (Lecompte *et al.* 2002a). The single species is *Heimyscus fumosus*.

Justina C. Ray & Jay R. Malcolm

Heimyscus fumosus AFRICAN SMOKY MOUSE

Fr. Souris fumeuse; Ger. Afrikanische Rauchmaus

Heimyscus fumosus (Brosset, Dubost and Heim de Balsac, 1965). Biologia Gabonica 1: 154. Makokou, Gabon.

Taxonomy Originally described in the genus *Hylomyscus*, but later allocated to a new genus by Misonne (1969a), a classification confirmed by Robbins *et al.* (1980) on the basis of marked differences in cranial and external characters between *Heimyscus* and *Hylomyscus*. Synonyms: none. Chromosome number: 2n = 40 (Primus *et al.* 2006).

Description Small delicate mouse with soft short greyish-brown pelage. Dorsal pelage greyish-brown with a faint reddish tint in some individuals. Ventral pelage greyish-white and not clearly delineated from flanks. Eyes very small. Ears relatively tall. Vibrissae whitish, giving the snout a frosted or powdered appearance. Fore-

and hindfeet with short white hairs. Hindfeet narrow; Digit 5 reaches slightly beyond base of Digit 4, and is longer than Digit 1. Six relatively small metatarsal pads regularly distributed on plantar surface of hindfoot. Tail long (ca. 100% of HB), appears naked. Females significantly heavier than ♂♂ (Duplantier 1982, Ray 1996). Skull: similar to *Hylomyscus*; upper incisors opisthodont; anterior palatal foramina end well anteriorly to M¹; mean length of M¹–M³ shorter than in *Hylomyscus* (except for *H. parvus* [shorter] and *H. allenii* [similar]); cusps on molar teeth well-developed, mostly to a greater extent than in *Hylomyscus* (Figure 67). See Brosset *et al.* 1965 for full description. Nipples: 1 + 2 = 6.

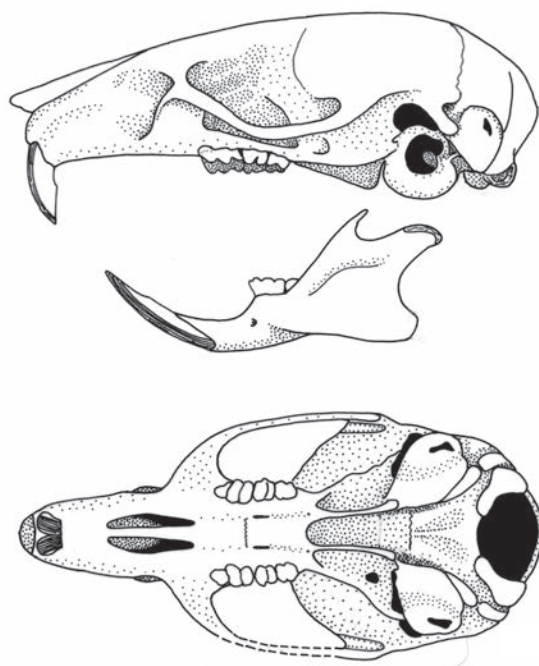


Figure 67. Skull and mandible of *Heimyscus fumosus* (RMCA 10035). Details of the occlusal surface of the upper molar teeth are obscure and not included.

Geographic Variation None recorded.

Similar Species

Hylomyscus spp. Tail considerably longer than head and body; Digits 1 and 5 of HF longer (Digit 5 semi-opposable), and tubercles larger and positioned closer together; pelage reddish in colour, rougher in texture; ventral pelage whiter and more clearly delineated from flanks; partially sympatric with *H. aeta*, *H. alleni*, *H. parvus* and *H. stella*.

Praomys spp. Usually larger and heavier; tail longer; eyes larger; hindfeet broader.

Distribution Endemic to Africa, Rainforest BZ (West Central Region, Gabon Subregion). Recorded only from Gabon, S Cameroon, S Central African Republic and Congo (Brosset *et al.* 1965, Petter & Genest 1970, Robbins *et al.* 1980, Granjon 1991, Ray 1996, Malcolm & Ray 2000, Nicolas *et al.* 2003a).

Habitat In Central African Republic, found in all forest habitats except close to streams (Ray 1996), with slightly higher capture rates in undisturbed forest than in secondary forest along logging roads (Malcolm & Ray 2000). In Gabon, more abundant in forest than in secondary habitats bordering cultivation (Brosset *et al.* 1965) and slash-and-burn cultivation (J.-M. Duplantier unpubl.). In primary rainforest prefers micro-habitats with relatively dense understorey and open canopy (Duplantier 1989, Ray 1996).

Abundance In undisturbed rainforest at Makokou, Gabon, comprised 4.6–20.5% (mean 11.5%, $n = 549$; 9 spp.) of small rodents and was the second or third commonest species (after *Hylomyscus stella*) depending on the time of year; density 0.4–2.7/ha (mean 1.4/ha) (Duplantier 1989). In Dzanga-Sangha, Central African

Republic, comprised 9.7% of terrestrial captures from unlogged forest (10 of 103 captures), 6.6% from skid trails (9 of 136), 6.9% from secondary logging roads (12 of 174), 5.2% from primary logging roads (10 of 191); and 0% from mono-dominant *Gilbertiodendron dewevrei* forest (0 of 34) (J. Malcolm & J. Ray unpubl.; Malcolm & Ray 2000). At Mont Doudou, Gabon, comprised 8% ($n = 675$; 11 spp.) and 12% ($n = 802$; 10 spp.) of trapped small rodents during the course of 12 months, and was the fourth commonest species after *Hylomyscus stella*, *Hybomys univittatus* and *Praomys* cf. *misonnei* (Nicolas & Colyn 2003).

Adaptations Strictly terrestrial (Duplantier 1982; Malcolm & Ray 2000). Digs underground burrows or lives within tree-root cavities; burrows have two exit passages. Nests are filled with dead leaves (Duplantier 1982).

Foraging and Food Diet composed of ca. 50% insects and 50% fruit seeds and pulp, with seeds especially common. Arthropods (cockroaches, caterpillars, beetle and fly larvae, termites and myriapodes) present in all stomachs examined (Duplantier 1982).

Social and Reproductive Behaviour In Makokou, Gabon, home-ranges slightly larger for ♂♂ ($2900 \pm 1608 \text{ m}^2$, $n = 12$) than ♀♀ ($2500 \pm 776 \text{ m}^2$, $n = 12$). Maximum recapture distance for ♂♂ averaged 50.5 m ($n = 22$), and for ♀♀ 37.5 m ($n = 30$) (Duplantier 1982).

Reproduction and Population Structure In Gabon, reproductive activity evident throughout the year with a peak of activity during the dry season (Jan–Mar) (Duplantier 1989). In another part of Gabon, ♀♀ were only reproductively active from Aug to Mar (Nicolas & Colyn 2003). Litter-size: 2.1 (1–3, $n = 7$; Dzanga-Sangha, Central African Republic; J. C. Ray & J. R. Malcolm unpubl.), 2.6 (2–4, $n = 7$; Gabon; Nicolas & Colyn 2003), 3 and 4



Heimyscus fumosus

($n = 2$; Makokou, Gabon; Dubost 1968, Duplantier 1982), 3 ($n = 1$; Kouilou Basin, Congo; Granjon 1991). Average number of captures of ♀♀ significantly greater than for ♂♂ at Makokou, Gabon (Duplantier 1982). In SW Gabon, the sex ratio not significantly different overall, between seasons or age classes (Nicolas *et al.* 2003b). The age class composition differed between seasons, the population experiencing a gradual ageing from Apr to Sep, simultaneously with an increase in mean body weight (Nicolas *et al.* 2003b). In SW Gabon, ♀♀ reached sexual maturity later than ♂♂ (Nicolas *et al.* 2003b).

Predators, Parasites and Diseases No information.

Conservation IUCN Category: Least Concern.

Measurements

Heimyscus fumosus

HB: 94.3 (81–105) mm, $n = 54$

T: 95.8 (88–108) mm, $n = 54$

HF: 21.9 (21–23) mm, $n = 54$

E: 17.1 (15–19) mm, $n = 54$

WT: 20.1 (13–28) g, $n = 54$

GLS: 26 (23.7–27.5) mm, $n = 20$

GWS: 11.8 (11.2–12.6) mm, $n = 20$

M^1 – M^3 : 3.5 (3.4–3.8) mm, $n = 20$

Dzanga-Sangha Special Reserve/Dzanga-Ndoki Park, Central African Republic (J. C. Ray and J. R. Malcolm unpubl., USNM)

Key References Brosset *et al.* 1965; Duplantier 1982; Nicolas *et al.* 2003a, b; Ray 1996.

Justina C. Ray & Jay R. Malcolm

GENUS *Hybomys*

Forest Mice

Hybomys Thomas, 1910. Ann. Mag. Nat. Hist., ser. 8, 5: 85. Type species: *Mus univittatus* Peters, 1876.



Hybomys univittatus.

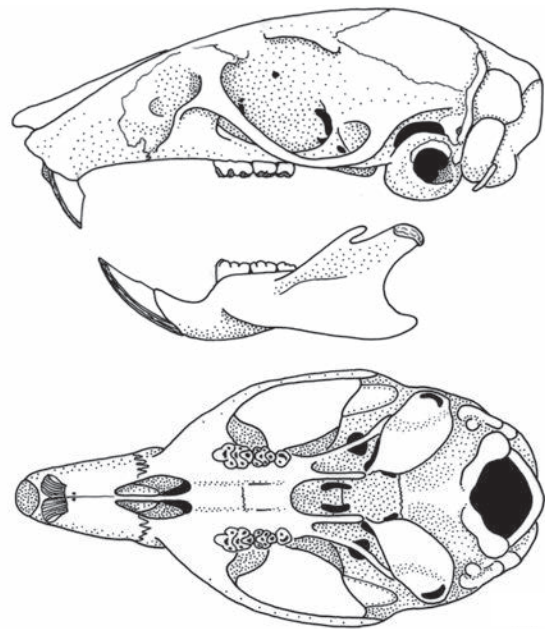


Figure 68. Skull and mandible of *Hybomys trivirgatus* (HC 977).

This genus contains six species of medium-sized, dark-coloured terrestrial rodents (Table 33), representing two well-defined subgenera: *Hybomys* with four species (*H. badius*, *H. basili*, *H. lunaris* and *H. univittatus*) and *Typomys* with two species (*H. planifrons* and *H. trivirgatus*). Their collective distribution is closely tied to the distribution of the Rainforest BZ (as well as montane rainforest). In West Africa, species in the genus are recorded from SW Guinea to S Nigeria (excluding the Dahomey Gap); in central Africa, from Cameroon to S Uganda, and southwards through Gabon, Congo and DR Congo to NC Zambia. They are found generally at lower altitudes (100–1000 m) but as high as 2600 m in the Rwenzori Mts.

Species in the genus are medium-sized murines with variable amounts of dark dorsal striping. The dorsal pelage is some shade of brown, with overtones ranging from drab yellowish to dark reddish, and the ventral pelage is typically dull whitish-grey. A single mid-dorsal black stripe is always present, sometimes weakly marked; and in *H. trivirgatus* it is bordered by an additional stripe on each side. The pelage is moderately soft and short; juvenile pelage colour is like that of adults but the texture softer and finer. Pinnae are darkly pigmented and thinly haired. Digits 1 and 5 of the hindfoot are relatively short, extending only to the base of Digits 2–4; plantar surfaces are black and hairless, with five plantar pads (hypothecar absent). Tail is shorter than

Table 33. Species in the genus *Hybomys* (see also Figure 69). Arranged according to number and conspicuousness of stripe(s).

| Species | Dorsal stripe(s) | Position of stripe(s) | Subgenus ^a | Chromosome number | Distribution and notes |
|-----------------------|--|--|-----------------------|-------------------|--|
| <i>H. trivirgatus</i> | Three, inner usually conspicuous; outer usually inconspicuous (see text) | Inner stripe: forehead to base of tail.
Outer stripes: shoulder to base of tail | <i>Typomys</i> | 2n = 40, 42 | Sierra Leone – W Nigeria |
| <i>H. planifrons</i> | One, conspicuous | Neck to base of tail | <i>Typomys</i> | 2n = 35, 38, 39 | Guinea – Côte d'Ivoire |
| <i>H. univittatus</i> | One, sometimes inconspicuous | Neck/shoulders to base of tail | <i>Hybomys</i> | 2n = 44, 46, 48 | SE Nigeria – Uganda – NW Zambia |
| <i>H. badius</i> | One, inconspicuous | Neck to base of tail | <i>Hybomys</i> | n. d. | S Cameroon only |
| <i>H. basilioi</i> | One, inconspicuous | Mid shoulders to base of tail | <i>Hybomys</i> | n. d. | Bioko I. only. Largest species (mean HB: 137 mm) |
| <i>H. lunaris</i> | One, inconspicuous | Mid shoulders to rump | <i>Hybomys</i> | 2n = 48 | Rwenzori Mts only. Smallest species (HB: 108 mm) |

^a See details in genus profile.

head and body (T: ca. 75–85% of HB), dusky to almost black. Skull characters include the following: moderate size (GLS: ca. 31–36 mm), braincase lacking prominent ridging even in old animals; interorbital region with slight supraorbital shelf and low beaded edges; zygomatic arches parallel-sided, low-slung over their mid-section; and auditory bullae medium-sized. The molars are strongly cuspidate, acuminate until heavily worn; M³ about one-half the size of M²; cusp t3 of M¹ smaller than t1; t7 absent; t9 variable in size and occurrence on M¹ and M² depending on the species; M³ with large t1 and without a t3; anteroconid of M₁ deeply bifurcate, with or without an anteromedial conulid; and the development of accessory cusps on labial cingula variable according to the species. Upper incisors opisthodont, without grooves; anterior surface yellow to yellowish-orange (Figure 68).

All species appear to be predominantly insectivorous, mostly diurnal and generally solitary in habits. Habitats within the Rainforest BZ include primary and secondary forest, densely vegetated 'gaps' formed by natural treefalls and by logging, and swampy areas with leaf litter and dense vegetation. *Hybomys* is mostly a rare genus, typically comprising <2% of the small rodent community and occasionally up to 30% when conditions are temporarily very favourable.

Variation of many characters within *Hybomys* concords with the two subgeneric divisions (e.g. see Rosevear 1969, Van der Straeten & Verheyen 1982, Carleton & Robbins 1985, Verheyen & Van der Straeten 1985). (1) Subgenus *Hybomys*: pectoral mammae present; skull profile evenly arched; zygomatic plate broad and vertical; anterior palatal foramina longer; alisphenoid strut present; accessory molar cusps usually present; M1/m1 roots = 5/5; limited to the

West Central, East Central and South Central Regions of the Rainforest BZ. (2) Subgenus *Typomys*: pectoral mammae absent; skull flatter; zygomatic plate narrow and slanted; anterior palatal foramina shorter; alisphenoid strut absent; accessory molar cusps usually absent; M1/m1 roots = 3/2; limited to the Western Region of the Rainforest BZ (sometimes called the 'Upper Guinea Forests') and the West Central Region (West Nigeria Subregion).

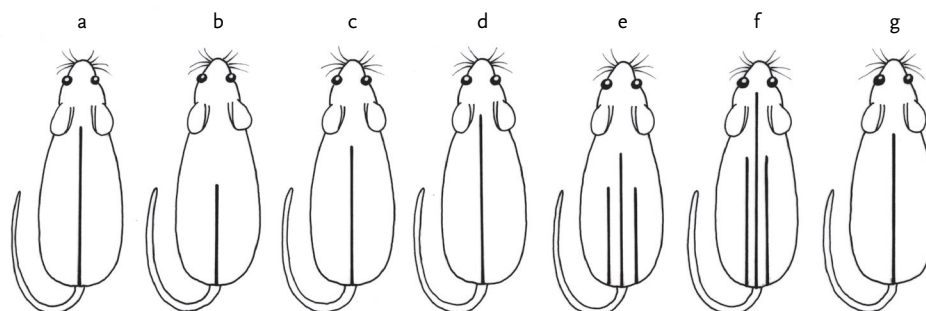
In view of the many morphological contrasts and their distributions within different biogeographic regions, some systematists have arranged *Hybomys* and *Typomys* as separate genera (Thomas 1911a, Van der Straeten 1984). Others have viewed their relationship as sister taxa, expressed at the level of distinctive subgenera (Allen 1939, Carleton & Robbins 1985), with general affinity to members of the arvicanthine assemblage (Ellerman 1941), in particular *Dephomys* (Misonne 1969a). Immunological data have supported the close relationship of *Hybomys univittatus* and *Stochomys longicaudatus* among 15 African murid genera studied, but other taxa critical to the issue of *Hybomys* and *Typomys* as genera or subgenera were not included (Watts & Baverstock 1995a). Resolution of the appropriate taxonomic ranking accorded to *Hybomys* and *Typomys* will require additional phylogenetic studies that include other rainforest rats, especially *Dephomys* and *Stochomys*.

The species are distinguished on the form and number and position of stripes on the back (Figure 69), cranial size and shape, development of the anterior palatal foramina, presence/absence of certain molar cusps, and karyological differences.

Michael D. Carleton

Figure 69. Schematic diagram of the stripes on the dorsal pelage of *Hybomys* spp.

(a) *H. badius*, (b) *H. basilioi*, (c) *H. lunaris*, (d) *H. planifrons*, (e) *H. trivirgatus* (Sierra Leone), (f) *H. trivirgatus* (Nigeria), (g) *H. univittatus* (after original by D. C. D. Happold). In some individuals, stripes may be inconspicuous or even absent (see text for details).



Hybomys badius CAMEROON FOREST MOUSE (CAMEROON HIGHLAND HYBOMYS)

Fr. Rat forestier du Cameroon; Ger. Kamerun-Streifenmaus

Hybomys badius Osgood, 1936. Zool. Ser. Field Mus. Nat. Hist. 20: 254. Southwest slope of Mt Cameroon, Cameroon.

Taxonomy Subgenus *Hybomys*. Originally described as a subspecies of *Hybomys univittatus*. The form *eisentrauti* was described as a separate species (Van der Straeten & Hutterer 1986) but is tentatively included in *H. badius* by Musser & Carleton (2005), an action that needs further study and documentation. Synonyms: *eisentrauti*. Subspecies: none. Chromosome number: not known.

Description Medium-sized dark brown forest mouse with single mid-dorsal stripe. Pelage silky and shiny; hairs fine, ca. 8 mm. Dorsal pelage dark reddish-brown to very dark brown, faintly flecked with yellowish-brown or chestnut-brown; hairs dark grey with yellowish-brown subterminal band and black tip; numerous slightly longer pure black hairs. Black mid-dorsal stripe from between ears or neck to base of tail; stripe weakly defined but mostly clearly visible. Ventral pelage greyish-brown, often tinged with buff; hairs pale grey at base, whitish-grey or buff at tip. Colour of ventral pelage not clearly delineated from colour of flanks. Head similar in colour to dorsal pelage. Head and neck thickset, muzzle blunt. Ears rounded, darkly pigmented. Fore- and hindfeet blackish-brown; soles of hindfeet black. Tail long (ca. 85% of HB) ringed with small blackish scales; numerous short dark bristles. Nipples: 1 + 2 = 6.

Geographic Variation The form *eisentrauti* (from Mt Lefo and Mt Oku, Cameroon) has greyish-white ventral pelage, and the indistinct mid-dorsal stripe usually extends from shoulders or mid-back to base of tail.

Similar Species

H. univittatus. Similar in size; hindfoot on average slightly longer; dorsal colour less dark, mid-dorsal stripe more obvious; rainforests of S Cameroon.

Distribution Endemic to Africa. Rainforest BZ (West Central Region, Eastern Nigeria sub-region). Known only from Mt Cameroon, Rumpi Hills and Mt Kupé (*badius*), and from Mt Lefo and Mt Oku in the Bamenda highlands (*eisentrauti*). Probably also other highlands in the Mamfe Region, W Cameroon (Eisentraut 1963, 1973).

Habitat Dense lowland forest (lowest altitude 30 m) and montane forest up to 2000 m.

Abundance Very common on Mt Cameroon (Eisentraut 1973).

Remarks Strictly terrestrial; active at day and night (Eisentraut 1973). Partly carnivorous; the stomach of one animal from Mt Oku

*Hybomys badius*

contained 60% animal matter (O. Fülling pers. comm.). Pregnant ♀♀ in Oct–Jan (no data for other months). Embryo number: 1.8 (1–2, mode 2; n = 6). Subadults were observed at the end of Oct and in Nov (Eisentraut 1973).

Conservation IUCN Category: Endangered.

Measurements

Hybomys badius

HB: 122.4 (105–137) mm, n = 16

T: 114.3 (108–121) mm, n = 12

HF: 29.3 (27–31) mm, n = 16

E: 16.7 (15–18) mm, n = 16

WT: 63.7 (55–75) g, n = 16

GLS: 34.7 (33.3–35.9) mm, n = 12

GWS: 16.2 (14.8–17.2) mm, n = 9

M¹–M³: 5.4 (5.2–5.6) mm, n = 12

Mt Cameroon, Mt Kupé, Rumpi Hills, Cameroon (ZFMK)

Key References Eisentraut 1973; Van der Straeten & Hutterer 1986.

R. Hutterer

***Hybomys basilioi* BASILIO'S FOREST MOUSE (BIOKO HYBOMYS)**

Fr. Rat forestier de Basilio; Ger. Basilius Streifenmaus

Hybomys basilioi Eisentraut, 1965. Zool. Jahrb. Syst. 92: 20. Mocaltal, Fernando Poo (= Bioko I., Equatorial Guinea). 1200 m.

Taxonomy Subgenus *Hybomys*. Originally described as a subspecies of *H. univittatus*; raised to specific rank by Van der Straeten (1985). Synonyms: none. Chromosome number: not known.

Description Medium-sized dark mouse, with indistinct mid-dorsal stripe on rump. Similar in general colour and form to other species in genus. Pelage long, soft and shiny. Dorsal pelage dark reddish-brown, slightly speckled with yellowish-brown; hairs grey at base, black at tip or with subterminal band of yellowish-brown and black tip. Black mid-dorsal stripe, if present, very inconspicuous, from mid-back to base of tail. Ventral pelage whitish-grey, colour usually limited to close to mid-ventral line; hairs grey at base, off-white or pale grey at tip. Other characters similar to other species in genus. Males are slightly larger than ♀♀.

Geographic Variation None recorded.

Similar Species All other *Hybomys* species are on average smaller and occur on the mainland.

Distribution Endemic to Africa. Occurs only on Bioko I. (Equatorial Guinea), and the only species of *Hybomys* on the island; 450–2000 m.

Habitat Closed and montane forests, also forest edges in dense cover (Eisentraut 1965).

Abundance In suitable habitats the species may be locally abundant.

Remarks Terrestrial. Mainly nocturnal but also active during the day (Eisentraut 1965). Pregnant ♀♀ found in Oct and Dec. Litter-size: 1–2 (Eisentraut 1965, 1973).

Conservation IUCN Category: Endangered.

Measurements*Hybomys basilioi*

HB: 137.0 (118–160) mm, n = 34

*Hybomys basilioi*

T: 114.3 (90–132) mm, n = 30

HF (c. u.): 31.2 (29–33) mm, n = 34

E: 17.2 (15–20) mm, n = 32

WT: 86.2 (70–95) g, n = 6

GLS: 35.9 (33.4–37.8) mm, n = 33

GWS: 17.3 (15.5–18.4) mm, n = 32

M¹–M³: 6.3 (5.9–6.7) mm, n = 34

Bioko I., Equatorial Guinea

Body and skull measurements: Van der Straeten (1985)

Weight: ZFMK

Key Reference Van der Straeten 1985.**R. Hutterer*****Hybomys lunaris* RWENZORI FOREST MOUSE (RWENZORI HYBOMYS)**

Fr. Rat forestier du Rwenzori; Ger. Rwenzori-Streifenmaus (Ruwendzori-Hybomys)

Hybomys lunaris (Thomas, 1906). Ann. Mag. Nat. Hist., ser. 7, 18: 145. Mubuku Valley, Rwenzori East, Uganda. 6000 ft (1830 m).

Taxonomy Originally described as *Mus univittatus lunaris*. Subgenus *Hybomys*. Although *lunaris* was described as a subspecies, it is now raised to specific rank on the basis of chromosomal traits (Verheyen & Van der Straeten 1985) and morphometric analyses (Van der Straeten *et al.* 1986). Carleton & Robbins (1985) suggested that *lunaris* from the region of the type locality is at present confined only to that area, a statement confirmed by Kerbis Peterhans *et al.* (1998). The variability

within the species (and hence its geographic range) is uncertain. The populations named as *H. lunaris* by Dieterlen (1985a, b) are now provisionally considered to represent *H. univittatus*. Synonyms: none. Chromosome number: 2n = 48 (Rwanda; Verheyen & Van der Straeten [1985]; however, this may not represent *H. lunaris* as defined here. See Musser & Carleton 2005).

Description Thomas (1906) wrote: '[This species has the] general characters of the typical western *M. univittatus*, but size smaller and colour more olivaceous, not turning rufous on the rump, which is blackish olivaceous. Belly-hairs greyish tipped with buffy; a line down outer edge of thighs also buffy. Dorsal streak not sharply defined and not extending on to neck and head. Upper surface of hands blackish-brown, of feet rufous-brown. Tail practically naked, black above, rather lighter below. Skull similar to that of true *univittatus*, but smaller and lighter throughout. Molars decidedly narrower.' Musser & Carleton (2005) referring to the holotype and to two specimens in the USNM from Kanyawara, a place near to the type locality, state that these 'precisely fit Thomas's description in their colouration, delicate skull, and small size. These two specimens contrast sharply with the larger robust skulls seen in our examples from Uwinka, Rwanda, the same locality where Verheyen and Van der Straeten obtained karyotypic preparations.'

Geographic Variation None recorded.

Distribution Endemic to Africa. Afromontane–Afroalpine BZ. Restricted to the Rwenzori Mts (Kerbis Peterhans *et al.* 1998). Van der Straeten *et al.* (1986) enlarged the range to include NE and E DR Congo, W Uganda and Rwanda. However, individuals from the enlarged area are not representative of true *lunaris*, which (morphologically) is known only from the Rwenzori Mts (Musser & Carleton 2005).

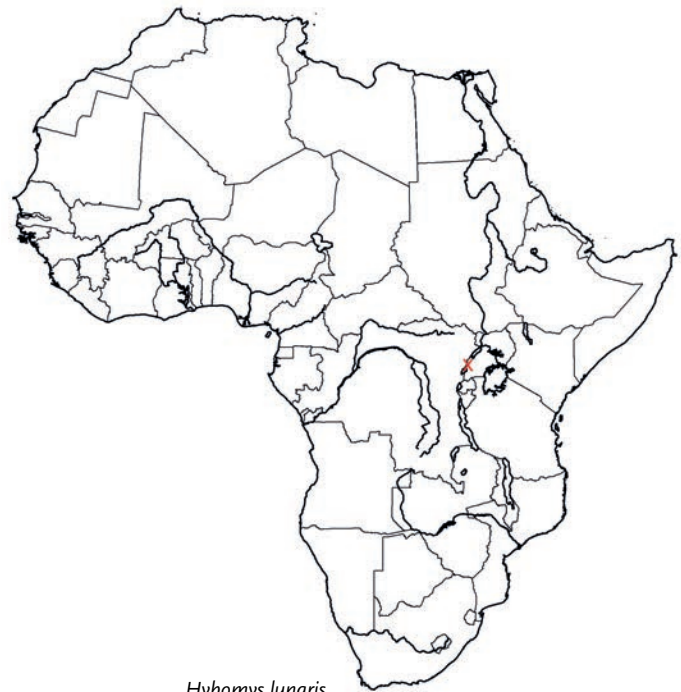
Habitat Montane forest on the eastern slopes of Rwenzori Mts, mostly between 1830 and 2440 m (Thomas & Wroughton 1910, Misonne 1963). On the western slopes of Rwenzori Mts, the altitudinal range of the montane forest is confined to 1900–2100 m (Misonne 1963).

Abundance R. B. Wroughton (in Thomas & Wroughton 1910) wrote: 'This was a rare species on Rwenzori and only two examples were obtained during many months' continuous trapping'.

Remarks Apparently no other information available.

Conservation IUCN Category: Vulnerable.

Montane forests on the Rwenzori Mts are under threat.



Hybomys lunaris

Measurements

Hybomys lunaris

HB: 108 mm

T: 115 mm

HF: 25 mm

E: 17 mm

WT: n. d.

GLS: 32 mm

GWS: 15.3 mm

M¹–M³: 5.1 mm

Rwenzori Mts, Uganda (holotype)

Key References Musser & Carleton 2005; Verheyen & Van der Straeten 1985.

Fritz Dieterlen

Hybomys planifrons LIBERIAN FOREST MOUSE (LIBERIAN FOREST HYBOMYS)

Fr. Rat forestier à front plat; Ger. Millers Streifenmaus

Hybomys planifrons (Miller, 1900). Proc. Washington Acad. Sci. 2: 641. Mount Coffee, 400–500 ft (122–152 m), Liberia.

Taxonomy Subgenus *Typomys*. Originally described as *Arvicanthis planifrons*, but subsequently considered to be a subspecies of either *Hybomys univittatus* (Allen 1939) or *H. trivirgatus* (Rosevear 1969). Re-established as a valid species on the basis of various cranial and dental attributes, and a different karyology from other species in the genus (Carleton & Robbins 1985). Synonyms: none. Chromosome number: 2n = 35, 38, 39; FN = 40, 42 (Tranier & Dosso 1979, Carleton & Robbins 1985).

Description Medium-sized, dark-coloured murine with a single mid-dorsal black stripe that extends from the level of the pinnae to base of tail. Dorsal pelage rich, dark brown; hairs dark grey at base with rufous subterminal band. Ventral pelage similarly dark; hairs dark grey at base with warm buff to ochraceous tips. Ears short and darkly pigmented, moderately covered with fine hairs. Upper surface of hindfeet dusky brown, plantar surfaces black and hairless. Tail short (ca. 75–80% of HB), sparsely haired, black all around or only slightly paler underneath. Skull of the *Typomys* configuration (see

Genus profile); anterior palatal foramina relatively long and reaching the level of the front edge of M^1 ; bony palate correspondingly shorter; interorbital constriction relatively narrow; cusp $t9$ of M^1 typically absent or present ($<7\%$) only as a bulge of the enamel crest linking $t6$ – $t8$. Sexual dimorphism in size negligible (Carleton & Robbins 1985). Nipples: $0 + 2 = 4$.

Geographic Variation None recorded.

Similar Species

H. trivirgatus. Dorsum with one dark mid-dorsal stripe bordered on each side by a less well-defined black stripe, from level with pinna (or shoulders/mid-back in some parts of range) to base of tail; skull with shorter anterior palatal foramina that terminate anteriorly to the level of M^1 ; interorbital constriction broader; cusp $t9$ of M^1 usually present; may be sympatric with *H. planifrons* from E Sierra Leone to SW Côte d'Ivoire.

Distribution Endemic to Africa. Rainforest BZ (Western Region). Recorded from SW (Kounankan Massif) and SE (Mt Nimba region) Guinea, Sierra Leone, Liberia and SW Côte d'Ivoire west of the Sassandra R. (Carleton & Robbins 1985, Barnett *et al.* 1996). Altitudinal range from ca. 100 m to 1000 m (Grubb *et al.* 1998).

Habitat Primary and secondary rainforest, and riverine forest, typically in micro-habitats with dense, moist ground cover. In Nimba Mts, Liberia, collected in dense vegetation of rainforest at lower altitudes than *H. trivirgatus* (Coe 1975). In Sierra Leone, found in moist semi-deciduous forest with luxuriant understorey and lush ground cover dominated by stands of *Marantachloa* sp. (Marantaceae) (Carleton & Robbins 1985), and in cocoa plantations with abundant vegetation (Grubb *et al.* 1998).

Abundance No census information available but locally restricted and uncommon (e.g. $<1\%$ of small rodents trapped in Outamba-Kilimi region, N Sierra Leone; M. D. Carleton unpubl.).

Remarks Terrestrial. Limited trapping records indicate that these striped forest mice are diurnal (Sierra Leone; Carleton & Robbins 1985). Forages on ground. Mainly insectivorous, but also feeds on fruits and other vegetable matter (Sierra Leone: Grubb *et al.* 1998). Two embryos recorded in one specimen (label, USNM) from Sierra Leone.



Hybomys planifrons

Conservation IUCN Category: Least Concern.

Measurements

Hybomys planifrons

HB: 124 (120–130) mm, $n = 8$

T: 97 (91–104) mm, $n = 8$

HF: 30.6 (28–32) mm, $n = 8$

E: 17.4 (16–19) mm, $n = 8$

WT: 51 (46–60) g, $n = 8$

GLS: 32.8 (32.0–33.8) mm, $n = 8$

GWS: 15.5 (15.1–15.8) mm, $n = 8$

M^1 – M^3 : 5.6 (5.4–5.9) mm, $n = 8$

Sierra Leone (M. D. Carleton unpubl., USNM)

Key References Carleton & Robbins 1985; Rosevear 1969.

Michael D. Carleton

Hybomys trivirgatus THREE-STRIPED FOREST MOUSE (WEST AFRICAN HYBOMYS)

Fr. Rat forestier à trois bandes dorsale; Ger. Dreistreifenmaus

Hybomys trivirgatus (Temminck, 1853). Esquisses zoologiques sur la Côte de Guinée. Part I, Mammifères, p. 159. Dabocrom, Ghana.

Taxonomy Originally described in the genus *Mus*. Subgenus *Typomys*. *Hybomys trivirgatus* formerly included Miller's (1900) *planifrons* as a well-defined subspecies (e.g. Rosevear 1969, Misonne 1974) until *planifrons* was reinstated to a full species based on morphological and karyotypic differences (Carleton & Robbins 1985). Ingoldby (1929) described *pearsei* (type locality = Lagos, Nigeria) as a subspecies of *H. trivirgatus*, an arrangement considered invalid by Rosevear (1969) and Happpold (1987). *Hybomys trivirgatus* is now considered to be a

monotypic species whose closest relative is *H. planifrons*, the other West African member of the subgenus *Typomys* (Carleton & Robbins 1985). Synonyms: *pearsei*. Subspecies: none. Chromosome number: $2n = 40, 42, 43$; $FN = 40, 42, 43$ (Tranier & Dosso 1979, Carleton & Robbins 1985, Verheyen & Van der Straeten 1985).

Description Medium-sized rodent with three dark dorsal stripes usually visible. Dorsal pelage yellowish- to greyish-brown and finely

*Hybomys trivirgatus*

speckled; hairs pale grey at base with ochraceous subterminal band. Mid-dorsal stripe black and prominent, usually extending from crown or forehead to rump but sometimes from shoulders/mid-back to rump in some populations; lateral stripes pale dusky and shorter, sometimes only faintly defined in certain individuals or populations (especially in Nigeria). Ventral pelage variable, typically drab greyish-white, occasionally with extensive suffusion of buff-tipped hairs. Upper surface of hindfeet pale brown; plantar surface black and naked. Tail long (ca. 80% of HB), dark brown to blackish, usually indistinctly paler ventrally. Skull of the *Typomys* configuration (see Genus profile); interorbital constriction relatively broad; anterior palatal foramina short and wide, not reaching the level of the anterior edge of M^1 , and bony palate correspondingly long; $t9$ usually present on M^1 (ca. 75–95% of specimens). Sexual dimorphism in size negligible (Van der Straeten & Verheyen 1982). Nipples: $0 + 2 = 4$.

Geographic Variation None recorded.

Similar Species

H. planifrons. Lateral stripes absent and mid-dorsal stripe terminating anteriorly about the level of the pinnae; interorbital constriction narrower; anterior palatal foramina longer; cusp $t9$ lacking on M^1 and M^2 ; may occur sympatrically with *H. trivirgatus* from E Sierra Leone to SW Côte d'Ivoire.

Distribution Endemic to Africa. Rainforest BZ (Western Region and West Central Region [Western Nigerian Subregion]). Recorded from E Sierra Leone to SW Nigeria, west of the Niger R. (Carleton & Robbins 1985, Happold 1987, Grubb *et al.* 1998). Not recorded

in S Togo and Benin (Dahomey Gap). Altitudinal range from near sea level to 1200 m (Coe 1975).

Habitat Undisturbed rainforest (Happold 1975b, 1977); also recorded in cocoa plantations and secondary bush adjacent to forest (Jeffrey 1977).

Abundance Rarely encountered using typical field census methods, e.g. comprised only 1–2% of small terrestrial rodents at various sites in SW Nigeria (Happold 1975b, 1977). Higher relative abundances recorded elsewhere, e.g. 11% in Ghana (Cole 1975).

Adaptations Terrestrial. Activity reported as diurnal (07:00–16:00h) (Ghana; Cole 1975) and as both diurnal and nocturnal (Nigeria; Happold 1977).

Foraging and Food Forages in natural thickets along valley bottoms and valley slopes, avoiding bare ground and retreating to fallen logs when disturbed. Mainly insectivorous (ants, termites, beetles, orthopterans) but feeds on some vegetable material (Ghana; Cole 1975).

Social and Reproductive Behaviour Trapping data suggest that animals live in small groups because individuals were frequently found in the same or adjacent traps within a restricted area (Cole 1975, Happold 1977).

Reproduction and Population Structure Pregnant ♀♀ recorded mainly in wet season (Mar, Jul and Sep). Litter-size: 2.8 (2–3, $n = 4$; Nigeria; Happold 1974, 1987).

Predators, Parasites and Diseases No information.

Conservation IUCN Category: Least Concern.

Measurements

Hybomys trivirgatus

HB: 124 (113–141) mm, $n = 19$

T: 100 (90–120) mm, $n = 19$

HF: 31.8 (30–34) mm, $n = 20$

E: 17.0 (15–18) mm, $n = 20$

WT: 56 (45–71) g, $n = 20$

GLS: 33.6 (32.3–35.1) mm, $n = 16$

GWS: 15.6 (14.6–16.8) mm, $n = 16$

M^1 – M^3 : 5.4 (5.0–5.9) mm, $n = 16$

Ghana (Carleton & Robbins 1985)

Key References Carleton & Robbins 1985; Happold 1987; Rosevear 1969.

Michael D. Carleton & D. C. D. Happold

***Hybomys univittatus* ONE-STRIPED FOREST MOUSE (PETERS'S HYBOMYS)**

Fr. Rat forestier bai; Ger. Einstreifenmaus

Hybomys univittatus (Peters, 1876). Monatsber. K. Preuss. Akad. Wiss. Berlin, p. 479. Dongila, Gabon.

Taxonomy Originally described in the genus *Mus*. Subgenus *Hybomys*. The definition of this form is uncertain. There is considerable morphological and karyotypic variation among populations assigned to *H. univittatus*, with several forms previously classified as subspecies now elevated to species level (Carleton & Robbins 1985, Verheyen & Van der Straeten 1985). The populations named as *H. lunaris* by Dieterlen (1967b, 1985a, b) are now provisionally considered to be *H. univittatus* (see also *H. lunaris*). Synonyms: *rufocanus*. Subspecies: none. Chromosome number: $2n = 44, 46, 48$ (Carleton & Robbins 1985, Verheyen & Van der Straeten 1985).

Description Medium-sized dark mouse with one black mid-dorsal stripe. Pelage soft and sleek; hairs long, 12–14 mm. Dorsal pelage dark reddish-brown to very dark brown, with yellowish-brown speckling. Hairs dark grey at base with black tip, or with subterminal band of yellowish-brown and black tip. Black mid-dorsal stripe from nape of neck or shoulders to base of tail (sometimes rather inconspicuous). Ventral pelage tawny to whitish-grey, hairs grey with off-white, buff or pale brown tip. Colour of dorsal pelage and ventral pelage clearly delineated on flank. Head and neck thickset, muzzle blunt. Ears small, very round and appearing naked. Eyes relatively large. Fore- and hindfeet black. Digits 1 and 5 reach only to the base of Digits 2, 3 and 4. Digit 5 slightly longer than Digit 1. Soles of hindfeet shiny black with five metatarsal pads on plantar surface. Tail long (ca. 85% of HB), very black, mostly naked, with dense rings of very short bristles; may be slightly bicoloured. Nipples: $1 + 2 = 6$.

Geographic Variation Colour of dorsal and ventral pelage variable, even at any given locality; dorsal stripe sometimes not detectable.

Similar Species

Hybomys badius. Pelage shorter; mid-dorsal stripe usually longer and often more visible; range very restricted (highland areas of Cameroon).

H. lunaris. Lighter, more delicate skull (E DR Congo only).

H. trivirgatus and *H. planifrons*. West Africa only.

Distribution Endemic to Africa. Rainforest BZ (West Central [Eastern Nigeria and Gabon Subregions], East Central and South Central Regions), and some outlier forests in Rainforest–Savanna Mosaics. Recorded from SE Nigeria (east of the Niger R.), Cameroon, Gabon, extreme S Central African Republic, N DR Congo, SC Uganda, W Rwanda and extreme NW Zambia (Delany 1975, Ansell 1978, Carleton & Robbins 1985, Happold 1987, Ray 1996). Outlier populations in C DR Congo and S DR Congo/NW Zambia (Ansell 1978, Carleton & Robbins 1985). Replaced by *H. trivirgatus* and *H. planifrons* in West Africa, west of the Niger R.

Habitat Rainforest, especially where gaps in the canopy allow dense herbaceous cover on the ground. Readily takes advantage of both natural and human-made secondary habitats within the Rainforest BZ,

provided cover is present. In SW Central African Republic, prefers habitats with dense understorey and low canopy cover (Ray 1996). Capture rates were higher along primary and secondary forestry roads than along narrower, less-damaged tracks (Malcolm & Ray 2000). In Kibale Forest, Uganda, population numbers were higher in gaps in mature and logged forests than in non-gaps, and where ground cover was most dense. Number of captures increased with increasing forest patch size (Struhsaker 1997). Frequently associated with moist forests near rivers or swamps, characterized by rich herbaceous flora, abundant leaf litter and heavy shade (Sanderson 1940, Delany 1964a, Kingdon 1974). Present in gallery forests or montane forests at elevations up to ca. 2000 m (Rosevear 1969, Carleton & Robbins 1985).

Abundance Abundance varies greatly according to location and forest disturbance. Generally an uncommon species although it is generally the commonest species in forests with extensive gaps. During 44 months of trapping in Kibale Forest, Uganda, density and relative abundance increased significantly with increased logging intensity, e.g. mean density was 0.14 individuals/ha (comprising 1.6% of all rodent species captured) in unlogged forest; 3.02/ha (22.5%) in lightly logged forest; and 4.14/ha (26.7%) in heavily logged forest (Struhsaker 1997). In SW Central African Republic, relative abundance was 0% along streams ($n = 200$), 0.7% in mono-dominant *Gilbertiodendron dewevrei* forest ($n = 406$), 4.1% ($n = 458$) in unlogged mixed-species forest, and 12.6% of all captures ($n = 704$) along secondary logging roads. In E DR Congo, it represented 15.1% of total captures ($n = 93$) in 'primary' forest and 9.5% ($n = 169$) in cultivated secondary bush (Rahm 1967). In undisturbed rainforest at Makokou, Gabon, relative abundance on

*Hybomys univittatus*

a 9-ha study site ranged from 0% to 4.2% (mean: 2.16%, 21 of 971 captures) during six trapping sessions over 15 months (Duplantier 1989). It was the most commonly captured species in an undisturbed forest in SW Gabon, representing 24% of 1531 captures (Nicolas & Colyn 2003). In undisturbed mixed forest in Ituri Forest, DR Congo, comprised 19 of 60 (31.7%) individuals captured (Gubista 1999).

Adaptations Terrestrial (Genest-Villard 1978a, Duplantier 1982, Malcolm & Ray 2000), although a good swimmer (Thomas 1888a). Diurnal and nocturnal (Rahm 1967, Rosevear 1969, Genest-Villard 1978). Trapping near L. Kivu, DR Congo, yielded 60% of total captures ($n = 30$) at 08:00h (caught overnight), 16.7% at 12:00h and 23.3% at 17:00h (Rahm 1967). Individuals live and breed in burrows found in cavities under tree roots, stumps, or rotting logs (Kingdon 1974, Duplantier 1982). Nests are made from twigs (Genest-Villard 1978b) or leaves (Duplantier 1982). An individual may have three or more burrows (with those of a ♀ often as close as 10 m apart), and there is a tendency to use one burrow more than the others (Genest-Villard 1978b). Males usually spend several nights in the same burrow, while ♀♀ seldom spend more than two consecutive nights in the same burrow unless they have young. Males emerge from the burrow between 07:20h and 08:50h, have resting periods in mid-morning and late afternoon, and return to the burrow for the night between 17:45h and 18:05h. Individuals cover about 500 m each day with a mean speed ranging from 80 to 90 cm/min in the afternoon and 110 cm/min in the mornings. Females are not as active as ♂♂, and cover shorter distances, generally not wandering more than 50 m from their burrow (Genest-Villard 1978b).

Foraging and Food Omnivorous and insectivorous; diet varies geographically. At M'Baiki, Central African Republic (Genest-Villard 1980), diet varied seasonally: 70% insects, 25% fruit pulp and 5% seeds in wet season, and 61% insects, 21% fruit pulp and 17% seeds in dry season. Most of the insect food consisted of termites and ants. At least 30 species of fruit were eaten in the wet season, fewer during the dry season, as well as cultivated fruit and seeds, particularly during the dry season. Although leaves are not important components of stomach

contents, feeding observations indicated that they were regularly sought after and consumed, although in small quantities. Radio-collared individuals foraged beneath the leaf litter or fallen woody debris, and insects were snapped up opportunistically when encountered (Genest-Villard 1980). In Makokou, Gabon, during the wet season, diet was mostly fruit pulp, although arthropods (cockroaches, caterpillars, beetle and fly larvae, ants, termites and myriapods) were present in 99% of stomachs, usually in small quantities. In the dry season, proportionately less pulp and more seeds and insects were consumed (Duplantier 1982). In Kibale Forest, Uganda, almost 70% of stomach contents comprised fruit pulp and seeds; other identifiable items of the diet were equal proportions of insects and herbaceous matter. Feeding experiments on captive individuals demonstrated a preference for dried seeds rather than fresh seeds and fruit (Struhsaker 1997). Reported to feed opportunistically from fruit scattered on the ground by arboreal frugivorous primates and birds (Kingdon 1974).

Social and Reproductive Behaviour Mainly solitary. Home-range of radio-collared individuals was 4.5–6.1 ha ($n = 6$ ♂♂) and 1.4–1.8 ha ($n = 4$ ♀♀). Home-ranges of neighbouring ♂♂ do not overlap and ♂♂ do not tolerate other ♂♂ in their home-range, suggesting strong territoriality. A ♂ gives chase and bites intruders within his home-range. There is little overlap in the ranges of any individuals, although the home-ranges of one or more ♀♀ may overlap with that of a ♂. Males exhibit home-range fidelity throughout their life-span, whereas ♀♀ may leave one home-range for another. Individuals do not sleep together in the same burrows. Young ♂♂ and ♀♀ disperse from their natal area (Genest-Villard 1978b).

Reproduction and Population Structure In Central African Republic, reproductive activity in ♂♂ and ♀♀ occurred at all times of the year, with a peak of activity during wet season (Aug–Nov) (Ray 1996). In E DR Congo, reproduction corresponded with the end of the wet season when fruiting is at its peak, and reproductive activity was not evident during dry season (Rahm 1970). Gestation: 29–31 days (Petter & Genest 1967). Litter-size: 2.5 (1–5, $n = 38$; Makokou, Gabon; Dubost 1968); 2.6 (2–6, $n = 10$; Dzanga-Sangha, Central African

Table 34. Species in the genus *Hylomyscus*. Arranged in order of increasing mean head and body length.
(n. d. = no data.)

| Species | HB mean (range) (mm) | Frontal bone at interorbital constriction | Supraorbital ridges | Posterior end of anterior palatal foramina | Length of molar cheekteeth mean (range) (mm) | Incisor teeth | |
|--------------------|----------------------|---|---------------------|--|--|---------------------------------|--|
| <i>H. parvus</i> | 67.4 (56–77) | Slight to obviously concave | Small | Anterior to M ¹ | 3.2 (3.0–3.4) | Orthodont or slightly pro-odont | |
| <i>H. alleni</i> | 83.6 (71–97) | Slightly concave | Absent | First lamina of M ¹ | 3.6 (3.4–3.9) | Slightly pro-odont | |
| <i>H. stella</i> | 85 (57–118) | Slightly concave | Small or absent | Anterior to M ¹ | 4.0 (3.4–4.3) | Slightly opisthodont | |
| <i>H. aeta</i> | 95.7 (79–114) | Smooth | Small | Anterior to or level with anterior end of M ¹ | 4.4 (4.2–4.6) | Slightly opisthodont | |
| <i>H. carillus</i> | 96 (ca.) | n. d. | Well developed | n. d. | 4.0 (3.8–4.4) | Orthodont | |
| <i>H. grandis</i> | 96.8 (89–110) | n. d. | n. d. | n. d. | 4.9 (4.8–5.0) | n. d. | |
| <i>H. denniae</i> | 98.3 (87–106) | Smooth | Small | First lamina of M ¹ | 4.2 (3.9–4.4) | Slightly opisthodont | |
| <i>H. baeri</i> | 105.9 (98–115) | Smooth | Small | Anterior to M ¹ | 4.2 (4.0–4.4) | Orthodont | |

Republic; J. C. Ray & J. R. Malcolm unpubl.); 2.6 (2–4, n = 20; SW Gabon; Nicolas & Colyn 2003). Mean body weights in Dzanga-Sangha were significantly lower in dry season than in the wet season. Head, body and tail fully grown at about Week 20 (Petter & Genest 1967). First parturition, on average, at 4.5 months of age (range: 11 weeks to 7 months). Male life-span ca. 12 months (Genest-Villard 1978b).

Predators, Parasites and Diseases Remains found in scats of mongooses and other small carnivores in Dzanga-Sangha, Central African Republic (Ray 1998). Hunted by pygmies using crossbows, especially in the wet season (Genest-Villard 1980).

Conservation IUCN Category: Least Concern.

Measurements

Hybomys univittatus

- HB (♂ ♂): 120.8 (96–138) mm, n = 103
- HB (♀ ♀): 119.2 (92–140) mm, n = 79
- T (♂ ♂): 112.0 (81–130) mm, n = 88
- T (♀ ♀): 110.4 (81–133) mm, n = 73

- HF (♂ ♂): 31.7 (28–36) mm, n = 104
 - HF (♀ ♀): 31.1 (29–36) mm, n = 80
 - E (♂ ♂): 17.5 (15–20) mm, n = 103
 - E (♀ ♀): 17.6 (15–20) mm, n = 79
 - WT (♂ ♂): 52.6 (30–78) g, n = 114
 - WT (♀ ♀): 49.4 (28–73) g, n = 82
 - GLS (♂ ♂): 34.7 (33–35.9) mm, n = 10
 - GLS (♀ ♀): 34.3 (33.6–35.2) mm, n = 10
 - GWS (♂ ♂): 16.6 (15.7–17.7) mm, n = 10
 - GWS (♀ ♀): 16.5 (15.7–17.2) mm, n = 10
 - M¹–M³ (♂ ♂): 5.4 (5.1–5.7) mm, n = 10
 - M¹–M³ (♀ ♀): 5.5 (5.3–5.7) mm, n = 10
- Dzanga-Sangha Special Reserve/Dzanga-Ndoki Park, Central African Republic
(J. C. Ray & J. R. Malcolm unpubl, USNM)

Key References Carleton & Robbins 1985; Genest-Villard 1978b; Rosevear 1969.

Justina C. Ray

GENUS *Hylomyscus*
Wood Mice

Hylomyscus Thomas, 1926. Ann. Mag. Nat. Hist., ser. 9, 17: 174. Type species: *Epimys aeta* Thomas, 1911.

The genus contains eight species (Table 34) and is endemic to Africa. It is widely distributed in lowland and montane rainforests of tropical Africa from Guinea to Angola and DR Congo, and in afroalpine habitats of East African mountains.

Species of *Hylomyscus* are very small to small arboreal mice, soft-furred, with a very long tail, slender and relatively short hindfeet, and large round ears. The skull is relatively broad, smooth and rounded, with small zygomatic plate, small auditory bullae and small narrow molars; upper incisor teeth are pro-odont, orthodont or opisthodont (depending on the species); and anterior palatal foramina

end well anterior to M¹ or level with anterior end of M¹ (Figure 70). Wood Mice are agile climbers, using the digits of the hindfeet to grip small branches and twigs. Digit 5 of the hindfoot is opposable or semi-opposable. Wood Mice are exclusively nocturnal and have an omnivorous diet. In many habitats only one species of *Hylomyscus* is present, but in others 3–4 species appear to be sympatric.

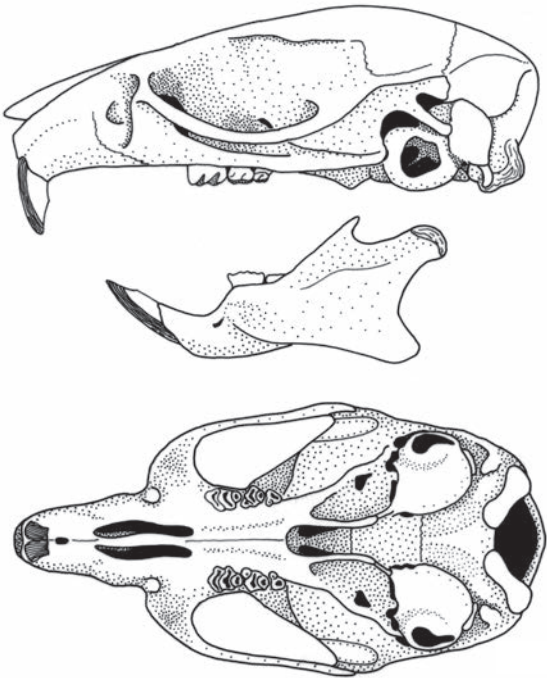


Figure 70. Skull and mandible of *Hylomyscus stella* (HC 890).

| | Colour of ventral pelage | Distribution |
|--|---------------------------------|--|
| | Dark grey at base, brown at tip | Scattered localities in Gabon, Congo, Central African Republic, S Cameroon, N DR Congo |
| | Grey at base, white at tip | Sierra Leone to Togo. Cameroon to Central African Republic |
| | Grey at base, white at tip | Rainforest. Widespread from Nigeria to Kenya |
| | Grey at base, white at tip | Rainforest BZ of central Africa |
| | Grey at base, white at tip | Angola; perhaps SE DR Congo |
| | Grey at base, white at tip | Mt Oku, Cameroon |
| | Grey at base, white at tip | E DR Congo, Rwanda, Burundi, Uganda, Kenya, Tanzania, WC Angola. Highland |
| | Pure white | Liberia, Côte d'Ivoire and Ghana |

Hylomyscus was previously treated as a subgenus of *Rattus* (e.g. by Ellerman 1941) or of *Praomys* (e.g. by Davis 1965 and Misonne 1974), but its generic status is now recognized by most authorities (e.g. Allen 1939, Hatt 1940a, Heim de Balsac & Aellen 1965, Rosevear 1966, 1969, Robbins *et al.* 1980). The genus is part of the monophyletic 'Praomys group' comprising *Praomys*, *Myomyscus* (formerly *Myomys*), *Mastomys* and *Hylomyscus* (Chevret *et al.* 1994), which is more closely related to *Mus* than to *Rattus*. Analysis of skeletal and dental traits

(Lecompte *et al.* 2002a), mitochondrial cytochrome *b* (Lecompte *et al.* 2002b) and other characters show that the first three genera cluster together and that *Hylomyscus* is clearly separate and monophyletic.

Species in the genus are distinguished primarily by size, tail length and pelage colour.

Fritz Dieterlen

Hylomyscus aeta BEADED WOOD MOUSE (BEADED HYLOMYSCUS)

Fr. Rat à poil doux de Thomas; Ger. Perlen-Waldmaus

Hylomyscus aeta (Thomas, 1911). Ann. Mag. Nat. Hist., ser. 8, 7: 591. Biteye, Dja River, Cameroon.

Taxonomy Originally described in the genus *Epimys*. Synonyms: *laticeps*, *schoutedeni*, *weileri*. Subspecies: none. The form *grandis*, described as a subspecies of *H. aeta*, is now considered to be a separate species. Chromosome number: $2n = 54$, $FN = 86$ (Robbins *et al.* 1980).

Description Small mouse with cinnamon-brown pelage and very long tail. Dorsal pelage cinnamon-brown; hairs dark grey at base, cinnamon-brown at tip. Some longer guard hairs present. Juvenile pelage black to grey-brown. Ventral pelage pure white in appearance; hairs dark at base, white at tip. Colour of dorsal pelage and ventral pelage clearly delineated on flanks and separated by buffy line. Rostrum short and blunt with long vibrissae. Eyes and ears large relative to head size. Hindfoot broad; Digit 5 rather long, ending near the middle of the terminal joint of Digit 4; Digit 1 ending beyond the base of Digit 2. On forefoot, Digit 5 about equal in length to Digit 2. Both fore- and hindfeet covered with short white hairs. Tail very long (ca. 145% of HB) with short hairs on the extreme end. Skull: supraorbital ridges very well developed (to a greater extent than other species in

the genus); frontal bone concave at interorbital constriction; anterior palatal foramina end anteriorly to or level with anterior end of M^1 ; upper incisors opisthodont. Nipples: $1 + 2 = 6$.

Geographic Variation None recorded.

Similar Species

H. allenii/stella. Skull and body on average smaller and lighter in weight; ventral pelage not as pure white; supraorbital ridges on skull absent; tail naked.

H. parvus. Tail shorter; skull smaller.

Praomys spp. On average larger body size; tail usually relatively shorter; Digit 5 of hindfoot short; non-arboreal.

Heimyscus fumosus. Digit 5 on hindfoot short; pelage darker; tail shorter; eyes smaller.

Distribution Endemic to Africa. Rainforest BZ (mostly East Central and South Central Regions, and Gabon Subregion of West Central Region). Recorded from Cameroon, Equatorial Guinea (including Bioko I.), Gabon, S Central African Republic, Congo, DR Congo, W Uganda and NW Burundi (Dubost 1968, Eisentraut 1969a, Petter & Genest 1970, Musser & Carleton 1993, 2005, Malcolm & Ray 2000). Geographic limits uncertain (Musser & Carleton 1993, 2005).

Habitat In Dzanga-Sangha, Central African Republic, strong positive correlation between number of captures and density of understorey, with slightly higher preference for primary logging roads over unlogged forest (Malcolm & Ray 2000). In W Cameroon and Bioko I., occurs at medium to high altitudes (1200–2100 m) (Eisentraut 1969a).

Abundance Less common than other sympatric *Hylomyscus* spp. Comprised 9.5% of 1187 small mammals captured in traps set at three different heights in Dzanga-Sangha, Central African Republic (Malcolm & Ray 2000).

Adaptations Arboreal. Of the relatively common species of rodents, *H. aeta* was the only species to increase in abundance with increasing height of traps set above ground (Malcolm & Ray 2000).

Foraging and Food Predominantly vegetarian (Rosevear 1969). At Makokou, Gabon, consumed fruit (pulp and seeds) and insects,



Hylomyscus aeta

slightly favouring fruit (56.5%) rather than insects (43.5%) during dry season, but preferring insects (92%) instead of fruit (8%) during wet season (Genest-Villard 1980).

Social and Reproductive Behaviour No information.

Reproduction and Population Structure Litter-size: 2.8 (2–3, $n = 8$; Makokou, Gabon; Dubost 1968); and 2.8 (2–3, $n = 4$; Dzanga-Sangha, Central African Republic; J. C. Ray & J. R. Malcolm unpubl.).

Predators, Parasites and Diseases No information.

Conservation IUCN Category: Least Concern.

Measurements

Hylomyscus aeta

HB (♂ ♂): 95.7 (79–114) mm, $n = 65$

HB (♀ ♀): 93.3 (78–110) mm, $n = 55$

T (♂ ♂): 136.9 (118–158) mm, $n = 64$

T (♀ ♀): 135.4 (121–161) mm, $n = 54$

HF (♂ ♂): 21.4 (20–23) mm, $n = 65$

HF (♀ ♀): 21.1 (20–22) mm, $n = 55$

E (♂ ♂): 16.0 (15–18) mm, $n = 65$

E (♀ ♀): 16.1 (15–17) mm, $n = 55$

WT (♂ ♂): 26.7 (16–39) g, $n = 85$

WT (♀ ♀): 23.4 (14–30) g, $n = 61$

GLS (♂ ♂): 27.8 (26.5–29.7) mm, $n = 10$

GLS (♀ ♀): 27.3 (25.8–28.3) mm, $n = 10$

GWS (♂ ♂): 13.9 (13.1–14.7) mm, $n = 10$

GWS (♀ ♀): 13.9 (13.4–14.8) mm, $n = 10$

M¹–M³ (♂ ♂): 4.4 (4.2–4.6) mm, $n = 10$

M¹–M³ (♀ ♀): 4.4 (4.2–4.6) mm, $n = 10$

Dzanga-Sangha, Central African Republic

(J. C. Ray and J. R. Malcolm unpubl., USNM)

Key References Eisentraut 1969a; Malcolm & Ray 2000.

Justina C. Ray & Jay R. Malcolm

Hylomyscus alleni ALLEN'S WOOD MOUSE (ALLEN'S HYLOMYSCUS)

Fr. Rat à poil doux d'Allen; Ger. Allens Waldmaus

Hylomyscus alleni (Waterhouse, 1838). Proc. Zool. Soc. Lond. 1837: 77 (publ. 1838). Fernando Poo (= Bioko I., Equatorial Guinea).

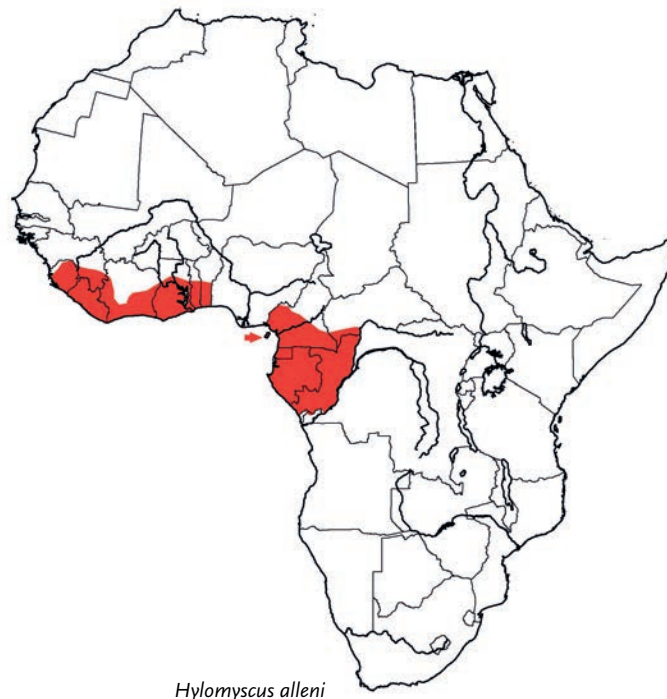
Taxonomy Originally described in the genus *Mus*. This species has had a history of taxonomic problems. Rosevear (1969) restricted *H. alleni* to Fernando Poo (= Bioko I.), but subsequent authors (e.g. Robbins *et al.* 1980) considered that it also occurs on the mainland of West Africa. The holotype was a juvenile specimen (Rosevear 1966, Robbins *et al.* 1980), which complicates definition of the species. *Hylomyscus alleni* is difficult to separate from *H. stella* using morphological characters, biometric analyses, or even cranial and dental features in some cases (Robbins *et al.* 1980, Iksandar *et al.* 1988). Synonyms: *canus*, *montis*, *simus*. Subspecies: none. Chromosome number: $2n = 46$, $FN = 68$ (Robbins *et al.* 1980).

Description Small climbing mouse with soft brownish pelage and very long tail. Dorsal pelage reddish-brown to greyish-brown; hairs grey at the base with brown-orange tips. Ventral pelage greyish-white; hairs grey on basal half, white on terminal half. Muzzle pointed. Eyes surrounded by faint dark ring. Ears large relative to head and covered by short fine red hairs that are barely detectable. Hindfoot narrow; Digit 1 of hindfoot reaches beyond the base of Digit 2; Digit 5 long, reaching as far as the middle of the terminal joint of Digit 4. On forefoot, Digit 5 about equal in length to Digit 2. Fore- and hindfeet covered with short white hairs. Tail very long (ca. 150% of HB), appears naked. Skull: no supraorbital ridges; incisors slightly proodont. No sexual dimorphism in size. Nipples: $2 + 2 = 8$.

Geographic Variation None recorded.

Similar Species

H. aeta. Body size on average larger; pronounced supraorbital ridges on skull, no eye-ring, foot broader, base of tail with hairs.



Hylomyscus alleni

H. stella. Incisors orthodont.

H. parvus. Tail on average shorter; skull smaller.

Praomys spp. Body size on average larger; tail usually relatively shorter; Digit 5 of hindfoot shorter; terrestrial.

Heimyscus fumosus. Digit 5 on hindfoot shorter, pelage darker; tail almost always shorter; eyes smaller; terrestrial.

Distribution Endemic to Africa. Rainforest BZ (Western Region and parts of West Central Region [Eastern Nigeria and Gabon Subregions]). Recorded from two separate areas: (a) Sierra Leone, Guinea (e.g. Mt Nimba), Côte d'Ivoire, S Ghana and Togo; and (b) Cameroon, Equatorial Guinea (incl. Bioko I.), Gabon and SW Central African Republic (Musser & Carleton 1993, Grubb *et al.* 1998, Malcolm & Ray 2000). Not recorded from Benin and Nigeria.

Habitat Rainforest. Prefers micro-habitats characterized by relatively sparse understorey, dense canopy cover and an abundance of large trees (Adam 1977, Ray 1996). Abundant in primary and old secondary forests where shrubs and creepers plentiful, and in dense farm bush (Grubb *et al.* 1998). On Bioko I., none captured in montane forest in spite of intensive trapping (Eisenbraut 1969a). Found in drier parts of the bare forest floor (Sanderson 1940).

Abundance Often the commonest species in relatively undisturbed forests; present but less abundant in degraded forests characterized by dense understorey and fewer large trees (Adam 1977, Ray 1996). In SW Central African Republic comprised 54.1% of all captures ($n = 458$) from unlogged mixed-species forest, 70.0% from monodominant *Gilbertiodendron dewevrei* forest ($n = 406$), 31.5% along secondary logging roads ($n = 704$) and 79.5% along streams ($n = 200$) (Ray 1996). In S Côte d'Ivoire, most commonly trapped small mammal (e.g. 46.6% of 670 and 47.4% of 78 captures) in undisturbed forest habitats; less abundant in highly degraded forests (0% of 83 and 8.7% of 23 captures), swamp forests (8.9% of 191) and gallery forests (12.5% of 40) (Adam 1977). In Tai Forest, Côte d'Ivoire, represented 18.4% of captures in forest habitats and 6.1% in rice and groundnut fields (Dosso 1975b). In sacred groves (forested 'islands' surrounded by savanna or secondary growth) of S Ghana, represented 12.9% of 280 small mammals, and second in abundance after *Praomys tullbergi* (Decher 1997). Because these mice are primarily arboreal (see below), terrestrial trapping may not reflect true relative abundance.

Adaptations Nocturnal (Sanderson 1940, Jeffrey 1975). Arboreal (Sanderson 1940, Rosevear 1969), although known to spend some time on ground (Dosso 1975b, Jeffrey 1975, Malcolm & Ray 2000). Agile climber (Grubb *et al.* 1998); climbing ability is enhanced because the elongated Digit 5 is almost opposable and is used for gripping small twigs, and the long tail is used as a counterbalance while climbing. Nests in holes are constructed in trees, bananas or plantains (Grubb *et al.* 1998). More commonly trapped in understorey and upper strata than on the ground (Adam 1977, Malcolm & Ray 2000). In forest at Adiopodoumé, Côte d'Ivoire, represented only 18.1% of small mammals captured on the ground, but 73.8% at 0–2 m, 87.9% at 2–5 m and 80% at >5 m (Adam 1977; see also Malcolm & Ray 2000). In contrast, trapping on logging roads in Dzanga-Sangha, Central African Republic, revealed some evidence for greater proportional abundance on the ground than at other heights (Malcolm & Ray 2000).

Foraging and Food Predominantly vegetarian (Rosevear 1969). In Sierra Leone, diet included seeds, roots, stems and fruits, with some insects (Taylor 1984, in Grubb *et al.* 1998).

Social and Reproductive Behaviour No information.

Reproduction and Population Structure Reproductive activity in ♂♂ and ♀♀ occurred at all times of the year, but with peaks of activity during the wet season (Ray 1996). During the dry season, relatively few ♀♀ were reproductively active, lactating and/or gravid; testes of ♂♂ were at their smallest size and only a small proportion of ♂♂ had scrotal testes. Litter-size: 2.7 (1–4, $n = 9$; Dzanga-Sangha, Central African Republic; J. C. Ray & J. R. Malcolm unpubl.). Mean body weights in Dzanga-Sangha significantly lower in dry season than in wet season.

Predators, Parasites and Diseases Found in scats of small carnivores from Dzanga-Sangha, although at disproportionately lower frequency than expected from population numbers revealed by trapping (Ray 1998).

Conservation IUCN Category: Least Concern.

Close association with undisturbed forests, and general absence from secondary forests, means that deforestation and degradation of forests (e.g. by logging and clearance for agriculture) constitute potential threats.

Measurements

Hylomyscus alleni

HB (♂♂): 83.6 (71–97) mm, $n = 205$
 HB (♀♀): 83.1 (69–100) mm, $n = 180$
 T (♂♂): 131.3 (108–157) mm, $n = 201$
 T (♀♀): 128.8 (103–156) mm, $n = 171$
 HF (♂♂): 19.8 (17–22) mm, $n = 205$
 HF (♀♀): 19.6 (18–22) mm, $n = 180$
 E (♂♂): 15.6 (13–18) mm, $n = 205$
 E (♀♀): 15.7 (14–18) mm, $n = 180$
 WT (♂♂): 19.2 (11–30) g, $n = 246$
 WT (♀♀): 18.1 (12–27) g, $n = 220$
 GLS (♂♂): 25.0 (24.2–27.2) mm, $n = 10$
 GLS (♀♀): 24.8 (23.2–25.4) mm, $n = 10$
 GWS (♂♂): 12.3 (11.3–12.9) mm, $n = 10$
 GWS (♀♀): 12.3 (11.9–12.7) mm, $n = 10$
 M¹–M³ (♂♂): 3.6 (3.4–3.9) mm, $n = 10$
 M¹–M³ (♀♀): 3.7 (3.6–3.9) mm, $n = 10$
 Dzanga-Sangha, Central African Republic
 (J. C. Ray and J. R. Malcolm, unpubl., USNM)

Key References Adam 1977; Malcolm & Ray 2000; Ray 1996.

Justina C. Ray

***Hylomyscus baeri* BAER'S WOOD MOUSE (BAER'S HYLOMYSCUS)**

Fr. Rat à poil doux de Baer; Ger. Baers Waldmaus

Hylomyscus baeri Heim de Balsac and Aellen, 1965. Biologia Gabonica 1: 175. Adiopoudomé, Côte d'Ivoire.**Taxonomy** Synonyms: none. Chromosome number: not known.**Description** Small arboreal mouse with very long tail and pure white ventral pelage. Pelage short and dense; dorsal hairs ca. 4 mm. Dorsal pelage medium brown, slightly paler on flanks; hairs dark grey at base, brown at tip. Ventral pelage pure white (cf. hairs grey base in all other *Hylomyscus* spp.). Colour of flanks and ventral pelage delineated by well-defined band of orange. Head similar in colour to dorsal pelage. Dark eye-ring; orange suborbital spot. Vibrissae long and stiff, usually black. Ears darkly pigmented. Chin, throat and chest pure white. Tail long (ca. 122% of HB), appears naked, but ringed with small scales, and many small dark bristles. Nipples: 2 + 2 = 8.**Geographic Variation** None recorded.**Similar Species***H. alleni*. On average smaller but with relatively longer tail; ventral pelage grey at base; sympatric.**Distribution** Endemic to Africa. Rainforest BZ (Western Region). Recorded from only a few localities in Liberia, Côte d'Ivoire and Ghana. Limits uncertain.**Habitat** Trees and bushes on the edge of the forest and in trees in cocoa plantations (Gautun & Bellier 1970). One specimen from Ghana was found in secondary forest (Robbins & Setzer 1979).**Abundance** No information. Known only from a few specimens.**Remarks** Apparently no other information available.**Conservation** IUCN Category: Endangered.**Measurements***Hylomyscus baeri*

HB: 105.9 (98–115) mm, n = 10

*Hylomyscus baeri*

T: 128.1 (111–141) mm, n = 10

HF: 21.8 (21–23) mm, n = 10

E: 16.3 (15–19) mm, n = 10

WT: 31.8 (25–36) g, n = 10

GLS: 25.8 (24.2–26.9) mm, n = 10

GWS: 13.5 (12.5–14.3) mm, n = 10

M¹–M³: 4.2 (4.0–4.4) mm, n = 10

Côte d'Ivoire (Gautun & Bellier 1970, RMCA)

Key References Gautun & Bellier 1970; Heim de Balsac & Aellen 1965.

D. C. D. Happold

***Hylomyscus carillus* ANGOLAN WOOD MOUSE (ANGOLAN HYLOMYSCUS)**

Fr. Rat à poil doux d'Angola; Ger. Angolische Waldmaus

Hylomyscus carillus (Thomas, 1904). Ann. Mag. Nat. Hist., ser. 7, 13: 418. Pungo Andongo, Angola. 1200 m.**Taxonomy** Originally described in the genus *Mus*. Sometimes considered to be related to *H. aeta* or *H. alleni*, but may be more closely related to *H. stella* (details in Musser & Carleton 2005). Definition of this species is uncertain: Crawford-Cabral (1998) lists it as the only species of *Hylomyscus* in Angola, but Musser & Carleton (2005) suggest that two other species (*H. denniae* and *H. stella*) may also occur there. Synonyms: none. Chromosome number: not known.**Description** Small very long-tailed climbing mouse; one of the larger species in the genus. Pelage soft, moderately dense, dorsal hairs ca. 8 mm. Dorsal pelage brown to rufous-brown; hairs dark grey at base, rufous, pale brown or black at tip. Grey colour of base may show on surface of pelage. Flanks slightly paler, sometimes more rufous. Ventral pelage whitish-grey; hairs dark grey on basal half, white on terminal half. Lips, cheeks, throat and chest white. Long dark vibrissae (up to 25 mm). Forelimbs short, white above; Digits

*Hylomyscus carillus*

2, 3, 4 and 5 long with short claws; Digit 1 reduced to tubercle, without claw. Hindlimbs slightly elongated, especially hindfoot. Hindfoot white above; Digit 1 short; Digits 2, 3, 4 and 5 long; all digits with claws. Tail very long (ca. 130% of HB), not bicoloured, appears naked but ringed with small scales; small tuft of hairs on tip. Skull with strong supraorbital ridges; incisor teeth orthodont. Nipples 1 + 2 = 6 or 2 + 2 = 8.

Geographic Variation None recorded.

Similar Species

H. stella. On average slightly smaller; supraorbital ridges small or absent; incisor teeth orthodont; ? allopatric.

H. aeta. Skull larger; supraorbital ridges well-developed; incisor teeth opisthodont; allopatric, possibly parapatric in SE DR Congo.

Distribution Endemic to Africa. Zambezan Woodland BZ (northern part). Recorded from W and C Angola; perhaps occurs in SE DR Congo (Crawford-Cabral 1998). Misonne (1974) gives a larger range, which includes Cameroon, Gabon, Congo, DR Congo, W Uganda, N Angola and Bioko I., but which probably includes specimens now allocated to *H. aeta* and *H. stella* (see also Musser & Carleton 2005). Limits uncertain.

Habitat Unknown; 'probably occurs throughout ... the more forested areas' (Hill & Carter 1941).

Abundance Uncertain. Known from only 12 localities (Crawford-Cabral 1998; but see also above).

Remarks One ♀ collected in Jun was pregnant with six embryos (label, BMNH). Three ♀♀ collected at Hanha in May were lactating (Hill & Carter 1941).

Conservation IUCN Category: Least Concern.

Measurements

Hylomyscus carillus

HB: 96 (89–107) mm, n = 8*

T: 128.5 (117–146) mm, n = 8

HF: 18.6 (18–19) mm, n = 8

E: 16.0 (15–18) mm, n = 8

WT: n. d.

GLS: 25.0 (24.7–25.6) mm, n = 6

GWS: 12.2, 12.3 mm, n = 2

M¹–M³: 4.0 (3.8–4.4) mm, n = 8

Pungo Andongo, Angola (BMNH)

*TL and T on labels; HB calculated

Key References Crawford-Cabral 1998; Hill & Carter 1941.

D. C. D. Happold

Hylomyscus denniae MONTANE WOOD MOUSE (MONTANE HYLOMYSCUS)

Fr. Rat à poil doux de montagne; Ger. Gebirgswaldmaus

Hylomyscus denniae (Thomas, 1906). Ann. Mag. Nat. Hist., ser. 7, 18: 144. Mubuku Valley, Rwenzori East, Uganda. 7000 ft (2130 m).

Taxonomy Originally described in the genus *Mus*. The definition of this species is unclear (Musser & Carleton 2005). Bishop (1979) listed three subspecies: the comparatively large *H. d. denniae* (from Mt Kenya and the Aberdare Ranges, Kenya), the smaller *H. d. vulcanorum* (from W Kenya and the Kigezi/Virunga Mts of SW Uganda and E DR Congo) and *H. d. anselli* (a new subspecies from Zambia and N Tanzania), although none of these are currently recognized. The species is morphologically close to *H. carillus*; specimens described as *H. carillus* from WC Angola (Hill & Carter 1941) are probably *H. denniae* (Musser & Carleton 2005). The form *endorobae*, assessed as close to *Praomys* (Van der Straeten & Robbins 1997), is considered a *Hylomyscus* by Musser & Carleton (2005).

Specimens from E DR Congo and Rwanda appear to be relatively large and to associate with *denniae*. Synonyms: *anselli*, *endorobae*, *vulcanorum*. Subspecies: none. Chromosome number: 2n = 48 (west of L. Kivu, DR Congo; det. J. Olert unpubl.).

Description One of the largest and darkest species in the genus. Pelage rather long (ca. 8–10 mm), soft and dense. Dorsal pelage dark brownish-grey, without rufous colouration as in some other species in the genus; hairs dark grey with brownish tip. Flanks similar to dorsum with tinge of rufous. Ventral pelage whitish-grey; hairs dark grey with white at tip. Head similar in colour to dorsum. Rufous-buff on cheek between eye and ear. Upper lips, chin and throat

whitish-grey (similar to ventral pelage). Vibrissae long, black. Large eyes, surrounded by narrow ring of black hairs. Upper surfaces of fore- and hindlimbs white. Upper surface of each digit of hindfeet with small tuft of white hairs. Tail very long (ca. 140% of HB), dark, ringed with small scales; appears naked but with many small dark bristles; hairs slightly longer at tip. Skull: small and delicate; frontal bone at interorbital constriction smooth; supraorbital ridges small; anterior palatal foramina long and wide, reaching to M^1 ; cheekteeth narrow, over 4 mm in length. Nipples: $2 + 2 = 8$.

Geographic Variation Bishop (1979) recognized three subspecies (now synonyms) on the basis of length of the anterior palatine foramina and ratio with the condylo-occipital length:

H. d. denniae: most of eastern Africa.

H. d. vulanorum: Virungu Volcanoes (DR Congo); Rwenzori Mts, Impenetrable Forest, Mt Elgon (Uganda) and Cherangani Hills (Kenya).

H. d. anselli: Tanzania and Zambia.

Similar Species

H. aeta. On average slightly smaller; sympatric only in E DR Congo.

H. stella. Smaller; frontal bone concave; sympatric only in E DR Congo.

Praomys delectorum. Slightly larger, with longer ears, shorter tail and longer hindfeet; not arboreal; sympatric only in Tanzania.

P. jacksoni. Larger in all respects except ear length; not arboreal; sympatric in Uganda, E DR Congo and N Zambia.

Distribution Endemic to Africa. Zambezian Woodland BZ, southern part of Somalia–Masai Bushland BZ and parts of the Eastern Rainforest–Savanna Mosaic. Recorded in several discrete areas: (a) Rwenzori Mts (DR Congo/Uganda), the Virunga Mts (DR Congo/Uganda/Rwanda) (Misonne 1963, Delany 1975, Verschuren *et al.*

1983), and west and east of L. Kivu (DR Congo/Rwanda/Burundi); (b) Mt Elgon (Uganda/Kenya), Cherangani Hills, Mt Kenya and Aberdare Ranges of Kenya; (c) Highland areas of Mt Kilimanjaro, Mt Meru and Ngorongoro Crater, South Pare Mts, Uzungwa Mts, Rungwe Mts and Ukinga in Tanzania (Bishop 1979, Kingdon 1974, Stanley *et al.* 1998a); (d) several localities in NE and N Zambia (Ansell 1978); and (e) WC Angola. The species is presumed to have had a wider and more continuous distribution in the past (Misonne 1969a).

Habitat In E DR Congo and Rwanda, lives in *Hagenia* forests, heath forests of *Erica arborea* and sub-alpine habitats with *Senecio* and *Lobelia*, from ca. 2000 m to ca. 4400 m. Occurs in most trapping sites within these habitats, e.g. recorded in 20 of 23 sites (F. Dieterlen unpubl.). On Mt Elgon, Uganda, found only in montane forest and bamboo (but not in heather, swamps or rocky habitats) (Clausnitzer & Kityo 2001). On South Pare Mts, Tanzania, occurs occasionally at 1100 m (Stanley *et al.* 1998a).

Abundance Mostly common, but abundance varies with habitat. Comprised 7–30% of small mammals in most habitats in E DR Congo and Rwanda (F. Dieterlen, unpubl.). Recorded as ‘extremely common’ in the Rwenzori Mts (Thomas & Wroughton 1910). In South Pare Mts, Tanzania, at 2000 m, recorded at two (of four) sites, and where caught comprised 11% ($n = 9$, 3 spp.) and 30% ($n = 33$, 6 spp.) of small rodents; in both instances, was the second most common species after *Praomys delectorum* (Stanley *et al.* 1998a).

Adaptations Arboreal and mostly nocturnal. Constructs nests in tree holes. The very long tail and short hindfeet appear to be adaptations for climbing among branches and vines.

Foraging and Food Omnivorous. Forages both on and above the ground. In E DR Congo, vegetable material is the principal food (remains in all 28 stomachs examined), but insects and other invertebrates are also eaten (remains in 10 of the 28 stomachs) (F. Dieterlen, unpubl.). In other localities, food varied slightly: mainly insects, but also fruits and starchy matter on the Virunga Mts (Verschuren *et al.* 1983), and invertebrates, seeds and fruit pulp on Mt Elgon, Uganda (Clausnitzer 2003).

Social and Reproductive Behaviour Individuals in captivity were peaceful and did not display agonistic behaviour towards conspecifics (F. Dieterlen unpubl.).

Reproduction and Population Structure Reproductive rate and embryo number varied seasonally near L. Kivu, E DR Congo (F. Dieterlen unpubl.). In the ‘dry’ season (Jul–Aug; rainfall 25–50 mm/month) and early wet season (Sep; ca. 150 mm/month) 80% of ♀♀ were pregnant or lactating ($n = 35$). During the wet season (Oct–May; rainfall ca. 150–210 mm/month), the reproductive rate decreased to 9% ($n = 34$) in Oct–Jan, but then increased to 47% ($n = 29$) in Feb–May. Embryo number: 4.55 (3–7, $n = 29$ ♀♀). Mean number of embryos was higher at the end of the dry season (Jul, Aug) and the beginning of the wet season (Sep) than at other times of the year. Testes length of adult reproductively active ♂♂ was 6–8 mm. Females mature when 22 g, and first pregnancies occur when 22–25 g; ♂♂ mature when 22 g and when testes are 5 mm in length (F. Dieterlen, unpubl.).



Hylomyscus denniae

Conservation IUCN Category: Least Concern.

Conservation of montane forests are necessary for the conservation of this species (Schlitter 1989).

Measurements

Hylomyscus denniae

HB: 98.3 (87–106) mm, n = 36

T: 139 (123–153) mm, n = 36

HF: 20.7 (19–23) mm, n = 36

E: 18.0 (16–19) mm, n = 36

WT: 30.0 (19–40) g, n = 36

GLS: 25.7 (24.6–27.1) mm, n = 25

GWS: 12.7 (12.0–13.7) mm, n = 21

M¹–M³: 4.2 (3.9–4.4) mm, n = 21

E DR Congo (F. Dieterlen unpubl., SMNS)

Key Reference Bishop 1979.

Fritz Dieterlen

Hylomyscus grandis LARGE WOOD MOUSE (MOUNT OKU HYLOMYSCUS)

Fr. Rat à poil doux grande; Ger. Grosse Waldmaus

Hylomyscus grandis Eisentraut, 1969. Z. Säugetierk. 34: 300. Oku Mts, West Cameroon. 2100 m.

Taxonomy Described as a subspecies of *H. aeta* by Eisentraut (1969a) and Musser & Carleton (1993). Raised to specific status by Hutterer *et al.* (1992). Synonyms: none. Chromosome number: unknown.

Description Small arboreal mouse; the largest species in the genus *Hylomyscus*. Pelage fine and soft; dorsal hairs ca. 10 mm on back. Dorsal pelage greyish-brown to bright cinnamon-brown; hairs medium grey, brownish at tip (some with black tip). Ventral pelage whitish-grey; hairs dark grey, white at tip. Ventral colour clearly delineated from colour of flanks. Head similar in colour to dorsal pelage. Nose, upper lips, chin, lower cheeks off-white or whitish-grey. Vibrissae long and black. Ears small, darkly pigmented, with slight covering of short dark brown or black hairs. Forefeet small, with sparse whitish hairs; five digits; Digit 1 reduced and without claw. Hindfeet relatively short, with sparse whitish hairs; five digits, all with claws. Tail very long (145% of HB), ringed with scales; appears naked but with very short black bristles; longer bristles at tip. Skull and molars larger than in *H. aeta*. Nipples 1 + 1 = 4.

Geographic Variation None recorded.

Similar Species

H. aeta. Mostly smaller in external dimensions, skull smaller and narrower; cheekteeth smaller; widespread including S Cameroon.

H. stella. Smaller on average in external dimensions; skull smaller and narrower; cheekteeth smaller; may occur in the same area.

Distribution Endemic to Africa. Recorded only from the region of Mt Oku in C Cameroon.

Habitat Montane forest at 2100 m.

Abundance Apparently rare; known only from four specimens.

Remarks Very long tail suggests a scansorial life-style. A pregnant ♀ collected on 22 Jan had 5–6 embryos (specimen in ZFMK).

Conservation IUCN Category: Critically Endangered.



Hylomyscus grandis

Measurements

Hylomyscus grandis

HB: 96.8 (89–110) mm, n = 4

T: 140.0 (130–150) mm, n = 4

HF: 20.0 (18–22) mm, n = 4

E: 16.5 (15–20) mm, n = 4

WT: 33.0 (25–41) g, n = 4

GLS: 27.6 (27.3–27.9) mm, n = 4

GWS: 14.0 (13.7–14.4) mm, n = 4

M¹–M³: 4.9 (4.8–5.0) mm, n = 4

Mt Oku (Eisentraut 1969a)

Key References Eisentraut 1969a.

R. Hutterer

***Hylomyscus parvus* LESSER WOOD MOUSE (LESSER HYLOMYSCUS)**

Fr. Rat à poil doux africain; Ger. Kleine Waldmaus

Hylomyscus parvus Brosset, Dubost and Heim de Balsac, 1965. Biologia Gabonica 1: 149. Belinga Mts, Gabon.

Taxonomy Synonyms: none. Chromosome number: $2n = 46$, $FN = 70$ (Robbins *et al.* 1980).

Description Very small climbing mouse with short round head and stout body; smallest species in the genus. Dorsal pelage chocolate-brown or dark brown; hairs dark grey at base, brown at tip. Paler on flanks. Ventral pelage brownish-white; hairs brown, some with white tip. No clear delineation between colour of dorsal and ventral pelage. Ears large, rounded, naked or with very short hairs. Limbs relatively long for a *Hylomyscus*. Forelimb with short white hairs; Digit 1 of forefoot very short, without claw; Digits 2–5 long, each with small claw. Hindfoot short; Digit 1 short. Tail very long (140–165% of HB), pale, sparsely covered with very short pale hairs. Juvenile pelage grey-brown to almost black, darker than in adults. Skull: small and delicate; incisor teeth orthodont or very slightly pro-odont; very slight supraorbital ridges; frontal bone slightly concave or obviously concave at supraorbital constriction; anterior palatal foramina long and wide, not reaching the level of the anterior edge of M^1 ; incisor and molar teeth narrow. Nipples: $1 + 2 = 6$.

Geographic Variation None recorded.

Similar Species

Other *Hylomyscus* spp. On average larger; dorsal pelage paler.

Heimyscus fumosus. Digit 5 on hindfoot shorter; pelage softer and darker; tail relatively shorter; eyes smaller.

Pracomys spp. Overall size larger; hindfoot longer; Digit 5 of hindfoot shorter.

Distribution Endemic to Africa. Rainforest BZ (West Central Region [Eastern Nigeria and Gabon Subregions] and East Central Region). Recorded only from two localities in Gabon, one in Congo (Brosset *et al.* 1965), one in Central African Republic (Genest-Villard 1980), six in South Cameroon (Robbins *et al.* 1980, Dudu *et al.* 1989) and one in N DR Congo (Dudu *et al.* 1989). Probably more widespread within the central African rainforests than these records indicate.

Habitat Primary and secondary forest (Brosset *et al.* 1965, Dudu *et al.* 1989, J.-M. Duplantier unpubl.), but also abandoned fields in DR Congo (Dudu *et al.* 1989).

Abundance Uncommon or rare. Represented 3.1% of rodents trapped at Masako, DR Congo (Dudu *et al.* 1989) and 2.6% at Makokou, Gabon (Duplantier 1982). Much less common at Masako than sympatric *H. stella* (very numerous) and *H. aeta* (uncommon).

Adaptations Terrestrial, scansorial and arboreal (Robbins *et al.* 1980).

Foraging and Food In Central African Republic, diet (as assessed by stomach contents) is fruit and insects, and similar to that of *H. stella*. In captivity, eats pulp of fruits and seeds (Genest-Villard 1980).

Social and Reproductive Behaviour Sex ratio: 1 : 1 at Makokou, Gabon ($n = 16$) (J.-M. Duplantier unpubl.).

Reproduction and Population Structure Embryo number: 2.4 (2–3, $n = 5$; Gabon; Dubost 1968, J.-M. Duplantier unpubl.).

Predators, Parasites and Diseases No information.

Conservation IUCN Category: Least Concern.

Measurements

Hylomyscus parvus

HB: 67.4 (56–77) mm, $n = 21$

T: 102.4 (87–120) mm, $n = 21$

HF (c.u.): 15.3 (14–16) mm, $n = 23$

E: 13.9 (13–15) mm, $n = 20$

WT: 12.7 (10–16) g, $n = 16$

GLS: 20.7 (19.4–21.9) mm, $n = 33$

GWS: 10.9 (10.1–11.7) mm, $n = 33$

M^1 – M^3 : 3.2 (3.0–3.4) mm, $n = 36$

Masako, DR Congo (Dudu *et al.* 1989)

Weight: Makokou, Gabon (J.-M. Duplantier unpubl.)

Key References Brosset *et al.* 1965; Dudu *et al.* 1989; Robbins *et al.* 1980.



Hylomyscus parvus

J.-M. Duplantier

Hylomyscus stella STELLA WOOD MOUSE (STELLA HYLOMYSCUS)

Fr. Rat à poil doux de Stella; Ger. Stella-Waldmaus

Hylomyscus stella (Thomas, 1911). Ann. Mag. Nat. Hist., ser. 8, 7: 590. Ituri Forest, between Mawambi and Avakubi, E DR Congo.

Taxonomy Originally described in the genus *Epimys*. Closely related to *H. alleni*, and difficult to separate from this species. Robbins *et al.* (1980) united the species with *H. alleni* in the 'alleni-group' because both species have a concave frontal bone at the interorbital constriction, narrow incisors and narrow molars. See also *H. alleni*. Synonyms: *kaimosi*. Subspecies: none. Chromosome number shows polymorphism, according to locality: $2n = 46$, $FN = 70$ and $2n = 46$, $FN = 72$ (DR Congo; Matthey 1963a); $2n = 46$, $FN = 74$ (Central African Republic; Viegas-Péquignot *et al.* 1983); $2n = 48$, $FN = 86$, $aFN = 82$ (Burundi; Maddalena *et al.* 1989).

*Hylomyscus stella*.

Description A small beautiful climbing mouse with very long tail. Pelage soft. Dorsal pelage rufous-brown; hairs dark grey, rufous-brown or dark brown at tip. In juveniles, dorsal pelage darker grey, without rufous tinge. Ventral pelage greyish-white or silvery-white; hairs grey at base, whitish at tip. Colour of ventral pelage clearly delineated from dorsal pelage. Head small, similar in colour to back. Ears large, rounded, slightly pigmented; appear almost naked, but with very short hairs. Hindfeet short and broad; Digit 5 opposable. Upper side of fore- and hindfeet white, sometimes yellowish- to reddish-brown. Tail very long (ca. 150% of HB), dark, ringed with small scales, almost naked but with very short bristles. Skull: small and delicate; supraorbital ridges small or absent; frontal bone slightly concave at interorbital constriction, incisors orthodont; incisors and molar teeth narrow. Nipples: $2 + 2 = 8$.

Geographic Variation None except for karyotypic variation (see Taxonomy).

Similar Species

H. alleni. Very similar; incisors pro-odont; marginally sympatric.

H. grandis. On average larger; very restricted distribution in Cameroon.

H. parvus. On average smaller in all respects.

Promys jacksoni. On average larger; partly arboreal; sympatric in DR Congo.

*Hylomyscus stella*

Distribution Endemic to Africa. Rainforest BZ (West Central, East Central and South Central Regions). Recorded from W Nigeria, S Cameroon, Gabon, SW Central African Republic, Congo, DR Congo (including Rwenzori Mts and Virunga Mts), SW Uganda, Rwanda and Burundi. Isolated records in Gotel Mts on Nigeria–Cameroon border (Hutterer *et al.* 1992), Imatong Mts in S Sudan (F. Dieterlen unpubl.), Uganda (Delany 1975) and Kakamega Forest and other forest relicts in W Kenya (Bishop 1979). Altitudinal distribution from near sea level (e.g. W Nigeria) to at least 2250 m (Burundi, Rwenzori Mts). Geographic range uncertain due to morphological similarity with *H. alleni*.

Habitat Primarily arboreal and associated with tangles, shrubs and the lower storeys of forest. In Nigeria, found in tangled vegetation in abandoned farmlands, 'palm bush', secondary growth bordering paths and roads in forested areas, and in open areas of rainforest where shrubs and creepers form a dense growth (Happold 1987). In the Virunga–Rwenzori region recorded in forests at 800–2250 m, in dense and dark places in bamboo forests, and in other forest types (Verschuren *et al.* 1983). Delany (1975) caught many more individuals at 0.5–9.0 ft above the ground, mostly at 1.5–6 ft, than on the ground. In lowland rainforest (800–1700 m) in E DR Congo, preferred habitat was primary forest on hills (where comprised 25% of captured small mammals); less favoured habitats were ravines with streams (17%), secondary forest (20%) and cultivation (5%) (F. Dieterlen unpubl., Rahm 1970). Although mainly arboreal, descends to the ground to forage and hence (in some localities) caught in considerable numbers on the ground (Duplantier 1989);

in contrast, very few were caught at ground level in rainforest in Nigeria (Happold 1977).

Abundance Difficult to assess because of arboreal habits. At Makokou, NE Gabon (where caught on the ground), comprised 58% of small mammals (9 spp., $n = 549$), ranging from 55 to 72% depending on time of year (Duplantier 1989). (A second species of *Hylomyscus*, *H. parvus*, comprised only 0.5–2.5%.) Likewise, the most abundant species at two localities at Monts Doudou, SE Gabon, comprising 26% ($n = 675$; 10 spp.) and 39% ($n = 802$; 10 spp.) of small mammals during a 12-month period (Nicolas & Colyn 2003). In E DR Congo, the third most numerous species after *Hybomys univittatus* and *Praomys jacksoni* (Dieterlen 1985a). In W Nigeria, comprised 58% of arboreal species in a forest–farmland habitat (Happold 1974), but only 5.6% of small rodents in a mark-recapture study over three years in rainforest (Happold 1977).

Adaptations Primarily arboreal, but also terrestrial. Nocturnal. Very active and agile when climbing amongst creepers and shrubs. Holds on to narrow twigs using long opposable Digit 5 of hindfoot, and uses long tail for balance.

Foraging and Food Forages on branches and on the ground. Besides feeding on live insects (see below), forages in leaf litter for dead insects. In Central African Republic, diet in the dry season (as assessed by analysis of stomach contents) was 56% vegetable material (mainly fruits) and 44% insects (mainly termites, with some ants and beetles). In the wet season, diet changed to 8% vegetable material and 92% insects (Genest-Villard 1980). Feeding is selective: in captivity, individuals ate 35 species of fruits and rejected 21 species. Different parts of fruits are eaten depending on the species (and probably also on nutritive value and ease of consumption): fruit pulp (47%) and seeds (28%) are preferred foods, and nuts (12%), arils (7.5%) and nutshells (2.5%) are less preferred (Genest-Villard 1980). The small incisor teeth and small narrow molar teeth limit which species of fruit, and which parts of a fruit, can be masticated and ingested. In E DR Congo, wild-caught individuals ate insects less often (remains in only 16 of 61 stomachs); captive animals consumed 35 spp. of fruits (Rahm 1972, F. Dieterlen unpubl.).

Social and Reproductive Behaviour No information.

Reproduction and Population Structure Reproduction occurs throughout the year with peaks of activity during the wet

season. In W Nigeria, pregnant ♀♀ recorded in all months except Dec and Feb (long dry season) and Aug (little dry season) (Happold 1974). On a yearly basis, pregnancy rate was just over 50%. A similar pattern of reproduction recorded in Uganda (Delany 1971) and Sudan (F. Dieterlen unpubl.). In E DR Congo (Dieterlen 1985a, b) pregnancy rate was 80% ($n = 132$) during the main wet season (Nov–May), 8–25% during the dry season (Jun–Aug) and 40% during the early wet season (Sep–Oct) (Dieterlen 1985a, b). Gestation: ca. 29.5 days (Delany 1971) – rather long for a rodent of this size. Mean embryo number varies according to season. During the wet season (Nov–Apr), it averaged 3.71 (range 3.3 [Mar] to 4.5 [Nov]); during the dry season and early wet season (May–Oct), it averaged 3.07 (range 2.0 [Jun] to 3.5 [Oct]). Mean embryo number also varies by locality: 3.4 (Gabon; Dubost 1968), 3.21 (Uganda; Delany 1971), 2.9 (1–4; Nigeria; Happold 1974). Females become mature at 13–16 g (Happold 1974, Dieterlen 1985a, Duplantier 1989, Dudu 1991), and most first pregnancies occur when weight is 15–20 g. At birth, young are naked and blind, and weigh 1.2–1.8 g. Dark pigmentation visible on Day 6–9. Thin covering of hair dorsally and ventrally Day 9–14. Adult pelage Day 25–48. Weight 4–8 g on Day 20 and 9–12 g on Day 40 (Delany 1971).

Predators, Parasites and Diseases No information.

Conservation IUCN Category: Least Concern.

Measurements

Hylomyscus stella

HB: 85 (57–118) mm, $n = 307$

T: 126 (61–152) mm, $n = 324$

HF: 17.0 (13–22) mm, $n = 298$

E: 14.8 (11–19) mm, $n = 236$

WT: 20.2 (16–32) g, $n = 319$

GLS: 24.4 (23.0–25.5) mm, $n = 27$

GWS: 12.4 (11.9–13.3) mm, $n = 19$

M^1 – M^3 : 4.0 (3.4–4.3) mm, $n = 22$

Body measurements: DR Congo (Dudu 1991)

Skull measurements: DR Congo (SMNS)

Key References Delany 1971; Dieterlen 1985a; Genest-Villard 1980; Happold 1974.

Fritz Dieterlen

GENUS *Lamottemys*

Mount Oku Rat

Lamottemys Petter, 1986. Cimbabesia, Ser. A, 8: 98. Type species: *Lamottemys okuensis* F. Petter, 1986.

A monotypic genus found only on Mt Oku, Cameroon. The genus is characterized by medium size, uniformly dark brown pelage, and tail about equal in length to the head and body. Digit 5 of forefoot very short with nail (as in *Desmomys*) and not with claw (as in *Oenomys*). Skull shape similar to a young *Oenomys*, upper incisors with faint groove (as in *Desmomys* but unlike *Oenomys*), upper molars stephanodont

(frequent connections between cusps) as in *Oenomys* (Figure 71). The genus appears to be closely related to *Oenomys* (Dieterlen & Van der Straeten 1988, Musser & Carleton, 1993) rather than to *Desmomys* as suggested by Petter (1986). The single species is *Lamottemys okuensis*.

R. Hutterer

Lamottemys okuensis MOUNT OKU RAT (MOUNT OKU LAMOTTEMYS)

Fr. Rat du Mont Oku; Ger. Oku-Lamotte-Maus

Lamottemys okuensis Petter, 1986. Cimbebasia, Ser. A, 8: 98. Mt Oku, W Cameroon.*Lamottemys okuensis*.

Taxonomy Externally similar to *Oenomys* but with distinctive cranial characters (see Genus profile). Synonyms: none. Chromosome number: not known.

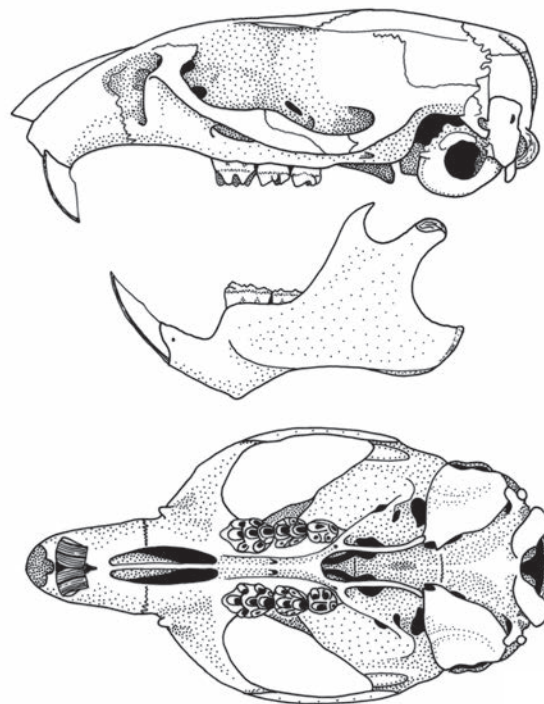
Description Small to medium-sized mouse, similar in colour to *Hybomys* spp. but without any dark mid-dorsal stripe. Pelage soft and shiny. Dorsal pelage dark blackish-brown tinged with russet-brown, speckled with yellowish-brown; hairs dark grey, with yellowish-brown subterminal band and black tip. Many long pure black guard hairs. No mid-dorsal dark stripe. Ventral pelage yellowish-grey, paler than dorsal pelage; hairs grey at base, yellowish at tip. Colour of dorsal pelage merges with colour of ventral pelage. Head similar in colour to dorsal pelage. Ears relatively large, darkly pigmented, with some short black or dark brown hairs. Forelimbs yellowish-brown with four digits; Digit 1 absent; Digit 5 reduced in size with nail (not claw). Hindlimbs yellowish-brown, five digits, each with claw. Tail long (ca. 100% of HB), black, ringed with scales, many very small black bristles. Skull: see genus profile. Nipples: not known.

Geographic Variation None recorded.

Similar Species

Hybomys badius. Externally similar but with faint black dorsal stripe; Digit 5 of forefoot with claw.

Distribution Endemic to Africa. Afromontane–Afroalpine BZ. Restricted to the Kilum-Ijim Forest of Mt Oku, an old volcano in North West Province, Cameroon; this forest is isolated and has an area of only 21 km² and a high level of endemism (Eisentraut 1968b).

Figure 71. Skull and mandible of *Lamottemys okuensis* (ZFMK 91232; after original photograph by R. Hutterer).*Lamottemys okuensis*.

Habitat Undisturbed montane forest, at 2100–3000 m, where there is a dense understorey of brush, thornbushes and herbaceous plants (Eisentraut 1982).

Abundance Appears to be rare or uncommon.

Remarks The characters and proportions of the body (in comparison with *Oenomys* and *Desmomys*) suggest that it is mainly terrestrial and herbivorous (O. Fülling pers. comm.). Litter-size perhaps small: one ♀ captured on 24 Jan during the dry season contained one embryo (Dieterlen & Van der Straeten 1988). Mongooses and genets occur in Oku forest (Maisels *et al.* 2001) and are likely predators. Like other rodents, this species is hunted for food by the local community (O. Fülling pers. comm.).

Conservation IUCN Category: Endangered.

Measurements

Lamottemys okuensis

HB: 126.0 (108–135) mm, n = 4

T: 124.8 (107–132 mm, n = 4

HF: 28.4 (25–31) mm, n = 4

E: 16.5 (16–17) mm, n = 4

WT: 43, 69 g, n = 2

GLS: 32.6, 33.9 mm, n = 2

GWS: n. d.

M¹–M³: 6.9 (6.8–7.1) mm, n = 4

Mt Oku, Cameroon (Dieterlen & Van der Straeten 1988)

Key References Dieterlen & Van der Straeten 1988; Petter 1986.

R. Hutterer

GENUS *Lemniscomys*

Grass Mice

Lemniscomys Trouessart 1881. Bull. Soc. Etud. Scient. Angers 10: 124. Type species: *Mus barbarus* Linnaeus, 1766.



Lemniscomys macculus.

The genus *Lemniscomys* is endemic to Africa and contains 11 species (Table 35) that inhabit grassland habitats north of the Sahara in NW Africa (one species) and large areas of savanna south of the Sahara (ten species). Striped grass mice are easily recognized by the attractive longitudinal stripes on the back and sides of the body, a cryptic pattern that elegantly blends the mice with the colour of their grassland habitat. Compared with Africa's other striped grass mice, genus *Rhabdomys*, Digit 5 of the forefoot in species of *Lemniscomys* is vestigial. The periosteum investing the braincase of *Lemniscomys*, as well as certain other arvicanthine rodents (*Arvicanthis*, *Pelomys*, *Rhabdomys*), is densely pigmented with melanin granules, an adaptation that is believed to provide protection from deleterious levels of ultraviolet radiation in these predominantly diurnal small mammals (Hill 1942, Timm & Kermott 1982).

Species of *Lemniscomys* are small to medium in size. Pelage relatively short (hairs ca. 5–8 mm over middle rump), closely adpressed to the body; hairs stiff to slightly hispid in some forms, especially over the rump. Dorsal pelage is characterized by a dark mid-dorsal stripe, dusky to black, that extends from the middle crown to the rump. On either side of this stripe are white or pale buff longitudinal lateral stripes on a dark grey or brown background. Three general patterns are evident: (a) lateral stripes absent or faint (*griselda* species-group); (b) continuous lateral stripes not broken into spots (*barbarus* species-group); and (c) lateral stripes that are normally continuous near the mid-dorsal line but broken into lines of spots more laterally (*striatus* species-group). The number and width of the lateral stripes vary according to species and populations. Ventral pelage is white, cream, or buff and sharply delineated from colour of back, sometimes accented by a buffy or pale orange lateral line. Pinnae short and broadly rounded, covered with tawny to rufescent hairs. Tail longer than head and body (T ca. 110–120% of HB); moderately hairy, partially obscuring annulations; bicolouration weakly defined, dorsal hairs blackish and ventral hairs reddish. Forefoot appearing three-fingered; Digits 2–4 normally developed, Digit 5 nearly as small as Digit 1 and, like it, equipped with a nail instead of a claw. Hindfoot narrow, with Digits 1 and 5 of hindfoot very short, their claws reaching the metatarsal–phalangeal joint of Digits 2–4. Plantar surface of metatarsus and digits naked, tarsus hairy; modal number of plantar pads variable according to species-group, typically six in *striatus* group, five in *griselda* species-group (hypotheneal indistinct or absent) and four in *barbarus* species-group (thenar and hypotheneal minute or absent).

Skull is narrow, rostrum short, cranial profile evenly arched. Zygomatic arches parallel-sided, lateral flaring slight even in old animals; zygomatic plate broad but short, leading edge straight to weakly concave, dorsal notch deeply incised. Interorbital region constricted, dorsal edges convergent and marked by a low supraorbital bead and small shelf. Braincase elongate, temporal ridging weak; interparietal comparatively short and narrow. Anterior palatal foramina

Table 35. Species in the genus *Lemniscomys*. Arranged in order of number and pattern of lateral stripes.
(n. d. = no data.)

| Species | Lateral stripe pattern (species-group) | Lateral stripes on each flank | Colour of ventral pelage | |
|-----------------------|--|--|--------------------------|--|
| <i>L. barbarus</i> | Continuous stripes not broken into spots (<i>barbarus</i>) | 7–8; pale yellow | White | |
| <i>L. zebra</i> | Continuous stripes not broken into spots (<i>barbarus</i>) | 6–7; honey-coloured | White or cream | |
| <i>L. hoogstraali</i> | Continuous stripes not broken into spots (<i>barbarus</i>) | 5; wide, white, interspersed with four narrow slightly spotted; very dark background | White | |
| <i>L. bellieri</i> | Some stripes broken into spots (<i>striatus</i>) | 8; similar in colour to background; all spotted | White | |
| <i>L. macculus</i> | Some stripes broken into spots (<i>striatus</i>) | 6–8; pale; upper stripes spotted | White | |
| <i>L. mittendorfi</i> | Some stripes broken into spots (<i>striatus</i>) | 8; pale; upper stripes spotted on dark background, lower stripes continuous | Greyish | |
| <i>L. striatus</i> | Some stripes broken into spots (<i>striatus</i>) | 4; obvious upper stripes, spotted; irregular pattern of spots below, not always in lines | White | |
| <i>L. roseveari</i> | Faint and obscure (<i>griselda</i>) | None (or obscure spotting not in stripes) | White | |
| <i>L. linulus</i> | Faint or none (<i>griselda</i>) | None (or obscure pale spotting) | Pure white | |
| <i>L. griselda</i> | None (<i>griselda</i>) | None | White | |
| <i>L. rosalia</i> | None (<i>griselda</i>) | None | White or off-white | |

long (ca. 75–82% of diastema length), extending between the anterior roots of the first molars; foramina broader and bluntly pointed anteriorly, narrower and acute posteriorly. Optic foramen large, nearly the size of the anterior alar fissure. Carotid circulation lacking supraorbital branch (sphenofrontal foramen and squamosal-alisphenoid groove absent, stapedia foramen present). Alisphenoid strut absent and auditory bullae medium-sized. Molars low crowned, moderately broad, with blunt cusps. Third molars approximately two-thirds the size of the second molars. Cusps t1 and t3 of M¹, as well as t4 and t6, approximately equal in size; t3 of M² tiny but present; t9 present on M¹⁻², small and closely connected to t8; M¹⁻² lacking t7 and posteroloph.

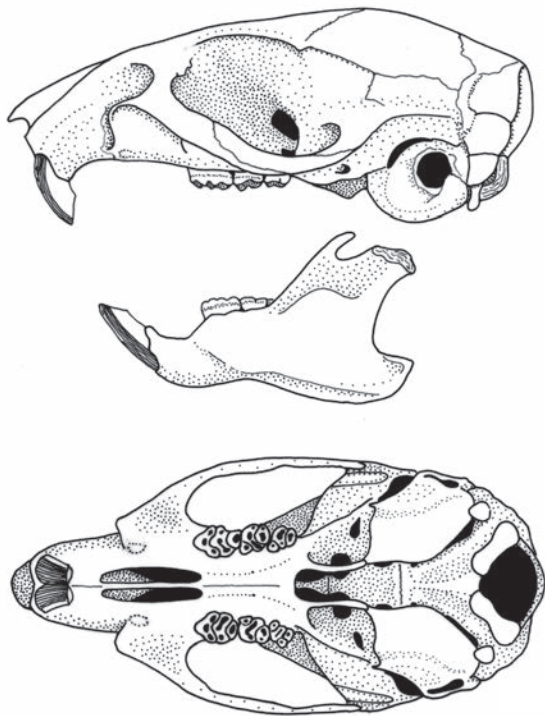


Figure 72. Skull and mandible of *Lemniscomys zebra* (HC 1322).

Anteromedian and labial cusplets variably developed on m₁₋₂, small if present; posterolophid of m₁₋₂ small, absent in some forms. Molar root formula: $\frac{5}{5}, \frac{4-5}{4}, \frac{3}{3}$. Upper incisors opisthodont and short, without grooves, enamel surface pale to medium orange (Figure 72). Grass mice are typically common where grass cover is suitably dense for nests and runways. They are recorded from natural savanna grasslands and woodlands, agricultural fields, abandoned farms and many other habitats where there is abundant grass cover. They are terrestrial and never dig burrows. Unlike many other grassland rodents, they are largely diurnal or crepuscular, and hence may be seen scampering through grasses during the daytime. When disturbed, they run quickly along little paths into the densest nearby cover. Grass mice feed principally on grass stems and seeds and, to a lesser extent, insects. The distribution and abundance of grass mice is patchy. Some species are widespread, others have very restricted distributions. In favoured habitats they may attain high population densities, but in other places, they are not common. When environmental conditions are good, grass mice are fecund, and hence population numbers increase rapidly. Population numbers oscillate greatly, especially in areas where savanna grasses are burned; after fire, when the grasses begin to sprout, recolonization occurs from unburnt grasslands nearby.

Lemniscomys is closely related to a group of genera that Misonne (1969a) informally acknowledged as the ‘*Arvicanthis* Division’. Although Misonne (1969a) affiliated certain Asian genera within this Division, subsequent studies (Musser 1987a, Ducroz *et al.* 2001) have supported its recognition as a radiation of six genera indigenous to Africa (*Arvicanthis*, *Desmomys*, *Lemniscomys*, *Mydomys*, *Pelomys*, *Rhabdomys*), and have separated Misonne’s Asian genera from the *Arvicanthis* Division. Within this clade of six genera, gene-sequence analyses portray *Lemniscomys* as the most basal lineage (Ducroz *et al.* 2001). The monophyly of the genus itself is corroborated by both morphological and molecular data (Ellerman 1941, Misonne 1969a, Ducroz *et al.* 2001). Fossils are so far recorded only from middle to late Pleistocene sites in Morocco (as *L. barbarus*, Amani & Geraads 1993), East Africa (as *L. aff. striatus*, Wesselman 1984) and DR Congo (as *L. rosalia*; Avery 1995, 1996).

| | Mid-dorsal stripe | HB mean (mm) | GLS mean (mm) | Chromosome number | Notes |
|--|---------------------------------------|--------------|---------------|-------------------|---|
| | Narrow | ca. 111 | 30.1 | 2n = 54 | Mahgreb of NE Africa; not south of the Sahara |
| | Narrow | 102 | 28.3 | 2n = 54, FN = 58 | Widespread West and East Africa; drier habitats than <i>L. striatus</i> ; not north of Sahara |
| | Well defined | 127 | 31.9 | n. d. | C Sudan only |
| | Well defined | 109 | 28.2 | 2n = 56 | Côte d'Ivoire, Ghana |
| | Obscure due to dark background colour | 99 | 27.1 | 2n = 56 | Eastern Africa |
| | Narrow | 92 | 25.9 | 2n = 56 | L. Oku, Cameroon |
| | Narrow | 116 | 28.4 | 2n = 44 | Widespread West, central and East Africa |
| | Well defined | 124 | 32.2 | n. d. | Zambia only. Rare |
| | Well defined | 107 | 27.5 | n. d. | Senegal, Côte d'Ivoire |
| | Well defined | 121 | 31.0 | n. d. | Angola, Zambia |
| | Wide | 136 | 31.9 | 2n = 54, FN = 64 | Widespread in Zambezan Woodland BZ |

No subgenera have been recognized, but the 11 species of *Lemniscomys* are divisible into three species-groups based on the pattern of their dorsal markings (see above): *griselda* species-group (*L. griselda*, *L. linulus*, *L. rosalia* and *L. roseveari*); *barbarus* species-group (*L. barbarus*, *L. hoogstraali* and *L. zebra*); and *striatus* species-group (*L. bellieri*, *L. macculus*, *L. mittendorfi* and *L. striatus*). Although these pelage-defined associations receive some support from other morphological traits (Carleton & Van der Straeten 1997) and craniodental morphometry

(Van der Straeten 1980b, Van der Straeten & Verheyen 1980), their monophyletic stature and phylogeographic relationships invite research using other information sources. Chromosome number is variable according to species, ranging from 2n = 44 to 2n = 56 (Van der Straeten & Verheyen 1978a, Gautun *et al.* 1986, Filippucci *et al.* 1986).

Michael D. Carleton

Lemniscomys barbarus BARBARY GRASS MOUSE (BARBARY LEMNISCOMYS)

Fr. Souris rayé de Barbarie; Ger. Mehrstreifen-Grasmaus

Lemniscomys barbarus (Linnaeus, 1766). Syst. Nat., 12th edn., 1. Addenda. Barbaria (= Morocco).

Taxonomy Originally described in the genus *Mus*. Species-group: *barbarus*. Most authors in the past, e.g. Rosevear (1969), Misonne (1974) and Musser & Carleton (1993), included all striped grass mice within a single species, *L. barbarus*. However, recent study has shown that the name *barbarus* should be used only for the North African representatives of the *barbarus* species-group (Carleton & Van den Straeten 1997). The North African *L. barbarus* is geographically isolated from other populations of the species-group south of the Sahara (see maps). It is likely that northern (*L. barbarus*) and southern (*L. zebra*) populations of the species-group were contiguous in the past when the Sahara was more mesic than at present. Much less is known about this species than about *L. zebra*, the most northerly of the sub-Saharan species of the genus. Synonyms: *ifniensis*. Subspecies: none. Chromosome number: 2n = 54 (Algeria; Filippucci *et al.* 1986).

Description Medium-sized grass mouse with pale lateral stripes. Dorsal pelage buffy-brown, with narrow dark mid-dorsal stripe and six or seven unbroken ochre or pale yellow stripes on each flank. Ventral pelage white. Head narrow and pointed, similar in colour to dorsal pelage. Ears large and rounded, covered with short rufous

hairs. Tail long (115% of HB), sparsely haired, dark above, pale below. Forefoot has only three functional digits. Nipples 2 + 2 = 8.

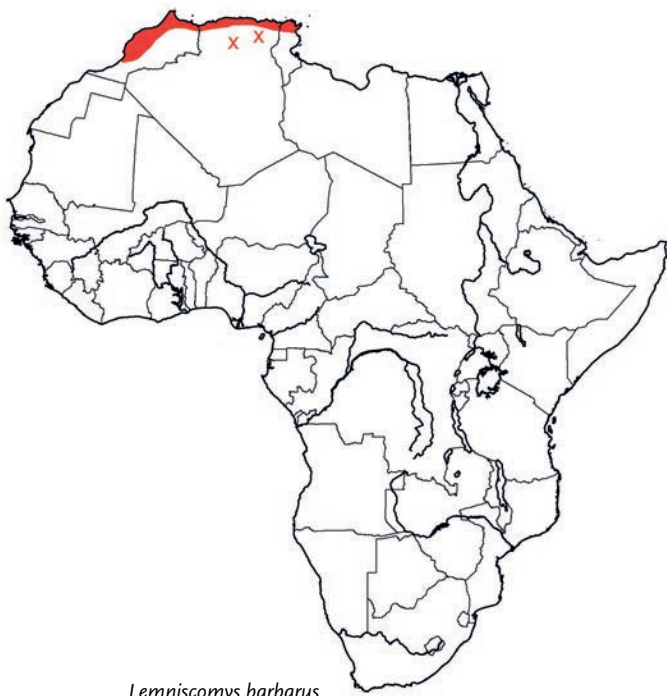
Geographic Variation None recorded.

Similar Species There are no other species of *Lemniscomys* in Africa north of the Sahara.

Distribution Endemic to Africa. Mediterranean Coastal BZ. Recorded from coastal regions (mostly north of the Atlas Mts) of Morocco, Algeria and Tunisia.

Habitat Bushes and grassy habitats along the coastal zone, where ground cover is dense. In Tunisia, also found in fields of lucerne, tomatoes and artichokes (Bernard 1969). Not recorded in the Haut Atlas or Saharan Atlas mountains (Aulagnier & Thévenot 1986, Kowalski & Rzebik-Kowalska 1991).

Abundance Mostly uncommon or rare even in preferred habitats, although densities may be high when conditions are suitable. In



Morocco, populations large in some years, very small in others (Brosset 1960).

Adaptations Terrestrial. Burrows are complex with 2–3 chambers, and are excavated under bushes and where food is available (e.g. in cultivated fields) (Lamine Cheniti & Sani 1989). Individuals in captivity were most active before and during sunset, and in the early morning after sunrise; a third lesser peak of activity occurred in the middle of the night. In cold weather, activity declined, especially at night (Lenkiewicz & Saint Girons 1964).

Foraging and Food Probably herbivorous (or omnivorous). These grass mice eat many sorts of food, often feeding close to the burrows;

may also feed on crops. Leaves of *Asphodelus microcarpus* (which have a high water content) found in burrows during dry season (Lamine Cheniti & Sani 1989).

Social and Reproductive Behaviour No information.

Reproduction and Population Structure Pregnant ♀♀ found in Tunisia in May, Jun and Sep; ♂♂ and ♀♀ not in reproductive condition during Nov–Jan. Adult ♂♂ reproductively active all year in Tunisia. Embryo number: 7.5 (3–11; Tunisia; Bernard 1969).

Predators, Parasites and Diseases Owls prey on striped grass mice in Algeria (Kowalski & Rzebik-Kowalska 1991).

Conservation IUCN Category: Least Concern.

These mice live in areas that have large human populations. Destruction of natural grassy habitats may be a threat to their survival.

Measurements

Lemniscomys barbarus

TL: 238 (211–266) mm, n = 37

T: 127 (110–145) mm, n = 37

HF: 27.1 (24–29) mm, n = 37

E: 15.2 (14–16) mm, n = 7

WT: 49 (28–56) g, n = 44

GLS: 30.1 (28.3–32.2) mm, n = 44

GWS: 14.2 (13.6–25.1) mm, n = 43

M¹–M³: 5.6 (5.2–6.0) mm, n = 44

Agadir Province, Morocco (Carleton & Van der Straeten 1997)

Ear measurement: Kowalski & Rzebik-Kowalska 1991

Key References Aulagnier & Thévenot 1986; Carleton & Van der Straeten 1997; Kowalski & Rzebik-Kowalska 1991.

D. C. D. Happold

Lemniscomys bellieri BELLIER'S GRASS MOUSE (BELLIER'S LEMNISCOMYS)

Fr. Souris rayée de Bellier; Ger. Belliers Grasmaus

Lemniscomys bellieri Van der Straeten, 1975. Rev. Zool. Afr. 89: 906. Ayeremou (= Lamto), Côte d'Ivoire.

Taxonomy Species-group: *striatus*. Related to *L. macculus*. Earlier studies included this species within *L. striatus*. Synonyms: none. Chromosome number: 2n = 56 (Van der Straeten 1975b).

Description Small grass mouse with well-defined black mid-dorsal stripe. Dorsal pelage yellowish-brown tending to grey on flanks; hairs grey at base. Eight lateral stripes on each flank broken into spots, pale buffy, and often not well differentiated from background colour. Only the spots of the 3rd, 4th and 5th stripes are arranged in well-defined lines. In extreme cases, the dorsal region has a close resemblance to that of *L. linulus*. Ventral pelage pure white, rarely washed with buff. Fore- and hindfeet washed with buff. Tail long (ca. 100% of HB), bicoloured, dark brown above, nearly white below. Nipples 2 + 2 = 8.

Geographic Variation None recorded.

Similar Species

L. linulus. Lateral stripes absent; may be sympatric.

L. striatus. Larger; lower lateral stripes broken into spots; sympatric.

L. macculus. Same body measurements but with different pattern of stripes; eastern Africa only.

L. zebra. All stripes continuous; paler; sympatric.

Distribution Endemic to Africa. Guinea Savanna BZ and Northern Rainforest–Savanna Mosaic. Recorded only west of the Dahomey Gap from Côte d'Ivoire and Ghana. One record from Guinea. May occur in Sierra Leone (Grubb *et al.* 1998). Probably more widely distributed than records indicate (Van der Straeten 1975a).



Habitat Grasslands, especially where *Isobertina doka* and *I. danielli* trees are common. In the Rainforest–Savanna Mosaic found in savanna

habitats, whereas *L. striatus* occurs closer to the forest edge (Van der Straeten 1975a).

Abundance No information.

Remarks Apparently no other information available.

Conservation IUCN Category: Least Concern.

Measurements

Lemniscomys bellieri

HB: 109 (91–127) mm, n = 251

T: 112 (94–134) mm, n = 251

HF: 25.4 (23–27) mm, n = 251

E: 15.9 (13–19) mm, n = 251

WT: 36 (26–46) g, n = 59

GLS: 28.2 (24.3–31.3) mm, n = 251

GWS: 12.8 (11.2–14.4) mm, n = 251

M¹–M³: 5.1 (4.6–5.7) mm, n = 251

Côte d'Ivoire (Van der Straeten 1975a)

Key Reference Van der Straeten 1975b.

Erik Van der Straeten

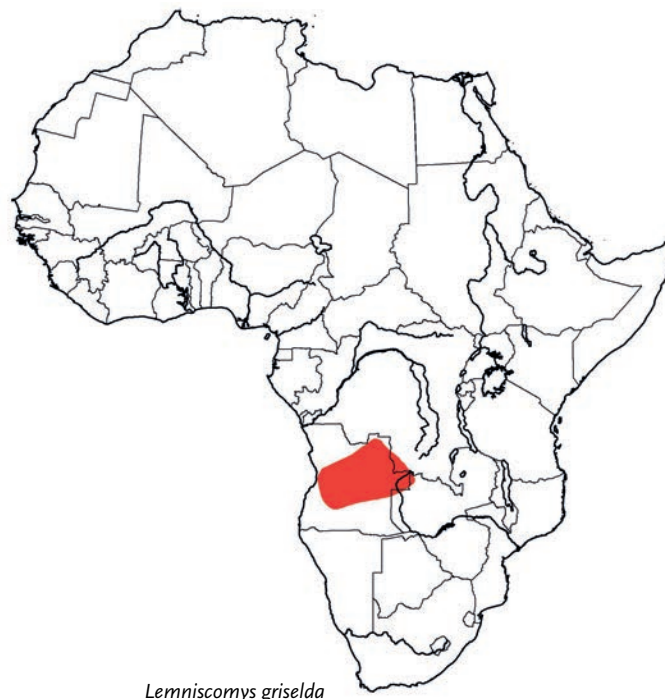
Lemniscomys griselda **GRISELDA'S GRASS MOUSE (GRISELDA'S LEMNISCOMYS)**

Fr. Souris rayée de Griselda; Ger. Griselda-Grasmaus

Lemniscomys griselda (Thomas, 1904). Ann. Mag. Nat. Hist., ser. 7, 13: 414. Muene Coshi, Angola.

Taxonomy Described as *Arvicanthis dorsalis griselda* (Thomas 1904c). Species-group: *griselda*. Formerly considered the nominate form of a polytypic species occurring in southern and eastern Africa. This species, *L. rosalia* and *L. roseveari* are morphometrically similar with considerable inter-species overlap in characters, and none have longitudinal lateral stripes. Van der Straeten (1980a) considered the nominate *griselda* to be a distinct species restricted to Angola, and separate from *L. rosalia* and *L. roseveari*. Ansell (1978) assigned specimens from NW Zambia to the nominate *L. griselda* and mentioned the possibility of intergradation with subspecies of *L. rosalia*. The *griselda* species-group (i.e. *L. griselda*, *L. linulus*, *L. rosalia* and *L. roseveari*) is in need of revision (Crawford-Cabral 1998, Musser & Carleton 2005). Synonyms: none. Chromosome number: not known.

Description Medium-sized grass mouse with coarse pelage and a single dark mid-dorsal stripe (similar to *L. rosalia*). Dorsal pelage pale grey-brown. Black mid-dorsal stripe extends along spine from neck to base of tail. Flanks slightly paler than dorsal pelage. No longitudinal lateral stripes on flanks. Ventral pelage white. Head with blunt nose and long vibrissae. Muzzle pale yellow. Ears medium-sized. Yellowish eye-ring present. Limbs medium-sized, same colour as flanks. Forefeet with three functional digits, Digits 1 and 5 greatly reduced. Hindfeet with three elongated digits, Digits 1 and 5 shorter. Tail long (ca. 100% of HB), dark with sparse short hairs.



Geographic Variation None recorded.

Similar Species

Lemniscomys rosalia. Very similar, no lateral stripes on flanks; greater suffusion of buff on dorsal pelage and flanks; allopatric and widespread.

L. roseveari. No lateral stripes; probably parapatric.

L. striatus. Well-defined lateral stripes on flanks.

Distribution Endemic to Africa. Zambezan Woodland BZ. Recorded from Angola and Zambia. Widespread on the Angolan plateau (Crawford-Cabral 1998), extending into NW Zambia (Ansell 1978).

Habitat No information.

Abundance Reported to be very common in Angola (Monard 1935). Considering the large number of localities from which museum specimens have been collected (Crawford-Cabral 1998), this species is probably not uncommon on the Angolan plateau.

Remarks Apparently no other information available.

Conservation IUCN Category: Least Concern.

Measurements

Lemniscomys griselda

HB: 121 mm, n = 1

T: 135 mm, n = 1

HF: 28 mm, n = 1

E: 14 mm, n = 1

WT: n. d.

GLS: 31.0 mm, n = 1

GWS: 12.5 mm, n = 1

M¹–M³: 6.1 mm, n = 1

Angola (Thomas 1904c)

Key References Crawford-Cabral 1998; Van der Straeten 1980a.

A. Monadjem

Lemniscomys hoogstraali HOOGSTRAAL'S GRASS MOUSE (HOOGSTRAAL'S LEMNISCOMYS)

Fr. Souris rayée de Hoogstraal; Ger. Hoogstraals Grasmaus

Lemniscomys hoogstraali Dieterlen, 1991. Bonn. Zool. Beitr. 42: 11. 12 miles N of Niayok, Paloich, Upper Nile Province, Sudan.

Taxonomy Known only from a single old adult male specimen. Species-group: *barbarus*. Status of this species is uncertain because the single specimen is imperfect (Musser & Carleton 2005). Synonyms: none. Chromosome number: not known.

Description Small grass mouse, similar to but larger than *L. zebra*; one of the darkest of *Lemniscomys* spp. (together with *L. mittendorfi*). Mid-dorsal black stripe. Flanks very dark with five wide white unbroken lateral stripes on each flank, narrow anteriorly near head, wider posteriorly on rump. Four small narrow white stripes, often broken into small spots and streaks, on each flank in between the wide unbroken stripes. The wide white lateral stripes on the black background are extremely marked, giving a very 'zebra-like' effect (more so than in *L. barbarus* and *L. zebra*). Ventral pelage almost pure white, without any cinnamon or yellowish border between colour of dorsal pelage and ventral pelage. Ears rounded, covered with short rusty-brown hairs, and rusty-brown hairs at base. Fore- and hindfeet whitish. Tail long (ca. 100% of HB; tail tip missing), bicoloured, with short bristles, black above, pale below. Skull larger than in *L. zebra*; anterior palatal foramina ending anteriorly to M¹. Nipples: not known.

Geographic Variation None recorded.

Similar Species

Lemniscomys zebra. Smaller body and skull (especially HF), fewer narrower longitudinal stripes; yellowish border between dorsal and ventral pelage, fore- and hindfeet yellowish or cream.

L. striatus. Lateral stripes broken into spots and streaks.

Distribution Recorded only from the type locality, east of the Nile R. and north of Malakal, EC Sudan.

Habitat Forested grassland with *Acacia mellifera* and *Balanites aegyptiaca* trees.

Abundance Very rare. Only a single specimen was obtained amongst ca. 100 small rodents (mainly *Mastomys* sp., *Acomys cinereus* and *Arvicanthis niloticus*) collected near the type locality. Another single specimen of *L. zebra* was collected nearby.



Lemniscomys hoogstraali

Remarks Apparently no other information available.

Conservation IUCN Category: Data Deficient.

Measurements

Lemniscomys hoogstraali

HB: 127 mm, n = 1

T: 128 mm, n = 1

HF (c.u): 28 mm, n = 1

E: 16 mm, n = 1

WT: n. d.

GLS: 31.9 mm, n = 1

GWS: n. d.*

M¹–M³: 5.4 mm, n = 1

Holotype, Sudan (Dieterlen 1991)

*Width of braincase: 13.1 mm, n = 1

Key References Carleton & Van der Straeten 1997; Dieterlen 1991.

Fritz Dieterlen

Lemniscomys linulus SENEGAL GRASS MOUSE (SENEGAL LEMNISCOMYS)

Fr. Souris rayée de Senegal; Ger. Senegal-Grasmaus

Lemniscomys linulus (Thomas, 1910). Ann. Mag. Nat. Hist., ser. 8, 6: 429. Gamon, French Gambia (= Senegal).

Taxonomy Originally described in the genus *Arvicanthis*. Species-group: *griselda*. Originally described as a species but Allen (1939) treated it as a subspecies of *L. griselda*. Re-instated as a valid species by Van der Straeten (1980b). Synonyms: none. Chromosome number: not known.

Description Small grass mouse. Dorsal pelage buffy-grey becoming more ochraceous posteriorly. Well-defined black mid-dorsal stripe. Many faint lateral stripes of very small pale spots, not well defined (and barely visible) in some individuals; hairs with pale tips where forming small spots. Spots obscure in museum specimens (so appearance is similar to *L. griselda*). Ventral pelage pure white with buff line separating colour of flanks and ventral pelage. Fore- and hindfeet with buff hairs. Tail long (ca. 105–110% of HB), dark above, ochraceous laterally and buff below. Nipples 2 + 2 = 8.

Geographic Variation None recorded.

Similar Species

L. striatus. Well-defined lateral stripes on flanks, mostly broken into spots.

L. zebra. Well-defined lateral stripes on flanks, not broken into spots.

Distribution Endemic to Africa. Guinea and Sudan Savanna BZs of West Africa west of the Dahomey Gap. Recorded from Côte d'Ivoire, Senegal and Mali (L. Granjon unpubl.). May have a more extensive distribution from Gambia to Ghana (Grubb *et al.* 1998).

Habitat Agricultural land, bush and grass (specimen labels) and dry woodland savanna (Bellier & Gautun 1967). Co-exists with *L. striatus* and *L. zebra* in some localities.

Abundance Rather common. In NE Côte d'Ivoire, five times as many specimens of this species were captured compared to other *Lemniscomys* (*L. zebra* and *L. striatus*) (Bellier & Gautun 1967).

Remarks Apparently no other information available.

Conservation IUCN Category: Least Concern.



Lemniscomys linulus

Measurements

Lemniscomys linulus

HB: 107 (93–126) mm, n = 170

T: 111 (85(?)–136) mm, n = 149

HF: 26 (23–28) mm, n = 169

E: 16.5 (14–18) mm, n = 165

WT: 27 (23–33) g, n = 3

GLS: 27.5 (25.2–31.4) mm, n = 145

GWS: 12.7 (11.9–14.3) mm, n = 160

M¹–M³: 5.4 (4.7–5.9) mm, n = 170

Côte d'Ivoire and Senegal (after Van der Straeten 1980b)

Key References Bellier & Gautun 1967; Van der Straeten 1980b.

Erik Van der Straeten

Lemniscomys macculus BUFFOON GRASS MOUSE (BUFFOON LEMNISCOMYS)

Fr. Souris rayée tachetée; Ger. Tüpfelgrasmaus

Lemniscomys macculus (Thomas & Wroughton, 1910). Trans. Zool. Soc. Lond. 19: 515. Mokia, SE Rwenzori, Uganda.

Taxonomy Originally described in the genus *Arvicanthis*. Species-group: *striatus*. Considered to be a valid species and not a small form of the larger *L. striatus* (Van de Straeten & Verheyen 1979a). Probably closely related to *L. bellieri*. Often confused with *L. striatus*, with which it is sympatric in Kenya and Ethiopia (Musser & Carleton 2005). Synonyms: *akka*. Subspecies: none. Chromosome number: $2n = 56$, $FN = 60$ (Ethiopia; Bulatova *et al.* 2002).

Description Small grass mouse, second smallest of all the grass mice, very similar morphologically to *L. striatus*. Dorsal pelage dark brown, mostly so dark that the mid-dorsal line is nearly inconspicuous. Seven (sometimes six or eight) pale (never white) longitudinal lateral stripes on each flank; upper stripes broken into irregular spots or streaks, lower stripes (from the 4th downwards) tend to be continuous. Ventral pelage white. Hindfeet small. Fore- and hindfeet white or whitish-yellow. Tail very long (ca. 110–120% of HB), bicoloured, upper surface brownish-black, lower surface paler. Nipples: $2 + 2 = 8$.

Geographic Variation None recorded.

Similar Species

L. striatus. Body and skull on average larger (HB: 116 [107–123] mm, HF: 25 [2–27] mm, GLS: 28.4 [26.1–30.9] mm); weight on average heavier (41 [31–48] g).

Distribution Endemic to Africa. Guinea Savanna BZ and Northern and Eastern Rainforest–Savanna Mosaic in eastern Africa.

*Lemniscomys macculus*

Recorded from NE DR Congo, Uganda, SE Sudan, N Kenya and SW Ethiopia. Possibly also occurs in Rwanda, Burundi and N Tanzania (E. Van der Straeten pers. comm.). Limits uncertain.

Habitat Dry river beds, open grasslands with *Acacia* and *Euphorbia candelabra* and, rarely, in dense grasslands (H. Rupp unpubl., Verheyen & Verschuren 1966). In SE Sudan, occurs in regions where annual rainfall is 800–1200 mm. Also occurs on rocky outcrops (Verheyen & Verschuren 1966). Unlike *L. striatus*, not found in cultivated areas.

Abundance Uncertain. In habitats in Uganda where *L. macculus* and *L. striatus* were sympatric (and sometimes syntopic), *L. macculus* was the least numerous of the two species (Verheyen & Verschuren 1966, Delany 1975).

Adaptations Terrestrial and partly diurnal. Constructs small underground burrows. Nests may be constructed on the surface of the ground, in burrows, or in natural holes, which are sometimes shared with the toad *Bufo regularis* (Verheyen & Verschuren 1966).

Foraging and Food Stomach contents consisted entirely of grasses (Verheyen & Verschuren 1966).

Social and Reproductive Behaviour No information.

Reproduction and Population Structure Pregnancies recorded in wet season in Sudan ($n = 5$ ♀♀). Embryo number: 6.0 (5–7). Pregnancies not recorded during dry season (H. Rupp unpubl.). Litter-size larger than in *L. striatus*, perhaps an adaptation to the drier environmental conditions and shorter period of reproduction.

Predators, Parasites and Diseases No information.

Conservation IUCN Category: Least Concern.

Measurements

Lemniscomys macculus

HB: 99.2 (81–118) mm, $n = 45$

T: 109.0 (70–150) mm, $n = 41$

HF: 22.6 (19.8–25.5) mm, $n = 55$

E: 14.6 (10–20) mm, $n = 45$

WT: 28, 28, 35 g, $n = 3$

GLS: 27.1 (25–29) mm, $n = 55$

GWS: 12.7 (11.6–13.7) mm, $n = 53$

M^1 – M^3 : 5.0 (4.6–5.7) mm, $n = 64$

Mostly Uganda and DR Congo (Van der Straeten & Verheyen 1979a)

Weight: Delany 1975

Key Reference Van der Straeten & Verheyen 1979a.

Fritz Dieterlen

***Lemniscomys mittendorfi* MITTENDORF'S GRASS MOUSE (MITTENDORF'S LEMNISCOMYS)**

Fr. Souris rayée de Mittendorf (Souris rayée du Lac Oku); Ger. Mittendorfs Grasmaus

Lemniscomys mittendorfi Eisentraut, 1968. Bonn. Zool. Beitr. 19: 7. L. Oku, Cameroon.

Taxonomy Species-group *striatus*. Shows morphometric affinities with *L. macculus* and *L. bellieri* (Van der Straeten & Verheyen 1980). Synonyms: none. Chromosome number: $2n = 56$, $FN = 66-72$ (Fülling 1992).

Description Small striped grass mouse with a striking dark-brown coloured pelage. One of the darkest of *Lemniscomys* spp. (together with *L. hoogstraali*). Dorsal pelage dark brown, with a small black mid-dorsal stripe; flanks greyish. Eight pale-spotted lateral stripes; top three stripes with clearly visible spots, lower stripes tend to be continuous without spots. Ventral pelage grey; hairs grey at base, white on terminal half but tending to brownish-yellow on chest. Eye-ring and nasal region buff. Fore- and hindfeet buff, sparsely haired. Tail long (ca. 86% of HB), bicoloured, thickly clothed with short hairs in the middle section, black above, whitish-buff below. Nipples: not known.

Geographic Variation None recorded.

Similar Species

L. macculus. Similar body size; tail on average longer (and relatively longer); ventral pelage pure white; longitudinal stripes similar to *L. mittendorfi*; East Africa and NE DR Congo.

L. bellieri. Similar size; ventral pelage pure white; faint pattern of pale lateral stripes; west of Dahomey Gap.

L. striatus. Larger; less dark; does not occur on Mt Oku, although widespread in surrounding regions.

Distribution Endemic to Africa. Afromontane–Afroalpine BZ. Known only from the type locality in Cameroon.

Habitat Afroalpine grass savanna with bushes above the montane forest zone on Mt Oku (ca. 2300 m).

Abundance Rare; known from only ten specimens.

Remarks Apparently no other information available.

Conservation IUCN Category: Vulnerable.
Geographic distribution very restricted.

*Lemniscomys mittendorfi***Measurements***Lemniscomys mittendorfi*HB: 92 (85–98) mm, $n = 5$ T: 79 (75–85) mm, $n = 5$ HF: 20.6 (19–22) mm, $n = 5$ E: 14.2 (13–15) mm, $n = 5$ WT: 28 (22–34) g, $n = 4$ GLS: 25.9 (24.9–26.9) mm, $n = 4$ GWS: 12.7 (12.0–13.3) mm, $n = 5$ M^1-M^3 : 5.1 (4.9–5.2) mm, $n = 5$

Mt Oku, Cameroon (ZFMK)

Key Reference Van der Straeten & Verheyen 1980.**Erik Van der Straeten*****Lemniscomys rosalia* SINGLE-STRIPED GRASS MOUSE (SINGLE-STRIPED LEMNISCOMYS)**

Fr. Rat rayée de Rosalie; Ger. Einsstreifen-Grasmaus

Lemniscomys rosalia (Thomas, 1904). Ann. Mag. Nat. Hist., ser. 7, 13: 414. Monda, Tanzania.

Taxonomy Originally described in the genus *Arvicanthis*. Species-group: *griselda*. Formerly known as *Lemniscomys griselda*, but now considered to be a different species, *L. rosalia* (Van der Straeten 1980a) and closely related to *L. griselda* and *L. roseveari*. See also *Lemniscomys griselda*. Synonyms: *calidior*, *dorsalis*, *fitzsimonsi*,

maculosus, *mearnsi*, *phaeotis*, *sabiensis*, *sabulatus*, *spinalis*, *zuluensis*. Subspecies: five recognized by Meester *et al.* (1986), but they are of dubious value and not recognized here. Chromosome number: $2n = 54$, $FN = 64$ (NE Tanzania; Fadda *et al.* 2001).

Description Medium-sized grass mouse with coarse pelage, without lateral stripes. Dorsal pelage variable shades of pale orange-brown grizzled with dark brown; dorsal hairs grey at base, orange-brown or brown at tip. Black mid-dorsal stripe extends from neck to base of tail. Colour of rump usually rich buffy. Flanks slightly paler than dorsal pelage. No lateral stripes on flanks. Ventral pelage white to off-white; hairs white. Head with blunt nose and long vibrissae. Muzzle same colour as dorsal pelage. Ears medium-sized, buffy. Yellowish-orange eye-ring often conspicuous. Limbs medium-sized, same colour as flanks. Forefeet with three functional digits; Digits 1 and 5 greatly reduced. Hindfeet with three elongated digits. Digits 1 and 5 shorter. Tail long (ca. 100% of HB), dark above, pale below. Nipples: $2 + 2 = 8$.

Geographic Variation Individuals from arid western regions of southern Africa are noticeably paler than individuals from the mesic east. This difference, however, appears to be clinal rather than discrete.

Similar Species

- L. griselda* and *L. roseveari*. Lateral stripes absent or very faint; allopatric.
- L. macculus*. Smaller; many lateral stripes; maybe parapatric in East Africa.
- L. striatus*. Many lateral stripes, some broken into spots; maybe parapatric in East Africa.
- L. zebra*. Many lateral stripes, all continuous (not broken into spots); maybe parapatric in East Africa.

Distribution Endemic to Africa. Zambezan Woodland BZ and southern part of Somalia–Masai Bushland BZ. Recorded from E and N South Africa, E Swaziland, Zimbabwe, Mozambique, Malawi, N Botswana, N Namibia (De Graaff 1981), S Angola (Crawford-Cabral 1998) and Zambia (Ansell 1978). A separate population occurs in Tanzania and S Kenya (Swynnerton & Hayman 1950).



Lemniscomys rosalia

Habitat Tolerates a wide range of savanna habitats, but tall, dense grass is essential. Vacates recently burnt areas (Korn 1981, Swanepoel 1981, Bowland & Perrin 1988) but may return after grass has recovered (Monadjem & Perrin 1997). Often occurs in agricultural landscapes, especially fallow fields. Not recorded from montane grasslands and forests (Monadjem 1999a).

Abundance Very varied; common to very common in suitable habitats, but often rare or absent in some parts of its range. In Swaziland, replaces *Mastomys natalensis* as the numerically dominant species in tall *Hyperthelia*–*Hyparrhenia* grasslands about one year after a fire. Density reaches 15/ha under natural conditions, but higher where supplementary food is available (Monadjem & Perrin 1997). In other parts of range, abundance is varied: e.g. in S Malawi comprised 1% ($n = 222$ small rodents; 9 spp.) in thicket-clump savanna during one year, and present in only six out of nine trapping periods (Happold & Happold 1991); in Mozambique, comprised 0% in Oct, Jan and Apr, and ca. 8% in Jul (Gliwicz 1985); and in Zimbabwe, 0% in miombo, mopane and thicket habitats during the course of one year (1992–93), although known to be present in small numbers in miombo and mopane woodland in a previous year during the cool dry season (Linzey & Kesner 1997a).

Adaptations Terrestrial and predominantly crepuscular (A. Monadjem unpubl.). Builds untidy nests of grass, which are placed on the ground, usually at the base of a clump of grass.

Foraging and Food Herbivorous tending toward granivorous. In Swaziland, diet was 85% vegetable material and 15% seeds ($n = 9$ stomachs; Swaziland; Monadjem 1997b).

Social and Reproductive Behaviour Home-ranges of individuals appear not to overlap. Individuals kept in captivity exhibit aggression towards each other (A. Monadjem unpubl.), suggesting that individuals may defend territories. In captivity, ♂♂ share a nest with a ♀ and assist with the care of the young.

Reproduction and Population Structure Reproduction confined to the wet season. In N KwaZulu–Natal, South Africa, ♀♀ reproductively active from Sep to Dec (Swanepoel 1972); juvenile recruitment mostly in Jan–Mar (Swaziland and South Africa). Mean litter-size: 6.1 (Swaziland; Monadjem 1998a) and 6.5 (6–7, $n = 4$; KwaZulu–Natal, South Africa; Taylor 1998). Litter-sizes from 2 to 11 recorded elsewhere (Skinner & Smithers 1990). Gestation (in captivity): ca. 24 days. Birth-weight: 2.6 g. Incisors erupt Day 6–8. Young weaned Day 20 (Scott & Meester 1988). Population numbers relatively stable between seasons, except after a fire when all individuals move out of the burnt area. Individuals return to former range about three months after the fire (Monadjem & Perrin 1997). Survival rates low, and few individuals live for more than a year.

Predators, Parasites and Diseases Preyed on by Black-shouldered Kites *Elanus caeruleus* (Mendelsohn 1982), and recorded from pellets of Barn Owls *Tyto alba* in Swaziland (M. Avery, in litt.).

Conservation IUCN Category: Least Concern.

This widespread and numerous species is unlikely to become threatened in the near future.

Measurements

Lemniscomys rosalia

HB (♂ ♂): 136.8 (102–168) mm, n = 25
 HB (♀ ♀): 115.7 (85–133) mm, n = 14
 T (♂ ♂): 132.1 (98–147) mm, n = 25
 T (♀ ♀): 127.7 (81–147) mm, n = 14
 HF (♂ ♂): 26.9 (24–30) mm, n = 25
 HF (♀ ♀): 25.2 (25–30) mm, n = 12
 E (♂ ♂): 11.3 (9–16) mm, n = 10
 E (♀ ♀): 11.4 (8–16) mm, n = 5
 WT (♂ ♂): 52.5 (19–70) g, n = 25

WT (♀ ♀): 55.8 (42–74) g, n = 14
 GLS: 31.9 (27.2–34.6) mm, n = 11
 GWS: 15.2 (13.5–16.5) mm, n = 11
 M¹–M³: 5.9 (5.3–6.7) mm, n = 13
 Body measurements: Swaziland (Monadjem 1998a)
 Skull measurements: southern Africa (Roberts 1951)

Key References Monadjem & Perrin 1997; Scott & Meester 1988.

A. Monadjem

Lemniscomys roseveari ROSEVEAR'S GRASS MOUSE (ROSEVEAR'S LEMNISCOMYS)

Fr. Rat rayée de Rosevear; Ger. Rosevears Grasmaus

Lemniscomys roseveari Van der Straeten, 1980. Ann. Cape Prov. Mus. Nat. Hist. 13 (5): 55. Balovale (= Zambezi), Zambia. 1015 m.

Taxonomy Species-group: *griselda*. Closely related to *L. griselda* and *L. rosalia*. The status of this species is uncertain (Musser & Carleton 2005). See also *L. griselda*. Synonyms: none. Chromosome number: not known.

Description Medium-sized grass mouse with black mid-dorsal stripe and obscure pale lateral spots. Dorsal pelage brownish, tending to greyish anteriorly and yellow-ochre posteriorly; well-defined black mid-dorsal stripe from between the ears to rump. Flanks covered with small spots of pale-tipped buff or ochraceous-buff hairs, which are not clearly aggregated into longitudinal lines. Ventral pelage pure white, edged with a buff line. Ears, fore- and hindfeet yellow-ochre. Hindfoot longer in ♂ ♂ than in ♀ ♀. Tail long (ca. 110% of HB), dark above, ochraceous-orange or yellow-ochre laterally, white below. Upper incisors mostly with faint grooves. Nipples 2 + 2 = 8.

Geographic Variation None recorded.

Similar Species

L. rosalia. Less brownish; Angola.

L. griselda. Less brownish; southern Africa and Tanzania.

Distribution Endemic to Africa. Zambezian Woodland BZ. Recorded from two localities in Zambia: the type locality (Zambezi [= Balovale]) and Solwezi. Probably more widely distributed than present records indicate.

Habitat No information.

Abundance No information.

Remarks Apparently no other information available.

Conservation IUCN Category: Data Deficient.

Measurements

Lemniscomys roseveari

HB (♂ ♂): 124 (113–137) mm, n = 15
 HB (♀ ♀): 126 (118–137) mm, n = 11

T (♂ ♂): 137 (123–151) mm, n = 14
 T (♀ ♀): 139 (129–153) mm, n = 11
 HF (♂ ♂): 28.3 (27–30) mm, n = 15
 HF (♀ ♀): 27.2 (26–29) mm, n = 11
 E (♂ ♂): 16.4 (16–18) mm, n = 15
 E (♀ ♀): 16.2 (13–19) mm, n = 11
 GLS (♂ ♂): 32.2 (30.7–33.9) mm, n = 17
 GLS (♀ ♀): 32.2 (30.8–33.9) mm, n = 11
 GWS (♂ ♂): 15.2 (14.3–15.8) mm, n = 29
 GWS (♀ ♀): 15.3 (14.5–16.3) mm, n = 11
 M¹–M³ (♂ ♂): 6.1 (5.7–6.4) mm, n = 17
 M¹–M³ (♀ ♀): 6.1 (5.7–6.4) mm, n = 11
 Zambia (BMNH, AM)

Key Reference Van der Straeten 1980a.

Erik Van der Straeten



Lemniscomys roseveari

Lemniscomys striatus STRIATED GRASS MOUSE (STRIATED LEMNISCOMYS)

Fr. Rat rayée d'Afrique; Ger. Streifengrasmaus

Lemniscomys striatus (Linnaeus, 1758). Syst. Nat, 10th edn., 1: 62. 'India' (= Sierra Leone; see Allen 1939: 394).

Taxonomy Originally described in the genus *Mus*. Species-group: *striatus*. Synonyms: *ardens*, *dieterleni*, *fasciatus*, *luluae*, *lynsei*, *massaicus*, *micropus*, *orientalis*, *pulchella*, *pulcher*, *spermophilus*, *venustus*, *versustus*, *wroughtoni*. Subspecies: five are recognized by Van der Straeten & Verheyen (1980) (see Geographic Variation), but their status is uncertain. Recent analysis suggests that *massaicus* may be a valid species (with *dieterleni* as subspecies), and *lynsei* may also be a distinct species (E. Van der Straeten in litt.). Therefore, probably only two subspecies (*L. s. striatus* and *L. s. venustus*) are valid. Chromosome number: $2n = 44$ (Côte d'Ivoire; Van der Straeten & Verheyen 1978a).

Description Small grass mouse with black mid-dorsal stripe and lines of pale spots on back and flanks. Dorsal pelage brown often flecked with ochre. Black mid-dorsal stripe from neck to base of tail; flanks with four lines of pale yellow lateral stripes on each upper flank, each stripe broken into oblong or roundish spots. Additional spots not arranged in lines on lower flanks. Shape and clarity of spots very variable. Some individuals rufous or cinnamon on rump and base of tail. Ventral pelage white, clearly delineated from flanks. Head rather narrow and pointed, similar in colour to dorsal pelage; eye-ring and nasal region sometimes rufous. Ears large and rounded, covered with short rufous hairs. Forefoot with three functional toes. Tail long (ca. 125% of HB), dark above, pale below, sparsely haired. Nipples: $2 + 2 = 8$.

Geographic Variation Considerable variation in colour in different parts of range: individuals in and close to Rainforest BZ are darker with well-defined spots; individuals in savanna and drier habitats are paler with spots less well defined, some merging to form continuous lines. Size also varies in different parts of range. Five subspecies recognized by Van der Straeten & Verheyen (1980); subspecies distinguished by width of black mid-dorsal stripe, number and pattern of lateral stripes, and geographic location. May be distinguished by discriminate function analysis.

L. s. dieterleni: DR Congo.

L. s. striatus: West Africa (Sierra Leone to Cameroon).

L. s. lynsei: Jebel Marra, Sudan.

L. s. massaicus: Kenya, Uganda, Tanzania, N Malawi, Burundi, Rwanda, Sudan.

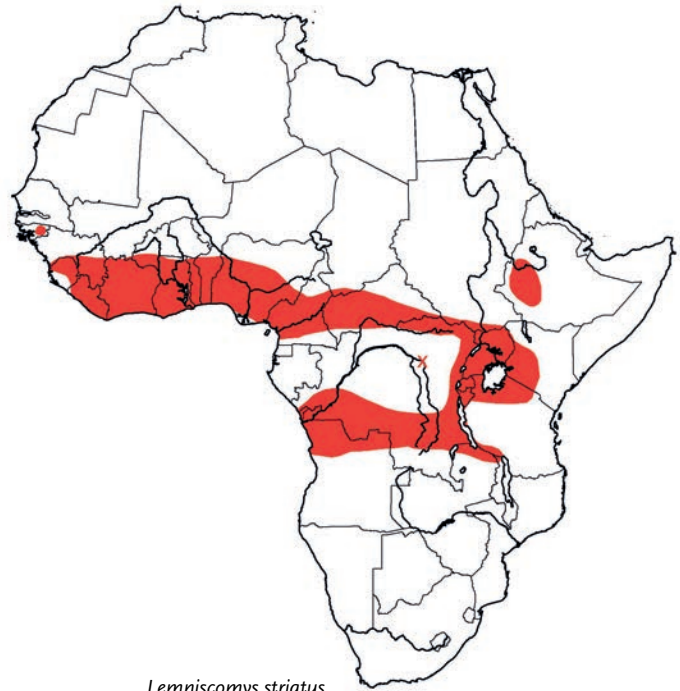
L. s. venustus: N Nigeria, N Benin (boundary Guinea and Sudan Savanna BZs); largest subspecies (HF: 26–33 mm; GLS: 28.4–34.6 mm).

Similar Species

L. zebra. Lateral stripes continuous (not broken into spots); usually paler; distribution further north but sympatric with *L. striatus* in southern parts of Guinea Savanna BZ.

L. bellieri. Upper lateral stripes broken into spots, lower stripes continuous; Côte d'Ivoire and Ghana.

L. linulus. Very well defined black mid-dorsal stripe; lateral stripes broken into spots, often obscure; Senegal and Côte d'Ivoire.



Lemniscomys striatus

L. macculus. On average smaller (HB: 99 (81–118) mm; 6–8 yellowish lateral stripes on each flank, upper stripes broken into irregular spots or streaks; partly sympatric in eastern Africa.

Distribution Endemic to Africa. The most widespread species in the genus. Guinea Savanna BZ, Rainforest–Savanna Mosaics, and northern parts of Zambezan Woodland BZ. Recorded from Sierra Leone to S Sudan and Uganda; W Kenya and N Tanzania; extreme N Malawi, NE Zambia; DR Congo and N Angola (including Cabinda). Also occurs in grassy patches in the Rainforest BZ, especially close to rainforest–savanna border. Isolated populations in C Sudan (Jebel Marra) and SW Ethiopia. Range expanding in Rainforest BZ due to human-induced environmental changes.

Habitat Dense cover of grasses or herbs in regions of moderate rainfall (1500–2000 mm/year). Found in woodland savannas, grassland savannas, rice fields, farmlands, abandoned fields and plantations (provided there is adequate grass cover). In Rainforest BZ, occurs only where there is natural or man-made grass cover, e.g. roadsides, farmlands, plantations. Not recorded from rainforest relicts in savanna. Rarely found in northern part of Guinea Savanna BZ or in Sudan Savanna BZ, where *L. zebra* occurs (see also below).

Abundance In optimal habitats, comprise the majority of small rodents, e.g. 48% (Foro-Foro, Côte d'Ivoire; Gautun 1975) and 47% (Queen Elizabeth National Park, Uganda; Cheeseman & Delany 1979). In other habitats, they are less numerous, e.g. 18% (Dabou, Côte d'Ivoire), 13% (grassbush, E DR Congo), 5% (*Pennisetum*, E DR

Congo) (Gautun 1975; Dieterlen 1967c). Many seemingly suitable habitats do not seem to contain any spotted grass mice.

The composition and structure of grasslands determine population numbers. In Queen Elizabeth N. P., Uganda, *L. striatus* occurs in all five major (unburnt) habitats. *Capparis* bush, *Themeda* and *Hyperrenia* grasslands contain higher numbers of grass mice than *Cymbopogon* and *Imperata* grasslands. In each of these habitats, grass mice form a varying proportion of the rodent fauna, from 40% in *Cymbopogon*, and *Themeda* to 27% in *Hyperrenia*. Population numbers fluctuate throughout the year in relation to reproductive activity, immigration and emigration (Neal 1970).

Burning of grasses at the beginning of the dry season also affects numbers. Immediately after burning, population numbers are reduced by 50–75% in all habitats. During the following months, numbers in burnt *Imperata* and *Themeda* grasslands gradually increase to their former levels whereas numbers decline in unburnt grasslands. In *Cymbopogon* grasslands – not a preferred habitat when unburnt – numbers increase dramatically (up to four-fold), because of rapid growth of good cover and immigration from less preferred habitats; after about ten months, numbers fall to pre-burn levels. All habitats that have been burnt contain higher populations of grass mice 3–10 months after burning than do unburnt habitats (Neal 1970, Delany 1972, Cheeseman & Delany 1979).

Seasonal changes in population parameters of grass mice in W Uganda are: density ranges from 2.6 to 16.1 individuals/ha; biomass (live trapping) from 233 to 467 g/ha in unburnt grasslands and from 374 to 1496 g/ha in burnt grasslands; net annual production from 1520 to 2804 g/ha/year (Cheeseman & Delany 1979).

Adaptations Terrestrial and crepuscular, with some activity at night prior to midnight. In unburnt grassland in Kivu, 62% of captures were during daytime (Dieterlen 1967a). Runways are made in grass and herbs; and nests are built of finely shredded grasses on the surface under dense cover. Body weight varies seasonally (usually 20% higher in wet season than dry season). Liver and body fat levels increase (especially in ♀♀) during the wet season (Field 1975) and decrease during the dry season when the fat is utilized. Increase in fat level is closely correlated with rainfall and with the quantity and quality of food. Spotted grass mice are adaptable: their populations exhibit seasonal changes in numbers (see above), they breed opportunistically, and move from one type of grassland to another as conditions dictate.

Foraging and Food Omnivorous or herbivorous. In Uganda, the most frequently eaten foods especially during the dry season were grass stems and inflorescences; seeds were eaten occasionally, but leaves were rarely eaten. During the wet season, insects (mainly termites) formed a major part of the diet (62–100% in some months). Insects formed an important source of protein during the breeding season (Field 1975). In coffee plantations in Central African Republic, from Aug to Oct, the diet was insects (up to 50%), seeds and fruits of several species (20%) and leaves (30%) (Genest-Villard 1980). In Kivu, stomachs contained 90% seeds and no insects (Dieterlen 1967a).

Social and Reproductive Behaviour Little information. Usually found singly or in pairs. Spotted grass mice have rapid flight reactions, and they appear to be 'nervous' when disturbed.

Reproduction and Population Structure Seasonal; closely related to pattern of rainfall. In Côte d'Ivoire (Gautun 1975), pregnancy rates vary seasonally: 70–100% during early wet season (Apr–Jun) and late wet season (Oct–Nov); 6–40% during mid wet season (Jul–Sep); and 0% during dry season (Dec–Mar). In Uganda (Neal 1977), where rainfall occurs in all months of the year, there are two peaks of rainfall: Mar–May and Aug–Dec. Pregnancies recorded in Apr–Jun and Sep–Dec, beginning from about one month after onset of rainfall peaks. Counts of placental scars after the two breeding seasons each year suggest 1–3 litters/♀ (one litter 16%; two litters 81%, three litters 3%; n = 37 ♀♀). Postpartum oestrus in ♀♀. Males reproductively active (increase in size of testes and seminal vesicles) in Apr–Jun and Sep–Dec. Timing and duration of reproduction related directly and indirectly to effects of rainfall (Neal 1977). Reproduction in burnt areas is slightly advanced compared to unburnt areas probably because of higher nutritive value of sprouting grass (Field 1975). Gestation: 22.6 ± 1.4 days. Mean embryo number in Côte d'Ivoire: 4.1 (first breeding season), 6.5 (second breeding season); in Uganda: 5.02 ± 0.18 (3–8), n = 58. Litter-size: 4.78 ± 0.17 (2–8 in Uganda). Embryo reabsorption: 4–50% (Côte d'Ivoire). Birth-weight: 1.6–1.8 g (in litter of five young). Body weight at maturity: 26 g (♀♀), 28 g (♂♂). Young sparsely haired at birth; pelage shows striped pattern as in adults.

Populations in Queen Elizabeth N. P., Uganda, contain individuals of most age groups in each month (age assessed on toothwear: classes I [young] to XIV [old]); proportion of each age-class changing in sequence each month due to effects of natality and mortality. Cohort born Sep–Dec forms Classes II–VI in Jan–Apr, and Classes V–VII (mature) in Apr–May. Some of these individuals are still alive in Nov (now age-classes XII–XIV, ca. 12 months old). Numbers of each cohort decline as members of the cohort increase in age. Second cohort (born Apr–Jul) form Classes II–VI in Jul–Nov and some individuals (age-class XII–XIV) are still alive in following Apr–May (Cheeseman & Delany 1979). Longevity in the wild rarely more than ca. 12 months.

Predators, Parasites and Diseases In Uganda, preyed upon by many species of birds of prey, mongooses *Herpestes ichneumon* and snakes.

Conservation IUCN Category: Least Concern.

This common, widespread and adaptable species is not threatened.

Measurements

Lemniscomys striatus

HB: 116 (107–123) mm, n = 10

T: 143 (133–152) mm, n = 10

HF: 25 (23–27) mm, n = 10

E: 16 (15–17) mm, n = 10

WT: 41.6 (31–48) g, n = 10

GLS: 28.4 (26.1–30.9) mm, n = 10

GWS: 13.5 (12.9–14.2) mm, n = 10

M¹–M³: 5.0 (4.7–5.3) mm, n = 10

Uganda (BMNH)

Key References Cheeseman & Delany 1979; Gautun 1975; Neal 1970, 1977; Van der Straeten & Verheyen 1980.

D. C. D. Happold

Lemniscomys zebra ZEBRA GRASS MOUSE (HEUGLIN'S LEMNISCOMYS)

Fr. Rat rayée zébrée; Ger. Zebragrasmaus

Lemniscomys zebra (Heuglin, 1864). Beit. Zool. Cent.-Afrika's Leopoldina 31: 10. Bahr el Ghazal, Sudan.

Taxonomy Originally described in the genus *Mus*. Species-group: *barbarus*. Previous authors, e.g. Rosevear (1969), Misonne (1974), Happold (1987) and Musser & Carleton (1993), considered *zebra* to be a synonym or subspecies of *L. barbarus*. However, Carlton & Van der Straeten (1997) showed that the striped grass mice immediately south of the Sahara should be considered as a separate species from the North African *L. barbarus*. Besides differences in the pattern of stripes, *L. zebra* has a smaller and less robust skull than *L. barbarus*. *Lemniscomys zebra*, as understood here, shows great variation in the colour and pattern of lateral stripes throughout its large range, and includes many forms, which, in the past, have had specific rank. Synonyms: *albolineatus*, *convictus*, *dunni*, *manteufeli*, *nigeriae*, *nubalis*, *olga*, *orientalis*, *oweni*, *spekei*. Subspecies: none. Chromosome number: $2n = 54$. FN = 58 (Niger; Dobigny *et al.* 2002b).

Description Small grass mouse with pale lateral stripes along flanks; the only species (with *L. barbarus*) with unbroken lateral stripes (i.e. not broken into spots or streaks). Dorsal pelage yellowish-brown or brown. Black mid-dorsal stripe from neck to base of tail. Six or seven honey-yellow or cream unbroken lateral stripes on each flank, each stripe as wide as the brownish 'background' colour. Ventral pelage white or cream. Head narrow and pointed, similar in colour to dorsal pelage. Ears large and rounded, covered with short pale rufous hairs. Tail long (ca. 110% of HB), sparsely haired, dark above, pale below. Forefoot has only three functional digits. Nipples: $2 + 2 = 8$.

Geographic Variation Considerable variation in colour in different parts of range, especially with respect to background colouration. Southern margins of Sahara: dorsal pelage yellowish-brown to pale brown with narrow dark mid-dorsal stripe and cream stripes on flanks. Guinea savanna: dorsal pelage medium brown to dark brown, well-defined black mid-dorsal stripe and cream stripes on flanks. S Sudan and East Africa: dorsal pelage dark brown or black, wide black mid-dorsal stripe, and thin cream stripes on flanks.

Similar Species

- L. barbarus*. Similar pattern of lateral stripes on back and flanks; on average larger; Morocco, Algeria and Tunisia only.
- L. striatus*. Pale lateral stripes broken into spots; moist savanna habitats including grassy areas in Rainforest BZ.
- L. bellieri*. Upper lateral stripes broken into spots, lower stripes continuous; Côte d'Ivoire and Ghana.
- L. linulus*. Well-defined black mid-dorsal stripe; spots and stripes often obscure; Senegal and Côte d'Ivoire.
- L. macculus*. 6–8 yellowish lateral stripes, upper stripes broken into irregular spots or streaks; partly sympatric in eastern Africa.

Distribution Endemic to Africa. Sahel, Sudan and Guinea BZs, and Northern and Eastern Rainforest–Savanna Mosaics; also southern part of Somalia–Masai BZ. Recorded from Senegal to C

*Lemniscomys zebra*

and S Sudan (including Jebel Marra [*dunni*]), Uganda, S Kenya and N Tanzania. Isolated populations in Niger (Damergou). Not recorded in Ethiopia although may occur close to the Sudan–Ethiopian border (Carleton & Van der Straeten 1997).

Habitat Dry grasslands and wooded grasslands in areas of low rainfall where there is good cover of grass, herbs or bushes. Prefers drier habitats than *L. striatus*. May be parapatric or sympatric with *L. striatus* in some habitats in West Africa and East Africa.

Abundance Mostly uncommon or rare, even in preferred habitats. Zebra Grass Mice formed 0.4% of all small rodents (9 spp.) at Foro-Foro, Côte d'Ivoire (Gautun & Petter 1972), and 12% in Karamoja, Uganda (Delany 1964a). Usually less abundant than *L. striatus*.

Adaptations Terrestrial, living and nesting on the surface. Zebra Grass Mice make runways through grass, and cut grass with their teeth for nests. When disturbed or frightened, they rush quickly under piles of dead grass or other dense vegetation where their striped pelage provides good camouflage. They are active mostly before and during sunset, and in the early morning after sunrise. In cold weather, activity declines especially at night. See also *L. barbarus*.

Foraging and Food No definite information, but probably herbivorous (or omnivorous) as for other species of *Lemniscomys*.

Social and Reproductive Behaviour Little information. Usually found singly or in pairs.

Reproduction and Population Structure Little information. Embryo number: 5 (n = 1; Uganda; Delany 1964a); 5 (n = 1; Togo; E. van der Straeten unpubl.).

Predators, Parasites and Diseases No information.

Conservation IUCN Category: Least Concern.

Although uncommon, this widespread species does not appear to be threatened.

Measurements

Lemniscomys zebra

HB: 102 (83–118) mm, n = 16

T: 124 (110–137) mm, n = 15
HF (c.u.): 24.5 (23–26) mm, n = 15
E: 15.1 (13–18) mm, n = 16
WT: 36.1 (24–49) g, n = 16
GLS: 28.3 (26.6–29.5) mm, n = 16
GWS: 13.2 (12.0–14.0) mm, n = 16
M¹–M³: 5.1 (4.8–5.4) mm, n = 18
S Sudan (SMNS)

Key References Carleton & Van der Straeten 1997; Rosevear 1969.

D. C. D. Happold & Fritz Dieterlen

GENUS *Malacomys* Swamp Rats

Malacomys Milne-Edwards, 1877. Bull. Sci. Soc. Philom. Paris, ser. 6, 12: 10. Type species: *Malacomys longipes* Milne-Edwards, 1877.



Malacomys longipes.

The genus *Malacomys* is endemic to Africa and contains three species, which live in rainforest habitats in West and central Africa. The genus is characterized by relatively large size, large naked ears, long vibrissae, elongated muzzle (more so than in most other small rodents) and long hindlimbs. Dorsal pelage is brown or very dark grey, soft and dense, and with a velvet-like texture. Ventral pelage is white or greyish-white, also short and velvet-like. Limbs are long, especially the hindfoot, which has loose-knit metatarsals that allow the digits to splay outwards. Hindfoot with five plantar pads (cf. *Praomys*). The skull is long and narrow, especially in the nasal region; posterior limit of anterior palatal foramina well anterior to M¹ (cf. *Praomys*), cheekteeth small and cuspidate; and t3 on M² small or absent (cf. *Praomys* where t3 is always present) (Figure 73). The common names – Long-footed Rats or Swamp Rats – refer to the relatively long hindfoot (longer than for other species of equivalent size, except for the semi-aquatic *Colomys*, *Deomys* and *Nilopegamys*) and the preference of these species for moist damp environments

Species in this genus are mostly terrestrial, and live in primary and secondary forest in the Rainforest BZ. They are usually (but not always) commonest near streams, in moist habitats on the lower slopes of valleys or in swampy areas of rainforests. When walking, especially on soft and water-logged soil, the body is lifted high off the ground

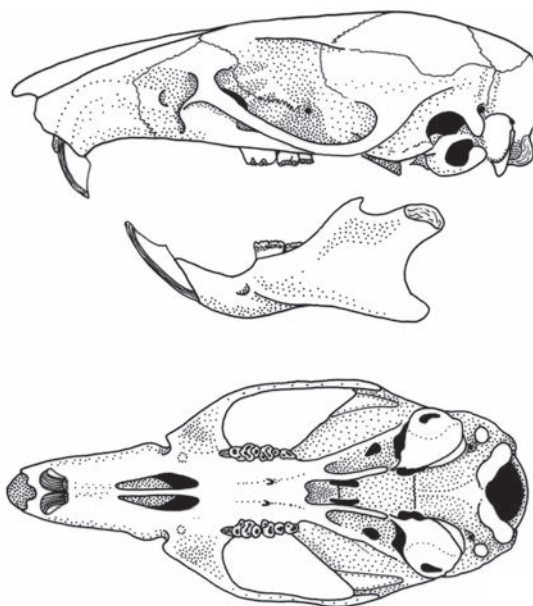


Figure 73. Skull and mandible of *Malacomys edwardsi* (HC 1354).

and the toes of the hindfeet are splayed to provide extra support. The diet is omnivorous, and includes slugs and earthworms. In body form and ecology (especially affinity for moist environments close to water), the genus shows similarities to *Colomys* and *Nilopegamys*. Abundance varies according to the species and location, contributing 7–23% of small terrestrial rodents in some localities.

The relationship of *Malacomys* to other genera is uncertain. Although previously considered to be distantly related to other genera (Misonne 1974), DNA hybridization shows a relationship to the *Praomys* group (i.e. *Praomys*, *Hylomyscus*, *Mastomys*, *Myomyscus* [= *Myomys*]) and to the *Mus* group (Chevret 1994). However, cladistic analysis suggests that the relationship with the *Praomys* group is not so close (Lecompte *et al.* 2002b). Two species formerly allocated to the genus *Malacomys* are currently in the genus *Praomys* (*P. lukolelae* and *P. verschurenii*), thus strongly suggesting a close relationship

between these two genera (see Rautenbach & Schlitter 1978, Van der Straeten & Verheyen 1979b, Musser & Carleton 1993, 2005). There is some evidence that *P. verschureni* and *P. lukolelae* may even represent a separate genus (E. van der Straeten pers. comm.).

The three species are distinguished by body size, length of hindfoot and geographic distribution.

D. C. D. Happold

***Malacomys cansdalei* CANSDALE'S SWAMP RAT (CANSDALE'S MALACOMYS)**

Fr. Rat palustre de Cansdale; Ger. Cansdales Sumpfratte

Malacomys cansdalei Ansell, 1958. Ann. Mag. Nat. Hist., ser. 13, 1: 342. Oda, Ghana.

Taxonomy This very long-footed rat from West Africa was described as a subspecies of *M. longipes* (Ansell 1958), and considered to be the western representative of *Malacomys longipes* of central Africa (Rautenbach & Schlitter 1978). Now considered to be a valid species (Van der Straeten & Verheyen 1979b, Grubb *et al.* 1998). Synonyms: *giganteus*. Subspecies: none. Chromosome number: not known.

Description Medium-sized long-footed rat, slimly built with large ears, long hindfeet and very long tail, similar in general dimensions to *M. edwardsi*. Pelage soft, dense and short, with a velvet-like texture. Dorsal pelage cinnamon; basal half of dorsal hairs medium grey, terminal half cinnamon; paler than in other species in the genus. Ventral pelage mostly white; ventral hairs white, pale grey at base; grey colouration visible on some parts of ventral pelage. Chin, chest and throat white. Head slender and muzzle elongated; vibrissae long; eyes large; ears elongated, rounded at tips, hairless, deeply pigmented, and very mobile. Tail very long (ca. 136% of HB), thin, almost hairless, dark above, pale below. Nipples 1 + 2 = 6.

Geographic Variation None recorded.

Similar Species

M. edwardsi. HF shorter (34 mm or less); nipples 0 + 2 = 4; sympatric in Ghana and further west.

M. longipes. Very similar in size; east of Niger R. only; allopatric.

Praomys tullbergi. Smaller body size; HF and T shorter; sympatric and syntopic at some localities.

Distribution Endemic to Africa. Rainforest BZ (Western Region only). Recorded only from Ghana, Côte d'Ivoire and E Liberia. Sympatric with *M. edwardsi* throughout its range.

Habitat Rainforest habitats, especially close to streams and in valley bottoms, on lower slopes of the forests, sand banks at the edge of water, and on mud (Cole 1975). Not recorded from cultivated areas in Rainforest BZ. Prefers moister swampier habitats than *M. edwardsi*.

Abundance In Ghana, individuals comprised 7% of the terrestrial rodents in rainforests (Cole 1975, as *M. longipes*). Studies in Ghana and Côte d'Ivoire suggest this species is less abundant than *M. edwardsi*.

Remarks Terrestrial and nocturnal, probably with similar adaptations as other species of *Malacomys*. In Ghana, captive individuals paddled in water, and sometimes defecated in water. Omnivorous. Forages on lower slopes of rainforest, usually in a different part of the rainforest to *M. edwardsi* (Cole 1975). In Ghana,



Malacomys cansdalei

diet was mainly vegetable material, earthworms and slugs, and was similar in most respects to that of *M. edwardsi*. The holotype (collected in early February) contained four embryos (Ansell 1958).

Conservation IUCN Category: Least Concern.

Lives primarily in rainforest, and hence destruction of rainforest habitats will reduce the geographic range and population numbers.

Measurements

Malacomys cansdalei

HB: 144 (133–162) mm, n = 17

T: 196 (178–208) mm, n = 16

HF (c.u.): 42.7 (40–44) mm, n = 17

E: 28.2 (27–31) mm, n = 15

WT: 81.7 (63–101) g, n = 14

GLS: 40.2 (39.1–42.2) mm, n = 11

GWS: 16.7 (15.4–17.8) mm, n = 14

M¹–M³: 5.6 (5.3–5.9) mm, n = 18

Ghana (Cole 1972)

Key References Cole 1972, 1975.

D. C. D. Happold

Malacomys edwardsi EDWARDS'S SWAMP RAT (EDWARDS'S MALACOMYS)

Fr. Rat palustre de Edwards; Ger. Edwards Sumpfratte

Malacomys edwardsi Rochebrune, 1885. Bull. Sci. Soc. Philom. Paris, ser. 7, 9: 87.

Mellacoree River, Liberia (= Melikhoure River, Rep. of Guinea).

Taxonomy Previously considered to be a subspecies of *Malacomys longipes* (e.g. Allen 1939, Heim de Balsac & Lamotte 1958) and then a full species (Rosevear 1969, Misonne 1974). *Malacomys edwardsi* is clearly distinguishable from *M. longipes* by the smaller size of its skull and external measurements (Rautenbach & Schlitter 1978, Van der Straeten & Verheyen 1979b). See also *Malacomys longipes*. Synonyms: none. Chromosome number: $2n = 48$, $FN = 52$ (Matthey 1958, Van der Straeten & Verheyen 1979b).

Description Medium-sized long-footed rat, slimly built with large ears, long hindfeet and very long tail. Pelage soft, dense and short, with a velvet-like texture. Dorsal pelage rusty-brown to warm brown; hairs dark grey at base, warm brown at tip. Ventral pelage whitish-grey; hairs grey at base with white tips. Throat and chest whitish-grey. Head slender with elongated muzzle; vibrissae long. Eyes large. Ears elongated, rounded at tips, hairless and very mobile. Fore- and hindfeet whitish; hindfeet long with three long central toes. Tail very long (ca. 130% of HB), thin, almost hairless, dark above, pale below. Pelage of juveniles and young smoky-grey. Nipples: $0 + 2 = 4$.

Geographic Variation None recorded.

Similar Species

M. cansdalei. On average HB, T and HF larger; Ghana to E Liberia only.

M. longipes. On average HB, T and HF larger; E Nigeria and further eastwards.

Praomys tullbergi. Smaller size, HF shorter; E shorter; less pointed muzzle; syntopic.

Distribution Endemic to Africa. Rainforest BZ (Western Region and West Central Region [Western Nigerian Subregion]). Recorded from Guinea, Sierra Leone, Liberia, Côte d'Ivoire, Ghana and W Nigeria (west of the Niger R.). Occurs very rarely in forest patches in E Ghana (Decher 1997); not recorded in forest relics in Togo and Benin (Robbins & Van der Straeten 1996). Populations in W Nigeria (Western Central Region [Nigerian Subregion]) are geographically isolated from those of the Western Region.

Habitat Primary and secondary rainforest, especially where the soil is moist and damp (on slopes leading down to streams and along the edges of streams). Some individuals found in secondary bush, and in cocoa plantations and farmlands adjacent to rainforest (Jeffrey 1977). Does not occur in grasslands or cleared forest regions, nor in forestry plantations (e.g. teak) in Rainforest BZ.

Abundance Varies according to locality. In Sierra Leone, comprised 18% (second most numerous species after *Praomys tullbergi* [59%]) at one locality, and 22% (third most numerous species after *P. tullbergi* [30%] and *Hybomys trivirgatus* [28%]) at a second locality (Cross 1977). In Ghana, formed 23% (the second most numerous rodent



Malacomys edwardsi

after *P. tullbergi* [37%]) and 14% (third most numerous species after *P. tullbergi* [57%] and *H. trivirgatus* [20%]; Jeffrey 1977, Cole 1975). In W Nigeria, comprised 9% (second most numerous species after *P. tullbergi* [63%]) during a three-year mark-recapture study (Happold 1977).

Adaptations Terrestrial and nocturnal; may swim occasionally. Walks carefully on moist ground with only the toes of the long limbs touching the ground. Builds saucer-shaped nests of intact forest leaves, usually under logs and buttress roots of large trees. Tends to be inquisitive, sniffing with the nostrils and twisting the very large mobile ear pinnae from side to side when searching for food or sensing danger. The cheekteeth are small and the toothrow is short in relation to the length of the skull, indicating that only soft non-abrasive foods are eaten.

Foraging and Food Omnivorous. In Nigeria, food consisted of 40% vegetable material and 60% invertebrates, mostly insects ($n = 6$) (D. C. D. Happold unpubl.). Likewise, in Ghana, the food was ca. 50% vegetable material and 50% invertebrates, including earthworms, slugs and some grasshoppers, butterfly caterpillars and adult beetles (Cole 1975).

Social and Reproductive Behaviour Quiet and unaggressive when handled. In captivity, several may be kept together without showing agonistic behaviour.

Reproduction and Population Structure In W Nigeria, reproduction occurs during the dry season and early wet season (Nov–

Jul); juveniles enter the population during main part of wet season (Happold 1977). Litter-size: 2.5 (2–3).

Conservation IUCN Category: Least Concern.

Lives primarily in rainforest, and hence destruction of rainforest habitats will reduce their geographic range and population numbers.

Measurements

Malacomys edwardsi

HB: 133 (120–152) mm, n = 30

T: 168 (141–186) mm, n = 30

HF: 33 (31–34) mm, n = 30

E: 25 (22–28) mm, n = 30

WT: 59 (46–74) g, n = 24*

GLS: 38.0 (34.5–40.3) mm, n = 30

GWS: 15.7 (14.3–16.9) mm, n = 30

M¹–M³: 5.2 (4.8–5.4) mm, n = 30

West Africa (Rosevear 1969)

*Nigeria only (D. C. D. Happold, unpubl.)

Key References Cole 1975; Happold 1977, 1987; Rosevear 1969.

D. C. D. Happold

Malacomys longipes LONG-FOOTED SWAMP RAT (COMMON MALACOMYS)

Fr. Rat palustre commun; Ger. Langfüssige Sumpfratte

Malacomys longipes Milne-Edwards, 1877. Bull. Sci. Soc. Philom. Paris, ser. 6, 12: 10.
Gaboon River, Gabon (= vicinity of Ogooué River, Gabon). (See Rautenbach and Schlitter 1978.)

Taxonomy Formerly considered to include *cansdalei* and *giganteus* from Côte d'Ivoire and Ghana (Bellier & Gautun 1968, Rosevear 1969, Rautenbach & Schlitter 1978). However, *giganteus* is a synonym of *M. cansdalei*, and *M. cansdalei* is considered now to be a valid species (Van der Straeten & Verheyen 1979b, Grubb *et al.* 1998). Consequently this species is now restricted geographically to E Nigeria and further eastwards. Synonyms: *australis*, *centralis*. Subspecies: three, validity uncertain. Chromosome number: 2n = 48 (Primus *et al.* 2006).

Description Large long-footed rat, slimly built with large ears, long hindfeet and very long tail; the largest species in the genus. Pelage soft, dense and short, with a velvet-like texture. Dorsal pelage medium to dark brown, usually without any tinge of cinnamon or russet; hairs dark grey, brown at tip. Ventral hairs greyish-white; hairs grey with white tips. Pelage colour varies between individuals and localities. Throat, chest and ventral pelage pale grey or milky-grey. Head slender with elongated muzzle; vibrissae long. Eyes large. Ears elongated, rounded at tips, hairless and very mobile. Fore- and hindfeet whitish; hindfeet long (longer than in *M. edwardsi*, but mostly shorter than in *M. cansdalei*) with three long central toes. Tail very long (ca. 120% HB), thin, almost hairless, dark above, pale below. Pelage of juveniles and subadults smoky-grey. Nipples: 1 + 2 = 6.

Geographic Variation Three subspecies are recognized by Rautenbach & Schlitter (1978), but the validity of these subspecies is uncertain and the differences in size may only reflect clinal variation.

M. l. longipes: E Nigeria, Cameroon, Gabon, Central African Republic, Congo and W DR Congo. Body and cranial measurements mostly within the lower to medium size range for the species.

M. l. centralis: NE and E DR Congo, Uganda, Burundi and NE Angola. Body and cranial measurements mostly at the upper size range for the species.

M. l. australis: Extreme NW Zambia. Similar to *M. l. centralis*, but geographically remote; some individuals have unique white triangular patch on ventral pelage (base of triangle between forelimbs, apex on abdomen).

Similar Species

M. edwardsi. Similar size, HF shorter; W Nigeria and further westwards; allopatric.

M. cansdalei. On average smaller; Ghana to E Liberia; allopatric.

Colomys goslingi. On average smaller in all external measurements; ventral pelage pure white; sympatric.

Praomys verschurenii. Smaller, shorter HF and T; sympatric with restricted distribution.

Deomys ferrugineus. Ventral pelage pure white, rich red-brown coarse-textured pelage, hindfeet on average shorter, and ears oval.

Distribution Endemic to Africa. West Central, East Central and South Central Regions of Rainforest BZ. Recorded from SE Nigeria, Cameroon, Gabon, Equatorial Guinea (Rio Muni and Bioko I.),



Malacomys longipes

Malacomys longipes.



Central African Republic, Congo, DR Congo, W Rwanda, W Uganda (Ankole) and NE Angola. Outlying populations occur in C Uganda (near Entebbe), S Sudan (near Yei) and NW Zambia. The distribution of *M. longipes* does not overlap with *M. edwardsi* and *M. cansdalei* (its ecological equivalents in West Africa).

Habitat Rainforest habitats especially moist areas close to streams (Rahm 1966); also found in some swampy habitats, in oil palm plantations and secondary forest. Occurs up to 1000 m on Mt Cameroon and the Rwenzori Mts in gallery forests, but not in bamboo or *Hagenia* forests (Rahm 1967). Rarely found in cultivated habitats (Rahm 1966). In Dzanga-Sangha, Central African Republic, exhibited extreme habitat specialization: relatively common in stream beds, but rare in upland forest habitats (Ray 1996). Rosevear (1969) and Sanderson (1940) also report a strong association of this species with water.

Abundance Varied, but not uncommon in some localities. Comprised 3–24% of the population of terrestrial small rodents in rainforest habitats (e.g. 3% in Mayanga Forest, Uganda; 20% near streams in E DR Congo and 24% in Kalinzu Forest, Uganda [Delany 1964a, Rahm 1972]). In Dzanga-Sangha, Central African Republic, it was the second most abundant terrestrial small rodent captured in stream beds (14.5%, $n = 200$; Ray 1996).

Adaptations Similar in most respects to *M. edwardsi*. May be more aquatic than *M. edwardsi* because favours moister habitats; probably spends a considerable amount of time in small water-courses in rainforest; likes to immerse body in water (Delany 1975). During daytime, rests in holes and crevices along river banks (Rahm 1966). One study found an individual in vines 2 m above a stream – an unusual observation because the feet are not adapted for climbing.

Foraging and Food Omnivorous. In E DR Congo, analysis of stomach contents indicated that 64% of individuals had fed only on vegetable material and 36% had fed on vegetable and insect material ($n = 55$). Other studies demonstrated relatively high percentage of soft invertebrates in stomachs, such as snails, slugs and earthworms (Genest-Villard 1980, Duplantier 1982, Struhsaker 1997).

Social and Reproductive Behaviour No information; probably similar to *M. edwardsi*.

Reproduction and Population Structure In E DR Congo, pregnancies recorded in Jan, Mar, May, Jul, Sep and Dec; monthly pregnancy rate ranged from 20% to 100% (Rahm 1970). Embryo number varies slightly according to locality: Cameroon: 2.5 (1–4, $n = 12$; Dubost 1968); E DR Congo: 3 (1–5, $n = 27$; Rahm 1970); Central African Republic: 2.3 (2–3, $n = 4$; J. C. Ray unpubl.).

Predators, Parasites and Diseases No information.

Conservation IUCN Category: Least Concern.

Lives primarily in rainforest, and hence destruction of rainforest habitats reduces the geographic range and population numbers.

Measurements

Malacomys longipes

HB: 158.2 (144–173) mm, $n = 14$

T: 186.1 (165–202) mm, $n = 14$

HF: 39.4 (36–41) mm, $n = 14$

E: 25.7 (25–27) mm, $n = 14$

WT: 105.6 (88–129) g, $n = 14$

GLS: 41.6 (40.0–43.9) mm, $n = 11$

GWS: 17.3 (16.6–18.2) mm, n = 11
M¹–M³: 5.7 (5.4–6.0) mm, n = 11
Irangi, DR Congo (SMNS)

Key References Rahm 1966, 1972; Rautenbach & Schlitter 1978; Van der Straeten & Verheyen 1979b.

D. C. D. Happold

GENUS *Mastomys*
Multimammate Mice

Mastomys Thomas, 1915. Ann. Mag. Nat. Hist., ser. 8, 16: 477. Type species: *Mus coucha* Smith, 1834.



Mastomys natalensis.

The genus *Mastomys* is endemic to Africa and currently contains eight species (Table 36). It is widespread in Africa south of the Sahara with a relic population of one species in Morocco. Species of the genus live mainly in grasslands, wooded savanna, cultivated areas and human dwellings or stores. They also occur in human settlements in the Rainforest BZ, but are not known from deserts.

Species in the genus are small in size with soft pelage, darkish-brown dorsally and greyish ventrally. The head is slender with an elongated muzzle and long vibrissae. Eyes are large, and ears are elongated, rounded at tips, hairless and very mobile. Tail is about the length of HB or somewhat shorter, with small scales and short fine hairs between the scales. One of the most obvious characters is the two rows of nipples, each with 8–12 nipples, arranged almost contiguously from axilla to inguinal region (hence the vernacular name of ‘Multimammate Mice’). The skull typically has the anterior palatal foramina reaching well posteriorly to between the cheekteeth often as far as the median root of M¹; t3 is present on M¹ but smaller than t1, which is placed quite far to the rear; the palatine bone never extends forward beyond the front of M²; and the mesopterygoid fossa is very narrow at the margin of the palatine bone, generally less than 1 mm (sometimes larger in *M. kollmannspergeri*) (Figure 74).

Most species have large litters, and are able to breed very rapidly when conditions are favourable. When this happens it can lead to a

Table 36. Species in the genus *Mastomys*. Arranged in order of increasing mean head and body length.
(n. d. = no data.)

| Species | HB
mean (range)
(mm) | Tail
mean (range)
(mm) [% of HB] | Adult dorsal pelage | Adult ventral
pelage | Nipples ^a | |
|----------------------------|---|---|---------------------------------|-------------------------|----------------------|--|
| <i>M. pernanus</i> | 78 (73–88) | 66 (60–78)
[85%] | Dark grey | Grey, white tips | n. d. | |
| <i>M. coucha</i> | 100 (77–132) | 85 (75–193)
[85%] | Rusty-brown | Dark grey | 12 × 2 = 24 | |
| <i>M. natalensis</i> | 108 (74–145) (♂ ♂),
106 (66–171) (♀ ♀) | 108 (63–147) (♂ ♂),
106 (70–175) (♀ ♀)
[ca. 100%] | Rusty-brown | Dark grey | 12 × 2 = 24 | |
| <i>M. shortridgei</i> | 120 (103–137) | 105 (86–118)
[88%] | Dark grey | Grey, white tips | 5 × 2 = 10 | |
| <i>M. awashensis</i> | 122 (116–127) | 118 (111–123)
[103%] | Blackish, greyish-rufous flanks | Grey | n. d. | |
| <i>M. huberti</i> | 139 (♂ ♂), 132 (♀ ♀) | 114 (♂ ♂), 113 (♀ ♀)
[84%] | Rusty-brown to blackish | Grey | 12 × 2 = 24 | |
| <i>M. kollmannspergeri</i> | 142 (118–166) (♂ ♂),
132 (120–148) (♀ ♀) | 118 (99–137) (♂ ♂),
113 (96–131) (♀ ♀)
[85%] | Grey | Pale grey to whitish | 9–12 × 2 = 18–24 | |
| <i>M. erythroleucus</i> | 142 (♂ ♂), 134 (♀ ♀) | 123 (♂ ♂), 121 (♀ ♀)
[89%] | Reddish-brown | Cream | 12 × 2 = 24 | |

^a Nipples equally spaced along ventral surface from axilla to inguinal region.

^b See text for further details.

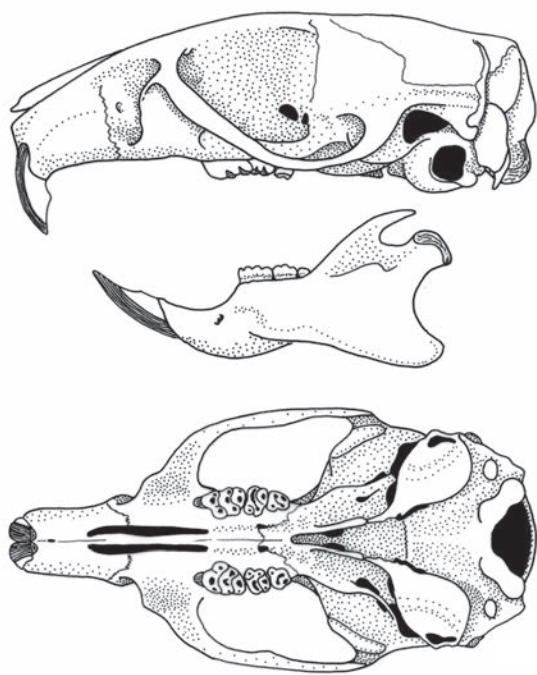


Figure 74. Skull and mandible of *Mastomys erythroleucus* (HC 1659).

‘population explosion’, but when conditions deteriorate population numbers decline very rapidly. Several species and populations display such irregular population explosions. Multimammate mice are among the most adaptable of African mice, are capable of surviving in a wide range of environmental conditions, and are often the most numerous

mice in savanna habitats and agricultural fields. Multimammate mice are common pest rodents in agricultural fields and pest stores. They are important, also, because they are natural hosts of pathogens that cause sickness in humans.

Mastomys has often been listed as a subgenus in the genus *Praomys*, but it is now well accepted as a separate genus. Very few species of *Mastomys* can be recognized by size or colour alone, and most are very difficult to distinguish on external morphology or on skull measurements. Definite identification is possible only by karyological analysis or molecular methods. Musser & Carleton (1993, 2005) recognized eight species, but only five species (*M. coucha*, *M. erythroleucus*, *M. natalensis*, *M. pernanus*, *M. shortridgei*) are common to both studies. Additional species in Musser & Carleton (2005) are *M. awashensis* and *M. huberti* (species shown to be karyotypically different to other named forms), as well as *M. kollmannspergeri* (originally described as a subspecies of *M. natalensis*, but now recognized as a separate species with *verheyeni* as a junior synonym). Two species listed in Musser & Carleton (1993) have been reallocated: *Mastomys angolensis* is now provisionally placed in the genus *Myomyscus*, and *Mastomys hildebrandtii* is provisionally placed as a synonym of *M. natalensis*, while most specimens earlier classified as *M. hildebrandtii* are now placed in *M. huberti* (see Musser & Carleton 2005 for further comment). Specimens from widespread regions in Africa have been attributed to *M. natalensis*, but this is probably a species complex; likewise *M. erythroleucus* was recently recognized as a species complex. The genus requires careful systematic revision.

Herwig Leirs

| | Chromosome number | Notes |
|--|----------------------------------|--|
| | n. d. | N Tanzania, S Kenya; white spot behind each ear; rare |
| | 2n = 36, FN = 54 | S and W Zimbabwe, C Namibia, South Africa; higher altitudes, rainfall <800 mm per annum |
| | 2n = 32, FN = 52–54 | Widespread in West, East, southern and central Africa; lower altitudes and higher rainfall |
| | 2n = 36, FN = 50 | NW Botswana, NE Namibia; moist and marshy habitats |
| | 2n = 32 | Ethiopia at low altitudes; rare |
| | 2n = 32, FN = 44 | Senegal, Mauritania, Mali, Burkina, Nigeria |
| | 2n = 38, FN = 40–41 | Cameroon, Chad, N Niger; limits uncertain |
| | 2n = 38, FN = 50–56 ^b | Senegal to Ethiopia, Cameroon to E DR Congo; very common; isolated population in Morocco |

***Mastomys awashensis* AWASH MULTIMAMMATE MOUSE (AWASH MASTOMYS)**

Fr. Souris à mamelles multiples d'Awash; Ger. Awash-Vielzitzenmaus

Mastomys awashensis Lavrenchenko, Likhnova & Baskevich 1998. Z. Saugetierk. 63: 44.

Banks of the Awash River near Koka L., Ethiopia (ca. 08° 23' N, 39° 09' E).

Taxonomy Distinguished from other species of *Mastomys* in Ethiopia by multivariate craniometry, phallic morphology, spermatozoan structure, allozymes and chromosome characters. Synonyms: none. Chromosome number: $2n = 32$ (as in syntopic *M. natalensis* but with different C-banding).

Description Medium-sized grey mouse similar in size to *M. erythroleucus* but with relatively shorter tail bearing smaller scales. Dorsal pelage blackish, with greyish-rufous flanks. Ventral pelage greyish. Colour of dorsal and ventral pelage clearly delineated. Head blackish, with yellowish-rufous cheeks. Upper parts of fore- and hindfeet whitish, claws pale. Tail long (ca. 103% of HB), scaly. Skull typical of *Mastomys*, straight and strongly rounded dorsal edge of anterior margin of zygomatic plate, narrow mesopterygoid fossa, anterior palatine foramina extending to middle of M^1 ; palatine bone reaching no further forward than the middle of M^2 . Externally similar to sympatric *M. erythroleucus* and *M. natalensis*. Nipples: not known.

Geographic Variation None recorded.

*Mastomys awashensis***Similar Species**

M. erythroleucus. Slightly larger mean HB and T; ventral pelage cream; widespread distribution; common; $2n = 38$.

M. natalensis. Smaller mean HB and T; ventral pelage dark grey; widespread distribution; common; $2n = 32$.

Distribution Endemic to Africa. Somalia–Masai Bushland BZ of Ethiopia. Recorded from only two localities: eastern bank of Koka L. and Awash N. P. Geographic limits uncertain, but probably more extensive than known at present. A further specimen from Zway (08° 00' N, 38° 48' E) may also represent this species (M. Corti unpubl.).

Habitat *Acacia–Commiphora* thornbush with high grass, and adjacent agricultural lands. Absent from buildings in human settlements.

Abundance Rare; known only from ten specimens.

Remarks Apparently no other information available.

Conservation IUCN Category: Vulnerable.

This species has a very limited geographic range and non-commensal life-style; there is progressive destruction of its habitat by agricultural development.

Measurements

Mastomys awashensis

HB: 122 (116–127) mm, $n = 6$

T: 118 (111–123) mm, $n = 6$

HF: 23.8 (23.5–24.3) mm, $n = 6$

E: 19.0 (18–20) mm, $n = 6$

WT: 46 (30–68) g, $n = 6$

GLS: 29.8 (28.8–30.7) mm, $n = 6$

GWS: 14.6 (13.5–15.6) mm, $n = 6$

M^1 – M^3 : 5.2 (5.1–5.4) mm, $n = 6$

Ethiopia (Lavrenchenko *et al.* 1998a)

Weight: L. A. Lavrenchenko (unpubl.)

Key References Lavrenchenko & Baskevich 1996; Lavrenchenko *et al.* 1998a.

Leonid A. Lavrenchenko & Herwig Leirs

***Mastomys coucha* SOUTHERN AFRICAN MULTIMAMMATE MOUSE (SOUTHERN AFRICAN MASTOMYS)**

Fr. Souris à mamelles multiples du sud; Ger. Südliches Vielzitzenmaus

Mastomys coucha (Smith, 1834). Rept. Exped. Exploring Central Africa, p. 43.

Northern Cape Province, between Orange River and Tropic of Capricorn, South Africa. (Type locality fixed as Kuruman.)

Taxonomy Originally described in the genus *Mus*. Traditionally considered to be conspecific with *M. natalensis* but now known to be a valid species on the basis of its karyology and a 'faster' haemoglobin in electrophoresis. Good biological information about *M. coucha* is rather sparse because many studies were carried out in areas where it is sympatric with *M. natalensis* and karyological confirmation of the studied specimens is not available. Both the wild form and a chamois-coloured pink-eyed laboratory strain are used in medical research, sometimes still misnamed as *M. natalensis* (Kruppa *et al.* 1990). Synonyms: *bradfieldi*, *breyeri*, *limpopoensis*, *marikquensis*, *sicalis*, *silaceus*, *socialis*. Subspecies: none. Chromosome number: $2n = 36$, $FN = 54$.

Description Small grey mouse. Dorsal pelage darkish-grey (young) to rusty-brownish (old adults). Ventral pelage dark grey; hairs with paler tip. Fore- and hindfeet whitish. Tail long (ca. 100% of HB), dark above and below. Skull distinguishable from *M. natalensis* by multivariate techniques only, but with considerable misclassification (Dippenaar *et al.* 1993, Lecompte *et al.* 2002b). Spermatozoa and genital morphology slightly different from other species of *Mastomys* (Gordon & Watson 1986, Lavrenchenko & Baskevich 1996). Nipples: 12 (equally spaced from axilla to inguinal region) = 24.

Geographic Variation None recorded.

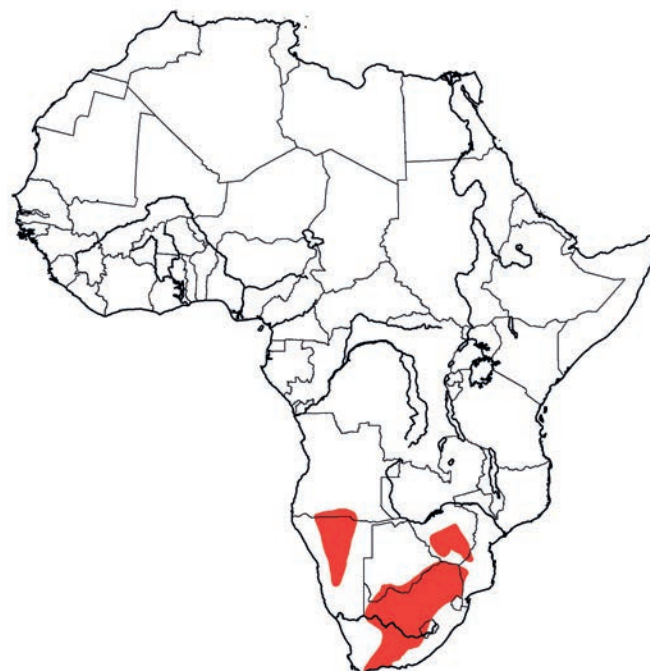
Similar Species

M. natalensis. Slightly larger mean HB and T; ventral pelage dark grey; broadly sympatric with *M. coucha* in southern Africa; common; $2n = 32$.

Distribution Endemic to Africa. Zambezian Woodland BZ and Highveld BZ. Recorded from S and W Zimbabwe, C Namibia and S Africa in areas receiving <800 mm annual rainfall. Partly overlaps with *M. natalensis*, and hence the identification of species in many earlier studies is uncertain. *Mastomys coucha* has a preference for higher altitude/relatively drier parts of South Africa, while *M. natalensis* prefers low altitude/high rainfall regions (Venturi *et al.* 2003). *Mastomys coucha* is currently thought to be the only *Mastomys* present in Free State, South Africa, meaning that a number of studies on biology there can now be ascribed to this species (N. Avenant unpubl.).

Habitat Grassland, woodland savanna, fields and human dwellings. Very common at disturbed sites. Due to the association of this species with such habitats, it can be used as an indicator species for the level of disturbance in, for example, nature reserves (Avenant 2000, 2002).

Abundance Common, particularly in disturbed habitats.

*Mastomys coucha*

Adaptations Probably similar to other species in the genus, but tolerates drier conditions than *M. natalensis*.

Foraging and Food Terrestrial and nocturnal. No specific information available but probably similar to *M. natalensis*.

Social and Reproductive Behaviour No information, but probably similar to *M. natalensis*.

Reproduction and Population Structure Reproduction is seasonal with a break in the dry winter months (Coetzee 1965), but other studies suggest that breeding continues throughout the year (Avenant 1996). Maturation is stimulated by chemicals present in germinating grasses (Linn 1991). Mean litter-size: ca. 8–10. Gestation: 21–22 days. Interval between litters 33 days (average). At birth, young altricial. Eyes open Day 15. Weaning Day 21 (Meester 1960). Sex ratio around 1 : 1.

Predators, Parasites and Diseases More susceptible to plague than *M. natalensis*. Distribution of outbreaks of plague in Zimbabwe and South Africa corresponds approximately to the distribution of *M. coucha*, although there are some exceptions (Taylor *et al.* 1981, Venturi *et al.* 2003).

Conservation IUCN Category: Least Concern.

Measurements*Mastomys coucha*

HB: 100 (77–132) mm, n = 26

T: 85 (75–103) mm, n = 26

HF: 20.0 (18–22) mm, n = 26

E: 17.8 (16–20) mm, n = 26

WT: 31 (15–54) g, n = 26

GLS: 26.9 ± 1.32 mm, n = 21GWS: 11.45 ± 0.31 mm, n = 19* M^1-M^3 : 4.95 ± 0.22 mm, n = 21

Body measurements and weight: Kuruman, South Africa (TM)

Skull measurements: Njobe 1997, as mean \pm 1 S.D.

* = Greatest breadth of braincase

Key References Avenant 1996; Gordon & Watson 1986; Linn 1991; Meester 1960; Venturi *et al.* 2003.**Herwig Leirs*****Mastomys erythroleucus* GUINEA MULTIMAMMATE MOUSE (REDDISH-WHITE MASTOMYS)**

Fr. Souris à mamelles multiples de Guinée; Ger. Guinea-Vielzitzenmaus

Mastomys erythroleucus (Temminck, 1853). Esquisses Zool. sur la Côte de Guinée, p. 160. (The cultivated parts of Guinea.)

Taxonomy Originally described in the genus *Mus*. Until a few years ago, *Mastomys erythroleucus* was thought to be clearly distinguishable from other *Mastomys* by its chromosome number of $2n = 38$. However, there are probably at least three forms with this same chromosome number but with different fundamental number, and which may deserve species status (Volobouev *et al.* 2001). One form has $FN = 40-41$ and occurs in Niger, Chad and Sudan and is now referred to as a separate species *Mastomys kollmannspergeri*. The second form (i.e. this species) has $FN = 50-56$, and is widely distributed throughout sub-Saharan Africa with karyotyped populations from Senegal, Côte d'Ivoire, Mali, Benin, Cameroon, DR Congo and Sudan (and probably also Morocco and Ethiopia). A third form has $FN = 59-60$ and is found in E DR Congo, Uganda and probably Mali and Chad, but so far has not been associated with a separate specific name. Synonyms: *calopus*, *gambianus*, *peregrinus*. Subspecies: none. Chromosome number: $2n = 38$, $FN = 50-56$ (see also above).

Description Medium-sized reddish-brown mouse. Dorsal pelage reddish-brown. Ventral pelage creamy. Colour of dorsal pelage more or less clearly delineated from ventral pelage. Fore- and hindfeet whitish. Tail long (89% of HB in Senegal), dark above, paler below. Skull closely resembles that of *M. natalensis* and *M. huberti*, and can be distinguished by multivariate techniques (Duplantier 1988). Sexually dimorphic: ♂♂ have larger HB, HF and weight than ♀♀. Nipples: 12 (equally spaced from axilla to inguinal region) = 24.

Geographic Variation None recorded.

Similar Species

M. huberti. Smaller mean HB and T; ventral pelage grey; restricted to West Africa; prefers wet areas; nipples $12 \times 2 = 24$; $2n = 32$.

M. kollmannspergeri. Similar mean HB and T; ventral pale grey or white; known only from around L. Chad, geographic limits uncertain; nipples $9-12 \times 2 = 18-24$; $2n = 38$.

M. natalensis. Smaller mean HB and T; tail longer as % of HB; ventral pelage dark grey; also widespread distribution with extensive sympatry in savanna habitats of West and Central Africa; nipples $12 \times 2 = 24$; $2n = 32$.

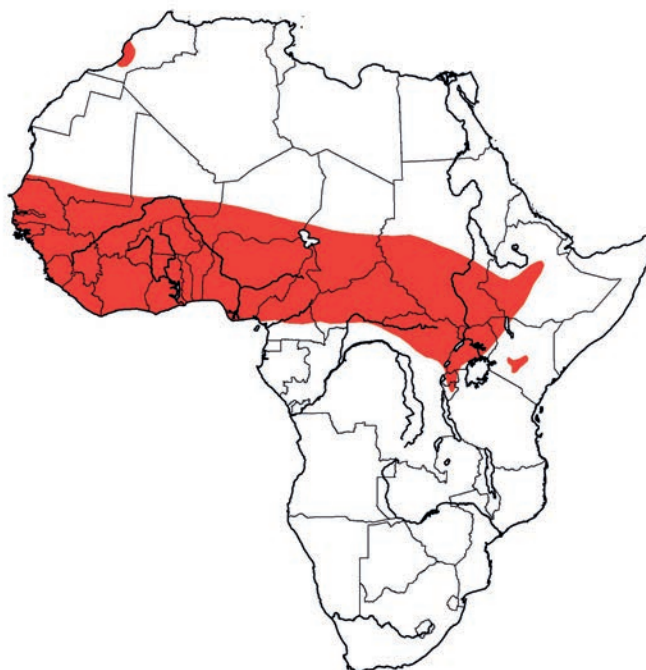
Praomys daltoni. Smaller mean HB and T; T longer as % of HB (110%); ventral pelage pure white; widespread distribution and

common in savanna habitats of West and Central Africa; nipples: $3 + 2 = 10$. $2n = 36$.

Praomys derooi. Smaller mean HB and T; ventral pelage grey, often with white spot on chest; restricted to savanna habitats from Ghana to W Nigeria; commensal; nipples $3 + 2 = 10$; $2n = 36$.

Distribution Endemic to Africa. Widespread in Sahel, Sudan and Guinea BZs, Northern and Eastern Rainforest–Savanna Mosaics; extends into suitable habitats in Rainforest BZ in West Africa. Recorded from Senegal to Ethiopia, and south to Cameroon and E DR Congo. Isolated populations in Morocco (Cabrera 1932, Tranier 1974).

Habitat Grasslands, disturbed areas, fields, near human habitations and in buildings (Duplantier & Granjon 1988). Occurs on a wide variety of soil types, but not in arid environments (Hubert *et al.* 1977). In Ghana, this species dominated in areas with tree plantations and secondary forest (Decher & Bahian 1999).

*Mastomys erythroleucus*

Abundance Very common. Population explosions occur irregularly; densities vary from 1/ha to more than 100/ha in Senegal (Hubert 1982, Hubert & Adam 1985). In Ethiopia, densities remained below 20/ha during two years of study, with lower densities during the dry season (Afework Bekele & Leirs 1997). When populations are high, these mice are a serious agricultural pest in fields and stores.

Adaptation In semi-arid areas, shortage of food during the late dry season induces a decrease of water loss and cessation of reproduction (Sicard *et al.* 1999). Fats are stored in body tissues during the period of highest availability of seeds in the early part of the dry season, and are used as a source of energy and metabolic water later in the season (Hubert & Demarne 1981).

Foraging and Food Mainly granivorous but other plant parts and insects are also eaten. Seeds of plants of the Cucurbitaceae family predominate in the diet during the early dry season, and seeds of Convolvulaceae during the late dry season. An increase in green vegetation in the diet increases during the wet season and coincides with the start of reproduction. Grass seeds and arthropods are eaten throughout the year (Hubert *et al.* 1981b). Supplementary food, provided experimentally, increased recruitment and survival but was unable to prevent population decline (Hubert *et al.* 1981a).

Social and Reproductive Behaviour Males have larger home-ranges than ♀♀ and move more often. Individual mice are not territorial or aggressive, and they do not form lasting group associations. These characters are even more evident in island populations than in mainland populations in Senegal (Granjon *et al.* 1986, Granjon & Duplantier 1991).

Reproduction and Population Structure Reproduction is seasonal, beginning early in the wet season and lasting well into the dry season (Hubert 1982, Afework Bekele & Leirs 1997). Gestation: 21 days. Litter-size: 11.8 (1–21, $n = 150$; Duplantier *et al.* 1996). Litter-size is higher in maize fields than in other habitats (Afework Bekele & Leirs 1997). Spontaneous ovulation; postpartum oestrus occurs within a few hours of parturition and then again after a few days. Vaginal plug formed after copulation (Brambell & Davis 1941).

Predators, Parasites and Diseases Hubert & Adam (1983) suspected a virus, Bandia virus, to play a role in the dynamics of populations of *M. erythroleucus* but no details of its epidemiology or pathology are known. The presence of a number of human pathogens (*Borrelia crocidurae*, *Leishmania*, several viruses) has been reported from this species in Senegal. Serological tests on these mice have been positive for antibodies against Lassa fever virus and Congo–Crimean haemorrhagic fever virus.

Conservation IUCN Category: Least Concern.

The status of the isolated populations in Morocco is unknown. This species is considered a pest in crops and therefore often controlled.

Measurements

Mastomys erythroleucus

HB (♂♂): 142 ± 12 mm, $n = 174$

HB (♀♀): 134 ± 10 mm, $n = 158$

T (♂♂): 123 ± 11 mm, $n = 174$

T (♀♀): 121 ± 10 mm, $n = 137$

HF (♂♂): 24.3 ± 1.1 mm, $n = 173$

HF (♀♀): 23.9 ± 1.0 mm, $n = 155$

E (♂♂): 19.1 ± 0.9 mm, $n = 170$

E (♀♀): 19.0 ± 0.9 mm, $n = 143$

WT (♂♂): 62.6 ± 17.8 g, $n = 174$

WT (♀♀): 50.3 ± 12.9 g, $n = 158$

GLS (♂♂): 30.7 ± 1.3 (27.7–32.9) mm, $n = 32$

GLS (♀♀): 30.3 ± 1.1 (27.5–32.6) mm, $n = 27$

GWS (♂♂): 15.6 ± 0.9 (13.7–17.4) mm, $n = 32$

GWS (♀♀): 15.5 ± 0.8 (14.0–17.3) mm, $n = 27$

M¹–M³ (♂♂): 4.8 ± 0.2 (4.5–5.3) mm, $n = 32$

M¹–M³ (♀♀): 4.8 ± 0.3 (4.2–5.4) mm, $n = 27$

Senegal, adult mainland individuals (Duplantier 1988, unpubl.)

Data given as mean \pm 1 S.D (range not available for body measurements and weight)

Key References Duplantier *et al.* 1996; Duplantier & Granjon 1988; Hubert 1982; Hubert *et al.* 1981b; Sicard *et al.* 1999.

Herwig Leirs

Mastomys huberti HUBERT'S MULTIMAMMATE MOUSE (HUBERT'S MASTOMYS)

Fr. Souris à mamelles multiples de Hubert; Ger. Huberts Vielzitzenmaus

Mastomys huberti (Wroughton, 1908). Ann. Mag. Nat. Hist., ser. 1, 8: 255. Zungeru, N Nigeria.

Taxonomy Originally described in the genus *Mus*. Although *huberti* was traditionally considered a name for a West African *Mastomys* species, Qumsiyeh *et al.* (1990) argued that the name *hildebrandtii* (with a type locality in Kenya) had priority over *huberti* for this species, but without comparing the type material. Their decision was based on the assumption that specimens from Kenya in their study were different from *M. natalensis* from South Africa and conspecific with specimens from Somalia, which Capanna *et al.* (1982) had named as *M. huberti*. Musser & Carleton (1993) thus also referred to this species as *M. hildebrandtii*. However, the karyology for the West African specimens assigned to *huberti* ($2n = 32$, $FN = 44$) is

different from that of the specimens from Kenya that Qumsiyeh considered to be *hildebrandtii* ($2n = 32$, $FN = 50$ – 54). Therefore, these taxa are not synonyms and *M. huberti* is maintained as a valid species, even though specimens from the type region have not yet been investigated karyologically, and the type locality lies outside the geographic range of what is currently called *M. huberti* (Granjon *et al.* 1997b). Synonyms: none. Chromosome number: $2n = 32$, $FN = 44$.

Description Medium-sized dark-grey mouse. Dorsal pelage darkish-grey (young), rusty-brownish (old adults) or blackish (in Senegal). Ventral pelage dark, hairs with greyish tip. Fore- and

hindfeet whitish. Tail long (84% of HB in Senegal), dark above, sometimes somewhat paler below. Skull closely resembles that of *M. natalensis*. Sexually dimorphic: on average ♂♂ have larger HB and HF and weigh more than ♀♀. Nipples: 12 (equally spaced from axilla to inguinal region) = 24.

Geographic Variation None recorded.

Similar Species

M. erythroleucus. Similar mean HB and T; ventral pelage cream; widespread distribution; common; $2n = 38$.

M. natalensis. Smaller mean HB and T; tail longer as % of HB; ventral pelage dark grey; widespread distribution in savanna habitats of West and Central Africa; $2n = 32$.

Pracomys daltoni. Smaller mean HB and T; T longer as % of HB (110%); ventral pelage pure white; widespread distribution and common in natural habitats; nipples: $3 + 2 = 10$. $2n = 36$.

Distribution Endemic to Africa. Sahel and Sudan Savanna BZs of W West Africa. Recorded (and confirmed by karyology) from Senegal, Mauritania, Mali and Burkina (Granjon *et al.* 1997b). Type locality (not karyotyped) in Nigeria. Sympatric with *M. erythroleucus* and *M. natalensis* in parts of its geographic range. Many records are uncertain because information on chromosomes is lacking.

Habitat Humid areas in natural grassland as well as agricultural fields. Also occurs on dry islands in the Saloum Delta in Senegal. Partly syntopic with *M. erythroleucus* in market gardens in Senegal (Duplantier & Granjon, 1988).

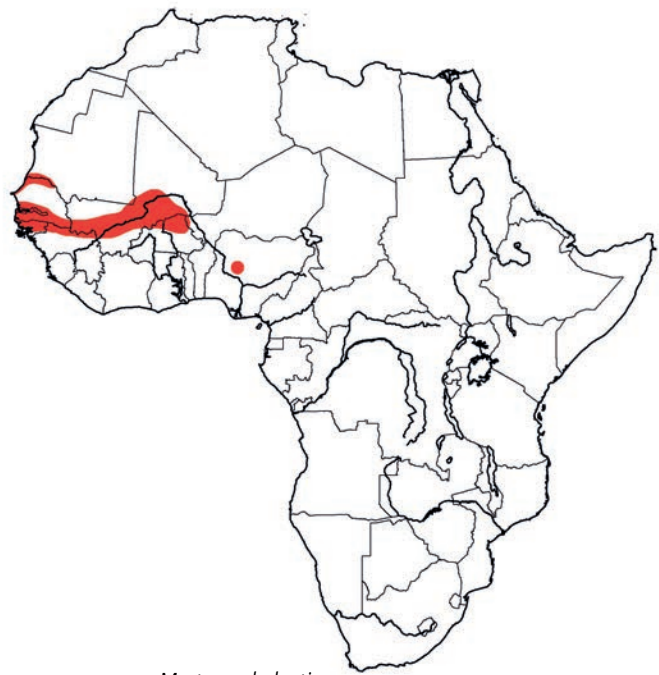
Abundance Common in suitable habitats. During a two-year period (Oct 1988 to Oct 1990) in the Saloum Delta of Senegal, 8–97 individuals were present on a 0.8 ha island (= 10–108/ha) and 19–37 individuals on a 2 ha study area (= 10–18/ha) on the nearby mainland (Granjon *et al.* 1994).

Adaptations Large variation in water metabolism in different individuals. Free water not needed for survival (Granjon *et al.* 1994, Ganem *et al.* 1995). Very good swimming abilities (Duplantier & Bâ 2001).

Foraging and Food Omnivorous. In Senegal, analysis of stomach contents showed that 97% contained insects, 59% grains or starchy tubers, 49% leaves stems and roots, and 9.7% fruit pulp ($n = 145$ stomachs; (Hester 1993).

Social and Reproductive Behaviour Inter-male relationships less aggressive than in *M. natalensis* and *M. erythroleucus* (Granjon *et al.* 1986). Multiple capture results suggested associations between adult ♂♂ (Granjon & Duplantier 1991).

Reproduction and Population Structure Reproductive activity occurs throughout the year in wet habitats (Sicard *et al.* 1999). Gestation: 21 days. Litter-size: 12.2 (1–27) (Duplantier *et al.* 1996). Populations in irrigated fields showed seasonal variations in population structure: in the dry season (Jan–Mar), juveniles represented more than 50% of captures, while in the wet season



Mastomys huberti

(Jul–Nov) old adults represented 50% or more. Pregnancy rate in adult ♀♀ was highest (45%) in Sep (end of wet season) and lowest (3%) in Jan (dry season). Sex ratio in adults was male-biased (J.-M. Duplantier unpubl.).

Predators, Parasites and Diseases Preyed on by Barn Owls *Tyto alba* in the Senegal Delta (Bâ *et al.* 2000). Known to be a carrier of *Borrelia crocidurae* (Godeluck *et al.* 1994, Duplantier & Sene 2000).

Conservation IUCN Category: Least Concern.

Considered to be a serious agricultural pest.

Measurements

Mastomys huberti

HB (♂♂): 139 ± 10 mm, $n = 120$

HB (♀♀): 132 ± 10 mm, $n = 115$

T (♂♂): 114 ± 10 mm, $n = 107$

T (♀♀): 113 ± 10 mm, $n = 109$

HF (♂♂): 25.1 ± 1.1 mm, $n = 120$

HF (♀♀): 24.6 ± 1.1 mm, $n = 115$

E (♂♂): 18.6 ± 0.9 mm, $n = 120$

E (♀♀): 18.4 ± 0.9 mm, $n = 115$

WT (♂♂): 59.1 ± 13.0 g, $n = 119$

WT (♀♀): 51.5 ± 11.3 g, $n = 115$

GLS (♂♂): 30.7 ± 1.2 (27.7–32.9) mm, $n = 20$

GLS (♀♀): 29.9 ± 1.3 (27.5–32.6) mm, $n = 21$

GWS (♂♂): 15.8 ± 0.7 (14.4–16.9) mm, $n = 20$

GWS (♀♀): 15.6 ± 0.7 (14.7–16.9) mm, $n = 21$

M¹–M³ (♂♂): 4.6 ± 0.2 (4.3–5.1) mm, $n = 20$

M¹–M³ (♀♀): 4.5 ± 0.2 (3.9–5.0) mm, $n = 21$

Senegal (mainland) (Duplantier 1988, unpubl.)

Data given as mean \pm 1 S.D. (range not available for body measurements and weight)

Key References Duplantier & Granjon 1988; Duplantier *et al.* 1990, 1996; Granjon *et al.* 1997b; Sicard *et al.* 1999.

Herwig Leirs

Mastomys kollmannspergeri KOLLMANNSPERGER'S MULTIMAMMATE MOUSE (KOLLMANNSPERGER'S MASTOMYS)

Fr. Souris à mammelles multiples de Kollmannsperger; Ger. Kollmannspergers Vielzitzenmaus

Mastomys kollmannspergeri (Petter, 1957). Mammalia 21: 129. 150 km north of Agadès, on the road from Agadès to In Abbangarit, near Tedjidda-n-Tesemt, where the road splits to In Gal, Aïr region, N Niger.

Taxonomy Originally described in the genus *Rattus*. Specimens from near the type locality (in Niger; see above) have a karyotype similar to one reported earlier from Sudan, Chad and Niger and recognized as a valid taxon different from *Mastomys erythroleucus* (Volobouev *et al.* 2001, Dobigny *et al.* 2002b). All these specimens were therefore attributed to *Mastomys kollmannspergeri*, which originally was described as a subspecies of *Mastomys natalensis*. Morphometric, cytogenetic and molecular data have shown that specimens from the type region of *Mastomys verheyeni* (a limited geographic area around L. Chad) are now considered to be conspecific with *kollmannspergeri* (Robbins & Van der Straeten 1989). The name for this species is provisionally considered to be *M. kollmannspergeri*, with *verheyeni* as a synonym (C. Denys unpubl.; Musser & Carleton 2005), but there may be older names that are applicable. The holotype of *Mastomys kollmannspergeri*, although described as an adult ♀♀, is considerably smaller than the smallest ♀♀ in the type series used for the description of *verheyeni*, so the existence of several *Mastomys* species around L. Chad should not be excluded. Synonyms: *verheyeni*. Subspecies: none. Chromosome number: $2n = 38$, $FN = 40-41$.

Description Medium-sized grey mouse, one of the largest species of *Mastomys*. Dorsal pelage medium-grey. Ventral pelage paler, hairs grey at base, usually with white tip. Upper surface of fore- and hindfeet with rather long white hairs. Tail long (85% of HB) with rather long hairs. Skull typical of *Mastomys*, but molars wider and molar row longer than in other *Mastomys* species; interorbital constriction narrow. Males slightly larger than ♀♀ in the specimens from around L. Chad. Nipples: 9–12 (equally spaced from axilla to inguinal region) = 18–24.

Geographic Variation None recorded.

Similar Species

M. erythroleucus. Similar mean HB and T; ventral pelage cream; widespread distribution; common; $2n = 38$, $FN = 50-56$.

M. natalensis. Smaller mean HB and T; tail longer as % of HB; ventral pelage dark grey; widespread distribution; $2n = 32$.

Distribution Endemic to Africa. Borders of the Sudan and Sahel Savanna BZ. Karyotypically known specimens recorded from the area immediately surrounding L. Chad in Nigeria and Cameroon; also recorded in S Chad and N Niger. Eastern and western limits unknown; may extend into large areas of Sahel and Sudan BZs, and parts of Sahara Arid BZ in Niger, Chad and Sudan (red line on map).

Habitat In Chad, found predominantly in annually flooded habitats characterized by a clay-rich soil with wide cracks, often with *Acacia seyal* as the main vegetation. In Niger, lives in open grassland habitats with desiccation cracks, and also near camps and in a village (Granjon *et al.* 2004).

Abundance In Zakouma N. P. in Chad, *M. kollmannspergeri* and *M. erythroleucus* were equally abundant and were about twice as common as other rodents. In other areas in Chad, it is not uncommon and may occur with other species of *Mastomys* (Robbins & Van der Straeten 1989; E. Van der Straeten pers. comm.).

Remarks Reproduction may be seasonal. Near L. Chad, in late Nov 1970, most trapped animals were young, and four out of eight ♀♀ were pregnant; in Aug 1972, nearly all animals were adults, ten out of 17 ♀♀ were pregnant or had recently given birth. Litter-size: 12 ($n = 1$) (E. Van der Straeten, unpubl.). In Chad, embryo numbers were 12, 12, 8 and 7/litter ($n = 4$; Granjon *et al.* 2004).

Conservation IUCN Category: Least Concern.



Mastomys kollmannspergeri

Measurements*Mastomys kollmannspergeri*

HB (♂ ♂): 142 (118–166) mm, n = 22

HB (♀ ♀): 132 (120–148) mm, n = 25

T (♂ ♂): 118 (99–137) mm, n = 20

T (♀ ♀): 113 (96–131) mm, n = 24

HF (♂ ♂): 27.2 (26–29) mm, n = 22

HF (♀ ♀): 26.0 (24–28) mm, n = 25

E (♂ ♂): 18.1 (16–20) mm, n = 22

E (♀ ♀): 17.4 (15–19) mm, n = 25

WT (♂ ♂): 105.9 (54–160) g, n = 22

WT (♀ ♀): 83.4 (60–116) g, n = 25

GLS (♂ ♂): 35.0 (31.8–38.9) mm, n = 20

GLS (♀ ♀): 33.0 (30.4–36.7) mm, n = 30

GWS (♂ ♂): 16.7 (15.2–18.4) mm, n = 22

GWS (♀ ♀): 16.1 (14.9–17.7) mm, n = 33

M¹–M³ (♂ ♂): 6.2 (5.7–7.3) mm, n = 24M¹–M³ (♀ ♀): 6.2 (5.8–6.8) mm, n = 34Nigeria and Cameroon (Robbins & Van der Straeten 1989, E. Van der Straeten unpubl.; as *Mastomys verheyeni*)**Key References** Dobigny *et al.* 2002b; Granjon *et al.* 2004; Robbins & Van der Straeten 1989; Volobouev *et al.* 2001.**Herwig Leirs*****Mastomys natalensis* NATAL MULTIMAMMATE MOUSE (NATAL MASTOMYS)**

Fr. Souris à multiples mamelles du Natal; Ger. Natal-Vielzitzenmaus

Mastomys natalensis (Smith, 1834). S. Afr. Quart. J., ser. 2, 2: 156. Port Natal (= Durban), South Africa.

Taxonomy Originally described in the genus *Mus*. For many years, the name *M. natalensis* has been used as the name for *Mastomys* mice from all over Africa (many papers actually using the naming *Praomys natalensis*). Recent studies have shown that there are not less than eight species of *Mastomys*, each characterized by its own karyotype, and now *M. natalensis* is restricted to populations with a chromosome number of $2n = 32$, $FN = 52–54$. The species has an extremely large geographic range (see below), and specimens from South Africa and from Senegal are reported to be conspecific (Granjon *et al.* 1996). However, chromosomal variation within the currently recognized species may indicate that *M. natalensis* is a species group with additional species still to be recognized. Synonyms: *caffer*, *cuninghamei*, *durumae*, *effectus*, *evelyni*, *fumatus*, *gardulensis*, *fusca*, *hildebrandtii*, *illovoensis*, *ismaillae*, *itigiensis*, *kerensis*,

komatiensis, *longicaudatus*, *microdon*, *muscardinus*, *neumanni*, *ovamboensis*, *pallida*, *panya*, *rufa*, *somereni*, *tana*, *tinctus*, *ugandae*, *victoriae*, *zuluensis*. Subspecies: none. Chromosome number: $2n = 32$, $FN = 52–54$.

Description Small, grey mouse. Dorsal pelage darkish-grey (young) to rusty-brownish (old adults). Ventral pelage dark grey; hairs with paler tip. Eyes dark and bulbous. Ears large, naked, rounded at tip. Fore- and hindfeet whitish. Tail long (ca. 100% of HB), dark above and below. Skull distinguishable from *M. coucha* and *M. huberti* by multivariate techniques only, but with considerable misclassification (Dippenaar *et al.* 1993, Lecompte *et al.* 2002b). Spermatozoa and genital morphology slightly different from other species of *Mastomys* (Gordon & Watson 1986, Lavrenchenko & Baskevich 1996) but these characters are cumbersome for species identification. Nipples: 12 (equally spaced from axilla to inguinal region) = 24.

Geographic Variation Uncertain.**Similar Species**

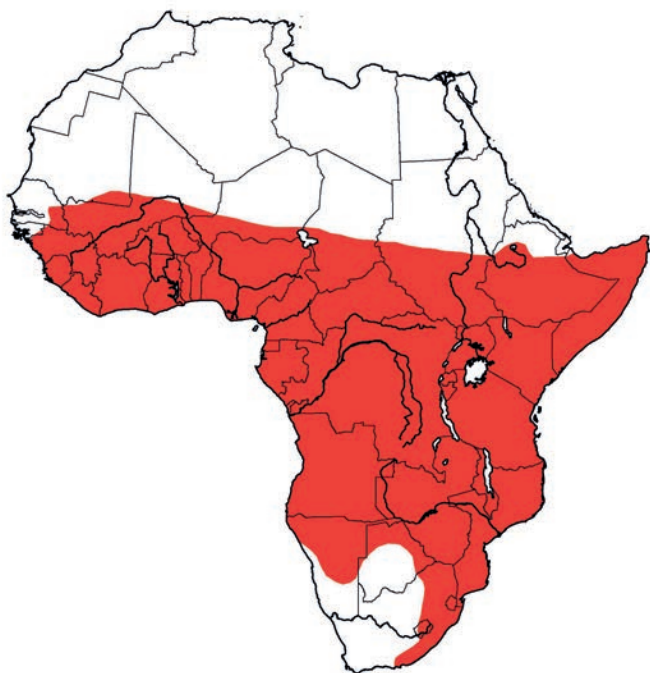
M. erythroleucus. Larger mean HB and T; ventral pelage cream; widespread distribution; common; overlap in geographic range in West Africa but not in eastern or southern Africa; $2n = 38$, $FN = 50–56$.

Praomys daltoni. Smaller mean HB and T; T longer as % of HB (110%); ventral pelage pure white; widespread distribution and common in savanna habitats of West Africa but not southern Africa; nipples: $3 + 2 = 10$; $2n = 36$.

M. coucha. Similar HB and T; ventral pelage dark grey; partially sympatric in southern Africa; common; prefers low altitude/high rainfall regions; nipples $12 \times 2 = 24$; $2n = 36$.

M. awashensis, *M. kollmannspergeri*, *M. pernanus*, *M. shortridgei*, *Myomyscus angolensis* and *Praomys derooi* are narrowly sympatric with *M. natalensis* in small and restricted areas (see profiles and maps).

Distribution Endemic to Africa. Very widely distributed throughout many biotic zones in western, central, eastern and

*Mastomys natalensis*

southern Africa but not in highland habitats such as alpine meadows. Recorded from Senegal, Mali, Benin, Burkina and Niger in West Africa to Ethiopia and Somalia in the east, and southwards through Kenya and Tanzania to Namibia and the eastern part of South Africa. *Mastomys natalensis* prefers low altitude/high rainfall regions (>600 mm annual rainfall), while *M. coucha* has a preference for higher altitude/relatively drier parts of South Africa (Dippenaar *et al.* 1993, Venturi *et al.* 2003). The species is absent from natural habitats in the Rainforest BZ in central Africa, but has been recorded in human settlements in that zone. Many records of *M. natalensis* throughout Africa, and the associated biological information, are uncertain because of lack of karyological identification and the large geographic overlap with most other *Mastomys* species. Molecular identification of tissue samples should resolve the distribution of this species in the near future.

Habitat Grassland, with or without bushes, thickets or trees, and disturbed patches. Very common in fields and fallow land as well as in and around buildings in human settlements. Does not occur in the rainforest but may be found in human settlements and agricultural fields within the Rainforest BZ. At the extremes of its geographic range may be limited to specific habitats, e.g. only inside villages in Senegal (Duplantier *et al.* 1990). It is a common pioneer species after fire (Meester *et al.* 1979).

Abundance One of the commonest species in savanna habitats, with densities of up to 1000/ha in disturbed areas. In farmland and fallow areas in Tanzania, 85% of the captured small mammals were multimammate mice while in natural miombo woodland and moist grassland 50 km away, they comprised only 27% of the trapped small mammals in a community of 17 different species (Leirs 1995). The species is well known for its seasonal fluctuations in numbers and irregular population explosions: maximum population numbers may be up to 40 times minimum numbers (Leirs *et al.* 1996). In a natural thicket-grassland savanna in Malawi, multimammate mice comprised 47% of small rodents in a community of ten species on an annual basis; densities fluctuated from 1/ha (dry season) to 40/ha (wet season) (Happold & Happold 1991). Abundance may be patchy, large numbers occurring in (preferred) habitats while other nearby habitats have no (or very few) individuals. Often the commonest of all rodents in food stores and houses where they may be very abundant and are regarded as a serious pest.

Adaptations Terrestrial and nocturnal. Activity is highest during the first half of the night, starting immediately after sunset. Multimammate mice can make their own burrows, but often use existing burrows or cracks in the soil. They can easily dig to a depth of more than 500 mm and can jump over 600 mm high (S. Vibe-Petersen unpubl.). The nest is constructed underground, often not very deep, and is a simple cavity lined with dried plant parts torn to pieces. The digestive system is adapted to a generalist diet (Perrin & Curtis 1980). Subadult animals become reproductively active very quickly after a period of heavy rainfall (Leirs *et al.* 1993, 1994). Survival of subadult and adult animals is affected in a complex way by a combination of density-dependent and density-independent (rainfall) factors (Leirs *et al.* 1997a).

Foraging and Food Opportunistic omnivores. The diet includes seeds of cereals, leaves and stems of grasses and dicotyledonous plants, insects and sometimes carrion (Leirs *et al.* 1994). Contents of stomachs reported in the literature often relate to the kind of habitat where the studies were carried out, illustrating the opportunistic nature of foraging. Seeds often make up a large proportion of the stomach contents (Field 1975, Taylor & Green 1976). Multimammate mice dig up newly-planted maize seeds, causing huge loss of potential harvest. They also climb maize stalks and damage the cobs. They are generally considered a pest in agriculture throughout their geographic range.

Social and Reproductive Behaviour Very lively, but generally not aggressive (although reported more aggressive than other *Mastomys* species). Home-ranges show a wide degree of overlap and there is no evidence of territoriality. For resident animals, home-ranges are rather small, ca. 1000 m², larger for males than for females (Leirs *et al.* 1997a). At times of dispersal, animals can move several hundred metres in only a few hours.

Reproduction and Population Structure Reproduction very seasonal, starting soon after the onset of the wet season and lasting well into the dry season. Germinating seed and young grass seedlings in the diet stimulate reproductive maturation (Leirs *et al.* 1994, Firquet *et al.* 1996). Mean litter-size varies widely between populations, e.g. 10–12 in Tanzania (with a reported maximum litter-size of 23) (Leirs 1995), 6.5 in Senegal (Duplantier *et al.* 1996) and 4.5 in E DR Congo (Rahm 1970). Gestation: 21–22 days. Postpartum oestrus a few days after parturition; mean litter interval 28 days during the breeding season. Copulatory plug only rarely formed (Johnston & Oliff 1954). Young altricial at birth; eyes open Day 15; weaned Day 21 (Baker & Meester 1977). Young animals rarely mature during the season of birth; they become reproductively active after abundant rainfall and vegetation growth in the next breeding season. When such rains come early, subadults may start reproducing at the age of three months. Most animals die towards the end of their first breeding season when not more than about 12 months of age. Sex ratio of subadults near 1:1, but strongly biased towards ♀♀ during the breeding season. Population structure is strongly influenced by the large litters, high reproductive rate and early mortality. In Malawi, the population in thicket-grassland savanna was composed primarily of subadults at end of dry season (when the population is at its lowest – see above); most of these subadults matured during the early wet season. Young began to enter the population towards the end of the wet season and early dry season, and soon formed the majority of the population as the adults died. By mid-dry season all young had become subadults. Population turnover was rapid due to dispersal of young, immigration of new animals from elsewhere and mortality of animals of all age-groups; individuals rarely live for more than 12 months (Happold & Happold 1991).

Predators, Parasites and Diseases Multimammate mice are a common prey of many owls, raptors, snakes and small ground-dwelling carnivores. Predation is an important source of mortality. The mice adapt their foraging behaviour and become more cautious in open spaces when the presence of raptors in the environment increases (Mohr *et al.* 2003). Attracting or excluding avian predators

has complex and sometimes compensatory effects on survival, reproduction and dispersal of the mice so there is no clear effect on the resulting population densities (Vibe-Petersen *et al.* 2006). Multimammate mice are the main reservoir for Lassa fever virus in West Africa, and also implicated in the epidemiology of bubonic plague and leptospirosis. Very little is known about diseases affecting the mice themselves.

Conservation IUCN Category: Least Concern.

One of the commonest small mammals in Africa. Considered to be a serious agricultural pest in many regions.

Measurements

Mastomys natalensis

HB (♂ ♂): 108 (74–145) mm, n = 801

HB (♀ ♀): 106 (66–171) mm, n = 751

T (♂ ♂): 108 (63–147) mm, n = 786

T (♀ ♀): 106 (70–175) mm, n = 736

HF (♂ ♂): 22.3 (17–25) mm, n = 797

HF (♀ ♀): 21.7 (16–25) mm, n = 747

E (♂ ♂): 17.2 (12–24) mm, n = 790

E (♀ ♀): 16.9 (11–25) mm, n = 741

WT (♂ ♂): 37.5 (9–84) g, n = 799

WT (♀ ♀): 35.3 (10–88) g, n = 752

GLS (♂ ♂): 28.5 (22.9–34.8) mm, n = 754

GLS (♀ ♀): 28.1 (22.3–32.3) mm, n = 699

GWS (♂ ♂): 13.6 (10.9–16.9) mm, n = 747

GWS (♀ ♀): 13.5 (10.9–16.4) mm, n = 702

M¹–M³ (♂ ♂): 5.0 (4.4–5.6) mm, n = 803

M¹–M³ (♀ ♀): 5.0 (4.5–5.7) mm, n = 754

Morogoro, Tanzania (H. Leirs unpubl., RMCA)

Key References Dippenaar *et al.* 1993; Duplantier *et al.* 1990; Granjon *et al.* 1996; Leirs 1995; Leirs *et al.* 1997a.

Herwig Leirs

Mastomys pernanus DWARF MULTIMAMMATE MOUSE (DWARF MASTOMYS)

Fr. Souris à mamelles multiples naine; Ger. Zwerg-Vielzitzenmaus

Mastomys pernanus (Kershaw, 1921). Ann. Mag. Nat. Hist., ser. 9, 8: 568. Amala River, Kenya (= upper course of the Mara River, situated at 00° 58' S, 25° 24' E according to Misonne & Verschuren 1964).

Taxonomy Originally described in the genus *Rattus*. The generic position of this species has been questioned, and recent molecular evidence indeed suggests that it should no longer be considered a member of *Mastomys* but is more closely related to *Hylomyscus* (Lecompte *et al.* 2002b). Synonyms: none. Chromosome number: not known.

Description Very small, grey mouse, smaller than all other *Mastomys*. Dorsal pelage darkish-grey with, in most specimens, an ochraceous stripe between flanks and ventral pelage. Ventral pelage grey, belly slightly washed with buff; hairs grey with white tip; small white chest patch in some individuals. Prominent spot of white hairs behind each ear. Tail long (85% of HB), well covered with short hairs (up to 1.5 mm). Typical *Mastomys* skull; mesopterygoid fossa triangular, very narrow on the posterior margin of the palatine and relatively wide towards the end (Van der Straeten 1999). Nipple number: not known.

Geographic Variation None recorded.

Similar Species

M. natalensis. Much larger mean HB and T; tail longer as % of HB; ventral pelage dark grey; widespread distribution and common; nipples 12 × 2 = 24; 2n = 32.

Distribution Endemic to Africa. Southern part of Somali–Masai Bushland BZ. Recorded from N Tanzania and S Kenya, with one morphologically somewhat aberrant specimen from Dakawa in C Tanzania. Unconfirmed records from Rwanda (Van der Straeten 1999).



Mastomys pernanus

Habitat The one specimen in Dakawa, Tanzania, was trapped in *Brachystegia* woodland (W. Verheyen, R. Verhagen & H. Leirs, unpubl.).

Abundance The very low number of specimens in collections indicates that the species is rare or not easily captured with usual trapping techniques. Only a single specimen was trapped at Dakawa Ranch, Tanzania, although 1333 other small mammals were collected at the same locality over a period of two years (W. Verheyen, R.

Verhagen & H. Leirs, unpubl.). In Rwanda, however, 14 out of 201 rodent specimens in owl pellets were identified as *M. pernanus* (Misonne & Verschuren 1964).

Remarks Apparently no other information available.

Conservation IUCN Category: Data Deficient.

Measurements

Mastomys pernanus

HB: 78 (73–88) mm, n = 7

T: 66 (60–78) mm, n = 6

HF: 16.1 (15–18) mm, n = 7

E: 14.9 (14–16), n = 7

WT: 18, 20 g, n = 2

GLS: 24.1 (23.2–25.1) mm, n = 3

GWS: 12.1 (11.8–12.5) mm, n = 3

M¹–M³: 4.0 (3.8–4.4) mm, n = 6

S Kenya, N Tanzania (Van der Straeten 1999; all known specimens)

Weight: E. Van der Straeten and H. Leirs unpubl.

Key Reference Van der Straeten 1999.

Herwig Leirs

Mastomys shortridgei SHORTRIDGE'S MULTIMAMMATE MOUSE (SHORTRIDGE'S MASTOMYS)

Fr. Souris à mammelles multiples de Shortridge; Ger. Shortridges Vielzitzenmaus

Mastomys shortridgei (St Leger, 1933). Proc. Zool. Soc. Lond. 1933: 411. Okavango–Omatako junction, Grootfontein District, Namibia.

Taxonomy Originally described in the genus *Myomys*. Van der Straeten & Robbins (1997) confirmed the classification of this species in the genus *Mastomys*. It has been suggested that *M. shortridgei* was conspecific with *M. angolensis*, but the nipple arrangement is different in the two species, and *angolensis* is now placed in the genus *Myomyscus*. Referred to as *Myomys shortridgei* by Shortridge (1934) and as *Praomys shortridgei* by Smithers (1971). Synonyms: *legerae*. Subspecies: none. Chromosome number: 2n = 36, FN = 50.

Description Medium-sized dark grey mouse. Dorsal pelage dark grey, sometimes nearly black; hairs grey at base with buffy tip. Ventral pelage grey; hairs grey at base with white tip. Upper surface of fore- and hindfeet white. Tail long (ca. 88% of HB), dark above and below. Skull typical of *Mastomys*, but pterygoid fossa wider than in other *Mastomys* and the anterior palatal foramina do not reach the inner root of M¹ (Meester *et al.* 1986). There is confusion in the literature about the number of nipples: Gordon (1985) mentioned two rows of eight nipples, but Van der Straeten (2001 in litt.) confirmed that the holotype has two rows of five nipples each (total ten).

Geographic Variation None recorded.

Similar Species

M. natalensis. Smaller mean HB; tail longer as % of HB; ventral pelage dark grey; widespread distribution and common; nipples 12 × 2 = 24; 2n = 32.

Distribution Endemic to Africa. Zambezi Woodland BZ. Usually thought to be endemic to extreme NW Botswana and NE Namibia in the region of the confluence of Okavango and Kwito rivers. However, Crawford-Cabral (1998) reported a few specimens from scattered localities in E Angola.

Habitat Marshes and the banks and terraces of rivers. Sometimes commensal.

Abundance Uncertain. Smithers (1971) recorded that it occurs with *M. natalensis* in Botswana but was the least common of the two



Mastomys shortridgei

species. Rare in collections from Angola (Crawford-Cabral 1998), although Shortridge (1934) mentioned that it was plentiful locally.

Remarks Terrestrial and nocturnal. Granivorous; probably omnivorous (Smithers 1971). None of 18 ♀♀ collected in Apr and May in NW Botswana showed signs of breeding, but a tiny juvenile was trapped in Feb (Smithers 1971).

Conservation IUCN Category: Least Concern.

Measurements

Mastomys shortridgei

HB: 120 (103–137) mm, n = 25

T: 105 (86–118) mm, n = 25

HF: 25 (23–27) mm, n = 25

E: 18 (17–20) mm, n = 25
 WT: 46 (35–74) g, n = 25
 GLS: n. d.
 GWS: n. d.
 M¹–M³: n. d.

Okavango Region and Western Caprivi, NE Namibia (Shortridge 1934)
 Weight: Smithers 1971

Key References Shortridge 1934; Skinner and Smithers 1990.

Herwig Leirs

GENUS *Muriculus* Ethiopian Striped Mouse

Muriculus Thomas, 1903. Proc. Zool. Soc. Lond. 1902 (2): 314. (publ. 1903). Type species: *Mus imberbis* Rüppell, 1842.



Muriculus imberbis.

A monotypic genus confined to higher altitudes in Ethiopia. The genus has been allied to *Mus* and *Zelotomys* (Osgood 1936) and especially to *Mus* (Ellerman 1941). The genus is characterized by pro-odont incisors (but without notch on the posterior side as in *Mus*), the cutting edges of the incisors form a semi-circular shape (similar to those of *Ammodillus*), the rostrum is thin and narrow (especially when viewed laterally), and the coronoid process on the mandible is low without a point and is approximately the same height as the articular condyle (Figure 75). There is a dark middle-dorsal stripe. The single species is *Muriculus imberbis*.

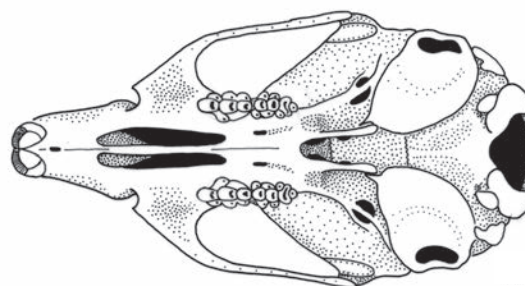
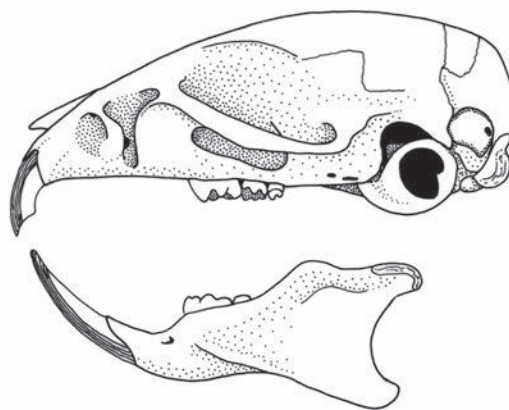


Figure 75. Skull and mandible of *Muriculus imberbis* (BMNH 28.1.1.153).

D. W. Yalden

Muriculus imberbis ETHIOPIAN STRIPED MOUSE

Fr. Souris à crinière; Ger. Simien-Maus

Muriculus imberbis (Rüppell, 1842). Mus. Senckenberg. 3: 110, pl. 6 (Fig. 4). Enschetgab, Ethiopia. 2800 m.

Taxonomy Originally placed in the genus *Mus*. Synonyms: *chilaloensis*. Subspecies: two. Chromosome number: not known.

Description Distinctive very small murine, with pro-odont upper incisors that distinguish the skull from related species. Pelage soft and dense. Dorsal pelage brown to olive-grey, with slight speckling; hairs dark grey at base, brownish at tip; some all-black hairs especially along mid-dorsal line. Faint mid-dorsal stripe along the middle of the back, which does not extend as far forward as the head nor over the rump. (Pelage colour very similar to *Mus mahomet* except for mid-dorsal

stripe.) Flanks paler, less black, often with yellowish line separating dorsal and ventral colours. Ventral pelage greyish to buff-white, with tinge of orange-buff in some individuals. Ears grey, with sparse short buffy hairs. Fore- and hindfeet whitish-grey dorsally. Tail (ca. 70% of HB) very clearly bicoloured with small hairs; dark above, pale below. Skull: see genus profile. Nipples: not known.

Geographic Variation

M. i. imberbis: Ethiopian plateau west of the Rift Valley. Ventral pelage greyish-white or buff.

*Muriculus imberbis*

M. i. chilaloensis: south-eastern plateau of Ethiopia, east of the Rift Valley. Ventral pelage white with a yellow tinge.

Similar Species

Mus mahomet. Very similar, but on average slightly smaller, lacks the mid-dorsal stripe; incisors orthodont (not pro-odont).

Distribution Endemic to Africa. Afromontane–Afroalpine BZ of Ethiopia. Confined to the grasslands (woina dega) of the high plateaux of Ethiopia, from 1900 to 3400 m. Known from only about nine localities (Yalden *et al.* 1976, Yalden & Lagen 1992).

Habitat Typically open upland grasslands, but also reported as commensal in Simien Mts (Müller 1977).

Abundance Rare. Only 12 specimens known (Yalden *et al.* 1976; Yalden & Lagen 1992). Collecting in Ethiopia (1968–98, $n = \text{ca. } 6300$ rodents) yielded no individuals of this species. Some individuals were found in houses in the Simien Mts in the 1970s (Müller 1977), but none were recorded there in the 1990s (Nievergelt *et al.* 1998). Despite extensive recent trapping, not known to occur in the Bale Mts.

Remarks Probably terrestrial and nocturnal. The pro-odont upper incisors suggest that these mice may dig their own burrows in the otherwise rather open habitat. Presumably granivorous. One juvenile found in Sep (label, BMNH).

Conservation IUCN Category: Endangered.

The grassland habitat is threatened by continuing modification and destruction by humans and their livestock; Yalden *et al.* (1976) speculated that the species was less common than 50 years previously. Schlitter (1989) recommended that the species should be classified as Vulnerable.

Measurements

Muriculus imberbis

HB: 70, 78 mm, $n = 2$

T: 50, 52 mm, $n = 2$

HF: 16.5 (16–17) mm, $n = 3$

E: 11, 12 mm, $n = 2$

WT: n. d.

GLS: 21.5 (20.6–22.5) mm, $n = 3$

GWS: 11.0 mm, $n = 1$

M^1 – M^3 : 4.0 (3.8–4.1) mm, $n = 3$

Ethiopia (D.W. Yalden unpubl.)

Key References Müller 1977; Nievergelt *et al.* 1998; Yalden *et al.* 1976; Yalden & Lagen 1992.

D.W. Yalden

GENUS *Mus*

Old World Mice and Pygmy Mice

Mus Linnaeus, 1758. Syst. Nat., 10th edn., 1: 59. Type species: *Mus musculus* Linnaeus, 1758.

*Mus minutoides*

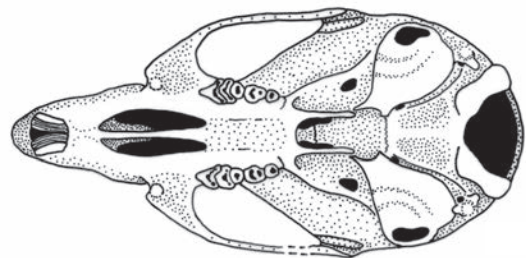
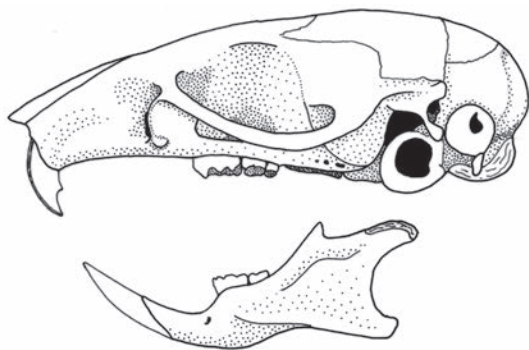
In Africa, the genus *Mus* is represented by about 20 species (Table 37). Species within the genus occur throughout most of the continent and are recorded from forest, savanna, highland grassland and semi-

arid habitats, and from sea level to ca. at least 2000 m. The only habitats where *Mus* does not occur are rainforests and arid deserts. Extraliminally, the genus is represented throughout the Old World. One species, *Mus musculus*, has been introduced into all continents (including Africa) and many islands, and has, in general, proved to be a very successful colonizer.

The genus, as exemplified by African species, is characterized by small size (HB: ca. 43–90 mm, GLS: 16–25 mm, WT: 3–20 g), delicate build, shortish pelage and shortish tail without a terminal pencil. Upper incisors opisthodont or slightly pro-odont; uniquely there is a notch on the posterior face of the upper incisors. Other diagnostic skull characters include pronounced masseteric knob on the zygomatic plate near the lower edge, anterior palatal foramina,

Table 37. Species in the genus *Mus*. Arranged in order of increasing mean head and body length. (n. d. = no data.)

| Species | Subgenus ^a | HB mean (range) (mm) | Tail mean (range) (mm) [% of HB] | GLS mean (range) (mm) | White spots on head | Choanae ^b | |
|-----------------------|-----------------------|----------------------|----------------------------------|-----------------------|--------------------------------------|----------------------|--|
| <i>M. tenellus</i> | N | 48.4 (43–53) | 34 (30–36) [70%] | 16.8 (16–17.5) | Subauricular and postauricular | U | |
| <i>M. haussa</i> | N | 49.7 (44–52) | 38 (35–42) [75%] | 16.6 (15–17) | None | U or V | |
| <i>M. mattheyi</i> | N | 52 (46–60) | 38.4 (33–44) [70%] | 16.6 (15–17) | None | U or V | |
| <i>M. indutus</i> | N | 53.2 (45–65) | 42 (30–52) [80%] | 17.7 (16.5–19.5) | Subauricular | U | |
| <i>M. minutoides</i> | N | 54.8 (45–68) | 41 (38–49) [75%] | 18.8 (17.5–20.4) | Subauricular, small | U | |
| <i>M. sorella</i> | N | 59.9 (51–73) | 38.9 (34–46) [65%] | 19.7 (17.8–21.0) | Subauricular, small | V | |
| <i>M. orangiae</i> | N | 59.6 (52–63) | 37.5 (36–39) [63%] | 18.6 (18.5–18.7) | n. d. | U | |
| <i>M. musculoides</i> | N | 60.8 (55–70) | 43.6 (32–55) [72%] | 19.3 (18.3–20.2) | Subauricular, small | U | |
| <i>M. goundae</i> | N | 61 (60–62) | 34 (31–37) [55%] | 19 (18–20) | Postauricular, large | V | |
| <i>M. setzeri</i> | N | 61 (ca.) | 36 (31–48) [59%] | 18.0 (17.5–18.3) | None | U | |
| <i>M. oubanguii</i> | N | 62.7 (50–75) | 38 (26–44) [61%] | 20 (18.6–21.5) | Postauricular, large | V | |
| <i>M. baoulei</i> | N | 65.9 (59–73) | 36.9 (32–45) [50–65%] | 18.8 (17.7–20.4) | Suborbital, and subauricular (ochre) | U | |
| <i>M. mahomet</i> | N | 67 (63–73) | 53.5 (46–60) [74%] | 19.9 (18.4–21.0) | None | U | |
| <i>M. bufo</i> | N | 68.4 (63–78) | 66.6 (61–74) [97%] | 20.9 (20.1–21.6) | None | U | |
| <i>M. spretus</i> | M | 77 (ca.) | 62 (55–71) [ca. 80%] | 19.8 (18.3–21.8) | None | U | |
| <i>M. triton</i> | N | 75.9 (69–80) | 54 (49–63) [71%] | 21.8 (20.5–22.7) | None | U | |
| <i>M. setulosus</i> | N | 81.8 (77–86) | 55.5 (52–59) [68%] | 21.1 (19.3–21.9) | None | U | |
| <i>M. musculus</i> | M | 83.7 (78–91) | 77.2 (66–85) [92%] | 21.6 (21–22.3) | None | U | |
| <i>M. neavei</i> | N | 88.8 (58–106) | 38.4 (33–48) [43%] | 18.5 (18–18.9) | ? | V | |
| <i>M. callewaerti</i> | N | 88.8 (84–97) | 44.8 (43–46) [50%] | 25.4 (23.4–25.1) | None | ?U | |

^a N = subgenus *Nannomys*; M = subgenus *Mus*. See genus profile for details.^b U = U-shaped choanae; V = V-shaped choanae.Figure 76. Skull and mandible of *Mus setulosus* (MNHN 1998/887).

| | Colour of ventral pelage | Chromosome number | Distribution and Notes |
|--|---------------------------------------|-----------------------------|---|
| | Pure white | n. d. | Sudan, S Ethiopia, S Somalia, S Kenya and C Tanzania; postauricular patch is obvious tuft |
| | Pure white | 2n = 28–34, FN = 38 | Sudan and Sahel Savanna BZs; Senegal to Sudan |
| | Pure white | 2n = 36, FN = 36 | Sudan and Guinea Savanna BZs; West Africa |
| | Pure white | 2n = 36, FN = 36–37 | Southern Africa |
| | Pure white | 2n = 18–34, FN = 36 | Southern and eastern Africa; widespread |
| | Pure white | n. d. | Central Africa |
| | Pure white | n. d. | C South Africa |
| | Pure white | 2n = 38 (polymorphic) | Guinea and Sudan Savanna BZs. W Africa (and towards central Africa) |
| | Pure white | 2n = 16–19, FN = 30 | Central African Republic. Very rare |
| | Pure white | n. d. | Namibia, Botswana, Zambia |
| | Pure white | 2n = 28, FN = 30–34 | Central African Republic |
| | Pure white | 2n = 20, FN = 32 | Guinea to Togo |
| | Greyish-white (sometimes with orange) | 2n = 36, aFN = 34 | Ethiopia, SW Kenya, SW Uganda |
| | Buff to greyish-buff | 2n = 36, FN = 36 | Mountains of Albertine Rift in E DR Congo, W Uganda and Burundi |
| | Whitish | n. d. | N Morocco to N Libya |
| | Medium-dark grey, white tips | 2n = 34, FN = 34 (variable) | Central Africa; widespread |
| | Pure white | 2n = 36, FN = 36 | Sierra Leone to S Sudan and Ethiopia |
| | Usually grey, sometimes white | 2n = 40 | Mostly ports on coastline |
| | Pure white | n. d. | Tanzania to South Africa; ears large and pale |
| | Medium-dark grey, white tips | n. d. | NE and C Angola, S and W DR Congo |

which extend well posterior to the anterior end of M¹, laminae of the molar teeth, which tilt posteriorly, t1 of M¹ distorted posteriorly and hence almost in line with t4 and t5, and very small M³ (Figure 76).

There is great variation in the distribution and abundance of species of *Mus* in Africa. Some are widespread and numerous (*M. minutoides*, *M. musculoides*, *M. setulosus*), some have very limited distributions (e.g. *M. bufo*, *M. goundae*, *M. oubanguii*), and others are known from only few widely scattered localities and their full geographic range is uncertain (e.g. *M. callewaerti*, *M. sorella*, *M. tenellus*). Typically, individuals of many species of *Mus* are numerous in favoured environments and contribute a relatively large percentage to the total rodent community; they have short life expectancies and high fecundity, and the population

turnover is rapid. They form an important source of food for smaller predators, and their remains often contribute a high percentage of total prey in the pellets of owls. Individuals of *Mus* spp. are mostly gregarious and non-territorial. They are granivorous or omnivorous, their small size necessitating that they eat only high quality foods.

The genus is divided into four subgenera, two of which are represented in Africa: subgenus *Mus* (typical Old World Mice) distinguished by larger size, flat anterior face to the zygomatic plate, masseteric knob at the lower anterior corner of the plate, and M³ with two (often inconspicuous) laminae (2 spp. – *M. musculus*, *M. spretus*); and the subgenus *Nannomys* (African Pygmy Mice), distinguished by smaller size, convex anterior face to the zygomatic plate, masseteric

knob at the lower centre of the plate, and M^3 usually without laminae (18 spp.). In the past, *Nannomys* was referred to as *Leggada* (e.g. De Graaff 1981, Smithers 1983, Meester *et al.* 1986) and has been raised to the rank of genus by some authorities (e.g. Allen 1939, Roberts 1951, Bonhomme 1992). The distinction between the two subgenera is not always clearcut (Petter 1963b) although, in West Africa, for example, the two can be easily separated (Rosevear 1969). For Africa, the recognition of *Nannomys* as a subgenus appears to be warranted (Musser & Carleton 2005). Here, the African species are allocated to the genus *Mus* (rather than *Leggada* or *Nannomys*) following Petter & Matthey (1975) and Musser & Carleton (2005).

Because all species of *Mus* (especially *Nannomys*) are small and morphologically similar, distinctions between species are often blurred. Geographical variation within widespread species is common and has resulted in the naming of many forms (species or subspecies), many of which are now regarded as synonyms. Within *Nannomys*, some species have been classified into groups implying at least some degree of relationship between the group-members. Based on some external and craniodental morphological similarities, Petter (1981) defined a 'sorella group', which included *M. sorella*, *M. goundae*, *M. neavei*, *M. oubanguii*, *M. kasaicus* (considered here to be conspecific with *M. minutoides* [but see Musser & Carleton 2005]) and two other species (*acholi*, *wamae*) now considered to be conspecific with *M. sorella*. Musser & Carleton (1993, 2005) indicate that the diagnostic characters of *M. baoulei* are closely similar to those of the *sorella* group, but suggest that the relationship of *M. baoulei* to other members of the *sorella* group requires fresh assessment. Musser & Carleton (2005) do not mention either *M. minutoides* or *M. musculoides* as belonging to the *sorella* group. Based on morphology of the sex chromosomes, two

groups within *Nannomys* can be distinguished. The first group (with acrocentric X and Y chromosomes) includes *M. bufo*, *M. indutus*, *M. mattheyi*, *M. mahomet* and *M. tenellus*, which all have 36 acrocentric chromosomes (diploid number $2n = 36$, and fundamental number $FN = 36$). Two additional species belong to this group: *M. setulosus* ($2n = 36$, $FN = 36$), which is distinguished from the others by large heterochromatin additions on several pairs of autosomes, and *M. haussa*, which is distinguished by a pericentric inversion and varying numbers of autosomal centric fusions ($2n = 28-34$, $FN = 38$) (Veyrunes *et al.* 2004). The second group (with metacentric X and/or Y chromosomes formed by sex-autosome translocations) includes *M. triton*, *M. oubanguii*, *M. musculoides*, *M. minutoides* and *M. goundae* (Matthey 1966a, b, Jotterand 1972, Veyrunes *et al.* 2004). This group is of special interest because of the large variation in the number and morphology of chromosomes between populations and even within populations ($2n = 18-34$, $FN = 30-36$). This is particularly evident for *M. minutoides* and probably also for *M. triton*. This diversity most likely indicates the occurrence of cryptic species (Veyrunes *et al.* 2004). In the absence of chromosomal data, the other species have not yet been assigned to either group (i.e. *M. baoulei*, *M. callewaerti*, *M. neavei*, *M. orangiae*, *M. setzeri* and *M. sorella*). Consequently, it is not yet possible to determine if the *sorella* group of Petter (1981) corresponds to the second of the groups based on chromosome morphology (although there is at least some overlap in species composition); pending resolution of this problem, the affinities of species to these groups are not given in the species profiles. Species in the genus may be distinguished by size, pelage colour, skull characters and karyology.

D. C. D. Happold & F. Veyrunes

Mus baoulei BAOULE PYGMY MOUSE

Fr. Souris naine de Baoulé; Ger. Baouli-Zwergmaus

Mus baoulei (Vermeiren & Verheyen, 1980). Rev. Zool. Afr. 94: 573. Lamto, Côte d'Ivoire.

Taxonomy Originally described in the genus *Leggada*. Subgenus *Nannomys*. Synonyms: none. Chromosome number: $2n = 20$, $FN = 32$ (M. Tranier unpubl.).

Description Very small mouse. Dorsal pelage grey-brown to dark-brown; hairs grey at base, brown at tip. Flanks paler than dorsal pelage, becoming yellowish- to reddish-brown towards ventral surface. Ventral pelage pure white, clearly delineated from dorsal pelage on flanks and cheeks. One ochre spot below each eye and one below each ear. Tail short (50–65% of HB), brown above, paler below, covered with fine and short hairs. Skull: anterior palatal foramina very long (3.65 mm, range 3.65–4.70), and longer than for sympatric species of *Mus*. Nipples: not known.

Geographic Variation None recorded.

Similar Species

M. goundae. Chromosome number: $2n = 16-19$, $FN = 30$; Central African Republic.

M. oubanguii. Chromosome number: $2n = 28$, $FN = 30-34$; Central African Republic.

M. kasaicus, *M. neavei* and *M. sorella*. All belong to the 'sorella' group of Petter (1981), are of similar size, and have a more easterly distribution.

M. setulosus. A little larger; chromosome number: $2n = 36$, $FN = 36$; no auricular spots; relatively longer tail; West to East Africa.

M. musculoides. Brighter pelage; chromosome number: $2n = 18-34$, $FN = 36$; relatively longer tail; West and East Africa.

M. haussa. Paler colour; chromosome number: $2n = 28-34$, $FN = 38$; West Africa.

M. mattheyi. Chromosome number: $2n = 36$, $FN = 36$; West Africa.

Cranial and dental characters also enable discrimination between these species (Vermeiren & Verheyen 1980, Musser & Carleton 1993).

Distribution Endemic to Africa. Guinea Savanna BZ and Northern Rainforest–Savanna Mosaic. Known only from E Guinea, Côte d'Ivoire and Togo (Vermeiren & Verheyen 1980, Musser & Carleton 1993, Robbins & Van der Straeten 1996).

Habitat Savanna.

Abundance Uncertain; may be locally abundant (e. g. Lamto, Côte d'Ivoire, cf *M. musculoides*, *L. setulosus*) (Vermeiren & Verheyen 1980).

Remarks Apparently no other information available.

Conservation IUCN Category: Least Concern.

Measurements

Mus baoulei

HB: 65.9 (59–73) mm, n = 47

T: 36.9 (32–45) mm, n = 35

HF (c.u.): 13.3 (12–15) mm, n = 40

E: 10 (8–12) mm, n = 35

WT: n. d.

GLS: 18.8 (17.7–20.4) mm, n = 6*

GWS: 9.1 (8.3–9.8) mm, n = 40

M¹–M³: 3.1 (2.8–3.4) mm, n = 66

Côte d'Ivoire (Vermeiren & Verheyen 1980, MNHN) and Guinea (MNHN)

*MNHN only

Key Reference Vermeiren & Verheyen 1980.



Mus baoulei

Laurent Granjon

Mus bufo TOAD PYGMY MOUSE (RWENZORI MOUSE)

Fr. Souris naine crapaud; Ger. Kröten-Zwergmaus

Mus bufo Thomas, 1906. Ann. Mag. Nat. Hist., ser. 7, 18: 145. Rwenzori East, Uganda, 6000 ft (1830 m).

Taxonomy Subgenus *Nannomys*. Morphologically similar to sympatric *Mus triton* but different in external, skull, dental, karyological and ecological characters (F. Dieterlen unpubl.). The form *ablutus* from Idjwi I. in L. Kivu could be a valid subspecies (Allen & Loveridge 1942). Electrophoretic analysis of protein enzymes at 24 loci indicates that *M. bufo* is more closely related to *M. gratus* (= *M. minutoides*) than to *M. triton* (Van Rompaey *et al.* 1984). Synonyms: *ablutus*, *wambutti*. Subspecies: none currently recognized. Chromosome number: 2n = 36, FN = 36 (Jotterand-Bellomo 1988, Maddalena *et al.* 1989).

Description Small mouse, smaller than sympatric *M. triton*. Dorsal pelage stiff and thick, hairs long (8–9 mm). Dorsal pelage dark coppery-brown, rather variable; hairs slate-grey to black at base, dull reddish-brown at tip; softer underfur black, grey or buff. Rump darkish. Ventral pelage buff to greyish-buff, shorter than dorsal pelage. Yellowish line between dorsal and ventral pelage in some individuals. Ears dark with scattered short buffy hairs. No postauricular or subauricular spots. Upper surface of forefeet and hindfeet brown with a tinge of buff. Tail long (ca. 97% of HB), finely scaled, with dense short blackish bristles above, whitish below. Skull stoutly built but less so than in *M. triton*; anterior palatal foramina long, extending nearly to the middle of M¹; mesopterygoid fossa broad compared to *M. triton* (Thomas 1906a). Nipples: 3 + 1 = 8.

Geographic Variation None currently recognized (see Taxonomy).



Mus bufo

Similar Species

M. triton. Larger; tail shorter (71% of HB); ventral pelage paler (usually greyish-white); different chromosome number (see species profile).

Distribution Endemic to Africa. Afromontane–Afroalpine BZ in montane regions of the Albertine Rift Valley, normally 1500–3000 m (Misonne 1963, Delany 1975, F. Dieterlen unpubl.). Recorded in Upper Ituri region west of L. Albert and on both sides of the Albertine Rift Valley from ca. 01° N to ca. 03° S. Specific locations include Rwenzori Mts (DR Congo, Uganda); Virunga Mts and mountains west of L. Edward (DR Congo); and on both sides of L. Kivu (E DR Congo, W Rwanda, NW Burundi) (Elbl *et al.* 1966, Dieterlen 1967a, Rahm 1967, Maddalena *et al.* 1989, J. Kerbis Peterhans, in litt.). One record from Itombwe Mts, west of L. Tanganyika (von Wettstein-Westersheim 1923). Records from lowland forests below 1000 m need verification, especially Ituri Forest (the type locality of *M. b. wambutti*; Lönnberg & Gyldenstolpe 1925) and Irangi, E DR Congo (Rahm 1967). An extralimital record from the Aberdare Mts, Kenya (Misonne 1963) also needs verification (not shown on map).

Habitat In Kahuzi-Biega N. P., E DR Congo (at 2300–2400 m), preferred habitats are bamboo forest (*Arundinaria alpina*) and stands of *Hagenia abyssinica*, both with grass cover (*Panicum massaiense*) (F. Dieterlen unpubl.). Other habitats include secondary growth on the edge of dense montane forest (2000–2200 m), low and dense afroalpine vegetation (e.g. with *Erica*, *Senecio*, *Lobelia*, *Helichrysum*) on the peak of Mt Kahuzi, E DR Congo (3260–3308 m), and dense stands of *Pennisetum purpureum* in the cultivated zone west of L. Kivu, DR Congo (1500–1900 m). On Rwenzori Mts, Uganda, recorded in grassland (1500 m), low montane forest (1900 m), high montane forest (2600 m) and bamboo (2960 m) (Kerbis Peterhans *et al.* 1998).

Abundance Generally rare in the cultivated zone west of L. Kivu (1500–1900 m). Less common than *M. minutoides* on Idjwi I. in L. Kivu (Rahm & Christiaensen 1966). Often occurs sympatrically with *M. triton* and *M. minutoides* in E DR Congo; e.g. at five locations, *M. bufo* comprised 4.38% of all small mammals (*M. minutoides* 8.24%, *M. triton* 3.91%, $n = 2340$) although the percentage values varied according to locality from 0.7% to 6.5% (Rahm 1967). Numbers varied from month to month over four years (at a single locality); *M. bufo* was

normally the second or third commonest species of the three species of *Mus*, and much less abundant than *M. minutoides* (Rahm 1967). More common in selected habitats in Kahuzi-Biega N. P., E DR Congo.

Adaptations Mainly nocturnal (Delany 1975, Kerbis Peterhans *et al.* 1998).

Foraging and Food Herbivorous, occasionally omnivorous. Most stomach contents (eight of 13) contained exclusively starch-like vegetable material, a whitish-brownish pulp of seeds and tubers; five stomachs contained animal food (chitinous parts, fibres, parts of intestines) comprising only up to ca. 20% of stomach contents (F. Dieterlen, unpubl.).

Reproduction and Population Structure Seasonal trends in reproduction not known. A few pregnant and/or lactating ♀♀ recorded in different seasons. Embryo number: 3 and 4 ($n = 2$). As for other species of the genus *Mus*, captures of ♂♂ outnumber ♀♀ (36 : 25; F. Dieterlen unpubl.).

Predators, Parasites and Diseases No information.

Conservation IUCN Category: Least Concern.

Measurements

Mus bufo

HB: 68.4 (63–78) mm, $n = 30$

T: 66.6 (61–74) mm, $n = 27$

HF: 15.3 (13–18) mm, $n = 30$

E: 11.8 (10–13) mm, $n = 30$

WT: 10.4 (6–16) g, $n = 30$

GLS: 21.0 (20.1–21.6) mm, $n = 11$

GWS: 10.1 (9.9–10.3) mm, $n = 9$

M¹–M³: 3.4 (3.1–3.5) mm, $n = 10$

Parc National de Kahuzi-Biega, DR Congo (F. Dieterlen unpubl., SMNS)

Key References Delany 1975; Misonne 1963.

Fritz Dieterlen

***Mus callewaerti* CALLEWAERT'S PYGMY MOUSE**

Fr. Souris naine de Callewaert; Ger. Callewaerts Zwergmaus

Mus callewaerti (Thomas, 1925). Ann. Mag. Nat. Hist., ser. 9, 15: 668. Lualaba, Luluabourg, DR Congo. 610 m.

Taxonomy Subgenus *Nannomys*. Described in the genus *Hylonomys* (Thomas 1925), a genus distinguished from *Leggada* (= *Nannomys*) by the presence of pro-odont incisors (a character now known to be present in several species of *Leggada*). *Hylonomys* now synonymized with *Mus* (Musser & Carleton 1993, 2005). Synonyms: none. Chromosome number: not known.

Description The largest species of the genus, similar externally to *M. triton*. Pelage stiff, dense and coarse. Dorsal pelage medium-brown, hairs dark grey at base, with subterminal medium brown

band and black tip. Ventral pelage whitish-grey; hairs dark grey on basal half, off-white on terminal half. (Hill & Carter [1941] state that ventral pelage may have a pale pinkish-brown tinge especially on chest.) Ears short, brown. Lips and chin white. No postauricular or subauricular spots. Fore- and hindfeet dirty-white. Tail short (ca. 50% of HB), indistinctly bicoloured, brown above, whitish below. Skull: large for the genus; supraorbital crests well developed; auditory bullae large; incisor teeth white on anterior surface, slightly pro-odont. Nipples: not known.

Geographic Variation None recorded.

Similar Species

M. triton. Smaller; ventral pelage grey; supraorbital crests on skull absent; auditory bullae small; incisor teeth yellowish-orange on anterior face; sympatric at some localities (e.g. Chitau, Angola).

M. sorella. Much smaller; ventral pelage pure white.

M. minutoides. Much smaller; dorsal pelage brownish-buff; ventral pelage pure white; incisor teeth yellowish on anterior surface.

Distribution Endemic to Africa. Zambezan Woodland BZ and Southern Rainforest–Savanna Mosaic. Recorded from C and NE Angola and S and SE DR Congo. Altitudes from 610 m (holotype) to 1810 m (SE DR Congo) (Crawford-Cabral 1998). Sympatric with *M. triton*.

Habitat ‘Forest’ (holotype in SE DR Congo; Cabrera & Ruxton 1926) and savanna (Sanborn 1952).

Abundance Uncertain; known by only a few specimens. Recorded as ‘peu commun’ (Sanborn 1952).

Remarks One specimen had eaten fruits of prickly pear *Opuntia* sp. In Angola, Hill & Carter (1941) remarked ‘Apparently in the debris they live on the many insects frequenting such places.’ Females collected in Jul and Aug were ‘apparently lactating’ (Hill & Carter 1941).

Conservation IUCN Category: Least Concern.

The limited number of records and rarity of specimens are causes for concern. In Angola, there are many seemingly suitable localities where the species has not been encountered (Crawford-Cabral 1998). Eaten by local people (Sanborn 1952).

Measurements

Mus callewaerti

HB: 88.8 (84–97) mm, n = 4



Mus callewaerti

T: 44.8 (43–46) mm, n = 4

HF: 15.3 (12–17) mm, n = 4

E: 11.3 (10–14) mm, n = 4

WT: n. d.

GLS: 24.5 (23.4–25.1) mm, n = 4

GWS: 11.3 (10.7–11.9) mm, n = 3

M¹–M³: 3.8, 3.8 mm, n = 2

Auditory bulla: 4.9, 5.1 mm, n = 2

Angola and DR Congo (Hill & Carter 1941, Misonne 1965b)

Key Reference Hill & Carter 1941; Misonne 1965b; Sanborn 1952.

D. C. D. Happold

Mus goundae GOUNDA RIVER PYGMY MOUSE

Fr. Souris naine de la Gounda; Ger. Gounda-Fluss Zwergmaus

Mus goundae Petter and Genest, 1970. Mammalia 34: 455. Gounda River, N Central African Republic.

Taxonomy Subgenus *Nannomys*. Related to *M. oubanguii*. Synonyms: none. Chromosome number: 2n = 16–19, FN = 30; chromosomal polymorphism caused by Robertsonian translocations (Jotterand 1970, 1972).

Description Very small brownish-orange mouse, with pure white ventral pelage. Dorsal pelage ochraceous-brown, with orange-rufous on flanks. Ventral pelage pure white. Colour of dorsal pelage and ventral pelage clearly delineated on lower flanks. Ears large, blackish, slightly pointed at tip. White postauricular patch present. Fore- and hindfeet comparatively large, white. Tail short (ca. 55% of HB). Skull: rostrum elongated; incisors slightly pro-odont, choanae V-shaped; anterior palatal foramina short (one tenth of M¹–M³), M¹

with prelobe and without accessory cusp; M³ small; M₁ with anterior lobe quadricuspidate. Nipples: 2 + 2 = 8.

Geographic Variation None recorded.

Similar Species

M. oubanguii. Similar size; dorsal pelage reddish-brown; large white postauricular patch; nipples 3 + 2 = 10; chromosome number: 2n = 28.

M. setulosus. Larger (HB: 81.8 [77–86] mm, T: 55.5 [52–59] mm, GLS: 21.1 [19.3–21.9]); dorsal pelage blackish-brown; no auricular patches; nipples not known; chromosome number: 2n = 36.

M. musculoides. Similar size; dorsal pelage golden-brown; no postauricular patch; nipples $2 + 2 = 8$; chromosome number: $2n = 25-32$ (polymorphic); common and widespread.

Distribution Endemic to Africa. Guinea Savanna BZ. Only known from near the Gounda R., north-east of N'Délé, N Central African Republic.

Habitat Wooded savanna.

Abundance No information; known only from the type locality.

Remarks Apparently no other information available.

Conservation IUCN Category: Data Deficient.

The single known population is very small, and the number of individuals is probably declining.

Measurements

Mus goundae

HB: 60, 62 mm, $n = 2$

T: 31, 37 mm, $n = 2$

HF: 12, 14 mm, $n = 2$

E: 12, 13 mm, $n = 2$

WT: n. d.

GLS: 18, 20 mm, $n = 2$

GWS: n. d.



Mus goundae

M^1-M^3 : 3.5, 3.7 mm, $n = 2$

Central African Republic (MNHN)

Key Reference Petter & Genest 1970.

F. Petter

Mus haussa HAUSA PYGMY MOUSE

Fr. Souris naine Haussa; Ger. Haussa Zwergmaus

Mus haussa (Thomas and Hinton, 1920). Novit. Zool. 27: 319. Farniso, near Kano, N Nigeria.

Taxonomy Originally described in the genus *Leggada*. Subgenus *Nannomys*. Morphologically and ecologically similar to *M. tenellus* (Rosevear 1969, Musser & Carleton 2005). Synonyms: none. Chromosome number: $2n = 28-34$, $FN = 38$ (Jotterand 1972, Veyrunes 2002, Granjon & Dobigny 2003).

Description Very small pale-coloured mouse; the smallest species of *Mus* in sub-Saharan Africa. Dorsal pelage pale sandy. Ventral pelage pure white. Colour of dorsal pelage and ventral pelage clearly delineated on flanks. Ears sandy-grey, with small whitish or sandy hairs. No postauricular patch of white hairs. Cheeks, lips and throat white. Fore- and hindfeet white. Tail short (ca. 75% of HB), scaly, pale or white, more or less naked. Skull: GLS 17 mm or less (cf. *M. minutoides*); upper incisors opisthodont, choanae U-V shaped, anterior palatal foramina elongated; M^1 elongated and 65–70% of M^1-M^3 ; M_1 with anterior lobe tricuspidate. Nipples: $3 + 2 = 10$.

Geographic Variation None recorded.

Similar Species

M. mattheyi. On average slightly larger (HB: 52 [46–60] mm); dorsal

pelage ochre-tawny to chestnut; parapatric.

M. musculoides. Larger (HB: 61 [55–70] mm, GLS: 18.4 [17.8–18.9] mm); dorsal pelage darker, golden-brown flecked with dark brown; distribution in less arid habitats.

Distribution Endemic to Africa. Sahel and Sudan Savanna BZs from Senegal to Chad and Sudan.

Habitat Semi-arid grassland savanna of the sub-Sahara region.

Abundance Evidence from remains in owl pellets (from Senegal, Nigeria and Chad) suggest this species may be locally common (see below).

Remarks Nocturnal and terrestrial. Tolerates the hottest and driest climates of all species of pygmy mice. Diet is seeds and insects (no detailed studies). Remains found in owl pellets in W Senegal (F. Petter unpubl.), Mali (Meinig 2000) and N Nigeria where they formed 13% of the rodent prey (Demeter 1978).

Conservation IUCN Category: Least Concern.

Measurements

Mus haussa

HB: 49.7 (44–52) mm, n = 7

T: 38 (35–42) mm, n = 7

HF: 12 (12–13) mm, n = 7

E: 8.8 (8–10) mm, n = 7

WT: 3 g, n = 1

GLS: 16.6 (15–17) mm, n = 6

GWS: 8.4 (8.2–8.6) mm, n = 4

M¹–M³: 2.9 (2.9–3.1) mm, n = 7

Senegal (St Louis), Niger (Niamey), Nigeria (Farniso, Kano) and Chad (Njamena); BMNH, MNHN, SMF

Key References Happold 1987; Rosevear 1969.

F. Petter



Mus haussa

Mus indutus DESERT PYGMY MOUSE

Fr. Souris naine du désert; Ger. Wüstenzwergmaus

Mus indutus (Thomas, 1910). Ann. Mag. Nat. Hist., ser. 8, 5: 89. Molopo River, South Africa.

Taxonomy Originally described as *Leggada bella induta*. Subgenus *Nannomys*. Formerly considered as a subspecies of *M. minutoides*. Currently, *indutus* refers to *Mus* from the western parts of southern Africa, but the limits of its distribution are not known. Synonyms: *deserti*, *pretoriae*, *valschensis*. Subspecies: two or three. Chromosome number: 2n = 36, FN = 36–37 (Matthey 1966a, Veyrunes *et al.* 2004).

Description Very small mouse with soft pelage. Dorsal pelage variable shades of pale buff or pale buffy-orange; hairs slate-grey at base, some with black tip giving a grizzled appearance. Flanks buffy-orange without black-tipped hairs. Ventral pelage (including chin) pure white. Clear delineation between colour of flanks and ventral pelage. Head with pointed nose and long vibrissae. Ears moderately sized and rounded, brownish; small white subauricular patch (usually absent in eastern part of distribution). Limbs short with whitish feet; four digits on forefeet; five digits on hindfeet. Digits 3 to 4 elongated on both forefeet and hindfeet. All digits with well-developed claws. Tail long (ca. 80% of HB), pale buff above, white below. Nipples: 2 + 2 = 8.

Geographic Variation

M. i. indutus: Botswana and Namibia. Dorsal pelage comparatively pale buff.

M. i. pretoriae/valschensis: Gauteng Province, South Africa. Dorsal pelage tawny ochraceous-buff, reminiscent of *Mus minutoides*.

Similar Species

M. minutoides. Dorsal pelage generally darker, tail dark above; allopatric.



Mus indutus

M. setzeri. Ears longer; white ventral pelage extends onto upper rump and muzzle; sympatric.

Distribution Endemic to Africa. Zambezian Woodland and South-West Arid (Kalahari Desert) BZs. Recorded from C and

N Namibia (Matson & Blood 1994), through Botswana to NW South Africa and W Zimbabwe. Extends northwards into S Angola (Crawford-Cabral 1998) and SW Zambia (Ansell 1978).

Habitat Tolerates a wide range of habitats in semi-arid savannas (Nel 1978); avoids open micro-habitats (Kerley *et al.* 1990).

Abundance Abundant to very abundant. May undergo population explosions during periods of high food supply (Smithers 1971). In the Kalahari Desert of South Africa, *M. indutus* is the third most abundant species of small mammal after *Rhabdomys pumilio* and *Gerbillurus paeba* (Nel 1978).

Adaptations Nocturnal and terrestrial. Excavates its own burrows in sandy soil, but also uses burrows excavated by other species; may hide under rocks, fallen logs or beneath the bark of trees. Spherical nests are constructed underground from grass or other soft fibres, in which young are born.

Foraging and Food Diet is predominantly grass seeds and pods of *Acacia* trees, but includes insects (Smithers 1971, Nel 1978). Green plant material may also be important (Kerley *et al.* 1990).

Social and Reproductive Behaviour Highly aggressive towards conspecifics, with cases of cannibalism reported in captivity (Skinner & Smithers 1990). Such aggressive behaviour suggests territoriality, but critical studies are lacking. Offspring remain with both parents until they are weaned.

Reproduction and Population Structure May breed throughout the year, but peaks in pregnancy are recorded in Botswana during the wet season (Oct–Apr; Smithers 1971). Embryo number: 4.9 (2–8, $n = 17$; Botswana; Smithers 1971). Population explosions in *M. indutus* occur at the same time as those of *Mastomys natalensis*. High numbers of *M. natalensis* may possibly provide predator cover for *M. indutus*.

Predators, Parasites and Diseases No information.

Conservation IUCN Category: Least Concern.
Widespread and abundant throughout its range.

Measurements

Mus indutus

HB: 53.2 (45–65) mm, $n = 12^*$

T: 42 (30–52) mm, $n = 90$

HF: 14 (13–16) mm, $n = 90$

E: 11 (8–12) mm, $n = 90$

WT: 5.4 (3–8) g, $n = 85$

GLS: 17.7 (16.5–19.5) mm, $n = 11$

GWS: 9.3 (8.5–10.0) mm, $n = 10$

M^1 – M^3 : 3.0 (2.8–3.1) mm, $n = 11$

Body measurements and weight: Botswana, unsexed individuals (Smithers 1971)

Skull measurements: Botswana, South Africa (Roberts 1951)

*Specimen labels (TM)

Key References Nel 1978; Smithers 1971.

A. Monadjem

Mus mahomet MAHOMET PYGMY MOUSE

Fr. Souris naine de Mahomet; Ger. Mohammed-Zwergmaus

Mus mahomet Rhoads, 1896. Proc. Acad. Nat. Sci., Philadelphia 1896: 532. Sheik Mahomet, Ethiopia.

Taxonomy Subgenus *Nannomys*. Within Ethiopia, *M. mahomet* is a distinctive species. The name *kerensis* Heuglin 1877 might be a prior name (Yalden *et al.* 1976). The status of this taxon is uncertain, and it may belong to another species from further south in Africa, such as *M. minutoides*, *M. bufo*, *M. sorella* or *bella* (synonym of *M. minutoides*) (Yalden & Largen 1992). Synonyms: *emesi*. Subspecies: none. Chromosome number: $2n = 36$, $aFN = 34$ (Aniskin *et al.* 1998).

Description Very small mouse, similar to *M. minutoides*. Pelage dense, short and slightly coarse. Dorsal pelage dark greyish-brown, slightly speckled with buff; hairs grey at base, brown or buff at tip. Ventral pelage greyish-white, sometimes with pale orange tinge; hairs grey at base, off-white at tip. Ventral pelage clearly delineated from flanks usually by thin orange-buff or sandy-yellow line. Ears darkly pigmented, prominent, covered with sparse short buffy hairs. No postauricular or subauricular white patches. Fore- and hindfeet white. Tail short (ca. 74% of HB), scaly, with many very short hairs; dark above, slightly paler below. Nipples: $3 + 2 = 10$.

Geographic Variation None recorded.

Similar Species

M. tenellus. Mostly smaller; dorsal pelage pale sandy-brown, ventral pelage pure white; white postauricular and/or subauricular patches; in Ethiopia, < ca. 2000 m).

M. triton. On average larger, dorsal pelage olive-brown; ventral pelage grey or whitish-grey; in Ethiopia, SE forests only.

M. musculoides. Similar size; sympatric in Uganda and Kenya.

M. setulosus. Slightly larger; dorsal pelage grey, ventral pelage pure white; sympatric or parapatric in Ethiopia; in Ethiopia, 1000–1500 m.

Distribution Endemic to Africa. Afromontane–Afroalpine BZ of Ethiopia and Eritrea; perhaps confined to the plateaux at 1500–3200 m (Yalden & Largen 1992). Considered by Musser & Carleton (1993, 2005) to occur also in SW Kenya and SW Uganda (not mapped). Limits unknown.

Habitat Upland forest-edges, scrub and grasslands, habitats partly shared with *Stenocephalemys albipes*, but unlike *S. albipes*, *M. mahomet* is not a true forest species (Yalden 1988, Yalden & Largen 1992).

Abundance Moderately common and widespread at middle altitudes in Ethiopia. Comprised 11% (n = 285) of rodents caught in Menagesha State Forest (Afework Bekele 1996a), and 6% (n = 905) in a wide range of sites in S Ethiopia (Rupp 1980).

Remarks Little is known about the biology of this species. Nocturnal and presumed to feed on seeds and insects. Parous ♀♀, and ♂♂ with enlarged testes, were trapped in Aug in Bale, Ethiopia, and a lactating ♀ was recorded in Jan at Illubabor, Ethiopia (1500 m; BMNH).

Conservation IUCN Category: Least Concern.

Measurements

Mus mahomet

HB: 67 (63–73) mm, n = 21

T: 53.5 (46–60) mm, n = 21

HF: 15 (14–15) mm, n = 21

E: 11.8 (9–13) mm, n = 21

WT: 10.3 (6–13) g, n = 17

GLS (CbL): 19.9 (18.4–21.0) mm, n = 21

GWS: n. d.

M¹–M³: 3.2 (3.0–3.6) mm, n = 21

Ethiopia (Rupp 1980, Yalden 1988)



Mus mahomet

Key References Afework Bekele 1996a; Rupp 1980; Yalden & Largen 1992.

D. W. Yalden

Mus mattheyi MATTHEY'S PYGMY MOUSE

Fr. Souris naine de Matthey; Ger. Mattheys Zwergmaus

Mus mattheyi Petter, 1969. Mammalia 33: 118. Accra, Ghana.

Taxonomy Subgenus *Nannomys*. Closely related to *M. haussa*. Musser & Carlton (1993, 2005) comment that they were 'unable to assign anything to *mattheyi* [and] the morphological traits used to distinguish *mattheyi* from *haussa* by Petter (1969) and by Petter & Matthey (1975) vary in a continuous fashion from typical *haussa* morphology to that considered diagnostic for *mattheyi*'. However, Veyrunes (2002) showed that *M. mattheyi* must be considered as a valid species because of its very high molecular divergence and chromosomal differences compared with *M. haussa*. Synonyms: none. Chromosome number: 2n = 36, FN = 36. The karyotype is considered to be ancestral for African *Mus* (Jotterand-Bellomo 1986).

Description Very small mouse, on average larger than *M. haussa* but on average smaller than *M. musculoides*. Dorsal pelage ochre-tawny to chestnut, usually darker along mid-dorsal line. Flanks fawn. Ventral pelage white. Colour of dorsal pelage and ventral pelage clearly delineated on flanks. Ears grey; no postauricular white patch. Fore- and hindfeet white. Tail short (ca. 70% of HB). Skull: upper incisors opisthodont; choanae V-shaped, sometimes tending to U-shaped (as in *M. haussa*); anterior palatal foramina elongated (but less than in *M. haussa*) reaching to level of posterior end of M¹; M¹ with prelobe; M₁ with anterior lobe tricuspidate. Nipples 2 + 2 = 8.



Mus mattheyi

Geographic Variation None recorded.

Similar Species

M. haussa. On average slightly smaller (HB: 49.7 [44–52] mm, HF: 12 [11.5–12.5] mm, GLS: 16.6 [15–17] mm); dorsal pelage pale sandy; distribution in more arid habitats.

M. musculoides. On average larger (HB: 61 [55–70] mm, HF: 13.6 [12–14] mm, GLS: 18.4 [17.8–18.9] mm); dorsal pelage darker, golden-brown flecked with dark brown; sympatric.

Distribution Endemic to Africa. Sudan Savanna and Guinea Savanna BZs. Recorded from Senegal to Côte d'Ivoire (and perhaps Togo), and Burkina (Veyrunes 2002), but distribution may be more extensive. Musser & Carleton (2005) record only from the type locality (see above). Geographic range is further south than for *M. haussa*.

Habitat Moist woodland savanna and grass savanna. The holotype was taken on the Accra plain.

Remarks Apparently no other information available.

Conservation IUCN Category: Least Concern.

Measurements

Mus mattheyi

HB: 52 (46–60) mm, n = 27

T: 38.4 (33–44) mm, n = 22

HF: 12.1 (11–13) mm, n = 27

E: 8.8 (7–10) mm, n = 27

WT: n. d.

GLS: 16.6 (15–17) mm, n = 6

GWS: 8.4 (8.2–8.6) mm, n = 4

M¹–M³: 2.9 (2.8–3.0) mm, n = 4

Throughout geographic range (MNHN)

Key Reference Petter 1969.

F. Petter

Mus minutoides TINY PYGMY MOUSE

Fr. Souris naine d'Afrique australe; Ger. Kleine Zwergmaus

Mus minutoides Smith, 1834. S. Afr. Quart. J., ser. 2, 2: 157. Cape Town, South Africa.

Taxonomy Subgenus *Nannomys*. Taxonomic status of this species is uncertain. Formerly, *M. indutus* and *M. orangiae* were considered subspecies of *M. minutoides*, but are now regarded as valid species (Musser & Carleton 1993, 2005). Currently, *minutoides* refers to *Mus* from the eastern side of Africa, from East Africa to South Africa, but the limits of the geographic range are uncertain. If *M. musculoides* is included in *M. minutoides* (as in Musser & Carleton 2005), then *M. minutoides* has a distribution throughout much of the savanna regions of Africa. The *minutoides*–*musculoides* complex and the relationship between *M. minutoides* and *M. musculoides* is not yet resolved. Diploid chromosome number apparently variable, suggesting *minutoides* may include sibling species. Synonyms: *kasaicus*, *marica*, *minimus*, *umbratus*. Subspecies: three, validity uncertain. Chromosome numbers: 2n = 18, FN = 36 (Western Cape Province, South Africa); 2n = 34 (KwaZulu–Natal, South Africa) (Matthey 1966a, Skinner & Smithers 1990, Veyrunes *et al.* 2004).

Description Very small mouse with soft, shiny pelage. Dorsal pelage variable shades of brownish-buff to brownish-orange; hairs slate-grey at base with black tip. Flanks buffy-orange. Ventral pelage (including chin) pure white. Clear delineation between colour of flanks and ventral pelage. Head with pointed nose and long vibrissae. Ears brownish, moderately sized and rounded. Limbs short. Feet white with well-developed digits; four digits on forefoot; five digits on hindfoot. Digits 2–4 elongated. All digits with well-developed claws. Tail short (ca. 75% of HB), brownish above, paler below. Nipples: 3 + 2 = 10.

Geographic Variation Meester *et al.* (1986) list three subspecies for southern Africa:

M. m. minutoides: Western Cape, Eastern Cape and KwaZulu–Natal Provinces, South Africa.

M. m. umbratus: Swaziland and NE South Africa.

M. m. marica: E Mpumalanga Province, South Africa; S Mozambique.

Specimens from Western and Eastern Cape Provinces (South Africa) are slightly darker than specimens from KwaZulu–Natal and E Mpumalanga Provinces (South Africa), Swaziland and S Mozambique. Differences, however, not very noticeable due to great variation within each region. Specimens from S Mozambique have fewer black-tipped hairs in dorsal pelage, resulting in brighter brownish-orange colour (but highly variable).

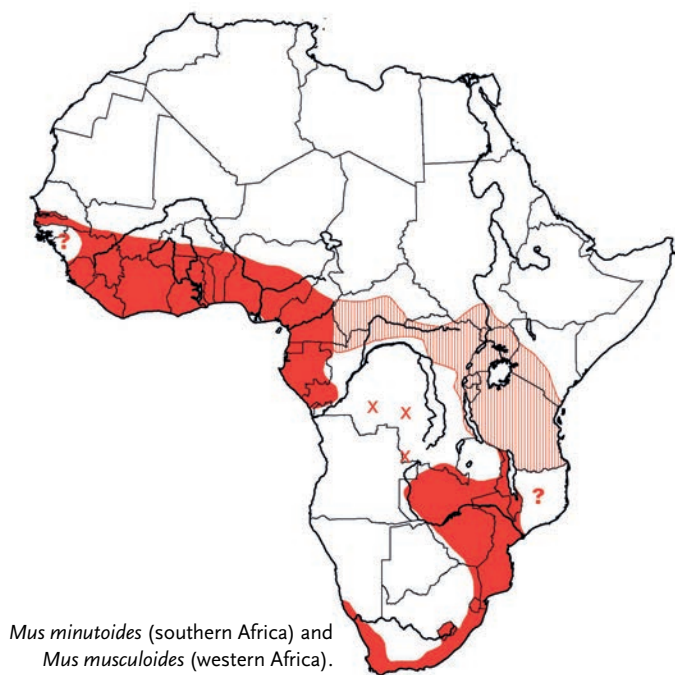
Similar Species

M. indutus. Dorsal pelage generally paler; tail pale above.

M. setzeri. Ears longer; white ventral pelage extends on to upper rump and muzzle.

Distribution Endemic to Africa. Zambezan Woodland BZ (eastern part), South-West Cape BZ and southern Somalia–Masai Bushland BZ. Also occurs at higher altitudes in Swaziland. Recorded in S and E South Africa, northwards through Swaziland and S Mozambique to Zimbabwe and Malawi. Two isolated records from NE Namibia (Matson & Blood 1994). Northern limit of the geographic range where it adjoins that of *M. musculoides* in eastern Africa is uncertain (shown by striped lines on map). Replaced by *M. indutus* in western part of Zambezan Woodland BZ.

Habitat Tolerates a wide range of habitats. In Swaziland, occurs in afro-montane and riparian forests, short to tall grasslands, rocky outcrops, all forms of *Acacia* and broad-leaved woodland, cultivated



Mus minutoides (southern Africa) and
Mus musculoides (western Africa).
See also text.

fields and recently burnt areas (Monadjem 1998a). May also occur in suburban gardens, young pine plantations and on the fringe of wetlands. Altitude range: near sea level to 2700 m (Rowe-Rowe & Meester 1982a).

Abundance Abundant to very abundant. Densities of up to 28/ha have been recorded (Monadjem 1998b), and presumably may reach much higher densities during favourable conditions.

Adaptations Nocturnal and terrestrial. Tiny Pygmy Mice excavate their own burrows in soft soil, and will also use holes excavated by other species, or will rest under rocks, fallen logs or beneath the

bark of trees. During the non-breeding season, shelters may be changed regularly. Construct spherical nests, under cover, from grass or other soft fibres in which young are born. In captivity, does not enter spontaneous torpor at low temperatures or during periods of reduced food availability (Webb & Skinner 1995, Downs & Perrin 1996).

Foraging and Food Omnivorous. Diet consists mostly of grass seeds and insects (Rowe-Rowe 1986), but foliage predominates in the Karoo of SW South Africa (Kerley 1992). Proportional contribution of food types in stomach contents: 44% vegetable material, 40% seeds, 16% arthropods (n = 17, Swaziland; Monadjem 1997b).

Social and Reproductive Behaviour Reported to forage independently, but frequently pairs are captured in the same live-trap, suggesting that they may forage together (Monadjem 1998a). In Swaziland, mean distance between successive monthly captures (on a 1 ha grid) was 18.6 m, indicating that movements are limited to a small area. In captivity, copulation is preceded by grooming of ♀ by her mate (Willan & Meester 1978). Females aggressively defend their nests when young are present. Self-grooming commences at 10–11 days of age and continues through adulthood.

Reproduction and Population Structure Poorly known for such an abundant species. Reproduction peaks in the wet season (Nov–Feb) but may continue throughout the year. Mean litter-size 4.5 (n = 4, KwaZulu–Natal, South Africa; Taylor 1998) and 4.0 (range 1–7, n = 27, in captivity; Willan & Meester 1978). Gestation (in captivity): 18–19 days. At birth, young hairless, weight 0.8 g. Incisors erupt Day 7–9. Young weaned Day 18. Sexual maturity attained Day 42 (Willan & Meester 1978). Mean interval between litters 22 days. Population numbers fluctuate widely at some localities (Monadjem 1999b) but not at others (Monadjem 1998b). Survival rates are low and few individuals live to one year of age. Sex ratio does not deviate from parity (Monadjem 1999b).



Mus minutoides.

Predators, Parasites and Diseases Preyed upon by several species of owls (Vernon 1972, Perrin 1982). Ectoparasites include 12 species of fleas, and three species of ticks (details in De Graaff 1981). Susceptible to plague in laboratory conditions.

Conservation IUCN Category: Least Concern.
Widespread and abundant throughout its range.

Measurements

Mus minutoides

HB: 54.8 (45–68) mm, n = 16

T: 41.0 (38–49) mm, n = 16

HF: 12.5 (11–14) mm, n = 15

E: 8.5 (6–11) mm, n = 11

WT: 6.2 (4–12) g, n = 16

GLS: 18.8 (17.5–20.4) mm, n = 4

GWS: 9.6 (8.8–10.3) mm, n = 4

M¹–M³: 3.0 (2.8–3.2) mm, n = 4

Body measurements: Swaziland (Monadjem 1998a)

Skull measurements: South Africa (Roberts 1951)

Key References De Graaff 1981; Downs & Perrin 1996; Monadjem 1999b; Smithers 1983; Willan & Meester 1978.

A. Monadjem

Mus musculoides WEST AFRICAN PYGMY MOUSE

Fr. Souris naine d'Afrique de l'Ouest; Ger. Westafrikanische Zwergmaus

Mus musculoides Temminck, 1853. Esquisses Zool. sur la Côte de Guinée, p. 161. 'Côte de Guinée', West Africa. Exact locality uncertain.

Taxonomy Subgenus *Nannomys*. The taxonomic relationship of this species with *M. minutoides* of eastern and southern Africa is uncertain. Within West Africa, this species has been referred to both *M. musculoides* and *M. minutoides*. The taxon *musculoides* has been placed as a subspecies of *M. minutoides* (Petter & Matthey 1975), as a valid species (Rosevear 1969, Happold 1987, Musser & Carleton 1993, Grubb *et al.* 1998), or placed in synonymy with *L. minutoides* (Musser & Carleton 2005). The species occurs throughout West Africa; however, its eastern geographic border is uncertain (see Distribution); Musser & Carleton (1993) consider this to be Ethiopia and Somalia, but R. Hutterer (pers. comm.) places the eastern limit as W Cameroon. Hence the identity of C African populations is questionable. Rosevear (1969) placed *Mus musculoides* in the subgenus *Leggada*, now a synonym of *Nannomys* (Musser & Carleton 1993). See also *Mus minutoides* for

further comment. Synonyms: *bella* (or *bellus*), *enclavae*, *gallarum*, *gondokorae*, *grata*, *marica*, *paulina*, *petila*, *soricoides*, *sungarae*, *sybilla*, *vicini* (Musser & Carleton 1993). Subspecies: none. Chromosome number shows Robertsonian polymorphism: at Ippy, Central African Republic, 2n = 25 to 2n = 32, with 2n = 28 and 2n = 29 forming about 60% of population (n = 31); another study at Ippy, 2n = 38, FN = 33 and 34 (n = 4) (Jotterand-Bellomo 1984); in Côte d'Ivoire, 2n = 33 (n = 6) and 2n = 33 (n = 2) (Jotterand-Bellomo 1984); in S Nigeria, 2n = 32 (n = 1), 2n = 33 (n = 4) and 2n = 34 (n = 7) (R. Matthey pers. comm.); in Mali, 2n = 18 (♀ ♀), 2n = 19 (♂ ♂) (n = 8) (Veyrunes *et al.* 2004).

Description Very small delicate mouse with short tail and white ventral pelage. Dorsal pelage golden-brown, flecked with dark brown; hairs pale grey at base, golden-brown at tip. Flanks similar in colour to dorsal pelage, becoming paler on lower flanks. Head similar in colour to dorsal pelage; small white subauricular patch. Ventral pelage pure white. Colour of flanks and ventral pelage clearly delineated. Chin, chest, fore- and hindlimbs white. Tail short (ca. 70% of HB) and slender, pale brown above, whitish below. Total length of skull more than 17 mm (cf. *M. haussa*). Nipples 2 + 2 = 8.

Geographic Variation None except in karyotype (see Taxonomy).

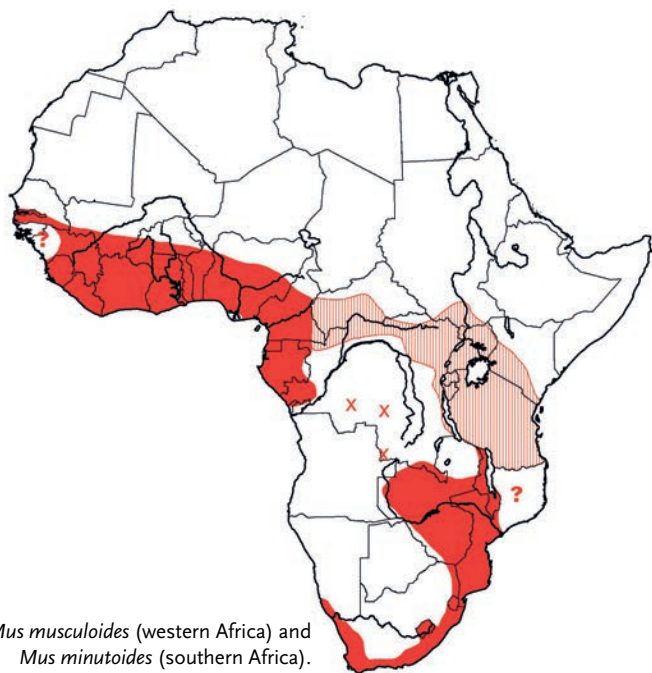
Similar Species

M. setulosus. Larger (HB: 81.8 [77–86] mm, HF: 14.1 [14–16] mm, M¹–M³: 3.58 [3.5–3.6] mm); dorsal pelage darker.

M. haussa. On average smaller (HB: 49.7 [44–52] mm, HF: 12 [11.5–12.5] mm, M¹–M³: 2.9 [2.9–3.1] mm); dorsal pelage paler; distribution further north, mostly in Sudan and Sahel Savanna BZs.

M. mattheyi. On average smaller (HB: 52 [46–60] mm, HF: 12 [11.5–12.5] mm, M¹–M³: 2.9 [2.9–3.1] mm); Ghana, distribution limits and status uncertain.

Distribution Endemic to Africa. Widely distributed in Guinea Savanna BZ, Northern Rainforest–Savanna Mosaic, and grassy patches in Rainforest BZ. May extend into southern parts of Sahel Savanna



Mus musculoides (western Africa) and
Mus minutoides (southern Africa).
See also text.

BZ in west of range. Recorded from Gambia and Senegal to Cameroon, and may extend further eastwards through N DR Congo, Central African Republic and Uganda to Ethiopia and Somalia (see above). Western extension of range to East Africa, and where *M. minutoides* replaces *M. musculoides*, also uncertain (shown by striped lines on map). Geographic range has extended southwards into 'savanna-like' habitats within the Rainforest BZ in recent years as a result of human-induced activities (clearing of rainforest, farming, urbanization).

Habitat Savanna woodlands and grasslands, as well as new and old farmlands, secondary bush and immature cocoa plantations. Grassy areas within Rainforest BZ, such as road verges, farmlands and clearings. Does not occur in rainforest except, very occasionally, in natural grassy clearings where trees have fallen.

Abundance At 14 widely separated savanna habitats in W Nigeria, comprised on average 14% (0–53%) of captured small rodents (Happold 1975b), and at Olokomeji F. R. (in Rainforest–Savanna Mosaic) they formed 56% of all small rodents in grasslands at certain times of year (Anadu 1973). Relative abundance (and absolute numbers) declines from south to north in W Nigeria from 90% in Rainforest–Savanna Mosaic to 11–41% in southern Guinea Savanna BZ and (usually) 0% in northern Guinea Savanna BZ (where *Tatera kemp* [now *Gerbilliscus kemp*], *Myomys daltoni* [now *Praomys daltoni*] and *Mastomys* spp. are common species) (Happold 1975b). In natural clearings in rainforest in Ghana they comprise ca. 2% of small rodents, the fifth most numerous species after *Lophuromys sikapusi*, *Praomys tullbergi*, *Dephomys defua* and *Hybomys trivirgatus* (Jeffrey 1977).

Population numbers vary seasonally and annually in W Nigeria (Anadu 1973). Numbers tended to be lowest at the end of the wet season (Oct/Nov), increasing during the dry season and early wet season, and declining gradually during the late wet season. Density: 2–4/ha (end of wet season) to 7–10/ha (end of dry season). In some years, highest density is 23–35/ha (early dry season).

Adaptations Terrestrial and nocturnal. Construct spherical or cup-shaped nests of shredded grass under logs and in shallow burrows. Locomotion is a rapid scuttle; when disturbed, individuals hide under logs, dry grass and any other available cover. Numbers decline markedly where savanna is burned during dry season (probably mostly due to emigration), but immigrants from unburnt areas return as soon as grasses sprout again (Anadu 1973).

Foraging and Food Herbivorous. In captivity, feeds on small seeds, grass stems and fruits.

Social and Reproductive Behaviour Gregarious. In captivity,

many individuals huddle together in a nest; huddling is probably an important aspect of thermoregulation in this small species, especially during cooler days of the dry season.

Reproduction and Population Structure Reproduction is seasonal in S Nigeria. Young born Aug–May; most litters at end of dry season and beginning of wet season (Mar–Apr), and at end of wet season (Sep–Dec). Embryo number (wild-caught ♀♀): 3.38 (2–6, mode 2, n = 13); embryo number (captive ♀♀): 3.00 (1–5, mode 3, n = 18 litters from seven ♀♀; Anadu 1976). Females may have several litters in close succession. Gestation: 22–24 days. Litter interval (in captivity): 41–58 days. At birth, young are naked, eyes are closed, and mean WT = 0.8 g. External ear open Day 11. Eyes open Day 14. Weaned at Day 24. Almost (92%) adult HB length by Day 30; adult size by Day 60. Sexual maturity 10–12 weeks. Longevity: probably not longer than ca. one year. Mice born at beginning of wet season (Apr) attain sexual maturity during the wet season and begin to breed in Aug; mice born at end of wet season (Nov–Dec) are not mature until the beginning of next breeding season in Mar–Apr. Hence continual recruitment of young throughout most of year, and high annual turnover (Anadu 1973). No details from other parts of range.

Predators, Parasites and Diseases Preyed upon by owls. Second most numerous species in pellets of Barn Owls *Tyto alba* on Mt Nimba, Liberia (Heim de Balsac & Lamotte 1958). In N Nigeria, comprised 4–8% of prey numbers (total n = 64) in pellets of Barn Owls and 3% of prey numbers (total n = 83) in pellets of Spotted Eagle-owls *Bubo africanus* (Demeter 1981).

Conservation IUCN Category: Least Concern (as *M. minutoides*). Widespread and not threatened.

Measurements

Mus musculoides

HB: 60.8 (55–70) mm, n = 8

T: 43.6 (32–55) mm, n = 8

HF: 13.6 (12–14) mm, n = 8

E: 9.6 (9–10) mm, n = 8

WT: 8.5 (6.5–10.3) g, n = 8

GLS: 19.3 (18.3–20.2) mm, n = 8

GWS: 9.5 (8.9–10.0) mm, n = 8

M¹–M³: 3.1 (2.6–3.2) mm, n = 8

W Nigeria (Happold 1987)

Key References Anadu 1976; Happold 1975b, 1987.

D. C. D. Happold

Mus musculus HOUSE MOUSE

Fr. Souris domestique; Ger. Haus-Maus

Mus musculus Linnaeus, 1758. Syst. Nat., 10th edn., 1: 62. Uppsala, Sweden.

Taxonomy Subgenus *Mus*. Many forms or subspecies of *Mus musculus* have been described, most of which are now considered as synonyms (see Musser & Carleton 1993, 2005) although others

may be species (Marshall & Sage 1981). The taxonomy of the 'house mouse' has been less well studied in Africa than elsewhere (but see Granjon *et al.* 1992, Prager *et al.* 1998). Recent research suggests

that the 'correct' name of the domestic mouse is likely to be *Mus domesticus* (Boursot *et al.* 1993, 1996, Din *et al.* 1996, Prager *et al.* 1998). One taxon (*M. spretus* of North Africa and S Europe), originally included in *Mus musculus*, is now considered to be a valid species. Traditionally, there appear to be two forms of *Mus musculus*: a domestic form (which lives only in houses and has a relatively longer tail) and a feral form (which lives in human-modified habitats and has a relatively shorter tail). Synonyms that refer to Africa include *brevirostris*, *domesticus*, *gentilis*, *praetextus*, *vignaudi* (all pale-bellied forms from North Africa – see Osborn & Helmy 1980, Aulagnier & Thévenot 1986) and *modestus* (dark-bellied form from southern Africa (see Meester *et al.* 1986). Musser & Carleton (2005) provide a full list of synonyms. Chromosome number: $2n = 40$, $FN = 38$ (Niger: Dobigny *et al.* 2002b; Senegal: Granjon *et al.* 1992); $2n = 22$ (Robertsonian populations in Tunisia; Said & Britton-Davidian 1991).

Description Very small greyish mouse, normally associated with houses. Dorsal pelage greyish or brownish-grey; hairs dark grey at base, pale grey or brown at terminal end, sometimes with black tip. Flanks paler. Ventral pelage buffy-brown, pale grey, or white, merging into colouration of flanks. Head rather pointed, dark 'beady' eyes; ears large, mostly naked. Fore- and hindlimbs short, greyish, with small naked unpigmented digits. Tail long (ca. 90–100% of HB), thin, almost naked, slightly darker above than below. Nipples: $3 + 2 = 10$.

Geographic Variation Throughout its range, *M. musculus* shows large differences in colour and pattern. For Africa, the following forms may be recognized:

gentilis (including *praetextus*): North Africa, Sudan, Ethiopia. Pale (usually white) ventral pelage.

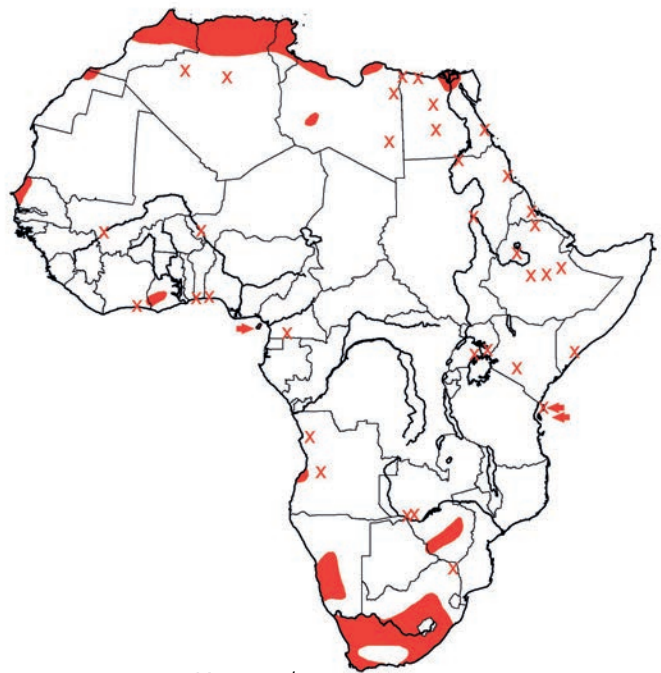
modestus (? *domesticus*): North Africa; South Africa (and perhaps Namibia and Zimbabwe). Buffy-brown or grey ventral pelage.

In North Africa, both dark and pale-bellied forms are usually distributed in a geographical mosaic in separate farms and oases (Marshall & Sage 1981).

Similar Species

Mus (Nannomys) spp. On average smaller body size; tail relatively shorter (i.e. usually less than 75% of HB); natural habitats (Table 37).

Distribution Not indigenous to Africa. Occurs in most countries of the world, but not widespread in Africa. Recorded in temperate Africa, especially in the northern parts of Morocco, Algeria, Libya and Tunisia, and in the Nile Valley. In Algeria and Libya, known from some oases in the desert. Occurs up to 2000 m in the High Atlas of Morocco. Introduced to sub-Saharan Africa by Arab and European shipping, but has formed permanent populations only in selected localities in South Africa (including Marion I.), Namibia, Zimbabwe and Senegal (north of Dakar). Mostly rare in tropical Africa, and recorded from only a few localities near the coastline where populations may not be permanent. Of the three species of small murid rodents introduced into Africa, *M. musculus* has not colonized the continent to the same extent as *Rattus rattus* but has been more successful than *R. norvegicus*.



Mus musculus

Habitat In Africa, mostly commensal and confined to houses, food stores and other urban buildings, although a few populations are feral (e.g. in Morocco [Aulagnier & Thévenot 1986], Algeria [Kowalski & Rzebik-Kowalska 1991] and southern Africa [Smithers 1983]). In Libya, recorded as commensal and quite widely distributed in the wild where the habitat is mesic and has a dense cover of plants (Ranck 1968). In Egypt, also found in a variety of natural habitats including gardens, barley fields, sand flats, salty waste land (with *Suaeda* and other halophytic plants), canal banks and palm groves (Osborn & Helmy 1980). In N Sudan, recorded only from Khartoum during winter months, but not in villages away from the Nile R. (Happold 1967c). In Senegal, House Mice are strictly commensal (J.-M. Duplantier, unpubl.).

Abundance In North Africa, may be fairly abundant in suitable habitats when conditions are optimal. Little information for Africa south of the Sahara; Smithers (1983) records that, in southern Africa, House Mice never occur in sufficient numbers to become a major problem, a contrasting situation to temperate regions of the world, and to some countries where they have been introduced, where they may be major pests, e.g. Australia.

Adaptations Nocturnal and diurnal; terrestrial and scansorial. Extreme adaptability with respect to food and climate has enabled House Mice to colonize many habitats in most parts of the world. Most populations are commensal, some are feral. House Mice require adequate water (as free water or in food) and hence do not survive in arid habitats (unless close to a river, a man-made water supply, or in oases). Nevertheless, in Senegal, they live in drier areas than *Rattus rattus*. Populations are able to breed (and remain viable) in a wide range of climates where the ambient temperatures are very high (as in hot deserts) or very low (sub-Antarctic islands). Rapid reproduction (see below) enables populations to increase rapidly when environmental conditions are good.

Foraging and Food Omnivorous. Primarily granivorous and herbivorous, but will feed on anything edible. Occasionally feed on insects and earthworms.

Social and Reproductive Behaviour Communal and sociable. In established groups, ♂♂ defend an area of variable size (which is related to food availability). When populations are low, any increase in resources promotes rapid reproduction; when populations are high, reproductive rate declines, and at very high densities and when food is limiting, reproduction may cease completely. House Mice are good colonizers, and in a very short period of time can become very numerous (Corbet & Southern 1977).

Reproduction and Population Structure Little information for Africa. Very prolific. In Egypt, pregnant ♀♀ and nestling young present throughout year (Osborn & Helmy 1980). Typically, in other parts of the world, ♀♀ may produce 5–10 litters/year. Gestation: 19–20 days; fertilization may occur during postpartum oestrus. Litter-size: ca. 5.5 (4–8). Young weaned by Day 20. Sexual maturity when 7.5 g (♀♀) to 10 g (♂♂) (Corbet & Southern 1977). Rapid reproduction maintains high population numbers even when predation rates are high.

Predators, Parasites and Diseases Many small mammalian carnivores, birds of prey and snakes feed on House Mice. Ectoparasites include several species of fleas and a sucking louse. The fleas *Xenopsylla cheopis*, *X. ramesis*, *Pulex irritans*, *Nosopsyllus londiniensis* and *Synosternus cleopatrae* are commonly found on House Mice in Egypt (Hoogstraal

& Traub 1965b). Several human diseases can be carried by House Mice including tularaemia, leptospirosis, borreliosis and several *Salmonella*-like bacteria that cause food poisoning.

Conservation IUCN Category: Least Concern.

House Mice are major pests in some parts of the world, and control of their populations is essential. They eat and contaminate stored foods, and are a threat to public health in many parts of the world. The domestic white mouse, used extensively for medical research, is derived from this species.

Measurements

Mus musculus

HB: 83.7 (78–91) mm, n = 10

T: 77.2 (66–85) mm, n = 10

HF: 18.0 (16–20) mm, n = 10

E: 13.7 (13–15) mm, n = 9

WT: 13.4 (9–20) g, n = 9

GLS: 21.6 (21.0–22.3) mm, n = 11

GWS: 11.2 (9.9–12.1) mm, n = 9

M¹–M³ (alveolar): 3.6 (3.3–3.8) mm, n = 9

Egypt (Osborn and Helmy 1980)

Key References (Africa only) Corbet & Southern 1977; Kowalski & Rzebik-Kowalska 1991; Osborn & Helmy 1980; Ranck 1968; Smithers 1983.

D. C. D. Happold

Mus neavei NEAVE'S PYGMY MOUSE

Fr. Souris naine de Neave; Ger. Neaves Zwergmaus

Mus neavei (Thomas, 1910). Ann. Mag. Nat. Hist., ser. 8, 5: 90. Petauke, Loangwe district, E Zambia. 2500 ft (762 m).

Taxonomy Originally described in the genus *Leggada*. Subgenus *Nannomys*. Described as *Leggada neavei* (Thomas 1910a). Belongs to the 'sorella group' (see *Mus sorella*). Considered as a subspecies of *M. sorella* (Verheyen 1965b, Smithers 1983, Meester *et al.* 1986), although Petter (1981) suggested that it should be treated as a valid species. Relationship to *M. oubanguii* and *M. baoulei* is uncertain (Musser & Carleton 2005). Synonyms: none. Chromosome number: not known.

Description Small mouse with rich tawny pelage. Dorsal pelage ochraceous-brown to rich tawny-brown, tending to blackish on mid-dorsal region. Ventral pelage pure white. Colour of dorsal pelage and ventral pelage clearly delineated on lower flanks. Head with pointed muzzle. Ears large, pale grey. Fore- and hindfeet white. Tail short (ca. 43% of HB). Skull: rostrum elongated, incisors slightly pro-odont, choanae V-shaped; M¹ with small prelobe. Nipples: not known.

Geographic Variation None recorded.

Similar Species

M. sorella. Mean HB smaller; mean GLS larger; mean M¹–M³ longer; dorsal pelage dark greyish-brown.



Mus neavei

M. minutoides. Mean HB smaller (51.3 [45–63] mm); mean M^1 – M^3 slightly smaller (3.0 (2.8–3.2) mm); dorsal pelage brownish-buff (variable).

Distribution Endemic to Africa. Zambezian Woodland BZ. Recorded from S Tanzania, S DR Congo, SE Zambia, S Zimbabwe, W Mozambique and South Africa (former Transvaal). Limits of geographic range unknown. Records from Malawi represent other species (Ansell & Dowsett 1988).

Habitat Woodland savanna.

Remarks Apparently no other information on this species.

Conservation IUCN Category: Data Deficient.

Measurements

Mus neavei

HB: 88.8 (58–106) mm, n = 5

T: 38.4 (33–48) mm, n = 5

HF: 13 (12–14) mm, n = 6

E: 11 (10–12) mm, n = 6

WT: n. d.

GLS: 18.5 (18–18.9) mm, n = 6

GWS: 9.4, 9.7 mm, n = 2

M^1 – M^3 : 3, 3.5 mm, n = 2

E Zambia (MNHN)

Key Reference Thomas 1910a.

F. Petter

Mus orangiae ORANGE PYGMY MOUSE

Fr. Souris naine d'Orange; Ger. Orange Zwergmaus

Mus orangiae (Roberts, 1926). Ann. Transvaal Mus. 11: 251. Viljoensdrift, near Vereeniging, Kruisementfontein, South Africa.

Taxonomy Originally described in the genus *Leggada*. Subgenus *Nannomys*. Formerly considered a subspecies of *Mus minutoides* (e.g. De Graaff 1981; Meester *et al.* 1986) but now considered as a valid species. Considered to be allied, on craniological grounds, to *Mus setzeri* (Vermeiren & Verheyen 1983). Synonyms: none. Chromosome number: not known.

Description Very small mouse with soft pelage. Dorsal pelage bright orange-buff; hairs with pale grey base; orange-buff at tip; black tips of some hairs result in a slightly grizzled appearance. Flanks orange-buff, without any black-tipped hairs. Ventral pelage pure white. Head with pointed nose and long vibrissae. Ears brownish,

relatively long and rounded; white subauricular patch (probably) absent. Limbs short with white feet and well-developed digits; four digits on forefeet; five digits on hindfeet. All digits with well-developed claws. Tail short (ca. 60% of HB), brownish above, paler below. Nipples: 2 + 2 = 8.

Geographic Variation None recorded.

Similar Species

M. minutoides. Similar size and shape; dorsal pelage reddish-brown with some black-tipped hairs; may differ craniologically; marginally parapatric.

M. indutus. On average slightly smaller; HF usually larger; dorsal pelage generally paler; tail pale above; marginally sympatric.

M. setzeri. Similar size; rump white; allopatric.

Distribution Endemic to Africa. Highveld BZ. Recorded from C South Africa and Lesotho. Taxonomic status of *Mus* occurring in the southern part of the Free State, South Africa, uncertain, but may represent *M. orangiae*. Limits of geographic range not known.

Habitat Lynch (1983, as *M. minutoides* but presumably referring to *M. orangiae*) records that in the Free State, specimens were mostly collected in short, open grassland.

Abundance 'Mus minutoides is not abundant in the Orange Free State' (Lynch 1983). No other information.

Remarks Nocturnal and terrestrial; constructs a grass nest amongst piles of rocks or in disused termitaria (Lynch 1983).

Conservation IUCN Category: Least Concern.

However, too little is known about this species to be able to assess its conservation status adequately.



Mus orangiae

Measurements

Mus orangiae

HB (♂♂): 59.6 (52–63) mm, n = 8

HB (♀♀): 60.7 (56–69) mm, n = 6

T (♂♂): 37.5 (36–39) mm, n = 8

T (♀♀): 37.8 (36–40) mm, n = 6

HF (♂♂): 12.9 (12–14) mm, n = 8

HF (♀♀): 13.5 (12–14) mm, n = 6

E (♂♂): 11.9 (9–14) mm, n = 8

E (♀♀): 12.7 (12–13) mm, n = 6

WT: n. d.

GLS: 18.5, 18.7 mm, n = 2

GWS: 9.0, 9.7 mm, n = 2

M¹–M³: 3.0, 3.3 mm, n = 2

South Africa

Body measurements: TM

Skull measurements: Roberts 1951

Key Reference Lynch 1983.

A. Monadjem

Mus oubanguii OUBANGUI PYGMY MOUSE

Fr. Souris naine de l'Oubangui; Ger. Oubangui-Zwergmaus

Mus oubanguii Petter and Genest, 1970. Mammalia 34: 454. Bangassou near La Maboké (near Mongoumba), Central African Republic.

Taxonomy Subgenus *Nannomys*. Synonyms: none. Chromosome number: 2n = 28; FN variable; polymorphism is non-Robertsonian (Matthey & Jotterand 1970, Jotterand 1972, Jotterand-Bellomo 1984).

Description Very small reddish-brown mouse with pure white ventral pelage. Dorsal pelage reddish-brown. Ventral pelage pure white. Colour of dorsal pelage and ventral pelage clearly delineated on flanks. Head with pointed muzzle. Ears large, blackish, slightly pointed at tip. Large white postauricular patch. Fore- and hindfeet white. Hindfeet comparatively large (cf. *M. mattheyi*). Tail short (ca. 60% of HB). Skull: rostrum elongated; incisors orthodont or slightly pro-odont; choanae V-shaped; anterior palatal foramina short; M¹ and M² well developed, M³ small; M¹ with well-developed prelobe and without accessory cusp; M₁ with anterior lobe quadricuspidate. Nipples: 3 + 2 = 10.

Geographic Variation None recorded.

Similar Species

M. goundae. Similar size; dorsal pelage ochraceous-brown; nipples 2 + 2 = 8; chromosome number: 2n = 16–19; N Central African Republic.

M. musculoides. Similar size; dorsal pelage golden-brown; no postauricular patch; nipples 2 + 2 = 8; chromosome number: 2n = 25–32 (polymorphic); common and widespread.

M. setulosus. Much larger (HB: 81.8 [77–86] mm, T: 55.5 [52–59] mm); dorsal pelage blackish-brown; no auricular patches; chromosome number: 2n = 36; widespread.

Distribution Endemic to Africa. Northern Rainforest–Savanna Mosaic. Recorded only from the type locality at Bangassou near La Maboké, and at Ippy on the right bank of Oubangui R., SW Central African Republic.

Habitat Savanna patches on sandy slightly lateritic soil, close to rainforest, with grasses (mostly *Loudetia arundinacea*) and trees (mostly *Hymenocardia acida*, *Annona senegalensis*, *Lophira alata* and introduced *Borassus aethiopium*). Type locality (and study site – see Genest-Villard 1973) was an unburnt reserve. Sympatric with *M. setulosus* and *M. minutoides* (Petter & Genest 1970).

Abundance Uncertain. In suitable habitats, 10–25 burrows/100 m² (Genest-Villard 1973). Distribution is very localized.

Adaptations Nocturnal and terrestrial. During the day, rests in simple underground burrows. Burrows are up to ca. 60 cm in length, with a spherical nest chamber (ca. 20 cm diameter) and an escape entrance. The nest is lined with leaves of grass and trees. The main entrance is blocked with fragments of grass and dead leaves. Burrows may be constructed close of those of *Tatera* (now *Gerbilliscus*) spp. and occasionally the burrows of the two species join up (Genest-Villard 1973).

Foraging and Food Mainly granivorous. In captivity, eats seeds and small insects.



Mus oubanguii

Social and Reproductive Behaviour Normally nest alone, except when ♀ has her young. Adult ♂ nest alone.

Reproduction and Population Structure Litter-size: 4–5. Births recorded in May and Jun (no data for other months) (Genest-Villard 1973).

Predators, Parasites and Diseases No information.

Conservation IUCN Category: Data Deficient.

The very limited geographic range, isolation of populations and decline in habitat are cause for concern.

Measurements

Mus oubanguii

HB: 62.7 (50–75) mm, n = 50

T: 38 (26–44) mm, n = 29

HF: 13.9 (13–15) mm, n = 50

E: 11.5 (9–14) mm, n = 50

WT: n. d.

GLS: 20 (18.6–21.5) mm, n = 26

GWS: 10 (9.5–10.7) mm, n = 21

M¹–M³: 3.5 (3.2–3.9) mm, n = 26

Central African Republic (MNHN)

Key References Genest-Villard 1973; Petter & Genest 1970.

F. Petter

Mus setulosus PETERS'S PYGMY MOUSE

Fr. Souris naine de Peters; Ger. Peters Zwergmaus

Mus setulosus Peters, 1876. Monatsb K. Preuss. Akad. Wiss. Berlin: 480. Victoria, Cameroon.

Taxonomy Subgenus *Nannomys*. One form (*proconodon*) from Ethiopia was considered to be a valid endemic species by Yalden *et al.* (1976). Synonyms: *pasha*, *proconodon*. Subspecies: none. Chromosome number: 2n = 36, FN = 36 (Matthey 1966a, Jotterand-Bellomo 1986).

Description Small dark-coloured mouse; the largest of pygmy mice in West Africa. Pelage short, slightly coarse (cf. soft in other pygmy mice); comparatively long (7 mm). Dorsal pelage blackish-brown, usually 'dull', very finely speckled with buff (without the 'bright' russet colouration of *M. musculoides*); hairs grey at base, buff or black at tip. Lower flanks slightly paler, with fewer black-tipped hairs. Ventral pelage pure white or off-white. Head similar in colour to dorsal pelage. Ears darkly pigmented, with sparse short grey or buff hairs. Upper lips with narrow white fringe (not wide as in *M. haussa* or *M. musculoides*). Auricular patches absent. Fore- and hindfeet white. Tail short (ca. 67% of HB), dark above and below, with small scaly rings and scattered short dark bristles. Skull: larger than in other species of pygmy mice in West Africa (see also below); total length of skull ca. 21 mm; anterior palatal foramina 4.8 (4.4–5.1) mm; M² with small antero-external cusp (Rosevear 1969).

Geographic Variation Individuals from Cameroon (see Measurements) are larger than *proconodon* (see Taxonomy) from Ethiopia.

Similar Species

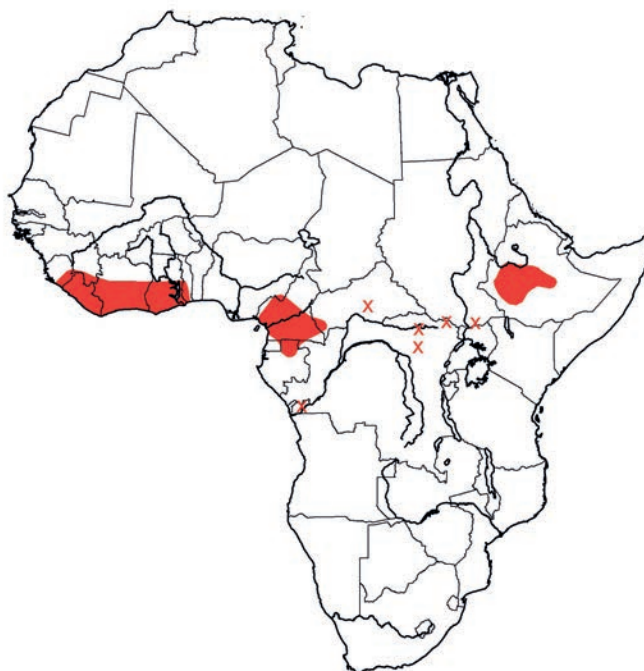
M. haussa. Smaller in most measurements; dorsal pelage sandy; auricular patches present; geographic range further north.

M. musculoides. Smaller; dorsal pelage buff or russet, usually rather bright; auricular patches present; sympatric.

Distribution Endemic to Africa. Rainforest BZ (Western and West Central Regions), Northern Rainforest–Savanna Mosaic and Afromontane–Afroalpine BZ of Ethiopia. Most locality records are from E Sierra Leone, Liberia, Côte d'Ivoire, Ghana and Togo; also

recorded from E Nigeria (Gotel Mts, Yelwa), S Cameroon (Adamaoua Mts, Victoria) and Gabon (Hutterer & Joger 1982, Hutterer *et al.* 1992, Grubb *et al.* 1998). Scattered localities in Central African Republic, NE DR Congo and S Sudan. Isolated populations in Ethiopia (as *proconodon*). Not recorded from Benin and S Nigeria, where perhaps it occurs. One locality in SE DR Congo (not mapped) needs verification.

Habitat Most records are from relict forests in the Rainforest BZ, and from gallery forests and grasslands in montane habitats, e.g. gallery forest (E Nigeria, Cameroon), montane grassland and gallery forest (Liberia), tropical deciduous forest and cultivated areas of cleared tropical forest (Ethiopia), and grassfields at edge of forest on



Mus setulosus

Mt Nimba (Guinea). Recorded from 1000 to 1750 m in Ethiopia (where it is considered a 'lowland species' – Yalden *et al.* 1976), at 1550–2300 m in highlands of Cameroon and Nigeria, and 500–1300 m on Mt Nimba, Liberia.

Abundance Generally uncommon, and not captured as often as sympatric *M. musculoides*. May be locally common, as in parts of S Cameroon (Eisentraut 1973).

Remarks There is no detailed biological information on this species. Rosevear (1969) suggested that it is probably very similar to *M. musculoides*.

Conservation IUCN Category: Least Concern.

Measurements

Mus setulosus

HB: 81.8 (77–86) mm, n = 6

T: 55.5 (52–59) mm, n = 6

HF: 14.1 (14–16) mm, n = 6

E: 11.8 (11–12) mm, n = 6

WT: n. d.

GLS: 21.1 (19.3–21.9) mm, n = 4

GWS: 9.9 (9.6–10.2) mm, n = 4

M¹–M³: 3.6 (3.5–3.6) mm, n = 4

Cameroon (BMNH)

Key Reference Rosevear 1969.

D. C. D. Happold

Mus setzeri SETZER'S PYGMY MOUSE

Fr. Souris naine de Setzer; Ger. Setzers Zwergmaus

Mus setzeri Petter, 1978. Mammalia 42: 377. 82 km west of Mohembo, Botswana.

Taxonomy Subgenus *Nannomys*. Craniologically most similar to *Mus orangiae*. Synonyms: none. Chromosome number: not known.

Description Very small mouse with soft pelage. Dorsal pelage variable shades of pale buff or pale buffy-orange; hairs slate-grey at base; some have black tip giving a slightly grizzled appearance (though less so than in *M. indutus*). Flanks lack black-tipped hairs and are buffy-orange. Ventral pelage pure white; white colour extends high up on flanks, and dorsally across rump to form white band anterior to tail – a unique character of this species. Head with pointed nose and long vibrissae. Chin, cheeks and muzzle white. Ears comparatively

long (cf. *M. minutoides*) and rounded, pale brown; small white patch at base of each ear. Limbs short with white feet; four digits on forefeet; five digits on hindfeet. All digits with well-developed claws. Tail short (ca. 60% of HB), whitish. Nipples: not known.

Geographic Variation None recorded.

Similar Species

M. minutoides. Dorsal pelage generally darker, tail dark above; white ventral pelage does not extend on to upper rump and muzzle; allopatric.

M. indutus. Ears shorter; white ventral pelage does not extend on to upper rump and muzzle; sympatric.

Distribution Endemic to Africa. Parts of South-West Arid Zone (Kalahari Desert) and Zambezian Woodland BZ. Recorded only from NE Namibia, NW Botswana and W Zambia, with a single record from S Botswana (Vermeiren & Verheyen 1983). Perhaps present in SE Angola. The record from S Botswana suggests a wider geographic range than currently known.

Habitat Poorly known. In Botswana, recorded from the fringes of pans and wetlands in relatively arid habitats (mean annual rainfall 400–450 mm).

Abundance No information. The species is poorly represented in museum collections, suggesting that it is not abundant.

Remarks Apparently no other information available.

Conservation IUCN Category: Least Concern.

The restricted geographic range, apparent rarity and lack of records from protected areas may be cause for concern.



Mus setzeri

Measurements*Mus setzeri*

HB: 61 mm, n = 1*

T: 36 (31–48) mm, n = 9

HF: 14 (13–15) mm, n = 11

E: 13.6 (13–14) mm, n = 11

WT: 6.8 (5–9) g, n = 11

GLS: 18.0 (17.5–18.3) mm, n = 11

GWS: 10.1 (9.6–10.5) mm, n = 17

M¹–M³: 3.3 (3.3–3.5) mm, n = 18Body measurements and weight: Botswana, unsexed individuals (as *Leggada* sp.; Smithers 1971)

Skull measurements: Zambia (Vermeiren & Verheyen 1983)

*From specimen label (TM)

Key References Petter 1978; Vermeiren & Verheyen 1983.**A. Monadjem*****Mus sorella* SORELLA PYGMY MOUSE (THOMAS'S PYGMY MOUSE)**

Fr. Souris naine de Thomas; Ger. Zentralafrikanische Zwergmaus

Mus sorella (Thomas, 1909). Ann. Mag. Nat. Hist., ser. 8, 4: 548. Kirui, Mt Elgon, W Kenya. 6000 ft (1830 m).

Taxonomy Originally described in the genus *Leggada*. Subgenus *Nannomys*. A species within the 'sorella group', characterized by the presence of V-shaped choanae, which also includes the closely related *M. goundae*, *M. neavei* and *M. oubanguii*. Phylogenetic relationships within the 'sorella group' need systematic revision (Musser & Carleton 1993, 2005). Synonyms: *acholi*, *kasaicus*, *wamae*. Subspecies: none. Chromosome number: not known.

Description Very small greyish mouse with pure white ventral pelage. Dorsal pelage dark greyish-brown, with pale-coloured speckles; hairs grey at base, beige or pale brown at tip; some hairs on back longer with black tip. Flanks paler, due to presence of rufous or pale brown hairs and absence of black-tipped hairs. Ventral pelage pure white. Colour of dorsal pelage and ventral pelage very clearly delineated high up on flanks (more so than in other species of *Mus*) without a brownish-orange line of delineation. Head long. Ear comparatively long, dark brown, sparsely covered with short fine hairs. Small white subauricular spot. Upper lips, lower cheeks, chin, throat and chest pure white. Fore- and hindfeet white. Tail short (ca. 65% of HB). Skull: rostrum slender; choanae V-shaped; incisors proodont, anterior palatal foramina long, reaching to the anteriolateral cusp of M¹. Nipples: 2 + 2 = 8.

Geographic Variation None recorded.

Similar Species

M. musculoides/minutoides. Similar in total length; HB on average smaller (*M. minutoides*); tail longer (mean 50 mm, ca. 100% of HB); ear on average shorter (mean 8.9 mm); common and widespread.

Distribution Endemic to Africa. Northern and Eastern Rainforest–Savanna Mosaics close to the Rainforest BZ (East Central and West Central Regions). Recorded from NE and SE DR Congo, Uganda, Kenya and N Tanzania (Musser & Carleton 1993). Presence in E Cameroon and EC Angola (Musser & Carleton 2005) uncertain (not mapped). Limits of geographic range unknown.

Habitat Savanna grasslands and woodlands, especially where grasses are tall; grassland areas close to gallery forests along rivers (NE DR Congo; Verheyen 1965b).

*Mus sorella*

Remarks In Garamba N. P., E DR Congo, sympatric with *M. minutoides* (Verheyen 1965b). Seeds and fragments of burnt material were the principal items in stomach contents (Verheyen & Verschuren 1966). Preyed on by owls in Kagera N. P., Rwanda (X. Misonne in Verheyen 1965b).

Conservation IUCN Category: Least Concern.

Measurements*Mus sorella*

HB: 59.9 (51–73) mm, n = 22

T: 39.8 (34–46) mm, n = 21

HF: 13.1 (12–14) mm, n = 22

E: 10.8 (10–12) mm, n = 22

WT: n. d.

GLS: 19.7 (17.8–21.0) mm, n = 26

GWS: 10.1 (9.3–10.7) mm, n = 20

M¹–M³: 3.4 (3.1–3.7) mm, n = 29
 Garamba N. P., NE DR Congo (Verheyen 1965)

Key References Petter 1981; Verheyen 1965b.

F. Petter

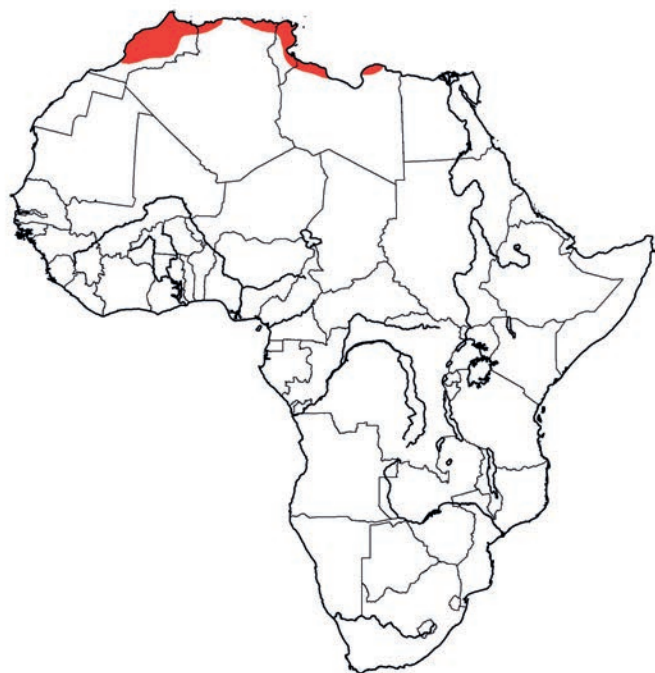
Mus spretus ALGERIAN MOUSE (WESTERN MEDITERRANEAN MOUSE)

Fr. Souris sauvage; Ger. Algerische Maus

Mus spretus Lataste, 1883. Actes Soc. Linn. de Bordeaux, ser. 7, 4: 27. Oued Magra, between M'sila and Barika, N of Hodna, Algeria.

Taxonomy Subgenus *Mus*. Various considered as a valid species, or as a subspecies of *M. musculus*. Karyology, electrophoresis, DNA hybridization and mitochondrial RNA sequences suggest *M. spretus* is linked with *M. spicilegus* and *M. musculus*, and is a member of the clade that includes *Mus macedonicus*, *M. spicilegus* (both non-African) and *M. musculus* (details in Musser & Carleton 2005). Synonyms: *caocci*, *hispanicus*, *lusitanicus*, *lynsei*, *mogrebinus*, *parvus*, *rifensis*. Subspecies: none. Chromosome number: 2n = 40, FN = 40.

Description Small mouse similar to *Mus musculus*, but smaller and often with shorter tail. Pelage short and dense. Dorsal pelage brownish, slightly flecked with pale brown; hairs dark grey with pale brown or black tip. Ventral pelage greyish-white, clearly delineated from colour of flanks; hairs grey on basal half, white on terminal half. Head similar in colour to dorsal pelage; face rather pointed. Ears darkly pigmented. Limbs short. Fore- and hindfeet with small sparse white hairs. Tail long (ca. 80% of HB), bicoloured, ringed with very small scales; many extremely small bristles. Notch on inner surface of upper incisors not well developed (cf. *M. musculus*); sometimes barely visible. Nipples: not known.



Mus spretus

Geographic Variation None recorded.

Similar Species

M. musculus. Dorsal pelage dark grey; ventral pelage grey; tail on average longer (66–85 mm, 90–100% of HB); notch on inner surface of upper incisors well developed; commensal.

Apodemus sylvaticus. Larger in all dimensions; tail ca. 107% of HB; often syntopic.

Distribution Mediterranean Coastal BZ and coastal regions of Sahara Arid BZ. In Africa, recorded from Morocco, Algeria, Tunisia and Libya. In Algeria, extends from sea level to the northern parts of Haut Plateaux (Kowalski & Rzebik-Kowalska 1991), and in Morocco from coastal regions near Tangiers to limits of cultivation in the sub-Sahara as well as some oases (Aulagnier & Thévenot 1986). Distribution in Libya uncertain; reference to the 'wild form' of *M. musculus* (Ranck 1968) probably refers to *M. spretus*, which is commoner in the interior than near the coast. Extralimital in S France, Spain, Portugal and Balearic Islands. Probably indigenous to the Maghreb and subsequently expanded northwards into southern Europe (Dobson 1998, Dobson & Wright 2000).

Habitat In Algeria, recorded from the seashore to alpine meadows at 1600 m (Kowalski & Rzebik-Kowalska 1991). Tends to prefer habitats with sparse woody vegetation interspersed with open ground, as well as agricultural fields (Khidas *et al.* 2002). In Morocco, lives on plains and hills, as well as cultivated areas, grasslands and forests (Aulagnier & Thévenot 1986). Although largely sympatric with *M. musculus*, it is usually not syntopic and is not commensal (cf. *M. musculus*).

Abundance Varies greatly according to habitat. Commonest species of small mammal in mixed woodlands (dominated by *Phylliria latifolia*, *Pinus halepensis* and *Arenia maritima*) near sea level in Algeria (*M. spretus* 46%, *Gerbillus campestris* 32%, *Apodemus sylvaticus* 12%, *Lemniscomys barbarus* 9%; n = 43). In an oak–olive forest, comprised 80% of two spp. of small mammals (n = 10) (Khidas 1993). Rare or absent in five other sampled habitats from 250 to 1800 m (Khidas 1993). Highest population numbers are often in agricultural fields.

Adaptations Terrestrial. Individuals appear to be less capable of coping with cold conditions than *M. musculus*. Experimentally, in both species, when Ta = 5–35 °C, Tb = 35–37 °C. When Ta is reduced to 0 °C, Tb decreased to ca. 33 °C (whereas for *M. musculus*, Tb remained

normal). At $T_a = 20\text{--}25^\circ\text{C}$, oxygen consumption (as a measure of metabolic rate) was $3\text{--}7\text{ cm}^3/\text{g/h}$ for both species; when $T_a = 0^\circ\text{C}$, metabolic rate remained at $3\text{--}7\text{ cm}^3/\text{g/h}$ in *M. spretus*, but increased to $11\text{--}20\text{ cm}^3/\text{g/h}$ in *M. musculus* (S.D. $\pm 0.63\text{--}\pm 1.07$). Although results are variable (and for *M. musculus* depend on where the individuals originated), *M. spretus* seems less capable of altering metabolic rate (and therefore maintaining Tb) when T_a is low than *M. musculus* (Gorecki *et al.* 1990).

Foraging and Food Mainly fruits and seeds (Aulagnier & Thévenot 1986, Khidas *et al.* 2002).

Social and Reproductive Behaviour No information.

Reproduction and Population Structure In Algeria, ♂♂ with enlarged testes from May–Nov, and lactating ♀♀ from Jun–Nov (Kowalski & Rzebik-Kowalska 1991). Embryo number: 4 ($n = 1$). In S Spain (a climate similar to that of the Mahgreb), reproductive season is from Mar–Nov, with peaks in reproductive activity in Apr–May and Aug–Sep (Antunez *et al.* 1990). Reproductive activity is probably associated with food abundance, and therefore varies from year to year (Duran *et al.* 1987, in Fons & Saint Girons 1993).

Predators, Parasites and Diseases Probably common in owl pellets in Algeria, although difficult to distinguish from *M. musculus* (Kowalski & Rzebik-Kowalska 1991). In Morocco, comprised 65% of small prey in pellets of Barn Owls *Tyto alba* (Aulagnier & Thévenot 1986). Ectoparasites include a flea, *Nosopsyllus barbarus* (Beaucornu & Kowalski 1985).

Conservation IUCN Category: Least Concern.

Measurements

Mus spretus

TL: 139.7 (125–155) mm, $n = 41$

T: 62.1 (55–71) mm, $n = 44$

HF: 16.0 (14–18) mm, $n = 44$

E: 12.8 (12–15) mm, $n = 41$

WT: 13.9 (12–16) g, $n = 7$

GLS (CBL): 19.8 (18.3–21.8) mm, $n = 40$

GWS: 11.0 (10.0–12.1) mm, $n = 41$

$M^1\text{--}M^3$: 3.6 (3.3–3.9) mm, $n = 44$

Algeria (Kowalski & Rzebik-Kowalska 1991)

Key References Khidas *et al.* 2002; Kowalski & Rzebik-Kowalska 1991.

D. C. D. Happold

Mus tenellus DELICATE PYGMY MOUSE

Fr. Souris naine délicate; Ger. Zarte Zwergmaus

Mus tenellus (Thomas, 1903). Proc. Zool. Soc. Lond. 1903: 298. Roseires, Blue Nile, Sudan.

Taxonomy Originally described in the genus *Leggada*. Subgenus *Nannomys*. Morphologically and ecologically similar to *M. haussa*. Setzer

(1956) placed *aequatorius* and *delamensis* (in the Sudan) as subspecies of *bellus* (now a synonym of *M. musculoides*), but Musser & Carleton (1993, 2005) allocated these forms to *M. tenellus*. Synonyms: *aequatorius*, *delamensis*, *gerbillus*, *suahelicus* (Petter 1972b, Musser & Carleton 1993). Subspecies: none. Chromosome number: not known.



Mus tenellus

Description Very small pale-coloured mouse, similar in colour to *M. haussa*. Dorsal pelage pale sandy, sometimes darker on mid-dorsal line. Ventral pelage pure white. Colour of dorsal pelage and ventral pelage clearly delineated on flanks. Chin and throat pure white. Ears short, grey. White sub- and postauricular patches (which may form a white ring around the base of each ear); the only species of *Mus* with such extensive patches. Fore- and hindfeet white. Hindfeet narrow. Tail of moderate length (ca. 70% of HB), scaly, with very small bristles, dark above, pale below. Skull: choanae U-shaped, anterior palatal foramina small, rounded; incisors opisthodont; M^1 56–61% of $M^1\text{--}M^3$, M^3 15–20% of $M^1\text{--}M^3$; M_1 with anterior lobe tricuspidate (cf. *M. haussa*). Nipples: $2 + 2 = 8$.

Geographic Variation None recorded.

Similar Species No other species of *Mus* has such an extensive postauricular patch (or tuft) of white hairs (see Description).

M. haussa. Similar size; no postauricular patch of white hairs; allopatric.
M. minutoides/musculoides. On average larger; dorsal pelage darker (golden-brown flecked with dark brown).

Distribution Endemic to Africa. Guinea Savanna and Somalia–Masai Bushland BZs. Recorded from C Sudan, Ethiopia (below 2000 m), S Somalia (not mapped) and southwards through Kenya to C Tanzania (Musser & Carleton 1993, 2005). Limits of geographic range unknown.

Habitat Grass steppe with thicket clumps.

Abundance Uncertain. Rarely collected. In S Ethiopia comprised <1% of 8 spp. (n = 138) and 2.5% of 6 spp. (n = 38) at two localities (1200–1500 m) (Rupp 1980).

Remarks Embryo number: 3 (n = 1; Nuba Mts, Sudan; Nov), 4 (n = 1; Darfur, Sudan; Sep) (labels; BMNH).

Conservation IUCN Category: Least Concern.

Measurements

Mus tenellus

HB: 53.8 (44–62) mm, n = 8

T: 38.4 (34–43) mm, n = 8

HF: 12.6 (12–14) mm, n = 8

E: 8.6 (8–10) mm, n = 8

WT: n. d.

GLS: 16.1 (15.5–16.5) mm, n = 6

GWS: 8.3 (7.9–8.6) mm, n = 6

M¹–M³: 2.9 (2.6–3.0) mm, n = 6

Sudan (BMNH)

Key Reference Petter 1972b.

F. Petter

Mus triton GREY-BELLIED PYGMY MOUSE

Fr. Souris naine à ventre gris; Ger. Graubauchzwergmaus

Mus triton (Thomas, 1909). Ann. Mag. Nat. Hist., ser. 8, 4: 548. Kirui, Mt Elgon, Kenya. 6000 ft (1830 m).

Taxonomy Originally described in the genus *Leggada*. Subgenus *Nannomys*. Despite differences in some measurements (e.g. HB and T), over a considerable altitudinal range (1000–3400 m), there generally seems to be a broad morphological uniformity in named forms (e.g. *triton* from Mt Elgon, *fors* from W Rwenzori [both Delany 1975], *birungensis* from west of L. Kivu and *imatongensis* from Imatong Mts in S Sudan [F. Dieterlen unpubl.]); hence subspecific distinctions are of dubious validity. Synonyms: *birungensis*, *fors*, *imatongensis*, *murilla*, *naivashae*. Subspecies: none recognized here. Chromosome

number: 2n = 32, FN = 34 (DR Congo); 2n = 20, 21, 22, FN = 34 ♂♂, 2n = 32 (♀♀) (Tanzania, Malawi) (Matthey 1963b, 1966b, Jotterand-Bellomo 1988).

Description Small mouse, although comparatively large for a pygmy mouse. Dorsal hairs 7–12 mm. Dorsal pelage darkish-brown, slightly flecked with buff or yellow; hairs dark grey at base, with black subterminal band and with black or buff or yellow at tip. Rump generally darker due to more black-tipped hairs. Flanks and head brownish due to more yellowish-tipped hairs. Ventral pelage medium grey to greyish-white, sometimes tinged with yellow; hairs dark grey at base, buff, off-white or white at tip. Ventral and dorsal colours delineated by buff or yellowish stripe (adults only). Ears dark with sparse covering of short brownish hairs. Fore- and hindfeet brownish or yellowish. Tail short (ca. 70% of HB), covered with short bristles, dark above, paler below. Skull stoutly built; mesopterygoid fossa narrow compared to *M. bufo*; anterior palatal foramina extending to the antero-internal root of M². Nipples: 3 + 2 = 10.

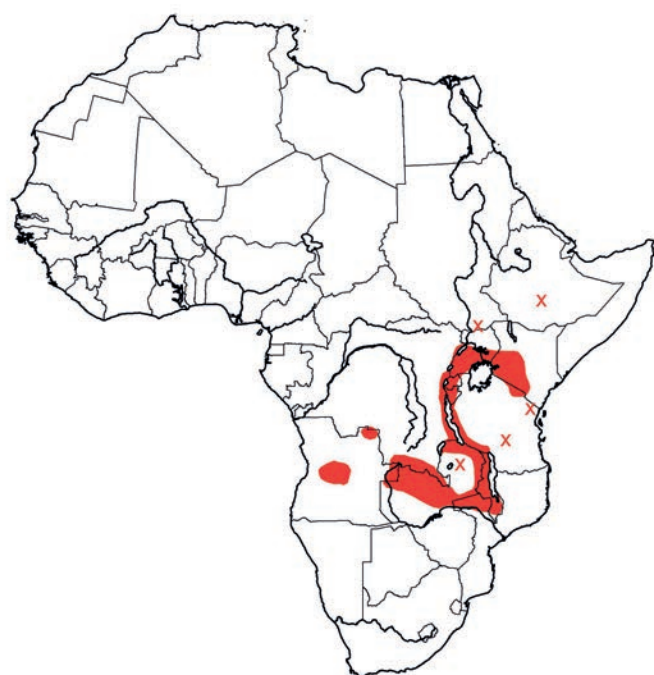
Geographic Variation See Taxonomy.

Similar Species

M. bufo. On average smaller; ventral pelage buff; tail longer and relatively longer; chromosome number: 2n = 36; mountains of Albertine Rift Valley.

M. mahomet. Smaller; ventral pelage greyish-white; tail similar in length; chromosome number: 2n = 36; mainly Ethiopia.

M. minutoides. Much smaller; ventral pelage pure white; tail shorter; chromosome number: 2n = 18–34; widely sympatric.



Mus triton

Distribution Endemic to Africa. Zambezi Woodland BZ and adjacent parts of Eastern and Southern Rainforest–Savanna Mosaics; also Afromontane–Afroalpine BZ in eastern Africa. Recorded from Ethiopia (Bale Mts), S Sudan (Imatong Mts only), NE and N DR Congo, Uganda, Rwanda, Burundi, Kenya, Tanzania, Malawi, Mozambique (Tete district) and Angola (mainly N and NE). In much of eastern Africa, restricted to isolated mountain and highland areas.

Habitat Recorded in many types of grasslands, scrublands, swampy areas and cultivations from 1000 to 3500 m. Typical habitats include grassy areas and slopes (Imatong Mts, Sudan; F. Dieterlen unpubl.), savanna with a dense moist grassy cover (NE DR Congo; Misonne 1963), ‘grass-bush’ and cultivated secondary savanna (west of L. Kivu, E DR Congo; Dieterlen 1967a), *Imperata–Hyparrhenia* grassland (Rwenzori Mountains N. P., Uganda; Delany 1972, 1975), and grasslands in high and moderate rainfall areas (including burnt grasslands) and cultivation (Malawi; Hanney 1965, Happold & Happold 1989a, b). Also recorded in wet montane grasslands at higher altitudes (Kenya, Tanzania; Martin & Dickinson 1985, Stanley *et al.* 1998b). In Bale Mts, Ethiopia, confined to forest habitats (Yalden 1988). On Rwenzori Mts, Uganda, found in low montane forest (1900 m) but not at higher altitudes (cf. *M. bufo*) (Kerbis *et al.* 1998).

On Zomba Plateau, Malawi (1900 m), trapping data showed that *M. triton* preferred montane grasslands (61% of captures) to bracken (26%) and tangles (7.5%), and no individuals were found in adjacent montane forest habitats. They also showed a slight preference for unburnt grasslands (39%) to burnt grasslands (22%), but they moved into burnt grasslands when the burnt grasses sprouted. There was also a clear preference for unburnt bracken (24%) that provided some cover to burnt bracken (2.5%) that provided no cover (Happold & Happold 1989a).

Abundance In montane grasslands on Zomba Plateau in Malawi, *Mus triton* was the most abundant species, forming 37% of all trappable small mammals on a yearly basis (8 spp. rodents, 1 sp. shrew; n = 218 individuals). Population numbers remained more or less constant throughout the year, although population structure changed seasonally – see below (Happold & Happold 1989a). Abundance varies by locality at any one time: in Malawi in Apr–May: 9% on Nyika Plateau (where *Rhabdomys pumilio* and *Lophuromys flavopunctatus* were the commonest species), 20% on Zomba Plateau (where *Lophuromys flavopunctatus*, *Mus triton* and *Praomys delectorum* were the commonest species) and 2% on Mulanje Mt (where *Lophuromys flavopunctatus*, *Rhabdomys pumilio* and *Praomys delectorum* were the commonest species) (Happold & Happold 1989b).

Adaptations Terrestrial and mainly nocturnal. Daily activity (as assessed by trapping) is both nocturnal (ca. 70%) and diurnal (30%) (Rahm 1967). Individuals run on the ground, probably using the runways made by larger rodents. They do not dig burrows, but make nests, which are hidden at the bases of clumps of grass.

Foraging and Food Omnivorous, primarily insectivorous. In Malawi, 81% of stomachs (n = 36) contained insects, mostly adult beetles, and one stomach contained only ant pupae; 28% of stomachs contained white vegetable material (but never green cells) and 8% contained earthworms (Hanney 1965). In DR Congo, five of nine stomachs contained vegetable material (mostly sorghum) and four

contained mainly insects (Dieterlen 1967a). Foraging appears to be opportunistic.

Social and Reproductive Behaviour No information.

Reproduction and Population Structure Reproductive season varies according to locality. In Queen Elizabeth N. P., Uganda, where rain may fall in every month, pregnant ♀♀ recorded during months when rainfall is greater than 50 mm/month (Apr–Jul, Aug–Dec); pregnancy rate varies monthly and in the same month in different years depending on seasonal and yearly changes in rainfall (Delany & Neal 1969, Neal 1986). In a single wet season, each ♀ produces two (sometimes three) litters. In Kivu, E DR Congo, most reproduction is during the wet season (Oct–Mar) when pregnant and/or lactating ♀♀ comprise ca. 40% of all adult ♀♀ with a peak of reproduction of ca. 65% in Jan–Feb. Mean annual reproductive rate of all adult ♀♀ is ca. 30%. No reproduction recorded at end of dry season (Aug–Sep) (Dieterlen 1967a). Further south in Malawi, young recorded during wet season (ca. Dec–Mar) and in the early dry season (Apr–Jul); young not recorded in late dry season (Aug–Nov) (Happold & Happold 1989a). Reproductive rate appears to be comparatively low. Gestation: not known. Embryo number: Uganda: 4.50 (2–6, n = 14; Delany 1975); Kivu: 4.31 (2–7, n = 16; Dieterlen 1967c); Malawi: 6.0 (2–7, n = 5; Hanney 1965). At birth, WT = 0.8 g, HB: 23 mm, T: 9 mm, HF: 4 mm, E: 0 mm and not yet open (n = 5). Day 25–30: WT: = 4–5 g. Day 50: WT: = ca. 8 g. Maturity: WT: = 9–10 g and HB: >70 mm (♀♀) (Dieterlen 1967c.)

In Malawi, during late dry season, most individuals in population are subadults (WT: 9–10 g). By early wet season (Nov), subadults are now adults and some ♀♀ are pregnant (WT: 12–20 g). During the wet season (Dec–Mar), populations composed of juveniles, subadults and adults (range 8–20 g). Mortality of many/most adults between Jun and Sep (dry season, often cool) (Malawi; Happold & Happold 1989a). Proportion of young in population varies seasonally: 0% in late dry season, 15–20% in early wet season, 43–45% in late wet season, and 11% in early dry season by which time young have become subadults and reproduction has ceased. Survival rate in population (data from CMR studies): two months – 0.4; four months – 0.2; six months – 0.1 (Happold & Happold 1989a).

Predators, Parasites and Diseases Occasionally preyed upon by African Grass-owls *Tyto capensis* in Malawi (Happold & Happold 1986); comprised 8–13% of prey in montane grasslands, contributing only 2% of prey biomass. In Malawi, 6.1% (n = 99) of individuals were diseased, mostly by diphyllbothriid larvae (tapeworms; Cestoda). Infection rate was 14–15% in Feb–May and 0% (n = 44) in Oct–Nov. The high infection rate by this parasite in *M. triton* is similar to that in *Lophuromys flavopunctatus* (see Hanney 1964), suggesting similar or identical feeding habits (Hanney 1965). Also parasitized by (adult) *Hymenolepis* sp. (Cestoda) (Hanney 1965).

Conservation IUCN Category: Least Concern.

Measurements

Mus triton

HB: 75.7 (69–80) mm, n = 27

T: 54.0 (49–63) mm, n = 27

HF (c.u.): 15.9 (15–17) mm, n = 27
 E: 12.7 (12–14) mm, n = 27
 WT: 12.1 (8–18) g, n = 27
 GLS: 21.8 (20.5–22.7) mm, n = 27
 GWS: 10.6 (10.3–11.3) mm, n = 26
 M¹–M³: 3.7 (3.2–4.1) mm, n = 24

Lwiro, E DR Congo (F. Dieterlen unpubl., SMNS)

Key References Delany 1975; Dieterlen 1967a, c; Hanney 1965; Happold & Happold 1989b, c.

Fritz Dieterlen & D. C. D. Happold

GENUS *Myiomys*

Mill Rats (Three-toed Grass Rats)

Myiomys Thomas, 1906. Ann. Mag. Nat. Hist., ser. 7, 18: 224. Type species:
Myiomys cunningghamei Thomas, 1906 (= *Golunda dybowskii* Pousargues, 1893).



Myiomys dybowskii.

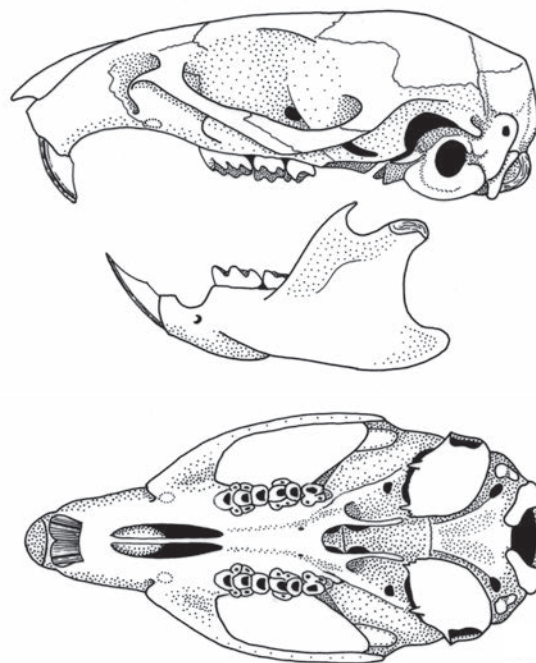


Figure 77. Skull and mandible of *Myiomys dybowskii* (RMCA 37016).

The genus *Myiomys* contains two species, one widely distributed in eastern and central Africa, and the other restricted to the type locality in Ethiopia. The preferred habitat is grassland and forest–grassland mosaic (*M. dybowskii*) or forest (*M. rex*).

The genus is characterized by reduction of the number of digits on the forefoot: Digits 1 and 5 are reduced or vestigial, so there are only three functional digits (cf. *Arvicanthis* and *Pelomys* with four digits [Digit 1 absent, Digits 2, 3 and 4 normal, Digit 1 reduced]). Skull with heavy rostrum, strong supraorbital ridges, large interparietal, thick zygoma, low zygomatic plate, and narrow palate. Upper incisors grooved (cf. ungrooved upper incisors in *Arvicanthis*, grooved in *Pelomys*). Molars unusually broad and strong, and cusps very prominent. Upper molar teeth closely crowded together (Ellerman 1941). The cusps of upper molars face backwards whereas the cusps of the lower molars face forwards (Figure 77).

There are some striking external similarities between *Myiomys* and species of *Pelomys* and *Arvicanthis*, but a real relationship exists only with *Pelomys* (Ellerman 1941, Musser & Carleton 2005). Although similarities in the characteristics of the teeth suggest that species of *Myiomys* should be placed with *Pelomys* (Heim de Balsac 1967a, Heim

de Balsac & Bellier 1967), most taxonomists consider *Myiomys* and *Pelomys* to be different genera. Morphological features link *Myiomys* to *Arvicanthis*, *Pelomys*, *Rhabdomys* and *Lemniscomys* (Musser 1987b), as do studies on mitochondrial DNA sequences (mitochondrial DNA cytochrome *b*, 12S and 16S rRNA gene sequences) (Ducroz *et al.* 2001). Molecular results suggest that *Myiomys*, *Pelomys* and *Arvicanthis* form a single lineage (Ducroz *et al.* 2001).

Musser & Carleton (1993) recognized only one species, *M. dybowskii*, with eight synonyms (originally described as species or subspecies). A giant specimen without skull from Ethiopia, described as *Desmomys (Arvicanthis) rex* (Thomas 1906b), was provisionally placed in synonymy (Musser & Carleton 1993), but is listed as a valid species *Myiomys rex* by Musser & Carleton (2005).

The two species are distinguished by size and geographic distribution.

Fritz Dieterlen

Mylomys dybowskii DYBOWSKI'S MILL RAT (DYBOWSKI'S THREE-TOED GRASS RAT, COMMON MYLOMYS)

Fr. Souris de Dybowski; Ger. Mylomys-Grasratte (Dybowskis Mühlenratte)

Mylomys dybowskii (Pousargues, 1893). Bull. Soc. Zool. France 18: 162.

Kemo River, French Congo (= Central African Republic). (06° 17' N, 17° 15' E).

Taxonomy Originally described in the genus *Golunda*. At one time placed in the genus *Pelomys* (e.g. by Ellerman 1941). Following Petter (1962), the form *lowei* from W Africa is maintained as a valid and separate species, *M. lowei*, by Rosevear (1969) and Grubb *et al.* (1998), but is considered here as a synonym of *M. dybowskii* (see Musser & Carleton 2005). The form *richardi* from lower DR Congo appears to be a special taxon and could be a distinct species (F. Dieterlen unpubl.). Synonyms: *alberti*, *christyi*, *cuninghamei*, *lowei*, *lutescens*, *massaicus*, *richardi*, *roosevelti*. Subspecies: none currently recognized. Chromosome number: $2n = 42$ from Central African Republic (Matthey 1970) and Guinea (Gautun *et al.* 1986). Autosomes comprise 8 large and 32 very small chromosomes – an unusual situation among murid rodents (Matthey 1970).

Description Large stoutly built and impressively coloured rat with a strong and rather thick tail as in most arvicanthine rats. Pelage glossy, dense, coarse and long (ca. 15 mm on back). Dorsal pelage pale brown, heavily streaked with black; hairs dark grey or black, with yellow or blackish tip. Scattered black guard hairs (up to ca. 19 mm), especially on back. Tips of hairs on rump and at base of tail russet. No mid-dorsal black stripe (cf. some *Pelomys* spp.). Ventral pelage off-white, shorter than dorsal pelage; hairs off-white. Colour of dorsal and ventral pelage clearly delineated. Head uniformly similar in colour to dorsal pelage. Lower cheeks, chin and chest off-white. Small patches of yellowish or orange hairs on nose, around the eyes and at the front base of ears in some individuals. Ears large and rounded at tip; pigmented and sparsely

covered with short pale brown and black bristles. Hairs on cheek may obscure base of ear. Fore- and hindfeet similar in colour to dorsal pelage. Forefeet small, with three functional toes (Digits 2, 3 and 4); Digit 1 and 5 small or vestigial; well-developed palmar pads. Hindfeet long and strong with five digits, Digits 2, 3 and 4 long (up to 7 mm) with long curved claws (3 mm); Digits 1 and 5 shorter, reaching to bases of Digits 2, 3 and 4. Tail long (ca. 92% of HB), ringed with small scales, bicoloured, dark and pigmented with short blackish bristles above, paler with whitish or yellowish bristles below. Skull: well-developed supraoccipital ridges; upper incisors each with a single groove towards the outer side of the tooth; orthodont. Cheekteeth extremely cuspidate in young animals. Each upper molar tooth angled posteriorly at 40–45° to supporting maxilla bone (more so than in other murids); each lower molar tooth angled anteriorly at ca. 40–45° to supporting mandibular bone. Nipples: 2 + 2 = 8.

Geographic Variation The western forms (*dybowskii*, *richardi* and *lowei*) from Guinea to the Central African Republic are slightly larger than those from eastern Africa.

Similar Species

Pelomys fallax. Ventral pelage similar in colour to dorsal pelage; mid-dorsal stripe (sometimes indistinct); each upper incisor with groove. *Arvicanthis* spp. Ventral pelage similar in colour to dorsal pelage; each upper incisor without groove.

Distribution Endemic to Africa. Northern and Eastern Rainforest–Savanna Mosaics; outlier populations in Zambezi Woodland and Somalia–Masai Bushland BZs and in parts of the Afromontane–Afroalpine BZ of eastern Africa. Distribution widespread but disjunct. Recorded from C and W Kenya, Uganda, W Tanzania (Mahali Mts), Malawi (Nyika Plateau), NE Rwanda, S Sudan (S Equatoria Province on both sides of Nile R.), DR Congo (non-forested areas west of L. Kivu and L. Edward, and on both sides of Lower Congo R. from near Kinshasa to the Atlantic coast); Congo (north of Lower Congo R. from near Brazzaville to the Atlantic coast), Central African Republic (north of Ubangi R. from ca. 04° N to ca. 06–07° N), and parts of E, C and W Cameroon: Outlier populations in W Ghana (Wenchi only, as *M. lowei*; Grubb *et al.* 1998), Côte d'Ivoire and Guinea (Mt Nimba). No records from Nigeria, Benin and Togo.

Habitat *Mylomys dybowskii* is – apart from a few exceptions – an inhabitant of the Rainforest–Savanna Mosaics. Preferred habitats are moist and tall grasslands with scattered trees and/or shrubs. Recorded from *Imperata cylindrica*, *Cymbopogon afronardus* and *Themeda triandra* grasslands (Queen Elizabeth N. P., Uganda; Neal 1970, Cheeseman & Delany 1979); forest–grassland mosaic (Didinga Mts, SE Sudan; H. Rupp unpubl.); montane grasslands up to 2300 m (NE

*Mylomys dybowskii*

and E DR Congo [Misonne 1963, Rahm 1967]; Malawi [Chitaukali *et al.* 2001]), and grasslands and clear-cut areas at the edge of rainforest (Côte d'Ivoire; Bellier 1967).

Abundance In most habitats, *M. dybowskii* is recorded as rare. In a few localities may be locally quite common: e.g. in one locality in Queen Elizabeth N. P., Uganda, it comprised 44% of all rodents (9 spp.; n = 140), yet was absent at five other savanna localities in the N. P. (Delany 1964b). In another study in Queen Elizabeth N. P., it comprised 7–21% (mean 13%) of all small rodents (6 spp.), and 12–35% (mean 22%) of total biomass during the eight months before the grasslands were burned (Cheeseman & Delany 1979). The proportion of *M. dybowskii* fell to 1–5% of all rodents during three of the nine months after burning, and to 0% during the other six months, including those 8–9 months after the fire when new grasses had sprouted. In this respect, *M. dybowskii* is similar to sympatric *Lophuromys sikapusi*, and it is much less 'fire-adapted' compared with other sympatric species (e.g. *Lemniscomys striatus*, *Mus triton*, *Mastomys natalensis*). In unburnt grasslands in Côte d'Ivoire, comprised 16%, and was the third most numerous species of small mammals after *Dasyms incomtus* and *Uranomys ruddi* (n = 177; 8 spp.) (Bellier 1967).

Adaptations Terrestrial and mostly diurnal. Probably fast-running, and perhaps leaping, as suggested by the rather short forefeet and the long hindfeet, which bear three long central toes with long claws. Verheyen & Verschuren (1966) report that they do not use burrows and their grass nests are normally on the ground. The alimentary canal has a very large caecum and colon (comprising ca. 60% of the total length), indicative of a mainly grass diet (Dieterlen 1967b).

Foraging and Food Herbivorous. Contents of 25 stomachs from W Uganda contained only grass leaves and stems (Delany 1964b). Two specimens from cultivated land in Kivu, DR Congo, had very large stomachs containing a homogeneous green pulp, mostly of green beans, grass and herbs (Dieterlen 1967b).

Social and Reproductive Behaviour No information.

Reproduction and Population Structure In Queen Elizabeth N. P., Uganda, reproduction occurs in most months of the year; pregnancies recorded in all months except Jan and Feb (no samples), Jul and Aug. For months when pregnancies were recorded, 50–100% of ♀♀ were pregnant except for Sep (n = 1–8 ♀♀/month; Delany & Neal 1969). Very young animals found in all months except Mar, Apr, Sep and Nov (Delany 1975). Embryo number: mean 4.32 (2–6, mode 5, n = 28 litters; Delany 1975). Dorsal pelage in young animals is dull blackish-brown, usually without yellowish tinge, and ventral pelage is greyish; subadults have a slight warm glossy yellowish tinge (and may be confused with young *Pelomys fallax*).

Predators, Parasites and Diseases Remains found in stomach of a Puff Adder *Bitis arietans* in Uganda (Cheeseman & Delany 1979). *Mylomys dybowskii* belongs to the small mammalian fauna of the endemic plague regions in NE and E DR Congo (Fain 1953, Misonne 1959). In Central African Republic, forms of *Toxoplasma* found in parasitizing Thrombiculids mites (Giroud *et al.* 1952).

Conservation IUCN Category: Least Concern.

Measurements

Mylomys dybowskii

HB: 160 (122–194) mm, n = 87

T: 147 (104–180) mm, n = 85

HF: 32.8 (29–37) mm, n = 87

E: 20.0 (14–25) mm, n = 83

WT: 114 (46–190) g, n = 84

GLS: 36.9 (34.4–39.1) mm, n = 15

GWS: 17.7 (17.0–18.7) mm, n = 15

M¹–M³: 8.1 (7.7–8.6) mm, n = 15

Queen Elizabeth N. P., Uganda (Delany 1975, BMNH)

Key References Cheeseman & Delany 1979; Delany 1975; Rosevear 1969.

Fritz Dieterlen

Mylomys rex KING MILL RAT (ETHIOPIAN THREE-TOED GRASS RAT, ETHIOPIAN MYLOMYS)

Fr. Souris d'Ethiopie; Ger. Königsmühlenratte

Mylomys rex (Thomas, 1906). Ann. Mag. Nat. Hist., ser. 7, 18: 304. Charada Forest, Ethiopia.

Taxonomy Originally described in the genus *Arvicanthis*. This species is known only from the holotype. When describing this species, Thomas (1906b) remarked that it was likely to be a large form of *Desmomyss*, a genus sometimes considered as a synonym or subgenus of *Pelomys*. Hence, *rex* has been referred to as *Pelomys rex* for the past 90 years (e.g. by Yalden *et al.* 1976; Yalden & Largen 1992). The species is known only from the holotype. However, Musser & Carleton (1993) correctly point out that *rex* is in fact a *Mylomys*; they doubted its separation from central and West African *M. dybowskii* and considered *rex* as a synonym. Later (in 2005) these authors reinstated *rex* as a valid species on the basis that it is larger than *M. dybowskii* and lives in tropical deciduous forest. Musser & Carleton (1993, 2005) questioned the locality of the holotype, but there is no doubt that it

was collected by Peter Zaphiro in Ethiopia: his distinctive hand-writing is evident on the original collection label, and the locality and date of collection are consistent with his published route map. There is a large gap in geographic range between the type locality in Ethiopia and the nearest localities of *M. dybowskii*. Without more specimens and a full taxonomic appraisal, it seems premature to sink this species into synonymy. Synonyms: none. Chromosome number: not known.

Description Very large, harsh-furred rat, looking like a large *Arvicanthis*. Dorsal pelage speckled sandy-brown, redder around the rump. Ventral pelage bluish-white, with a sharp delineation between dorsal and ventral colours. Tail long (ca. 83% of HB), coarsely ringed. Forefeet with only three functional toes.

Geographic Variation None recorded.

Similar Species

M. dybowski. Similar in form, but smaller in external dimensions; widespread but not recorded in Ethiopia.

Pelomys fallax. Ventral pelage similar in colour to dorsal pelage; each upper incisor with groove.

Arvicanthis spp. Ventral pelage similar in colour to dorsal pelage; each upper incisor without groove.

Distribution Endemic to Africa. Afromontane–Afroalpine BZ. Only known from the holotype collected in Charada Forest, Kaffa, Ethiopia (ca. 07° 25' N, 36° 45' E; 1800 m).

Habitat Moist evergreen montane forest.

Abundance Only known from the holotype.

Remarks Apparently no other information available.

Conservation IUCN Category: Data Deficient.

Measurements

Mylomys rex

HB: 212 mm, n = 1

T: 175 mm, n = 1

HF: 35 mm, n = 1

E: 24 mm, n = 1

WT: n. d.

GLS: n. d.*

GWS: n. d.*



Mylomys rex

M¹–M³: n. d.*

Ethiopia (Thomas 1906)

*Skull missing

Key References Musser & Carleton 2005; Thomas 1906b; Yalden & Largen 1992.

D.W.Yalden

GENUS *Myomyscus*

Meadow Mice

Myomyscus Shortridge, 1942. Ann. S. Afr. Mus. 36: 93. Type species: *Mus verroxii* (= *verreauxii*) A. Smith, 1834.



Myomyscus brockmani.

The genus *Myomyscus* contains three species, each widely separated geographically from each other. All species live in grassland or heathland habitats, and some may be associated with rocky habitats. The genus is characterized by small body size, long or very long tail (100–140% of HB), brown or grey dorsal pelage, white or whitish ventral pelage, and four or five pairs of nipples. The skull is similar to that of the genera *Mastomys* and *Praomys* (Figure 78).

Two of the species currently assigned to *Myomyscus* were formerly placed in *Myomys*. The genus *Myomyscus* was proposed because, according to some authorities, *Myomys* was an invalid name (Musser & Carleton 1993). However, *Myomys* was still accepted as valid by Musser & Carleton (1993), but current opinion replaces *Myomys* by *Myomyscus*. As a consequence, the six species previously allocated to *Myomys* are reallocated to different genera as follows: *Myomys albipes* (now *Stenocephalemys albipes*), *Myomys daltoni* (now *Praomys daltoni*), *Myomys derooi* (now *Praomys derooi*), *Myomys fumatus* (now *Myomyscus brockmani*), *Myomys ruppi* (now *Stenocephalemys ruppi*) and *Myomys verreauxii* (now *Myomyscus verreauxii*). Thus only two of the original *Myomys* remain within *Myomyscus*, two have been transferred to *Stenocephalemys* (a purely Ethiopian genus) and two have been transferred to *Praomys*. The third species within the genus *Myomyscus* is *M. angolensis* (formerly *Mastomys angolensis*), transferred primarily because it has only five pairs of nipples and is not a 'multimammate rat' with up to 12 pairs of nipples.

The genus *Myomyscus* appears to be polyphyletic (Musser & Carleton 2005). The relationships of the genus are uncertain and contradictory.

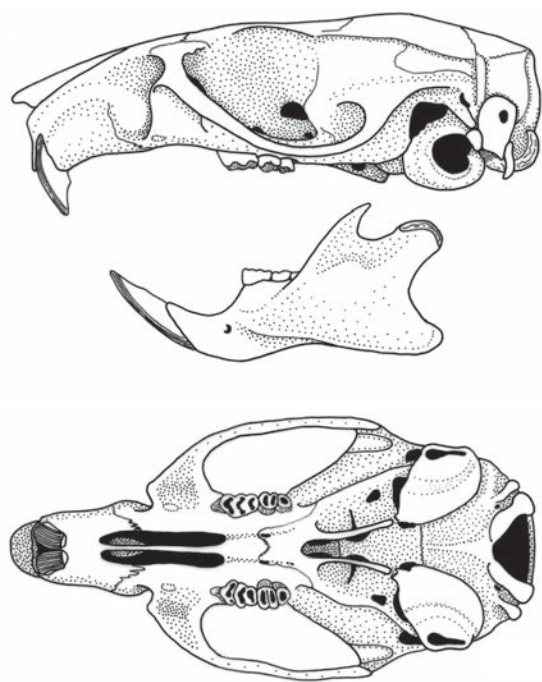


Figure 78. Skull and mandible of *Myomyscus brockmani* (HC 266).

Analysis of complete mitochondrial DNA cytochrome *b* sequences places *M. verreauxii* as a sister-group to *Colomys* and *Zelotomys*, and *M. brockmani* as a sister-group to *Mastomys* and *Stenocephalemys*. Chromosomal and immunological studies relate *Myomyscus brockmani* (as *Myomys fumatus*) to species of *Mastomys* (Qumsiyeh *et al.* 1990), and morphometric analysis places *M. verreauxii* closer to *Mastomys* than to other species of *Myomyscus* (Van der Straeten & Dieterlen 1983, Van der Straeten & Robbins 1997). Molecular analysis clusters *Myomyscus* with *Praomys*, *Mastomys*, *Hylomyscus*, *Heimyscus* and *Stenocephalemys* (Fadda *et al.* 2001). These relationships are fully discussed by Musser & Carleton (2005).

The species are distinguished by body size and colouration, tail length, skull characters and geographic distribution.

D. C. D. Happold

Myomyscus angolensis ANGOLAN MEADOW MOUSE (ANGOLAN MYOMYSCUS)

Fr. Souris d'Angola; Ger. Angolische Wiesenmaus

Myomyscus angolensis (Bocage, 1890). Journ. Sci. Math., Phys. Nat., Lisboa, ser. 2, 12.
Capangombe, interior of Moçâmedes District, Angola (15°06' S, 13°09' E). 527 m.

Taxonomy Originally described in the genus *Mus*. This species was known previously as *Mastomys angolensis* but lacks the typical large number of nipples, arranged almost contiguously in two rows, that is so characteristic of multimammate mice. Now assigned to *Myomyscus* (= *Myomys*) (e.g. Hill & Carter 1941, Robbins & Van der Straeten 1989, Crawford-Cabral 1998), an arrangement confirmed by molecular data (Lecompte 2003). Crawford-Cabral (1988) argued that all specimens previously identified as *M. angolensis* were so different from the description of the holotype (now no longer extant), and also in their ecological distribution, that he grouped them in a new species *angolae* in the genus *Mastomys*. Musser & Carleton (1993) considered this to be no more than a renaming of *angolensis*. Synonyms: *angolae*. Subspecies: none. Chromosome number: not known.

Description Medium-sized grey mouse. Dorsal pelage brown to reddish-brown. Ventral pelage grey; hairs dark at base, with white tip. Fore- and hindfeet white. Tail long (ca. 100% of HB); dark reddish-brown above, pale grey below. Skull with considerably wider interpterygoid region than in *Mastomys* species, with which it sometimes is confused. Nipples: 3 + 2 = 10.

Geographic Variation None recorded.



Myomyscus angolensis

Similar Species

Mastomys natalensis. Smaller mean HB and T; tail similar as % of HB; ventral pelage similarly dark grey; much larger geographic distribution; nipples $12 \times 2 = 24$; $2n = 32$.

Mastomys shortridgei. Similar mean HB; mean T shorter and as % of HB; ventral pelage grey with white tips; nipples $5 \times 2 = 10$.

Distribution Endemic to Africa. Zambezian Woodland BZ. Recorded from Angola; may also be present in S DR Congo. Sympatric or altitudinally parapatric with *M. natalensis*.

Habitat Humid grasslands in mountain and highland areas above 1000 m. Tolerates more adverse climatic and soil conditions than *M. natalensis*.

Abundance Not common (Hill & Carter 1941).

Remarks Apparently no other information available.

Conservation IUCN Category: Least Concern.

Measurements

Myomyscus angolensis

HB: 121 (109–127) mm, $n = 5$

T: 122 (103–128) mm, $n = 5$

HF: 24.2 (24–25) mm, $n = 5$

E: n. d.

WT: n. d.

GLS: 31.1 (30.5–32.0) mm, $n = 5$

GWS: 15.3 (14.8–15.5) mm, $n = 5$

M^1 – M^3 : 5.2 (5.4–5.5) mm, $n = 5$

Chitau and Humpata, Angola (Hill & Carter 1941)

Key References Crawford-Cabral 1988; Robbins & Van der Straeten 1989.

Herwig Leirs

Myomyscus brockmani BROCKMAN'S MEADOW MOUSE (SMOKY MEADOW MOUSE, BROCKMAN'S MYOMYSCUS)

Fr. Souris fuligineuse; Ger. Rauchgraue Wiesenmause

Myomyscus brockmani (Thomas, 1908). Ann. Mag. Nat. Hist., ser. 7, 18: 298. Upper Sheikh, Somalia.

Taxonomy Originally described in the genus *Mus*. Previously referred to as *Myomys fumatus* (Peters, 1878) by, e.g. Musser & Carleton (1993) and earlier authors. However, Musser & Carleton (2005), following Van der Straeten & Robbins (1997), showed that the holotype of *fumatus* is a species of *Mastomys* and therefore that the oldest available name for this species is *brockmani*. Placed in genus *Praomys*, subgenus *Myomyscus* (together with *M. albipes* [now *Stenocephalemys albipes*], *M. verreauxii* [now *Myomyscus verreauxii*] and *M.*

daltoni [now *Praomys daltoni*] by some authors, e.g. Kingdon, 1974, Misonne 1974, Delany 1975, Nader *et al.* 1983). Synonyms: *allisoni*, *niveiventris*, *oweni*, *subfuscus*, *ulae*. Subspecies: none. Chromosome number: $2n = 38$, $FN = 48$ (Qumsiyeh *et al.* 1990).

Description Small pale brown mouse, with pure white ventral pelage and long tail. Dorsal pelage soft medium brown, especially in mid-line, becoming paler (smoky) on flanks; dorsal hairs dark grey at base with brown tip on mid-line, pale brown or ochre on flanks. Ventral pelage pure white, clearly delineated from colour of flanks. Head similar to dorsal pelage, with white on chin and throat. Ears fairly large, darkly pigmented with scattered short pale hairs. Limbs short, upper surface similar in colour to flanks, undersurface white. Forefoot with four digits; Digit 1 absent. Hindfoot with five digits; Digit 1 small, ending level with base of Digit 5. Tail long (ca. 140% of HB), scaly with scattered short bristles, medium brown above, paler below. Nipples $2 + 2 = 8$, $3 + 2 = 10$ (labels, BMNH).

Geographic Variation None recorded.

Similar Species

Mastomys natalensis. Ventral pelage grey; nipples 16–24 in two equal rows.

Distribution Endemic to Africa. Mainly southern Somalia–Masai Bushland BZ at higher altitudes. Recorded in SE Ethiopia, S Sudan, NW Somalia, N Uganda, Kenya and N Tanzania. Isolated populations on Jebel Marra (W Sudan) and the Central African Republic (Nader *et al.* 1983).



Myomyscus brockmani

Habitat Smoky Meadow Mice live amongst rocks and boulders, usually at altitudes of 3000–6000 ft (1000–3000 m), where rainfall is low and there is a sparse cover of trees and grasses. They have also been found in caves, and amongst volcanic lava (Mt Suswa, Kenya) and in dry *Acacia* savanna (Uganda). Their preference for rocks suggests an alternative common name ‘rock rat’ (Misonne & Verschuren 1966). On Jebel Marra they were found only in dense grassy vegetation beside a stream (Happold 1966b). Sometimes found in local buildings in NE Somalia (labels, BMNH).

Abundance Populations dispersed and often isolated. Generally uncommon, although may be locally abundant. At one locality beside a stream on Jebel Marra, meadow mice formed 90% of the small mammals ($n = 42$).

Adaptations Terrestrial, nocturnal. Domiciles under and amongst rocks and boulders, and in crevices in volcanic lava; presumably does not dig burrows.

Foraging and Food Misonne & Verschuren (1966) record that stomach contents contain ‘matières amylacées’. The rather narrow cheekteeth suggest that these mice eat soft foods.

Social and Reproductive Behaviour Very little information. The density of individuals on Jebel Marra suggest that meadow mice are sociable and non-aggressive.

Reproduction and Population Structure On Jebel Marra in Dec (dry season), 60% of collected animals were juveniles, suggesting that births occurred in the late wet season (Jul–Sep). Embryo number: 6 ($n = 1$; Mt Suswa, Kenya; Aug; BMNH); 7 ($n = 1$; Ethiopia; Jan; BMNH).

Predators, Parasites and Diseases No information.

Conservation IUCN Category: Least Concern.

Measurements

Myomyscus brockmani

HB: 104 (93–125) mm, $n = 15$

T: 146 (115–175) mm, $n = 15$

HF: 20.7 (18–22) mm, $n = 15$

E: 17 (14–20) mm, $n = 15$

WT: 29.7 (22–39) g, $n = 11$

GLS: 27.7 (25.5–29.9) mm, $n = 14$

GWS: 13.3 (12.7–13.9) mm, $n = 13$

M^1 – M^3 : 4.4 (4.2–4.6) mm, $n = 14$

Sudan, Somalia, Kenya (BMNH; as *Myomys fumatus*)

Key References Happold 1966b; Misonne & Verscharen 1966; Musser & Carleton 2005.

D. C. D. Happold

Myomyscus verreauxii VERREAUX’S MEADOW MOUSE (WHITE-FOOTED MOUSE)

Fr. Souris de Verreaux; Ger. Verreauxs Wiesenmaus

Myomyscus verreauxii (Smith, 1834). S. Afr. Quart. J., ser. 2, 2: 156. Cape of Good Hope near Cape Town, South Africa.

Taxonomy Originally described in the genus *Mus*. Allocated to the genus *Praomys* (subgenus *Myomyscus*) by De Graaff (1981), Smithers (1983) and Corbet & Hill (1986). Placed in the genus *Myomys* by Musser & Carleton (1993) but now, with the elevation of *Myomyscus* to a valid genus, allocated to the genus *Myomyscus* (Musser & Carleton 2005). The original species name, *verroxii*, was amended to *verreauxi* by Sclater (1901) to agree with the correct name of P. J. Verreaux (taxonomist and curator of the South African Museum in the 1830s) after whom this mouse was named (De Graaff 1997). Relationship uncertain: analyses of mitochondrial DNA cytochrome *b* sequences separate *M. verreauxii* from *M. brockmani* (formerly *Myomys fumatus*) and *M. yemeni* and suggest it may be related more closely to *Colomys* and *Zelotomys* than to other species currently in the genus *Myomyscus* (Lecompte *et al.* 2002b). Musser & Carleton (2005) suggest that ultimately *M. verreauxii* may prove to be the only species of *Myomyscus*. Synonyms: *verreauxi* (only one ‘i’), *verroxii*. Subspecies: none. Chromosome number: not known.

Description Small brown mouse, similar in general appearance to *Mastomys* spp. Pelage long (8–12 mm) and soft. Dorsal pelage buffy-brown; hairs dark grey at base, buffy-brown at tip. Longer thicker black guard hairs scattered throughout most of dorsal pelage, especially on lower back and rump. Flanks similar, paler, with fewer guard hairs. Ventral pelage shorter than dorsal pelage, whitish-grey;



Myomyscus verreauxii

hairs dark grey at base, white at tip. Head similar to dorsal pelage; lip, chin and throat pale buffy-brown. Long black vibrissae. Ears large, naked. Fore- and hindlimbs and feet white. Tail very long (ca. 135% of HB), scaly with very small bristles; darker above, paler below. Juveniles paler than adults. Skull: similar to *Praomys*, but broader; supraorbital ridges absent; anterior palatal foramina end near anterior edge of M¹; mid-point of zygomatic arch tends to bow inwards towards cranium (De Graaff 1981). Nipples: 3 + 2 = 10.

Geographic Variation None recorded.

Similar Species

Mastomys spp. Usually larger; more than ten nipples.

Distribution Endemic to Africa. South-West Cape BZ. Known only from SW Cape Province, South Africa, from Olifants R. in the west to near Plettenberg Bay and Knysna in the east.

Habitat Meadow banks near the coast, and near fallen trees and in grassy vleis in forests. Grasslands with *Protea* spp. may be favoured habitat (De Graaff 1981). In the Cederberg region, north of Cape Town, found mostly in forested valleys (Rautenbach & Nel 1980).

Abundance Little information, although may be locally abundant, e.g. 50% of small mammals (n = 28) trapped in forested valleys in the Cederberg area (Rautenbach & Nel 1980).

Remarks Nocturnal and terrestrial. Two stomachs contained 95% insects and 5% white plant material (Rautenbach & Nel 1980). Feeds

on *Protea* seeds and insects (De Graaff 1981). Three species of fleas (*Dinopsyllus abaris*, *D. ellobius*, *Epirimia aganippes*) and two species of ticks (*Ixodes* sp., *Haemaphysalis leachii*), as well as endoparasitic worms, have been recorded (details in De Graaff 1981).

Conservation IUCN Category: Least Concern.

Listed in the South African Red Data Book of 1976–77; now excluded because quite common in suitable habitats, even though populations are dispersed.

Measurements

Myomyscus verreauxii

HB: 106 (90–118) mm, n = 15

T: 143 (124–154) mm, n = 15

HF: 24 (20–28) mm, n = 15

E: 18 (17–20) mm, n = 11

WT: 44 (41–54) g, n = 4

GLS: 29.5, 30.0 mm, n = 2

GWS: 14.8, 14.9 mm, n = 2

M¹–M³: 4.6, 4.6 mm, n = 2

South Africa

Body measurements and weight: ♂♂ only (De Graaff 1981)

Skull measurements: HZM

Females are slightly larger, i.e. HB: 110 (102–133) mm.

Key References De Graaff 1981; Smithers 1983.

D. C. D. Happold

GENUS *Nesokia*

Bandicoot Rats

Nesokia Gray, 1842. Ann. Mag. Nat. Hist., ser. 1, 10: 264. Type species: *Arvicola indica* Gray, 1830.

A genus of large robust rats comprising one or two species. The most widespread species, *Nesokia indica*, is distributed mainly in the Middle East and Asia extending as far west as the extreme NE of Africa. The characteristics of the genus are given in the species account below.

D. C. D. Happold

Nesokia indica SHORT-TAILED BANDICOOT RAT (EGYPTIAN PEST RAT)

Fr. Rat à queue courte; Ger. Kurzschwanz-Bandicootratten

Nesokia indica (Gray and Hardwicke, 1830). Illustr. Indian Zool. 1: pl 11. India (locality uncertain).

Taxonomy Originally described in the genus *Arvicola*. Recorded as *Nesokia bacheri* in Anderson & Winton (1902) and described as a separate species *Nesokia suilla* by Thomas (1907b); *suilla* is now considered to be a junior synonym of the widespread *N. indica*. Considerable morphological variation throughout the worldwide geographic range (see below) suggests that there may be more than one species (Musser & Carleton 1993). External, cranial and dental morphology indicates close relationship with the genus *Bandicota*,

the bandicoot rats of Asia. Bandicoot rats are not related in any way to the marsupial Bandicoots of Australia and New Guinea (Marsupialia: Paramelidae). Synonyms: *suilla* (plus 16 non-African synonyms – see Musser & Carleton 1993, 2005 for details). Subspecies: none. Chromosome number in 90% of population: 2n = 42; polymorphism of sex chromosomes results in 2n = 39, 40 or 41 in 10% of population (Indian specimens; Rao *et al.* 1983).

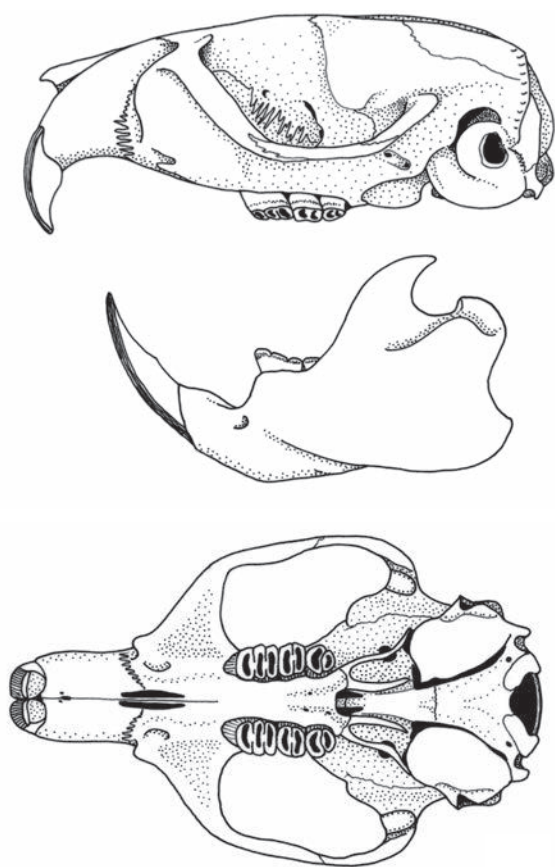


Figure 79. Skull and mandible of *Nesokia indica* (BMNH 4.8.4.3).

Description Large solidly built rat with dense pelage of relatively coarse hair and short tail. Dorsal pelage medium brown; hairs greyish-brown at base, buff-brown or black on terminal third or half. Scattered long black guard hairs (20–30 mm) project beyond surface of dorsal pelage. Flanks paler. Ventral pelage greyish-brown, sometimes with irregular white patches on chest. Head robust, similar in colour to dorsal pelage. Muzzle blunt. Eyes relatively large. Ears small, slightly pointed at tip, mostly naked, with short black vibrissae. Fore- and hindfeet broad, greyish-brown. Forelimbs with four digits; hindlimbs, five digits. Tail short (ca. 66% of HB), thick, scaly, sparsely covered with short dark bristles. Pelage colouration variable. Skull thickset and robust. Upper incisor teeth broad and slightly pro-odont. Incisors without grooves. Cheekteeth laminate, without cusps in adults. Supraorbital and supraoccipital ridges well developed. Auditory bullae well developed (Figure 79). Nipples: 8.

Geographic Variation None in Egypt other than variation in the size of white patch on chest. Osborn & Helmy (1980) refer to the Egyptian Bandicoot Rat as *N. i. suilla* on account of its smaller size compared with other subspecies.

Similar Species

Rattus norvegicus. Slightly larger with long tail (ca. 90% of HB); hindfoot 40–51 mm; dorsal pelage shaggy brownish-black; ventral pelage grey without white markings.



Nesokia indica

Rattus rattus. On average smaller but with long tail (ca. 120% of HB); hindfoot 25–34 mm; dorsal pelage blackish; ventral pelage pale to dark brown, or lemon-yellow, or white.

Distribution Sahara Arid BZ. In Africa, known only from the western margins of the Nile Delta, El Faiyum, Wadi Natron, Bahariya oasis and near Suez in Egypt. Extraliminally recorded from Saudi Arabia, Israel, Iran, Iraq and eastwards to Pakistan and northern India; and north-eastwards to Turkmenistan and NW China. Distribution in Egypt was more widespread during the wetter periods of the Pliocene, Oligocene and Miocene. Such wet periods probably allowed the species to reach Wadi Natron and the Faiyum (now surrounded by desert) from the Nile valley. Fossil remains of *Nesokia indica* have been found at late Pleistocene sites near Aswan and Wadi Halfa in Nubia on the Sudan border (Osborn & Helmy 1980).

Habitat Although within the Sahara Arid BZ, known only from cultivated areas, gardens, canal banks, borders of saline lakes and palm groves, especially where soil is damp (Osborn & Helmy 1980).

Abundance Populations are scattered and local. May be common in suitable habitats. When numerous, regarded as a pest by local farmers.

Adaptations Nocturnal. Burrows are usually less than 0.5 m below the surface, and vary from 2.5 to 9 m in length (Osborn & Helmy 1980). They are mostly situated in damp soils (e.g. on canal banks). Spill heaps of excavated soil often indicate the position of burrows. A nest may be situated 0.6–1.0 m below the surface (Hoogstraal 1963), apparently deeper than most of the burrow. These rats are regarded as very aggressive, and will bite without hesitation when handled.

Foraging and Food In Egypt, fleshy roots of *Alhagi mannifera* and *Typha elaphantina* were found in storage chambers in burrows. Also feeds on crops of maize, barley and vegetables (Hoogstraal 1963).

Social and Reproductive Behaviour No information.

Reproduction and Population Structure Embryo number: 4.7 (1–8). Gestation: 26–28 days. Females nurse young for 30 days after parturition (Iraq; Harrison & Bates 1991). In Egypt, reproductive activity recorded from Feb to Oct; extent and possible seasonality of reproduction in Egypt unknown.

Predators, Parasites and Diseases Fleas have not been recorded from this species, probably because the dampness of the burrows is unsuitable for fleas (Hoogstraal & Traub 1965b). In Iraq, jungle cats, snakes and owls are the main predators (Al-Jumaily *et al.* in Harrison & Bates 1991).

Conservation IUCN Category: Least Concern.

Measurements

Nesokia indica

HB: 183 (165–197) mm, n = 5

T: 121 (110–134) mm, n = 5

HF: 39 (36–42) mm, n = 5

E: 20 (20–21) mm, n = 5

WT: 244 (205–280) g, n = 5

GLS: 44.2 (42.0–46.1) mm, n = 8

GWS: 27.7 (26.1–29.3) mm, n = 7

M¹–M³: 9.7 (9.0–10.4) mm, n = 8

Egypt (Osborn & Helmy 1980)

Key Reference Osborn & Helmy 1980.

D. C. D. Happold

GENUS *Nilopegamys* Ethiopian Water Rat

Nilopegamys Osgood, 1928. Field Mus. Nat. Hist., Zool. Ser., 12: 185. Type species: *Nilopegamys plumbeus* Osgood, 1928.

A monotypic genus occurring only in the highlands of Ethiopia. The genus was described to accommodate the single species *N. plumbeus*, which exhibits many characters associated with a semi-aquatic life-style, and which is far-removed geographically from similar species of the Rainforest BZ. The genus was accepted by Allen (1939) and Ellerman (1941), but subsequently included in *Colomys* by Hayman

(1966), Dieterlen (1983) and Musser & Carleton (1993). Reinstated as a valid genus after the detailed study by Kerbis Peterhans & Patterson (1995) (see also Musser & Carleton 2005). Further details are given in the species profile.

D. C. D. Happold

Nilopegamys plumbeus ETHIOPIAN WATER RAT

Fr. Rat aquatique d’Ethiopie; Ger. Äthiopische Wasserratte

Nilopegamys plumbeus Osgood, 1928. Field Mus. Nat. Hist., Zool. Ser. 12: 185.

Between Sakalla and Njabarra (= Enjibara, Injibarra), Gojam, Ethiopia. 8500 ft (2800 m).

Taxonomy Hayman (1966) placed *N. plumbeus* as a subspecies of *Colomys goslingi*, an arrangement followed by most subsequent authorities (e.g. Misonne 1974; Yalden *et al.* 1976, Dieterlen 1983, Musser & Carleton 1993). Following Kerbis Peterhans & Patterson (1995), *N. plumbeus* is now considered to be a valid species. Known only by the holotype (♂) collected in 1927. Synonyms: none. Chromosome number: not known.

Description Medium-sized semi-aquatic black and white rodent with very long tail and long broad hindfeet. Pelage very soft and dense, suffused with long guard hairs. Dorsal pelage greyish-black; hairs grey at base, blackish at tip. Ventral pelage pure white. Dorsal and ventral colours very clearly delineated. Head rather elongated; muzzle bulbous with vertical cleft on rhinarium and upper lip, and long vibrissae. Eyes small, set high on side of head. Ears small, projecting above pelage, dark, with white fringing hairs on posterior and ventral margins. White postauricular spot. Side of face, upper lips, chin, throat and chest pure white. Shoulder and upper thighs greyish-black as dorsal pelage. Forelimb, greyish-black above, white

below; forefeet pure white. Hindlimbs white; hindfeet white, long and broad, with five digits; Digit 1 with large claw, Digit 5 elongated; soles edged with fringing hairs. Tail very long (ca. 120% of HB), rather broad at base and not laterally flattened, ringed with scales, black above, white below with sharp thin median mid-ventral black line; tip of tail totally black. Skull with flattened dorsal profile (when viewed from side), rostrum straight without ridges, and enlarged foramen magnum (Figure of skull not available). Nipples: not known.

Geographic Variation None recorded.

Similar Species

Colomys goslingi. Similar in colour and pattern; smaller HB, T and WT; HF similar in length but less broad; longer ears; Cameroon to Uganda, Kenya and S Sudan.

Deomys ferrugineus. Dorsal pelage bright rusty-red; ventral pelage white; long naked ears; hindfeet long and slim; S Cameroon and Gabon to Rwanda and Uganda.

*Nilopegamys plumbeus*

Distribution Endemic to Africa. Afromontane–Afroalpine BZ. Recorded only from the type locality in the highlands of Ethiopia, about 70 km south of L. Tana.

Habitat The holotype was taken ‘in a small clear stream, probably nameless but tributary to the Little Abbai not far from its source ... in a little runway leading from the water across a tiny islet’ (Osgood 1928).

Abundance Extremely rare; not seen since 1927.

Adaptations External characters suggest it is semi-aquatic: these include the bulbous muzzle and long vibrissae, the flattened form of the head and high-set eyes, the dense woolly pelage, the stark contrast between dark dorsal pelage and white ventral pelage, and the long

broad hindfeet. It shares some of these characters with *Colomys goslingi* and *Deomys ferrugineus* (and *Malacomys* spp. to a lesser extent), which are also semi-aquatic, although these species are more inclined to be ‘waders’ rather than ‘swimmers’. The flattened profile of the upper surface of the skull and the large foramen magnum are similar to those in other African and non-African semi-aquatic rodents. The brain is enlarged (about 1.5 times larger than expected for a murid rodent of this size), which may indicate that *N. plumbeus* lives in a complex three-dimensional environment (such as rivers and streams) (Kerbis Peterhans & Patterson 1995). The broad hindfoot suggests an ability to swim; however, *N. plumbeus* does not show the adaptations for aquatic life (webs between digits, thick laterally flattened tail) as seen in the otter-shrews (Afrosoricida: Tenrecidae).

Remarks The stomach contents of the holotype had a ‘strong fishy smell’, which may suggest that fish (and perhaps other animal foods) are eaten. The foraging behaviour of *Colomys goslingi* (see Dieterlen & Statzner 1981) may be applicable to *N. plumbeus*.

Conservation IUCN Category: Critically Endangered.

Measurements

Nilopegamys plumbeus

HB: 148 mm

T: 180 mm

HF: 40 mm

E: 14.4 mm*

WT: 71–81 g*

GLS: 35.1 mm

GWS: 15.4 mm

M¹–M³: 5.8 mm

Gojjam, Ethiopia (holotype)

Kerbis Peterhans & Patterson (1995)

*Estimated

Key References Kerbis Peterhans & Patterson 1995; Osgood 1928.

D. C. D. Happold

GENUS *Oenomys* Rufous-nosed Rats

Oenomys Thomas, 1904. Ann. Mag. Nat. Hist., ser. 7, 13: 416. Type species: *Mus hypoxanthus* Pucheran, 1855.

The genus *Oenomys* contains two species, *O. ornatus* and *O. hypoxanthus*, which live parapatrically in the Rainforest BZ and in isolated rainforest relics in restricted areas of western and eastern Africa. Although a ‘rainforest’ genus, typical habitats are grasslands, tangles and secondary growth, not rainforest itself.

The genus is characterized by greyish-brown dorsal pelage, with bright russet patches on rump and thighs, bright russet on nose and cheeks, whitish ventral pelage, a medium-sized and relatively long tail, forefoot with four digits and hindfoot with five digits, Digits 1 and 5 considerably shorter than Digits 2, 3 and 4. Principal characters of the long narrow and strongly built skull are: narrow interorbital width with well-developed supraorbital ridges; wide anterior palatal

foramina; supraoccipital ridges with well-developed keels laterally; opisthodont incisors without grooves; cuspidate molars, angled posteriorly; M¹ without t9; and the large central cusps of M¹, M² and M³ form a prominent straight row along length of molars (Figure 80).

The two species of the genus are terrestrial, but capable of climbing in tangles and low branches. Individuals are often active during daylight as well as at night. Nests of grass are built on the ground and up to about 3 m above ground (Dieterlen 1967b, Rosevear 1969). Although uncommon in many areas, population numbers may be very high in preferred habitats (Dieterlen 1967b, Happold 1987). The diet is mainly green vegetation.



Oenomys hypoxanthus.

The genus is considered as closely related to *Thamnomys* (an arboreal genus), suggesting that the two genera had a common ancestor (Hatt 1940a, Lopez-Martinez *et al.* 1998). However, there are important differences in skull and molar morphology between these genera (F. Dieterlen unpubl.). Interestingly, *Oenomys* shares characters of the molar pattern with *Lamottemys* (Dieterlen & Van der Straeten 1988).

The two species are distinguished on body size, dental characters, chromosome number and geographic distribution. Variations in the

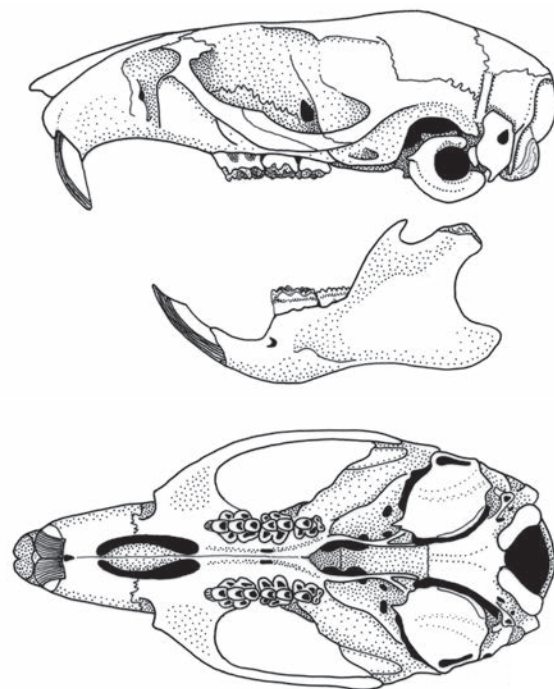


Figure 8o. Skull and mandible of *Oenomys hypoxanthus* (BMNH 26.7.6.26o).

shape and size of the molars along climatic gradients suggest the existence of an additional cryptic species in central Africa (Renaud 1999).

Fritz Dieterlen

Oenomys hypoxanthus COMMON RUFOUS-NOSED RAT (COMMON OENOMYS)

Fr. Rat à museau roux commun; Ger. Gemeine Rotnasenratte

Oenomys hypoxanthus (Pucheran, 1855). Rev. Mag. Zool. Paris, ser. 2, 7: 206. Gabon.

Taxonomy Originally described in the genus *Mus*, but assigned to *Oenomys* by Thomas (1904c) when he proposed the new genus. Shows extensive geographic variation in pelage colour and morphological characters, which has resulted in descriptions of 12 forms, either as species or subspecies (Hollister 1919, Hatt 1940a, Rosevear 1969, Dieterlen & Rupp 1976, F. Dieterlen unpubl.). Variation also occurs within populations from a single locality (Rosevear 1969). Synonyms: *albiventris*, *anchietae*, *bacchante*, *editus*, *marungensis*, *moerens*, *oris*, *rufinus*, *talangae*, *unyor*, *vallicola*. Subspecies: none. Chromosome number: $2n = 32$, $FN = 58$, $aFN = 54$ (Matthey 1963a, Maddalena *et al.* 1989).

Description Medium-sized to large slender rat with a very long tail, and rufous nose and cheeks. Pelage long (up 13 mm), dense, rather harsh. Dorsal pelage greyish-brown to rufous-brown, slightly speckled with yellowish-buff; hairs grey at base, with yellow tip or with black tip. Longer black hairs (ca. 15–23 mm, with buff tip) overlay pelage especially on mid-dorsal line. Rump and upper thighs orange or russet, contrasting with remainder of dorsal pelage. Flanks similar to dorsal pelage, sometimes with greenish-yellow tinge. Ventral pelage pure white or creamy-white, often richly suffused with orange;

clearly delineated from colour of flanks. Head similar to dorsal pelage. Nose, lips and cheeks bright orange or russet. Eyes with dark russet rings in some individuals. Ears large, rounded, covered by short reddish hairs. Vibrissae long, black. Fore- and hindfeet brown or russet, with pale claws. Tail very long (ca. 114–133% of HB), scaly and almost naked, dark above, yellowish below, with short dark bristles. Skull rather long and narrow (see also Genus profile). Nipples: usually $2+1 = 6$, but $1+2 = 6$, $2+2 = 8$ and $1+1 = 4$ in some individuals.

Geographic Variation Pelage colour varies geographically and with altitude. At lower altitudes (in Rainforest BZ), orange-russet colour on rump is darker and more extensive, and ventral pelage is strongly tinged with orange. At higher altitudes (e.g. montane forests, Rwenzori East, 2000 m), rump colouration is paler and less contrasting with colour of mid-back, and ventral pelage is whitish rather than orange/russet (Dieterlen & Rupp 1976).

Similar Species

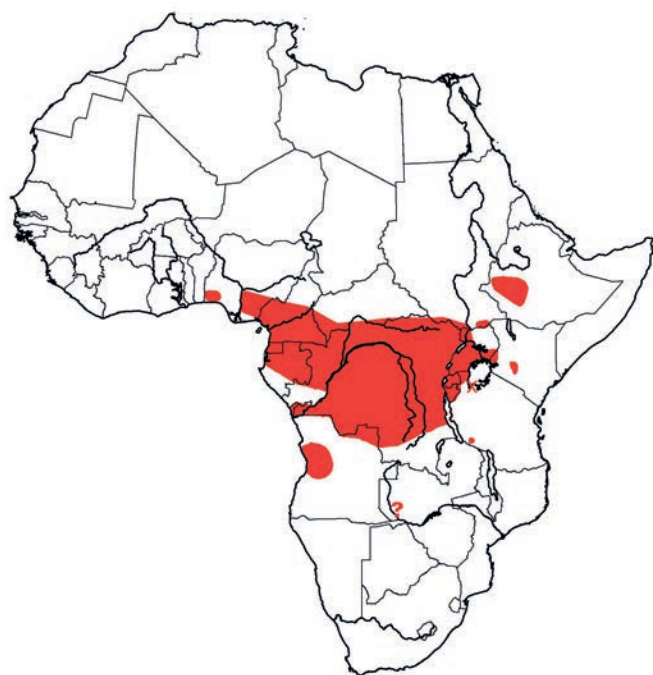
O. ornatus. On average smaller; relatively longer tail; chromosome number: $2n = 46$; occurs only to the west of the Dahomey Gap.

Grammomys spp. Smaller HB and HF; Digit 5 of hindfoot elongated; without russet colour on nose; arboreal.

Distribution Endemic to Africa. Rainforest BZ (South Central, East Central and West Central Regions) and Rainforest–Savanna Mosaics; Afromontane–Afroalpine BZ in Uganda. Recorded in Nigeria (E and W of the Niger R.), C Cameroon, Equatorial Guinea, Gabon, S Central African Republic, Congo and DR Congo. Also recorded in isolated forest patches in S Sudan, Uganda, Rwanda, Burundi, W and C Kenya, W Tanzania, N, NE and C Angola and SW Ethiopia.

Habitat Tall, moist, dense grasslands and shrubby vegetation at the edge of gallery forests, in forest clearings, along borders of marshes, farmlands, plantations and abandoned cultivation. Frequently found in elephant-grass *Pennisetum* spp. In East and central Africa, lives in dense vegetation at the edge of montane forests (2000–3000 m). On the Rwenzori Mts (Uganda) occurs in grasslands and forest from ca. 1500–2900 m, but not in bamboo or in afroalpine habitats (Kerbis Peterhans *et al.* 1998). In regions where the dry season lasts longer than 4–5 months, populations are confined to permanently moist habitats, and hence tend to be isolated from other populations. Suitable habitats are often disjunct, and hence populations also tend to be localized (Rosevear 1969). Habitats range from near sea level to ca. 3300 m (montane forest in Aberdare Range, Kenya; Hollister 1919).

Abundance Very varied. In preferred habitats may be common, e.g. in elephant-grass habitats of E DR Congo comprised up to 26% of trapped small mammals and was often the most numerous species of small mammal (Dieterlen 1967a, b). In E Nigeria, comprised 58% of small rodents ($n = 11,300$) in the herbaceous ground layer of oil palm plantations (Greaves 1964 in Happold 1987). In other seemingly suitable habitats, rare or absent.



Oenomys hypoxanthus

Adaptations Terrestrial, but also climbs in small bushes and on thick grasses; most activity is probably above ground rather than on the ground. Nests are usually constructed at 50–300 cm above ground, and are attached between thick stems of grasses or on forks or twigs of shrubs, and are rarely built on the ground (Sanderson 1940, F. Dieterlen unpubl.). Nests (diameter 12–18 cm) are woven from dry grass and other plant material; on the outside, the grasses are coarsely shredded, but inside are finely shredded. The entrance is directed slightly downwards. Nests are used as sleeping quarters and for raising the young (Rosevear 1969). Rufous-nosed Rats are diurnal and nocturnal (Dieterlen 1967c). When alarmed, they can remain motionless high up in elephant-grass, move ‘in slow motion’, or dive to the ground or even into water (F. Dieterlen unpubl.). Defecation seems to take place on the ground (F. Dieterlen unpubl.; observations in captivity). The alimentary canal is characteristic of a herbivore, the stomach and caecum being particularly large (Dieterlen 1967b, unpubl., Rahm 1972).

Foraging and Food Herbivorous. The diet (as assessed by stomach contents) of individuals living close to rainforests was primarily grass and herbs (46%), but also flesh and kernels of forest and cultivated fruits (48%), including *Carica papaya*, *Coffea robusta*, *Psidium guayava*, *Elaeis guineensis*, *Musanga cecropioides* and *Staudtia stipitata* (Genest-Villard 1980). Some stomachs contained remains of bark (30%) and invertebrates (4–5%, not insects). In E DR Congo preferred food was shoots and leaves of elephant-grass (Dieterlen 1967b). In S Cameroon, damage to bark and leaves of *Hevea* trees – formerly extensively cultivated in African rainforests – has been attributed to these rats (Jeannin 1936).

Reproduction and Population Structure In E DR Congo, reproductive activity varies with altitude and season of the year. (1) At higher altitudes (2000–2400 m), reproductive activity appears to be aseasonal and mean litter-size is 2.27. (2) At 1500–2000 m west of L. Kivu, reproduction is seasonal: 22% ($n = 100$) of adult ♀♀ were pregnant or lactating during the dry season (Jul–Sep), and 55% of adult ♀♀ were pregnant or lactating during the wet season (Oct–Jun), with a peak of 81% in Nov ($n = 254$); mean litter-size varies from 1.95 (dry season) to 2.55 (wet season), with a range (both seasons) of 1–5 (Dieterlen 1967c). (3) At 800–1000 m, in lowland rainforest habitats towards the Congo Basin, reproduction is seasonal with reduced reproductive activity during the drier months (Jul–Sep); mean litter-size 2.61 ($n = 33$; Dieterlen 1985a). In Gabon, mean litter-size: 2.54 (Dubost 1968).

Gestation: not less than 22 days; postpartum oestrus observed for some ♀♀ in captivity (F. Dieterlen unpubl.). At birth, young altricial, naked with short (ca. 1 mm) dorsal pelage and a few long yellow guard hairs (ca. 5–7 mm). Acoustical reactions and ability to crawl away and hide on Day 5–6. Eyes open Day 7–9. Lower incisors erupt Day 7–9. Nose and rump become typically rufous Day 7–9. Many behavioural characteristics (running, undirected jumping) Day 15 when ca. 15 g. Consume green plant material Day 15. Weaned by Day 30–35. Adult size: ca. 3–5 months. One captive ♀♀ produced first litter at age of 141 days. Males from lower altitudes reach maturity earlier (body weight 50–60 g) than those from high altitudes (body weight 75–80 g) (Dieterlen 1967c, 1985a). Sex ratio: 51.9% ♂♂ to 48.1% ♀♀ ($n = 1249$, E DR Congo; Dieterlen 1967a, 1985a, unpubl.).

Predators, Parasites and Diseases Predators include the Civet *Civettictis civetta*, Genet *Genetta maculata*, Palm Civet *Nandinia binotata*, Egyptian Mongoose *Herpestes ichneumon*, Green Mamba *Dendroaspis jamesoni kaimosae* and Nose-horned Viper *Bitis nasicornis* (Kenya; Allen & Lawrence 1936).

Conservation IUCN Category: Least Concern.

Measurements

Oenomys hypoxanthus

HB: 150 (137–165) mm, n = 20

T: 179 (154–201) mm, n = 20

HF: 32.3 (30–34) mm, n = 20

E: 19.7 (18–23) mm, n = 20

WT: 97 (70–124) g, n = 20

GLS: 37.6 (34.0–40.3) mm, n = 20

GWS: 17.8 (17.0–19.3) mm, n = 20

M¹–M³: 7.0 (6.5–7.7) mm, n = 20

Lwiro, E DR Congo (Dieterlen 1967b, SMNS)

Key References Dieterlen 1967a, b; Dieterlen & Rupp 1976; Rosevear 1969.

Fritz Dieterlen

Oenomys ornatus WEST AFRICAN RUFOUS-NOSED RAT (WEST AFRICAN OENOMYS)

Fr. Rat à museau roux d'Afrique de l'Ouest; Ger. Westafrikanische-Rotnasenratte

Oenomys ornatus Thomas, 1911. Ann. Mag. Nat. Hist., ser. 8, 7: 378. Bibianaha, near Dunkwa, Ghana.

Taxonomy Although considered to be a valid species by Allen (1939) and Ellerman (1941), treated as a subspecies of *O. hypoxanthus* by Rosevear (1969), who commented that although the two taxa could be distinguished when viewed together, there was considerable overlap in colour and size. Karyotype and distribution are different to those of *O. hypoxanthus*. Synonyms: none. Chromosome number: 2n = 46 (with 12 meta- and submetacentric and at most 34 acrocentric chromosomes) (Tranier & Gautun 1979).

Description Medium-sized slender rat with a very long tail, and rufous nose and cheeks, similar to *O. hypoxanthus*. Dorsal pelage pale greenish-grey to greenish-brown without any tinge of rufous; hairs dark grey at base, yellow to greenish-yellow at tip. Rump bright pale rufous. Ventral pelage pure white, slightly suffused with rufous, clearly delineated by thin orange band from colour of flanks. Head similar to dorsal pelage; cheeks and nose bright rufous. Ears large and rounded with small tuft of rufous on inner front margin of ear, and rufous-red around backs and sides of ears (particularly visible in young animals). Hindlimbs rufous, as on rump. Fore- and hindfeet pale. Tail very long (ca. 132% of HB), scaly, dark above, yellowish below, with short dark bristles. Skull: see genus profile. Nipples: 1 + 2 = 6.

Geographic Variation None recorded.

Similar Species

Oenomys hypoxanthus. HB on average larger; tail on average shorter; dorsal pelage greyish-brown or rufous-brown; chromosome number: 2n = 32; occurs only to the east of the Dahomey Gap.

Distribution Endemic to Africa. Rainforest BZ (Western Region) and western part of Northern Rainforest–Savanna Mosaic. Recorded from the Loma Mountains in Sierra Leone eastwards to Guinea, Liberia, Côte d'Ivoire and C Ghana. Not recorded from Togo (Robbins & Van der Straeten 1996) or further eastwards.

Habitat Similar to *O. hypoxanthus*. Recorded in open areas with dense undergrowth and grass in Rainforest BZ (Grubb *et al.* 1998). Also found in cultivated areas bordering rainforest in Guinea (Roche 1971).



Oenomys ornatus

Abundance Rarely encountered and considered to be rare; known only from a few localities in each of the countries where recorded (Sierra Leone [2 localities; Grubb *et al.* 1998], Guinea [9 localities; Heim de Balsac & Lamotte 1958, Roche 1971, Misonne & Verschuren 1976], Liberia [2 localities; Kuhn 1965], Côte d'Ivoire [2 localities; Tranier & Gautun 1979, Gautun *et al.* 1986] and Ghana [3 localities; Heim de Balsac & Lamotte 1958, Rosevear 1969, Grubb *et al.* 1998]). In some habitats, may be comparatively common, e.g. near Sérédou (Guinea), where 28 specimens were obtained by local collectors (Roche 1971).

Remarks Presumed similar to *O. hypoxanthus*. One nest in Guinea was made entirely from ears of rice (Roche 1971). Herbivorous (Misonne & Verschuren 1976). One specimen was identified among 374 pellets of a Barn Owl *Tyto alba* in Guinea (Heim de Balsac &

Lamotte 1958). Two juveniles (HB: 70, 72 mm) found in Jan (Ghana; BMNH).

Conservation IUCN Category: Least Concern.

Probably should be considered as Vulnerable in most parts of its range. Individuals may cause damage in some rice fields (Roche 1971).

Measurements

Oenomys ornatus

HB: 143 (131–154) mm, n = 10

T: 189 (180–203) mm, n = 10

HF: 33.5 (31–36) mm, n = 10

E: 18.5 (18–19) mm, n = 10

WT: 95 (80–103) g, n = 4

GLS: 35.6 (34.0–37.7) mm, n = 10

GWS: 16.9 (15.6–17.8) mm, n = 9

M¹–M³: 6.9 (6.3–7.4) mm, n = 10

Ghana (Rosevear 1969); Guinea (Roche 1971)

Key References Grubb *et al.* 1998; Heim de Balsac & Lamotte 1958; Rosevear 1969.

Fritz Dieterlen

GENUS *Pelomys*

Creek Rats

Pelomys Peters, 1852. Bericht Verhandl. K. Preuss. Akad. Wiss. Berlin, 17: 275. Type species: *Mus (Pelomys) fallax* Peters, 1852.



Pelomys fallax.

The genus *Pelomys* contains five species widely distributed in savanna habitats in eastern and central Africa (Table 38). Species of the genus are found mainly in moist habitats and mostly near to water.

The genus is characterized by medium to large size (HB: ca. 120–170 mm), speckled or ‘pepper and salt’ dorsal pelage, with a dark mid-dorsal stripe in some species. Skull strongly built with heavy supraorbital ridges, broad interorbital constriction, a single groove on each upper incisor (as in *Myomys*) and relatively large auditory bullae. Molar teeth heavy with broad cusps, especially in the central and lingual rows (Figure 81).

Pelomys spp. are terrestrial and mainly diurnal. Preferred habitats include savanna with permanent cover of grass or bush, flood-plains, marshes, edges of bogs, and close to streams. All species in the genus require moist conditions, and hence are confined mostly to swamps and marshes in the drier parts of their geographic ranges. Although not morphologically adapted to water, two species (*P. fallax* and *P. hopkinsi*) are known to be semi-aquatic (no data for other species). They are herbivorous, feeding primarily on green vegetable material. In some localities, two species of *Pelomys* may be sympatric or parapatric (e.g. *P. fallax* and *P. campanae*) and in one locality in Angola there are probably three species (*P. campanae*, *P. fallax* and *P. minor*).

Table 38. Species in the genus *Pelomys*. Arranged in order of increasing mean head and body length.

| Species | Subgenus ^a | HB mean (range) (mm) | T mean (range) (mm) [% of HB] | Digit 5 of forefoot has | M ¹ –M ³ | Mid-dorsal stripe | Notes |
|--------------------|-----------------------|----------------------|-------------------------------|-------------------------|--------------------------------|--|---|
| <i>P. minor</i> | P | 122 (101–161) | 113 (100–131) [93%] | Nail | 5.3 (4.9–5.7) | Between ears to base of tail; thin, distinct | Central Africa south of Rainforest BZ |
| <i>P. hopkinsi</i> | K | 122 (116–127) | 164 (160–166) [135%] | Claw | 6.1 (5.8–6.6) | Centre of forehead to base of tail | Swamps near L. Victoria and Albertine Rift Valley; rare |
| <i>P. isseli</i> | K | 132 (114–149) | 149 (135–171) [113%] | Claw | 6.1 (5.9–6.3) | Forehead to base of tail; very distinct | Ssese I., L. Victoria, Uganda only |
| <i>P. campanae</i> | P | 144 (118–170) | 145 (125–158) [100%] | Nail | 6.4 (5.8–6.9) | Mid-back to base of tail; indistinct or absent | Angola, W DR Congo |
| <i>P. fallax</i> | K | 147 (125–174) | 133 (109–156) [90%] | Nail | 6.8 (6.4–7.3) | Neck to base of tail; may be indistinct | East, central and southern Africa; widespread |

^a Subgenera: K = *Komomys*; P = *Pelomys* (see genus profile for details).

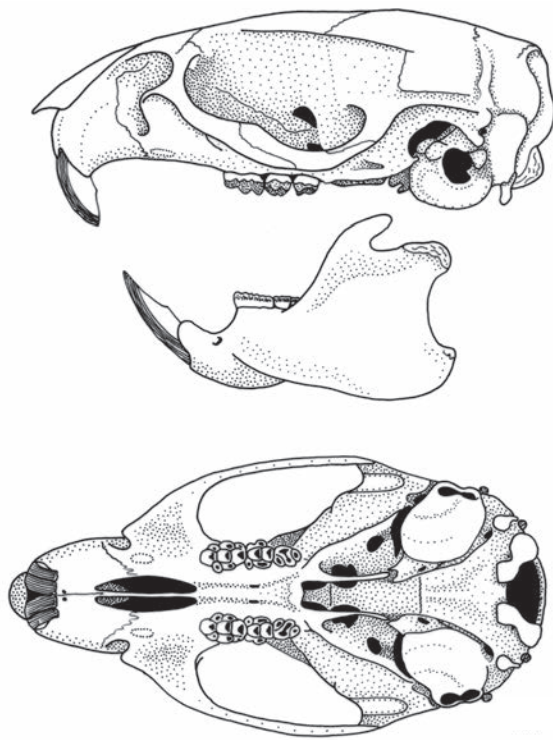


Figure 81. Skull and mandible of *Pelomys fallax* (HC 2299).

Pelomys campanae ANGOLAN CREEK RAT (ANGOLAN PELOMYS)

Fr. Rat à fourrure des marais; Ger. Angolanische Bachratte

Pelomys campanae (Huet, 1888). Le Naturaliste, ser. 2, 10 (31): 143. Landana, west coast of Angola.

Taxonomy Originally described in the genus *Golunda*. Subgenus *Pelomys*. Probably evolved from a peripheral population of the more widely distributed *P. fallax* through isolation by invasive Kalahari sands in S DR Congo (Crawford-Cabral 1983). Synonyms: none. Chromosome number: $2n = 48$, FN uncertain, probably ca. 60 (Matthey 1963a).

Description Distinctive, medium-sized species, similar in overall size to *P. fallax*. Dorsal pelage similar to *P. fallax* (see that species profile). Black mid-dorsal stripe from mid-back to base of tail (in ca. 70% of specimens); indistinct in some individuals. Ventral pelage dull white, yellowish-white or honey-yellow, delineated from colour of flanks. Reddish-yellow patches on neck and ventral surface in some (mostly subadult) individuals. Hairs on nasal region, ears and around eyes rusty-brown. Forefoot with five digits: Digits 2, 3 and 4 normal, Digit 1 very small (almost invisible), Digit 5 small, bearing a nail (as in *P. fallax*). Hindfoot with five digits; Digits 2, 3 and 4 long, Digits 1 and 5 short, not reaching base of other digits; all with short claws. Tail long (ca. 100% of HB), colour variable, mostly darkish above, paler below, bristles short above, slightly longer laterally and below. Skull similar to *P. fallax*, but more delicately built, with less developed median row of cusps (t2, t5, t8) on M^1 and M^2 . Each upper incisor with groove. Nipples: $2 + 2 = 8$.

The genus is a member of the arvicanthine group of species (Musser & Carleton 2005), which also includes *Arvicanthis*, *Desmomys*, *Lemniscomys*, *Mylomys* and *Rhabdomys*. Morphologically it is closely related to *Mylomys* and *Desmomys*. Two subgenera may be recognized (F. Dieterlen unpubl.): (a) subgenus *Pelomys*: tail equal or less than HB, mid-dorsal stripe incomplete or absent, margin of ears without black hairs, and Digit 5 of forefoot relatively short with a nail; (b) subgenus *Komemys*: tail longer than HB, mid-dorsal stripe complete, margin of ears with black hairs, and Digit 5 of forefoot relatively long with claw. Subgeneric distinctions are not recognized by Musser & Carleton (2005).

Species are distinguished by size, relative length of tail, presence/absence of mid-dorsal stripe, and presence of nail or claw on Digit 5 of forefoot.

Fritz Dieterlen

Geographic Variation None recorded.

Similar Species

P. fallax. Mid-dorsal stripe mostly shorter or lacking; ventral pelage usually buff or yellowish; tail shorter (ca. 90% of HB); skull more robust; median row of cusps on M^1 and M^2 well developed.

Distribution Endemic to Africa. North-western part of Zambezi Woodland BZ and Southern Rainforest–Savanna Mosaic. Recorded from Angola, mostly west of 16°E and from ca. 07°S to 17°S including the Cabinda enclave, and from W and SW DR Congo, from the mouth of the Congo R. eastwards to the catchment of the Kwango, Kwilu and Kasai rivers to about 06°S and 23°E . Northernmost locality is Bolobo on the Congo R. Occurs sympatrically or parapatrically with *P. fallax* in parts of its range (Crawford-Cabral 1983).

Habitat Grassland savannas. Sometimes occurs close to but never inside rainforests. In Angola (including Cabinda), occurs on the coastal plains, the Escarpment zone and on the Western Angolan plateau. Also found in old gardens, and in local cornfields with grassy patches (field notes on museum labels). Juveniles (HB: ca. 75 mm) found in Apr, Jun and Jul (Angola; BMNH).



Pelomys campanae

Pelomys fallax EAST AFRICAN CREEK RAT (EAST AFRICAN PELOMYS)

Fr. Rat à fourrure des ruisseaux; Ger. Rillenzahn-Bachratte

Remarks Apparently no other information available.

Conservation IUCN Category: Least Concern.

Measurements

Pelomys campanae

HB: 144 (118–170) mm, n = 31

T: 145 (125–158) mm, n = 31

HF: 32 (27–35) mm, n = 31

E: 18.3 (18–19) mm, n = 31

WT: n. d.

GLS: 35.5 (33.8–36.4) mm, n = 40

GWS: 16.8 (15.7–17.5) mm, n = 9

M¹–M³: 6.4 (5.8–6.9) mm, n = 40

Angola and DR Congo (AMNH, BMNH, FMNH, ICCA, MNHN, RMCA)

Key References Crawford-Cabral 1983, 1998.

Fritz Dieterlen

Pelomys fallax (Peters, 1852). Monatsb. K. Preuss. Akad. Wiss. Berlin 17: 275. Caya district, Zambezi River, Mozambique.

Taxonomy Originally described in the genus *Leggada*. Subgenus *Pelomys*. Because there is considerable variation in size and pelage colour, Musser & Carleton (2005) suggest that *P. fallax* may contain more than one species. The most distinctive forms (which may represent one or more valid species or subspecies, e.g. *frater* in parts of Angola) occur at the margins of the geographic range of the species (F. Dieterlen unpubl.). Synonyms: *australis*, *concolor*, *frater*, *insignatus*, *iridescens*, *luluae*, *rhodesiae*, *vumbae*. Subspecies: none. Chromosome number: not known.

Description Large species, similar in size and colour to *Arvicanthis* spp. Largest species of the genus. Pelage glossy, speckled, with a greenish-brown or olive iridescence. Dorsal pelage golden-yellow to rusty-brown; hairs dark blackish-grey at base, yellow at tip; interspersed with thick black guard hairs, black or yellowish-brown at tip. Mid-dorsal black stripe from neck to base of tail, clearly defined or indistinct, but usually conspicuous in juveniles. Base of tail dull rusty-brown. Ventral pelage variable, usually buff or yellowish anteriorly, dirty-white in axillary and inguinal regions. Head similar in colour to dorsal pelage. Ears sparsely covered with short rufous hairs. Nasal region sometimes rufous. Forefoot with four digits: Digit 1 absent or vestigial; Digits 2, 3 and 4 long, with long claws; Digit 5 very short with nail. Hindfoot with Digits 2, 3 and 4 long with long claws; Digits 1 and 5 short with short claws. Tail long (ca. 90% of HB), black above, whitish below. Skull strongly built with heavy supraorbital ridges, broad interorbital constriction, and relatively large auditory bullae. In most specimens, anterior palatal foramina reach to level of M¹, but not in some populations. Each upper incisor

with groove. Molar teeth heavy with broad cusps, especially in the central and lingual rows. Nipples: 2 + 2 = 8.

Geographic Variation In many parts of its range *P. fallax* shows a relatively large variation in size and pelage colour. The population of *rhodesiae* in the SW corner of its geographic range (SW Zambia and Caprivi Strip) is a distinct form (F. Dieterlen, unpubl.). The typical *iridescens* is distributed in SE Kenya and NE Tanzania. Large areas within the distribution of *P. fallax* – C and S Tanzania, N Mozambique, Malawi, most of Zambia, most of S DR Congo and parts of Angola – have indistinctive forms assigned to *insignatus* and *vumbae*.

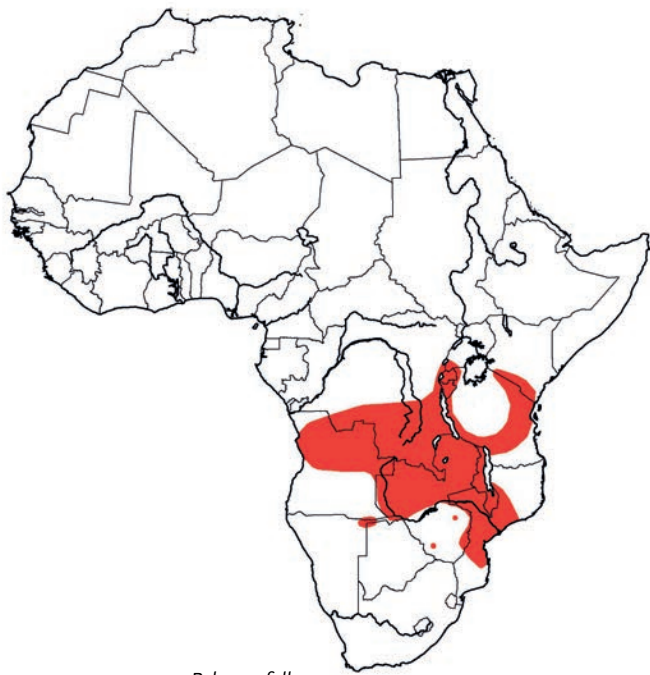
Similar Species

P. campanae. Mid-dorsal stripe distinct (in most individuals); ventral pelage whitish; tail on average longer; median row of cusps on M¹ and M² slightly smaller.

P. hopkinsi. Digit 5 of forefoot with claw.

Arvicanthis spp. Some forms have a slight mid-dorsal stripe; rostrum and nasal region narrower; incisors not grooved; nipples 1 + 2 = 6.

Distribution Endemic to Africa. Zambezian Woodland BZ (north of the Zambezi R.) and Southern Rainforest–Savanna Mosaic; also Afromontane–Afroalpine BZ of central Africa. The most widespread of all species in the genus. Recorded from S Kenya, SW Uganda, Tanzania, Rwanda, Burundi, E and S DR Congo, N Angola, Zambia, Malawi, Mozambique, N Botswana, N Zimbabwe and NE Namibia (Caprivi Strip). Wide altitudinal distribution: in N Tanzania 150–2400 m (Hubbard 1972), and in E DR Congo up to 2000 m and

*Pelomys fallax*

also in open grassy montane areas at higher altitudes (F. Dieterlen unpubl.).

Habitat Generally restricted to savanna habitats with permanent cover of grass or bush or cultivation. In regions where some parts of the year are dry, confined to permanent damp habitats, e.g. flood-plain grasslands, marshes, edges of bogs, stream sides, the perimeter of forests, and all habitats 'where access to water is possible throughout the year and where the overhead shelter is not normally destroyed by fire' (Vesey-Fitzgerald 1966). In regions where the wet season is long (up to nine months of the year, e.g. SW Uganda, E DR Congo), distribution is more or less continuous and populations are not restricted to swamps and marshes, etc.; in such localities, recorded from stands of *Pennisetum* and other grasslands, swampy secondary bush and dense cultivation (Dieterlen 1967a, Rahm 1967).

Abundance Not rare, but never abundant, in the cultivated habitats west of L. Kivu, E DR Congo. In dense elephant-grass, and in more open grassy bushland, numbers estimated at ca. 3% of the small mammal community (5 spp., $n > 100$; Dieterlen 1967a, c).

Adaptations Terrestrial, nocturnal and diurnal. Activity may vary with habitat: in Botswana, where occurs only in swampy areas, it is almost entirely diurnal (Smithers 1971); in Uganda, where the environment is generally moist, they are considered as 'equally diurnal and nocturnal' (Delany 1975). The colouration and pattern of the pelage appears to provide excellent camouflage during daylight hours. Runs quickly and hides under grass. In southern Africa, they dig their own burrows, often in dry ground adjacent to wet places (Smithers 1983). In contrast, in dense grasslands of E DR Congo, the thick layer of rotten vegetation provides excellent shelter. Nests of grass are either built amongst grass debris, or in burrows. In the Okavango swamps, Shortridge (1934) recorded that individuals were 'often observed sunning themselves like water voles on the fringe of

the reed-beds, now and again taking short plunges into the water from one patch of vegetation to another. They were rather wary and on alarm disappeared behind the reeds'. In moister habitats, they are parapatric with *Otomys* spp., and in drier habitats with *Lemniscomys* spp. and *Arvicanthis* spp.

Foraging and Food Mainly herbivorous. Feeds on leaves, shoots, stems of various grasses and swamp vegetation, often leaving behind small piles of cut grass stems (a behaviour also seen in some other species of grass-eating rodents). Stomach contents in cultivated areas contained green vegetation – green stems, leaves and pods of beans, but also grains of sorghum and whitish matter of tubers etc. May also feed on seeds (Smithers 1983). In Malawi, contents of three stomachs contained only green vegetation, one contained white material (presumably from seeds) and one contained insect remains (Hanney 1965).

Social and Reproductive Behaviour Little information. Captive animals are docile and communal (Hanney 1965). Nests where young were found in E DR Congo were made of very finely shredded grass, mostly situated under rotten vegetation or in very large tussocks of elephant-grass (*Pennisetum purpureum*).

Reproduction and Population Structure Reproductive activity occurs throughout most of the year near L. Kivu, E DR Congo, without any clear relationship to wet and dry seasons. Most births occurred in Jan–Jul when 58% of adult ♀♀ were reproductively active ($n = 26$); activity declined in Aug–Dec when 33% of adult ♀♀ were reproductively active ($n = 15$). In Botswana and Zimbabwe, reproduction occurred in the warmer and wetter months between Aug and Apr (Smithers 1971, 1975). Gestation: not known. Embryo number: 5.45 (4–7, $n = 11$; DR Congo; Dieterlen 1967c). Embryo number: 2 and 7 (Nyika Plateau, Malawi; Hanney 1965). Nests found with complete litters in Kivu, E DR Congo, had 3–7 young. Development as follows (mean values from two litters; F. Dieterlen unpubl.). Day 1–2: HB: 40 mm, WT: 2.8 g; skin darkly pigmented with fluffy yellowish hairs (1 mm). Day 4–5: HB: 46 mm, WT: 4.5 g. Day 7–8: HB: 52 mm, WT: 5.1 g, dorsal stripe visible, lower incisors erupting (0.5 mm). Day 10: eyes open. Day 22: HB: 73 mm, WT: 13.5 g. Day 65: HB: 119 mm, WT: 50 g, scrotum visible in ♂♂. Day 105: HB: 140 mm, WT: 78 g, adult pelage fully developed.

Predators, Parasites and Diseases Predators include owls (several records of remains in owl pellets from Malawi; Hanney 1965) and genets (Hubbard 1972). Heavily parasitized, more so than most other species of small mammals near L. Kivu, DR Congo. Most free-living young supported many fleas. Subadults and adults were often infested with larvae of bot-flies (*Cordylobia* sp.), up to 10 mm long, under the skin near the base of tail, on the belly and on the neck (F. Dieterlen unpubl.). In Malawi, parasitized by nematodes *Longistriata* sp., cestodes *Inermicapsifer guineensis*, and fleas *Ctenophthalmus calceatus*, *Dinopsyllus lypusus* (Hanney 1965). In Tanzania, six species of fleas reported – the two spp. listed above, *D. longifrons*, *C. blandulus*, *C. verutus* and *C. evidens* (Hubbard 1972). Reported to be plague-positive in East Africa (Hubbard 1972). Parasitized by 11 spp. of mites (from four families) and 13 spp. of fleas (from three families) in southern Africa (Zumt 1961, details in De Graaff 1981).

Conservation IUCN Category: Least Concern.

Measurements

Pelomys fallax

HB: 147 (125–174) mm, n = 116

T: 133 (109–156) mm, n = 108

HF: 32 (27–35) mm, n = 117

E: 9.2 (15–22) mm, n = 115

WT: 105 (70–151) g, n = 116

GLS: 35.1 (32.0–38.2) mm, n = 51

GWS: 17.1 (16.0–18.8) mm, n = 41

M¹–M³: 6.8 (6.4–7.3) mm, n = 53

Lwiro, Kivu, E DR Congo (F. Dieterlen unpubl., AMNH, BMNH, FMNH, RMCA, SMNS)

Key References Dieterlen 1967a, c; De Graaff 1981.

Fritz Dieterlen

Pelomys hopkinsi HOPKINS'S CREEK RAT (HOPKINS'S PELOMYS)

Fr. Rat à fourrure de Hopkins; Ger. Hopkins Bachratte

Pelomys hopkinsi Hayman, 1955. Rev. Zool. Bot. Afr. 52: 323. Rwamachuchu, Gombolola, Rukiga County, Kigezi District, Uganda.

Taxonomy Subgenus *Komemys*. Morphologically similar to *P. isseli*, but differences in pelage colouration, skull, distribution and habitat distinguish the two species. Synonyms: none. Chromosome number: not known.

Description Small to medium-sized speckled rat with a long tail. Dorsal pelage blackish, speckled with tawny or ochraceous; hairs dark blackish-grey at base with tawny or yellowish tip; some hairs thicker, pure black. Distinct black mid-dorsal stripe running from the centre of the forehead to base of tail, usually contrasting conspicuously with the blackish speckled pelage. Ventral pelage variable, but usually slate-grey with buff tinge; hairs grey on basal half, yellow or buff on terminal half. Inner surface of ears with short rufous hairs; outer surface of ear pale except for contrasting band (2–3 mm wide) of black hairs on upper outer surface. Nasal region gingery-orange. Limbs and feet similar in colour to dorsal pelage; soles of feet blackish (cf. *P. isseli*). Digit 5 of forefoot with claw. Tail very long (ca. 135% of HB), blackish above, paler or dirty white below. Each upper incisor with groove. Nipples: 1 + 2 = 6.

Geographic Variation None recorded.

Similar Species

P. isseli. Pelage not dark-coloured; soles of feet not blackish.

Distribution Endemic to Africa. Eastern Rainforest–Savanna Mosaic. Recorded mostly between L. Victoria and the Albertine Rift Valley: Kigesi in SW Uganda (1 specimen), S and C Rwanda (5) and W Kenya (2).

Habitat Swamps. The holotype was collected at the edge of a papyrus swamp in Kigezi, Uganda. Of five specimens from Rwanda, four are also from the edge of papyrus swamps in the catchment area of the Akanyaru and Kagera rivers (Hayman 1955, Misonne 1965a).

Abundance Rare; known only by eight specimens.

Remarks Presumed to be adapted to the swampy environment, and to be semi-aquatic. Apparently no other information available.

Conservation IUCN Category: Data Deficient.

Schlitter (1989) classified it as Vulnerable 'because of the tenuous nature of its preferred habitat and the small area of occurrence'.

Measurements

Pelomys hopkinsi

HB: 116, 127 mm, n = 2

T: 160, 166 mm, n = 2

HF: 30.2, 31.5 mm, n = 2

E: 15.0, 16.8 mm, n = 2

WT: 41, 68 g, n = 2

GLS: 33.7 (30.8–36.3) mm, n = 6

GWS: 15.9 (14.0–17.2) mm, n = 5

M¹–M³: 6.1 (5.8–6.6) mm, n = 7

Uganda (BMNH, RMCA)

Key References Afework Bekele & Schlitter 1989; Hayman 1955.

Fritz Dieterlen



Pelomys hopkinsi

Pelomys isseli SSESE ISLANDS CREEK RAT (LAKE VICTORIA PELOMYS)

Fr. Rat à fourrure des Iles Ssese; Ger. Ssese Inseln Bachratte

Pelomys isseli (De Beaux, 1924). Annali Mus. Civ. Stor. Nat. Giacomo Doria 51: 207. Kome I., L. Victoria, Uganda.

Taxonomy Subgenus *Komomys*. Morphologically similar to *P. hopkinsi*, but significant distinguishing traits suggest that *P. hopkinsi* and *P. isseli* should be treated as separate species (Afework Bekele & Schlitter 1989). Synonyms: none. Chromosome number: not known.

Description Medium-sized buffy slightly speckled rat with a very long tail; externally looks very similar to *Lemniscomys rosalia*. Dorsal pelage warm tawny-buff slightly speckled with black; hairs blackish at base, buff or tawny at tip. Very distinct black mid-dorsal stripe from forehead to base of tail; base of tail rusty. Ventral pelage brownish-grey tending to yellowish-grey on flanks; neck grey. Margins of ears bordered with black hairs (2–3 mm long). Hairs orange, yellowish or rusty on the nose, around the eyes and at base of ears. Digit 5 of forefoot with claw (cf. *P. fallax*). Soles of feet not (or only slightly) blackish (cf. *P. hopkinsi*). Tail very long (ca. 113% of HB), blackish above, yellowish below. Each upper incisor with groove. Nipples: not known.

Geographic Variation None recorded.

Similar Species

P. hopkinsi. Blackish pelage, black mid-dorsal stripe not contrasting conspicuously with the blackish pelage; soles of feet blackish.

Lemniscomys rosalia. Dorsal pelage orangey-brown to dark brown with obvious thin mid-dorsal black stripe; tail shorter (ca. 130 mm, 100% of HB); Digit 5 of forefoot with nail; each upper incisor without groove.

Distribution Endemic to Africa. Recorded from some of the Ssese Is. (Kome, Bugala, Bunyama) in NW L. Victoria, Uganda. It is the only species of *Pelomys* on the islands, and is not known from the mainland where *P. hopkinsi* and *P. fallax* are present. It has not been recorded on other islands of the archipelago.

Habitat The collecting habitat on Bugala I. was abandoned farmland covered with herbs and perennials. The species was not found in forest, nor in natural grassland (Delany 1969, 1975); unlike *P. hopkinsi* on the mainland of Uganda, it does not show a preference for swamps.

Abundance Comprised 13% of rodents of the rodent community (5 spp.) in abandoned farmland on Bugala I. (n = 30; Delany 1969).

Remarks Two lactating ♀♀ and one ♀ with four placental scars

*Pelomys isseli*

was found in Apr (the only month of sampling) (Delany 1969).

Conservation IUCN Category: Data Deficient.

Schlitter (1989) classified it as Vulnerable because it occurs only on three islands in L. Victoria.

Measurements

Pelomys isseli

HB: 132 (115–149) mm, n = 6

T: 149 (135–171) mm, n = 6

HF: 31 (28–32) mm, n = 6

E: 15 (12.5–18.5) mm, n = 6

WT: 54 (46–60) g, n = 4

GLS: 32.7 (30.6–34.4) mm, n = 5

GWS: 16 (14–16.5) mm, n = 5

M¹–M³: 6.1 (5.9–6.3) mm, n = 8

Ssese Islands, Uganda (BMNH)

Key Reference Delany 1975.

Fritz Dieterlen

***Pelomys minor* LEAST CREEK RAT (LEAST PELOMYS)**

Fr. Rat à fourrure plus petit; Ger. Kleine Bachratte

Pelomys minor Cabrera & Ruxton, 1926. Ann. Mag. Nat. Hist., ser. 9, 17: 601. Luluabourg, DR Congo.

Taxonomy Subgenus *Pelomys*. Synonyms: none. Chromosome number: not known.

Description Small rat with a long tail; the smallest species in the genus. Dorsal pelage similar in colour to *P. fallax* and *P. campanae*. Black mid-dorsal stripe, usually thin but distinct, from between ears to base of tail; indistinct in some individuals. Base of tail dull rusty-brown, not always distinguishable from colour of mid-back. Ventral pelage dull white, buff or yellowish. Hairs on nasal region, ears, at base of ears and around eyes rusty-brown. Digit 5 of forefoot very short, with nail. Hindlimbs rusty; hindfeet yellowish-buff. Tail long (ca. 93%, but may be $\geq 100\%$), blackish above, grey below. Each upper incisor with groove. M^1 – M^3 short (mean 5.3 mm), much shorter than in *P. fallax* and *P. campanae* (see Measurements). Nipples: not known.

Geographic Variation None recorded.

Similar Species

P. fallax. On average larger in most respects; M^1 – M^3 longer.

P. campanae. On average larger; M^1 – M^3 longer.

Lemniscomys rosalia and *L. griselda*. Black mid-dorsal stripe; each upper incisor without groove: M^1 – M^3 longer (ca. 6.2 mm); cusps of upper molars relatively small and low.

Distribution Endemic to Africa. Zambezian Woodland BZ and Southern Rainforest–Savanna Mosaic. Recorded from NE Angola (8 localities), N Zambia (4), SW, C and E DR Congo (11) and W Tanzania (1) (F. Dieterlen unpubl.). In one locality in N Angola (Duque de Braganca) appears to be sympatric with *P. fallax* and *P. campanae*.

Habitat Moist savanna, e.g. savanna with tall grass, near to cultivated land, on slopes near rivers and in wooded valleys (Sanborn 1952). Highest locality is Ujamba, Mahari Mts, W Tanzania, ca. 2160 m in montane grassland (where grass is ca. 3 ft high).

Remarks Juvenile (HB: ca. 75 mm) caught in Aug (Angola; BMNH). Apparently no other information available.

Conservation IUCN Category: Least Concern.

*Pelomys minor***Measurements**

Pelomys minor

HB: 122.5 (101–161) mm, n = 16

T: 113.3 (100–131) mm, n = 19

HF: 24.2 (21–27) mm, n = 13

E: 14.5 (13–16) mm, n = 6

WT: 42, 56 g, n = 2

GLS: 29.2 (27.4–32.3) mm, n = 40

GWS: n. d.

M^1 – M^3 : 5.3 (4.9–5.7) mm, n = 44

Several localities throughout range (AMNH, BMNH, RMCA, SMNS)

Key Reference Sanborn 1952.

Fritz Dieterlen

GENUS *Praomys***Soft-furred Mice**

Praomys Thomas, 1915. Ann. Mag. Nat. Hist., ser. 8, 15: 4. Type species: *Epimys tullbergi* Thomas, 1894.

The genus *Praomys* is endemic to tropical Africa and is here considered to contain 16 species (but see also below) (Table 39). Most species in the genus live in primary rainforest, secondary forest, gallery forests in savanna habitats, and montane forests, over a range of altitudes from near sea level to 3000 m. Some may also occur in forest plantations, and

some species may be found in agricultural fields and in dense grasslands in and close to rainforests. Only one species, *P. daltoni*, lives in savanna habitats (where the closely related genera *Myomyscus* and *Mastomys* are common), and only one species, *P. derooi*, lives in commensal habitats in savanna (where it may cohabit with *Mastomys* spp. and *Rattus rattus*).



Praomys tullbergi.

Members of the genus are called ‘Soft-furred Mice’ because of their smooth dense soft pelage. They are medium-sized (ca. HB: 100–130 mm, WT: 30–60 g) with brown to reddish-brown or greyish-brown dorsal pelage, and grey or white ventral pelage. The muzzle is pointed, ears are large and naked, hindfoot is neither short and broad as in *Hylomyscus*, nor long and elongated as in *Malacomys*, and the tail is long and more-or-less naked. The dorsal surface of the mouth has seven or nine palatal ridges, and there are six plantar pads on the sole of the hindfoot (cf. five pads in *Malacomys*). The skull is elongated, with a narrow interorbital constriction and a marked supraorbital ridge above each orbit; the palatine bone extends well forward to end level with M¹ (cf. *Myomyscus* [= *Myomys*] and *Mastomys*) and long

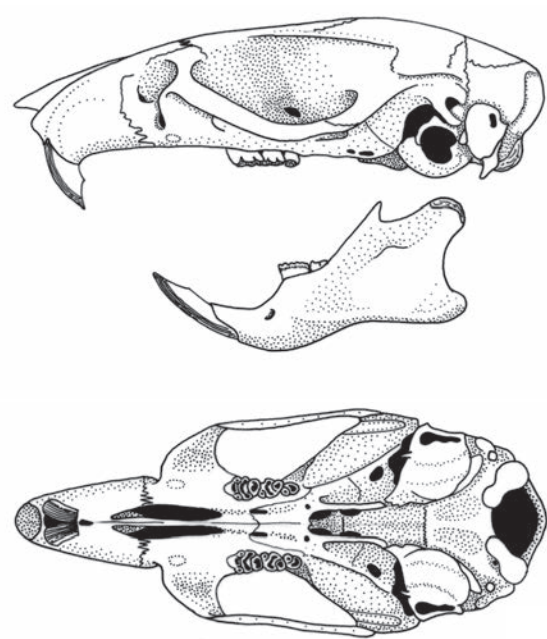


Figure 82. Skull and mandible of *Praomys tullbergi* (HC 673).

anterior palatal foramina extend posteriorly to the level of the first row of cusps of M¹ (cf. *Malacomys*). Incisor teeth are opisthodont and cheekteeth are rather small (Figure 82). There are usually 1 + 2 = 6 nipples (sometimes 2 + 2 = 8 in *P. degraaffi*).

Table 39. Species in the genus *Praomys*. Arranged in order of increasing mean head and body length. (n. d. = no data.)

| Species
[Species-group] ^a | HB
mean (range)
(mm) | HF
mean (range)
(mm) | GLS
mean (range)
(mm) | Palatal
ridges | Colour of hairs of
ventral pelage | Supraorbital ridge | |
|---|----------------------------|----------------------------|-----------------------------|-------------------|---|-----------------------------------|--|
| <i>P. derooi</i> [R] | 97 (73–124) | 21.4 (19–23) | 26.7 (23.9–3.2) | 2 + 5 = 7 | Uniformly grey | Small or absent | |
| <i>P. delectorum</i> [D] | 100 (92–109) | 23.8 (22–26) | 28.6 (27.6–29.5) | 2 + 5 = 7 | Grey at base, white at tip | Small or absent | |
| <i>P. minor</i> [J] | 102 (91–114) | 21.7 (21–22.5) | 28.1 (27.4–29.3) | 2 + 5 = 7 | Grey at base, white at tip | Well developed, straight | |
| <i>P. tullbergi</i> [T] | 103 (100–115) | 22.5 (20–24) | 32.2 (31.1–34.0) | 2 + 7 = 9 | Grey at base, white at tip | Small or absent | |
| <i>P. degraaffi</i> [J] | 105 (98–122) | 26 (25–29) | 31.2 (30.6–31.6) | 2 + 5 = 7 | n. d. | Well-developed, straight | |
| <i>P. daltoni</i> [R] | 108 (87–133) | 20 (16–24) | 28.7 (24.7–29.1) | 2 + 5 = 7 | Pure white | Small or absent | |
| <i>P. misonnei</i> [T] | 111.6 (89–123) | 24.3 (21–26) | 31.0 (29.9–32.3) | 2 + 7 = 9 | Grey at base, white at tip | Small or absent | |
| <i>P. morio</i> [T] | 113.5 (100–130) | 23.5 (21–25) | 30.2 (28.1–32.9) | 2 + 7 = 9 | Very dark grey at base,
white at tip | Small or absent | |
| <i>P. rostratus</i> [T] | 114 (97–134) | 26.5 (25–29) | 33.7 (30–37.4) | 2 + 7 = 9 | Grey at base, white on
terminal two-thirds | Small or absent | |
| <i>P. mutoni</i> [J] | 114 (97–139) | 22 (20–24) | 31.8 (29.2–33.1) | 2 + 5 = 7 | Grey at base, white at tip | Well developed, bends
outwards | |
| <i>P. jacksoni</i> [J] | 115 (94–131) | 25.0 (12–28) | 31.0 (28.1–34.2) | 2 + 5 = 7 | Grey at base, white at tip | Well developed, straight | |
| <i>P. petteri</i> [T] | 119 (73–143) | 26.0 (24–28) | 34.1 (30.5–36.7) | 2 + 7 = 9 | Grey at base, white at tip | Small or absent | |
| <i>P. obscurus</i> [T] | 121 (108–137) | 27.1 (26–28) | 31.4 (29.7–33.1) | 2 + 7 = 9 | Dark grey at base,
off-white at tip | n. d. | |
| <i>P. verschureni</i> [L] | 121 (109–135) | 30.1 (28–32) (c.u.) | 34.4 (33.1–36.1) | 2 + 6 = 8 | Dark grey, white at tip | Absent | |
| <i>P. lukolelae</i> [L] | 123 (109–144) | 30.2 (28–32) (c. u.) | 31.5 (28.5–33.7) | 2 + 5 = 7 | Grey at base, white at tip | Small, not raised | |
| <i>P. hartwigi</i> [T] | 125 (115–134) | 26.5 (24–28) | 32.6 (31.6–33.6) | 2 + 7 = 9 | Grey at base, off-white
at tip | n. d. | |

^aT = *tullbergi* species-group. J = *jacksoni* species-group. D = *delectorum* species-group. L = *lukolelae* species-group. R = *daltoni* species-group.

Soft-furred Mice are often the most numerous of terrestrial small mammals in African forests (e.g. forming up to 75% of individuals in a community of seven species). Two species (*P. tullbergi*, *P. jacksoni*) have very widespread distributions, others (*P. rostratus*, *P. delectorum*) are less widespread, and some have very restricted distributions (e.g. *P. morio* on Mt Cameroon and *P. hartwigi* on montane habitats in Cameroon, and *P. degraaffi* on mountains of the Albertine Rift Valley). In many localities there is only one species of *Praomys*, but in some localities in central Africa there may be at least three species of *Praomys* living parapatrically and/or syntopically. They are terrestrial and nocturnal. During the day they hide under logs and within the crevices of buttress roots. The diet is mainly fruits and seeds that fall to the forest floor, new green shoots and occasionally insects. They are social, unaggressive animals; home-ranges tend to be small and to overlap extensively, and there is no indication of territoriality. Reproduction (for those species that are well studied) is seasonal, with peaks in pregnancy rate during the wet season and early dry season. Litter-size is large (usually 3–5, but up to eight), ♀♀ have a postpartum oestrus, and reproductive rate is high.

The taxonomy of the genus is controversial and has been the subject of debate for many years. The definition of the genus, and its constituent species, is still uncertain. Historically, species have been variously placed in the genera *Mus*, *Rattus* and *Epimys* (Rosevear 1969), and the genus *Praomys* has included species now considered to represent *Hylomyscus*, *Mastomys* and *Myomys* (e.g. Misonne 1974). In recent years, the recognition of 'cryptic species' (as a result of new methods of analysis and more extensive sampling) has resulted in descriptions of additional

species of *Praomys*. Hence the number of species in the genus has varied from 21 (with four subgenera) (Misonne 1974) to nine (Musser & Carleton 1993) to 15 (Musser & Carleton 2005). Many authors have used the term 'Praomys-complex' to refer to these four closely related taxa. How these genera are viewed taxonomically is determined, to some extent, by the type of analysis. For example, Van der Straeten & Dieterlen (1983), using canonical analysis, considered *Myomys*, *Mastomys* and *Myomyscus* as subgroups or subgenera within *Praomys*, whereas Chevret *et al.* (1994), using DNA/DNA hybridization experiments, considered that *Mastomys* and *Hylomyscus* are independent genera, and that *Praomys* and *Myomys* are closely related and may be synonymous. However, there now seems to be general consensus (Lecompte *et al.* 2002a) that *Praomys*, *Myomys* (now *Myomyscus*), *Hylomyscus* and *Mastomys* are independent genera, although the relationships between and within these genera are not yet well understood.

Within the genus *Praomys* (as understood here), five species-groups can be distinguished on the basis of karyology, number of palatal ridges and cranial characters: three species-groups (a, b, c) were listed by Lecompte *et al.* (2002a, b), Van der Straeten & Kerbis Peterhans (1999) and E. Van der Straeten (pers. comm.). In addition, Van der Straeten & Duda (1990) recognize a fourth species-group (d), and a fifth species-group (e) is included for species formerly in *Myomys*. These species-groups are:

- (a) *tullbergi* species-group (*P. tullbergi*, *P. hartwigi*, *P. misonnei*, *P. morio*, *P. rostratus*, *P. obscurus*, *P. petteri*): palatal ridges 2 + 7 = 9; plantar pads 6; anterior palatal foramina reach to front edge of first root of M¹; t3 of M¹ obsolete or difficult to detect; weak supraorbital ridges not raised. Chromosome number: 2n = 34 (*P. tullbergi*, *P. morio*, *P. rostratus*); 2n = 42 (*P. petteri*). Habitat usually primary rainforest.
- (b) *jacksoni* species-group (*P. jacksoni*, *P. mutoni*, *P. minor*, *P. degraaffi*): palatal ridges 2 + 5 = 7; plantar pads 6; anterior palatal foramina reach to middle of first root of M¹; t3 of M¹ well developed; supraorbital ridges raised. Chromosome number: 2n = 28 (*P. jacksoni*). Habitat usually secondary forest and more open habitats.
- (c) *delectorum* species-group (*P. delectorum* only): palatal ridges 2 + 5 = 7; plantar pads 6; smaller size than other groups; anterior palatal foramina reach to front edge of first root of M¹; t3 of M¹ well developed; t3 in M² larger than in other species of *Praomys*; weak supraorbital ridges not raised. Chromosome number: 2n = 48. Habitat only montane forest in eastern Africa.
- (d) *lukolelae* species-group (*P. lukolelae*, *P. verschureni*): palatal ridges 2 + 5 = 7; plantar pads 6; anterior palatal foramina short not reaching to M¹; t3 on M¹ obsolete; weak supraorbital ridges not raised. The long hindfoot, long ears and the form of the skull are more typical of *Malacomys* than of *Praomys*. Chromosome number: 2n = 58 (*P. verschureni*). Habitat rainforest.
- (e) *daltoni* species-group (*P. daltoni*, *P. derooi*): palatal ridges 2 + 5 = 7; plantar pads 6; anterior palatal foramina reach to front edge of first root of M¹; t3 of M¹ well developed; supraorbital ridges not raised. Chromosome number: 2n = 36. Habitat savanna (*P. daltoni*) and houses (*P. derooi*). These species were formerly allocated to *Myomys* (= *Myomyscus*).

The *Praomys*-complex is considered to be monophyletic (as are the closely related genera *Hylomyscus*, *Praomys*, *Myomyscus* [= *Myomys*])

| Chromosome number | Notes |
|---------------------|---|
| n. d. | Savanna; commensal. West Africa |
| 2n = 48 | Montane forests. East Africa |
| n. d. | Rainforest. DR Congo (south bank of Congo R.) |
| 2n = 34 | Rainforest and forest relicts. West Africa (Gambia to Central African Republic) |
| 2n = 26, FN = 28 | Montane forests of Albertine Rift Valley. Burundi, Rwanda, Uganda |
| 2n = 36 | Savanna. Senegal to SW Sudan |
| n. d. | Rainforest. E and NE DR Congo |
| 2n = 34 | Montane forest at higher altitudes. Mt Cameroon only |
| 2n = 34 | Rainforest. Senegal to Ghana |
| n. d. | Rainforest. DR Congo (N of Congo R.) |
| 2n = 28, FN = 30 | Rainforest and forest relicts. Central Africa |
| 2n = 42, FN = 62 | Rainforest. Cameroon, Gabon, Congo |
| n. d. | Gallery montane forest. E Nigeria (Gotel Mts) |
| 2n = 58, FN = 58/60 | Rainforest and sub-montane forest. DR Congo (north and east of Congo R.) |
| n. d. | Rainforest. DR Congo (south of Congo R.). Similar to <i>Malacomys</i> |
| n. d. (? 2n = 34) | Gallery montane forest. Cameroon (near L. Oku only) |

and *Mastomys*) (Lecompte *et al.* 2002a). About 3–4 mya, the ancestral lineage is thought to have diverged to form the four taxa (here considered as genera) (Chevret *et al.* 1994). At this time, the climate was hot and humid, and forests were expanding. It is hypothesized that later, 3–3.5 mya, a cooler, drier period led to the expansion of savanna and fragmentation of the forests into a mosaic of isolated forest patches (the largest of which may be termed ‘forest refuges’). Some populations adapted to the savanna habitats and evolved into the genera *Myomyscus* (= *Myomys*) and *Mastomys*; others remained in forest patches and evolved into *Hylomyscus* and into the *tullbergi* species-group and *jacksoni* species-group. The present distribution of species is a result of these climatic events. Some species occur only around a former refuge, e.g. *P. rostratus* in Upper Guinea; *P. morio* and *P. hartwigi* in the mountainous regions of Cameroon; *P. misonnei* and *P. mutoni* in the central Congo Basin (although the distribution of these species is not fully known);

P. degraaffi in the mountains of the Albertine Rift Valley; and *P. delectorum* in montane regions of E Africa (Lecompte *et al.* 2002a; see also Happold & Happold 1989b, Happold 1996). Other species (*P. jacksoni*, *P. tullbergi*) are more widespread, due perhaps to greater habitat tolerance, but also to dispersal when rainforests expanded after the Pleistocene. The genus *Praomys* is now considered as paraphyletic (Lecompte *et al.* 2002a). Further investigations may show that *P. jacksoni* and perhaps *P. tullbergi* (as now understood) are comprised of a complex of different species (E. Van der Straeten unpubl.).

The species in the genus are distinguished by size, locality, pelage colour (to some extent) and cranial characteristics. However, some species are very difficult to identify by external characteristics, and can be distinguished only by special methods of craniometry.

D. C. D. Happold

Praomys daltoni DALTON’S SOFT-FURRED MOUSE (DALTON’S PRAOMYS)

Fr. Souris sylvestre de Dalton; Ger. Daltons Weichhaarmaus

Praomys daltoni (Thomas, 1892). Ann. Mag. Nat. Hist., ser. 6, 10: 181. West Africa (see Rosevear 1969).

Taxonomy Originally described in the genus *Myomys*. Species-group: *daltoni*. Traditionally referred to as *Myomys daltoni*. Now allocated to the genus *Praomys* on the basis of morphological (Musser & Carleton 2005), molecular (Lecompte *et al.* 2002b) and DNA/DNA hybridization (Chevret *et al.* 1994) data. Constitutes a separate species-group with *P. derooi* (= *Myomys derooi*). Synonyms: *butleri*, *ingoldbyi*, *saturatus*, *tuareg*. Subspecies: none. Chromosome number: 2n = 36, all autosomes acrocentric (Granjon *et al.* 1992 and unpubl.).

Description Small savanna mouse with pure white ventral pelage. Dorsal pelage variable in colour, from yellowish-brown in the Sahel Savanna BZ to chocolate-brown near the Rainforest BZ; hairs grey at base, brown at tip. Ventral pelage pure white, clearly delineated from dorsal pelage on flanks and cheeks. Ears fairly large, oval-shaped. Eyes relatively small. Back of fore- and hindfeet white. Hindfeet rather short, with a short Digit 5 and a relatively long Digit 1. Tail long (ca. 110% of HB), with small scales arranged in rings, almost naked. Skull: anterior palatal foramina reach to front edge of first root of M¹; t3 of M¹ well developed; supraorbital ridges not raised. Nipples: 3 + 2 = 10.

Geographic Variation None recorded.

Similar Species

P. derooi. Slightly smaller on average (especially in skull and dental measurements); ventral pelage uniformly grey; commensal.

P. tullbergi and *P. rostratus*. Ventral pelage grey; tail and hindfoot on average longer; rainforest habitats.

Distribution Endemic to Africa. Widespread in Sahel, Sudan and Guinea Savanna BZs and Rainforest–Savanna Mosaic close to the edge of the Rainforest BZ. Recorded in most West African countries from Senegal to S Chad, N Central African Republic and SW Sudan.

Habitat Rocky hillsides, inselbergs, open dry forest and savanna habitats where grass and often rocks are present. Often found near or in human settlements, in gardens or cultivated farms (Rosevear 1969; Happold 1975b). In Nigeria, preferred habitat is Guinea Savanna; it is less numerous in savannas of the Rainforest–Savanna Mosaic and Sudan Savanna BZ and has not penetrated ‘savanna-like’ habitats in the Rainforest BZ (cf. *Mus musculoides*, *Lemniscomys striatus*) (Happold 1987). An ability to cope with human-modified environments undoubtedly accounts for the northward extension of the geographic range as far north as the Adrar des Iforas Massif in Mali (Dobigny *et al.* 2001a).



Praomys daltoni

Abundance In W Nigeria, comprised 0–78% (mean 50%) of small rodents at 11 localities, and at six of these localities it was the commonest species (Happold 1975b). Especially abundant on inselbergs throughout Nigeria in the Guinea Savanna BZ (Happold 1987). Populations of Dalton's Mice fluctuate during the year; in the savannas of the Rainforest–Savanna Mosaic in S Nigeria, highest population numbers occurred in the mid-late dry season (8–10/ha) and the lowest in the mid wet season (3–4/ha) (Anadu 1973). At Foro, Côte d'Ivoire, comprised 24% of small mammals, the second most numerous species after *Lemniscomys zebra* (Gautun 1975). In SE Senegal, densities ranged from 0 to 20/ha during a 3-year study (Bâ 2002).

Adaptations Nocturnal, with a main peak of activity during the first half of the night in captivity (Duplantier & Granjon 1990). Often considered arboreal, and said to have its nests in tree holes or even under the bark (Hubert *et al.* 1973). Displays good swimming performances under laboratory conditions (Duplantier & Bâ 2001).

Foraging and Food Predominantly granivorous; insects (mainly termites) also eaten at the beginning of the dry season. In Senegal, seeds of *Trianthema portulacastrum* (Ficoidaceae) are preferred at any season (Moro & Hubert 1983).

Social and Reproductive Behaviour Lactating ♀♀ show considerable maternal care, and ♂♂ may assist with the care of the young. Observations in captivity suggest that *M. daltoni* is a territorial species (Anadu 1979a).

Reproduction and Population Structure The period of reproduction varies at different localities. At Foro in C Côte d'Ivoire, pregnant and lactating ♀♀ were observed in Feb–Jul and in Sep–Nov, with periods of quiescence in Jan–Feb and Aug–Sep. The length of each period of reproduction varied annually (during a 3-year period), but there was no clear relationship with rainfall (Gautun 1975). In Nigeria, reproduction occurred throughout the year, with peaks at the beginning and the end of the wet season (Anadu 1979a). In SE Senegal, pregnant ♀♀ were recorded in the dry season (Apr and Jun), and the highest proportion of young were present in November, about one month after the end of the wet season (Bâ 2002). Gestation: 23 days. Monthly means of 3.0–6.5 embryos/

female in Côte d'Ivoire (Gautun 1975). Litter-size (in captivity): 5.6 (3–10, $n = 13$; Anadu 1978); young weaned during Week 3; age at sexual maturity 4.5–5.5 months; interval between successive litters 21–37 days (mean = 29.1; Anadu 1979a). Individuals recaptured up to 21 months after their initial capture in Senegal (Bâ 2002).

In SW Nigeria (Anadu 1973), proportion of each of three age-classes fluctuated seasonally. In mid wet season (Jul–Oct) population comprised mostly adults (80–100% of population); juveniles first appeared in Oct, reached a peak in numbers (80–100% of population) in early dry season (Dec), by which time many adult animals had left the population (and are presumed to have died). By mid-late dry season (Jan–Apr), juveniles had become subadults. A second peak of juveniles occurred during early wet season (May–Jun), the progeny of old adults and perhaps some of the youngest adults (born 6–7 months previously). Population turnover 1–2 times each year.

Predators, Parasites and Diseases In Senegal, present but rare in pellets of Barn Owls *Tyto alba* (Granjon *et al.* unpubl.).

Conservation IUCN Category: Least Concern.

Measurements

Praomys daltoni

HB: 108.8 (87–133) mm, $n = 172$

T: 115.8 (90–150) mm, $n = 122$

HF: 20 (16–24) mm, $n = 54$

E: 17 (13–20) mm, $n = 88$

WT: 33.9 (20–66) g, $n = 129$

GLS: 27.8 (24.7–29.1) mm, $n = 34$

GWS: 13.8 (12.8–15.4) mm, $n = 30$

M¹–M³: 4.2 (3.8–4.6) mm, $n = 35$

Body measurements: Senegal, Mali, Burkina, Côte d'Ivoire and Central African Republic (MNHN)

Skull measurements: Mali (MNHN)

(see Van der Straeten & Verheyen [1978b] for other measurements)

Key References Anadu 1979a; Gautun 1975; Happold 1975b; Van der Straeten & Verheyen 1978b.

Laurent Granjon

Praomys degraaffi DE GRAAFF'S SOFT-FURRED MOUSE (DE GRAAFF'S PRAOMYS)

Fr. Souris sylvestre de De Graaff; Ger. De Graaffs Weichhaarmaus

Praomys degraaffi Van der Straeten and Kerbis Peterhans, 1999. S. Afr. J. Zool. 34: 81. Abris Nyamugari, Burundi. 2200 m.

Taxonomy Species-group: *jacksoni* (Van der Straeten & Dudu 1990). Distinguished from *P. jacksoni* by pelage colour, number of nipples and karyology (Van der Straeten & Kerbis Peterhans 1999). Synonyms: none. Chromosome number: $2n = 26$, $FN = 28$ (Maddelena *et al.* 1989, as *Praomys cf. jacksoni*). One pair of acrocentric chromosomes fewer than in *P. jacksoni*.

Description Medium-sized mouse, with overall dark pelage. Overall pelage typically dark grey or sooty-black. Hindfoot with

six large plantar pads (usual murid arrangement) and usually one small accessory plantar pad; hindfoot narrow (cf. *P. jacksoni*). Tail very long (ca. 129% HB). Skull: supraorbital ridges well developed and straight, originating at anterior end of frontal bone; t3 of M¹ well developed; posterior limit of anterior palatal foramina level with second root of M¹. Nipples: 2 + 2 = 8.

Geographic Variation None recorded.

Similar Species

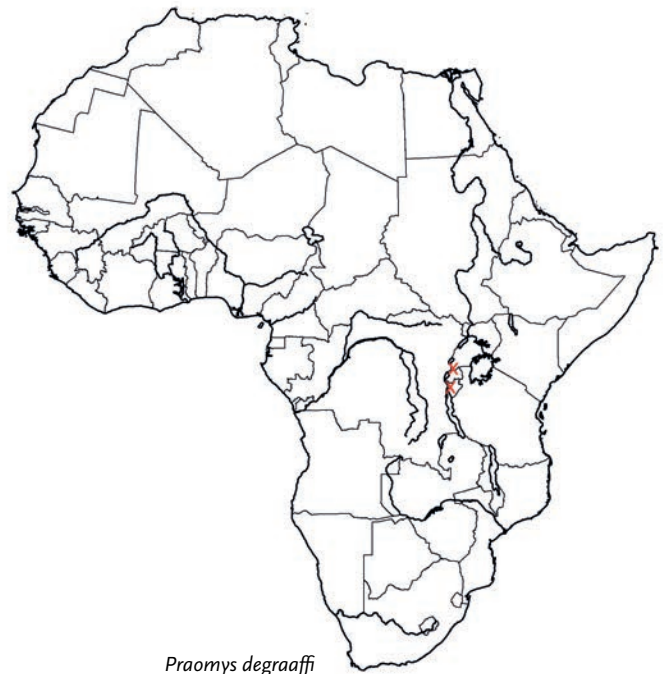
P. jacksoni. Dorsal pelage grey or rufous; nipples 1 + 2 = 6; chromosome number $2n = 28$; HF broader (mean 4.6 mm); four accessory plantar pads; may be syntopic at 1800–2500 m; widespread geographic distribution.

Distribution Endemic to Africa. Afroalpine–Afroalpine BZ. Recorded from mountainous regions bordering the eastern side of the Albertine Rift Valley in Burundi (Bururi F. R., 1880–2170 m; Kibira N. P.), Ruanda (Nyungwe N.P.; Parc National des Volcans) and Uganda (Mgahinga Gorilla N. P.; Bwindi Impenetrable N. P.; Echuya F. R.). Occurs at successively lower altitudes with increasing latitude (Van der Straeten & Kerbis Peterhans 1999). In certain localities at high altitude (e.g. 2680 m in Mgahinga N. P. and 2380 m in Echuya F. R.), the only member of the genus. In Bwindi Impenetrable N. P., it is sympatric with *P. jacksoni* at 2350 m but it has not been found at lower altitudes (1500–1850 m) where *P. jacksoni* is the sole representative of the genus.

Habitat High altitude montane forests. In Echuya F. R. prefers thick stands of bamboo, secondary herbaceous growth, edges of fast-flowing streams, dense shrubs in wet forest and, on one occasion, *Rubus* habitats between Echuya Swamp and bamboo forest. In Mgahinga Gorilla N. P. consistently but infrequently occurs in monodominant stands of *Hagenia* and in patches of *Myrianthus* sp. In Bwindi Impenetrable N. P. it prefers the dry slopes at high altitudes (2350 m) rather than wet valley bottoms. In S Burundi favours secondary forest above 2000 m and primary forest and open valleys dominated by *Entandophragma*.

Abundance Varies according to locality and vegetation, becoming more common with increasing altitude. Comprised 16% of captured small mammals in and near Echuya Forest (Van der Straeten & Kerbis Peterhans 1999) and 6–7% in Mgahinga Gorilla N. P. at ca. 2680 m. Especially common in southern localities, where it comprised 40% (Bururi F. R., Burundi; 2000 m) and 54% (Mumushwizi Valley, Kibira N. P., Burundi) of small mammals.

Remarks Nocturnal and terrestrial. Pregnancies were recorded in Feb (1 of 2 adult ♀♀; Kibira N. P.), Mar (1 of 5; Bururi F. R.), Apr (1 of 4) and Aug (1 of 6; Bururi F. R.). None of the ♀♀ collected in March (n = 18) in Kibira N. P. was pregnant. No information for other months. Embryo number: 2 (n = 1), 4 (n = 3).



Praomys degraaffi

Conservation IUCN Category: Vulnerable.

Measurements

Praomys degraaffi

HB: 111 (92–124) mm, n = 38

T: 136.0 (115–151) mm, n = 40

HF: 26.4 (24–29) mm, n = 48

E: 19.6 (17–22) mm, n = 41

WT (♂♂): 41 (29–58) g, n = 80

WT (♀♀): 37.5 (26–59) g, n = 45

GLS: 31.3 (29.1–32.9) mm, n = 48

GWS: 14.7 (13.2–15.7) mm, n = 48

M¹–M³: 5.2 (4.9–5.6) mm, n = 49

Burundi, Rwanda and Uganda (Van der Straeten & Kerbis Peterhans 1999; FMNH, RMCA)

Key References Van der Straeten & Kerbis Peterhans 1999.

Julian C. Kerbis Peterhans & Sean O. Bober

***Praomys delectorum* DELICATE SOFT-FURRED MOUSE (EAST AFRICAN PRAOMYS)**

Fr. Souris sylvestre délicate; Ger. Reizende Weichhaarmaus

Praomys delectorum (Thomas, 1910). Ann. Mag. Nat. Hist., ser. 8, 6: 430. Mulanje Plateau, Malawi.

Taxonomy Species-group: *delectorum*. Described in the genus *Epimys* (Thomas 1910d). Synonyms: *melanotus*, *octomastis*, *taitae*. Van der Straeten & Kerbis Peterhans (1999) recognized these forms as valid species but, following Musser & Carleton (2005), they are considered to be synonyms here. Subspecies: none. Chromosome number: $2n = 48$ (as *taitae*; Matthey 1965).

Description Small delicate mouse with soft, smooth, dense pelage. Dorsal pelage dark brown from nose to base of tail, dorsal hairs dark

brownish-grey with dark brown tips; hairs of flanks tipped with rusty-brown. Flanks slightly paler. Ventral pelage whitish-grey; ventral hairs dark grey, whitish-grey at tip. Chin and throat similar to ventral colouration. Head narrow, with pointed nose, long black vibrissae and large eyes. Ears elongated, rounded at tips, dark brown; very mobile, held upwards and forwards from head. Fore- and hindlimbs short and slender, with sparse short white hairs; four digits on forefeet (Digit 1 almost vestigial); five digits on hindfeet (Digit 1 short). Tail very long (ca. 125% of HB), thin, with many small dark scales and

short dark bristles. Skull: supraorbital ridges small (or absent), originating half way along frontal bone; posterior limit of anterior palatal foramina at second root of M^1 ; t_3 of M^1 well developed. Palatal ridges $2 + 5 = 7$. Nipples: $2 + 2 = 8$.

Geographic Variation None recorded.

Similar Species This is the only species of *Praomys* on the mountains of eastern Africa.

Distribution Endemic to Africa. Afroalpine–Afroalpine BZ of eastern Africa. Disjunct, confined to riverine and montane forests above ca. 1500 m. Recorded from Malawi (Cholo Mt, Mlanje Mt, Zomba Plateau, Dedza Mt, Vipya Plateau, Nyika Plateau, Misuku Hills); Tanzania (Mt Kilimanjaro, Mt Meru, Ngorogoro Crater, Southern Highlands, Uzungwa Mts, Uluguru Mts, Usambara Mts); Zambia (Makutu Mts, Mafinga Mts); Mozambique (Namuli Mt) and SE Kenya (Shimba Hills) (Swynnerton & Hayman 1951, Hanney 1965, Ansell 1978, Rodgers *et al.* 1982, Ansell & Dowsett 1988, Happold & Happold 1992). May also occur on other highlands of the Eastern Arc Mountains in Tanzania.

Habitat Montane forests, riverine forests and tangles along margins of forests in highland regions where average annual rainfall is not less than ca. 2000 mm. May occur in bracken adjacent to forest, mostly during the wet season, but rarely found in grassland adjacent to forest even when grasses are tall and dense. This species shows a statistically significant preference for montane forest habitats compared with all other montane habitats (grasslands, bracken, etc.) (Happold & Happold 1989b, c).

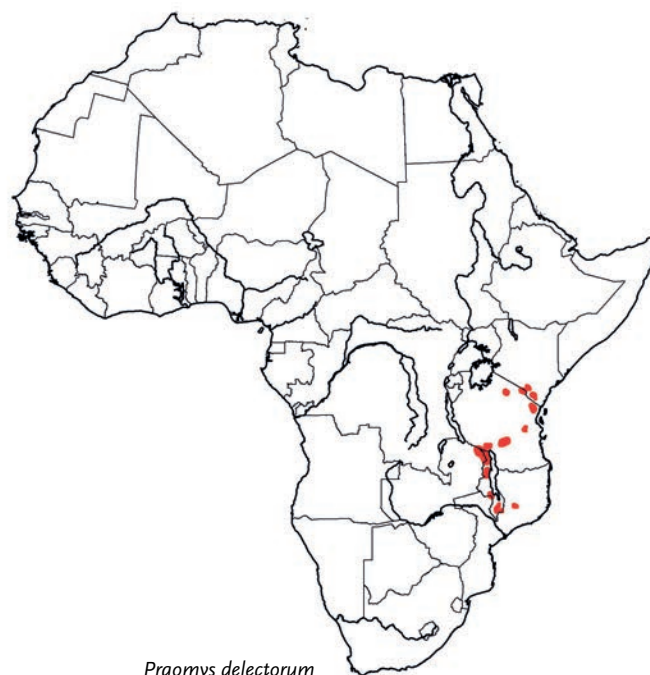
Abundance Common in suitable habitats, especially at the end of the breeding season (see below). Comprised 29–33% of small mammals trapped in forest/grassland mosaic habitats and 50–88% in montane forest habitats in Malawi (Happold & Happold 1989b, c, 1992).

Adaptations Terrestrial and scansorial. Nocturnal. Lives in burrows amongst the roots of large forest trees, and under large logs.

Foraging and Food Forages on ground in leaf-litter. Omnivorous. Analyses of stomach contents: 78% contained vegetable material, 82% contained insects (caterpillars, adult insects) ($n = 45$, Malawi; Hanney 1965).

Social and Reproductive Behaviour No information. Individuals in captivity do not exhibit agonistic behaviour (D. C. D. Happold, unpubl.).

Reproduction and Population Structure Pregnancies during late dry season and wet season (Sep–Apr) but mostly in Dec–Feb (Malawi). On Zomba Plateau, Malawi, young animals enter population during late wet season and early dry season (Feb–Apr). Litter-size usually 4 (2–6). Population numbers (on Zomba Plateau)



Praomys delectorum

low at end of dry season (Aug–Nov), increasing to maximum (up to $\times 10$ minimum) at end of wet season and beginning of early dry season (Mar–Jun); young form 50–80% of population in late wet season. Individuals rarely survived for more than six months (Happold & Happold 1989c).

Predators, Parasites and Diseases Preyed upon infrequently by African Grass-owls *Tyto capensis* on Zomba Plateau, Malawi, probably only during the wet season when they move into bracken at the forest edge (Happold & Happold 1986), and when they climb to the top of grass stalks to feed on the seed heads.

Conservation IUCN Category: Least Concern.

Because of restricted habitat requirements, populations on separate highland areas are isolated from other populations.

Measurements

Praomys delectorum

HB: 100.1 (92–109) mm, $n = 17$

T: 124.2 (108–133) mm, $n = 17$

HF: 23.8 (22–26) mm, $n = 17$

E: 20.6 (18–21) mm, $n = 17$

WT: 28.7 (20–34) g, $n = 16$

GLS: 28.6 (27.6–29.5) mm, $n = 17$

GWS: 13.2 (12.3–13.8) mm, $n = 17$

M^1 – M^3 : 4.5 (4.3–4.7) mm, $n = 17$

Rungwe Forest, Tanzania (RMCA)

Key References Hanney 1965; Happold & Happold 1989b, c, 1992.

D. C. D. Happold

Praomys derooi DE ROO'S SOFT-FURRED MOUSE (DE ROO'S PRAOMYS)

Fr. Souris sylvestre de De Roo; Ger. Deroos Weichhaarmaus

Praomys derooi Van der Straeten and Verheyen, 1978. Z. Säugetierk. 43: 33. Borgou, Togo.

Taxonomy Species-group: *daltoni*. Traditionally referred to as *Myomys derooi*. Now allocated to the genus *Praomys* (see also the phylogenetically closely related *P. daltoni*). Considered a commensal form of *Myomys daltoni* (now *Praomys daltoni*) by Heim de Balsac (1967a) and Rosevear (1969), before being described as a new species by Van der Straeten & Verheyen (1978b). In contrast, Musser & Carleton (2005) suggest that this species may represent local populations of *P. daltoni*. Synonyms: none. Chromosome number: $2n = 36$, all autosomes acrocentric (Granjon 1992, L. Granjon unpubl.).

Description Small brownish commensal mouse. Dorsal pelage variable in colour, from pale brown to dark grey-brown; hairs grey at base with brown tip. Flanks paler than the back, with a gradual transition to the uniformly grey ventral pelage. White spot often present on chest. Tail long (115–120% of HB), unicoloured, with rather long hairs, especially in the mid-dorsal region and at tail tip. Skull: see *P. daltoni*. Palatal ridges $2 + 7 = 9$. Nipples: $3 + 2 = 10$.

Geographic Variation None recorded.

Similar Species

P. daltoni. Larger on average (especially in skull and dental measurements); ventral pelage pure white; natural savanna habitats.

P. tullbergi and *P. rostratus*. On average longer tail and hindfoot; ventral pale grey, hairs with white tip; rainforest habitats.

Mastomys spp. On average larger; ♀♀ with up to 24 nipples equally spaced along abdomen; natural savanna and commensal habitats.

Distribution Endemic to Africa. Guinea Savanna BZ. Recorded from Ghana, Togo, Benin and W Nigeria (Van der Straeten & Verheyen 1978b, Happold 1987, Decher *et al.* 1997). Also possibly Guinea (one juvenile ♂; Ziegler *et al.* 2002; but see Musser & Carleton 2005).

Habitat Commensal in savanna habitats (Van der Straeten & Verheyen 1978b).

Abundance Locally abundant, although not present in many areas.

Remarks Appears to be a rather highly specialized commensal species. May live sympatrically in human dwellings and stores with *Rattus rattus* and *Mastomys erythroleucus*. Reproductive data available only for Jul, Aug, Nov and Dec. Pregnant ♀♀ recorded in each of these months (wet season and early dry season); pregnancy rates: Jul 11% ($n = 27$ adult ♀♀), Aug 28% ($n = 7$), Nov 20% ($n = 5$), Dec 39% ($n = 66$); lactating ♀♀ in Jul, Aug and Dec. Many juveniles

*Praomys derooi*

in Dec. Embryo number: 3.75 (2–5) (Van der Straeten & Verheyen 1978b). Because of commensal habits, reproduction may occur during a longer period of the year than present records indicate.

Conservation IUCN Category: Least Concern.

Measurements

Praomys derooi

HB: 97.1 (73–124) mm, $n = 111$

T: 115.7 (84–136) mm, $n = 89$

HF (c.u.): 21.4 (19–23) mm, $n = 110$

E: 14.3 (12–18) mm, $n = 110$

WT: 32 (24–45) g*

GLS: 26.7 (24.0–30.2) mm, $n = 110$

GWS: 12.5 (11.3–14) mm, $n = 110$

M^1 – M^3 : 4.3 (4.0–5.1) mm, $n = 111$

Throughout geographic range (recalculated from Van der Straeten & Verheyen 1978b)

*Nigeria (no sample size; Happold 1987, as *Myomys derooi*)

Key Reference Van der Straeten & Verheyen 1978b.

Laurent Granjon

Praomys hartwigi HARTWIG'S SOFT-FURRED MOUSE (HARTWIG'S PRAOMYS)

Fr. Souris sylvestre de Hartwig; Ger. Hartwigs Weichhaarmaus

Praomys hartwigi Eisentraut, 1968. Bonn. Zool. Beitr. 19: 8–11. L. Oku, Bamenda Highlands, Cameroon.

Taxonomy Species-group: *tullbergi* (Lecompte *et al.* 2001, Lecompte *et al.* 2002a), as indicated by its palatal ridges (Fülling 1992). Synonyms: none. Chromosome number: not known (presumably $2n = 34$; Eisentraut 1970).

Description Medium-sized dark reddish-brown rodent. Pelage soft and long (13–15 mm on back). Dorsal pelage rich dark reddish-brown or russet-brown; hairs dark grey with reddish-brown tip. Flanks similar, less rich. Ventral pelage whitish-grey; hairs grey at base, off-white at tip. Head similar to dorsal pelage. Lips and lower cheeks greyish or pale russet. Chin and throat greyish-white. Forefeet whitish, five digits; Digit 1 reduced to tubercle with very small claw. Tail very long (ca. 140% of HB), medium brown, ringed with scales, appears more or less naked but covered with very small dark bristles. Nipples: $1 + 2 = 6$.

Geographic Variation None recorded.

Similar Species

P. obscurus. Similar in external measurements and pelage texture, but dorsal pelage darker and skull smaller; occurs only in the Gotele Mts, Nigeria.

P. jacksoni. On average smaller in external and cranial measurements; pelage long and less soft; occurs sympatrically with *P. hartwigi* on Mt Oku.

Distribution Endemic to Africa. Afromontane–Afroalpine BZ. Recorded only from Mt Oku and L. Manengouba in the Bamenda Highlands, Cameroon (Eisentraut 1970, Hutterer *et al.* 1992).

Habitat Strictly confined to montane forest habitats. Mainly found on the forest floor, but may climb on trees and branches (O. Fülling pers. comm.).

Abundance Common in the undisturbed montane forest slopes of Mt Oku.

Remarks Terrestrial and nocturnal. Limb proportions suggest adaptations to a scansorial life. Omnivorous; up to 10% of stomach contents are animal remains, such as arthropods and worms. Animals forage mainly on the ground. Hunted with traps and eaten by the local Oku people (all information: O. Fülling pers. comm.).



Praomys hartwigi

Conservation IUCN Category: Endangered.

Measurements

Praomys hartwigi

HB: 125 (115–134) mm, $n = 11$

T: 162.1 (152–173) mm, $n = 11$

HF: 26.5 (24–28) mm, $n = 11$

E: 19.2 (17–21) mm, $n = 11$

WT: 57.2 (44–70) g, $n = 11$

GLS: 32.6 (31.6–33.6) mm, $n = 8$

GWS: 15.6 (15.0–16.2) mm, $n = 8$

M^1 – M^3 : 5.6 (5.4–5.8) mm, $n = 9$

Bamenda Highlands, Cameroon (Hutterer *et al.* 1992)

Key Reference Eisentraut 1970.

R. Hutterer

Praomys jacksoni JACKSON'S SOFT-FURRED MOUSE (JACKSON'S PRAOMYS)

Fr. Souris sylvestre de Jackson; Ger. Jacksons Weichhaarmaus

Praomys jacksoni (de Winton, 1897). Ann. Mag. Nat. Hist., ser. 6, 20: 318. Entebbe; Uganda.

Taxonomy Originally described in the genus *Mus*. Species-group: *jacksoni*. The definition of this species is problematic because the holotype is a juvenile with insufficient data, and the species currently

regarded as '*P. jacksoni*' may include other forms or species. Van der Straeten & Dudu (1990) used topotype specimens in order to define the species, and proposed that those with a karyotype of $2n = 28$,

FN = 30 and AA = 26 represent *P. jacksoni*. Van der Straeten & Dudu (1990) and Van der Straeten & Kerbis Peterhans (1999) regard *montis* (from Uganda), *peromyscus* (from Kenya), *sudanensis* (from Sudan) and *viator* (from Nigeria) as valid species on the basis of canonical analysis; in contrast Musser & Carleton (2005) refer these to synonyms of *P. jacksoni*. Synonyms: *montis*, *peromyscus*, *sudanensis*, *viator*. Subspecies: none. Chromosome number: $2n = 28$, FN = 30.

Description Small rufous-grey soft-furred mouse, similar in external appearance to several other species of the genus. Pelage soft and long (9–10 mm). Dorsal pelage grey or rufous (see below), hairs dark grey at base, grey or rufous at tip. Dorsal pelage varies with age: dark grey in juveniles and subadults, rufous in adults and deep rufous in old adults. Changes in colour due to age less pronounced in montane populations, where the dorsal pelage is mostly darker. Ventral pelage greyish-white, hairs grey at base, white at tip. Forefeet whitish. Hindfeet pale with brownish tinge, comparatively wide (4.6 mm; cf. *P. degraaffi*); toes whitish. Ears relatively large, round, darkish, inconspicuously haired. Tail very long (ca. 118% [Uganda] to 140% [Nigeria]), almost naked, dark grey above, slightly paler below. Skull: supraorbital ridges well developed and straight, originating at anterior end of frontal bone; posterior limit of anterior palatal foramina at second root of M^1 ; $t3$ of M^1 well developed. Palatal ridges: $2 + 5 = 7$. Nipples $1 + 2 = 6$.

Geographic Variation None recognized here, but see Taxonomy.

Similar Species

- P. misonnei*. $t3$ on M^1 absent; interorbital breadth small (especially when compared with *P. jacksoni*); partly sympatric; restricted geographic range.
- P. tullbergi*. Palatal ridges $2 + 7 = 9$; supraorbital ridges weak or absent; sympatric in parts of range; widespread and common; allopatric.
- P. mutoni*. On average slightly smaller; rare; partly sympatric.



Praomys jacksoni

Hylomyscus spp. HF usually shorter and broader; tail relatively longer; scansorial and arboreal; widespread and common.

Distribution Endemic to Africa. Rainforest BZ (East Central and South Central Regions) and rainforest relicts in Rainforest–Savanna Mosaics from Nigeria to Kenya and Tanzania. Widespread in DR Congo, S Central African Republic, Gabon and Equatorial Guinea (Rio Muni). Also recorded in Afromontane–Afroalpine BZ as follows: Nigeria (Jos Plateau, Abuja, Gotele Mts, Mambilla Plateau; Happold 1987, Hutterer *et al.* 1992), Cameroon (Adamaoua Highlands and western montane regions; Eisentraut 1975, Hutterer & Joger 1982) and Tanzania (Eastern Arc mountains). Altitudinal range: ca. 300 m in lowland rainforest to ca. 3000 m in montane forests (e.g. Mt Tshiaberimu, Virunga N. P., DR Congo [3000 m; Verschuren *et al.* 1983], Mt Kinyetti, S Sudan [3187 m; F. Dieterlen unpubl.] and Mt Elgon, Uganda [3250 m; Clausnitzer & Kityo 2001]). Probably absent from the alpine and sub-alpine zones of mountains.

Habitat Primarily lowland rainforest and secondary forest; also recorded in cultivated and fallow land, montane forests and rainforest relicts in Rainforest–Savanna Mosaics. Occasionally lives in bamboo forest and around marshes and swamps.

Abundance One of the most common species of small mammal in the rainforests of central and eastern Africa. In montane forests of E DR Congo (1900–3300 m), comprised 28.9% of small rodents and was often the most abundant species ($n = 2043$; F. Dieterlen unpubl.). At lower altitudes in E DR Congo, abundance varied: overall the most numerous (19%) of 14 species, ranging from 14% (rainforests) to 20% (forested hills) and 21% (abandoned farmland in rainforest) (Rahm 1972). In Mayanga Forest, Uganda, was the second most numerous species (28%, as *P. morio*) after *Lophuromys flavopunctatus* (51%) (Delany 1971).

Adaptations Terrestrial, nocturnal and crepuscular. May also scramble over dead logs and tree stumps and climb small branches up to ca. 2 m (6 ft) and very occasionally higher (Delany 1971). Activity is primarily nocturnal (ca. 89% of captures), and occasionally diurnal (ca. 11%) ($n = 293$; E DR Congo; Rahm 1972). Runways are made under debris and tree roots. Nests are built under roots and are constructed of cut grasses and ferns (Rahm 1967). The alimentary canal is typical of an omnivore: it is long (about 6.5 times length of head and body) and has the following proportions: small intestine 85%, caecum 5%, large intestine 10% ($n = 18$, Clausnitzer 2003; see also Rahm 1972).

Foraging and Food Mainly frugivorous; partly omnivorous. Forages mainly on the ground, as described by Vesey-Fitzgerald (1966): ‘The home-range of a group may be restricted to the vicinity of a single forest tree such as *Parinari*, which sheds its fruit on the ground. It collects the fruit by making sorties from a convenient shelter. The fruit is then carried back to the shelter, where the hard shell is gnawed at leisure in order to get at the kernel; the debris of continual feeding indicates that such shelters are used during a prolonged period possibly amounting to the life span of several generations.’

The diet is mainly seeds, nuts, kernels and fruits. In E DR Congo, 31 out of 38 stomachs contained vegetable material, and only two

stomachs were full of insects – mainly *Pseudacanthotermes* termites (Rahm 1972). Analysis of 54 stomachs (F. Dieterlen unpubl.) in E DR Congo showed the following: most (44) contained vegetable material, mainly kernels and pulp from fruits; 11 contained sorghum from nearby cultivations; 20 contained small amounts of insects; and ten contained large numbers of insects – mostly ants and other invertebrates. Few stomachs (5%) contained fresh green plant material. On Mt Elgon, diet was seeds and fruit pulp, with some arthropods and herbs (Clausnitzer 2003).

Social and Reproductive Behaviour Little information. Females nipple-drag their young when disturbed or alarmed (F. Dieterlen unpubl.).

Reproduction and Population Structure Reproduction occurs during many months of the year in relation to rainfall and the availability of fruits. In lowland rainforests (Irangi, E DR Congo; 800–1000 m), reproductively active ♀♀ (as assessed by pregnancy and/or lactation) comprised, on a yearly basis, 65% of adult ♀♀, rising to 71% during wet season (Sep–Mar) with peak in Dec–Feb, and falling to 46% during dry season (Jun–Aug). In montane forests of E DR Congo (1900–2700 m), equivalent percentages were 56%, rising to 68% (n = 234) in Jan–Apr, and falling to 39% in May–Jun. In both lowland and montane regions, reproductive activity of ♂♂ (assessed by length of testes) showed a similar and corresponding trend to that of ♀♀ (F. Dieterlen unpubl.).

Gestation: uncertain – 25–31 days (F. Dieterlen unpubl.); 36 (34–37) days (Delany 1971). Embryo number varies according to locality. In lowland forests of DR Congo: 3.18 (1–5, n = 91), increasing to 3.68 in Dec–Jan. In montane forests: 3.60 (1–6,

n = 215; F. Dieterlen unpubl.). At other localities, litter-size: 3.0 (Kisangani, C DR Congo; Dudu 1991), 3.33 (1–5, n = 67; Uganda; Delany 1971) and 3.8 (2–6, n = 11; Gabon; Dubost 1968). At birth, young altricial, blind, naked and with some dorsal pigmentation; weight ca. 2.5 g. Short pelage present Day 10. Eyes open and limb coordination Day 10–16. Weaned by Day 29 (just before ♀ has next litter). Testes fully formed in ♂♂ by Day 74. Males first copulate at ca. Day 85, and first parturition in ♀♀ about Day 112 (Delany 1971). Females have a postpartum oestrus.

Predators, Parasites and Diseases No information.

Conservation IUCN Category: Least Concern.
Widespread and common; not threatened at present.

Measurements

Praomys jacksoni

HB: 115.4 (94–131) mm, n = 88

T: 146.9 (125–168) mm, n = 82

HF: 25.0 (12–28) mm, n = 88

E: 18.4 (15–22) mm, n = 80

WT: 40 (28–58) g, n = 53

GLS: 31.0 (28.1–34.2) mm, n = 89

GWS: 14.7 (13.3–16.1) mm, n = 86

M¹–M³: 5.0 (4.6–5.5) mm, n = 87

E DR Congo (Van der Straeten & Dieterlen 1987, SMNS)

Key References Delany 1971; Dieterlen 1985a.

Fritz Dieterlen

Praomys lukolelae LUKOLELA SOFT-FURRED MOUSE (LUKOLELA PRAOMYS)

Fr *Souris sylvestre* de Lukolela; Ger. Lukolele-Weichhaarmaus

Praomys lukolelae Hatt, 1934. Amer. Mus. Novit. 708:13. Lukolela, Central African Republic.

Taxonomy Originally described as *Praomys tullbergi lukolelae*. Species-group: *lukolelae*. Exhibits characteristics of both *Malacomys* and *Praomys*. Long hindfeet, large naked ears and elongated face suggest affinities to *Malacomys*; six plantar pads on hindfoot and some characteristics of cranium and teeth suggest affinities to *Praomys*. Sometimes included in genus *Malacomys* (e.g. Musser & Carleton 1993; Leirs *et al.* 1999), but now considered to belong to *Praomys* (Musser & Carleton 2005). Probably closely related to *P. verschureni*. The similarities between *P. lukolelae* and *P. verschureni* suggest a close relationship; together they may represent a new genus, distinct from *Praomys* and *Malacomys* (E. Van der Straeten pers. comm.). Synonyms: none. Chromosome number: not known.

Description Medium-sized russet-brown rodent, with long hindfeet and large naked ears. Pelage lies close to body; without a velvet texture as in *Malacomys* spp. Dorsal pelage medium-brown or russet-brown, paler on flanks; hairs grey at base, brown terminal band. Ventral pelage whitish-grey; hairs grey at base, white at tip. Head with elongated muzzle; ears relatively large, brown, naked, rounded at tip. Pre- and subauricular spot, pinkish-cinnamon. Limbs and feet whitish-grey.

Hindfoot long and slender; six plantar pads (as in *Praomys* spp.; cf. five in *Malacomys*). Tail long (ca. 115% of HB), mostly naked, dark above, pale below. Skull: supraorbital ridges small, not raised; posterior limit of anterior palatal foramina anterior to M¹ (as in *Malacomys*); t3 on M¹ absent. Palatal ridges 2 + 5 = 7. Nipples: not known

Geographic Variation None recorded.

Similar Species

P. verschureni. Similar in many characters; NE DR Congo only; probably allopatric.

Praomys (other spp). Ear length shorter relative to GLS; on average T and HF shorter.

Malacomys longipes. Larger (HB: ca. 158 mm, HF: ca. 39 mm); pelage similar in texture to velvet; five plantar pads on hindfoot; sometimes parapatric.

Distribution Endemic to Africa. Rainforest BZ (South Central Region). Known only from Lukolela, Kikwit and SE of Kisangani, DR Congo. Perhaps more widespread than these records suggest.

*Praomys lukolelae*

Habitat Rainforest.

Abundance Uncertain; very local. At Kikwit, formed 1.9% of all small mammals collected in forest and grassland habitats ($n = 1879$) (Leirs *et al.* 1999).

Remarks Terrestrial and nocturnal. No other information available.

Conservation IUCN Category: Least Concern.

Distribution restricted, and no detailed information on conservation status. Destruction of rainforest is likely to be a major threat.

Measurements

Praomys lukolelae

HB: 123.8 (109–144) mm, $n = 31$

T: 141.2 (116–159) mm, $n = 32$

HF (c.u.): 30.2 (28–32) mm, $n = 34$

E: 22.9 (18–26) mm, $n = 34$

WT: 41.1 (27–57) g, $n = 32$

GLS: 31.5 (28.5–33.7) mm, $n = 32$

GWS: 13.8 (12.7–15.0) mm, $n = 33$

M^1 – M^3 : 4.9 (4.6–5.4) mm, $n = 34$

Kikwit, DR Congo (E. Van der Straeten pers. comm.)

Key Reference Hatt 1934.

D. C. D. Happold

Praomys minor LEAST SOFT-FURRED MOUSE (LEAST PRAOMYS)

Fr. Souris sylvestre plus petite; Ger. Kleine Weichhaarmaus

Praomys minor Hatt, 1934. Amer. Mus. Novit. 708: 11. Lukolela, DR Congo.

Taxonomy Species-group: *jacksoni*. Described as a subspecies of *P. jacksoni* but now treated as a distinct species (Van der Straeten & Dudu 1990). Synonyms: none. Chromosome number: not known.

Description Small mouse. Dorsal pelage warm brown in older individuals, dark brown in younger ones. Flanks paler. Ventral pelage whitish-grey; hairs grey at base, white at tip. Dark eye-ring. Palatal ridges $2 + 5 = 7$. Hands and feet white. Some ♂♂ have a white patch or stripe just in front of the penis. Tail very long (ca. 120–130% of HB), unicoloured, dark brown, with a few short hairs between the scales. Some animals have irregular pale spots on the tail. Skull: supraorbital ridges well developed and straight, originating at anterior end of frontal bone; posterior limit of anterior palatal foramina at second root of M^1 ; t_3 of M^1 well developed. Nipples $1 + 2 = 6$.

Geographic Variation None recorded.

Similar Species

P. jacksoni. On average larger; HF on average longer (mean 25 mm).

P. lukolelae. On average much larger; HF longer (mean 30.2 mm).

*Praomys minor*

Distribution Endemic to Africa. Rainforest BZ (South Central Region). Recorded only from the type locality on the left bank of the Congo R., DR Congo.

Habitat No information.

Abundance Apparently rare; known only from a few specimens.

Remarks Apparently no other information available.

Conservation IUCN Category: Data Deficient.

Measurements

Praomys minor

HB: 102 (91–114) mm, n = 6

T: 129 (120–137) mm, n = 7

HF: 21.7 (21–23) mm, n = 7

E: 14.7 (13–17) mm, n = 7

WT: n. d.

GLS: 28.1 (27.4–29.3) mm, n = 4

GWS: 13.1 (12.8–13.3) mm, n = 3

M¹–M³: 4.6 (4.5–4.7) mm, n = 7

DR Congo (AMNH, RMCA)

Key References Hatt 1934; Van der Straeten & Dudu 1990.

Erik Van der Straeten

Praomys misonnei MISONNE'S SOFT-FURRED MOUSE (MISONNE'S PRAOMYS)

Fr. Souris sylvestre de Misonne; Ger. Misonnes Weichhaarmaus

Praomys misonnei Van der Straeten and Dieterlen, 1987. Stuttgart. Beitr. Naturk., Serie A, 402: 3. Irangi, Kivu, DR Congo.

Taxonomy Species-group: *tullbergi*. Closely related to *P. tullbergi*, *P. rostratus* and *P. morio*. In E DR Congo, occurs sympatrically with *P. jacksoni*, from which it can be distinguished by characters of the skull (Van der Straeten & Dieterlen 1987, Van der Straeten & Dudu 1990). Musser & Carleton (1993, 2005) point out that *P. misonnei* could simply be a form of *P. tullbergi* at the eastern margin of its geographical range, but Van der Straeten & Dieterlen (1987) found highly significant differences in ten skull and tooth characters. The specimens of *P. misonnei* from Kenya, identified as such by Qumsiyeh *et al.* (1990), are now considered to represent a new species, *P. degraaffi* (Van der Straeten & Kerbis Peterhans 1999). Synonyms: none. Chromosome number: not known.

Description Small rufous soft-furred mouse, similar in external appearances to *P. jacksoni*. Pelage soft and long (9–10 mm). Dorsal pelage rufous or grey; hairs dark grey at base, rufous or grey at tip. Dorsal pelage varies with age: dark grey in subadults, rufous in adults and deep rufous in old adults. Ventral pelage greyish-white; hairs grey at base, white at tip. Forefeet whitish and hindfeet pale with whitish tinge, toes whitish. Tail very long (ca. 123% of HB), almost naked, dark grey above, slightly paler below. Skull: similar to *P. tullbergi*; the most obvious distinction is the narrower breadth of M¹ and the narrower interorbital breadth compared with *P. jacksoni*; supraorbital ridges absent or small (if present, originate half-way along frontal bone); posterior limit of anterior palatal foramina at anterior edge of M¹; t3 of M¹ absent or difficult to detect. Palatal ridges 2 + 7 = 9. Nipples 1 + 2 = 6.

Geographic Variation None recorded.

Similar Species

P. jacksoni. HB on average slightly larger; tail slightly longer; palatal ridges 2 + 5 = 7; skull characters as for *jacksoni* species-group; sympatric.

Distribution Endemic to Africa. Rainforest BZ (East Central Region). Recorded only from Irangi, Masako Forest (near

Kisangani), Ituri Forest and Gamangui, all in E and NE DR Congo (Van der Straeten & Dudu 1990, Dudu 1991). Extent of range unknown but likely to occur in most of the lowland and sub-montane rainforest of E DR Congo. Possibly occurs in some localities in Uganda and W Kenya (not mapped). A record by Nicolas & Colyn (2003) of '*Praomys cf. misonnei*' at Mont Doudou, SW Gabon (02° 09' S, 10° 30' E) is much further west than other records and needs investigation.

Habitat Similar to that of *P. jacksoni*. Recorded from lowland rainforest (500–850 m) at Masako and Irangi, and sub-montane forest (up to 1650 m) at Irangi. Has not been found at higher



Praomys misonnei

altitudes, e.g. in montane forest (1800–3000 m) in Kahuzi–Biega N. P. Preferred habitat is undisturbed rainforest, although may also occur (less frequently) in secondary forest and fallow cultivated habitats within rainforest; never found in wet areas (cf. *P. mutoni*).

Abundance Abundance varies according to habitat and altitude. In general, not nearly as common as the sympatric *P. jacksoni*. In lowland rainforest at Irangi (altitude 850–950 m), *P. misonnei* was less numerous (27%, $n = 103$) than *P. jacksoni* (73%, $n = 282$), but in the sub-montane rainforest above Irangi at 1250–1650 m, it was more numerous (78%, $n = 54$) than *P. jacksoni* (22%, $n = 17$) (F. Dieterlen unpubl.). It was never found at higher altitudes in the montane forest (1800–3000 m) in Kahuzi–Biega N. P.

Remarks Mostly terrestrial but also semi-arboreal. Reproductive activity mostly during the wet season: 80% of adult ♀♀ ($n = 21$) were pregnant or lactating during the wet season (Sep–May; $n = 21$); and only 7% during the dry season (Jun–Aug; $n = 15$) (Dieterlen 1985a, b). Embryo number: 3.2 (2–5, $n = 14$ litters). Sex ratio: 3:2 ($n = 150$).

Conservation IUCN Category: Least Concern.

Although recorded from only a few localities, this species is likely to be fairly widespread in rainforests.

Measurements

Praomys misonnei

HB: 111.6 (89–123) mm, $n = 51$

T: 137.3 (113–163) mm, $n = 50$

HF: 24.3 (21–26) mm, $n = 49$

E: 18.5 (16–21) mm, $n = 46$

WT: 34.7 (27–48) g, $n = 68$

GLS: 31.0 (29.2–32.4) mm, $n = 33$

GWS: 14.2 (13.5–15.2) mm, $n = 33$

M¹–M³: 5.0 (4.7–5.4) mm, $n = 33$

Irangi, E DR Congo (Van der Straeten & Dieterlen 1987, F. Dieterlen unpubl.)

Key Reference Van der Straeten & Dieterlen 1987.

Fritz Dieterlen

Praomys morio CAMEROON SOFT-FURRED MOUSE (CAMEROON PRAOMYS)

Fr. Souris sylvestre du Mont Cameroon; Ger. Kamerun-Weichhaarmaus

Praomys morio (Trouessart, 1881). Bull. Soc. Etudes Sci. Angers 10: 121. Mount Cameroon, Cameroon. 7000 ft (2135 m).

Taxonomy Originally described in the genus *Mus*. Species-group: *tullbergi*. Attempts to breed *P. morio* with *P. tullbergi* in captivity were unsuccessful (Eisentraut 1973), indicating that *P. morio* is specifically distinct. The name *morio* has been used for specimens from localities far from Mt Cameroon (e. g. in Central African Republic), but these are now known to represent *P. tullbergi* or *P. petteri* (Musser & Carleton 1993, 2005). Synonyms: *maurus*. Subspecies: none. Chromosome number: $2n = 34$ (same as *P. tullbergi*; Matthey in Eisentraut 1973).

Description Small dark montane forest mouse. Pelage dense and soft, dorsal hairs 10–12 mm. Dorsal pelage dark rufous-brown to blackish-brown; hairs dark grey at base, rufous-brown to dark brown at tip. Ventral pelage pale to dark grey; hairs dark grey at base, white at tip; colour of base often shows through to surface. Ears relatively long, darkly pigmented, rounded at tip. Head, cheeks, muzzle and throat similar to dorsal pelage. Fore- and hindlimbs dark brown. Tail very long (ca. 112% of HB), darkly pigmented, with small dark bristles. Skull similar to *P. tullbergi*: supraorbital ridges small or absent, originating half way along frontal bone; posterior limit of anterior palatal foramina at anterior edge of M¹; t3 of upper M1 absent or difficult to detect; rostrum shorter and narrower and M¹–M³ longer than in *P. tullbergi* (Eisentraut 1969b, Lecompte *et al.* 1999). Palatal ridges $2 + 7 = 9$. Nipples: $1 + 2 = 6$.

Geographic Variation Specimens from lower altitudes are rufous-brown to dark brown; those from higher altitudes are darker and blacker because there is more melanin in the hairs. Specimens from Bioko I. tend to be slightly smaller, on average, to those from Mt Cameroon (Eisentraut 1970).

Similar Species

P. tullbergi. HB on average smaller (mean 103 mm); T on average longer (mean 145 mm); M¹–M³ shorter (mean 4.5 mm); widespread in rainforests of West Africa.

P. jacksoni. T on average longer (mean 146.9 mm); GLS and M¹–M³ similar; palatal ridges $2 + 5 = 7$; chromosome number: $2n = 28$; widespread in rainforests of central Africa.



Praomys morio

P. hartwigi. T longer; GWS and M^1 – M^3 larger; only known from Mt Oku and L. Manengouba in the Bamenda Highlands of Cameroon.

Distribution Endemic to Africa. Afromontane–Afroalpine BZ. Recorded only from Mt Cameroon and Bioko I. On Mt Cameroon, known from ca. 1000–3000 m, but not recorded at lower altitudes on the mountain nor on neighbouring mountains at similar altitudes. On Bioko I. recorded at 1200–2000 m. Appears not to be syntopic or sympatric with *P. tullbergi*.

Habitat Montane forest at higher altitudes, and alpine grasslands towards the summit of Mt Cameroon.

Abundance Uncertain; tends to be more abundant at higher altitudes.

Remarks Probably similar to *P. tullbergi* in most respects. Gestation: 26–30 days. Females have a postpartum oestrus. Embryo number (Mt Cameroon): 4.6 (3–6); mode 5, $n = 14$ litters. Litter-size (in captivity): 4.7 (2–6), mode 4 and 5, $n = 61$. Weight at birth: 2.25–2.64 g. Eyes open on Day 17–19. Growth

to 25 g in ca. 80 days. Minimum age to first conception: 136 days (Eisentraut 1961).

Conservation IUCN Category: Endangered.

The limited distribution of the species and destruction of rainforest habitats are cause for concern.

Measurements

Praomys morio

HB: 113.5 (100–130) mm, $n = 83$

T: 129.9 (110–147) mm, $n = 83$

HF: 23.5 (21–25) mm, $n = 83$

E: 18.3 (16–20) mm, $n = 83$

WT: 43.0 (27–62) g, $n = 83$

GLS: 30.2 (28.1–31.9) mm, $n = 83$

GWS: 12.4 (11.7–12.8) mm, $n = 83$

M^1 – M^3 : 5.2 (5.0–5.4) mm, $n = 83$

Mt Cameroon, Cameroon (Eisentraut 1970)

Key References Eisentraut 1970, 1973.

D. C. D. Happold

Praomys mutoni RIVERINE SOFT-FURRED MOUSE (MASAKO SOFT-FURRED MOUSE, RIVERINE PRAOMYS)

Fr. Souris sylvestre de la rivière (Souris à poil doux de Masako); Ger. Muton-Weichhaarmaus

Praomys mutoni Van der Straeten and Dudu, 1990. In: Vertebrates in the Tropics (eds G. Peters & R. Hutterer). Museum Alexander Koenig, Bonn, p. 75. Batiabongena, Masako Forest Reserve, DR Congo.

Taxonomy Species-group: *jacksoni* (Van der Straeten and Dieterlen 1987). Synonyms: none. Chromosome number: not known.

Description Small dark brown mouse. Dorsal pelage soft sepia-brown; dorsal hairs 9–10 mm. Ventral pelage whitish-grey; hairs grey at base, white on terminal end; more greyish in ♀♀ than in ♂♂. Most ♂♂ have a white patch or stripe in front of the penis. Tail very long (ca. 120–140% HB), unicoloured, rather dark, with a few short hairs between the scales. Skull: supraorbital ridges well developed and clearly bending outwards (not straight as in other species of the *jacksoni* species-group); posterior limit of anterior palatal foramina at second root of M^1 ; t_3 of M^1 well developed. Palatal ridges $2 + 5 = 7$. Nipples $1 + 2 = 6$.

Geographic Variation None recorded.

Similar Species

P. jacksoni. Pelage colour paler; supraorbital ridges straight; widespread in Rainforest BZ of central Africa.

Distribution Endemic to Africa. Rainforest BZ (East Central Region). Only known from the type locality (Masako F. R., DR Congo; $00^\circ 36' N$, $25^\circ 13' E$). Probably widespread in suitable habitats north of the Congo R.

Habitat Very wet areas along rivers and rivulets within secondary forest and in old farmlands, where syntopic with *P. jacksoni*.

Abundance Rare and localized. In preferred wet habitats, comprised 2.1% of trapped small mammals; overall in Masako F. R. comprised 0.85% of rodents ($n = 4000$ rodents).



Praomys mutoni

Remarks Pregnant ♀♀ recorded at beginning (Dec) and end (Feb) of dry season. Embryo number: 2–3 (Dudu 1991).

Conservation IUCN Category: Data Deficient.

Measurements

Praomys mutoni

HB: 114 (97–139) mm, n = 29

T: 146 (113–171) mm, n = 28

HF: 22 (20–24) mm, n = 28

E: 18 (16–20) mm, n = 25

WT: 45 (31–57) g, n = 29

GLS: 31.8 (29.2–33.1) mm, n = 29

GWS: 14.9 (13.4–16.0) mm, n = 29

M¹–M³: 5.1 (4.9–5.5) mm, n = 29

DR Congo (Van der Straeten & Dudu 1990)

Key References Dudu 1991; Van der Straeten & Dieterlen 1987; Van der Straeten & Dudu 1990.

Erik Van der Straeten

Praomys obscurus OBSCURE SOFT-FURRED MOUSE (GOTEL MOUNTAIN PRAOMYS)

Fr. Souris sylvestre obscure; Ger. Dunkel Weichhaarmaus

Praomys obscurus Hutterer and Dieterlen, 1992. Bonn. Zool. Beitr. 43: 402. Gangirwal, Gotel Mts, Mambilla Plateau, SE Nigeria. 2300 m.

Taxonomy Species-group: *tullbergi*. Originally described as a subspecies of *P. hartwigi* (Hutterer *et al.* 1992). The status of *obscurus* is uncertain: it may be a subspecies of *P. hartwigi* or a valid species. Here (following Musser & Carleton 2005), *P. obscurus* is given specific rank. The two species, *P. hartwigi* and *P. obscurus*, have very restricted geographic ranges in separate montane forests, separated from each other by about 100 km of savanna. Synonyms: none. Chromosome number: not known.

Description Medium-sized dark rainforest mouse, but comparatively large for a species in this genus. Pelage soft and long (13–15 mm on back). Dorsal pelage dark brown to greyish-black, especially on mid-dorsal line, without any russet tinge as in *P. hartwigi*; hairs dark grey with subterminal band of pale brown or beige, and black at tip. Dorsal pelage slate-grey in young animals. Flanks slightly paler. Ventral pelage whitish-grey; hairs dark grey at base, off-white

at tip. Colour of flanks and ventral pelage delineated by thin line of pale reddish-brown. Head similar in colour to dorsal pelage. Ears large, darkly pigmented with sparse short dark hairs. Forelimbs pale, with sparse short whitish hairs; five digits, Digit 1 reduced to tubercle with very small claw. Hindfeet pale as forefeet; five digits each with claw. Tail very long (ca. 140% of HB), ringed with scales, appears more or less naked but covered with very small dark bristles. Palatal ridges: 2 + 7 = 9. Skull narrow and long, similar to that of *P. hartwigi* but on average shorter. Upper tooththrow short, M¹ short and narrow, molar crown pattern simplified as compared to *P. hartwigi*. Palatal ridges: 2 + 7 = 9. Nipples: 1 + 2 = 6.

Geographic Variation None recorded.

Similar Species

P. hartwigi. Overall similar, but dorsal pelage less dark, mostly reddish-brown; on average heavier (mean WT: 57.2 g); skull (mean GLS: 32.6 mm) on average larger; upper tooththrow (mean M¹–M³: 5.6 mm) longer; occurs further south on the Bamenda Plateau, not in sympatry with *P. obscurus*.

Distribution Endemic to Africa. Afromontane–Afroalpine BZ. Known only from two localities (Mt Gangirwal and Chappal Waddi) in the Gotel Mts of Nigeria (Hutterer *et al.* 1992).

Habitat Relict montane forest at 1900–2300 m on the slopes of the Gotel Mts, a plateau of about 21 km² (Chapman *et al.* 2004). Of a total of 38 specimens, 14 were collected in fern-grassland, 11 in forest, eight along streams in forest, three in gallery forest and two in forest swamp (Hutterer *et al.* 1992).

Abundance May be locally common in the Gotel Mts, but in an extremely restricted habitat.

Remarks Terrestrial and nocturnal. Females probably start to reproduce at a minimum weight of 40 g. In the Gotel Mts in 1988, four of 11 adult ♀♀ were reproductively active in the second half of Mar: one was lactating and three were pregnant. Embryo number: 3 (n = 1), 4 (n = 2). Maturation of ♂♂ at ca. 30–35.



Praomys obscurus

Conservation IUCN Category: Endangered.

Measurements

Praomys obscurus

HB: 121.0 (108–137) mm, n = 22

T: 161.0 (149–174) mm, n = 22

HF: 27.1 (26–28) mm, n = 22

E: 20.1 (19–21) mm, n = 22

WT: 47.2 (34–60) g, n = 22

GLS: 31.4 (27.7–33.1) mm, n = 15

GWS: 15.4 (14.4–16.3) mm, n = 15

M¹–M³: 5.3 (5.2–5.4) mm, n = 22

Nigeria, Gotel Mts (Hutterer *et al.* 1992)

Key Reference Hutterer *et al.* 1992.

R. Hutterer

Praomys petteri PETTER'S SOFT-FURRED MOUSE (PETTER'S PRAOMYS)

Fr. Souris sylvestre de Petter; Ger. Petters Weichhaarmaus

Praomys petteri Van der Straeten, Lecompte and Denys, 2003. Bonn. Zool. Beitr. 50: 333. Boukoko, Central African Republic.

Taxonomy Species-group: *tullbergi*, and a sibling species of *P. rostratus*. The species was first documented as a *Praomys* with 2n = 42 (Matthey 1965), but without a formal name, and has subsequently been referred to as 'morio' (when considered to be the same as *P. morio* from Cameroon [Matthey 1965, Petter 1975b]) or *P. lukolelae* (Petter 1975b). Phylogenetic studies show that populations in Cameroon, Gabon and Congo are not *P. morio* or *P. lukolelae*, and they are now allocated to *P. petteri* (Van der Straeten *et al.* 2003). Synonyms: none. Chromosome number: 2n = 42, aFN = 62 (Matthey 1965).

Description Small to medium-sized brown forest mouse, although one of the larger species in the genus and similar in colour to *P. rostratus*. Pelage dense and soft; hairs ca. 10 mm on mid-back. Dorsal pelage dark brown, sometimes very dark. Ventral pelage whitish-grey. Short white hairs along edge of the ears. Feet with white hairs. Tail very long (115–125% of HB), unicoloured dark brown, with irregular pale spots; a few short hairs between the scales. Skull: supraorbital ridges small or absent; posterior limit of anterior palatal

foramina at anterior edge of M¹; t3 of M¹ absent or difficult to detect. Palatal ridges 2 + 7 = 9. Nipples 1 + 2 = 6.

Geographic Variation None recorded.

Similar Species

P. tullbergi. HF smaller; GLS on average smaller; similar pelage colour; chromosome number: 2n = 34; mainly West Africa.

P. rostratus. Similar colour; chromosome number: 2n = 34 (as in *P. tullbergi*); Senegal to Ghana.

P. jacksoni. Similar colour; can only be distinguished by skull characters; chromosome number: 2n = 42; widespread in central Africa.

Distribution Endemic to Africa. Rainforest BZ (West Central Region, Gabon Subregion). Recorded from S Cameroon, SW Congo and S Central African Republic.

Habitat Secondary forest, savanna developed after deforestation, and dry thickets. Sometimes in the neighbourhood of small villages, and occasionally within villages (Granjon, 1991). Specimens of *P. petteri* frequently occur sympatrically with *P. tullbergi* and *P. jacksoni*.

Abundance In Congo (Granjon 1991) and Cameroon (E. Van der Straeten unpubl.), this species seems to be more abundant than the syntopic *P. cf. tullbergi*.

Remarks Mainly insectivorous. Diet (as indicated by stomach contents) is mainly insects (>75% by volume) as well as grains and fruit, especially in the dry season (Genest-Villard 1980). One of the eight ♀♀ trapped in Sep was pregnant. Embryo number: 4 (n = 1; Congo; Granjon 1991).

Conservation IUCN Category: Least Concern.

Measurements

Praomys petteri

HB: 119 (73–143) mm, n = 38

T: 140 (99–165) mm, n = 38

HF: 26.0 (24–28) mm, n = 42

E: 18.5 (15–22) mm, n = 42



Praomys petteri

WT: 49 (40–61) g, n = 12

GLS: 34.1 (30.5–36.7) mm, n = 49

GWS: 15.4 (13.5–17.2) mm, n = 48

M¹–M³: 5.1 (4.6–5.5) mm, n = 52

Cameroon, Congo and Central African Republic (Van der Straeten *et al.* 2003)

Key References Granjon 1991; Petter 1975b; Van der Straeten *et al.* 2003.

Erik Van der Straeten

Praomys rostratus WEST AFRICAN SOFT-FURRED MOUSE (WEST AFRICAN PRAOMYS)

Fr. Souris sylvestre d'Afrique de l'Ouest; Ger. Wald-Weichhaarmaus

Praomys rostratus (Miller, 1900). Proc. Washington Acad. Sci., 2: 637. Mount Coffee, Liberia.

Taxonomy Originally described as *Mus tullbergi rostratus*. Species-group: *tullbergi*. Subsequently *Praomys rostratus* was described as a distinct species (separate from *P. tullbergi* because of its larger mean size) by Van der Straeten & Verheyen (1981). In 1958, Heim de Balsac & Lamotte (1958) recorded two species of *Praomys* at Mt Nimba: *P. tullbergi* (incorrectly referred to as *P. morio*) and *P. rostratus* (incorrectly referred to as *P. jacksoni*). Synonyms: none. Chromosome number: 2n = 34 (as in *P. tullbergi*; E. Van der Straeten unpubl.).

Description Small brown forest mouse, similar in colour to *P. tullbergi*. Pelage dense and soft, ca. 10 mm on mid-back. Dorsal pelage reddish-brown to yellowish-brown in older animals; dark brown in younger ones. Ventral pelage nearly white in adult specimens; ventral hairs grey at base, white on terminal two-thirds. Hands and feet white. Some ♂♂ have white patch or stripe just in front of penis. Tail very long (ca. 115–125% of HB), dark brown, with a few short hairs between the scales; unicoloured with irregular pale spots. Skull: supraorbital ridges small or absent, originating half-way along frontal bone; posterior limit of anterior palatal foramina at anterior edge of M¹; t3 of M¹ absent or difficult to detect. Palatal ridges 2 + 7 = 9. Nipples 1 + 2 = 6.

Geographic Variation None recorded.

Similar Species

P. tullbergi. Skull and external measurements on average smaller; cannot be distinguished by pelage colour.

Distribution Endemic to Africa. Rainforest BZ (Western Region) and Northern Rainforest–Savanna Mosaic. Recorded from Senegal (Basse Casamance) to Ghana; all records west of the Dahomey Gap.

Habitat Rainforest and forest relicts, dry thickets and cultivated land (Lim & Van Coeverden de Groot 1997, Van der Straeten & Verheyen 1981). Often syntopic with *P. tullbergi*.

Abundance At Adiopodoumé (Côte d'Ivoire), *P. rostratus* was more abundant (70%) than *P. tullbergi* (30%).

Remarks Terrestrial, but also found in trees at heights of 1 m and 2.5 m in Côte d'Ivoire. Reproductively active in Feb (no samples in other months): ♂♂ had scrotal testes, and all ♀♀ (n = 6) were pregnant. Embryo number: 2–4 (Lim & Van Coeverden de Groot 1997).



Praomys rostratus

Conservation IUCN Category: Least Concern.

Measurements

Praomys rostratus

HB: 114 (97–134) mm, n = 87

T: 138 (109–161) mm, n = 80

HF: 26.5 (25–29) mm, n = 87

E: 15.5 (12–18) mm, n = 87

WT: 50 (30–67) g, n = 87

GLS: 33.7 (30.0–37.4) mm, n = 87

GWS: 14.9 (13.2–16.5) mm, n = 87

M¹–M³: 5.2 (4.7–5.6) mm, n = 87

Adiopodoumé, Côte d'Ivoire (Van der Straeten & Verheyen 1981)

Key References Heim de Balsac & Lamotte 1958; Lim & Van Coeverden de Groot 1997; Van der Straeten & Verheyen 1981.

Erik Van der Straeten

Praomys tullbergi TULLBERG'S SOFT-FURRED MOUSE (TULLBERG'S PRAOMYS)

Fr. Souris sylvestre de Tullberg; Ger. Tullbergs Weichhaarmaus

Praomys tullbergi (Thomas, 1894). Ann. Mag. Nat. Hist., ser. 6, 13: 205. Ankober River, Wasa, Ashanti, Ghana.

Taxonomy Originally described in the genus *Mus*. Species-group: *tullbergi*. Synonyms: *burtoni*. Subspecies: none. Chromosome number: $2n = 34$ (Central African Republic; Petter 1975b); $2n = 34$ (Côte d'Ivoire; Matthey 1958); $2n = 34$, $FN = 32$, all acrocentric autosomes (Senegal; Granjon *et al.* 1992).

Description Small forest mouse. Pelage soft. Dorsal pelage reddish-brown; hairs grey at base, greyish-brown to rufous-brown tips. Ventral pelage greyish; hairs grey at base, white at tip. Chin, throat and chest whitish. Head narrow and pointed, moderate to large eyes, large fleshy ears. Palatal ridges $2 + 7 = 9$. Fore- and hindfeet white. Tail very long (ca. 140% of head and body), with short sparse bristles. Considerable variation in pelage colour: dark grey in juveniles, greyish-brown in young adults and rufous-brown to reddish-brown in old individuals. Males often slightly larger than ♀♀. Skull: supraorbital ridges small or absent, originating half-way along frontal bone; posterior limit of anterior palatal foramina at anterior edge of M^1 ; $t3$ of M^1 absent or difficult to detect. Nipples: $1 + 2 = 6$.

Geographic Variation None recorded.

Similar Species

P. daltoni. Ventral hairs pure white; nipples $3 + 2 = 10$; savanna habitats only.

P. rostratus. On average larger; sympatric west of Dahomey Gap.

P. jacksoni. On average larger; palatal ridges $2 + 5 = 7$; mostly allopatric but may be sympatric in parts of Cameroon.

Hylomyscus stella. Primarily arboreal; hindfeet smaller and usually shorter; tail on average relatively longer; nipples $2 + 2 = 8$.

Distribution Endemic to Africa. Rainforest BZ (Western Region and West Central Region) and Northern Rainforest–Savanna Mosaic. Recorded from Gambia and SW Senegal to Ghana, and from W Nigeria to Cameroon, Gabon and Central African Republic. Isolated populations in Togo and Benin (Dahomey Gap), and in forest relicts in Northern Rainforest–Savanna Mosaic. Lower altitudes of Mt Cameroon (up to ca. 600 m); replaced by *P. morio* at higher altitudes on the mountain. Eastern limit of geographic range uncertain.

Habitat Primary and secondary rainforest, where soil is covered by leaf litter and small well-spaced forest herbs and shrubs. Also recorded in cultivated areas close to the forest, abandoned farmlands, cocoa plantations, oil palm plantations, forest clearings and along logging tracks in the Rainforest BZ. Occurs in forest relicts in savanna habitats where structure and characteristics resemble rainforest (Happold 1975b; Decher 1997). Not recorded in savanna grasslands.

Abundance Often the most abundant species of small terrestrial rodent in rainforest habitats of West Africa, e.g. comprised 30–57% of all terrestrial rodents in Sierra Leone (Cross 1977), 37% (Cole 1975) and 57% (Jeffrey 1977) in Ghana, and 75–86% in Nigeria



Praomys tullbergi

(Happold 1975b, 1977). In some areas (e.g. Côte d'Ivoire), they were the second most abundant small rodent (32%) after *Hylomyscus alleni* (as *H. simus*) (34%) (Adam 1977). In Central African Republic, the percentage abundance varied by habitat: 15% in *Gilbertiodendron* forest, 20% in natural mixed species forest and 40% in more open habitats along forest tracks (Ray 1998). Density ranges from 0.4 to 2.7 individuals/ha in Gabon (Duplantier 1989). During a 3-year period at a single study site in Gambari Forest, Nigeria, population density varied from 9.5/ha to 27.9/ha depending on year and season (Happold 1977, 1978, 1979). Mean biomass ranged from 47 g/ha (range 15–86 g/ha) in Gabon (Duplantier 1989) to 514 g/ha (range 185–920 g/ha) in Nigeria (Happold 1977).

Adaptations Terrestrial and nocturnal; occasionally scansorial. Lives in holes in fallen logs, in crevices under living trees and buttress roots, old termite mounds and in cracks in the soil. Not known to dig burrows. Constructs nests of dead forest leaves, laid flat to form a saucer-shaped depression. Radio-collared individuals exhibited several peaks of activity during the night; ♂♂ showed greater activity than ♀♀. Average distance travelled each night was 227 m by males and 169 m by females (Duplantier 1982).

Foraging and Food Omnivorous, and probably opportunistic. In Ghana, diet was mainly vegetable material (fruits, shoots and seeds) but also some insects (ants, termites, grasshoppers and beetles) (Cole 1975). In Gabon, mostly fruit pulp and seeds with some insects (Duplantier 1982), and in Central African Republic, insects (mostly ants and termites, 70–75% by volume), many species of seeds and

fruits (ca. 25%) and a few other invertebrates (6–8%) (Genest-Villard 1980).

Social and Reproductive Behaviour Home-ranges of ♂♂ and ♀♀ are similar in area (♂♂: 0.23 [0.11–0.39] ha, $n = 19$; ♀♀: 0.22 [0.13–0.30] ha, $n = 14$), with extensive overlap between individuals (Happold 1977). Social organization is communal, and individuals show a high frequency of amicable behaviour. Individuals of different sexes nest together, and young often nest with the mother after weaning.

Reproduction and Population Structure Time of reproduction is similar throughout the geographic range of the species. In Nigeria, for example, reproduction occurs in all months of the year, with two peaks of reproductive activity, one at the end of the dry season and during the early wet season (Feb–Apr), and the second after the little dry season (Oct, Nov) (Happold 1977, 1987). Reproduction is rapid because of the following characters: oestrus cycle 6–7 days; gestation 23–24 days, young weaned at Day 24–25, first conception at 84 (62–115) days, and minimum time between consecutive litters (in captivity) 23–30 days (Happold 1978). Embryo number varies slightly by locality: Sierra Leone 3.45 (2–4) (Cross 1977); Ghana 3.7 (2–6), mode 3 or 4 (Jeffrey 1975, 1977); and Nigeria 3.6 (2–6), mode 3 or 4 (Happold 1978). Litter-size at birth for 103 parturitions in captivity was 3 (1–6; Happold 1978).

In Nigeria (Happold 1977), population structure remains fairly constant throughout the year as a result of more-or-less continuous reproduction and a steady rate of mortality and/or emigration. All five age-weight classes (<1 month, 1–2 months, 3–4 months, 4–6 months, 6–18 months) present in most months; two youngest age-

classes absent when reproductive rate declines. Commonest age-classes: 3–4 months and 4–6 months. Survival rate of young entering the population is 0.52 after one month, 0.29 after three months, 0.20 after five months and 0.11 after 11 months; maximum known age in the wild is 18 months; 83% of population replaced every six months.

Predators, Parasites and Diseases In Central African Republic, comprised nearly 10% of small mammal remains in scats of various carnivores (total $n = 732$), and 29% of rodents less than 100 g ($n = 251$) (Ray 1998).

Conservation IUCN Category: Least Concern.

Measurements

Praomys tullbergi

HB: 103 (100–115) mm, $n = 10$

T: 145 (135–160) mm, $n = 10$

HF: 22.5 (20–24) mm, $n = 10$

E: 16.8 (15–17) mm, $n = 10$

WT: 38 (32–42) g, $n = 10$

GLS: 32.2 (31.1–34.0) mm, $n = 10$

GWS: 14.2 (13.3–14.9) mm, $n = 10$

M¹–M³: 4.5 (4.2–4.9) mm, $n = 10$

Males only. Females often slightly smaller

Western Nigeria (Happold 1974)

Key References Happold 1975b, 1977, 1978, 1987.

D. C. D. Happold

Praomys verschureni VERSCHUREN'S SOFT-FURRED MOUSE (VERSCHUREN'S PRAOMYS)

Fr. Souris sylvestre de Verschuren; Ger. Verschurens Weichhaarmaus

Praomys verschureni (Verheyen and Van der Straeten, 1977). Rev. Zool. Afr. 91: 739. Mamiki, DR Congo.

Taxonomy Originally described in the genus *Malacomys*, on the basis of one specimen. Four additional specimens were obtained between 1977 and 1993 (Robbins & Van der Straeten 1982, Dieterlen & Van der Straeten 1984), and a further 31 were collected in Irangi, DR Congo (F. Dieterlen unpubl.). Although described in the genus *Malacomys*, *verschureni* is close to *Praomys* and is considered here as a species of *Praomys* (Van der Straeten & Kerbis Peterhans 1999, Musser & Carleton 2005). Species-group: *lukolelae*. This taxon, together with *P. lukolelae*, may represent a separate genus (E. Van der Straeten unpubl.). Synonyms: none. Chromosome number: $2n = 58$, FN = 58 or 60 (Robbins & Van der Straeten 1982).

Description Medium-sized with very long tail and long hindfeet, showing characters of both *Praomys* and *Malacomys* (see also *P. lukolelae*). Pelage soft and long (ca. 12 mm), texture sleek as in *Praomys*. Dorsal pelage dark grey washed with some brown; hairs dark grey at base with white at extreme base, brown at tip. In older animals, pelage becomes brownish, similar to that of *P. jacksoni*. Flanks brownish, especially anteriorly. Ventral pelage grey; hairs dark grey at base, white at tip. Colour of dorsal and ventral pelage clearly delineated. Ears rounded, inner and outer surfaces sparsely covered with short brownish hairs.

Vibrissae long (30–40 mm). Palatal ridges $2 + 6 = 8$. Upper sides of fore- and hindfeet whitish (unpigmented) with very short white hairs. Hindfeet comparatively long; soles with six plantar pads, claws short. Tail very long (ca. 120% of HB), dark (sometimes partly unpigmented), mostly naked, but sparsely covered with short whitish bristles. Skull: not very elongated, as in *Praomys* (cf. *Malacomys*); posterior limit of anterior palatal foramina anterior to M¹ (as in *Malacomys* spp.); sides of frontal bones rounded and without supraorbital ridges. Upper incisors between ortho- and opisthodont. t3 of M² usually present (rarely present in *Malacomys* spp.). t9 on M¹ and M² absent (same as in *Malacomys* spp.). Mandible relatively large (as in *Malacomys* spp.). Nipples: $1 + 2 = 6$.

Geographic Variation None recorded.

Similar Species

Praomys (other spp. groups) Hindfeet on average shorter (means 22–25 mm).

Malacomys longipes. Hindfeet longer (39.4 [36–41] mm).

Distribution Endemic to Africa. Rainforest BZ (East Central Region). Known from four localities: Irangi, E DR Congo; Mamiki

near Beni, NE DR Congo; Epulu (Ituri), NE DR Congo (J. Kerbis unpubl.); and Tandala near Gemena, N DR Congo. All localities are east and north of the Congo R. Distribution is probably limited to the west and south by the Congo R., and to the east and north by the northern edge of the rainforest.

Habitat Lowland rainforest and sub-montane forest. The holotype was captured close to water in *Cynometra* forest. At Irangi (850 m), found in hilly rainforest where typical trees were *Pygnanthus angolensis*, *Annonidium manni*, *Julbernardia seretii*, *Gilbertiodendron dewevrei*, *Staudtia stipitata* and *Uapaca* sp. In sub-montane forest (1000–1800 m), preferred habitat contained *Strombosia scheffleri*, *Ocotea usambarensis*, *Bridelia brideliiifolia*, *Polyscias kivuensis*, *Carapa grandiflora*, *Lebrunia bushaie* and *Musanga leo-errerae*.

Abundance Rather varied. Extremely rare in lowland rainforest, comprising <0.01% of captures, and 0.6% in pure primary forest. In contrast, comprised 12.3% and was the fourth commonest species of all small mammals (17 spp.) in sub-montane forest at 1250–1650 m (F. Dieterlen unpubl.).

Remarks Omnivorous. Stomach contents (n = 11) were either only invertebrate remains – mainly arthropods and their larvae discernible by pieces of chitin, fatty tissues and muscle fibres (n = 6) – or were invertebrate remains with 50% plant material, which was mostly whitish homogeneous material (probably from nuts, kernels or tubers) without any typical plant fibres or green matter (n = 5) (F. Dieterlen unpubl.). At Irangi, E DR Congo, ♀♀ in reproductive condition (pregnant or lactating) were caught between Sep and Apr (n = 13 adults), months when most other small mammals were also reproducing (limited sampling in other months). Embryo number: 3 (n = 1). Five of the seven lactating ♀♀ were obtained in Apr, and none of the lactating ♀♀ was pregnant. Sex ratio of captures unusually biased (35 : 65%, n = 34) towards ♀♀.

Conservation IUCN Category: Data Deficient.



Praomys verschureni

Measurements

Praomys verschureni

HB: 121.3 (109–135) mm, n = 29

T: 143.0 (123–162) mm, n = 27

HF (c.u): 30.1 (28–32) mm, n = 27

E: 20.3 (19–23) mm, n = 24

WT: 50.8 (40–65) g, n = 28

GLS: 34.4 (33.1–36.1) mm, n = 22

GWS: 15.5 (14.8–16.1) mm, n = 14

M¹–M³: 5.3 (4.7–5.9) mm, n = 26

Irangi, E DR Congo (F. Dieterlen unpubl.)

Key References Dieterlen & Van der Straeten 1984; Verheyen & Van der Straeten 1977.

Fritz Dieterlen

GENUS *Rattus*

Rats

Rattus Fischer, 1803. Natl Mus. Nat. Paris, 2: 128. Type species: *Mus decumanus* Pallas, 1778 (= *Mus norvegicus* Berkenhout, 1769).

The genus *Rattus* is one of the most widespread of rodent genera in the world, occurring on all continents of the world except Antarctica, and also on many islands where it has been introduced (mostly inadvertently) by humans (see also Rosevear 1969). The number of species is uncertain, but is in the order of 56 (Musser & Carleton 1993) to 66 species (Musser & Carleton 2005); of these only two species occur in Africa, both of them introduced by humans in recent times (see Rodentia profile). The following notes are mostly restricted to the two African species.

The genus is characterized by large body size for a murid (mean HB length in Africa at least 165 mm), typically ‘rat-like’ shape,

coarse pelage and long naked tail with small scales. The dorsal pelage and flanks are dull brownish or blackish, and ventral pelage is grey, yellow or white. There are no stripes or colour patterns on the pelage. The skull (Figure 83) is relatively narrow, with mean length of at least 39 mm, slender zygomatic arches, strong supraorbital ridges, moderate-sized auditory bullae and relatively small cheekteeth. Incisors are wide, smooth, without notch on posterior surface (cf. *Mus*), ungrooved and opisthodont. M¹ has five roots.

The genus is not indigenous to Africa, and is assumed to have entered Africa by various means of human transport, notably by ships arriving at African ports. The two species in Africa have restricted

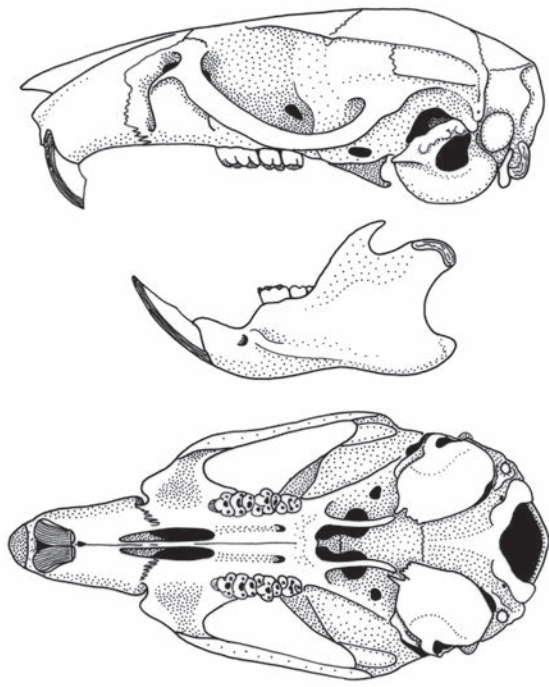


Figure 83. Skull and mandible of *Rattus rattus* (HC 463).

Rattus norvegicus BROWN RAT (NORWAY RAT)

Fr. Surmulot (Rat d'égouts); Ger. Wanderratte

D. C. D. Happold

Rattus norvegicus (Berkenhout, 1769). Outlines of the Natural History of Great Britain and Ireland, 1:5. Great Britain (no precise locality stated).

Taxonomy Originally described in the genus *Mus*. Original distribution assumed to be SE Siberia, N China and parts of Japan but now an introduced species in many parts of the world. The Brown Rat is the wild ancestor of the laboratory white rat extensively used in medical and pharmacological research. Synonyms: many, mostly non-African (see Musser & Carleton 2005 for details). Chromosome number: $2n = 42$.

Description Large rat with long coarse shaggy blackish-brown pelage, and tail shorter than head and body. Dorsal pelage dark brown or blackish-brown, often flecked with rufous; hairs grey at base, blackish-brown at tip. Flanks paler, grey-brown. Ventral pelage grey; hairs grey sometimes with white tips. Ears relatively short (ca. 44% of GLS) with many small darkish hairs. Muzzle blunt. Fore- and hindlimbs similar in colour to ventral pelage; fore- and hindfeet with sparse white hairs above, naked and fleshy below. Tail thick at base, relatively long (ca. 90% of HB), mostly naked with scattered short bristles; brownish above, whitish below. Skull: supraorbital and temporal ridges well-defined; curve strongly outwards from interorbital constriction and then run parallel along edge of braincase. Nipples: usually $3 + 3 = 12$.

Geographic Variation None recorded in Africa.

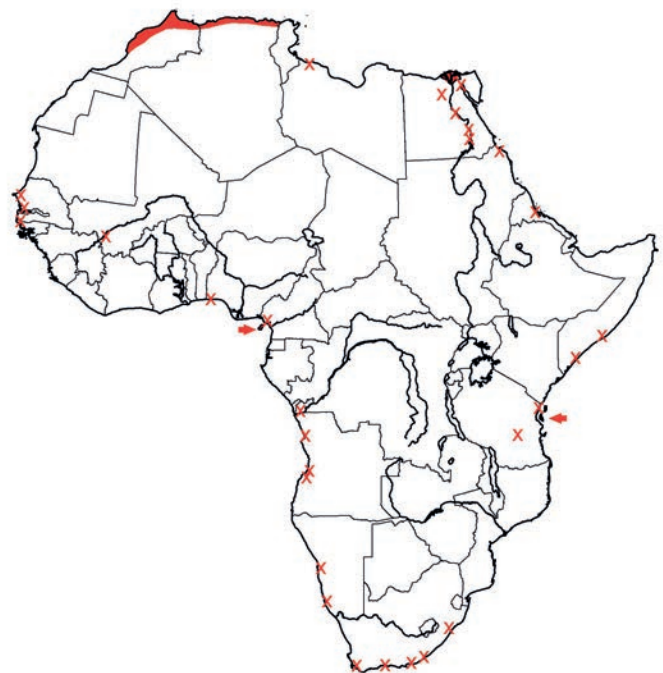
Similar Species

R. rattus. On average smaller; tail longer than HB; HF less than ca.

geographic distribution on the continent, *R. norvegicus* more so than *R. rattus*. Neither species has invaded natural ecosystems to any significant extent: *R. norvegicus* is restricted to coastal ports and *R. rattus* has invaded the interior but is mostly confined to human habitations and some farmlands. Importantly, both species are pests of stored food (as are some indigenous species, notably *Mastomys* spp.) and are reservoir hosts of some human diseases (see species profiles).

The number of species in the genus was larger in the past than now. After the definition of the genus by Fischer, most 'rats' were placed in the genus *Rattus*. In 1915, Thomas reduced the number of species, by placing various 'Rattus-like' species in subgenera, which, in 1926, were raised to generic rank. These generic ranks are maintained to the present time (although Ellerman [1940] lumped them all in *Rattus* again) and include, *inter alia*, the African genera *Aethomys*, *Stochomys*, *Praomys*, *Hylomyscus* and *Mastomys* (see Misonne 1969a, De Graaff 1981). A full discussion of the genus is given in Musser & Carleton (2005).

The two African species are distinguished by body size and shape, length of hindfoot, relative size of ears, and shape of the supraorbital ridges.



Rattus norvegicus

35 mm; ears naked, ca. 59% of GLS; more widespread in Africa. *Nesokia indica*. Smaller with much shorter tail; skull robust with laminate molars; Egypt only.

Distribution Introduced to Africa by ships to seaports on the coast, and recorded only at major ports, and at some localities on the Nile R. in Egypt. Unlike other introduced small rodents in Africa (e.g. *R. rattus* and *Mus musculus*), has not normally dispersed away from the coastal towns and cities of Africa south of the Sahara. Unknown in Morocco, except in coastal ports, prior to 1910; since 1910 has spread throughout N Morocco (Aulagnier & Thévenot 1986). Recorded from Bamako (on the Niger R. in Mali) (Meinig 2000). Outside Africa, occurs in all continents (except Antarctica) and on many islands.

Habitat Houses and human habitations; drains, rubbish tips and sewers. Requires permanent water, and may live in swampy ground and in drainage banks. Commensal with humans.

Abundance Little information for Africa. In suitable habitats (outside Africa) may be very numerous because of high reproductive rate (see below). In Lagos, Nigeria, during 1931–34, Brown Rats comprised only 5% of the population of Black Rats and Brown Rats.

Adaptations On a worldwide basis, Brown Rats are very successful because of commensalism, high reproductive rate, omnivorous diet and fearless nature. Well adapted to colonize cold climates – a character that partly explains why they have not been successful colonists in Africa. Nocturnal and terrestrial; scansorial (but less so than Black Rats). They are bold and aggressive, bite if handled; and tend to be more wary of humans than Black Rats. They can chew wood and other materials with their large incisor teeth in order to gain access to new habitats. Individuals living on irrigation banks (e.g. in Egypt) dig shallow burrows and are good swimmers. Brown Rats have not been studied extensively in Africa because of their limited distribution and importance, although they (and the diseases they transit) have been well studied in temperate countries (see, e.g. Macdonald *et al.* 1999).

Foraging and Food Omnivorous, feeding on almost anything that is edible, including human food and stored crops.

Social and Reproductive Behaviour Gregarious. Brown Rats often form multimale, multifemale groups, which may defend a clan territory, especially where resources are abundant. Social organization within a group determines many aspects of behaviour and survival. Larger, dominant individuals (i.e. those with high social status) are the most successful members of a group. Social dominance confers great advantages: access to food, higher reproductive success and reduced susceptibility to adverse conditions. Social pressures determine which individuals remain and which leave the group. Young subordinate ♂♂ are usually forced to emigrate to less favourable habitats. Reproductive behaviour is complex: a dominant ♂ does not

necessarily have the highest reproductive success because ♀♀ mate with several ♂♂ while in oestrus, and ♀♀ exercise mate choice. Olfaction is a very well-developed sense, and the various odours produced by individuals convey important signals to other members of the group (Macdonald *et al.* 1999, and references therein).

Reproduction and Population Structure Little information is available on reproduction in Africa. In Lagos, pregnancies occurred throughout year, pregnancy rate varying from 7 to 8% of ♀♀ in the dry season (Dec–Apr) to 8–15% in the wet season (May–Nov) (Buxton 1936). Brown Rats breed prolifically, and ♀♀ may produce several litters in a breeding season; hence populations can increase rapidly when conditions are optimal. Typical reproductive data: gestation: 21–24 days; litter-size 6–12; young born naked and blind; eyes open Day 6, weaned at Day 21; maturity in ♀♀ at about 11 weeks (Corbet & Southern 1977). Because of large litter-size and prolonged breeding season, populations usually consist mostly of young and subadult animals.

Predators, Parasites and Diseases Like Black Rats, Brown Rats are pests because of their unsanitary habits and because they harbour parasites that transmit diseases to humans (including plague). Many species of fleas and mites have been recorded from wild-living rats (De Graaff 1981). *Xenopsylla cheopis* was the commonest species of flea (of four species) found on Brown Rats in Egypt (Hoogstraal & Traub 1965b).

Conservation IUCN Category: Least Concern.

Control of Brown Rats is essential to reduce the damage they cause to buildings and food supplies, and to minimize the spread of disease.

Measurements

Rattus norvegicus

HB: 219.9 (196–254) mm, n = 13

T: 196.0 (145–234) mm, n = 13

HF: 43.4 (40–51) mm, n = 13

E: 20.8 (20–23) mm, n = 13

WT: 259.3 (208–360) g, n = 4

GLS: 46.8 (43.2–52.2) mm, n = 12

GWS: 23.2 (20.9–26.9) mm, n = 7

M¹–M³: 7.4 (6.8–7.8) mm, n = 12

Egypt (Osborn & Helmy 1980)

Key References (Africa only) Buxton 1936; De Graaff 1981; Osborn & Helmy 1980.

D. C. D. Happold

Rattus rattus BLACK RAT

Fr. Rat noir; Ger. Hausratte

Rattus rattus (Linnaeus, 1758). Syst. Nat., 10th edn., 1: 61. Uppsala, Sweden.

Taxonomy Originally described in the genus *Mus*. The widespread distribution and large variation in colour has resulted in many taxonomic names being applied to this species. Most of these names

are now considered to be synonyms, although some are used to describe the clearly recognizable colour forms. Musser & Carleton (2005) list 84 synonyms worldwide. In Africa, there are three colour

forms (see Geographic Variation), which, in the past, have sometimes (incorrectly) been referred to as subspecies. More than one form may occur at a single locality, and sometimes a single litter may contain more than one colour form (Rosevear 1969). Nevertheless, a specified locality normally contains only one colour form. Synonyms: see details in Musser & Carleton (2005). Subspecies: none. Chromosome number: $2n = 38$, $FN = 58$ (Niger; Dobigny *et al.* 2002b). The same chromosome number has been recorded in Black Rats from Benin (Capanna *et al.* 1997), Senegal, South Africa and Djibouti (Capanna & Civitelli 1971).

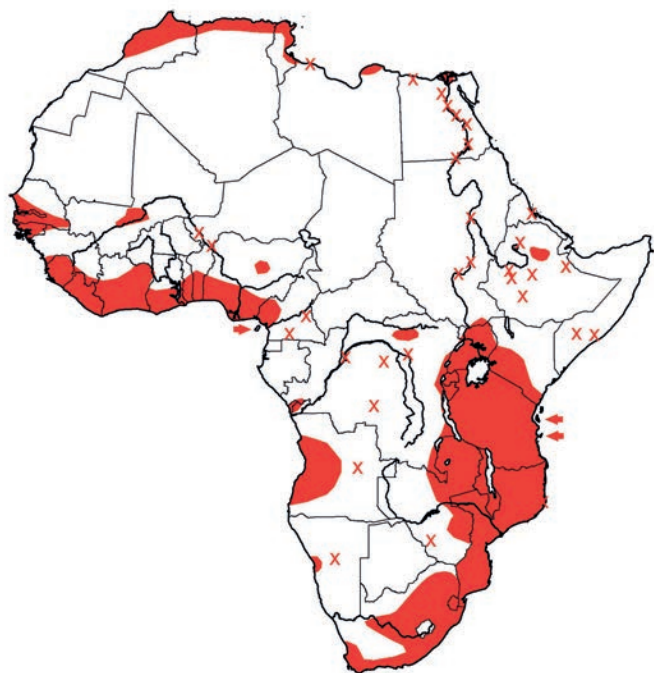
Description Large rat, with blackish-brown dorsal pelage and long scaly naked tail. Pelage coarse and dense, sleek, lying close to body. Dorsal pelage dark brown or blackish-brown, usually darker along mid-dorsal line; hairs medium grey at base, with pale brown, dark brown or black tip. Many long dark guard hairs scattered throughout dorsal pelage. Ventral pelage varied, either pale to dark brown, or lemon-yellow, or white. Individuals with brown ventral pelage may have white patches on chest and throat. Ears naked; ca. 59% of GLS. Fore- and hindlimbs dark greyish-brown. Well-developed digits, upper surfaces with greyish-brown hairs. Forefoot with four digits; hindfoot with five digits. Tail very long (ca. 120% of HB), thin, with scales arranged in rings along length of tail and many short dark bristles. Skull: supraorbital and temporal ridges well defined; curve strongly outwards from interorbital and then curve inwards along edge of braincase. Nipples: $3 + 2 = 10$, $3 + 3 = 12$.

Geographic Variation Three colour forms are known in Africa:

frugivorous: ventral pelage white or lemon-yellow; dorsal pelage pale brown or reddish-brown.

alexandrinus: ventral pelage grey-brown; dorsal pelage grey-brown or medium-brown.

rattus: ventral pelage pale brown or dark brown; dorsal pelage blackish or dark brown.



Rattus rattus

Similar Species

R. norvegicus. On average larger; ears with short hairs, ca. 44% of GLS; HF > 35 mm; tail shorter than HB; restricted to coastal districts.

Mastomys spp. Smaller; pelage soft; ♀♀ with continuous rows of nipples (up to a total of 24 nipples).

Distribution Introduced to sub-Saharan Africa by Arab and European ships, and subsequent dispersal within Africa mainly by river, rail and road transport. Recorded in many biotic zones (see map). Occurs mainly in moister habitats, although some populations live in arid habitats where there is permanent water (e.g. upper reaches of the Niger R. and lower reaches of the Nile R.). More widespread in savanna habitats of eastern Africa than in western Africa. Fairly widespread in temperate habitats of North Africa and southern Africa (but see Habitats). Outside Africa, occurs in all continents (except Antarctica) and on many islands.

The dispersal of Black Rats is well documented in parts of Africa. In Senegal, for example, Black Rats were present in towns along the Senegal R. during nineteenth century when the river was the only trade route to Mali. They colonized the centre of Senegal from Dakar eastwards during the building of the railway to Mali and hence are now present in Bamako (Duplantier *et al.* 1991). At the end of the twentieth century, they invaded SE Senegal along the tarmac road through the Niokolo-Koba N. P. (Bâ 2002). In East Africa, Black Rats may have been present on the coast for many centuries, arriving in sailing ships and dhows, and then travelling along caravan routes to the interior (Dieterlen 1979b). They were recorded from Mombasa and Dar-es-Salaam in 1895; the building of railway lines and roads enabled Black Rats to colonize the interior of East Africa: they were first recorded in Tabora in 1895, Kisumu in 1901 and Kampala in 1911 (Misonne 1963, Delany & Happold 1979, Dieterlen 1979b). Some individuals probably crossed L. Victoria by boat, since they were recorded in W Uganda (at Katwe) in 1906–09. Later, during the late 1930s, they spread throughout most of W Uganda and in the early 1950s reached E DR Congo (Misonne 1963). In some parts of Tanzania, dispersal from Dar-es-Salaam was slower, and Black Rats did not reach Serengeti (at Seronera) until 1976 (Senzota 1982). The pattern of dispersal has been similar in all parts of Africa: arrival at a port and subsequent transportation to locations where there are human habitations. Undoubtedly, the distribution of Black Rats is still expanding, and their numbers are increasing. Of the three introduced species of small rodents in Africa, *R. rattus* has colonized the continent to a much greater extent than *Mus musculus* and *R. norvegicus*.

Habitat Houses, food stores and warehouses in cities, towns and villages; abandoned farmland and close to streams in urban areas. Commensal with humans. Rarely found in natural habitats.

Abundance In preferred habitats, Black Rats may be very common, although population numbers may vary greatly between years and between seasons.

Adaptations Nocturnal and diurnal, terrestrial and scansorial. Black Rats are agile climbers, and frequently live in roofs of houses, under wooden floors, and high up in multi-storey buildings. Their boldness, lack of fear of humans and ability to eat many sorts of foods (see below) allow them to live in close association with humans

where they may cause damage to buildings and food stores. These characters, coupled with their high reproductive rate, result in rapid increases in population numbers when conditions are suitable, and increase their impact as a pest species. Although they may be rarely seen, their presence is indicated by their large faecal pellets and by stains along runways (produced by urine and secretions from skin glands).

Black Rats rarely invade natural habitats in Africa (although they may occur in abandoned farmlands close to urban settlements), hence they do not compete or displace indigenous species of rodents in natural habitats. However, because of their larger size and competitive supremacy, Black Rats have displaced *Mastomys natalensis* (and other *Mastomys* spp.) as the major rat pest in houses in Uganda and E DR Congo (Misonne 1963).

Foraging and Food Omnivorous, feeding on almost anything that is edible, including many foods stored for human consumption (e.g. wheat, maize, millet, etc.).

Social and Reproductive Behaviour Sociable and gregarious. In a wild-living population in Ghana (Ewer 1971) there was a single dominant ♂, and at times a linear male hierarchy was formed. Usually 2–3 mutually tolerant top-ranking ♀♀ were subordinate to the dominant ♂. A group territory was established around a feeding location, and was defended against non-members of the group. Both sexes chased non-members away, but non-member ♀♀ were mainly chased by the resident ♀♀. Territorial boundaries were marked by rubbing secretions from the cheeks and ventral surface onto branches and other objects. Black Rats exhibit well-documented behaviour: tooth gnashing (response to unfamiliar stimuli), piloerection and posturing with stretched legs (threat signals), vibrations of the tail (a sign of defeat or frustration) and social grooming (bonding between individuals). Black Rats are good at 'problem-solving'; once a solution has been found, it is remembered and subsequently perfected. Rats also appear to learn by imitating the behaviour of other members of the group. Lactating ♀♀ show aggression when other members approached the nest. Play is an important pastime for young animals (Ewer 1971).

Reproduction and Population Structure Very prolific. When conditions are suitable (as in human habitations where food and water are available at all times), breeding occurs throughout the year, e.g. in Uganda (Delany 1975), Zimbabwe (Smithers 1975) and Nigeria (Buxton 1936). Although reproduction within a population may be continuous, in Uganda only 37% of all females were pregnant at any one time (Delany 1975). In Lagos and Dakar, pregnancies occurred in all months, pregnancy rates varying from 11 to 13% of females in the dry season to 13–14% in the wet season in Lagos, and up to 38% in the wet season in Dakar (Buxton 1936). Continuous reproduction, large litter-size and rapid development can result in rapid increases in population numbers within a short period of time; hence populations are very responsive to changing environmental conditions. Gestation for primiparous ♀♀: ca. 21 days; for lactating ♀♀: 23–29 days (Ewer 1971). Postpartum oestrus usually within 24 hours of parturition. Mean litter-size: 6 (n = 55, mode 6 or 7)

(Uganda; Delany 1975). Typical range of litter-size: 5–10. Growth and development is rapid – fine fur all over body by Day 8, eyes open Day 10–14; solid food eaten Day 15–18, weaned Day 30; sexual maturity Day 100–120. Females may have many litters per year (often one litter/month).

Predators, Parasites and Diseases Black Rats occur primarily in urban areas, and hence the only predators are those mammalian carnivores, raptors and snakes that also occur in urban environments (e.g. domestic cats and dogs, Barn Owls, etc.). In Egypt, *Xenopsylla cheopis*, *Synosternus cleopatrae* and *Echidnophaga gallinacea* were found frequently on Black Rats; and almost any species of flea occurring in towns and gardens may parasitize these rats (Hoogstraal & Traub 1965b). Black Rats also carry many species of mites, ticks and parasitic worms (De Graaff 1981). One species of flea, *Xenopsylla cheopis*, is of particular concern to humans because it transmits a bacterium *Yersinia pestis* that causes the disease called plague or 'Black Death', which is usually fatal in humans. Black Rats also die very quickly from plague, so fleas living on them have to find another host, which in urban environments is usually a human. When Black Rats and humans are living in close association, it is difficult to break the cycle of transmission from rat to human, and human to rat. Plague was very common in Europe during the Middle Ages and caused severe epidemics that killed many thousands of humans. In more recent times (1993, 1994), Black Rats have been responsible for outbreaks of plague in some harbours and large towns in Mozambique, Tanzania, DR Congo and Zimbabwe (Gratz 1997). There is always the chance of future outbreaks wherever there are large populations of humans and Black Rats living together in unsanitary conditions. (Some species of indigenous rodents [*Mastomys* spp., *Tatera* (now *Gerbilliscus*) spp.] are also known to be reservoirs of the bacterium and so they form natural foci of the disease in Africa). Black Rats are the main reservoir of murine typhus in Africa (Gratz 1997) and of leptospirosis in Zimbabwe (Dalu & Feresu 1997).

Conservation IUCN Category: Least Concern.

Control of Black Rats is essential to reduce the damage they cause to buildings and food supplies, and to minimize the spread of disease.

Measurements

Rattus rattus

HB: 165.3 (133–180) mm, n = 12

T: 195.6 (180–209) mm, n = 11

HF: 31.7 (25–34) mm, n = 12

E: 23.1 (22–26) mm, n = 12

WT: 132 (100–186) g, n = 12

GLS: 39.3 (36.9–41.4) mm, n = 6

GWS: 19.0 (18.3–19.6) mm, n = 6

M¹–M³: 6.3 (6.2–6.4) mm, n = 6

Irangi, Kivu Province, DR Congo (ZFMK)

Key References (Africa only) Buxton 1936; Dieterlen 1979b; Ewer 1971.

D. C. D. Happold

GENUS *Rhabdomys*

Four-striped Grass Mouse

Rhabdomys Thomas, 1916. Ann. Mag. Nat. Hist., ser. 8, 18: 69. Type species: *Mus pumilio* Sparrman, 1784.



Rhabdomys pumilio.

A monotypic genus of small mice distributed throughout southern Africa and the eastern side of the continent as far north as Uganda. In East Africa, the genus is restricted to higher altitudes, but in southern Africa it is widely distributed from near sea level to 1800–2200 m. These mice live in many types of grassland, bush and woodland habitats in dry, wet, hot and cold environments. The single species is widespread and common in the southern part of its range, but less common with a very disjunct distribution in the north of its range.

The genus is characterized by the unique pattern of lateral stripes on the dorsal pelage and flanks (cf. *Lemniscomys*, *Pelomys* and *Hybomys*). The skull has ungrooved incisors, well-developed supraorbital ridges, cheekteeth with well-developed cone-like cusps, and the zygomatic plate has an almost vertical anterior face. The surface of the skull and the inner surface of the skin are often black or darkened due to deposits of melanin, as in *Lemniscomys* (see species profile for further details) (Figure 84).

Hill & Carter (1941) recognized two species in Angola on the basis of colour and size of the auditory bullae: *R. pumilio* (central and southern regions) is smaller and darker, with well-developed stripes and small auditory bullae; *R. bechuanae* (arid regions) is larger and very pale, with indistinct stripes and larger auditory bullae. Currently only one species is recognized. Variability in pelage colouration has resulted in the description of many subspecies, most of dubious validity. The phylogenetic relationship and taxonomic status of the many isolated populations in eastern Africa await investigation.

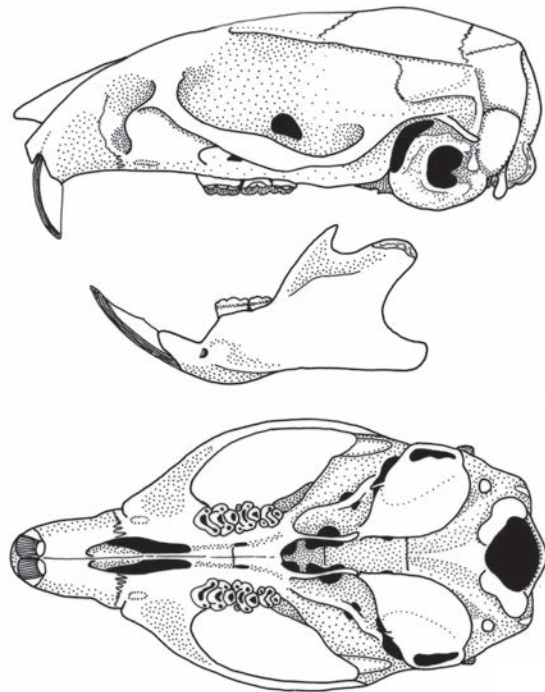


Figure 84. Skull and mandible of *Rhabdomys pumilio* (HC 2738).

Morphological characters place *Rhabdomys* in a group with *Arvicanthis*, *Lemniscomys*, *Myiomys* and *Pelomys*. Analysis of mitochondrial DNA, cytochrome *b* and rRNA sequences support such a grouping, but also show that *Rhabdomys* is in the same lineage as *Desmomys*, and separate from the lineage containing *Lemniscomys* (despite the somewhat similar pattern of longitudinal stripes on the pelage) and from the lineage containing *Arvicanthis*, *Myiomys* and *Pelomys* (Ducroz *et al.* 2001, Musser & Carleton 2005). Based on the sequence of mtDNA of cytochrome *b*, Rambau *et al.* (2003) suggest the existence of two species in southern Africa: *R. pumilio* representing the western form in arid habitats, and *R. dilectus* (= *R. dilectus* [de Winton 1897]) representing an eastern and northern form inhabiting more mesic habitats. Musser & Carleton (2005) recognize both *R. pumilio* and *R. dilectus* as valid species, giving the range of *R. pumilio* as restricted to 'xeric grasslands and savannas from W South Africa north through Namibia and C and S Botswana to SW Angola'. Thus populations from Uganda and Kenya southwards to E Zimbabwe and E South Africa are considered as *R. dilectus*. The biological information given below may, therefore, refer to either one or both species. Further study is required to ascertain the number of species in this genus.

D. C. D. Happold

Rhabdomys pumilio FOUR-STRIPED GRASS MOUSE

Fr. Rat rayé champêtre; Ger. Vierstreifengrasmaus (Striengrasmaus)

Rhabdomys pumilio (Sparrman, 1784). K. Svenska Vet.-Akad. Handl. Stockholm, p. 236. Slangrivier, Tsitsikamma Forest, east of Knysna, S Western Cape Province, South Africa.

Taxonomy Originally described in the genus *Mus*. Historically placed in either the genus *Mus* or the genus *Arvicanthis*. Meester *et al.* (1964) suggested that at most two subspecies, a darker eastern and a paler western, can be recognized in southern Africa. However, there is a complex pattern of geographic variation involved, in which more subspecies may well be distinguishable. Meester *et al.* (1986), broadly following Ellerman *et al.* (1953), provisionally listed seven subspecies in southern Africa. Many names have been associated with the species, but the status of subspecies is uncertain, and none is recognized here (but see also below). A revision of the species by Rambau *et al.* (2003) using mtDNA shows that there are two highly divergent clades within the species. One clade (named as *R. pumilio*) represents populations with $2n = 46$, which occur throughout the western more arid range of the species (Namibia, W South Africa). The second clade, named as *R. dilectus*, represents populations with $2n = 46$ or 48 and occurs in the eastern and northern more mesic parts of the range. This second clade is comprised of two subgroups, which can be considered as subspecies: *R. d. dilectus* ($2n = 46$) from the northern parts of the range (Uganda [Mt Elgon], Malawi [Nyika Plateau, Mt Mlanje], Zimbabwe [Inyanga Highlands] and N South Africa [three known localities centred on Limpopo Province]) and *R. d. chakae* ($2n = 48$) from NE and SE South Africa. The two 'subspecies' appear to be parapatric in N South Africa, but presumably not syntopic. Information is not available for the many isolated populations in East Africa (see Distribution). Synonyms: 27 (details in Musser & Carleton 2005). Subspecies: uncertain (see comments above). Chromosome number: $2n = 46$ or 48 .

Description Small mouse with black and cream lateral stripes. Dorsal pelage harsh, yellowish-brown to speckled buff (see also Geographic Variation); hairs black at base, yellowish-brown at tip; numerous thick black guard hairs darken dorsal pelage. No black mid-dorsal stripe (cf. *Lemniscomys*). Whitish or cream lateral stripe, one on either side of mid-dorsal line, from behind ears to base of tail, each bordered by a black or brown lateral stripe above and below (hence four black stripes). Ventral pelage paler than dorsal pelage, without black guard hairs. Head similar in colour to dorsal pelage, with a longitudinal median black stripe from between eyes to between ears. Ears well covered with short reddish-brown or orange hairs. Chin, throat and abdomen paler than head, or off-white; bases of hairs dark grey. Fore- and hindfeet paler than dorsal pelage, soles of hindfoot darkly pigmented. Tail comparatively short (ca. 80% of HB; see also below) with sparse short hairs, black above, yellowish-brown or grey below. Nipples: $2 + 2 = 8$.

Geographic Variation Pelage colour and tail length vary geographically. In southern Africa, individuals from eastern areas are dark grizzled greyish-buff, with black lateral stripes; those from the western (drier) areas are whitish-grey with reddish-brown lateral stripes. In parts of Botswana, dorsal pelage pale yellowish-

buff, lateral stripes brown. One melanistic specimen recorded from Molopolo, Botswana (specimen in TM). Mean head and body length, and tail, vary according to locality and climate; e.g. Zimbabwe: HB: 100 mm, T: 85 mm; Botswana: HB: 105 mm, T: 106 mm (Smithers 1983); Mt Elgon: HB: 107–112 mm, T: 78–80 mm (Clausnitzer 2003). Variation in size is positively correlated with mean minimum temperature of the coldest month (Yom-Tov 1993). Where *Rhabdomys pumilio* is parapatric with *Lemniscomys* spp. (also a diurnal herbivore but often larger in size), individuals are significantly smaller than those from regions where *Lemniscomys* does not occur. Possibly two subspecies (see Taxonomy above).

Similar Species

Lemniscomys spp. Black mid-dorsal stripe; many pale-coloured lateral stripes (sometimes continuous, sometimes broken into spots) on flanks in most species.

Distribution Endemic to Africa. Widespread in South-West Arid, South-West Cape and Highland BZs, SW Zambezan Woodland BZ, and in Afromontane–Afroalpine BZ, from southern Africa to eastern Africa. Recorded extensively in South Africa and Namibia. Patchy and discontinuous in Swaziland, S Mozambique, E Zimbabwe, C and S Angola, S Botswana, Zambia (Nyika Plateau), Malawi (Mt Mlanje, Nyika Plateau), SE DR Congo, Tanzania (highland areas including Mt Kilimanjaro, Livingstone Mts, Uzungwa Mts, Mt Rungwe, Poroto Mts and Ngorongoro crater rim), Kenya (Mt Kenya and central highlands) and Uganda (Mt Elgon). Recorded from close to sea level



Rhabdomys pumilio

in South Africa, to 3500–4200 m on Mt Elgon and ca. 4000 m on Mt Kenya. Occurs over a range of rainfall regimes from <100 mm/year in Namibia, to >1200 mm/year in E Zimbabwe and W Mozambique, and to ca. 3000 mm/year on Mt Mlanje (Malawi). (See also genus profile.)

Habitat In southern Africa, recorded from bush and savanna habitats, dry river beds, high grassveld, karoo, succulent karoo, forest and woodland ecotones, edges of agricultural lands, and montane grasslands up to 2700 m. Confined to montane grasslands and swamps, and afroalpine habitats, in northern part of geographic range (e.g. in Malawi [Happold & Happold 1989b] and Mt Elgon, Uganda [Clausnitzer 2001]).

Abundance Widespread and fairly common species in southern Africa, and often the most numerous species of small mammal (rodents and shrews), e.g. ca. 40–70% in grasslands and shrublands at 1500–1700 m in the Drakensburg Mts, South Africa (Rowe-Rowe & Meester 1982a), and by far the most numerous species in river bed, dune and plateau habitats in Namibia (Nel 1978). In high altitude grasslands of Malawi, *Rhabdomys* was the most numerous species of small rodent (47%, $n = 45$; 5 spp.) on the Nyika Plateau, and the third most abundant species (22%, $n = 46$; 6 spp.) on Mt Mlanje (Happold & Happold 1989b). Density also varies greatly by locality and season: 9–13/ha (Nyika Plateau, Malawi), 2–8/ha (Mt Mlanje, Malawi), up to 10/ha (Mt Elgon, Uganda), up to 14/ha (Mt Kilimanjaro, Tanzania) and 6–34/ha (Kenya) (Delany & Roberts 1978, Happold & Happold 1989b, Shore & Garbett 1991, Clausnitzer 2003). In some habitats densities may be even greater, especially when (temporarily) there are many juveniles in the population (e.g. 37–171/ha in succulent karoo, South Africa; Schradin & Pillay 2005b). Biomass in Eastern Cape Province, South Africa, fluctuates greatly within and between years by several orders of magnitude (e.g. 0.1–1.0 kg/ha; Perrin 1980b).

Adaptations Terrestrial and scansorial. Diurnal and crepuscular. Constructs shallow burrows in some areas, usually not deeper than ca. 50 cm), with the entrance hidden under vegetation. Runways radiate from the burrow entrance, and are usually well hidden under grass cover. Nests are built in burrows, clumps of grass or amongst low-growing bushes. In contrast, in the Kalahari (Nel 1978), grasslands (Choate 1971) and succulent karoo of South Africa, nests are typically above ground and burrows are not constructed (Schradin & Pillay 2004). In the southern Kalahari and Namib deserts, and the succulent karoo, these mice climb in low bushes (for foraging), a habitat not utilized by other syntopic small mammals (Nel 1978). The large geographic range, from hot semi-arid grasslands to damp cold sub-alpine moorlands, indicates very wide habitat tolerance. Diurnal activity and acclimation to cold regulate heat production and body temperature (Haim & Fourie 1980). Body fat fluctuates irregularly during the year, mostly in response to ingestion of nutritious foods and/or seasonal change. Insects provide additional fat and proteins during the breeding season (Perrin 1980a, b).

Foraging and Food Opportunistic omnivore. Individuals in semi-arid succulent karoo habitats forage alone (Schradin & Pillay 2004). Diet varies seasonally (Perrin 1980a, Churchfield 1985) and is predominantly granivorous in many areas (Brooks 1974, Rowe-Rowe & Meester 1982b, Kerley 1989). Percentage composition of

the diet, in terms of green plant material, seeds and insects, varies temporally; for example, in Eastern Cape Province, South Africa, the diet in mid-summer (Jan–Feb) was 83% insects, 2% seeds, 0% fruits, 7% leaves and 9% stems; in mid-winter (Jun–Jul) it was 0% insects, 19% seeds, 49% fruits, 4% leaves and 27% stems (Perrin 1980a). Similar changes in diet are recorded in other localities (Rowe-Rowe 1986). Also eats fruits of *Ziziphus mucronata* (buffalo thorn), *Grewia* spp. (raisin bush) and the pods of *Acacia* spp. in Botswana (Smithers 1971). In some localities, feeds on the succulent bracts of low-growing *Protea* flowers, and probably assists in pollination (Rourke & Wiens 1977). Snails and worms are eaten occasionally. In the succulent karoo, feeds on leaves and fruits from shrubs (*Zygophyllum retrofractum*), wildflowers (during spring) and succulents. At some times of the year, especially in winter, diet includes roots and bark of trees in commercial *Pinus patula* plantations, causing considerable damage (Taylor & Perrin 1996). The periods of the year when insects form a large proportion of the diet are correlated with the highest rates of pregnancy (Perrin 1980a, b).

Social and Reproductive Behaviour Social behaviour varies according to habitat and population density. In non-arid habitats of South Africa, individuals are solitary and territorial (Willan 1982) and levels of aggression are not density-dependent (Ercoli 1994). Adult ♂♂ are more aggressive and less amicable than adult ♀♀ (Perrin *et al.* 2001). Adults, particularly ♀♀, are inhibited from attacking juveniles and subadults owing to kin-selection. They are less aggressive to kin than to unknown individuals within a population (Perrin *et al.* 2001).

In semi-succulent Karoo, individuals live in communal groups, typically comprised of one adult breeding ♂, four adult breeding ♀♀ and 5–28 non-breeding adults (progeny of the breeding ♀♀). Each group lives in a large surface grass nest within a bush (typically *Zygophyllum retrofractum*). Interactions between members of the group are mostly amicable; for example sitting in bodily contact, sniffing at each other and allogrooming. Territorial behaviour (chasing and fighting) is exhibited by all group members. Territorial aggression is greatest in front of the group nest and lower at territory boundaries. Males are more aggressive towards ♂♂ of other groups than towards ♀♀ of other groups. Females are aggressive towards strangers of both sexes. Behavioural characters of *Rhabdomys pumilio* suggest it is a 'territorial group-living solitary forager' (Schradin 2004). Under conditions of extreme low population density in the succulent karoo (as during the exceptional drought of winter 2003), the social system changes from a social to a solitary life-style (as typically exhibited by conspecifics living in grasslands), but reverts to group living with increasing population density (C. Schradin & N. Pillay unpubl.). This species is a good example of the way in which social behaviour varies with the environment (in particular with food abundance, availability of suitable nesting sites and the possibility of sun-basking): individuals living in arid habitats form territorial groups (up to 30 adult mice) but forage alone, whereas individuals living in mesic environments are solitary, and have exclusive territories although the territory of a ♂ overlaps the territories of several ♀♀ (Schradin 2005).

Rhabdomys pumilio exhibits paternal care of the young. In group-living individuals from the succulent Karoo, ♂♂ participate in looking after the young (huddling, retrieving, grooming) in a similar way to ♀♀ (Schradin & Pillay 2003). There is some evidence for

allonursing (a ♀ suckling young other than her own) (Schradin & Pillay 2004).

In group-living populations of the succulent karoo, individuals of one group have largely overlapping home-ranges, and the home-range areas for each sex are not statistically different (Schradin & Pillay 2004). Radio-tracking revealed a home-range size of $1305 \pm 225 \text{ m}^2$ for ♂♂ and $912 \pm 93 \text{ m}^2$ for females. In grasslands of KwaZulu–Natal, home-ranges are much larger, and ♂♂ ($12,466 \pm 2000 \text{ m}^2$) have significantly larger home-ranges than ♀♀ ($5760 \pm 1098 \text{ m}^2$; Schradin & Pillay 2005a).

Reproduction and Population Structure In South Africa, reproduction is seasonal and occurs in summer after rainfall and when nutritious food (especially insects) is available; reproduction is inhibited in winter and is associated with a low protein vegetarian diet, little rainfall and cool temperatures (Brooks 1974, Smithers & Wilson 1979, Perrin 1980b, Henschel *et al.* 1982). In the succulent karoo (with winter rain), reproduction occurs during three months in spring (mid-Aug to mid-Nov) after winter rains, but not during the dry summer (Schradin & Pillay 2005b). Reproduction in Zimbabwe is also seasonal (Smithers & Wilson 1979). Embryo number: 4.91 ± 1.73 ($n = 21$; South Africa; Perrin 1980b); 6.5 (3–10, $n = 42$ litters in captivity; Brooks 1982); 4.7 (3–6, $n = 6$; Zimbabwe; Smithers & Wilson 1979); 4.5 (3–7, $n = 22$; South Africa – Drakensberg Mts; Rowe-Rowe & Meester 1982b); 6.1 (1–11, $n = 24$; South Africa – KwaZulu–Natal; Taylor 1998); 3.6 (3–4, $n = 5$; Uganda – Mt Elgon; Clausnitzer 2003). Litter-size can be reduced to two young under conditions of low food availability, such as in the Namib Desert (Krug 2002) or in the succulent karoo after extreme drought (C. Schradin & N. Pillay unpubl.). Average gestation: 25 days (Brooks 1974). Females have a postpartum oestrus (Choate 1971). At birth, young are altricial and weigh 2.5 g. Eyes open Day 7–8. Weaned Day 16. Sexual maturity ca. 2 months (Brooks 1974). Young do not nipple-cling. *Rhabdomys pumilio* is considered to be a comparatively r-selected species (Perrin 1980b).

Population structure fluctuates on an annual basis. In Eastern Cape Province, South Africa, during summer and early winter (Jan–Jun), the population (as indicated by tooth wear and eye-lens weight) is composed of juveniles and older breeding adults. In late summer and early winter (Jul–Oct), younger animals form the majority of the population because of the high mortality of older animals. Prior to reproduction in spring (Nov–Dec), population is composed of the young of the previous year (now ca. 8–11 months) and no juveniles (Perrin 1979). Population numbers fluctuate greatly during the year

(see above). In the succulent karoo, reproduction occurs in spring by individuals born the previous spring. Juveniles first appear in Sep (16% of the population) and comprise ca. 50% of the population in Oct (when population densities are highest – see above) and ca. 10% in Dec when the breeding season has terminated (Schradin & Pillay 2005b). Mice lose 12% of body weight during the dry summer, and mortality is highest during the following cold and wet winter. However, the annual mortality of ca. 80% is lower than in grasslands (ca. 93%). No information available on reproduction and population structure in other parts of the geographic range.

Predators, Parasites and Diseases Many predators have been recorded, including several species of snakes, several species of owls and diurnal raptors, servals, wildcats, jackals, genets and mongooses. In some areas, this species is also eaten by humans, e.g. in KwaZulu–Natal (South Africa) and Mozambique. Many ectoparasites have been recorded, including mites, chiggers, fleas (41 spp.; Zumpt 1961, 1966) and ticks (11 spp.; Theiler 1962). Endoparasites include nine species of tapeworms and six species of round worms. Full lists of parasites are given in De Graaff (1981).

Conservation IUCN Category: Least Concern.

This common and abundant species is not threatened in the southern part of its range. However, the small populations on isolated mountains in East Africa require adequate conservation.

Measurements

Rhabdomys pumilio

HB: 109 (99–124) mm, $n = 45$

T: 86 (71–101) mm, $n = 43$

HF: 21 (19–24) mm, $n = 45$

E: 13 (11–15) mm, $n = 42$

WT: 43.1 (41–53) g, $n = 22$

GLS: 28.2 (27.1–29.4) mm, $n = 10$

GWS: 14.1 (13.3–15.1) mm, $n = 10$

M¹–M³: 4.5 (4.3–4.6) mm, $n = 10$

Body measurements and weight: South Africa (De Graaff 1981)

Skull measurements: KwaZulu–Natal, South Africa (TM)

Key References De Graaff 1981; Haim & Fourie 1980; Perrin 1980a, b; Perrin *et al.* 2001; Schradin & Pillay 2004, 2005a, b; Smithers 1983.

D. C. D. Happold

GENUS *Stenocephalemys*

Ethiopian Rats

Stenocephalemys Frick, 1914. Ann. Carnegie Mus., 9: 7. Type species: *Stenocephalemys albocaudata* Frick, 1914.

The genus *Stenocephalemys* is endemic to Ethiopia, mostly in the Afromontane–Afroalpine BZ, and contains four species (Table 40); two species live in high altitude grassland and moorlands (2400–4400 m) and two live in bush and forest habitats at lower altitudes (1500–3000 m).

Species in this genus are medium to large rats with long tails (ca. 86–123% of HB). Skull with curved braincase (when viewed laterally), well-developed zygomatic plate, thick wide zygoma, anterior palatal foramina reach to mid-line of M¹, orthodont incisors without groove, relatively large molar toothrow, and narrow interorbital constriction

Table 40. Species in the genus *Stenocephalemys*. Arranged in order of increasing mean head and body length. All measurements in mm. (n. d. = no data.)

| Species | HB
mean
(mm) | T
% of HB | WT
average
(g) | M ¹ –M ³
(mm) | Interorbital constriction
(shape in cross-section) | Notes |
|-----------------------|--------------------|--------------|----------------------|--|---|--|
| <i>S. albipes</i> | 132 | 125% | 59 | 5.5 | Rounded | Widely distributed 1500–3000 m east and west of Rift Valley |
| <i>S. ruppi</i> | 131 | 122% | 60 | 6.7 | Rounded | Gughe Mts, west of Rift Valley only. Rare |
| <i>S. griseicauda</i> | 154 | 93% | 99 | 6.8 | Rounded, flat dorsally | High plateaux east and west of Rift Valley. 2400–3900 m |
| <i>S. albocaudata</i> | 164 | 86% | 130 | 7.9 | Square | High plateaux of Bale and Arssi Provinces, east of Rift Valley. 3000 m |



Stenocephalemys griseicauda.

(Figure 85). This arrangement (stenocephaly) positions the eyes in a more dorsal position than in most other small rodents. Skull shape within species of the genus appears to be correlated with altitude, stenocephaly being more pronounced in higher altitude species than in those living at lower altitudes (Fadda & Corti 2000) (Figure 86). Pelage texture is silky to woolly. Dorsal pelage is sandy-brown, ventral pelage is paler; there are faint darker rings around the eyes, prominent thin ears and unremarkable feet. Superficially *Stenocephalemys* looks very much like *Mastomys*, *Myomyscus* and *Praomys*.

Species of the genus are nocturnal. Species at higher altitudes have a thick woolly pelage. The diet is granivorous and herbivorous, but there are no detailed quantitative studies for most species. The period of reproduction varies by species and altitude; at lower altitudes reproduction occurs throughout the year (*S. albipes*); at higher altitudes it is seasonal, mainly during the wet season but not during the cold season (*S. albocaudata*, *S. griseicauda*). Recruitment of young animals into the population is low. Two species are abundant (*S. albipes*, *S. albocaudata*) and are an important prey for raptors, but not for Ethiopian Wolves (see *Arvicanthus blicki* and *Lophuromys melanonyx*).

The genus was erected for *S. albocaudata* in 1914. Another species, *S. griseicauda*, was recognized in 1972. A third species, *S. albipes*, was previously allocated to the genus *Praomys*, and later to *Myomys* (now *Myomyscus*) (see Yalden *et al.* 1976, Musser & Carleton 1993). *Stenocephalemys ruppi*, regarded originally as a narrow-headed form of *S. albipes*, was described as a full species in 1983. The four species are now considered to represent a group of rodents endemic to Ethiopia. The genus is phylogenetically related to species of *Praomys*, *Mastomys*, *Myomyscus*, *Heimyscus* and *Hylomyscus*

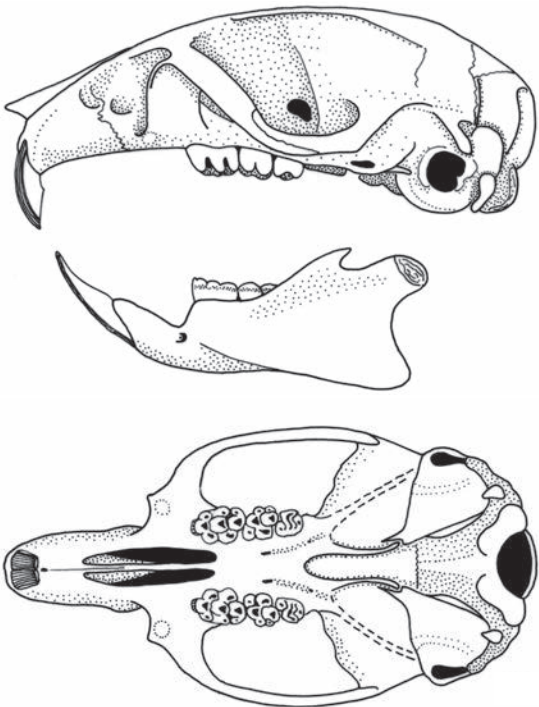


Figure 85. Skull and mandible of *Stenocephalemys albocaudata* (BMNH 72.1196).

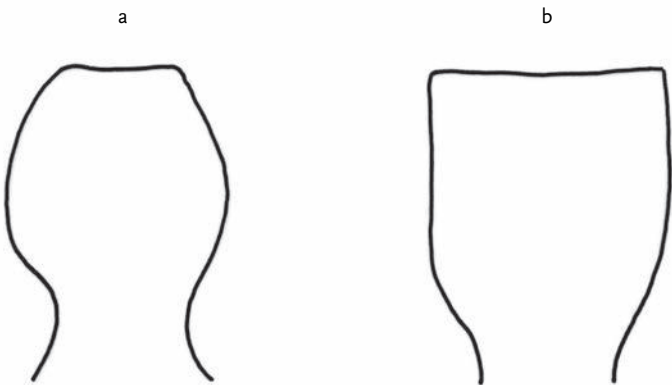


Figure 86. Cross section of the interorbital region of the skull of *Stenocephalemys*. (a) rounded, e.g. *S. albipes*, *S. ruppi*; (b) square, e.g. *S. albocaudata*, *S. griseicauda* (after Yalden *et al.* 1976).

(Lecompte *et al.* 2002b). Analysis of allozymes, karyology, mitochondrial 16S rRNA and mitochondrial DNA cytochrome *b* gene sequences link *S. albipes*, *S. albicaudata* and *S. griseicauda* (*S. ruppi* not included in the analysis) and indicate that these species form a monophyletic group (Lavrenchenko *et al.* 1999, 2000, Fadda & Corti 2000), which is distinct from *Praomys* and *Myomyscus* (= *Myomys*). *Stenocephalemys griseicauda* is more closely related to *S.*

albipes than to *S. albicaudata*. Detailed analysis of the genus is given by Musser & Carleton (2005).

The four species are distinguished by size, skull characters and distribution.

D.W. Yalden

Stenocephalemys albipes WHITE-FOOTED ETHIOPIAN RAT (WHITE-FOOTED STENOCEPHALEMYS)

Fr. Rat d'Éthiopie à pieds blancs; Ger. Weissfüssige Äthiopien-maus

Stenocephalemys albipes (Rüppell, 1842). Mus. Senckenberg. 3: 107. Massawa [?], Ethiopia. (The type locality, at sea level, is misleading since the species is not currently known from below ca. 800 m.)

Taxonomy Originally described by Rüppell as *Mus albipes*, but usually allocated to the genus *Myomys* or *Praomys* (Yalden *et al.* 1976, Yalden 1988). Karyologic al analysis (Corti *et al.* 1995, 1999), DNA mitochondrial cytochrome *b* sequences (Lecompte *et al.* 2002b) and other studies indicate that *S. albipes* clusters with *S. albicaudata* and *S. griseicauda* in a monophyletic group confined to the Ethiopian plateaux. Synonyms: *alettensis*, *ankoberensis*, *leucopus*, *minor*. Subspecies: none. Chromosome number: $2n = 46$, $FN = 50-53$ (Corti *et al.* 1999).

Description Medium-sized, silky-furred rat, on average much smaller than *S. albicaudata* and *S. griseicauda*, comparable in size with *Mastomys* spp. in Ethiopia. Pelage sleek and long (hairs 10–12 mm). Dorsal pelage sandy-brown, slightly darker towards mid-line; hairs dark grey at base, sandy-brown on terminal third. Juveniles greyer than adults, gaining sandy colour by about three months of age. Ventral pelage pale grey; hairs dark grey at base, white on terminal third. Colour of dorsal and ventral pelage sharply delineated. Eye with faint dark ring. Ears grey, large, rounded, appearing naked but finely furred. Forelimbs small, brownish-grey. Forefeet white, with four digits. Hindfeet white above, with characteristic dark mark over metatarsals; Digits 1 and 5 short. Tail very long (ca. 125% of HB), bicoloured, lightly furred, appearing naked, black dorsally, white ventrally. Skull: interorbital constriction less marked than in congeners; rounded in cross-section (Figure 86). Nipples: $3 + 2 = 10$.

Geographic Variation None recorded.

Similar Species

- S. albicaudata*. Larger (mean WT: 130 g); mean M^1-M^3 : 7.9 mm; tail uniformly white, or white with grey patches, relative tail length ca. 86% of HB; interorbital constriction square in cross-section.
- S. griseicauda*. On average larger (mean WT: 99 g); M^1-M^3 : 6.8 mm; tail grey, relative tail length 93% of HB, darker dorsally than ventrally; interorbital constriction rounded laterally, but flat dorsally, in cross-section.
- S. ruppi*. Slightly larger (mean WT: 60 g); M^1-M^3 : 6.7 mm; tail grey, relative tail length 122% of HB, darker dorsally than ventrally; interorbital constriction more marked, rounded, in cross-section.

Distribution Endemic to Africa. Afromontane–Afroalpine BZ of Ethiopia. Widely distributed in many mid-elevation highland habitats



Stenocephalemys albipes

in Ethiopia, particularly at 1500–3000 m. May also occur in some lowland forest habitats at 1285 and 820 m (Yalden & Largen 1992; Afework Bekele 1996a), but not known to occur in grasslands at 3700 m in the Simien Mts nor in grasslands at lower altitudes (Yalden & Largen 1992; Afework Bekele 1996a, Afework Bekele & Corti 1997) (see also below).

Habitat Recorded from a wide range of habitats including bush, grasslands, forest and *Erica* scrub. Trapping shows that forest habitats are preferred to shrub and grassland (Afework Bekele 1996b). In areas of human disturbance, occurs in the 'living fences' surrounding tukuls (local homesteads).

Abundance The most common rodent trapped at altitudes above 1500 m within and close to forest habitats, especially at 2800–3000 m. Probably the second most widespread rodent in Ethiopia after *Lophuromys flavopunctatus*. In Menagesha State Forest, comprised 54% of rodents in all habitats, and 71% in forest locations (Afework Bekele 1996a). With increasing altitude, forms a higher percentage of

the population of small mammals in its preferred habitats (Afework Bekele & Corti 1997).

Adaptations Nocturnal and terrestrial. Semi-arboreal activity has been observed on trees close to the ground.

Foraging and Food Herbivore and frugivore. In bushland and scrub habitats in Menagesha State Forest, diet (as indicated by occurrence in stomachs) was berries of *Carissa edulis* (in 94% of stomachs) and green leaves (38%) (n = 53 stomachs). In forest habitats, the diet was berries of *Olea* (in 60% of stomachs), *Juniperus* (57%), *Rosa abyssinica* (25%), *Rubus* (13%) and green leaves (63%) (n = 60 stomachs) (Afework Bekele 1996b). Animal material in stomachs was insignificant.

Social and Reproductive Behaviour The mean home-range length was 29 ± 12.9 m for ♀♀, and 65 ± 31.2 m for ♂♂. Male home-range lengths overlapped, while those of ♀♀ did not overlap.

Reproduction and Population Structure Reproduction occurs throughout the year with the highest pregnancy rates during the end of wet season (Sep and Nov). Reproductively active ♂♂ (with scrotal testes) were recorded throughout the year. Gestation: 23 days. Embryo number: 5 (2–8, n = 18 pregnancies). Litter-size: 4.1 (2–6, mode 5, n = 42 litters). At birth, young are naked and weigh ca. 3 g. Ear pinnae unfold Day 4–5. Pelage visible Day 7–10. Incisors (lower) erupt Day 10–12, (upper) Day 13–17. Eyes open Day 13–18. Weaned at Day 24–29. Weight gain is rapid up to eight weeks, and slower thereafter, and after weight of 45 g. Recruitment rate of young into the population is usually less than 20% (perhaps

due to heavy predation). Survival rate for adults was less than a year in the wild and three years in captivity (Afework Bekele 1995).

Predators, Parasites and Diseases Nocturnal predators such as owls may be a controlling factor on population numbers. Nematode worms found in at least 17 (of 60) stomachs, with up to ten worms per stomach.

Conservation IUCN Category: Least Concern.

Although deforestation has (and is) continued at an alarming rate, White-footed Mice survive well on the forest fringes and in the bush where *Carissa edulis*, *Rosa abyssinica* and *Rubus* are common, and close to human habitations.

Measurements

Stenocephalemys albipes

HB: 132.5 (120–152) mm, n = 30

T: 161.8 (137–182) mm, n = 30

HF: 26.6 (25–29) mm, n = 30

E: 22.9 (20–25) mm, n = 30

WT: 59.0 (40–79) g n = 30

GLS: 32.3 (30.7–34.8) mm, n = 17

GWS: 15.6 (13.7–16.8) mm, n = 17

M¹–M³: 5.5 (5.0–5.8) mm, n = 17

Ethiopia (BMNH)

Key References Afework Bekele 1995, 1996a, b; Afework Bekele & Corti 1997; Rupp 1980; Yalden & Lagen 1992.

Afework Bekele

Stenocephalemys albicaudata WHITE-TAILED ETHIOPIAN RAT (WHITE-TAILED STENOCEPHALEMYS)

Fr. Rat d’Ethiopie à queue blanche; Ger. Weisschwänzige Äthiopien-maus

Stenocephalemys albicaudata Frick, 1914. Ann. Carnegie Mus. 9: 8, pls 1–2. Inyala Camp, Chilalo Mts, Ethiopia (ca. 07° 50' N, 39° 20' E).

Taxonomy *Stenocephalemys albicaudata* is the nominate species in the genus. It is closely related to the other species in the genus, *S. griseicauda* and *S. albipes* (formerly *Myomys albipes*) and *S. ruppi*. The chromosome number (2n = 54) is the same as in *S. griseicauda* (Lavrenchenko *et al.* 1997). On the basis of 16S rRNA sequences and allozyme data, this species is more distinct from *S. griseicauda* and *S. albipes* than they are from each other; morphologically and cytogenetically, *S. albicaudata* is much closer to *S. griseicauda* than to *S. albipes*. Synonyms: none. Chromosome number: 2n = 54, FN = 60–62 (Corti *et al.* 1999; Lavrenchenko *et al.* 1999).

Description Large, soft-furred rat, larger on average than the other three species in the genus. Pelage woolly and dense, uniformly longer (hairs 16–18 mm on mid-back) and softer than in *Praomys* and *Myomyscus*. Dorsal pelage dark sandy-brown to ginger (adults appearing much brighter than *S. griseicauda*); hairs dark grey at base, sandy on tip; many slightly longer black-tipped hairs especially on mid-dorsal line. Flanks paler, brownish, without black-tipped hairs. Ventral pelage greyish-white; hairs grey with off-white tip; pure

white mid-ventral stripe in some individuals. Dorsal and ventral pelage delineated by a sharp yellowish line. Eyes with dark rings. Ears grey, prominent, lightly furred. Fore- and hindfeet white. Tail long (86% of HB), scaly, almost naked but with short white hairs; appearing uniformly white or white with grey patches proximally. Juvenile pelage much greyer than in adults. Skull: interorbital constriction narrow, squared off dorsally in cross-section (Figure 86). Nipples: 3 + 2 = 10.

Geographic Variation None recorded.

Similar Species

S. albipes. Much lighter (mean WT: 59 g); mean M¹–M³: 5.5 mm; tail bicoloured, black dorsally and white ventrally, relative tail length ca. 125% of HB; interorbital constriction rounded in cross-section.

S. griseicauda. On average lighter (mean WT: 99 g); M¹–M³ shorter; tail grey, relative tail length 93% of HB, darker dorsally than ventrally; interorbital constriction rounded laterally, but flat dorsally, in cross-section.

S. ruppi. Much lighter (mean WT: ca. 60 g); M^1 – M^3 shorter; tail dark grey above, pale below, relative tail length 122% of HB; interorbital constriction rounded laterally, but flat dorsally, in cross-section.

Distribution Endemic to Africa. Afromontane–Afroalpine BZ of Ethiopia. Confined to the high plateaux in Bale and Arssi (Arussi) Provinces, SE Ethiopia, at 3000–4377 m. Not known from west of the Rift Valley (Yalden *et al.* 1976, Yalden & Lagen 1992).

Habitat Typically found in upland moorland, above 3500 m (Yalden 1988), but extends to lower grasslands along river valleys. Habitat preference distinguishes this species from both *S. albipes* (a forest species) and *S. griseicauda* (a scrub species). In the Web Valley, Bale, commonly found in *Alchemilla* pastures and mesa slopes dominated by low *Artemisia* and *Helichrysum* scrub, which provide good cover.

Abundance The most common rodent on the high plateau, above 4000 m, contributing 32% (994 of 3083) of the rodents caught in Bale Province (Sillero-Zubiri *et al.* 1995a). Density estimated at 42/ha (16–60/ha in different months) in the Web Valley grasslands and 26/ha (16–44/ha in different months) in the moorland of the Sanetti plateau (Sillero-Zubiri *et al.* 1995a). Commonly syntopic with diurnal species, e.g. *Arvicanthis blicki*, *Lophuromys melanonyx* and *Tachyoryctes macrocephalus*.

Adaptations Nocturnal (over 99% of 752 captures were at night; Sillero-Zubiri *et al.* 1995a). Large size (compared with other Ethiopian rodents) and woolly pelage are assumed to be responses to the low night-time temperatures at high altitude (Rupp 1980, Yalden & Lagen 1992, Sillero-Zubiri *et al.* 1995a). Narrow interorbital region causes the eyes to face more dorsally than in other species of the genus, which might be an adaptation for detecting raptors in its open upland habitat (Yalden & Lagen 1992).

Foraging and Food Dentition and habitat suggest a granivorous and herbivorous diet; no detailed information.

Social and Reproductive Behaviour No information.

Reproduction and Population Structure In Bale Province, pregnant animals were found during wet season (May–Oct) with a sharp peak in reproductive activity in May–Jun. No pregnancies recorded during the dry season (Dec–Apr). Very young animals (<40 g) found mainly Aug–Jan. Beginning of the wet season probably triggers reproduction (Sillero-Zubiri *et al.* 1995a). Embryo number: 3.59 ± 0.93 , $n = 27$ ♀♀. Even when most numerous in Aug–Nov, juveniles comprise only 30% of the population and ca. 10% in Feb–Jul (Sillero-Zubiri *et al.* 1995a), suggesting a low rate of recruitment.

Predators, Parasites and Diseases Nocturnal habits probably protect these rats from the largely diurnal predators such as raptors and from Ethiopian Wolves *Canis simensis* (which feed mainly on the



Stenocephalemys albocaudata

diurnal *Arvicanthis blicki* and *Lophuromys melanonyx*). Ethiopian Wolves avoided these rats in ‘cafeteria’ tests (Sillero-Zubiri & Gotelli 1995). Forms the main prey of Abyssinian Long-eared Owls *Asio abyssinicus* (53% by prey number, 63% by prey mass; Yalden 1973), and is probably eaten also by other owls.

Conservation IUCN Category: Least Concern.

Lives at higher altitudes than the majority of Ethiopians and their livestock, and hence its habitat should be relatively safe from destruction; however, the limited range of the habitat should class this species as ‘vulnerable’. Preferred habitat is protected within the proposed Bale Mountains National Park.

Measurements

Stenocephalemys albocaudata

HB: 164 (106–195) mm, $n = 590$

T: 141 (112–175) mm, $n = 583$

HF: 32 (21–36) mm, $n = 218$

E: 27 (24–32) mm, $n = 218$

WT: 130 (83–198) g, $n = 592$

GLS: 39.4 (37.6–41.8) mm, $n = 7$

GWS: 20.7 (19.3–22.2) mm, $n = 7$

M^1 – M^3 : 7.9 (7.5–8.0) mm, $n = 7$

Body measurements and weight: Bale Province, Ethiopia (Sillero-Zubiri *et al.* 1995b)

Skull measurements: Ethiopia (BMNH)

Key References Lavrenchenko *et al.* 1999; Sillero-Zubiri *et al.* 1995a, b; Yalden & Lagen 1992; Yalden *et al.* 1976.

D.W.Yalden

***Stenocephalemys griseicauda* GREY-TAILED ETHIOPIAN RAT (GREY-TAILED STENOCEPHALEMYS)**

Fr. Rat d'Éthiopie à queue grise; Ger. Grauschwänzige Äthiopien-maus

Stenocephalemys griseicauda Petter, 1972. Mammalia 36: 171. Dinshu, Bale Mts, Ethiopia.

Taxonomy Distinguished from *S. albicaudata* (the nominate species of *Stenocephalemys*) by its smaller size and grey tail (Petter 1972a). Synonyms: none. Chromosome number: $2n = 54$. Two chromosomal forms in the Bale Mts may represent cryptic species (Lavrenchenko *et al.* 1997). One chromosomal form (from high altitudes) has a metacentric X chromosome, and the other (medium altitudes) has a submetacentric X chromosome. These two forms are also distinguished by several other genetic polymorphisms.

Description Large, soft-furred rat, intermediate in size between *S. albipes* and *S. albicaudata*. Pelage woolly and long (hairs ca. 1415 mm on mid-back); uniformly longer and softer than in *Praomys* and *Myomyscus*. Dorsal pelage sandy-brown to dull brown, darker over the mid-line; hairs dark grey at base, sandy-brown at tip; many slightly longer black-tipped hairs, especially on mid-dorsal line. Flanks paler than back. Ventral pelage greyish-white; hairs dark grey at base, off-white or pale grey at tip. Faint dark ring around eyes. Ears grey, prominent, slightly furred. Fore- and hindfeet off-white or pale brown. Tail moderately long (ca. 93% of HB), grey above or all over. Skull: mean M^1-M^3 : 6.8 mm; interorbital constriction narrow, flat dorsally but rounded laterally in cross-section (Figure 86). Nipples: not known.

Geographic Variation None recorded except for altitudinal variation in chromosomal and genetic characters (see Taxonomy).

Similar Species

S. albipes. On average lighter (mean WT: 59 g); mean M^1-M^3 shorter; tail bicoloured, black dorsally and white ventrally,

relative tail length ca. 125% of HB; interorbital constriction rounded in cross-section.

S. albicaudata. On average heavier (mean WT: 130 g); mean M^1-M^3 longer; tail uniformly white, or white with grey patches, relative tail length 86% of HB; interorbital constriction square in cross-section.

S. ruppi. Lighter (mean WT: 60 g); tail bicoloured, black dorsally and white ventrally, relative tail length ca. 122% of HB; interorbital constriction rounded in cross-section.

Distribution Endemic to Africa. Afromontane–Afroalpine BZ of Ethiopia. Confined to the high plateaux of Ethiopia, at 2400–3900 m. Widespread both east and west of the Rift Valley from Simien in the north to Bale in the south (Yalden *et al.* 1976, Yalden & Largen 1992).

Habitat Typically found in upland grasslands (dega) and scrub, at 2900–3500 m, extending uphill into the edge of moorland (Yalden 1988, Sillero-Zubiri *et al.* 1995a). Habitat preference separates this species ecologically from both *S. albipes* (forest species) and *S. albicaudata* (moorland species), though their general distributions overlap. In the Web Valley, Bale Province, preferred habitat is mesa slopes dominated by low *Artemisia* and *Helichrysum* scrub, which provide good cover (Sillero-Zubiri *et al.* 1995a). Often occurs with *Lophuromys flavopunctatus*.

Abundance Common in upland grassland communities, contributing 23% of the rodents caught in appropriate habitats in Bale (Yalden 1988).

Adaptations Nocturnal (97% of 71 captures being made at night; Yalden 1988, Sillero-Zubiri *et al.* 1995a). Large size (compared with other Ethiopian rodents) and woolly pelage are assumed to be adaptations to the low night-time temperatures at high altitude (Rupp 1980, Yalden & Largen 1992, Sillero-Zubiri *et al.* 1995a). Narrow inter-orbital region causes the eyes to face more dorsally, which might be an adaptation for detecting raptors in the open upland habitat (Yalden & Largen 1992).

Foraging and Food Dentition and habitat suggest a granivorous and herbivorous diet; no detailed information available.

Social and Reproductive Behaviour No information.

Reproduction and Population Structure In Simien, pregnant animals were found just before, during and immediately after the wet season (May–Dec), but not in the dry cold season (Jan–Apr). Very young animals (<40 g) were found mainly in Sep–Dec (Müller 1977).

Predators, Parasites and Diseases Nocturnal habits probably protect these rats from largely diurnal predators such as raptors and Ethiopian Wolves *Canis simensis*. Probably preyed upon by various owls, a suggestion which requires confirmation.

*Stenocephalemys griseicauda*

Conservation IUCN Category: Least Concern.

Although relatively common, lives in habitats that suffer from continuing destruction by many humans and their livestock.

Measurements

Stenocephalemys griseicauda

HB: 154 (130–175) mm, n = 97

T: 142 (105–160) mm, n = 97

HF: 30 (25–33) mm, n = 86

E: 24 (20–30) mm, n = 85

WT: 99 (70–136) g, n = 98

GLS: 35.9 (34.1–37.9) mm, n = 11

GWS: 18.0 (16.0–19.7) mm, n = 11

M¹–M³: 6.8 (6.5–7.1) mm, n = 11

Body measurements and weight: Bale, Ethiopia (Yalden 1988, Sillero-Zubiri *et al.* 1995b)

Skull measurements: Ethiopia (BMNH)

Key References Lavrenchenko *et al.* 1997; Müller 1977; Rupp 1980; Yalden & Lagen 1992.

D.W. Yalden

Stenocephalemys ruppi RUPP'S ETHIOPIAN RAT (GUGHE HIGHLANDS RAT, RUPP'S STENOCEPHALEMYS)

Fr. Rat d'Ethiopie de Rupp; Ger. Rupp's Äthiopien-maus

Stenocephalemys ruppi (Van der Straeten and Dieterlen, 1983). Ann. Mus. Roy. Afr. Centr., Sci. Zool. 237: 121. Bonke, N. of Bulta, Gemu-Gofa, Ethiopia. 2800–3200 m.

Taxonomy First described as *Praomys ruppi*, then placed in the genus *Myomys*. Subsequently allocated to the genus *Stenocephalemys* on account of its intermediate morphology between *S. albipes* and *S. griseicauda*, particularly on the character of the interorbital region, and because (like the other species in genus) it is an Ethiopian endemic (see Musser & Carleton 2005). Considered as a narrow-headed form of *S. albipes* (Rupp 1980, as *M. albipes*) and closely related to it (Van der Straeten & Dieterlen 1983). Perhaps not distinguishable from *S. albipes*, but encompassed within the range of variation of that species (Fadda & Corti 2000; M. Corti pers. comm.). Synonyms: none. Chromosome number: not known.

Description Medium-sized, soft-furred rat, intermediate in size and other respects between two other endemic Ethiopian rodents, *S. albipes* and *S. griseicauda*. Dorsal pelage sandy-brown; hairs dark grey basally, uniform sandy-brown distally. Ventral pelage greyish-white; hairs dark grey basally, white distally. Sharp, yellowish delineation along flanks between dorsal and ventral colours. Ears grey, prominent, lightly furred. Forefeet white, hindfeet all white or with dark patch over metatarsals. Tail very long (ca. 122% of HB), dark grey above, pale below. Skull: mean M¹–M³: 6.65 mm; interorbital constriction narrow, rounded in cross-section (Figure 86). Nipples: 3 + 2 = 10.

Geographic Variation None recorded.

Similar Species

S. albipes. M¹–M³ shorter; tail more distinctly bicoloured, black dorsally and white ventrally, relative tail length ca. 125% of HB; interorbital constriction rounded in cross-section.

S. albicaudata. M¹–M³ longer; tail uniformly white, or white with grey patches, relative tail length 86% of HB; interorbital constriction square in cross-section.

S. griseicauda. Tail grey, relative tail length 93% of HB, darker dorsally than ventrally; interorbital constriction rounded laterally, but flat dorsally, in cross-section.



Stenocephalemys ruppi

Distribution Endemic to Africa. Afromontane–Afroalpine BZ of Ethiopia. Confined to the Gughe Mts, west of the Rift Valley on the southern plateaux of Ethiopia, at 2800–3200 m. Syntopic with *S. albipes* (Yalden & Lagen 1992).

Habitat Montane forest and scrub, a habitat shared with *S. albipes*.

Abundance Presumably rare; described on the basis of nine specimens from the Gughe Highlands.

Remarks Presumably a nocturnal seed- and berry-feeder, like *S. albipes*.

Conservation IUCN Category: Data Deficient.

The very limited distribution in an area where there is a high density of humans suggests this species should be considered as vulnerable.

Measurements

Stenocephalemys ruppi

HB: 131 (124–138) mm, n = 9

T: 160 (143–179) mm, n = 9

HF: 31 (29–33) mm, n = 8

E: 24 (23–26) mm, n = 8

WT: n. d.*

GLS (CbL): 31.6 (30.8–32.5) mm, n = 7

GWS: 16.2 (15.5–16.9) mm, n = 7

M¹–M³: 6.7 (6.3–7.2) mm, n = 7

Gughe, Ethiopia (Van der Straeten & Dieterlen 1983)

*Probably ca. 60 g

Key References Van der Straeten & Dieterlen 1983; Yalden & Lagen 1992.

D. W. Yalden

GENUS *Stochomys*

Target Rat

Stochomys Thomas, 1926. Ann. Mag. Nat. Hist., ser. 9, 17: 176. Type species: *Dasymys longicaudatus* Tullberg, 1893.



Stochomys longicaudatus.

Monotypic genus, widely distributed in the Rainforest BZ from W Nigeria to E DR Congo and W Uganda. The genus is 'rat-like' and characterized by medium body size, very long naked tail and large

heavily built skull (see *Stochomys longicaudatus* for further details). The type species of the genus was described as *Dasymys longicaudatus*. The genus *Stochomys* was created by Thomas (1926) to contain the single species, thus separating it from the genera *Dasymys*, *Rattus*, *Mus*, *Epimys* and *Aethomys* to which it had previously been allocated (see Rosevear 1969 for details).

The genus is closely related to (and morphologically similar to) *Dephomys* (Musser & Carleton 2005), although this relationship is uncertain (Van der Straeten 1984). Pelage, skull and dentition are similar to some species of *Aethomys*, suggesting that both genera belong to the same clade and are ecological equivalents in rainforest (*Stochomys*) and savanna (*Aethomys*) (Visser & Robinson 1986). On the basis of microcomplement fixation, *Stochomys* groups with *Hybomys*, both genera well removed from *Aethomys* (Watts & Baverstock 1995a). The systematic and phylogenetic position of *Stochomys* is ambiguous and far from clear, and awaits further study. The single species is *Stochomys longicaudatus*.

D. C. D. Happold

Stochomys longicaudatus TARGET RAT

Fr. Rat à collière; Ger. Zielscheibenratte

Stochomys longicaudatus (Tullberg, 1893). Nova Acta Reg. Soc. Sci. Uppsala, ser. 3, 16: 36. Cameroon.

Taxonomy Originally described in the genus *Dasymys*. The Target Rat has the dubious distinction of having been placed in six different genera at various times since its original description (Rosevear 1969; see also Genus profile). Now recognized as being the only species in the genus *Stochomys*. Can be confused with *Dephomys* except for differences in distribution. Synonyms: *hypoleucus*, *ituricus*, *sebastianus*. Subspecies: two of dubious validity. Chromosome number: not known.

Description Medium-sized robustly built rat with dense pelage and very long tail. Dorsal pelage reddish-brown to chocolate-brown; hairs almost unicoloured, sometimes pale grey at base. Dorsal pelage interspersed with long black shiny guard hairs (some with white tip), which extend beyond the contours of the body, especially on rump. These guard hairs project slightly upwards and backwards resembling

small arrows fired into a target. Flanks brownish-grey with fewer shorter guard hairs. Ventral pelage whitish or whitish-brown; hairs brownish on basal half, whitish on terminal half. Head large and broad, long vibrissae, large eyes, and large rounded ears sparsely covered with short hairs. Forefoot with five digits; Digit 1 very reduced, with nail. Hindfoot long and broad with five digits, each with claw; Digits 1 and 5 short; Digits 2, 3 and 4 long and subequal. Tail very long (ca. 146% of HB), small scales, seemingly naked but covered with small fine bristles. Dorsal pelage of juveniles greyish-brown with dark guard hairs visible. Moulting individuals often have patchy colouration. Skull: large and robust; GLS: >36 mm; supraorbital ridges well developed; anterior palatal foramina not reaching (or just reaching) level of M¹; width of palate at level of M¹ less than 1.5 times width of M¹; incisors well-developed, rather thick in anterior-posterior

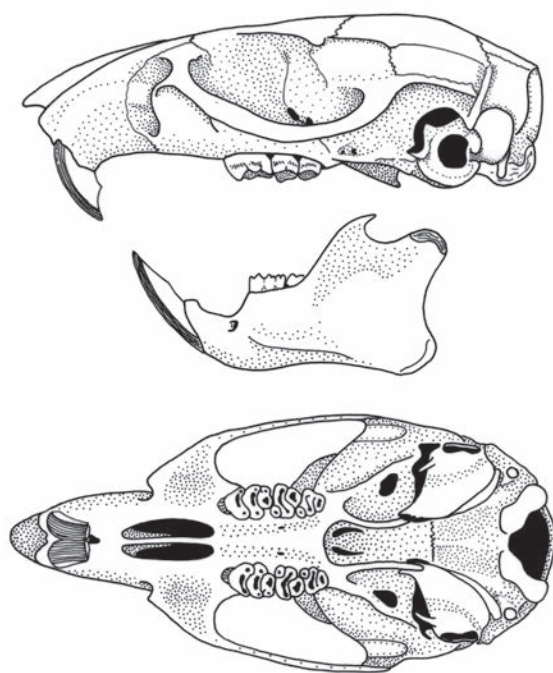


Figure 87. Skull and mandible of *Stochomys longicaudatus* (HC 1349).

plane, opisthodont, not grooved; upper molar teeth canted outwards; t7 on M¹ absent; t9 of M¹ reduced to small displaced cusp; cusps on M¹ linear and almost laminate; t3 on M² very reduced and displaced (Figure 87). Nipples 1 + 2 = 6.

Geographic Variation Van der Straeten (1984) recognized two subspecies based on canonical analysis of skull characters: *S. l. longicaudatus* west of the Congo R. and *S. l. ituricus* to the east of the river. The validity of subspecies is questionable.

Similar Species

Dephomys defua. On average smaller, with smaller less-obvious guard hairs; geographic range only west of Dahomey Gap, not overlapping with *S. longicaudatus*.

Distribution Endemic to Africa. Rainforest BZ (West Central, East Central and South Central Regions). Recorded from W Nigeria to E DR Congo, including lower slopes of Rwenzori Mts. Populations on the periphery of main geographic range known from forest relicts in Togo and Dahomey (Robbins & Van der Straeten 1996), S Central African Republic (Genest-Villard 1980, Morvan *et al.* 1999, Malcolm & Ray 2000) and W Uganda (Delany 1975).

Habitat Primary and secondary rainforest, especially near rivers and streams; individuals have been found less commonly in oil palm plantations and cultivated land. Also occur in evergreen shady forests and gallery forests up to 800–1000 m on Mt Cameroon and in Rwenzori Mts (Misonne 1963). Considered as ‘gap specialists’ that take advantage of both natural and human-made secondary habitats within the Rainforest BZ, although not in open areas without cover. Significantly more abundant along primary and secondary logging roads than in unlogged forest (Malcolm & Ray 2000). Favours habitats characterized by relatively dense understorey, low tree species



Stochomys longicaudatus

diversity, low tree diameter, low sapling density and open canopy cover (Ray 1996, Malcolm & Ray 2000).

Abundance One of the rarest of rainforest rodents, comprising only 1–2% of the small terrestrial rainforest rodents trapped in Nigeria (Happold 1975b, 1977). In E DR Congo, relative abundance depended on habitat, e.g. 1.8% in cultivated land, 9% in forest near rivers, 1% on forested hills and 4% in oil palm plantations (Rahm 1967, 1972). In SW Central African Republic, comprised 3.2% of all captures (n = 704) along secondary logging roads, 0.2% (n = 458) in unlogged mixed-species forest, 1.5% in monodominant *Gilbertiodendron dewevrei* forest (n = 406) and 0.5% along streams (n = 200) (Ray 1996). At M’passa (Gabon), biomass was ca. 8 g/ha (Duplantier 1989), equivalent to ca. 1 individual/11 ha.

Adaptations Nocturnal and terrestrial or scansorial. A few individuals have been obtained in creepers 2–3 m above the ground. Individuals in captivity made spherical nests of shredded forest leaves and herbs (Happold 1987). In Dzanga-Sangha, Central African Republic, occurred only in lower strata (on ground and understorey at 2 m), and was more abundant in the understorey than on the ground and never captured in the canopy (Malcolm & Ray 2000).

Foraging and Food Analysis of stomach contents suggest a mainly vegetarian diet (Rahm 1966). Individuals in captivity ate fruits and seeds, as well as insects (Happold 1987). Diet was mostly fruit and seeds at Makokou (Gabon; Duplantier 1982) and at Mbaiki (Central African Republic; Genest-Villard 1980).

Social and Reproductive Behaviour May be nomadic, changing domiciles (and home-range) as conditions change. In W Nigeria most individuals in a study area were captured only once (Happold 1977). A few individuals were resident for up to four weeks; they then ‘disappeared’ for several months, and were recaptured

again at exactly the same place as previously. One individual resided for 25 months, including absences of 12 months and six months. Similar behaviour and nomadism has also been observed in Gabon.

Reproduction and Population Structure Pregnancies recorded in Mar and Jun, and young in Jan, Jun and Dec in W Nigeria (Happold 1977), and in Jan and in Apr–Sep inclusive in E DR Congo (Rahm 1970). Litter-size: 3 (n = 2; Happold 1987). Embryo number: 2.1 (1–4, n = 17, mode 2; DR Congo; U. Rahm in Delany 1975); 2.5 (1–4, mode 2; Gabon; Dubost 1968). The limited data suggest that Target Rats have small litters, breed during most months of the year and have the potential to live for a comparatively long period of time (cf. *Praomys tullbergi*, which lives syntopically with *S. longicaudatus* in Nigeria).

Predators, Parasites and Diseases In Dzanga-Sangha Forest Reserve, Central African Republic, *S. longicaudatus* comprised 6% of small rodent prey (WT: <100 g) of Long-nosed Mongooses *Herpestes naso* (n = 86 scats with small mammal remains), more than expected on the basis of trapping results. Similar data for all small carnivores is 4% (n = 251 scats). Small carnivores appear to prey selectively on this species (Ray 1998).

Conservation IUCN Category: Least Concern.

Target Rats are dependent on moist rainforest habitats, so their conservation is dependent on extensive areas of rainforest.

Measurements

Stochomys longicaudatus

HB: 145 (132–155) mm, n = 20

T: 213 (191–230) mm, n = 20

HF: 30.7 (27–34) mm, n = 20

E: 20.3 (17–23) mm, n = 19

WT: 94.5 (84–102) g, n = 10

GLS: 38.8 (37.7–40.6) mm, n = 15

GWS: 18.9 (17.9–19.8) mm, n = 14

M¹–M³: 6.4 (6.2–6.6) mm, n = 14

DR Congo (SMNS, BMNH)

Key References Happold 1977, 1978; Misonne 1963; Rahm 1967, 1972.

D. C. D. Happold

GENUS *Thallomys* Acacia Rats (Tree Rats)

Thallomys Thomas, 1920. Ann. Mag. Nat. Hist., ser. 9, 5: 141. Type species: *Mus nigricauda* Thomas, 1882.

The genus contains four species (Table 41) widely distributed in arid and savanna habitats in southern and eastern Africa. The genus is characterized by medium size, long brown or dark-coloured tail, dark facial markings (usually present), four digits on forefoot (Digit 1 absent or reduced to very small tubercle), relatively short hindfeet with five digits, Digit 1 much shorter than Digits 2–5. The skull is *Rattus*-like, with broad palate, long and wide anterior palatal foramina extending posteriorly to the first row of cusps of M¹, and moderately well-developed supraorbital ridges (Figure 88). The generic name is derived from the Greek *thallos* meaning a fine twig, and refers to the

fact that these rats feed on the young leaves and twigs of *Acacia* trees and use them for nest construction.

All species in the genus are arboreal – an unusual feature for murids, shared only with *Grammomys*, *Thamnomys* and *Hylomyscus*. Nocturnal; during the day individuals rest in nests built among the branches of trees, which they construct from cut twigs. The diet is vegetarian, primarily leaves and shoots of the trees where they live. The gastrointestinal tract exhibits some unusual characters not seen in most murid rodents. The stomach is unilocular and hemiglandular, and also has folds that channel the movement of

Table 41. Species in the genus *Thallomys*. Arranged in alphabetical order. (n. d. = no data.)

| Species | HB
mean (range)
(mm) | T
mean (range)
(mm) [% of HB] | M ¹ –M ³
mean (range)
(mm) | Nipple
number | Chromosome
number | Black markings
on face | Colour of
dorsal pelage | |
|-----------------------|----------------------------|-------------------------------------|--|-------------------------|----------------------|---------------------------|---|--|
| <i>T. loringi</i> | 144 (140–160) | 159 (143–183)
[110%] | 5.6 (5.2–5.8) | 0 + 2 = 4 | n. d. | Conspicuous | Brown with
blackish wash;
some brown guard
hairs | |
| <i>T. nigricauda</i> | 135 (117–147) | 146 (127–156)
[120%] | 5.2 (4.7–5.7) | 1 + 2 = 6 | 2n = 47–50 | Very conspicuous | Grey with yellow
wash; some black
guard hairs | |
| <i>T. paedulus</i> | 140 (130–155) | 166 (157–179)
[120%] | 4.9 (4.1–5.4) | 0 + 2 = 4,
1 + 2 = 6 | 2n = 43–46 | Conspicuous | Yellowish-grey to
pale brown | |
| <i>T. shortridgei</i> | (140–150) | (183–210)
[ca. 145%] | (5.5–5.7) | 0 + 2 = 4 | n. d. | Often obscure | Brown | |



Thalomys paedulus.

foods, and parts have papillae that increase the surface area of the stomach. Some parts are cornified. The stomach contains bacteria that are presumed to assist in the breakdown and fermentation of food (Perrin 1986). The caecum is comparatively large (Perrin & Curtis 1980). These characters may be related to feeding almost exclusively on *Acacia* trees (see below). No other rodents has exploited this feeding niche, and hence competition with any other species is minimized.

The status and relationships of the genus are uncertain. Thomas (1920) separated this genus from *Rattus*, and Ellerman (1941) retained it as a separate genus. Ellerman *et al.* (1953) placed *Thalomys* with the subgenus *Aethomys* in the genus *Rattus*. Subsequent authors (De Graaff 1981, Smithers 1983, Musser & Carleton 1993, 2005) retain *Thalomys* as a valid genus. The number of species in the genus is also controversial. Misonne (1974) and De Graaff (1981) recognize one species, *T. paedulus*. Meester *et al.* (1986) also recognize one species, with 14 subspecies in the southern African region. Petter (1973) recognizes two species, *T. paedulus* and *T. damarensis*, as did Dippenaar *et al.* (1983) on the basis of karyotypes. Gordon (1987) found *T. paedulus sensu lato* to comprise two chromosomal species, *T. paedulus* ($2n = 43-47$) and *T. nigricauda* ($2n = 47-50$). The ranges

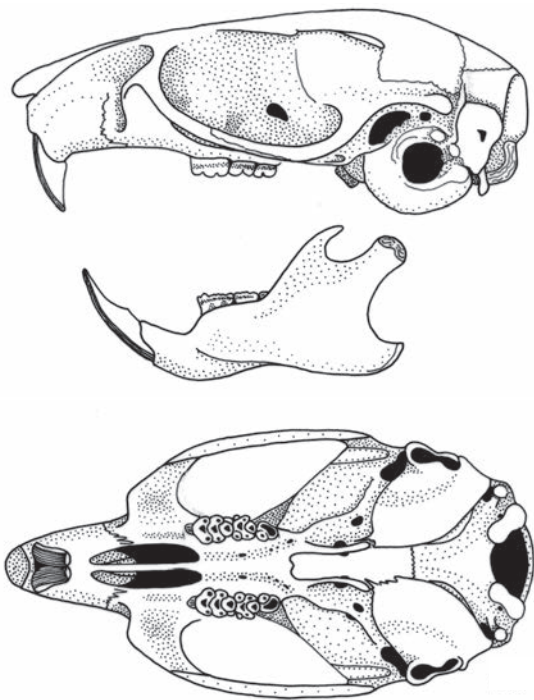


Figure 88. Skull and mandible of *Thalomys nigricauda* (BMNH 25.12.4.152).

of these two species appear to be parapatric, *T. paedulus* being associated with the Zambezian Woodland BZ and *T. nigricauda* with the South-West Arid BZ (Taylor 1998). Taylor *et al.* (1995) used discriminant analysis to derive craniometric criteria for the two chromosomal species and plotted revised distribution maps, which indicated a complicated pattern of widespread sympatry throughout southern Africa. The situation remains unclear and requires further biogeographic, karyotypic, morphometric and molecular studies to resolve species limits.

Four species are recognized here, and are distinguished by size (to limited extent), pelage colour, chromosome number and distribution.

Mike Perrin

| | Colour of ventral pelage | Notes |
|--|----------------------------|---|
| | Creamy-white; grey at base | Gregorian Rift Valley; Kenya and N Tanzania. Possibly sympatric with <i>T. paedulus</i> |
| | White | South-West Arid BZ; Botswana, South Africa, SW Angola |
| | White; white at base | Zambezian Woodland BZ and S Somalia–Masai Bushland BZ; Kenya to South Africa |
| | White; slate-grey at base | South-West Arid BZ; South Africa (localized) |

Thallomys loringi LORING'S ACACIA RAT (LORING'S THALLOMYS)

Fr. Rat arboricole de Loring; Ger. Lorings Baumratte

Thallomys loringi (Heller, 1909). Smithsonian Misc. Coll. 52: 471. L. Naivasha, Kenya.

Taxonomy Originally described in the genus *Thamnomys*, but Thomas & Hinton (1923b) correctly transferred it to the genus *Thallomys*. Subsequently, most authors have considered *loringi* to warrant only subspecies recognition, either within *T. nigricauda* (Hollister 1919, Allen 1939, Ellerman, 1941) or *T. damarensis* (Petter 1973). Musser & Carleton (1993) reinstated *loringi* to species based on its distinctive morphology and viewed the form as most similar to (and probably phylogenetically closely allied with) *T. nigricauda*. No detailed evaluation of their degree of differentiation and level of relationship has yet been presented. Synonyms: none. Chromosome number: not known.

Description Medium- to large-sized rodent with prominent black facial markings and predominantly brown dorsally. Pelage medium-long (hairs 11–13 mm on rump), thick and soft. Dorsal pelage wood-brown, with blackish wash on middle back and rump; hairs pale plumbeous-grey on basal two-thirds, medium buff to pale ochraceous on distal one-third. Guard hairs dusky-brown. Ventral pelage creamy-white to whitish-grey; hairs pale grey at base, white or creamy-white distally. Flanks paler brown tending towards grey. Colour of ventral pelage sharply delineated from colour of flanks. Head brownish-grey; blackish-brown around eyes and side of muzzle forming a dark facial mask. Ears medium in length, with black epidermis and clothed externally and internally with ochraceous hairs. Upper surfaces of fore- and hindfeet with dull white hairs. Hindfoot relatively short and broad, Digit 5 nearly as long as Digits 2, 3 and 4, and much longer than Digit 1; plantar pads six, large and set close to one another. Tail long (ca. 110% of HB), dark all around, brown at base and becoming black toward tip; hairs black, short and inconspicuous over proximal two-thirds of tail, longer over distal third and forming a weak pencil. Skull large for the genus, with laterally bowed zygomatic arches and narrow interorbital constriction. Supraorbital ridging weakly developed, in adults forming an obtuse projection at rear of orbit. Anterior palatal foramina relatively short, terminating posteriorly in front of or in line with anterior root of M¹; bony palate correspondingly long. Auditory bullae large. Nipples: 0 + 2 = 4.

Geographic Variation None recorded.

Similar Species

T. paedulus. Dorsal pelage exhibiting more grey, especially over the head, forequarters and flanks; ventral pelage pure white, hairs white to base; tail blacker throughout length, hence more noticeably contrasting with dorsal pelage; anterior palatal foramina longer, terminating posteriorly between M¹'s, bony palate correspondingly shorter. Possibly sympatric with *T. loringi* in W Kenya or N Tanzania.

Distribution Endemic to Africa. Somalia–Masai Bushland BZ. Recorded from the Gregorian Rift Valley in W, C and SW Kenya and extreme N Tanzania; limits of geographic range uncertain. Known altitudinal range ca. 1000–2300 m.

*Thallomys loringi*

Habitat *Acacia* trees, shrubby woodlands and brushy thickets in East African savanna. Specimens have been obtained in traps placed 'on limb of acacia,' 'near hole at base of thorn tree in shrubby area,' 'at base of thorn tree in grassy area with scattered trees and shrubs,' and in 'runway in thick growth of weedy herbs' (habitat notes, USNM field labels).

Abundance No information.

Adaptations Nocturnal. Trapping results indicate both arboreal and terrestrial activity and well-developed scansorial abilities (Heller 1910 [in Roosevelt 1910], Loring 1910 [in Roosevelt 1910]). The natural history of *T. loringi* is very poorly documented, but anecdotal observations by collectors suggest that its ecology, food habits, behaviour and reproduction may generally resemble *T. nigricauda* and *T. paedulus*, the better known species in southern Africa.

Foraging and Food No information.

Social and Reproductive Behaviour Nests in branches of thorn trees or bushes, perhaps also in burrows near the base of trees; arboreal nests about 16 cm in diameter, fashioned of sticks, leaves and grasses (Heller 1910, Loring 1910 [both in Roosevelt 1910]). Heller (1910 [in Roosevelt 1910]) noted that runways lead from trees that contained active nests to ground burrows.

Reproduction and Population Structure Four embryos recorded for a ♀ (collected in Apr) from the Loita Plains, Kenya.

Predators, Parasites, and Diseases No information.

Conservation IUCN Category: Least Concern.

Measurements

Thallomys loringi

HB: 144 (140–160) mm, n = 9

T: 159 (143–183) mm, n = 9

HF: 27.0 (25–30) mm, n = 12

E: 22.7 (21–25) mm, n = 6

WT: 80 g, n = 1

GLS: 34.3 (31.5–37.2) mm, n = 11

GWS: 18.2 (16.1–19.7) mm, n = 12

M¹–M³: 5.6 (5.2–5.8) mm, n = 20

Kenya (USNM; M. D. Carleton unpubl.)

Key References Heller 1909; Heller 1910 [in Roosevelt 1910]; Thomas & Hinton 1923b.

Michael D. Carleton

Thallomys nigricauda BLACK-TAILED ACACIA RAT (BLACK-TAILED THALLOMYS)

Fr. Rat arboricole à queue noire; Ger. Schwarزشwänzige Baumratte

Thallomys nigricauda (Thomas, 1882). Proc. Zool. Soc. Lond. 1882: 266. Hountop (= Hudup or Hutop) River, west of Gibeon, Namibia.

Taxonomy Originally described as *Mus nigricauda*, but later assigned to the newly described genus *Thallomys* by Thomas (1920). Misonne (1974), De Graaff (1981), Smithers (1983) and Meester *et al.* (1986) refer to *nigricauda* as a subspecies of *T. paedulus*. Currently recognized as a valid species because of differences in chromosome number, body size and geographical distribution compared with *T. paedulus* (Gordon 1987). Geographical variation in external characters resulted in descriptions of 13 subspecies (see Meester *et al.* 1986), all now regarded as synonyms. Synonyms: *bradfieldi*, *damarensis*, *davisi*, *kalaharicus*, *molopensis*, *nitela*, *quissamae*, *robertsi* (two other forms, *herero* and *leuconoe* may represent *T. paedulus*). Subspecies: uncertain. Chromosome number: 2n = 47–50 (Gordon 1987).

Description Medium-sized rodent with soft, woolly pelage. Hairs long (15 mm on mid-back, 17 mm on rump). Dorsal pelage slate-grey with a wash of yellow; hairs pale slate-grey, yellow at tip, with liberal sprinkling of longer black hairs. Flanks pale grey. Ventral pelage, including chin and throat, white. Sides of face pale grey. Black band extends from nose to around eyes, and in some individuals tapers to below ears (indistinct in some populations). Long vibrissae and large eyes. Ears large, oval, especially prominent in juveniles, set at angle to head. Upper parts of legs pale grey. Feet short, broad, with strong claws and white upper parts. Four digits on forefeet. Five digits on hindfeet; Digit 5 elongated, almost as long as Digit 2. Tail long (ca. 120% HB), with black scales and short bristly black hairs; tip with longer black hairs. Nipples: 1 + 2 = 6.

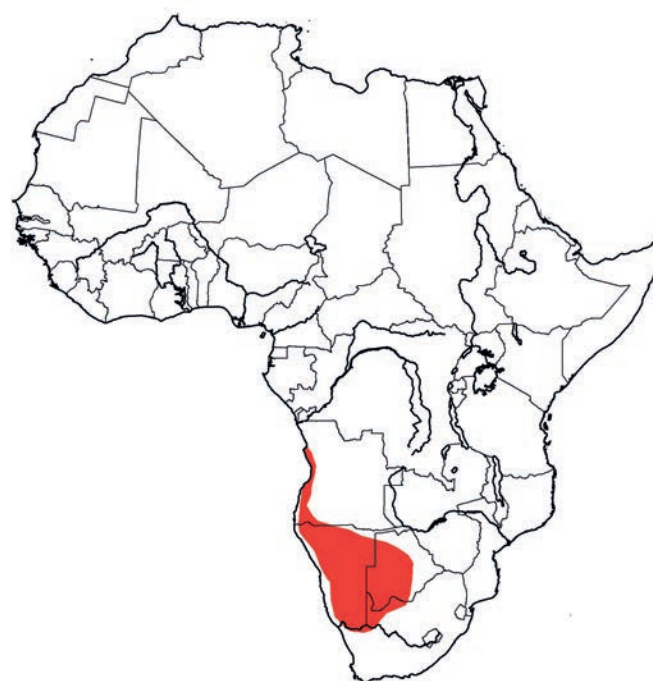
Geographic Variation Until the degree of similarity or difference between the external characters of *T. nigricauda* and *T. paedulus* is resolved, as well as their geographical relationship (see Taylor *et al.* 1995), no comments on geographical variation in *T. nigricauda* are possible.

Similar Species

T. paedulus. External differences still unresolved (Taylor *et al.* 1995).

Whereas Gordon (1987) found allopatry between the two species, Taylor *et al.* (1995) suggest extensive overlap in distribution. Chromosome number: 2n = 43–46.

T. shortridgei. Similar body size; tail longer, less hairy; dorsal pelage brown (not grey); ventral pelage slatey-grey at base; feet longer;



Thallomys nigricauda

marked reduction in black facial markings; skull on average slightly larger; nipples 0 + 2 = 4; chromosome number not known.

Distribution Endemic to Africa. South-West Arid BZ (particularly Kalahari Desert). Recorded in Namibia (except Namib Desert and dwarf shrublands), Botswana (except NE), NW South Africa and marginally in SW Angola. Degree of allopatry with *T. shortridgei* unknown (Thomas & Hinton 1923b, Taylor *et al.* 1995).

Habitat Arid savanna, especially Kalahari thornveld with *Acacia erioloba*, *A. luederitzii*, *Boscia albitrunca* and *Terminalia sericea* trees and *A. mellifera* shrubs. Also lives in habitats with *A. karoo* (interior plateau of Namibia) and *Euclea pseudobenus* (Naukluft Mts). Occurs mostly in dense or open stands of trees, but also in large isolated trees ca. 150 m away from stands.

Abundance Common in stands of suitable trees, especially *A. erioloba*, which contains cracks or nesting hollows in the trunks or between branches. Localized reduction of population numbers occurs in the SW Kalahari, perhaps due to smoke from bushfires filtering through nests and crevices. The number of inhabited trees in unburnt and burned areas differs significantly, even where many trees are only singed by the fire in 'burned' areas (J. A. J. Nel unpubl.). Single individuals, or (presumed family groups) of 2–8 inhabit specific trees (Lovegrove 1997).

Adaptations Nocturnal and arboreal. Black-tailed Acacia Rats are agile climbers; they use the prehensile tail for balancing, and the strong claws and broad feet for climbing. They construct conspicuous nests in hollow trunks and forks of trees; in the SW Kalahari, nests are 20–50 cm in diameter and there may be 1–3 nests per tree. Not all nests are occupied. Along one stretch of dry river bed, 50% of *Acacia erioloba* trees (n = 50) were inhabited. Larger trees with a circumference of 2.3 m are inhabited to a greater extent (44%) than smaller trees with a circumference of 1.7 m (15%). No correlation exists between tree size and number of nests. However, 80% of trees with signs of use (presence of faeces) by these acacia rats had no visible nests (J. A. J. Nel unpubl.). Untidy piles of interlaced twigs and thorns may hinder predators trying to enter the nest or the crevice in the tree trunk or branch. Nests are larger and better constructed than those of *T. paedulus* (Roberts 1951, Van Huyssteen 1978), but only buffer ambient temperatures by a few degrees (Lovegrove *et al.* 1991). Evaporative cooling helps to maintain body temperature well below ambient temperatures up to $T_a = 42^\circ\text{C}$, and conserves energy during the day by dropping body temperature by about 3°C (Lovegrove *et al.* 1991, Lovegrove 1997). Mean T_b is 38.2°C for males (n = 2) and 38.8°C for females (n = 6) (Nel & Rautenbach 1977). Black-tailed Acacia Rats can subsist on a vegetarian diet without free water, and their kidneys have a high urine concentrating ability (Frean *et al.* 1998).

Foraging and Food Emerges from the nest and starts to forage at dusk. Active throughout the night, with a peak of activity in the early evening that lasts longer (19:00–22:00h) in the breeding season than in the non-breeding season (19:00–21:00h) (Eccard *et al.* 2004); during the breeding season, a second peak of activity occurs near the end of the night (04:00–07:00h). These acacia rats forage in the upper levels of tree canopies, where there are no other rodent competitors, and in *Acacia* shrubs (Eccard *et al.* 2004). Foraging seldom occurs on the ground. The diet comprises young leaves, buds, the outer tunic of *Acacia* seed pods and gum obtained from grooves that the rats make by gnawing into the branches and trunks of *Acacia* trees. Occasionally, insects are eaten.

Social and Reproductive Behaviour Lives in groups of 2–8 in a single tree; groups probably consist of a breeding pair and one or more litters (Lovegrove 1997). Branches are marked by perineal dragging (Earl & Nel 1976). Single, large isolated trees or stands of trees with interlacing branches probably constitute the home-range of an individual. During the breeding season, home-ranges of ♂♂, assessed by the minimum convex polygon method, are larger (5.9–

11.5 ha, n = 3) than those of ♀♀ (0.02–0.17 ha, n = 3). In the non-breeding season, the home-ranges of ♂♂ are smaller (1.9 and 3.2 ha, n = 2) but still larger than those of ♀♀ (0.1–0.5 ha, n = 4). Males also have larger core areas than ♀♀. Females always use two core areas: one at the nest and one at a preferred feeding site (Eccard *et al.* 2004). The home-range of a ♂ usually overlaps with those of one or more ♀♀, but the core areas do not overlap (Eccard *et al.* 2004). Several social structures have been described: a breeding pair per nest with their offspring of different ages (De Graaff 1981); a family of related individuals (Roberts 1951) and a colony (Nel 1975). By following individuals with radio transmitters, Eccard *et al.* (2004) found that these acacia rats lived solitarily or with their offspring, and that they had a promiscuous breeding system. It may be that social structure varies according to the habitat.

Reproduction and Population Structure Births occur from Oct to Apr. Litter-size: 3.6 (2–5) (Skinner & Smithers 1990). Young nipple-cling (aided by prominent notches in the deciduous upper incisors) and can be carried in this way by the mother when moving to a new nest (J. A. J. Nel unpubl.) or when escaping predators (Lovegrove 1997), but not when foraging. Hair begins to grow on Day 3, pelage is completely developed at Day 9 when the tail starts getting darker and the eye-rings become noticeable. Climbing begins at Day 17 and is proficient at Day 19 (Van Huyssteen 1978). Weaned at Day 33.

Predators, Parasites and Diseases Predators include snakes, e.g. Cape Cobras *Naja nivea*, and owls to a small extent. Ectoparasites recorded for *Thallomys paedulus sensu lato* (i.e. including *T. nigricauda*) include fleas of the families Pulicidae, Hystrihopsyllidae and Chimaeropsyllidae (including some spp. that are vectors of plague), mites and ticks (details in De Graaff 1981). One endoparasite, a cestode *Inermicapsifer madagascariensi*, has been recorded (De Graaff 1981).

Conservation IUCN Category: Least Concern.

Measurements

Thallomys nigricauda

HB: 135.0 (117–147) mm, n = 6

T: 146.8 (127–156) mm, n = 6

HF (c. u.): 24.7 (22–26) mm, n = 6

E: 20.5 (20–22) mm, n = 6

WT: 73.8 (50–84) g, n = 5

GLS: 33.3 (32–36) mm, n = 24

GWS: 14.1 (17–19) mm, n = 24

M^1 – M^3 : 5.2 (4.7–5.7) mm, n = 24

Body measurements and weight: SW Kalahari, South Africa (J. A. J. Nel unpubl.)

Skull measurements: Taylor *et al.* (1995) and Roberts (1951); specimens of Taylor *et al.* positively karyotyped as *T. nigricauda*

Key References De Graaff 1981; Lovegrove 1997; Shortridge 1934; Skinner & Smithers 1990.

Jan A. J. Nel

Thallomys paedulus SUNDEVALL'S ACACIA RAT (ACACIA THALLOMYS)

Fr. Rat arboricole des Acacias; Ger. Sundevalls Baumratte

Thallomys paedulus (Sundevall, 1846). Ofv. K. Svenska Vet.-Akad. Forhandl. Stockholm, 3: 120. 'In Caffrania interiore, prope tropicum'. Davis (1965) defines the type locality as Crocodile Drift, Brits, Transvaal, South Africa.

Taxonomy Originally described in the genus *Mus*. The limits of this species have been controversial, and there have been many changes in the definition of the species. De Graaff (1981) and Smithers (1983) considered that *T. paedulus* was the only species in southern Africa. Meester *et al.* (1986) likewise recognized only *T. paedulus*, and listed 14 forms as subspecies in southern Africa. Smithers (1971) listed three subspecies in Botswana, and Smithers & Wilson (1979) listed two subspecies in Zimbabwe. Two of these forms are now considered to be valid species (*T. nigricauda*, *T. shortridgei*), the remainder are regarded as synonyms of this species or of *T. nigricauda* (see De Graaff 1981 and Meester *et al.* 1986 for detailed reviews). Because *T. nigricauda* was included in *T. paedulus* until recently, some of the biological information for *T. paedulus* in southern Africa may refer to *T. nigricauda*. Synonyms: *acaciae*, *lebomboensis*, *moggi*, *rhodesiae*, *ruddi*, *scotti*, *somaliensis*, *stevensoni*, *zambeziensis*. Subspecies: none. Chromosome numbers: $2n = 43, 44, 45$ and 46 ; species-specific X chromosome (Gordon & Rautenbach 1980, Bowland & Gordon 1983, Gordon 1987).

Description Medium-sized arboreal mouse with very long black or blackish-brown tail. Pelage generally long and soft. Dorsal pelage yellowish-grey, pale rufous, cinnamon or pale brown; dorsal hairs medium-grey at base, with buff, cinnamon or yellowish-brown at tip; scattered fine black guard hairs. Flanks often greyer than dorsal pelage. Ventral pelage pure white. Pelage colour varies geographically and seasonally (see below). Head similar in colour to dorsal pelage. Black markings on face extend from nose to the eye, around each eye and more diffusely to the ear in some individuals. Eyes large and black. Ears conspicuous, rounded, pigmented, with sparse buff hairs. Chin and throat pure white. Limbs short. Upper surface of forefeet and hindfeet with dense, short, white hair, and strong, short claws. Tail long (ca. 120% of HB), black or blackish-brown, scaly, with numerous small black bristles. Skull: auditory bullae unusually large for a murid rodent (ca. 6 mm); anterior palatal foramina long, extending posteriorly to between M^1 's (cf. *P. loringi*). Nipples: $0 + 3 = 6$, $0 + 2 = 4$, $1 + 2 = 6$.

Geographic Variation Pelage colour varies geographically. In Botswana, for example, pelage is grey with a yellow tinge in drier habitats (Kalahari), and buffy-brown with darker flanks in moister habitats (Okavango Delta) (Smithers 1971). In Zimbabwe, some individuals have brown forefeet rather than white forefeet (Smithers & Wilson 1979). In Kenya, dorsal pelage tends to be pale rufous or cinnamon. Length of M^1 – M^3 varies geographically, but the significance of this variation is uncertain. Pelage varies seasonally in Botswana: in Nov–Apr (warm wet season), pelage is shorter, darker and less dense than in Jun–Oct (cool dry season) when it is longer, paler (yellow or reddish) and denser (Smithers 1971).

Similar Species

T. nigricauda. Similar in size; black markings on head more conspicuous; tail black; may be parapatric in Botswana.

T. loringi. Similar size; dorsal pelage brown (not grey); possibly sympatric in Kenya and Tanzania.

Graphiurus spp. Smaller; bushy tails.

Distribution Endemic to Africa. Zambezi Woodland BZ and southern part of Somalia–Masai BZ. Recorded from E South Africa (Transvaal and KwaZulu–Natal Provinces), Angola, Botswana, Zimbabwe, Mozambique (south of the Zambezi R.), Swaziland, S Zambia, S DR Congo, Malawi, Tanzania, Kenya, S Ethiopia and S Somalia. Limits uncertain. Widespread in southern Africa; localized in East Africa.

Habitat Savanna habitats, especially woodlands of *Acacia* spp. In East Africa, associated mainly with *A. xanthophloea* and *A. tortilis* trees (Kingdon 1974).

Abundance Locally common in suitable habitats but populations may be small and isolated; no quantitative information available.

Adaptations Arboreal and nocturnal. Lives more or less continuously in trees and is well adapted for arboreal life. In Zimbabwe, makes nests of grass, sticks and leaves, which are dragged into hollow trunks or under the bark of trees (Smithers & Wilson 1979). Probably independent of free drinking water. In most respects, these acacia rats appear to resemble *T. nigricauda*. See also genus profile.

Thallomys paedulus has a complex sacculated stomach comprising a non-glandular forestomach with diverticulae (pouches) that

*Thallomys paedulus*

contain symbiotic bacteria, a glandular stomach and also complex folds and sphincters that control regurgitation and the passage of the digesta (flow of the food) (Perrin 1986). The stomach is one of the most complex described for any rodent. Its function is aided by the microflora, which are thought to detoxify chemical plant defences as well as digest complex polysaccharides.

Foraging and Food Predominantly vegetarian. Most food is obtained in trees. Forages mainly in the canopy, and has regular pathways along the lower branches. The principal food is fresh young leaflets and green twigs of *Acacia* trees and, less frequently, *Acacia* flowers, the green or outer coating of *Acacia* pods and the berries of *Zizyphus macronata* (Smithers & Wilson 1979). At times, may forage on the ground for *Acacia* pods.

Social and Reproductive Behaviour Little information; acacia rats probably live in small communities of an adult pair and their offspring (De Graaff 1981).

Reproduction and Population Structure In Zimbabwe, pregnant ♀♀ recorded in Aug, Nov, Feb (four pregnancies in sample of 23, taken throughout year) (Smithers & Wilson 1979). In Botswana, pregnant ♀♀ recorded in Oct, Feb, Mar and Apr (five pregnancies in sample of 93, taken throughout year). In southern Africa, most pregnancies recorded in the warmer months of the year; no information for eastern Africa. Reproductive data for captive individuals (originally from Transvaal) kept at ambient temperatures (Meester & Hallett 1970) are: litter-size: 2.7 (range not given; $n = 23$ litters); minimum interval between litters: 26 days. At birth, WT: 2.5–2.8 g, altricial and hairless. Incisors erupt Day 1; ear pinna open Day 1; eyes open

Day 15; efficient walking Day 15; weaned Day 28–31; minimum age at maturity (age at first litter) Day 107. Young attached to nipples until Day 25; mother nipple-draws until Day 15.

Predators, Parasites and Diseases Predators include the Giant Eagle-owl *Bubo lacteus* (Pitman & Adamson 1978). Ectoparasites include many species of fleas and mites, and are probably similar to those of *T. nigricauda* (details in De Graaff 1981). Host to the flea *Xenopsylla brasiliensis*, which is a vector of plague (De Meillon *et al.* 1961).

Conservation IUCN Category: Least Concern.

Measurements

Thallomys paedulus

HB: 140.3 (130–155) mm, $n = 6$

T: 166.2 (157–179) mm, $n = 5$

HF: 25.3 (24–27) mm, $n = 6$

E: 20.8 (19–22) mm, $n = 6$

WT: 72.3 (55–85) g, $n = 6$

GLS: 32.8 (30.2–34.6) mm, $n = 9$

GWS: 16.4 (14.9–17.6) mm, $n = 9$

M¹–M³: 4.9 (4.1–5.4) mm, $n = 10$

Auditory bulla: 6.9 (6.3–7.9) mm, $n = 9$

Zambia and South Africa (TM, HZM)

Key References De Graaff 1981; Meester *et al.* 1986; Skinner & Smithers 1990.

Mike Perrin

Thallomys shortridgei SHORTRIDGE'S ACACIA RAT (SHORTRIDGE'S THALLOMYS)

Fr. Rat arboricole de Shortridge; Ger. Shortridges Baumratte

Thallomys shortridgei Thomas & Hinton, 1923. Proc. Zool. Soc. Lond. 1923: 492. Louisvale on the south bank of the Gariep (= Orange) River, near Upington, Northern Cape Province, South Africa.

Taxonomy Described by Thomas & Hinton (1923) as a distinct species on the basis of external and skull characters, especially the weakly developed facial markings and smaller auditory bullae. This view was accepted by Roberts (1951), who recognized four species of *Thallomys* in southern Africa: *T. nigricauda*, *T. shortridgei*, *T. damarensis* (now synonym of *T. nigricauda*) and *T. moggi* (now synonym of *T. paedulus*). However, Ellerman (1941) regarded *shortridgei* as a subspecies of *Thallomys nigricauda*. More recent assessments have maintained *shortridgei* as a valid species (Skinner & Smithers 1990, Musser & Carleton 1993, 2005, Bronner *et al.* 2003). Synonyms: none. Chromosome number: not known.

Description 'A brown species with slightly developed face markings. Size about as in *T. nigricauda*, or slightly smaller. General colour above brown – near "Brussels Brown" – not as greyish as in other species. Under surface white, but the bases of the hairs are mostly slaty ... Face grey, but the brown of the crown reaches as far forward as between the eyes. Dark facial markings hardly developed at all, the darker edges of the orbit quite narrow and inconspicuous, and not

extending forwards or backwards as an ocular streak. Ears about the colour of the head; hairs behind them buffy-brown. Hands and feet white, with darker patches on the metapodials. Tail long, black. ... Skull with well-marked supraorbital ridges, long anterior palatal foramina, and rather small bullae ...' (Thomas & Hinton 1923b). Nipples: 0 + 2 = 4.

Geographic Variation None recorded.

Similar Species

T. nigricauda. Grey above (not brown), black facial markings much more prominent, tail more haired, shorter; ears slightly smaller; auditory bullae slightly larger. Nipples: 1 + 2 = 6.

Distribution Endemic to Africa. South-West Arid BZ. Recorded only in South Africa, from the south bank of the Gariep (= Orange) River, from near Upington westwards to Goodhouse. Degree of allopatry with *T. nigricauda* not known.

Habitat *Acacia* thornveld and scrub.

Abundance No information.

Remarks Apparently no other information available.

Conservation IUCN Category: Data Deficient.

Measurements

Thallomys shortridgei

HB: 140–150 mm, n = 4

T: 183–210 mm, n = 4

HF: 27–28 mm, n = 4

E: 23–25 mm, n = 4

WT: n. d.

GLS: 34.2–37 mm, n = 4

GWS: 18–18.7 mm, n = 4

M¹–M³: 5.5–5.7 mm, n = 4

South Africa (Roberts 1951)

Mean values not recorded

Key Reference Thomas & Hinton 1923b.



Thallomys shortridgei

Jan A. J. Nel

GENUS *Thamnomys*

Thicket Rats

Thamnomys Thomas, 1907. Ann. Mag. Nat. Hist., ser. 7, 19: 121. Type species: *Thamnomys venustus* Thomas, 1907.

The genus *Thamnomys* contains three species, each with a very restricted distribution in the Rainforest BZ of DR Congo, or in the montane forests of the Albertine Rift Valley. The genus is not well known because of its restricted distribution and rarity.

All species in the genus are medium-sized with soft long pelage and a very long tail ending in a small pencil. Dorsal pelage is brownish, usually orange-rufous on the rump, and ventral pelage is whitish. Hindfeet are broad and relatively short. The cheekteeth are distinguished by the strongly developed postero-internal cusp (t7) on M¹ and M²; in this respect, it differs from the closely related genus *Grammomys* in which the cusp is reduced to a narrow ridge between t4 and t8 (see genus profile). This difference is considered to be large enough to warrant generic recognition (Ellerman 1941, Rosevear 1969, Hutterer & Dieterlen 1984, Musser & Carleton 1993). The almost rectangular-shaped molars of *Thamnomys* are in contrast to the rounded shape of the upper molars of *Grammomys*. The skull has a long rostrum, broad braincase, well-developed supraorbital ridges, long open anterior palatal foramina, which reach nearly to the level of M¹, medium-sized auditory bullae, and the zygomatic plate is more or less straight anteriorly (Figure 89). The molar pattern shows great similarities to that of the genus *Oenomys*.

All species in the genus are arboreal and, like *Grammomys* spp., show adaptations for climbing on branches and twigs. Collectively, less is known about the biology of *Thamnomys* spp. than for *Grammomys* spp., although it is presumed that both genera are rather similar in many respects (see *Grammomys* profiles). All species of *Thamnomys* are



Thamnomys venustus.

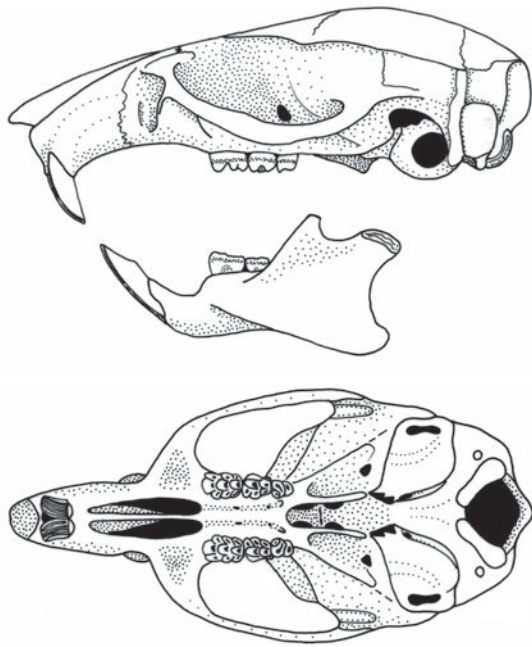


Figure 89. Skull and mandible of *Thamnomys venustus* (BMNH 65.3777).

Thamnomys kemp KEMP'S THICKET RAT (KEMP'S THAMNOMYS)

Fr. Rat des fourrés de Kemp; Ger. Kemps Dickichtratte

Thamnomys kemp Dollman, 1911. Ann. Mag. Nat. Hist., ser. 8, 8: 658. Buhamba, near L. Kivu, DR Congo. 6000 ft (1830 m).

Taxonomy Although described as markedly different from *Thamnomys venustus*, *T. kemp* was often considered to be a subspecies of *T. venustus* (e.g. Ellerman 1941, Misonne 1974). Important differences in skull characters, especially larger size, longer anterior palatal foramina than in the other species, and the absence of t9 on M¹ and M², justify recognition of *T. kemp* as a valid species. *Thamnomys kemp* may represent a subgenus, separate from *T. venustus* and *T. schoutedeni* (Dieterlen 1999 and unpubl.). Synonyms: *major*. Subspecies: none recognized here, although *major* was considered to be a subspecies by Musser & Carleton (1993) and a distinct species by Musser & Carleton (2005). Chromosome number: not known.

Description Large arboreal rat with bright orange-rufous pelage and very long tail; the largest species of the genus. Dorsal pelage soft and long (ca. 15 mm), bright orange-rufous especially on rump; hairs black at base, rufous at tip; brown hairs interspersed in pelage, especially on anterior part of body. Flanks slate-grey, washed with bright yellowish-buff. Ventral pelage whitish, often with yellowish or yellowish-orange tint; hairs dark at base, whitish at tip. Colour of flanks clearly delineated from ventral pelage, sometimes with thin line of yellow. Head greyish-buff; tip of nose black. Narrow dark eye-ring. Ears with dark brownish hairs on outer surface and short golden-buff hairs on inner surface. No subauricular tuft. Hindfeet broad and comparatively short. Fore- and hindlimbs and fore- and hindfeet buff, with conspicuous dark patches on upper surfaces of feet. Tail very long (ca. 130% of HB), slightly scaly, dark above, slightly paler below, with short bristles, and longer hairs at tip

probably vegetarian, and limited evidence suggests that they have small litters. The genus has a very limited distribution compared with *Grammomys*, and each species within the genus has a much smaller distribution than most species of *Grammomys*.

Phylogenetically *Thamnomys* is close to *Oenomys*. The genus *Thamnomys* at one time contained all those species now assigned to the genus *Grammomys*, or to the subgenus *Thamnomys* (*Grammomys*); hence *Thamnomys* now contains fewer species than previously.

The species in the genus may be distinguished by body size (see species profiles).

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forming pencil. In young individuals, dorsal pelage dark brownish-grey, ventral pelage whitish (but less so than in adults), sometimes with orange tint. Skull with long anterior palatal foramina (mean 8.80 mm); t7 on M¹ and on M² elongated and well developed; t9 on M¹ and on M² absent. Nipples: 0 + 2 = 4.

Geographic Variation Two forms may be distinguished:

kemp: Virunga Mts southwards on both sides of the Albertine Rift Valley to ca. 02° 20' S. Characters as described above.

major: Virunga Mts above 3000 m (parts only). Pelage longer; skull measurements on average longer than in *kemp*.

Similar Species

T. venustus. On average smaller than *T. kemp*; skull smaller, anterior palatal foramina shorter (mean 6.50 mm), molar teeth smaller and narrower; large t9 on M¹ and smaller t9 on M²; partially sympatric.

T. schoutedeni. Smallest species of genus (means: HB: 119 mm, HF: 25 mm); skull smaller; anterior palatal foramina shorter (mean 6.81 mm); large t9 on M¹; not sympatric.

Distribution Endemic to Africa. Afromontane–Afroalpine BZ of the Albertine Rift Valley on both sides of L. Kivu. Recorded from a relatively small area between ca. 01° S and 03° S; known from the Virunga Mts and Kahuzi–Biega N. P. west of L. Kivu in DR Congo, Nyungwe F. R. in Rwanda, and from NW Burundi. The presence of



Thamnomys kempi

T. kempi from north of the Virunga Mts to the highlands west of L. Albert is uncertain (because of the problems of identification and separation from *T. venustus*). Altitudinal range ca. 1800–3500+ m.

Habitat Preferred habitat is thickets in open areas of montane secondary forests (and occasionally in primary forests) (F. Dieterlen unpubl.). The thickets are composed mainly of two vines *Sericostachys scandens* and *Urera hypselodendron*, a herb *Brillantaisia cicatricose*, and a tree fern *Marattia fraxinea*; the forest includes *Neobutonia macrocalyx*, *Hagenia abyssinica* and *Myrianthus holstii* trees. Not recorded from bamboo forests or marshes near to thickets.

Abundance Generally rare; in four regions of E DR Congo, comprised 2.5% (1.6–13.5%) of all small rodents obtained (regardless of habitat; $n = 5883$). Occasionally may be quite common in suitable thickets; in one thicket comprised 39% ($n = 40$) of small rodents. More common than the other species of *Thamnomys*.

Adaptations Kemp's Thicket Rats are good climbers, which live most of the time in thickets, although they may also descend to the ground. They build large nests. Activity is chiefly nocturnal and crepuscular (ca. 60%; Rahm 1967). Morphological adaptations for climbing include short broad hindfeet and long tail. The alimentary tract is unusually long, six times longer than HB length, indicating

a pure vegetarian diet. Stomachs are large and when full weigh up to 22% of body weight. Length and volume of caecum and colon are also large and typical of a herbivore. Measurements (means and ranges for freshly caught specimens): stomach 52 (45–60) mm; small intestine 450 (380–480) mm; caecum 97 (85–115) mm; colon 340 (290–380) mm (F. Dieterlen unpubl.).

Foraging and Food Herbivorous. The diet appears to be almost exclusively green material. Stomach contents consisted of a uniform green pulp with only very small fibres, sometimes with fruit pulp. Since herbs were not abundant near thickets, the 'green pulp' is assumed to be from leaves, buds and fruits of thicket plants. An individual in captivity preferred fruits (bananas etc.) (F. Dieterlen unpubl.).

Social and Reproductive Behaviour No information.

Reproduction and Population Structure Reproduction recorded in all months from Jan to Sep, when 70–100% (mean 72%) of 47 adult ♀♀ were pregnant and/or lactating; reproduction lower in Oct–Dec (mean 30%, $n = 10$) (F. Dieterlen unpubl.). Embryo number: 1.43 (1–2), $n = 23$ ♀♀. Young are born in nests, and nipple-cling even when mother is active outside the nest (Hatt 1940a). Sexual maturity attained when 70 g. Sex ratio of trapped individuals: 61% ♀♀ : 39% ♂♂ ($n = 161$ captures); ratio more biased towards ♀♀ than in other murids in central Africa.

Conservation IUCN Category: Vulnerable.

Montane forests along the Albertine Rift Valley are under threat, and hence the species should be considered as vulnerable or endangered (as are other endemic species in the Albertine Rift Valley).

Measurements

Thamnomys kempi

HB: 155 (130–173) mm, $n = 48$

T: 202 (170–226) mm, $n = 48$

HF (c.u.): 29.3 (27–32) mm, $n = 48$

E: 23.6 (20–26) mm, $n = 48$

WT: 84 (62–108) g, $n = 48$

GLS: 37.5 (35.3–39.7) mm, $n = 24$

GWS: 17.5 (16.9–18.6) mm, $n = 11$

M^1 – M^3 : 6.8 (6.4–7.2) mm, $n = 31$

Kivu region, DR Congo (SMNS, F. Dieterlen unpubl.)

Key References Dieterlen 1999; Dollman 1911d.

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Thamnomys schoutedeni SCHOUTEDEN'S THICKET RAT (SCHOUTEDEN'S THALLOMYS)

Fr. Rat des fourrés de Schouteden; Ger. Schoutedens Dickichtratte

Thamnomys schoutedeni Hatt, 1934. Amer. Mus. Novit. 708: 9. Medje, Ituri District, DR Congo.

Taxonomy The form *schoutedeni* was first described as a subspecies of *Thamnomys venustus* by Hatt (1934). Raised to specific rank by Dieterlen (1999) on the basis of its smaller body and skull measurements.

Musser & Carleton (2005) place *schoutedeni* as a synonym of *T. venustus*. Synonyms: none. Chromosome numbers: not known.

Description Small to medium-sized arboreal rodent; smallest species in the genus. Pelage long and soft. Dorsal pelage brown or russet-brown; hairs grey at base, brownish at tip. Flanks paler. Ventral pelage whitish; hairs grey at base, white at tip; colour of base shows on surface of pelage. Colour of flanks clearly delineated from ventral pelage, without any separating line of colour. Head similar in colour to dorsal pelage. No dark eye-ring. Ears dark brownish. White subauricular tuft. Hindfeet comparatively short. Upper surface of feet similar in colour to flanks. Tail very long (ca. 155% of HB), brown, almost naked, with slight pencil at tip. Skull with relatively long anterior palatal foramina (mean 6.81 mm); t7 on M¹ and on M² elongated and well developed; large t9 on M¹ and smaller t9 on M². Nipples: not known.

Geographic Variation None recorded.

Similar Species

T. kempi. Much larger in all measurements; skull with longer anterior palatal foramina (mean 8.80 mm); t9 on M¹ and on M² absent.

T. venustus. Larger in all measurements; skull larger, anterior palatal foramina shorter (mean 6.50 mm), large t9 on M¹.

Grammomys kuru. Similar in size (perhaps very slightly smaller); pelage shorter, ventral pelage pure white, molars with rounded shape, t7 and t9 of M¹ and M² smaller.

Distribution Endemic to Africa. Rainforest BZ (East Central Region). Recorded only at Medje (800 m) in Ituri Forest, DR Congo, and at Irangi, E DR Congo (ca. 800–1450 m).

Habitat At Irangi, primary rainforest, secondary forest and submontane forest.

Abundance Extremely rare, known only by a few specimens. Appears to be much rarer than *G. kuru*, with which it is syntopic.

Remarks Nothing is known about this species, but it is assumed that it has a similar life-style to other species in the genus, and to *G. kuru*.

Conservation IUCN Category: Data Deficient.



Thamnomys schoutedeni

Measurements

Thamnomys schoutedeni

HB: 119 (114–122) mm, n = 4

T: 185 (171–203) mm, n = 4

HF: 25 (24–26) mm, n = 4

E: 18.5 (16–20) mm, n = 4

WT: 40, 50 g, n = 2

GLS: 32.8, 34.1 mm, n = 2

GWS: 15.9, 16.0 mm, n = 2

M¹–M³: 5.7, 6.1 mm, n = 2

Medje and Irangi, DR Congo (SMNS)

Two specimens were between subadult and adult

Key References Dieterlen 1999; Hatt 1934, 1940a.

Fritz Dieterlen

Thamnomys venustus CHARMING THICKET RAT (THOMAS'S THAMNOMYS)

Fr. Rat des fourrés charmant; Ger. Anmutige Dickichtratte

Thamnomys venustus Thomas, 1907. Ann. Mag. Nat. Hist., ser. 7, 19: 122. Rwenzori East, Uganda. 7000 ft (2130 m).

Taxonomy Type species of the genus *Thamnomys*. Specimens recorded as *T. venustus* from parts of Uganda and DR Congo (see below) may not be this species and hence biological information from these specimens is not included here. Synonyms: *kivuensis*. Subspecies: the form *kivuensis* was considered to be a subspecies by Allen & Loveridge (1942) but it is not recognized as such here. Chromosome number: not known.

Description Medium-sized arboreal species with a very long tail; rather similar to *T. kempi* but smaller, although larger than *T. schoutedeni*. Dorsal pelage long (ca. 15 mm), dark brown; hairs slate-grey at base,

reddish-brown or yellowish-brown at tip. Flanks yellowish-brown; hairs with bright yellow tip. Ventral pelage whitish, sometimes tinted with yellow; hairs greyish at base, whitish at tip; colour of base shows on surface of pelage. Colour of flanks clearly delineated from ventral pelage, sometimes with thin line of yellow. Head similar in colour to dorsal pelage. Narrow dark eye-ring. Ears reddish-brown. No subauricular tuft. Fore- and hindlimbs as well as fore- and hindfeet reddish-brown; toes whitish. Dark patches on upper surface of feet (as in *T. kempi*). Hindfeet broad and comparatively short. Tail very long (ca. 135% of HB), dark above, slightly paler below, with short hairs, longer hairs form a pencil at tip. Skull large with relatively

long anterior palatal foramina (mean 6.50 mm), but shorter than in *T. kemp*i); t9 on M¹ and on M² elongated and well developed; large t9 on M¹ and a smaller t9 on M². Nipples: 0 + 2 = 4.

Geographic Variation None recognized here.

Similar Species

*T. kemp*i. On average larger in most respects; skull larger; anterior palatal foramina longer (mean 8.80 mm); t9 on M¹ and M² absent. *T. schoutedeni*. Smaller in all respects, anterior palatal foramina longer (mean 6.81 mm); t9 on M¹ large.

Distribution Endemic to Africa. Afroalpine–Afroalpine BZ of the Albertine Rift Valley in a comparatively small area between ca. 01° N and 03° S. Recorded from East Rwenzori, Uganda; Kahuzi–Biega N. P., DR Congo (Dieterlen 1999); and on Idjwi I. in L. Kivu, DR Congo (Allen & Loveridge 1942). The identification of other specimens, purported to be *T. venustus*, from west of L. Albert (Blukwa, Djugu) and from the Lubero–Butembo highlands (both in DR Congo; Misonne 1963), Kigezi (Uganda; Delany 1975) and from the Virunga Mts (Verschuren *et al.* 1983) is uncertain. Altitudinal range ca. 1800–3000 m.

Habitat Thickets in montane forests; habitats similar to those of *T. kemp*i.

Abundance Uncertain; rarely collected.

Remarks Very little is known about the species, but it is probably similar in many ways to *T. kemp*i. Of two ♀♀ captured in the region of Kahuzi–Biega N. P. in Jun and Jul, one contained one embryo, the other was lactating.

Conservation IUCN Category: Vulnerable.

Montane forests along the Albertine Rift Valley are under threat, and hence the species should be considered as vulnerable or endangered (as are other endemic species in the Albertine Rift Valley). Recorded by Schlitter (1989) as ‘insufficiently known’ to place in any threat category.



Thamnomys venustus

Measurements

Thamnomys venustus

HB: 146 (140–160) mm, n = 6

T: 198 (183–209) mm, n = 6

HF: 26.3 (25–27) mm, n = 6

E: 21.3 (20–23) mm, n = 6

WT: 64 (59–70) g, n = 6

GLS: 35.2 (34.8–35.7) mm, n = 6

GWS: 16.5 (15.9–17.0) mm, n = 3

M¹–M³: 6.1 (5.8–6.5) mm, n = 6

Kivu, DR Congo (SMNS, F. Dieterlen unpubl.)

Key References Dieterlen 1999; Thomas 1907a.

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GENUS *Zelotomys* Broad-headed Mice

Zelotomys Osgood, 1910. Field Mus. Nat. Hist. Publ. Zool. ser. 10 (2): 7. Type species: *Mus hildegardae* Thomas, 1902.

The genus contains two species, one (*Z. hildegardae*) in grasslands of the Zambezian Woodland BZ of central and eastern Africa, and the other (*Z. woosnami*) in arid and semi-arid habitats of the South-West Arid BZ of southern Africa.

The genus is characterized by its medium size, scaly white tail, ten nipples in ♀♀ of both species, and a superficial similarity to *Mastomys*. The skull is short and broad with very short braincase, ungrooved incisors, which are either pro-odont (*Z. hildegardae*) or orthodont (*Z. woosnami*), and very broad molars with rather high-crowned cusps (Figure 90). M¹ longer than M² + M³, and M² broader than long.

Zelotomys shows relationships to *Colomys* in respect of the molar teeth (Misonne 1969a), mitochondrial DNA cytochrome *b* (Lecompte *et al.* 2002b) and nuclear IRBP gene sequences (E. Lecompte, in Musser & Carleton 2005). *Zelotomys*, *Colomys* and *Myomyscus* appear to form a monophyletic cluster within a larger group composed of *Praomys*, *Mastomys*, *Myomyscus*, *Hylomyscus*, *Heimyscus* and *Stenocephalemys* (Musser & Carleton 2005).

Zelotomys is a rare or uncommon genus, and forms only a small percentage of rodent communities. Individuals of both species appear to be insectivorous or omnivorous, and mostly solitary. One species, *Z. hildegardae*, is noted for its very strong, offensive odour. Because

of their rarity, information on the genus is sparse. The species are distinguished by the form of the incisors and geographic distribution.

Jan A. J. Nel



Zelotomys hildegardae.

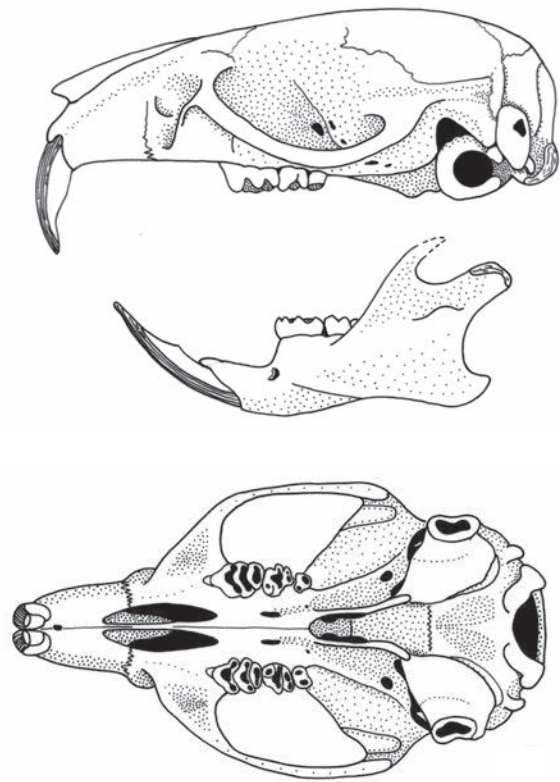


Figure 90. Skull and mandible of *Zelotomys hildegardae* (RMCA 82.11.M.531).

***Zelotomys hildegardae* HILDEGARDE'S BROAD-HEADED MOUSE (HILDEGARDE'S ZELOTOMYS)**

Fr. Souris de Hildegarde; Ger. Hildegardes Breitkopfmaus

Zelotomys hildegardae (Thomas, 1902). Ann. Mag. Nat. Hist., ser. 7, 9: 219. Machakos, Kenya.

Taxonomy Originally described in the genus *Mus*. Synonyms: *instans*, *kuvelaiensis*, *lillyana*, *shortridgei*, *vinacaus*. Subspecies: none. Chromosome number: not known.

Description Medium-sized mouse with slightly broadened skull and long slightly pro-odont incisors. Pelage soft and dense. Dorsal pelage grey or greyish-brown, slightly flecked with buff; hairs dark grey at base, buff at tip. Ventral pelage pale grey to brownish-grey; hairs grey at base, white at tip. Colour of dorsal and ventral pelage merge on flanks. Head somewhat broadened; cheeks pale grey to white. Chin and throat pale grey to white. Vibrissae dark. Ears oval, darkly pigmented, sparsely haired with scattered short white or buff hairs. Fore- and hindlimbs short, whitish above and below. Feet off-white, sometimes brown above. Tail moderately short (70% of HB), mostly naked and ringed with small scales; hairs sparse and short, white to grey-brown (sometimes hair white below, brown with white tips above). Emanates a very strong smell. Skull: broad (due to flaring zygomatic arches); postorbital ridge absent; upper incisor teeth ungrooved, long and pro-odont. Nipples $3 + 2 = 10$.

Geographic Variation Overall considerable variation in pelage colour (Hollister 1919, Misonne 1965a, Ansell 1978).



Zelotomys hildegardae

Similar Species

Z. woosnami. Incisors orthodont; southern Africa only.

Mastomys spp. (primarily *M. erythroleucus* and *M. natalensis*). On average slightly larger, upper incisor teeth orthodont; tail grey and relatively longer (ca. 90% of HB); up to 24 nipples arranged in two longitudinal rows.

Distribution Endemic to Africa. Eastern and Southern Rainforest–Savanna Mosaics, and Zambezian Woodland BZ in central and East Africa. Recorded from Angola, N Zambia, N Malawi, Tanzania, Kenya, W Uganda, Rwanda, Burundi, NE DR Congo and S Sudan. Musser & Carleton (2005) also list Central African Republic.

Habitat Moist grassy savanna and scrub, edge of swamps and forests (Misonne 1965a), and grasslands. Favours *Imperata* grasses in Serengeti N. P., Tanzania (Misonne & Verschuren 1966) and Queen Elizabeth N. P., Uganda (Delany 1964b, 1975). Syntopic in Virunga N. P. in E DR Congo with *Otomys irroratus*, *Aethomys kaiseri* and *Arvicanthis abyssinicus* (Verschuren *et al.* 1983). On the Nyika Plateau, Malawi, recorded from pine plantations and near houses (Hanney 1965).

Abundance Fairly low; usually comprises <3% of captured rodents. Comprised 2.15% of rodents caught in Queen Elizabeth N. P., Uganda, occurring in only two of four habitats sampled (Delany 1964b); 0.31% in Virunga N. P., DR Congo (Verschuren *et al.* 1983); and 2.6% (n = 349) in grassland of Rwenzori Mountains N. P., Uganda (Cheeseman 1975). In the crater area of Rwenzori Mountains N. P., estimated population density throughout year varied from 0.44 to 1.33 individuals/ha (Cheeseman 1975), dropping immediately after burning of savanna grasses. In Rwanda (Misonne 1965a), comprised 1.5% of rodents trapped, but 3.37% of rodents (n = 267) in owl pellets; perhaps more common in some areas than trapping results indicate.

Adaptations Terrestrial and nocturnal. In captivity, constant activity occurs throughout the night (n = 3 animals; Cheeseman 1975). Like shrews, these mice have a strong unpleasant smell, which may protect them from predators (Kingdon 1974). Makes a high-pitched whistling call (Delany 1975).

Foraging and Food Mainly insectivorous. Probably forages underneath grass cover (Kingdon 1974). Contents of stomachs have included Orthoptera (Delany 1964b), ‘insects’ (Misonne 1965a) and ‘remains of insects and fruits’ (Misonne & Verschuren 1966); myriapods and dung beetles are also eaten (Kingdon 1974). In captivity, eats meat (Delany 1975).

Social and Reproductive Behaviour No information.

Reproduction and Population Structure Pregnant ♀♀ recorded in Jun and Nov in Kenya (Hollister 1919, Southern & Hook 1963), and Feb, Mar, May–Jul in Uganda (Delany 1975); no information for other months. Litter-size: 3–7.

Predators, Parasites and Diseases Remains found in pellets of raptors in Rwanda (Misonne 1965a). Harbours various ectoparasites, e.g. Anoplura and Acarina (Benoit 1959, Colbo 1973, Fain 1976, Fain & Lukoschus 1977).

Conservation IUCN Category: Least Concern.

Measurements

Zelotomys hildegardae

HB: 125.8 (104–142) mm, n = 28

T: 87.9 (80–100) mm, n = 26

HF: 22.5 (21–26) mm, n = 27

E: 14.6 (12–18) mm, n = 23

WT: 59.8 (38–74) g, n = 25

GLS: 31.4 (30.6–32.3) mm, n = 9

GWS: 17.8 (16.8–18.2) mm, n = 7

M¹–M³: 5.3 (4.7–5.6) mm, n = 9

Body measurements and weight: Uganda (Delany 1975)

Skull measurements: Kenya, Uganda, Malawi (BMNH)

Key References Delany 1975; Kingdon 1974.

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Zelotomys woosnami WOOSNAM'S BROAD-HEADED MOUSE (WOOSNAM'S ZELOTOMYS)

Fr. Souris de Woosnam; Ger. Woosnams Breitkopfmaus

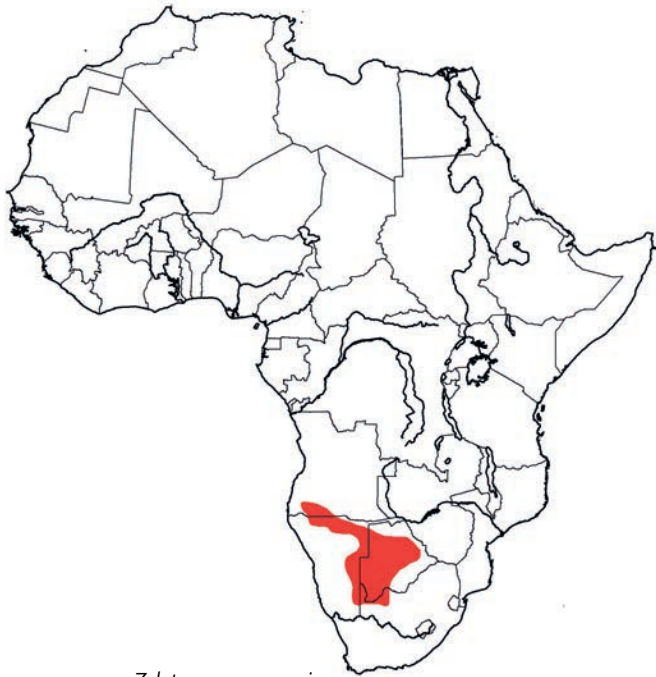
Zelotomys woosnami (Schwann, 1906). Proc. Zool. Soc. Lond. 1906: 108. Kuruman, South Africa.

Taxonomy Originally described in the genus *Mus* and subsequently placed in the genus *Ochromys* (e.g. Shortridge 1934), and allied with *Aethomys*, *Rattus* and *Thallomys* (Musser & Carleton 2005). Synonyms: none. Chromosome number: not known.

Description Medium-sized, somewhat slender mouse with white tail. Pelage soft and smooth; hairs 15 mm on back. Dorsal pelage uniform pale grey to buff-grey; hairs slate-grey on basal two-thirds, pale grey on terminal third, some with black tip. Ventral pelage white; hairs pale grey at base, white at tip. Vibrissae soft, fine, dark, about 35 mm long. Ears medium-sized, oval, sparsely haired with a

narrow white ring around the base in adults. Chin and throat white. Fore- and hindlimbs short and slender, white above and below. Forefeet with four functional digits; Digit 1 vestigial. Hindfeet with five digits; Digits 1 and 5 shorter than other digits. Tail long (ca. 85% of HB), thin, entirely white, with short white hairs above and below, sometimes with dark tip. Juveniles darker in colour than adults. Head not broadened as in *Z. hildegardae*. Upper incisor teeth opisthodont, slender, ungrooved; molar cusps prominent. Nipples 3 + 2 = 10 (Shortridge 1934).

Geographic Variation None recorded.

*Zelotomys woosnami*

Similar Species

Z. hildegardae. Upper incisor teeth pro-odont; eastern Africa only; allopatric.

Mastomys spp. (primarily *M. coucha* and *M. natalensis*). On average slightly larger, upper incisor teeth orthodont; tail grey and relatively longer (ca. 90% of HB); up to 24 nipples arranged in two longitudinal rows.

Distribution Endemic to Africa. South-West Arid BZ (Kalahari Desert). Sparsely distributed where mean annual rainfall is 200–500 mm. Recorded from N and E Namibia, N, SW and C Botswana, NW South Africa, and extreme SW Angola.

Habitat Sparsely vegetated *Acacia* woodlands, savannas, riparian *Acacia*, open shrublands of *Acacia*, *Grewia* and *Terminalia*, and *Rhigozum* woodlands (SW Kalahari only). Prefers sandy to fine, consolidated soil (J. A. J. Nel unpubl.). In SW Kalahari, recorded in high dunes, *Acacia* savanna, and low dunes flanking dry river beds (Nel & Rautenbach 1975).

Abundance Generally occurs in low numbers over most of its range (but see below) (Nel & Rautenbach 1975). In the SW Kalahari, over 24 years of sampling, comprised 0.74% of small rodents ($n = 1905$) in the habitats where they were recorded. However, within a particular habitat, numbers may fluctuate widely; e.g. on the low dunes flanking the dry Nossob R., they comprised 0.62% (7 out of 1125) of rodents caught during 26 trapping sessions spanning 24 years. They were totally absent during 22 of these trapping sessions and comprised 0.87%, 1.64%, 1.90% and 4.55% of the rodents in four sessions. In a high dune habitat, ca. 4 km distant from the Nossob R., they comprised 0.97% of all rodents ($n = 304$) caught during 11 trapping sessions spanning 13 years; they were absent during nine trapping sessions, and comprised 4.65% and 2.22% of rodents in two sessions.

Adaptations Primarily terrestrial, but also adept climbers and able to jump from branch to branch, using the tail for balance (Birkenstock & Nel 1977). In captivity, observed to climb to 1 m. Nocturnal with three peaks of activity; active in short, regular cycles in captivity (Birkenstock & Nel 1977). They dig their own burrows under shrubs and trees; two excavated burrows were 40–55 cm deep with nest chambers filled with finely-shredded grass (Birkenstock & Nel 1977). At times, may inhabit burrows of other rodents, e.g. *Tatera* (now *Gerbilliscus*) (Shortridge 1934) or *Desmodillus* (Roberts 1951).

Foraging and Food Granivorous (Smithers 1971), omnivorous and carnivorous (Birkenstock & Nel 1977). Forage on ground. One stomach contained seeds (79%) and insects (21%); a second contained 100% flesh (Birkenstock & Nel 1977) and a third contained 75% seeds and 25% insects as well as nematode worms (De Graaff 1981). There is some evidence that the carcasses of other rats are eaten, and that scavenging may occur.

Social and Reproductive Behaviour Solitary and mutually intolerant. Individuals will attack, kill and partly consume conspecifics in captivity. In SW Kalahari, a ♂ and ♀ have been caught at the same trap station (twice) during the same trapping session while singletons were spaced 10–100 m apart ($n = 6$). Adults normally nest alone (Birkenstock & Nel 1977). Allogrooming between sexes is a prelude to mating.

Reproduction and Population Structure Birth of young occurs during wet months (Dec–Mar) (Smithers 1971, J. A. J. Nel unpubl.) as well as during the dry winter months (May–Aug) (J. A. J. Nel unpubl.). Litter-size: 4.7 (4–5; Birkenstock & Nel 1977). Embryo number: 2–11 (Shortridge 1934, Smithers 1971). Females have a postpartum oestrus. Minimum time between litters: 31 days. Sex ratio at birth in captivity 1 : 1.33. At birth, young altricial and hairless; hairs erupt by Day 6. First leave nest Day 12. Ears open Day 14. Eyes open Day 16–17. Weaned ca. Day 30. Young attain 80% of adult weight by Day 40 (Birkenstock & Nel 1977). Young do not nipple-cling.

Predators, Parasites and Diseases Predators unknown. Ectoparasites include two species of flea (one a vector of bubonic plague) and one species of tick (De Graaff 1981). Maggots of a parasitic fly (probably *Cordylobia* sp.) have been found in the scrotum, producing pus and disease (and in one animal had destroyed the testis) (Dollman 1910). Harbours nematodes *Physaloptera aduensis* adults and larvae, and *Spirura* sp. ♀♀ (A. Verster in litt.).

Conservation IUCN Category: Least Concern.

Measurements

Zelotomys woosnami

HB: 128.4 (102–151) mm, $n = 33$

T: 108.9 (89–118) mm, $n = 30$

HF (c. u.): 26.4 (21–29) mm, $n = 33$

E: 18.9 (15–20) mm, $n = 33$

WT: 59.5 (42–85) g, $n = 18$

GLS: 31.9 (27.3–35.3) mm, $n = 14$

GWS: 16.1 (13.9–17.4) mm, n = 13

M¹–M³: 5.4 (4.9–6.0) mm, n = 14

Body measurements: Kalahari (Smithers 1971, J. A. J. Nel unpubl.)

Skull measurements: Nxai Pan, Botswana (Smithers 1971)

Key References Birkenstock & Nel 1977; De Graaff 1981; Smithers 1971.

Jan A. J. Nel

Subfamily OTOMYINAE – Vlei Rats and Whistling Rats

Otomyinae Thomas, 1897. Proc. Zool. Soc. Lond. 1896: 1017 (publ. 1897).

| | | |
|------------------------------|----------------|--------|
| <i>Otomys</i> (15 species) | Vlei Rats | p. 574 |
| <i>Parotomys</i> (2 species) | Whistling Rats | p. 596 |

The Otomyinae contains two genera and 17 species (Table 42) and represents a localized murid radiation that took place in sub-Saharan Africa. Species richness is highest in southern Africa and the East African mountains, with outlying species found in the highlands of Ethiopia, E Nigeria and Cameroon, and Angola. Species with morphologically primitive traits (*Parotomys* spp. and certain *Otomys* [*O. sloggetti* and *O. unisulcatus*]) are confined to drier regions of southern Africa; derived morphologies characterize more broadly distributed species groups, particularly those inhabiting the mountains and savannas of East Africa. The subfamily collectively occupies a wide range of environments and moisture conditions, but individual species tend to be stenotopic, occurring in savannas, sandy and semi-desert veldts, rocky or dense shrub associated with montane forest, sub-alpine and alpine grasslands, and wetlands (marshes, swamps, river edges and moorlands). Species are uniformly terrestrial, mostly diurnal and predominantly herbivorous; the diet of some species supplemented by seeds and berries.

Otomyinae rodents are stocky in build and medium to large in size. The pelage is long, soft and somewhat shaggy in mesic forms, or shorter and stiffer in xeric-adapted species. Dorsal pelage is normally brown, ranging from pale sandy or tawny-buff to dusky, with rufescent highlights in some forms; ventral pelage is usually greyish-white to dark grey, only weakly delineated from dorsal pelage. Pinnae are small and rounded, sparsely to densely furred. The hindfeet are relatively short and wide, with Digits 1 and 5 short and the plantar surface bearing six pads; otomyines characteristically possess a tuft of long ungual hairs that overarch the claws of the hindfeet. The tail is notably short, only half to three-quarters the length of head and body, and moderately well haired. There are four nipples in all species, arranged as two inguinal pairs.

The cranium is heavily built, moderately to strongly arched, with a narrow interorbital constriction and pronounced supraorbital ridges; rostrum is relatively short, with the nasal bones broadened near their tips, abruptly so in certain *Otomys*; zygomatic arches are nearly parallel-sided, deep over their mid-section and the zygomatic plate broad; anterior palatal foramina narrow, nearly as long as diastema; hard palate narrow and deeply corrugated; pterygoid fossa compressed and deeply recessed; anteroventral maxillary foramen very large, stapedial foramen present (except *O. angoniensis*), sphenofrontal foramen and squamosal-alisphenoid groove absent, alisphenoid strut present; ectotympanic part of auditory bullae are large (*Otomys*) or very large (*Parotomys*) relative to most Muridae, except certain Gerbillinae; malleus transitional between perpendicular and parallel form, the orbicular apophysis absent or minute; mandibular ramus very deep,

coronoid process short (Cockerell *et al.* 1914, Thomas 1918, Bohmann 1952, Carleton & Musser 1984, Pocock 1987). Dental features collectively define the subfamily as unique among murids: upper incisors are broad, opisthodont, each with at least one conspicuous groove (except *Parotomys littledalei*) and a second faint groove in some species; lower incisors also with one (most species) or two (*O. typus*) grooves, or none (*Parotomys* and some *Otomys*). Molar rows long, close set and moderately hypsodont; occlusal surfaces planar, formed of compressed transverse laminae with individual cusps suppressed; M¹ (three laminae) and M² (two laminae) much shorter than M³; M³ and M₁ longest in their respective toothrows; M³ with two or three laminae (*P. brantsii*, *P. littledalei*), four, five or six laminae (*O. denti*, *O. saundersiae*, *O. sloggetti*, *O. unisulcatus*), commonly seven or eight (*O. burtoni*, *O. cuanzensis*, *O. irroratus*, *O. lacustris*, *O. anchietae*, *O. angoniensis*, *O. typus*, *O. tropicalis*, *O. barbouri*, *O. occidentalis*), and exceptionally nine or ten (*O. laminatus*, some *O. typus*); lower first molar with two laminae (*O. unisulcatus*), three or four laminae in most species, five to seven in certain *Otomys* (*O. anchietae*, *O. barbouri*, *O. lacustris*, *O. laminatus*, *O. occidentalis*) (Dollman 1915, Thomas 1918, Roberts 1951, Bohmann 1952). The transverse laminae on the molar teeth are very characteristic of the genus, and are associated with mastication of abrasive silica-rich grasses (Figure 91).

Adaptations to an herbivorous trophic niche and grassland ecology impart a characteristic otomyine form, one reminiscent of other muroid lineages that have radiated into similar niches around the world. Many authors (e.g. Kingdon 1974) have emphasized external similarities between otomyine species (Muridae) and those of Arvicolinae (Cricetidae), notably as expressed by their stocky body form and short limbs, blunt rostrum and small pinnae, and a tail shorter than head and body. The resemblance extends even to details of molar size, form and variability of the molar teeth, especially the posterior portion of M³ and anterior portion of M₁ (e.g. Guthrie 1971); such dental differences have figured prominently in the taxonomic diagnoses of genera and species within both groups. No otomyine, however, has attained ever-growing molars (hypsodonty) nor the derived arrangements of enamel microstructure as found in arvicolines (von Koenigswald 1980). Phylogenetic augmentation of molar triangles (Arvicolinae) or laminae (Otomyinae) and increased crown height, accompanied by remodelling of the cranium and attached zygomasseteric musculature, have served to enhance propalinal grinding in both groups and in part explain their dietary specialization and evolutionary success in grassland environments. Further, otomyines, like arvicolines (Vorontsov 1967), possess a long and anatomically elaborate caecum and colon (Perrin & Curtis 1980, Jackson & Spinks 1998), which are the principal sites for microbial fermentation of cellulose-rich foods. Morphological convergence and eco-behavioural equivalence are equally striking between otomyines and certain other muroids. For example, *Otomys*

and New World Cotton Rats (*Sigmodon*, Sigmodontinae) are similar in external appearance and form, degree of molar hypsodonty and precocial development of young; likewise, *Parotomys* and African Sand Rats (Gerbillinae: *Psammomys*) are convergent in pelage colour and form, colonial social structure and alarm calls, existence in xeric habitats, and dietary reliance upon salt-rich plants.

Following Thomas (1897), otomyines have been ranked as a subfamily of Muridae, whether the family is defined *sensu lato* (Ellerman 1941, Roberts 1951) or *sensu stricto* (Miller & Gidley 1918, Simpson 1945). Although some have classified Otomyinae with Cricetidae (Kingdon 1974, Misonne 1974) or Nesomyidae (Chaline *et al.* 1977, Lavocat 1978), anatomical and palaeontological evidence unequivocally affirms their phyletic origin from early African murids, possibly arvicanthine-like forms (Pocock 1976, Carleton & Musser 1984, Breed 1995, S  n  gas 2001). Similarly, a diverse suite of molecular data uniformly portrays the evolutionary heritage of *Otomys* as murid, not cricetid (Contrafatto *et al.* 1994, Watts & Baverstock 1995a, Michaux & Catzeflis 2000, Michaux *et*

al. 2001, Jansa & Weksler 2004), in particular as a sister-group to *Arvicanthis* and its kin, which constitute a large clade within African Murinae (Chevret *et al.* 1993a, Ducroz *et al.* 2001). Molecular clock estimates place the split from arvicanthine murids about 7–9.5 mya (Chevret *et al.* 1993a, Ducroz *et al.* 2001), a time-frame in broad agreement with fossil data insofar as known (S  n  gas 2001) and with the late Miocene proliferation of C₄ grass-dominated savannas in Africa (Jacobs *et al.* 1999).

The geological occurrence of Otomyinae ranges from the late Miocene to Recent in southern Africa (S  n  gas & Avery 1998) and from the early Pleistocene to Recent in East Africa (Denys 1989b). Extinct species certainly assignable to *Otomys* proper appear in the middle Pliocene of South Africa (Pocock 1987) and early Pleistocene of Tanzania (Denys 1989b). One other fossil murid, the Miocene *Microtia* from the Gargano Islands off Italy (Freudenthal 1976), exhibits comparably enlarged M³ and M₁, but it retains a chevron arrangement of cusps, not the planar laminate occlusion and cusp suppression characteristic of Otomyinae.

Table 42. Species in the subfamily Otomyinae. Arranged in order of increasing number of laminae on M³. Note that although 17 species are listed below, recent reviews in 2011 suggest that several of these are composite species and therefore the total number of species is 31 (see also text).

| Species | Laminae on M ³ ^a | Laminae on M ₁ ^a | Grooves on each upper incisor | Grooves on each lower incisor | Petrotympenic foramen | Nasal bones ^b | |
|--|--|--|-------------------------------|---|-----------------------|--------------------------|--|
| <i>Parotomys brantsii</i> | 2 | 4 | 2 (deep outer, shallow inner) | 0 | Round | Barely expanded | |
| <i>Parotomys littledalei</i> | 3 | 3 | 0 | 0 | Round | Barely expanded | |
| <i>Otomys unisulcatus</i> | 4 ^c | 3 ^d | 1 | 0 | Round | Barely expanded | |
| <i>Otomys sloggetti</i> | 4, 5 | 4 | 1 | 1 | Slit-like | Barely expanded | |
| <i>Otomys denti</i> ^c | 5, 6 | 4 | 1 | 1 | Round | Moderately expanded | |
| <i>Otomys saundersiae</i> ^f | 6 (5) | 4 | 1 | 2 (deep medially, shallow laterally) | Round | Moderately expanded | |
| <i>Otomys burtoni</i> | 6, 7 | 4 | 2 (deep inner, shallow outer) | 2 (deep medially, shallow laterally) | Slit-like | Moderately expanded | |
| <i>Otomys cuanzensis</i> | 6, 7 | 4 | 1 | 2 (deep medially, shallow laterally) | Round | Moderately expanded | |
| <i>Otomys irroratus</i> ⁱ | 6 (7) | 4 | 1 | 2 (deep medially, shallow laterally) | Round (large) | Sharply expanded | |
| <i>Otomys lacustris</i> | 6 (7) | 5 | 1 | 1 | Round | Moderately expanded | |
| <i>Otomys anchietae</i> | 7 (6, 8) | 5 (6) | 2 (one deep, 1 shallow) | 1 | Round | Moderately expanded | |
| <i>Otomys angoniensis</i> | 7 (6) | 4 | 1 | 2 (deep medially, shallow laterally); sometimes 1 | Slit-like | Moderately expanded | |
| <i>Otomys typus</i> s.l. ^g | 6, 7, 8, 9 | 4 | 1 | 2 (deep) | Round | Sharply expanded | |
| <i>Otomys tropicalis</i> ^h | 7 (8) | 4 | 1 | 2 (deep medially, shallow laterally) | Round | Moderately expanded | |
| <i>Otomys barbouri</i> | 7 (8) | 5 | 1 | 1 | Round | Sharply expanded | |
| <i>Otomys occidentalis</i> | 8 (7) | 5 | 1 | 1 | Slit-like | Sharply expanded | |
| <i>Otomys laminatus</i> | 8–10 | 7 | 1 | 2 (deep medially, shallow laterally) | Round | Sharply expanded | |

^a Where two numerals are given, each is observed in roughly equal frequency; numerals in brackets indicate a less frequently observed number of laminae.

^b See Fig 92 for illustration of the shape of nasal bones.

^c Plus small circular posterior lamina on M³.

^d Plus partial incomplete anterior lamina on M₁.

^e Taylor *et al.* (2009a) recognize *sungae* from the Eastern Arc as a distinct species, previously regarded to be a synonym of *denti*.

^f Taylor *et al.* (2009a) provide evidence that *saundersiae* should be retained as a synonym of *irroratus* and the name *karoensis* should instead be used to describe the small, pallid species from the Cape.

For so small and morphologically distinctive a group, the taxonomy of otomyine rodents remains unsettled at the family, genus, and species levels. Disclosure of close relationship to arvicanthine rodents has led investigators to propose that otomyines should be ranked as a tribe within Murinae (Ducroz *et al.* 2001, S  n  gas 2001). Although close phyletic association of otomyine rodents with other African murids is incontestable, decision on their taxonomic rank will be better informed by expanded sampling of genera from Asia and Indo-Australia. Generic arrangements within the subfamily have ranged from only a single genus *Otomys* (Bohmann 1952), to the customary two, *Otomys* and *Parotomys* (Ellerman 1941, Misonne 1974), to as many as three (*Otomys*, *Parotomys* and *Myotomys* – Thomas 1918, Musser & Carleton 2005) or five genera (*Otomys*, *Parotomys*, *Myotomys*, *Anchotomys* and *Lamotomys* – Roberts 1951). Improved comprehension of phyletic relationships among species should provide a sounder basis for delimiting genera. Recent studies, for example, have revealed that *Otomys*, as its specific contents are usually denoted, is polyphyletic; in particular, the species *O. sloggetti* and/or *O. unisulcatus* (both placed in

the genus *Myotomys* by Musser & Carleton [2005]) demonstrate close kinship with species of *Parotomys* (Taylor *et al.* 1989, Bernard *et al.* 1991, Meester *et al.* 1992, Contrafatto *et al.* 1994, Musser & Carleton 2005). Specific diversity within *Otomys* has been historically masked by uncritical application of the biological species concept and an exceptionally forgiving interpretation of subspecies. This practice, applied over the middle 1900s, culminated in morphologically indefinable species, such as *O. irroratus*, *O. tropicalis* and *O. typus*, whose altitudinal and geographic distributions were improbably broad (e.g. Bohmann 1952, Ellerman *et al.* 1953, Dieterlen 1968, Misonne 1974, Petter 1982). The removal of diagnosable, genetically homogeneous species from these polyphyletic constructs is progressing but still requires much basic revision (see Taylor & Kumirai 2001 and Musser & Carleton 2005 for different estimates of species diversity). In view of this on-going research, only the two traditional genera – *Otomys* with 15 species and *Parotomys* with two species – are recognized here.

Michael D. Carleton

| HB
mean (range)
mm
[T as % of HB] | Notes |
|--|--|
| 151 (136–173) [63%] | South-West Arid BZ (South Africa, S Namibia, SW Botswana) |
| 153 (124–175) [70%] | South-West Arid BZ (South Africa) |
| 158 (128–190) [60%] | South-West Arid BZ (South Africa) |
| 127 (93–170) [49%] | Afromontane–Afroalpine BZ (South Africa, Lesotho) |
| 155 (131–183) [54%] | Afromontane–Afroalpine BZ (Rwenzori Mts, Albertine Rift Mts, EC Tanzania, N Malawi) |
| 145 (210–180) [73%] | South Africa |
| 156 (145–167) [50%] | Mt Cameroon |
| 180 (178–184) [58%] | NE Angola |
| 161 (147–186) [60%] | Southern Africa, south of Zambesi R. |
| 158 (150–165) [65%] | Afromontane–Afroalpine BZ (Kenya, Tanzania, Malawi) |
| 213 (209–217) [56%] | NE Angola |
| 155 (105–207) [55%] | Zambesian Woodland and Somalia–Masai BZs; widespread from eastern Africa to South Africa |
| 147 (120–210) [47%] | Afromontane–Afroalpine BZ (Ethiopia to Zambia/Malawi) |
| 178 (147–201) [46%] | Afromontane–Afroalpine BZ (eastern Africa) |
| 177 (162–210) [45%] | Afromontane–Afroalpine BZ (Mt Elgon) |
| 143 (131–160) [54%] | Afromontane–Afroalpine (W Cameroon, E Nigeria) |
| 199 (188–213) [57%] | Afromontane–Afroalpine BZ (South Africa) |

^gThis species represents a highly variable complex comprising 12 composite species. The values presented here cover the range of the complex and were obtained from Taylor *et al.* (2011).

^hCarleton & Byrne (2006) regard *dollmani* as a distinct species, previously recognized as a synonym of *tropicalis*.

ⁱTaylor *et al.* (2009b) and Engelbrecht *et al.* (2011) recognize two species within *irroratus s.l.*, these being *irroratus s.s.* and *auratus*.

GENUS *Otomys*

Vlei Rats

Otomys F. Cuvier, 1824. Dents des Mammifères, p. 255. Type species: *Euryotis irrorata* Brants, 1827.

The genus *Otomys* contains at least 15 species (Table 42, but see also below) and has a widespread distribution in semi-arid, montane and mesic grassland savanna habitats in southern Africa, and, more discontinuously, in montane, alpine and mesic grassland savanna habitats in East Africa, Angola, E DR Congo, Rwanda, Burundi, Ethiopia, S Sudan and the highlands of Cameroon and E Nigeria. Most species in the genus have rather restricted distributional and altitudinal ranges, and most (except *O. unisulcatus*) are associated with

damp grasslands and swamps from close to sea level to ca. 4300 m on mountains. The diet is exclusively grass, which is masticated by the highly specialized molar teeth.

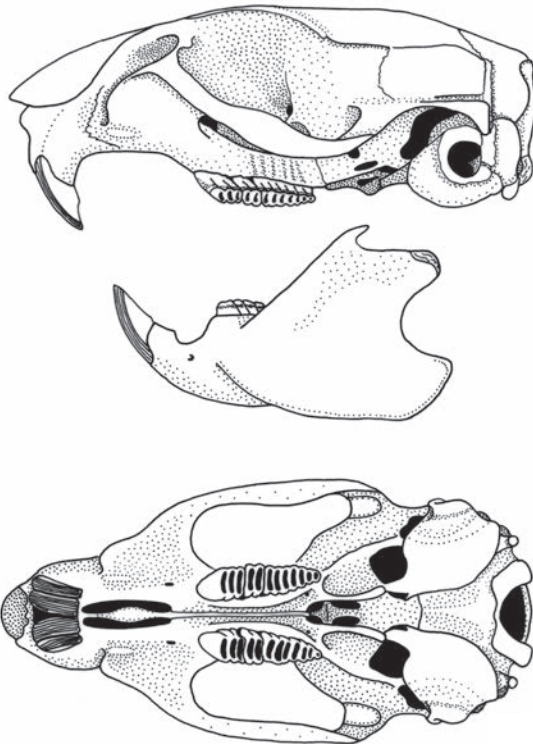
The genus is characterized by medium to large body size, stocky build, shaggy, dark greyish-brown dull pelage, short tail, short limbs and four digits on each fore- and hindfoot. In their conservative, vole-like appearance they are thus very similar to the whistling rats (*Parotomys*), although the latter tend to be much paler in colouration, with proportionately larger head and expanded auditory bullae (Taylor *et al.* 2004b), the last-mentioned feature being an adaptation common to many species of rodents living in arid habitats. The skull is solidly built, zygoma are thick and almost parallel, zygomatic plate is large with forwardly curving anterior edge, anterior palatine foramina are short ending well anterior to M^1 , and the upper incisors are wide and opisthodont, each with one or two grooves (Figure 91). The upper and lower cheekteeth ($M1-M3$) are very distinctive with a highly derived lamellar molar pattern, and M^3 and M_1 are especially elongated, more so than in members of *Parotomys*. The nasal bone varies in shape in different species – it is either small and barely expanded or large and greatly expanded (Figure 92). The petrotympanic (or stapedial) foramen may be round or slit-like (Figure 93). Further details of the external and skull morphology of this genus are shared with species of *Parotomys* (see also subfamily profile).

The common names for the genus (Vlei Rats, Groove-toothed Rats, Laminate-toothed Rats) refer to their preferred habitat (vlei = swamp) and to the structure of the incisors (grooved) and cheekteeth (laminate).

The number of species in the genus is controversial. Musser & Carleton (1993) recognized 12 species, and later (2005) recognized 19 species (excluding two species they classified in *Myotomys*, which we here retain in *Otomys*: *O. unisulcatus* and *O. sloggetti*). Whilst acknowledging that it is an underestimate (and pending more accurate definition of species limits), we here recognize 15 species (following Dieterlen & Van der Straeten 1992, Musser & Carleton 1993, Taylor & Kumirai 2001, Taylor *et al.* 2005): *O. anchietae*, *O. angoniensis*, *O. barbouri*, *O. burtoni*, *O. cuanzensis*, *O. denti*, *O. irroratus*, *O. lacustris*, *O. laminatus*, *O. occidentalis*, *O. saundersiae*, *O. sloggetti*, *O. tropicalis*, *O. typus* and *O. unisulcatus*. Musser & Carleton (2005) recognize a further six species: *maximus* (considered here to be a subspecies of *angoniensis*; see Bronner & Meester 1988, and sequence

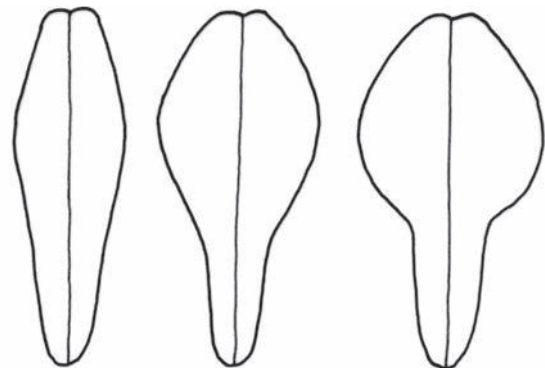


Otomys typus.



ABOVE: Figure 91. Skull and mandible of *Otomys angoniensis* (HC 2776).

RIGHT: Figure 92. Evolutionary trend in the shape of the nasal bone (viewed dorsally with anterior end at top) in species of the subfamily Otomyinae. Left: barely expanded anteriorly, the primitive state, e.g. *Parotomys* spp. Centre: moderately expanded anteriorly, e.g. *Otomys angoniensis*. Right: sharply expanded anteriorly, the most advanced state, e.g. *Otomys irroratus* (after original by P. Taylor).



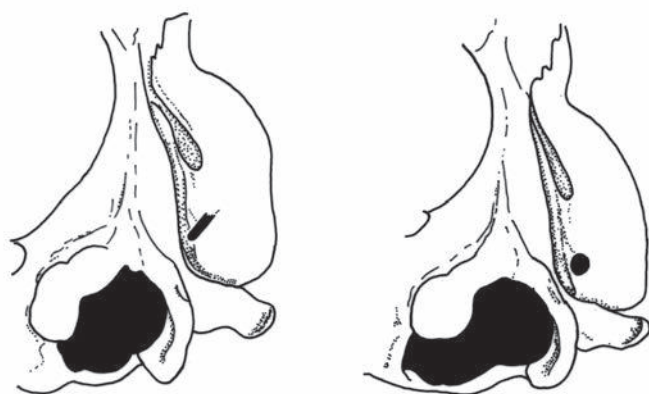


Figure 93. Basicranial region of skull of *Otomys* showing the two shapes of the petrotympanic foramen. *O. angoniensis* (left) with slit-like petrotympanic foramen; *O. irroratus* (right) with round petrotympanic foramen (after Meester *et al.* 1986). Foramen magnum black; mastoid process points to right below the auditory bulla.

data of Maree 2002), *orestes* (previously a synonym of *O. tropicalis* or *O. typus*), *dollmani* (previously a synonym of *O. tropicalis*), *jacksoni*, *dartmouthi* and *uzungwensis*. The last three listed species were previously considered as southern alpine-adapted forms of *O. typus* but recent molecular and morphological data (Taylor *et al.* 2011) support their validity (and that of *zinki* from Mt Kilimanjaro and *thomasi* from the Mau Escarpment of Kenya) as distinct taxa unrelated to *typus* s.s. from Ethiopia. Taylor *et al.* (2011) also provide evidence of further speciation within *O. typus* s.s. from Ethiopia, with six Ethiopian species proposed, including *typus*, *fortior*, *helleri* and three newly described species, *cheesmani*, *simiensis* and *yaldeni*. Further justification of the status of *dollmani* and *orestes* as valid species is provided by Carleton & Byrne (2006) and Taylor *et al.* (2011). Taylor *et al.* (2009a) elevated *sungae* (previously a synonym of *O. denti*) to species status. Musser & Carleton (2005) follow Taylor *et al.* (2005) in considering *saundersiae* to be a valid taxon; however Taylor *et al.* (2009b) endorse Taylor *et al.* (1993b), providing convincing molecular and karyotypic evidence to show that *saundersiae* is a synonym of *irroratus*, and *karoensis* is the valid name for the smaller-sized species from the Western Cape. The small-sized species from northern Eastern Cape and southern Free State Provinces of South Africa are provisionally assigned to *karoensis* although ongoing molecular study seems to show they may be distinct. Within *O. irroratus*, Taylor *et al.* (2009b) and Engelbrecht *et al.* (2011) demonstrate two divergent molecular clades: one from the Fynbos Biome (*O. irroratus* s.s.) and the second from the Highveld of South Africa extending into the Zimbabwe Highlands (for which the name *O. auratus* is available). These studies suggest that there are now 31 species of *Otomys*; it has not been possible to include separate profiles for the new species described in 2009 and 2011.

The genus *Otomys* (Vlei Rats) is closely related to the genus *Parotomys* (Whistling Rats); together the two genera comprise the

Afrotropical murid subfamily Otomyinae. The monophyly of *Otomys* has been questioned on biochemical, molecular and morphological grounds. Two species, *O. unisulcatus* and *O. sloggetti* (*Myotomys* of Thomas [1918]), group phylogenetically closer to *Parotomys* than to other species of *Otomys* (Pocock 1976, Taylor *et al.* 1989, Contratto *et al.* 1994, Maree 2002, Taylor *et al.* 2004a, b). Although Musser & Carleton (2005) recognize the genus *Myotomys*, the monophyly of *Myotomys* is not supported by recent molecular and morphological cladistic analyses, and the most cladistically correct solution may be to include *Parotomys* species in the genus *Otomys* (Maree 2002, Taylor *et al.* 2004a).

Some authors recognize Vlei Rats as a distinct subfamily within the Muridae, or as a family, while others have placed them within Cricetidae and even Nesomyidae. Here, *Otomys* is included with *Parotomys* in the subfamily Otomyinae of the family Muridae. An alternative arrangement, based on recent palaeontological and molecular data, supports the allocation of *Otomys* and *Parotomys* in a tribe (the Otomyini) within the family Muridae (Ducroz *et al.* 2001, S  n  gas 2001). The South African fossil species, *Euryotomys pelomyoides* (6.0–4.5 mya) and *E. boliti* (4–5 mya) provide strong links between true murids and modern *Otomys* (Pocock 1976, Denys 1989b, Chevret *et al.* 1993a, Avery 1998, S  n  gas & S  n  gas 2001). The earliest true *Otomys* appeared first in South Africa (*O. cf. gracilis*, 3.0–3.5 mya), and later in East Africa (*O. petteri*, at 1.5–2.0 mya), suggesting a southern African origin of this genus. On the basis of DNA–DNA hybridization (Chevret *et al.* 1993a), the ancestor of Otomyini split from the Arvicanthine division of murids at around 7 mya. According to the protein molecular clock, *Otomys* and *Parotomys* may have split at around 6.5–5.5 mya (Taylor *et al.* 1989).

A relatively low number of five to six laminae in M^3 was present in ancestral *Otomys* species, as evidenced by the extinct *O. gracilis* in South Africa, with a subsequent trend towards an increasing number of laminae as shown in extant species (Denys 1989b, Chevret *et al.* 1993a). Bohmann (1952) postulated that successive radiations within the genus occurred from South Africa northwards into East Africa, Angola and West Africa, coinciding with mesic pluvial periods during the Pleistocene. At this time, montane forest–grassland mosaics extended to lower altitudes and became geographically continuous between southern Africa and East Africa. However, on fossil evidence, Denys (2003) postulated a single northwards dispersal followed by further speciation in East Africa, a scenario supported by recent molecular and morphometric data (P. J. Taylor, in litt.).

The taxonomy of the group is highly unstable due to variability in diagnostic characters. Species are distinguished by the number of laminae in M^3 and M_1 , the number and form of grooves on the incisors, shape of the nasal bone and shape of the petrotympanic foramen (see Table 42).

P. J. Taylor

***Otomys anchietae* ANCHIETA'S VLEI RAT (ANGOLAN VLEI RAT)**

Fr. Rat du vlei d'Anchiete; Ger. Anchietas Lamellenzahnratte

Otomys anchietae (Bocage, 1882). J. Sci. Acad. Lisbon 9: 26. Caconda, Huila, Angola.

Taxonomy Originally described in the genus *Euryotis*. Based on having five laminae in M_1 , some authors include *lacustris*, *occidentalis* and *barbouri* in this species. However, Dieterlen & Van der Straeten (1992) treated it as a species separate from *lacustris*, *occidentalis* and *barbouri*, a decision supported on morphometric and morphological grounds (Taylor & Kumirai 2001, Taylor *et al.* 2004a). Synonyms: none. Chromosome number: not known.

Description Very large, stoutly built rat with large, blunt head and short tail. Mean HB larger than any other *Otomys* (HB: >209 mm, skull length: >45 mm). Pelage soft, fine and thick. Dorsal pelage blackish tinged with 'pinkish buff'. Ventral pelage near cinnamon. Tail short (ca. 56% of HB), black above, paler below, sparsely haired. Each upper incisor with one deep and one shallow groove, each lower incisor with one deep groove, very occasionally a second faint groove. M^3 with six, seven (typically) or eight laminae. M_1 with five or (occasionally) six laminae. Petrotympanic foramen round. Nasal bones moderately expanded. Nipples $0 + 2 = 4$.

Geographic Variation None recorded.

Similar Species

O. angoniensis: M_1 with four laminae; petrotympanic foramen slit-like; partially sympatric in Angola (*O. o. maximus* only).

O. cuanzensis: M_1 with four laminae; HB, HF and M^1 – M^3 probably longer, marginally sympatric.

Distribution Endemic to Africa. Zambezian Woodland BZ. Recorded only in NE Angola, where associated with the rivers of the Congo Basin drainage, and in C and SW Angola, where it is narrowly sympatric with *Otomys cuanzensis* and *Otomys angoniensis maximus* (Crawford-Cabral 1998).

Habitat Riverine habitats in the Congo Basin in NE Angola, and mesic grasslands and moist savannas at higher altitudes of the central plateaux (>1500 m) of Angola.

Abundance No information.

Remarks Very little is known about this species. Apparently makes a screeching sound 'like a squirrel'. Lactating ♀♀ collected in Aug (Hill & Carter 1941).

Conservation IUCN Category: Least Concern.

*Otomys anchietae***Measurements***Otomys anchietae*

HB (♂♂): 213 (209–217) mm, n = 5

HB (♀♀): 197 (187–209) mm, n = 6

T (♂♂): 119 (115–127) mm, n = 5

T (♀♀): 111 (87–121) mm, n = 6

HF (♂♂): 41 (40–41) mm, n = 5

HF (♀♀): 37 (36–38) mm, n = 6

E: n. d.

WT: n. d.

GLS: 49.4 (46.2–52.8) mm, n = 5

GWS: 26.5 (25.0–28.0) mm, n = 5

 M^1 – M^3 : 12.0 (11.3–12.5) mm, n = 5

Body measurements: Chitau, Angola (Hill & Carter 1941)

Skull measurements: Angola (Taylor & Kumirai 2001)

Key References Crawford-Cabral 1998; Hill & Carter 1941.

P. J. Taylor

Otomys angoniensis ANGONI VLEI RAT

Fr. Rat du vlei d'Angoni; Ger. Angonis-Lamellenzahnratte

Otomys angoniensis Wroughton, 1906. Ann. Mag. Nat. Hist., ser. 7, 18: 274. M'Kombhuie, Malawi (= Matipa Forest, Misuku Range, Malawi; *fide* Ansell & Dowsett 1991). 7000 ft (2120 m).

Taxonomy *Otomys angoniensis maximus* may be a distinct species (Musser & Carleton 1993, 2005, Crawford-Cabral 1998), but morphometric overlap (Bronner & Meester 1988, P. J. Taylor unpubl.) and genetic similarity (Maree 2002) suggest *maximus* should be retained as a subspecies of *O. angoniensis*. The Angolan *cuanzensis*, previously allocated to *angoniensis*, is recognized as a distinct species following Musser & Carleton (2005). Synonyms: *canescens*, *divinorum*, *elassodon*, *mashona*, *maximus*, *nyikae*, *pretoriae*, *rowleyi*, *sabiensis*, *tugelensis*. Subspecies: three. Chromosome number: $2n = 56$, $aFN = 54$. All chromosomes are acrocentric. X-chromosome is second largest member of the karyotype and Y-chromosome is smallest. Limited G-band homology detected between this species and *O. irroratus* (Contrafatto *et al.* 1992c).

Description Large stocky rat with dense shaggy pelage. Dorsal pelage pale to dark greyish-buffy. Colour varies geographically from darker to paler, with the palest individuals on Mt Kilimanjaro. Ventral pelage dark grey. Head large. Small, well-haired ears held close to head. Tail short (ca. 55% of HB). Each upper incisor with single groove. Each lower incisor with one deep and one shallow groove (except for *O. a. maximus* where the shallow groove is practically invisible). M^3 with seven laminae (occasionally six). M_1 with four laminae. Nasal bones moderately expanded. Petrotympanic foramen small, slit-like (as in *O. burtoni* and *O. sloggetti*). Baculum spatulate basally with central raised portion in ventral view; length of proximal portion ca. 4 mm, maximum width ca. 1 mm (Davis 1973). Body size varies geographically (see Measurements). Nipples: $0 + 2 = 4$.

Geographic Variation Three subspecies may be recognized (P. J. Taylor unpubl.):

- O. a. angoniensis*: Kenya, Tanzania, Malawi, Mozambique, Zimbabwe. Similar size to *O. a. tugelensis*, smaller than *O. t. maximus*; HB: 141–189 mm, GLS: 35–40 mm, but wider interorbital distance (>4.5 mm; P. J. Taylor, unpubl.). Each lower incisor with deep outer and shallow inner groove.
- O. a. maximus*: N Botswana, NW Zambia, SW & SE Angola, SE & E DR Congo. Largest subspecies; HB: 154–207 mm, GLS: 40–49 mm (Roberts 1951, P. J. Taylor unpubl.). Each lower incisor with single groove.
- O. a. tugelensis*: South Africa, SE Botswana. Similar size to *O. a. angoniensis*, comparatively narrow interorbital distance (<4.5 mm). Each lower incisor with deep outer and shallow inner groove.

Similar Species

- O. irroratus*. Petrotympanic foramen round in shape; dorsal pelage less buffy-coloured; on average larger; six (occasionally seven) laminae in M^3 ; partly sympatric.
- O. laminatus*. More than eight laminae in M^3 .

O. tropicalis. Round petrotympanic foramen.

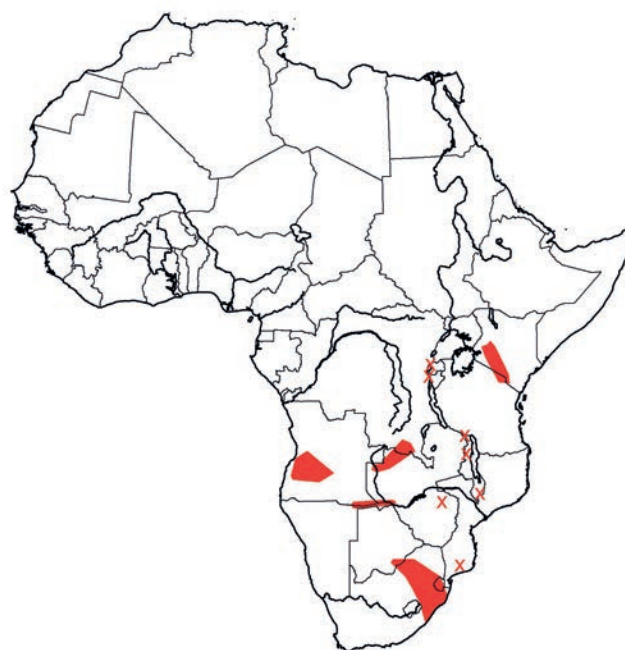
O. denti, *O. sloggetti* and *O. unisulcatus*. Single groove in each lower incisor.

O. typus. Two deep grooves in each lower incisor.

O. anchietae, *O. barbouri*, *O. lacustris*, *O. occidentalis*. Five laminae in M_1 .

Distribution Endemic to Africa. Zambezan Woodland BZ and southern part of the Somalia–Masai Bushland BZ; also present in highland habitats throughout the eastern side of the continent. Recorded from South Africa, Swaziland, Zimbabwe, Mozambique, Malawi, Angola, Zambia, DR Congo, Rwanda, Tanzania and Kenya (Ansell 1960, Misonne 1974, Ansell & Dowsett 1988, Bronner & Meester 1988, Crawford Cabral 1998). Records from outlying Eastern Cape Province, South Africa (De Graaff 1981, Bronner & Meester 1988) could not be corroborated on the basis of known museum specimens (Lynch 1994). Specimens having slit-like petrotympanic foramina from Uvira (SMNS) and Albert N. P. (MNHN) extend the known distribution into E DR Congo and Rwanda, respectively. Distribution in East Africa is patchy. See also Geographic Variation above.

Habitat Mesic grassland and savanna woodland habitats (from coastal to high montane habitats, mostly at <1000 m in South Africa), generally in close proximity to wetlands or water. Drier habitats may also be occupied during the wet season. Where in sympatry with *O. irroratus*, *O. angoniensis* occupies more xeric habitats (plant associations providing lower ground cover). On a study area near Pretoria (South Africa), positive association recorded between *O. a. tugelensis* and



Otomys angoniensis

several plant species including *Helictotrichon turgidulum*, *Cynodon dactylon*, *Melilotus alba*, *Hyparrhenia dregeana*, *Berkheya radula*, *Chironia palustris* and *Conyza podocephala*. On the same study area, *O. irroratus* was negatively associated with the above plants, preferring species that provide denser ground cover (Davis 1973). In Malawi, occurs only in montane grasslands (Hanney 1965).

Abundance Abundant in suitable habitats. A stable population in the highlands of Kenya had a density of 30/ha. Population size appears to be regulated by availability of cover (Taylor & Green 1976). Presence of this species is indicated by short chopped lengths of grass and green moist faecal pellets.

Adaptations Diurnal, crepuscular or nocturnal, depending possibly on the level of owl predation. Shaggy dark pelage, vole-like body form with short tail, and sturdy skull are adaptations for camouflage and burrowing through runways in dense swampy habitats. Large nasal bones are adaptation for enhanced olfactory ability. Laminate molars, long spiralled small intestine and large complex caecum are adaptations for strict herbivory. Coprophagy may aid caecal fermentation and vitamin metabolism (Perrin & Curtis 1980). Distinctive 'runways' are constructed in dense grass, and are used by other species of small mammals. Constructs dome-shaped grass nests.

Foraging and Food Stems and rhizomes of grass, fine reeds and other monocotyledonous plants. In Kenya, diet includes dicotyledonous plants (particularly in winter), bark of shrubs and trees (e.g. *Lantana*, *Eucalyptus*) and seeds from wheat (Taylor & Green 1976). In Malawi, diet is entirely green grass (Hanney 1965).

Social and Reproductive Behaviour Solitary, pairs or small family groups. In captivity, less vocal (very few audible sounds recorded) but less shy than *O. irroratus* (N. Pillay pers. comm.).

Reproduction and Population Structure Polyoestrous. In Kenya, breeding continues throughout the year with a peak of activity in the wet season (Taylor & Green 1976). In Malawi, pregnant ♀♀ recorded in the dry season (May, Jul and Nov) (Hanney 1965). In southern Africa, young recorded only in spring and summer (Sep–Jan); no breeding recorded during mid-winter (Jun, Jul). Embryo number: 1–5, usually 2 or 3 (Bronner & Meester 1988). In captivity, gestation: 37 days. Mean litter-size: 3.1 (2–5), n = 48 (Phillips *et al.* 1997). At birth, young precocial with erupted incisors and capable of nipple-clinging immediately after birth; mean weight at birth 11.4 g. Minimum age at sexual maturity: five weeks (♀♀) to eight weeks (♂♂). *Otomys angoniensis* is less K-selected than either *O. irroratus* or *O. sloggetti robertsi* and more K-selected than *O. unisulcatus* (Phillips *et al.* 1997).

Predators, Parasites and Diseases Predators include owls (African Grass-owl *Tyto capensis*, Marsh Owl *Asio capensis*, Barn Owl *Tyto alba*, Spotted Eagle-owl *Bubo africanus*), felids (e.g. Serval *Felis serval*), jackals (Black-backed Jackal *Canis mesomelas*, Side-striped Jackal *Canis adustus*), mongooses (e.g. Grey mongoose *Herpestes ichneumon* and

Water Mongoose *Atilax paludinosus*), genets (*Genetta tigrina*), Civet (*Civettictus civetta*), snakes (e.g. Puff Adder *Bitis arietans*) and humans (e.g. tribespeople in Botswana, where many are eaten following annual reed-burning ceremonies) (Shortridge 1934, Dean 1978b, Skinner & Smithers 1990). On Zomba Plateau, Malawi, was the most numerous prey item of African Grass-owls, comprising 47% of small mammals (n = 101) in disintegrating pellets, and 58% of the food biomass; and 24% of prey items and 40% of prey biomass in 21 intact pellets (Happold & Happold 1986).

Bronner & Meester (1988) list some 30 species of ecto- and endoparasites, including fleas (13 species), mites (2 species), lice (1 species), ticks (4 species), chiggers (2 species), filaria and nematodes (2 species), and at least three zoonoses in which Angoni Vlei Rats may be intermediate hosts of diseases of humans (rickettsia, plague and melioidosis). They are susceptible themselves to bilharzia.

Conservation IUCN Category: Least Concern.

Measurements

Otomys angoniensis

HB: 155 (105–207) mm, n = 116

T: 86 (43–131) mm, n = 117

HF: 26 (19–39) mm, n = 116

E: 20 (9–30) mm, n = 116

WT (♂♂): 89.9 (25–138) g, n = 56*

WT (♀♀): 96.6 (47–216) g, n = 56*

GLS: 37.5 (26.3–49.1) mm, n = 105

GWS: 18.9 (16.1–23.4) mm, n = 104

M¹–M³: 9.2 (7.8–11.5) mm, n = 101

Pan-African (TM; Bronner & Meester 1988)

*Weight: Former Transvaal, South Africa (Rautenbach 1982)

O. a. maximus

HB: 183 (154–207) mm, n = 17

T: 110 (81–131) mm, n = 17

HF (c.u.): 34 (29–39) mm, n = 16

E: 23 (20–30) mm, n = 16

WT (♂♂): 178.4 (112–242) g, n = 11*

WT (♀♀): 205.3 (140–255) g, n = 5*

Botswana (TM; Bronner & Meester 1988)

*Weight: Botswana (Smithers 1971)

O. a. angoniensis

HB: 172 (141–189) mm, n = 12

T: 80 (65–91) mm, n = 12

HF (c.u.): 26 (20–28) mm, n = 12

E: 22 (20–26) mm, n = 12

Kenya (TM; Bronner & Meester 1988)

Key References Ansell & Dowsett 1991; Bronner & Meester 1988; Davis 1973; Phillips *et al.* 1997; Taylor & Green 1976.

R. J. Taylor

Otomys barbouri BARBOUR'S VLEI RAT

Fr. Rat du vlei de Barbour; Ger. Barbours Lamellenzahnratte

Otomys barbouri Lawrence and Loveridge, 1953. Bull. Mus. Comp. Zool., Harvard 110: 63. Mt Elgon, Uganda. 10,500 ft (3200 m).

Taxonomy Musser & Carleton (1993) consider *barbouri* to be a synonym of *O. anchietae*. In contrast, *barbouri* was recognized as a valid species by Dieterlen & Van der Straeten (1992) and Musser & Carleton (2005) on the basis of morphometrics and cranial variables. Taylor & Kumirai (2001) also recognize *barbouri* as a valid species on the basis of PCA and discriminant functions analysis for 16 cranial variables. Synonyms: none. Chromosome number: $2n = \text{'at least 66'}$ (P. J. Taylor, unpubl.).

Description Large vole-like rat with a long shaggy pelage. Hairs very long (20–35 mm). Dorsal pelage dull reddish-brown speckled with black, dorsal hairs reddish-brown, with black tips. Flanks slightly paler. Ventral pelage conspicuously paler than dorsal pelage. Fore- and hindfeet greyish-brown. Tail short (ca. 45% of HB), blackish-brown, with scales and short dark bristles. Each upper incisor and each lower incisor with single groove. M^3 with seven (occasionally eight) laminae. M_1 with five laminae. Nasal bones sharply expanded. Petrotympanic foramen round. Sexual dimorphism present: HB and T significantly larger in adult ♂♂, ears significantly larger in ♀♀, but no significant difference in hindfoot length (Clausnitzer 2003). Nipples: $0 + 2 = 4$.

Geographic Variation None recorded.

Similar Species

O. lacustris. Tail longer (ca. 65% of HB); M^3 with six (occasionally seven) laminae; Tanzania, Malawi and Kenya (?) only.



Otomys barbouri

O. typus. Smaller; two grooves in each lower incisor; M^3 with seven laminae; M_1 with four laminae; highlands of Ethiopia, Kenya, Uganda, Tanzania, Zambia, Malawi. Sympatric on Mt Elgon.

Distribution Endemic to Africa. Afromontane–Afroalpine BZ. Recorded only above 3200 m on Mt Elgon (Uganda, Kenya).

Habitat Afroalpine grasslands and glades above 3200 m up to the peaks (4300 m). Preferred habitats are richly structured dense grasslands, bush–grassland mosaics on moist soils, and swamps with *Carex runsoroensi*. Pure tussock grasslands (mainly *Festuca pilgeri*) on drier soils are avoided, and inhabited by the syntopic *Otomys typus* (Clausnitzer 2000, 2001, 2003).

Abundance Abundant in and near swamps, and common in grasslands and bush–grassland mosaics (Clausnitzer 2001, 2003). Density varies from 15/ha (grassland, bush–grassland mosaic) to 25/ha (swamps). Comprised 45–50% of all rodents trapped in suitable habitats on Mt Elgon (V. Clausnitzer unpubl.). Density remains constant throughout the year.

Adaptations Diurnal and terrestrial. Lives in an extensive, surface and very shallow subterranean runway system, and seeks shelter in dense vegetation. Temperature in preferred habitat is often below freezing at night; however, these *Otomys* do not build nests or show eusocial behaviour (huddling) as a protection from the cold. The teeth and digestive system are modified for an entirely herbivorous diet: the molars are laminate, and the caecum and large intestine are relatively long (small intestine 40%, caecum 21%, large intestine 39%) (Clausnitzer 2003). See also genus profile.

Foraging and Food Herbivorous. Forages on leaves and flowers; prefers receptacles of *Helichrysum* flowers. Diet (on an annual basis) as assessed by analysis of faecal and stomach contents: 24% *Festuca pilgeri*, 21% other grasses, 30% parts of Compositae flowers (mainly *Helichrysum*), 6% other flowers, 18% dicotyledons (leaves) (n [faeces] = 89, n [stomach] = 32; Uganda; V. Clausnitzer unpubl.). Diet shows slight seasonal variation (Clausnitzer 2003).

Social and Reproductive Behaviour Solitary (except when ♀♀ are looking after young) and unsociable. Individuals utter chittering warning noises whenever they meet. Non-territorial; home-ranges overlap to a large extent. Home-range: 361 m^2 ($n = 49$, range: $0.21\text{--}2461 \text{ m}^2$). No significant difference in home-range area between the sexes and between seasons (Clausnitzer 2000, 2001, 2003).

Reproduction and Population Structure Reproduction is non-seasonal and occurs in all months of the year. In each month of the year, 20–60% of ♀♀ pregnant, and 20–100% lactating. Litter-

size: one ($n = 8$, Clausnitzer 2003). At birth, young are precocial and fully furred. Females have more than one litter/year. Populations are stable throughout the year without any seasonal fluctuations in numbers. Juveniles form about 10% of the population at all times (Clausnitzer 2003). Sex ratio 1 : 1 throughout year. Life expectancy: at least 15 months.

Predators, Parasites and Diseases Servals are a major predator: teeth of *Otomys* (*O. typus* and *O. barbouri*) comprised 95% of all teeth present in 100 faecal samples (Clausnitzer 2003). Birds of prey (including Augur Buzzard *Buteo rufofuscus*) may be minor predators. Fleas (species unknown) normally found on most adult individuals. No records of endoparasites (Clausnitzer 2003).

Conservation IUCN Category: Endangered.

Conservation of the very small geographical range (Mt Elgon above 3000 m) is essential.

Measurements

Otomys barbouri

HB (♂ ♂): 177 (162–210) mm, $n = 10$

HB (♀ ♀): 155 (125–175) mm, $n = 14$

T (♂ ♂): 79 (66–96) mm, $n = 10$

T (♀ ♀): 70 (57–80) mm, $n = 14$

HF (♂ ♂): 27 (23–30) mm, $n = 10$

HF (♀ ♀): 27 (24–30) mm, $n = 14$

E (♂ ♂): 23 (21–26) mm, $n = 10$

E (♀ ♀): 25 (22–28) mm, $n = 14$

WT (♂ ♂): 117.8 (83–161) g, $n = 83$

WT (♀ ♀): 106.2 (78–144) g, $n = 9$

GLS: 36.6 (32.4–39) mm, $n = 8$

GWS: 18.5 (16.5–19.7) mm, $n = 10$

M¹–M³: 8.9 (8.6–9.3) mm, $n = 8$

Mt Elgon, Uganda

Body measurements: Clausnitzer 2003

Skull measurements: Taylor & Kumirai 2001

Key References Clausnitzer 2001, 2003; Dieterlen & Van den Straeten 1992; Lawrence & Loveridge 1953; Taylor and Kumirai 2001.

Viola Clausnitzer

Otomys burtoni BURTON'S VLEI RAT

Fr. Rat du vlei de Burton; Ger. Burtons Lamellenzahnratte

Otomys burtoni Thomas, 1918. Ann. Mag. Nat. Hist., ser. 9, 2: 210. Cameroon Mt, Cameroon. 7000 ft (2100 m).

Taxonomy Previously treated as a subspecies or synonym of *O. tropicalis*. The presence of a slit-like petrotympanic foramen, shared with *O. angoniensis* and *O. sloggetti* (cf. round-shaped in all other *Otomys*), together with six or seven laminae in M³ (cf. seven in *O. angoniensis*, and four or five in *O. sloggetti*), allies this form with *O. angoniensis* (Taylor *et al.* 2004a) rather than with *O. tropicalis* as was previously thought. However, because of its very disjunct distribution, *O. burtoni* is here maintained as a distinct species following Musser & Carleton (2005). Synonyms: none. Chromosome number: not known.

Description Large, stoutly built rat with large, blunt head. Pelage long and soft (ca. 20 mm on mid-back). Dorsal pelage dull grizzled brown with a slight coppery tint. Hands and feet dark brown. Tail relatively short (50% of HB). Each upper and lower incisor with deep inner and shallow outer groove. M³ with six or seven laminae. M₁ with four laminae. Nasal bones moderately expanded. Petrotympanic foramen slit-like. Nipples: four.

Geographic Variation None recorded.

Similar Species

O. occidentalis. M³ with eight (occasionally seven) laminae; M₁ with five laminae; petrotympanic foramen slit-like (Dieterlen & Van der Straeten 1992).

O. angoniensis. M³ with seven laminae; petrotympanic foramen slit-like; not found in Cameroon.



Otomys burtoni

Distribution Endemic to Africa. Afromontane–Afroalpine BZ. Recorded only from Mt Cameroon, Cameroon, and the only known species of *Otomys* on the mountain.

Habitat Montane wetlands. Type specimen was collected at 2100 m.

Abundance No information.

Remarks Apparently no other information available.

Conservation IUCN Category: Endangered.

Listed as Endangered because of restricted geographic range and degradation of wetland habitats by overgrazing.

Measurements

Otomys burtoni

HB: 156 (145–167) mm, n = 6

T: 78 (75–84) mm, n = 6

HF: 30 (29–32) mm, n = 4

E: 24 (22–26) mm, n = 6

WT: 90 (71–105) g, n = 3

GLS: 37.2 (35.9–38.3), n = 5

GWS: 18.4 (18.1–18.7), n = 3

M¹–M³: 9.1 (8.9–9.2), n = 4

Cameroon (Dieterlen & Van der Straeten 1992, P. J. Taylor, unpubl.)

Key References Dieterlen & Van der Straeten 1992; Musser & Carleton 2005; Taylor & Kumirai 2001; Taylor *et al.* 2004.

P. J. Taylor

Otomys cuanzensis CUANZA VLEI RAT

Fr. Rat du vlei de Cuanza ; Ger. Cuanza Lamellenzahnratte

Otomys cuanzensis Hill and Carter, 1937. Amer. Mus. Novit. 913: 7. Chitau, Angola. 4930 ft (1500 m).

Taxonomy Mistakenly treated as a synonym of *maximus* (= *angoniensis*) by Musser & Carleton (1993). The presence of six to seven laminae in M³, and a round petrotympanic foramen, indicates a closer relationship with either *O. irroratus* or *O. tropicalis*. Since *O. cuanzensis* differs clearly from *O. irroratus* in having much narrower nasal bones and a uniformly brown pelage, and from *O. tropicalis* in having six rather than seven laminae in M³, it is treated as a distinct species pending a definitive study of its specific relationships (Musser & Carleton 2005). Synonyms: none. Chromosome number: not known.

Description Large, stoutly built rat with large, blunt head and relatively short tail. Pelage moderately long, soft, fine and thick. Dorsal pelage brown mixed with iridescent black, general colour 'near Bister' (Hill & Carter 1937, 1941). Flanks with black overlay less evident. Ventral pelage paler, deep neutral grey overlaid with cinnamon-buff or even paler. Eyes without paler rings. Ears of medium length, well haired, somewhat paler than body. Limbs short. Tail relatively short (ca. 58% HB), bicoloured and paler below, with short bristles. Each upper incisor with single groove, each lower incisor with one deep groove and additional faint or very faint groove, occasionally absent. M³ with six or seven laminae. M₁ with four laminae. Nasal bones moderately expanded. Petrotympanic foramen round. Nipples: four.

Geographic Variation None recorded.

Similar Species May co-exist sympatrically with two other species of *Otomys* in Angola:

O. angoniensis maximus. M₁ with four laminae; petrotympanic foramen slit-like.

O. anchietae. M₁ with five or six laminae; HB, HF, M¹–M³ probably shorter.

Distribution Endemic to Africa. Zambezan Woodland BZ. Distribution coincides largely with the drainage of the Cuanza R. in NW Angola, and other rivers in the north of Angola, which empty



into the Atlantic Ocean. Although occurring sympatrically with *O. anchietae* at Chitau, and with *O. angoniensis maximus* at Mt Soque, its geographic range appears to be parapatric to those of the other two Angolan species.

Habitat No information.

Abundance No information.

Remarks Apparently no other information available. Presumably similar to *Otomys irroratus*.

Conservation IUCN Category: Least Concern.

Measurements*Otomys cuanzensis*

HB: 180.3 (178–184) mm, n = 3

T: 104.7 (100–109) mm, n = 3

HF: 32 (31–33) mm, n = 3

E: 22 (22) mm, n = 3

WT: n. d.

GLS: 41.9 (40.4–43.5) mm, n = 3

GWS: 20.1 (19.5–20.9) mm, n = 3

M¹–M³: 9.4 (8.9–9.8) mm, n = 4

Angola (Hill & Carter 1941)

Key References Crawford-Cabral 1998; Hill & Carter 1937, 1941.**P. J. Taylor***Otomys denti* DENT'S VLEI RAT

Fr. Rat du vlei de Dent; Ger. Dents Lamellenzahnratte

Otomys denti Thomas, 1906. Ann. Mag. Nat. Hist., ser. 7, 18: 142. Mabuku Valley, east slope of Mt Rwenzori, Uganda.**Taxonomy** Synonyms: *kempi*, *sungae*. Subspecies: none. Chromosome number: not known.**Description** Large, stoutly built rat with large, blunt head. Pelage soft, fine and thick. Slightly smaller than *O. tropicalis*. Dorsal pelage dark blackish-brown with coppery tinge (distinctly different to other *Otomys* spp.). Ventral pelage similar to dorsal pelage. Tail short (54% of HB), black above and below (all other *Otomys* spp. have bicoloured tails). Each upper and lower incisor with single groove. M³ with five or six laminae. M₁ with four laminae. Nasal bones moderately expanded. Petrotympanic foramen round. Nipples: 0 + 2 = 4.**Geographic Variation** None recorded.**Similar Species***O. saundersiae*. Dorsal pelage paler, tail bicoloured, endemic to South Africa.*O. tropicalis*. Dorsal pelage paler, tail bicoloured, M³ with more than six laminae.*O. angoniensis*. Dorsal pelage paler, tail bicoloured, slit-like petrotympanic foramen.*O. sloggetti*. Dorsal pelage paler, tail bicoloured, slit-like petrotympanic foramen, endemic to South Africa.*O. anchietae*, *O. occidentalis*, *O. barbouri*, *O. lacustris*. M₁ with five laminae.**Distribution** Endemic to Africa. Afroalpine–Afroalpine BZ. Disjunct distribution on widely separated mountain ranges. Recorded from Uganda and DR Congo (Rwenzori and Albertine Rift Valley Mountains), EC Tanzania (Usambara and Uluguru Mts), N Malawi (Nyika Plateau) and extreme E Zambia. Based on widespread occurrence of fossils during the Pleistocene, historical distribution was much more widespread. On Rwenzori Mts, altitudinal range is 1860–3900 m (eastern side) and 2100–2700 m (western side) (J. Kerbis unpubl.).**Habitat** Damp montane grasslands and *Protea* scrub (Malawi; Ansell & Dowsett 1988) and secondary growth associated with forests in east-central Africa (Kingdon 1974). On Nyika Plateau, Malawi, mostly found near water and on swampy ground (Hanney 1965).**Abundance** No information.**Adaptations** Apparently more specialized than *O. tropicalis*. The two species only occur together in diversified habitats, but *O. denti* tends to displace *O. tropicalis* in montane situations, e.g. the earliest collecting records in the Rwenzori Mts show that *O. tropicalis* was the dominant species, but by the early 1960s it had been replaced by *O. denti* (Misonne 1963, Rahm 1967).**Foraging and Food** Presumably herbivorous as for other members of the genus. According to Kingdon (1974), individuals of this species have been reported to damage cypress trees, eating the bark and cambium of trees 1–8 years old.**Social and Reproductive Behaviour** No information.**Reproduction and Population Structure** In Malawi, pregnant ♀♀ recorded during the cool dry season (May, Jun and Nov). Embryo number: 1 (n = 4), 4 (n = 1) (Hanney 1965).*Otomys denti*

Predators, Parasites and Diseases Remains have been found in the stomach of a the Pallid Harrier *Circus macrourus* and an African Grass-owl *Tyto capensis* as well as comprising the bulk of the faeces of a leopard (Lawrence & Loveridge 1953).

Conservation IUCN Category: Least Concern.

Measurements

Otomys denti

HB: 154.9 (131–183) mm, n = 18

T: 82.6 (64–96) mm, n = 18

HF: 26.9 (26–28) mm, n = 18

E: 20.0 (18–22) mm, n = 18

WT: n. d.

GLS: 37.7 (35.2–40.4) mm, n = 15

GWS: 19.3 (18.3–20.2) mm, n = 12

M¹–M³: 8.4 (8.0–9.0) mm, n = 15

Body measurements: DR Congo (W. Van Neer unpubl., ex. alcohol)

Skull measurements: Rwanda (P. J. Taylor unpubl.)

Key References Kingdon 1974; Lawrence & Loveridge 1953.

P. J. Taylor

Otomys irroratus SOUTHERN AFRICAN VLEI RAT

Fr. Rat du vlei d’Afrique du Sud; Ger. Gemeine Lamellenzahnratte

Otomys irroratus (Brants, 1827). Het Geslacht der Muizen, p. 94. Constantia, Cape Town, Western Cape Province, South Africa.

Taxonomy Originally described in the genus *Euryotis*. Some authors have included *Otomys tropicalis* in *Otomys irroratus* (Bohmann 1952, Petter 1982, Dieterlen & Van der Straeten 1992), but Misonne (1974) and Musser & Carleton (1993, 2005) regarded each as separate species. On morphometric grounds, the two species are distinct (Taylor & Kumirai 2001). Meester *et al.* (1986) recognized eight subspecies, but none is currently recognized. Synonyms: *auratus*, *bisulcatus*, *capensis*, *coensus*, *cupreoides*, *cupreus*, *natalensis*, *obscura*, *orientalis*, *randensis*, *typicus*. Subspecies: none recognized here (but see below). Chromosome numbers: 2n = 23–32, aFN = 24–50.

The species has undergone major karyotypic evolution when compared with its congeners (Robinson & Elder 1987). Five parapatric ecologically distinct but genetically similar cytotypes are recognized: A, A1, A2, B and C (Contrafatto *et al.* 1992b, c, Taylor *et al.* 1992, 1993a, Contrafatto 1996, Taylor 2000). Cytotypes differ in the morphology of the seven largest chromosome pairs: all are single-armed (acrocentric) in A, A1 and A2, four pairs are biarmed or submetacentric in C (due to addition of heterochromatic whole arms), and all are submetacentric in B. Cytotype A2 bears two additional unidentified chromosome pairs not found in other cytotypes. Populations of cytotype A1 are reproductively isolated from other populations due to a complex tandem fusion rearrangement involving chromosome pairs 7 and 12 (Contrafatto *et al.* 1992b, Contrafatto 1996, Rambau *et al.* 2001). In all cytotypes, numerical variation (from 0 to 4) occurs between the number of small variable-morphology B-chromosomes (Contrafatto *et al.* 1992b). See also ‘Geographic Variation’ and ‘Social and Reproductive Behaviour’ below.

Description Large stocky rat with dense shaggy pelage. Dorsal pelage varies in colour geographically from dark slatey-greyish buff or ‘olive-brown’ with black-tipped hairs (KwaZulu–Natal Province) to a richer buffy or ‘cinnamon-brown’ with buffy-tipped hairs (Eastern Cape and Free State Provinces). Ventral pelage dark grey to paler greyish-buffy. Large head. Small well-haired ears held close to head. Tail short (ca. 60% of HB). Each upper and lower incisor with

single groove, although a shallow inner groove is additionally present in each lower incisor. M³ with six laminae (very occasionally seven). M₁ with four laminae. Nasal bones sharply expanded. Petrotympenic foramen round and large. Nipples: not known.

Geographic Variation Five cytotypes of indeterminate evolutionary status are recognized:

Cytotype A: lower altitudes (<1400 m) from C KwaZulu–Natal to Eastern Cape Province, South Africa.

Cytotype A1: Drakensberg mountain slopes (ca. 1400–1800 m) from KwaZulu–Natal to Eastern Cape Province, South Africa.

Cytotype A2: central mistbelt of KwaZulu–Natal, South Africa, 1000–1400 m.

Cytotype B: South Africa (lower-lying region of Eastern Cape Province from Grahamstown to Port Elizabeth and Fish River Valley) and Zimbabwe.

Cytotype C: winter-rainfall region of Western Cape Province, and highveld of Free State and Gauteng Provinces, South Africa.

According to Rambau *et al.* (2001), only two cytotype-groups should be recognized: A1 (with the composite chromosomal rearrangement), and all other cytotypes lacking this rearrangement. However, Taylor *et al.* (2009b) and Engelbrecht *et al.* (2011) recognize, on molecular and morphological grounds, two evolutionary lineages (species), which correspond with bioregions rather than karyotype, these being *irroratus* s.s. (from fynbos and thicket biomes) and *auratus* (from high-lying grasslands).

Similar Species

O. angoniensis. M³ with seven laminae; petrotympanic foramen slit-like; distribution in South Africa mostly <1000 m in savanna habitats, therefore largely parapatric with *O. irroratus* (>1000 m, highland grasslands).

O. laminatus. M³ with eight to ten laminae; M₁ with seven laminae; narrow distribution in South Africa, sympatric with *O. irroratus*.

*Otomys irroratus*

O. saundersiae. M³ with five to seven laminae; paler colour and smaller size; rocky hillside habitats in fynbos and thicket biomes of Western and Eastern Cape Provinces.

O. tropicalis. M³ with seven or more laminae; East and central Africa.

O. cuanzensis. M³ with seven laminae; restricted to Angola.

Distribution Endemic to Africa. Highveld and South-West Cape BZs and montane habitats of South Africa and Zimbabwe; extends marginally into southern parts of South-West Arid BZ. Recorded in South Africa from Cape Town to E KwaZulu–Natal and the central highveld of Gauteng Province; isolated populations are present in the southern parts of South-West Arid BZ at Kuruman (Northern Province) and into the Karoo along the Fish River Valley. Also recorded from Lesotho and Swaziland, and from E Zimbabwe and adjacent parts of W Mozambique. Altitudinal range is sea level to 2400 m.

Habitat Montane and sub-montane grasslands, fynbos and heath habitats. May occur in great abundance in rank grassy verges and overgrown garden lawns. Populations are mostly continuous in montane, high-rainfall areas, but disjunct at lower altitudes where they occur in areas of lush grass, sedge and herbs on damp wetland soils.

Abundance Abundant in suitable habitats. In a population near Pretoria, density increased from 17/ha in Sep to 72/ha in May. Mean density throughout year was 36/ha (Davis 1973).

Adaptations Mainly crepuscular. Creates distinctive 'runways' in the grass, which are used by other species of small mammals. The gut is modified for specialized herbivory: e.g. the stomach is U-shaped with an oesophageal sac capable of tremendous expansion, and the caecum is large and complex with a mean length of 149 mm (Davis 1973). Digestion of vegetation relies greatly on caecal fermentation. Coprophagy common.

Foraging and Food Diet is only green plant material with a fairly stable nutrient content (Perrin 1980a). Preferred food plants include stems and leaves of palatable grasses (e.g. *Panicum* spp.) and herbs. May feed on the soft outer bark of pine trees in forestry plantations and may cause extensive damage. Piles of discarded stems and leaves of grasses betray the location of their feeding spots along the runways.

Social and Reproductive Behaviour Solitary and aggressive. Levels of aggression are greatest in scrotal ♂♂, and decline successively from perforate ♀♀ to non-scrotal ♂♂ to imperforate ♀♀. Mean home-range 1730 m² in males and 1252 m² in females (Davis 1973). Adults partly territorial, defending a small area around the nest. Intraspecific conflict is minimized by anal-gland marking and indiscriminate urination and defecation along runways. Individual encounters are characterized by nose–nose contact with the body held low and extended, threat displays and by chases and fights, which may result in serious wounds. Submissive individuals rear upright with the forelimbs extended, exposing the vulnerable belly, and vocalize with a soft chittering (Davis 1972). In captivity, male–female aggression is high at initial contact, but declines over about four days, after which mating occurs. When individuals of particular cytotypes were paired, there was delayed mating due to heightened aggression, as well as significant ♀ choice of homotypes over heterotypes (Pillay *et al.* 1995b). Reproduction between different cytotypes resulted in 96% loss of fertility in hybrids (Pillay *et al.* 1995a).

Reproduction and Population Structure Gestation: 5–6 weeks. Females polyoestrus; 3–4 births/year. Near Pretoria, reproduction declined in mid-winter (Jun, Jul) but resumed in Aug following an increase in daylength and before there was an increase in food quality and quantity (Davis & Meester 1981). In Eastern Cape Province, reproduction declined in mid-summer, and was linked to a reduction in food availability rather than to variations in rainfall (Perrin 1980b). Mean litter-size: 1.5 in Eastern Cape Province (Perrin 1980b), 1.6 in Drakensberg Mts (Rowe-Rowe & Meester 1982b), 2.8 near Pretoria (Davis & Meester 1981); range (at all locations): 1–4. At birth, weight 12.5 g; incisors erupted. Young nipple-cling immediately after birth. Growth rapid: adult behaviour patterns attained at two weeks; 71% of adult weight attained in ten weeks; sexual maturity reached at 96 g (ten weeks for ♀♀ and 14 weeks for ♂♂) (Davis & Meester 1981). Greatest longevity in captivity: 22 months (Davis 1973).

Predators, Parasites and Diseases Bronner *et al.* (1988) list 21 known predator species, including humans, snakes (e.g. python *Python sebae* and Mole Snake *Pseudaspis cana*), birds (e.g. Grey Heron *Ardea cinerea*, and four species of owls), and mammalian carnivores (e.g. Serval *Felis serval*, Wild Cat *Felis lybica* and genet *Genetta* spp.). *Otomys irroratus* is typically by far the commonest prey item found in owl pellets and in faeces of Servals (Davis 1973, Bowland & Perrin 1983). Bronner *et al.* (1988) list 63 species of parasites (e.g. nematodes, cestodes, trematodes, mites, fleas, ticks and lice), and at least four zoonoses for which this species is probably a reservoir (bluetongue virus, bubonic plague, tick-bite fever and Q-fever).

Conservation IUCN Category: Least Concern.

Measurements

Otomys irroratus

HB: 161 (147–186) mm, n = 79

T: 98 (82–117) mm, n = 79

HF: 32 (29–34) mm, n = 79

E: 21 (19–23) mm, n = 79

WT: 144 (102–206) g, n = 79

GLS: 41.0 (32.6–45.9) mm, n = 105

GWS: 20.5 (16.8–24.1) mm, n = 104

M¹–M³: 9.7 (8.5–11.5) mm, n = 105

South Africa and Zimbabwe

Body measurements: Bronner *et al.* 1988; Taylor *et al.* 2005

Skull measurements: Taylor & Kumirai 2001

Key References Bronner *et al.* 1988; Contrafatto *et al.* 1992b, Pillay *et al.* 1995a, b; Taylor *et al.* 1992, 1993a; Taylor & Kumirai 2001.

P. J. Taylor

Otomys lacustris LAKE VLEI RAT

Fr. Rat du vlei du lac; Ger. Wasser-Lamellenzahnratte

Otomys lacustris Allen and Loveridge, 1933. Bull. Mus. Comp. Zool. Harvard 75: 120. Madehani, Ukinga Mts, Tanzania.

Taxonomy Lawrence & Loveridge (1953) described *lacustris* as a subspecies of *O. anchietae*, an arrangement followed by Bohmann (1952). Musser & Carleton (1993) placed *lacustris* as a synonym of *O. anchietae*. Recognized as a valid species by Dieterlen & Van der Straeten (1992) on the basis of morphometrics and cranial variables, and by Taylor & Kumirai (2001) on the basis of PCA and discriminant functions analysis of 16 cranial variables. Synonyms: none. Chromosome number: not known.

Description Large with comparatively long tail and very dark pelage. Pelage smoother and less brightly coloured than other species of *Otomys*. Dorsal pelage dark blackish-brown, hairs black or brown at base with narrow rusty subterminal band and black tip. Flanks dark brown. Ventral pelage paler. Tail comparatively long (ca. 65% of HB). Each upper and lower incisor with one single groove. M³ with six (occasionally seven) laminae; M₁ with five laminae. Nasal bones moderately expanded. Petrotympanic foramen round. Nipples: 0 + 2 = 4.

Geographic Variation None recorded.

Similar Species

Otomys anchietae. Much larger (HB: >187 mm); M³ with six (occasionally seven) laminae; M₁ with five (occasionally six) laminae; Angola only.

O. barbouri. Tail shorter (ca. 45% of HB); M³ with seven (occasionally eight) laminae; Mt Elgon only.

O. typus. Each lower incisor with two grooves; M³ with seven laminae, M₁ with four laminae; Afromontane–Afroalpine BZ of eastern Africa; sympatric at some localities.

Distribution Endemic to Africa. Afromontane–Afroalpine BZ of eastern Africa. Recorded from Kenya (one dubious record from the Aberdare Mts), Malawi (Mugesse Forest, as *O. anchietae*), Zambia (Abercorn = Mbala) and Tanzania (Ukinga Mts, Poroto Mts, Ufipa Plateau, Uzungwe Mts and Ilolo). The Kenya specimen clustered with *O. lacustris* (Taylor & Kumirai 2001).



Otomys lacustris

Habitat Montane habitats. Found in wet forest close to small stream (Mugesse Forest, Malawi); and in 'forest' on Ufipa Plateau, Tanzania (Dieterlen & Van der Straeten 1992). Detailed descriptions of habitat are lacking. The dubious record from Kenya (see above) was obtained in afroalpine habitat.

Abundance Uncertain. Rare in collections.

Remarks Apparently no other information available. See genus profile.

Conservation IUCN Category: Vulnerable.
Restricted to mountain ranges in eastern Africa.

Measurements*Otomys lacustris*

HB: 158 (150–165) mm, n = 4

T: 102.5 (90–110) mm, n = 4

HF (c.u.): 30.6 (30–31) mm, n = 4

E: 21 (20–22) mm, n = 4

WT: n. d.

GLS: 38.6 (36.8–39.9) mm, n = 3

GWS: 18.9 mm, n = 1

M¹–M³: 8.8 (8.6–9.1) mm, n = 3

Tanzania

Body measurements: Dieterlen & Van der Straeten 1992

Skull measurements: Taylor & Kumirai 2001

Key References Allen & Loveridge 1933; Dieterlen & Van der Straeten 1992; Taylor & Kumirai 2001.**Viola Clausnitzer*****Otomys laminatus* LAMINATE VLEI RAT (KWAZULU VLEI RAT)**

Fr. Rat du vleï laminé; Ger. Kap-Lamellenzahnratte

Otomys laminatus Thomas and Schwann, 1905. Abstr. Proc. Zool. Soc. Lond. 1905 (18): 23. Sibhudeni, Nkandhla Forest, KwaZulu–Natal, South Africa. 1050 m.**Taxonomy** Thomas (1918) erected a subgenus *Lamotomys* for this species, which was raised to generic rank by Roberts (1951), a view not currently followed. Synonyms: *fannini*, *mariepsi*, *pondoensis*, *silberbaueri*. Subspecies: five were recognized by Roberts, but Meester *et al.* (1986) consider it more likely that the four eastern forms are synonymous with the nominate form. Chromosome number: not known.**Description** Medium-sized, heavy-set rat with short tail. Pelage soft and shaggy; hairs ca. 20 mm. Dorsal pelage dark buffy-brown or 'raw umber'; hairs black at base with subterminal brown band and black tip. Indistinguishable from darker individuals of *Otomys irroratus*. Ventral pelage dull yellowish; hairs grey at base. Throat dull yellowish-white. Ears naked. Tail short (ca. 57% of HB), well haired, blackish above and dull buffy below. Each upper and lower incisor with single deep groove, with additional inner shallow groove ineach lower incisor. M³ with 8–10 laminae, usually nine, and distinctively more than any other species of *Otomys*. M₁ with seven laminae, also exceeding the number for any other *Otomys*. Nasal bones sharply expanded. Petrotympanic foramen round. Sexual dimorphism in some body measurements. Nipples: four.**Geographic Variation** None recognized here.**Similar Species***O. irroratus*. M³ with 6–7 laminae.*O. angoniensis*. M³ with 6–7 laminae; petrotympanic foramen slit-like.**Distribution** Endemic to Africa. Afromontane–Afroalpine and Highveld BZs; sometimes in parts of Coastal Forest Mosaic BZ. Recorded only in South Africa. Occurs along eastern foothills of Drakensberg range from Eastern Cape Province through KwaZulu–Natal into Mpumalanga Province, with a relic population in the Cape Peninsula and Paarl Valley of Western Cape Province.**Habitat** Mesic sub-montane grasslands along the Drakensberg foothills in KwaZulu–Natal, also recorded from coastal forests in KwaZulu–Natal, and from *Restio*-dominated coastal fynbos and mountain fynbos habitats in the Western Cape Province (De Graaff 1981, Taylor *et al.* 1994, Taylor 1998). May occur in pine plantations.**Abundance** Much less common than *O. irroratus*, with which it shares the same habitats. Occasionally common, e.g. *O. laminatus* was the only species of *Otomys* trapped in a single pine plantation (n = 56; P. J. Taylor unpubl.).**Remarks** As described for *O. irroratus*. Since increasing laminae number is surmised to be associated with an evolutionary trend towards increased specialization to mesic habitats (Pocock 1976, Denys 1989b), this species is presumably the most specialized species of *Otomys* in this respect. Probably entirely vegetarian, feeding on shoots and stems of grasses, *Restio* and small shrubs (De Graaff 1981).**Conservation** IUCN Category: Least Concern.

Measurements

Otomys laminatus

HB (♂ ♂): 199 (188–213) mm, n = 5
 HB (♀ ♀): 178 (158–197) mm, n = 3
 T (♂ ♂): 109 (97–115) mm, n = 5
 T (♀ ♀): 107 (105–111) mm, n = 3
 HF (♂ ♂): 30 (22–34) mm, n = 5
 HF (♀ ♀): 30 (30–31) mm, n = 3
 E (♂ ♂): 21 (17–26) mm, n = 5
 E (♀ ♀): 24 (22–26) mm, n = 3
 WT (♂ ♂): 190, 264 g, n = 2
 WT (♀ ♀): 140 (140–140) g, n = 3

GLS: 44.6 (42.7–41.7) mm, n = 7
 GWS: 22.5 (20.2–25.0) mm, n = 7
 M¹–M³: 10.5 (9.7–11.0) mm, n = 7
 South Africa
 Body measurements: De Graaff 1981
 Weights: P. J. Taylor unpubl.
 Skull measurements: Roberts 1951

Key References De Graaff 1981; Taylor 1998; Taylor *et al.* 1994.

P. J. Taylor

Otomys occidentalis WESTERN VLEI RAT

Fr. Rat du vlei occidental; Ger. Westliche Lamellenzahnratte

Otomys occidentalis Dieterlen and Van der Straeten, 1992. Bonn. Zool. Beitr. 43: 386. Chappal Waddi, Gotel Mts, south-east Nigeria.

Taxonomy Closely related to *O. anchietae*, *O. lacustris* and *O. barbouri* in having five laminae in M₁. Synonyms: none. Chromosome number: not known.

Description Medium-sized, stoutly built rat, but one of the smallest species of the genus (see also *O. saundersiae*). Pelage soft, fine and thick; hairs 20–27 mm. Dorsal pelage brown to blackish-brown, slightly more reddish in individuals from Mt Oku than those from Gotel Mts. Flanks slightly paler; hairs with yellowish tip. Ventral pelage blackish-grey, silky and glossy (more so than dorsal pelage); individuals from Mt Oku paler and more brownish than those from Gotel Mts. Head large and blunt. Tail short (ca. 54% of HB) and bicoloured. Each upper and lower incisor with single groove. Nasal bones sharply expanded. M³ with eight, occasionally seven, laminae. M₁ with five laminae. Petrotympanic foramen slit-like (n = 1). Nipples: 0 + 2 = 4.

Geographic Variation None recorded.

Similar Species

O. burtoni. Mean values for measurements slightly larger; pelage paler and more buffy; M³ with six or seven laminae; M₁ with four laminae; petrotympanic foramen round; Mt Cameroon only.
O. barbouri. HB on average larger, M³ with seven to eight laminae; petrotympanic foramen round; longer dorsal hairs 20–35 mm; Mt Elgon only.

Distribution Endemic to Africa. Afroalpine–Afroalpine BZ in Nigeria and Cameroon. Known from only two localities: Mt Oku (2100–3000 m) in W Cameroon and Gotel Mts (1900–2300 m) in E Nigeria.

Habitat Alpine heath and grassland with ferns in montane forest clearings, 1900–3000 m (Dieterlen & Van der Straeten 1992).

Abundance No information.

Remarks One ♀ with two embryos was collected in Mar (Dieterlen & Van der Straeten 1992).

Conservation IUCN Category: Vulnerable.

The restricted geographic range and continuing decline in area, extent and quality of its montane habitat are cause for concern.

Measurements

Otomys occidentalis

HB: 143 (131–160) mm, n = 4
 T: 78 (68–88) mm, n = 4
 HF: 28 (24–29) mm, n = 4
 E: 20 (18–22) mm, n = 5
 WT: 77 (69–88) g, n = 3



Otomys occidentalis

GLS: 35.7 (34.3–36.9) mm, $n = 3$

GWS: n. d.

M^1 – M^3 : 8.9 (8.5–9.6) mm, $n = 4$

Cameroon and Nigeria (Dieterlen & Van der Straeten 1992)

Key Reference Dieterlen & Van der Straeten 1992.

P. J. Taylor

Otomys saundersiae SAUNDERS'S VLEI RAT

Fr. Rat du vlei de Saunders; Ger. Saunders Lamellenzahnratte

Otomys saundersiae Roberts, 1929. Ann. Transvaal Mus. 13: 115. Grahamstown, Eastern Cape Province, South Africa.

Taxonomy *Otomys saundersiae* is retained as a valid species here, although Musser & Carleton (2005) regard *saundersiae* as a subspecies of *O. irroratus*. *Otomys saundersiae* is distinct from *O. irroratus* on the basis of consistent but subtle differences in chromosomal, allozyme, DNA (PCR–RAPD), pelage colour and/or morphometric characters (Meester *et al.* 1986, Taylor *et al.* 1993b, 2005). Synonyms: *karoensis*. Subspecies: two, but both may prove to deserve specific status. Chromosome number: $2n = 28$, $aFN = 42$ – 44 (Taylor 2000, Taylor *et al.* 2005).

Description Medium-sized stocky rat. Pelage dense and shaggy, 13–16 mm on mid-back. Dorsal and ventral pelage variable – see Geographic Variation. Head large. Small well-haired ears held close to head. Tail bicoloured, short (ca. 73% of HB), but relatively longer than other *Otomys* spp. Each upper and lower incisor with single deep groove; additional inner shallow groove on each lower incisor. M^3 with six, sometimes five, laminae (although seven in holotype). M_1 with four laminae. Nasal bones moderately expanded (Taylor *et al.* 1993b). Petrotympanic foramen round. Nipples: $0 + 2 = 4$.

Geographic Variation

O. s. saundersiae: coastal and low-lying parts of the Eastern Cape Province, south of 33°S. On average slightly larger, intermediate between *O. irroratus* and *O. s. karoensis*; dorsal pelage pale buffy, speckled with dark brown-tipped hairs; dorsal hairs 13 mm; flanks paler buffy; ventral pelage grey; throat and distal appendages whiter in colour; tail buffy-white dorsally, grey below; tip of muzzle, ring around eye and tuft of hair in front of the ears buffy-yellow; hair immediately behind ears buffy to white.

O. s. karoensis: mountainous areas of the Western and Eastern Cape Provinces and extreme SW Free State. Dorsal pelage pallid greyish-buffy, conspicuously paler than in *O. irroratus* but less buffy than in *O. s. saundersiae*; dorsal hairs generally 16 mm, pencilled with black due to numerous interspersed longer (26 mm) black-tipped hairs; ventral pelage less buffy-grey.

Similar Species

O. irroratus. Body size on average larger; GLS on average larger; pelage darker; M^3 with six to seven laminae; upper incisor with single groove; nasal bones widen more abruptly anteriorly.

O. unisulcatus, *O. sloggetti*, *Parotomys brantsii*, *P. littledalei*. Pelage paler; lower incisors ungrooved; not found in winter rainfall region of Western Cape Province.



Otomys saundersiae

Distribution Endemic to Africa. South-West Cape BZ and Highveld BZ. *Otomys s. saundersiae* confined to coastal and low-lying areas of the Eastern Cape Province, South Africa, south of 32°S from King William's Town in the east to Port Elizabeth in the west, possibly as far west as the Bredasdorp area. *Otomys s. karoensis* occupies two separate areas: (1) mountainous winter rainfall areas of Western Cape Province, from the Cape Peninsula north to the Citrusdal district; and (2) summer rainfall areas of southern portion of the Drakensberg range in Eastern Cape Province (north of 32°S and west of Lesotho), and into Free State where it has been recorded in the Bloemfontein district (Taylor *et al.* 2005).

Habitat *Otomys s. saundersiae* prefers open grassland habitats on the drier upper slopes in hilly terrain. *Otomys s. karoensis* prefers rocky mountain fynbos habitats on the upper mountain slopes where *Restio* is a dominant species; exceptionally *O. s. karoensis* has been found in open grassland and scrubland in the Bloemfontein and Fauresmith districts of SW Free State (Taylor *et al.* 2005).

Abundance Based on the proportionately fewer numbers of museum specimens, and difficulty in trapping them, *O. s. saundersiae* is much less common than *Otomys irroratus* in Eastern Cape Province.

Otomys s. karoensis may be easily trapped in fair numbers in mountainous habitats in Western Cape Province (P. J. Taylor unpubl.).

Remarks In captivity, individuals of *O. s. karoensis* are docile and curious, contrasting with the typical aggressive and shy behaviour of *O. irroratus* (A. Kumirai & P. J. Taylor unpubl.). Three species of laelaptid mites, four species of fleas (of the families Hystrichopsyllidae and Chimaeropsyllidae) and four species of ticks (one species of soft tick and three species of hard ticks) have been described (De Graaff 1981).

Conservation IUCN Category: Least Concern.

In 1996, listed as Near Threatened.

Measurements

Otomys saundersiae

O. s. saundersiae

HB: 145 (120–180) mm, n = 13

T: 86 (70–106) mm, n = 11

HF: 25 (20–29) mm, n = 13

E: 21 (16–25) mm, n = 13

WT (♂ ♂): 111 (100–134) g, n = 7

WT (♀ ♀): 95 (84–107) g, n = 4

GLS: 35.7 (32.2–38.7) mm, n = 11

GWS: 17.6 (16.2–19.5) mm, n = 11

M¹–M³: 8.6 (7.9–9.6) mm, n = 11

Eastern Cape Province, South Africa (A. Kumirai & P. J. Taylor unpubl.)

Weights: Eastern and Western Cape Provinces, South Africa (De Graaff 1981)

O. s. karoensis

HB: 134 (110–154) mm, n = 11

T: 98 (86–111) mm, n = 10

HF: 27 (25–30) mm, n = 11

E: 21 (18–23) mm, n = 11

WT: 108 (78–139) g, n = 4

GLS: 35.6 (32.4–38.4) mm, n = 10

GWS: 17.4 (16.0–18.3) mm, n = 11

M¹–M³: 8.5 (7.8–9.3) mm, n = 10

Western Cape Province, South Africa (A. Kumirai & P. J. Taylor unpubl.)

Key References De Graaff 1981; Taylor *et al.* 1993b.

P. J. Taylor

Otomys sloggetti SLOGGETT'S VLEI RAT

Fr. Rat du vlei de Sloggett; Ger. Sloggetts Lamellenzahnratte

Otomys sloggetti Thomas, 1902. Ann. Mag. Nat. Hist., ser. 7, 10: 311. Deelfontein, Northern Cape, South Africa.

Taxonomy Closely related to *O. unisulcatus* (Thomas 1918, Roberts 1951, Taylor *et al.* 1989) but not as sister species (Taylor *et al.* 2004a). Placed in the genus *Myotomys* by Musser & Carleton (2005). Synonyms: *basuticus*, *jeppiei*, *robertsi*, *turneri*. Subspecies: five. Chromosome number: 2n = 42, aFN = 48, comprising 16 acrocentric, two metacentric and two subtelocentric pairs, a medium-sized acrocentric X-chromosome and a small acrocentric Y-chromosome (Contrafatto *et al.* 1992a). Allozyme data show reduced gene flow between high altitude populations of *O. s. robertsi* from north Eastern Cape and NE Lesotho (Contrafatto *et al.* 1992a).

Description Medium-sized, stoutly built rat. Pelage soft, fine and thick. Dorsal pelage pale greyish-buffy. Flanks pale greyish-brown. Ventral pelage whitish-buffy. Large blunt head. Area around facial vibrissae red-brown, a character that can be used to distinguish this species from other *Otomys* spp. Ears small, dark on posterior edge. Tail short (ca. 49% of HB), bicoloured, black above, pale buffy below. Each upper incisor with one groove; each lower incisor with one very faint groove. M³ with four or five laminae, M₁ with four laminae. Nasal bones barely expanded. Petrotympanic foramen slit-like. Anterior expansion of nasal bones makes an obtuse angle (ca. 150 degrees). Nipples: 2 + 0 = 4.

Geographic Variation Five subspecies recognized but with poorly defined geographical boundaries:

O. s. sloggetti: Northern Cape Province, South Africa.

O. s. turneri: E Free State Province, South Africa.

O. s. robertsi (Ice Rat): high Drakensberg Mts in Lesotho and N Eastern Cape Province, South Africa.

O. s. jeppiei: Northern Cape Province, South Africa.

O. s. basuticus: low-lying parts of SE Lesotho.

Similar Species

O. unisulcatus. M³ with six or five laminae; petrotympanic foramen round; semi-arid habitats.

O. saundersiae. Dorsal pelage less pallid; M³ with six (rarely five or seven) laminae; petrotympanic foramen round; winter rainfall biome of Western and Eastern Cape Provinces.

Distribution Endemic to Africa. Highveld BZ and Afroalpine BZ of South Africa and Lesotho. Recorded throughout the high Drakensberg Mts, South Africa (i.e. the western border of KwaZulu–Natal, NE Free State, Eastern Cape Provinces) and Lesotho, to about 27°S in Mpumalanga Province (only at Wakkerstroom). Isolated relict populations in the Karoo near Hanover, Orange R., and as far west as Deelfontein in Northern Cape Province (De Graaff 1981, Lynch 1983, 1989, Lynch & Watson 1992, P. J. Taylor unpubl.). It is likely that this species previously occupied a much wider distribution, and range of altitudes and habitats, as evidenced by its presence in late Holocene sites (<1000 years ago) in the upper Tugela River basin in KwaZulu–Natal, which are now covered by savanna (Avery 1991). Altitudinal range: above 2000 m (most of range) and above 2600 m in Lesotho (Rowe-Rowe & Meester 1982b, Lynch 1994).

*Otomys sloggetti*

Habitat Montane and alpine grasslands on xeric or mesic soils, with or without rocky outcrops. Typically individuals live in piles of loose stones and boulders, both natural and man-made (e.g. stone walls throughout Lesotho). In boggy situations, these vlei rats construct their burrows on raised hummocks, which they create by their own burrowing activities (Lynch & Watson 1992). In the Drakensberg Mts of the KwaZulu–Natal, burrows maybe found in alluvial soils along river banks (D. Rowe-Rowe pers. comm.). Isolated populations occupy dry semi-desert habitats in the eastern Karoo, but these recorded localities are in the vicinity of inselbergs and mountain ranges at >1500 m.

Abundance Densities of over 100/ha have been estimated in suitable rocky habitats (Willan 1990).

Adaptations Diurnal. Individuals sun themselves on exposed rocks (or at the entrance to burrows) intermittently throughout the day to gain heat. Burrow-dwelling, and hoarding of food in burrows, may be adaptations for surviving periods of intense cold. Such behaviour may facilitate the *ad libitum* suckling of young by lactating ♀♀, and thereby delay emergence of young from the nest until about five weeks of age. Survival of young is thus enhanced by greater protection from predators, and by postnatal development of thermoregulatory ability necessary to cope with cold temperatures. Reduced length of HB and extremities (tail, hindfoot and ear) of young Ice Rats (*O. sloggetti robertsi*), compared to young *O. irroratus*, is also a thermoregulatory adaptation to reduce surface area/volume ratios and to minimize heat loss in intensely cold environments (Willan 1990). Similarly, adults have significantly shorter tails than other *Otomys* spp. (Richter 1997). Adults are best able to thermoregulate at lower, rather than higher, temperatures compared to other *Otomys* spp., which might explain their restriction to higher altitudes and cold habitats (Richter *et al.* 1997).

As with other species of *Otomys* and *Parotomys*, the structure of the gut is adapted to a high fibre diet. The slightly larger size of the small intestine, caecum, stomach and parts of the colon in the Ice Rat (*O.*

sloggetti robertsi) compared with other species of Otomyinae could be an adaptation for increased energy uptake and/or poor diet quality in alpine environments. The dimensions of the gut of female Ice Rats increase during summer, possibly in response to the increased energy requirements of lactation and pregnancy (Schwaibold & Pillay 2003).

Foraging and Food Specialist herbivore, feeding on stems, leaves and floral parts of a range of green plants. Food plants are hoarded in burrows, including *Knopfia caulescens*, *Cyperus* spp., *Eumorphia sericea*, *Anthraxia fontana*, *Euryops* sp., *Arctotis arctoides*, *Selago flanaganii*, *Senecio asperulus* and two grass species, *Bromus* sp. and *Vulpia bromoides*. Foraging is usually limited to regions in close proximity to burrow entrances (Hinze *et al.* 2003). In summer, food is mostly eaten *in situ*. In contrast, in winter, food is usually carried back to the burrow thus avoiding long exposure to extreme cold temperatures and, possibly, helping to avoid injury due to aggressive competition when food resources are limited (Schwaibold & Pillay 2003).

Social and Reproductive Behaviour Burrows may be occupied by pairs or family groups within which only a single pair breeds (Willan 1990). Burrows comprise an intricate tunnel system, usually 200–300 mm deep, with one or two active nest sites lined with finely shredded grass leaves, and 2–12 tunnel entrances. Faeces are deposited at or just inside tunnel entrances (Lynch & Watson 1992, Hinze *et al.* 2003).

Sociality in Ice Rats *O. s. sloggetti* varies spatially and seasonally. When above ground, individuals of a group are partly territorial, maintaining overlapping home-ranges and competing aggressively for limited food resources between themselves as well as against non-group members (Hinze *et al.* 2003). One or more sentinels apparently maintain vigilance for the group. When underground, individuals huddle to conserve heat and there is no evidence of territoriality. Groups comprise 4–16 individuals. Individuals of a group make synchronized above-ground appearances each day, but do not follow generalized behaviour patterns. They are active throughout the year, although in winter they spend more time each day underground in their burrows. Individuals are highly inquisitive and relatively unafraid of humans (Hinze *et al.* 2003).

Reproduction and Population Structure Pregnancies recorded during mid- to late summer (Oct–Mar) in Lesotho. Mean litter-size: 2.5 (2–5; Lynch 1994). In captivity, gestation 38 days, litter-size 1.4 (1–2), reproductive effort 0.5, and fecundity about six young/annum (Willan 1990).

Predators, Parasites and Diseases Predators include Small Grey Mongooses *Galerella pulverulenta*, Barn Owls *Tyto alba*, Steppe Buzzards *Buteo buteo* and Jackal Buzzards *B. rufofuscus*. Mites (two species), fleas (11 species) and ticks (two species) have been recorded (details in De Graaff 1981).

Conservation IUCN Category: Least Concern.

Measurements

Otomys sloggetti

HB: 127 (93–170) mm, n = 73

T: 62 (47–84) mm, n = 73

HF: 28 (21–30) mm, n = 73
 E: 18 (14–22) mm, n = 72
 WT: 84 (45–155) g, n = 61
 GLS: 37.6 (35.0–40.0) mm, n = 11
 GWS: 19.8 (19.0–21.8) mm, n = 12
 M¹–M³: 8.4 (7.9–9.7) mm, n = 14
 Body measurements: Lesotho (Lynch 1994)

Skull measurements: South Africa (Roberts 1951)

Key References Lynch 1994; Lynch & Watson 1992; Richter 1997; Richter *et al.* 1997; Willan 1990.

P. J. Taylor

Otomys tropicalis TROPICAL VLEI RAT (EAST AFRICAN VLEI RAT)

Fr. Rat du vlei du tropique; Ger. Tropische Lamellenzahnratte

Otomys tropicalis Thomas, 1902. Ann. Mag. Nat. Hist., ser. 7, 10: 314. West slope of Mt Kenya, Kenya. 10,000 ft (3000 m).

Taxonomy Although regarded by some authors to be conspecific with *O. irroratus* (Misonne 1974, Petter 1982, Dieterlen & Van der Straeten 1992), this species has been shown to be distinct on morphometric and dental evidence (Taylor & Kumirai 2001, Taylor *et al.* 2004b). Musser & Carleton (2005) consider *dollmani* and *orestes* from Kenya (here retained as synonyms) to be valid species, distinct from *O. tropicalis* in pelage and skull-shape characters and in having six laminae on M³. Because it possesses a slit-like petrotympanic foramen (Taylor *et al.* 2004a), *burtoni* from Cameroon, previously considered to be a subspecies of *tropicalis* (Dieterlen & Van Straeten 1992), is here considered to be a distinct species. Synonyms (of *tropicalis*): *elgonis*, *dollmani*, *faradjius*, *ghighi*, *giloensis*, *orestes*, *nubilis*, *rubeculus*, *vivax*, *vulcanis* (of *orestes*): *malleus*, *percivali*, *thomasi*, *squalus*, *zinki*. Subspecies: uncertain; several have been described but their validity remains to be tested. Chromosome number: not known.

Description Large, stoutly built rat with large, blunt head and short tail. Pelage soft, fine and thick. Dorsal pelage dark brown, close to 'raw umber'. Flanks clear brown. Ventral pelage slatey, hairs buffy at tip. Eyes without paler rings. Ears of medium length, well haired, somewhat paler than body. Tail short (ca. 46% of HB), black above, dull white below. Each upper incisor with single groove; each lower incisor with one deep groove and additional faint or very faint groove (occasionally absent). M³ with seven (usually) or eight laminae. M₁ with four laminae. Nasal bones moderately expanded. Petrotympanic foramen round. Nipples: 0 + 2 = 4.

Geographic Variation Disjunct populations associated with different mountain ranges vary slightly in pelage colour, size and cranial characters (shape of nasal bones and the number of laminae on M³), making it difficult to delineate species or subspecies (although *orestes* and *dollmani* mentioned above may prove to represent distinct species coexisting with contiguous populations of *tropicalis* on the slopes of Mt Kenya).

Similar Species Four other species of *Otomys* occur in eastern Africa, but at higher altitudes than *O. tropicalis*:

- O. typus*. M³ with eight (sometimes six, seven or nine) laminae; two deep grooves on each lower incisor.
- O. barbouri*. M₁ with five laminae.
- O. lacustris*. M³ with six laminae; M₁ with five laminae.

O. denti. Much blacker pelage, tail not bicoloured, M³ with five or six laminae; M₁ with four laminae.

Distribution Endemic to Africa. Afromontane–Afroalpine BZ in eastern Africa, and some nearby areas at lower altitudes. Recorded from E DR Congo, Uganda, Rwanda, Burundi, S Sudan, W and N Kenya and possibly NE Tanzania. Specific localities are Rwenzori Mts, Mt Elgon, Mt Kenya, Aberdare Ranges and Imatong Mts. One isolated record from Nyika Plateau, Malawi. Also occurs at lower altitudes such as Kampala in Uganda, and Garamba N. P. in NE DR Congo. Specimens from Mt Kilimanjaro and Msinga (NE Tanzania) are probably this species. Misonne's comment (1963) that *O. tropicalis* does not occur on the Rwenzori Mts is incorrect. Altitudinal range is very varied, from below 1000 m to over 3000 m; on Rwenzori Mts, range is ca. 840–2250 m.

Habitat Occupies a wide range of dense, moist grassland and scrub habitats, ranging from savanna to alpine heath, as well as cultivated areas (e.g. coffee and banana plantations). Avoids natural forested habitats except where these are highly degraded or where clearings and secondary growth are formed as a result of fire or destruction of the forest



Otomys tropicalis

(Verheyen & Verschuren 1966, Dieterlen & Van der Straeten 1992); also avoids very dry and permanently flooded marsh habitats (Misonne 1963). Not recorded in local houses. Sympatric with *O. denti* and *O. typus* in Rwenzori Mts, but each species has a different altitudinal range.

Abundance Common. In Haut Ituri, DR Congo, abundance varied according to habitat. Comprised ca. 40% of all small rodents in preferred habitats; estimated densities ranged from ca. 16.1/ha in seasonally flooded marsh, to 42.5/ha in savanna with secondary growth near villages (Misonne 1963). Densities decreased in savanna habitats away from villages (ca. 23.3/ha) (Misonne 1963).

Adaptations Presumably similar to *Otomys irroratus*.

Foraging and Food Herbivorous, feeding on a range of green grass, reed and herb stems, shoots, bark and occasionally roots, seeds and berries (Kingdon 1974). Verheyen & Verschuren (1966) noted fragments of ants in stomach contents. They may damage forest plantations; in DR Congo, 65% of trees in one plantation had been damaged, with trees of 3–15 mm diameter being completely ring-barked.

Social and Reproductive Behaviour Activity mostly crepuscular. Timid and sensitive to noise in captivity. Few vocalizations, but squeaks and a loud screech have been noted (Kingdon 1974).

Reproduction and Population Structure Litter-size 1 or 2, always <4. Births recorded throughout year; up to five litters per year. Capable of breeding before three months of age. Adult behaviour is attained within two weeks. Mean birth-weight 12.5 g; young grow at a rate of 10 g per week (Kingdon 1974).

Predators, Parasites and Diseases Major predators in East Africa include the African Grass-owl *Tyto capensis* and Augur Buzzard *Buteo rofufuscus*. They have been implicated as a plague reservoir (F. Dieterlen in Kingdon 1974), but as contact with humans is limited, their role as an immediate transmitter of the disease must be slight.

Conservation IUCN Category: Least Concern.

Measurements

Otomys tropicalis

HB: 178.0 (147–201) mm, n = 10

T: 81.5 (69–94) mm, n = 10

HF: 28.7 (26–33) mm, n = 10

E: 23.3 (20–24) mm, n = 7

WT: 111.3 (81–133) g, n = 9

GLS: 39.0 (29.0–43.5) mm, n = 52

GWS: 19.0 (15.0–21.8) mm, n = 52

M¹–M³: 9.2 (8.4–10.4) mm, n = 52

Body measurements: throughout geographic range (BMNH, DM, MNHN)

Skull measurements: throughout geographic range (Taylor & Kumirai 2001)

Key References Dieterlen & Van der Straeten 1992; Kingdon 1974; Taylor & Kumirai 2001; Taylor *et al.* 2004a; Verheyen & Verschuren 1966.

P. J. Taylor

Otomys typus ETHIOPIAN VLEI RAT

Fr. Rat du vlei d'Éthiopie; Ger. Äthiopische Lamellenzahnratte

Otomys typus (Heuglin, 1877). Reise in Nordost-Afrika 2: 77. Simien Mts, Ethiopia.

Taxonomy Originally described in the genus *Oeromys*. The taxonomy of *O. typus* is uncertain. In Ethiopia, there are two genetically distinct *Otomys*, 'Sp. A' and 'Sp. B', both currently included in *O. typus* (Lavrenchenko *et al.* 1997); subsequently formally named as *O. yaldeni* sp. nov. and *O. helleri*, respectively (Taylor *et al.* 2011). Because there are variations in the number of laminae on M³, size, skull shape and pelage, Musser & Carleton (2005) recognize *jacksoni* (with seven laminae), *dartmouthi* (six laminae) and *uzungwensis* (seven laminae) as distinct species, thus restricting the range of *O. typus sensu stricto* (eight or nine laminae) to the Ethiopian Highlands. However, similar variation has been observed even within Ethiopian populations (six to nine laminae, large size and shape variation), and a recent molecular, morphological and cytogenetic synthesis (Taylor *et al.* 2011) restricts *typus s.s.* to certain mountains west of the Great Rift Valley in Ethiopia (Simien and Guna Mountains in the north, extending to the highlands of the western rim of the Rift Valley) and recognizes a further 11 valid taxa: *cheesmani* sp. nov. (Ethiopia), *dartmouthi* Thomas, 1906 (Rwenzori Mts), *fortior* Thomas, 1906a (south-western Ethiopia), *helleri* Frick, 1914 (Bale Mts, Ethiopia), *jacksoni* Thomas, 1891 (Mt Elgon), *orestes* Thomas, 1900 (Mt Kenya and Abderdare Mts), *simiensis* sp. nov. (Simien

Mts, Ethiopia), *thomasi* Osgood, 1910 (central Kenya), *uzungwensis* Lawrence and Loveridge, 1953 (Eastern Arc Mts to Nyika Plateau), *yaldeni* sp. nov. (Bale Mts, Ethiopia), *zinki* Bohmann, 1943 (Mt Kilimanjaro). Synonyms: *degeni*, *malkensis*, *percivali*. Subspecies: none. Chromosome number: 2n = 52 (Mt Elgon; A. Kumirai & P. J. Taylor unpubl.), 2n = 56 (Sp. A; Ethiopia) and 2n = 57–58 (Sp. B; Ethiopia).

Description Medium-sized, smooth-coated rat. Dorsal pelage speckled bright tawny-brown. Ventral pelage grey. Colours of dorsal and ventral pelage merge along the flanks. Ears grey, short, prominent and rounded. Feet dark grey to black. Tail short (ca. 46% of HB). Each upper incisor with single groove; each lower incisor with two deep grooves. M³ with typically seven or eight laminae; however, 'Sp. A' is believed to have six laminae and 'Sp. B' has seven or eight laminae. M₁ with four laminae. Males tend to be larger than ♀♀. Nasal bones expanded. Petrotympanic foramen round. Nipples: presumably 0 + 2 = 4.

Geographic Variation None recorded.

Similar Species In Ethiopia, only one species is currently

recognized. Elsewhere in East Africa other *Otomys* spp. have fewer laminae on M³.

Distribution Endemic to Africa. Afromontane–Afroalpine BZ. Widespread in moist localities at higher altitudes in Ethiopia, and discontinuously southwards to Zambia. Recorded from Ethiopia (many localities, as *O. typus*, *cheesmani*, *fortior*, *helleri*, *simiensis*, *yaldeni*), Mt Elgon (Uganda/Kenya, as *jacksoni*), Aberdare Ranges (as *orestes*), Kilimanjaro (as *zinki*), Mau Plateau (as *thomasi*) and Rwenzori Mts (Uganda/DR Congo, as *dartmouthi*). Also recorded from Uzungwa Mts (WCTanzania), Nyika Plateau (Malawi) and Nyika Plateau (NE Zambia) as *uzungwensis*. Altitudinal range on Rwenzori Mts 3300–3900 m.

Habitat Occurs only in moist grasslands and swamps from 1300 to 4300 m. Prefers habitat with dense grass cover, and avoids wet marshlands (Clausnitzer 2003). In afroalpine habitats on Mt Elgon, this species is broadly syntopic with *O. barbouri*; however, *O. typus* prefers drier grasslands and *O. barbouri* prefers wetter habitats.

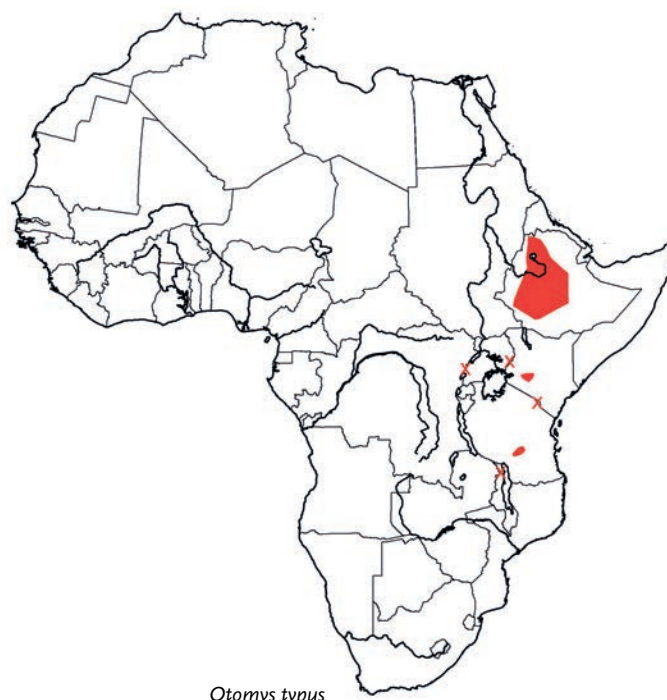
Abundance May be abundant in suitable habitats, but abundance often underestimated because of acute trap-shyness (Sillero-Zubiri *et al.* 1995a, Clausnitzer 2003). Comprised 6% of rodents in grasslands of Simien Mts, Ethiopia (Müller 1977). On Mt Elgon (Kenya/Uganda), population numbers rather stable throughout year; density is ca. 15/ha to 30/ha, and mean biomass is 937–1941 g/ha depending on the vegetation (Clausnitzer 2003).

Adaptations Terrestrial. Active throughout 24 hours in the Bale Mts, Ethiopia; about 75% of captures in morning and 25% at night (Sillero-Zubiri *et al.* 1995a). In the Simien Mts, Ethiopia, as likely to be trapped during daytime as at night (Müller 1977). Animals are nervous during daylight and tend to stay under cover.

Foraging and Food Herbivorous, specializing on grass stems and leaves. Well-used runways radiate from good cover to feeding sites. On Mt Elgon, major food items were *Festuca pilgeri* (ca. 50%) and other grasses (*Kolera capensis*, *Argosies gracilifolia*) (ca. 50%). Flowers of the shrubby composite *Helichrysum*, when available, were the only other significant item of food (Clausnitzer 2003).

Social and Reproductive Behaviour Aggressive, but not territorial. Median home-range on Mt Elgon varies according to sex and habitat: 401–728 m² for ♂♂ (n = 45) and 181–481 m² for ♀♀ (n = 45) (Clausnitzer 2003). Home-ranges of individuals have considerable overlap.

Reproduction and Population Structure Limited samples from Simien Mts, Ethiopia, where rainfall is seasonal, suggest seasonal breeding during the wet season (May–Dec) (Müller 1977). On Mt Elgon, where seasonal changes in climate are slight, reproductively active adults (scrotal ♂♂, pregnant and parous ♀♀) and juveniles were trapped throughout the year (Clausnitzer 2003). Litter-size: 1.1 (1–2), n = 9. Young precocial; nipple-cling to mother. No evidence that ♀♀ use nests (Clausnitzer 2000, 2003). Sex ratio of captures close to unity. On Mt Elgon, population numbers rather stable throughout year; juveniles form about 20% of population throughout the year (Clausnitzer 2003).



Otomys typus

Predators, Parasites and Diseases In Bale Mts, Ethiopia, form a significant prey of Ethiopian Wolves *Canis simensis* (17% of prey numbers and 8% of prey biomass), greater than would be expected from trapping (Sillero-Zubiri *et al.* 1995b). On Mt Elgon, Servals *Leptailurus serval* are a major predator: teeth of *Otomys* (*O. typus* and *O. barbouri*) comprised 95% of all teeth present in 100 faecal samples (Clausnitzer 2003). Probably also prey for owls and diurnal raptors.

Conservation IUCN Category: Least Concern.

Although abundant in suitable localities, geographic ranges are small and populations are disjunct. Populations in swamps and wetlands may be threatened by conversion of wetlands into agricultural land.

Measurements

Otomys typus

HB (♂♂): 147 (120–171) mm, n = 19

HB (♀♀): 139 (125–155) mm, n = 16

T (♂♂): 67 (57–76) mm, n = 19

T (♀♀): 68 (61–82) mm, n = 17

HF (♂♂): 24 (22–26) mm, n = 19

HF (♀♀): 22 (19–24) mm, n = 17

E (♂♂): 22 (20–26) mm, n = 19

E (♀♀): 23 (19–26) mm, n = 16

WT (♂♂): 92.1 (70–121) g, n = 29

WT (♀♀): 86.4 (78–101) g, n = 15

GLS (CbL): 38.5 (36–41.1) mm, n = 20

GWS: 19.5 (18.3–21.3) mm, n = 20

M¹–M³: 9.4 (9.0–9.9) mm, n = 20

Body measurements: Mt Elgon, Uganda (Clausnitzer 2000)

Skull measurements: Ethiopia (Rupp 1980)

Key References Clausnitzer 2003; Lavrenchenko *et al.* 1997; Sillero-Zubiri & Gottelli 1995.

D.W.Yalden

Otomys unisulcatus KAROO VLEI RAT (BUSH KAROO RAT)

Fr. Rat du vlei de Karoo; Ger. Karoo-Lamellenzahnratte

Otomys unisulcatus F. Cuvier, 1829. Hist. Nat. Mammifères, Pt. 60. South Africa. (Type locality nominated as Matjiesfontein, Western Cape Province, South Africa; Roberts 1951.)

Taxonomy Referred to as *Myotomys unisulcatus* by Musser & Carleton (2005). This species and *O. sloggetti* show close affinities to *Parotomys* spp. Synonyms: *abaniensis*, *bergensis*, *broomi*, *granti*. Subspecies: none. Chromosome number: $2n = 28$ (Robinson & Elder 1987).

Description Large to medium-sized rat with distinct black line on upper surface of tail. Pelage long, dense and shaggy. Dorsal pelage buffy-brown to dark chocolate-brown; hairs grey at base, buffy-yellow at tip. Long pure black hairs interspersed throughout pelage, especially on head and back (but not on flanks). Ventral pelage buffy-white; hairs grey at base, buffy-yellow at tip. Head blunt, similar in colour to back. Eyes without eye-ring. Ears darkly pigmented, large and rounded, well covered with hair, partly obscured by hair on cheeks. Fore- and hindfeet buffy-white. Tail short (ca. 60% of HB), covered with short bristles, black above, dull white or black below. Each upper incisor with single shallow groove towards outer edge; each lower incisor ungrooved (occasionally with faint shallow groove). M^3 with four laminae and a small circular posterior section. M_1 with three laminae (and one partial anterior lamina). Nasal bones barely expanded. Petrotympanic foramen round. ♂♂ on average larger than ♀♀ for most measurements. Nipples: $0 + 2 = 4$.

Geographic Variation None recorded.

Similar Species Four species of *Otomys* are potentially sympatric, but not necessarily syntopic:

Otomys irroratus. Slightly larger mean HB; M^3 with 6(7) laminae; M_1 with four laminae; two grooves on each lower incisor tooth; does not build stick nests; does not whistle.

Otomys saundersi. Smaller mean HB; M^3 with 6(5) laminae; M_1 with four laminae; two grooves on each lower incisor tooth; does not build stick nests; does not whistle.

Parotomys brantsi. Smaller mean HB; M^3 with two laminae; M_1 with four laminae; two grooves on each upper incisor tooth; constructs large complex underground burrow systems; whistles when alarmed.

Parotomys littledalei. Slightly smaller mean HB; M^3 with three laminae; M_1 with three laminae; no grooves on upper incisor teeth; constructs large complex above-ground burrow systems; whistles when alarmed.

Distribution Endemic to Africa. South-West Cape and South-West Arid (Karoo) BZs. Largely confined to the Nama- and Succulent-Karoo regions within the Northern Cape, Eastern and Western Cape Provinces, South Africa, and not found north of the Orange R. Also extends southwards marginally into fynbos. Distribution may be limited by veld fires, which can easily destroy their stick lodges (see below), especially in areas such as the Kalahari that are prone to lightning strikes (Kerley & Erasmus 1992b).



Otomys unisulcatus

Habitat Shrub- and Karoo-like vegetation, including rocky outcrops or rocky areas. Often associated with the beds and banks of dry water-courses (Dieckmann 1979). In Eastern Cape Province, South Africa, associated with areas of cover provided by various *Lycium* bushes (Brown & Willan 1991). On the west coast of South Africa, often associated with coastal dunes predominantly in lower-lying sandy areas protected from the prevailing SW wind (Vermeulen & Nel 1988). Tends to shun damp situations and dense riverine habitats.

Abundance Common in suitable habitats throughout its range. Maximum recorded density of 64/ha in Eastern Cape Province, South Africa (Brown 1987). In Western Cape Province, a density of 155 lodges/ha (Vermeulen & Nel 1988) suggests that much higher population densities are possible. The presence of these rats is conspicuous due to the presence of their nesting lodges, characterized by a build-up of accumulated sticks (see below).

Adaptations Diurnal and terrestrial. In Eastern Cape Province, South Africa, activity peaks during the cooler hours in summer (06:00–10:00h, 16:00–18:00h) but during the warmer hours (10:00–15:00h) in the winter (Brown & Willan 1991). In Western Cape Province, South Africa, Karoo Rats are crepuscular (Vermeulen & Nel 1988); nocturnal activity has not been recorded. Activity periods outside the nest last from less than five minutes to more than an hour, amounting to approximately three hours per day (Brown & Willan 1991).

Bush Karoo Rats construct elaborate, dome-shaped lodges made of intricately interwoven sticks and twigs (Vermeulen & Nel 1988). Lodges are constructed at the base of shrubs or shrubby trees (Brown & Willan 1991), mostly on level ground (88%, $n = 43$; Vermeulen & Nel 1988). Active lodges have a series of 1–5 runways radiating out from them, mostly less than 5 m long (Brown 1987). These runways may interconnect lodges, or run to trees and bushes without any lodges beneath them. Maximum recorded size of sticks used to build a lodge is 20×300 mm, though typically sticks are less than 10×100 mm (diameter \times length) (Brown 1987). Lodges may be up to 0.45 m high and 1.3 m in diameter (Brown 1987, Du Plessis & Kerley 1991). Each lodge has a number of entrances (6–11), which open at or above ground level. Internally, lodges are criss-crossed by passages and tunnels leading to nests, latrines and entrances. Beneath the lodge, one or two tunnels extending to 30 cm below the ground surface may be present; these provide protection from predators and buffer ambient weather conditions (Vermeulen & Nel 1988, Brown & Willan 1991). Some smaller lodges have no underlying tunnels, whilst some tunnels underneath the canopy of a shrub are not covered with sticks. Each lodge has 1–2 nest chambers, incorporated at the base of tunnels and lined with shredded wood. Bush Karoo Rats have also been recorded sheltering under rocky outcrops and log piles, as well as gaps in stone walls (Brown 1987). In Eastern Cape Province, they use as many as 20% of suitable shrubs for nesting (Brown 1987). While these provide protection from both predators and climatic extremes, they do not afford the same thermal buffering as provided by tunnels (Du Plessis *et al.* 1992, Jackson *et al.* 2002). Brown & Willan (1991) suggest the inclusion of tunnel systems beneath lodges in Eastern Cape Province, but not in Western Cape Province, may relate to the colder conditions where extreme minimums reach ca. -7.5°C , compared to 0.7°C .

The thermal physiology of Bush Karoo Rats appears to be better suited to the microclimate of their surface lodges than to the macroclimate of the arid and semi-arid environment. Thus, individuals exhibit relatively low thermal conductance and show considerable signs of heat stress at 37°C (Du Plessis *et al.* 1989, Jackson *et al.* 2004). The kidneys are only moderately adapted to xeric conditions (Pillay *et al.* 1994, Jackson *et al.* 2004); and urine osmolality, and possibly hindgut water retention, are more similar to that of otomyine rodents from mesic habitats than many other arid-living rodents (Jackson & Spinks 1998, Jackson *et al.* 2004).

Foraging and Food Strictly herbivorous, feeding on the leaves and fruits of a wide range of plant species (Brown 1987, Du Plessis *et al.* 1991). Foraging pathways radiate outwards from lodges to food plants; here, individuals collect food and refuge-building materials, but generally do not travel more than ca. 5 m from their lodges. Herbaceous vegetation is typically eaten *in situ*, whereas cropped material is carried back to the protection of a shrub or lodge. Individuals may forage alone, or sometimes in groups of up to eight individuals (Brown & Willan 1991). When more than one animal is foraging in the open, individuals tend to move greater distances from the protective bush (Brown 1987). They may also feed within the shelter of bushes, which they climb readily, typically to a height of <1 m, although they occasionally climb as

high as 3 m to feed. Bushes where the rats have been feeding are noticeable because of circular ‘windows’ of vegetation (diameter ca. 15 cm) that have been removed by foraging rats. Bush Karoo Rats forage mainly on the trees and bushes within which their lodges are built and nearby herbaceous vegetation. Occasionally Bush Karoo Rats forage up to 50 m from their home lodge (Brown & Willan 1991).

Stomach analysis shows that both plant stems (30%) and leaves (70%) are included in the diet, but not insects (Vermeulen & Nel 1988). Generally, plant species are consumed in proportion to availability; 60 species of food plants have been recorded in the southern Karoo (Du Plessis *et al.* 1991). Shrubs rather than annuals or trees dominate the diet (Du Plessis *et al.* 1991). In the Eastern Cape Province, Karoo Rats feed on *Acacia karroo*, *Atriplex* sp., *Lycium austrinum*, *L. horridum*, *Mesembryanthem* sp. and *Tribulus* sp. Both the leaves and highly hydrated fruits of *Lycium* bushes are heavily utilized (Brown & Willan 1991). In the southern Karoo, *Lycium* bushes, *Galenia africana*, *Drosanthemum* sp. and *Psilocaulon* sp. predominate in the diet (Du Plessis *et al.* 1991), while in the coastal region of the Western Cape Province, *Ruschia* sp., *Exomis microphylla* and *Zygophyllum flexuosum* are important in the diet (Vermeulen & Nel 1988). The nature of the herbivorous diet is of key importance to survival within semi-arid areas.

Social and Reproductive Behaviour Several individuals may share a lodge, up to a maximum of eight individuals (Brown 1987). The exact nature of the relationship between individuals is not understood, though they probably represent an extended family group. Individuals move frequently between a limited number of lodges. The most common social group is an adult pair, though various combinations including up to four adult $\delta \delta$, three adult ♀ , as well as subadults and juveniles have been recorded. Laboratory studies show that most interactions between lodge mates appear to be amicable, with a degree of ritualized aggression between $\delta \delta$. However, interactions between residents of different lodges are characterized by high levels of direct aggression, particularly by $\delta \delta$, in which individuals may receive fatal wounds during fights (Brown 1987).

Reproduction and Population Structure Reproductive activity varies geographically. In areas receiving mixed summer and winter rainfall, the highest percentage of reproductively active animals occurs during the summer months (83.3% in Nov) and drops to 50.0% during Jul (Brown 1987). In Eastern Cape Province (average annual rainfall 396 mm, with rain in both summer and winter), breeding occurs throughout the year, although at a reduced rate in winter (Brown 1987). In Namaqualand, South Africa, young have been observed in Aug–Sep, following winter rainfall, whilst individuals trapped in Jan showed no signs of pregnancy or lactation (T. Jackson pers. obs.). Along the coast of Western Cape Province, which also receives predominantly winter rainfall, a pregnant ♀ was trapped in May, while young were heard or seen in Jun and Jul. Together, these data suggest breeding is opportunistic and occurs in relation to local rainfall patterns.

Gestation: 37 days. Litter-size (in captivity): 2.09 (1–3); reproductive effort: 0.58. At birth young are semi-precocial; dorsal and lateral pelage well developed, ventral pelage absent; upper and

lower incisors erupted; weight 6.1–9.6 g. Ability to smell, and ears open, on Day 4. Eyes fully open Day 6. Young nipple-cling until ca. Day 6. Age of first reproduction: 6 weeks (♂♂), 5 weeks (♀♀). Inter-litter interval of 40 days suggests ♀♀ exhibit a postpartum oestrus (Pillay *et al.* 1993, Pillay 2001).

Predators, Parasites and Diseases Preyed upon by small carnivores, snakes and raptors. Within the Little Karoo of Western Cape Province, Bush Karoo Rats are the commonest prey of the Pale Chanting Goshawk *Melierax canorus*. They are also preyed upon by Jackal Buzzards *Buteo rufofuscus* in northern Namaqualand. Nests of bush rats have been destroyed by Black-backed Jackals *Canis mesomelas*. Potential predators are the Small Grey Mongoose *Galerella pulverulenta*, Water Mongoose *Atilax paludinosus*, Yellow Mongoose *Cynictis penicillata*, Small Spotted Genet *Genetta genetta*, Cape Fox *Vulpes chama*, Bat-eared Fox *Otocyon megalotis*, Mole Snake *Pseudaspis cana*, Sweep-slang *Psamophis notostictus*, Cape Cobra *Naja nivea*, Boomslang *Dispholidus typus* and Black Eagle *Aquila verreauxi* (Vermeulen & Nel 1988). Other predators may include African Wild Cat (*Felis lybica*). Ectoparasites include 26 spp. of fleas and eight species of ticks (De Graaff 1981, and references therein), as well as sucking lice (Vermeulen & Nel 1988). The ticks are of veterinary significance, and may carry babesias, rickettsias and theileriosis. Bush Karoo Rats are important vectors of plague (De Graaff 1981). Three of eight individuals dissected harboured 1–3 tapeworms (Vermeulen & Nel 1988).

Conservation IUCN Category: Least Concern.

Measurements

Otomys unisulcatus

HB (♂♂): 158 (128–190) mm, n = 18

HB (♀♀): 147 (110–205) mm, n = 22

T (♂♂): 94 (78–106) mm, n = 18

T (♀♀): 90 (63–105) mm, n = 22

HF (♂♂): 29 (27–32) mm, n = 18

HF (♀♀): 28 (22–30) mm, n = 22

E (♂♂): 24 (21–27) mm, n = 18

E (♀♀): 23 (20–33) mm, n = 22

WT (♂♂): 105 (61–156) g, n = 18

WT (♀♀): 87 (67–122) g, n = 22

GLS (♂♂): 35.7 (31.9–39.4) mm, n = 18

GLS (♀♀): 34.7 (32.5–37.5) mm, n = 22

GWS (♂♂): 18.5 (15.2–20.9) mm, n = 18

GWS (♀♀): 17.4 (15.8–19.1) mm, n = 22

M¹–M³ (♂♂): 6.9 (5.9–7.7) mm, n = 18

M¹–M³ (♀♀): 7.0 (5.9–7.9) mm, n = 22

Northern and Western Cape Provinces, South Africa (TM)

Key References Brown 1987; Brown & Willan 1991; Du Plessis *et al.* 1991; Pillay 2001; Vermeulen & Nel 1988.

Tim P. Jackson

GENUS *Parotomys*

Whistling Rats

Parotomys Thomas, 1918. Ann. Mag. Nat. Hist., ser. 9, 2: 205. Type species: *Euryotis brantsii* A. Smith, 1834.



Parotomys brantsii.

The genus *Parotomys* contains two species, *Parotomys brantsii* and *P. littledalei*. Both species are endemic to the South-West Arid BZ of southern Africa and are the most arid-occurring of all otomyine rodents. They are restricted to sandy habitats suitable for the construction of their complex burrow systems. Both are herbivorous and diurnally active above ground.

Parotomys is similar in many respects to *Otomys*, but is distinguished from *Otomys* principally by the enlarged auditory meatus, which has a strongly projecting thickened process on its anterior edge, a narrow basioccipital, lower incisors that lack grooves or are only faintly grooved, and inflated auditory bullae (De Graaff 1981) (Figure 94). The molar teeth are laminate, but are much less laminate than in *Otomys*, and M³ has only two or three laminae (cf. 4–10 in *Otomys*). The upper incisors of *P. brantsii* have a deep outer and shallow inner groove, those of *P. littledalei* are without grooves. Nasal bones are barely expanded (Figure 92). *Parotomys* is noteworthy amongst the Otomyinae in producing high-pitched, single note, whistle-like calls, that may be repeated in non-rhythmic bouts.

The current generic distinction of the genus *Parotomys* from *Otomys* is questionable and is principally based on one morphological character – the size of the auditory bullae (Misonne 1974, Meester *et al.* 1986). Significantly, Pocock (1976) suggested that the dental characters of *O. sloggetti* and *O. unisulcatus* are more similar to *Parotomys* than to other *Otomys* species, while the diameter of their bullae and nasal width are intermediate between the more mesic *Otomys* species and the arid-occurring *Parotomys*. The original morphological characters for separation of the genera are not supported by more recent biochemical and cytogenetic analyses. These studies – protein electrophoresis (Taylor *et al.*

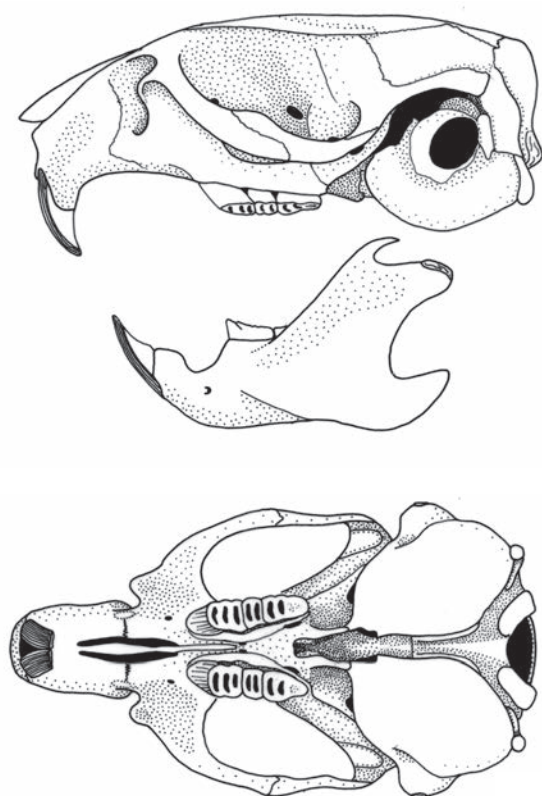


Figure 94. Skull and mandible of *Parotomys littledalei* (BMNH 23.5.9.89).

1989), immuno-electrotransfer analysis (Contrafatto *et al.* 1994), immunoblot analysis (G. Contrafatto in litt.) and mitochondrial DNA (Maree 2002) – variously suggest a closer phylogenetic relationship between the species of *Parotomys* and *O. sloggetti* or *O. unisulcatus* than between the two *Parotomys* species. Furthermore, Rambau *et al.* (1997) concluded that a high degree of chromosomal homology exists between *P. brantsii* and *O. unisulcatus*, but not between *O. unisulcatus* and *O. irroratus*, which they relate to habitat

fragmentation processes for *O. irroratus*. *Liutomys*, named as a subgenus by Thomas (1918) and used by Roberts (1951) as a genus, is now regarded as a synonym (Musser & Carleton 1993, 2005).

These relationships are, in part, supported by differences in sperm and kidney morphology. Sperm morphologies are similar for *P. brantsii* and *O. sloggetti*, and differ from those of mesic species. *Otomys unisulcatus* differs from any other species by having very small mitochondria in the mid-piece (Bernard *et al.* 1991). Indeed, several studies suggest that the southern African otomyine rodents may best be divided into an arid group and a mesic group (Pocock 1976, Taylor *et al.* 1989, Contrafatto *et al.* 1994). This is confirmed by Pillay *et al.* (1994), who found a dichotomy between arid species and mesic species with respect to kidney morphology, primarily with respect to relative cortex and medulla proportions. However, while the *Parotomys* species and *O. unisulcatus* could be included in an arid group, *O. sloggetti* grouped with the mesic otomyines.

Present evidence suggests that *Prototomys campbelli*, which occurred ca. 3.6 mya, was ancestral to all modern Otomyinae (Pocock 1976). Biochemical, palaeontological and morphological data support the existence of two evolutionary lineages of otomyines in southern Africa that were presumably derived from this extinct fossil species, one essentially arid-adapted and the other mesic-adapted. The arid-adapted group includes the two *Parotomys* species, as well as *O. unisulcatus* and *O. sloggetti*. These data do not, however, support a generic distinction between *Otomys* and *Parotomys*, suggesting either that the arid *Otomys* species be included in *Parotomys* or *Parotomys* should be considered a synonym of *Otomys* (Meester *et al.* 1992).

The two species are distinguished on the characteristics of their whistle-like calls, their enlarged auditory meatus and on the form of the incisor teeth.

Tim P. Jackson

Parotomys brantsii BRANTS'S WHISTLING RAT

Fr. Rat de Brant; Ger. Brants Pfeifratte

Parotomys brantsii (A. Smith, 1834). S. Afr. Quart. J. 2: 150. Little Namaqualand, Cape Province, South Africa; 'towards the mouth of the Orange River'. (Type locality fixed as Port Nolloth, Northern Cape Province, South Africa [Thomas & Schwann 1904].)

Taxonomy Originally described as *Euryotis brantsii*. Synonyms: *brantsi*, *deserti*, *luteolus*, *pallida*, *rufifrons*. Subspecies: none. Chromosome number: $2n = 42$ (Meester 1988).

Description Medium- to large-sized rat, very similar to *P. littledalei*, with blunt head and reddish-brown tail. Pelage soft and dense (hairs ca. 6–7 mm). Dorsal pelage sienna-yellow speckled with blackish-brown; hairs dark grey at base, yellowish at tip; long pure black hairs, especially on mid-dorsal line. Flanks slightly paler. Ventral pelage greyish-white; hairs grey at base, off-white or pale yellow at tip. Head greyish-white, with blunt muzzle; nasal region and forehead russet. Ears large and rounded, darkly pigmented, with short brown or pale hairs. Limbs short; forefeet

with four long digits and long slender claws (Digit 1 reduced, hardly visible); hindfeet with five well-developed digits and long slender claws. Tail short (ca. 63% of HB), covered with hair; dark brown above, reddish-orange on sides and below. Each upper incisor one deep outer groove and one shallow inner groove; lower incisors without grooves. M^3 small (cf. *Otomys*) with two laminae. Nasal bones barely expanded. ♂♂ on average larger than ♀♀ for most measurements. Vocalizes using a single, high-pitched, alarm whistle (see below). Nipples: $0 + 2 = 4$.

Geographic Variation Mean HB length and weight of individuals in South Africa are greater than those in Namibia, and ♂♂ are also larger than ♀♀ (e.g. in South Africa: ♂♂ HB: 215 [177–249] mm,

*Parotomys brantsii*

T: 87 [70–154] mm, WT: 138 [84–206] g; ♀♀ HB: 202 [161–236] mm, T: 82 [58–97], WT: 121 [80–214] g [T. Jackson unpubl.] (see also Measurements).

Similar Species

P. littledalei. Similar HB; on average lighter weight; more pointed ears and nose; M³ with three laminae; upper incisors without grooves. Alarm whistle shorter and lower pitched.

Distribution Endemic to Africa. South-West Arid BZ (Karoo and southern parts of the Kalahari Desert). Recorded from Western and Northern Cape Provinces of South Africa, S Namibia and SW Botswana. Distribution mostly in areas with mean annual rainfall <300 mm (Smithers 1983).

Habitat Hard sandy soils throughout the Nama and Succulent Karoo, as well as the southern Kalahari. In the Kalahari Gemsbok N. P., South Africa and Botswana, distribution is largely correlated with the presence of the shrub *Rhigozum trichotomum* on dune slopes and banks of dry river beds (Nel & Rautenbach 1974).

Abundance Populations undergo large-scale fluctuations in numbers in response to environmental conditions. During favourable periods, densities exceed 50 animals/ha, with populations increasing as much as four-fold through the course of a breeding season (T. Jackson unpubl.).

Adaptations Diurnal and terrestrial; occasionally scansorial. Feeding and foraging activity is mostly during the early morning and late afternoon (Nel & Rautenbach 1974, Jackson 1998a). Probably polyphasic, with most nocturnal activity restricted to underground movements. However, also recorded foraging on moonlit nights in the southern Kalahari. In Namaqualand, remains above ground all day during winter, mainly resting through the middle of the day,

though retiring underground during the hottest period of the day in summer (Jackson 1998a).

Brants's Whistling Rats construct large and complex burrows (De Graaff & Nel 1965, Du Plessis & Kerley 1991). Many burrows are constructed in relatively open localities (cf. *P. littledalei*), as well as under bushes (e.g. *Rhigozum trichotomum*, *Lycium* sp. and *Zygophyllum retrofractum*). Burrows often associated with raised mima-like mounds (*heuweltjies*). In Namaqualand, some burrows contain 1–6 nest chambers, and are accessed by more than 500 entrances (mean 92) and cover an average area of 72.9 m². Individuals switch nest chambers, on average, every 1.6 nights (Roper *et al.* 2002). Such behaviour may reduce the rate at which ectoparasites, especially fleas, accumulate (Roper *et al.* 2002). Many tunnels bifurcate shortly before they reach the surface of a burrow, thus increasing the number of entrances. The numerous entrances provide many quick 'escape holes' into the burrows – a useful feature for a diurnal rodent living in an open habitat (Jackson 2000a). The burrows are well buffered from variations in ambient temperature, and have a narrow average diel temperature range (<4 °C) compared with the temperature at the surface (>14 °C). Maximum burrow temperatures are independent of maximum ambient shade temperature (Jackson *et al.* 2002).

Rather surprisingly, in view of the aridity of their habitat, Brants's Whistling Rats do not show any unusual physiological adaptations to reduce water loss (Jackson *et al.* 2004). They are strictly herbivorous and the water content of the food is probably of greater importance to survival than in many other arid-occurring rodents. They exhibit hyperthermia at 37 °C, and are the most tolerant of the southern African Otomyinae to such high ambient temperatures. Unlike many desert rodents, they do not exhibit a lower resting metabolic rate (recorded as 1.15 ml O₂/g/h) than expected for body size, while their lower critical temperature (23 °C) is comparatively low and the thermal neutral zone of 23–37 °C is broad (Jackson *et al.* 2004).

Alarm calls, used to signal predators, have a dominant frequency of 10.0 kHz and mean call duration of 164 ms – longer and higher pitched than those of *P. littledalei* (Le Roux *et al.* 2002). These whistling rats do not differentiate predator types by means of vocalizations; rather their calls are 'urgency-based' and indicate perceived threat levels. Thus, high-risk encounters such as those evoked by a fast-flying raptor provoke a short-duration call before the rat bolts underground, whereas low-risk encounters such as those provoked by a slow-moving snake elicit a relatively long-duration call while the caller remains above ground and continues to observe the threat (Le Roux *et al.* 2002).

Foraging and Food Exclusively herbivorous. Feeds on a wide range of plants (Du Plessis *et al.* 1991, Jackson 1998b), including woody shrubs, annuals, geophytes, grasses and various succulents, but not seeds or other dry plant material. In suitable habitats, whistling rats restrict much of their foraging to the confines of their extensive burrows and individuals are seldom more than 30 cm from an entrance. Typically pieces of vegetation are nipped off and eaten, whilst some individuals occasionally climb into shrubs to feed. Whistling rats may be described as 'central-place foragers', carrying larger food items greater distances than small ones (Jackson 2001). During the hot dry summer, individuals have also been observed digging for bulbs. Fresh plant material may be eaten immediately, particularly in the early morning and late afternoon when animals are most active.

Larger items of fresh material are typically stored underground (less often stored above ground at a burrow entrance), usually near a nest chamber, rather than being eaten immediately. Much of this stored material is collected in the late afternoon, and is believed to act as an overnight food source (Jackson 2001). In some areas, such as N Namaqualand, foraging is largely confined to above-ground areas within the boundaries of a burrow. However, individuals will also move between adjacent burrows, located a mean distance of 5.1 m apart in Namaqualand, in search of food. Burrows are inter-connected by a series of well-used pathways. When visiting neighbouring burrows, individuals do so largely to feed and not to collect material for later consumption (Jackson 2001).

The burrowing and foraging behaviour plays a key ecological role. In natural ecosystems, when population numbers are high, whistling rats are capable of causing heavy disturbance to plant communities with a concurrent reduction in plant species richness and abundance (T. Jackson unpubl.). Soils associated with their burrows have higher mineral concentrations: sodium may be 8.7 times more concentrated than in the surrounding soils, and magnesium may be 1.5 times more concentrated. This is paralleled by an increase in soil alkalinity. However, at lower population densities, they play an important role in rehabilitating mined areas, by creating soil patches around their burrows with higher pH, reduced conductivity and increased microbial activity, which are conducive to plant growth (Desmet & Cowling 1999).

Social and Reproductive Behaviour Typically, individuals occupy separate burrows and may be considered solitary. Burrows are, however, normally situated in close proximity to one another (e.g. range of distances between burrows is 1–25 m in Namaqualand), such that interactions can be frequent between individuals. At high population densities, a maximum of four individuals may share a burrow. Even so, rats will maintain discreet territories in a burrow. The breeding system is based on scramble competition polygyny (Jackson 1999); ♂♂ solicit ♀♀ during the breeding period searching actively for mates in burrows near to their own. Males are, therefore, seen away from their burrows on more occasions than are ♀♀. However, while the maximum distances that ♂♂ are observed away from their burrows (mean = 33 m) is greater than for ♀♀ (mean = 20 m), average movement distances from the centre of their ranges (males = 9 m, females = 6 m) do not differ between the sexes (T. Jackson, P. Fleming & N. Bennett, unpubl.). Aggressive behaviour is mostly directed by ♀♀ towards intruding ♂♂, and male–male aggression is limited. Natal dispersal distances are short and do not differ with gender, averaging 38 m for ♀♀ and 40 m for ♂♂. More than 50% of adults disperse less than 20 m from their natal burrows (T. Jackson, P. Fleming & N. Bennett unpubl.) and many individuals, both ♂ and ♀, may be considered philopatric.

Reproduction and Population Structure Reproduction is opportunistic, and dependent on rainfall. In areas of summer rainfall, including the southern Kalahari, the pregnancy rate is greatest during the summer months. In winter rainfall areas, such as Namaqualand, the greatest number of reproductively active (pregnant or lactating) ♀♀ is during winter–spring (May–Oct), though lactating ♀♀ have also been captured in Jan (Jackson 2000b). Gestation: ca. 38 days. Embryo number: 2.1 (1–3, n = 9; SW Botswana; Smithers 1971).

Litter-size: 3.4 (3–4, n = 14; Namaqualand; Jackson 2000b). No information available on birth-weight or ontogeny. Young forage above ground from Day 7. Growth rate: 1.2 g/day until independence from mother at 6–7 weeks of age and 55% of adult weight (Jackson 2000b). Young have the ability to make overnight food stores, collect nest material and defend a burrow against conspecifics by Day 35. Sexual maturity: Day 35 (♀♀), unknown (♂♂). Young disperse from their natal nest area at the time when ♀♀ potentially reach sexual maturity. Females have a postpartum oestrus, and may produce at least four litters during the annual breeding period. Females typically survive to breed for 1–2 years.

The behaviour of ♀♀ is modified as a result of the birth of their young. After parturition, they spend extended periods (>50% during daytime) underground, interspersed with bouts of food collection (Jackson 2000b). At this time, feeding activity above ground is reduced compared to that during pregnancy and after the emergence of young, although the times of day when foraging occurs remain unchanged. Females carry 43% of food material underground after the birth of the young and prior to their emergence, compared to only 10% during pregnancy. By the time young are 12–14 days of age, ♀♀ spend at least 75% of time above ground again. Female anti-predator vigilance increases from 5.5% of activity when young are underground to 14.1% when they emerge above ground. After the birth of young (Day 1), mothers nipple-drag their young for about 12% of the time when they are above ground; this increases to 35% until Day 8–9, and declines thereafter. Nipple-clinging by young no longer observed from Day 14 (Jackson 2000b). In some regions, a disproportionately greater die-off of ♂♂ has been recorded during the breeding period, with almost all ♂♂ disappearing from the population (T. Jackson unpubl.).

Predators, Parasites and Diseases Common raptor predators include Pale Chanting Goshawks *Melierax canorus*, Jackal Buzzards *Buteo rufofuscus*, Lanner Falcons *Falco biarmicus* and Booted Eagles *Hieraaetus pennatus*, as well as Barn Owls *Tyto alba* and Spotted Eagle-owls *Bubo africanus* at dusk. Small mammalian predators include Yellow Mongooses *Cynicits penicillata*, Ratels *Mellivora capensis*, Black-backed Jackals *Canis mesomelas* and African Wild Cats *Felis lybica*. Snake predators include Puff Adders *Bitis arietans*, Black Spitting Cobras *Naja nigricollis*, Mole Snakes *Pseudaspis cana* and Cape Cobras *Naja nivea*. Whistling rats have also been recorded in the diet of the Black Heron *Ardea melanocephala*. Ectoparasites include at least eight species of fleas and three species of ticks. Whistling rats are susceptible to natural outbreaks of plague, making them important vectors of the disease (De Graaff 1981, and references therein).

Conservation IUCN Category: Least Concern.

Measurements

Parotomys brantsii

HB (♂♂): 151 (136–173) mm, n = 21

HB (♀♀): 148 (116–178) mm, n = 42

T (♂♂): 95 (84–107) mm, n = 21

T (♀♀): 95 (73–110) mm, n = 42

HF (♂♂): 29 (27–31) mm, n = 21

HF (♀♀): 28 (25–30) mm, n = 42

E (♂♂): 16 (14–21) mm, n = 20

E (♀ ♀): 17 (14–21) mm, n = 42
 WT (♂ ♂): 120 (100–163) g, n = 7
 WT (♀ ♀): 119 (77–153) g, n = 20
 GLS (♂ ♂): 36.5 (34.5–38.3) mm, n = 14
 GLS (♀ ♀): 36.7 (34.0–40.5) mm, n = 26
 GWS (♂ ♂): 19.4 (18.0–21.0) mm, n = 17
 GWS (♀ ♀): 19.5 (17.5–21.3) mm, n = 25
 M¹–M³ (♂ ♂): 8.3 (7.4–9.1) mm, n = 19

M¹–M³ (♀ ♀): 8.3 (7.7–8.9) mm, n = 35
 Namibia (N. Coetzee, unpubl.)

Key References Jackson 1999, 2000b, 2001; Jackson *et al.* 2002; Le Roux *et al.* 2002.

Tim P. Jackson

Parotomys littledalei LITLEDALÉ'S WHISTLING RAT

Fr. Rat de Littledale; Ger. Littledales Pfeifratte

Parotomys littledalei Thomas, 1918. Ann. Mag. Nat. Hist., ser. 9, 2: 205. Kenhardt, Northern Cape Province, South Africa.

Taxonomy Synonyms: *molopensis*, *namibensis*. Subspecies: none. Chromosome number: 2n = 50 (Meester 1988).

Description Medium- to large-sized rat with blunt head and dark tail. Pelage soft and long (up to 13 mm). Dorsal pelage cinnamon-buff; hairs medium grey at base, cinnamon-buff at tip; long pure black hairs, especially on mid-dorsal line. Flanks and ventral pelage pale buff; hairs grey at base, buff or off-white at tip. Head with blunt muzzle, similar in colour to back, without russet on forehead and nasal region. Ears large and rounded, darkly pigmented, covered with short yellowish hairs. Limbs short. Forefeet with four long digits and long slender claws. Digit 1 reduced, hardly visible; hindfeet with five well-developed digits and long slender claws, all digits well covered with short off-white hairs. Tail short (ca. 70% of HB), covered with hair, dark buff above, paler below; tip may be black. Skull: upper and lower incisors without grooves. M³ with three laminae. Nasal bones moderately expanded. ♂♂ on average larger than ♀♀ for most measurements. Vocalizes using a single, high-pitched, alarm whistle of approximately 0.5 sec in duration (Le Roux *et al.* 2002). Nipples: 0 + 2 = 4.

Geographic Variation Mean HB and weight of individuals in South Africa are greater than those in Namibia (although tails are shorter), and ♂♂ are also larger than ♀♀, e.g. in South Africa: ♂♂ – HB: 238 (176–276) mm, T: 100 (78–118) mm, WT: 120 (72–153) g; ♀♀ – HB: 222 (205–246) mm, T: 92 (79–107) mm, WT: 95 (80–116) g (T. Jackson unpubl.) (see also Measurements).

Similar Species

P. brantsii. HB similar; often weight heavier; nose and ears more rounded; each upper incisor with two grooves; M³ with two laminae. Alarm whistle longer with a higher dominant frequency of 10 kHz.

Distribution Endemic to Africa. South-West Arid BZ (Namib Desert and Karoo). Recorded from the coastal areas of N Namibia to the Western and Northern Cape Provinces, South Africa. Absent from the central Namib Desert.

Habitat Coastal hummocks, sand dunes and gravel plains of the Namib Desert, and (dry) riverine systems extending inland from the coastal plains of Namibia (Coetzee 1969, Coetzee & Jackson 1999).



Parotomys littledalei

Abundance Comparatively common in suitable habitat (although infrequently caught using small rodent traps). Avoids open habitats. Rarely seen but frequently heard.

Adaptations Diurnal and terrestrial. In Namaqualand, lives in moderate-sized burrows extending over an average of 4.7 m², with an average of eight entrances. Burrows are constructed below bushes and contain several nest chambers filled with shredded vegetation (Jackson 2000a). Burrows are linked by surface pathways. Littledale's Whistling Rats show several physiological adaptations to reduce water loss: the large kidneys (1.4% of body mass compared with 0.6% in *P. brantsii*) enable production of the most concentrated urine of any southern African otomyine rodent (Jackson *et al.* 2004); and the long intestine (proportionately the longest large intestine of any southern African otomyine rodent [Jackson & Spinks 1998]) probably enhances water absorption. Exhibits hyperthermia at ambient temperatures higher than 31 °C, although in this respect thermophysiology does not differ markedly from otomyine rodents inhabiting more mesic habitats (Jackson *et al.* 2004).

A high-pitched alarm whistle (dominant frequency 7.7 kHz, duration 53 ms; Le Roux *et al.*, 2002) is emitted when disturbed by predators. No other vocalizations as yet recorded.

Foraging and Food Exclusively herbivorous, feeding on a variety of fresh plant material including annuals, succulent perennials, non-succulent perennials and grasses. Feeds under the cover of bushes, where runways link foraging areas to burrows. In some areas, probably feeds only on one plant species such as *Salsola nollothensis*, due to lack of variety of available plants (Coetzee & Jackson 1999). In coastal Namibia, the diet includes *Tribulus zeyheri*, *Psilicaulon salicornioides*, *Atriplex lindleyi*, *Lycium tetrandum*, Aizoaceae spp. and *Salsola* sp. Fresh plant cuttings, including *Lycium* sp., *Schismus inermis*, *Psilicaulon absimile*, *Messembryanthemum guerichianum* and *Galenia sarcoophylla* have been collected at burrow entrances in Namaqualand, indicating that these species are included in the diet (T. Jackson, unpubl.).

Social and Reproductive Behaviour Individuals inhabit burrows built at the base of bushes (e.g. *Psilicaulon absimile*, *Atriplex ganescense*, *Salsola* sp., *Zygophyllum stapffii*, *Lycium tetrandum*) in suitable habitat. Whilst small bushes probably include the burrows of single individuals, burrows under large bushes may be occupied by several individuals (Coetzee & Jackson 1999). Social organization probably parallels that of *P. brantsii*, with individuals maintaining separate territories within a bush.

Reproduction and Population Structure Reproductive activity is related to rainfall. In Namibia, reproductively active ♀♀ caught during the period of summer rainfall (Sep–Mar). In contrast, in Namaqualand, 75% (n=4) of ♀♀ were lactating in Sep following the winter rainfall, and none was reproductively active in Apr (n=4) prior to rain. Gestation: 41 days. Embryo number: 2.4 (1–3; Namibia; Coetzee & Jackson 1999). Litter-size (in captivity): 2.4 (2–3; Pillay 2002). At birth, young precocial, eye slits visible, incisors erupted; mean weight 12.7 g. Sense of smell developed by Day 4. Auditory meatus and eyes open Day 4–6. Weaned Day 8–12, when mean weight 38.4 g (Pillay 2002). Sexual maturity: 6 weeks (♂♂), 5 weeks (♀♀).

Predators, Parasites and Diseases Remains recorded from the pellets of Pale Chanting Goshawks *Melierax canorus* (G. Malan unpubl.). Judging by their hunting activity, other potential predators include Yellow Mongooses *Cynictis penicillata*, African Wild Cats *Felis lybica* and Jackal Buzzards *Buteo rufofuscus*. Ectoparasites include eight species of fleas and one species of mite (De Graaff 1981, and references therein).

Conservation IUCN Category: Least Concern.

Measurements

Parotomys littledalei

HB (♂♂): 153 (124–175) mm, n = 44

HB (♀♀): 146 (119–172) mm, n = 68

T (♂♂): 108 (85–124) mm, n = 43

T (♀♀): 105 (85–126) mm, n = 64

HF (♂♂): 27 (23–30) mm, n = 43

HF (♀♀): 26 (23–31) mm, n = 68

E (♂♂): 19 (18–25) mm, n = 42

E (♀♀): 19 (17–22) mm, n = 66

WT (♂♂): 105 (93–115) g, n = 3

WT (♀♀): 97 (55–151) g, n = 14

GLS (♂♂): 36.2 (33.0–39.8) mm, n = 36

GLS (♀♀): 35.5 (32.8–39.5) mm, n = 63

GWS (♂♂): 19.3 (15.6–21.8) mm, n = 39

GWS (♀♀): 18.9 (18.0–21.5) mm, n = 60

M¹–M³ (♂♂): 7.9 (7.0–9.2) mm, n = 46

M¹–M³ (♀♀): 7.8 (7.6–9.7) mm, n = 70

Namibia (C. G. Coetzee unpubl.)

Key References Coetzee & Jackson 1999; Jackson 2000a, b; Le Roux *et al.* 2002; Pillay 2002.

Tim P. Jackson

Family ANOMALURIDAE

ANOMALURES

Anomaluridae Gervais, 1849. In: D'Orbigny, Dict. Univ. Hist. Nat., 11: 203. f

| | | |
|-------------------------------|--------------------|--------|
| <i>Anomalurus</i> (4 species) | Anomalures | p. 603 |
| <i>Idiurus</i> (2 species) | Pygmy Anomalures | p. 611 |
| <i>Zenkerella</i> (1 species) | Cameroon Anomalure | p. 615 |

The family is endemic to Africa, and comprises three genera and seven living species. All living anomalures are restricted to the Rainforest BZ, with the single exception of *Anomalurus derbianus*, which also occurs in well-developed woodlands where trees of the family Caesalpiniaceae are either dominant or abundant.

The most obvious feature of all anomalures (with the exception of *Zenkerella insignis*) is the presence of a patagium (or flight membrane) stretched between each forelimb and hindlimb, from wrist to ankle, and a smaller interfemoral patagium (or tail membrane) between each hindlimb from the ankle to the proximal end of the tail. A cartilaginous spur, the calcaneum, supports the anterior part of each patagium between the elbow and outer edge of the patagium. The patagia, when stretched, form an aerofoil that enables the anomalure to glide from tree to tree. The patagia cannot be flapped (as for the wing of a bird or bat). Dorsal pelage colour is greyish, brownish or black, frosted with white in some species, and the ventral pelage is pale or whitish. Pelage colour in *Anomalurus* spp. (except *A. pusillus*) varies geographically, the proportion of the various colour morphs varying in different parts of the geographic range (Schunke & Hutterer 2004). The tail is long and well covered with hair, but the hairs are not as long or as bushy as in squirrels, except for the last third of the tail. On the undersurface of the tail, near the base, are two rows of scales; the scales overlap slightly and each scale has a posteriorly directed sharp point. The scales are used for supporting the body when resting or when climbing the vertical trunk of a tree. There are four digits on the forefoot and five digits on the hindfoot; all digits have long curved pointed claws. The head has large eyes, relatively large ears and well-developed vibrissae. *Zenkerella insignis* does not have patagia and is unable to glide.

The skull is diagnostic and shows many differences from the skull of squirrels (family Sciuridae). The postorbital process is small or absent (well-developed in squirrels), the infraorbital foramen is large and contains a very large masseter muscle (very small in squirrels), the zygomatic arches are curved outwards so the head has a rounded appearance (not markedly curved and head narrower in squirrels), and the palate is narrow, especially at the level of the single premolar

(P⁴) and M¹, becoming broader posteriorly as the line of cheekteeth curves outwards (also broad in squirrels, and of similar width along its length between the parallel rows of cheekteeth). The posterior surface of the incisors is smooth (*Anomalurus*, *Zenkerella*) or notched (*Idiurus*). Dental formula: I ¹/₁, C ⁰/₀, P ¹/₁, M ³/₃ = 20 (as in Sciuridae – squirrels). Size categories of species in the family (based on mean head and body length) are given in the order Rodentia profile.

Anomalures are arboreal and scansorial, and occasionally terrestrial. They are nocturnal, resting during the day in hollows and cavities of large trees. Before gliding, an individual climbs up a tree with a 'humping gait', the two forefeet alternating with the two hindfeet. It launches itself into the glide with the limbs spread-eagled so the patagia are extended to form a taut aerofoil (or a curved umbrella-shaped structure – Sanderson 1940). Before landing – at a lower elevation from where the glide began – the anomalure assumes a vertical position; on landing, the long claws on the digits and the pointed scales on the undersurface of the tail securely grip the trunk of the tree. By climbing up trunks and gliding from tree to tree, an anomalure can move easily throughout its home-range in the forest. Anomalures are vegetarians, feeding on leaves, fruits, seeds, nuts, bark and phloem exudates. Little is known about their reproductive biology, other than that litter-size is usually one. Longevity in the wild is unknown.

The seven living species of Anomaluridae represent specialized vestiges of an ancient, uniquely African group of rodents that were diverse (20 genera) and abundant in the Oligocene (36.6–23.7 mya). This diversity would seem to have disappeared under the competitive influence of other families of rodents, which invaded from Eurasia in the Miocene and later. The anomalures have evolved independently in Africa from the ecologically equivalent gliding rodents of Eurasia and the Americas and from gliding marsupials in Australia. Their survival would seem to be based upon their having adopted successful gliding niches before any other incoming rodents could compete.

The living Anomaluridae have some very distant relationship with the Springhares, family Pedetidae. Presumably both derive from a very ancient and primitive type of anomalurid. Because fossil anomalurids were diverse and abundant before Africa's reconnection with the Eurasian land mass it is likely that they evolved from a primitive rodent group that became established in Africa during the long isolation of Africa during the Palaeocene and Cretaceous.

Table 43. Species in the family Anomaluridae.

| Species | Patagium | Eye-mask | HB mean (range) (mm) | T mean (range) (mm) [% of HB] | GLS mean (range) (mm) | Dorsal pelage | |
|-----------------------------|----------|----------|----------------------|-------------------------------|-----------------------|----------------------------|--|
| <i>Anomalurus derbianus</i> | Present | Present | 306 (283–379) | 284 (227–327) [90%] | 58.7 (57.8–60.2) | Grey, reddish, or brownish | |
| <i>Anomalurus pelii</i> | Present | Absent | 421 (400–460) | 403 (325–450) [95%] | 67.8 (65.5–69.5) | Black | |
| <i>Anomalurus beecrofti</i> | Present | Absent | 278 (261–300) | 213 (190–238) [75%] | 56.3 (53.8–58.8) | Grey, silvery-grey | |
| <i>Anomalurus pusillus</i> | Present | Absent | 231 (221–238) | 136 (130–140) [60%] | 44.4 (43.8–44.8) | Blackish-tan (flecked) | |
| <i>Idiurus macrotis</i> | Present | Absent | 88.4 (73–105) | 132.4 (110–186) [150%] | 26.1 (25–27) | Sepia-grey | |
| <i>Idiurus zenkeri</i> | Present | Absent | 69.5 (63–75) | 94.9 (83–104) [130%] | 20.9 (20.4–22.0) | Brown | |
| <i>Zenkerella insignis</i> | Absent | Absent | 202.7 (180–225) | 172.5 (165–180) [85%] | 45.7 (44.8–46.3) | Slate-grey | |

Although the Anomaluridae have traditionally been placed next to the Sciuridae in the suborder Sciurognathi of the order Rodentia (Wilson & Reeder 1993, Rosevear 1969), or as the sole representative of the superfamily Anomalurioidea in the ‘Sciuromorpha’ (Anderson & Jones 1984), new phylogenetic analyses using morphological and mitochondrial genes suggest that the Anomaluridae and Pedetidae form a suborder Anomaluromorpha in the order Rodentia (Montgelard *et al.* 2001, 2002, Huchon *et al.* 2002). Thus the family is no longer associated closely with the Sciuromorpha

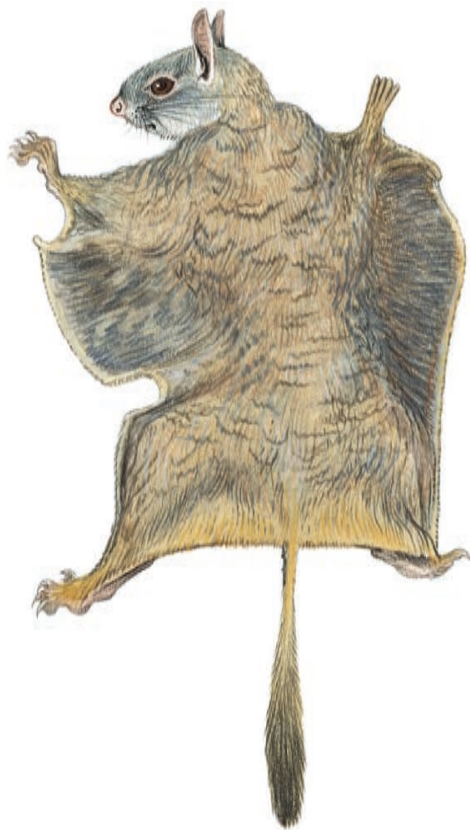
(squirrels and their relations) (Musser & Carleton 2005) but is associated in a way not yet fully comprehended or acknowledged with the Pedetidae.

The three genera (*Anomalurus*, *Idiurus* and *Zenkerella*) and six species (Table 43) are distinguished by the size of the body and hindfoot, the presence/absence of patagia, the form of the tail and the shape and position of the maxillary branch of the maxillary process.

Jonathan Kingdon

GENUS *Anomalurus*
Anomalures (Scaly-tailed Squirrels)

Anomalurus Waterhouse, 1843. Proc. Zool. Soc. Lond. 1842: 124 (1843). Type species: *Anomalurus fraseri* Waterhouse, 1843 (= *Pteromys derbianus* Gray, 1842).



Anomalurus pusillus.

The genus contains four species, all of which live in the rainforests of West and central Africa. Species in the genus are characterized by extensive flight patagia on either side of the body between long, very lightly built limbs; and small interfemoral patagia between the hindlimbs and the proximal end of the tail. The undersurface of the basal part of the tail bears two rows of closely packed, sharply pointed scales; hence the alternative vernacular name ‘scaly-tail’. A cartilaginous spur on the elbow provides support for the flight membrane. The species of *Anomalurus* are large and heavy, with a long

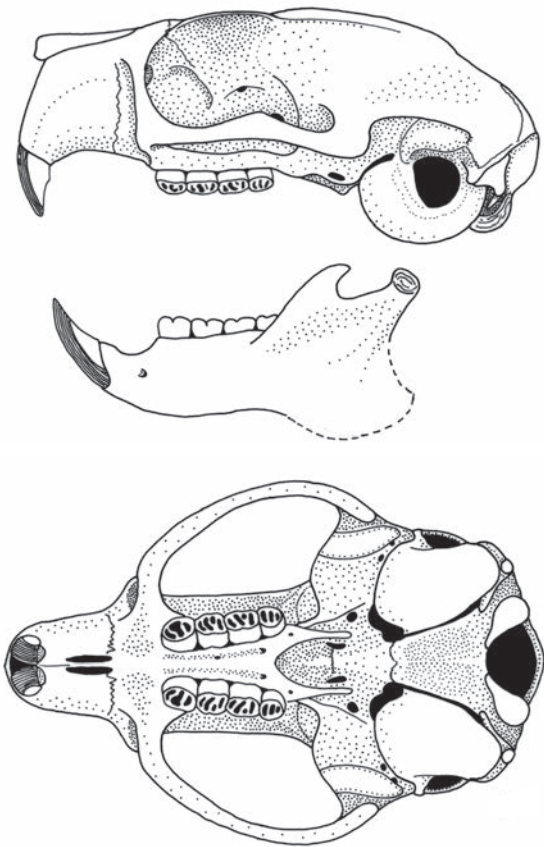


Figure 95. Skull and mandible of *Anomalurus derbianus* (BMNH 64.1075). Angular process of mandible broken; details added from Ellerman (1940) and other specimens.

| | Distribution and Notes |
|--|--|
| | Widespread in Rainforest BZ and adjacent Mosaics |
| | Liberia – Ghana. Tail black or white |
| | Widespread in Rainforest BZ and adjacent Mosaics |
| | Cameroon–Uganda, Liberia |
| | Sierra Leone–Ghana, SE Nigeria–Gabon, NE DR Congo, NE Tanzania |
| | Cameroon–Gabon, E DR Congo–Uganda |
| | Cameroon–Congo, Central African Republic |

tail ending in a well-developed brush (cf. *Idiurus*). On the skull, the posterior surface of each upper incisor is smooth without a notch (cf. *Idiurus*), the lower branch of the maxillary process is immediately anterior to M¹ (cf. *Idiurus*, *Zenkerella*), and the nasal bone is comparatively shallow (cf. *Idiurus*, *Zenkerella*) (Figure 95). The skulls of each species of *Anomalurus* are very similar morphologically, but differ in size. See also Family profile.

One species, *A. beecrofti*, has sometimes been allocated to a distinct genus or subgenus, *Anomalurops*, because of its narrower skull and differences in dentition compared with *Anomalurus* (e.g. Rosevear 1969, Grubb *et al.* 1998).

Anomalurus beecrofti BEECROFT'S ANOMALURE (BEECROFT'S SCALY-TAILED SQUIRREL)

Fr. Anomalure de Beecroft; Ger. Beecrofts Dornschwanzhörnchen

Jonathan Kingdon

Anomalurus beecrofti Fraser, 1853. Proc. Zool. Soc. Lond. 1852: 17. 'Fernando Po' (= Bioko I., Equatorial Guinea).

Taxonomy This species has been separated from the other large anomalures into the genus *Anomalurops* (Matschie 1914, Rümmler 1933, Dekeyser 1955, Rosevear 1969) on the basis of many skull characters including narrower zygomatic width, wider frontals between the orbits, more inflated auditory bullae, nasal bones, which extend well forward of the incisors, wedge-shaped palate due to the pronounced out-curving of the cheekteeth row at the rear of the palate, specialized palate and muzzle that are exceptionally narrow, and unusual dentition (see Description). Recent authors (e.g. Dieterlen 1993a, 2005a) have retained *A. beecrofti* in the genus *Anomalurus*, although it is possible that further studies of its anatomy, behaviour and genetics may justify the validity of the genus *Anomalurops* (see Rosevear 1969 for additional comment).

A large number of forms have been described. Some of these may reflect regional differences; Rosevear (1969), in comparing the types of *argenteus* and *citrinus*, stated that although they are different, these forms are extremes and that many intermediate forms exist. The form *schou tedeni* was considered a valid species by Crawford-Cabral (1971), and *fulgens*, from Gabon, has been treated as a full species by some authors (e.g. Dorst & Dandelot 1970, Haltenorth & Diller 1980) because of its entirely orange pelage; however, yellowish or orange tints are characteristic of most populations and are probably poor criteria for erecting taxa. Indeed, Rosevear (1969) was of the opinion that *fulgens* was little more than an erythristic form. Schunke & Hutterer (2004) showed that the species is polymorphic, with different proportions of each colour morph in different populations, and hence subspecies are not recognized. Synonyms: *argenteus*, *chapini*, *citrinus*, *fulgens*, *hervoi*, *laniger*, *schoutedeni*. Subspecies: three of dubious validity (but see Geographic Variation). Chromosome number: not known.

Description Very large arboreal rodent with well-developed patagia and long narrow tail. Pelage colour varies geographically (see below). Dorsal pelage soft, long and dense, agouti grey or silvery-grey often with golden-brown stripe from neck over larger part of back, or wholly orange, or without any orange colouration. Ventral pelage pale grey or orange with yellow/orange mid-ventral stripe, or uniformly orange, or grey without yellow mid-ventral stripe; ventral hairs less dense than on dorsal pelage. Dorsal surface of flight patagia

At least one species of *Anomalurus* is of great ecological interest for its possible influence on forest dynamics. Sustained 'pruning' by *A. derbianus* of vegetation around their food trees may favour the survival of preferred food trees; this may determine (in the long term) the composition of rainforest plant communities by favouring some species of trees at the expense of other species.

The species are distinguished by size of head and body, size of skull, and the colour of pelage and tail.

grey or brown; interfemoral patagia grey or ochre (similar to dorsal pelage). Ventral surface of patagia ochre-yellow, less densely haired than dorsal surface. Cartilaginous spur projects outwards (within the membrane) from the elbow to margin of patagium. Head somewhat narrower, with longer muzzle, than in other *Anomalurus* spp. Face pale coloured (grey or yellowish) without dark 'eye-mask' around the eyes. Many individuals have a small white spot on the upper forehead. Ears pale, narrow and somewhat pointed, bordered by an arc of black hairs on the temple. Vibrissae clustered on densely haired and swollen pads of the upper lips. Chin and top of the head with shorter, finer individual vibrissae. Upper surfaces of limbs grey (as dorsal pelage). Digits with long sharp claws. Tail short (ca. 75% of HB), with sparse short grey hairs; very small whitish brush at tip; up to nine pairs of sharp pointed scales on ventral surface near base of tail near where it becomes free of the interfemoral patagia. Skull similar to *A. derbianus* but with very narrow palate (especially at level of P⁴ and M¹), narrow cheekteeth (<3 mm), nasal bones that project well forward of the incisors, cheekteeth row slightly curved outwards, and larger auditory bullae. Nipples: 1 + 1 = 4 (or 2 + 0 = 4).

Geographic Variation Dorsal and ventral colouration is polymorphic and varies geographically and within populations (see Schunke & Hutterer [2004] for details, and Rosevear [1969] for further comment). Three subspecies have been recognized (as given below), but the presence of different colour forms within single populations suggests that the subspecies are perhaps invalid.

A. b. beecrofti: Bioko I. Dorsal pelage dark brown or golden-brown, without any orange colouration; ventral pelage pale orange, or grey with central orange stripe.

A. b. argenteus: Sierra Leone to Cameroon. Dorsal pelage silvery-grey with golden-brown mid-dorsal stripe (sometimes absent); ventral pelage pale grey or yellowish with or without central yellow stripe.

A. b. fulgens: Gabon. Dorsal pelage orange; ventral pelage grey with orange, or wholly orange.

Similar Species

A. pusillus. Smaller, dorsal pelage relatively uniformly brownish; tail black-tipped and bushy.



A. derbianus. On average larger, eye-mask, muzzle and surroundings of ear black or brown; tail black and bushy.

Distribution Endemic to Africa. Rainforest BZ (all regions) and Southern Rainforest–Savanna Mosaic. Widely distributed from Senegal, Guinea-Bissau and Sierra Leone (though not yet known from Gambia) to E DR Congo and throughout the Rainforest BZ north and south of the Congo R. Also relict forests in Angola and NW Zambia, Bioko I., reliably reported from Bwamba, W Uganda. Altitudinal range: near sea level to 2500 m.

Habitat Preferred habitats are swamp forests with abundant wild palms; there is a close correspondence between the natural distribution of the oil palm (*Elaeis guineensis*) and this anomalure. Also recorded from cultivated areas, notably oil palm plantations.

Abundance Uncertain, but may be comparatively common in suitable habitats. Individuals are difficult to observe (due to their exceptional powers of concealment). Lack of observations may reflect low densities, even in suitable habitat.

Adaptations Arboreal and mostly nocturnal. Beecroft's Anomalures are considered to be wholly nocturnal (Dekeyser & Villiers 1951), although some authors (e.g. Sanderson 1940) have suggested they are diurnal perhaps because they have been seen resting on tree trunks during the day (something almost unknown in Lord Derby's Anomalure, *Anomalurus derbianus*). In such situations, their mottled agouti pattern seems to represent an effective camouflage against predators. Although recorded from areas with tall trees, this species appears to be less dependent than other *Anomalurus* spp. on long, unobstructed flight paths.

Sanderson (1940) reported that Beecroft's Anomalures prefer the upper strata of forest and sleep in dense conglomerations of leaves and twigs at the very summits of trees. One individual has been

observed asleep at 08:00h clinging to the trunk of a palm tree, more than 6 m up, under the shelter of a dead frond (T. S. Jones in Rosevear 1969). These and other reports of opportunistic roosting in relatively exposed temporary sites suggest that Beecroft's Anomalure may be considered to be much more of a 'camper' than other anomalures.

Branch pruning, as practised by *A. derbianus*, has not been recorded but some twig cutting is likely to occur. The narrower, more elongated muzzle and narrow incisors probably constrain its foraging to only the slenderest twigs. Moving between short-trunked, swamp forest trees that are quite close together, among sprays of palm fronds and across obstructed spaces poses many problems for a glider and suggests that *A. beecrofti* may scramble through vegetation more than other anomalures. How its gliding differs from the commoner *A. derbianus* is not known, but its smaller size and weight probably help while the long, whippy tail is generally concerned with maintaining balance. The special significance of its elongated and slightly down-turned, tubular nose is not known but could suggest that the scent of foods can be very closely monitored while being gnawed.

Foraging and Food Little known. Reported to feed on various fruits, bark, leaves, flowers and occasional insects, but some authors (Dekeyser & Villiers 1951) have found they feed only on the pulp of oil palm fruits, *Elaeis guineensis*. Although ripening bunches of oil palm fruits are protected by short spines, the anomalures mainly chew the pulp *in situ* (Dekeyser and Villiers 1951). The special problems associated with getting at the pulp of palm fruits growing in large, densely packed bunches might favour a narrow muzzle, permitting the incisors to reach deeper into the spaces between hard-stoned fruits.

Social and Reproductive Behaviour Because the few records have always been of single individuals, they have been assumed to be solitary. Information is lacking on territoriality, interactions between individuals and on social organization. The only known vocalization (Bates 1905) is a low noise in the forest at night characterized as something between a whistle and a hoot.

Reproduction and Population Structure In Ibadan, Nigeria, two ♀♀, each with a small young, were obtained in early Oct and late Jan (Happold 1987). In Cameroon, a pregnant ♀ was found in Jul (Sanderson 1940).

Predators, Parasites and Diseases Alp & Kitchener (1993) recorded a jaw fragment of this species in faecal remains from a Robust Chimpanzee *Pan troglodytes* in the Tenkere area of Sierra Leone. Other potential predators include Crowned Eagles, Long-tailed Hawks and pythons. A microfilaria has been reported from the blood of West African specimens (Dekeyser & Villiers 1951).

Conservation IUCN Category: Least Concern.

Possibly declining locally but still widespread. These anomalures are too small and rare to warrant being hunted for food. Although they are known to feed on oil palm fruits, they are unlikely to represent any threat to oil palm production.

Measurements

Anomalurus beecrofti argenteus

HB: 278 (261–300) mm, n = 10

T: 213 (190–238) mm, n = 10
 HF: 49 (37–55) mm, n = 10
 E: 27 (22–28) mm, n = 10
 WT: n. d.
 GLS: 56.3 (53.8–58.8) mm, n = 14
 GWS: 35.3 (33.2–36.9) mm, n = 14
 P⁴–M³: 12.0 (11.3–12.7) mm, n = 14

Throughout geographic range (Rosevear 1969)

Key References Bates 1905; Dekeyser & Villiers 1951; Rosevear 1969; Sanderson 1940; Schunke & Hutterer 2004.

Jonathan Kingdon

Anomalurus derbianus LORD DERBY'S ANOMALURE (LORD DERBY'S SCALY-TAILED SQUIRREL)

Fr. Anomalure de Derby; Ger. Derbys Dornschwanzhörnchen

Anomalurus derbianus (Gray, 1842). Ann. Mag. Nat. Hist., ser. 1, 10: 262. Sierra Leone.

Taxonomy Originally described in the genus *Pteromys*. Validity of the specific name *derbianus* is questioned by Rosevear (1969) as it antedates *Anomalurus fraseri* Waterhouse 1842 from Bioko, Equatorial Guinea (now considered a synonym of *derbianus*). The type specimen is in very poor condition and without skull. Considerable variability in pelage colour within and between populations. Synonyms: *beldeni*, *chrysophaenus*, *cinereus*, *erythronotus*, *fortior*, *fraseri*, *griselda*, *imperator*, *jacksoni*, *jordani*, *laticeps*, *neavei*, *nigrensis*, *orientalis*, *perustus*, *squamicaudus*. Subspecies: at least 15 subspecies have been described, none of which is recognized now. Chromosome number: not known.

Description Very large anomalurid with dark grey, long, fine-textured fur with silvery grizzle. Dorsal pelage long, dense and fine in texture, greyish or brownish to reddish-brown; hairs dark grey at base with subterminal ring and inconspicuous black tip, giving dorsal pelage a somewhat mottled appearance (see also Geographic Variation). Hairs silver-tipped around head and shoulders. Ventral pelage dense, pure white, greyish or yellowish. Flight patagia stretch between forelimb and hindlimb, and interfemoral patagia are present between the ankle and the proximal end (ca. 5 cm) of the tail. Cartilaginous spur projects outwards (within the membrane) from the elbow to margin of patagium. Hairs on membrane similar in colour to dorsal pelage but shorter and sparser; ventral surface almost naked. Roundish head with relatively short, pointed muzzle and large eyes. Black mask surrounds eyes and ears; forehead and throat almost uniformly pale grey. Ears large, elliptical, erect and naked, surrounded at bases with long back hair. Limbs long, feet powerfully built. Forefeet have four digits, hindfeet have five digits, all with thin, strong, sharp, curved claws. Upper surface of feet covered with hairs; black bristles cover hindclaws. Tail long (ca. 90% of HB), narrow, short-haired at base widening to long-haired brush at tip; basal portion pale turning to black distally; strong, pointed scales on basal ventral surface of tail. Skull with narrow palate, narrow cheekteeth (<3 mm), lower branch of maxillary process ending just anterior to first cheektooth, molar row slightly curved outwards, three depressions between transverse enamel ridges of each cheektooth, and without a sharp, backward pointing postero-internal cusp on each molar. Nipples: 2 + 0 = 4.

Geographic Variation Dorsal colouration is polymorphic and varies geographically and within populations; the brownish colour morph is usually the commonest colour in all populations. From S Cameroon to the lower Congo and Ubangi rivers, the dorsal colour



Anomalurus derbianus

of most individuals is reddish-brown (although some 'brownish' individuals are also present) and the patagia are grey. In SE DR Congo and S Tanzania, some individuals have silvery-grey dorsal pelage. Ventral colouration is usually white or greyish; in some populations, some individuals are yellowish mixed with grey (C DR Congo and Zambia) and some are pale yellow (Kenya). The colour of ear, throat and shoulders also exhibits inter- and intra-population variation (details in Schunke & Hutterer 2004).

Similar Species

A. beecrofti. On average smaller; ear shorter; tail with very small terminal brush; snout narrow and pointed; pelage somewhat longer, softer and sometimes darker.

Distribution Endemic to Africa. Rainforest BZ (all regions), Rainforest–Savanna Mosaics, and northern parts of Zambezi Woodland BZ. Recorded from Sierra Leone to W Kenya, and from N Angola, S DR Congo, Zambia, N Malawi, and S and N Tanzania. Two records in N Mozambique (Smithers & Wilson 1979). Zanzibar I. (requires confirmation).

Habitat Catholic in habitat requirements as long as forest cover is adequate and naturally hollow trees are present for resting and nesting. Found in broad spectrum of forest types, ranging from moist rainforest to savanna woodlands, from sea level to 2400 m (Rahm 1969b, Rosevear 1969, Jones 1971, Kingdon 1974, Grubb *et al.* 1998). May prefer relatively open forest with well-spaced tree trunks and scarce vines (Happold 1987). While abundant in relatively undisturbed forest, also found nesting in dead standing trees in burned areas cleared for cultivation and near villages (Rahm 1969b, Jones 1971), provided living trees are within gliding distance (Rosevear 1969).

Abundance Commonest of the larger anomalurids (Rosevear 1969). Estimated density in central Gabon 27–54 individuals/km²; biomass 30–65 kg/km² (Julliot *et al.* 1998). Most abundant of three anomalurids in E DR Congo, representing 60% of 30 individuals collected (Rahm 1969b).

Adaptations Nocturnal and arboreal. Usually rests during day unless disturbed, and regularly emerges from resting areas shortly after dusk (Rosevear 1964, Rahm 1969b, Jones 1971, Julliot *et al.* 1998). Marked individuals in central Gabon began activity as soon as the light level in the forest became low (18:10–18:55h; *n* = 27) and returned to the nest at sunrise (05:20–06:20h; *n* = 14). During night, no clear pattern of activity was exhibited (Julliot *et al.* 1998).

Derby's Anomalures are almost completely arboreal, rarely venturing to the ground. Individuals rest while clinging to sides of trees, 8–25 m above the ground, with the head up and body parallel to the bole. The long sharp claws grip the bark, and the scales on the undersurface of the tail also provide support (Rosevear 1969). Gliding is performed with the patagia outstretched, and the distance that can be covered is determined by gravity and the height at take-off. The patagia do not flap during gliding and have very limited manipulability, and hence a glide ends at a lower level to where it began. Observations on two individuals in Tanzania recorded the downward glide angle (from the horizontal) as 24 degrees, regardless of the height above the ground where the glide began and the length of the glide (animal 1: horizontal glide distance 4.5 m; glide distance 5.4 m; glide from 5 m to 3 m above ground; animal 2: horizontal glide distance 40 m; glide distance 44 m; from 23 m to 4.5 m above ground) (Corbin & Cordeiro 2006). The glide angle of 24 degrees is probably the most efficient angle that allows for the longest glide distance; the morphology of the pelvis (Scheibe & Essner 2000) and large thigh muscles (Kingdon 1974) contribute to the ability of the anomalure to 'leap' into the glide rather than 'dropping' before 'gliding'. On landing on a tree trunk (fore- and hindlimbs landing at the same time, with the body almost vertical), the anomalure climbs up immediately with a 'humping gait', forefeet alternating with hindfeet, to gain height once again (Rosevear 1969). Anomalures can glide up to 50 yards (Rosevear 1969) and sometimes up to 100 m (Kingdon 1974). One radio-collared ♀ covered an average distance of 540 m per night, alternating between localized movements and directed glides up to 100 m (Julliot *et al.* 1998). Anomalures are awkward and clumsy on the ground, heading immediately for a vertical surface in a series of jumps if disturbed. They ascend trees and vertical structures rapidly (Rahm 1960a, Rosevear 1969). Further details of gliding are given by Rahm (1969b), Rosevear (1969) and Sanderson (1940).

Rests during the day in nests within hollows, often in trees that have lost their crowns and are open at the top (Rahm 1960a, 1969b, Jones 1971, Julliot *et al.* 1998). The size and species of tree do not seem to be important in nest selection – more important is the position and quality of the entrance hole. In C Gabon, primary nests (80%; *n* = 10) had both basal and high entrance holes, while secondary nests had high entrance holes only (Julliot *et al.* 1998). In Equatorial Guinea, hollows where nests were situated ranged from 0.3 to 2.5 m diameter and up to ca. 40 m above the ground (Jones 1971). One radio-collared female in Gabon used six nesting trees, one primary and five secondary. Individuals apparently exhibit some degree of fidelity to nests, with the same ♀ using the same nest for four months (Julliot *et al.* 1998). Fidelity to a particular nest was observed in E DR Congo, where the same individual is thought to occupy the same nest for at least 2.5 years (Rahm 1969b).

Like other anomalures, Derby's Anomalure engages in pruning behaviour, using its incisors to clear bark and cut small branches. This branch-cutting behaviour is thought to enhance access to food supplies and also keep flight paths open (Kingdon 1997).

Colour and markings of the pelage blend well with the background of a tree where an individual may sun itself during the day (Rosevear 1969, Kingdon 1974), although well-lit resting places are avoided (Julliot *et al.* 1998). Anomalures have powerful jaw musculature for gnawing bark or chewing woody twigs. Large ears with well-developed auditory bullae suggest that hearing plays a large role in sensory perception (Rosevear 1969). Structure of the male penis was described as 'remarkable' by Sanderson (1940), who noted the presence of a cartilaginous 'spear'.

Foraging and Food Wholly vegetarian; diet consists of leaves, fruits, flowers and soft inner bark (Rahm 1960a, Rosevear 1969). In C Gabon, anomalures forage by scratching bark of trees (mostly of the family Caesalpiniaceae) with the teeth, cutting the bark open, licking exuding material and ingesting the phloem sap (but not the bark itself). Stomach contents of one individual consisted of leaves and petioles, bark fragments, and ants and termites (Julliot *et al.* 1998). Other records indicate actual ingestion of bark and/or gnawing of twigs and branches (Rahm 1960a, Kingdon 1974). In E DR Congo, individuals have been observed feeding on fruits and leaves and inner bark, while avoiding trees that exude latex (Rahm 1960a). Flowers and fruits are thoroughly masticated (Sanderson 1940).

Social and Reproductive Behaviour Nests usually contain a single individual (*n* = 6 out of 10) but up to three individuals have been found in nests in central Gabon. Except for mother/young pairs, individuals enter and leave nests individually. Two individuals (other than mother/young) may feed close together, and one may glide after the other (Julliot *et al.* 1998). In Equatorial Guinea, Jones (1971) found 1–3 individuals resting in tree hollows (*n* = 10 trees). Larger groupings have also been recorded (Rosevear 1969, Kingdon 1974). Known to share the same hollow occasionally with bats and other species of anomalures (Julliot *et al.* 1998). Home-range of a radio-collared ♀ in C Gabon was 3.37 ha, with 50% of locations in a small central area comprising 11.3% of home-range (Julliot *et al.* 1998).

Reproduction and Population Structure One to three young (Sanderson 1940, Kingdon 1974) have been recorded. Mother/young observations in C Gabon were all of single young (Julliot *et al.* 1998). In Equatorial Guinea, lactating ♀♀ were collected in Feb and May (Jones 1971). In S Cameroon, pregnant ♀♀ were collected in the beginning of the wet season (Jun/Jul) (Sanderson 1940). In Uganda and W Kenya, four births were recorded in Jan, two pregnancies in Mar and a lactating mother in May. In S Tanzania, well-grown young were observed in May/Jul corresponding with the early dry season (Kingdon 1974). Young are born in nests in hollow trees, and at birth are large, well-furred and the eyes are open (Kingdon 1974). Vagina of pregnant ♀♀ sealed with hard plug (Sanderson 1940).

Predators, Parasites and Diseases In C Gabon, one record of predation by an eagle (Julliot *et al.* 1998). A Blue Monkey *Cercopithecus mitis* in Budongo Reserve, Uganda was seen feeding on a Derby's Anomalure during the dry season when food availability is generally at its lowest (Fairgreave 1997). Rahm (1969b) noted the tendency of some people of E DR Congo to season food with the aromatic gut contents of Derby's Anomalures. A species of malarial plasmodium has been found in some specimens (Kingdon 1974).

Conservation IUCN Category: Least Concern.

Listed under CITES Appendix III in Ghana. Otherwise considered to be the most widely distributed and tolerant of the anomalures (Kingdon 1974). Deforestation constitutes an on-going threat to the survival of some populations.

Measurements

Anomalurus derbianus

HB: 306 (283–379) mm, n = 11

T: 284 (227–327) mm, n = 11

HF: 56 (51–64) mm, n = 11

E: 40 (36–47) mm, n = 11

WT: 595.3 (588–605) g, n = 3*†

GLS: 58.7 (57.8–60.2) mm, n = 15

GWS: 38.7 (36.8–41.0) mm, n = 15

P⁴–M³: 12.8 (11.9–13.5) mm, n = 15

West Africa (Rosevear 1969)

*Central African Republic (J. C. Ray & J. R. Malcolm unpubl., USNM)

†In Gabon, WT: 720 (700–740) g, n = 2 (Julliot *et al.* 1998)

Key References Jones 1971; Julliot *et al.* 1998; Kingdon 1974, 1997; Rahm 1969b.

Justina C. Ray

Anomalurus pelii PEL'S ANOMALURE (PEL'S SCALY-TAILED SQUIRREL)

Fr. Anomalure de Pel; Ger. Pels Dornschwanzhörnchen

Anomalurus pelii (Schlegel & S. Müller, 1845). In: Temminck (1843–1845): Verh. Nat. Gesch. Nederland. Overz. Bezitt., Zool., Mammalia, p. 109. 'Daboerom, aan de Goudkust' (= Dabacrom, Ghana).

Taxonomy Originally described in the genus *Pteromys*, a genus of 'flying squirrels' (Sciuridae, Petauristinae) that occurs only in the Palearctic. Synonyms: *auzembergeri*, *peralbus*. Subspecies: three. Chromosome number: not known.

Description Very large anomalure, usually with fringe of white hairs around the edges of the patagia, and a black or white tail. The largest species of anomalure. Pelage soft and long; colour varies geographically; description for *A. p. pelii* follows (but see Geographic Variation for other subspecies). Dorsal pelage pure black, with narrow band of white around edge of flight patagia and interfemoral patagia. Ventral pelage grey or off-white; less dense than dorsal pelage. Cartilaginous spur projects outwards (within the membrane) from the elbow to margin of flight patagium. Head black with large white nose-spot. Vibrissae long, black, growing from black-furred pads on upper lips and muzzle. Ears large, rounded at tip, with pale pigmentation and conspicuous dense tuft of white hairs along dorsal margin. Forelimbs with four digits, black above, pale below, and well-developed narrow short claws. Hindlimbs with five digits, black above fringed with white (where patagium joins limb), pale below; well-developed claws. Tail long (ca. 95% of HB), pure white (*peralbus*, *pelii*) or black (*auzembergeri*), well covered with rather coarse hairs; hairs short near base, becoming longer towards tip and forming large brush

at terminal end; 6–7 pairs of sharp pointed scales on ventral surface near base of tail near where it becomes free of the patagium. Skull similar to *A. derbianus*, but larger in all dimensions. Nipples: 2 + 0 = 4.

Geographic Variation Rosevear (1969) detailed two subspecies (*A. p. auzembergeri* and *A. p. pelii*). Schunke & Hutterer (2005) reviewed colour variation in the species and described a third subspecies (*A. p. peralbus*).

A. p. peralbus: Côte d'Ivoire, between Bandama and Sassandra rivers; flight patagia with very wide white border on dorsal surface, reaching almost to the body; wide white border on interfemoral membrane; tail white; large white patch at base of each ear; fore- and hindfeet white.

A. p. pelii: Côte d'Ivoire (east of Bandama R.) and Ghana (west of Volta R.); flight patagia with narrow white border on dorsal surface; narrow white border on interfemoral membrane; tail whitish; white patch at base of each ear; forefeet blackish and hindfeet whitish (see Rosevear 1969 for colour picture).

A. p. auzembergeri: Côte d'Ivoire (west of Bandama R.) and Liberia; flight patagia black without any white border on dorsal surface; interfemoral membrane black without white border; tail black; without white patch at base of each ear; fore- and hindfeet black.

Similar Species

A. derbianus. Smaller and more variable in colouring with distinctive eye-mask; dorsal pelage mottled; tail black; widespread and common.

A. beecrofti. Smaller, dorsal pelage mottled; ventral pelage orange or yellow; tail relatively short (ca. 75% of HB), grey with small (or non-existent) pale-coloured brush.

Distribution Endemic to Africa. Rainforest BZ (Western Region). Recorded from E Liberia to Ghana west of the Volta R. In Liberia, apparently limited to the vicinity of the Cavally R., with only one record from further west in Deaple (Kuhn 1966). No records from Sierra Leone (Grubb *et al.* 1998).

Habitat Moist low-altitude rainforests with annual rainfall of 1400–3900 mm. Prefers primary forest with numerous tall emergents and palm trees.

Abundance Formerly regarded as quite common in rainforest but nocturnal habits and shyness make assessment of abundance very difficult. Sharing of hollows by up to six individuals suggests that local abundance and dispersion might be strongly influenced by availability of holes. Extensive logging of moist low-altitude rainforests implies a corresponding decline in overall abundance.

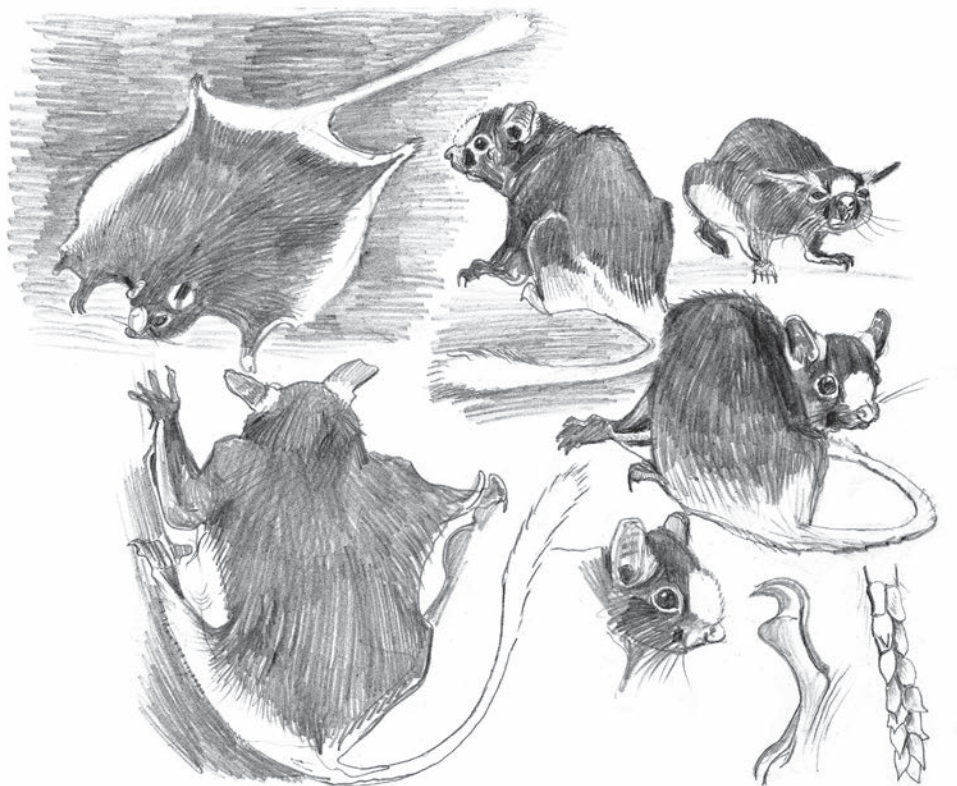
Adaptations Nocturnal and arboreal. During the daytime, Pel's Anomalures sleep in holes and hollow branches high in large trees. They emerge from their nests well after sunset and return long before daybreak (Adams 1894). One nest in a felled tree was contained in a large hollow some 5 feet deep and covered at the bottom with sticks and small branches. Cansdale (1946) took one of his specimens from



Anomalurus pelii

a hollow *Terminalia superba* tree. It is not known to what extent they make their own holes and hollows. There is some evidence that they modify their environment by pruning branches out of glide-paths (but not yet confirmed).

When disturbed in a hollow, Pel's Anomalures growl, hiss and snap their teeth (all noises that are amplified in a hollow). This behaviour may deter birds of prey, primates and small carnivores, as well as hornbills (which may compete for nest-hollows). Bold colouring,



Anomalurus pelii.

large size and aggressiveness may make this species less vulnerable to predation than the smaller species. Black and white colouring (with the exception of the melanistic subspecies *A. p. auzembergeri*) could also imply higher visibility and unambiguous postural signalling during intra-specific interactions. Strictly nocturnal activity probably diminishes the number of potential visual predator species, and apparently obviates the need for cryptic colouring. Forefeet primarily adapted for clinging on to bark and clasping branches; the absence of Digit 1 restricts handling of food, which is generally gnawed directly at source (although Adams [1894] noted that fruits are taken back to the nest and peeled).

At night, Pel's Anomalures glide from tree to tree, and are only visible when there is a full moon (Adams 1894). The surface area of the volplane (ventral surface of body and patagia) is ca. 2000 cm², larger than for other anomalures, probably because this species is substantially heavier than other species in the family.

Foraging and Food Little known. The diet is likely to be bark, probably from a few large tree species, fruits (especially oil palm *Elaeis guineensis* and other palm dates), leaves and flowers. Cansdale (1946) observed finely chewed leaves and 'mealy seed' in the stomach of one animal, and records that the droppings are green and oval. How the consumption of oil palm fruits by this species might differ from Beecroft's Anomalure remains undetermined.

Social and Reproductive Behaviour Adams (1894) never found more than three individuals sharing a hole, although he was informed that up to six may be found. Nothing is known about social interactions or home-range but contact calls have been described as deep hoots. Scent from well-developed inguinal glands suggests that olfactory communication is important.

Reproduction and Population Structure Cansdale (1946) recorded a ♂ with dilated testes in Aug, while a ♀ taken in Oct carried one embryo. Up to four young, more commonly 2–3, can be born at a time and two litters a year have been recorded. It seems

likely that competition for suitable resting and breeding holes is one of the primary determinants of reproductive and social life, but there is no corroborating data.

Predators, Parasites and Diseases There are currently no records of predation, although likely predators include large owls, hole-hunting hawks (such as African Harrier-hawks *Polyboroides typus* and Crowned Hawk-eagles *Stephanoaetus coronatus*), hornbills, snakes and palm civets. Nothing is known about parasites or diseases. They are, however, considered to be quite tasty and may be preyed upon by villagers in some localities.

Conservation IUCN Category: Data Deficient, previously assessed as Near Threatened.

Wholesale logging of the forests in the Upper Guinea rainforests has removed the larger part of the preferred habitat. The following National Parks are within the range of this species: Loffa-Mano, Cestos Sankwan and Sapo in Liberia; Taï and Azagny in Côte d'Ivoire; and Nini-Suhien and Bia in Ghana.

Measurements

Anomalurus pelii pelii

B: 421 (400–460) mm, n = 6

T: 403 (325–450) mm, n = 6

HF: 72 (70–75) mm, n = 6

E: 44 (42–48) mm, n = 6

WT (♀): 1400 g, n = 1

GLS: 67.8 (65.5–69.5) mm, n = 9

GWS (ZW): 45.8 (43.7–49.4) mm, n = 9

P⁴–M³: 15.5 (14.4–16.0) mm, n = 9

Throughout geographic range (Rosevear 1969)

Key References Adams 1894; Cansdale 1946; Rosevear 1969.

Jonathan Kingdon

Anomalurus pusillus LESSER ANOMALURE (DWARF SCALY-TAILED SQUIRREL)

Fr. Anomalure pygmée; Ger. Zwerg-Dornschwanzhörnchen

Anomalurus pusillus Thomas, 1887. Ann. Mag. Nat. Hist., ser. 5, 20: 440. 'Bellima and Tingasi, Monbuttu', DR Congo (= Niangara, DR Congo).

Taxonomy Synonyms: *batesi*. Subspecies: none. Chromosome number: not known.

Description Large dark speckled anomalure with black-tipped tail and without facial markings. Pelage long and soft. Dorsal pelage blackish to tan, speckled and agouti-like; hairs medium grey at base darkening towards tip; buff or pale brown at tip. Well-developed patagia, dark brown tending to yellowish on interfemoral patagia. Ventral pelage shorter than dorsal pelage, white or creamy-white or greyish-white. Cartilaginous spur projects outwards (within the membrane) from the elbow to margin of patagium. Head greyish without any markings. Muzzle rather slender. Vibrissae long, black. Ears slightly pigmented, naked. Limbs similar in colour to body. Hindlimbs with yellow bristle-like hairs covering claws. Tail relatively short (ca.

60% of HB), thin, hairs yellow at basal end turning to black-tipped at terminal end. Skull similar to *A. derbianus*. Nipples: not known, but presumably 2 + 0 = 4.

Geographic Variation In contrast to the other species in the genus, *A. pusillus* does not show any geographic variation (Schunke & Hutterer 2004).

Similar Species

A. derbianus. Larger; darker and heavier; black markings at base of ears; tail long, grey, with well-developed black brush at tip.

A. beecrofti. Larger; dorsal pelage grey, agouti; ventral pelage orange or yellow; tail long, thin, grey and with small blackish brush at tip.

*Anomalurus pusillus*

Distribution Endemic to Africa. Rainforest BZ (Western, West Central and East Central Regions). Recorded from isolated dispersed localities in Liberia, Cameroon, Equatorial Guinea (Rio Muni), Gabon and NE DR Congo. One record in Central African Republic. May also occur in W Uganda. Whether the Liberian specimens represent an isolated population or whether the species occurs elsewhere in West Africa is not known (Grubb *et al.* 1998); however, also recorded from Côte d'Ivoire (A. Schunke pers. comm.; not shown on map).

Habitat Equatorial rainforest. In Gabon and DR Congo, recorded only from rainforest, not from the outer margins or mosaics of the Congo Basin. Too few specimens have been collected to identify any preferences for forest type or structure. Mainly recorded at lower altitudes, but one specimen known from montane forest at 2200 m in E DR Congo (Rahm & Christiaensen 1963).

Abundance The rarest of the *Anomalurus* spp., and possibly very localized. After many years of collecting in E DR Congo, Rahm (1969b) listed data for only three specimens. In a 75 ha area in C Gabon, Julliot *et al.* (1998) estimated the density of Lesser Anomalures at about 5/km² (cf. 27–54/km² for *A. derbianus* and 164–437/km² for *Idiurus macrotis* in the same area).

Adaptations Arboreal and strictly nocturnal. In C Gabon (Julliot *et al.* 1998), nests were in hollows either near the base, or high up, in medium or large trees. The muscles of the jaws are relatively much less developed for chewing and gnawing than in *A. derbianus*, and therefore it is unlikely that branches are pruned to the same extent. Local variations in colour of the dorsal pelage in different populations may suggest that predators have exerted selection pressure for colour matching of the pelage with that of the trunks and branches.

Foraging and Food Little information. Rahm (1969b) recorded that the drupes of the Parasol tree *Musanga cecropioides* were eaten, and fruits of other trees suggested. A generalized resemblance of the teeth and jaws with those of Lord Derby's Anomalure suggests that Lesser Anomalures may also eat bark but possibly select softer, less fibrous barks, as are found on newer growth and some lianas. This implies that this species may find little food on large tree trunks and big boles.

Social and Reproductive Behaviour Lesser Anomalures seem to nest alone (Julliot *et al.* 1998), although Rahm (1960a) records one individual nesting with *A. jacksoni* (= *A. derbianus*).

Reproduction and Population Structure No information.

Predators, Parasites and Diseases No information.

Conservation IUCN Category: Least Concern.

Measurements

Anomalurus pusillus

HB: 231 (221–238) mm, n = 3

T: 136 (130–140) mm, n = 3

HF: 38 (37–39) mm, n = 3

E: 28 (27–29) mm, n = 3

WT: 170 g, n = 1*

GLS: 44.4 (43.8–44.8) mm, n = 3

GWS (ZW): 28.3 (27.7–29.1) mm, n = 3

P⁴–M³: 8.8 (8.7–8.8) mm, n = 3

Gabon (as *A. p. batesi*; Rosevear 1969)

*Adult ♂, Gabon (Julliot *et al.* 1998)

Key References Grubb *et al.* 1998; Julliot *et al.* 1998; Rahm 1969b.

Jonathan Kingdon

GENUS *Idiurus* Pygmy Anomalures

Idiurus Matschie, 1894. Sber. Ges. Naturf. Freunde Berlin 8: 194. Type species: *Idiurus zenkeri* Matschie, 1894.

The genus *Idiurus* contains two species, which occur in the Rainforest BZ from Sierra Leone to W Uganda and W Tanzania. They occur only in the rainforest where there are large forest trees.

The genus is characterized by small size (HB less than 100 mm, GLS less than ca. 26 mm), flight patagia between the fore- and hindlimbs,

and small interfemoral patagia between the hindlimbs and the proximal end of the tail. The tail is long, thin and feathery, and there are small backwardly pointed scales on the undersurface of the tail. The outer margins of the flight patagium are fringed with fine hairs. A cartilaginous spur on the elbow provides support for the flight membrane. The



postorbital process of the frontal bone is absent and the infraorbital foramen is large, in contrast with that of squirrels. The nasal bone is comparatively deep in the dorsal–ventral plane, and the mandible is also deep in this plane giving the skull a rather ‘box-like’ shape. The lower process of each maxillary process extends anteriorly almost to the incisor (cf. *Anomalurus*). The posterior surface of each upper incisor has a well-defined notch (cf. *Anomalurus*), the premolar (P^4) is large and the last molar (M^3) is small (Figure 96).

Pygmy anomalures are arboreal and nocturnal. When resting in tree hollows during the day they are very gregarious, and often many tens of individuals will cluster together. In contrast, individuals are solitary when travelling and foraging at night. They are vegetarian, feeding on a variety of fruits and saps. Throughout the geographic range, abundance varies according to species and habitat, from rare to quite common; however, because of their small size, nocturnal activity and the density of preferred habitat, individuals are often difficult to observe. They are very efficient gliders (see *I. macrotis*), and when running along branches and tree trunks they use a running gait, rather than the bounding gait of *Anomalurus* spp.

Two species are recognized: *I. macrotis* and *I. zenkeri*. Some authorities recognize subspecies within *I. zenkeri* based on variation in pelage colouration. The two species are distinguished by size; their distribution is similar except that *I. zenkeri* does not occur in the Western Region of the Rainforest BZ. A multivariate study on 57 craniometric characters of the skulls of *Idiurus* supports the division into two species; however, although there is some geographic variation between populations of each species, these differences are not sufficient to warrant subspecific differentiation (Schunke & Hutterer 2007).

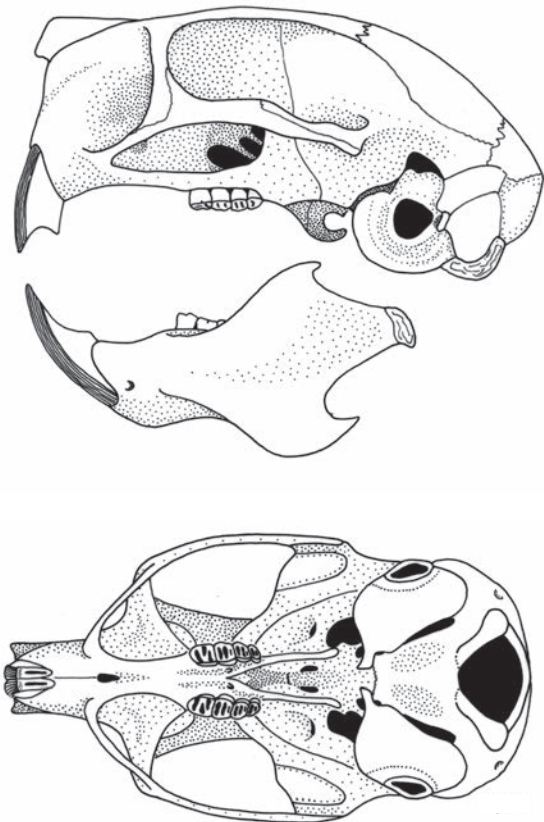


Figure 96. Skull and mandible of *Idiurus macrotis* (BMNH 3.2.4.16).

Richard W. Thorington, Jr

Idiurus macrotis LONG-EARED PYGMY ANOMALURE (LONG-EARED SCALY-TAILED FLYING SQUIRREL)

Fr. Anomalure nain à grandes oreilles; Ger. Großohr-Gleitbilch

Idiurus macrotis Miller, 1898. Proc. Biol. Soc. Washington 12: 73. Efulen, Cameroon.

Taxonomy Synonyms: *cansdalei*, *langi*, *panga*. Subspecies: none. Chromosome number: not known.

Description Very small anomalurid with feathery tail. Dorsal pelage sepia-grey to mouse-grey; hairs deep chocolate at base. Longer brown hairs interspersed throughout dorsal pelage. Ventral pelage

paler, sometimes slightly pinkish; hairs blackish-grey at base. Flight patagia and interfemoral patagia naked close to body, but covered with short dark hairs at edges. Ears relatively large and brown, mostly naked. Vibrissae black and extremely long. Forelimbs and hindlimbs short; wrist and ankles with sparse tuft of bristles; digits covered with fringe of hairs. Tail very long (ca. 150% of HB), thin, with long

delicate dark brown feather-like hairs on lateral sides. Ventral surface of tail with two rows of very short bristles and with small horny scales arranged in transverse rows of three or more near to basal end. Skull box-like in shape; maxillary process reaches well forward of the first premolar (almost to the incisor); incisor teeth with deep notch on posterior surface, M^3 small but more than half the size of M^1 or M^2 . Nipples: $2 + 0 = 4$.

Geographic Variation Individuals from Ghana are buffy-brown and paler than the darker brown individuals from elsewhere (Côte d'Ivoire and further west; Nigeria and further east).

Similar Species

I. zenkeri. Smaller in body and skull measurements; relatively smaller ears.

Anomalurus spp. Considerably larger; tail well covered with hairs, not 'feathery' as in *Idiurus* spp.

Distribution Endemic to Africa. Rainforest BZ (Western, West Central and East Central Regions). Distribution disjunct. Recorded from: (1) Sierra Leone to Ghana west of Volta R. (not recorded from Guinea but expected to occur there); (2) SE Nigeria, SW Cameroon, Equatorial Guinea (Rio Muni) and Gabon; and (3) NE DR Congo, WTanzania.

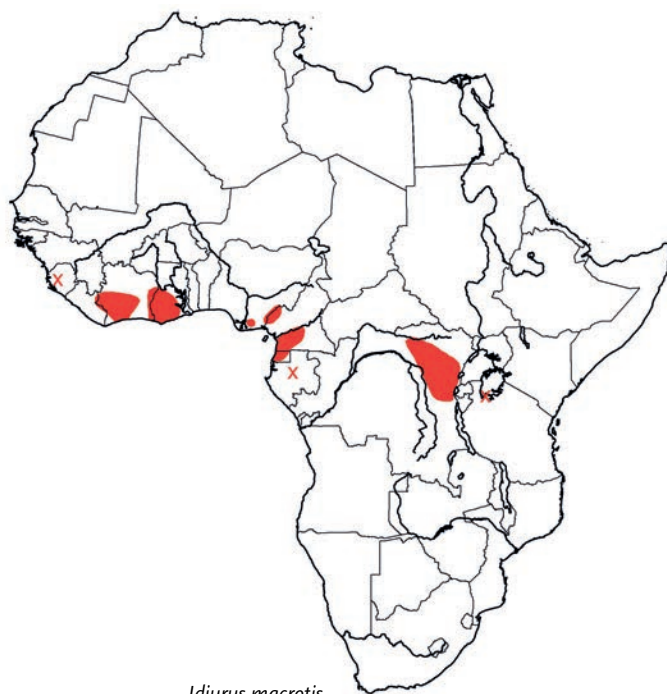
Habitat Rainforest where there are large trees with hollows and holes in the trunks.

Abundance Uncertain. In favoured habitats in Gabon, density is 164–437 ind/km² (Julliot *et al.* 1998).

Adaptations Arboreal and nocturnal. During the day, individuals rest in hollows and holes of many species of large forest trees. The preferred trees have hollows with entrances low down. Emergence from the hollow begins at 18:15 to 19:00h, and activity continues until 06:00h but without any clear pattern of activity during the night. There is some evidence of fidelity to a particular hollow, the same hollows being occupied by the same species (but not necessarily the same individuals) for many months or years (Julliot *et al.* 1998). Pygmy Anomalures (and Zenker's Anomalures) are very expert gliders.

Foraging and Food Vegetarian, mainly frugivorous. Gnaws and peels bark and probably feeds on sap (Julliot *et al.* 1998). In captivity, feeds only on palm nuts (Durrell 1952).

Social and Reproductive Behaviour Gregarious, but solitary at night. In Gabon, during the day, individuals rest in hollows, singly, in pairs, or in groups of up to 40 individuals (Julliot *et al.* 1998). When resting in groups, individuals huddle up to each other in a similar manner to communal bats. A particular hollow may contain only conspecifics, or may include other species such as *Anomalurus derbianus*, *A. beecrofti*, *A. pelii*, *Idiurus zenkeri* and *Graphiurus hueti* (now *G. nagtglasii*) or species of bats (*Hipposideros cyclops*, *Tadarida leonis*, *Tadarida* sp.) (Rahm 1966, Rosevear 1969, Jones 1971, Jeffrey



Idiurus macrotis

1975, Julliot *et al.* 1998). Home-range was about 3 ha for one ♂ radio-tracked during 48 hours; this ♂ travelled about 780 m per night (Julliot *et al.* 1998).

Reproduction and Population Structure In E DR Congo, embryo number: 1 ($n = 5$). Pregnancies recorded in Jun and Aug in E DR Congo (Rahm 1966); ♀♀ found with infants and young in Jun in Cameroon (Durrell 1952).

Predators, Parasites and Diseases No information.

Conservation IUCN Category: Least Concern.

Conservation of rainforest with tall forest trees with hollows is essential for the survival of the species.

Measurements

Idiurus macrotis

HB: 88.4 (73–105) mm, $n = 10$

T: 132.4 (110–186) mm, $n = 13$

HF: 20.3 (19–22) mm, $n = 8$

E: 17.4 (17–18) mm, $n = 8$

WT: 26.3 (23–30) g, $n = 4$

GLS: 26.1 (25–27) mm, $n = 8$

GWS: 14.8 (13.6–16.1), $n = 9$

P^4-M^3 : 3.6 (3–4) mm, $n = 6$

Throughout geographic range (BMNH, and literature records)

Key References Julliot *et al.* 1998; Miller 1898; Schunke & Hutterer 2007.

Brian J. Stafford & Richard W. Thorington, Jr

Idiurus zenkeri ZENKER'S PYGMY ANOMALURE (PYGMY SCALY-TAILED FLYING SQUIRREL)

Fr. Anomalure nain de Zenker; Ger. Zenkers Gleitbilch

Idiurus zenkeri Matschie, 1894. Sber. Ges. Naturf. Freunde Berlin 8: 197. Yaounde, Cameroon.

Taxonomy Synonyms: *haymani*, *kivuensis*. Subspecies: none recognized here. Chromosome number: not known.

Description The smallest of the anomalures, with a feathery tail. Pelage soft and dense, fine; ca. 8 mm on back. Dorsal pelage medium-brown; hairs dark grey at base, medium to pale brown at tip; grey colour of base often visible on surface. Ventral pelage similar to dorsal pelage. Well-developed flight patagia, supported anteriorly by calcaneum on forearm; small interfemoral patagia. Dorsally, pelage extends from back on to inner part of flight patagia, most of patagia covered by sparse short blackish hairs. Ventrally, also covered with sparse short blackish hairs, but ventral pelage does not extend on to inner part of flight patagia. Head similar in colour to dorsal pelage, without any contrasting markings. Long vibrissae (ca. up to 35 mm). Ears moderately large, rounded at tip, mostly naked. Forelimbs short, with feathering on outer surface of forefeet; four digits of equal length, each with small blackish claw. Hindfeet slightly elongated; five digits,

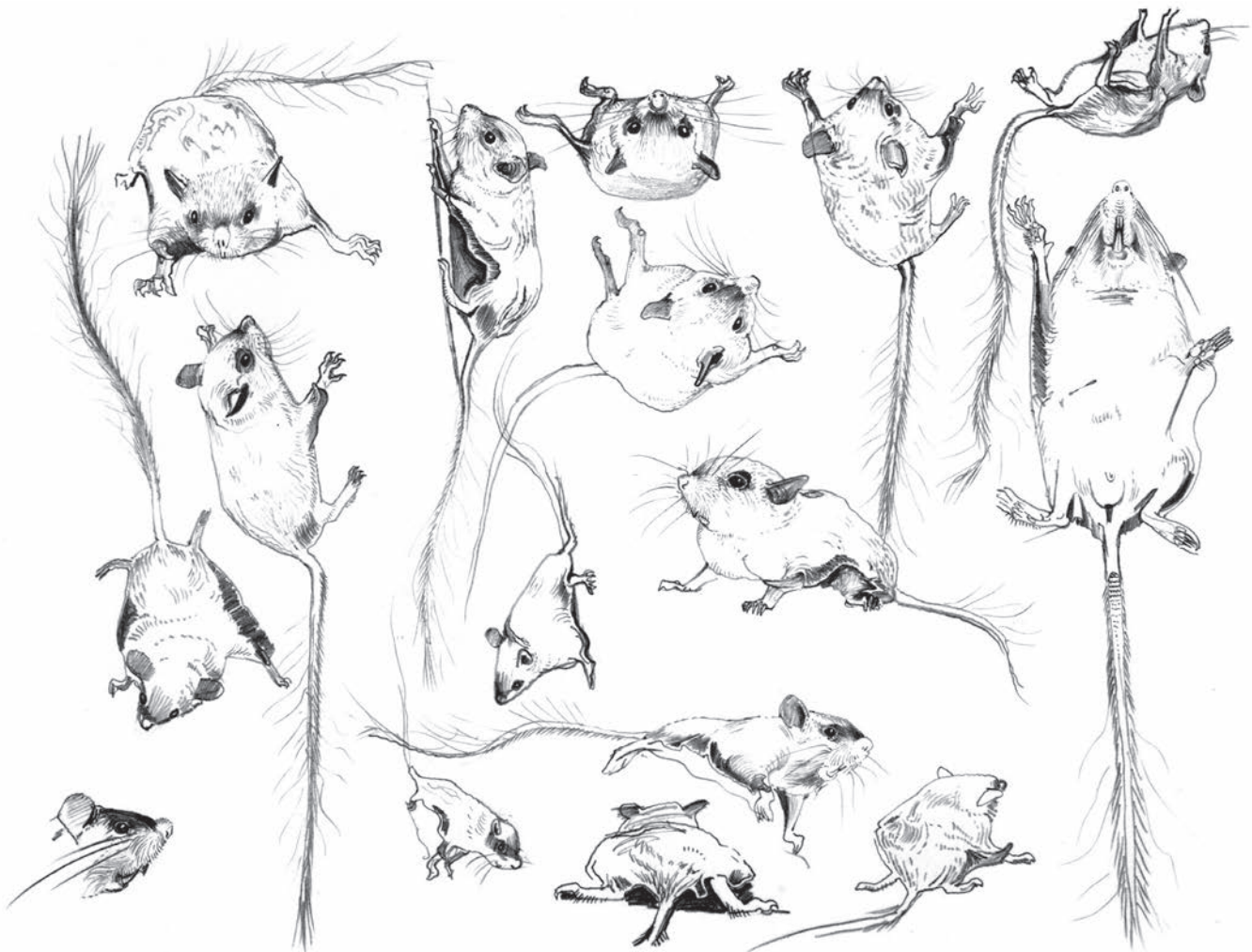
more or less equal in length. Tail very long (ca. 130% of HB), with two lines of short hairs (ca. 3 mm) placed laterally, interspersed with many long dark brown or black hairs (20–25 mm), which slant backwards at ca. 45 degrees to line of tail. Skull: maxillary process reaches well forward of the first premolar; incisor teeth with deep notch in posterior surface, M^3 small, and less than half the size of M^1 and M^2 . Nipples: not known.

Geographic Variation None recognized here (but see Genus profile).

Similar Species

I. macrotis. Larger (HB: 73–105 mm, T: 110–186 mm, WT: ca. 23–30 g); more widespread distribution.

Distribution Rainforest BZ (East Central and West Central Regions). Two separate ranges: (1) S Cameroon, Equatorial Guinea



Idiurus zenkeri.

(Rio Muni) and NW Gabon; (2) NE and E DR Congo, W Uganda. Also a few records from S Central African Republic.

Habitat Moist equatorial rainforest (Rahm 1966).

Abundance No information.

Remarks Less well known than *I. macrotis*, but probably similar in many respects. Gregarious. Rests in hollows and holes in trees with other species (see *I. macrotis*) during the day. In Cameroon, Sanderson (1940) recorded up to 100 individuals of this species and *I. macrotis* resting in the same tree. In Equatorial Guinea (Rio Muni), Jones (1971) found two *Anomalurus derbianus* and four *I. zenkeri* in the same hollow. Very agile, especially when running up the trunk of a tree (Kingdon 1974). The only information on reproduction is that none of the ♀♀ caught in May–Sep in E DR Congo was pregnant (Rahm 1966). A captive individual uttered mouse-like squeaks when captured (Kingdon 1974).

Conservation IUCN Category: Least Concern. Destruction of mature rainforest, especially the larger trees, which contain hollows for nesting, is a major threat to the species.

Measurements

Idiurus zenkeri

HB: 69.5 (63–75) mm, n = 11

T: 94.9 (83–104) mm, n = 10

HF: 15.4 (14–17) mm, n = 11

E: 13.2 (11–15) mm, n = 10

WT: 17.4 g, n = 1

GLS: 20.9 (20.4–22.0) mm, n = 6

GWS: 12.0 (11.6–12.4) mm, n = 6



Idiurus zenkeri

P⁴–M³: 2.5 (2.5–2.6) mm, n = 6

Throughout geographic range

Body measurements and weight: Delany 1975, Matschie 1894, Rahm 1967

Skull measurements: BMNH

Key References Kingdon 1974; Schunke & Hutterer 2007.

Brian J. Stafford & Richard W. Thorington, Jr

GENUS *Zenkerella* Cameroon Anomalure

Zenkerella Matschie, 1898. Sber. Ges. Naturf. Freunde Berlin 4: 23. Type species: *Zenkerella insignis* Matschie, 1898.

The genus *Zenkerella* is monotypic, and distributed in parts of the West Central Region of the Rainforest BZ. The genus is distinguished

from all other genera of anomalurids by a thick bushy black tail, and by the absence of any patagia (and therefore it is unable to glide as can all other species of the family). As in other anomalurids, there are pointed scales on the undersurface of the tail. The skull is similar in

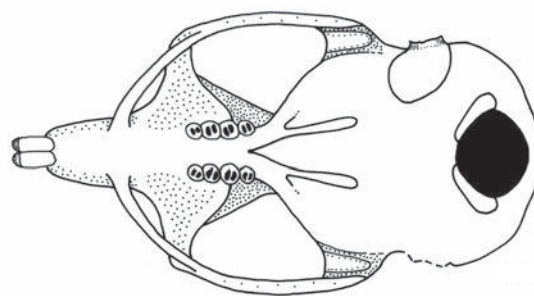
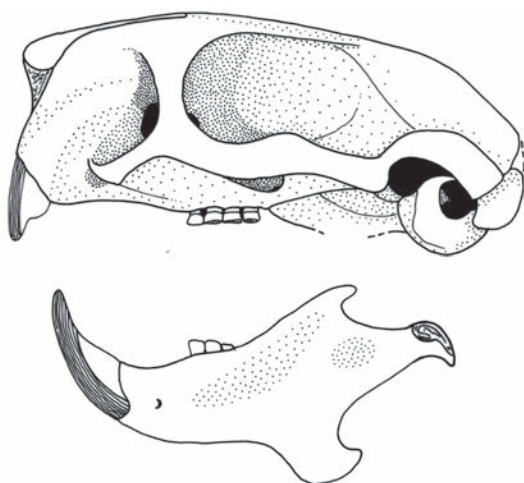


Figure 97. Skull and mandible of *Zenkerella insignis* (MNHN 1970/112). The basicranial region of the skull is partially broken and displaced, and details of the ventral surface are obscured by dry tissue.

general form to that of *Idiurus* spp. although much larger and more box-shaped. The premaxilla is comparatively deep in the dorsal-ventral plane (as in *Idiurus*). The lower branch of each maxillary process extends anteriorly almost to the incisor teeth (as in *Idiurus*; cf. *Anomalurus*). The infraorbital foramen is relatively very large (as in *Idiurus*). The posterior surface of each upper incisor has a slight notch

(less so than in *Idiurus*; cf. *Anomalurus*), and upper M^1 and upper M^2 are larger than upper P^4 and upper M^3 , which are similar in size (Figure 97). Other characters are given in the species profile. The single species is *Zenkerella insignis*.

D. C. D. Happold

Zenkerella insignis CAMEROON ANOMALURE (CAMEROON SCALY-TAIL)

Fr. Zenkerelle; Ger. Kameruner Dornschwanzbilch

Zenkerella insignis Matschie, 1898. Sber. Ges. Naturf. Freunde Berlin 4: 24. 'Kamerun, Afr. Occ., Yaunde' (= Yaounde, Cameroon).

Taxonomy Synonyms: *glirinus*. Subspecies: none. Chromosome number: not known.

Description Medium-sized anomalure without patagia. Pelage soft and dense. Dorsal pelage slate or ashy-grey. Ventral pelage silver or grey, paler than dorsal pelage. Head ashy-grey; ears large, naked and rounded at tip. Long strong black vibrissae. Chin and chest ashy-grey. Limbs short, similar in colour to dorsal pelage, sometimes with ochre tinge on forelimbs. Forefeet with four digits. Hindfeet with five digits; tufts of stiff hairs on outer surface of ankles (function uncertain). Patagia absent. Tail long (ca. 85% of HB), with two rows of seven scales on undersurface close to base of tail; black hairs arranged distichously form a thick bushy tail, hairs shorter at base becoming progressively longer towards tip. Skull: see genus profile. Nipples: not known.



Zenkerella insignis.

Geographic Variation None recorded.

Similar Species

Idiurus spp. Patagia present; without black bushy tail.

Anomalurus spp. Patagia present.

Graphiurus spp. Patagia absent; no scales on undersurface of tail.

Funisciurus and *Heliosciurus* spp. Patagia absent; no scales on undersurface of tail.

Distribution Rainforest BZ (West Central Region, Gabon Subregion). Recorded from S Cameroon, Equatorial Guinea (Rio Muni and Bioko I.), Congo and Central African Republic. Not recorded from N Gabon, but likely to occur there. Kingdon (1997, map) records the species in E Nigeria (east of the Cross R.) but there is no evidence that the species has ever been recorded in Nigeria (Rosevear 1953, Happold 1987).

Habitat Rainforest, probably in canopy although may descend to ground level. Also recorded from semi-deciduous forest, close to savanna habitats (Pérez del Val *et al.* 1995).



Zenkerella insignis

Abundance The rarest of all the anomalures; known only from 11 specimens.

Remarks Arboreal and terrestrial (Pérez del Val *et al.* 1995). De Winton (1898) suggested that these anomalures may be diurnal (on the basis that, like squirrels, they do not have patagia); conversely Bates (1905) suggested that they are nocturnal, hiding in tree hollows during the day. Probably vegetarian.

Conservation IUCN Category: Least Concern; previously assessed as Data Deficient (2004) and Near Threatened (1996).

Measurements

Zenkerella insignis

HB: 202.7 (180–225) mm, n = 3

T: 172.5 (165–180) mm, n = 4

HF: 41 (40–42) mm, n = 3

E: 19.5 (14–23) mm, n = 3

WT: 460 g, n = 1

GLS: 45.7 (44.8–46.3) mm, n = 3

GWS: 26.5 mm, n = 1

P⁴–M³: 6, 7 mm, n = 2

Throughout geographic range (de Winton 1898, Malbrant & Maclatchy 1949, Matschie 1898, Pérez del Val *et al.* 1995)

Key References de Winton 1898; Matschie 1898; Pérez del Val *et al.* 1995.

**Brian J. Stafford &
Richard W. Thorington, Jr**

Family PEDETIDAE
SPRINGHARES

Pedetidae Gray, 1825. Ann. Philos., n. s., 10: 342.

| | | |
|---------------------|-------------|--------|
| Pedetes (2 species) | Springhares | p. 618 |
|---------------------|-------------|--------|

The family Pedetidae is endemic to Africa; it contains one genus and two species, one in East Africa and one in southern Africa. It is restricted to arid and semi-arid, relatively flat and open habitats with short grass, usually where there is little or no woody vegetation.

Characters of the family include large body size (HB: ca. 390 mm, WT: ca. 2.8 kg), long hindlimbs, long hindfeet (ca. 155 mm), short forelimbs, large eyes and long tail (ca. 425 mm). The lower trachea is unique among mammals in that it has a septum similar to that present in some birds (Nowak 1999). The skull is robust, dorsally flattened in lateral view with large expanded nasal bones, the lower maxillary process (of the zygomatic plate) extends anteriorly towards the cutting edge of the upper incisor teeth, orbits are large, tympanic bullae are well developed (especially the occipital part, visible in dorsal view), as is the pterygoid process (see photos in De Graaff 1981). Dental formula: $I^{1/1}, C^{0/0}, P^{1/1}, M^{3/3} = 20$. Upper incisor teeth opisthodont. Cheekteeth hypsodont, continuously growing, flattened, with a single re-entrant fold on the lingual side of each cheektooth. Mandible robust, coronoid process much reduced, and short angular process; strong ridge for muscle attachment on angular process. The species of Pedetidae are among the largest of the Rodentia (similar in size to species of Hystricidae and Thryonomidae), and are the only large saltatorial rodents in Africa. Size categories of species in the family (based on mean head and body length) are given in the order Rodentia profile.

The earliest known fossils (*Parapedetes namaquensis* from Namibia and *Megapedetes pentadactylus* from Kenya) are from the early Miocene (20 mya) (Montgelard *et al.* 2001). *Megapedetes* is larger than *Pedetes*, but otherwise already morphologically very similar (MacInnes 1957). Two extinct species of *Pedetes* are known from the fossil record; *P. gracilis* and *P. hagenstadi*, both from South Africa. The oldest fossil of *P. capensis* comes from the Pleistocene of Zimbabwe (De Graaff 1981). The pre-Miocene fossil history and origin of Pedetidae is not known, but it is likely that Pedetidae emerged in the early Tertiary (Bugge 1974a), either in Africa or Asia (Montgelard *et al.* 2001).

The affinities of pedetids are among the most obscure of all rodents and, therefore, subject to much debate and enquiry (Luckett

& Hartenberger 1985, Carleton & Musser 2005). There is some agreement that pedetids represent a very early, independent, lineage within Rodentia. In recognition of this, Ellerman (1940) erected the superfamily Pedetoidea within the suborder Sciuromorpha. Simpson (1945) also placed pedetids in Sciuromorpha, but in the superfamily Anomaluroidea. More recently, Bugge (1974a, b) erected the suborder Anomaluromorpha (to include both Pedetidae and Anomaluridae), and Landry (1999) erected the suborder Pedetomorpha (to include only Pedetidae).

The subordinal position is uncertain as pedetids share both hystricognath and sciurognath morphological characters (Jaeger 1988a, Huchon *et al.* 2000, Dieterlen 2005b). Recent molecular findings, however, strongly support inclusion of Pedetidae within Sciurognathi (Matthee & Robinson 1997a). This position is further supported by studies of foetal membranes and reproductive features (Luckett 1985, Otianga'a-Owiti *et al.* 1992). The emerging view is that the hystricognath characters of pedetids are due to parallelisms and, therefore, are not useful for phylogenetic inference (Luckett & Hartenberger 1985, Matthee & Robinson 1997a).

The familial relationships of pedetids are also uncertain. The two most critical questions are whether pedetids and anomalurids comprise a natural clade, and if so, where does this sister-group fit cladistically among the other major rodent associations (Carleton & Musser 2005). Although the microstructure of incisor enamel (Martin 1995, Huchon *et al.* 2000) and some palaeontological data (Jaeger 1988a, Landry 1999) do not support a close relationship between Pedetidae and Anomaluridae, some anatomical features (e.g. middle-ear structure [Lavocat & Parent 1985] carotid arterial pattern [Bugge 1974a, b, 1985]) and molecular data (Montgelard *et al.* 2001) strongly support the relationship between these two families (Montgelard *et al.* 2001) and, therefore, recognition of the suborder Anomaluromorpha (Bugge 1974a, b). Here Pedetidae and Anomaluridae are placed together in the suborder Anomaluromorpha (following Dieterlen 2005b; see also Carleton & Musser 2005).

Thomas M. Butynski

GENUS *Pedetes*
Springhares

Pedetes Illiger, 1811. Prodr. Syst. Mamm. Avium., p. 81.

The genus contains two species widely distributed in eastern and southern Africa. Characters of the genus are given in the family profile. Until recently, the genus was considered to be monotypic (e.g. Dieterlen 1993b), but recent research shows that the populations in East Africa are distinct and allopatric from those in southern Africa.

Based on phenotypic and morphological characters, *P. capensis* has been considered by some authorities to represent the only species in the genus (Allen & Loveridge 1927, Ellerman *et al.* 1953, Kingdon

1974, 1997, Misonne 1974, De Graaff 1981, Meester *et al.* 1986, Skinner & Smithers 1990, Dieterlen 1993b). In contrast, on the basis of skull characters and molecular data (see family profile), the East African Springhare is sufficiently distinct to warrant recognition as a separate species *Pedetes surdaster* (Thomas 1902b, Hollister 1918, 1919, Allen 1939, Coe 1967, Davies 1982, Dieterlen 2005b). The two species also differ in physiological characters (basal metabolic rate, thermal conductance and thermal neutral zone) and chromosome

number (see species profiles). While the morphology of skulls of *Pedetes* from the northern part of the range (S Kenya) and from the southern part of the range (Cape of Good Hope) differ considerably (Thomas 1902b, Hollister 1918), many of these differences are not apparent when intermediate populations are examined. For example, skulls from Tabora (W–C Tanzania; Allen & Loveridge 1927) and Dodoma (C Tanzania; Miller 1927) resemble more closely those of *P. capensis* from the Cape of Good Hope (>3000 km to south) than *P. surdaster* from L. Naivasha, Athi Plains and Sotik regions of Kenya (ca. 600 km to north), even though the East Africa and southern Africa populations are (apparently) separated by ca. 350 km.

The species are distinguished by size and shape of bones of the skull (especially the nasals, bullae and premaxillary processes), size and shape of the teeth, and shape of the braincase.

Thomas M. Butynski

Pedetes capensis SOUTHERN AFRICAN SPRINGHARE

Fr. Lièvre Sautteur du Sud; Ger. Südafrikanischer Springhase



Pedestes surdaster.

Pedetes capensis (Forster, 1778). K. Svenska Vet.-Akad. Handl. Stockholm (1) 39: 109. Cape of Good Hope, Western Cape Province, South Africa.

Taxonomy Originally described in the genus *Yerbua*. The taxonomy of this species is much debated. Here, following Dieterlen 2005b (see also family profile), *P. capensis* is the southern representative of the genus (see also *P. surdaster*). Synonyms: *albaniensis*, *angolae*, *cafer*, *damarensis*, *fouriei*, *orangiae*, *salinae*, *typicus*. Subspecies: none recognized here. Chromosome number: $2n = 38$ (Matthee & Robinson 1997b).

Description The only large, saltatorial-bipedal rodent in southern Africa. Pelage straight, long and soft. Dorsal pelage sandy to cinnamon-buff with scattered, long black-tipped guard hairs (ca. 35 mm) that decrease in density towards tail. Underfur of dorsal pelage thick, 25–33 mm long; hairs grey on basal half, glossy-brown on distal half. Ventral pelage white, yellowish, pale buff or pale orange; hairs 20–30 mm long, fine and sparse. Colour of pelage varies geographically (see below). Head broad, short and blunt. Face and lower half of ears sandy, yellowish-brown, cinnamon-buff, or rufous-brown. Vibrissae and eyelashes black. Nose, cheeks, forehead and crown cinnamon overlain with varying amounts of brownish-black. Ears long (70–80 mm); lower half yellowish-brown, upper half brownish-black. Inner surface of limbs, as for ventral pelage. Forelimbs short with five digits, each with long curved, sharp claws (ca. 19 mm); plantar pad near base of Digit 1 large, rounded and naked; plantar pad at base of Digit 5 smaller and oval. Hindlimbs very long and robust, with four digits (Digit 1 absent); Digit 3 elongated; each digit with large, triangular, hoof-like nail (see photographs in De Graaff 1981). Pelage on undersurface of hindfeet cream or pale grey. Tail long (ca. 110% of HB) and bushy, similar in colour to dorsal pelage with brownish-black to jet black on terminal 25–37% and black patch on underside at base; hairs 50–60 mm long, coarser and duller than on body, lacking grey on basal half. Skull stoutly constructed, thick; breadth of premaxillary processes (on side of nasal bones) ca. 3 mm (cf. ca. 1 mm in *P. surdaster*); auditory bullae large (ca. 19 mm long; cf. ca. 13 mm in *P. surdaster*), extending posteriorly behind the foramen magnum (Thomas 1902b) (Figure 98). Infant

and juvenile pelage softer and paler, underfur of dorsal pelage cream rather than grey, and pelage at base of tail and on undersurface of hindfeet blackish. Faecal pellets distinctive: rectangular but irregular with raised point at one end (ca. $8 \times 8 \times 15$ mm to ca. $10 \times 10 \times 21$ mm). Nipples: $2 + 0 = 4$ (not $1 + 0 = 2$ as given in Skinner & Smithers 1990); anterior pair just below axilla.

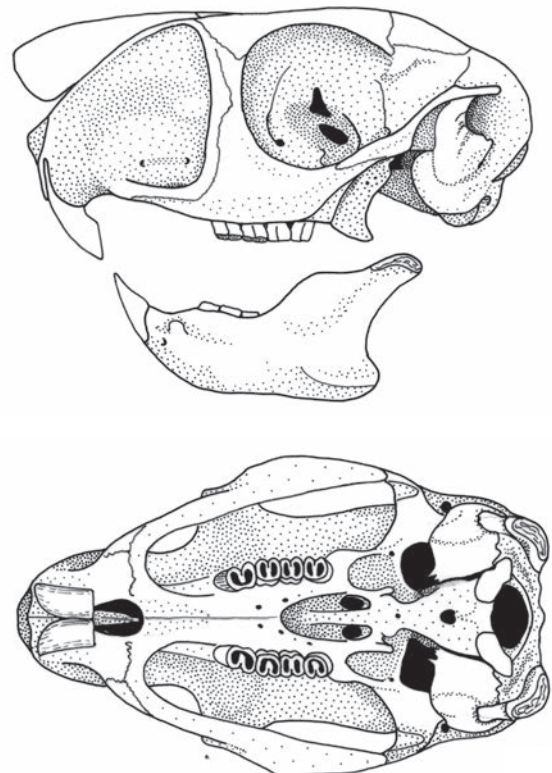


Figure 98. Skull and mandible of *Pedetes capensis* (RMCA 305).

Geographic Variation Nine subspecies have been described, but their validity is uncertain (Misonne 1974, Meester *et al.* 1986, Skinner & Smithers 1990, Matthee & Robinson 1997b, Dieterlen 2005b). There appears to be a slight north–south decline in body size from N Botswana (Smithers 1971) through SE Botswana (Butynski 1979a) to S South Africa (Lynch 1983, Anderson 1996) (see Measurements). A very dark, almost melanistic, individual (black pelage over most of body; ventral pelage whitish cream; hairs with silvery-brown tip) is in the collection of the AMNH.

Similar Species

P. surdaster. External morphology similar; breadth of premaxillary processes ca. 1 mm; length of bullae ca. 13 mm; reflective eye shine at night from only one eye at same time (as in *P. capensis*); chromosome number $2n = 40$; East Africa only.

Galago moholi. Much smaller (total length ca. 375 mm; body weight ca. 170 g); arboreal but may hop bipedally on ground; reflective eye shine at night from both eyes at same time; sympatric.

Distribution Endemic to Africa. Zambezan Woodland, South-West Arid (Kalahari Desert, Namib Desert and Karoo subzones), Highveld, South-West Cape and Coastal Forest Mosaic BZs. Present in Angola, Namibia, South Africa, SDR Congo, SW Zambia, Botswana, W and S Zimbabwe and S Mozambique (De Graaff 1981, Skinner & Smithers 1990). No records for Swaziland and Lesotho. Distribution highly fragmented due to lack of suitable habitat over much of geographic range. Range limits are from 08° S to 34° S and from 13° E to 35° E. Altitudinal range: ca. 10–2000 m (Lynch 1983, Kofron 1987, G. Kerley pers. comm.), with mean annual rainfall ca. 200–800 mm, either falling during one or two wet seasons per year (Smithers 1971, Butynski 1979b, Lynch 1983).

Habitat Arid and semi-arid, relatively flat and open areas with short grass, with little or no woody vegetation, and where the soil

is sandy, deep and compact, and suitable for digging burrows. Also found on agricultural lands. Generally absent from areas of tall grass, dense woodland and from mopane (*Colophospermum mopane* dominant) and miombo (*Brachystegia* spp. dominant) scrub and woodland where the soils are clay and poorly drained. Highest densities of *P. capensis* are attained on and near flood-plains of rivers, lakes and swamps, and on fossil lake beds (pans) where the vegetation is open, the grass is short and green, rhizomes and corms are present all year, and sandy soils are available. Such preferred habitats have some of the most succulent, protein-rich, mineral-rich grasses in southern Africa and, therefore, also receive more or less continuous heavy grazing from other herbivores, both wild and domestic. The flat, open terrain of these habitats is ideal for bipedal locomotion, for detection and avoidance of predators, and may also facilitate social behaviours such as finding mates (Smithers 1971, Butynski & Mattingly 1979, Skinner & Smithers 1990, Anderson 1996, Peinke & Brown 2006).

Abundance Common and widespread over much of southern Africa. In seven habitat types near Kimberley, South Africa, densities range from 3/km² in 'Kalahari thorn/sandveld' to 19/km² in 'panveld' (Anderson 1996). At 15 sites in Eastern Cape Province, South Africa, densities range from 1/km² to 99/km² (Peinke & Brown 2006). Other known densities include ca. 40/km² in Sandveld Nature Reserve, South Africa (Watson 1992), ca. 100/km² in S. A. Lombard Nature Reserve, South Africa, and ca. 370/km² on pan-associated habitats in S. A. Lombard Nature Reserve (Van der Walt 1989).

Adaptations Nocturnal and terrestrial. *Pedetes capensis* combines morphological features for living in an open, nocturnal, terrestrial environment (where a high level of mobility is required) with morphological features for excavation of burrows and life underground. External features associated with terrestrial activities include elongated and powerful hindlegs, long tail and large ears and eyes. Features associated with subterranean life include strong, long claws on forefeet for digging, valvular nostrils that can be closed, and ears with well-developed antitragus capable of folding back and lengthwise along the mid-line preventing entry of soil. The long whiskers, long sensory hairs on dorsal pelage, long eyelashes and patch of long sensory bristles just above the eye probably assist in orientation in the burrow (Skinner & Smithers 1990). Sharp, chisel-like teeth are capable of cutting through roots and other soft objects during excavation.

Although *P. capensis* hops bipedally when moving to and from foraging sites, it moves on all four legs when foraging, putting the weight on the short forelegs and then moving the hindlegs forward in a hare-like manner. When eating, weight is placed on the hindfeet, perineum and tail, leaving the forefeet free to manipulate food. To avoid predators, *P. capensis* makes bipedal 'ricochet' leaps of up to 2 m in length as it moves towards its burrow. Although the forefeet are well-adapted for digging, they are also dexterous, allowing for the extraction of plant parts from both above and below ground, and for manipulation of the food so that the most nutritious portions can be selected (e.g. green seeds and subterranean storage organs). When sleeping, the body is bent forward until the forelimbs are between the thighs, and the top of head is resting on the ground between the feet.

Vision, hearing and sense of smell are acute. The large eyes allow running and avoidance of objects on moonless nights, and the frequent movement of the ears and regular sniffing of the air are



Pedetes capensis

vital to intra-specific communication and social interactions with conspecifics, as well as the detection of predators – both above and below ground. Underground predators include snakes and mongooses (Butynski & Mattingly 1979, Anderson 1996).

Although primarily nocturnal, there are a few records of activity during daylight hours (Shortridge 1934, Anderson 1996). Generally, Southern African Springhares do not emerge from the burrow until ca. 30 minutes after sunset, and do not return to the burrow later than 30 minutes before sunrise. In Kalahari Desert, most activity above ground is during middle of night (i.e. 4–8 hours after sunset; Butynski 1984). Near Kimberley, numbers above ground increase up to ca. 24:00h and then decline steadily until ca. one hour before sunrise (Anderson 1996). In Eastern Cape Province, activity is fairly constant through the night with a decline starting two hours before sunrise (Brown & Peinke 2007).

The number of *P. capensis* on Kalahari pans declines as air temperature declines, with few above ground at temperatures below +1 °C. They remain active during light rains but move into burrows when rains are moderate to heavy (Butynski 1984). Near Kimberley, low air temperatures also affect foraging activity. In winter, they forage closer to their burrows (<120 m) than in summer (150–400 m). As in Botswana, *P. capensis* remain active during light rain, but move into burrows when rain is moderate to heavy. *Pedetes capensis* tend to stay close to their burrows under windy conditions (Anderson 1996). In Eastern Cape Province, temperature and wind do not seem to affect activity, although very strong wind does reduce activity (Brown & Peinke 2007). These behaviours probably help conserve energy and avoid thermoregulatory stress.

In the Kalahari Desert, activity on pans is greatly influenced by moonlight. The distance of individuals away from the burrows and onto the pans is inversely correlated with intensity of moonlight. When there is no moonlight, mean distance onto pans is ca. 58 m, but only 4 m when there is a full moon. Intensity of moonlight, however, does not affect the numbers of individuals on pans (Butynski 1984). Similarly, near Kimberley, they feed up to 400 m from burrows when there is no moonlight and seldom >40 m from burrows when the moon is full (Anderson 1996). In Eastern Cape Province, they are less active on full moon nights than on new moon nights, and activity begins to decrease earlier on full moon nights. As the moon rises in the sky, and as shadows produced by trees and shrubs become reduced in size, individuals move closer to trees and shrubs to remain within shadows. This 'shadow-seeking' behaviour is probably an adaptation for predator avoidance (Butynski 1984).

Limiting above-ground activity until dark (when air temperature is lowest and humidity highest), and selectively feeding on moist plant parts, are behavioural adaptations that considerably reduce water loss. Physiologically, Southern African Springhares are fairly well adapted to an arid environment. They do not drink water even when available; meeting moisture requirements from rain and dew on vegetation, and from food as preformed and metabolic water (Butynski & Mattingly 1979, Anderson 1996, Peinke & Brown 1999). They are able to survive seven days of water deprivation and tolerate a 30% loss of body weight – twice the level that is fatal in most other mammals. The ability to be highly selective, and to feed on rhizomes, tubers and leaf bases, ensures a plentiful and relatively stable food (and water) supply throughout the year (during most years), even in a highly seasonal environment.

Peinke & Brown (2003) found that *P. capensis* (unlike *P. surdaster*; Müller *et al.* 1979) has a higher than expected basal metabolic rate and a lower than expected minimum thermal conductance. This, together with a relatively low, lower critical temperature and broad thermal neutral zone, indicates physiological adaptations suitable for the low (below freezing) night-time temperatures that occur during the southern African winter. Like other desert-adapted species, *P. capensis* is a good osmoregulator and is similar to some true desert species in its ability to tolerate dehydration and maintain blood plasma volume. It also produces relatively dry faeces but, surprisingly, does not produce highly concentrated urine (Peinke & Brown 1999).

Burrows provide a relatively stable, moderate temperature and humidity in which to live and raise young, and some protection against predators. Burrows are typically 70–122 cm deep, 36–46 m long, and have up to nine entrance holes (Butynski & Mattingly 1979). Burrows lack food, nesting materials and chambers. The porous soil in which burrows are excavated provides good insulation and a micro-environment of relatively moderate, stable temperature, and air saturated with water vapour. In the Eastern Cape Province, mean monthly temperature at more than 1.5 m inside of one burrow located in open grassland ranged from 12 to 22 °C through the year. In this region, mean monthly maximum air temperatures outside are +19 °C to +27 °C, and mean minimum air temperatures are +5 °C to +16 °C; absolute air temperatures range from –5 °C to +45 °C (Peinke & Brown 2003, 2006).

Southern African Springhares often exert a large influence on the vegetation structure and plant diversity around burrows and on feeding sites through exposure of fresh soil, preferential utilization of plant species and deposition of plant material and dung. The effect of digging up rhizomes, corms and tubers is that patches of soil are often totally worked-over and temporarily denuded of vegetation. These denuded patches are often >3 m in diameter (Peinke & Brown 2006), but can be in excess of 240 m² (Anderson 1996, T. Butynski pers. obs.). This disturbance encourages growth of several species of grass that are a preferred food, and which make up the bulk of the diet. These and other effects of burrow excavation and feeding are documented in detail for sites in Botswana (Butynski & Mattingly 1979) and South Africa (Anderson 1996, Peinke & Brown 2006).

They are generally silent, but occasionally give 'grunts' and soft 'growls'. 'Screams' (also termed 'squeals' or 'bleats') are emitted when distressed or frightened, such as when captured by a predator, and 'grunts' and 'growls' are given when annoyed or uncomfortable. 'Sighs' are given but their function is not known (Anderson 1996, T. Butynski pers. obs.).

Many of the specialized morphological, physiological and behavioural features of *P. capensis* are best explained as adaptations to a semi-arid, open environment, and for avoidance of predators. Nutritious, short grasses occur during the dry months on relatively moist and fertile flood-plains and pans. As a medium-sized, bipedal mammal, *P. capensis* is small enough to be a selective forager, yet mobile enough to avoid predators and to travel several hundred metres from the burrow to the foraging sites. The major 'trade-off' is that a medium-sized herbivore attracts a large array of predators, both small and large.

Foraging and Food Herbivorous, feeding primarily on grasses. The burrow represents the 'core area' for foraging activities, with

foraging routes emanating out from the burrow. Individuals on the Kalahari pans are frequently 25–250 m, and occasionally as far as 400 m, from their burrows (Smithers 1971, Butynski 1984). Near Kimberley, the core area is within ca. 40 m of the burrows, and maximum distance is ca. 400 m (Anderson 1996).

Southern African Springhares are highly selective feeders, feeding on the most nutritious parts of plants. Diet in the Kalahari Desert is comprised almost entirely of grass parts – roots, corms, green stems, green leaves and green seeds (Butynski 1984). Here, green seeds of grasses, especially of *Urochloa* spp., comprise much of the diet during the wet season (Butynski & Mattingly 1997). Small invertebrates are ingested incidentally (Butynski 1982a). Lumps of soil frequently found in stomachs (T. Butynski pers. obs.).

Near Kimberley, Anderson (1996) found that the diet comprises at least 20 species of plants (eight grasses, five dwarf shrubs, one geophyte, five trees and shrubs, one herb). Together, *Cynodon dactylon* (41%), *Schmidtia pappophoroides* (17%), *Eragrostis lehmanniana* (8%) and *Gladiolus permealibis* (8%) comprise ca. 74% of the diet. Plant parts eaten include rhizomes, stolons, green culms and green leaves, but, unlike in the Kalahari Desert, not seeds. In Eastern Cape Province, the diet is predominantly rhizomes of *C. dactylon*, tubers of yellow nut sedge *Cyperus esculentus* and leaf bases of *Eragrostis curvula* (Peinke & Brown 2006). At all sites, the diet includes the roots, stems and leaves of shrubs and small trees, but these items are a minor part of the diet (Butynski 1982b, 1984, Anderson 1996, Peinke & Brown 2006).

Underground storage organs are extracted from the ground with claws of forefeet and nipped off with the teeth. Green grass seeds are readily removed from the stem by pulling, with one hand, the stem through diastema between incisors and premolars. Where abundant, rhizomes of *C. dactylon* are the most important food. *Pedetes capensis* often reach high densities when *C. dactylon* is abundant (Smithers 1971, Anderson 1996, Peinke & Brown 2006, T. Butynski pers. obs.).

Data on sex and age differences in the quantity and quality of foods eaten by *P. capensis*, on seasonal changes in their physical condition, and on seasonal changes in food availability and quality, are presented in Butynski (1979b, 1982a, b) and Anderson (1996).

Social and Reproductive Behaviour Solitary and polygamous. Individuals are solitary when in the burrow except when a mother has her single young (Butynski & Mattingly 1979, Anderson 1996); on one occasion, an adult ♂ shared a burrow with an adult ♀ but remained 2–3 m apart (Peinke & Brown 2005). Above ground, they may form temporary groups (when densities are suitably high). In Botswana, 36% of individuals on pans and 35% off pans occur in groups ($n = 2545$). Group size ranges from two to six and increases with time after sunset. Of the 2545 individuals encountered, 62% were alone, 25% were in pairs and 9% were in groups of three. Of five age/sex categories considered, only adult ♂♂ are represented in groups more than expected by chance. Forming groups probably facilitates predator detection and avoidance, as well as foraging, learning and reproduction (Butynski 1984).

Mating is preceded by prolonged chasing of the ♀, usually by two adult ♂♂, for up to 45 minutes. Copulation lasts 3–5 seconds and is usually undertaken by fastest ♂ (Anderson 1996).

Intra-specific aggression, defence of sites, or other acts typical of territorial species have not been observed. Southern African Springhares have widely overlapping home-ranges and often join feeding groups

without any overt aggression (Anderson 1996, Peinke & Brown 2005, T. Butynski pers. obs.). In Eastern Cape Province, 70% of burrows were, over the course of one year, used by a single animal, suggesting that burrows are ‘defended’ against conspecifics. Scent marks from the perineal glands, and urine (which is frequently deposited at the burrow entrance), may indicate to conspecifics that the burrow is occupied; under these conditions, occupancy by another individual will seldom occur until the scent marks of the previous inhabitant are more than one month old. Changing burrows frequently, and the non-occupancy of a burrow, may help to reduce the numbers of potential predators attracted by the odour of a frequently used burrow, and to reduce the number of parasites and parasite eggs that accumulate in the burrows (Peinke & Brown 2005).

Near Kimberley, minimum home-range size over periods of 2–6 months varied from 0.3 to 2.8 ha (mean 1.4 ha, $n = 4$) (Anderson 1996). In Eastern Cape, the minimum area covered by the burrows used by seven *P. capensis* radio-tracked for 1–12 months ranged from 0.4 to 28.5 ha (mean 10.6 ha) (Peinke & Brown 2005). Distances separating burrows and preferred feeding sites, and the size and quality of burrowing and feeding sites, play a major role in determining the size and shape of the home-range (Butynski 1984, Anderson 1996, D. Peinke pers. comm.).

There is no evidence that ♂♂ assist in raising young.

Reproduction and Population Structure Monotocous with aseasonal reproduction in most localities. Southern African Springhares breed throughout the year in Botswana (Butynski 1979b, Butynski & Hanks 1979) and in Eastern Cape Province, South Africa (Peinke & Bernard 2005), and show slight seasonality at Kimberley (Anderson 1996). In all locations, more-or-less continuous reproduction occurs despite living in strongly seasonal, sometimes severe, environments where there are distinct wet/hot and dry/cold seasons and considerable variations both in daylength and food supply. However, during prolonged droughts when there is extreme shortage of food, reproductive activity is greatly restricted or ceases completely (Kofron 1987).

Median length of gestation is assumed to be the same as for *P. surdaster*, i.e. 78 days (range: 72–82 days, $n = 3$ in captivity) (Rosenthal & Meritt 1973, Velte 1978; see also Kofron 1987). Litter-size: one. Only three cases of twinning have been recorded (0.8%, $n = 380$ pregnancies; Shortridge 1934, Van der Horst 1935, Butynski 1979b, Lynch 1983, Anderson 1996, Peinke & Bernard 2005, R. H. N. Smithers pers. comm.). Of 404 fetuses, 200 recorded in the right uterine horn and 204 in left uterine horn (Smithers 1971, Butynski 1979b, van der Merwe *et al.* 1980, Kofron 1987, Gewers 1993, Anderson 1996, Peinke & Bernard 2005).

Mean birth-weight is assumed to be the same as for *P. surdaster* (i.e. 273 g, range 238–319 g, $n = 7$ in captivity; Hediger 1950, Coe 1967, Rosenthal & Meritt 1973, Velte 1978). At birth, young covered with dense hair, except on throat, ventrum, genitalia, insides of legs and soles of feet, which are nearly naked (Butynski 1982b). Full covering of hair at ca. Week 3 (F. F. Velte pers. comm.). Precocious; able to move, dig and face-wash within a few hours of birth. Bipedal hopping Day 4. Ears erect within few days of birth. Eyes may be open at birth, but sometimes not fully open until Day 14 (Butynski 1980, Peinke & Bernard 2005). First emergence from burrow and weaning occurs at ca. Week 7 (Botswana; Butynski 1979b, 1982b) or ca. Week

5 (Kimberley; Anderson 1996). Newborns weigh ca. 10% as much as mothers, with ears and hindfeet 56% adult length. Predicted weight of 'newborn litter' for a mammal the weight of adult ♀ (ca. 3.0 kg) is 426 g, or 14% the mother's weight. Although the weight of the newborn *P. capensis* is large (ca. 300 g), it is ca. 30% less than expected in relation to the weight of the mother (Butynski 1980).

Sexual maturity in ♂♂ attained when 2.3 kg (Botswana; n = 286; Butynski & Hanks 1979), 2.5 kg (Kimberley; n = 126; Anderson 1996) and 2.8 kg (Eastern Cape Province; n = 59; Peinke & Bernard 2005). Some ♂♂ spermatogenically active at ca. eight months but most not until ca. 12 months (Kofron 1987, Anderson 1996). Adult males produce active sperm throughout year. Females reach sexual maturity and conceive for first time when 2.7–3.0 kg (Butynski 1979b, Anderson 1996, Peinke & Bernard 2005). Youngest pregnant ♀♀ are 13 months old, but some do not conceive until 24 months (Anderson 1996). Sexual maturity is attained at a much older age compared to other rodents of similar size (Peinke & Bernard 2005).

Females are polyoestrous with pregnancies separated by non-pregnant period. Reproductive parameters vary according to locality. In Botswana, adult ♀♀ have a mean non-pregnant period of ca. 24 days, a mean interval between conceptions of ca. 101 days, and a mean of ca. 3.6 pregnancies/year (Butynski 1979b). Near Kimberley, adult ♀♀ have a mean non-pregnant period of ca. 39 days, a mean interval between conceptions of ca. 116 days, and a mean of ca. 3.1 pregnancies/year (Anderson 1996); in Eastern Cape Province, the figures are 49 days, 126 days and 2.9 pregnancies/year, respectively (Peinke & Bernard 2005). The reproductive rate is unusually low for a rodent, even for a rather large one. Mean length of lactation in Botswana is ca. 50 days, with some ♀♀ lactating for >60 days. Lactation ceases when young are ca. 1.3 kg, ca. seven weeks of age and beginning to forage above ground. Lactation lasts for longer than predicted for a mammal of this size (Eisenberg 1981). In Botswana, no ♀ with a foetus heavier than 59 g was lactating (n = 34) (Butynski 1979b). Likewise, in Eastern Cape Province, no ♀ with a foetus heavier than 54 g was lactating (n = 10) (Peinke & Bernard 2005). Near Kimberley, only two of 16 ♀♀ (12%) with a foetus heavier than 100 g were lactating (Anderson 1996). A foetus reaches 59 g and 100 g at ca. 57 days and ca. 62 days post-conception, respectively (Butynski 1980). Hence most pregnant ♀♀ stop lactating before the final trimester of pregnancy, but a few lactate during at least 80% of the pregnancy.

Male:female ratio at parity (60 : 61) among foetal *P. capensis* large enough for sex determination (Butynski 1979b, Anderson 1996). Male:female ratios at parity for juveniles + adults in all three of the better-studied populations (Botswana, 321 : 312 [Smithers 1971, Butynski 1979b]; near Kimberley, 187 : 180 [Anderson 1996]; Eastern Cape, 59 : 61 [Peinke & Bernard 2005]). However, in SE Zimbabwe, Kofron (1987) obtained 51 ♂♂ and 72 ♀♀ during the third year of a three-year drought.

Some juvenile:adult ratios are as follows: 1 : 2.6 (Botswana; Butynski 1979b), 1 : 3.0 (Kimberley; Anderson 1996), 1 : 3.6 (Eastern Cape Province; Peinke & Bernard 2005) and 1 : 2.4 (SE Zimbabwe; Kofron 1987). No longevity data available for *P. capensis* (maximum longevity for *P. surdaster* in captivity is 14 years [Jones 1982]). Peinke & Bernard (2005) suggest that the life-span of *P. capensis* in the wild is typically 6–12 years, but T. Butynski (pers. obs.) believes that the mean life-span in the wild is much shorter than this and is probably closer to 2–3 years.

Predators, Parasites and Diseases At least 23 known or potential species of predators prey on *Pedetes capensis* in the Kalahari Desert (Butynski & Mattingly 1979), and Anderson (1996) lists 31 predators in the Kimberley area. In a combined sample of 602 stomachs of Black-backed Jackals *Canis mesomelas* from Botswana, Zimbabwe (Skinner & Smithers 1990) and South Africa (Bothma 1966, Anderson 1996), 48 (8%) contained remains of *P. capensis*. Anderson (1996) observed 11 attempts by Black-backed Jackals to catch *P. capensis*; only two (18%) were successful. Given their size, abundance and sympatric distribution over most or all of their geographic range, the Black-backed Jackal, Cape Fox *Vulpes chama* and Caracal *Felis caracal* are likely to be the most important mammalian predators. In the Kalahari Gemsbok N. P., South Africa/Botswana, *P. capensis* constitute a large part of the diet of Cheetahs *Acinonyx jubatus* (W. Labuscagne pers. comm. in Smithers 1971). Similarly, Skinner & Smithers (1990) record that Southern African Springhares form a major part of the diet of Cheetahs in the drier areas of Botswana.

Many ectoparasites have been recorded. Mites: *Radfordiella capensis*, *Radfordiella meridionalis*, *Androlaelaps marshalli* and *Histioglyphus santos-diasi*. Lice: *Eulinognathus denticulatus*. Pulicid fleas: *Echidnophaga bradyi*, *Echidnophaga gallinacea*, *Ctenocephalides conatus*, *Ctenocephalides felis*, *Synosternus caffer*, *Parodontis riggenbachii* and *Xenopsylla cryptonella*. Ticks: *Amblyomma hebraeum*, *Haemaphysalis leachii*, *Hyalomma marginatum*, *Rhipicephalus appendiculatus*, *Rhipicephalus sanguineus*, *Rhipicephalus simus*, *Rhipicephalus tricuspis* and *Rhipicephalus capensis*. Endoparasites include the following nematodes: *Dermatophys veligara*, *Hyracofilaria hyracis*, *Oesophagostomum susannae*, *Physaloptera capensis* and *Trichuris pedetei* (De Graaff 1981, Butynski 1982a, Anderson 1996, Anderson & Kok 2003). There is no evidence to suggest that parasites or diseases play a significant role in the regulation of population numbers (Butynski 1982a). Because of their parasites, *P. capensis* may play a role in the transmission to man and domestic stock of bubonic plague, rickettsiosis, babesiosis, theileriosis and toxicosis paralysis (De Graaff 1981).

Conservation IUCN Category: Least Concern.

Although widespread and even abundant at many localities, populations of *P. capensis* are in rapid decline over much of their geographic range (Lynch 1983). While most of the decline is related to habitat degradation as a result of overgrazing by domestic stock, and to habitat loss as a result of conversion of natural habitats to agriculture, over-hunting is also partly responsible for the decline in some areas (Butynski 1973, Lynch 1983, C. Anderson pers. comm.).

Pedetes capensis are a major source of bushmeat and an important pest of crops (Smithers 1971, De Graaff 1981, Anderson 1996). In Botswana, they are probably the most important wild animal in the diet of local humans. A single band of bushmen may kill more than 200 annually. It is estimated that the people of Botswana kill 2.5 million individuals each year. This represents ca. 2.2 million kg of meat each year, the equivalent of 20,000 cattle (Butynski 1973). Bushmen make the skin into garments, use the long sinew of the tail as thread and smoke dried faecal pellets. Butynski (1973) estimated that 10–15% of maize, sorghum, beans and groundnuts grown in Botswana are destroyed by *P. capensis*. Elsewhere they sometimes cause extensive damage to wheat, oats, maize and other crops (Shortridge 1934).

Pedetes capensis is one of Africa's most biologically unique and economically important mammals. In addition, it is likely to be a

keystone species in some ecosystems. As such, the long-term survival of this species needs to be ensured. As one of Africa's most studied, widespread, locally abundant and easily located and observed mammals, there is considerable opportunity for additional research. Applied research might focus on obtaining more information on the economic importance of this species, and on what the sustainable harvest is under various natural and man-made conditions. Interesting theoretical questions involve behaviour and how it is affected by environmental conditions and population density. Comparative ecological, behavioural and physiological studies with *P. surdaster* (which lives near the Equator in a much less seasonal environment) would be particularly enlightening.

Measurements

Pedetes capensis

HB (♂ ♂): 402 (?–?) mm, n = 12
 HB (♀ ♀): 401 (?–?) mm, n = 14
 T (♂ ♂): 448 (417–485) mm, n = 12
 T (♀ ♀): 429 (410–443) mm, n = 12
 HF (♂ ♂): 161 (150–170) mm, n = 14
 HF (♀ ♀): 161 (153–182) mm, n = 14
 E (♂ ♂): 75 (70–80), n = 14
 E (♀ ♀): 75 (69–79), n = 14
 WT (♂ ♂): 3.26 (?–?) kg, n = 13
 WT (♀ ♀): 3.26 (?–?) kg, n = 13
 GLS: 88.6 (84.9–91.9) mm, n = 14*
 GWS: 54.3 (50.3–60.4) mm, n = 14*
 P⁴–M³: 16 (14.2–17.8) mm, n = 14*
 Western Okavango, NW Botswana (Smithers 1971)
 *Males and females combined; South Africa and Namibia (BMNH)

HB (♂ ♂): 390 (?–?) mm, n = 185
 HB (♀ ♀): 396 (?–?) mm, n = 180
 T (♂ ♂): 431 (423–492) mm, n = 181
 T (♀ ♀): 425 (418–484) mm, n = 176
 HF (♂ ♂): 156 (153–167) mm, n = 186
 HF (♀ ♀): 155 (153–168) mm, n = 180
 E (♂ ♂): 72 (72–85) mm, n = 186
 E (♀ ♀): 72 (70–77) mm, n = 182
 WT (♂ ♂): 2.98 (2.51–4.01) kg, n = 184
 WT (♀ ♀): 3.07 (2.62–3.71) kg, n = 182
 SE Botswana (Butynski 1979a)

HB (♂ ♂): 380 (364–385) mm, n = 101
 HB (♀ ♀): 379 (356–397) mm, n = 97
 T (♂ ♂): 412 (370–465) mm, n = 91
 T (♀ ♀): 406 (354–463) mm, n = 86
 HF (♂ ♂): 150 (136–158) mm, n = 101
 HF (♀ ♀): 148 (138–157) mm, n = 86
 E (♂ ♂): 76 (69–82) mm, n = 101
 E (♀ ♀): 75 (67–81) mm, n = 97
 WT (♂ ♂): 2.81 (2.05–3.50) kg, n = 91
 WT (♀ ♀): 2.86 (2.10–3.65) kg, n = 86
 Kimberley, Northern Cape Province, South Africa (Anderson 1996)

Key References Anderson 1996; Butynski 1979a, b, 1982a, b, 1984; Butynski & Mattingly 1979; Peinke & Bernard 2005; Peinke & Brown 2005.

Thomas M. Butynski

Pedetes surdaster EAST AFRICAN SPRINGHARE

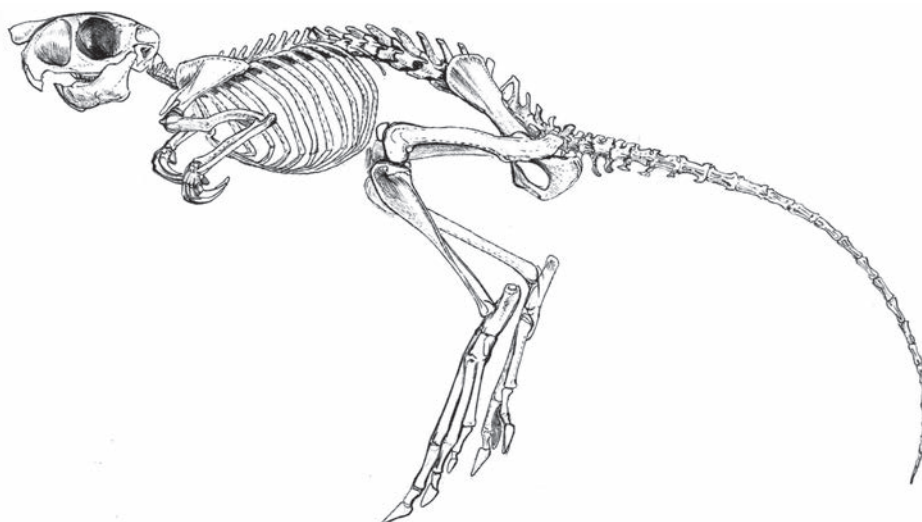
Fr. Lièvre Sautteur de l'Est; Ger. Ostafrikanischer Springhare

Pedetes surdaster Thomas, 1902. Ann. Mag. Nat. Hist., ser. 7, 9: 440. Mordat, Naivasha Prov., mile 365 of Uganda Railway, Kenya. 2000 m.

Taxonomy See *Pedetes capensis* profile. Based on phenotypic and morphological differences, it is debatable whether *surdaster* should be designated as a full species or as a subspecies of *P. capensis* (Dieterlen 1993b, 2005a). Standard body measurements for *surdaster* fall within the range for six populations of *capensis* (Hollister 1919, see *P. capensis* profile). Thomas (1902b), Hollister (1919), Miller (1927) and Davies (1982) note that, relative to *P. capensis*, *P. surdaster* has smaller nasal bones and smaller auditory bullae, narrower premaxillary processes, a less deeply concave anterior palate, narrower and shallower incisors and molars, and a more vaulted braincase. Thomas (1902b), Hollister (1918, 1919), Ellerman (1940), Coe (1969), De Graaff (1981), Davies (1982) and Dieterlen (2005a) treat *surdaster* as a full species. Recent molecular data also support this position (Matthee & Robinson 1997b). Among the molecular differences is a difference in chromosome number. Some significant physiological differences also exist (Müller *et al.* 1979, Peinke & Brown 2003). Synonyms: *currax*, *dentatus*, *larvalis*, *taborae*. Subspecies: none recognized here (but see Geographic Variation). Chromosome number: 2n = 40 (Matthee & Robinson 1997b).

Description The only large, saltatorial bipedal rodent in East Africa (morphologically similar to *P. capensis* of southern Africa; see *P. capensis*). Pelage straight, long and soft. Dorsal pelage sandy, yellowish-brown, or cinnamon-buff. Guard hairs sparse, black. Underfur of dorsal pelage grey over proximal half and glossy brown over distal half. Ventral pelage off-white to light yellow, without underfur. Head relatively large. Eyes large. Ears long, narrow, upright. Forelimbs very short with five digits, each with long, curved, sharp claw. Hindlimbs very long and robust, with four digits (Digit 1 absent). Tail long (ca. 106% of HB) and bushy. Infants and juveniles similar in colour to adults. Skull stoutly constructed, thick. Skull: breadth of premaxillary process (on side of nasal bones) ca. 1 mm (cf. ca. 3 mm in *P. capensis*); auditory bullae large (ca. 13 mm long; cf. 19 mm in *P. capensis*) not extending posteriorly behind foramen magnum (Thomas 1902b). Sexes alike in colour and body size (♂ ♂ may, on average, be slightly larger). Males may have linear body measurements 3–5% longer than ♀ ♀, but sample size small. Faecal pellets distinctive (see *P. capensis*). Nipples: 2 + 0 = 4.

Pedetes surdaster.



Geographic Variation Five subspecies have been described but there is no consensus about how many of these, if any, should be recognized (Misonne 1974, Meester *et al.* 1986, Skinner & Smithers 1990, Matthee & Robinson 1997b, Dieterlen 2005b). Assessing validity of the named subspecies is hampered by lack of knowledge of the geographic limits of each, as well as by the apparent absence of major barriers to gene flow; close examination might reveal that such barriers are provided by large areas of hard-packed ground (e.g. lava flows, black cotton soil) or unsuitable vegetation (e.g. forest). Differences may be clinal rather than absolute. No subspecies are recognized here.

Similar Species

P. capensis. External colouration and morphology similar; breadth of premaxillary processes ca. 3 mm; length of auditory bullae ca. 19 mm; reflective eye shine at night from only one eye at same time (as *P. capensis*); chromosome number: $2n = 38$; southern Africa only.

Galago senegalensis and *Otolemur garnettii*. Much smaller (<300 g and <1200 g, respectively); usually arboreal but sometimes hop bipedally on the ground; reflective eye shine at night from both eyes at same time; sympatric.

Distribution Endemic to Africa. Sudan Savanna, Somalia–Masai Bushland, Coastal Forest Mosaic and Zambezian Woodland BZs. Recorded from SC Kenya and Tanzania. Reports from C Kenya (Laikipia, Samburu and Meru Districts) and coastal Kenya need verification. No confirmed records north of Nakuru, Gilgil or Thika in SC Kenya, or south of L. Rukwa in SW Tanzania. Distribution sometimes extremely patchy as suitable habitats often widely scattered.

Habitat Semi-arid, relatively open and flat areas with short, nutrient-rich grasses, with little or no woody cover, and where soils are well-drained, compact, deep and sandy, and suitable for digging burrows. Also on agricultural lands where suitable burrowing sites are present. Preferred habitats often present along the margins of rivers and lakes, in alluvial valleys, sandy plateaux, near human dwellings, gardens, bomas and boreholes. These sites are also highly

attractive to many other herbivores, tend to be heavily grazed and are relatively nutrient-rich due to the heavy deposit of manure and urine (Kingdon 1974, Stelfox 1986, Augustine *et al.* 1995, T. Butynski pers. obs.). Generally absent from areas of tall grass, dense bush, dense woodland and forest, and from most miombo (*Brachystegia* spp. dominant) woodlands where the soils are lateritic ('hard-pan') and poorly drained. However, may occur within miombo woodlands where sandy soils are present (e.g. along river courses). The broad features of the habitats of *P. surdaster* are similar to those of *P. capensis* in southern Africa (Smithers 1971, Butynski & Mattingly 1979, Butynski 1984, Anderson 1996, Peinke & Brown, 2006). Altitudinal range ca. 100–2000 m (Thomas 1902b, Kasigwa & Howell 1975, T. Butynski & Y. de Jong pers. obs.), but mostly above 1000 m. Mean annual rainfall ca. 400–1200 mm, but mostly 600–1100 mm.

On the Athi-Kapiti Plains, Kenya, *P. surdaster* prefers areas near sources of perennial water that are subject to heavy grazing, both by



Pedetes surdaster

native ungulate species (primarily Wildebeest *Connochaetes taurinus* and Thomson's Gazelles *Eudorcas thomsonii*) and by cattle. Star (or couch) grass *Cynodon dactylon* covers ca. 67% of the ground in such areas (Augustine *et al.* 1995). Stelfox (1986) found that the high input of nitrogen and phosphorus from ungulate faeces around cattle bomas and boreholes leads to dramatically higher levels of crude protein and lower fibre levels in the vegetation in comparison to more distant sites. *Cynodon dactylon* is able to out-compete other grass species in these highly disturbed but fertile sites.

Abundance Few data available. On Athi-Kapiti Plains numbers seen during surveys ranged from 1/km² in *Themeda-Balanites/Acacia drepanolobium* short woodland to 24/km² in *Cynodon-Balanites* grassland (n = 361 animals; Augustine *et al.* 1995). Absent from very large areas within geographic range and, where present, density often <1/km² (T. Butynski & Y. de Jong pers. obs.).

Adaptations Nocturnal and terrestrial. Many of the adaptations of *P. capensis* probably also apply to *P. surdaster* (see *P. capensis* profile). Kingdon (1974) discusses the several peculiar anatomical adaptations related to bipedal hopping and how this mode of locomotion has benefits for moving over flat, open ground, but is ill-adapted to circumventing obstacles, as is required when running over broken ground, or ground with anything more than short, sparse vegetation.

Augustine *et al.* (1995) did not find any difference in the number of animals seen between 22:00 and 24:00h and between 01:00 and 03:00h. There are only four records for daylight hours: one at daybreak (06:30h) (O'Brien 1982), one at 10:20–11:30h (Kasigwa & Howell 1975), one on a 'dark day' (Hollister 1919) and the fourth in 'broad daylight' (S. Thomsett pers. comm.).

Individuals probably always construct their own burrows. Burrows are generally less than 1 m deep. The entrances are often temporarily sealed with sand from the inside. Each burrow system usually harbours but one animal; at most two adults and one young (Kingdon 1974). When sleeping, *P. surdaster* assumes the same pose as for *P. capensis* (see above); contact of the top of the head with the ground may allow detection of vibrations through the ground that are created by movements of conspecifics and predators (Kingdon 1974, as *P. capensis*).

Pedetes surdaster are generally quiet, but emit 'bleats' and 'grunts' (Kingdon 1974, as *P. capensis*). Infants give 'squeaks' and high-pitched 'bleats' (Coe 1967).

Compared to *P. capensis* (Peinke & Brown 2003), *P. surdaster* has a low basal metabolic rate and high rate of thermal conductance (n = 2; Müller *et al.* 1979). This combination reduces the endogenous heat load and facilitates heat loss – adaptations typical of mammals that are seldom, if ever, exposed to low temperatures (e.g. tropical mammals and mammals that spend all or part of their time underground).

Where abundant, East African Springhares have a large influence on vegetation structure and plant diversity around their burrows and on feeding sites. This influence is a result of the exposure of fresh soil, preferential utilization of plant species, and deposition of plant material and dung. Individuals often totally dig over extensive areas as they forage for plant parts, mixing dung and seeds into the soil (T. Butynski pers. obs.).

Many of the specialized morphological, physiological and behavioural features of *P. surdaster* are best explained as adaptations to a semi-arid, open environment, and avoidance of predators. Nutritious,

short grasses occur during the dry months on comparatively moist and fertile (often seasonally flooded) flood-plains, lake shores and valley bottoms. Smaller mammals could harvest these grasses, but they would be extremely susceptible to predators as these habitats lack vegetative cover and the soils are often too hard and/or too wet for burrowing. As a medium-sized, bipedal mammal, *P. surdaster* is small enough to be a selective forager, yet mobile enough to avoid predators and to travel several hundred metres from the burrow to the foraging sites. The major 'trade-off' here is that a medium-sized herbivore attracts a large array of predators, both small and large.

Foraging and Food Herbivorous. Probably very similar to *P. capensis*. Feeds primarily, and selectively, on grass parts: roots, rhizomes, corms, stems, leaves and seeds, and crops such as sweet potatoes, groundnuts, pumpkins, maize and wheat. Prefers green grasses high in protein and water, especially *C. dactylon*. Reported to eat locusts and beetles (Kingdon 1974, Augustine *et al.* 1995). One record of feeding (at day break) on the flesh and bone of a Cape Hare *Lepus capensis* killed by a vehicle the previous day (O'Brien 1982).

Social and Reproductive Behaviour Solitary and polygamous. Probably similar to *P. capensis*. No territorial behaviour reported. Of 361 individuals encountered during transects on the Athi-Kapiti Plains, 59% were alone and 41% were in groups of two to six, with one group of 11. Of 104 sighted from viewing towers, 58% were alone and 42% were in groups of two or three (Augustine *et al.* 1995). These results are similar to those for *P. capensis* in Botswana (Butynski 1984).

Reproduction and Population Structure Little-studied. Probably similar to *P. capensis*. Pregnant ♀♀ were collected in Mar, Apr, Aug, Sep, Oct and Nov (no sample sizes given) suggesting that females breed throughout the year (Coe 1969). Females collected in Mar contained very small embryos (8 and 15 mm) as well as full-term foetuses. Estimated median length of gestation in captivity is 78 days (range: 72–82 days, n = 3) (Rosenthal & Meritt 1973, Velte 1978). Monotocous (n = 27 births); no records of twinning but few observations. Mean birth-weight of seven young born in captivity: 273 g (range 238–319 g) (Hediger 1950, Coe 1967, Rosenthal & Meritt 1973, Velte 1978). The 238 g neonate survived to >4 months of age (Velte 1978), indicating that it was probably not born prematurely. Total length at birth of three young born in captivity was 343, 368 and 375 mm (Jones 1941, Rosenthal & Meritt 1973). Detailed information on the anatomy of the reproductive tract is given by Coe (1969).

Young are born in a burrow in an unlined chamber (Kingdon 1974). After parturition, the mother cleans the neonate, chews the umbilical cord off near the point of attachment to the neonate and eats the placenta. At birth, head, back, tail and outer surface of limbs are well-covered with pale fawn-brown pelage (ca. 5 mm long on back) but chin, throat, ventral surface and insides of limbs have only a sparse covering of hair. At birth, eyes partly open, ears open and almost erect. Neonates are able to move about and to wash face, ears and top of head. Urination and defecation accomplished spontaneously. Like adults, infants sleep with the body bent forward between the legs with the top of head on the ground (Jones 1941, Hediger 1950, Coe 1967, Rosenthal & Meritt 1973, Velte 1978). Captive-born young

attained the following weights: 250 g at birth, 530 g at Day 21 (Hediger 1950); 238 g at birth, 410 g at Day 19; 272 g at birth, 370 g at Day 20 (Velte 1978). The smallest animal collected ($n = >22$) above ground by Coe (1969) was 1473 g, indicating that young do not leave the burrow until they achieve a weight close to this. There is no evidence that food is carried into the burrow and so young presumably suck until they depart the burrow and begin to feed above ground (as for *P. capensis*). Maximum longevity in captivity is 14 years (Jones 1982).

Predators, Parasites and Diseases No information. Likely to have many of the same predators as for *P. capensis*; many of the species of predators present in the range of *P. capensis* also occur over the range of *P. surdaster*. Black-backed Jackals *Canis mesomelas* and Caracals *Felis caracal* are likely to be the main predators of *P. surdaster*, as they appear to be for *P. capensis*.

Conservation IUCN Category: Least Concern.

Unlikely to be threatened as a species. Fairly widespread and locally common, but populations have been reduced or extirpated from some localities due to habitat degradation, habitat loss and/or over-hunting. *Pedetes surdaster* is a source of bushmeat and a pest of crops, but how important it is to the people of East Africa is not known.

The two species of *Pedetes* are among Africa's most biologically unique mammals. In addition, they are likely to be keystone species in those ecosystems where they are most abundant. As such, the long-term survival of these two species needs to be ensured. Where extirpation appears likely, conservation actions should be taken to remove the threats. While *P. capensis* is one of Africa's most studied smaller mammals, *P. surdaster* remains comparatively poorly known. Both are very similar phenotypically and morphologically, but each lives under very different climatic and biotic conditions. For example, most of the plant species differ between the ranges of the two species,

and *P. surdaster* probably never experiences temperatures lower than +5 °C, whereas *P. capensis* frequently forages when temperatures are below 0 °C, and sometimes as low as -8 °C. Applied research might focus on assessing the economic importance of this species, and on what the sustainable harvest is under various natural and man-made conditions.

Measurements

Pedetes surdaster

HB (♂ ♂): 393 (336–457) mm, $n = 27$

HB (♀ ♀): 387 (350–440) mm, $n = 26$

T (♂ ♂): 418 (390–484) mm, $n = 30$

T (♀ ♀): 418 (390–451) mm, $n = 26$

HF (♂ ♂): 156 (140–161) mm, $n = 30$

HF (♀ ♀): 148 (130–159) mm, $n = 27$

E (♂ ♂): 77 (67–89) mm, $n = 12$

E (♀ ♀): 73 (65–85) mm, $n = 13$

WT (♂ ♂): 2.7 (?–?) kg, $n = 10$

WT (♀ ♀): 2.8 (?–?) kg, $n = 12$

GLS (♂ ♂): 85 (80–88) mm, $n = 3$

GLS (♀ ♀): 87 (86–88) mm, $n = 4$

GWS (♂ ♂): 55 (52–57) mm, $n = 13$

GWS (♀ ♀): 54 (52–57) mm, $n = 15$

P⁴–M³ (♂ ♂): 15 (13–16) mm, $n = 13$

P⁴–M³ (♀ ♀): 16 (15–17) mm, $n = 14$

Kenya (mostly Naivasha and Machakos) and Tanzania (AMNH, BMNH, CUMV, FMNH, NMK, USNM, Hollister 1918, 1919, Miller 1927, Allen & Loveridge 1927, Coe 1969, S. Thomsett pers. comm.)

Key References Augustine *et al.* 1995; Coe 1969; Kingdon 1974.

Thomas M. Butynski & Jan Kalina

Family CTENODACTYLIDAE

GUNDIS AND PECTINATOR

Ctenodactylidae Gervais, 1853. Ann. Sci. Nat. (Paris), ser. 3, 20: 245.

| | | |
|----------------------------------|--------------------|--------|
| <i>Ctenodactylus</i> (2 species) | Gundis | p. 629 |
| <i>Felovia</i> (1 species) | Felou Gundi | p. 634 |
| <i>Massoutiera</i> (1 species) | Mzab Gundi | p. 636 |
| <i>Pectinator</i> (1 species) | Speke's Pectinator | p. 638 |

The family is endemic to Africa, and contains four genera and five species (Table 44) widely distributed in arid and semi-arid habitats north of the Equator. Typically, all species (commonly known as 'gundis') are associated with rocky habitats. 'Gundi' is the name given by Berbers to *Ctenodactylus* spp. and this name is applied indiscriminately now to all the living species of the family.

Members of the family are very similar in external appearance. The head and body is of medium size (typically HB: 160–193 mm), thickset, with short limbs and a very small brushy tail. Pelage is very dense (173–289 hairs/cm²; George 1978a). The fore- and hindlimbs are short with four digits on each foot. The family name, Ctenodactylidae, is derived from the comb-like bristles surmounting the digits of the hindfeet (George 1978a). The claws are sharp and usually do not touch the ground; they are used exclusively for climbing and are not for excavating or for grooming. Skull: broad posteriorly due to wide flaring zygomatic arches, large auditory bullae and large orbits. Auditory bullae weakly to moderately inflated, size varying in relation to the aridity of the habitat, but not as well developed as in gerbils (Gerbillinae) and jerboas (Dipodidae). Dental formula: $I^{1/1}, C^{0/0}, P^{1-2/1-2}, M^{3/3} = 20$ or 24 ; P^4 smaller than molars. Zygomatic arches wide and thick, maxillary process of zygomatic arch well developed, zygomatic plate small extending dorsally only to mid-way on maxillary process. Each upper incisor with single faint groove (absent in some specimens of *Massoutiera mzabi*). Cheekteeth rootless except in *Pectinator spekei* (Jaeger 1971). Mandible thin with almost no development of coronoid process, condylar process in line with cheekteeth; angular process short in *Felovia* and *Pectinator*, but pointed and well-developed in *Ctenodactylus* and *Massoutiera*. Size categories of species in the family (based on mean head and body length) are given in the order Rodentia profile.

Gundis are not able to dig burrows although they may push small stones with their forefeet or nose in order to improve the entrances of their shelters. Gundis are restricted to rocky habitats that provide shelters (George 1974). They are able to ascend almost perpendicular rock faces by pressing the body against the rock face and using their claws to cling to the slightest irregularities of the rock. The flat broad head with ears that can be flattened, and a compressible thorax, enable gundis to edge into narrow crevices in order to escape danger. Inside a crevice, a gundi can work its way up or down or sideways (George 1974). Female gundis have two pairs of nipples, one pectoral and one thoracic. Gestation is long for a small mammal (50–70 days), and the young are born fully furred, with their eyes open (George 1978b). Gundis make species-specific calls that are readily identifiable (George 1981a).

Gundis are mainly, if not completely, diurnal (George 1974, Gouat, P. 1991a) and have behavioural adaptations for temperature regulation. They change their resting position according to the ambient temperature, and stay in the shade during the hottest part of the day. The temperature threshold initiating behavioural responses varies between species according to the aridity of the habitat (Gouat 1991a). Nevertheless, these behavioural adaptations are not sufficient to explain how gundis cope with their water balance. Renal function and concentrating ability are unspecialized, at least in *Ctenodactylus vali* and *Massoutiera mzabi* – the two species that live in the central Sahara (de Rouffignac *et al.* 1981, George 1988). Gundis are herbivorous and do not drink free water. Efficient water absorption may occur in the long large intestine (which may be as long as 100 cm in *C. gundi* and hence five times as long as the head and body length); faecal pellets are very dry (Gouat 1993). Detailed physiological studies are required.

The family Ctenodactylidae is the only recent family of the infraorder Ctenodactylomorpha of the suborder Hystricomorpha (Dieterlen 2005c). This taxon (previously referred to as the superfamily Ctenodactyloidea) includes some of the oldest of rodent fossils (Dawson *et al.* 1984). It is characterized by a combination of an hystricomorphous

Table 44. Species in the family Ctenodactylidae. Arranged in alphabetical order.

| Species | HB mean (range) (mm) | T mean (range) (mm) [% of HF] | Groove on each upper incisor | Auditory bulla | Shape of forehead | Length of faecal pellets mean (range) (mm) | Notes |
|----------------------------|----------------------|-------------------------------|------------------------------|---------------------|-------------------------|--|--------------------------------------|
| <i>Ctenodactylus gundi</i> | 193 (150–228) | 31 (20–45) [81%] | Present | Moderately inflated | Large and straight | 11.0 (9.8–11.9) | E Morocco to W Libya |
| <i>Ctenodactylus vali</i> | 160 (124–185) | 36 (27–43) [102%] | Present | Greatly inflated | Narrow; slightly hooked | 7.9 (7.3–8.2) | Morocco, Algeria, Libya |
| <i>Felovia vae</i> | 179 (169–190) | 73 (67–80) [221%] | Present | Slightly inflated | Large and straight | 10.6 (10.0–10.9) | Mali, Mauritania |
| <i>Massoutiera mzabi</i> | 176 (125–210) | 52 (33–85) [148%] | Absent (or slight groove) | Greatly inflated | Large and straight | 7.3 (6.6–7.9) | Algeria, Mali, Niger, Chad |
| <i>Pectinator spekei</i> | 170 (155–190) | 74 (60–80) [224%] | Absent | Moderately inflated | Large and straight | n. d. | Ethiopia, Eritrea and Horn of Africa |

skull with a sciurognathous jaw, and a non-molariform P⁴ (Jaeger 1971). From these observations, and others, Hartenberger (1985) concluded that ctenodactylids may be the stem group of all other rodents. More recent studies, based on molecular analysis, proved the relatedness between Ctenodactylidae and hystricognathous rodents (Beintema *et al.* 1991). Huchon *et al.* (2000) confirmed that Ctenodactylidae and Hystricognathi robustly cluster together, and proposed the formation of a new clade named Ctenohystrica. This clade, together with other lineages (Sciuroidea and Gliridea), is thought to have emerged close to the Cretaceous–Tertiary boundary (Huchon *et al.* 2000). Following their emergence and radiation in Asia during the Eocene, Ctenodactyloidea extended its range to the west and disappeared from the Far East (Dawson *et al.* 1984). The Ctenodactylidae reached the Mediterranean region and northern Africa during the late Eocene (Dawson *et al.* 1984). Two genera, *Africanomys* and *Metasayimys*, are described from the late Miocene from North Africa. During the early Pleistocene, *Irhoudia* was common in

North Africa (Jaeger 1971). Nowadays, the Ctenodactylidae is reduced to four living genera and five species. See Rosevear (1969) for further discussion.

The five species can be classified into three groups according to their phylogenetic affinities and distribution (George 1974, 1979b, 1985a). Speke's Gundi *Pectinator spekei* is the most primitive species (Jaeger 1971) and occurs only in the Horn of Africa. North of the Sahara Desert are the two species of *Ctenodactylus*. The two other species, *Felovia vae* and *Massoutiera mzabi*, are closely related and are typically sub-Saharan species (George 1979b, 1985a), although *M. mzabi* also occurs further north to the northern edge of the Sahara (Gouat *et al.* 1984, Gouat 1988a, 1991a).

The genera may be distinguished by tail length and visibility, alarm calls, size of auditory bullae, size of faecal pellets and geographic distribution.

Patrick Gouat

GENUS *Ctenodactylus* Gundis

Ctenodactylus Gray, 1830. *Spicilegia Zoologica* 2: 10. Type species: *Ctenodactylus massonii* Gray, 1830 (= *Mus gundi* Rothmann, 1776).



Ctenodactylus gundi.

The genus contains two species that live in rocky habitats of the northern Sahara Desert BZ from Morocco to Libya. The first-named species was described as *Mus gundi* by Rothman in 1776. In 1830, Gray proposed the current definitive name *Ctenodactylus* (derived from Greek *ctenos*, comb; and *dactylos*, toe). Characters of the genus include: palate extends posteriorly to the cheekteeth, toothrows converge anteriorly, upper molar teeth simple without infoldings on both sides (Figure 99), and tail shorter or about equal in length (ca. 80–102%) to the hindfoot (Misonne 1974). The two species are difficult to differentiate in the field. The species can be distinguished by body size, shape of the forehead, distance between the auditory bullae, type of alarm call and the mean length of the faecal pellets.

Patrick Gouat

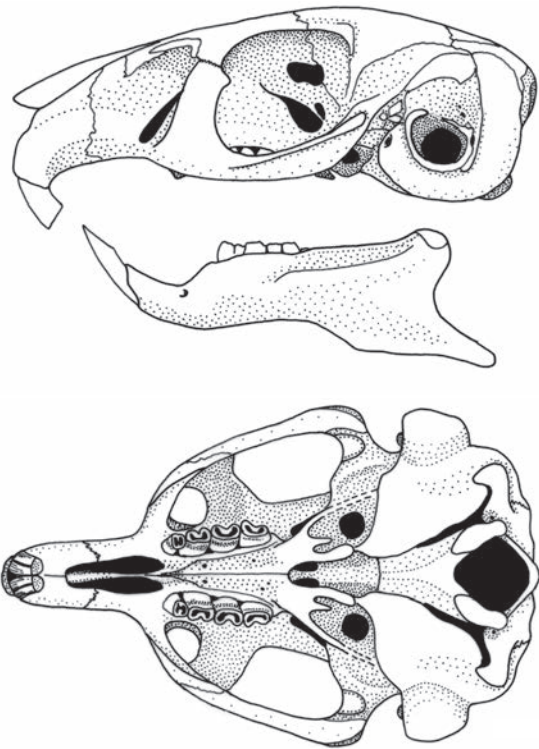


Figure 99. Skull and mandible of *Ctenodactylus gundi* (BMNH 19.7.7.2918).

Ctenodactylus gundi ATLAS GUNDI (COMMON GUNDI)

Fr. Goundi de l'Atlas; Ger. Atlas-Gundi

Ctenodactylus gundi (Rothman, 1776). In: A.L. Schölzer (ed.), Briefwechsel, Book 6, Part 1, Göttingen: 339. Gharian, 80 km S of Tripoli, Libya.

Taxonomy Originally described in the genus *Mus*. Synonyms: *arabicus*, *massonii*, *typicus*. Subspecies: none. Chromosome number: $2n = 40$ (George 1979b).

Description General appearance of a small guinea-pig with a short hairy tail and small ears. Pelage very dense and soft. Dorsal pelage buffy-brown, dull grey underfur. Ventral pelage buff to yellowish-grey. Head flat and broad. Forehead large and straight. Muzzle short with long black vibrissae. Nostrils naked and black. Eyes large and round surmounted by long vibrissae. Ears flattened on the head, oval, black inside bordered by a dense fringe of short stiff whitish-grey hairs. Fore- and hindlimbs short; four digits on each foot. Digits of the hindfeet surmounted by comb-like bristles. Claws sharp; do not reach the ground in the normal position. Tail relatively short (ca. 81% of HF), usually hidden by pelage of rump and not visible. Skull: see family and genus profiles; each upper incisor with single groove, angular process of mandible elongated posteriorly forming the most posterior part of the mandible (as in *Massoutiera*, cf. *Felovia*, *Pectinator*), auditory bullae moderately inflated (ca. 15.4 mm, 51% of GLS), distance between bullae ca. 10 mm) (Figure 99). Emits whistle alarm call when disturbed. Mean length of faecal pellets: 11.0 (9.8–11.9) mm. Nipples: $2 + 0 = 4$. In lactating ♀♀, nipples appear as black dots on the buff pelage.

Geographic Variation None recorded.

Similar Species

C. vali. On average smaller; forehead narrow and slightly hooked; auditory bullae inflated to a greater extent; chirp alarm call; mean length of faecal pellet <9 mm; partially parapatric.

Massoutiera mzabi. On average smaller; tail relatively longer; present in northern Sahara; allopatric.

Distribution Endemic to Africa. Mediterranean Coastal BZ and northern fringe of Sahara Arid BZ in NW Africa. Recorded from E Morocco to W Libya. In E Morocco: High Atlas east of wadi Dades, and upper Moulouya basin in the Middle Atlas (Petter & Saint-Girons 1965, Aulagnier & Thévenot 1986, P. Gouat pers. obs.). Algeria: Saharan Atlas from Ksour Mts in the west to Nemencha Mts in the east (Gouat & Gouat 1984, Gouat 1988b). Tunisia: High Tell south of a line Enfida–Kasserine, Matmata Mts, Dahar Hamada, and slopes bordering the Djefara depression (Séguignes 1979, 1983, Séguignes & Vernet 1996). Western Libya: Tripolitanian Mts (Nefusa, Tigrina and Jefren Mts) (Ranck 1968).

Habitat Semi-desert mountainous rocky habitats that contain natural shelters. Large rocks ($>2 \text{ m}^3$) are necessary for main shelters (Gouat & Gouat 1983). Natural caves and human constructions (retaining walls along roads, piles of stones along fields, small rocky dams) may also be used as shelters. Atlas Gundis avoid forests and dense vegetation cover (e.g. esparto grass *Stipa tenacissima* steppe),

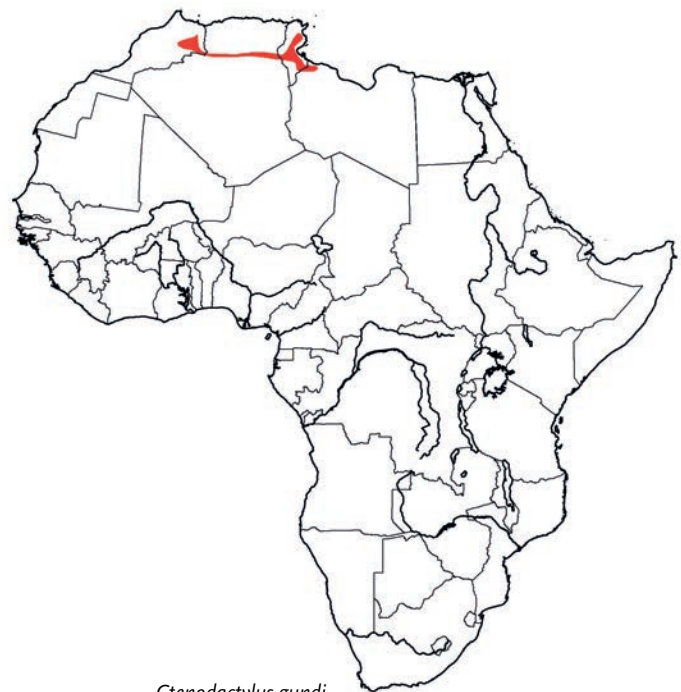
preferring sites with sparse vegetation, where the average annual rainfall is 100–400 mm (Gouat & Gouat 1983, Séguignes 1983). Dispersing animals may be found in isolated small rocky massifs up to 10 km away from normal preferred habitat (Gouat 1988a, Séguignes & Vernet 1998).

Abundance Common in suitable habitats when food resources are abundant: e.g. 20–25 animals/km² (evaluated from data in Séguignes 1979). Rare in desert habitats (Séguignes & Vernet 1996). One year without rain may cause the disappearance of gundis from previously suitable habitat (Gouat & Gouat 1982).

Adaptations Similar to *C. vali* (see Species profile).

Foraging and Food Herbivorous. Atlas Gundis are selective feeders. The species of plants eaten vary greatly from place to place. For example, in a semi-desert site of the Aures Mts (E Algeria), the diet consisted of *Anabasis articulata*, *Artemisia herba-alba*, *Asparagus acutifolius*, *Astragalus armatus*, *Haloxylon articulata*, *Lycium afrum*, *Rhus tripartitus* and grass. In a high elevation site, 10 km away, the diet was *Euphorbia buplroides*, *Lamium* sp., *Rhamnus alaternus*, *Rhamnus lycioides* and grass (P. Gouat & J. Gouat 1987). In both sites, the diet comprised only ca. 30% of the plant species present. These gundis are capable of climbing small trees or bushes in order to eat the leaves.

Social and Reproduction Behaviour Gundis live in small colonies (up to 11 adults) with typically one adult ♂ and several adult ♀♀ with young and juveniles (Séguignes 1979, Gouat 1988a).

*Ctenodactylus gundi*

The social group is stable and long lasting; one adult reproductive ♂, for example, was observed in the same colony in the Aures Mts for more than three years (Gouat 1988a). Members of the colony occupy a common home-range, which remains stable throughout the year, and from one year to the next. The size of home-ranges depends on food abundance, stability of resources and on local social constraints. In the Aures Mts, the home-range of three colonies was 1031 m² and 5468 m² in semi-desert habitats, and 685 m² in a high elevation habitat (Gouat 1991b). The whole of the home-range is equivalent to a territory. It is actively marked and defended against conspecific intruders (Gouat 1991a). Animals deposit scent marks all around their territory, and the entrances to shelters are covered with piles of faecal pellets, which are a good indication that gundis are present (George 1974). Animals mark and dust-bathe at least once each day in a specific place near the main shelter (P. Gouat & J. Gouat 1987). Gundis may chase conspecific intruders. In captivity, even in large cages, intruders are chased and bitten to death (Eisentraut 1977, P. Gouat & J. Gouat 1987).

Animals in a colony share a common shelter during the night. In addition to this night shelter, numerous secondary shelters used during the day are scattered throughout the home-range. Activity starts at sunrise. Animals come out of the night shelter, and after a period of amicable interaction around the entrances, disperse throughout their home-range to feed individually or in small groups (Gouat 1988a, 1991a). The territory appears as a mosaic of foraging patches adjacent to their rocky shelters. Atlas Gundis spend a large amount of time sun-bathing on the ground or on rocks. Adults and juveniles cooperate to detect predator and conspecific intruders. Animals take turns to watch the surroundings from the top of rocks and to give alarm calls when a potential predator is detected (Gouat & Gouat 1989). Alarm calls are typically simple, monosyllabic chirps which are emitted in quick succession (up to 20 at a time) (George 1981a), but they vary according to the age of the emitter and the circumstances (Séguignes 1979, Gouat *et al.* 1985). On hearing alarm chirps, members of the colony stop their activity and stay vigilant. The sudden appearance of a predator elicits one or two very loud chirps, and all the members of the colony run into shelters. Sound emissions are numerous and varied. The repertoire includes audible range communication (vocalizations, tooth chattering and foot drumming) and some ultrasonic vocalizations (Gouat *et al.* 1985). These sounds are mainly displayed during interactions between conspecifics.

At mid-day, animals rest in the shade or inside the shelters, individually or in small groups. The length of the resting period depends on the ambient temperature. In the hot period (Apr–Sep) in the southern part of the Aures Mts, this resting period lasts from 10:00h until 16:00h. During the cold period (Dec–Feb), or in high elevation sites, resting periods may be absent or may last only one hour (Gouat 1991a). In the late afternoon, animals forage again. Around sunset, they return individually to the main shelter. Interactions are rare at this time except when there is a change of night shelter. One animal may stay at the entrance of the old night shelter and drive the incoming animals to the new night shelter (Gouat 1988a).

In the semi-desert sites of Aures Mts, reproduction starts in Dec. It begins with the exclusion of supernumerary ♂♂ by both the ♀♀ and the reproducing ♂ (Gouat 1988a). This time of the year is one of the rare occasions when gundis are aggressive (P. Gouat & J. Gouat 1987). Copulation may occur outside the shelter (Gouat 1985). Prior

to mating, ♂ approaches ♀ by walking with measured tread with the head bent down slightly, and emits a sexual trill of low intensity (Gouat *et al.* 1985). He sniffs the genital area of ♀. Mounting is followed by some long pelvis thrusts, which precede ejaculation. After ejaculation, ♂ remains on ♀ for ca. 30 sec. In natural conditions, ♂♂ have been observed ejaculating five times during a 45 min period with the same or different ♀♀ (Gouat 1985).

Reproduction and Population Structure Polyoestrous. Two litters are produced each year. In the semi-desert sites of Aures Mts, reproduction begins in late Dec. First litters born in late Feb to early Mar. The birth of young is preceded by a prepartum oestrus (Gouat 1985; see also *C. vali*). Second births occur between late Apr and mid-May. In high altitude sites of the Aures Mts, this reproductive schedule is delayed by two months. Females have two litters per year only under favourable conditions, and scarcity of food may preclude any reproduction and promote the exclusion of supernumerary ♂♂ (Nutt, 2005). Gestation: 73 days. Litter-size: 2 (1–3, n = 17; Gouat 1985). At birth, young are precocial, fully furred, with the eyes and ears open and functional, and able to walk and to chew solid food (Gouat 1985). Birth-weight: 29.9 ± 11.9 g (range 18–40 g, n = 15; Gouat 1985). Weaning: ca. Week 6. Males and ♀♀ do not breed until the reproductive season following their birth, when aged 7–9 months of age (Gouat 1985). Detailed physiological studies on reproduction are required.

Communal nursing is the rule, but young have seldom been observed sucking any ♀♀ other than their mother (J. Gouat & P. Gouat 1987). Young gundis emit an extension trill when approaching their mother, or when the mother leaves them after feeding (Gouat *et al.* 1985). This vocalization accompanies lordosis and anogenital eversion by the young. The extension trill is attractive to adults and may elicit similar trills in other young animals (J. Gouat & P. Gouat 1987). Young animals emit a modulate trill during sucking (Gouat *et al.* 1985). During their first week, young animals remain near the main shelter watched over by an adult ♀ or a juvenile. Adults may carry the young animals in their mouth, one by one, from one shelter to another (J. Gouat & P. Gouat 1987). At the end of the second week, play behaviour (running and head-shaking) and young vocalizations tend to disappear, and agonistic behaviour develops. At three weeks of age, young animals display most behavioural patterns of the adult but sexual behaviour remains absent until the next reproductive season (J. Gouat & P. Gouat 1987). Young animals from about two weeks of age feed mainly on vegetation, but weaning seldom occurs before six weeks of age (Gouat & Gouat unpubl.). Females may supplement young with water through long-lasting mouth to mouth contact (Gouat 1988a).

Three types of population structure have been observed dependent on the bioclimatic conditions. (1) In high altitude habitats, and in habitats with a Mediterranean climate, where mean annual rainfall is ca. 400 mm and food resources are abundant from spring to autumn, high levels of reproduction and a high turnover of the population are observed. Colonies in these habitats, however, may disappear suddenly if devastated by summer storms or by a long period of snow cover during winter (Séguignes 1979, Gouat & Gouat 1983). (2) In semi-desert habitats, populations are more stable, and the level of reproduction is correlated with the abundance of resources. Summer is the most difficult period of the year for gundis because the vegetation becomes dry and sparse. When the conditions are good enough, and

the resources remain abundant, mortality may be low during summer. In this case, in summer or autumn, a group composed of adults and juveniles may migrate to establish themselves in a vacant site (Gouat 1988b). (3) In desert habitats on the edge of the Sahara Desert, where mean annual rainfall is less than 100 mm, social units are generally composed of only one breeding pair. Generally, animals are unable to survive in the desert habitats when there is more than one year without any rain. The maintenance of populations under these conditions depends primarily on recolonization from more favourable sites (Gouat & Gouat 1982, Séguignes & Vernet 1998).

Predators, Parasites and Diseases Gundis are hunted and eaten by humans in the Maghreb. The most dangerous predators are snakes because they are able to enter the rocky shelters of gundis, even during the night. The presence of a large adder (Daudin's Viper *Vipera lebetina*), 1.20 m long, caused a colony of gundis to change their main shelter and to modify the way they used their home-range (Gouat 1991a). Other predators are dogs, foxes, birds of prey and ravens (Séguignes 1979, Gouat 1988a).

Conservation IUCN Category: Least Concern.

Measurements

Ctenodactylus gundi

HB: 193 (150–228) mm, n = 25

T: 31 (20–45) mm, n = 20

HF: 38 (33–44) mm, n = 113*

E: 18 (14–22) mm, n = 113*

WT: 268 (185–396) g, n = 22

GLS: 48.6 (42.9–53.5) mm, n = 44

GWS: 32.1 (27.8–35.9) mm, n = 43

M¹–M³: 9.3 (7.5–10.8) mm, n = 48**

Algeria and Tunisia (MNHN); Aures Mts (Algeria) and from their descendants born in captivity (P. Gouat & J. Gouat unpubl.)

*Beni Kheddache, Tunisia (K. J. Nutt unpubl.)

**P⁴ may occur in some adults; if so cheekteeth measurement is P⁴–M³

Key References Gouat 1985; Gouat, P. 1991b; Gouat & Gouat, 1983; Gouat & Gouat 1989; Gouat *et al.* 1985.

Patrick Gouat

Ctenodactylus vali THOMAS'S GUNDI

Fr. Goundi de Thomas (Goundi du Sahara); Ger. Thomas Gundi

Ctenodactylus vali Thomas, 1902. Proc. Zool. Soc. London 1902: 11. 'Wadi Bey' (NW of Bonjem, Tripoli), Libya.

Taxonomy Corbet (1978) included *vali* as a synonym of *gundi*, but George (1982) listed *vali* and *gundi* as separate valid species (see also Dieterlen 2005c). The form *joleaudi* (originally described as a species, *C. joleaudi*) is considered to be a subspecies of *vali* by Petter (1961) and subsequent authors. Synonyms: *joleaudi*. Subspecies: none. Chromosome number: 2n = 40 (George 1979b).



Ctenodactylus vali

Description General appearance of a small guinea-pig with a short hairy tail and small ears. Pelage very dense and soft. Dorsal pelage buffy-brown with dull grey underfur. Ventral pelage yellowish-grey. Head flat and broad. Forehead narrow and slightly hooked. Muzzle short with long black vibrissae. Nostrils naked and black. Eyes large and round surmounted by long vibrissae. Ears flattened on the head, oval, black inside bordered by a dense fringe of short stiff whitish-grey hairs. Fore- and hindlimbs short; four digits on each foot. Digits of the hindfeet are surmounted by comb-like bristles. Claws sharp, not reaching the ground in normal position. Tail relatively short (ca. 102% of HF), usually hidden by pelage of rump and not visible. Skull: see family and genus profiles; each upper incisor with single groove; angular process of mandible elongated posteriorly forming the most posterior part of the mandible (as in *Massoutiera*, cf. *Felovia*, *Pectinator*); hugely inflated auditory bullae (ca. 17.9 mm, 39% of GLS), distance between bullae ca. 7 mm. Emits chirp alarm call when disturbed. Mean length of faecal pellets: 7.9 (7.3–8.2) mm. Nipples: 2 + 0 = 4.

Geographic Variation None recorded.

Similar Species

C. gundi. HB on average larger; forehead large and straight; whistle alarm call; less inflated auditory bullae; mean length of faecal pellets >9.5 mm; partially parapatric.

Massoutiera mzabi. HB similar; tail relatively longer; present in northern Sahara; allopatric.

Distribution Endemic to Africa. Northern edge of Sahara Arid BZ. Distributed in two discrete and widely separated areas of NW

Africa: (1) Algeria and Morocco in the west, and (2) Libya in the east. Morocco: hamada of Wadi Ziz. Algeria: Saharan Atlas from Beni Ounif to Bechar, basin of Wadi Saoura, and hamada of Wadi Guir, Ougarta Mts. Libya: Tripolitania, transitional desert between Soda Mts and the Gulf of Sirte (Ranck 1968). Often parapatric with *C. gundi*. See also below.

Habitat Wide range of rocky desert habitats such as mountain slopes, edges of hamadas, wadis, rift and small mountainous massifs. Also found in semi-desert areas, on the southern slopes of the Saharan Atlas in Algeria and SE Morocco.

Abundance Generally sparsely distributed, but high density may be observed under favourable climatic conditions during the breeding period (e.g. 18 animals/ha; George 1981a).

Adaptations Thomas's Gundis are diurnal and have similar activity patterns to Atlas Gundis: they are active at sunrise and in the early morning, rest at the hottest time of the day, and are active again in the afternoon before sunset. Thomas's Gundis are parapatric with Atlas Gundis on the western edge of the Saharan Atlas and in the south-eastern part of Morocco. In semi-desert habitats, the highly structured occupation of space displayed by Atlas Gundis prevents any extension of the geographic range of Thomas's Gundis further to the west. However, Thomas's Gundis are capable of rapid colonization of sites left vacant by Atlas Gundis following a period of severe drought (Gouat 1988b). The present distribution of Thomas's Gundis in two isolated areas of distribution is best explained by competition with Atlas Gundis and the climatic fluctuations of the Sahara Desert. The relationships between the two species may be explained as follows (Gouat 1988a):

- (1) *Ctenodactylus gundi*, thought to belong to the ancestral species, originally occupied their present range. Following an extension of the Sahara Desert to the north, populations of *Ctenodactylus gundi* gradually moved away and settled in the northern mountains (e.g. Tel Atlas Mts in Algeria). Several rocky corridors may have allowed this resettlement from southern sites to northern sites (e.g. Hodna Mts in Algeria).
- (2) *Ctenodactylus vali* appears to have evolved in one of the populations of *Ctenodactylus gundi* remaining in the Saharan Atlas, in response to the drought caused by the extension of the Sahara Desert to the north. This new species extended its range throughout the range occupied previously by *Ctenodactylus gundi* where desert conditions prevail.
- (3) Regression of the Sahara Desert to the south enabled *Ctenodactylus gundi* to return to its previous range, and as a consequence, the range of *Ctenodactylus vali* became smaller and restricted to more arid desert habitats. As a result, the range of *Ctenodactylus vali* was split into two parts and the species is present only in habitats where *Ctenodactylus gundi* is unable to survive.

Foraging and Food Herbivorous, feeding mainly on grasses and herbaceous plants. The diet encompasses food plants such as *Eremophyton chevallieri*, *Amberboa leucantha*, *Cymbopogon* sp. and *Aristida* sp. (George 1974). Animals forage mainly in early morning and late in the afternoon, alternating foraging with resting. Animals pick up food

items while they travel through their home-range, without having any clear foraging places. The area of foraging each day varies from 20 m² to 275 m² (Gouat 1988a).

Social and Reproduction Behaviour Thomas's Gundis, in contrast to Atlas Gundis, are mainly solitary; social bonds are weak, and animals behave as 'floaters' for a large part of the year. At the end of autumn, ♀ settles at a place where she will produce her young. Several ♂♂ may try to join ♀, but only one ♂ will succeed. A familiarization period is necessary for ♂ to become accepted by ♀. In captivity, reproduction was successful in groups composed of one ♀ and 2–3 ♂♂ (Grenot 1973); ♂♂ develop a hierarchy (George 1978b). In captivity, confrontation between unfamiliar animals may cause the death of the intruder (Grenot 1973, Gouat 1988a). During these agonistic encounters, animals emit different vocalizations, including the 'trilled whistle' and the 'repeated whistle', and non-vocal sounds such as foot-drumming and tooth-chattering (J. Gouat 1991). The repeated whistle is composed of a repetition of short whistles (mean frequency of the plateau: 4.5 KHz; each unit lasts between 0.12 and 0.5 sec). This vocalization is also displayed in the case of a sudden alert and is named the 'alarm call' by George (1981a); on hearing this call, conspecifics respond by adopting an alert posture, or by disappearing inside a shelter. The trilled whistle is emitted only in an agonistic context. It consists of a modulate whistle followed by a trill. The trilled whistle is emitted alone or coupled with the alarm call.

Thomas's Gundis have two litters each year (see also below). In Dec in Djeniene Bou Rezg (Beni Ounif region, Algeria), individuals settle in a suitable habitat after several months of nomadic existence and become sedentary. A ♀ and several ♂♂ establish a territory where ♀ will later give birth to her young. By Jan, ♀ and one of the ♂♂ have developed a social bond; and the supernumerary ♂♂ have disappeared. The pair may spend the night in a common shelter but each forages independently. First copulation occurs in the days following pair formation. Male stays with ♀ during gestation but leaves her soon after the parturition oestrus and no later than the birth of the first litter in Jan–Mar. Young animals are precocial but have difficulty in moving around and remain close to the shelter. Even before they are weaned, the mother leaves her young at night. She joins them in the morning, and may spend the afternoon rest with them. Young animals emit a calling trill quite similar to the extension trill of the Atlas Gundi (J. Gouat 1991), but without lordosis or anogenital eversion by the young. This vocalization attracts the mother and the littermates. Littermates continue to use a common shelter during the night. Young animals of the first litter disperse before the birth of the second litter in Apr–May. In captivity, mothers may become aggressive towards their young of the first litter in the days preceding birth of the second litter. In natural conditions, however, dispersion does not seem to be caused by the mother. Young animals disperse simply by extending their home-range. The mother uses a similar strategy with her second litter. Even while she is still lactating, the mother spends the night alone. She forages on her own, and shortly before her young are weaned, she increases her home-range significantly. In Djeniene Bou Rezg (Beni Ounif region, Algeria), the size of the daily home-range varies from 100 to 500 m² in Dec–Mar, and increases to 1125 m² in May and Jun. At this time of the year, the mother is still lactating. There is no significant correlation between the size of the daily home-range, either with food abundance or with the presence

of young. From day to day, animals use different parts of their habitat and the percentage of overlap between the daily home-range on two consecutive days varies from 12% to 33%, with a minimum in May and Jun. In the early summer, mothers leave their reproductive home-range and become nomadic. The young animals may stay for a while on their natal home-range, but soon become nomadic and solitary. Animals become sedentary again in Dec, with the beginning of the next reproductive season.

Reproduction and Population Structure Two litters per year under favourable conditions; first litter in late Jan–Mar; second litter Apr–May. Gestation: 2 months. Litter-size: 2 (1–3), $n = 21$ litters (combined data from Grenot 1973, George 1978b, Gouat 1988a). Females are lactating and pregnant with the second litter at the same time. Young precocial, fully furred, with eyes and ears open and functional at birth. Weaned: 1–2 months. Young reach sexual maturity and adult size in Dec when aged 7–9 months. In times of severe drought (more than one year without rain), there is no sedentary period and no reproduction. First copulations occur at the end of the autumn (late Nov–Jan). The period of mating may vary between animals of a given region. In the Taghit region, two ♀♀ were captured 20 km apart during the same week of Mar, and one gave birth four weeks before the other (Gouat 1988a). As in Atlas Gundis, a prepartum oestrus is suspected for the second copulation. Female is able to store spermatozoa in her genital tract for at least two months, and to use these spermatozoa without further copulation in order to produce a replacement litter (Gouat 1986). Young animals disperse soon after weaning and recolonization of vacant sites occurs rapidly (Gouat 1988b).

In times of severe drought, reproduction stops and the density of local populations decreases slowly. At such times, Thomas's Gundis may extend their home-range in order to find sufficient resources

to survive. After four years without significant rainfall, Thomas's Gundis were still present in the Beni Abbes region but at a very low density (Gouat & Gouat 1984). When the climatic conditions became favourable again, reproduction recommenced (Gouat 1988a).

Predators, Parasites and Diseases Preyed upon by humans, shepherd's dogs, foxes, birds of prey, snakes (Gouat 1988a) and jackals (George 1974).

Conservation IUCN Category: Data Deficient.

Probably not threatened. Human population density is very low in the geographic range of the species; any decreases in population density are probably due to climatic changes.

Measurements

Ctenodactylus vali

HB: 160 (124–185) mm, $n = 13$

T: 36 (27–43) mm, $n = 13$

HF: 35 (30–39) mm, $n = 9$

E: 17 (15–20) mm, $n = 9$

WT: 129.6 (87–180) g, $n = 7$

GLS: 47.8 (45.1–50.9) mm, $n = 19$

GWS: 32.0 (28.4–34.4) mm, $n = 20$

M^1 – M^3 : 8.4 (7.4–9.7) mm, $n = 20$

Algeria (MNHN); and individuals from the Taghit region (Algeria) and their descendants born in captivity (J. Gouat & P. Gouat unpubl.)

Key References George 1974; J. Gouat, 1986, 1991; P. Gouat, 1988b; Grenot 1973.

Patrick Gouat

GENUS *Felovia*

Felou Gundi

Felovia Lataste, 1886. Le Naturaliste 7 (36): 287. Type species: *Felovia vae* Lataste, 1886.



Felovia vae.

Felovia is a monotypic genus, restricted to the semi-desert rocky habitat of the Felou Hills of the upper Senegal R. in Mali and Mauritania. Originally proposed as a subgenus of *Massoutiera* but recognized as a valid genus by Thomas (1913) and St Leger (1931). Characters of the genus include: palate extends posteriorly to the cheekteeth, toothrows converge anteriorly, upper molar teeth simple with large infoldings on both sides (Figure 100), and tail about double the length (ca. 221%) of the hindfoot (Misonne 1974); further details are given in the species profile. The single species is *Felovia vae*.

Patrick Gouat

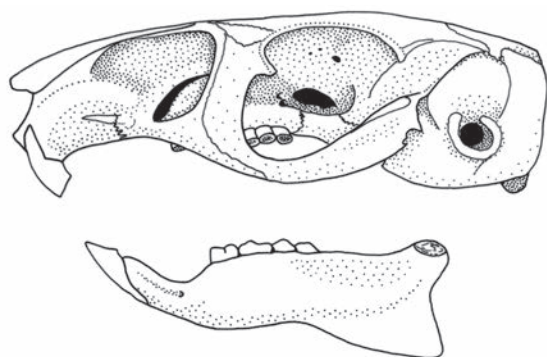
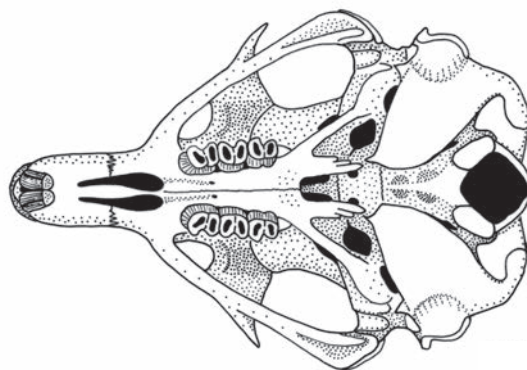


Figure 100. Skull and mandible of *Felovia vae* (BM 19.7.7.3698).



Felovia vae FELOU GUNDI

Fr. Goundi du Félou; Ger. Felou-Gundi

Felovia vae (Lataste, 1886). Le Naturaliste, 7 (36): 287. Upper Senegal River, Felou Hills, Medine, south of Kayes, Mali.

Taxonomy Originally described in the genus *Massoutiera*. Phylogenetic evidence suggests this species is closely related to *Massoutiera mzabi* (George 1979a, 1985a). Synonyms: none. Chromosome number: $2n = 36$ (George 1979a).

Description General appearance of a small guinea-pig with small ears and a short movable hairy tail. Pelage very dense and soft. Dorsal pelage reddish-brown. Ventral pelage russet. Head flat and broad. Ears small, with a whitish tuft at the base but without white on the back of the ear; flattened on the head. Fore- and hindlimbs short; four digits on each foot. Digits of the hindfeet surmounted by comb-like bristles. Tail relatively long (ca. 221% of HF), longer than in other gundis (except *P. spekei*). Tail is folded back on the rump when the gundi is at rest, but begins to flick as soon as the gundi begins to move. Skull: see family and

genus profiles; each upper incisor with single groove; angular process of mandible not elongated posteriorly; auditory bullae not greatly inflated (ca. 13.8 mm, 29% of GLS, least inflated of all species of gundis). Mean length of faecal pellets: 10.6 (10.0–10.9) mm. Nipples: $2 + 0 = 4$.

Geographic Variation None recorded.

Similar Species

Massoutiera mzabi. Upper incisors not grooved or slightly grooved; auditory bullae greatly inflated. All other species of gundis are allopatric.

Distribution Endemic to Africa. Sahel Savanna BZ. Known only from Felou Hills, upper Senegal R. in Mali, and the Tagant and Adrar regions in Mauritania. Suspected to occur in Senegal.

Habitat Long deep fissures of ancient sandstone hills, in semi-desert habitats with some trees (e.g. *Adenium obesum*, 2 spp. of fig trees) and shrubs (*Tephrosia mossiensis*) (George 1974). In Mauritania, animals have been found in an oasis on the rocky banks of wadis, on rocky mountain slopes, on the edges of hamada (F. Colas pers. comm.) and on gueltas (i.e. water ponds) where they drink free water (Vale *et al.* 2012).

Abundance Very limited geographic distribution, but in selected localities up to 25 animals/ha (George 1981a).

Remarks Herbivorous. During the dry season (Mar) feeds on leaves of a leguminous shrub *Tephrosia mossiensis*, dropped petioles of fig trees, dry grass and seeds (George 1974). Food resources fluctuate seasonally. Felou Gundis lives in family groups, not far from other family groups. They are noisy animals and in alert situations they emit repeated ‘chee-chee-chee’ calls (George 1981a). They occupy the same shelters for a long time; in 1972, they were still present at the same site where Lataste found them in 1885 (George 1974). Births recorded between mid-Dec and Jan. One young per litter (George 1978b). African Wild Cats *Felis sylvestris* are likely predators (George 1974). See Rosevear (1969) for further information.



Felovia vae

Conservation IUCN Category: Data Deficient, previously assessed as Vulnerable.

Felou Gundis are the most threatened of all species of gundis (but see Abundance above). They are not preyed on by humans in Mauritania.

Measurements

Felovia vae

HB: 179 (169–190) mm, n = 5

T: 73 (67–80) mm, n = 4

HF: 33.6 (31–37) mm, n = 9

E: 15.7 (14–17) mm, n = 7

WT: 185.8 ± 8 g, n = 10

GLS: 45.1 (42.8–47.3) mm, n = 8

GWS: 29.7 (27.4–31.8) mm, n = 8

M¹–M³: 8.5 (7.5–8.9) mm, n = 8**

Mauritania (MNHN)

Weight: George (1978b)

**P⁴ may occur in some adults; if so, cheekteeth measurement is P⁴–M³

Key References George 1974, 1978a, 1981a; Rosevear 1969.

Patrick Gouat

GENUS *Massoutiera*

Mzab Gundi

Massoutiera Lataste, 1885. Le Naturaliste 7 (3): 21. Type species: *Ctenodactylus mzabi* Lataste, 1881.

A monotypic genus distributed in desert and semi-desert rocky habitats in the Sahel Savanna BZ and the Sahara Arid BZ. The type species, although originally named *Ctenodactylus mzabi* by Lataste (1881), was transferred by him to his new genus, *Massoutiera*, on the basis of the bilobate pattern of the upper molar teeth. Characters of the genus include: palate extends posteriorly to the cheekteeth, toothrows converge anteriorly, upper molar teeth simple with narrow infoldings on both sides, and tail about one and a half times the length (ca. 148%) of the hindfoot (Misonne 1974); further details are given in the species profile. The single species is *Massoutiera mzabi*.

Patrick Gouat



Massoutiera mzabi.

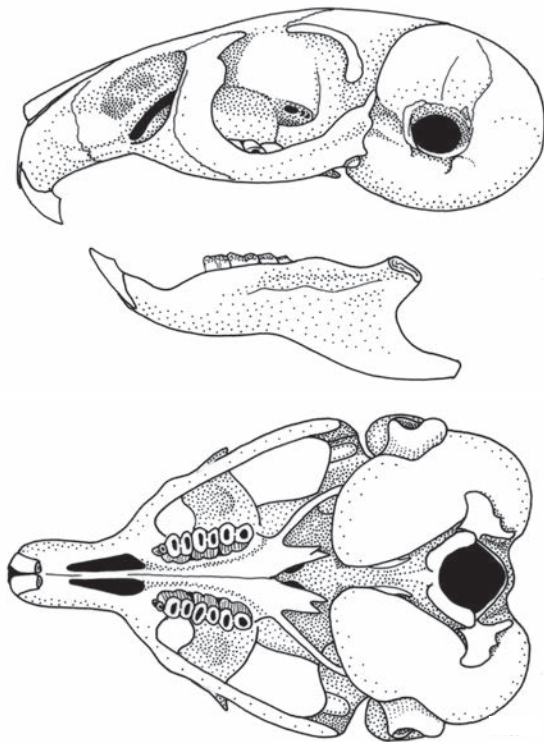


Figure 101. Skull and mandible of *Massoutiera mzabi* (BMNH 19.7.7.2923).

Massoutiera mzabi MZAB GUNDI

Fr. Goundi du Mzab; Ger. Sahara-Gundi

Massoutiera mzabi (Lataste, 1881). Bull. Soc. Zool. de France 6: 214. Ghardaia, Mzab, Algeria.

Taxonomy Two other species have been described in this genus (*Massoutiera haterti* and *Massoutiera rothschildi*), but although there are slight differences in the two forms, similar differences may be observed within a single population (Petter & Roche 1958). Synonyms: *harterti*, *rothschildi*. Subspecies: none. Chromosome number: $2n = 36$ (George 1979b).

Description General appearance of a small guinea-pig with small ears and a short, movable hairy tail. Pelage very dense and soft. Dorsal pelage cream to reddish-brown. Ventral pelage paler. Young have a pinker colouration than their parents. Head flat and broad. Forehead large and straight. Muzzle short with long black vibrissae. Nostrils naked and black. Eyes large and round surmounted by long vibrissae.

Ears flattened on head, oval, black inside bordered by a dense fringe of short stiff whitish-grey hairs. Fore- and hindlimbs short; four digits on each foot. Digits of the hindfeet are surmounted by comb-like bristles. Claws are sharp, not reaching to the ground in normal position. Tail of medium relative length (ca. 148% of HF), longer than in *Ctenodactylus* spp. but shorter than in *Felovia vae*; tail conspicuous (with flicking movements) when gundi is moving. Skull: see family and genus profiles; each upper incisor with single faint groove or without groove; angular process of mandible elongated posteriorly, but not to the extent as in *Ctenodactylus*; auditory bullae hugely inflated (ca. 18.2 mm, 40% of GLS) (Figure 101). Mean length of faecal pellets: 7.3 (6.6–7.9) mm. Nipples: $2 + 0 = 4$.

Geographic Variation None recorded.

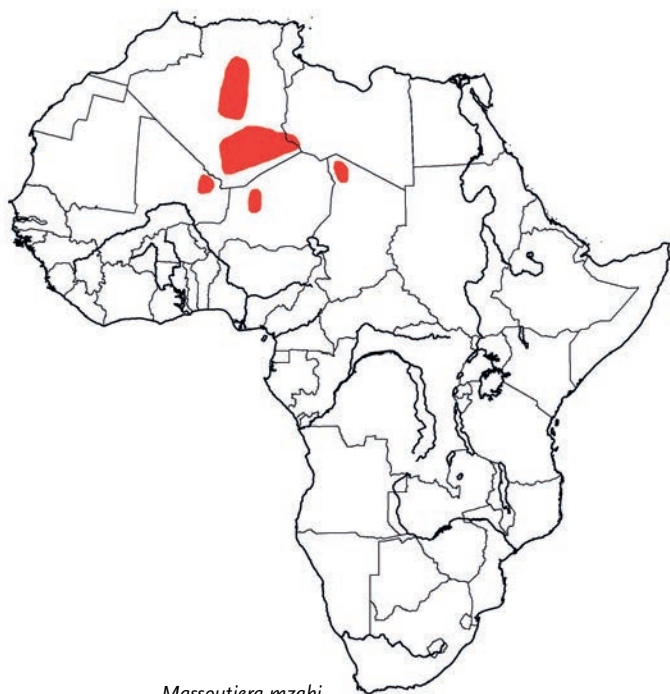
Similar Species

Ctenodactylus gundi and *Ctenodactylus vali*. Tail smaller, less visible; unilobate pattern of the upper molar teeth.

Felovia vae. Tail longer; upper incisors each with single groove; less inflated auditory bullae.

Pectinator spekei. Tail similar size; ears only partially flattened on the head; occurs only on the Horn of Africa. *Pectinator spekei* and *Felovia vae* are allopatric, and there is no risk of confusion with *M. mzabi* in the field.

Distribution Endemic to Africa. Sahara Arid BZ (northern edge) and Sahel Savanna BZ of NW Africa. Range discontinuous in Algeria, Libya, Mali, Niger and Chad. Algeria (north): Mzab region, Oued Mya Bassin, Tademaït. Algeria (south): Mouydir, Tefedest, Hoggar (= Ahaggar) Mts and Tassili n' Ajjer. Libya: Maghides Plateau, Akakus, Massak Mallat, Massak Mastafat, Al Haruj al Aswad, Djebel Sawda, Djebel Al Hasawinah. Mali: Adrar des Ifoghas. Niger: Aïr Massif. Chad: Tibesti Massif. The distribution in Libya is not shown on the map.



Massoutiera mzabi

Because of the close phylogenetic relationship of this species to *Felovia vae*, and its behavioural characteristics (Gouat 1991a), it is highly probable that *Massoutiera mzabi* evolved in the Sahel and spread northwards across the Sahara when the climate was less arid. The present geographical range of the species is discontinuous and is probably a relict of a formerly more widespread distribution (Jaeger 1977b, George 1988).

Habitat Mountainous regions of deserts and semi-deserts where rocks are present, but also in rolling hills of Mzab, and on the edges of hamadas in the Wadi Mya basin and Tademaït.

Abundance Patchily distributed in family groups (see below), and never abundant. Isolated animals are common, mainly during the summer. Density in the Mzab region (Algeria): 0.3–3.2 animal/ha (George 1981a, Gouat 1988a).

Adaptations See family profile.

Foraging and Food Herbivorous. Animals forage individually but may forage close to each other. In the Mzab during winter (Nov–Mar), they forage continuously from sunrise to sunset. In contrast, during the summer (Apr–Sep) they are partly nocturnal – foraging begins before sunrise and continues until 10:00h, when animals retreat into the shade or into their rocky shelters; foraging resumes in late afternoon and may continue until after sunset (Gouat 1991a). There is no specific place for foraging; animals collect food items while they travel through their territory.

Principal foods are the leaves, flowers, seeds and stalks of several species of herbs and grasses including *Moricandia arvensis*, *Reseda villosa*, *Launea angustifolia*, *Stipa retorta*, *Peganum harmala*, *Chrysanthemum macrocarpum*, *Centaurea incana*, *Limonium sinuatum*, *Scabiosa arenaria*, *Odontospermum pygmaeum* (George 1988).

Social and Reproductive Behaviour In the Mzab region of Algeria, adult ♀♀ are sedentary and territorial. An adult ♀ occupies a permanent territory (1000–2000 m²) throughout the year. In autumn (Sep–Dec), ♂ joins ♀ in her territory, and stays with her until the first mating (Nov–Dec) and the birth of the first litter (Jan–Mar). Depending on food availability, he remains with the ♀ until at least the time of the second mating (Mar–Apr), and at most until the beginning of summer (Jun). During the period of cohabitation, ♂ and ♀ cooperate to actively defend the territory against conspecific intruders. Mzab Gundis may modify their use of space from one day to another; night and day shelters may differ every day. An alarm call may be emitted in response to a potential predator. This vocalization is a whistle that begins with a sudden decrease of frequency from an ultrasonic frequency far exceeding 16 KHz, and then reaches a plateau at 11–13 KHz. When the animal is worried by an unusual situation, the frequency of the plateau may fluctuate between 8 and 12 KHz. Both adults and juveniles emit alarm calls. The same vocalization is used during agonistic encounters.

After the birth of the young, ♂ may watch them from a distance but rarely interacts with them during their first month of life. During this period, the young remain in the vicinity of their shelter. During the day or at night, ♀ may carry her young, one at a time, in her mouth from one shelter to another, holding the young across its body. During

daytime, the mother comes occasionally to feed the young and seems to spend at least a part of the night with them. This maternal behaviour appears to serve as a defence against predators (Gouat 1988a). In the presence of their mother, young gundis emit a 'modulated whistle', part of which is a 'hiss'. The whistle starts at 2 KHz and ends as an ultrasonic vocalization far exceeding 16 KHz, and is emitted in successive pulses, each lasting 0.15–0.35 sec. The 'modulated whistle' appears to have the same function as the 'extension trill' of the Atlas Gundi. When the young grow older, they become more mobile and follow the mother when they wish to suck. During exploration, juveniles emit low frequency chuckles (1–4 KHz) (J. Gouat pers. comm.). Juveniles interact amicably with both adult ♂♂ and ♀♀. With the arrival of the second litter, ♀ becomes aggressive towards her first young in order to avoid contact between juveniles and her new young. Juveniles are not aggressive to the young. Young of both litters remain within the territory of their mother until the beginning of the summer. Juvenile ♂♂ then disperse, while juvenile ♀♀ tend to stay with their mother for a longer time and try to establish themselves in a vacant territory near their mother. The formation of a group of related ♀♀ seems to be possible.

Reproduction and Population Structure Two litters each year in the Mzab region, Algeria. First mating: Nov–Dec. Birth of first litter: Jan–Mar; second litter: Apr–May. Gestation: ca. nine weeks (captive animal; Gouat 1988a). Litter-size: 2 (1–3), $n = 17$ litters (combined data from George 1978a, Gouat 1988a). Data from other localities is inconclusive: at Mt Baguezan (Aïr, Niger), three ♀♀ with fetuses were captured in May; at Hoggar (Algeria), one ♀ with two well-developed fetuses obtained in mid-Apr (Thomas & Hinton

1921); at Al Haruj al Aswad (Libya), one ♀ with a ca. two-week old young in late Dec.

Predators, Parasites and Diseases Preyed on by humans, canids, birds of prey and snakes (Gouat 1988a).

Conservation IUCN Category: Least Concern.

Measurements

Massoutiera mzabi

HB: 176 (125–210) mm, $n = 16$

T: 52 (33–85) mm, $n = 14$

HF: 35 (33–36) mm, $n = 10$

E: 17 (15–17) mm, $n = 10$

WT: 200 (132–234) g, $n = 7$

GLS: 45.5 (39.8–48.5) mm, $n = 24$

GWS: 29.3 (25.3–32.5) mm, $n = 24$

M^1 – M^3 : 8.4 (7.8–9.2) mm, $n = 23^*$

Algeria, Chad and Mali (MNHN) and Berriane region (Mzab, Algeria), and from their descendants born in captivity (J. Gouat & P. Gouat unpubl.)

* P^4 may occur in some adults; if so, cheekteeth measurement is P^4 – M^3

Key References George 1988; P. Gouat 1988a, 1991a; Gouat *et al.* 1984.

Patrick Gouat

GENUS *Pectinator*

Speke's Pectinator

Pectinator Blyth, 1856. Journ. Asiatic Soc. Bengal, for 1855, (2) 24: 294 [1856]. Type species: *Pectinator spekei* Blyth, 1855.

Monotypic genus distributed in desert and semi-desert rocky habitats in Ethiopia, Eritrea, Djibouti and Somalia. The characters of the genus include: ears partially flattened on top of head (all other species 'flattened'); palate does not extend posteriorly to the cheekteeth (cf. all other genera of gundis), tooththrows more or less parallel and not converging anteriorly; upper molar teeth simple

with narrow infoldings on both sides, and tail about double the length (ca. 224%) of the hindfoot (Misonne 1974); further details are given in the species profile. The single species is *Pectinator spekei*.

Patrick Gouat

Pectinator spekei SPEKE'S PECTINATOR

Fr. Pectinator de Speke; Ger. Buschschwanz-Gundi

Pectinator spekei Blyth, 1856. J. Asiat. Soc. Bengal for 1855 (2) 24: 294. Between Goree Bunder and Nogal, Somalia.

Taxonomy Synonyms: *legerae*, *meridionalis*. Subspecies: none. Chromosome number: $2n = 40$ (George 1979b).

Description General appearance of a small guinea-pig with ears only partially flattened on the head, and a short, movable hairy tail. Pelage very dense and soft. Dorsal pelage ashy-grey, suffused with black or brown. Flanks greyish. Ventral pelage greyish-white. Head flat and broad. Muzzle short with long black vibrissae. Ear broadly

ovoid, almost naked, with a fringe of whitish hairs on anterior margin. Fore- and hindlimbs short; four digits on each foot. The digits of the hindfeet have three-tiered combs (George 1978a). Tail hairy and long for a gundi (ca. 224% of HF); white on the basal half, black on terminal half with white tip; tail conspicuous even when gundi is resting. The tail appears whitish along its middle, with two lateral black lines externally fringed with dull white. Skull: see family and genus profiles; each upper incisor without groove; angular process of mandible



Pectinator spekei.

short, not reaching level of coronoid process; auditory bullae moderately inflated (ca. 14.9 mm, 33% of GLS) (Figure 102). Mean length of faecal pellets: not known. Nipples: $2 + 0 = 4$.

Geographic Variation None recorded.

Similar Species No other species of gundi lives on the Horn of Africa.

Distribution Endemic to Africa. Somalia–Masai Bushland BZ. Recorded from rocky habitats in Ethiopia, Eritrea, Djibouti and Somalia.

Habitat In Ethiopia, Speke's Pectinator inhabits volcanic and limestone rocky cliffs in desert or semi-desert areas. Altitudinal range: 0–1200 m (Yalden *et al.* 1976). Also lives in man-made rocky escarpments bordering roads (George 1974). Recorded up to 1950 m in N Somalia (N. Redman pers. comm.).



Pectinator spekei

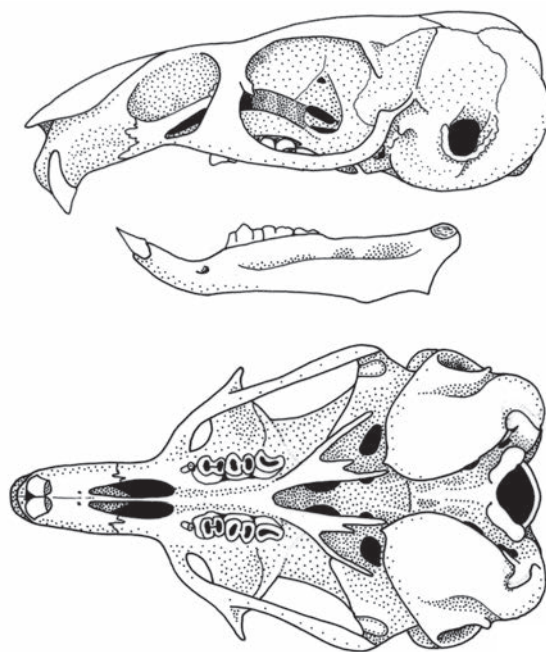


Figure 102. Skull and mandible of *Pectinator spekei* (BMNH 14.2.9.2).

Abundance Speke's Pectinators live at much higher densities than any other species of gundi. In the Danakil Desert of Ethiopia, densities range from 24 to 237 animals/ha (George 1981a).

Adaptations Terrestrial and diurnal. Emerges from rocky shelters at sunrise; maximum activity occurs 0–3 hours after sunrise when ambient temperature is 23–29°C; retreats to shelters during the daytime when temperature reaches 33–34°C and emerges again in late afternoon. Pectinators climb trees and may rest on branches in the shade (George 1974). (See also family profile.)

Foraging and Food Herbivorous. Feeds on dry grass (stalks and seeds), and on leaves of *Caboda rotundifolia*, *Acacia senegal* and *A. seyal* trees (George 1974). Food resources fluctuate seasonally from abundant during the wet season to scarce during the dry season.

Social and Reproduction Behaviour Sociable, living in colonies based on extended family units. When there is a perceived danger, animals emit an alarm call that begins with a chirp, then a long whistle and finally three to six chirps (duration: 0.6–1.5 s, frequency: 1–4 KHz) (George 1981a). Pectinators share their habitat with Rock Hyraxes *Procapra capensis*.

Reproduction and Population Structure In the Danakil desert, births occur from late Aug to mid-Sep after the short wet season. Elsewhere in Ethiopia (no precise locality) births occur in ca. Jan. Litter-size: 1.2 (1–2, n = 6). Birth WT: ca. 20 g; young precocial, fully furred at birth. Time to attain adult weight: ca. 174 days. Growth rate is regular (George 1978b).

Predators, Parasites and Diseases Gabar Goshawks *Micronisus gabar* attempt to catch pectinators (George 1974).

Conservation IUCN Category: Data Deficient.

Measurements

Pectinator spekei

HB: 170 (155–190) mm, n = 8

T: 74 (60–80) mm, n = 10

HF: 33.1 (30–36) mm, n = 11

E: 19.0 (16–21) mm, n = 11

WT: 178.2 ± 0.9 g, n = 4

GLS: 44.9 (42.5–47.6) mm, n = 13

GWS: 26.5 (25.1–28.9) mm, n = 11

P⁴–M³: 8.2 (6.9–9.0) mm, n = 13

Body and skull measurements: Djibouti, Somalia and Ethiopia (MNHN)

Weight: George (1978b)

Key References George 1974, 1978a, b, 1981a.

Patrick Gouat

Family BATHYERGIDAE

MOLE-RATS

Bathyergidae Waterhouse, 1841. Ann. Mag. Nat. Hist., ser. 1, 8: 81.

| | | |
|-----------------------------------|------------------|--------|
| <i>Bathyergus</i> (2 species) | Dune Mole-rats | p. 644 |
| <i>Cryptomys</i> (10 species) | Mole-rats | p. 648 |
| <i>Georchus</i> (1 species) | Cape Mole-rat | p. 662 |
| <i>Heliophobius</i> (1 species) | Silvery Mole-rat | p. 664 |
| <i>Heterocephalus</i> (1 species) | Naked Mole-rat | p. 667 |

The Bathyergidae is a polygeneric family, distributed throughout most of tropical and sub-tropical sub-Saharan Africa, in habitats ranging from open forest to savannas and semi-deserts. All species in the family are subterranean, living in soils that range from soft coastal sands to soils that are extremely hard when dry. There are five genera and at least 15 species, all endemic to Africa (Ellerman 1940, De Graaff 1964a, 1981, Skinner & Smithers 1990, Faulkes *et al.* 1997b, Bennett & Faulkes 2000). The genera *Georchus* and *Bathyergus* are restricted to South Africa, *Heterocephalus* and *Heliophobius* occur only in eastern Africa, and *Cryptomys* occurs in eastern, western and southern Africa. Several genera are sympatric and syntopic, especially in southern Africa. The Bathyergidae is one of the most specialized families of African rodents, and has been the subject of many studies.

All members of the family show morphological adaptations to life underground. Head and body cylindrical in shape, without distinct neck. Limbs short. Fore- and hindfeet have five digits each and naked soles; the radiale (scaphoid) and intermedium (lunar) carpal bones are separate, a feature unique to Bathyergidae and Ctenodactylidae. Pelage short and thick; longer sensory hairs are present over much of the body and are especially numerous on the head. Skin very loosely attached and, in those genera with hair, can be shaken vigorously (20–25 vibrations/sec) to clean pelage of soil. Digits and outer borders of the feet fringed with stiff hairs. Tail very short and fringed with stiff hairs in all genera except *Heterocephalus*. Eyes very small and unable to form images, usually kept closed. Lacks ear pinnae, opening of external auditory meatus is slightly raised; hearing is good. Nostrils housed in a flat horseshoe-shaped nasal area situated above prominent extra-buccal incisors. Muscular folds, covered with medially directed stiff hairs, meet behind the incisors and keep soil out of the mouth when digging. Skull tends to be stoutly built; infraorbital foramina small and secondarily reduced, varied in shape and dimensions and in the thickness of the bone on the outer wall; cheekteeth (premolars and molars) strongly hypsodont and rooted, number varying in number in the different genera. Upper incisors pro-odont and sharp, with either a single groove on the anterior surface of each incisor (*Bathyergus*) or ungrooved (all other genera). Upper incisors of *Bathyergus* are rooted above the anterior cheekteeth, those of other genera more procumbent and rooted posteriorly to the cheekteeth (Ellerman 1940, De Graaff 1964a, 1981). Lower incisors ungrooved. The angle of the lower jaw strongly flared outwards to allow passage of a specialized portion of the superficial masseter lateralis muscle. The two halves of the mandible not firmly ankylosed, permitting lateral splaying of the lower incisors (Jarvis & Bennett 1991; *contra* De Graaff 1981). Dental formula varied, but usually $I^{1/1}, C^{0/0}, P^{1/1}, M^{3/3} = 20$. *Heliophobius* is unusual because the complete cheekteeth formula (P and M) is $s^{6/6}$, but at any one time it is $5/4$ or $4/4$, and occasionally $4/5$ or $6/6$; the

anterior premolars are usually shed before the posterior molars have erupted. *Heterocephalus* only has three molariform teeth in each ramus and on occasion this is reduced to two. In *Cryptomys*, M^3 erupts early in life, and in *Georchus* M^3 erupts late in life (De Graaff 1981). All cheekteeth are molariform in structure and differ only in size.

All genera are strictly subterranean (see Table 15); individuals live and feed in an extensive network of burrows, the majority of which are superficial foraging burrows running at depths close to those of their food. Deeper burrows link foraging areas with nest, toilet area and, where present, a food store. Loose skin facilitates turning in the tight confines of the burrow. All genera, except *Bathyergus*, are chisel-tooth diggers, biting at the soil face with their sharp rapidly growing incisors. All genera use fore- and hindfeet to push the loosened soil behind them; fringes of hairs on feet and tail help contain the soil as a mole-rat reverses down the burrow and up a side-branch where the soil is disposed of as a mound (or mounds) at the surface (Jarvis & Sale 1971). Except at the inception of mound formation, all genera, except *Heterocephalus*, have a plug of soil between the burrowing animal and the outside. Once the mound is fully formed, the side-branch is packed with soil thereby sealing the burrow system from the surface. Mole-rats are most vulnerable to predation by snakes, birds and small carnivores during mound formation, the only time when an above-ground predator can accurately locate them. Activity patterns appear to vary seasonally, largely in response to temperature changes in superficial foraging burrows; mole-rats show poor ability to entrain their circadian rhythms to light. Peak burrowing activity, and mound formation, occur after rainfall when soil is easily worked. When the soil is very dry, excavated soil is packed into disused sections of the burrow system and not disposed of on the surface (Jarvis & Sale 1971, Jarvis & Bennett 1991).

Mole-rats have little exposure to sunlight and exhibit signs of vitamin D3 deficiency. Nevertheless, unlike most mammals that need vitamin D3 for calcium uptake, mole-rats absorb calcium in the intestine and kidneys via specialized vitamin D3-independent paracellular processes (Buffenstein *et al.* 1994). The diet is high in cellulose and fibre, and is digested by symbiotic micro-organisms in a large caecum and hindgut. Digestive efficiency is high (>80%), facilitating maximum returns for foraging effort (Buffenstein & Yahav 1991a, 1994, Bennett & Jarvis 1995), and is further enhanced by re-ingesting partly digested faecal pellets. This autocoprophagy contributes to digestive efficiency, reinoculates the mole-rat with endosymbionts and provides an additional source of protein and energy from digestion of the microbes themselves. For their size, members of the Bathyergidae have lower than predicted metabolic rates (McNab 1966, Lovegrove 1986, Buffenstein & Yahav 1991b) and long maximum life-spans: >26 years for captive *Heterocephalus glaber* and >12 years for *Cryptomys damarensis* (O'Connor *et al.* 2002, Sherman & Jarvis 2002, J. U. M. Jarvis & N. C. Bennett unpubl.).

Bathyergus, *Heliophobius* and *Georchus* are solitary, each individual aggressively defending its burrow system against conspecifics. All breed seasonally. *Bathyergus* and *Georchus* communicate through the soil by drumming with their hindfeet. Occupancy of a burrow by

more than one animal occurs briefly at mating; young leave the maternal burrow at about two months; 1–2 litters are born during the breeding season (Jarvis & Bennett 1991, Sumbera *et al.* 2003a). In contrast, *Heterocephalus* and *Cryptomys* are social: colonies consist of family units usually with a single reproductive ♀, 1–3 consort ♂♂ and a number of non-reproductive (but not infertile) helpers (Jarvis 1981, Bennett 1988, Jarvis & Bennett 1991, Jarvis *et al.* 1994). New colonies of *Cryptomys* are formed from an out-bred pair and their offspring; the colony fragments on the death of the reproductive animals (Jarvis & Bennett 1993, Jarvis *et al.* 1994, Bishop *et al.* 2004, Burland *et al.* 2004). *Heterocephalus* is strongly xenophobic, frequently inbreeds, and replacement of reproductive animals often occurs from within the colony; occasionally out-breeding may occur (O’Riain *et al.* 1996, O’Riain & Braude 2001). Some *Cryptomys* breed seasonally (e.g. *C. h. hottentotus*) and others aseasonally (e.g. *C. damarensis*; Bennett 1988, Spinks *et al.* 1999). Breeding in *Heterocephalus* is aseasonal. Gestation is long: 56–111 days in *Cryptomys* and *Heliophobius*, and 66–74 days in *Heterocephalus* (Bennett *et al.* 1991). In seasonal breeders, a maximum of two litters are born annually, whereas aseasonal breeders have 3–4 litters each year. In all genera, testes lie abdominally or in inguinal pockets, and there is no development of a scrotum. Non-reproductive ♀♀ have small nipples and a vagina closure membrane. Litter-sizes are usually 2–6 young/litter, but reach 28 young/litter in *Heterocephalus*. Maximum recorded colony sizes are 41 animals for *Cryptomys damarensis* (Jarvis & Bennett 1993) and >300 for *Heterocephalus* (Brett 1991a, S. Braude unpubl.).

Bathyergus dig extensive foraging burrows with their strongly clawed forefeet; other genera bite at the soil with large, rapidly growing, extra-buccal incisors. All feed on underground portions of plants, particularly roots, bulbs, corms and tubers located while digging extensive, superficial foraging burrows. *Bathyergus* and *Georchus* also eat aerial parts of plants by loosening the soil under the roots, and then pulling the entire plant into the burrow. Most genera store small food items in a chamber or blind-ending burrow situated close to the nest. Larger items are eaten *in situ*, often being partly eaten and then left to regenerate (Jarvis & Bennett, 1991). Mole-rats do not drink free water. Solitary genera are usually restricted to mesic habitats where food items are spaced close together and where rainfall is frequent allowing frequent opportunities to burrow. Sociality has enabled *Cryptomys* and *Heterocephalus* to also inhabit arid regions where food is widely dispersed and patchy and where rainfall is sparse and unpredictable, allowing for only limited opportunities to burrow (Jarvis & Bennett 1993, Jarvis *et al.* 1994). After rainfall, colonies can dig >1 km of foraging burrows in a month, rapidly expanding their home-range while the cost of digging is relatively low. Most of the food needed to sustain the colony until the next rains is located at this time. All species peel their food, holding onto small items of food with their forefeet while eating, with frequent pauses to shake it, or hold it, between their incisors and to brush it with the forefeet. All except *Heterocephalus* balance on the hindfeet while feeding on small items; *Heterocephalus* rests on the elbows.

The Bathyergidae is a monophyletic group currently placed with the suborder Hystricomorpha, infraorder Hystrignathi. The Bathyergidae are the most species-rich of the four African families of the Hystricognatha, which also includes the families Hystricidae, Petromuridae and Thryonomyidae. Bathyergids show a number of unique features. All five genera have a highly flared angle of the lower

jaw, secondarily reduced infraorbital foramina, and unfused carpal bones. Few genera of other families of rodents have such a variable number of cheekteeth (3–6 in both upper and lower jaws) (Ellerman 1940, De Graaff 1981). Closest, but still distant, relatives are the other phiomorph families of the Hystricognathi: Rock Rats (Petromuridae), Cane Rats (Thryonomyidae) and Old World Porcupines (Hystricidae). Fossils from two extinct genera of bathyergids and of *Heterocephalus* date from the early Miocene (ca. 25 mya) in East Africa and Namibia. Molecular evidence also indicates early divergence of *Heterocephalus* and *Heliophobius* from extant members of the family (Allard & Honeycutt 1992, Faulkes *et al.* 1997b, 2004).

Taxonomy of the Bathyergidae, particularly of *Cryptomys*, is under review. *Cryptomys* spp. from C Zambia and around Pretoria, South Africa, show much genetic divergence and several, as yet undescribed, species have been found. Little is known of the relationships of *Cryptomys* spp. from West Africa and Uganda. Additionally, genetically divergent *Heliophobius* have been found in WTanzania and Malawi, and divergent *Heterocephalus* in Ethiopia (Faulkes *et al.* 1997b, 2004). The significance of these genetic divergences is unclear.

The family is traditionally divided into two subfamilies, Bathyerginae and Georchichinae (De Graaff 1981, Allard & Honeycutt 1992) and currently 15 species are recognized (Table 45). The Bathyerginae has grooved upper incisors whose roots originate above the cheekteeth, enlarged forefeet and claws and large body size (up to ca. 2000 g), and contains one genus (*Bathyergus*) and two species. The Georchichinae has ungrooved upper incisors with roots originating behind the molars, forefeet and claws which are not enlarged, and a smaller body size (<500 g), and contains four genera (*Georchus*, *Heliophobius*, *Heterocephalus*, *Cryptomys*) and about 13 species. However, the above subfamilial groupings are not supported by molecular phylogenies, and are not considered here. *Bathyergus* forms either a clade within the paraphyletic Georchichinae or it groups with *Georchus* in a monophyletic clade. Thus it would appear that the long claws on forefeet and grooved upper incisors are derived traits peculiar to *Bathyergus* (Faulkes *et al.* 2004). All molecular studies agree that *Heterocephalus* is basal and divergent in the family. Woods & Kirkpatrick (2005) place the genera *Bathyergus*, *Cryptomys*, *Georchus* and *Heliophobius* in the subfamily Bathyerginae, and the genus *Heterocephalus* in a subfamily of its own, the Heterocephalinae.

The five genera recognized here are:

Bathyergus: silvery to tan pelage with darker mid-dorsal band, colour very variable; head darker with paler areas round the eyes, ears, nose and chin; upper and lower cheekteeth, simple; the only genus with elongated claws and grooved upper incisor teeth; weight up to 2000 g.

Georchus: strikingly marked head and face: black to charcoal head with white patches on muzzle; eyes and ears on top of head; four upper and lower cheekteeth with persistent re-entrant folds; palate extends behind tooththrow; ungrooved upper incisor teeth; weight up to 350 g (1 sp.).

Heliophobius: silver to tan pelage, sometimes lacking white head-patch; up to six upper and lower simple cheekteeth (not usually all present at the same time); palate not extending behind tooththrow; ungrooved upper incisor teeth; weight up to 260 g (possibly 2 spp.).

Heterocephalus: skin pink-brown, lacking a pelage although isolated sensory hairs are present; only genus with long tail; three upper

Table 45. Species in the family Bathyergidae. Arranged alphabetically.

| Species | HB mean (mm) | GLS mean (mm) | Pelage colour | Groove on each upper incisor | Infra-orbital foramen (longest dimension) | Other characters | Notes |
|--------------------------------------|--------------|---------------|---|------------------------------|---|---|---|
| <i>Bathyergus janetta</i> | 205 | 51.9 | Silvery-fawn (variable) | Single | Small, almost round (2 mm dia.) | White eye-ring. Angle of mandible extends posteriorly to skull | South-West Arid BZ (parts) |
| <i>Bathyergus suillus</i> | 281 | 65.1 | Cinnamon-brown | Single | Small, almost round, (2–3 mm dia.) | Pale eye-ring. Mandible as <i>B. janetta</i> | South-West Cape BZ |
| <i>Cryptomys anelli</i> | 121 | 33.9 | Slate-grey (young); golden-ochre (adult) (variable) | Absent | Elliptical, wide at base (n. d.) | White patch on forehead (most) | Zambia (Lusaka region) |
| <i>Cryptomys bocagei</i> | 151 | 31.1 | Grey, silvery-grey | Absent | Small, teardrop (1.5–2 mm) | White patch on forehead | Zambezian Woodland BZ |
| <i>Cryptomys damarensis</i> | 164 | 36.2 | Fawn, brown or black | Absent | Small, teardrop (1.5–2 mm) | Mid-dorsal and mid-ventral stripes | Zambezian Woodland and South-West Arid (Kalahari) BZs |
| <i>Cryptomys darlingi</i> | 145 | 33.3 | Blackish to silvery-grey (variable) | Absent | Small, teardrop (1.5–2 mm) | White ventral stripe or patch | Zambezian Woodland BZ (Zimbabwe, C Mozambique) |
| <i>Cryptomys foxi</i> | 145 | 40.7 | Sepia-brown | Absent | Oval teardrop (1.5–2 mm) | Subcircular white patch on forehead | Highlands of C Nigeria and Cameroon |
| <i>Cryptomys hottentotus</i> | 122 | 30.6 | Cinnamon-buff to dark grey (variable) | Absent | Elliptical (ca. 3 mm) | | Widespread in South-West Cape, South-West Arid, Highveld and parts of Coastal Forest Mosaic BZs |
| <i>Cryptomys kafuensis</i> | 112 | 33.5 | Slate-grey to golden-ochre | Absent | Elliptical (n. d.) | Small conspicuous white patch on forehead | S Zambia |
| <i>Cryptomys mechowii</i> | 190 | 52.0 | Greyish-brown to golden-ochre | Absent | Elliptical (ca. 5 mm) | No white patch on forehead (usually). Bristles on margins of feet | Zambezian Woodland BZ and Southern Rainforest Mosaic |
| <i>Cryptomys ochraceocinereus</i> | 169 | 43.2 | Medium brown | Absent | Round-oval (ca. 2 mm dia.) | Conspicuous round white head patch. White eye-ring | Northern Rainforest–Savanna Mosaic |
| <i>Cryptomys zechi</i> | 167 | 42.7 | Pale cinnamon-buff | Absent | Round-oval (ca. 2 mm dia.) | White patch on forehead | NW Ghana, Togo |
| <i>Georchus capensis</i> | 189 | 48.3 | Russet-brown | Absent | Small, round (ca. 1–1.5 mm) | Distinctive black and white markings on head. White eye-ring | South-West Cape and Highveld BZs |
| <i>Heliophobius argenteocinereus</i> | 161 | 39.1 | Silvery-grey to tan | Absent | Round (dia. 1.5 mm) | White patch on forehead (some). Bristles on margins of feet | Zambezian Woodland and southern part of Somalia–Masai Bushland BZs |
| <i>Heterocephalus glaber</i> | 84 | 21.4 | Naked (no pelage) | Absent | Round, very small (ca. 0.5 mm) | Tail comparatively long (ca. 50% of HB) | Somalia–Masai Bushland BZ (Somalia–SE Kenya) |

and lower cheekteeth; Digit 3 of forefoot longer than Digit 4; ungrooved upper incisor teeth; weight highly variable 25–80 g (1 sp.).

Cryptomys: pelage colour varies from silver, grey, tan, charcoal and black; many have a white head-patch; four upper and lower cheekteeth with only traces of infolding; ungrooved upper incisor teeth; weight up to 600 g. Two groups/subclades have been

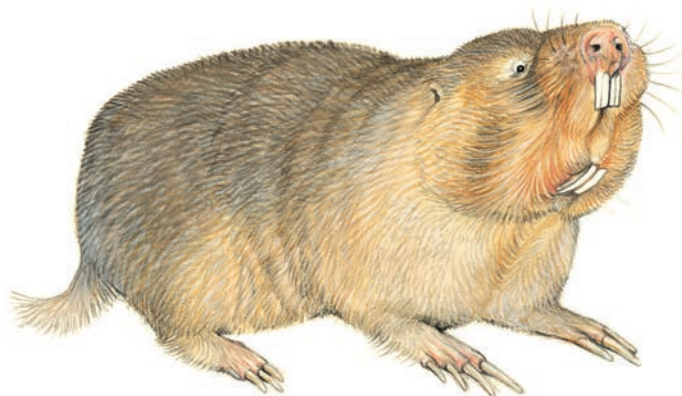
identified in this genus, as a result of differences in the infraorbital foramina and in mitochondrial cytochrome *b*. One subclade has small thick-walled infraorbital foramina (at least 6 spp.), the other has elliptically shaped and thin-walled infraorbital foramina (at least 3 spp.).

J. U. M. Jarvis

GENUS *Bathyergus*

Dune Mole-rats

Bathyergus Illiger, 1811. Prodr. Syst. Mamm. Avium., p. 86. Type species: *Mus maritimus* Gmelin, 1788 (= *Mus suillus* Schreber, 1782).



Bathyergus suillus.

This small genus contains two species distributed along the SE and NW coastal regions of South Africa and the SW coast of Namibia. Both are restricted to sandy soils, hence their common name 'Dune Mole-rats'.

Bathyergus contains the largest mole-rats, and is the only genus with the following set of characters: enlarged strongly clawed forelimbs (Digits 2, 3 and 4 bearing largest claws); grooved upper incisors that are less protruding than other genera and are rooted above the anterior cheekteeth; and with the angular process of mandible extending backwards behind the skull more than in all other genera of mole-rats (Ellerman 1940, De Graaff 1981).

Members of the genus dig with strongly clawed forelimbs (the only bathyergids to do so), using the teeth to sever roots that they encounter. When the soil is dry, foraging burrows often run deeper than food items, reducing the risk of these large-diameter burrows collapsing in the very loose sandy soil; the mole-rats dig upwards every now and then to locate their food. Up to 60% of diet is aerial (above ground) parts of plants; dune mole-rats dig up under the plant, isolate or sever the roots, and pull the entire plant underground; some is eaten and some used as nesting. They also eat roots and the subterranean storage organs of geophytes (Davies & Jarvis 1986). Dune mole-rats are solitary, drum with the hindfeet to advertise territory and perhaps to attract mates. There is marked sexual dimorphism: ♂♂ are larger with very thick skin (up to 10 mm) on the ventral surface of neck – perhaps as a protection during fighting for mates. Reproduction is seasonal, with a maximum two litters of 1–6 young/season (Jarvis 1969b, Herbst *et al.* 2004). Occasionally animals are found wandering on the surface, where they are very vulnerable to predators (Davies & Jarvis 1986, J. U. M. Jarvis unpubl.).

The species are distinguished by size, colour of pelage, and skull characters. The two species are allopatric over most of their geographic range but are sympatric near Groenriviersmond and Rondawel (31° S, 18° E) on the west coast of South Africa (Faulkes *et al.* 2004).

J. U. M. Jarvis

Bathyergus janetta NAMAQUA DUNE MOLE-RAT

Fr. Rat-taupe des dunes de Namaqua; Ger. Namaqua-Strandgräber

Bathyergus janetta Thomas and Schwann, 1904. Abstr. Proc. Zool. Soc. Lond. 2: 6. Port Nolleth, coastal Little Namaqualand, NW Cape Province, South Africa.

Taxonomy Originally described as a subspecies of *B. suillus* but De Graaff (1981) believed it to be a valid species, a view followed by later authors and supported by genetic information (Nevo *et al.* 1987, Faulkes *et al.* 1997b). Synonyms: *inselbergensis*, *plowski*. Subspecies: none recognized here although there is considerable geographic variation in size and colour that may indicate the existence of coastal and inland subspecies. Roberts (1951) recognized three subspecies but they were not recognized by De Graaff (1981) because the sample sizes were small. Subspecies: none. Chromosome number: $2n = 54$, $FN = 104$ (Nevo *et al.* 1986).

Description Medium to large mole-rat (although smaller than *B. suillus*). Pelage colour varies geographically (see below). Pelage with silvery sheen. Dorsal pelage silvery-fawn with broad band of dark seal-brown or dark grey from nape of neck to rump. Flanks silvery-grey or seal. Ventral pelage darker than flanks. Long pale-coloured tactile hairs scattered over body. Head dark brown or black, white patch or stripe on muzzle and sometimes on chin. Eyes with white eye-ring. Ear opening often surrounded by white patch. Limbs and feet dark slaty-

grey above, dull white below; strong curved claws. Tail very short (ca. 24% of HB), pink above, white below with long dull white bristles (De Graaff 1981, Skinner & Smithers 1990). Skull rounded (more so than in *B. suillus*); sagittal and occipital ridges small; each upper incisor with a single deep groove; auditory bullae rather swollen; palate does not extend posteriorly beyond the molars; infraorbital foramen small, almost round (2 mm dia.), with thick outer wall. Angular process of mandible extends posteriorly well beyond end of skull. Males on average larger than ♀♀. Nipples: $2 + 1 = 6$.

Geographic Variation Individuals near the coast are smaller and paler in colour (description above). Individuals further inland are larger and may be almost black with silvery flanks.

Similar Species

Bathyergus suillus. HB larger; less contrasting pelage, without sheen; skull much flatter, larger sagittal and occipital ridges, auditory bullae not markedly swollen, and palate extending posteriorly beyond level of M^3 .



Bathyergus janetta

Distribution Endemic to Africa. Recorded in South-West Arid BZ (Namib and Karoo) from near Rndawel in W Northern Cape Province northwards along the coast to the Orange R., and about 90 km into Namibia (Faulkes *et al.* 2004). Inland extends from Springbok and Kamieskroon to Ezelfontein in the Kamiesberg Mts at an altitude of 1350 m (Roberts 1951, De Graaff 1981). Over much of the inland range, occurs in sympatry with *Cryptomys hottentotus*; near Groenriviersmond and Rndawel, the southernmost part of range, occurs in sympatry with *B. suillus* (Faulkes *et al.* 2004).

Habitat Coastal sand dunes and consolidated sandy alluvial soils inland where mean annual rainfall is <400 mm. Vegetation is typical of the Namaqualand Namib Domain of the Succulent Karoo floristic region (Jürgens 1991), with winter rainfall, abundant spring flowers, herbs and grass after good winter rains. These ephemeral plants die down at the onset of the prolonged, hot, dry season, leaving a sparse covering of low shallow-rooted and drought-resistant shrubs with succulent leaves, patches of grass, a variety of succulents and abundant geophytes. Range of habitats within this floristic region is slightly more diverse than in the habitat of *B. suillus* and includes the coastal Sandveld, southern Namib Desert and Richtersveld.

Abundance Occurs in small isolated patches, particularly in the most arid part of range where often associated with seepage areas where geophytes abound. Densities are greatest inland, where the rainfall is higher: up to 44 individuals/km². The mean home-range is 806 m² (range 398–12,438 m², n = 6) (Herbst 2002).

Adaptations Subterranean. Burrow systems are usually 57–175 m in length but may be as long as 250 m; foraging burrows are 250–400 mm below the surface and 107–136 mm in diameter (N. C. Bennett, J. U. M. Jarvis & R. Tharm unpubl.). Method of digging and burrow configuration are similar to *B. suillus*. Nests are located 40–58 cm below ground, each has a single entrance, and nests contain

pieces of grass and outer husks of geophytes; there may be up to five nests per burrow. In the inland part of the range, burrows may overlap, but at different depths, with those of *Cryptomys h. hottentotus* (J. U. M. Jarvis & N. Bennett unpubl.).

Foraging and Food Herbivorous. In spring after the winter rainfall, Namaqua Dune Mole-rats eat aerial vegetation—daisies, grasses and herbs—which is pulled into their burrows. In dry conditions when most of this aerial vegetation has died down, they subsist on geophytes (bulbs, tubers, corms) and also succulent roots and stems of *Herrea* spp. and *Trachyandra* spp.; these succulents are often abundant and probably enable Namaqua Dune Mole-rats to occur in arid regions. Namaqua Dune Mole-rats store food (geophytes and roots) in a side branch in the burrow (1–2 stores per burrow system). Partly eaten roots of *Herrea* plants that are still growing next to the burrows have been found in excavated burrows (N. Bennett, J. U. M. Jarvis & R. Tharm unpubl., Herbst 2002). Most foraging burrows are dug after rainfall.

Social and Reproductive Behaviour Solitary. Territorial drumming is used to inform conspecifics of their presence. More drumming occurs at the onset of the breeding season, presumably to communicate with prospective mates. Drumming is achieved by simultaneously hitting the burrow floor with both hindfeet. Occupancy of a burrow by more than one adult animal has been recorded in May–Aug, possibly indicating the onset of mating (Herbst 2002). Nothing known about reproductive behaviour.

Reproduction and Population Structure Reproduction is seasonal. Individuals become reproductively active towards end of winter and at onset of early spring rains. The concentration of testosterone is raised Jul–Nov, as is oestradiol Jul–Aug and progesterone Jul–Sep (Herbst 2002). Pregnant ♀♀ captured in spring and early summer (Aug–Nov); and ♀♀ with young in Sep–Dec. A newly dispersed juvenile (62 g) captured in Dec. Minimum length of gestation: 52 days (time of capture to birth of litter, n = 2 animals). One, sometimes two, litters per season. Litter-size: 2–7 (n = 13). At birth, young weigh 15.4 g (11.4–19.9 g, n = 9). Solid foods first eaten ca. Day 10. Weaned ca. Day 34. Eyes open Day 14. Inter-sibling sparring begins around Day 44 and young disperse from ca. Day 60 (Herbst *et al.* 2004). One coastal ♀ weighing 198 g was pregnant, indicating the small adult body size in this part of the geographic range (J. U. M. Jarvis unpubl.).

Predators, Parasites and Diseases Mole-snakes *Pseudapsis cana* prey on Namaqua Dune Mole-rats. Large raptors, jackals and other carnivores may be potential predators. No information on parasites and diseases.

Conservation IUCN Category: Least Concern.

Listed as rare in South African Red Data Book (1986). The restricted distribution and damage to the habitat by strip-mining for diamonds on the coast are cause for concern.

Measurements

Bathyergus janetta

HB (♂ ♂): 205 (170–235) mm, n = 9

HB (♀ ♀): 183 (170–205) mm, n = 10
 T (♂ ♂): 47 (41–52) mm, n = 9
 T (♀ ♀): 44 (40–50) mm, n = 10
 HF (♂ ♂): 41 (38–43) mm, n = 9
 HF (♀ ♀): 37 (34–40) mm, n = 10
 WT (♂ ♂): 412 (242–500) g, n = 7
 WT (♀ ♀): 306 (198–460) g, n = 12
 GLS (CbL) (♂ ♂): 51.9 (41.1–54.8) mm, n = 5
 GLS (CbL) (♀ ♀): 43.9 (40.4–50.7) mm, n = 12
 GWS (♂ ♂): 31.2 (26.5–37.2) mm, n = 6
 GWS (♀ ♀): 28.4 (26.5–33.8) mm, n = 11
 P³–M³ (♂ ♂): 8.2 (7.5–9.1) mm, n = 6
 P³–M³ (♀ ♀): 7.6 (7.0–8.2) mm, n = 11

Port Nolloth, South Africa (coastal animals; De Graaff 1964a)
 Weights: Oranjemund and Spergabiet, Namibia (J. U. M. Jarvis unpubl.)

Inland animals (from Kamieskroon, South Africa) are larger and heavier: ♂ ♂: total body length 283 mm (n = 28); WT: 439 (208–794) g (n = 28); ♀ ♀: total body length 273 mm (n = 26); WT: 330 (198–511) g (n = 26) (M. Herbst unpubl.)

Key References De Graaff 1981; Herbst 2002; Jarvis 1997; Roberts 1951; Skinner & Smithers 1990.

J. U. M. Jarvis

Bathergus suillus CAPE DUNE MOLE-RAT

Fr. Rat-taupe des dunes du Cap; Ger. Kap-Strandgräber

Bathergus suillus (Schreber, 1782). Die Säugethiere 4: 715. Cape of Good Hope, South Africa.

Taxonomy Originally described in the genus *Mus*. Formerly included *janetta* (now considered to be a valid species). Synonyms: *africana*, *intermedius*, *maritimus*. Subspecies: none. Chromosome number: 2n = 56, FN = 102 (Nevo *et al.* 1986).

Description Large mole-rat, the largest of all subterranean mammals in Africa, with strong curved claws on forefeet. Pelage thick and woolly, without sheen. Dorsal pelage cinnamon-brown,

sometimes with darker mid-dorsal band, hairs black or dark grey at base, cinnamon-brown at tip. Long pale-coloured sensory hairs interspersed in pelage. Flanks paler. Ventral pelage greyish. Head similar in colour to dorsal pelage, with small white markings on muzzle and (in some individuals) on back of head. Eyes small, with pale eye-ring. External ears absent, with pale patch around ear opening. Forelimbs short with large forefeet and strong curved claws (largest on Digits 2, 3 and 4). Tail broad, very short (ca. 18% of HB), fringed on the edge with stiff pale buff bristles. Skull robust and dorsoventrally flattened; well-developed sagittal and occipital ridges; each upper incisor with a single deep groove; palate extends posteriorly to beyond M³; auditory bullae not markedly swollen; infraorbital foramen small, almost round (2 mm dia.), with thick outer wall. Molar teeth simple with re-entrant folds only in juveniles (as in Figure 103). Angle of mandible extends posteriorly well beyond end of skull (Figure 103). Males on average larger than ♀ ♀. Nipples: 2 + 1 = 6.

Geographic Variation Individuals from the drier west coast localities (north of Cape Town) are paler in colour, but often with a slightly darker mid-dorsal band compared with those from the moister south coast localities (Cape Town to Knysna) (De Graaff 1981).

Similar Species

B. janetta. HB smaller; dorsal pelage silvery-fawn with sheen and a darker mid-dorsal band; skull with smaller sagittal and occipital ridges; auditory bullae markedly swollen; and palate does not extend posteriorly beyond the level of M³.

Cryptomys hottentotus. HB much smaller; incisors not grooved; forefeet without elongated claws.

Georchus capensis. Smaller; dorsal pelage russet; head blackish with white muzzle and large white patch around ear opening; incisors not grooved; forefeet without elongated claws.

Distribution Endemic to Africa. South-West Cape BZ. Recorded only from South Africa; ranges from coastal areas of Western Cape Province from near Ronddawel on the Groenrivier (Faulkes *et al.* 2004)

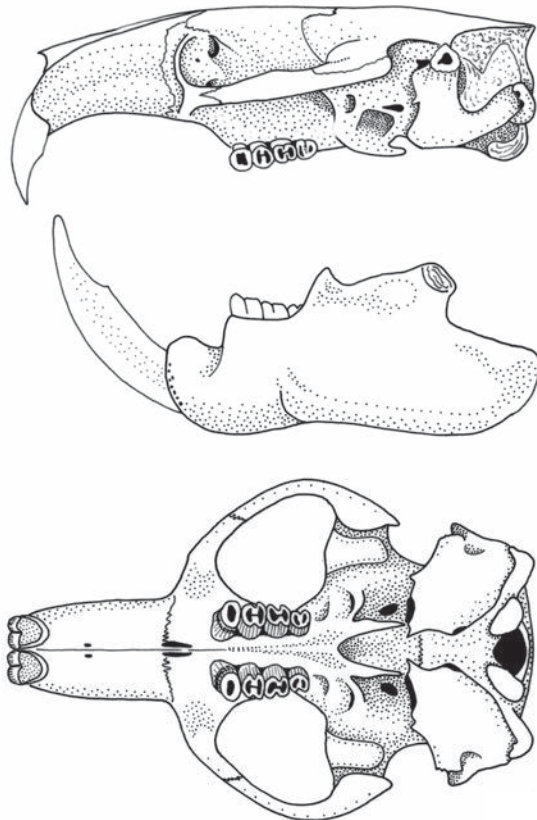
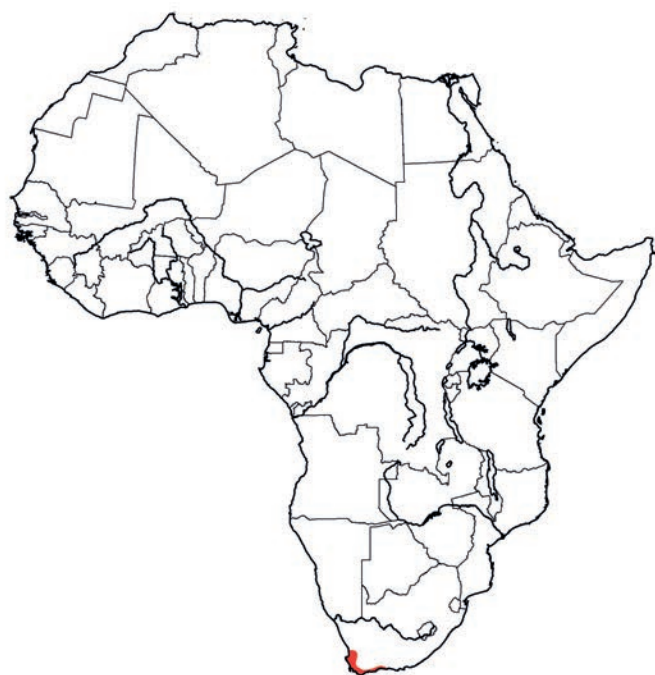


Figure 103. Skull and mandible of *Bathergus suillus* (BMNH 4.2.2.6).



Bathyergus suillus

in the north-west to Knysna on the south coast. Rarely occurs above 300 m. Where sand is more consolidated, may occur sympatrically with *Georchus capensis* and/or *Cryptomys hottentotus*. Near Ronsdale occurs in sympatry with *B. janetta*.

Habitat Loose coastal sands and sandy loams along the coast, and on banks of rivers close to the coast. Favours Sandveld vegetation where grasses, herbs and restionaceous sedges abound.

Abundance Sometimes extremely abundant locally. Density has been recorded as 0.9 mole-rats/ha in coastal fynbos (Davies & Jarvis 1986); and as high as >300 individuals/ha in grasslands and wheat fields so that the entire ground surface is covered by their large mounds (J. U. M. Jarvis unpubl.). Their abundance was noted by Europeans as early as 1660; Van Riebeeck (in his journals) referred to the Berg River region as 'the kingdom of the moles'; he commented that horse riders were forced to keep to rhinoceros trails to prevent the horses from stumbling and throwing their riders or breaking their legs when they stumbled into the mole-rat's burrows.

Adaptations Subterranean. The large size of Cape Dune Mole-rats restricts them to easily worked soils where the energetic cost of excavating soil is lowest. They dig with their strongly clawed forelimbs. Burrows are extensive (up to 420 m), not as finely branching as those of other genera. Foraging burrows are 350–650 mm deep and 150–220 mm in diameter. Nest chambers are often slightly deeper than foraging burrows; nests are lined with grass and twigs and are often associated with blind-ending 'bolt-holes' (>2 m deep) into which an animal retreats if alarmed, blocking the burrow behind it. Blind-ending toilet burrows occur also near the nest chamber, and food stores are sometimes present. Burrow configuration is constantly changing but animals remain in one area (Davies & Jarvis 1986). Burrows may overlap with those of *Georchus capensis* and/or *Cryptomys h. hottentotus*, the burrows of each species being at different

depths (Skinner & Smithers 1990, Jarvis & Bennett 1991). Telemetry studies reveal that animals are active throughout 24 h, with peaks of activity at 12:00h–16:00h (J. U. M. Jarvis unpubl.).

Foraging and Food Herbivorous. The diet consists of up to 60% above-ground vegetation (herbs, grasses, sedges of the family Restionaceae) collected by digging up under the plant and pulling it into the burrow. Bulbs, tubers, roots also eaten (Davies & Jarvis 1986) whenever encountered during digging. Cape Dune-rats rarely forage above ground.

Social and Reproductive Behaviour Solitary and aggressively territorial. Cape Dune Mole-rats communicate through soil by drumming with both hindfeet simultaneously on the ground (two beats, pause, two beats, etc.; J. U. M. Jarvis unpubl.). They make snorting grunts and drum when threatened or alarmed. Vacant burrows are quickly taken over by neighbours. Little is known about reproductive behaviour, and there have been no successful matings in captivity. During courtship, ♂♂ and ♀♀ drum in unison, move soil and lock incisors; ♀ raises her tail and vocalizes while ♂ follows and attempts to mount (J. U. M. Jarvis unpubl.). Marked sexual dimorphism and thick protective skin on the neck suggests ♂♂ fight for ♀♀. Males seem to have more linear burrows than neighbouring ♀♀, possibly providing access to several ♀♀ (Davies & Jarvis 1986). Mean home-range of adults at one site in coastal fynbos was 0.27 ha (0.14–0.35 ha) (Davies & Jarvis 1986); home-range can be much smaller elsewhere when densities are high.

Reproduction and Population Structure Reproduction is seasonal, occurring during the wet winter (Apr–Nov), with pregnancies peaking in Aug. During the reproductive season, testes in ♂♂ change from abdominal to inguinal, but there is no real development of a scrotum. Usually one (occasionally two) litter/season. Gestation: 2 months (estimate). Litter-size: 3.3 (1–6), n = 99. At birth, young weigh 27–52 g (n = 10). Eyes open Day 7. First solid foods eaten ca. Day 15. Weaned ca. Day 30. Inter-sibling sparring begins at Day 12, and later escalates to fighting. Young disperse either above or below ground ca. Day 60–65, when weight is ca. 300 g. Sexual dimorphism beginning to be evident at one year of age, when weight is 420–638 g (n = 4). Smallest wild sexually active individuals at weight of 529 g (♂♂) and 494 g (♀♀) (J. U. M. Jarvis unpubl.). Growth continues for several years. Longevity: >6 years. Sex ratio is parity (M. J. O'Riain & J. U. M. Jarvis unpubl.).

Predators, Parasites and Diseases Despite their large size, even adult Cape Dune Mole-rats are eaten by Mole-snakes *Pseudapsis cana* and probably also by the Cape Cobra *Naja nivea*. Jackals, caracals, other small carnivores and even herons and some raptors, will capture animals working close to the surface or wandering above ground. During the winter, Cape Dune Mole-rats occupying low-lying areas such as temporary vleis, sometimes get flooded out of their burrow systems. They have little resistance to cold and are easy prey to these predators. Ectoparasites include three species of mites, one species of flea, one species of sucking louse and two species of ticks. Three species of endoparasitic worms have been recorded (De Graaff 1964b, 1981). Close to habitations, Cape Dune Mole-rats are often infested with the cysts of the dog tapeworm.

Conservation IUCN Category: Least Concern.

Cape Dune Mole-rats may be pests. They undermine roads, damage earthen dam walls, chew through underground communication cables and irrigation pipes. Their large mounds damage combine harvesters. They are trapped extensively, and eaten by local people.

Measurements

Bathyergus suillus

HB (♂♂): 281 (240–330) mm, n = 39

HB (♀♀): 256 (204–300) mm, n = 45

T (♂♂): 52 (30–70) mm, n = 28

T (♀♀): 46.6 (25–61) mm, n = 32

HF (♂♂): 51.9 (45–65) mm, n = 37

HF (♀♀): 46.9 (42–55) mm, n = 43

E (♂♂): 0 mm

E (♀♀): 0 mm

WT (♂♂): 896 (529–2200) g, n = 208

WT (♀♀): 670 (494–900) g, n = 257

GLS (♂♂): 65.1 (56–76.7) mm, n = 27

GLS (♀♀): 55.1 (39.4–69.3) mm, n = 32

GWS (♂♂): 40.1 (34.2–47.3) mm, n = 28

GWS (♀♀): 38.1 (28.5–41) mm, n = 32

P⁴–M³ (♂♂): 11.4 (10.6–12.5) mm, n = 27

P⁴–M³ (♀♀): 10.9 (9.3–13) mm, n = 32

South Africa (TM, AM, MM)

Weights: J. U. M. Jarvis unpubl.

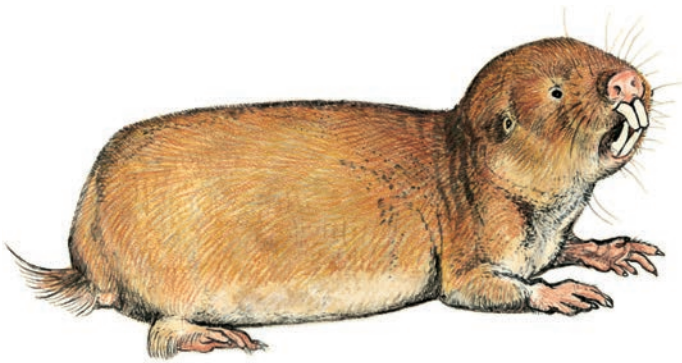
Key References Davies & Jarvis 1986; De Graaff 1981; Jarvis & Bennett 1991; Skinner & Smithers 1990.

J. U. M. Jarvis

GENUS *Cryptomys*

Mole-rats

Cryptomys Gray, 1864. Proc. Zool. Soc. Lond. 1864: 124. Type species: *Georchus holosericeus* Wagner, 1842 (= *Bathyergus hottentotus* Lesson, 1826).



Cryptomys hottentotus.

The genus *Cryptomys* contains ten species distributed throughout western, central and southern Africa, but is absent from the Horn of Africa, tropical rainforests of central and West Africa, and the Sahara. It is distributed in a wide range of soil types – fine clays to coarse sand and occasionally brecciated soils – and occurs in a variety of biomes, from mesic to arid.

These mole-rats are of intermediate size, being larger than *Heterocephalus* but smaller (except for *C. mechowii*) than *Bathyergus*, *Georchus* and *Heliophobius*. Pelage colour is cinnamon, fawn, grey and black amongst the different species. The muzzle is flat; tail is shorter than the hindfeet; the toes of fore- and hindfeet, and their claws, are short. The skull is less robust than in *Bathyergus*. Cheekteeth are simple folds in adults. The premaxilla bones, housing the incisors, do not bulge out laterally as much as in *Bathyergus* and *Georchus*. The jugal fits into an elongate groove on the outer upper side of the zygomatic. Upper incisors, without grooves, are rooted in the pterygoid bones posterior to the cheekteeth (Figure 104).

Cryptomys mole-rats are social, occurring in colonies with reproductive division of labour, overlap of generations, cooperative

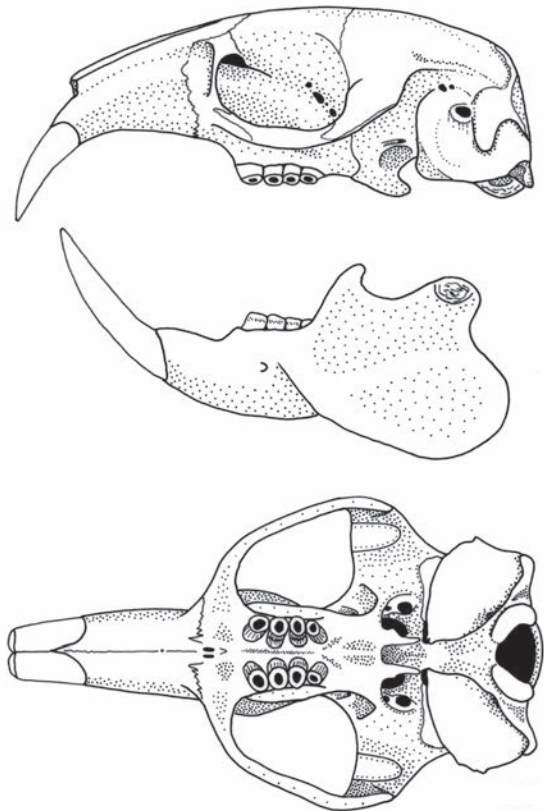


Figure 104. Skull and mandible of *Cryptomys hottentotus* (BMNH 98.4.4.23).

care of young and high reproductive skew. All species studied to date are obligate outbreeders. In mesic areas, *Cryptomys* spp. are loosely social, whereas species in arid areas have well-developed social structures. Each colony is characterized by having a single reproductive ♀ and between one and two reproductive ♂♂. Non-reproductive animals exhibit socially induced infertility ranging from strict incest

avoidance in mesic species through to physiological suppression in arid species. In the clade (see below) containing *C. hottentotus*, courtship and copulation is usually initiated by ♂, whereas in the *C. damarensis* clade it is initiated by ♀. All species are subterranean and chisel-tooth diggers; they excavate extensive burrow systems by disposing of excavated soils as mounds on the surface.

Approximately 49 forms have been named (Ellerman 1940). Size, colour and external appearance are poor criteria for making comparisons between species in this genus. The genus *Cryptomys* is composed of two highly divergent clades, whose genetic distance can exceed that between some of the other genera in the family (Faulkes *et al.* 1997b), a division also supported by morphological characters of the skull. DNA sequence analysis has gone some way in clarifying the taxonomic problems of the genus (e.g. Allard & Honeycutt 1992, Faulkes *et al.* 1997b, Bennett & Faulkes 2000, Walton *et al.* 2000). The first clade contains all species except for *C. hottentotus*, has thick-walled infraorbital foramina and is distributed widely throughout savanna habitats in southern, central and eastern Africa, with two species with restricted distributions in West Africa. This clade is karyotypically very diverse (Burda *et al.* 1999), ranging from $2n = 40$ in *C. mehowi* to $2n = 74$ in *C. damarensis*. The second clade contains only *C. hottentotus*, has thin-walled elliptically shaped infraorbital foramina, and is karyotypically conserved ($2n = 54$).

The smallest genetic distance between *Cryptomys* species is 8.4% for *C. mehowi* and *C. bocagei*. *Cryptomys anelli* from Zambia and *C. darlingi* from Zimbabwe have traditionally been classified as subspecies

of *C. hottentotus*, but are highly divergent from this species and are indeed distinct species. Within the *C. hottentotus* clade, *C. h. nimrodi* from Zimbabwe, *C. h. natalensis* from South Africa (KwaZulu–Natal) and *C. h. pretoriae* from South Africa (Gauteng) are also genetically divergent from one another and should possibly be considered as separate species. There are no data for the genetic relationships between *C. foxi*, *C. zechi* and *C. ochraceocinereus*; all three species have a small thick-walled infraorbital foramina, as in *C. damarensis*.

These differences within *Cryptomys* have shown that the genus, as currently defined, may be composed of two genera. The genus *Fukomys* has been proposed (Kock *et al.* 2006) to contain all species (*anselli*, *bocagei*, *damarensis*, *darlingi*, *foxi*, *kafuensis*, *mehowi*, *ochraceocinereus*, *zechi*) except for *hottentotus*, which remains in the genus *Cryptomys*. *Fukomys* cannot be separated from *Cryptomys* on the grounds of morphological or morphometric characters. *Fukomys* is distinguished from *Cryptomys* by nuclear and mitochondrial DNA (Faulkes *et al.* 2004, Ingram *et al.* 2004) and high karyotypic diversity with diploid karyotypes ranging from $2n = 40$ to 80, as opposed to a very conservative $2n = 54$ in *Cryptomys* (van Daele *et al.* 2004, Deuve *et al.* 2008). The separation into two genera is supported by reciprocal monophyly of the two lineages based on nuclear and mitochondrial data sets and the level of sequence divergence observed between the two lineages for nuclear and mitochondrial DNA (e.g. *Bathyergus* and *Georchus*) (Faulkes *et al.* 1997b, Ingram *et al.* 2004).

Nigel C. Bennett

Cryptomys anelli ANSELL'S MOLE-RAT

Fr. Rat-taupe d'Ansell; Ger. Ansell's Graumull

Cryptomys anelli Burda, Zima, Scharff, Macholan and Kawalika, 1999. Z. Säugetierkunde 64: 36–50. Chainama Hills, Lusaka, Zambia.

Taxonomy Prior to 1999, this species was included in *C. hottentotus* (e.g. Ansell 1978). It was referred to as *C. hottentotus* or *Cryptomys* 'population Lusaka, karyotype $2n = 68$ ' in papers published between 1987 and 1999. This species has been placed in the genus *Fukomys* by Kock *et al.* (2006) (see genus *Cryptomys*). Synonyms: none. Allozyme profile (Filippucci *et al.* 1994, 1997) and DNA sequences (Ingram *et al.* 2004) clearly separate this species from other species of *Cryptomys*. Chromosome number: $2n = 68$, FN = 79–82 (Burda *et al.* 1999).

Description Medium-sized mole-rat. Pelage colour is age- and weight-dependent: dark slate-grey (neonates), greyish-brown (weaned young), brown (juveniles and subadults) and golden-ochre (adult animals). Head with conspicuous white patch on forehead in most (but not in all) individuals. Tail very short (ca. 14% HB). Skull: infraorbital foramina elliptical, wide at base, thick-walled. Upper incisors ungrooved. Nipples: $2 + 1 = 6$.

Geographic Variation None recorded.

Similar Species

Cryptomys kafuensis. Similar in appearance, head spot white, usually larger; chromosome number $2n = 58$.



Cryptomys anelli

Distribution Endemic to Africa. Zambezan Woodland BZ. Recorded only from several localities in C Zambia (Lusaka and its surroundings, to a maximum of ca. 100 km from Lusaka, but not across the Kafue R.).

Habitat Savanna bushland, cultivated fields, gardens and golf courses where mean annual rainfall is ca. 820 mm.

Abundance Detailed assessment of abundance not available, but the species appears to be rather abundant in the Lusaka and Central Provinces.

Adaptations Subterranean. Ansell's Mole-rat has a low resting metabolic rate of 0.63 ± 0.06 ml O₂/g/h (67% of expected). Has a low body temperature of 33.8 °C and a high thermal conductance of 0.12 ml O₂/h/ °C (Bennett *et al.* 1994a).

Foraging and Food Herbivorous; feeds on rootstocks, tubers, bulbs, corms and rhizomes (Scharff 1998).

Social and Reproductive Behaviour Social. Lives in family groups of about 12 animals (range 2–25, $n = 12$) (Scharff 1998). A colony consists of a founding reproductive pair and their offspring from several litters. These offspring do not reproduce due to incest avoidance based on individual recognition of the family members. Offspring are (in many cases probably lifelong) helpers at the nest (Burda 1995, Burda *et al.* 2000).

Reproduction and Population Structure Reproduction is aseasonal and one or two (rarely three) litters can be produced each year in captivity. Gestation: 98 (84–112) days. Litter-size: 2 (1–5), $n = 102$ litters. Sex ratio of neonates: 1 : 1.4 ($n = 159$). Weight of neonates: 7.9 (5.7–10.7) g. Pelage first visible on Day 8–10. Eyes open at weight 12.9 g on Day 23 (13–50). Solids first eaten ca. Day 22. Weaned at weight 34 g, on ca. Day 82 (75–105) (Burda 1989, 1990, Begall & Burda 1998). Non-reproductive ♀♀ have reduced

follicular development; tertiary follicles luteinize or atrophy so that ovulation does not occur (Willingstorfer *et al.* 1998).

Predators, Parasites and Diseases Apart from humans, no predators are known that have specialized on Ansell's Mole-rats. Ectoparasites have not been found. Low infestation with a nematode (*Protospirura muricola*) has been reported (Scharff 1998).

Conservation IUCN Category: Near Threatened.

Ansell's Mole Rats are considered to be agricultural and horticultural pests; they are hunted by local people and are a highly valued food.

Measurements

Cryptomys anselli

HB (♂♂): 121.5 ± 10.9 (109–135) mm, $n = 20$

HB (♀♀): 119.3 ± 8.0 (108–132) mm, $n = 30$

T (♂♂): 17.9 ± 1.9 (15.6–21.7) mm, $n = 20$

T (♀♀): 18.3 ± 2.3 (13.9–22.9) mm, $n = 30$

HF (♂♂): 22.6 ± 3.1 (21.8–25.8) mm, $n = 20$

HF (♀♀): 23.3 ± 0.9 (21.8–25.2) mm, $n = 30$

E (♂♂): 0 mm

E (♀♀): 0 mm

WT (♂♂): 96.1 ± 14.7 (80–145) g, $n = 40$

WT (♀♀): 79.1 ± 12.7 (65–122) g, $n = 100$

GLS (♂♂): 33.9 ± 1.9 (29.0–38.8) mm, $n = 10$

GLS (♀♀): 31.8 ± 1.7 (29.8–34.7) mm, $n = 10$

GWS (♂♂): 26.5 ± 2.3 (22.6–30.0) mm, $n = 10$

GWS (♀♀): 23.9 ± 1.8 (22.1–26.1) mm, $n = 10$

P⁴–M³ (♂♂): 6.1 ± 0.3 (5.6–6.9) mm, $n = 10$

P⁴–M³ (♀♀): 6.0 ± 0.4 (5.4–6.8) mm, $n = 10$

Zambia (H. Burda unpubl.)

Key References Begall & Burda 1998; Bennett *et al.* 1994a; Burda 1989.

Nigel C. Bennett & Hynek Burda

Cryptomys bocagei BOCAGE'S MOLE-RAT

Fr. Rat-taupe de Bocage; Ger. Bocages Graumull

Cryptomys bocagei (de Winton, 1897). Ann. Mag. Nat. Hist., ser. 6, 20: 323. Hanha, Angola.

Taxonomy Originally described in the genus *Georchus*. Included within *C. hottentotus* by De Graaff (1981) and Smithers (1983), but now considered as a valid species by Woods (1993) and Woods & Kirkpatrick (2005). Recognized as a distinct species by Honeycutt *et al.* (1991) based on the character of the infraorbital foramina. This species has been placed in the genus *Fukomys* by Kock *et al.* (2006) (see genus *Cryptomys*). Synonyms: *kubangensis*. Subspecies: none. Chromosome number: $2n = 58$ (G. H. Aguilar unpubl.).

Description Medium-sized mole-rat with white patch on head. Dorsal and ventral pelage drab-grey to silvery-grey. Head blunt, usually with variably shaped white patch on forehead; incisor teeth visible outside lips. Long vibrissae. Eyes very small. External ear absent. Limbs short, feet pink and naked. Tail very short (ca.

7% of HB). Skull broad, strong; zygomatic arches slightly bowed anteriorly; infraorbital foramina small, teardrop-shaped (1.5–2 mm), thin-walled. Upper incisors ungrooved. Males slightly larger than ♀♀. Nipples: 2 + 1 = 6.

Geographic Variation None recorded.

Similar Species

Cryptomys mechowii. On average much larger in size.

Distribution Endemic to Africa. Zambezan Woodland BZ. Recorded in C and S Angola, N Namibia (particularly Ondjeva, Ongha and Ondongera in Ovamboland Province), extreme S DR Congo and W Zambia.

Habitat No information.

Abundance No information. Probably common.

Remarks Recorded to feed on geophytes (G. H. Aguilar unpubl.). Social behaviour: four animals were caught from one colony that was not completely trapped-out.

Conservation IUCN Category: Data Deficient.

Measurements

Cryptomys bocagei

HB (♂♂): 151 (141–165) mm, n = 4

HB (♀♀): 155 (150–165) mm, n = 4

T (♂♂): 10 (7–12) mm, n = 4

T (♀♀): 11 (6–15) mm, n = 4

HF (♂♂): 20 (19–22) mm, n = 4

HF (♀♀): 22 (20–24) mm, n = 4

E (♂♂): 0 mm

E (♀♀): 0 mm

WT (♂♂): n. d.

WT (♀♀): n. d.

GLS (♂♂): 31.9 (29.9–34.4) mm, n = 4

GLS (♀♀): 33.5 (32.5–35.0) mm, n = 4

GWS (♂♂): 22.5 (21–24.6) mm, n = 4

GWS (♀♀): 23.6 (23.3–24.4) mm, n = 4

P⁴–M³ (♂♂): 5.3 (5.0–5.7) mm, n = 4

P⁴–M³ (♀♀): 5.1 (4.8–5.3) mm, n = 4



Cryptomys bocagei

Throughout geographic range (De Graaff 1964a)

Key Reference De Graaff 1964a.

Nigel C. Bennett

Cryptomys damarensis DAMARALAND MOLE-RAT

Fr. Rat-taupe du Damara; Ger. Damaraland Graumull

Cryptomys damarensis (Ogilby, 1838). Proc. Zool. Soc. Lond. 1838: 5. Damaraland, Namibia.

Taxonomy Originally described in the genus *Bathyergus*. Included within *C. hottentotus* by Ellerman *et al.* (1953), De Graaff (1981) and Smithers (1983), but now considered as a valid species by Woods (1993) and Woods & Kirkpatrick (2005). Described as a distinct species by Honeycutt *et al.* (1991) on characters of the infraorbital foramina. Faulkes *et al.* (1997b) confirmed specific status by showing that an 11% sequence divergence in 12S rRNA occurred between haplotypes of *C. hottentotus* and *C. damarensis*. This species has been placed in the genus *Fukomys* by Kock *et al.* (2006) (see genus *Cryptomys*). Synonyms: *lugardi*, *micklei*, *ovamboensis*. Subspecies: none. Chromosome number: 2n = 74 or 2n = 78, aFN = 92 (Nevo *et al.* 1986).

Description Medium-sized colonial mole-rat with white patch on dorsal region of head. Pelage short, thick, with a sheen. Dorsal and ventral pelage fawn, or very dark brown to black. In a single colony, a single colour morph, or both colour morphs, may be present. Mid-dorsal and mid-ventral white stripes in some individuals. Isolated tactile hairs protrude from pelage, especially on the face. Head with large white patch on forehead, sometimes with flecks of pelage colour. Incisor teeth visible outside lips. Eye small. External ear

pinnae absent. Limbs short and feet pink and naked. Tail very short (ca. 18% of HB), with stiff bristles that radiate from tail. Skull: dorsoventrally flattened; sagittal crest well developed; zygomatic arch strongly bowed outwards; infraorbital foramina small, teardrop-shaped (1.5–2 mm), thin-walled; upper incisors ungrooved; angular process on mandible not extending far backwards. Nipples: 2 + 1 = 6.

Geographic Variation Individuals from South Africa (Kalahari), Botswana (Okavango swamps) and Zimbabwe are black in colour. Those from C Namibia (Dordabis and Rheoboth) may be either black or fawn in colour.

Similar Species

C. darlingi. On average smaller; pelage fawn (similar to the fawn-coloured morph of *C. damarensis*); chromosome number: 2n = 54; Zimbabwe and Mozambique.

C. hottentotus. On average smaller; pelage grey; chromosome number: 2n = 54; Western Cape, Northern Cape, Eastern Cape, KwaZulu–Natal, Free State, Gauteng and Mpumalanga Provinces. Occurs in sympatry with *C. hottentotus* in Van Zyl's Rus, Northern Cape Province.

*Cryptomys damarensis*

Distribution Endemic to Africa. Zambezi Woodland BZ and South-West Arid BZ (Kalahari Desert). Recorded from most of Botswana (except extreme east), NW South Africa, C and N Namibia, SW Zimbabwe and extreme W Zambia. Distribution closely associated with red Kalahari arenosols, but also occurs in coarse sandy soils.

Habitat Semi-arid thorn scrub, woodland savanna and grasslands associated with red Kalahari sands and sandy soils; rainfall is typically low and sporadic (200–400 mm/annum) and burrow temperatures range from a mean of 30 °C in summer to 19 °C in winter (Bennett *et al.* 1988).

Abundance Localized, but may be abundant in suitable habitats where population numbers can exceed 380 individuals/km². However, abundance of subterranean mammals is not easy to estimate.

Adaptations Subterranean. Activity is discontinuous throughout the day and night. Damaraland Mole-rats excavate extensive burrow systems that can extend for more than 1 km and appear to radiate from a central nest and nearby food store (Jarvis *et al.* 1998). The nest is deep, sometimes exceeding 2.4 m below the surface, and has two to three entrances. Toilet areas have not been found. Individuals within a colony remain resident in the same home-range for many years (>8 years; N. C. Bennett & J. U. M. Jarvis unpubl.).

When threatened, a Damaraland Mole-rat has a unique defensive posture, rolling onto its back, exposing its belly, with the mouth agape and incisors bared. It braces itself with its limbs and rolls from side to side (Bennett 1990). Like other species of *Cryptomys*, it can also throw its head back with mouth agape and produce a threatening grunt.

Damaraland Mole-rats have one of the lowest resting metabolic rates of all mammalian species: 0.66 ± 0.07 ml O₂/g/h (85% of expected), a low body temperature (35.1 °C) and a low thermal conductance 0.065 ml O₂/g/h/ °C (Bennett *et al.* 1992).

Foraging and Food Herbivorous. Superficial foraging burrows are excavated as the animals search for underground storage organs of geophytes (bulbs, tubers and rootstocks). There is selective storage of geophytes: geophytes that are proportionately larger may possibly have a longer 'shelf life', or it may be more cost-effective to transport large geophytes to the store than small ones. Geophytes include various genera of Hyacinthaceae (e.g. *Dipcadi*, *Ledebouria*, *Ornithogalum*), Portulacaceae (e.g. *Talinum*) and Cucurbitaceae (e.g. *Acanthosicyos*), a number of which are toxic to livestock but not to mole-rats. Portable bulbs and corms are stored whereas the very large tubers (e.g. *Acanthosicyos*) are partly eaten *in situ*, and will often regenerate (Bennett & Faulkes 2000, Jarvis *et al.* 2000).

Social and Reproductive Behaviour Social. Lives in medium-sized colonies of around 12 animals (range 2–41) (Bennett & Jarvis 1988, Jarvis & Bennett 1993). The colony consists of a founding reproductive pair and their progeny from several litters; these younger individuals do not breed while in the natal colony. Sex ratios of captured colonies range from 0.8 to 2.1 in favour of ♂♂. Mean body mass of individuals in the colony may vary from 103 to 202 g in ♂♂ and 88 to 145 g in ♀♀ (n = 6 colonies, n = 107 individuals) depending upon the ages of the adult non-reproductive animals in the colony (Jacobs *et al.* 1990). The reproductive pair consists of the most dominant individuals; the non-reproductive ♂♂ are more dominant than non-reproductive ♀♀. The non-reproductive members of the colony can be placed into work-related groups based on body mass: there is a tendency for smaller (not necessarily younger) animals to perform more burrow maintenance than larger (but not necessarily older) animals. An oestrus ♀ solicits the ♂ prior to mating. Multiple mating occurs following a ritualized courtship of tail-to-tail chasing, vocalizations and head mounting by the reproductive ♀ (Bennett & Jarvis 1988).

Reproduction and Population Structure In most ♂♂, the testes are abdominal and the penis is contained in a penile sheath; in a reproductive ♂, the penis is usually visible beyond the sheath and the testes are often in inguinal pockets. Females have external labial flaps and an os-clitoris, that is only exposed during sexual activity, and is the same length as the penis of the ♂. A vaginal closure membrane is present in non-reproductive ♀♀. The reproductive ♀ can be identified by her open vagina and prominent nipples.

Reproduction is aseasonal, with up to three litters per annum. Ovulation is spontaneous. Gestation: 78–92 days (Bennett & Jarvis 1988). Litter-size: 3 (1–6), n = 8 litters. At birth, young weigh 8–9 g and are mobile. Pelage develops from Day 6. Solid foods first eaten ca. Day 6–8. Eyes open on Day 18. Weaned Day 28. Inter-sibling sparring begins at Day 18–25. Young do not disperse but join the natal colony (Bennett *et al.* 1991).

Non-reproductive ♂♂ have functional gonads but are oligospermic and occasionally azoospermic, although they have similar hormone profiles to the reproductive ♂ (Maswanganye *et al.* 1999). In contrast, the non-reproductive ♀♀ do not ovulate and show reduced follicular development with tertiary follicles luteinizing or atresing. The hormone profiles of non-reproductive ♀♀ have lower concentrations of oestrogen, progesterone and LH than the reproductive ♀ (Bennett *et al.* 1993, 1994c). Reproductive suppression is due to two components: a suppressive action from the

social environment, and incest avoidance in the form of obligatory out-breeding. Removal of a non-reproductive ♀ from the colony releases her suppression and her gonads become active. In a functional colony, the oldest non-reproductive animals are the primary dispersers; however, when either a reproductive ♂ or ♀ dies, the entire colony will fragment. In either instance, dispersal occurs after rain when the costs of digging are lowest (Bennett *et al.* 1996).

Predators, Parasites and Diseases The Damaraland Mole-rat is at particular risk from predation during mound formation. Mole-snakes *Pseudapsis cana* appear to detect such freshly turned soil. They seize a mole-rat from behind, constrict and kill it. Cobras *Naja nivea* also enter the open holes of mole-rat burrows. Dispersing animals are particularly vulnerable to owls and small carnivores such as jackals, mongooses, Caracals *Caracal caracal* and occasionally Brown Hyenas *Hyaena brunnea*. Damaraland Mole-rats have conspicuously few parasites; the predominant parasites are intestinal nematodes.

Conservation IUCN Category: Least Concern.

There is little conflict with agriculture (unlike some other species of mole-rats) because most of the habitat is arid.

Measurements

Cryptomys damarensis

HB (♂ ♂): 164 (150–185) mm, n = 20

HB (♀ ♀): 151 (141–164) mm, n = 4

T (♂ ♂): 25 (23–30) mm, n = 20

T (♀ ♀): 28 (25–32) mm, n = 4

HF (♂ ♂): 27 (26–30) mm, n = 20

HF (♀ ♀): 27 (26–28) mm, n = 4

E (♂ ♂): 0 mm

E (♀ ♀): 0 mm

WT (♂ ♂): 161 (56–234) g, n = 17

WT (♀ ♀): 119 (49–206) g, n = 25

GLS (♂ ♂): 36.2 (32.2–44.1) mm, n = 20

GLS (♀ ♀): 35.3 (31.6–38.2) mm, n = 4

GWS (♂ ♂): 25 (23.3–33.0) mm, n = 20

GWS (♀ ♀): 27.1 (25.1–30.3) mm, n = 4

P⁴–M³ (♂ ♂): 5.8 (5.2–6.7) mm, n = 20

P⁴–M³ (♀ ♀): 6.0 (5.5–6.4) mm, n = 4

South Africa and Namibia (De Graaff 1964a; Bennett *et al.* 1990)

Key References Bennett & Jarvis 1988; Bennett *et al.* 1994c; Jarvis & Bennett 1993; Jarvis *et al.* 1998.

Nigel C. Bennett

Cryptomys darlingi DARLING'S MOLE-RAT (MASHONA MOLE-RAT)

Fr. Rat-taupe de Darling; Ger. Darlings Graumull

Cryptomys darlingi (Thomas, 1895). Ann. Mag. Nat. Hist., ser. 6, 16: 239. Salisbury, Rhodesia (now Harare, Zimbabwe).

Taxonomy Originally described in the genus *Georchus*. Included within *C. hottentotus* by Ellerman *et al.* (1953), De Graaff (1981), Smithers (1983) and Woods (1993) but now considered as a valid species (Woods & Kirkpatrick 2005). This species has been placed in the genus *Fukomys* by Kock *et al.* (2006) (see genus *Cryptomys*). Synonyms: *beirae*, *nimrodi*, *zimbitiensis*. Subspecies: none. Chromosome number: 2n = 54, aFN = 80 (Aguilar 1993).

Description Medium-sized mole-rat with a longitudinal white stripe on ventral surface. Pelage short and thick. Dorsal and ventral pelage blackish, seal-brown, slate- or silvery-grey. White stripe or patch on ventral pelage; variable in width and length, may extend for length of body. Head blunt, sometimes with white patch on forehead; incisor teeth visible outside lips. Isolated tactile hairs protrude from pelage, especially on the face. Eye small. External ear absent. Fore- and hindfeet naked with soft pink skin. Tail very short (ca. 7% of HB), naked with coarse vibrissae. Pelage of juveniles is darker than in adults. Skull broad, braincase large and rounded; infraorbital foramina small, teardrop (1.5–2 mm), thin-walled; upper incisors ungrooved. Nipples: 2 + 1 = 6.

Geographic Variation None recorded.

Similar Species

Cryptomys damarensis. Fawn-coloured morph very similar; on average larger; pelage fawn, or very dark brown to black; chromosome

number: 2n = 74; South Africa, Namibia, Zimbabwe, Botswana and Zambia.



Cryptomys darlingi

Distribution Endemic to Africa. Zambezian Woodland BZ. Recorded only in N and E Zimbabwe, extending into C Mozambique. Mainly restricted to the Mashonaland plateau at altitudes above 1000 m. Limits of geographic range not known.

Habitat Miombo woodland predominated by *Brachystegia* and *Julbernardia*. Also found in valley grasslands, and on sandstone and granitic derived soils in areas of relatively high and predictable rainfall (ca. 700 mm/annum) (Genelly 1965, as *C. hottentotus*).

Abundance Common in miombo woodlands and grasslands.

Adaptations Subterranean. Mashona Mole-rats have a low resting metabolic rate of 0.98 ± 0.14 ml O₂/g/h (97% of expected) and a low body temperature of 33.3 ± 0.5 °C. They have strong poikilothermic tendencies in body temperature below ambient temperatures of 25 °C, whereas above 25 °C they are endothermic (Bennett *et al* 1993a).

Foraging and Food Herbivorous. These Mole-rats sometimes burrow around the root systems of *Brachystegia* and *Julbernardia* trees, where they feed on geophytes and on the swollen roots of these trees (N. C. Bennett unpubl.).

Social and Reproductive Behaviour Social. Mashona Mole-rats live in small colonies of 5–9 individuals consisting of a founding reproductive pair and the offspring from several litters, who remain non-reproductive while resident in the natal burrow. Sex ratios of all individuals from captured colonies appear to be biased towards ♂♂. Mean body mass of all individuals in a colony varies from 52 to 75 g (n = 5 colonies), this depending upon number of adults in the colony. The reproductive animals are the most dominant, thereafter ♂♂ are more dominant than ♀♀ (Gabathuler *et al.* 1996). Non-reproductive members of the colony cannot be placed into clearly defined work-related groups based on body mass (cf. *C. damarensis*). When in oestrus, ♀ solicits ♂ prior to mating. Multiple copulations occur over two days (Bennett *et al.* 1994b). Reproductive inhibition in the non-breeding animals appears to be maintained by incest avoidance alone (Bennett *et al.* 1994b).

Reproduction and Population Structure Reproduction is aseasonal, with up to four litters per annum. Gestation (estimated): 56–61 days. Litter-size: 2 (1–3), n = 7 litters. Sex ratio at birth is parity. At birth, young weigh 6.9–8.2 g (n = 4). Pelage first appears Day 4. First solid foods eaten Day 14. Eyes open Day 14. Weaned ca. Day 45. Non-breeding ♂♂ are smaller than breeding ♂♂, the penis is enclosed by a sheath, and they lack prominent bulging inguinal testes. Non-reproductive ♀♀ have an imperforate vagina.

Predators, Parasites and Diseases No information.

Conservation IUCN Category: Least Concern.

Measurements

Cryptomys darlingi

HB (♂♂): 145 (125–165) mm, n = 38

HB (♀♀): 141 (135–150) mm, n = 18

T (♂♂): 10 (8–13) mm, n = 38

T (♀♀): 10 (10–10) mm, n = 18

HF (♂♂): 23 (21–30) mm, n = 38

HF (♀♀): 22 (20–24) mm, n = 18

E (♂♂): 0 mm

E (♀♀): 0 mm

WT (♂♂): 76.4 (60–88) g, n = 11

WT (♀♀): 77.0 (54–92) g, n = 7

GLS (♂♂): 33.3 (30.6–37.9) mm, n = 38

GLS (♀♀): 32.6 (31–36.5) mm, n = 18

GWS (♂♂): 24.4 (20.8–28.2) mm, n = 38

GWS (♀♀): 23.3 (21.3–27.2) mm, n = 18

P⁴–M³ (♂♂): 5.3 (4.7–5.6) mm, n = 38

P⁴–M³ (♀♀): 5.1 (4.7–5.5) mm, n = 18

Harare and Goromonzi, Zimbabwe (De Graaff 1964a, N. C. Bennett unpubl.)

Key References Bennett *et al.* 1994a; Gabathuler *et al.* 1996; Genelly 1965.

Nigel C. Bennett

Cryptomys foxi Fox's MOLE-RAT

Fr. Rat-taupe de Fox; Ger. Foxs Graumull

Cryptomys foxi (Thomas, 1911). Ann. Mag. Nat. Hist., ser. 8, 7: 462. Panyam, Jos Plateau, Nigeria.

Taxonomy Originally described in the genus *Georychus*. De Graaff (1975) placed *foxi* as a subspecies of *C. ochraceocinereus*, an arrangement followed by Happold (1987). Currently considered as a valid species. Detailed analysis of skull characters provided by Williams *et al.* (1983). This species has been placed in the genus *Fukomys* by Kock *et al.* (2006) (see genus *Cryptomys*). Synonyms: none. Chromosome number: 2n = 66, FN = 122 (n = 6), 2n = 70, FN = 130 (Cameroon; Williams *et al.* 1983). See Rosevear (1969) for further information.

Description Sepia-coloured mole-rat, sometimes with whitish markings on head or body. Pelage soft and short, with velvet-like

texture. Dorsal and ventral pelage sepia-brown. Head blunt, usually with sub-circular white patch on forehead; incisor teeth visible outside lips. Long vibrissae. Eyes very small. External ear absent. Limbs short and feet naked. Fore- and hindfeet well-developed. Five digits on fore- and hindfeet. Tail very short (ca. 8% of HB), covered with stiff bristles. Skull: widest part of nasal bones anteriorly; upper incisors ungrooved and comparatively narrow (ca. 2.4 mm); infraorbital foramina teardrop-shaped (1.5–2 mm), thin-walled; upper cheekteeth comparatively short (mean 7.6 [range 7.2–8.3] mm). Individuals from Cameroon are larger than those from Nigeria (see Measurements). Nipples: 2 + 1 = 6.

Geographic Variation None recorded.

Similar Species

C. zechi. Pelage pale cinnamon; on average larger; widest part of nasal bones posteriorly; upper cheekteeth longer (ca. 8.3 mm); incisor teeth comparatively wider (ca. 3.2 mm); Ghana and Togo only.

Distribution Endemic to Africa. Afromontane–Afroalpine BZ. Recorded only from near Panyam (1220 m) on the Jos Plateau, N Nigeria (Thomas 1911b, Rosevear 1969), and Ngaoundere, Cameroon (Williams *et al.* 1983). Occurs only at altitudes above 1000 m.

Habitat On the Jos Plateau, Nigeria (ca. 1000–1800 m), typical habitats are extensive grasslands, rocky areas and riverine forest along streams (Happold 1987).

Abundance Uncertain; very localized and probably uncommon.

Remarks Virtually nothing is known about this species. Subterranean, living in colonies. Twelve animals were trapped from one colony but it is not known whether these animals constituted the whole colony. The Rev. G. T. Fox, who collected the holotype, recorded that these mole-rats ate earthworms in captivity (Thomas 1911b), an unusual situation for members of a genus that is primarily vegetarian.

Conservation IUCN Category: Data Deficient.

Measurements

Cryptomys foxi

HB: 145 (135–159) mm, n = 10

T: 14 (11–17) mm, n = 10

HF: 29 (26–31) mm, n = 10

E: 0 mm

WT: n. d.

GLS: 40.7 (39.3–43.0) mm, n = 10

GWS: 28.2 (25.7–30.0) mm, n = 10

P⁴–M³: 7.7 (7.2–8.3) mm, n = 10

Nigeria (Rosevear 1969)

HB (♂♂): 176.6 (161–191) mm, n = 7

HB (♀♀): 174.8 (162–191) mm, n = 10



Cryptomys foxi

T (♂♂): 20.1 (16–23) mm, n = 7

T (♀♀): 20.5 (17–25) mm, n = 10

HF (♂♂): 32.4 (30–36) mm, n = 7

HF (♀♀): 31.2 (29–34) mm, n = 10

E (♂♂): 0 mm

E (♀♀): 0 mm

WT (♂♂): n. d.

WT (♀♀): n. d.

GLS (♂♂): 44.8 (42.0–48.4) mm, n = 7

GLS (♀♀): 42.7 (39.7–46.4) mm, n = 10

GWS (♂♂): 31.0 (28.9–33.1) mm, n = 7

GWS (♀♀): 29.8 (28.7–32.8) mm, n = 10

P⁴–M³ (♂♂): 7.5 (6.8–8.4) mm, n = 7

P⁴–M³ (♀♀): 7.3 (6.7–8.0) mm, n = 10

Cameroon (Williams *et al.* 1983)

Key References Thomas 1911b; Williams *et al.* 1983.

Nigel C. Bennett

Cryptomys hottentotus COMMON MOLE-RAT (HOTTENTOT MOLE-RAT)

Fr. Rat-taupe hottentot; Ger. Hottentotten-Graumull

Cryptomys hottentotus (Lesson, 1826). Voyage Monde Coquille, Zool. 1: 166. Paarl, Cape Province, South Africa.

Taxonomy Originally described in the genus *Bathyergus*. *Cryptomys hottentotus* is a geographically variable polytypic species (hence the many synonyms), and is in need of revision. Meester *et al.* (1986) refer to five subspecies (each with many synonyms): *hottentotus* (17 synonyms), *damarensis* (3), *darlingi* (3), *bocagei* (1) and *natalensis* (16). Corbet & Hill (1991) recognize *natalensis* as a valid species without comment. The taxa *damarensis*, *darlingi* and *bocagei* are currently regarded as three valid species and are placed in the same clade as *C. hottentotus* (see genus

profile), and *natalensis* is placed as a synonym of *C. hottentotus*. *Cryptomys hottentotus* is placed within its own clade within the genus (see genus profile). All the available evidence indicates that the *C. hottentotus* clade is chromosomally conserved ($2n = 54$), and is distributed throughout South Africa, extending into Mozambique and parts of Zimbabwe. Mitochondrial DNA sequence analysis consistently resolves six groups within the *C. hottentotus* clade as follows: *natalensis* (KwaZulu–Natal and Mpumalanga Provinces), *pretoriae* (Gauteng, North West and Limpopo

Provinces), *nimrodi* (SW Zimbabwe), *hottentotus* (Western Cape, Northern Cape and Eastern Cape Provinces), *mahali* (Gauteng Province) and *aberrans* (Eastern Cape Province) (Faulkes *et al.* unpubl.). The first four forms are considered as subspecies (see below), but the status of *mahali* and *aberrans* is uncertain (Faulkes *et al.* unpubl.) Synonyms: *aberrans*, *albus*, *amatus*, *arenius*, *beirae*, *bigalkei*, *caecutiens*, *cradockensis*, *darlingi*, *exenticus*, *holosericius*, *jamesoni*, *jorisseni*, *kopmotiensis*, *langi*, *lugwigii*, *mahali*, *melanoticus*, *montanus*, *natalensis*, *nemo*, *nimrodi*, *orangiae*, *pretoriae*, *rufulus*, *stellatus*, *talpoides*, *transvaalensis*, *valschensis*, *vandami*, *vrybergensis*, *whytei*, *zimbitiensis*, *zuluensis*. Subspecies: four. Chromosome number (*C. h. hottentotus*): $2n = 54$, $FN = 106$; (*C. h. natalensis*): $2n = 54$, $FN = 104$ (Nevo *et al.* 1986).

Description Medium-sized mole-rat with flattened body. Pelage short, thick and silky. Dorsal pelage cinnamon-buff, fawn or dark grey but with considerable geographical variation. Ventral pelage paler. Flanks may or may not be paler than dorsal pelage. Head similar in colour to body, with small white patch on forehead in some individuals. Isolated tactile hairs protrude through the pelage, more numerous on face than on body. Limbs short. Feet naked and pink. Tail very short (ca. 15% of HB), pink, with hairs fringing from the tail itself. Body size is variable, depending on habitat, status within the colony and reproductive state. Skull with strong convex curvature dorsally; sagittal crest poorly developed; infraorbital foramina elliptical (ca. 3 mm), thin-walled; upper incisors ungrooved; four cheekteeth without re-entrant folds and decreasing in size from P to M³. No (or very little) sexual dimorphism; sexes difficult to distinguish. Nipples: $2 + 1 = 6$.

Geographic Variation

- C. h. hottentotus*: Western, Eastern and Northern Cape Provinces and Free State of South Africa; $2n = 54$; pelage cinnamon-buff to fawn with or without head-patch.
- C. h. natalensis*: KwaZulu–Natal and Mpumalanga Provinces of South Africa; $2n = 54$; pelage dark grey to black with characteristic black colouration around snout (usually without distinct head-patch).
- C. h. pretoriae*: Gauteng, North West, Limpopo and Mpumalanga Provinces of South Africa; $2n = 54$; pelage silvery-fawn to grey, with or without head-patch.
- C. h. nimrodi*: Limpopo Province, South Africa, and S Zimbabwe; pelage silvery-fawn to cinnamon-buff, with or without head-patch.

Similar Species

- Bathyergus suillus*. HB much larger; pelage without sheen; skull much flatter with large sagittal and occipital ridges; forefeet with elongated claws; upper incisors grooved.
- B. janetta*. HB larger; dorsal pelage silvery-fawn with sheen; skull with smaller sagittal and occipital ridges; auditory bullae markedly swollen; palate extends posteriorly to level of M³; forefeet with elongated claws; upper incisors grooved.
- Georchus capensis*. On average larger; dorsal pelage russet; head blackish with white muzzle and large white patch around ear opening; forefeet without elongated claws; upper incisors ungrooved.

Distribution Endemic to Africa. Widespread in several BZs (South-West Cape BZ, South-West Arid Zone BZ [Karoo], Highveld

BZ, and parts of Coastal Forest Mosaic BZ). Recorded from South Africa, Lesotho, Swaziland and S Zimbabwe. In South Africa, known from Stellenbosch and Somerset West on the Cape Peninsula, north-west to Steinkopf and inland to Prieska and Calvinia (Northern Cape Province); also in consolidated sands of the east coast and throughout Eastern Cape Province and southern parts of Free State; and in grasslands and savanna woodlands of KwaZulu–Natal, Mpumalanga, North-West and Gauteng Provinces in a range of soils from granitic sandstones to coarse clays. In Zimbabwe, found in granitic sandstones and in brecciated soils.

Habitat Fynbos, grassland, savanna and Succulent and Nama Karoo with rainfall of 200–1000 mm per annum. Occurs in a range of substrates from friable sandy loams to exfoliated schists and sandy soils. Does not occur in heavy clay or very brecciated soils.

Abundance Uncertain. In preferred habitats, density may exceed 150/km². Abundance of subterranean mammals is not easy to estimate.

Adaptations Subterranean. Capable of running forwards and backwards with equal ease in the burrow (Bennett 1992). Common Mole-rats have a low resting metabolic rate 0.92 ± 0.1 ml O₂/g/h (90% of expected), low body temperature of 34.4°C and high thermal conductance of 0.14 ml O₂/g/h/°C (Bennett *et al.* 1992). Body size varies with environment: in arid habitats, the mean body size (mean weight ± 1 SE) is much lower (57.8 ± 0.7 g; $n = 722$) than in mesic habitats (75.2 ± 1.0 g; $n = 865$) (Spinks 1998, Spinks *et al.* 2000). This reduction in body size in arid environments may be an adaptation to burrowing and to dispersed food, which requires less soil to be excavated per metre of burrow (Bennett *et al.* 1992).

Foraging and Food Herbivorous. Common Mole-rats specialize on bulbs, corms and tubers, especially those of *Albuca*, *Lachenalia*,



Cryptomys hottentotus

Ornithogalum (Hyacinthaceae), *Romulea*, *Micranthus*, *Homeria* (Iridaceae) and *Oxalis* (Oxalidaceae). They select the larger-sized geophytes and place them in a store situated close to the nest. The stored geophytes are packed in soil and disbudded when they shoot. In areas with seasonal flooding, the store and nest are often sited in raised areas. In arid areas, where some geophytes are too large to carry to the store, they are left growing and hollowed out *in situ*; these partly eaten geophytes can often regenerate. Small quantities of above-ground vegetation may also be consumed. In mesic parts of their range, where food occurs in closely spaced clumps and rainfall is frequent, mole-rats are able to search for new resources for many months of the year. In arid regions, food is more dispersed and there are few opportunities to greatly extend the foraging burrows. A number of geophytes containing cardiac glycosides that are extremely toxic to livestock (e.g. *Ornithogalum* spp., *Homeria* spp., *Morea* spp.) are eaten by Common Mole-rats (Davies & Jarvis, 1986).

Social and Reproductive Behaviour Social. Lives in small colonies of around five animals (2–14, $n = 109$). A colony consists of a founding reproductive pair and number of non-reproductive offspring. Sex ratios of captured colonies ($n = 4$) ranged from 0.5 to 1.6. Sex ratio of a population is 1.28 : 1 in favour of ♂♂ ($n = 1053$). Reproductive animals are the dominant animals in the colony; of the non-reproductive animals, ♂♂ are more dominant than ♀♀. The non-reproductive members of the colony cannot be placed into clearly defined work-related groups based on body mass; there is, however, a tendency for smaller (not necessarily younger) animals to perform more burrow maintenance than their larger (not necessarily older) counterparts. Sexual differences are minimal and Common Mole-rats are difficult to sex. In ♂♂, the testes are abdominal and the penis is retracted into a penile sheath. A vaginal closure membrane is present in all ♀♀ that are not actively reproducing. In the reproductive ♀, the vagina is open, and axillary and inguinal nipples are prominent. The gonads of non-reproductive ♂♂ are active and incest avoidance prevents the non-reproductive ♂ offspring from breeding. The reproductive ♂ solicits the ♀ prior to mating. Multiple copulations occur between the pair following ritualized courtship by the ♂, who grasps the hind region of the ♀ with his incisors, sometimes also urinating on her head (Bennett 1989, Spinks 1998, Malherbe *et al.* 2003).

Common Mole-rats are strictly obligate outbreeders. A colony will remain resident in the same area for a number of years, and will aggressively defend its home-range against invasion by other colonies. In the more mesic parts of their distribution, there is some mixing of animals from different colonies, whereas in the arid parts, mixing rarely occurs (Bishop *et al.* 2004). Dispersal in the Common Mole-rat occurs more frequently in ♂♂ than in ♀♀.

Reproduction and Population Structure Reproduction is seasonal, occurring in summer (Oct–Jan), with up to two litters per annum. Litter-size: 3 (1–6), $n = 6$ (Bennett 1989, Bennett & Faulkes 2000). However, there is no regression of gonads in winter, perhaps because this is when adult non-reproductive animals can disperse and find mates. Elevated levels of reproductive hormones (testosterone, progesterone and oestrogen) at this time would promote bonding, and prepare a new reproductive pair for breeding during the following summer. Ovulation is induced (Spinks *et al.*

1999). Gestation: 59–66 days (Bennett 1989, Malherbe *et al.* 2003). At birth, young weigh 8–9 g and are altricial. Pelage developed from Day 8. First solid foods eaten ca. Day 10. Eyes open on Day 13. Weaned at Day 28. Inter-sibling sparring begins on Day 10–14. Young do not disperse but remain in the natal colony (Bennett 1989).

Predators, Parasites and Diseases Common Mole-rats are at particular risk to predation during mound formation. They are eaten by a wide range of predators, including Mole-snakes *Pseudapsis cana*, Shield-nosed Snakes *Aspidelaps scutatus*, Cobras *Naja naja*, Barn Owls *Tyto alba*, Marsh Owls *Asio capensis*, Grey Herons *Ardea cinerea* and a number of small carnivores. Ectoparasites include eight species of fleas (one of which, *Cryptopsylla ingrami*, is specific to this mole-rat), one species of tick, one species of louse and ten species of mites (De Graaff 1981).

Conservation IUCN Category: Least Concern.

In parts of its range, Common Mole-rats are agricultural pests.

Measurements

Cryptomys hottentotus hottentotus

HB (♂♂): 122 (90–190) mm, $n = 70$

HB (♀♀): 118 (100–160) mm, $n = 62$

T (♂♂): 17.4 (8–27) mm, $n = 69$

T (♀♀): 18 (10–25) mm, $n = 54$

HF (♂♂): 21.3 (18–33) mm, $n = 58$

HF (♀♀): 21.5 (17–25) mm, $n = 48$

E (♂♂): 0 mm

E (♀♀): 0 mm

WT (♂♂): 65.8 (56–79) g, $n = 19$

WT (♀♀): 46.8 (41–54) g, $n = 19$

GLS (♂♂): 30.6 (29–38.6) mm, $n = 44$

GLS (♀♀): 30.6 (27.2–34.3) mm, $n = 42$

GWS (♂♂): 22.0 (19.6–28.0) mm, $n = 47$

GWS (♀♀): 21.9 (18.4–25.3) mm, $n = 43$

P⁴–M³ (♂♂): 5.1 (4.5–6.1) mm, $n = 39$

P⁴–M³ (♀♀): 5.1 (4.6–5.9) mm, $n = 36$

Cape Province, South Africa

Body measurements: De Graaff (1964a)

Weights: Bennett (1989)

C. h. pretoriae

HB (♂♂): 143.4 (103–172) mm, $n = 19$

HB (♀♀): 139.9 (123–165) mm, $n = 20$

T (♂♂): 13.6 (10–15) mm, $n = 19$

T (♀♀): 13.8 (10–17) mm, $n = 20$

HF (♂♂): 25.6 (19–27) mm, $n = 19$

HF (♀♀): 25.8 (23–29) mm, $n = 20$

E (♂♂): 0 mm

E (♀♀): 0 mm

WT (♂♂): 87.9 (59–148) g, $n = 19$

WT (♀♀): 80.6 (51–135) g, $n = 20$

GWS (♂♂): 25.4 (19–31.6) mm, $n = 71$

GWS (♀♀): 24.1 (18.6–29.3) mm, $n = 123$

GLS (♂♂): 38.7 (31.2–44.4) mm, $n = 7$

GLS (♀♀): 37.1 (29.2–41.2) mm, $n = 123$

P⁴–M³ (♂ ♂): 6.7 (5.1–7.7) mm, n = 71

P⁴–M³ (♀ ♀): 6.6 (4.7–7.6) mm, n = 123

Gauteng Province, South Africa (Van Rensburg 2000)

Key References Bennett 1989; Davies & Jarvis 1986; Spinks *et al.* 1999, 2000.

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Cryptomys kafuensis KAFUE MOLE-RAT

Fr. Rat-taupe du Kafue; Ger. Kafue Graumull

Cryptomys kafuensis Burda, Zima, Scharff, Macholan and Kawalika, 1999. Z. Säugetierkunde 64: 36–50. 'Hot Springs' in Itezhi-Tezhi, Kafue National Park, Zambia.

Taxonomy Prior to 1999, this species was included in *C. hottentotus* (e.g. Ansell 1978). Allozyme profile (Filippucci *et al.* 1994, 1997), chromosome number (Burda *et al.* 1999) and DNA sequences (Ingram *et al.* 2004) clearly separate this species from other species of *Cryptomys*. This species has been placed in the genus *Fukomys* by Kock *et al.* (2006) (see genus *Cryptomys*). Synonyms: none. Chromosome number: 2n = 58, FN = 82 (Burda *et al.* 1999).

Description Medium-sized mole-rat. Pelage dark slate-grey (young) to golden-ochre (adults). Head blunt with conspicuous white patch on forehead (in most but not in all individuals), variable in shape. Tail very short (15% of HB). Skull: infraorbital foramina elliptical, thin-walled; upper incisors ungrooved. Nipples: 2 + 1 = 6.

Geographic Variation None recorded.

Similar Species

C. anselli. Similar in appearance; white patch on the head tends to be smaller; chromosome number: 2n = 68.

Distribution Endemic to Africa Zambebian Woodland BZ. Recorded only in Itezhi-Tezhi, Southern Province, Zambia. (Degree square of 1526C of Ansell 1978.)

Habitat Grasslands and cultivated fields near villages where mean annual rainfall is 787 mm.

Abundance Abundant in this restricted area.

Remarks Little is recorded about the biology of this species. Subterranean and social. In many aspects of ecology, reproductive biology and behaviour apparently similar to *C. anselli*. Apart from humans (mole-rats are considered agricultural pests and are hunted for food), no predators are known to specialize on Kafue Mole-rats. Ectoparasites have not been found on this species. Endoparasites include two species of cestodes (*Inermicapsifer madagascariensis* and an undetermined species) and a nematode (*Protospirura muricola*); in one study, proportion of individuals with endoparasites was low (three out of 18) (Scharff *et al.* 1997).

Conservation IUCN Category: Vulnerable.

Measurements

Cryptomys kafuensis

HB (♂ ♂): 112 (105–129) mm, n = 4

HB (♀ ♀): 104 (96–115) mm, n = 5

T (♂ ♂): 16.6 (14.3–19.0) mm, n = 4

T (♀ ♀): 16.7 (13.5–20.0) mm, n = 5

HF (♂ ♂): 23.1 (19.9–25.0) mm, n = 4

HF (♀ ♀): 23.0 (18.9–24.3) mm, n = 5

E (♂ ♂): 0 mm

E (♀ ♀): 0 mm

WT (♂ ♂): 95 ± 32 g, n = 6

WT (♀ ♀): 75 (61–93) g, n = 6

GLS (♂ ♂): 33.5 (31.5–35.6) mm, n = 5

GLS (♀ ♀): 32.3 (30.3–34.2) mm, n = 5

GWS (♂ ♂): 23.7 (21.9–26.0) mm, n = 5

GWS (♀ ♀): 22.0 (20.6–23.9) mm, n = 5

P⁴–M³ (♂ ♂): 6.0 (5.6–6.8) mm, n = 5

P⁴–M³ (♀ ♀): 5.9 (5.5–6.2) mm, n = 5

Zambia (H. Burda unpubl.)

Key Reference Burda *et al.* 1999.

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Cryptomys kafuensis

Cryptomys mechowii GIANT MOLE-RAT

Fr. Rat-taupe géant; Ger. Riesiger Graumull

Cryptomys mechowii (Peters, 1881). Senckenberg. Ges. Naturw. Freunde Berlin, p. 133. Malanje, North Angola.

Taxonomy Originally described in the genus *Georychus*. Recently placed in the genus *Fukomys* by Kock *et al.* (2006) (see genus *Cryptomys*). Synonyms: *ansorgi*, *blainei*, *mellandi*. Subspecies: none. Chromosome number: $2n = 40$, $FN = 80$ (Macholan *et al.* 1993).

Description Large, stout mole-rat, the heaviest of all species in the genus (but not as large and heavy as *Bathyergus* spp.). Pelage short and dense, almost woolly in texture. Pelage colour age- and weight-dependent: dark slate-grey (neonates), greyish-brown (weaned young), brown (juveniles and subadults) and golden-ochre (adult animals); hairs pale brown at base, variable as dorsal pelage at tip. Ventral pelage pale brown. Head large, without white spot on forehead (except very small spot in some individuals). Eyes small. No external ears (small ears hidden in pelage in specimens from Mt Moko). Mouth rusty-stained (some individuals). Fore- and hindfeet large and broad, naked with fringe of whitish bristles on outer border of each foot. Tail very short (up to 15 mm); longish white bristles, which extend beyond end of tail. Males on average larger than ♀♀. Skull: robust and dorsoventrally flattened; infraorbital foramina elliptical (ca. 5 mm), thin-walled and slender; upper incisors ungrooved, large and broad. Nipples: $2 + 1 = 6$.

Geographic Variation Individuals from Mt Moko, Angola are larger than those from elsewhere (see below).

Similar Species Several sympatric species; none are usually as large or weigh as much as *C. mechowii*.

Distribution Endemic to Africa. Zambezian BZ and Southern Rainforest–Savanna Mosaic. Recorded from N Zambia, S and E DR Congo, E Angola (and perhaps N Malawi).

Habitat Savanna bushland, cultivated and abandoned fields, gardens, dambos (temporary swamps), pine plantations and dense *Acacia* woodland. Found in a variety of soil types from quite stony to pure sand and clay. The area of distribution is characterized by an annual rainfall of more than 1100 mm (Scharff *et al.* 2001a).

Abundance Detailed assessment of abundance not available, but appears to be rather abundant in the Copperbelt Province of Zambia.

Adaptations Subterranean. Extensive burrow system comprises a deep nest (60–160 cm deep) with three or four entrances, food stores and toilet areas (Scharff *et al.* 2001a). Giant Mole-rats have a low resting metabolic rate 0.6 ± 0.08 ml O_2 /g/h (96% of expected), low body temperature of $34 \pm 0.4^\circ\text{C}$, and a low thermal conductance 0.09 ± 0.01 ml O_2 /g/h/ $^\circ\text{C}$ (Bennett *et al.* 1994a).

Foraging and Food Predominantly herbivorous. Food in non-cultivated areas includes grass rhizomes, roots, bulbs and tubers of diverse weeds, shrubs and trees; in cultivated areas, they probably

*Cryptomys mechowii*

feed on crop plants such as sweet potatoes, cassava and groundnuts (Scharff *et al.* 2001a). Giant Mole-rats are unusual amongst bathyergids, because they apparently supplement their diet with invertebrate and vertebrate commensals found in their burrows (Burda & Kawalika 1993, Scharff *et al.* 2001a).

Social and Reproductive Behaviour Social. Lives in colonies of 2–20+ (probably up to 40 or more) individuals (Burda & Kawalika 1993, Scharff *et al.* 2001a). Sex ratio within colonies is in favour of ♀♀ (Scharff *et al.* 2001a). The colony consists of a founding reproductive pair and non-reproductive offspring from several litters (Burda & Kawalika 1993, Wallace & Bennett 1998, Scharff *et al.* 2001a). The reproductive animals are the most dominant, and the non-reproductive ♂♂ are more dominant than ♀♀. The non-reproductive members of the colony cannot be placed into clearly defined work-related groups based on body mass (Wallace & Bennett 1998). Giant Mole-rats are very vocal compared to other species of *Cryptomys* (Burda & Kawalika 1993, Credner *et al.* 1997).

Reproduction and Population Structure Giant Mole-rats breed aseasonally both in the laboratory and in the field, producing up to three litters per annum (Burda & Kawalika 1993, Bennett & Aguilar 1995, Scharff *et al.* 1999). Gestation: 112 (89–118) days. Litter-size: 2.6 (1–5), $n = 41$. Sex ratio (mean of 41 litters) at birth biased in favour of ♀♀ (1 : 1.9). At birth, young weigh 19.6 (12.6–27.7) g. Thin pelage appears within the first week. Eyes open on Day 6. First solid foods eaten ca. Day 14. Weaned ca. Day 90. Inter-sibling sparring begins at Day 10 (Bennett & Aguilar 1995, Scharff *et al.*

1999). Growth is comparatively slow: weight increases in an almost linear fashion until ca. 120 g at age ca. Day 170; thereafter increase in weight continues until ca. 250–300 g at ca. Day 450 (n = 1; Scharff *et al.* 1999).

A colony consists of a founding reproductive pair and several litters of their offspring. In the laboratory, genetic studies have shown that female offspring may sometimes mate with the reproductive ♂ (M. J. O'Riain & J. Bishop unpubl.). Offspring can be denoted as (in many cases probably lifelong) helpers at the nest (Burda & Kawalika 1993, Bennett & Aguilar 1995, Scharff *et al.* 1999, 2001a, Burda *et al.* 2000).

Predators, Parasites and Diseases Giant Mole-rats are eaten by Mole-snakes and other large snakes, and also by humans. Ectoparasites have not been found on animals or in the nests of Giant Mole-rats. Endoparasites include three species of cestodes (*Inermicapsifer madagascariensis*, *Raillietina* sp., *Inermicapsifer madagascariensis*) and two species of nematodes (*Protospirura muricola*, *Cappilaria* sp.). Proportion of individuals with endoparasites is relatively low (12 out of 35) compared to most other rodents (Scharff *et al.* 1997, Scharff *et al.* 2001a).

Conservation IUCN Category: Least Concern.

Giant Mole-rats are detrimental to agriculture and horticulture and are considered as pests. They are an important source of protein for local people and their meat is highly valued in some areas of Zambia.

Measurements

Cryptomys mechow

HB (♂ ♂): 190 ± 22 (156–262) mm, n = 10

HB (♀ ♀): 165 ± 18 (135–205) mm, n = 10
 T (♂ ♂): 27.3 ± 2.3 (23–31) mm, n = 10
 T (♀ ♀): 27.8 ± 3.8 (23–33.7) mm, n = 10
 HF (♂ ♂): 35.3 ± 2.0 (30.6–37.8) mm, n = 10
 HF (♀ ♀): 32.2 ± 1.0 (31–34) mm, n = 10
 E (♂ ♂): 0 mm
 E (♀ ♀): 0 mm
 WT (♂ ♂): 370 ± 94 (250–560) g, n = 20
 WT (♀ ♀): 245 ± 34 (200–295) g, n = 22
 GLS (♂ ♂): 52.0 (45.6–59.2) mm, n = 5
 GLS (♀ ♀): 42.2 (34–49.7) mm, n = 5
 GWS (♂ ♂): 46.7 (40.3–53.2) mm, n = 5
 GWS (♀ ♀): 33.2 (28.6–37.0) mm, n = 5
 P⁴–M³ (♂ ♂): 9.1 (7.9–10.2) mm, n = 5
 P⁴–M³ (♀ ♀): 7.8 (6.9–9.2) mm, n = 5
 Zambia (H. Burda unpubl.)

HB: 241.1 (222–260) mm, n = 5

T: 26.0 (20–32) mm, n = 4

HF: n. d.

E: 46.8 (42–50) mm, n = 5

WT: n. d.

GLS: 55.7 (53.8–57.2) mm, n = 5

GWS: 38.0 (35.7–39.1) mm, n = 5

P⁴–M³: 9.0 (8.8–9.4) mm, n = 5

Mt Moko, Angola (BMNH)

Key References Burda & Kawalika 1993; Bennett & Aguilar 1995; Scharff *et al.* 1999, 2001a.

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Cryptomys ochraceocinereus OCHRE MOLE-RAT

Fr. Rat-taupe ocre; Ger. Ockerfarbiger Graumull

Cryptomys ochraceocinereus (Heuglin, 1864). Nova Acta Acad. Caes. Leop., Dresden 31: 3. Upper Bahr-el-Ghazal, Sudan.

Taxonomy Originally described in the genus *Georychus*. Recently placed in the genus *Fukomys* by Kock *et al.* (2006) (see genus *Cryptomys*). Synonyms: *kummi*, *lechei*. Subspecies: none recognized here (but see Geographic Variation). Chromosome number: not known.

Description Medium-sized mole-rat. Pelage short, dense and soft. Dorsal pelage medium-brown, sometimes with silvery tinge. Ventral pelage similar in colour to dorsal pelage. Conspicuous roundish white head-spot (5–15 mm diameter) on forehead in some individuals, although absent in others (e.g. in parts of Uganda). Eyes blue. Conspicuous white eye-ring. Fore- and hindfeet small, broad and naked. Forefoot with five digits, hindfoot with five digits; all with sharp claws. Small fringe of pale white hairs around base of hindfoot. Tail (ca. 10% of HB) barely visible, mostly obscured by hair-like bristles. Skull: infraorbital foramina round-oval (ca. 2 mm diam.), thick-walled; upper incisors ungrooved. Nipples: 1 + 1 = 4.

Geographic Variation De Graaff (1975) records two subspecies: *C. o. ochraceocinereus* from Upper Bahr el Ghazal, Sudan, and *C. o. oweni* from S Sudan.

Distribution Endemic to Africa. Primarily Northern Rainforest–Savanna Mosaic of central Africa. Recorded from S Sudan, N Uganda, N DR Congo and Central African Republic. Locality records are widely distributed. Presence in W Cameroon and NW Kenya (as shown on map) is uncertain.

Habitat Wooded savanna (e.g. *Isberlinia* woodlands) and cultivated land.

Abundance Uncertain; widespread but localized. In Didinga Hills, S Sudan, recorded as 'Plentiful in mountain-meadows' (Setzer 1956).

*Cryptomys ochraceocinereus*

Remarks Subterranean. The burrow is a network of tunnel passages, which may attain an overall length of 315 m with up to 32 mounds of excavated soil. The mounds are irregularly placed and in

groups of three or four close together. An enlarged area in a passage forms the nest, which is lined with grasses on the outside and with roots of trees and leaves on the inside (Verheyen & Verschuren 1966). Mounds are 7–10 cm high and 20–25 cm at the base (Hatt 1940a). Herbivorous. In Garamba N. P. (NE DR Congo) feeds on roots, principally on those of *Dioscorea abyssinica* (Verheyen & Verschuren 1966, as *C. lechei*).

Conservation IUCN Category: Least Concern.

Measurements

Cryptomys ochraceocinereus

HB: 169 (157–200) mm, n = 14

T: 18 (14–27) mm, n = 24

HF: 31 (27–35) mm, n = 14

E: 0 mm

WT: n. d.

GLS: 43.2 (39.7–48.2) mm, n = 16

GWS: 29.4 (27.1–32.9) mm, n = 16

P⁴–M³: 7.2 (6.9–8.8) mm, n = 16

N DR Congo (Hatt 1940a, as *C. lechei*)

Key References Setzer 1956; Verheyen & Verschuren 1966.

Nigel C. Bennett

Cryptomys zechi TOGO MOLE-RAT

Fr. Rat-taupe du Togo; Ger. Togo Graumull

Cryptomys zechi (Matschie, 1900). Sber. Ges. naturf Freunde, Berlin, p. 146. Near Kete Krachi, Middle Volta, Togo. (Old Kete Krachi, now inundated by L. Volta, is in present-day Ghana, not Togo [Grubb *et al.* 1998]).

Taxonomy Originally described in the genus *Georychus*. Recently placed in the genus *Fukomys* by Kock *et al.* (2006) (see genus *Cryptomys*). Synonyms: none. Chromosome number: not known. See Rosevear (1969) for further information.

Description Pale-coloured mole-rat, sometimes with whitish markings on head or body. Pelage soft and short, with velvet-like texture. Dorsal pelage pale cinnamon to buff (and slightly variable); hairs unicoloured, may be white very close to base. Ventral pelage not recorded. Head blunt, usually with white patch on forehead; incisor teeth visible outside lips. Long vibrissae. Eyes very small. External ear absent. Limbs short. Fore- and hindfeet well-developed and naked. Five digits on fore- and hindfeet. Tail very short (ca. 8% of HB), covered with stiff bristles. Skull: widest part of nasal bones posteriorly; infraorbital foramina round-oval (ca 2 mm diam.), thick-walled; upper incisors ungrooved and comparatively wide (ca. 3.2 mm). Nipples: 2 + 1 = 6.

Geographic Variation None recorded.

Similar Species

C. foxi. On average smaller; pelage dark sepia-brown; widest part of nasal bones anteriorly; P⁴–M³ shorter (ca. 7.6 mm); incisor teeth comparatively narrow (ca. 2.4 mm). Nigeria only.

*Cryptomys zechi*

Distribution Endemic to Africa. Guinea Savanna BZ. Recorded from NW Ghana and between the Oti and Volta rivers in Togo. One specimen (BMNH) allocated to this species from SW Sudan (Rosevear 1969) is probably *C. ochraceocinereus* (Grubb *et al.* 1998).

Habitat Grasslands with a few scattered trees (typically *Khaya senegalensis*, *Butyrospermum parkii*, *Adansonia digitata*, *Parkia clappertoniana* and *Ceiba pentandra*) (Yeboah & Dakwa 2002).

Abundance Unknown; presumably rare with a rather restricted distribution.

Remarks Colony size 1–7 (average four animals). Sex ratio of colony members is parity. It is believed that animals occur in small colonies comprising a reproductive pair and their litter. Reproduction restricted to the reproductive pair (Yeboah & Dakwa 2002).

Conservation IUCN Category: Least Concern.

Measurements

Cryptomys zechi

HB: 167 mm, n = 4

T: 15 mm, n = 4

HF: 27 mm, n = 4

E: 0 mm, n = 4

WT: 217 (155–283) g, n = 48

GLS: 42.7 mm, n = 4

GWS: 31.0 mm, n = 4

P⁴–M³: 8.3 mm, n = 4

Throughout geographic range (Rosevear 1969; mean values only, range not given)

Weight: Atebubu District, Ghana (Yeboah & Dakwa 2002)

Key References Grubb *et al.* 1998; Rosevear 1969; Yeboah & Dakwa 2002.

Nigel C. Bennett

GENUS *Georychus*

Cape Mole-rat

Georychus Illiger, 1811. Prodr. Syst. Mamm. Avium., p. 87. Type species: *Mus capensis* Pallas, 1778.



Georychus capensis.

A monotypic genus with a restricted distribution in South Africa. The genus occurs from the Cape Peninsula of Cape Province eastwards through Eastern Cape Province to KwaZulu–Natal and Mpumalanga Provinces. Preferred habitat is loose sandy soils and loams in mesic regions of South Africa, usually where mean annual rainfall is >500 mm.

Georychus mole-rats are of intermediate size, being larger than most species of *Cryptomys* but smaller than *Bathyergus*. The pelage is distinctive: head black with flat white muzzle, white lips and eye-ring; and large white patch around auditory meatus. Dorsal pelage of body varies from dark grey, russet to orange-cinnamon; ventral pelage whitish. Digits of fore- and hindfeet are short, with short claws. Tail is short and white. The skull is less robust than in *Bathyergus* and is characterized by upper incisors without grooves, which have their roots in the pterygoid bones behind the cheekteeth. Each upper cheektooth has one narrow inner and one outer fold that persist in adults (the only genus without simplified ovate cheekteeth in adults). The jugal bone dovetails into a backward projection of the zygomatic arch (Figure 105). Other characters of the genus are given in the species profile. The single species is *Georychus capensis*.

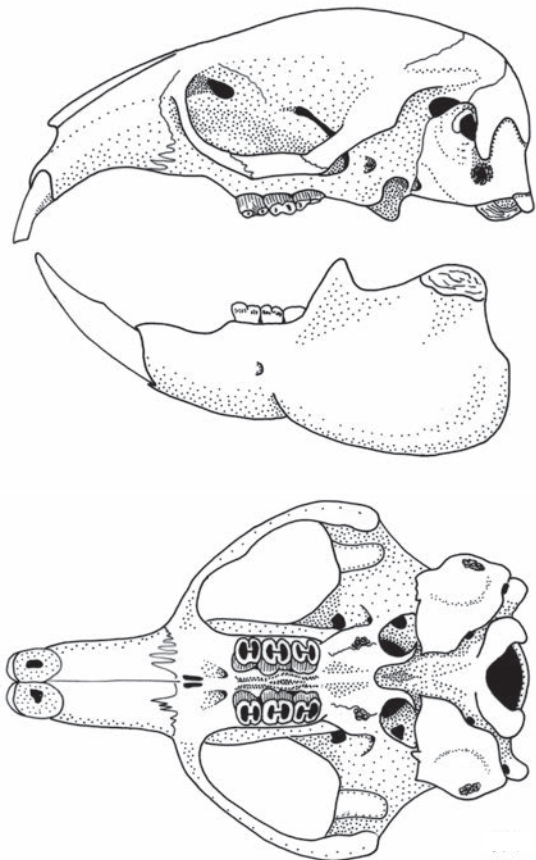


Figure 105. Skull and mandible of *Georychus capensis* (BMNH 95.9.3.18).

Nigel C. Bennett

Georychus capensis CAPE MOLE-RAT (BLES MOL)

Fr. Rat-taupe du Cap; Ger. Kap-Blessmulle

Georychus capensis (Pallas, 1778). Nova. Spec. Quad. Glir. Ord., 76: 172. Cape of Good Hope, South Africa.

Taxonomy Originally described in the genus *Mus*, but later placed in *Marmota* (see de Graff 1981). In 1811, Illiger proposed the genus *Georychus* with *Mus capensis* as the type. In 1832, Smuts referred to the species as *Bathyergus capensis*. Modern authors, e.g. De Graaff (1981) and Smithers (1983), refer to the species as *Georychus capensis*. The populations from Western Cape Province and from KwaZulu–Natal could represent two different species as allozyme and mitochondrial DNA RFLP analyses suggest they are divergent (Honeycutt *et al.* 1987; Nevo *et al.* 1987). Synonyms: *buffonii*, *canescens*, *leucops*, *yatesi*. Subspecies: none. Chromosome number: $2n = 54$, $aFN = 100$ (Taylor *et al.* 1985, Nevo *et al.* 1986).

Description Medium-sized mole-rat with distinctive black and white colouration on head. Pelage thick and woolly. Dorsal pelage russet, often with a brownish tinge. Ventral pelage silvery-white. Unlike other genera, tactile hairs do not project from the pelage on the body. Head large and blunt, black, charcoal or deep russet, with a pattern of white markings unlike that of any other mole-rat. Muzzle and lips white. Eyes black (a little larger than other bathyergids) with large white eye-ring. Large white patch around auditory meatus. Fore- and hindfeet usually white. Tail very short (ca. 13% of HB), pink with a number of coarse white hairs radiating from it. Skull: dorsoventrally flattened; old animals possess distinctive sagittal and nuchal crests; jugal dovetails into backward projection of the zygomatic arch; infraorbital foramina small, round (ca. 1–1.5 mm), thick-walled. Upper cheekteeth each with one narrow inner and outer fold that persist in adults. Upper incisors ungrooved. No sexual dimorphism. Nipples $2 + 1 = 6$.

Geographic Variation None except for some genetic characters.

Similar Species

Bathyergus suillus. Larger; pelage cinnamon-brown, and sometimes with darker mid-dorsal band; forefeet with elongated claws; upper incisors with grooves.

Cryptomys hottentotus. On average much smaller; pelage fawn to grey.

Distribution Endemic to Africa. South-West Cape BZ and some parts of the Highveld BZ. Recorded only from South Africa; distribution is disjunct in mesic regions where mean annual rainfall is >500 mm. Recorded from Cape Peninsula in SW Western Cape Province northwards to Citrusdal and Nieuwoudtville, and eastwards to Port Elizabeth and W Eastern Cape Province (formerly Transkei). Isolated populations occur in KwaZulu–Natal Province near the border with Lesotho, and at Belfast, Wakkerstroom and Ermelo in Mpumalanga Province (formerly Eastern Transvaal). In S Western Cape Province, found at 12–510 m and in KwaZulu–Natal at 1372–1700 m.

Habitat Coastal and montane fynbos, forest and savanna grassland, where mean annual rainfall is 500–800 mm. Occurs in sandy loams, alluvium and clay soils. In coastal regions, occurs where annual rainfall

*Georychus capensis*

is 279–728 mm (mean ca. 500 mm) and in KwaZulu–Natal where annual rainfall is 954–1278 mm (mean ca. 800 mm). Sympatric with *Bathyergus suillus* and *Cryptomys hottentotus* in coastal areas where the sands are more consolidated.

Abundance Uncommon and localized, but densities may exceed 30 animals/km² in Cape Town.

Adaptations Strictly solitary and highly territorial. Multiple occupancy of burrows only during the breeding season, when the mate is present or when ♀ has young. Territorial drumming, using both hindfeet simultaneously, is frequently performed to advertise presence in the burrow system. The burrow system can exceed 130 m in length, and the burrow diameter is typically 100 mm. The burrow system comprises a central nest, a food store and a toilet area located away from the nest area. The food store consists of geophytes packed with soil; stored geophytes are disbudded when they sprout. Mounds are thrown up after rain when the soil is moist. Cape Mole-rats have been observed above ground on occasions, particularly after dusk. It is thought that in mountainous regions, where there are pockets of soil interspersed with rocky barriers, they disperse above ground.

Cape Mole-rats have a low basal metabolic rate of 0.59 ml O₂/g/h, and low body temperature (36°C).

Foraging and Food Herbivorous. Food is located as the mole-rats excavate their superficial (5–25 mm deep) foraging tunnels of diameter 7–8 cm. Most extensions to the burrows occur after rainfall when the costs of burrowing are lowest. The diet consists predominantly

of geophytes – bulbs, corms and tubers – but also ca. 6% above-ground vegetation. The geophytes include species of Hyacinthaceae (e.g. *Albuca*, *Lachenalia* and *Ornithogalum*), Iridaceae (e.g. *Romulea*, *Micranthus* and *Homeria*) and Oxalidaceae (e.g. *Oxalis*). A number of these contain cardiac glycosides and are toxic to livestock but not to mole-rats. Cape Mole-rats selectively store the larger-sized geophytes of many species, and food stores may exceed 5000 items. The food in the store is probably eaten when ♀ has young or during unfavourable periods when soils are difficult to excavate (Lovegrove & Jarvis 1986).

Social and Reproductive Behaviour Solitary, aggressive and territorial. Seismic signalling (which differs from territorial drumming) occurs at the onset of reproduction. Males and ♀ ♀ drum at different frequencies. The onset of courtship seismic signalling in ♂♂ is accompanied by raised urinary testosterone concentrations, and enlargement of the testes and accessory reproductive glands. Hindfoot seismic signalling by ♂♂ is extremely fast, each drum pulse in ♂♂ lasting two minutes with a beat length of 0.035 seconds. Females do not drum as fast, with a beat length of 0.05 per second. Courtship is usually initiated by ♂ and copulation is brief, involving multiple intromissions of 2–3 thrusts per second, interspersed by short periods during which the animals are involved in bouts of grooming, particularly around the genitalia (Bennett & Jarvis 1988, Narins *et al.* 1992).

Reproduction and Population Structure Reproduction is seasonal; young are born in summer (Aug–Dec), and ♀ produces a maximum of two litters/summer. Gestation: ca. 44 days. Litter-size: 6 (3–10), *n* = 19. At birth, young naked and blind. Pelage with the distinctive markings Day 7. Eyes open Day 9. First solid foods eaten ca. Day 17. Weaned Day 28. Pup development is comparatively rapid compared with that of social species. Inter-sibling aggression begins around Day 35, and young disperse (either below or above ground) at about Day 50.

Predators, Parasites and Diseases Cape Mole-rats are particularly vulnerable to predation during mound formation and

when moving above ground. Preyed upon by Mole-snakes *Pseudapsis cana*, cobras, owls, herons and small carnivores. Few parasites are associated with these mole-rats: ectoparasites includes four species of mites, a tick and a flea; endoparasites include a tapeworm (*Echinococcus* sp.) and a nematode (*Trichurus* sp.). Mole-rats are susceptible to bubonic plague (De Graaff 1981).

Conservation IUCN Category: Least Concern.

Cape Mole-rats are occasionally an agricultural pest, and can cause problems for horticulturists and green-keepers.

Measurements

Georchus capensis

HB (♂♂): 189 (177–200) mm, *n* = 12

HB (♀♀): 182 (155–204) mm, *n* = 29

T (♂♂): 31 (25–40) mm, *n* = 12

T (♀♀): 26 (20–33) mm, *n* = 29

HF (♂♂): 32 (30–35) mm, *n* = 12

HF (♀♀): 29 (27–35) mm, *n* = 29

E (♂♂): 0 mm

E (♀♀): 0 mm

WT (♂♂): 181 g, *n* = 51*

WT (♀♀): 180 g, *n* = 37*

GLS (♂♂): 48.3 (44.1–53.3) mm, *n* = 12

GLS (♀♀): 45.1 (41–51.2) mm, *n* = 29

GWS (♂♂): 37.9 (35.1–39.9) mm, *n* = 12

GWS (♀♀): 32.8 (30.1–40.4) mm, *n* = 29

P⁴–M³ (♂♂): 8 (7.6–9.4) mm, *n* = 12

P⁴–M³ (♀♀): 7.8 (6.8–8.5) mm, *n* = 29

Western Cape Province, South Africa (De Graaff 1964a, Taylor *et al.* 1985)

*Range not recorded

Key References Bennett & Jarvis 1988; Taylor *et al.* 1985.

Nigel C. Bennett

GENUS *Heliophobius*

Silvery Mole-rat

Heliophobius Peters, 1846. Bericht Verhandl. K. Preuss. Akad. Wiss. Berlin 11: 259. Type species: *Heliophobius argenteocinereus* Peters, 1846.



Heliophobius argenteocinereus.

Currently considered to be a monotypic genus distributed from Kenya southwards through Tanzania to E DR Congo, N Zambia, Malawi and Mozambique north of the Zambezi R. Occurs in a variety of savannas and woodlands, and in many soil types from 'black cotton' soil (very sticky when wet, hard when dry) to well-drained sandy soils.

The genus is distinguished from other genera in the family by long, silky pelage, up to six simple upper and lower cheekteeth (not usually all present at the same time), and a narrow palate that does not extend posteriorly beyond the level of the cheekteeth. Cheekteeth show re-entrant folds in young animals. Unlike *Bathyergus*, and like the other genera of mole-rats, the angular process of the lower jaw does not extend far posteriorly to the skull (Figure 106).

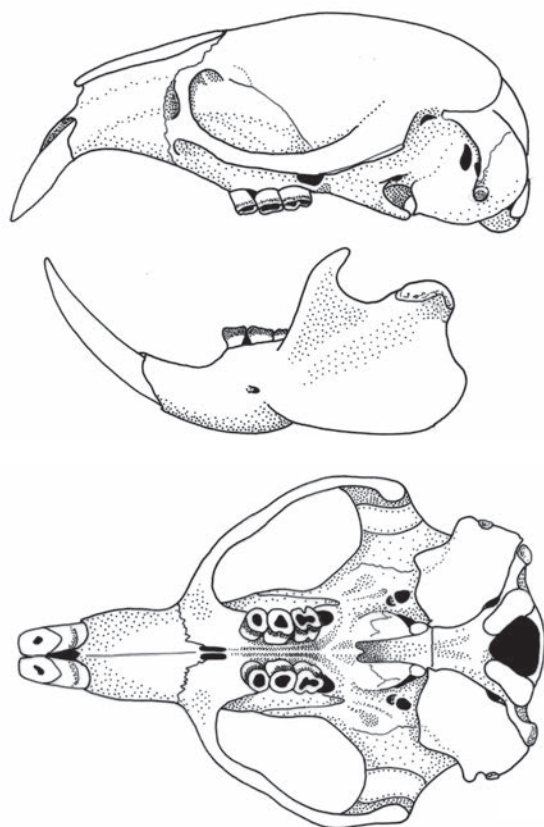


Figure 106. Skull and mandible of *Heliophobius argenteocinereus* (HC 2438). Subadult: only three cheek-teeth visible (cf. 4–5 in adults).

Heliophobius argenteocinereus SILVERY MOLE-RAT

Fr. Rat fouisseur gris-argent; Ger. Silbergrauer Erdbohrer

Heliophobius argenteocinereus Peters, 1846. Bericht Verhandl. K. Preuss. Akad. Wiss. Berlin 11: 259. Tete, Mozambique. (See also below.)

Taxonomy Ellermann (1940) listed two species of *Heliophobius*: *H. argenteocinereus* and *H. spalax*, as well as eight subspecies of *H. argenteocinereus* (Honeycutt *et al.* 1991). All forms currently considered to be synonyms of *H. argenteocinereus*. However, genetic differences between animals from Kenya and from Malawi suggest that populations in different parts of the geographic range may be specifically or subspecifically different (see genus profile). Molecular studies suggest that there is a good case for recognizing five genetically divergent clades within the species: *robustus/mottoulei* species complex (clade 1), *H. kapiti* (clade 2a), *H. spalax* (tentatively clade 2b), *H. emini* (clade 3), *argenteocinereus/angonicus* complex (clade 4) and *H. marungensis* (clade 5) (C. Faulkes and N. Bennett, pers. comm.). Synonyms: *albifrons*, *angonicus*, *emini*, *kapiti*, *marungensis*, *mottoulei*, *pallidus*, *robustus*, *spalax*. Subspecies: none currently recognized (but see above and Geographic Variation). Chromosome number: $2n = 60$ (George 1979a), $2n = 62$ (Scharff *et al.* 2001b).

Description Medium-sized silvery-grey mole-rat with soft silvery pelage. Pelage silky and long (20–25 mm). Dorsal pelage silvery-grey to tan. Nose, eye region, lateral parts of head, limbs and ventral pelage paler. Head similar to dorsal pelage, paler around muzzle, eyes and nose; small white patch or fleck on forehead in some individuals (ca. 50% of those in Malawi, R. Sumner pers. comm.).

Biological characters of the genus include solitary behaviour, seasonal breeding, and a long gestation (87–101 days) that limits ♀♀ to having one litter a year (up to five young/litter). The other solitary genera (*Bathyergus*, *Georchus*) have shorter gestations that allow two litters in the breeding season after winter rainfall (late winter, early spring). *Heliophobius* has a wider geographic distribution than the other solitary genera (Jarvis & Bennett 1991, Sumner *et al.* 2003a).

Ellerman (1940) recognized two species, *H. argenteocinereus* and *H. spalax* (from Kilimanjaro, Tanzania) although Honeycutt *et al.* (1991) consider the genus to be monotypic with variations that are age-related. Recent studies have shown large genetic divergencies between animals from Kenya and from Malawi (up to 15.4% HKY85 corrected cytochrome *b* sequence differences; C. G. Faulkes pers. comm.). Furthermore, there are chromosomal differences between the Zambian populations ($2n = 62$, Scharff *et al.* 2001b) and those in Kenya ($2n = 60$, George 1979a). The systematics of this genus requires further study. The single species is *Heliophobius argenteocinereus*.

J. U. M. Jarvis

Incisor teeth long, slightly curved and lying outside the lips. Limbs short. Feet, pale-coloured, not enlarged, outer edges fringed with stiff hairs. Five digits, not strongly clawed. Tail very short (8–9% of HB), pale-coloured, with fringe of stiff hairs. Sexual dimorphism occurs in some regions (see below). Infraorbital foramen round (diam. 1.5 mm), thick-walled. Upper incisors ungrooved. (See also genus profile.) Nipples: $2 + 1 = 6$.

Geographic Variation Silvery Mole-rats from Malawi are larger than those recorded elsewhere; they also have shorter pelage (10–15 mm) and show sexual dimorphism with ♂♂ being about 15% larger than ♀♀ (Sumner *et al.* 2003a). Tail length is shorter than in specimens from Kenya, and ♀♀ have significantly longer tails (12.9 ± 1.8 mm) than the ♂♂ (12.4 ± 1.7) (R. Sumner pers. comm.). There is a white patch in the axilla of animals from Athi Plains, Kenya, but not from Malawi (J. Jarvis & R. Sumner unpubl.). The pelage is darker and the head-patch is larger in animals from Morogoro, Tanzania (C. Faulkes pers. comm.). Molecular genetic studies also show considerable geographic variation (see above).

Similar Species

Tachyoryctes splendens. Similar size; ear pinnae present, but small; eyes larger; incisors orange. (Although subterranean in habit, as are

*Heliophobius argenteocinereus*

bathyergid mole-rats, *Tachyoryctes splendens* belongs to a different family of rodents – Spalacidae: Tachyoryctinae.)

Distribution Widespread in Zambezian Woodland BZ and southern part of Somalia–Masai Bushland BZ. Recorded from C and S Kenya, Tanzania, Malawi, E Zambia, C and N Mozambique, and E DR Congo. Occurs from ca. 100 m to >2000 m and where annual rainfall is usually 250–900 mm, and up to 1500 mm (in Malawi). The type locality is given as Tete (which is on the southern (right) bank of the Zambezi R.); however, the type description records that the holotype (and specimens of other species) came from ‘Tette’ without saying precisely where they were caught. Smithers & Lobão Tello (1976) show that all records in Mozambique come from north of the Zambezi R., although Smithers (1983), which considers only Africa south of the Zambezi, shows a small range south of the Zambezi. As pointed out by Skinner & Smithers (1990), it seems unlikely that the species occurs south of the Zambezi.

Habitat *Combretum* and *Brachystegia* woodlands, rocky hillsides and sub-montane grasslands. In Malawi, frequently invades crops of banana, cassava and sweet potato (R. Sumbera pers. comm.). Occurs in a wide range of soils from well-drained easily worked sandy soils to heavy ‘cotton soils’ that are very hard when dry but sticky and waterlogged when wet (Kingdon 1974, Ansell & Dowsett 1988, J. U. M. Jarvis unpubl.).

Abundance Little information. Densities are low on the Athi Plains, Kenya (J. U. M. Jarvis unpubl.). In Malawi, density is 5.2/ha at Blantyre (Sumbera *et al.* 2003a, b). Sex ratio is parity (Sumbera *et al.* 2003a).

Adaptations Subterranean. Silvery Mole-rats dig using their chisel-like incisor teeth. On the Athi Plains, Kenya, foraging burrows are 12–23 mm below the surface, 50 mm in diameter and average

47 m (range 39–61, $n = 4$) in length (Jarvis & Sale 1971). In Malawi, mean burrow lengths are 73 m (range 22–138) at Blantyre, and 105 m (range 39–188) at Mulanje (Sumbera *et al.* 2003b, R. Sumbera unpubl.). Nest chambers are slightly deeper (300 mm) and contain a hollow ball of nesting material (grass, corm husks, skins of tubers); deeper still is a bolt-hole (up to 540 mm) where a mole-rat can retreat when threatened. Toilet areas are in blind-ending tunnels (Sumbera *et al.* 2003b). When the black cotton soil is wet, the animals use balls of mud to repair damaged burrows. Burrow systems often associated with slightly raised areas with better drainage (J. U. M. Jarvis unpubl.). Individuals show no particular activity pattern, and are active during the day and night (Jarvis 1973b).

Foraging and Food Herbivorous. Little known of the diet in the wild. In Kenya and Malawi, partly eaten tubers of *Dolichos* sp. and *Vigna* sp., still growing *in situ*, were apparently harvested as needed by the mole-rats (Jarvis & Sale 1971, R. Sumbera pers. comm.). Of the two tubers, *Vigna* is the preferred food and appears to be the key species determining the occurrence of Silvery Mole-rats near Blantyre (R. Sumbera pers. comm.). In Malawi, other species such as *Gladiolus dallenii*, *Imperata cylindrica* and *Hypoxis* sp., as well as a variety of cultivated root crops, have also been found in food stores (either in special chambers or blind-ending tunnels) (R. Sumbera pers. comm.). In captivity, animals are strongly selective, preferring bulbs and tubers, which they peel before eating. They practise coprophagy, seizing faecal pellets as they are voided from the anus with their incisors, and eating up to 12 pellets at one time (Jarvis 1969b).

Social and Reproductive Behaviour Silvery Mole-rats aggressively defend burrows against conspecifics. Animals emit a snorting hiss when cornered, assume a rigid stance with the feet braced and head thrown up, and with mouth and eyes wide open. When fighting, opponents lock incisors and sometimes roll over while still maintaining a grip on the opponent. Territorial drumming has not been reported (Jarvis 1969a, Sumbera *et al.* 2003a), but short, fast, repeated drumming with the forelimbs occurs during highly aggressive encounters (Sumbera 2001). In Kenya, animals are unusual amongst bathyergids in emitting an almost continuous cry (similar to a newborn baby) when alarmed (such as being transported by car; Jarvis 1969a). Silvery Mole-rats from Malawi are not very aggressive and will often coexist in captivity. Courtship behaviour (Sumbera 2001) is initiated by ♂, who follows ♀, sometimes sniffing her anogenital region. The animals face each other, gently nibble each other or lock incisors. Sometimes one of them (of either sex) lies on its back. Both animals vocalize, ♀ more so than ♂. The ♂ frequently urinates on vertical surfaces. Repeated intromissions (10–30) and rapid thrusting (7.3/sec) occur during copulation. Aggression has not been observed at the end of mating (Sumbera 2001).

Reproduction and Population Structure Reproduction is seasonal. In Malawi, mating occurs during the beginning of the cold dry season (Apr–Jun) and young are born when it is hot and dry (Aug–Oct) (Sumbera *et al.* 2003a), whereas limited data from Kenya indicate that young are born at the onset of the long rains (Apr–Jun) (Jarvis 1969a). Gestation: 87–101 days ($n = 3$ litters; Jarvis & Bennett 1991, Sumbera *et al.* 2003a). Litter-size: 3.2 (2–5), $n = 27$ litters (Sumbera *et al.* 2003a). At birth, mean weight of young 12.8 g

(n = 5). First solids eaten Day 8–11. Eyes open Day 13–14. Weaned ca. 2 months. Mean adult weight ca. 12 months. The ability to engage in serious sparring/fighting appears to be correlated with attainment of a specific body weight (and not with age), ranging from ten weeks (♂ WT: 94 g) to 22 weeks (♂ 80 g) (Sumbera *et al.* 2003a). The long gestation precludes the ability of ♀ to have more than one litter each breeding season. The lack of seismic signalling, ‘relatively high pacifism in captive animals’, capture of mature animals above ground, and no evidence of interlinking burrows suggest that this species may find its mates by moving above ground (Sumbera *et al.* 2003a).

Predators, Parasites and Diseases Little information available. However, predators are probably snakes, raptors and small carnivores. Endoparasites include four species of *Eimera* (Koudela *et al.* 2000, Modry *et al.* 2005), *Protospirura muricola* and *Inermicapsifer arvicanthidis* (Tenora *et al.* 2003). Ectoparasites include an unidentified species of mite (Trombiculidae, Acarina) (R. Sumbera unpubl.).

Conservation IUCN Category: Least Concern.

Measurements

Heliophobius argenteocinereus

HB (♂ ♂): 161 (131–195) mm, n = 69

HB (♀ ♀): 158 (131–191) mm, n = 129

T (♂ ♂): 12.4 (6–16) mm, n = 64

T (♀ ♀): 12.9 (8–17) mm, n = 62

HF (♂ ♂): 28.3 (18–31) mm, n = 69

HF (♀ ♀): 28.4 (23–34) mm, n = 129

E (♂ ♂): 0 mm

E (♀ ♀): 0 mm

WT (♂ ♂): 145 (107–220) g, n = 70

WT (♀ ♀): 153 (110–259) g, n = 128

GLS (♂ ♂): 39.1 (33.9–45.0) mm, n = 68

GLS (♀ ♀): 38.1 (32.9–43.0) mm, n = 124

GWS (♂ ♂): 30.3 (26.8–35.3) mm, n = 69

GWS (♀ ♀): 30.6 (25.3–34.8) mm, n = 124

P⁴–M³ (♂ ♂): 7.5 (6.1–9.4) mm, n = 69

P⁴–M³ (♀ ♀): 7.7 (6.1–9.3) mm, n = 125

Morogoro and Mlali, Tanzania (W. Verheyen unpubl.)

HB (♂ ♂): 155.3 (106–193) mm, n = 64

HB (♀ ♀): 148.8 (108–180) mm, n = 62

HF (♂ ♂): 29.8 (24–36) mm, n = 64

HF (♀ ♀): 28.7 (23–35) mm, n = 62

WT (♂ ♂): 190.1 (63–331) g, n = 70

WT (♀ ♀): 162.1 (51–271) g, n = 74

Malawi (Sumbera *et al.* 2003a)

Key References Jarvis 1973b; Jarvis & Sale 1971; Sumbera 2001; Sumbera *et al.* 2003a.

J. U. M. Jarvis

GENUS *Heterocephalus*

Naked Mole-rat

Heterocephalus Rüppell, 1842. Mus. Senckenbergianum Abh. 3 (2): 99. Type species: *Heterocephalus glaber* Rüppell, 1842.

Heterocephalus glaber.



Heterocephalus is a monotypic genus distributed only in NE Africa (parts of Kenya, Ethiopia and Somalia). The habitat is semi-desert where the annual rainfall is <400 mm, with long periods without rain, and where many species of plants have underground storage organs.

Heterocephalus is unique among the Bathyergidae (and indeed amongst adult rodents) in having no pelage. The skin is pink-brown and naked, with isolated sensory hairs, the tail is comparatively long, and Digit 3 of forefoot is longer than Digit 4. There are three cheekteeth in each ramus of the skull and mandible. Body weight is highly variable. Other characteristics of the genus are given in the species account.

The single species in the genus, as for other species in the family, is subterranean. Individuals live in colonies that have a very special social system that has been likened to the eusocial system of termites (for reviews, see Sherman *et al.* 1991, Bennett & Faulkes 2000, Jarvis & Sherman 2003). Because of the many unique characteristics of Naked Mole-rats, the genus has been placed in a subfamily of its own, Heterocephalinae, separate from all the other genera of the Bathyergidae (see Woods & Kirkpatrick 2005 and references therein). The single species is *Heterocephalus glaber*.

J. U. M. Jarvis

Heterocephalus glaber NAKED MOLE-RAT

Fr. Hétérocéphale glabre; Ger. Nacktmull

Heterocephalus glaber Rüppell, 1842. Mus. Senckenbergianum Abh. 3(2): 99. Shoa, Ethiopia.

Taxonomy Several species and subspecies have been described primarily based on body size, number of cheekteeth (two or three) and number of ribs (11 or 12 pairs), but *Heterocephalus* is currently considered to be monotypic (Honeycutt *et al.* 1991, Allard & Honeycutt 1992). However, mean genetic divergence between haplotypes from E Ethiopia and S Kenya is 10% for cytochrome *b* gene, a value exceeding interspecific differences in some other genera of mole-rats (Faulkes *et al.* 1997b, 2004). Captive animals from Lerata, N Kenya and Mtito Andei, S Kenya, have a genetic distance of 3% and are able to interbreed. Few samples from Ethiopia and Somalia are currently available for taxonomic study and nothing is known of their biology. Synonyms : *ansorgei*, *dunni*, *phillipsi*, *progreiens*, *scortecchi*, *stygius*. Subspecies: none. Chromosome number: $2n = 60$ (George 1979b).

Description Small mole-rat, the smallest species in the family, naked, without pelage and with a comparatively long tail. Skin loose, heavily creased, brownish-pink, darker dorsally than ventrally in

younger animals. Isolated pale-coloured tactile hairs all over body, especially on face and tail. Head large, cone-shaped, blunt anteriorly. Eyes tiny, eyelids thickened with minute eyelashes. Ears lack pinnae; external auditory meatus slightly raised. Limbs short and slender, tapering rapidly toward feet. Forefeet small and stubby, hindfeet longer and fringed on outer edge with stiff hairs; digits slender. All digits, with small claws, not modified for digging. Tail moderately short (ca. 50% of HB); naked. Adult body size very variable and changeable depending on status of individual within colony and on the abundance of food (Jarvis *et al.* 1991, O'Riain 1996, O'Riain & Jarvis 1998). No sexual dimorphism, except that reproductive ♀♀ have elongated bodies (O'Riain *et al.* 2000). A darkish-pink horizontal line, between the anus and clitoris, denoting the position of the sealed vaginal opening, distinguishes non-breeding ♀♀ from ♂♂. Skull: more rounded than other genera of bathyergids; infraorbital foramen round, very small (ca. 0.5 mm), thick-walled; upper incisors strongly pro-odont, ungrooved and extrabuccal; upper incisors protrude from just below a flattened nasal area; three upper and three lower cheekteeth (the only genus of Bathyergidae with this number) possibly reduced to two in some populations; re-entrant folds on cheekteeth visible only in young animals (Figure 107). Nipples arranged in two parallel rows from the axilla to the inguinal region; mean number of nipples 11.9 (range 9–15, $n = 249$) (Sherman *et al.* 1999).

Geographic Variation Animals from a population in S Kenya, where food was more abundant, were larger (mean 33.9 g, $n = 715$) than those from a population at Lerata in N Kenya (mean 21.3 g, $n = 204$) (Jarvis 1985, Brett 1991a, b).

Similar Species No other species is naked.

Distribution Endemic to Africa. Somalia–Masai Bushland BZ. Recorded from hot dry regions of Djibouti, Somalia, E Ethiopia (excluding the highlands), and N and SE Kenya.

Habitat Semi-deserts characterized by high temperatures, low irregular rainfall (200–450 mm/annum) and plants with underground storage organs. Preferred soil type is hard consolidated lateritic loam, but may occur in many types of soil, ranging from fine sand to pure gypsum (Hill *et al.* 1957, Jarvis 1985). In Ethiopia, known only from arid lowlands at ca. 400–1500 m (Yalden *et al.* 1976).

Abundance Distribution is patchy; colonies are often widely dispersed but burrows of adjacent colonies can approach within a few metres of each other. Mean colony size is ca. 75 animals (range 2–300, $n = >50$). Population size difficult to estimate because mole-rats are subterranean.

Adaptations Subterranean, but may very occasionally venture above ground. Naked Mole-rats run forwards and backwards with equal ease, using their tail and sensory hairs to navigate. Burrow

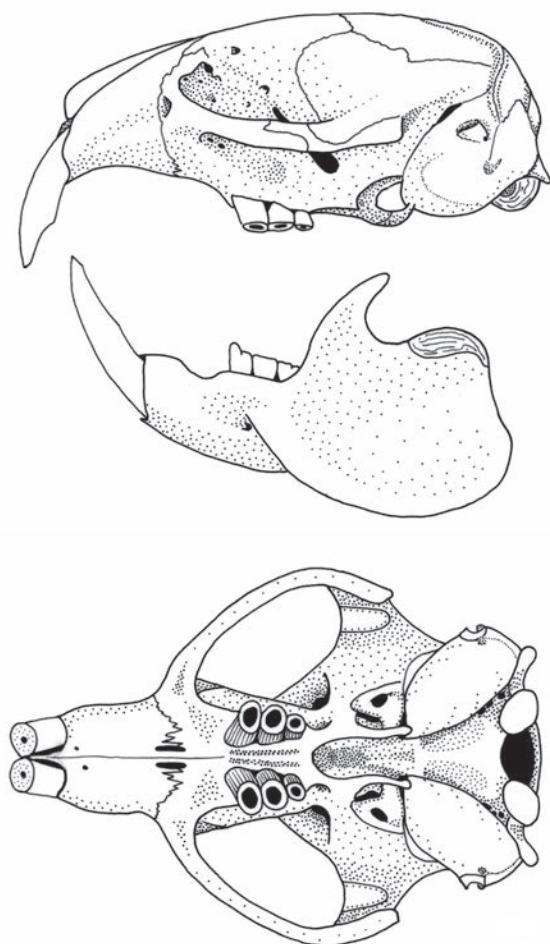


Figure 107. Skull and mandible of *Heterocephalus glaber* (BMNH 7.4.1.12).

*Heterocephalus glaber*

system length depends on colony size and local food abundance. One completely excavated system containing 60 animals was 595 m long (Jarvis 1985), another with 85–90 animals was estimated (from telemetry studies over 12 months) to be 3 km long (Brett 1991b). Burrow systems consist of superficial networks (2–20 cm deep) of narrow (2.5–3 cm) foraging burrows, which are blocked off once the animals have finished foraging in the area. Superficial burrows lead down to wide (4–5 cm), long and relatively un-branched main burrows (>30 cm deep), which are dug to locate large tubers and patches of food; they also lead to nests (with several entrances), blind-ending toilet burrows and deep ‘bolt-holes’ – these may descend steeply to ca. 2 m (Jarvis 1985, Brett 1991b).

Temperatures in the main burrows vary little diurnally and seasonally (ca. 28–32 °C), and the humidity is high (ca. 80%). Naked Mole-rats are poikilothermic over most ambient temperatures, using behavioural means (huddling, basking close to the surface) to maintain body temperature close to ambient temperature (Buffenstein & Yahav 1991b). The well-vascularized hairless skin facilitates rapid heat exchange; and the high humidity in the burrow reduces water loss but prevents evaporative cooling. The basal metabolic rate is exceptionally low (40% of expected; McNab 1966); other energy-demanding features such as eyes and the optic regions in the brain are reduced to conserve energy. Energy-saving features help reduce life-time expenditure of energy, reduce cumulative oxidative damage and may possibly promote longevity of >26 years for captive breeders and non-breeders (O’Connor *et al.* 2002, Sherman & Jarvis 2002). In the wild, longevity is <3 years for non-reproductive animals and >10 years for reproductive animals (S. Braude unpubl.).

Foraging and Food Herbivorous, feeding exclusively on roots and swollen underground storage organs of plants. Food is widely dispersed in patches of small items or single large tubers (up to 50 kg). After rain, Naked Mole-rats dig long prospecting foraging burrows (up to 1 km/month) whose pattern is modified depending on the type

of food encountered. Burrows branch finely when patches of food are encountered, but not when they encounter large tubers, as these occur singly. Large tubers are partly eaten *in situ*, and the cavities are then packed with soil; many tubers are not totally destroyed and will regenerate (Brett 1991a, b). Non-reproductive animals of both sexes cooperate to dig foraging burrows: one animal bites the earth face, others collect excavated soil and form a chain to kick it back along the burrow to a larger animal who kicks it onto the surface through an open hole (Jarvis & Sale 1971, Braude 1991). Active mounds resemble an erupting volcano and are the site where most predation occurs. Most mounds are produced between 02:00 and 08:00h, times when predatory snakes are least active (Brett 1991a, b). In the laboratory, foragers (the non-reproductive animals) returning to the nest leave scent trails back to the food (Judd & Sherman 1996). Small items of food may be carried back to the nest where they are eaten by the young or by other colony members. Naked Mole-rats do not store food and all colony members (including the reproductive animals) will visit the primary source of food to feed.

Social and Reproductive Behaviour Naked Mole-rats are highly social, indeed they resemble eusocial insects in having reproductive division of labour, overlap of generations and cooperative care of young (Jarvis 1981, Sherman *et al.* 1991). Only one ♀ per colony is reproductively active (occasionally two); she is the dominant ♀ and suppresses reproduction in subordinates, not through pheromones but through stress-inducing behavioural interactions (shoving, passing over, etc.). She solicits mating with 1–3 consorts, who may remain her consorts throughout her life, occasionally continuing as reproductive ♂♂ to the succeeding reproductive ♀. When in oestrus, she emits a distinctive call and crouches in front of the ♂ or ♂♂ with tail to one side. Multiple paternity may occur in a litter (Faulkes *et al.* 1997a). There are no castes of workers but smaller non-reproductive animals (both adults and subadults) tend to perform more maintenance and foraging tasks than larger adults and also devote more time caring for the young. Larger adults tend to act as defenders in times of danger. The reproductive ♀ may remain as the only reproductive ♀ for many years (sometimes >20 years in the laboratory and >10 years in the wild). The oldest, largest ♀♀ (irrespective of relatedness) typically fight viciously for reproductive succession when a vacancy occurs (O’Riain 1996, Van der Westhuizen 1997, Jarvis & Sherman 2003). This is usually when the dominant reproductive ♀ dies, but also sometimes if she is sick or in some other way unable to dominate her colony; on such occasions she is usually killed by rivals. The lumbar vertebrae of the new dominant ♀ elongate during her first pregnancies, rendering her morphologically distinct from other ♀♀; this unusual situation is the first mammalian example of a behaviourally and morphologically distinct caste (O’Riain *et al.* 2000). Her enlarged abdomen enables her gut to hypertrophy to cope with the greatly increased energy demands of having large litters. It also enables her to remain mobile in the narrow confines of the burrow and thereby to maintain dominance over her colony. Males and ♀♀ remain fertile for >23 years (Buffenstein & Jarvis 2002, O’Connor *et al.* 2002, Sherman & Jarvis 2002). Colonies are strongly xenophobic, recognizing colony members by a cocktail of odours acquired from huddling in the communal nest and grooming in the communal toilet (O’Riain & Jarvis 1997). Because reproductive succession often occurs within the colony, many colonies are highly

inbred (Faulkes *et al.* 1997a). Occasionally fat, highly sexed, dispersers appear who, in laboratory experiments, will actively solicit foreign animals but not members of their own colony (O'Riain *et al.* 1996). These individuals may disperse to found new colonies, and perhaps even enter other colonies, but it is not known if dispersal is above or below ground. Small incipient and out-bred colonies are occasionally found in the wild; such colonies rarely last more than a year, indicating the high risks taken in attempting to 'go it alone' (O'Riain & Braude 2001, Jarvis & Sherman 2003).

The vocal repertoire of Naked Mole-rats is unusually large for a rodent (>18 vocalizations). Most vocalizations are in the 1–9 kHz frequency range and include high-pitched contact and aggressive chirps, a prolonged alarm scream, and aggressive grunting towards outside sources of danger. Larger individuals are mobilized, through the alarm calls, to defend the colony. Some vocalizations are restricted to specific animals in the colony, e.g. juveniles, reproductive animals (Pepper *et al.* 1991). Although most activities in the colony are accompanied by frequent vocalizations, the primary modes of communication, odour and touch, are also used (Sherman *et al.* 1991, O'Riain & Jarvis 1997).

Reproduction and Population Structure The one (occasionally two) reproductive ♀♀ in a colony breed throughout the year and have 3–4 litters/year. Gestation: 70–74 days. Litter-size 11.4 (1–28), *n* = 190. Postpartum oestrus Day 10. At birth, young weigh 1–2 g. First solids eaten by Day 14. Fully weaned at ca. 5 weeks (Jarvis 1991, O'Riain 1996). Young do not disperse but join the non-reproductive workforce. Only the reproductive ♀ lactates but, in many captive colonies, the entire colony (♂♂ and ♀♀) develop nipples prior to the birth of the young. This hormonal response to the pregnancy of the dominant ♀ by the colony may prime the animals to accept, and help care for, her young. The energetic costs of breeding are high; during pregnancy energy demands of the breeding ♀ increase by ca. 1300 kJ per gestation cycle, and lactation requires an additional 1515 kJ per day for an average-sized litter (Urison & Buffenstein 1995). Lactation lasts about five weeks. On weaning, the juveniles solicit caecotrophs from adults (special nutritious faeces routinely eaten by mole-rats as they are voided), and also eat food brought to the nest. The reproductive ♀ is the only adult that can solicit caecotrophs from other adults; they form an important dietary supplement to enhance her reproductive success.

Of all the ♀♀ in the colony, the dominant (reproductive) ♀ is identified by her elongated body, prominent nipples and perforate vagina. Reproductive ♂♂, often small emaciated-looking animals, are strongly bonded to the ♀ through repeated mutual anonasal interactions. In colonies with >1 reproductive ♂, there is no apparent competition for mating rights (Jarvis 1991). In the wild, the

reproductive ♀ and reproductive ♂♂ are usually the oldest members of the colony, and are distinctive in being less counter-shaded than non-reproductive animals (S. Braude unpubl.). Non-reproductive ♀♀ are prepubescent, have a vaginal closure membrane, small inactive ovaries and low levels of reproductive hormones (Faulkes & Abbott 1997); they can begin to have oestrus cycles within a week of removal from the colony. Non-reproductive ♂♂ have lower sperm counts, lower levels of reproductive hormones, and the sperm have low motility (Faulkes *et al.* 1994, Faulkes & Abbott 1997). Testes of reproductive and non-reproductive ♂♂ are abdominal. Over 95% of non-reproductive animals never have opportunity to breed (Sherman *et al.* 1992, Jarvis & Sherman 2003).

Predators, Parasites and Diseases Naked Mole-rats are preyed on by snakes (especially the Rufous-beaked Snake *Rhamphiophis oxyrhynchus* and Sand Boa *Eryx columbrinus*) and various raptors. They are especially vulnerable when they build mounds and eject soil onto the surface. Probably because of their nakedness, Naked Mole-rats have few ectoparasites; the most numerous are subcutaneous mites and chiggers (Parona 1895). Endoparasitic nematodes and cestodes are very rare (<1% of >300 animals autopsied from Mtito Andei; J. U. M. Jarvis unpubl.).

Conservation IUCN Category: Least Concern.

Local populations often highly inbred, and therefore potentially at risk from extinction by disease. There is little conflict with farmers because much of their habitat is not suitable for agriculture.

Measurements

Heterocephalus glaber

HB: 83.4 (66–110) mm, *n* = 131

T: 42.1 (34–50) mm, *n* = 123

HF: 20.1 (18–22) mm, *n* = 127

WT: 33.9 (25–80) g, *n* = 715

GLS: 21.4 (16.5–24.4) mm, *n* = 119

GWS: 16.8 (12.6–20.1) mm, *n* = 105

M¹–M³: 3.4 (3.1–3.9) mm, *n* = 100

Mtito-Andei, S. Kenya (J. U. M. Jarvis unpubl.)

Weight: Mtito-Andei, S. Kenya (Brett 1991)

In areas where food is limiting, body size is considerably smaller (see Jarvis, 1985)

Key References Bennett & Faulkes 2000; Hill *et al.* 1957; Jarvis & Sherman 2003; Sherman *et al.* 1991, 1992.

J. U. M. Jarvis

Family HYSTRICIDAE

PORCUPINES

Hystricidae G. Fischer, 1817. Mem. Soc. Imp. Nat., Moscow 5: 372.

| | | |
|------------------------------|------------------------|--------|
| <i>Atherurus</i> (1 species) | Brush-tailed Porcupine | p. 672 |
| <i>Hystrix</i> (2 species) | Crested Porcupines | p. 674 |

The Hystricidae contains three genera and 11 species distributed in Africa, the Middle East, the Indian sub-continent and South Asia, and on various islands in Indonesia and the Philippines (Woods 1984, Woods & Kirkpatrick 2005). The family, as a whole, is represented in many habitats including rainforest, savanna and semi-desert, although each species is rather restricted in its requirements. Two genera and three species occur in Africa.

Porcupines are best known for their large size and weight, and the possession of very coarse hair and spines on the back in some species. The spines (or quills) vary in size, shape, length and pattern according to the species and position on the body; however, all are pointed at the tip and provide a very effective defence against potential predators. The limbs are short, the fore- and hindfeet are plantigrade and each foot has five digits with claws. Locomotion is either a rather clumsy walk or a trot. The tail is short, and covered by quills, some of which may be modified into 'rattle quills'. Most species are brown or black in colour, although white bands on the spines of some species result in a generally paler colouration. Size categories of species in the family (based on mean head and body length) are given in the order Rodentia profile.

The skull is massive and high domed with an inflated nasal region in some species (*Hystrix* spp.), and with large pro-odont smooth-faced incisors, a large infraorbital foramen and relatively small zygomatic arches. Dental formula is $I^{1/1}, C^{0/0}, P^{1/1}, M^{3/3} = 20$. Upper incisor teeth without grooves. The premolar is retained for most of the individual's life, but is replaced late in life. The four cheekteeth have a unique wavy and complex pattern of enamel and dentine. On the upper molars, there are three labial (outer) folds and one lingual (inner) fold of the enamel. These folds usually become isolated early in life (due to wear) and then form 'islands' so that there are alternating lines and rings of enamel and dentine (Figure 108).

Porcupines are vegetarians, feeding on a wide variety of grasses, fruits, bark, bulbs and roots. They are nocturnal and travel at night along well-defined paths, often covering long distances in search of food. During the day they rest in burrows, which they may dig themselves, caves, or cavities under forest trees (such resting places are sometimes referred to as 'dens'). They are primarily terrestrial and unable to climb (except for one species in Asia).

Porcupines are solitary or gregarious, according to the species. In the social species, groups of several individuals of mixed sexes rest together in a single burrow. In *Hystrix*, parental care is well developed: ♂♂ look after young in the nest and accompany them when they begin

to forage above ground. Development of porcupines is slow (by comparison with other rodents), mainly because of their large size: gestation is 90–120 days, suckling continues for about two months, weaning occurs at about four months and adult size and reproductive maturity are not attained until about one year (or longer in the largest species). Porcupines are long-lived; in captivity, African species have survived for at least 20 years.

The family comprises genera and species that are very different from other rodents and the taxonomy of the family is not controversial. Hystricidae are placed in the suborder Hystricognathi (synonym: Hystricomorpha), together with the Bathyergidae, Petromuridae and Thryonomidae. Fossil porcupines in Africa date back to the Pleistocene, but older fossils are known from India and Eurasia (Woods 1984). Porcupines have radiated into two major groupings, which are sometimes considered as subfamilies (e.g. by Rosevear 1969): Atherurinae (*Atherurus*, *Triorchys*) consists of the smaller forest-living Brush-tailed Porcupines with poorly developed quills, and Hystricinae (*Hystrix*) consists of the larger savanna-living Crested Porcupines with well-developed quills. Following Woods (1993) and Woods & Kirkpatrick (2005), subfamilies are not listed here, even though there are considerable differences in the morphology and biology of each subfamily.

The two genera (*Atherurus*, *Hystrix*) in Africa are distinguished by size, tail length, character and size of the quills on the tail, and by the length of the nasal bones.

D. C. D. Happold

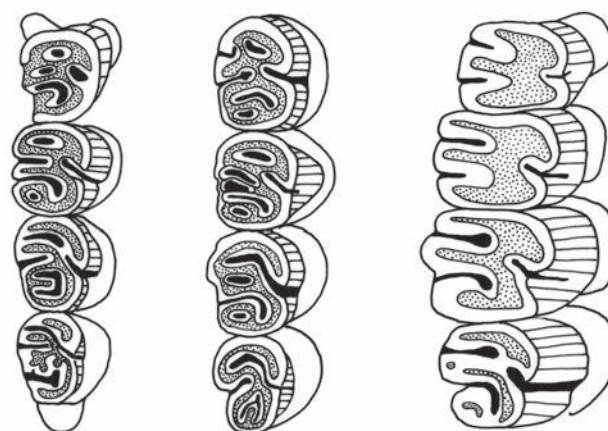


Figure 108. Cheekteeth of *Atherurus africanus* (left), *Hystrix cristata* (centre), *Thryonomys swinderianus* (right). White = enamel, stipple = dentine, black = infolding from outer surface, or space within enamel 'island'.

Genus *Atherurus*

Brush-tailed Porcupines

Atherurus F. Cuvier, 1829. Dict. Sci. Nat. 59: 483. Type species: *Hystrix macroura* Linnaeus, 1758.

The genus contains one African species and one Asian species. The genus is characterized by comparatively small size (cf. *Hystrix*), relatively long tail with a brush of 'rattle-quills' at the terminal end, and comparatively short dark quills on back which do not form a crest. The skull has small nasal bones which are shorter than the

frontal bones and end anteriorly to the anterior end of the zygomatic arches (cf. *Hystrix*). The genus is represented only in rainforest habitats. The single African species is *Atherurus africanus*.

D. C. D. Happold



Atherurus africanus.

Atherurus africanus AFRICAN BRUSH-TAILED PORCUPINE

Fr. Athérure d'Afrique; Ger. Afrikanischer Quastenstachler

Atherurus africanus Gray, 1842. Ann. Mag. Nat. Hist, ser.1, 10: 261. Sierra Leone (exact locality not specified).

Taxonomy Synonyms: *africanus* and *armatus* (West Africa), *centralis* (DR Congo) and *turneri* (East Africa). Subspecies: none. Chromosome number: not known.

Description Extremely large dark rodent, with comparatively short spines (quills) on back and flanks, and long tail ending in 'rattle quills'. Dorsal pelage dark brown; hairs rather sparse, modified into coarse thick spines, off-white at base, darkening towards the middle, blackish-brown (without alternating black and white bands as in *Hystrix* spp.) and sharply pointed at tip. Length of spines variable: 20 mm on neck, 35 mm on mid-back, up to 90 mm on rump and 25–45 mm on flanks. Fine hairs grow between the spines. Ventral pelage off-white to pale brown; 'hairs' softer and less spiny than dorsal hairs; length ca. 10–15 mm. Head sparsely covered with short dark coarse hairs; very long black vibrissae. Ears darkly pigmented, mostly naked. Fore- and hindfeet short and thick-set, covered with coarse dark brown hairs; five digits on each foot, all with small claws (except for short Digit 1 of forefoot). Tail short (ca. 40% of HB), thick and swollen at base with short black spines; tapers towards tip; terminal end with off-white or yellow 'rattle-quills', each with 4–5 hollow cavities along its length. When tail is shaken, the hollow cavities of the rattle-quills produce a rustling sound. Skull rather elongated (cf. *Hystrix* spp.) with 'normal' non-inflated nasal bones that end anteriorly to zygomatic arch; incisor teeth smooth and without grooves on outer surface (Figure 109, see also Figure 108). Nipples: 2 + 0 = 4.

Geographic Variation None recorded.

Similar Species

Hystrix cristata. Much larger, and with longer spines (up to 30 cm); nasal region of skull more inflated; rattle-spines of tail with only one large elongated hollow.

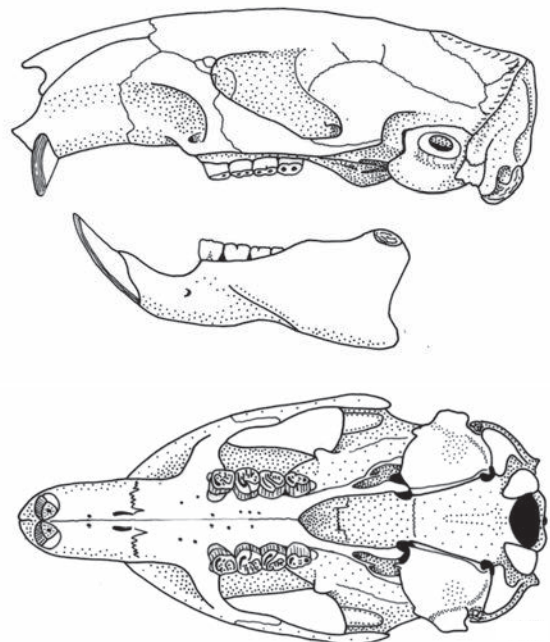


Figure 109. Skull and mandible of *Atherurus africanus* (RMCA 15288).



Atherurus africanus

Thryonomys swinderianus. Pelage coarse (without spines); tail without spines; each upper incisor tooth with three longitudinal grooves.

Distribution Endemic to Africa. Rainforest BZ and Rainforest–Savanna Mosaic from Gambia and throughout West Africa to E DR Congo; small populations in Uganda, Kenya and S Sudan. Bioko I. (Eisenbraut 1973).

Habitat Evergreen rainforests and gallery forests where there are hollow trees, buttress roots and soft soil, especially close to streams in little valleys. May occur in farmlands adjacent to forest within Rainforest BZ. Occurs over a range of altitudes from near sea level to 1400 m in E DR Congo (on volcanoes and Rwenzori Mts) and 1500 m on Mt Cameroon.

Abundance May be very abundant in some localities. Estimates vary according to locality (and method of calculation), e.g. 2.4–13.2/km² in Bayanga, Central African Republic (Noss 1998); 55/km² in Equatorial Guinea (Fa *et al.* 1995); 174 kg/km² = ca. 58/km² in Gabon (Feer 1993 in Jori *et al.* 1998).

Adaptations Nocturnal, terrestrial. Brush-tailed Porcupines do not dig burrows, but hide during the day in a den in hollow trees and hollow logs, or under roots of large trees. At Makokou, Gabon, they leave their hiding places at ca. 17:00h and return at about 05:30h (Emmons 1983). The activity pattern is usually trimodal, with two rest periods during the night, although bimodal on moonlit nights. Rest periods of 10–50 min are taken during each hour – these tend to be longer in the middle of the night than at the beginning or end, and when there is bright moonlight. On dark nights, ♀♀ do not normally take a rest period in the middle of the night (23:00–01:00h), although ♂♂ rest for some of the time. On nights close to full moonlight, the average time of inactivity/night was 3.5 hours, whereas on nights close to no moonlight, the average time of inactivity/night was 1.89 hours.

Brush-tailed Porcupines walk and trot on the forest floor, but they can also scramble and climb to a limited extent. While moving, the tail is held slightly upwards and backwards from the body, and sometimes at night the rustling of the ‘rattle quills’ can be heard even though the animal appears invisible. When alarmed or threatened, the spines on the back are raised and the rattle-quills are shaken; if attacked, the animal moves sideways and backwards with the pointed quills facing towards the opponent.

Brush-tailed Porcupines usually defecate regularly at the same place, either under a rock or in the den (Rahm & Christiaensen 1963).

Foraging and Food Vegetarian; feeds primarily on the leaves, flowers and fruits of forest trees (most of which have fallen from the higher storeys of the forest) and on some roots (Rahm 1962b). Where farms are adjacent to forest, maize, manioc (cassava), bananas and palm nuts are favourite foods. Occasionally, porcupines feed on carrion and earthworms (Rosevear 1969).

Social and Reproductive Behaviour At night, Brush-tailed Porcupines usually travel alone, although they may meet at feeding places. During the day, when resting in dens, they may be gregarious. In 22 dens investigated in Gabon, there were one (n = 12), two (n = 7) three (n = 1) or four (n = 1) animals in each den; associations were either ♂♂ and ♀♀, all ♂♂, or all ♀♀ (Emmons 1983). When living together (in captivity), porcupines show mutual grooming and auditory displays of dominance and submission. In some instances, they may form family groups (♂ and ♀ and young) (Rahm 1962b). The social organization of porcupines seems to be rather fluid, without the formation of monogamous pairs or cohesive groups.

Home-ranges (measured by radio-telemetry in Gabon) of adults varied from ca. 11 ha to 22 ha, ♂♂ on average having larger home-ranges than ♀♀. During the night, individuals travel rapidly along a well-defined network of pathways, averaging about 100 m in ca. 4 mins. Pathways connect dens with resting sites and foraging areas. Average nightly distances travelled are impressively large: ♂♂ covered 1697 m (on moonlit nights) and 2333 m (on dark nights), and ♀♀ covered 1646 m (on moonlit nights) and 1953 m (on dark nights) (Emmons 1983). Home-ranges of ♂♂ and ♀♀ tend to overlap. Most ♂♂ travel through most of the home-range every night (Emmons 1983), but do not display territorial behaviour.

Reproduction and Population Structure In E DR Congo, young animals have been found in most months of the year (Rahm 1962a), and it is likely that this pattern of reproduction occurs at other localities within the Rainforest BZ (see e.g. Jeffrey 1975). Gestation: 100–120 days (Rahm 1962a). Litter-size: 1–2 (Rahm 1962a, Weir 1974); 1–4 (Kingdon 1974). Females probably polyovular, so litter-size of only one young/litter in captivity may be related to captive conditions. Weight at birth: 150 g. The young are precocious at birth: the eyes are open, there are very soft spine-like hairs on the back and flanks, and walking on all four legs is possible. Sucking continues for ca. 2 months; solid food is first eaten at 2–3 weeks. Growth rate is comparatively slow: adult size is attained in ca. 300 days; but adult weight and sexual maturity are not reached until about two years (Rahm 1962a, Rosevear 1969). Females probably have 2–3 litters/year. Breeds well in captivity. Longevity: up to 22 years (Fa *et al.* 1995).

Predators, Parasites and Diseases The main predators are humans and Leopards *Panthera pardus*. Brush-tailed Porcupines are vigorously hunted by humans because of their succulent flesh and because (to a lesser extent) they may cause damage to crops. Carcasses are seen for sale as 'bushmeat' in many parts of the Rainforest BZ (see also *Thryonomys swinderianus*). In countries where surveys have been conducted (e.g. Nigeria [Martin 1983, Anadu *et al.* 1988], DR Congo [Colyn *et al.* 1987], Equatorial Guinea [Colell *et al.* 1994, Fa *et al.* 1995] and NE Gabon [Lahm 1993, quoted by Fa *et al.* 1995]), porcupines formed 6–19% of carcasses for sale in local markets on an annual basis. They are usually the third or fourth most numerous 'species' after antelopes (*Cephalophus* spp.), Cane Rats (*Thryonomys swinderianus*) and giant rats (*Cricetomys* spp.). In S Cameroon, they comprised 61% of carcasses (Muchaal & Ndjangui 1995, quoted by Jori *et al.* 1998). Studies to assess the impact of hunting on populations suggest that, in most places at the present time, Brush-tailed Porcupines are not overhunted, although their supposed rate of recruitment (based on rather slow reproduction) seems contrary to this assessment. One study (Feer 1993), where biomass was estimated at 174 kg/km² (= 58 individuals/km²), suggested that maximum sustained annual yield could be 44 kg/km²/year (= 14 individuals/km²/year).

Brush-tailed Porcupines are host to a malarial parasite, *Plasmodium atheruri* (Van den Berghe *et al.* 1958).

Conservation IUCN Category: Least Concern.

Brush-tailed Porcupines appear to be able to retain their population numbers except where hunting pressure is very high. However, loss of forest habitat as well as hunting are cause for concern in some parts of their range.

Measurements

Atherurus africanus

HB: 534 (508–560) mm

T: 204 (177–230) mm

HF: 72 (71–73) mm

E: 39 (38–39) mm

WT: (2500–3400) g

GLS: 98.0 (87.5–104.3) mm

GWS: 49.2 (45.7–52.2) mm

M¹–M³: 18.5 (16.7–20.3) mm

West Africa (Rosevear 1969)

Weight: Rahm 1962a

Sample sizes not stated

Key References Emmons 1983; Rahm 1956, 1962a, b; Rosevear 1969.

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Genus *Hystrix* Crested Porcupines

Hystrix Linnaeus, 1758. Syst. Nat., 10th edn, 1: 56. Type species: *Hystrix cristata* Linnaeus, 1758.

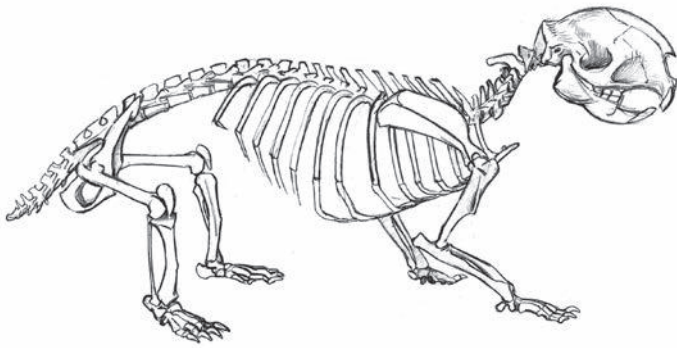
The genus contains eight species (with many synonyms) widely distributed in Africa, the Middle East, India, South-East Asia and islands of the Indonesian archipelago (Woods & Kirkpatrick 2005). The genus may be divided into three subgenera: *Thecurus*, *Acanthion* and *Hystrix*, the latter subgenus containing both African species and being characterized

by having long quills along the length of the back, which can be erected to form a 'crest'. Representatives of the genus occur in savannas, woodlands, rocky areas, forests and plantations, but not in rainforests.

The genus is characterized by extremely large size (HB up to ca. 800 mm, WT up to ca. 20 kg, and the largest of African



Hystrix cristata.



Skeleton of *Hystrix cristata*.

rodents), coarse black bristles on head, limbs and ventral surface, long spines (quills) with alternating black and white bands on the back and flanks, short tail covered with black-and white banded 'rattle quills', and large thickset head. The hairs on the head and the quills on the back can be erected to form a backwardly facing crest when the animal is stressed or in danger. Quills are periodically lost (moulted) and replaced. Tail very short, with spines but without 'brush' of 'rattle-quills' (cf. *Atherurus*). The skull is large and thickset, rather narrow with a high domed forehead; nasal bones very large (extending over much of the top of the skull and exceeding in length the frontal and parietal bones combined) and ending posteriorly in line with the anterior or posterior end of the orbit (cf. *Atherurus*); zygomatic arch short; upper incisor teeth large, pro-odont and without grooves; and with four cheekteeth on each ramus (Rosevear 1969) (Figure 110). The common name, Crested Porcupines, refers to the erectile crest on the back (cf. *Atherurus*).

Crested porcupines are nocturnal and terrestrial, and live in holes or caves during the day. They live singly or in small family groups. They are vegetarian, eating a wide range of roots, tubers, bark and fallen fruits. On occasion they may gnaw bones, presumably to obtain additional calcium.

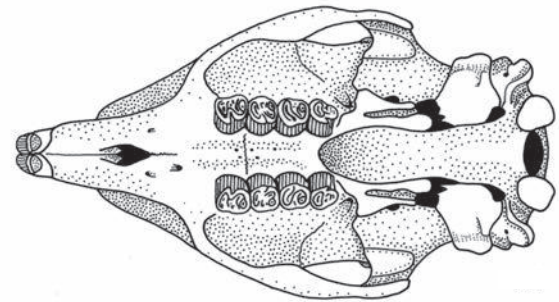
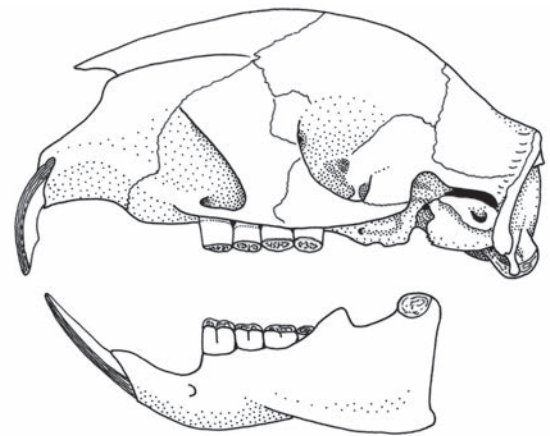


Figure 110. Skull and mandible of *Hystrix africaeaustralis* (RMCA 6191).

Within Africa, Ellerman (1940) recognized four species, although Corbet & Jones (1965) reduced the number to two, placing *stegmanni* as a synonym of *H. africaeaustralis* and *galeata* as a synonym of *H. cristata*. The two species are distinguished by length of the nasal bone, the ratio of the frontal bone to the nasal bone (frontal : nasal ratio), the characteristics of the rattle-quills, and colour of the rump (Table 46).

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Table 46. Characters of *H. cristata* and *H. africaeaustralis* (mostly after Corbet & Jones 1965).

| Character | <i>H. cristata</i> | <i>H. africaeaustralis</i> |
|---|-----------------------------------|---|
| Length of rattle-quills | 5 cm or less | 6 cm or more |
| Diameter of rattle-quills | 2–5 mm | 5–7 mm |
| Colour of nuchal crest | Mostly dark | Mostly white |
| Colour of rump | Black | White |
| Relative length (%) of frontal bone to nasal bone | 23–38%, i.e. nasal bone very long | 49–68%, i.e. nasal bone not especially long |
| Relative length (%) of nasal bone to occipital–nasal length | 58–68% | 51–58% |

***Hystrix africaeaustralis* CAPE CRESTED PORCUPINE (CAPE PORCUPINE)**

Fr. Porc-épique de l'Afrique du Sud; Ger. Südafrikanisches Stachelschwein

Hystrix africaeaustralis Peters, 1852. Reise nach Mossambique, Säugethiere, p. 170. Near Tette, Querimba coast, Mozambique (exact locality uncertain, but ca. 10° 30' to 12° 00' S, 40° 30' E, at sea level).

Taxonomy Synonyms: *capensis*, *prittwitzi*, *stegmanni*, *zuluensis*. Subspecies: none. Chromosome number: $2n = 66$, $NF = 114$ (George & Weir 1974).

Description Extremely large rodent, the largest in Africa (together with *H. cristata*), with extremely long stiff hairs and spines (quills). Very similar in external appearance to *H. cristata*. Dorsal pelage with long stiff black or white hairs anteriorly, and with long smooth quills on mid-back and rump. Quills with alternating wide black and narrow white bands (usually four or five of each), ending in long white pointed tip; length varies, maximum 30 cm on rump. Nuchal crest (on neck and shoulders) formed of long wiry hairs, up to 45 cm, mostly white with black base. Crest and quills erectile when animal is frightened or threatened. Head, neck and limbs with coarse dark bristles (up to 50 mm). Mid-line of rump white. Head rather broad with short muzzle, swollen nasal region and long dark vibrissae. Eyes small and dark. Ears short, darkly pigmented. Limbs with short black hairs, relatively short and broad; five digits on each foot (Digit 1 of forefoot greatly reduced), each with claws. Tail very short, covered with short weak quills, usually invisible beneath quills of rump; some tail quills modified to form 'rattle-quills' or 'wine-glass quills' (ca. 6 cm long, 5–7 mm diameter), which rattle when tail is shaken. Skull large and rounded. Upper incisor teeth smooth; cheekteeth with complex folds of enamel and dentine; nasal bones long, 51–58% of occipito-nasal length, wide, extending posteriorly almost to level of anterior end of orbit; frontal-nasal ratio 49–68%. Nipples: 2 or 3 + 0 = 4 or 6.

Geographic Variation None recorded.

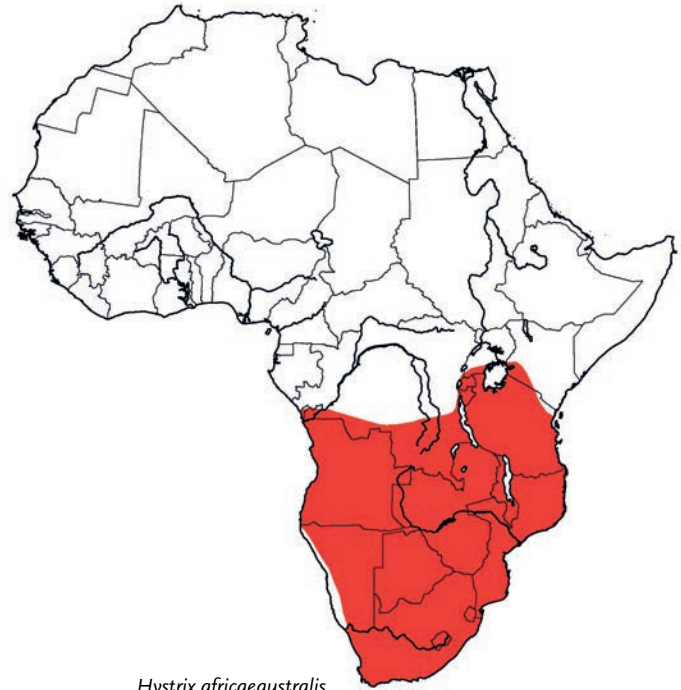
Similar Species

H. cristata. Nasal bones >57% of occipital-nasal length; frontal-nasal ratio 23–38%; mid-line of rump black or mottled; western and central Africa; sympatric with *H. africaeaustralis* in parts of S Uganda, S Kenya and Tanzania.

Distribution Endemic to Africa. Widespread throughout southern Africa in four biotic zones (Zambezian Woodland, South-West Arid, Highveld and Coastal Forest Mosaic BZs). Recorded from South Africa northwards to Angola, S DR Congo, Tanzania, S Kenya and S Uganda. Parapatric with *H. cristata* in East Africa. Probably not present on Zanzibar I. (*contra* Kingdon 1974; see *H. cristata*).

Habitat Savanna, semi-deserts and forested areas, but not in swamps, moist forests and barren deserts. Common in rocky hill country; shows preference for *Burkea* savanna (see below). Also occurs in farmlands and forest plantations.

Abundance Relatively common in suitable habitats, although rarely seen because of nocturnal habits. Many records are based on the presence of discarded quills.



Hystrix africaeaustralis

Adaptations Nocturnal and terrestrial. Rests during daytime in caves, natural crevices and burrows. Cape Crested Porcupines are good diggers and may excavate their own burrows or may take over burrows made by other animals (e.g. Aardvarks). Burrows may be complex with several chambers. The gait is either a shuffling plantigrade walk or (if frightened or in danger) a clumsy gallop.

In South Africa, Cape Crested Porcupines may have a significant effect on their environment due to their habit of chewing the bark and roots of many species of trees, and digging for food. They are especially fond of the bark of *Burkea africana* and *Dombeya rotundifolia* and preferentially chew on these species (De Villiers & Van Aarde 1994); by removing the bark, trees are more susceptible to fire and may be killed during subsequent savanna fires. Chewing bark also results in coppicing and a reduction in the number of trees reaching maturity (Yeaton 1988). The combination of fire and Cape Crested Porcupines has a strong effect on the species composition and structure of *Burkea* savanna, and helps to maintain the mosaic of grasslands and woodland patches. Cape Crested Porcupines rarely feed on the bark of *Acacia* trees and do not prevent the development of mature *Acacia* woodlands. As a result, *Acacia* woodland has the potential to spread into regions where *Burkea* woodlands have been partly destroyed. Digging for food disturbs the soil and increases the chances of seed germination; seedling density and diversity may be higher where porcupines (as well as Aardvarks *Oryzomys afer* and Bat-eared Foxes *Otocyon megalotis*) have been digging than on flat hard soil surfaces (Dean & Milton 1991).

Cape Crested Porcupines have a lower metabolic rate than expected for their size, and can maintain a constant body temperature (T_b) when

ambient temperature (T_a) ranges between 13 °C and 30 °C. When T_a is low, T_b is maintained at about 37 °C mostly by increasing metabolic rate and decreasing heat loss. When T_a is 30 °C, there is an increase in ventilation rate and loss of water through the lungs, which prevents body temperature from rising to a dangerously high level. If T_a is 37 °C—a condition not normally experienced by free-living porcupines because they are nocturnal—hyperthermia occurs. Low metabolic levels, efficient heat loss when ambient temperature is high and ability to regulate body temperature over a wide range of conditions, enable these porcupines to live in a wide variety of habitats (Haim *et al.* 1990a, b).

Foraging and Food Omnivorous. Feeds primarily on roots, bark, bulbs, tubers, berries and other fruits, and shoots of herbs (De Graaff 1981, De Villiers *et al.* 1994). Cape Crested Porcupines forage above ground, digging for roots and bulbs. They may cause damage to crops and forestry plantations. In captivity, they eat more during winter (10 °C and short days) than during summer; an increase in food consumption (and hence energy production), together with a decrease in heat loss, appear to be mechanisms that allow porcupines to be active during cold weather (Haim *et al.* 1990b). Food consumption is correspondingly reduced during summer conditions.

Social and Reproductive Behaviour Live in monogamous pairs, usually with their young. Family groups live together in burrows, although group may split up while foraging at night. Size and the duration of family group seem to depend on opportunities for young to disperse when they become mature. Family groups may, on occasion, be large—up to 14 individuals have been found in a single burrow—and composed of two (or more?) pairs with young (Van Aarde 1987a). Within a family group, only the monogamous pair reproduces. Offspring disperse when mature provided there are areas where territories may be established and where food is not limiting. If dispersal opportunities are limited, offspring may stay with parents, forming large family groups, but reproductive suppression prevents offspring from being reproductively active (Corbet & Van Aarde 1996).

Home-ranges are large. In *Burkea* savanna in South Africa (Corbet & Van Aarde 1996), mean home-range area in summer was 215 ha, although only about 80 ha of the range (the 'core area') was used extensively. Home-ranges of different individuals overlapped, especially during winter, although the core area was used exclusively by a single individual. Hence individuals are probably territorial with a small territory, advertised by scent marking, within a larger home-range. Winter home-ranges and territories are smaller than those in summer (e.g. 142 ha and 55 ha, respectively). Each territory has 1–3 burrow systems (Van Aarde 1987b). Porcupines that live and feed in crop areas have larger ranges than those living in natural savanna, and without any seasonal differences in area.

Porcupines communicate with each other with various piping calls and pig-like grunts. Members of a monogamous pair indulge in daily bonding behaviour (grooming, etc.), and ♀ conceives only after living with her partner for at least 90–100 days. Parental care of young is well developed. In the burrow, mother suckles young while in a crouching position. Male lives in the burrow with ♀ and young and, later, escorts them on foraging excursions and protects them from predators (Van Aarde 1997). Family group remains intact until young disperse at adulthood.

Reproduction and Population Structure Breeding season varies according to locality. In South Africa (30° S), in the wild, births occur mostly in spring and summer, from Aug to Mar with a peak in Jan (Van Aarde 1987a). Most ♀ ♀ more than 24 months of age are reproductively active (88–95%) during the breeding season. Younger ♀ ♀ (12–24 months) are less reproductively active (63–88%), and ♀ ♀ aged less than 12 months rarely breed. In the drier regions of the Karoo in South Africa, births coincide with peaks in rainfall (Skinner *et al.* 1984). Times of reproductive activity in northern parts of geographic range are uncertain, although there is some evidence that births may occur in all months of the year.

Mean oestrus cycle: ca. 35 days (Weir 1974). In South Africa, captive ♀ ♀ are polyoestrous, with most ♀ ♀ cycling every 28–36 days (Van Aarde 1985). Gestation: 93–94 days. In captivity (in South Africa), litter-size 1.5 (1–3); of 165 litters, 58% had a single young, 32% had twins and 9% had triplets (Van Aarde 1985). Weight at birth 300–440 g. Each young (whether singletons or twins) weighs ca. 2% of maternal weight; overall litter weight (young, placenta, etc.) weighs ca. 10% of maternal weight (Weir 1974). Mammary glands are situated on the side of the thorax. Twins usually suck from opposite nipples. The average length of lactation is 101 days, but may continue for 163 days. Mean litter interval of captive ♀ ♀ is 385 (269–500) days; thus mothers give birth to only one litter/year (Van Aarde 1985).

Young are precocious (although relatively small) at birth, with eyes open and with soft spines and soft quills on the back. They remain in the burrow for 7–9 weeks, a much longer period of time compared with other rodents, emerging for the first time when the quills have hardened. This behaviour (as well as huddling with siblings and parents) probably conserves energy, which can be channelled into growth rather than being used for activity above ground, and provides protection before the quills are fully developed. Growth in body weight is linear until a weight of 11–12 kg is attained at about 52 weeks; thereafter, there is a slow increase in weight to the full adult size of 12–18 kg (Van Aarde 1987a). Sexual maturity occurs when 12–24 months of age. The approximate age of an individual can be determined by tooth wear until adult weight is attained; thereafter age cannot be determined.

Little is known about age structure of populations. In N South Africa, age structure varied markedly during a 2-year study (Van Aarde 1987b). When categorized into four age categories (<6 months, 6–12 months, 12–24 months and >24 months), the proportions of each age category during one of the years were 20–40%, 10–25%, <10–25% and 30–50%, respectively ($n = 118$). Because young are born in many months of the year, there is no period when young of the year form a really large proportion of the population (cf. small rodents). In the second year, the presence of young was more seasonal, perhaps because fewer adults were breeding. The probability of survival of young to 18 months of age was 0.46 in the first year and 0.33 in the second year (Van Aarde 1987b). Changes in the age at first reproduction are probably responsible for changes in population growth rates and population structure. There is no information on porcupine populations in the northern part of their geographic range.

Predators, Parasites and Diseases Predators include large cats and hyaenas, although the quills and behavioural characteristics

(see above) provide considerable protection from predators. Some humans hunt Cape Crested Porcupines for food, and the quills are used for ornaments. Many species of mites, fleas and ticks have been recorded (details in De Graaff 1981).

Conservation IUCN Category: Least Concern.

Not listed in any category of threat in South Africa (Smithers 1986b). As for *H. cristata*, the species is generally uncommon and populations are scattered, although some areas maintain good population numbers (see above).

Measurements

Hystrix africaeaustralis

HB: 655 (649–674) mm, n = 3

T: 105, 130 mm, n = 2

HF: 99 (89–102) mm, n = 4

E: 40 (39–41) mm, n = 4

WT: up to 18 kg (♂ ♂), up to 22.6 kg (♀ ♀)

GLS: 160, 161 mm n = 2

GWS: 86.3, 89.6 mm, n = 2

P⁴–M³: 38.6, 39.0 mm, n = 2

Southern Africa and Kenya

Body measurements: South Africa (De Graaff 1981)

Skull measurements: NMK

Key References Corbet & Van Aarde 1996; De Graaff 1981; De Villiers *et al.* 1994.

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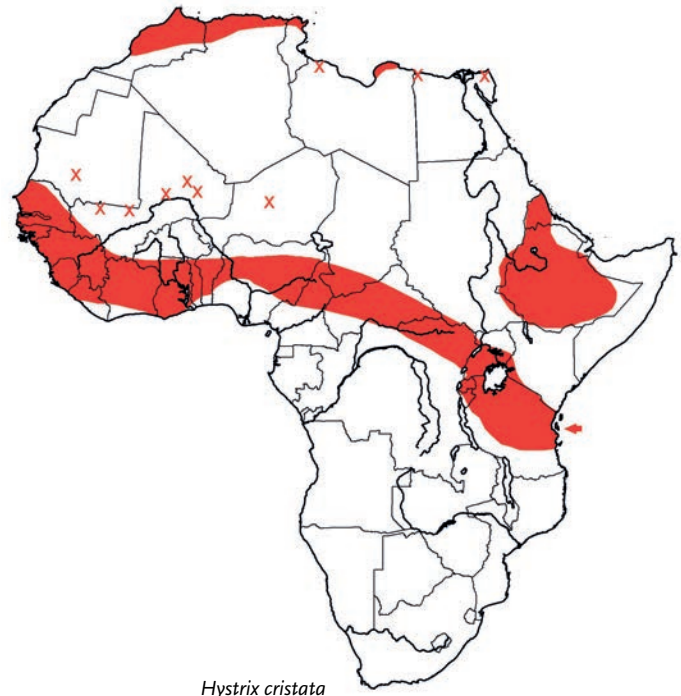
Hystrix cristata NORTH AFRICAN CRESTED PORCUPINE (CRESTED PORCUPINE)

Fr. Porc-épique de l'Afrique du Nord; Ger. Nordafrikanisches Stachelschwein (Kamm-Stachelschwein)

Hystrix cristata Linnaeus, 1758. Syst. Nat., 10th edn, 1: 56. 'Asia' (restricted to Rome, Italy by Thomas 1911).

Taxonomy The Crested Porcupines of Africa north of the Equator were known as *H. cristata* (western and northern Africa) and *H. galeata* (eastern Africa). Corbet & Jones (1965) showed that *cristata* and *galeata* exhibit wide overlap in all characters, and therefore should be regarded as conspecific. Likewise, various described races also show overlap in characters. The holotype, from Italy, was probably descended from North African individuals that had been imported, perhaps during Roman times. Synonyms: *aerula*, *cuvieri*, *daubentoni*, *europaea*, *galeata*, *occidanea*, *senegalica*. Subspecies: none recognized here (but see Geographic Variation). Chromosome number: 2n = 66, NF = 114 (George & Weir 1974).

Description Extremely large rodent, the largest in Africa (together with *H. africaeaustralis*), with extremely long stiff hairs and spines. Very similar in external appearance to *H. africaeaustralis*. Dorsal pelage with long stiff black or white hairs anteriorly, and with long smooth spines (quills) on mid-back and rump. Quills with alternating wide black and narrow white bands (usually four or five of each), ending in long white pointed tip; length varied, maximum 30 cm on rump. Nuchal crest (on neck and shoulders) formed of long wiry hairs, up to 45 cm, mostly black. Crest and quills erectile when animal is frightened or threatened. Head, neck and limbs with coarse dark bristles (up to 50 mm). Mid-line of rump black or mottled. Head rather broad with short muzzle, swollen nasal region and long dark vibrissae. Eyes small and dark. Ears short, darkly pigmented. Limbs with short black hairs, relatively short and broad; five digits on each foot (Digit 1 of forefoot greatly reduced), each with claws. Tail short, usually invisible beneath quills of rump; tail covered with short weak quills, some modified to form 'rattle-quills' or 'wine glass quills' (ca. 5 cm long, 2–5 mm diameter), which rattle when tail is shaken. Skull large and rounded. Incisor teeth smooth; cheekteeth with complex folds of enamel and dentine; nasal bones very long, >57% of occipito-nasal length, wide, extending posteriorly almost to level of posterior margin of orbit; frontal : nasal ratio 23–38%. Nipples: 2 or 3 + 0 = 4 or 6.



Hystrix cristata

Geographic Variation Populations show differences in occipito-nasal length, zygomatic width, length of nasals and in overall size. North African (and Italian) individuals are the smallest in size, those from West Africa are intermediate, and those from eastern African (*galeata*) are the largest. However, there is considerable overlap, and differences are probably clinal (Corbet & Jones 1965). In West Africa, Rosevear (1969) refers to two races (subspecies) that differ in size: the largest is *senegalica* from the savanna woodlands (total length about 900 mm, HF 120 mm, GLS over 140 mm, and P⁴–M³ over 32 mm), and the smallest is *aerula* from the semi-desert (TL about 700 mm, HF 80–90 mm, GLS under 140 mm, and P⁴–M³ 30 mm or less).

Similar Species

H. africae australis. Nasal bones 51–58% of occipito-nasal length; frontal-nasal ratio 49–68%; mid-line of rump white; southern Africa; parapatric with *H. cristata* in parts of S Uganda, S Kenya and Tanzania.

Distribution Widespread in Mediterranean Coastal BZ, Sudan Savanna and Guinea Savanna BZs, Northern Rainforest–Savanna Mosaic, and Afromontane–Afroalpine BZ of Ethiopia. Disjunct distribution in parts of Sahel Savanna and Sahara Arid BZs. Recorded from coastal regions and parts of Atlas mountains of Morocco, Algeria and Tunisia; coastal areas of Libya. Probably extinct in Egypt (Osborn & Helmy 1980). Isolated populations in semi-desert habitats in Air (Niger) and Adrar des Iforas (Niger). Widespread throughout West Africa from Senegal to Cameroon, and in NE DR Congo, Rwanda, Ethiopia, Uganda, Kenya and N Tanzania, Zanzibar I. Probably present in S Chad and Central African Republic. In Ethiopia, occurs from sea level to about 3550 m. Also occurs (as an introduced species) in Italy, Sicily, Albania and N Greece (Woods & Kirkpatrick 2005).

Habitat Semi-desert, woodland and grassland savannas, especially where rocks and caves are present. In Algeria and Morocco, lives in forested hills and steppes, but not in the Sahara Desert. Appears to be very tolerant of a wide range of habitats and climates, including warm coastal scrub, dry semi-desert and cold grasslands on mountains. In Ethiopia, may be attracted to irrigated large-scale farmlands, where they can become pests on crops (Yalden *et al.* 1976).

Abundance Uncertain because rarely seen; thought to be quite common in suitable habitats in most parts of range. Many records are based on the presence of discarded quills.

Adaptations Nocturnal, although in captivity may be active in daylight. Terrestrial. During the day, these crested porcupines rest in caves, holes under trees or made by other animals, and in rocky crevices. They do not dig their own burrows. Locomotion is a walk or slow trot, and because of their large size, they are unable to climb. When frightened or threatened, the crest and quills can be erected (making the animal look much bigger than it really is) and the quills are rattled. If in danger, the animal moves sideways or backwards with the pointed tips of the erect quills facing the source of danger, and stamps its feet (Ewer 1968). If really provoked by a potential predator, an individual charges backwards forcing some of its quills into the predator; the quills are easily detached and may stick (like arrows) in the predator. Quite severe wounds can be caused by these quills. This behaviour, and the sharpness of the quills, provides the porcupine with a very effective defence mechanism (even against potential predators such as Lions *Panthera leo*).

There are many reports of porcupines (this species and probably also Cape Crested Porcupines) gathering and chewing on bones, and dens being littered with bones. These habits are thought to be associated with wearing and sharpening the incisor teeth, perhaps with the added benefit of providing an additional source of calcium and minerals (Kingdon 1974).

Foraging and Food Herbivorous. Principal foods are fruits, roots, bulbs and bark. Cassava, sweet potatoes and groundnuts are eaten in savanna farmlands.

Social and Reproductive Behaviour Crested Porcupines are social and gregarious. Secretions from anal glands are used to mark home-ranges and to indicate an individual's presence, and vocal sounds are used (as in many species of hystricomorph rodents) for male–female interactions, to warn conspecifics of danger and during aggressive encounters. During courtship, ♂ approaches ♀ using a 'bipedal approach' gait, and he also grooms the ♀. Females solicit copulation by a 'tail-up rump' display (Mohr 1965, Kleiman 1974). Several individuals may rest together in a burrow (Delany 1975).

Reproduction and Population Structure Gestation: 112 days. Litter-size: 2 (1–4). Weight of young at birth ca. 1000 g. Ratio of litter weight/maternal weight is 10% – a low percentage compared with most hystricomorph rodents (6–60%) (Weir 1974). Young born with eyes open and soft spines (Rosevear 1969). Mother suckles while sitting because nipples are placed on the side of thorax. Males assist with retrieving and grooming young, and will rest with young in the burrow (Mohr 1965). Young weaned at 16 weeks of age.

Predators, Parasites and Diseases North African Crested Porcupines have few predators because of their defensive behaviour (see above). Humans may hunt them for food, but they are not a major source of 'bushmeat' (cf. *Atherurus africanus*, *Thryonomys swinderianus* and duikers; for details, see references in profiles for these species). Two species of tsetse flies (*Glossina submorsitans* and *G. tachinoides*), which transmit sleeping sickness to humans, are recorded as feeding on the blood of porcupines.

Conservation IUCN Category: Least Concern.

North African Crested Porcupines are uncommon and populations are scattered (see above) and hence may be in need of protection.

Measurements

Hystrix cristata

HB: 650–850 mm

T: 120–170 mm

HF: ca. 95 mm

E: ca. 40 mm

WT: ca. 20 kg

GLS: 158 (152–170) mm

GWS: 83 (81–88) mm

P⁴–M³: 33.6 (32.3–34.4) mm

Body measurements: Morocco (*H. c. cristata*; Aulagnier & Thévenot 1986; no sample sizes given)

Skull measurements: West African savanna (*H. c. senegalica*; Rosevear 1969; no sample sizes given)

Key References Corbet & Jones 1965; Rosevear 1969.

D. C. D. Happold

Family PETROMURIDAE
NOKI (DASSIE RAT)

Petromuridae Wood, 1955. J. Mamm. 3: 184.

| | | |
|-----------------------------|------|--------|
| <i>Petromus</i> (1 species) | Noki | p. 681 |
|-----------------------------|------|--------|

The family contains only a single species, *Petromus typicus*. It is restricted to Namaqualand (South Africa), Namibia and extreme SW Angola, occurring only on mountains and rocky outcrops of the semi-arid western escarpment and adjoining areas of the Namib Desert.

The single species is unusual in its external appearance, looking like a mixture of a rat and a squirrel. It is about 200 mm long, with brownish or brownish-grey coarse pelage, and longish tail covered with long dark bristle-like hairs. The head is relatively large, rather flattened with pointed muzzle and long vibrissae. Eyes large; ears moderate and rounded, not protruding above the line of the head. Limbs are short, and feet are broad and naked with well-developed pads; forefoot with four digits (Digit 1 rudimentary); hind-foot with five digits, all with short sharp claws. The ribs are particularly flexible so the body can be pressed flat (when under boulders and rock slabs) without injury. Pectoral nipples are situated laterally behind the shoulders (as in Cane Rats). Size categories of species in the family (based on mean head and body length) are given in the order Rodentia profile.

The skull exhibits typical hystricomorph characters as well as those associated with a rupicolous life-style: infraorbital foramen enlarged,

jugal bone of zygomatic arch enlarged dorsoventrally, cranium flattened dorsoventrally (height above M¹ about 43% of zygomatic width), rostrum narrow (especially in relation to the wide orbital area, zygomatic arches and braincase), and without an interorbital constriction. Dental formula: I ¹/₁, C ⁰/₀, P ¹/₁, M ³/₃ = 20. Upper incisors narrow, not grooved, opisthodont, yellowish. Anterior palatal foramina wide at both ends (similar in width to the upper molars), reaching posteriorly to between premolars; septum between each foramen very narrow. Cheekteeth show a unique structure: four cheekteeth (one premolar, three molars), hypsodont and four-rooted. Each upper cheektooth has deep infolding on the lingual side giving the impression that it consists of two sections. Similar infoldings occur on the labial side but, because of increased wear on this side, they are less obvious in older animals. Each lower cheektooth has deep infoldings on the labial side, and most wear on the lingual side. Auditory bullae considerably inflated, with a well-developed paraoccipital process on the posterior side, which does not project below the level of the bullae. Mandibles very wide posteriorly, with a distinct ridge on the lower outer side, stretching from below the first molar to the narrow angular process (Figure 111).

Nokis are adapted for desert and semi-desert life on rocky habitats. They live in family groups amongst boulders of outcrops and mountainsides, or amongst rock slabs in broken terrain. They are diurnal, but less active during the warmer hours of the day, and they forage on grass and leaves of shrubs and trees up to 20 m away from the protection of rocks.

The phylogenetic relationship of the Petromuridae to other hystricognaths is uncertain. Simpson (1945) grouped Petromuridae with the Octodontoidea, a superfamily proposed by him. Wood (1955) re-established the suborder name Hystricognomorpha for Old World taxa of the hystricognaths and proposed the superfamily name Thryonomyoidea (for the Cane Rats and Dassie Rat) as well as the use of Petromuridae to replace Petromyidae (see Woods & Kirkpatrick 2005). Lavocat (1974) supports the differentiation between Hystricognathi of the Old and New World by using the terms Phiomorpha and Caviomorpha respectively, but prefers to group them together into a higher clade Hystricognathi (suborder). Mess (1999), using the analysis of molecular data (Catzeflis *et al.* 1995), the structure of the rostrum (Ade 1998) and of the ethmoid- and orbital regions (Mess 1997), grouped *Petromus*, *Hystrix* and *Thryonomys* under the Hystricoidea – a name proposed by Gill in 1874. Patterson & Wood (1982) split the Petromuridae in three subfamilies: the Petromurinae for the extant *Petromus*, and the Phiomiyinae and Diamantomyinae for extinct species. At present, there is one genus and one species, *Petromus typicus*.

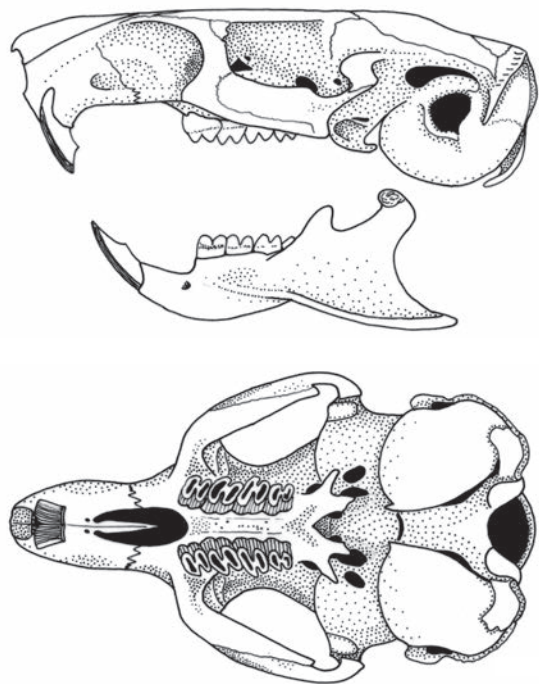


Figure 111. Skull and mandible of *Petromus typicus* (BMNH 28.9.11.377). This specimen is from a young animal and shows infoldings on the labial side of the cheekteeth. See family profile for details.

C. G. Coetzee

Genus *Petromus* Noki (Dassie Rat)

Petromus A. Smith, 1831. S. Afr. Quart. J. 1(5): 10. Type species: *Petromus typicus* A. Smith, 1831.

A monotypic genus occurring only in the South-West Arid BZ. Characters of the genus are given in the family profile above. The single species is *Petromus typicus*.

C. G. Coetzee



Petromus typicus.

Petromus typicus NOKI (DASSIE RAT)

Fr. Rat des rochers du Namibie; Ger. Felsenratte

Petromus typicus A. Smith, 1831. S. Afr. Quart. J., ser. 1, 5: 11. Mountains towards the mouth of the Orange River, Little Namaqualand, Northern Cape Province, South Africa.

Taxonomy Originally described in the genus *Petromus*, but in 1834 Smith referred to the genus as *Petromys*. This mis-spelling prevailed for some time and influenced the spelling of the higher categories – Petromyidae (e.g. Roberts 1951) and Petromyinae (Ellerman 1940). The erroneous spelling was used also in the descriptions of 11 of the 13 described forms (based mainly on coat colour). Synonyms: *ausensis*, *barbiensis*, *cinnamomeus*, *coetzeei*, *cunealis*, *greeni*, *guinasensis*, *karasensis*, *kobosensis*, *majoriae*, *namaquensis*, *pallidior*, *tropicalis*, *windhoeckensis*. Subspecies: none recognized here (but see Geographical Variation). Chromosome number: not known.

Description Large, squirrel-like diurnal rodent with longish pelage and hairy tail. (The term 'large' is ambivalent here; the species is large by murid or sciurid standards, but it is the smallest of non-fossorial hystricomorpha rodents; see Order profile.) Dorsal pelage dark blackish-brown, dark grey or pale buffy-yellow (depending on locality; see below); hairs pale grey at base. Ventral pelage slightly paler than dorsal pelage. Head dorsoventrally flattened, similar in colour to dorsal pelage, paler on nose, lips and around the eyes. Vibrissae long. Eyes large. Ears slate-gray to black, sparsely covered with extremely short hair, small, oval, not protruding above the line of the head. Limbs short; feet broad, well covered with hair on upper surface, naked on undersurface. Forefoot with four digits (Digit 1 rudimentary), three plantar pads at the base of digits and two on palm. Hindfoot with five digits, three plantar pads at base of the toes and only one pad on sole. All digits with short sharp claws. Tail long (ca. 85% of HB), densely covered with long hairs (but not as long as in a squirrel), similar in colour to rump at base, black on terminal three-quarters; tail normally rests on (or is held close to) the ground, not squirrel-like over the body. The scrotum is not conspicuous. Skull: see family profile. Nipples: 2 + 1 = 6; anterior nipples placed laterally behind shoulders; inguinal nipples often absent.

Geographic Variation Although no subspecies are recognized here, three groups may be distinguished, based on the colour of the dorsal pelage, which varies from dark brown in the south to pale brown in the north, and pale to dark grey towards the higher rainfall area of the Otavi Mts complex, leading to south–north and west–east coat clines in colour. The geographical groups may be linked to named forms, as follows:

- Southern buffy-brown group (Namaqualand, along the Orange R., and S Namibia) corresponding to the nominate form (*typicus*) and to *ausensis*, *barbiensis*, *cinnamomeus*, *karasensis* and *namaquensis*.
- Pale brown group (C and NW Namibia to SW Angola) corresponding to *coetzeei*, *greeni*, *kobosensis*, *majoriae*, *pallidior*, *tropicalis* and *windhoeckensis*.
- Grey group (Otavi Mountain area towards the eastern Kaokoveld and northwards to the Kunene R. valley below the Rua Cana Falls and east of the Baines Mts) corresponding to *cunealis* and *guinasensis*.

However, preliminary cranial measurements do not support these divisions (C. G. Coetzee & C. Chimimba unpubl.).

Similar Species

Procavia spp. Similar in appearance, especially when the Noki has lost its tail, as is the case in about 10% of animals; sympatric and often syntopic.

Xerus princeps. Larger; comparatively longer HB; tail with long bushy hairs; may be sympatric and syntopic.

Graphiurus spp. Smaller HB; pelage woolly, nocturnal; upper incisors form an inverted V-shape.

Distribution Endemic to Africa. South-West Arid BZ (Namib Desert). Recorded in rocky habitats in extreme SW Angola, W Namibia and extreme NW South Africa where mean annual rainfall

*Petromus typicus*

is ca. 50–400 mm. Found in canyons of the Namib where the mean annual rainfall can be as low as 35 mm/year. In Angola, limited to the outcrops and broken terrain on the eastern side of the Namib, approximately as far north as 16°S, 12°E and along the Kunene R. inland to the Rua Cana Falls.

Habitat Occurs amongst granite, schist slabs and sedimentary rocks; and amongst the boulders of outcrops, canyons and mountain slopes where rock crevices provide shelter and nesting sites. May also occur amongst boulders and rock accumulations that are some distance away from mountains and outcrops. Normally absent on steep, rather bare rock faces although such rock faces may be used during the day for basking. Habitats with deciduous and evergreen trees and perennial shrubs provide a more stable food resource on outcrops and mountains of the Namib (Rathbun & Rathbun 2005). Also recorded in marginal habitats where annual rainfall is <100 mm and grasses are restricted to narrow strips in gullies and below boulders; here, run-off of water after sporadic rains and from condensed fog, provides additional moisture.

Abundance Generally rare. Populations widely scattered, and localized, but may be quite abundant in favoured localities. At Tumasberg, Namibia (a very arid locality with mean annual rainfall of 39 mm), density was 2.8/ha (biomass 431 g/ha) (Withers 1979). In the winter rainfall region of SW Namibia, where succulents and shrubs provide a year-round source of food, maximum density was 28/ha (biomass 3221 g/ha) (Coetzee 2002). At Tumasberg, *P. typicus* comprised 16% of trapped small mammals, and was less numerous than two other sympatric rodents, *Petromyscus collinus* (60%) and *Aethomys namaquensis* (16%) (n = 250; 6 spp.; Withers 1979).

Adaptations Nokis are well adapted to life in rocky habitats in arid environments. Diurnal and rupicolous. Temperature regulation plays an important role in their activities. They are most active during early morning and late afternoon. Significantly more time is spent basking

during the first three hours after sunrise than during a similar period during the late afternoon (Rathbun & Rathbun 2006b). During daytime, they bask on the tops of boulders or on ledges, or rest underneath rocky overhangs that protect them from avian predators and prevailing dry winds. Basking is less common during the hot season than during the cold season of the year (Rathbun & Rathbun 2006b). Nokis tend to bask on the eastern side of a small outcrop or rock accumulation in the morning, and on the western side during the afternoon (C. G. Coetzee unpubl.). They may even lie spread-eagled on warm rocks (Shortridge 1934, Coetzee 2002). Solar basking, moving from sunny to shady areas, and sheltering at night amongst rocks to avoid extreme external temperatures, form an important part of the Noki's behavioural control of temperature (Rathbun & Rathbun 2006b). Withers *et al.* (1980) recorded a body temperature (T_b) of 34.9 ± 0.5 °C (n = 6) in laboratory animals. Temperature recorders on the necks of three wild-living Nokis recorded a mean temperature of 34.9 °C (range 27.8–42.2 °C) when basking in the sun, 33.3 °C (range 25.8–38.2 °C) when active during the day, and 34.8 °C (range 29.2–38.4 °C) when resting in a night shelter; thus the mean temperature near the skin (and hence not T_b) remains fairly constant (with similar ranges) during the various daily activities and changing environmental temperatures at different locations (Rathbun & Rathbun 2006b). Nokis do not enter torpor at any time.

Nocturnal activity outside nests is restricted (and hence remains of Nokis in owl pellets are rare). Nests are built between rocks and underneath boulders and rock slabs, often with an untidy accumulation of sticks at the entrances. Rock entrances leading to shelters are small, averaging only ca. 44–69 mm high (Augrabies Falls N. P., South Africa; George & Crowther 1981). Nokis are well adapted to squeezing into rock crevices partly because the skull is dorsoventrally flattened and the ribs are compressible (see family profile).

Nokis have a low minimum water turnover rate (0.029 ml/g/day), comparatively large medullary area of the kidney and low daily energy expenditure. Their diet is water-rich stems and succulents; when fed experimentally on dry seeds and without water, they lose 20–35% of their body weight and are unable to survive (Withers *et al.* 1980). George (1981b) found that '*Petromus* can maintain its weight in captivity on 5.7 g dry weight of mixed vegetation containing 0.5 g protein.' In the wild, there is some evidence that water turnover rate is higher when advective fog is present (Withers *et al.* 1980), suggesting that they may drink condensed fog water in areas and at times when this water source is available. The daily energy expenditure of captive individuals fed on dry bird seed (with *ad libitum* water) was 0.55 kJ/g/day, which is 55% of the expected value on the basis of size (Withers *et al.* 1980). The physiological characters of Nokis suggest that they are well adapted to xeric conditions (Withers *et al.* 1980).

Foraging and Food Herbivorous. Nokis feed on a wide variety of leaves, flowers, stems and fruits, with variations depending on season and locality. They forage by cutting leaves or grass stalks, and then quickly return to the shelter. They climb shrubs and small trees such as *Scotia afra*, *Hermannia stricta* (George 1981b), *Boscia* and *Lycium* species to nibble the leaves. Fruit of cucurbitaceous plants (e.g. *Cucumis dinteri*) and flowers of daisies such as *Arctotis*, *Gazania* and *Dimorphotheca* sp., leaves of *Mesembryanthemum* succulents and *Aloe* sp. are also eaten. When herbs such as *Tribulus zeyheri* are collected and brought to the resting area, the stems are usually eaten before the

leaves (Coetzee 2002). In the wild (and in captivity), they collect and eat both green and dry grass stalks when both are available. In the central Namib and near Windhoek, these grasses include species of *Eragrostis*, *Enneapogon* and *Stipagrostis*, as well as *Cenchrus ciliaris* and *Anthehora pubescens*. During the dry season, they eat new green leaves on the stems of *Grewia flavescens* and *G. tenax*, dry leaves on the ground, flowers on the stems (and on the ground) of *Sterculia africana* and *Adenolobus garipensis*, and the flowers and/or seed pods from stems of *Boscia albitrunca* (Rathbun & Rathbun 2005). In the winter rainfall area of Namaqualand and SW Namibia, succulents such as the numerous species of Mesembryanthemaceae and Fabaceae form an important part of their diet. At Augrabies Falls, South Africa, George (1981b) found that 55–90% of the diet consisted of monocotyledons, even though the water content (57% in green grass and 18% in dry grass blades and stalks) was lower than in dicotyledons (75%). At Tumasberg, stomach contents ($n = 13$) contained seeds (3%), leaves (24.8%), stems (49.7%) and insect remains (21.0%) (Withers 1979). In the Erongo Mts of Namibia, Nokis consumed 28 species of plants (green leaves and stems, flowers, fruits, dry stems and leaves, according to the plant species). The diet changed seasonally depending on the phenology of each species (Rathbun & Rathbun 2005). Some species of plants were avoided, probably because of the presence of secondary defence compounds. The diet of Nokis is very flexible and varies from locality to locality depending on the plant species available.

Nokis have a simple typical rodent-like stomach and a large caecum. Cellulose-rich food is most likely to be fermented by micro-organisms in the intestine. Coetzee (1983) recorded 'jack-knife' movements of the head and body whereby food is regurgitated and rechewed, but Rathbun & Rathbun (2005) and Mess & Ade (2005) did not record such movements nor regurgitation. Leaf remains in stomachs vary from fresh and green fragments of ca. 2 mm (e.g. *Boscia albitrunca* and *Lycium* spp.) to those the size of sand-grains. Nokis are coprophagous; two sorts of faecal pellets are produced: dark, dry, brown ones and wet softer greenish ones. The greenish ones are often eaten, but the dry ones are not (Mess & Ade 2005). The two main longitudinal ridges in the proximal colon result in two distinct grooves, which separate the contents of the caecum. Coprophagy is likely to be an important method of increasing digestive efficiency, especially when the diet is coarse and fibrous.

Social and Reproductive Behaviour Socially monogamous (Rathbun & Rathbun 2006a). Lives in family groups that vary in size from one ♂, one ♀ and one young (Rathbun & Rathbun 2006a) to five animals (in an overnight shelter). Occasionally groups are larger, e.g. 22 animals from (presumably) two family groups, which were using granite boulders as overnight abodes (Coetzee 2002, unpubl.). A family group may congregate and rest on a rock or in shelters. Allogrooming takes place throughout the day, but self-grooming in the morning is more common. Grooming and suckling of young takes place at these resting sites. Young frequently bask and nap curled up on the extended front limbs ('lap resting'), or on top of the extended base of the tail ('tail resting'), of one of the parents (Rathbun & Rathbun 2006a).

The mean home-range of a male–female pair (95% minimum convex polygon) for five pairs of individuals in the Erongo Mts is 0.34 ha for ♀♀ and 0.23 ha for ♂♂ (Rathbun & Rathbun 2006a). The home-range of ♂ had a 56% overlap (on average) with that of ♀, and the home-range of ♀ had an 81% overlap (on average) with

that of ♂. There was virtually no overlap in the home-ranges of adjacent pairs. Male home-ranges (territories) are exclusive and are maintained by male–male aggression; ♀♀ are more tolerant and will allow intruding ♂♂ and other ♀♀ into their home-range. Home-ranges of both ♂♂ and ♀♀ contract greatly after the birth of the young, especially during the first week, when one parent, either ♂ or ♀, remains with the young nearly all the time. Rathbun & Rathbun (2006a) suggest that 'mate-guarding' is the principal adaptive factor in the evolution of social monogamy in Nokis (as it is for Kirk's Dik-dik *Madoqua kirkii* [Brotherton & Rhodes 1996] and Eastern Rock Sengi *Elephantulus myurus* [Ribble & Perrin 2005]).

Adults occasionally make soft 'tjijrrrrrr' squeaks whilst resting and at night; each squeak lasts for ca. 1.5 seconds and is repeated in a series (e.g. 13 squeaks in 90 seconds). The interval between series varies considerably (Coetzee 2002).

Reproduction and Population Structure In the winter rainfall area of SW Namibia and Namaqualand, reproduction is mainly during spring. In the summer rainfall areas of Namibia and Angola, fecund ♀♀ were mostly recorded during Sep to Apr (spring to autumn) with a peak in the autumn months. Gestation: ca. 12 weeks (Mess 2005). Litter-size: 1.97 ± 0.7 (1–3, $n = 37$). At birth, young weigh ca. 14.7 g (range 10.5–20 g; Coetzee 2002), precocial with eyes and ear pinnae open, fully furred and able to jump over their mother when ca. 10 minutes old (C. G. Coetzee unpubl.); first eat solid food on Day 14; weaned ca. Day 20 when 3–4 times birth-weight; adult weight (ca. 150 g) at 9–12 months (Coetzee 2002).

Predators, Parasites and Diseases Important mammal predators probably include: *Felis lybica*, *Galerella sanguinea*, *Galerella pulverulenta*, *Cynictis penicillata*, *Canis mesomelas* and *Vulpes chama*. Predation by *Galerella nigrata* is well documented (Rathbun & Rathbun 2006a). Snake predators may include *Python anchietae*, *Pseudapsis cana*, *Naja nigricollis*, *Naja haja*, *Bitis arietans* and *B. caudalis* (at the base of mountains). Captive *Petromus* react strongly to overhead movements. Raptors that are possible predators are *Falco biarmicus*, *Hieraaetus spilogaster*, *Aquila verreauxi*, *Cicaetus cinereus* and *Cicaetus pectoralis* (H. Berry pers. comm.). There are few records of parasites: ectoparasites include one cosmopolitan flea (*Echignophaga gallinacea*) (De Meillon *et al.* 1961) and endoparasites include a nematode worm (*Acanthoxyuris shortridgei*) (Monnig 1931, in De Graaff 1981). Not known to play any role in the spread of diseases.

Conservation IUCN Category: Least Concern.

Conserved in several nature reserves and national parks in South Africa, Namibia and Angola.

Measurements

Petromus typicus

HB (♂♂): 171.0 (140–224) mm, $n = 50$

HB (♀♀): 173.0 (135–200) mm, $n = 47$

T (♂♂): 142.6 (119–175) mm, $n = 50$

T (♀♀): 145.7 (116–168) mm, $n = 41$

H (♂♂): 32 (27–40) mm, $n = 57$

HF (♀♀): 32 (28–38) mm, $n = 47$

E (♂♂): 13.8 (11–17) mm, $n = 47$

E (♀♀): 13.2 (10–16) mm, $n = 49$

WT (♂ ♂): 160.9 (102–285) g, n = 17
WT (♀ ♀): 161.5 (88–219) g, n = 22
GLS (♂ ♂): 42.5 (38.2–49.7) mm, n = 65
GLS (♀ ♀): 47.9 (39.5–47.0) mm, n = 78
GWS (♂ ♂): 25.6 (22.2–36.1) mm, n = 66
GWS (♀ ♀): 26.6 (23.4–36.1) mm, n = 78
P–M³ (♂ ♂): 9.7 (9.1–11.4) mm, n = 66

P–M³ (♀ ♀): 9.9 (9.1–11.3) mm, n = 78
Namibia, South Africa (C. G. Coetzee unpubl.)

Key References Coetzee 2002; De Graaff 1981; Rathbun & Rathbun 2006a, b; Skinner & Smithers 1990.

C. G. Coetzee

Family THRYONOMYIDAE

CANE RATS

Thryonomyidae Pocock, 1922. Proc. Zool. Soc. Lond. 1922: 423.

| | | |
|------------------------|-----------|--------|
| Thryonomys (2 species) | Cane Rats | p. 686 |
|------------------------|-----------|--------|

The family Thryonomyidae is endemic to Africa and contains a single genus distributed widely in the savanna regions throughout the continent. Cane rats are characterized by their large size (second only to *Hystrix* spp. and *Pedetes*), long coarse hairs, massive blunt head, short limbs and a rather short tail. Each foot has three well-developed digits (Digits 2, 3 and 4), ending in thick claws; Digits 1 and 5 are short or rudimentary and without a claw. The skull is easily recognizable by its large size, strong build and wide upper incisor teeth, orange in colour, each with three deep longitudinal grooves on the outer face (a character not seen in any other African rodent), well-developed supraoccipital crests, small auditory bullae, long finger-like paraoccipital process and thick zygomatic arches. There is a large infraorbital foramen

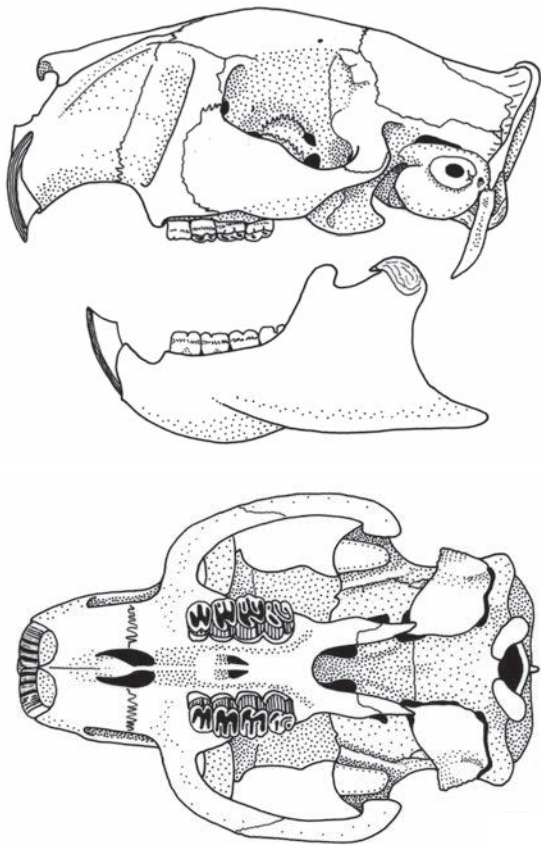


Figure 112. Skull and mandible of *Thryonomys swinderianus* (RMCA RG 22.827).

as in the other hystricomorph rodents (Figure 112). Dental formula: $I^{1/1}, C^{0/0}, P^{1/1}, M^{3/3} = 20$. The deciduous premolar is retained throughout life so there are always four cheekteeth. The molar teeth have an intricate pattern of enamel and dentine. The basic design is three transverse ridges; each upper molar has two infoldings on the outer (labial) side and one infolding on the inner (lingual) side (Figure 108), and each lower molar has one infolding on the outer side and two on the inner side. This design of alternating ridges of enamel and dentine results in very efficient mastication of the fibrous plant material in the diet. Size categories of species in the family (based on mean head and body length) are given in the order Rodentia profile.

Both species live in long grass savanna, swamps and reed-beds, and normally rest during the day in the dense grasses. They do not make proper nests and do not dig burrows. They are mostly nocturnal, although they may be active during the day in some situations. They tend to live in small groups and have a wide repertoire of calls and behaviours for communication between individuals. Cane rats are strict herbivores that feed primarily on coarse grasses, but they also feed on crops in agricultural areas. Because of their large size and succulent flesh, they are hunted by humans in many parts of their geographic range.

The Thryonomyidae is thought to be closely related to the Petromuridae (which contains just a single extant species, *Petromus typicus*). Some authorities place *P. typicus* within the Thryonomyidae, but here, following Woods (1993) and Woods & Kirkpatrick (2005), the two families are maintained. The geological record of the Thryonomyidae is sparse; fossils are known from the Oligocene of N Africa, and the Pleistocene of Niger, Sudan and Namibia (De Graaff 1981, Woods 1984), suggesting a wider distribution in the past than at the present time.

Thomas (1922) proposed the ‘*Choeromys* group’ for the cane rats of central and eastern Africa (*gregorianus*, *logonensis*), thereby separating them from the ‘*Thryonomys* group’ of western Africa (*swinderianus*). The ‘groups’ were differentiated primarily on overall size, the amount of inflation of the skull, the position of the grooves on the incisor teeth and the length of the tail. These differences are no longer considered of any value at the generic or subgeneric level (Rosevear 1969), although they are of value for identification at the species level.

The family contains a single genus with two species, *T. gregorianus* and *T. swinderianus*.

D. C. D. Happold

Genus *Thryonomys*
Cane Rats

Thryonomys Fitzinger, 1867. Sitzb. Akad. Wiss. Wein 56 (1): 141. Type species: *Aulacodus swinderianus* Temminck, 1827.



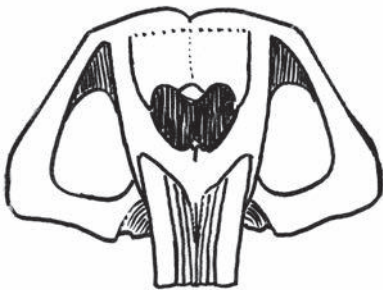
Thryonomys swinderianus.



Thryonomys sp.

The genus contains two species (Table 47) and is widely distributed throughout sub-Saharan Africa. Both species live in grassland habitats, especially where the grass is thick and lush. Characters of the genus are given in the family profile above. The two species are distinguished by body size, shape of frontal bone, position of grooves on the upper incisor teeth and length of tail.

D. C. D. Happold



Frontal view of incisor teeth of *Thryonomys gregorianus* (top) and *T. swinderianus* (below). (From Kindgon 1974)

Table 47. Characters of *Thryonomys swinderianus* and *Thryonomys gregorianus*.

| Character | <i>T. swinderianus</i> | <i>T. gregorianus</i> |
|--------------------------------------|---|---|
| Tail length ^a | 170–262 mm, at least twice as long as HF; longer than in <i>T. gregorianus</i> | 90 (65–173) mm, about equal to, or slightly longer than, HF; shorter than in <i>T. swinderianus</i> |
| Grooves on upper incisor tooth | Three grooves; outermost in mid-line of tooth; two inner grooves faint and close together | Three grooves; outermost nearer to outer edge than to mid-line; two inner grooves clearly separated |
| Skull size and shape | Arched in frontal region when viewed from side | More or less flat when viewed from side |
| Height of skull | ca. 44 mm | ca. 34 mm |
| Shape of zygomatic arch ^b | Zygomatic arch slopes outwards from top of head | Zygomatic arch slopes almost perpendicularly from top of head |
| Zygomatic width | 53–60 mm | 49–60 mm |
| Weight ^b | 3.2–5.2 kg (♂ ♂)
3.4–3.8 kg (♀ ♀) | 1.4–2.38 kg (♂ ♂)
1.7–1.9 kg (♀ ♀) |

^aTail length, and tail length relative to hindfoot (HF) length, appear to be good distinguishing characters in East Africa (Kindgon 1974), although not in southern Africa (Smithers 1983).

^bSouthern Africa (Smithers 1983).

Thryonomys gregorianus LESSER CANE RAT (LESSER GRASS CUTTER)

Fr. Petit Aulacode ; Ger. Kleine Rohrratte

Thryonomys gregorianus (Thomas, 1894). Ann. Mag. Nat. Hist., ser. 6, 13: 202. Kiroyo, Luiji Reru River, Kenya (00° 3'5 S, 36° 05' E).

Taxonomy Originally described in the genus *Aulacodus*. Thomas (1922) proposed that *T. gregorianus* should be placed in a separate genus, *Choeromys*, because of supposed differences between it and *T. swinderianus*. This proposal is no longer accepted. Rosevear (1969) recognized *T. longonensis* (from N Cameroon) and *T. camerunensis* (from S Cameroon) as species within the 'Choeromys group'. Synonyms: *camerunensis*, *congius*, *harrisoni*, *logonensis*, *pusillus*, *rutschuricus*, *sclateri*. Subspecies: none recognized here. Meester *et al.* (1986) listed two subspecies, *T. g. gregorianus* and *T. g. sclateri*, without giving reasons, and they were unable to comment on the validity of other taxa as subspecies. Chromosome number: not known.

Description Extremely large rodent (although smaller than *Hystrix* spp. and *T. swinderianus*), with large blunt head and coarse dense brownish pelage. Similar in form and colour to *T. swinderianus* (see description), although smaller. Tail short (ca. 38% of HB) and 2.5 times the length of HF. Skull strongly built. Upper incisor teeth broad (total width: 10–12 mm), orange on outer surface, each with three longitudinal well-separated grooves, the outer groove nearer to the outside than to the mid-line. Frontal region relatively flat when viewed from the side. Zygomatic arch slopes almost perpendicularly downwards from top of head. Cheekteeth with complex folds; each tooth with two folds on outer surface and one fold on inner surface. Cheekteeth cant outwards. M³ erupts well after other cheekteeth are in use. Well-developed supraoccipital crest and paraoccipital processes. Some ♂♂ tend to be heavier than ♀♀. Nipples: 0 + 2 = 4 placed laterally (Ansell 1966).

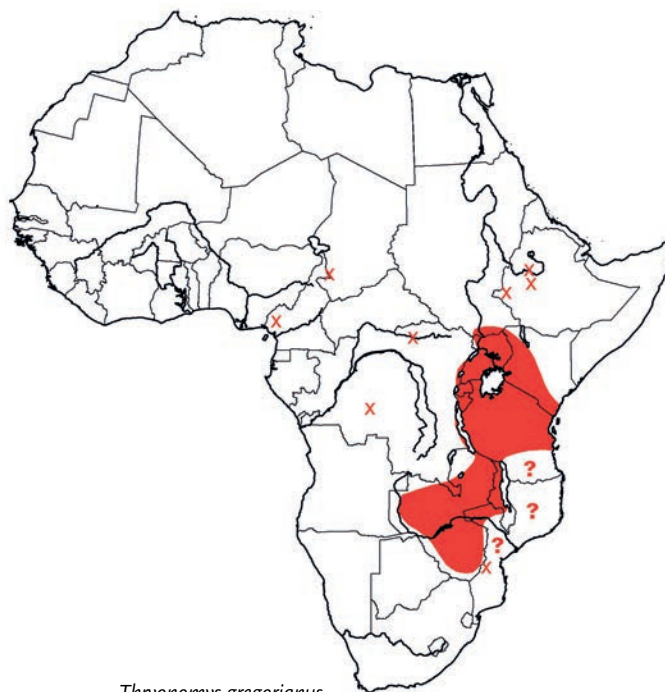
Geographic Variation Specimens from the northern part of the geographic range have a shorter tail and on average longer hindfoot compared with specimens from the southern part (see Measurements), e.g. four individuals from Kenya and E DR Congo have the following body measurements: T: 100 (90–112) mm, HF: 85 (74–92) mm.

Similar Species

T. swinderianus. Larger and heavier; tail at least twice length of HF; more extensive geographic range; including western and southern Africa.

Distribution Endemic to Africa. Parts of Zambezan Woodland Savanna BZ, Eastern Rainforest–Savanna Mosaic and southern part of Somalia–Masai Bushland BZ. Widely distributed in tall grass savanna in S Sudan, Uganda, Kenya, Tanzania, Zambia, Malawi and Zimbabwe. Isolated populations in Cameroon, DR Congo and Ethiopia. Likely to occur in Mozambique, but no definite records available.

Habitat Grasslands, tussock grasslands, swamps and rocky habitats in savanna habitats. Prefers drier habitats than *T. swinderianus*. Maybe be semi-aquatic at the edges of swamps.

*Thryonomys gregorianus*

Abundance Uncertain. Appears to be less common than *T. swinderianus*.

Adaptations Probably similar to *G. swinderianus*. Well-defined paths are made in long grass, often forming 'tunnels' (10–12 cm wide and 15–18 cm high) overhung by vegetation (Rahm & Christiaensen 1963).

Foraging and Food Herbivorous. In E DR Congo, Lesser Cane Rats feed on the stems of many sorts of plants, including the grasses *Pennisetum*, *Hyparrhenia*, *Setaria*, *Melinis* and *Exothea*, bracken *Pteridium* and wild ginger *Aframomum* (Rahm & Christiaensen 1963). In cultivated areas, feeds on cassava, stems of maize and sugarcane. Cane rats (both species) practise coprophagy, which occurs at a set time, usually between 08:00h and 11:00h, when faecal pellets are taken directly from the anus and reingested (Ewer 1969). It is assumed that coprophagy allows additional nutrients, including vitamins produced by the bacterial fauna of the caecum, to be absorbed during a second passage through the gut in much the same way as in species of Lagomorpha.

Social and Reproductive Behaviour Probably similar to Greater Cane Rats. Home-range in E DR Congo estimated to be 3000–4000 m² (Rahm & Christiaensen 1963).

Reproduction and Population Structure Information is sparse and inconclusive. In Uganda, one pregnancy recorded in Aug (two embryos; Delany 1975); in Kenya, pregnancies in Nov and Dec

(two ♀♀, three embryos each; Hollister 1919, as *T. pusillus*); in Zimbabwe, pregnancies in May (one ♀, two embryos) and Nov (one ♀, three embryos) (Smithers & Wilson 1979).

Predators, Parasites and Diseases Predators include Leopards *Panthera pardus*, Servals *Leptailurus serval*, pythons, viverrids and some eagles (De Graaff 1981). In Zimbabwe, preyed upon by Cape Eagle-owls *Bubo capensis* (Gargett & Grobler in De Graaff 1981). Humans hunt Lesser Cane Rats but they are not as important as a source of protein as Greater Cane Rats.

Conservation IUCN Category: Least Concern.

Measurements

Thryonomys gregorianus

TL (♂♂): 519 (410–575) mm, n = 7

TL (♀♀): 518 (495–540) mm, n = 3

T (♂♂): 144 (110–175) mm, n = 7

T (♀♀): 132 (125–140) mm, n = 3

HF c.u. (♂♂): 60 (55–90) mm, n = 7

HF c.u. (♀♀): 62 (70–75) mm, n = 3

E (♂♂): 29 (27–30) mm, n = 7

E (♀♀): 29 (25–31) mm, n = 3

WT (♂♂): 1.9 (1.4–2.4) kg, n = 7

WT (♀♀): 1.9 (1.7–1.9) kg, n = 3

GLS: 81.9 (75.2–89.6) mm, n = 10

GWS: 51.9 (46.6–58.9) mm, n = 10

P⁴–M³: 16.2 (14.4–17.3) mm, n = 9

Body measurements: southern Africa (Smithers 1983)

Skull measurements: East Africa (MRAC, NMK)

Key References De Graaff 1981; Smithers 1983.

D. C. D. Happold

Thryonomys swinderianus GREATER CANE RAT (CUTTING-GRASS, GRASS CUTTER)

Fr. Grand Aulacode ; Ger. Grosse Rohrratte

Thryonomys swinderianus (Temminck, 1827). Monogr. Mamm. 1: 248. Sierra Leone (exact locality not stated).

Taxonomy Originally described in the genus *Aulacodus*. Synonyms: *angolae*, *calamophagus*, *logani*, *raptorum*, *semipalmatus*, *variegatus*. Subspecies: none currently recognized. Thomas (1922) recognized four forms based on colour, size and geography, all of which are now regarded as synonyms. Within West Africa, Thomas (1922) referred to the savanna race as *swinderianus* and the forest race as *raptorum*. Chromosome number: 2n = 44, NF = 86 (Benin; Civitelli *et al.* 1996).

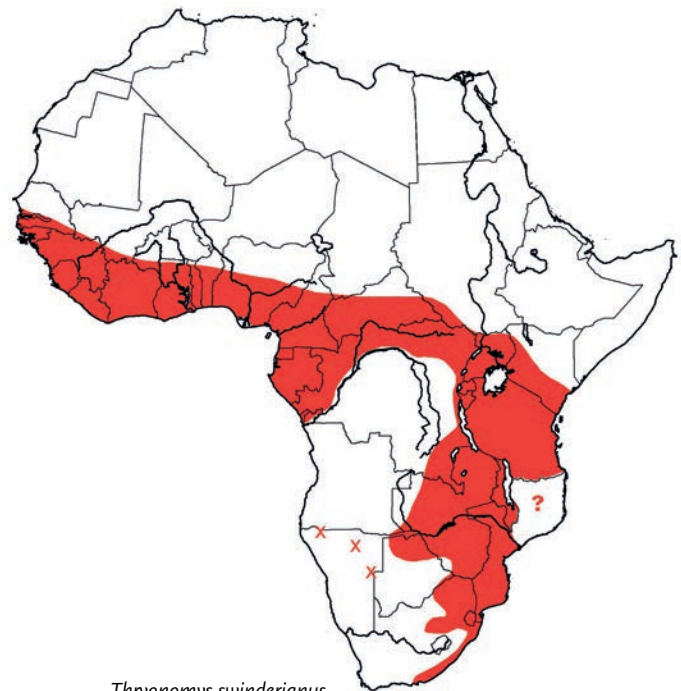
Description Extremely large rodent (surpassed only in size by *Hystrix* spp. and *Pedetes* spp.), with large blunt head and coarse dense brownish pelage. Dorsal pelage deep brown to rufous-brown, flecked with yellow and black. Dorsal hairs thick and coarse, mostly brown, with yellowish terminal band and (usually) black tip. Flanks similar to dorsal pelage merging into greyish-white ventral pelage. Body thickset. Head blunt with broad flattened muzzle; eyes small; mouth situated ventrally, set back from the enlarged nasal region; ears short and rounded, with short hairs and often partly obscured by cheek hairs. Limbs short and strong with well-developed claws. Forefeet with five digits: Digit 1 short, Digit 5 rudimentary. Hindfeet with four digits: Digit 1 absent, Digit 5 very small. Tail short (ca. 36% of HB and about twice the length of HF); thick at base tapering to tip; densely covered with short bristles similar in colour to dorsal pelage. Skull strongly built. Upper incisor teeth broad, orange on outer surface, each with three longitudinal grooves, the outermost groove in midline of tooth. Frontal region arched when viewed from the side. Zygomatic arch slopes outwards from top of head. Cheekteeth with complex folds; each tooth with two folds on outer surface and one fold on inner surface. Cheekteeth cant outwards. M³ erupts well after other cheekteeth are in use. Well-developed supraoccipital crest and paraoccipital processes. Males tend to be heavier than ♀♀. Nipples: 0 + 3 = 6, placed laterally.

Geographic Variation Colour variations associated with different geographic regions have been named as different forms (see Taxonomy).

Similar Species

Thryonomys gregorianus. Smaller and less heavy; tail about same length as HF; restricted to parts of central and eastern Africa.

Distribution Widely but patchily distributed in several savanna biotic zones south of the Sahara. May also occur, in smaller numbers, in grassy regrowth areas on the fringes of the Rainforest BZ. Rarely



Thryonomys swinderianus

recorded north of about 15°N in the north-west of the continent, north of 5–10°N in the north-east, or south of ca. 25°S except in some eastern coastal regions of South Africa. Not present in rainforests of central Africa, nor in arid habitats of Angola, Namibia, Botswana and South Africa.

Habitat Swamps, reed-beds, semi-aquatic habitats and long grass savannas where grass cover is dense. Also occurs in habitats subject to seasonal flooding, and in fields of sugarcane, maize and guinea corn.

Abundance Probably common in suitable habitats, although rarely seen. The large number killed for bushmeat (see below) suggests that Greater Cane Rats are very common in some regions. The commonest evidence of cane rats is the piles of droppings and the characteristic cut stems of grasses.

Adaptations Nocturnal, although may be active during the day in sheltered environments and on dull days. Although Greater Cane Rats have short limbs, they run quickly when disturbed, often 'freezing' after running for some distance. They make runways through dense grasses and reeds, and are good swimmers. During the day, an individual rests in a 'form', a simple depression in the grass often lined with cut grass stems (in much the same way as a hare), and occasionally in a rock crevice or burrow excavated by a large mammal. Eyesight is not particularly good, but hearing is very acute. Greater Cane Rats produce several vocal sounds, each of which is emitted as a specific communication signal to other individuals: the 'boom', sometimes accompanied by thumping with the hindfeet, is a warning signal when there is disturbance or potential danger; the 'growl' is a threat signal used during agonistic behaviour and sometimes by ♂♂ during courtship; the 'wheet' is a contact call by young, the 'squeak' indicates fear and may also indicate appeasement, and the 'quirr' is probably for close-contact communication with other Greater Cane Rats (Cox 1978). Each of these vocalizations may vary in emphasis, duration, repetition and amplitude depending on the motivation of the animal and the context in which each is given. The diversity of methods of communication suggests that Greater Cane Rats have a well-defined social organization (Cox 1978).

Greater Cane Rats are coprophagous (as are many Lagomorphs and *T. gregorianus*), and the caecum is enlarged and used for fermentation of food. These characteristics enable them to feed on grasses and stems with a high fibre content. In the dry season, when grasses are dead and particularly high in fibre, cane rats adapt by increasing the size of the caecum and colon, and the rate of coprophagy. Even though the daily intake of food is increased, protein intake and the rate of growth is reduced (van Zyl *et al.* 1999). The ability of these cane rats to extract nutrients from low quality fibrous food enables them to survive when only coarse dry grass is available.

The four cheekteeth in each ramus of the jaw erupt sequentially, and the age of an individual (up to about nine months when half adult weight) can be determined by the number of cheekteeth visible above the gum. From birth to ca. one month, only one tooth (P4) is visible; from 1 to 5 months only P4 and M1, from 5 to 9 months only P4, M1 and M2, and from nine months onwards all cheekteeth (P4, M1, M2 and M3) are present (van der Merwe 2000). The width of the cheekteeth and length of the toothrow in relation to

length of the skull is comparatively greater than in most other rodents – a condition related to the fibrous nature of the diet.

Foraging and Food Herbivorous; feeds primarily on the stems of thick coarse grasses and reeds. Greater Cane Rats have a unique way of cutting thick stems: the side of the head is placed along the length of the stem, but rotated so that the outer edge of the incisor teeth touches the stem. In this way, the incisor teeth bite at an angle of about 45 degrees to the long axis of the stem. The fallen piece of stem is then picked up in the mouth, grasped on either side of the mouth and sliced through the middle with the incisors. The two cut ends, each held in a forefoot, are fed into the mouth and sliced into small pieces by the incisors. Short bouts of incisor slicing are alternated with bouts of cheekteeth chewing, with a predominantly sideways action (Ewer 1969). The seed heads of grasses are eaten in a different manner: the stem is held in a forefoot and then pulled through the mouth stripping off the seeds. In cultivated areas, cane rats will feed on sugarcane, maize and guinea corn. A pile of short grass stems, cut at 45 degree angles, is a good indication of where a Greater Cane Rat has been feeding. They produce characteristically shaped faecal pellets, often where they have been feeding.

Social and Reproductive Behaviour Greater Cane Rats are normally encountered in small groups, although some groups may be large (e.g. 15 individuals seen together in Guinea; Gautun *et al.* 1986). Little is known about the composition of groups. In captivity (Ewer 1969), observations suggest that the social unit is single ♂ with one or two ♀♀ and their young. Greater Cane Rats exhibit many social interactions with conspecifics. Males determine their dominance by nose-pushing. Two ♂♂ approach each other, and when their noses touch, they push against each other. One of them may, alternatively, attempt to push against the cheek of his opponent, temporarily knocking him off-balance. If one individual relaxes for a moment, the other quickly flips round and tries to knock his opponent on the rump with his rump. These nose-pushes and rump-pushes continue until the loser jumps away and flees. The opponents do not attempt to bite with their incisors during these contests, nor do they threaten by gnashing their teeth (as do many species of rodents) (Ewer 1969).

Mutual grooming occurs between members of a group. An individual solicits grooming by turning the head so the throat is exposed. When two members approach each other and display in this manner, mutual grooming may commence. Grooming of the throat appears to be especially pleasurable (and, incidentally, is an area which the animal cannot groom by itself).

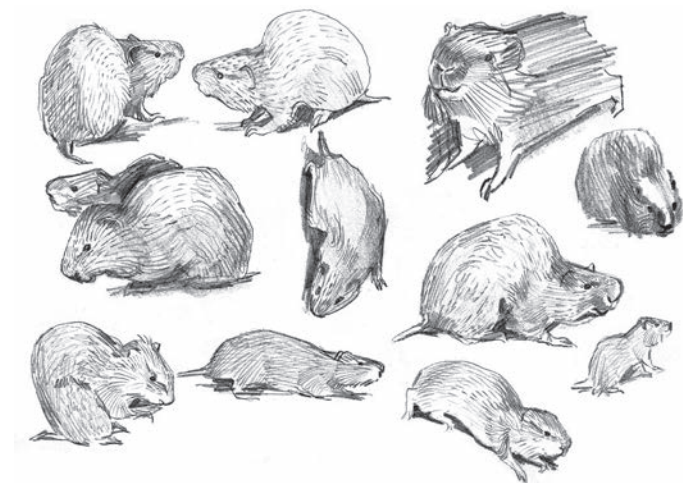
The tail is used to express submission. Wagging the tail from side to side appears to inhibit aggression by the individual to whom the signal is made. Youngsters have been observed to wag the tail when approached by an adult from behind, and ♂♂ wag their tails when courting ♀♀ (Ewer 1969).

Female suckles her young while lying on her belly, taking some of the weight of her body on fore- and hindlimbs. The lateral position of the nipples allow the young to suck from either side.

Reproduction and Population Structure Reproductive activity varies according to locality and climate. In Ghana, pregnancies occur in all months. In S Ghana, monthly pregnancy rate was 64–

93% ($n = 523$), with >80% during 10 months of the year, and in N Ghana, pregnancy rate was 26–95%, with >80% during the four months of the wet season (May–Aug) (Asibey 1974b). No information available on months when young are born, but seasonality of birth rate is probably related to seasonality of rainfall and grass growth. Information from elsewhere is inconclusive: young recorded in Jun and Aug in Botswana (Smithers 1971), and in Aug and Nov in Zimbabwe but information is lacking for other months (Smithers & Wilson 1979). Gestation 155 days (137–172), $n = 33$ litters (Asibey 1974b). Postpartum oestrus likely. Embryo number: 3 (1–5); $n = 18$ females (South Africa; van der Merwe 1999); 3.8 (2–5), $n = 6$ litters (van der Merwe & van Zyl 2001); 4–6, mode 4, $n = 480$ litters (Ghana; Asibey 1974b). Some evidence of embryo reabsorption (Asibey 1974b). Mean weight of young at birth: 128 (75–190) g ($n = 9$ litters). Total litter weight at birth is ca. 15–20% of maternal weight ($n = 112$ litters), and there is no relationship between litter weight and weight of the mother (Asibey 1981). Great variation in weight of young within and between litters. Mean litter-size varies according to age of mother: 3.1 for primiparous ♀♀ and 3.9 for parous mothers (Asibey 1974b). At birth, young are fully furred with eyes open, and can follow the mother within an hour of birth. In captivity, growth rates and adult weights greater for ♀♀ than for ♂♂; ♀♀ reach adult size at ca. Day 300, and ♂♂ at ca. Day 390 (van der Merwe & van Zyl 2001). Sexual maturity is attained at about seven months and a ♀ gives birth to her first litter when about one year old. Females probably produce two litters each year (Booth 1960, Asibey 1974b). In captivity, in South Africa, ♀♀ may have two litters per year (van der Merwe & van Zyl 2001). Histological changes during the oestrous cycle are described by Adjanohoun (1992). Longevity up to four years in captivity.

Predators, Parasites and Diseases Leopards, servals, hunting dogs, eagles, eagle-owls and pythons are potential natural predators (De Graaff 1981). Greater Cane Rats are vigorously hunted by humans



Thryonomys gregorianus.

because of their succulent flesh. Carcasses are seen for sale as 'bushmeat' in many parts of Africa, especially in the Rainforest BZ (see also *Atherurus africanus*). Greater Cane Rats are hunted with dogs and by burning savanna grasses, and are caught by snares. In Bendel State, S Nigeria, carcasses of cane rats formed 20–34% of all bushmeat for sale, and were either the most abundant or second most abundant species in local markets (Martin 1983, Anadu *et al.* 1988). In Accra, Ghana, about 110,000 kg of Greater Cane Rats were traded during a 12-month period in 1970–71 (Asibey 1974a) – equivalent to 40,000–55,000 individuals. In less suitable habitats, e.g. Equatorial Guinea, they form only a small proportion of 'bushmeat' (Juste *et al.* 1995). The meat of Greater Cane Rats has a higher percentage of protein and less fat per unit weight than does rabbit and chicken, and is also rich in calcium and phosphorus (Jori *et al.* 1995). Because of the desirability of these animals for food, studies in several African countries are investigating the possibility of domesticating and farming them commercially (Ajayi & Tewe 1980, Hardouin 1995, Jori *et al.* 1995).

Many species of ticks have been recorded (De Graaff 1981, Aeshlimann 1967), as well as gastrointestinal cestode and nematode worms (De Graaff 1981).

Conservation IUCN Category: Least Concern.

In spite of the very high hunting pressure on Greater Cane Rats, in some parts of the geographic range, numbers do not appear to be threatened at present. However, there is some evidence that population numbers are falling near large urban centres.

Measurements

Thryonomys swinderianus

TL (♂♂): 715 (670–792) mm, $n = 5$

TL (♀♀): 666 (654–670) mm, $n = 3$

T (♂♂): 188 (180–192) mm, $n = 6$

T (♀♀): 183 (165–195) mm, $n = 3$

HF (♂♂): 94 (80–100) mm, $n = 6$

HF (♀♀): 89 (88–90) mm, $n = 3$

E (♂♂): 33 (30–35) mm, $n = 6$

E (♀♀): 35 (34–45) mm, $n = 3$

WT (♂♂): 4.5 (3.2–5.2) kg, $n = 6$

WT (♀♀): 3.6 (3.4–3.8) kg, $n = 3$

GLS: 90.6 (86.5–95.1) mm, $n = 4$

GWS: 58.0 (55.6–61.3) mm, $n = 4$

P⁴–M³: 18.8 (18.1–19.5) mm, $n = 4$

Body measurements: southern Africa (Smithers 1983)

Skull measurements: Nigeria (forest; Rosevear 1969)

Key References Asibey 1974a, b; Ewer 1969; De Graaff 1981; Smithers 1983.

D. C. D. Happold

Family MYOCASTORIDAE

COYPU

Myocastoridae Ameghino, 1904. *Anales Soc. Cient. Argentina* 56–58: 103.

This family of South American aquatic rodents contains only a single genus and single species, *Myocastor coypus*. The family belongs to the suborder Hystricomorpha (together with the African endemic families Bathyergidae, Hystricidae, Petromyidae and Thryonomyidae). This species is not indigenous to Africa, and only one introduced

population (now feral) is known to exist in Africa; therefore details of the family and genus are not given here (see Woods *et al.* 1992 [and references therein] and Woods & Kirkpatrick [2005] for further details).

D. C. D. Happold

Genus *Myocastor*

Coypu

Myocaster Kerr, 1792. In: Linnaeus, *Anim. Kingdom*, p. 23. Type species: *Mus coypus* Molina, 1782.

The genus is monotypic. Further information is given in the family and species profiles.

Myocastor coypus COYPU (NUTRIA)

Fr. Ragondin; Ger. Nutria

Myocastor coypus (Molina, 1782). *Sagg. Stor. Nat. Chile*, p. 287. Bio Maipo, Chile.

Taxonomy No information available for African populations. See Woods & Kirkpatrick (2005) for details of synonyms and subspecies in natural geographic range of species. Unless otherwise stated, this profile refers to the introduced population in Kenya – the only feral population known on the African continent. Synonyms: eight (world-wide). Subspecies: none in Africa. Chromosome number: $2n = 42$, $FN = 76$.

Description Extremely large shaggy rodent with dark lustrous pelage, long tail and webbed hindfeet. Pelage thick with long coarse guard hairs (dull or shiny) and dense underfur. Dorsal pelage brown, tending to blackish-brown in some individuals; guard hairs thin and long (up to 50 mm), pale or dark brown, usually with pale brown band(s) below tip. Ventral pelage similar to dorsal pelage in colour and texture. Underfur dark brown to black; dense and woolly. Head broad and thickset, similar in colour to dorsal pelage; muzzle and chin with some hairs pale or white or with white tip. Vibrissae very long and coarse. Ears dark, small and rounded. Fore- and hindlimbs short with dark brown or black hairs. Forefeet with five digits; Digit 1 short, Digits 2–5 long, each with long claw and without webbing between digits. Hindfeet long with webbing (skin) between digits, especially between Digits 1–2, 2–3 and 3–4; long claw on all digits. Tail short to long (ca. 72% of HB), with scales, sparsely covered with short dark brown hairs. Skull large and strong; zygomatic arches deep; infraorbital foramen very large; large pointed paraoccipital processes; mandible deep with angular process extending far posteriorly to condylar process and paraoccipital process; dental formula: $I\ 1/1$, $C\ 0/0$, $P\ 1/1$, $M\ 3/3 = 20$; incisor teeth smooth, without grooves, usually orange in colour on outer surface; cheekteeth flattened, converge anteriorly and camber outwards; each cheektooth with complex foldings of dentine and enamel on outer and inner surfaces (Figure 113). Nipples: 4–5 pairs situated dorsolaterally.

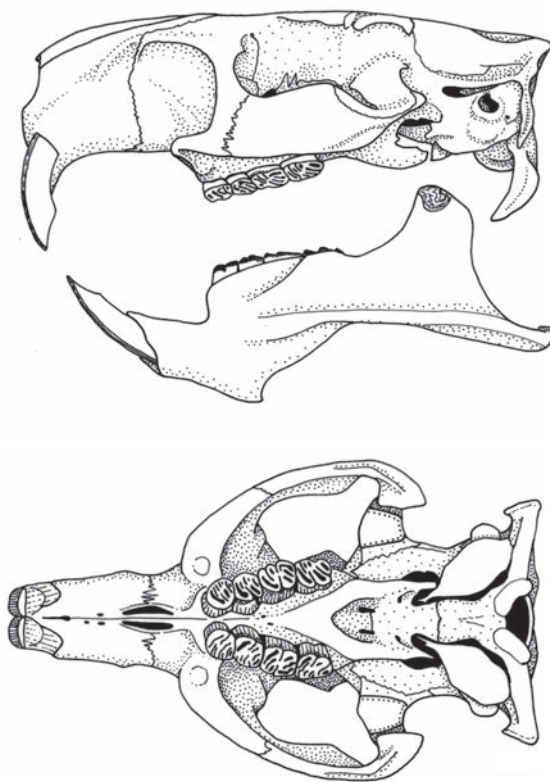


Figure 113. Skull and mandible of *Myocastor coypus* (BMNH 60.1948).

Geographic Variation None recorded in Africa.

Similar Species

Thryonomys swinderianus. HB of similar size, but shorter T (mean 183–188 mm); without webbing on hindfeet; smaller skull (GLS, GWS and P^4-M^3); terrestrial or semi-aquatic.

Thryonomys gregorianus. Smaller in size (mean HB: ca. 375 mm), with much shorter tail (mean 132–144 mm; ca 38% of HB); without webbing on hindfeet; skull smaller; terrestrial or semi-aquatic.

Distribution Introduced. In Africa, recorded only from aquatic habitats in C Kenya. Introduced (as captive animals) at Nanyuki in ca. 1947 (see also below). Later (ca. 1950), some animals were released (or escaped) and gradually spread throughout rivers, dams and swamps of the Central Highlands east of the Rift Valley (Ian Parker in litt.), as well into the Rift Valley at L. Naivasha (ca. 1960). They have been recorded, at various times, from the Ewaso Nyiro and Ewaso Narok rivers on the Laikipia Plateau, Ol Pejeta Conservancy and Mt Kenya Safari Club near Nanyuki, the Ark waterhole in the eastern Aberdare Ranges, near Sagana (possibly), L. Naivasha, L. Ol-Bolosat and near Kiserian (south of Nairobi) (data from many local sources). They have not been recorded from the alkaline lakes Elmenteita and Nakuru in the Rift Valley. Nor, as yet, have they been recorded from the highlands west of the Rift Valley (where the climate is similar to that east of the valley) and where they might be expected to occur. Map not given.

De Vos (1965) recorded that ‘coypu have been established in the wild in Zambia’ (see also Haltenorth & Diller [1980], Lever [1985] and Long [2003]). However, Ansell (1978), commenting on De Vos’ statement, wrote: ‘I am unaware of the basis for this assertion, but even if correct no more appears to have been heard of them.’ Local sources (in litt. 2005/2006) state that there is no evidence for the presence of coypu in Zambia. Haltenorth & Diller (1980) record that ‘from 1960 [coypu] has gone feral in the coastal swamps of Tanzania’ (see their map showing small range in the extreme NE corner of the country). Lever (1985) and Long (2003), both following Haltenorth and Diller (1980), also record the presence of Coypu in Tanzania. However, local sources (2005, with records back to the 1960s) have no knowledge of Coypu in Tanzania. On the basis of the present evidence, it appears that Coypu do not occur in the wild in Zambia or Tanzania. Lever (1985) records, without detail, that Coypu have been farmed in Zimbabwe and South Africa, and have not become feral in these countries. Other authors have also commented on the presence of Coypu in southern Africa. Aliev (1967) records Coypu in Botswana and Zimbabwe (as dots on a map) without comment or reference, and Carter & Leonard (2002) show the presence of Coypu in Zambia, Zimbabwe and Botswana (map, mostly following Aliev 1967) but also comment (as pers. comm. J. du Toit) that the species is not feral anywhere in southern Africa. Local sources in Zimbabwe and South Africa (M. van der Merwe, F. P. D. Cotterill, D. Spears pers. comm. 2007) record that the species is not present (farmed or feral) in these countries. The overall evidence suggests that, at the present time, Coypu are feral only in Kenya.

The natural distribution of the species is South America, but it has been widely introduced into North America, Europe and N Asia (Lever 1985, Long 2003, Woods & Kilpatrick 2005). (Map not given.)

Habitat Rivers, lakes, streams and swamps. Coypu are able to disperse from one aquatic habitat to another when conditions are favourable.

Abundance In Kenya, distribution is patchy. Very numerous in some habitats, e.g. the rivers and dams on the Laikipia plateau (N. Gregory in litt.). One dam at Ol Pejeta Conservancy contained eight individuals (ca. 4/ha; Butynski pers. comm.). Presence and abundance varies seasonally and annually; local populations may become extinct, but recolonization of a habitat may occur when conditions are suitable.

Remarks Aquatic and nocturnal. There are no detailed studies on the species in Kenya; the following remarks refer to populations extralimital to Africa. The webbed hindfeet are adaptations for swimming, and the thick water-repellent pelage helps to maintain a more or less constant core body temperature, especially when the water is cool or cold. Other adaptations for aquatic life include the ability to stay submerged for at least 10 minutes, and to preferentially maintain blood flow, during a dive, to the brain and heart while restricting blood flow to the muscles, intestines and kidney. Vegetarian, feeding on a large variety of aquatic and terrestrial herbs, stems and roots. Often gregarious. Litter-size: usually 3–6 (1–12); young precocial at birth; weaned at Week 8; attain adult weight at ca. 16–18 months (Britain; Southern 1964); maximum longevity in the wild probably 5–6 years. See Woods *et al.* (1992) for a review.

Conservation IUCN Category: Least Concern (worldwide).

Introduced into Kenya to provide pelts (skins) for making coats (see above). Population numbers in Kenya are kept in check by many predators (N. Gregory in litt.). Introduction of Coypu to L. Naivasha, together with the introduction of crayfish and Floating Water-fern *Salvinia molesta* in the 1960s and 1970s, has had dramatic adverse effects on the indigenous aquatic flora (Harper *et al.* 1990); additionally unwise water usage and inappropriate land management of the water catchment of the lake are having detrimental effects on the lake ecosystem. Geographic range is unlikely to expand in Kenya to any great extent because aquatic habitats in a cool climate are required for the survival of the species.

Measurements

Myocastor coypus

HB: 521 (472–575) mm

T: 375 (340–405) mm

HF: 135 (120–150) mm

E: 27 (25–30) mm

WT (♂♂): ca. 6.7 kg

WT (♀♀): ca. 6.36 kg

GLS: 114.2 (102–106) mm

GWS: 68.1 (60–76) mm

P^4-M^3 : 27.8 (22.5–29.3) mm

Locality not stated, presumably North America; sample sizes not recorded (Woods *et al.* 1992)

Key References Woods *et al.* 1992; Woods & Kilpatrick 2005.

D. C. D. Happold

Order *LAGOMORPHA* – *Hares, Rock-hares, Rabbits and Pikas*

Lagomorpha Brandt, 1855.

| | | |
|----------------------------------|----------------------------|--------|
| Leporidae (5 genera, 13 species) | Hares, Rock-hares, Rabbits | p. 694 |
|----------------------------------|----------------------------|--------|

The order Lagomorpha contains two extant families (Leporidae, Ochotonidae), 13 extant genera and about 87 species (Hoffmann & Smith 2005). Of these, only the Leporidae, with five genera and 13 species, is represented in Africa. The order was once considered to be a suborder of rodents (because of the superficial similarity of the teeth). The modern view is that the Lagomorpha is an order in its own right. Based on molecular and morphological evidence, the Lagomorpha and Rodentia may be grouped together in the cohort Glires (see for example Scally *et al.* 2001, Bronner *et al.* 2003). The order is represented naturally in all continents except Antarctica, South America and Australia.

The principal characteristics of the order include: two pairs of upper incisors, the second pair being very small and located behind the first principal pair where they have no cutting function; incisor teeth which grow throughout life and are rooted in the premaxilla bone; no canine teeth; a diastema between the incisors and the cheekteeth (as in rodents and artiodactyls); five or six high-crowned cheekteeth (P¹, P², P³, M¹, M², M³), which may or may not have roots (depending on the family); large caecum; no baculum in the penis; and testes that are anterior to the penis. In size and habitat, members of the two families are rather different. Species of Leporidae are

the largest members of the order (details below), have long narrow upright ears, small fluffy tails, and live in grasslands and scrublands. In contrast, species of Ochotonidae (no longer present in Africa) are small (HB: ca. 125–300 mm, WT: 125–400 g), with small rounded ears close to the head, and most species are associated with rocks and talus (Nowak 1999). All members of the order are terrestrial and vegetarian.

The fossil record of the Lagomorpha in Africa is relatively poor and fragmentary (Cooke 1972). The earliest fossils, from the early Miocene (ca. 20 mya), are ochotonids from Kenya, Uganda, Namibia, Morocco and Libya (Erbajeva 1994, Winkler *et al.* 2005). It is assumed that these ochotonids arrived in Africa from Eurasia. The leporids are first known from Africa in the late Miocene (oldest is 6.5–6.6 mya) of Kenya (Winkler 2002, 2003; Mein & Pickford 2003) and Ethiopia (Haile-Selassie *et al.* 2004). From this time, leporids have radiated extensively (perhaps due to the expansion of grassland). Ochotonids are last known from Africa in the middle Miocene (14–15 mya; Mein & Pickford 2003, Winkler 2003) and now survive only in Eurasia and western North America.

The single family of the Lagomorpha in Africa is the Leporidae. Further details are given in the family profile below.

D. C. D. Happold

Family LEPORIDAE

HARES, ROCK-HARES AND RABBITS

Leporidae Fischer, 1817. Mém. Soc. Imp. Nat. Moscow, 5: 372.

| | | |
|--------------------------------|-----------------|--------|
| <i>Bunolagus</i> (1 species) | Riverine Rabbit | p. 696 |
| <i>Lepus</i> (6 species) | Hares | p. 698 |
| <i>Oryctolagus</i> (1 species) | Rabbit | p. 708 |
| <i>Poelagus</i> (1 species) | Bunyoro Rabbit | p. 710 |
| <i>Pronolagus</i> (4 species) | Rock-hares | p. 712 |

The family Leporidae occurs widely in the Palaearctic, Oriental and Ethiopian Regions, and certain species have been introduced into parts of South America, Australia and New Zealand, and many oceanic islands. Representatives of the family live in arctic, temperate semi-tropical, tropical, semi-arid and arid habitats. There are 11 genera and about 61 spp. in the family of which five genera and 13 species occur in Africa (see above); three of these genera are endemic to Africa (*Bunolagus*, *Poelagus*, *Pronolagus*). See Flux & Angermann (1990), Hoffmann (1993) and Hoffmann & Smith (2005) for further details.

Species in the Leporidae in Africa are easily recognized by their relatively large size for a ‘small mammal’ (mean HB: 300–600 mm, mean WT: 1–3 kg, according to species), which is larger than the majority of rodents, long (or very long) narrow ears, which project upwards from the head, large eyes, small fluffy tail and thick woolly pelage. Other distinguishing characters of the family include two patches of different-textured pelage – the nuchal patch on the back of the neck and the gular patch on the throat and anterior part of the chest, relatively long limbs (hindlimbs usually longer than forelimbs), four or five digits on each foot, and thick dense hairs on the soles of the feet. The skull is lightly built and arched with moderate restriction between the orbits, prominent supraorbital processes, well-developed thick zygomatic arches, maxilla bone with numerous

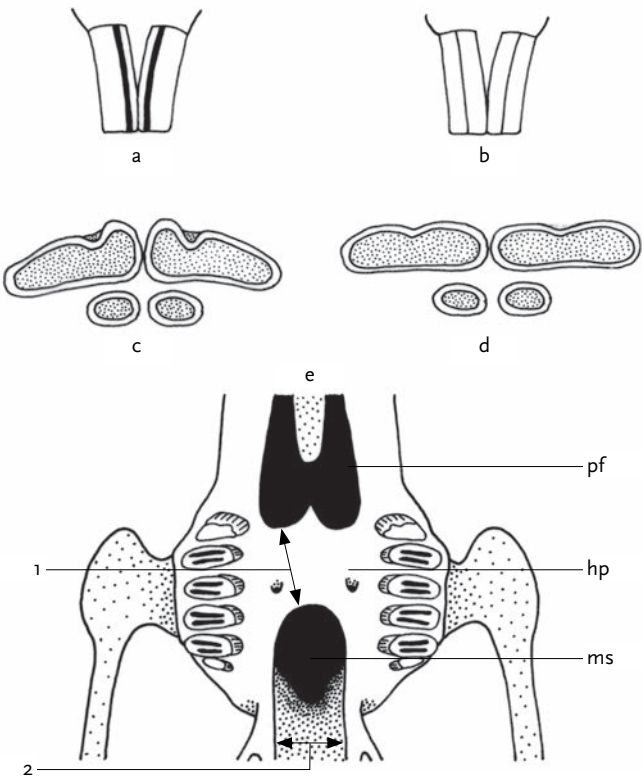


Figure 114. **Selected characters of the skull of Leporidae.** (a) upper front incisor teeth (frontal view) with deep groove filled with cement, (b) upper front incisor teeth (frontal view) with shallow groove not filled with cement, (c) cross-section of (a) above with the smaller second incisor posteriorly, (d) cross-section of (b) above with the smaller second incisor posteriorly, (e) ventral view of part of skull showing ‘minimum length of hard palate’ and ‘width of mesopterygoid space’. pf = palatal foramen, hp = hard palate, ms = mesopterygoid space, 1 = minimum length of hard palate, 2 = width of mesopterygoid space.

Table 48. Genera of Lagomorpha in Africa. Arranged in order of increasing mean length of ear. (n.d. = no data.)

| Genus | E (mean)
(mm)
[E/HF as %] | HB
(mean)
(mm) | T (mean)
(mm) | HF
(mean)
(mm) | E (mean)
(mm)
[E/GLS as %] | Width
mesopterygoid
space (mm) | Minimum
length
hard palate
(mm) | |
|--|----------------------------------|----------------------|------------------|----------------------|----------------------------------|--------------------------------------|--|--|
| <i>Poelagus</i>
(1 sp.) | 65 [67%] | 415 | 56 | 97 | 64.7 [81%] | 6.71 | 7.95 | |
| <i>Oryctolagus</i>
(1 sp.) | 73 [87%] | 368 | 69 | 84 | 73 [98%] | 5.32 | 5.86 | |
| <i>Pronolagus</i>
(4 spp.) ^a | 74 [81%]–94 [102%] | 447–508 | 65–97 | 91–100 | 74 [81%]–94 [116%] | 4.8–5.8 | 6.9–9.5 | |
| <i>Bunolagus</i>
(1 sp.) | 116 [111%] | 429 | 92 | 104 | 116 [146%] | 7.54 | 5.12 | |
| <i>Lepus</i>
(6 spp.) ^a | 88 [92%]–140 [101%] ^b | 452–561 | 68–126 | 95–138 | 88.2 [101%]–140 [139%] | 7.5–10 | 6.0–7.5 | |

^a For genera with more than one species, values for the smallest and largest species are given.

^b Only *L. fagani* has a mean ear length of less than 100 mm, and the smallest values for T and HF.

fenestrae; a small hard palate (= bony palate, palatal bridge); and wide internal choanae (= mesopterygoid space). The skull is also notable for having two pairs of upper incisors, the secondary pair being very small and located behind the first principal pair where they have no cutting function; incisor teeth, which grow throughout life and are rooted in the premaxilla bone; no canine teeth; and well-developed diastema (as in rodents and artiodactyls). There are six high-crowned cheekteeth (P^1 , P^2 , P^3 , M^1 , M^2 , M^3) on each side of the skull and five on each side of the maxilla. The first tooth (P^1) of the upper cheekrow is smaller than the four succeeding teeth (P^2 , P^3 , M^1 , M^2), and the last tooth (M^3) is very small and sometimes missing (Figure 114). Dental formula: $I^{2/1}$, $C^{0/0}$, $P^{3/2}$, $M^{3/3}$ = 28. There is no baculum in the penis, and the testes are situated anteriorly to the penis.

Hares, rock-hares and rabbits are terrestrial, living in open, rocky, grassland or bushy habitats. They are primarily nocturnal, but may be active close to dawn and dusk on cool cloudy days. During the day, hares rest in 'forms' (small open nests in the grass), rock-hares rest in rocky crevices or under boulders, and rabbits hide in complex underground burrows (or 'warrens'), which they dig themselves. All species are noted for their fast quadrupedal running and manoeuvrability, and rock-hares are capable of jumping from rock to rock and running up steep rock faces. All leporids are herbivorous, grazing on short fresh grass and herbs. Digestion of plant tissue is notoriously difficult; in leporids, efficiency of digestion is enhanced by a very large caecum in the hindgut and by coprophagy (a process whereby faecal pellets are eaten and food passes twice through the digestive system).

Hares and rock-hares are solitary, and only occasionally seen in groups of up to three or four. In contrast, rabbits (particularly *Oryctolagus cuniculus*) are gregarious; several individuals share a burrow and may feed in small groups. Most species of hares and rock-hares have small litters, usually 1–3 young/litter; young are precocial at birth, fully furred with the eyes open, and capable of walking and running within a few hours. Rabbits have larger litters, up to 10–12/litter; young are altricial at birth, naked with the eyes closed, and they remain in the nest until 2–3 weeks of age.

The terms 'hare' and 'rabbit' are not clearly defined. However, 'hares' are usually larger than 'rabbits', have comparatively longer hindlimbs, are solitary, run with a fast loping gait, have small litters

and do not dig burrows. 'Rabbits' exhibit a converse set of characters. Some genera do not fit precisely into either 'hare' or 'rabbit' categories, and show a mixture of characteristics. Here, the term 'hare' is used for species that live in non-rocky habitats, do not dig burrows, have small litters and precocial young; 'rabbit' for species that live in non-rocky habitats, dig burrows, usually have large litters and altricial young; and 'rock-hares' for species that live in rocky habitats, do not dig burrows, have small litters and (probably) altricial young. One genus, *Polagus*, shows a mixture of hare and rabbit characteristics.

Taxonomic relationships within the family are uncertain, especially for the genus *Lepus*. Many specific names have been given to the hares of Africa, mainly because some have large geographic ranges and show great variation in colour, size and length of ear in different parts of their ranges. Historically each 'new' form was described as a new species. Current taxonomic methods have reduced the number of species of *Lepus* in Africa to six, some with many synonyms; however, there may be many 'cryptic species' within the species currently allocated to *Lepus*. Molecular analysis confirms that leporids are a monophyletic group (Robinson & Matthee 2005) and speciation into the major clades occurred 3–6 millions years ago. Within Africa, the alternating periods of wet and dry climates and the concomitant expansion and contraction of forests and savannas has been an important factor in leporid evolution.

The genera are distinguished by selected body and skull characters, chromosome number and geographic distribution (see Table 48). African hares and rabbits range in HB size from 368–432 mm (small), 433–496 mm (medium-sized) to 497–561 mm (large). Tail length ranges from 56–79 mm (short), 80–103 mm (medium-sized) to 104–127 mm (long). Ear length ranges from 65–90 mm (short), 91–115 mm (medium-sized) to 116–140 mm (long). Ear length relative to GLS ranges from 77–100% (relatively short), 101–123% (medium relative length) to 124–146% (relatively long). The ratio of the mean width of the mesopterygoid space to the mean minimum length of the hard palate (abbreviated to MS/HP) ranges from 52–84% (low), 85–117% (medium) to 118–149% (high). All of the above categories are based on means.

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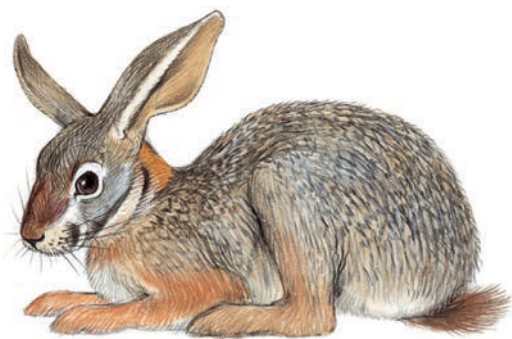
| MS/HP (as %) ^c | Chromosome number | Incisor teeth | Notes |
|---------------------------|-------------------|---|--|
| 80 | n.d. | Deep groove, no cement | Central Africa |
| 90 | 2n = 44 | Deep groove, no cement | North Africa (islands off South Africa) |
| 30–80 | 2n = 42 | Deep groove, no cement | Southern and eastern Africa |
| 150 | 2n = 44 | No cement | South Africa only. Dark stripe from mouth to base of ear |
| 100–150 | 2n = 48 | Deep groove, with cement (except <i>L. starki</i>) | Throughout Africa |

^c For MS = width of mesopterygoid space, HP = minimum length of hard palate (see Figure 114e).

GENUS *Bunolagus*

Riverine Rabbit

Bunolagus Thomas, 1929. Proc. Zool. Soc. Lond. 1929: 109. Type species: *Lepus monticularis* Thomas, 1903.



Bunolagus monticularis.

A monotypic genus occurring only in South Africa in bushy habitats close to streams and rivers. The genus is characterized by long ears (longer than in *Pronolagus*), a dark stripe on the lower jaw from near mouth to base of ear, soft silky hairs on soles of feet, uniformly coloured tail, and hard palate shorter than width of mesopterygoid space. *Bunolagus* exhibits significant difference in karyotype which separates it clearly from *Lepus* (Robinson & Skinner 1983): there are fewer chromosomes ($2n = 44$) than in *Lepus* ($2n = 48$). Of the species of Lagomorpha examined, this species has the most derived karyotype, differing from the hypothesized ancestor by seven fusions and five fissions (Robinson *et al.* 2002). Further details are given in the species profile.

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Bunolagus monticularis RIVERINE RABBIT

Fr. Lapin des Boschimans; Ger. Flusskaninchen (Buschmannhase)

Bunolagus monticularis (Thomas, 1903). Ann. Mag. Nat. Hist., ser. 7, 11: 78. Deelfontain, Cape Colony, South Africa.

Taxonomy Originally described in the genus *Lepus*. Synonyms: none. No subspecies. Chromosome number: $2n = 44$ (Robinson & Skinner 1983).

Description Small dark rabbit with long ears. Pelage soft and fluffy. Dorsal pelage grizzled (agouti) blackish-brown, without rufous patch on rump; hairs grey at base, with white subterminal band and black tip. Flanks similar to dorsal pelage, becoming rufous on lower flanks. Ventral pelage white or pale rufous, usually confined to narrow band on mid-ventral line. Nuchal patch rich rufous. Head similar to dorsal pelage, with conspicuous white or pale buff eye-ring; white or buff colouration may extend anteriorly to nasal region. Thin brown or black stripe along lower jaw to base of ear. Ears comparatively and relatively long, broad, inner margin lined with white hairs, tips rounded and bordered by short black hairs on outer surface. Forelimbs similar colour to flanks; soles of forefeet with thick dense pale rufous hairs. Hindlimbs similar colour to flanks; hindfoot medium brown above, pale rufous-brown below; soles of forefeet with thick dense pale rufous hairs. Tail medium-sized, dark brown; hairs long and fluffy, slightly grizzled, without any white hairs. Skull characteristics include: GLS comparatively short; minimum length of hard palate comparatively short; MS/HP ratio high (ca. 147%); lacks antero-external shoulders on zygoma (cf. other African lagomorph genera); single groove on each principal upper incisor tooth not filled with cement (Figure 115, see also Table 48). Nipples: not known.

Geographic Variation None recorded.

Similar Species

Lepus capensis. Dorsal pelage grizzled, greyish, less fluffy; tail black above, white below; no black stripe on lower jaw; groove on each upper incisor filled with cement; grassy habitats.

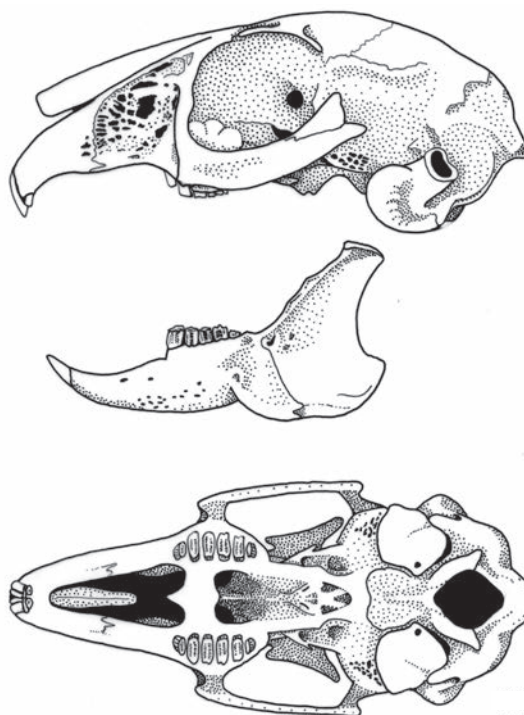


Figure 115. Skull and mandible of *Bunolagus monticularis* (BMNH 2.12.1.26).



Bunolagus monticularis

Pronolagus spp. Pelage dense and harsh; tail uniformly rufous or rufous-black; ears relatively short or medium-sized; no black stripe on lower jaw; rocky habitats.

Distribution Endemic to Africa. South-West Arid (Karoo) BZ. Restricted to a small area in Northern and Western Cape Provinces, South Africa (Districts of Victoria West, Beaufort West Sutherland, Calvinia, Touws River and Frazerburg; additional details in Duthie *et al.* 1989).

Habitat Thick riverine bushland along seasonal rivers, especially where *Sasola glabrescens* and *Lycium* spp. predominate. In this habitat, grasses are uncommon and represent only about one-fifth of the cover provided by dicotyledonous plants (Duthie *et al.* 1989). The habitat is shared with Cape Hares (*Lepus capensis*).

Abundance Uncertain, but rare with a very small geographic range. Two censuses suggested densities of 0.064–0.166 individuals/ha, i.e. about one individual/6–15 ha. Extrapolation of these figures suggests that, in 1989, the remaining suitable habitat could not support more than ca. 1500 individuals (Duthie 1989, in Duthie & Robinson 1990), although the current population size is estimated to be less than 250 mature individuals (IUCN Red List 2004).

Adaptations Terrestrial and nocturnal. Constructs burrows with length of 200–300 mm, and entrance of 90–115 mm wide; nest chamber (120–170 mm wide) is formed at end of burrow. Burrow entrance plugged with soil and twigs when not in use. Locomotion rather slow compared with other leporids (Robinson 1981b).

Foraging and Food Herbivorous. Forages by browsing on flowers and leaves of dicotyledons, particularly *Pteronia erythrocaetha*, *Kochia pubescens*, *Salsola glabrescens*, *Rosenia humilis* and several species

of the Mesembryanthemaceae. Grasses are eaten only when available in the wet season (Duthie 1989, in Duthie & Robinson 1990).

Social and Reproductive Behaviour Solitary with a polygamous mating system. Mean home-range for ♂♂ is 20.9 ha and for ♀♀ is 12.9 ha; home-range of a ♂ can overlap with that of several ♀♀ (Duthie 1989, in Duthie & Robinson 1990). Young born in nest lined with fur and grass in a burrow, rather similar to that of the European Rabbit.

Reproduction and Population Structure Reproductive season extends from Aug to May during the warmer seasons of the year. Litter-size: one (occasionally two). Females may have a postpartum oestrus. At birth, young weigh ca. 40 g. Like other species of rabbits, the young are born altricial, blind and helpless at birth, and will only leave the burrow when old enough to look after themselves.

Predators, Parasites and Diseases Little information. Predators include African Wild Cats *Felis silvestris*, domestic dogs and Cape Eagle-owls *Bubo capensis*.

Conservation IUCN Category: Critically Endangered.

The rarest of all African lagomorphs, and the only African lagomorph placed in this IUCN category. Before 1948 was seen commonly, but in recent years has become increasingly rare (Robinson 1981b, Duthie *et al.* 1989). Much of the former range (never large) is now used for cultivation (Duthie & Robinson 1990). Rarity is presumed to be due mainly to habitat changes and a reduction in the area of suitable habitat; in addition, reduction in the numbers of jackals has resulted in an increase in the numbers of Wild Cats *Felis libyca* and Caracals *Felis caracal*, which prey on Riverine Rabbits (Robinson 1981b). The species is now the focus of various conservation programmes.

Measurements

Bunolagus monticularis

HB: 429 (337–470) mm, n = 14

T: 92 (70–108) mm, n = 13

HF: 104 (90–120) mm, n = 15

E: 116 (107–124) mm, n = 15

WT: n. d. (ca. 1.0–1.5 kg)

GLS: 79.7 (78.5–81.5) mm, n = 6

GWS: 36.3 (35.8–37.9) mm, n = 6

P²–M³: 11.62 (11.2–11.9) mm, n = 6

Mesopterygoid space (width): 7.5 (7.2–7.8) mm, n = 6

Hard palate (minimum length): 5.1 (4.4–5.7) mm, n = 6

Upper principal incisor width: 2.0 (1.9–2.0) mm, n = 5

Bulla width: 9.0 (8.3–9.6) mm, n = 5

South Africa

Body measurements: Smithers 1983

Skull measurements: TM

Key References Duthie & Robinson 1990; Duthie *et al.* 1989; Robinson & Skinner 1983; Thomas 1903.

D. C. D. Happold

GENUS *Lepus*

Hares

Lepus Linnaeus, 1758. Syst. Nat., 10th edn, 1: 57. Type species: *Lepus timidus* Linnaeus, 1758.



Lepus saxatilis.

The genus *Lepus* contains the largest number of species of any genus in the order Lagomorpha: about 32 spp. worldwide (Hoffmann & Smith 2005), six of these occurring in Africa. Members of the genus occur widely in arid, semi-arid and savanna habitats throughout the African continent. Two species (*Lepus capensis*, *L. victoriae*) have particularly large geographic ranges. Usually only one or two species occur in a single region (here often separated by habitat considerations), but three species are sympatric or syntopic on the Ethiopian Plateau and the Horn of Africa.

Species in the genus are characterized by their long limbs (especially the hindlimbs), their fast movement (the fastest of all

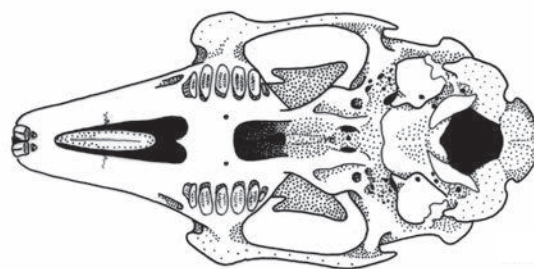
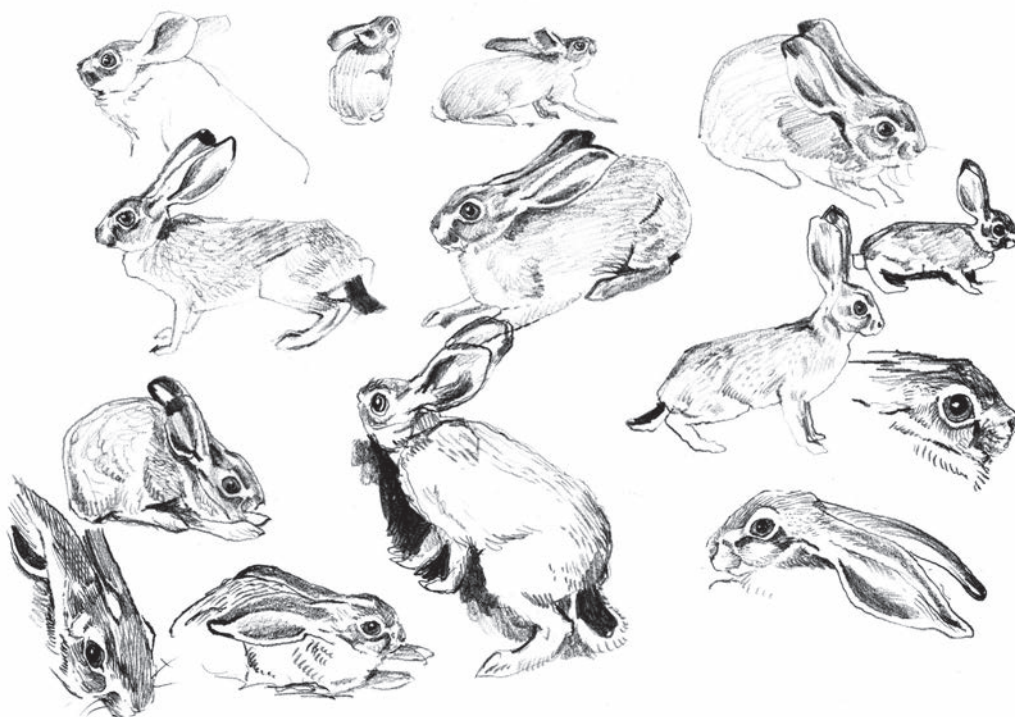


Figure 116. Skull and mandible of *Lepus victoriae* (RMCA 92-149-M-0010, as *Lepus crawshayi*).



Lepus capensis.

the lagomorphs) and their comparatively and relatively medium-sized to long ears (except comparatively short in *L. fageni*). Skull characteristics include: mean GLS > 87 mm (longer than other African lagomorphs except *Pronolagus crassicaudatus* and *P. randensis*); minimum length of hard palate short or medium-sized; MS/HP ratio high (except in *L. fageni*) as in *Bunolagus*; antero-external shoulders present on zygoma; single groove on each principal upper incisor tooth filled with cement (except *L. starki*, cf. all other African lagomorph genera) (Figure 116, Table 48). Species of *Lepus* live in open grassland and bushland habitats, and are not associated with rocks. They do not dig burrows. During the day they rest in ‘forms’ in the open, and they remain motionless to avoid detection. Young are precocial at birth, fully furred, the eyes are open, and they are capable of running within a few hours of birth. Hares are solitary, and associate with other hares only for courtship and mating, and when several congregate at highly favoured feeding areas.

The taxonomy of the genus is controversial (see also order profile). Species of the genus that have large geographic ranges show great variation in overall size, pelage colour and length of ear. The two particularly widespread species in Africa, *L. capensis* and *L. victoriae*, each have many synonyms, testimony to the large variation within each

species. Taxonomic uncertainties are exemplified by (a) some forms (now synonyms) that may be valid species, (b) currently recognized species that may in fact not be valid species, e.g. *L. habessinicus* may be a subspecies of *L. capensis* (Azzaroli-Puccetti 1987a, Flux & Angermann 1990), and (c) different viewpoints on what is the correct name for a species, e.g. *L. victoriae* (see Hoffmann 1993) is considered to be *L. microtis* by Hoffmann & Smith (2005) – although the name *microtis* is considered to be *nomina dubia* by Petter (1972c) because the holotype is a young animal. The genus is in need of revision. It is not possible to identify hares (or indeed lagomorphs in general) using only one or two characters; a combination of many characters, and ratios between selected measurements, are required for precise identification (Azzaroli-Puccetti 1987a, b). Chromosome numbers do not vary across the world range, but DNA analyses seem likely to resolve many taxonomic problems in the future (Alves *et al.* 2003).

The six species in the genus in Africa are distinguished by body size, ratio of width of mesopterygoid space to minimum length of hard palate, amount of black colouration on tip of ear, shape of groove on principal incisor tooth and presence/absence of cement in that groove.

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Lepus capensis CAPE HARE

Fr. Lièvre du Cap; Ger. Kap-Hase

Lepus capensis Linnaeus, 1758. Syst. Nat., 10th edn, 1: 58. ‘ad Cap. b. Spei’ (Cape of Good Hope, South Africa).

Taxonomy Specimens of this species from Kenya are almost identical to those of *L. victoriae* where the two species are parapatric or sympatric (Flux & Flux 1983, as *L. crawshayi*). A similar situation occurs in Somalia where some specimens have been difficult to identify and appear to exhibit characters intermediate between the two species (Azzaroli-Puccetti 1987a). Because of its widespread distribution and inter-population variation, many forms of *L. capensis* have been described; these were originally given species rank but are now considered to be synonyms even though some of them may yet prove to be valid species (Flux & Angermann 1990). Synonyms: 38 African synonyms are listed by Hoffmann & Smith (2005), of which the following are considered by them to be subspecies: *aegyptius*, *aquilo*, *carpi*, *granti*, *hawkeri*, *isabellinus*, *sinaiticus*. The taxonomic limits of this species, and its relationships with *L. victoriae*, are uncertain, and require detailed investigation. Subspecies: none recognized here. Chromosome number: probably $2n = 48$ (Robinson 1981a).

Description Medium-sized. Pelage soft, not as ‘fluffy’ as in *Pronolagus* spp. and *Bunolagus*. Dorsal pelage silvery-grey, grizzled (agouti) with black; hairs white at base with wide black subterminal band, whitish terminal band, and black or white tip. Underfur white or greyish-white. Flanks similar to dorsal pelage, becoming very pale buff on lower flanks. Ventral pelage pure white; long. Head similar in colour to dorsal pelage. Lateral profile of head (from forehead to nasal region) distinctly angular (i.e. with obtuse bend downwards above the eye (cf. smoothly convex in *L. victoriae*) (Flux & Flux 1983). Eye-ring white, often with rufous markings above and below eye-ring. Cheeks greyish-brown. Upper lips pale rufous. Chin and throat white. Gular collar buffy-white or buffy. Ears relatively long (ca. 142% of GLS),

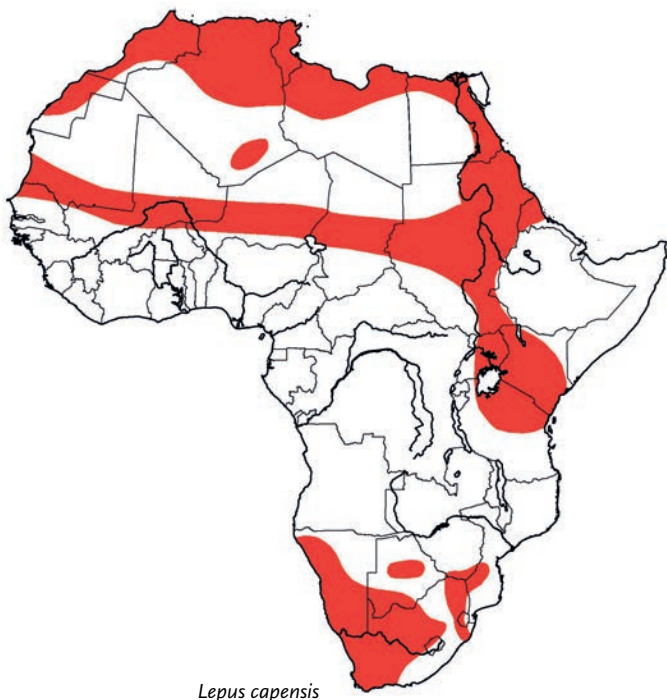
finely covered with buffy hairs; inner margin fringed with long white hairs; outer margin fringed with very short white hairs; tip of ear rounded, fringed with short black hairs especially on outer surface. Nuchal patch brownish-pink; rather inconspicuous. Forelimbs pale rufous above, white below. Hindlimbs pale rufous. Soles of all feet with buffy-brown hairs. Tail comparatively long, fluffy, black above, white laterally and below. MS/HP ratio high (ca. 140%). Each principal incisor tooth with small groove filled with cement.

Geographic Variation Pelage colour varies through range (and hence many synonyms). Individuals from arid and semi-arid habitats are paler in colour (dorsal pelage beige, oatmeal, with only a small amount of black speckling) than those from more mesic habitats (see Description above). Length of ear and hindfoot increase with increasing aridity of the habitat (see table below; BMNH):

| Form (n) | Locality | HF (mm) | E (mm) | Ratio E/HF % |
|------------------------|----------------|---------|---------|--------------|
| <i>aethiopicus</i> (5) | E Sudan | 80–102 | 110–118 | 114–132 |
| <i>hawkeri</i> (5) | W Sudan | 99–104 | 93–106 | 93–102 |
| <i>sefranus</i> (3) | Algeria | 99–110 | 100–112 | 91–113 |
| <i>whitakeri</i> (7) | Niger, Algeria | 95–114 | 117–135 | 114–127 |

Similar Species

L. victoriae. Dorsal pelage brown, grizzled with black; lateral profile of head smoothly convex; nuchal patch orange/brownish-orange; scrub, bush and grassland habitats.



L. saxatilis. Dorsal pelage grizzled dark buffy-brown; ears with narrow band of black on tip; nuchal patch large, pale rufous; soles of feet dark rufous; open and scrub habitats; southern Africa only.

Distribution Widespread in Mediterranean Coastal, Sahel Savanna and Somalia–Masai BZs, and several BZs in southern Africa. Recorded in two regions: (1) savanna and semi-desert regions of South Africa, Namibia, Botswana, S Zimbabwe, S Angola and S Zambia; (2) Kenya, Somalia and Ethiopia, and throughout much of the dry savanna regions of central, western and northern Africa, including parts of the Sahara Desert. Not present in rainforest habitats. There is a gap in distribution in eastern Africa (S Tanzania, Malawi, N Zimbabwe, parts of Mozambique). Extraliminally occurs throughout most of the Middle East and eastwards north of Himalaya Mts to China.

Habitat Grasslands and open habitats, including *Acacia* and *Brachystegia* savanna, Sahel and Sudan savanna, and semi-desert. Avoids bush habitats. Cape Hares are extremely adaptable and live in many environments. Prefer open habitats to closed habitats (cf. *L. victoriae*), and move into burnt areas when grasses begin to sprout. Hence, the range of Cape Hares has increased with bush clearance and extensive savanna fires (Flux & Flux 1983).

Abundance Probably the commonest lagomorph in Africa. Densities of 4.7–24.8 hares/km² have been recorded in South Africa (Wessels 1978 in Flux & Angermann 1990), and densities of 4.2 hares/km² (short grass habitats) to 9.2 hares/km² (long grass habitats) in Serengeti N. P., Tanzania (but see *L. victoriae* for further comments). Significantly fewer hares are observed with increasing number of larger mammals (Eltringham & Flux 1971).

Adaptations Terrestrial and nocturnal. During the day Cape Hares rest in ‘forms’ (as do other *Lepus* spp.) but may feed during the day when overcast. When disturbed, they run into the open (not

into cover as do *L. victoriae*) (Flux & Flux 1983). Cape Hares may be affected by larger mammals in the same way as *L. victoriae*, but detailed information is lacking. Cape Hares may assist dispersal of seeds for those species that have seeds with hooks or barbs. Agnew & Flux (1970) list 17 species of plants (mainly grasses) that have been found attached to the pelage of hares. The commonest seed was *Tragus berteronianus* (76% of seeds), followed by *Achyranthes aspera*, *Pupalia lapacea* and *Boerhavia repens* (all <1%). Only about half the hares examined carried seeds; for hares that carried seeds, the mean number of seeds/hare was 3.3 for ♀♀ and 1.2 for ♂♂; and rarely did any hare carry more than 20 seeds.

Foraging and Food Herbivorous. Grazes at night on grasses. Analysis of faecal pellets from dead specimens at Magadi (in the Rift Valley, Kenya) was dicotyledons 20%, grass (epidermis) 34%, sedge 2% and ‘stem fibres’ 35%. The principal grasses were *Sporobolus* sp., *Aristida* sp., *Chloris* sp., *C. dactylon*, *Enneapogon* sp. and *Eragrostis* sp. There were differences in the proportion of each grass species eaten at different sites, but seasonal differences in diet at each site were surprisingly small even though there were marked wet and dry seasons. It appears that hares are reasonably opportunistic, eating different grass species according to availability (Stewart 1971c).

Social and Reproductive Behaviour Mainly solitary; very occasionally in small groups. In Kenya, only four groups of three animals were encountered in 800 animals observed (Flux 1981b).

Reproduction and Population Structure Reproductive activity varies in different localities. In Kenya near the Equator, ♂♂ are fecund and ♀♀ are pregnant in all months (Flux 1969, 1981a). Pregnancy rate is 80–100% for most months of the year except in Apr (wettest month of the year) and Jun–Jul (end of wet season). Mean litter-size 1.5. Weight of young at birth: ca. 100 g. Number of litters/year: 6–8. Mean number of young/year: 11.6 (equivalent to 55% of adult female weight – a high percentage by lagomorph standards, but not as high as for *L. victoriae*). Mean litter-size varies seasonally: 1.0 in Sep to 1.9 in Jan, probably in response to changes in rainfall and forage. Litter-size also varies by altitude: hares at higher altitudes having smaller litters (mean 1.24 at 1800 m) than those at lower altitudes (mean 1.75 at 600 m). Growth rate of young hares: ca. 10 g/day. Adult size attained in 4–5 months (Flux & Jarvis 1970).

In Botswana, pregnant ♀♀ were found in Feb, Jun and Nov (only seven months sampled) but there are indications that hares continue to breed even in drought years (Smithers 1971). Litter-size: 1.9 (1–3); singletons 4, twins 6, triplets 3. See also *L. victoriae*.

Predators, Parasites and Diseases In Serengeti N. P., predators include Black-backed Jackals *Canis mesomelas*, Golden Jackals *Canis aureus*, Leopards *Panthera pardus*, Caracals *Caracal caracal* and Cheetahs *Acinonyx jubatus* as well as avian predators.

Conservation IUCN Category: Least Concern.

Widespread and common especially in reserved areas.

Measurements

Lepus capensis

HB: 478 (445–550) mm, n = 19

T: 117 (100–145) mm, n = 19
 HF: 119 (110–138) mm, n = 19
 E: 124 (110–140) mm, n = 19
 WT: 2.04 (1.70–2.45) kg, n = 19
 GLS: 87.6 (84.9–89.4) mm, n = 5
 GWS: 39.7 (38.4–40.5) mm, n = 5
 P²–M³: 13.0 (12.6–13.5) mm, n = 5
 Mesopterygoid space (width): 8.4 (8.1–8.6) mm, n = 5
 Hard palate (minimum length): 6.0 (5.5–6.4) mm, n = 5

Upper principal incisor width: 2.7 (2.4–3.0) mm, n = 5
 Bulla width: 9.0 (8.4–9.4) mm, n = 5
 Body measurements and weight: Cape Province, South Africa (Smithers 1983)
 Skull measurements: Cape Province, South Africa; TM

Key Reference Flux & Angermann 1990.

D. C. D. Happold

Lepus fagani ETHIOPIAN HARE

Fr. Lièvre éthiopien; Ger. Äthiopischer Hase

Lepus fagani Thomas, 1903. Proc. Zool. Soc. Lond. 1902 (2): 315 [1903]. Zegi, L. Tsana (= L. Tana), Ethiopia. 4000 ft (1220 m).

Taxonomy Taxonomic status uncertain; possibly a subspecies of either *L. victorae* or *L. capensis* (Flux & Angermann 1990). Considered to be closely related to *L. saxatilis* and *L. victorae*, and sometimes to be part of a *L. victorae*/*L. saxatilis* complex. However, Azzaroli-Puccetti (1987a) considered *fagani* to be a distinct species because its characters are unusually uniform throughout its geographic range. *Lepus fagani* is geographically isolated (on the mountains of Ethiopia north of the Rift Valley) from populations of *L. capensis* in the surrounding lowlands, and Flux & Angermann (1990) suggest that this probably resulted in the evolution of *L. fagani* as a distinct species. Following Azzaroli-Puccetti (1987a, b), Flux & Angermann (1990) and Hoffmann & Smith (2005), *L. fagani* is maintained here as a valid species. Synonyms: none. Chromosome number: probably 2n = 48 (as in all other *Lepus* spp.).

Description Large lagomorph with dense rather coarse pelage; dorsal hairs 20–25 mm. Dorsal pelage brownish-buff, finely grizzled (agouti) with black; hairs pale grey at base, white subterminal band, buff terminal band and (usually) black tip. Underfur whitish-grey. Flanks buff; hairs white at base, buff (not black) at tip. Ventral pelage white, fluffy. Head darker than dorsal pelage, blacker on crown. Chin and throat white. Ears comparatively short (cf. other Ethiopian hares – *L. habessinicus* and *L. starcki*) but of medium relative length (ca. 101% of GLS), buffy, with buff fringe on upper outer margin, white or buff fringe on lower outer margin; narrow black rim around inner surface of tip. Nuchal patch rich cinnamon-ginger extending on to sides of neck. Forelimbs cinnamon-brown; soles of forefeet with blackish-brown hairs. Hindlimbs brownish-buff above, white below; soles of hindfeet with blackish-brown or ginger-brown hairs. Tail medium-sized, fluffy, black above, buff at sides, buffy-white below. MS/HP ratio medium (ca. 99%). Each principal incisor tooth with deep simple groove entirely filled with cement; front face of each upper incisor tooth slopes laterally, thus forming an angled anterior surface.

Geographic Variation None recorded.

Similar Species

L. habessinicus. Dorsal pelage soft; ears longer; tail on average longer; Ethiopian plateaux and Horn of Africa.
L. starcki. Ears longer, upper quarter conspicuously black; tail longer;

principal upper incisor with groove not filled with cement; Ethiopian plateaux both sides of Rift Valley.

L. capensis. Pelage grizzled greyish; ears longer; nuchal patch brownish-pink, rather inconspicuous; open grasslands and semi-arid habitats; widespread.

Distribution Endemic to Africa. Afromontane–Afroalpine BZ of Ethiopia, and extending marginally into Sudan Savanna BZ. Recorded from the Ethiopian Plateau region west of the Rift Valley, mainly at 500–2500 m. Possibly also recorded from SE Sudan and extreme NW Kenya (Yalden *et al.* 2003; Flux & Angermann 1990; not mapped).

Habitat Scrub and forest margins; preferred habitat is less open than that of *L. habessinicus*, and similar to that preferred by *L. victorae* in Kenya (Yalden *et al.* 1986). ‘Wet grasslands with scattered thickets’ and ‘Bush cultivated area’ (labels, BMNH).



Lepus fagani

Remarks Apparently no other information available.

Conservation IUCN Category: Data Deficient.

Measurements

Lepus fagani

HB: 506 (450–540) mm, n = 5

T: 68 (50–82) mm, n = 4

HF: 95 (90–110) mm, n = 5

E: 88.2 (81–95) mm, n = 5

WT: n. d.

GLS: 87.6 (83.3–90) mm, n = 5

GWS: 40.8 (39.9–42.2) mm, n = 5

P²–M³: 16.4 (15.7–16.9) mm, n = 5

Mesopterygoid space (width): 7.5 (6.4–8.5) mm, n = 5

Hard palate (minimum length): 7.5 (6.9–8.2) mm, n = 5

Upper principal incisor width: n. d.

Bulla width: n. d.

Ethiopia (Azzaroli-Puccetti 1987a)

Key References Azzaroli-Puccetti 1987a; Flux & Angermann 1990; Yalden *et al* 1986.

D. C. D. Happold

Lepus habessinicus ABYSSINIAN HARE

Fr. Lièvre d'Abyssinie; Ger. Abessinischer Hase

Lepus habessinicus Hemprich and Ehrenberg, 1832. Symbolae Puhsciae, Mamm., dec 2; sheet P, pl. 15, fig. 2. Near Arkiko, Ethiopia.

Taxonomy Status of this species uncertain; related to *L. capensis* (Azzaroli-Puccetti 1987b). Angermann (1983) and Hoffmann (1993) list *habessinicus* as a synonym of *L. capensis*. In contrast, Petter (1963a, 1972c), Yalden *et al.* (1986), Azzaroli-Puccetti (1987a, b) and Flux & Angermann (1990) consider *habessinicus* to be a valid species on account of its larger ears, well-developed interparietal bone, larger bullae and its isolation in the Horn of Africa. Flux & Angermann (1990) and Azzaroli-Puccetti (1987a), although recording *L. habessinicus* as a species, suggest that when other evidence is available, *habessinicus* may prove to be a subspecies or synonym of *L. capensis*. Because the evidence is still equivocal, Hoffmann & Smith (2005) retain *L. habessinicus* as a valid species. Synonyms: *abyssinicus*, *berberensis*, *cordeauxi*, *crispit*, *somaliensis*, *tigrensis*. Subspecies: none. Chromosome number: 2n = 48, aFN = 88 (as in all other *Lepus* spp.) (Azzaroli-Puccetti *et al.* 1996).

Description Medium-sized lagomorph with conspicuously long ears. Pelage soft and dense; dorsal hairs up to 20 mm. Dorsal pelage silvery-grey, grizzled (agouti) with varying amounts of black on shoulders, back and rump; dorsal hairs greyish-white at base, with broad black subterminal band, and buff or silvery-white terminal band, often with black tip. Grey underfur. Flanks paler; hairs pure white at base, subterminal band narrower than on dorsal pelage, whitish-buff at tip. Lower flanks very pale. Ventral pelage pure white, less dense than dorsal pelage; fluffy. Wide cinnamon or rufous stripe from forelimbs to hindlimbs separate ventral colour from flanks. Head similar in colour to dorsal pelage; nasal region and cheeks silvery-white, finely grizzled (agouti). Whitish eye-ring in some individuals. Chin grey or whitish. Ears relatively long (ca. 130% of GLS) and wide, brown or silvery-brown on outer surface, whitish-buff on inner surface; white fringe on lower part of outer margin; narrow black rim around tip of ear. Nuchal patch pale brownish-cinnamon, not extending laterally onto sides of neck. Forelimbs long, brownish-cinnamon above, pale whitish-buff below. Hindlimbs long, silvery-grey, grizzled (agouti) with black above, white or pale cinnamon-rufous below. Hindfeet cinnamon above and below. Soles of all feet with dense cinnamon hairs. Tail medium-sized, pure black above, pure white on sides and below. MS/HP



Lepus habessinicus

ratio high (ca. 125%). Each principal incisor with a deep groove entirely filled with cement.

Geographic Variation Pelage varies geographically: sandy-coloured in Eritrea, and greyer on Ethiopian plateau (*tigrensis*); probably related to soil colour (Yalden *et al.* 1986).

Similar Species

L. starki. Ears with upper quarter conspicuously black; principal upper incisor with groove not filled with cement; Ethiopian plateaux only.

L. fagani. Pelage coarse; ears shorter; Ethiopian plateaux.

L. victoriae. Dorsal pelage brown, grizzled with black; ears relatively shorter; ear tip black on inner and outer surfaces (amount of black variable); nuchal patch orange to brownish-orange; allopatric.

Distribution Endemic to Africa. Somalia–Masai Bushland BZ (and possibly some parts of Afroalpine–Afromontane BZ in Ethiopia). Recorded from E Ethiopia, Eritrea, Djibouti, N and C Somalia, and perhaps extreme NE Kenya. A record from Kamisa, Dinder R., E. Sudan mapped by Yalden *et al.* (1986) refers to a record by Setzer (1956) of *L. capensis dinderus* which they considered to represent *L. habessinicus*.

Habitat Desert and semi-desert from sea level to 2000 m; may extend up 2500 m on arid NE plateau of Ethiopia/Eritrea (Yalden *et al.* 1986).

Abundance Widespread, locally very common in Djibouti (Laurent & Laurent 2002).

Remarks Apparently no other information available.

Conservation IUCN Category: Least Concern.

Measurements

Lepus habessinicus

HB: 452.4 (400–550) mm, n = 12

T: 85.1 (75–100) mm, n = 10

HF: 107.5 (100–118) mm, n = 12

E: 112.7 (105–121) mm, n = 11

WT: n. d.

GLS: 86.8 (82.2–91.8) mm, n = 11

GWS: 39.1 (32.7–41.1) mm, n = 10

P²–M³: 14.4 (12.7–15.7) mm, n = 10

Mesopterygoid space (width): 7.8 (6.5–8.8) mm, n = 11

Hard palate (minimum length): 6.2 (5.5–6.9) mm, n = 11

Upper principal incisor width: 2.7 (2.4–3.1) mm, n = 4

Bulla width: 12.4 (11.7–13.2) mm, n = 4

Ethiopia (Azzaroli-Puccetti 1987a; BMNH)

Key References Azzaroli-Puccetti 1987a; Yalden *et al.* 1986.

D. C. D. Happold

Lepus saxatilis SCRUB HARE

Fr. Lièvre des buissons; Ger. Busch-Hase

Lepus saxatilis F. Cuvier, 1823. Dict. Sci. Nat. 26: 309. (Cape of Good Hope, South Africa.)

Taxonomy The taxonomic relationship between this species and *L. victorae* is uncertain. *Lepus saxatilis* and *L. victorae* are conventionally viewed as allopatric. Smithers (1983) considered *L. saxatilis* and *L. victorae* (as understood here) to be a single species, *L. saxatilis*, and therefore his distribution map for *L. saxatilis* combines the ranges of both species. Here, following Flux & Angermann (1990), Hoffmann (1993) and Hoffmann & Smith (2005), *L. saxatilis* is limited to the larger southern African form, and *L. victorae* to the smaller form to the north (Kryger *et al.* 2004).

Evidence from mtDNA suggests *L. saxatilis* comprises three lineages (Kryger *et al.* 2004). One lineage, long isolated and confined to SW South Africa (mainly Western Cape and Northern Cape Provinces), may be specifically distinct and is referred to here as *L. s. saxatilis*. The second lineage occurs in C and SE South Africa (mainly Eastern Cape and parts of Free State and KwaZulu–Natal Provinces) and the third lineage occurs in N South Africa, Namibia, Botswana and SW Zimbabwe. Together, these two lineages contain at least seven of the forms listed below as synonyms. For convenience, the second lineage is referred to here as *L. cf. saxatilis*. The third lineage is not referred to by any name in this profile, and its distribution is not included in the map. Synonyms of *L. saxatilis (sensu lato)*: *aurantii*, *bechuanae*, *chiversi*, *chobiensis*, *damarensis*, *fumigatus*, *gungunyanae*, *khanensis*, *longicaudatus*, *megalogotis*, *ngamiensis*, *nigrescens*, *orangensis*, *rufinucha*, *subrufus*, *timidus*. Subspecies: none recognized here. Chromosome number: probably 2n = 48 (as in other *Lepus* spp.).

Description *Lepus saxatilis* is medium to large with medium to long broad ears. Pelage soft. Dorsal pelage dark buffy-brown, grizzled (agouti) with black; hairs buff at base, with black subterminal band, buff terminal band and black tip. Underfur greyish-white. Flanks paler than dorsal pelage. Ventral pelage pure white. Pale buff band between

flanks and ventral pelage usually absent (cf. *L. capensis*). Head similar in colour to dorsal pelage. Grey or buff eye-ring, extending anteriorly to nasal region. Ears densely covered with small buffy-brown hairs; inner margin fringed with long buff hairs; outer margin fringed with very short white hairs; tip with narrow band of black on both inner and outer surfaces. Ears relatively long (ca. 139% of GLS in *L. s. saxatilis*) or of medium length (ca. 119% in *L. cf. saxatilis*). Nuchal patch large, pale rufous extending anteriorly under ears to base of head. Forelimbs brownish above, white below. Hindlimbs brownish-buff above, white below. Soles of all feet covered with thick dark rufous hair. Tail medium to long, black above, white below. MS/HP ratio high (ca. 149% in *L. s. saxatilis*; 123% in *L. cf. saxatilis*). Each principal incisor tooth with complex groove, filled with cement. (There is no consistent morphological or phenotypic distinction [other than greater size] to distinguish *Lepus s. saxatilis* from scrub hares in the more northerly parts of South Africa; T. J. Robinson, unpubl.)

Geographic Variation There is clinal variation in size within *L. saxatilis (sensu lato)*: *L. s. saxatilis* from the south-west of the range (Western Cape Province) are much larger than *L. cf. saxatilis* in the former Transvaal and KwaZulu–Natal Provinces of South Africa and further north in Zimbabwe. Measurements (mean and range) for ♂♂ from Western Cape Province, Transvaal and Zimbabwe (respectively) are: TL 558 (545–595) mm, 554 (450–640) mm, 529 (400–564) mm; ear: 140 (130–150) mm, 109 (95–148) mm, 99 (92–108) mm; weight: 3.19 (2.70–3.75) kg, 2.2 (1.4–2.9) kg, 2.04 (1.5–2.5) kg (various sources in Smithers 1983).

Similar Species

L. capensis. Dorsal pelage grizzled greyish; tip of ear fringed with short black hairs; nuchal patch brownish-pink, rather inconspicuous;

soles of feet buffy-brown; open grasslands and semi-arid habitats; widespread.

L. victoriae. Ear comparatively and relatively shorter (cf. *L. s. saxatilis*); nuchal patch orange to brownish-orange; soles of feet brown; scrub and bushland habitats; widespread.

Distribution Endemic to Africa. South-West Cape BZ (extending north and east into parts of South-West Arid BZ [mainly Karoo], Highveld BZ and Coastal Forest Mosaic BZ). *Lepus s. saxatilis* is endemic to SW South Africa (mainly Western Cape and Northern Cape Provinces). *Lepus* cf. *saxatilis* is widespread in C and N South Africa, eastwards to KwaZulu–Natal Province, Swaziland (Monadjem 1998a) and probably Lesotho (Lynch 1994). Records from some localities are dubious because it is difficult to distinguish this species from sympatric *L. capensis* in the field, and hence the northern boundary of the geographic range is very uncertain. Flux & Angermann (1990) place the northern limit of the range in C KwaZulu–Natal. However, Taylor (1998) and Kryger *et al.* (2004) refer to specimens of *L. saxatilis* from Zimbabwe and Botswana, implying the northern limit is in these countries (see also Taxonomy). Therefore the northern boundary of *L. saxatilis* (*sensu lato*) may be further north than shown in the map.

Habitat Occurs in a variety of open and scrub habitats. In KwaZulu–Natal, South Africa, recorded in open grasslands, thornveld and roadside verges (Taylor, 1998). In Namibia, prefers rocky and stony habitats, although also known from open sand-plain, bushveld and forest (Shortridge 1934). Attracted to cultivated areas and gardens.

Abundance Common in South Africa. No detailed information from elsewhere.

Adaptations Nocturnal. During the day, Scrub Hares rest singly in a 'form' in the grass or under a bush. When disturbed in the daytime, they run in a zig-zag fashion to the nearest cover. Sometimes

two hares will lie close together, but in different forms, and when disturbed, each runs in a different direction.

Foraging and Food Forages at night. Grazes on grass leaves, rhizomes and stems, with a preference for green grass (K. Collins pers. comm.).

Social and Reproductive Behaviour Solitary, occasionally in pairs.

Reproduction and Population Structure Pregnant ♀♀ recorded in Aug, Oct, Dec, Jun and Jul ($n = 15$) in South Africa, suggesting that reproduction occurs throughout most (if not all) of the year (Taylor 1998). Embryo number: 3.5 (1–4), $n = 15$ (KwaZulu–Natal; Taylor 1998). In Zimbabwe (as *L. saxatilis*, but may be *L. victoriae*), pregnant ♀♀ have been recorded in all months of the year, with peak in reproduction during the warmer months (Sep–Feb); embryo number 1.6 (1–3), $n = 25$ (Smithers & Wilson 1979).

Predators, Parasites and Diseases No information.

Conservation IUCN Category: Least Concern.

However, *Lepus s. saxatilis* is restricted to a small area of south-western South Africa, where habitats are highly modified by farming, and populations are subject to over-hunting. Consequently, these hares should be considered as 'rare'.

Measurements

Lepus saxatilis saxatilis

TL: 688 (551–768) mm, $n = 12$

T: 126.6 (91–175) mm, $n = 12$

HF: 138 (128–155) mm, $n = 12$

E: 140 (130–150) mm, $n = 12$

WT: n. d.

GLS: 100.9 (96.3–104.9) mm, $n = 8$

GWS: 45.0 (43.7–46.8) mm, $n = 11$

P²–M³: n. d.

Mesopterygoid space (width): 10.0 (9.1–11.4) mm, $n = 12$

Hard palate (minimum length): 6.7 (6.0–6.9) mm, $n = 12$

Upper principal incisor width: 3.1 (2.8–3.4) mm, $n = 12$

Bulla width: 9.4 (8.7–9.8) mm, $n = 12$

Western Cape Province, South Africa (various sources; T. J. Robinson, unpubl.)

Lepus cf. *saxatilis*

TL: 570.3 (450–628) mm, $n = 120$

T: 93.3 (70–122) mm, $n = 120$

HF: 113.2 (99–128) mm, $n = 120$

E: 110.8 (95–148) mm, $n = 120$

WT: 2.4 (1.4–3.5) kg, $n = 120$

GLS: 93.5 (88.4–99.8) mm, $n = 21$

GWS: 43.6 (41.5–46.3) mm, $n = 21$

P²–M³: 15.9 (13.8–17.6) mm, $n = 21$

Mesopterygoid space (width): 8.5 (7.7–9.4) mm, $n = 21$

Hard palate (minimum length): 6.9 (5.8–8.0) mm, $n = 21$

Upper principal incisor width: 3.1 (2.8–3.4) mm, $n = 21$

Bulla width: 8.3 (7.4–9.0) mm, $n = 20$



Body measurements and weight: Transvaal, South Africa (Rautenbach 1978 in Smithers 1983); ♂♂ (n = 50) and ♀♀ (n = 70) combined. Skull measurements: KwaZulu–Natal, South Africa (Robinson & Dippenaar 1987); ♂♂ (n = 8) and ♀♀ (n = 12 or 13) combined. Females on average larger (but not significantly larger) than ♂♂ in most measurements

Key References Flux & Angermann 1990; Kryger *et al.* 2004; Smithers 1983.

D. C. D. Happold

Lepus starcki ETHIOPIAN HIGHLAND HARE (STARCK'S HARE)

Fr. Lièvre des haut plateaux d'Éthiopie; Ger. Äthiopischer Hochland Hase

Lepus starcki Petter, 1963. Mammalia 27: 239. Jeldu Liban, Shoa, 40 km W Addis Ababa, Ethiopia. 2720 m.

Taxonomy Originally described as a subspecies of *L. capensis*, but raised to species rank by Angermann (1983). Azzaroli-Puccetti (1987a, b) also lists *L. starcki* as a valid species, but suggests that it may be a relict form of *L. europaeus* because of the similarity between their skulls; she suggests that after the retreat of glaciers during an inter-glacial period, populations of *L. europaeus* were isolated on the Ethiopian Plateau and evolved in isolation to the subspecific level, and therefore the name might be *L. europaeus starcki*. Hoffmann (1993) and Hoffmann & Smith (2005) follow Angermann (1983) in assigning *L. starcki* to specific rank. Synonyms: none. Chromosome number: 2n = 48 (as in all other *Lepus* spp.) (Azzaroli-Puccetti *et al.* 1996).

Description Medium-sized dark lagomorph, darker than *L. habessinicus*. Pelage thick and dense; dorsal hairs 20–25 mm. Dorsal pelage buffy-white, grizzled (agouti) with dots and streaks of black. Dorsal hairs whitish-grey at base, with wide black subterminal band, whitish terminal band and black tip. Underfur dense, grey or greyish-white. Flanks paler; hairs pale grey at base with broad white or buff subterminal band, and black or white tip. Lower flanks pale cinnamon-rufous; hairs white with cinnamon tip. Ventral pelage pure white, fluffy. Head similar in colour to back. White eye-ring in some

individuals. Ears of medium length (ca. 122% of GLS) with upper quarter conspicuously black on both surfaces; outer surface with wide fringe of white or buff hairs along inner margin, and narrow fringe of white hairs along outer margin, except at tip; in some individuals, the black extends along the outer margin of the outer surface, and on the inner margin of the inner surface, to base of ear. Chin whitish, with tinge of cinnamon on lips. Nuchal patch bright cinnamon or rufous, not extending onto sides of neck. Forelimbs long, pale cinnamon. Hindlimbs whitish-grey above, cinnamon and white below. Hindfeet cinnamon-buff above, medium-brown below. Soles of all feet with dense brown hairs. Tail medium-sized, pure black above, white on sides and below; tail colour variable – holotype has pure white tail. MS/HP ratio high (ca. 128%). Each principal upper incisor tooth with wide groove not filled with cement.

Geographic Variation None recorded.

Similar Species

- L. habessinicus*. Dorsal pelage grizzled silvery-grey; ears with narrow black rim around tip; nuchal patch pale brownish-cinnamon; Ethiopian Plateaux and Horn of Africa.
- L. fagani*. Pelage rather coarse; ears shorter with narrow black rim around inner surface of tip; nuchal patch rich cinnamon-tinger extending onto sides of neck; groove on each upper incisor filled with cement; Ethiopian plateaux west of Rift Valley.
- L. victoriae*. Dorsal pelage brown, grizzled with black; ears with much less black on tip; nuchal patch orange to brownish-orange; widespread but not recorded from Ethiopian plateaux.

Distribution Endemic to Africa. Afroalpine–Afromontane BZ of Ethiopia. Recorded only in restricted areas in the highlands, especially in the mountains of Arussi and Bale regions; 2500–4000 m. Does not occur in the Ethiopian Rift Valley separating these mountain regions.

Habitat Open highland habitats, especially grasslands and montane moorlands (Yalden *et al.* 1986).

Abundance Widely distributed within its restricted geographic range. In places, may be very common; e.g. Leslie Brown (in Flux & Angermann 1990) wrote: 'I have never seen so many [hares], even on some Scottish moors, as there are in the heath zone of the Arussi Mountains ... at over 11,000 ft.' Sympatric in part of range with *L. habessinicus* (Angermann 1983). Estimated densities 0.3/ha in afroalpine grasslands on Sanetti Plateau, 0.2/ha in *Helichrysum* scrub



Lepus starcki

at Tullu Deemtu, and 0.17/ha in grasslands of the Web valley in Bale (Sillero-Zubiri & Gottelli 1995).

Remarks One ♀ pregnant and one ♀ lactating in Dec. Embryo number: 1 (n = 1). Reproduction in the dry season would be expected at this altitude (D. W. Yalden, pers. comm.). Preyed on by Ethiopian Wolves *Canis simensis* (composing 1.6% of diet numerically but 11.6% by weight; Sillero-Zubiri & Gottelli 1995) and by Tawny Eagle *Aquila rapax* (L. Brown in Flux & Angermann 1990).

Conservation IUCN Category: Least Concern.

Measurements

Lepus starcki

HB: 482.0 (440–545) mm, n = 12

T: 96.3 (82–115) mm, n = 12

HF: 106.8 (88–120) mm, n = 12

E: 107.9 (100–115) mm, n = 12

WT: 2.5 (1.9–3.0) kg, n = 5

GLS: 89.0 (77.3–92.7) mm, n = 8

GWS: 42.4 (40.1–44.5) mm, n = 7

P²–M³: 16.2 (13.5–17.6) mm, n = 8

Mesopterygoid space (width): 9.1 (8.0–10.5) mm, n = 8

Hard palate (minimum length): 7.1 (6.8–8.0) mm, n = 8

Upper principal incisor width: 3.2 mm, n = 1

Bulla width: n. d.

Ethiopia (Azzaroli-Puccetti 1978a; BMNH)

Key References Azzaroli-Puccetti 1987a, b; Flux & Angermann 1990; Sillero-Zubiri & Gottelli 1995.

D. C. D. Happold

Lepus victoriae AFRICAN SAVANNA HARE

Fr. Lièvre des savanes; Ger. Afrikanischer Savannen Hase

Lepus victoriae Thomas, 1893. Ann. Mag. Nat. Hist., ser. 4, 12: 268. Nassa, Speke Gulf, L. Victoria, Tanzania.

Taxonomy The status of this species, and its various synonyms (including *crawshayi*, *canopus*, *whytei* and *zechi* which are widely used in the older literature) is debatable. The form *victoriae* was included with *L. saxatilis* by Robinson & Dippenaar (1987) and Smithers (1983). Petter (1972c) referred to this species as *L. whytei* and listed *victoriae* and *microtis*, amongst others, as *nomina dubia*. Subsequently, Angermann & Feiler (1988), Flux & Angermann (1990) and Hoffmann (1993) considered *L. victoriae* to be a valid species. However, Hoffmann & Smith (2005) refer to this species as *L. microtis*, on the basis that *microtis* Heuglin, 1865 predates *victoriae*. Some taxonomic confusion has arisen because the type skull of *victoriae* is missing (and its characters are unknown) and because the type of *whytei* seems to be aberrant and not 'typical' of others in nearby localities. Azzaroli-Puccetti (1987b) considers that *whytei* (from Malawi) is close to *L. fagani* (from Ethiopia), although distinguishable on cranial and dental characters, and that the wide geographic separation between the two forms merits recognition of *whytei* as a valid species. *Lepus victoriae* may be considered as the northern allospecies of the southern *L. saxatilis* (see *L. saxatilis*). Here, *L. victoriae* is maintained as a valid species. Synonyms: *angolensis*, *ansorgei*, *canopus*, *crawshayi*, *herero*, *kakumegae*, *mickleimi*, *microtis*, *meridionalis*, *raineyi*, *senegalensis*, *whytei*, *zairensis*, *zechi*, *zuluensis*. Subspecies: none. Chromosome number: probably 2n = 48 (as in all other *Lepus* spp.).

Description Based on *crawshayi* from Nigeria. Medium-sized brown lagomorph. Pelage soft but slightly coarse; dorsal hairs up to 20 mm. Dorsal pelage brown, grizzled (agouti) with black, but showing geographic variation; hairs whitish-grey at base, black subterminal band, yellow-buff terminal band, black at tip. Flanks buff, with fewer black-tipped hairs than dorsal pelage. Whitish-grey underfur. Crown of head and nasal region similar to dorsal pelage. Lips, cheeks and around eyes greyish, without black-tipped hairs. Ventral pelage white or buff. Chin white. Gular collar rufous or buffy. Lateral profile of head (from forehead to nasal region) shallowly and smoothly convex (cf. angular in *L. capensis*) (Flux & Flux 1983). Throat

buffy-brown. Ears of medium length (ca. 114% of GLS), brownish, grizzled (agouti), outer surface with wide fringe of white or buff hairs along inner margin, and narrow fringe of white hairs along outer margin, except at tip; tip black on both outer and inner surfaces, amount of black variable. Nuchal patch orange to brownish-orange. Forelimbs long, buffy-brown. Hindlimbs cinnamon-brown; hindfeet cinnamon-brown above, brown below. Soles of all feet with dense brown hairs. Tail medium-sized; black or dark brown above, white or off-white laterally and below. MS/HP ratio high (ca. 124%). Each principal incisor tooth with wide deep groove filled with cement.

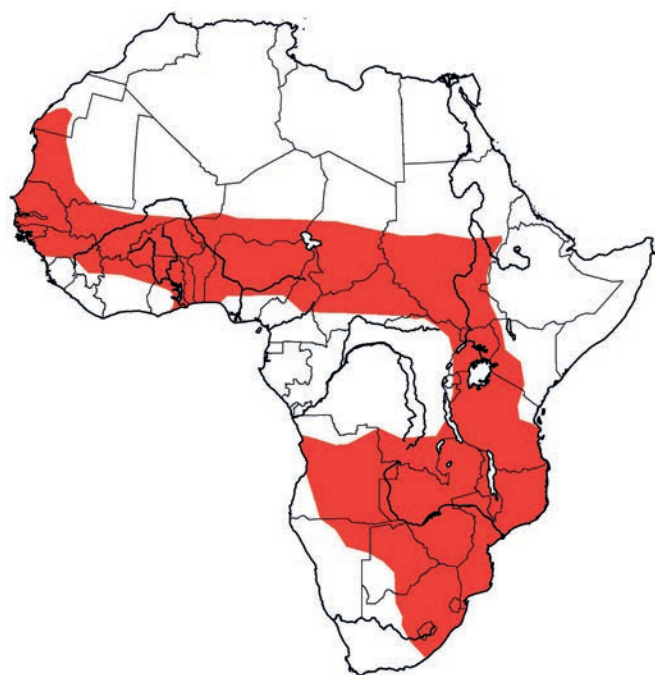
Geographic Variation Pelage colour varies geographically. Montane forms are more rufous and darker than lowland forms (Flux & Angermann 1990).

Similar Species

L. capensis. Dorsal pelage grizzled silvery-grey; nuchal patch brownish-pink, rather inconspicuous; lateral profile of head angular; grasslands, open habitats and semi-desert; widespread.

L. saxatilis. Dorsal pelage grizzled dark buffy-brown; nuchal patch large, pale rufous; soles of feet dark rufous; open and scrub habitats; southern Africa only.

Distribution Endemic to Africa. Sahel Savanna and Guinea Savanna BZs, Rainforest–Savanna Mosaics, Zambezian Woodland BZ and parts of the Somalia–Masai Bushland BZ. Widespread in savanna and semi-desert regions of Africa south of the Sahara, but not present in southern Africa where it is replaced by an allopatric species, *L. saxatilis*. Occurs in mountain regions up to about 3600 m on Mt Kenya (Flux & Flux 1983). A relict population (probably of this species) occurs near Beni Abbas, Algeria, in the Sahara Desert (Petter 1959a as *L. crawshayi*; Kowalski & Rzebik-Kowalska 1991 as *L. saxatilis*); the status of this population is uncertain and needs confirmation. Not present in rainforest habitats.



Lepus victoriae

Habitat Scrub, bush and grasslands habitats, preferring less open habitats compared with *L. capensis*. Also semi-arid grasslands.

Abundance Uncertain because it is difficult to distinguish this species from *L. capensis* in the field. For both species combined, Curry-Lindahl (1981) records biomass estimates that vary greatly according to habitat, e.g. 131 kg/km² in Tsavo N. P., Kenya; 182 kg/km² in Upemba N. P., DR Congo; 242 kg/km² in Serengeti N. P., Tanzania; and 362 kg/km² in Virungu N. P., DR Congo. For Serengeti N. P., this biomass is equivalent to ca 1.2 hares/ha (assuming mean wt of 2 kg/hare). Other estimates have given much lower densities of hares; for example, 8.5 hares/km² (= 0.09 hares/ha) in Serengeti N. P. (Frame & Wagner 1981). The characteristics of the habitat determine the density of hares: in Serengeti N. P., density ranged from a minimum of 0.4 hares/km² in short grass savanna to 3.1 hares/km² in *Themeda* savanna, 10.4 hares/km² in *Pennisetum* savanna and 18.6 hares/km² in medium-height grassland with >50% shrub cover (Frame & Wagner 1981). Numbers vary according to season of the year and habitat: in Queen Elizabeth N. P., Uganda, the number of hares seen during night counts ranged from 6.6 to 9.1 hares/km (annual mean 7.8 hares/km) in short grass/sparse thickets, to 0.6–2.3 hares/km (annual mean 1.4 hares/km) in short grass/dense thickets (Ogen-Odoi & Dilworth 1987). Hares are attracted to areas where grasses are sprouting after burning. Most estimates of density and biomass should be taken with caution because hares are difficult to census.

The numbers of hares remains relatively constant during each season, probably because they breed throughout the year (see below). In this respect, they differ markedly from some temperate species in the genus that exhibit marked annual and multi-annual fluctuations in numbers.

Adaptations Terrestrial and nocturnal. Normally run for cover when disturbed (cf. *L. capensis*) (Flux & Flux 1983). The number of hares may be partly determined by other species of mammals. Light to moderate grazing of grasslands by Common Hippopotami

Hippopotamus amphibius in Queen Elizabeth N. P., Uganda stimulates the growth of new sprouts, which, in turn, attract hares (Ogen-Odoi & Dilworth 1987). When numbers of large grazing mammals increase, the number of hares declines significantly (Eltringham & Flux 1971). The relationship between the numbers of larger mammals and hares is not clearcut; little is known about the responses of hares to each species of large mammal, or the role of large grazing mammals in modifying grasslands and how such modification may be beneficial or detrimental to hares.

Foraging and Food Herbivorous. In Kenya, identified species in the diet (as assessed by faecal analysis) were *Digitaria* sp. 19%, *Hyparrhenia* sp. 11%, *Cynodon dactylon* 4% and dicotyledonous epidermis 1.4%; nearly 50% of the diet was unidentified grass leaf epidermis, stems and grass fibres (Stewart 1971b).

Social and Reproductive Behaviour Mostly solitary; sometimes in groups of 2–3 while feeding. Home-range 5–10 ha (Flux & Angermann 1990).

Reproduction and Population Structure Reproduction occurs throughout the year in Kenya on the Equator, with all sampled ♀♀ being pregnant except in May and Nov when 80% of sampled ♀♀ were pregnant (Flux 1981a). Mean litter-size: 1.6. Weight of young at birth: ca. 100 g. Number of litters/year: 6–8. Mean number of young/year: 13.9 (equivalent to 68% of adult female weight – a very high percentage by lagomorph standards). This hare, like *L. capensis* in Kenya, is a good example of the reproductive strategy in a tropical hare near the Equator (i.e. long reproductive season, many litters/year, small number of young/litter and a high reproductive effort); such a strategy is possible because the environment (primarily rainfall and food resources) enables reproductive activity throughout the year (Flux 1981a). No information available from other localities.

Predators, Parasites and Diseases No information.

Conservation IUCN Category: Least Concern (as *L. microtis*).

Measurements

Lepus victoriae (as *L. crawshayi*)
 HB: 495 (415–575) mm, n = 13
 T: 92 (68–121) mm, n = 13
 HF: 113 (103–127) mm, n = 13
 E: 102 (93–119) mm, n = 13
 WT: 2.31 (1.36–3.17) kg, n = 5
 GLS: 89.2 (84.9–93.6) mm, n = 5
 GWS: 41.4 (39.4–43.2) mm, n = 5
 P²–M³: 13.5 (12.9–14.3) mm, n = 5
 Mesopterygoid space (width): 8.3 (7.4–9.1) mm, n = 5
 Hard palate (minimum length): 6.7 (6.2–8.0) mm, n = 5
 Upper principal incisor width: 3.0 (2.8–3.3) mm, n = 5
 Bulla width: 11.0 (9.6–13.3) mm, n = 5
 Kenya (BMNH)

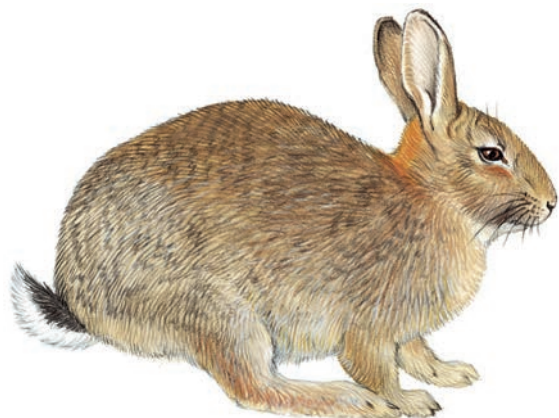
Key Reference Flux & Angermann 1990.

D. C. D. Happold

GENUS *Oryctolagus*

European Rabbit

Oryctolagus Lilljeborg, 1873. Sverig. Og Norges Ryggradsdjur 1: 417. Type species: *Lepus cuniculus* Linnaeus, 1758.



Oryctolagus cuniculus.

A monotypic genus, widespread in Europe but confined in Africa to the extreme north-west of the continent and some islands off southern Africa. The genus is distinguished by its comparatively small body size, small hindfeet and short ears. Skull characteristics include: GLS short (shortest of all African lagomorphs); mean minimum length of hard palate short; MS/HP ratio medium (90%); antero-external shoulders present on zygoma; single groove on each principal upper incisor tooth not filled with cement (Figure 117, Table 48). The single species, *O. cuniculus*, is unique among African lagomorphs because it is a social species, constructs large subterranean burrows and has large litters. Other characteristics of the genus are given in the species profile.

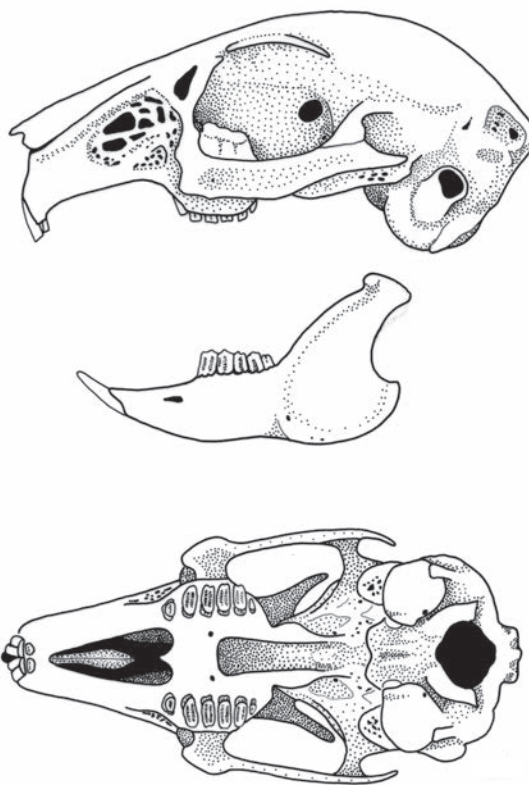


Figure 117. Skull and mandible of *Oryctolagus cuniculus* (BMNH 19.17.7.2533).

D. C. D. Happold

Oryctolagus cuniculus EUROPEAN RABBIT

Fr. Lapin de garenne; Ger. Europäisches Wildkaninchen

Oryctolagus cuniculus (Linnaeus, 1758). Syst. Nat., 10th edn, 1: 58. 'in Europa australis' (= Germany).

Taxonomy Originally described in the genus *Lepus*. The European Rabbit has been rarely studied in Africa. Populations in Morocco and Algeria were probably introduced in the eighteenth century (Kowalski & Rzebik-Kowalska 1991). Loche (1867, in Kowalski & Rzebik-Kowalska 1991) referred to the Algerian Rabbit as *Cuniculus algirus*; more recent authors place *algirus* as a subspecies of *Oryctolagus cuniculus* on the basis of its smaller size. Populations on islands off the coast of South Africa (see below) are descended from domesticated strains of *O. cuniculus* first released in the 1650s (Smithers 1983). Synonyms: nine (all extralimital to Africa; Hoffmann 1993). Subspecies (Africa only): *algirus*. Chromosome number: $2n = 44$ (Schroder & Van der Loo 1979).

Description *Oryctolagus cuniculus algirus* is a small greyish-brown lagomorph, smaller than all other lagomorphs in Africa. Dorsal pelage pale brown, slightly flecked with black and buff; hairs ginger-

brown at base, buff terminally, sometimes with black tip. Underfur grey. Ventral pelage white tinged with pale ginger-buff; hairs white, some with ginger-buff tip. Head similar in colour to dorsal pelage. Chin and throat white. Eye-ring absent. Ears comparatively and relatively short (ca. 98% of GLS), dark brown, darker than dorsal pelage. Nuchal patch pale rufous-brown. Gular patch ginger-buff tinged with orange. Fore- and hindlimbs short (cf. *Lepus* spp.), pale brown. Hindfeet white above, soles thickly covered with pale brown hair. Tail short, same colour as dorsal pelage above, brown or white laterally, white below. Skull: see family and genus profile.

Geographic Variation Extraliminally, pelage colour varies geographically. Specimens from North Africa are paler than those from Spain. Domestic rabbits (and feral descendants) vary in colour from white to brown and black, with or without different colour patches.

Similar Species

Lepus capensis. Much larger in all measurements, ears comparatively and relatively much longer; each principal incisor tooth with groove filled with cement; widespread.

Distribution Mediterranean Coastal BZ. Recorded from N Morocco and N Algeria (coastal regions and Tell Atlas), but not further eastwards to Libya; also on Habibas Is (west of Oran, Algeria). Introduced in the 1600s on to several islands near the coast of South Africa and Namibia: currently present on Jutten, Schaapen, Vondeling, Dassen and Robben Islands near Cape Town, Bird I. near Port Elizabeth, and Possession I. near Luderitz (Smithers 1983, Lever 1985, Flux *et al.* 1990). (Distribution on these islands not shown on map.) Introduced to several other smaller islands near the South African coast, but now locally extinct. Extralimittally widespread throughout continental Europe (natural populations); introduced into Britain (probably in eleventh century), Australia, New Zealand and several South American countries, and many oceanic islands (Flux & Fullager 1983, Flux *et al.* 1990, Lever 1985).

Habitat High mountains, dense bushy regions, and arid habitats in Morocco (Aulagnier & Thévenot 1986). Tends to avoid forested habitats and open areas in Algeria (Kowalski & Rzebik-Kowalska 1991). Sometimes found in cultivated areas.

Abundance Common in W Algeria, less common in E Algeria (Kowalski & Rzebik-Kowalska 1991). Populations in Algeria were reduced when the disease myxomatosis was introduced.

Adaptations Mainly nocturnal, but active at dawn and dusk when conditions are suitable. Dig extensive underground burrows ('warrens') for resting in during the day, and for protection when threatened. Considered a pest in cultivated crops when population numbers are high. As for European Rabbits elsewhere, very adaptable

and prolific. Apart from North Africa, European Rabbits have not colonized Africa (as they have in other continents where they have been released); it seems that competition and predation have prevented individuals (whether introduced purposely, or escaped from captivity) from establishing permanent populations.

Foraging and Food Herbivorous. Graze on grasses. No detailed information for African populations.

Social and Reproductive Behaviour No information for North Africa, but likely to show similar behaviour to populations elsewhere. Social and territorial. A dominant ♂ associates with several ♀♀ and their young. When population numbers are low, groups are small; when high, social groups may defend territories but may join other groups to feed at night.

Reproduction and Population Structure No detailed information for North Africa. Elsewhere very prolific, with an ability to breed opportunistically when conditions are favourable. In general, the reproductive season is shorter at higher latitudes and longer at lower latitudes, and more opportunistic in drier arid habitats than in wetter temperate climates. No data on reproductive season in North Africa, but probably occurs during summer months (Apr–Sep) in Atlas Mts, and in spring and autumn (or even winter) on the semi-arid Mediterranean coast and opportunistic reproduction in summer when conditions are favourable. In North Africa, it is probable that reproductive data are similar to elsewhere in southern Europe (as given below). Young born in burrow, in nest of fur made by mother. Gestation: 28–30 days. Litter-size: 3–9, 4–6 or 3–4, depending on season and environmental conditions. Females have postpartum oestrus. At birth, young are altricial, naked, with eyes closed. Weaned ca. Day 20, when first leave nest. Maturity: 3–4 months. Population numbers fluctuate, often greatly. High productivity of young is matched by heavy predation by predators. Population numbers increase during the reproductive season and decline at other times of the year (Gibb 1990). The reproductive strategy of the European Rabbit contrasts greatly with that of hares (genus *Lepus*).

Predators, Parasites and Diseases Occasionally preyed on by owls, and hunted by humans in Algeria (Kowalski & Rzebik-Kowalska 1991). Probably has numerous other predators. The disease myxomatosis (caused by the virus *Myxoma*) has reduced population numbers in many parts of the world.

Conservation IUCN Category: Least Concern (worldwide).

Although common and widespread (and regarded as pests at times) in some continents, status in North Africa is not known.

Measurements

Oryctolagus cuniculus

HB: 368 (355–380) mm, n = 5

T: 69.0 (65–70) mm, n = 5

HF: 84.4 (80–89) mm, n = 5

E: 73 (70–76) mm, n = 4

WT: n. d.

GLS: 74.5 (72.7–77.2) mm, n = 5

GWS 35.9 (34.6–36.7) mm, n = 5



Oryctolagus cuniculus

P²–M³: 11.8 (10.0–12.5) mm, n = 5*

Mesopterygoid space (width): 5.3 (5.0–5.7) mm, n = 5

Hard palate (minimum length): 5.9 (5.5–6.1) mm, n = 5

Upper principal incisor width: n. d.

Bulla width: n. d.

Morocco (Petter & Saint-Girons 1972)

*Algeria (Kowalski & Rzebik-Kowalska 1991)

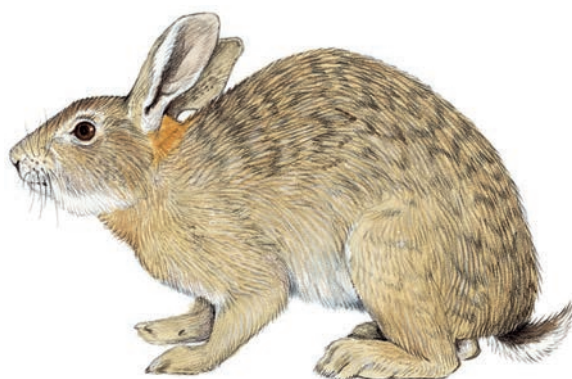
Key References (Africa only) Flux *et al.* 1990; Kowalski & Rzebik-Kowalska 1991; Smithers 1983.

D. C. D. Happold

GENUS *Poelagus*

Bunyoro Rabbit

Poelagus St Leger, 1932. Proc. Zool. Soc. Lond. 1932 (1): 119. Type species: *Lepus marjorita* St Leger, 1929.



Poelagus marjorita.

A monotypic genus distributed in savanna habitats in eastern and central Africa to the north of the Rainforest BZ. The genus lacks unique features (Corbet 1983). Like most *Lepus*, the body is medium-sized, individuals are mostly solitary, do not live in extensive underground burrows, and litters are small. As in *Oryctolagus*, the skeleton is not built for fast movement, the ears are comparatively and relatively short, and the young are altricial at birth. Skull characteristics include: GLS of medium length; minimum length of hard palate medium; MS/HP ratio low (ca. 84%) as in *Pronolagus*; antero-external shoulders present on zygoma; single groove on each principal upper incisor tooth not filled with cement (Figure 118, Table 48).

The mixture of characteristics suggest that the single species does not fit into any other genus of Lagomorpha, and that a separate genus, *Poelagus*, is warranted. Other characteristics of the genus are given in the species profile.

D. C. D. Happold

Poelagus marjorita BUNYORO RABBIT (UGANDA GRASS HARE)

Fr. Lapin sauvage d'Afrique centrale; Ger. Bunyoro-Buschkaninchen

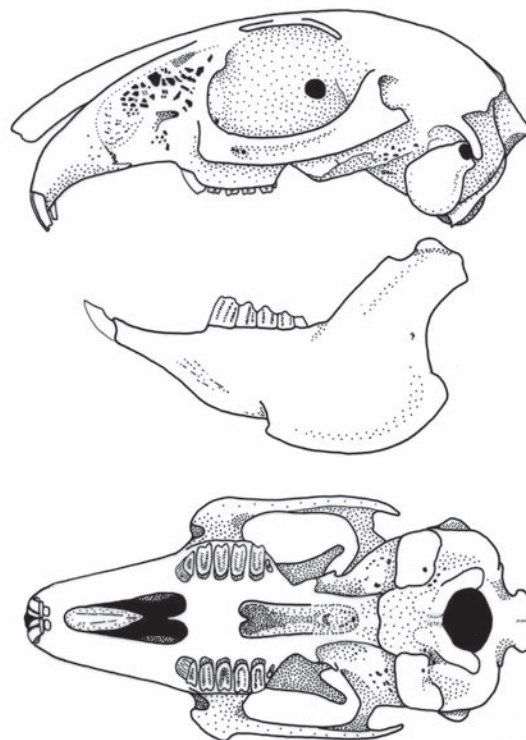


Figure 118. Skull and mandible of *Poelagus marjorita* (RMCA no number).

Poelagus marjorita (St Leger, 1929). Ann. Mag. Nat. Hist., ser. 10, 4: 292. Near Masindi, Bunyoro, Uganda.

Taxonomy Originally described in the genus *Lepus*. Synonyms: *larkeni*, *oweni*. Subspecies: none. Chromosome number: not known.

Description Medium-sized lagomorph with comparatively

short ears. Dorsal pelage buffy-brown, grizzled (agouti) with black hairs; hairs whitish-grey at base, with wide black subterminal band, pale brown to buff terminal band, and black tip. Underfur greyish-white. Flanks paler, mainly buffy-brown; most hairs without black

tips. Ventral pelage yellowish-buff; hairs whitish-grey on basal half, yellowish-buff on terminal half. White mid-ventral stripe from chest (ca. 20–30 mm wide) to lower abdomen (ca. 40–50 mm wide), extending posteriorly on to inner surface of hindlimbs; hairs pure white. Ventral underfur pure white. Head similar in colour to dorsal pelage; chin and throat white. Ears comparatively and relatively short (ca. 77% of GLS), similar in colour to dorsal pelage, usually without fringe of white hair on ear margins; brown hairs on inner surface; no black on tip. Nuchal patch rufous, not extending on to sides of neck. Fore- and hindlimbs brownish-buff, soles of feet with dense rufous or blackish hairs. Tail short; same colour as dorsal pelage above and on sides, paler (often with some white hairs) below. Both sexes have glandular slits on either side of the genitalia. Juveniles with deep rufous nuchal patch; hairs on soles of feet whitish or grey. Skull: see family and genus profiles. Nipples: not known.

Geographic Variation None recorded.

Similar Species

L. victoriae. Tail longer; ear comparatively and relatively longer (ca. 114% of GLS); each principal incisor tooth with wide deep groove filled with cement; more widespread.

L. capensis. Dorsal pelage silvery-grey, grizzled with black; tail and hindfoot longer; ear comparatively and relatively longer (ca. 142% of GLS); each principal incisor tooth with wide deep groove filled with cement; more widespread.

Distribution Endemic to Africa. Eastern Rainforest–Savanna Mosaic and Guinea Savanna BZs. Recorded from C and W Uganda, S Sudan, NE DR Congo and NE Central African Republic. There is no evidence for the species in Ruanda, Burundi, Kenya, S Chad, S DR Congo and N Angola (*contra* Duthie & Robinson 1990 and Kingdon 1997) (see Happold & Wendelen 2006).

Habitat Primarily woodland savanna; also stony habitats and hills with short grass (Hatt 1940a). May also occur in forests (e.g. in S Sudan; Setzer 1956).

Abundance Uncertain. Reported to be common in open savanna scrub in S Sudan (Setzer 1956), and in Garamba N. P., DR Congo (Verheyen & Verschuren 1966). In Uganda, reported in 1928 as ‘Abundant in certain localities at night grazing on grassy tracks and roads’, and in 1958 as ‘Very common grazing by roads at night’ (labels, BMNH).

Adaptations Terrestrial and primarily nocturnal. During the day, rests alone in a form in thick vegetation. Locomotion is more similar to that of a rabbit than of a hare (Kingdon 1974). This is probably because the skeleton is rabbit-like, e.g. scapula is long and narrow (broad and ‘shovel-like’ in hares), ulna is sturdy (reduced in hares), transverse processes of lumbar vertebrae are narrow (expanded in hares) and cervical vertebrae are short (elongated in hares) (St Leger 1932); however, in some specimens, these characters are not so pronounced and are more similar to those of *Lepus* (Hatt 1940a).

Foraging and Food Forages at night on flowers and sprouting grasses. Tends to prefer pastures that have been heavily grazed by



Poelagus marjorita

larger mammals, newly mown fields and burnt areas where the grasses are sprouting (Kingdon 1974). Quantitative data on diet is not available.

Social and Reproductive Behaviour Probably solitary when resting in a form; feeds at night in small groups (pairs, or ♀♀ with young). May be found on rocky habitats with Rock Hyraxes (Kingdon 1974).

Reproduction and Population Structure Newborn young recorded in Jan, Feb, Mar, Jun, Aug and Oct in Garamba N. P., NE DR Congo (Hatt 1940a, Verheyen & Verschuren 1966), and juveniles (WT: 185–200 g) recorded in Jan, Feb, May and Aug (labels, RMCA) suggest that reproduction occurs in most (if not all) months of the year. One large embryo recorded in mid-Aug (Faradje, DR Congo; Hatt 1940a). Gestation thought to be about five weeks (Kingdon 1974). Litter-size: 1–2. Young born in short burrow, the entrance concealed by grass and soil (Kingdon 1974). At birth, young are blind and helpless, with sparse covering of short hair (as in *Oryctolagus cuniculus*).

Predators, Parasites and Diseases No detailed information, but likely to include Servals *Felis serval*, Genets *Genetta* spp., hawks and owls (Kingdon 1974). In Uganda, hunted with nets and dogs.

Conservation IUCN Category: Least Concern.

Measurements

Poelagus marjorita

HB: 451.9 (400–605) mm, n = 17

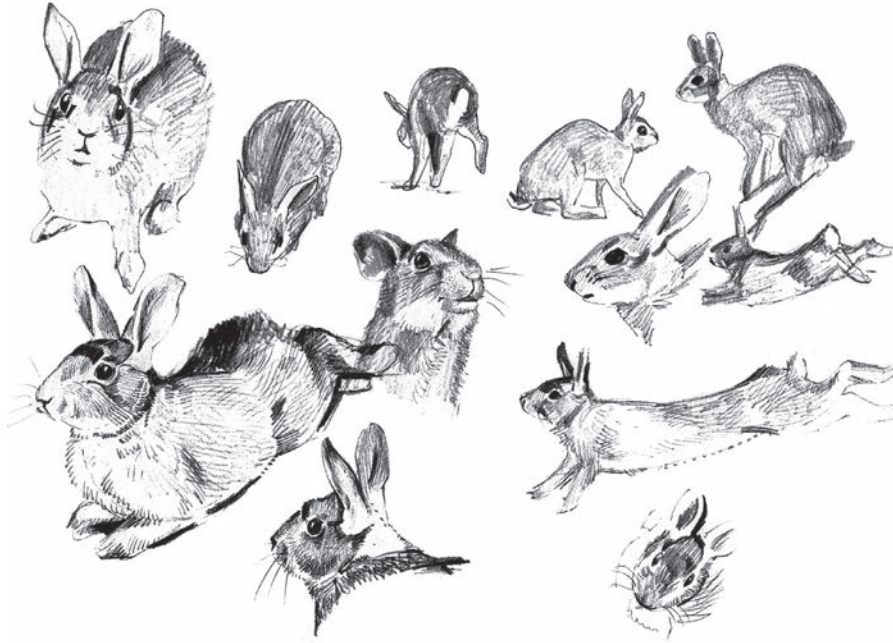
T: 55.6 (38–70) mm, n = 17

HF: 97.5 (65–108) mm, n = 17

E: 64.7 (61–70) mm, n = 5

WT: 2.68 (2.26–3.17) kg, n = 5*

Poelagus marjorita.



GLS: 83.8 (78.0–89.6) mm, n = 20
 GWS: 40.3 (38.8–42.6) mm, n = 20
 P²–M³: 13.6 (13.1–14.4) mm, n = 5*
 Mesopterygoid space (width): 6.7 (6.1–7.6) mm, n = 9*
 Hard palate (minimum length): 8.0 (7.3–8.7) mm, n = 9*
 Upper principal incisor width: 3.0 (2.9–3.3) mm, n = 9*
 Bulla width: 9.3 (8.4–10.2) mm, n = 9*

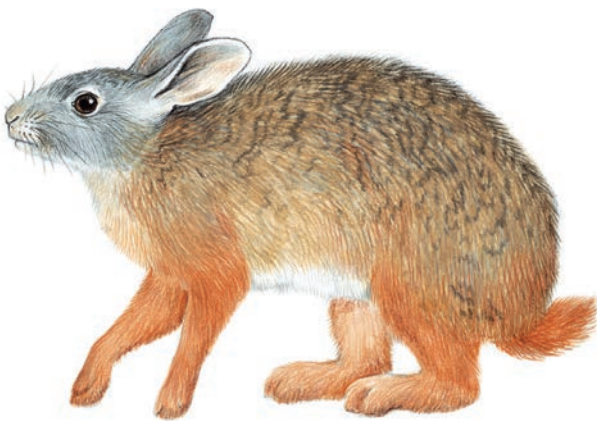
Uganda (BMNH) and DR Congo (Hatt 1940)
 *BMNH only

Key References Duthie & Robinson 1990; Happold & Wendelen 2006; Kingdon 1974.

D. C. D. Happold

GENUS *Pronolagus* Rock-hares

Pronolagus Lyon, 1904. *Smithson. Misc. Coll.* 45:416. Type species: *Lepus crassicaudatus* I. Geoffroy, 1832.



Pronolagus rupestris.

The genus *Pronolagus* – the Rock-hares – contains three or four species that occur mainly in southern Africa. One species, *P. rupestris*, is also represented in eastern Africa, but its taxonomic status is uncertain. Rock-hares (unlike other lagomorphs) are always associated with rocky habitats. Diagnostic characters of the genus are medium to large size (as in most *Lepus* spp.), hindlimbs

that are only slightly longer than forelimbs (cf. *Lepus*), ears short to medium-sized, uniformly coloured rufous or rufous-black tail, and a considerable amount of reddish or rufous colouration on the limbs and ventral surface. Skull characters include: GLS short to medium-sized; minimum length of hard palate medium to long (depending on species); MS/HP ratio low; antero-external shoulders present on zygoma; and a single groove on each principal upper incisor tooth not filled with cement (Figure 119, Table 48) (cf. most *Lepus* spp.).

Rock-hares are unique in their ability to run and jump over rocks and boulders; they live in small colonies (perhaps because of restrictions in the extent of their habitat) and litter-size is small. Young are altricial at birth (like rabbits) and are born in a nest lined with fur.

Traditionally three species have been recognized (*P. crassicaudatus*, *P. randensis*, *P. rupestris*) (Hoffmann & Smith 2005). Here, the form *saundersiae* (listed as a synonym of *P. rupestris* by Hoffmann & Smith 2005) is also considered to be a valid species (Whiteford 1995, Matthee & Robinson 1996).

The species are mainly distinguished by the size of body, hindfoot and ear, geographic range and by selected ratios (see profiles).

D. C. D. Happold

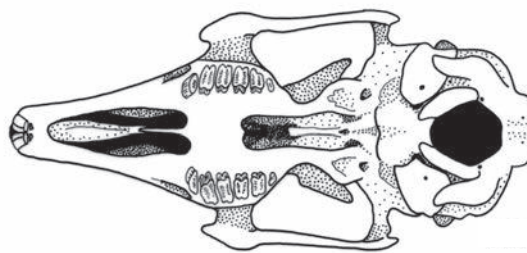
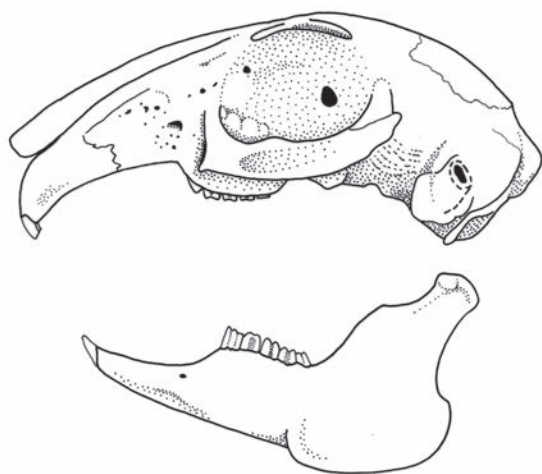


Figure 119. Skull and mandible of *Pronolagus crassicaudatus* (RMCA RG2624).

Pronolagus crassicaudatus NATAL RED ROCK-HARE

Fr. Lièvre Roux du Natal; Ger. Natal-Rotkaninchen

Pronolagus crassicaudatus (I. Geoffroy, 1832). Mag. Zool. Paris 2: cl. 1, pl. 9. 'Port Natal' (= Durban South Africa).

Taxonomy Originally described in the genus *Lepus*. Formerly treated as a subspecies of *P. randensis* but now considered to be a valid species. Synonyms: *kariageae*, *lebombo*, *lebomboensis* (*lapsus*), *ruddi*. Subspecies: possibly five (see below). Chromosome number: $2n = 42$ (as in all *Pronolagus* spp.).

Description Large lagomorph with reddish-coloured limbs. Pelage rather dense and harsh. Dorsal pelage brown, grizzled (agouti) and flecked with black, becoming bright rufous on rump; hairs pale rufous at base, with cream subterminal band, black at tip. Underfur grey. Flanks paler than dorsal pelage, with fewer black-tipped hairs. Ventral pelage pale rufous, with irregular white patches and streaks; hairs mostly with white tips. Head greyish-brown, slightly grizzled. Chin, lower cheeks and throat grey or greyish-white; with greyish-white band extending laterally along edge of jaw to nuchal patch. Nuchal patch brown to grey. Gular patch brownish-rufous (contrasting with colour on throat and chest). Ears relatively short (ca. 81% of GLS) and sparsely furred; whitish-grey on outer surface, grey (similar to cheek) on inner surface. Fore- and hindlimbs dull rufous; soles of all feet rufous-brown. Tail short, bright rufous above and below (but not as dark or as black as in other *Pronolagus* spp.). MS/HP low (ca. 61%). Each principal incisor tooth with groove (close to inner margin of tooth) not filled with cement.

Geographic Variation Petter (1972c), Meester *et al.* (1986) and Flux & Angermann (1990) list five subspecies, but their status, characteristics and geographic limits are uncertain and their validity is doubtful. Listed here without comment: *P. c. crassicaudatus*, *P. c. ruddi*, *P. c. kariageae*, *P. c. bowkeri* (considered to be a subspecies of *P. rupestris* by Smithers 1983, Hoffmann & Smith 2005) and *P. c. lebombo*. Subspecies distinguished partly by colour of nuchal patch (see Taylor 1998).

Similar Species

P. saundersiae. HB on average shorter (mean 447 mm; ear shorter

(80–105 mm); tail on average longer (mean 86 mm); sympatric in part of range.

Distribution Endemic to Africa. Coastal Forest Mosaic, Highveld and parts of Afromontane–Afroalpine BZs in SE South Africa. Recorded from eastern South Africa (primarily KwaZulu–Natal and Mpumalanga Provinces), Lesotho, Swaziland and extreme S Mozambique (Meester *et al.* 1986, Duthie & Robinson 1990). Occurs from sea level to 1550 m. Syntopic in northern and eastern part of range with *P. saundersiae*. Distribution is patchy (see below). Two records from Mozambique (Smithers & Lobão Tello 1976) are not assignable.



Pronolagus crassicaudatus

Habitat Rocky kopjes, rocky hills and ravines where grasses and shrubs grow among the rocks or at base of rocks.

Abundance Relatively common and widespread in KwaZulu-Natal (Taylor, 1998). No detailed information from elsewhere.

Adaptations Nocturnal. During the day, hides in crevices in rocks and under boulders, or in forms in dense grass. Relies heavily on rocks and boulders for cover, and rarely moves far away from rocks when foraging. The skeleton is 'rabbit-like' since the hindlimbs are only slightly longer than the forelimbs. Droppings are deposited in middens, which are often far from resting sites (Duthie 1997).

Foraging and Food Herbivorous. No detailed information.

Social and Reproductive Behaviour Lives in small colonies consisting of a few individuals (Duthie 1997).

Reproduction and Population Structure In KwaZulu-Natal, pregnant ♀♀ have been recorded in Jun and Aug, and lactating ♀♀ in Aug, Oct and Feb (Taylor, 1998). These data suggest that reproduction occurs throughout much of the year. Embryo number: 1 (n = 1) or 2 (n = 3).

Predators, Parasites and Diseases No information.

Conservation IUCN Category: Least Concern.

Measurements

Pronolagus crassicaudatus

HB: 508 (460–560) mm, n = 28

T: 65 (35–110) mm, n = 26

HF: 112 (100–125) mm, n = 12

E: 74 (60–80) mm, n = 17

WT: 2.6 (2.4–3.05) kg, n = 13

GLS: 91.3 (85.3–94.8) mm, n = 27

GWS: 39.6 (36.0–41.8) mm, n = 25

P²–M³: 15.5 (15.2–18.2) mm, n = 28

Mesopterygoid space (width): 5.8 (4.6–6.8) mm, n = 27

Hard palate (minimum length): 9.5 (8.4–11.2) mm, n = 28

Upper principal incisor width: 3.2 (2.9–3.6) mm, n = 24

Bulla width: 6.1 (5.1–7.0) mm, n = 27

South Africa

Robinson & Dippenaar 1983a

*Smithers 1983

Key References Duthie & Robinson 1990; Smithers 1993; Taylor, 1998.

D. C. D. Happold

Pronolagus randensis JAMESON'S RED ROCK-HARE

Fr. Lièvre Roux de Jameson; Ger. Jamesons Rotkaninchen (Rand-Wollschwanzhase)

Pronolagus randensis Jameson, 1907. Ann. Mag. Nat. Hist., ser. 7, 20: 404. 'Observatory kopje', Johannesburg, South Africa. 5900 ft (1798 m).

Taxonomy Formerly included *P. crassicaudatus* as a subspecies. Synonyms: *capricornis*, *caucinus*, *ekmani*, *kaokoensis*, *kobosensis*, *maka-pani*, *powelli*, *waterbergensis*, *whitei*. Subspecies: none. Chromosome number: 2n = 42 (as in all *Pronolagus* spp.).

Description Medium-sized; brownish, with rufous limbs and rump. Pelage dense, woolly with silky texture. Dorsal pelage brown, grizzled (agouti), pale rufous on rump and flanks; hairs pale cinnamon at base, with white or cream subterminal band and often black tip. Usually darker on upper back due to many black-tipped hairs. Underfur rufous-brown. Flanks paler. Ventral pelage pale cinnamon, sometimes with white patches; hairs cinnamon with white tip. Head grizzled brownish-grey (without any rufous). Lower cheeks and throat whitish-grey. Ears short (ca. 93% of GLS); brownish-grey with white hairs at tip. Nuchal patch rufous. Gular patch brownish-rufous; hairs with white tips. Fore- and hindlimbs pale rufous, similar to flanks; soles of feet dark brown. Tail medium-sized; blackish-rufous, with black-tipped hairs especially towards tip. MS/HP ratio low (ca. 52%). Each principal incisor tooth with groove (close to inner margin of tooth) not filled with cement.

Geographic Variation A preliminary study of mtDNA collected from specimens from six South African localities reveals no geographic variation among populations representing four previously

recognized subspecies (*P. r. randensis*, *P. r. powelli*, *P. r. makapani* and *P. r. capricorni*) (Matthee 1993). Thus there is little geographic variation within the western *P. randensis* group as suggested by Meester *et al.* (1986), who recognized only two subspecies: *P. r. caucinus* (Namibia) and *P. r. randensis* (South Africa, Zimbabwe and Botswana).

Similar Species

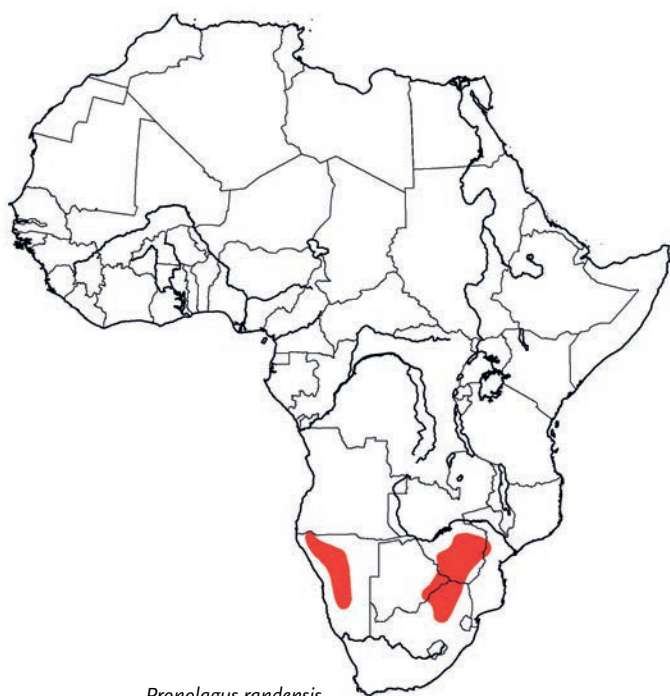
P. crassicaudatus. Ear shorter (60–80 mm); tail on average shorter (mean 65 mm); eastern South Africa; allopatric.

P. rupestris. HB: on average shorter (mean 447 mm), but with ear on average longer (mean 94 mm) and tail on average shorter (mean 86 mm); South Africa, and Malawi northwards to Kenya; allopatric.

P. saundersiae. Ear on average longer (mean 94 mm); tail on average shorter (mean 86 mm); marginally sympatric in part of range.

Distribution Endemic to Africa. South-West Arid (Namib) and Zambezi Woodland BZs. Two disjunct populations: (1) NE South Africa, E Botswana and Zimbabwe; (2) C and NW Namibia, and perhaps extreme SW Angola. Distribution is patchy because of specialized habitat requirements (see below).

Habitat Rocky kopjes, gorges and cliffs, and rocky hills with boulders. Rock crevices and boulders are an essential component of the habitat. In Botswana, occurs on isolated kopjes up to 22 km from



Pronolagus randensis

nearest kopjes (and from other populations) so, when necessary, individuals have to disperse across intervening non-rocky habitat. Where sympatric with *P. saundersiae* in hilly mountainous areas, *P. randensis* tends to be found on the drier low-lying mountain slopes where there are many jumbled boulders and rock crevices, whereas *P. saundersiae* is found at higher altitudes with fewer boulders and crevices, and higher rainfall.

Abundance Very common in the granite hills of Matopos Hills in Zimbabwe and sandstone formations of E Botswana (Smithers 1983).

Adaptations Mainly nocturnal but may feed and sunbathe in the late afternoon. During the day, rests in rock crevices, under boulders, or in thick grass close to rocks. If disturbed, stays under cover until the last moment and then disappears behind nearby rocks. Like all rock-hares, can leap from rock to rock, and run up steep rock faces to reach crevices. Characteristic flattened pellet-like droppings are deposited in middens (as in other *Pronolagus* spp.). Unlike hyraxes, which also live in rocky habitats, Jameson's Red Rock-hares do not expose themselves on observation boulders (Smithers 1983).

Foraging and Food Herbivorous. Grazes on grasses amongst rocks or at base of rocky hills. Congregates on recently burnt areas to feed on newly sprouting grass. No detailed information on diet.

Social and Reproductive Behaviour Generally solitary; sometimes seen in small groups of ♀ and young, or adult ♀ with one or two ♂♂. Several individuals may congregate when grazing (Smithers 1983). In Matopos Hills, Zimbabwe, most nocturnal observations were of single animals, and only 15% were of pairs (Peddie 1975, in Duthie & Robinson 1990).

Reproduction and Population Structure Probably breeds throughout the year in Zimbabwe (Peddie 1975, in Duthie & Robinson 1990). Pregnancies recorded in Jan, Jul and Aug; and lactating ♀♀ in Jun, Jul and Aug in Zimbabwe (no data for Feb, Mar, Apr, May, Nov, Dec; Smithers & Wilson 1979, as *P. crassicaudatus*). Litter-size: 1.1 (1–2), n = 8 (Smithers 1983). No information on rate of growth or age at maturation.

Predators, Parasites and Diseases No information.

Conservation IUCN Category: Least Concern.

Measurements

Pronolagus randensis

HB: 463 (420–500) mm, n = 12

T: 97 (60–135) mm, n = 13

HF: 100 (87–110), n = 13

E: 84 (80–100) mm, n = 13

WT: 2.3 (1.82–2.95) kg, n = 43*

GLS: 90.0 (86.1–92.9) mm, n = 14

GWS: 40.6 (38.6–42.6) mm, n = 14

P²–M³: 15.5 (14.7–16.3) mm, n = 14

Mesopterygoid space (width): 4.8 (3.9–5.3) mm, n = 14

Hard palate (minimum length): 9.3 (8.1–10.1) mm, n = 14

Upper principal incisor width: 3.0 (2.6–3.4) mm, n = 14

Bulla width: 6.3 (5.5–7.0) mm, n = 14

South Africa, Zimbabwe (Robinson & Dippenaar 1983a)

*Smithers 1983

Key References Duthie & Robinson 1990; Smithers 1983.

D. C. D. Happold

Pronolagus rupestris SMITH'S RED ROCK-HARE

Fr. Lièvre Roux de Smith; Ger. Smiths Rotkaninchen

Pronolagus rupestris (A. Smith, 1834). S. Afr. Quart. J. 2: 174. 'Rocky situations, South Africa' (probably Rhynsdorp District, South Africa).

Taxonomy Originally described in the genus *Lepus*. Formerly included in *P. crassicaudatus*. The taxonomic status of the East African *P. rupestris* is uncertain and requires investigation, and is here treated as conspecific with the southern African *P. rupestris*. Synonyms: *curryi*, *fitzsimonsi*, *melanurus*, *mülleri*, *nyikae*, *vallicola*. Subspecies: none. Chromosome number: 2n = 42 (as in all *Pronolagus* spp.).

Description Medium-sized. Pelage thick and dense, woolly and frequently characterized by a reddish undertone. Dorsal pelage grizzled (agouti) brown anteriorly; hairs pale cinnamon at base, with subterminal white band and black tip; dorsal pelage rufous posteriorly and bright rufous on rump; hairs rufous with white tip. Flanks paler; hairs mostly with white tip and fewer with black tip. Ventral pelage pale rufous to whitish-rufous. Head greyish-

brown. Cheeks greyish-white. Ears ca. 116% of GLS; similar in colour to head with many small off-white or brown hairs. Gular patch brownish. Nuchal patch rufous. Forelimbs bright rufous, contrasting with body colour. Hindlimbs pale rufous (not as bright as forelimbs); hairs whitish-rufous at tip. Soles of all feet very densely covered with dark grey hair. Tail medium-sized, usually black, or black and dark red. MS/HP ratio low (ca. 77%). Each principal incisor tooth with groove (close to inner margin of tooth) not filled with cement. Length of frontal bone almost equal to length of muzzle (cf. *P. saundersiae*).

Geographic Variation Pelage colour varies geographically (Smithers 1983).

Similar Species

P. randensis. Ear on average shorter (mean 84 mm); tail on average longer (mean 97 mm); allopatric.

P. saundersiae. Length of frontal bone shorter than length of muzzle; marginally sympatric in part of range.

Distribution Endemic to Africa. South-West Arid and Zambeian Woodland BZs; also some areas of Afroalpine–Afroalpine BZ. Two disjunct ranges: (1) NW South Africa; (2) SW Kenya, C Tanzania, Malawi and E Zambia. The two ranges are separated by ca. 1200 km. Not recorded from Botswana (Smithers 1971), Zimbabwe (Smithers & Wilson 1979), Swaziland (Monadjem 1998a) and Mozambique (Smithers & Lobão Tello 1976).

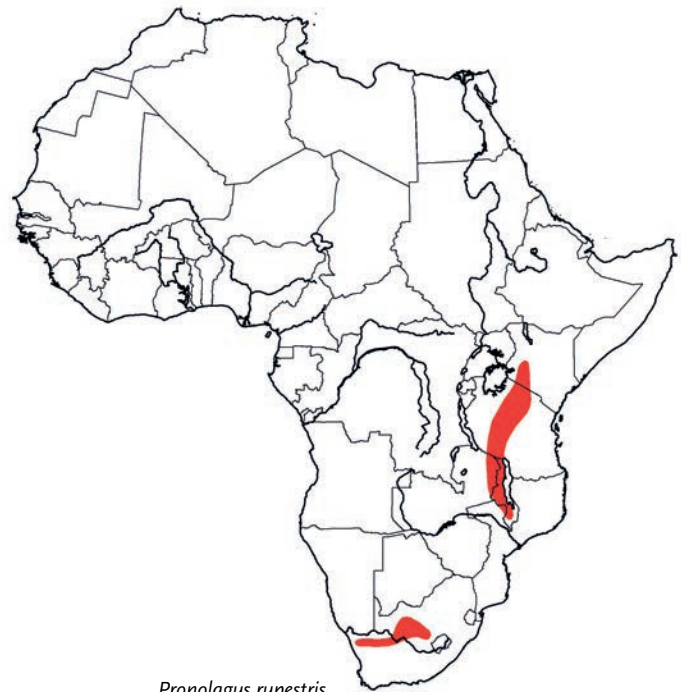
Habitat Rocky kopjes and rocky hillsides with boulders. Rock crevices and boulders are essential components of the habitat. Habitat very similar to other species of *Pronolagus*. In South Africa, generally found at lower elevations than *P. saundersiae* (Matthee & Robinson 1996).

Abundance In South Africa, fairly abundant throughout range; expected total population size exceeds 10,000 mature individuals (T. J. Robinson, unpubl.). No information on abundance for East African populations.

Adaptations Nocturnal. Emits a wide range of vocalizations: an alarm ‘tu ... tu’ when approached at night, and a grunt when disturbed before sunrise. Young individuals produce a scream when handled, and a ‘churring sound’ when disturbed under a rock (Duthie 1997). Large disc-shaped faecal pellets are deposited in middens (Duthie 1997). Adaptations likely to be similar to those of other rock-hares.

Foraging and Food Herbivorous. Forages near rocks, grazing mainly on grasses. In the Ngong Hills, Kenya, plant items in faecal pellets were grass epidermis (mainly *Ischaemum afum* 33.5%) and stem fibres (30.6%); small amounts of other grass were present, and a very small amount of dicotyledon epidermis (Stewart 1971b).

Social and Reproductive Behaviour Female prepares nest of fur from her body, suggesting that young remain for some time in a nest (Smithers 1983).



Pronolagus rupestris

Reproduction and Population Structure Females give birth to young from spring to summer (Sep–Feb) in South Africa. Gestation: 35–45 days. Litter-size: one or two (Duthie 1997). At birth young are likely to be altricial, with sparse covering of hair and eyes closed (Smithers 1983).

Predators, Parasites and Diseases No information.

Conservation IUCN Category: Least Concern.

Measurements

Pronolagus rupestris

HB: 447 (380–535) mm, n = 15

T: 86 (50–115) mm, n = 15

HF: 92 (85–100) mm, n = 15

E: 94 (80–105) mm, n = 15

WT: 1.62 (1.35–2.05) kg, n = 18

GLS: 80.7 (75.1–85.3) mm, n = 67*

GWS: 36.7 (34.5–39.4) mm, n = 67*

P²–M³: 14.1 (13.2–15.6) mm, n = 15

Mesopterygoid space (width): 5.3 (4.3–6.8) mm, n = 81*

Hard palate (minimum length): 6.9 (5.4–8.5) mm, n = 81*

Upper principal incisor width: 2.5 (2.1–3.0) mm, n = 78*

Bulla width: 7.2 (6.0–8.5) mm, n = 72*

South Africa

Body measurements: Robinson & Dippenaar 1983a

Weight: Smithers 1983

Skull measurements: TM; *Whiteford 1995

Key References Duthie 1997; Smithers 1983.

D. C. D. Happold

Pronolagus saundersiae HEWITT'S RED ROCK-HARE

Fr. Lièvre Roux de Hewitt; Ger. Hewitts Rotkaninchen

Pronolagus saundersiae Hewitt, 1927. S. Afr. Quart. J. 2: 174. 'Rocky situations, South Africa' (probably Albany district, South Africa).

Taxonomy Originally described as *Pronolagus crassicaudatus saundersiae*. Referred to as a subspecies of *P. rupestris* by Meester *et al.* (1986) and Hoffmann & Smith (2005) but here, following Whiteford (1995) and Matthee & Robinson (1996), it is considered to be a valid species. Synonyms: *australis*, *barretti*. Subspecies: none. Chromosome number: $2n = 42$ (as in all *Pronolagus* spp.).

Description Medium-sized. Pelage thick and dense, woolly. Dorsal pelage grizzled (agouti) brown anteriorly; hairs pale cinnamon at base, with subterminal white band and black tip; dorsal pelage rufous posteriorly and bright rufous on rump; hairs rufous with white tip. Flanks paler; hairs mostly with white tip and some with black tip. Ventral pelage pale rufous to whitish-rufous. Head greyish-brown. Cheeks greyish-white. Ears ca. 116% of GLS; similar in colour to head with many small off-white or brown hairs. Gular patch brownish. Nuchal patch rufous. Forelimbs bright rufous, contrasting with body colour. Hindlimbs pale rufous (not as bright as forelimbs); hairs whitish-rufous at tip. Soles of all feet very densely covered with dark grey hair. Tail usually red or pale sandy colour. MS/HP ratio low (ca. 77%). Each principal incisor tooth with groove (close to inner margin of tooth) not filled with cement. Length of frontal bone shorter than length of muzzle (cf. *P. rupestris*).

Geographic Variation Pelage colour varies geographically (Smithers 1983).



Pronolagus saundersiae

Similar Species

P. crassicaudatus. HB on average longer; ear shorter (60–80 mm); tail on average shorter (mean 65 mm); sympatric in part of range.
P. randensis. Ear on average shorter (mean 84 mm); tail on average longer (mean 97 mm); marginally sympatric in part of range.
P. rupestris. Length of frontal bone almost equal to length of muzzle; marginally sympatric in part of range.

Distribution Endemic to Africa. South-West Arid (Karoo), South-West Cape and Highveld BZs. Recorded from Western Cape, Eastern Cape, KwaZulu–Natal and Mpumalanga Provinces, South Africa, along the Great Escarpment of South Africa.

Habitat Rocky kopjes and rocky hillsides with boulders. Rock crevices and boulders are an essential component of the habitat. Habitat very similar to that of other species of *Pronolagus*. Generally found at higher elevations than *P. rupestris* (Matthee & Robinson 1996).

Abundance Fairly abundant throughout the range and it is expected that their total population size exceeds 10,000 mature individuals (T. J. Robinson unpubl.).

Remarks Since this species was formerly included within *P. rupestris*, its biology is likely to be similar to that of *P. rupestris*. Comparative studies are required. No other information available.

Conservation IUCN Category: Least Concern.

Measurements

Pronolagus saundersiae

HB: 447 (380–535) mm, $n = 15$

T: 86 (50–115) mm, $n = 15$

HF: 92 (85–100) mm, $n = 15$

E: 94 (80–105) mm, $n = 15$

WT: 1.62 (1.35–2.05) kg, $n = 18$

GLS: 81.3 (70.6–91.9) mm, $n = 109$

GWS: 36.72 (32.7–41.4) mm, $n = 89$

P^2-M^3 : n. d.

Mesopterygoid space (width): 5.4 (4.1–8.5) mm, $n = 105$

Hard palate (minimum length): 6.9 (5.0–8.8) mm, $n = 106$

Upper principal incisor width: 2.5 (2.0–3.3) mm, $n = 99$

Bulla width: 6.6 (5.6–7.8) mm, $n = 3$

South Africa

Body measurements: Robinson & Dippenaar 1983a (not differentiated from *P. rupestris*)

Weight: Smithers 1983

Skull measurements: Whiteford 1995

Key References Duthie 1997; Smithers 1983.

Appendix: New Taxa 2005–2010

Gliridae

Graphiurus walterveyeni Holden and Levine, 2009. Bull. Amer. Mus. Nat. Hist. 331: 341. Distribution: riparian equatorial tropical rainforest, central Congo Basin, Democratic Republic of the Congo. Known altitude 398–431 m.

Muridae

Dendromus ruppi Dieterlen, 2009. Bonn. zool. Beitr. 56: 190. Distribution: Gilo, Imatong Mts, East Equatoria, South Sudan; altitude ca. 1800–1900 m.

Grammomys brevirostris Kryštufek, 2008. Acta Zool. Lituanica 18: 222. Distribution: Lemesikio, Loliondo, Loita Plains, Kenya (01° 30' S, 35° 09' E).

Hylomyscus anelli Carleton and Stanley, 2005. Proc. Biol. Soc. Washington 118: 636. Distribution: highlands in northern Zambia and westernmost Tanzania (Ufipa Plateau); known altitude 1220–2300 m. Remarks: Described as a subspecies of *Praomys denniae*; elevated to species by Carleton & Stanley (2005).

Hylomyscus arcimontensis Carleton and Stanley, 2005. Proc. Biol. Soc. Washington 118: 629. Distribution: Forested highlands from the Misuku Mts, northern Malawi; to Mt Rungwe and contiguous highlands, south-western Tanzania; eastwards through the Eastern Arc Mountain chain to the South Pare Mts, north-eastern Tanzania; known altitude 900–2410 m.

Hylomyscus endorobae (Heller, 1910: 3). Distribution: Highlands of west-central Kenya, including Mt Kenya, the Aberdare Mts and Mau Escarpment; ... known altitude 2135–3260 m. Remarks: Long considered a synonym of *H. denniae*; elevated to species by Carleton *et al.* 2006.

Hylomyscus pamfi Nicolas, Olayemi, Wendelen & Colyn, 2010. Zootaxa 2579: 38. Distribution: type locality Lalama forest, Benin (06° 57' N, 02° 09' E); also recorded from Lougha and Gotcha (Benin), Palimé (Togo), and Asijire and Osogbo (Nigeria).

Hylomyscus vulcanorum (Lonnberg and Gyldenstolpe, 1925: 4). Distribution: Mountains bordering the central Albertine Rift Valley, from south-western Uganda and east-central Democratic Republic of Congo, through Rwanda, to southern Burundi; known altitude 1670–3100 m. Remarks: Described as, and conventionally recognized as, a subspecies of *H. denniae*; elevated to species by Carleton *et al.* 2006.

Hylomyscus walterveyeni Nicolas, Wendelen, Barriere, Dudu and Colyn, 2008. J. Mammal. 89: 225. Distribution: Doudou Mounts, Ogooue-Maritime Province, SW Gabon (02° 09' S, 10° 30' E); 110 m.

Lophuromys chercherensis Lavrenchenko, W. Verheyen, E. Verheyen, Hulselmans and Leirs, 2007. Bull. Inst. R. Sci. Nat. Belg. Biol. 77:

102. Distribution: 22 km north-east Hirna (near road Hirna–Deder), Chercher Mts, eastern Ethiopia (09° 19' N, 41° 15' E, 2700 m).

Lophuromys kilonzoii W. Verheyen, Hulselmans, Dierckx, Mulungu, Leirs, Corti and E. Verheyen, 2007. Bull. Inst. R. Sci. Nat. Belg. Biol. 77: 33. Distribution: Magamba (04° 45' S, 38° 17' E; altitude 1550 m) (Tanzania).

Lophuromys machangui W. Verheyen, Hulselmans, Dierckx, Mulungu, Leirs, Corti and E. Verheyen, 2007. Bull. Inst. R. Sci. Nat. Belg. Biol. 77: 34. Distribution: Mt Rungwe (09° 10' S, 33° 39' E; altitude 2300 m), forest (Tanzania).

Lophuromys makundii W. Verheyen, Hulselmans, Dierckx, Mulungu, Leirs, Corti and E. Verheyen, 2007. Bull. Inst. R. Sci. Nat. Belg. Biol. 77: 38. Distribution: 'Gerodom' (foot of Mt Hanang along a brook (04° 28' S, 35° 23' E; altitude ca 2000 m) (Tanzania).

Lophuromys menageshae Lavrenchenko, W. Verheyen, E. Verheyen, Hulselmans and Leirs, 2007. Bull. Inst. R. Sci. Nat. Belg. Biol. 77: 99. Distribution: Suba Forest Station, Menagesha Forest, Central Ethiopia (08° 57' N, 38° 33' E, 2600 m).

Lophuromys pseudosikapusi Lavrenchenko, W. Verheyen, E. Verheyen, Hulselmans and Leirs, 2007. Bull. Inst. R. Sci. Nat. Belg. Biol. 77: 106. Distribution: Sheko Forest, south-west Ethiopia (07° 04' N, 35° 30' E, 1930 m). Remarks: The exact place of capture was in disturbed humid afro-montane forest situated ca. 800 m northwards from the local agricultural office of the Sheko settlement.

Lophuromys sabunii W. Verheyen, Hulselmans, Dierckx, Mulungu, Leirs, Corti and E. Verheyen, 2007. Bull. Inst. R. Sci. Nat. Belg. Biol. 77: 36. Distribution: Mbizi on the Ufipa Plateau, Tanzania (07.42° S, 31.40° E; altitude ±1750 m). Remarks: found on forest rim.

Lophuromys stanleyi W. Verheyen, Hulselmans, Dierckx, Mulungu, Leirs, Corti and E. Verheyen, 2007. Bull. Inst. R. Sci. Nat. Belg. Biol. 77: 31. Distribution: Mt Rwenzori-Bujuku, Uganda (00.22° N, 29.58° E; altitude 3700 m).

Praomys coetzeei Van der Straeten, 2008. Stuttgart. Beitr. Naturk. A, Neu. Ser. 1: 124. Distribution: Duque de Bragança (25 km N – 15 km E), Angola.

Otomys dollmani Heller, 1912: 5. Distribution: Known only from Mt Gargues, Mathews Range, central Kenya. Remarks: Long considered a subspecies of *O. irroratus* or *O. tropicalis*; specific validity clarified by Carleton & Byrne (2006).

Otomys orestes Thomas, 1900: 175. Distribution: Discontinuous in alpine habitats, ca. 2700–4200 m, from western and central Kenya. Remarks: Various considered as a synonym of *O. irroratus*, *O. tropicalis*, or *O. typus*; specific validity clarified by Carleton & Byrne (2006).

Otomys uzungwensis Lawrence and Loveridge, 1953: 61. Distribution: Mountain ranges in west central Tanzania to the Nyika Plateau, northern Malawi; altitude 1800–2750 m. Remarks: Conventionally considered a synonym of *O. typus*; specific validity clarified by Carleton & Byrne (2006).

Glossary

abbrev. = abbreviation

adj. = adjective

cf. = *confer*, compare with; as opposed to

Lat. = Latin

pl. = plural

q.v. = *quod vide*, 'which see'

acrocentric: describes a chromosome that has the centromere very near one end and therefore appears to have only one arm (= telocentric [*q.v.*] for practical purposes).

ad libitum: (*Lat.*) as much as one likes; having unrestricted access to a resource (e.g. water or food).

aestivate: state of torpor (*q.v.*) induced by cold or drought; usually associated with a reduced metabolic rate and inactivity.

aFN: (*abbrev.*) the total number of chromosomal arms in the autosomal chromosome complement of a species (*cf.* fundamental number [FN], which includes the chromosomal arms of the sex chromosomes as well as those of the autosomal [*q.v.*] chromosomes). Each metacentric (*q.v.*), submetacentric (*q.v.*) or subtelocentric (*q.v.*) chromosome is given a value of 2; each acrocentric chromosome is given a value of 1. *See also* fundamental number.

afroalpine: describes habitats and/or vegetation occurring above the treeline on African mountains. Includes montane grassland and heathlands.

afromontane: refers to mountainous regions in Africa, e.g. afromontane forests and afromontane grasslands.

agouti: the alternation of pale and dark bands of colour on a hair resulting in the pelage having a grizzled, speckled or 'pepper and salt' appearance.

Albertine Rift Valley: *see* Rift Valley (*q.v.*).

alisphenoid: bone in the skull.

allele: an alternative form of a gene. A diploid organism carries two alleles (which may be same or different) for each gene locus. At any one locus, there may be several possible alleles (although only two are present in a single organism).

allopatry (*adj.* **allopatric**): the situation where populations of the same or different species have non-overlapping geographic ranges; refers also to populations of the same, or different, species that are geographically separated. *cf.* sympatry (*q.v.*); syntopy (*q.v.*).

altimontane: collective term for the belts of ericaceous and afroalpine vegetation on the high mountains of tropical East Africa (White 1983).

altricial: describes young born in an undeveloped state. *cf.* precocial.

alveolus (*pl.* **alveoli**, *adj.* **alveolar**): small cavity; socket that houses the root of a tooth.

angular process: process at the posterior lower corner of the mandible; situated ventrally to the coronoid process (*q.v.*).

anteorbital: in front of the orbit (*q.v.*).

anterior palatal foramen (*pl.* **foramina**): foramen (*q.v.*) in the premaxilla and/or maxilla bone on the ventral surface of the skull

situated in rodents between the incisor teeth and the cheekteeth; foramina always in pairs and elongated in an anterior–posterior direction; sometimes referred to as the anterior incisive foramen. *See also* posterior palatal foramen.

anteroloph: a low transverse enamel ridge that forms part of the anterior cingulum located on the anterior rim of the upper molars of many rodents.

anterolophid: a low transverse enamel ridge that forms part of the anterior cingulum located on the anterior rim of the lower molars of many rodents.

anthropophilic: living or thriving with humans; inhabiting domiciles in man-made structures and buildings; thriving in habitats substantially modified by humans (e.g. towns, farmlands). *cf.* lithophilic (*q.v.*), phytophily (*q.v.*).

apomorphy (*adj.* **apomorphic**): a character state that distinguishes a group of biological organisms from others descended from a common ancestor. *cf.* plesiomorphy (*q.v.*).

arboreal: living above the ground (in trees and shrubs). *cf.* scansorial (*q.v.*); terrestrial (*q.v.*).

auditory bulla (*pl.* **bullae**): bony structure encapsulating the middle and inner ear, situated on the ventral surface of the skull. Often greatly inflated in some taxa of arid zone rodents (e.g. Gerbillinae, Dipodidae). Composed of several separate bones, which vary in size and inflation in different genera. Sometimes referred to as tympanic bulla. *See also* ectotympanic bulla.

auditory meatus (*pl.* **auditory meati**): the external opening of the ear; the passage leading from the tympanic membrane (ear drum) to the external ear.

autapomorphy: derived trait uniquely characteristic of a taxon.

autosomal: pertaining to any chromosome other than the sex chromosomes.

baculum (*pl.* **bacula**, *adj.* **bacular**): the os penis, or penis bone, which supports the penis in some mammals.

basal metabolic rate: metabolic rate required for survival in the thermal neutral zone (*q.v.*); a state that requires the lowest expenditure of energy when at rest.

basicranial axis: a line drawn in the lateral view of the skull indicating the position of the floor of the braincase, in the median line (Harrison & Bates 1991).

basisphenoid: cranial bone in middle of base of skull; the median posterior part of the sphenoid bone, forming part of the floor of the braincase.

bicuspid: having two points or cusps (particularly of teeth).

bifid: divided by a shallow or deep notch.

bipedal: body supported by the two hindlimbs; movement not using the forelimbs.

biserial: arranged in pairs (as in the cusps of molar teeth in some mammals, e.g. some rodents).

blastula: a hollow ball of undifferentiated cells (derived from a fertilized ovum by cell division), which represents one of the earliest stages of embryonic development.

- brachydont**: describes a premolar or molar tooth with low crowns.
cf. hypsodont (*q.v.*).
- braincase (= cranium)**: that part of the skull housing the brain; the part of the skull posterior to the front line of the orbits. *cf.* rostrum (*q.v.*).
- bushmeat**: meat for human consumption derived from non-domesticated mammals, birds and reptiles taken from their natural habitats and domiciles.
- bushveld**: savanna vegetation type characterized by a grassy ground layer and a moderately dense upper layer of shrubs and scattered trees.
- BZ**: (*abbrev.*) Biotic Zone.
- C or c**: (*abbrev.*) canine tooth; upper case denotes adult dentition, lower case denotes deciduous dentition (milk teeth). *See also* canine.
- c.u.**: (*abbrev.*) (*Lat. cum unguis* = with nail) sometimes added as a suffix to the hindfoot measurement (HF) to emphasize that the measurement includes the claw. *cf.* s.u. (*q.v.*).
- canine**: the tooth situated immediately posterior to the incisors or, if incisors are absent, the most anterior tooth. Tall and pointed in most mammals, but absent in rodents and lagomorphs, and in some other orders. By definition, situated on the maxilla bone. *See also* diastema (*q.v.*), dental formula (*q.v.*).
- cauda epididymides**: the ducts of the epididymides at the posterior end of the testes, which carry sperm from the testes to the vas deferens, which, in turn, carries sperm to the penis. Sometimes used to store sperm prior to copulation.
- CbL**: (*abbrev.*) *see* condylobasal length.
- cement**: bone-like material that covers part of tooth; material that anchors tooth into its socket. In lagomorphs, may be present in groove on front surface of incisor tooth.
- central Africa**: Cameroon (south of the Sanaga R.), Central African Republic (but only south of ca. 7° N), Equatorial Guinea, Gabon, DR Congo (except SE). Mainly rainforest habitats and rainforest–savanna mosaics.
- cf.** (in general usage): compare or compare with. In the context of descriptions, implies a difference or contrast: e.g. Upper incisors do not have a longitudinal groove (*cf.* *Meriones*).
- cf.** (in taxonomy): precedes the specific name if there is uncertainty in the assignment.
- cheekteeth**: the premolar (*q.v.*) and molar (*q.v.*) teeth combined; the chewing surface for rodents and lagomorphs.
- choana (pl. choanae)**: the openings of the internal nostrils on the skull, situated immediately posterior to the bony palate.
- chromosome**: one of the thread-like bodies within the nucleus of a cell that carry the genes (genetic material) in linear order; each chromosome is composed of one long molecule of DNA (and two long molecules at cell division). Chromosomes occur in pairs (one from each parent) and are visible as rod-like bodies in cells that are dividing. The total number of chromosomes in a cell is expressed as the diploid number (2n).
- cingulum (pl. cingula)**: ridge around the base of the crown of a tooth.
- clade**: branch of a phylogenetic tree containing the set of all organisms descended from a common ancestor.
- cladistic (analysis)**: a methodology that provides a classification in which organisms are grouped in terms of the time when they had a common ancestor.
- cline (adj. clinal)**: in context of geographic variation, a gradual and sequential change of a character(s) without a significant break such as would justify division into separate subspecies or species.
- CNL**: (*abbrev.*) condylo-nasal length; measurement from the most anterior part of the nasal bone to the most posterior part of the occipital condyle (exoccipital) on the same side of the skull; a similar measurement to ‘greatest length of skull’.
- comparatively**: used in the context of describing the size of one character compared with the size of the same character in a different species. Sizes described as small, medium or large (if range is divided into three) or very small, small, medium, large, very large (if range is divided into five). *cf.* relatively (*q.v.*).
- competitive exclusion**: the principle that two different species cannot indefinitely occupy the same ecological niche.
- concave**: having a curvature that curves inwards; having an outline or a surface curved like the interior of a circle or sphere. *cf.* convex (*q.v.*).
- concavity**: a concave depression in an outline or surface.
- conceptus**: embryo prior to implantation.
- conductance**: in thermal biology, the rate at which heat passes across a temperature gradient, e.g. the density and thickness of the pelage affects the rate at which body heat passes from the body to the outside. Thick pelage, which traps and holds air, results in low thermal conductance.
- condylar process**: process at the posterior upper corner of the mandible, which forms the lower hinge of the jaw articulation; fits into the glenoid fossa of the skull.
- condyle**: a rounded process on a bone, which articulates with a socket-like concavity in another bone.
- condylobasal length (CbL)**: the length of the skull from the most posterior point of one occipital condyle to the most anterior point of the premaxilla on the same side.
- congeneric**: belonging to the same genus.
- conspecific**: belonging the same species.
- convex**: having a curvature that bulges outwards; having an outline or a surface curved like the exterior of a circle or sphere. *cf.* concave (*q.v.*).
- coprophagy (adj. coprophagous)**: condition in which an individual reingests its own faeces; any animal that feeds on faeces.
- copulatory plug**: plug formed in the vagina of the female after copulation; formed from seminal fluids of the male. Prevents or reduces the chance of sperm from another male(s) entering the female reproductive tract if the female copulates again soon after copulation with the first male.
- coronoid process**: angular pointed process on the upper margin of the mandible, situated anteriorly to the condylar process (*q.v.*); does not participate in the jaw articulation.
- corpus luteum (pl. corpora lutea)**: a glandular mass of tissue on the surface of an ovary, that develops after the extrusion of an ovum from a Graafian follicle (*q.v.*); secretes the hormone progesterone.
- cotype**: originally synonymous with syntype but now used as synonym of paratype (*q.v.*).
- CR**: (*abbrev.*) *see* crown–rump length.
- cranial profile**: the shape of the cranium (that part of the skull that surrounds the brain) when viewed from the side.
- craniodental**: pertaining to the skull and teeth.

- cranium:** that part of the skull housing the brain. Also called braincase.
- crepuscular:** pertaining to the twilight, or active during twilight, when light intensity is higher than at night but lower than during the day. *cf.* diurnal (*q.v.*); nocturnal (*q.v.*).
- crown:** (1) top of head; (2) exposed part of a tooth (visible above gum), especially the grinding surface.
- crown–rump length (CR):** distance from the crown of head to the rump of a foetus (i.e. maximum length of a foetus in its natural form).
- cursorial:** pertaining to running.
- cusp** (*adj.* **cuspidate**): a prominence or sharp point, such as on the occlusal surface of some teeth. *See also* t.
- Cyrenaica:** a region of north-east Libya. Includes the Cyrenaican Plateau and that part of the Mediterranean Coastal Biotic Zone between the plateau and the sea, as well as drier terrain south of the plateau.
- cytochrome b:** a protein involved in electron exchange in the mitochondria. It is the product of a gene in the mitochondrial genome. The sequence of this gene is often compared between species in phylogenetic studies to infer relatedness.
- Dahomey Gap:** the geographic region where savanna habitat extends southwards to the West African coast in E Ghana, Togo, Benin (formerly Dahomey) and extreme SW Nigeria. The presence of savanna forms a break (or gap) in the extensive Rainforest Biotic Zone, which extends along the West African coast from Sierra Leone to Cameroon. The Dahomey Gap is an important biogeographical barrier separating the faunas to the east and west of the Gap.
- Dega:** Ethiopian word for the temperate agricultural/economic altitudinal zone, about 2300–3000 m, warm enough for cereal-based agriculture.
- delayed implantation:** a means of lengthening the interval between copulation and parturition by delaying the implantation of the blastula (*q.v.*), so that both copulation and parturition can occur in the most optimal seasons. Development to blastula stage is followed by a period of halted development lasting several weeks or months; then the blastula implants and embryonic development proceeds normally, usually without any further interruption, until the young is born.
- deme:** a unit of population that is interbreeding and separate from any other such population.
- dental formula:** a simple numerical method of denoting the number of incisor (I), canine (C), premolar (P) and molar (M) teeth on one side of the upper jaw and lower jaw, and the total number of teeth. For example, the dental formula of a primitive mammal is $I^{3/3}, C^{1/1}, P^{4/4}, M^{3/3} = 44$, which means there are three incisors, one canine, four premolars and three molars on each side of the upper jaw and also the lower jaw, making a total of 44 teeth. The formula may also be expressed in the form $^{3143}/_{3143} = 44$. Each incisor, premolar and molar is numbered according to its position in the tooththrow; superscript numbers indicate upper jaw, subscript numbers indicate lower jaw (mandible), e.g. P^4 (upper fourth premolar), M_2 (lower second molar). Dental formula, with respect to the presence and number of each of the four types of teeth, varies greatly between orders, families and genera of mammals. *See also* incisor (*q.v.*), canine (*q.v.*), premolar (*q.v.*) and molar (*q.v.*).
- diastema:** space in the mouth between the incisor teeth and cheekteeth in those mammals that feed on grasses, herbs etc. (e.g. rodents, hares, rabbits, ruminants, etc.).
- dichromatism:** condition in which members of a species show one of only two distinct colours or colour-patterns.
- diphyly:** the derivation of a taxon from two separate lines of descent. *cf.* monophyly (*q.v.*).
- diploid number (2n):** total number of chromosomes (including sex chromosomes) in a somatic cell of an organism.
- distal:** the end of any structure furthest away from the mid-line of the body or furthest from the point of its attachment. *cf.* proximal (*q.v.*).
- distichous:** arranged in two rows; e.g. long hairs of the tail in some anomalurids and some dormice (as opposed to the hairs being evenly spread all around the tail).
- diurnal:** pertaining to the daytime, or active during daytime, when light intensity is high. *cf.* crepuscular (*q.v.*); nocturnal (*q.v.*).
- DNA:** (*abbrev.*) deoxyribonucleic acid; the very large self-replicating molecule that carries the genetic information of a chromosome; each molecule is composed of two complementary chains of DNA.
- DNA hybridization:** technique of comparing the similarity between two DNA molecules by reassociating single strands from each molecule and determining the extent of double-helix formation. In phylogenetics, this technique is used to determine the relatedness of two or more taxa.
- dorsoventral** (*adj.* **dorsoventrally**): from dorsal to ventral surface; from back to belly of an animal.
- E:** length of external (outer) ear (= pinna), measured from tip of ear to the posterior point of the ear conch. For all mammals, length (and shape) is often affected by preservation.
- East Africa:** Kenya, Uganda, Rwanda, Burundi and Tanzania.
- eastern Africa:** SE Sudan, Ethiopia, Eritrea, Djibouti, Somalia, Kenya, Uganda, Rwanda, Burundi, Tanzania, Malawi (but only south of L. Malawi and east of the Shire R. Valley) and Mozambique (but only east of Malawi and north of the Zambezi R.).
- ectotympanic bone:** sheathing bone, typically hemiglobular in shape, that encloses the middle ear chamber and auditory ossicles in rodents and supports the tympanic membrane. *See also* auditory bulla.
- edaphic:** influenced by conditions of soil or substratum.
- emargination:** a distinct notch or indentation.
- embryo number:** number of foetuses within the uterus or uteri of the female (as assessed by autopsy). Expressed as mean number (with range from minimum to maximum, and sample size). *cf.* litter-size (*q.v.*).
- endemic:** restricted to, peculiar to, or prevailing in, a specified country or region.
- entoconid:** principal cusp located at the posterior lingual (inner) side of a lower molar.
- Eocene:** geological epoch (within the Tertiary period), 38–55 mya.
- epiphysis** (*pl.* **epiphyses**): any part of a long bone that is formed from a different centre of ossification and which later fuses with the bone to form its terminal part.
- evaporative water loss:** the loss of water from the body through the skin and/or the lungs. A mechanism used by mammals to reduce T_b (*q.v.*) when T_a (*q.v.*) is high. Excessive evaporative water loss may lead to dehydration if sufficient water is unavailable.

- exfoliating:** shedding flakes (e.g. of bark), or breaking into relatively thin slabs (e.g. of granitic rock).
- exoccipital condyles:** a pair of projections from the occipital bone on either side of the foramen magnum (*q.v.*), which articulate with the first vertebra.
- extant:** living at the present time. *cf.* extinct.
- extrabuccal:** condition in which incisor teeth extend anteriorly to the lips and are visible externally.
- F. R.:** (*abbrev.*) Forest Reserve.
- facultative:** having the capacity to switch from one mode of life or action to another depending on conditions or circumstances. *cf.* obligate (*q.v.*).
- fenestra** (*pl. fenestrae*): opening on a bone, or between two bones, e.g. on maxilla.
- flank:** the side of the body of a mammal.
- FN:** (*abbrev.*) *see* fundamental number.
- folivore** (*adj. folivorous*): an animal that eats leaves.
- foramen** (*pl. foramina*): an aperture (which is usually small, round or elliptical) in a bone, or between bones, for the passage of a nerve, blood vessel or muscle.
- foramen magnum:** the large opening at the posterior end of the skull through which the spinal cord passes.
- forest island:** *see* relict forest.
- form:** in taxonomy, a taxonomic unit (usually named) whose status as either a species or a subspecies is uncertain; one of the varieties found in a polymorphic species.
- fossorial:** adapted for digging; burrowing. *cf.* subterranean (*q.v.*).
- fovea:** small pit or depression.
- frontal bone:** one of a pair of bones forming the anterior part of the braincase.
- frugivorous:** fruit-eating.
- fundamental number (FN):** an ambiguous term sometimes defined as (1) the total number of chromosomal arms in the full chromosomal complement of an organism (i.e. including the sex chromosomes), or (2) the total number of chromosomal arms found in the autosomal chromosomes only (i.e. excluding the sex chromosomes). When only the autosomal chromosomes are included, some authors (but not all) use aFN instead of FN to avoid ambiguity. For further details, *see* aFN.
- fynbos:** the heath shrublands characteristic of the Cape Floristic Kingdom (within the South-West Cape Biotic Zone) of South Africa. Dominant plants are sclerophyllous, evergreen, low (<3 m), bushy and fine-leaved, but there are also scattered taller bushes and, less often, very widely spaced trees. Contains an exceptionally high number of endemic species of plants. The three main components on nutrient-poor sandy soils are species of Ericaceae, Restionaceae and Proteaceae. Also includes 'renosterveld' (dominated by species of Asteraceae) on nutrient-rich silt or clay soils.
- G. R.:** (*abbrev.*) Game Reserve.
- gallery forest:** type of forest outlier (in a savanna region) found in narrow sheltered valleys and ravines on hillsides, where soils are moist enough, and conditions humid enough, to support rainforest trees (Rosevear 1953).
- genotype:** genetic term to describe the genetic constitution of an individual inherited from its parents. *cf.* phenotype (*q.v.*).
- gestation:** the development of embryo/foetus that takes place in the uterus; the period during which this development takes place.
- The gestation period is defined as the interval between conception and parturition (birth). Strictly speaking, the gestation period is not the interval between copulation (mating) and parturition (birth), although many authors take it to be this interval.
- glans penis:** the bulbous tip of the penis.
- glenoid fossa (= glenoid):** the cavity (fossa) in the squamosal bone of the skull for the articulation of the condyle of the mandible (lower jaw) in mammals; visible on lateral and/or ventral views of skull depending on the taxon.
- GLS:** greatest length of skull, measured from anterior end of incisor teeth or nasal bone (whichever is most anterior) to the posterior end of the skull (occiput, occipital condyles or auditory bullae, whichever is most posterior).
- Graafian follicle:** the structure in the mammalian ovary that contains the developing ovum, and from which the ovum is released at the time of ovulation.
- gracile:** lightly built. *cf.* robust
- granivore** (*adj. granivorous*): an animal that eats grains and seeds.
- gregarious:** living together in groups, flocks, herds.
- Gregorian Rift Valley:** *see* Rift Valley.
- guard hair:** long thin bristle-like hairs, mainly on the back and flanks, which project beyond the soft hairs of the pelage; when present, conspicuous but never as numerous as soft hairs; probably tactile in function.
- gular:** pertaining to the upper part of the throat (the gula) as in gular gland, gular pouch, gular region. *See also* gular patch.
- gular patch:** in lagomorphs, patch of hair on throat, often contrasting in colour with that of the surrounding pelage; may be referred to as gular collar when extends dorsally on neck. *See also* nuchal patch.
- GWS:** (*abbrev.*) greatest width of skull; in rodents, usually across the widest point of the zygomatic arches, although in some species the widest point is across the braincase. *See also* zygomatic arch.
- hallux:** the first digit of the hindlimb; the big toe.
- hamada:** flat plain covered with pebbles of various sizes on a hard substrate in an arid environment. Much of the Sahara Desert is formed of hamada.
- hard palate:** the bony ventral part of the skull (*see also* palate). In lagomorphs, the hard palate is much reduced; the shortest longitudinal distance between posterior end of the palatal foramina and the anterior end of the mesopterygoid fossa (across the 'bony palate') is a diagnostic character. *See* Figure 114. *See also* mesopterygoid space.
- HB:** (*abbrev.*) length of head and body (measured from the tip of the nose to the most posterior point of the pelvis (anterior to the first tail vertebra).
- HF:** (*abbrev.*) length of hindfoot measured from the 'ankle bone' to the tip of the longest digit; usually measured without including the claw. *See also* c.u.; s.u.
- hibernaculum** (*pl. hibernacula*): a place, domicile or roost where an animal hibernates.
- hibernation:** a state of inactivity accompanied by a reduction in metabolic rate (below basal metabolic rate [*q.v.*]), lower T_b and slow breathing. Occurs when T_a is low and food is scarce; usually lasts for weeks or months; not common in African mammals (*cf.* torpor).

- high-crowned:** refers to structure of the teeth in the toothrow of herbivorous mammals in which the premolar and/or molar teeth are tall; such teeth have open roots, grow continuously, and the crown is worn down (due to the abrasive action of chewing grass) at the same rate as the tooth grows.
- high forest:** rainforest that has matured, stabilized and reached the climax stage of succession.
- highveld:** high plateau characteristic of inland southern Africa, dominated by grasses.
- Holocene:** epoch of the Quaternary period (*q.v.*) following the Pleistocene epoch (*q.v.*), present time to ca. 11,000 years ago. Sometimes referred to as the 'Recent' epoch.
- holotype (= type):** the single specimen designated or indicated by the original author of the original description of a new species or subspecies, to be the standard reference to the essential characters of the new taxon. *see also* cotype (*q.v.*), lectotype (*q.v.*), neoparatype (*q.v.*), neotype (*q.v.*), paratype (*q.v.*), syntype (*q.v.*), topotype (*q.v.*) and type locality (*q.v.*).
- home-range:** the area (expressed in square metres, or square kilometres) routinely used by an animal for its day-to-day activities and requirements, and which contains the resources required for survival and reproduction. Within the home-range there may be a 'core area' or 'centre of activity', which is utilized more frequently than other parts (e.g. 80% or 90% of known time-based observations). *cf.* territory (*q.v.*).
- homoplasy:** similarity between different organisms or taxa resulting from evolution along similar lines (e.g. convergent evolution) rather than descent from a common ancestor.
- hyperthermia:** elevation of body temperature above normal limits due to increase in T_a (*q.v.*) or increase in metabolic rate. *cf.* hypothermia (*q.v.*).
- hypocone:** in rodents, the cusp (t8) located centrally in the posterior lamina of an upper molar tooth.
- hypoconid:** principal cusp located at the posterior lingual side of a lower molar in rodents.
- hypothermia:** drop in body temperature below normal limits; occurs in some small mammals when T_a (*q.v.*) falls, and is a means of conserving energy in cold weather. *cf.* hyperthermia (*q.v.*).
- hypsodont:** describes a premolar or molar tooth with high crowns; has short roots.
- I or i:** (*abbrev.*) incisor (*q.v.*) tooth; upper case denotes adult dentition, lower case denotes deciduous dentition (milk teeth). *See also* incisor.
- I. (pl. Is.):** (*abbrev.*) Island.
- I¹–M³:** (*abbrev.*) the length of the toothrow from the anterior end of the first upper incisor to the posterior end of the last molar. In taxa where the last molar is M² (instead of M³), the measurement is I¹–M².
- implantation:** the embedding of a blastula (*q.v.*) in the lining of the uterus.
- incertae sedis:** (*Lat.*) refers to a taxon of uncertain status and which may be taxonomically invalid.
- incisive foramen (pl. foramina):** *see* anterior palatal foramen (*q.v.*).
- incisor:** tooth rooted in the premaxillary bone (most anterior bone of upper jaw) and in an equivalent position in the mandibular bone (lower jaw); always anterior to the canine teeth, if present.
- In rodents, there is always one incisor tooth in each side of upper and lower jaws. The number and form of incisor teeth varies in different species in other orders of mammals. *See also* dental formula.
- infraorbital foramen (pl. foramina):** foramen that connects the orbit (eye-socket) with the rostrum (premaxilla and maxilla bones); outer surface often expanded to form part of the zygomatic plate (*q.v.*); foramen contains the masseter medialis muscle.
- inner:** nearest to mid-line of body, e.g. inner incisor, inner margin of ear.
- insectivore (adj. insectivorous):** an animal that eats insects.
- inselberg:** isolated rocky hill; term used mainly in western Africa. *See also* jebel; kopje.
- interaual:** between the ears.
- interorbit (= interorbital constriction):** narrowest part of the skull between the orbits when viewed dorsally at the level of the frontal bones.
- interparietal:** bone (not paired) on dorsal surface of the skull, lying between and partly posterior to the parietal bones.
- inter-specific:** between different species.
- intra-specific:** within one species; between members of the same species.
- invagination:** the formation of a cavity by the in-sinking of the outside wall or surface of a tissue or structure, thereby drawing an exterior layer into the interior of the structure to form the lining of the cavity; a cavity formed by the process of invagination.
- Isoptera:** taxonomic order containing the termites (within the phylum Insecta).
- isozyme:** any one of several different forms of an enzyme encoded by the same or different genes that differ in properties such as optimum pH or isoelectric point.
- iteroparous:** repeated reproduction throughout a season or a lifetime (*cf.* semelparous – reproduces once and then dies).
- jebel:** isolated rocky hill in savanna and arid habitats; term used mainly in northern Africa. *See also* inselberg; kopje.
- jugal:** bone of the skull that forms the middle part of the zygomatic arch (*q.v.*); anteriorly joins the maxillary process (*q.v.*) of the maxilla bone and posteriorly joins the squamosal process of the squamosal bone.
- Kaokoveld:** area of sandstone and lava hills of the Namib Desert (Biotic Zone 11b) in NW Namibia, inland from the Skeleton Coast.
- Karoo:** southern African term for grassy dwarf shrubland on the semi-arid central plateau of the western half of South Africa at altitudes of 500–2000 m.
- karyogram:** a photographic representation of a karyotype (*q.v.*) as it appears at mitosis. Individual chromosomes are arranged in pairs from largest to smallest.
- karyological:** pertaining to the chromosomes.
- karyotype:** the chromosomes in the cell of an animal. *See also* karyogram.
- Kolla:** Ethiopian term for the tropical agricultural/economic altitudinal zone, about 800–1500 m, warm enough for coffee-growing.
- kopje:** rocky hill with boulders, rock crevices and sparse vegetation; term used mainly in southern Africa. *See also* inselberg (*q.v.*); jebel (*q.v.*).

- labial:** pertaining to the lips; situated near the lips; on the outer side of the teeth within the mouth. *cf.* lingual (*q.v.*).
- labially:** in the direction of the lips. *cf.* lingually (*q.v.*).
- lachrymal bone:** small bone in skull situated at the upper anterior margin of the orbit, near the lachrymal (tear) gland.
- lambdoid crest (= supraoccipital crest):** crest or ridge of bone running transversely across back of the skull at the junction of the dorsal (parietal) and posterior (occipital) bones of the braincase.
- lambdoid suture:** the line at the junction of the occipital and parietal bones of the skull. May be clearly defined in juveniles or obscured by complete fusion in adults, or by the formation of a lambdoid crest.
- lamina** (*pl.* **laminae**): in the context of premolar and molar teeth, a transverse row of cusps (e.g. t1, t2 and t3, or t4, t5 and t6, etc.), which, when worn, form a transverse ridge of bone and dentine across the tooth.
- lectotype:** a specimen chosen from syntypes (*q.v.*) to stand as 'the type' of a species or subspecies when no holotype (*q.v.*) was designated by the author who described the new species or subspecies.
- lenticular:** lens-shaped.
- limiting factor:** the principle that the growth or functioning of an organism is limited when any essential factor (or resource) is lacking or in short supply, regardless of the quantity available of any other factor (or resource). The principle may also be applied to the proliferation and/or distribution of a population or species.
- lingual:** pertaining to the tongue; situated near the tongue; on the inner (tongue) side of the mouth. *cf.* labial (*q.v.*).
- lingually:** in the direction of the tongue. *cf.* labially (*q.v.*).
- lithophilic:** loving, or thriving amongst, stones, rocks; inhabiting domiciles in caves, on cliffs, or under or amongst rocks etc. *cf.* anthropophilic (*q.v.*); phytophilyc (*q.v.*).
- litter-size:** number of young born to a female. Expressed as mean number (with range from minimum to maximum, and sample size). *cf.* embryo number (*q.v.*).
- lobule:** small lobe.
- localized movements:** movements of an animal within part or all of its home-range within a single day or within a limited period of time. *cf.* migration (*q.v.*); nomadic movements (*q.v.*).
- longitudinal:** lengthwise; running in a head to tail direction. *cf.* transverse (*q.v.*).
- loph:** enamel crest or ridge on the cheekteeth of rodents whose principal orientation is transverse to the longitudinal axis of the teeth.
- lophate:** condition in which the cross-connections of enamel elements, on the cheekteeth of rodents, are emphasized, forming a series of more-or-less well defined lophs (*q.v.*).
- lowveld:** savanna at lower altitudes below the Great Escarpment of South Africa, with vegetation consisting of a grassy lower layer and a woody upper layer of shrubs and/or trees, at either high density (woodland) or intermediate density (bushveld, *q.v.*).
- M:** (*abbrev.*) molar tooth. *See also* molars.
- M¹–M³:** (*abbrev.*) measurement of the length of the three upper cheekteeth (first molar to third molar) in small rodents (e.g. Muridae, Dipodidae, etc.).
- Maghreb:** *see* North-West Africa.
- malleus:** the most external bone of the three ossicles of the middle ear, the handle of which is joined to the ear drum.
- mandible:** lower jaw.
- mandibular ramus:** one of the two branches (sides) of the mandible (*q.v.*); the two rami are joined at the mandibular symphysis.
- masseteric tubercle:** knob-like bony projection on maxilla bone (for attachment of part of the masseter muscle) just anterior to first cheektooth, present in some rodents (e.g. squirrels).
- mastoid:** a bone on the posterior ventral part of the skull, immediately behind the auditory meatus (*q.v.*); usually small in size, but largely swollen, as is the auditory bullae, in some arid-adapted rodents (e.g. gerbils, jerboas).
- matorral:** Mediterranean bush-like vegetation.
- maxilla** (*pl.* **maxillae**): one of the pair of bones in the skull that forms that part of each upper jaw in which the canine (*q.v.*) if present and cheekteeth (premolars and molars) (*q.v.*) are rooted.
- maxillary:** pertaining to the maxilla (*q.v.*).
- maxillary process:** projection of bone from the maxilla, which forms the anterior portion of the zygomatic arch (*q.v.*); usually oriented vertically to the anterior–posterior line of the skull.
- meatus:** a passage or channel; the opening of a passage.
- medial:** situated in the middle.
- melanistic:** having an abnormally large amount of black or dark pigment in pelage and skin.
- mesa:** Ethiopian word for the micro-habitat (usually on slopes) within afroalpine moorlands and grasslands, where it is higher and drier than surroundings areas, so dominated by (usually) *Alchemilla*.
- mesoloph (-id):** low transverse enamel ridge found on the molar teeth of many rodents, situated between the paracone (*q.v.*) and metacone (*q.v.*) and extending laterally from the mid-line of the tooth.
- mesopterygoid fossa:** U- or V-shaped depression on the ventral aspect of the skull posterior to the palate and between the pterygoid processes (*q.v.*).
- mesopterygoid space:** the maximum lateral distance across the mesopterygoid fossa (*q.v.*); a diagnostic measurements in lagomorphs. *See also* bony palate.
- metabolic rate:** *see* basal metabolic rate (*q.v.*).
- metabolic water:** water produced by oxidative processes within the body; an important source of water for arid-adapted mammals when free (drinking) water and water within the food is in short supply or unavailable.
- metacarpals:** the long bones of the hand, situated between the carpal bones of the wrist and the proximal phalanges of the fingers.
- metacentric:** describes a chromosome with the centromere at or very near the middle of its length, so there are two arms of equal or almost equal length (ratio not greater than 1 : 1.1). *cf.* submetacentric (*q.v.*).
- metacone:** in rodents, the cusp (t9) located on the labial side of the posterior lamina of an upper molar tooth.
- metatarsals:** the long bones of the foot, situated between the tarsal bones of the ankle and the most proximal phalanges of the toes; very elongated in saltatorial species (e.g. jerboas).

- microcomplement fixation:** in molecular evolutionary studies, species can be compared by the extent to which antibodies to the proteins of one species cross-react to the proteins of another species. The extent of cross-reaction is indicative of the similarity of the proteins and, by inference, the evolutionary affinity of the two species. Albumin is a protein commonly used for these studies.
- migration:** movements of species that travel, predictably and more-or-less directly, from one habitat to another (and back again), along predetermined routes, in response to seasonal changes in climate, food supply or any other resource. *cf.* localized movements (*q.v.*); nomadic movements (*q.v.*).
- milk teeth:** teeth (usually simple) occurring in newborn mammals, or appearing soon after birth, and preceding the permanent teeth of the adult animal. Also called deciduous teeth.
- Miocene:** geological epoch (within the Tertiary period), ca. 5–23 mya.
- miombo:** a vernacular name applied to trees in the genus *Brachystegia*; a type of savanna woodland in the Zambezian region where *Brachystegia* spp. are the commonest trees or one of the commonest trees.
- Mistbelt:** foothills along the eastern Great Escarpment that experience regular fogs, with vegetation comprising mainly grasslands and patches of afro-montane forest in protected valleys and ravines.
- mitochondrial DNA:** the small amount of DNA contained within the mitochondria of a cell.
- molar:** grinding tooth or teeth on the maxilla bone; the most posterior teeth of the cheekteeth in adult mammals. Not preceded by deciduous (milk) teeth. Each molar tooth has many cusps arranged in a standardized way that is diagnostic for the taxon. The number of molars varies in different taxa, but is usually three in each ramus of the upper and lower jaw of rodents. The relative size of M1, M2 and M3 varies according to taxon; commonly M1 is the largest and M3 is the smallest. Because the molar teeth do not grow continuously, wear of the molars (resulting in differing patterns of dentine and enamel) provide a relative (but rarely absolute) measure of the age of an individual rodent. *See also* dental formula.
- molariform:** similar in form to a molar tooth; used to describe the form of the premolar teeth in some taxa.
- monoestrous:** having one litter per year. For species and/or populations described as being monoestrous, each female has one litter/year. *cf.* polyoestrous (*q.v.*).
- monogamy** (*adj.* **monogamous**): a mating system in which one male mates with one female, usually for the whole of an animal's life. Neither sex has the opportunity of monopolizing additional members of the opposite sex. Fitness often maximized through shared parental care. *cf.* polygyny (*q.v.*).
- monophyletic:** describes a taxonomic group descended from a common ancestor that was itself a member of that taxonomic group, and including *all* the descendants of that ancestor. *cf.* paraphyletic (*q.v.*); polyphyletic (*q.v.*).
- monophyly:** derivation of taxa from a common ancestor. *cf.* diphyly (*q.v.*), polyphyly (*q.v.*).
- monotocous:** normally having only one young per litter (twinning, if it occurs, is very rare and abnormal). *cf.* polytocous (*q.v.*).
- monotypy** (*adj.* **monotypic**): describes a taxon containing only one immediately subordinate taxonomic unit, e.g. a monotypic family contains only one genus; a monotypic genus contains only one species, a monotypic species contains no subspecies. *cf.* polytypy (*q.v.*).
- mopane:** a vernacular name applied to the tree *Colophospermum mopane*; a type of savanna woodland in the Zambezian region in which *C. mopane* is the commonest species of trees.
- MS/HP:** in Lagomorpha, the ratio of the mean width of the mesopterygoid space (MS) to the mean minimum length of the hard palate (HP), expressed as a percentage. *See* Figure 114.
- Mt:** (*abbrev.*) Mount.
- mtDNA:** (*abbrev.*) mitochondrial DNA (*q.v.*).
- Mts:** (*abbrev.*) Mountains.
- muzzle:** the snout; the nose and jaws of a mammal.
- mya:** (*abbrev.*) millions of years ago.
- n. d.:** (*abbrev.*) no data.
- N. P.:** (*abbrev.*) National Park.
- neonate:** a newly born animal.
- neoparatype:** any specimen described at the same time as the neotype (*q.v.*).
- neotype:** a specimen selected as the type in cases where the primary types are definitely known to be lost or destroyed.
- nipple:** external opening of a mammary gland. Nipple number and position vary according to the taxon, but are consistent within a species. Nipples arranged in pairs, one of the pair on each side of the body. Nipple number given as: number on one side of the body, and total for both sides. For example, in some murid rodents, nipples are found in the pectoral and inguinal regions, and the number is given as, e.g. 1 (pectoral) + 2 (inguinal) (all on one side) = 6 (both sides). In squirrels, nipples are more evenly spaced, and are given as axillary + pectoral + abdominal + inguinal (all on one side) = total (both sides).
- nipple-clinging:** the behaviour of neonates and unweaned young that remain semi-permanently attached to the nipples of the mother (including while she is foraging) for a period of several days to several weeks. In some species, there is a gap between the two deciduous upper incisor teeth, which assists in nipple-clinging.
- nipple-dragging:** situation when a mother drags her neonates and unweaned young, firmly attached to her nipples, when she is active outside her nest. *cf.* nipple-clinging.
- nocturnal:** pertaining to the night, or active during the night, when light intensity is at its lowest; between sunset and sunrise. *cf.* crepuscular (*q.v.*); diurnal (*q.v.*).
- nomadic movements:** irregular and unpredictable movements, from one locality to another, made by species living in unpredictable habitats. *cf.* localized movements (*q.v.*); migration (*q.v.*).
- nomen dubium:** when the available evidence is not sufficient to permit the identification of a species, its name is considered to be a *nomen dubium* and therefore not available for taxonomic purposes.
- nomen nudum:** a name that is not valid because, when it was originally published, the organism to which it referred was not adequately described, defined or sketched. The name is therefore invalid because it is impossible to associate it indisputably with any specific organism.
- nominate subspecies:** the subspecies that bears the name of the species to which it belongs, only brought into existence by the

- creation of one or more other subspecies in the same species. Subspecies are rarely used in rodent and lagomorph taxonomy at the present time.
- North Africa:** those parts of Mauritania, Morocco, Algeria, Tunisia, Libya and Egypt that are north of the Sahara Desert.
- north-central Africa:** southern Chad and southern Sudan, west of the Nile R. and south of the Sahara Desert. Mainly savanna habitats.
- North-West Africa:** (= the Mahgreb) those parts of Mauritania, Morocco, Algeria, Tunisia and NW Libya that are north of the Sahara Desert.
- nuchal patch:** patch of hair on back of neck, often contrasting in colour with that of the surrounding pelage (in lagomorphs). *See also* gular patch.
- nulliparous:** not having given birth.
- obligate:** obligatory; limited to one mode of life or action irrespective of conditions or circumstances. *cf.* facultative (*q.v.*).
- occipitonasal length:** the length from the most anterior margin of the nasal bones to the posterior part of the occiput. *cf.* greatest length of skull (*q.v.*).
- occiput:** the posterior part of the skull, above and lateral to the foramen magnum (*q.v.*).
- occlusal:** pertaining to the biting surface of a tooth.
- olecranon process:** large bony process at the proximal end of the ulna bone (forearm); very well developed in some subterranean mammals.
- Oligocene:** geological epoch (within the Tertiary period), ca. 23–38 mya.
- omnivore** (*adj.* **omnivorous**): an animal that eats a wide range of foods.
- opisthodont:** of the incisor teeth, directed posteriorly. *cf.* proodont (*q.v.*); orthodont (*q.v.*).
- orbit:** bony cavity (eye-socket) in which the eye is situated.
- orthodont:** of the incisor teeth, directed more or less in a vertical plane. *cf.* pro-odont (*q.v.*); opisthodont (*q.v.*).
- outer:** furthest from the mid-line of the body.
- ovulation:** the release of female gametes (ova, egg cells) from the ovary.
- ovum:** the female gamete or egg cell.
- owl pellets:** waste material, normally cylindrical with rounded ends, regurgitated by owls, which contains undigested fragments of bone, hair, feathers and scales etc. from the prey; for mammalogists, useful in determining indirectly the species of small mammals in a habitat.
- P or p:** (*abbrev.*) premolar tooth; upper case denotes adult dentition, lower case denotes deciduous dentition (milk teeth). *See also* premolar.
- P⁴–M³:** (*abbrev.*) measurement of the length of the four cheekteeth (fourth premolar to third molar) in Sciuridae etc. *cf.* M¹–M³.
- Palaearctic:** a zoogeographic region comprising temperate Europe, North Africa and the Arabian peninsula.
- Palaeocene:** geological epoch (within the Tertiary period), 55–65 mya.
- palatal ridges:** a series of ridges on the roof of the mouth (soft palate) arranged transversely; not visible on bony palate of skull. The number and arrangement of ridges are useful diagnostically in some genera of murids.
- palate:** the roof of the mouth. The anterior part (hard palate) comprises the bony palate (*q.v.*, formed by the premaxillae, maxillae and palatine bones), and a covering mucous membrane. The soft palate (covering the bony palate and extending posteriorly) is composed only of muscular tissue covered by a mucous membrane. *See also* bony palate.
- palpably pregnant:** describes a pregnant female whose pregnancy has been detected only by feeling the foetus(es), not by dissection. It is not possible to detect the early stages of pregnancy by palpation.
- papilla** (*pl.* **papillae**): a small projection or protuberance.
- paracone:** in rodents, the cusp (t6) located on the labial side of the central lamina of an upper molar tooth.
- paraconid:** principal cusp located at the anterior lingual side of lower molars in basal groups related to rodents; absent in Rodentia proper and believed to be a synapomorphy for the Order.
- paraoccipital process:** narrow strut-like bone, which projects ventrally from the paraoccipital bone on the posterior part of the skull.
- parapatry** (*adj.* **parapatric**): the situation where two or more species have geographic ranges that are contiguous but do not overlap. This abutting may be along a line of habitat discontinuity, an ecotone, or an altitudinal/climatic contour, but may also arise from competitive exclusion of one (or both) by the other.
- paraphyletic:** describes a taxon containing units that have evolved from a single ancestral taxon but which do not contain all of the descendants of the most recent common ancestor.
- paratype:** a specimen collected at the same time and place as the holotype (*q.v.*) and designated by the original authority as such. There may be one or more paratypes.
- parietal:** one of the pair of bones forming the vault of the braincase, situated between the frontal and the occipital bones.
- parous:** having given birth.
- partim:** in taxonomy, used in context of taxon names and synonyms to indicate that not all material that has been referred to the name is currently considered to belong to that name.
- parturition:** the act of giving birth.
- patagium** (*pl.* **patagia**): membranous flap of skin stretching between forelimb and hindlimb, and between hindlimb and tail; when stretched, forms an aerofoil that facilitates gliding (non-flapping flight) from tree to tree in some taxa of rodents. The same term is used for the flight membranes in bats.
- pectoral:** pertaining to or situated on the chest.
- pelage:** the hairy, woolly or furry covering of the body in mammals. The pelage variously consists of hairs, guard hairs and underfur according to the species.
- pencil:** hairs on terminal end of tail, which form a small slight tuft; hairs usually rather short (5–10 mm); hairs may extend beyond the end of the bony tail (e.g. *Gerbillus*, *Tatera*, *Taterillus*, *Grammomys*).
- phalanx** (*pl.* **phalanges**): one of the bones in a finger.
- phenotype:** the visible characters of an individual resulting from the interaction between the genotype (*q.v.*) and the environment.
- philopatry:** the tendency to remain in, or consistently return to, the place where one was born.
- philtrum:** the groove present in some mammals on the median line of the upper lip.
- phylogeny** (*adj.* **phylogenetic**): the evolutionary history and line of descent of a species or higher taxonomic unit.

- phytophilic**: living or thriving with plants; inhabiting domiciles in foliage, on tree trunks, in hollow trees, under bark etc. *cf.* anthropophilic (*q.v.*); lithophilic (*q.v.*).
- piloerection**: the erection of hairs, which occurs as a means of conserving heat (*see* temperature regulation) and, in some mammals, as a threat display.
- pinna** (*pl.* **pinnae**): the external (outer) ear.
- placental scar**: a scar on the inner surface of the uterus of a mammal indicating the site where a placenta was attached during pregnancy. If the average number of young/litter is known, the number of placental scars can give an indication of the number of litters that a female has had during her life-time.
- planar**: the condition in which the occlusal surface of the cheekteeth in rodents is flat, lying in one plane; a specialization usually found in species with high-crowned teeth whose chewing motion is primarily propalinal.
- plantar**: of the sole of the foot.
- Pleistocene**: geological epoch (within the Quaternary period), ca. 10,000 to 1.7 million years ago.
- plesiomorphy** (*adj.* **plesiomorphic**): having a similar form; a character state shared by different groups of biological organisms and inherited from a common ancestor. *cf.* apomorphy (*q.v.*).
- Pliocene**: geological epoch (within the Tertiary period), ca. 2–5 mya.
- poikilothermic**: describes animals whose resting body temperature is the same as, or within 1–2 degrees of, the ambient temperature.
- pollex**: Digit 1 ('thumb') of forefoot ('hand').
- polymorphism** (*adj.* **polymorphic**): the existence, within a species or population, of individuals having different forms (colour, size, shape etc.).
- polyoestrous**: having two or more litters/year. For species and/or populations that are described as polyoestrous, each female has two or more litters/year. *cf.* monoestrous (*q.v.*).
- polyphyletic**: describes a taxon derived from two or more ancestral sources; not of a single, immediate line of descent (Mayr *et al.* 1953). *cf.* monophyletic (*q.v.*).
- polyphyly**: derivation of a taxon from two or more ancestral sources. *cf.* monophyly (*q.v.*).
- polytocous**: normally or often having more than one young per litter. *cf.* monotocous (*q.v.*).
- polytypy** (*adj.* **polytypic**): a taxon that has several taxa in the next lower taxonomic category, e.g. a polytypic family contains two or more genera, a polytypic genus has two or more species, a polytypic species has two or more subspecies. *cf.* monotypy (*q.v.*).
- postauricular**: behind the external ear (pinna).
- posterior palatal foramen** (*pl.* **foramina**): foramen (*q.v.*) (often inconspicuous) in the palatine bone on the ventral surface of the skull situated in rodents between the cheekteeth; foramina are always in pairs and elongated in an anterior–posterior direction. *cf.* anterior palatal foramen (*q.v.*).
- posteroloph**: transverse enamel ridge that forms part of the posterior cingulum, defining the posterior rim of the upper molar teeth.
- postorbital**: behind (posterior to) the orbit.
- postorbital process**: a process that projects laterally from the parietal bone above the orbit; well developed in some species of squirrels.
- postpartum oestrus**: an oestrus cycle immediately after (or very soon after) parturition and while lactating. *See* Vol. 4.
- precocial**: describes young in which fur covers the body, eyes and ears are open, and adult-like movements are possible immediately or very soon after birth. *cf.* altricial.
- pregnancy rate**: the proportion of adult females in a population which are pregnant at any one time; usually expressed as a percentage of the total number of adult females.
- premaxilla**: one of a pair of bones at the anterior end of the skull, which bears the incisor teeth.
- premolar**: tooth or teeth on the maxilla bone situated immediately anterior to the molar teeth; usually preceded in time by deciduous (milk) teeth; multi-cusped. Structure and function of premolar teeth vary according to species and are diagnostic for a taxon. In many taxa of rodents, premolar teeth are not present; in others, only P⁴ is present. *See also* dental formula.
- preorbital**: anterior to the eye.
- prismatic**: high crowned molar tooth of rodents in which conical cusp definition is lost and the flat occlusal surface appears as interlacing triangular-shaped prisms.
- promiscuity**: a mating system in which each male mates with several females and each female mates with several males.
- pro-odont**: of the incisor teeth, directed anteriorly. *cf.* orthodont (*q.v.*); opisthodont (*q.v.*).
- propalinal**: chewing motion in certain rodents, typically associated with the evolution of high-crowned molars, in which the prevalent movement of the mandible is anterior–posterior (as in species of Arvicolinae).
- protocone**: in rodents, the cusp (t5) located centrally in the middle lamina of an upper molar tooth.
- protoconulid**: small accessory cusp found in certain species of gerbilline rodents, situated between the protoconid and anteroconid and assimilated with the latter after a little wear. Presence of protoconulid is considered as a primitive trait.
- proximal**: nearest to the body or to the mid-line of the body; nearest to the point of attachment. *cf.* distal (*q.v.*).
- pterygoid**: one of a pair of cranial bones forming part of the roof of the mouth.
- Quaternary**: geological period, present time to ca. 2 mya, comprising two epochs: Pleistocene (*q.v.*) and Holocene (Recent) (*q.v.*).
- R.**: (*abbrev.*) River.
- ramus**: one half (left or right) of the lower jaw or mandible.
- range length**: distance between the most distant captures (by live-trapping) of an individual; a rough method of assessing home-range (*q.v.*).
- relatively**: used in the context of describing the size of one character relative to the size of a different character in the same individual. Usually expressed as a percentage. e.g. Tail 80–90% of HB. *cf.* comparatively (*q.v.*).
- relict forest**: a forest that persists where local conditions are favourable after the disappearance of forest from the surrounding area as a result of climate change or human activity. Relict forests include those at the base of inselbergs that are watered by rainwater running off the inselberg, and forests growing in graveyards and sacred sites that are protected. Sometimes known as forest islands.

- relict population:** one that persists where local conditions are favourable after the extinction of the species from at least part of its former range.
- reproductive capacity:** number of young produced by a female during the breeding season.
- reproductive chronology:** the timing and duration of events, such as spermatogenesis, copulation, ovulation, gestation, parturition, lactation and reproductive inactivity, throughout the year.
- ridge:** in teeth, a ridge connecting two cusps. Also called commissure.
- Rift Valley:** deep valley extending from the Red Sea through Ethiopia and East Africa to Malawi; formed ca. 12 mya by subsidence of the valley floor and uplifting of the edges to form mountains and highlands. Comprised of four parts: (1) Ethiopian Rift Valley dividing the Ethiopian plateau into two parts; (2) Albertine Rift Valley (Western Rift Valley) in Uganda, E DR Congo and W Tanzania; (3) Gregorian Rift Valley (Eastern Rift Valley) in N Kenya, C Kenya and N Tanzania; (4) Malawian Rift Valley – the extension of the Albertine Rift Valley in Malawi. The Rift Valleys are noted for their many deep and beautiful lakes.
- riverine forest:** forest growing along the banks of a river or stream where conditions are moister than in the surrounding area. Sometimes referred to as ‘fringing forest’.
- Robertsonian fusion:** a chromosomal event involving the apparent fusion of non-homologous single-armed (telocentric *q.v.*) chromosomes to form a bi-armed (metacentric *q.v.* or submetacentric *q.v.*) chromosome. Modern studies have revealed that all chromosomes have two arms, even if the smaller one is not detectable by light microscopy. Consequently, the term Robertsonian translocation is becoming more commonly used than Robertsonian fusion.
- rostral:** pertaining to the rostrum.
- rostrum:** that portion of the skull anterior to the front line of the orbits and supporting the upper part of the muzzle, comprised of the nasals, premaxillae and maxillae bones.
- rupicolous:** rock-living.
- s.u.:** (*abbrev.*) (*Lat. sans unguis* = without claw) sometimes added as a suffix to the hindfoot measurement to emphasize that HF has been measured without the claw. However, since this is the standard method of measurement for rodents and lagomorphs (that often have broken or worn claws), most authors write ‘HF’, not ‘HF s.u.’. *cf.* c.u. (*q.v.*).
- sagittal crest:** longitudinal crest of raised bone on the mid-dorsal line of the cranium.
- saltatorial:** jumping on the two hindlimbs, as in jerboas and springhares.
- sand-bathing:** a method of cleaning the pelage by lying in the sand; during sand-bathing, the body is wriggled and the limbs kick and throw sand over the body. Observed in many species of desert rodents.
- scansorial:** climbs or scrambles over logs and in low vegetation close to the ground. *cf.* terrestrial (*q.v.*); arboreal (*q.v.*).
- sclerophyllous:** describes vegetation having hard leaves that are resistant to drought.
- scrotal:** pertaining to, or within, the scrotum (*q.v.*).
- scrotum:** an external sac containing the testes and epididymides in male mammals.
- scuttling:** rapid cursorial locomotion over the ground (or similar surfaces) in which the limbs move quickly; for rats and other small mammals, scuttling is quadrupedal.
- Senegambia:** Senegal and Gambia.
- sensu lato:** (*Lat.*) in a broad sense.
- sensu stricto:** (*Lat.*) in a strict sense.
- septum:** a dividing wall separating two cavities.
- sex ratio:** the number of males to the number of females, usually expressed as a proportion to one male, e.g. 1 : 1 (equal numbers of males and females), 1 : 0.5 (= twice as many males as females), 1 : 2 (= twice as many females as males).
- sexual dimorphism:** observable (phenotypic) difference(s) (e.g. in colour, size or form) between the males and females of a species or higher taxon.
- sibling species:** true species that are reproductively isolated and do not interbreed but are difficult to separate solely on basis of morphological characters.
- side-stripe:** longitudinal stripe(s) of contrasting colour on each flank, usually from shoulder to rump or upper part of hindlimb. Number of side-stripes on each flank varies from one (as in some squirrels) to about four (as in some species of *Lemniscomys*). Most side-stripes are continuous, but in some species of *Lemniscomys* some side-stripes are broken into spots and streaks.
- singleton:** a neonate born singly as opposed to being one of a larger litter.
- sister species:** species thought to have arisen from a single dichotomous splitting event.
- south-central Africa:** Angola, SE DR Congo, Zambia and Malawi (but only west of L. Malawi and the Shire R. Valley).
- southern Africa:** south of the Cunene and Zambezi Rivers, i.e. Namibia, Botswana, Zimbabwe, southern Mozambique and South Africa (after Smithers 1983).
- sperm:** any male gamete; the male cell that fuses with a female gamete (ovum, egg cell) to produce a fertilized egg or zygote from which an embryo will develop.
- spermatogenesis:** the formation of sperm in the testes.
- sub, sub-:** prefix meaning under, signifying beneath or ventral to (as in anatomical features) or south of (as in sub-Saharan); less than (as in subsonic); not quite, nearly, almost, somewhat (as in subequal, subtriangular). In taxonomy, indicates a group just below the status of the taxa immediately following it (e.g. a genus may contain two or more subgenera).
- subauricular:** below the ear.
- subcaudal:** below the tail.
- submetacentric:** describes a chromosome with the centromere somewhat nearer one end than the other, so there are two arms of somewhat unequal length (ratio 1 : 1.2–1.9). *cf.* metacentric (*q.v.*); subtelocentric (*q.v.*).
- subspecies:** a geographically localized and isolated subdivision of a species, which differs genetically, morphologically and taxonomically from other subdivisions of the species.
- subtelocentric:** describes a chromosome with the centromere much nearer one end than the other, so there are two arms of very unequal length (ratio 1 : >2).
- subterminal:** just below the end or tip.
- subterranean:** living permanently below the ground; subterranean mammals show many adaptations for life underground, e.g. short

- limbs, thickset shoulder blades and forelimbs, reduced eyes, reduced ability to see, reduction (or absence) of ear pinnae, large extra-buccal incisors, sensory hairs over all the body, feet fringed with hairs, extensive subterranean burrows, etc. (e.g. species of Bathyergidae and Spalacidae). *cf.* fossorial (*q.v.*).
- suckling:** the act of a mother giving milk directly from her breast (mammary glands) to her young. Mothers suckle; their young suck.
- supraorbital:** above (dorsal to) the orbit.
- supraoccipital crest:** crest or ridge of bone, oriented transversely across the back of the skull, at the junction of the parietal and/or supraoccipital bones and the occipital bone. Sometimes referred to as the lambdoid crest.
- supraorbital process:** bony process on outer edge of frontal bone extending outwards above the orbit in lagomorphs.
- supraorbital ridge:** ridge of bone along upper rim of orbit (eye-socket); can be well developed, low or absent.
- sympatry** (*adj.* **sympatric**): the situation where populations of two or more different species have overlapping geographic ranges; refers also to populations of two or more species whose geographic ranges are partly or wholly overlapping. They may or may not interact. *cf.* allopatry (*q.v.*); syntopy (*q.v.*).
- symplesiomorphy:** a primitive or ancestral character shared by two or more groups, which is inherited from ancestors older than the last common ancestor.
- synanthropic:** associated with humans and/or their houses and other buildings.
- synapomorphy** (*adj.* **synapomorphic**): situation in which a homologous character is present in two or more taxa and is thought to have originated in their most recent common ancestor. *See also* apomorphy.
- synonym:** one or more of different names for the same taxonomic unit. A synonym may be a 'senior synonym' (the oldest name), or a 'junior synonym' (a more recent name), which is no longer considered to be valid. May be used to refer to all names that have been associated, at some time in the past, with the taxonomic unit as currently understood.
- syntopy** (*adj.* **syntopic**): describes the situation where two or more species use the same or similar habitats and activity times. They may or may not interact. *cf.* allopatry (*q.v.*); sympatry (*q.v.*).
- syntype:** any specimen, or one of a series of specimens, used to designate a species when a holotype (*q.v.*) and paratype(s) (*q.v.*) have either not been selected, or have been lost or destroyed.
- systematics:** the science of arranging organisms in a way that reflects their evolutionary relationships; such relationships may be expressed as a phylogeny (*q.v.*). Often defined (somewhat incorrectly) as a synonym of taxonomy (*q.v.*).
- t:** (*abbrev.*) (= tubercle) as used to describe and number the cusps on premolar and molar teeth, e.g. t1, t3, t5. The presence/absence, position and size of longitudinal ridges between cusps are diagnostic for many taxa of rodents.
- T:** (*abbrev.*) length of tail, measured from the anterior end of the first caudal vertebra to the posterior end of the last caudal vertebra (excluding any tufts, bristles etc. at tip of tail).
- T_a:** (*abbrev.*) ambient temperature; the temperature in which an animal is living. *cf.* T_b (*q.v.*).
- taloid:** heel at the posterior end of a lower molar tooth.
- tapetum lucidum:** light-reflecting layer in the retina of the eyes of some vertebrates.
- taxon** (*pl.* **taxa**): any defined unit (e.g. family, genus, species, subspecies) in the classification of organisms.
- taxonomy:** the science of biological nomenclature; the study of the rules, principles and practice of naming and classifying species and other taxa. Sometimes considered as an integral part (and near synonym) of systematics (*q.v.*).
- T_b:** body temperature; the temperature of the core (central) part of an animal. *cf.* T_a (*q.v.*).
- telocentric:** describes a chromosome that appears to have a terminal centromere and therefore only one arm. Modern studies have revealed that all chromosomes have two arms but the smaller arm of telocentric chromosomes is not visible under a light microscope.
- termitarium** (*pl.* **termitaria**): a place where termites (Insecta: Isopoda) live. Often a large mound of modified hard soil. The shape and size of a termitarium is unique to each species of termite.
- terrestrial:** living on the ground. *cf.* arboreal (*q.v.*); scansorial (*q.v.*).
- territory:** an area defended by an individual against certain other members of the species, usually by overt aggression or advertisement; territory is marked by the urine, faeces or glandular secretions of the territory's owner. *cf.* home-range. The boundary of a territory is a line across which the status of the territory holder changes from dominant to subordinate.
- Tertiary:** geological period, 2–65 mya, comprising five epochs: Palaeocene, Eocene, Oligocene, Miocene and Pliocene (*q.v.*); followed by the Quaternary period (*q.v.*).
- testes:** the male gonads, or testicles, in which spermatozoa are formed and in which the male hormone is produced.
- thermoneutral zone:** the range of body temperatures within which an animal does not have to increase its metabolic rate to increase T_b (*q.v.*) (when T_a (*q.v.*) is low) and reduce T_b (when T_a is high).
- thermoregulation:** regulation of body temperature, either by metabolic or behavioural means (or both simultaneously) so that T_b (*q.v.*) is kept more or less constant.
- thoracic:** pertaining to, or situated upon, the chest.
- TL:** (*abbrev.*) total length from tip of snout to posterior end of tail. Equivalent to the head and body length and tail length added together. *See also* HB and T.
- toothrow:** the teeth situated posterior to the diastema in rodents and lagomorphs (and some other orders of herbivorous mammals). The upper and lower tooththrows are comprised of premolar and molar teeth, or only molar teeth. Although small cusps are present on the surface of each tooth in a tooththrow in young animals, these cusps wear with age to form a smooth grinding surface; the pattern of enamel and dentine of the grinding surface may be used to assess the age of the individual. A tooththrow may contain three teeth (all molars, e.g. most murid rodents), four teeth (one premolar, three molars, e.g. some squirrels, porcupines, springhares), five teeth (two premolar, three molars, e.g. some squirrels) or six teeth (three premolars, three molars, e.g. lagomorphs).

- topotype**: any specimen from the type locality (*q.v.*), i.e. the same locality as that from which the holotype (*q.v.*) was taken.
- topotypical**: pertaining to the type locality (e.g. a topotypical population is one found at the type locality).
- torpor** (*adj.* **torpid**): a state in which there is reduction of metabolic rate and a lowering of T_b (*q.v.*) when T_a (*q.v.*) declines; arousal from torpor occurs when T_a increases and without high energy costs to the individual. Torpor is associated with a state of inactivity and reduced responsiveness to stimuli. Torpor lasts for only short periods of time (hours or days) (*cf.* hibernation).
- transverse**: in a direction across the body from side to side. *cf.* longitudinal (*q.v.*).
- tricuspid**: having three points or cusps (particularly of teeth).
- tubercle**: a small rounded protuberance, e.g. a cusp of a tooth.
- tympanic bulla** (*pl.* **tympanic bullae**): one of a pair of usually rounded bony capsules, on underside of skull (one on each side), housing structures of the middle and inner ear in many mammals. Also called auditory bulla (*q.v.*).
- type description**: the original description of a species; the original description of the holotype (and paratype[s] if included).
- type locality**: the locality from which a holotype (*q.v.*), lectotype or neotype was collected. Also called topotypical locality.
- type series**: the holotype and all specimens collected at the same place and time and used, together with the holotype, to describe a new species.
- type species**: usually the species that was the first to be described under the name of a new genus. Not all genera had a designated type species when they were first created; in such cases, other rules determine which species will be the type species.
- type specimen**: *see* holotype.
- underfur**: dense and often woolly layer of the pelage, situated close to the skin and below the soft hairs and guard hairs; usually short and present in those species that experience lower T_a .
- unicuspid**: having one cusp or point (particularly of teeth).
- vagrant**: an individual that has been found well outside the normal geographic range of its species, e.g. a bat or bird that has been wind-borne, or an animal that has been transported as a stowaway on a ship, to a distant locality.
- vascularized**: infiltrated with capillaries.
- vasoconstriction**: constriction of the capillaries of the blood system near the surface of the skin in order to reduce the rate of heat loss through the skin; a mechanism used by many mammals to conserve heat when T_a (*q.v.*) is low. *cf.* vasodilation (*q.v.*).
- vasodilation**: the dilation (or opening) of the capillaries of the blood system near the surface of the skin in order to increase the rate of heat loss through the skin; a mechanism used by many mammals to cool themselves when T_a (*q.v.*) is high. *cf.* vasoconstriction (*q.v.*).
- veld**: Afrikaans word, used mainly by southern African biologists, to refer to a wide variety of grassland vegetation types typically used for grazing. *See also* bushveld, highveld, lowveld.
- vertebra** (*pl.* **vertebrae**): any of the bones that make up the backbone.
- vibrissa** (*pl.* **vibrissae**): long stiff hairs on the face, especially around nostrils and lips; often associated with the perception of tactile sensation; 'whiskers'.
- vlei**: southern African term for a marsh or swamp, either permanent or seasonal.
- wadi**: a desert valley, usually dry at the surface except after heavy rainfall.
- water turnover**: the rate at which water (fluids) is utilized and replaced in the body per unit time (normally expressed as ml/kg body weight/day); the amount of water an animal processes through its body each day. Water turnover is related to water availability, the urine concentrating ability of the kidney, amount of protein in the diet and T_a (*q.v.*). Water turnover rates are characteristically low in arid-adapted mammals when compared with non arid-adapted mammals.
- West Africa**: ca. south of 18°N from Senegal to the Sanaga R. in Cameroon, and Bioko I. (Equatorial Guinea) (Rosevear 1965).
- Wurch**: Ethiopian word for the alpine agricultural/economic altitudinal zone, above about 3000 m, too cold for most agriculture.
- Woina Dega**: Ethiopian word for the warm-temperate agricultural/economic altitudinal zone, about 1500–2300 m, warm enough for most agriculture.
- WT**: (*abbrev.*) weight of an individual, usually expressed in grams (g) or kilograms (kg).
- ZW**: (*abbrev.*) *see* zygomatic width.
- zygomatic arch**: one of a pair of cheekbones, formed of the maxillary process anteriorly, jugal bone medially and squamosal bone posteriorly. Ranges from massive, broad, widely flared and bony, to frail, slender and cartilaginous. When present provides protection to the eyes and orbits. Also called zygoma.
- zygomatic plate**: expanded and flattened lower part of the maxillary process on the outer side of the infraorbital foramen (*q.v.*); variations in size and shape are useful for identification of some rodents.
- zygomatic width (ZW)**: greatest width between the outer aspect of one zygomatic arch to the equivalent position on the opposite zygomatic arch. *See also* GWS.

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MAMMALS OF AFRICA

VOLUME IV

HEDGEHOGS, SHREWS AND BATS

EDITED BY MEREDITH HAPPOLD AND DAVID HAPPOLD

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HEDGEHOGS, SHREWS AND BATS



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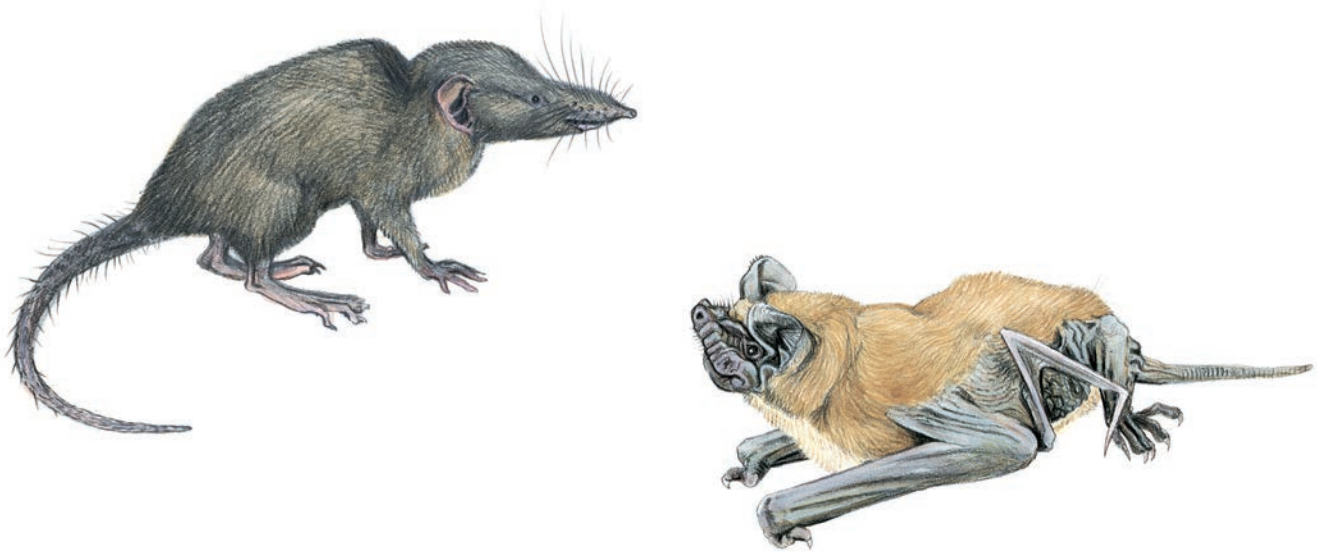
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ABOVE LEFT: Jan Kalina.

ABOVE: From left to right: Jonathan Kingdon, Thomas Butynski, Meredith Happold, David Happold and Andrew Richford.

LEFT: Jonathan Kingdon (left) and Michael Hoffmann.

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Mammals of Africa: *An Introduction and Guide*

David Happold, Michael Hoffmann, Thomas Butynski and Jonathan Kingdon

Mammals of Africa is a series of six volumes that describes, in detail, every extant species of African land mammal that was recognized at the time the profiles were written (Table 1). This is the first time that such an extensive coverage has been attempted; all previous books and field guides have either been regional in coverage, or have described a selection of mammal species – usually the larger species. These volumes demonstrate the diversity of Africa's mammals, summarize what is known about the distribution, ecology, behaviour and conservation status of each species, and serve as a guide to identification.

Africa has changed greatly in recent decades because of increases in human populations, exploitation of natural resources, agricultural development and urban expansion. Throughout the continent, extensive areas of forest have been destroyed and much of the forest that remains is degraded and fragmented. Savanna habitats have been altered by felling of trees and development for agriculture. Many of the drier areas are threatened with desertification. As a result, the abundance and geographic ranges of many species of mammals have declined – some marginally, some catastrophically, some to

extinction. Hence, it seems appropriate that our knowledge of each species is recorded now, on a pan-African basis, because the next few decades will see even more human-induced changes. How such changes will affect each mammalian species is uncertain, but this series of volumes will act as a baseline for assessing future change.

The study of African mammals has taken several stages. During the era of European exploration and colonization, the scientific study of African mammals was largely descriptive. Specimens that were sent to museums were described and named. As more specimens became available, and from different parts of the Continent, there was increasing interest in distribution and abundance, and in the ecological and behavioural attributes of species and communities. At first, it was the largest and most easily observed species that were the focus of most studies but, as new methodologies and equipment became available, the smaller, seldom seen, secretive species became better known. Many species were studied because of their suspected role in diseases of humans and livestock, and because they were proven or potential 'pests' in agricultural systems. During the past decade or so, there has been greater emphasis on the karyotypic and molecular/genetic characters of species. These studies have produced a wealth of information, especially during the past 40 years or so. These volumes are not only a distillation of the huge literature that now exists on African mammals: they also contain much previously unpublished information.

There is a huge discrepancy among species in the amount of information available. Some species have been studied extensively for many years, especially the so-called 'game species', some species of primates and a few species that are widespread and/or easily observed. In contrast, other species are known only by one or a few specimens, and almost nothing is known about them. Likewise, some areas and countries have been well studied, while other areas and countries have been neglected. During the preparation of these volumes, the editors have often been surprised by the wealth of information about some species when little was anticipated, and by the paucity of information about others, some of which were assumed to be 'well known'. In addition to presenting information that is based on sound scientific evidence, the aims of these volumes are to point out where there are gaps in knowledge and to correct inaccurate information that has become embedded in the literature. For most taxa, the detail provided in the species profiles allows accurate identification.

Mammals of Africa comprises six volumes (Table 2). The volumes consist mainly of species profiles – each profile being a detailed

Table 1. The mammals of Africa.

| Order | Number of families | Number of genera | Number of species |
|-----------------|--------------------|------------------|-------------------------|
| Hyracoidea | 1 | 3 | 5 |
| Proboscidea | 1 | 1 | 2 |
| Sirenia | 2 | 2 | 2 |
| Afrosoricida | 2 | 11 | 24 |
| Macroscelidea | 1 | 4 | 15 |
| Tubulidentata | 1 | 1 | 1 |
| Primates | 4 | 25 | 93 |
| Rodentia | 15 | 98 | 395 ^a |
| Lagomorpha | 1 | 5 | 13 |
| Erinaceomorpha | 1 | 3 | 6 |
| Soricomorpha | 1 | 9 | 150 |
| Chiroptera | 9 | 49 | 224 |
| Carnivora | 9 | 38 | 83 |
| Pholidota | 1 | 3 | 4 |
| Perissodactyla | 2 | 3 | 6 |
| Cetartiodactyla | 6 | 41 | 93 |
| 16 | 57 | 296 | 1116^b |

^a Including five introduced species. ^b Species profiles in *Mammals of Africa*.

Table 2. The six volumes of *Mammals of Africa*.

| Volume | Contents | Number of species | Editors |
|--------|--|-------------------|--|
| I | Introductory chapters. Afrotheria (Hyraxes, Elephants, Dugong, Manatee, Otter-shrews, Golden-moles, Sengis and Aardvark) | 49 | Jonathan Kingdon, David C. D. Happold, Michael Hoffmann, Thomas M. Butynski, Meredith Happold and Jan Kalina |
| II | Primates | 93 | Thomas M. Butynski, Jonathan Kingdon and Jan Kalina |
| III | Rodents, Hares and Rabbits | 408 | David C. D. Happold |
| IV | Hedgehogs, Shrews and Bats | 380 | Meredith Happold and David C. D. Happold |
| V | Carnivores, Pangolins, Equids and Rhinoceroses | 93 | Jonathan Kingdon and Michael Hoffmann |
| VI | Pigs, Hippopotamuses, Chevrotain, Giraffes, Deer and Bovids | 93 | Jonathan Kingdon and Michael Hoffmann |

account of the species. They have been edited by six editors who distributed their work according to the orders with which they were most familiar. Each editor chose authors who had extensive knowledge of the species (or higher taxon) and, preferably, had experience with the species in the field. Each volume follows the same general format with respect to arrangement, subheadings and contents. Because *Mammals of Africa* has contributions from 356 authors (each with a different background and speciality), and because each volume was edited by one or more editors (each with a different perspective), it has not been possible or even desirable to ensure exact consistency throughout. Species profiles are not intended to be exhaustive literature reviews, partly for reasons of space. None the less, they are written and edited to be as comprehensive as possible, and to lead the reader to the most important literature for each species. Inevitably, not all information available could be accommodated for the better-known species, and so such profiles are a précis of available knowledge. Extensive references in the text alert the reader to more detailed information.

In addition to the species profiles, there are profiles for the higher taxa (genera, families, orders, etc.). Thus, there is a profile for each order, for each family within the order, for each genus within the family, and for each species within the genus. For some orders there are additional taxonomic levels, for example, tribes (e.g. in Bovidae), subgenera (e.g. in *Procolobus*) and species-groups, or 'super-species' (e.g. in *Cercopithecus*). The taxonomy used in these volumes mostly follows that presented in the third edition of *Mammal Species of the World: A Geographic and Taxonomic Reference* (2005), although authors have employed alternative taxonomies when there were good reasons for doing so. Volume I differs from the other volumes in that it contains a number of introductory chapters about Africa and its environment, and about African mammals in general.

The continent of Africa

For the purposes of this work, 'Africa' is defined as the continent of Africa (bounded by the Mediterranean Sea, the Atlantic Ocean, the Indian Ocean, the Red Sea and the Suez Canal) and the islands on the continental shelf that, at some time in their history, have been joined to the African continent. The largest of the 'continental islands' are Zanzibar (Unguja), Mafia and Bioko (Fernando Po). All 'oceanic islands', e.g. São Tomé, Príncipe, Annobón (Pagulu), Madagascar, Comoros, Seychelles, Mauritius, Socotra, Canaries, Madeira and Cape Verde are excluded, with the exception of Pemba, which is included because of its close proximity (ca. 50 km) to the mainland.

The names of the countries of Africa are taken from the *Times Atlas* (2005). The Republic of Congo is referred to as 'Congo' and the Democratic Republic of Congo (formerly Zaire) as 'DR Congo'. Smaller geographical or administrative areas within countries are rarely referred to except for Provinces in South Africa, which are used extensively in the literature. Maps showing the political boundaries of Africa (Figure 1a), the Provinces of South Africa (Figure 1b) and the physical features of Africa with the major rivers and lakes (Figure 1c) are provided, as well as a list of the 47 countries together with their previous names that are used in the older literature on African mammals (Table 3).

Africa is the second largest continent in the world (after Asia), but it differs from other continents (except Australia and Antarctica) in being essentially an island. At various times in the past, Africa has been joined to other continents – a situation that has had a strong influence on the fauna and flora of the continent. Africa is a vast continent (29,000,000 km², 11,200,000 mi²) that straddles the Equator, with about two-thirds of its area in the northern hemisphere and one-third in the southern hemisphere. As a result, Africa has many varied climates (with seasons in each hemisphere being 6 months out of phase), many habitats (including deserts, savannas, woodlands, swamps, rivers, lakes, moist forests, monsoon forests, mountains and glaciers), and altitudes ranging from 155 m (509 ft) below sea level at L. Assal, Djibouti, in the Danakil (Afar) Depression, to 5895 m (19,341 ft) on Mt Kilimanjaro, Tanzania. Africa is comprised of 47 countries, some of which are very large (e.g. Sudan [2,506,000 km²; 967,000 mi²], Algeria (2,382,000 km², 920,000 mi²], and Democratic Republic of Congo [2,345,000 km², 905,000 mi²]), and others that are relatively small (e.g. Djibouti [23,200 km², 9,000 sq miles], Swaziland [17,400 km², 6,700 mi²] and The Gambia [11,300 km², 4,400 mi²]). The human population of each country also varies greatly, from about 346/km² in Rwanda to only about 2.5/km² in Namibia. With its great size and varied habitats, Africa supports a high biodiversity, including a large number of species of mammals. Likewise, most countries have a high diversity of mammals (especially when compared with temperate countries).

Africa may also be divided into biotic zones (Figure 2). A biotic zone (BZ) is defined as an area within which there is a similar environment (primarily rainfall and temperature) and vegetation, and which differs in these respects from other biotic zones. Thirteen biotic zones are recognized, two of which may be divided into smaller categories. The biotic zones exploited by each species of mammal are listed in each profile for several reasons. They indicate the environmental conditions in which the species lives and they provide data with which the geographic distribution can be explained



Figure 1. (a) Political map of Africa; (b) provinces of South Africa; (c) altitudes and major rivers of Africa. South Sudan and Somaliland are not identified as separate countries in the text.

Table 3. The countries of Africa: names, areas and human population density.

| Country name | Area
(km ²) '000 | Area
(miles ²) '000 | Human population
'000 (2006) | People per km ² |
|--|---------------------------------|------------------------------------|---------------------------------|----------------------------|
| Algeria | 2,382 | 920.0 | 33,500 | 14.1 |
| Angola (includes Cabinda) | 1,247 | 481.0 | 15,800 | 12.7 |
| Benin * [Dahomey] | 113 | 43.0 | 8,700 | 77.0 |
| Botswana [Bechuanaland] | 582 | 225.0 | 1,800 | 3.1 |
| Burkina Faso * [Upper Volta; Burkina] | 274 | 106.0 | 13,600 | 49.6 |
| Burundi [part of Ruanda-Urundi (= part of Belgian Congo)] | 27.8 | 10.7 | 7,800 | 280.5 |
| Cameroon [includes former French Cameroon, German Cameroon and part of Eastern Nigeria] | 475 | 184.0 | 17,300 | 36.2 |
| Central African Republic # | 623 | 241.0 | 4,300 | 6.9 |
| Chad [Tchad] | 1,284 | 496.0 | 10,000 | 5.8 |
| Congo [Republic of Congo] | 342 | 132.0 | 3,700 | 10.8 |
| Côte d'Ivoire * [Ivory Coast] | 322 | 125.0 | 19,700 | 61.2 |
| Democratic Republic of Congo [Belgian Congo; Congo (Kinshasha); Zaire] | 2,345 | 905.0 | 62,700 | 26.7 |
| Djibouti [French Somaliland] | 23.2 | 9.0 | 800 | 34.5 |
| Egypt | 1,001 | 387.0 | 75,400 | 75.3 |
| Equatorial Guinea # (includes Rio Muni [Spanish Guinea] and Bioko I. [Fernando Po]) | 28.1 | 10.8 | 500 | 17.8 |
| Eritrea (formerly part of Ethiopia) | 94 | 36.0 | 4,600 | 48.9 |
| Ethiopia [Abyssinia] | 1,128 | 436.0 | 74,800 | 66.3 |
| Gabon # | 268 | 103.0 | 1,400 | 5.2 |
| The Gambia | 11.3 | 4.4 | 1,500 | 132.7 |
| Ghana [Gold Coast] | 239 | 92.0 | 22,600 | 94.6 |
| Guinea * | 246 | 95.0 | 9,800 | 39.8 |
| Guinea-Bissau [Portuguese Guinea] | 36 | 13.9 | 1,400 | 38.9 |
| Kenya | 580 | 224.0 | 34,700 | 59.8 |
| Lesotho [Basutoland] | 30.4 | 11.7 | 1,800 | 59.2 |
| Liberia | 111 | 43.0 | 3,400 | 30.6 |
| Libya | 1,760 | 679.0 | 5,900 | 3.6 |
| Malawi [Nyasaland] | 118 | 46.0 | 12,800 | 108.5 |
| Mali * | 1,240 | 479.0 | 13,900 | 11.2 |
| Mauritania * | 1,030 | 412.0 | 3,200 | 3.1 |
| Morocco [includes former Spanish Morocco and French Morocco; (now also includes Western Sahara = former Spanish Sahara)] | 447 | 172.0 | 32,100 | 71.8 |
| Mozambique [Portuguese East Africa] | 802 | 309.0 | 19,900 | 24.8 |
| Namibia [South-west Africa] | 825 | 318.0 | 2,100 | 2.5 |
| Niger * | 1,267 | 489.0 | 14,400 | 11.3 |
| Nigeria | 924 | 357.0 | 134,500 | 145.6 |
| Rwanda [part of Ruanda-Urundi (= part of Belgian Congo)] | 26.3 | 10.2 | 9,100 | 346.0 |
| Senegal * | 197 | 76.0 | 11,900 | 60.4 |
| Sierra Leone | 71.7 | 27.7 | 5,700 | 79.5 |
| Somalia § [British Somaliland and Italian Somaliland; Somali Republic] | 638 | 246.0 | 8,900 | 13.9 |
| South Africa | 1,220 | 471.0 | 47,300 | 38.7 |
| Sudan § [Anglo-Egyptian Sudan] | 2,506 | 967.0 | 41,200 | 16.4 |
| Swaziland | 17.4 | 6.7 | 1,100 | 63.2 |
| Tanzania [German East Africa; Tanganyika] (now includes Zanzibar I., Mafia I. and Pemba I.) | 945 | 365.0 | 37,900 | 40.1 |
| Togo [Togoland] | 56.8 | 21.9 | 6,300 | 110.9 |
| Tunisia | 164 | 63.0 | 10,100 | 61.6 |
| Uganda | 236 | 91.0 | 27,700 | 117.4 |
| Zambia [Northern Rhodesia] | 753 | 291.0 | 11,900 | 15.8 |
| Zimbabwe [Southern Rhodesia] | 391 | 151.0 | 13,100 | 33.5 |
| Totals/mean density | 29,448 | 11,383 | 902,600 | 56.8 |

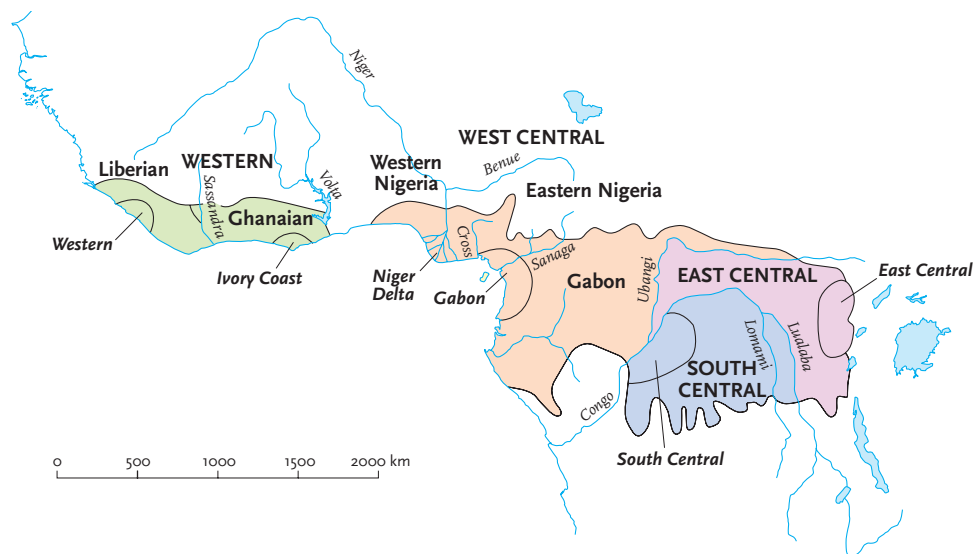
Former names are listed in chronological order in square brackets, with the oldest name listed first. Obsolete names are listed because much of the older literature refers to past colonial entities. * = formerly part of French West Africa. # = formerly part of French Equatorial Africa. § At the time of going to press, the country of Sudan had been divided into two: the Republic of Sudan in the north, and the Republic of South Sudan in the south. § The former British Somaliland is now a self-declared state under the name of the Republic of Somaliland, but remains internationally unrecognized.



Figure 2. The biotic zones of Africa.

and predicted. Furthermore, the number of biotic zones exploited by a species indicates its level of habitat tolerance and the extent to which it is vulnerable to loss of a particular type of habitat. The Rainforest Biotic Zone (Figure 3) and the South-West Arid Biotic Zone are divided into regions and subregions that reflect the different biogeographical distributions of species within the zone, each region/subregion having a community of mammals and other animals that is different to any other. Details of the biotic zones of Africa, and the regions and subregions of the Rainforest Biotic Zone, are given in Volume I of *Mammals of Africa*.

Figure 3. The Rainforest Biotic Zone showing the regions, subregions and refugia. Regions are indicated in capital letters and colours: Western region – green; West Central region – brown; East Central region – purple; South Central region – blue. Subregions are indicated in lower case letters. Refugia are indicated in lower case italics and yellow (after Happold 1996 and references therein; see also Happold & Lock, Volume I, *Mammals of Africa*).



The hedgehogs, shrews and bats of Africa

This volume is devoted to the orders Erinaceomorpha (hedgehogs), Soricomorpha (shrews) and Chiroptera (bats). These orders comprise 380 species (i.e. about 34% of all African mammals). Two of the orders contain many species – Soricomorpha (150 species) and Chiroptera (224 species) – and are the second and third most speciose orders after the Rodentia (395 species) (see Table 1). The seven orders that are considered to be the ‘small mammals of Africa’ (orders Afrosoricida and Macroscelidea [Volume I], Rodentia and Lagomorpha [Volume III], and Erinaceomorpha, Soricomorpha and Chiroptera [this volume]) collectively comprise 74.1% (827 of 1116) of all African mammalian species. Many species in the orders described in this volume have not been studied in detail because of their rarity and small geographic ranges; however, there is considerable knowledge about many of the species of bats.

There are two editors for this volume: Meredith Happold (Chiroptera; 224 species) and David C. D. Happold (Erinaceomorpha and Soricomorpha; 156 species).

The profiles for Volume IV were submitted to the editors between 2001 and 2005. It has not been possible to revise profiles since then; however, notes have sometimes been added to draw attention to important changes in taxonomy and distribution, the IUCN Categories of threat in the conservation sections have been updated, and citations of papers previously given as ‘in press’ have been completed. An Appendix has been added listing new taxa described during the period 2005–2010.

Species profiles

Information about each species is given under a series of subheadings. The amount of information under each of these subheadings varies greatly between species; where no information is available, this is recorded as ‘No information available’ or words to this effect. The sequence of subheadings is as follows:

Scientific name (genus and species) The currently accepted name of the species.

Vernacular names English, French and German names are given, as available. The first given English name is the preferred vernacular name for the species; alternative names are given in parentheses for some species. Wilson & Cole (2000) list proposed vernacular names for all the world's mammals; most of these names were also given in the third edition of *Mammal Species of the World* (Wilson & Reeder 2005). Although these works have been consulted, the names used have not always been adopted in *Mammals of Africa*. For the names of bats, there was collaboration between the authors of profiles, other bat specialists and Nancy Simmons (Simmons 2005): consequently the bat names, with very few exceptions, are the same in both publications. French names were either provided by Stéphane Aulagnier (bats), other profile authors, or taken from Gunther (2002). Most of the German names were provided by Jakob Fahr and Cornelia Rumpff (bats) and by Anke Hoffman (other taxa).

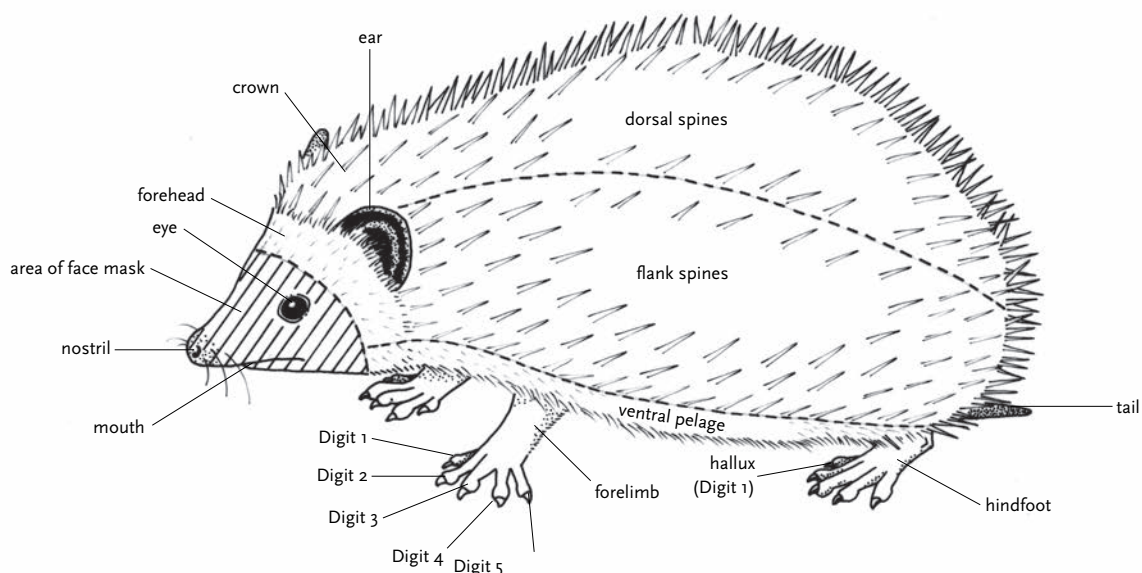
Scientific Citation This provides the full scientific name of the species, i.e. genus name, species name, authority name and date of authority. Parentheses around the authority's name and date indicate that the species was originally named in a different genus to the one it is placed in now. The scientific name is followed by the publication where the species was described, and the type locality (i.e. where the holotype [or type series] was obtained). Most of this information is taken from Wilson & Reeder (2005).

Taxonomy This section contains information about previous scientific names of the species, and problems and controversies (if any) associated with its nomenclature and relationships with other species. Major synonyms are listed (without the taxonomic authority unless essential for clarity), and the number of subspecies (usually only in Africa) is given: most of this information is from Wilson & Reeder (2005). The chromosome number is given if available,

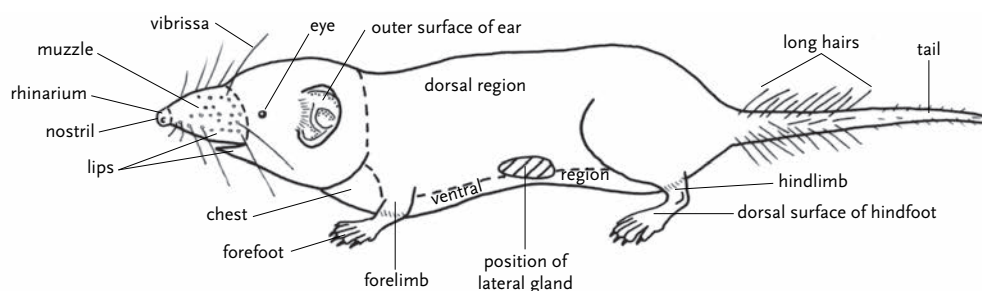
and in some cases this is followed by other information relevant to the chromosomes. In late 2006, a revised edition of the *Atlas of Mammalian Chromosomes* was published (O'Brien *et al.* 2006), but it has not been possible to incorporate the findings of that important work here.

Description This section, together with the illustrations and relevant tables, includes sufficient information to identify the species as well as describing characters that are relevant to the habits and life-style of the species. The section begins with a brief overall description of the species, including an indication of size. (For the bats, the first sentence lists the most useful diagnostic characters of the species, ending with those that distinguish it from its most similar species.) This is followed by a more detailed description of the external characters and skulls (including the diagnostic characters); the information given covers all subspecies (if any). It was not possible – or desirable – to describe the same suite of characters for every species. Instead, an appropriate selection was made for each family and/or genus, and therefore the same suite of characters is described for all members of the relevant taxon. Consequently the descriptions of related species are comparable and compatible. The table-keys (referred to as tables in the text) function as keys to the species, and should be read from the left column to the right column, which gives the name of the species thereby identified. The number and arrangement of nipples in adult females (for taxa other than bats) is noted wherever this feature varies between the taxa being discussed (see Glossary). The tables allow easy comparison between taxa within a genus or family.

Geographic Variation Variation within the species may be clinal (without subspecies) or subspecific. If the variation is clinal, there is a description of the character(s) that alters clinally across the geographic range of the species. If the variation is subspecific, each subspecies is listed together with its geographic range and the characters that distinguish it from the other subspecies.



External characters of a hypothetical hedgehog.



External characters of a hypothetical shrew.

Similar Species A list of similar species is given together with the diagnostic characters and/or measurements most useful to distinguish that particular species from the profiled species. If a character of a similar species is described as being 'larger' or 'smaller' than that of the profiled species, there is no known overlap in the ranges of measurements of this character. In contrast, if the ranges overlap but the means are different, a character is said to be 'larger on average' or 'smaller on average'. For the Order Chiroptera, similar species are considered to be those that share a specified combination of characters, whether or not they live sympatrically. For other orders, with some exceptions, the lists of similar species are restricted to those that are sympatric or parapatric with the profiled species; this section is omitted for the genus *Crocidura* because of the very large number of species (but see Table 8).

Distribution The first sentence is often 'Endemic to Africa' indicating that the species is found (in the wild) only in Africa. Alternatively, the section begins with the distribution in Africa, and the extralimital distribution is given at the end of the section. The Biotic Zone (or Zones) in which the species has been recorded are listed because this information indicates the sorts of environments exploited by that species, and the extent to which it is likely to be threatened by habitat change. Also, it is the basis for predictions of its distribution outside the currently known limits. Next, the distribution in African countries, or parts of countries, is described, and altitudinal ranges may be given. As a general rule, descriptions of the ranges of species with very restricted distributions are more precise in terms of information given (including, for example, geographic coordinates) than for more widespread species, where a more generalized statement is adequate. A distribution map (see below) augments the information given here.

Habitat This section provides a description of the habitat, or range of habitats, where the species lives. Details of plant communities, plant species, vegetation structure, soil type and/or structure, and water availability, etc. (if available) may be recorded. Other information may include average annual rainfall, altitudinal limits and seasonal variation in habitat characteristics.

Abundance This section attempts to indicate the comparative abundance of the species. For many species, quantitative data are unavailable but the species can be assessed as 'abundant', 'common', 'rare', 'rarely seen but often heard', 'rarely collected' etc. For some species, abundance is indicated by quantitative estimates of density (e.g. number/ha or number/km²), or relative abundance within the

community (e.g. 'comprised 40% of small mammals captured', 'the second most numerous species captured'). For the better-known or rare species, actual numbers of individuals for the species may be given. Other information may include seasonal changes in density, frequency of observations, or the relative abundance of specimens in collections.

Adaptations This section describes morphological, physiological and behavioural characteristics, which show how the species uniquely interacts with its environment, with conspecifics, and with other animals. This section may also describe species-specific adaptations for locomotion, burrowing, mechanisms for orientation, production of sound, sensory mechanisms and activity patterns. It may also include descriptions of domiciles and population movements (such as migration). In some instances, comparison with related or convergent species allows the unique adaptations of the species under discussion to be detailed or emphasized.

Foraging and Food The first sentence briefly describes the diet of the species (e.g. insectivorous, carnivorous, granivorous, etc.). This may be followed by the methods of collecting food (foraging), size of home-range and daily distance moved, and descriptions of feeding behaviour. The diet, if well-known, is then described in one or more of the following ways: a list of the taxa of animals or plants consumed, a quantitative measure based on direct observations, or by a qualitative or quantitative analysis of the stomach contents or faeces.

Social and Reproductive Behaviour Topics in this section may include social organization (e.g. solitary, social or colonial), group size and composition, agonistic and amicable behaviour, territoriality and home-range (including quantitative data), courtship and mating, parental behaviour and parent–young interactions, cooperative breeding and social vocalizations.

Reproduction and Population Structure If data are available, this section describes the reproductive strategy of the species, this being determined by the litter-size and the timing of reproductive events (i.e. the reproductive chronology). Reproductive chronologies cover the times of year when spermatogenesis, ovulation, copulation, gestation, parturition and lactation occur, and consequently this indicates the duration of pregnancy and lactation, and the number of pregnancies each female may have in one year. Reproductive chronologies give data for both individuals and local populations. Special adaptations such as reproductive delays (e.g. delayed implantation) and postpartum oestrus are mentioned, and

the timing of reproductive events in relation to climatic seasons, availability of food and other relevant events are discussed. This section may also include birth-weights and sizes of young, growth-rates, age at weaning and sexual maturity, and longevity. Finally, if data are available, population structure is discussed. This includes sex ratios, adult/young ratios, the abundance of different cohorts in the population at different times of the year, and mortality rates. In general, information on reproduction is much better known for bats than for other species described in this volume.

Predators, Parasites and Diseases The known predators, known parasites (usually ectoparasites only) and some diseases are listed. Additional information is given if the species is a host to diseases that affect humans and domestic stock, and if it is utilized as food for humans ('bushmeat').

Remarks This subheading subsumes five of the above subheadings (Adaptations, Foraging and Food, Social and Reproductive Behaviour, Reproduction and Population Structure, and Predators, Parasites and Diseases) in those instances where there is little or no information available.

Conservation The conservation status of the species (i.e. its IUCN Category) is taken from the 'Red List of Threatened Species' prepared by the International Union for Conservation of Nature (IUCN). The IUCN Red List Categories follow the definitions given in the *IUCN Red List Categories and Criteria Version 3.1* (see www.iucnredlist.org) and are listed in Table 4. For those species classified as threatened (i.e. 'Vulnerable', 'Endangered' and 'Critically Endangered'), readers may obtain detailed reasons (the criteria) for the classification on the IUCN Red List website. The status of some species has been changed in recent years because

of improved knowledge, changes in taxonomy, or the impact of threatening processes or conservation action; detailed reasons for the present status, and past status, are given on the IUCN Red List website. If a species is listed on an Appendix I or Appendix II under CITES (Convention on International Trade in Endangered Species; www.cites.org), this is also indicated. For some species, additional information is provided, such as presence in protected areas, major threats, and current or recommended conservation measures.

Measurements A series of morphological measurements is provided. For each species in a particular order there is a standard set of measurements. The abbreviation (and definition) for each measurement are given in the Glossary. A measurement is cited as the mean value (with minimum value to maximum value in parentheses) and sample size. For some, the standard deviation (mean \pm 1 S.D.) is given instead of, or in addition to, the range. For most measurements, data for males and females are combined but where there is sexual dimorphism, measurements for males and females are given separately. Where possible, the localities of the measured specimens and the source of the data are provided. Sources are either cited publications, or specimens in museums, or unpublished information from the authors or others. The acronyms for museums where specimens were examined and measured are given in Table 5. Most museum records have been provided by the author of the profile; others – when an author did not have the measurements or did not have the opportunity to visit museums – were provided by the editors.

Key References A select list of references provides more information on the species. Each reference is given in full in the Bibliography.

Table 4. IUCN Red List Categories (from IUCN – International Union for Conservation of Nature).

| Category | Description |
|-----------------------------------|--|
| Extinct (EX) | A taxon is Extinct when there is no reasonable doubt that the last individual has died. A taxon is presumed Extinct when exhaustive surveys in known and/or expected habitat, at appropriate times (diurnal, seasonal, annual), throughout its historic range have failed to record an individual. Surveys should be over a time frame appropriate to the taxon's life-cycles and life form. |
| Extinct in the Wild (EW) | A taxon is Extinct in the Wild when it is known only to survive in cultivation, in captivity or as a naturalized population (or populations) well outside the past range. A taxon is presumed Extinct in the Wild when exhaustive surveys in known and/or expected habitat, at appropriate times (diurnal, seasonal, annual), throughout its historic range have failed to record an individual. Surveys should be over a time frame appropriate to the taxon's life-cycle and life form. |
| Critically Endangered (CR) | A taxon is Critically Endangered when the best available evidence indicates that it meets any of the criteria A to E for Critically Endangered, and it is therefore considered to be facing an extremely high risk of extinction in the wild. |
| Endangered (EN) | A taxon is Endangered when the best available evidence indicates that it meets any of the criteria A to E for Endangered, and it is therefore considered to be facing a very high risk of extinction in the wild. |
| Vulnerable (VU) | A taxon is Vulnerable when the best available evidence indicates that it meets any of the criteria A to E for Vulnerable, and it is therefore considered to be facing a high risk of extinction in the wild. |
| Near Threatened (NT) | A taxon is Near Threatened when it has been evaluated against the criteria but does not qualify for Critically Endangered, Endangered or Vulnerable now, but is close to qualifying for (or is likely to qualify for) a threatened category in the near future. |
| Least Concern (LC) | A taxon is Least Concern when it has been evaluated against the criteria and does not qualify for the Critically Endangered, Endangered, Vulnerable or Near Threatened categories. Widespread and abundant taxa are included in this category. |
| Data Deficient (DD) | A taxon is Data Deficient when there is inadequate information to make a direct, or indirect, assessment of its risk of extinction based on its distribution and/or population status. Data Deficient is not a category of threat. Listing of taxa in this category indicates that more information is required and acknowledges the possibility that future research will show that a threatened classification is appropriate. |
| Not Evaluated (NE) | A taxon is Not Evaluated when it has not yet been evaluated against the criteria. |

Table 5. Acronyms for museum and private collections.

| Acronym | Museum name |
|---------|--|
| AM | Amatole Museum, King William's Town, South Africa. [formerly Kaffrarian Museum]. |
| AMNH | American Museum of Natural History, New York, USA. |
| BMNH | Natural History Museum, London, UK [formerly British Museum (Natural History)]. |
| CAS | California Academy of Sciences, San Francisco, USA. |
| CM | Carnegie Museum of Natural History, Pittsburgh, USA. |
| CZL | Centro de Zoologia, Lisboa, Portugal. |
| DM | Durban Natural Science Museum, Durban, South Africa. |
| EBD | Estación Biológica de Doñana, Seville, Spain. |
| FC | Fahr Collection, Ulm, Germany (private collection). |
| FMNH | Field Museum of Natural History, Chicago, USA. |
| HC | Happold Collection, Canberra, Australia (private collection). |
| HNHM | Hungarian Natural History Museum, Budapest, Hungary. |
| HZM | Harrison Zoological Museum, Sevenoaks, Kent, UK. |
| ICN | Instituto da Conservação da Natureza, Lisboa, Portugal. |
| IICT/CZ | Instituto de Investigação Científica Tropical, Centro de Zoologia, Lisboa, Portugal. |
| IRSN | Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium. |
| KU | Kansas Museum of Natural History, Lawrence, USA. |
| LACM | Los Angeles County Museum, Los Angeles, USA. |
| MCZ | Museum of Comparative Zoology, Harvard University, Cambridge, USA. |
| MHNC | Musée d'Histoire Naturelle, La Chaux-de-Fonds, Switzerland. |
| MHNG | Muséum d'Histoire Naturelle, Genève, Switzerland. |
| MHNS | Musée d'Histoire Naturelle, Strasbourg, France. |
| MMB | Museums of Malawi, Blantyre, Malawi. |
| MNHN | Muséum National d'Histoire Naturelle, Paris, France. |
| MSNM | Museo Civico di Storia Naturale di Milano, Milan, Italy. |
| MUMZ | Makerere University, Museum of Zoology, Kampala, Uganda. |
| MZUF | Museo Zoologico 'La Specola', Università di Firenze, Italy. |

| Acronym | Museum name |
|---------|---|
| MZUT | Museo di Zoologia, Università di Torino, Italy. |
| NAU | Northern Arizona University Museum of Vertebrates, Flagstaff, Arizona, USA. |
| NHMB | Naturhistorisches Museum, Berlin, Germany. |
| NMB | National Museum (Bloemfontein), South Africa. |
| NMBE | Naturhistorisches Museum, Bern, Switzerland. |
| NMK | National Museums of Kenya, Nairobi, Kenya. |
| NMP | Natal Museum, Pietermaritzburg, South Africa. |
| NMW | Naturhistorisches Museum, Wien (Vienna), Austria. |
| NMZB | Natural History Museum of Zimbabwe, Bulawayo, Zimbabwe. |
| NRM | Naturhistoriska Riksmuseet, Stockholm, Sweden. |
| OSU | Oklahoma State University, Stillwater, USA. |
| RMCA | Royal Museum for Central Africa, Tervuren, Belgium. |
| RMNH | Nationaal Natuurhistorisch Museum, Leiden, the Netherlands. (formerly Rijksmuseum Natuurlijke Historie) |
| ROM | Royal Ontario Museum, Toronto, Canada. |
| SAM | South African Museum, Cape Town, South Africa. |
| SBPU1 | Station Biologique de Paimpont, Université de Rennes 1, F-35380 Paimpont, France. |
| SMF | Senckenberg Museum, Frankfurt, Germany. |
| SMND | Staatliches Museum für Naturkunde, Dresden, Germany. |
| SMNS | Staatliches Museum für Naturkunde, Stuttgart, Germany. |
| TM | Transvaal Museum, Pretoria, South Africa. |
| USNM | United States National Museum of Natural History, Smithsonian Institution, Washington, USA. |
| YPM | Yale Peabody Museum, New Haven, Connecticut, USA. |
| ZFMK | Museum Alexander Koenig, Bonn, Germany. |
| ZMA | Zoologisch Museum, Amsterdam, the Netherlands. |
| ZMB | Museum für Naturkunde, Humboldt University, Berlin, Germany. |
| ZMMU | Zoological Museum, Moscow University, Moscow, Russia. |
| ZMUC | Zoologisk Museum Universitet, København, Denmark. |
| ZMUZ | Zoologisches Museum der Universität, Zurich, Switzerland. |

Author The name of the author, or authors, is given at the end of each profile. All profiles should be cited using the author name(s).

Tables For selected taxa (mainly families and genera) tables (sometimes in the form of table-keys) provide details of the main characteristics of these taxa and can be used as an aid to identification. The tables were prepared by the editors.

Higher order profiles

The profiles for orders, families and genera are less structured than for the species profiles. Each profile usually begins with a listing of the taxa in the next lower taxon; for example, each family profile lists the genera in that family. An exception to this arrangement is where a taxon has only one lower taxon. Higher taxa profiles provide the characteristics common to all members of that taxon. Some of these characteristics may not be repeated in lower taxon profiles (unless essential for identification) so readers are encouraged to consult also the next higher taxon profile, e.g. the species profile for *Crocridura olivieri* should be consulted in association with the genus

Crocridura profile. For the Chiroptera, the higher taxon profiles end with information that enables readers to recognize and distinguish the next lowest taxa (e.g. family profiles end with the diagnostic characters of the genera in that family).

Distribution maps

Each species profile, with a very few exceptions, contains a pan-African map showing the geographic range of the species. Most maps were provided by the author of the profile and were compiled from literature records and museum specimens; some maps were provided by the editor(s) when it was not possible for the author to do so. Each map shows the boundaries of the 47 countries of Africa, some of the major rivers (Nile, Niger–Benue, Congo [with the tributaries Ubangi, Lualaba and Lomani], Zambezi and Orange), and Lakes Chad, Tana, Turkana (formerly Rudolf), Albert, Edward, Victoria, Kyoga, Kivu, Tanganyika, Malawi, Mweru, Bangwuela and Kariba. The map projection is 'Transverse Mercator, with the following parameters: False Easting: 0; False Northing: 0; Central Meridian: 20; Linear Unit: metre; Datum: Clarke 1866'. The geographic

distribution of a species is indicated as:

- red shading = current range(s).
- × = individual localities when only a few localities are known, or isolated localities considered to be separate from the main geographic range(s). Some localities indicated by × may include two or more closely spaced localities.
- ? = locality of uncertain validity; relevant information usually in text.
- red arrow = recorded from the island indicated by the arrow.

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Order ERINACEOMORPHA – Hedgehogs

Erinaceomorpha Gregory, 1910.

| | | |
|-----------------------------------|-----------------|-------|
| Erinaceidae (3 genera, 6 species) | Spiny Hedgehogs | p. 29 |
|-----------------------------------|-----------------|-------|

The order Erinaceomorpha contains one family, ten genera and 20 species, distributed throughout Eurasia and Africa (Corbet 1988, Reeve 1994). The single family contains two subfamilies: the Galericinae (the Gymnures or Hairy Hedgehogs) and the Erinaceinae (the Spiny Hedgehogs). The five genera and six species of Hairy Hedgehogs live in the temperate and tropical forests of Asia, and are not considered further in this account. The Spiny Hedgehogs – usually referred to as just ‘Hedgehogs’ – occur widely in temperate Eurasia and Africa; currently, they are classified into five genera and 14 species, of which six species (in two or three genera) live in Africa.

The order (as family Erinaceidae) was previously included within the order Insectivora (Hutterer 2005a). Although the name Erinaceomorpha is not new – it was originally proposed by Gregory in 1910 – recent research has indicated that the Insectivora (hedgehogs and moonrats, shrews, moles, golden-moles, otter-shrews and tenrecs) are not a closely related group, and that the order Insectivora should be divided into three orders – Erinaceomorpha (hedgehogs and moonrats), Soricomorpha (shrews and moles) and Afrosoricida (golden-moles, otter-shrews, tenrecs). The following account deals only with the African hedgehogs – the sole representatives of the Erinaceomorpha in Africa.

The two best known characteristics of hedgehogs are their short pointed spines, which densely cover all of the back and flanks, and their ability to curl up into a ball when disturbed. Each spine is thought to be the equivalent of several hairs, where the follicles have coalesced, rather than of a single hair. The spines grow in lines, each spine pointing outwards in a slightly different direction; this results in a dense mat of spines that point in all directions. The spines are shed and replaced, just like normal hairs but more slowly. Hedgehogs can curl into a ball so that the head, limbs, tail and ventral surface are protected by the spiny back and flanks. Under the spiny skin are two large muscles, the orbicularis and panniculus carnosus, which encircle the back, chest and flanks forming a hood-like structure over the animal. Other muscles run downwards from the orbicularis and overlie the forehead, shoulders and rump; when a hedgehog is disturbed, these muscles contract very rapidly pulling the orbicularis downwards. At the same time, the orbicularis itself contracts and the whole body becomes enveloped within the stretched panniculus muscle. This movement stretches the very flexible skin and causes the spines to erect, providing additional protection (Reeve 1994). Hedgehogs can remain in this state for hours on end; they also roll up (but not so tightly) when asleep or in torpor and hibernation. Hedgehogs are characteristically parasitized by many fleas, which may be observed frequently among the spines.

Hedgehogs are small mammals, weighing on average 130–205 g as adults (African species). They are compact, rotund little animals because the neck, tail and limbs are short. The head is broad, the snout is slightly elongated and mobile, and the well-developed sense of smell is used for locating prey. The eyes are of moderate

size but sight is primarily monochrome and highly developed. The ears vary from being quite small to very large, and hearing is very acute; some desert species have enlarged auditory bullae (as do some desert rodents), which enhances detection of very quiet noises in open spaces. Olfaction and hearing are the dominant senses for hedgehogs. The skull is strongly built with wide zygomatic arches so that the head appears rather broad. The dental formula is $I^{3/2}, C^{1/1}, P^{3/2}, M^{3/3} = 36$. The teeth are similar in structure and function to other small species of insectivores. One of the upper incisors is long and caniform, and points anteriorly. The canine teeth are small, as are the front premolars. The last premolar and the molars are large with well-developed pointed cusps that crush and slice through the exoskeletons of arthropod prey.

Hedgehogs live in a very wide range of habitats from cold temperate steppes to hot tropical savannas. In the cooler parts of their range (where sub-zero temperatures, frosts and snow occur in winter), they enter hibernation (see below). In the hotter parts of their range, they may be active all year, but may enter torpor during the dry season when food is scarce. Unlike many mammals, they adapt to human-modified environments and may be common (but rarely seen) in towns, cities and gardens. They do not live in rainforests or in very dry deserts. Although sometimes considered as rather ‘primitive’ mammals with rather few species, their widespread distribution and adaptability show that, as a family, they are very successful.

Hedgehogs are terrestrial, although some species are scansorial and can climb over logs and fences. They have short limbs, each with four or five digits ending in claws. They walk or trot on the soles of the feet, and can move surprisingly quickly for their size. They are nocturnal and active during most of the night, usually with peaks of activity before midnight and around 03:00h. During the day, they rest in a variety of habitats – under logs and piles of stones, in caves and rocky crevices, and in dense litter and hedgerows; some species dig burrows or rest in the burrows made by other animals. Surprisingly, most species can swim.

Hedgehogs are omnivorous, but their preferred prey is arthropods (mainly insects), earthworms, snails, small reptiles and eggs. Some species eat fruits and fungi in season. They appear to be resistant to toxins produced by some of their prey (such as centipedes and bees). When food is abundant, hedgehogs store fat under the skin and around some organs, and increase in weight. Fat is utilized (and weight declines) when food is scarce during the colder and drier months of the year.

Hedgehogs have the ability to change their metabolic rate in relation to environmental conditions. When the climate is cool or cold (and food may be limited), hedgehogs lower their metabolic rate and reduce their body temperature, and enter a state known as torpor or hibernation. The ability to hibernate is well understood and documented in temperate species, but it appears that African species enter torpor during the cold season of North Africa and South Africa, and during the dry season of tropical Africa. Torpor is physiologically different to hibernation and the metabolic rate

does not decline to the same extent, but it does enable individuals to reduce their energy expenditure and heat loss when environmental conditions are unfavourable.

African hedgehogs, like temperate ones, are mostly solitary. Very little is known about their behaviour and social organization in Africa. Likewise, little is known about their reproduction in the wild; the few observations that are available suggest that birth of young in most localities is seasonal. There are usually 2–6 young in a litter, and growth is rather slow. Most individuals probably do not breed until they are about a year old.

In Africa, fossil remains of hedgehogs are known from the early Miocene (Yates 1984). All the extant species of African hedgehogs are rather similar, but each of the six species has radiated into a different environment. The species are essentially allopatric with very limited overlap in their geographical ranges. African hedgehogs are found throughout the continent except in the Rainforest BZ and the driest parts of the Sahara and South-West Arid BZs.

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Table 6. Characteristics of species in the family Erinaceidae in Africa. See also Figure 5.

| Species | Mean HB (mm) | Central parting of spines | Surface of spines | Face-mask | Digit 1 on hindfoot | Ears (length as % of HF) | |
|--------------------------------|--------------|---------------------------|--|---|------------------------------|--|--|
| <i>Atelerix albiventris</i> | 167 | Narrow | Smooth | Black; well defined, slight posterior extension on to lower cheek | Absent (or very rudimentary) | Small, rounded, shorter than adjacent spines (73%) | |
| <i>Atelerix algirus</i> | ca. 235 | Narrow | Smooth | None; black 'spotting' on muzzle in some individuals | Small | Small, rounded, shorter than adjacent spines (77%) | |
| <i>Atelerix frontalis</i> | ca. 190 | Narrow | Smooth | Black or dark brown; well defined, extends ventrally to merge with black ventral pelage | Small | Small, rounded, shorter than adjacent spines (76%) | |
| <i>Atelerix sclateri</i> | 225 | Narrow | Smooth | Black; well defined, extends slightly on to cheek | Small | Small, rounded, shorter than adjacent spines (88%) | |
| <i>Hemiechinus auritus</i> | 179 | Absent | Papillate with fine longitudinal grooves | None | Large | Large, considerably longer than adjacent spines (114%) | |
| <i>Paraechinus aethiopicus</i> | 196 | Wide | Papillate with fine longitudinal grooves | Black; well defined | Large | Large, slightly pointed, protrude above adjacent spines (132%) | |

Family ERINACEIDAE

HEDGEHOGS

Erinaceidae G. Fischer, 1817. Mem. Soc. Imp. Nat., Moscow, 5: 372.

| | | |
|--------------------------------|---------------------|-------|
| <i>Atelerix</i> (4 species) | Hedgehogs | p. 30 |
| <i>Hemiechinus</i> (1 species) | Long-eared Hedgehog | p. 37 |
| <i>Paraechinus</i> (1 species) | Ethiopian Hedgehog | p. 39 |

The family Erinaceidae occurs widely in temperate Eurasia and Africa; currently, they are classified into five genera and 14 species. Characteristics of the family are given in the order profile above.

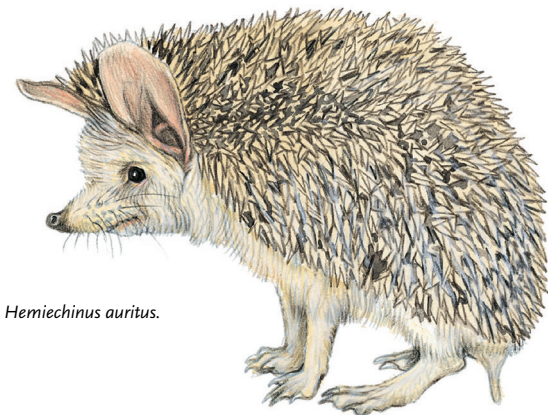
African hedgehogs are placed in three genera, *Atelerix*, *Hemiechinus* and *Paraechinus* (Figure 4). *Atelerix* has been considered as a subgenus of *Erinaceus* (Corbet 1974a, Yates 1984), which contains several species of European and temperate Asian species, but Robbins & Setzer (1985) showed that it warrants generic distinction (see also Hutterer 2005a). The genera are distinguished by many characters (Figure 5, Table 6), the most important being the presence or absence of a central parting between the spines of the scalp (and if present, its comparative width), the presence or absence of papillae on the spines, the size of the ears and their size relative to the length of the adjacent spines, the form of some of the teeth, the width and form of the palatal shelf, the form of the auditory bullae and (in ♂♂)

Atelerix albiventris.



the structure of the glans penis (Corbet 1988). Compared with the European Hedgehog *Erinaceus europaeus*, there are few detailed studies on African hedgehogs, especially in the wild.

African hedgehogs range in size (mean HB) from 167 mm to ca. 235 mm. Species are considered as ‘small’ (mean HB of <180 mm), ‘medium-sized’ (mean HB 180–200 mm) or ‘large’ (mean HB >201 mm). Ear length is considered as ‘small’ (<30 mm) or ‘large’ (>30 mm) (see Table 6).



Hemiechinus auritus.



Paraechinus aethiopicus.

Figure 4. The three genera of African hedgehogs.

| | Colour of ventral pelage and limbs | Number of roots on premolar | Notes |
|--|---|-----------------------------|--|
| | White; limbs pale | 2 | Widespread in savanna and semi-arid. Senegal to Ethiopia; E Africa north of Zambezi R. |
| | White; limbs pale | 3 | Morocco to Libya north of Sahara |
| | Grey to black; limbs grey to black | 2 or 3 | Southern Africa only |
| | White or buffy-white; limbs dark | 2 (barely divergent) | Somalia |
| | White; limbs long, white | 1, 2 (barely divergent), 3 | Egypt and Libya |
| | White, dark posteriorly; limbs long, dark brown | 1 | Sahara Desert and surrounding semi-arid regions |

The genera are distinguished by the presence/absence of the central parting on the forehead, whether the spines are papillate or smooth, and the width of the palatal shelf.

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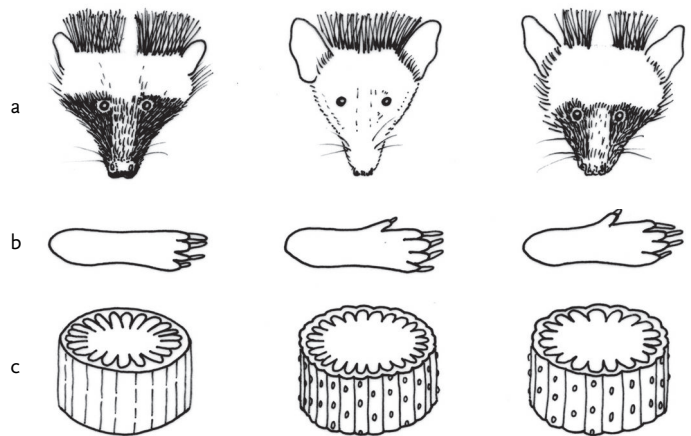


Figure 5. External characters of African hedgehogs: *Atelerix* (left), *Hemiechinus* (centre) and *Paraechinus* (right). (a) Head showing parting and face-mask. (b) Left hindfoot. (c) Section of spine. After Corbet (1988).

GENUS *Atelerix* Hedgehogs

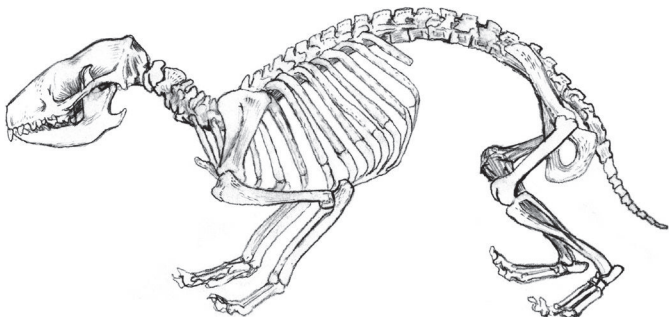
Atelerix Pomel, 1848. Arch. Sci. Phys. Nat. Geneve 9: 251. Type species: *Erinaceus albiventris* Wagner, 1841.

The genus *Atelerix* contains four species endemic to Africa, which occur throughout the savanna regions of the continent. All species in the genus have a narrow parting of the spines on the head, smooth spines (without papillae), rather small ears, broad palatal shelf and small auditory bullae (Figure 6). The hallux (Digit 1 of hindfoot) is

small or absent. The genus *Atelerix* has often not been recognized, and the four species have been included within the genus *Erinaceus* (which includes three species very widely distributed in the Palearctic regions). However, multivariate analysis of cranial characteristics (Robbins & Setzer 1985) as well as other non-cranial characters



Atelerix albiventris.



Atelerix sp.

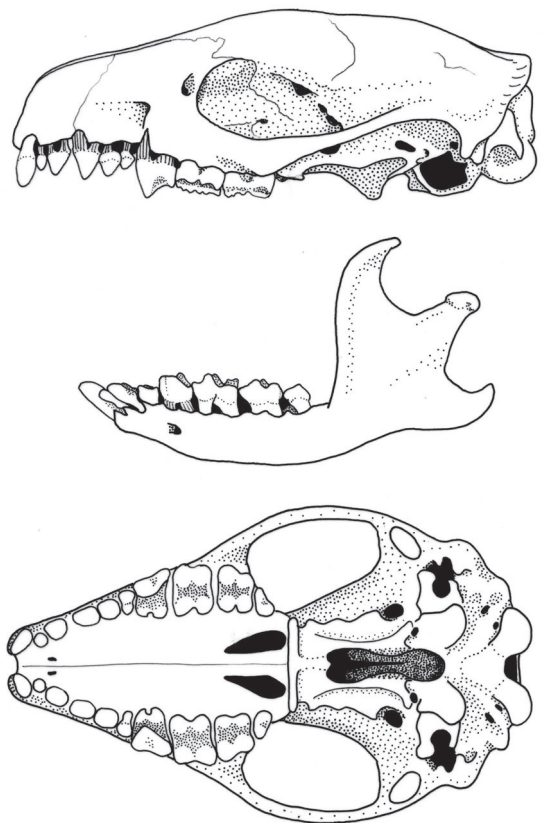


Figure 6. Skull and mandible of *Atelerix frontalis* (BMNH 34.10.10.213).

Atelerix albiventris.



and distribution patterns, clearly warrant separation of the African species in a separate genus (Corbet 1988, Hutterer 2005a). The four species are allopatric; one species – *A. albiventris* – is very widespread in central, East and West Africa, and the other species have more limited geographic distributions.

The species are distinguished by presence/absence of face-mask, colour of ventral pelage, presence/absence of Digit 1 on hindfoot, body size and geographic distribution (see Table 6).

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Atelerix albiventris WHITE-BELLIED HEDGEHOG (FOUR-TOED HEDGEHOG)

Fr. Hérisson à ventre blanc; Ger. Weissbauchigel

Atelerix albiventris (Wagner, 1841). In Schreber. Die Säugethiere, Suppl. 2: 22. Probably Senegal or Gambia.

Taxonomy Originally described in the genus *Erinaceus*. The species, as now understood, includes many taxa originally considered to be species and subspecies; all are now treated as synonyms. Synonyms: *adansoni*, *atratus*, *diadematus*, *faradjius*, *heterodactylus*, *hindei*, *kilimanus*, *langi*, *lowei*, *oweni*, *pruneri*, *sotikae*, *spiculus*, *spinifex*. Subspecies: none recognized here; the large variation within populations suggests that subspecific differentiation is not justified (Corbet 1988, Reeve 1994). Chromosome number: $2n = 48$, $aFN = 96$ (Hübner *et al.* 1991).

Description Small hedgehog with four digits on hindfoot. Dorsal pelage of dark spines; spines 15–20 mm, basal half off-white, terminal half dark brown or blackish-brown, often with white tip. Considerable variation in banding pattern on spines. Surface of spines smooth without papillae. Ventral pelage of non-spiny hairs; rather sparse; hairs white or buffy-white. Spiny dorsal pelage and hairy ventral pelage clearly delineated on lower flanks. Head with wide white forehead from cheek to cheek; narrow central parting of spines on crown of head; face-mask on muzzle and around eyes black, well-defined, extending posteriorly on lower cheek (see also below). Ears small, rounded, shorter than adjacent spines; ca. 73% of HF. Limbs short, white or pale; forefeet with

five digits; hindfeet with four digits, Digit 1 absent or rudimentary. Tail relatively very short (ca. 7% of HB), barely visible, with small pale hairs. Nipples: not known. Glans penis without spiny or papillate pads. Some ♂♂ tend to be larger and heavier than ♀♀. Skull: auditory bullae comparatively small (see Measurements); P^3 with two roots. See Table 6.

Geographic Variation Specimens from drier habitats appear paler because they have a greater number of white-tipped spines; some individuals do not have a black face-mask.

Similar Species

Paraechinus aethiopicus. On average larger (HB: 196.1 [169–217] mm); wide central parting on crown; spines with papillae and grooves; ears much longer (41–45 mm), longer than adjacent spines; hindfeet with five digits; Sahara and northern semi-arid regions.

Atelerix sclateri. On average larger (HB: 225.0 [210–263] mm); Digit 1 of hindfoot present, small but not rudimentary; Somalia only.

A. frontalis. On average slightly larger (HB (♂♂): 185 [170–190] mm, HB (♀♀): 196 [186–210] mm); face-mask extending ventrally to merge with black ventral pelage; south of Zambezi R. only.

Distribution Endemic to Africa. The most widespread of the African hedgehogs. Recorded from Sudan Savanna and Guinea Savanna BZs, Northern and Eastern Rainforest–Savanna Mosaics and most of the Somalia–Masai Bushland BZ. Penetrates the northern margins of the Rainforest BZ where habitat destruction has created grasslands and cultivations. Recorded from Senegal to Ethiopia, Djibouti and Somalia, and southwards through East Africa to Zambia (north of the Zambezi R.) and Malawi. Only known overlap in geographic range with other species of hedgehogs is with *Paraechinus aethiopicus* in C Sudan and N Ethiopia (and possibly at other places where the northern savannas meet the Sahara Desert), and with *A. sclateri* in N Somalia. (Note: the record of this species from Liberia [Lienhardt 1982] is presumably an error.)

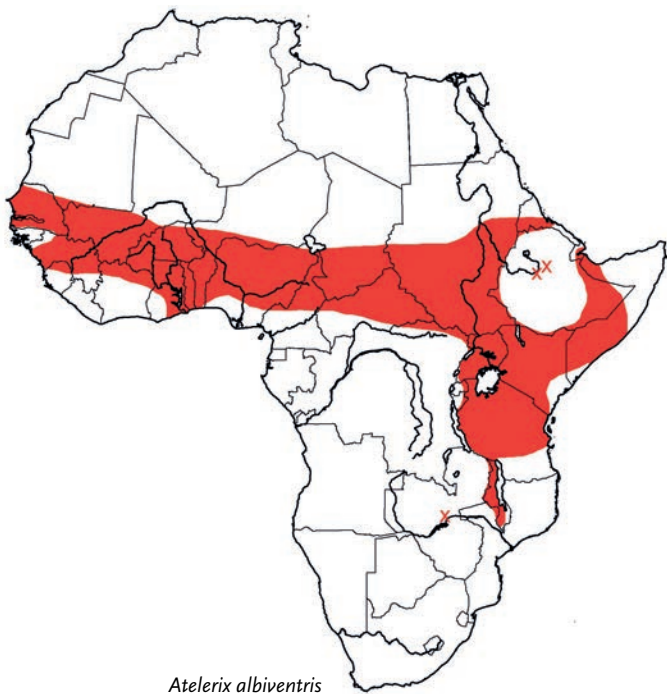
Habitat Savanna and semi-arid habitats, including rocky inselbergs. Tends to avoid waterlogged habitats, marshes and swamps. Often found in suburban gardens and cultivated fields.

Abundance May be common in suitable habitats. Individuals are seen more often at the beginning of the wet season when more individuals are killed by vehicles on roads.

Adaptations Nocturnal and terrestrial. During day, rests under rocks and logs, and in crevices and termitaria. In captivity, two peaks of nocturnal activity are evident: 21:00–24:00h and around 03:00h (Herter 1965). When active, hedgehogs walk and trot on all four limbs.

Body temperature (T_b) is maintained at 32.9–35.4 °C at normal ambient temperatures (Herter 1971). In captivity, when T_a is 19–24 °C, individuals become torpid and less active than normal. A similar drop in T_b is likely to occur in those regions where cool nights are experienced at some times of the year.

Foraging and Food Detailed information unavailable; probably similar to other species of hedgehogs (see order and family profiles).



In East Africa, the diet is reported to consist of earthworms, snails, slugs, crabs, fruit, fungi, roots and groundnuts (Kingdon 1974). Hedgehogs usually forage alone.

Social and Reproductive Behaviour Primarily solitary. Several vocal sounds are emitted, which enable communication between individuals and express mood. Five categories of audible vocal sounds have been recorded (Gregory 1975). (1) Twitter – a very quiet sound emitted through the closed mouth, and often accompanied by sniffing; usually associated with unfamiliar situations. Each twitter is of very short duration (5–40 msec) and several are emitted in pulses lasting for several seconds. (2) Hiss – a short noise of lower pitch than the twitter, emitted during stressful situations. (3) Snort – similar to the hiss, but louder and emitted when severely stressed or attacked, often repeated rapidly. (4) Scream – a rare sound, emitted under extreme stress. (5) Serenade – a series of low-pitched sounds ranging from a pure whistle to a course squawk, emitted by ♂♂ during courtship behaviour.

The faecal pellets have a strong odour, and may be a means of advertising the presence of an individual. Likewise, 'self-anointing' (licking the spines of the flank with copious amounts of saliva) may be a means of advertising and ensuring recognition (Reeve 1994).

Courtship behaviour is said to be similar to that of the European Hedgehog *Erinaceus europaeus* (M. W. Gregory, in Reeve 1994). When the ♂ approaches, the ♀ reacts aggressively, bristling her spines and snorting. The ♂ attempts to circle the ♀, who may try to run away; the ♀ responds by vigorously pushing the ♂ on his flank with the spines on her head. Such behaviour may last for minutes or hours. Copulation occurs when the ♂ mounts the ♀ from behind; the ♂ has a particularly long penis, perhaps because the spines on the rump of the ♀ prevent him from getting too close to the ♀.

Reproduction and Population Structure Times of reproductive activity vary in different parts of the range: probably active all year in East Africa (Kingdon 1974), but seasonal in drier and cooler habitats. Collections in Nairobi for a complete year include the following: pregnancies in Jul and Aug; litters in Apr–May; juveniles (<200 g) in Jan, Feb, Mar, Apr, May, Jun and Jul (Gregory 1976). Gestation: 35–37 days. Litter-size in captivity: 3.1 (1–6), $n = 52$ litters (1 young [$n = 8$], 2 [$n = 14$], 3 [$n = 11$], 4 [$n = 6$], 5 [$n = 9$], 6 [$n = 4$]). Young altricial at birth; WT: 5–11 g. Increase in weight is rapid: 25 g by Day 7, 50 g by Day 13, 70–75 g by Day 20, 110–120 g by Day 28, 130–150 g by Day 34, 170–190 g by Day 40 (Brodie *et al.* 1982, Lienhardt 1982). Maturity attained in ca. 5–6 months, but in the wild young probably do not breed until the next breeding season, when about one year old. Young are blind and naked at birth.

Predators, Parasites and Diseases The spines provide good protection against predators; however, remains of this species have been found in the pellets of Giant Eagle-owls *Bubo lacteus* in East Africa (Brown 1965) and in Nigeria (Happold 1987). In some parts of their geographical range, hedgehogs are eaten by humans, and they are vulnerable to being killed by vehicles on roads. In East Africa, the skin and spines are sometimes used as fertility charms.

Many ectoparasites have been recorded from hedgehogs in Kenya, Nairobi and Sudan, including fleas (*Ctenocephalides felis*, *C. crataepus*,

Echidnophaga gallinacea, *Xenopsylla cheopis*), ticks (*Haemophysalis leachi*, *H. spinulosa*, *Rhipicephalus sanguineus*, *R. simus*) and mites (*Caparinia erinacei*, *Notoedres oudemansi*, *Rodentopus sciuri*, *Sarcoptes scabiei*) (Gregory 1981, Okaeme & Osakwe 1985, Reeve 1994). Hedgehogs are also hosts to endoparasites; in Nairobi many hedgehogs were parasitized by tapeworms, nematodes and acanthocephalines (Gregory 1981).

Conservation IUCN Category: Least Concern.

This widespread species is unlikely to be threatened at present.

Measurements

Atelerix albiventris

HB: 167.5 (140–258) mm, n = 10

T: 12.5 (9–16) mm, n = 10

HF: 27.2 (26–29) mm, n = 10

E: 19.9 (15–23) mm, n = 10

WT: 422 (270–680) g, n = 10

GLS: 43.5 (41.9–44.8) mm, n = 10

GWS: 28.0 (26.5–29.8) mm, n = 10

I¹–M³: 21.5 (20.3–22.1) mm, n = 9

Auditory bulla: 4.6 (4.3–5.0) mm, n = 4*

Dakar, Senegal (ZFMK)

*Sudan (BMNH)

Key References Corbet 1988; Reeve 1994.

D. C. D. Happold

Atelerix algirus ALGERIAN HEDGEHOG

Fr. Hérisson d'Algérie; Ger. Algerischer Igel

Atelerix algirus Lereboullet, 1842. Mem. Soc. Hist. Nat. Strasbourg 3 (2), art. QQ: 4. Oran, Algeria.

Taxonomy Synonyms: *caniculus*, *fallax*, *girbaensis*, *lavaudeni*, *vagans*. Subspecies: none recognized here. Several have been described for mainland and introduced island populations (see below); the insular populations show variation in pelage colouration but subspecific recognition is considered unwarranted by Corbet (1988). In contrast, Hutterer (2005a) recognizes *girbaensis* and *vagans* as subspecies. Chromosome number: not known.

Description Large hedgehog with five digits on hindfoot. Dorsal pelage of dark spines often with some pure white spines. Surface of spines smooth and without papillae. Ventral pelage of non-spiny hairs; hairs white or buffy-white, sometimes with dark patches. Spiny dorsal pelage and hairy ventral pelage clearly delineated on lower flanks. Head with wide white forehead from cheek to cheek; narrow central parting of spines on crown of head; muzzle white without dark face-mask (or with only a slight 'spotting' of dark hairs). Ears small, rounded, shorter than adjacent spines; ca. 77% of HF. Limbs short, white or pale; forefeet with five digits; hindfeet with five digits, Digit 1 may be slightly shorter than other digits. Tail relatively very short (<10% of HB), barely visible, with small pale hairs. Glans penis without spiny or papillate pads, expands laterally. Skull: auditory bullae moderate size; P³ with three roots. Nipples: not known. See Table 6.

Geographic Variation Individuals from Morocco are paler than those from Algeria, Tunisia and Libya (Corbet 1988).

Similar Species

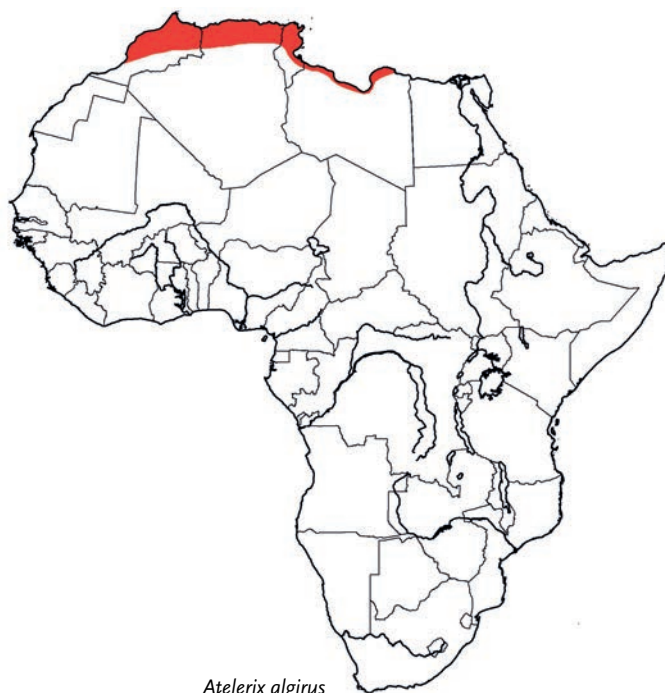
Paraechinus aethiopicus. Wide central parting on crown; spines with papillae and grooves; black face-mask; ears longer than adjacent spines; Sahara and northern semi-arid regions.

Hemiechinus auritus. No central parting on crown; spines with papillae and grooves; no face-mask; ears very large, much longer than adjacent spines; Egypt and Libya only.

Distribution Endemic to Africa. Mediterranean Coastal BZ and (infrequently) coastal regions of the Sahara Arid BZ. Recorded

from Morocco, Algeria and Tunisia between the Mediterranean coast and the semi-arid habitats north of the Sahara Desert, including the Atlas Mts. In Libya, occurs only in a few localities near the coast, as far west as Cyreniaca. Djerba Is. (Tunisia). Introduced into several islands of the Balearic and Canary Is., and into parts of the Mediterranean coastal regions of France and Spain. Overlaps marginally with *Paraechinus aethiopicus* in the southern part of its range.

Habitat Mediterranean scrublands and grasslands, cultivations, palm groves and suburban gardens. May occur up to 2000 m in the Middle Atlas of Morocco (Aulagnier & Thévenot 1986).



Atelerix algirus

Abundance Common in cultivated regions and palm groves (Aulagnier & Thévenot 1986). In Libya, more abundant than the other two species of hedgehogs (*P. aethiopicus* and *H. auritus*).

Adaptations Nocturnal and terrestrial. It seems likely that Algerian Hedgehogs enter torpor during the winter.

Foraging and Food Primarily insectivorous and opportunistic; the diet includes worms, eggs and fruits (Aulagnier & Thévenot 1986), snails and insects (Hufnagl 1972). Introduced animals in the Balearic Is. are reported to feed on snails, centipedes, insects, snakes, lizards and a truffle-like fungus (J. A. Alcover, in Corbet 1988).

Social and Reproductive Behaviour No information.

Reproduction and Population Structure Reproduction appears to be limited to spring and summer. In Libya, breeding occurs from Apr to Jun, and occasionally a second litter is produced in Jul. Gestation: 30–48 days; litter-size: 3–7. Young remain close their mother for several months (Hufnagl 1972).

Predators, Parasites and Diseases Remains are infrequently found in owl pellets in Algeria (Kowalski & Rzebik-Kowalska 1991). May be eaten by humans in the Balearic Is. (Corbet 1988). Frequently killed by vehicles on roads in all parts of its range. Ectoparasites

include the flea *Echidnophaga gallinacea* (also found on chickens); endoparasites include nematode worms (Reeve 1994).

Conservation IUCN Category: Least Concern.

Measurements

Atelerix algirus

HB: 200–270 mm

T: 15–30 mm

HF: 30–40 mm

E: 25–30 mm

WT: n. d.

GLS: 54.7 (43.6–58.3) mm, n = 8

GWS: 32.3 (27.4–34.6) mm, n = 7

I-M³: 27.8 (24.7–29.7) mm, n = 8

Auditory bulla: 6.6 (5.6–7.8) mm, n = 5*

Body measurements: Morocco (Aulagnier & Thévenot 1986; no means or sample sizes recorded)

Skull measurements: Algeria (Kowalski & Rzebik-Kowalska 1991)

*Algeria (BMNH)

Key References Aulagnier & Thévenot 1986; Corbet 1988; Hufnagl 1972; Kowalski & Rzebik-Kowalska 1991.

D. C. D. Happold

Atelerix frontalis SOUTHERN AFRICAN HEDGEHOG

Fr. Hérisson du Cap; Ger. Kap-Igel

Atelerix frontalis (A. Smith, 1831). S. Afr. Quart. J., ser. 1, 5: 10. N Graaff Reinet district, South Africa.

Taxonomy Originally described in the genus *Erinaceus*. Synonyms: *angolensis*, *capensis*, *diadematus*, *fractilis*. Subspecies: two of uncertain validity. Chromosome number: not known.

Description Medium-sized hedgehog with five digits on hindfoot. Dorsal pelage of dark spines; spines white at base, with broad black or dark-brown subterminal bands and white or buffy tip. Surface of spines smooth without papillae. Ventral pelage of non-spiny hair, dark grey, brown or black. Head with white forehead; narrow central parting of spines on crown of head; black or dark brown face-mask on muzzle and around eyes extending posteriorly and ventrally to merge with the dark colouration on throat and chest (Figure 4). Ears small and rounded, shorter than adjacent spines; ca. 76% of HF. Limbs short, grey-brown to dark brown; hindfeet with five digits. Tail relatively very short (ca. 15% of HB). Nipples: 2 + 1 = 6. Skull: auditory bulla comparatively small.

Geographic Variation Shortridge (1934) and Meester *et al.* (1986) list two subspecies without comment:

A. f. angolae: SW Angola, N and C Namibia.

A. f. frontalis: W and C Zimbabwe, E Botswana and South Africa.

Similar Species

Atelerix albiventris. Ventral pelage white or buffy-white; four digits on

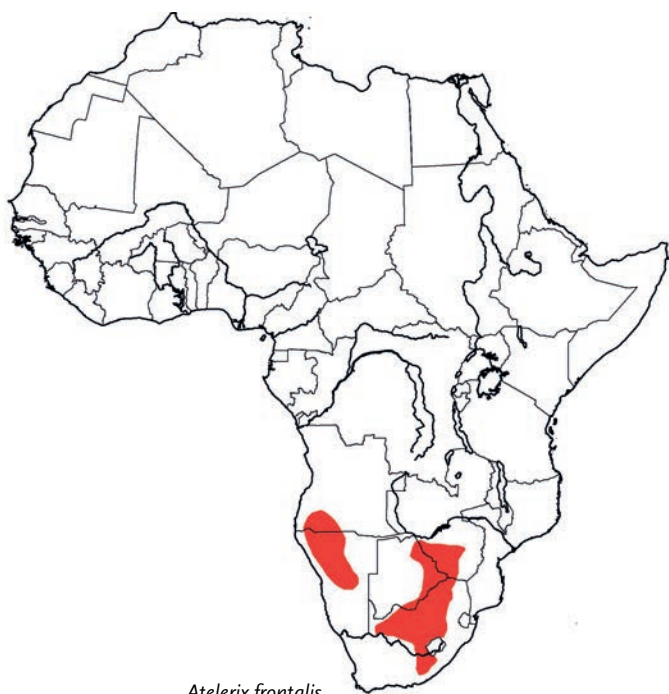
HF; widespread in savanna habitats south of the Sahara and north of the Zambezi R. Allopatric.

Distribution Endemic to Africa, Zambezian Woodland BZ (SE and SW parts), Highveld BZ and parts of South-West Arid BZ (Karoo). Distribution disjunct with two separate ranges: (a) SW Angola, and N and C Namibia; (b) W and C Zimbabwe, E Botswana, and South Africa west of 31°E and southwards towards Grahamstown and the eastern Karoo (Smithers 1968, Rautenbach 1982, Lynch 1983, Skinner & Smithers 1990). Not recorded north of the Zambezi R. or from Swaziland (Monadjem 1998c) or KwaZulu–Natal (Taylor, P. 1998). Geographic range not known to overlap with *Atelerix albiventris*.

Habitat Occurs in many habitats in semi-arid and sub-temperate regions where annual rainfall is 300–800 mm and where there is ample ground cover. Not found in deserts or mesic habitats. Regularly found in suburban gardens.

Abundance Generally uncommon or rare (Shortridge 1934, Smithers 1983); tend to be commoner in suburban gardens where there is cover and food. In South Africa, numbers have declined with increased usage of domestic and agricultural pesticides.

Adaptations Terrestrial. Southern African Hedgehogs spend the day curled up in a ball under the cover of vegetation or in holes



Atelerix frontalis

in the ground, emerging in the evening to forage. Locomotion is slow, but agile when in flight. They are predominantly nocturnal, but exhibit some diurnal activity after rain has fallen, probably to feed on emerging earthworms.

Southern African Hedgehogs enter torpor during the cool dry season (= winter) when T_a is low. Torpor is characterized by low oxygen consumption, low respiration rate and a lowered body temperature. Experimental study has shown that at 15 °C and a 10 : 14 hour light : dark photoperiod, hedgehogs readily enter torpor. Similarly, on a restricted diet (about 40% of weekly maximum consumption) they display longer periods of torpor (Gillies *et al.* 1991). During torpor, fat reserves accumulated during the wet season are utilized to obtain energy (Smithers 1983). It appears that hedgehogs can modify the length of torpor in response to the availability of food and energy.

The timing and duration of torpor is likely to vary geographically. In the colder regions of the geographic range (eastern Free State, South Africa) where ambient temperatures fall to -9 °C during the winter, hedgehogs are inactive and remain in their burrows from Jun to Aug. During this period, there may be a 11–19% loss of body weight. If there is a warm spell during winter, hedgehogs may emerge and feed briefly before resuming torpor again (Smithers 1983). Torpor ends when temperatures increase in spring (Sep).

The dorsal spines are an effective means of defence when accompanied by rolling into a ball with the head, limbs and soft ventral surface in the centre. Smithers (1983) reported the sighting of a Lion *Panthera leo* in Hwange N. P., Zimbabwe, which was rolling a balled hedgehog between its paws and trying to bite it; the hedgehog survived and was none the worse for the encounter!

Foraging and Food Omnivorous. Hedgehogs forage in litter and just under the soil surface, and food is located mainly by scent. The diet includes variety of invertebrates such as beetles, earwigs, grasshoppers, termites, slugs and snails (which form the bulk of their diet) and small vertebrates such as small mammals, eggs and chicks

of terrestrial birds, frogs and lizards. Some vegetable matter (e.g. fungi) may also be eaten. In captivity, hedgehogs eat invertebrates, minced beef, bread and dogfood (Smithers 1966, Smithers & Wilson 1979, Lynch 1989, Skinner & Smithers 1990). They do not seem to be dependent on free water, which is often not available, or available only seasonally, in their preferred habitat.

Social and Reproductive Behaviour Usually solitary, but also recorded in pairs and as a ♀ with young (Lynch 1983). Aggressive behaviour includes head butting accompanied by vocalizations that have been described as snuffling, snorting and growling. The alarm call is a high-pitched screech (Smithers 1983).

Females give birth to young in sheltered nests in debris or in holes lined with dry leaves. In the Free State, South Africa, they sometimes utilize termitaria for nesting (Lynch 1983). The young remain in or around the nest for 4–6 weeks after birth, and then can be seen foraging in the company of the ♀. Males do not participate in parental care (Skinner & Smithers 1990).

Reproduction and Population Structure Reproduction occurs during the warm wet summer months (Oct–Apr), and ♀♀ are seasonally polyoestrous. Gestation: 5–6 weeks. Litter-size: usually four (range 1–9; Smithers 1983). At birth: 5 cm in length, WT: 9 g, blind and hairless, ears closed, and rudimentary spines visible beneath skin. Development of spines is rapid; tips of unpigmented spines emerge through skin 1–3 h after birth and lengthen to about 6.5 mm by Day 2. Pigmented spines appear on Day 3, and by Day 7 a distinctly hedgehog-like appearance is attained and characteristic behaviour described as frowning, puffing and jerking is evident. Eyes open Day 10. Infant spines shed at 4–6 weeks. Weaned at about five weeks (Jacobsen 1982). A ♀ may produce more than one litter each year (Skinner & Smithers 1990).

Predators, Parasites and Diseases The Giant Eagle-owl *Bubo lacteus* preys on hedgehogs (Smithers 1968); when feeding, it peels and discards the spines from the body (Kemp & Calburn 1987). Some humans catch hedgehogs for food.

Conservation IUCN Category: Least Concern.

Originally listed as a threatened species but now thought to be less threatened. In South Africa, considered as 'rare' (Smithers 1986) and protected by local ordinances. Numbers have probably declined because of changing land-use and increased use of pesticides (which kill prey species).

Measurements

Atelerix frontalis frontalis

| | |
|----------|-----------------------------|
| HB (♂♂): | 185 (170–190) mm, n = 7 |
| HB (♀♀): | 196 (186–210) mm, n = 4 |
| T (♂♂): | 24 (20–30) mm, n = 7 |
| T (♀♀): | 24 (20–25) mm, n = 4 |
| HF (♂♂): | 34 (32–36) mm, n = 7 |
| HF (♀♀): | 34 (31–36) mm, n = 4 |
| E (♂♂): | 25 (20–27) mm, n = 7 |
| E (♀♀): | 27 (25–29) mm, n = 4 |
| WT (♂♂): | 362 (291–479) g, n = 9 |
| WT (♀♀): | 410, 450 g, n = 2 |
| GLS: | 47.4 (44.6–50.6) mm, n = 12 |

GWS: 29.2 (26.9–31.8) mm, n = 12
 I¹–M³: 23.4 (22.2–25.0) mm, n = 12
 Auditory bulla: 5.3 (5.2–5.5) mm, n = 4
 Body measurements and weight: Zimbabwe (Smithers & Wilson 1979)
 Skull measurements: South Africa (BMNH)

Key References Gillies *et al.* 1991; Jacobsen 1982; Smithers 1983.

N. J. Dippenaar & R. M. Baxter

Atelerix sclateri **SOMALI HEDGEHOG**

Fr. Hérisson de Somalie; Ger. Somalischer Igel

Atelerix sclateri Anderson, 1895. Proc. Zool. Soc. Lond. 1895: 415. Taf, central Somalia.

Taxonomy The least well-known of African hedgehogs. Originally described in the genus *Erinaceus*, then moved to *Aethechinus*, but now considered to belong to *Atelerix* and closely related to *A. albiventris*. In N Somalia, populations of *A. sclateri* occur within about 100 km of populations of *A. albiventris* (Corbet 1988) without intergradation, and without any physical boundaries separating them. Possibly *sclateri* is a subspecies of *A. albiventris* (Corbet 1988). Synonyms: none. Chromosome number: not known.

Description Large hedgehog with five digits on hindfoot. Dorsal pelage of dark spines. Surface of spines smooth and without papillae. Ventral pelage of non-spiny hairs; hairs white or buffy-white with dark patches posteriorly. Spiny dorsal pelage and hairy ventral pelage clearly delineated on lower flanks. Head with white forehead from cheek to cheek; narrow central parting of spines on crown of head; black face-mask with slight posterior extension of black colouration on cheek. Ears small, rounded, shorter than adjacent spines; ca. 88% of HF. Limbs short, dark; forefeet with five digits; hindfeet with five digits, Digit 1 small. Tail very short with small pale hairs, barely visible. Nipples: not known. Glans penis – no information. Skull: auditory bullae comparatively small; P³ with two roots, barely divergent. See Table 6.

Geographic Variation None recorded.

Similar Species

Atelerix albiventris. Four digits on HF; limbs pale; widespread in savanna habitats south of the Sahara and north of the Zambezi R. Allopatric.

Distribution Endemic to Africa. Somalia–Masai Bushland BZ. Known only from a few localities in N Somalia. Not recorded from neighbouring Djibouti (Pearch *et al.* 2001) or Ethiopia (Yalden *et al.* 1976).

Habitat Most specimens found on ‘maritime plain close to hills’ near Berbera. Altitude range: 10 m (near Berbera) to 1360 m (near Upper Sheik).

Abundance Uncertain; known from only a few specimens from about seven localities. Said to be ‘fairly common on the maritime plain’ (R. E. Drake-Brockman; label, BMNH).

Remarks Apparently no other information available. Presumed to be similar in many respects to other hedgehogs in arid habitats.



Atelerix sclateri

Conservation IUCN Category: Least Concern.

The few known specimens, small distribution and absence in locations where it would be expected to occur suggest that the species is threatened and should be classified as Vulnerable.

Measurements

Atelerix sclateri

HB: 225.0 (206–263) mm, n = 4

T: 18.5 (14–20) mm, n = 4

HF: 26.8 (25–28) mm, n = 4

E: 24.0 (22–27) mm, n = 4

WT: n. d.

GLS: 41.8 (40.3–42.8) mm, n = 4

GWS: 25.1 (24.0–26.0) mm, n = 4

I¹–M³: 20.0 (19.1–20.4) mm, n = 4

Auditory bulla: 4.6 (4.4–4.8) mm, n = 4

Somalia (BMNH)

Key Reference Corbet 1988.

D. C. D. Happold

GENUS *Hemiechinus*

Long-eared Hedgehog

Hemiechinus Fitzinger, 1866. Sitzb. Akad. Wiss. Wien 54, 1: 565. Type species:
Erinaceus platyotis Sundevall, 1842 (= *Erinaceus auritus* Gmelin, 1770).

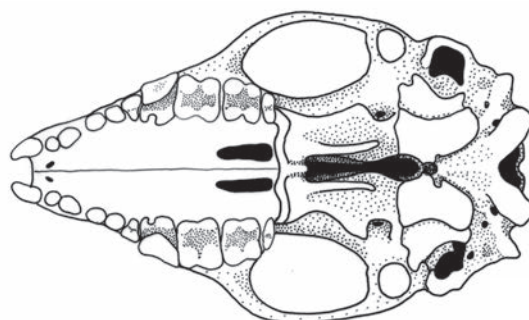
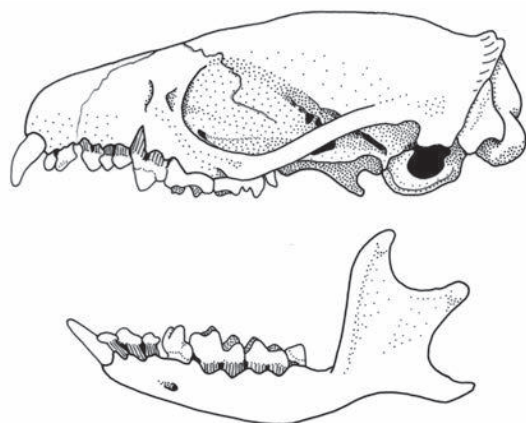


Figure 7. Skull and mandible of *Hemiechinus frontalis* (BMNH 92.7.1.2).

The genus contains four species widely distributed in the temperate and semi-desert regions from NE Africa and the Middle East to central China and NW India. Species in the genus are distinguished by the absence of a parting of the spines on the crown of the head, papillate spines with grooves, very large ears, narrow palatal shelf and enlarged auditory bullae (Figures 4 and 7). Digit 1 of the hindfoot

is well developed. Hutterer (2005a) includes *Paraechinus* within this genus, but following Corbet (1988), *Paraechinus* is retained as a valid genus here. The single species in Africa, *Hemiechinus auritus*, occurs only in the extreme NE of the continent.

D. C. D. Happold

Hemiechinus auritus LONG-EARED HEDGEHOG

Fr. Hérisson à grandes oreilles; Ger. Langohr-Igel (Grossohrige)

Hemiechinus auritus (Gmelin, 1770). Nova Comm. Acad. Sci. Petropoli 14: 519. Astrakhan, S. Russia.

Taxonomy Originally described in the genus *Erinaceus*. A central Asian and Middle Eastern species, which has its extreme western boundary in coastal Egypt and Libya. Many synonyms (extralimital to Africa; see Corbet 1988, Hutterer, 1993, 2005a). Synonyms: many (mostly extralimital to Africa – see Hutterer 2005a). Subspecies: two (Egypt only). Chromosome number: $2n = 48$, $aFN = 92$ (Hübner *et al.* 1991).

Description Small pale hedgehog with five digits on hindfoot. Dorsal pelage of dark spines; spines banded, whitish at base, with two wide black bands separated by white band, and white tip. Surface of spines rough with numerous papillae and with many shallow longitudinal grooves. Ventral pelage of non-spiny soft white hairs. Spiny dorsal pelage and hairy ventral pelage clearly delineated on lower flanks. Head white without dark face-mask; no central parting of spines on crown of head (cf. all other African hedgehogs). Ears large, slightly pointed, flexible and mobile, considerably longer than adjacent spines; ca. 114% of HF. Limbs rather long for a hedgehog, white; forefoot with five digits; hindfoot with five digits. Tail relatively very short and barely visible (ca. 15% of HB) with small pale hairs. Nipples: usually 5 pairs. Glans penis with two tracts of spines on upper surface; not expanded laterally. Skull: auditory bullae enlarged, but smaller than in *Paraechinus aethiopicus* (see Measurements); P^3 with 1–3 roots. See Table 6.

Geographic Variation Considerable variation throughout range. In Egypt, Osborn & Helmy (1980) recognize two subspecies:

- H. a. aegyptius*: Nile Delta and Sinai. Darker colouration, tail longer.
- H. a. libycus*: coastal desert regions west of the Nile Delta. Paler colouration, tail shorter.

Similar Species

- Paraechinus aethiopicus*. Wide central parting on crown; black face-mask; Sahara and northern semi-arid regions.
- Atelerix algirus*. Narrow central parting on crown; spines smooth; ears shorter than adjacent spines; Morocco to Tunisia only.

Distribution North-eastern part of Sahara Arid BZ. Recorded from coastal Egypt and Libya. Extraliminally throughout Middle East, central Asia north of the Himalayan Mts to Mongolia and China (see Corbet 1988).

Habitat Coastal semi-desert and scrub with dense vegetation. Prefers mesic habitats such as gardens, olive groves and cultivated areas.

Abundance Not uncommon in suitable habitats.

*Hemiechinus auritus*

Adaptations Nocturnal and terrestrial. Although the Long-eared Hedgehog lives in semi-arid countries, it is not desert-adapted as is the Ethiopian Hedgehog *Paraechinus aethiopicus*. Nevertheless, it is moderately tolerant of heat and drought, and the large ears may be used for thermoregulation (Hufnagl 1972). During the day animals rest in burrows 20–90 cm long, which they dig themselves or in burrows originally made by rodents; at other times they rest in caves and crevices and under piles of rocks and bricks. Their long limbs enable them to walk and run quickly.

Comparative studies show that metabolic rate is 64% of that predicted on the basis of weight (cf. European Hedgehog *Erinaceus europaeus*: 98%). Evaporative water loss is similar to that of the European Hedgehog at low T_a , but lower at high T_a ; for example, at $T_a = 30^\circ\text{C}$ water loss is 1.0 ml/g/h and at $T_a = 40^\circ\text{C}$ water loss is 4.0–8.2 ml/g/h (see also *Paraechinus aethiopicus*) (Shkolnik 1980). In this respect, Long-eared Hedgehogs fall midway between the temperate *Erinaceus europaeus* and the desert-adapted *Paraechinus aethiopicus*. During the cold season in North Africa (ca. Dec–Feb) they may go into torpor and remain in their burrows for periods of 5–40 days (Schoenfeld & Yom-Tov 1985).

Studies in Israel (where the climate is similar to that of North Africa) have revealed other aspects of the biology of the species (Schoenfeld & Yom-Tov 1985). During the course of a year, hedgehogs undergo regular fluctuations in weight. Mean maximum weight of 280 g is in summer (when food is abundant); weight declines in autumn to 260 g and to the minimum of 235 g during winter. Loss of weight is associated with torpor when hedgehogs utilize their fat reserves. In an area of ca. 500 ha, mean home-ranges were 4.9 ha for ♂♂ and 2.8 ha for ♀♀. Home-ranges for lactating

♀♀ were larger (mean = 3.5 ha) than for non-lactating ♀♀ (mean = 1.3 ha). Radio-tracking showed that individuals sometimes walk 1000 m during the course of night.

Foraging and Food Primarily insectivorous. In Israel, the diet (of this species and *Erinaceus europaeus*) included many insects (bugs, beetles, grasshoppers and ants), millipedes and snails. During spring, snails were a favoured food (Schoenfeld & Yom-Tov 1985).

Social and Reproductive Behaviour No information for Africa. Courtship behaviour is well developed, and includes sniffing, licking of the genitalia and flank-rubbing (Poduschka & Poduschka 1986, in Reeve 1994).

Reproduction and Population Structure In Egypt, litters of one and two young were recorded in May, and five in Aug (Flower 1932). Births were recorded in Jun (Israel; Schoenfeld & Yom-Tov 1985), and in Jun or Jul–Oct, with a peak in Aug (India; Prakash 1966 in Nader 1968). Litter-size: 2.5 (1–6) (Prakash 1960). Typically eyes open ca. Day 16, solid food eaten Day 21–28, and young are weaned at ca. Day 40 (Poduschka & Poduschka 1986).

Predators, Parasites and Diseases In Israel, ectoparasites include one species of tick *Rhipicephalus sanguineus* and one species of flea *Archaeopsylla erinacei* (Schoenfeld & Yom-Tov 1985). In Egypt, 11 species of fleas in seven genera have been recorded; many of these are widespread species, which also parasitize other mammalian species (Lewis 1967).

Conservation IUCN Category: Least Concern.

A widespread species and unlikely to be threatened.

Measurements

Hemiechinus auritus aegyptius

HB: 179.1 (156–206) mm, n = 35

T: 24.4 (18–39) mm, n = 36

HF: 35.9 (28–39) mm, n = 37

E: 41.0 (34–45) mm, n = 37

WT: up to ca. 500 g

GLS: 44.6 (42.4–46.7) mm, n = 32

GWS: 26.5 (24.1–29.7) mm, n = 32

I–M³: 21.9 (19.3–23.9) mm, n = 20*

Auditory bulla: 6.5 (6.3–6.7) mm, n = 5**

Egypt (Osborn & Helmy 1980)

*Middle East (Harrison & Bates 1991)

**Egypt (BMNH)

Key References Osborn & Helmy 1980; Schoenfeld & Yom-Tov 1985.

D. C. D. Happold

GENUS *Paraechinus*

Desert Hedgehog

Paraechinus Troussart, 1879. Rev. et Mag. de Zool. 3 (7): 242. Type species: *Erinaceus micropus* Blyth.

Contains three species of 'desert hedgehogs', which live in arid habitats of North Africa and the Middle East. The genus is distinguished by the wide central parting of spines on crown of head, papillate spines with grooves, large ears, broad palatal shelf and especially enlarged auditory bullae (Figures 4 and 8). Digit 1 of hindfoot is well developed (cf. *Atelerix* spp.). Members of the genus are better adapted to arid conditions than other hedgehogs. *Paraechinus* is considered to be a subgenus of *Hemiechinus* by Hutterer (1993, 2005a), although retained as a valid genus by Corbet (1988). The single African species occurs only in the arid and semi-arid regions in and around the Sahara Desert.

D. C. D. Happold

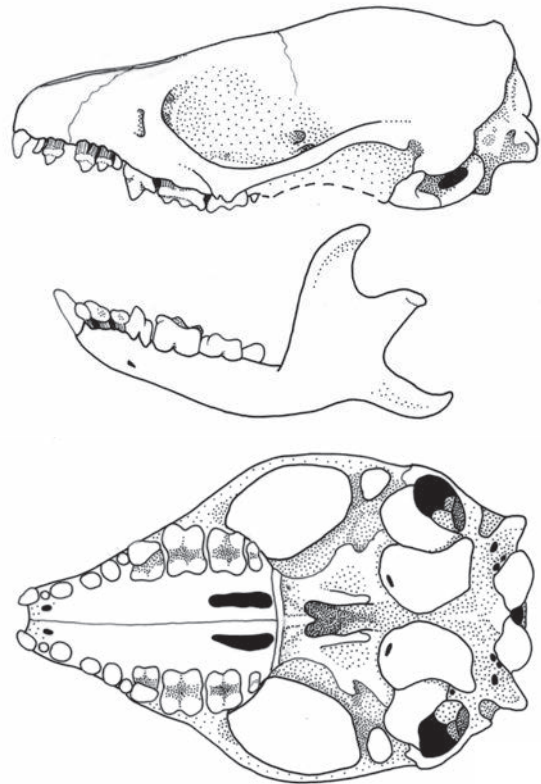


Figure 8. Skull and mandible of *Paraechinus aethiopicus* (BMNH 66.5581).

Paraechinus aethiopicus DESERT HEDGEHOG (ETHIOPIAN HEDGEHOG)

Fr. Hérisson du désert; Ger. Wüstenigel

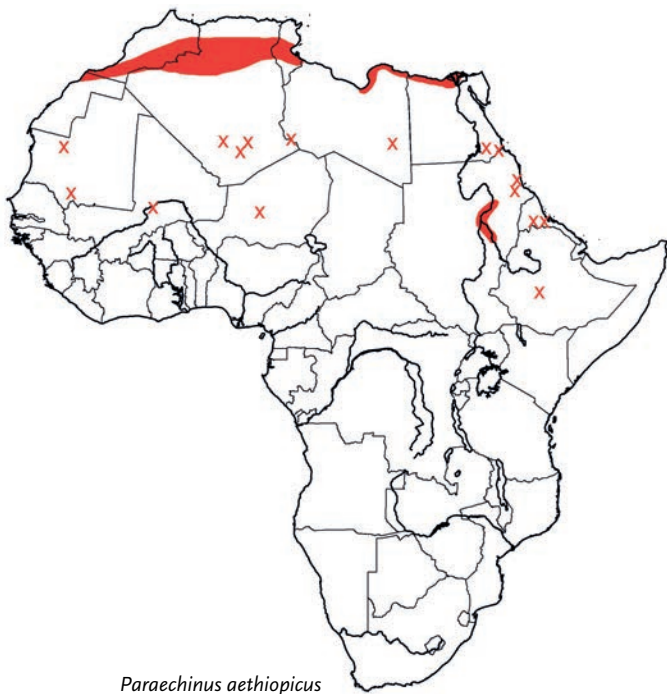
Paraechinus aethiopicus (Ehrenberg, 1832). Symb. Phys. Mamm. 2; footnote. Dongola desert, Sudan.

Taxonomy Originally described in the genus *Erinaceus*. The widespread distribution, and the large amount of individual variation, has resulted in many names, at species and subspecies level, being applied to this species. Osborn & Helmy (1980) regard *aethiopicus*, *dorsalis* and *deserti*, all of which occur in Egypt, as full species, a view not supported by Corbet (1988) and Hutterer (1993, 2005a). Here, placed in the genus *Paraechinus* (following Corbet 1988), not in the genus *Hemiechinus* as given by Hutterer (2005a). See also genus profile. Synonyms: *albatus*, *albior*, *blancalis*, *brachydactylus*, *deserti*, *dorsalis*, *ludlowi*, *oniscus*, *pallidus*, *pectoralis*, *senaariensis*, *wassifi*. Subspecies: none recognized here. Chromosome number: $2n = 48$, $FN = 90$ (Saudi Arabia; Harrison & Bates 1991).

Description Medium-sized hedgehog with five digits on hindfoot (as in *Hemiechinus*). Dorsal pelage of dark spines; spines banded, whitish at base, with two wide black bands separated by white band, and white tip. Surface of spines rough with numerous papillae and with many shallow longitudinal grooves. Ventral pelage of non-spiny hairs;

rather sparse; hairs mostly white but may be brown posteriorly or have brown patches on chest in some individuals. Spiny dorsal pelage and hairy ventral pelage clearly delineated on lower flanks. Head with broad white forehead from cheek to cheek; wide central parting of spines on crown of head; face-mask on muzzle and around eyes black, well defined, extending posteriorly on to the lower cheek (see also below). Ears large, slightly pointed, usually longer than adjacent spines; ca. 132% of HF. Limbs rather long for a hedgehog, dark brown; forefeet with five digits; hindfeet with five digits (Digit 1 may be slightly reduced). Tail relatively very short (<1% of HB), barely visible, with small pale hairs. Glans penis with two tracts of spines (sometimes each with two rows of spines) on upper surface. Skull: auditory bullae enlarged (more so than in other species of hedgehogs; see Measurements); P^3 with one root. Nipples: four pairs. See Table 6.

Geographic Variation There is considerable variation in the extent of the brown colouration of the ventral pelage in different parts of the range.



Similar Species

Atelerix albiventris. Narrow central parting on crown; spines smooth; four digits on HF; ears shorter than adjacent spines; widespread in savanna habitats south of the Sahara and north of the Zambezi R.

A. algirus. Narrow central parting on crown; spines smooth; no face-mask (some 'spotting' on muzzle); five digits on HF; ears shorter than adjacent spines; Morocco to Tunisia only.

Hemiechinus auritus. No central parting on crown; no face-mask; five digits on HF; ears very large, much longer than adjacent spines; Egypt and Libya only.

Distribution Sahara Arid BZ and in the semi-arid regions to the north and south of the desert. Widely distributed. Recorded from Mauritania and Morocco to Egypt, Sudan and N Ethiopia. Also Djerba I. (Tunisia). Populations are mostly scattered and isolated (as a result of increasing aridity in the area of distribution in recent millennia). Not recorded from coastal regions of Morocco, Algeria or Tunisia. Also occurs extralimittally in Saudi Arabia, Israel, Jordan, Iraq and the Gulf States (Harrison & Bates 1991).

Habitat Desert and dry scrub, often on stony plains, jebels and in mountainous desert country (e.g. Hoggar); also in more mesic regions such as near oases and vegetated wadis.

Abundance Generally uncommon, but may be common in selected localities. Populations are scattered and isolated, and do not occur throughout the whole geographic range. Not uncommon in (irrigated) gardens and fields in parts of the range (e.g. Libya; Hufnagl 1972).

Adaptations Little is known about this species in the wild (Corbet 1988). Desert Hedgehogs appear to be better adapted to arid conditions than the other species of African hedgehogs. Nocturnal and terrestrial. During the day, rest in crevices in cliffs, under clumps

of vegetation, or in burrows and, unlike other hedgehogs, may dig their own burrows (Herter 1968). During the winter (cool season) in the desert, when the night air is cold and food is less abundant, they enter torpor (and hence are rarely seen). In Algeria, hedgehogs are torpid during the months of Nov–Mar (Kowalski & Rzebik-Kowalska 1991); during these months they usually emerge every few days to feed (Harrison & Bates 1991).

Desert hedgehogs show two adaptations that are clearly associated with the desert habitat: low metabolic rate and low evaporative water loss. In captive animals, metabolic rate (as measured by oxygen consumption) is only 51% of what is predicted on the basis of weight (cf. European Hedgehog: 98%). Evaporative water loss is comparatively lower than that of the European Hedgehog; for example, in the Desert Hedgehog at $T_a = 30^\circ\text{C}$ water loss is 0.55 ml/g/h; at $T_a = 40^\circ\text{C}$ water loss is 3.3–4.5 ml/g/h; equivalent figures for the European Hedgehog are 2.6 and 6.7–10 ml/g/h (Shkolnik 1980). T_b at normal T_a is around 34°C ; there is no information on the T_b of torpid Desert Hedgehogs.

Long limbs enable fast walking and trotting: one individual was followed at a steady 10 km/h for five minutes in Libya (Hufnagl 1972).

Foraging and Food Primarily insectivorous. In Algeria, the diet comprises insects, eggs, agamid lizards and snakes, and they are also reported to eat scorpions (Sellami *et al.* 1989, Kowalski & Rzebik-Kowalska 1991).

Social and Reproductive Behaviour No information.

Reproduction and Population Structure Litter-size: 2–5. Weight of young at birth: 8–9 g. Growth rate: 20 g at Day 10; 40 g at Day 20; 60 g at Day 30; 80 g at Day 40; 150 g at Day 60. Growth rate to 6 weeks: 1.7 g/day; from 6 to 9 weeks: 3.5 g/day. Eyes open: Day 21–22. Solid foods eaten: Day 44. Fully weaned: Day 58 (Eisentraut 1952, Reeve 1994). Growth to weaning is longer than in other species of hedgehogs. Thermoregulation fully developed at about Day 44 when solid food is first eaten. No information on number of litters/year, or on average longevity.

Predators, Parasites and Diseases In Algeria, hunted by jackals. Remains of young hedgehogs found in the pellets of owls (species unknown) (Kowalski & Rzebik-Kowalska 1991). Also eaten by humans in some parts of the range (e.g. in Algeria; Sellami *et al.* 1989). Two species of fleas recorded on Desert Hedgehogs in Egypt: *Synosternus pallidus* (common on several species of hedgehogs and carnivores) and *S. cleopatrae* (common on gerbils) (Lewis 1967).

Conservation IUCN Category: Least Concern.

Measurements

Paraechinus aethiopicus

HB: 196.1 (169–217) mm, n = 7

T: 19.1 (15–22) mm, n = 7

HF: 32.8 (30–37) mm, n = 7

E: 43.6 (41–45) mm, n = 7

WT: ca. 500 g

GLS: 43.4 (41.1–45.1) mm, n = 8

GWS: 26.5 (25.1–27.5) mm, n = 8

I¹–M³: 20.5 (19.8–21.5) mm, n = 8

Auditory bulla: 9.4 (8.6–10.3) mm, n = 6

Body measurements and weight: Egypt (Osborn & Helmy 1980)

Skull measurements: Egypt and Sudan (BMNH)

Key References Corbet 1988; Eisentraut 1952; Reeve 1994.

D. C. D. Happold

Order SORICOMORPHA – Shrews, Moles, Shrew Moles, Desmans and Solenodons

Soricomorpha Gregory, 1910. Bull. Amer. Mus. Nat. Hist. 37: 465.

| | | |
|--|--------|-------|
| Soricidae (9 genera, 150 species) | Shrews | p. 43 |
|--|--------|-------|

The order Soricomorpha includes a multitude of shrew-like forms that feed primarily on invertebrates, including insects, other arthropods, molluscs and earthworms. They have elongated, flexible snouts, prominent vibrissae and numerous small pointed teeth. The external ears are small and rounded. The eyes are minute. The pelage is short and dense with a velvety touch. They are mostly terrestrial and ground-dwelling, and run with a plantigrade gait. They include some of the smallest of all living mammals, and range in size from the tiny shrews such as *Suncus etruscus* and *Sorex minutissimus* weighing 1.5–2 g, to the stoutly built solenodons such as *Solenodon paradoxus*, weighing up to 1 kg. Although soricomorphs resemble more closely the generalized, primitive mammalian condition than other Recent placental mammals, the earlier viewpoint that they were ancestral to the other eutherian (placental) orders of mammals and defined by primitive characters has largely been abandoned (Butler, 1988). Their geological range is early Eocene to Recent (Miocene to Recent in Africa).

Extant members of the Soricomorpha are distributed widely throughout Eurasia, North America, Africa and southern Asia. Only after the formation of the Pliocene land bridge did they reach South America, but only one genus, the shrew *Cryptotis*, has successfully colonized the Neotropics. They have never been present in Australia and are absent from the polar regions.

The soricomorphs (as currently understood) were previously assigned to the order Insectivora, along with many other small fossil and extant mammals with primitive characters such as hedgehogs

(Erinaceidae), golden-moles (Chrysochloridae), tenrecs (Tenrecidae) and elephant shrews or sengis (Macroscelidae). It was long argued that, because of the primitive features possessed by all these insectivorous mammals, they exhibit closer affiliations with the ancestral stock of mammals than do any other living groups. However, the composition of the group has never been fully agreed upon and the proposal that they represent a monophyletic group descended from a single common ancestor has been hotly debated. Cladistic analysis suggests that living insectivores are united by derived anatomical features (MacPhee & Novacek 1993). Molecular studies have cast further doubt on the phylogeny and affiliations of these insectivorous mammals and alternative groupings have been proposed (Springer *et al.* 1997, Stanhope *et al.* 1998, Madsen *et al.* 2001, Murphy *et al.* 2001a).

The taxonomy adopted by Wilson & Reeder (2005) is followed here: the order Insectivora is replaced by three orders, these being Afrosoricida (Tenrecidae, Chrysochloridae), Erinaceomorpha (Erinaceidae) and Soricomorpha (Soricidae [shrews], Talpidae [moles, shrew moles and desmans], Solenodontidae [solenodons] and the extinct Nesophontidae [West Indian shrews]). The Macroscelidae has, for many years, been placed in an order of its own, the Macroscelidea (Schlitter 1993, 2005). The Afrosoricida and Macroscelidae are now placed in the Afrotheria (see Volume I of *Mammals of Africa*). Within the Soricomorpha, only the Soricidae are found in Africa. In comparison with the wealth of information about the biology and ecology of shrews from temperate regions, African species are poorly documented.

Sara Churchfield

Table 7. Genera in the family Soricidae.

| Genera
(number of
species) | Long
hairs
on tail | External
ear | Very
long
claws on
forefeet | Number
of upper
unicuspid
teeth | P ₃ | Crown
pattern
on P ₄ | Vascular
foramina
on
cranium | Notes |
|-----------------------------------|--------------------------|-----------------|--------------------------------------|--|----------------------|---------------------------------------|---------------------------------------|--|
| <i>Congosorex</i>
(3 spp.) | Absent | Very
reduced | No | 3 | Absent or
present | Myosorine | Present | Rainforests of DR Congo and
Congo |
| <i>Crocidura</i>
(106 spp.) | Present | Large | No | 3 | Absent | Crocidurine | Absent | All of Africa |
| <i>Myosorex</i>
(14 spp.) | Absent | Reduced | No | 4 | Present | Myosorine | Present | Mountains of central and East
Africa; southern Africa |
| <i>Paracrocidura</i>
(3 spp.) | Present | Reduced | No | 3 | Absent | Crocidurine | Absent | Montane and rainforest of
central Africa |
| <i>Ruwenzorisorex</i>
(1 spp.) | Absent | Reduced | No | 4 | Absent | Crocidurine | Absent | Mountains of Albertine Rift
Valley |
| <i>Scutisorex</i>
(1 spp.) | Absent | Large | No | 4 | Absent | Crocidurine | Absent | E DR Congo, Uganda |
| <i>Suncus</i>
(7 spp.) | Usually
present | Large | No | 4 | Absent | Crocidurine | Absent | Widespread, but not western
Africa |
| <i>Surdisorex</i>
(2 spp.) | Absent | Absent | Yes | 3 | Absent | Myosorine | Present | Mt Kenya and Aberdare
highlands. Fossorial |
| <i>Sylvisorex</i>
(13 spp.) | Usually
absent | Large | No | 4 | Absent | Crocidurine | Absent | Rainforest and montane forests
of central and East Africa |

Family SORICIDAE

SHREWS

Soricidae Fischer, 1815. Mem. Soc. Imp. Nat. Moscow 5: 372.

| | | |
|-----------------------------------|-------------------------------|--------|
| <i>Congosorex</i> (3 species) | Congo Shrews | p. 50 |
| <i>Crociodura</i> (105 species) | Shrews (White-toothed Shrews) | p. 54 |
| <i>Myosorex</i> (14 species) | Shrews | p. 149 |
| <i>Paracrociodura</i> (3 species) | Large-headed Shrews | p. 164 |
| <i>Ruwenzorisorex</i> (1 species) | Rwenzori Shrew | p. 167 |
| <i>Scutisorex</i> (1 species) | Armoured Shrew | p. 169 |
| <i>Suncus</i> (9 species) | Dwarf Shrews | p. 172 |
| <i>Surdisorex</i> (2 species) | Mole-shrews | p. 183 |
| <i>Sylvisorex</i> (12 species) | Forest Shrews | p. 186 |

The family Soricidae – the shrews – contains 23 Recent genera and some 374 species (Hutterer 2005b), and has many more representatives than any other family of insectivorous mammals. The Soricidae has radiated to fill the terrestrial insectivore niche in most habitats in both temperate and tropical regions. It has the widest distribution of any family of insectivorous mammals, being found in Eurasia, South-East Asia and the Americas, as well as in Africa. Shrews are by far the most numerous and widespread of the terrestrial insectivorous mammals found in Africa. The number of species of shrews in Africa is uncertain and is under constant review as more species are encountered, particularly

in little-known forested and montane areas, and as other previously described taxa are placed in synonymy. Wolsan & Hutterer (1998) record 149 species of shrews in Africa, and Hutterer (2005b) lists 148 species. Here, nine genera and 150 species are recognized (Tables 7 and 8). Within the Soricidae, three clades are recognized, supported by allozyme data and rRNA sequence data (Maddalena & Bronner 1992, Quérrouil *et al.* 2001). Hutterer (2005b) retains these clades at the subfamily level: Soricinae (red-toothed shrews), Crocidurinae (white-toothed shrews) and Myosoricinae. All African shrews are members of the Crocidurinae or Myosoricinae, and the most widespread genus is *Crociodura*, with ca. 105 species recognized at present. The taxonomy of *Crociodura* is complex and some species are morphologically so similar that they are assigned to ‘species groups’. Multivariate analyses of morphological characters to distinguish species is hampered by the lack of specimens available in many cases but recent genetic analyses are providing a means of differentiating morphologically similar species, and molecular approaches are giving further insights into species boundaries and phylogenetic relationships within African *Crociodura* species groups (e.g. Quérrouil *et al.* 2001, 2005). This profile from here on primarily pertains to the Soricidae of Africa. Detailed information on the natural history of shrews is given by Churchfield (1990).

Table 8. Shrews of Africa arranged by size (mean HB and then CI) within eight size categories.

Habitat: a = arid/semi-arid, s = savanna, f = rainforest, fs = rainforest + savanna, m = montane, com = commensal.

Regions: c = central Africa, e = eastern Africa, n = northern Africa, s = southern Africa, w = western Africa, ec = east-central Africa.

| Genus | Species | Mean HB (mm) | Mean CI (mm) | T % of HB (approx) | Habitat | Regions |
|---------------------------------------|-----------------------------|--------------|--------------|--------------------|---------|---------|
| MINUTE (mean HB: <50 mm) | | | | | | |
| <i>Crociodura</i> | <i>nana</i> | 40 | 16 | 75 | s | e |
| <i>Suncus</i> | <i>etruscus</i> | 44 | 13 | 60 | s | n |
| <i>Crociodura</i> | <i>pasha</i> | 46 | 14 | 70 | a | w, e |
| <i>Suncus</i> | <i>remyi</i> | 47 | 13 | 41 | f | c |
| <i>Crociodura</i> | <i>obscurior</i> | 48 | 15 | 60–70 | f | w |
| <i>Crociodura</i> | <i>bottegi</i> | 48 | 16 | 60 | m | e |
| <i>Sylvisorex</i> | <i>johnstoni</i> | 49 | 15 | 50–60 | f | w, c |
| VERY SMALL (mean HB: 50–59 mm) | | | | | | |
| <i>Crociodura</i> | <i>nanilla</i> | 50 | 15 | 70 | s | e |
| <i>Sylvisorex</i> | <i>vulcanorum</i> | 50 | 16 | 100 | m | ec |
| <i>Crociodura</i> | <i>pitmani</i> | 50 | 18 | 72 | s? | c |
| <i>Suncus</i> | <i>infinitesimus</i> | 51 | 15 | 55 | f, s | s |
| <i>Myosorex</i> | <i>schalleri</i> (juvenile) | 53 | 9 | 80 | m | ec |
| <i>Suncus</i> | <i>hututsi</i> | 53 | 14 | 60 | m | ec |
| <i>Crociodura</i> | <i>douceti</i> | 53 | 17 | 80 | f, fs | w |
| <i>Crociodura</i> | <i>religiosa</i> | 54 | 15 | 65 | a | n |
| <i>Crociodura</i> | <i>bottegoides</i> | 54 | 15 | 82 | m | e |
| <i>Suncus</i> | <i>varilla</i> | 56 | 16 | 60 | s | s, e |
| <i>Sylvisorex</i> | <i>granti</i> | 56 | 17 | 100 | m | e |
| <i>Crociodura</i> | <i>yankariensis</i> | 56 | 19 | 67 | s | w, e |

| Genus | Species | Mean HB (mm) | Mean CI (mm) | T % of HB (approx) | Habitat | Regions |
|---|----------------------|--------------|--------------|--------------------|---------|---------|
| <i>Crocidura</i> | <i>ansellorum</i> | 57 | 17 | 80 | s | c |
| <i>Crocidura</i> | <i>fuscumurina</i> | 58 | 16 | 65 | s | w, e, s |
| <i>Crocidura</i> | <i>polia</i> | 58 | 18 | 124 | f, s? | c |
| <i>Sylvisorex</i> | <i>camerunensis</i> | 58 | 18 | 100 | m | w |
| <i>Congosorex</i> | <i>verheyeni</i> | 59 | 18 | 32 | f | c |
| <i>Sylvisorex</i> | <i>isabellae</i> | 59 | 19 | 90 | m | w |
| <i>Crocidura</i> | <i>cinderella</i> | 59 | 19 | 70 | s | w |
| SMALL (mean HB: 60–69 mm) | | | | | | |
| <i>Crocidura</i> | <i>lusitania</i> | 60 | 16 | 56 | s | w, e? |
| <i>Crocidura</i> | <i>aleksandrasi</i> | 60 | 17 | 70 | a | n |
| <i>Crocidura</i> | <i>allex</i> | 60 | 17 | 82 | m | e |
| <i>Congosorex</i> | <i>polli</i> | 60 | 20 | 40 | rs | c |
| <i>Crocidura</i> | <i>planiceps</i> | 61 | 17 | 72–78 | s | w, e |
| <i>Crocidura</i> | <i>whitakeri</i> | 61 | 17 | 50 | a | n |
| <i>Crocidura</i> | <i>muricauda</i> | 61 | 18 | 120–150 | f | w |
| <i>Suncus</i> | <i>megalaria</i> | 61 | 18 | 118 | s | w, e, c |
| <i>Crocidura</i> | <i>virgata</i> | 61 | 20 | 65 | m | w |
| <i>Sylvisorex</i> | <i>howelli</i> | 62 | 16 | 70 | m | e |
| <i>Crocidura</i> | <i>elgonius</i> | 62 | 17 | 55 | m | e |
| <i>Crocidura</i> | <i>maquassiensis</i> | 62 | 19 | 71 | m, s | s |
| <i>Crocidura</i> | <i>denti</i> | 63 | 21 | 65–70 | f | c, w? |
| <i>Sylvisorex</i> | <i>konganensis</i> | 64 | 17 | 56 | f | c |
| <i>Crocidura</i> | <i>floweri</i> | 64 | 18 | 75–100 | a | n |
| <i>Crocidura</i> | <i>tarfayensis</i> | 64 | 19 | 60 | a | n |
| <i>Crocidura</i> | <i>somalica</i> | 64 | 20 | 66 | a | e |
| <i>Crocidura</i> | <i>gracilipes</i> | 65 | n. d. | 80 | m | e |
| <i>Crocidura</i> | <i>dolichura</i> | 65 | 19 | 125–150 | f | w, c |
| <i>Crocidura</i> | <i>ludia</i> | 66 | 18 | 84–87 | f | c |
| <i>Sylvisorex</i> | <i>morio</i> | 67 | 20 | 75 | m | w |
| <i>Crocidura</i> | <i>roosevelti</i> | 67 | 22 | 85 | f, s | c, e |
| <i>Crocidura</i> | <i>crossei</i> | 68 | 19 | 84 | f | w |
| <i>Crocidura</i> | <i>phaeura</i> | 68 | 20 | 53 | m | e |
| <i>Sylvisorex</i> | <i>oriundus</i> | 68 | 21 | 91 | ? | c |
| <i>Crocidura</i> | <i>russula</i> | 69 | 19 | 50 | s | n |
| <i>Crocidura</i> | <i>silacea</i> | 69 | 20 | 70 | f, s | s |
| <i>Suncus</i> | <i>lixus</i> | 69 | 20 | 64 | f, s | w, e, s |
| SMALL–MEDIUM (mean HB: 70–79 mm) | | | | | | |
| <i>Crocidura</i> | <i>harennia</i> | 70 | 19 | 66 | m | e |
| <i>Crocidura</i> | <i>macowi</i> | 70 | 20 | 80 | s? | e |
| <i>Crocidura</i> | <i>caliginea</i> | 70 | 22 | 70 | f | c |
| <i>Congosorex</i> | <i>phillipsorum</i> | 71 | 19 | 55–60 | m | s |
| <i>Crocidura</i> | <i>greenwoodi</i> | 71 | 21 | 72 | f, s | e |
| <i>Crocidura</i> | <i>hildegardeae</i> | 72 | 19 | 70 | m | e |
| <i>Crocidura</i> | <i>crenata</i> | 72 | 19 | 120 | f | c |
| <i>Crocidura</i> | <i>eisentrauti</i> | 72 | 20 | 79 | m | w |
| <i>Myosorex</i> | <i>geata</i> | 72 | 21 | 57 | m | e |
| <i>Crocidura</i> | <i>jacksoni</i> | 73 | 21 | 75 | f | e |
| <i>Myosorex</i> | <i>okuensis</i> | 73 | 22 | 55 | m | w |
| <i>Sylvisorex</i> | <i>pluvialis</i> | 74 | 19 | 90 | f | c |

| Genus | Species | Mean HB (mm) | Mean CI (mm) | T % of HB (approx) | Habitat | Regions |
|-----------------------------------|----------------------|--------------|--------------|--------------------|---------|---------|
| <i>Crocidura</i> | <i>niobe</i> | 74 | 20 | 82 | m | ec |
| <i>Crocidura</i> | <i>smithii</i> | 74 | 21 | 54 | s? | e |
| <i>Crocidura</i> | <i>nigricans</i> | 74 | 22 | 75 | m | c |
| <i>Crocidura</i> | <i>kivuana</i> | 75 | 21 | 89 | m | ec |
| <i>Crocidura</i> | <i>jouvenetae</i> | 75 | 22 | 66 | f | w |
| <i>Crocidura</i> | <i>glassi</i> | 75 | 23 | 67 | m | e |
| <i>Crocidura</i> | <i>latona</i> | 76 | 20 | 85 | f | c |
| <i>Crocidura</i> | <i>congolbelgica</i> | 76 | 21 | 75 | f | c |
| <i>Crocidura</i> | <i>picea</i> | 76 | 22 | 55 | m | w |
| <i>Paracrocidura</i> | <i>schoutendeni</i> | 76 | 23 | 50 | f | c |
| <i>Crocidura</i> | <i>parvipes</i> | 77 | 20 | 45–60 | s | c, e |
| <i>Myosorex</i> | <i>kihaulei</i> | 77 | 20 | 53 | m | e |
| <i>Suncus</i> | <i>aequatorius</i> | 77 | 21 | 78 | f | e |
| <i>Myosorex</i> | <i>eisentrauti</i> | 77 | 23 | 45–55 | f | w |
| <i>Crocidura</i> | <i>macmillani</i> | 77 | 23 | 70 | m | e |
| <i>Crocidura</i> | <i>monax</i> | 77 | 24 | 70 | m | e |
| <i>Crocidura</i> | <i>montis</i> | 78 | 22 | 72 | m | e |
| <i>Crocidura</i> | <i>macarthuri</i> | 78 | 23 | 56 | s | e |
| <i>Crocidura</i> | <i>batesi</i> | 78 | 24 | 60–75 | f | w, c |
| MEDIUM (mean HB: 80–89 mm) | | | | | | |
| <i>Crocidura</i> | <i>fumosa</i> | 80 | 21 | 50–80 | m | e |
| <i>Crocidura</i> | <i>mariquensis</i> | 80 | 21 | 70 | s | c, s |
| <i>Sylvisorex</i> | <i>lunaris</i> | 80 | 23 | 65 | m | ec |
| <i>Crocidura</i> | <i>attila</i> | 81 | 21 | 55–65 | m | w, c? |
| <i>Crocidura</i> | <i>usambarae</i> | 81 | 22 | 70 | m | e |
| <i>Crocidura</i> | <i>grassei</i> | 81 | 23 | 95 | f | c |
| <i>Crocidura</i> | <i>cyanea</i> | 82 | 21 | 69 | fs | s |
| <i>Crocidura</i> | <i>manengubae</i> | 82 | 22 | 75 | m | w |
| <i>Crocidura</i> | <i>voi</i> | 82 | 23 | 45–55 | ? | w, e |
| <i>Crocidura</i> | <i>nimbae</i> | 82 | 26 | 40 | f, s | w |
| <i>Myosorex</i> | <i>varius</i> | 83 | 22 | 50 | s | s |
| <i>Myosorex</i> | <i>tenuis</i> | 83 | 22 | 41–59 | s | s |
| <i>Crocidura</i> | <i>selina</i> | 83 | 23 | 70 | f | e |
| <i>Myosorex</i> | <i>longicaudatus</i> | 83 | 23 | 79 | f | s |
| <i>Paracrocidura</i> | <i>graueri</i> | 83 | 28 | 55 | m | ec |
| <i>Myosorex</i> | <i>rumpii</i> | 84 | 23 | 40 | m | w |
| <i>Crocidura</i> | <i>nigrofusca</i> | 84 | 24 | 75 | f | e, c |
| <i>Crocidura</i> | <i>poensis</i> | 84 | 24 | 75 | f | w |
| <i>Myosorex</i> | <i>babaulti</i> | 85 | 22 | 45 | m | ec |
| <i>Crocidura</i> | <i>luna</i> | 85 | 23 | 61 | f, s | e |
| <i>Crocidura</i> | <i>wimmeri</i> | 85 | 25 | 75 | f | w |
| <i>Crocidura</i> | <i>buettikoferi</i> | 86 | 21 | 70 | f | w |
| <i>Myosorex</i> | <i>blarina</i> | 86 | 22 | 42 | m | ec |
| <i>Crocidura</i> | <i>baileyi</i> | 86 | 22 | 51 | m | e |
| <i>Crocidura</i> | <i>lucina</i> | 86 | 23 | 62 | m | e |
| <i>Crocidura</i> | <i>hirta</i> | 86 | 23 | 55–90 | m, s | e, s |
| <i>Crocidura</i> | <i>fischeri</i> | 86 | 27 | 53–59 | s | e |
| <i>Crocidura</i> | <i>lamottei</i> | 87 | 25 | 53 | f, s | w |
| <i>Crocidura</i> | <i>thalia</i> | 87 | 25 | 70 | m | e |
| <i>Crocidura</i> | <i>maurisca</i> | 88 / 79 | 21 | 89 | s | ec |

| Genus | Species | Mean HB (mm) | Mean CI (mm) | T % of HB (approx) | Habitat | Regions |
|--|---------------------|--------------|--------------|--------------------|---------|---------|
| <i>Myosorex</i> | <i>cafer</i> | 88 | 23 | 50 | f | s |
| <i>Crocidura</i> | <i>desperata</i> | 89 | 26 | 75 | m | e |
| LARGE (mean HB: 90–99 mm) | | | | | | |
| <i>Crocidura</i> | <i>ultima</i> | 90 | 23 | 70 | m | e |
| <i>Crocidura</i> | <i>viaria</i> | 90 | 25 | 70 | a | n, w, e |
| <i>Surdisorex</i> | <i>polulus</i> | 90 | 25 | 30 | m | e |
| <i>Crocidura</i> | <i>theresae</i> | 91 | 23 | 52 | s | w |
| <i>Crocidura</i> | <i>raineyi</i> | 91 | 25 | 69 | ? | e |
| <i>Crocidura</i> | <i>tarella</i> | 91 | 25 | 63 | f | e |
| <i>Crocidura</i> | <i>stenocephala</i> | 92 | 24 | 77 | m | ec |
| <i>Paracrocidura</i> | <i>maxima</i> | 92 | 26 | 53 | m | ec |
| <i>Crocidura</i> | <i>xantippe</i> | 93 | 23 | 66 | s | e |
| <i>Crocidura</i> | <i>littoralis</i> | 93 | 24 | 73 | f | c |
| <i>Myosorex</i> | <i>zinki</i> | 94 | 23 | 38 | m | e |
| <i>Myosorex</i> | <i>sclateri</i> | 94 | 25 | 43–63 | s | s |
| <i>Crocidura</i> | <i>erica</i> | 96 | 22 | 56 | s? | c |
| <i>Crocidura</i> | <i>lanosa</i> | 96 | 25 | 80 | f | ec |
| <i>Ruwenzorisorex</i> | <i>suncoides</i> | 96 | 25 | 40 | m | ec |
| <i>Crocidura</i> | <i>tansaniana</i> | 96 | 25 | 60–70 | m | e |
| <i>Surdisorex</i> | <i>norae</i> | 97 | 26 | 30 | m | e |
| <i>Crocidura</i> | <i>nigeriae</i> | 98 | 26 | 60–70 | f, s | w |
| VERY LARGE (mean HB: 100–149 mm) | | | | | | |
| <i>Crocidura</i> | <i>turba</i> | 100 | n. d. | 58 | f, s | e, c |
| <i>Crocidura</i> | <i>flavescens</i> | 100 | 26 | 49 | s, m | s |
| <i>Sylvisorex</i> | <i>ollula</i> | 103 | n. d. | 57 | f | c |
| <i>Crocidura</i> | <i>foxi</i> | 103 | 25 | 50–63 | s | w |
| <i>Crocidura</i> | <i>zaphiri</i> | 105 | n. d. | 57 | ? | e |
| <i>Crocidura</i> | <i>longipes</i> | 105 | 25 | 60 | s? | w |
| <i>Crocidura</i> | <i>telfordi</i> | 105 | 26 | 65–85 | m | e |
| <i>Crocidura</i> | <i>fulvastra</i> | 110/90 | 23 | 60 | s | e |
| <i>Suncus</i> | <i>murinus</i> | 114 | 32 | 40 | comm | e |
| <i>Crocidura</i> | <i>mutae</i> | 115 | 25 | 60–75 | f | c |
| <i>Crocidura</i> | <i>grandiceps</i> | 117 | 26 | 55–65 | f | w |
| <i>Crocidura</i> | <i>zimmeri</i> | 118 | 27 | 45 | s? | c |
| <i>Crocidura</i> | <i>olivieri</i> | 125 | 33 | 70–80 | f, s | w, e, c |
| <i>Scutisorex</i> | <i>somerani</i> | 137 | 33 | 63 | f, m | c |
| EXTREMELY LARGE (mean HB: >150 mm) | | | | | | |
| <i>Crocidura</i> | <i>goliath</i> | 165 | 38 | 68 | f | c |

Shrews are typically small, fast-running, terrestrial or semi-fossorial insectivores with long pointed snouts, minute eyes, small ears, short limbs, long tails and short dense fur. The eyes are small, and most species have poor eyesight so prey are located largely by smell, touch and by random searching. African shrews range in size from the tiny *Suncus etruscus* and *S. infinitimus* of about 2.0 g to the large, rat-sized *Crocidura olivieri*, *C. goliath* and *Scutisorex somerani*, which have mean weights of ca. 60 g. The limbs are unspecialized, with five digits on each limb. Shrews have a generalized quadrupedal

locomotion and a plantigrade gait, running with the sole and heel of the foot touching the ground. Neither the thumb nor big toe is opposable, so items such as food cannot be grasped freely by the hand. The radius and ulna are separate but the tibia and fibula are fused near the ankle. Like all soricomorphs, shrews possess clavicles. Members of the Soricidae have primitive brains and depend more on olfaction than on vision: the olfactory bulbs are very large but the eyes and optic foramina are small, and visual acuity is poor. Unlike most other eutherian mammals, the cerebral hemispheres are

smooth and with little convolution, and they usually do not extend backwards to cover the cerebellum or corpora quadrigemina. The neopallium and corpus callosum are very small. In outline, the skull is low and flat, and often long and slender. The braincase is small, the orbits open laterally, auditory bullae are absent, and zygomatic arches are absent or much reduced.

The first set of teeth of shrews is deciduous and is shed before birth. All the teeth are rooted. Unlike rodents, the incisors do not grow throughout life and they wear down as the animal ages. In the soricine shrews, the tips of the teeth are reddish in colour resulting from the deposition of iron in the outer enamel, a condition that is thought to increase resistance to wear. The total number of teeth in extant species of shrews varies between 28 and 32. Shrews normally have six teeth on each side of the lower jaw but a variable number in the upper jaw. The anterior dentition is specialized by the enlargement of the first upper incisor, which is large and hooked, and bears a notch and a cusp. The first lower incisor is also enlarged and is procumbent. Together these teeth function as fine forceps for grasping small invertebrates. The first upper incisor is followed by several small, unicuspid teeth (I^2 , I^3 , C, P^1 , P^2 , P^3), all rather similar in form; the number varies according to the genus, but in some genera there are only three unicuspid teeth (I^2 , I^3 , C; also referred to as U^1 , U^2 and U^3). The remaining premolars and molars (P^4 , M^1 , M^2 and M^3) are large and possess sharp, high-pointed cusps, which can crush the tough, chitinous exoskeletons of invertebrate prey (Figure 9).

The genital and urinary systems of shrews have a common exit through a cloaca. The sexes are difficult to distinguish externally, particularly in immature individuals. The penis is usually retracted into the abdomen when not in use and, in immature $\sigma \sigma$, is small and poorly developed. The testes are abdominal and do not descend into a scrotal sac, even when the $\sigma \sigma$ are mature. However, breeding $\sigma \sigma$ can be distinguished by the swollen testes on either side of the anus. In breeding ♀ the nipples are easily seen. In immature ♀ of many species, a small dark patch of fur marks the position of each nipple.

Shrews can be found in most terrestrial habitats, including forest, scrub and grassland, and at a wide range of altitudes. Some are fossorial (e.g. *Scutisorex*) and some (e.g. *Ruwenzorisorex*) are semi-aquatic. Shrews are most abundant in moist, well-vegetated habitats but a few are well adapted for life in xeric habitats. Some inhabit montane areas, for example *Crociodura montis* occurs in the afroalpine zone on Mt Elgon, Uganda at altitudes of 3300–4200 m. Many are commonly found in man-made habitats, especially in plantations and cultivated areas. Several are commensal with humans, and frequent gardens, shambas, houses and outbuildings, e.g. *Crociodura russula*, *C. olivieri* and *Suncus murinus*.

Many are proficient burrowers, and most can climb and swim well. The small size of shrews permits them to exploit a variety of habitats and penetrate narrow spaces, cracks and crevices in search of food and suitable nest sites. Many may utilize the tunnels of other small mammals for shelter and foraging. They frequent dense vegetation and find shelter

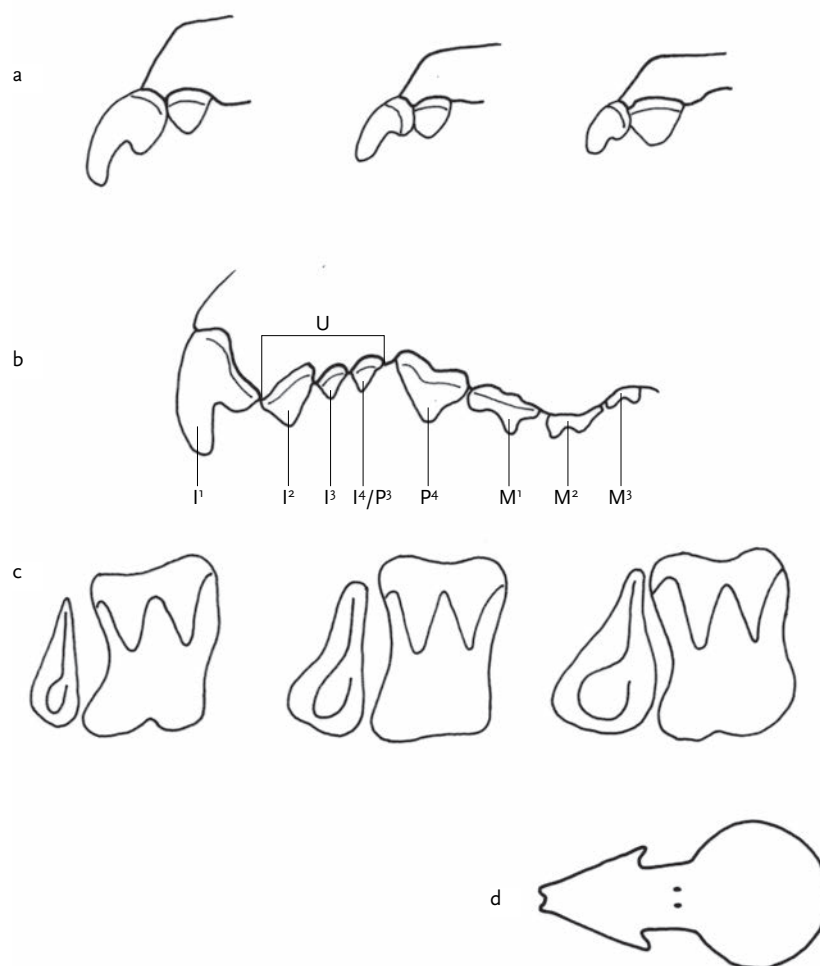


Figure 9. Some skull characteristics of shrews. (a) Size of upper I^1 relative to upper I^2 : long and hooked (left), medium-sized and hooked (centre) and small and slightly hooked (right). (b) Upper left toothrow to show terminology: I = incisor, P = premolar, M = molar, U = unicuspid. (c) Right upper M^2 and upper M^3 (occlusal view) to show relative size of upper M^3 to upper M^2 : small (left), medium (centre), large (right). Labial (outer side) pointing upwards. (d) Dorsal view of skull to show position of vascular foramina in the genera *Myosorex*, *Surdisorex* and *Congosorex*.

under logs, among rocks, beneath the roots of trees and under piles of dry brush and grass, and hence are rarely seen. Even the larger forms can remain unseen in dense forest with thick undergrowth.

Shrews feed on a variety of invertebrates. The principal prey of most species is arthropods (primarily insects), molluscs and earthworms. But they are highly opportunistic and larger species will also prey upon fish, amphibians and small reptiles. They may augment the diet with carrion and many consume some plant material, particularly seeds. No African shrews have been found to possess venomous saliva. Shrews have a reputation for voracious appetites and little resistance to starvation, needing to feed frequently day and night in order to survive. They have average daily energy expenditures significantly greater than those of rodents of similar size, and their basal metabolic rates are well above those predicted on the basis of size and weight. Soricine shrews have particularly high metabolic rates and energy requirements. Crocidurine shrews have lower metabolic rates and smaller food requirements. *Sorex araneus* (a non-African species) of about 9 g body mass requires 90% of its body weight in food or 9.7 kJ/g/day whereas *Crocidura russula* of similar size requires only 48% of its body weight or 3.4 kJ/g/day (Genoud 1985, Churchfield 1990). The large food requirements of these mammals are attributed to the high water content and indigestible chitin content of prey, as well as high metabolic rate. With their high metabolic rates, small body size and inability to store large quantities of fat as a food reserve, shrews are incapable of hibernating or entering extended torpor during critical periods of stress due to cold, heat, drought or food shortage. However, many crocidurine shrews exhibit short, daily periods of torpor with hypothermia. The African species *C. russula* can be induced to enter daily torpor by decreasing the availability of its food, during which the metabolic rate and body temperature are reduced (Genoud 1985).

It is common for several species of shrew to be syntopic as well as sympatric. It is not unusual for five or more species to coexist in the same habitat. In the forests of West and central Africa between eight and 16 syntopic species of shrews have been found (Dieterlen & Heim de Balsac 1979, Ray & Hutterer 1995, Churchfield *et al.* 2004, Dudu *et al.* 2005). In multi-species communities of shrews there is evidence of resource partitioning on the basis of body size: very small species are primarily epigeal foragers on small invertebrates active on the ground surface whereas large species are hypogeal foragers, subsisting mostly on larger, soil-dwelling prey (Churchfield *et al.* 1999, Dudu *et al.* 2005).

Shrews generally have poor vision, and they rely on tactile, auditory and olfactory senses for navigation and orientation around their home-ranges, for locating prey and for intra-specific communication. The sense of touch is well developed. The long flexible snout so characteristic of these mammals is well furnished with touch-sensitive vibrissae whose follicles are well supplied with nerve endings and which are useful in orientation and location of prey. Hearing is keen and shrews are able to produce and perceive a wide range of sounds, from squeaks and shrieks to grunts and snuffles, both in the audible range of human hearing and at ultrasonic frequencies. Shrews are highly vocal, particularly during social interactions and agonistic behaviour (Gould 1969). They emit high-pitched twitters as they explore and forage, and during interactions between the ♀♀ and her young. Young shrews produce staccato 'barks' to attract the mother's attention. Loud

squeaks and rolling 'churls' are used by shrews when threatened or alarmed, and in aggressive meetings between individuals. Scent forms an important means of intra-specific communication, being used to indicate gender and reproductive condition and to delineate territories. Shrews have lateral flank glands situated mid-way between the fore- and hindlimbs. These are small, well-vascularized oval areas, which are present in both sexes but which are best developed in sexually mature ♂♂. They exude a greasy secretion that rubs off on vegetation as they pass by. Shrews frequently defecate in prominent places, suggesting another means of scent-marking. The musk shrews, *Crocidura* spp., are particularly odoriferous, exuding a sweet, musky scent. Females, and especially ♂♂, of *C. flavescens* actively scent-mark by rubbing the lateral glands against objects (Baxter & Meester 1982). Crocidurine shrews also possess anal or caudal glands at the base of the tail, and chin/neck glands, that are used for scent-marking. In *C. flavescens* scent-marking is very evident after aggressive encounters.

Most shrews are solitary and intolerant of conspecifics. There is evidence of territoriality in crocidurine and soricine shrews. They generally occupy individual territories that are largely mutually exclusive, although during the breeding season the territory or home-range of the ♂ is extended to overlap those of several ♀♀ (Churchfield 1990). Meetings between conspecifics, when they occur, are aggressive affairs: shrews squeak loudly, bite and wrestle with each other. Some species are more social: crocidurine shrews such as *C. hirta* and *C. russula* are aggressive towards strangers but will share nests with familiars (Meester 1963, Cantoni & Vogel 1989). Territoriality and sociability may vary seasonally. In winter, the home-ranges of individuals of *C. russula* overlap extensively, but there is strict territoriality between ♂♂ and between ♀♀ in summer and the formation of monogamous breeding pairs, which share nests (Cantoni & Vogel 1989). Home-ranges or territories range greatly in size between species, e.g. 75–395 m² in *Crocidura russula* and 400–2800 m² in (non-African) *Sorex araneus* (Genoud 1978, Churchfield 1990).

Many crocidurine and mysoricine shrews are capable of breeding whenever conditions are favourable, but most African species breed mostly during warm, wet months and reproduction declines in the dry season (Dieterlen & Heim de Balsac 1979, Rowe-Rowe & Meester 1985b). The breeding season of *Myosorex* shrews in southern Africa coincides with the onset of the rains but is also influenced by temperature; those at higher altitudes commence breeding later than those at lower altitudes (Rowe-Rowe & Meester 1985b, Baxter 2005). Shrews normally produce 2–3 litters during a breeding season. They have a postpartum oestrus allowing litters to be produced in quick succession when conditions are favourable. Gestation varies from about 24 to 33 days, according to species. Litter-size is generally large but it varies between species; crocidurine shrews have smaller litter-sizes (usually 3–4 young/litter) than soricines (5–7 young/litter). Young shrews are born naked and hairless but growth is rapid and within a few days the pelage is evident. In *Crocidura* and *Myosorex*, the eyes are open between Day 12 and 18 and they take their first invertebrate prey at around Day 19. Weaning occurs at about three weeks of age. Caravanning behaviour has been observed in some species, notably crocidurine shrews such as *C. bicolor*, *C. russula* and *Suncus etruscus*; when the young first leave the nest, the mother leads them along in a line, each young grasping the base of the tail of the

one in front (Ansell 1964, Fons 1974, Churchfield 1990). In tropical species there is rapid growth to sexual maturity, e.g. crocidurine shrews can mature and commence breeding within a couple of months of birth. Paternal care is rare amongst shrews, and the presence of the ♂ is usually not tolerated by the ♀. However, in some crocidurine shrews (e.g. *C. russula* and *Suncus varilla*) monogamous breeding pairs are formed, and the ♂ stays in attendance and may help to shelter the young (Cantoni & Vogel 1989, Lynch 1990, 1991).

Shrews undergo seasonal cycles in abundance. These are particularly well-documented in species in temperate regions where many mark–recapture studies have been carried out. Numbers are high in the temperate summer when breeding occurs but decline through autumn and into winter as young disperse and old adults die after breeding is completed. Similar trends in population dynamics have been found in *Myosorex* spp. in southern Africa (Rowe-Rowe & Meester 1985b). In contrast, there is little information about population dynamics of African shrews in the tropics. Population densities vary greatly according to species and habitat and to the alternation of dry and wet seasons. Population densities of African shrews appear to be much lower than those of temperate species. For example, reported densities of *Suncus varilla* in southern Africa are 0.25–8.0/ha (Lynch 1990, 1991) while those of *Crocidura suaveolens* and *Sorex araneus* in Europe vary from 12–100/ha (Genoud 1978, Churchfield 1990).

Longevity varies largely according to size. Shrews are amongst the shortest-lived mammals. Life-span of wild-living *Myosorex varius* in southern Africa is about 12–17 months (Rowe-Rowe & Meester 1985b), very similar to that of soricine shrews (Churchfield *et al.* 1995). *Suncus varilla* can survive for 24–30 months (Lynch 1990, 1991). Although small crocidurine shrews such as *Crocidura russula* can live up to 4 years in captivity, few survive longer than 1.5 years in the wild (Vogel 1972, Jeanmaire-Besançon 1986). Mortality is highest in young animals as they disperse after weaning. Some 30–50% of soricine shrews die or disperse during the first two months of life and only 20–40% of the original cohort survive to breed (Churchfield *et al.* 1995).

The fossil record of shrews in Africa is fragmentary. The earliest known fossils (*Latetium* sp.) are from the mid-Miocene of Morocco (ca. 14 mya) and from the late-Miocene of Tunisia (ca. 12 mya) (Butler 1998). More recent fossils, from the Pliocene (ca. 2.5–3 mya) and Pleistocene (ca. 0.5 mya) are more widespread in distribution and have been found in NW Africa (Morocco, Algeria and Tunisia), East Africa (Omo and Hadar in Ethiopia, Kobi Fora, Rusinga and Isenya in Kenya, Olduvai and Laetoli in Tanzania), and in Zimbabwe and South Africa. Fossil shrews have not been found in the Sahara, West and central Africa. The fossil record suggests that shrews probably entered Africa from south-west Asia in the early Miocene when a land bridge connected south-west Asia with Arabia (and hence Africa). Additionally, and at a later date, some shrews entered North-West Africa from the western Mediterranean. *Myosorex* and *Sylvisorex* are known from the middle–late Miocene.

Crocidura (now the most speciose of the genera of African shrews) seems to have originated in Africa, although it is now widespread in Eurasia. Radiation of this genus seems to have started in Africa at the end of the Miocene (Butler 1998). The origins of other genera are less well known. Both morphological and molecular investigations indicate rapid radiation of *Crocidura* in Africa (Butler 1998, Quéroutil *et al.* 2005) with rapid morphological divergence occurring in

response to palaeo-environmental changes. The expansion of forested habitats during warm moist periods and their contraction in cool dry periods, during the Pleistocene and Holocene promoted the speciation of shrews, especially *Crocidura* spp., and allowed some to adapt to arid and semi-desert environments. In localities where the fossil record is good, several species may be distinguished; e.g. Butler & Greenwood (1979) recognized nine species from mandibular fragments (*Sylvisorex*, *Suncus* and *Crocidura* spp.) at Olduvai in Tanzania – a rich community similar to communities of shrews in some forested habitats today. Good reviews of fossil shrews are given by Heim de Balsac & Lamotte (1956, 1957) and Butler (1998) (and references therein).

Recent molecular findings (with rRNA sequencing) support evidence from external, cranial and dental characters that, amongst the genera of African shrews, two major lineages have emerged (Meester 1953, Heim de Balsac & Lamotte 1956, 1957, Quéroutil *et al.* 2001). The first includes *Myosorex* and *Congosorex* (supporting the existence of a myosoricine taxon) and the second includes the six remaining genera (*Crocidura*, *Paracrocidura*, *Ruwenzorisorex*, *Scutisorex*, *Suncus* and *Sylvisorex*). Although *Sylvisorex* appears to be polyphyletic, *Crocidura* is monophyletic and all species investigated, with representatives from India and Europe as well as Africa, seem to be closely related (Quéroutil *et al.* 2001). Grouping patterns of species from different continents suggest that there have been multiple exchanges between Africa and Eurasia (Quéroutil *et al.* 2001).

The genera, and species within each genus, are arranged alphabetically. In the Descriptions, an indication of the size of each species is recorded comparatively to other species in the family. The size categories (see also Table 8) based on head and body length (HB), are:

minute: less than 49 mm; very small: 50–59 mm; small: 60–69 mm; small–medium: 70–79 mm; medium: 80–89 mm; large: 90–99 mm; very large: 100–149 mm; extremely large: more than 150 mm.

The size categories of tail length as a percentage of head and body (see also Table 8) are: short: <40%; medium: 41–60%; long: 61–80%; very long: 81–100%; extremely long >101%.

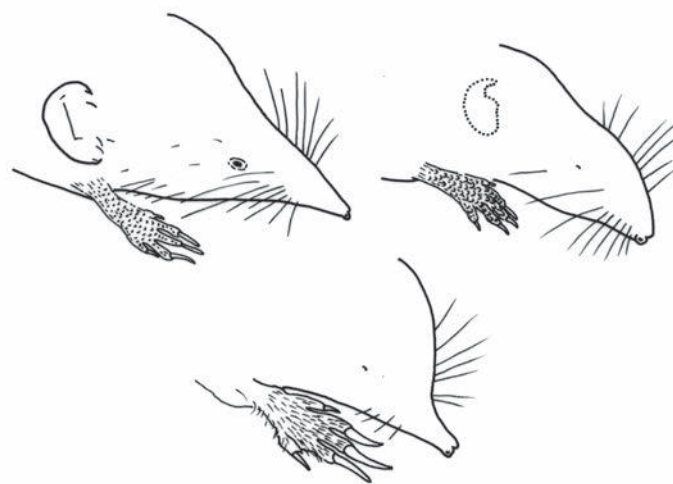


Figure 10. Head and right forefoot of *Myosorex* (upper left), *Congosorex* (upper right) and *Surdisorex* (bottom) to show variation in shape of head, size of eye, shape of forefoot and length of claws (after Hutterer *et al.* 2001).

Shrews are not easy to identify. The most important characteristics are size and mass (Table 8), pilosity of the tail (Figure 11), and the fine details of the skull and teeth. Within Africa, the geographical distribution and habitat may help to narrow the number of possibilities for a correct identification. Because of the large numbers of species of shrews in Africa, and because the geographic distributions of many species overlap, it is not possible to provide full details of similar species in the species profiles. For *Crocidura*, the section on ‘Similar Species’ is omitted and for the other genera, ‘Similar Species’ is restricted to other species in the genus (see also Tables 7 and 8 for comparisons between genera and species).

Sara Churchfield

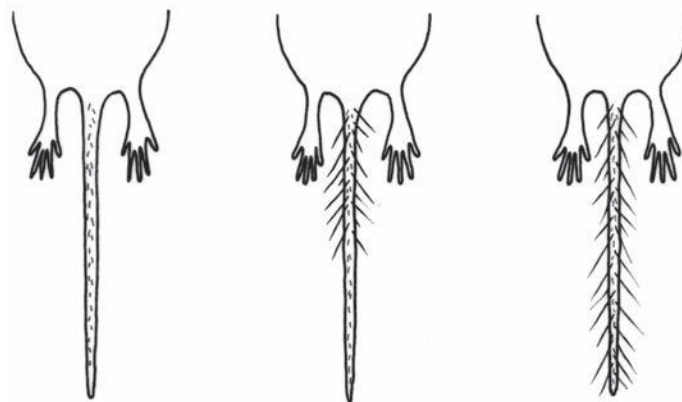


Figure 11. Pilosity of the tails of shrews: 0% (left), 50% (centre), 100% (right).

GENUS *Congosorex* Congo Shrews

Congosorex Heim de Balsac and Lamotte, 1956. Mammalia 20: 167. Type species: *Myosorex polli* Heim de Balsac and Lamotte, 1956.



Congosorex polli.

The genus contains three species: two (*C. polli*, *C. verheyeni*) live in primary and secondary lowland rainforest, gallery forest and small savanna patches within the forest of the Congo Basin, and the third species (*C. phillipsorum*) lives in isolated montane forest, bamboo, or marshy habitats in the Eastern Arc Mts of SW Tanzania above 1500 m.

Congosorex was described as a subgenus of *Myosorex* (Heim de Balsac & Lamotte 1956), and treated as a full genus by Heim de Balsac (1967) and subsequent authors (Hutterer 1993, 2005b, Stanley *et al.* 2005a). The original description compared *Congosorex* with *Myosorex* (*sensu stricto*) and *Surdisorex*. The full variability and species composition of the genus is not yet known.

The characters of *Congosorex* are somewhat cryptic. Species of the genus resemble species of *Myosorex* externally, but limbs and tail in *Congosorex* are generally shorter (tail length 30–58% of HB, cf. 42–84% in *Myosorex*). Other characteristics of the genus are short dense pelage (long and dense in *Myosorex* and *Surdisorex*), large head relative to rest of body, moderate or large-sized ears (normal or reduced in *Myosorex*, atrophied in *Surdisorex*), moderate-sized forefeet and claws (large in *Myosorex*, very large in *Surdisorex*) (Heim de Balsac & Lamotte 1956), prominent scales on fore- and hindfeet, absence of long hairs on the tail (as in *Myosorex* and *Surdisorex*) and minute eyes (Hutterer *et al.* 2001). On the skull, braincase is wide and rostrum is short (giving a broader-looking skull than in other genera of African shrews), there are three upper unicuspid, fourth upper unicuspid

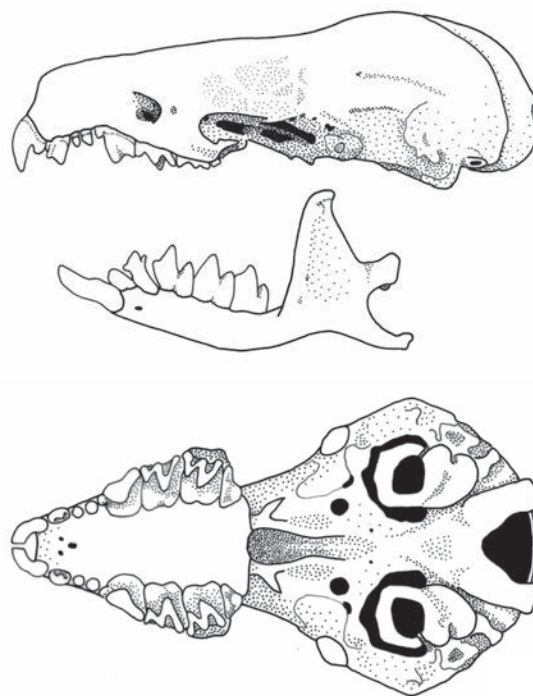


Figure 12. Skull and mandible of *Congosorex verheyeni* (ZFMK 99.932 [holotype]).

(P³) is absent (present in *Myosorex*, absent in *Surdisorex*) and M³ is large. Dental formula: I ³/₂, C ¹/₀, P ¹/₁, M ³/₃ = 28 (Figure 12). The tip of the phallus of male *Congosorex* is pointed, in contrast to the rounded condition found in *Myosorex* (Stanley *et al.* 2005a). Two vascular foramina are present between the parietal bones of the cranium, as in *Myosorex* and *Surdisorex* (see also Table 7).

The biology of any of the species is hardly known. Most specimens were collected in primary rainforest and, less frequently,

in secondary rainforest. The reduction of the limbs, tail and ear may indicate that foraging occurs in leaf litter or under logs, mosses or other cover.

Genetic data show that *Congosorex* is a sister taxon of *Myosorex*, and that both are members of the subfamily Myosoricinae (or tribe Myosoricini), which comprises *Myosorex*, *Congosorex* and probably

Surdosorex, and is the most ancient taxon of all living African shrews (Quérrouil *et al.* 2001, Hutterer *et al.* 2002).

The species are distinguished by tail and hindfoot length, and distribution.

Rainer Hutterer & William T. Stanley

Congosorex phillipsorum PHILLIPS'S CONGO SHREW

Fr. Musaraigne de Phillips; Ger. Phillips Kongo-Spitzmaus

Congosorex phillipsorum Stanley, Rogers and Hutterer 2005. J. Zool., Lond. 265: 271. Ndundulu Forest, Udzungwa Mountains, Tanzania.

Taxonomy A member of the Myosoricini with some characters shared with *Myosorex*. Synonyms: none. Chromosome number: not known.

Description Small-medium robust shrew with dark brown pelage and relatively large head. Dorsal pelage dark brown; hairs slate-grey, dark brown at tip. Hairs 5 mm (dorsal), 3 mm (ventral). Ventral pelage only slightly paler than dorsal pelage; hairs brown at tip. Head large relative to body (measuring about one-third of HB length). Vibrissae long (10–14 mm), thin, translucent. Ears barely visible, covered with long hairs. Fore- and hindfeet covered in dark conspicuous scales. Tail relatively medium long (55–60% of HB), only slightly bicoloured. Male phallus pointed. Nipples: not known.

Geographic Variation None recorded.

Similar Species

Congosorex polli. Smaller (HB: 60 mm, n = 1), tail shorter (T: 24 mm, n = 1). DR Congo.

Congosorex verheyeni. On average smaller (HB: 59 [53–95] mm; tail shorter T: 20 [19–26] mm). Congo and Central African Republic.

Distribution Endemic to Africa. Afromontane–Afroalpine BZ of Tanzania. Known only from the Ndundulu and Nyumbanitu forests of the Udzungwa Mts, Tanzania.

Habitat Undisturbed or slightly disturbed montane forests above 1500 m in Ndundulu and Nyumbanitu forests of the Udzungwa Mts where soil is moist; occasionally found in bamboo forests and marshy habitats (Stanley *et al.* 2005a). Known altitudinal range 1500–2086 m.

Abundance In one survey in Ndundulu Forest, Udzungwa Mts, comprised 53% of all shrews (4 spp., including *Myosorex kishaulei*, *Crocridura hildegardae* and *C. monax*).

Remarks Terrestrial and predominantly nocturnal. A sample of nine individuals (collected in July 2003) consisted of six ♂♂ and three ♀♀. The two ♀♀ examined were not pregnant. Testes length of four ♂♂ examined ranged from 5–7 mm (mean = 5.7); width 2.5–4 mm (mean = 3.4), with 50% of the sample exhibiting convoluted epididymes.



Conservation IUCN Category: Critically Endangered.

Threatened because of fragmented distribution and decline in suitable habitat.

Measurements

Congosorex phillipsorum

HB: 71.3 (68–76) mm, n = 9

T: 37.1 (35–40) mm, n = 9

HF: 12.7 (12–14) mm, n = 9

E: 7.4 (7–8) mm, n = 9

WT: 7.9 (7.4–8.3) g, n = 9

CI: 19.2 (18.8–20.0) mm, n = 17

GWS: 10.7 (10.2–10.9) mm, n = 20

I¹–M³: 8.2 (7.7–8.7) mm, n = 20

Ndundulu Forest, Udzungwa Mts, Tanzania (Stanley *et al.* 2005a)

Key Reference Stanley *et al.* 2005a.

William T. Stanley

Congosorex polli GREATER CONGO SHREW

Fr. Musaraigne du Congo; Ger. Grosse Kongo-Spitzmaus

Congosorex polli (Heim de Balsac and Lamotte, 1956). Mammalia 20: 155.
Lubondai via Tshimbulu (06° 30' N, 22° 39' E), Kasai Province, DR Congo.

Taxonomy Originally described in the genus *Myosorex*. Type species of the genus *Congosorex* (as defined by Heim de Balsac & Lamotte 1956, Hutterer *et al.* 2002); a sister taxon of *Myosorex* (Quéroutil *et al.* 2001) and probably also of *Surdisorex*. Synonyms: none. Chromosome number: not known.

Description Small shrew. Dorsal and ventral pelage brown, body hairs short. Head large compared to the rest of the body. Ear reduced but larger than in *C. verheyeni*. Eyes small and hidden by pelage. Forefeet short with moderately developed digits and claws; scales large, covering the dorsal surface of the forefeet. Hindfoot also short with short claws and large scales. Tail relatively short (ca. 40% of HB), covered with short hairs over its entire length; no longer hairs present. Skull with a short rostrum, narrow maxillary, wide interorbit and a wide and inflated braincase. Nipples: not known. See also genus profile.

Geographic Variation None recorded.

Similar Species

Congosorex phillipsorum. Larger (HB: 68–76 mm). Tail longer (T: 35–40 mm). Udzungwa Mts, Tanzania.

Congosorex verheyeni. Skull perhaps shorter (CI: 17.8–19.1 mm). Congo and Central African Republic.

Distribution Endemic to Africa. Southern Rainforest–Savanna Mosaic. Known only from the type locality in Kasai Province, DR Congo.

Habitat Not recorded; probably gallery forest in the savanna.

Abundance No information; one of the rarest African shrews.

Remarks Like *Congosorex verheyeni*, *C. polli* has short limbs and reduced eyes and ears, which may indicate a secretive life under litter, logs or below ground.

Conservation IUCN Category: Data Deficient.
Known only by a single specimen collected in 1955.

*Congosorex polli***Measurements**

Congosorex polli

HB: 60 mm, n = 1

T: 24 mm, n = 1

HF: 10 mm, n = 1

E: 6.5 mm, n = 1

WT: n. d.

CI: 20.3 mm, n = 1

GWS: 10.4 mm, n = 1

I¹–M³: 8.7 mm, n = 1

Kasai Province, DR Congo (Hutterer *et al.* 2002)

Key References Heim de Balsac & Lamotte 1956; Hutterer *et al.* 2002.

Rainer Hutterer

Congosorex verheyeni LESSER CONGO SHREW

Fr. Musaraigne petite du Congo; Ger. Kleine Kongo-Spitzmaus

Congosorex verheyeni Hutterer, Barrière and Colyn 2001. Bull. Inst. Roy. Sci. Nat. Belgique, Biol. 71 (suppl.): 7–16.

Mbomo (00° 24' N, 14° 44' E), Parc National d'Odzala, Congo.

Taxonomy Synonyms: none. Chromosome number: not known.

Description Very small, stout shrew with a very short tail. Dorsal and ventral pelage dark brown. Body hairs short: 5 mm (dorsum), 3 mm (ventrum). Head comparatively large, distance from tip of nose to back of ear about one-third of head and body length. Nose and lips flesh-coloured. Vibrissae sparse, longest 12 mm. Ear present, reduced in size and covered by hairs. Eye opening minute, hidden by pelage. Forefeet short with moderately developed digits and claws; large scales cover dorsal surface of forefoot. Hindfoot also short with short claws and large scales. Tail very short (ca. 32% of HB), with 11 short and weak caudal vertebrae; pale-coloured, covered with short, black hairs over entire length. Nipples: 0 + 2 = 4.

Geographic Variation None recorded.

Similar Species

Congosorex phillipsorum. On average larger (HB: 71.3 [68–76] mm); tail longer (T: 35–40 mm). Udzungwa Mts, Tanzania.

Congosorex polli. Skull perhaps longer (CI: 20.3 mm, n = 1). DR Congo.

Distribution Endemic to Africa. Rainforest BZ (Gabon sub-region) and adjacent Rainforest–Savanna Mosaic. Known from three localities in Odzala National Park, Congo, and four localities in Ngotto forest, Central African Republic. All localities are on the right (northern) bank of the Congo R.

Habitat Primary and secondary lowland rainforest. One specimen was collected in adjacent savanna and a few others in newly regenerated forest patches (Barrière *et al.* 2000).

Abundance Only 53 specimens have been collected at the present time. Never a dominant species of the community of shrews but may be locally common. In Odzala N. P. comprised only 1% of shrews (n = 255) in primary forest, and 3% (n = 142) in disturbed forest (Barrière 1997). In Ngotto N. P., comprised 2% of shrews in Batouri (primary forest, n = 1350, 18 spp.); 4% in Bambio (secondary forest, n = 27, 7 spp.); 8% in Grima (secondary forest, n = 63, 10 spp.); and 9% in Massangai (secondary forest, n = 66, 8 spp.) (Barrière *et al.* 2000).

Remarks Short limbs, reduced eyes and ears may indicate adaptations to a secretive life under litter, logs or below ground. May feed preferentially on subterranean invertebrates such as earthworms. Embryo number: 2 (n = 1; Ngotto forest; wet season; P. Barrière, unpubl.).



Congosorex verheyeni

Conservation IUCN Category: Least Concern.

Occurs in two National Parks in Congo and in Central African Republic.

Measurements

Congosorex verheyeni

HB: 59 (53–95) mm, n = 15

T: 20 (19–26) mm, n = 15

HF: 9 (9–11) mm, n = 15

E: 6 (4–8) mm, n = 12

WT: 7.1 (4–12) g, n = 14

CI: 18.4 (17.8–19.1) mm, n = 10*

GWS: 10.0 (9.7–10.3) mm, n = 10*

I¹–M³: 8.1 (7.7–8.4) mm, n = 11*

Odzala National Park, Congo and Ngotto National Park, Central African Republic (Hutterer *et al.* 2001)

*Stanley *et al.* 2005a

Key References Barrière *et al.* 2000; Hutterer *et al.* 2001; Quéroutil *et al.* 2001.

Patrick Barrière & Rainer Hutterer

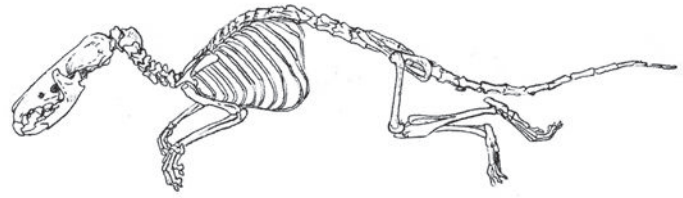
GENUS *Crocidura*

Shrews (White-toothed Shrews)

Crocidura Wagler, 1832. Isis, p. 275. Type species: *Sorex leucodon* Herman, 1780.



Crocidura flavescens.



Skeleton of *Crocidura* sp.

The genus *Crocidura* contains more species than any other genus of African mammals (see below), and is found throughout the whole continent and in every biotic zone. Because of the widespread geographic range of the genus, one or more species of the genus is found in almost every habitat except in the driest of deserts.

The characters of the genus include rather small size and slender build. Head and body ranges (according to species) from very small (*C. bottegoides*; HB: ca. 50 mm, HF: 10 mm, WT: 3 g) to large (*C. olivieri*; HB: up to 140 mm, HF: ca. 23 mm, WT: 65 g). The largest species (*C. goliath*, *C. olivieri*) are equivalent in size to a medium-sized murid rodent. Pelage colour is usually undistinguished – drab brown or grey, often paler on the ventral pelage, and without any special markings or colours. The head is pointed (more so than in other genera of shrews), with a long muzzle, which projects anteriorly beyond the nasal bones of the skull and, in life, is constantly wiggled from side to side (see below, and order profile). The rhinarium is simple, divided into two by a vertical slit between the two nostrils. Eyes are small but visible, and ears are small and rounded (slightly more prominent than in *Myosorex*) with a complex arrangement of folds on the inner surface. The fore- and hindfeet are short and simple, without hairs on the outer side of the hindfeet; forefeet have five digits, hindfeet have five digits, all with small claws. The tail is usually thicker towards the base, tapering to the tip, and (in most species) covered with small bristles and scattered long (usually) pale hairs. These long hairs are almost unique to this genus of shrews (also present, to a lesser extent, in *Suncus* and *Paracrocidura*) and are useful for species identification. The proportion of the tail covered with these long hairs is expressed as the ‘pilosity’ of the tail (Fig. 27); pilosity is the percentage of tail, measured from the base, which supports these long hairs (e.g. 0% [no long hairs], 50% [basal half of tail]; 75% [basal three-quarters of tail] and 100% [all of tail]). In external characteristics (except for size), *Crocidura* shrews show great morphological similarity and hence are very difficult to distinguish. The skull is elongated and low, without zygomatic arches (as in all shrews), the teeth are white (not pigmented). Dental formula: $I^{3/1}$,

$C^{1/1}$, $P^{1/1}$, $M^{3/3}$ = 28. All teeth are cuspidate, a typical condition in shrews and other insectivores. I^1 is long and hooked with two denticulations (cusps), the anterior one being larger than the posterior one, and is followed posteriorly by three unicuspid teeth (U^1 , U^2 , U^3) – not four as in most other genera of shrews (see Table 7), which are morphologically I^2 , I^3 and C (Hutterer 2005c). The unicuspid teeth are small; they usually vary in size, the smallest being the most posterior. There is only one premolar; this is P^4 (P^1 , P^2 and P^3 are lost) and is usually the largest tooth in the molar row. The premolar is followed by three molars; M^1 and M^2 are similar in size to P^4 , and like P^4 have a complicated W-shaped pattern of cusps and ridges. M^3 is much smaller and variable in size, with a simple cusp. The widest point of the skull is across the braincase. The mandible is elongated with only six teeth in each ramus; I_1 does not have denticulations, the coronoid process is tall, vertical and rises well above the mandibular process, and the angular process is elongated and usually the most posterior part of the mandible (Figure 13). Some species of *Crocidura* shrews have a very strong pungent odour, produced by numerous secretory glands in the skin and tail. See Table 7 for comparisons with other genera of shrews.

The number of extant species in the genus is uncertain, and has varied according to the authority and the methods of study. Dollman (1915a, b, c, d, e, f, 1916) recorded 126 species (plus five indeterminate) in Africa, and Hutterer (2005b) recognized 171 species worldwide, of which 106 (62%) are African. Here, 105 species of *Crocidura* are recognized and described; many other previously described taxa are now regarded as synonyms. *Crocidura* is also the most speciose of the nine genera of African shrews, comprising 70% of the 150 of the currently recognized species of African shrews.

Crocidura shrews are terrestrial, although a few species are scansorial. None are fossorial (cf. *Surdisorex*) or semi-aquatic (cf. *Ruwenzorisorex*). Little is known about the ecology of *Crocidura* shrews in Africa. Like other shrews, all are insectivorous, consuming a high proportion of their body weight in a 24-hour period. Species that have been studied feed on a wide variety of insects and other invertebrates (Churchfield *et al.* 2004). It is evident that many species of *Crocidura* (together with species from other shrew genera) can live syntopically, implying that there must be important mechanisms for avoiding competition. Studies in Gabon have recorded five species of *Crocidura* (plus up to four other species belonging to different genera) in the same study area (Nicolas *et al.* 2003).

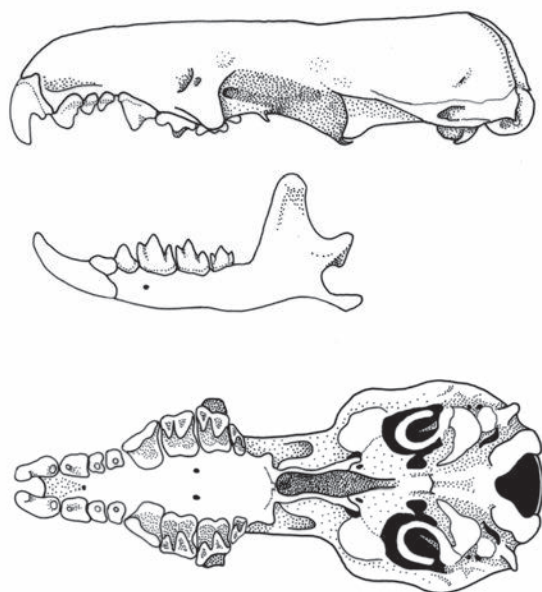


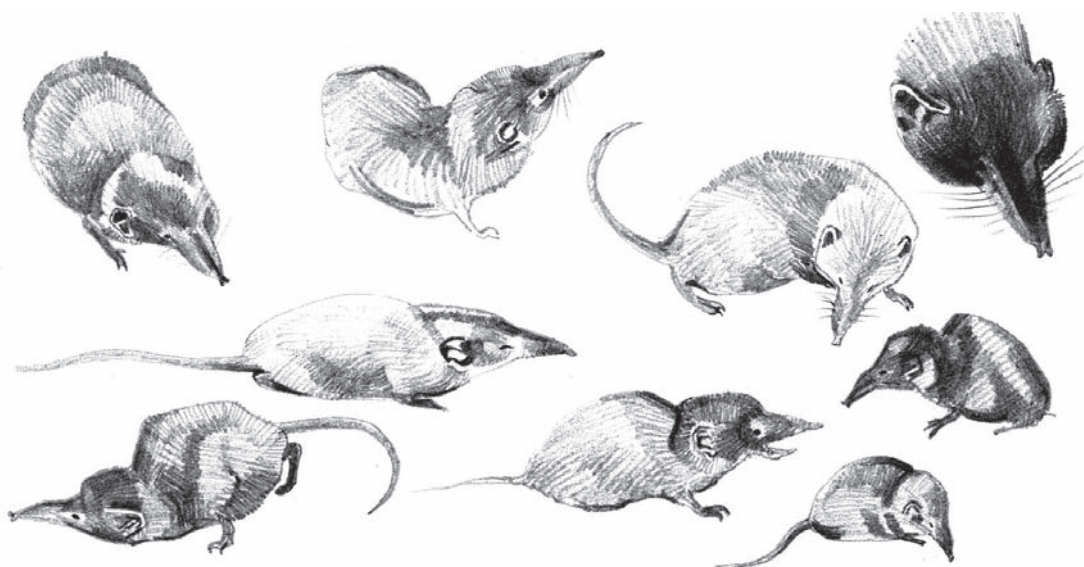
Figure 13. Skull and mandible of *Crocidura olivieri* (HC 579).

Crocidura shrews rely on their olfactory senses rather than visual senses for communication and foraging. They have scent glands on many parts of the body, which determine social relationships. The eyes of *Crocidura* shrews are small (size varying by species) and are thought to be of limited value other than providing a general impression of light intensity. Shrews make a variety of vocalizations (see e.g. *C. flavescens*, *C. hirta* and order profile), which indicate specific emotions. *Crocidura* shrews are mostly solitary, except during mating and care of the young; the best known of social behaviours is caravanning of the young in some species (e.g. *C. hirta*, *C. fuscomurina* and *C. russula* among African species). The small size of *Crocidura* shrews (and other shrews) means thermoregulation is an important aspect of metabolism; very little is known about these topics for African species, although it is well known that individuals of *Crocidura* shrews are often torpid if kept in cool conditions, particularly if food is unavailable.

The systematics of *Crocidura* is difficult because of the similarity between species. Dollman (1915a *et seq.*) divided the genus into 22 groups on the basis of size, pelage colour, length of hairs, relative size and width of the second and third unicuspid teeth, size of M^3 , and pilosity of the tail – characters that are still considered to be useful at the present time. Heim de Balsac (in a series of papers) divided the African *Crocidura* into four groups: *dolichura* group (Brosset *et al.* 1965), *smithii* group (Heim de Balsac 1966), *flavescens* group (Heim de Balsac & Barloy 1966) and *bicolor* (*fuscomurina*) group (Heim de Balsac 1958).

Butler *et al.* (1989) studied the mandibles (a structure often found in owl pellets) and, using principal component analysis, sorted them into six groups (but with many outliers). Hutterer & Happold (1983) divided the 21 *Crocidura* shrews of Nigeria into seven groups on the basis of size, length of tail and habitat (forest or savanna). Karyological and molecular studies have not assisted, to any great extent, with the systematics of shrews; the chromosome number is known for some species (see e.g. Schlitter *et al.* 1999), but since most species have not been studied in this respect, such methods are, at the present time, of limited value for identification.

The genus is considered to be monophyletic (Quérrouil *et al.* 2001). Within the African Soricidae as a whole, two lineages are apparent. One of these corresponds to the subfamily Crocidurinae, contains *Crocidura*, *Sylvisorex*, *Suncus*, *Scutisorex* and *Ruwenzorisorex* (and *Paracrocidura*) (see also family profile). The second lineage (subfamily Myosoricinae [see Hutterer 2005b]) contains *Congosorex* and *Myosorex*. (*Surdisorex* was not included in this study.) An alternative view by Butler *et al.* (1989) is that *Crocidura* is not a natural taxonomic unit, rather it is polyphyletic and includes several lineages. Studies on the chromosomes of *Crocidura* (Maddalena & Ruedi 1994), but with only a limited number of species, show that within the genus, three evolutionary trends are apparent. The first retains a karyotype close to the ancestral state and is represented by species throughout the worldwide geographic range (and includes the African *C. luna*, *C. cf. bottegi* and *C. bottegi*); the second exhibits an increase in both the number of chromosomes and the fundamental number (due to fission) and includes most of the African *Crocidura*; and the third shows a reduction of both the number of chromosomes



Crocidura maurisca.

and the fundamental number (due to Robertsonian fusions) and is typical of the Palaearctic–Oriental species. Thus the majority of African *Crocidura* form a single clade, strongly suggesting that there was rapid evolution of the genus within Africa (Butler *et al.* 1989, Quérouil *et al.* 2001, 2005).

The fossil record of the genus (and indeed all shrews) in Africa is limited (Butler 1978). Shrews are thought to have originated in Eurasia (see family profile) in the Oligocene. The radiation of *Crocidura* seems to have started at the end of the Miocene (Butler 1978, 1998) just after a period of major extinction when many ecological niches became vacant (Maglio 1978). There are fossil *Crocidura* from the late

Pliocene (ca. 2 mya) of South Africa, and from the early Pleistocene (ca. 1.5 mya) of Tanzania (Butler 1978, 1998). Alternation of wet and dry periods during the Pleistocene undoubtedly assisted the amazingly successful adaptive radiation of *Crocidura* shrews.

The species of the genus are very difficult to identify on gross morphological characteristics. The following characters are helpful: body dimensions and weight, pilosity and relative length of tail, shape of skull, shape of I¹, relative size and shape of unicuspid teeth and M³, habitat and distribution.

D. C. D. Happold

Crocidura Aleksandrisi CYRENAICA SHREW

Fr. Crocidure de Libye; Ger. Cyrenien-Spitzmaus

Crocidura Aleksandrisi Vesmanis, 1977. Bonn. Zool. Beitr. 28: 3. Cyrenaica, 5 km W Toca, Libya (32° 31' N, 20° 34' E).

Taxonomy Looks like a small form of the European *C. suaveolens*. This species was referred to as *C. russula* by Ranck (1968). Synonyms: none. Chromosome number: 2n = 40 (P. Benda pers. comm.).

Description Small shrew. Pelage soft and short (hairs ca. 2 mm). Dorsal pelage greyish-brown, with slight tinge of russet; hairs dark grey at base, brown at tip. Ventral pelage grey to brownish-grey; hairs dark grey at base, grey to pale brown at tip. Colour of head similar to dorsal pelage. Chin, throat and chest grey. Fore- and hindfeet brown. Tail relatively long (ca. 70% of HB), brown above, slightly paler below; pilosity 90%. Skull unspecialized; rostrum and maxillary medium, interorbit wide, braincase width medium, and braincase height high. First upper incisor long and hooked, third molar wide (cf. Vesmanis 1977). Nipples: not known.

Geographic Variation None recorded.

Distribution Endemic to Africa. Mediterranean Coastal BZ. Recorded from only a few localities in Cyrenaica, Libya (Hutterer 1993).

Habitat Wadis and bushland with Mediterranean-type vegetation in the northern part of Cyrenaica.

Abundance No information.

Remarks Remains of this shrew were abundant in pellets of Barn Owls collected in Wadi al Kuf, Cyrenaica (R. Hutterer, unpubl.).

Conservation IUCN Category: Least Concern.

Measurements

Crocidura Aleksandrisi

HB: 60.2 (56–65) mm, n = 6

T: 43.2 (39–46) mm, n = 6



Crocidura Aleksandrisi

HF: 11.8 (11–12) mm, n = 6

E: 7.8 (7.6–8.0) mm, n = 2

WT: 4.8 (4–6.5) g, n = 3

CI: 17.4 (16.6–18.1) mm, n = 4

GWS: 7.9 (7.7–8.2) mm, n = 3

I¹–M³: 7.4 (6.8–8.0) mm, n = 57

Cyrenaica, Libya (Vesmanis 1977, R. Hutterer unpubl.)

Key Reference Vesmanis 1977.

Rainer Hutterer

Crocidura allex EAST AFRICAN HIGHLAND SHREW

Fr. Crocidure des montagnes; Ger. Hochland-Spitzmaus

Crocidura allex Osgood, 1910. Field Mus. Nat. Hist. Publ., Zool. ser. 10 (3): 20. Kenya, 'Naivasha, British East Africa'.

Taxonomy Synonyms: *alpina*, *zinki* (see Heim de Balsac & Meester 1977). Subspecies: none. Gureev (1979) listed *alpina* as a distinct species without comment.

Description Small dark brown shrew. Pelage thick and dense, 3–4 mm dorsally. Dorsal pelage burnt umber, hairs dark grey, burnt umber at tip. Ventral pelage brownish-grey; hairs grey on basal half, brownish-grey on terminal half. Fore- and hindfeet dark brown, digits with sharp pointed claws. Tail relatively very long (ca. 82% of HB), dark brown, pilosity 40%. Rostrum short, maxillary width medium, and interorbital constriction wide. Braincase wide and of medium height. First incisor moderately long and hooked, third molar wide. Nipples: not known.

Geographic Variation Uncertain. Heim de Balsac (1957a) described a subspecies (*zinki*) from a high elevation (3550 m) on Mt Kilimanjaro, but this has not been recognized by subsequent authors.

Distribution Endemic to Africa. Afromontane–Afroalpine BZ. Recorded only from the highlands of C Kenya (e.g. Mt Kenya, Aberdare Ranges, Mau Forest, Nanyuki – see Aggundey & Schlitter 1986) and N Tanzania (Mt Kilimanjaro, Mt Meru and Ngorogoro Crater).

Habitat Occurs from the forest to the alpine zones (Grimshaw *et al.* 1997). On Mt Meru collected in the bamboo zone between 2550 and 2750 m (Demeter & Hutterer 1986). Recorded to at least 3700 m on Mt Kilimanjaro (Child 1965) and up to 4100 m on Mt Kenya (Coe & Foster 1972).

Abundance Rather common on Mt Kilimanjaro at 3500 m in habitats with highest ground cover (Shore & Garbett 1991). The second most abundant small mammal on the Shira Plateau (Mt Kilimanjaro), with densities of 2.9–5.8/ha (Shore & Garbett 1991). Not common on the montane grasslands of Mt Kilimanjaro (W. N. Verheyen pers. comm. 2003).

Remarks On Mt Kenya, found on pathways made by *Otomys* spp. (Otomysinae: Rodentia) (Coe & Foster 1972). One pregnant ♀ found on Mt Kilimanjaro (17 Jul–7 Aug; n = 23 shrews; Shore & Garbett 1991). Remains of *C. allex* were found in faeces of Servals *Leptailurus serval* in Ngorogoro Crater, Tanzania (Geertsema 1985). Raptors may also be predators.

*Crocidura allex*

Conservation IUCN Category: Vulnerable.

Measurements*Crocidura allex*

HB: 60.7 (55–64) mm, n = 8

T: 49.5 (45–55) mm, n = 8

HF: 11.4 (10–12) mm, n = 8

E: 7.9 (7–9) mm, n = 7

WT: 5.2 (4–8) g, n = 9

CI: 17.3 (16.8–18.2) mm, n = 6

GWS: 7.7 (6.9–8.1) mm, n = 6

I¹–M³: 7.1 (7.0–7.3) mm, n = 5

Mt Meru, Tanzania (Demeter & Hutterer 1986, R. Hutterer unpubl.)

Key References Child 1965; Shore & Garbett 1991.

Rainer Hutterer

Crocidura ansellorum ANSELL'S SHREW

Fr. Crocidure des Ansell; Ger. Ansell's Spitzmaus

Crocidura ansellorum Hutterer and Dippenaar, 1987. Bonn. Zool. Beitr. 38: 1 (see also below).

Kasombu stream (= Isombu River), Mwinilunga Distr., Zambia. 4100 ft.

Taxonomy The species was originally named *C. anselli* but was emended to *C. ansellorum* (Hutterer & Dippenaar 1987b). The phylogenetic relations of the species are unknown. Synonyms: none. Chromosome number: not known.

Description Very small shrew. Pelage soft, hairs ca. 4 mm. Dorsal pelage dark chocolate-brown. Ventral pelage slightly washed with greyish-brown (most notable on the throat of the holotype). Limbs and ears dark chocolate-brown. Tail relatively long (ca. 80% of HB), greyish-brown; pilosity ca. 51%. Skull broad and high-domed. Upper incisor long and hooked. First unicuspid large and pointed, second and third subequal in size, all three with a well-developed cingulum. Third upper molar medium-sized. Nipples: not known.

Geographic Variation None recorded.

Distribution Endemic to Africa. Zambezian Woodland BZ. Recorded only from N Zambia; regarded as endemic to the Ikelenge Pedicle, NW Zambia (Cotterill 2002b).

Habitat Gallery forest along streams.

Abundance Rare; known from only three specimens.

Remarks Apparently no other information available.

Conservation IUCN Category: Endangered.

Measurements*Crocidura ansellorum*

HB: 57.3 (56–58) mm, n = 3

T: 46.3 (41–51) mm, n = 3

HF: 11.2 (10.5–12) mm, n = 3

*Crocidura ansellorum*

E: 7.7 (7.5–8) mm, n = 2

WT: 4.6 (4.2–5) g, n = 2

CI: 17.4 (16.8–17.7) mm, n = 3

GWS: 8.2 (8.0–8.4) mm, n = 3

I¹–M³: 7.4 (7.2–7.6) mm, n = 3

N Zambia (Hutterer & Dippenaar 1987a)

Key References Cotterill 2002b; Hutterer & Dippenaar 1987a.**Rainer Hutterer***Crocidura attila* HUN SHREW (CAMEROON SHREW)

Fr. Crocidure du Cameroun; Ger. Hunnen-Spitzmaus

Crocidura attila Dollman, 1915. Ann. Mag. Nat. Hist., ser. 8, 15: 512; ser. 8, 16: 141. Bitye, South Cameroon. 2000 ft.

Taxonomy Originally described as a subspecies of *C. poensis*; included in *C. buettikoferi* by Heim de Balsac & Meester (1977) but now considered to be a distinct species (Hutterer & Joger 1982). Very similar to *C. poensis*. Synonyms: none. Chromosome number: 2n = 50, FN = 66 (Cameroon; Schlitter *et al.* 1999).

Description Medium-sized shrew. Dorsal pelage brown, paler laterally with fairly abrupt transition to paler ventral pelage; lateral gland silvery-white. Dorsal surface of fore- and hindfeet bicoloured.

Tail relatively short (55–65% of HB), dark brown above, paler below; pilosity 85–90%. Skull: second and third unicuspid subequal in size, third upper molar moderately broad. Nipples: not known.

Geographic Variation None recorded.

Distribution Endemic to Africa. Montane habitats in Rainforest BZ. Found on Mt Cameroon and the Adamaoua Highlands near Banyo, Cameroon (Heim de Balsac 1957b, Hutterer & Joger 1982).

and in the Gote Mts, SE Nigeria at 1900 m (Hutterer *et al.* 1992b). Perhaps extends eastwards from Nigeria/Cameroon border to E DR Congo (Hutterer *et al.* 1992b, Wolsan & Hutterer 1998). Eastern part of range needs confirmation.

Habitat Primarily montane forests.

Abundance No information.

Remarks Principal prey probably comprises a range of common invertebrates. Principal predators likely to be owls, reptiles and small carnivores such as mongooses, genets and small cats, which are known to feed on shrews.

Conservation IUCN Category: Least Concern.

Formerly considered as Vulnerable. Major threats are human-induced habitat loss and degradation.

Measurements

Crocidura attila

HB: 80.9 (75–90) mm, n = 8

T: 49 (45–55) mm, n = 8

HF: 13.5 (12–15) mm, n = 8

E: 10 (9–11) mm, n = 7

WT: 5 g

CI: 21.0 (19.5–21.7) mm, n = 8

GWS: 9.0 (8.3–9.5) mm, n = 9

I¹–M³: 9.0 (8.2–9.5) mm, n = 10

Measurements: Cameroon and DR Congo (BMNH)

Weight: Young ♀, Cameroon (Hutterer *et al.* 1992b)



Crocidura attila

Key References Heim de Balsac & Meester 1977; Hutterer & Joger 1982; Hutterer *et al.* 1992b.

P. D. Jenkins & S. Churchfield

Crocidura baileyi BAILEY'S SHREW (SIMIEN SHREW)

Fr. Crocidure de Bailey; Ger. Baileys Spitzmaus

Crocidura baileyi Osgood 1936. Field Mus. Nat. Hist., Zool. ser. 20 (21): 225.

Ras Dashan, Simien Mts, Ethiopia. 3400 m (ca. 13° 14'N, 38° 25'E).

Taxonomy Specimens recorded as *C. baileyi* by Osgood (1936) and Yalden *et al.* (1976) are now allocated to *C. lucina* (Dippenaar & Meester 1989). A member of the endemic Ethiopian *C. glassi* complex (*C. glassi*, *C. lucina*, *C. thalia*, *C. macmillani* and *C. baileyi*) (Dippenaar & Meester 1989). Synonyms: none. Chromosome number: not known.

Description Medium-sized *Crocidura* with a distinctly bicoloured pelage and tail. Pelage long, woolly and soft. Dorsal pelage brownish to reddish-brown; hairs grey at base, rufous at tip. Ventral pelage creamy-white, hairs grey at the base, white at tip. Dorsal surface of fore- and hindfeet whitish. Tail of medium relative length (ca. 51% of HB), brown above and whitish below; pilosity 100%. Skull with inflated braincase, as typical for the high altitude Ethiopian *Crocidura*. Nipples: not known.

Geographic Variation None recorded.

Distribution Endemic to Africa. Afroalpine–Afroalpine BZ. Recorded only in Ethiopia in the highlands west of the Ethiopian Rift Valley (Simien Mts, Amedamit Mts, Enjiabara, Debre Sina and Ankober), 2700–3550 m.

Habitat Humid localities with tall grasses in afroalpine moorland and humid heather forest (Guttinger *et al.* 1998).

Abundance Relatively common in suitable habitats. Comprised 9.8% (17 of 173) of small mammals caught in the Simien Mts (Guttinger *et al.* 1998).

Remarks Woolly fur and relatively short tail might be adaptations to the cold at high altitudes. Presumed to be insectivorous or omnivorous.

Conservation IUCN Category: Endangered.

*Crocidura baileyi*

Previously considered as Vulnerable. Populations conserved within the Simien Mountains N. P.

Measurements

Crocidura baileyi

HB: 86 (72–93) mm, n = 8

T: 44 (41–46) mm, n = 8

HF: 14.4 (14–16) mm, n = 8

E: n. d.

WT: n. d.

CI: 22.0 (21.6–22.8) mm, n = 5

GWS: 10.2 (10.0–10.4) mm, n = 3

I¹–M³: 10.1 (9.9–10.2) mm, n = 3

Ethiopia

Body measurements: Osgood 1936

Skull measurements: Dippenaar 1980a, Hutterer 1980

Key References Dippenaar 1980a; Guttinger *et al.* 1998.

Leonid A. Lavrenchenko

Crocidura batesi BATES'S SHREW

Fr. Crocidure de Bates; Ger. Bates Spitzmaus

Crocidura batesi Dollman, 1915. Ann. Mag. Nat. Hist., ser. 8, 15: 143. Como River, Gabon.

Taxonomy Often included in *C. poensis* (Hutterer 2005b). Specimens from Cameroon and Gabon recorded as *C. wimmeri* belong to this species. Synonyms: none. Chromosome number: 2n = 50, FN = 76 (Schlitter *et al.* 1999).

Description Small to medium-sized dark chocolate-brown shrew. Dorsal pelage uniform dark chocolate-brown; hairs greyish-brown at base; chocolate-brown at tip. Ventral pelage similar to dorsal pelage or slightly paler. Upper surface of fore- and hindfeet brownish. Tail relatively long (ca. 60–75% of HB), brown above, paler below; pilosity ca. 20–60%. Nipples: not known.

Geographic Variation None recorded.

Distribution Endemic to Africa. Rainforest BZ (Gabon sub-region). Known only from S Cameroon, Gabon, Equatorial Guinea (Rio Muni) and SW Central African Republic (Hutterer 1993, Ray & Hutterer 1995). Perhaps occurs in N Congo. Distribution limits uncertain.

Habitat Lowland rainforest. Recorded at all three altitudinal zones (110 m, 375 m, 625 m) on Mt Doudou, Gabon; seems to have preference for lower and wetter habitats near river margins (Goodman & Hutterer 2004).

Abundance Uncommon or rare. Represented 1.2% (2 of 160; 11 spp.) of captures in Belinga-Makokou, Gabon (Brosset 1988), 11.2% at Mt Alen, Equatorial Guinea (Lasso *et al.* 1996), 11.1% in

*Crocidura batesi*

Ngotto Forest, Central African Republic (Barrière & Nicolas 2000) and 9% in SW Gabon (Nicolas *et al.* 2003). On Mt Doudou, Gabon, found at four of nine localities sampled; where found, comprised 6–17% of all shrews (1 of 16, 8 spp.; 1 of 6, 5 spp.; 1 of 11, 6 spp.; 1 of 8; 3 spp.) (Goodman & Hutterer 2004).

Remarks Found in 3.2% of 311 small carnivore scats collected in Dzanga-Sangha, Central African Republic (Ray & Hutterer 1995, Ray 1998). One ♀ caught in Feb contained two small embryos (label, BMNH; Dja R., Cameroon).

Conservation IUCN Category: Least Concern.

Measurements

Crocidura batesi

HB: 78 (72–88) mm, n = 4

T: 57.9 (52–60) mm, n = 4

HF: 14.3 (14–15) mm, n = 4

E: 11.5 (11–12) mm, n = 4

WT: 12.7 (9.1–15.5) g, n = 4

CI: 24.0 (23.1–25.2) mm, n = 3

GWS: 10.0 (9.2–10.9) mm, n = 4

I¹–M³: 11.6 (10.6–12.2) mm, n = 4

Body measurements and weight: Mt Doudou, Gabon (Goodman & Hutterer 2004)

Skull measurements: Cameroon (BMNH)

Key Reference Goodman & Hutterer 2004.

Justina C. Ray & Rainer Hutterer

Crocidura bottegi BOTTEGO'S SHREW

Fr. Crocidure de Bottego; Ger. Bottegos Spitzmaus

Crocidura bottegi Thomas, 1898. Ann. Mus. Civ. Stor. Nat. Genova, ser. 2, 18: 677. 'Between Badditu and Dime', NE L. Turkana, Ethiopia.

Taxonomy West African populations previously allocated to *C. bottegi* (Hutterer & Happold 1983) are now considered to represent *C. obscurior*. Synonyms: none. Chromosome number: not known.

Description Minute shrew. Dorsal pelage rich chocolate-brown with russet tinge. Ventral pelage slightly paler. Ears dark brown. Fore- and hindlimbs with brown hairs; claws short. Tail of medium relative length (ca. 60% of HB); pilosity ca. 80%. Skull with high and rounded braincase, rostrum short, interorbital and maxillary region short but wide. Front dentition weak. Third upper molar rather wide. Nipples: not known.

Geographic Variation None recorded. Populations from Ethiopia should be compared with those from Kenya.

Distribution Endemic to Africa. Afromontane–Afroalpine BZ. Known from three localities in the highlands of Ethiopia (Yalden *et al.* 1976) and from Marsabit, N Kenya (Aggundey & Schlitter 1986).

Habitat No detailed habitat information is available.

Abundance No information.

Remarks Apparently no other information available.

Conservation IUCN Category: Data Deficient.

Measurements

Crocidura bottegi

HB: 46, 51 mm, n = 2

T: 29, 30 mm, n = 2

HF: 9, 9 mm, n = 2

E: 7 mm, n = 1

WT: 4 g, n = 1

CI: 14.9, 15.2 mm, n = 2

GWS: 6.5, 7.2 mm, n = 2

I¹–M³: 6.2 (6.1–6.2) mm, n = 3

Ethiopia (Hutterer & Yalden 1990)

Key Reference Hutterer & Yalden 1990.

Rainer Hutterer



Crocidura bottegi

***Crociodura bottegoides* BALE SHREW (TRICOLOURED PYGMY SHREW)**

Fr. Crocidure de Bale; Ger. Bale Spitzmaus (Dreifarbige Zwergspitzmaus)

Crociodura bottegoides Hutterer and Yalden, 1990. In: Vertebrates in the Tropics (eds G. Peters & R. Hutterer), Bonn, p. 67. Katcha Camp, Harenna Forest, Bale Mts, Ethiopia. 2400 m.

Taxonomy Synonyms: none. Chromosome number: $2n = 36$, $FN = 60$ (Lavrenchenko *et al.* 1997).

Description Very small shrew with tricoloured pelage. Narrow dark brown band (6–8 mm) runs from top of the head along mid-back towards tail, bordered on each side by a yellowish-brown band of about the same breadth. Ventral pelage, limbs and tail creamy-brown (two specimens) or reddish-brown (one specimen). Claws short. Tail relatively very long (ca. 82% of HB); pilosity 0%. Braincase high and rounded, rostrum short and broad, interorbit and maxillary region short but wide. Dentition gracile, particularly the first upper incisor. Third upper molar medium. Nipples: not known.

Geographic Variation None recorded.

Distribution Endemic to Africa. Afromontane–Afroalpine BZ of Ethiopia. Known only from two regions in Ethiopia: Harenna Forest in the Bale Mts, and Mt Albasso, Arussi (Hutterer & Yalden 1990, Yalden & Largen 1992, Lavrenchenko *et al.* 1997). Allopatric to *C. bottegi* (of similar size), which is also an Ethiopian endemic.

Habitat Relict forests. Found in a grassy clearing in *Schefflera* / *Hagenia* forest at 2400 m, and beneath a log in *Erica arborea* woodland at 3280 m (Hutterer & Yalden 1990). A larger species, *C. harenna* (mean WT: 7.8 g,) also lives in Harenna Forest, but in forested habitats.

Abundance Appears to be uncommon in Harenna Forest (Yalden 1988).

Remarks Apparently no other information available.

Conservation IUCN Category: Endangered.

Measurements

Crociodura bottegoides

HB: 54 (46–57) mm, $n = 3$



Crociodura bottegoides

T: 44.3 (43–47) mm, $n = 3$

HF: 10.3 (10–11) mm, $n = 3$

E: 7 (6–8) mm, $n = 3$

WT: 3.1 (2.5–3.5) g, $n = 3$

CI: 14.7 (14.3–15.1) mm, $n = 3$

GWS: 7.1 (7.1) mm, $n = 3$

I^1 – M^3 : 5.9 (5.9–6.0) mm, $n = 3$

Harenna Forest, Ethiopia (Hutterer & Yalden 1990)

Key Reference Hutterer & Yalden 1990.

Rainer Hutterer

***Crociodura buettikoferi* BÜTTIKOFER'S SHREW**

Fr. Crocidure de Büttikofer; Ger. Büttikofers Spitzmaus

Crociodura buettikoferi Jentink, 1888. Notes Leyden Mus. 10: 47. Robertsport, Liberia.

Taxonomy This species formerly included *attila*, now regarded as a separate species (Hutterer & Joger 1982). Referred to as *Crociodura occidentalis nigeriae* by Sanderson (1940) and Cozens & Marchant (1952) (see Hutterer & Happold 1983). The specimen ascribed to this species from Oda, Ghana (Heim de Balsac 1958) is, in fact, *C. poensis* (Grubb *et al.* 1998). Synonyms: none. Chromosome number: not known.

Description Medium-sized dark-coloured shrew. Dorsal pelage dark chocolate-brown. Ventral pelage paler, greyish-brown. Limbs dark. Tail relatively long (ca. 70% of HB), dark, very sparsely covered with hairs and bristles; pilosity ca. 50%. Skull with a slightly domed braincase, nearly oval in dorsal view; skull smaller and more slender than in sympatric *C. poensis*. Upper first incisor medium and hooked. First unicuspid larger than second and third.

Third molar large. Nipples: not known.

Geographic Variation None recorded.

Distribution Endemic to Africa. Rainforest BZ (Western Region and Western Nigeria sub-region). Recorded from S Guinea, Liberia, Côte d'Ivoire, Ghana and Nigeria. Two specimens from Njala, Sierre Leone, and specimens from Wenchi, Ghana are perhaps this species (Grubb *et al.* 1998). Presence in Guinea-Bissau is uncertain.

Habitat Grassland habitats within the Rainforest BZ (rather than rainforest itself), forest relicts in derived savanna, secondary growth, cocoa plantations and cleared land.

Abundance Very varied, according to locality and habitat. In three sacred groves on the Accra plains, Ghana, only one individual was found out of a total of 14 shrews of four species of *Crocidura* (Decher & Bahian 1999). At Umuahia, Nigeria, it was considered to be 'one of the commonest ground-living mammals', and at Owerri, Nigeria, 32 specimens were obtained (Cozens & Marchant 1952). In Tai N.P., Côte d'Ivoire, comprised 13% and was the fourth commonest species of shrew (10 spp.) (Churchfield *et al.* 2004). In another study in Tai N.P., uncommon in forest (7.2% of 390 shrews, 9 spp.) but one of the two most abundant species in cocoa-coffee plantations (29.3% of 140 shrews, 7 spp.) (Barrière *et al.* 1999). In Ziama Biosphere Reserve, Guinea, uncommon in primary forest, secondary forest, fields, fallow land and young forest plantations (4.8%–13.2%), but the commonest species (36.4% of 441 shrews, 9 spp.) in old forest plantations (P. Barrière unpubl.).

Remarks In Tai N. P., Côte d'Ivoire, commonest prey items (% frequency of occurrence) in 28 stomachs were representatives of the following taxa: Araneae (46%), ants (46%), adult Coleoptera (36%), Isoptera (32%), Diplopods (18%), Blattodea (18%), Gryllidae (14%), Diptera larvae (11%) and earthworms (11%). Several other taxa were each represented by frequencies of <10%. Most (82%) of the prey were 15 mm or less in length (Churchfield *et al.* 2004).

Conservation IUCN Category: Near Threatened.



Crocidura buettikoferi

Measurements

Crocidura buettikoferi

HB: 72–100 mm, n = 3

T: 51–62 mm, n = 3

HF: 12–15 mm, n = 3

E: 7–9.5 mm, n = 3

WT: n. d.

CI: 21.4–22.7 mm, n = 3

GWS: 9.2–9.9 mm, n = 3

I¹–M³: 10.0–10.1 mm, n = 3

♀ only; mean values not recorded

Umuahia, Nigeria (Hutterer & Happold 1983)

Key References Happold 1987; Hutterer & Happold 1983.

D. C. D. Happold

Crocidura caliginea AFRICAN DUSKY SHREW (DUSKY WHITE-TOOTHED SHREW)

Fr. Crocidure sombre; Ger. Dunkle Weißzahnschmaus

Crocidura caliginea Hollister, 1916. Bull. Am. Mus. Nat. Hist. 35: 664. Medje, NE DR Congo.

Taxonomy In skull characters resembles *C. yankariensis* (Hutterer & Jenkins 1983). It also shares unusual characteristics with *Paracrocidura schoutedeni* (Hutterer & Duda 1990). Synonyms: none. Chromosome number: not known.

Description Small to medium-sized dark-brown shrew. Pelage 3.5 mm (on back). Dorsal pelage dark brown. Ventral pelage dark brown. Snout, ears, fore- and hindfeet covered by very short whitish hairs that contrast sharply with the uniformly dark pelage of the body. Ear small relative to head, pale, covering only half the height of the head. Hindfeet relatively short. Tail relatively long (70%

of HB), brown; pilosity 20–30%. Skull strongly built, with heavy maxillary processes. The skull differs from the general *Crocidura* type by its rectangular shape, broad maxillary region and narrow interorbital region and long rostrum. Teeth comparatively large and well developed. First upper incisor long and hooked. Second upper incisor (= first unicuspid) most unusual in being twice as large as the second and third upper unicuspid, and in having (mostly in ♂♂) a secondary cusp. Upper molars large. Molar teeth of mandible very well developed. Nipples: not known.

Geographic Variation None recorded.

Distribution Endemic to Africa. Rainforest BZ (East Central Region) of NE DR Congo. Until 1990, recorded from only two localities (Medje [type locality] and Masako Forest [near Kisangani]) (Hollister 1916, Hutterer & Dudu 1990), but has since been found to occur in various forests in the vicinity of Kisangani (Mukinzi *et al.* 2006). The geographic range of the species still appears to be very limited.

Habitat In Masako Forest, most *C. caliginea* have been found in secondary forest (40-year-old regrowth) surrounded by primary forest (mono-dominant *Gilbertiodendron* forest). Some have been found in fallow land and in moist areas along creeks (Hutterer & Dudu 1990, Dudu *et al.* 2005). In recent surveys near Kisangani (Mukinzi *et al.* 2006, and unpubl.), it has been found also in primary forest.

Abundance Considered a rare, endemic species but may be relatively abundant locally. Numerically the commonest species during three years of trapping in Masako Forest where it comprised 47% of shrews in secondary forest ($n = 36$; 8 spp.) and 33% of shrew captures in all habitats ($n = 72$, 9 spp.) (Dudu *et al.* 2005).

Adaptations External characters of *C. caliginea* suggest a terrestrial species with some modifications towards a semi-fossorial life. Large, heavy teeth are particularly well adapted for crushing tough, chitinous exoskeletons of arthropods.

Foraging and Food Feeds on a wide range of invertebrates, primarily arthropods. Stomach analyses ($n = 20$) from rainforest in Masako Forest showed that Formicidae were major prey items (100% by frequency), followed by Isoptera (60%), Araneae (60%), adult Coleoptera (55%) and Diplopoda (45%). Invertebrate prey ranged in body length from 3 mm to 20 mm with 85% being <10 mm (Dudu *et al.* 2005).

Social and Reproductive Behaviour No information. The possession of an additional cusp on the second upper incisor in significantly more ♂♂ than ♀♀ (see above) suggests partial sexual dimorphism, which would be most unusual in the Soricidae.

Reproduction and Population Structure No information.

Predators and Diseases No information but principal predators likely to be owls and small mammalian carnivores such as mongooses, genets and small cats known to feed on shrews (Demeter 1981, Ray & Hutterer 1995).



Crocidura caliginea

Conservation IUCN Category: Least Concern.

Formerly assessed as Critically Endangered. A rare endemic species with a very restricted range. Major threats are human-induced habitat loss and degradation of the rainforests.

Measurements

Crocidura caliginea

HB: 69.6 ± 4.4 mm, $n = 14$

T: 48.7 ± 3.7 mm, $n = 12$

HF: 11.7 ± 0.5 mm, $n = 14$

E: 7.1 ± 0.3 mm, $n = 12$

WT: 8.3 ± 1.3 g, $n = 12$

CI: 21.8 ± 0.5 mm, $n = 20$

GWS: 9.6 ± 0.2 mm, $n = 20$

I¹–M³: 10.1 ± 0.3 mm, $n = 24$

DR Congo

Measurements: Hutterer & Dudu 1990

Weight: Dudu *et al.* 2005

Mean \pm 1 S.D.

Key References Hollister 1916; Hutterer & Dudu 1990.

S. Churchfield, R. Hutterer & A. Dudu

Crocidura cinderella CINDERELLA SHREW

Fr. Crocidure cendr  e; Ger. Cinderellas Spitzmaus

Crocidura cinderella Thomas, 1911. Ann. Mag. Nat. Hist., ser. 8, 8: 119. 'Gemenjulla, French Gambia' (= Senegal).

Taxonomy The species may be related to *C. tarfayensis* of Morocco and Mauritania (Hutterer 1987). Synonyms: none. Chromosome number: not known.

Description Very small to small pale-coloured shrew. Pelage short (ca. 2 mm) and dense. Dorsal pelage brownish-grey; hairs dark grey on basal two-thirds, pale cream or pale brown subterminally, with russet-brown to pale brown at tip. Ventral pelage pale grey;

hairs grey at base, white at tip. Colour of ventral pelage delineated from dorsal pelage on lower flanks, especially from shoulder to base of tail. Chin, throat and chest grey. Fore- and hindfeet white; claws transparent, pointed and sharp. Tail relatively long (ca. 70% of HB), bicoloured, pale brown above, white below; pilosity ca. 80%. Skull with flat dorsal roof and flat braincase. Rostrum, interorbital and braincase of medium length, maxillary wide. First incisor long and hooked. Third molar medium. Nipples: not known.

Geographic Variation None recorded.

Distribution Endemic to Africa. Sudan Savanna and Sahel Savanna BZs of West Africa. Known from scattered localities in Senegal, Mauritania, Gambia, Mali and Niger (Hutterer 1993).

Habitat A specimen from Bandia, Senegal, was collected in dry *Acacia seyal* forest (Böhme & Hutterer 1978); another in a banana plantation at Keur Moussa monastery. *Crocidura cinderella* shares these habitats with *C. fuscomurina*, *C. lamottei*, *C. lusitania* and *C. olivieri* (R. Hutterer unpubl.).

Abundance Appears to be rare. Known from fewer than ten specimens.

Remarks The flat skull and the pale grey pelage perhaps indicates an adaptation to life in rocky fissures in arid habitats.

Conservation IUCN Category: Least Concern.

Measurements

Crocidura cinderella

HB: 67, 50 mm, n = 2

T: 45, 49 mm, n = 2

HF: 11, 12 mm, n = 2



Crocidura cinderella

E: 8.5 mm, n = 1

WT: 5.6 g, n = 1

CI: 18.8 mm, n = 1

GWS: 7.7 mm, n = 1

I¹–M³: 8.0, 8.3 mm, n = 2

Senegal (ZFMK)

Key Reference Hutterer 1987.

Rainer Hutterer

Crocidura congobelgica CONGO SHREW (CONGO WHITE-TOOTHED SHREW)

Fr. Crocidure du Congo; Ger. Kongo-Weißzahnschmaus

Crocidura congobelgica Hollister, 1916. Bull. Amer. Mus. Nat. Hist. 35: 670. Lubila, near Bafwasende, NE DR Congo.

Taxonomy Probably related to sympatric *C. latona*, which it closely resembles in appearance (Hollister 1916); however, *C. congobelgica* has a larger skull, much wider palate, stronger maxillary processes and larger teeth, but lacks a fovea on the hypoconid of M₃ (present in *C. latona* and *C. caliginea*). Resembles sympatric *C. caliginea* in size and proportions but differs in colour, and is also very similar to *C. buettikoferi*. Synonyms: none. Chromosome number: not known.

Description Small-medium, unicoloured, dark-brown shrew. Dorsal pelage glossy dark-brown, finely streaked with cinnamon-buff. Ventral pelage slightly paler in colour. Fore- and hindfeet thinly clothed in brown hairs. Tail relatively long (ca. 75% of HB), brownish-black, paler underneath at base; nearly naked except for scattered short hairs; pilosity 25%. Skull with large maxillary processes. Unicuspid teeth rounded; first upper unicuspid relatively larger, oval in crown pattern, and with well-developed cingulum. Second and

third unicuspid similar to first and approximately equal in size; third unicuspid slightly overlapping the second. Last upper premolar lacks conspicuous posterior emargination, the median space between it and the first molar being very small; length approximately equal to its breadth. Nipples: not known.

Geographic Variation None recorded.

Distribution Endemic to Africa. Rainforest BZ (East Central Region). Found only in NE DR Congo and probably endemic to this region. Latterly found in and around Masako Forest Reserve (NE of Kisangani) and in Ituri Forest (NE DR Congo).

Habitat Primary and secondary rainforest. Captured only in fallow land adjacent to rainforest in Masako Forest, DR Congo (Dudu *et al.* 2005).

Abundance Appears to have small, localized populations and is rare in trapped samples. Comprised 14% of shrews ($n = 21$; 6 spp.) in fallow land, and only 4% of shrews ($n = 72$; 9 spp.) in all habitats during three years of trapping in Masako Forest, DR Congo (Dudu *et al.* 2005).

Remarks A terrestrial, ground-dwelling species. Feeds on a wide range of invertebrates, primarily arthropods. Stomach analyses ($n = 3$) contained the following prey: Isoptera, Formicidae, Diptera and Lepidoptera larvae, Heteroptera, Araneae, Chilopoda and Diplopoda. Invertebrate prey ranged in body length from 3 mm to 30 mm but most were <10 mm (Dudu *et al.* 2005).

Conservation IUCN Category: Least Concern.

Species insufficiently known. Probably a species of conservation concern because of its very restricted distribution and small population numbers. At risk from habitat modification and isolation, particularly deforestation.

Measurements

Crociodura congobelgica

HB: 74 mm, $n = 1^*$, 79 mm, $n = 2^{**}$

T: 59 mm^{*}

HF: 14 mm^{*}

E: n. d.

WT: 17.0 g^{**}

CI: 20.7 mm^{*}

GWS: 9.1 mm^{*}

I¹–M³: n. d.

DR Congo



Crociodura congobelgica

*Hollister 1916 – holotype

**Dudu *et al.* 2005

Key References Dudu *et al.* 2005; Heim de Balsac 1968b; Hollister 1916.

S. Churchfield, R. Hutterer & A. Dudu

Crociodura crenata JUMPING SHREW

Fr. Crocidure sautante; Ger. Springende Weißzahnspitzmaus

Crociodura crenata Brosset, Dubost and Heim de Balsac, 1965. Mammalia 29: 268. Belinga, Gabon.

Taxonomy A comparison of 16s rRNA gene fragments reveals that *C. crenata* is closely related to *C. dolichura* (Quérouil *et al.* 2005). Synonyms: none. Chromosome number $2n = 48$ (Primus *et al.* 2006).

Description Small–medium sized, reddish-brown shrew with long hindfoot and long tail. Pelage short (hairs ca. 4 mm) and dense. Dorsal pelage and ventral pelage reddish-brown or russet-brown; hairs grey on basal half, reddish-brown on terminal half. Head similar in colour to dorsal pelage. Long vibrissae. Ears relatively large, darkly pigmented, not concealed by pelage. Fore- and hindfeet flesh-coloured, appear naked but with very short ginger hairs. Tail relatively extremely long (ca. 120% of HB, relatively longer than in most other *Crociodura* of similar size), dark brown, slightly bicoloured; pilosity 0%. Skull long and narrow. Rostrum long, wide and high. Maxillary and braincase narrow, interorbit wide. Braincase highly inflated. Dentition very weak (even compared to *C. dolichura*). First upper incisor short and slightly hooked. Third upper molar medium. Incisor of mandible has two denticles on inner surface. Nipples: not known.

Geographic Variation None recorded.

Distribution Endemic to Africa. Rainforest BZ (West Central Region [Eastern Nigeria and Gabon sub-regions]). Recorded from S Cameroon, N Gabon, N Congo and S Central African Republic (Brosset 1988, Hutterer 1993, Hutterer & Schlitter 1996, Ray & Hutterer 1995, Goodman *et al.* 2001, Nicolas *et al.* 2003, Barrière *et al.* 2005). One possible record from Rainforest BZ (East Central Region).

Habitat Rainforest and marshy habitats in rainforest, mostly at lower altitudes; recorded from rainforest in ‘montagne’ at Belinga, Gabon (Brosset 1988).

Abundance Varies according to habitat and locality. At Mt Doudou, Gabon, found at three altitudes (110 m, 375 m, 625 m), and the second most common species of shrew (17%; 9 spp.) after *Sylvisorex johnstoni* (Goodman & Hutterer 2004). In another study, comprised 9.7% of shrews (14 of 144; 9 spp.) (Nicolas *et al.* 2003). In Minkébé Forest, Gabon, only one specimen was obtained (out of

11) in marshy habitats, and it was not present in drier parts of the forest (Goodman *et al.* 2001). Comprised 1.2% (2 of 160; 11 spp.) in NE Gabon (Brosset 1988).

Remarks Hindfeet extremely long in relation to body size, which may assist in jumping rather than climbing (Brosset 1988). Tail very long; may allow a scansorial life on vines and in dense vegetation; however, not caught in traps placed above ground at Mt Doudou (Goodman & Hutterer 2004).

Conservation IUCN Category: Least Concern.
Status insufficiently known.

Measurements

Crocidura crenata

HB: 72.4 (62–79) mm, n = 7

T: 85.1 (72–91) mm, n = 7

HF: 15.7 (15–16) mm, n = 7

E: 10.1 (7–11) mm, n = 7

WT: 8.4 (7.8–9.1) mm, n = 7

CI: 19 mm, n = 1

GWS: 7.7 mm, n = 1

I¹–M³: 8.8 mm, n = 1

Body measurements and weight: Gabon (Goodman & Hutterer 2004)

Skull measurements: Gabon (Brosset *et al.* 1965a; holotype)



Crocidura crenata

Key References Brosset 1988; Brosset *et al.* 1965a; Goodman *et al.* 2001.

Rainer Hutterer & Patrick Barrière

Crocidura crossei CROSSE'S SHREW

Fr. Crocidure de Crosse; Ger. Crosses Moschusspitzmaus

Crocidura crossei Thomas, 1895. Ann. Mag. Nat. Hist., ser. 6, 16: 53. 'Asaba, 150 miles [241 km] up the River Niger', Nigeria.

Taxonomy Resembles *C. gracilipes* in size and colouration. Heim de Balsac & Meester (1977) included *ebriensis*, *ingoldbyi* and *jouvenetae* in *C. crossei*, an arrangement followed by Hutterer (1993). However, Hutterer (2005b) considers the larger *jouvenetae* to represent a separate species (with *ebriensis* as a synonym). Sympatric with *C. juvenetae* for most of its range. Synonyms: *ingoldbyi*. Subspecies: none. Chromosome number: 2n = 44, FN = 66 (Côte d'Ivoire; Meylan & Vogel 1982; this karyology may be based on specimens of *C. crossei* or *C. juvenetae*).

Description Small shrew. Dorsal pelage slaty-grey or greyish-brown to chocolate-brown. Ventral pelage greyish and paler. Chin white. Limbs usually dark; fore- and hindfeet brownish-buff. Tail relatively very long (about 84% of HB), quite stout; grey-brown above, paler below; well furnished with small dark hairs and sparsely but evenly distributed with long bristles along most of its length; pilosity ca. 85%. Skull long, with a flat braincase. Dorsal profile of skull angular, sometimes with a marked mid-dorsal break (see also *C. douceti*). Rostrum slender, maxillary region narrow. Anterior upper incisors small and delicate; second and third upper unicusps approximately equal, their tips about level with the basal cusp of P⁴. Nipples: not known.

Geographic Variation Considerable variation in pelage colour from one locality to another, even within the same vegetation zone. Rainforest individuals are generally darker than those in forest–savanna mosaic habitats (Hutterer & Happold 1983).

Distribution Endemic to Africa. Rainforest BZ (Western Region and West Central Region), Northern Rainforest–Savanna Mosaic and Guinea Savanna BZ from Guinea and Sierra Leone to W Cameroon.

Habitat Forest habitats, including lowland rainforest, relic forests in savanna, and tree plantations (Hutterer & Happold 1983, Decher *et al.* 1997). Found at various altitudes, from closed canopy forests along the R. Niger to forests on Mt Cameroon.

Abundance In Gambari Forest, Nigeria, comprised 71% of shrews (2 spp., n = 56) trapped during three years; much more common than the other syntopic species (*C. nigeriae*) (Happold 1977).

Adaptations Primarily terrestrial but also clammers over fallen tree trunks and branches.

Foraging and Food No information, but searches for invertebrate prey in leaf litter, soil crevices and rotting wood.

Social and Reproductive Behaviour Low recapture rates suggest that individuals wander widely and do not remain in the same area for very long. Of 40 marked individuals in rainforest of S Nigeria, only four were captured a second time; of these, three were seen a second time within one month, and the fourth was seen again five months later (Happold 1977, 1987).

Reproduction and Population Structure Pregnant ♀♀ were found in the wet season (Apr, May, Oct and Nov) in S Nigeria (Happold 1977), and in early Dec in Ghana (Decher *et al.* 1997). Litter-size: 2–4 (Nigeria; Happold 1987).

Predators, Parasites and Diseases No information but principal predators likely to be owls, reptiles and small carnivores such as mongooses, genets and small cats known to feed on shrews.

Conservation IUCN Category: Least Concern.

A widespread and relatively common species of no immediate conservation concern.

Measurements

Crociodura crossei

TL (♂♂): 116.6 (114–122) mm, n = 5

TL (♀♀): 117.0 (115–119) mm, n = 4

T (♂♂): 48.0 (45–57) mm, n = 5

T (♀♀): 47.8 (45–50), n = 4

HF (♂♂): 12.2 (11.0–13.0) mm, n = 5

HF (♀♀): 12.3 (12.0–13.0) mm, n = 4

E (♂♂): 9.8 (8.0–11.0) mm, n = 5

E (♀♀): 9.8 (8.0–11.0) mm, n = 4

WT (♂♂): 5.6 (5.0–7.0) g, n = 5

WT (♀♀): 5.1 (4.5–6.0) g, n = 4

CI (♂♂): 18.7 (17.9–19.4) mm, n = 5

CI (♀♀): 18.8 (18.1–19.6) mm, n = 4

GWS (♂♂): 8.0 (7.7–8.2) mm, n = 5

GWS (♀♀): 7.8 (7.5–8.1) mm, n = 4

I¹–M³ (♂♂): 8.0 (7.7–8.3) mm, n = 5

I¹–M³ (♀♀): 8.1 (7.9–8.5) mm, n = 4

Ghana (Decher *et al.* 1997)



Crociodura crossei

HB (both sexes): 54–80 mm, n = 10

T (both sexes): 48–57 mm, n = 10

HF (both sexes): 10–12 mm, n = 10

E (both sexes): 6–8 mm, n = 10

WT (both sexes): 6.3–8.0 g, n = 10

CI (both sexes): 18.5–19.9 mm, n = 10

GWS (both sexes): 7.8–8.5 mm, n = 10

I¹–M³ (both sexes): 7.7–8.6 mm, n = 10

Nigeria (Hutterer & Happold 1983; mean values not recorded)

Key References Decher *et al.* 1997; Happold 1977, 1987; Heim de Balsac & Meester 1977.

S. Churchfield & P. D. Jenkins

Crociodura cyanea REDDISH-GREY SHREW

Fr. Crocitude de Cyané; Ger. Rotgraue Moschusspitzmaus

Crociodura cyanea (Duvernoy, 1838). Mem. Soc. Hist. Nat. Strasbourg. 'La rivière des Elephants, au sud de l'Afrique' (= Citrusdal, South Africa).

Taxonomy Originally described in the genus *Sorex*. Polytypic. The taxonomic limits of the species are uncertain; and many of the subspecies listed by Heim de Balsac & Meester (1977) are now considered as valid species, or as synonyms of other species. Some names, e.g. *infumata* and *cyanea*, are considered as subspecies by Meester *et al.* (1985), but as synonyms here. Synonyms: *argentatus*, *capensis*, *?capensoides*, *?concolor*, *electa*, *infumata*, *martensii*, *pondoensis*, *vryburgensis* (see Hutterer 2005b for details). Subspecies: none. Chromosome number: not known.

Description Small–medium (♀♀) to medium-sized (♂♂) shrew. Dorsal pelage brownish-grey, grizzled with pale yellow; hairs

slaty-grey at base, with pale-grey or yellowish subterminal bands and brown tip. Ventral pelage paler grey with a yellow or brown tinge in older specimens; hairs slaty-grey at base with silvery-grey tip. Head slender with long, narrow pointed muzzle, small eyes and rounded ears. Fore- and hindfeet yellow to pale brown; each with five digits. Tail relatively long (ca. 69% of HB), pale to dark brown above; paler below; pilosity ca. 50%. Males on average larger than ♀♀. Nipples: 0 + 3 = 6.

Geographic Variation Western forms are generally paler than the eastern ones. There is also variation in size in different parts of the range.

Distribution Endemic to Africa. Widespread in Zambezan Woodland BZ and South-West Arid BZ (but excluding much of the Kalahari Desert). Recorded from N Zambia and N Mozambique southwards to southern Africa, and then northwards through C Namibia. Conspicuously absent from E Namibia, N Botswana, N–C Karoo and C Mozambique.

Habitat Montane forest and grassland, vleis, dense shrubs, savanna, grasslands and rocky outcrops. Has a remarkably wide habitat tolerance.

Abundance Widespread and comparatively common in some areas.

Adaptations Predominantly nocturnal and terrestrial. In C Namibia, there is a cave-dwelling population where individuals penetrate 150 m into the cave, apparently thriving on the numerous invertebrates, such as ptinid beetles, apterous crickets and pseudoscorpions that are found there (Marais & Irish 1990). Shrews were collected from areas in the cave where large numbers of bats roost, and may well feed on carcasses that are fairly common at those sites.

Foraging and Food Insectivorous (Monadjem 1997).

Social and Reproductive Behaviour Solitary.

Reproduction and Population Structure In South Africa, reproductive activity occurs during the wet season (Sep–Apr) (Rautenbach 1982, Lynch 1983, Skinner & Smithers 1990). In KwaZulu–Natal Province, South Africa, a pregnant specimen was collected during the dry season (Jul) (Taylor, P. 1998). Probably breeds opportunistically. Mean litter-size: 3.3 (range 2–6; mode 4; n = 12) (Rautenbach 1982, Lynch 1983, Taylor, P. 1998).

Predators, Parasites and Diseases Remains of this species have been recovered from the pellets of Barn Owls *Tyto alba*.

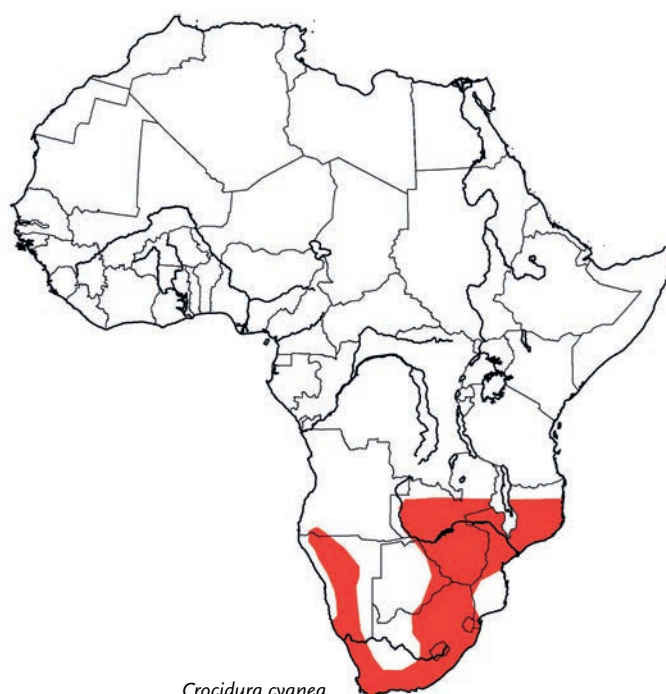
Conservation IUCN Category: Least Concern.
A relatively common shrew.

Measurements

Crociodura cyanea

HB (♂♂): 89 (67–93) mm, n = 23

HB (♀♀): 74.7 (68–89) mm, n = 19



Crociodura cyanea

T (♂♂): 52.8 (42–69) mm, n = 23

T (♀♀): 48.0 (33–55) mm, n = 19

HF (♂♂): 13.0 (11–14.5) mm, n = 21

HF (♀♀): 12.5 (12–14) mm, n = 19

E (♂♂): 9.3 (8–11) mm, n = 22

E (♀♀): 8.6 (7.5–11) mm, n = 17

WT: n. d.

CI (♂♂): 21.1 (19.6–22.0) mm, n = 19

CI (♀♀): 20.5 (19.6–21.4) mm, n = 11

GWS (♂♂): 9.3 (8.4–9.8) mm, n = 18

GWS (♀♀): 9.1 (8.8–9.4) mm, n = 12

I¹–M³ (♂♂): 9.0 (7.9–9.5) mm, n = 24

I¹–M³ (♀♀): 8.8 (8.3–9.6) mm, n = 16

Citrusdal, South Africa (Meester 1963, as *C. c. cyanea*)

Key References Lynch 1983; Meester 1963; Skinner & Smithers 1990.

R. M. Baxter & N. J. Dippenaar

Crociodura denti DENT'S SHREW (DENT'S WHITE-TOOTHED SHREW)

Fr. Crociodure de Dent (Crociodure d'Ituri); Ger. Dents Spitzmaus

Crociodura denti Dollman, 1915. Ann. Mag. Nat. Hist., ser. 8, 16: 377. Between Mawambi and Avakubi, Ituri Forest, DR Congo.

Taxonomy Originally described as a subspecies of *C. jacksoni*. West African records for this species (Ziegler *et al.* 2002) need confirmation. Preliminary genetic data suggest that the species is composite and perhaps includes more than one species (Quérroul *et al.* 2005). No synonyms. Chromosome number: not known.

Description Small dark brown shrew with hairy tail. Dorsal pelage dark brown. Ventral pelage slate-grey. Tail relatively long (ca. 65–70% of HB), brown above, paler below; pilosity 66–75%. Skull stout with short and broad snout. Nipples: not known.

Geographic Variation None recorded.

Distribution Endemic to Africa. Rainforest BZ; widespread but disjunct. Recorded from Cameroon, Gabon and NE DR Congo; may occur in N Congo. Records from Guinea and Sierra Leone need confirmation (see above).

Habitat Swamp forest in Guinea (Ziegler *et al.* 2002), gallery forest in montane savanna in Adamoua Highlands, Cameroon (Hutterer & Joger 1982), secondary forest in Masako Forest Reserve (Dudu *et al.* 2005).

Abundance The most common shrew captured by owls (25% of 64) in the Adamaoua Highlands, Cameroon (Hutterer & Joger 1982). Formed 19.4% of shrew captures ($n = 72$) in Masako Forest, DR Congo (Dudu *et al.* 2005). Elsewhere, rarely captured.

Remarks Stomach analyses from rainforest in Masako Forest showed that Isoptera were major prey items (30% by composition), followed by Diplopoda (13.6%), Formicidae (11.4%), Coleoptera (9.6%), Araneae (8.5%), Blattoidea (6.0%), Heteroptera (5.5%), Lepidoptera (5.5%), Diptera larvae (4.3%) and Acrididae (<1%) (Dudu *et al.* 2005). Remains of this species were found in 2.9% of 311 small carnivore scats collected in Dzanga-Sangha, Central African Republic (Ray & Hutterer 1995; Ray 1998).

Conservation IUCN Category: Least Concern.

Measurements

Crocidura denti

HB: 63 mm, $n = 1$

T: 46 mm, $n = 1$

HF: 13 mm, $n = 1$

E: 8 mm, $n = 1$

WT: 10.5 (8–12) g, $n = 8$



Crocidura denti

CI: 20.6 mm, $n = 1$

GWS: 9.3 mm, $n = 1$

I¹–M³: 9 mm, $n = 1$

Measurements: Ituri Forest, DR Congo (Dollman 1915e; holotype)

Weight: Central African Republic (Ray & Hutterer 1995)

Key References Dudu *et al.* 2005; Hutterer & Joger 1982.

Justina C. Ray & Rainer Hutterer

Crocidura desperata DESPERATE SHREW

Fr. Crocidure triste; Ger. Rasende Spitzmaus

Crocidura desperata Hutterer, Jenkins and Verheyen, 1991. Oryx 25: 165. Rungwe Mts, S Tanzania. Above 2000 m.

Taxonomy Relationships of this shrew are still unresolved (Hutterer 2005b). Synonyms: none. Chromosome number: not known.

Description Medium-sized greyish-brown shrew. Pelage long, dense and woolly; dorsal hairs 10 mm. Dorsal pelage deep greyish-brown, slightly speckled. Ventral pelage pale grey. Colour of dorsal and ventral pelages merge. Fore- and hindfeet pale grey (as ventral pelage). Claws well developed: claws on forefeet 2.5–2.6 mm, claws on hindfeet 2.6–2.9 mm. Tail relatively long (ca. 75% of HB), thick at base, bicoloured, brown above, grey below; pilosity 70–76%. Skull large, rather flat. First incisor long and hooked. Skull large, rostrum elongated, interorbital region narrow. Upper incisor long and gracile. First unicuspid larger, second and third unicuspid smaller and equal. Upper last molar small. Nipples: not known.

Geographic Variation None recorded.

Distribution Endemic to Africa. Known only from the Rungwe and Udzungwa (Uzungwa) Mts, S Tanzania. Not known from any of the other Eastern Arc Mts in Tanzania.

Habitat Bamboo zone and relict montane forests above 2000 m (Hutterer *et al.* 1991).

Abundance Extremely localized.

Remarks Some of the characteristics of the body, e.g. long claws on hindfeet (similar to those of *Myosorex* spp.), comparatively small ears and dorsal surface of hindfoot with small scales and relatively few hairs suggest that these shrews may be partly fossorial. Elongated incisors suggest that earthworms may form part of the diet (Hutterer *et al.* 1991).

Conservation IUCN Category: Endangered.

Measurements

Crocidura desperata

HB: 89.0 (80–101) mm, n = 4

T: 67 mm, n = 4

HF: 18.7 (18.5–19) mm, n = 4

E: 8.1 (7.1–8.5) mm, n = 4

WT: 23.3 (16–27) mm, n = 4

CI: 25.9 (25.0–27.0) mm, n = 4

GWS: 10.9 (10.6–11.0) mm, n = 4

I¹–M³: 11.2 (10.6–11.8) mm, n = 4

Tanzania (ZFMK)

Key Reference Hutterer *et al.* 1991.

Rainer Hutterer



Crocidura desperata

Crocidura dolichura LONG-TAILED SHREW (LONG-TAILED MUSK SHREW)

Fr. Crocidure à queue longue; Ger. Langschwanz Spitzmaus

Crocidura dolichura Peters, 1876. Monatsb. K. Preuss. Akad. Wiss. Berlin 1876: 475. Bonjongo, Cameroon.

Taxonomy The taxa *latona*, *ludia*, *muricauda* and *polia* were included in *C. dolichura* by Heim de Balsac & Meester (1977) but are regarded as valid species by Hutterer & Dippenaar (1987a) and Hutterer (1993, 2005b). Sister taxon of *C. crenata* (Quérouil *et al.* 2005). Synonyms: none. Chromosome number: not known.

Description Small grey-brown shrew. Dorsal pelage uniform deep greyish-brown. Ventral pelage slightly paler grey. Hindfeet relatively short. Hind- and forefeet with scattered white hairs. Tail relatively extremely long (125–150% of HB); pilosity 0%. Skull laterally depressed and rounded, braincase oval. Dorsal profile with straight rostrum and inflated braincase. Dentition weak, I¹ and subsequent unicuspid very small; M³ large. Nipples: not known.

Geographic Variation None recorded.

Distribution Endemic to Africa. Rainforest BZ (West Central and East Central Regions). Recorded from S Nigeria, S Cameroon, N Gabon, S Central African Republic, DR Congo (N of Congo R.), Uganda and Burundi. Also Bioko I.

Habitat Primary and secondary rainforests over a wide range of altitudes. In E DR Congo, found in primary rainforests, secondary rainforests and montane forests (e.g. *Neoboutonia* and mixed forests), but not found in swamps or in cultivations (Dieterlen & Heim de Balsac 1979).

Abundance Uncommon. Proportional abundance varies from 4% to 9% depending on the shrew community and location. Comprised 4% of captured shrews at Mt Alen, Equatorial Guinea (n = 26; 8 spp.; Lasso *et al.* 1996), 4% at Mt Doudou, SE Gabon (n = 503; 9 spp.; Nicolas *et al.* 2004), 4.5% in SW Gabon at 110 m (n = 44; 9 spp.; Nicolas *et al.* 2004).



Crocidura dolichura

spp.; Goodman & Hutterer 2004), 7.5% at Belinga-Makokou, Gabon (n = 160; 11 spp.; Brosset 1988), 8% in Korup National Park, S Cameroon (n = 24; 9 spp.; Hutterer & Schlitter 1996) and 9% in marshland at Minkébé Reserve, Gabon (n = 11, 7 spp.; Goodman *et al.* 2001).

Remarks The long tail may be used for balance (Hutterer & Happold 1983). Embryo number: 2.5 (2–3, n = 2; Belinga-Makokou, Gabon; Brosset 1988). Stomach contents (n = 1) includes representatives of the following: Formicidae, adult Diptera, Lepidoptera larvae, Diplopoda and Araneae (Dudu *et al.* 2005). Found in 3.9% of 311 small carnivore scats collected in Dzanga-Sangha, Central African Republic (Ray & Hutterer 1995; Ray 1998).

Conservation IUCN Category: Least Concern.

Measurements

Crocidura dolichura

HB: 60, 70 mm, n = 2

T: 73, 75 mm, n = 2

HF: 12, 13 mm, n = 2

E: 9, 10 mm, n = 2

WT: 5.6 (4–7) g, n = 11

CI: 18.8, 19.5 mm, n = 2

GWS: 8.1, 8.4 mm, n = 2

I¹–M³: 7.9, 8.3 mm, n = 2

Measurements: Nigeria (Hutterer & Happold 1983)

Weight: Central African Republic (Ray & Hutterer 1995)

Key References Dieterlen & Heim de Balsac 1979; Hutterer & Happold 1983.

Justina C. Ray & Rainer Hutterer

Crocidura douceti DOUCET'S SHREW (DOUCET'S MUSK SHREW)

Fr. Crocidure de Doucet; Ger. Doucets Moschusspitzmaus

Crocidura douceti Heim de Balsac, 1958. Mem. Inst. Fr. Afr. Noire 53: 329. Adiopodoume, Côte d'Ivoire.

Taxonomy Very similar to *C. muricauda* but apparently not closely related; exact genetic relations unknown (Quérouil *et al.* 2005). Synonyms: none. Chromosome number: not known.

Description Very small shrew. Dorsal pelage greyish-brown to chocolate-brown; hairs uniformly coloured. Ventral pelage grey to off-white. Fore- and hindlimbs with pale hairs. Tail relatively long (ca. 80% of HB), dark and thin, with small hairs and dark bristles; pilosity 20%. Skull similar to *C. crossi* (dorsal profile flatter) and *C. muricauda* (skull larger); rostrum short. Upper and lower dentition weak, particularly the first incisor and unicuspid. M³ large. Nipples: not known.

Geographic Variation Dorsal pelage darker in northern populations. Heim de Balsac & Aellen (1958) remarked that specimens from Serédou, Guinea, had longer tails and differed in colouration from the typical form and could represent a 'slightly different race'. The phylogenetic relations between the populations from Guinea to Nigeria are unresolved.

Distribution Endemic to Africa. Primarily Guinea Savanna BZ and margins of Rainforest BZ (Western Region, Guinea); also coastal forest relicts (Côte d'Ivoire). Recorded from Guinea and Côte d'Ivoire (Hutterer 2005b). Records from Nigeria (Hutterer & Happold 1983) are questionable (and not mapped). Distribution limits uncertain.

Habitat Relict and riverine forests in savannas. Also found in mixed secondary forest and swampy areas in the Taï Forest (Churchfield *et al.* 2004), and in moist tall grass-forest habitats near Adiopodoumé, Côte d'Ivoire (Heim de Balsac & Aellen 1958). Also found in a relict forest at base of inselberg (Abuja, Nigeria) (D. C. D. Happold unpubl.).

Abundance Rarely collected and abundance usually low: comprised 7% of shrews (n = 194) caught in secondary forest of

Taï N. P., Côte d'Ivoire (Churchfield *et al.* 2004); 3.2% of shrews (n = 390; 9 spp.) in forest and 1.4% of shrews (n = 140; 7 spp.) in cocoa-coffee plantations in Taï N. P. (Barrière *et al.* 1999); 1% of shrews (n = 96) in the Mt Nimba area (Heim de Balsac 1958); 1.3% of shrews (n = 79) in lower Côte d'Ivoire (Heim de Balsac & Aellen 1958); and 3.6% (n = 303; 10 spp.) in forest plantations, 5.6% (n = 500; 11 spp.) in primary forest and up to 8.8% (n = 272, 9 spp.) in fields in Ziama Biosphere Reserve, Guinea (P. Barrière unpubl.).



Crocidura douceti

Adaptations The long tail may be a modification towards a scansorial life. A nest containing two juveniles was found some 10 m above ground in a cavity of a palm tree (Heim de Balsac & Vuattoux 1969), and another specimen was found in a glue trap in the canopy of Taï Forest (Churchfield *et al.* 2004).

Foraging and Food Feeds on a wide range of invertebrates, primarily arthropods. Stomach analyses ($n = 14$) from Taï N. P. showed that Formicidae were major prey items (50% by frequency of occurrence), followed by Coleoptera (29%), Araneae (29%), Isoptera (29%) and some other groups of minor importance. Invertebrate prey ranged in body length from 3–20 mm with ca. 80% being <10 mm (Churchfield *et al.* 2004).

Reproduction and Population Structure Embryo number: 2 ($n = 1$; Côte d'Ivoire; Heim de Balsac 1958).

Conservation IUCN Category: Data Deficient.

Crocidura eisentrauti EISENTRAUT'S SHREW

Fr. Crocidure d'Eisentraut; Ger. Eisentrauts Spitzmaus

Crocidura eisentrauti Heim de Balsac, 1957. Zool. Jahrb. Abt. Syst. Oekol. Geogr. Tiere 85: 616.
Johann-Albrecht-Hütte, 2900 m, Mt Cameroun, Cameroon.

Taxonomy This species is not conspecific with *C. vulcani* (*contra* Heim de Balsac 1957b; see Hutterer 2005b). Synonyms: none. Chromosome number: not known.

Description Small-medium brown shrew. Pelage soft and dense; hairs 4–5 mm on mid-dorsal line. Dorsal pelage brown to soft reddish-brown; hairs grey on basal half, brown on terminal half. Ventral pelage greyish-brown; hairs grey at base, pale brown to greyish-brown or white at tip. Ears dark, anterior part partly concealed by hairs. Fore- and hindfeet brown or greyish-brown. Tail relatively long (ca. 79% of HB), bicoloured, brown above, pale or whitish below; pilosity 33–50%. Skull flattish rising slightly at posterior end. Upper incisor small and hooked. First unicuspid large and slightly pointed; second and third unicuspid subequal in size; all three with weakly developed cingulum. Third upper molar medium-sized. Nipples: not known.

Geographic Variation None recorded.

Distribution Endemic to Africa. Afromontane–Afroalpine BZ. Recorded only on Mt Cameroon, Cameroon (1850–3000 m).

Habitat At higher altitudes (Pic Isabel, ca. 3000 m), lives in alpine grasslands. Habitat at lower altitudes (e.g. Refugium, 2000 m) is 'Schefflera montane forest' (1400–2600 m).

Abundance Uncertain; at 3000 m, Heim de Balsac (1959a) found six specimens of this species, and one specimen of *Sylvisorex morio*.

Remarks Two pregnant ♀♀ at 3000 m in Apr; one contained two embryos (Heim de Balsac 1959a) and the other contained three embryos (labels ZFMK).

Measurements

Crocidura douceti

HB: 50–55 mm, $n = 5$

T: 40–45 mm, $n = 5$

HF: 10 mm, $n = 5$

E: 8 mm, $n = 5$

WT: 4–5 g, $n = 5$

CI: 16.4–17.3 mm, $n = 5$

GWS: 7.0–7.5 mm, $n = 5$

I¹–M³: 6.8–7.5 mm, $n = 5$

Nigeria (Hutterer & Happold 1983; mean values not recorded)

Key References Churchfield *et al.* 2004; Happold 1987; Hutterer & Happold 1983.

Rainer Hutterer & D. C. D. Happold

Conservation IUCN Category: Vulnerable.

Measurements

Crocidura eisentrauti

HB: 72.3 (68–78) mm, $n = 9$

T: 57.2 (53–62) mm, $n = 9$

HF: 12.7 (11–14) mm, $n = 9$

E: 8.7 (6–10) mm, $n = 9$



Crocidura eisentrauti

WT: 9.1 (8–11) g, n = 8
 CI: 19.7 (19.5–20.4) mm, n = 6
 GWS: 8.6 (8.4–9.0) mm, n = 6
 I¹–M³: 8.3 (7.9–8.8) mm, n = 6
 Mt Cameroon, Cameroon (ZFMK)

Key Reference Eisentraut 1963.

Rainer Hutterer

Crocidura elgonius ELGON SHREW

Fr. Crocidure du Mont Elgon; Ger. Elgon-Spitzmaus

Crocidura elgonius Osgood, 1910. Ann. Mag. Nat. Hist., ser. 8, 5: 369. Kirui, Mt Elgon, Kenya.

Taxonomy Originally described as a subspecies of *C. bicolor* (now *C. fuscomurina*) but regarded as a separate species by Heim de Balsac & Meester (1977) and Hutterer (1983b, 1993). Synonyms: none. Chromosome number: not known.

Description Small brown shrew with short hairs. Dorsal hairs ca. 2 mm; ventral hairs ca. 1.5 mm. Dorsal pelage brown; hairs brown along entire length. Ventral pelage dirty white speckled with grey; hairs dirty white, grey at base. Colour of dorsal pelage clearly delineated from ventral pelage. Ears prominent and devoid of long hairs. Forefeet pale relative to dorsal pelage. Hindfeet dark brown on the distal two toes and edge of foot; yellowish on the inside. Tail of medium relative length (ca. 55% of HB), bicoloured, dark above, pale below; pilosity ca. 66%. Nipples: not known.

Geographic Variation None recorded.

Distribution Endemic to Africa. Afromontane–Afroalpine BZ of eastern Africa. Recorded from Kenya (Cherangani Hills, Eldoret, Kisumu, L. Nakuru, Mt Elgon [holotype], Muguga, Nairobi) and Tanzania (East and West Usambara, Uluguru and Udzungwa

Mountains) (Aggundey & Schlitter 1986 [and references therein], Stanley *et al.* 1998, Swynnerton & Hayman 1951).

Habitat Disturbed habitats near montane forest and in other habitats in highlands. In the Udzungwa Mts, common in dry forests at 600 m and absent in wetter forests above 1000 m. Recorded in rotting vegetation at the edge of a swamp (Allen & Loveridge 1942).

Abundance The most numerous shrew in drier forests of the Udzungwa Mts (70% of the shrews observed; n = 23). In the East Usambara Mts, the most common shrew in tea plantations, but absent from samples taken in nearby fragments of montane forests (W.T. Stanley unpubl.).

Remarks Terrestrial and nocturnal. In a sample from forests of the Udzungwa Mts in Aug (1995), ♂ : ♀ ratio was 11 : 5, and age ratio was 1 juvenile : 4 adults (n = 10). Similar ratios were found in samples from the East and West Usambara Mts collected between Jul and Sep (between 1991 and 1993): ♂ : ♀ ratio was 3 : 1 (n = 20), and age ratio was 1 juvenile : 3 adults (n = 16) (W. T. Stanley unpubl.). Remains found in owl pellets collected at Nairobi and L. Nakuru, Kenya (Hutterer 1983b).

Conservation IUCN Category: Least Concern.

May be 'Vulnerable' because of fragmented distribution and decline in suitable habitat.

Measurements

Crocidura elgonius

HB: 62 (55–68) mm, n = 16

T: 36 (33–40) mm, n = 16

HF: 10 (9–11) mm, n = 16

E: 7 (7–8) mm, n = 16

WT: 3.4 (2–4.6) g, n = 16

CI: 16.5 (15.5–17.1) mm, n = 10

GWS: 7.2 (6.1–7.6) mm, n = 10

I¹–M³: 7.0 (6.6–7.3) mm, n = 10

Udzungwa Mts, Tanzania (W. T. Stanley unpubl.)

Key Reference Hutterer 1983b.

William T. Stanley



Crocidura elgonius

Crocidura erica HEATHER SHREW (ANGOLAN WHITE-TOOTHED SHREW)

Fr. Crocidure d'Angola occidental; Ger. Angola-Spitzmaus

Crocidura erica Dollman, 1915. Ann. Mag. Nat. Hist. ser. 8, 15: 514; ser. 8, 16: 145. Pungo Andongo, Angola.

Taxonomy Relationship to *C. nigricans* uncertain (Crawford-Cabral 1987) but listed as a distinct species (Hutterer 1993, 2005b). Resembles *C. hirta* in cranial dimensions. Synonyms: none. Chromosome number: not known.

Description Large pale-coloured shrew. Dorsal pelage pale grey faintly washed with brown. Flanks greyer, gradually merging with dull grey ventral pelage. Dorsal surface of feet greyish-white. Tail of medium relative length (56% of HB), finely haired, brown above, greyish-white below; pilosity 45%. Skull: second unicuspid larger than third; third upper molar medium in size; talonid of third lower molar reduced to a single cusp. Nipples: not known.

Geographic Variation None recorded.

Distribution Endemic to Africa. Zambezan Woodland BZ. Recorded only from W Angola (Heim de Balsac & Meester 1971, Hutterer 1993, 2005b).

Habitat No information. The holotype was found at 1098 m.

Abundance No information.

Remarks Apparently no other information available.

Conservation IUCN Category: Data Deficient.

Major threats are human-induced habitat loss and degradation, and restricted distribution.

Measurements

Crocidura erica

HB: 96 mm, n = 1

T: 54 mm, n = 1

HF: 15 mm, n = 1



Crocidura erica

E: 8 mm, n = 1

WT: n. d.

CI: 22.4, 23.3 mm, n = 2

GWS: 9.7, 10.2 mm, n = 2

I¹–M³: 10.2, 10.3 mm, n = 2

Pungo Andongo, Angola (Dollman 1915d)

Key References Crawford-Cabral 1987; Wolsan & Hutterer 1998.

P. D. Jenkins & S. Churchfield

Crocidura fischeri FISCHER'S SHREW

Fr. Crocidure de Fischer; Ger. Fischers Spitzmaus

Crocidura fischeri Pagenstecher, 1885. Jahrb. Wiss. Anst., Hamburg 2: 34, pl. 1, f. 1–3. Nguruman, Kenya.

Taxonomy Most of the records for this species listed by Heim de Balsac & Meester (1977) are not this species (Hutterer 1986a). Synonyms: none. Chromosome number: not known.

Description Medium-sized shrew. Dorsal pelage bluish-grey with brownish tinge. Ventral pelage white; hairs grey on basal half, white on terminal half. Upper lips, throat, and behind ears white; fore- and hindfeet white; all hairs grey on basal half, white on terminal half. Tail of medium relative length (ca. 59% of HB in ♀♀; 53% of HB in ♂♂), pale pink (skin) thick at base, tapering towards

tip, pilosity 100%. Skull: upper first incisor long and hooked. First upper unicuspid very large, double the size of second and third unicuspids. Third upper molar small. Nipples: not known.

Geographic Variation None recorded.

Distribution Endemic to Africa. Somalia–Masai Bushland BZ. Only known from Nguruman in S Kenya (north of L. Natron) and Himo, N Tanzania.

*Crocidura fischeri*

Habitat Grasslands of *Acacia* savanna woodland where widely scattered *Acacia tortilis* are the dominant species of tree, and *Themeda*, *Hyparrhenia* and *Cenchrus* are the common grasses. Due to heavy grazing by livestock, the area becomes denuded during the dry season and when daytime temperatures may reach 40 °C.

Abundance Locally abundant forming 78% of shrew captures at Nguruman.

Remarks Terrestrial and nocturnal. In Jun (1998), seven individuals were captured; of the four ♀♀, three had a perforate vagina suggesting they were in reproductive condition. The three ♂♂ were not in reproductive condition.

Conservation IUCN Category: Data Deficient.

More information is required before a valid assessment can be given.

Measurements

Crocidura fischeri

HB (♂♂): 89 (82–97) mm, n = 3

HB (♀♀): 82 (65–92) mm, n = 4

T (♂♂): 47 (41–57) mm, n = 3

T (♀♀): 49 (42–57) mm, n = 4

HF (♂♂): 13.3 (13.2–13.5) mm, n = 3

HF (♀♀): 12.7 (12–13) mm, n = 4

E (♂♂): 9 (7.5–10.5) mm, n = 3

E (♀♀): 10.3 (9.4–11.7) mm, n = 4

WT (♂♂): 14.8 (14.5–15) g, n = 3

WT (♀♀): 13.1 (11–15) g, n = 4

CI: 26.0*, 27.4** mm n = 2

GWS: 11.5 mm, n = 1**

I¹–M³: 11.4 mm, n = 1**

Body measurements and weight: Nguruman, SE Kenya (N. O. Oguge unpubl.)

*Holotype – Nguruman, SE Kenya (see Hutterer 1986a)

**Tanzania (Hutterer 1986a)

Key Reference Hutterer 1986a.

N. Oguge

Crocidura flavescens GREATER RED SHREW (GREATER RED MUSK SHREW)

Fr. Crocidure grande; Ger. Afrikanische Riesenspitzmaus

Crocidura flavescens (I. Geoffroy, 1827). Dict. Class. Hist. Nat. 11: 324; Mem. Mus. Hist. Nat. Paris 15: 126.

‘La Cafrérie et le pays de Hottentots’ (= King William’s Town, South Africa).

Taxonomy Originally described in the genus *Sorex*. The name *flavescens* previously used for forms now considered as species or synonyms of other species, especially *C. oliveri*, e.g. *atlantis*, *bueae*, *darfurea*, *hedenborgiana*, *hera*, *manni*, *martiensseni*, *occidentalis*, *spurelli*, *sururæ*, *zuleika*. The name *flavescens* is now restricted to giant shrews from southern Africa. Synonyms: *capensis*, *cinnamomeus*, *knysnae*, *rutilus*. Subspecies: none. Chromosome number: 2n = 50 (South Africa; Maddalena *et al.* 1987).

Description Very large brown shrew. Dorsal pelage fawn to cinnamon-brown; hairs slaty-grey at base, pale subterminal band and brown tip. Ventral pelage pale grey or yellowish-grey; hairs dark grey at base, off-white to pale yellow at tip; ventral colour merges fairly abruptly with dorsal colour on flanks. Head slender with long, narrow pointed muzzle, small eyes and rounded ears. Fore- and hindfeet fawn with five digits. Tail of medium relative length (ca. 49% of HB), brown above, pale grey below; covered with sparse long hairs; pilosity ca. 65–80%. Nipples: 0 + 3 = 6.

Geographic Variation None recorded.

Distribution Endemic to Africa. Occurs in several biotic zones close to the coast of South Africa, and parts of the Highveld BZ. In South Africa, recorded along the escarpment of E Mpumalanga Province, the coastal regions of Western Cape and Eastern Cape Provinces, and throughout most of KwaZulu–Natal. Also recorded in E Lesotho, Swaziland and the Inhambane district of S Mozambique (Meester 1963, Meester *et al.* 1986, Monadjem 1998a, c, Taylor, P. 1998).

Habitat Usually occurs close to water where there is adequate ground cover. Trapped in a variety of vegetation types including fynbos, grasslands (montane, temperate and sub-tropical), coastal forest, woodlands, savanna and disturbed habitats in higher rainfall regions of South Africa. Commensal with humans and enters dwellings. Wide habitat tolerance.



Crocidura flavescens

Abundance Relatively common especially in sub-tropical habitats of its range. Very abundant in gardens in Pietermaritzburg, South Africa.

Adaptations Predominantly nocturnal with greatest peak of activity at dawn and a secondary peak at dusk (Baxter *et al.* 1979). Enters spontaneous torpor (Baxter 1996) during adverse environmental conditions, but exhibits no other special physiological adaptations (Brown *et al.* 1997). Very high levels of aggression (Baxter & Irwin 1995) assist it in killing vertebrate prey larger than itself.

Foraging and Food Feeds opportunistically on invertebrates and vertebrates; cannibalistic and also a scavenger. Diet includes insects, snails, earthworms, reptiles and rodents (Baxter 1977).

Social and Reproductive Behaviour Aggressive and territorial with probable overlap of male and female territories (Baxter & Irwin 1995). Territories are probably demarcated through scent-marking using lateral, chin and ano-genital glands and strongly scented faecal piles (Baxter & Meester 1982).

Vocalization includes (a) a loud, strident squeak when alarmed, (b) squeaks interspersed with 'chirrs' or chattering sounds during aggressive encounters, (c) chattering in female-young interactions and (d) soft, repetitive squeaks when foraging (Baxter & Meester 1982). Although vocalization has ultrasonic properties (up to 50 kHz), it is not used for echolocation (Irwin & Baxter 1980). Grooming behaviour includes scratching with the hindfeet, face-washing and occasionally licking of the pelage. Stretching and yawning have also been observed. Licking of the everted rectum and coprophagy are common behaviours (Baxter & Meester 1982).

Mating behaviour includes 'flehmen' when the ♂ sniffs the ano-genital region of the female (Baxter 1981), and chases last for up to 35 minutes. During the chasing, the ♀ occasionally pauses and the ♂ attempts to mount. Eventually the ♂ bites the rump of the ♀ and

she stops. Successful intromission lasts for seven seconds with the male biting strongly on her mid-back. After ejaculation, this grip is released and the ♀ moves off, dragging the male by his penis for a short period. After disengagement, the ♀ is usually aggressive towards the ♂ (Baxter & Meester 1982). Nests are spherical or saucer-shaped, often placed in rock crevices or under cover. Lactating ♀♀ show no aggression to strange young and will foster them (Baxter 1993a).

Reproduction and Population Structure Pregnancies occur during late dry season and wet season (Aug–Apr), but mostly in Oct–Dec. Gestation: ca. 28 days. Mean litter-size: 3.65 ($n = 51$), commonly 4. At birth: HB: 36.3 mm, T: 11.1 mm, HF: 6.2 mm, E: 2.5 mm, weight 1.8 g ($n = 186$). Young born naked, blind and helpless but development is rapid. Weaning at Day 18–22; by Day 28 young are adult size in all measurements except weight. Walking begins ca. Day 5, when caravanning first observed. Eyes and ears open ca. Day 12. Full pelage present ca. Day 14. Caravanning ceases ca. Day 16. Young leave nest ca. Day 28 (R. M. Baxter unpubl.). Young displaced from nest emit a high-pitched squeak after which they are retrieved by the female and carried in her mouth back to the nest. Females have a postpartum oestrus and litters can be conceived consecutively. Maturity usually attained by Day 90, but might occur as early as Day 28. Longevity 14–18 months in the wild but can be 2.5 years in captivity (R. M. Baxter unpubl.).

Predators, Parasites and Diseases Known predators include Banded Mongooses *Mungos mungo* (Baxter 1993b), Water Mongooses *Atilax paludinosus*, Zorillas *Ictonyx striatus*, Striped Weasels *Poecilogale albinucha* and two species of owl. Domestic cats capture but seldom consume these shrews (Baxter 1977).

Conservation IUCN Category: Least Concern.

A common shrew in urban gardens over much of its range.

Measurements

Crocidura flavescens

HB (♂♂): 99.3 (81–112) mm, $n = 70$

HB (♀♀): 100.3 (83–117) mm, $n = 50$

T (♂♂): 48.8 (41–59) mm, $n = 69$

T (♀♀): 48.6 (36–58) mm, $n = 50$

HF (♂♂): 14.8 (13–16) mm, $n = 70$

HF (♀♀): 14.8 (13–16) mm, $n = 50$

E (♂♂): 10.3 (9–11) mm, $n = 70$

E (♀♀): 10.2 (9–11) mm, $n = 50$

WT (♂♂): 30 (20–40) g, $n = 10$

WT (♀♀): 25.2 (20–38) g, $n = 17$

CI (♂♂): 26.6 (24.7–28.6) mm, $n = 64$

CI (♀♀): 26.2 (24.5–28.3) mm, $n = 49$

GWS (♂♂): 10.8 (10.2–11.4) mm, $n = 56$

GWS (♀♀): 10.7 (10.0–11.4) mm, $n = 43$

I¹–M³ (♂♂): 11.9 (10.9–12.7) mm, $n = 85$

I¹–M³ (♀♀): 11.7 (10.7–12.7) mm, $n = 62$

Measurements: South Africa (Meester 1963, Taylor 1998 [weight]).

Key References Baxter 1977; Baxter & Irwin 1995; Baxter & Meester 1982; Baxter *et al.* 1979.

R. M. Baxter & N. J. Dippenaar

Crocidura floweri FLOWER'S SHREW

Fr. Crocidure de Flower; Ger. Flowers Spitzmaus

Crocidura floweri Dollman, 1915. Ann. Mag. Nat. Hist. ser. 8, 15: 515; 1916 Ann. Mag. Nat. Hist., ser. 8, 17: 192. Giza, Egypt.

Taxonomy Hutterer & Harrison (1988) suggested that this species may be related to *C. arabica* (a non-African species) and *C. crossei*. Synonyms: none. Chromosome number: not known.

Description Small shrew. Dorsal pelage pale cinnamon-brown. Ventral pelage paler to whitish; hairs grey at base, white at tip. Abrupt delineation laterally of dorsal and ventral colours. Feet dirty white. Tail relatively long to very long (75–100% of HB), cinnamon-brown above, whitish below; bristle hairs bicoloured; pilosity 50%. Skull: second and third unicuspid subequal; third upper molar moderately broad; talonid basin present on third lower molar. Molars with a metaloph and metaconule (Heim de Balsac & Mein 1971). Nipples: not known.

Geographic Variation None recorded.

Distribution Endemic to Africa. Sahara Arid BZ. Recorded from Nile Delta and El Faiyum (Osborn & Helmy 1980), and Wadi el Natrun, Egypt (Goodman 1989). Unconfirmed record in S Sudan (Wolsan & Hutterer 1998). Also identified in ancient mummified remains at Thebes in S Egypt (Heim de Balsac & Mein 1971).

Habitat Unknown except that specimens have been collected in fields.

Abundance No information.

Remarks Little information available. One specimen was obtained from the stomach of a cattle egret (Flower 1932, in Osborn & Helmy 1980) and another from regurgitated pellets of a Little Owl *Athene noctua* at Wadi el Natrun.

Conservation IUCN Category: Data Deficient.

Major threats are human-induced habitat loss and degradation, and restricted distribution.

Measurements*Crocidura floweri**Crocidura floweri*

HB: 57–71 mm*

T: 55–58 mm*

HF: 12–13.5 mm*

E: 8 mm*

WT: n. d.

CI: 18.4 (18.0–19.2) mm, n = 4

GWS: 7.8 (7.6–8.2) mm, n = 4

I¹–M³: 7.5 (7.3–7.7) mm, n = 4

Giza, Egypt (BMNH, Osborn & Helmy 1980)

*Flower 1932 (no means or sample sizes recorded)

Key Reference Osborn & Helmy 1980.

P. D. Jenkins & S. Churchfield

Crocidura foxi FOX'S SHREW

Fr. Crocidure de Fox; Ger. Foxs Moschusspitzmaus

Crocidura foxi Dollman, 1915. Ann. Mag. Nat. Hist., ser. 8., 15: 514. Panyam, Nigeria.

Taxonomy Considered as a member of the *poensis* group, and probably closely related to *C. theresae* (see Hutterer & Happold 1983, Hutterer 2005b). A series from Owerri, S Nigeria, referred to *C. foxi* by Hutterer & Happold (1983) now considered to represent a dark form of *C. lamottei*. Synonyms: *tephra*. Subspecies: none. Chromosome number: not known.

Description Large to very large shrew. Dorsal pelage chocolate-brown to russet-brown; hairs grey at base with brown tip. Ventral pelage grey; hairs grey, sometimes white at tip. Colour of ventral pelage well delineated from colour of dorsal pelage. Flanks, chest and throat grey. Tail relatively short (50–63% of HB), pale, coarsely haired; pilosity ca. 20–35%. Skull: braincase flat (more so than in

C. poensis and *C. nigeriae*). First upper incisor long and hooked. First unicuspid larger than second or third unicuspid. Third molar small. Nipples: not known.

Geographic Variation Specimens from Senegal are darker than those from elsewhere.

Distribution Endemic to Africa. Sudan Savanna BZ. Recorded from Jos Plateau, Nigeria (type series), and from Senegal to S Sudan (Hutterer 2005b).

Habitat In Nigeria, found in long grass, secondary bush, near to farmlands, and in rocky grasslands recently burned (Hutterer & Happold 1983). In Senegal, found in cultivated irrigated areas between series of dunes, and in swampy zones with grasses; coexists with *Dasymys rufulus* and *Mastomys huberti* (Niayes region, north of Dakar; J.-M. Duplantier unpubl.).

Abundance Locally abundant in Nigeria (Hutterer & Happold 1983).

Remarks Embryo number: 2 (n = 1: Nigeria; Happold 1987). Embryo number: 3.25 (range 2–4, n = 4; Senegal; J.-M. Duplantier unpubl.).

Predators, Parasites and Diseases Found in pellets of Barn Owls *Tyto alba* in Senegal (J.-M. Duplantier unpubl.).

Conservation IUCN Category: Least Concern.

Measurements

Crocidura foxi

HB: 103.5 (91–114) mm, n = 30

T: 60.7 (53–72) mm, n = 27



Crocidura foxi

HF: 16.9 (15.5–18.5) mm, n = 30

E: 10.0 (8–11) mm, n = 30

WT: 16.8 (13–22) g, n = 30

CI: 24.5 (23.5–25.8) mm, n = 25

GWS: 10.5 (8.8–11.2) mm, n = 24

I¹–M³: 10.6 (9.9–11.3) mm, n = 25

Niayes, Senegal (J.-M. Duplantier & L. Granjon unpubl., MNHN)

Key References Hutterer 2005b; Hutterer & Happold 1983.

J.-M. Duplantier & L. Granjon

Crocidura fulvastra SAVANNA SHREW

Fr. Crocidure de savane; Ger. Savannen-Spitzmaus

Crocidura fulvastra (Sundevall, 1843). K. Svenska Vetensk-Akad. Handl. Stockholm, 1842: 172 (publ. 1843). Bahr el Abiad, Sudan.

Taxonomy Originally described as *Sorex fulvaster*. Synonyms: *arethusa*, *beta*, *diana*, *fulvaster*, *macrodon*, *marrensis*, *sericeus*, *strauchii* (see Hutterer 1983c, 2005b, Hutterer & Happold 1983, Hutterer & Kock 1983). Subspecies: none. Chromosome number: not known.

Description Very large shrew. Dorsal pelage pale brown to cinnamon; hairs bluish-grey tipped with cinnamon. Ventral pelage and flanks whitish-grey clearly delineated from dorsal pelage; hairs grey with white tips. Tail of medium relative length (ca. 60% of HB), thin, brownish; pilosity 80–85%. Skull long and narrow in general shape, with long rostrum, narrow interorbital constriction. Braincase oval. Zygomatic process of maxilla angular. First upper incisor long and sharp, passing straight downwards. Upper premolars and molars narrow compared with *C. viaria*, *C. lamottei* and *C. butleri*. Shows considerable sexual dimorphism (Hutterer & Happold 1983). Nipples: not known.

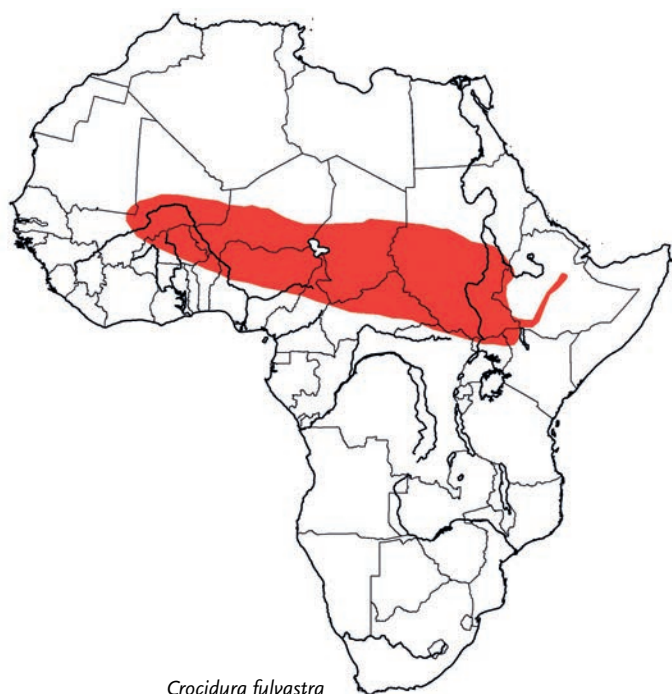
Geographic Variation None recorded.

Distribution Endemic to Africa. Sudan and Sahel Savanna BZs as well as parts of Guinea Savanna BZ in Sudan, and the Rift Valley of Ethiopia. Locality records very disjunct. Recorded from Mali, N Nigeria, S and C Sudan, Ethiopia and N Kenya. May occur in Mauritania and Senegal. One mummified specimen recorded from ancient Egypt (Hutterer 1983c).

Habitat Drier savanna habitats but likely also to inhabit a variety of mesic habitats.

Abundance Occurs quite frequently in savanna habitats in Nigeria (Hutterer & Happold 1983).

Remarks Comprised 0.3% of all shrews found in pellets of the



Spotted Eagle-owl *Bubo africanus* in Awash N. P., Ethiopia (Demeter 1982). Remains have also been found in owl pellets in Nigeria (Hutterer & Jenkins 1980, Demeter 1981). Other likely predators include small carnivores such as mongooses, genets and small cats known to feed on shrews.

Conservation IUCN Category: Least Concern.

Not uncommon and hence of no immediate conservation concern.

Measurements

Crocidura fulvastra

HB (♂♂): 99–120 mm, n = 4

HB (♀♀): 86–94 mm, n = 5

T (♂♂): 57–64 mm, n = 4

T (♀♀): 49–55 mm, n = 5

HF (♂♂): 14–17 mm, n = 4

HF (♀♀): 14–15 mm, n = 5

E (♂♂): 12–13 mm, n = 4

E (♀♀): 10–11 mm, n = 5

WT (♂♂): 16–29 g, n = 4

WT (♀♀): 10–18 g, n = 5

CI (♂♂): 23.6–25.7 mm, n = 4

CI (♀♀): 21.1–22.7 mm, n = 5

GWS (♂♂): 10.0–10.6 mm, n = 4

GWS (♀♀): 9.1–9.7 mm, n = 5

I¹–M³ (♂♂): 10.0–10.8 mm, n = 4

I¹–M³ (♀♀): 8.9–10.0 mm, n = 5

Nigeria (Hutterer & Happold 1983; mean values not recorded)

Key References Hutterer 2005b; Hutterer & Happold 1983; Hutterer & Jenkins 1980.

S. Churchfield & P. D. Jenkins

Crocidura fumosa SMOKY MOUNTAIN SHREW (SMOKY WHITE-TOOTHED SHREW)

Fr. Crocidure du Mont Kenya; Ger. Smoky Mountain Spitzmaus

Crocidura fumosa Thomas, 1904. Ann. Mag. Nat. Hist., ser. 7, 14: 238. Western slope of Mt Kenya. 2600 m.

Taxonomy Revised by Dippenaar & Meester (1989). Similar to *C. montis*. Synonyms: *alchemillae*. Subspecies: none. Chromosome number: not known.

Description Medium-sized shrew. Dorsal pelage dark grey-brown, slightly paler ventrally. Feet pale greyish- to yellowish-brown. Tail medium-long (50–80% of HB), greyish to reddish-brown above, paler below; pilosity 50–90%. Skull with wide interorbital region and broad high-domed braincase. Third unicuspid usually larger than second. Third upper molar moderately broad; talonid of lower third molar with entoconid and talonid basin. Nipples: not known.

Geographic Variation None recorded.

Distribution Endemic to Africa. Afromontane–Afroalpine BZ. The revision by Dippenaar & Meester (1989) restricts this species to the Aberdare Range and Mt Kenya, Kenya. Also recorded from the Cherangani Hills, Kenya. Previously reported to occur widely in Kenya, Tanzania and Uganda.

Habitat Montane forest. A specimen from Mt Kenya was obtained



in a *Carex-Lobelia keniensis* bog at 12,500 ft (3800 m) (Coe & Foster 1972).

Remarks Apparently no other information available.

Conservation IUCN Category: Vulnerable.

Major threats are human-induced habitat loss and degradation, and restricted distribution.

Measurements

Crocidura fumosa

HB: 80 (65–92) mm, n = 115

T: 52 (39–63) mm, n = 114

HF: 16 (10–18) mm, n = 112

E: 9 (5–11) mm, n = 31

WT: n. d.

CI: 20.9 (19.3–21.9) mm, n = 66

GWS: 9.8 (9.2–10.5) mm, n = 65

I¹–M³: 9.0 (8.1–9.6) mm, n = 103

Aberdare Range and Mt Kenya, Kenya (Dippenaar & Meester 1989)

Key Reference Dippenaar & Meester 1989.

P. D. Jenkins & S. Churchfield

Crocidura fuscumurina BICOLOURED SHREW (BICOLOURED MUSK SHREW, TINY MUSK SHREW)

Fr. Crocidure petite; Ger. Zweifarben-Spitzmaus

Crocidura fuscumurina (Heuglin, 1865). Leopoldina 5. In: Nouv. Acta Acad. Caes. Leop.-Carol. 32: 36.

Meshra-el-Req (08° 25' N, 29° 16' E), Bahr-el-hazal, Sudan.

Taxonomy Originally described as *Sorex fusco murinus*. Polytypic with several described forms. The taxonomic status of the lowveld populations in Limpopo and Mpumalanga Provinces, South Africa, requires re-examination as there is some evidence that a second species might be involved. Known as *C. bicolor* for some 50 years, but now referred to by the previously described older name of *C. fuscumurina* (Hutterer 1983b). Synonyms: *bicolor*, *bovei*, *cunninghami*, *fuscumurinus*, *?glebula*, *hendersoni*, *marita*, *sansibarica*, *tephragaster*, *tephronotus*, *woosnami*. Subspecies: none. Chromosome number: 2n = 56 (Burundi; Maddalena & Ruedi 1994).

Description Very small, predominantly grey-brown shrew grizzled with grey. Dorsal pelage grey-brown; hairs slaty-grey at base with a fawn subterminal band and brown or buffy-brown tip. Ventral pelage silvery-grey, sometimes with a yellow tinge; hairs slate-grey at base, white or off-white at tip. Dorsal and ventral colours sharply delineated. Fore- and hindfeet pale brown to off-white. Tail relatively long (ca. 65% of HB), pale to dark brown above, paler below; colours sharply demarcated; pilosity at least 75%. Western forms are paler and larger. Nipples: not known.

Geographic Variation Several forms have been described as subspecies (now listed above as synonyms). Following Heim de Balsac & Meester (1977), as *C. bicolor*, these are:

bicolor: Angola, S Zambia, S Malawi; Zimbabwe, Mozambique, Swaziland, South Africa (areas with rainfall exceeding 500 mm).

cunninghami: E Uganda, Kenya.

fuscumurina: Sudan (Bahr-el-Ghazal; holotype).

hendersoni: NE Zambia, N Malawi, Tanzania.

marita: Sudan (Jebel Marra, Darfur).

tephragaster: Sudan (Torit, Equatoria).

woosnami: N Namibia, Botswana, South Africa (Northern Cape Province).

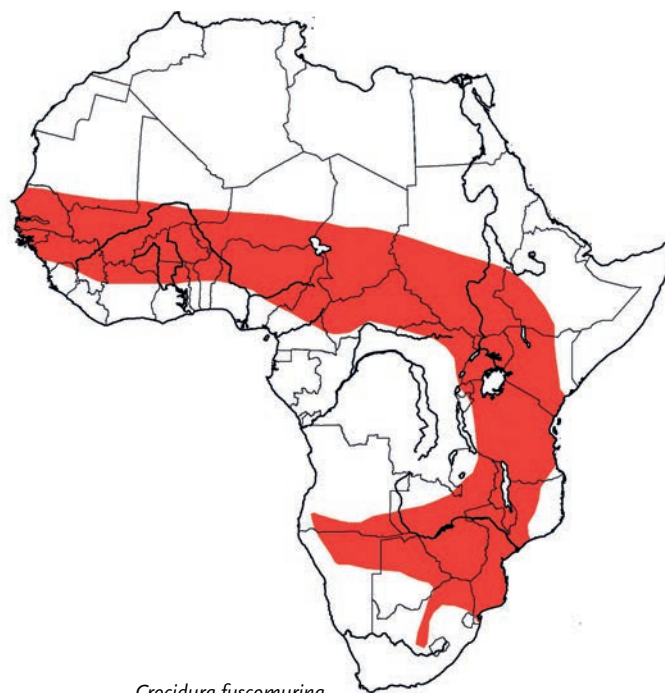
Distribution Endemic to Africa. Widely distributed in parts of Sahel, Sudan, Guinea, Somalia–Masai and Zambezan Woodland

BZs. Recorded from many countries in West, East, east-central and southern Africa.

Habitat Woodland savannas and semi-arid regions. Recorded from grasslands, woodlands, Kalahari sand and riverine scrub habitats. Found in termite mounds, fallen logs and marshy areas. May enter domestic dwellings (Meester 1963, Smithers 1971, Lynch 1983, Monadjem 1998a, c).

Abundance Widespread but rarely collected.

Adaptations Nocturnal and terrestrial. Appears to have wide habitat tolerance and can live in mesic and moderately arid habitats.



Crocidura fuscumurina

Foraging and Food Insectivorous. Prefers moths but also eats grasshoppers, praying mantids, dragonflies and crickets in captivity (Dippenaar 1979a).

Social and Reproductive Behaviour Presumably solitary.

Reproduction and Population Structure In southern Africa, reproductive activity occurs during the wet season (Nov–Apr). Mean litter-size: 3.4 (range 2–5, $n = 8$). Weight at birth: 0.25 g to ca. 1 g. Young are born virtually hairless but after a week are fully furred. Behavioural development is rapid during the second week with the emergence of traits such as face-wiping, sniffing, scratching, yawning, jumping and the ability to climb vertically. Eyes open Day 12. Active exploration is evident from Day 17; solid food first taken Day 14–19. Initially the ♀ carries young in her mouth but this ceases when caravanning commences around Day 6. Caravanning ends just before weaning. In one litter from the Kruger National Park, caravanning was replaced by ‘back riding’, possibly an aberrant form of caravanning (Watson & Watson 1986) (see also Ansell 1964, Dippenaar 1979a).

Predators, Parasites and Diseases Remains have been found in owl pellets (Meester 1963).

Conservation IUCN Category: Least Concern.

Although uncommon, unlikely to be at risk to because of extensive geographic range and secretive habits.

Measurements

Crocidura fuscumurina

(as *C. bicolor bicolor*)

HB: 57.9 (48–75) mm, $n = 11$

T: 38.5 (27.5–48) mm, $n = 11$

HF: 9.8 (8–11) mm, $n = 11$

E: 7.6 (6.5–9) mm, $n = 10$

WT: 3.7 (2–5) g, $n = 11$

CI: 16.2 (15.1–17.4), $n = 10$

GWS: 7.2 (6.7–7.7), $n = 7$

I^1-M^3 : 6.6 (6.2–7.2), $n = 30$

Measurements: Southern Africa (Meester 1963)

Weight: Transvaal, South Africa (Rautenbach 1982), Swaziland (Monadjem 1998a)

Key References Ansell 1964; Dippenaar 1979a; Meester 1963; Watson & Watson 1986.

N. J. Dippenaar & R. M. Baxter

Crocidura glassi GLASS'S SHREW (ETHIOPIAN MOUNTAIN SHREW)

Fr. *Crocidure de Glass*; Ger. Äthiopien-Gebirgsspitzmaus

Crocidura glassi Heim de Balsac, 1966. Mammalia 30: 448. Gara Mulatta, Harar, Ethiopia (ca. 09° 16' N, 41° 44' E). 2700 m.

Taxonomy Considered as a well-defined species (Dippenaar 1980a, Hutterer 1980). A member of the endemic Ethiopian *C. glassi* complex (*C. glassi*, *C. lucina*, *C. thalia*, *C. macmillani* and *C. baileyi*) (Dippenaar & Meester 1989). Synonyms: none. Chromosome number: $2n = 36$ (Lavrenchenko *et al.* 1997). The level of genetic (allozyme) differentiation among populations from the Bale Mts is very high (Lavrenchenko *et al.* 1997).

Description Small-medium greyish-brown shrew. Dorsal pelage greyish-brown; hairs grey at base, brown at tip. Ventral pelage silvery-grey, hairs grey at the base, pale yellowish at tip. Dorsal surface of fore- and hindfeet pale grey. Tail relatively long (ca. 67% of HB), brown above, whitish to yellowish below; pilosity 80%. Skull with inflated braincase, as typical for the high altitude Ethiopian *Crocidura*. Nipples: not known.

Geographic Variation None recorded.

Distribution Endemic to Africa. Afroalpine–Afroalpine BZ. Recorded only from Ethiopia, where confined to highlands east of the Ethiopian Rift Valley (Bale Mts, Mt Badda and Chercher Highlands), 2700–4050 m.

Habitat Upland grasslands, ericaceous scrub and afroalpine moorland, over a range of altitudes.

Abundance Numerous in suitable habitats. Comprised 18% of 229 small mammals in ericaceous scrub on the Bale Mts; the second most numerous species after *Lophuromys brevicaudus* (51%).



Crocidura glassi

Remarks Presumed to be insectivorous or omnivorous. In the Bale Mts, pregnant ♀♀ were found during the late dry season and the beginning of the wet season (late Mar–May). Embryo number: 3.13 (2–4), $n = 16$ pregnant ♀♀. Sex ratio close to unity. Contributed 15% of 92 small mammals in pellets of the Abyssinian Long-eared Owl *Asio abyssinicus* (Yalden 1973). Not eaten by Simien Wolves *Canis simensis*, presumably because distasteful (Sillero-Zubiri & Gottelli 1995).

Conservation IUCN Category: Vulnerable.

Occurs in a very restricted area, although abundant where found.

Measurements

Crociodura glassi

HB: 75 (65–85) mm, $n = 20$

T: 51.7 (43–58) mm, $n = 21$

HF: 15.9 (14.8–18.0) mm, $n = 20$

E: 10.0 (7.8–11.0) mm, $n = 20$

WT: 11.2 (7–14) g, $n = 19$

CI: 23.3 (22.3–24.2) mm, $n = 21$

GWS: 10.3 (9.7–11.1) mm, $n = 21$

I¹–M³: 10.3 (9.7–10.8) mm, $n = 21$

Ethiopia (L. A. Lavrenchenko & R. Hutterer unpubl.)

Key References Dippenaar 1980a; Hutterer 1980; Lavrenchenko *et al.* 1997.

Leonid A. Lavrenchenko

Crociodura goliath GOLIATH SHREW

Fr. Crociodure géante; Ger. Goliath-Spitzmaus

Crociodura goliath Thomas, 1906. Ann. Mag. Nat. Hist., ser. 7, 17: 177. Efulen, Cameroon.

Taxonomy Often included in *C. flavescens* or *C. olivieri*, but apparently a distinct species that lives in sympatry with *C. olivieri* in the central African rainforests (Hutterer 2005b). Synonyms: *nimbasilvanus*, *guineensis*. Subspecies: none. The names *aequatorialis* and *odorata*, which are currently listed under *olivieri*, may eventually turn out to represent *goliath*, pending the discovery of the holotypes; in that case, the species name needs to be changed. The taxa *guineensis* (preoccupied) and *nimbasilvanus* were provisionally included in *goliath* by Hutterer (2005b) but represent a distinct species endemic to West Africa (not considered in this volume). Chromosome number: $2n = 50$ (Primus *et al.* 2006).

Description Extremely large brownish-red shrew. Pelage long, sparse, slightly coarse and glossy, hairs 8–10 mm, occasionally up to 20 mm. Dorsal pelage dark rufous to chestnut-brown; hairs grey on basal half, rufous on terminal half; some individuals with long thick dark rufous hairs on back from shoulders to rump. White-tipped hairs, if present, give slight frosted appearance to pelage. Ventral pelage greyish-rufous or greyish; hairs grey at base, grey or greyish-rufous at tip. Lateral gland large and usually very obvious. Head similar to dorsal pelage. Chin, throat and chest rufous-brown. Ears relatively small. Fore- and hindlimbs dark rufous-brown; claws whitish. Tail relatively long (ca. 68% of HB), rufous-brown; pilosity 50%. Skull: large and heavily built with long CI length (see Measurements; cf. other large shrews) and robust, semi-squarish molars. In old animals, the dorsal surface of the braincase may be sculptured with inconspicuous irregular bony ripples (as seen in *Scutisorex somereni* to a much greater extent). First incisor long and hooked. Third molar narrow. Nipples: not known.

Geographic Variation Individuals from S Cameroon (Efulen), N DR Congo (Kisangani) and NE Gabon (Minkébé Forest) are larger than those at Mt Doudou, SW Gabon (Goodman & Hutterer 2004). A small coastal form may represent the taxon *odorata*, currently listed under *C. olivieri* (see Taxonomy). Mean values for four adults

at Mt Doudou are: HB: 136.8 (122–150) mm; T: 92.0 (89–96) mm; HF: 21.6 (19–23) mm; E: 14.8 (13–16 mm, WT: 48.1 (38–57) g (cf. Measurements below).

Distribution Endemic to Africa. Rainforest BZ (mainly in West Central Region, Gabon sub-region). Recorded from S Cameroon, Gabon, Equatorial Guinea (Rio Muni), N Congo, SW Central African Republic and DR Congo (north of Congo R.).

Habitat Primary rainforest (Thomas 1906a), marshes and mixed rainforest (Goodman *et al.* 2001); riparian forest and marshy forest (Nicolas *et al.* 2004).



Crociodura goliath

Abundance Varies according to habitat. In Gabon, the following abundances from short-term studies have been recorded: 8% (1 of 12 shrews, 7 spp.; marsh, Minkebe Forest), 57% (4 of 7 shrews, 4 spp.; heterogeneous rainforest, Minkebe Forest), 14% (6 of 44, 9 spp.; 110 m, Mt Doudou) and 17% (4 of 23, 6 spp.; 625 m, Mt Doudou) (Goodman *et al.* 2001; Goodman & Hutterer 2004). In a long-term study at Mt Doudou, *C. goliath* comprised 5% (25 of 503) of shrews captured in several habitats, and was the seventh most abundant species (out of nine spp.) (Nicolas *et al.* 2004).

Remarks Occurs syntopically with another very large shrew (*C. oliveri*) in Minkébé Forest, Gabon. In a study of 16s rRNA sequences, *C. goliath* clustered near *C. oliveri*, *C. flavescens*, *C. viaria* and *C. hirta* (Quéroutil *et al.* 2005). Embryo number: 3 (range not given), *n* = 5 (Mt Doudou, Gabon; Nicolas *et al.* 2004).

Conservation IUCN Category: Least Concern.

Measurements

Crociodura goliath

HB: 165.4 (155–175) mm, *n* = 5*

T: 112.8 (100–132) mm, *n* = 5

HF: 25.4 (23–27) mm, *n* = 5

E: 16.6 (15–17) mm, *n* = 5

WT: 61.2 (51–76) g, *n* = 5

CI: 38.1 (37.1–38.9) mm, *n* = 10**

GWS: 14.6 (13.9–15.4) mm, *n* = 10**

I¹–M³: 17.3 (16.6–17.6) mm, *n* = 10**

Minkébé Forest, NE Gabon (Goodman *et al.* 2001)

*Original data given as TL; HB calculated by authors

**DR Congo (ZFMK)

Key References Goodman & Hutterer 2004; Goodman *et al.* 2001.

Rainer Hutterer & D. C. D. Happold

Crociodura gracilipes SHORT-FOOTED SHREW (PETERS'S MUSK SHREW)

Fr. Crocidure à pieds courts; Ger. Kleinfüßige Spitzmaus

Crociodura gracilipes Peters, 1871. Monatsber. K. Preuss. Akad. Wiss. Berlin 1870: 590 (publ. 1871).

Unidentifiable but generally accepted as Mt Kilimanjaro, Tanzania (Moreau *et al.* 1946).

Taxonomy Known only from the original specimen; possibly conspecific with *C. cyanea* (see Hutterer 1993, 2005b). Synonyms: none. Chromosome number: not known.

Description Small shrew. Dorsal pelage cinnamon-brown. Ventral pelage grey-brown; base of hairs slate-grey. Feet with sparse cinnamon-coloured hairs. Tail relatively long (ca. 80% of HB), thin, brown above, greyish-brown below, with scattered bristle hairs; pilosity not known. Nipples: not known.



Crociodura gracilipes

Geographic Variation None recorded.

Distribution Endemic to Africa. Afromontane–Afroalpine BZ. Distribution uncertain but type locality usually accepted as Mt Kilimanjaro, Tanzania. Reports of *C. gracilipes* occurring more widely in eastern and western Africa cannot be confirmed because many specimens have been wrongly attributed.

Habitat No information.

Abundance Known only from the holotype.

Remarks No information.

Conservation IUCN Category: Data Deficient.

Distribution extremely restricted.

Measurements

Crociodura gracilipes

HB: 65 mm, *n* = 1

T: 52 mm, *n* = 1

HF (c.u.): 13 mm, *n* = 1

E: 6.5 mm, *n* = 1

WT: n. d.

CI: n. d.

GWS: n. d.

I¹–M³: 8.7 mm, *n* = 1

Holotype (Peters 1871)

Key References Hutterer 2005b; Peters 1871.

P. D. Jenkins & S. Churchfield

***Crocidura grandiceps* LARGE-HEADED SHREW**

Fr. Crocidure à grande tête; Ger. Großköpfige Spitzmaus

Crocidura grandiceps Hutterer, 1983. Rev. Suisse Zool. 90: 699. Krokosua Hills, N of Asempanaya (Asampaniye), Sedfwi Wiaso, Ghana.

Taxonomy Genetically allied to the *turba-poensis* complex (Quérrouil *et al.* 2005). Some of the specimens reported as *C. poensis* (Happold 1977) belong to this species. Synonyms: none. Chromosome number: $2n = 46$, $FN = 68$ (Schlitter *et al.* 1999).

Description Very large brown shrew, similar to (and difficult to distinguish from) *C. nigeriae*. Dorsal pelage clove-brown. Ventral pelage similar to dorsal pelage, but paler. Fore- and hindfeet dark brown. Tail medium-long (ca. 55–65% of HB), slightly bicoloured, brown above, paler below; pilosity not known. Skull large (when compared with species of similar size, e.g. *C. longipes*, *C. nigeriae*); slightly domed. Upper incisor long, almost straight. First unicuspid pointed, larger than second and third unicuspid; second and third unicuspid equal; all three with cingulum. Third upper molar medium to large. Nipples: not known.

Geographic Variation None recorded.

Distribution Endemic to Africa. Rainforest BZ (Western Region and parts of West Central Region). Recorded from Guinea, Côte d'Ivoire, Ghana, W Nigeria, and possibly Cameroon (not mapped).

Habitat Primary and degraded rainforest.

Abundance Uncertain because of problems with identification. Probably an uncommon species. The following percentages (of shrews captured) were obtained in Taï N. P. (Côte d'Ivoire): 0.5% ($n = 390$, 9 spp.) in forest and 2.1% ($n = 140$) in cocoa-coffee plantations (Barrière *et al.* 1999). In Ziam Biosphere Reserve (Guinea), percentage abundances were 1.6% ($n = 509$, 10 spp.) in secondary forest, 1.6% ($n = 484$, 9 spp.) in old fallow land, 1.2% ($n = 303$, 10 spp.) in young forest plantations and 0.8% ($n = 500$, 11 spp.) in primary forest. This species was not captured in fields ($n = 272$, 9 spp.) nor in old forest plantations (441 shrews, 9 spp.) (P. Barrière, unpubl.).

Remarks Probably similar to *C. nigeriae* and *C. poensis*. See Happold (1987) and Hutterer & Happold (1983) for further details.

*Crocidura grandiceps*

Conservation IUCN Category: Near Threatened.

Measurements*Crocidura grandiceps*HB: 117 (98–119) mm, $n = 19$ T: 65 (55–74) mm, $n = 19$ HF: 18.1 (17–19) mm, $n = 19$ E: 11 (10–12) mm, $n = 18$ WT: 23.5 (19–27) g, $n = 18$ CI: 26.1 (25.4–27.4) mm, $n = 15$ GWS: 10.9 (10.6–11.7) mm, $n = 12$ I^1-M^3 : 11.4 (10.6–11.7) mm, $n = 17$

Nigeria (Hutterer 1983a, Hutterer & Happold 1983)

Key Reference Hutterer & Happold 1983.

Rainer Hutterer

***Crocidura grassei* GRASSÉ'S SHREW**

Fr. Crocidure de Grassé; Ger. Grasses Spitzmaus

Crocidura grassei Brosset, Dubost and Heim de Balsac, 1965. Biologia Gabonica 1: 165. Belinga, Gabon.

Taxonomy Related to the *maurisca-littoralis* group (Quérrouil *et al.* 2005). Synonyms: none. Chromosome number: $2n = 40$ (Primus *et al.* 2006).

Description Medium-sized grey shrew, the largest of the *dolichura*-group. Pelage soft and dense; hairs 2–3 mm. Dorsal pelage greyish-brown; hairs grey at base, greyish-brown at tip.

Ventral pelage greyish-beige, paler than dorsal pelage; hairs grey at base, beige at tip. Head similar colour to dorsal pelage. Fore- and hindfeet not pigmented, sparsely covered with short white hairs. Tail relatively very long (ca. 95% of HB), bicoloured, medium to dark brown above, whitish below; long white hairs on tail; pilosity ca. 15%. Braincase slightly domed. First upper incisor long, hooked. Unicuspid pointed; first unicuspid larger than second and third; second and third subequal; all three with well developed cingulum. Third upper molar medium. Nipples: not known.

Geographic Variation None recorded.

Distribution Endemic to Africa. Rainforest BZ (Gabon sub-region). Recorded from Gabon, Central African Republic, S Cameroon and Equatorial Guinea (Rio Muni). Perhaps occurs in N Congo.

Habitat Rainforest, especially riparian habitats and marshes (Nicolas *et al.* 2004).

Abundance Considered as rare (Nicoll & Rathbun 1990, Goodman *et al.* 2001), but may be locally quite common. Frequency of occurrence in various regions includes 9% (one of 11; 7 spp.) in a marsh in Minkébé Forest, NE Gabon (Goodman *et al.* 2001), 10% (8 of 72; 9 spp.) at Mt Doudou (Goodman & Hutterer 2004) and 9% (46 of 503; 9 spp.) at Mt Doudou (Nicolas *et al.* 2004).

Remarks Apparently no other information available.

Conservation IUCN Category: Least Concern.

Measurements

Crocidura grassei

HB: 81.3 (76–86) mm, n = 4

T: 76.8 (69–80) mm, n = 4

HF: 15.8 (15–16) mm, n = 4



Crocidura grassei

E: 10.8 (10–12) mm, n = 4

WT: 11.6 (11–13) g, n = 4

CI: 22.9 (22.5–23.3) mm, n = 6

GWS: 9.6 (9.4–9.8) mm, n = 6

I¹–M³: 10.2 (9.9–10.7) mm, n = 6

Body measurements and weight (adults only): Mt Doudou, Gabon (Goodman & Hutterer 2004)

Skull measurements: ZFMK

Key References Goodman *et al.* 2001; Nicolas *et al.* 2004.

Rainer Hutterer

Crocidura greenwoodi GREENWOOD'S SHREW

Fr. Crocidure de Greenwood; Ger. Greenwoods Spitzmaus

Crocidura greenwoodi Heim de Balsac, 1966. Monitore Zool. Ital. 74 (Suppl.): 215. Gelib, Somalia.

Taxonomy Related to *C. fulvastra* and *C. hirta* (Hutterer 1993, 2005b), with which it shares the same karyotype (Schlitter *et al.* 1999). Synonyms: none. Chromosome number: 2n = 50, FN = 66 (Schlitter *et al.* 1999).

Description Small–medium shrew. Dorsal pelage grey tinged with brown. Ventral pelage whitish, hairs grey at base. Feet greyish. Tail relatively long (ca. 72% of HB), thick; pilosity 75%. Braincase broad and flattened. Second and third unicuspid subequal in size. Third upper molar medium. Talonid of third lower molar with a talonid basin and entoconid small or absent. Nipples: not known.

Geographic Variation None recorded.

Distribution Endemic to Africa. Somalia–Masai Bushland BZ. Recorded only from S Somalia.

Habitat Gallery forest, savanna, bush and arid regions; cultivated land.

Abundance No information.

Remarks Apparently no other information available.

Conservation IUCN Category: Least Concern.

Major threats are human-induced habitat loss and degradation, and restricted distribution.

Measurements

Crocidura greenwoodi

HB: 71 mm, n = 1

T: 51 mm, n = 1

HF: 13 mm, n = 1

E: n. d.

WT: n. d.

CI: 21.4 (21–22) mm, n = 3

GWS: 9.0 (8.5–9.6) mm, n = 3

I¹–M³: 9.1 (9.0–9.3) mm, n = 3

Somalia (Heim de Balsac 1966, BMNH)

Key References Heim de Balsac 1966; Hutterer 1993, 2005b.

P. D. Jenkins & S. Churchfield



Crocidura greenwoodi

Crocidura harena HARENNA SHREW

Fr. Crocidure de Harena; Ger. Harena Spitzmaus

Crocidura harena Hutterer and Yalden, 1990. In: Vertebrates in the Tropics (eds G. Peters and R. Hutterer), Bonn. p. 64. Katchja clearing, Harena Forest, Bale, Ethiopia.

Taxonomy One of the nine endemic species of Ethiopian shrews (Hutterer & Yalden 1990, Hutterer 2005b). Specimens referred to as *Crocidura* sp. A by Yalden (1988a) became the type series for this species. May be related to *C. phaera*, which is known only from Sidamo, Ethiopia. Synonyms: none. Chromosome number: 2n = 36, FN = 50 (Lavrenchenko *et al.* 1997).

Description Small–medium grey shrew. Pelage soft and dense; hairs 4.5 mm on back. Dorsal and ventral pelage dark slate-grey, without any trace of brown colour. Snout, ears, fore- and hindlimbs also slate-grey. Tail relatively long (ca. 66% of HB), with numerous long bristle hairs (<6 mm); pilosity ca. 80% (cf. sympatric *C. bottegoides*: 0%). Skull high-domed; braincase almost hexagonal in dorsal view. First upper incisor moderately long and hooked. First upper unicuspid large, second and third unicuspid about half height of first unicuspid. Third upper molar relatively large. Nipples: not known.

Geographic Variation None recorded.

Distribution Endemic to Africa. Afromontane–Afroalpine BZ. Known only from the type locality (Harena forest; 06°42'N, 39°44'E) in the Bale Mts of Ethiopia at 2400 m where it co-exists with the smaller *C. bottegoides* (Yalden 1988a).

Habitat *Schefflera*–*Hagenia* montane forest; this contrasts with *C. bottegoides*, which is a grassland species in the same area.



Crocidura harena

Abundance Rare. Known from six specimens (type series) out of 100 shrews (5 spp.) trapped in all habitats in Bale N. P. in 1971–1986 (Yalden 1988a), and the only species in the *Schefflera*–*Hagenia* montane forest. Also eight specimens (of 82 shrews) trapped in 1995 from various sites in Bale N. P. (Lavrenchenko *et al.* 1997).

Remarks One pregnant ♀♀ (WT: 11.5 g) and two sexually active ♂♂, recorded in Aug (D.W.Yalden unpubl.); no data for other months.

Conservation IUCN Category: Critically Endangered.

The limited distribution of the species, and the threat of habitat destruction, are cause for concern.

Measurements

Crocidura harena

HB: 70.1 (65–76) mm, n = 5

T: 46.5 (44–48) mm, n = 6

HF: 13.1 (12.5–14) mm, n = 6

E: 8.6 (8–9) mm, n = 5

WT: 7.8 (7.0–9.5) g, n = 4

CI: 19.0 (18.7–19.2) mm, n = 4

GWS: 9.2 (9.0–9.4) mm, n = 4

I¹–M³: 8.1 (7.9–8.2) mm, n = 5

Harena Forest, Ethiopia (Hutterer & Yalden 1990)

Key Reference Hutterer & Yalden 1990.

Rainer Hutterer & D.W.Yalden

Crocidura hildegardeae HILDEGARDE'S SHREW

Fr. Crocidure de Hildegarde; Ger. Hildegardes Spitzmaus

Crocidura hildegardeae Thomas, 1904. Ann. Mag. Nat. Hist., ser. 7, 14: 240. Fort Hall, Kenya.

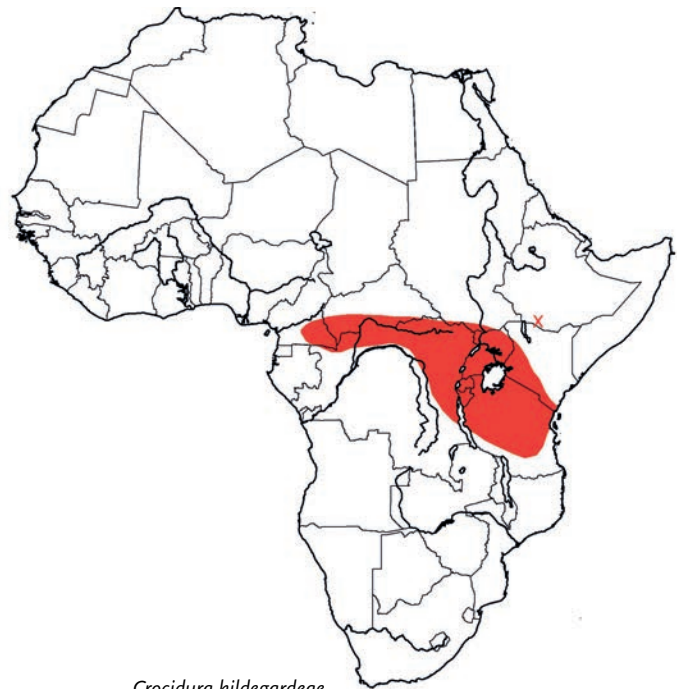
Taxonomy Considered a subspecies of *C. gracilipes* by Heim de Balsac & Meester (1977) but a valid species by Dieterlen & Heim de Balsac (1979), Demeter & Hutterer (1986) and Hutterer (1993, 2005b). Synonyms: *altae*, *holobrunneus*, *ibeana*, *lutreola*, *maanjan*, *phaios*, *procera*, *rubecula*. Hutterer (2005b) lists *virgata* (from Cameroon), previously listed as a synonym of this species, as a valid species on the grounds that it has a different chromosome number ($2n = 52$, $FN = 86$; Schlitter *et al.* 1999) to *C. hildegardeae*. Subspecies: none. Chromosome number: $2n = 52$, $FN = 76$ (Burundi; Maddalena & Ruedi 1994). Taxonomic revision of this species is required.

Description Small-medium shrew with prominent ears. Hairs 3.5 mm on rump, 3 mm on neck and back, 2.4 mm on ventral surface. Dorsal pelage milk-chocolate-brown; dorsal hairs chocolate-brown, dark brown at tip. Ventral pelage pale brown. Forelimbs chocolate-brown, hindlimbs dark brown on outer side, yellowish-brown on inner side. Tail relatively long (ca. 70% of HB), subtly bicoloured, black above, brown below; pilosity ca. 35%. Males usually larger than ♀♀ (Stanley *et al.* 1996a). Nipples: not known.

Geographic Variation None recorded.

Distribution Endemic to Africa. Rainforest BZ (West Central Region [Gabon sub-region] and East Central Region), Northern and Eastern Rainforest–Savanna Mosaics, and Afromontane–Afroalpine BZ of eastern and central Africa. Recorded from SE Cameroon and Congo to Kenya and Tanzania. In Tanzania, known from Mt Meru, the South Pare, East and West Usambara and the Udzungwa Mts (Dieterlen & Heim de Balsac 1979, Demeter & Hutterer 1986, Hutterer 1993, Stanley *et al.* 1996a, 1998). Limits of distribution uncertain.

Habitat Dry forest and wetter forests of montane and highland areas in eastern Africa. Found in both undisturbed and moderately disturbed sub-montane forests of East Usambara Mts. More common at mid-elevation dry forests than at higher elevation wetter montane forests of South Pare and Udzungwa Mts (Stanley *et al.* 1996a, W.T. Stanley unpubl.). In Rwanda, known from cultivated areas and moist savannas (Hutterer *et al.* 1987).



Crocidura hildegardeae

Abundance Varies by habitat and elevation. In Tanzania, the most abundant shrew at 1100 m (78% of total sample; n = 37), but the least abundant (30% of total sample; n = 10) at 2000 m in the South Pare Mts (Stanley *et al.* 1996a).

Remarks Terrestrial and nocturnal. Pregnancy rates were 25% (n = 12; Jul; South Pare Mts, Tanzania) and 50% (n = 6; Aug; East Usambara Mts). Embryo number: 2 (n = 3; East Usambara Mts). In Aug (1993), 64% of sample were juveniles (East Usambara Mts; Stanley *et al.* 1996, W.T. Stanley unpubl.). ♂ : ♀ ratio was 1 : 1 (South Pare Mts, 1100 m) and 1 : 3 (East Usambara Mts). Remains found in small carnivore scats in the Central African Republic (Ray & Hutterer 1995), and in the stomach of a sedge viper (*Atheris nitschei*) (Allen & Loveridge 1942).

Conservation IUCN Category: Least Concern.

Measurements

Crocidura hildegardeae

HB: 71.5 (64–77) mm, n = 25

T: 50.1 (39–56) mm, n = 25

HF: 13.0 (12–14) mm, n = 17

E: 9.0 (8–11) mm, n = 25

WT: 6.3 (4.6–7.7) g, n = 25

CI: 18.8 (18.2–19.3) mm, n = 25

GWS: 8.5 (8.2–8.8) mm, n = 25

I¹–M³: 7.9 (7.6–8.1) mm, n = 25

South Pare Mts, Tanzania (calculated from Stanley *et al.* 1996a)

Key Reference Stanley *et al.* 1996a.

William T. Stanley

Crocidura hirta LESSER RED SHREW (LESSER RED MUSK SHREW)

Fr. Crocidure petite rousse; Ger. Kleine Moschusspitzmaus

Crocidura hirta Peters, 1852. Reise nach Mossambique, Zool. 1, Säugetiere: 78, pl. 18, fig. 2. Tete, Zambezia, Mozambique (17S).

Taxonomy Polytypic. Synonyms: *annellata*, *beirae*, *bloyeti*, *canescens*, *deserti*, *flavidula*, *langi*, *luimbalensis*, *velutina* (see Heim de Balsac & Meester 1977). The two southern African forms are relatively well delimited. Subspecies: none (see also below). Chromosome number: 2n = 50 (Maddalena & Ruedi 1994).

Description Medium-sized shrew. Dorsal pelage cinnamon-brown, grizzled with reddish-fawn to dark-brown; hairs slaty-grey at base, with fawn subterminal band and brown or buffy-brown tip. Ventral pelage paler with yellow to fawn tinge; hairs grey at base with yellow to fawn tip. Dorsal colour can be sharply delineated from central colour. Head slender with long, narrow pointed muzzle, small eyes and rounded ears. Fore- and hindfeet fawn. Tail of medium to very long relative length (ca. 55% of HB in South Africa, up to 90% in central Africa) (Ansell & Dowsett 1988), brown above, pale grey below; pilosity up to 100%. Nipples: 0 + 3 = 6.

Geographic Variation Heim de Balsac & Meester (1977) recognized four forms as subspecies (here listed as synonyms):

deserti: W and S Angola, Zambia, NE Namibia, NE South Africa, Botswana. Dorsal pelage creamish-brown.

hirta: Zambia, SE Tanzania, Zimbabwe, N South Africa, Mozambique, Swaziland.

langi: DR Congo.

velutina: N Tanzania.

Distribution Endemic to Africa. Primarily Zambezan Woodland BZ and southern part of Somalia–Masai Bushland BZ. Recorded from SE Angola, SE DR Congo, Tanzania, Malawi, Zimbabwe, Zambia, Mozambique, Botswana, Swaziland, NW Namibia and N South Africa. Perhaps occurs in Kenya and Somalia. Limits of distribution uncertain.

Habitat Montane forest, bushveld, savanna and woodlands; requires some cover such as piles of debris, fallen logs or urban compost heaps (Smithers & Wilson 1979). Often commensal with humans, as is the Greater Musk Shrew (*Crocidura flavescens*) and African Giant Shrew (*C. olivieri*). Very wide habitat tolerance.

Abundance Uncertain, but common in urban gardens in Pretoria (South Africa), Bulawayo and Harare (Zimbabwe) as well as in suitable habitats throughout its range.

Adaptations Appears to be similar to the Greater Musk Shrew *Crocidura flavescens* but is less aggressive.

Foraging and Food Largely insectivorous, but will also prey on vertebrate prey (Meester 1960) as well as molluscs.

Social and Reproductive Behaviour Predominantly nocturnal with greatest peak of activity at dusk with a secondary peak at dawn (Baxter *et al.* 1979); thus there is temporal separation between this species and *C. flavescens* in their zone of sympatry. Vocalizations include a short, loud squeak when encountering a strange conspecific or when alarmed.

Scent marking using lateral glands has been observed. Faecal piles are strongly scented, suggesting some form of territoriality. Grooming behaviour includes scratching with the hindfeet and face-washing. Rectum licking has been observed (Baxter & Meester 1980).

Mating behaviour includes ‘flehmen’, when the male sniffs the ano-genital region of a female (Baxter 1981), and chasing. Copulation is



Crocidura hirta

brief after a chase of seven minutes. As in *C. flavescens*, the ♂ may be dragged along by his penis before disengagement. Nests are usually saucer-shaped (Baxter & Meester 1980) and are often situated at the end of a long tunnel underneath a rock (Meester 1960).

Reproduction and Population Structure In South Africa, pregnancies recorded during wet season and early dry season (Sep–May), but mostly in Jan–Feb. Gestation: ca. 28 days. Litter-size: 4.1 (2–5), mode 4, $n = 8$ (R. M. Baxter unpubl.). In (former) Transvaal, South Africa, breeding occurs from Nov–May and mean litter-size is 3.8 ($n = 7$) (Rautenbach 1982); in Zimbabwe, breeding is recorded in Sep, Dec and Feb, and mean litter-size is 3.6 ($n = 5$) (Smithers & Wilson 1979). At birth, HB = 31 mm, T = 8.1 mm, HF = 5.1 mm, E = 2.5 mm and weight = ca. 1 g ($n = 29$). Young are born naked, blind and helpless but development is rapid. When the young start to walk on Day 9, caravanning can be observed. Eyes and ears open around Day 12. Full pelage is present by Day 14, and caravanning ceases after Day 18. Weaning occurs at ca. Day 18. A postpartum oestrus is present and consecutive litters may be produced (Meester 1963, R. M. Baxter unpubl.).

Predators, Parasites and Diseases Known predators include African Grass-owls *Tyto capensis* and Barn Owls *Tyto alba*, as well as

Black-necked Cobras *Naja nigricollis*. As with *C. flavescens*, domestic cats kill but do not eat this shrew.

Conservation IUCN Category: Least Concern.

A relatively common shrew in urban gardens throughout its range.

Measurements

Crocidura hirta hirta

HB: 85.7 (69–96) mm, $n = 26$

T: 47.3 (39–59) mm, $n = 26$

HF: 14.3 (12–16) mm, $n = 25$

E: 10.1 (8–12) mm, $n = 23$

WT: 15.6 (8–24) g, $n = 48$

CI: 23.2 (22.0–24.3) mm, $n = 23$

GWS: 9.9 (9.3–10.8) mm, $n = 20$

I¹–M³: 10.0 (9.1–10.7) mm, $n = 27$

Measurements: Pretoria, South Africa (Meester 1963)

Weight: (Former) Transvaal (Rautenbach 1982)

Key References Baxter & Meester 1980; Meester 1960, 1963.

R. M. Baxter & N. J. Dippenaar

Crocidura jacksoni JACKSON'S SHREW

Fr. Crocidure de Jackson; Ger. Jacksons Spitzmaus

Crocidura jacksoni Thomas, 1904. Ann. Mag. Nat. Hist., ser. 7, 14: 238. Ravine Station, Kenya.

Taxonomy Synonyms: *amalae* (see Heim de Balsac & Meester 1977). Subspecies: none. Chromosome number: not known.

Description Small–medium shrew with soft, smooth short pelage. Dorsal pelage fawn to dark brown; hairs grey at base, brown at tip. Flanks similar to dorsal pelage. Ventral pelage whitish-grey; ventral hairs dark grey, whitish-grey at tip. Chin and throat similar to ventral colour. Head narrow with long-pointed muzzle with long dark brown vibrissae and very small eyes. Ears small, oval and dark brown; held laterally and backwards from head. Fore- and hindlimbs short and slender, with sparse short pale brown hairs. Tail thin and relatively long (ca. 75% of HB); buff above and on sides, grey below; small dark scales, pilosity at least 66%. Nipples: 0 + 3 = 6.

Geographic Variation None recorded.

Distribution Endemic to Africa. Somalia–Masai Bushland BZ, Eastern Rainforest–Savanna Mosaic and some parts of Afromontane–Afroalpine BZ in eastern Africa. Recorded from Uganda, Kenya, N Tanzania and E DR Congo.

Habitat Forests, wet bushlands and cultivated areas where annual rainfall is more than 1000 mm. In East Africa, inhabits moist forests in highland regions from 1400 m. In the eastern Rift Valley of Kenya, has been captured in cultivated areas (C. O. Odhiambo & N. O. Ouge, unpubl.) at elevations of over 1800 m.

Abundance Common in the Taita Hills, Kenya, where widely distributed in forest fragments. Collected in 11 of 14 forest fragments, comprising 13% of all shrews captured; the second most abundant species of shrew (after *C. hildegardeae*) (Ouge *et al.* 2004).



Crocidura jacksoni

Remarks Diet includes a wide range of invertebrates, including ants, beetles and termites. Preyed on by Barn Owls *Tyto alba* (skull recovered from pellets collected in Rongai Division, Kenya). Ectoparasites have not been recovered from this species.

Conservation IUCN Category: Least Concern.

Reduction in size and extent of forest fragments has probably reduced the geographic range of the species in recent years. Its presence in farming lands may suggest adaptability to environmental disturbance.

Measurements

Crocidura jacksoni

HB (♂♂): 75.3 (61–85) mm, n = 16

HB (♀♀): 69.9 (53–80) mm, n = 9

T (♂♂): 58.7 (49–69) mm, n = 15

T (♀♀): 54 (48–58) mm, n = 9

HF (♂♂): 12.9 (11.4–14.5) mm, n = 16

HF (♀♀): 12.8 (12–13.9) mm, n = 9

E (♂♂): 8.6 (6.7–9.7) mm, n = 15

E (♀♀): 8.2 (7.4–9.4) mm, n = 9

WT (♂♂): 8.5 (7–11) g, n = 16

WT (♀♀): 8.1 (6–12) g, n = 9

CI (♂♂): 20.6 (20.3–21) mm, n = 5

CI (♀♀): 20.4 (19.9–20.9) mm, n = 3

GWS (♂♂): 9.0 (8.9–9.1) mm, n = 5

GWS (♀♀): 8.9 (8.6–9.2) mm, n = 3

I¹–M³ (♂♂): 9 (8.8–9.4) mm, n = 5

I¹–M³ (♀♀): 8.7 (8.6–8.9) mm, n = 3

Taita Hills, Kenya (N. Oguge, unpubl.)

Key Reference Oguge *et al.* 2004.

N. Oguge

Crocidura jouvenetae JOUVENET'S SHREW

Fr. Crocidure de Jouvenet; Ger. Jouvenet Spitzmaus

Crocidura jouvenetae Heim de Balsac, 1958. Mém. Inst. Fr. Afr. Noire 53: 331. Ziéla, Mt Nimba, Guinea.

Taxonomy Referred to as a subspecies of *C. crossei* by Hutterer (1993) and Grubb *et al.* (1998). However, *jouvenetae* and *ebriensis* (described as a subspecies of *C. jouvenetae* by Heim de Balsac & Aellen 1958) are larger animals and represent a separate species (Hutterer 2005b). The form *ebriensis* was listed as a species by Maddalena & Ruedi (1994) and Schlitter *et al.* (1999). Synonyms: *ebriensis*. Subspecies: none. Chromosome number: 2n = 44, FN = 66.72 (Maddalena & Ruedi 1994, as *C. ebriensis*).

Description Small-medium greyish-brown shrew. Pelage short and dense. Dorsal pelage greyish-brown. Ventral pelage paler without any clear delineation with colour of flanks. Head long, similar in colour to dorsal pelage, paler under chin. Upper part of face dark grey to black; lower part silvery, delineated clearly from upper face. Ears large and well developed. Fore- and hindfeet pale or flesh-coloured. Tail relatively long (ca. 66% of HB), thick (especially at base; diameter 5–6 mm), bicoloured; pilosity ca. 75%. Nipples: not known.

Geographic Variation Specimens from forests at Mt Nimba are smaller and darker than those elsewhere (Heim de Balsac 1968a).

Distribution Endemic to Africa. Rainforest BZ (Western Region). Recorded from S Guinea, Liberia and S Côte d'Ivoire (Hutterer 2005b). May also occur in Sierra Leone (Grubb *et al.* [1998], as *C. crossei jouvenetae*).

Habitat Primary and secondary lowland forest and cocoa-coffee plantations within the forest. Specimens also caught in moist rainforest near coastal lagoons, and near savanna (Dabou, Côte d'Ivoire). At Mt Nimba, found in forested habitats at the base of the mountains (Heim de Balsac 1958).

Abundance Common in all localities where it has been captured. In Taï N.P., Côte d'Ivoire, common in secondary forest (18.5%, n = 390 shrews, 9 spp.) and in cocoa-coffee plantations (16.5%, n = 140 shrews, 7 spp.) (Barrière *et al.* 1999). In Ziama Biosphere Reserve, Guinea, common in young forest plantations, primary forest, old fallow land and secondary forest (25.1%, n = 303 shrews, 10 spp.; 22.4%, n = 500, 11 spp.; 18.2%, n = 484, 9 spp.; and 15.7%, n = 509, 10 spp., respectively), but less common in fields (14.7%, n = 272, 9 spp.) and in old forest plantations (10.9%, n = 441, 9 spp.) (P. Barrière, unpubl.). At Adiopoudome, Côte d'Ivoire, more abundant than syntopic *C. poensis* (Heim de Balsac & Aellen 1958).



Crocidura jouvenetae

Remarks The commonest prey items (% frequency of occurrence) in 26 stomachs in Taï N.P., Côte d'Ivoire, were representatives of the following taxa: Formicidae (80.8%), Araneae (42.3%), Diplopoda (26.9%), Coleoptera adults (23.1%), Blattodea (11.5%), Gryllidae (7.7%), Lepidoptera larvae (3.8%), Mantidae (3.8%), Diptera adults (3.8%) and Isopoda (3.8%). This analysis suggests that *C. jouvenetae* is a specialist feeder on ants. (Churchfield *et al.* 2004).

Conservation IUCN Category: Least Concern.

Measurements

Crocidura jouvenetae

HB: 74.8 (64–86) mm, n = 22

T: 55.8 (47–63) mm, n = 20

HF: 13.8 (13–14.5) mm, n = 22

E: 9.4 (9–10) mm, n = 5*

WT: 9.4 (7.5–12) g, n = 7

CI: 21.6 (20.6–23.0) mm, n = 21

GWS: 8.8 (8.3–9.9) mm, n = 22

I¹–M³: 9.7 (9.2–10.2) mm, n = 22

Côte d'Ivoire (Heim de Balsac & Aellen 1958)

*RMCA

Key References Heim de Balsac 1958; Heim de Balsac & Aellen 1958.

D. C. D. Happold

Crocidura kivuana KIVU SHREW

Fr. Crocidure de Kivu; Ger. Kivu-Spitzmaus

Crocidura kivuana Heim de Balsac, 1968. Biologia Gabonica 4: 319. Tshibati, Kivu, DR Congo.

Taxonomy Belongs to the *monax* species-group, a complex of 12 related species occurring in high montane areas of Cameroon, central and East Africa, four of which (*C. kivuana*, *C. lanosa*, *C. littoralis* and *C. stenocephala*) are endemics of the Albertine Rift Valley (Hutterer 1986b). Resembles *C. maurisca* and *C. congobelgica* (Heim de Balsac 1968c, Heim de Balsac & Meester 1977). Synonyms: none. Chromosome number: not known.

Description Small–medium shrew with a relatively long tail. Dorsal pelage blackish with a distinct brownish tinge, especially on the head; hairs silvery ash-grey at base, blackish with brownish tinge at tip. Ventral pelage ashy-grey without brownish tinge, paler than dorsal pelage; hairs silvery ash-grey at base, grey with brownish tinge at tip. Ears naked, usually not covered by pelage. Hindfeet brownish, short-haired; forefeet paler. Tail relatively very long (ca. 89% of HB), not tapering towards tip, blackish brown above, slightly paler below; pilosity 0–20%; some specimens have slight pencil at tip. Skull: cranium domed, with broad maxillary width. Upper third unicuspid larger than upper second unicuspid (cf. *C. maurisca* and *C. congobelgica* in which the third upper unicuspid is smaller than the second). Nipples: not known.

Geographic Variation None recorded.

Distribution Endemic to Africa Afromontane–Afroalpine BZ flanking the Albertine Rift Valley. Confined to a small montane region west of L. Kivu between Lwiro (1700 m) and the peak of Mt Kahuzi (3300 m). Probably widely distributed in undisturbed areas above 2000 m.

Habitat At lower altitudes, swamps with *Cladium mariscus* and *Cyperus latifolius* are the preferred habitat. At higher altitudes, recorded from swamps with *Cyperus latifolius*, primary and secondary mixed montane forests, and (rarely) bamboo forest. One individual was obtained in the afroalpine vegetation on the top of Mt Kahuzi at 3300 m (Dieterlen & Heim de Balsac 1979).

Abundance Abundant in some swampy habitats, representing ca. 50% of captured shrews. Often syntopic with *C. stenocephala* in some swampy habitats on Mt Kahuzi, E DR Congo.

Remarks Four ♀♀ were pregnant during the wet season (Oct, Nov, Mar). Embryo number: 1.67 (1–2), n = 3.

Conservation IUCN Category: Vulnerable.

Threatened because of its rarity and very restricted geographic and ecological range; adequate conservation of this species is similar to that of the other endemic species of the Albertine Rift Valley region.



Crocidura kivuana

Measurements

Crocidura kivuana

HB: 75.0 (64–88) mm, n = 34

T: 66.5 (60–75) mm, n = 34

HF: 13.0 (10–16) mm, n = 34

E: 8.0 (5–10) mm, n = 34

WT: 9.9 (5–13) g, n = 34

CI: 20.9 (20.1–21.8) mm, n = 20

GWS: 9.3 (8.9–9.7) mm, n = 20

I¹–M³: 9.1 (8.3–9.4) mm, n = 20

Kivu, E DR Congo (Dieterlen & Heim de Balsac 1979, SMNS)

Key References Dieterlen & Heim de Balsac 1979; Heim de Balsac 1968c.

Fritz Dieterlen

Crocidura lamottei LAMOTTE'S SHREW

Fr. Crocidure de Lamotte; Ger. Lamottes Spitzmaus

Crocidura lamottei Heim de Balsac, 1968. Mammalia 32: 386. Lamto, Côte d'Ivoire.

Taxonomy Synonyms: *elegans*. Subspecies: none. Chromosome number: 2n = 52, FN = 68 (Meylan 1971).

Description Medium-sized shrew with relatively pale-coloured pelage. Dorsal pelage pale brown to grey-brown, without flecking; hairs bluish-grey, brown at tip. Ventral pelage grey or silvery-grey washed with yellowish tint; hairs medium grey at base, creamy-grey at tip. Vibrissae long. Ears conspicuous, not concealed by pelage; appear naked but covered with short hairs. Hindfoot relatively short. Fore- and hindlimbs flesh-coloured covered with short pale brown hairs. Tail medium length (ca. 53% of HB), thick, broad at base narrowing towards tip; flesh-coloured with reddish blotches; pilosity 100%. Skull similar to *C. butleri* but larger. First incisor long and hooked. Third molar narrow. Mandible very robust, particularly the coronoid process. Nipples: not known.

Geographic Variation Specimens from the north of the range are paler dorsally and pure grey ventrally compared with specimens from the south, and have slightly larger skull measurements providing possible justification of a subspecies (? *C. l. elegans*) (Hutterer 1986a, Hutterer & Schlitter 1996).

Distribution Endemic to Africa. Sudan and Guinea Savanna BZs of West Africa. Recorded from Senegal to W Cameroon, including Nigeria, Côte d'Ivoire, Liberia, Senegal and possibly Togo (Heim de Balsac & Meester 1977, Hutterer 1981b, Hutterer & Happold 1983). Specimens from Owerri, S Nigeria recorded as *C. foxi* (Hutterer & Happold 1983) are in fact *C. lamottei* (Hutterer 2005b). One record from the Rainforest BZ (Korup N. P., Cameroon; Hutterer & Schlitter 1996).

Habitat Recorded from a variety of habitats; found primarily in dry forest, grasslands in savanna, amongst dry grasses on rocky hillside, and in grassy clearings (Heim de Balsac 1968a, Hutterer & Happold 1983, Hutterer 1986a, Hutterer & Schlitter 1996, Decher *et al.* 1997).

Abundance No information.

Remarks Found inhabiting termitaria (Heim de Balsac 1968a). One pregnant ♀ bearing a single embryo was found at the beginning of the dry season in Ghana (Decher *et al.* 1997).

Conservation IUCN Category: Least Concern.



Crocidura lamottei

Measurements

Crocidura lamottei

HB: 85, 90 mm, n = 2

T: 35.5–55 mm, n = 8

HF: 14–16 mm, n = 8

E: 11–12 mm, n = 3

WT: 18–23 g, n = 3

CI: 24.7–26.0 mm, n = 10

GWS: 10.1–10.6 mm, n = 3

I¹–M³: 10.4–11.8 mm, n = 12

Guinea, Côte d'Ivoire, Togo, Nigeria (Heim de Balsac 1968a, Hutterer & Happold 1983)

Mean values not recorded

Key References Decher *et al.* 1997; Heim de Balsac 1968a; Hutterer 1981b, 1986a; Hutterer & Happold 1983; Hutterer & Schlitter 1996.

P. D. Jenkins & S. Churchfield

Crocidura lanosa KIVU LONG-HAIRED SHREWFr. *Crocidura laineuse* de Kivu; Ger. Kivu-Langhaarspitzmaus*Crocidura lanosa* Heim de Balsac, 1968. Biologia Gabonica 4: 309. Lemera. Kivu Province, DR Congo.

Taxonomy Belongs to the *monax* species-group, a complex of 12 related species occurring in high montane areas of Cameroon, central and East Africa, four of which (*C. kivuana*, *C. lanosa*, *C. littoralis* and *C. stenocephala*) are endemic to the Albertine Rift Valley (Hutterer 1986b). Synonyms: none. Chromosome number: not known.

Description Large shrew (the largest of the *monax*-group). Pelage long and dense, woolly with dull texture. Dorsal pelage almost unicoloured blackish-grey with a superficial brownish tinge; hairs with white tip. Ventral pelage blackish-grey, but slightly paler than dorsal pelage, possibly with a brownish tinge. Eyes small. Ears medium-sized, partly covered by pelage. Fore- and hindfeet brownish. Hindfoot relatively long. Tail relatively long (ca. 80% of HB), dark, covered with short dark bristles except at terminal end; pilosity ca. 33%. (Some specimens have whitish hairs at tip of tail, forming a small pencil.) Skull elongated; maxillary and cranial regions broad; cutting edge of lower incisor normally smooth, rarely with a denticle. Nipples: 0 + 3 = 6.

Geographic Variation None recorded.

Distribution Endemic to Africa. Afromontane–Afroalpine BZ. Recorded from montane forests on the slopes of the Albertine Rift Valley of E DR Congo and Rwanda (Rugege Forest, now Nyungwe Forest) on both east and west sides of L. Kivu at 1800–2500 m (Heim de Balsac 1968b, Dieterlen & Heim de Balsac 1979, Hutterer *et al.* 1987).

Habitat Primarily montane forest including thick undergrowth and glens (n = 24), and mixed forests (primary and secondary) with bamboo (n = 9). Not recorded from open habitats nor from montane swamps.

Abundance Comprised 15% of shrews (33 of 222; 10 spp.) caught in all montane habitats (1800–3300 m) W of L. Kivu, DR Congo, and 23% of shrews in habitats where the species was present (Dieterlen & Heim de Balsac 1979).

Remarks Dense woolly pelage is possibly an adaptation to cold temperatures and wet conditions in the mountains. Pregnant ♀♀ found during the wet season (Oct, Nov, Jan) but not at other times of the year. Embryo number: 2 (n = 2), 6 (n = 1). Sex ratio of captured shrews: ca. 2 : 1.

*Crocidura lanosa*

Conservation IUCN Category: Endangered.

This species is threatened because of its rarity and very restricted geographic and ecological range; in this respect it is similar to the other endemic species of the Albertine Rift Valley region.

Measurements*Crocidura lanosa*

HB: 95.6 (87–105) mm, n = 33

T: 77.6 (69–85) mm, n = 33

HF: 19.3 (16–22) mm, n = 33

E: 8.6 (6–10) mm, n = 33

WT: 22.6 (18–34) g, n = 33

CI: 25.4 (24.2–26.0), mm, n = 17

GWS: 11.0 (10.6–11.4) mm, n = 17

I¹–M³: 11.0 (10.4–11.3) mm, n = 17

Kivu, E DR Congo (1800–2500 m) (Dieterlen & Heim de Balsac 1979, SMNS, ZFMK)

Key References Dieterlen & Heim de Balsac 1979; Heim de Balsac 1968b.

Fritz Dieterlen

Crocidura latona LATONA'S SHREW

Fr. Crocidence de Latona; Ger. Latonas Spitzmaus

Crocidura latona Hollister, 1916. Bull. Amer. Mus. Nat. Hist. 35: 667. Medje, NE DR Congo.

Taxonomy Similar to *C. niobe* in size, but *C. latona* is distinguishable by its uniform dark brownish colouration on upper and lower parts. Skull and teeth very similar to *C. maurisca* and *C. littoralis*, but smaller. May be related to the paler-coloured *C. jacksoni*, which is similar in size and also possesses a fovea on M₃. Brosset *et al.* (1965b) suggested that *C. ludia* may be a synonym, but this seems unlikely since it has a smaller skull and a longer more sparsely haired tail than *C. latona*. Synonyms: none. Chromosome number: not known.

Description Small-medium, lightly built dark-coloured shrew. Dorsal pelage rich dark-brown. Ventral pelage slightly paler brown than on back and sides. Lateral flank glands russet. Fore- and hindfeet buffy-brown, very thinly haired. Tail relatively very long (ca. 85% of HB), blackish-brown, very slightly paler below at base; pilosity ca. 20%. Skull small. Unicuspid rather narrow with small cusps and large cingula; second and third unicuspid relatively wide and inclined to be circular. Last upper premolar is longer than wide. A fovea is present on the talonid of M₃. Nipples: not known.

Geographic Variation None recorded.

Distribution Endemic to Africa. Rainforest BZ of NE DR Congo. Known only from four localities: near Medje, near Kisangani (Masako Forest Reserve), Okapi Faunal Reserve (Katuala *et al.* 2005) and Irangi.

Habitat Lowland primary and secondary rainforest. Captured in secondary forest, along creek-sides and in fallow land in Masako Forest, near Kisangani (Dudu *et al.* 2005).

Abundance Appears to have small, highly localized populations and is rarely found in trapped samples. Comprised 7% of shrews (5 of 72; 9 spp.) during three years of trapping in Masako Forest, DR Congo (Dudu *et al.* 2005).

Adaptations Ground-dwelling species. Feeds on a wide range of invertebrates, primarily arthropods. Stomach analyses (n = 5) showed that major prey comprised Formicidae and Diptera (each 17% by composition), Isoptera, Coleoptera, Acrididae, Araneae and Diplopoda (each 10–12%). Invertebrate prey ranged in body length from 3 mm to 30 mm with 80% being <10 mm (Dudu *et al.* 2005).

Conservation IUCN Category: Least Concern.

Previously assessed as Vulnerable (B1 + 2c). Major threats are habitat modification, particularly deforestation, and the restricted geographic range.

*Crocidura latona***Measurements***Crocidura latona*

HB: 76 mm*

HB: 64.7 mm, n = 3**

T: 59 mm*

HF: 14 mm*

E: 9 mm*

WT: 6.6 g, n = 5**

CI: 19.8 mm*

GWS: 8.9 mm*

I¹–M³: n. d.

*DR Congo (Hollister 1916 – holotype)

DR Congo (Dudu *et al.* 2005)Key References** Dudu *et al.* 2005; Hollister 1916.**S. Churchfield, R. Hutterer & A. Dudu**

Crocidura littoralis NAKED-TAILED SHREW

Fr. Crocidure des rives; Ger. Nacktschwanz-Spitzmaus

Crocidura littoralis Heller, 1910. *Smithson. Misc. Coll.* 56 (15): 5. Butiabi, east shore of L. Albert, Uganda.

Taxonomy Formerly included in *C. monax*, but now considered a distinct species (Dieterlen & Heim de Balsac 1979, Hutterer 1993). The subspecies *C. l. stenocephala* (see Dieterlen & Heim de Balsac 1979) is now regarded as a valid species. The specimens referred to *C. maurisca* from Kenya (Hollister 1918) are probably *C. littoralis* (Dieterlen & Heim de Balsac 1979). Synonyms: *oritis*. Subspecies: none. Chromosome number: not known.

Description Large shrew. Dorsal pelage blackish or dark brown; hairs ash-grey at base, brownish at tip. Ventral pelage (including undersurface of head and neck) similar to dorsal pelage or greyish-brown; hairs silvery-grey at base, brownish-grey at tip. Ears darkly pigmented, with very short dark hairs on outer edge. Hindfeet dark brown, forefeet medium-brown. Tail relatively long (ca. 73% of HB), blackish above, slightly paler below; appears naked, with a few longer bristles at base of tail (pilosity ca. <25%). Skull similar to that of *C. stenocephala*, but clearly broader; cutting edge of mandibular incisors with (two) inconspicuous denticles. Nipples: not known.

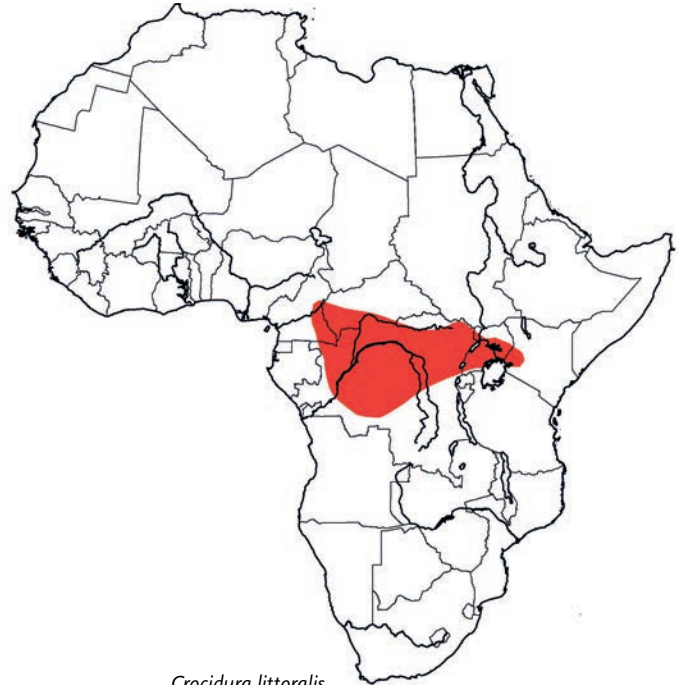
Geographic Variation None recorded.

Distribution Endemic to Africa. Rainforest BZ (West Central [Gabon sub-region], South Central and East Central Regions) and Eastern Rainforest–Savanna Mosaic. Recorded from a few localities in SW Central African Republic, Cameroon, Congo, DR Congo, Uganda and Kenya (Dieterlen & Heim de Balsac 1979, Hutterer 1993, Ray & Hutterer 1995).

Habitat Closed-canopy rainforest. Appears unevenly distributed on both a local and regional basis (Dieterlen & Heim de Balsac 1979).

Abundance Usually rare, but can be locally abundant (Dieterlen & Heim de Balsac 1979).

Remarks In Masako Forest, E DR Congo, one of the rarest shrews, comprising ca. 1% (1 of 72) of the shrew community (equal eighth commonest species; 9 spp.) (Dudu *et al.* 2005). Diet includes species of Formicidae, Diptera and Lepidoptera larvae, Heteroptera, Isoptera and Araneae (n = 1; Dudu *et al.* 2005). Litter-size: 2–4 (n = 2; Kivu, DR Congo) (Dieterlen & Heim de Balsac 1979). Found in 2.3% of 311 small carnivore scats collected in Dzanga-Sangha, Central African Republic (Ray & Hutterer 1995, Ray 1998).

*Crocidura littoralis*

Conservation IUCN Category: Least Concern.

Measurements*Crocidura littoralis*

HB: 93 (85–100) mm, n = 5

T: 68 (64–77) mm, n = 5

HF: 16 (13–17) mm, n = 5

E: 9.5 (8–11) mm, n = 5

WT: 21 (20–24) g, n = 5

CI: 24.4 (23.8–24.8) mm, n = 3

GWS: 10.6 (10.4–10.7) mm, n = 3

I¹–M³: 10.2 (10.1–10.5) mm, n = 3E DR Congo (Dieterlen & Heim de Balsac 1979, as *C. littoralis littoralis*)

Key Reference Dieterlen & Heim de Balsac 1979.

Justina C. Ray & Rainer Hutterer

***Crocidura longipes* LONG-FOOTED SHREW (SAVANNA SWAMP SHREW)**

Fr. Crocidure à longs pieds (Crocidure des marais); Ger. Savannen-Sumpfspitzmaus

Crocidura longipes Hutterer and Happold, 1983. Bonn. Zool. Monogr. 18: 53. Dada, Nigeria.**Taxonomy** Synonyms: none. Chromosome number: not known.**Description** Very large chocolate-brown shrew with long hindfeet. Dorsal pelage and ventral pelage uniformly dark brown. Fore- and hindfeet dark brown. Hindfeet comparatively long (ca. 17% of HB). Tail of medium relative length (ca. 60% of HB), brown; pilosity unknown ('sparsely haired'). Skull long and pointed; interorbital and maxillary regions narrow; dentition weak, especially upper molars. Nipples: not known.**Geographic Variation** None recorded.**Distribution** Endemic to Africa. Guinea Savanna BZ. Recorded from only two localities in Nigeria – Dada and Iella (2 miles E of Bahindi).**Habitat** Swampy areas with tall grasses (1–2 m in height), palm trees and scattered other trees. May occur in other swamps along major river systems in Guinea Savanna BZ. Syntopic with *Crocidura olivieri* in one swamp (C. B. Robbins in Hutterer & Happold 1983).**Abundance** Unknown. Known only from seven specimens.**Remarks** Apparently no other information available.**Conservation** IUCN Category: Data Deficient.
Previously considered as Endangered.**Measurements***Crocidura longipes*

HB: 105 (95–111) mm, n = 6

T: 62 (56–69) mm, n = 6

HF: 18.2 (18–19) mm, n = 6

*Crocidura longipes*

E: 11 (10–12) mm, n = 6

WT: 19.3 (15–24) g, n = 6

CI: 24.9 (24.2–25.4) mm, n = 6

GWS: 10.4 (10.1–10.8) mm, n = 5

I¹–M³: 10.7 (10.3–10.9) mm, n = 6

Nigeria (Hutterer & Happold 1983)

Key Reference Hutterer & Happold 1983.**D. C. D. Happold*****Crocidura lucina* LUCINA'S SHREW**

Fr. Crocidure de Lucina; Ger. Lucinas Spitzmaus

Crocidura lucina Dippenaar, 1980. Ann. Transvaal Mus. 32: 134. Web River, near Dinshu, Bale, Ethiopia (ca. 07°06' N, 39°46' E). 3000 m.**Taxonomy** Specimens recorded as *C. baileyi* by Osgood (1936) and Yalden *et al.* (1976) are now allocated to this species (Dippenaar & Meester 1989). A member of the endemic Ethiopian *C. glassi* complex (*C. glassi*, *C. lucina*, *C. thalia*, *C. macmillani* and *C. baileyi*) (Dippenaar & Meester 1989). Synonyms: none. Chromosome number: 2n = 36 (Lavrenchenko *et al.* 1997).**Description** Medium-sized shrew, with a distinctly bicoloured pelage and tail. Pelage long and soft. Dorsal pelage greyish-brown to reddish-brown; hairs grey at base, rufous at tip. Ventral pelage greyish-white, hairs grey at the base, white at tip. Dorsal surface of fore- and hindfeet whitish. Tail relatively short (ca. 62% of HB), brown above, whitish below; pilosity 100%. Skull with inflated braincase, as typical for the high altitude Ethiopian *Crocidura*. Nipples: not known.**Geographic Variation** None recorded.**Distribution** Endemic to Africa. Afromontane–Afroalpine BZ. Recorded only in the highlands east of the Ethiopian Rift Valley (Bale Mts and Mt Badda), Ethiopia, 3000–4050 m.

Habitat Afroalpine moorland, and grasslands at lower altitudes (Yalden 1988, Lavrenchenko *et al.* 1997).

Abundance Rare. Comprised 1.9% ($n = 535$) of small mammals caught in the Bale Mts (Yalden 1988a, b).

Remarks Woolly fur and relatively short tail might be adaptations to the cold at high altitudes. One pregnant ♀ (with two embryos) trapped in the Bale Mts in the late dry season (early Mar; L. Lavrenchenko unpubl.). Seems to be avoided as prey by Simien Wolves *Canis simensis* (Sillero-Zubiri & Gottelli 1995).

Conservation IUCN Category: Least Concern.

Distribution very limited. Protected within the proposed Bale Mountains N. P.

Measurements

Crocidura lucina

HB: 86 (80–92) mm, $n = 5$

T: 53 (47–55) mm, $n = 5$

HF: 17 (16–17) mm, $n = 5$

E: 12 (11–12) mm, $n = 5$

CI: 23.1 (22.7–24.0) mm, $n = 9$

GWS: 10.3 (10.1–10.5) mm, $n = 4$

I¹–M³: 10.4 (10.1–10.8) mm, $n = 4$

Ethiopia (Dippenaar 1980a)



Crocidura lucina

Key References Dippenaar 1980a; Dippenaar & Meester 1989.

Leonid A. Lavrenchenko

Crocidura ludia LUDIA'S SHREW

Fr. Crocidure de Ludia; Ger. Ludias Spitzmaus

Crocidura ludia Hollister, 1916. Bull. Amer. Mus. Nat. Hist. 35: 668. Medje, DR Congo.

Taxonomy Included in *C. dolichura* by Heim de Balsac & Meester (1977), but reinstated as a full species by Hutterer & Dippenaar (1987a). The species may include more than one species (Quérrouil *et al.* 2005). Synonyms: none. Chromosome number: not known.

Description Small brown shrew. Dorsal pelage uniformly brown; hair grey at base, brown at tip. Ventral pelage brown, rather similar to dorsal pelage. Fore- and hindfeet buff, thinly haired, with brown streak along outside. Tail relatively very long (84–87% of HB), blackish-brown above, paler on basal third below; appears naked but covered with short dark bristles; long hairs restricted to base of tail (pilosity 20–30%). Skull (depicted in Hollister 1916, pl. 7, fig. 4) small and gracile, similar to *C. dolichura* in general configuration. Braincase rounded, rostrum slender; skull tapering from the interorbital region to the tip of the skull; braincase strongly inflated in lateral view. Dentition weak; upper first incisor short and small; M³ large. Nipples: not known.

Geographic Variation None recorded.

Distribution Endemic to Africa. Rainforest BZ and Northern Rainforest–Savanna Mosaic. Recorded from DR Congo (Medje, Tandala, Masako forest near Kisangani, Yoko forest south of Kisangani; Hollister 1916, Hutterer & Dippenaar 1987, Dudu *et al.*

2005, Mukinzi *et al.* 2006) and Central African Republic (Dzanga-Sangha F.R., Batouri, Bohou; Ray & Hutterer 1995, Barrière *et al.* 2005).

Habitat In Masako Forest, found only in secondary forest (not in primary forest, along creeks, or in fallow land) (Dudu *et al.* 2005). In Bohou (Central African Republic), found in gallery forest and moist savanna habitats (Barrière *et al.* 2005).

Abundance Rarely collected. In Masako Forest, comprised ca. 3% (2 of 72, 9 spp.) of shrews captured (Dudu *et al.* 2005). In Bohou (Central African Republic) surprisingly constituted the dominant species, with 71% (41 of 58, 7 spp.) of shrews captured (Barrière *et al.* 2005).

Remarks Stomach contents ($n = 2$) include representatives of the following: adult Coleoptera, Formicidae, Lepidoptera larvae, Blattodea, Diplopoda, Araneae and seeds (Dudu *et al.* 2005). Occasionally recorded (1.3% of 311 shrews; 16 spp.) in scats of carnivores from Central African Republic; one of the predators was *Herpestes naso* (Ray & Hutterer 1995). Three other similar species are potentially sympatric with *C. ludia*: *C. polia*, *C. dolichura* and *C. latona*.

Conservation IUCN Category: Least Concern.

Measurements

Crocidura ludia

HB: 69, 63 mm, n = 2

T: 60, 53 mm, n = 2

HF: 14, 12 mm, n = 2

E: 9, 9 mm, n = 2

WT: 6.5, 6.5 g, n = 2

CI: 18.2, – mm, n = 2

GWS: 8.2, – mm, n = 2

I¹–M³: 7.8, – mm, n = 2

Measurements: Medje, DR Congo (holotype and topotype; Hollister 1916). HB calculated from TL.

Weight: Masako Forest, DR Congo (Dudu *et al.* 2005)

Key References Dudu *et al.* 2005; Hollister 1916; Ray & Hutterer 1995.

Rainer Hutterer



Crocidura ludia

Crocidura luna MOONSHINE SHREW (GREY-BROWN MUSK SHREW)

Fr. Crocidure sélène; Ger. Grosse graubraune Moschusspitzmaus

Crocidura luna Dollman, 1910. Ann. Mag. Nat. Hist., ser. 8, 5: 175. Bunkeya River, Katanga, Shaba Province, DR Congo.

Taxonomy A member of the *luna-fumosa* complex (Dippenaar & Meester 1989). Synonyms: *electa*, *garambae*, *inyangai*, *johnston*, *schistacea*, *umbrosa*. Subspecies: none. Chromosome number: 2n = 36 (Maddalena & Ruedi 1994).

Description Medium-sized shrew. Dorsal pelage brownish-grey to very dark brownish-grey; hairs slaty-grey at base, pale fawn or grey subterminal band and paler or darker at tip. Ventral pelage slightly to obviously paler and greyer; hairs slaty-grey at base, pale fawn to olive at tip. Head slender with long, narrow pointed muzzle, small eyes and rounded ears. Fore- and hindfeet usually pale brownish-grey to yellowish-brown or brown. Tail relatively long (ca. 61% of HB), dark brown to blackish-brown above, paler below. Nipples: 0 + 3 = 6.

Geographic Variation None recorded.

Distribution Endemic to Africa. Zambezian Woodland BZ, extending into southern part of Somalia–Masai Bushland BZ and Eastern Rainforest–Savanna Mosaic. Recorded from extreme NE DR Congo, Uganda, Kenya, most of Tanzania, Zambia, SE DR Congo, WC Mozambique and Malawi; outlier population in Inyanga Highlands of Zimbabwe and adjacent Mozambique (Dippenaar & Meester 1989).

Habitat Moist, cool areas, typically on the fringes of montane forest where there is dense cover, in matted grass along streams where rainfall exceeds 1000 mm (Smithers & Lobão Tello 1976,

Smithers & Wilson 1979), on hillsides with tussock grass (Skinner & Smithers 1990), and in *Pinus* plantations (Happold & Happold 1987). Recorded up to 1400 m on Mt Kilimanjaro (Grimshaw *et al.* 1995), and at 1900 m on Zomba Plateau (Malawi) (Happold & Happold 1989a).



Crocidura luna

Abundance Uncertain, but mostly rarely encountered. Three individuals captured in Afromontane grasslands on Zomba Plateau during monthly sampling (10 months); the only species of shrew recorded in this habitat. Recorded in most plantations of *Pinus patula* (ages 1–32 years) where abundant grass cover is present (Happold & Happold 1987).

Remarks Nocturnal, with peaks of activity at dawn and dusk; terrestrial (Smithers & Wilson 1979). Reproductive activity has been reported in Oct and Nov when 3–4 young are born (Smithers & Wilson 1979).

Conservation IUCN Category: Least Concern.

Measurements

Crocidura luna

HB: 85 (60–107) mm, n = 397

T: 52 (31–69) mm, n = 396

HF: 14.5 (7–21) mm, n = 399

E: 9.5 (5–14) mm, n = 396

WT: n. d.

CI: 22.6 (20.0–25.1), n = 268

GWS: 9.9 (9.1–11.3), n = 251

I¹–M³: 10.7 (9.9–11.3), n = 19

Throughout geographic range (Dippenaar & Meester 1989)

Key References Dippenaar & Meester 1989; Meester 1963; Smithers 1983.

R. M. Baxter & N. J. Dippenaar

Crocidura lusitania MAURITANIAN SHREW

Fr. Crocidure de Mauritanie; Ger. Mauritanien-Spitzmaus

Crocidura lusitania Dollman, 1915. Ann. Mag. Nat. Hist., ser. 8., 15: 516. Trarza country, Mauritania.

Taxonomy Synonyms: none. Chromosome number: 2n = 38, aFN = 70 (Oursi, Burkina; Maddalena & Ruedi 1994).

Description Very small to small shrew. Dorsal pelage cinnamon-brown with very short hairs. Ventral pelage pure white (Nigeria) to greyish. Head grey. Lips, chin and throat white. Fore- and hindfeet white. Hindfeet short. Tail of medium relative length (ca. 56% of HB), bicoloured, ashy-grey above, white below; pilosity 100%. Skull very flat and very small. Nipples: not known.

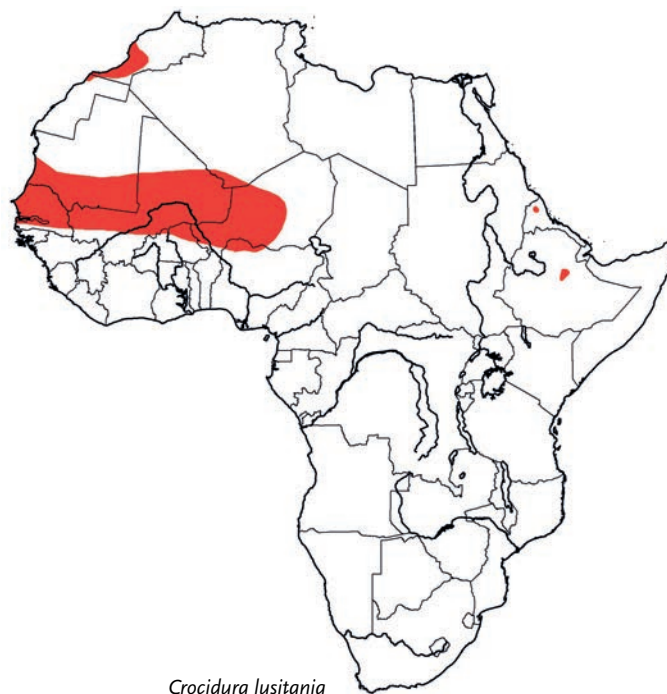
Geographic Variation None recorded.

Distribution Endemic to Africa. Sudan and Sahel Savanna BZs of West Africa and southern part of Mediterranean Coastal BZ. Recorded from Morocco, Mauritania, Senegal, Côte d'Ivoire, Burkina, Niger and N Nigeria. Two isolated records from Eritrea and Ethiopia (Aulagnier & Thévenot 1986, Happold 1987, Ag Sidiyène 1989, Hutterer 1993, Maddalena & Ruedi 1994).

Habitat Tree and bush savannas and traditionally cultivated fields in Senegal. Also present in sandy areas and coastal dunes along the Senegalese and Mauritanian coasts (Granjon *et al.* 1997, J.-M. Duplantier unpubl.). In Senegal, syntopic with *C. cinderella*, *C. fuscomurina*, *C. lamottei* and *C. olivieri* at Mbour, and probably with *C. viaria* and *C. lamottei* in *Acacia* bush savanna at Ferlo (J.-M. Duplantier unpubl.). Sometimes occupies termite mounds.

Abundance Can be locally abundant. Comprised nearly 50% of shrews trapped at Mbour, Senegal, between Sep and Dec 1988 (J.-M. Duplantier unpubl.). Comprised 50% of all prey in pellets of Barn Owls *Tyto alba* in Fètè-Olè, Senegal (Poulet 1982), and one-third of all shrews found in pellets of Barn Owls in the Senegal delta (Bâ *et al.* 2000).

Remarks Apparently no other information available.



Crocidura lusitania

Conservation IUCN Category: Least Concern.

Measurements

Crocidura lusitania

HB: 59.8 (45–68) mm, n = 9

T: 33.8 (29–37) mm, n = 9

HF: 9.4 (9–10) mm, n = 6

E: 5, 8 mm, n = 2

WT: 3.9 (3–5.1) g, n = 8

CI: 16.1 (15.1–17.0) mm, n = 14

GWS: 7.1 (6.7–7.6) mm, n = 13

I^1-M^3 : 6.9 (6.4–7.4) mm, $n = 14$

Mbour, Senegal (J.-M. Duplantier unpubl.); Fété Olè, Senegal (A. R. Poulet unpubl.); MNHN, ZFMK

Key References Heim de Balsac 1968a; Hutterer 1993.

L. Granjon & J.-M. Duplantier

Crocidura macarthuri **MACARTHUR'S SHREW**

Fr. Crocidure de MacArthur; Ger. MacArthurs Spitzmaus

Crocidura macarthuri St Leger, 1934. Ann. Mag. Nat. Hist., ser. 10, 13: 559. Merifano, 32 km from mouth of Tana River, Kenya.

Taxonomy Recorded from Somalia as *smithi* (e.g. Heim de Balsac 1966; see Hutterer 2005b). Synonyms: none. Chromosome number: not known.

Description Medium-sized shrew very similar to, but smaller than, *C. fischeri*. Dorsal pelage bluish-grey with brownish tinge. Ventral pelage white; hairs grey on basal half, white on terminal half. Upper lips, throat, behind ears, fore- and hindfeet white; hairs grey on basal half, white on terminal half. In some specimens, white hairs are washed with buff or grey. Tail of medium relative length (56% of HB), white, thick at base, tapering towards tip; pilosity not known. Nipples: not known.

Geographic Variation None recorded.

Distribution Endemic to Africa. Somalia–Masai Bushland BZ. Recorded in widely dispersed localities from S Kenya (Nguruman) to central Somalia (Belet Amin).

Habitat Wooded grassland with widely scattered tree species, e.g. *Acacia tortilis*, interspersed with *Themeda*, *Hyparrhenia* and *Cenchrus* grasses (S Kenya). These habitats are generally hot and daytime temperatures may reach 40 °C, and are marginal for agriculture.

Abundance Very rare. No quantitative information.

Remarks Apparently no other information available.

Conservation IUCN Category: Least Concern.

Should perhaps be classified as Data Deficient.

Measurements

Crocidura macarthuri

HB: 78–85 mm, $n = 5$

T: 35–45 mm, $n = 5$



Crocidura macarthuri

HF: 12–13 mm, $n = 5$

E: 7–10 mm, $n = 5$

WT: 11–13 g, $n = 6^*$

CI: 22.5–23.9 mm, $n = 5$

GWS: 9.6–9.7 mm, $n = 5$

I^1-M^3 : 9.7–10.7, $n = 5$

Kenya and Somalia (Hutterer 1986a; mean values not recorded)

*Includes one ♀ (11 g) from Nguruman, SE Kenya (N. O. Ogue unpubl.). Mean values not recorded

Key References Aggundey & Schlitter 1986; Hutterer 1986a.

N. Ogue

Crocidura macmillani **MACMILLAN'S SHREW**

Fr. Crocidure de Macmillan; Ger. Macmillans Spitzmaus

Crocidura macmillani Dollman, 1915. Ann. Mag. Nat. Hist., ser. 8, 15: 514. Koteke, Walamo, Ethiopia (ca. 06° 45' N, 37° 53' E). 1900 m.

Taxonomy Considered as a well-defined species of the endemic Ethiopian *glassi* complex (*C. glassi*, *C. lucina*, *C. thalia*, *C. macmillani* and *C. baileyi*) (Dippenaar 1980a, Dippenaar & Meester 1989). Although previously considered to be phylogenetically distant from

this endemic Ethiopian group (Bannikova *et al.* 2001), molecular phylogenetic analysis (Inter-SINE-PCR) supports the validity of the species (Bannikova *et al.* 2005). Formerly included in *C. fumosa* (Yalden *et al.* 1976) or *C. luna* (Heim de Balsac & Meester 1977,

Hutterer 1980). Synonyms: none. Chromosome number: $2n = 28$ (L. Lavrenchenko unpubl.).

Description Small-medium dark shrew with narrow skull. Dorsal pelage dark brownish-grey to blackish-grey; hairs grey at base, black at tip. Ventral pelage dark grey; hairs uniformly grey to dark grey. Upper surface of fore- and hindfeet dark grey. Tail relatively long (ca. 70% of HB), blackish-grey above, grey below; pilosity 75%. Skull narrow with inflated braincase as typical for the endemic Ethiopian *Crocidura*. Nipples: not known.

Geographic Variation None recorded.

Distribution Endemic to Africa. Afromontane–Afroalpine BZ. Known only from Koteke (06° 45' N, 37° 53' E), the Middle Godjeb Valley (07° 15' N, 36° 47' E) and Sheko Forest (07° 04' N, 35° 30' E) in Ethiopia.

Habitat Humid afromontane forests; humid woodland *Terminalia*–*Combretum* savanna with high grass.

Abundance Rare; known only from four specimens (L. Lavrenchenko & R. Hutterer unpubl.). Comprised 2.5% of 79 small mammals trapped in the Middle Godjeb Valley (L. Lavrenchenko unpubl.).

Remarks Apparently no other information available.

Conservation IUCN Category: Vulnerable.
Distribution very limited.

Measurements

Crocidura macmillani

HB: 77 (73–87) mm, $n = 3$

T: 55 (52–57) mm, $n = 3$



Crocidura macmillani

HF: 14.1 (13.8–14.5) mm, $n = 3$

E: 9, 9 mm, $n = 2$

WT: 8, 8 g, $n = 2$

CI: 22.6 (22.3–22.9) mm, $n = 3$

GWS: 9.9 (9.8–10.0) mm, $n = 3$

I¹–M³: 9.9 (9.8–10.0) mm, $n = 3$

Ethiopia (L. A. Lavrenchenko & R. Hutterer unpubl.)

Key References Bannikova *et al.* 2001, 2005; Dippenaar 1980a; Dippenaar & Meester 1989.

Leonid A. Lavrenchenko

Crocidura macowi NYIRO SHREW

Fr. Crocidure du Mont Nyiro; Ger. Nyiro-Spitzmaus

Crocidura macowi Dollman, 1915. Ann. Mag. Nat. Hist., ser. 8, 16: 378. Mt Nyiro, S of L. Rudolf [L. Turkana], Kenya.

Taxonomy Regarded as a synonym of *C. hildegardae* by Osgood (1936), but retained as a species by Heim de Balsac & Meester (1977), who noticed similarities to *C. niobe* (Hutterer 2005b). Synonyms: none. Chromosome number: not known.

Description Small shrew. Dorsal pelage dark brown. Ventral pelage greyish-brown or slate-grey. Fore- and hindfeet dark brown. Tail relatively long (ca. 80% of HB); pilosity ca. 55%. Third unicuspid larger than second; third upper molar medium in size, talonid of third lower molar with entoconid and talonid basin. Nipples: not known.

Geographic Variation None recorded.

Distribution Endemic to Africa. Somalia–Masai Bushland BZ. Known only from the type locality, Mt Nyiro, south of L. Rudolf (L. Turkana), Kenya.

Habitat No information.

Abundance No information.

Remarks Apparently no other information available.

Conservation IUCN Category: Data Deficient.

Previously considered as Critically Endangered. Major threats are human-induced habitat loss and degradation, and very restricted distribution.

Measurements

Crocidura macowi

HB: 71, 68 mm, n = 2

T: 58, 57 mm, n = 2

HF: 13.5, 13 mm, n = 2

E: 9.5, 8.5 mm, n = 2

CI: 19.7 mm, n = 1

GWS: 9.0 mm, n = 1

I¹–M³: 8.3 mm, n = 1

Kenya (BMNH; holotype and topotype). Weight not recorded.

Key References Dollman 1915d; Heim de Balsac & Meester 1977.

S. Churchfield & P. D. Jenkins



Crocidura macowi

Crocidura manengubae MANENGUBA SHREW

Fr. Crocidure des Monts Manengouba; Ger. Manenguba-Spitzmaus

Crocidura manengubae Hutterer, 1982. Bonn. Zool. Beitr. 32: 242. Lager III, L. Manenguba, Bamenda Highlands, Cameroon. 1800 m.

Taxonomy Synonyms: none. Chromosome number: not known.

Description Medium-sized brown shrew without any long hairs on tail. Pelage soft and dense; hairs 5–6 mm. Dorsal pelage medium-brown tinged russet; hairs grey on basal two-thirds, russet-brown on terminal third. Ventral pelage brownish-grey, contrasting slightly with dorsal pelage; hairs grey at base with pale brown, grey or beige at tip. Fore- and hindfeet dark russet-brown. Tail relatively long (ca. 75% of HB), very dark blackish-brown; pilosity 0%. First incisor long and hooked. Third incisor medium to wide. Nipples: not known.

Geographic Variation None recorded.

Distribution Endemic to Africa. Afromontane–Afroalpine BZ. Recorded only from the Bamenda and Adamaoua highlands, Cameroon. Unconfirmed report from highlands near Yaounde, Cameroon (see Heim de Balsac 1968d).

Habitat Swamp on the shoreline of L. Manenguba (an extinct crater lake), and in grass and shrub habitats close to the edge of the lake. The forested regions on the steeply sloping sides of the crater lake are also the only known habitat of *Praomys hartwigi*.

Abundance Very rare; known only by the holotype and paratype, and from remains in owl pellets.

Remarks Recorded from owl pellets in the Adamaoua highlands, Cameroon, near the border with Nigeria (Hutterer & Joger 1982).

Conservation IUCN Category: Vulnerable.



Crocidura manengubae

Measurements*Crocidura manengubae*

HB: 87, 77 mm, n = 2

T: 61, 62 mm, n = 2

HF: 16, 16 mm, n = 2

E: 11, 9 mm, n = 2

WT: 15, 13 g, n = 2

CI: 22.1, 21.5 mm, n = 2

GWS: 9.5, 9.3 mm, n = 2

I¹–M³: 9.4, 9.1 mm, n = 2

L. Manenguba, Cameroon (Hutterer 1982). Holotype and paratype respectively.

Key Reference Hutterer 1982.**Rainer Hutterer*****Crocidura maquassiensis* MAKWASSIE SHREW**

Fr. Crocidure de Maquassie; Ger. Makwassie-Moschusspitzmaus

Crocidura maquassiensis Roberts, 1946. Ann. Transvaal Mus. 20: 312. Klipkuil, Makwassie, Wolmaransstad district, North West Province, South Africa.**Taxonomy** Might be a southern form of *C. suaveolens* (Pallas, 1811) – a Palaearctic species – and may be closely related to *C. pitmani* (Meester *et al.* 1986). Synonyms: *malani*. Subspecies: none. Chromosome number: not known.**Description** Very small to small shrew. Dorsal pelage grey-brown washed with grey; hairs slaty-grey with a fawn subterminal annulation and brown tip. Ventral pelage grey tinged with fawn; hairs slaty-grey with pale grey tip. Colours of dorsal and ventral pelage merge on flanks. Head slender with long, narrow pointed muzzle, small eyes and rounded ears. Fore- and hindfeet pale brown. Tail relatively long (ca. 71% of HB), dark brown above, paler below; pilosity ca. 70%. Nipples: 0 + 3 = 6.**Geographic Variation** None recorded.**Distribution** Endemic to Africa. Southern part of Zambezan Woodland BZ. Distribution disjunct, generally restricted to rocky or montane habitats above 1500 m (two specimens known from coastal northern KwaZulu–Natal, South Africa). Recorded from Zimbabwe (Nyamaziwa Falls, Inyanga; Matopo Hills), Swaziland (Mantenga Falls), South Africa (North West, Limpopo, Gauteng, Mpumalanga and KwaZulu–Natal Provinces).**Habitat** Montane vegetation or rocky areas (Meester 1963); but P. Taylor (1998) suggests a broader habitat preference.**Abundance** Rare. Although known from Swaziland, not recorded during recent extensive mammal surveys (A. Monadjem unpubl.).**Remarks** One pregnant ♀ collected in Oct contained three embryos (Skinner & Smithers 1990).**Conservation** IUCN Category: Least Concern.**Measurements***Crocidura maquassiensis*

HB: 62.2 (54.5–74) mm, n = 3

*Crocidura maquassiensis*

T: 44.3 (43–46) mm, n = 3

HF: 11.3 (11–11.5) mm, n = 3

E: 8.3 (8–9) mm, n = 3

WT: n. d.

CI: 18.5 (17.6–19.2), n = 9

GWS: 8.6 (8.3–8.7), n = 9

I¹–M³: 7.7 (7.6–7.7), n = 3

Southern Africa (Meester 1963, N. J. Dippenaar unpubl.)

Key References Meester 1963; Skinner & Smithers 1990; Taylor, P. 1998; Taylor *et al.* 1994.**R. M. Baxter & N. J. Dippenaar**

Crocidura mariquensis SWAMP SHREW

Fr. Crocidure des marais; Ger. Sumpf-Moschusspitzmaus

Crocidura mariquensis (A. Smith, 1844). Illustr. Zool. S. Afr. Mamm. pl. 44, fig. 1. 'A wooded ravine near the Tropic of Capricorn'
(= Marico River near its junction with Limpopo River, North West Province, South Africa).

Taxonomy Originally described in the genus *Sorex*. Synonyms: *neavei*, *pilosa*, *shortridgei*, *sylvia*. Subspecies: three. Chromosome number: not known.

Description Small-medium to medium-sized shrew. Dorsal pelage blackish-brown grizzled lightly with reddish-fawn; hairs slaty-grey at base, with reddish-fawn to reddish-brown subterminal bands and blackish-brown tip. Ventral pelage paler; dark brown grizzled with fawn; hairs slaty-grey at base, fawn to pale brown at tip. Colours of dorsal and ventral pelage merge on flanks. Head slender with long, narrow pointed muzzle, small eyes and rounded ears. Fore- and hindfeet yellowish-brown, brown or blackish-brown. Tail relatively long (ca. 70% of HB), brown, reddish-brown to blackish-brown above, sometimes paler below; pilosity 26–53% (see below). There is distinct geographical variation and sexual dimorphism in size (see below; also Dippenaar 1977, 1979b). Nipples: 0 + 3 = 6.

Geographic Variation

C. m. mariquensis: South Africa, Swaziland, S Mozambique. Dark subspecies; pilosity 51%.

C. m. neavei: SC Angola; SE DR Congo, Zambia. Dark subspecies; smaller than *C. m. mariquensis*; pilosity ca. 26%.

C. m. shortridgei: NE Namibia, Botswana (Okavango Delta, along the Chobe R. and south to Maun), extreme NW Zimbabwe. Pale subspecies; pilosity 35%.

Distribution Endemic to Africa. Zambezan Woodland BZ, parts of Highveld BZ and marginally into the Coastal Forest Mosaic BZ (in South Africa). Distribution disjunct. Restricted to marshes and inundated grasslands in three distinct regions: (a) C Angola, SE DR Congo, and W and C Zambia; (b) NE Namibia, N Botswana and extreme NW Zimbabwe; (c) N and NE South Africa, Swaziland and S Mozambique (Dippenaar 1977, Heim de Balsac & Meester 1977, Ansell 1978, Monadjem 1998a, c).

Habitat Riverine and semi-aquatic vegetation and reed-beds; only found in close proximity to open water, with a distinct preference for marshy conditions (Dippenaar 1977). Very strict habitat requirements.

Abundance Relatively common in suitable habitats. On the Kafue Flats, Zambia, populations highest in the wet season and early dry season; comprised 37% (57 of 153) of all species of shrews (4 spp.) captured during one year, and was the commonest species of shrew (*C. hirta* 35%, *C. occidentalis* 27%) (Sheppe 1973).

Adaptations The digits of hindfeet are conspicuously splayed when walking and this may be an adaptation to marshy habitats (Baxter & Meester 1980). In Zambia (Kafue Flats), during the wet season (Jan–Jul), 40% of individuals ($n = 48$) contained fat reserves whereas none ($n = 8$) contained fat in dry season (Aug–Dec; Sheppe 1973).

*Crocidura mariquensis*

Foraging and Food Feeds on snails and termites in captivity (Baxter & Meester 1980).

Social and Reproductive Behaviour Predominantly nocturnal (Baxter *et al.* 1979), although some authors record diurnal activity as well (e.g. Rautenbach 1982). When moving, the tail may uniquely be curved slightly upwards (Baxter & Meester 1980). This species is particularly active and agile (compared with other species) and shows little or no animosity towards conspecifics (Goulden & Meester 1978, Baxter & Meester 1980). Vocalizations include short, sharp squeaks and short 'chirrs' during aggressive encounters. Scent-marking has not been observed, although both the body of the shrew and the faecal piles are strongly scented. Digging and rooting behaviour are virtually absent. Nests are not actively built in captivity but an individual will creep into nesting material where, by moving about, it makes a hollow (Baxter & Meester 1980). One instance of a spherical nest is known (Meester 1963). In the field, nests have been found deep in clumps of tussock grass and in debris about 30 cm above ground.

Reproduction and Population Structure In South Africa, reproductive activity in the subspecies *mariquensis* has been recorded during the wet season (Sep–Feb); litter-size: 4.1 (2–7), $n = 18$ (Taylor, P. 1998, R. M. Baxter unpubl.). In Botswana, reproductive activity in the subspecies *shortridgei* occurs during the wetter warmer months of the year (Aug–Apr); embryo number: 3.3 (range 2–5), $n = 22$ (Smithers 1971). In Zambia (Kafue Flats), three pregnant

♀ ♀ found in Aug, and one each in Sep and Oct (Flats flooded); and one each in Feb and Apr (wet season); embryo number: 3.8 (range 2–5), $n = 6$ (Sheppe 1972, 1973).

Predators, Parasites and Diseases Preyed on by Fiscal Shrikes *Lanius collaris* (Meester 1963), Barn Owls *Tyto alba* and African Grass-owls *Tyto capensis* (Vernon 1972).

Conservation IUCN Category: Least Concern.
Destruction of wetlands could threaten this species.

Measurements

Crocidura mariquensis shortridgei

HB (♂ ♂): 82 (63–105) mm, $n = 108$

HB (♀ ♀): 77 (62–90) mm, $n = 68$

T (♂ ♂): 62 (45–72) mm, $n = 106$

T (♀ ♀): 56 (45–71) mm, $n = 67$

HF (♂ ♂): 17 (15–20) mm, $n = 110$

HF (♀ ♀): 16 (14–19) mm, $n = 69$

E (♂ ♂): 9 (7–11) mm, $n = 108$

E (♀ ♀): 9 (6–10) mm, $n = 68$

WT (♂ ♂): 11.7 (9.8–16.5) g, $n = 46$

WT (♀ ♀): 9.0 (6.1–13.9) g, $n = 50$

CI (♂ ♂): 20.8 (19.2–21.9), $n = 66$

CI (♀ ♀): 19.8 (18.3–21.7), $n = 41$

GWS (♂ ♂): 9.0 (8.3–9.5), $n = 62$

GWS (♀ ♀): 8.7 (8.2–9.1), $n = 35$

I¹–M³ (♂ ♂): 8.8 (8.4–9.4), $n = 21$

I¹–M³ (♀ ♀): 8.5 (8.2–9.0), $n = 21$

Kasane, Botswana (Dippenaar 1979b)

WT from Smithers (1971); I¹–M³ from Dippenaar (1977)

The two other subspecies are slightly smaller

Key References Baxter & Meester 1980; Dippenaar 1977, 1979b.

R. M. Baxter & N. J. Dippenaar

Crocidura maurisca GRACILE NAKED-TAILED SHREW (DARK SHREW)

Fr. Crocidure maure; Ger. Grazile Nacktschwanzspitzmaus

Crocidura maurisca Thomas, 1904. Ann. Mag. Nat. Hist., ser. 7, 14: 239. Entebbe, Uganda.

Taxonomy The 23 specimens from Kaimosi, Kenya, named as *maurisca* (Hollister 1918) are now considered to represent *C. littoralis* (Dieterlen & Heim de Balsac 1979). Belongs to the *C. maurisca*–*littoralis* species-group (Hutterer 2005b). Synonyms: none. Chromosome number: not known.

Description Medium-sized greyish-black shrew. Dorsal hairs long (7–8 mm). Dorsal pelage black. Ventral pelage grey. Upper surface of fore- and hindfeet black (as dorsal pelage). Hindfeet relatively long (20% of HB). Tail relatively very long (ca. 89% of HB), with dense short hairs; pilosity: 10–15%. Skull with long rostrum, narrow maxillary width (5.75–6.2 mm), elongate maxillary unicusps with small cusps and large cingula. Males are mostly larger than ♀ ♀ (see Measurements). Nipples: not known.

Geographic Variation None recorded.

Distribution Endemic to Africa. Eastern Rainforest–Savanna Mosaic. Only recorded with certainty from six localities, mostly high elevation swamps in Uganda (Echuya, Mubwindi, Ngoto), and Burundi, and one record from Gitebe (near Rutshuru), E DR Congo (Dieterlen & Heim de Balsac 1979). A single record of an unsexed, young specimen from Gabon (Goodman *et al.* 2001) at 600 m is far removed from the main distribution of the species and needs verification. The species has not been collected at the type locality (Entebbe) since described (see above) and it is possible that it was not collected there. Specimens from Kaimosi, Kenya (Hollister 1918) are probably *C. littoralis* (Dieterlen & Heim de Balsac 1979).

Habitat Prefers montane sedge swamps of the Albertine Rift Valley (1500–2400 m). In Kibira National Park (Burundi, 2180 m),



Crocidura maurisca

and Echuya and Mubwindi Swamps (Uganda, 2380 and 2070 m), the typical habitat is sedge swamp with water-loving herbs, bracken and shrubs (*Hypericum* sp., *Rubus* sp. and *Brillantasia cicatricosa*). A single record comes from Ngoto Swamp (a papyrus swamp, 1500 m), while another came from the edge of shallow stream adjacent to the sedge habitat in Burundi.

Abundance Although exceedingly rare, may be relatively common in its restricted favoured habitats; comprised 15% of captured small mammals in Echuya Swamp and was one of the most common species (28%) within a sedge meadow in the Gitenge Valley, Kibira N. P., Burundi.

Remarks Although mostly nocturnal (84%, $n = 18$), some individuals were collected during the day. The relatively long hindfeet may be an adaptation to the swampy environment. Stomach contents have yielded remains from the following invertebrate groups: Orthoptera, Homoptera, Araneida and Diptera (FMNH). Trapping results in more ♂♂ (8 of 9 specimens in Burundi, and 6 of 8 specimens in Uganda) than ♀♀. Information on reproduction not available.

Conservation IUCN Category: Least Concern.

Measurements

Crocidura maurisca

HB (♂♂): 88.5 (79–97) mm, $n = 14$

HB (♀♀): 79 (75–81) mm, $n = 5$

T (♂♂): 67.7 (60–72) mm, $n = 14$

T (♀♀): 62 (60–64) mm, $n = 5$

HF (♂♂): 18 (17–19.5) mm, $n = 14$

HF (♀♀): 16 (14.5–17) mm, $n = 5$

E (♂♂): 8.7 (8–10) mm, $n = 13$

E (♀♀): 8.5 (8–9) mm, $n = 4$

WT (♂♂): 13 (10–18) g, $n = 14$

WT (♀♀): 9.2 (8.3–10) g, $n = 4$

CI (♂♂): 21.8 (21.3–22.7) mm, $n = 11$

CI (♀♀): 20.6 (20.0–20.9) mm, $n = 5$

GWS (♂♂): 9.6 (9.3–9.8) mm, $n = 10$

GWS (♀♀): 9.3 (9.2–9.4) mm, $n = 5$

I¹–M³ (♂♂): 9.1 (8.8–9.6) mm, $n = 12$

I¹–M³ (♀♀): 8.7 (8.5–8.9) mm, $n = 5$

Burundi (FMNH), Uganda (BMNH holotype, FMNH)

Key References Dieterlen & Heim de Balsac 1979.

Julian C. Kerbis Peterhans & Sean O. Bober

Crocidura monax KILIMANJARO SHREW (ROMBO SHREW)

Fr. Crocidure du Mont Kilimanjaro (Crocidure de Rombo); Ger. Kilimanjaro-Spitzmaus

Crocidura monax Thomas, 1910. Ann. Mag. Nat. Hist., ser. 8, 6: 310. Rombo, Mt Kilimanjaro, Tanzania. 6000 ft (1829 m).

Taxonomy Considered to be distinguishable from *C. littoralis*, but part of the *monax*–*littoralis* species-complex (Dieterlen & Heim de Balsac 1979, Hutterer 1993). Heim de Balsac & Meester (1977) considered *ultima* to be a subspecies of *C. monax*, but Hutterer (1993) recognized *C. ultima* as a distinct species. Burgess *et al.* (2000a) considered that *monax* was endemic to Mt Kilimanjaro, while Stanley *et al.* (1998a) listed it from a number of mountains in N Tanzania. Synonyms: none. Chromosome number: not known.

Description Small–medium shrew with rich brown pelage. Hairs 6 mm on back, 5.5 mm on shoulders, 4.5 mm on ventral surface. Dorsal pelage rich brown; hairs steel-grey at base, brown at tip. Ventral pelage similar in colour to dorsal pelage; hairs pale brown at tip. Ears visible but not prominent. Fore- and hindlimbs slightly paler than dorsal pelage. Claws on forefeet 1.9 mm; on hindfeet 2.4 mm. Tail relatively long (70% of HB), very dark above, paler below; pilosity ca. 50%. Nipples: not known.

Geographic Variation None recorded.

Distribution Endemic to Africa. Afromontane–Afroalpine BZ. Montane habitats of W Kenya (Amala R.) and Tanzania. Recorded from Amala R. in W Kenya, Mt Kilimanjaro, and some of the Eastern Arc Mountains in Tanzania, including the West Usambara and Uluguru Mountains (Allen & Loveridge 1927, Aggundey & Schlitter 1986, Hutterer 1993, Stanley *et al.* 1998a).

Habitat Moist undisturbed montane forest. Not observed in disturbed forests or agricultural areas at the same elevation.



Crocidura monax

Abundance The most numerous species in undisturbed forest in the West Usambara Mts, comprising 77% of shrews sampled ($n = 26$) (W.T. Stanley unpubl.).

Remarks No juveniles of this species were recorded while sampling shrews in the West Usambara Mts in Jul–Sep 1991–1993. Within the same sample, the ♂ : ♀ ratio was 17 : 5 ($n = 22$). No

pregnant ♀♀ were recorded, and ♂♂ had testes lengths of 3–6 mm and widths of 2–4 mm (W.T. Stanley unpubl.).

Conservation IUCN Category: Least Concern.

Probably Vulnerable because of fragmented distribution and decline in suitable habitat.

Measurements

Crociodura monax

HB: 77 (70–84) mm, n = 21*

T: 66 (60–71) mm, n = 21

HF: 16 (15–17) mm, n = 21

E: 10 (10–12) mm, n = 21

WT: 14 (10–16) g, n = 21

CI: 23.7 (22.9–24.3) mm, n = 13

GWS: 10.7 (10.1–11.0) mm, n = 13

I¹–M³: 10.4 (10.1–10.8) mm, n = 13

West Usambara Mts, Tanzania (W.T. Stanley unpubl.)

*HB calculated by subtracting tail length from total length

Key Reference Allen & Loveridge 1927.

William T. Stanley

Crociodura montis MONTANE SHREW (MONTANE WHITE-TOOTHED SHREW)

Fr. Crocidure de montagne d'Afrique; Ger. Hochland-Weißzahnschneckenmaus

Crociodura montis Thomas, 1906. Ann. Mag. Nat. Hist., ser. 7, 18: 138. Rwenzori East, Uganda. 12,000 ft (= Bujongolo, Mubuku Valley, E slope of Mt Rwenzori, Uganda; see Dippenaar & Meester 1989).

Taxonomy Formerly included in *C. fumosa* but separated by Dippenaar & Meester (1989). Synonyms: none. Chromosome number: not known.

Description Small-medium, very dark shrew. Pelage soft and dense; hairs ca. 4 mm. Dorsal pelage and ventral pelage very dark brown to blackish-brown; hairs dark grey on basal half, dark brown with slight russet tinge on terminal half. Head similar in colour to dorsal pelage. Ears small, partially concealed by pelage. Fore- and hindfeet pale golden-brown to brown. Tail relatively long (ca. 72% of HB), dark blackish-brown; pilosity 60–70% (mean 70%, range 51–89%, n = 75; Dippenaar & Meester 1989). Skull compact. Rostrum short, interorbital region wide, braincase rounded in dorsal and inflated in lateral view. Infraorbital bridge wide. First incisor long and hooked; third molar wide. Molariform teeth wide and contrasting with the row of small unicuspid. Nipples: not known.

Geographic Variation None recorded.

Distribution Endemic to Africa. Afromontane–Afroalpine BZ of eastern Africa. Recorded from Mt Kilimanjaro, Ngorongoro Crater and Mt Meru (Tanzania), Mt Rwenzori and Mt Elgon (Uganda), Imatong Mts (S Sudan) and Cherangani Hills and Mt Kenya (Kenya). Also occurs in a few other isolated montane habitats (details in Dippenaar & Meester 1989). Distribution disjunct. The record of this species in Bwindi Impenetrable N. P., Uganda, is in error (J. Kerbis, *in litt.*).

Habitat Montane forests on Mt Meru (Demeter & Hutterer 1986). On Mt Elgon, Uganda (Clausnitzer *et al.* 2003), was recorded from a variety of habitats at 3200–4120 m including *Erica* forest (3460 m), grassland/*Erica* forest (3200 m), montane grassland (3870 m), *Alchemilla* shrub (3850 m), and in bogs in montane grasslands (3590 and 4120 m); it occurred in both dry and wet boggy sites, although dry sites (85% of 93 captures) were preferred; not recorded in montane forest (cf. Mt Meru).

Abundance In preferred habitats on Mt Elgon (montane grasslands, *Erica* forest and *Alchemilla* shrub), *C. montis* comprised 59% (n = 131) of the two insectivorous small mammals (i.e. *Lophuromys flacopunctatus* and this species) (Clausnitzer *et al.* 2003). On Mt Meru, Tanzania, it was the commonest (79%) of two species of shrews on the escarpment at 'Meru East' (1550–2750 m) (*C. montis*: 26 of 33; cf. *C. allex*: 7 of 33; Demeter & Hutterer 1986).

Remarks Sympatric with *C. allex* on Mt Kilimanjaro and Mt Meru. The only species of shrew at higher altitudes on Mt Elgon. May be confused with *C. fumosa* in other parts of East Africa. Generalist, opportunistic insectivore. Primarily insectivorous, with lesser amounts of other invertebrates. On Mt Elgon, Uganda, feeds on 20 groups of invertebrates; the commonest food items



Crociodura montis

(as assessed by frequency of occurrence in stomach contents, in order of frequency) were Araneae, adult Coleoptera, Lepidoptera larvae and earthworms. Less frequently eaten foods were Coleoptera larvae, adult Diptera, Heteroptera and Diplopoda, as well as small amounts of other invertebrates. Seeds and plant leaves/stems occurred in 35–42% of stomachs (% frequency of occurrence; $n = 40$ stomachs; Clausnitzer *et al.* 2003). This species and *Lophuromys flavopunctatus* are the only insectivorous small mammals at the higher elevations of Mt Elgon. The dietary overlap of the two species is 36%; *C. montis* eat fewer Diptera larvae and earthworms, and more adult Coleoptera and Araneae, than *L. flavopunctatus*. Both species consumed seeds to a similar extent (ca. 7% dietary occurrence), but *C. montis* ate far less vegetable material (ca. 6% dietary occurrence) than *L. flavopunctatus* (ca. 27% dietary occurrence) (Clausnitzer *et al.* 2003).

Conservation IUCN Category: Least Concern.

Rainer Hutterer

Crocidura muricauda WEST AFRICAN LONG-TAILED SHREW (MOUSE-TAILED SHREW)

Fr. Crocidure à queue de souris; Ger. Westafrikanische Langschwanzspitzmaus

Crocidura muricauda (Miller, 1900). Proc. Wash. Acad. Sci. 2: 645. Mount Coffee, Liberia.

Taxonomy Originally described in the genus *Myosorex*. Formerly included as a subspecies in *C. dolichura* but differs from this species by the hairiness of tail (cf. no long hairs on tail of *C. dolichura*) (Hutterer & Happold 1983). Genetically not closely related to *C. dolichura* (Quérrouil *et al.* 2005). May include different morphological forms, perhaps representing sibling species (Quérrouil *et al.* 2005). Synonyms: none. Chromosome number: not known.

Description Small shrew with large ears and long tail. Pelage soft; hairs ca. 3 mm. Dorsal pelage greyish-brown; hairs grey at base, brown at tip. Ventral pelage whitish-grey; hairs grey at base, white at tip. Head similar in colour to dorsal pelage. Ears large in relation to head, more or less naked. Fore- and hindfeet flesh-coloured, sparsely covered with short white hairs. Tail pale brown, extremely long (120–150% of HB), not bicoloured; tail hairs tend to be short and less visible than in other *Crocidura*; pilosity varies from 50 to 80%. Skull long and narrow, braincase round in dorsal view and inflated in lateral view. Rostrum slender. First incisor small. Upper dentition weak, third molar large (Miller 1900, Heim de Balsac & Aellen 1958). Nipples: not known.

Geographic Variation High variability of tail length, pilosity and genetic distances suggest that more than one species is included in *C. muricauda* (Quérrouil *et al.* 2005).

Distribution Endemic to Africa. Rainforest BZ (Western Region). Recorded from Sierra Leone, Liberia, SE Guinea, Côte d'Ivoire and W Ghana.

Habitat Rainforest and secondary forest. Sibling forms also found in degraded forest, including plantations and fields.

Abundance Locally common. Comprised 21.5% of all shrews captured ($n = 553$) in Tã N. P. with pit traps, and the second

Measurements

Crocidura montis

HB: 78 (63–95) mm, $n = 78$

T: 56 (46–69) mm, $n = 77$

HF: 15 (10–17) mm, $n = 79$

E: 10 (6–12) mm, $n = 72$

WT: n. d.

CI: 21.7 (19.9–23.0) mm, $n = 62$

GWS: 10.2 (9.6–10.8) mm, $n = 58$

I¹–M³: 9.5 (8.6–10.3) mm, $n = 80$

Throughout geographic range (except Mt Elgon) (Dippenaar & Meester 1989)

Key References Clausnitzer *et al.* 2003; Dippenaar & Meester 1989.

most numerous species of shrew ($n = 10$ spp.) (Churchfield *et al.* 2004). Rare in cocoa–coffee plantations in Tã N. P. (Barrière *et al.* 1999). In Ziama Biosphere Reserve, Guinea, the commonest species in primary forest (32%, $n = 500$, 11 spp.) and secondary forest (28.4%, $n = 509$, 10 spp.), but uncommon in young forest plantations (8%, $n = 303$, 10 spp.) and fields (6%, $n = 272$, 9 spp.) (P. Barrière, unpubl.). Surveys with snap traps yield lower values, such as 4.3% in the Mt Nimba area ($n = 96$) (Heim de Balsac 1958).



Crocidura muricauda

Remarks A climbing species, as is *C. dolichura* (Heim de Balsac & Aellen 1958). Diet includes a wide range of invertebrates (Churchfield *et al.* 2004). The commonest prey items (% frequency of occurrence) in 44 stomachs in Taï N. P., Côte d'Ivoire, were representatives of the following taxa: Araneae (55%), ants (44%, several families), Gryllidae (23%), Blattodea (14%), adult Coleoptera (14%) and Lepidoptera larvae (9%). Twelve other taxa were also present (at values less than 7% frequency of occurrence). Most of the prey was 10 mm or less in size.

Conservation IUCN Category: Least Concern.

Measurements

Crocidura muricauda

HB: 61 (56–66) mm, $n = 5$

T: 77 (62–95) mm, $n = 5$

HF: 12.2 (11.8–13) mm, $n = 5$

E: 9 (8.5–10) mm, $n = 4$

WT: 4.4 (3–8) g, $n = 26$

CI: 18.2 (17.8–18.8) mm, $n = 4$

GWS: 8.4, 8.4 mm, $n = 2$

I^1 – M^3 : 8.1 (7.8–8.4) mm, $n = 5$

Measurements: Liberia, Côte d'Ivoire (Miller 1900), Guinea (Heim de Balsac & Aellen 1958, and unpubl.)

Weight: Côte d'Ivoire (Churchfield *et al.* 2004)

Key References Churchfield *et al.* 2004; Heim de Balsac & Aellen 1958.

Rainer Hutterer

Crocidura mutesae UGANDAN SHREW (UGANDAN MUSK SHREW)

Fr. Crocidure d'Uganda; Ger. Uganda-Moschusspitzmaus

Crocidura mutesae Heller, 1910. *Smithson. Misc. Coll.* 56 (15): 3. Kampala, Uganda.

Taxonomy Alternatively assigned to *C. hirta* (Allen 1939) or *C. suahelae* (Heim de Balsac & Meester 1977). Recorded as *C. mutesae* from Central African Republic (Ray & Hutterer 1995). The taxonomic status is far from being settled (Hutterer 2005b), but for the present the species is considered to be valid pending further studies. A study of 16s rRNA sequences revealed that eight specimens of *C. cf. mutesae* from Central African Republic exhibited eight different haplotypes, five of which were shared with *C. olivieri*. These haplotypes were interspersed with those of *C. olivieri* and *C. goliath* (Quéroutil *et al.* unpubl.). Synonyms: none. Chromosome number: $2n = 50$ (NW DR Congo; R. Hutterer & B. Robbins unpubl.).

Description Very large shrew with thick hairy tail and long pelage. Dorsal and ventral pelage greyish. Feet and tail darker in colour. Hindfeet long and broad. Tail relatively long (ca. 60–75% of HB), dark with tightly packed long bristles (10–12 mm); pilosity 70–80%. Similar to *C. olivieri*, but size is at the lower limit (or below) of the size range of that species. Skull shape similar to *C. olivieri* but less robust and smaller in size (see Hollister 1918: plate 8, figs. 1–2). Nipples: not known.

Geographic Variation None recorded.

Distribution Endemic to Africa. Rainforest BZ (West Central Region, Gabon sub-region) and Eastern Rainforest–Savanna Mosaic. Morphotype described from Kampala, Uganda, and identified as such from SW Central African Republic (Hutterer 1993, Ray 1996, Ray & Hutterer 1995, Morvan *et al.* 1999, Barrière *et al.* 2000) and N DR Congo (R. Hutterer & B. Robbins unpubl.).

Habitat In SW Central African Republic, four (of 12 individuals) were captured in unlogged forest, four in mono-dominant *Gilbertiodendron dewevrei* forest and four in secondary forest along

logging roads. The preferred habitat is where the understorey is relatively open (Ray 1996).

Abundance Comprised 33.3% of shrews ($n = 36$) captured in a mosaic of primary and secondary forest habitats at Salo, Central African Republic (Morvan *et al.* 1999).

Remarks Found in 2.3% of 311 small carnivore scats collected in Dzanga-Sangha, Central African Republic (Ray & Hutterer 1995, Ray 1998).

Conservation IUCN Category: Data Deficient.



Crocidura mutesae

Measurements*Crocidura mutesae*

HB: 115 mm

T: 64 mm

HF: 16 mm

E: n. d.

WT: n. d.

CI: 24.6 mm

GWS: 11.0 mm

I¹–M³: 11.3 mm

Uganda (holotype; Hollister 1918)

Key References Hollister 1918; Ray 1998.**Justina C. Ray & Rainer Hutterer*****Crocidura nana* SOMALI DWARF SHREW**

Fr. Crocidure naine; Ger. Somalia-Zwergspitzmaus

Crocidura nana Dobson, 1890. Ann. Mag. Nat. Hist., ser. 6, 5: 225. Dollo, Somalia.

Taxonomy The name *C. nana* has been given to various small shrews of Somalia, Ethiopia and Egypt, leading to the proposal (Setzer 1957) that *C. nana* is conspecific with *C. religiosa* (which it does not antedate), a conclusion followed by Heim de Balsac & Mein (1971) and Osborn & Helmy (1980). However, the holotype of *C. nana* is a juvenile of a species that is larger than the holotype of *C. religiosa* (Hutterer 1993), and hence the proposal that *C. nana* is conspecific with *C. religiosa* is not acceptable (see Corbet 1978, Hutterer 1993). The relationship of *C. nana* to other very small species has yet to be clarified. Synonyms: none. Chromosome number: not known.

Description Minute shrew. Dorsal hairs short (3–4 mm). Dorsal pelage and flanks slaty-brown. Ventral pelage greyish-white. Upper surface of fore- and hindfeet white. Tail relatively long (ca. 75% of HB), finely haired, dull brown above, white below; numerous whitish bristles on tail. Pilosity 90%. Skull very small with markedly flattened braincase; maxillary region rather narrow; teeth very small; third upper unicuspid a little broader than second (Dollman 1916); talonid of third lower molar reduced to a single cusp. Nipples: not known.

Geographic Variation None recorded.

Distribution Endemic to Africa. Somalia–Masai Bushland BZ. Recorded at lower altitudes in Somalia and Ethiopia (Heim de Balsac & Meester 1977).

Habitat Little information; appears to inhabit dry grassland and scrub.

Abundance No information; rarely collected.

Remarks Apparently no other information available.

Conservation IUCN Category: Least Concern.

*Crocidura nana***Measurements***Crocidura nana*

HB: 40 mm*

T: 30 mm*

HF: 8.5 mm*

E: n. d.

CI: 15.8, 16 mm, n = 2

GWS: 7.0, 7.0 mm, n = 2

I¹–M³: 6.4, 6.8 mm, n = 2

Somalia (Dollman 1916, BMNH)

*Dried preserved specimen

Key References Dollman 1916; Heim de Balsac & Meester 1977; Hutterer 2005b.

S. Churchfield & P. D. Jenkins

Crocidura nanilla SAVANNA DWARF SHREW (TINY WHITE-TOOTHED SHREW)

Fr. Crocidure naine de savane; Ger. Savannen Zwergspitzmaus

Crocidura nanilla Thomas, 1909. Ann. Mag. Nat. Hist., ser. 8, 4: 499. Uganda, probably Entebbe.

Taxonomy Determination of this species is difficult because of its similarity to *C. pasha* (Heim de Balsac & Verschuren 1968). Synonyms: *denti*, *nancilla* (*lapsus* for *nanilla*), *rudolfi*. Subspecies: none. Chromosome number: uncertain. (Maddalena & Ruedi 1994, quoted by Hutterer 2005b, give a chromosome number of $2n = 42$, $FN = 74$ from Côte d'Ivoire, a location which is not considered to be within the range of the species.)

Description Minute to very small dark shrew. Pelage short and dense (hairs ca. 3 mm). Dorsal pelage dark greyish-brown to dark blackish-brown; hairs brown on terminal third. Ventral pelage medium grey, paler than dorsal pelage; hairs grey on basal half, pale grey to whitish-grey on terminal half. Colours of dorsal and ventral pelage merge on lower flanks. Colour of head similar to dorsal pelage. Chin and throat white or grey. Fore- and hindfeet dark brown, well covered with short hairs. Tail relatively long (ca. 70% of HB), dark brown above, paler below; pilosity 85%. Dorsal surface of skull convex, and crowns of teeth relatively high (Heim de Balsac 1968a). First incisor long and hooked. Third molar medium. Nipples: not known.

Geographic Variation Pelage colour varies geographically: dorsal pelage dark (e.g. Guinea) to grey with slight rufous tinge (Senegal).

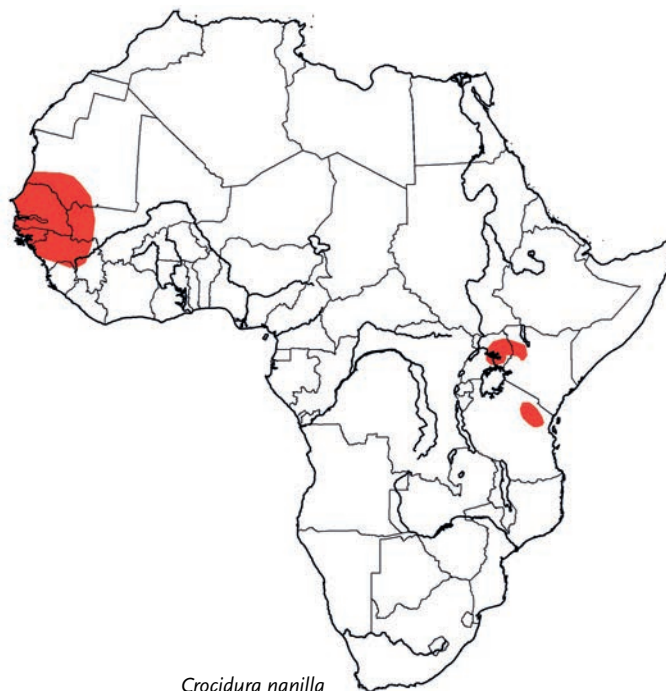
Distribution Endemic to Africa. Sahel and Sudan BZs of West Africa; Eastern Rainforest–Savanna Mosaic and part of Somalia–Masai BZ of eastern Africa. Distribution very disjunct. Recorded from Mauritania to Kenya, Uganda and Tanzania. Limits of distribution uncertain.

Habitat Dry and moist savanna (Hutterer 1993). One individual was found in irrigated crops at Richard-Toll, Senegal (L. Granjon unpubl.).

Abundance No detailed information; rarely captured. Only one specimen captured (out of 172 shrews, 13 spp.) in Garamba N. P., DR Congo (Heim de Balsac & Verschuren 1968).

Remarks Remains of this species (and the similar *C. pasha*) found in owl pellets in Kagera N. P., Rwanda (Heim de Balsac & Verschuren 1968).

Conservation IUCN Category: Least Concern.

*Crocidura nanilla***Measurements***Crocidura nanilla*HB: 41, 58 mm, $n = 2$ T: 31, 41 mm, $n = 2$ HF: 8.2, 10.5 mm, $n = 2$ E: 6.3, 8 mm, $n = 2$

WT: n. d.

CI: 15, – mm, $n = 2$ GWS: 6.8, – mm, $n = 2$ I^1 – M^3 : 6.2, 6.7 mm, $n = 2$

Uganda (1st measurement: holotype, measured in alcohol; Thomas 1909) and Senegal (2nd measurement: L. Granjon, unpubl.)

Key Reference Heim de Balsac 1968a.

D. C. D. Happold

Crocidura nigeriae NIGERIAN SHREW (NIGERIAN MUSK SHREW)

Fr. Crocidure du Nigeria; Ger. Nigeria-Moschusspitzmaus

Crocidura nigeriae Dollman, 1915. Ann. Mag. Nat. Hist., ser. 8, 15: 524. Asaba ('150 miles up the Niger'), Nigeria.

Taxonomy Very similar in size and colour to *C. longipes*, *C. grandiceps* and *C. foxi*. Previously referred to as *C. occidentalis nigeriae* and *C. poensis nigeriae* (e.g. Happold 1977). Formerly included in *poensis* (*C. p. nigeriae*) but see Heim de Balsac (1957b), Meylan & Vogel

(1982) and Hutterer & Happold (1983). Both *C. nigeriae* and *C. poensis* show considerable variation in colour, specimens of both species from Cameroon being much darker than those from Nigeria. Size and shape of skull, and karyotype, provide distinguishing characters.

Karyotype is identical to that of *C. batesi*, and the two species may be conspecific (Hutterer 2005b). Synonyms: none. Chromosome number: $2n = 50$, $FN = 76$ (Meylan & Vogel 1982).

Description Large shrew. Dorsal pelage very dark brown with a grizzled appearance. Ventral pelage paler, dark grey or greyish-brown. Tail relatively long (60–70% of HB), dark with small black hairs; pilosity 65%. Skull large and flat in profile, with a broad maxillary region and a broad braincase. Third upper molar large, not reduced. Similar to *C. poensis* (paler pelage, hindfoot slightly longer, and tail slightly longer in *C. nigeriae*; see Hutterer & Happold 1983). Nipples: not known.

Geographic Variation Considerable variation in colour is evident, specimens from Cameroon being much darker than those from Nigeria.

Distribution Endemic to Africa. Rainforest BZ (West Central Region [Eastern Nigeria and Western Nigeria sub-regions] and Western Region [Ghanaian sub-region]), Northern Rainforest–Savanna Mosaic, and Guinea Savanna BZ. Recorded from W Cameroon, Nigeria, Ghana and Côte d'Ivoire. Bioko I. Distribution disjunct.

Habitat Widespread in rainforest habitats but also recorded in farmlands and grasslands in the Rainforest BZ, and some relict forests in the Rainforest–Savanna Mosaic and Guinea Savanna BZ in Nigeria (Hutterer & Happold 1983, Happold 1987). Recorded only in northern Guinea Savanna in Ghana (Decher *et al.* 1997). Found at 600 m on Mt Cameroon (Heim de Balsac 1957b).

Abundance Uncertain. Some of specimens recorded as *C. poensis* by Happold (1977) may be this species (see *C. poensis*).

Remarks Apparently no other information available.

Conservation IUCN Category: Least Concern.
Widespread and reported to be relatively common.

Measurements

Crociodura nigeriae

TL (♂♂): 159.0 (144–170) mm, $n = 3$

TL (♀♀): 156.0 (148–161) mm, $n = 4$

T (♂♂): 56.7 (53–61) mm, $n = 3$



Crociodura nigeriae

T (♀♀): 60.3 (58–64), $n = 4$

HF (♂♂): 17.0 (16–18) mm, $n = 3$

HF (♀♀): 17.0 (16–18) mm, $n = 4$

E (♂♂): 11.3 (9–14) mm, $n = 3$

E (♀♀): 10.0 (9–11) mm, $n = 4$

WT (♂♂): 20.3 (15–24) g, $n = 3$

WT (♀♀): 15.3 (11–19) g, $n = 4$

CI (♂♂): 25.8 (24.4–26.6) mm, $n = 3$

CI (♀♀): 25.1 (24.3–25.7) mm, $n = 4$

GWS (♂♂): 10.7 (10.3–11.3) mm, $n = 3$

GWS (♀♀): 10.5 (10.1–11.0) mm, $n = 4^*$

I¹–M³ (♂♂): 11.6 (11.2–12.0) mm, $n = 3$

I¹–M³ (♀♀): 11.3 (11.0–11.5) mm, $n = 4$

Ghana (Decher *et al.* 1997)

*Corrected measurements; original published data were in error

Key References Decher *et al.* 1997; Heim de Balsac 1957b; Hutterer & Happold 1983.

S. Churchfield & P. D. Jenkins

Crociodura nigricans BLACKISH SHREW (BLACKISH WHITE-TOOTHED SHREW)

Fr. Crocidure d'Angola; Ger. Schwarze Weißzahnschmaus

Crociodura nigricans Bocage, 1889. J. Sci. Math. Phys. Nat. Lisboa (2) 1: 28. Quindumbo, Benguela District, Angola.

Taxonomy Status uncertain; considered to be unidentifiable by Heim de Balsac & Meester (1977) but accepted as a species by Crawford-Cabral (1987) and Hutterer (2005a). Synonyms: none. Chromosome number: not known.

Description Small–medium shrew. Dorsal pelage blackish-blue, slate-grey. Ventral pelage paler. Tail relatively long (ca. 75%

of HB); pilosity ca. 60%. Talonid of M³ lacks a fovea. Nipples: not known.

Geographic Variation None recorded.

Distribution Endemic to Africa. Zambezan Woodland BZ. Recorded only from Angola.

Habitat Mountainous region of central Angolan plateau (Crawford-Cabral 1987). Reports of *C. nigricans* occurring widely in eastern Africa cannot be confirmed due to the uncertain status of this species.

Abundance No information.

Remarks Apparently no other information available.

Conservation IUCN Category: Least Concern.
Species insufficiently known.

Measurements

Crocidura nigricans

HB: 73.6 (62–89) mm, n = 11

T: 54.1 (46–63.5) mm, n = 11

HF (c.u.): 13 (11–16) mm, n = 9

E: 7.2 (4–9) mm, n = 11

WT: n. d.

CI: 21.5 (20.5–22.4) mm, n = 7

GWS: 9.0 (8.5–9.4) mm, n = 8

I¹–M³: 9.2 (8.5–10.0) mm, n = 10

Angola (Crawford-Cabral 1987)



Crocidura nigricans

P. D. Jenkins & S. Churchfield

Key Reference Crawford-Cabral 1987.

Crocidura nigrofuscus AFRICAN BLACK SHREW

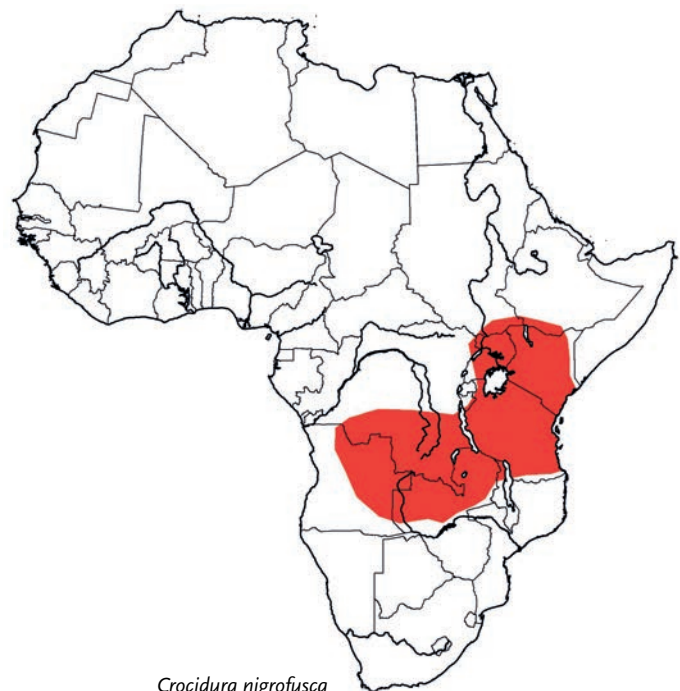
Fr. Crocidure noirâtre; Ger. Afrikanische Schwarzspitzmaus

Crocidura nigrofuscus Matschie, 1895. Säugetiere Deutsch-Ost-Afrikas, p. 33. 'Wukalala, Kinyawanga im Westen des Semliki' (= Semliki Valley, DR Congo).

Taxonomy The species has been quoted under various names and still requires careful systematic revision (Hutterer 2005b). Referred to as *C. luluae* and *C. zaodon* by Heim de Balsac & Meester (1977), and as *C. ansorgei*, *C. nilotica* and *C. zena* by Gureev (1979). Synonyms: *ansorgei*, *cabrerai*, *kempi*, *lakiundae*, *luluae*, *nilotica*, *nyikae*, *provocax*, *zaodon*, *zena*. Subspecies: none. Chromosome number: 2n = 48, FN = 78 (Maddalena & Ruedi 1994). In an allozyme study of 21 African and European species of *Crocidura* (Maddalena 1990a), *C. nigrofuscus* clustered with *C. hildegardae*, *C. poensis* and *C. theresae*.

Description Medium-sized very dark shrew. Pelage soft and dense with silky sheen; hairs 4–5 mm. Dorsal pelage very dark blackish-brown or black; hairs grey at base with dark brown to blackish tip. Ventral pelage similar to dorsal pelage; may be slightly paler. Ears darkly pigmented. Tail relatively long (ca. 75% of HB), black, not bicoloured; pilosity 80–90%. Skull elongated and without sharp edges; braincase oval in dorsal view; dorsal profile straight in lateral view (depicted in Heim de Balsac & Verschuren 1968, fig. 7). First upper incisor short. Third molar medium. Nipples: not known.

Geographic Variation There exist differences in size between geographical samples, but the amount of variation has not been studied. Dippenaar (1982) demonstrated morphometric differences between *C. nigrofuscus* (as *C. zaodon*) and *C. turba* in Zambia.



Crocidura nigrofuscus

Distribution Endemic to Africa. Zambesian Woodland BZ and parts of Somalia–Masai Bushland BZ and Eastern Rainforest–Savanna Mosaic. Recorded from S Ethiopia, S Sudan, most of East Africa, Zambia, Angola and C and S DR Congo. May also occur in Cameroon (Hutterer 2005b). Detailed distribution maps or records (under the name *zaodon*) available for Zambia (Ansell 1978), Malawi (Ansell & Dowsett 1988), Kenya (Aggundey & Schlitter 1986) and Uganda (Hollister 1918).

Habitat Damp habitats near water-courses (Ansell & Dowsett 1988, as *C. zaodon*). Also secondary forest, forest patches, swampy areas in forest–savanna mosaic (Rwanda), and montane forest (S Sudan).

Abundance Uncertain; widely distributed but does not occur in high numbers. In SE Kenya, six individuals (2%, $n = 302$ shrews) were captured in 13 forest fragments (Oguge *et al.* 2004).

Remarks The species represents a general type of terrestrial shrew. Mean litter-size 3.3 (T. Maddalena, in Innes 1994); two embryos reported from Garamba Parc, NE DR Congo (Heim de Balsac & Verschuren 1968).

Conservation IUCN Category: Least Concern.

Measurements

Crocidura nigrofusca

HB: 83.7 (65–95) mm, $n = 3$

T: 64.3 (55–72) mm, $n = 3$

HF: 15 (13.9–15.9) mm, $n = 3$

E: 9.4 (9.1–9.9) mm, $n = 3$

WT: 16.8 (13–23.5) g, $n = 3$

CI: 23.9, 23.9 mm, $n = 2$

GWS: 10.3 (10.1–10.4) mm, $n = 2$

I¹–M³: 10.2 (10.0–10.8) mm, $n = 4$

Body measurements and weight: SE Kenya (Oguge *et al.* 2004)

Skull measurements: DR Congo (ZFMK)

Key References Ansell 1978; Maddalena & Ruedi 1994.

Rainer Hutterer

Crocidura nimbae NIMBA SHREW

Fr. Crocidure du Mont Nimba; Ger. Nimba-Spitzmaus

Crocidura nimbae Heim de Balsac, 1956. Mammalia 20: 131. Zouguépo, Mt Nimba, Guinea.

Taxonomy A distinct species, now known not to be conspecific with *C. wimmeri* (Hutterer 1993, 2005a; *contra* Hutterer 1983a). Synonyms: none. Chromosome number: not known. (Note: the record of $2n = 46$, $FN = 68$ from a specimen referred to as *C. cf. nimbae* from Yealé, Côte d'Ivoire (Meylan & Vogel 1982) is incorrect since the specimen represents *C. grandiceps* (Hutterer 1983a, Schlitter *et al.* 1999).

Description Medium-sized dark shrew with relatively short tail. Pelage short and dense with silky sheen; hairs 3 mm. Dorsal pelage dark brownish-grey to grey, with sparse flecking; hairs dark grey at base becoming browner towards tip; some hairs with pale tip. Ventral pelage slightly paler and greyer than dorsal pelage; hairs grey on basal half, brownish-grey on terminal half, sometimes with whitish tip. Ears conspicuous, not concealed by pelage. Flank gland visible as small oval patch of bare skin. Fore- and hindfeet flesh-coloured, with sparse short brown hairs on upper surface; whitish hairs on toes. Tail relatively short (ca. 40% of HB), bicoloured, dark brownish-grey above, paler ventrally; pilosity ca. 70%. First incisor long and hooked. Third molar narrow to medium. Nipples: not known.

Geographic Variation None recorded.

Distribution Endemic to Africa. Rainforest BZ. Recorded from Sierra Leone, SE Guinea, Liberia and W Côte d'Ivoire.

Habitat Sub-montane and lowland rainforest. Often with a preference for marshy habitats (Heim de Balsac 1956a, 1958).

Abundance Uncommon or rare. In Taï N. P., Côte d'Ivoire, comprised 4% of shrews in several habitats ($n = 553$ shrews; fifth

commonest species; 10 spp.) (Churchfield *et al.* 2004), 3.6% in forest ($n = 390$ shrews, 9 spp.) and 4.3% in cocoa–coffee plantations ($n = 140$ shrews, 7 spp.) (Barrière *et al.* 1999). In Ziam Biosphere Reserve, Guinea, it was very rare or absent: percentage occurrences were 0.6% in secondary forest ($n = 509$ shrews, 10 spp.), 0.2% in primary forest ($n = 500$, 11 spp.) and 0.2% in old forest plantations ($n = 441$ shrews, 9 spp.). The species was not recorded in old fallow



Crocidura nimbae

land, young forest plantations and fields ($n = 484$ shrews, 9 spp.; 303 shrews, 10 spp.; and $n = 272$, 9 spp., respectively) (P. Barrière unpubl.).

Remarks Primarily insectivorous, with lesser amounts of other invertebrates. In Tâi N. P. feeds on nine groups of invertebrates; the commonest food items (as assessed by frequency of occurrence in stomach contents, in order of frequency) were Formicidae (53%), adult Coleoptera (41%), Araneae (29%), Diplopoda (18%), Isopoda (17%), Blattodea (12%) and Heteroptera, Isoptera and Mantidae (6% each) (Churchfield *et al.* 2004).

Conservation IUCN Category: Near Threatened.

Listed as a species of conservation concern by Nicoll & Rathbun (1990).

Measurements

Crocidura nimbae

HB: 81.7 (75–90) mm, $n = 3$

T: 53 (50–57) mm, $n = 3$

HF: 16.5 (16–17) mm, $n = 3$

E: n.d

WT: 12.5 (8–19) g, $n = 22$

CI: 26 (25.5–26.5) mm, $n = 3$

GWS: 10 mm, $n = 1$

I^1 – M^3 : 12 (12–12) mm, $n = 3$

Measurements: Mt Nimba (Heim de Balsac 1956a, 1958); holotype (♀) and two ♂♂

Weight: Tâi N. P., Côte d'Ivoire (Churchfield *et al.* 2004; juveniles and adults)

Key References Churchfield *et al.* 2004; Heim de Balsac 1958.

Rainer Hutterer

Crocidura niobe NIOBE'S SHREW

Fr. Crocidure de Niobé; Ger. Niobes Spitzmaus

Crocidura niobe Thomas, 1906. Ann. Mag. Nat. Hist., ser. 7, 18: 138. Mubuku Valley, E Rwenzori, Uganda. 1829 m.

Taxonomy Synonyms: none. Chromosome number: not known.

Description Small–medium dark shrew with slight silver mottling on dark greyish back. Hairs short, ca. 5 mm on back. Dorsal hairs slate-grey at base (80%), brownish at tip (20%). Ventral pelage slightly paler. Fore- and hindfeet pale brown. Claws on forefeet slightly shorter than on hindfeet. Tail relatively very long (ca. 82% of HB), slender, uniformly blackish, sometimes with white tip; pilosity: 0–10%. Skull with low braincase; muzzle stout and conical; unicuspid broader than long. Nipples: not known.

Geographic Variation None recorded.

Distribution Endemic to Africa Afromontane–Afroalpine BZ associated with the Albertine Rift Valley. Recorded from Rwenzori Mts of both Uganda and DR Congo. Also recorded in Uganda (Bwindi–Impenetrable N. P., Mgahinga Gorilla N. P. [3000 m]), Burundi (Kibira N. P. and Bururi F. R. [1950–2250 m]) and E DR Congo (Irangi [800–900 m]). Not yet recorded from Rwanda, but likely to occur in Nyungwe N. P. and Parc National des Volcans. A specimen from Ethiopia (Corbet & Yalden 1972) is probably *C. harena* or a closely related species (Hutterer & Yalden 1990).

Habitat In Irangi, E DR Congo, found in montane rainforest, secondary forest and adjacent to cultivated areas (Dieterlen & Heim de Balsac 1979). In the Rwenzori Mts, recorded in elephant grass below the forest (Thomas & Wroughton 1910) as well as montane forest at 1920 m (Kerbis Peterhans *et al.* 1998). In Kibira N. P., favours mesic habitats along shallow streams and sedge marshes. In Mgahinga Gorilla N. P., collected within and adjacent to sedge marshes at a high altitude.

Abundance Generally rare, but may be common in favoured locations; e.g. comprised 44% of shrews and was the commonest species ($n = 23$, 7 spp.) at Kyoha River, Rwenzori Mts, but did not occur at five other localities on these mountains (Kerbis Peterhans *et al.* 1998). Comprised 40% of the shrew fauna ($n = 10$) along the Nyabikona River in Kibira N. P.

Remarks Nocturnal. Stomach contents of five specimens from Burundi contained remains of Araneida, Diptera, Chilopoda



Crocidura niobe

(including *Chilopoda mesostigmata*) and Coleoptera (adult & larva). Pregnant ♀♀ recorded in Mar (Mgahinga Gorilla N. P.); Apr (Irangi, E DR Congo); May and Aug (Kibira N. P.), Burundi; and Nov (Rwenzori Mountains N. P., Uganda). Records refer to only one to three ♀♀ at each occasion. Embryo number: 1–4.

Conservation IUCN Category: Near Threatened.

Measurements

Crocidura niobe

HB: 74.3 (65–81) mm, n = 22

T: 61.1 (56–66) mm, n = 21

HF: 14.1 (13–15) mm, n = 21

E: 9.3 (8–12) mm, n = 22

WT: 8.2 (5.5–10) g, n = 20

CI: 19.6 (18.5–20.3) mm, n = 17

GWS: 8.9 (8.5–9.2) mm, n = 17

I¹–M³: 8.4 (7.6–8.8) mm, n = 19

Burundi, Uganda and DR Congo (FMNH)

Key References Dieterlen & Heim de Balsac 1979; Thomas & Wroughton 1910.

Sean O. Bober & Julian C. Kerbis Peterhans

Crocidura obscurior WEST AFRICAN PYGMY SHREW

Fr. Crocidure obscure; Ger. Westafrika-Zwergspitzmaus

Crocidura obscurior Heim de Balsac, 1958. Mém. Inst. Fr. Afr. Noire 53: 328. Mt Nimba, Guinea; montane prairie.

Taxonomy Described as a subspecies of *C. bottegi* (see Heim de Balsac & Meester 1977); now considered as valid species (Hutterer 2005b). (The name *C. bottegi* is now restricted to populations found only in Ethiopia.) Synonyms: *eburnea*. Subspecies: none. Chromosome number: 2n = 36, FN = 56 (Côte d'Ivoire; Maddalena & Ruedi 1994), and 2n = 40, FN = 60 (Meylan 1971 as *C. bottegi*).

Description Minute to very small dark brown shrew. Pelage soft, dense and velvety; hairs 1–2 mm. Dorsal pelage dark brown, with slight russet tinge and silky sheen; hairs almost unicoloured, some with dark brown tip. Ventral pelage greyish-brown. Head similar to dorsal pelage. Ears darkly pigmented, not concealed by pelage; appear naked but covered with short dark hairs. Chin and throat similar to ventral pelage. Tail relatively long (ca. 60–70% of HB), dark brown above, slightly paler below; long white hairs on tail – pilosity ca. 50%. Braincase high-domed. First upper incisor long and hooked. Third upper molar wide. Nipples: not known.

Geographic Variation None recorded.

Distribution Endemic to Africa. Rainforest BZ (Western Region and W Nigeria). Recorded from Sierra Leone, Côte d'Ivoire, S Guinea and Ghana; probably also W Nigeria. Not known to occur east of Nigeria (*contra* Heim de Balsac & Meester 1977).

Habitat Rainforest and on edges of forest. Specimens (as *C. bottegi eburnea*) found in swampy habitats (Adiopoudoumé, Côte d'Ivoire), in or near forest (near Mt Nimba), and in highland grasslands (near a wooded ravine at 1600 m) (Heim de Balsac & Aellen 1958).

Abundance Common in most habitats. In Taï N. P., Côte d'Ivoire, it was the commonest species of shrew in forest and plantations, comprising 38.2% (n = 390, 9 spp.) of shrews in forest, and 37.2% (n = 140, 7 spp.) in cocoa–coffee plantations (Barrière *et al.* 1999). In Ziama Biosphere Reserve, Guinea, it was the commonest species of shrew in young forest plantations and fallow land (39.6%, n = 303, 10 spp. and 33.6%, n = 484, 9 spp., respectively). In primary and secondary forests at Ziama, it was co-dominant with *C. muricauda*

(30.4%, n = 500, 11 spp. and 27.6%, n = 509, 10 spp., respectively), and less common in old forest plantations and fields (25.2%, n = 441, 9 spp. and 14.8%, n = 272, 9 spp., respectively) (P. Barrière unpubl.).

Remarks The commonest prey items (% frequency of occurrence) in 59 stomachs in Taï N.P., Côte d'Ivoire, were representatives of the following taxa: Formicidae (71%), Araneae (52.5%), Gryllidae (17%), Coleoptera adults (15.3%), Diplopoda (11.9%), Isopoda (10.2%), Blattodea (8.5%), Heteroptera (7.7%), Isoptera (5.1%), Lepidoptera adults (5.1%) and Coleoptera larvae (3.4%). Diptera adults, Lepidoptera larvae, Gastropoda, Lumbricidae, plant material and Acrididae were represented by lower percentage occurrences. Noteworthy features are the presence of small amounts of earthworms and plant material in the diet, and the exceptionally long intestine for a species of this size (Churchfield *et al.* 2004).



Crocidura obscurior

Conservation IUCN Category: Least Concern.

Measurements

Crociodura obscurior

HB: 45–50 mm, n = 3

T: 30–35 mm, n = 3

HF: 10–10 mm, n = 3

E: 6–8 mm, n = 3

WT: 2.5–4 g, n = 3

CI: 15.6–15.9 mm, n = 3

GWS: 7.1–7.3 mm, n = 3

I¹–M³: 6.7–6.9 mm, n = 3

W Nigeria (Hutterer & Happold 1983)

Mean values not recorded

Key Reference Churchfield *et al.* 2004; Heim de Balsac & Aellen 1958.

Rainer Hutterer

Crociodura olivieri AFRICAN GIANT SHREW (MANN'S MUSK SHREW, EUCHAREENA'S MUSK SHREW)

Fr. Crocidure grande africaine; Ger. Große Afrikanische Riesenspitzmaus

Crociodura olivieri (Lesson, 1827). Manuel de Mammalogie, p. 121. Sakkara, Egypt; neotype collected near Giza.

Taxonomy Originally described in the genus *Sorex*. First described from embalmed animals found in Egyptian tombs at Sakkara. *Crociodura olivieri* is the valid name for the large shrews previously known as *C. flavescens* (now the valid name for a smaller species restricted to South Africa). Synonyms: *aequatorialis*, *anchietae*, *atlantis*, *bueae*, *cara*, *cinereoaeana*, *daphnia*, *darfurea*, *detae*, *doriana*, *ferruginea*, *fuscusa*, *giffardi*, *guineensis*, *hansruppi*, *hedenborgi*, *hedenborgiana*, *hera*, *herero*, *kijabae*, *kivu*, *luluana*, *manni*, *martienseni*, *nyansae*, *petersii*, *occidentalis*, *odorata*, *spurelli*, *suruae*, *tatiana*, *toritensis*, *zuleika*. Many of these names have been used as subspecies, or have been considered as allospecies of a *flavescens* superspecies (Hutterer 2005b). Many authors also distinguished between pale (*occidentalis*, *manni*, *spurelli*) and black (*giffardi*, *hedenborgiana*, *martienseni*, *odorata*) colour morphs, regarding them as different species; biochemical evidence has shown that they are merely colour morphs of a single and highly variable species (Maddalena 1990a). Subspecies: none recognized here; but see above and Hutterer (2005b). Chromosome number: 2n = 50, FN = 66, aFN = 62 (Meylan & Vogel 1982).

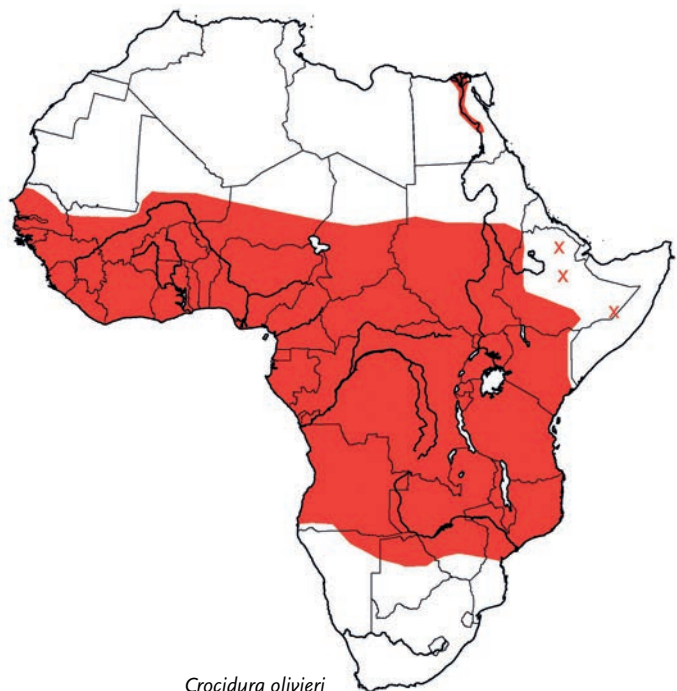
Description Very large shrew, highly variable in colour and size (see below). Dorsal pelage reddish-brown to dark brown or black. Ventral pelage buffy-brown to dark grey. Tail relatively long (70–80% of HB), thick, with many short bristles; pilosity ca. 100%. Skull large, heavy and flat in profile, with large rostrum but relatively small cranium. Rostrum, maxilla and braincase broad but interorbital constriction long and narrow. Teeth large and heavy, particularly the incisors. Well-developed lateral flank glands exude a sweet, musky odour, particularly strong and pungent in West African forms (*manni* and *odorata*). Nipples: 1 + 2 = 6 (in some specimens nipples are equally spaced on each side of the ventral surface).

Geographic Variation Very variable in respect of size (see below) and pelage colour. West African forms (*manni*, *odorata*) are the largest (HB: 98–154 mm; adult WT: 37–78 g). Pelage colour ranges from reddish-brown to dark brown or blackish dorsally, and from buffy-brown to dark grey ventrally (Maddalena 1990a).

Distribution Endemic to Africa. Widely distributed throughout many biotic zones from the Sahel Savanna BZ to the Rainforest BZ,

and in most of the Somalia–Masai BZ and the Zambezian Woodland BZ. Recorded from Senegal eastwards to Sudan and Ethiopia, and southwards towards southern Africa. Found in the Nile Valley of Egypt but not in the arid Sahara Desert nor the arid parts of Somalia and Ethiopia. Occurs along Okavango and Chobe Rivers, and in Okavango Swamp in northern Botswana but its distribution further south is apparently limited by ecological factors, particularly aridity. Occurs from close to sea level to high up on mountains. Recorded on Mts Kenya, Elgon and Umengo, and on the Aberdare Ranges (Aggundey & Schlitter 1986), and at altitudes up to 3300 m in DR Congo and Kenya (Dieterlen & Heim de Balsac 1979, Aggundey & Schlitter 1986).

Habitat Common and widespread, mostly in well-vegetated moist habitats including lowland and montane evergreen forest, riverine and flood-plain grassland and swamp (Sheppe & Osborne 1971, Sheppe 1973) but also in scrub and in burnt and grazed



Crociodura olivieri

grassland (Delany 1964a). Occasionally found in pine plantations and montane grasslands (Happold & Happold 1986). Common in farmland, plantations, around houses and food stores (Delany 1964a, Hutterer *et al.* 1987, Brosset 1988).

Abundance No data on population densities. A frequent but variable contributor to sorcid communities. In DR Congo, comprised 8% of shrew captures in montane habitats at 1900–3300 m (10 spp.), 77% in rainforest at 800–900 m (7 spp.) and 31% in cultivated areas (9 spp.) (Dieterlen & Heim de Balsac 1979). In Uganda, it constituted 20–80% of captures in communities of 2–8 shrew species (Delany 1964a), but only 8.5% of shrew captures (4 spp.) in the Pare Mts, Tanzania (Stanley *et al.* 1996a) and 3.1% in Gabon (Brosset 1988).

Adaptations Terrestrial, and adaptable, and able to occupy many different habitats and to live commensally with humans. Wild and captive individuals almost completely nocturnal with peaks of activity just before dawn (Vogel *et al.* 1981, Brosset 1988). Moulting shrews found in Mar, May, Jul and Aug in Zambia (Sheppe 1973).

Foraging and Food Feeds on invertebrates, particularly arthropods, and possibly carrion. Analyses of stomach contents ($n = 16$) from rainforest in DR Congo showed that major prey comprised Formicidae (20% by composition), Coleoptera and Diplopoda (each 16%), Isoptera and Araneae (each 12%) with smaller amounts of Acrididae and insect larvae. Prey were 3 mm to >30 mm in length with 67% being <10 mm (Dudu *et al.* 2005). Food energy consumption was 2.02–2.56 kJ/g/day (mean 2.27 kJ) in captive animals weighing 26–37 g (Hunkeler & Hunkeler 1970). Mean oxygen consumption was 2.07 kJ/g/h (Vogel 1976).

Social and Reproductive Behaviour Essentially solitary but individuals often live in close proximity. They utter loud shrieks and churls when angry or threatened.

Reproduction and Population Structure Breeding activity varies according to locality. In DR Congo, pregnant ♀♀ found in all months, but breeding declined during dry season (Dieterlen & Heim de Balsac 1979). Pregnant ♀♀ caught in dry and wet seasons in Zambia (Sheppe 1973). In Uganda, all ♀♀ examined in Jul–Aug, and one ♀ in Dec, were pregnant (Delany 1964a). Embryo number: 4 (1–5) in eastern Africa (Delany 1964b, Sheppe 1973, Dieterlen & Heim de Balsac 1979), and 2 (1–4) in central and western Africa (Dubost 1968, Happold 1987). Usually four young/litter in Nigeria (Happold 1987). Breeding ♀♀ captured in and around human settlements in Gabon have greater fecundity (3–4 embryos) than those in natural habitats (1–2 embryos) (Dubost 1968). Pregnant and parous ♀♀ weighed 34–57 g, non-breeding females 35–42 g (Sheppe 1973). Testis length 4–8 mm, width 3 mm (Delany 1964b, Stanley *et al.* 1996a). Sex ratio of captured animals ca. 1 : 1 ($n = 32$)

in eastern Africa (Sheppe 1973) but male-biased (66% ♂ to 34% ♀) in central Africa (Dieterlen & Heim de Balsac 1979). Little is known about other aspects of the life history of the species.

Predators, Parasites and Diseases Main predators are raptors, particularly owls (including *Tyto alba* and *Bubo africanus*), and small carnivores such as mongooses, genets and wild cats (Demeter 1981, Ray & Hutterer 1995). Contributed 5% and 15–23% to the diets of *T. alba* and *T. capensis*, respectively, in Malawi (Hanney 1962, Happold & Happold 1986). Even the large and odoriferous *manni* and *odorata* have been found in owl pellets. Comprised 0.3% of shrews (16 spp.) identified in carnivore scats from the Central African Republic (Ray & Hutterer 1995). Host to a diversity of helminths.

Conservation IUCN Category: Least Concern.

A common and widespread species of no immediate conservation concern.

Measurements

Crociodura olivieri

HB: 110–140 mm, $n = 5$

T: 85–100 mm, $n = 5$

HF: 21–23 mm, $n = 5$

E: 12–14 mm, $n = 5$

WT: 37–65 g, $n = 5$

CI: 32.0–34.3 mm, $n = 5$

GWS: 13.2–14.4 mm, $n = 5$

I¹–M³: 14.0–15.4 mm, $n = 5$

Nigeria (Hutterer & Happold 1983; as *C. o. manni*)

Mean values not recorded

HB (♂♂): 119 (115–131) mm, $n = 5$

HB (♀♀): 124 (115–129) mm, $n = 7$

T (♂♂): 82 (75–87) mm, $n = 5$

T (♀♀): 78 (70–83) mm, $n = 6$

HF (♂♂): 21 (20–23) mm, $n = 5$

HF (♀♀): 21 (18–22) mm, $n = 7$

E (♂♂): 12 (10–14) mm, $n = 5$

E (♀♀): 11 (9–12) mm, $n = 6$

WT (♂♂): 35.4 (33.3–37.0) g, $n = 3$

WT (♀♀): 33.8 (31.0–37.0) g, $n = 4$

Zimbabwe (Smithers & Wilson 1979)

Body dimensions vary greatly at different locations within the geographic range

Key References Brosset 1988; Dieterlen & Heim de Balsac 1979; Hutterer & Happold 1983; Hutterer *et al.* 1987; Maddalena 1990; Sheppe 1973.

Sara Churchfield & Rainer Hutterer

Crocidura parvipes SMALL-FOOTED SHREW

Fr. Crocidure à petits pieds; Ger. Kleinfüßige Savannenspitzmaus

Crocidura parvipes Osgood, 1910. Field Mus. Nat. Hist. Publ., Zool. Ser. 10: 19. Voi, Kenya.

Taxonomy Subgenus *Afrosorex* (Hutterer 1986a). Synonyms: *boydi*, *chitauensis*, *cuanzensis*, *katharina*, *lutrella*, *nisa*. Subspecies: none. Chromosome number: $2n = 50$ (Bannikova *et al.* 2001; Ethiopia), $2n = 52$, $FN = 66$ (Schlitter *et al.* 1999; Cameroon).

Description Small-medium greyish-brown shrew. Pelage soft and dense with silky sheen; hairs ca. 4 mm. Dorsal pelage mid-brown, washed with pale brownish-grey; hairs medium grey on basal two-thirds, pale brownish-grey subterminal band, and brown at tip (see also below). Ventral pelage creamy-grey, sometimes silvery-white; hairs grey with creamy-grey at tip. Appears to be clear delineation between colour of dorsal and ventral pelage. Flank gland elongated, covered by short white hairs. Ears large and comparatively conspicuous, not concealed by pelage. Fore- and hindfeet flesh-coloured, covered with short pale brown or creamy hair. Hindfeet relatively short. Tail of medium relative length (ca. 45–60% of HB), thick at base and tapering towards tip; bicoloured, medium brown above, flesh-coloured below; pilosity ca. 85%. First incisor moderately long and slightly hooked. Third molar medium to narrow. Nipples: not known.

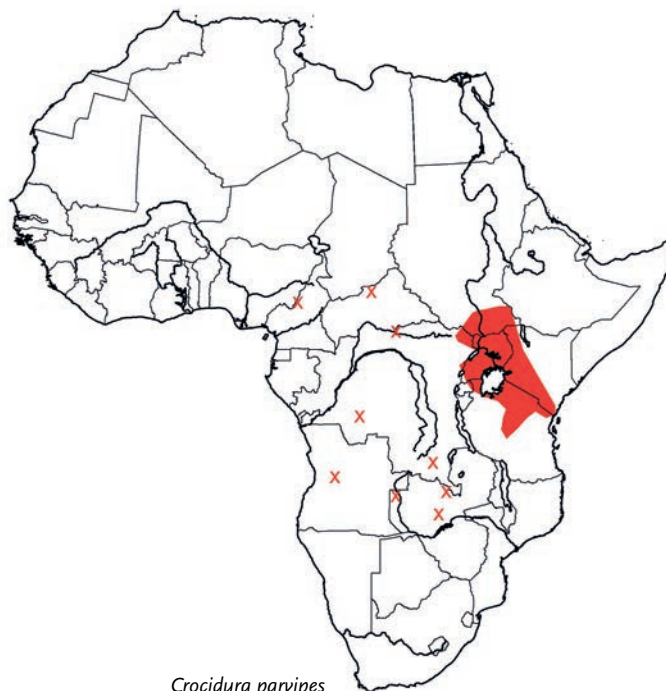
Geographic Variation Dorsal pelage varies in colour from 'drab grey' to greyish-brown and brown (Hutterer 1986a). Considerable variation in size may indicate that there may be more than one species involved (Hutterer 2005b).

Distribution Endemic to Africa. Primarily Eastern Rainforest–Savanna Mosaic, and parts of the Guinea, Zambezian Woodland and Somalia–Masai Bushland BZs of eastern Africa; isolated scattered records throughout central Africa. Recorded from Cameroon, Central African Republic, S Sudan, Uganda, Ethiopia, Kenya, Tanzania, DR Congo, Zambia and Angola. Limits of distribution uncertain.

Habitat Savanna. In Garamba N. P., DR Congo, usually found in dry savanna habitats and occasionally in gallery forest (Heim de Balsac & Verschuren 1968; as *C. boydi*).

Abundance No information.

Remarks Little is known about this species. Remains have been found in the pellets of Barn Owls *Tyto alba* (Heim de Balsac & Verschuren 1968).

*Crocidura parvipes*

Conservation IUCN Category: Least Concern.

Measurements

Crocidura parvipes

HB: 68–85 mm

T: 32–52 mm

HF: 10–13 mm

E: 5–10 mm

WT: 8–12 g

CI: 19.3–20.7 mm

GWS: 8.4–9.2 mm

I^1 – M^3 : 8.4–9.2 mm

Throughout geographic range (Hutterer 1986a; mean and sample sizes not recorded)

Key Reference Hutterer 1986a.

Rainer Hutterer

Crocidura pasha SAHELIAN TINY SHREW

Fr. Crocidure naine du Soudan; Ger. Sahel-Zwergspitzmaus

Crocidura pasha Dollman, 1915. Ann. Mag. Nat. Hist., ser. 8, 15: 517. 1916. Ann. Mag. Nat. Hist., ser. 8, 17: 195. Atbara River, Sudan.

Taxonomy Similar to *C. nana* and *C. nanilla* but with a smaller skull. Often confused with *C. nanilla* and *C. lusitania*. Does not include *glebula* (a synonym of *C. fuscomurina*) or *C. planiceps* (see Hutterer & Kock 1983). A specimen from Zunguru, Nigeria, was described as the holotype of *C. glebula* (Dollman 1916) and has been referred to as *C. glebula* by Rosevear (1953) but as *C. pasha glebula* by Heim de Balsac & Meester (1977). Synonyms: none. Chromosome number: not known.

Description Minute shrew. Dorsal pelage cinnamon mottled with grey. Ventral pelage white. Flanks similar to dorsal pelage. Upper surface of fore- and hindfeet whitish-buff. Tail relatively long (ca. 70% of HB), finely haired, cinnamon-brown above, whitish below, with numerous long, white bristle hairs; pilosity ca. 95%. Skull flattened, sides of braincase rather less parallel, more convex. Teeth small; second upper unicuspid slightly smaller in horizontal section than the third, which slightly overlaps it; third upper unicuspid moderately narrow; talonid of third lower molar a single cusp. Nipples: not known.

Geographic Variation None recorded.

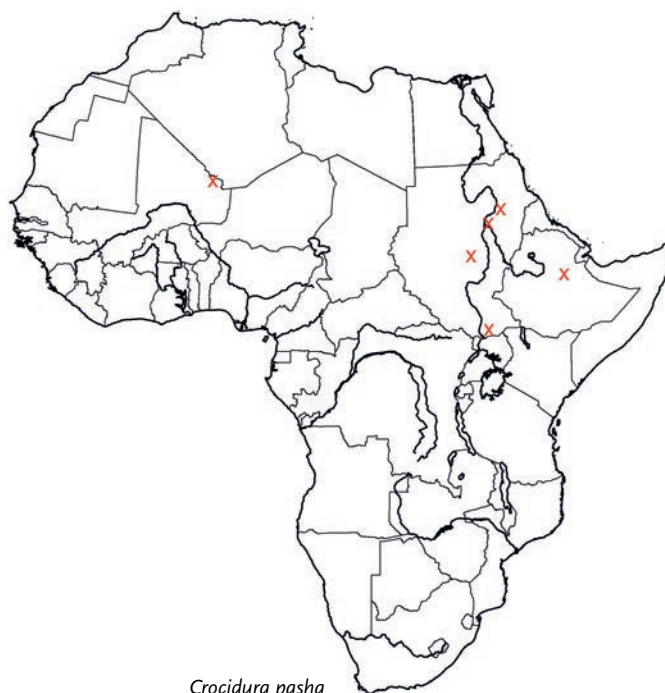
Distribution Endemic to Africa. Sahel Savanna and Sudan Savanna BZs. Widespread in semi-arid habitats, but known populations very disjunct. Recorded in Sudan from Atbara R. (Dollman 1916), Khartoum and Torit (Setzer, 1956) and Nuba Mts (Hutterer & Kock 1983). Also known from Awash N. P., Ethiopia (Demeter 1982) and Adrar des Iforas, N Mali (Dobigny *et al.* 2001).

Habitat Semi-arid savannas.

Abundance Little information. Common in Adrar des Iforas, N Mali (Dobigny *et al.* 2001; see also below).

Remarks Remains of one individual (out 344 shrews) found in pellets of a Spotted Eagle-owl *Bubo africanus* in Awash N. P., Ethiopia (Demeter 1982). The commonest species of shrew (of three species) in owl pellets from Adrar des Iforas (Dobigny *et al.* 2001).

Conservation IUCN Category: Least Concern.
Insufficiently known.

*Crocidura pasha***Measurements***Crocidura pasha*

HB: 42, 50 mm, n = 2

T: 29, 38 mm, n = 2

HF: 7.5, 9 mm, n = 2

E: 5, 8 mm, n = 2

WT: n. d.

CI: 14.2 (13.9–15.1) mm, n = 4

GWS: 6.5 (6.3–6.6) mm, n = 4

I¹–M³: 5.9 (5.6–6.4) mm, n = 4

Sudan (BMNH)

Key References Demeter 1982; Hutterer & Happold 1983; Hutterer & Kock 1983.

S. Churchfield & P. D. Jenkins

Crocidura phaeura GURAMBA SHREW

Fr. Crocidure du Mont Guramba; Ger. Guramba Spitzmaus

Crocidura phaeura Osgood, 1936. Field Mus. Nat. Hist. Publ., Zool. ser. 20: 228. Mt Guramba (west base), NE of Allata, Sidamo, Ethiopia.

Taxonomy Taxonomic relationships uncertain. Originally described as a subspecies of *C. hildegardeae* (Osgood 1936). Included as a subspecies of *C. hildegardeae* by Yalden *et al.* (1976); now considered a valid species (Hutterer 2005b). Cranial characteristics

place the species close to *C. montis* and *C. fumosa*, both members of the *luna-fumosa* complex (see Dippenaar & Meester 1989). Related to *C. harensa* (Hutterer & Yalden 1990). Synonyms: none. Chromosome number: not known.

Description Small to medium-sized dark shrew, similar to *C. hildegardeae*. Dorsal pelage dark blackish-brown. Ventral pelage similar but slightly paler. Relatively large hindfeet (18.6% HB). Tail of medium relative length (ca. 53% of HB); entirely dark; pilosity not known. Braincase relatively broad and deep. Second unicuspid slightly smaller than third unicuspid (Osgood 1936). M^3 more robust than in any other African *Crocridura* (Dippenaar & Meester 1989). Appreciably smaller than other Ethiopian endemics of the *glassii* group. Nipples: not known.

Geographic Variation None recorded.

Distribution Endemic to Africa. Afromontane–Afroalpine BZ of Ethiopia. Recorded only from Mt Guramba (type locality) (Osgood 1936) and Nechisar N. P. at 1100 m (Duckworth *et al.* 1993). Specimens from four other localities (Sakalla, west of L. Zwai, Arba Minch, and Dolo) originally allocated to *C. phaeura* (Yalden *et al.* 1976) are now considered to represent *C. hildegardeae* (Yalden & Largen 1992).

Habitat Forested localities, including riverine forest at Nachisar (1100 m) and Mt Guramba (2600 m).

Abundance Apparently rare with very restricted geographic range.

Remarks One of five endemic species of shrews (*C. bottegoides*, *C. glassii*, *C. harenna*, *C. lucina*, *C. phaeura*) known only from Ethiopia east of the Rift Valley (Hutterer & Yalden 1990). Apparently no other information available.

Conservation IUCN Category: Endangered.
Previously considered as Critically Endangered.

Measurements

Crocridura phaeura

HB: 68.0 (60–80) mm, $n = 11$



Crocridura phaeura

T: 52.1 (48–57) mm, $n = 11$

HF: 12.7 (12–14) mm, $n = 11$

E: 8.4 (8–10) mm, $n = 10$

WT: n. d.

CI: 19.7 (18.9–20.6) mm, $n = 11$

GWS: 9.0 (8.8–9.4) mm, $n = 11$

I^1-M^3 : 8.7 (8.2–9.3) mm, $n = 11$

Nechisar N. P., Ethiopia (Duckworth *et al.* 1993)

Key References Duckworth *et al.* 1993; Yalden & Largen 1992.

D. C. D. Happold & D. W. Yalden

Crocridura picea CAMEROON SHREW (ASSUMBO SHREW)

Fr. Crocidure d'Assumbo; Ger. Kamerun-Spitzmaus

Crocridura picea Sanderson, 1940. Trans. Zool. Soc. Lond. 24: 682. Tinta, Assumbo, Mamfe Division, Cameroon. 2300 ft (701 m).

Taxonomy Originally described as a subspecies of *C. occidentalis*. Synonyms: none. Chromosome number: $2n = 58$, $FN = 66$ (Schlitter *et al.* 1999).

Description Small–medium dark shrew. Pelage soft and dense with silky sheen; hairs 4–5 mm. Dorsal pelage medium to dark greyish-brown or black with sparse inconspicuous flecking; hairs dark grey on basal two-thirds, brown or greyish-brown on terminal third. Ventral pelage slightly paler and greyer; hairs grey at base; medium grey on terminal third. Ears moderately large and conspicuous, not concealed by pelage. Fore- and hindfeet blackish-brown, with dark brown short hairs; sharp claws. Tail of medium relative length (ca. 55% of HB), blackish-brown, not bicoloured; pilosity ca. 78%. Braincase medium. First upper incisor long and hooked. Third upper molar medium. Nipples: not known.

Geographic Variation None recorded.

Distribution Endemic to Africa. Afromontane–Afroalpine BZ. Recorded only from Bamenda Highlands, Cameroon.

Habitat 'False mountain grass; dry locality with sandy soil' (Sanderson 1940).

Abundance Very rare; known only by a few specimens.

Remarks Apparently no other information available.

Conservation IUCN Category: Endangered.

Measurements

Crocidura picea

HB: 76, 75 mm, n = 2

T: 43, 47 mm, n = 2

HF: 13, 14 mm, n = 2

E: 8, 9 mm, n = 2

WT: 12, 13 g, n = 2

CI: 21.8, 22.0 mm, n = 2

GWS: 8.9, 9.1 mm, n = 2

I¹–M³: 9.4, 9.7 mm, n = 2

Mt Oku and Bamenda Highlands, Cameroon (ZFMK)

Key Reference Sanderson 1940.

Rainer Hutterer



Crocidura picea

Crocidura pitmani PITMAN'S SHREW

Fr. Crocidure de Pitman; Ger. Pitmans Spitzmaus

Crocidura pitmani Barclay, 1932. Ann. Mag. Nat. Hist., ser. 10, 10: 440. Maluwe-Serenje District, Zambia. 3800 ft (1158 m).

Taxonomy Similar to but smaller than *C. bicolor*. Placed as synonym of *C. gracilipes* by Ansell (1978). Synonyms: none. Chromosome number: not known.

Conservation IUCN Category: Data Deficient.

Previously assessed as Vulnerable. Major threats are human-induced habitat loss and degradation, and restricted distribution.

Description Very small shrew with comparatively long pelage (hairs 4–5 mm). Dorsal pelage mouse-grey slightly tinged with brown. Ventral pelage paler and slightly flecked with a few white hairs, especially under chin and throat. Dorsal and ventral pelage not clearly delineated at flanks. Upper surface of fore- and hindfeet greyish-brown. Tail relatively long (ca. 72% of HB), unicoloured grey-brown; pilosity ca. 35–40%. Skull relatively large with a broad braincase; third unicuspid larger than second; third upper molar moderately broad, entoconid present on talonid of third lower molar. Nipples: not known.

Geographic Variation None recorded.

Distribution Endemic to Africa. Zambezian Woodland BZ. Recorded definitively only from the type locality. The location of the holotype is uncertain but is thought to be on the Luomba R. (ca. 13° 30' S, 30° 30' E) (Ansell 1978). Limits uncertain: perhaps occurs throughout C and N Zambia (Hutterer 2005b).

Habitat No information.

Abundance No information.

Remarks Apparently no other information available.



Crocidura pitmani

Measurements*Crocidura pitmani*

HB: 50 mm, n = 1

T: 36 mm, n = 1

HF: 10.1 mm, n = 1

E: 5.6 mm, n = 1

WT: n.d.

CI: 18 mm, n = 1

GWS: 8.4 mm, n = 1

I¹–M³: 7.5 mm, n = 1

Zambia (holotype; Barclay 1932)

Key Reference Barclay 1932.**S. Churchfield & P. D. Jenkins*****Crocidura planiceps* FLAT-HEADED SHREW**

Fr. Crocidure à tête plate; Ger. Flachkopf-Spitzmaus

Crocidura planiceps Heller, 1910. Smithson. Misc. Coll. 56 (15): 5. Rhino Camp, Lado Enclave, Uganda.

Taxonomy Closely related to and very similar to *C. fuscomurina*, if not conspecific (see Heim de Balsac 1968a, Hutterer 1983b, 2005a). Synonyms: none. Chromosome number: 2n = 44, FN = 72 (Meylan & Vogel 1982).

Description Small to very small shrew similar to *C. fuscomurina*. Dorsal pelage cinnamon-brown to greyish-brown; hairs uniform in colour to roots. Ventral pelage paler, tending to yellowish-grey or silvery-grey. Flank glands distinctly marked by an oblong patch of whitish hair. Feet paler in colour than dorsal pelage. Tail relatively long (72–78% of HB); pilosity 70–80%. Skull smaller and slimmer than that of *C. fuscomurina*, especially in the maxillary region and the braincase. Braincase very flat, with a marked depression at its termination in the interorbital region; the profile of the rostrum ascends slightly anterior to this depression. Upper tooththrow shorter than in *C. fuscomurina*. Nipples: not known.

Geographic Variation Some evidence of local variation in pelage colour and skull size in Nigeria (Hutterer & Happold 1983).

Distribution Endemic to Africa. Guinea Savanna and Sudan Savanna BZs. Recorded from N Nigeria, N DR Congo, Uganda, Sudan and Ethiopia (Hutterer & Happold 1983, Hutterer 2005b). Distribution appears to be disjunct. Limits uncertain.

Habitat In Yankari G. R., N Nigeria, found in *Cyperus* swamp near a stream (Happold 1987).

Abundance No information.

Remarks Some evidence of breeding in Nov in Nigeria. Remains have been found in owl pellets in Nigeria (Hutterer & Happold, 1983).

Conservation IUCN Category: Data Deficient.

Measurements*Crocidura planiceps*

HB: 50–66 mm, n = 4 [71 mm]

*Crocidura planiceps*

T: 39–48 mm, n = 4 [53 mm]

HF: 9–11 mm, n = 4 [12.5 mm]

E: 6–8 mm, n = 4

WT: 2–3 g, n = 4

CI: 16.4–17.1 mm, n = 4 [18.3 mm]

GWS: 6.5–7.4 mm, n = 4 [8 mm]

I¹–M³: 6.5–7.1 mm, n = 4 [8 mm]

Nigeria (Hutterer & Happold 1983; mean values not recorded)

Measurements of the holotype from Uganda given in square brackets

Key References Happold 1987; Hutterer 2005b; Hutterer & Happold 1983; Meylan & Vogel 1982.

S. Churchfield & P. D. Jenkins

Crocidura poensis FRASER'S SHREW (FRASER'S MUSK SHREW)

Fr. Crocidure de Fraser; Ger. Frasers Moschusspitzmaus

Crocidura poensis (Fraser, 1843). Proc. Zool. Soc. Lond. 1842: 200 (publ. 1843). Clarence, Fernando Poo (= Bioko I., Equatorial Guinea).

Taxonomy Originally described in the genus *Sorex*. Definition of this species is uncertain (Hutterer 2005b). Included in *C. dolichura* by Heim de Balsac & Meester (1977) but considered as a distinct species by Hutterer (1993, 2005a). Synonyms: *calabarensis*, *pamela*, *schweitzeri*, *soricoides*, *stampflii*. Subspecies: none. Chromosome number: $2n = 52$, $FN = 70$ (Côte d'Ivoire; Meylan & Vogel 1982).

Description Medium-sized musk shrew. Dorsal pelage dark brown to blackish. Ventral pelage paler, greyish-brown. Ear pinnae prominent. Limbs dark. Tail relatively long (ca. 75% of HB), thin and dark, covered with short bristles; pilosity ca. 50%. Both sexes have oval-shaped lateral scent glands on the flanks, surrounded by short stiff hairs that exude a greasy secretion with a prominent sweet, musky odour (hence 'musk shrew'). Distinguishable from other similar species by sonographic differences in frequency and duration of defence calls (Hutterer & Vogel 1977). Nipples: not known.

Geographic Variation None recorded.

Distribution Endemic to Africa. Widely distributed in the Rainforest BZ (Western Region and West Central Region) and Guinea Savanna BZ of West Africa. Recorded from Sierra Leone and Guinea to Cameroon. Also Bioko I. and (extraliminally) Príncipe I.

Habitat Mostly found in primary and secondary lowland evergreen rainforest, forest relicts up to 1000 m. Also occurs in rough grass, farmland, plantations, gardens and around houses.

*Crocidura poensis*

Abundance Frequently the most numerous species in West African shrew communities. It was the most abundant species, comprising 48% ($n = 160$) of forest-dwelling shrews in Gabon (10 spp.; Brosset 1988); and also the most abundant species (equal in abundance with *Sylvisorex schoutedeni*; 29%, $n = 24$; 9 spp.) in Korup N. P., Cameroon (Hutterer & Schlitter 1996). Reported to be common in some rainforest localities in Nigeria (Happold 1987). In Gambari Forest, Nigeria, comprised 29% of shrews (2 spp., $n = 56$) during a mark-recapture study over three years, and 28% over the following five years (2 spp., $n = 29$) (Happold 1977). It was much less common than the other syntopic species (*C. crossi*) (Happold 1977). No data on population densities.

Adaptations Ground-dwelling, adaptable and able to live in anthropogenic habitats and commensally with humans. Mostly nocturnal, increasing in activity before dawn (Vogel *et al.* 1981, Brosset 1988).

Foraging and Food Feeds on invertebrates, particularly arthropods. Major prey items (in order of importance) based on analysis of faecal material from live-trapped shrews in Nigeria ($n = 8$) are species of Gryllidae, Diplopoda, Coleoptera, Heteroptera, Formicidae, Lepidopteran larvae and Araneae (Churchfield 1982). Captive individuals readily ate grasshoppers and mantids. Most prey were 5–20 mm in length but captive shrews took prey up to 50 mm in length. Mean food energy consumption was 3.49 kJ/g body mass/day (range 3.32–3.86, $n = 4$) in captive animals weighing 14–20 g (Hunkeler & Hunkeler 1970). Mean oxygen consumption of captive animals with mean body weight of 16.7 g ($n = 4$) was 1.05 kJ/h (Vogel 1976).

Social and Reproductive Behaviour Primarily solitary and aggressive towards conspecifics, but with partial overlap of home-ranges. Scent is probably important in the social and spatial organization of these highly odoriferous shrews.

Reproduction and Population Structure Little information. Mean embryo number: 3 (range 1–4). Fecundity greater than in other sympatric forest-dwelling crocidurine shrews (Brosset 1988). Pregnant ♀ with three embryos (each 16 mm crown–rump) captured in Jun in Cameroon; testes of males 5–7 mm (Hutterer & Schlitter 1996).

Predators, Parasites and Diseases Main predators are raptors, particularly owls. Shrews, including *C. poensis*, comprised 31% by number and 6% by weight in the diet of Spotted Eagle-owls *Bubo africanus*, and 25–29% by number and 8–16% by weight in the diet of Barn Owls *Tyto alba*, in and around Yankari G. R., Nigeria (Demeter 1981). Also preyed on by mongooses, genets and small cats. Host to a diversity of helminth worms.

Conservation IUCN Category: Least Concern.

Primarily a forest-dwelling species; relatively common, widespread and adaptable, and of no immediate conservation concern.

Measurements

Crocidura poensis

HB (♂ ♂): 83.7 (77–98) mm, n = 15*

HB (♀ ♀): 85.0 (75–93) mm, n = 5*

T (♂ ♂): 59.4 (48–64) mm, n = 15*

T (♀ ♀): 52.6 (48–59) mm, n = 5*

HF (♂ ♂): 16.0 (15–18) mm, n = 13*

HF (♀ ♀): 15.2 (15–16) mm, n = 5*

E (♂ ♂): 10.3 (9–11) mm, n = 4**

E (♀ ♀): 10, 11 mm, n = 2**

WT (♂ ♂): 11.1 (9–13) g, n = 4**

WT (♀ ♀): 17 g, n = 1*

CI: 23.7–24.5 mm, n = 8†

GWS: 10.1–10.5 mm, n = 8†

I¹–M³: 9.7–11.1 mm, n = 8†

*Côte d'Ivoire (Heim de Balsac & Aellen 1958)

**Cameroon (Hutterer & Schlitter 1996)

†Nigeria (Hutterer & Happold 1983)

Key References Brosset 1988; Churchfield 1982; Hutterer & Happold 1983.

Sara Churchfield & Rainer Hutterer

Crocidura polia POLIA'S SHREW

Fr. Crocidure de Medje; Ger. Polias Spitzmaus

Crocidura polia Hollister, 1916. Bull. Amer. Mus. Nat. Hist. 35: 669. Medje, DR Congo.

Taxonomy Included in *C. dolichura* by Heim de Balsac & Meester (1977). Synonyms: none. Chromosome number: not known.

Description Very small greyish-brown shrew. Dorsal pelage greyish-brown, sparsely speckled with silvery-grey. Ventral pelage pale greyish-brown. Fore- and hindfeet whitish. Tail relatively extremely long (ca. 124% of HB), slightly bicoloured, blackish brown above, paler below; uniquely covered with short hairs, which increase in number and length on the terminal half to form a distinct white brush at tip. Skull profile flat, rising gently from rostrum to occiput. First upper incisor small. Uniscupids pointed; first uniscupid larger than second and third; second and third subequal. Third upper molar medium. Nipples: not known.

Geographic Variation None.

Distribution Endemic to Africa. Rainforest BZ/Northern Rainforest–Savanna Mosaic. Known only from the type locality at Medje, DR Congo.

Habitat Not known. The vegetation at Medje is a mosaic of rainforest and savanna.

Abundance Very rare. Known only by the holotype.

Remarks Apparently no other information available.

Conservation IUCN Category: Data Deficient.

Measurements

Crocidura polia

TL: 130 mm, n = 1

T: 72 mm, n = 1

HF: 13 mm, n = 1



Crocidura polia

E: 9 mm, n = 1

WT: n. d.

CI: 18.2 mm, n = 1

GWS: 8.2 mm, n = 1

I¹–M³: 7.3 mm, n = 1

Medje, DR Congo (holotype; Hollister 1916)

Key Reference Hollister 1916.

Rainer Hutterer

***Crocidura raineyi* RAINEY'S SHREW**

Fr. Crocidure de Rainey (Crocidure de Mt Garguez); Ger. Raineys Spitzmaus

Crocidura raineyi Heller, 1912. Smithson. Misc. Coll. 60 (12): 7–8. North Creek, Mt Garguez, Kenya (= Warges, Kenya).

Taxonomy A species of the *luna-fumosa* group (Dippenaar & Meester 1989); the largest species in the group. Not a synonym of *C. luna* as given by Heim de Balsac & Meester (1977). Synonyms: none. Chromosome number: not known.

Description Large brownish-grey shrew. Dorsal pelage grizzled brownish-grey. Ventral pelage paler than dorsal pelage. Fore- and hindfeet very pale yellowish-brown (not black). Tail relatively long (ca. 69% of HB); bicoloured, brownish-grey above, whitish below; pilosity 61–71%. Skull medium-sized, braincase narrow and low. Unicuspid subequal. Upper third molar robust. (Description after Dippenaar & Meester 1989.) Nipples: not known.

Geographic Variation None.

Distribution Endemic to Africa. Somalia–Masai Bushland BZ. Known only from the type locality at Mt Garguez, Kenya.

Habitat No information.

Abundance Very rare. Known only from the holotype and eight paratypes collected in 1911.

Remarks Apparently no other information available.

Conservation IUCN Category: Data Deficient; formerly Critically Endangered.

Measurements*Crocidura raineyi*

HB: 91 (90–92) mm, n = 9

T: 63 (59–65) mm, n = 8

HF: 16 mm, n = 9*

E: n. d.

*Crocidura raineyi*

WT: n. d.

CI: 24.9 (24.6–25.3) mm, n = 7

GWS: 10.6 (10.3–10.9) mm, n = 8

I¹–M³: 10.9 (10.8–11.0) mm, n = 8

Mt Garguez, Kenya (Dippenaar & Meester 1989)

*Range not given

Key Reference Dippenaar & Meester 1989.**Rainer Hutterer*****Crocidura religiosa* EGYPTIAN PYGMY SHREW**

Fr. Crocidure naine d'Égypte; Ger. Ägypten-Zwergspitzmaus

Crocidura religiosa (L. Geoffroy, 1827). Mem. Mus. Hist. Nat. Paris 15: 128. Giza, Egypt.

Taxonomy Originally described as *Sorex religiosa* from embalmed specimens from ancient Egyptian tombs at Thebes. Referred to as *C. nana* by Osborn & Helmy (1980), a name that has been applied to various small shrews of Somalia, Ethiopia and Egypt (see Hutterer 2005b for discussion). The name *religiosa* is now restricted to the small endemic shrew of the Nile Valley in Egypt (Hutterer 2005b). Synonyms: none. Chromosome number: not known.

Description Very small grey shrew. Dorsal pelage greyish with tinge of brown. Ventral pelage pale grey; hairs grey at base, white

at tip. Chin and throat paler than ventral pelage. Fore- and hindfeet whitish. Tail relatively long (ca. 65% of HB), bicoloured, grey above, whitish below; pilosity uncertain ('bristles numerous'). Skull small and delicate, and rather 'flat'. (Description modified from Osborn & Helmy 1980.) Nipples: not known.

Geographic Variation None recorded.

Distribution Endemic to Africa. Sahara Arid BZ. Recorded only in Egypt in the southern part of the Nile delta near Giza, and at

Thebes. May occur along Nile Valley between Giza and Thebes.

Habitat Recorded under stones, bricks and clumps of earth in moist cultivated fields (Hoogstraal 1962); also found along canal banks and under piles of grass, cotton and corn stalks (Osborn & Helmy 1980). Nest made of cotton bolls and sticks (label; Osborn & Helmy 1980).

Abundance No information.

Remarks Apparently no other information available.

Conservation IUCN Category: Data Deficient.

Measurements

Crocidura religiosa

HB: 53.8 (48–62) mm, n = 8

T: 34.8 (28–40) mm, n = 8

HF: 9.4 (9–10) mm, n = 8

E: 7.0 (6–9) mm, n = 7

WT: n. d.

CI: 15.3 (14.4–16.1) mm, n = 8

GWS: 6.8 (6.6–7.1) mm, n = 12

I¹–M³: 6.2 (5.5–6.7) mm, n = 12

Egypt (Osborn & Helmy 1980, as *C. nana*)



Crocidura religiosa

Key Reference Osborn & Helmy 1980.

D. C. D. Happold

Crocidura roosevelti ROOSEVELT'S SHREW

Fr. Crocidure de Roosevelt; Ger. Roosevelts Spitzmaus

Crocidura roosevelti (Heller, 1910). Smithson. Misc. Coll. 56 (15): 6. Rhino Camp, Lado Enclave, Uganda.

Taxonomy Originally described in the genus *Heliosorex*. Genetic data suggest that this species is not closely related to *C. dolichura* and allies (Quérrouil *et al.* 2005). Clusters preferentially with the Euro-African *C. russula*, secondarily with the European *C. leucodon* and the African *C. obscurior* (Quérrouil *et al.* 2001). Synonyms: none. Chromosome number: not known.

Description Small greyish-brown shrew. Pelage soft and comparatively long; hairs 3–4 mm. Dorsal pelage greyish-brown; hairs grey at base, mid-brown to cinnamon-brown at tip. Ventral pelage whitish-grey, hairs pale grey at base, white at tip. Head similar in colour to dorsal pelage. Ears relatively large. Fore- and hindlimbs flesh-coloured, with sparse covering of short white hairs on upper surface. Hindlimbs relatively long; whitish. Soles of hindfeet with granular surface between plantar pads. Tail relatively very long (ca. 85% of HB to 94% and 96% of HB in Angola), bicoloured, pale brown above, paler below; pilosity ca. 70%. First incisor moderately long and hooked. Third molar narrow to medium. Nipples: not known.

Geographic Variation None recorded.

Distribution Endemic to Africa. Northern, Eastern and Southern Rainforest–Savanna Mosaics of central Africa. Recorded



Crocidura roosevelti

from Central African Republic, DR Congo, Uganda, Rwanda, Tanzania and NE Angola (Hutterer 1981a).

Habitat Margins of forest and savanna (Hutterer 2005b).

Abundance Uncertain. Only recorded from a few localities within the geographical range.

Remarks Recorded occasionally in pellets of Barn Owls *Tyto alba* in Garamba N. P., DR Congo (5 of 172 shrews; 13 spp.) (Heim der Balsac & Verschuren 1968).

Conservation IUCN Category: Least Concern.

Measurements

Crocidura roosevelti

HB: 72, 62 mm, n = 2

T: 68, 59 mm, n = 2

HF: 14, 14 mm, n = 2

E: n. d.

WT: n. d.

CI: 22 mm, n = 1

GWS: n. d.

I¹–M³: 8.9 mm, n = 1

Angola (Hayman 1963)

Key Reference Hutterer 1981a.

D. C. D. Happold

Crocidura russula GREATER SHREW (GREATER WHITE-TOOTHED SHREW)

Fr. Crocidure musette; Ger. Große Weißzahnschnecke

Crocidura russula (Hermann, 1780). In: Zimmermann, Geogr. Gesch. Mensch. Vierf. Tiere 2: 382. Near Strasbourg, Bas Rhin, France.

Taxonomy Originally described in the genus *Sorex*. Although two subspecies are recognized here, molecular data has provided evidence that populations of this species in Tunisia may represent a separate species, *C. ichneusi* (listed as such in Hutterer 2005b), within the 'russula group', separate from populations in Morocco (Vogel *et al.* 2004, Cosson *et al.* 2005). Synonyms (Africa only): *chaouiensis*, *foucauldi*, *heljanensis*, *yebalensis* (see Hutterer 2005b for non-African synonyms and comment). Subspecies: two. Chromosome number: 2n = 42, FN = 60 in Morocco (Catzefflis *et al.* 1985, Vogel *et al.* 1992), aFN = 68 in Tunisia (Sarà & Zanca 1992).

Description Small to small-medium shrew. Pelage soft and moderately dense; hairs ca. 4 mm. Dorsal pelage greyish-brown to reddish-brown; hairs dark grey at base, reddish-brown at tip. Flanks similar in colour to dorsal pelage, or paler and greyer. Ventral pelage grey to whitish-grey, sometimes tinged with russet; hairs grey at base, off-white or russet at tip. Ears relatively large, not concealed by pelage. Hindfeet dark on dorsal surface. Tail of medium relative length (ca. 50% of HB), dark brown; pilosity 60%. Skull elongated, rostrum narrow. Third unicuspid tooth relatively large, even larger than the second, and larger than the adjacent cusp (parastyle) of the fourth upper premolar. Parastyle of the fourth upper premolar poorly developed, standing off the metacone. Mandible length and height of coronoid process (see Measurements) are useful distinguishing characters. Nipples: not known.

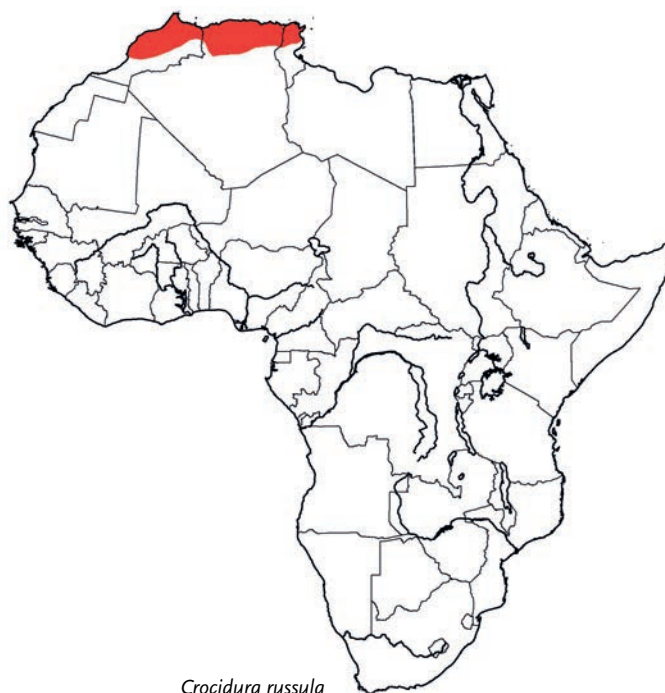
Geographic Variation A stepped cline, with changes in shape and size, and in chromosome characteristics, occurs from the eastern to the western Maghreb (Sarà & Vogel 1996). Although recognized as two subspecies, Vogel *et al.* (2004) and Cosson *et al.* (2005) suggest each subspecies represents a species:

C. r. russula: Morocco; western part of geographic range (the 'modern' part of range) including the form *yebalensis*.

C. r. ichneusi: Tunisia; eastern part of range (the 'ancient' part of the range) (Brändli *et al.* 2005, Hutterer 2005b).

Distribution Mediterranean Coastal BZ. Recorded from Morocco, Algeria and Tunisia north of the Atlas Mts, from sea level up to at least 2800 m (Hutterer 1986e, Vogel & Maddalena 1987, Kowalski & Rzebik-Kowalska 1991). Extraliminally widespread in S and W Europe, including some Mediterranean islands.

Habitat Semi-open grasslands, cultivated areas and gardens (sheltering mainly in hedgerows and dry stone walls between the fields), low shrubs, halophyte vegetation of estuaries and matorrals. All habitats are characterized by being quite humid and covered with vegetation.



Crocidura russula

Abundance Quite common and widely distributed. Populations may attain high densities; fluctuations in density are probably related to rainfall.

Adaptations Active day and night with peaks of activity after dusk and around dawn. Activity periods are longer during night than day, and vary according to climate (Genoud & Vogel 1981).

Foraging and Food Mainly insectivorous. Principal prey includes insects, snails and earthworms. Occasionally eats small vertebrates such as lizards and young rodents. Daily energetic expenditure requires a food intake of ca. 50% of body weight/day (Genoud 1985, Churchfield 1990).

Social and Reproductive Behaviour Territorial in summer during the reproductive season, but may live in small groups during winter.

Reproduction and Population Structure Reproduction occurs from Feb to Nov in the Mediterranean regions of Europe, and peaks of reproductive activity occurs in late spring to early summer. Gestation: 28–33 days. Litter-size: 1–6 (mean: 3.5–4.6 in Europe). Weaned at Day 18–20 (Genoud & Vogel 1991). Age at first breeding: ca. 3 months. Maximal longevity: 1–1.5 years. Females may have up to eight litters (4–5 in a single breeding season). Dispersal of young is highly female-biased (Favre *et al.* 1997). Males may pair simultaneously with up to four ♀♀, and ♀♀ paired with multiple-mated ♂♂ wean significantly more offspring (Bouteiller & Perrin 2000); consequently a high level of genetic diversity can be observed in subpopulations.

Predators, Parasites and Diseases Regular prey of Barn Owls

Tyto alba in N Morocco, forming ca. 2% to 22% of the diet (Aulagnier *et al.* 1999) and of Tawny Owls *Strix aluco* in Boukhalfa (Algeria), forming up to 13.9% of the diet (Hamdine *et al.* 1999). Occasional prey of the Pharaoh Eagle-owl *Bubo ascalaphus* and the Marsh Owl *Asio capensis*. Ectoparasites include *Nosopsyllus barbarus* (Siphonaptera, Leptopsyllidae) (Hastriter & Tipton 1975).

Conservation IUCN Category: Least Concern.

Because of its synanthropic habits, this shrew can suffer from the use of insecticides and other toxic chemicals.

Measurements

Crociodura russula

HB: 69.4 (61–79) mm, n = 27

T: 37.0 (27–45) mm, n = 27

HF: 12.2 (11–13) mm, n = 27

E: 8.9 (8–11) mm, n = 26

WT: 6.4 (5–9) g, n = 27

CI: 19.0 (18.1–19.8) mm, n = 23

GWS: 8.7 (8.4–9.3) mm, n = 23

I–M³: 8.2 (7.7–8.6) mm, n = 23

Mandible length: 10.8–12.1 mm

Height of coronoid process: 4.4–4.9 mm

Morocco (Vesmanis & Vesmanis 1980)

Specimens from humid areas (rainfall 1200 mm/year) are larger than those from drier areas (400 mm/year)

Key References Aulagnier & Thévenot 1986; Hutterer 1986e; Kowalski & Rzebiak-Kowalska 1991; Vogel & Maddalena 1987.

Stéphane Aulagnier & Peter Vogel

Crociodura selina UGANDAN LOWLAND SHREW

Fr. Crociodure de forêt d'Ouganda; Ger. Uganda-Tieflandspitzmaus

Crociodura selina Dollman, 1915. Ann. Mag. Nat. Hist., ser. 8, 16: 371–372. Chagwe, Mabira Forest, Uganda.

Taxonomy Previously included in *C. fumosa* or *C. luna*, but considered a distinct species by Dippenaar & Meester (1989). Synonyms: none. Chromosome number: not known.

Description Medium-sized shrew. Dorsal pelage dark brownish-grey to slate-grey. Ventral pelage slightly paler. Feet reddish-brown to yellowish-brown. Tail dark reddish-brown above, slightly paler below. Tail relatively long (ca. 70% of HB); pilosity 68–78%. Skull with a proportionally wide interorbital region (4.8 [4.7–5.0] mm, n = 5), moderately robust rostrum, narrow and flat braincase, robust unicusps and moderately wide M³ (Dippenaar & Meester 1989). Nipples: not known.

Geographic Variation A newly discovered population in SE Kenya (Oguge *et al.* 2004) may be slightly larger and requires detailed comparison with the Uganda populations.

Distribution Endemic to Africa. Isolated records in Uganda (Mabira Forest, Kibanda Forest, Mbanga Forest) and SE Kenya (Kyulu Hills).

Habitat Lowland evergreen forest in Uganda (Mabira, Kibanda and Mbanga Forests). In Kenya (Kyulu Hills) the species was found at 1700 m in mist forest consisting primarily of the plants *Alangium chinense*, *Ilex mitis*, *Ficus* spp., *Xymalos* sp., *Neuboutonia* sp., *Schefflera* sp., *Prunus africana*, *Olea capensis* and *Rapanae* sp. (Oguge *et al.* 2004).

Abundance In Uganda, the species is known from only a few specimens collected in three different forests; no population study has been conducted so far. In Kenya (Kyulu Forest), *C. selina* occurs in reasonably high numbers (63% of all shrew captures), together with *C. luna* and *C. hildegardeae* (Oguge *et al.* 2004).

Remarks A medium-sized terrestrial shrew; no other available information.

Conservation IUCN Category: Data Deficient (previously Endangered).

Measurements

Crocidura selina

HB: 83 (79–88) mm, n = 5

T: 58 (55–62) mm, n = 5

HF: 14 (13–15) mm, n = 2

E: 10 (10–11) mm, n = 2

WT: n. d.

CI: 23.2 (22.8–23.5) mm, n = 4

GWS: 10.0 (9.8–10.3) mm, n = 4

I¹–M³: 10.4 (10.2–10.6) mm, n = 6

Uganda (Dippenaar & Meester 1989)

HB: 87.3 (77–100) mm, n = 14

T: 62 (58–68) mm, n = 14

HF: 15 (13–16) mm, n = 14

E: 8.3 (6.6–9.8) mm, n = 14

WT: 12.4 (11–15) g, n = 14

Kyulu Hills, SE Kenya, Uganda (Oguge *et al.* 2004)

Key Reference Dippenaar & Meester 1989.

Rainer Hutterer

Crocidura selina



Crocidura silacea LESSER GREY-BROWN SHREW (LESSER GREY-BROWN MUSK SHREW)

Fr. Crocidure grisâtre; Ger. Kleine graubraune Moschusspitzmaus

Crocidura silacea Thomas, 1895. Ann. Mag. Nat. Hist., ser. 6, 16: 53. Figtree Creek, De Kaap, Barberton district, Mpumalanga Province, South Africa.

Taxonomy Monotypic. Although described as a valid species, there has been some doubt in the literature about the status of *silacea*. Meester (1963) considered it to be a monotypic species, Heim de Balsac & Meester (1977) referred to it as a subspecies of *C. gracilipes*, Smithers (1971) listed it as a synonym of *Crocidura cyanea infumata* while Meester *et al.* (1986) reverted to the original designation of *C. silacea*. Morphometric studies by Meester *et al.* (1985), Taylor *et al.* (1994) and Taylor & Contrafatto (1996) support its status as a valid species. Synonyms: *holobrunneus*. Subspecies: none. Chromosome number: not known.

Description Small to small-medium shrew. Dorsal pelage buffy-brown to brown grizzled with pale grey or fawn; hairs slaty-grey at base, pale grey to fawn subterminal band, brown at tip. Ventral pelage pale grey with brown tinge; hairs slaty-grey at base, pale grey or fawn at tip. Colours of dorsal and ventral pelage merge gradually on flanks. Summer pelage is darker than winter pelage. Head slender with long, narrow pointed muzzle, small eyes and rounded ears. Fore- and hindfeet brown. Tail relatively long (ca. 70% of HB), pale to dark brown above, paler below; pilosity not known. Nipples: 0 + 3 = 6.

Geographic Variation None recorded.

Distribution Endemic to Africa. Zambezian Woodland BZ and Highveld BZ. Recorded from Zimbabwe, N Botswana, South Africa (North West, Northern, Gauteng, Mpumalanga and KwaZulu–Natal

Provinces), Swaziland and S Mozambique (Wolsan & Hutterer 1998) in areas with rainfall exceeding 500 mm/year (Meester 1963). Because of uncertainty over the taxonomic status of the species, its geographical range possibly also includes Angola, S Zambia and



Crocidura silacea

S Malawi to Kenya and Uganda (Meester *et al.* 1986). Geographic limits uncertain.

Habitat Montane forest and grassland, coastal forest, savanna woodland, bush, grassland and even rocky habitats (Meester 1963, Rautenbach 1982, Skinner & Smithers 1990). Wide habitat tolerance.

Abundance Uncommon; seldom collected.

Adaptations A physiological trial on a single specimen produced an average daily metabolic rate slightly lower than expected for a crocidurine of its size (R. M. Baxter unpubl.).

Foraging and Food No detailed information; presumably insectivorous.

Social and Reproductive Behaviour Vocalizations include an occasional short, strident squeak during aggressive encounters. A similar squeak is given when alarmed. Digging and rooting has rarely been observed in captivity. Nests are spherical with 2–4 entrances.

Reproduction and Population Structure No information.

Predators, Parasites and Diseases Remains of the species have been recovered from pellets of Barn Owls *Tyto alba* (Vernon 1972). Domestic cats also prey on these shrews (Meester 1963).

Conservation IUCN Category: Least Concern.

Measurements

Crocidura silacea

HB: 69.2 (60–80) mm, n = 17

T: 48.8 (43–56) mm, n = 17

HF: 11.9 (10.5–13) mm, n = 18

E: 8.4 (7–10) mm, n = 17

WT: 7 (6–8) g, n = 2

CI: 19.7 (19.0–20.3) mm, n = 14

GWS: 8.9 (8.7–9.2) mm, n = 12

I¹–M³: 8.3 (7.9–8.7), n = 19

South Africa

Measurements: Meester 1963

Weight: Rautenbach 1982

Key Reference Meester 1963.

R. M. Baxter & N. J. Dippenaar

Crocidura smithii DESERT SHREW (DESERT MUSK SHREW)

Fr. Crocidure de Smith; Ger. Wüsten-Moschusspitzmaus

Crocidura smithii Thomas, 1895. Ann. Mag. Nat. Hist., ser. 6, 15: 51. Finik, Webi Shebeli, Ethiopia.

Taxonomy Specimens reported from Somalia by Heim de Balsac (1966) represent *C. macarthuri*. The widespread disjunct distribution (see below) may indicate that the two populations represent different species (Hutterer 1986a). Synonyms: *debalsaci*. Subspecies: none. Chromosome number: not known.

Description Small–medium shrew. Dorsal pelage slate-grey to pale yellowish-brown; hairs grey at base. Ventral pelage white; hairs grey at base, white at tip. Clear delineation between colours of dorsal and ventral pelage rather high up on the flanks; including almost to the top of the ears and the cheeks. Ears naked, sticking out from side of body. Fore- and hindlimbs white; hindfeet short. Tail of medium relative length (ca. 54% of HB), white, thick at base; pilosity ca. 100%. Nipples: not known.

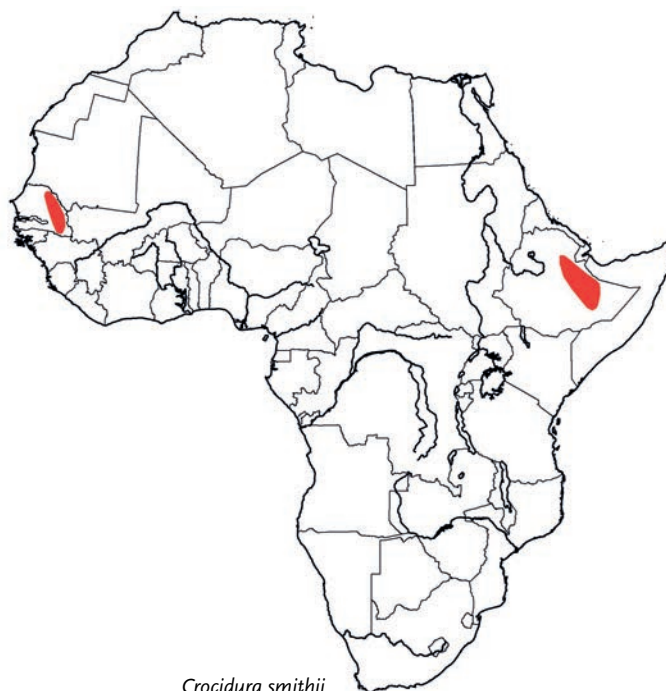
Geographic Variation The form *debalsaci* from Senegal (described as a subspecies – see Hutterer 1981b – but now considered as a synonym) is larger in size than specimens from Ethiopia.

Distribution Endemic to Africa. Sudan Savanna BZ (Senegal) and Somalia–Masai Bushland BZ (Ethiopia). Recorded only from lowland Ethiopia and Senegal, but not recorded from any locality between these countries

Habitat Not known. One specimen found in a termitarium in Senegal (Hutterer 1981b).

Abundance Very rare; known only by a few specimens.

Remarks Apparently no other information available.



Crocidura smithii

Conservation IUCN Category: Least Concern.

Measurements

Crocidura smithii

HB: 64–85 mm

T: 31–51 mm

HF: 11–13 mm

E: 7.5–8 mm

WT: n. d.

CI: 20.6–22.9 mm

GWS: 7.9–9.2 mm

I¹–M³: 8.8–10.1 mm

Ethiopia (Hutterer 1986a; means and sample sizes not recorded)

Key References Hutterer 1981b, 1986a.

D. C. D. Happold

Crocidura somalica SOMALI SHREW

Fr. Crocidure de Somalie; Ger. Somalia-Spitzmaus

Crocidura somalica Thomas, 1895. Ann. Mag. Nat. Hist., ser. 6, 16: 52. Middle Webi Shebeli (about 05° 30' N, 44° 00' E) near Geledi (Galadi), Ethiopia.

Taxonomy Revised by Hutterer & Jenkins (1983). Similar to *C. yankariensis* but relationships unknown. The subspecies *dhofarensis* (Hutterer & Harrison 1988, Harrison & Bates 1991) from Oman is now considered to be a separate species (Hutterer *et al.* 1992a, Hutterer 2005b). Synonyms: none. Chromosome number: not known.

Description Small–medium shrew. Dorsal hairs 3–4 mm in length. Dorsal pelage slaty-grey, more or less variegated with brown. Ventral pelage clearly grey. Chin white. Ears whitish, very finely haired. Fore- and hindfeet white. Tail relatively long (ca. 66% of HB), slender, slightly thicker at base; pale brown above, white below, bristles white (partly quoted from Thomas 1895); pilosity ca. 80%. Skull small and slender (figured in Hutterer & Jenkins 1983); dorsal profile straight, slopes gradually upwards from rostrum to back of braincase; rostrum relatively long and slender; zygomatic process subangular, aligned with paracone of M² region gradually increasing in width from anterior to posterior; braincase suboval in dorsal view. Coronoid process of mandible medium in height and width. Dentition as in other crocidurines, lacks special features. I¹ short; M³ medium. Nipples: not known.

Geographic Variation None recorded.

Distribution Endemic to Africa. Sudan Savanna BZ and Somalia–Masai Bushland BZ. Recorded from three localities in Ethiopia (Hutterer 1980, Demeter 1982), and in Sudan (Kordofan Province; Hutterer & Kock 1983) and Mali (Hutterer *et al.* 1992a). Probably also in Somalia (Hutterer 2005b). The locality of the holotype, ‘Webi Shebeli, Somaliland’, is in fact in Ethiopia near the border with Somalia (see Moreau *et al.* 1946).

Habitat Dry savanna and semi-desert. Granite rocks and sandy valleys in the Adrar de Iforas (Mali) (Dobigny *et al.* 2001).

Abundance Uncertain. An owl pellet assemblage from Kordofan, Sudan, contained four specimens (= 3.4%) among 123 shrews of five species (Hutterer & Kock 1983). Also present in small numbers in another assemblage from Adrar de Iforas, Mali (Dobigny *et al.* 2001).

Remarks Skull remains have been found in pellets of Spotted Eagle-owls *Bubo africanus* in Awash N. P., Ethiopia (Demeter 1982), and in pellets of Barn Owls *Tyto alba* in Kordofan, Sudan (Hutterer & Kock 1983) and in Adrar de Iforas, Mali (Dobigny *et al.* 2001). Two individuals were found drowned in a calabash full of milk in the desert of NE Mali (Hutterer *et al.* 1992a). *Crocidura yankariensis* – a similarly small species – coexists with *C. somalica* in Sudan and Ethiopia; *C. yankariensis* differs by having a densely haired tail, short hindfoot (9–10 mm), larger ears, lower part of hindlimb (tibia) without long body hairs (figured in Hutterer & Jenkins 1983), and a more rectangular skull with heavier dentition.

Conservation IUCN Category: Least Concern.

Measurements

Crocidura somalica

HB: 64.3 (63–77) mm, n = 3



Crocidura somalica

T: 42.8 (40–46) mm, n = 3
 HF: 12 (11–13) mm, n = 3
 E: 6.4 (5–7) mm, n = 3
 WT: 8 g, n = 1
 CI: 19.8 (19.2–20.1) mm, n = 3
 GWS: 8.8 (8.5–9.1) mm, n = 3

I¹–M³: 8.5 (8.4–8.7) mm, n = 3
 Ethiopia (Hutterer & Jenkins 1983)

Key References Hutterer & Jenkins 1983; Hutterer *et al.* 1992a.

Rainer Hutterer

Crocidura stenocephala **KAHUZI SWAMP SHREW**

Fr. Crocidure du Mont Kahuzi; Ger. Kahuzi Sumpfspitzmaus

Crocidura stenocephala Heim de Balsac, 1979. Säugetierk. Mitt. 27: 258. Kahuzi-Biega National Park, E DR Congo.

Taxonomy Described as a subspecies of *C. littoralis* but regarded as a full species by Hutterer (1982, 2005a). Synonyms: none. Chromosome number: not known.

Description Large shrew. Dorsal pelage blackish, superficially brownish; hairs silvery-ash grey at base, brownish at tip. Ventral pelage brownish-grey, sometimes with olive tinge, paler than dorsal pelage; hairs pale grey at base, pale brownish at tip. Undersurface of head and neck ash-grey. Ears covered with short hairs and partly covered by pelage. Hindfeet dark brown, forefeet pale brown. Tail relatively long (ca. 77% of HB), dark brown above, paler below; appears naked but with very short inconspicuous bristles; does not taper towards tip, pilosity <20%. Skull similar to that of *C. littoralis*, but clearly narrower; cutting edge of mandibular incisors with two denticles. Nipples: not known.

Geographic Variation None recorded.

Distribution Endemic to Africa. Afromontane–Afroalpine BZ, in regions around the Albertine Rift Valley in E DR Congo and SW Uganda. Recorded from only three montane swamps (2100–2300 m) at the foot of Mt Kahuzi, E DR Congo (Dieterlen & Heim de Balsac 1979) and in Bwindi Impenetrable N. P., SW Uganda (Kasangaki *et al.* 2003).

Habitat Swamps dominated by *Cyperus latifolius* (E DR Congo). Water in the swamps is normally slightly above ground level, but covered by a thick layer of floating plants, which provide shelter and nesting facilities (see also below).

Abundance This species (and *C. kivuana*) are often the commonest shrews in some swamps in E DR Congo. In one swamp, there were 14 *C. stenocephala*, one *Sylvisorex megalura*, one *S. granti*, but no *C. kivuana*. In another swamp, there were 19 *C. stenocephala*, 22 *C. kivuana* and seven specimens of four additional species.

Remarks Although there appear to be no special morphological adaptations for living in swamps, it is assumed that these shrews must accommodate to a very moist habitat and changing water levels. Frequently the swamps are flooded and the water level is 20–30 cm above ground level. One pregnant ♀ (out of 13) was found during the wet season (Mar). Sex ratio (captures): 23 ♂♂ to 13 ♀♀ (E DR Congo; F. Dieterlen unpubl.).



Crocidura stenocephala

Conservation IUCN Category: Endangered.

This species is threatened because of its rarity and very restricted geographic range; in this respect it is similar to the other endemic species of the Albertine Rift Valley.

Measurements

Crocidura stenocephala

HB: 92.1 (82–106) mm, n = 36
 T: 71.0 (61–81) mm, n = 36
 HF: 16.2 (15–20) mm, n = 36
 E: 8.5 (5–11) mm, n = 36
 WT: 21.0 (16–35) g, n = 36
 CI: 23.7 (22.9–24.4) mm, n = 20
 GWS: 9.6 (9.0–10.0) mm, n = 20
 I¹–M³: 9.9 (9.5–10.3) mm, n = 20
 E DR Congo (Dieterlen & Heim de Balsac 1979, SMNS)

Key Reference Dieterlen & Heim de Balsac 1979.

Fritz Dieterlen

Crocidura tansaniana TANZANIAN SHREW (AMANI MUSK SHREW)

Fr. Crocidure de Tanzanie; Ger. Tansania-Spitzmaus

Crocidura tansaniana Hutterer, 1986. Bonn. Zool. Beitr. 37: 27. Amani, East Usambara Mts, Tanzania.

Taxonomy Considered to be part of the *C. monax-littoralis* species group (Hutterer 1986b). Synonyms: none. Chromosome number: not known.

Description Large stout shrew with dark chocolate-brown pelage. Pelage dense and short (5 mm on back, 4 mm on neck, 4.5 mm ventrally). Dorsal pelage chocolate-brown; hairs silvery-grey with brown tip. Ventral pelage silvery-brown, paler than dorsal pelage; hairs grey with pale brown tip. Colours of dorsal and ventral pelage merge on flanks. Vibrissae long. Ears prominent with very small hairs. Flank gland usually not visible in ♂♂ unless pelage is parted. Fore- and hindfeet paler than dorsal pelage; hindfeet dark on outer edge and paler on inner edge with short silvery hairs on the upper surface. Tail relatively long (60–70% of HB), unicoloured; pilosity ca. 30%. First incisor long and hooked. Third molar medium. Nipples: not known.

Geographic Variation None recorded.

Distribution Endemic to Africa. Afromontane–Afroalpine BZ. Recorded only from the East Usambara Mts, N Tanzania.

Habitat Undisturbed or slightly disturbed montane forests in the Amani area of the East Usambara Mts where soil is moist. Not recorded in smaller disturbed forest patches in the same area (30 ha or smaller), nor in agricultural areas.

Abundance The most abundant species of shrew recorded in surveys of undisturbed forest in the East Usambara Mts; comprised ca. 50% of shrews collected ($n = 33$). Syntopic with *C. hildegardae*, *C. olivieri* and *Sylvisorex howelli* (Stanley *et al.* 2011).

Remarks Terrestrial and nocturnal. Males tended to outnumber females during three years of sampling (♂ : ♀ ratios were: 2 : 0 [$n = 2$, 1991]; 3 : 1 [$n = 12$, 1992]; 18 : 17 [$n = 35$, 1993]; and 29 : 20 [$n = 49$, 1991–93]). Average testes length 4.5 mm (3–6 mm), average width 2.5 mm (2–4 mm) ($n = 17$, 1991–93). Most of the ♀♀ examined (Jul–Sep 1991–93) were nulliparous and two were pregnant ($n = 13$). Embryo number: two ($n = 2$), one embryo in each horn; crown–rump lengths of the largest embryos: 8 and 14 mm. Ratio of juveniles to adults (based on toothwear) was 11 : 23 in 1993 (Stanley *et al.* 2011).

*Crocidura tansaniana*

Conservation IUCN Category: Endangered.

Measurements*Crocidura tansaniana*HB: 96 (80–110) mm, $n = 42$ T: 68 (58–76) mm, $n = 49$ HF: 17 (15–19) mm, $n = 49$ E: 11 (8–14) mm, $n = 49$ WT: 14.8 (9.5–20) g, $n = 49$ CI: 25.1 (23.8–26.1) mm, $n = 43$ GWS: 10.8 (10.3–11.4) mm, $n = 43$ I¹–M³: 11.1 (10.7–12.0) mm, $n = 43$ East Usambara Mts, Tanzania (Stanley *et al.* 2011)

Key References Hutterer 1986b; Stanley *et al.* 2011.

William T. Stanley

Crocidura tarella TARELLA SHREW

Fr. Crocidure de Tarella (Crocidure d'Ouganda); Ger. Tarella-Spitzmaus

Crocidura tarella Dollman, 1915. Ann. Mag. Nat. Hist., ser. 8, 15: 511; ser. 8, 16: 135. Chaya, near Ruchuru, Congo Belge (= near Rutshuru, DR Congo).

Taxonomy Described as a subspecies of *C. turba* (Dollman 1915a, d) and also considered as a subspecies of *C. zaodon* (Heim de Balsac

& Meester 1977); now recognized as a distinct species by Dippenaar (1980b). Synonyms: none. Chromosome number: not known.

Description Large shrew. Dorsal pelage dark reddish-brown. Ventral pelage grey with reddish-brown wash and silvery sheen. Feet dark reddish-brown. Tail relatively long (63% of HB), blackish-brown above, paler below; pilosity 85–90%. Skull: wide interorbital region; wide maxillary region; narrow braincase. Unicuspid broad; third upper molar moderately broad; talonid of third lower molar with entoconid and talonid basin. Nipples: not known.

Geographic Variation None recorded.

Distribution Endemic to Africa. Eastern Rainforest–Savanna Mosaic. Recorded from NE DR Congo and Uganda. Distribution disjunct; limits uncertain.

Habitat Forest.

Abundance No information.

Remarks Apparently no other information.

Conservation IUCN Category: Endangered.

Measurements

Crociodura tarella

HB: 91 mm, n = 1

T: 57 mm, n = 1

HF: 17 mm, n = 1

E: 9.5 mm, n = 1

WT: n. d.

CI: 24.5 mm, n = 1



Crociodura tarella

GWS: 10.4 mm, n = 1

I¹–M³: 10.9 mm, n = 1

DR Congo (Dollman 1915d, BMNH)

Key Reference Dollman 1915d.

P. D. Jenkins & S. Churchfield

Crociodura tarfayensis SAHARAN SHREW (TARFAYA'S SHREW)

Fr. Crocidure de Tarfaya; Ger. Sahara-Spitzmaus

Crociodura tarfayensis Vesmanis and Vesmanis, 1980. Zool. Abh. Mus. Tierk. Dresden 36: 47. 8 km south Tarfaya, Agadir Prov., Morocco.

Taxonomy All related forms described as species or subspecies by Vesmanis & Vesmanis (1980). Relationship with possible conspecific *Crociodura* species from West Africa and Europe needs to be more carefully evaluated. Synonyms: *agadiri*, *gouliminensis*, *tiznitensis*. Subspecies: none. Chromosome number: not known.

Description Small shrew, a little smaller than *C. russula*. Dorsal pelage pale greyish-brown, hairs long (4–6 mm) and smooth. Ventral pelage whitish, sharply contrasting with dorsal pelage. Hindfeet pale on upper surface. Tail of medium relative length (ca. 60% of HB); hairy; pilosity not known. Teeth stronger than those of *C. russula*, sharing some characteristics with those of *C. whitakeri*: third unicuspid tooth smaller than the second unicuspid, and the same size as the adjacent, well-developed cusp (parastyle) of the fourth upper premolar. First and second upper molars short and broad. Nipples: not known.

Geographic Variation None recorded.

Distribution Endemic to Africa. Sahara Arid BZ. Restricted to the Atlantic coast of Morocco, south of Agadir, and parts of Western

Sahara into Mauritania. The specimens reported as *C. whitakeri* by Heim de Balsac (1948, 1968e) undoubtedly belong to *C. tarfayensis* according to the measurements of Vesmanis (1976). All records of *C. whitakeri* from south of Oued Draa probably represent *C. tarfayensis*.

Habitat Stony and sandy habitats with scarce vegetation, such as bushy steppe with *Euphorbia*, where rainfall is low. Probably also inhabits stone screes (because it is abundant in pellets of rock-dwelling owls) and bare gravel plains. Avoids human habitats.

Abundance Uncertain. May be locally abundant (as suggested by abundance in owl pellets). Population numbers seem to fluctuate depending on the alternation of dry and moister periods. May be declining following recent climate changes, which have reduced its geographic range.

Remarks May comprise a major part (over 30%) of the diet of Barn Owls *Tyto alba* and Pharaoh Eagle-owls *Bubo ascalaphus*, and occasionally of Little Owls *Athene noctua* (Thévenot *et al.* 1988).

Conservation IUCN Category: Data Deficient.

Most of the known specimens were collected some time ago when shrews were apparently more numerous. The recent desertification and northern expansion of the Sahara might cause a serious threat for the survival of this species.

Measurements

Crocidura tarfayensis

HB: 63.8 (61–69) mm, n = 6

T: 38.7 (33–40) mm, n = 6

HF: 13.3 (13–14) mm, n = 6

E: 10.2 (9–11) mm, n = 6

WT: 6.5 (6–7) g, n = 6

CI: 18.5 (17.9–18.9) mm, n = 5

GWS: 8.4 (8.3–8.6) mm, n = 5

I¹–M³: 8.1 (7.8–8.6) mm, n = 5

Mandible length: 10.5–11.6 mm

Height of coronoid process: 4.3–5.1 mm

Morocco (Vesmanis & Vesmanis 1980)

Key References Aulagnier & Hermas 1989; Aulagnier & Thévenot 1986; Heim de Balsac 1968e; Hutterer 1986e; Vesmanis & Vesmanis 1980.



Crocidura tarfayensis

Stéphane Aulagnier

Crocidura telfordi TELFORD'S SHREW

Fr. Crocisure de Telford; Ger. Telfords Spitzmaus

Crocidura telfordi Hutterer, 1986. Bonn. Zool. Beitr. 37: 28. Morningside, Uluguru Mts, Tanzania. 1150 m.

Taxonomy Considered to be part of an endemic group of shrews in the Eastern Arc Mts (Hutterer 2005b). Synonyms: none. Chromosome number: not known.

Description Very large shrew with chocolate-brown pelage. Dorsal pelage chocolate-brown; hairs silvery-grey with brown tips; hairs 5–6 mm on back, 4 mm on neck. Ventral pelage slightly paler brown than dorsal pelage; hairs 3 mm, brown at tip. Vibrissae long. Ears prominent with few hairs. Fore- and hindfeet paler than dorsal pelage. Hindfeet relatively long (17–19% of HB). Tail relatively long (65–85% of HB), slightly bicoloured; pilosity 5%. Nipples: not known.

Geographic Variation None recorded.

Distribution Endemic to Africa. Afromontane–Afroalpine BZ. Known only from montane forests of the Uluguru and Udzungwa Mts, Tanzania.

Habitat Undisturbed or slightly disturbed montane forests where soil is moist. Not recorded in smaller disturbed forest patches in the same area (30 ha or smaller), nor in agricultural areas.

Abundance In samples of shrews from the montane forests of the Uluguru and Udzungwa Mountains, *C. telfordi* was one of the species that was the least well represented. In an elevational survey of the Udzungwa Mts, *C. telfordi* comprised 1% of total shrews sampled



Crocidura telfordi

(n = 145). Other shrews that occurred in this sample include *C. elgonius*, *C. desperata*, *C. hildegardeae*, *C. monax*, *C. olivieri* and *Myosorex kihaulei* (W.T. Stanley unpubl.).

Remarks Terrestrial. Nocturnal and diurnal: two individuals were caught during the night and two were caught during the day ($n = 4$; W.T. Stanley unpubl.). A single adult ♀ collected in Aug–Sep from Udzungwa Mts was not pregnant. One ♂ collected in Aug–Sep from the Uluguru Mts had testes length of 4 mm and width of 3 mm (W.T. Stanley unpubl.).

Conservation IUCN Category: Endangered.

The geographic distribution is fragmented and suitable habitat is declining.

Measurements

Crocidura telfordi

HB: 105.3 (104–108) mm, $n = 3$

T: 76 (70–83) mm, $n = 3$

HF: 19.7 (19–20) mm, $n = 3$

E: 9.3 (9–10) mm, $n = 3$

WT: 19.8 (16.5–22) g, $n = 3$

CI: 25.9 (25.8–26.1) mm, $n = 3$

GWS: 11.1 (10.9–11.3) mm, $n = 3$

I¹–M³: 11.8 (11.5–11.9) mm, $n = 3$

Udzungwa Mts, Tanzania (W.T. Stanley unpubl.)

Key Reference Hutterer 1986b.

William T. Stanley

Crocidura thalia THALIA'S SHREW

Fr. Crocidure de Thalia; Ger. Thalias Spitzmaus

Crocidura thalia Dippenaar, 1980. Ann. Transvaal Mus. 32 (6): 138. Gedeb Mts, SE of Dodola, Bale, Ethiopia (ca. 06° 55' N, 39° 10' E). 2600 m.

Taxonomy A member of the endemic Ethiopian *C. glassi* complex (*C. glassi*, *C. lucina*, *C. thalia*, *C. macmillani* and *C. baileyi*) (Dippenaar & Meester 1989). Synonyms: none. Chromosome number: $2n = 36$ (L. Lavrenchenko unpubl.).

Description Medium-sized greyish-brown shrew. Dorsal pelage greyish-brown (west of the Ethiopian Rift Valley) to dark grey with brown to reddish-brown wash (east of the Rift Valley); hairs grey at base, brown or reddish-brown at tip. Ventral pelage pale grey to blackish with ochre wash; hairs grey to dark-grey at base, pale-yellowish to ochre-yellowish at tip. Dorsal surface of fore- and hindfeet brownish, greyish-brown or yellowish-grey. Tail relatively long (ca. 70% of HB), dark brown above, brown below; pilosity 80%. Skull with inflated braincase as is typical for other high altitude Ethiopian *Crocidura*. Nipples: not known.

Geographic Variation Pelage colouration of populations west of the Ethiopian Rift Valley differ in colour from those east of the valley – see above (Dippenaar 1980a).

Distribution Endemic to Africa. Afromontane–Afroalpine BZ, mostly in highland regions in Ethiopia. The most widespread of the endemic shrews of Ethiopia, found both east and west of the Ethiopian Rift Valley, from 515 to 3300 m (Yalden & Lagen 1992). Records currently suggest four separate regions, three in the highlands and one at lower altitude (Baro R., near border with Sudan).

Habitat Open habitats from humid woodland savanna to highland grasslands and scrub. Largely absent from the afromontane forest with a dense canopy where it inhabits only moist riverine habitats (Lavrenchenko 2000).

Abundance Generally uncommon. Comprises 7% of small mammals captured ($n = 88$) in Harennia Forest and neighbouring ericaceous bush; may be rather abundant locally (up to 40% of small mammals on some trapping lines) (L. Lavrenchenko unpubl.)



Crocidura thalia

Remarks Presumed to be nocturnal and insectivorous or omnivorous. In the Bale Mts not known to breed during most of the dry season (no pregnant ♀♀ trapped during Dec–Feb).

Conservation IUCN Category: Least Concern.

Measurements

Crocidura thalia

HB: 87 (77–100) mm, $n = 14$

T: 61 (55–69) mm, $n = 14$

HF: 17.1 (15–19) mm, $n = 14$

E: 11.2 (10–13) mm, $n = 14$

WT: 16 (9–26) g, $n = 14$

CI: 25.2 (23.7–26.1) mm, n = 12
 GWS: 11.1 (10.6–11.5) mm, n = 12
 I¹–M³: 11.3 (10.5–11.7) mm, n = 13
 Ethiopia (L. A. Lavrenchenko and R. Hutterer unpubl.)

Key References Dippenaar 1980a; Yalden & Lagen 1992.

Leonid A. Lavrenchenko

***Crocidura theresae* THERESE'S SHREW**
 Fr. Crocidure de Thérèse; Ger. Thérèses Spitzmaus

Crocidura theresae Heim de Balsac, 1968. Mammalia 32: 398. Nzerekore, Guinea.

Taxonomy First described as *Crocidura* aff. *foxi*, within the *C. poensis* group (Heim de Balsac 1958), then considered as a valid species (Heim de Balsac 1968a). Morphologically closely related to *C. foxi* and *C. poensis* (Heim de Balsac 1968a), and electrophoretically to *C. poensis* (Maddalena 1990a). Synonyms: none. Chromosome number: 2n = 50 (Côte d'Ivoire; Meylan 1971), FN = 82–86 (Guinea; Maddalena 1990b).

Description Medium to large shrew. Dorsal pelage grey to brown. Ventral pelage paler, exceptionally whitish. No clear delineation between colours of dorsal and ventral pelage on flanks. Fore- and hindfeet brown. Tail medium to long (52% [39–62%] of HB), thickset, with sparse brown hairs; pilosity ca. 75%. Nipples: not known.

Geographic Variation None recorded.

Distribution Endemic to Africa. Guinea Savanna BZ. Recorded from Sierra Leone and Guinea to Ghana.

Habitat All types of grasslands up to 1600 m, and also ricefields (Heim de Balsac 1968a).

Abundance Locally abundant; hundreds trapped in savannas at Dabou, Côte d'Ivoire (L. Bellier, in Heim de Balsac 1968a). In Ziamia Biosphere Reserve, Guinea, common in fields (16.2%, n = 272 shrews, 9 spp.), but extremely rare in all other habitats (primary–secondary forest, old fallow land and forest plantations) (P. Barrière unpubl.).

Remarks Apparently no other information available.

Conservation IUCN Category: Least Concern.

Measurements

Crocidura theresae
 HB: 91.3 (78–101) mm, n = 20



Crocidura theresae

T: 47.5 (34–55) mm, n = 19
 HF: 14.8 (13–16) mm, n = 20
 E: n. d.
 WT: 13.3 (7–18.4) g, n = 20
 CI: 22.8 (21.3–24.4) mm, n = 19
 GWS: 9.6 (8.8–10.2) mm, n = 19
 I¹–M³: 10.1 (9.4–10.8) mm, n = 19
 Foro and Dabou, Côte d'Ivoire (MNH)

Key Reference Heim de Balsac 1968a.

J.-M. Duplantier & L. Granjon

***Crocidura turba* TURBO SHREW**
 Fr. Crocidure de Chilui; Ger. Turbo-Spitzmaus

Crocidura turba Dollman, 1910. Ann. Mag. Nat. Hist., ser. 8, 5: 176. 'Chilui Island, Lake Bangweolo' (= Chilubi I., Zambia).

Taxonomy Aggundey & Schlitter (1986) list this species as *C. zaodon* with four subspecies (*zaodon*, *provocax*, *lakiundae* and *kempi*). The species has been confused with *zaodon* (now placed as a synonym

of *C. nigrofusca*) (Hutterer 2005b). Synonyms: *angolae*. Subspecies: none. Chromosome number: not known.

Description Large to very large shrew with short soft pelage. Dorsal pelage blackish-brown or dark-brown; hairs grey at base, dark brown at tip. Ventral pelage grey with a brownish tinge medially, shorter than on dorsal surface or flanks. Throat pale or ashy-grey. Head narrow, with long muzzle with sparkling bright brown vibrissae that appear darker at base. Nose with a conspicuous blob on tip. Pinnae oval, slanting posteriorly towards shoulders; slightly paler than dorsal pelage. Limbs small. Each digit with small straight sharp pointed claw. Tail of medium relative length (ca. 58% of HB), brown; pilosity ca. 75%. Nipples: not known.

Geographic Variation None recorded.

Distribution Endemic to Africa. Widely distributed. Forest–savanna mosaics and Zambezan Woodland BZ. Recorded from NW Cameroon to Kenya, and southwards to Zambia and Angola. Limits of distribution uncertain. In Zambia, probably limited to areas that have a rainfall of at least 900 mm/year, so not present in low-lying valleys (Ansell 1978).

Habitat Dry forests, montane forests, riverine habitats, bushlands and grasslands.

Abundance Locally common. In Kenya, locally uncommon but widely distributed.

Remarks A ♂ captured in mid-dry season (Jan) in Ololua Forest, Kenya, was in reproductive condition.

Conservation IUCN Category: Least Concern.

Despite loss of many suitable habitats in Kenya where the species occurs, it is probably not under threat at the present time as some of its habitats are in protected areas.

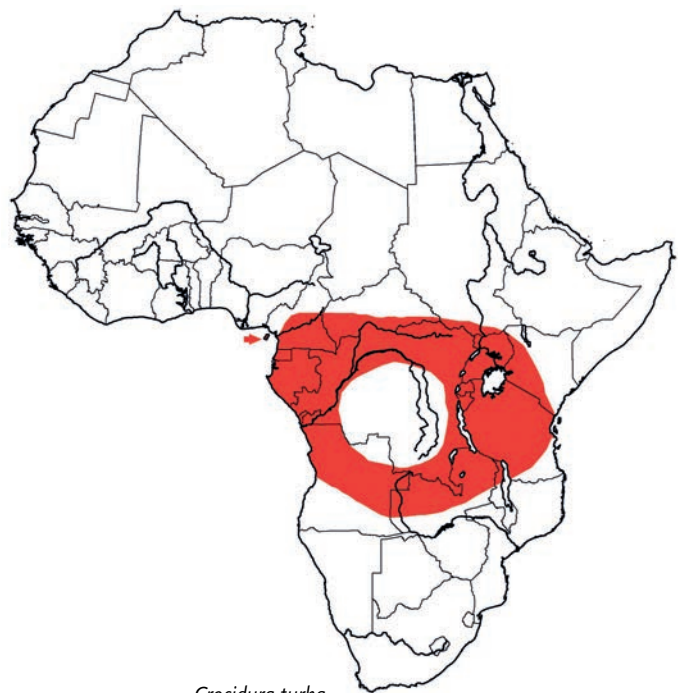
Measurements

Crocidura turba

HB (♂ ♂): 99, 102 mm, n = 2

HB (♀ ♀): 101 mm, n = 1

T (♂ ♂): 56, 59 mm, n = 2



Crocidura turba

T (♀ ♀): 55 mm, n = 1

HF (♂ ♂): 16, 16 mm, n = 2

HF (♀ ♀): 15 mm, n = 1

E (♂ ♂): 8.1 mm, n = 1

E (♀ ♀): 7.7 mm, n = 1

WT (♂ ♂): 17, 21 mm, n = 2

WT (♀ ♀): 17 mm, n = 1

CI: n. d.

GWS: n. d.

I¹–M³: n. d.

Ololua forest, Nairobi, Kenya (N. Ogue unpubl.)

Key Reference Aggundey & Schlitter 1986.

N. Ogue

Crocidura ultima ULTIMATE SHREW

Fr. Crocidure de Nyeri; Ger. Ultimative Spitzmaus

Crocidura ultima Dollman, 1915. Ann. Mag. Nat. Hist., ser. 8, 15: 517. 1916. Ann. Mag. Nat. Hist., ser. 8, 17: 204. Jombeni Range, Nyeri District, Kenya. 1424 m.

Taxonomy Placed as a synonym of *C. monax* by Heim de Balsac & Meester (1977) but considered to be a distinct species within the *littoralis*–*monax* group by Dippenaar (1980b). Known only from the holotype. Synonyms: none. Chromosome number: not known.

Description Large shrew. Dorsal pelage reddish-brown mottled with grey. Ventral pelage greyer, not clearly delineated from the brownish colour of the flanks. Upper surface of fore- and hindfeet pale buffish-brown. Claws of hindfeet slightly larger than those of forefeet. Tail relatively long (ca. 70% of HB), reddish-brown above and below, covered with very short brownish hairs; pilosity ca. 20%.

Skull broad with a rather blunt muzzle. Teeth small; second upper unicuspid conspicuously smaller than (and overlapped by) third unicuspid, circular in section with well-developed cingula. Third upper molar broad, entoconid present on talonid of third lower molar. Nipples: not known.

Geographic Variation None recorded.

Distribution Endemic to Africa. Afromontane–Afroalpine BZ. Known only from the Jombeni Range near Nyeri, Kenya.

*Crocidura ultima*

Habitat No information; type locality suggests habitat may be montane forest.

Abundance No information.

Remarks Apparently no other information available.

Conservation IUCN Category: Data Deficient.
Previously assessed as Critically Endangered.

Measurements

Crocidura ultima

HB: 90 mm, n = 1

T: 62 mm, n = 1

HF: 16 mm, n = 1

E: 13 mm, n = 1

CI: 22.9 mm, n = 1

GWS: 10.2 mm, n = 1

I¹–M³: 10.2 mm, n = 1

Kenya (holotype; Dollman 1915, BMNH)

Key References Dollman 1915a, 1916.

S. Churchfield & P. D. Jenkins

Crocidura usambarae USAMBARA SHREW

Fr. Crocidure des Monts d'Usambara; Ger. Usambara-Spitzmaus

Crocidura usambarae Dippenaar, 1980. Ann. Transvaal Mus. 32: 128. Shume, 16 miles N of Lushoto, West Usambara Mts, Tanzania.

Taxonomy Dippenaar (1980a) suggested that *C. usambarae* is related to *C. monax*. Synonyms: none. Chromosome number: not known.

Description Medium-sized reddish-brown shrew. Dorsal hairs ca. 6 mm on back, ventral hairs 4 mm. Dorsal pelage reddish-brown; hairs slate-grey at base, reddish-brown on terminal quarter. Ventral pelage pale reddish-brown (paler than dorsal pelage); hairs slate-grey at base (ca. 60–75% of the hair), yellowish-white subterminal band, pale reddish-brown at tip. Fore- and hindfeet reddish-brown, with long hairs on upper surface. Tail relatively long (ca. 70% of HB), dark above, slightly paler below; pilosity 10–20% (hairs black). Males on average larger than ♀♀ (Stanley *et al.* 1996a). Nipples: not known.

Geographic Variation None recorded.

Distribution Endemic to Africa. Afromontane–Afroalpine BZ. In N Tanzania, recorded from the South Pare (Stanley *et al.* 1996a), West Usambara Mts (Dippenaar 1980a, Howell & Jenkins 1984), and East Usambara Mts (Stanley *et al.* 2011). One specimen (skin only) from the Poroto Mts, S Tanzania, has been tentatively identified as *C. usambarae* (Dippenaar 1980a).

Habitat Moist montane forest and adjacent habitats. One specimen found in an agricultural field adjacent to montane forest in the South Pare Mts (Stanley *et al.* 1996a). Howell & Jenkins (1984)

*Crocidura usambarae*

recorded a specimen from the edge of montane forest, and another in disturbed montane forest in the West Usambara Mts.

Abundance In Chome F. R. South Pare Mts, comprised 70% of all shrews sampled ($n = 10$) at 2000 m, but only 8% of all shrews sampled ($n = 37$) at 1100 m (Stanley *et al.* 1996a).

Remarks In Chome F.R., ♂ : ♀ ratio was 1 : 2 ($n = 3$) at 1100 m, and 6 : 1 ($n = 7$) at 2000 m (Stanley *et al.* 1996a). Of the three ♀♀ in these samples (collected Jul–Sep), two were nulliparous, the third was pregnant. Embryo number: 5 ($n = 1$); three embryos in left uterine horn, two in right horn; crown–rump length of largest embryo 6 mm. One pregnant ♀ from West Usambara Mts in Jan 1981 contained two embryos (one in each horn; maximum crown–rump length 8 mm) (Howell & Jenkins 1984).

Conservation IUCN Category: Endangered.

The distribution is fragmented and suitable habitat is declining.

Measurements

Crocidura usambarae

HB (♂♂): 84 (82–87) mm, $n = 6$

HB (♀♀): 76, 80 mm, $n = 2$

T (♂♂): 59 (56–62) mm, $n = 5$

T (♀♀): 54, 57 mm, $n = 2$

HF (♂♂): 16 (15–16) mm, $n = 7$

HF (♀♀): 15 mm, $n = 1$

E (♂♂): 10 (9–10) mm, $n = 6$

E (♀♀): 9, 10 mm, $n = 2$

WT (♂♂): 9.7 (9–10) g, $n = 6$

WT (♀♀): 8.4, 8.9 g, $n = 2$

CI (♂♂): 22.2 (21.4–22.7) mm, $n = 6$

CI (♀♀): 22.1, 22.3 mm, $n = 2$

GWS (♂♂): 10.0 (9.5–10.3) mm, $n = 6$

GWS (♀♀): 9.8, 10.0 mm, $n = 2$

I¹–M³ (♂♂): 9.7 (9.5–9.9) mm, $n = 6$

I¹–M³ (♀♀): 9.8, 9.9 mm, $n = 2$

South Pare Mts, Tanzania (Stanley *et al.* 1996a)

Key References Dippenaar 1980a; Stanley *et al.* 1996a.

William T. Stanley

Crocidura viaria SAVANNA PATH SHREW

Fr. Crocidure de savanna sèche; Ger. Savannen-Wegspitzmaus

Crocidura viaria (I. Geoffroy, 1834). In: Zool. Voy. de Belanger Indes-Orient., p. 127. 'Senegal'.

(Restricted to region between Dakar and St Luis by Hutterer 1984.)

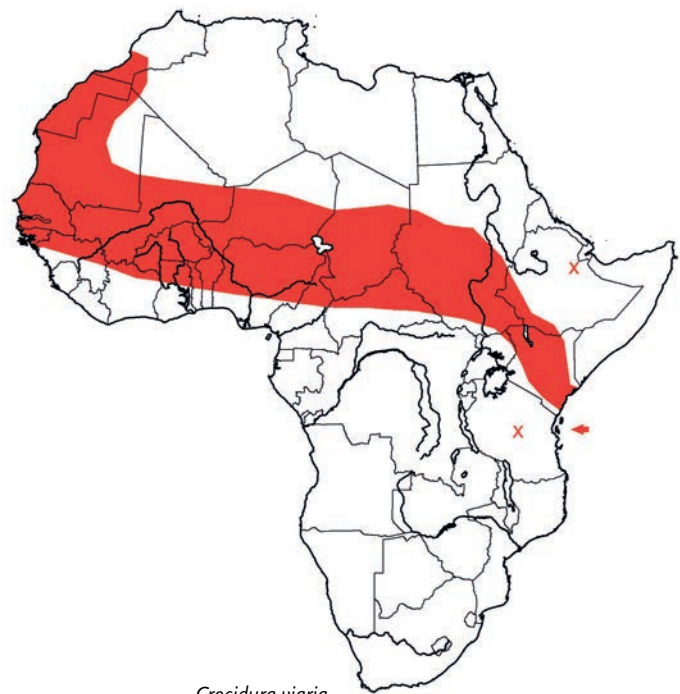
Taxonomy Originally described as *Sorex viarius* (see Hutterer 1983c for details). Member of the *flavescens* species-group (Maddalena 1990a). Synonyms: *bolivari*, *hindei*, *suahelae*, *tamrinensis*. Subspecies: none. Chromosome number: $2n = 50$, $FN = 66$ (Maddalena & Ruedi 1994).

Description Large pale-coloured shrew. Pelage dense, soft, with silky sheen; dorsal hairs 5 mm. Dorsal pelage pale medium brown, with a mottled appearance; hairs dark grey on basal half, pale brown on terminal half, medium brown at tip. Ventral pelage medium reddish-brown or creamy-grey; hairs grey on basal two-thirds, creamy-grey on terminal third. Head similar in colour to dorsal pelage. Ears pale brown, conspicuous, not concealed by pelage. Chin, throat and chest medium reddish-brown (see also below). Fore- and hindfeet pale, slightly pinkish, covered with creamy short hairs. Tail relatively long (ca. 70% of HB), medium brown, slightly paler below; thick at base, tapering to tip; pilosity 75–90%. Braincase flat and broad. First upper incisor long and hooked. Third upper molar medium to wide. Nipples: not known.

Geographic Variation In Morocco, pelage colour of chin and throat same as ventral pelage ($n = 3$); in Senegal, chin and throat have irregular reddish-ginger patches of longer hair ($n = 3$).

Distribution Endemic to Africa. Sahara Arid BZ (in the west of the continent), Sahel Savanna, Sudan Savanna and parts of Guinea Savanna BZs. Recorded from S Morocco to Senegal and eastwards to Sudan, W Ethiopia and Kenya.

Habitat In S Morocco, most numerous in cultivated fields (e.g. lucerne) and dense scrubby vegetation (which is sometimes



Crocidura viaria

inundated) beside seasonal rivers. Also recorded on vegetated sand dunes, and on dunes with thick cover of *Chenopodium murale* or *Euphorbes cactoides* (and boulders).

Abundance Common in certain habitats. In S Morocco, comprised 75% of all small mammals ($n = 8$, 1 sp. of shrew, 2 spp.

of rodent) in dense scrubby vegetation, and 70% in cultivated fields (n = 7, 1 sp. shrew, 1 sp. rodent) (Vogel *et al.* 2000).

Remarks Strictly nocturnal. In Morocco, may use abandoned burrows of rodents for shelter. A specimen from Nigeria was found in owl pellets (Hutterer & Happold 1983).

Conservation IUCN Category: Least Concern.

Measurements

Crocidura viaria

HB: 90 (75–100) mm, n = 6

T: 55.7 (42–63) mm, n = 6

HF: 16.2 (14–17) mm, n = 6

E: n. d.

WT: n. d.

CI: 24.7 (22.6–26.4) mm, n = 6

GWS: 10.6 (10.2–11.0) mm, n = 6

I¹–M³: 10.8 (10.0–11.6) mm, n = 6

Senegal (♀ only; Hutterer 1983c)

Mean measurements of four ♂♂ are slightly larger

Key References Hutterer 1983c; Vogel *et al.* 2000.

Rainer Hutterer

Crocidura virgata MAMFE SHREW

Fr. Crocidure de Mamfe; Ger. Mamfe-Spitzmaus

Crocidura virgata Sanderson, 1940. Trans. Zool. Soc. Lond. 24: 682. Tinta, Assumbo, Mamfe, Cameroon. 2300 ft (06° 15' N, 09° 31' E).

Taxonomy Originally described as a subspecies of *C. occidentalis* (now a synonym of *C. oliveri*). Formerly allocated as a subspecies to *C. gracilipes* (Heim de Balsac & Meester 1977), a species now considered as of uncertain status and restricted to Mt Kilimanjaro; and later included in *C. hildegardae* (Hutterer 1993). Now considered a valid species (Hutterer 2005b) on the basis of different karyotype from *C. hildegardae* (2n = 52, FN = 76) and differences in skull size and shape (Heim de Balsac 1968d). Synonyms: *vulcani*. Subspecies: none. Chromosome number: 2n = 52, FN = 86 (Meylan & Vogel 1982).

Description Small shrew. Dorsal pelage and tail pale chocolate-brown. Ventral pelage gradually changing into greyish-brown. Fleishy parts paler pinkish-grey. Tail relatively long (65% of HB); pilosity 80%. Hindfeet short; metatarsal joint well covered with hairs. Skull similar to that of *C. hildegardae*, but slightly smaller, with shorter and more slender rostrum. I¹ small; M³ large. Nipples: not known.

Geographic Variation None recorded.

Distribution Endemic to Africa. Afromontane–Afroalpine BZ. Restricted to E Nigeria (Meylan & Vogel, 1982), Tinta in the Mamfe highlands of W Cameroon (Sanderson 1940), Bibundi near Mt Cameroon (*vulcani*; 1500–1600 m; Heim de Balsac 1957b), and Mt Kupé, Cameroon (Heim de Balsac 1968d). Limits of distribution unknown.

Habitat False mountain grass; dry habitat (Sanderson 1940), open forest at 850 m at foot of Mt Kupé (Eisentraut 1973a), and in the crater of Bibundi on Mt Cameroon (Heim de Balsac 1957b).

Abundance No information.

Remarks Meylan & Vogel (1982) reported on a karyotype of a specimen from Okpuje, Nigeria, under the name *Crocidura* cf. *gracilipes*, a name used by Heim de Balsac & Meester (1977) for the *C. hildegardae* group.

Conservation IUCN Category: Data Deficient.



Crocidura virgata

Measurements

Crocidura virgata

HB: 61 mm, n = 1

T: 40 mm, n = 1

HF: 12 mm, n = 1

E: 10 mm, n = 1

WT: 7 g, n = 1

CI: 19.5 mm, n = 1

GWS: 8.6 mm, n = 1

I¹–M³: 8.2 mm, n = 1

Mt Kupé, Cameroon (ZFMK)

Key References Heim de Balsac 1968d; Meylan & Vogel 1982.

D. C. D. Happold & R. Hutterer

Crocidura voi VOI SHREW

Fr. Crocidure de Voi; Ger. Voi-Spitzmaus

Crocidura voi Osgood, 1910. Field Mus. Nat. Hist. Publ., Zool. Ser. 10: 18. Voi, British East Africa (= Kenya).

Taxonomy Synonyms: *aridula*, *butleri*, *percivali*. Subspecies: none. Chromosome number: not known.

Description Small-medium to medium-sized shrew. Dorsal pelage cinnamon to greyish-brown; hairs grey at base, cinnamon at tip. Ventral pelage and flanks yellowish-grey to greyish-white; hairs grey at base, creamy-yellow at tip. Tail of medium relative length (ca. 45–55% of HB), broad, pale and usually bicoloured; pilosity ca. 100%. Skull: hour-glass shaped, broad and flat. Nipples: not known.

Geographic Variation None recorded.

Distribution Endemic to Africa. Sudan Savanna and Somalia–Masai Bushland BZs. Recorded from Mali, N Nigeria, Sudan, Ethiopia, Somalia and Kenya. Distribution disjunct.

Habitat No information. Not obtained during an extensive survey (302 shrews, 12 spp.) in ‘montane forests’ (Shimba Hills, Taita Hills and Kyulu Hills) in SE Kenya, not far from the type locality at Voi (Oguge *et al.* 2004).

Abundance Probably rare; known only from a few specimens at each locality where captured.

Remarks Apparently no other information available.

Conservation IUCN Category: Least Concern.

Measurements*Crocidura voi*

HB: 75–89 mm

T: 34–53 mm

HF: 12–14 mm

E: 10–12 mm

*Crocidura voi*

WT: 13.4 g

CI: 22.8–24.8 mm

GWS: 9.4–10 mm

I¹–M³: 9.2–10 mm

Throughout geographic range (Hutterer 1986a; mean values and sample sizes not recorded)

Key Reference Hutterer 1986a.

D. C. D. Happold

Crocidura whitakeri WHITAKER'S SHREW (LESSER MAGHREBI SHREW)

Fr. Crocidure de Whitaker; Ger. Whitakers Spitzmaus

Crocidura whitakeri de Winton, 1898. Proc. Zool. Soc. Lond. 1897: 954. Sierzet, between Marrakech and Essaouira, Morocco.

Taxonomy Described as a subspecies of *C. suaveolens*, but now considered as a valid species. Despite description of several local forms, no consistent geographical variation is currently recognized. Synonyms: *essaouiranensis*, *matruhensis*, *mesatanensis*, *zaianensis*. Subspecies: none. Chromosome number: not known.

Description Small pale shrew, smaller than *C. russula*, with a comparatively larger head and ears. Pelage short (3–4 mm on back). Dorsal pelage short and silky, buffy-brown flecked with white (speckled in the holotype); hairs ash-grey at base with subterminal

band of white, and brownish tip. Ventral pelage whitish; hairs grey on basal half, white on terminal half. Fore- and hindfeet pale or white on upper and lower surfaces. Tail of medium relative length (ca. 50% of HB), pale above, whitish below; pilosity up to 100%. Skull relatively flat with short rostrum. Third upper unicuspid tooth smaller than the second unicuspid, and about the same size as the adjacent, well developed and attached cusp (parastyle) of the fourth upper premolar. Nipples: not known.

Geographic Variation None recorded.

Distribution Endemic to Africa. Mediterranean Coastal BZ. Recorded in the Atlantic and Mediterranean parts of Morocco, Algeria and Tunisia, from sea level to 1800 m. Particularly widely distributed on the Atlantic coast of Morocco, but absent from most of the coastal zone of Algeria where its distribution is along the southern border of the Saharan Atlas. One record (previously listed as *C. suaveolens matruhensis*) from the coastal area of Egypt (Hutterer 1994). May occur in suitable habitats all along the North African coast from NW Africa to Egypt (Hutterer 1994).

Habitat Dry and stony habitats, with sparse vegetation (i.e. steppe or semi-deserts); also sandy coastal dunes. Shelters among rocks as well as in rodent burrows. In Egypt (Setzer 1960, as *C. suaveolens matruhensis*), recorded from 'burrows of the fat sand rat, *Psammomys obesus*, in damp saline depressions just behind the sea' (see also Osborn & Helmy 1980).

Abundance Highest densities recorded in the Atlantic part of Morocco. Common in owl pellets in semi-arid regions of Algeria, but not in the Sahara Desert (Kowalski & Rzebik-Kowalska 1991).

Remarks Mainly nocturnal. Represented 2.1% of the diet of Barn Owls *Tyto alba* in N Morocco, and up to 9.8% in one locality (Aulagnier *et al.* 1999). Also preyed on by Tawny Owls *Strix aluco*, Pharaoh Eagle-owls *Bubo ascalaphus* and Black-winged Kites *Elanus caeruleus*.

Conservation IUCN Category: Least Concern.

Can be adversely affected by pesticides massively used against locusts in the southern part of its range.

Measurements

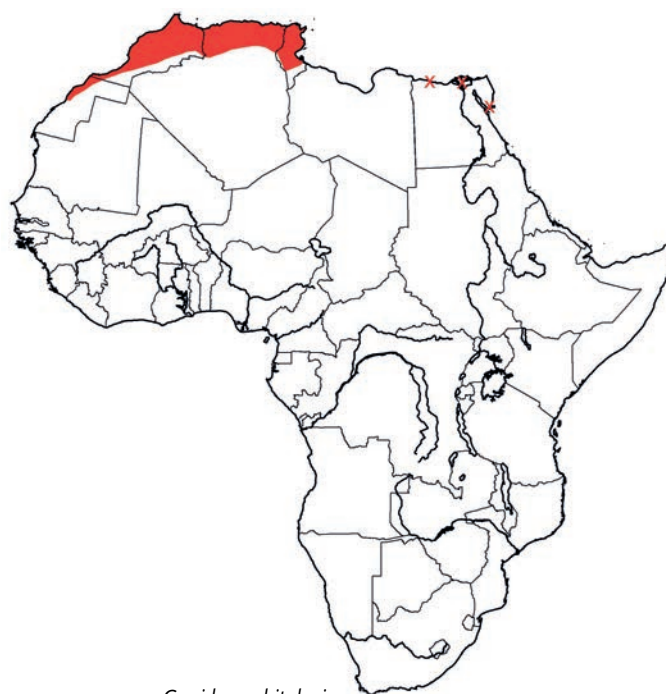
Crocidura whitakeri

HB: 61.4 (56–64) mm, n = 8

T: 32.8 (28–39) mm, n = 8

HF: 11.8 (11–13) mm, n = 8

E: 9.5 (8–11) mm, n = 6



Crocidura whitakeri

WT: 6.0 (5–7) g, n = 5

CI: 17.2 (16.8–17.4) mm, n = 7

GWS: 8.0 (7.7–8.3) mm, n = 8

I¹–M³: 7.4 (6.9–7.7) mm, n = 9

Mandible length: 9.5–10.9 mm

Height of coronoid process: 3.7–4.5 mm

Morocco (Vesmanis 1976, Vesmanis & Vesmanis 1980)

Key References Aulagnier & Thévenot 1986; Hutterer 1986e; Kowalski & Rzebik-Kowalska 1991; Sarà & Zanca 1992; Vogel *et al.* 2000.

Stéphane Aulagnier

Crocidura wimmeri WIMMER'S SHREW

Fr. Crocidure de Wimmer; Ger. Wimmers Spitzmaus

Crocidura wimmeri Heim de Balsac and Aellen, 1958. Rev. Suisse Zool. 65: 952. Adiopodoumé, S Côte d'Ivoire.

Taxonomy Resembles *C. nimbae*, *C. foxi* and *C. nigeriae* in appearance and cranio-dental characteristics, but differs in details of the skull and teeth. Records of this species from Cameroon and Gabon (Brosset 1988) refer to *C. batesi* (Hutterer 2005b). Synonyms: none. Chromosome number: 2n = 50, FN = 84 (Meylan & Vogel 1982).

Description Medium-sized species. Dorsal pelage dark ash-grey to brown. Ventral pelage paler. Tail relatively long (ca. 75% of HB), not densely haired; pilosity not known. Skull elongated, facial region well developed and maxillary region broad (see Heim de Balsac & Aellen 1958 for details). Nipples: not known.

Geographic Variation None recorded.

Distribution Endemic to Africa. Rainforest BZ (Western Region [Ghanian sub-region]). Known only from around Adiopodoumé near Abidjan, S Côte d'Ivoire (Heim de Balsac & Aellen 1958, Vogel 1976).

Habitat Wet, swampy forest near the coast (Heim de Balsac & Aellen 1958).

Abundance Rare and localized.

Remarks Nocturnal. In captivity, mean total activity was 340 min/24 h in 22 phases; 6–45 min/h at night but for only 0–4 min/h during the day (Vogel *et al.* 1981). Energy consumption in captivity was 1.9 kJ/g/h for an individual weighing 23.5 g (Vogel 1976). Can be distinguished from several other African *Crocidura* by its distinctive

defence calls; calls last an average of 217 msec with a frequency of 11.7–15.0 kHz (Hutterer & Vogel 1977).

Conservation IUCN Category: Critically Endangered.

Measurements

Crocidura wimmeri

HB: 80, 90 mm, n = 2

T: 57, 57 mm, n = 2

HF: 17, 17 mm, n = 2

E: n. d.

WT: 22, 28 g, n = 2

CI: 25, 24 mm, n = 2

GWS: 9.5, 10.0 mm, n = 2

I¹–M³: 12.0, 11.3 mm, n = 2

Côte d'Ivoire

Measurements: Heim de Balsac & Aellen (1958); 2 ♂♂

Weight: Vogel *et al.* 1981

Key References Heim de Balsac & Aellen 1958; Vogel 1976, Vogel *et al.* 1981.

S. Churchfield & P. D. Jenkins



Crocidura wimmeri

Crocidura xantippe XANTHIPPE'S SHREW (YELLOW-FOOTED SHREW)

Fr. Crocidure à pieds jaunes; Ger. Xantippes Spitzmaus

Crocidura xantippe Osgood, 1910. Field Mus. Nat. Hist. Publ., Zool. Ser. 10: 19. Voi, Kenya.

Taxonomy Status uncertain, but probably related to *C. hirta* (Hutterer 1993, 2005a). Synonyms: none. Chromosome number: not known.

Description Large species. Dorsal pelage pale brown with a fine speckling of paler colour; hairs slate-grey, some tipped with brown (resulting in a speckled pattern). Pelage short; hairs 3.6 mm on shoulders, 3.3 mm on chest, 3.7 mm on rump. Ventral pelage whitish-grey with yellowish wash along the ventral mid-line, narrow on neck and wider on chest and abdomen; hairs greyish-white or grey on basal half, yellowish-white on distal half. Ears prominent. Forefeet pale brown to yellowish-brown; hindfeet paler than forefeet. Tail relatively long (ca. 66% of HB), slightly bicoloured, whitish-grey below turning browner on distal third; pilosity 75%. Nipples: not known.

Geographic Variation None recorded.

Distribution Endemic to Africa. Somalia–Masai Bushland BZ. Recorded from SE Kenya and NE Tanzania (Heim de Balsac & Meester 1977, Aggundey & Schlitter 1986). Identification of a specimen in N Kenya (near L. Turkana) is uncertain.

Habitat The holotype was collected in dry thorn scrub habitat in Kenya. Three specimens from the West Usambara Mts came from a variety of habitats at 1100–1300 m, including slightly disturbed montane forest and a *Eucalyptus* plantation (Stanley *et al.* 2011).



Crocidura xantippe

Abundance Uncertain; probably rare. Comprised 1.5% of shrews captured in the West Usambara Mts (n = 53) (W. T. Stanley unpubl.), but not encountered amongst 303 shrews (10 spp.) obtained

in montane forests of SE Kenya within the area of distribution of this species (Oguge *et al.* 2004).

Remarks One ♀ (of three) lactating in Jul (West Usambara Mts; W.T. Stanley unpubl.).

Conservation IUCN Category: Least Concern.

Geographic range is fragmented and the number of suitable habitats are declining.

Measurements

Crocidura xantippe

HB: 93 (89–98) mm, n = 3

T: 63 (55–67) mm, n = 3

HF: 15 (14–16) mm, n = 3

E: 11 (10–12) mm, n = 3

WT: 12.5 (12–14) g, n = 3

CI: 22.5 (22.1–22.8) mm, n = 3

GWS: 9.7 (9.4–10.0) mm, n = 3

I¹–M³: 9.7 (9.6–9.8) mm, n = 3

West Usambara Mts, Tanzania (W.T. Stanley unpubl.)

Key Reference Osgood 1910.

William T. Stanley

Crocidura yankariensis YANKARI SHREW

Fr. Crocisure de Yankari; Ger. Yankari-Spitzmaus

Crocidura yankariensis Hutterer and Jenkins, 1980. Bull. Brit Mus. (Nat Hist.) Zool., 39: 305. Futuk (16 km E of Yankari G. R. boundary), Bauchi Province, N Nigeria.

Taxonomy Specimens of this species were previously misidentified as *C. somalica* (see Hutterer & Jenkins 1983). Synonyms: none. Chromosome number: 2n = 68, FN = 122 (Schlitter *et al.* 1999).

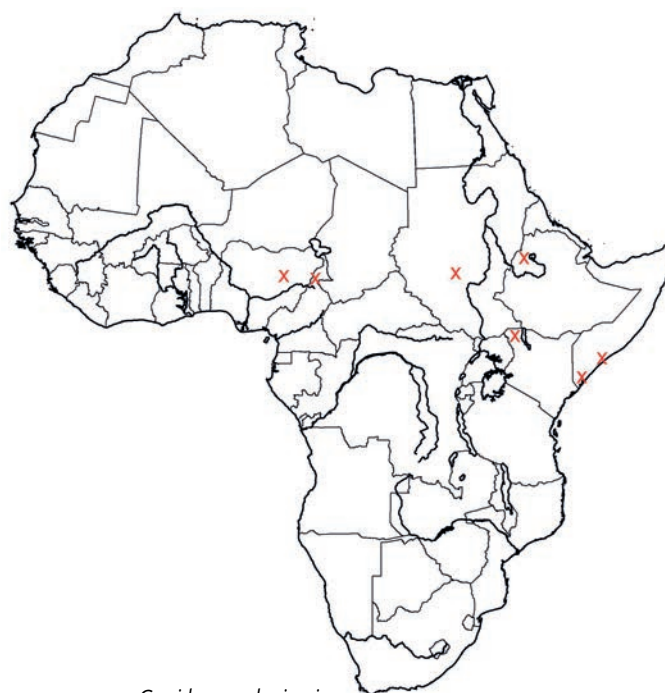
Description Very small species. Pelage short; hairs 2–3 mm. Dorsal pelage olive-brown; hairs grey at base, brown at tip. Ventral pelage smoky-grey or greyish-olive; hairs grey. Colours of dorsal and ventral pelage merge without delineation. Muzzle from nose-tip to eyes with fine short hairs, and without long vibrissae. Ears large, with short fine hairs; stiff bristles on inner folds. Fore- and hindfeet white. Lower part of hindlimb without brownish hair (cf. other *Crocidura* in which body hairs extend to ankle). Tail relatively long (ca. 67% of HB); bicoloured, brown above, whitish below; pilosity almost 100%. Skull: profile slopes gradually upwards anteriorly, then angles downwards sharply posteriorly; least interorbital width 3.9–4.1 mm (further details of skull in Hutterer & Jenkins 1983). Nipples: not known.

Geographic Variation A specimen from Ethiopia has dorsal pelage of deep fuscous, and ventral pelage of pale grey.

Distribution Endemic to Africa. Sudan Savanna BZ and parts of Somalia–Masai Bushland BZ. Recorded from Nigeria, Cameroon, Sudan, Ethiopia, NW Kenya and Somalia (Hutterer 2005b). Distribution very disjunct.

Habitat Primarily dry savanna. A specimen from Ethiopia was found amongst shrubs and boulders in wet grasslands (which are usually waterlogged during the wet season).

Abundance Uncertain. Present in owl pellets from near Yankari N. P., Nigeria (Hutterer & Jenkins 1980); also, but rarely (2 of 344 shrews), in pellets of Spotted Eagle-owls *Bubo africanus* from Awash N. P., Ethiopia (Demeter 1982).



Crocidura yankariensis

Remarks In Sudan and Ethiopia, coexists with *C. somalica* (a similarly small species; see profile for further details).

Conservation IUCN Category: Least Concern.

Measurements

Crocidura yankariensis

HB: 56.1 (52–66) mm, n = 8

T: 37.8 (35–41) mm, n = 9

HF: 9.7 (9–10) mm, n = 9

E: 6.8 (6–8) mm, n = 7

WT: 4.5 g, n = 1

CI: 18.9 (18.4–19.5) mm, n = 7

GWS: 8.3 (8.2–8.5) mm, n = 6

I¹–M³: 8.2 (7.7–8.5) mm, n = 10

Throughout geographic range (mean values calculated from Hutterer & Jenkins 1983)

Key Reference Hutterer & Jenkins 1983.

Rainer Hutterer

Crocidura zaphiri **ZAPHIR'S SHREW**

Fr. Crocidure de Zaphir; Ger. Zaphirs Spitzmaus

Crocidura zaphiri Dollman, 1915. Ann. Mag. Nat. Hist., ser. 8, 15: 509. Ann. Mag. Nat. Hist., ser. 8, 16: 66. Charada Forest, Kaffa, S Ethiopia.

Taxonomy Similar but smaller than *C. olivieri*. This species may also include *mutuae* and *suaelae* (see *C. viaria*), in which case it would be a widely distributed species (Hutterer & Yalden 1990, Hutterer 2005b). Synonyms: *simiolus*. Subspecies: none. Chromosome number: unknown.

Description Very large shrew. Dorsal pelage dull slaty-brown to cinnamon-brown. Ventral pelage slightly paler and greyer. Feet pale, contrasting with body colour. Tail of medium relative length (ca. 57% of HB), brown above and below; pilosity 95%. Second upper unicuspid smaller than third upper unicuspid; third upper molar moderately broad; talonid basin on third lower molar. Nipples: not known.

Geographic Variation None recorded.

Distribution Endemic to Africa. Somalia–Masai Bushland BZ. Recorded in SW Ethiopia and SW Kenya (Dollman 1915a, Aggundey & Schlitter 1986).

Habitat No information.

Abundance No information.

Remarks Apparently no other information available.

Conservation IUCN Category: Data Deficient.
Species insufficiently known.

Measurements

Crocidura zaphiri

HB: 105 mm, n = 1

T: 60 mm, n = 1

HF: 19 mm, n = 1



Crocidura zaphiri

E: 11 mm, n = 1

WT: n. d.

CI: n. d.

GWS: n. d.

I¹–M³: ca. 12.0 mm, n = 1

Ethiopia (holotype; BMNH, skull damaged)

Key References Aggundey & Schlitter 1986; Dollman 1915a.

S. Churchfield & P. D. Jenkins

Crocidura zimmeri **UPEMBA SHREW**

Fr. Crocidure d'Upemba; Ger. Upemba-Spitzmaus

Crocidura zimmeri Osgood, 1936. Field Mus. Nat. Hist. Publ., Zool. Ser. 20: 223. 'Lualaba River, Katobwe', near Bukama, Katanga Prov., DR Congo.

Taxonomy Species status of this little-known species is beyond doubt (Hutterer 2005b). Relationships unknown, but possibly part of the *C. turba* species complex. Synonyms: none. Chromosome number: not known.

Description Very large, strikingly coloured shrew. Dorsal pelage very dark blackish-brown. Ventral pelage considerably paler with a silvery tinge, not sharply separated from colour of dorsal pelage. Hindfeet dark brown. Tail of medium relative length (45% of HB),

*Crocidura zimmeri*

thickened at base, blackish and not bicoloured, with numerous long bristle hairs; pilosity 70–80%. Skull large and heavy, with dorsal profile somewhat arched or convex rather than straight; interorbital region broad; sagittal crest well developed and extending forward nearly to nasal bones. Dentition heavy but less so than in *C. oliveri*; second upper unicuspid slightly larger than third (Osgood 1936). Nipples: not known.

Geographic Variation None recorded.

Distribution Endemic to Africa. Zambezian Woodland BZ. Recorded only from the region of Upemba N. P., Katanga Province, S DR Congo.

Habitat Uncertain. Upemba N. P. is situated on the Kibara plateau and bordered in the west by the Lualaba (or Upper Congo) river and numerous lakes. The habitat of the plateau consists mainly of gently rolling grasslands at altitudes of between 1750 m and 1800 m. These are cut by numerous streams, which rise on the plateau and are lined with gallery forest. The grasslands are bordered by *Uapaca*-dominated woodland (Birdlife International 2006).

Abundance Rare. Known only by three specimens from type locality.

Remarks The species was found to co-exist with *C. oliveri* and *C. hirta* at Katobwe (Osgood 1936). There have been no known studies on this species since 1936 when the type series were collected.

Conservation IUCN Category: Data Deficient, previously Vulnerable.

Measurements

Crocidura zimmeri

HB: 112, 123 mm, n = 2

T: 48, 56 mm, n = 2

HF (c. u.): 17.5, 18.2 mm, n = 2

E: n. d.

WT: n. d.

CI: 27.1 mm*

GWS: 11.1 mm*

I¹–M³: 12.0 mm*

DR Congo (type locality; Osgood 1936)

*Holotype

Key Reference Osgood 1936.

Rainer Hutterer

GENUS *Myosorex*

Mouse Shrews

Myosorex Gray, 1838. Proc. Zool. Soc. Lond. 1837: 124 (publ. 1838). Type species: *Sorex varius* Smuts, 1832.

*Myosorex* sp.

The genus *Myosorex* contains 14 species occurring mainly in isolated mountain forests of central and south-east Africa. Populations on Bioko I. and the Cameroon Mts are widely isolated from populations in the mountains of the Rift Valley of eastern Africa and in the Eastern

Arc Mts of Tanzania. Most species are confined to montane forest or montane grasslands, and are less common in mid-elevation forests, lowland estuarine habitats and other vegetation close to water.

All species of *Myosorex* have dark-brown to blackish-brown pelage. Tail length varies from medium (42% of head and body length) to very long (84% in *Myosorex longicaudatus*) and does not have long white bristle hairs as in *Crocidura* and *Paracrocidura*. The limbs are of medium length as in other terrestrial shrews. Fore- and hindfeet are covered by small scales (cf. large in *Congosorex*) and the forefeet bear long claws (shorter in *Congosorex*, longer in *Surdisorex*). The outer ear is visible but embedded in the pelage. Eyes are small, but clearly visible (tiny in *Congosorex*, not visible in *Surdisorex*). The tip of the phallus of a male *Myosorex* is round (pointed in *Congosorex*). Cranially, *Myosorex* (and *Congosorex* and *Surdisorex*) differ from all other African shrews in having a pair of vascular foramina close to the suture

between the nasal and frontal bones (Figure 9). There are four upper unicuspid teeth in each jaw (see also Table 7).

Biological details are known for only a few species. They are active burrowers but also use existing runways in dense vegetation. They seem to be solitary and terrestrial. Some kind of social behaviour seems to exist because caravanning behaviour has been observed in some species (R. Baxter in litt.).

Myosorex and *Congosorex* are closely related and, on the basis of morphology, molecular genetics and similar adaptations for a semi-fossorial life-style, are placed together in the subfamily Myosoricinae (Hutterer *et al.* 2001, Quéroutil *et al.* 2001). *Surdisorex* is likely also to belong to this subfamily (see family profile). Partial reviews of *Myosorex* were provided by Heim de Balsac (1967, 1968a), Heim de Balsac & Lamotte (1956), Meester & Dippenaar (1978) and Stanley & Hutterer (2000). Although 14 species have been described, there are undoubtedly additional species, as yet undescribed.

The species currently recognized are not easy to distinguish, but usually differ in relative tail length and skull size (Stanley & Hutterer 2000). Since many species occur allopatrically, the locality is a major source for species determination. Sympatric species of the genus occur in southern Africa; they can be identified with keys provided by Meester *et al.* (1986) and Meester & Dippenaar (1978), except for *M. sclateri* and *M. tenuis*.

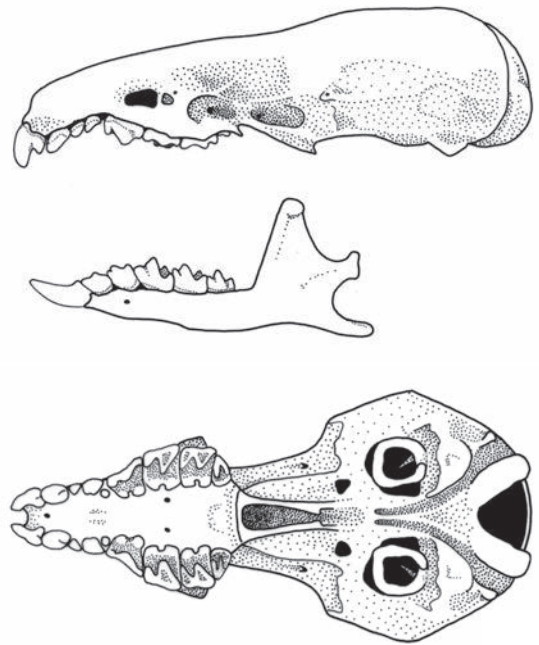


Figure 14. Skull and mandible of *Myosorex sclateri* (BMNH 4.12.3.14).

Rainer Hutterer

Myosorex babaulti BABAULT'S MOUSE SHREW (KIVU MOUSE SHREW)

Fr. Musaraigne des bois de Babault; Ger. Babaults Kivu-Spitzmaus.

Myosorex babaulti Heim de Balsac and Lamotte, 1956. *Mammalia* 20: 150. 'Kivu', DR Congo.

Taxonomy Formerly included in *C. blarina* but now recognized as a valid species (see Heim de Balsac & Lamotte 1956 and Dieterlen & Heim de Balsac 1979). A single specimen collected on Idjwi I. in L. Kivu (Allen & Loveridge 1942) is provisionally retained in *C. babaulti*. Synonyms: none. Chromosome number: not known.

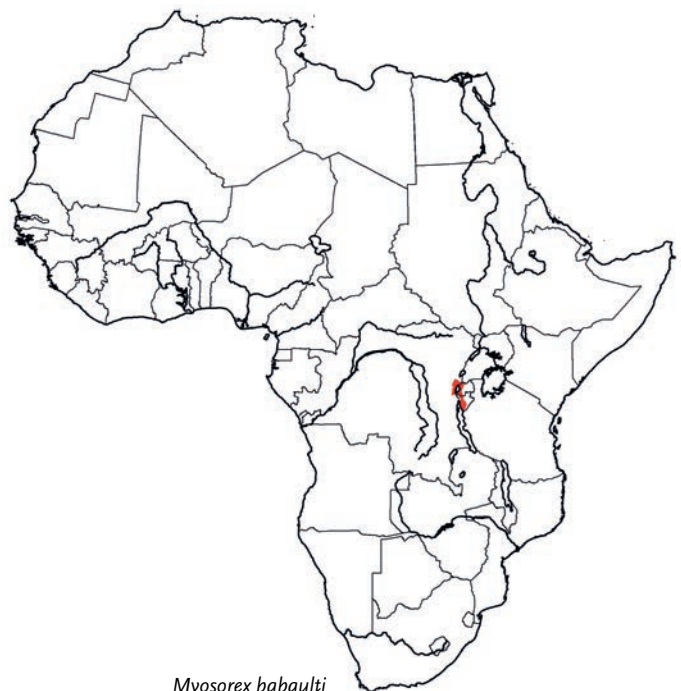
Description Medium-sized shrew, rather similar in form to a mole and to *M. blarina*. Pelage soft and dense, with slightly longer hairs at posterior end of body. Dorsal pelage uniformly blackish with a slight brownish tinge; hairs silvery ash-grey at base, brownish-black at tip. Ventral pelage paler than dorsal pelage; hairs ash-grey at base, brown at tip. Muzzle elongated. Eyes small with slit-like eye opening. External ears reduced and almost unpigmented; comprise only a forward directed broad flap (2–3 mm), which covers the wide opening of the auditory canal. Fore- and hindfeet brownish. Forefeet broad and mole-like with long claws (max. 2.5–3.0 mm). Tail of medium relative length (ca. 45% of HB), pale in colour, almost naked, with some short hairs below. Skull with well-marked interparietal bone and tiny much-reduced upper premolar (P^4). Nipples: not known.

Geographic Variation None recorded.

Similar Species

Myosorex blarina. Similar in size and form except maxillary region and dentition less heavily built; M^3 smaller and more compressed

from front to back. Geographic distribution very close in E DR Congo (Rwenzori Mts only).



Myosorex babaulti

M. schalleri. Based on one juvenile specimen, head and body smaller (HB: 50–55 mm); tail longer (T: 44 mm) and relatively longer (ca. 80% of HB). Pelage entirely black. Apparently allopatric but distribution close (Itombwe Mts, E DR Congo).

Distribution Endemic to Africa. Afromontane–Afroalpine BZ. Montane habitats in E DR Congo (west and east of L. Kivu, including Idjwi I. in L. Kivu), Rwanda and Burundi. Also recorded in Bwindi Impenetrable N. P., Uganda (Kasangaki *et al.* 2003), where it is apparently the only species of *Myosorex* (J. Kerbis in litt.).

Habitat Montane forests (including disturbed secondary montane forests) and, less frequently, swampy areas with *Cyperus latifolius* and shrubs (e.g. near Lwiro, west of L. Kivu [1750 m]). All localities are moist and shady (Dieterlen & Heim de Balsac 1979). Altitudinal range: ca. 1750–2300 m.

Abundance Uncertain, presumed to be rare.

Remarks Reduction of external ears and eyes, broad forefeet with long and strong claws, and a rather robust mole-like skull

suggest a subterranean life-style. One pregnant ♀ and one lactating ♀ recorded during the wet season (F. Dieterlen, unpubl.). Sex ratio (captures) 1 : 1 (n = 12).

Conservation IUCN Category: Near Threatened.

Measurements

Myosorex babaulti

HB: 84.5 (79–91) mm, n = 11

T: 37.9 (34–40) mm, n = 12

H: 12.8 (10–16) mm, n = 12

E: ca. 2–3 mm

WT: 17.6 (12–22) g, n = 12

CI: 22.3 (21.8–22.7) mm, n = 9

GWS: 12.0 (11.6–12.2) mm, n = 6

I¹–M³: 9.5 (9.3–9.8) mm, n = 10

E DR Congo (Dieterlen & Heim de Balsac 1979, SMNS)

Key Reference Dieterlen & Heim de Balsac 1979.

Fritz Dieterlen

Myosorex blarina RWENZORI MOUSE SHREW (MOUNTAIN MOUSE SHREW)

Fr. Musaraigne des bois du Rwenzori; Ger. Rwenzori-Waldspitzmaus

Myosorex blarina Thomas, 1906. Ann. Mag. Nat. Hist. ser. 7, 18: 139. Mubuku Valley, Rwenzori Mts, Uganda. 10,000 ft (3048 m).

Taxonomy The forms *babaulti* and *zinki* were formerly subsumed within this species (see Heim de Balsac & Meester 1977), but are now considered valid species (see Dieterlen & Heim de Balsac 1979 for *babaulti*, and Stanley *et al.* 2005b and Hutterer 2005b for *zinki*). Synonyms: none. Chromosome number: not known.

Description Medium-sized dark shrew with a medium-length tail. Pelage thick and velvet-like. Dorsal pelage blackish-brown, slightly iridescent; hairs long (8 mm) interspersed with longer hairs (12–13 mm) on rump. Ventral pelage slightly more grey. Ears short, hidden by pelage. Fore- and hindfoot blackish; claws on forefoot very large. Tail of medium relative length (ca. 42% of HB), blackish, naked. Skull stout and heavy with prominent angle in squamosal region. Teeth small, anterior incisors delicate. First unicuspid the largest, second unicuspid just under half the size of the first, third unicuspid three-quarters the size of the first, fourth unicuspid minute. Nipples: not known.

Geographic Variation None recorded.

Similar Species

Myosorex babaulti. Similar in size and form except maxillary region and dentition more heavily built; M³ larger and less compressed from front to back. Geographic distribution very close in E DR Congo but not recorded from Rwenzori Mts.

M. schalleri. Based on one juvenile specimen, head and body smaller (HB: 50–55 mm); tail longer (T: 44 mm) and relatively longer (ca. 80% of HB); skull shorter (CI: 8.9 mm). Pelage entirely black. Apparently allopatric but distribution close (Itombwe Mts, E DR Congo).

Distribution Endemic to Africa Afromontane–Afroalpine BZ. Restricted to the Rwenzori Mts of Uganda and DR Congo at 1920–4000 m. The published record of this species in Bwindi Impenetrable N. P. (Kasangaki *et al.* 2003) is incorrect (J. Kerbis in litt.)



Myosorex blarina

Habitat Occurs in several diverse habitats associated with changing elevation. Recorded from the lower forests along the Mubuku R. amidst bracken and at the edges of streams (1900 m), in the ericaceous zone at 3370 m (sphagnum moss in valley with *Lobelia*), and the alpine zone with *Lobelia* and *Senecio* (Kerbis Peterhans *et al.* 1998). The type series was taken near a stream in very swampy ground using ‘worms’ as bait (Thomas & Wroughton, 1910).

Abundance Rare. Comprised 11% of shrews ($n = 65$; 8 spp.) at six habitats in Rwenzori Mts (Kerbis Peterhans *et al.* 1998). Less common in forested habitats.

Remarks Terrestrial. Elongated foreclaws facilitate rummaging through leaf litter and humus. Mostly nocturnal, but was one of three specimens taken during the day (Kerbis Peterhans *et al.* 1998). Sexes collected in equal proportions ($n = 10$; FMNH). Two ♀♀ collected in Nov and May were not pregnant (FMNH).

Conservation IUCN Category: Endangered.

The rarity and restricted distribution are cause for concern.

Measurements

Myosorex blarina

HB: 86.0 (81–93) mm, $n = 9$

T: 34 (31–40) mm, $n = 9$

HF: 15.0 (13–16) mm, $n = 9$

E: 6.5 (6–7) mm, $n = 7$

WT: 16 (13.5–18) g, $n = 6$

CI: 22.1 (21.7–22.5) mm, $n = 3$

GWS: 11.8 (11.7–12.0) mm, $n = 3$

I¹–M³: 9.5 (9.1–9.7) mm, $n = 4$

Rwenzori Mts, Uganda and DR Congo (FMNH)

Key Reference Kerbis Peterhans *et al.* 1998.

Sean O. Bober & Julian C. Kerbis Peterhans

Myosorex cafer DARK-FOOTED MOUSE SHREW

Fr. Musaraigne des bois à pieds sombre; Ger. Dunkelfuß-Waldspitzmaus

Myosorex cafer (Sundevall, 1846). Ofv. Kongl. Svenska Vet.-Akad. Forhandl. Stockholm 3 (4): 119. ‘E Caffraria interiore et Port-Natal’ (= Durban, KwaZulu–Natal Province, South Africa).

Taxonomy Originally described in the genus *Sorex*. The status of the Zimbabwe/Mozambique populations is uncertain (Meester 1958a); variation in chromosome number in the more central parts of the geographic range in South Africa suggests the presence of another species. The form *sclateri*, from KwaZulu–Natal, has for long been regarded as a subspecies of *M. cafer* (Meester *et al.* 1986), but is now recognized as a distinct species (Maddalena & Bronner 1992). Likewise *tenuis*, previously regarded as a subspecies (Meester *et al.* 1986), is now recognized as a valid species (Hutterer 2005b). Synonyms: *swinyi*. Subspecies: none. Chromosome number: $2n = 38$ or 40 (South Africa; Dippenaar *et al.* 1983).

Description Medium-sized shrew with medium-length tail. Dorsal pelage dark brown with buffy tinge; hairs slaty-grey at base, off-white to brown subterminal band, and dark-brown to black tip. Ventral pelage buffy-brown. Spring and autumn moults have a marked effect on pelage length, density and sometimes colour (Meester 1958b). Head slender with long, narrow pointed muzzle, small eyes and rounded ears. Fore- and hindfeet dark brown. Tail of medium relative length (ca. 50% of HB), dark-brown to black above, dark-brown below. Nipples: $0 + 3 = 6$.

Geographic Variation None recorded.

Similar Species

Myosorex longicaudatus. Tail on average longer (T: 66 [46–79] mm) and relatively longer (ca. 79% of HB). Allopatric but distribution fairly close along southern coast of South Africa.

M. sclateri. Pelage colour and hindfeet similar; skull on average larger (CI: 24.6 [23.9–25.5] mm). Sympatric in KwaZulu–Natal, South Africa.

M. tenuis. Head and body on average smaller (HB: 83.2 [75–92] mm). Skull on average shorter (CI: 21.5 [20.6–22.4] mm). Distribution close in Mpumalanga Province (formerly part of Transvaal), South Africa.

M. varius. Dorsal pelage mottled grey-brown to dark grey-brown; ventral pelage pale grey. Fore- and hindfeet pale grey. Tail pale to dark brown above, fawn to white laterally and below. Sympatric in part of South Africa; in the Amatola mountains of the Eastern Cape Province, *M. varius* is on average smaller than *M. cafer*.

Distribution Endemic to Africa. Zambezan Woodland, Highveld and Coastal Forest Mosaic BZs of southern Africa. Distribution disjunct. Recorded from three separate regions: (a) eastern highlands of Zimbabwe and adjacent Mozambique; (b) Soutpansberg Range in far northern South Africa and Swaziland; (c) eastern escarpment of Limpopo and Mpumalanga Province and into afro-montane and coastal forests of southern KwaZulu–Natal and the Eastern Cape Province (Meester 1958a, Smithers & Lobão Tello 1976, Smithers & Wilson 1979, Rautenbach 1982, Meester *et al.* 1986, Monadjem 1998a,c, Taylor, P. 1998).

Habitat In South Africa, typically occurs in forest although may also be found in montane grassland (e.g. in the Wolkberg, where *M. varius* is commonest in the adjacent forest [Rautenbach 1982]). More abundant in damp microhabitats. Appears to have stricter habitat requirements than *M. varius*, which occurs throughout its South African geographic range; *M. cafer* tending to be the commonest species in the forests and *M. varius* in the grasslands.

Abundance Reasonably common in suitable habitats. In the Amatola forests of Eastern Cape Province, South Africa, it and the

Woodland Dormouse *Graphiurus murinus* are the most common small mammals (trap success of 4%) (R. M. Baxter unpubl.).

Adaptations Predominantly nocturnal with a higher level of diurnal activity than *M. varius* (Baxter *et al.* 1979). In contrast to *M. varius*, no rooting and burrowing behaviour has been observed.

Foraging and Food Insectivorous. In Zimbabwe, prey includes spiders and earthworms, Lepidopteran larvae, Coleoptera, Isoptera, Isopoda and centipedes. Small amounts of seed and green plant material are also consumed (Churchfield 1985, Monadjem 1997).

Social and Reproductive Behaviour Mildly aggressive; vocalizations include a short squeak when encountering a strange conspecific. Scent-marking with lateral glands has been observed, and faecal piles are strongly scented. Saucer-shaped nests are built in captivity (Baxter & Meester 1980).

Reproduction and Population Structure Reproductive activity appears to occur during the wet season from Oct to Apr (Skinner & Smithers 1990, Taylor, P. 1998). Litter-size in Zimbabwe: 3 (2–4), *n* = 3 (Smithers & Wilson 1979); KwaZulu–Natal, South Africa: 3.5 (2–5), *n* = 6 (Taylor, P. 1998).

Predators, Parasites and Diseases Known predators include Barn Owls *Tyto alba* and African Grass-owls *Tyto capensis*.

Conservation IUCN Category: Least Concern.

Destruction of forest habitats is a potential threat to this species.

Measurements

Myosorex cafer

HB: 88 (78–105) mm, *n* = 46

T: 44 (36–50) mm, *n* = 46

HF: 14.7 (13–16) mm, *n* = 46

E: 10.1 (9–11) mm, *n* = 46



Myosorex cafer

WT: 11.9 (9–17) g, *n* = 26

CI: 23.3 (22.1–24.3) mm, *n* = 31

GWS: 11.1 (10.4–11.8) mm, *n* = 22

I¹–M³: 9.8 (9.1–10.2) mm, *n* = 39

Measurements: Port St Johns, South Africa (Meester & Dippenaar 1978)

Weight: Northern Province and Mpumalanga Province, South Africa (Rautenbach 1982)

Key References Baxter & Meester 1980; Baxter *et al.* 1979; Meester 1958a; Smithers & Wilson 1979; Taylor, P. 1998.

R. M. Baxter & N. J. Dippenaar

Myosorex eisentrauti EISENTRAUT'S MOUSE SHREW

Fr. Musaraigne des bois d'Eisentraut; Ger. Eisentrauts Waldspitzmaus

Myosorex eisentrauti Heim de Balsac, 1968. Bonn. Zool. Beitr. 19: 20. Pic Santa Isabel, Fernando Po (= Bioko I.), Equatorial Guinea. 2400 m.

Taxonomy The forms *okuensis* and *rumpii* (neither of which occurs on Bioko I.) were included in *C. eisentrauti* by Heim de Balsac & Meester (1977), but now both are regarded as distinct species (see Hutterer 1993, 2005a). Synonyms: none. Chromosome number: not known.

Description Small–medium, dark shrew. Pelage soft and dense with silky sheen; hairs ca. 6 mm. Dorsal pelage uniformly very dark blackish-brown; hairs dark grey at base, dark brown or dark chestnut-brown at tip. Ventral pelage slightly paler, dark brown with shot-silk appearance; hairs dark grey, very dark reddish-brown at tip. Ears small and inconspicuous, mostly concealed by pelage. Fore- and hindfeet brown, with dark scales, well covered by dark brown hairs; claws sharp and relatively long. Tail of medium relative length

(45–55% of HB), dark brown, not bicoloured, with many short dark brown hairs. Braincase high domed. First upper incisor moderately long and hooked. Third upper molar wide. Nipples: 2 + 0 = 4.

Geographic Variation None.

Similar Species

Myosorex rumpii. Apparently very similar but data limited. One specimen; Rumpi Hills, Cameroon.

Distribution Endemic to Bioko I. (Equatorial Guinea).

Habitat Found only on the Pic Santa Isabel at 2400 m and at 'Refugium' at 2000 m. At higher altitudes (Pic Isabel, ca. 3000 m),

lives in alpine grasslands. Habitat at lower altitudes (e.g. Refugium, 2000 m) is 'Schefflera montane forest' (1400–2600 m).

Abundance Uncertain; known only from a few specimens.

Remarks Apparently no other information available.

Conservation IUCN Category: Critically Endangered.

Measurements

Myosorex eisentrauti

HB: 77.3 (71–82) mm, n = 4

T: 40 (37–42) mm, n = 4

HF: 12.6 (12–13.5) mm, n = 4

E: 6, 7 mm, n = 2

WT: 13.7 (12–15) g, n = 4

CI: 22.6 (22–23.2) mm, n = 5*

GWS: 11.1 (11.0–11.2) mm, n = 5*

I¹–M³: 9.4 (9.1–9.6) mm, n = 5*

Bioko I., Equatorial Guinea (Heim de Balsac 1968d)

*Skulls re-measured by author

Key Reference Heim de Balsac 1968d.



Myosorex eisentrauti

Rainer Hutterer

Myosorex geata GEATA MOUSE SHREW

Fr. Musaraignes des bois des montagnes Uluguru; Ger. Uluguru-Waldspitzmaus

Myosorex geata (Allen and Loveridge, 1927). Proc. Boston Soc. Nat. Hist. 38: 417. Nyingwa, Uluguru Mountains, Tanzania.

Taxonomy Originally described in the genus *Crocidura* but later placed in the genus *Myosorex* (Heim de Balsac 1967). Synonyms: none. Chromosome number: not known.

Description Small–medium, dark shrew. Pelage 6.5–7 mm (rump), 4.5–5.0 mm (neck and ventral pelage). Dorsal pelage rich dark brown; hairs slate-grey (75% of length), yellowish-gold subterminal band, dark brown at tip. Ventral pelage similar in colour to dorsal pelage, hairs lack brown tip. Fore- and hindfeet brown with scaly reticulation and small claws. Tubercles of hindfeet small. Tail of medium relative length (ca. 57% of HB), dark, only slightly bicoloured. Nipples: not known.

Geographic Variation None recorded.

Similar Species

Myosorex kahaulei. HB on average larger (HB: 77 [70–84] mm), skull almost always slightly smaller (CI: 20.2 [19.7–20.8] mm); hindfoot tubercles larger and more rounded. Allopatric but distribution fairly close in Tanzania (Udzungwa Mts only; Stanley & Hutterer 2000).

Distribution Endemic to Africa. Afromontane–Afroalpine BZ. Recorded only on Uluguru Mts, Tanzania.



Myosorex geata

Habitat Montane forests at 1345 and 1535 m. Allen & Loveridge (1927) recorded the holotype from 7500 ft (= 2250 m) and another specimen from 2000 ft (= 600 m).

Abundance Comprised 5% of shrews recorded at 1525 m (n = 103). Syntopic shrews in this sample include *C. monax* and *Sylvisorex howelli* (W.T. Stanley unpubl.).

Remarks In Jul and Aug (1996), none of the ♀♀ examined was pregnant (n = 2). On the basis of toothwear, all individuals (n = 6) were young adults (W.T. Stanley unpubl.). Sex ratio 1 : 1 (n = 6).

Conservation IUCN Category: Endangered.

The geographic range is limited and fragmented, and the number of suitable habitats is declining.

Measurements

Myosorex geata

HB: 72.1 (68–75) mm, n = 6

T: 41.0 (40–43) mm, n = 6

HF: 13.2 (12–14) mm, n = 6

E: 7.2 (5–9) mm, n = 6

WT: 9.2 (7.6–10.5) g, n = 6

CI: 20.9 (20.7–21.1) mm, n = 6

GWS: 10.5 (10.3–10.7) mm, n = 6

I¹–M³: 9.1 (8.9–9.2) mm, n = 6

Uluguru Mts, Tanzania (W.T. Stanley unpubl.)

Key References Allen & Loveridge 1927; Stanley & Hutterer 2000.

William T. Stanley

Myosorex kahaulei KHAULE'S MOUSE SHREW

Fr. Musaraigne des bois de Kihale; Ger. Kihaulis Waldspitzmaus

Myosorex kahaulei Stanley and Hutterer, 2000. Bonn. Zool. Beitr. 49: 19–29. Udzungwa Scarp Forest Reserve, Udzungwa Mts, Tanzania. 1460 m.

Taxonomy Synonyms: none. Chromosome number: not known.

Description Small–medium, dark brownish shrew similar to *M. geata* in pelage characteristics. Dorsal pelage dark brown; hairs dark at base, brown at tip. Ventral pelage brown (but not as ‘rich’ as in *M. geata*). Hindfoot tubercles large and well rounded. Claws on feet robust. Tail of medium relative length (ca. 53% of HB). Skull robust (especially the rostrum), but slightly smaller than that of *M. geata*. Nipples: not known.

Geographic Variation None recorded.

Similar Species

Myosorex geata. HB on average smaller (HB: 72.1 [68–75] mm), skull almost always slightly larger (CI: 20.9 [20.7–21.1] mm); hindfoot tubercles small. Allopatric but distribution fairly close in Tanzania (Uluguru Mts only; Stanley & Hutterer 2000).

Distribution Endemic to Africa. Afromontane–Afroalpine BZ. Recorded only on Udzungwa Mts, Tanzania.

Habitat Wetter areas of montane forest including swampy areas and bamboo forests above 1400 m. Not recorded below 900 m in Udzungwa Scarp F. R. in 1995 (W. T. Stanley unpubl.).

Abundance Comprised 15% of shrews sampled (n = 108) at 1460 m and 2000 m on the Udzungwa Mts (1995; W. T. Stanley unpubl.).

Remarks Short tail and robust claws may allow for foraging in thick vegetation. While mostly nocturnal, diurnal movement has

been observed (W. T. Stanley, unpubl.). In Jul and Aug (1995), all specimens were adult, and one ♀ was pregnant. Embryo number: 2 (n = 1). Sex ratio 3 : 1 (n = 12) (W.T. Stanley unpubl.). Owl pellets found at 1800 m near Massiwe, Udzungwa Scarp Forest, contained one skull of *Myosorex kahaulei* (W. T. Stanley, unpubl.).

Conservation IUCN Category: Endangered.

The geographic range is limited and fragmented, and the number of suitable habitats is declining.



Myosorex kahaulei

Measurements*Myosorex kahaulei*

HB: 77 (70–84) mm, n = 16

T: 41 (36–46) mm, n = 16

HF: 13 (12–14) mm, n = 16

E: 8 (6–9) mm, n = 16

WT: 10.1 (8–12.5) g, n = 16

CI: 20.2 (19.7–20.8) mm, n = 10

GWS: 10.4 (9.7–10.7) mm, n = 10

I¹–M³: 8.6 (8.0–9.0) mm, n = 10

Udzungwa Mts, Tanzania (Stanley & Hutterer 2000, W. T. Stanley unpubl.)

Key Reference Stanley & Hutterer 2000.**William T. Stanley*****Myosorex longicaudatus* LONG-TAILED MOUSE SHREW**

Fr. Musaraigne des bois à longue queue; Ger. Langschwanz-Waldspitzmaus

Myosorex longicaudatus Meester and Dippenaar, 1978. Ann. Transvaal Mus. 31: 30. Diepwalle State Forest, 14 km NNE of Knysna (33° 57'S, 23° 10'E), Western Cape Province, South Africa.**Taxonomy** Polytypic. Dippenaar (1995) described *boosmani* as a subspecies on the basis of slight differences in cranial morphology and geographic location. Synonyms: none. Subspecies: two. Chromosome number: not known.**Description** Medium-sized shrew with long tail. Dorsal pelage dark grey heavily washed with greyish-yellow, brown or brownish-black; hairs slaty-grey at base, off-white to buffy subterminal band, dark-brown at tip. Ventral pelage somewhat paler, dark grey washed with brownish-black to dark brown, mostly paler than dorsal pelage; hairs slaty-grey, buffy at tip. Colours of dorsal and ventral pelage merge on flanks. Head slender with long, narrow pointed muzzle. Eyes small. Ears rounded. Fore- and hindfeet brownish-black, greyish yellow-brown, or dull yellowish-brown above. Tail relatively long (ca. 79% of HB); brownish-black above, usually somewhat to distinctly paler below. Males tend to weigh more than ♀♀. Nipples: 0 + 3 = 6.**Geographic Variation** Two subspecies can be distinguished only by discriminant function analysis.*M. l. boosmani*: Boosmansbos Forest and its ecotone in the Langeberg Mts; geographically isolated from the nominate subspecies by the dry Gouritz River valley. Differs from the nominate subspecies by its more slender rostrum, shallower braincase, usually narrower P³ and usually shorter but wider M³.*M. l. longicaudatus*: Knysna Forest from Lottering State Forest near Nature's Valley in the east to Ruitersbos State Forest north-north-west of Mossel Bay in the west.**Similar Species***Myosorex cafer*: Tail on average shorter (T: 44 [36–50] mm) and relatively shorter (49% of HB). Allopatric but distribution fairly close along southern coast of South Africa.*M. varius*: Tail almost always shorter (T: 42 [38–48] mm) and relatively shorter (ca. 50% of HB); fore- and hindfeet pale grey. Sympatric in extreme southern part of South Africa.**Distribution** Endemic to Africa. South-West Cape BZ. Occurs in the extreme southern parts of South Africa along almost the entire altitudinal gradient from 240 m above sea level near Nature's Valleyto 2000 m in the Outeniqua Mts north-north-west of Mossel Bay. Sympatric with *M. varius* throughout range.**Habitat** Primary forest, forest ecotones, fynbos and boggy grassland. Micro-habitats are always moist.**Abundance** It is usually readily trapped but is never as abundant as *M. varius*.**Remarks** When descending from objects, the terminal portion of the long tail is used in a prehensile fashion. The tail also braces the animal when it sniffs the air, forming a tripod with the hindlimbs. Insectivorous, but seeds have been found in stomach contents (Skinner & Smithers 1990). In captivity, readily eats a variety of insects, mealworms and minced meat, often dragging the food to the nest box before consuming it. In captivity, these shrews are surprisingly docile and can be handled with ease.*Myosorex longicaudatus*

Conservation IUCN Category: Vulnerable.

Destruction of forest and fynbos habitats is a potential threat to this species. Present evidence suggests that the subspecies *M. l. boosmani* in the Langeberg Mts should also be considered as 'Vulnerable'.

Measurements

Myosorex longicaudatus

HB: 83 (73–93) mm, n = 123

T: 66 (46–79) mm, n = 121

HF: 17.1 (14–19) mm, n = 123

E: 10.5 (10–12) mm, n = 21

WT (♂♂): 14 (9–21) g, n = 72

WT (♀♀): 9, 10 g, n = 2

CI: 23.2 (21.5–24.4) mm, n = 100

GWS: 11.3 (10.7–12.0) mm, n = 96

I¹–M³: 9.9 (9.6–10.1) mm, n = 27

South Africa (Meester & Dippenaar 1978, Dippenaar 1995)

Key References Dippenaar 1995; Meester & Dippenaar 1978.

N. J. Dippenaar & R. M. Baxter

Myosorex okuensis OKU MOUSE SHREW

Fr. Musaraigne des bois du Mont Oku; Ger. Oku-Waldspitzmaus

Myosorex okuensis Heim de Balsac, 1968. Bonn. Zool. Beitr. 19: 20. L. Oku, Mt Oku, Bamenda Highlands, Cameroon. 2100 m.

Taxonomy Originally described as a subspecies of *Myosorex eisentrauti* (see Heim de Balsac 1968d, Heim de Balsac & Meester 1977), but cranially very distinct (Hutterer 2005b). Synonyms: none. Chromosome number: not known.

Description Small-medium very dark shrew. Pelage relatively long, soft and dense; hairs 7–8 mm. Dorsal pelage dark brownish-black; hairs dark blackish-grey, dark brown at tip. Ventral pelage similar in colour to dorsal pelage or slightly paler (depending on angle of view), with shot-silk appearance. Ears reduced, concealed by pelage and barely visible. Fore- and hindlimbs slightly pigmented, with dark brown short hairs; relatively long claws. Tail of medium relative length (ca. 55% of HB), dark brownish-black. Braincase high domed. First upper incisor moderately long and hooked. First upper unicuspid large, second and third smaller and subequal, fourth minute. Third upper molar medium. Nipples: not known.

Geographic Variation None recorded.

Similar Species

Myosorex rumpii. Head and body probably larger (HB: 84 mm); tail probably shorter (T: 35 mm) and relatively shorter (ca. 40% of HB) but data limited (n = 1). Allopatric but distribution fairly close (Rumpi Hills, Cameroon).

Distribution Endemic to Africa. Afromontane–Afroalpine BZ. Recorded only on the Bamenda Highlands, Cameroon (L. Manenguba, Mt Oku, Mt Lefo). Populations disjunct.

Habitat Montane forests.

Abundance No information.

Remarks Apparently no other information available.

Conservation IUCN Category: Endangered.



Myosorex okuensis

Measurements

Myosorex okuensis

HB: 72.7 (72–73) mm, n = 3

T: 40, 41 mm, n = 2

HF: 12.7 (12–13) mm, n = 3

E: 8 (8–8) mm, n = 3

WT: 12.3 (11–12) g, n = 3

CI: 21.5, 21.7 mm, n = 2

GWS: 11.4, 11.5 mm, n = 2

I¹–M³: 9.0, 9.3 mm, n = 2

L. Oku, Bamenda Highlands, Cameroon (ZFMK)

(see also Heim de Balsac 1968d for other measurements)

Key References Heim de Balsac 1968d.

Rainer Hutterer

Myosorex rumpii RUMPI MOUSE SHREW

Fr. Musaraigne des bois de Rumpi; Ger. Rumpi-Waldspitzmaus

Myosorex rumpii Heim de Balsac, 1968. Bonn. Zool. Beitr. 19: 20. Rumpi Hills, Cameroon. 1100 m.

Taxonomy Originally described as a subspecies of *M. eisentrauti*; however, Heim de Balsac was uncertain about the status of this taxon, and while he formally named it *M. eisentrauti rumpii*, he labelled all figures and the map with '*Myosorex rumpii*'. Now regarded as a full species (Hutterer 2005b). Synonyms: none. Chromosome number: not known.

Description Medium-sized, dark short-tailed shrew. Pelage soft, dense and velvety with silky sheen; hairs ca. 6 mm. Dorsal pelage dark blackish-brown; hairs dark grey on basal two-thirds, blackish-brown or dark chestnut-brown on terminal third. Ventral pelage blackish-brown, paler than dorsal pelage (depending on angle of view) with shot-silk appearance; hairs dark grey on basal two-thirds, dark reddish-brown on terminal third. Head similar in colour to dorsal pelage. Fore- and hindfeet whitish with conspicuous brown scales, short blackish-brown hairs on upper surface; claws relatively long and sharp. Tail relatively short (ca. 40% of HB), blackish-brown, not bicoloured. First incisor moderately long and hooked. Third upper molar narrow. Nipples: not known.

Geographic Variation None recorded.

Similar Species

Myosorex eisentrauti. Apparently very similar but data limited. Only known from Bioko I.

M. okuensis. Head and body probably smaller (HB: 72–73 mm); tail probably longer (40, 41 mm) and relatively longer (ca. 55% of HB), but data limited. Allopatric but distribution fairly close (Bamenda Highlands, Cameroon).

Distribution Endemic to Africa. Afromontane–Afroalpine BZ. Known only from the type locality in the Rumpi Hills, Cameroon.

Habitat Not known.

Abundance Not known.

Remarks Apparently no other information available.

Conservation IUCN Category: Endangered.



Listed as a species of conservation concern by Nicoll & Rathbun (1990).

Measurements

Myosorex rumpii

HB: 84 mm, n = 1

T: 35 mm, n = 1

HF: 14 mm, n = 1

E: 10 mm, n = 1

WT: 15 g, n = 1

CI: 22.7 mm, n = 1

GWS: 12.2 mm, n = 1

I¹–M³: 9.6 mm, n = 1

Rumpi Hills, Cameroon (type locality; ZFMK)

Key Reference Heim de Balsac 1968d.

Rainer Hutterer

Myosorex schalleri SCHALLER'S MOUSE SHREW

Fr. Musaraigne des bois de Schaller; Ger. Schallers Waldspitzmaus

Myosorex schalleri Heim de Balsac, 1966. C.R. Acad. Sci. Paris 263: 889. Nzombe (Mwenga), Itombwe Mts, E DR Congo.

Taxonomy Provisionally named by Heim de Balsac (1966) and fully described by Heim de Balsac (1967). The type locality was erroneously given as 'Albert N. P.' by Heim de Balsac & Meester (1977) but is located

in the Itombwe Mts (Hutterer 1986c). The description was based on a juvenile ♂, which still remains the only known specimen. The relation of the species within the genus is unresolved. Synonyms: none.

Description Very small (smallest species of the genus), comparable in size to *Sylvisorex granti*, with entirely black pelage and limbs (Heim de Balsac 1967). Pelage short and not dense. Tail relatively very long (ca. 80% of HB); appearing naked, without long bristles. Ear conch visible, not reduced or hidden in pelage. Skull small with an oval (not hexagonal) braincase and a narrow interparietal bone. Due to the juvenile condition of the holotype, the normal adult shape of the skull is not known. Dentition as in other *Myosorex*, but weaker. For a full description see Heim de Balsac (1967). Nipples: not known.

Geographic Variation None recorded.

Similar Species

Myosorex babaulti. Head and body perhaps larger (HB: 79–91 mm); tail perhaps shorter (T: 34–40 mm) and relatively shorter (ca. 45% of HB). Pelage not entirely black, hairs ash-grey at base. Apparently allopatric but distribution close in E DR Congo.

M. blarina. Head and body larger (HB: 81–93 mm); tail probably shorter (T: 31–40 mm) and relatively shorter (ca. 42% of HB); skull longer (CI: 21.7–22.5 mm, $n = 3$). Apparently allopatric but distribution close (Rwenzori Mts of Uganda and E DR Congo).

Distribution Endemic to Africa. Afromontane–Afroalpine BZ. Recorded only from the Itombwe Mts of E DR Congo.

Habitat Montane forest. The holotype was found dead on a forest road near Nzombe during a gorilla survey. Schaller (1963) provided a photograph of the site and commented: ‘A mountain rain forest covers the chaotic jumble of ridges and valleys in the Mwenga-Fizi region.’

Abundance Very rare. Known only from the type locality.

Remarks *Myosorex schalleri* seems to form, together with *Paracrociodura graueri*, part of the endemic small mammal fauna of the Itombwe Mts (Hutterer 1986c).

Conservation IUCN Category: Data Deficient, previously Critically Endangered.



Myosorex schalleri

Measurements

Myosorex schalleri

HB: 50–55 mm*

T: 44 mm

HF: 10.5 mm

E: n. d.

WT: n. d.

CI: 8.9 mm

GWS: 8.5 mm

I¹–M³: 8.4 mm

Holotype, a juvenile from Itombwe Mts, DR Congo (Heim de Balsac 1967, Stanley & Hutterer 2000)

*Approximate value (as stated in Heim de Balsac 1967)

Key Reference Heim de Balsac 1967.

Rainer Hutterer

Myosorex sclateri SCLATER'S MOUSE SHREW

Fr. Musaraigne de bois de Sclater (Musaraigne du Kwazulu); Ger. Sclaters Waldspitzmaus

Myosorex sclateri Thomas and Schwann, 1905. Abstr. Proc. Zool. Soc. Lond. 1905 (15): 10. Ngoye Hills, Zululand, South Africa.

Taxonomy Sometimes regarded as a subspecies of *M. cafer* (Meester *et al.* 1986). Differences in karyotype (Wolhuter in Smithers 1983) and habitat suggest that *sclateri* should be recognized as a valid species (see Hutterer 2005b), sympatric with *M. cafer*. *Myosorex sclateri* can also be distinguished from *M. cafer* and *M. varius* on biochemical evidence (Maddalena & Bronner 1992) and morphological grounds (T. Kearney in Taylor, P. 1998). Synonyms: *affinis*, *talpinus*. Subspecies: none. Chromosome number: $2n = 38$.

Description Large shrew but with considerable variation in size. Dorsal pelage bright reddish-brown or blackish-brown. Ventral pelage yellowish-brown. Feet broad and digits relatively long. Hindfeet brown to black. Tail short to medium (43–63% of HB), uniformly brown, maybe slightly paler below. Skull: CI = 24–27 mm (cf. Similar Species). Nipples: not known.

Geographic Variation None recorded.

Similar Species

Myosorex cafer. Pelage colour and hindfeet similar; skull on average smaller (CI: 23.3 [22.1–24.3] mm). Sympatric in KwaZulu–Natal, South Africa.

M. varius. Dorsal pelage dull mottled grey-brown to dark grey-brown; hindfeet pale grey. On average smaller (HB: 83 [76–88] mm; T: 42 [38–48] mm). Skull shorter (CI: 20.3–22.4 mm). Sympatric in N KwaZulu–Natal, South Africa.

Distribution Endemic to Africa. Coastal Forest Mosaic BZ. Restricted to KwaZulu–Natal Province, South Africa.

Habitat Estuarine reed-beds and other wet habitats; also grassland and forest close to water. Coastal and lowland regions.

Abundance Fairly common (Taylor, P. 1998).

Remarks Habitat preferences rather similar to those of *M. varius* (Taylor, P. 1998).

Conservation IUCN Category: Near Threatened.

Although not uncommon in favoured habitats, distribution is very restricted.

Measurements

Myosorex sclateri

HB: 94 (81–114) mm, n = 18

T: 51 (46–57) mm, n = 18

HF: 16 (13–18) mm, n = 18

E: 9.7 (8–11) mm, n = 18

WT: n. d.



Myosorex sclateri

CI: 24.6 (23.9–25.5) mm, n = 9

GWS: 12.0 (11.4–12.4) mm, n = 7

I¹–M³: 10.4 (10.0–10.7) mm, n = 16

KwaZulu–Natal Province, South Africa (BMNH)

Key References Taylor, P. 1998.

P. D. Jenkins & S. Churchfield

Myosorex tenuis THIN MOUSE SHREW (TRANSSVAAL FOREST SHREW)

Fr. Musaraigne des bois du Transvaal; Ger. Transvaal-Waldspitzmaus

Myosorex tenuis Thomas and Schwann, 1905. Proc. Zool. Soc. Lond. 1905: 131–132. Zuurbron, Wakkerstroom Highlands, Transvaal, South Africa.

Taxonomy Traditionally considered as synonym (Meester *et al.* 1986) or subspecies (Smithers 1983) of *M. cafer*. Now recognized as valid species because of different karyotype (see Smithers 1983, Hutterer 2005b). Synonyms: none. Chromosome number: 2n = 40 (Wolluter in Smithers 1983).

Description Medium-sized dark shrew. Dorsal pelage dark brown. Ventral pelage paler, with a silvery wash in some specimens. Feet dark brown, slender with long claws. Ears smaller and less conspicuous than in *M. sclateri*. Tail of medium relative length (41–59% of HB), dark above, paler beneath. Skull moderately small (CI: 20–22 mm). Nipples: not known.

Geographic Variation None recorded.

Similar Species

Myosorex cafer. Head and body on average larger (HB: 88 [78–105] mm). Skull on average longer (CI: 23.3 [22.1–24.3] mm).

Distribution close in Mpumalanga Province (formerly part of Transvaal), South Africa.

M. varius. Dorsal pelage mottled grey-brown to dark grey-brown. Very similar in size. Sympatric in Mpumalanga Province (formerly part of Transvaal), South Africa.

Distribution Endemic to Africa. Highveld BZ. Recorded from Mpumalanga Province (formerly part of Transvaal), South Africa; possibly also W Mozambique.

Habitat Thick grass at edge of stream (eight specimens), under a tree in forest (two specimens) and in a vlei (one specimen) (labels, BMNH). Recorded from 1600 m in Wakkerstroom Highlands, Transvaal (Thomas & Schwann 1905).

Abundance No information. Rarely collected.

Remarks Apparently no other information available.

Conservation IUCN Category: Data Deficient.

Formerly considered as Vulnerable. Known only from a very restricted area.

Measurements

Myosorex tenuis

HB: 83.2 (75–92) mm, n = 13

T: 42.0 (37–45) mm, n = 13

HF: 13.7 (12–14.5) mm, n = 13

E: 9.2 (8–10) mm, n = 13

WT: n. d.

CI: 21.5 (20.6–22.4) mm, n = 10

GWS: 10.6 (10.1–11.2) mm, n = 11

I¹–M³: 8.9 (8.6–9.4) mm, n = 13

Zuurbron, Wakkerstroom Highlands and Woodbush Hills, Transvaal, South Africa (BMNH)

Key Reference Thomas & Schwann 1905.

P. D. Jenkins & S. Churchfield



Myosorex tenuis

Myosorex varius SOUTH AFRICAN MOUSE SHREW

Fr. Musaraigne des bois sud-africaine; Ger. Südafrika-Waldspitzmaus

Myosorex varius (Smuts, 1832). Enumer. Mamm. Cap. p. 108. Algoa Bay, South Africa (= Port Elizabeth, Eastern Cape Province, South Africa).

Taxonomy Originally described in the genus *Sorex*. Synonyms: *herpestes*, *pondoensis*, *transvaalensis*. Subspecies: none. Chromosome number: 2n = 40 or 42 (South Africa; Dippenaar *et al.* 1983).

Description Medium-sized shrew. Dorsal pelage mottled grey-brown to dark grey-brown; hairs slaty-grey at base, white to off-white subterminal band, dark-brown at tip. Ventral pelage pale grey, sometimes with yellowish tinge; hairs slaty-grey at base, white to fawn at tip. Colours of dorsal and ventral pelage merge gradually. Head slender with long, narrow pointed muzzle, eyes small, ears rounded. Fore- and hindfeet pale grey. Tail of medium relative length (ca. 50% of HB), pale to dark brown above, fawn to white laterally and below, with sparse hairs along its length. Nipples: 0 + 3 = 6.

Geographic Variation Individuals from higher altitudes in the Drakensberg Mts are significantly smaller (in HB, E and WT) than individuals from lower altitudes (Rowe-Rowe & Meester 1985a). In contrast, populations in Eastern Cape Province exhibit the opposite trend between sea level and 1800 m (R. M. Baxter unpubl.).

Similar Species

Myosorex cafer. Dorsal pelage dark brown with buffy tinge; ventral pelage buffy-brown. Fore- and hindfeet dark brown. Tail dark-brown to black above, dark-brown below. Sympatric in the Amatola mountains of the Eastern Cape Province, South Africa, where *M. cafer* is on average larger than *M. varius*.

M. longicaudatus. Tail almost always longer (T: 66 [46–79] mm) and relatively longer (ca. 79% of HB); fore- and hindfeet brownish-

black, greyish yellow-brown, or dull yellowish-brown above. Sympatric in extreme southern part of South Africa.

M. sclateri. Dorsal pelage bright reddish-brown or blackish-brown. Hindfeet brown to black. On average, larger (HB: 94 [81–114] mm; T: 51 [46–57] mm). Skull longer (CI: 23.9–25.5 mm). Sympatric in N KwaZulu–Natal, South Africa.

M. tenuis. Dorsal pelage dark brown. Very similar in size. Sympatric in Mpumalanga Province (formerly part of Transvaal), South Africa.

Distribution Endemic to Africa. Widespread in parts of South-West Arid (Karoo), South-West Cape, Highveld and Coastal Forest Mosaic BZs. Recorded from Lesotho, W Swaziland and the southern parts of South Africa. In South Africa, known from the eastern half of Limpopo Province, southwards and westwards through Mpumalanga, Gauteng, NE Free State and KwaZulu–Natal Provinces. Also occurs along the western coast of Northern Cape Province, southwards to Western Cape Province and eastwards across much of Eastern Cape Province (Rautenbach 1982, Lynch 1983, 1994, Meester *et al.* 1986, Monadjem 1998a, c, Taylor, P. 1998).

Habitat Savanna and grassland habitats, typically in dense, moist grassland. Also recorded in forest (Rautenbach 1982, Rowe-Rowe & Meester 1982a) and in drier regions along the west coast and in Karoo N. P. where mists provide a moist micro-habitat. Measurements in different micro-habitats along an altitudinal gradient indicate a relatively stable environment despite considerable variation in climate (R. M. Baxter & C. R. Brown unpubl.); it is probably this stability that allows this species (and possibly other species) to

occupy a diverse range of vegetation types. Recorded in grasslands, *Protea* woodlands, scrub, forest and *Erica*–*Helichrysum* habitats, from 1500–3000 m, in the Drakensberg Mts, South Africa (Rowe-Rowe & Meester 1982a).

Abundance Common in many habitats in the Drakensberg Mts, South Africa (Rowe-Rowe & Meester 1982a) and Eastern Cape Province (R. M. Baxter unpubl.). Recorded in all of ten montane habitats (1500–1800 m) in the Drakensberg Mts, where it was mostly the second most numerous small mammal after the rodent *Rhabdomys pumilio*, and at all of eight sub-alpine and alpine habitats where it was usually the most abundant small mammal (Rowe-Rowe & Meester 1982a). In Eastern Cape Province, abundance (as frequency of occurrence in traps) increased from 1.9% at 600 m to 3.0–7.7% at 1500 m and 6.3–11.5% at 1800 m (R. M. Baxter unpubl.).

Adaptations Terrestrial and generally nocturnal (Baxter *et al.* 1979) but becoming predominantly diurnal in mid-winter (Brown *et al.* 1997). This change in circadian rhythm is an adaptation that probably allows these shrews to conserve energy by resting in a well-insulated nest during the coldest hours of the night. Possess relatively long claws on the forefeet, and are active burrowers.

Foraging and Food Mostly insectivorous. Analysis of stomach contents indicates that feeding is largely opportunistic and changes seasonally (Rowe-Rowe 1986, Wirminghaus & Perrin 1992, Monadjem 1997). In the Drakensberg Mts, the commonest prey (frequency of occurrence, wet and dry seasons combined) are adult Coleoptera (58%), Hymenoptera (53%), Orthoptera (24%), Lepidoptera larva (22%), Coleoptera larva (20%), Arachnida (20%), Blattoidea (16%), Hemiptera (11%) and six other orders (each <10%) (n = 55; Rowe-Rowe 1986). In captivity, readily eats earthworms, locusts, grasshoppers, bagworms, termites and beetles (Goulden & Meester 1978). Small amounts of vegetable matter form part of the diet (Wirminghaus & Perrin 1992), and there is circumstantial evidence that green plant material might be important in initiating breeding in captivity (R. M. Baxter unpubl.). May be cannibalistic. Refection (rectum-licking) has been observed (Baxter & Meester 1980).

Social and Reproductive Behaviour Mostly an aggressive species, especially at the beginning of the breeding season. In captivity individuals need to be kept apart in order to avoid fighting and potential death. Both ♂♂ and ♀♀ maintain territories during the wet and dry season. Territory size is in the region of 0.08–0.2 ha and, in general, male and female territories have areas of overlap. Scent-marking of territories is performed using secretions from the lateral and chin glands and the faecal pile is strongly scented (Baxter & Meester 1980). When individuals are alarmed, they exude a strong odour that humans can smell several metres away (R. M. Baxter unpubl.).

Vocalizations include a short, sharp squeak when encountering strange conspecifics and when alarmed. This squeak is repeated frequently and interspersed with occasional drawn-out ‘chirrs’ during aggressive encounters. A soft ‘chittering’ is heard occasionally from male–female pairs, and when the young are nursed. The young emit a keening squeak during their first few days. Grooming includes scratching with the hindfeet, nibbling and licking of the fur and paws, and face-washing with the forepaws (Goulden & Meester 1978).



Myosorex varius

Courtship behaviour involves extensive chasing by the male (Goulden & Meester 1978). Nests of grass are spherical with 2–4 entrances, often at the end of a short burrow under a rock. Maternal care is well developed. The young nipple-cling from birth to Day 5 or 6, thereafter caravanning is observed until weaning. A female has never been observed to carry the young in her mouth (Baxter & Lloyd 1980).

Reproduction and Population Structure Geographic variation in the breeding season is apparent. Generally pregnancies occur in the wet season but can occur at any time if unseasonable rain falls (R. M. Baxter unpubl.). In most locations, breeding occurs from Aug, Sep or Oct to Feb–Apr (data from Gauteng Province, KwaZulu–Natal Province, Drakensberg Mts and Lesotho). However, year-round breeding occurs in the Western Cape, with most pregnancies in Jun–Sep (where there is winter rainfall) (R. M. Baxter unpubl.). Embryo number: 3.3 (1–6), mode 3, n = 125) but mean embryo number varies with location, e.g. Western Cape 2.5 (n = 26), KwaZulu–Natal midlands 3.0 (n = 26) (R. M. Baxter unpubl.), KwaZulu–Natal Drakensberg 2.8 (n = 19) (Rowe-Rowe & Meester 1982b) and Lesotho 3.8 (n = 45) (Lynch 1994). Larger litters occur in locations where the breeding season is shorter, e.g. Lesotho.

Young are born blind, naked and helpless. Development is rapid and weaning occurs at Day 20–24 when the young (HB: 75–78 mm) are almost adult size (HB: 84–87 mm) (Baxter & Lloyd 1980). Longevity is 12–16 months, with a die-off of old adults towards the end of the breeding season. In captivity, individuals survive for up to 2.5 years (R. M. Baxter unpubl.).

During the dry season, populations are usually composed of sub-adults (50–60%; toothwear class 2; Dippenaar 1977) and adults (ca. 30%; toothwear class 3) with a few older animals. Approximately two months after the start of the wet season, juveniles (toothwear class 1) first appear, and by mid and late wet season, the population is composed of juveniles (ca. 20%), subadults (40%) and adults (40%) (R. M. Baxter unpubl.).

Predators, Parasites and Diseases Remains of this species are often found in the pellets of Barn Owls *Tyto alba* (*inter alia* Baxter & Matshili 2003). Other known predators include Marsh Mongooses *Atilax paludinosus*, Striped Weasels *Poecilogale albinucha* and Zorillas *Ichonyx striatus*.

Conservation IUCN Category: Least Concern.

A widely distributed, common species.

Measurements

Myosorex varius

HB: 83 (76–88) mm, n = 32

T: 42 (38–48) mm, n = 32

HF: 14.7 (14–16) mm, n = 32

E: 9.3 (6–11) mm, n = 32

WT: 13.3 (9.5–18.0) g, n = 54

CI: 21.5 (20.3–22.4) mm, n = 71

GWS: 10.6 (10.1–11.1) mm, n = 62

I¹–M³: 9.0 (8.2–9.5) mm, n = 86

Diepwalle, South Africa (Meester & Dippenaar 1978)

Weight: R. M. Baxter (unpubl.)

Key References Baxter & Lloyd 1980; Meester 1958a; Rowe-Rowe & Meester 1985b.

R. M. Baxter & N. J. Dippenaar

Myosorex zinki KILIMANJARO MOUSE SHREW

Fr. Musaraigne des bois du Kilimanjaro; Ger. Kilimanjaro-Waldspitzmaus

Myosorex zinki Heim de Balsac and Lamotte, 1956. Mammalia 20: 148. South-east slope of Mt Kilimanjaro, Tanzania. 3700 m.

Taxonomy Described as a subspecies of *Myosorex blarina*, and often referred to as such (e.g. Heim de Balsac & Meester 1977, Shore & Garbett 1991). Synonyms: none. Chromosome number: not known.

Description Very large and distinctive dark shrew. Pelage soft, dense with silky sheen; hairs ca. 6 mm. Dorsal pelage uniformly dark greyish-brown with conspicuous shot-silk appearance; hairs dark grey at base, shiny brown at tip. Some hairs with subterminal band of white resulting in flecked appearance. Ventral pelage slightly to moderately paler (depending on angle of view) with shot-silk appearance; hairs grey, greyish-brown at tip. Ears inconspicuous and densely covered with hairs, well concealed by pelage. Fore- and hindfeet brown, darkly pigmented, well-covered with dark brown short hairs. Tail relatively short (ca. 38% of HB), blackish-brown, with dark brown short hairs above, brown below. Braincase high-domed. First upper incisor moderately long and hooked. Third upper molar wide. No sexual dimorphism in body and skull measurements. Nipples: not known.

Geographic Variation None recorded.

Distribution Endemic to Africa. Afromontane–Afroalpine BZ. Recorded only at higher altitudes (2470–4000 m) on Mt Kilimanjaro, Tanzania (Grimshaw *et al.* 1997, Stanley *et al.* 2005b).

Habitat Montane forest, heathland, moorland, and the edges of alpine desert (Stanley *et al.* 2005b). One specimen collected on a grassy river bank (Shore & Garbett 1991).

Abundance Widely distributed along an elevational gradient ranging from 2470–4000 m (Stanley *et al.* 2005b); may be common in some localities.

Remarks This is the only species of *Myosorex* currently known to occur on Mt Kilimanjaro. No other information available.

Conservation IUCN Category: Vulnerable.

Measurements

Myosorex zinki

HB: 93.7 (84–100) mm, n = 6

T: 35.8 (33–37) mm, n = 6

HF: 16.3 (15–18) mm, n = 6

E: 7.5 (6–8) mm, n = 6

WT: 16.5 (14.5–19.5) g, n = 6

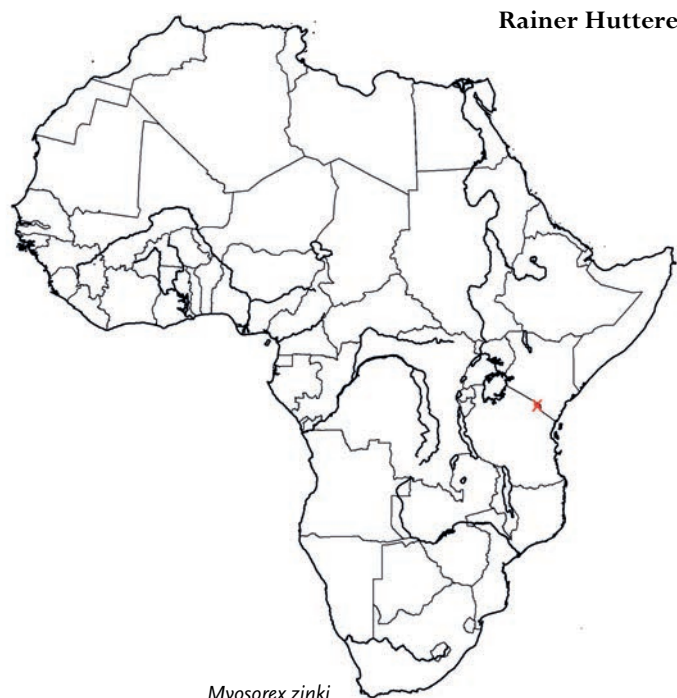
CI: 22.9 (22.1–23.7) mm, n = 5

GWS: 11.6 (11.3–11.8) mm, n = 5

I–M³: 9.5 (9.2–9.7) mm, n = 5

Males only; no significant difference between ♂♂ and ♀♀
Mt Kilimanjaro, Tanzania (Stanley *et al.* 2005b)

Key Reference Stanley *et al.* 2005b.



Rainer Hutterer

Myosorex zinki

GENUS *Paracrocidura*

Large-headed Shrews

Paracrocidura Heim de Balsac, 1956. Rev. Zool. Bot. Afr. 54: 137. Type species: *Paracrocidura schoutedeni* Heim de Balsac, 1956.



Paracrocidura schoutedeni.

The genus contains three species distributed in rainforest and montane forest habitats of central Africa, and has been recorded from Cameroon, Gabon, Equatorial Guinea, Congo, DR Congo, Central African Republic, Uganda, Rwanda and Burundi. The species in the genus are often found close to small streams, at altitudes of 600–2350 m.

The body form is that of a terrestrial shrew. The head is especially large (hence the vernacular name ‘large-headed shrew’) with long protruding incisors, and the ear pinnae are small, thinly haired and vertically inserted. The limbs are short (HF: 9–16 mm), and the tail is short (HB: 24–46 mm), thick and covered with long bristle-hairs (as in *Crociodura*). The pelage is short and uniformly dark brown. Females have only one pair of nipples. Skull characteristics include broad and flat braincase, narrow interorbital region, broad bimaxillary region, and three upper unicuspid teeth in each ramus (see also Table 7). The upper incisors are strongly hooked and have spade-like tips; upper and lower molars are very broad (Figure 15).

The biology of the species of this genus is not well known. One species lives in lowland forest, the two others in montane forest. Tree ferns and running water are typical characteristics of such habitats. It is assumed that Large-headed Shrews forage in leaf litter and under logs. The reduced number of nipples in ♀♀ and very low litter size (1–2) suggest a special but as yet not understood social organization and reproductive strategy.

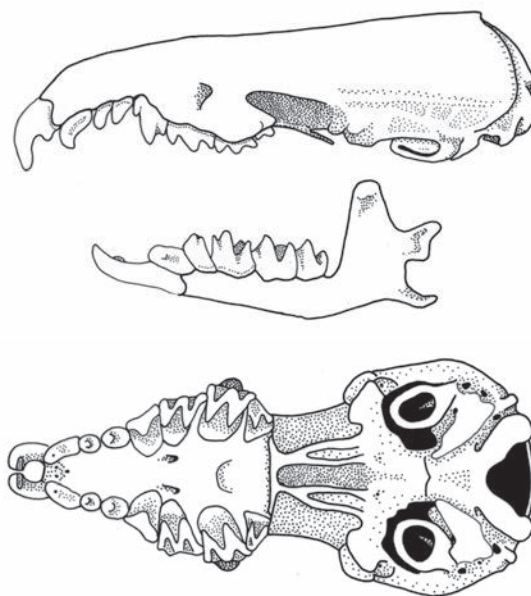


Figure 15. Skull and mandible of *Paracrocidura schoutedeni* (ZFMK 22920, with some information from BMNH 63.1813).

The genus (and its three species) was revised by Hutterer (1986c). A study of 16s rRNA sequences placed *Paracrocidura* in one clade with *Crociodura* (Quérrouil *et al.* 2001). However, unique external and cranial features distinguish *Paracrocidura* from all other genera.

The three species of the genus are distinguished by absolute size, and especially by length of hindfoot and tail.

Rainer Hutterer

Paracrocidura graueri GRAUER'S LARGE-HEADED SHREW

Fr. Crociodure à grande tête de Grauer; Ger. Grauers Großkopfspitzmaus

Paracrocidura graueri Hutterer, 1986. Bonn. Zool. Beitr. 37: 81. Sibatwa, Itombwe Mts, DR Congo. 2000 m.

Taxonomy Synonyms: none. Chromosome number: not known.

Description Medium-sized shrew. Pelage short and dense. Pelage uniform in colour; dorsal and ventral pelage dark brown (presumably – faded in the only specimen). Ears conspicuous but short, not concealed by pelage. Fore- and hindfeet pale and covered by very short hairs. Tail of medium relative length (ca. 55% of HB), unicoloured, paler than dorsal pelage; pilosity ca. 80%. Skull with a relatively long braincase and long rostrum. First incisor long and hooked. Third molar wide. Nipples: not known.

Geographic Variation None recorded.

Similar Species

Paracrocidura maxima. Skull perhaps shorter (CI: 25.9 [25.1–26.9] mm); toothrow shorter (I^1-M^3 : 12.3–13.6 mm). Allopatric.
P. schoutedeni. Tail shorter (T: 34.5 [33–38] mm); hindfoot perhaps shorter (HF: 11.3 [10–13] mm). Allopatric.

Distribution Endemic to Africa. Afromontane–Afroalpine BZ. Known only from the type locality in the Itombwe Mts, E DR Congo.

Habitat Montane forest.

Abundance Very rare; known only from the holotype.

Remarks Apparently no other information available.

Conservation IUCN Category: Data Deficient.
Formerly assessed as Critically Endangered.

Measurements

Paracrocridura graueri

HB: 83 mm

T: 46 mm

HF: 14.8 mm

E: 6.4 mm

WT: n. d.

CI: 27.7 mm

GWS: 12.2 mm

I¹–M³: 14.2 mm

Itombwe Mts, E DR Congo holotype; Hutterer 1986c)

Key Reference Hutterer 1986c.

Rainer Hutterer



Paracrocridura graueri

Paracrocridura maxima GREATER LARGE-HEADED SHREW

Fr. Crocidure à grande tête à dents blanches; Ger. Größere Großkopfspitzmaus

Paracrocridura maxima Heim de Balsac, 1959. Rev. Zool. Bot. Afr. 59: 26. Tshibati, E DR Congo.

Taxonomy Originally described as a subspecies of *Paracrocridura schoutedeni*, but regarded as a full species by Hutterer (1986c, 2005a). Genetic data suggest that the genus *Paracrocridura* is a monophyletic clade, recently derived from the genus *Crocridura* (Quéroutil *et al.* 2001). Synonyms: none. Chromosome number: not known.

al. 2003) and Mgahinga–Gorilla N. P. (Uganda), Nyungwe N. P. (Rwanda) and Kibira N. P. (NW Burundi); and on the western side from Kahuzi-Biega N. P. (E DR Congo). Altitude range: mostly 1600–2680 m, with one record from Irangi, E DR Congo (850 m).

Description Large blackish shrew with dense, very short pelage; hairs 3–4 mm. Dorsal pelage and ventral pelage blackish-grey or dark grey-brown. Head large, with small ears. Tail of medium relative length (ca. 53% of HB), very fat, with long (4–5 mm) bristle hairs; pilosity 90%. Skull: braincase box-shaped in dorsal view (figured in Thorn and Kerbis Peterhans 2009); incisors spade-like at tip. Temporalis muscles well developed. Nipples: 0 + 1 = 2, inguinal and bifurcate.

Geographic Variation None recorded.

Similar Species

Paracrocridura graueri. Skull perhaps longer (CI: 27.7 mm); tooththrow perhaps longer (I¹–M³: 14.2 mm, n = 1). Allopatric.

P. schoutedeni. Hindfoot shorter (HF: 11.3 [10–13] mm); tail almost always shorter (T: 34.5 [33–38] mm); skull shorter (CI: 22.1–23.2 mm). Allopatric.

Distribution Endemic to Africa. Afroalpine–Afroalpine BZ. Recorded only in eastern Africa on both sides of the Albertine Rift Valley. Recorded on the eastern side from Rwenzori Mts (DR Congo and Uganda). Bwindi-Impenetrable N. P. (Kasangaki *et*



Paracrocridura maxima

Habitat Mostly recorded from montane forest (with one record from Irangi in lowland rainforest). Specimens have been captured in understorey habitats in primary and secondary forest, *Brillantasia* swamp forest, and beside a stream running through *Cyperus* swamp. Not recorded in alpine habitats (e.g. above treeline).

Abundance Probably rare – only about 19 specimens known at the present time. May be locally common as suggested by three specimens captured at Lwiro Falls (E DR Congo) during three days. Represented 3.4% of the soricid fauna ($n = 117$; 14–15 spp., captured in conventional traps and pitfall traps) in Bwindi-Impenetrable N. P. (Thorn & Kerbis Peterhans 2009) and 0.5% ($n = 207$; 17–18 spp.) in Kibira N. P., Burundi at 1600–2459 m.

Remarks A captive ♀ (WT: 20.6 g) gave birth to a full-term foetus (1.6 g, crown–rump length = 25 mm) on 4 April 1996 (Ruhija, Uganda). This ♀ was remarkable in the possession of a single pair of enlarged and bifurcate teats.

Conservation IUCN Category: Near Threatened.

This species is threatened because of its rarity and very restricted geographic range; in this respect it is similar to the other endemic species of the Albertine Rift Valley.

Measurements

Paracrocidura maxima

HB: 92.1 (80–97) mm, $n = 15$

T: 42.8 (37–48) mm, $n = 15$

HF: 15.1 (14–16) mm, $n = 15$

E: 6.2 (4–8) mm, $n = 9$

WT: 17.1 (16–21) g, $n = 6$

CI: 25.9 (25.1–26.9) mm, $n = 15$

GWS: 11.5 (10.9–11.9) mm, $n = 14$

I¹–M³: 13.2 (12.3–13.6) mm, $n = 16$

Burundi, DR Congo, Rwanda, Uganda (FMNH, AMNH, MUMZ, Hutterer 1986c)

Key Reference Hutterer 1986c.

Julian C. Kerbis Peterhans

Paracrocidura schoutedeni SCHOUTEDEN'S LARGE-HEADED SHREW (LESSER LARGE-HEADED SHREW)

Fr. Crocidure à grande tête de Schouteden; Ger. Schoutedens Großkopfspitzmaus

Paracrocidura schoutedeni Heim de Balsac, 1956. Rev. Zool. Bot. Afr. 54: 137. Tshimbulu, Lubondaie, Kasai, DR Congo.

Taxonomy The subspecies *camerunensis* from Mt Cameroon (Heim de Balsac 1968b) is not currently recognized (Hutterer 2005b). Synonyms: *camerunensis*. Subspecies: none. Chromosome number: not known

Description Small–medium shrew with short dense pelage. Dorsal and ventral pelage blackish-brown. Short, robust snout. Ears small and covered with short, fine grey hairs. Hindfeet short with naked soles. Tail of medium relative length (ca. 50% of HB), thick; pilosity ca. 100%. Incisors with laterally flattened cutting edge. Nipples: not known.

Geographic Variation None recorded.

Similar Species

Paracrocidura graueri. Tail longer (T: 46 mm, $n = 1$); hindfoot perhaps longer (HF: 14.8 mm, $n = 1$). Allopatric.

P. maxima. Hindfoot longer (HF: 15.1 [14–16] mm); tail almost always longer (T: 42.8 [37–48] mm); skull longer (CI: 25.1–26.9 mm). Allopatric.

Crocidura caliginea: Tail with only a few long hairs (pilosity 20–30%); rostrum shorter.

Distribution Endemic to Africa. Rainforest BZ (mainly West Central and South Central Regions). Recorded from Cameroon, Congo, Gabon, Central African Republic and S DR Congo (Hutterer 1986c).

Habitat Found in a variety of forest and forest edge habitats at mid-altitudes up to ca. 950 m (Hutterer 1986c). Considered as a typical member of the fauna of the lowland rainforest of the Congo Basin

(Goodman & Hutterer 2004). On Mt Doudou, Gabon, occurred at 110 m and 375 m, but not at 625 m (Goodman & Hutterer 2004).

Abundance May be quite common and, where present, represents 8–24% of shrews in various communities as follows: 11% at Belinga-Makokou (third most numerous after *Crocidura poensis* [48%] and *Sylvisorex johnstoni* [25%]; $n = 160$; 11 spp.; Brosset



Paracrocidura schoutedeni

1988); 24% at Moueva, SW Gabon (second commonest species after *S. johnstoni* [40%]; $n = 144$; 9 spp.; Nicolas *et al.* 2003); 13% at Minkébé Forest, Gabon (= third commonest species [with one other]; $n = 30$; 11 spp.; Goodman *et al.* 2001); 8% at Korup N. P. Cameroon (= third commonest species; $n = 24$; 9 spp.; Hutterer & Schlitter 1996); 11% at Mt Doudou, Cameroon (= fourth commonest species; $n = 56$ shrews captured at 110 m and 375 m; 9 spp.; Goodman & Hutterer 2004); 10% at Mt Alen, Gabon (third commonest species; $n = 40$; 8 spp., Lasso *et al.* 1996); and 11% at Ngotto, Central African Republic (fourth commonest species; $n = 81$; 11 spp.; Morvan *et al.* 1999).

Remarks Embryo number: 1.7 (1–2), $n = 4$ (Beling-Makokou, Gabon; Brosset 1988). Capture rates were changeable throughout the year in Ngotto, Central African Republic, with peak abundance recorded during May and Nov (Barrière & Nicolas 2000). It was the second most abundant species of shrew in small carnivore scats (frequency of occurrence: 24.1% of 311 scats) collected in Dzanga-Sangha, Central African Republic (Ray & Hutterer 1995, Ray 1998).

Conservation IUCN Category: Least Concern.

Measurements

Paracrocidura schoutedeni

HB: 75.7 (65–90) mm, $n = 6$

T: 34.5 (33–38) mm, $n = 6$

HF: 11.3 (10–13) mm, $n = 6$

E: 7.3 (5.5–8) mm, $n = 5$

WT: 7, 10 g, $n = 2$

CI: 22.8 (22.1–23.2) mm, $n = 4$

GWS: 10.0 (9.8–10.2) mm, $n = 4$

I¹–M³: 11.2 (11.0–11.5) mm, $n = 4$

Cameroon, Gabon and DR Congo (Hutterer 1986c, Hutterer & Schlitter 1996)

Key References Heim de Balsac 1956b; Hutterer 1986c.

Justina C. Ray & Rainer Hutterer

GENUS *Ruwenzorisorex*

Rwenzori Shrew

Ruwenzorisorex Hutterer, 1986. Z. Säugetierk. 51: 260. Type species: *Sylvisorex suncoides* Osgood, 1936.



Ruwenzorisorex suncoides.

Ruwenzorisorex is a monotypic genus distributed in the Albertine Rift Valley (E DR Congo, W Uganda, Rwanda and Burundi). The single species lives in shallow streams and swamps in montane forest.

Ruwenzorisorex is the only genus of African shrews with characteristics for a semi-aquatic life-style, such as water-repellent pelage, reduced ears, a slightly bicoloured tail and an enlarged brain with an expanded foramen magnum (Stephan *et al.* 1991). In some respects it resembles *Sylvisorex*, with which it was previously associated (Osgood 1936) – both species have a similar external appearance (naked tail) and possess an extra unicuspid tooth. However, *Ruwenzorisorex* is larger than any species of *Sylvisorex*, the upper and lower teeth are heavy and unique in shape (Hutterer 1986d), the lower first incisor is without denticulations and the skull is dorsoventrally compressed and concave when viewed laterally (Figure 16). Dental similarity with *Suncus* (small and medially inset fourth upper unicuspid, P⁴) was first pointed out by Osgood (1936), despite his allocation of the species to *Sylvisorex*. The close relationship between *Suncus* and *Ruwenzorisorex* has since been supported with

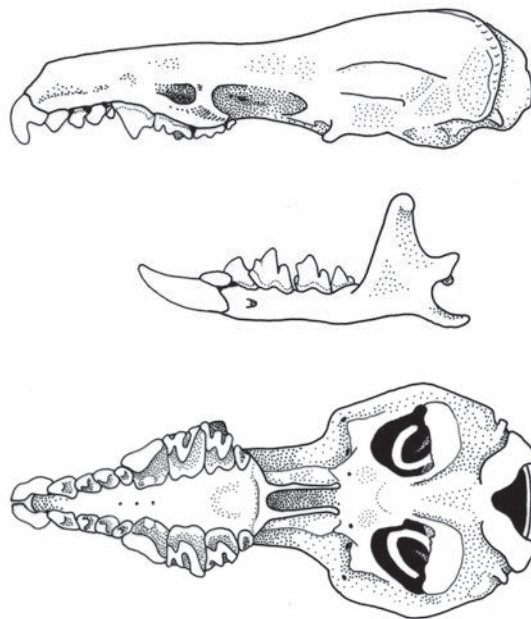


Figure 16. Skull and mandible of *Ruwenzorisorex suncoides* (ZFMK 148267).

genetic data (Quéroutil *et al.* 2001). Additional information and a key to the genus are given in Thorn & Kerbis Peterhans (2009) (see also Tables 7 and 8).

Rainer Hutterer & Julian C. Kerbis Peterhans

Ruwenzorisorex suncoides RWENZORI SHREW

Fr. Musaraigne du Rwenzori; Ger. Rwenzori-Spitzmaus

Ruwenzorisorex suncoides (Osgood, 1936). Field Mus. Nat. Hist. Publ., Zool. ser. 20: 217. Kalongi, western slope of Rwenzori Mts, E DR Congo. 7000 ft (2135 m).

Taxonomy Originally described as a species of *Sylvisorex* (Osgood 1936). Transferred to the new genus *Ruwenzorisorex* by Hutterer (1986d). More recently aligned with *Suncus* (Quérrouil *et al.* 2001) on the basis of molecular characteristics. Synonyms: none. Chromosome number: not known.

Description Large dark shrew with small ears and woolly, water-repellent pelage. Dorsal pelage blackish-grey, ticked with paler grey; hairs slate-grey at base, brownish at tip; 6 mm long. Long, pale-coloured guard hairs on rump. Ventral pelage slate-grey; hairs grey at base, pale grey or brownish at tip. Muzzle swollen, with well-developed facial vibrissae. Eyes small. Ears small, not protruding from pelage. Fore- and hindfeet without any special adaptations for aquatic life; claws 1–1.3 mm in length. Tail relatively short (ca. 40% of HB), slightly bicoloured, dark above, paler below especially at terminal end, and without long bristle hairs. Skull elongated, dorsoventrally compressed, concave profile in lateral view, with four unicuspid (I^2 , I^3 , C, P^3); lower incisor smooth, without denticulations (see also Table 8 and genus profile; Thorn and Kerbis Peterhans [2009]). Nipples: not known.

Geographic Variation None recorded.

Distribution Endemic to Africa. Afromontane–Afroalpine BZ on both sides of the Albertine Rift Valley extending marginally into the Rainforest BZ of E DR Congo. Recorded from Irangi, Kalongi and Rwenzori Mts (E DR Congo), Uwinka (Nyungwe N. P., Rwanda), Bwindi-Impenetrable N. P. (Uganda) and Bururi Forest and Kibira N. P. (Burundi). Not recorded from the Ugandan side of the Rwenzori Mts.

Habitat Found near clear, shallow streams in montane forest (usually 1800–2350 m) but one record at 850 m (Irangi, E DR Congo). Also typically found by clear streams overhung with herbaceous undergrowth. The forested stream habitats where it has been collected in Burundi are characterized by scattered *Syzygium*, *Symphonia*, *Arundinaria* (bamboo) with *Cyathea* (tree ferns) and *Tabernaemontana*. The first record in Uganda was from a stream meandering through *Brillantasia* swamp (Bwindi-Impenetrable N. P., Uganda; Kasangaki *et al.* 2003). Not recorded from alpine habitats.

Abundance Extremely rare, known by only about ten specimens. This status is probably accurate because the large size of this species allows it to be caught by traditional collecting methods.

Remarks Semi-aquatic. Found exclusively along clear shallow streams (less than 20 cm deep) in montane forests. Exclusively nocturnal. Attracted to animal baits (e.g. fish and worms). The short dense water-repellent pelage, bicoloured tail and small ears are typical of semi-aquatic small mammals, but other characteristics often associated with such mammals (e.g. feet fringed with stiff hairs, webbed feet, keel on the tail) are not present. The enlarged medulla oblongata and enlarged foramen magnum are associated with an



Ruwenzorisorex suncoides

expanded trigeminal nerve system, which provides enhanced tactile acuity to the facial vibrissae when foraging in shallow streams; such an adaptation is also typical of other semi-aquatic mammals (Stephan *et al.* 1991).

Conservation IUCN Category: Vulnerable.

Considered to be threatened because of its rarity, very restricted geographic range, and specific micro-habitat requirements. The conservation threats to this species are similar to those of other endemic species of the Albertine Rift Valley. Of particular concern for this species are the detrimental effects of coltan mining on the streams in E DR Congo and NW Burundi.

Measurements

Ruwenzorisorex suncoides

HB: 96.1 (84–102) mm, n = 9

T: 64.2 (55–70) mm, n = 9

HF: 17.3 (16–19) mm, n = 9

E: 7.3 (7–8) mm, n = 6

WT: 19.8 (18–23) mm, n = 6

CI: 25.3 (24.4–25.9) mm, n = 5

GWS: 11.5 (11.1–12.2) mm, n = 5

I^1 – M^3 : 11.3 (10.7–11.7) mm, n = 7

Burundi, DR Congo, Uganda (FMNH; J. C. Kerbis Peterhans unpubl.)

Key Reference Hutterer 1986d.

Julian C. Kerbis Peterhans

GENUS *Scutisorex*

Armoured Shrew (Hero Shrew)

Scutisorex Thomas, 1913. Ann. Mag. Nat. Hist., ser. 8, 11: 321. Type species: *Sylvisorex somereni* Thomas, 1910.

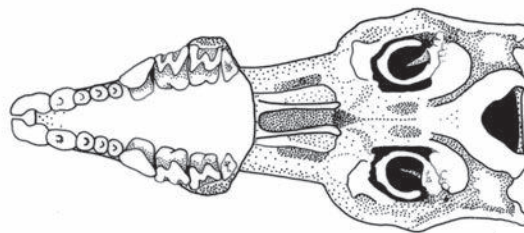
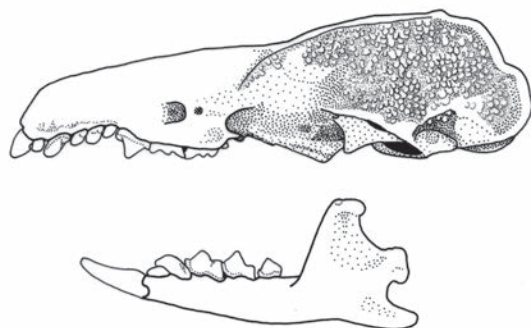


Figure 17. Skull and mandible of *Scutisorex somereni* (ZFMK 68.514).

A monotypic genus, belonging to the subfamily Crocidurinae (although, because of its very special characteristics, Heim de Balsac & Bourlière [1955] placed it in its own subfamily, Scutisorinae). The genus occurs only in rainforests and montane forests of NE DR Congo, Uganda, Rwanda and Burundi.

The genus is characterized primarily by the unique structure of the vertebral column (see species profile). Other characteristics include large size, and large skull sculptured with irregular bony ripples on the dorsal surface of the braincase (Figure 17). The teeth show similarities to those of *Sylvisorex*: comparatively small size, and lower horizontally placed incisors with denticulations. Dental formula: $I^{3/1}, C^{1/1}, P^{2/1}, M^{3/3} = 30$. There are four

upper unicuspid teeth behind I^1 (I^2, I^3, C, P^2); P^3 is well developed and molar-like with cusps. Further characteristics are given in the species profile.

Although *Scutisorex* has evolved to a giant shrew, it shows fewer modifications than the giant species of *Crocidura* and *Suncus* (Heim de Balsac & Lamotte 1957). Its origin can be found in the archaic evolutionary line of *Sylvisorex*, but the early point of divergence is a matter of speculation. Genetical studies place *Scutisorex* next to *Sylvisorex* (Quérouil *et al.* 2001).

There is a single species, *Scutisorex somereni*.

Fritz Dieterlen

Scutisorex somereni ARMoured SHREW (HERO SHREW)

Fr. Musaraigne cuirassée; Ger. Schildspitzmaus (Panzerspitzmaus)

Scutisorex somereni (Thomas, 1910). Ann. Mag. Nat. Hist., ser. 8, 6: 113. Kyetume, near Kampala, Uganda.

Taxonomy Originally described in the genus *Sylvisorex*. *Scutisorex somereni* is endemic to the Albertine Rift Valley (and nearby regions) and considered as the only species in the genus. The form *congicus* (Thomas 1915) from NE DR Congo was described as ‘probably only superficially distinct from the nominate race’ (Heim de Balsac & Lamotte 1957, Heim de Balsac & Meester 1977) and is now considered as a synonym. Synonyms: *congicus*. Subspecies: none. Chromosome number: not known.

Description Very large shrew with a unique and extraordinary vertebral column. Dorsal pelage long (15–17 mm on rump), dense, soft and woolly with projecting guard hairs. Dorsal pelage blackish-grey with a brownish (but variable) tinge, hairs sometimes with white tip. Ventral pelage similar to dorsal pelage, rather uniform in colour. In most adult specimens, dorsal and ventral pelages may have yellowish and brownish stains, mostly irregular in shape, due to secretions from the lateral glands. Muzzle, ears, upper surface of fore- and hindfeet blackish-brown. Tail relatively long (ca. 63% of HB), darkly pigmented and with short fine blackish hairs; pilosity 0%. Skull large and robust, with enormously developed lambdoid crests projecting posteriorly

beyond the level of the condyles (forming a ‘shield’ over the back of the skull). In old individuals, low sagittal crest present on the cranium. On both sides of the crest, the surface is not smooth, but sculptured with irregular bony ripples (as in *C. goliath* to a lesser extent). Nipples: $0 + 2 = 4$. The special characteristics of the vertebral column (see below) are not visible exteriorly.

Geographic Variation None recorded.

Distribution Endemic to Africa. Rainforest BZ (East Central Region), Afromontane–Afroalpine BZ (Albertine Rift Valley) and parts of Eastern Rainforest–Savanna Mosaic. Distribution disjunct. Recorded from NE and E DR Congo (Kisangani, Bafwasende, Medje, Ituri, Irangi, Semliki R., Rutshuru, mountains west of L. Kivu); Rwanda (Rugege Forest, now Nyungwe Forest); NW Burundi (Kibira N.P.); and Uganda (east of L. Albert, near Semliki R., east of L. Edward, west of the Victoria Nile including near Kampala) (Allen 1917b, Pirlot 1964, Rahm & Christiaensen 1963, Rahm 1966, Elbl *et al.* 1966, Kingdon 1974, Dieterlen & Heim de Balsac 1979, Hutterer *et al.* 1987, Cullinane & Aleper 1998, Dudu *et al.* 2005).



Habitat Lowland and montane forests from ca. 400 m (near Kisangani, DR Congo) to ca. 2500 m (highlands of E DR Congo and Rwanda). Also recorded, less frequently, from secondary lowland forests and montane bamboo (Dieterlen & Heim de Balsac 1979). Allen (1917b) reported similar habitats in NE DR Congo. Not recorded from open habitats, or from swamps and marshes. Kingdon (1974) recorded the habitat in Uganda as mainly swampy, but the species is not found in such habitats in DR Congo.

Abundance Uncommon. Comprised 4.8% (seven individuals) of small mammals trapped in montane forest at Rugege Forest, Rwanda (in Aug and Sep) (Dieterlen & Heim de Balsac 1979). In Masako Forest, DR Congo, comprised 7% of shrews (5 of 72; 9 spp.) and was the equal fourth commonest species (Dudu *et al.* 2005).

Adaptations The structure of the vertebral column is unique. Like most other mammals *Scutisorex* has seven cervical, 14 thoracic and five sacral vertebrae; but 11 (rather than the usual five) lumbar vertebrae. The vertebral column is heavily and strongly built. Although the cervical vertebrae are similar in structure to those of other mammals, the vertebrae from about the mid-thoracic region to last lumbar vertebra (and especially in the mid-lumbar region) are highly modified. The unique features of each of these vertebrae

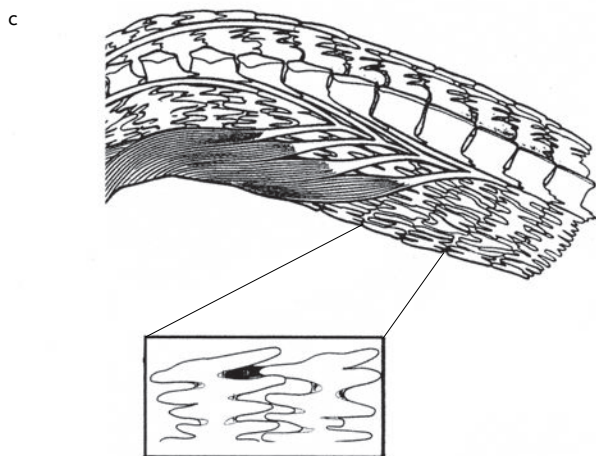


Figure 18. *Scutisorex somereni*. (a) Skeleton. (b) Myology. (c) Details of lumbar region of vertebral column to show the interlocking pattern of tubercles (after Cullinane & Aleper 1998).

are increase in size and diameter, and profuse development of spines (called trabeculae or tubercles) arising mainly on the lateral sides of each vertebra. The spines face forwards and backwards and interlock with each other and with adjacent vertebrae (Figure 18). The arrangement provides great strength. The relative mass of the spine (3.97% of body mass) is considerably larger than in other mammals (0.69–1.58% in 12 other species of small mammals) (Cullinane *et al.* 1998). The increase in size and mass, and the unique structure, allows the spine to resist large compressive forces and to resist axial torsion. The ribs have larger diameters than expected for an animal of this size, and show similarities in structure to those of fossorial small mammals. Paradoxically, the appendicular skeleton (limbs) does not show any modifications for handling heavy loads or compression. The unique structure of the vertebrae has resulted in modifications of some of the spinal muscle groups (Cullinane & Aleper 1998). Locomotion in this species is ‘serpentine’ and unlike that of other shrews; undoubtedly the highly modified vertebral column reduces mobility to some extent (particularly in the sagittal plane). When standing, the vertebral column is slightly arched, especially behind the shoulder blade where the thickened part of the vertebral column begins, and consequently the rib cage is more vertical than horizontal. The strength and protective ability of the vertebral column is well illustrated by Herbert Lang (in Allen 1917b) who described how a local man (of about 160 pounds) balanced himself on one leg on the back of an Armoured Shrew for several minutes; when released, the shrew shook itself and seemed none the worse for the experience. Although Kingdon (1974) suggested that the structure of the vertebral column may be due to the fact that Armoured Shrews live in swamps and need to get the body well clear of the ground (as do other small mammals without any special modifications to the vertebral column), Ahmed & Klima (1978), Seip (1980), Schäfer (1980) and Cullinane *et al.* (1998) concluded that there is no known satisfactory ecological, behavioural or functional explanation for this unique vertebral morphology.

Studies on the embryos of Armoured Shrews show that the special characteristics of the vertebral column are visible in embryos. The enlarged vertebrae and tubercles are formed as cartilage and then ossified (as occurs during the development of any other mammal); they are not formed as secondary ossifications later in life (Ahmed & Klima 1978), nor because of a modified calcium–phosphorus metabolism as suggested by Heim de Balsac & Lamotte (1957).

The intestine is longer than in any other species of shrew (396.0 ± 43.5 mm, $n = 5$), a condition partly related to the large size of the shrew. Of greater interest is the high intestine/body length ratio of 3.7, which is considerably greater than for the other seven other species of smaller shrews (typically 2.1–2.9) in Masako Forest, DR Congo (Dudu *et al.* 2005). The significance of the relatively long intestine is uncertain.

Foraging and Food During foraging ‘the deeply grooved nose is moved in every direction and continually quivering ... the undersides of leaves and even stones are inspected. Fair sized pebbles, pieces of bark and decayed wood [are] turned over and pulled away with the assistance of the incisors’ (Herbert Lang in Allen 1917b). Dewdrops may be licked from the margins of the leaves or grasses (Allen

1917b). Diet, as indicated by analysis of stomach contents ($n = 5$), includes earthworms (100% frequency of occurrence); Diptera larvae, Diplopoda, Araneae (all 60%); adult Coleoptera, Formicidae, Acari (all 40%); and Heteroptera, Isoptera, Blattodea, Acrididae, Chiloptera (all 20%) (Dudu *et al.* 2005; Masako Forest, DR Congo). Of nine species of shrews in Masako Forest, DR Congo, only *S. somereni* ate earthworms. Prey size included a greater proportion of prey >30 mm in length than for any other species of shrew (Dudu *et al.* 2005).

Social and Reproductive Behaviour Scent marking behaviour appears to have high intra-specific (and possibly inter-generic) importance. On each side of the rump, adult individuals have a gland producing a strong-smelling yellow secretion (see Description). The odour is very characteristic and can be detected by humans at a distance of 5 m, e.g. when trapped or when running on the forest floor (Dieterlen & Heim de Balsac 1979). Captive specimens show very conspicuous marking postures and rhythmic rubbing with the hindquarters, suggestive of territorial marking (Kingdon 1974). The behavioural characteristics of Armoured Shrews are unknown. However, they have ‘a mild disposition’, which could suggest that they are more social than other species of shrews (Kingdon 1974) but this needs confirmation.

Reproduction and Population Structure Reproduction in rainforest habitats of E DR Congo has been recorded from Dec to Aug (no data from Sep to Nov). Pregnancy rate was higher during wet season (Dec–Apr; nine ♀♀ pregnant/lactating, three non-pregnant) than during the dry season (Jun–Aug; seven ♀♀ pregnant/lactating, nine non-pregnant). Embryo number: 1.85 (1–3), $n = 14$ ♀♀; mode 2 (Dieterlen & Heim de Balsac 1979). In Uganda, in May, two ♀♀ were lactating and three ♀♀ were not lactating (Kingdon 1974).

Predators, Parasites and Diseases Ticks (*Ixodes alluaudi* and *Ixodes* sp.) have been recorded from this species in Rugege Forest, Rwanda (Elbl *et al.* 1966).

Conservation IUCN Category: Least Concern.

Measurements

Scutisorex somereni

HB: 136.5 (120–153) mm, $n = 40$

T: 86.7 (76–99) mm, $n = 40$

HF: 23.6 (22–27) mm, $n = 40$

E: 12.7 (9–16) mm, $n = 40$

WT: 65.1 (42–92) g, $n = 40$

CI: 33.1 (32.0–34.9) mm, $n = 20$

GWS: 14.4 (13.4–15.1) mm, $n = 20$

I¹–M³: 14.7 (13.8–15.6) mm, $n = 20$

Kahuzi-Biega region, E DR Congo (Dieterlen & Heim de Balsac 1979), SMNS, ZFMK

Key References Allen 1917b; Cullinane *et al.* 1998; Dieterlen & Heim de Balsac 1979.

Fritz Dieterlen & D. C. D. Happold

GENUS *Suncus*

Dwarf Shrews

Suncus Ehrenberg, 1832. In: Hemprich and Ehrenberg. Symb. Phys. Mamm. 2: k. Type species: *Suncus sacer* Ehrenberg, 1832 (= *Sorex murinus* Linnaeus, 1766).



Suncus lixus.

The genus *Suncus* contains 18 species worldwide, of which nine species occur in Africa (Hutterer 2005b) – one of which has probably been introduced. The genus has a large geographic range, which also includes the Middle East, Madagascar, India, Sri Lanka, South-East Asia and China. In Africa, the distribution of each species is limited in extent and patchy, and the genus is not represented in western Africa nor in arid habitats.

The genus (in Africa) is characterized by very small size (all species weigh less than 8 g and the two smallest weigh only 1.5–2.5 g), short or long tail (ca. 40–65% of HB) with long hairs (as in *Crociodura* and *Paracrociodura*), large naked ears and small eyes. The skull is small with flattened braincase and four upper unicuspid (although the fourth unicuspid is often very small and may be vestigial). Dental formula: $I^{3/2}, C^{1/0}, P^{2/1}, M^{3/3} = 30$ (Figure 19). There are two exceptions to the above: (1) *Suncus murinus*, an Asiatic member of the genus, which is presumed to have been introduced in historical times into coastal East Africa, is very large (weight 67–105 g); (2) *Suncus megalura* has a relatively extremely long tail (ca. 118% of HB), long hindfeet and is scansorial; this species has previously been allocated to *Sylvisorex* (e.g. Hutterer 1993), but genetic data show that it should be allocated to *Suncus* (Quérrouil *et al.* 2001). See also Table 7.

These shrews are capable of living in a wide range of habitats, although moister habitats are preferred. The small size of most species suggests that thermoregulation is likely to be a major determinant of ecology and metabolism. Several species are associated with termitaria, where a moist, warm and constant environment (and plenty of food) provide a suitable environment for such a small

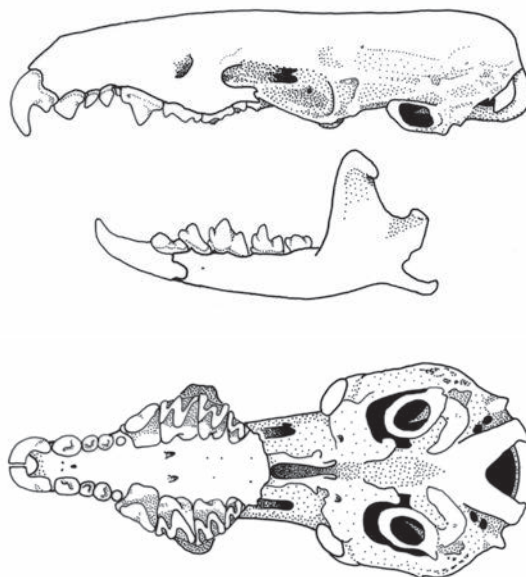


Figure 19. Skull and mandible of *Suncus murinus* (ZFMK 84.550).

mammal. Physiological studies on the small species of the genus would be of great interest.

Phylogenetically, *Suncus* is placed between *Crociodura* and *Sylvisorex* (Heim de Balsac & Lamotte 1957). The three genera are closely related and similar. Some authors (e.g. Harrison & Bates 1991) suggest that *Suncus* is retained as a matter of convenience and that the only real difference between *Suncus* and *Crociodura* is the possession of the small fourth upper unicuspid in *Suncus* – and this tooth is often vestigial. Quérrouil *et al.* (2001) suggest that, on the evidence of mtDNA data, *Suncus* originated in Africa from a *Sylvisorex*-like ancestor, perhaps 7–9 mya. Because *Sylvisorex* is endemic to Africa, it is likely that *Suncus* evolved in Africa, and later migrated to Asia. The oldest fossils of *Suncus*, from 3–5 mya, are from East and South Africa (Butler 1998), and are much older than any from Europe or Asia. The alternative view (Butler *et al.* 1989) is that *Suncus* evolved in Asia and migrated to Africa.

The species in the genus are distinguished by size, relative length of the tail, habitat and distribution.

D. C. D. Happold

Suncus aequatorius TAITA DWARF SHREW

Fr. Pachyure du Taita; Ger. Taita-Zwergspitzmaus

Suncus aequatorius (Heller, 1912). Smithsonian Misc. Coll. 60, 12: 4. Summit of Mt Sagalla, Taita Hills, Kenya.

Taxonomy Originally described as a subspecies of *Pachyura lixa* by Heller (1912) and subsequently transferred to genus *Suncus* (see Heim de Balsac & Meester 1977). Referred to as a subspecies of *S. lixus* by

Aggundey & Schlitter (1986), and as a synonym of *S. lixus* by Hutterer (1993). Now considered as a full species (Oguge *et al.* 2004, Hutterer 2005b). Synonyms: none. Chromosome number: not known.

Description Small–medium shrew with soft, smooth short pelage. Dorsal pelage grey; hairs grey at base, brown at tip. Flanks similar to dorsal pelage. Ventral pelage pale grey. Chin and throat similar in colour to ventral pelage. Head broad (greatest width similar to incisor–molar length). Muzzle pink, covered with long (18.5 mm) clear white vibrissae. Eyes small. Ears large, oval and pale, almost white and bare; held laterally and backwards from head at an oblique angle. Fore- and hindfeet each with five claws. Forelimbs below ‘elbow’ covered with short fine white hair; soles naked, toes with white claws. Hindlimbs below ‘knee’ covered with short fine white hair; conspicuous white claws. Tail thin and relatively long (ca. 78% of HB), covered by dirty whitish fine fur along its length; fine white scales ventrally, decreasing in density laterally and even more so dorsally; pilosity at least 50%. Males tend to be larger (on average) than ♀♀ (see Measurements). Nipples: not known.

Geographical Variation None recorded.

Similar Species

Suncus lixus. Dorsal pelage greyish-brown. Tail shorter (T: 36–51 mm) and relatively shorter (64% of HB), brown above, whitish or yellow below; pilosity 80–100%.

S. megalura. Head and body smaller (HB: 50–65 mm); tail much longer (T: 82–97 mm) and relatively much longer (ca. 118% of HB). Perhaps parapatric in SE Kenya.

Distribution Endemic to eastern Africa. In SE Kenya, recorded only from two locations: Mt Sagalla (1500 m; 03° 30' S, 38° 35' E), and Chawia Forest (1600 m; 03° 28' S, 38° 28' E) in the Taita Hills (Oguge *et al.* 2004). Not recorded from the other 12 of 14 locations sampled (1400–2228 m) (Oguge *et al.* 2004). Perhaps occurs in NE Tanzania (Hutterer 2005b, not mapped).

Habitat Disturbed remnant forest in highland regions (1500–1600 m), where annual rainfall is more than 1000 mm (Oguge *et al.* 2004); dominant vegetation includes *Tabernaemontana stapfiana* (tree) and *Dracaena steudner* (shrub).

Abundance Common in the highly degraded forests of Mt Sagalla, comprising 69% of captures (11 of 16 shrews captured; 4 spp.). Rare in the Dabida massif with captures only in Chawia Forest (1 of 72 shrews captured; 10 spp.) (Oguge *et al.* 2004).

Remarks Distribution is disjunct and abundance (where present) is varied. The commonest species of syntopic shrews in Chawia Forest are *Crocidura hildegardae* and *C. jacksoni* (Oguge *et al.* 2004). *Suncus aequatorius* is considerably larger than *S. lixus* (condyloincisive length 21.3 mm [cf. 19.7 mm in *S. lixus*], tail 51–67 mm [cf. 36–51 mm in *S. lixus*]; see Meester & Lambrechts 1971), and geographically separated by some 800 km from the northernmost population of *S. lixus* in the Udzungwa Mts, S Tanzania (Stanley & Hutterer 2007).



Suncus aequatorius

Conservation IUCN Category: Critically Endangered.

Reduction in the size and extent of forest fragments has probably reduced the geographic range of the species in recent years.

Measurements

Suncus aequatorius

HB (♂♂): 76.4 (66–85) mm, n = 10

HB (♀♀): 80, 85 mm, n = 2

T (♂♂): 56.7 (53–67) mm, n = 10

T (♀♀): 51, 55 mm, n = 2

HF (♂♂): 12.8 (11.2–13.6), n = 10

HF (♀♀): 11.5, 14 mm, n = 2

E (♂♂): 7.4 (5.5–9.5) mm, n = 10

E (♀♀): 6.4, 7.3 mm, n = 2

WT (♂♂): 8.9 (7.5–11) g, n = 10

WT (♀♀): 8, 9.5 g, n = 2

CI (♂♂): 21.3, 21.3 mm, n = 2

CI (♀♀): n. d.

GWS (♂♂): 9.2, 9.3 mm, n = 2

GWS (♀♀): n. d.

I¹–M³ (♂♂): 9.2, 9.2 mm, n = 2

I¹–M³ (♀♀): n. d.

Taita Hills, Kenya (Oguge *et al.* 2004), NMK

Key Reference Oguge *et al.* 2004.

N. Oguge & Rainer Hutterer

***Suncus etruscus* ETRUSCAN DWARF SHREW (PYGMY WHITE-TOOTHED SHREW)**

Fr. Pachyure étrusque; Ger. Etrusker-Zwergspitzmaus

Suncus etruscus (Savi, 1822). Nuovo Giorn. de Letterati, Pisa 1: 60. Pisa, Italy.

Taxonomy Originally described in the genus *Sorex*. African specimens are considered to be the nominate form. Synonyms: none in Africa (but see Hutterer 2005b for extralimital synonyms). Chromosome number: $2n = 42$, $FN = 74$, $aFN = 68$ (Meylan 1968, Catalan 1984, Zima & Kral 1984).

Description Minute shrew, one of the smallest terrestrial mammals in the world (see also *S. remyi*). Dorsal pelage greyish-brown. Ventral pelage pale grey. Long hairs scattered through pelage. Eyes small. Ears large. Snout elongated with long vibrissae. Hindfeet very small (useful character for distinguishing this species from the young of larger species). Tail of relative medium length (ca. 60% of HB), same colour as body, with some scattered long hairs. Braincase flat, interorbital region narrow; mandible gracile. Nipples; not known.

Geographic Variation None recorded in Africa.

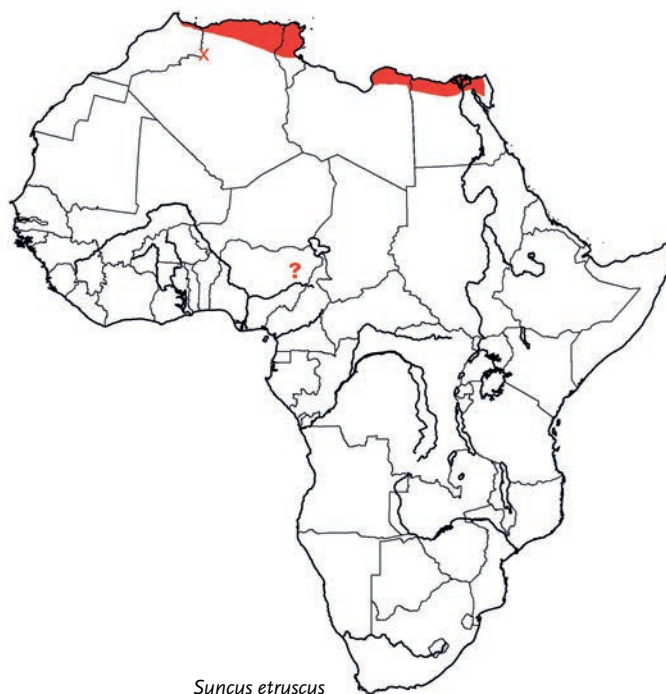
Similar Species No other species of *Suncus* occurs in northern Africa.

Distribution Mediterranean Coastal BZ. Recorded from the Mediterranean region of N Morocco, N Algeria (reaching south to the northern limit of Hauts Plateaux) and N Tunisia. Also recorded from N Libya (Cyrenaica) and N Egypt. Altitudinal range: sea level to 1000 m. Some records outside this range can be associated with synanthropic habits, e.g. at Figuig oasis in SE Morocco, Biskra oasis in Algeria and Nefta oasis in Tunisia (not shown on map). Three records need confirmation: Sherifuri and Futuk (both in N Nigeria) and Bahar-Dar (in Ethiopia; not mapped). Extraliminally known from S Europe to the Arabian peninsula, Asia Minor, the Himalaya Mts, Thailand and Yunnan (China).

Habitat Preferred habitats include abandoned olive groves, vineyards and other cultivated areas overrun by Mediterranean shrubs, but also gardens, low maquis, scrub and open forest of Mediterranean oaks and pines provided that old dry stone walls are available as shelters. Particularly common in river banks in Tunisia (Müller 1956) and near humid habitats in Algeria (Baziz *et al.* 2002). Avoids sand dunes, dense forests and intensively cultivated land.

Abundance Much less common than other species of shrews (e.g. *Crocodyrus russula* and *C. whitakeri*) living in the same area in Algeria (as assessed by trapping and in owl pellets, e.g. 1 : 7.2; Rzebik-Kowalska 1985). In Africa, greatest abundance recorded in the coastal zone of Algeria.

Adaptations More active during the night than during the day, with a peak of activity at dawn. Exhibits daily variations of weight, hypothermy and torpor; these variations are necessary regulatory

*Suncus etruscus*

mechanisms because of the small body size, high level of activity and high energy consumption (oxygen consumption: 6 ml O_2 /g/h). A respiratory rate of up to 894 breaths/minute, and a heart rate up to 1500 beats/minute, has been recorded (Fons 1975, Fons *et al.* 1997).

Foraging and Food Captive individuals eat wild-caught invertebrates and small vertebrates. They appear to feed on any species except chemical-protected arthropods (e.g. some chilopods and Heteroptera) and insects with strong chitinous exoskeletons (e.g. some Coleoptera).

Social and Reproductive Behaviour Social interactions were observed during the breeding season. During the rest of the year, animals are solitary and aggressive. Territoriality is established by vocalizations and fights.

Reproduction and Population Structure Reproductive season in Africa uncertain, but occurs in spring to autumn (Mar–Oct) in W Europe. Gestation: 27–28 days. Litter size: 3.9 (2–5). At birth, young naked and blind; HB: 4–15 mm; WT: 0.2 g. Weaned at Day 19–21. A ♀ may have up to six litters during her life. Breeding occurs only after the winter following birth. Very few animals probably survive to breed after a second winter in the wild.

Predators, Parasites and Diseases May represent 5% of the diet of Barn Owls *Tyto alba* in the coastal zone of Algeria, and up to

10% in some locations, but only 1% further inland (Rzebiak-Kowalska 1985). Also preyed on by the Pharaoh Eagle-owl *Bubo ascalaphus*, Little Owl *Athene noctua* and occasionally by some carnivores and reptiles. Apart from some ectoparasites, four helminths have been described from this shrew.

Conservation IUCN Category: Least Concern.

Etruscan shrews are vulnerable to insecticides and herbicides.

Measurements

Suncus etruscus

HB: 43.5 (40–46) mm, n = 4

T: 26.8 (25–28) mm, n = 4

HF: 7.2 (7–7.5) mm, n = 4

E: 5.1 (4.0–6.2) mm, n = 189*

WT: 1.5–2.5 g

CI: 13.2 (13.0–13.5) mm, n = 3

GWS: 5.8, 5.9 mm, n = 2

I¹–M³: 5.5 (5.4–5.5) mm, n = 4

Tunisia (Vesmanis & Vesmanis 1980)

*Specimens from western Europe

Key References Aulagnier & Thévenot 1986; Fons 1975; Kowalski & Rzebiak-Kowalska 1991; Rzebiak-Kowalska 1985; Vesmanis *et al.* 1980.

Stéphane Aulagnier & Roger Fons

Suncus hututsi HUTU-TUTSI DWARF SHREW

Fr. Pachyure des Hutus et Tutsis; Ger. Hutu-Tutsi Zwergspitzmaus

Suncus hututsi Kerbis Peterhans and Hutterer 2009. Bonn. Zool. Monog. 55: 144. Ruhondo, Kibira National Park, NW Burundi. 2040 m.

Taxonomy Synonyms: none. Chromosome number: not known.

Description Very small dark shrew. Pelage very short (hairs 1–2 mm). Dorsal pelage blackish-grey. Ventral page slightly paler. Eyes tiny. Ears visible in dorsal view. Tail of relative medium length (ca. 60% of HB), dark brown above, slightly paler below; small bristle hairs; pilosity ca. 50%. Skull very small, short upper tooththrow, four upper unicusps; mandible lightly built with short tooththrow, lower first incisor without denticulations, and low coronoid process (3.0 [range 2.9–3.2] mm). (See also key in Thorn & Kerbis Peterhans 2009.) Nipples: 0 + 3 = 6.

Geographic Variation None recorded.

Similar Species

Suncus megalura. On average larger (HB: 60.8 [50–65] mm); tail much longer (T: 82–97 mm) and relatively much longer (ca. 118% of HB); skull longer (CI: 16.8–18.6 mm). Perhaps parapatric in Burundi; mostly associated with moist savanna.

S. murinus. Much larger and heavier (HB: ca. 105–155 mm, T: 50–85 mm, WT: ca. 65–105g). Geographic distribution overlaps in Burundi; only one specimen known; commensal.

Distribution Endemic to Africa. Afromontane–Afroalpine BZ. Known only from the highlands on the east side of the Albertine Rift Valley. Recorded from Burundi (Kibira N. P.) and Uganda (Bwindi-Impenetrable N. P., Mujuzi F. R. and Kasana Kasambya F. R.; Kasangaki *et al.* 2003). Altitude range: 1170–2350 m.

Habitat Well-drained closed-canopy montane forest amidst *Dombeya joatizen* (holotype). Also recorded in upland bamboo (*Arundinaria alpina*) with mixed hardwoods, amongst forbs, sedges, grasses and *Begonia* sp. (Burundi), on the edge of a swamp beneath *Laconia* sp. (Bwindi-Impenetrable N. P., Uganda), and on dry forested slopes (Kasana Kasambya F. R., Uganda).

Abundance Extremely rare in collections, known at present by only 14 specimens. Its (apparent) rarity may be because it is very difficult to capture such a very small shrew. All known captures are from pitfall traps, a relatively recent innovation for surveys of small mammals in Africa.

Remarks Nocturnal. Although a rare species, a ♂ and ♀ have been collected in the same trapline, although not at the same time. Stomach contents (n = 3) include spiders (Araneae) and immature and adult Coleoptera (J. Boone in litt.). Ectoparasites include ticks of the families Ixodidae (larvae, on head), Trombiculidae (on ear pinnae, tail and back), Laelapidae (on back) and Glycyphagidae (on face and back) (B. O'Connor in litt.).



Suncus hututsi

Conservation IUCN Category: Vulnerable.

This species is threatened because of its rarity and very restricted geographic range; in this respect it is similar to other endemic species of the Albertine Rift Valley.

Measurements

Suncus hututsi

HB: 52.6 (44–58) mm, n = 9

T: 31.1 (28–33) mm, n = 9

HF: 8.4 (8–9) mm, n = 9

E: 5.7 (4–7) mm, n = 9

WT: 1.9 (1.7–2.4) g, n = 9

CI: 13.8 (13.3–14.2) mm, n = 9

GWS: 6.3 (6.1–6.6) mm, n = 12

I¹–M³: 5.5 (5.3–5.7) mm, n = 13

Burundi, Uganda (FMNH, MUMZ)

Key Reference Kerbis Peterhans & Hutterer 2009.

Julian C. Kerbis Peterhans

Suncus infinitesimus LEAST DWARF SHREW

Fr. Pachyure de Heller; Ger. Kleinere Zwergspitzmaus

Suncus infinitesimus (Heller, 1912). *Smithson. Misc. Coll.* 60 (12): 5. Rumruti, Laikipia Plateau, Kenya. 7000 ft (2135 m).

Taxonomy Originally described as *Pachyura infinitesimus*. Polytypic with three geographically widely separated forms. Hutterer (2005a) lists these forms as synonyms, but their status is uncertain. Clusters genetically with *Suncus remyi*, and may also be related to the widely distributed species *S. etruscus* (Quéroutil *et al.* 2001). Synonyms: *chriseos*, *ubangiensis*. Subspecies: none. Chromosome number: not known.

Description Very small shrew. Dorsal pelage darkish grey-brown; hairs dark slaty-grey at base, narrow white subterminal band, brown at tip. Ventral pelage grey; hairs dark slaty-grey at base, white at tip. Colours of dorsal and ventral pelage merge gradually. Head slender with long, narrow pointed muzzle. Eyes small. Ears rounded. Fore- and hindfeet greyish-brown. Tail of medium relative length (ca. 55% of HB), brown above, paler below. Nipples: 0 + 3 = 6.

Geographic Variation Three forms have been described (see Heim de Balsac & Meester 1977):

chriseos: South Africa: (Eastern Cape, Gauteng, KwaZulu–Natal,

North West and Free State Provinces) and Swaziland (Malolotja).

infinitesimus: Kenya and perhaps Uganda.

ubangiensis: Central African Republic (Bangui) and Cameroon.

Similar Species

Suncus megalura. Tail much longer (T: 82–97 mm) and relatively much longer (ca. 118% of HB). Skull longer (CI: 16.8–18.6 mm). Dorsal and ventral colours merge. Geographic distribution overlaps in Central African Republic, SW Kenya, and perhaps Cameroon.

S. varilla. Dorsal pelage greyish-chestnut; ventral pelage whitish-grey; colours of dorsal and ventral pelage clearly delineated. Geographic distribution overlaps in some areas of South Africa.

Distribution Endemic to Africa. Distribution disjunct. Primarily Coastal Forest Mosaic BZ of South Africa and adjacent Afromontane–Afroalpine and South-West Cape BZs (plus scattered records in savanna zones further north). Recorded from three well-separated areas: (a) South Africa (Gauteng, North West and Free State Provinces, coastal regions of the Eastern Cape Province) (Meester

& Lambrechts 1971, Skinner & Smithers 1990), KwaZulu–Natal (Taylor, P. 1998) and W Swaziland (Monadjem 1998a, c); (b) Kenya (Aggundey & Schlitter 1986); (c) Central African Republic (Petter & Chippaux 1962) and Cameroon (Hutterer & Joger 1982).

Habitat Primary forest, montane grassland, savanna and mixed bushveld. In South Africa, commonly associated with disused termitaria of the snouted harvester termite *Trinervitermes trinervoides* (Lynch 1983).

Abundance Uncommon. Probably more abundant than indicated by surveys. Fairly widespread in the lower-lying regions of central and eastern KwaZulu–Natal (Taylor, P. 1998).

Adaptations These tiny shrews are able to reduce their costs of metabolism by making use of termitaria, where the microclimate is mild and comparatively stable. They might also utilize torpor, a



Suncus infinitesimus

characteristic of crocidurines (Taylor, J.R.E. 1998). Ball-shaped nests (100 mm diam.) are constructed in the termitaria (Lynch 1983).

Foraging and Food Insectivorous. Readily eats beetles in captivity.

Social and Reproductive Behaviour Usually solitary (Rautenbach 1982). Mating behaviour involves nose-to-tail chasing culminating in a brief copulation (R. M. Baxter pers. obs.).

Reproduction and Population Structure Appears to be reproductively active during the wet season (Lynch 1983, Taylor, P. 1998). Litter size probably 2–3 (Taylor, P. 1998).

Predators, Parasites and Diseases Preyed on by owls, occasionally caught by domestic cats and dogs (Dippenaar 1997).

Conservation IUCN Category: Least Concern.

Measurements

Suncus infinitesimus

HB: 50.7 (42–62) mm, n = 16

T: 28.1 (23–31) mm, n = 16

HF: 7.9 (7–9) mm, n = 8*

E: 4.8 (3–7) mm, n = 8*

WT: 2.8, 3.1 g, n = 2*

CI: 14.5 (13.9–15.2) mm, n = 12

GWS: 6.3 (6.1–6.6) mm, n = 8

I¹–M³: 5.8 (5.3–6.3) mm, n = 33

South Africa (Meester & Lambrechts 1971)

*KwaZulu–Natal Province, South Africa (Taylor, P. 1998)

Key References Meester & Lambrechts 1971; Skinner & Smithers 1990.

R. M. Baxter & N. J. Dippenaar

Suncus lixus GREATER DWARF SHREW

Fr. Pachyure de Thomas; Ger. Größere Zwergspitzmaus

Suncus lixus (Thomas, 1898). Proc. Zool. Soc. Lond. 1897: 930. Nyika Plateau, Malawi.

Taxonomy Originally described in the genus *Crociodura*. The form *aequatorius* was included formerly with *S. lixus* (e.g. Heim de Balsac & Meester 1977, Hutterer 1993). In contrast, Hutterer (2005a) treats *aequatorius* as a full species with a geographic range in SE Kenya and N Tanzania (see below). Synonym: *gratulus*. Subspecies: none. Chromosome number: not known.

Description Small shrew with a moderately long tail. Dorsal pelage greyish-brown. Ventral pelage pale grey. Colours of dorsal and ventral pelage merge gradually on flanks. Head slender with long, narrow pointed muzzle. Eyes small; ears rounded. Fore- and hindfeet whitish. Tail moderately long (ca. 64% of HB), brown above, whitish or yellow below; pilosity 80–100% (Meester & Lambrechts 1971). Nipples: 0 + 3 = 6.

Geographic Variation Heim de Balsac & Meester (1977) listed three forms:

lixus: N Botswana, Zambia, Malawi and Tanzania.

gratulus: South Africa.

(*aequatorius*: now considered to be a separate species [see *Suncus aequatorius*])

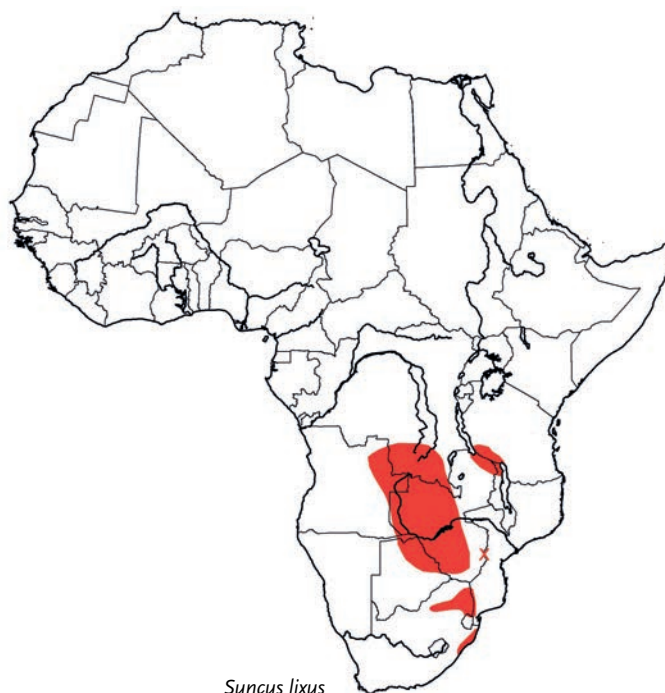
Similar Species

Suncus aequatorius. Dorsal pelage grey. Tail longer (T: 53–67 mm) and relatively longer (ca. 78% of HB), covered by dirty whitish, fine fur along its length, pilosity at least 50%. Kenya only.

S. megalura. Tail much longer (T: 82–97 mm) and relatively much longer (ca. 118% of HB). Geographic distribution overlaps in S DR Congo, Zambia, SW Tanzania and E Angola.

S. varilla. Colours of dorsal and ventral pelage clearly delineated. Skull shorter (CI: 15.1–17.0 mm). Geographic distribution overlaps or almost overlaps in S DR Congo, NE Zambia, Zimbabwe and N South Africa.

Distribution Endemic to Africa. Widely distributed mainly in the Zambezan Woodland BZ and southern part of the Somalia–



Suncus lixus

Masai Bushland BZ. Recorded from NE Angola, S DR Congo, S Tanzania, W Zambia, N Malawi, N Botswana, Zimbabwe, SW Mozambique, N South Africa and Swaziland. In South Africa, occurs widely in eastern parts of Limpopo Province (with a south-westerly extension into North West Province), Mpumalanga Province and the lower-lying areas of KwaZulu–Natal Province (Meester & Lambrechts 1971, Heim de Balsac & Meester 1977, Wirminghaus & Nanni 1989, Skinner & Smithers 1990, Monadjem 1998a, c, Taylor, P. 1998).

Habitat Moist riverine forest, coastal lowland forest, savanna woodland, thornveld, semi-arid scrub and grassland. Capable of living in a wide range of vegetation types.

Abundance Uncommon. Probably more abundant than indicated by surveys. In most of the countries listed above, known only from very few specimens from scattered localities.

Remarks Known to inhabit termite mounds. Might utilize torpor, a characteristic of crocidurines (Taylor, J. R. E. 1998). Insectivorous. In South Africa, reproductive activity recorded in the wet season (Jan), but a lactating ♀ has been reported in Aug from KwaZulu–

Natal (Wirminghaus & Nanni 1989). Litter size: three. Preyed on by Barn Owls (Vernon 1972).

Conservation IUCN Category: Least Concern.

Measurements

Suncus lixus

HB: 69.2 (52–81) mm, n = 6

T: 44.5 (36–51) mm, n = 6

HF: 12 (12–12) mm, n = 3*

E: 6.7 (5–8) mm, n = 3*

WT: 4.9 g, n = 1*

CI: 19.7 (19.2–20.7) mm, n = 10

GWS: 8.6 (8.3–8.9) mm, n = 8

I¹–M³: 8.1 (7.4–8.7) mm, n = 36

South Africa (Meester & Lambrechts 1971)

*KwaZulu–Natal Province, South Africa (Taylor, P. 1998)

Key References Meester & Lambrechts 1971; Skinner & Smithers 1990; Wirminghaus & Nanni 1989.

R. M. Baxter & N. J. Dippenaar

Suncus megalura CLIMBING DWARF SHREW

Fr. Pachyure grimpeuse; Ger. Kletter-Zwergspitzmaus

Suncus megalura (Jentink, 1888). Notes Leyden Mus. 10: 48. Schlieffelinsville, Junk R., Liberia.

Taxonomy Originally described in the genus *Pachyura*. Formerly considered to be a species of *Sylvisorex*, but genetic data (Quérroul *et al.* 2001) suggest that it should be allocated to the genus *Suncus*. Synonyms: as listed below. Subspecies: none. Chromosome number: 2n = 48 (Côte d'Ivoire; Meylan 1975).

Description Small shrew with an extremely long, thin tail and long hindfeet. Pelage soft and moderately dense; dorsal hairs 5 mm. Dorsal pelage greyish with brown tinge; hairs grey on basal two-thirds, brown on terminal third. Ventral pelage off-white to pale-buffy; hairs grey, with white or buff tip. Flanks similar to dorsal pelage or grey; colours of flanks and ventral pelage merge. Head slender with long, narrow pointed muzzle, small eyes and rounded ears. Fore- and hindfeet brown, slender and relatively long (ca. 25% of HB). Tail relatively extremely long (ca. 118% of HB), dark brown above, pale buffy below; ringed with small scales and covered with minute dark bristles. Nipples: 0 + 3 = 6.

Geographic Variation Seven forms (listed as subspecies by Heim de Balsac & Meester 1977) are recognized (see also Hutterer 2005b):

angolensis: Angola, NW Zambia.

gemmeus: Kenya, Uganda, NE DR Congo, Rwanda.

infuscus: Cameroon, Gabon, Central African Republic.

megalura: Guinea, Liberia, Côte d'Ivoire.

phaeopus: Ethiopia.

sheppardi: Zimbabwe, W Mozambique.

sorella: Mozambique (northern Tete district)

Similar Species

Suncus aequatorius. Head and body larger (HB: 66–85 mm); tail much shorter (T: 51–67 mm); and relatively much shorter (ca. 78% of HB). Perhaps parapatric in SE Kenya.

S. hututsi. On average smaller (HB: 52.6 [44–58] mm); tail much shorter (T: 28–33 mm) and relatively much shorter (ca. 60% of HB); skull shorter (CI: 13.3–14.2 mm). Perhaps parapatric in Burundi. Montane forest and upland bamboo.

S. infinitesimus. Tail much shorter (T: 23–31 mm) and relatively much shorter (ca. 55% of HB). Skull shorter (CI: 13.9–15.2 mm). Dorsal and ventral colours sharply delineated. Geographic distribution overlaps in Central African Republic, SW Kenya, and perhaps Cameroon.

S. lixus. Tail much shorter (T: 36–51 mm) and relatively much shorter (ca. 64% of HB). Geographic distribution overlaps in S DR Congo, SW Tanzania, Zambia and E Angola.

S. murinus. Much larger and heavier (HB: ca. 105–115 mm, WT: ca. 65–105g). Geographic distribution overlaps in Rwanda and Tanzania but *S. murinus* is commensal.

S. remyi. Smaller (HB: 42–48 mm); tail much shorter (T: 17–21 mm) and relatively much shorter (ca. 41% of HB). Apparently allopatric but geographic distribution fairly close in Cameroon, Gabon and Congo.

S. varilla. Colours of dorsal and ventral pelage clearly delineated. Tail much shorter (T: 25–45 mm) and relatively much shorter (ca. 60% of HB). Geographic distribution overlaps or almost overlaps in S DR Congo, W Tanzania, N Zambia, Malawi, N Zimbabwe and C Mozambique.

Distribution Endemic to Africa. Widespread, but apparently disjunct in many biotic zones: Rainforest BZ of West Africa, Rainforest–Savanna Mosaics and parts of Zambezian Woodland BZ. Not recorded in the Rainforest BZ of central Africa. Recorded from West, central and East Africa and southwards into E Zimbabwe, C Mozambique and Angola. The southern extension has an annual rainfall of 800–1200 mm (Smithers & Lobão Tello 1976, Heim de Balsac & Meester 1977, Ansell 1978, Smithers & Wilson 1979, Ansell & Dowsett 1988).

Habitat Very varied, and mostly associated with moist savanna. In Zimbabwe, recorded in thick scrub and on the fringe of an orchard near tall grass (Smithers 1983). In Zambia, found in tall grass of a drying stream bed (Ansell 1960a). In Kivu Province, DR Congo, captured in regenerating bush (30 specimens), long elephant grass (13) and in grassy scrub (11) (Dieterlen & Heim de Balsac 1979). Most specimens captured between 1600 m and 1900 m; relatively uncommon at higher altitudes.

Abundance One of the rarest species of shrew in Taï N. P. (Côte d'Ivoire), representing only 0.25% (n = 390 shrews; 9 spp.) in forest, and 0% in cocoa–coffee plantations (n = 140; 7 spp.) (Barrière *et al.* 1999). In Ziama Biosphere Reserve (Guinea), abundance varied according to habitat: 26.5% (n = 272 shrews; 9 spp.) in fields where it was the commonest species, 5.2% (n = 303; 10 spp.) in young forest plantations, 4.13% (n = 484; 9 spp.) in old fallow land, 2.7% (n = 441; 9 spp.) in old forest plantations, 1.6% (n = 500; 11 spp.) in primary forest and 0% (n = 509; 10 spp.) in secondary forest (P. Barrière unpubl.).

Adaptations The long tail is prehensile and used extensively in climbing. When stretching towards a distant branch, can support itself using its tail and relatively large hindfeet. In captivity, captures grasshoppers above the ground (Vogel 1974).

Foraging and Food Insectivorous. In Taï N. P. (Côte d'Ivoire), this species (as *Sylvisorex megalura*) was the only species of shrew that ate centipedes (Chilopoda) (n = 1 stomach; Churchfield *et al.* 2004).

Social and Reproductive Behaviour A single nest in Zimbabwe was spherical and constructed of broadleaf grasses; it was situated 1 m above ground in the branches of a bush (Dieterlen & Heim de Balsac 1979).

Reproduction and Population Structure Eight of 15 females collected in Mar (1 specimen), Jun (3), Aug (1) and Nov (3) in Kivu Province, E DR Congo, were reproductively active. Litter size: 1.8 (no range), mode 2, n = 5 (Dieterlen & Heim de Balsac 1979).



Suncus megalura

Predators, Parasites and Diseases No information.

Conservation IUCN Category: Least Concern.
Widely distributed; survives well in disturbed habitats.

Measurements

Suncus megalura

HB: 60.8 (50–65) mm, n = 36

T: 88.8 (82–97) mm, n = 36

HF: 15.5 (14–17) mm, n = 36

E: 8.3 (6–10) mm, n = 36

WT: 5.5 (3–8) g, n = 36

CI: 18.0 (16.8–18.6) mm, n = 12

GWS: 8.2 (7.8–8.5) mm, n = 12

I¹–M³: 7.5 (6.9–7.8) mm, n = 12

Kivu district, DR Congo (Dieterlen & Heim de Balsac 1979, as *Sylvisorex megalura*)

Individuals closer to the Rainforest BZ tend to be smaller than those from higher elevations.

Key References Dieterlen & Heim de Balsac 1979; Vogel 1974.

R. M. Baxter & N. J. Dippenaar

Suncus murinus ASIAN HOUSE SHREW

Fr. Musaraigne asiatique des maisons (Pachyure musquée); Ger. Hausspitzmaus

Suncus murinus (Linnaeus, 1766). Syst. Nat., 12th Ed., 1: 74. Java, Indonesia.

Taxonomy Originally described in the genus *Sorex*. Very variable species with a number of genetically distinct populations (Hutterer 2005b). Many synonyms, mostly extralimital to Africa (see Hutterer

2005b for full details). Synonyms (Africa only): *albicauda*, *auriculata*, *crassicaudus*, *duvernoyi*, *geoffroyi*, *leucura*, *mauritiana*, *sacer*. See also Hutterer & Tranier (1990) and Heim de Balsac & Meester (1977).

Subspecies: none. Chromosome number: $2n = 40$ (Djibouti; E. Pequignot in Hutterer & Tranier 1990).

Description Very large, rat-sized shrew. Dorsal pelage greyish-brown. Ventral pelage paler, no clear delimitation between dorsal and ventral pelage. Cutaneous scent-gland situated behind the shoulder, present in both sexes. Ears short and rounded. Palms and soles naked. Tail relatively long (ca. 63% of HB), thick. Four upper unicuspid; the fourth very small – much smaller than the third. Nipples: $0 + 3 = 6$.

Geographic Variation None recorded.

Similar Species

Suncus hututsi. Much smaller and lighter (HB: 44–58 mm, T: 28–33 mm, WT: ca. 1.7–2.4 g). Geographic distribution overlaps in Burundi; montane forest.

S. megalura. Much smaller and lighter (HB: 50–65 mm, WT: 3–8 g). Geographic distribution overlaps in Rwanda and Tanzania but *S. megalura* is not commensal.

Distribution Introduced recently into Africa (Hutterer & Tranier 1990). First recorded in Egypt during the eighteenth century, but no other records since then and now probably locally extinct (Osborne & Helmy 1980). Also recorded from Sudan (one record, Hutterer & Tranier 1990), Eritrea (one; Hutterer & Tranier 1990), Djibouti (two; Hutterer & Tranier 1990, Pearch *et al.* 2001), Kenya (two; Schlitter & Aggundey 1986), Tanzania (five; Hutterer & Tranier 1990) and Rwanda (one; Hutterer *et al.* 1987). Pemba and Zanzibar Is (Hutterer & Tranier 1990). With exception of specimens from Rwanda and Tanzania, found only in harbours. Extraliminally widespread from Burma and Afghanistan to China and throughout most of South-East Asia, including the Philippines and Japan; Madagascar and some islands of the Indian Ocean (Hutterer 2005b).

Habitat Commensal in Africa, but also lives in natural habitats in Asia (Nowak 1999).

Abundance There is no evidence that any population is firmly established on mainland Africa. All records refer to very few individuals. Present for only a short period (mostly before 1920, although one individual found in Djibouti in 1999 [Pearch *et al.* 2001]). It seems that individuals are introduced from time to time, and survive (breed?) within harbours before becoming locally extinct; a few reached further inland on transport routes.

Remarks Nocturnal. There is no information on the species in Africa. Elsewhere (Nowak 1999 and references therein), the diet is insectivorous plus items of human food and refuse. Individuals are



Suncus murinus

solitary and intolerant of one another. Gestation: 30 days. Litter size: 2.1 (1–4) on Guam Island; 2.8 (1–6) on Madagascar. Weaned at Day 17–20 (Hasler *et al.* 1997).

Conservation IUCN Category: Least Concern.

Numerous strains maintained in captivity. Extensively used as a laboratory animal, mainly for physiological studies (Oda *et al.* 1980). Regarded as a pest when population numbers are large.

Measurements

Suncus murinus

TL: 184.9 (155–240) mm, $n = 23$

T: 71.4 (50–85) mm, $n = 24$

HF: 19.6 (16–22) mm, $n = 26$

E: 12.2 (9–15) mm, $n = 26$

WT (♂♂): ca. 105 g

WT (♀♀): ca. 67 g

CI: 31.6 (28.6–35.0) mm, $n = 17$

GWS: 13.6 (12.0–15.6) mm, $n = 18$

I¹–M³: 13.5 (12.3–15.2) mm, $n = 21$

Measurements: Arabian peninsula (Harrison & Bates 1991); no data for mainland Africa

Weight: India (Nowak 1999)

Key Reference (Africa only) Hutterer & Tranier 1990.

J.-M. Duplantier

***Suncus remyi* REMY'S DWARF SHREW (REMY'S PYGMY SHREW)**

Fr. Pachyure de Remy; Ger. Remys Zwergspitzmaus

Suncus remyi Brosset, Dubost and Heim de Balsac, 1965. Biologia Gabonica 1: 170. Makokou, Gabon.

Taxonomy Genetically related to *S. infinitesimus* (Quéroutil *et al.* 2001). Synonyms: none. Chromosome number: not known.

Description Minute shrew, one of the smallest of all shrews. Pelage fine, short and dense. Dorsal pelage rich reddish-brown to rufous-brown; hairs grey on basal third, rich reddish-brown on terminal two-thirds. Ventral pelage slightly paler than dorsal pelage. Ears small and naked, clearly visible, not concealed by pelage. Fore- and hindfeet dark reddish-brown, with small claws. Tail relatively short or of medium length (ca. 41% of HB), dark brown; small dark hairs on basal 50–80%. Nipples: not known.

Geographic Variation None recorded.

Similar Species

Suncus megalura. Larger (HB: 50–65 mm); tail much longer (T: 82–97 mm) and relatively much longer (ca. 118% of HB). Apparently allopatric but geographic distribution fairly close in Cameroon, Gabon and Congo.

Distribution Endemic to Africa. Rainforest BZ (West Central Region [Gabon sub-region]). Recorded from N Gabon, Congo and SW Central African Republic.

Habitat In Gabon, found in a variety of habitats: primary rainforest especially where moist, and secondary marshy forest (Brosset *et al.* 1965b, Brosset 1988), and in heterogeneous and homogeneous rainforest (Goodman *et al.* 2001).

Abundance Uncommon or rare. Comprised 11% (2 of 18; 10 spp.) in two habitats at Minkébe Forest, Gabon (Goodman *et al.* 2001); 6% (1 of 16; 8 spp.) in one habitat at 110 m on Mt Doudou (Goodman & Hutterer 2004); 5% (8 of 160; 11 spp.) at Belinga and Makokou (Brosset 1988); and only 1% (5 of 503; 9 spp.) at another site on Mt Doudou (Nicolas *et al.* 2004). It has not been encountered at other study sites where shrews have been captured.

Remarks Embryo number: 1, n = 3 (Brosset 1988). One ♀ caught in Aug contained one full-term embryo; no information for other months (Brosset *et al.* 1965b).



Suncus remyi

Conservation IUCN Category: Least Concern.

Measurements

Suncus remyi

HB: 46.5 (42–48) mm, n = 5

T: 19.2 (17–21) mm, n = 5

HF: 7 mm, n = 1*

E: 5 mm, n = 1*

WT: 1.8 g, n = 1*

CI: 13.4 (13.1–13.6) mm, n = 4

GWS: n. d.

I¹–M³: 6.0 (5.8–6.2) mm, n = 4

Gabon (Brosset *et al.* 1965b)

*Gabon (Goodman *et al.* 2001)

Key References Brosset *et al.* 1965b.

D. C. D. Happold

***Suncus varilla* LESSER DWARF SHREW**

Fr. Pachyure petite; Ger. Zierliche Zwergspitzmaus

Suncus varilla (Thomas, 1895). Ann. Mag. Nat. Hist., ser. 6, 16: 54. East London, Cape Province, South Africa.

Taxonomy Originally described as *Crocidura (Pachyura) varilla*. Heim de Balsac & Meester (1977) list five subspecies, and Hutterer (2005a) lists six synonyms (as given here). Synonyms: *meesteri*,

minor, *natalensis*, *orangiae*, *tulbaghensis*, *warreni*. Subspecies: none. Chromosome number: not known.

Description Very small shrew with a long tail. Dorsal pelage greyish-chestnut; hairs pale slaty-grey at base, silvery-white sub-terminal band, buffy-brown at tip. Ventral pelage whitish-grey; hairs pale slaty-grey at base, with broad white to fawn tip. Colour of dorsal and ventral pelage clearly delineated. Head slender with long, narrow pointed muzzle. Eyes small, ears rounded. Fore- and hindfeet white. Tail relatively long (ca. 60% of HB), brown above, paler below, with numerous long bristles over its length. Nipples: not known.

Geographic Variation Heim de Balsac & Meester (1977) listed five forms, without comment:

minor: DR Congo and Tanzania.

orangiae: NE Zimbabwe, Malawi (?); C Mozambique, South Africa (North West, Gauteng, Free State, NE Eastern Cape and KwaZulu–Natal Provinces).

tulbaghensis: South Africa (limited parts of Western Cape Province).

varilla: South Africa (East London in Eastern Cape Province).

warreni: South Africa (from Port Nolloth in Northern Cape Province to van Rhynsdorp in Western Cape Province).

Similar Species

Suncus infinitesimus. Dorsal pelage darkish grey-brown; ventral pelage grey; colours of dorsal and ventral pelage merge gradually. Geographic distribution overlaps in some areas of South Africa.

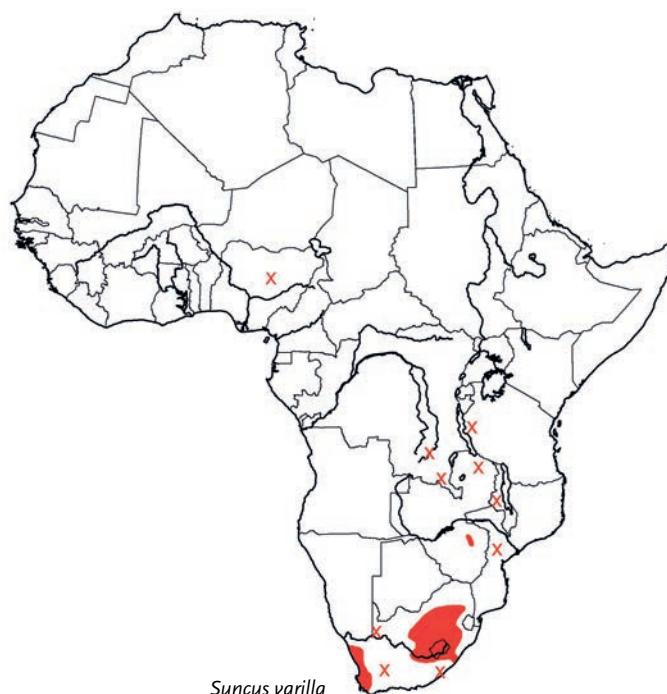
S. lixus. Colours of dorsal and ventral pelage merge. Skull longer (CI: 19.2–20.7 mm). Geographic distribution overlaps or almost overlaps in S DR Congo, NE Zambia, Zimbabwe and N South Africa.

S. megalura. Colours of flanks and ventral pelage merge. Tail much longer (T: 82–97 mm) and relatively much longer (ca. 118% of HB). Geographic distribution overlaps or almost overlaps in S DR Congo, W Tanzania, N Zambia, Malawi, N Zimbabwe and C Mozambique.

Distribution Endemic to Africa. Zambezan Woodland BZ, and parts of the Highveld and South-West Cape BZs. Recorded from DR Congo, W Tanzania, NE Zambia, Malawi, NE Zimbabwe, C Mozambique and South Africa. Records are widely separated and disjunct, especially in the north of the geographical range. One isolated record (skull fragments from an owl pellet) from N Nigeria (see Hutterer & Happold 1983).

Habitat Occurs in a great variety of vegetation types. In South Africa, usually recorded in grassland habitats, and often (but not always) associated with the termitaria of Harvester Termites *Trinervitermes trinervoides*. In KwaZulu–Natal also found in piles of wood, suburban gardens, open savanna and on the secondary margins of coastal forests (Taylor, P. 1998). Appears to be dependent on the disused mounds of these termites, in which it constructs spherical nests of grass (Lynch 1983, 1986). No information about habitat in northern part of range.

Abundance Widespread in South Africa, but mostly uncommon. Thirty specimens were collected from 27 localities throughout Free State Province (Lynch 1983) and 15 specimens were collected from



Suncus varilla

ten localities in (former) Transvaal (Rautenbach 1982). Densities of 0.25–8 individuals/ha recorded in central Free State Province of South Africa (Lynch 1991).

Adaptations Spherical nests are built in termite mounds, mostly in the centre or oriented towards the north or west (the warmer sides) of the mound, and mostly below ground level (Lynch 1985). The close association with termite mounds provides a thermally stable and insulated micro-habitat, which reduces the cost of thermoregulation and expenditure of energy. This very small shrew enters torpor, as do other crocidurines (Taylor, J. R. E. 1998), as a means to further reduce energy expenditure.

Foraging and Food Insectivorous. In captivity, feeds on grasshoppers, crickets, termites and ox-liver (Taylor, P. 1998).

Social and Reproductive Behaviour Thought to be monogamous, with 65% of adults occurring in pairs, regardless of the time of year. Young animals accompany ♀♀ for up to nine months. Parental care is well developed. Caravanning has been observed (Lynch 1985). Young leave the ♀ in the dry season (ca. May), and pair before breeding commences in Aug (Lynch 1990, 1991).

Reproduction and Population Structure In Free State Province, South Africa, pregnancies recorded during late dry season (Aug–Sep) and the wet season (Oct–Mar), but mostly in Aug–Nov. Embryo number: 3.7 (2–7). Litter size: 3.3 (2–7). There is no noticeable die-off, with 92% of population comprising adults during the dry season (May–Jul). By end of the wet season, 42% of population comprises juveniles or subadults. Longevity is estimated at 24–30 months during which time females produce 2–3 litters. A postpartum oestrus occurs, but only 18% of ♀♀ produce a second litter in a breeding season. Most ♀♀ do not breed during the season of birth (Lynch 1990, 1991).

Predators, Parasites and Diseases No information.

Conservation IUCN Category: Least Concern.

A widely distributed species that is not threatened at present.

Measurements

Suncus varilla

HB: 55.8 (44–68) mm, n = 79

T: 33.3 (25–45) mm, n = 79

HF (c.u.): 9 (9–10) mm, n = 22*

E: 8 (7–9) mm, n = 19*

WT: 6.5 g*

CI: 16.2 (15.1–17.0) mm, n = 65

GWS: 7.1 (6.3–7.6) mm, n = 60

I¹–M³: 6.6 (6.0–7.1) mm, n = 91

South Africa (Meester & Lambrechts 1971)

*Free State Province, South Africa (Skinner & Smithers 1990)

Key References Lynch 1986, 1990, 1991; Meester & Lambrechts 1971.

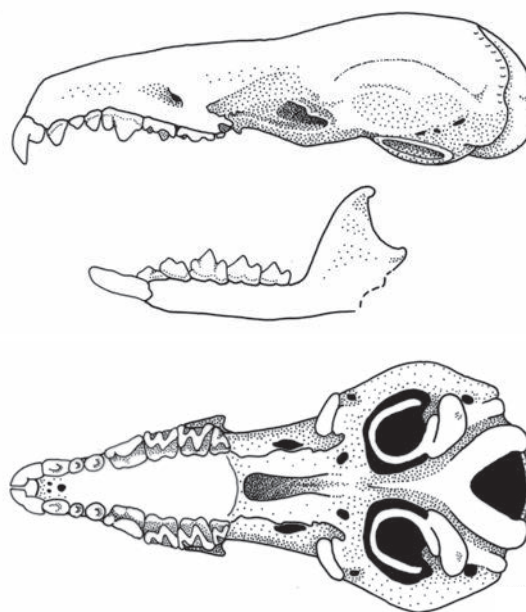
R. M. Baxter & N. J. Dippenaar

GENUS *Surdisorex*

Mole-shrews

Surdisorex Thomas, 1906. Ann. Mag. Nat. Hist., ser. 7, 18: 223. Type species: *Surdisorex norae* Thomas, 1906.

The genus *Surdisorex* contains two species, both of which live only in the highlands of Kenya. The distinguishing characters of *Surdisorex* are the absence of external ears, enlarged forelimbs and claws, very short tail (ca. 30% of HB), large elongated skull (24–27 mm), and wide braincase (GWS 50–55% of CI; other genera <50% of CI). There are three unicuspid teeth in each upper jaw (as in *Congosorex*; Figure 20; see also Table 7). In all these respects, *Surdisorex* differs from the genus *Myosorex* to which it is closely related. Both species of the genus look more like small moles (family Talpidae) or golden-moles (family Chrysochloridae) than like shrews. They show some similarity in their ecology to moles, and hence have the common name of mole-shrews. The genus was formerly included in *Myosorex* but retained as a full genus by Hollister (1918), Meester (1953), Heim de Balsac (1966), Hutterer (1993) and Hutterer *et al.* (2001). Genetic and molecular data are not yet available (the genus was not included in the analysis of Quérrouil *et al.* 2001), but morphological characters support the view that the genus belongs to the Myosoricinae, as defined by Hutterer *et al.* (2001). The two species are rather similar and may be distinguished on the basis of size and geographic distribution.



D. C. D. Happold & Rainer Hutterer

Figure 20. Skull and mandible of *Surdisorex polulus* (BMNH 74.650).

Surdisorex norae ABERDARE MOLE-SHREW

Fr. Musaraigne des Aberdares; Ger. Aberdare-Wühlspitzmaus

Surdisorex norae Thomas, 1906. Ann. Mag. Nat. Hist., ser 7, 18: 223. East side of Aberdare Range, near Nyeri, Kenya.

Taxonomy Heim de Balsac & Meester (1977) and Aggundey & Schlitter (1986) refer to this species as *Myosorex (Surdisorex) norae*. Following Thomas (1906b) and Hutterer (1993, 2005a), the species is retained in the genus *Surdisorex*. Synonyms: none. Chromosome number: not known.

Description Large mole-like shrew with long claws on forelimbs, and short tail. Pelage thick and dense, with the texture of velvet. Dorsal and ventral pelage dark chocolate-brown, hairs 6–7 mm, with long black guard hairs on rump. Head broad with

pointed muzzle. Eyes very small, almost vestigial and hidden by pelage. External ears very short, just a raised area of skin around auditory meatus; not visible unless hair is displaced. Forelimbs short. Forefeet broad with five digits: Digits 3, 4 and 5 long, with long pale claws 4–6 mm; Digits 1 and 5 shorter, reaching only to level of first phalanges of other digits; claws 2–3 mm. Hindlimbs short; hindfeet short, five digits with pale claws. Tail short (ca. 30% of HB), black, covered with dense short black bristles. Skull: condyloincisive length 26–27 mm (Heim de Balsac & Meester 1977). Nipples: 0 + 3 = 6.

Geographic Variation None recorded.

Similar Species

Surdisorex polulus. Lighter (WT: 18.3 [16–21] g). Mt Kenya only.

Distribution Endemic to Africa. Afromontane–Afroalpine BZ. Recorded only from the Aberdare Range, C Kenya. The few known specimens were collected at 2820–3300 m. The geographic distribution is probably limited by soil texture and the abundance of earthworms (see below).

Habitat Swamps in moorlands in the Aberdare highlands (Duncan & Wrangham 1971).

Abundance Very rare, known by only a few specimens.

Adaptations Nocturnal and diurnal. The forelimbs are broad with long digits and claws, and the skull is shorter, broader and stronger compared with the skulls of closely related shrews. Similar adaptations are seen in moles (Talpidae) and in golden-moles (Chrysochloridae). Mole-shrews forage and travel along runways on the soil surface, under grass and under leaf-litter. Sympatric species, which also use the runways, include *Crocidura* spp., *Sylvisorex granti*, *Lophuromys flavopunctatus*, *Mus* sp., *Praomys jacksoni*, *Hylomyscus? denniae* and *Otomys tropicalis* (Duncan & Wrangham 1971). It seems unlikely that mole-shrews excavate subterranean burrows, as do talpid moles. The mole-like characteristics of Aberdare Mole-shrews indicate that they are the ecological equivalent to moles (Talpidae) of the Palearctic, and to *Chrysochloris stuhlmanni* (Chrysochloridae), which also occurs in other East African highlands (but not sympatrically with *S. norae* in the Aberdares).

Foraging and Food Carnivorous. The diet is mainly earthworms, which are bitten into small pieces before swallowing. Small vertical holes, 1–2 cm in diameter, found in the swamps are probably made by the mole-shrews while foraging for worms (Duncan & Wrangham 1971).

Social and Reproductive Behaviour No information.

Reproduction and Population Structure Embryo number: 2 ($n = 1$). One pregnant ♀ was recorded in October (Hollister 1918). No information for other months.

Predators, Parasites and Diseases No information.



Surdisorex norae

Conservation IUCN Category: Vulnerable.

The very small geographical range, small and fragmented populations, and limited probability of recolonization (if locally extinct) are causes for concern. Habitat conservation, especially where populations are within the borders of a National Park, is essential.

Measurements

Surdisorex norae

HB: 96.8 (82–110) mm, $n = 5$

T: 30.0 (20–35) mm, $n = 5$

HF: 15.0 (14–16) mm, $n = 5$

E: 6.9 (6.7–7.3) mm, $n = 4$

WT: 25.0 (22.5–27.5) g, $n = 4$

CI: 26.3 mm, $n = 1$

GWS: 14.4 mm, $n = 1$

I¹–M³: 11.1 mm, $n = 1$

Aberdare Range, Kenya (BMNH)

Key References Duncan & Wrangham 1971; Kingdon 1974.

D. C. D. Happold

Surdisorex polulus MOUNT KENYA MOLE-SHREW

Fr. Musaraigne du Mont Kenya; Ger. Mount Kenya Wühlspitzmaus

Surdisorex polulus Hollister, 1916. Smithsonian Misc. Coll. 66 (1): 1. West side of Mount Kenya, Kenya. 10,731 ft (3261 m).

Taxonomy Heim de Balsac & Meester (1977) and Aggundey & Schlitter (1986) refer to this species as *Myosorex (Surdisorex) polulus*, and Heim de Balsac & Meester (1977) suggest that it may be no more than a subspecies of *S. norae*. Following Hutterer (1993, 2005a), the species is retained in the genus *Surdisorex*. Synonyms: none.

Chromosome number: not known.

Description Large mole-like shrew with long claws on forelimbs, and short tail, very similar to *Surdisorex norae* (see Description of *S. norae*). Pelage thick and dense, with the texture

of velvet. Dorsal pelage dark chocolate-brown; hairs 5–6 mm, dark grey at base, chocolate-brown at tip; long black guard hairs on rump. Ventral pelage paler, sometimes with russet tinge. Head broad with pointed muzzle. Eyes very small, almost vestigial and hidden by pelage. No external ears, or with only a small raised area of skin on posterior margin of meatus. Forelimbs short. Forefeet broad with five digits: Digits 3, 4 and 5 long, with long pale claws 4–6 mm; Digits 1 and 5 shorter reaching only to level of first phalanges of other digits, claws 2–3 mm. Hindlimbs short; hindfeet short; five digits with pale claws. Tail relatively short (ca. 30% of HB), black, covered with dense short black bristles. Skull: condyloincisive length 24–25 mm (Heim de Balsac & Meester 1977). Nipples: not known.

Geographic Variation None recorded.

Similar Species

Surdisorex norae. Heavier (WT: 25.0 [22.5–27.5] g). Aberdare Range, Kenya.

Distribution Endemic to Africa. Afromontane–Afroalpine BZ. Only recorded from the west side of Mount Kenya at altitudes of about 10,000 ft (3300 m). As for *S. norae*, the geographic distribution is probably limited by soil texture and the abundance of earthworms.

Habitat *Podocarpus*-bamboo forests and swamps near the forests, often where there is a ground layer of short grasses and/or leaf litter.

Abundance Rare or very rare; although may be not uncommon in favoured habitats.

Adaptations Similar to *S. norae*.

Foraging and Food Carnivorous. The diet is mainly earthworms, which are bitten into small pieces before swallowing. In captivity, mole-shrews use their forefeet to hold earthworms on the ground. Usually the earthworm is eaten, starting at the anterior end, only as far as the clitellum; hence the long intestine (full of soil and detritus) is not ingested. Thereafter another worm is seized and eaten in the same way (Duncan & Wrangham 1971).

Social and Reproductive Behaviour No information.

Reproduction and Population Structure Embryo number: 1 (n = 1) and 2 (n = 1), late Aug (BMNH), Oct (Hollister 1918); no data for other months.



Surdisorex polulus

Predators, Parasites and Diseases One species of flea, *Ctenophthalmus c. cophurus*, has been recorded; this species is also found on the sympatric golden-mole *Chrysochloris stuhlmanni* (Duncan & Wrangham 1971).

Conservation IUCN Category: Vulnerable.

The very small geographical range, small and fragmented populations, and very limited probability of recolonization (if locally extinct) are cause for concern. Habitat conservation, especially where populations are within the borders of a National Park, is essential.

Measurements

Surdisorex polulus

HB: 90 (85–92) mm, n = 6

T: 30.3 (26–32) mm, n = 6

HF: 14.7 (14–16) mm, n = 7

E: 0 mm, n = 6

WT: 18.3 (16–21) g, n = 6

CI: 24.9 mm, n = 1

GWS: 12.6 mm, n = 1

I¹–M³: 10.5 mm, n = 1

Mt Kenya, Kenya (BMNH)

Key References Duncan & Wrangham 1971; Kingdon 1974.

D. C. D. Happold

GENUS *Sylvisorex*

Forest Shrews

Sylvisorex Thomas, 1904. Abstr. Proc. Zool. Soc. Lond. 1904 (10): 12. Type species: *Crociodura morio* Gray, 1862.

The genus *Sylvisorex* contains 12 species distributed from SE Nigeria to NE Tanzania. All species live in primary and secondary forest habitats, and are called 'Forest Shrews' or 'Forest Musk Shrews'.

Shrews of the genus *Sylvisorex* are small to medium-sized and terrestrial. Tail length varies from short (*S. johnstoni*; mean 32 mm) to long (*S. vulcanorum*; mean 67 mm). Hindfeet are small and narrow, without special adaptations (Table 7). Ear pinnae are large and well visible. Eyes are small, as in most shrews. The pelage of most species in the genus is uniformly dark brown to blackish-brown, and only one species (*S. pluvialis*) has a whitish-grey ventral pelage. The narrow and sometimes elongated rostrum, and the round and highly domed braincase, are characteristic. The incisors and unicuspid teeth are weak; four unicuspid teeth are present in each upper jaw (Figure 21).

Biological details of any species are hardly known. *Sylvisorex johnstoni* is common in the lowland forest of the Congo Basin and may be the most numerous species in some shrew communities (Nicolas *et al.* 2003). Up to four species of the genus have been found to occur sympatrically in the lowland forests of Central African Republic (Ray & Hutterer 1995). Although most species are terrestrial, *S. vulcanorum* is sometimes scansorial.

The genus was regarded as part of *Suncus* by Smithers & Lobão Tello (1976), but was retained as a valid species by Ansell (1978). Quéroutil *et al.* (2001) studied 16s rRNA sequences of four species and found the genus, as currently understood, to be polyphyletic. As a consequence, *S. megalura* is now excluded from *Sylvisorex* and included in *Suncus*. Further taxonomic research will require a careful analysis of all taxa. Heim de Balsac (1968d) and Jenkins (1984) figured and discussed most of the species in the genus. Maddalena & Ruedi (1994) and Schlitter *et al.* (1999) described karyotypes of five species.

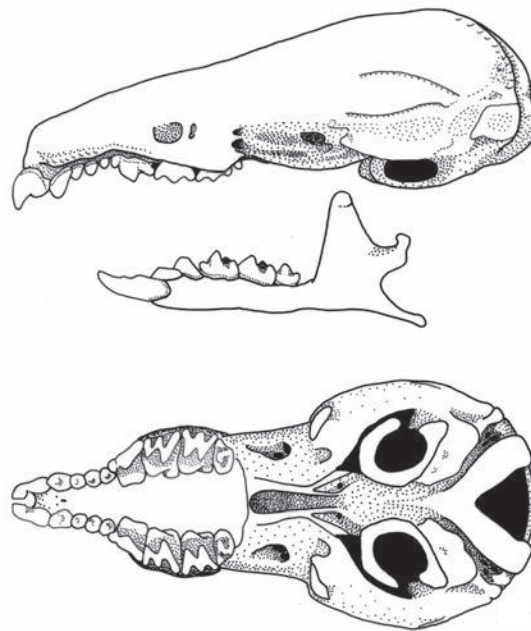


Figure 21. Skull and mandible of *Sylvisorex granti* (BMNH 88.55).

The 12 species recognized at present are not easily distinguished. Helpful characters and measurements are provided by Jenkins (1984), Hutterer and Schlitter (1996) and Ray & Hutterer (1996).

Rainer Hutterer

Sylvisorex camerunensis CAMEROONIAN FOREST SHREW

Fr. Musaraigne sylvestre du Cameroun; Ger. Kamerun-Waldmoschusspitzmaus

Sylvisorex camerunensis Heim de Balsac, 1968. Bonn. Zool. Beitr. 19: 35. L. Manengouba, Cameroon. 1800 m.

Taxonomy Originally described as a subspecies of *Sylvisorex granti* but now considered as a full species (Hutterer *et al.* 1992b). Synonyms: none. Chromosome number: not known.

Description Very small dark brown shrew. Pelage soft, dense and shiny; hairs ca. 6 mm on back. Dorsal pelage dark brown; hairs dark grey; dark brown at tip. Ventral pelage similar to dorsal pelage, or a little paler, sometimes with silvery sheen; hairs grey, brown at tip. Fore- and hindlimbs sparsely haired with short dark hairs. Tail relatively very long (ca. 100% of HB), dark brown to black, with numerous small dark bristles. Skull small and delicate; slightly domed. First upper incisor small, not hooked. First unicuspid large; second to fourth unicuspid smaller and subequal. M³ large. Nipples: not known.

Geographic Variation None recorded.

Similar Species

Sylvisorex johnstoni. Dorsal pelage pale brown. Tail much shorter (T: 25–36 mm) and relatively shorter (ca. 50–60% of HB), with very short, barely visible hairs. Skull shorter (CI: 14.4–14.9 mm).

Distribution Endemic to Africa. Recorded only from W Cameroon (Mt Oku, L. Manengouba) and SE Nigeria (Gotel Mts).

Habitat Specimens from Mt Gangirwal in the Gotel Mts, Nigeria, were found in farm and grassland habitats (labels, ZFMK). Montane forests in Cameroon (Hutterer 2005b).

Abundance No information.

Remarks Apparently no other information available.

Conservation IUCN Category: Vulnerable.

Measurements

Sylvisorex camerunensis

HB: 58.3 (55–60) mm, n = 7

T: 58.8 (55–61) mm, n = 7

HF: 11.7 (11–13) mm, n = 7

E: 8.9 (8–10) mm, n = 7

WT: 4.9 (4–5) g, n = 6

CI: 17.5 (17.0–18.1) mm, n = 7

GWS: 8.2 (7.7–8.5) mm, n = 7

I¹–M³: 7.4 (7.3–7.7) mm, n = 7

Cameroon and Nigeria (ZFMK)

Key Reference Heim de Balsac 1968d.

Rainer Hutterer



Sylvisorex camerunensis

Sylvisorex granti GRANT'S FOREST SHREW

Fr. Musaraigne sylvestre de Grant; Ger. Grants Waldmoschusspitzmaus

Sylvisorex granti Thomas, 1907. Ann. Mag. Nat. Hist., ser. 7, 19: 118. Mubuku Valley, Rwenzori East, Uganda. 10,000 ft (3048 m).

Taxonomy Considered on morphological grounds to be the most archaic species of the genus (Heim de Balsac & Lamotte 1957). The form *camerunensis* is now considered as a separate species (Hutterer *et al.* 1992b). Synonyms: *mundus*. Subspecies: none. Chromosome number: not known.

Description Very small shrew with tail similar in length to head and body. Pelage length on back varies: ca. 4 mm (Kivu, DR Congo; 1700 m), 7 mm (Mt Kilimanjaro; 3500 m) (F. Dieterlen unpubl.). Dorsal pelage blackish with brownish tinge. Ventral pelage greyish-brown, slightly paler than dorsal pelage. Ears dark grey, very finely haired. Eyes very small (0.7 mm diameter). Fore- and hindfeet brownish. Tail relatively very long (ca. 100% of HB), appearing naked, but bearing very short bristles. Skull with domed cranium and short muzzle. Lower incisors with two marked denticulations. Lower first premolar with two cusps. Nipples: 0 + 2 = 4.

Geographic Variation None recorded.

Similar Species

Sylvisorex johnstoni. Dorsal pelage pale brown, ventral pelage orange and contrasting markedly with dorsal pelage. Tail shorter (T: 25–36 mm) and relatively shorter (ca. 50–60% of HB). Rainforest habitats; parapatric in E DR Congo and Uganda. Both figured in Hutterer & Verheyen (1985).

S. lunaris. Head and body larger and much heavier (HB: 70–93 mm; WT: 9–20 g). Tail relatively shorter (ca. 65% of HB); blackish-

brown, very finely haired without longer bristles. Sympatric in montane areas of Albertine Rift Valley.

S. vulcanorum. Head and body on average larger (HB: 49.6 [43–56] mm). Skull usually shorter (CI: 15.5–16.1 mm). Marginally parapatric with *S. granti* in Rwanda and Uganda. Both figured in Hutterer & Verheyen (1985).

Distribution Endemic to Africa. Afromontane–Afroalpine BZ. Recorded from E DR Congo (west of L. Albert, W Rwenzori Mts, Virunga Volcanoes, west of L. Kivu, Idjwi I. in L. Kivu); Rwanda (Nyungwe Forest); Uganda (E Rwenzori Mts, Virunga Mts, Mt Elgon); Kenya (Mt Kenya, Mt Elgon, Cherangani Hills, Aberdare Ranges); and Tanzania (Mt Kilimanjaro). Altitudinal distribution: 1510 m (Idjwi I., L. Kivu) to 3800 m (Lac Marion, Rwenzori Mts) (Heim de Balsac 1968b). A record from Bwindi Impenetrable N. P. is uncertain and requires verification (J. Kerbis in litt.).

Habitat Swamps, montane forests and moist bushy vegetation at altitudes above 1500 m where montane forests are the dominant vegetation. In the mountains west of L. Kivu, 22 specimens (= 66% of shrews) were collected in swamps dominated by *Cyperus latifolius* and/or *Cladium mariscus* at 1700 m, 19 from swamps (*Cladium mariscus*) in cultivated land at 1700 m, and three from montane swamps (*Cyperus latifolius*) at 2100–2300 m. Eight were captured in non-swampy habitats: four in forests and four in moist bushy vegetation (Dieterlen & Heim de Balsac 1979).

Abundance May be very abundant in swampy habitats (see above).

Remarks In E DR Congo, half of the ♀♀ (6 of 12) collected during the wet season (Oct–Jan) were pregnant or lactating. In the dry season (Jun–Aug), only one (of two) ♀♀ was pregnant. Embryo number: 1.6 (1–2), $n = 5$.

Conservation IUCN Category: Least Concern.

Measurements

Sylvisorex granti

HB: 56.1 (45–65) mm, $n = 20$

T: 55.8 (47–63) mm, $n = 20$

HF: 13 (8–14) mm, $n = 20$

E: 7.7 (6–10) mm, $n = 20$

WT: 3.8 (3–6) g, $n = 20$

CI: 16.9 (16.1–17.0) mm, $n = 9$

GWS: 8.0 (7.8–8.3) mm, $n = 7$

I^1 – M^3 : 6.8 (6.7–7.1) mm, $n = 7$

Kivu, E DR Congo

Dieterlen & Heim de Balsac 1979, SMNS

Key Reference Dieterlen & Heim de Balsac 1979.

Fritz Dieterlen



Sylvisorex granti

Sylvisorex howelli HOWELL'S FOREST SHREW (ULUGURU FOREST SHREW)

Fr. Musaraigne sylvestre de Howell; Ger. Howells Waldmoschusspitzmaus

Sylvisorex howelli Jenkins, 1984. Bull. Brit. Mus. (Nat. Hist.), Zool. 47: 65. Morningside, Uluguru Mts, Tanzania.

Taxonomy Includes *usambarensis*, which was previously considered as a separate species (e.g. Hutterer 1986b). Two subspecies are currently recognized: *S. h. howelli* and *S. h. usambarensis* (Hutterer 1986b), and there is some evidence that they may be separate species (Ray & Hutterer 1995). Phylogenetic analysis showed that there is considerable molecular variation among each of the Eastern Arc Mountain populations (see below), suggesting that each population has been isolated for a long period of time (Stanley & Olson 2005). Synonyms: *usambarensis*. Subspecies: two. Chromosome number: not known.

Description Small shrew with long bristle-hairs on the basal one-half to two-thirds of the tail. Dorsal pelage dark chocolate-brown. Ventral pelage paler brown. Dorsal and ventral hairs steel-grey at base, with chocolate-brown or brown at tip. Delineation between dorsal and ventral pelage not striking, but most obvious where the limbs join the body. Forelimbs chocolate-brown on dorsal and ventral surfaces. Pads on soles of hindfeet very dark brown. Tail relatively long (ca. 70% of HB), subtly bicoloured (darker above than below) with short hairs along entire length interspersed with longer bristle hairs on basal two-thirds. Nipples: not known.

Geographic Variation Jenkins (1984) and Hutterer (1986b) recognize two subspecies:

S. h. howelli: Uluguru Mts, Tanzania (based on a larger and higher skull).

S. h. usambarensis: Usambara Mts, Tanzania (based on a smaller and flatter skull). Stanley & Olson (2005) analysed all six known populations (see below), but did not formally describe any new subspecies. They found that specimens from East Usambara had the shortest and most narrow skulls, and specimens from Nguru had the longest and widest skulls.

Similar Species No other species of *Sylvisorex* has been recorded from the Eastern Arc Mts of Tanzania.

Distribution Endemic to Africa. Afrotropical–Afroalpine BZ. Disjunct distribution on several Eastern Arc Mts in Tanzania above 900 m. Recorded from the East Usambara, West Usambara, Nguu, Ukaguru, Nguru and Uluguru Mts (Jenkins 1984, Hutterer 1986b, 1993, Stanley *et al.* 1998, Stanley & Olson 2005).

Habitat Montane and sub-montane forests above 900 m. Rarely found in disturbed or drier regions of forest.

Abundance In areas of occurrence, the most common shrew of its size. In 1992, in the West Usambara Mts, comprised 90% of the total sample of shrews ($n = 43$) and 34% of the total sample of all non-volant small mammals ($n = 116$) (W.T. Stanley, unpubl.).

Remarks Nocturnal. In the West Usambara Mts in Aug, one ♀ was pregnant ($n = 10$). Embryo number: 2 ($n = 1$; one in each uterine horn; crown–rump length 3 mm; W. T. Stanley, unpubl.).

Males more commonly captured than ♀♀ – ratio 22 : 14. Of 28 individuals examined, all were assessed (by toothwear) as adults.

Conservation IUCN Category: Endangered.

The geographic range is fragmented and the number of suitable habitats is declining.

Measurements

Sylvisorex howelli

HB: 62 (53–72) mm, n = 58

T: 42 (36–48) mm, n = 61

HF: 11 (9–13) mm, n = 62

E: 8 (7.5–12) mm, n = 62

WT: 3.9 (2.5–5) g, n = 61

CI: 16.4 (15.5–16.9) mm, n = 52

GWS: 7.5 (7.3–7.9) mm, n = 52

I¹–M³: 6.8 (6.4–7.1) mm, n = 52

West Usambara Mts, Tanzania (W. T. Stanley, unpubl.)

Key References Hutterer 1986b; Jenkins 1984.

William T. Stanley



Sylvisorex howelli

Sylvisorex isabellae ISABELLA FOREST SHREW (BIOKO FOREST SHREW)

Fr. Musaraigne sylvestre d'Isabella; Ger. Bioko-Waldmoschusspitzmaus

Sylvisorex isabellae Heim de Balsac, 1968. Bonn. Zool. Beitr. 19: 31. Pic Santa Isabel, Refugium, Fernando Po (= Bioko I.), Equatorial Guinea. 2000 m.

Taxonomy Originally described as a subspecies of *Sylvisorex morio* (Heim de Balsac 1968d) but now considered to represent a distinctly smaller species on Bioko I. (Hutterer 2005b). *Sylvisorex morio* now restricted to Mt Cameroon. Included in *S. morio* by Heim de Balsac & Meester (1977). Synonyms: none. Chromosome number: 2n = 36, FN = 50 (Bamenda highlands, Schlitter *et al.* 1999; see also below).

Description Very small to small dark shrew. Pelage soft and dense; hairs ca. 5 mm. Dorsal pelage dark reddish-brown; hairs dark grey, brown at tip. Ventral pelage reddish-brown, usually slightly paler than dorsal pelage (depending on angle of view) with shot-silk appearance; hairs grey on basal two-thirds, pale brown on terminal third. Head similar in colour to dorsal pelage. Fore- and hindfeet brown, with inconspicuous dark brown scales and sparse short dark brown hairs; claws sharp. Tail relatively very long (ca. 90% of HB), blackish-brown, not bicoloured but slightly paler below. Braincase high-domed. First incisor long and hooked. First unicuspid large; second to fourth unicuspid smaller and subequal. Third molar medium. Nipples: not known.

Geographic Variation None recorded.

Similar Species

Sylvisorex johnstoni. Dorsal pelage on Bioko I. rufous-brown. Smaller (HB: 45–53 mm; CI: 14.4–14.9 mm). Bioko I. and the mainland.

Distribution Endemic to Africa. Rainforest BZ/Afromontane–

Afroalpine BZ. Recorded only from Bioko I. (Equatorial Guinea). A similar species (referred to as this species by Schlitter *et al.* 1999) occurs in the Bamenda Highlands, Cameroon, but its status at present is uncertain (Hutterer 2005b).



Sylvisorex isabellae

Habitat Montane forest and grassland from 2000 to 2400 m (Heim de Balsac 1968d).

Abundance Uncertain. Probably rare and with a restricted distribution.

Remarks Sympatric with *Myosorex eisentrauti*, also endemic to 'Pic Santa Isabel' and 'Refugium' on Bioko I.

Conservation IUCN Category: Endangered.

Measurements

Sylvisorex isabellae

HB: 59.3 (54–63) mm, n = 4

T: 55.5 (54–59) mm, n = 4

HF: 12.0 (10–13) mm, n = 4

E: 8.6 (8–9) mm, n = 4

WT: 7.6 (5.5–9) g, n = 4

CI: 18.6 (18.3–18.8) mm, n = 4

GWS: 8.8 (8.3–9.2) mm, n = 4

I¹–M³: 8.0 (7.7–8.2) mm, n = 4

Bioko I.

Body measurements and weight: Heim de Balsac (1968d)

Skull measurements: ZFMK

Key Reference Heim de Balsac 1968d.

Rainer Hutterer

Sylvisorex johnstoni JOHNSTON'S FOREST SHREW (PYGMY FOREST SHREW)

Fr. Musaraigne sylvestre de Johnston; Ger. Johnstons-Waldmoschusspitzmaus

Sylvisorex johnstoni (Dobson, 1888). Proc. Zool. Soc. Lond. 1887: 577 [1888]. Rio del Rey, Cameroon.

Taxonomy Originally described in the genus *Myosorex*. Populations in S Gabon and W Congo exhibit considerable genetic distances, suggesting that cryptic species may be involved (Quéroutil *et al.* 2003). Synonyms: none. Chromosome number: 2n = 30, FN = 38 (Schlitter *et al.* 1999); one of the lowest diploid numbers of any species of African shrew.

Description Minute to very small shrew. Dorsal pelage pale brown (see also below). Ventral pelage orange, contrasting markedly with dorsal pelage. Short rostrum. Ears moderate, covered with short hairs. Tail of relative medium length (ca. 50–60% of HB), dark above and below with very short, barely visible hairs. Nipples: not known.

Geographic Variation Specimens from Bioko I. have rufous-brown dorsal pelage, and paler ventral pelage (BMNH).

Similar Species

Sylvisorex camerunensis. Dorsal pelage dark brown. Tail much longer (T: 55–61 mm) and relatively longer (ca. 100% of HB), dark brown to black, with numerous small dark bristles. Skull longer (CI: 17.0–18.1 mm).

S. granti. Dorsal pelage blackish with brownish tinge, ventral pelage slightly paler than dorsal pelage and not contrasting with it. Tail longer (T: 47–63 mm) and relatively longer (ca. 100% of HB). Montane habitats; parapatric in E DR Congo and Uganda. Both figured in Hutterer & Verheyen (1985).

S. isabellae. Dorsal pelage dark reddish-brown. Larger (HB: 54–63 mm; CI: 18.3–18.8 mm). Only known on Bioko I.

S. konganensis. Dorsal pelage brownish-grey. Tail pale brownish-grey, covered with short bristles, with a few longer bristles (1–3 mm) on basal 50%. Probably larger (HB: 64 mm; CI: 16.9 mm, n = 1). Sympatric only in SW Central African Republic and perhaps in N Congo.

S. lunaris. Dorsal pelage moderately dark greyish-brown to mid-brown; ventral pelage paler, not contrasting markedly with dorsal pelage. Much larger (HB: 70–93 mm; T: 45–56 mm; CI: 22.2–

22.9 mm). Parapatric in region of N Albertine Rift Valley.

S. morio. Much larger (HB: 61–71 mm; T: 50–59 mm; CI: 19.4–19.9 mm). Montane forest at 1000 m and above; recorded only from Mt Cameroon; possibly parapatric in Mt Cameroon area.

S. ollula. Much larger (HB: 91–110 mm; T: 59–71 mm). Sympatric throughout most of geographic range.

S. vulcanorum. Dorsal pelage dark sepia-brown to blackish-brown; ventral pelage slightly greyer. Tail much longer (T: 47–51 mm) and relatively longer (ca. 100% of HB). Skull longer (CI: 15.5–16.1 mm). Parapatric in region of N Albertine Rift Valley. Both figured in Hutterer & Verheyen (1985).

Distribution Endemic to Africa. Rainforest BZ (West Central Region, mainly in Gabon sub-region), and Eastern Rainforest–Savanna Mosaic. Recorded from two areas: (a) SW Cameroon, Gabon, Congo, and Central African Republic; and (b) E DR Congo, Uganda, Burundi and NW Tanzania. Also recorded from Bioko I.

Habitat Disturbed and undisturbed rainforest habitats (Hutterer & Schlitter 1996, J. C. Ray unpubl.); favours micro-habitats with relatively dense understorey (J. C. Ray unpubl.). In Gabon, occurs in rainforest and, to a lesser extent, marshy forest and riparian forest (Nicolas *et al.* 2004).

Abundance Consistently a common species in many central African shrew communities, representing (where found) 13–60% of shrews captured. Comprised 14% in Ngotto Forest, Central African Republic (n = 81; 11 spp.; Morvan *et al.* 1999), 15% in Belinga-Makokou, Gabon (n = 160; 11 spp.; Brosset 1988), 29% in Korup, Cameroon (n = 24, 9 spp.; Hutterer & Schlitter 1996), 31% at Mt Alen, Equatorial Guinea (n = 26; 8 spp.; Lasso *et al.* 1996), 35% at Mt Doudou, Gabon (n = 79; 9 spp.; Goodman & Hutterer 2004), 45% at Mt Doudou, Gabon (n = 693, 10 spp.; Nicolas *et al.* 2005) and 60% in Dzanga-Sangha, Central African Republic (J. C. Ray unpubl.). In all localities given above, it was the commonest species, except for Ngotto and Belinga-Makokou, where it was the second commonest species.

Remarks At Mt Doudou, Gabon, reproductive activity occurred throughout the year (Nicolas *et al.* 2003). Mean embryo number: 2 (n = 3) at Belinga-Makokou, Gabon (Brosset 1988) and 1.4 (n = 15) at Mt Doudou, Gabon (Nicolas *et al.* 2004). Most abundant species of shrew species found in small carnivore scats (frequency of occurrence: 36.7% of 311 scats) collected in Dzanga-Sangha, Central African Republic (Ray & Hutterer 1995, Ray 1998).

Conservation IUCN Category: Least Concern.

Measurements

Sylvisorex johnstoni

HB: 48.5 (45–53) mm, n = 15

T: 32.1 (25–36) mm, n = 17

HF: 9.2 (8–12) mm, n = 17

E: 8.2 (7–9) mm, n = 14

WT: 2.9 (2.3–3.5) g, n = 11

CI: 14.8 (14.4–14.9) mm, n = 4

GWS: 7.4 (7.2–7.6) mm, n = 4

I¹–M³: 6.4 (6.1–6.7) mm, n = 4

Body measurements and weight: Mt Doudou, Gabon (Goodman & Hutterer 2004)

Skull measurements: Bioko I. (as Fernando Po; BMNH)



Sylvisorex johnstoni

Justina C. Ray & Rainer Hutterer

Key Reference Brosset 1988; Nicolas *et al.* 2005.

Sylvisorex konganensis KONGANA FOREST SHREW

Fr. Musaraigne sylvestre de Kongana; Ger. Kongana-Waldmoschusspitzmaus

Sylvisorex konganensis Ray and Hutterer, 1996. Ecotropica 1: 93. Kongana, Dzanga-Sangha Forest Reserve, Central African Republic.

Taxonomy Comparison of 16s rRNA sequences shows a close relationship to *S. ollula* (Quérrouil *et al.* 2001). Synonyms: none. Chromosome number: not known.

Description Small shrew. Dorsal pelage brownish-grey. Ventral pelage, tail, limbs and outer ear slightly paler in colour than dorsal pelage. Snout covered by numerous facial vibrissae. Ear small, rounded, paler than dorsal pelage, and covered by short hairs. Fore- and hindfeet pale, with relatively elongated digits; Digit 1 of hindfoot unusually long; tubercles absent from the inner surface of the sole. Tail of medium relative length (ca. 56% of HB), pale brownish-grey, covered with short bristles, with a few longer bristles (1–3 mm) on basal 50%. Nipples: not known.

Geographic Variation None recorded.

Similar Species

Sylvisorex johnstoni. Dorsal pelage pale brown or rufous-brown. Tail dark above and below with very short, barely visible hairs. Smaller (HB: 45–53 mm; CI: 14.4–14.9 mm). Sympatric only in SW Central African Republic and perhaps in N Congo.

S. pluvialis. Tail and hindfoot longer (T: 67 mm; HF: 14 mm, n = 1). Tail relatively longer (ca. 90% of HB). Ventral pelage whitish-grey with white-tipped hairs. Possibly sympatric in SW Central African Republic and N Congo.



Sylvisorex konganensis

Distribution Endemic to Africa. Rainforest BZ (West Central Region [Gabon sub-region]). Recorded only from SW Central African Republic (Ray & Hutterer 1995; Barrière & Nicolas 2000). Likely to occur also in N Congo.

Habitat One specimen collected in unlogged mixed forest with relatively open understorey (Ray & Hutterer 1995).

Remarks Probably very rare. Found in only 1.3% of 311 small carnivore scats collected in Dzanga-Sangha, Central African Republic (Ray & Hutterer 1995); comprised 0.8% of 1350 shrews captured in Ngotto Forest, Central African Republic (Barrière & Nicolas 2000).

Conservation IUCN Category: Data Deficient.

Measurements

Sylvisorex konganensis

HB: 64 mm, n = 1

T: 36 mm, n = 1

HF: 11.3 mm, n = 1

E: 8 mm, n = 1

WT: 3 g, n = 1

CI: 16.9 mm, n = 1

GWS: n. d.

I¹–M³: 7.5 mm, n = 1

Holotype

Dzanga-Sangha Forest Reserve, Central African Republic (Ray & Hutterer 1995)

Key Reference Ray & Hutterer 1995.

Justina C. Ray & Rainer Hutterer

Sylvisorex lunaris MOON FOREST SHREW

Fr. Musaraigne sylvestre des Monts de la Lune; Ger. Mond-Waldmoschusspitzmaus

Sylvisorex lunaris Thomas, 1906. Ann. Mag. Nat. Hist., ser. 7, 18: 139. Mubuku Valley, Rwenzori East, Uganda. 12,000 ft (3810 m).

Taxonomy Synonyms: *ruandae*. Subspecies: none. Chromosome number: 2n = 58, FN = 80 (Maddalena & Ruedi 1994).

Description Small-medium to medium dark shrew. Pelage soft and dense with silky sheen; hairs ca. 4 mm. Dorsal pelage moderately dark greyish-brown to mid-brown; hairs dark grey on basal three-quarters, dark brown on terminal quarter. Head colour similar. Ventral pelage brownish-grey, paler than dorsal pelage (depending on angle of view) with shot-silk appearance; hairs grey on basal two-thirds, pale brown or beige on terminal third. Fore- and hindfeet dark brown with dark brown hairs; claws fairly long, sharp. Tail blackish-brown, relatively long (ca. 65% of HB); not bicoloured. First incisor moderately long and hooked. Third molar medium. Braincase high-domed. Nipples: 6.

Geographic Variation None recorded.

Similar Species

Sylvisorex granti. Head and body smaller and much lighter (HB: 45–65 mm; WT: 3–6 g). Tail relatively longer (ca. 100% of HB); appearing naked but bearing very short bristles. Sympatric in montane areas of Albertine Rift Valley.

S. johnstoni. Dorsal pelage pale brown; ventral pelage orange, contrasting markedly with dorsal pelage. Much smaller (HB: 45–53 mm; T: 25–36 mm; CI: 14.4–14.9 mm). Parapatric in region of N Albertine Rift Valley.

S. vulcanorum. Head and body much smaller and much lighter (HB: 43–56 mm, n = 5; WT: 3.5 g, n = 2). Skull shorter (CI: 15.5–16.1 mm). Dorsal pelage dark sepia-brown to blackish-brown. Sympatric in montane areas of Albertine Rift Valley.

Distribution Endemic to Africa. Afromontane–Afroalpine BZ. Recorded from Uganda (Rwenzori Mts), E DR Congo (mountains west of L. Kivu), Rwanda (Virunga Mts) and Burundi (mountains east of L.

Kivu). Also recorded on Idjwi I. (1500 m) in L. Kivu (Heim de Balsac 1968b). Altitudinal range: 1500–4100 m.

Habitat Very varied. In the Kivu district of E DR Congo, commonest in swamp and secondary bush (27 specimens) but also found in grass-bush (7), elephant-grass (6), and gallery woodland at 1600–1900 m; also recorded in secondary forest (3), bamboo (1) and montane swamp (1) at 1900–3300 m (Dieterlen & Heim de Balsac 1979). At higher altitudes in Rwenzori Mts, found in *Lobelia–Senecio* vegetation (J. Verschuren in Dieterlen & Heim de Balsac 1979).



Sylvisorex lunaris

Abundance Uncommon to common. In E Kivu, comprised 10% (6 of 56; 4 spp.) in elephant-grass, 17% (7 of 41; 6 spp.) in grassbush, and 32% (27 of 83; 8 spp.) in swamp and secondary bush habitats. At higher altitudes, the species is less common, comprising 0% (0 of 81; 8 spp.) in primary montane forest, 7% (2 of 28; 7 spp.) in mixed primary and secondary montane forest, 5% (1 of 20; 7 spp.) in bamboo and 1–2% (1 of 76; 6 spp.) in montane swamp habitats (Dieterlen & Heim de Balsac 1979).

Remarks Pregnancies recorded in Feb (1 of 1), Mar (2 of 5), Jun (1 of 2) and Jul (1 of 1); no pregnancies recorded in Jan (0 of 3) and Aug (0 of 6); no data for other months. Embryo number: 2.6 (2 [n = 2] to 4 [n = 1]) (Dieterlen & Heim de Balsac 1979).

Conservation IUCN Category: Vulnerable.

Measurements

Sylvisorex lunaris

HB: 80.0 (70–93) mm, n = 39

T: 52.2 (45–56) mm, n = 39

HF: 14.7 (12–16) mm, n = 39

E: 9.1 (7–10) mm, n = 39

WT: 13.2 (9–20) g, n = 39

CI: 22.5 (22.2–22.9) mm, n = 11

GWS: 10.6 (10.2–11.0) mm, n = 11

I¹–M³: 9.7 (9.3–10.0) mm, n = 11

E DR Congo (Dieterlen & Heim de Balsac 1979)

Key Reference Dieterlen & Heim de Balsac 1979.

D. C. D. Happold & Fritz Dieterlen

Sylvisorex morio MOUNT CAMEROON FOREST SHREW

Fr. Musaraigne sylvestre du Mont Cameroun; Ger. Kamerunberg-Waldmoschusspitzmaus

Sylvisorex morio (Gray, 1862). Proc. Zool. Soc. Lond. 1862: 180. Cameroon Mountain, Cameroon.

Taxonomy The form *isabella* from Bioko I., originally described as a subspecies of *S. morio* by Heim de Balsac (1968d), is now considered to be a separate species (Hutterer 2005b; see *S. isabella*). Synonyms: none. Chromosome number: 2n = 38 (Schlitter *et al.* 1999).

Description Small dark shrew. Pelage soft and dense; dorsal hairs 6 mm. Dorsal pelage dark russet-brown to black without conspicuous silky sheen; hairs dark grey with dark brown on tip. Ventral pelage slightly or moderately paler (depending on angle of view) with silky sheen; hairs grey with medium brown or pale brown tip. Ears short, partly concealed by pelage. Fore- and hindfeet brown, with short brown hairs. Tail relatively long (ca. 75% of HB), thin, blackish-brown, without long hairs. Skull slender in dorsal view with a semi-hexagonal braincase. Lateral view of dorsal profile flat from nasal to frontal. Braincase slightly domed. Upper toothrows gradually tapering inwards from M² to I¹ in ventral view. I¹ moderately long and hooked. M³ wide. Nipples: not known.

Geographic Variation None recorded.

Similar Species

Sylvisorex johnstoni. Much smaller (HB: 45–53 mm; T: 25–36 mm; CI: 14.4–14.9 mm). Rainforest; possibly parapatric in Mt Cameroon area.

S. ollula. Much larger (HB: 91–110 mm); tail almost always longer (T: 59–71 mm) and relatively longer (ca. 57% of HB). Lowland rainforest; possibly parapatric in S Cameroon.

S. pluvialis. Dorsal pelage paler (greyish-brown). Tail relatively a little longer (ca. 90% of HB), with short dark hairs and a few longer bristles on basal 40%. In S Cameroon, recorded only from Korup N. P.

Distribution Endemic to Africa. Afromontane–Afroalpine BZ. Recorded only from Mt Cameroon, Cameroon.

Habitat Montane forest at 1000 m and up to the limit of forest

at ca. 2100 m (Eisentraut 1973a, Heim de Balsac 1968d). One specimen in alpine grass and bushland at 3000 m (Eisentraut 1973a).

Abundance Probably fairly common although distribution is restricted. Heim de Balsac (1968b) commented that ‘à 1850 m (Musake-Hütte), l’animal est très commun ... et Eisentraut en capture de bonnes séries à chacun de ses voyages’ and also (Heim de Balsac 1958) that this species ‘parut ... le plus abondant des Soricidé du biotope’.

Remarks Apparently no other information available.

Conservation IUCN Category: Endangered.



Sylvisorex morio

Measurements*Sylvisorex morio*

HB: 66.6 (61–71) mm, n = 3

T: 53.3 (50–59) mm, n = 3

HF: 13.5 (12.5–15) mm, n = 3

E: 9.6 (9–10) mm, n = 3

WT: 8, 8 g, n = 2

CI: 19.7 (19.4–19.9) mm, n = 3

GWS: 9.3 (9.2–9.4) mm, n = 3

I¹–M³: 8.4 (8.3–8.6) mm, n = 3

Cameroon (ZFMK)

Key References Eisentraut 1973a; Heim de Balsac 1968d.**D. C. D. Happold & Rainer Hutterer***Sylvisorex ollula* GREATER FOREST SHREW

Fr. Musaraigne sylvestre d'Ollula; Ger. Große Waldmoschusspitzmaus

Sylvisorex ollula Thomas, 1913. Ann. Mag. Nat. Hist., ser. 8, 11: 321. Dja R., Bitye, Cameroon. 2000 ft (610 m).

Taxonomy Phylogenetic studies showed little difference between populations from W Congo and SW Cameroon (Quérrouil *et al.* 2003). Synonyms: none. Chromosome number: 2n = 38, FN = 64 (Schlitter *et al.* 1999).

Description Very large dark shrew, the largest species in the genus. Pelage dense and velvety with silky sheen; hairs 4–5 mm. Dorsal pelage medium to dark brown, or blackish, with slight russet tinge; hairs dark grey on basal two-thirds, dark greyish-brown to russet-brown on terminal third. Ventral pelage greyish-brown to medium brown, paler than dorsal pelage; hairs grey on basal two-thirds, greyish-brown on terminal third. Ears partly concealed by pelage. Fore- and hindfeet dark brown, sparsely covered by dark brown hairs. Tail of relative medium length (ca. 57% of HB), thin, blackish-brown, mostly naked with some bristles on basal 10%. Skull flat with braincase slightly domed. First upper incisor long and hooked. Third upper molar narrow. Sagittal and occipital crests on braincase well developed. Nipples: not known.

Geographic Variation None recorded.

Similar Species

Sylvisorex johnstoni. Much smaller (HB: 45–53 mm; T: 25–36 mm).

Sympatric throughout most of geographic range.

S. konganensis. Dorsal pelage brownish-grey. Smaller and much lighter (HB: 64 mm; WT: 3 g, n = 1). Tail shorter (T: 36 mm, n = 1).

Possibly sympatric in SW Central African Republic and N Congo.

S. morio. Much smaller (HB: 61–71 mm); tail almost always shorter (T: 50–59 mm) and relatively shorter (ca. 75% of HB). Montane forest above 1000 m; Mt Cameroon only; possibly parapatric in S Cameroon.

S. pluvialis. Smaller (HB: 74 mm, n = 1). Tail relatively longer (ca. 90% of HB); ventral pelage whitish-grey with white-tipped hairs. Sympatric in Korup N. P., SW Cameroon and possibly in SW Central African Republic.

Distribution Endemic to Africa. Rainforest BZ (West Central Region [Gabon sub-region]). Recorded from S Cameroon, E Nigeria (Gotel Mts, 1900 m, adjacent to Cameroon border [Hutterer *et al.* 1992b]), Equatorial Guinea (Rio Muni), Gabon and SE Central African Republic. May also occur in W Congo. One record from SE DR Congo. One of the most widespread species of shrews within its principal geographic range (see Goodman *et al.* 2001).

Habitat Lowland rainforest. In Ngotto Forest, Central African Republic, abundant in dense unlogged forest characterized by a high frequency of natural disturbances (Morvan *et al.* 1999). In Minkébé Forest, Gabon, found only in marshland and homogeneous forest (Goodman *et al.* 2001).

Abundance Rare to common, depending on the locality. Comprised 0.5–33% of captured shrews, and sometimes one of the commonest of species, e.g. 5% (8 of 160; 11 spp.) at Belinga-Makokou, Gabon (Brosset 1988); 4% (1 of 24; = sixth of 9 spp.) at Korup N. P., Cameroon (Hutterer & Schlitter 1996); 10% (49 of 503; fourth of 9 spp.) at Mt Doudou, Gabon (Nicolas *et al.* 2004); 10% (8 of 79; = fourth of 9 spp.) at Mt Doudou (Goodman & Hutterer 2004); 11% (3 of 26; fourth of 8 spp.) at Mt Alen National Park, Equatorial Guinea (Lasso *et al.* 1996); 31% (25 of 81; first of 11 spp.) at Ngotto Forest, Central African Republic (Morvan *et al.* 1999); and 33% (4 of 12; = first of 7 spp.) in marshland at Minkébé Forest, Gabon (Goodman *et al.* 2001).

*Sylvisorex ollula*

Remarks Despite the commonness of this species, little has been recorded about its biology. Mean litter size: 2, $n = 2$; Belinga-Makokou, Gabon (Brosset 1988). Mean embryo number: 3.5, $n = 4$; Mt Doudou, Gabon (Nicolas *et al.* 2004). Found in 3.5% of 311 small carnivore scats collected in Dzanga-Sangha, Central African Republic (Ray & Hutterer 1995; Ray 1998). Ebola virus RNA detected in extracts of organs of one individual collected from Ngotto Forest, Central African Republic (Morvan *et al.* 1999).

Conservation IUCN Category: Least Concern.

Measurements

Sylvisorex ollula

HB: 103.8 (91–110) mm, $n = 5$

T: 67.0 (59–71) mm, $n = 5$
 HF: 15.2 (14–17) mm, $n = 5$
 E: 13.8 (12–17) mm, $n = 5$
 WT: 18.2 (18–22) g, $n = 5$
 CI: n. d.
 GWS: n. d.
 I¹–M³: n. d.
 Gabon (Goodman *et al.* 2001)
 HB calculated from TL

Key References Brosset 1988; Goodman & Hutterer 2004; Goodman *et al.* 2001.

Justina C. Ray & Rainer Hutterer

Sylvisorex oriundus LESSER FOREST SHREW

Fr. Musaraigne sylvestre naine; Ger. Kleine Waldmoschusspitzmaus

Sylvisorex oriundus Hollister, 1916. Bull. Amer. Mus Nat. Hist. 35: 672. Medje, DR Congo.

Taxonomy Often included in *C. ollula* but regarded as distinct by Dieterlen & Heim de Balsac (1979). Synonyms: none. Chromosome number: not known.

Description Small dark shrew, with relatively long hindfoot. Dorsal pelage dark olive-brown to dark sepia-brown; hairs dark grey, olive-brown at tip. Flanks and ventral pelage dark greyish-brown, paler than dorsal pelage. Paler colouration on throat. Fore- and hindfeet pale buffy-brown; ankles blackish. Hindfoot relatively long (ca. 26% of HB). Tail relatively very long (ca. 91% of HB), dark above (darker than dorsal pelage), pale brown (on basal two-thirds) below. Upper first incisor hooked. Unicuspid form a graded series in size: first slightly larger than second, etc. (Description after Hollister 1916.) Nipples: not known.

Geographic Variation None recorded.

Similar Species No other species of *Sylvisorex* has been recorded from NE DR Congo.

Distribution Endemic to Africa. Rainforest BZ (East Central Region) and/or Northern Rainforest–Savanna Mosaic. Recorded only from NE DR Congo.

Habitat No information; presumably rainforest or rainforest–savanna mosaic.

Abundance Uncertain; known only by the holotype.

Remarks Apparently no other information available.

Conservation IUCN Category: Data Deficient; previously assessed as Vulnerable.

Measurements

Sylvisorex oriundus

TL: 130 mm, $n = 1$

T: 62 mm, $n = 1$
 HF: 18 mm, $n = 1$
 E: 8 mm, $n = 1$
 WT: n. d.
 CI: 20.5 mm, $n = 1$
 GWS: n. d.
 I¹–M³: 8.9 mm, $n = 1$
 Medje, DR Congo (Hollister 1916; holotype)

Key Reference Hollister 1916.

Rainer Hutterer



Sylvisorex oriundus

Sylvisorex pluvialis RAINFOREST SHREW

Fr. Musaraigne sylvestre de forêt pluvieux; Ger. Korup-Waldmoschusspitzmaus

Sylvisorex pluvialis Hutterer and Schlitter, 1996. In: Contributions in Mammalogy: A Memorial Volume Honoring Dr. J. Knox Jones, Jr. p.: 61. Ikenge Research Station (05° 16' N, 09° 08' E), Korup N. P., SW Province, Cameroon. 160 m.

Taxonomy Synonyms: none. Chromosome number: not known.

Description Small-medium shrew similar to *Suncus megalura*. Pelage soft; hairs 3.6 mm dorsally, 3 mm ventrally. Dorsal pelage greyish-brown, paler than in other species of the genus. Ventral pelage whitish-grey with white-tipped hairs, a feature shared with *Suncus megalura* and unlike that of other species of *Sylvisorex*. Ears small, rounded, covered with short hairs. Fore- and hindfeet paler in colour than body; with slightly elongated digits. Tail relatively very long (ca. 90% of HB), with short dark hairs and a few longer bristles. Skull flat. First upper incisor small. Third upper incisor large (as in *Suncus megalura* and *Sylvisorex morio*). (Description from Hutterer & Schlitter 1996.) Nipples: not known.

Geographic Variation None recorded.

Similar Species

- Sylvisorex johnstoni*. Much smaller (HB: 45–53 mm; T: 25–36 mm, 50–60% of HB). Ventral pelage orange, hairs not white-tipped. Sympatric in Korup N. P., SW Cameroon; possibly sympatric in SW Central African Republic.
- S. konganensis*. Tail and hindfoot shorter (T: 36 mm; HF: 11.3 mm, n = 1). Tail relatively shorter (ca. 56% of HB). Possibly sympatric in SW Central African Republic and N Congo.
- S. morio*. Dorsal pelage darker (dark russet-brown to black). Tail relatively a little shorter (ca. 75% of HB), without long hairs. In S Cameroon, recorded only from Mt Cameroon.
- S. ollula*. Larger (HB: 91–110 mm). Tail relatively shorter (ca. 57% of HB); ventral pelage brown. Sympatric in Korup N. P., SW Cameroon and possibly in SW Central African Republic.

Distribution Endemic to Africa. Rainforest BZ (West Central Region [Eastern Nigeria and Gabon sub-regions]). Recorded only from the type locality, and from Kongana, Central African Republic (Ray & Hutterer 1995).

Habitat Rainforest.

Abundance Uncertain. Known only from the holotype in Cameroon and from carnivore scats in Central African Republic.

Remarks In Korup N. P., only one specimen was recorded amongst 24 shrews of nine spp. (three other species also represented only by a single specimen) (Hutterer & Schlitter 1996). Recorded from carnivore scats at Kongana, Central African Republic (Hutterer



Sylvisorex pluvialis

2005b). Ray & Hutterer (1995) refer to this species as *Sylvisorex* sp. A, and record that a single specimen of *Sylvisorex* sp. A was obtained among remains of 145 shrews (16 spp.).

Conservation IUCN Category: Data Deficient.

Measurements

Sylvisorex pluvialis

HB: 74 mm, n = 1

T: 67 mm, n = 1

HF: 14 mm, n = 1

E: 8 mm, n = 1

WT: 5 g, n = 1

CI: 19.3 mm, n = 1

GWS: 8.8 mm, n = 1

I¹–M³: 8.6 mm, n = 1

Korup N. P., Cameroon (Hutterer & Schlitter 1996; holotype)

Key Reference Hutterer & Schlitter 1996.

D. C. D. Happold

***Sylvisorex vulcanorum* VOLCANO FOREST SHREW (VOLCANO SHREW)**

Fr. Musaraigne sylvestre des volcans; Ger. Vulkan-Zwergspitzmaus

Sylvisorex vulcanorum Hutterer and Verheyen, 1985. Karisoke, Parc National des Volcans, Rwanda. 3100 m.**Taxonomy** Synonyms: none. Chromosome number: not known.

Description Minute to very small dark shrew (smallest in the genus) with relatively long tail. Pelage soft and fine; dorsal hairs 3–4 mm. Dorsal pelage dark sepia-brown to blackish-brown; hairs grey, sepia-brown at tip. Ventral pelage similar to dorsal pelage but slightly greyer; some hairs with white tips. Head similar colour to dorsal pelage. Ears small, slightly concealed by pelage. Fore- and hindlimbs darkly pigmented, covered by small dark brown hairs. Tail relatively very long (ca. 100% of HB), dark with many small black bristles. Braincase slightly domed. First upper incisor short and slightly hooked. Third upper molar wide. Nipples: not known.

Geographic Variation None recorded.**Similar Species**

Sylvisorex granti. Head and body on average smaller (HB: 56.1 [45–65] mm). Skull usually longer (CI: 16.1–17.0 mm). Marginally parapatric with *S. vulcanorum* in Rwanda and Uganda. Both figured in Hutterer & Verheyen (1985).

S. johnstoni. Dorsal pelage pale brown; ventral pelage orange, contrasting markedly with dorsal pelage. Tail much shorter (T: 25–36 mm) and relatively shorter (ca. 50–60% of HB). Skull shorter (CI: 14.4–14.9 mm). Parapatric in region of N Albertine Rift Valley. Both figured in Hutterer & Verheyen (1985).

S. lunaris. Head and body much larger and much heavier (HB: 70–93 mm; WT: 9–20 g). Tail relatively shorter (ca. 65% of HB). Skull longer (CI: 22.2–22.9 mm). Dorsal pelage moderately dark greyish-brown to mid-brown. Sympatric in montane areas of Albertine Rift Valley.

Distribution Endemic to Africa. Afromontane–Afroalpine BZ. Mountains flanking the Albertine Rift Valley in E DR Congo, SW Uganda, Rwanda and Burundi. Marginally parapatric with *S. granti* in Rwanda and Uganda.

Habitat Remnant montane forest at 1900–3100 m (Hutterer *et al.* 1987).

Abundance Uncertain.

Remarks The relatively long tail suggests that this species may be partly scansorial.

*Sylvisorex vulcanorum***Conservation** IUCN Category: Near Threatened.**Measurements***Sylvisorex vulcanorum*

HB: 49.6 (43–56) mm, n = 5

T: 48.8 (47–51) mm, n = 5

HF: 10.4 (10–11) mm, n = 5

E: 6.6 (6–7) mm, n = 5

WT: 3.5, 3.5 g, n = 2

CI: 15.8 (15.5–16.1) mm, n = 5

GWS: 7.8 (7.7–7.9) mm, n = 5

I¹–M³: 6.6 (6.5–6.8) mm, n = 5

E DR Congo (volcanoes) and Rwanda (calculated from data in Hutterer & Verheyen 1985)

Key Reference Hutterer & Verheyen 1985.**Rainer Hutterer**

Order CHIROPTERA – Bats

Chiroptera Blumenbach, 1779. *Handbuch der Naturgeschichte*, p. 58.

| | | |
|---|---------------------------|--------|
| Pteropodidae (14 genera, 28 species) | Old World Fruit Bats | p. 223 |
| Rhinolophidae (1 genus, 27 species) | Horseshoe Bats | p. 300 |
| Hipposideridae (4 genera, 18 species) | Old World Leaf-nosed Bats | p. 357 |
| Megadermatidae (2 genera, 2 species) | False Vampire Bats | p. 401 |
| Rhinopomatidae (1 genus, 3 species) | Mouse-tailed Bats | p. 409 |
| Emballonuridae (3 genera, 7 species) | Sheath-tailed Bats | p. 418 |
| Nycteridae (1 genus, 13 species) | Slit-faced Bats | p. 438 |
| Molossidae (6 genera, 33 species) | Free-tailed Bats | p. 464 |
| Vespertilionidae (17 genera, 93 species) | Vesper Bats | p. 541 |

Bats are the only mammals that can fly (although there are gliding mammals in other orders) and approximately 20% of the mammals of Africa are bats. Worldwide, there are 1116 species, placed in 18 families and 202 genera, of which 42% are monotypic and 16% have only two species. About 221 species of bats live in Africa; three other species have been reported but they are probably either vagrants or erroneously reported. Furthermore, some of the species undoubtedly contain subspecies or cryptic forms that will eventually be recognized as distinct species, and some species are of dubious status. Indeed, since these profiles were submitted in 2006, one new species has been described and six subspecies have been restored to specific status (details in Appendix) with the consequent addition of three species to the number recorded from Africa: these are not profiled individually but are mentioned in profiles of closely related taxa.

Of the 221 species recognized when this profile was submitted, 28 are megabats traditionally considered to belong to the suborder Megachiroptera, and 193 are microbats traditionally considered to belong to the suborder Microchiroptera. Evidence from recent phylogenetic studies supports the monophyly of the Megachiroptera, but the Microchiroptera is not currently considered to be a monophyletic taxon (see below). Nevertheless, megabats and microbats are sufficiently different in their morphology and habits to justify retaining their names here, in non-taxonomical contexts, at least until the relationships between the families of bats are fully understood.

All megabats belong to one family, the Pteropodidae (Old World Fruit Bats). In Africa, the Old World Fruit Bats are usually referred to simply as fruit bats and therefore, in African contexts, the terms megabat and fruit bat are interchangeable. In the profiles below, the megabats are referred to as fruit bats. In contrast, there are 17 families of microbats, of which eight are represented in Africa and, in the profiles below, species in these families are referred to collectively as microbats (not insect-bats or insectivorous bats, which are commonly used alternatives in other literature). Megabats (which are not always larger than microbats) feed almost exclusively on fruit and/or flower products, and perceive their surroundings mainly

by sight. In contrast, most microbats feed on insects, and perceive their surroundings mainly by echolocation. All African microbats are insectivorous, although some species also eat other arthropods, and at least two species also eat small vertebrates (see Food and Foraging): there are no blood-sucking microbats in Africa. Elsewhere, although most of the microbats are insectivorous, some feed on fruit and/or flower products, some feed on small fish, some feed on blood, and some of the insectivorous species also eat nocturnally migrating birds or small terrestrial vertebrates.

Almost all bats are nocturnal, and some of the explanations for this are given by Speakman (1995). Because the vast majority of species can echolocate and fly (self-powered flight as opposed to gliding), they can feed at night on flying insects (a resource that no other mammal and very few birds can exploit efficiently) and they can roost in totally dark day-roosts. The advantages of these resources to bats have directed the evolution of their morphology, physiology, behaviour, life-histories and almost every other aspect of their biology. However, the origin and early evolution of bats is poorly understood, mainly because the fossil record is very poor. The conventional view is that both megabats and microbats evolved from a common ancestor, which possessed gliding membranes between the fingers, and between the legs and tail, as well as between the arms and legs as in other gliders. Lengthening of the fingers followed, with the result that fully evolved bats can fly as competently as flying birds. However, despite this evolution of arms and legs into wings, many species of bats are also able to scuttle over the ground and/or climb with considerable agility.

Form and structure

In both megabats and microbats, there are species of different size. The length of the forearm (FA) gives a fair indication of overall size. Here, bats are described as very small, small, medium-sized, large or very large on the basis of FA, where each increment is one-fifth of the total range found in African species. For megabats, the total range is 38–163 mm; for microbats the total range is 20–124 mm; therefore the size-categories for megabats are slightly different to those for microbats. In all profiles of bats, when two similar species are distinguished on the basis of the size of FA (or any other character), one is only said to be ‘larger’ or ‘smaller’ than the other if there is no overlap in the ranges of FA of each species. If there is overlap, but the means are different, it is stated that one is ‘larger on average’ than the other or ‘smaller on average’. In contrast, some authors (especially taxonomists) may use ‘larger’ or ‘smaller’ in both of the above contexts. Bats have dorsal and ventral pelage on the head and body, sometimes extending onto the flight-membranes. Mid-dorsal hairs of African bats range in length from 2 to 19 mm. Hairs may be unicoloured or banded with different colours (used diagnostically). Most bats are grey or brown: striking colours or colour patterns are uncommon and, in Africa, limited to some of the species that roost by day in open places where camouflage is valuable. Microbats

are colour-blind and are unlikely to use colour patterns in social behaviour.

Some species have two colour-phases, grey-brown and orange: it has been suggested that the pelage changes from grey or brown (after the yearly moult) to orange or bright russet as it is oxidized by fumes within the day-roost (Constantine 1958, Brosset 1968, Wolton *et al.* 1982). Pelage colour can be bleached by ammonia from bat guano and stained by urine or glandular secretions. In *Miniopterus minor*, older browner pelage is replaced by blacker pelage when the bats moult (McWilliam 1988c); variation in colour in relation to moulting deserves investigation in other species, especially when taxa are distinguished mainly by colour. The effect of environmental humidity on colour also needs further investigation; there is a tendency for forms to be darker in more humid habitats.

Heads of bats are more varied in form than the heads of mammals in other orders. Megabats have dog-like heads with simple muzzles, simple erect ears and very large eyes. In contrast, many microbats have extraordinary heads. Those that emit echolocation calls through the mouth have simple, unadorned muzzles, but those that emit the calls through the nostrils, have a bizarre fleshy outgrowth (noseleaf) on the muzzle, which modifies the emitted sound. Furthermore, the pinnae (external ears) of microbats range from small and simple, to large and extremely complex in shape and structure. The inner surface is often heavily ridged and, in some species, is also creased, so the ears can be folded compactly against the head to reduce loss of heat and water during rest or hibernation. This is achieved by closing valves in blood-vessels so the pinnae deflate; when the valves open, the pinnae inflate very rapidly. Ears that are very large are often connected by a fold of skin linking the inner margins, and have thick cartilaginous margins and bracing, all of which maintain the aerodynamic shape of the ears during flight. Ears of microbats usually have a tragus – a cartilaginous structure arising near the external opening of the ear on the outer side of the pinna. Its presence or absence, size and shape are diagnostic characters. Microbats usually also have an antitragus (lobe near the base of the outer margin of the pinna). Eyes of megabats are very large and are modified to increase visual acuity at night: there is a tapetum lucidum, which causes the eyes to shine red in a spotlight. Eyes of microbats are much smaller and may be minute and partly hidden by pelage or a noseleaf. Bodies of all bats tend to be dorso-ventrally flattened, and tapered from shoulders to hips. Most female bats have one pair of nipples located in the pectoral region: some Vespertilionid species (e.g. *Otonycteris hemprichii*) have two pairs. Bats in the families Rhinolophidae, Hipposideridae and Megadermatidae (and in the extralimital Craseonycteridae) have an additional pair of nipples in the pubic region just anterior to the vagina, which provide holdfasts for the young: these may have at least some lacteal function in many species (Simmons 1993).

Wings of bats vary in shape (see Wing Morphology and Flight). The wing skeleton has the same bones as the forelimbs of other mammals: humerus essentially the same; ulna reduced and fused to radius to form the forearm; wrist as in other mammals but less flexible because the radius does not rotate. The bones supporting the outer part of each wing (the hand-wing) are the same as in the human hand except that the metacarpals and phalanges of the fingers are greatly elongated. The thumb (= first finger) is short and has a claw. Megabats also have a claw at the end of the second finger. The wing-membranes and interfemoral membrane are stretched around

and between the skeletal framework, as in Figure 22. Although these flight-membranes are extremely thin and elastic, they are supplied with blood vessels, muscles and nerves. The hindlimbs are slender and elongated with long toes and with sharp curved claws from which a bat can hang when it is not flying. The hindlimbs are seldom weight-bearing except in some species that are adapted for cursorial locomotion as well as flight and, as an adaptation for flight, they are rotated so the knees point backwards instead of forwards. As a consequence of this, the first toe (or hallux) of a bat is the one on the outside whereas, in all other five-toed mammals, it is the fifth toe which is outermost. The tail is short, vestigial or absent in megabats, but medium to very long in most megabats. Most bats have an interfemoral membrane, which stretches between the hindlimbs and usually encloses the tail. The camber of the interfemoral membrane can be altered during flight by a bony or cartilaginous spur (calcar), which projects from each heel into the trailing edge of the membrane. Each family of bats can be distinguished by the relative length of the tail, and the shape of the interfemoral membrane and the extent to which it encloses the tail.

Skulls of bats vary from family to family and from species to species, depending mainly on (a) diet and how strong the teeth, jaws and jaw muscles must be, (b) the presence or absence of a noseleaf, which requires skeletal support, (c) the emission of vocalizations (ultrasonic or otherwise), which may require resonating chambers in the rostrum and (d) habits such as nectarivory (which may require long narrow muzzles) or roosting in narrow cracks (which may require flattened skulls or other modifications). The following characters of skulls (Figure 23) are widely used to distinguish bats:

Zygomatic arches (= *cheekbones*). Range from massive, broad, widely flared and bony, to frail, slender and cartilaginous.

Sagittal crest. This is the ridge of bone running lengthwise along the top of the braincase; it can be well developed, low or absent.

Lambdoid crest. This is a ridge of bone running transversely across the back of skull at the junction of the dorsal and posterior bones of braincase; it can be well developed, low or absent.

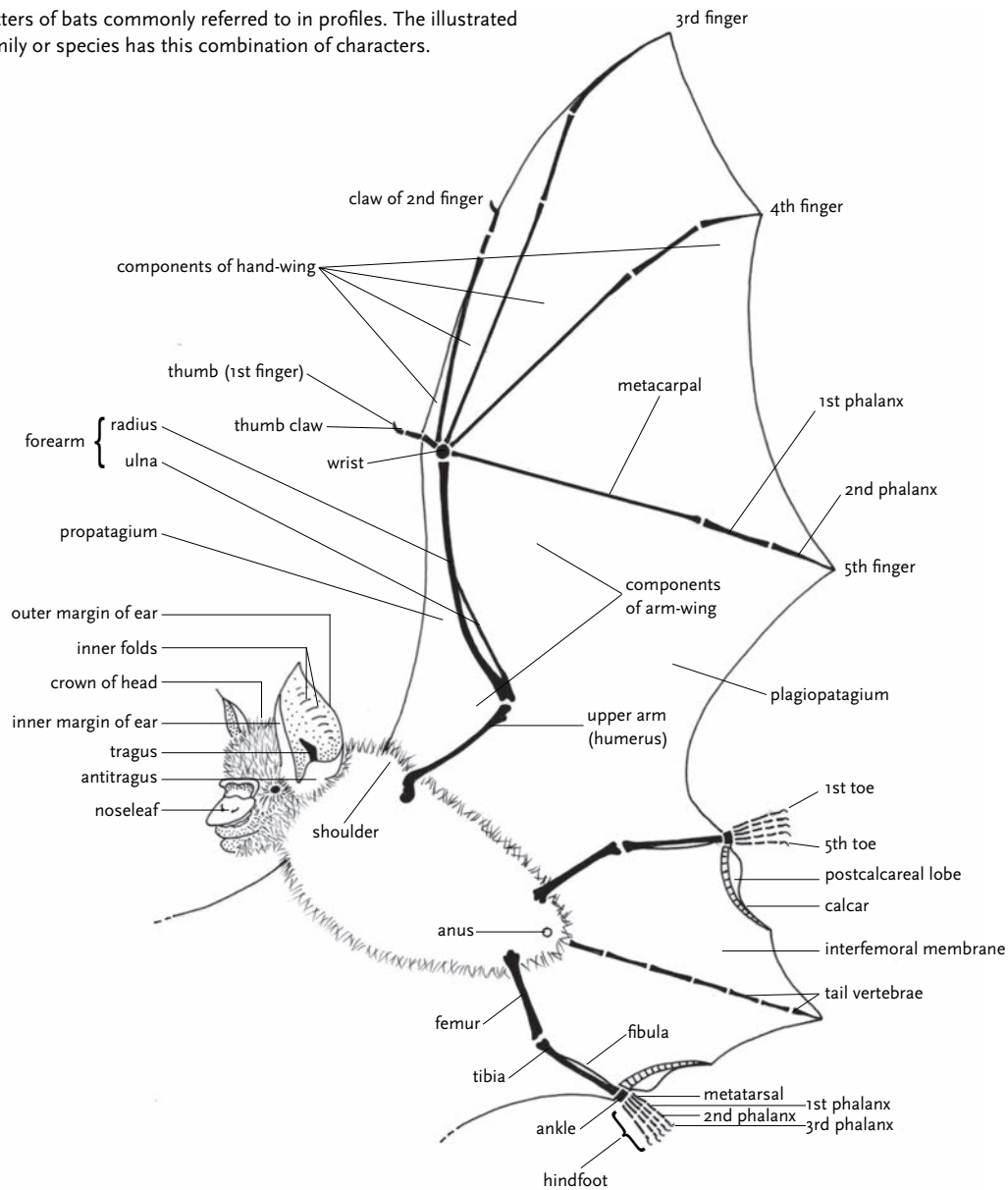
Occipital helmet. This is a backward-pointing projection formed when sagittal and lambdoid crests are well developed and united; it can be present or absent.

Supraorbital crest. This is a ridge of bone along the upper rim of the orbit (eye-socket); it can be present or absent.

Postorbital process. This is a bony projection arising from the upper rim of each orbit and projecting outwards and downwards around the posterior of the orbit: it can be present or absent, long, slender and conspicuous, or concealed as result of merging with the supraorbital ridge.

Premaxillae (sing. *premaxilla*). These are the pair of bones that carry the incisors. Each premaxilla is comprised of a nasal branch that forms one side of the anterior end of the rostrum, and a palatal branch that forms one side of the anterior end of the bony palate (roof of mouth). Either the nasal branches, or the palatal branches, or both branches,

Figure 22. External characters of bats commonly referred to in profiles. The illustrated bat is hypothetical: no family or species has this combination of characters.



may be present or absent, well developed or reduced, independent or fused with other bones.

Anterior palatal emargination. This is an emargination in the anterior of the bony palate associated with loss or reduction of the palatal branches of the premaxillae (see above). It can be closed (non-existent), shallow (barely reaching incisors), deep (reaching level of canines) or very deep (reaching level of premolars or beyond), narrow or wide, and can vary in shape (e.g. U-shaped, V-shaped, bulb-shaped) (Figure 24).

Basiscranial axis. This is the line of the ventral profile of the skull, viewed laterally; usually mentioned when the alignment of the cranial (braincase) region relative to the alignment of the region anterior to the braincase is significant.

Bats have milk-teeth, which erupt prior to birth or soon after: they are shaped to enable neonates to 'lock' themselves onto a

nipple to prevent falling from the mother. Adult bats typically have fully differentiated incisors, canines, premolars and molars. The number of each type of tooth, and the shapes, positions and relative sizes of the teeth, are of taxonomic importance. Teeth may be separated or in contact; within the toothrow (in alignment with other teeth) or displaced either labially (towards the lips) or lingually (towards the tongue); and they may be unicuspid, bicuspid or tricuspid depending on the number of points (cusps) on the crown. Molar teeth of megabats have ridges around the outside with a shallow trough in the middle. Molar teeth of microbats, if fully developed, have a W-shaped pattern of sharp ridges (= commissures) on the grinding surface (Figure 23). However, a molar may be reduced (with the concomitant loss or partial loss of one or two of the most posterior ridges) in which case the pattern usually becomes N-shaped, incomplete N-shaped or V-shaped (for details see Family Molossidae). The length of the maxillary toothrow in bats is $C-M^1$, $C-M^2$ or $C-M^3$ depending on which molar is the most posterior molar.

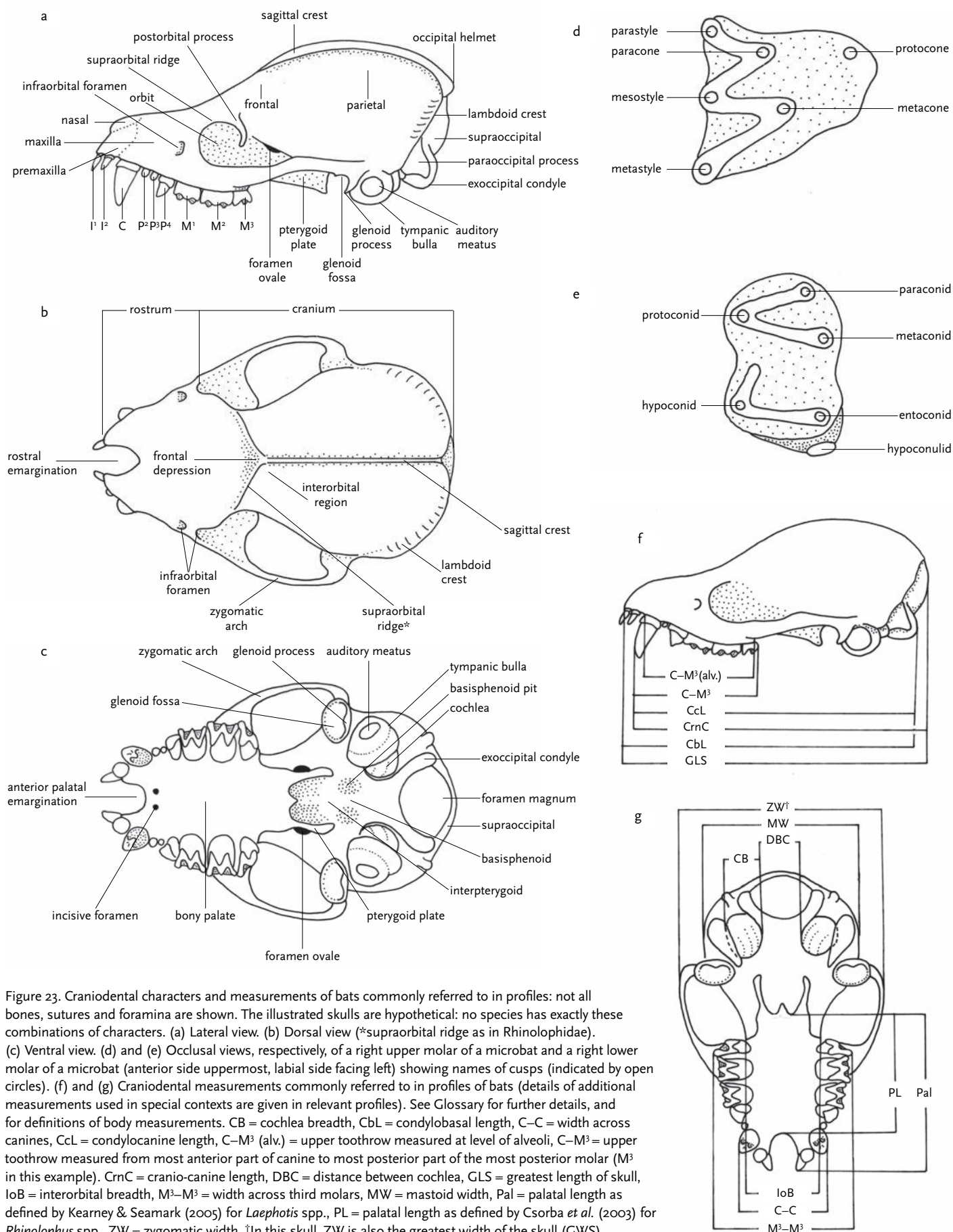


Figure 23. Craniodental characters and measurements of bats commonly referred to in profiles: not all bones, sutures and foramina are shown. The illustrated skulls are hypothetical: no species has exactly these combinations of characters. (a) Lateral view. (b) Dorsal view (*supraorbital ridge as in Rhinolophidae). (c) Ventral view. (d) and (e) Occlusal views, respectively, of a right upper molar of a microbat and a right lower molar of a microbat (anterior side uppermost, labial side facing left) showing names of cusps (indicated by open circles). (f) and (g) Craniodental measurements commonly referred to in profiles of bats (details of additional measurements used in special contexts are given in relevant profiles). See Glossary for further details, and for definitions of body measurements. CB = cochlea breadth, CbL = condylobasal length, C-C = width across canines, CcL = condylocanine length, C-M³ (alv.) = upper tooththrow measured at level of alveoli, C-M³ = upper tooththrow measured from most anterior part of canine to most posterior part of the most posterior molar (M³ in this example). CrnC = cranio-canine length, DBC = distance between cochlea, GLS = greatest length of skull, IoB = interorbital breadth, M³-M³ = width across third molars, MW = mastoid width, Pal = palatal length as defined by Kearney & Seamark (2005) for *Laephotis* spp., PL = palatal length as defined by Csorba *et al.* (2003) for *Rhinolophus* spp., ZW = zygomatic width. †In this skull, ZW is also the greatest width of the skull (GWS).

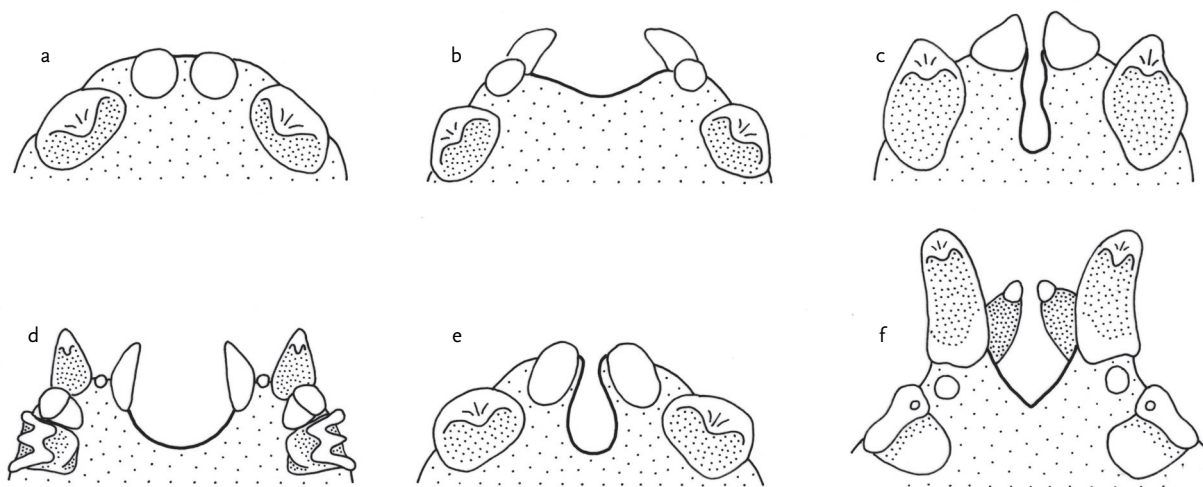


Figure 24. Shapes of the anterior palatal emargination in bats. (a) Closed (e.g. some *Tadarida pumila*); (b) shallow (perhaps does not occur in African bats); (c) deep and narrow (e.g. *Otomops martiensseni*); (d) very deep, wide and U-shaped (e.g. *Glauconycteris poensis*); (e) bulb-shaped (e.g. *Tadarida bivittata*); (f) V-shaped (e.g. *Taphozous perforatus*).

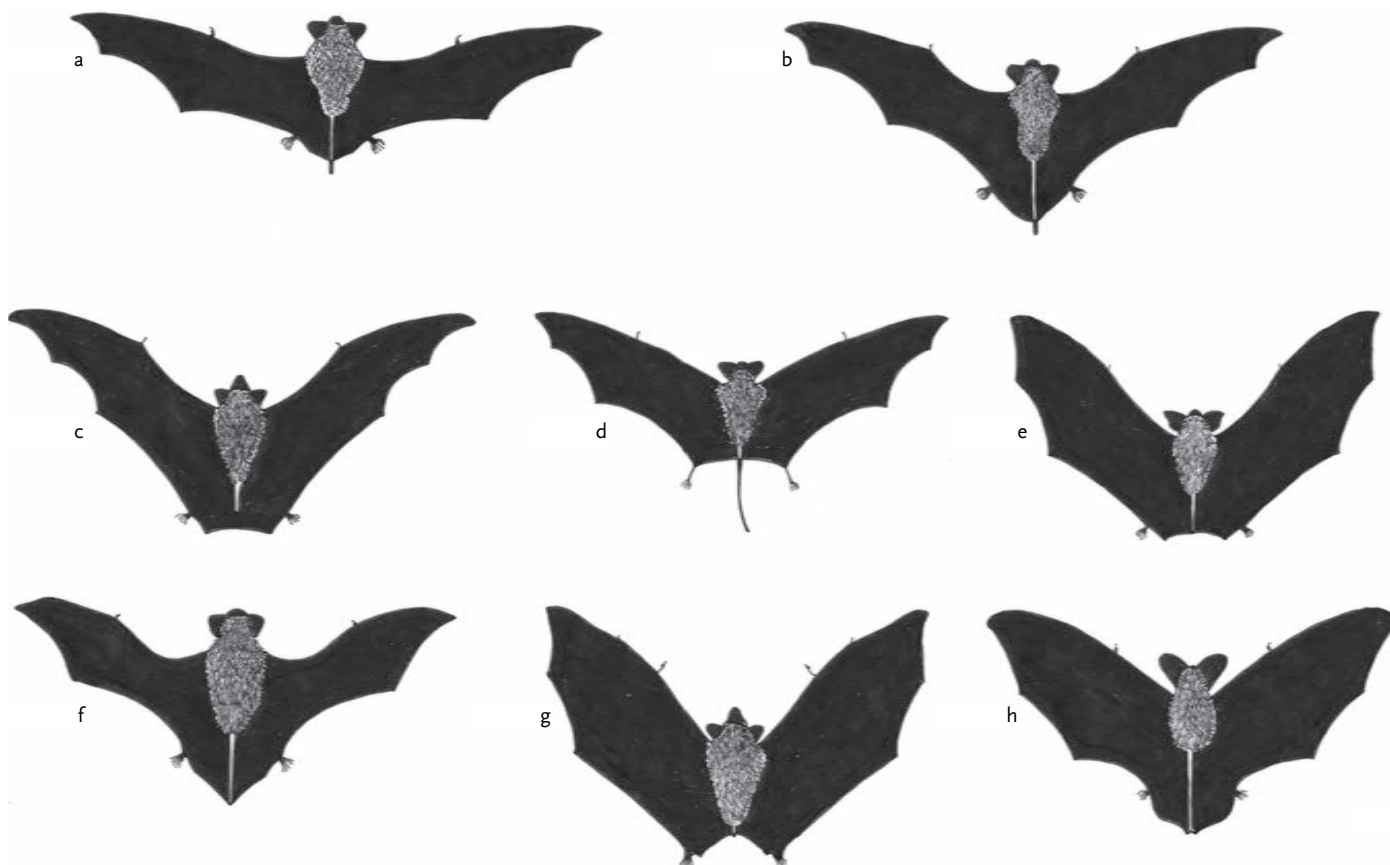


Figure 25. Outlines of flight membranes, bodies and ears of bats with aspect ratios ranging from very high to very low. In all examples except *Rhinopoma* and *Mimetillus*, the layout of the wings follows McKenzie & Rolfe (1986) and the outlines were traced from fresh specimens. (a) *Tadarida nigeriae* (Molossidae): aspect ratio very high. (b) *Tadarida pumila* (Molossidae): aspect ratio high. (c) *Taphozous mauritanus* (Emballonuridae): aspect ratio: medium. (d) *Rhinopoma hardwickii* (Rhinopomatidae): aspect ratio low. (e) *Rhinolophus blasii* (Rhinolophidae): aspect ratio low. (f) *Mimetillus moloneyi* (Vespertilionidae): aspect ratio low. (g) *Epomophorus labiatus* (Pteropodidae): aspect ratio very low. (h) *Nycteris hispida* (Nycteridae): aspect ratio very low.

Wing morphology and flight

Wings of bats differ in shape: there are marked differences between families (Figure 25) and less obvious differences between species belonging to the same genus. The area and shape of the wings in relation to the mass of the bat determine how fast and how slowly the bat can fly, how fast it must be travelling in order to fly, how rapidly and effectively it can turn and manoeuvre, and whether it can hover or take off from the ground. From family to family, these are highly variable. The parameters of greatest significance are aspect ratio (ratio of wing-length to wing-breadth), wing-loading (mass divided by wing-area) and tip-shape. Wingspans and wing-areas can be measured in several ways. Two methods in common usage are those of (a) Norberg & Rayner (1987) and (b) McKenzie & Rolfe (1986) (Figure 26). In method (a), the bat is laid out with the leading edges of its wings at right-angles to the mid-line of the body; wingspan is distance between the tips of each wing and wing-area is the combined area of the wings, interfemoral membrane and body. In (b), the wings are angled forward into a position that approximates the position of the wings when wing-loading is minimal during the downstroke; wingspan is more complex than simply the distance between the wing-tips, and the wing-area includes the area of the head and ears. Measurements obtained by these different methods are not the same. Furthermore, the numerical differences are not consistent because in (b) the wings are always evenly stretched irrespective of species, whereas in (a) the wings are almost evenly stretched in species with long narrow wings but very unevenly stretched in species with short broad wings (M. Happold unpubl.). Here, the problems associated with differences in method are avoided by using the following conventions in the species profiles:

Wingspan (WS). Given in 'Measurements' (with method in brackets), to give a rough indication of the bat's size.

- (a) Wings with leading edges at right-angles to mid-line of body: $WS = \text{distance from wing-tip to wing-tip}$ (Figure 26a; Norberg & Rayner 1987).
- (b) Wings angled forward with all flight-membranes fully and evenly stretched: $WS = \text{approximately the distance from wing-tip to wing-tip via centre of body}$ (Figure 26b; McKenzie & Rolfe 1986).
- (c) Wings forward as in (b) but $WS = \text{straight distance from wing-tip to wing-tip}$. An old method commonly recorded with museum specimens.
- (d) Method not known.

Aspect ratio. Calculated by dividing the square of the wingspan by the wing-area. Described as very low, low, medium, high or very high, where each increment is one-fifth of the total range found in African bats. Methods (a) and (b) for measuring wingspan and wing-area, yield similar (albeit not identical) results for aspect ratios, and the range for African bats is 4.8–10. Narrow wings have high aspect ratios.

Wing-loading = mass (kg) divided by wing-area (m^2). Described as very low, low, medium, high or very high, where each increment is one-fifth of the total range found in African bats. For wingspan method (a) the range for the African species for which reliable data

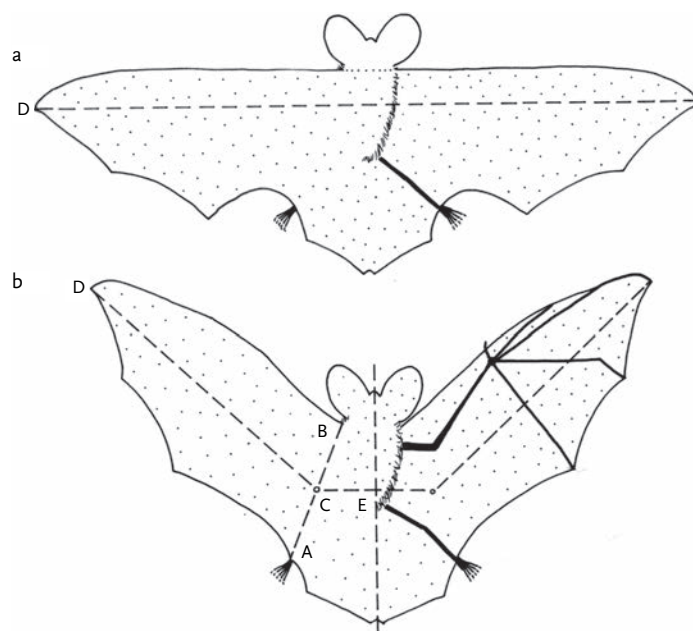


Figure 26. Calculating wingspan and 'wing area' using the methods of (a) Norberg & Rayner (1987) in which the leading edge of the wing is at right angles to the mid-line and (b) McKenzie & Rolfe (1986) in which only the humerus is at right angles to the mid-line. The illustrated species is *Nycteris thebaica* (HC 2942) that maximally demonstrates the different results of each method; the outlines were traced from one fresh specimen. A = point of attachment of wing to ankle, B = closest point on the leading edge of the wing to A, C = mid-point between A and B, D = wing-tip, E = point at which a line from C meets the mid-line at right angles. The areas used in each method of calculating aspect ratio are stippled. For method (a), wingspan = distance between wing-tips in straight line. For method (b), wingspan = $2(CD + CE)$.

are available is 4.5–20 Newton/ m^2 . Wing-loadings above this range are described as exceptionally high, but they need confirmation. For method (b), the range is 4–18 N/ m^2 . Bats with narrow wings have high wing-loadings unless the wings are also long.

Tip-shape. Refers to the length, area and pointedness of the hand-wing (between the fingers) relative to the arm-wing (between the body, hindlimb and fifth finger). Here we describe tip-shape very roughly as short or long, rounded or pointed (for further information see Norberg & Rayner 1987).

Some of the characteristics of a bat's flight and the parameters with which they are correlated are:

Speed. High speed is correlated with high wing-loading. Bats with high wing-loadings must travel at high speed to maintain flight. Flight speeds of at least 27 m/sec (9.72 km/h) (in a molossid) are known (Norberg & Rayner 1987). Here, flight speeds are described as very slow, slow, medium (= average) or fast, but the ranges of flight speeds for each of these categories have not been defined.

Turning. Bats initiate a turn by altering the form of their flight-membranes so one wing has more lift than the other and the bat rolls. The turn itself is then achieved by adjusting the wings, legs and/or interfemoral membrane so drag increases on the side of the dipped wing and the bat turns with the dipped wing on the inside of the turn. Radius of turn is proportional to speed. For this reason, some

bats swoop upwards to lose speed before rolling; some almost stall and therefore achieve 'stall-and-twist' turns, which are extremely tight and wonderfully acrobatic to watch. A 'banked' turn is one in which there is little change in height or speed.

Manoeuvrability is a measure of the minimum space required for a turn at a given speed. Because the radius of a turn increases with increased speed, manoeuvrability is favoured by slow flight and therefore low wing-loading. Manoeuvrability in confined spaces (i.e. in densely cluttered environments) is also favoured by short wings and small overall size. Small, lightweight bats with short broad wings, such as *Nycteris hispida*, can keep flying and manoeuvring very easily within a cubic metre of space. Large heavyweight bats with broad wings need more space because of their larger size.

Agility is the rate at which a turn can be initiated. It is favoured by fast flight and high wing-loading. Bats with great agility make high-speed swerves and swoops in pursuit of insects.

Energetic cost of flight is the energy used per unit time or per unit distance. It is lowest when aspect ratio is highest. Economical slow flight is favoured by long narrow wings; economical fast flight by short narrow wings.

Hovering is favoured by relatively long wings, low wing-loading, small overall size and rounded wing-tips. The wing-beat in hovering is very complex.

Losing height. Some bats, such as the European *Nyctalus noctula*, lose height by rolling through 180° and flying upside down; in this position, the lift-force on the wings is directed downward and this force, together with gravity, results in very rapid descent. Some bats, such as *Otomops martiensseni*, perform a series of side-slips (fish-tailing) to lose height (for details see Norberg 1976).

Landing. Some bats land directly on vertical surfaces, often after swooping upwards to lose speed, and they adjust their posture to head-down after landing. Others perform a half-roll while slowing to stalling speed, which enables them to grasp a perch with their hindfeet and hang freely from it.

Taking-off. Flight requires speed and the higher the wing-loading, the greater the speed that is required. Diving from a high site is the most economical way to accelerate to achieve the required speed and, for bats such as molossids with very high wing-loadings, the necessary speed cannot be achieved in any other way. For bats with low wing-loadings, it is possible to muster enough energy to beat the wings and achieve sufficient acceleration to reach the comparatively slow speeds required for flight, and these bats can take off from level surfaces such as the ground.

Load-carrying. Some bats carry extra heavy loads after feeding, during pregnancy and while carrying young, heavy prey or heavy loads of seasonally accumulated fat. Bats that habitually carry heavy loads have relatively large wings and low wing-loading. Small bats have greater reserves of power and can carry additional weight more easily than larger bats.

Long-distance flight. Long distances are flown by bats that are nomadic or migratory, those that fly long distances between roosts and feeding-grounds, and those that spend many hours flying to obtain flying insects. Economical flight is favoured by high aspect ratios, so these bats have narrow wings. Migratory bats do not necessarily have to fly fast, so many have rather low wing-loadings in conjunction with high aspect ratios. In contrast, bats such as molossids and some emballonurids which forage at high speeds for long periods have high aspect ratios in conjunction with high wing-loadings.

The flight characteristics of bats can be compared in many ways (e.g. Aldridge & Rautenbach 1987). A very simple way is to observe individuals in a 1 × 1 × 1 m enclosure (mosquito netting over a frame) and record whether or not they can fly across the enclosure, complete a full circuit, fly a figure-of-eight with banked turning, gain height, take off from the ground and land on the ceiling (M. Happold unpubl.). The maximum number of circuits flown per flight reflects how easily a bat can manoeuvre in this very confined space, and the minimum radius of banked turns can be determined from the complexity of the manoeuvres (e.g. a figure-8 with banked turns indicates minimum radius <25 cm). Bats that cannot turn around within one cubic metre can be tested in small rooms. The flight characteristics of 36 species of Malawian microbats (six families, 15 genera) were assessed in this way, and the maximum number of circuits/flight and other flight characteristics are given here (see profiles).

Foraging and food

Most megabats feed on soft ripe fruits of trees. For convenience, figs (which are really the flowers of fig trees – *Ficus* spp.) are included here in the category of soft fruits. Some megabats also eat the buds, flowers, pollen and/or nectar of other trees; some feed only on pollen and nectar, and some only on nectar. Megabats have excellent night-vision, colour-vision and a highly developed sense of smell. They detect food at great distance by smell, and at close range also by sight. Most megabats obtain fruit and/or flower products by landing on the vegetation and then feeding. Some carry fruit to a nearby perch before eating it. Some hover briefly before landing, but apparently no African megabats sustain hovering while feeding (cf. the frugivorous phyllostomid bats of the Americas) (Hill & Smith 1984). Some land to take fruit from the ground.

All African microbats are insectivorous but some species also eat other arthropods (e.g. *Nycteris thebaica*, *Otonycteris hemprichii*). *Nycteris grandis* also eats small terrestrial vertebrates and *Nyctalus lasiopterus* also eats nocturnally migrating birds. However, no African microbats are currently known to habitually eat fruit, flower products, fish or blood (as some microbats do elsewhere). There are no blood-sucking bats in Africa. Some species specialize on hard-shelled insects such as beetles, some on soft-bodied insects such as moths, and some are opportunistic feeders that take whatever comes provided the size is manageable. Diets often change between seasons and bats tend to be more opportunistic when insects are scarce.

Depending on their flying abilities and what they are able to perceive visually and by echolocation, microbats forage for different sorts of insects in different ways and places and thereby avoid excessive competition with other species. The methods of foraging exemplified

by African microbats, and the situations where each method takes place, are listed below with examples. Some bats use more than one method.

Fast-hawking. High above ground and vegetation, in very open spaces. Flying insects are detected at long range; pursued with high speed and great agility but poor manoeuvrability; eaten in flight. Foraging flights last several hours and cover long distances. (Emballonurids and molossids.)

Slow-hawking. Semi-open spaces below or close to canopies, small clearings and tunnels in vegetation, and closer to the ground than in fast-hawking. Flying insects are detected at short-range; pursued with moderate speed, moderate agility and moderate to great manoeuvrability; eaten in flight. Foraging flights shorter; interspersed with rest periods. (Most vespertilionids.)

Moderately fast-hawking. Intermediate between fast- and slow-hawking. Combines foraging at moderately high speed in open spaces fairly high above ground and vegetation, with foraging at slower speeds with great manoeuvrability in moderately cluttered spaces. (Some vespertilionids.)

Fly-catching. Close to vegetation and ground in moderately cluttered spaces. The bat hangs from a perch and waits until an approaching flying insect is detected at close range. The prey is pursued during a brief flight with considerable manoeuvrability, and taken to the perch before being eaten. In some literature, this behaviour is included in perch-hunting. (Some rhinolophids and hipposiderids.)

Gleaning. Very close to vegetation and/or the ground in densely cluttered spaces. Non-flying prey is taken from surfaces including foliage, tree-trunks, walls and ground. Hover-gleaners glean while hovering or flying slowly. Foliage-gleaners specialize in taking prey from foliage and tree-trunks and are usually hover-gleaners. Ground-gleaners often land to catch prey but may also take it while flying slowly. Gleaners, especially ground-gleaners, are often perch-hunters (see below). (Some nycterids, rhinolophids and hipposiderids, and a few vespertilionids.)

Perch-hunting. A general term referring to any foraging behaviour in which the bat hangs from a perch while searching for its prey and then returns to the perch to eat and/or to resume searching. Fly-catching is a type of perch-hunting. Ground-gleaning (and perhaps gleaning from other surfaces) is often combined with perch-hunting.

Trawling. Refers to the taking of insects (or small fish) from water surfaces. Prey is taken by the hindfeet: trawling bats have long toes and sharp claws, which act as grapnels. (*Myotis capaccinii*, *M. bocagii*.)

Chasing. Refers to the detection and pursuit of non-flying prey (e.g. cockroaches, resting moths) by bats that scuttle over horizontal and sloping surfaces, or the ground, in pursuit of the prey. (*Taphozous mauritanus*, *Tadarida condylura*, *T. pumila*.)

Foraging strategies are very complex. They are determined not only by 'capture' techniques but also by trade-offs between quantity of food versus its quality, duration of foraging and feeding versus

duration of other activities, and the advantages of obtaining food versus the risk of predation and/or aggression from competitors. African bats whose foraging strategies have been studied in detail (albeit not necessarily in Africa) include *Hypsignathus monstrosus*, *Hipposideros vittatus*, *Cardioderma cor*, *Lavia frons*, *Nycteris grandis*, *N. thebaica*, *Nyctalus leisleri*, *Myotis emarginatus*, *M. nattereri* and to a lesser extent *Epomophorus wahlbergi*, *Hipposideros caffer*, *Tadarida teniotis*, *Pipistrellus capensis*, *P. kuhlii* and *Scotophilus leucogaster*.

Echolocation

Microbats are not blind but, in most species, eyesight is poorly developed and they use vision mainly to tell when it is dark enough to begin foraging, and when moonlight is bright enough to increase danger from predators. Possibly, migrating microbats use vision to perceive landmarks, and some species use vision, at least to some extent, to locate and catch prey, and to detect the approach of predators. Also, in well-known environments, some rely considerably on memory to avoid obstacles (which is why they can be caught in mist-nets). However, microbats mainly perceive their surroundings and locate targets (prey) by using reflected ultrasonic sound instead of light to 'see' in the dark. This procedure is called echolocation, and it enables microbats to perceive range, movement, size, shape and texture with a degree of sophistication that is almost unimaginable to humans (Simmons *et al.* 1979, 1995, Pye 1980, Simmons & Stein 1980, Simmons & Grinnell 1988 and others). In contrast, eyesight is well developed in megabats, and echolocation probably occurs in only one genus, *Rousettus*. Species in this genus produce clicks with their tongues and use these to orientate in total darkness but, unlike the sophisticated echolocation calls made by microbats, these clicks are broad bandwidth, impulse sounds with no clearly defined wave structure, no evidence of frequency modulation, and amplitude patterns that are rapid and transient (Pye 1980). Echolocation calls of microbats are produced in the larynx, modified by the surrounding tissues and spaces, and emitted through the mouth or through the nostrils. Noseleaves, which surround the nostrils of some microbats, beam the sound in front of the bat. Some bats emit echolocation calls that are extremely loud (100–110 decibels at 10 cm distance from the bat); in contrast there are 'whispering' bats whose calls are very quiet (60 decibels at 10 cm). To prevent deafening by their own calls, bats block their hearing mechanism while each call is being produced. Echolocation calls are of very short duration (e.g. 0.2–84 ms in African species), and the dominant frequencies range from ca. 10–212 kHz in African bats. Humans can hear 3–18 kHz, so the echolocation calls of a few species of bats are audible to humans. Echolocation calls may be constant in frequency (CF), or the frequency may be modulated (FM) which means that the frequency increases or decreases evenly within a few microseconds. Many bats emit calls that have both CF and FM components.

Echolocation enables microbats to perceive acoustic images that correspond to the visual images perceived by animals with eyesight. Range (distance) of an object is perceived by the time taken for an echo to return and for this purpose short calls are better than long calls. Sizes of objects can be perceived with greater accuracy by using high-frequency calls (the higher the better) and this is the main reason why bats use ultrasonic calls. With a call of 50 kHz (which has a wavelength of 6.8 mm) objects as small as 6.8 mm can

be measured accurately. However, high-frequency sounds do not travel as far as lower-frequency sounds, so a bat that emits calls of 160 kHz, for example, can only detect prey that is closer than 30 cm and it must fly slowly to avoid collisions. In contrast, bats that emit lower-frequency sounds (e.g. 20 kHz) can detect prey at distances of up to 20 m and have no need to fly slowly. Echoes from stationary objects come back to a stationary bat with the same frequency as the emitted call and this informs the bat that the objects are stationary. In contrast, the frequency of an echo from an object that is moving towards the bat, or away from it, will be increased or decreased by the Doppler effect, and this enables bats to perceive the speed and direction of the moving object (Möhres 1953, Schnitzler 1968, Bell & Fenton 1984). If the bat is moving as well as the object, it can make allowance for Doppler shifts created by its own movement, and can still perceive how objects are moving in relation to itself. Long CF calls are best suited for perceiving Doppler shift and rhinolophids and hipposiderids emit these calls to detect 'flutter' – the fluctuating rise and fall in the frequency of an echo reflected from an object that is moving to and fro, such as the fluttering wing of a moth. Long CF calls are also good for detecting prey that is moving in front of a stationary background and, although they are not good for perceiving range, they are often emitted by bats that forage in cluttered environments. In contrast, short CF calls are good for detecting the presence and range of prey in open spaces, but provide little other information.

To distinguish a stationary moth from the bark of a tree, or a flying beetle from a flying moth, a bat needs to perceive size, shape and texture and for these purposes it needs to emit a broad range of frequencies simultaneously or as near to simultaneously as possible. This can be done by producing FM calls or by producing harmonics. Harmonics are produced by having anatomical structures around the larynx, mouth and nasal cavities that vibrate in sympathy with the vocal cords. The lowest frequency produced by the cords is the fundamental frequency or first harmonic. The second harmonic is twice the frequency of the fundamental; the third is three times the fundamental and so on. Many microbats place maximum sound energy in the second harmonic, but by producing up to four harmonics they greatly improve the discriminating qualities of the call.

Frequency modulated (FM) calls are 'steep' if the frequency changes rapidly with time, or 'shallow' if the frequency changes slowly. Harmonics may be present. The difference between the highest and lowest frequency of any harmonic is the bandwidth: bandwidths range from broad to narrow. FM calls can provide a bat with enough information about size, shape and texture to perceive a camouflaged moth on a tree-trunk, which would probably be overlooked by a bird in daylight. However, FM calls do not provide detailed information about the speed and direction of travel of a flying target. Bats compensate for this by emitting up to 200 calls per second, and comparing the echoes of consecutive calls. Call repetition-rate increases as a bat approaches a target and needs more accurate information. These rapidly emitted FM calls are referred to as feeding-buzzes.

Because CF and FM calls differ in what they enable a bat to perceive, and how effective they are in cluttered environments or open spaces, at close range or at long range, most bats produce multi-purpose calls that have both CF and FM components. They can also emphasize either the CF component or the FM component, or switch entirely from one type to the other, depending on what information they require at the time. Likewise, they can add or delete

the harmonics. Some bats are more versatile than others. Extreme versatility is shown by some vespertilionids and molossids (Figure 27). When searching for prey in open spaces, their search-phase calls are lower-frequency short CF or short shallow FM sweeps with only one harmonic: these narrow bandwidth calls are very appropriate for long-range target detection. As a bat approaches a target, it makes approach-phase calls in which a broad FM sweep is introduced at the beginning of the call: these calls are good for target detection and resolution of its size, shape and movement. As the bat comes even closer, the CF component shortens and disappears and the calls become short, rapidly repeated broad steep FM sweeps that provide superb resolution of target range. In sequence, such a bat might 'see' something at a distance that looks promising; as it comes closer it has a good 'look' to see if it is moth, beetle or some other suitable prey and then, having decided to catch it, it concentrates only on where exactly it is and what it might be doing to avoid capture. Some insects are able to 'hear' ultrasonic calls in the range 20–50 kHz, and respond to the sound of an approaching bat by closing their wings and falling out of the way (Fenton & Fullard 1981, Jacobs 2000).

Echolocation calls, habitat preferences, food, wing morphology and flying ability have evolved in unison and there are strong relationships between them (e.g. Fenton 1982, Norberg & Rayner 1987, Neuweiler 1989, Jones 1993, Schnitzler & Kalko 2001). Therefore it is not surprising that bats with different phylogenies and life-styles emit different echolocation calls. Bats belonging to different families have very different life-styles and they emit echolocation calls that are different and therefore characteristic of each family (see family profiles). If the calls are made audible to humans by a bat-detector, the calls of different families can be recognized by ear. It was once thought that bats emitted species-specific calls and that bats, like birds, could be recognized by their calls (e.g. Fenton & Bell 1981). While this is largely true, recent studies have shown that intra-specific variation is common and that it can be linked, for example, to the purpose of the call, to geographic distribution, to differences in the habitat or foraging areas being occupied at the time, and to the presence of conspecifics. Nevertheless, in particular areas, echolocation calls are a useful means of recognizing species and this has various ecological and behavioural applications, such as following activity patterns at particular localities. Differences in echolocation call characteristics have also enabled cryptic species to be recognized, e.g. the European *Pipistrellus pygmaeus* was discovered because its echolocation calls differ from those of *P. pipistrellus* (Jones & Van Parijs 1993).

Distinguishing the calls of different species by ear is rarely possible, but sonograms (graphs of frequency against time, Figure 28) and computer software that analyses data contained in recordings and sonograms, enable researchers to see and measure the most important physical characteristics of calls. Complete sonograms show all harmonics, but bat biologists often use sonograms that only show the harmonic with maximum energy (= dominant harmonic). Search-phase calls are more useful than approach-phase calls and feeding-buzzes as a means of distinguishing species, but different authors describe these calls in various ways using different characteristics and different terms. Here, search-phase calls are described using the following parameters and using the following terms, which have been derived from diverse sources, including Simmons & Stein (1980), Fenton & Bell (1981), Taylor (1999a), Schnitzler & Kalko (2001) and M. Happold (unpubl.):

Call-shape. The way frequency changes with time as shown on sonograms (spectrograms). Described by terms (or combinations of terms) such as CF, FM, linear, sigmoid, curvilinear, steep or shallow, angular or smooth, and Q (quasi = almost); e.g. the hockey-stick

shaped calls of some vespertilionids are described here as steep FM/QCF (where / marks the transition from the steep FM component to the 'heel', which is almost CF). For call-shapes of African species, and the terms used here to describe them, see Figure 28.

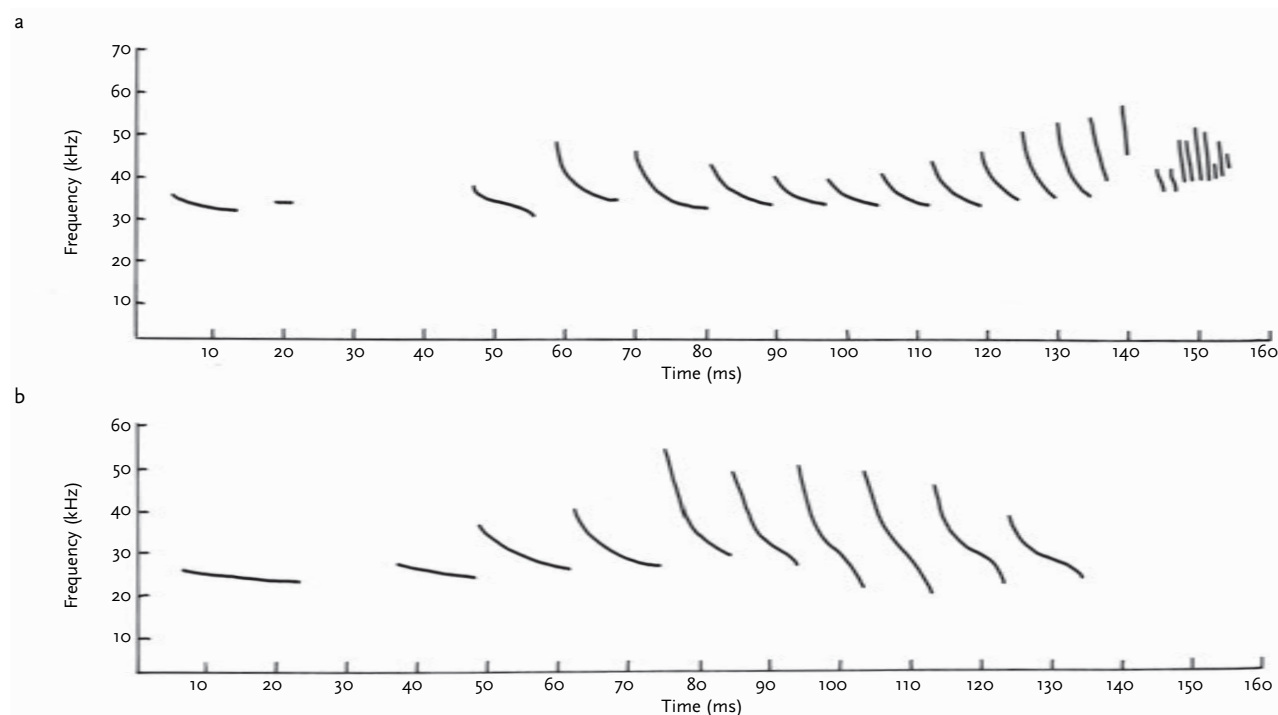


Figure 27. Sonograms of sequences of echolocation calls that have very diverse shapes (M. Happold unpubl.). (a) Calls emitted by a vespertilionid (*Scotoecus hirundo* from Malawi) while searching for prey (search-phase), approaching prey (approach-phase) and then catching it ('feeding buzz'). (b) One search-phase call followed by approach-phase calls associated with rapid acceleration, emitted by a molossid (*Tadarida pumila*); this sequence lacks a 'feeding buzz' indicating that the potential prey was not attacked and captured. Time axis marked at intervals of 10 ms.

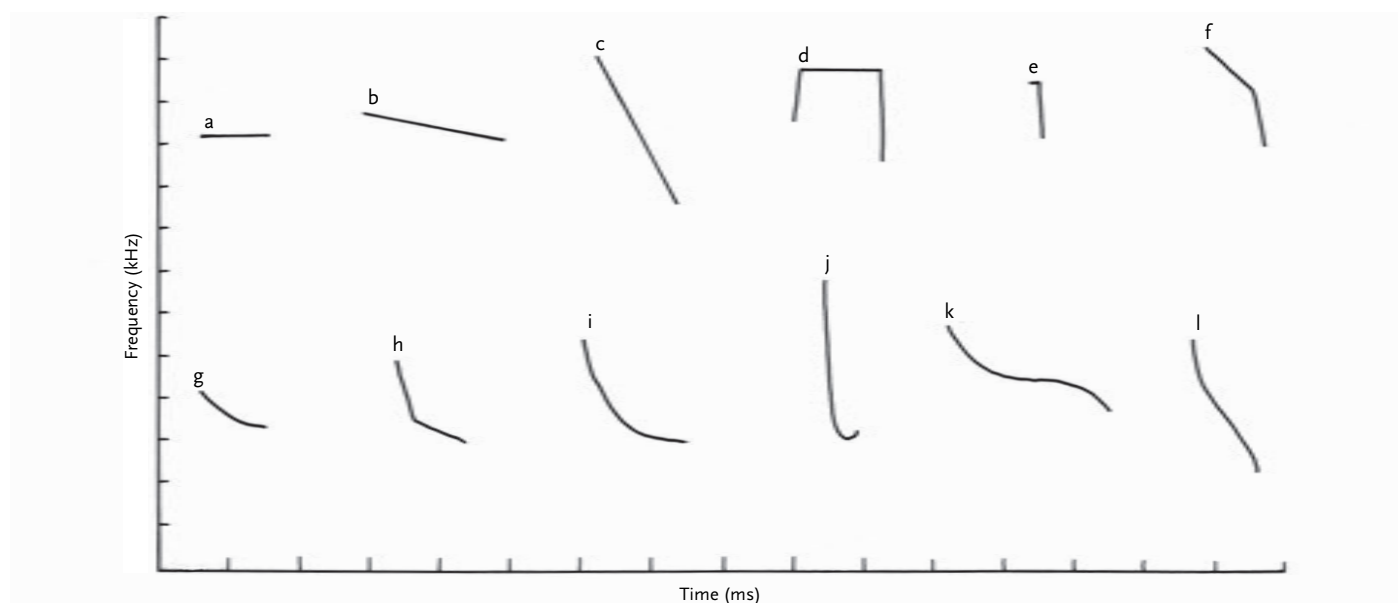


Figure 28. Sonograms of echolocation call-shapes of African bats and the terminology used here to describe them. (a) CF. (b) Shallow linear FM. (c) Steep linear FM. (d) FM/CF/FM. (e) CF/FM. (f) Angular shallow/steep FM. (g) Shallow curvilinear. (h) Angular steep/shallow FM. (i) Smooth steep/shallow FM. (j) Steep FM/QCF. (k) Shallow sigmoid FM. (l) Steep sigmoid FM. All call-shapes, except (d) and (e), are traced from sonograms in which the frequency and time scales are the same: frequency axis marked at intervals of 10 kHz, time axis marked at intervals of 10 ms. For calls-shapes (d) and (e), each interval on the time axis corresponds to 50 ms. Abbreviations: CF = constant frequency, FM = frequency modulated, QCF = quasi (almost) constant frequency. Slashes indicate transitions between different components of a call.

Table 9. Resource partitioning within a community of microbats in miombo woodland in Liwonde N. P., Malawi (M. Happold & D. C. D. Happold pers. obs.). Diets are based mainly on data from Zambia and Zimbabwe. Insects that apparently form a major part of the diet are listed: for details see species profiles. Probably all microbats are opportunistic feeders to some extent, but the size of a bat and its dentition and jaw-strength impose limitations on what it can eat. For definitions of terms, see text.

| Family | Species | Size | Aspect ratio | Wing-loading N/m ² | Foraging | Level of clutter | |
|------------------|--|------------------|--------------|-------------------------------|--|------------------------|--|
| Molossidae | <i>Tadarida condylura</i> | Small | High | Very high | Fast-hawking | Very low | |
| Molossidae | <i>Tadarida pumila</i> | Very small | High | Medium | Fast-hawking | Very low | |
| Emballonuridae | <i>Taphozous mauritanus</i> | Medium | Medium | Medium | Fast-hawking | Very low | |
| Vespertilionidae | <i>Scotophilus dinganii</i> | Small | Medium | Medium | Moderately fast-hawking | Low–moderate | |
| Vespertilionidae | <i>Miniopterus fraterculus</i> | Small | High | Low | Fast- and slow-hawking | Low–moderate | |
| Vespertilionidae | <i>Scotophilus viridis</i> | Small | Low | Medium | Slow-hawking | Low–moderate | |
| Vespertilionidae | <i>Scotoecus hirundo</i> | Very small | Low | Medium | Moderately fast-hawking | Low | |
| Hipposideridae | <i>Hipposideros vittatus</i> | Very large | Low | High | Fly-catching | Moderate | |
| Rhinolophidae | <i>Rhinolophus hildebrandtii</i> | Medium | Low | Low | Perch-hunting and slow-hawking | Moderate | |
| Rhinolophidae | <i>Rhinolophus fumigatus</i> | Medium–small | Low | Low | Fly-catching, slow-hawking and ? gleaning | Moderate | |
| Rhinolophidae | <i>Rhinolophus blasii</i> | Small | Low | Low | Slow-hawking, fly-catching and gleaning | Moderate–high | |
| Vespertilionidae | <i>Myotis tricolor</i> | Small | Low | Low | Slow-hawking, ? gleaning | Moderate (? also high) | |
| Vespertilionidae | <i>Nycticeinops schlieffeni</i> | Very small | Low | Very low | Slow-hawking | Low–moderate | |
| Rhinolophidae | <i>Rhinolophus clivus</i> | Small | Low | Very low | Slow-hawking, fly-catching and ? gleaning | Moderate | |
| Rhinolophidae | <i>Rhinolophus simulator</i> | Small | Low | Very low | Slow-hawking and ? gleaning | Moderate | |
| Vespertilionidae | <i>Myotis welwitschii</i> | Medium–small | Low | Very low | Uncertain | ? Moderate–high | |
| Vespertilionidae | <i>Pipistrellus rueppellii</i> | Very small | Low | Very low | Slow-hawking mainly over water and marshes | Moderate–high | |
| Vespertilionidae | <i>Myotis bocagii</i> | Small–very small | Low | Very low | Slow-hawking and trawling | Moderate–high | |
| Vespertilionidae | <i>Pipistrellus zuluensis</i> | Very small | Low | Very low | Slow-hawking | Moderate–high | |
| Vespertilionidae | <i>Pipistrellus</i> cf. <i>melckorum</i> | Very small | Low | Very low | Slow-hawking | Moderate–high | |
| Vespertilionidae | <i>Pipistrellus nanus</i> | Very small | Low | Very low | Slow-hawking | Moderate–high | |
| Vespertilionidae | <i>Kerivoula argentata</i> | Very small | Low | Very low | ? Gleaning | Very high | |
| Nycteridae | <i>Nycteris grandis</i> | Medium–small | Very low | Low | Slow-hawking, fly-catching and gleaning | Very high | |
| Nycteridae | <i>Nycteris macrotis</i> | Small | Very low | Very low | ? Gleaning | Very high | |
| Nycteridae | <i>Nycteris thebaica</i> | Small | Very low | Very low | Slow-hawking, fly-catching and gleaning | Moderate–very high | |
| Nycteridae | <i>Nycteris hispida</i> | Small–very small | Very low | Very low | Slow-hawking and gleaning | Very high | |

Intensity. Usually described either as low (<75 dB at 10 cm distance) or high (ca. 100–110 dB at 10 cm). In this context, intensity = sound pressure level.

CF-frequency. The frequency of the CF component; particularly useful when the CF component is the main component of the call (e.g. calls of rhinolophids and hipposiderids).

Start-frequency. Frequency at beginning of call. Because high frequencies attenuate rapidly (and therefore cannot be heard and/or

recorded as far away as lower frequencies), sonograms often do not show the highest frequencies that were emitted by the bat. Therefore start-frequencies appear to be very varied and are of comparatively little use as a means of identifying calls.

End-frequency. Frequency at end of call. For FM calls ending with lower frequencies than their start-frequencies, the end-frequency is an important means of identifying calls.

Peak-frequency. Frequency with maximum energy and intensity. Often

Resource partitioning

The number of species in African bat communities ranges from ten or less (e.g. in some montane habitats) to at least 36. Each bat in a community is adapted to exploit a different combination of resources, and to obtain them in different ways, places or times, so that competition between species is minimal. To achieve this, bats have become almost as diverse as birds in their size, morphology, flying abilities, food and foraging behaviour, dependence on water, day-roosts and other habits (O'Shea & Vaughan 1980, Findley & Black 1983, Aldridge & Rautenbach 1987, Rautenbach & Fenton 1992, Decher 1997). Some of the differences between 26 microbats in a community in Malawi, which enable them to co-exist without excessive competition for resources, are given in Table 9.

Day-roosts and roosting behaviour

Bats are most active at night and they roost during the day. Bats are found in a wide range of day-roosts but few species have identical preferences. Lithophilic species depend on natural day-roosts found in caves, rock-crevices, holes under rocks and boulders, and gaps under exfoliating rock. Some lithophilic species also use man-made structures that have similar characteristics, e.g. mines, culverts, cavernous buildings, and nooks and crannies in buildings. Some also use burrows. Phytophilic species roost in trees or shrubs: among foliage or bare branches, on tree-trunks, under exposed roots, inside furled leaves, in small holes in trunks or branches, or in hollow trunks. Some phytophilic species also use man-made structures that have similar characteristics, including exterior walls of buildings (especially under eaves), and nooks and crannies in and under thatch and other structures. Some use holes made by birds such as woodpeckers (Picidae) and barbets (Capitonidae), or bird-nests such as those of weavers (Ploceidae). Some species are adaptable and tolerant and can use a variety of roosts. Others are limited to roosts where temperature, humidity, light-level, noise-level and proximity to food and water meet particular specifications. Some species roost singly or in monospecific groups of varying size. Others commonly roost with bats of other species. When this happens, in a cave for example, the different species will be found in different parts of the cave if their requirements are dissimilar, but may be found in close contact if their requirements are similar. Tolerance may vary seasonally depending on the special requirements of young or hibernating bats. Because many species have specific roost requirements, conservation plans must include protection of the natural day-roosts, and it is very important that bats in caves are not disturbed – especially if they are torpid or hibernating. Not all bats roost in dark places: some commonly cling to the outside walls of houses and exposed tree-trunks. Some bats move to a different roost every few days; others show varying degrees of roost-fidelity. Roost-fidelity is usually strong in species that roost in caves, hollow trees and buildings that provide permanent sites. In contrast, foliage-roosting bats often show fidelity to a home-area rather than to a specific roost. Some bats show fidelity to one or more roosts, which they use alternately. Roost-fidelity is often strongest during maternity.

Bats roost in several ways. Bats in some families hang from one or both hindfeet, with the toes curled round slender twigs or toe-holds

| Search-phase
Echolocation | Diet |
|---|--|
| Shallow linear FM and shallow sigmoid FM | Hard-shelled beetles and various soft-bodied insects |
| Shallow linear FM | Mainly soft-bodied insects |
| CF and short shallow linear FM | Mainly moths |
| Very shallow linear FM and steep/shallow FM | Mainly beetles; also various other insects |
| Steep FM/QCF | Mainly Diptera; some beetles and moths |
| Steep FM/QCF (in moderate clutter) | Mainly beetles; also various other insects |
| Very shallow linear FM and steep/shallow FM | Not known |
| CF/FM | Mainly hard-shelled beetles |
| FM/CF/FM | Mainly beetles and moths |
| FM/CF/FM | Beetles, moths and other insects |
| FM/CF/FM | Moths |
| Steep linear FM | Not known |
| Steep/shallow FM | Beetles, Diptera and various other insects |
| FM/CF/FM | Moths, small beetles |
| FM/CF/FM | Mainly moths |
| Steep linear FM | Includes beetles |
| Steep FM/QCF | Includes beetles |
| Steep linear FM | Minute insects including moths and beetles |
| Steep FM/QCF | Includes moths and beetles |
| Steep FM/QCF | Not known |
| Steep FM/QCF | Mainly small beetles and moths |
| Whispering | Not known |
| Whispering | Small vertebrates, insects |
| Whispering | Orthoptera, beetles, termites |
| Whispering | Various insects (opportunistic) |
| Whispering | Small moths and other small insects |

analysed by computer software and particularly useful as a means of identifying calls.

Call-duration. The duration (in ms) of each call (= pulse) within a sequence of calls. Sometimes means and ranges are given, sometimes only maximum durations.

Intercall-interval. The interval (in ms) between successive calls in a sequence of calls.

on rough surfaces. The weight of the bat's body causes tendons in the hindlimbs to pull the toes into the curled position so that hanging is effortless but the bat must exert effort to release its grip. Bats may hang freely, or in contact with vertical surfaces such as walls or tree-trunks. Some species always hang freely; others hang either freely or in contact. Some species hang apart (with no contact with other bats) while other species huddle together in tight clusters. Bats in other families do not hang: instead they either crouch on surfaces that are horizontal, or cling (head down) to surfaces that are sloping or vertical. In both cases, they hold on with their thumbs as well as their hindfeet. Some species crouch or cling on exposed surfaces; others tuck themselves into crevices. Some crouch or cling apart; others huddle. Most bats fold their wings against the sides of their bodies, but pteropodids, rhinolophids and hipposiderids wrap them around the body.

Torpor and hibernation

Daily torpor

Bats are warm-blooded and, because they are small, they require a great deal of food to maintain a high constant temperature at all times, even in the tropics. Because of this, some species of microbats do not attempt to maintain a constant temperature. Instead, during the day, these bats go into torpor, allowing the body temperature to fall from around 34–39°C to approximately the ambient temperature. Torpid bats move very sluggishly and are unable to fly, but they are perfectly healthy. At dusk, they warm themselves up by shivering, a process that takes ca. 20 minutes. When they become warm enough, they become active, investigate their surroundings, yawn, communicate with their neighbours, and indulge in long sessions of meticulous grooming before taking off to forage for food. Only one African megabat, *Megaloglossus woermanni*, is known to enter torpor. In contrast, one or more species of African microbats in each of the families Rhinolophidae, Hipposideridae, Rhinopomatidae, Emballonuridae, Molossidae and Vespertilionidae becomes torpid during the day.

Hibernation

In temperate regions (including those in North Africa and South Africa), when temperatures are low and flying insects very scarce during 'winter', many microbats spend most of the time (day and night for many days) in a deep state of torpor referred to as hibernation. During this time, they slowly metabolize large reserves of fat that are laid down during the autumn. Bats also accumulate reserves of brown fat in autumn, and deposits of the two kinds of fat can result in a bat's weight being 20–30% higher in autumn than in spring. The brown fat is used if and when bats arouse themselves during the hibernation period – which they do occasionally in order to urinate, defecate, drink, feed or move to a more favourable roost. Arousal also occurs if bats are disturbed during hibernation and, because the precious reserves of fat are depleted each time this happens, bats are unable to survive if they are disturbed more than a very few times. Consequently, populations may be endangered by excessive disturbance of large numbers of bats at the roosts where they are hibernating. Roosts used during hibernation are called hibernacula. Invariably, hibernacula must be very humid to

prevent the bats becoming dehydrated, and often hibernating bats glisten with droplets of water that have condensed on their pelage. Furthermore, each species requires a particular ambient temperature for hibernation. For this reason, roosts used as hibernacula are often different to the day-roosts used in summer, and hibernacula such as caves and other underground cavities are often occupied by several species of bats, which may choose to hibernate in different parts (with different temperatures) if their temperature preferences are different. During hibernation, bats often huddle together and usually adopt special postures to reduce the area of their body surface; both facilitate the conservation of energy and water. Their heart-rates drop to as low as 18–80 beats/min (cf. as high as 880 beats/min when active) (E. Kulzer in Schober & Grimmberger 1989), and there can be as much as 60–90 min between breaths of air. Furthermore, hibernating bats are almost incapable of body-movement, so it is easy to think that they are dead. In North Africa, hibernation has been observed in 12 species (*Rhinolophus euryale* and two other rhinolophids, *Tadarida teniotis*, *Barbastella barbastellus*, *Nyctalus leisleri*, *Pipistrellus pipistrellus*, *Myotis capaccinii* and other species of *Myotis*, and *Miniopterus schreibersii*). In South Africa, hibernation has been observed in five species (*Rhinolophus capensis*, *R. clivosus*, *Myotis tricolor*, *Miniopterus fraterculus* and *M. natalensis*).

Drinking, water balance and kidneys

Bats, like other mammals, must balance water loss (mainly from evaporation, urination and defaecation) with water obtained by drinking water, eating moist foods and metabolizing fats and carbohydrates. For bats, evaporative water loss during flight is extremely high: in one species it is 3.1% body weight/h compared with 0.05% during rest (Carpenter 1969). The rate of water loss through the kidneys varies greatly, depending on the amount of waste products that need to be excreted and on the urine-concentrating ability of the kidney. Megabats obtain copious amounts of water from their food, and their diet is low in protein and salts. Their kidneys excrete large volumes of very dilute urine while maximally retaining valuable solutes, and their faeces are moist. For example, *Rousettus aegyptiacus* produces urine concentrations ranging from 88 to 1800 mOsmol/kg. It is unlikely that megabats need to drink once they have started to feed but those that roost in sunny or windy places probably need to drink soon after leaving their roosts, especially if their feeding-grounds are far away. Some species usually roost near water, and some species skim over water, dip into it and presumably drink although this has not been confirmed (Bergmans 1978). Some flying-foxes (including *Pteropus seychellensis*) sometimes drink seawater, possibly to obtain salts. In contrast to megabats, insectivorous microbats obtain much less water in their diet, and need additional water to excrete waste products. Although they obtain some water by metabolizing fat from insects, it is predicted that they also need to drink, and many species come to pools and rivers presumably for this purpose. Insectivorous microbats produce dry faeces and their kidneys conserve water by producing concentrated urine. Mean maximum urine concentration can be predicted reliably from the ratio of cortex width to medulla length, which is very variable (Figure 29); the longer the medulla relative to the width

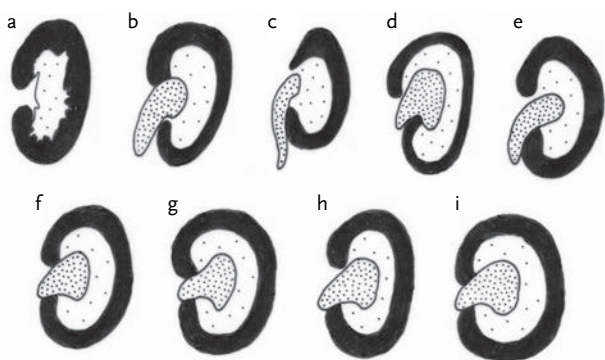


Figure 29. Outlines of mid-sagittal sections of kidneys from Malawian bats and, in brackets, the predicted mean maximum urine concentration ranking for the microbats. (a) *Epomophorus wahlbergi* (fruit-bat), (b) *Pipistrellus zuluensis* (very high), (c) *Nycticeinops schlieffeni* (very high), (d) *Taphozous mauritanus* (high), (e) *Laephotis botswanae* (medium), (f) *Hipposideros ruber* (low), (g) *Rhinolophus clivosus* (low), (h) *Nycteris thebaica* (low) and (i) *Tadarida condylura* (very low). Cortex in black. In (a) entire medulla lightly stippled. In others, outer zone of medulla lightly stippled, inner zone of medulla heavily stippled. Based on Happold & Happold (1988).

of the cortex, the more concentrated the urine can be (Geluso 1980). In 28 species of microbats, representing five families, which live in diverse African habitats, predicted mean maximum urine concentration ranges from 2298 to 4709 mOsmol/kg (Happold & Happold 1988). This is comparable with the range 2390–5010 mOsmol/kg, determined from water deprivation experiments or predicted from renal morphology, for 27 species of insect-eating microbats from elsewhere (Geluso 1980). Efficient water-conserving kidneys are probably particularly advantageous to species that do not drink during sustained periods of torpor or hibernation. Although some desert microbats have efficient water-conserving kidneys, some do not: the ability of bats to live in desert habitats, and also to roost in hot dry day-roosts, seems to depend on their ability to fly to sources of water and not on their ability to reduce urinary water loss (cf. desert rodents).

Distributions, habitats and species richness

Profiles include a distribution section in the text as well as a map. Both must be consulted for a complete record of known localities because the text sometimes includes localities that are not mapped.

Bats are found throughout Africa with the exception of some extremely hot and dry desert regions (where water, food and/or cool day-roosts are limiting factors) and the tops of high mountains (where food, day-roosts and low temperatures are limiting factors). Of the 220 species in Africa (excluding *Mormopterus acetabulosus*, *M. francoismoutoui*, *Pipistrellus permixtus* and *Phoniscus aerea*, which are not likely to be true residents of Africa), 65% are found only or mainly in the tropics, 25% inhabit both tropical and temperate habitats, and 10% are found only in temperate habitats. Of the 22 temperate species, only *Rhinolophus capensis* and *Cistugo lesueuri* are found in southern Africa, and most of those found in North Africa are Palearctic species that extend into Africa across the Mediterranean Sea, or via the Middle East. Some species are found in many biotic zones and are distributed very widely. Of the 220 species for which data are available, 9% are found only in the coastal

and/or montane habitats of the Maghreb and Cyrenaica in North Africa. Elsewhere, 24% occur only in forests (rainforests, montane and riverine forests), 25% in both forests and savannas, 28% only in savannas, 7% in savannas and arid zones, 4% only in arid zones (where food and suitable day-roosts are available), 2% are able to exploit forest, savanna and arid habitats and 1% are island specialists. Ninety-two species (42%) are able to exploit montane habitats, but only two rhinolophids and six vespertilionids have been found only in montane habitats. Although all bats can fly, they vary in how far they can fly without resting and how easily they can orientate and travel across unfamiliar or inhospitable terrain. Consequently, the distributions of some species are restricted by geographical barriers such as drought corridors, the Dahomey Gap and other belts of unfavourable habitat (natural or man-made), the Rift Valleys and the Lower Zambezi Valley, and some of the largest rivers. In contrast, the distributions of many species have been extended by corridors of suitable habitat such as riverine and gallery forests in savannas. Because the requirements of bats may have patchy distributions, or vary seasonally, the bats themselves may have patchy distributions, and distribution maps often give a misleading impression that species are more widely distributed than they are in reality.

For species with wide distributions, the sources of locality records are too numerous to list in the profiles. In many of these cases, the major sources are country checklists and surveys including the following. **Algeria:** Kowalski & Rzebik-Kowalska 1991. **Angola:** Crawford-Cabral 1986. **Benin:** Robbins 1980. **Botswana:** Smithers 1971. **Burkina:** Koopman *et al.* 1978, Koch-Weser 1984. **Burundi:** Kock 1980, Verschuren 1980. **Cameroon:** Aellen 1952, Perret & Aellen 1956, Eisentraut 1973a. **Central African Republic:** Schlitter *et al.* 1982, Lunde *et al.* 2001. **Chad:** Viellard 1974. **Congo:** Aellen & Brosset 1968, Dowsett *et al.* 1991. **Côte d'Ivoire:** De Vree 1971, Lim & Van Coeverden de Groot 1997. **Djibouti:** Pearch *et al.* 2001. **DR Congo:** Hayman *et al.* 1966. **Egypt:** Gaisler *et al.* 1972, Qumsiyeh 1985. **Equatorial Africa (Bioko I.):** Eisentraut 1964, 1973a, Juste & Ibáñez 1994. **Equatorial Africa (mainland):** Jones 1971. **Ethiopia & Eritrea:** Lagen *et al.* 1974, Yalden *et al.* 1996. **Gabon:** Brosset 1966. **Gambia and Ghana:** Grubb *et al.* 1998. **Guinea:** Veiga-Ferreira 1948, 1949, Eisentraut & Knorr 1957. **Guinea-Bissau:** Monard 1939. **Kenya:** Aggundey & Schlitter 1984, Schlitter *et al.* 1986. **Lesotho:** Lynch 1994. **Liberia:** Kuhn 1965, Koopman 1989, Koopman *et al.* 1995. **Libya:** Qumsiyeh & Schlitter 1982. **Malawi:** Happold *et al.* 1987, Ansell & Dowsett 1988, Happold & Happold 1997. **Mali:** Meinig 2000. **Morocco:** Aulagnier & Thévenot 1986, Benda *et al.* 2004d. **Mozambique:** Smithers & Lobão Tello 1976. **Namibia:** Shortridge 1934. **Niger:** Braestrup 1935. **Nigeria:** Happold 1987. **Senegal:** Adam & Hubert 1972, Verschuren 1982. **Sierra Leone:** Grubb *et al.* 1998. **Somalia:** Funaioli 1971, Varty & Hill 1988. **South Africa:** Herselman & Norton 1985, Smithers 1983, Taylor, P. 1998, 2000. **Sudan:** Kock 1969a, Koopman 1975, McLellan 1986. **Swaziland:** Monadjem 1998a. **Tanzania:** Swynnerton & Hayman 1951, Kulzer 1962, Cockle *et al.* 1998. **Togo:** De Vree *et al.* 1969, 1970, De Vree & Van der Straeten 1971, Robbins 1980. **Tunisia:** Aellen & Strinati 1969. **Uganda:** Kityo & Kerbis 1996. **Zambia:** Ansell 1978. **Zanzibar I., Pemba I. and Mafia I.:** Moreau & Pakenham 1940, Kock & Stanley 2009. **Zimbabwe:** Smithers & Wilson 1979, Hutton 1986, Cotterill 1996a, b, 2001b, c, 2002b. A great many other localities

have been obtained from other literature and museum specimens, and all maps were reviewed at a Global Mammal Assessment workshop, held in Jan 2005, and attended by ca. 40 mammalogists currently working on bats and/or small mammals in Africa. Since the profiles were submitted in 2006, new locality records have been published. If the new records significantly change the distribution of a species, they are now mentioned in the species profile but it was not possible to update the maps. For this reason, and others, the distribution sections in the profiles often contain localities that are not shown on the maps.

Species richness is greatest in areas where there are diverse day-roosts for both phytophilic and lithophilic bats, abundant food of different sorts, and diverse habitats suitable for species with different foraging strategies. On a broad scale, it seems that there are usually more species near the Equator than at higher latitudes, as roughly indicated by the following examples: 57 species in savanna at 08°45'N in Comoe N. P., Côte d'Ivoire (Fahr & Kalko 2011), 51 species at ca. 07°40'N on Mt Nimba, in Guinea, Côte d'Ivoire and Liberia (A. Monadjem pers. comm.), 40 species in rainforest at 05°50'N in Tai N. P., Côte d'Ivoire (Fahr & Kalko 2011), although only 25 species in thorn scrub at 02°18'S at Masalani, near Kibwezi, Kenya (O'Shea & Vaughan 1980). For comparison, there are 27 species in miombo woodland at 15°02'S in Liwonde N. P., Malawi (Happold & Happold 1997), and ca. 36 species in diverse woodlands at ca. 18°S at Sengwa Wildlife Research Area in Zimbabwe (Fenton 1985). However, climate, habitat diversity, the area included in the locality, differences in sampling methods and in the amount of time spent sampling, mean that these data give only a rough estimate of latitudinal variation in species richness.

Localized movements, migration and nomadic movements

Localized movements

These occur when bats fly within part or all of their home-ranges within a single night or within a limited period of time. They include movements between different day-roosts, which are used during a particular season, and foraging flights from the day-roosts. Some fruit bats routinely fly 10 km from their day-roosts to their foraging-grounds and another fruit bat, *Eidolon helvum*, forages as far away as 59 km from the day-roost when not migrating (Richter & Cumming 2008). Molossids, which fly very fast (e.g. 27 m/sec) for most of the night, must also travel long distances although not necessarily so far from their day-roosts.

Migration

This describes the movements of species that travel predictably, and more-or-less directly, from one habitat to another (and back again) along predetermined routes, in response to seasonal changes in climate, food supply or any other resource. Migrating species do not migrate continuously. Some fruit bats, including *Eidolon helvum*, *Myonycteris torquata* and *Nanonycteris veldkampii* (see species profiles) migrate from the Rainforest–Savanna Mosaic to savanna zones (such as the Guinea Savanna BZ in West Africa), and then back again. In West Africa, round-trip distances of at least 750 km have

been reported for *Myonycteris torquata* and *Nanonycteris veldkampii* (see species profiles), and *Eidolon helvum* is reported to travel round-trip distances of ca. 1500 km in West Africa (Thomas 1983). Elsewhere, *E. helvum* ♂♂ travel at least 2000 km in three months, from NC Zambia to N DR Congo (Richter & Cumming 2008). In West Africa, the migration of fruit bats follows the rains associated with the Intertropical Convergence Zone, which oscillates north and south, creating bimodal peaks in rainfall in the Rainforest–Savanna Mosaic, and a unimodal peak in the Guinea Savanna BZ. In contrast, other West African fruit bats apparently do not migrate and therefore there are resident or nomadic populations of these species either in the rainforest, or in the savannas, throughout the year. Thomas (1983) investigated the seasonal migrations of the four fruit bats listed above, and suggested that the seasonality of fruit production, population levels of the resident species and the levels of competition for food resources may interact to create the conditions necessary for migration. He suggested that the high amplitude of the seasonal fluctuations in abundance of fruit in savanna habitats creates a wet-season surplus of food, which results in low intra-specific and inter-specific competition levels in these habitats compared with the levels in the rainforest where fluctuations in the abundance of food are of much smaller amplitude. Migration driven by the search for food is sometimes referred to as alimentary migration.

Several species of African microbats are also migratory, but often for reasons different to those of fruit bats. For example, in South Africa, some species migrate from warmer regions where they roost in summer to cooler regions where they can find the conditions enabling them to hibernate during the winter; these species include *Rhinolophus simulator*, *Nycteris thebaica*, *Myotis tricolor*, *Miniopterus fraterculus* and *M. natalensis* (see species profiles). Most species of North African bats are also reported to migrate between summer- and winter-roosts – in Europe if not in Africa. In East Africa, it has been suggested that some species avoid the long dry season (Oct–Dec) and associated shortage of insects experienced in inland lowland localities by migrating to coastal or montane habitats that receive rain during this period; these alimentary migratory species include *Hipposideros vittatus*, *Taphozous hildegardeae* (but not all populations) and *Scotoecus hirundo* (see species profiles).

An interesting consequence of migration in bats is that two taxa may be sympatric during part of the year and allopatric during another part, and unless the time of mating is known, it is impossible to determine whether or not these two taxa have an opportunity to interbreed (Koopman 1983). As reproductive isolation is the crux of the biological species concept, when taxa are raised to specific status on the grounds that they are geographically isolated, it is important to be certain that migratory patterns do not bring the taxa together sympatrically during their mating seasons when interbreeding would be possible. Conversely, two taxa could be sympatric for much of the time, but geographically isolated during the mating period and therefore reproductively isolated.

Nomadic movements

Unlike migration, nomadic movements are unpredictable and irregular, and are undertaken by species that live in unpredictable habitats (Delany & Happold 1979). They do not occur at any particular season, or at yearly intervals, and the direction and

extent of nomadic movements vary according to local conditions. Within fairly localized areas in savannas and arid zones, and even in rainforests, trees flower and fruit at different times in neighbouring areas depending mainly on where and when localized rainfall occurs, and this drives nomadic movements by some fruit bats. African fruit bats that are thought to be nomadic include *Epomophorus crypturus*, *E. gambianus*, *E. wahlbergi* and *Megaloglossus woermanni* (see species profiles). Vagaries of rainfall also create unpredictable rises and falls in the abundance of insects in neighbouring areas as, for example, when a local downpour stimulates the emergence of flying termites in that area. However, as yet there appear to be no documented accounts of nomadic movements in African microbats.

Social and reproductive behaviour

Very little is known about the social behaviour of most species, and most of our knowledge comes from observations of a few species at their day-roosts. Some species of bats are solitary. Other species live in pairs (i.e. one ♂ with one ♀) or monogamous family groups, some form harems (one ♂ with two or more ♀) and some live in groups of other kinds. Groups range in size from three to many thousands of individuals and sometimes several millions (e.g. five million *Eidolon helvum* at one locality in Zambia). Following Ansell (1960a), groups are described as small (3–15), medium (15–30), large (30–100), or very large (more than 100). Some groups are comprised of roughly equal numbers of ♂♂ and ♀♀, while others may be comprised mainly or solely of ♂♂ or of ♀♀. Some species spend the dry seasons or winters in groups of adult ♂♂ and ♀♀, but form maternity colonies comprised of pregnant ♀♀ and/or lactating ♀♀ and their young in the warmer, wetter months.

Bats interact with each other in many ways. They communicate with vocalizations (many of them audible to humans), and with olfactory, tactile and occasionally visual signals. Bats that belong to groups recognize each other and may roost and forage together. Individuals that are not recognized may be threatened with specific vocalizations, swiped by the claw of a thumb, or they may be pursued, attacked and bitten. Many species defend feeding territories and/or roosts. Although group-members may roost together, many maintain some distance between themselves and their nearest neighbour; this space may be established and maintained with vocal protest and jostling. Territorial disputes for the best places are a common occurrence and the outcome may influence mate-selection.

Compared with other mammals, little is known about the reproductive behaviour and social organizations of bats, but there are some notable exceptions and several types of social organization and mating systems have been defined (e.g. Bradbury & Vehrencamp 1976, Emlen & Oring 1977, Bradbury 1979, 1981). These include (with African examples):

Monogamy. One ♂ mates with one ♀ and that ♀ only mates with that ♂ (e.g. *Hipposideros beatus*, *Lavia frons*).

Polygyny. One ♂ mates with several ♀♀. Polygynous social organizations and mating systems include harem-formation (one ♂ resides with and mates with a stable group of ♀♀). Harem-

formation may be based on the defence of a group of ♀♀ (female-defence polygyny) as in *Coleura afra*, or on the defence of one or more resources (e.g. roosts and/or foraging areas) to which small groups of ♀♀ are attracted (resource-defence polygyny) as in *Pipistrellus* cf. *helios*, or a combination of both as in *Taphozous hildegardeae*, *Tadarida pumila* and *Myotis bocagii*, and perhaps *Otomops martiensseni*.

Promiscuity. Each ♂ mates with several ♀♀ and each ♀ with several ♂♂ (e.g. *Pipistrellus nanus*). This possibly gives rise to sperm competition (Fenton 1984, Bernard *et al.* 1997).

Classical lekking. Defined loosely, ♂♂ aggregate at traditional sites (leks), compete for a status or position that conveys maximal attractiveness to ♀♀, and display to attract ♀♀. Receptive ♀♀ visit the lek and mate with the ♂ of their choice. For the crucial definitive criteria of classical lekking, see Bradbury (1977) and *Hypsignathus monstrosus* (species profile). Leks are widely spaced, and within leks, the ♂♂ are clustered in fairly close proximity to each other. Lekking allows ♀♀ to examine a large number of ♂♂ in the least possible time, and enables younger ♀♀ to benefit from the knowledge of how older ♀♀ have selected their mates (Bradbury 1981).

Exploded lekking. Described as an intermediate stage in the evolution of lekking (Bradbury 1981). Similar to classical lekking except that exploded leks are not so widely spaced, and within exploded leks, the ♂♂ are not so close together. Nevertheless, the ♂♂ are aggregated to some extent – an essential criterion of exploded lekking is that the sites at which individual ♂♂ display are not uniformly dispersed.

Life-histories and reproductive strategies

Most small mammals have 'live fast – die young' life-histories characterized by short life-spans, rapid reproduction and high mortality. In contrast, bats 'live slow and die old' – their life-histories are characterized by longevity (as much as 30 years in the wild), many reproductive events in a life-time, small litter-sizes and delayed onset of sexual maturity (Barclay & Harder 2003, Barclay *et al.* 2004). The evolution of nocturnal flight has been a key factor in shaping the life-histories and reproductive strategies of bats for two main reasons – first because it reduces predation and hence mortality rate, and second because flight dictates that young bats must be large enough and developed enough to fly before they are weaned, and this means that lactation periods (which are energetically costly) must be relatively long (1–3 months) (Pomeroy 1990, Barclay 1994).

Reproductive strategies are determined primarily by litter-size and reproductive chronology. Most bats are monotocous (litter-size one: twinning abnormal), but some are polytocous (litter-size normally or often more than one). In Africa, litter-size is known for 103 species: 83% are normally monotocous, 17% are normally or often polytocous. These polytocous species include 12 species (all vespertilionids) that normally or very often have twins, and two species (*Nycticeinops schlieffeni*, *Scotophilus dinganii*) that usually have 2–3 young/litter. In Africa, polytocous has been observed only in the families Pteropodidae and Vespertilionidae. Of 19 pteropodids for

which information is available, polytocry (as a normal strategy) has been reported in only one species (*Epomops dobsonii*), but 48% of the 31 African species of vespertilionids for which data are available are often or normally polytocous. In bats, litter-size is limited by the constraints of flight, and also by the energetic demands of long lactation periods. In Africa, most of the polytocous species have mean weights <10 g, but three notable exceptions are *Scotophilus viridis* (16.5 g), *S. leucogaster* (19.7 g) and *S. dinganii* (23.9 g). This could be because smaller species can carry relatively larger weights while flying (Aldridge & Brigham 1988). In Africa, polytocry is only known to occur in species that are monoestrous (each ♀ has one litter/year), with the possible exception of *Myotis bocagii*.

Reproductive chronologies are defined by the number of litters/year and the timing of reproductive events. Events (e.g. mating and giving birth) are said to be 'seasonal' if they occur only at particular times of the year (e.g. in mating-seasons and parturition-seasons). Consequently, a reproductive chronology can be described, for example, as 'restricted seasonal monoestry' if all young in a specified area are born during a short parturition-season. Seasonal events in reproductive chronologies are usually, but not always, linked to seasonal changes in climate and the availability of resources, but 'seasonal' in the context of a reproductive chronology is not the same as 'seasonal' in the climatic sense. Females may be monoestrous (each ♀ has one litter/year) or polyoestrous (each ♀ has more than one litter/year). For 67 African species for which valid data are available, polyoestry has only been recorded in 22 species (34%); these include 7 of 9 species of pteropodids, 3 of 4 species of emballonurids, 2 of 3 species of nycterids, 6 of 9 species of molossids and 3 of 24 species of vespertilionids. The reproductive chronologies of 51 species are known for at least one locality within their geographic ranges in Africa. Thirty-seven (73%) of these species have only been reported as monoestrous, 12 (24%) have only been reported as polyoestrous and two (*Epomophorus wahlbergi*, *Rousettus aegyptiacus*) are monoestrous in some localities and polyoestrous in others. Bernard & Cumming (1997) suggest that polyoestry is the ancestral strategy of bats, with monoestry evolving as an adaptation to higher latitudes where conditions are optimal only once per year. In Africa, most polyoestrous species have two litters/year, but *Tadarida pumila* has three, four or five litters/year depending on locality. Polyoestry is not easy to prove and the literature on African bats contains many cases where polyoestry has been suggested, implied or claimed on the basis of evidence that is inappropriate and invalid. Here, following Happold & Happold (1990a), a species is said to be polyoestrous only if one or more of the following observations have been made at one locality: (1) the observation of two or more births/year in marked or captive individuals, (2) the simultaneous occurrence of pregnancy and lactation (which also indicates postpartum oestrus), (3) observation or evidence of copulation while the ♀ is still lactating, (4) histological confirmation of postpartum oestrus, (5) the occurrence of pregnancy with evidence of very recent lactation and (6) the observation that 80% or more of the ♀♀ in a population were pregnant during each of two or more breeding seasons within one year. The occurrence of births in two or more seasons (without any of the above observations) is not considered to be proof of polyoestry: alternative explanations include the possibilities that there are monoestrous bats with austral and boreal cycles at that

locality, or that there are two species involved. Conclusions have not been drawn from data that come from several localities because the timing of reproduction in different localities is not necessarily the same. This is especially true of localities north and south of the Equator where seasons are six months out of phase.

Ten reproductive chronologies have been observed in African bats (Happold & Happold 1990a) and their characteristics are illustrated schematically in Figure 30. Note that the black bars in this illustration represent the periods during which ♀♀ are pregnant (not the periods in which rain falls as erroneously indicated by Racey & Entwistle 2000).

(a) *Restricted seasonal monoestry*. Each ♀ has one litter/year. Females are in close or fairly close reproductive synchrony and therefore all young are born at the same time each year. The season of parturition may vary from a few days to not more than two months and is restricted to one climatic season or the transition between two climatic seasons. E.g. *Eidolon helvum*, *Rhinolophus capensis*, *Hipposideros caffer*, *Nycteris thebaica*, *Pipistrellus nanus*, *Miniopterus natalensis* and many others.

(b) *Extended seasonal monoestry*. Each ♀ has one litter/year. Females are not in close reproductive synchrony, the single season of parturition is 2–7 months and may span more than one climatic season. E.g. *Rousettus aegyptiacus* and *Rhinolophus blasii*.

(c) *Aseasonal monoestry*. Each ♀ has one litter/year. Females are not in reproductive synchrony and young are born in eight or more months of the year and in all climatic seasons, e.g. perhaps *P. nanus* in some equatorial habitats (Happold & Happold 1990b), but this needs confirmation because the available data perhaps came from different cryptic species.

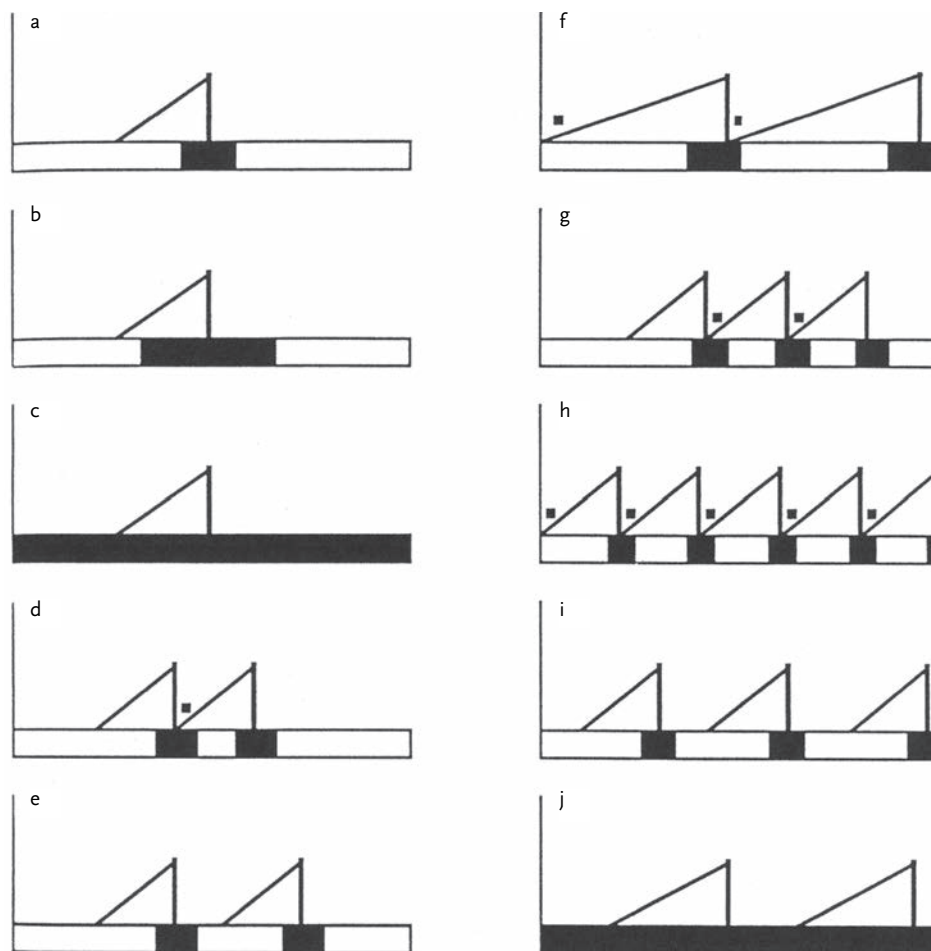
(d) *Seasonal bimodal polyoestry with postpartum oestrus*. Each ♀ has two litters/year. Females are in reproductive synchrony and therefore young are born in two distinct seasons of parturition that usually occur during one climatic season. The first birth is followed by a postpartum oestrus and a period of simultaneous pregnancy and lactation. The second birth is followed by lactation only, and then a period of reproductive inactivity. E.g. *Tadarida condylura* in Malawi.

(e) *Seasonal bimodal polyoestry without postpartum oestrus*. Each ♀ has two litters/year. Females are in reproductive synchrony and therefore young are born in two distinct seasons of parturition. Neither birth is followed by a postpartum oestrus. In all known examples, seasons of parturition occur during similar climatic seasons (e.g. in each of two wet seasons where rainfall is bimodal). E.g. *Tadarida condylura* and *T. pumila* in Kenya, and *T. thersites* in Uganda.

(f) *Continuous bimodal polyoestry with postpartum oestrus*. Each ♀ has two litters/year and a gestation of 5–6 months. Females are in reproductive synchrony and therefore young are born in two distinct seasons of parturition ca. six months apart. Each parturition is followed by a postpartum oestrus. Seasons of parturition do not necessarily coincide with a particular climatic season. E.g. *Epomophorus wahlbergi*, *Epomops buettikoferi*, *E. franqueti*, *Hypsignathus monstrosus*, *Micropteropus pusillus* and *Rousettus aegyptiacus*.

Figure 30. Schematic illustrations of the reproductive chronologies of African bats (after Happold & Happold 1990a). In each illustration, the horizontal axis covers 12 months. Sloped lines indicate pregnancy in one individual, and vertical lines indicate parturition in that same individual. Black bars indicate the season(s) of parturition in one population as a whole: they do not indicate periods of rainfall. ■ = postpartum oestrus. The duration of pregnancy and season of parturition varies according to species and locality.

(a) Restricted seasonal monoestry. (b) Extended seasonal monoestry. (c) Aseasonal monoestry. (d) Seasonal bimodal polyoestry with postpartum oestrus after first parturition. (e) Seasonal bimodal polyoestry without postpartum oestrus. (f) Continuous bimodal polyoestry (note postpartum oestrus after both parturitions). (g) Seasonal multimodal polyoestry with postpartum oestrus after all but the last parturition in the season. (h) Continuous multimodal polyoestry with postpartum oestrus after every parturition. (i) Continuous multimodal polyoestry without postpartum oestrus. (j) Aseasonal polyoestry. This could theoretically occur with or without postpartum oestrus: the latter is illustrated here.



(g) *Seasonal multimodal polyoestry with postpartum oestrus*. Each ♀ has three or more litters/year, with a postpartum oestrus after all except the last birth, which is followed by a period of reproductive inactivity. Females are in reproductive synchrony and therefore young are born in distinct seasons of parturition all (or most) of which occur during one climatic season. E.g. *Tadarida pumila* in Malawi and South Africa. (Seasonal multimodal polyoestry without postpartum oestrus has not been observed.)

(h) *Continuous multimodal polyoestry with postpartum oestrus*. Each ♀ has three or more litters/year with a postpartum oestrus after every birth. Females are in reproductive synchrony and therefore young are born in three or more distinct seasons of parturition. The seasons of parturition are not restricted to one climatic season. E.g. some *Tadarida pumila* in Ghana.

(i) *Continuous multimodal polyoestry without postpartum oestrus*. Each ♀ has three or more litters/year; none of the births is followed by a postpartum oestrus. Females are in reproductive synchrony and therefore young are born in three or more distinct seasons of parturition. The seasons of parturition are not restricted to a particular climatic season. E.g. *Tadarida pumila* in Uganda.

(j) *Aseasonal polyoestry*. Each ♀ has two or more litters/year. Females are not in reproductive synchrony and young are born in eight or more months of the year and in all climatic seasons. (Theoretically,

this chronology could occur with or without postpartum oestrus but, as yet, the only species that perhaps exemplifies this strategy is *Nanonycteris veldkampii* (see species profile), but this needs confirmation.

Bimodal monoestry has been suggested for *Scotonycteris zenkeri* (see species profile) but the data come from different localities and were collected in different years, so this strategy needs confirmation.

Because spermatogenesis, pregnancy and particularly lactation are energetically costly, it is best if they occur when food is most abundant, and these reproductive events tend to be timed with greater force and precision in habitats where food is abundant during one season but scarce at other times. Often it is impossible for both spermatogenesis and lactation to occur when food is most abundant unless the gestation period (defined in this context as the time between mating and parturition) is made substantially longer than the minimum time for normal development of the embryo (Bernard & Cumming 1997, Racey & Entwistle 2000). However, bats exemplify three mechanisms of reproductive delay, which make this possible:

Delayed fertilization combined with sperm storage. Spermatogenesis and lactation occur in summer (or wet season). Sperm is then stored in the cauda epididymides of ♂♂ until autumn (or cool dry season) when mating occurs after the young have been weaned for a few weeks. Sperm is then stored in the female reproductive tract (as well

as cauda epididymides) throughout the winter (when hibernation may occur) or the dry season. In the spring (or late dry season), ovulation, fertilization and implantation occur, uninterrupted development of the embryo takes place, and the young is born in the summer (or early wet season). This is the most common reproductive delay. In Africa, reproductive delay achieved by storage of sperm in the reproductive tract of the ♀♀ has been recorded in *Rhinolophus clivosus*, *R. simulator*, *Nycticeinops schlieffeni* and *Pipistrellus nanus*. It also occurs in European populations of *R. ferrumequinum* and *R. hipposideros* (no data from Africa).

Delayed implantation. Spermatogenesis and lactation occur in summer; ovulation, mating and fertilization occur in autumn. Development begins but the blastocyst does not implant and develop any further until the spring when implantation occurs and development proceeds, usually without any further interruption, until the young is born in early summer. Delayed implantation has been recorded in *Eidolon helvum*, *Rhinolophus landeri*, *Taphozous hildegardeae*, *Miniopterus fraterculus*, *M. natalensis*, probably *M. minor* and, extraliminally, *M. schreibersii*.

Retarded embryonic development. Spermatogenesis and lactation occur in summer; ovulation, mating, fertilization and implantation occur in autumn, then the implanted embryo enters a period of retarded (slowed) growth, which may last 4–8 months, after which development proceeds normally and the young is born in early summer. In some extralimital species, the delay is not a facultative response to low temperatures or shortage of food but, in Africa, retarded development seems to be facultative. It has been recorded in *Hipposideros caffer*, *H. ruber*, *Coleura afra* and *Miniopterus natalensis*.

The timing of reproductive events is usually determined by seasonal changes in the availability of food. For example, a comparison of year-round rainfall, insect abundance and the timing of parturition, at different latitudes in Africa, showed that insect abundance peaks ca. one month after the peak rainfall, and that microbats (with the possible exception of molossids) commonly give birth one month before peak rainfall, presumably so the young bats are newly weaned at the time when insects are most abundant (Cumming & Bernard 1997). It is not surprising, therefore, that intra-specific variations in reproductive strategy have been observed in species that live in diverse environments. Intra-specific variation can be achieved by changes in litter-size, changes in chronology, or both. Intra-specific variation has been observed, for example, in *Epomophorus wahlbergi*, *Rhinolophus blasii*, *Rousettus aegyptiacus*, *Hipposideros caffer*, *Miniopterus fraterculus*, *Miniopterus natalensis*, *Pipistrellus nanus*, *Tadarida condylura* and *T. pumila*.

Relative to other mammals, newborn bats are enormous (Tuttle & Stevenson 1982). They may weigh 15–33% of their mother's postpartum weight. Neonates of megabats are often well furred and have their eyes open. Neonates of microbats are usually pink and naked and their eyes are usually closed; pigmentation appears within a few hours and pelage within a few days. In all bats, the wings are small and crumpled at birth, but reach near adult-size before weaning. Neonates have recurved milk-teeth and disproportionately large thumbs and feet, which enable them to cling tenaciously to the nipples, fur and pubic nipples (if present) of the mother. Usually

after a few days, the young are left at the roost while their mothers forage. Young microbats emit 'isolation calls' when left behind; these are audible to humans until the bat's voice breaks and then the calls of most species become wholly ultrasonic. The ability to echolocate develops before microbats learn to fly. Juveniles are suckled for 1–3 months, until they approach adult size and learn to fly and obtain food for themselves. Volant young may accompany their mothers to learn how and where to forage and how to find the way back to the day-roost. These young bats can be distinguished from adults by the presence of whitish cartilaginous epiphysal plates at the ends of the finger bones, which give the joints a knobby, whitish appearance. Females of monoestrous species usually reach sexual maturity during their first year, and breed during the next breeding season; ♂♂ often take a year longer.

Predators, parasites and diseases

The main predators of African bats are humans, Bat Hawks *Macheiramphus alcinus* and other raptors, owls, hornbills, shrikes, snakes, genets (*Genetta* spp.) and other small carnivores. Bat Hawks have large eyes and a large gape and are specialist bat-eaters, but regular hunting of flying bats at dusk, and sometimes after dark, has also been recorded for African Goshawk *Accipiter tachiro*, Little Sparrow-hawk *A. minullus*, Gabar Goshawk *Micronisus gabar*, Lanner Falcon *Falco biarmicus*, Peregrine Falcon *F. peregrinus*, Eurasian Hobby *F. subbuteo*, Black Kite *Milvus migrans* and Wahlberg's Eagle *Aquila wahlbergi* (see bat species profiles). Owls known to feed on African bats include Spotted Eagle-owl *Bubo africanus*, Mackinder's Eagle-owl *B. capensis mackinderi*, Giant Eagle-owl *B. lacteus* and Barn Owl *Tyto alba*. Silvery-cheeked Hornbills *Bycanistes brevis* prey on small fruit bats, which are attacked at their day-roosts (Kingdon 1973). However, because bats fly at night and usually roost in inaccessible places, predation is assumed to play a very minor role in bat mortality (e.g. Speakman 1995).

Bats are parasitized by a wide variety of internal parasites, including protozoans (e.g. *Plasmodium*), and worms in the classes Trematoda, Cestoda and Nematoda (for a catalogue of endoparasites of African bats, see Anciaux de Faveaux 1984). Bats are also parasitized by a wide variety of ectoparasites (Figure 31) including some families of arthropods that exclusively or almost exclusively parasitize bats (Marshall 1982, Hill & Smith 1984). However, bats are seldom heavily infested, they are unlikely to infest human dwellings with dangerous parasites, and bat parasites are not known to play a significant role in transmission of diseases to humans although some have the potential to do so. African bats, like other mammals, are parasitized by blood-sucking insects such as mosquitoes, midges and assassin bugs, which land briefly on the host, bite and then move elsewhere (for catalogue, see Anciaux de Faveaux 1984). Ectoparasites of African bats also include bed-bugs (order Hemiptera, family Cimicidae), which are blood-sucking insects that live in the day-roosts of bats and other mammals and move temporarily on to their hosts to feed, and their blood-sucking allies (Polycstenidae), which live permanently in the fur of bats and are not known to parasitize other animals. There are also blood-sucking fleas (order Siphonaptera) in the families Pulicidae (which parasitize a variety of mammals) and

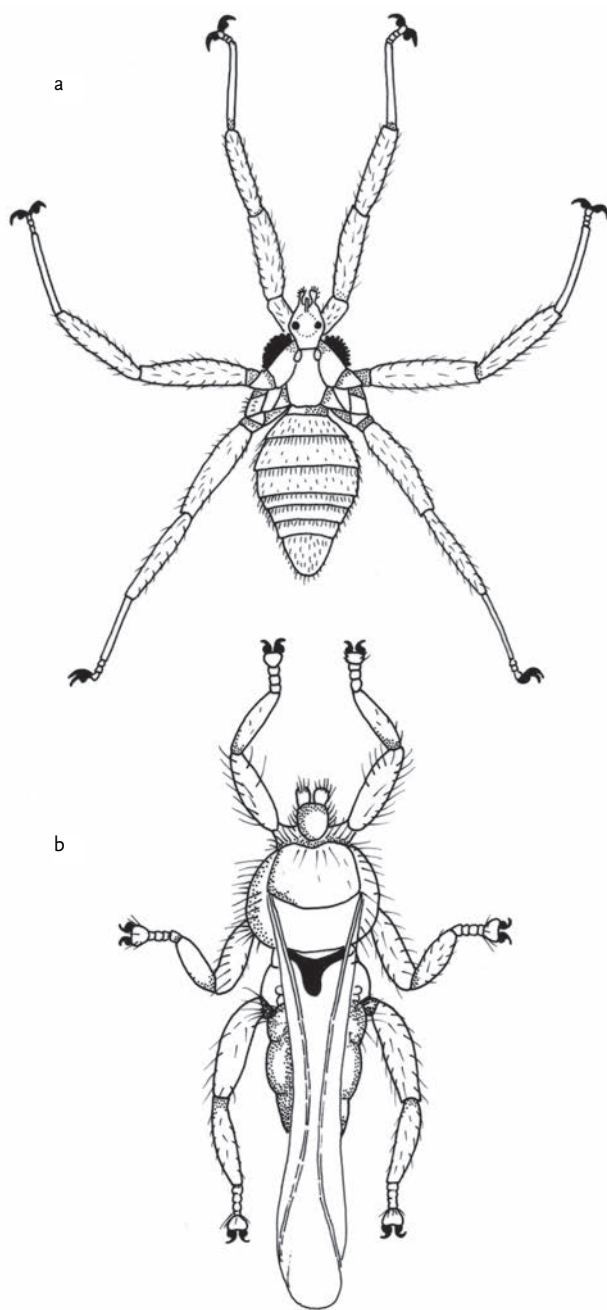


Figure 31. Two commonly seen bat-flies of the order Diptera that are ectoparasites of African bats. (a) *Cylopodia greeffi* (Nycteribiidae), an ectoparasite of the fruit-bat *Eidolon helvum* (based on Happold 1987). (b) A winged bat-fly (Streblidae) (redrawn from Hill & Smith 1984).

Ischnopsyllidae (which parasitize bats only), and bat-flies (order Diptera, families Nycteribiidae and Streblidae) which parasitize only bats. Nycteribiids, which are wingless, can be seen scuttling through the pelage. Streblids of both sexes are winged, but the ♀♀ burrow into the skin (usually behind the ears), shed their wings and legs, and then develop into large, flask-shaped sacs with only the hind-parts exposed. Other Arthropods that parasitize African bats belong to the order Acari, and include ticks (families Argasidae and Ixodidae), which move temporarily on to bats (or other animals) to suck blood, and mites belonging to 16 families including the Spinturnicidae, which only parasitize bats. Some

mites live permanently on their hosts whereas others spend only part of their life-cycle on the bat host. Most mites feed on skin and skin products such as dead cells, hairs and secretions, and most mites live on specific sites on the host. For example, mites in the families Dermanyssidae, Laelapidae, Spinturnicidae, Cheyletidae and some species in the family Macronyssidae live on the skin, particularly in the ears, around the base of the tail, around the eyes, or on the wings. Mites in the family Erythetidae and some in the families Trombiculidae and Gastronyssidae live in the nasal passages. Some in the family Macronyssidae live in the mouth and feed on tissue between the teeth and gums, sometimes causing loss of teeth. Mites in the families Myobiidae and Chirodiscidae attach themselves to the hairs, and some in the family Gastronyssidae live on the corneae of the eyes. Mites in the family Sarcoptidae burrow into the skin and cause mange and scabies. Ectoparasites likely to be observed on African bats are listed in each species profile; the data are taken mainly from the catalogue compiled by Anciaux de Faveaux (1984), although since then there have been some changes in the names of both the ectoparasites and their hosts, and some of the hosts have been re-identified. Ectoparasites can be collected from both living and freshly killed bats, and are easily found by examining the bat under a 10–70 power zoom dissecting microscope. More information about collecting, preserving and studying ectoparasites of bats is given by Whitaker (1988).

The diseases of bats are poorly known. Anciaux de Faveaux (1984) catalogues bacteria, fungi and viruses that have been found in African bats but (with very few exceptions) they are not mentioned in the species profiles unless they are known to cause illness in humans and/or domestic livestock. A fungal disease of both bats and humans is histoplasmosis, a respiratory disease caused by inhaling the spores of *Histoplasma capsulatum* and *H. duboisii*, fungi that grow in soils with high content of organic matter including bat guano (Hill & Smith 1984). Histoplasmosis can be fatal to humans, although serious infections are rare: therefore people entering guano-rich roosts of bats should wear masks and, if possible, avoid disturbing the guano. Other fungi from guano in bat caves include *Microsporum gypseum* and *Trichophyton mentagrophytes* (which cause ringworm in humans and livestock). Viruses that have been isolated from African bats and that are known to cause fevers and more serious illnesses in humans include Bangui, Bunyamwera group, Chikungunya, Rift Valley Fever, Sindbis, West Nile, Yellow Fever and Zika viruses. These are arboviruses (transmitted by mosquitoes and/or other blood-feeding arthropods). Rift Valley fever and West Nile viruses infect both humans and livestock, Rift Valley fever being of particular importance in Africa. In addition, African bats have been shown to be infected with three rabies virus-like lyssaviruses, which can be transmitted to humans, via bites or scratches, when saliva from infected animals contacts exposed tissue and nerve endings. These are Duvenhage virus (which causes a rabies-like illness and has caused the death of at least one human), Mokola virus (also known to cause fatal human infections) and Lagos bat virus. Rabies virus has rarely been reported in African bats, although it occurs in some other African mammals. Other viruses that have been found in African bats, but are not known to cause illness in humans, include Bukalasa bat, Dakar bat, Entebbe bat, Fomede, Ife, Kasokero, Mt Suswa bat, Saboya, Uganda S and Yogue viruses. Of these, Uganda S virus is an arbovirus but the others, *contra* Anciaux de Faveaux (1984), are not

arboviruses (C. H. Calisher pers. comm.). In the aftermath of the 1995 Ebola haemorrhagic fever epidemic at Kikwit, DR Congo, 538 bat specimens (representing four families and 18 species) were collected at Kikwit in 1995 and examined for the presence of Ebola virus, but none was found in these bats (Van Cakenberghe *et al.* 1999). Recently, Ebola-viral RNA was detected in liver and spleen tissues of *Hypsignathus monstrosus*, *Epomops franqueti* and *Myonycteris torquata*, and Ebola virus-specific antibody was detected in the same species; however, Ebola-viral RNA was not detected in those with antibody, and antibody was not detected in those with Ebola-viral RNA (Leroy *et al.* 2005). It is not yet known whether the Ebola virus involved can be transmitted to humans, or whether it is pathogenic, and more studies are needed to determine whether these or other bats are susceptible to Ebola viruses and whether they play a role in Ebola-viral transmission (C. H. Calisher pers. comm.). Several of the viruses that can cause illness in humans have been isolated from unidentified species of bats, and therefore have not been mentioned in species profiles. These include Bangui virus from *Tadarida* sp., *Pipistrellus* sp. and *Scotophilus* sp. in Central African Republic; Chikungunya from *Scotophilus* sp., Duvenhage virus from *Miniopterus* sp., Sindbis from *Rhinolophus* sp. and *Hipposideros* sp., West Nile virus from *Rousettus* sp., *Scotophilus* sp. and *Tadarida* sp. and Zika virus from *Rousettus* sp. and *Tadarida* sp. Furthermore, viruses that have been isolated from Palaearctic bats have not been included in the profiles of these species. The fungi, ectoparasites and viruses mentioned above, and the diseases they cause, do not comprise a comprehensive record. They have been compiled from Anciaux de Faveaux (1984), Hill & Smith (1984), Calisher *et al.* (2006) and Internet sources, with additional information from P. Boland (pers. comm.). Since the profiles were submitted in 2006, there have been numerous publications about viruses found in African bats, but it was not possible to update the profiles.

Pests and benefactors

An extremely small percentage of the species of bats in Africa are justifiably considered pests. These include several species of very smelly molossids (e.g. *Tadarida pumila*, *T. condylura*), which roost in very large numbers in the roofs of houses, and a few species of fruit bats (e.g. *Hypsignathus monstrosus* and *Epomops franqueti*), which make very loud and monotonous calls at night. The vast majority of species are not only harmless to people, but are of great value. Many megabats play a major role in pollinating trees and dispersing their seeds and, although some have the reputation of raiding orchards, they almost always feed only on fully ripe fruits, which should have been picked earlier to be of commercial value (Baker & Harris 1957, 1959, Tuttle 1986). By removing over-ripe fruits, fruit bats may help to control fungal diseases and fruit-flies. Microbats are mainly insectivorous and their prey includes insects such as mosquitos, midges, flies and cotton-boll moths, which are very serious pests. Microbats, although seldom seen by humans, are very numerous and their impact on insect numbers is enormous. It was estimated that the 500,000 occupants of just one cave in Gabon consumed 3000 kg of insects each night within a radius of ca. 12 km (Brosset 1969). There are no blood-sucking vampire bats in Africa and there appear to be no records of humans being bitten by African bats unless the bats were captive and

being handled. Furthermore, the likelihood of someone contracting a disease as a result of being bitten by a captive bat that is being handled, or from a parasite of a bat, seems to be very low but not negligible (see Predators, Parasites and Diseases above).

Abundance

It is extremely difficult to determine the abundance of bats accurately. For most African species, there are no data. For others, it has only been possible to indicate comparative abundance, very roughly, from how often they are encountered and how well they are represented in collections. Even these estimations are of dubious value because bats are seldom encountered in countable numbers (except sometimes when their day-roosts are known) and, in most parts of Africa, methodical and comprehensive collecting and/or recording of bats has not been carried out. Also, the fact that a species is well represented in collections does not necessarily mean that it is comparatively abundant – it might just be easier to collect for one or more of several reasons. Species that roost in large numbers in accessible caves, mines and buildings may be collected from their roosts much more easily than those that roost singly or in small groups in inconspicuous roosts. Catching and/or detecting bats while they are flying around at night is very difficult and estimations of abundance based on these methods are unreliable. Although bats have been mist-netted and trapped close to the ground for some time, the setting of mist-nets and traps in and above the canopy is a recent and comparatively rare activity and, consequently, bats that fly in these environments are likely to be under-represented in collections. Furthermore, even the most sophisticated bat-traps and mist-nets only operate in a minute fraction of the space utilized by bats, and species that fly high (such as emballonurids, molossids and some vespertilionids) and species that are good at detecting and dodging mist-nets and traps (such as nycterids and *Kerivoula* spp.), are often poorly represented in surveys and collections. The ‘rarest’ of bats may well prove to be those that can avoid mist-nets and traps, those whose day-roosts are not known, those that live in areas where collecting effort has been minimal, and those whose echolocation calls are too low in intensity to be easily detected with bat-detectors.

Conservation

Two important assessments of the conservation status of bats that contain much relevant information are Mickleburgh *et al.* (1992), which is an action plan for the conservation of Old World fruit bats compiled by the IUCN/SSC Chiroptera Specialist Group, and Hutson *et al.* (2001), which is a global status survey and conservation action plan for microbats also compiled by the same organization. Since then, the conservation status (IUCN Categories) of many species have been updated from the Global Mammal Assessment Africa Workshop. The IUCN Categories (given in the species profiles) have been taken from the IUCN website (www.redlist.org). Additional information in species profiles is often taken from this website; some authors have also made their own comments. Although much effort has been given to the assessment of the conservation status of African bats, there are many species that are impossible to assess accurately,

either because they live in habitats that are rarely surveyed or because they are particularly difficult to capture.

Based on the 2010.4 version of the IUCN website, of the 224 species of bats in Africa, 14% are regarded as threatened to some extent: of these, five microbats (*Rhinolophus hilli*, *R. macclaudi*, *R. ziama*, *Hipposideros lamottei* and *Kerivoula africana*) are Endangered or Critically Endangered, two megabats and nine microbats are Vulnerable, and two megabats and 13 microbats are Near Threatened. There are 20 megabats and 124 microbats that are of Least Concern, and there are four megabats and 44 microbats referred to as 'Data Deficient' because their conservation status cannot be assessed from the available information. One new species has not yet been evaluated. The rapid increase in human population (and the concomitant increase in human activities that are detrimental to bats) is the single most serious threat to bat populations. Human activities that pose the greatest threats to bats in Africa include destruction of natural habitat, interference with day-roosts, hunting, and use of pesticides. In 1992, 18 species (64%) of the megabats were considered threatened by deforestation, and four (including the vulnerable *Pteropus voeltzkowi*) by hunting. The vast majority of microbats are threatened by destruction of natural habitats, reduction in abundance and diversity of insects, destruction of day-roosts in old and dead trees, disturbance of colonies in caves and old mines, and/or the use of pesticides. There are only ca. nine species that appear to thrive by roosting in human habitations and/or foraging over farmlands and gardens, and some of these are considered pests and their roosts are sometimes fumigated. Microbats are particularly susceptible to insecticides; they can be poisoned by eating contaminated insects, by contacting insecticides in buildings fumigated to eradicate insect pests, and they can be starved when insect numbers are reduced by insecticides. If the human population increases five-fold during the twenty-first century, as predicted by Bongaarts (1994), the outlook for most species of bats in Africa is bleak.

Chromosome numbers: a problem with terminology

The taxonomy sections of species profiles give information about chromosomes, if available to the authors of the profiles. This information includes the chromosome number (the usually constant number of chromosomes in a somatic cell of an organism): because chromosomes are paired, this number is referred to as $2n$. Some profiles also give the fundamental number. Fundamental number (FN) was originally defined as 'The number of chromosomal arms of the autosomal complement (excluding the sex pair) of a given species' (Matthey 1951). Subsequently, some authors included the sex chromosomes in their assessment of FN, and this made the term FN ambiguous. To avoid ambiguity, some authors then used 'aFN' to specify that only the arms of autosomal chromosomes were counted. Others continued to use FN, but specified whether or not the count was restricted to the autosomal chromosomes. Some used FN without specifying which chromosomes were included. For all profiles in the Order Chiroptera, it has been ascertained that only autosomal chromosomes were included, and therefore the number of arms is given as aFN whether or not this term was used in the cited source of the information.

Chiropteran origins, systematics and the families of African bats

Based on fossils and molecular evidence, bats are thought to have evolved from an ancestor living ca. 64 mya, and it seems that they diversified into four major microbat lineages (among which the megabats are nested) in the early Eocene, 50–52 mya (Teeling *et al.* 2005). At this time, mean annual global temperatures had increased by ca. 7°C, land plants were increasing in diversity and abundance, and insects were at the peak of their Tertiary diversity; consequently it is probable that the diverse echolocation and foraging strategies exemplified by microbats resulted from differential niche exploitation at this time. Teeling *et al.* (2005) suggest that bats originated in Laurasia (possibly in North America) and that, of the four major microbat lineages, three were Laurasian in origin and the fourth Gondwanan. The extant African bat fauna contains representatives of the three Laurasian lineages; the Gondwanan lineage is represented only by South American microbats.

The closest relatives of bats appear to be colugos (order Dermoptera) and, to a lesser degree, tree-shrews (order Scandentia) and primates (order Primates). Colugos are gliding lemur-like mammals with a large membrane extending from the fingers to the toes and to the tip of the long tail, and webbing between the fingers. Until 1970, it was assumed that all bats were monophyletic and that their common ancestor was the first flying mammal. Then it was suggested that self-powered flight evolved twice – in an ancestral megabat related to the primates, and in an ancestral microbat related to a small terrestrial insectivore (Jones & Genoways 1970, Smith & Madkour 1980, Pettigrew 1986, 1991). Although the morphological differences between megabats and microbats are substantial, and there are similarities (particularly in the nervous system) between megabats and primates, there is now convincing evidence that the order Chiroptera is monophyletic, and the 'diphyly controversy' has waned (Simmons 1994, 1995, Volleth *et al.* 2002, Teeling *et al.* 2005).

The higher-level classification of bats is controversial. Prior to the late 1900s, the megabats and microbats were placed in two suborders – the Megachiroptera and Microchiroptera, respectively. These taxa were supported by phylogenetic analyses based on morphological data (reviewed by Simmons & Geisler 1998), and both were considered to be monophyletic. However, phylogenetic studies based on different sets of data, and especially molecular evidence, strongly suggest that the suborder Microchiroptera is not monophyletic (Simmons 2005, Teeling *et al.* 2005); more details are given below. Therefore, following Simmons (2005) and pending further studies, the suborders Megachiroptera and Microchiroptera are not recognized here but, for convenience, the terms megabat and microbat are used when it is useful to distinguish between the fruit bats (family Pteropodidae) and the bats belonging to all other families. The main morphological differences between megabats and microbats are as follows:

Megabats (fruit bats). The membrane between the second and third fingers is more extensive than in microbats and these two fingers have some independence of movement. Both the thumb and the second finger have a claw. The muzzle is simple and there are no noseleaves (although in ♂♂ of *Hypsignathus*, the muzzle ends in a flat fleshy

plate). The ears are simple and well separated; the margin of each ear forms a complete ring around the auditory orifice. The eyes are very large and orientation is primarily by eyesight (not by echolocation). In all African megabats, the tail is short or absent; the interfemoral membrane is merely a flange of skin around the inner margins of the legs. The skull has a well-developed postorbital processes, and the bony palate extends well beyond the last molars (except *Casinycteris*). The molars are simple in all African genera (except, to some extent, *Hypsignathus*) and are without W-shaped patterns of cusps. There is only one family, the Pteropodidae, with 42 extant genera and 186 species worldwide (Simmons 2005).

Microbats. The second finger is closely associated with the third, and only the thumb has a claw. The muzzle may be simple or adorned by fleshy outgrowths (noseleaves). The external ear is often complicated; the margin does not form a complete ring, and a tragus is usually present. The eyes are small to very small and orientation is primarily by echolocation, not eyesight. The tail is usually long and fully or partly enclosed by a large interfemoral membrane, which stretches from heel to heel (but in one family, the tail is absent). The postorbital processes of the skull are usually absent, rudimentary or concealed (except in the Emballonuridae). The bony palate does not extend beyond the last molars. The molars have a W-shaped pattern of cusps

(albeit reduced in some species). There are 17 extant families, 160 extant genera and 930 species worldwide (Simmons 2005).

This usage of the terms megabat and microbat is not meant to be taken as support for the monophyly of these two groups. Indeed, recent evidence (summarized by Simmons 2005) suggests that the Microchiroptera are not monophyletic, and that microbats in the families Rhinolophidae, Hipposideridae, Megadermatidae, Rhinopomatidae (and the non-African family Craseonycteridae) are more closely related to megabats than to other microbats, including those in the African families Emballonuridae, Nycteridae, Molossidae and Vespertilionidae. This raises an interesting question – did laryngeal echolocation evolve more than once in bats, or did it evolve only once then become lost in megabats? This is only one of many unresolved problems associated with the relationships between the families of bats and, for this reason, following Simmons (2005), no taxa above the level of family are included here. On the other hand, again following Simmons (2005), the families are presented in the sequence that is consistent with the most recent classifications (see list above), and some interfamilial relationships are mentioned in each family profile.

In Africa, there are nine families. They are distinguished mainly by their heads (noseleaves, ears, tragus), and their tails and interfemoral membranes (Table 10, Figures 32 and 33).

Table 10. Key to the African families in the order Chiroptera. Data pertain to African representatives only. Ear lengths are relative and derived from mean E as percentage of mean FA for all species within each family: very short (22–37%), short (38–52%), medium (52–67%), long (68–82%), very long (83–97%).

| Second finger | Noseleaf | Tail and interfemoral membrane | Ears | Family |
|-----------------------|--|--|---|------------------------------|
| Terminating with claw | None | Tail absent or rudimentary. Interfemoral membrane reduced to narrow band along inside margin of hindlimbs | Very short; well separated; margin of ear uniquely forming a complete ring. No tragus | Pteropodidae (14 genera) |
| Without claw | None | Tail more or less completely enclosed by interfemoral membrane | Very short to very long; widely separated or joined. Tragus conspicuous | Vespertilionidae (17 genera) |
| Without claw | None | Terminal portion of tail projecting upwards through centre of interfemoral membrane when bats are not flying | Very short; widely separated, backward-pointing. Tragus conspicuous | Emballonuridae (3 genera) |
| Without claw | None | Terminal portion of tail projecting freely well beyond hind-margin of interfemoral membrane when bats are not flying; length of 'free' portion ca. half width of interfemoral membrane | Short; inner margins widely separated or meeting or joined by band of skin. Tragus inconspicuous | Molossidae (6 genera) |
| Without claw | Rudimentary, rounded | Tail extremely long; most of tail projecting freely beyond interfemoral membrane; 'free' portion very much longer than width of interfemoral membrane | Short; inner margins joined by band of skin across forehead. Tragus conspicuous | Rhinopomatidae (1 genus) |
| Without claw | Longitudinal slit bordered by fleshy outgrowths | Tail completely enclosed by interfemoral membrane; last vertebra T-shaped or Y-shaped | Medium to long; inner margins joined by inconspicuous low band of skin across forehead. Tragus conspicuous, not bifid | Nycteridae (1 genus) |
| Without claw | Very large; comparatively simple | Tail absent; interfemoral membrane very large | Long; inner margins joined for at least one-third of length. Tragus very conspicuous, bifid | Megadermatidae (2 genera) |
| Without claw | Very large; posterior component subtriangular with erect tip | Tail more or less completely enclosed by interfemoral membrane | Short to medium; well separated. No tragus | Rhinolophidae (1 genus) |
| Without claw | Very large; posterior component elliptical or with three pointed projections | Tail completely enclosed by interfemoral membrane or projecting slightly beyond it | Very short to medium; well separated. Tragus inconspicuous | Hipposideridae (4 genera) |

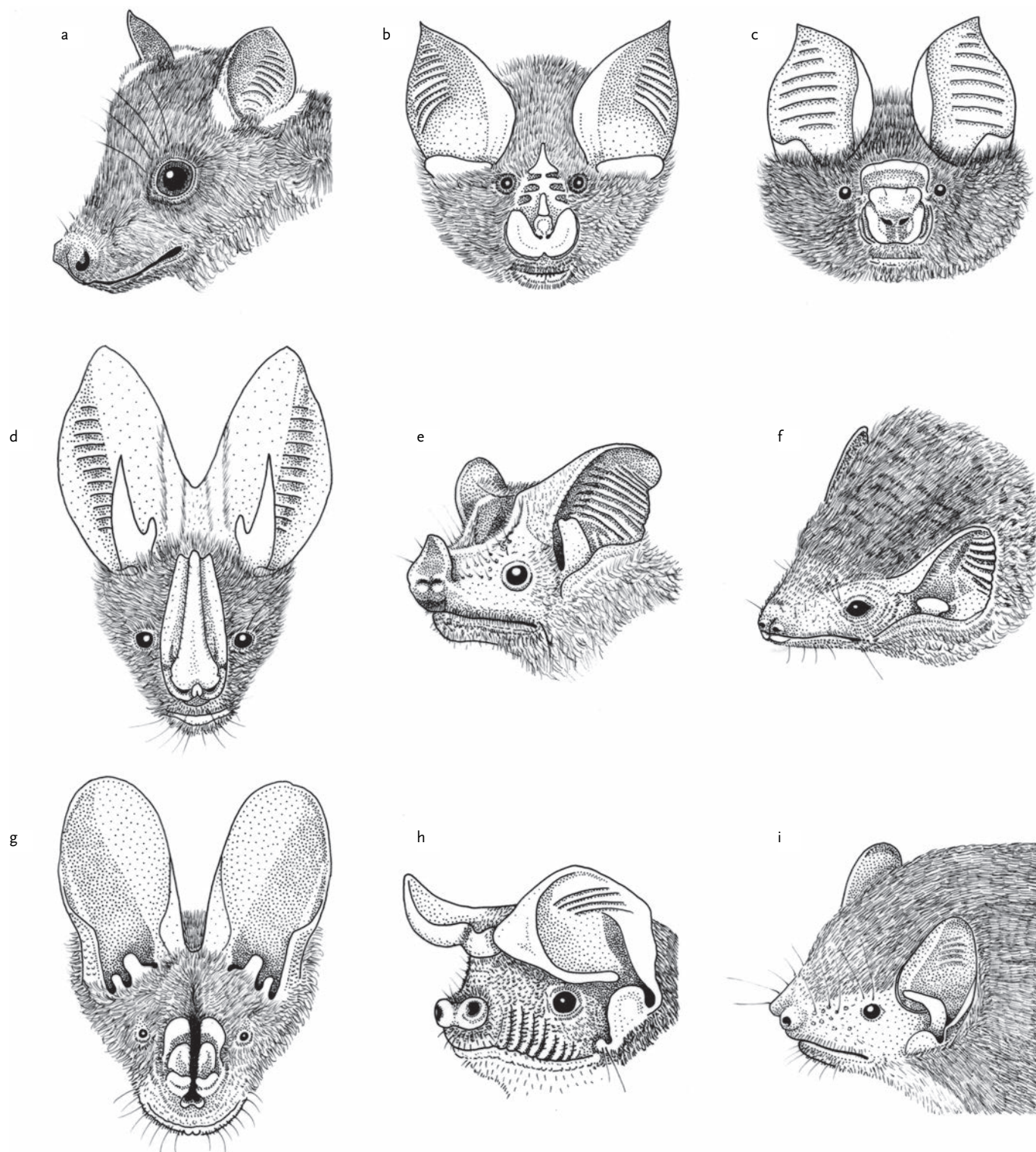


Figure 32. Heads of bats in the nine families represented in Africa. (a) Pteropodidae (*Epomophorus*), (b) Rhinolophidae (*Rhinolophus*), (c) Hipposideridae (*Hipposideros*), (d) Megadermatidae (*Lavia*), (e) Rhinopomatidae (*Rhinopoma*), (f) Emballonuridae (*Taphozous*), (g) Nycteridae (*Nycteris*), (h) Molossidae (*Tadarida*) and (i) Vespertilionidae (*Scotophilus*).

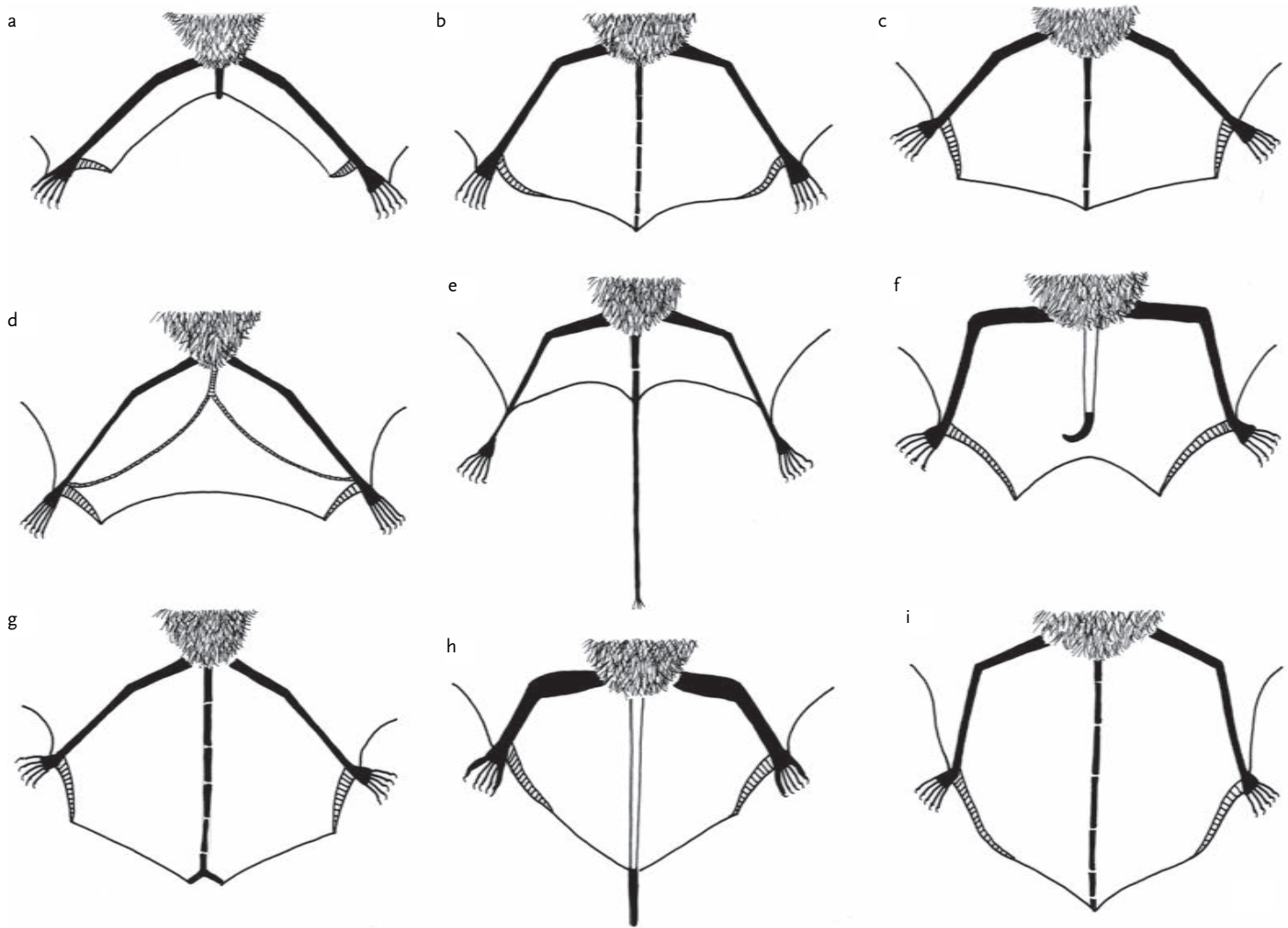


Figure 33. Tails and interfemoral membranes of bats in the nine families represented in Africa. (a) Pteropodidae, (b) Rhinolophidae, (c) Hipposideridae, (d) Megadermatidae, (e) Rhinopomatidae, (f) Emballonuridae, (g) Nycteridae, (h) Molossidae and (i) Vespertilionidae.

Update

Since this profile and all others were submitted in 2006, there have been many new publications (many referred to in *African Bat Conservation News*; www.Africanbats.org) but it was not usually possible to rewrite profiles or tables. However, sentences have been added to draw attention to new publications that substantially contribute to the taxonomy and distributions of African bats, and the

IUCN Categories of all species have been updated. Other sections of species profiles have not been updated. A very important publication – Monadjem *et al.* 2010 – contains some new information and references about the bats of southern and central Africa, and it contains photographs of skulls and living bats.

Meredith Happold

Family PTEROPODIDAE

FRUIT BATS (OLD WORLD FRUIT BATS)

Pteropodidae Gray, 1821. London Med. Repos., 15: 299.

| | | |
|-----------------------------------|--------------------------------|--------|
| <i>Casinonycteris</i> (1 species) | Short-palated Fruit Bat | p. 229 |
| <i>Eidolon</i> (1 species) | Straw-coloured Fruit Bats | p. 231 |
| <i>Epomophorus</i> (8 species) | Epauletted Fruit Bats | p. 234 |
| <i>Epomops</i> (3 species) | Singing Epauletted Fruit Bats | p. 252 |
| <i>Hypsignathus</i> (1 species) | Hammer-headed Fruit Bat | p. 259 |
| <i>Lissonycteris</i> (1 species) | Soft-furred Fruit Bat | p. 262 |
| <i>Megaloglossus</i> (1 species) | African Long-tongued Fruit Bat | p. 266 |
| <i>Micropteropus</i> (2 species) | Lesser Epauletted Fruit Bats | p. 268 |
| <i>Myonycteris</i> (2 species) | Collared Fruit Bats | p. 272 |
| <i>Nanonycteris</i> (1 species) | Dwarf Epauletted Fruit Bat | p. 277 |
| <i>Plerotes</i> (1 species) | Broad-faced Fruit Bat | p. 280 |
| <i>Pteropus</i> (2 species) | Flying-foxes | p. 282 |
| <i>Rousettus</i> (2 species) | Rousettes | p. 288 |
| <i>Scotonycteris</i> (2 species) | Tear-drop Fruit Bats | p. 294 |

The family Pteropodidae currently contains 42 extant genera and 186 species of which 14 genera and 28 species are found in Africa (Simmons 2005); some of the 28 species are considered to contain more than one species by some authors (see profiles). Traditionally, the pteropodids were placed in the suborder Megachiroptera (but see order Chiroptera). Consequently, they are often referred to as megabats but, in Africa, pteropodids are usually referred to, collectively, as fruit bats. Fruit bats have dog-like faces with very large eyes, well-separated erect ears and no noseleaf (Figure 32a); the tail is short or absent and the interfemoral membrane is merely a flange of skin around the inner margins of the legs (Figure 33a). There is a claw on the thumb and also at the end of the second finger (Figure 34a). All fruit bats feed on fruits and/or flowers or products of flowers and, in Africa, they are the only bats known to feed on plant products. Fruit bats are delightful animals. If handled gently, and encouraged with a mouthful of banana, they quickly lose their fear of people and it becomes obvious that they are very intelligent, very adaptable and curious enough to apparently enjoy new experiences as long as they bring comfort and nice things to eat! A few are regarded as pests when they raid orchards. However, although they may damage some fruits by biting to test ripeness, they only eat fruit that is too ripe for commercial value and, by removing this over-ripe fruit, they may help to control fungal disease and fruit-flies (Tuttle 1986). Fruit bats also play a vital role in the pollination of many trees including some which are not pollinated in any other way (Baker & Harris 1957, 1959, Harris & Baker 1959). They also play a vital role in the dispersal of the seeds of fruit-bearing trees (Thomas 1987, 1991). Bat-pollinated flowers are often large and robust, located at the edge of the foliage, and they only open and smell strongly during the night.

African fruit bats range in size from very small (FA: 38–62 mm) to very large (FA: 138–163 mm). In the larger species, ♂♂ are usually larger, on average, than ♀♀; however, the differences diminish with decrease in overall size and, in the very small *Nanonycteris*, the ♀♀ are larger, on average, than the ♂♂ (Bergmans 1989). Males often have secondary sexual characters (Figure 34). The pelage is typically of medium length and soft; the colour is usually uniformly fawn, grey, or brown, but some species have dark dorsal pelage and a contrasting bright red or yellow mantle across the neck and shoulders, and some

species have white markings (patches of white pelage) on the head that are of diagnostic importance. These markings include a white patch on the rostrum, a white spot behind each eye, white or whitish basal ear-patches and white upper lips (Figure 34). The basal ear-patches are often referred to as basal ear-tufts, however they are not strictly tufts but white hairs lining the basal parts of the margin of the ear. The body is elongated and robust; the head somewhat dog-like with short to very long muzzle and no noseleaf. The ears are well separated and simple; the bases of inner and outer margins join to form a complete ring around the auditory orifice; there is no tragus and no defined antitragus (Figure 34). The eyes are very large and are specially adapted to improve vision at night, as is typical of nocturnal mammals that do not echolocate. Although members of one genus (or perhaps two genera) have primitive echolocation, the majority of fruit bats cannot echolocate. The lips and cheeks of fruit-eating species are often wrinkled and expansible (i.e. able to stretch to form cheek-pouches in which large amounts of fruit can be carried). The tongue is either long, without backward-pointing hair-like papillae and with or without an expanded tip (fruit-eating species), or long with some hair-like papillae at the tip (*Plerotes*: diet uncertain), or very long with a brush of long hair-like papillae at the tip (nectar-eating species) (Figure 35). The tongues of fruit bats also have conical papillae for tasting food, and those of many (if not all) species also have a patch of tridentate papillae, stiff enough to serve as a rasp, fairly close to the tip. The soft palate has ridges forming patterns of diagnostic importance (Figure 34). The patterns include well-defined, conspicuous ridges, which are either thick or thin, interdental (between the rows of teeth) or postdental (further back than the last molars), and divided (if there is a median gap or groove across the centre) or undivided. Typically, there is a series of 3–12 of these conspicuous ridges beginning at the front of the palate, with a series of thin, flat, serrated ridges further back. Only the conspicuous ridges are of diagnostic importance. The wings of fruit bats are typically moderately short and broad. The thumb is usually long with a long claw, and the second finger has a metacarpal, two phalanges and a small claw. The wing-membrane on each side is usually attached (= inserted) to the first (= outer) toe or to the second toe; sometimes it is attached between these toes and, in some *Megaloglossus woermanni*, it is attached to the third toe (Figure 36). The hindlimbs are slender and moderately long; the toes are very long with long, sharp, curved claws, and all toes (except the first [= hallux]) have three phalanges. The tail is either short, vestigial or absent. The interfemoral membrane is poorly developed; typically, short calcars are present. There are no pubic nipples. Secondary sexual characters of adult ♂♂ include epaulettes, ruffs, mantles, which are more rigid and greasy than those of ♀♀, and (especially in *Hypsignathus*) various modifications of the head, skull and larynx associated with the production of loud vocalizations. An epaulette is a tuft of long white or yellowish hairs on each shoulder, which can be hidden within a deep pouch or displayed during courtship as a conspicuous circular whorl. It is often suggested that glands in the epaulette-pouches secrete scent, which is dispersed by the beating of the wings during courtship, but Püscher (1972) found fewer glands in the pouch than in normal skin, and concluded that

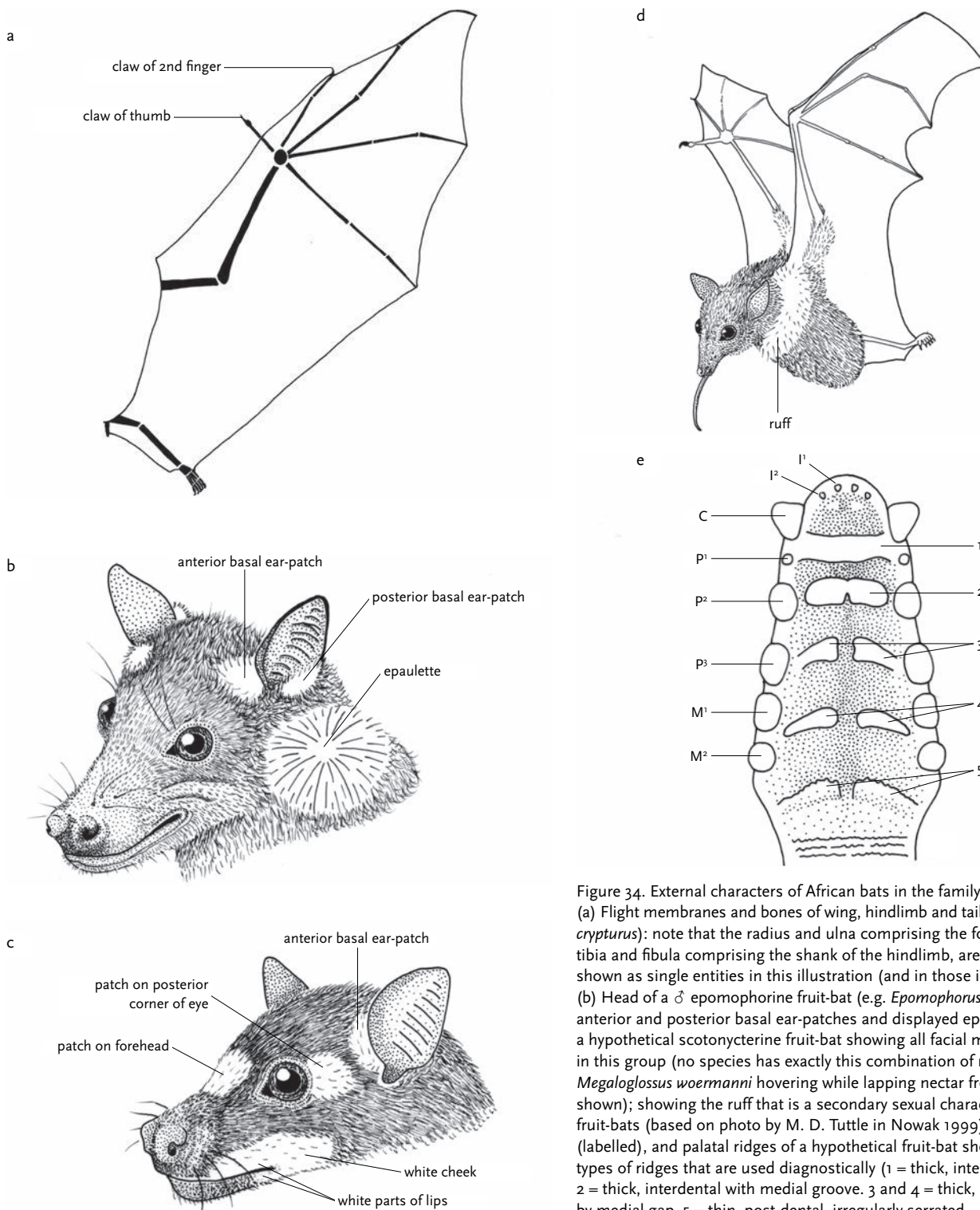


Figure 34. External characters of African bats in the family Pteropodidae. (a) Flight membranes and bones of wing, hindlimb and tail (e.g. *Epomophorus crypturus*): note that the radius and ulna comprising the forearm, and the tibia and fibula comprising the shank of the hindlimb, are fused and therefore shown as single entities in this illustration (and in those in other profiles). (b) Head of a ♂ epomophorine fruit-bat (e.g. *Epomophorus wahlbergi*) showing anterior and posterior basal ear-patches and displayed epaulette. (c) Head of a hypothetical scotonycterine fruit-bat showing all facial markings occurring in this group (no species has exactly this combination of markings). (d) Male *Megaloglossus woermanni* hovering while lapping nectar from a flower (not shown); showing the ruff that is a secondary sexual character of myonycterine fruit-bats (based on photo by M. D. Tuttle in Nowak 1999). (e) Upper teeth (labelled), and palatal ridges of a hypothetical fruit-bat showing the main types of ridges that are used diagnostically (1 = thick, interdental, not divided. 2 = thick, interdental with medial groove. 3 and 4 = thick, interdental, divided by medial gap. 5 = thin, post-dental, irregularly serrated).

epaulettes make purely visual signals. The possibility that wing-beating wafts scents bearing olfactory signals from other parts of the body invites investigation. A ruff (or collar) is a wide band of hairs that differ in colour, length and/or texture, extending from the shoulders across the throat and upper chest; in some species, ruffs arise from glandular skin and are stained by glandular secretions.

The skulls of fruit bats are easily distinguished from the skulls of microbats. The rostrum can be short to very long, tapering or (in

Hypsignathus) domed and square-ended. Postorbital processes are well developed and slender, and they curve outwards and downwards behind the orbit (as in Emballonuridae). There are no supraorbital ridges; the sagittal crest is low or absent, the lambdoid crest is very low or absent and there is no occipital helmet. The premaxillae have only the nasal branches present; the palatal branches are absent leaving a deep-wide anterior palatal 'emargination', which may, or may not, open anteriorly between the incisors. The bony palate extends

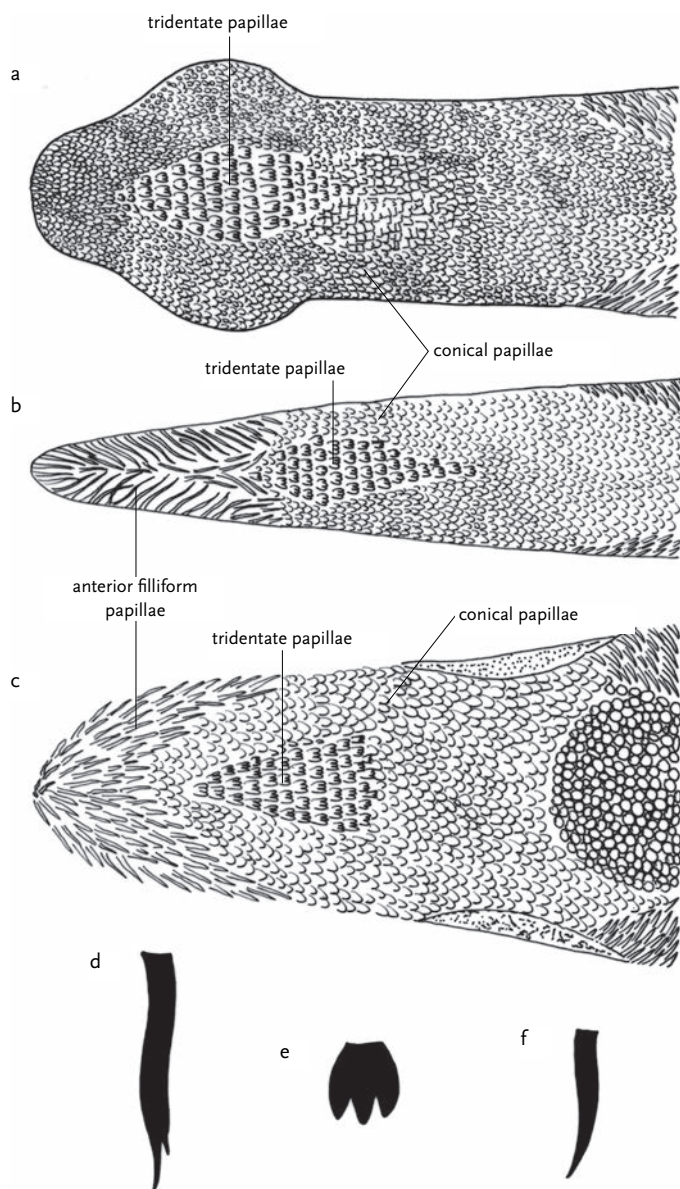


Figure 35. Characteristics of the papillae on tips of tongues of some fruit-bats. (a) *Hypsignathus monstrosus* (based on Lang & Chapin 1917b), (b) *Megaloglossus woermanni* (based on photo in Kulzer 1982) and (c) *Pterotes anchietae* (based on Harrison 1960). (d) anterior filiform papilla for collecting nectar. (e) Tridentate papilla, stiff enough to serve as a rasp. (f) Posterior hair-like papilla. Tongues not drawn to scale.

posteriorly well beyond the teeth (except in *Casinycteris*). The teeth are in an evolutionary process of becoming simpler (e.g. by losing cusps), smaller (especially the first premolars and posterior molars) and fewer. Dental formulae are usually $2^{121}/_{2132} = 28$ or $2^{132}/_{2133} = 34$. The teeth are well separated (cf. in close contact in microbats). The canines are long and curved; the molars are with or without cusps and the cusps are separated by smooth shallow troughs (cf. with a W-shaped pattern of sharp cusps in microbats [reduced in some species]). The dentition is highly specialized for crushing pulpy fruit.

Most African fruit bats for which data are available ($n = 8$) have low to very low aspect ratios (medium in *Micropteropus pusillus*), and medium to exceptionally high wing-loadings. Most can fly fast and direct in the open, or slowly with considerable manoeuvrability through branches and foliage. Most fly most of the time that they are

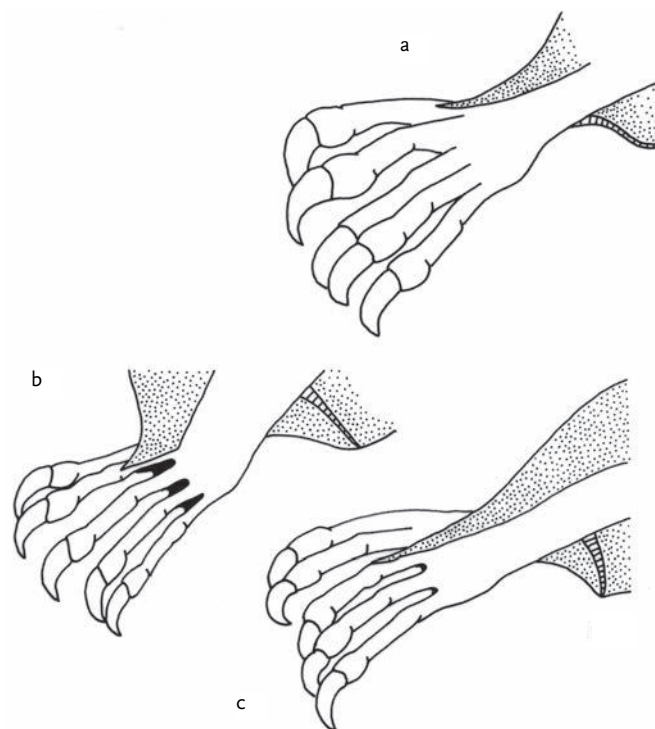


Figure 36. Left hindlimbs of three fruit-bats showing attachment of the wing to (a) the first toe (e.g. *Rousettus aegyptiacus*), (b) the second toe (e.g. *Myonycteris torquata*) and (c) the third toe as in some *Megaloglossus woermanni*. In some species, the wing is sometimes attached between the first and second toes.

airborne and only glide very short distances, but some flying-foxes (*Pteropus*) have become specialist gliders and soarers (Norberg *et al.* 2000). Some fruit bats can hover briefly and sometimes do so while collecting nectar or fruit. Some can take off from the ground, which enables them to feed on fallen fruit. Most species glide towards a perch and, at the last moment, stall, somersault and grasp the perch with their hindfeet. Others, such as some flying-foxes, fly slowly over a perch, grasp it with the hindfeet and then topple down into the hanging position. Many also make rather uncontrolled crash-landings on to foliage. Because they do not fly in pursuit of moving prey, they typically lack agility and do not perform aerial acrobatics (cf. microbats). Most African fruit bats eat the ripe soft-skinned fruits (sometimes also flowers) of rainforest, savanna and cultivated trees. Typically, they land onto fruit-bearing vegetation and use thumbs, wings and sometimes a foot, to manipulate the fruit so it can be bitten. The thumb can be opposed against the fingers, and the second finger has more mobility than in microbats; consequently the wing can be used somewhat like a hand. Whole fruits, or large pieces, are packed into the cheek-pouches and then carried to a perch where the bat hangs and slowly chews the fruit. To avoid carrying extraneous weight, only the energy-rich juice and small amounts of pulp are swallowed – the fibre and seeds are discarded. Juice is extracted by crushing the pulp between the teeth, sucking it and squeezing it against the palatal ridges. Fruits are a poor source of proteins and minerals: some fruit bats chew leaves and swallow the juices, presumably to obtain these nutrients. Furthermore, some flying-foxes fly off-shore apparently to drink seawater, possibly as a means of obtaining salts (Ratcliffe 1961, Bergmans 1978, Iudica & Bonaccorso 2003). The passage of food through the digestive tract is

very rapid (average 30 min) (Nowak 1999). The kidneys are adapted to excrete large volumes of very dilute urine, and to maximize the retention of salts and other solutes (Happold & Happold 1988). However, despite the large amount of water in the diet, several African fruit bats (*Eidolon helvum*, *Rousettus aegyptiacus*, *Hypsignathus monstrosus*) drink in captivity and, in the wild, *Eidolon helvum* and *Epomophorus gambianus* have been seen skimming over open water and making contact with the surface, but it is not yet certain that they do this to obtain water for drinking (Bergmans 1978). It is conceivable that *Eidolon helvum*, which dips its hindlimbs into the water, might be trawling for fish (Bergmans 1978). Some fruit bats, including *Megaloglossus woermanni* in Africa, are specialist nectar/pollen eaters that hover or land on flowers that are adapted for pollination by bats, and lap the nectar and/or pollen with their very long, brush-tipped tongues. Fruit bats locate food by smell, often at very long range; their olfactory lobes and sense of smell are highly developed (Möhres & Kulzer 1956). Fruit bats have colour-vision and, at close range, fruits are located by sight. Some fruit bats fly as much as 60 km between day-roost and feeding-ground, and then back again.

African fruit bats are dependent on trees for food and most are also dependent on trees for shelter. The abundance of fruit bats at many localities is determined by the seasonal availability of fruits and flowers; some species migrate and many are nomadic for this reason. Fruit bats are not adapted for cursorial locomotion such as scuttling, but some are fairly competent climbers; they swing along under thin branches, holding on with the claws of their thumbs and toes, and moving the wings in alternation. Some can also climb head-first up or down vertical surfaces. Some, if not all, can swim by using their wings as oars, but swimming is not a normal occurrence. During the day, most African fruit bats roost in trees or shrubs, hanging freely from thin branches, usually well concealed in the shade of foliage but sometimes in the open. Brownish pelage, white markings on the heads of many species, and pale skin over the wing-bones, probably contribute to the cryptic appearance of roosting fruit bats (Fenton 1992). Some fruit bats habitually roost in caves: *Rousettus* in dark caves, *Lissonycteris* in dimly lit caves. *Rousettus*, like all other fruit bats, perceive their surroundings by eyesight, even at night. However, at least three species also use a primitive form of echolocation (clicks made by the tongue) to find their way inside dark caves. Most roosting fruit bats temporally hang by their thumbs while urinating or defaecating. Fruit bats are mainly nocturnal, but some species leave their day-roosts at sunset and some in the late, or even early, afternoon. Some fruit bats roost singly, others in small to very large groups. Some are very noisy and restless during the day; others stay quiet and still. Fruit bats do not hibernate. Little is known about their social behaviour and mating systems with the exceptions of *Hypsignathus* (which has a classical lek mating system), *Epomops buettikoferi* and *E. franqueti* (which have exploded lek mating systems [sensu Bradbury 1981]) and *Pteropus seychellensis* (which appears to have a harem mating system of some sort). Some aspects of the social behaviour of *Epomophorus wahlbergi* and *Rousettus aegyptiacus* are also known although the mating systems of these species have not yet been elucidated. Males of some species attract mates by performing calling displays during which they make loud calls, beat their wings and display their epaulettes; they have a well-developed larynx and amplifying chambers.

Most fruit bats are monogamous (Hill & Smith 1984) but twinning has been reported in *Epomops dobsonii* (Hill & Smith 1984) and very

occasionally in *Eidolon helvum*, *Epomophorus wahlbergi*, *Megaloglossus woermanni*, *Nanonycteris veldkampii* and *Rousettus aegyptiacus*. Reproductive chronologies include restricted seasonal monoestry, extended seasonal monoestry, aseasonal monoestry, continuous bimodal polyoestry with postpartum oestrus, seasonal bimodal polyoestry without postpartum oestrus, perhaps aseasonal polyoestry and perhaps bimodal monoestry. One species, *Rousettus aegyptiacus*, exemplifies four of these chronologies at four different localities! Investigations of fruit bat reproductive chronologies are often hampered by the nomadic movements of the bats; there may be reliable evidence of births in one season but no data for other times when second births may be occurring elsewhere. *Eidolon helvum*, which has delayed implantation, is the only African fruit bat known to show any form of reproductive delay (Bernard & Cumming 1997). There appears to be a trend (exemplified intra-specifically by *Rousettus aegyptiacus* and *Epomophorus wahlbergi*) towards polyoestry in the tropics and monoestry at higher latitudes (Happold & Happold 1990a, Bernard & Cumming 1997, and species profiles). In the tropics, ten species are polyoestrous, four probably polyoestrous, one monoestrous, two probably monoestrous and there is no information for 11 species. In southern Africa, there are three monoestrous species (including the migratory *E. helvum*, which does not give birth in the region), and there is no information for one species. There is also evidence suggesting that some of the species in equatorial rainforests, peripheral savannas and/or woodland savannas north of the Equator, have inflexible chronologies that are, perhaps, better suited to some environments than others (Fayenuwo & Halstead 1974, Thomas & Marshall 1984, Happold & Happold 1990a).

Fruit bats are distributed mainly in forests and woodlands throughout the tropical and sub-tropical regions of the Old World (including islands in the Indian and Pacific oceans), wherever flowering and fruiting trees are present to provide food. They are not found in the New World, where the fruit and nectar-feeding niche is exploited by the Phyllostomidae, a family of microbats that is not represented elsewhere. Of the 28 species in Africa, 24 are found only in the tropics and sub-tropics, and four are mainly tropical but extend southwards into the temperate region of southern Africa. Eight species are found only or mainly in forests, nine in both forests and savannas, nine only or mainly in savannas and two only on islands. Eighteen species are found only on the mainland, eight mainland species also occur on Bioko I. and/or on at least one of the islands off the coast of East Africa (Pemba I., Zanzibar and Mafia I.), and two species are island specialists found only on Pemba I. or Mafia I. Only one species (*Rousettus lanosus*) is found mainly in montane habitats, but 13 species (48%) extend into montane habitats. Most localities suitable for fruit bats are probably exploited by more than one species; some localities have 4–10 species, for example:

Mt Nimba, Liberia (Rainforest and Montane Forest): *Eidolon helvum*, *Epomops buettikoferi*, *Hypsignathus monstrosus*, *Lissonycteris angolensis*, *Megaloglossus woermanni*, *Myonycteris torquata*, *Nanonycteris veldkampii*, *Rousettus aegyptiacus*, *Scotoonycteris ophiodon* and *S. zenkeri* (Coe 1975).
Luluabourg, DR Congo (Rainforest–Savanna Mosaic): *Casinycteris argynnis*, *Eidolon helvum*, *Epomophorus wahlbergi*, *Epomops franqueti*, *Hypsignathus monstrosus*, *Megaloglossus woermanni*, *Micropteropus intermedius* and *M. pusillus* (Hayman *et al.* 1966).
Zomba, Malawi (miombo woodland): *Eidolon helvum*, *Epomophorus crypturus*, *E. labiatus* and *E. wahlbergi* (Happold & Happold 1997).

The geological range of the Pteropodidae is early Miocene to Recent in Africa, Pleistocene to Recent in Madagascar and East Indies, and Recent in other parts of its geographic range (Koopman 1984, McKenna & Bell 1997); the early Oligocene *Archaeopteropus transiens* from Europe was removed from Pteropodidae by Schutt & Simmons (1998). There is also a late Eocene premolar from Thailand attributed to Pteropodidae, probably an epomophorine (Ducrocq *et al.* 1993), although some authors have not accepted the pteropodid affinities of this fossil (Teeling *et al.* 2005). A phylogeny based on DNA hybridization suggests that the Pteropodidae originated in the Australo-Pacific or South-East Asia at the end of the Cretaceous (Kirsch *et al.* 1995). An Australasian origin has been confirmed by Giannini & Simmons (2005). Collectively these results also suggest that, having initially specialized in eating mainly fruit (as opposed to insects), the pteropodids have diverged, repeatedly, towards eating either both fruit and nectar, or mainly flower products. For example, Giannini & Simmons (2005) demonstrated that specialist nectar-eating probably evolved at least three times in pteropodids. At the present time, there are ca. 37 fruit-eating genera and only six nectar-eating genera. Kirsch *et al.* (1995) suggest that the prevalence of fruit-eating pteropodids does not mean that fruit-eating is primitive, but Giannini & Simmons (2005) recovered specialized nectarivores nested within clades of frugivores, suggesting a primitively frugivorous feeding habit for pteropodids. Kirsch *et al.* (1995) also pointed out that the food preferences of pteropodids are not tightly correlated with anatomy, and they see this as further evidence that there have been repeated shifts between nectar-eating and fruit-eating in this family. In contrast, Giannini & Simmons (2005) reported fewer instances of parallel evolution of the nectarivorous habit and therefore lesser incongruence between anatomy and dietary habits. Other recent studies indicate that cave-dwelling has originated several times, and it is not yet known if echolocation has evolved only once in the Pteropodidae (as indicated by Giannini & Simmons 2003, 2005), or more than once (see Genus *Rousettus*). The number of times that Africa has been colonized by pteropodids is controversial. Kirsch *et al.* (1995), Springer *et al.* (1995) and Romagnoli & Springer (2000), for example, conclude that Africa has been invaded by one taxon that gave rise to all of the African genera (except possibly *Eidolon*, whose affinities are unclear); this has been referred to as the endemic-African-clade hypothesis (e.g. by Giannini & Simmons 2003). In contrast, Juste *et al.* (1999) suggest that at least three colonization events have occurred, the first (probably in the Miocene via forested corridors linking African and Asian rainforests) associated with the diversification that gave rise to most of the extant African fruit bats including *Rousettus* (*Stenonycteris*) *lanosa* (as *Stenonycteris*), a more recent event for the African *Rousettus* (from which they exclude *Stenonycteris*), and a third associated with *Eidolon*. Giannini & Simmons (2003) suggest an even more complicated scenario in which fruit bats colonized Africa at least four independent times; they indicate that *Stenonycteris* nests among Indomalayan species, which suggests that it is not a member of an African clade and that its occurrence in Africa must have been associated with a separate colonization event, and also that the colonization of islands in the western Indian Ocean and off the East African coast by *Pteropus* should also be counted as one or more separate colonization events (see Genus *Pteropus*).

With all this in mind, it is not surprising that the systematics of the Pteropodidae is controversial. On the basis of morphological

characters, Andersen (1912a) divided the pteropodids into three subfamilies – the Macroglossinae (containing all of the specialized nectar-feeding pteropodids including the African genus *Megaloglossus*), the Pteropodinae (containing most other pteropodids including all of the other African genera) and the Harpyionycterinae (containing one aberrant genus, which does not occur in Africa). Andersen (1912a) also divided the Pteropodinae into five ‘sections’ – the Eonycterine, Notopterine, *Epomophorus*, *Cynopterus* and *Rousettus* sections. Andersen’s *Epomophorus* section contained the African genera *Epomophorus*, *Hypsignathus*, *Epomops*, *Micropteropus*, *Casinycteris*, *Scotonycteris*, *Plerotes* and *Nanonycteris* – a group often referred to as the epomophorine fruit bats. Many of Andersen’s conclusions were supported by the results of subsequent studies, but some were challenged (e.g. Haiduk *et al.* 1983, Bergmans 1988, 1989, 1990, Kirsch *et al.* 1995, Springer *et al.* 1995, Juste *et al.* 1997) and, based on these studies and other work of his own, Bergmans (1997) tentatively proposed a new classification of the Recent Megachiroptera in which the African genera were placed into the following subfamilies and tribes:

Subfamily Rousettinae:

Tribe Rousettini: *Rousettus*, *Eidolon*

Subfamily Pteropodinae

Tribe Pteropodini: *Pteropus*

Subfamily Epomophorinae

Tribe Epomophorini: *Epomophorus*, *Epomops*, *Hypsignathus*, *Micropteropus*, *Nanonycteris*

Tribe Myonycterini: *Lissonycteris*, *Megaloglossus*, *Myonycteris*

Tribe Scotonycterini: *Casinycteris*, *Scotonycteris*

Tribe Plerotini: *Plerotes*.

Some phylogenetic studies based on molecular characters have indicated that (a) high levels of homoplasy have resulted in misleading taxonomic arrangements based on morphological characters, (b) the Epomophorinae *sensu* Bergmans is perhaps not monophyletic, (c) there is support for a large clade of endemic African taxa including genera previously placed in several different subfamilies or tribes and (d) the position of *Eidolon* is not clear (Hollar & Springer 1997, Álvarez *et al.* 1999, Romagnoli & Springer 2000, Giannini & Simmons 2003 and others [see Simmons 2005]). However, the most recent phylogenetic analyses (Giannini & Simmons, 2005) have suggested that Bergmans’s (1997) classification is largely corroborated with regard to the African taxa, with the exception of the placement of *Eidolon*, which does not belong in the Rousettinae and may instead be a member of a pteropodine clade. However, the relationships between pteropodid genera are not yet fully resolved and therefore, pending a re-evaluation of pteropodid classification, Simmons (2005) does not recognize any subfamilial or tribal groups. Likewise no subfamilial or tribal groups are included here.

The 14 genera of fruit bats in Africa are distinguished by size and the various characters given in Table 11. Following Simmons (2005), the genera of fruit bats, and the species within each genus, are presented in alphabetical order.

Table 11. Key to the African genera in the family Pteropodidae. The number of cheekteeth very occasionally varies from the usual numbers given below; for details, see genus profiles.

| Tongue brush-tipped | White or whitish markings on head | Epaulettes on shoulders of adult ♂♂ | FA range (mm) | Muzzle | Cheek-teeth (upper/lower) | Miscellaneous | Genus |
|---------------------|--|-------------------------------------|--------------------|---------------------------------|--|---|----------------------|
| Yes | None | Absent | 38–49 | Elongated | $\frac{5}{6}$ | Toes not webbed or very weakly webbed
Adult ♂♂ have ruffs | <i>Megaloglossus</i> |
| Moderately | No white markings on face
Basal ear-patches present (sometimes inconspicuous) | Absent | 47–53 | Simple | $\frac{4}{6}$ or $\frac{4}{5}$
or $\frac{5}{6}$ | Interfemoral membrane reduced to very narrow flange along legs
Calcars absent | <i>Plerotes</i> |
| No | None | Absent | 145–163 | Simple | $\frac{5}{6}$ | Red or yellow mantle present
Not on mainland Africa | <i>Pteropus</i> |
| No | None | Absent | 105–135 | Simple | $\frac{5}{6}$ | No mantle
Present on mainland Africa and some offshore islands | <i>Eidolon</i> |
| No | None | Absent | 82–106 | Simple | $\frac{5}{6}$ | Toes not webbed
Echolocates
M ² not greatly reduced
Ruffs absent | <i>Rousettus</i> |
| No | None | Absent | 68–90 | Simple | $\frac{5}{6}$ | Toes partly webbed
No echolocation
M ² not greatly reduced
Adult ♂♂ have ruffs | <i>Lissonycteris</i> |
| No | None | Absent | 56–75 | Simple | $\frac{5}{6}$ or $\frac{5}{5}$ | Toes not webbed
No echolocation
M ² greatly reduced
Adult ♂♂ have ruffs | <i>Myonycteris</i> |
| No | White markings on face
Basal ear-patches inconspicuous or absent | Absent | 47–87 ^a | Simple | $\frac{3}{5}$ | Bony palate extending well beyond teeth
Rostrum (viewed laterally) not upturned | <i>Scotonycteris</i> |
| No | White markings on face
Basal ear-patches present (sometimes inconspicuous) | Absent | 50–62 | Simple | $\frac{3}{5}$ | No postdental bony palate
Rostrum (viewed laterally) slightly upturned | <i>Casinycteris</i> |
| No | No white markings on face
Basal ear-patches present (sometimes inconspicuous) | Absent | 112–139 | Truncated; ends in fleshy plate | $\frac{3}{5}$ | | <i>Hypsignathus</i> |
| No | No white markings on face
Basal ear-patches present | Present | 54–100 | Simple | $\frac{3}{5}$ | Interfemoral membrane wide
Calcars present
6 thick palatal ridges | <i>Epomophorus</i> |
| No | No white markings on face
Basal ear-patches present | Present | 77–102 | Simple | $\frac{3}{5}$ | Interfemoral membrane wide
Calcars present
3 or 5 thick palatal ridges | <i>Epomops</i> |
| No | No white markings on face
Basal ear-patches present | Present | 46–64 | Simple | $\frac{3}{5}$ | Interfemoral membrane wide
Calcars present
5–6 palatal ridges; all divided except first
C–M ¹ : 8.0–ca. 10.6 mm | <i>Micropteropus</i> |
| No | No white markings on face
Basal ear-patches present | Present | 46–54 | Simple | $\frac{3}{5}$ | Interfemoral membrane wide
Calcars present
12–13 palatal ridges; posterior group of 8–9 narrowly divided
C–M ¹ : 6.8–7.7 mm | <i>Nanonycteris</i> |

^a Includes specimens from Congo, which are larger than those from elsewhere (see genus profile).

GENUS *Casinycteris*

Short-palated Fruit Bat

Casinycteris Thomas, 1910. Ann. Mag. Nat. Hist., ser. 8, 6: 111. Type species: *Casinycteris argynnis* Thomas, 1893.



Casinycteris argynnis.

This monotypic genus is endemic to Africa and found only in the Rainforest BZ and Rainforest–Savanna Mosaic in S Cameroon, Central African Republic and DR Congo. Diagnostic characters: white markings on the nose, upper lips and near the eyes; white basal ear-patches (sometimes inconspicuous); adult ♂♂ without epaulettes; FA: 50–62 mm; practically no bony palate posterior to the teeth; rostrum (viewed laterally) slightly upturned; canines long; three upper and five lower cheekteeth. Similar to *Scotonycteris* but see Table 11, p. 228. The palatal ridges and craniodental characters of *Casinycteris argynnis* are illustrated in Figure 37.

Although many microbats are short-palated, no other African fruit bat has a reduced palate and it is assumed to be a derived character (Bergmans 1990). Morphologically, *Casinycteris* closely resembles *Scotonycteris*, with *S. ophiodon* being intermediate between *Casinycteris* and *S. zenkeri* (Bergmans 1990). It has been argued that the reduction of the palate might be a relatively simple genetic

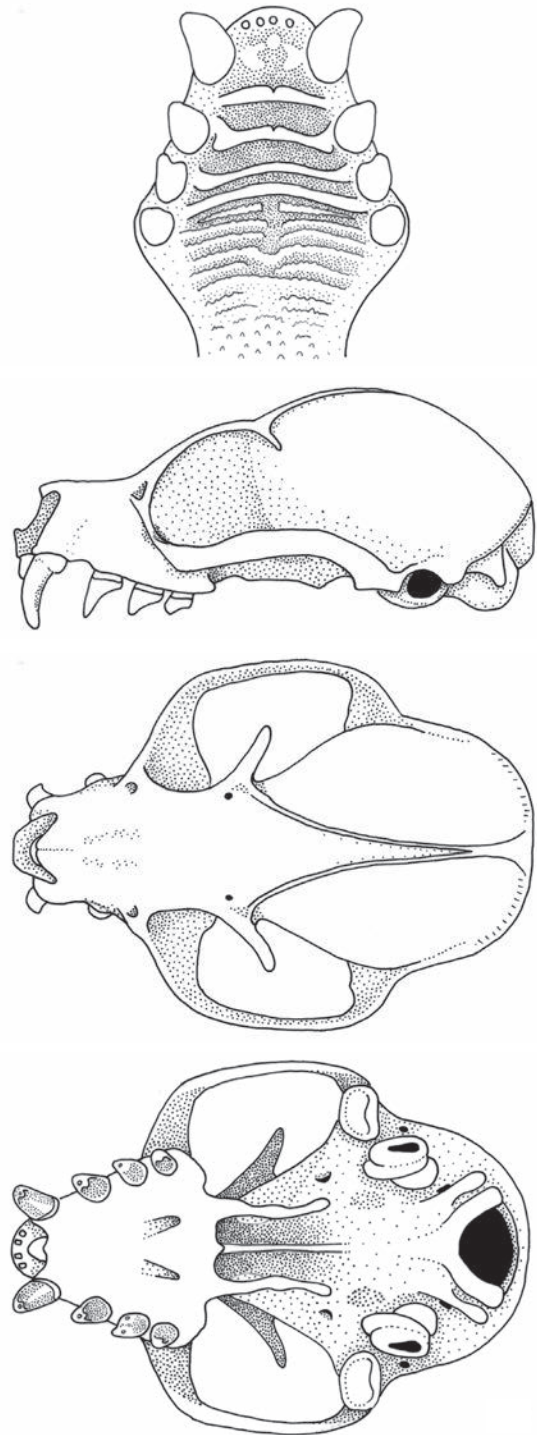


Figure 37. *Casinycteris argynnis*. Palatal ridges (RMCA F 75-56-M-98; see Meirte 1983 for variations). Skull (RMCA 97-021-M-579, adult ♀).

change not important enough to serve as the basis of a genus (Pohle 1943), but Bergmans (1990) gives several other reasons for maintaining *Casinycteris* as a genus as opposed to a subgenus or synonym of *Scotonycteris*. These include the following differences. In

Casinycteris, the orientation of the foramen magnum is rather more horizontal than in *Scotonycteris*. In *Casinycteris*, the rostrum profile is slightly upturned (cf. not upturned in *Scotonycteris*), and there is a distinct angle between rostrum and braincase in the profile of the skull (viewed laterally) (cf. in *Scotonycteris* the border is not so sharply marked). In *Casinycteris*, the orbital cavity is relatively larger than in *Scotonycteris*, and the ears are relatively larger. Differences between *Casinycteris* and *S. zenkeri* are more marked: as well as the reduced palate, *Casinycteris* has a shorter rostrum, stronger and more widely spread zygomatic arches, more strongly developed postorbital and cranial ridges, and generally higher and more pointed teeth (Thomas 1910). These differences suggest that the diet and feeding behaviour of these two species are different (Lang & Chapin 1917b, Bergmans

1990) and that competition between these species, where they occur sympatrically, is reduced accordingly (Andersen 1912a).

Casinycteris is reviewed by Bergmans (1990). *Casinycteris* was placed in the *Epomophorus* section of Andersen (1912a). Subsequently, based on morphological characters, *Casinycteris* was placed (with *Scotonycteris*) in the subfamily Epomophorinae and tribe Scotonycterini by Bergmans (1997). The close relationship of *Casinycteris* and *Scotonycteris*, and the grouping of these genera with other genera in the *Epomophorini*, is supported by the phylogenetic analyses of Springer *et al.* (1995) and Romagnoli & Springer (2000).

The single species is *Casinycteris argynnis*.

Meredith Happold

Casinycteris argynnis SHORT-PALATED FRUIT BAT

Fr. Casinyctère dorée; Ger. Goldener Kurzgaumen-Flughund

Casinycteris argynnis Thomas, 1910. Ann. Mag. Nat. Hist., ser. 8, 6: 111. Dja River, Bitye, Cameroon.

Taxonomy Synonyms: none. Chromosome number: not known.

Description Very small, brown fruit bat with face-markings (white patch on forehead, white posterior eye-spots, partly white lips, white cheeks); whitish anterior basal ear-patches (sometimes indistinct); no epaulettes; snout and finger-joints yellowish; forehead region of skull strongly concave; bony palate uniquely shortened; FA: 50–64 mm. Males and ♀♀ similar in colour (juveniles probably darker); ♀♀ larger, on average, than ♂♂. Pelage woolly; extending dorsally and ventrally over upper arm and halfway along each forearm; mid-dorsal hairs 7–8 mm, shorter and sparser ventrally. Dorsal pelage medium brown (sepia to slightly russet); hairs beige with dark brown at base and medium brown at tip. Ventral pelage medium brown on flanks merging into paler brown on throat, neck and mid-ventrally. No epaulettes. Head brown with white patch on forehead, white patch at posterior corner of each eye, whitish anterior basal ear-patches (sometimes inconspicuous), white cheeks, white chin and white lips (posterior half only). No posterior basal ear-patch. Ears relatively long for a fruit bat (26–35% of FA), rounded. Ears, nostrils and lips with yellow or yellowish-brown pigmentation. Lips and cheeks fleshy and expansible. Palate with three or four thick and one thin serrated interdental ridges (the last of which is sometimes divided), and many crowded, irregular, thin and serrated postdental ridges (Figure 37). Wings brown with some parts orange-brown or yellowish-brown when alive, and with distinctly darker reticulation lines; wing-membranes attaching to first toe. Wing-bones dark except at joints, which are pale yellow or pale yellowish-brown. Thumbs long (ca. 26 mm). No visible tail.

Skull (Figure 37) short for an African fruit bat. Braincase strongly rounded; rostrum relatively short, slightly upturned. Profile of forehead region (viewed laterally) strongly concave (cf. *Scotonycteris*). Zygomatic width relatively great (71–79% of GLS); zygomatic arches comparatively strong with ventral margins almost at level of alveolar line (Bergmans 1990) (cf. *Scotonycteris*). Bony palate extremely reduced so there is practically no postdental palate (cf. all other African fruit bats), although soft palate continues as far back as in other fruit bats. For specimens with the soft palate

intact, the posterior margin of the bony palate can be felt with a blunt probe. Upper incisors comparatively short (cf. *Scotonycteris ophiodon*). Upper canines tall, markedly curved backwards (as in *Scotonycteris ophiodon*); inner edges usually smooth, sometimes with slightly serrated appearance when worn. Premolars and molars with well-developed inner cusps (especially P⁴, P₃ and P₄) (cf. *Scotonycteris zenkeri*). Dental formula $\frac{2121}{2132} = 28$.

Geographic Variation None known.

Similar Species Only two other African fruit bats have white markings on the forehead, upper lip and behind the eyes:

Scotonycteris ophiodon. Much larger (FA: 73–87 mm; GLS: >35 mm).

Forehead region of skull only weakly concave; rostrum not upturned; bony palate extending well beyond last teeth.

S. zenkeri. Forearm often shorter (47–55 mm). Finger-joints brown.

Forehead region of skull almost straight; rostrum not upturned; bony palate extending well beyond last teeth.

Distribution Endemic to Africa. Known from 17 localities in Rainforest BZ and Southern Rainforest–Savanna Mosaic, in S Cameroon, Central African Republic and DR Congo (Bergmans 1990, Lunde & Beresford 1997), but likely to occur more widely within these zones. More recently, in 2000 and 2003, ten specimens were collected from Mabira F. R. in C Uganda (00° 23' N, 33° 01' E) (Kityo *et al.* 2009): this locality, which extends the known range eastwards by ca. 500 km, is not mapped.

Habitat Wetter and drier types of lowland rainforest, disturbed secondary forest, mosaics of forest with secondary grassland, and riverine forests (Bergmans 1990, Van Cakenberghe *et al.* 1999). Also swamp forest where few other fruit bats have been found (Bergmans 1990).

Abundance Very rarely recorded, but perhaps locally abundant: several specimens were mist-netted on one day at one locality

*Casinycteris argyrenis*

(Meirte 1983); 14 caught in five weeks at Irangi, DR Congo (Bergmans 1990).

Remarks Aspect ratio very low; wing-loading medium ($n = 1$); flight predicted to be slow and manoeuvrable. One ♀ was found hanging singly in the dense foliage of a bush 3 m above the ground (Lang & Chapin 1917b). The yellowish colour and reticulation of the wings suggest reliance on camouflage while roosting in foliage. The uniquely reduced bony palate, and several other characters of the skull and dentition, suggest that the food and feeding behaviour might be different from that of most other fruit bats (Lang & Chapin 1917b).

Reproduction and Population Structure No conclusive data. Within three degrees of the Equator, two pregnant ♀♀ (one also lactating), one lactating ♀ and one immature ♀ were taken

in Jan–Feb; one ♀ with one foetus was recorded in Apr, and an immature ♂ was recorded in May. These data suggest that litter-size is one and that the reproductive chronology is polyoestry, but this needs confirmation.

Conservation IUCN Category: Least Concern.

Bergmans (1999) indicated that this listing would be appropriate because of the wide distribution of this species in the Rainforest BZ in central Africa and its apparent abundance in one of the better-searched localities (Irangi). Major threat: deforestation.

Measurements

Casinycteris argyrenis

FA (♂♂): 52.9 (50–56) mm, $n = 12$

FA (♀♀): 58.9 (56–62) mm, $n = 23$

WS (d): 280–380 mm, $n = 3$

HB (♂♂): 80 mm, $n = 1$

HB (♀♀): 82.6 (70–100) mm, $n = 9$

T: 0 mm, $n = 4$

E: 18.1 (15–20) mm, $n = 10$

Tib: 24.0 (22–26) mm, $n = 9^*$

HF: 13.4 (12–14) mm, $n = 9^*$

WT (♂♂): 29 g, $n = 1$

WT (♀♀): 30 (24–41) g, $n = 14$

GLS (♂♂): 24.9 (22.4–26.9) mm, $n = 24$

GLS (♀♀): 26.1 (22.2–28.4) mm, $n = 30$

GWS (♂♂): 18.6 (16.0–19.8) mm, $n = 23$

GWS (♀♀): 19.1 (16.4–20.5) mm, $n = 28$

C–M¹ (♂♂): 8.3 (7.0–9.5) mm, $n = 24$

C–M¹ (♀♀): 8.6 (7.2–9.8) mm, $n = 28$

Throughout geographic range (Perret & Aellen 1956, Meirte 1983, Bergmans 1990, Van Cakenberghe *et al.* 1999, AMNH, BMNH, RMCA, SMNS, D. Lunde pers. comm.)

*Tibia and hindfoot: ♀♀ only

Key References Bergmans 1990; Lang & Chapin 1917b; Meirte 1983.

Meredith Happold

GENUS *Eidolon*

Straw-coloured Fruit Bats

Eidolon Rafinesque, 1815. Analyse de la Nature, p. 54. Type species: *Vespertilio vampirus helvus* Kerr, 1792.

Eidolon is a polytypic genus with two species: *E. helvum* on mainland Africa, *E. dupreanum* on Madagascar. Diagnostic characters: no white markings on head; no white basal ear-patches; adult ♂♂ without epaulettes; FA: 105–135 mm; no red or yellow mantle contrasting with blackish-brown dorsal pelage, no ruff of stiff hairs around the neck; five upper and six lower cheekteeth (Table 11, p. 228). The palatal ridges and craniodental characters of *Eidolon helvum* are illustrated in Figure 38.

The genus was revised by Bergmans (1990). *Eidolon* was placed in the *Rousettus* section of Andersen (1912a), and in the subfamily Rousettinae (tribe Rousettini) by Bergmans (1997). Juste *et al.*

(1999) indicate that *Eidolon* is not phylogenetically related to any other African fruit bat. Giannini & Simmons (2005) recovered *Eidolon* as sister to a pteropodine clade (including *Acerodon*, *Pteralopex* and *Pteropus*) in some but not all analyses, suggesting that more data are needed to corroborate this hypothesis and its interesting biogeographic implications. Based on this and other recent studies, the position of *Eidolon* is considered uncertain by Simmons (2005).

The African species is *Eidolon helvum*.

Meredith Happold

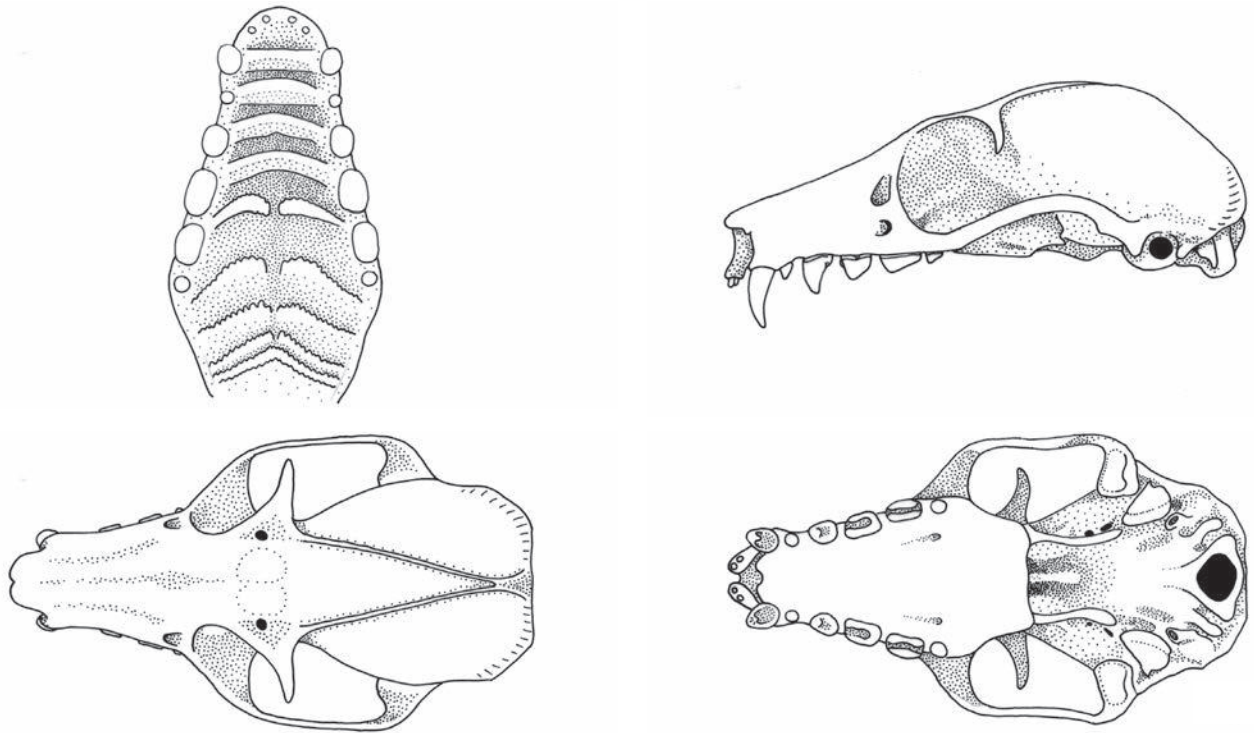


Figure 38. African *Eidolon*. Palatal ridges of *E. helvum*. Skull of *E. helvum* (BMNH 98.10.24.2, adult ♂).

Eidolon helvum AFRICAN STRAW-COLOURED FRUIT BAT

Fr. Rousette des palmiers africaine; Ger. Afrikanischer Palmflughund

Eidolon helvum (Kerr, 1792). In: Linnaeus, Anim. Kingdom 1 (1): xvii, 91. Senegal.

Taxonomy Originally *Vespertilio vampyrus helvus*. Synonyms: *annobonensis*, *buettikoferi*, *leucomelas*, *mollipilosus*, *paleaceus*, *palmarum*, *sabaeum*, *stramineus*. Hayman & Hill (1971) also included *dupreanum* from Madagascar, but Bergmans (1990) regards *E. dupreanum* as a distinct species. Subspecies: two, but only the nominate in Africa. Chromosome number: $2n = 34$ (Matthey 1962); aFN not known.

Description Large, yellowish fruit bat with no basal ear-patches; no white markings on head; no red or yellow mantle contrasting with dorsal pelage; no ruff of stiff hairs (although longer, pale yellowish-brown to bright orange hairs on throat); FA: 105–135 mm. Little sexual dimorphism. Hairs 6–8 mm mid-dorsally, longer ventrally; dorsal pelage extending to half-way along forearm (but not on to wing-membranes) and narrowing on mid-back (between wing-membranes); sparse on head. Dorsal pelage variable between individuals and between different regions of body; can be dull yellow, brownish-yellow, pale yellowish-grey to dark sepia-grey, or dull brown; head darker than shoulders, interscapular region and rump often darker and less yellow than mid-dorsal region and adjacent to wing-membranes; hairs pale yellowish, mostly tipped with brown or greyish-brown. Ventral pelage (except on throat) grading from pale yellow (buff) on flanks to pale brown mid-ventrally. Throat with ruff of longer (but not stiff) hairs, ranging from pale yellowish-brown to bright orange; breeding ♂ brighter than ♀. Males without epaulettes. Head

without markings; muzzle long, narrow, almost naked; cheeks only moderately extensible; lips fine and smooth. Ears rounded, naked, dark brown. Eyes large, orange-brown. Palate with four undivided thick ridges followed by four divided, serrated, thin ridges (Figure 38). Wing-membranes dark brown (in marked contrast to dorsal pelage), inserting unusually high on back (for an African fruit bat) and attaching to first toe. Thumb very long with a powerful, sickle-shaped, hook-like claw. Legs strikingly long. Interfemoral membrane narrow (especially near tail). Tail relatively long for a fruit bat.

Skull (Figure 38), on average, medium-long for an African fruit bat. Braincase domed, rostrum of medium relative length for this family; premaxillae not fused anteriorly. Basicranial axis considerably deflected; upper alveolar line straight. Tympanic bulla protruding to form a short tube around the auditory meatus. M_1 comparatively long (length = combined length of M_2 and M_3) (cf. *Rousettus* and *Lissonycteris*). Dental formula $2^{132}/_{2133} = 34$.

Geographic Variation Two subspecies are recognized by Bergmans (1990): *E. h. helvum* in Africa and *E. h. sabaeum* in SW Arabia. Geographic variation in size in Africa is not apparent, but detailed investigations have not yet been undertaken. Four specimens (♂♂) from Bioko I. (Eisentraut 1964) have comparatively large skulls (GLS: 55.8–58.7 mm). Unconfirmed records from Somalia possibly represent *E. h. sabaeum* (Bergmans 1990).

Similar Species Two other large African fruit bats have no basal ear-patches and no white markings on head; FA: >108 mm:

Pteropus voeltzkowi. Dorsal pelage blackish-brown with bright rusty-red or rusty-orange mantle. Larger (FA: 145–163 mm). Pemba I. only.

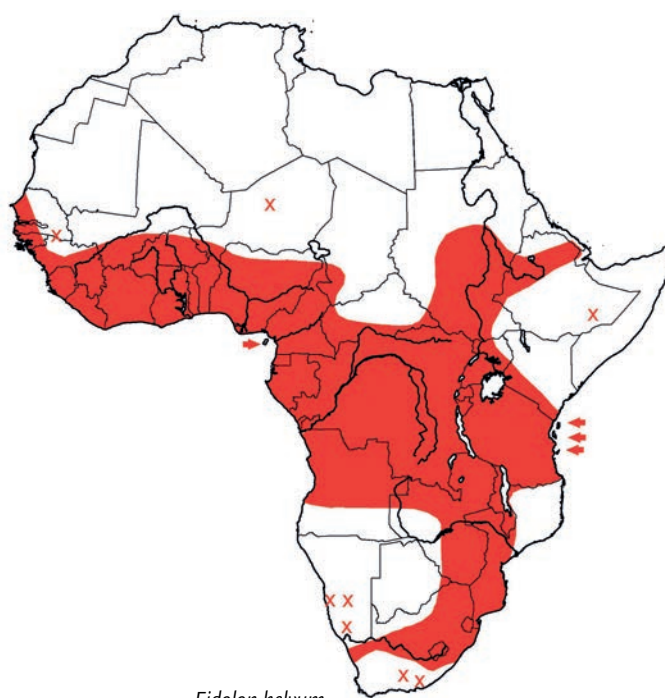
P. seychellensis comorensis. Dorsal pelage blackish-brown with golden or rusty-yellow mantle. Larger (FA: 147–158 mm). Mafia I.

Distribution In Africa, this migratory species has been recorded from all countries and all biotic zones and mosaics south of the Sahara (except the South-West Cape BZ), but there are no records in most parts of the Sahel Savanna, Somalia–Masai Bushland and South-West Arid BZs and also in some large parts of the Sudan Savanna, Guinea Savanna and Zambezian Woodland BZs. Some authors (e.g. Kingdon 1974, DeFrees & Wilson 1988) suggest that the Rainforest BZ, and the Rainforest–Savanna Mosaics and the Coastal Forest Mosaic BZ, from West Africa to East Africa (including Zanzibar, Mafia and Pemba Is.) comprise ‘prime habitat’ from which colonies migrate seasonally into the dry forest, woodland savanna and Sahel zones, and only reach the northern and southern limits seasonally and/or irregularly. Although Bergmans (1990) maintains that this is an overgeneralization that ignores the absence of records from very large parts of the area involved, this view is not held here. Extraliminally: SW Arabian Peninsula.

Habitat Probably inhabits all forest and woodland savanna habitats when and where trees are producing succulent fruits.

Abundance Extremely abundant locally, with largest colonies in forest regions possibly exceeding 1 million, and with one colony in savanna at Kasanka N. P., Zambia reaching 5–10 million (see below). Huge colonies are often associated with tall trees in city parks, making this fruit bat the most observable bat in Africa. Seasonally abundant to irregular at northern and southern limits due to fragmentation of colonies during seasonal migrations (Thomas 1983, Cosson *et al.* 1996). Comparatively rare in mist-netting samples taken at ground level because these fruit bats usually fly fairly high.

Adaptations Aspect ratio medium-low; wing-loading exceptionally high; wing-tip slightly pointed (Norberg & Rayner 1987). Flight straight and comparatively non-agile; slow, regular wing-beats often interrupted by short glides; mean speed (tested indoors) 4.5 m/sec (Rosevear 1965, Kulzer 1968 in Norberg 1987), but wing morphology and personal observations suggest that flight speeds are considerably higher in the field. Must dive 1–2 m to gain sufficient speed for flight, which might explain preference for canopy foraging. Makes long-range migrations: ♂♂ tracked by satellite telemetry are known to migrate at least 2000 km in three months, from Kasanka N. P., Zambia (where the bats presumably aggregate to exploit an exceptional rich seasonal peak in food) to N DR Congo (Richter & Cumming 2008); no data for ♀♀. Has been recorded at sea 240 km from land (Rosevear 1965). Remarkably long thumbs and legs facilitate agile climbing. By day, usually roosts colonially in tall trees exposed to full sunlight, but one small colony roosted on rock face of escarpment in C Mali (Thomas 1983). Heart very large, with massive anterior vena cava, allowing great flight endurance.



Eidolon helvum

Anastomoses permit regulation of blood flow into wing-membranes, probably to allow off-loading of heat during long-distance flight and mid-day roosting. Shows well-developed wing-licking and wing-fanning when roosting in full sun. Exhibits a strong homeothermic response down to 10°C, but rapidly becomes hypothermic below 10°C. Tongue has long backward-directed papillae, probably to facilitate rapid collecting of nectar. Skin of the neck contains a large sebaceous gland complex, better developed in ♂♂ than in ♀♀, suggesting that the throat ruff provides olfactory cues (Mainoya & Howell 1979).

Foraging and Food At dusk, colonies become active; groups fly up to 100–200 m above ground and non-migrating individuals forage as far as 59 km from the roost in one night (Richter & Cumming 2008). Commonly feeds in noisy groups. Diet includes great diversity of flowers (10 genera, 6 families), fruits (33 genera, 23 families) and leaves (4 genera, 3 families) (Marshall 1985). Unusual in specializing on small figs and small fruits (5–15 mm diameter), including *Ficus vogellii* and berries *Bridelia ferruginea*. Good climbing agility may make the harvesting of small fruits economical.

Social and Reproductive Behaviour Roosts in groups (colonies) varying in size from tens to hundreds of thousands, sometimes ca. 1 million and, in Kasanka N. P., Zambia, colonies of 5–10 million assemble each year in Nov–Dec (Richter & Cumming 2008). Cycles in colony occupation and size are intimately associated with migrations and reproductive chronology. North of Equator, colonies in rainforest habitats reach peak size at onset of dry season in northern savannas (Sep–Oct at Kampala, Uganda; Oct–Nov at Abidjan, Côte d'Ivoire). Colonies include juveniles and yearlings until Nov–Dec (Kampala), when these age-groups may disperse elsewhere (Kingdon 1974). Pregnant ♀♀ and adult ♂♂ remain until births (Jan–Feb at Abidjan; Feb–Mar at Kampala) and mating (probably Feb at Abidjan; Apr–Jun at Kampala). North of Equator,

colonies in forest habitats disperse with northward progression of rains into the savanna (Feb–Mar at Abidjan; May–Jun at Kampala). Migration into the savanna occurs in groups that fragment, creating progressively smaller colonies as they move northwards to at least 13° N (Thomas 1983). During the pregnancy and parturition period, multi-female groups associate with one or few ♂♂, suggesting polygyny and harem-formation, but the associations appear labile. There are no detailed studies of social structure in colonies.

Reproduction and Population Structure Litter-size: normally one ($n = \text{ca. } 200$); twins reported once. In Uganda, Nigeria and Côte d'Ivoire, the reproductive chronology is restricted seasonal monoestry with delayed implantation – a chronology not known in any other African fruit bat. At 00° 20' N (Kampala, Uganda), copulation and fertilization occur in Apr–Jun followed by development to blastocyst stage and then delayed implantation for ca. three months (during migration); implantation and onset of developmental gestation in Oct; births ca. four months later (Feb–Mar); lactation for ca. one month (Mutere 1965, 1967). Males gain mass prior to the mating season, suggesting increase in body condition. At Kampala, rain falls throughout the year but there are peaks in Oct–Nov and Apr–May, and the reproductive chronology is such that both spermatogenesis and lactation coincide with periods of high rainfall, and births during the relatively dry periods are avoided. At 07° 30' N (Ife, Nigeria), copulation and fertilization occur in May–Jul; implantation in Nov after a delay of ca. five months; births in Mar–Apr (Fayenuwo & Halstead 1974, Funmilayo 1979 in Bernard & Cumming 1997). At Ife, there is a long wet season (Mar–Jun), a short wet season (Sep–Oct) and a hot dry season (Nov–Feb). Here, both spermatogenesis and lactation occur during the long wet season, and the longer period of delayed implantation ensures that births do not occur until the long wet season is well established. At Ife, implantation coincides exactly with the start of the hot dry season, which suggests that the sudden change in weather or body condition might provide the stimulus for implantation (Fayenuwo & Halstead 1974). In contrast, at Kampala, implantation does not appear to coincide with any marked climatic factor. Reproduction south of the Equator has not been documented; an austral cycle is predicted but needs confirmation.

Predators, Parasites and Diseases Snakes, carnivorous birds (African Eagle-owl *Bubo africanus* and Kite *Milvus migrans*) and

mammals (Palm Civet *Nandinia binotata*, genets *Genetta* spp., even Potto *Perodicticus potto*) are probable predators, but few observations of non-human predation exist. Hunters with shotguns, and boys with sling-shots, kill large numbers (hundreds) for personal consumption or sale in markets. Ectoparasites include: a bed-bug *Afrocmex constrictus* (Hemiptera: Cimicidae); three species of fleas (Siphonaptera: Ischnopsyllidae); six species of bat-flies (Diptera: Nycteribiidae); pentastomids *Armillifer* sp. (Pentastomida: Porocephalidae), *Linguatula* sp. (Pentastomida: Linguatulidae); two species of ticks (Acari: Argasidae, Ixodidae); and 12 species of mites (Acari: Spinturnicidae, Macronyssidae, Myobiidae, Ereynetidae, Chirodiscidae, Sarcoptidae, Gastronyssidae, Teinocoptidae) (Anciaux de Faveaux 1984). Can harbour the following viruses: Bunyamwera, Entebbe bat, Lagos bat, West Nile, Yellow Fever, Zika and others (Anciaux de Faveaux 1984).

Conservation IUCN Category: Near Threatened.

Often seen in large numbers but the population of this species is declining because of over-harvesting for food and medicine.

Measurements

Eidolon helvum

FA: 118.6 (105–135) mm, $n = 97$

WS (d): 815.1 (720–950) mm, $n = 7$

TL: 193 (146–237) mm, $n = 68$

HB: 186.4 (161–227) mm, $n = 41$

T: 14.6 (4–24) mm, $n = 92$

E: 27.8 (22–33) mm, $n = 96$

Tib: 50.2 (45–54) mm, $n = 35$

HF: 30.4 (24–37) mm, $n = 28$

WT: 208.3 (110–350) g, $n = 13$

GLS: 57.0 (51.9–59.9) mm, $n = 41$

GWS: 31.9 (30.1–35.1) mm, $n = 38$

C–M²: 20.9 (19.0–22.8) mm, $n = 22$

Throughout geographic range (BMNH and literature)

Key References Kingdon 1974; Marshall 1985; Mutere 1965, 1967; Thomas 1983.

Don Thomas & Mickaël Henry

GENUS *Epomophorus*

Epauletted Fruit Bats

Epomophorus Bennett, 1836. Proc. Zool. Soc. Lond. 1835: 149 [publ. 1836]. Type species: *Pteropus gambianus* Ogilby, 1835.

Epomophorus is a polytypic genus, endemic to Africa (with the exception that *E. labiatus* also occurs in SW Saudi Arabia). Diagnostic characters: white basal ear-patches but no other white markings on the head; epaulettes on shoulders of adult ♂♂; FA: 54–100 mm; muzzle simple; interfemoral membrane well developed and with calcars; six thick palatal ridges; usually three upper and five lower cheekteeth (very occasionally four upper cheekteeth) (Table 11, p. 228). Palatal ridges of six species are illustrated in Figure 39. The skull of a representative of the genus is illustrated in Figure 40,

but there are inter-specific variations, especially in size and relative dimensions (see below). *Epomophorus* has eight species, more than any other genus of fruit bat endemic to Africa. Seven of the species occur mainly in savanna woodland habitats, one species occurs in both forest and savanna habitats.

Epomophorus was placed in the *Epomophorus* section of Andersen (1912a), and in the subfamily Epomophorinae (tribe Epomophorini) of Bergmans (1997) together with *Epomops*, *Hypsiphatius* and *Micropteropus*, which seem closely related morphologically and

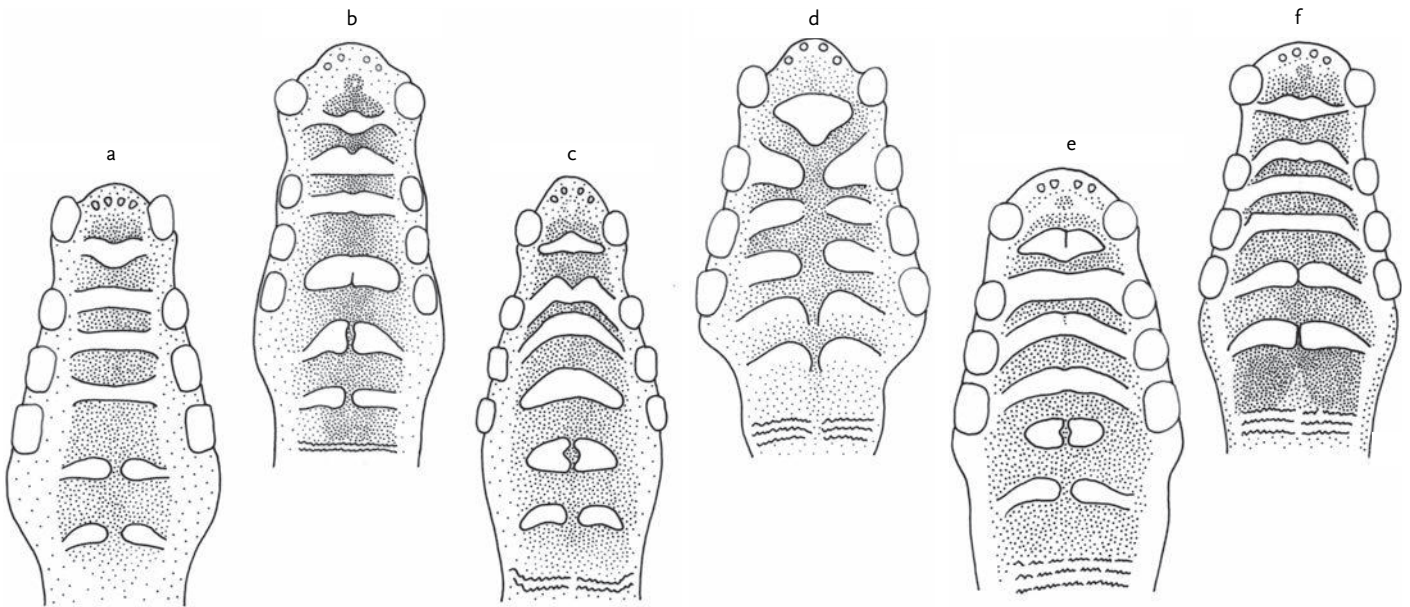


Figure 39. Palatal ridges of six species of *Epomophorus*. (a) *Epomophorus angolensis*, (b) *E. crypturus*, (c) *E. gambianus*, (d) *E. grandis* (based on Bergmans 1988 with permission of the author), (e) *E. labiatus* and (f) *E. wahlbergi*.

karyotypically (Haiduk *et al.* 1980). *Nanonycteris*, which was not studied by Haiduk *et al.* (1980), was also placed in this tribe by Bergmans (1997). However, more recently, the monophyly of the Epomophorinae (*sensu* Bergmans 1997) has been questioned (up to now, only by Springer *et al.* 1995 and Romagnoli & Springer 2000) and, pending a thorough revision of the Pteropodidae, Simmons (2005) does not recognize any of these subfamilial or tribal groups.

Andersen (1912a) recognized eight species: *E. gambianus*, *E. wahlbergi*, *E. labiatus*, *E. crypturus*, *E. angolensis*, *E. anurus*, *E. minor* and *E. pousarguesi*. Subsequently, *E. reii*, *E. grandis* (previously *Micropteropus grandis*) and *E. anelli* were added to this list. *Epomophorus wahlbergi*, *E. angolensis* and *E. grandis* have been regarded consistently as well-defined species, but the systematics of the other species has been controversial. These fall into two groups, one containing the larger species *E. gambianus*, *E. crypturus*, *E. pousarguesi* and *E. reii*, and the second containing the smaller species *E. anurus*, *E. labiatus*, *E. minor* and *E. anelli*.



Epomophorus labiatus. ♂ during courtship.

On the basis of standard measurements and qualitative characters, Bergmans (1988) concluded that *crypturus* was a synonym of *E. gambianus*, that *reii* was a synonym of *E. g. gambianus*, and that *pousarguesi* was a subspecies of *E. gambianus*. Subsequently, on the basis of zoogeography and the univariate and multivariate analyses of skull characters, Claessen & DeVree (1990a) concluded that both *E. crypturus* and *E. gambianus* were well-defined species and that *reii* and *pousarguesi* are synonyms of *E. gambianus*. There

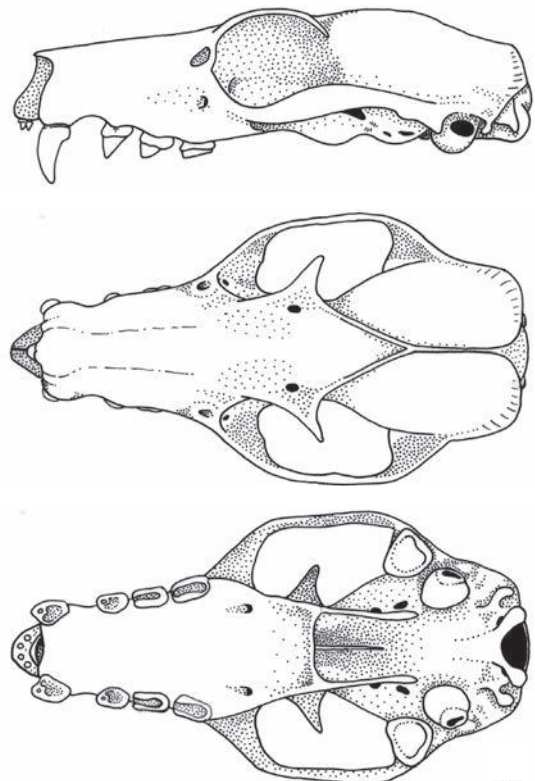


Figure 40. Skull of *Epomophorus wahlbergi* (BMNH 64.1.9.5, adult ♂).

are only four ‘*pousarguesi*’ specimens. They come from a different habitat and possibly belong to an isolated population, but their dimensions overlap with those of the largest specimens of *E. gambianus* and therefore Claessen & De Vree (1990a) concluded that it is premature to give these specimens subspecific rank. The specific status of *E. crypturus* is not widely accepted (e.g. Koopman 1993, Bergmans 1997), but this form is presented here as a distinct species partly because this is the most convenient option pending resolution of its true status. Simmons (2005), who also presents *E. crypturus* as a distinct species, points out that genetic studies, and more collecting in the wide gap between the distributions of *crypturus* and *gambianus*, may be necessary to resolve the relationship between these taxa.

Bergmans (1988) tentatively recognized both *E. labiatus* and *E. minor* but he discussed the status relationships of these species and regarded his arrangement as temporary. Bergmans (1988) also considered that *anurus* was a synonym of *E. labiatus*. Subsequently, on the basis of multivariate and discriminant analyses, Claessen & De Vree (1990b) concluded that *E. anurus*, *E. labiatus* and *E. minor* separated into two groups: a first group with an obvious clinal variation in size, consisting of specimens formerly identified as *E. anurus*, *E. labiatus* and partly as *E. minor*, and a second group with no geographic variation in size, consisting of specimens formerly identified as *E. minor*. They identified the first group as representatives of *E. labiatus*, and placed the second

group into a new species *E. minimus*. Bergmans (1997) accepted *E. minimus*, but indicated that there are several problems associated with *E. labiatus* as defined by Claessen & De Vree (1990b) (see species profile *E. labiatus*). Finally, in 2004, Bergmans & Van Strien described, as a new species named *E. anelli*, two specimens from Malawi, which are intermediate in size between specimens of *E. crypturus* and Malawian specimens of *E. labiatus*.

For convenience, we tentatively recognize eight species but acknowledge that the status of *E. crypturus* is uncertain, and that the content of *E. labiatus* is controversial. Most of these species can be distinguished by the characteristics and information given in Table 12. Differences in skull shape are derived from the relative dimensions listed in Table 13. *Epomophorus labiatus* and *E. minimus* can usually be distinguished by the length of their skulls: GLS: >36.5 mm (♀ ♀) or GLS: >40.0 mm (♂ ♂) indicates *E. labiatus*. In N Tanzania, however, these species are not easily distinguished. Claessen & De Vree (1990b) published a discriminant function for this purpose but, according to N. P. Giannini & N. B. Simmons (pers. comm.), it is flawed and not reliable.

The species are placed in three species-groups following Simmons (2005), but presented in alphabetical order irrespective of their species-groups.

Meredith Happold

Table 12. Key to the species in the genus *Epomophorus*. For an explanation of the diagnostic characteristics of the palatal ridges, see Family Pteropodidae. Size categories are based on the ranges of mean forearm lengths and mean GLS exemplified by the genus *Epomophorus*. Ranges are as currently known, but data for some species are derived from very small samples: *E. angolensis* (for FA, n = 9, for GLS, n = 6), *E. anelli* (n = 3 including one not fully adult ♀) and *E. grandis* (n = 3).

| Number of thick postdental palatal ridges | Palatal ridges 2, 3 & 4 | Size FA (mm) | Size GLS (mm) | Miscellaneous | Species |
|---|-------------------------|--|--|---|----------------------|
| 1 | Not divided | Large
♂ ♂ 81.9 (72–95)
♀ ♀ 78.1 (67–88) | Medium
♂ ♂ 50.5 (44.4–57.3)
♀ ♀ 44.8 (41.0–49.3) | | <i>E. wahlbergi</i> |
| 1 | Divided | Small
♂ ♂ 62, 63
♀ ♀ 66 | Small
♂ ♂ 35.4, 36.7
♀ ♀ 36.4 | | <i>E. grandis</i> |
| 2 in ♂
1 plus 1 partly postdental in ♀ ♀ | Not divided | Medium
♂ ♂ 77
♀ ♀ 68 >74 | Medium
♂ ♂ 47.1
♀ ♀ 38.7, > 41.2 | As yet known only from Malawi and SW Tanzania. In these localities, probably distinguished from <i>E. labiatus</i> by size | <i>E. anelli</i> |
| 2 | Not divided | Large
♂ ♂ 88.2 (85–94)
♀ ♀ 83.3 (81–86) | Large
♂ ♂ 56.4, 60.0
♀ ♀ 50.1 (49.4–50.6) | 4th palatal ridge nearer 3rd than 5th
Angola, Namibia; west of 18° E | <i>E. angolensis</i> |
| 2 | Not divided | Large
♂ ♂ 88.5 (80–100)
♀ ♀ 83.3 (75–95) | Large
♂ ♂ 58.7 (51.8–63.6)
♀ ♀ 50.8 (44.0–56.8) | 4th palatal ridge mid-way between 3rd and 5th
Distributed north of 4° N | <i>E. gambianus</i> |
| 2 | Not divided | Large
♂ ♂ 84.5 (80–88)
♀ ♀ 79.0 (75–83) | Large
♂ ♂ 53.6 (51.8–55.7)
♀ ♀ 46.1 (44.0–48.8) | 4th palatal ridge mid-way between 3rd and 5th
Distributed south of 8° S and east of 18° E | <i>E. crypturus</i> |
| 2 | Not divided | Medium
♂ ♂ 69.4 (60–80)
♀ ♀ 68.3 (58–76) | Small–Medium
♂ ♂ 42.7 (35.4–48.6)
♀ ♀ 39.3 (33.5–46.0) | In N Tanzania, not easily distinguished from <i>E. minimus</i> . Elsewhere GLS > 36.5 mm (♀ ♀), >40.0 mm (♂ ♂). In Malawi (and probably SW Tanzania), distinguished from <i>E. anelli</i> by size (see Similar Species) | <i>E. labiatus</i> |
| 2 | Not divided | Small
♂ ♂ 61.6 (54–67)
♀ ♀ 60.4 (57–66) | Small
♂ ♂ 35.7 (32.9–39.0)
♀ ♀ 33.3 (31.2–36.4) | In N Tanzania, not easily distinguished from <i>E. labiatus</i> . Elsewhere GLS < 36.5 mm (♀ ♀), < 40.0 mm (♂ ♂) | <i>E. minimus</i> |

Table 13. Relative dimensions of the skull in species of *Epomophorus* (based on Bergmans 1988). ZW = zygomatic width, GLS = greatest length of skull, RL = rostrum length, Pal = palatal length and C–C = width across upper canines (see Bergmans 1988 for definitions of these parameters). Sample size given in brackets.

| Species | <i>E. angolensis</i> | <i>E. anselli</i> | <i>E. crypturus</i> | <i>E. gambianus</i> | <i>E. grandis</i> | <i>E. labiatus</i> | <i>E. minimus</i> | <i>E. wahlbergi</i> |
|-----------------------|----------------------|-------------------|---------------------|---------------------|-------------------|--------------------|-------------------|---------------------|
| ZW as % of GLS (♂ ♂) | 46 (1) | 50 (1) | 44–45 (10) | 46–50 (31) | 57–61 (2) | ca. 52 | ca. 56 | 51–58 (52) |
| ZW as % of GLS (♀ ♀) | 52 (1) | 53 (3) | 41–43 (10) | 48–54 (38) | 60 (1) | ca. 54 | ca. 58 | 52–60 (70) |
| RL as % of GLS (♂ ♂) | 47–48 (2) | 42 (1) | 44–45 (10) | 44–47 (20) | 37 (2) | n. d. | n. d. | 38–43 (16) |
| RL as % of GLS (♀ ♀) | 45 (3) | 40 (1) | 41–43 (10) | 42–46 (27) | 37 (1) | n. d. | n. d. | 37–41 (37) |
| Pal as % of GLS (♂ ♂) | 62–63 (2) | 63 (1) | 63–65 (10) | 65–68 (17) | 57 (2) | n. d. | n. d. | 55–61 (14) |
| Pal as % of GLS (♀ ♀) | 60–61 (3) | 61 (1) | 61–64 (10) | 63–67 (26) | 56 (1) | n. d. | n. d. | 57–62 (33) |
| C–C as % of GLS (♂ ♂) | 17 (2) | 18 (1) | 18–20 (16) | 17–18 (12) | 19–20 (2) | n. d. | n. d. | 19–21 (13) |
| C–C as % of GLS (♀ ♀) | 17–18 (3) | 20 (1) | 18–21 (16) | 17–19 (16) | 21 (1) | n. d. | n. d. | 19–23 (32) |

Epomophorus angolensis ANGOLAN EPAULETTED FRUIT BAT

Fr. Épomophore d'Angola; Ger. Angola-Epaulettenflughund

Epomophorus angolensis Gray, 1870. Cat. Monkeys, Lemurs, Fruit-eating Bats Brit. Mus., p. 125. Benguela, Angola.

Taxonomy Species-group: *gambianus*. Synonyms: none. Chromosome number: not known.

Description Small to medium-sized, dorsally pale to medium brown fruit bat with anterior and posterior basal ear-patches but no other white markings on head; epaulettes on adult ♂ ♂; six palatal ridges of which two are postdental and fourth is closer to third than to fifth. Sexes with some differences in colour; ♂ ♂ mostly larger than ♀ ♀. Pelage soft, slightly fluffy; extending (dorsally and ventrally) ca. half-way along forearm; mid-dorsal hairs ca. 10 mm. Dorsal pelage pale brown to medium reddish-brown, sometimes paler on shoulders; hairs darker reddish-brown at base. Ventral pelage paler except, in adult ♂ ♂, chin, throat and chest are darker reddish-brown and this colour extends dorsally to form a ring around each epaulette. Adult ♂ ♂ with a white epaulette on each shoulder (retracted into pouch except when displayed). Head dog-like with anterior and posterior whitish basal ear-patches. Muzzle relatively long and narrow for an *Epomophorus*; lips and cheeks fleshy and expansible (especially in ♂ ♂). Ears short, rounded, dark brown. Eyes large. Palate with four thick interdental and two thick postdental ridges, the fourth closer to the third than the fifth (Figure 39a) (cf. *E. crypturus*); ridges 2, 3 and 4 not divided (cf. *E. grandis*). Wing-membranes brown; attaching to second toe. Tail absent or very short.

Skull on average medium-sized for an African fruit bat; large for an *Epomophorus*. Zygomatic width relatively narrow; rostrum relatively long and narrow, and palate of medium relative length for an *Epomophorus* (Table 13, p. 237). Postdental palate markedly concave (cf. *Epomops*). Dental formula $^{2121}/_{2132} = 28$.

Geographic Variation Based on its relatively restricted and continuous distribution, geographic variation is unlikely (Bergmans 1988).

Similar Species Thirteen other species of fruit bats have simple muzzles; basal ear-patches but no other markings on head; adult ♂ ♂ with epaulettes; three upper and five lower cheekteeth; only nine occur south of the Equator:



Epomophorus angolensis

Epomophorus crypturus. Fourth palatal ridge mid-way between third and fifth ridges. East of 18° E.

E. anselli and *E. labiatus*. Smaller (Table 12, p. 236).

E. wahlbergi. Only one thick postdental palatal ridge.

E. grandis. Much smaller (Table 12).

E. minimus. Much smaller (Table 12).

Epomops dobsonii. Three thick interdental palatal ridges.

Micropteropus (2 spp.). Much smaller (FA: 46–64 mm).

Distribution Endemic to Africa. Zambezi Woodland BZ and marginally in the north of the South-West Arid BZ, in W and SW Angola and Ovamboland in N Namibia (Bergmans 1988). An outlying record from 'Swakopmund', Namibia (not mapped) was queried by Shortridge (1934) and Bergmans (1988).

Habitat Known from drier regions than other species of *Epomophorus*, although probably found mainly in riverine habitats within these regions, e.g. reported roosting in exposed situations in *Acacia* trees along the Cunene R. by Shortridge (1934). The holotype was collected from Bushy Karoo–Namib scrubland at Benguela, Angola. Other records are from wetter miombo woodland, undifferentiated woodland, mopane woodland and the transition from mopane woodland to Bushy Karoo–Namib scrubland (Bergmans 1988; terminology from White 1983).

Abundance Uncertain; considered ‘Rare’ by Mickleburgh *et al.* (1992).

Remarks Individuals were observed hanging from the bare branches of large *Acacia* trees near the Cunene R. in Namibia; they were exposed to direct sunlight (Shortridge 1934). Five of six adult ♀♀ taken in Sep or Oct at Cunene R. (ca. 17° 20' S) had swollen nipples and appeared to be lactating, and of these, two had single neonates clinging to them (Shortridge 1934 and evidence from his specimens in BMNH).

Conservation IUCN Category: Near Threatened.

Provisionally listed as such because its population may be declining significantly and because of the loss of riverine roosting and fruit trees.

Measurements

Epomophorus angolensis

FA (♂♂): 88.2 (85–94) mm, n = 4

FA (♀♀): 83.3 (81–86) mm, n = 5

WS (d): 670 mm, n = 1

HB (♂): 158 mm, n = 1

HB (♀♀): 146 (130–155) mm, n = 12

T: (♂): 5 mm, n = 1

T: (♀♀): 3.3 (3–5) mm, n = 6

E (♂): 28 mm, n = 1

E (♀♀): 24 (23–26) mm, n = 12

Tib (♂♂): 36.8 (36–39) mm, n = 4

Tib (♀♀): 37.6 (32–39) mm, n = 7

HF: n. d.

WT: n. d.

GLS (♂♂): 56.4, 60.0 mm, n = 2*

GLS (♀♀): 50.1 (49.4–50.6) mm, n = 4*

GWS (♂): 27.4 mm, n = 1*

GWS (♀): 25.1 mm, n = 1*

C–M¹ (♂♂): 19.5 (17.0–21.6) mm, n = 4*

C–M¹ (♀♀): 17.4 (17.1–17.9) mm, n = 5*

Angola and Namibia (BMNH, Shortridge 1934, Hill & Carter 1941, *Bergmans 1988)

Two of the four ♀♀ skulls have fractures, which might have affected their GLS

Key References Bergmans 1988, 1999; Mickleburgh *et al.* 1992; Shortridge 1934.

P. J. Taylor

Epomophorus anelli ANSELL'S EPAULETTED FRUIT BAT

Fr. Épomophore d'Ansell; Ger. Ansell's Epaulettenflughund

Epomophorus anelli Bergmans and Van Strien, 2004. Acta Chiropterologica 6: 258. Lisanthu (13° 00' S, 33° 10' E), 1000 m, Kasungu N. P., Malawi.

Taxonomy Species-group: *gambianus*. Described from two specimens from Kasungu N. P., Malawi. A further two specimens (from Karonga, Malawi) almost certainly represent *E. anelli*, and three other specimens from Karonga are possibly referable, or partly referable, to this species (Bergmans & Van Strien 2004). Recognized as a valid species, although its describers considered the possibility that the specimens of *E. anelli* may be hybrids of *E. crypturus* and *E. labiatus*. These two species are found sympatrically at both localities in Malawi from which the form *anelli* has been recorded, and *anelli* is intermediate in size (Bergmans & Van Strien 2004). However, at one of these localities (Karonza), five *E. labiatus*, possibly 4–5 *E. anelli* (but identity not certain) and two *E. crypturus* were obtained, side by side, during two days of collecting and, in this collection, the proportion of specimens probably representing *E. anelli* appears too high for it to be a hybrid unless an extraordinary and highly unlikely amount of interbreeding had occurred. Synonyms: none. The holotype has been referred to as *Epomophorus anurus* by Bergmans & Jachmann (1983), *E. crypturus* by Happold *et al.* (1987) and *E. labiatus* by Bergmans (1988) and Claessen & De Vree (1990b). Subsequently, a further specimen was found, this time from SW Tanzania (NMW B5112; W. Bergmans unpubl.). This specimen was first identified as *E. minor*, then as *E. wahlbergi*, then published as *E. labiatus* (Bergmans 1988). Chromosome number: not known.

Description Small, medium brown fruit bat with anterior and posterior basal ear-patches but no other white markings on head; epaulettes on adult ♂♂; six palatal ridges of which, in ♂, two are postdental and in ♀ the fifth is partly interdental and the sixth postdental. A poorly known species with only one adult ♂, one nearly adult ♀ and one adult ♀ known; identity of some more specimens awaits confirmation. Males apparently larger than ♀♀ and with dark band on the chest. Pelage soft; mid-dorsal hairs 12–15 mm; extending dorsally and ventrally along each upper arm and up to a third of each forearm. Dorsal pelage medium brown (fawn); hairs very slightly darker brown at base. Ventral pelage very pale brown mid-ventrally, becoming slightly darker on flanks; no whitish mid-ventral patch; adult ♂ with dark brown band high on the chest, running transversely between the epaulettes. Adult ♂♂ with white epaulette on each shoulder (retracted within pouch except when displayed). Ears relatively short (26–28% of FA, n = 2), rounded, naked, brown with dark brown rim. Anterior and posterior white basal ear-patches present. Muzzle moderately long and broad. Lips and cheeks fleshy and very expansible, especially in ♂♂. Palate in ♂ with four thick, undivided interdental ridges and two thick divided postdental ridges, the fourth mid-way between third and fifth (cf. *E. angolensis*); in both ♀♀, the fifth ridge is only partly postdental. Wing-membranes brown; attaching to second toe. Tail very short.

Skull medium-sized for an African fruit bat; medium-sized in ♂ but short in ♀♀ for an *Epomophorus*. Zygomatic width medium for this genus; rostrum of medium relative length and breadth in one ♂, but relatively short and broad in one ♀; palate relatively short (Table 13, p. 237). Postdental palate markedly concave (cf. *Epomops*). Dental formula $^{2121}/_{2132} = 28$.

Geographic Variation Not known.

Similar Species Thirteen other species of fruit bats have simple muzzles; basal ear-patches but no other markings on head; adult ♂♂ with epaulettes; three upper and five lower cheekteeth:

Epomophorus grandis. Six thick palatal ridges of which 2–6 are divided.

Apparently smaller, but data are limited (Table 12, p. 236).

E. angolensis. Larger (Table 12).

E. crypturus. Apparently slightly larger (Table 12).

E. labiatus. In Malawi (and probably SW Tanzania), smaller (FA ♂♂: 60–67 mm, n = 19, FA ♀♀: 58–65 mm, n = 15; GLS ♂♂: 35.4–40.3 mm, n = 16, GLS ♀♀: 33.2–37.7 mm, n = 15).

E. wahlbergi. Fifth palatal ridge interdental. On average larger (Table 12).

E. gambianus. Apparently slightly larger (Table 12). North of Equator.

E. minimus. Smaller (Table 12). Nearest record N Tanzania.

Epomops (3 spp.). Three or five thick palatal ridges.

Micropteropus (2 spp.). Smaller (FA: 46–64 mm).

Nanonycteris veldkampii. Much smaller (FA: 46–54 mm). North of Equator.

Distribution Endemic to Africa. Known with certainty only from Lisanthu (13°00'S, 33°10'E) in Kasungu N. P., Malawi (the type locality), from Lifupa Camp (13°05'S, 33°08'E) in Kasungu N. P., Malawi, and from Ugano (10°56'S, 35°00'E) in SW Tanzania (Bergmans & Van Strien 2004, Bergmans unpubl.). The Tanzanian locality became known too late to be mapped. Almost certainly, it has also been recorded from Karonga (09°56'S, 33°56'E), Malawi (Bergmans & Van Strien 2004). All of these localities are in the Zambezian Woodland BZ but the Tanzanian locality is on the edge of the Afromontane–Afroalpine BZ.

Habitat The holotype was captured at 1000 m, over a stream between two Water Berry trees *Syzygium cordatum*, which were bearing fruit. Both Lisanthu and Lifupa Camp are located at 1000–1100 m, in wetter Zambezian miombo woodland dominated by *Brachystegia* and *Julbernardia* (Bergmans & Jachmann 1983; terminology: White 1983). Details of habitat at Karonga are not known. The Tanzanian locality, at 1560 m, lies on the boundary between wetter Zambezian miombo woodland and undifferentiated afromontane vegetation (terminology: White 1983).

Abundance Not known. Only two specimens (the holotype and paratype from Kasungu N. P.) are known with certainty from Malawi. Two others from Malawi (from Karonga) almost certainly represent this species, and there are three other specimens from Karonga, some or all of which might represent this species (details in Bergmans & Van Strien 2004). The Tanzanian specimen appears to be the only one known from that country.



Epomophorus anelli

Remarks Within Kasungu N. P., *E. anelli* has been collected at the same locality as *Epomophorus labiatus*, *Epomops dobsonii* and *Eidolon helvum*, while *Epomophorus crypturus* (as *E. gambianus crypturus*) was collected less than 2 km away in similar vegetation (Bergmans & Van Strien 2004). At Karonga, *Epomophorus anelli* has been collected at the same time as *E. crypturus*, *E. labiatus* and *E. wahlbergi* (MMB). The diet possibly includes fruits of *Syzygium cordatum*, but this needs confirmation. The ♂ holotype, collected on 19 Mar, had scrotal testes of 8.2 mm in length (measured through the skin). The nearly adult ♀ paratype was collected on 19 May, and the adult ♀ from Tanzania, collected in Jun, had large nipples, suggesting lactation at time of capture.

Conservation IUCN Category: Data Deficient.

Although very few specimens are known, and although they come from only three areas within a small rectangle between 09°56'S and 13°05'S, and 33°08'E and 35°00'E, there is no reason to believe that this species is in any danger. Furthermore, the available data are few and based on specimens collected between 1961 and 1988.

Measurements

Epomophorus anelli

FA: 77, 68, >74 mm

WS: n. d.

HB: ca. 145, 104, – mm

T: 4, 2, – mm

E: 20, 19, – mm

Tib: n. d.

HF: n. d.

WT: –, ca. 57, – g

GLS: 47.1, 38.7, >41.2 mm

GWS: 23.6, 22.0, – mm

C–M¹: 16.4, 13.9, 14.8 mm

Malawi and Tanzania (measurements of holotype [adult ♂, ZMA

21.693b], paratype [nearly adult ♀, ZMA 26.105] and Tanzanian specimen [adult ♀, NMW B5112], respectively)

The Tanzanian specimen is prepared as skull and skin, and the forearm bones and skull are damaged and incomplete – hence the approximate FA and GLS measurements and lack of other measurements

Epomophorus crypturus PETERS'S EPAULETTED FRUIT BAT

Fr. Épomophore de Peters; Ger. Peters' Epaulettenflughund

Epomophorus crypturus Peters, 1852. Naturwissenschaftliche Reise nach Mossambique. Zoologie I. Säugetiere.
Georg Reimer, Berlin. Tete, Mozambique.

Taxonomy Species-group: *gambianus*. Synonyms: *parvus*. Subspecies: none. On the basis of standard measurements and qualitative characters, *crypturus* is considered a subspecies of *E. gambianus* by Bergmans (1988). However, on the basis of univariate and multivariate analyses and geographical distribution, *E. crypturus* is considered to be a well-defined species by Claessen & De Vree (1990a). Bergmans (1997) gives reasons for rejecting the arguments of Claessen & De Vree (1990a). Simmons (2005) suggests that genetic studies and further collecting between the geographic ranges of the two taxa may be necessary to resolve their relationship. Here, the status of *crypturus* is considered uncertain, but it is tentatively treated as a distinct species because it is easier to combine data from two species, if they are later shown to be conspecific, than vice-versa. Chromosome number (Zimbabwe): $2n = 35$ (♂♂), 36 (♀♀); aFN = 68 (Peterson & Nagorsen 1975).

Description Small to medium-sized, pale brown fruit bat with anterior and posterior basal ear-patches but no other white markings on head; epaulettes on adult ♂♂; six palatal ridges of which two are postdental; fourth ridge mid-way between third and fifth ridges. Males on average larger and with darker throat than ♀♀. Pelage soft, slightly fluffy; extending dorsally and ventrally along each upper arm and some distance along each forearm; mid-dorsal hairs 10–11 mm. Dorsal pelage usually pale brown (fawn), paler on shoulders and often suffused with yellow on head, neck and rump; hairs dark brown at base. Some individuals (usually ♂♂) are darker (almost sepia brown) and some much paler (as though bleached). Ventral pelage slightly to considerably paler than dorsal pelage; throat sometimes rusty-brown, especially in adult ♂♂. Adult ♂♂ with white epaulette on each shoulder (retracted within pouch except when displayed). Head dog-like with anterior and posterior white basal ear-patches. Muzzle relatively very long and broad, especially in ♂♂. Lips and cheeks fleshy and very expansible, especially in ♂♂. Ears relatively short (26–36% of FA, $n = 8$), rounded, naked, brown with dark brown rim. Eyes large, brown. Palate with four thick interdental and two thick postdental ridges, the fourth mid-way between third and fifth (Figure 39b) (cf. *E. angolensis*); ridges 2, 3 and 4 not divided (cf. *E. grandis*). Wing-membranes brown; attaching to second toe. Tail absent or very short.

Skull medium-sized for an African fruit bat; long and robust for an *Epomophorus*. Zygomatic width relatively narrow for this genus; rostrum relatively long and broad (♂♂) or of medium breadth (♀♀); palate relatively long (Table 13, p. 237). Postdental palate markedly concave (cf. *Epomops*). Dental formula $^{2121}/_{2132} = 28$.

Key Reference Bergmans & Van Strien 2004.

Wim Bergmans

Geographic Variation None recorded.

Similar Species Thirteen other species of fruit bats have simple muzzles; basal ear-patches but no other markings on head; adult ♂♂ with epaulettes; three upper and five lower cheekteeth:

- Epomophorus angolensis*. Fourth palatal ridge nearer to third ridge than fifth. Angola, Namibia, west of 18° E.
- E. anelli*. Apparently slightly smaller (Table 12, p. 236) but data very limited.
- E. labiatus*. Almost always smaller (Table 12).
- E. wahlbergi*. Only one postdental palatal ridge (but *E. anelli* ♀♀ also have only one).
- E. grandis*. Smaller (Table 12).
- E. minimus*. Smaller (Table 12).
- E. gambianus*. North of Equator.
- Epomops* (3 spp.). Three or five thick palatal ridges.
- Micropteropus* (2 spp.). Much smaller (FA: 46–64 mm).
- Nanonycteris*. Much smaller (FA: 46–54 mm). North of Equator.

Distribution Endemic to Africa. Zambezan Woodland BZ and Coastal Forest Mosaic BZ. Recorded from E Angola to coast of Mozambique and from S Tanzania to E South Africa (Bergmans 1988 as *E. gambianus crypturus*). Indentations in the distribution might reflect insufficient sampling in those areas or, especially in Zambia and S Mozambique, the prevalence of less favourable drier habitats.

Habitat Apparently restricted to tropical and sub-tropical woodland savannas (including undifferentiated woodland and wooded grassland, and miombo), and the coastal forest mosaics of East Africa. Often found where evergreen trees are present, and sometimes follows riverine forests into drier regions. Not usually found in drier associations of *Colophospermum mopane*, *Acacia* spp. or *Terminalia* (Smithers 1983), although recorded from mopane woodland in Zimbabwe (Volpers & Kumirai 1995).

Abundance Common to very common, but local numbers are determined by the seasonal availability of fruits.

Adaptations Aspect ratio low; wing-loading very high (M. Happold unpubl.). Flight fast and direct in the open, slow and highly manoeuvrable through dense foliage. Can hover briefly and take off from the ground. Locomotion over flat surfaces is extremely awkward, and clambering around branches has not been reported. By day, hangs



Epomophorus crypturus

from small branches and twigs, shaded by foliage, usually in the canopies of evergreen trees. In Zimbabwe, commonly roosts in wild fig-trees *Ficus* spp. and sausage-trees *Kigelia africana*. At one locality, two radio-tracked individuals roosted in different trees on five of six consecutive days (Thomas & Fenton 1978). The wings, especially the thumbs and wrists, are used for holding and manipulating food. The tongue, which is used for lapping nectar from flowers and juice from fruits, is long with rasp-like backward-pointing papillae near the tip. The kidney has a thin medulla and no protruding papilla (as in *E. wahlbergi*, Figure 29a), enabling production of dilute urine.

Foraging and Food Feeds on soft fruits and/or nectar of trees. When visiting flowers, individuals hang on with their feet, and often support themselves by flapping their wings while lapping nectar with their long tongues. Sometimes roosts within half a kilometre of food, and movements (followed by radio-tracking) were confined to the vicinity of these resources over a period of six days (Thomas & Fenton 1978). During this study, *E. crypturus* began foraging almost two hours earlier than cave-dwelling *Rousettus aegyptiacus*, which had to commute from much further away, but subsequently both species fed together. Sometimes also feeds with *Epomophorus labiatus*, *E. wahlbergi* and/or *Epomops dobsonii*. At some localities *E. crypturus* seems to come and go, suggesting nomadic movements in response to seasonal changes in abundance of food (Pienaar *et al.* 1980, Smithers 1983). Apparently feeds opportunistically on the soft fruits and/or nectar of at least 20 species of trees (listed by Mickleburgh *et al.* 1992). Accumulations of skins, seeds and chewed pulp under some fruiting trees where this species feeds indicate that only the juices of the fruits are swallowed. Fruits eaten include orchard and garden soft-fruits such as guavas, apricots, peaches, loquats and papayas, but not hard-fruits such as apples and pears. This avoidance of hard-fruits implies that soft-fruits are only eaten when they are fully ripe and therefore over-ripe for commercial harvesting. If this is correct, *E. crypturus* probably helps to control fungal diseases and fruit-flies (see Tuttle 1986). In Zimbabwe

during the dry season, apparently specializes on only a few fruit-bearing trees (e.g. *Parinari curatellifolia*) (Volpers & Kumirai 1995).

Social and Reproductive Behaviour Roosts singly or in groups, which may be small to very large (several hundreds). Individuals space themselves at least 0.3 m apart and contact is negligible (except between mothers and young). When these bats fly into a roost at dawn, there is much bickering and the clawed thumbs on the wings are used to slash out at other bats that attempt to hang too close (Smithers 1983). Mating-system not known. Males make a moderately loud bell-like 'pink' repeated frequently (Volpers & Kumirai 1995). They are known to call at their roosts soon after dusk, but there appears to be no published observations of any associated displays, or mating, at the roosts or elsewhere.

Reproduction and Population Structure Litter-size: one, perhaps twins very rarely. Reproductive chronology not known. Lactation recorded in summer (Nov–Jan) in the former Transvaal (Pienaar *et al.* 1980) and in the wet season (Nov, Mar and Apr) in Malawi and E Zambia (Happold & Happold 1990a) but no conclusive data for other months. In Zimbabwe, pregnancies were recorded Jul–Mar with a particularly high proportion (73%) in Aug, and no pregnancies were recorded in Apr–Jun: this suggested a Sep peak in births (Smithers & Wilson 1979, Smithers 1983), but embryo size and lactation were not recorded and therefore year-round timing of births cannot be determined from this information. It has been suggested (e.g. Mickleburgh *et al.* 1992) that ♀♀ have one litter/year, but this cannot be confirmed from the above data. Young are born with eyes closed, sparse dorsal pelage, no ventral pelage, weight ca. 11 g. Each neonate attaches itself to one of its mother's two pectoral nipples, and clings with well-developed hindfeet and thumbs to its mother's pelage. For some time, juveniles are carried while their mothers forage. When too big to carry conveniently, they are left at a roost while the mothers forage.

Predators, Parasites and Diseases No information.

Conservation IUCN Category: Least Concern.

Measurements

Epomophorus crypturus

FA (♂♂): 84.5 (80–88) mm, n = 51*

FA (♀♀): 79.0 (75–83) mm, n = 40*

WS (a) (♂): 571 mm, n = 1

HB (♂♂): 156 (130–170) mm, n = 35

HB (♀♀): 132 (110–140) mm, n = 31

T: 1.4 (0–5) mm, n = 6

E (♂♂): 25.6 (21–27) mm, n = 35

E (♀♀): 23.3 (22–25) mm, n = 30

Tib: 31, 32 mm, n = 2

HF (♂♂): 21.6 (16–26) mm, n = 50

HF (♀♀): 20.4 (17–24) mm, n = 59

WT (♂♂): 115 (91–140) g, n = 11*

WT (♀♀): 83 (56–100) g, n = 13*

GLS (♂♂): 53.6 (51.8–55.7) mm, n = 47*

GLS (♀♀): 46.1 (44.0–48.8) mm, n = 33*

GWS (♂♂): 26.4 (25.5–27.4) mm, n = 24*

GWS (♀♀): 24.5 (23.5–25.7) mm, n = 29*

C–M¹ (♂♂): 18.2 (16.7–19.5) mm, n = 31*

C–M¹ (♀♀): 15.9 (14.7–16.8) mm, n = 25*

Throughout geographic range (BMNH, HC, TM and literature)

*Bergmans 1988

Key References Bergmans 1988; Claessen & De Vree 1990a; Mickleburgh *et al.* 1992; Smithers 1983; Thomas & Fenton 1978.

Meredith Happold

Epomophorus gambianus GAMBIAN EPAULETTED FRUIT BAT

Fr. Épomophore de Gambie; Ger. Gambia-Epaulettenflughund

Epomophorus gambianus (Ogilby, 1835). Proc. Zool. Soc. Lond. 1835: 100. Gambia.

Taxonomy Originally *Pteropus gambianus*. Species-group: *gambianus*. Synonyms: *epomophorus*, *guineensis*, *macrocephalus*, *megacephalus*, *pousarguesi*, *reii*, *whitei*, *zechi*. Subspecies: two recognized here; Bergmans (1988) also recognized *crypturus* as a subspecies, but this taxon is treated here as a distinct species. Chromosome number: not known.

Description Small to medium-sized, pale brown fruit bat with anterior and posterior basal ear-patches but no other white markings on head; epaulettes on adult ♂♂; six palatal ridges of which two are postdental. Males larger, on average, than ♀♀ and often with dark brown necks and chests. Pelage soft, slightly fluffy; extending dorsally and ventrally along each upper arm and some distance along each forearm; mid-dorsal hairs ca. 10 mm. Dorsal pelage usually pale brown (fawn), paler on shoulders and often suffused with yellow on head, neck and/or rump; hairs dark brown at base. Some individuals (especially ♂♂) are darker (almost sepia brown) and some much paler (as though bleached). Ventral pelage slightly to considerably paler than dorsal pelage: ♂♂ sometimes with a pale or white ventral patch. Adult ♂♂ with white epaulette on each shoulder (retracted within pouch except when displayed). Head dog-like with anterior and posterior white basal ear-patches. Muzzle relatively long (especially in ♂♂), and narrow. Lips and cheeks fleshy and very expansible, especially in ♂♂. Ears relatively short (22–32% of FA, n = 41), rounded, naked, brown with dark brown rim. Eyes large, brown. Palate with four thick interdental and two thick postdental ridges, the fourth mid-way between third and fifth; ridges 2, 3 and 4 not divided (cf. *E. grandis*) (Figure 39c). Wing-membranes brown; attaching to second toe. Tail absent or very short.

Skull long and robust for an *Epomophorus*. Zygomatic width relatively narrow (♂♂) or of medium relative width (♀♀); rostrum relatively long and narrow in both sexes, and palate relatively long for this genus (Table 13, p. 237). Postdental palate extremely concave (cf. *Epomops*). Dental formula $^{2121}_{2132} = 28$.

Geographic Variation Two of the three subspecies recognized by Bergmans (1988) are listed below. Possibly, *crypturus* is also a subspecies of *E. gambianus* but, here, this form is tentatively treated as a distinct species (see profile).

Epomophorus g. gambianus: Senegal to Ethiopia, excluding part of Central African Republic. Smaller (FA ♂♂: 81–95 mm, FA ♀♀: 76–90 mm; GLS ♂♂: 53.3–62.5 mm, GLS ♀♀: 46.1–55.4 mm).

E. g. pousarguesi: Four specimens, collected in Central African Republic at ca. 4°N and 18–19°E in Guinea-Congo lowland rainforest/secondary grassland mosaic, are considered to represent a distinct subspecies by Bergmans (1988), but Claessen & De Vree (1990a)

consider *pousarguesi* to be a synonym of *E. gambianus*. Larger (FA ♂: 100 mm, FA [n = 3 ♀♀]: 91–95 mm; GLS ♂: 63.6 mm, GLS [n = 3 ♀♀]: 54.4–56.8 mm).

Similar Species Thirteen other species of fruit bats have simple muzzles; basal ear-patches but no other markings on head; adult ♂♂ with epaulettes; three upper and five lower cheekteeth:

Epomophorus crypturus. South of Equator.

E. angolensis. Fourth palatal ridge closer to third ridge than fifth. South of Equator.

E. wahlbergi. Only one postdental palatal ridge.

E. anelli. Apparently slightly smaller (Table 12, p. 236) but data are limited.

E. grandis. Smaller (Table 12). One postdental palatal ridge; ridges 2, 3 and 4 divided. South of Equator.

E. minimus. Much smaller (Table 12).

E. labiatus. Almost always smaller (Table 12).

Epomops (3 spp.). Three or five thick palatal ridges.

Micropteropus (2 spp.). Much smaller (FA: 46–64 mm).

Nanonycteris veldkampii. Much smaller (FA: 46–54 mm).

Distribution Endemic to Africa. Mainly Sudan and Guinea Savanna BZs and the Northern Rainforest–Savanna Mosaic from Senegal to Central African Republic, and the Afromontane–Afroalpine BZ of Ethiopia. The gap between 23–35°E probably reflects insufficient sampling in that area. The outlying locality marked with a cross in CAR is that of *E. g. pousarguesi*. Map based on Bergmans (1988).

Habitat A woodland savanna species rarely found syntopically with forest fruit bats even though it also colonizes forest–savanna mosaics and derived savanna habitats in the Rainforest BZ, and sometimes also exploits fringes of rainforest habitats (Bergmans 1988). In West Africa, mainly found in *Isobrerlinia* woodland and undifferentiated woodland, and in forest–grassland mosaics bordering the rainforest. There are some records from drier types of lowland rainforest and mangrove forest, but probably in areas cleared for farming. Localities along the West African coast are in forest–grassland mosaics. In Sudan and Ethiopia, found in woodland and transitions to deciduous bushland and wooded grasslands, and also in afromontane vegetation, evergreen and semi-evergreen bushland and thicket (Bergmans 1988; terminology from White 1983).

Abundance Well represented in collections; probably common throughout most of geographic range when and where fruiting and/or flowering trees are present.



Epomophorus gambianus

Adaptations Aspect ratio very low; wing-loading high. Flight fast and direct in the open, slow and manoeuvrable through dense foliage. Can hover briefly. By day, hangs from small branches and twigs, shaded by foliage, usually high in the canopy of the tallest savanna trees. Several species of trees are used, including *Khaya senegalensis*, *Kigelia africana*, *Azadirachta indica*, *Mangifera* sp., *Cola* sp. and *Ficus* spp. (Boulay & Robbins 1989). The wings, especially the thumbs and wrists, are used for holding and manipulating food. The long tongue is used for lapping nectar from flowers and juice from fruits. This species has been seen skimming over rivers, close enough to drink water directly or by wetting the pelage and then licking it, but there is no certainty that this behaviour serves to obtain water for drinking (Bergmans 1978).

Foraging and Food Feeds on soft fruits and nectar. Usually forages earlier in the evening than some of the species (e.g. *Nanonycteris veldkampii*) with which it competes (Baker & Harris 1957, 1959). At other times, it arrives and feeds with *N. veldkampii* and *Micropteropus pusillus*. Foraging occurs throughout the night. At some localities, *E. gambianus* is nomadic in response to seasonal changes in the abundance of food (Happold & Happold 1978). Individuals visiting flowers hang on with their feet, and often support themselves by flapping the wings, while the nectar is lapped with the long tongue. Feeds opportunistically on soft fruits of endemic and cultivated trees and on the nectar (but apparently not the pollen or flowers) of several trees, including some whose flowers are adapted for pollination by fruit bats. In West Africa, obtains food from at least 18 species (listed in Mickleburgh *et al.* 1992). More species are utilized during the wet season, when resources are abundant, than in the dry season (Thomas & Marshall 1984). *Epomophorus gambianus* plays an important role in the dispersal of tree seeds and the regeneration of abandoned farmlands: the seeds of eight species were found in the faeces of individuals from Wango Fitini, Côte d'Ivoire (Thomas & Marshall 1984). Laps nectar from

the flowers of *Ceiba pentandra* and *Parkia clappertoniana* (Baker & Harris 1957, 1959), *Adansonia digitata*, *Kigelia africana* and mango trees. Like other nectar-lapping fruit bats, it collects pollen on its pelage and may transfer it to other flowers. Probably pollinates *Parkia*, but its importance (compared with that of other fruit bats) as a pollinator of other species of trees is not known.

Social and Reproductive Behaviour Roosts singly or in groups of two to more than 100 (Marshall & McWilliam 1982). Individuals space themselves at least 0.3 m apart and contact is negligible (except between a mother and her young). Some 'traditional' roosts are used year after year although individuals may change roosts every few days and nomadic movements sometimes result in these roosts being periodically deserted. These bats return to their roosts at first light; from sunrise to sunset there is silence and little movement except for occasional grooming. At sunset, they start flying about the roost and 'quarrelsome' calls are uttered if individuals come too close together. Adult ♂♂ may hang from perches and perform a calling-display during which they utter a moderately loud bell-like 'ping' at intervals of 1–3 seconds, display their epaulettes, and beat their wings in the interval between each call. Calling-displays at the roost may last up to 35 minutes. Individuals leave the roost singly or in groups, and may forage singly or in groups (including mixed-species groups). During the night, adult ♂♂ perform more calling-displays of up to three hours' duration, at sites remote from the roost. The calling-displays of this species probably attract ♀♀ and culminate in mating (as in *Hypsignathus*) but this needs confirmation and, even so, the mating system will not necessarily be lekking (see *Hypsignathus monstrosus*). The calling-displays and concomitant mating behaviour attributed to *E. gambianus* by Tuttle (1986) must be that of another species of *Epomophorus* (presumably *E. wahlbergi*) because *E. gambianus* does not occur in Kenya where his observations were made.

Reproduction and Population Structure Litter-size: normally one. At 09° 50' N (Wango Fitini, Comoé N. P., Côte d'Ivoire), the reproductive chronology of *E. g. gambianus* is continuous bimodal polyoestry with postpartum oestrus. Each ♀ has two litters/year. Gestation 5–6 months. Females are in reproductive synchrony; young are born during two seasons of parturition – at the beginning of the single wet season (Apr) and at the end of the wet season (Oct). Consequently both lactations occur when 3–6 species of fruit are available, cf. 2–3 in dry season (Thomas & Marshall 1984). At ca. 10° N (Mole N. P., Ghana), births occur at beginning of wet season (no data for other months) (Marshall & McWilliam 1982). Other published records from West Africa are inconclusive.

Predators, Parasites and Diseases While raising their young, Pied Crows *Corvus albus* sometimes prey on roosting *E. gambianus*. Ectoparasites include bat-flies *Cyclopodia greeffi*, *Eucampsipoda africana* (Diptera: Nycteribiidae) (Anciaux de Faveaux 1984).

Conservation IUCN Category: Least Concern.

Measurements

Epomophorus gambianus

FA (♂♂): 88.5 (80–100) mm, n = 271

FA (♀♀): 83.3 (75–95) mm, n = 351

HB (♂♂): 140.5 (108–170) mm, n = 15*
 HB (♀♀): 137 (130–162) mm, n = 13*
 T (♂♂): 3.5 (0–6) mm, n = 12*
 T (♀♀): 2.2 (0–8) mm, n = 10*
 E (♂♂): 23.2 (21–27) mm, n = 15*
 E (♀♀): 22.5 (19–28) mm, n = 13*
 Tib (♂♂): 36.6 (33–40) mm, n = 16
 Tib (♀♀): 33.9 (30–37) mm, n = 12
 HF: 23.3 (20–27) mm, n = 26
 WT (♂♂): 128 (96–155) g, n = 33
 WT (♀♀): 106 (87–145) g, n = 24
 GLS (♂♂): 58.7 (51.8–63.6) mm, n = 203

GLS (♀♀): 50.8 (44.0–56.8) mm, n = 270
 GWS (♂♂): 27.5 (26.1–28.9) mm, n = 34
 GWS (♀♀): 25.5 (24.1–27.0) mm, n = 36
 C–M¹ (♂♂): 20.3 (18.8–22.0) mm, n = 30
 C–M¹ (♀♀): 18.2 (16.5–22.6) mm, n = 66
 Throughout geographic range (Bergmans 1988)
 *Nigeria only (D. C. D. Happold & M. Happold unpubl.)

Key References Bergmans 1988; Boulay & Robbins 1989; Marshall & McWilliam 1982; Thomas & Marshall 1984.

Meredith Happold

Epomophorus grandis SANBORN'S EPAULETTED FRUIT BAT

Fr. Épomophore de Sanborn; Ger. Sanborns Epaulettenflughund

Epomophorus grandis (Sanborn, 1950). Publções Companhia de Diamantes de Angola 10: 55. Dundo, Lunda, Angola.

Taxonomy Originally *Micropteropus grandis*. Species-group: *grandis*. Synonyms: none. Transferred from *Micropteropus* to *Epomophorus* by Bergmans (1988). Chromosome number: not known.

Description Small, pale brown fruit bat with anterior and posterior basal ear-patches but no other white markings on head; epaulettes on adult ♂♂; six palatal ridges of which numbers 2–6 are divided and only one is postdental. A poorly known species – only three adults and one juvenile known. Sexual dimorphism: no conclusive data. Pelage dense dorsally, sparser ventrally. Dorsal pelage pale reddish-brown; hairs slightly darker at base (W. Bergmans pers. comm.). Ventral pelage very pale brown to whitish-brown. Throat nearly naked. Adult ♂♂ with white epaulette on each shoulder (retracted within pouch except when displayed). Head pale brown without markings except for anterior and posterior white basal ear-patches. Muzzle longish, although relatively short and broad for an *Epomophorus*. Lips and cheeks of ♂♂ fleshy and expansible (no data for ♀♀). Ears relatively short, slightly pointed, naked with brown pigmentation. Eyes large. Palate with six thick ridges of which 2–6 are divided by medial gap, 5 is level with last molars and 6 is postdental (Figure 39d). In juveniles, palatal ridges 2–4 are not divided. Wing-membranes light brown; attaching to second toe. Tail absent or very short.

Skull short for an African fruit bat and for an *Epomophorus*. Zygomatic width relatively large, rostrum relatively short and broad, and palate relatively short for this genus (Table 13, p. 237); rostrum of medium relative length for an African fruit bat. Postdental palate weakly concave (N. P. Giannini pers. comm.). Dental formula $2^{121}/_{2132} = 28$.

Geographic Variation None recorded.

Similar Species Thirteen other species of fruit bats have simple muzzles; basal ear-patches but no other markings on head; adult ♂♂ with epaulettes; three upper and five lower cheekteeth:

Epomophorus anselli. Six thick palatal ridges of which only 5 and 6 are divided. Apparently larger, but data are limited (Table 12, p. 236).

E. crypturus. Larger (FA: >70 mm; GLS: >40 mm).

E. angolensis. Much larger (Table 12).

E. wahlbergi. Larger (Table 12). Only one thick postdental palatal ridge.

E. minimus. Two thick postdental palatal ridges; ridges 2, 3 and 4 not divided. East Africa, Ethiopia, Somalia.

E. gambianus. Larger (Table 12). Two postdental palatal ridges; ridges 2, 3 and 4 not divided. North of Equator.

E. labiatus. Two thick postdental palatal ridges; ridges 2, 3 and 4 not divided.

Epomops (3 species). Three or five thick palatal ridges.

Micropteropus intermedius. Smaller in most skull and tooth dimensions including, in particular, rostrum length (11.2–11.6 mm), palatal length (17.3–18.5 mm) and C–M¹ (10.2–10.6 mm). Of the six palatal ridges, only 5 and 6 are divided.

M. pusillus. Smaller (FA: 46–55 mm; GLS: <32 mm).

Nanonycteris veldkampii. Smaller (FA: 46–54 mm).

Distribution Endemic to Africa. Known only from two localities in the Southern Rainforest–Savanna Mosaic: Dundo near northern border of Angola, and Pointe Noire on coast of Congo.

Habitat The above localities lie just south of the Rainforest BZ, where long fingers of rainforest project along the river valleys into secondary grasslands and woodland savannas (Hayman 1963, Bergmans 1988). Not recorded from the rainforest itself. The specimen from Pointe Noire was mist-netted in a stand of *Borassus* palms and lower shrubs behind the beach (Bergmans 1979). Bergmans (1988) predicts that *E. grandis* is a woodland species that might also be found in woodland savanna habitats E and S of the two known localities.

Abundance Only three adults and one juvenile have been collected, but this species perhaps occurs in some parts of the Zambezian Woodland BZ where few collections have been made.

Remarks The holotype, collected in Sep, was carrying a juvenile with milk teeth and FA: 46 mm (Sanborn 1950), suggesting this birth occurred shortly before the wet season.



Epomophorus grandis

Conservation IUCN Category: Data Deficient.

No evidence of rarity in the field; habitat preferences, distributional limits and population dynamics not known (Bergmans 1999). The area where it occurs has been inaccessible for years.

Measurements

Epomophorus grandis

FA (♂♂): 63, 62 mm

FA (♀): 66 mm

WS: n. d.

HB (♂♂): —, 99 mm

T (♂♂): —, 4 mm

T (♀): 8 mm

E (♂♂): 17, 18 mm

E (♀): ca. 16 mm

Tib (♂♂): 27, 29 mm

Tib (♀): 26 mm

HF (♂♂): 18, 18 mm

HF (♀): 19.6 mm

WT: n. d.

GLS (♂♂): 36.7, 35.4 mm

GLS (♀): 36.4 mm

GWS (♂♂): 20.8, 21.6 mm

GWS (♀): 21.8 mm

C–M¹ (♂♂): 12.3, 11.8 mm

C–M¹ (♀): 12.3 mm

Angola and Congo (♂♂: BMNH, ZMA respectively; ♀: FMNH, holotype; Bergmans 1988)

Key References Bergmans 1979, 1988, 1999; Hayman 1963.

Meredith Happold

Epomophorus labiatus LITTLE EPAULETTED FRUIT BAT

Fr. Épomophore de Temminck; Ger. Temmincks Epaulettenflughund

Epomophorus labiatus (Temminck, 1837). Monogr. Mamm., 2: 83. Given as 'Abyssinia', but probably Sennar, Blue Nile Province, Sudan (see Bergmans 1988, p. 105).

Taxonomy Originally *Pteropus labiatus*. Species-group: *gambianus*. Claessen & De Vree (1990b) conducted principal component analyses of skull measurements of specimens previously identified as *E. anurus*, *E. labiatus* and *E. minor*, and concluded that only two groups were represented by the material examined. The first group (a cluster of larger specimens with geographic variation in size) consisted of specimens formerly identified as *E. anurus*, *E. labiatus* and partly as *E. minor*, and these were considered to represent *E. labiatus*. The second group (a cluster of small specimens with no geographic variation in size) consisted of specimens formerly identified as *E. minor*, and these were described as a new species, *E. minimus*. While tentatively accepting the validity of *E. minimus*, Bergmans (1997) points out that there are many unresolved problems with *E. labiatus* as defined by Claessen & De Vree (1990b). Bergmans (1997) raised the possibility that *E. labiatus* (*sensu* Claessen & De Vree 1990b) contained more than one species and subsequently described *E. anelli*, the holotype of which was considered to represent *E. labiatus* by Claessen & De Vree (1990b). It is possible that *E. labiatus sensu* (Claessen & De Vree 1990b) contains still more species but, until the taxonomy of the small *Epomophorus* is fully resolved, information for all of the forms (excluding *E. minimus* and *E. anelli*) is given in the following profile. Synonyms:

anurus, *doriae*, *minor*, *schoensis*, *schovanus*. Subspecies: none. For a specimen formerly referred to as *E. anurus*, chromosome number (W Uganda): $2n = 36$ (♀) (Dulić & Mutere 1973a).

Description Small, pale brown fruit bat with anterior and posterior basal ear-patches but no other white markings on head; epaulettes on adult ♂♂; six palatal ridges. Not easily identified by its size and palatal ridges (see Similar Species). Males often darker and, on average, slightly larger than ♀♀. Pelage soft, fluffy; extending dorsally and ventrally along each upper arm and for some distance along each forearm; mid-dorsal hairs ca. 10 mm. Dorsal pelage (♂♂) pale brown; hairs pale brown with dark brown at base. Ventral pelage (♂♂) pale brown merging into pure white on abdomen; some ♂♂ with dark brown shoulders and throat. Adult ♂♂ with white epaulette on each shoulder (retracted within pouch except when displayed). Dorsal pelage (♀♀) pale brown (fawn); hairs beige with pale brown at tip. Ventral pelage (♀♀) pale fawn on chest becoming darker on abdomen. Head dog-like with anterior and posterior white basal ear-patches. Muzzle longish, although relatively medium-short and broad for an *Epomophorus*. Lips and cheeks fleshy and very expansible, especially in ♂♂. Ears relatively short, rounded, naked, brown with dark

brown rim. Eyes large, brown. Palate with six thick ridges, the fourth mid-way between third and fifth, the fifth partly or fully postdental and the sixth postdental; ridges 2, 3 and 4 not divided (cf. *E. grandis*) (Figure 39e). Wing-membranes brown; attaching to second toe. Tail very short or absent.

Skull medium (♂♂) or short (♀♀) for an African fruit bat and for an *Epomophorus*, and of medium relative breadth for this genus (Table 13, p. 237). Rostrum relatively short and broad (♀♀), also broad but possibly a little longer in ♂♂ (based on data for both *E. labiatus sensu* Bergmans and *E. minor* in Bergmans 1988). Postdental palate moderately concave. Dental formula $\frac{2121}{2132} = 28$.

Geographic Variation Clinal geographic variation in skull length is characteristic of this species as defined by Claessen & De Vree (1990b). However, some data were ignored when it was concluded that the variation was clinal, and the variation may also reflect the existence of more than one species in *E. labiatus* (Bergmans 1997).

Similar Species Thirteen other species of fruit bats have simple muzzles; basal ear-patches but no other markings on head; adult ♂♂ with epaulettes; three upper and five lower cheekteeth:

Epomophorus anelli. In Malawi (and probably SW Tanzania), larger (FA ♂♂: 77 mm, FA ♀♀: 68, >74 mm; GLS ♂♂: 47.1 mm, GLS ♀♀: 38.7, >41.2 mm).

E. crypturus. Almost always larger (Table 12, p. 236).

E. angolensis. Larger (Table 12).

E. wahlbergi. Only one thick postdental palatal ridge.

E. grandis. Only one thick postdental palatal ridge; ridges 2, 3 and 4 divided.

E. minimus: Skull usually shorter (GLS ♂♂: almost always <40 mm, GLS ♀♀: almost always <36.5 mm). In NTanzania, differences are minimal and the discriminate function of Claessen & DeVree (1990b) is flawed (see Genus *Epomophorus* and see also Bergmans 1997).

E. gambianus. Almost always larger (Table 12).

Epomops (3 spp.). Three or five thick palatal ridges.

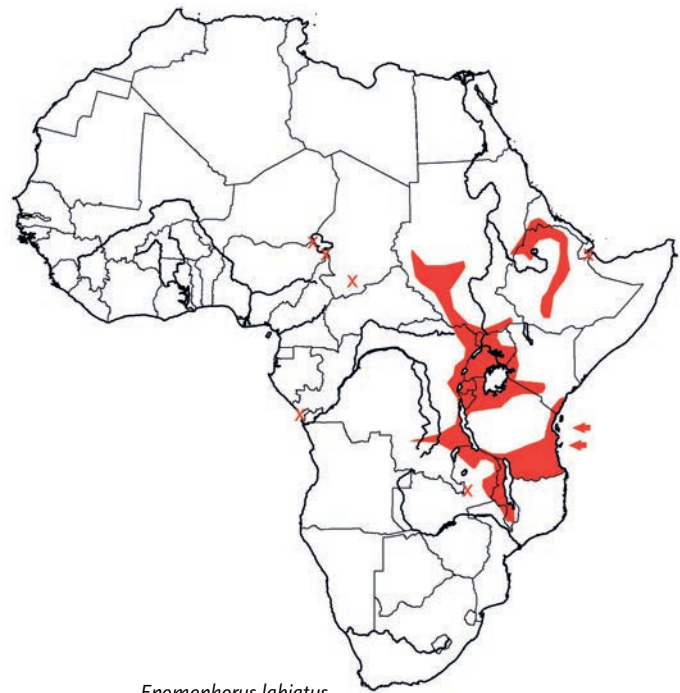
Micropteropus intermedius. Palatal ridges 2–4 divided by medial gap.

M. pusillus. Smaller (FA: 46–56 mm).

Nanonycteris veldkampii. Smaller (FA: 46–54 mm).

Distribution Mainly found in the Sudan and Guinea Savanna BZs, all Rainforest–Savanna Mosaics and the Coastal Forest Mosaic BZ, the Zambesian Woodland BZ and (in Ethiopia) the Afromontane–Afroalpine BZ, but apparently not widespread in any zone except the Eastern Rainforest–Savanna Mosaic. Recorded from NE Nigeria and S Congo eastwards to Djibouti, Eritrea and the Tanzanian coast (including Mafia I.; Kock & Stanley 2009), and southwards to Malawi. Extraliminally: SW Saudi Arabia (Gaucher 1992). Map adapted from Claessen & de Vree (1990b) with additional records from Bergmans (1988): this map should be regarded as tentative pending resolution of taxonomic problems.

Habitat Found in a wide variety of savannas including undifferentiated woodland, wetter miombo woodland, evergreen and semi-evergreen bushlands, *Acacia–Commiphora* deciduous bushland and thicket and *Acacia* wooded grassland (Bergmans 1988; terminology from White 1983). Also found in a variety of mosaics,



Epomophorus labiatus

(including rainforest–savanna, coastal forest–savanna, and evergreen bushland–grassland) and afromontane vegetation (Bergmans 1988). In Saudi Arabia, found in juniper forest at 2200 m from May to Sep but presumably moves to lower altitudes during the colder months (Gaucher 1992).

Abundance Well represented in collections. Probably common throughout most of its range but local abundance may depend on seasonal availability of fruit and flowers.

Adaptations Aspect ratio very low; wing-loading medium. Flight fast and direct when commuting, or slow with considerable manoeuvrability when foraging through the canopies of trees. Can hover briefly and take off from the ground. Locomotion over ground is extremely awkward – the wings flap in synchrony and the hindfeet are not used. Can clamber along thin branches and can climb head-first up or down rough surfaces: in both cases, the bat holds on with the thumbs and hindfeet and moves the wings and hindfeet in alternation (M. Happold pers. obs.). By day, hangs freely from branches of trees and shrubs (usually but not always under dense foliage), under banana leaves, and from roots exposed by the erosion of river-banks (Verschuren 1957). The thumbs and second fingers are opposable and are used with great dexterity during feeding (see below). The thumbs are also used to hold onto a perch while the bat hangs, with legs dangling, to defecate or urinate. Defaecation and urination also occur during flight. The tongue is long with small, rasp-like, backward-pointing papillae near the tip. During grooming, it is protruded from the front or sides of the mouth and used to lick the face, genital region and both surfaces of the wings. The claws of the hindfeet are used to comb the dorsal and ventral pelage, and individuals also shake themselves during grooming. Captive individuals did not drink.

Foraging and Food Primarily frugivorous. In Malawi, *E. labiatus* feeds on wild figs, and sometimes visits trees at the same

time as *E. crypturus* and *E. wahlbergi* (M. Happold unpubl.). Lands on clusters of figs and uses the thumbs and second fingers in conjunction to pull food towards the mouth and, subsequently, to hold and manipulate it while it is chewed. Food is initially packed into the expansible cheeks, carried to a perch and then chewed slowly, small amounts at a time. If a bat is hanging while feeding, one hindfoot is sometimes used to manipulate food in the mouth. Captive bats land to eat fruit on the ground suggesting that fallen fruits might be collected in the wild. Captive bats feed at intervals throughout the night. Feeds on soft fruits of endemic and cultivated trees including *Ficus*, *Terminalia*, *Mangifera*, *Irvingia* and *Salvadoria* (Verschuren 1957, 1965a, Okia 1974a, Mickleburgh *et al.* 1992). Visits the flowers of *Parkia* and *Kigelia*, but it is not known what components are eaten.

Social and Reproductive Behaviour Often roosts singly. Also observed roosting in groups of up to 40, but the individuals were 'hanging singly or scattered amid the branches of a grove of trees' (Lang & Chapin 1917b as *E. anurus*). Adult ♂♂ probably perform calling-displays as do other epauletted fruit bats, but the larynx is not very large and the calls can be heard only a short distance. A captive ♀ called intermittently throughout each night of her week in captivity (M. Happold unpubl.). The call was a soft bell-like 'ping' uttered at intervals of 1–7 seconds. A similar 'ping' made by an electronic watch elicited 'pinging' by the bat.

Reproduction and Population Structure Litter-size: one. At 00° 05'N (Entebbe) and 01° 30'N (Sebei, Uganda), the reproductive chronology is continuous bimodal polyoestry with postpartum oestrus (Okia 1974a). Gestation 5–6 months. Females are in reproductive synchrony. Parturition and postpartum mating occur in late Mar to early Apr, and late Sep to early Oct. Uganda has two wet seasons (Mar–May and Oct–Dec), so lactation and early pregnancy occur during each wet season. The relationship between reproductive chronology and availability of food is not known. Birth-weight ca. 11 g. At ca. 8–15°S in Malawi and Zambia, where there is one wet season (Nov to early Apr), ♀♀ are not in reproductive synchrony. Births have been recorded from Oct–Feb (no data for other months) (Happold & Happold 1990a as *E. minor*). Pregnant ♀♀ (n = 2), which appeared to have been lactating recently, were recorded in Oct and late-Jan, suggesting polyoestry, but this needs confirmation. In the Shire Highlands (Malawi), although young were mist-netted in Mar–May, no adults were mist-netted from Mar–Jun, or in Sep (no data for Jul–Aug), suggesting these bats are sometimes nomadic. If bimodal polyoestry occurs in this population, the first and second litters are presumably born at different localities.

Predators, Parasites and Diseases Predators include Silvery-cheeked Hornbill *Bycanistes brevis* (Kingdon 1973). Ectoparasites include a bat-fly *Basilia blainvillii* (Diptera: Nycteribiidae) and 11 species of mites (Acari: Spinturnicidae, Myobiidae, Trombiculidae, Ereynetidae, Chirodiscidae, Sarcoptidae, Gastronyssidae, Teinocoptidae) (Anciaux de Faveaux 1984).

Conservation IUCN Category: Least Concern.



Epomophorus labiatus.

Measurements

Epomophorus labiatus

FA (♂♂): 69.4 (60–80) mm, n = 247

FA (♀♀): 68.3 (58–76) mm, n = 182

WS (c) (♂♂): 438.0 (425–455) mm, n = 3*

WS (c) (♀♀): 413.0 (400–422) mm, n = 4*

HB (♂♂): 109.0 (105–113) mm, n = 4*

HB (♀♀): 94.8 (90–98) mm, n = 5*

T: 2.0 (0–5) mm, n = 10*

E: 18.5 (17–21) mm, n = 13*

Tib (♂♂): 27.6 (26–29) mm, n = 6*

Tib (♀♀): 25.8 (24–28) mm, n = 7*

HF: 16.1 (12–18) mm, n = 9

WT (♂♂): 54.4 (48–64) g, n = 4*

WT (♀♀): 40.6 (34–51) g, n = 10*

GLS (♂♂): 42.7 (35.4–48.6) mm, n = 216

GLS (♀♀): 39.3 (33.5–46.0) mm, n = 158

GWS (♂♂): 22.4 (19.0–25.7) mm, n = 225

GWS (♀♀): 21.4 (18.9–24.2) mm, n = 158

C–M¹ (♂♂): 14.2 (11.4–18.7) mm, n = 234

C–M¹ (♀♀): 13.2 (10.7–15.6) mm, n = 168

Throughout geographic range (Claessen & De Vree 1990b)

*Malawi only (HC). Bergmans (1997) considers the ranges of these measurements exceptionally large for one species, and indicates that the species content needs further research

Key References Bergmans 1988, 1997; Claessen & De Vree 1990b; Okia 1974a.

Meredith Happold

Epomophorus minimus LEAST EPAULETTED FRUIT BAT

Fr. Épomophore nain; Ger. Winziger Epaulettenflughund

Epomophorus minimus Claessen and De Vree, 1991. Senckenberg. Biol. 71: 209–238. Bahadu, Shewa, Ethiopia.

Taxonomy Species-group: *gambianus*. Synonyms: none. Included in *E. minor* by Bergmans (1988), but considered to be a distinct species by Claessen & De Vree (1990b); for details, see *E. labiatus*. Chromosome number: not known.

Description Small, fawn fruit bat with anterior and posterior white basal ear-patches and epaulettes on adult ♂♂, which very closely resembles *E. labiatus* (see profile). There are six thick palatal ridges; both fifth and sixth are fully postdental; ridges 2, 3 and 4 are not divided (cf. *E. grandis*). The skull is short for an *Epomophorus* and, in both sexes, the zygomatic width is relatively large (Table 13, p. 237). Postdental palate almost flat. Dental formula $^{2121}_{2132} = 28$.

Geographic Variation None recorded. No geographic variation in skull length (cf. *E. labiatus*).

Similar Species Thirteen other species of fruit bats have simple muzzles; basal ear-patches but no other markings on head; adult ♂♂ with epaulettes; three upper and five lower cheekteeth:

Epomophorus angolensis and *E. gambianus*. Much larger (Table 12, p. 236).

E. crypturus. Larger (FA: >70 mm; GLS >40 mm).

E. anelli. Larger (Table 12). Nearest record Malawi.

E. wahlbergi. Only one postdental palatal ridge. Larger (FA: almost always >67 mm; GLS: >40 mm).

E. grandis. Only one postdental palatal ridge; ridges 2, 3 and 4 divided. Congo, Angola.

E. labiatus. Skull usually longer (GLS ♂♂: almost always >40 mm, GLS ♀♀: almost always >36.5 mm). In N Tanzania, differences are minimal and the discriminate function of Claessen & De Vree (1990b) is flawed (see Genus *Epomophorus* and also Bergmans 1997).

Epomops (3 spp.). Three or five thick palatal ridges.

Micropteropus (2 spp.). Palatal ridges 2–4 divided by median gap.

Nanonycteris veldkampii. Smaller (FA ♂♂: 46–52 mm, FA ♀♀: 47–54 mm). Nine thick or partly thick palatal ridges.

Distribution Endemic to Africa. Known from ca. 40 localities, mostly in the Sudan Savanna and Afromontane–Afroalpine BZs, in C Ethiopia, C, N and E Kenya, and Somalia (Claessen & De Vree 1990b). Also recently recorded from the northern and western floral regions of W Uganda (Kityo & Kerbis 1996). Discontinuities in the distribution probably reflect insufficient sampling.

Habitat Poorly known. Most localities appear to be in deciduous bushland and thicket dominated by *Acacia* and *Commiphora* (usually near rivers and/or highlands), or in afromontane vegetation on the slopes of the Ethiopian and Kenyan Highlands. Also penetrates marginally into semi-desert grasslands and shrublands, but probably stays near rivers. In W Uganda, *E. minimus* is common in mosaics

*Epomophorus minimus*

of savanna and riverine forest in the northern floral region and less common in blocks of lowland rainforest in the western floral region (Kityo & Kerbis 1996).

Abundance Kityo & Kerbis (1996) reported *E. minimus* to be the second most abundant bat (after *Micropteropus pusillus*) in the northern floral region of Uganda. No information from elsewhere.

Remarks *Epomophorus minimus* is a newly described species that cannot be distinguished easily from *Epomophorus labiatus* with which it is sympatric in some areas. There appear to be no recent, detailed studies of its biology. Because species in the *E. anurus–labiatus–minor* complex were confused prior to the work of Claessen & De Vree (1990b), and because the taxonomy of species in this complex (which now includes *E. anelli*) is not yet fully resolved, observations in areas where these species occur sympatrically *Epomophorus* must be treated with caution.

Conservation IUCN Category: Least Concern.

Measurements

Epomophorus minimus

FA (♂♂): 61.6 (54–67) mm, n = 92

FA (♀♀): 60.4 (57–66) mm, n = 101

WS (d): 420 mm, n = 1*

HB: 103.5 (96–115) mm, n = 6*

T: 0 mm, n = 2*

E: 18.2 (16–20) mm, n = 6*

Tib: n. d.
 HF: n. d.
 WT: n. d.
 GLS (♂ ♂): 35.7 (32.9–39.0) mm, n = 91
 GLS (♀ ♀): 33.3 (31.2–36.4) mm, n = 149
 GWS (♂ ♂): 20.1 (19.0–21.6) mm, n = 94
 GWS (♀ ♀): 19.4 (17.9–20.7) mm, n = 150
 C–M¹ (♂ ♂): 11.8 (10.7–13.1) mm, n = 93

C–M¹ (♀ ♀): 11.1 (6.5–13.0) mm, n = 150
 Throughout geographic range (Claessen & De Vree 1990b)
 *Ethiopia and Kenya only (BMNH)

Key References Bergmans 1988; Claessen & De Vree 1990b.

Meredith Happold

***Epomophorus wahlbergi* WAHLBERG'S EPAULETTED FRUIT BAT**

Fr. Épomophore de Wahlberg; Ger. Wahlbergs Epaulettenflughund

Epomophorus wahlbergi (Sundevall, 1846). Ofv. Kongl. Svenska Vet.-Akad. Forhandl. Stockholm 3: 118.
 Near Durban, KwaZulu–Natal, South Africa.

Taxonomy Originally *Pteropus wahlbergi*. Species-group: *wahlbergi*. Synonyms: *haldemani*, *neumanni*, *stuhlmanni*, *unicolor*, *zenkeri*. Subspecies: two of dubious validity. Chromosome number (Kenya, Zimbabwe): 2n = 36; aFN = 68 (Dulić & Mutere 1973a, Peterson & Nagorsen 1975).

Description Small to medium-sized, fawn fruit bat with anterior and posterior basal ear-patches but no other white markings on head; epaulettes on adult ♂ ♂; six thick palatal ridges of which only one is postdental. Males on average larger than ♀ ♀, sometimes darker, sometimes with band of brown pelage around epaulettes and across throat and around testes (when sexually active). Pelage soft, slightly fluffy; extending dorsally and ventrally along each upper arm and for some distance along each forearm; mid-dorsal hairs ca. 10 mm. Dorsal pelage fawn, paler on shoulders, sometimes suffused with yellow on hindlimbs and around tail (especially in ♀ ♀); hairs (on back) fawn with dark brown at base. Ventral pelage slightly to considerably paler, sometimes suffused with grey. Adult ♂ ♂ with white epaulette on each shoulder (retracted into pouch except when displayed). Head dog-like with anterior and posterior white basal ear-patches. Muzzle long (although relatively short and broad for an *Epomophorus*). Lips and cheeks fleshy and very expansible, especially in ♂ ♂; ♂ ♂ can be distinguished at a distance by their expansible cheeks, which appear to form a pad under each eye. Ears relatively short, rounded, naked, brown with dark rim. Eyes large, brown. Palate with five thick interdental ridges and one thick postdental ridge; ridges 2, 3 and 4 not divided (cf. *E. grandis*) (Figure 39f): in exceptional cases, the fifth ridge is partly postdental. Wing-membranes brown; attaching to second toe. Tail absent or very short.

Skull (Figure 40) medium-sized for an African fruit bat but long and robust for an *Epomophorus*. Zygomatic width relatively large, rostrum relatively short and broad, and palate relatively short for this genus (Table 13, p. 237). Postdental palate markedly concave. Dental formula $^{2121}/_{2132} = 28$.

Geographic Variation Two subspecies, *E. w. wahlbergi* and *E. w. haldemani* have been described, but their ranges overlap and their diagnostic characters are poorly defined (for details see Bergmans 1988).

Similar Species Thirteen other species of fruit bats have simple muzzles; basal ear-patches but no other markings on head; adult ♂ ♂ with epaulettes; three upper and five lower cheekteeth:

Epomophorus grandis. Smaller (Table 12, p. 236). Palatal ridges 2–4 divided by medial gap.

E. anselli. Fifth palatal ridge postdental in ♂ ♂, partly interdental in ♀ ♀. On average smaller (Table 12).

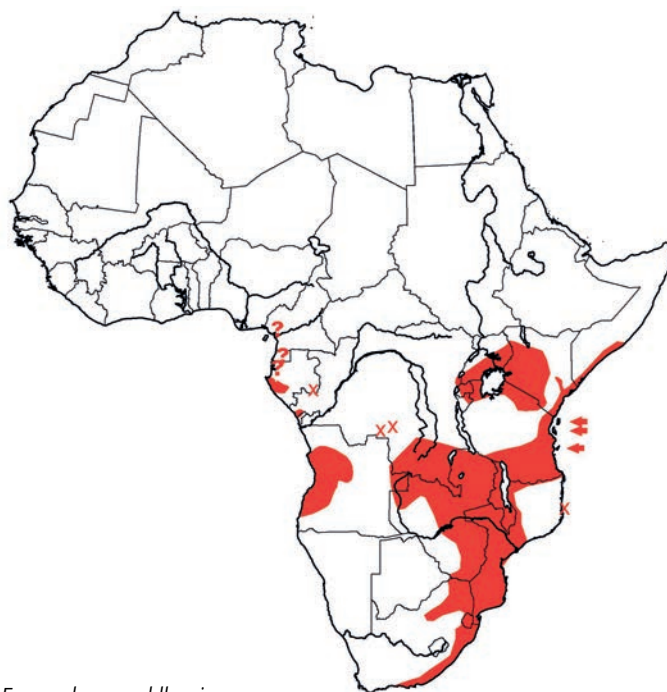
Epomophorus (5 other spp.). Two thick postdental palatal ridges.

Epomops (3 spp.). Three or five thick palatal ridges.

Micropteropus (2 spp.). Smaller (FA: 46–64 mm). Palatal ridges 2–4 divided by medial gap.

Nanonycteris veldkampii. Much smaller (FA: 46–54 mm).

Distribution Endemic to Africa. Mainly found in the Zambezan Woodland BZ, Eastern Rainforest–Savanna Mosaic, Coastal Forest Mosaic BZ and Somalia–Masai Bushland BZ. Recorded from Gabon (and perhaps Cameroon and Equatorial Guinea) to Somalia, and



Epomophorus wahlbergi

southwards to Angola in the west and South Africa in the east. Also Mafia I. (Kock & Stanley 2009), Pemba I. and Zanzibar I. (Bergmans 1988). The distribution is disjunct, partly for ecological reasons, but some gaps, and the apparent absence of records in Mozambique north of the Zambezi R. might reflect insufficient sampling.

Habitat Mainly recorded from woodland savannas (including wetter and drier miombo woodlands and mopane woodland) where fruiting trees are present. Also recorded from fingers of woodland penetrating the rainforest zone, and in mangrove forests and *Acacia–Commiphora* deciduous bushland and thicket. In southern Africa, *E. wahlbergi* is only found in river valleys and on the eastern slopes of mountains – habitats that have a high proportion of evergreen trees, a good water supply, humid conditions and a relatively even climate (Smithers 1983, Volpers & Kumirai 1995). Possibly also found only in similar habitats in the northern part of the range. Ornamental gardens are exploited for food and roosts. In South Africa, *E. wahlbergi* is also found in cities where fig trees have been planted (S. Sowler pers. comm.).

Abundance Uncertain; probably fairly common.

Adaptations Aspect ratio low; wing-loading: no information; flight moderately fast to slow; manoeuvrability moderate. Can turn by banking at very slow speeds (minimum radius <50 cm). Can hover briefly, glide short distances and take off from the ground. Locomotion on ground is clumsy and slow. In contrast, climbing up and down tree-trunks is very competent; forearms move in alternation with thumbs extended to find thumb-holds; strides are long. Climbs along under slender branches, clinging with thumbs and toes and with limbs moving in alternation. Crash-lands on foliage and bunches of fruit, but landing under a ceiling, palm-leaf or branch is accomplished by swooping upwards, hooking the thumbs to the perch with the last wing-stroke, swinging the feet up to grip the perch and then letting go with the thumbs (Wickler & Seibt 1976).

By day, usually hangs in foliage of trees with dense canopies (including evergreen trees in riverine woodlands, ornamental gardens and city parks). Also often hangs from living fronds of palms or the skirts of dead fronds surrounding the stems of *Borassus* palms. Occasionally hangs from thatched ceilings of large open buildings and from eaves of tall buildings. Roost-fidelity varies according to duration of residence in a particular area, and perhaps the safety of the roost. One roost in Kenya was occupied continuously for at least five years and, although the number of individuals at this roost varied from 40 to 100 over this period, group-size usually remained stable for 1–2 weeks at a time. Nomadic individuals perhaps return to familiar roosts in each locality they visit – some roosts have been occupied for several weeks during consecutive years but the individual identity of the occupants was not determined. Some individuals switch between several roosts in one area, for the duration of their stay in that area – possibly to avoid predation or in response to disturbance. Roosting bats hang from one or both feet, with the head either visible or tucked against the belly and covered by the wings. They are motionless for long periods, but may groom, stretch, yawn, or swing intermittently throughout each day; purpose of swinging not known. For details see Wickler & Seibt (1976).

Not known to drink water but *E. wahlbergi* has been seen flying low over water and wetting the ventral pelage (S. Sowler pers. comm.). The kidneys (Figure 29a) are adapted for excreting copious water from diet while maximally retaining salts and other solutes (Happold & Happold 1988). Adaptations enabling the lungs to extract the large amount of oxygen needed for flight include relatively large lungs, extensive alveolar surface area, a thin blood–gas barrier and a high capacity for diffusing oxygen through the body (Maina 1982, Maina *et al.* 1982, in Acharya 1992).

Foraging and Food Feeds on soft fruits, pollen and nectar. Foraging begins around dusk. Individuals move up to 4 km from roosts to feeding areas (Fenton *et al.* 1985). Nomadic movements occur where abundance of food fluctuates seasonally. Fruit is carried to an often regularly used feeding perch, then chewed slowly while the tongue mashes the fruit against the palate. Large pieces of fruit are held in one foot while bites are taken, and the thumbs are used to manipulate food. Pellets of skin, seeds and fibre are spat out (and can be analysed to reveal the diet). Feeds mainly on figs *Ficus* and the soft pulpy ripe fruits, pollen and nectar of trees and shrubs, including species of *Diospyrus*, *Anacardium*, *Terminalia*, *Uapaca*, *Voacanga*, *Tabernaemontana*, *Eugenia*, *Bridelia*, *Euclea*, *Annona*, *Sclerocarya*, *Podocarpus*, *Syzygium*, *Adansonia*, *Sideroxylon*, *Mimusops* and at least eight other genera (Mickleburgh *et al.* 1992, Taylor 2000). Figs sometimes comprise most of the diet. Also eats cultivated fruits but usually when too ripe to have commercial value. Pollinates baobabs *Adansonia* (Kock 1972) and probably other trees including *Parinari*. Chews leaves of *Balanites*, and swallows the juice possibly to obtain steroidal sapagenins (from which steroidal hormones are synthesized) and proteins (Wickler & Seibt 1976). Remains of beetles and other insects have been found in stomach contents (Pienaar *et al.* 1980), but although protein may be obtained in this way, this insectivory might be accidental.

Social and Reproductive Behaviour Usually roosts in mixed-sex groups throughout the year; group-size three to over 100, sex ratio ca. equal in large or very large groups but individual ♂♂ may roost with up to three adult ♀♀ and young. Rarely found roosting singly or in pairs. Sometimes roosts with *E. crypturus*. In Kenya, a detailed study of social interactions in a colony of 40–100 individuals was made during Jan each year, for five years (Wickler & Seibt 1976). The bats return to their roosts at dawn, and most social interactions at the roost occur at this time. These include nose-to-nose sniffing (and occasionally nose-licking), probably to allow group-members to recognize each other. Group-members clump together, but maintain a mean \pm S.D. distance of 16.5 ± 4 cm between neighbours. Individuals strike out with their clawed thumbs if approached too closely, and may half-open the wings, screech and occasionally bite. Mutual-grooming has not been seen, nor any other interactions between roosting adults. In Jan, the bats left precisely between 18:50h and 19:00h, and did not return until ca. 05:30h next morning. They departed one by one and often in different directions. Aggregations occurred at fruiting trees, but it is not known if these were comprised of individuals that roosted together. Elsewhere, bats of this species are reported to leave their day-roosts for 1–2 h and then return (Kirk in Eisentraut 1945).

Courting ♂♂ fly from the roost to perches, 2–20 m above ground, in nearby trees. There, they inflate their cheeks and make a moderately loud gong-like honk repeated at intervals of ca. one second. The epaulettes are displayed, and the wings are half opened, quiver constantly and beat once or twice with each call. Species-specific differences between the calls of sympatric *E. wahlbergi* and *E. crypturus* have been documented (Volpers & Kumirai 1995). The vocalizations and wing-beating displays of *Epomops franqueti* and *Hypsignathus* are substantially different to those of *E. wahlbergi* (see profiles). Rival *E. wahlbergi* ♂♂ are usually separated by at least 50 m. When approached by ♀♀, the ♂♂ double their call repetition-rates and turn towards the approaching ♀. The approaching ♀ hovers for nose-to-nose contact, and often utters a series of soft calls, each call being uttered in the interval between consecutive calls made by the ♂ (sonograms in Wickler & Seibt 1976). Males usually call from one perch for 15 min to over one hour, then move to other perches. Individuals apparently have several preferred perches to which they return on consecutive nights. These observations indicate that *E. wahlbergi* does not have a lek mating-system of any kind (for definitions, see order Chiroptera).

Parturition takes place at the roost in the presence of both male and female group-members (Wickler & Seibt 1976). Females deliver in the normal hanging posture but with the wings folded loosely. The neonate immediately clings to the mother, using the well-developed claws of its thumbs and toes and also its milk-teeth, which are hooked to facilitate gripping the mother's nipples. The placenta is chewed within five minutes of its appearance. The mother licks her vulva, and extensively licks her neonate. During the first 30 minutes, the neonate is placed horizontally across its mother's chest, and is turned (or turns itself) around several times so that its head is at one or other of the nipples. Older juveniles either cling horizontally or vertically with the head upwards. At first, the neonate is carried (attached to nipples and fur) while the mother forages. When volant, the young follow their mothers and maintain contact by calling to each other: the mother's calls are soft honks, the juvenile's are sparrow-like 'tweets' (M. Happold pers. obs.).

Reproduction and Population Structure Litter-size: one, rarely two. In tropical localities, the reproductive chronology appears to be aseasonal polyoestry (or possibly seasonal bimodal polyoestry in some localities [e.g. see Bergmans 1979]), but conclusive year-round data are not yet available. Furthermore, proof of polyoestry appears limited to the record of 2 of 5 ♀♀ simultaneously pregnant and post-lactating in Jan at ca. 15°S in Malawi, and the percentage of ♀♀ that breed more than once/year is not known (Happold & Happold 1990a). At 02°18'S (Masalani, inland Kenya), where *E. wahlbergi* was present throughout year but at low density in Jul–Sep, pregnant ♀♀, lactating ♀♀ and volant young were present continuously from Nov to Apr; polyoestry was proposed (O'Shea & Vaughan 1980) but without published evidence. On the Kenyan coast, lactating ♀♀ were observed in Apr and Oct (A. N. McWilliam in Thomas & Marshall 1984). At 03°54'S (Kikambala, Kenya), parturition occurs in Jan (observations for Jan only with no year-round data [Wickler & Seibt 1976]) and the interpretation that

this indicates seasonal monoestry (Bernard & Cumming 1997) was a mistake. Anciaux de Faveaux (1983) pooled data from different localities, and his conclusion that the species exemplifies bimodal polyoestry or possibly 'continuous polyoestry' (sic) in Shaba (DR Congo) and Rwanda is not justified and needs confirmation.

In South Africa, the majority of ♀♀ are aseasonally monoestrous but a few are polyoestrous. At 28°57'S (Mtunzini, KwaZulu–Natal), births were recorded throughout the year, with peaks in Jul and Nov–Jan (C. Sapsford in Taylor, P. 1998). At ca. 30°S, copulation, ovulation and fertilization peaked in May–Jul; 83% of all births were in Oct–Jan but there were some births in Feb–Jun and 3 of 83 ♀♀ were both pregnant and lactating in April (i.e. polyoestrous) (Sowler 1983). Females were not in close reproductive synchrony and spermatogenesis was continuous. Gestation 160 days. Females reached sexual maturity in their first year; ♂♂ in their second year.

Predators, Parasites and Diseases Ectoparasites include a bed-bug *Africimex constrictus* (Hemiptera: Cimicidae), bat-flies *Ascoapteron semirasum*, *Brachytarsina alluaudi* (Diptera: Streblidae), and seven species of mites (Acari: Spinturnicidae, Myobiidae, Gastronyssidae, Teinocoptidae) (Anciaux de Faveaux 1984). Lagos bat virus was isolated from specimens from the Durban area, South Africa (Mickleburgh *et al.* 1992).

Conservation IUCN Category: Least Concern.

Measurements

Epomophorus wahlbergi

FA (♂♂): 81.9 (72–95) mm, n = 133*

FA (♀♀): 78.1 (67–88) mm, n = 184*

WS (c): 581 (556–610) mm, n = 5

HB (♂♂): 144.1 (106–183) mm, n = 38

HB (♀♀): 134.9 (113–171) mm, n = 54

T (♂♂): 0–4 mm, n = 3

T (♀♀): 3.3 (0–6) mm, n = 14

E: 23.5 (20–28) mm, n = 71

Tib (♂♂): 36.6 (33–40) mm, n = 16

Tib (♀♀): 33.9 (30–37) mm, n = 12

HF: 23.2 (20–27) mm, n = 25

WT (♂♂): 99.9 (68–138) g, n = 22

WT (♀♀): 93.9 (69–140) g, n = 42

GLS (♂♂): 50.5 (44.4–57.3) mm, n = 122*

GLS (♀♀): 44.8 (41.0–49.3) mm, n = 155*

GWS (♂♂): 27.1 (24.6–29.0) mm, n = 58*

GWS (♀♀): 24.8 (22.9–27.4) mm, n = 80*

C–M¹ (♂♂): 17.5 (15.7–18.9) mm, n = 37*

C–M¹ (♀♀): 15.6 (14.0–17.4) mm, n = 53*

Throughout geographic range (HC, MMB and literature)

*Bergmans 1988

Key References Bergmans 1988; Fenton *et al.* 1985; Volpers & Kumirai 1995; Wickler & Seibt 1976.

Meredith Happold

GENUS *Epomops*

Singing Epauletted Fruit Bats

Epomops Gray, 1870. Cat. Monkeys, Lemurs, Fruit-eating Bats Brit. Mus. p. 126. Type species: *Epomophorus franqueti* Tomes, 1860.

Epomops is a polytypic genus endemic to Africa. Diagnostic characters: white basal ear-patches but no other white markings on the head; epaulettes on shoulders of adult ♂♂; FA: 77–102 mm; muzzle simple; interfemoral membrane well developed and with calcar; three or five thick palatal ridges (and others); usually three upper and

five lower cheekteeth, very occasionally four upper cheekteeth and often only four lower cheekteeth (Table 11, p. 228). Palatal ridges are illustrated in Figure 41. Craniodental characters of a representative of the genus are illustrated in Figure 42, but there are inter-specific variations, especially in the dorsal profile (viewed laterally) of the rostrum (Figure 43).

Epomops currently contains three well-defined species of which two (*E. buettikoferi* and *E. franqueti*) occur mainly in rainforest habitats and appear closely related, and one (*E. dobsonii*) occurs mainly in woodland savannas. *Epomops dobsonii*, however, shows some morphological affinity to *Epomophorus* and Bergmans (1989) questioned its placement in *Epomops* (see profile of *E. dobsonii*).

The social behaviour of *Epomops* spp. is very interesting. *Epomops franqueti* and *E. buettikoferi*, which mainly occur in the Rainforest BZ, exemplify an exploded lek mating system (*sensu* Bradbury 1981), which appears to be an intermediate stage in the evolution of classical lekking (see order Chiroptera). The mating system of the less common, savanna species, *E. dobsonii*, is not known but, based on factors that appear to have brought about the evolution of classical lekking (reviewed by Bradbury 1981), its mating system is not likely to be exploded lekking, and even less likely to be classical lekking. If so, this would add to the differences between *E. dobsonii* and the other species of *Epomops*. During courtship, ♂♂ of *E. buettikoferi* and *E. franqueti* perform calling-displays during which they make very loud monotonous 'honks' resembling the ringing of a cracked bell. These are intermediate in loudness between the extremely loud 'honks' of *Hypsognathus* and the quieter 'pings' of *Epomophorus*, but they are loud enough for these species to be regarded as nocturnal pests. In *E. franqueti*, the larynx is enlarged and ossified, larger in ♂♂ than in ♀♀, and located partly in the thoracic cavity and partly in the neck (no data for other species). There is no equivalent information for *E. dobsonii*.

The genus was reviewed by Bergmans (1989). *Epomops* was placed in the *Epomophorus* section of Andersen (1912a), and in the subfamily



Epomops franqueti male.

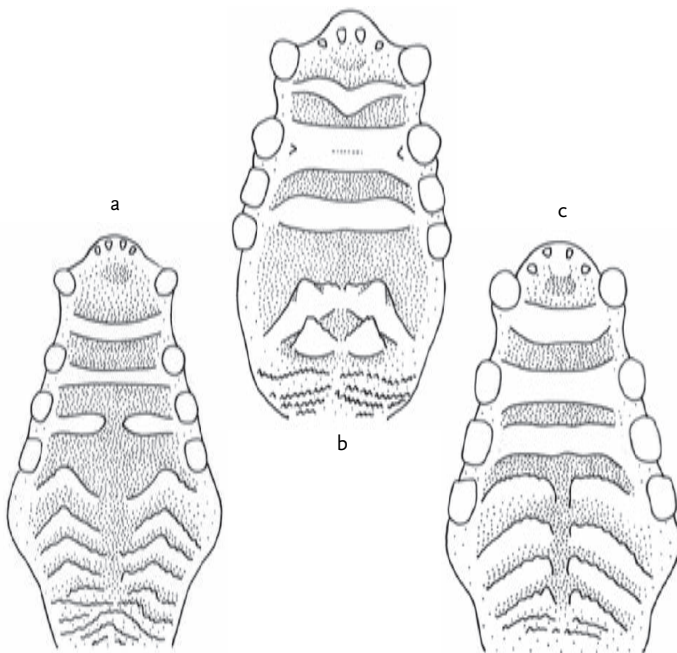


Figure 41. Palatal ridges of (a) *Epomops buettikoferi* (based on Bergmans 1997 with permission of the author), (b) *E. dobsonii* (based on Bergmans 1997 and Andersen 1912a) and (c) *E. franqueti* (based on Happold 1987).

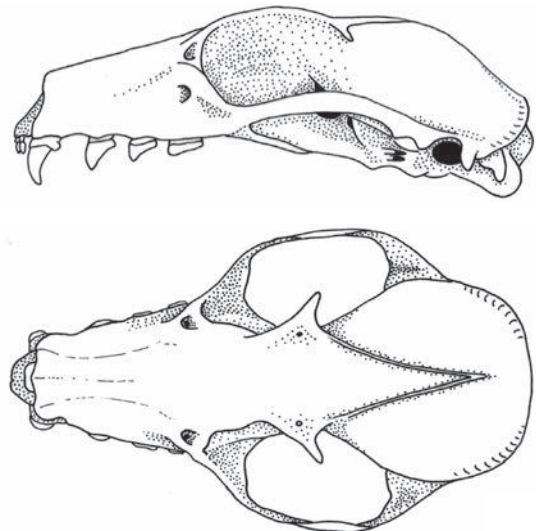


Figure 42. Skull of *Epomops franqueti* (ZFMK 69.580, adult ♂).

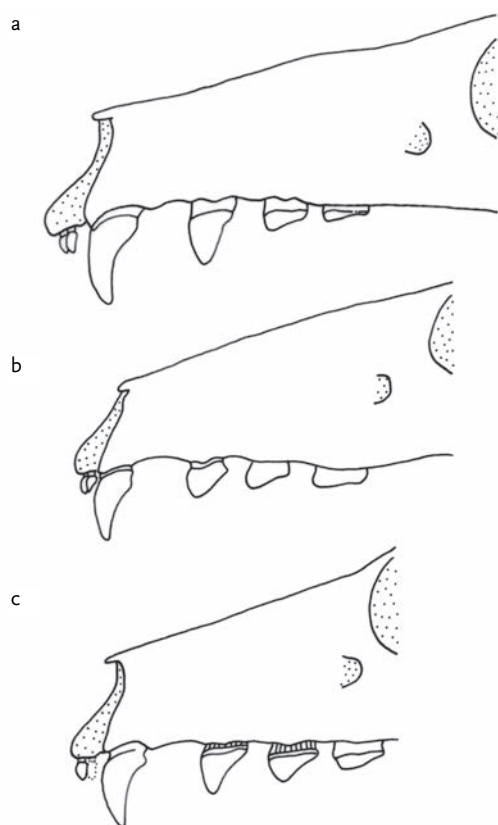


Figure 43. Rostral profiles of *Epomops* spp. showing (a) the convex dorsal profile and relatively long rostrum typical of *E. dobsonii* (BMNH 66.5402, ♂), (b) the slightly convex dorsal profile and relatively long rostrum of some *E. buettikoferi* (BMNH 77.327, ♂) (dorsal profile straight in some specimens) and (c) the straight dorsal profile and relatively short rostrum of some *E. franqueti* (BMNH 68.866, ♂) (dorsal profile slightly concave in some specimens). To emphasize the differences in relative length of the rostrum, the tooththrows are drawn to the same length for each species. Following Bergmans (1989).

Epomophorinae (tribe Epomophorini) of Bergmans (1997). Based on its anatomy, especially that of the larynx, *Epomops* (perhaps excluding *E. dobsonii*) appears to be more closely related to *Hypsignathus* than to *Epomophorus* and the other genera in the Epomophorinae (Andersen 1912a, Bergmans 1989). Chromosomally, based on data from *E. franqueti* and *H. monstrosus*, these genera also seem closely related: the karyotypes of these species cannot be distinguished, but their G- and C-bands differ in two aspects (Haiduk *et al.* 1980, 1981). Phylogenetic relationships between *Epomops*, *Epomophorus* and *Micropteropus* have also been studied by Álvarez *et al.* (1999) and Giannini & Simmons (2003) and, based on genetic data, both studies also indicate a close relationship between these genera. *Hypsignathus* and *E. dobsonii* were not included in these studies.

The species can usually be distinguished by the following characters:

- E. dobsonii*. Five thick and 3–4 thin palatal ridges (Figure 41b).
- E. franqueti*. Three thick palatal ridges; third ridge normally not divided (Figure 41c); West and central Africa between 5°W and 35°E. In area of sympatry with *E. buettikoferi*, usually smaller (FA ♂♂: 83–95 mm, ♀♀ 76–89 mm; GLS ♂♂: 43–51 mm, ♀♀: 37–46 mm).
- E. buettikoferi*. Three thick palatal ridges; third ridge normally divided medially (Figure 41a); West Africa between 14°W and 10°E. In area of sympatry with *E. franqueti*, usually larger (FA ♂♂: 92–103 mm, ♀♀: 82–95 mm; GLS ♂♂: 50–61 mm, ♀♀: 45–53 mm).

Meredith Happold

Epomops buettikoferi BÜTTIKOFER'S EPAULETTED FRUIT BAT

Fr. Épomophore de Büttikofer; Ger. Büttikofer's Epaulettenflughund

Epomops buettikoferi (Matschie, 1899). Megachiroptera Berlin Mus., p. 45. Schlieffelsville, Junk River, Liberia.

Taxonomy Originally *Epomophorus buettikoferi*. Synonyms: none. Chromosome number: not known.

Description Medium-sized, robustly built fruit bat with anterior and posterior basal ear-patches but no other white markings on head; epaulettes on adult ♂♂; three thick palatal ridges of which the third is almost always divided. Males usually darker, larger and heavier than ♀♀. Pelage soft, slightly fluffy; extending half-way along forearm; sparser on throat; mid-dorsal hairs 10–11 mm, shorter ventrally. Dorsal pelage variable, rich chocolate brown to pale golden-brown, tinged with orange or rusty-red on nape and legs; hairs unicoloured. Ventral pelage slightly paler and greyer grading to off-white or white mid-ventrally, or with clearly demarcated white or whitish mid-ventral patch; chin and throat medium brown in ♂♂ but only slightly darker than chest in ♀♀. Adult ♂♂ with a conspicuous white epaulette on each shoulder (retracted within pouch except when displayed); ♀♀

with a small, inconspicuous invagination on each shoulder containing short hairs of same colour as dorsal pelage. Head usually larger and more robust in ♂♂; muzzle long and broad; lips and cheeks fleshy and expansible (especially in ♂♂). Ears brown. Eyes large and brown. Palate with three thick ridges of which 1 and 2 are undivided whereas 3 is almost always divided by wide medial gap, occasionally divided by a narrow gap or very rarely undivided (cf. *E. franqueti*), and five to eight thin, irregularly serrated ridges (Figure 41a; Bergmans 1989). Wing-membranes brown; attaching to second toe. No tail.

Skull, on average, medium-sized for an African fruit bat. Rostrum relatively long for an African fruit bat and for an *Epomops* (rostral length ♂♂: 44–48% of GLS, ♀♀: 41–44% of GLS); dorsal profile (viewed laterally) straight or somewhat convex (Figure 43b; Bergmans 1989). Postdental palate almost flat (cf. *Epomophorus* spp. of similar size). Dental formula usually $2^{121}/_{2132} = 28$ but outer upper incisor sometimes absent.

Geographic Variation No subspecies are recognized. Body and skull dimensions decrease from west to east, specimens being larger west of Ghana and smallest towards E Ghana and in Nigeria (Bergmans 1989). *Epomops franqueti* also increases in size from west to east and therefore these species show their greatest difference in size in their zone of sympatry.

Similar Species Thirteen other species of fruit bats have simple muzzles; basal ear-patches but no other markings on head; adult ♂♂ with epaulettes; three upper and five lower cheekteeth:

Epomops dobsonii. Five thick palatal ridges. South of Equator.

E. franqueti. Third palatal ridge usually undivided. Comparatively widespread. In sympatric zone, smaller (FA ♂♂: <91 mm, FA ♀♀: <86 mm; GLS ♂♂: <51 mm, GLS ♀♀: usually <45.8 mm), but note that subadult *E. buettikoferi* and adult *E. franqueti* overlap in size and are difficult to distinguish.

Epomophorus (8 spp.). Six thick palatal ridges.

Micropteropus (2 spp.). Smaller (FA: 46–64 mm).

Nanonycteris veldkampii. Smaller (FA: 46–54 mm).

Distribution Endemic to Africa. Known mainly from the Rainforest BZ and Northern Rainforest–Savanna Mosaic (but with some records in the Guinea Savanna BZ), in West Africa. West of the Dahomey Gap, the distribution appears contiguous from Guinea just north-west of the Sierra Leone border to somewhere between the line connecting Kumasi and Takoradi in Ghana and the western border of Togo (Bergmans 1975). There are also some records from Senegal, Guinea-Bissau, Côte d'Ivoire and E Ghana, which appear isolated but might not be so. Not known from Togo or Benin, but 13 specimens taken in Nigeria indicate the existence of a possibly disjunct population east of the Dahomey Gap (Bergmans 1982).



Habitat Appears to be a moist savanna species that penetrates into lowland rainforest. It is most closely associated with patches of disturbed forest, secondary bush, cultivated land, gallery forest and the edges of areas of closed forest (Wolton *et al.* 1982, Bergmans 1988).

Abundance Locally abundant, especially in disturbed forest and along forest edge. More commonly caught in mist-nets set at ground level (0–3 m) than in canopy (>5 m). A year-round resident in Guinea savanna, with numerous recaptures of marked individuals.

Adaptations Males and ♀♀ highly dimorphic, with ♂♂ having a large palpable larynx designed for sound production. Pelvic girdle highly dimorphic. Immature ♂♂ identifiable by nearly closed and palpable pubis anterior to penis. Thumbs relatively short and weak. Clumsy when crawling along branches, so accesses fruits only by flight. Roosts by day well hidden in dense forest, ca. 8 m above ground; details not known.

Foraging and Food Primarily frugivorous. Foraging begins at dusk, distributed evenly throughout the night for ♀♀. Males more active after midnight, when calling dies down (see below). Carries fruit to feeding-roost 50–100 m from fruiting tree. Holds fruit with foot and thumb and fills large cheek-pouches to bulging with pulp. Sucks slowly to ingest only juices and small seeds before spitting out fibre and seed pellet. Feeding-roosts are used for >10 nights if fruit abundant, and accumulate large amounts of fibre pellets. Will visit *Ceiba pentandra* flowers, but is primarily frugivorous. Diet includes 15 genera (13 families; Marshall 1985) but, in Guinea Savanna, diet is dominated by large-fruited *Ficus capensis* and *F. vallis-choudae* (>20 g). In captivity, ingests ca. 150% of body mass and 1350 kJ/kg^{0.75} nightly (Thomas 1984a). In captivity, mean \pm 1 S.D. nightly consumption of food by ♂♂ was 103.7 \pm 14.2 g (n = 7) and by ♀♀ was 145.0 \pm 11.3 g (n = 10); mean consumption per unit body weight was 0.92 g/g^{bwt}; the mean through-put time was 69 \pm 14 min, and the percentage dry weight assimilated was 87% (Wolton *et al.* 1982).

Social and Reproductive Behaviour At night, ♂♂ congregate in great numbers along stretches of rivers to chorus in exploded leks (*sensu* Bradbury 1981) for hours with loud rhythmic 'kyonks'. Rhythm increases periodically from ca. 1/sec to staccato 'ki-kong-ki-kong-kaa-kaa-kaa', apparently as ♀ approaches. Males call year-round, but activity on lek varies seasonally (Thomas & Marshall 1984). During mating periods (Feb–Apr, Aug–Oct), all territories are occupied and calling begins at ca. 19:42h. Outside mating period, few ♂♂ call on bright moonlit nights and they start 90 minutes later. On dark nights, most ♂♂ call, but start 30 minutes later. Calling dies down after midnight, coinciding with increased mist-net captures. Radio-tagged bats roosted solitarily in dense foliage along edge of gallery forest. A report of large colony in Monrovia, Liberia (Kofron & Chapman 1994) is probably erroneous.

Reproduction and Population Structure Litter-size: one (n = ca. 20). In Côte d'Ivoire and Liberia, the reproductive

chronology is continuous bimodal polyoestry with postpartum oestrus. At 06° 13' N (Lamto, Côte d'Ivoire: Savanna in Rainforest–Savanna Mosaic; rain throughout year with peaks in Apr–Jun and Sep, minimal in Dec–Jan), births occur at onset of long wet season and the major increase in availability of fruit (Feb–Mar), and six months later, roughly at onset of short wet season and a minor increase in availability of fruit (Aug–Sep) (Thomas & Marshall 1984). Gestation ca. six months. Lactation (for population as a whole) for ca. 7–8 weeks after the Feb–Mar births, and ca. 13 weeks after the Aug–Sep births – the longer second period possibly due to less synchrony between ♀♀. During second month of lactation, >90% of ♀♀ are palpably pregnant, indicating occurrence of postpartum oestrus. Adult testes length constant throughout the year at 7.6 mm. Juvenile ♂♂ and ♀♀ become volant in May–Jun and Nov–Dec, with similar body mass (45–65 g) and forearm (74–76 mm). Females mature at six months and give birth at 12 months. Males below 140 g have small (<3 mm) or abdominal testes and no epaulettes. Males begin puberty at ca. nine months and by 15 months are indistinguishable from adults. At ca. 6° N (C Liberia; Rainforest BZ; rainfall unimodal, wet season Mar–Nov, dry season Dec–Feb), the reproductive chronology, and dates of events, are the same as at Lamto (Kofron & Chapman 1994).

Predators, Parasites and Diseases Ectoparasites not known (Anciaux de Faveaux 1984).

Conservation IUCN Category: Least Concern.

Measurements

Epomops buettikoferi

FA (♂♂): 96.2 (89–102) mm, n = 67

FA (♀♀): 89.1 (82–95) mm, n = 89

WS: n. d.

HB (♂♂): 162.2 (142–195) mm, n = 5

HB (♀♀): 146.0 (103–160) mm, n = 5

T: 0 mm, n = 10

E (♂♂): 25.2 (24–26) mm, n = 5

E (♀♀): 21.6 (20–23) mm, n = 5

Tib: 40.8 (38–43) mm, n = 8

HF: 21.4 (21–22) mm, n = 3

WT (♂♂): 185 (160–215) g, n = 112*

WT (♀♀): 130 (110–145) g, n = 69*

GLS (♂♂): 56.7 (50.9–61.0) mm, n = 61

GLS (♀♀): 49.7 (45.8–52.9) mm, n = 86

GWS (♂♂): 28.7 (27.0–30.3) mm, n = 23

GWS (♀♀): 26.1 (23.9–27.3) mm, n = 23

C–M¹ (♂♂): 20.7 (17.2–20.3) mm, n = 36

C–M¹ (♀♀): 18.3 (14.9–17.9) mm, n = 42

Throughout geographic range (BMNH, Rosevear 1965, Bergmans 1987)

*Côte d'Ivoire only (D. Thomas unpubl.)

Key References Bergmans 1975, 1989; Kofron & Chapman 1994; Marshall 1985; Thomas 1984a; Thomas & Marshall 1984.

Don Thomas & Mickaël Henry

Epomops dobsonii DOBSON'S EPAULETTED FRUIT BAT

Fr. Épomophore de Dobson; Ger. Dobsons Epaulettenflughund

Epomops dobsonii (Bocage, 1899). J. Sci. Math. Phys. Nat. Lisboa, ser. 2, 1: 1. Quindumbo, Benguela, Angola.

Taxonomy Originally *Epomophorus dobsonii*. Although Bergmans (1989), and also Simmons (2005), retained *dobsonii* in *Epomops*, Bergmans (1989) recognized important characters that make this form distinct from *Epomops* and closer to *Epomophorus*, and he suggested that *dobsonii* is possibly not well placed in *Epomops*. These include the strongly concave interdental palate of *dobsonii*, differences in the palatal ridges and differences in the form of the pterygoid wing of the skull. Synonyms: none. Chromosome number: not known.

Description Small, fawn to grey-brown fruit bat with anterior and posterior basal ear-patches but no other white markings on head; epaulettes on adult ♂♂; and, uniquely, five thick palatal ridges. Males on average larger than ♀♀. Pelage soft, slightly fluffy; extending along each upper arm and half-way along each forearm; mid-dorsal hairs ca. 13 mm. Dorsal pelage pale yellowish-brown to greyish-brown; some individuals with a bleached appearance; hairs pale brown with greyish-brown at base and fawn to greyish-brown at tip. Ventral pelage pale cinnamon-brown suffused with grey, pale brown or creamy-brown; usually palest on throat and belly; ♂♂ with chest distinctly darker greyish-brown. Adult ♂♂ with white epaulette on each shoulder (retracted within pouch except when displayed); adult ♀♀ apparently without shoulder pouches (n = 5). Head dog-like;

larger and more robust in ♂♂. Muzzle long and broad. Lips fleshy and moderately expansible. Ears dark brown. Eyes large. Palate with three thick interdental ridges, two thick, postdental ridges, each with two triangular projections, and three or four thin ridges (Figure 41b). Wing-membranes dark brown; attaching to second toe. Tail very short or absent.

Skull medium-sized for an African fruit bat. Rostrum relatively long for this family and for an *Epomops* (rostral length ♂♂: 46–47% of GLS, ♀♀: 43–45% of GLS); dorsal profile (viewed laterally) convex (Figure 43a) (Bergmans 1989). Postdental palate almost flat (cf. *Epomophorus* spp. of similar size). Dental formula usually $^{2121}/_{2132} = 28$.

Geographic Variation Data too limited to be conclusive.

Similar Species Thirteen other fruit bats have simple muzzles; basal ear-patches but no other markings on head; three upper and five lower cheekteeth:

Epomops franqueti and *E. buettikoferi*. Three thick palatal ridges.

Epomophorus (8 spp.). Six thick palatal ridges.

Micropteropus (2 spp.). Smaller (FA: 46–64 mm).

Nanonycteris veldkampii. Smaller (FA: 46–54 mm).

Distribution Endemic to Africa. Widespread across the Zambezian Woodland BZ between 8 and 18°S, from Angola to Tanzania and Malawi (Bergmans 1989). Outlying records north of 8°S in Tanzania and Rwanda (Bergmans 1989) are currently considered questionable (W. Bergmans pers. comm.). Predicted to occur east of L. Malawi.

Habitat Mainly wetter miombo woodland and mosaics of the above with adjacent types of vegetation. Also afro-montane vegetation at 1890 m at Kibweli, Tanzania, and (if this dubious record proves valid) the mosaic of East African evergreen bushland and secondary *Acacia* wooded grassland at Rubona, Rwanda. Bergmans (1989) expects *E. dobsonii* to occur in miombo woodland bordering the eastern side of L. Malawi and in the tongue of this vegetation extending northwards to L. Victoria. The distribution appears restricted by the belts of shrublands and desert vegetation lining the Atlantic coast in the west, by rainforest in the north and by drier vegetation in the south, south-east and east.

Abundance Moderately rare in collections, but occurs in poorly surveyed areas and is perhaps more common than the records indicate (see also below).

Remarks Litter-size: one or commonly two according to Hill & Smith (1984) but the exact frequency of occurrence of twins is not known. Three ♀♀ caught at Mt Soque in Angola at end of Aug were either pregnant or lactating (Mickleburgh *et al.* 1992). Apparently there is no other information about the biology of this species. There is as yet no evidence that *E. dobsonii* has an exploded lek mating system (cf. *E. buettikoferi* and *E. franqueti*); unlike these species, it has not been reported to be a nocturnal pest because of the noise made by aggregations of displaying ♂♂. Also, Bradbury (1981) suggests that lekking is most likely to evolve in species that are common because territoriality and female-defence become increasingly less viable as population density increases. It would be most interesting to know if *E. dobsonii* is really as uncommon as it appears to be, and if it exemplifies a mating system very different to that of the other two species of *Epomops*. Possibly lekking and exploded lekking are more suited to rainforest habitats than to savannas. Lagos bat virus has been isolated from *E. dobsonii* (Calisher *et al.* 2006).

Conservation IUCN Category: Least Concern.

Measurements

Epomops dobsonii

FA (♂♂): 87.6 (84–92) mm, n = 13*



Epomops dobsonii

FA (♀♀): 83.2 (80–88) mm, n = 15*

WS: n. d.

HB (♂♂): 163.7 (138–185) mm, n = 9

HB (♀♀): 138.0 (130–145) mm, n = 7

T: 0, 10, 12 mm, n = 3

E: 26.8 (24–30) mm, n = 16

Tib (♂♂): 34.3 (34–35) mm, n = 3†

Tib (♀♀): 30.9 (30–33) mm, n = 3†

HF: n. d.

WT (♂): 120 g, n = 1

GLS (♂♂): 53.8 (52.4–55.3) mm, n = 14*

GLS (♀♀): 46.7 (45.6–49.4) mm, n = 13*

GWS (♂♂): 26.4 (25.2–26.9) mm, n = 7*

GWS (♀♀): 24.4 (23.6–25.4) mm, n = 7*

C–M¹ (♂♂): 15.8 (14.5–16.7) mm, n = 6*

C–M¹ (♀♀): 14.1 (13.6–14.6) mm, n = 8*

Throughout geographic range (BMNH, IRSN, RMCA and literature)

*Bergmans 1989

†Angola only (Hill & Carter 1941)

Key Reference Bergmans 1989.

Meredith Happold

Epomops franqueti FRANQUET'S EPAULETTED FRUIT BAT

Fr. Épomophore de Franquet; Ger. Franquets Epaulettenflughund

Epomops franqueti (Tomes, 1860). Proc. Zool. Soc., Lond. 1860: 54. Gabon.

Taxonomy Originally *Epomophorus franqueti*. Synonyms: *comptus*, *streptitans*. Subspecies: none recognized by Bergmans (1989) but see Geographic Variation. Apparently closely related to *Epomops*

buettikoferi. Chromosome number (Cameroon): 2n = 36; aFN = 66 (Haiduk *et al.* 1981); (Gabon): 2n = 35; aFN = 66 (Primus *et al.* 2006).

Description Small to medium-sized, fawn to reddish-brown fruit bat with anterior and posterior basal ear-patches but no other white markings on head; epaulettes on adult ♂♂; three thick palatal ridges, which are usually undivided. Males and ♀♀ similar in colour; ♂♂ on average larger than ♀♀. Pelage soft, slightly fluffy, extending along each upper arm and half-way along each forearm; mid-dorsal hairs ca. 8 mm. Dorsal pelage fawn, pale brown or medium to dark reddish-brown; hairs unicoloured. Shoulders and nape sometimes greyish-brown. Ventral pelage pale brown often merging into white on abdomen and chest. Adult ♂♂ with white epaulette on each shoulder (retracted within pouch except when displayed); ♀♀ with a small, inconspicuous invagination on each shoulder containing pale brown hairs ca. 12 mm long. Head dog-like; larger and more robust in ♂♂. Muzzle moderately long and broad; lips and cheeks fleshy and expansible (especially in ♂♂). Ears dark brown. Eyes large. Palate with three thick ridges (1–2 undivided, 3 usually undivided [cf. *E. buettikoferi*]), and 5–8 thin, narrowly divided, finely serrated ridges (Figure 41c). Wing-membranes medium to dark brown; attaching to second toe. Tail very short or absent.

Skull (Figure 42) medium-sized for an African fruit bat. Rostrum of medium relative length for this family but short for an *Epomops* (rostral length ♂♂: 39–43% of GLS, ♀♀: 37–40% of GLS); dorsal profile (viewed laterally) slightly concave or straight, very rarely slightly convex (Figure 43c) (Bergmans 1989). Postdental palate almost flat (cf. *Epomophorus* spp. of similar size). Dental formula usually $2^{121}/_{2132} = 28$ but outer upper incisor often absent.

Geographic Variation A western subspecies (*E. f. strepitans*) was described by Andersen (1912a) but Bergmans (1989) was unable to delimit subspecific ranges and predicted that the species has a continuous distribution with clinal increase in body and skull dimensions from west to east: e.g. in West Africa (Ghana and Côte d'Ivoire), FA (♂♂): 87.6 (83.5–93.9) mm, n = 74, FA (♀♀): 81.6 (76.5–87.1) mm, n = 78; GLS (♂♂): 46.8 (43.3–49.9) mm, n = 73, GLS (♀♀): 41.9 (37.8–45.3) mm, n = 71; in central Africa (Gabon to Uganda), FA (♂♂): 95.6 (89.9–100.9) mm, n = 51, FA (♀♀): 89.3 (84.2–93.8) mm, n = 53; GLS (♂♂): 50.7 (47.4–52.4) mm, n = 39, GLS (♀♀): 45.2 (42.6–47.8) mm, n = 43 (data derived from Bergmans 1989). In contrast, *E. buettikoferi* decreases in size from west to east so these species show their greatest difference in size in their zone of sympatry.

Similar Species Thirteen other species of fruit bats have simple muzzles; basal ear-patches but no other markings on head; three upper and five lower cheekteeth:

Epomops dobsonii. Five thick palatal ridges.

E. buettikoferi. Third palatal ridge usually divided. West Africa only, between 14°W and 10°E. In sympatric zone, larger (FA ♂♂: 92–102 mm, FA ♀♀: 89–96 mm; GLS ♂♂: 53.8–60.2 mm, GLS ♀♀: 45.8–56.6 mm). Note: *E. franqueti* from further east tend to be larger on average than those from the sympatric zone.

Epomophorus (8 spp.). Six thick palatal ridges.

Micropteropus (2 spp.). Smaller (FA: 46–64 mm).

Nanonycteris veldkampii. Smaller (FA: 46–54 mm).



Epomops franqueti

Distribution Widespread in the Rainforest BZ and Rainforest–Savanna Mosaics with very marginal extensions into the Guinea Savanna BZ and Zambezian Woodland BZ. Recorded from Côte d'Ivoire to L. Victoria and southwards to Angola and S DR Congo. Previous reports from Guinea are erroneous (J. Fahr, in Simmons 2005). Map based on Bergmans (1989).

Habitat Mainly recorded from wetter and drier types of lowland rainforest, but also recorded from afromontane vegetation and mosaics of rainforest with woodland and grassland, and occasionally from *Isoberlinia* woodland and wetter miombo woodland (Bergmans 1989). In the Guinea Savanna and Zambezian Woodland BZs, they probably reside in relict and riverine forests. In Gabon, various types of secondary forest are preferred to primary forest, and hence the habitat is patchy mosaic (Bradbury 1981). Often caught in clearings close to dense undergrowth, and in gardens.

Abundance Common in Nigeria (Happold 1987), Gabon (Brosset 1966) and DR Congo (Lang & Chapin 1917b). Probably fairly common in the Rainforest BZ, but abundance apparently varies with seasonal changes in abundance of fruit and flowers, at least in some areas.

Adaptations Aspect ratio low; wing-loading very high. Flight slow and manoeuvrable. Commonly flies through the canopy and close to the ground (Jones 1972). Can take off from the ground (Brosset 1966). Lands neatly without crashing into vegetation. Roosts in dense foliage of large trees such as *Terminalia*, hanging freely from small branches usually 4–6 m above ground. Sometimes roosts in low bushes. Often roosts near or over water. Monthly home-ranges for five ♀♀ in Gabon ranged from 1.2 to 1.6 km in diameter (Bradbury 1981). Based on differences in foraging strategies, ♂♂ are likely to have much larger home-ranges. When individuals were exposed to decreased ambient temperatures, their body temperatures declined

generally in accordance with ambient temperature: the T_A averaged mostly 10 °C greater than the T_B (cf. *Eidolon helvum*, *Micropteropus pusillus*) (Jones 1972).

Foraging and Food Frugivorous. Sometimes congregates in large numbers at particular sources of food. Takes fruits from canopies of trees and also collects fallen fruits from the ground (Brosset 1966). Whole fruits, or large pieces, are often engulfed in the lips and carried to a perch 200 m or more away. At the perch, food is held by a hindfoot, the mouth, wrists or in the pocket formed by the wing-membrane when a wrist is flexed. Thumbs are rarely used to hold food, but individuals often hold onto a branch or leaf with one thumb and one hindfoot while feeding. Lips and tongue squeeze and suck out the juice, which is swallowed; pulp and seeds discarded. This species helps to disperse seeds but is not known to assist in pollination. In Equatorial Guinea (Rio Muni), based on direct observations and also captures in mist-nets set 0–2 m and 4–6 m above ground, Jones (1972) noted that *E. franqueti* forages and roosts in the same habitat, and at the same time, as *Eidolon helvum* and *Micropteropus pusillus*, but competition is reduced because the species for the most part utilize different strata – of the netted fruit bats, 100% of *Eidolon*, 73% of *Epomops* and only 10% of *Micropteropus* were caught in the higher nets.

As in *Hypsignathus monstrosus*, the foraging strategies and diets of ♂♂ and ♀♀ are different (Bradbury 1981). In Gabon, 36% of the diet of ♀♀ is fruits of *Solanum torvum*, which produces fruit throughout the year but only 1–2% of fruits are ripe on any one night and the quality of this food is comparatively poor. Females fly to the same locations on consecutive nights, take a few fruits from each plant and then move on to other plants. Twenty-one per cent of the diet is figs from *Ficus* spp., which are hard to locate and produce fruit for only 5–10 days at intervals of 1–3 years, but fruiting trees produce abundant figs of high quality. The remaining 43% of the diet is *Musanga*, guavas and bananas. In contrast, for ♂♂, figs comprise a much larger fraction of the diet. For implications of these differences, see Bradbury (1981) and profile of *Hypsignathus monstrosus*. In Equatorial Guinea, *E. franqueti* has been seen most frequently feeding on fruits of *Terminalia*, but it also ate fruits of *Artocarpus*, *Annona* and mangoes (Jones 1972). It also eats fruits of *Persea* and *Cecropia*, and captive bats eat plantains and avocados (Bradbury 1981, Mickleburgh *et al.* 1992).

Social and Reproductive Behaviour Usually roosts singly, very occasionally in twos, rarely in threes (Rosevear 1965, Jones 1972). Captive individuals roost as far from each other as possible (Jones 1972). *Epomops franqueti* has an exploded lek mating system (*sensu* Bradbury 1981). In Gabon, ♂♂ typically hold territories ca. 200 m or more in diameter. These are large enough to contain significant amounts of resources required by ♀♀, but the ♂♂ also place their territories over sites in which roosting ♀♀ and food resources are scarce or absent (Bradbury 1981). These territories are clustered (not uniformly dispersed as in resource-based territories). Adult ♂♂ display within their territories and the territories are presumably selected not for their resources but for qualities that optimize the effectiveness of the displays while minimizing opportunities for predation. The territories are, in some ways, similar to the sites within classical leks from which male *Hypsignathus* display (see profile). However, the territories of *E. franqueti* are very much

larger and are not as tightly clustered as sites held by ♂♂ within classical leks. For this reason, they are known as exploded leks. In Gabon, the gaps between exploded leks range from 2 to 4 km. While displaying, ♂♂ beat their half-open wings, display their epaulettes and make a loud metallic ‘honk’ at intervals of a second or less. At a distance, this very distinctive call sounds like a cracked bell; close to, it has been described as ‘kurnk’ or ‘kyurnk’ (Lang & Chapin 1917b). Calling-displays occur throughout the night. The call repetition-rate usually increases rapidly just before calling ceases.

Reproduction and Population Structure Litter-size: one. In equatorial Uganda, the reproductive chronology is continuous bimodal polyoestry with postpartum oestrus (Okia 1974b). Gestation 5–6 months. Females are in reproductive synchrony; births occur in Mar and Sep. Young probably not weaned until a few weeks before the next birth. The presence of lactating ♀♀ in almost all months may have misled earlier observers into thinking reproduction was aseasonal. In S Congo, seasonal bimodal polyoestry, with births in Feb and Sep, was proposed by Bergmans (1979) but without corroborative evidence.

Predators, Parasites and Diseases Ectoparasites include a bat-fly *Basilia tenuispina* (Diptera: Nycteribiidae) and a mite *Teinocoptes epomophori* (Acari: Teinocoptidae) (Anciaux de Faveaux 1984). Rift Valley fever virus been isolated from *E. franqueti* (Addy *et al.* 1978).

Conservation IUCN Category: Least Concern.

Measurements

Epomops franqueti

FA (♂♂): 91.7 (84–101) mm, n = 160*

FA (♀♀): 85.5 (77–96) mm, n = 192*

WS (d): ca. 600 mm

HB (♂♂): 140 (110–165) mm, n = 34

HB (♀♀): 155 (115–180) mm, n = 22

T: 0–1 mm, n = 21

E: 24 (23–27) mm, n = 47

Tib: 34.1 (32–38) mm, n = 29

HF (♂♂): 25.8 (24–28) mm, n = 6

HF (♀♀): 23.1 (21–25) mm, n = 14

WT (♂♂): 92–172 g, n = 47*

WT (♀♀): 61–130 g, n = 45*

GLS (♂♂): 48.5 (43.7–53.3) mm, n = 144*

GLS (♀♀): 43.4 (37.8–47.8) mm, n = 161*

GWS (♂♂): 27.8 (25.8–30.0) mm, n = 45*

GWS (♀♀): 25.6 (21.2–27.8) mm, n = 52*

C–M¹ (♂♂): 16.5 (14.7–17.9) mm, n = 43*

C–M¹ (♀♀): 14.7 (12.2–16.5) mm, n = 54*

Throughout geographic range (BMNH, RMCA and literature)

*Bergmans 1989

Specimens are larger in the central African part of the range (see Geographic Variation); means biased by uneven sampling in different parts of the range

Key References Bergmans 1989; Jones 1972; Okia 1974b.

Meredith Happold

GENUS *Hypsignathus*

Hammer-headed Fruit Bat

Hypsignathus H. Allen, 1861. Proc. Acad. Nat. Sci. Philadelphia, p. 156. Type species: *Hypsignathus monstrosus* H. Allen, 1861.

Hypsignathus is a monotypic genus endemic to Africa. Diagnostic characters: white basal ear-patches (sometimes inconspicuous) but no other white markings on the head; FA: >112 mm; head with humped nose and truncated muzzle, which ends in a fleshy plate; usually three upper and five lower cheekteeth (very occasionally four upper cheekteeth) (Table 11, p. 228). Palatal ridges as in Figure 44. The single species is the largest bat on the African mainland, and shows more sexual dimorphism than any other bat in the world (Figure 44). The genus is based mainly on the extraordinary anatomy of the skull (Figure 44), lips, dentition, vocal chords and air-sacs of the ♂ (see species profile). These characters are associated with the production of such extremely loud vocalizations that this species is sometimes considered to be one of Africa's greatest nocturnal pests. The vocalizations are part of courtship displays carried out by ♂♂ at traditional sites referred to as classical leks (see species profile); no other African bat is known to have a classical lek mating system although two species of *Epomops* have an exploded lek mating system, which has some of the characteristics of classical lekking and may represent an intermediate stage in the evolution of classical

Hypsignathus monstrosus
male.

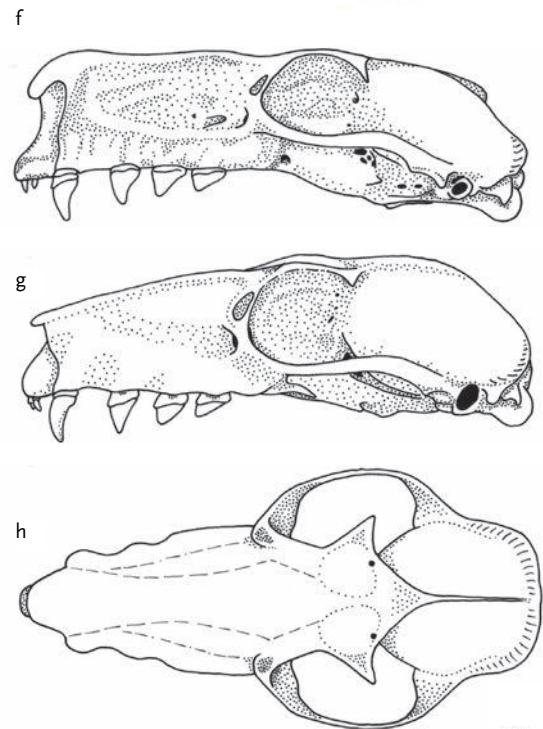
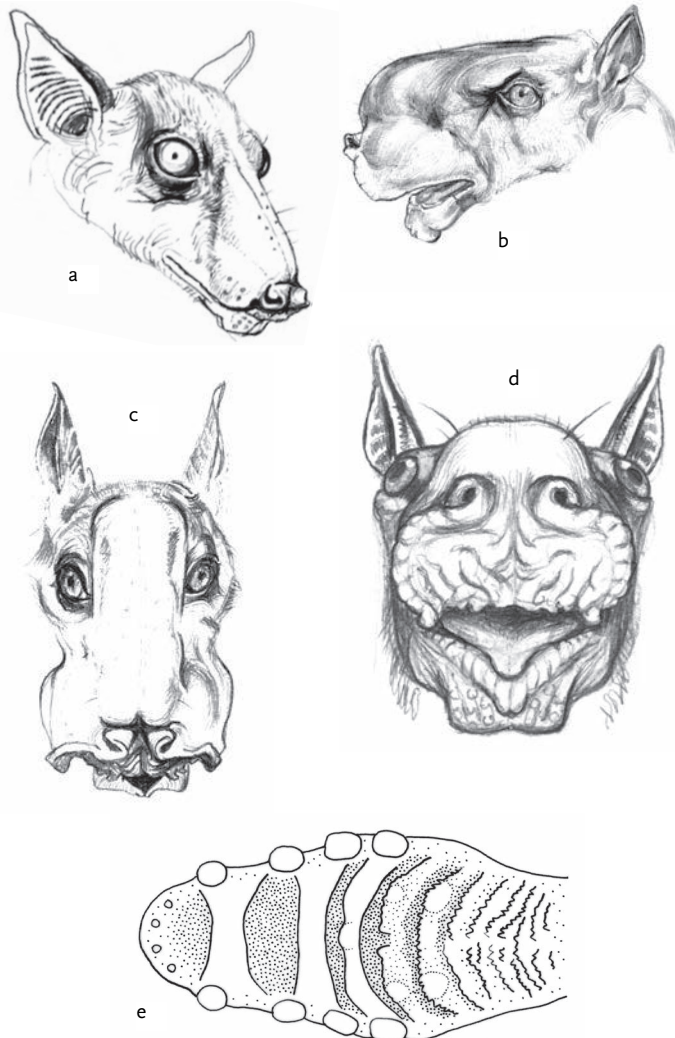


Figure 44. *Hypsignathus monstrosus*. Lateral views of head of (a) adult ♀ and (b) adult ♂. (c) and (d) Frontal views of ♂ head. The latter shows the mobile carunculated flanges surrounding the sound amplifying lips, here constricted around extruded spatulate tongue. (e) Palatal ridges (from photo in Bergmans 1989). (f) Lateral view of skull of adult ♂ (BMNH 98.10.7.2). (g) Lateral view of skull of adult ♀ (RMCA 93-079-M-0367). (h) Dorsal view of skull of adult ♂ (BMNH 98.10.7.2).

lekking (Bradbury 1981). Based on its anatomy, especially that of the larynx, *Hypsignathus* appears to be more closely related to *Epomops* than to *Epomophorus* and other genera (Andersen 1912a, Bergmans 1989). However, von Zeller (1984) discusses differences in the topography of the thoracic organs of *Hypsignathus* and *Epomops*, which suggest that the enlargement of the larynx took place independently in the phylogeny of both genera. The karyotypes of *Hypsignathus* and *Epomops franqueti* cannot be distinguished, but their G- and C-bands differ in two aspects (Haiduk *et al.* 1980, 1981). Males have the unusual sex chromosome combination of XO instead of XY (Bogart *et al.* 1977).

Hypsignathus monstrosus HAMMER-HEADED FRUIT BAT

Fr. *Hypsignathe monstrueux*; Ger. Hammerkopf-Flughund

Hypsignathus monstrosus H. Allen, 1861. Proc. Acad. Nat. Sci. Phil., p. 156. Gabon.

Taxonomy Synonyms: *labrosus*, *macrocephalus*. Subspecies: none. Chromosome number (DR Congo, Gabon): $2n = 36$; $aFN = 68$ (Haiduk *et al.* 1980, Primus *et al.* 2006).

Description Large, dark brown fruit bat with pale, woolly mantle; anterior and posterior white basal ear-patches, which are sometimes inconspicuous, but no other white markings on head; no epaulettes; easily recognized by its size and uniquely hammer-shaped head (Figure 44). The largest of all bats on the mainland of Africa. Males and ♀♀ similar in colour; ♂♂ almost twice as heavy as ♀♀, usually larger, and morphologically very different. Pelage soft, extending dorsally along each upper arm and for some distance along each forearm; mid-dorsal hairs ca. 13 mm. Dorsal pelage sepia brown (sometimes suffused with pale greyish-brown) becoming rusty-brown on rump and legs; hairs unicoloured or with pale greyish-brown at tip. Shoulders and neck with mantle of longer, woollier, pale greyish-brown pelage. Ventral pelage slightly paler than dorsal pelage with a whitish collar joining the mantle. Head (especially in ♂♂) large with greatly expanded, humped muzzle, which, instead of tapering, ends bluntly in a flat, fleshy plate formed by the upper and lower lips (see Adaptations). Females with considerably less monstrous heads! Ears blackish-brown, triangular. Eyes very large. Palate with three thick ridges that have wide extremities and narrower centres, a fourth, partly postdental, weakly serrated ridge, which has a wide, cushion-like pad near each extremity and a shallow, concave middle, a fifth ridge, which is similar to the fourth but more strongly serrated and less shallow in the middle, and five or six thin, serrated, irregular ridges, which are sometimes divided (Figure 44c). Tongue with expanded tip (Figure 35a). Wings blackish-brown with woolly brown dorsal pelage extending along the forearm and a strip of whitish pelage on the ventral surface; wing-membranes attaching to second toe. No tail. For further information, see Langevin & Barclay (1990).

Skull (Figure 44) larger and more robust than in any other African fruit bat. Rostrum massive, relatively long, very deep but laterally compressed, especially in ♂♂. Basicranial axis markedly deflected. Interdental palate concave from side to side and from front to back, but postdental palate lacks the raised sides. Dental formula usually $^{2121}/_{2132} = 28$ but an extra upper premolar (P^1) is present very occasionally. Inner ridges of posterior upper premolar, upper molar, posterior lower premolar and lower molars are much more

Hypsignathus was placed in the *Epomophorus* section of Andersen (1912a) and in the subfamily Epomophorinae (tribe Epomophorini) of Bergmans (1997). Apparently, the phylogenetic relationships between *Hypsignathus* and other genera of fruit bats have not yet been investigated using genetic data. Morphology suggests affinities with typical *Epomops* (Andersen 1912a).

The single species is *Hypsignathus monstrosus*.

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developed than in *Epomophorus*, and the median furrows of these teeth are correspondingly deepened.

Geographic Variation None recorded.

Similar Species None.

Distribution Endemic to Africa. Found throughout most of the Rainforest BZ and some distance into the surrounding Rainforest–Savanna Mosaics. Also a few records in the Guinea Savanna, Zambezian Woodland and Afromontane–Afroalpine BZs. Recorded from Sierra Leone to W Kenya, and south-westwards to NW Angola. Map based on Bergmans (1989).

Habitat Wetter and drier types of lowland rainforest, swamp forest and mosaics of these forests with secondary grasslands (Bergmans 1989). Records outside the rainforest zone are uncommon, but



Hypsignathus monstrosus

riverine forests appear to serve as passageways into woodland savannas such as *Isoberlinia* woodland to the north and miombo woodland to the south (Bergmans 1989). Relict forests and afromontane vegetation are also inhabited and there are some records from palm forests and a mangrove swamp. The rare records from savanna habitats are perhaps those of vagrants. Not recorded above 1800 m.

Abundance Said to be common in the Rainforest BZ, although local abundance is probably determined by the availability of ripe fruit. Rare outside the rainforest.

Adaptations Aspect ratio low; wing-loading exceptionally high (Norberg & Rayner 1987), but this needs confirmation. Flies directly up to 10 km at a time to find food, but can also manoeuvre and hover moderately well. Cannot take off from the ground. Typically roosts by day in the forest canopy 20–30 m above ground. Hangs from exposed branches beneath an umbrella of dense foliage, and shows no preference for particular species of trees. Also recorded roosting in undergrowth (Lang & Chapin 1917b), a cave (Nowak 1999, but not confirmed), among rocks (Sanderson 1939) and in a hut (Van Deusen 1968), but these roosts are probably unusual. Roost-fidelity is low (Bradbury 1977). Individuals typically change roosts after 5–9 days; some stay in one area and move only 50–100 m from one roost to the next while others move 1–10 km away. The marked sexual dimorphism and peculiar morphology of the head in ♂♂ is associated with the production of calls that attract ♀♀ (see Social and Reproductive Behaviour). These calls – extremely loud monotonous honking – are produced in a greatly enlarged larynx and amplified by resonating chambers. The larynx is one-half the length of the vertebral column and fills most of the thoracic cavity. The resonating chambers are a pair of inflatable pharyngeal air-sacs that open into a large sinus in the humped muzzle, and the gaping mouth, which has expansible cheeks and widely flaring lips (Lang & Chapin 1917b, von Zeller 1984). The tongue is large and powerful, with backward-pointing papillae; used for rasping fruit so juice can be extracted. The stomach and intestines are long and narrow with many folds in the interior wall to facilitate digestion of fruit. A captive individual drank regularly by flying low and scooping water into its mouth.

Foraging and Food Feeds mainly on the fruits of trees in forests, secondary growth and old plantations. Forages mainly in the canopy, but commuting may be above the canopy or as low as 1–4 m above the ground. There are two foraging strategies (Bradbury 1977, 1979, 1981). Females, subadults and non-displaying adult ♂♂ forage along regular routes and exploit dependable sources of food – the fruits of *Anthocleista* trees – although these are not of the highest quality. These trees grow in monospecific stands well known to the bats and, during each mating season of *H. monstrosus*, they bear thousands of fruits of which less than 1% are ripe and maximally nutritious at any one time. In contrast, sexually active ♂♂ fly from their roost to their leks (see below) where they display for 3–4 hours before flying directly to, or in search of, sources of particularly high-quality food such as figs *Ficus* spp. Fig trees bear small crops for ca. 10 days, do not fruit again for 6–24 months, and are randomly distributed in the forest. They are hard to find but, once located, provide a substantial supply of high-quality food for several days. They are usually ca. 7 km

away but may be up to 10 km away. Many sexually active ♂♂ forage until dawn and then return to their roosts: others return to the lek.

Diet: includes the fruits of *Ceiba*, *Musanga*, *Chlorophora*, *Solanum*, *Adenia* and especially figs *Ficus* and fruits of *Anthocleista*, and also bananas, guavas, mangoes and soursops (Lang & Chapin 1917b, Rosevear 1965, Bradbury 1977, Fujita & Tuttle 1991 and Thomas 1982 in Mickleburgh *et al.* 1992). Faeces usually contain seeds, suggesting that these bats play an important role in the dispersal of rainforest trees. Observed to attack chickens (one bat collected; identity confirmed), and to eat scraps of meat and the skinned carcasses of small birds that a museum collector frequently left lying on the ground in a well-lit area outside his house in Gabon (Van Deusen 1968). A bat would hover briefly over the carcass, reach down and seize it in the mouth, and carry it off. One individual, which regularly roosted during the day in a nearby hut, carried carcasses to this roost during the night and ate them there. It is not known if *H. monstrosus* regularly eats meat, but the observer suggests that birds that roost in the open in rainforests could provide a readily available source of food for this fruit bat.

Social and Reproductive Behaviour Bradbury (1977) conducted an outstanding study of the behaviour of *H. monstrosus* in NE Gabon. Both ♂♂ and ♀♀ very often roost singly. Groups are usually small (4.4 ± 2) but sometimes include up to 25 individuals, and at any particular roost, group-size is extremely labile. Groups can include one or both sexes and all age-classes, and apparently group-composition is also labile. A distance of 10–15 cm is maintained between roosting bats (except for ♀♀ with young), and ♂♂ often roost at the periphery of the group. Behaviour at roosts is minimal. The bats often defecate early in the day, then rest or sleep until dusk. They do not vocalize, groom each other or squabble over positions, and ♂♂ do not approach the ♀♀. At sunset, all of the bats groom themselves and then leave quietly and independently to forage or visit a lek.

There are two breeding seasons per year, with mating occurring in two periods of 1–3 months' duration. During these periods, aggregations of 20–135 ♂♂ gather in trees along rivers and streams, in special arenas (leks) that are usually ca. 40 m wide and 400–1600 m long. Males compete aggressively for display-territories (ca. 10 m in diameter) within these arenas, and then carry out a display of honking and wing-beating, which attracts ♀♀. Females fly along the arena, choose a ♂ and may land beside him. If this happens, the ♂ makes a 'staccato-buzz' call and may copulate immediately. The ♀ then departs and the ♂ resumes his display. This behaviour meets the specifications of a mating-system referred to as classical lekking, which is defined by the following criteria. (1) Males do not participate in parental care. (2) Males aggregate in particular areas (leks) and establish display-territories there, which are very much smaller than their home-ranges. (3) Display-territories contain no resources for ♀♀ other than access to a ♂. (4) Females have the opportunity to select a ♂ to mate with, and all matings occur at the lek. Lekking (which occurs in some birds and some other mammals) is often associated with 'secondary' features, and these also occur in *H. monstrosus*. (a) There is marked sexual dimorphism. (b) Males mature much later than ♀♀ (18 months versus six months). (c) Lek-locations are traditional. (d) Displays are extremely ritualized. (e) The mating success of ♂♂ in any one lek is highly skewed (in *H. monstrosus*, the top 6% achieves 79% of the total matings). (f) The most successful ♂♂ are found in a few particular centres within each lek.

Reproduction and Population Structure Litter-size: one. At 00°04'N (Makokou, Gabon), the reproductive chronology is continuous bimodal polyoestry with postpartum oestrus (Bradbury 1977). Each ♀ has two litters/year; gestation 5–6 months. Females in reproductive synchrony. Parturition occurs in the two dry seasons (Dec–Feb and Jun–Jul) so pregnancy and lactation occur mainly in the wet seasons. Data from elsewhere are minimal and inconclusive but consistent with bimodal polyoestry. Sex ratio at birth 1 : 1.

Predators, Parasites and Diseases Ectoparasites include a bat-fly *Dipseliopoda arcuata* (Diptera: Nycteribiidae) and mites *Ancystropus aethiopicus* (Acari: Spinturnicidae), *Mycteronyssus polli* (Acari: Gastronyssidae), *Teinocoptes auricularis* (Acari: Teinocoptidae) (Anciaux de Faveaux 1984).

Conservation IUCN Category: Least Concern.

Measurements

Hypsignathus monstrosus

FA (♂♂): 132.5 (120–139) mm, n = 80*

FA (♀♀): 120.4 (112–127) mm, n = 64*

WS (d) (♂♂): ca. 750 mm

HB (♂♂): 228 (160–297) mm, n = 9

HB (♀♀): 197 (165–255) mm, n = 15

T: 0 mm, n = 17

E (♂♂): 35 (30–41) mm, n = 9

E (♀♀): 31 (25–38) mm, n = 13

Tib (♂♂): 56.0 (54–60) mm, n = 4

Tib (♀♀): 52.0 (49–55) mm, n = 3

HF (♂♂): 38.1 (36–40) mm, n = 10

HF (♀♀): 32.0 (25–36) mm, n = 6

WT (♂♂): 376 (290–419) g, n = 8*

WT (♀♀): 249 (207–302) g, n = 13*

GLS (♂♂): 72.6 (67.9–74.0) mm, n = 70*

GLS (♀♀): 59.9 (56.8–63.8) mm, n = 46*

GWS (♂♂): 36.5 (32.9–38.7) mm, n = 25*

GWS (♀♀): 32.8 (31.6–34.7) mm, n = 19*

C–M¹ (♂♂): 23.2 (21.8–24.7) mm, n = 29*

C–M¹ (♀♀): 20.3 (18.4–21.2) mm, n = 36*

Throughout geographic range (BMNH, RMCA, ZFMK and literature)

*Bergmans 1989

Key References Bergmans 1989; Bradbury 1977, 1979; Lang & Chapin 1917b; Langevin & Barclay 1990.

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GENUS *Lissonycteris*

Angolan Soft-furred Fruit Bat

Lissonycteris K. Andersen, 1912. Cat. Chiroptera Brit. Mus. I. Megachiroptera 23: 814. Type species: *Cynonycteris angolensis* Bocage, 1898.

Lissonycteris is currently considered to be a monotypic genus. It is endemic to Africa. Diagnostic characters: no white basal ear-patches and no white markings on the face; FA: 68–90 mm, adult

♂♂ with ruff of stiff hairs around throat; toes partly webbed (Figure 45), five upper and six lower cheekteeth; M² not greatly reduced (Table 11 p. 228). The palatal ridges and craniodental

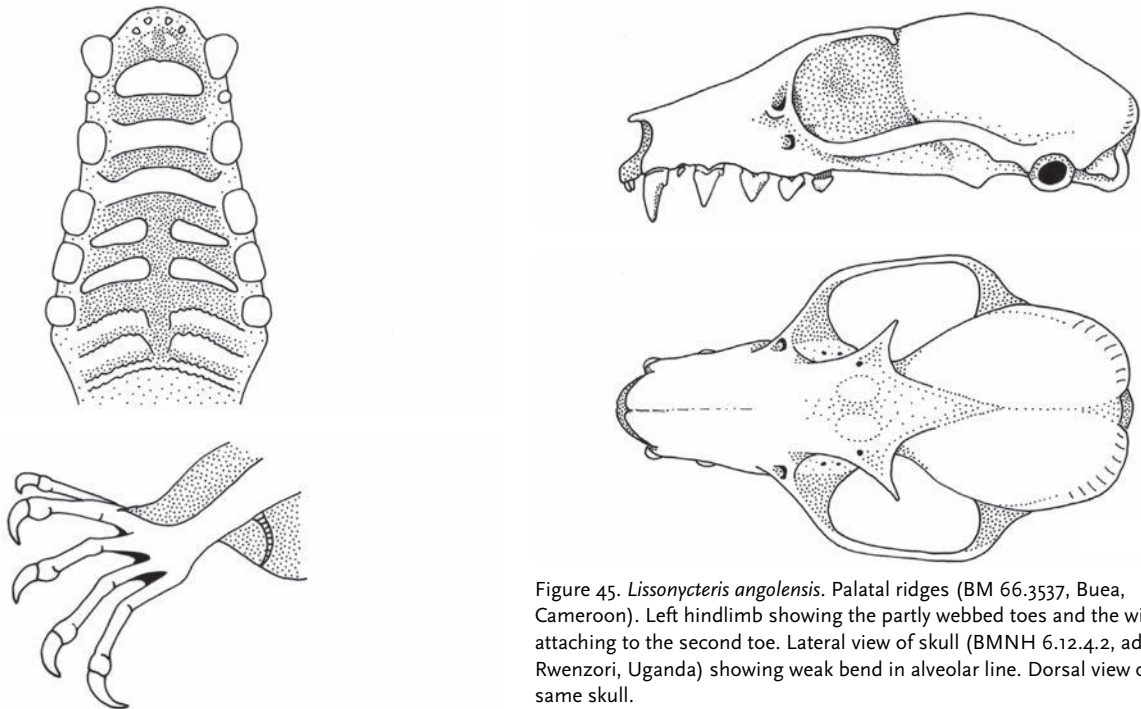


Figure 45. *Lissonycteris angolensis*. Palatal ridges (BM 66.3537, Buea, Cameroon). Left hindlimb showing the partly webbed toes and the wing attaching to the second toe. Lateral view of skull (BMNH 6.12.4.2, adult ♂, Rwenzori, Uganda) showing weak bend in alveolar line. Dorsal view of same skull.

characters of *Lissonycteris* are shown in Figure 45. *Lissonycteris* has longer silkier pelage than other fruit bats. It and the two endemic species of *Rousettus* are the only African fruit bats that normally roost in caves but, unlike *Rousettus* which roost in dark caves and orientate acoustically with a simple form of echolocation (as well as with vision), *Lissonycteris* uses only the eyes and it roosts in caves that are dimly lit. The tiny web between the toes, and the ruff of specialized hairs around the throat in adult ♂♂, are characters that *Lissonycteris* shares with *Myonycteris*.

Lissonycteris was proposed as a subgenus of *Rousettus* by Andersen (1912a) and then raised to generic status by Schwartz (1920). Subsequently, *Lissonycteris* has been considered synonymous with *Rousettus* by Koopman (1975), as a subgenus of *Rousettus* by Hayman & Hill (1971) and Koopman (1993), and as a synonym (or perhaps subgenus) of *Myonycteris* by Peterson *et al.* (1995). In contrast, the generic status of *Lissonycteris* has been maintained by Novick (1958a), Lawrence & Novick (1963), Rosevear (1965), Haiduk *et al.* (1981), Kirsch *et al.* (1995) and many others (see Bergmans 1997) and by Simmons (2005). Based on his own observations, and those of several other authors (including Benedict 1957, Lawrence & Novick 1963 and Kingdon 1974), Bergmans (1997) reported that *Lissonycteris* differs

from *Rousettus* in its skull morphology, dentition, its webbed toes, ruff, the scales of its hairs, its karyotype and chromosomal evolution, its lack of acoustic orientation and its feeding, roosting, locomotion and social behaviour. Bergmans (1997) considers that *Lissonycteris* and *Myonycteris* are more closely related to each other than each is to *Rousettus*. Kirsch *et al.* (1995), on the basis of DNA hybridization, also concluded that *Lissonycteris* is not part of *Rousettus*. Juste *et al.* (1997), on the basis of molecular data, concluded that *Lissonycteris angolensis*, *Myonycteris torquata* and *M. brachycephala* were a monophyletic group, and that the maintenance of *Lissonycteris* within the genus *Rousettus* was not sustainable. Consequently, *Lissonycteris*, which (as subspecies of *Rousettus*) was placed in the *Rousettus* section of Andersen (1912a), was placed in the subfamily Epomophorinae (tribe Myonycterini) by Bergmans (1997). Subsequently, other phylogenetic studies have supported the close relationship between *Lissonycteris* and *Myonycteris* (e.g. Álvarez *et al.* 1999, Giannini & Simmons 2003, 2005).

Following Bergmans (1997) and Simmons (2005), *Lissonycteris* is provisionally considered here to contain only one species, *L. angolensis*.

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Lissonycteris angolensis ANGOLAN SOFT-FURRED FRUIT BAT

Fr. Lissonyctère d'Angola; Ger. Angolanischer Samtfell-Flughund

Lissonycteris angolensis (Bocage, 1898). J. Sci. Math. Phys. Nat. Lisboa, ser. 2, 5: 133. Pungo Andongo, Cahata, Quibula, Angola.

Taxonomy Originally *Cynonycteris angolensis*. Synonyms: *crypticola*, *goliath*, *petraea*, *ruwenzorii*, *smithii*. Subspecies: five. Peterson *et al.* (1995) and Cotterill (2001a) consider *smithii* to be a distinct species, but Kock *et al.* (2002) agrees with Bergmans (1997) that *smithii* is a subspecies of *L. angolensis*. Based mainly on the apparent geographic isolation of the populations of *goliath* and *petraea* (and differences in size), *goliath* and *petraea* are considered to be distinct species by Cotterill (2001a). However, it is not certain that these populations are really isolated, and the differences in size possibly reflect clinal variation. Therefore, pending further studies, *smithii*, *goliath* and *petraea* are tentatively treated here as subspecies of *L. angolensis* (following Bergmans 1997), but the possibility that *L. angolensis* might contain more than one species is recognized. Since this profile was submitted, specimens were collected from Malawi that appeared to be intermediate in size between *goliath* and *ruwenzorii*, thereby supporting clinal variation (Šklíba *et al.* 2007). Chromosome number (Cameroon): $2n = 36$; $aFN = 66$ (Haiduk *et al.* 1981).

Description Small fruit bat with long silky dark brown pelage; head without white or pale markings; no epaulettes; toes partially webbed (sometimes inconspicuous); ruff of coarse hairs around the throat of ♂♂. Sexes similar in colour and size. Pelage soft, dense and without sheen; extending dorsally and ventrally along each upper arm and for some distance along each forearm, and also extending dorsally onto the interfemoral membrane and hindlegs as far as the ankles; mid-dorsal underfur ca. 10 mm long interspersed with longer hairs. Dorsal pelage ranging from rich dark rusty-brown to dark golden-brown or greyish-brown (becoming darker

on head and rusty-brown on hindlegs and wing margins in some individuals); hairs with basal half pale brown, terminal half dark brown. Ventral pelage slightly paler and greyer. Adult ♂♂ with a ruff of stiff coarse hairs on throat and sides of neck that ends with a whorl on each shoulder. Ruff sometimes sticky. Females lack a ruff of coarse hairs, but the hairs in this region are sparser and longer than elsewhere. No markings on head. Muzzle comparatively short giving the head a puppy-like appearance; lips and cheeks expansible. Ears rounded at tip, naked, dark brown. Antitragus distinct (cf. *Rousettus lanosus*). Palate normally with three undivided thick ridges, and four divided thick ridges of which two are postdental (Figure 45). Wing-membranes dark brown; attaching to second toe. Hindfeet with webbing between the proximal quarter or third of the first phalanges of the toes (Figure 45). Tail very short (8–21 mm).

Skull (Figure 45) on average short for an African fruit bat. Rostrum of medium relative length. Premaxillae fused, including anteriorly (cf. *Eidolon*, *Rousettus* and usually *Myonycteris*). Braincase only slightly deflected; upper alveolar line with weak angle between the two large premolars (Figure 46a) (cf. *Rousettus*, Figure 46c). Upper cheekteeth, particularly the posterior upper premolar (P^4) and anterior upper molar (M^1), are squarish in occlusal view (Figure 46d) (cf. *Myonycteris* Figure 46e). Dental formula $2^{132}/_{2133} = 34$.

Geographic Variation Five subspecies are recognized by Bergmans (1997):

L. a. angolensis: west of 22° E from Angola to E Nigeria (but not yet recorded in Gabon). FA: 72.0–83.0 mm ($n = 44$); GLS: 38.7–41.7 mm ($n = 20$).

L. a. smithii: West Africa, west of 2° E. Less extensively webbed toes. Relatively small and little-differentiated teeth. FA: 67.8–77.7 mm (n = 74); GLS: 36.6–40.1 mm (n = 52) (Bergmans 1997).

L. a. ruwenzorii: east of 22° E and between 6° N and 12° S. Slightly smaller than nominate subspecies (FA: 72.3–84.4 mm [n = 177]; GLS: 39.1–43.8 mm [n = 115]).

L. a. petraea: east of 34° E and north of 6° N; Ethiopian Highlands. FA: 71.7–76.3 mm (n = 10); GLS: 38.5–41.3 mm (n = 6); canines and cheekteeth short and low.

L. a. goliath: east of 30° E and south of 16° S; Mozambique and Zimbabwe. FA: 81.9–89.6 mm (n = 7); GLS: 42.2–46.0 mm (n = 7).

Similar Species Four other African mainland species of fruit bats are small to medium-sized (FA: 56–107 mm) with no basal ear-patches and no other white or pale markings on the head:

Rousettus aegyptiacus. Usually larger (FA: 82–106 mm). Dorsal pelage shorter; no ruff in adult ♂♂; toes not webbed; wing-membranes attaching to first toe or between first and second toes. Upper alveolar line straight. Orientates acoustically as well as visually.

R. lanosus. Usually larger (FA: 85–95 mm). No ruff in adult ♂♂; antitragus indistinct; toes not webbed; wing-membranes attaching to second toe or between first and second toes. Upper alveolar line straight; cheekteeth narrow. Probably orientates acoustically as well as visually.

Myonycteris torquata. Smaller (FA: 56–67 mm). Distal quarter to third of tibia practically naked. Skull with premaxillae not fused; posterior upper premolar (P⁴) and first upper molar (M¹) oblong (occlusal view). Not known to roost in caves.

M. relicta. Interfemoral membrane with pelage only close to the legs. Skull with premaxillae not fused; posterior upper premolar and first upper molar oblong (occlusal view); five lower cheekteeth on each side. Not known to roost in caves.

Distribution Endemic to Africa. Appears to have a very disjunct distribution in the Rainforest BZ and adjacent Rainforest–Savanna Mosaics, the Afroalpine–Afroalpine BZ of Ethiopia, and the Guinea Savanna and Zambezian Woodland BZs. Recorded from Senegal to Ethiopian Highlands (mostly south of 11° N), and southwards to 20° S. Also Bioko I. Some of the gaps, but not all, separate the five subspecies (see Geographical Variation). Map based on Bergmans (1997). Subsequently recorded from Zomba Plateau, Malawi (Šklíba *et al.* 2007); not mapped.

Habitat Rainforest, montane forest, forest transitions and mosaics and, to a lesser extent, woodland savannas, from sea level to 2200 m, where fruiting trees (and usually caves) are present. Most localities in rainforest are near the edges, and much of the rainforest is apparently not inhabited. In the Guinea Savanna and Zambezian Woodland BZs, usually found in relict and riverine forests or in nearby wetter types of woodland.

Abundance Unknown. Apparently common in some localized areas where fruiting trees and caves or cave-like day-roosts are present, but the distribution is likely to be very patchy because of the patchy distribution of this combination of resources.

Adaptations Aspect ratio low; wing-loading not known. Flight predicted to be slow and highly manoeuvrable; this species can probably fly through thicker vegetation than can many other African fruit bats. Unlike all African fruit bats except *Rousettus* spp., most often reported roosting by day in caves and mine-adits, but has also been found in a hollow tree, an open tunnel-like space between huge rocks, a subterranean bunker and a hut (Bergmans 1997). Roosting in foliage seems abnormal but there is a record of two under dead palm-leaves (Bergmans 1979). Because it orientates visually, without

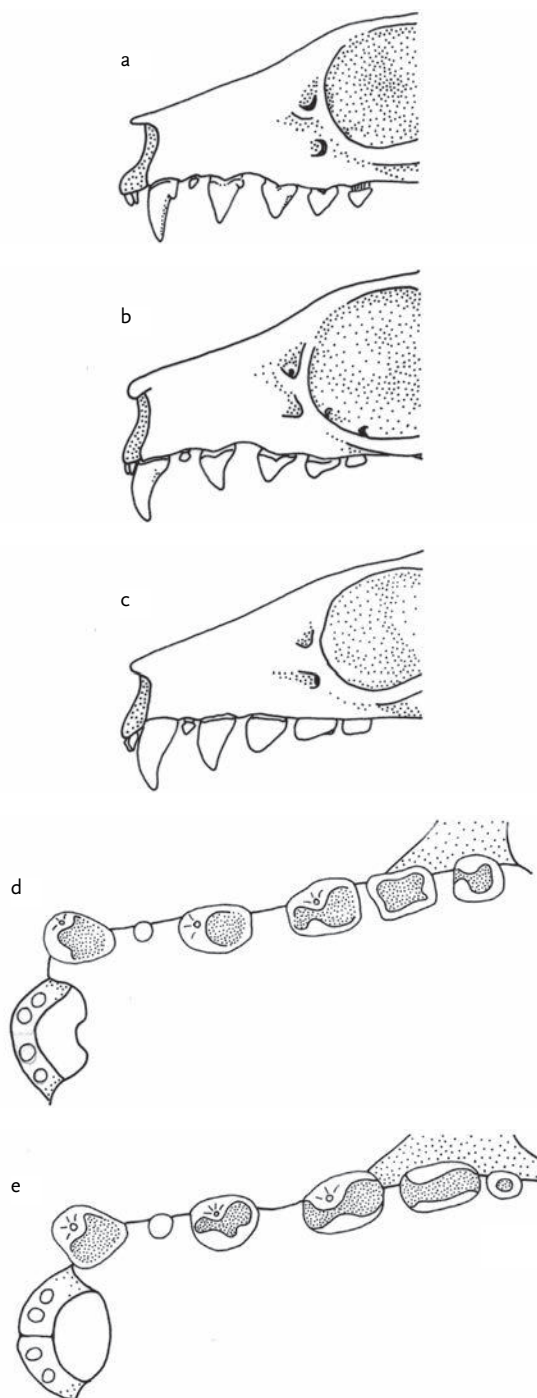
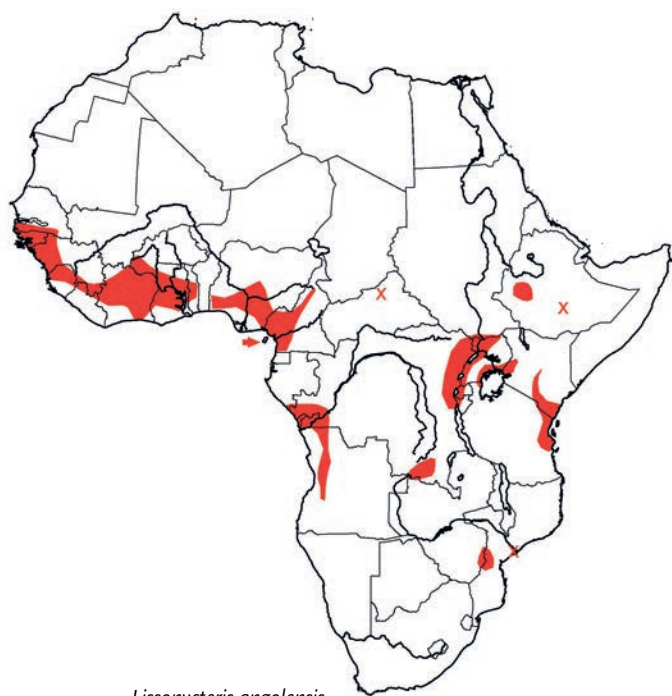


Figure 46. Some diagnostic characters of *Lissonycteris*, *Myonycteris* and *Rousettus*. Lateral views of upper alveolar lines in (a) *Lissonycteris angolensis*, (b) *Myonycteris torquata* and (c) *Rousettus aegyptiacus*. Occlusal views of upper teeth in (d) *Lissonycteris angolensis* and (e) *Myonycteris torquata*.

*Lissonycteris angolensis*

echolocation, it roosts where it is never totally dark. Hangs freely from ceilings of caves, using footholds that can be reached from flight. Does not use its wings for any form of locomotion except flight and, unlike species of *Rousettus*, does not clamber around or crawl into crevices (Lawrence & Novick 1963). Known to share caves with *Rousettus aegyptiacus* and microbats including *Rhinolophus macclaudi*, *Hipposideros caffer* and *H. cyclops*.

Foraging and Food Frugivorous. Forages below the canopy (Juste & Perez del Val 1995). Lands directly on fruits and does not clamber over branches (Lawrence & Novick 1963). Fruit is chewed *in situ*, or carried in the expansible cheeks to a nearby perch where it is chewed, the juice swallowed and the rest discarded. Food in the mouth is manipulated with a hindfoot but not with the wrists or thumbs. Feeds on soft fruits of endemic and introduced trees including *Ficus*, *Anthocleista*, *Chlorophora*, *Solanum* and *Adenia* (Marshall 1985) and orchard fruits including mangoes and guavas. Apparently there are no records of this species visiting flowers. Carnivory has been observed in captivity: on several occasions a captive individual settled over an adult *Myonycteris torquata*, enclosed it with the wings and then ate it, discarding only the feet and fragments of the wings (Coe 1975). In captivity, the mean \pm 1 S.D. nightly consumption of food was 68.9 ± 6.5 g ($n = 17$); the mean consumption per unit body weight was $1.18 \text{ g/g}^{\text{bwt}}$ ($n = 7$); the mean through-put time was 50 ± 14 min, and the percentage dry weight assimilated was 86% (Wolton *et al.* 1982).

Social and Reproductive Behaviour Usually roosts in groups of 2–50 (rarely up to 100); occasionally roosts singly. Females near parturition or lactating roost in maternity-roosts in which adult δ δ are absent or rare (Eisentraut 1942, 1956, 1963, Happold & Happold 1978). Evidence from Liberia suggests that the adult δ δ move away from some areas leaving the females behind until parturition and lactation are over (Wolton *et al.* 1982). Kingdon (1974) reports that the ‘stickiness’ of the males’ ruffs appears to increase and decrease

from time to time and he suggested that this may be caused by glandular secretion associated with sexual behaviour, and Hickey & Fenton (1987) found that the form of ‘glandular hairs’ from the ruff was consistent with a scent-dispersing function. However, Mainoya & Howell (1979) found almost no glandular tissue in the neck skin, and suggest that the ruff provides visual rather than olfactory cues.

Reproduction and Population Structure Litter-size: one. Reproductive chronology uncertain – probably polyoestry at least in some localities. At ca. $07^{\circ}40'N$ (Mt Nimba, Liberia), 71% of 49 females were pregnant in Jul and gave birth in Sep (Wolton *et al.* 1982), and near-parturient females were also recorded in late Nov (Coe 1975). At $07^{\circ}35'N$ (Ipole, Nigeria), a maternity group in Jul included six palpably pregnant females , one lactating female , five parous and seven non-parous females of undetermined reproductive condition, and two adult-sized males with abdominal testes (Happold & Happold 1978). On Bioko I., 29 of 32 females were pregnant and three reproductively inactive in Feb, 5 of 5 pregnant in Mar, 9 of 16 pregnant and seven (including three subadults) reproductively inactive in Oct, 2 of 3 pregnant and one lactating in Nov, and 2 of 4 lactating and two reproductively inactive in Dec (no useful data for other months) (Eisentraut 1964); this suggests polyoestry. In S Congo, near-parturient females have been recorded from May to Sep and in Nov, and lactation in Jan–Feb and Jun (Adam & Le Pont 1974). Longevity record (in captivity) 22 years 11 months (Jones 1982).

Predators, Parasites and Diseases Ectoparasites include bat-flies *Cyclopodia greeffi*, *Dipseliopoda biannulata*, *D. setosa* (Diptera: Nycteribiidae); mites *Microtrombicula hexasternalis*, *Riedlinia rousetti*, *Chiroptella adami* (Acari: Trombiculidae), *Nycteridocoptes macrophallus* (Acari: Sarcoptidae), *Teinocoptes ituriensis*, *Chirobia squamata* (Acari: Teinocoptidae) (Anciaux de Faveaux 1984).

Conservation IUCN Category: Least Concern.

Assessment includes all subspecies. Subspecies *goliath* and *petraea* are threatened by destruction of habitat and are likely to be taken from caves for bushmeat.

Measurements

Lissonycteris angolensis

FA: 68–90 mm, $n = 299^*$

WS (d): ca. 200 mm, $n = 1$

HB: 115.4 (90–140) mm, $n = 58$

T: 12.6 (6–21) mm, $n = 61$

E: 20.8 (15–25) mm, $n = 52$

Tib: 30.0 (25–37) mm, $n = 94$

HF: 20.6 (16–25) mm, $n = 45$

WT: 60–87 g, $n = 102^*$

GLS: 36.6–46.0 mm, $n = 189^*$

GWS: 20.1–26.7 mm, $n = 125^*$

C–M²: 13.9–17.2 mm, $n = 142^*$

Throughout geographic range (BMNH, ZFMK, Happold & Happold 1978)

*Bergmans 1997; mean values not recorded

Key References Bergmans 1997; Lawrence & Novick 1963.

Meredith Happold

GENUS *Megaloglossus*

Woermann's Long-tongued Fruit Bat

Megaloglossus Pagenstecher, 1885. Zool. Anz. 8: 245. Type species: *Megaloglossus woermanni* Pagenstecher, 1885.

Megaloglossus is a monotypic genus, endemic to Africa. Diagnostic characters: no white basal ear-patches; no white markings on face; FA: 38–49 mm; tongue very long with conspicuous long papillae on the pointed tip (Figure 35c); adult ♂ with a white, yellow or orange ruff; five upper and six lower cheekteeth (Table 11, p. 228). Selected characters of *Megaloglossus woermanni* are illustrated in Figure 47.

Megaloglossus has been placed in the Eonycterine section of Andersen (1912a) and in the subfamily Macroglossinae with all other specialized nectar-feeding pteropodids (e.g. Koopman 1993). However, DNA hybridization (Kirsch *et al.* 1995) and characters of the female reproductive system (Hood 1989) indicate that *Megaloglossus* and the other genera in this subfamily do not have a monophyletic origin, and

that *Megaloglossus* acquired nectarivory independently of the other genera. Based on these and other studies, Bergmans (1997) placed *Megaloglossus* in the subfamily Epomophorinae (tribe Myonycterini). The close relationship between *Megaloglossus*, *Myonycteris* and *Lissonycteris* is supported by the recent molecular studies of Álvarez *et al.* (1999) and Giannini & Simmons (2003). Several morphological characters of the integument and the postcranial skeleton also support Myonycterinae containing *Megaloglossus*, *Myonycteris* and *Lissonycteris* (Giannini & Simmons, 2005).

The single species is *Megaloglossus woermanni*.

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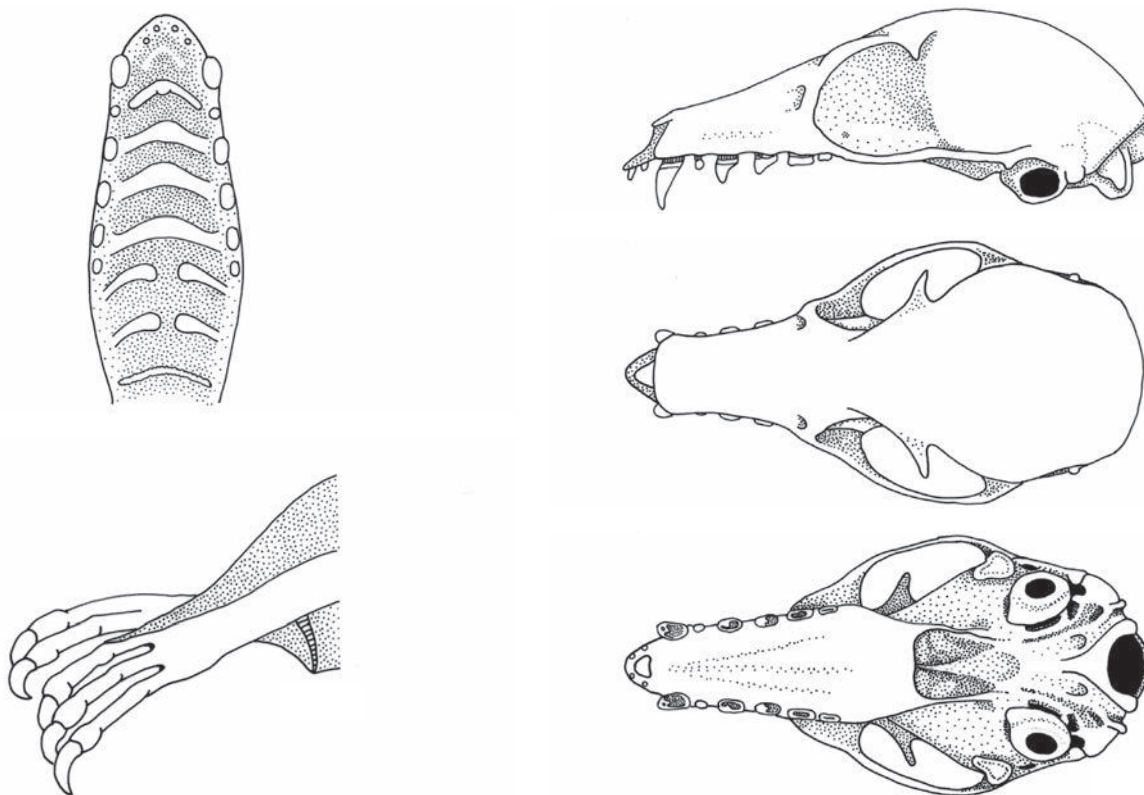


Figure 47. *Megaloglossus woermanni*. Palatal ridges. Left hindlimb showing wing attached to third toe as it is in some individuals, and weak webbing between the toes that occurs occasionally. Skull (BMNH 77.372).

Megaloglossus woermanni WOERMANN'S LONG-TONGUED FRUIT BAT

Fr. Mégaloglosse de Woermann; Ger. Woermanns Langzungen-Flughund (Afrikanishchen Langzungen-Flughund)

Megaloglossus woermanni Pagenstecher, 1885. Zool. Anz. 8: 245. Sibange Farm, Gabon [probably near Libreville, Gabon].

Taxonomy Synonyms: *prigoginei*. Subspecies: none currently recognized, but see Geographic Variation. Chromosome number (Cameroon, Gabon): $2n = 34$; $aFN = 62$ (Haiduk *et al.* 1980, Primus *et al.* 2006).

Description Very small, dainty, dark brown fruit bat with long, pointed muzzle and long, brush-tipped tongue; no markings on head; no epaulettes. Sexes similar in size. Pelage soft, moderately dense; mid-dorsal hairs 6–8 mm. Dorsal pelage dark brown; hairs pale brown with dark brown at tip. Ventral pelage paler. Adult ♂ with

ruff of stiff white, yellow or orange hairs on throat, neck and upper part of chest; hairs sometimes slightly sticky. Head small and narrow, with long, pointed muzzle; uniformly dark brown. Ears rounded at tip, blackish-brown. Eyes large. Tongue long and narrow; tip pointed and covered with brush of hair-like papillae (Figure 35b). Palate with seven ridges; ridges 5 and 6 divided by median groove (Figure 47). Wings dark brown; wing-membranes attaching to second or third toes, or between these toes; fifth finger shorter than third. Toes occasionally very weakly webbed (Figure 47). Tail very short (two vertebrae).

Skull (Figure 47) short for an African fruit bat. Braincase very rounded, sloping fairly steeply downwards from near front to back. Rostrum relatively long, narrow and tapering. Teeth weak (except canines); cheekteeth very low, narrow and devoid of cusps. Dental formula $^{2132}_{2133} = 34$.

Geographic Variation Two subspecies have been described:

M. w. woermanni: Throughout most of geographic range.

M. w. prigoginei: E DR Congo. FA: 43–49 mm; GLS: 27.7–30.3 mm.

However, the subspecific distinction between the supposedly larger *prigoginei* and smaller *woermanni* is not substantiated because there is considerable variation in size in all populations, as well as a gradual clinal increase in FA and GLS from west to east (Bergmans & Van Bree 1972, Bergmans 1997). There is also a large specimen from Angola (Bergmans 1997).

Similar Species None. This is the only African fruit bat with a long, narrow, pointed, brush-tipped tongue, no basal ear-patches and no other markings on the head.

Distribution Endemic to Africa. Widespread throughout the Rainforest BZ from Guinea and Sierra Leone to E DR Congo, Gabon and Bioko I., with some records from the Afromontane–Afroalpine BZ. Isolated populations have been recorded close to the Rainforest BZ in the adjacent Rainforest–Savanna Mosaics in West Africa, Uganda, N Angola and S DR Congo. Map based on Bergmans (1997).

Habitat Primary and secondary lowland rainforest, and clearings, banana plantations and other cultivated patches in rainforest. On Bioko I., occurs in rainforest at sea level, montane forest (800–1400 m) and in mossy forest (1400–1800 m) (Juste & Perez del Val 1995). Many specimens have been caught within a few metres of the ground, but the feeding habits of *M. woermanni* suggest that it probably also exploits the higher strata of the rainforest. However, when mist-nets were set in rainforest in Taï N. P., Côte d'Ivoire, at five elevations ('understorey' [1.5 m], 'canopy' [16.5, 20.5, 24.5 and 36.5 m above ground]), six *M. woermanni* were netted in the understorey and only one in the canopy (height 24.5 m; P. Barrière pers. comm.) (Henry *et al.* 2004).

Abundance Until recently, thought to be rare because there were few specimens in collections. However, in selected localities (where food resources are abundant) they may be common. For example: 'very common at Bélinga' in Gabon (Brosset 1966) and 'numerous in clearings in disturbed forest' in Congo (Dowsett *et al.* 1991).



Megaloglossus woermanni

Adaptations By day, hangs freely from half-dried banana and plantain leaves and amongst foliage of shrubs (Rosevear 1965). Also, one was taken inside a hut and another inside a house that had ripe bananas just outside the door (Rosevear 1965). The tongue is modified for lapping nectar from flowers: it is long (20 mm), thin (maximum breadth 5 mm) and tapers towards the tip, which is densely covered by rows of backward-pointing hair-like papillae. The papillae form a felt-like brush in which the nectar is entrapped. During lapping, the tongue is extruded with the tip curled downwards; then the tip is brought forward, and sometimes curled upwards, to scoop nectar into the spaces between the papillae (Kulzer 1982). The tongue moves in and out ca. seven times/second. As in other nectarivorous pteropodids, the cheekteeth are very small and non-functional, sometimes barely breaking through the gums. Because nectar is very easily digested and absorbed, the alimentary canal is short (twice HB) compared with ca. 6.5 HB in fruit-eating pteropodids (Kingdon 1974). Because of its small size, and the limitations imposed by nectarivory, *M. woermanni* does not maintain a constant body temperature (Kulzer & Storf 1980). When the ambient temperature is 31 °C, the body temperature is ca. 34 °C. When the ambient temperature falls to 23 °C (as it often does during cooler days and nights in the rainforest), the body temperature falls to ca. 26 °C, the metabolic rate is reduced to ca. one-half that at 31 °C, and the bat becomes torpid. Torpor is a means of saving energy when foraging would be energetically too expensive. Has been mist-netted over water (Jones 1971), suggesting that it might need to drink water – perhaps after roosting and prior to feeding.

Foraging and Food Feeds mainly on nectar and, to a lesser extent, pollen (Brosset 1966). Individuals in captivity refused to eat fruits and insects but avidly drank honey-water (Brosset 1966). Unlike nectarivorous phyllostomid bats of the Americas, which hover like humming-birds while feeding, *M. woermanni* apparently lands on or adjacent to flowers before feeding (Hill & Smith 1984). It feeds

by inserting the long tongue into the corolla of flowers and lapping the nectar (see Adaptations). In Nigeria (Happold & Happold 1978) and Bioko I. (Juste & Perez del Val 1995), they have been found in the lower strata (subcanopy) of the rainforest with frugivorous *Scotonycteris zenkeri* and, on Bioko I., also with *Rousettus aegyptiacus* and *Lissonycteris angolensis*. It is likely, however, that *M. woermanni* also forages in the higher strata: further investigations with elevated mist-nets are needed to confirm this prediction. Plants known to be exploited for food include *Kigelia* flowers (Eisentraut 1963) and pawpaw flowers for nectar (Jeffrey 1975), but it is highly likely that nectar is also taken from a wide variety of rainforest plants. Although flowers are present throughout the year in the rainforest, *M. woermanni* is not always present at particular localities, suggesting that it might be nomadic. For new information about home-range and foraging behaviour, see Weber *et al.* (2009).

Social and Reproductive Behaviour Very little is known. The only records of roosting are for male bats that were found singly (Brosset 1966). In Gabon (Brosset 1966) and Ghana (Jeffrey 1975), ♂♂ alone have been captured in large numbers ($n = 86$, Belinga, Gabon over several years; $n = 11$ on one night in Ghana), but at other times and localities both sexes have been obtained, although ♂♂ have predominated (e.g. 79% ♂♂ [$n = 109$] at Mt Nimba, Liberia; Wolton *et al.* 1982). Many ♂♂ have been mist-netted together at the same time, suggesting that they were part of a 'feeding flock', or that there was a 'male roosting area' nearby (Wolton *et al.* 1982). These observations suggest a social organization in which ♂♂ and ♀♀ segregate at least during some parts of the year (Happold 1987), but this needs confirmation.

Reproduction and Population Structure Litter-size: one, occasionally two (Eisentraut 1973b, Czekala & Benirschke 1974). Reproductive chronology uncertain. In equatorial Uganda, Okia (1987) recorded simultaneous pregnancy and lactation in one ♀ in May, and one birth in Jan. He recorded 1 of 3 ♀♀ pregnant in Jan,

1 of 3 pregnant in Feb, 1 of 1 pregnant in Apr and in May and 4 of 4 near parturition in Sep. These data are consistent with bimodal polyoestry with births in Jan and Sep (as in three other species of fruit bats in Uganda), but this needs confirmation: aseasonal polyoestry is an alternative possibility. Data from elsewhere are fragmentary and inconclusive (e.g. Eisentraut 1964, Jones 1971, Bergmans 1979, Wolton *et al.* 1982). Gestation not known.

Predators, Parasites and Diseases Ectoparasites include a mite *Binuncus megaloglossus* (Acari: Myobiidae) (Anciaux de Faveaux 1984).

Conservation IUCN Category: Least Concern.

Major threats: reduction in area of rainforest, and changes in the structure and biodiversity of the rainforest.

Measurements

Megaloglossus woermanni

FA: 42.7 (38–49) mm, $n = 180$

WS (d): ca. 225–255 mm, $n = 17$

HB: 68.3 (60–79) mm, $n = 46$

T: 0 mm, $n = 49$

E: 14.4 (9–20) mm, $n = 98$

Tib: 16.8 (16–19) mm, $n = 32$

HF: 12.2 (12–13) mm, $n = 11$

WT: 15 (10–25) g, $n = 100$

GLS: 27.3 (24.5–30.3) mm, $n = 85$

GWS: 13.7 (11.5–14.9) mm, $n = 48$

C–M²: 8.9 (8.1–9.7) mm, $n = 50$

Throughout geographic range (BMNH, NMK, SMNS and literature)

Key References Bergmans 1997; Bergmans & Van Bree 1972; Happold 1987; Kulzer & Storf 1980, 1982.

D. C. D. Happold

GENUS *Micropteropus* Lesser Epauletted Fruit Bats

Micropteropus Matschie, 1899. Megachiroptera Berlin Mus., p. 36, 57. Type species: *Epomophorus pusillus* Peters, 1868.

Micropteropus is a polytypic genus with two species, *M. pusillus* and *M. intermedius*, which are endemic to Africa. Diagnostic characters: white basal ear-patches but no other white markings on the head; FA: 46–64 mm, epaulettes on shoulders of adult ♂♂; muzzle simple; interfemoral membrane well developed and with calcars; 5–6 thick palatal ridges of which all but the first are divided by a wide median groove; C–M¹: 8.0–ca. 10.6 mm; usually three upper and five lower cheekteeth (very occasionally four upper cheekteeth) (Table 11, p. 228). Selected characters of *Micropteropus* are illustrated in Figure 48.

Micropteropus was placed in the *Epomophorus* section of Andersen (1912a), and is in the subfamily Epomophorinae (tribe Epomophorini) of Bergmans (1997). *Micropteropus* is evidently very closely related to *Epomophorus*: the type species was originally assigned to *Epomophorus* and *Micropteropus* was originally proposed as a subgenus of *Epomophorus*. It was raised to generic status by Andersen (1910) mainly because

of the relatively short muzzle and aberrant soft palate of the type, *M. pusillus* (the other criteria are listed and discussed by Bergmans 1989). More recent phylogenetic studies, based on molecular characters, support the close relationship between *Micropteropus* and *Epomophorus* (e.g. Álvarez *et al.* 1999, Giannini & Simmons 2003). Many morphological characters also support a close phylogenetic relationship of *Micropteropus* and *Epomophorus* (Giannini & Simmons 2005). Whereas most species of *Epomophorus* have six thick palatal ridges of which ridges 2, 3 and 4 are undivided, *M. pusillus* and *M. intermedius* have essentially six of which all but the first are close together and divided by a wide median groove. In *M. pusillus* and *M. intermedius*, partial fusions between ridges 2 and 3, and/or 3 and 4, may result in the number of ridges appearing to be less than six. A third species, *M. grandis*, which is morphologically intermediate between *M. intermedius* and *Epomophorus* (especially *E. labiatus*), was transferred to

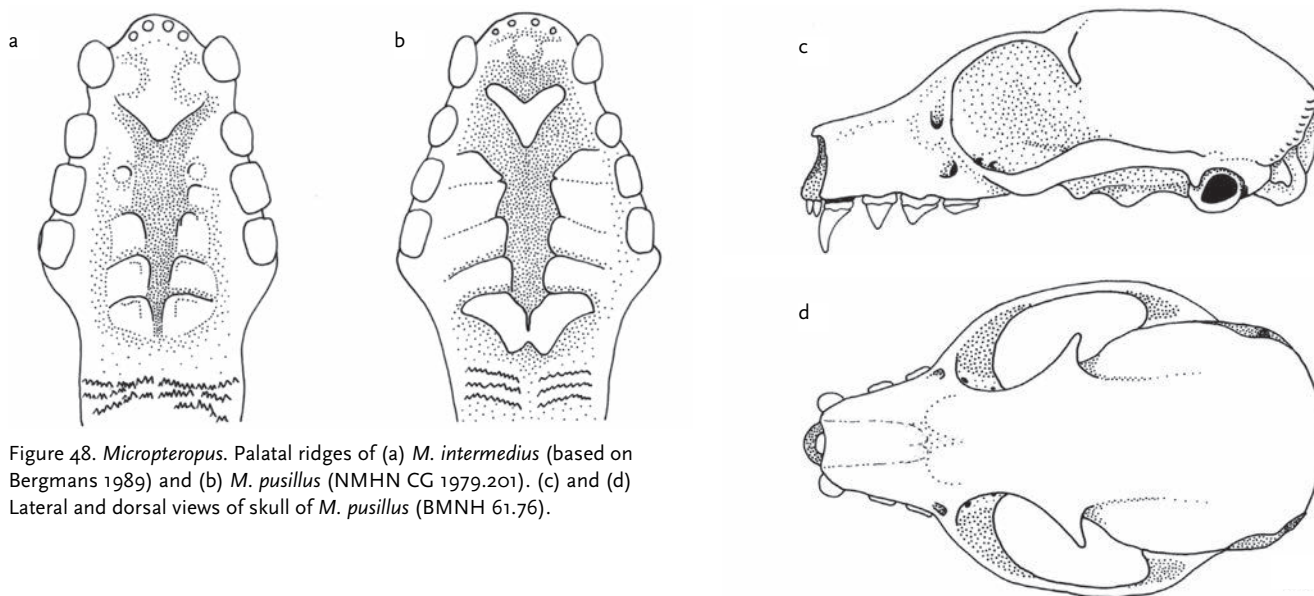


Figure 48. *Micropteropus*. Palatal ridges of (a) *M. intermedius* (based on Bergmans 1989) and (b) *M. pusillus* (NMHN CG 1979.201). (c) and (d) Lateral and dorsal views of skull of *M. pusillus* (BMNH 61.76).

Epomophorus by Bergmans (1988). Chromosomal differences between *Epomops*, *Hypsignathus*, *Micropteropus* and *Epomophorus* offer an additional argument for maintaining the generic status of *Micropteropus* (Haiduk *et al.* 1980, 1981). Further investigations may resolve the affinities of *E. grandis* and perhaps indicate when and where the two genera became separated.

The two species can be distinguished by the following characters:

M. intermedius. Larger, FA: 57–64 mm, GLS: 32–34 mm. Palatal ridges 2 and 3 weakly developed and apparently fused in some specimens. *M. pusillus*. Smaller, FA: 46–56 mm, GLS 26–31 mm. All palatal ridges prominent and well defined; 2 and 3 may be fused, 4 and 5 fused occasionally.

Meredith Happold

Micropteropus intermedius HAYMAN'S LESSER EPAULETTED FRUIT BAT

Fr. Microptéropode de Hayman; Ger. Haymans Kleiner Epaulettenflughund

Micropteropus intermedius Hayman, 1963. Publç. Cult. Comp. Diamantes de Angola, 66: 100. Dundo, Lunda, Angola.

Taxonomy Synonyms: none. Chromosome number: not known.

Description Very small to small, fawn fruit bat with anterior and posterior basal ear-patches but no other white markings on head; epaulettes on adult ♂♂; six thick palatal ridges of which the posterior five are divided, all except numbers 2 and 3 are well developed and two are clearly postdental; FA: 57–64 mm. A poorly known species – only one adult ♂ and four adult ♀♀ known. Sexes apparently similar. Pelage soft, moderately long. Dorsal pelage pale brown (fawn) becoming paler on shoulders; hairs with medium sepia brown at base. Ventral pelage pale brown becoming darker on flanks. Adult ♂♂ have a conspicuous white epaulette on each shoulder, which retracts into a pouch rimmed by sepia brown pelage: adult ♀♀ have a whorl of hairs, same colour and length as dorsal hairs, on each shoulder. Head round and puppy-like, pale brown with medium sepia brown chin and throat; white basal ear-patches. Muzzle relatively short and blunt; lips and cheeks not very expansible. Six palatal ridges, 5 and 6 divided by medial gap (Figure 48a); ridges 2 and 3 weakly developed and apparently fused in some specimens (cf. *M. pusillus*). Ears rounded, naked, with brown pigmentation. Eyes very large. Wing-membranes brown; attaching to second toe. Interfemoral membrane narrow; calcaris present. Tail rudimentary.

Skull short for an African fruit bat. Rostrum of medium relative length (34–35% of GLS [$n = 3$]), but broad (Bergmans 1989). Postdental palate almost flat. Dental formula usually $^{2121}_{2132} = 28$ very occasionally an extra upper premolar (P^1) is present.

Geographic Variation None.

Similar Species Thirteen other species of fruit bats have simple muzzles; basal ear-patches but no other markings on head; adult ♂♂ with epaulettes; three upper and five lower cheekteeth:

Micropteropus pusillus. Smaller (FA: 46–56 mm; GLS: 26.8–31.0 mm).

All palatal ridges prominent and well defined.

Epomophorus grandis. Larger in most skull and tooth dimensions including, in particular, rostrum length (13.1–13.7 mm), palatal length (20.2–20.9 mm) and C–M¹ (11.8–12.3 mm). In adults, palatal ridges 2–6 are divided.

Epomophorus (all other species). Palatal ridges 2–4 not divided by medial gap.

Epomops (3 spp.). Three or five thick palatal ridges.

Nanonycteris veldkampii. Smaller (FA: 46–54 mm, GLS: 23.6–27.1 mm).

Distribution Endemic to Africa. Known from only four localities in the Southern Rainforest–Savanna Mosaic, in NE Angola and SW DR Congo (Hayman 1963, Bergmans 1989). Bergmans suggests that this species is likely to occur in woodland savannas of the Zambezian Woodland BZ, but is not likely to occur in the Rainforest BZ.

Habitat Mosaics of forests (including lowland rainforest, mangrove forest and coastal forest) with open vegetation such as secondary grasslands (Bergmans 1989).

Abundance Very rarely collected.

Remarks A pregnant ♀ with one foetus (FA: ca. 14 mm) was taken in Jun–Jul (Bergmans 1989). Nothing else is known about the biology of this species.

Conservation IUCN Category: Data Deficient.

There is no evidence that this species is rare in the field, and its habitat preferences, distributional limits and population dynamics have not been investigated (Bergmans 1999).

Measurements

Micropteropus intermedius

FA (♂): 58 mm

FA (♀ ♀): 67, 58, 57 mm

WS: n. d.

T (♂): 3 mm

T (♀ ♀): ca. 5 mm

E (♂): 15 mm

E (♀ ♀): ca. 17, 14.3, – mm

Tib (♂): 24 mm

Tib (♀ ♀): ca. 26, 25, – mm

HF (♂): 16 mm

HF (♀ ♀): 18, 17, 17 mm

WT: n. d.



Micropteropus intermedius

GLS (♂): 33.3 mm

GLS (♀ ♀): 33.3, 32.2, 32.0 mm

GWS (♂): ca. 20.5 mm

GWS (♀ ♀): –, 20.2, 19.9 mm

C–M¹ (♂): ca. 10.6 mm

C–M¹ (♀ ♀): 10.2, 10.5, 10.2 mm

All known specimens: ♂ RMCA 22661, DR Congo; ♀ ♀ holotype BMNH 62.2073, Angola, SMF 2509, DR Congo, and RMCA 32380, DR Congo, respectively (Kock 1987, Bergmans 1989)

Key References Bergmans 1989; Hayman 1963; Kock 1987.

Meredith Happold

Micropteropus pusillus PETERS'S LESSER EPAULETTED FRUIT BAT

Fr. Petit microptéropode; Ger. Peters' Kleiner Epaulettenflughund

Micropteropus pusillus (Peters, 1868). Monatsber. K. Preuss. Akad. Wiss. Berlin 1867: 870 (publ. 1868). Yoruba, Nigeria.

Taxonomy Originally *Epomophorus pusillus*. Synonyms: none. Chromosome number (Cameroon): 2n = 35; aFN = 64 (Haiduk *et al.* 1981).

Description Very small fruit bat with anterior and posterior basal ear-patches but no other white markings on head; epaulettes on adult ♂ ♂; six thick palatal ridges of which the posterior five are divided and well developed (including 2 and 3), and two are clearly postdental; FA: 46–56 mm. Sexual dimorphism not pronounced; ♀ ♀ with, on average, larger forearms. Pelage soft, dense dorsally, sparser ventrally especially on throat; extending onto forearm, propatagium and interfemoral membrane; mid-dorsal hairs 7–9 mm. Dorsal pelage medium brown, reddish-brown, greyish-brown to pale brown; hairs with pale base. Ventral

pelage paler, sometimes off-white but without a demarcated whitish mid-ventral patch. Adult ♂ ♂ have a white epaulette on each shoulder (retracted into a pouch rimmed by dark hairs except when displayed); adult ♀ ♀ have a whorl of hairs, same colour and length as dorsal hairs on each shoulder. Ears brown. Eyes large. Head rounded and puppy-like with white or pale yellow basal ear-patches but no other markings; muzzle short and broad; lips and cheeks moderately expansible. Palate with six thick ridges, the first hastate (pointing backwards), all others divided by a medial gap decreasing in width from front to back and ending with V-shaped notch in ridge 6, ridges 2 and 3 not weakly developed (cf. *M. intermedius*), ridge 4 partly postdental, ridges 5 and 6 postdental (cf. *E. grandis*) (Figure 48b). Wing-membranes chocolate brown; attaching to second toe. Tail rudimentary or absent.

Skull (Figure 48) short for an African fruit bat. Rostrum, on average, relatively short (31–36% of GLS) and broad (Bergmans 1989). Postdental palate almost flat. Dental formula: $^{2121}_{2132} = 28$.

Geographic Variation Specimens are quite uniform throughout geographic range, with no clear clinal variation being apparent (Bergmans 1989). One exception is that specimens from Côte d'Ivoire have slightly longer forearms than specimens from elsewhere and weigh ca. 20% more than specimens from Equatorial Guinea.

Similar Species Thirteen other species of fruit bats have simple muzzles; basal ear-patches but no other markings on head; adult ♂ with epaulettes; three upper and five lower cheekteeth:

Micropteropus intermedius. Larger (FA: 57–64 mm; GLS: 32.0–33.3 mm, $n = 3$). Palatal ridges 2 and 3 weakly developed.

Epomophorus grandis. Larger (FA: 62–66 mm; GLS: 35.4–36.7 mm, $n = 3$).

Epomophorus (all other spp.). Palatal ridges 2–4 not divided by medial gap.

Epomops (3 spp.). Three or five thick palatal ridges.

Nanonycteris veldkampii. Nine thick or partly thick palatal ridges, all interdental ridges undivided.

Distribution Endemic to Africa. Recorded mainly from the Guinea Savanna BZ and Rainforest–Savanna Mosaics, with extensions into the Sudan Savanna, Rainforest, Somalia–Masai Bushland and Zambezan Woodland BZs. Recorded from Senegal to Ethiopia and southwards to Angola, S DR Congo and NW Tanzania – but avoiding the Congolian rainforest except around its edges.

Habitat Essentially a low elevation, savanna-forest ecotone species found along edges of gallery forests and in secondary growth in moist Guinea Savanna habitats, and in woodland copses in Sudan Savanna. Probably penetrates into rainforests along roadways, cut-overs, plantations and agricultural clearings. Generally uncommon in closed rainforest habitats. Mostly recorded below 800 m.

Abundance Uncommon in closed-canopy forest, but locally very common in regeneration and secondary growth and along forest edge, particularly where free-standing fig trees are abundant. A year-round resident with numerous recaptures of marked individuals.

Adaptations Aspect ratio high; wing-loading medium; flight rapid, manoeuvrable, agile and erratic (resembling that of some microbats) (Jones 1972, Norberg & Rayner 1987). Flies beneath, between and through clumps of fairly dense vegetation; begins flights with direct take-off from branches (Jones 1972), and is able to hover well (Kingdon 1974). Thumbs are relatively short and weak. Clumsy when crawling along branches, so accesses fruits only by flight. Roosts by day, hanging freely from branches of low shrubs and trees. Sometimes roosts, well hidden, between leaves of dense bushes, and seldom flies away when disturbed (Lang & Chapin 1917b). Sometimes roosts in places with little cover and considerable exposure to the sun (Verschuren 1957). There is one record of an individual roosting in a palm tree (Rosevear 1965). Some captive individuals exhibited a strong homeothermic response when subjected to temperatures down to 5 °C, but others



Micropteropus pusillus

permit hypothermia, allowing body temperature to decline as low as 22 °C (Jones 1972).

Foraging and Food Primarily frugivorous. Begins foraging at dusk. Typically flies into a fruiting tree, grasps fruit in mouth, and flies off to a feeding-roost 10–50 m distant. Can carry fruits up to 75% of body mass. When feeding, holds large fruit between foot, thumb and second finger, fills cheek pouches to bulging with pulp and small seeds. Slowly sucks to extract juices and some seeds before spitting out fibre-seed pellet. Feeding-roosts used for several days, accumulate piles of spat-out fibre-seed pellets. Feeds on flowers seasonally (5 genera, 4 families), but is primarily frugivorous. Moth scales left on fruits may appear intact in faeces, so do not indicate insectivory (Thomas 1984b). Marshall (1985) lists 11 genera (9 families) of figs and fruit in diet. All figs and fruits are sweet, succulent, larger than 20 mm. In Guinea Savanna of Côte d'Ivoire, diet dominated by *Ficus capensis* and *F. vallis-choudae* (49%), *Vitex doniana* (15%), *Cola gigantea* (12%). Ingests up to 250% of body mass and 1002.2–1428.7 kJ/kg^{0.75} nightly in captivity, adjusting intake by protein content of diet (Thomas 1984a).

Social and Reproductive Behaviour Poorly known. Roosts singly, in twos or in small groups of up to a dozen individuals (Lang & Chapin 1917b, Verschuren 1957). Pregnant ♀♀ continue to roost with immature young. Males make a shrill ringing note similar to that of larger epauletted fruit bats (Kingdon 1974). Calling ♂♂ common and widespread in Sudan Savanna, but not commonly heard in some patches of regenerating Guinea Savanna in Côte d'Ivoire, despite high capture-rates in mist-nets. May suggest geographic or habitat-related differences in social structure and mating behaviour.

Reproduction and Population Structure Litter-size: one ($n = \text{ca. } 20$). In Côte d'Ivoire, the reproductive chronology is continuous bimodal polyoestry with postpartum oestrus. At

06° 13' N (Lamto; Guinea savanna in Rainforest–Savanna Mosaic; rain throughout year with peaks in Apr–Jun and Sep, minimal in Dec–Jan), births occur at onset of the long wet season and the major increase in fruit availability (Mar) and ca. six months later, roughly at onset of short wet season and minor increase in fruit availability (Sep). Gestation ca. six months. Lactation (for population as a whole) for ca. 7–8 weeks after the Mar births, and ca. 11 weeks after the Sep births – the longer second period possibly due to less synchrony between ♀♀. Adult testes length constant at 5.6–6.0 mm, with no annual cycle in size. At 09° 50' N (Wango Fitini in northern part of Comoé N. P.; Guinea Savanna BZ; rainfall unimodal), births occur at onset of wet season (Apr) and at end of wet season (late Oct). At both localities, the first birth period seems timed to match increasing availability of fruit, but the second seems set by the six-month gestation. Juveniles appear in flying population in Apr–May and Nov–Dec at body mass 14–18 g and forearm 46–48 mm. Females mature at six months and give birth to their first young at 12 months. Males begin puberty at seven months and become adult by nine months. Reference: Thomas & Marshall (1984).

Predators, Parasites and Diseases Ectoparasites include mites *Ancystropus aethiopicus* (Acari: Spinturnicidae), *Nycteridocoptes pteropodi* (Acari: Sarcoptidae), *Teinocoptes epomophori*, *T. auricularis* (Acari: Teinocoptidae) (Anciaux de Faveaux 1984). Rift Valley Fever virus (Family, Bunyaviridae; genus, *Phlebovirus*) identified in 7% of individuals in Guinea. Lagos bat virus (strain AnCb-672d, identical to that of *Eidolon helvum*) isolated from brain, heart and spleen in Central African Republic.

Conservation IUCN Category: Least Concern.

Measurements

Micropteropus pusillus

FA (♂♂): 50.9 (46–55) mm, n = 149*

FA (♀♀): 52.2 (50–56) mm, n = 201*

WS: n. d.

HB: 78.2 (67–103) mm, n = 81

HB (♀♀): 77 (67–85) mm, n = 17

T: 1.4 (0–4) mm, n = 74

E: 15.2 (13–19) mm, n = 81

Tib: 22.0 (20–24) mm, n = 44

HF: n. d.

WT: 32.3 (20–43) g, n = 139

GLS (♂♂): 29.2 (27.8–30.6) mm, n = 57*

GLS (♀♀): 28.7 (26.8–29.8) mm, n = 48*

GWS (♂♂): 18.1 (16.9–19.0) mm, n = 10

GWS (♀♀): 17.9 (16.7–19.1) mm, n = 14

C–M¹ (♂♂): 9.0 (8.1–9.9) mm, n = 58*

C–M¹ (♀♀): 8.8 (8.0–10.1) mm, n = 77*

Throughout geographic range (BMNH, Happold & Happold 1978, Bergmans 1979, Thomas & Marshall 1984)

*Bergmans 1989

Key References Bergmans 1979, 1989; Jones 1972; Owen-Ashley & Wilson 1998; Thomas & Marshall 1984; Thomas 1984a.

Don Thomas & Mickäel Henry

GENUS *Myonycteris*

Collared Fruit Bats

Myonycteris Matschie, 1899. Megachiroptera Berlin Mus., p. 61, 63. Type species: *Cynonycteris torquata* Dobson, 1878.



Myonycteris torquata male.

Myonycteris has three species: two in Africa and one (*M. brachycephala*) on the oceanic islands of São Tomé and Príncipe in the Gulf of Guinea. Diagnostic characters: no white basal ear-patches; no white markings on the face; FA: 56–75 mm; ruff of stiff hairs on lower neck of adult ♂♂; tongue moderately long, rounded at tip, with inconspicuous rasp-like papillae; toes partly webbed; visual

orientation only; premaxillae seldom fused; five upper and five or six lower cheekteeth; M² greatly reduced (Table 11, p. 228). The partly webbed toes, palatal ridges and skull of *M. torquata* are shown as a representative of the genus in Figure 49. Figure 49 also shows interspecific differences in upper teeth.

The genus was revised by Bergmans (1976). *Myonycteris* was placed in the *Cynopterus* section of Andersen (1912a), but Bergmans (1997) transferred it to the subfamily Epomophorinae (tribe Myonycterini) on the basis of previous cladistic analyses of morphological characters, which indicated that *Myonycteris* should be excluded from the *Cynopterus* section (Springer *et al.* 1995), and on the basis of phylogenetic relationships (Juste *et al.* 1997), which showed that *Myonycteris torquata* and *M. brachycephala* and *Lissonycteris angolensis* form a monophyletic group. Subsequently, cladistic analysis of other skull and/or genetic characters has repeatedly confirmed this conclusion (e.g. Álvarez *et al.* 1999, Giannini & Simmons 2003, 2005). Two subgenera are recognized by Koopman (1994) and Simmons (2005):

M. (Myonycteris). Cheekteeth comparatively weak; outer and inner ridges of posterior lower premolar fused anteriorly; lower canine at least as high as middle lower premolar; no sagittal crest. Contains African mainland species *M. relictus* and *M. torquata*.

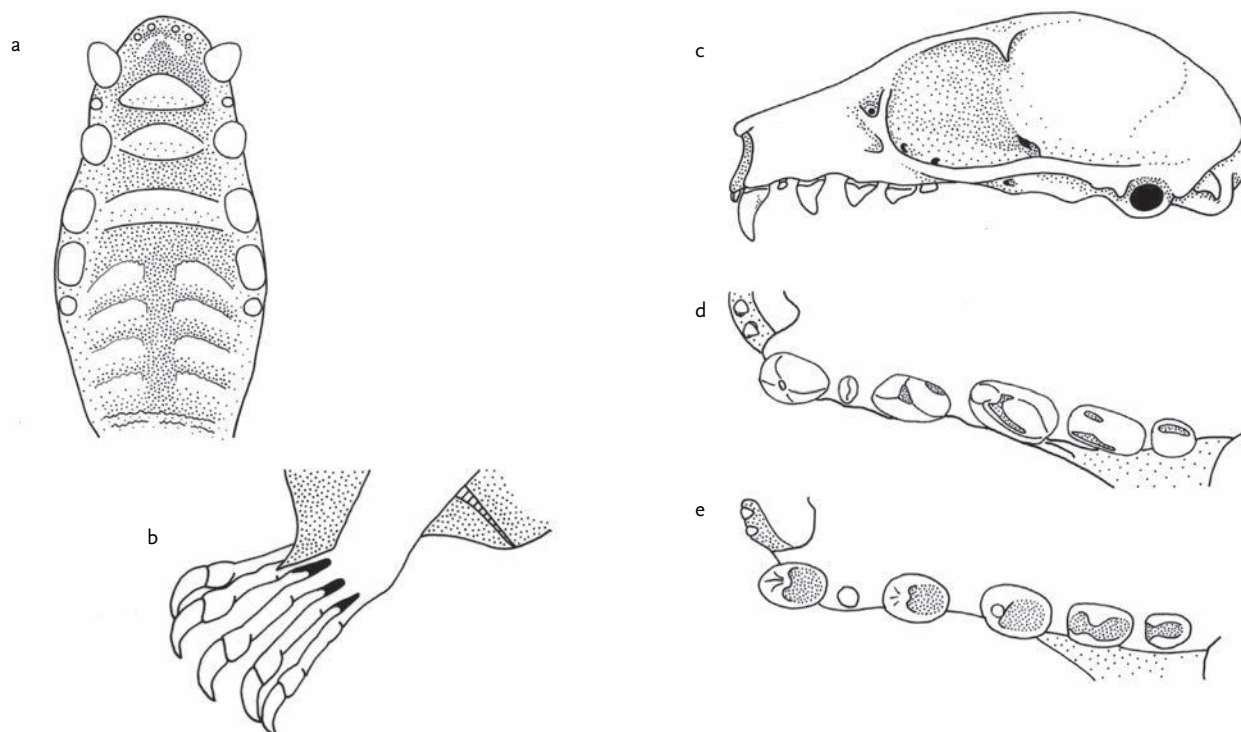


Figure 49. *Myonycteris*. (a) Palatal ridges of *M. torquata* (BMNH 84.799; see De Vree 1971 for variations). (b) Left hindlimb of *Myonycteris torquata* showing attachment of wing to second toe. (c) Lateral view of skull of *M. torquata* (BMNH 77.352, adult M). (d) Occlusal view of upper teeth of *M. relicta* (based on Bergmans 1980). (e) Occlusal view of upper teeth of *M. torquata leptodon* (C-M² drawn to same size in both species).

M. (Phygetis). Cheekteeth comparatively strong; outer and inner ridges of posterior lower premolar well separated; lower canine not as high as middle lower premolar; sagittal crest present. Contains *M. brachycephala* from São Tomé and Príncipe.

However, Bergmans (1976, 1997) does not recognize the subgeneric status of *Phygetis* and, furthermore, the cladistic analyses of Álvarez *et al.* (1999) and Giannini & Simmons (2003) indicate that *M. brachycephala* and *M. torquata* are more closely related than either is to *M. relicta*.

The two African mainland species can be distinguished by size and geographic distribution:

M. relicta. FA: 65–75 mm; GLS: 35.5–39.2 mm. African mainland east of 32° E.

M. torquata. FA: 56–67 mm; GLS: 30.2–35.2 mm. African mainland west of 32° E and Bioko I.

Meredith Happold

Myonycteris relicta BERGMANS'S COLLARED FRUIT BAT

Fr. Myonyctère d'Afrique orientale; Ger. Reliktärer Halskrausen-Flughund

Myonycteris relicta Bergmans, 1980. Zool. Meded. Rijksmus. Nat. Hist. Leiden 14: 126. Mukanda River, Lukore area, Shimba Hills, Kwale District, Coastal Province, Kenya.

Taxonomy Placed in subgenus *Myonycteris* by some authors, but see Genus *Myonycteris*. Synonyms: none. Peterson *et al.* (1995) consider *relicta* to be a species of *Rousettus*. Chromosome number: not known.

Description Small, reddish-brown fruit bat with no basal ear-patches; no white markings on head; no epaulettes; no mantle; ♂♂ with ruff of stiff hairs; interfemoral membrane with pelage only near legs; five lower cheekteeth: FA: 65–75 mm. Sexes similar except for ruff. Pelage dense, woolly on head; extending half-way along forearm and marginally onto wing-membrane, along leg (but

not as far as ankle) and on to interfemoral membrane but only adjacent to legs; mid-dorsal hairs 7–8 mm. Dorsal pelage pale to medium reddish-brown; hairs pale pinkish-brown with reddish-brown at tip. No epaulette or white markings on shoulder. Ventral pelage pinkish-brown; hairs with slightly darker bases. Adult ♂♂ with ruff of comparatively coarse, pale orange to pale orange-brown, specialized hairs on chin, throat and upper chest extending to shoulders. Head without markings; muzzle moderately long; lips quite thick and only slightly expansible. Ears dark brown. Eyes large. Palate with six (possibly sometimes seven) thick ridges, 1–3 undivided, 4–6 divided by narrow medial gaps. Wing-membranes

dark brown; attaching to second toe. Toes 'webbed' to middle of first phalanges.

Skull short and delicate for an African fruit bat. Rostrum of medium relative length (ca. 36–37% of GLS). Dentition comparatively strong (cf. *M. torquata*) and simple; two lower incisors on each side; M^2 and M_2 reduced; M_3 absent (cf. *M. torquata*); P^4 and M^1 oblong and subrectangular in occlusal outline, with longitudinal axes pointing (in forward direction) slightly lingually (Figure 49d) (Bergmans 1980, 1997, Schlitter & McLaren 1981). Dental formula $21^{132}/_{2132} = 32$.

Geographic Variation Not yet assessed but, as the distribution is disjunct, geographic variation is a possibility.

Similar Species Four other African mainland species of fruit bats are small to medium-sized (FA: 56–107 mm) with no basal ear-patches and no other white or pale markings on the head:

Myonycteris torquata. Usually larger (FA: 56–67 mm; GLS: 30.2–35.2 mm). Interfemoral membrane entirely covered by pelage. Six lower cheekteeth on each side.

Lissonycteris angolensis. Interfemoral membrane well covered with pelage. Skull with premaxillae fused; P^4 and M^1 squarish (occlusal view: Figure 46d); six lower cheekteeth on each side. Roosts in caves.

Rousettus (2 spp.). Larger (FA: 82–106 mm).

Distribution Endemic to Africa. Recorded disjunctly from the Coastal Forest Mosaic BZ (from SE Kenya to SE Tanzania), and from two isolated localities in the Zambezian Woodland BZ – at the eastern escarpment of the Uzungwa Mts in Tanzania, and at the confluence of the Haroni and Rusitu Rivers (= Lusitu River) in E Zimbabwe (Schlitter & McLaren 1981, Burgess *et al.* 1992, Mickleburgh *et al.* 1992, Burgess & Muir 1994, Clarke 1995, Clarke & Dickinson 1995, Cotterill 1995, Bergmans 1997, Burgess *et al.* 2000a, b, D. Kock unpubl.).

Habitat Forests in the coastal forest mosaic of East Africa, and inland lowland forests, at altitudes of 120–1000 m (D. Kock pers. comm., Burgess *et al.* 2000a). Holotype was collected over Mukanda R. in the Shimba Hills, in open country interspersed with patches of forest (Bergmans 1997). Has not been recorded from East African savannas, suggesting a close association with forest (Burgess *et al.* 2000a, b). The specimen from Zimbabwe was collected in forest at the southern end of the Chimanimani Mts (Bergmans 1997).

Abundance Between one and seven individuals were mist-netted from each of six coastal forests in a survey of 16 Tanzanian coastal forests (Cockle *et al.* 1998), making it the most commonly captured fruit bat after *Epomophorus wahlbergi*. This suggests that it may be fairly common locally in suitable forests in Tanzania and SE Kenya.



Myonycteris relicta

Remarks A pregnant ♀ was collected in Nov, and a lactating ♀ and two subadult specimens were collected in Feb (SMF, D. Kock unpubl.). Nothing else is known about this species.

Conservation IUCN Category: Vulnerable.

Major threat: the coastal, Eastern Arc and Zimbabwean forest habitats of this species are subject to intense human pressure and are fragmenting.

Measurements

Myonycteris relicta

FA: 70.9 (65–75) mm, n = 9

WS: n. d.

HB: 102.5 (90–115) mm, n = 6

T: 9.1 (5–14) mm, n = 7

E: 18.8 (17–20) mm, n = 7

Tib: 27.4 (26–29) mm, n = 3

HF: 16.5 (9–22) mm, n = 8

WT: 51.2 (48–54) g, n = 5

GLS: 36.7 (35.5–39.2) mm, n = 10

GWS: 21.4 (20.6–22.5) mm, n = 9

C– M^2 : 13.5 (12.9–14.9) mm, n = 10

Kenya, Tanzania, Zimbabwe (Bergmans 1980, 1997, Schlitter & McLaren 1981, D. Kock unpubl.)

Key References Bergmans 1980, 1997; Cotterill 1995.

P. J. Taylor

Myonycteris torquata LITTLE COLLARED FRUIT BAT

Fr. Petite myonctère; Ger. Kleiner Halskrausen-Flughund

Myonycteris torquata (Dobson, 1878). Cat. Chiroptera Brit. Mus., p. 71, 76. Northern Angola, restricted to area of Golungo Alto by Crawford-Cabral (1986).

Taxonomy Originally *Cynonycteris torquata*. Placed in subgenus *Myonycteris* by some authors, but see Genus *Myonycteris*. Synonyms: *collaris*, *leptodon*, *wroughtoni*. Subspecies: none. Chromosome number (Cameroon, Gabon): $2n = 36$; $aFN = 66$ (Haiduk *et al.* 1981, Primus *et al.* 2006).

Description Small fruit bat with no basal ear-patches; no white markings on head; no epaulettes; no mantle; ♂♂ with ruff of stiff hairs; interfemoral membrane entirely covered by pelage; six lower cheekteeth; FA: 56–67 mm. Sexes similar except for ruff. Pelage dense, silky; extending half to two-thirds of way along forearm and marginally onto wing, along leg (but not as far as ankle) and over the entire interfemoral membrane; mid-dorsal hairs 6–7 mm. Dorsal pelage variable, rich dark rusty-brown to medium yellowish-brown, head, neck and shoulders usually paler and greyer: hairs unicoloured or with pale brownish-grey at base. No epaulette or white marking on shoulder. Ventral pelage slightly paler than dorsal pelage, medium brown to greyish-brown or pale grey. Juveniles darker than adults. Adults and juveniles of both sexes with a pronounced woolly throat ruff; adult ♂♂ with ruff of dense, coarse, brushy hairs, on chin, throat and upper chest, which are seasonally stained yellow-orange by oily secretions from underlying glands. Head without markings; muzzle moderately long and stout; cheeks only slightly expansible; lips thin and smooth. Ears dark brown with somewhat pointed tip. Palate usually with seven thick ridges, 1–3 undivided, 4–5 divided by narrow medial gaps (Figure 49a) but some variations are known (De Vree 1971, Bergmans 1976). Wing-membranes dark brown; attaching to second toe. Toes ‘webbed’ to middle of first phalanges or a little less.

Skull (Figures 46b and e, and 49c) short and delicate for an African fruit bat. Rostrum of medium relative length (ca. 34–35% of GLS). Dentition comparatively weak (cf. *M. relicta*) and simple; one or two lower incisors on each side; P^1 , M^2 and M_2 strongly reduced; M_3 usually present (cf. *M. relicta*) (Bergmans 1980, 1997). Posterior upper premolar (P^4) and first upper molar (M^1) oblong and subrectangular in occlusal outline, with longitudinal axes parallel to the line of the toothrow (Rosevear 1965). Dental formula usually $2^{132}/_{2133} = 34$ or $2^{132}/_{1133} = 32$, but other variations are known.

Geographic Variation No subspecies recognized by Bergmans (1976). There is some geographic variation in size with the smallest form (formerly *M. torquata*) in Cameroon, W Congo Basin and Angola, the largest form (formerly *M. wroughtoni*) in NE DR Congo and Uganda, and an intermediate form (formerly *M. leptodon*) west of the Niger R. (Bergmans, 1976).

Similar Species Four other African mainland species of fruit bats are small to medium-sized (FA: 56–107 mm) with no basal ear-patches and no other white or pale markings on the head:

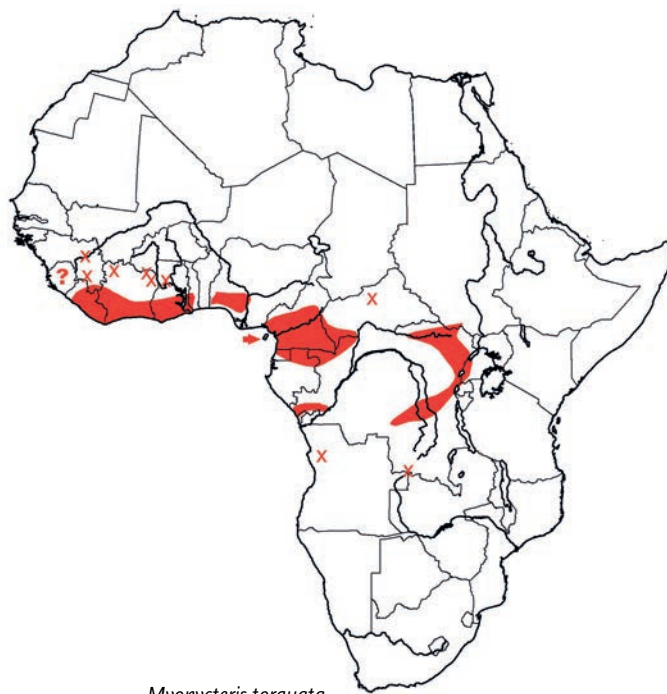
Myonycteris relicta. Usually smaller (FA: 65–75 mm; GLS: 35.5–39.2 mm). Interfemoral membrane with pelage only near legs. Five lower cheekteeth on each side.

Lissonycteris angolensis. Larger (FA: 68–90 mm). Tibia with pelage extending to ankle. Skull with premaxillae fused; posterior upper premolar and first upper molar squarish (occlusal view). Roosts in caves. More docile when handled.

Rousettus (2 spp.). Larger (FA: 82–106 mm). No ruff of coarse hairs.

Distribution Endemic to Africa. Recorded mainly from the Rainforest and Afromontane–Afroalpine BZs and the Rainforest–Savanna Mosaic, with marginal records in the Guinea Savanna and Zambezan Woodland BZs. Recorded disjunctly from Sierra Leone and Guinea to W Uganda and southwards to N Angola and S DR Congo, but absent from most of the Congolian rainforest. Also Bioko I. Recorded up to 1350 m. The exact locality of the specimen from Sierra Leone (the type locality of the form *leptodon*) is not known. Also recorded from Beletta Forest, Ethiopia, by Lavrenchenko *et al.* (2004): not mapped.

Habitat In central part of its distribution, most consistently associated with lowland rainforest, and appears to be most abundant in the canopy stratum (Cosson 1995). In West Africa, absent from savanna habitats in dry season (Jan–Apr), but penetrates into moist Rainforest–Savanna Mosaic and drier Guinea Savanna BZ in early wet season (Apr–May).



Myonycteris torquata

Abundance Various described as rare, uncommon and very common, depending on site, date and collector. Local abundance probably reflects changes in vertical stratification and seasonal migrations. In both Rainforest–Savanna Mosaic and Guinea Savanna BZ in Côte d'Ivoire, captures show a clear bimodal distribution with peaks in May–Jun and Nov–Dec, probably representing seasonal expansion from forest into savannas (Thomas 1983). Becomes the most common species in the Rainforest–Savanna Mosaic in the wet season (May–Jun).

Adaptations Very little is known. Flight 'has been described as slow and feeble' (Kingdon 1974). By day, one was found hanging from the branch of a *Combretum* tree, ca. 2 m above ground, directly exposed to the sunlight (Verschuren 1957), and there are two records of individuals hanging in bushes by day (Lang & Chapin 1917b, Rosevear 1965). Seasonal movements made by this fruit bat are described below (see Reproduction and Population Structure).

Foraging and Food Frugivorous. Little known about foraging behaviour and movements, but individuals captured at edge of gallery forest in Rainforest–Savanna Mosaic defecated *Solanum* seeds apparently from patches located several kilometres distant, suggesting wide foraging movements within single nights. Lack of any recaptures of banded individuals also suggests extensive movements. Has been described as a generalist, accepting a variety of soft fruits in captivity. Known to feed on figs *Ficus* and fruits of *Musa*, *Adenia*, *Solanum* and *Musanga* (Marshall 1985). The only systematic study of diet is from Guinea Savanna habitat where bitter *Solanum verbascifolium* fruits constitute 90% of diet (Thomas 1982). Apparently will visit flowers seasonally, as pollen (*Ceiba pentandra*?) was found on fur in Dec in Guinea Savanna. In captivity, the mean \pm S.D. nightly consumption of food (fruit) by ♂♂ was 50.0 ± 0.7 g ($n = 3$) and by ♀♀ was 55.5 ± 1.4 g ($n = 2$); mean consumption per unit body weight was $1.09 \text{ g/g}^{\text{bwt}}$; mean through-put time was 28 ± 12 min, and the percentage dry weight assimilated was 86% (Wolton *et al.* 1982).

Social and Reproductive Behaviour An adult ♂ was found roosting singly (Verschuren 1957), and a ♀ was found roosting with a half-grown young ♀ (Lang & Chapin 1917b). No other information.

Reproduction and Population Structure Litter-size: one ($n = 13$) (Jeffrey 1975). In Côte d'Ivoire, and also in Gabon, the reproductive chronology appears to be seasonal bimodal polyoestry. In Côte d'Ivoire (see below), births probably occur in Feb–Mar and ca. six months later in Aug–Sep (as in *Micropteropus pusillus*) – this is based on the observation that 87% of ♀♀ at Lamto were palpably pregnant with small embryos in May–Jun, and 100% of parous ♀♀ at Taï N. P. ($n = 26$) were pregnant with small fetuses in Nov (Thomas 1983). Near the Equator in Gabon, births occur Dec–Jan and in Jun (Brosset 1966). Length of gestation and lactation, and the timing of oestrus and mating are not known at either locality.

Myonycteris torquata is remarkable for sex- and age-related seasonal movements in Côte d'Ivoire, elucidated from capture numbers at Taï N. P. (05° 30' N; Rainforest BZ), Lamto (06° 13' N; Rainforest–Savanna Mosaic) and Wango Fitini (09° 50' N, Guinea Savanna BZ) (Thomas 1983). During the dry season (Nov–Mar), they are common in the Rainforest BZ and not captured in the Rainforest–Savanna Mosaic nor in the Guinea Savanna BZ. At the onset of the wet season (Apr–May), ♂♂, and to a lesser extent ♀♀, expand northwards into savanna habitats in the Rainforest–Savanna Mosaic, creating a peak in population numbers at Lamto in May–Jun. Only ca. 75% of these ♂♂ are mature and have throat ruffs, and ca. 87% of the ♀♀ are pregnant. All of the ♀♀ apparently then return to the rainforest in time to give birth later in the wet season (Aug–Sep). In contrast, at least some of the ♂♂ follow the inter-tropical front (and the rains) further northwards into the Guinea Savanna BZ, reaching Wango Fitini, for example, during the wettest months at that latitude. While in the north, testicular growth occurs in all of the ♂♂, and an oily exudate develops on the throat ruff. On the return journey, they pass through the Rainforest–Savanna Mosaic in Oct–Dec and create a second 'males only' peak in population numbers. These ♂♂ then return to the Rainforest BZ in time for the Feb–Mar births and presumably participate in the following mating season (having been absent from the Rainforest during the mating season that followed the Aug–Sep births).

Predators, Parasites and Diseases No information.

Conservation IUCN Category: Least Concern.

Measurements

Myonycteris torquata

FA: 61.3 (56–67) mm, $n = 73$

WS (d): ca. 280–305 mm*

HB: 107.9 (88–120) mm, $n = 50$

T (♂♂): 8.0 (0–13) mm, $n = 42$

E: 17.4 (13–21) mm, $n = 44$

Tib: 25.7 (22–28) mm, $n = 14^\dagger$

HF: n. d.

WT: 41.5 (27–60) g, $n = 50$

GLS: 33.1 (30.2–35.2) mm, $n = 71$

GWS: 19.4 (18.2–21.6) mm, $n = 71$

C–M²: 12.2 (11.0–13.3), $n = 73$

Throughout geographic range (derived from Bergmans 1976, 1997)

*Rosevear 1965

†West Africa only

Key References Bergmans 1976, 1997; Brosset 1966; Cosson 1995; Marshall 1985; Thomas 1982, 1983.

Don Thomas & Mickaël Henry

GENUS *Nanonycteris*

Veldkamp's Dwarf Epauletted Fruit Bat

Nanonycteris Matschie, 1899. Die Fledermäuse des Berliner Museums für Naturkunde. I. Megachiroptera, pp. 36, 58.

Type species: *Epomophorus veldkampii* Jentink, 1888.

Nanonycteris is a monotypic genus, endemic to Africa, and found in western tropical Africa from Guinea to Central African Republic, mainly in the Rainforest BZ and the adjacent Northern Rainforest–Savanna Mosaic. Diagnostic characters: white basal ear-patches but no other white markings on head; FA: 46–54 mm; ♂♂ on average smaller than ♀♀; epaulettes in adult ♂♂, muzzle slender and simple; interfemoral membrane well developed and with calcars; four thick interdental palatal ridges and 8–9 thin ridges of which only the posterior group is narrowly divided; postdental bony palate very short and broad, its lateral margins more or less parallel; C–M¹: 6.8–7.7 mm; usually three upper and five lower cheekteeth (very occasionally four upper cheekteeth) (Table 11, p. 228). Selected characters of *Nanonycteris veldkampii* are illustrated in Figure 50.

Nanonycteris was described as a subgenus of *Epomophorus*, but raised to generic status by Andersen (1912a). *Nanonycteris* was placed in the epomophorine section of Andersen (1912a); he considered it to be closely related to *Scotonycteris* and *Casinycteris*, and grouped these genera in the ‘*Nanonycteris* branch’. Bergmans (1997) classified *Nanonycteris* as a member of the tribe Epomophorini within the subfamily Epomophorinae. This is supported by recent phylogenetic analyses in which *Nanonycteris*

grouped with other epomophorine genera, i.e. *Epomophorus*, *Epomops*, *Hypsignathus* and *Micropteropus* (Springer *et al.* 1995, Jones *et al.* 2002). However, Romagnoli & Springer (2000) found *Nanonycteris* as a basal member of a clade including the genera mentioned above plus *Scotonycteris* and *Casinycteris*. According to their results, *Nanonycteris* and *Plerotes* would form the basal stem of an extended epomophorine clade, i.e. similar to the arrangement of Andersen (1912a) except that *Scotonycteris* and *Casinycteris* would represent a derived epomophorine clade.

The single species is *Nanonycteris veldkampii*.

Jakob Fahr



Nanonycteris veldkampii female.

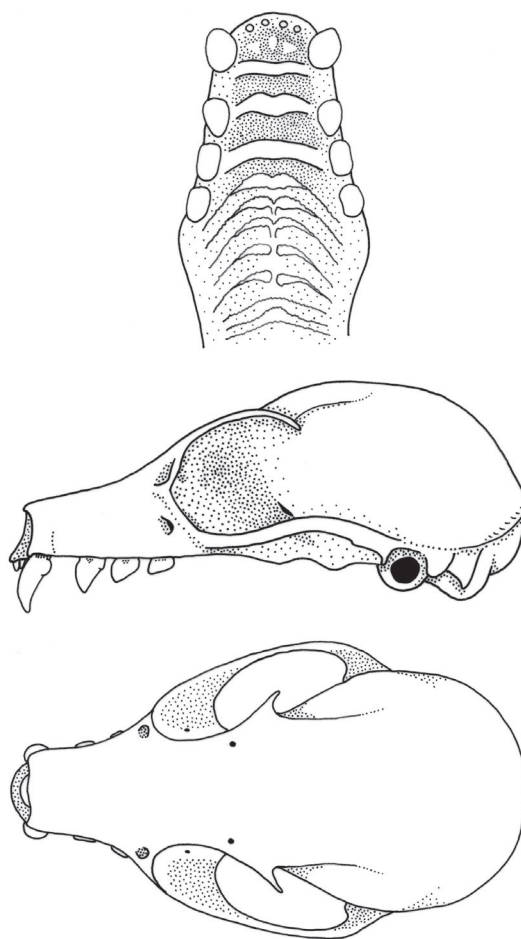


Figure 50. *Nanonycteris veldkampii*. Palatal ridges. Skull (RMCA RG 35013).

Nanonycteris veldkampii VELDKAMP'S DWARF EPAULETTED FRUIT BAT

Fr. Roussette naine de Veldkamp; Ger. Veldkamps Zwergflughund

Nanonycteris veldkampii (Jentink, 1888). Notes Leyd. Mus. 10: 51. Buluma, Fisherman L., Liberia.

Taxonomy Originally *Epomophorus veldkampii*. Synonyms: none. Sometimes spelled *N. veldkampii* but the correct spelling is *veldkampii*. Chromosome number: not known.

Description Very small fruit bat with anterior and posterior basal ear-patches but no other white markings on head; epaulettes on adult ♂♂; 8–9 thick or partly thick palatal ridges; FA: 46–54 mm. Not easily distinguished from *Micropteropus pusillus* except by palatal ridges. Sexes similar in colour; ♂♂, on average, with slightly smaller body measurements. Pelage dense, soft; mid-dorsal hairs 6–7 mm. Dorsal pelage brown, reddish-brown, greyish-brown to pale brown. Ventral pelage much paler. Adult ♂♂ with a white or yellowish epaulette on each shoulder (retracted into pouch except when displayed; sometimes stained yellow by pollen in dry season); ♀♀ with patch of soft, off-white hairs on each shoulder. Head with anterior and posterior basal ear-patches; muzzle moderately short, very slender, evenly tapering; lips slightly expansible (more wrinkled in adult ♂♂). Ears dark brown, naked, narrow. Eyes large, yellowish-brown. Palate with three narrow but thick ridges (the first two undivided, the third usually undivided, rarely notched, or very narrowly divided), 5–6 ridges, which are thick in middle, notched anteriorly or divided by narrow gap, and have serrated, backward-directed lateral arms, and 3–4 thin ridges (Figure 50). Wing-membranes dark brown; attaching to second toe. No visible tail.

Skull (Figure 50) short and delicate for an African fruit bat. Braincase rounded and deflected against rostrum. Rostrum of medium relative length (34–37% of GLS) and slender. Zygomatic arches slender. Postdental palate very broad, about same width as distance between upper molars. Upper toothrow short, not nearly reaching ventral margin of orbital cavity. Dentition comparatively weak. Dental formula $^{2121}_{2132} = 28$ (P¹ present very occasionally).

Geographic Variation None.

Similar Species Thirteen other species of fruit bats have simple muzzles; basal ear-patches but no other markings on head; adult ♂♂ with epaulettes; three upper and five lower cheekteeth:

Micropteropus pusillus. Six palatal ridges; muzzle broader at tip; lips more expansible. Sympatric in West Africa, Cameroon, Central African Republic.

M. intermedius. Six palatal ridges. Not sympatric.

Epomophorus (8 spp.). Six thick palatal ridges.

Epomops (3 spp.). Three or five thick palatal ridges. Larger (FA: >76 mm).

Distribution Endemic to Africa. Recorded from the Guinea Savanna BZ, Northern Rainforest–Savanna Mosaic, Rainforest BZ (West and West Central Regions) and Afromontane–Afroalpine BZ. Known from Guinea and Sierra Leone to C and SW Cameroon, and Bangui in Central African Republic. Additional specimens from the

*Nanonycteris veldkampii*

apparent gap between C Cameroon and Central African Republic are necessary to establish a more complete picture of the eastern part of the distribution.

Habitat This migratory species occupies a wide range of habitats (see also Adaptations). In Rainforest BZ, found mainly in farmland, small-scale plantations and secondary forest; also found in coastal and montane forest and (rarely) in undisturbed lowland rainforest (Coe 1975, Jeffrey 1975, Bergmans 1989). Has also been found in mangroves. Within Guinea Savanna BZ and Rainforest–Savanna Mosaic, mainly found where gallery and relict forests are present (Van Orshoven & Van Bree 1968, Marshall & McWilliam 1982, J. Fahr unpubl.). Not yet recorded from wettest parts of S Liberia and SW Côte d'Ivoire; rarely recorded from Dahomey Gap. Mostly found at lower altitudes, but found up to 1200 m on Mt Nimba, Liberia (Verschuren 1976).

Abundance Locally rare to very common, depending on habitat and season. In Jul–Aug (wet season), more common than *Micropteropus pusillus* and *Epomophorus gambianus* in the Guinea Savanna BZ at Mole N. P., Ghana (245 of 379 individuals; Marshall & McWilliam 1982). In the Guinea Savanna BZ of Comoé N. P., Côte d'Ivoire, comprised 22% of fruit bats captured in wet season (n = 1528) and was the second most abundant species (after *M. pusillus*) in a community of nine species of fruit bats (J. Fahr unpubl.). In *Borassus*-savanna with gallery forest at Lamto, Côte d'Ivoire, comprised only 1.7% of fruit bats captured in wet season (n = 2071) and was the seventh most abundant species in a community of nine species of fruit bats (Thomas 1982). In undisturbed rainforest of Tai N. P., Côte d'Ivoire, comprised only 0.6% of fruit bats

captured throughout year ($n = 1216$; J. Fahr & S. Pettersson unpubl.); rarest species in community of eight species of fruit bats. However, along disturbed fringes of Tai N. P. during dry season, comprised 9.9–29.4% of fruit bats captured (Thomas 1982, T. Gordon pers. comm.). At Mt Nimba, comprised 16.5–25.3% of fruit bats captured; either the most or second most abundant species (after *Myonycteris torquata*) in a community of ten species of fruit bats if study period included the dry season (Coe 1975, Verschuren 1976, A. Forbes-Watson in Wolton *et al.* 1982). In contrast, completely absent during wet season (Wolton *et al.* 1982).

Adaptations Flight faster and more agile than that of *E. gambianus* (Baker & Harris 1957). Day-roosts mostly unknown. Local people of Mt Nimba region, Liberia, report roosting in old barbet (Capitonidae) and woodpecker (Picidae) holes, and one individual was found in such a situation in a newly felled tree (Coe 1975). Seasonally migratory (Thomas 1982, 1983). During dry season (Oct–Feb), resident in Rainforest BZ of West Africa (Coe 1975, Wolton *et al.* 1982, J. Fahr & S. Pettersson unpubl.). At onset of wet season (Mar–Apr), both sexes migrate northwards, inhabiting the Rainforest–Savanna Mosaic (e.g. Lamto, Côte d’Ivoire) in Mar–Jun with a peak in catch-rate in Apr, and the Guinea Savanna BZ (e.g. Wango Fitini, S Comoe N. P.) in Apr–Jul with peak in catch-rate in May (Thomas 1983, J. Fahr unpubl.). In the Sudan Savanna further north (e.g. Wango Fitini, Mole N. P.), recorded during Apr, May, Jul and Aug (Marshall & McWilliam 1982, Thomas 1982, J. Fahr unpubl.). At end of wet season in the north, all but a few return to Rainforest BZ via the Rainforest–Savanna Mosaic, where they have been recorded in Aug–Jan with a second peak in catch-rate in Oct (Thomas 1982). Small numbers of this species remain in the Guinea Savanna BZ (Comoe N. P.) between Oct and Dec (J. Fahr & N. Ebigo unpubl.). Possibly the temporal and spatial pattern of the southward migration is more diffuse. During this time, many trees such as *Adansonia digitata*, *Ceiba pentandra*, *Kigelia africana* and *Parkia biglobosa* are flowering and are exploited by this bat (see below). The distance between rainforest and savanna locality records indicates a round-trip migration of 300–1100 km, depending on the width of the respective vegetation zones in a given region (Thomas 1982, 1983, J. Fahr unpubl.). Preliminary data from Ghana suggest that this bat also moves south during the wet season where suitable habitat is available (J. Fahr unpubl.). In the savanna-dominated Accra Plains south of the rainforest zone, it has been recorded during Mar, Jul, Aug and Sep. In this area, movements might be rather local between the rainforest and adjacent coastal savannas.

Foraging and Food Feeds on figs, fruits, nectar and pollen. Capture data, using mist-nets 0–25 m above ground in Comoe N. P., suggest preferential foraging fairly near ground and comparatively close to vegetation (median capture height 4.9 [0.9–23.6] m, $n = 332$) (J. Fahr unpubl.). Activity, based on frequency of captures, is fairly continuous throughout night with three indistinct peaks (around 20:00h, 23:00h and 01:00h), and least activity around 03:00h. In Mole N. P., Ghana, sometimes forages later than *Micropteropus pusillus*, and has major activity between 22:00h and 02:30h (Marshall & McWilliam 1982). Also observed to visit flowering *Parkia* trees later than *E. gambianus*, and to harass this larger species which then usually flew away (Baker & Harris 1957). However, *N. veldkampii* (and/or *M. pusillus*) sometimes visits flowering or fruiting trees

in mixed-species flocks of 15–20 bats, including *E. gambianus* and/or *M. pusillus*, but the arrival and departure of the different species was not highly synchronized (Marshall & McWilliam 1982). Diet includes fruits, nectar and pollen. Probably better adapted to nectarivory than *M. pusillus* (Marshall & McWilliam 1982) but not entirely nectarivorous as assumed by Wilson (1973). Flowering trees visited include *Kigelia* sp., *Adansonia digitata*, *Ceiba pentandra*, *Eperua falcata*, *Maranthes polyandra*, *Parkia biglobosa* and *Protea elliptica* (Baker & Harris 1957, Harris & Baker 1959, Lock & Marshall 1976, Lack 1978, Dobat & Peikert-Holle 1985). Marshall & McWilliam (1982) questioned some of the identifications based on observations of flying bats because *N. veldkampii* is easily confused with *M. pusillus*. Baker & Harris (1957) and Harris & Baker (1959) made detailed observations and photographed the visits to the pendulous inflorescences of *Parkia biglobosa*: individuals approached an inflorescence, clasped it with the wings and licked the nectar while holding on with their thumbs; visits lasted 1–30 sec. In contrast, when taking nectar from *Ceiba pentandra*, they land on the branches, crawl over them and lap from flowers as they encounter them (Baker & Harris 1959). During peak flowering of *C. pentandra* (Nov–Dec) these bats are stained bright yellow by the pollen, mistakenly attributed to a particular fruit by Coe (1975). Also feeds on figs *Ficus umbellata* and fruits of *Vitellaria paradoxa*, *Cola cordifolia*, *Solanum erianthum*, *Mangifera indica*, *Carica papaya*, *Psidium guajava* and *Musa* spp. (Baker & Harris 1957, Ayensu 1974, Coe 1975, Marshall & McWilliam 1982, Thomas 1982, J. Fahr unpubl.). Captive bats ingest 1–2 times their body weight per day, and gain ca. 1.5 g between dusk and dawn (Coe 1975, Marshall & McWilliam 1982). According to Coe (1975), single bats consumed much more in captivity than groups of bats although all were fed *ad libitum*.

Social and Reproductive Behaviour Males probably call during the night to attract ♀♀ (as do other epauletted fruit bats). Monotonously repeated high-pitched calls were heard frequently in gallery forests and relict forests in Comoe N. P. The unseen animals appeared to call solitarily, from widely spaced perches high in the trees. Temporarily caged ♂♂ responded by making identical calls, so the unseen callers were probably also *N. veldkampii*. Males presumably display their epaulettes during courtship as do other epauletted fruit bats.

Reproduction and Population Structure Litter-size: one. Reproductive chronology uncertain but records from West Africa (Guinea, Côte d’Ivoire, Liberia and Ghana combined) include evidence of polyoestry and some evidence that ♀♀ are not in close reproductive synchrony, which suggests that births occur either aseasonally or during fairly extended seasons. Several sympatric species of fruit bats exemplify polyoestry at these localities, but none are known to have extended seasonal or aseasonal parturition. The simultaneous occurrence of lactation and pregnancy has been observed (Thomas 1982, J. Fahr unpubl.), indicating that polyoestry and postpartum oestrus occur in at least some ♀♀. Percentages of pregnant ♀♀ exceeding 50% of all ♀♀ captured (including subadults) have been reported in Nov–Dec (75%, $n = 13$; Coe 1975) and also in May (55%, $n = 87$, J. Fahr unpubl.), indicating that many births occur during at least two seasons. Furthermore, in Jul–Aug, almost 50% of the ♀♀ were either pregnant or lactating while the remainder were immature ($n = 49$; Marshall & McWilliam

1982), which also indicates births during more than one season. However, pregnancies have been reported in all months except Sep (for which there are no data), and lactation has been observed during all months except Sep and Mar (Van Orshoven & Van Bree 1968, Coe 1975, Jeffrey 1975, Verschuren 1976, Marshall & McWilliam 1982, Thomas 1982, Lim & Van Coeverden de Groot 1997, J. Fahr unpubl.). These observations indicate a lack of close reproductive synchrony, but whether the chronology is aseasonal or extended seasonal polyoestry remains to be determined and, although ♀♀ are not likely to have more than two litters/year, this and the length of gestation are not yet known.

When capture data for a whole year are combined, the ratio of ♂♂ to ♀♀ is close to unity, e.g. 1 : 1.3 (n = 342) in Comoé N. P., Côte d'Ivoire (J. Fahr unpubl.). Contrary to Thomas (1982), there is at least some partial segregation of the sexes during migration. In Comoé N. P., captures were dominated by ♀♀ between Mar and Jun and by ♂♂ during Jul, Oct and Dec. Between Dec and Mar, Verschuren (1976) found a ratio of 1 ♂ : 3.2 ♀ (n = 42) at Mt Nimba, Liberia. According to Wolton *et al.* (1982), ♀♀ arrive on their southward migration one month later in the rainforest zone than ♂♂.

Predators, Parasites and Diseases Ectoparasites include a mite *Binuncus (Binuncus) myonycteris* (Acari: Myobiidae) (Uchikawa 1986).

Conservation IUCN Category: Least Concern.

Large-scale degradation of habitat might disrupt pattern of migration.

Measurements

Nanonycteris veldkampii

FA (♂♂): 47.1 (46–52) mm, n = 88

FA (♀♀): 50.6 (47–54) mm, n = 112

WS (c): 340 (300–378) mm, n = 10

HB (♂♂): 74.2 (69–80) mm, n = 28

HB (♀♀): 81.5 (75–87) mm, n = 14

T: 2.5 (1–4) mm, n = 26

E: 16.7 (14–18) mm, n = 43

Tib: 19.5 (17–22) mm, n = 9

HF (♂♂): 14.2 (12–16) mm, n = 29

HF (♀♀): 14.8 (13–16) mm, n = 12

WT (♂♂): 20.4 (16.0–27.0) g, n = 109

WT (♀♀): 24.9 (19.0–36.0) g, n = 131

GLS: 25.8 (23.6–27.1) mm, n = 37*

GWS: 14.9 (14.5–15.3) mm, n = 14*

C–M¹: 7.2 (6.8–7.7) mm, n = 20*

Guinea, Liberia, Côte d'Ivoire, Ghana, (FC, IRSN, RMCA, ROM, SMF, USNM, J. Fahr unpubl.)

*Throughout geographic range (Bergmans 1989)

Key References Bergmans 1989; Harris & Baker 1959; Marshall & McWilliam 1982; Thomas 1982, 1983; Wolton *et al.* 1982.

Jakob Fahr

GENUS *Plerotes*

Anchieta's Broad-faced Fruit Bat

Plerotes K. Andersen, 1910. Ann. Mag. Nat. Hist., ser. 8, 5: 97. Type species: *Epomophorus anchietae* Seabra, 1900.

Plerotes is a monotypic genus, endemic to Africa. Diagnostic characters: white basal ear-patches (sometimes inconspicuous); no other white markings on the head; FA: 47–53 mm; adult ♂♂ without epaulettes; muzzle simple; interfemoral membrane greatly reduced; calcars absent; four curved undivided palatal ridges followed

by 4–5 serrated ridges, which are more or less divided; four or five upper cheekteeth and five or six lower cheekteeth (Table 11, p. 228). Selected characters of *Plerotes anchietae* are illustrated in Figure 51.

Plerotes was placed in the *Epomophorus* section of Andersen (1912a) and *Epomops* was considered to be its nearest ally (Andersen 1910,

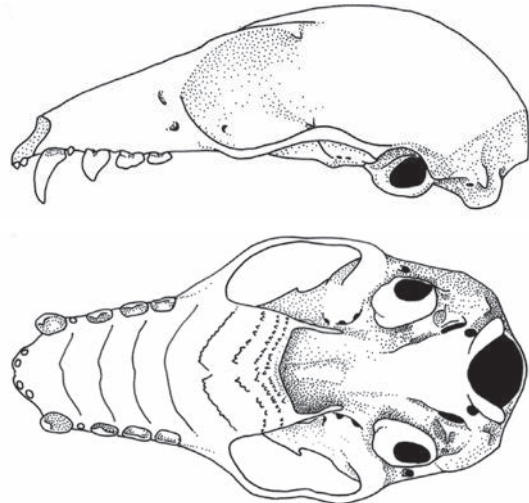
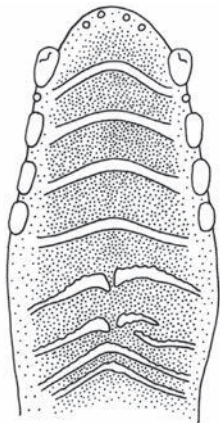


Figure 51. *Plerotes anchietae*. Palatal ridges drawn from skull with dried soft palatal tissue *in situ* (BMNH 43.45). Skull (neotype, immature ♀) (based on Bergmans 1982 with permission of the author): the ventral view also shows dried soft palate *in situ* and Bergman (1982) notes that it masks the margin of the post-dental palate.

1912a). Cladistic analyses of 33 morphological characters placed *Plerotes* in the same clade as *Rousettus* and *Lissonycteris*, suggesting that it should be excluded from the *Epomophorus* section (Springer *et al.* 1995). Bergmans (1997) retained *Plerotes* within Epomophorinae, Tribe Plerotini, but later (based on Springer *et al.* 1995 and new information from Kock *et al.* 1998a) W. Bergmans (pers. comm.) expressed uncertainty about his placement of *Plerotes* within the Epomophorinae. The more recent cladistic analyses of Álvarez *et al.* (1999), Giannini & Simmons (2003) and others have not included *Plerotes* in their analyses, but N. P. Giannini & N. B. Simmons (pers. comm.) have unpublished data suggesting that *Plerotes* is better

placed in Epomophorinae than in Rousettinae.

The single species of *Plerotes* was originally assigned to *Epomophorus*, and then to *Epomops*. Andersen (1910) raised it to generic status on the basis of 11 characters of its skull and dentition that differentiate it from *Epomops*. The 11 characters are listed and discussed by Bergmans (1989). Since Andersen, the generic status of *Plerotes* has not been disputed.

The single species is *Plerotes anchietae*.

Meredith Happold

Plerotes anchietae ANCHIETA'S BROAD-FACED FRUIT BAT (BENGUELA FRUIT BAT)

Fr. Plérote d'Anchieta; Ger. Anchietas Breitgesicht-Flughund

Plerotes anchietae (Seabra, 1900). J. Sci. Math. Phys. Nat. Lisboa, ser. 2, 6: 116. Galanga, Benguela, Angola.

Taxonomy Originally *Epomophorus anchietae*. Synonyms: none. Chromosome number: not known.

Description Very small, pale greyish-brown fruit bat with yellowish-white moustache and beard, and posterior whitish basal ear-patches (sometimes inconspicuous) but no other white markings on head; no epaulettes; greatly reduced interfemoral membrane; four or five upper cheekteeth. Only 11 specimens known. Sexes apparently similar. Pelage soft; mid-dorsal hairs ca. 8 mm. Dorsal pelage uniformly pale greyish-brown; hairs pale creamy-brown with darker, greyish-brown at tip. Ventral pelage pale creamy-brown. No mantle or collar of contrasting pelage. No epaulettes, but both sexes with white spot on each shoulder and a whitish patch (sometimes inconspicuous) at the posterior base of each ear. Head with relatively broad muzzle. Eyes large, narrowly ringed with reddish-brown pelage and with band of reddish-brown pelage from each eye-ring to the nostril. Moustache of stiff yellowish-white hairs on upper lip, and beard of similar hairs on chin. According to Seabra (in Harrison 1960), there are cheek-pouches on each side of the muzzle surrounding the eye, but there is no evidence that these are sound-amplifying pouches as stated by Kingdon (1997). In contrast, Kock (pers. comm.) did not find pouches around the eyes of an adult male specimen, and Kock *et al.* (1998a) noted that the lips and cheeks do not stretch to form cheek-pouches, and that the lips are smooth. Ears brown. Palatal ridges simple; 1–4 curved and undivided, 5–8 serrated and more or less divided (Figure 51). Tongue with filiform papillae covering the tip (as in *Megaloglossus woermanni*), but the papillae are rather short (cf. greatly elongated in *Megaloglossus*) (Harrison 1960) (Figure 35c). Wing-membranes brown; attaching to second toe. No tail. Interfemoral membrane, uniquely, no more than a narrow flange; no calcars.

Skull (Figure 51) short and delicate for an African fruit bat. Rostrum of medium relative length and relatively broad. Dentition weak. Incisors minute; one or two upper incisors on each side; original function probably lost. Premolars long and narrow; anterior premolar (P^1) present but rudimentary. Molars simple, without cusps; M^2 , M_2 and M_3 rudimentary or absent. Cheekteeth $4/6$, $4/5$ or $5/6$ (some cheekteeth are prone to being deciduous), therefore dental formula very variable – maximally $2^{132}/_{2133} = 34$.

Geographic Variation None recorded. Apparently inhabits two separate areas, so intra-specific variation is likely (Bergmans 1989).

Similar Species None. Other fruit bats of similar size lack reddish-brown markings on the head, do not have a white moustache and beard, and do not have interfemoral membranes which are reduced to a very narrow flange.

Distribution Endemic to Africa. Appears to have a disjunct distribution in the Zambezian Woodland BZ and nearby Afromontane–Afroalpine BZ. Western range in Angola; eastern range in S DR Congo, N Zambia and Malawi. Map based on Bergmans (1989).

Habitat Most records are from wetter miombo woodland dominated by *Brachystegia*, *Julbernardia* and *Isoberlinia*, but some are from mosaics of the above with dry evergreen forest, and



Plerotes anchietae

afromontane vegetation. Recorded from 1000 to 2000 m, which suggests a preference for montane and sub-montane habitats, but this needs confirmation.

Abundance Uncertain. Very rarely collected (only 11 specimens).

Remarks Nothing is known about the habits of this species. The diet is not known (*contra* Kingdon 1997). The simplicity of the palatal ridges, the presence of filiform papillae on the tip of the tongue, the delicacy of the skull and the weakness of the dentition suggest a diet of pollen and perhaps also nectar, and the moustache and beard of stiff hairs perhaps serve to transport pollen. However, the tongue is not particularly long nor as extensible as it is in nectar-feeding fruit bats such as *Megaloglossus* (Harrison 1960). Based on the short tongue and Seabra's indication that cheek-pouches are present, Harrison (1960) concluded that the diet of *Plerotes* is unlikely to be solely nectar, and he suggested that it might consist partly of soft fruit and partly of pollens. One specimen (BMNH 63.45) was caught at a fruiting *Parinari curassifolia* tree, although it is not known whether it was feeding on the fruit. Consequently, the diet of *P. anchietae* is an intriguing mystery, which should be investigated if individuals are captured in the future.

Conservation IUCN Category: Data Deficient.

Major threat: deforestation.

Measurements

Plerotes anchietae

FA: 49.0 (47–53) mm, n = 11

WS: n. d.

HB: 82.4 (70–96) mm, n = 7

T: 0 mm, n = 7

E: 16.9 (15–18) mm, n = 7

Tib: 20.6 (19–24) mm, n = 5

HF: n. d.

WT: 20, 20 g, n = 2

GLS: 27.6 (25.4–29.5) mm, n = 7

GWS: 14.5 (13.6–16.2) mm, n = 7

C–M¹: 7.8 (7.2–8.6) mm, n = 10

Throughout geographic range (BMNH, IRSN, Bergmans 1989, Kock *et al.* 1998a). Includes some immature specimens

Key References Bergmans 1989; Kock *et al.* 1998a.

Meredith Happold

GENUS *Pteropus*

Flying-foxes

Pteropus Brisson, 1762. Regnum Animale, Ed. 2, pp. 13, 153. Type species: *Vespertilio vampirus niger* Kerr, 1792.



Pteropus seychellensis.

Pteropus is a polytypic genus with 65 species (Simmons 2005), the majority of which are found on islands in the Pacific and Indian Oceans. Two species occur on islands off the coast of East Africa. These species can be distinguished from other African fruit bats by the following characters: no white basal ear-patches; no white markings on the face; FA: 145–163 mm; dorsal pelage blackish-grey with a contrasting red or yellow mantle; no ruff of stiff hairs around the neck; five upper and six lower cheekteeth (Table 11, p. 228). The heads of the African species and craniodental characters of *P. voeltzkowi* are shown in Figure 52.

No species of *Pteropus* occurs on the African mainland, but *P. voeltzkowi* occurs on Pemba I. (where it is endemic), and a species currently considered to be *P. seychellensis comorensis* occurs on Mafia I. (and extraliminally in the Comoros). These species are considered closely related. Speciation is facilitated by the isolation of populations on islands, so it is not surprising that there is a high level of endemism on the islands of the W Indian Ocean: eight species (nine subspecies) on nine islands or clusters of islands. Five of these islands or island-clusters are inhabited by only one species but, currently or in the recent past, three islands (Comoros, Réunion, Mauritius) have two sympatric species, which shows that the process of speciation in *Pteropus* of the Indian Ocean took place long ago and that colonization of some of the islands has occurred more than once.

Flying-foxes are very large fruit bats. Those for which data are available have low aspect ratios and extremely high wing-loadings (Norberg & Rayner 1987). Although their flight can appear laboured and not particularly fast, some species fly 40–60 km from roost to feeding-ground and back again in one night, and satellite-tracking of two individuals showed that some *Pteropus poliocephalus* make migratory round-trip journeys of at least 2000 km along the east coast of Australia (Tidemann & Nelson 2004). Furthermore, one Australian flying-fox flew ca. 2000 km to New Zealand (Daniel 1975). At least one species, *Pteropus poliocephalus* in coastal Australia, uses prevailing winds for assistance (Tidemann & Nelson 2004), and some species have become specialist gliders, which soar on updrafts and then glide most of the way to their feeding-grounds (Norberg *et al.* 2000). Some flying-foxes land gracefully by flying slowly over

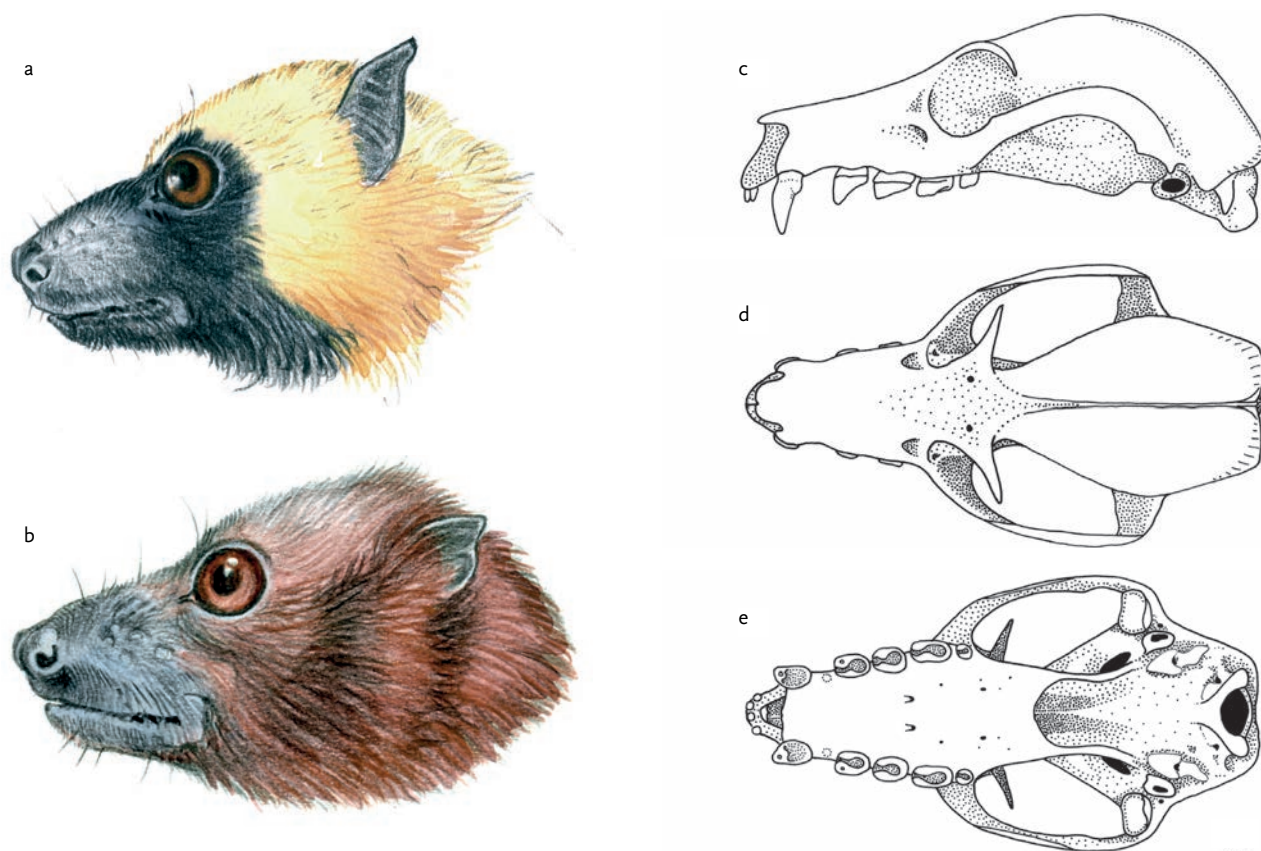


Figure 52. African *Pteropus*. (a) Head of *P. seychellensis comorensis*. (b) Head of *P. voeltzkowi*. (c), (d) and (e) Skull of *Pteropus voeltzkowi* (BMNH 55.163, adult ♂). The minute anterior upper premolar is absent in this specimen: in the ventral view, its position is shown by dotted circle between the canine and second premolar on each side.

a perch, grasping it with the hindfeet and then toppling down into the hanging position. Others often make crash-landings into foliage or onto bunches of fruit or flowers. However, unlike most African fruit bats, they are very agile climbers. The fingers fold the wing-membranes close to the forearms, which then resemble long legs with a large hook (the clawed thumb) at the end. Flying-foxes swing along under thin branches, holding on with the claws of the thumbs and toes, and moving the wings in alternation. They climb, head first, up or down vertical surfaces in a similar fashion. Flying-foxes also use their forearms and thumbs to pull fruits or flowers within reach and to manipulate food while eating. Some species on islands will often cross water to forage on other islands, and some occasionally swim in the sea albeit probably only after accidentally falling in (Bergmans 1978).

Flying-foxes inhabit forests and swamps, and most are found near coasts. Some species are found on continents and large islands; others (including *P. seychellensis comorensis* and *P. voeltzkowi*) are small-island specialists, which are often found on small islands near the coasts of much larger islands or continents. Flying-foxes feed mainly on the juices of soft fruits: pulp is crushed in the mouth and the juice swallowed; fibre and seeds are discarded. They also chew flowers to obtain juices and pollen. Most species roost in groups, ranging from about 20 to several hundreds of thousands, and their roosting-sites are usually referred to as camps. Flying-foxes hang freely from the branches, often choosing trees that rise above the forest canopy. Colonies of roosting flying-foxes may be divided into family groups,

territorial ♂♂ with harems, juvenile packs and/or guard groups that roost on the periphery and give warning of intruders. Vocal communication is sophisticated: *P. polycephalus* (in Australia) has more than 20 situation-specific calls (Churchill 1998). Some roosts or 'camps' may be used for many decades, and they are often remote from the feeding-grounds. Most flying-foxes are nocturnal, but some island species are partly diurnal. Most species have one young/litter and one litter/year with births occurring seasonally and in synchrony (Pierson & Rainey 1992).

The colonization, by *Pteropus*, of the African off-shore islands and the other islands in the W Indian Ocean has been discussed by authors including Kingdon (1974), Meirte (1984) and Bergmans (1997). These authors agree that *Pteropus* colonized these islands from Asia but the details are controversial and, as yet, unresolved. The presence of flying-foxes on Pemba I. and Mafia I., but not on the mainland, has led to the conjecture that flying-foxes, spreading westwards from islands in the Indian Ocean, may not have been able to compete against the fruit-eating mammals on the African mainland. However, on Pemba I., *P. voeltzkowi* successfully co-exists with other fruit-eaters including three other fruit bats (*Eidolon helvum*, *Rousettus aegyptiacus*, *Epomophorus wahlbergi*), a monkey *Cercopithecus aethiops nesiotes* (now *Chlorocebus pygerythrus*) and a Greater Galago *Galago crassicaudatus agisymbanus* (now *Otolemur garnetti*) (Moreau & Pakenham 1940, Kingdon 1974). Another conjecture is that flying-foxes may have been too vulnerable to predators to survive on the mainland. However, Pemba I. has

several species of owls and falcons, a python and a monitor lizard and, on the mainland, other sorts of carnivores are not important predators of fruit bats. The majority of flying-foxes are island specialists, which led Kingdon (1974) to ask 'what is peculiar to islands that might eventually leave its mark on fruit bats which have adapted to living on them?' It has been suggested that *Pteropus* might depend on seawater as a source of salts, which would prevent them from inhabiting central parts of Africa (Kingdon 1990), but this does not explain why they do not live along coastal Africa (McNab & Armstrong 2001). Nevertheless, it is curious that the vast majority of species in this genus are restricted to coastal areas and small islands, and there are anecdotal reports of *Pteropus* flying out to sea, dipping their muzzles into the water and appearing to drink (Iudica & Bonaccorso 2003). It is not yet known if they can assimilate mineral salts from ingested seawater, but ascertaining this might lead to an explanation as to why most species live near the sea (Iudica & Bonaccorso 2003). The reproductive biology of 23 species of *Pteropus* was reviewed by Pierson & Rainey (1992); all

are monotocous and, for most species, the chronology is restricted seasonal monoestry; gestation is on average 5.5 months; young become volant at ca. three months and are weaned at 4–6 months; ♀♀ reach reproductive maturity at 1.5–2.0 years.

Pteropus was placed in the *Rousettus* section of Andersen (1912a), but was placed in the subfamily Pteropodinae (tribe Pteropodini) by Bergmans (1997) (see family profile). Andersen (1912a) divided the species into 17 groups of which only the *niger* group is represented in Africa. The African representatives are:

P. seychellensis comorensis. Mantle bright yellow or brownish-yellow; face with dark mask (Figure 52a). Mafia I. and extraliminally Comoros.

P. voeltzkowi. Mantle bright rusty-red; face without dark mask (Figure 52b). Pemba I. only.

Meredith Happold

Pteropus seychellensis SEYCHELLES FLYING-FOX

Fr. Grande roussette des Seychelles; Ger. Seychellen-Flugfuchs

Pteropus seychellensis Milne-Edwards, 1877. Bull. Sci. Soc. Philom. Paris, ser. 7, 2: 221. Marianne I., Seychelles.

Taxonomy Species-group: *niger* – with *P. rufus* (Madagascar), *P. voeltzkowi* (Pemba I. [Tanzania]), *P. aldabrensis* (Aldabra Atoll) and *P. niger* (Reunion and Mauritius) (Koopman 1994). Synonyms: *comorensis*. Two subspecies are recognized by Bergmans (1990): *P. s. seychellensis* in the Seychelles and *P. s. comorensis* on four islands (Grande Comore, Anjouan, Mohéli and Mayotte) in the Comoros, and Mafia I. (Tanzania). However, recent studies of *Pteropus* in the Western Indian Ocean (O'Brien *et al.* 2009, Chan *et al.* 2011) have indicated that paraphyly exists in members of the *Pteropus seychellensis* complex, but the taxonomy of *P. seychellensis* is still in a state of flux (S. Goodman pers. comm.). For this reason, the *Pteropus* on Mafia I. is referred to here as *P. s. comorensis*, and the remainder of this account refers to this taxon. Because information from Mafia I. is limited, some data from the Comoros are included. Chromosome number: not known.

Description Very large, dorsally blackish-brown fruit bat with conspicuous bright yellow, pale gold or brownish-yellow mantle; fox-like head with dark face-mask; no ear-patches; no white markings on head; no epaulettes. Sexes similar. Pelage dense; mid-dorsal hairs ca. 14 mm. Dorsal pelage: crown golden-yellow or brownish-yellow; nape with longer, coarser (especially in ♂♂), golden-yellow or rusty-yellow pelage forming the mantle; back and rump blackish-brown, sometimes with scattered pale grey hairs. Dorsal hairs yellow or blackish-brown. Ventral pelage: chin and throat dark brown merging into bright orange, rusty-yellow or bright rusty-brown on chest, merging into dark brown with pale yellow wash on belly and flanks. Hairs on belly and flanks dark brown with yellow at tip. Muzzle long and tapering, giving head its fox-like appearance; muzzle and anterior half of face dark brown contrasting with the posterior half, which is yellow (Figure 52a). Ears pointed, naked, very dark brown. Wing-membranes very dark brown; attaching to

second toe. Interfemoral membrane well developed; in centre ca. 15 mm deep. No tail.

Skull long and robust for an African fruit bat. Rostrum of medium relative length. Dental formula $2^{132}/_{2133} = 34$.

Geographic Variation Two subspecies are recognized (but see Taxonomy). Specimens of *P. s. comorensis* from Mafia I. have more grey in the dorsal pelage, but variation between populations here and in the Comoros needs further analysis (Bergmans 1990).

Similar Species Two other species of large African fruit bats have no basal ear-patches; no white markings on head; FA: >108 mm:

Pteropus voeltzkowi. Mantle rusty-brown ('red'); no dark face-mask. Pemba I. only.

Eidolon helvum. Dorsal pelage usually pale and yellowish, no mantle. Smaller (FA: 105–135 mm). Mainland and islands including Pemba I. and Mafia I.

Distribution Currently, *P. s. comorensis* is considered to occur on Mafia I. off the coast of Tanzania and, extraliminally, Comoros. Moreau & Pakenham (1940) suggested that immigrant Comorians possibly imported the fruit bats to Mafia I. from Comoros as a potential source of food.

Habitat *Pteropus s. comorensis* is a small-island specialist. Mafia I., area 622 km², lies ca. 20 km from the mainland. It is a recent continental island isolated in the Pleistocene (Moreau & Pakenham 1940). There are remnants of evergreen forest (once widespread), and East African coastal forest mosaic, mangroves, palms and swamps. No rivers, many pools. Wet season (85% of rainfall) Dec–May, but rain in all months. On Comoros, this fruit bat roosts



Pteropus seychellensis

between sea level and 720 m and utilizes lowland and agricultural areas to a greater extent than the sympatric *P. livingstonii*, which roosts at higher altitudes and is more dependent on primary upland forest (Trehwella *et al.* 2001).

Abundance No recent information for Mafia I. except that two camps were seen in Oct 1990 (N. Payne in Mickleburgh *et al.* 1992). Common in Comoros.

Adaptations Aspect ratio very low; wing-loading exceptionally high. Able to glide, but spends the majority of its flight-time flapping rather than gliding, and is less well adapted for soaring than *P. livingstonii* (Norberg *et al.* 2000). By day, hangs freely from branches of shaded trees including *Ceiba*, *Tamarindus* and *Casuarina*. In Comoros, camps are sited where topographical features such as ravines and volcanic craters give protection from high winds, facilitate thermoregulation, and create updraughts, which may help the bats gain height before they set off towards feeding-grounds, which may be 5 or more kilometres away (Cheke & Dahl 1981). Individuals urinate on their wings and fan themselves to achieve evaporative cooling. They leave their roosts early in the afternoon, probably to maximize the use of updraughts and gliding to reach distant feeding-grounds with minimal loss of energy and minimal production of heat generated by flapping the wings (Norberg *et al.* 2000). From the late afternoon until shortly after sunset, individuals have been observed flying a short distance out to sea and then flying down to dip their hind-quarters into the down-slope of incoming waves. The purpose of this behaviour is open to conjecture: possibly to obtain salts lacking in fruit. This complex manoeuvre was observed many times at close range and the bats were never seen to grasp anything with their hindfeet so it is unlikely that they were trawling fish or collecting floating fruits.

Foraging and Food Feeds on soft fruits, pollen, nectar and leaves (Mickleburgh *et al.* 1992, Trehwella *et al.* 2001). In Comoros,

individuals begin flying to feeding-grounds as early as mid-day, but most leave their roosts between 14:00h and 17:30h with a peak at 14:45h (Trehwella *et al.* 2001). They feed at intervals throughout the night, and most return to the roost during the hour before and the hour after sunrise. Diet is mainly the juices of figs *Ficus*, and soft fruits (including, in Comoros, those of *Ceiba*, *Terminalia*, *Vitex*, *Carica papaya* and a variety of other cultivated fruits) and nectar from *Ceiba* and *Erythrina* (Cheke & Dahl 1981, Trehwella *et al.* 2001). Trehwella *et al.* (2001) observed many more individuals in *Ceiba pentandra* trees when they were flowering than subsequently when they were fruiting. A preliminary examination of faecal samples suggested that there is little overlap in the fruits eaten by *P. s. comorensis* and *P. livingstonii* (Trehwella *et al.* 2001). On Mafia I., food plants include *Mangifera* (mango), *Musa* (banana), *Syzygium* (Java plum) and *Terminalia* (Tropical Almond) (Clark 1994 in Trehwella *et al.* 2001). An important cross-pollinator.

Social and Reproductive Behaviour Roosts in colonies (camps) of ca. 20 to more than 2000. Camps are often noisy during the day: individuals fly or clamber from perch to perch, often disturbing their neighbours and starting quarrels. Within each camp, there are different sorts of social groups: pairs of adults, harems comprised of one ♂ with several ♀♀, maternity associations of ♀♀ with young, and groups of subadults. Communication is vocal, visual, olfactory and tactile. Courtship behaviour includes a croaking cry and clapping and rattling of the wings, and it occurs within harems (Cheke & Dahl 1981).

Reproduction and Population Structure Litter-size: one. Reproductive chronology on Mafia I. not known. On Mafia I. one female with large nipples and one placental scar in right uterine horn was found dead in early Aug, and a subadult in late Jul (Kock & Stanley 2009). In the Comoros, the chronology is restricted seasonal monoestry with copulation during the transition between the wet and dry seasons in Apr–Jun (Cheke & Dahl 1981, Trehwella *et al.* 1995). Very small young, still clinging to their mothers, were observed in Jan (Trehwella *et al.* 1995), but the age of these young, and the timing of parturition, is uncertain.

Predators, Parasites and Diseases Humans are probably the main predators.

Conservation IUCN Category: Least Concern (as *P. seychellensis* including *P. s. comorensis*: assessed mainly from extralimital data).

Population trend is stable for nominate subspecies in Seychelles: no data for *P. s. comorensis*. Flying-foxes are particularly prone to electrocution on electricity wires (e.g. Verschuren 1985), and cyclones and severe storms probably reduce their population numbers.

Measurements

Pteropus seychellensis comorensis

FA (♂♂): 147–158 mm, n = 13

FA (♀♀): 151–154 mm, n = 4

WS: n. d.

TL: 202, 235 mm, n = 2*

T: n. d.

E: 35 mm, n = 2*
 Tib: 64.8 mm, n = 1*
 HF: 38, 49 mm, n = 2*
 WT: 370, 390 g, n = 2*
 GLS (♂♂): 65.2–68.2 mm, n = 12
 GLS (♀♀): 65.4, 65.6 mm, n = 2
 GWS (♂♂): 35.7–39.3 mm, n = 11
 GWS (♀♀): 35.1 mm, n = 1
 C–M² (♂♂): 23.6–25.4 mm, n = 14

C–M² (♀♀): 24.2, 24.4 mm, n = 2
 Throughout geographic range of this subspecies (Bergmans 1990)
 *Mafia I. only (Kock & Stanley 2009)

Key References Bergmans 1990; Cheke & Dahl 1981; Clark 1994; Mickleburgh *et al.* 1992; Trehwella *et al.* 2001.

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Pteropus voeltzkowi PEMBA FLYING-FOX

Fr. Grande rousette de Pemba; Ger. Pemba-Flugfuchs

Pteropus voeltzkowi Matschie, 1909. Sitzb. Ges. Naturf. Fr. Berlin, p. 486. Fufuni, Pemba I., Tanzania.

Taxonomy Species-group: *niger* – with *P. rufus* (Madagascar), *P. seychellensis* (Seychelles, Comoros and Mafia I. [Tanzania]), *P. aldabrensis* (Aldabra Atoll) and *P. niger* (Reunion and Mauritius) (Koopman 1994). Synonyms: none. *Pteropus voeltzkowi* shows strong morphological similarities to *P. seychellensis* but differs from *P. seychellensis* and other Indian Ocean *Pteropus* in the red colour of its mantle and, for this reason, has retained specific status (Bergmans 1990). Chromosome number: not known.

Description Very large, blackish-brown fruit bat with conspicuous bright rusty-red or rusty-orange mantle; fox-like head without dark face-mask; no ear-patches; no white face-markings; no epaulettes; found only on Pemba I. Sexes similar in colour; ♂♂ on average larger than ♀♀. Pelage dense; mid-dorsal hairs ca. 15 mm. Dorsal pelage: crown dark brown or rusty-brown, with some grey hairs; nape with longer, coarser, rusty-red or rusty-orange pelage forming the 'red' mantle; back and rump black, blackish-brown or dark reddish-brown with some pale grey or rusty-brown hairs. Dorsal hairs rusty-red or blackish-brown. Ventral pelage: chin and throat dark brown merging into dark golden-brown on chest and golden-brown on belly and flanks. In some individuals, the ventral pelage is more uniformly rusty-brown or dark brown becoming paler on the flanks. Muzzle long, tapering, giving head a fox-like appearance; face uniformly rusty-brown (Figure 52b). Ears pointed, naked, very dark brown. Wing-membranes very dark brown (not grey as in Kingdon 1997); attaching to second toe. No tail.

Skull (Figure 52c, d and e) long and robust for an African fruit bat. Rostrum of medium relative length. Dental formula $2^{132}/_{2133} = 34$.

Geographic Variation None.

Similar Species Two other species of large African fruit bats have no basal ear-patches; no white markings on head; FA: >108 mm:

Pteropus seychellensis comorensis. Mantle golden or rusty-yellow ('yellow'); dark face-mask present. Mafia I. only.

Eidolon helvum. Dorsal pelage usually pale and yellowish; no mantle. Smaller (FA: 105–135 mm). Mainland Africa and islands including Pemba I. and Mafia I.

Distribution Endemic to Pemba I. (Tanzania) and its associated islets. Has not been recorded on Zanzibar I., Mafia I., or on the African mainland.

Habitat *Pteropus voeltzkowi* is a small-island specialist. Pemba I. (ca. 984 km²) lies ca. 40 km from the mainland and ca. 40 km from Zanzibar I. Terrain undulating; west side with ridges and steep valleys that are often forested, east side flatter and more arid. Formerly, primary evergreen forest must have been widespread, with evergreen bush in less favourable areas, and mangrove swamps around coast. The primary forest is now reduced to remnants, including two forest reserves and traditional graveyards. Secondary forest is regenerating in extensive abandoned clove plantations. No rivers, many pools (Moreau & Pakenham 1940, Entwistle & Corp 1997a).

Abundance Total world population (June 1995) estimated to be 4600–5500 individuals (Entwistle & Corp 1997a). Nineteen



Pteropus voeltzkowi

occupied camps were located: ten contained 94% of the population. On the basis of a week-long survey in 1989, Seehausen (1991a) suggested that the species was almost extinct; however, the five areas he surveyed did not include the areas where *P. voeltzkowi* was found in 1995.

Adaptations Very little is known, but *Pteropus voeltzkowi* resembles other flying-foxes and its adaptations are likely to be typical of the genus *Pteropus*. By day, hangs in the canopies of leafy trees. Camps are found in primary and secondary forests, mangroves and occasionally in isolated trees. Of the 19 camps located in 1995, 12 were on western side of Pemba. In hilly areas, camps were located on the ridge tops. As in other island-dwelling species of *Pteropus*, many individuals roost on the offshore islets and fly to Pemba for foraging; Pakenham (1984) observed 'hundreds' flying from the islets at dusk. In 1995, one camp was found in a village: the others were 100 m to 5 km away from villages. Many camps are traditional but the extent to which they are occupied may vary seasonally.

Foraging and Food Feeds on fruits, leaves and flowers. Foraging begins when individuals fly from their camps at dusk. Fruits are chewed and crushed against the palatal ridges, pulp and juice is swallowed, fibre and seeds are spat out as pellets. *Pteropus voeltzkowi* feeds on many species of indigenous trees (O. Seehausen in Mickleburgh *et al.* 1992), but shows a preference now for human-introduced species such as mango, breadfruit, jackfruit and papaya. Based on the analysis of 573 faecal pellets collected from 11 camps in Jun and Jul, the diet (expressed as the percentage of pellets containing each different food) was 57% mango, 18% breadfruit, 8% leaves, 5% figs, 7% other fruits and 5% flowers and pollen (Entwistle & Corp 1997b). However, individuals from different camps have different diets, depending on what is available in their foraging areas (e.g. Camp A: leaves 50%, mango 30%, other fruits 15%, flowers 5%. Camp B: figs 70%, breadfruit 20%, leaves 10%). Leaf-eating (which also occurs in *Eidolon helvum*, *Epomophorus wahlbergi* and some other fruit-eating bats) may be a means of obtaining important proteins and minerals that are not obtainable from fruits (Kunz & Diaz 1995). *Pteropus voeltzkowi* probably plays a part in the pollination of some trees (e.g. Kapok *Ceiba pentandra*), and in the transport of seeds from the parent trees to other locations.

Social and Reproductive Behaviour Very little known. Roosts in large to very large groups of mixed sexes and ages.

Reproduction and Population Structure Litter-size and reproductive chronology not known, the available information is inconclusive. Seehausen (1990 in Mickleburgh *et al.* 1992) recorded births 'between the rains' (Jun–Aug). However, Entwistle & Corp

(1997a) did not find evidence of births in Jun and Jul in 1995. 'Young' were recorded in Oct (Seehausen 1991b in Entwistle & Corp 1997a) and are 'first seen' in Aug and Sep (Pemba villagers, in Entwistle & Corp 1997a). There appear to be no reliable data for other times of the year, and therefore it should not be concluded that these observations indicate monoestry.

Predators, Parasites and Diseases Hunted for food by humans (Mickleburgh *et al.* 1992). Voeltzkow (in Pakenham 1984) reported the ectoparasitic bat-fly *Cyclopodia greeffi* (Diptera: Nycteribiidae) to be very numerous. No other ectoparasites recorded (Anciaux de Faveaux 1984).

Conservation IUCN Category: Vulnerable.

Major threats: (apart from extremely restricted distribution and small population size) deforestation, hunting (Seehausen 1990, Mickleburgh *et al.* 1992) and accidental mortality. The increasing human population and pressure on land for agriculture has reduced the areas of the forest that are essential for foraging and roosting. On the other hand, fruit trees planted by humans provide an important source of food. Population trend: stable.

Measurements

Pteropus voeltzkowi

FA (♂ ♂): 156 (147–163) mm, n = 8
 FA (♀ ♀): 151 (145–160) mm, n = 4
 WS (d) (♂ ♂): 480, 515 mm, n = 2
 WS (d) (♀ ♀): 510 (465–570) mm, n = 3
 HB (♂ ♂): 247 (240–260) mm, n = 6
 HB (♀ ♀): 237 (220–265) mm, n = 5
 T: 0 mm, n = 11
 E (♂ ♂): 27 (25–30) mm, n = 6
 E (♀ ♀): 25 (20–30) mm, n = 5
 Tib: n. d.
 HF: n. d.
 WT (♂ ♂): 470–610 g, n = 3*
 WT (♀ ♀): 430–600 g, n = 4*
 GLS (♂ ♂): 65.8 (60.7–68.0) mm, n = 8
 GLS (♀ ♀): 65.1 (63.0–67.9) mm, n = 7
 GWS (♂ ♂): 36.1 (32.6–37.8) mm, n = 8
 GWS (♀ ♀): 33.5 (30.9–36.3) mm, n = 7
 C–M² (♂ ♂): 25.8 (24.4–27.0) mm, n = 8
 C–M² (♀ ♀): 25.0 (24.2–26.5) mm, n = 7
 Pemba I. (BMNH, HZM and Bergmans 1990)
 *Mean values not recorded

Key References Bergmans 1990; Entwistle & Corp 1997a, b; Pakenham 1984.

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GENUS *Rousettus**Rousettus*

Rousettus Gray, 1821. London Med. Repos. 15: 299. Type species: *Pteropus aegyptiacus* E. Geoffroy, 1810.

Rousettus is a polytypic genus with, according to Simmons (2005), eight species of which two occur in Africa, one on Madagascar, one on the Comoros Is., one from Sri Lanka and Pakistan to S China and Indonesia, and the others in South-East Asia. Diagnostic characters of African species: no white basal ear-patches; no white markings on face; FA: 82–106 mm; no ruff of stiff hairs around the neck; toes not partly webbed; five upper and six lower cheekteeth; M^2 not greatly reduced (Table 11, p. 228). Roosts in caves; some, if not all, species orientate using echolocation as well as vision. Selected characters of African *Rousettus* are illustrated in Figure 53.

Rousettus was placed in the *Rousettus* section of Andersen (1912a), and in the subfamily Rousettinae (tribe Rousettini) by Bergmans (1997). *Rousettus* is considered to contain two or three subgenera by some authors – *Lissonycteris* (Africa), *Stenonycteris* (Africa and Madagascar) and *Boneia* (Indonesia). *Lissonycteris* is now considered a distinct genus, or possibly a synonym or subgenus of *Myonycteris*, and is no longer placed in the subfamily Rousettinae (see genus profile). The status of *Stenonycteris* is controversial. Lawrence & Novick (1963) used differences in behaviour and locomotion (amongst others) to support generic status for *Lissonycteris*, and Kingdon (1974) likewise

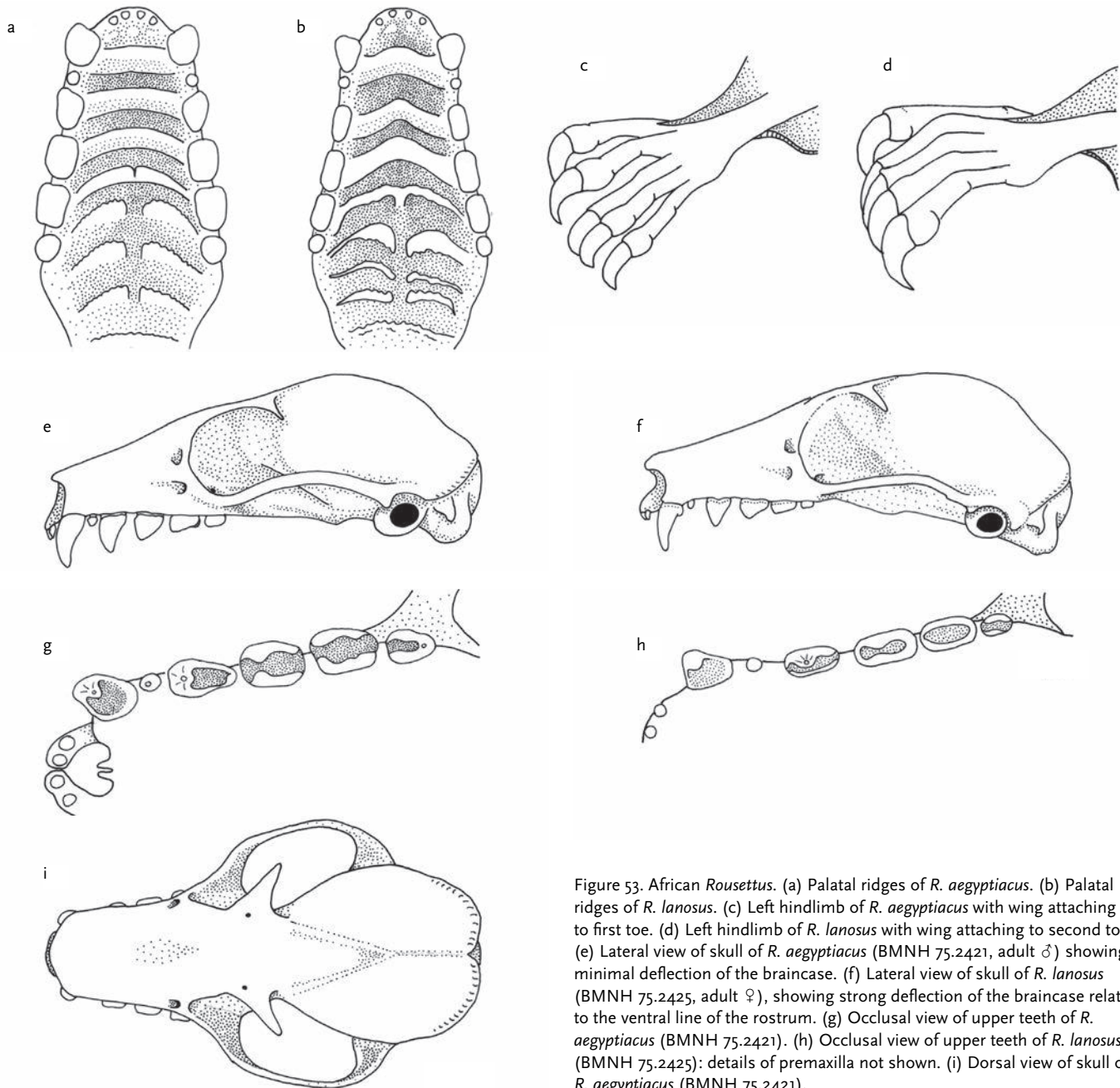


Figure 53. African *Rousettus*. (a) Palatal ridges of *R. aegyptiacus*. (b) Palatal ridges of *R. lanosus*. (c) Left hindlimb of *R. aegyptiacus* with wing attaching to first toe. (d) Left hindlimb of *R. lanosus* with wing attaching to second toe. (e) Lateral view of skull of *R. aegyptiacus* (BMNH 75.2421, adult ♂) showing minimal deflection of the braincase. (f) Lateral view of skull of *R. lanosus* (BMNH 75.2425, adult ♀), showing strong deflection of the braincase relative to the ventral line of the rostrum. (g) Occlusal view of upper teeth of *R. aegyptiacus* (BMNH 75.2421). (h) Occlusal view of upper teeth of *R. lanosus* (BMNH 75.2425); details of premaxilla not shown. (i) Dorsal view of skull of *R. aegyptiacus* (BMNH 75.2421).

Rousettus lanosus.

used differences in behaviour and locomotion between *Rousettus* and *Stenonycteris*, and some craniodental characters, to indicate generic status for *Stenonycteris*. In contrast, Bergmans (1977a, 1994) considers *lanosus* to be a species of *Rousettus*, and does not recognize *Stenonycteris* either as a genus or a subgenus, and he considers *Rousettus madagascariensis* from Madagascar to be intermediate between typical *Rousettus* and *Stenonycteris* in all morphological characters except the narrowness of its cheekteeth, which places it closer to *Stenonycteris*. Cladistic analyses based on molecular genetics are also controversial. According to Álvarez *et al.* (1999) and Juste *et al.* (1999), *R. (Stenonycteris) lanosus* appears more closely related to the myonycterine

clade than to *Rousettus (sensu stricto)*. In contrast, Giannini & Simmons (2003) found that '*Stenonycteris lanosus*' clustered with *Rousettus (sensu stricto)* and *Eonycteris spelaea* (both in the tribe Rousettini of Bergmans 1997) and not with the myonycterine clade. Their analysis also suggests that *lanosus* is more closely related to Indomalayan species of *Rousettus* than to the African *R. aegyptiacus*. *Rousettus aegyptiacus* and other *Rousettus* spp. echolocate, and *R. (S.) lanosus* probably echolocates. If *Stenonycteris* and *Rousettus* are sister taxa, echolocation by tongue-clicks has evolved only once in fruit bats (Giannini & Simmons 2003). Alternatively, if *Stenonycteris* belongs to the myonycterine clade (an endemic African clade) echolocation may have evolved twice (Giannini & Simmons 2003). Pending further information, following Simmons (2005), *Stenonycteris* is presented here as a subgenus of *Rousettus* and it is considered to contain two species, *R. (S.) lanosus* in Africa, and *R. (S.) madagascariensis* in Madagascar.

The species of *Rousettus* in Africa are:

- R. aegyptiacus*. Dorsal pelage sleek and shorter (underfur 6–7 mm, longest hairs ca. 12 mm); antitragal lobe of ear distinct; wing attached to first toe (Figure 53c) or between first and second toes; tibiae dorsally practically naked; skull not delicate; braincase only slightly deflected (Figure 53e); cheekteeth comparatively broad. Widespread and not restricted to mountainous areas.
- R. lanosus*. Dorsal pelage shaggy and longer (underfur 7–8 mm, longest hairs 16–18 mm); antitragal lobe of ear indistinct; wing attached to second toe (Figure 53d) or occasionally between first and second toes; tibiae dorsally well furred; skull delicate; braincase strongly deflected (Figure 53f); cheekteeth narrow. Mountainous areas of eastern Africa.

Meredith Happold

Rousettus aegyptiacus EGYPTIAN ROUSETTE

Fr. Rousette d'Egypte; Ger. Ägyptischer Höhlenflughund (Nilflughund)

Rousettus aegyptiacus (E. Geoffroy, 1810). Ann. Mus. Natn. Hist. Nat. Paris 15: 96. Giza, Egypt.

Taxonomy Originally *Pteropus egyptiacus*. The specific name was corrected to *aegyptiacus* by its author in 1818. This emendation was not accepted by Corbet & Hill (1992) and Bergmans (1994) but is considered justified by Kock (2001a): *aegyptiacus* is the name most often used and it is retained here (following Kock 2001a) and also in the interests of stability. Synonyms: *arabicus*, *egyptiacus*, *geoffroyi*, *hottentotus*, *leachii*, *occidentalis*, *princeps*, *sjostedti*, *thomensis*, *tomensis*, *unicolor*. Subspecies in Africa: four. Chromosome number (*R. a. leachii*, W Uganda): $2n = 36$; $aFN = 68$ (Dulić & Mutere 1973a).

Description Small to medium-sized, dark brown to greyish-brown fruit bat with no white markings; no mantle; no epaulettes; no ruff of coarse hairs; no webbing between toes; pelage moderately long and fairly sleek; wing-membranes usually attaching to first toe. Sexes similar in colour; ♂♂ on average slightly larger than ♀♀. Pelage soft, fairly sleek; extending dorsally and ventrally along each upper arm and ca. half-way along each forearm; mid-dorsal length of underfur hairs 6–7 mm interspersed with hairs up to 4 mm longer. Dorsal pelage dark sepia brown to greyish-brown (pale brown in

Egypt); paler and sparser on neck; hairs on back unicoloured, hairs on neck pale with darker tip. Ventral pelage slightly to considerably paler. Males with stiffer, paler hairs around neck and throat, but without a conspicuous coarse ruff (cf. *Lissonycteris*, *Myonycteris*). Head without markings; muzzle long; lips and cheeks not very expansible. Ears naked, brown, tip rounded; antitragus distinct although weakly developed. Palate usually with four undivided ridges, three divided ridges and one very thin ridge at posterior end of palate (Figure 53a), but the ridge pattern is variable (for details see Bergmans 1994). Wings blackish-brown, wing-membranes attaching to first toe (Figure 53c) or occasionally between the first and second toes. Dorsal side of tibia practically naked (cf. *R. lanosus*). Tail short, protruding up to 17 mm beyond interfemoral membrane.

Skull, on average, medium-sized for an African fruit bat and moderately robust. Zygomatic arches not extremely slender (cf. *R. lanosus*). Rostrum of medium relative length. Premaxillae not fused anteriorly (cf. *Lissonycteris*). Braincase minimally deflected; upper alveolar line straight (Figure 53e). Upper cheekteeth comparatively wide in occlusal view (Figure 53g), breadth of large premolars and

molars clearly greater than half their lengths; cf. *R. lanosus*); M^2 not greatly reduced (cf. *Myonycteris*). Dental formula $^{2132}/_{2133} = 34$.

Geographic Variation Six subspecies are recognized by Juste & Ibáñez (1993a) and Bergmans (1994), of which four occur partly or only in mainland Africa:

Rousettus a. aegyptiacus: Nile Valley of Egypt (and extraliminally northwards to Cyprus and extreme S Turkey, and eastwards to W Arabia).

R. a. arabicus: possibly Djibouti (and extraliminally S Arabia and eastwards to Pakistan).

R. a. unicolor: Senegal to Cameroon, Bioko I. and southwards to Angola.

R. a. leachii: NE DR Congo to Ethiopia and southwards to South Africa; also Pemba I., Zanzibar I. and Mafia I.

Similar Species Four other African mainland species of fruit bats are small to medium-sized (FA: 56–107 mm) with no basal ear-patches and no other white or pale markings on the head:

Rousettus lanosus. Dorsal pelage longer, shaggy. Antitragus indistinct. Wing-membranes attaching to second toe (occasionally between first and second toes); tibiae dorsally well furred. Skull delicate; braincase strongly deflected; cheekteeth narrow.

Lissonycteris angolensis. Usually smaller (FA: 68–90 mm). Dorsal pelage fairly long; ruff of coarse hairs in adult ♂♂. Toes partly webbed. Upper alveolar line with weak angle between 3rd and 4th premolars. Does not orientate acoustically.

Myonycteris spp. Smaller (FA: 56–75 mm). Adult ♂♂ with ruff of coarse hairs.

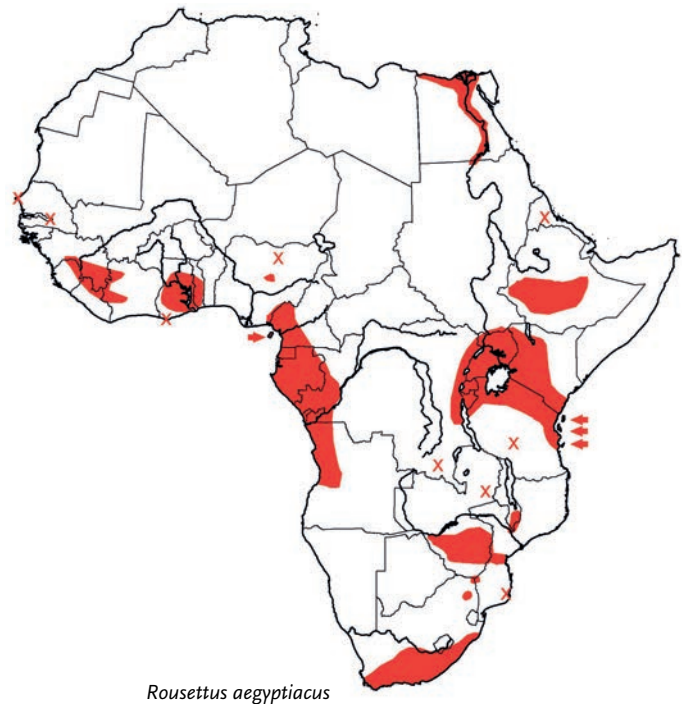
Distribution In Africa, the distribution is disjunct (see Geographic Variation) and restricted to areas with fruiting trees and caves (except in Nile Valley where man-made day-roosts are used), but there are records in all biotic zones and mosaics except the Mediterranean Coastal BZ and the Sahel Savanna BZ. Map based on Bergmans (1994). Not recorded from Somalia (*contra* Kingdon 1997) nor as widely elsewhere as his map indicates. Extraliminally: Cyprus, Turkey, Middle East, Arabian Peninsula, Pakistan, NW India. Also São Tomé I. and Príncipe I. in Gulf of Guinea.

Habitat South of the Sahara, found in most habitats where caves and fruiting trees are present, from 0 to 2500 m. In Egypt, *R. a. aegyptiacus* inhabits cultivated areas in the Nile Valley and Nile Delta and some oases, and it roosts in man-made cave-like day-roosts where caves are absent.

Abundance Common; sometimes very abundant near large caves.

Adaptations This species is particularly well studied, e.g. Möhres & Kulzer (1956), Kulzer (1958, 1963, 1969a, b, 1979), Novick (1958c), Noll (1979a), Laburn & Mitchell (1975), Jacobsen & Du Plessis (1976), Herzig-Straschil & Robinson (1978), Mutere (1968) and Korine *et al.* (1994). For review and more references, see Kwiecinski & Griffiths (1999).

Aspect ratio very low; wing-loading very high to exceptionally high; wing tips short and rounded. Flight-speed slow, reaches 4.4 m/sec; agile at slow speeds, manoeuvrability poor. Sometimes glides when



travelling from higher to lower localities; glide speeds 5.3–11 m/sec. Can hover briefly and take off from the ground. Physiological adaptations associated with the high demand for oxygen during flight include a relatively large heart, high haemoglobin concentration and very high carrying capacity for blood oxygen (Jürgens *et al.* 1981). Locomotion on ground is slow and clumsy, but climbing is efficient (Lawrence & Novick 1963). Frequently hangs from branches or fruits in a sloth-like position with one foot and one thumb on each side of the branch, and frequently moves along underside of branches in this position, using all four limbs (cf. *Lissonycteris angolensis*).

By day, roosts mainly in large humid caves and lava tunnels where temperatures are stable, sometimes choosing dimly lit areas and sometimes choosing areas of total darkness. Hangs in dense clusters, preferring to pack into holes and crevices in the roof, but will hang from ceilings if necessary. In Egypt, it roosts in cave-like buildings including temples, tombs and mosques. Sometimes shares day-roosts with several species of microbats, each species occupying its own area. Mean daily temperatures inside day-roosts sometimes reach 28 °C during the hottest months in Egypt, but are usually lower. However, the thermoneutral zone for *R. aegyptiacus* is narrow and the lower critical temperature (31 °C) is invariably higher than the day-roost temperature; consequently this species must live in colonies and individuals must huddle together to stay within the thermoneutral zone. They do not become torpid and do not hibernate. They warm themselves by huddling, shivering, breathing more rapidly and increasing metabolic heat production (including by metabolizing brown fat) but they cannot survive cold conditions for very long. To cool themselves, normally hydrated individuals move apart, pant, salivate copiously, lick most of the body, dilate the blood-vessels of the wings (but do not fan the wings) and lower the testes.

Rousettus aegyptiacus, and at least two other species of *Rousettus*, echolocates in dark caves and sometimes while flying outside. The echolocation calls always occur in groups of two clicks; they are made with the tongue and emitted through the mouth. The clicks have broad

bandwidths with frequencies of 7–70 kHz; parts of the calls are audible to humans as clicks. Frequencies around 10–12 kHz and 20 kHz contain the most energy, and the hearing curve is finely tuned at ca. 10 kHz with a second peak at 20 kHz. The cochlea is not specialized as in microbats (Hinchcliffe & Pye 1968). The pinnae are highly mobile and are most sensitive to click stimuli in front of the bat when they are directed forwards, and least sensitive when directed backwards; during flight, the ears flicker to and fro and the clicks are emitted when the ears are moving from their least sensitive to their most sensitive position (Holland & Walters 2005). The eyes are large and (as in other fruit bats) are specially adapted for night vision. The sense of smell is highly developed. The follicles of the stiff hairs around the neck and throat are associated with non-specialized sebaceous glands, more active in ♂♂ than ♀♀, suggesting that scent from these hairs provides behavioural cues (Mainoya & Howell 1979). The mean daily total intake of water (from the diet) is 71.7 ml; the kidney has a thin medulla and extremely short papilla, enabling production of dilute urine (113–1800 mOsmol/kg under varying dietary regimes) (Kulzer 1979, Arad & Korine 1993).

Foraging and Food Feeds on fruits, nectar and probably pollen. Sometimes commutes 10–24 km between day-roost and foraging ground, and consequently sometimes arrives much later than competing species that roost in trees nearby (Thomas & Fenton 1978). Fruits are carried to feeding perches. Hard-skinned fruits are peeled before the pulp is chewed and mashed against the palate. Up to 25% of gathered fruit is discarded, often because of attempted pilfering. In South Africa, alimantal migration (seasonal search for food) is implied by fluctuations in colony sizes (Lombard 1961), and marked bats have been recaptured at day-roosts 32–500 km apart. However, these movements might be nomadic rather than migratory. In contrast, in Uganda where food is available year-round, caves shelter thousands of individuals throughout the year. *Rousettus aegyptiacus* eats ripe fruits of many native trees and shrubs and also ripe cultivated fruits. Considered a pest in some areas although damage to orchards is often exaggerated. Takes nectar and probably pollen from flowers including those of *Bombax*, *Kigelia*, *Adansonia*, *Eriobotrya* and *Musa*, and pollinates at least some of these species (Kock 1972). Sometimes chews leaves. In captivity, the mean \pm S.D. nightly consumption of food was 120.3 ± 23.2 g; the mean consumption per unit body weight was $0.94 \text{ g/g}^{\text{bwt}}$ ($n = 7$); the mean through-put time was 20 ± 1 min (Wolton *et al.* 1982), more than twice as fast as in *Lissonycteris angolensis*.

Social and Reproductive Behaviour Roosts in groups (colonies) of ca. 50–4000 or more individuals of both sexes. A cave may contain several clusters of huddled bats, but the composition and stability of clusters is apparently not known. Fluctuations in adult sex ratios of colonies are recorded in South Africa and Israel; ♀♀ usually outnumber ♂♂ by as much as 3 : 1, suggesting polygamy (Jacobsen & Du Plessis 1976). During pregnancy and lactation, two caves in South Africa and one in Israel contained 25–33% adult ♂♂, suggesting that ♀♀ do not form maternity colonies in separate caves. However, Lombard (1961) noted that, in captivity, ♂♂ tended to form groups, ignoring the ♀♀ and juveniles, and therefore the possibility that occupants of a single cave segregate into maternity clusters and bachelor clusters needs investigation. There appears to be no other evidence of sexual separation (*contra* Kwiecinski & Griffiths 1999), nor any records of day-roosts occupied exclusively by ♀♀ with young.

Colonies remain active and noisy throughout much of the day. There is often competition for the darkest sites, and bats will move from lighter to darker positions if light levels increase during the day. Competition for particular positions within clusters is evident from aggressive interactions including screaming, striking out with the forearms, hooking an opponent and biting. Individuals are recognized primarily by their scent, and olfactory cues probably influence many social interactions. A wide range of vocalizations are made, many probably associated with communication.

Copulation occurs at the roost. During birth, the ♀ remains quiescent in the normal resting posture. Eventually the head of the baby appears and then the baby slowly squirms its way out of the vagina, thus participating actively in its own delivery. The wings are freed first and then the legs. Still attached to the umbilical cord, it climbs down over the mother's pelage, searches for a nipple and attaches firmly with its milk-teeth. Only then is the placenta delivered and eaten (Kulzer 1966, 1969b). The neonate remains attached to its mother for ca. 16 days, and is carried when she forages. Later, juveniles are left in the day-roost, in clusters of other juveniles.

Reproduction and Population Structure Litter-size: usually one, occasionally two. Reproductive chronology varies geographically – both monoestry and polyoestry and both seasonal and aseasonal chronologies are known. In Egypt, copulation and births occur in all months, gestation 105–107 days; not known if this population is polyoestrous. At 00° 22'S (Kasokero, Uganda), the chronology is seasonal bimodal polyoestry without postpartum oestrus, with gestation four months and births just before peaks in rainfall (Mar and Sep), and an interval of two months between parturition and the next conception (Mutere 1968). At 22° 25'S (Pafuri, Kruger N. P., South Africa), the chronology is restricted seasonal monoestry with copulation in winter (Jul–Aug), births in summer (Nov–Dec) with 95% pregnancy rate, and lactation for ca. two months (Penzhorn & Rautenbach 1988). In contrast, at ca. 24° S in the former Transvaal, South Africa, there is extended seasonal monoestry with copulation in Jun–mid-Sep, births in late Oct–Dec with a peak in Nov–Dec (Jacobsen & Du Plessis 1976). Further south at ca. 34° S (Tsitsikama Coastal N. P., Eastern Cape Province), the chronology for most ♀♀ is extended seasonal monoestry with births from Oct–Jun with a peak in Dec (Herzig-Straschil & Robinson 1978), but the possibility that births in Jun are the result of polyoestry in a few ♀♀ needs investigation. Data from other African localities are inconclusive.

Neonates have thin downy fur on the head and back; eyes are closed; ear pinnae pressed against head; birth-weight 18–25 g. Ears become erect and eyes open ca. day 10. By day 36, wing-span is 75% of adult span. Adult-size and weight attained ca. nine months (Kulzer 1979, Noll 1979b). Sex ratio at birth is 1 : 1.

Predators, Parasites and Diseases Predators include Genets *Genetta* spp., Lanner Falcons *Falco biarmicus*, hawks (species not identified) and owls *Bubo bubo* (Kulzer 1969b, Jacobsen & Du Plessis 1976 and Qumsiyeh 1985). In some areas, taken by humans for food, or because of supposed damage to crops. Ectoparasites include bed-bugs *Afrocmex leleupi*, *A. constrictus* (Hemiptera: Cimicidae), another bug *Eothenes intermedius* (Hemiptera: Polyctenidae); fleas *Archaeopsylla erinacei* (Siphonaptera: Pulicidae), *Thaumapsylla breviceps* (Siphonaptera: Ischnopsyllidae); bat-flies *Basilia blainvillii*,

Dipseliopoda biannulata, *D. setosa*, *Eucampsipoda hyrtlai*, *E. africana* (Diptera: Nycteribidae), *Brachytarsina diversa*, *B. alluaudi* and *B. bequaerti* (Diptera: Streblidae) (Anciaux de Faveaux 1984). Viruses isolated from *R. aegyptiacus* include Chikungunya virus, isolated from Ugandan material (Addy *et al.* 1978).

Conservation IUCN Category: Least Concern.

Measurements

Rousettus aegyptiacus

FA (♂♂): 95.9 (82–106) mm, n = 99*

FA (♀♀): 94.9 (85–106) mm, n = 106*

WS (d) (♂♂): 628 (550–670) mm, n = 8

WS (d) (♀♀): 604 (485–670) mm, n = 20

HB (♂♂): 136.8 (125–192) mm, n = 36

HB (♀♀): 131.9 (109–153) mm, n = 55

T (♂♂): 17.0 (13–22) mm, n = 38

T (♀♀): 16.8 (8–24) mm, n = 53

E: 21.9 (13–27) mm, n = 101

Tib (♂♂): 44.1 (41–47) mm, n = 24*

Tib (♀♀): 42.8 (39–48) mm, n = 39*

HF: n. d.

WT (♂♂): 130.5 (88–170) g, n = 19

WT (♀♀): 120.7 (83–166) g, n = 35

GLS (♂♂): 43.4 (42.1–45.7) mm, n = 49*

GLS (♀♀): 42.3 (38.3–44.0) mm, n = 48*

GWS (♂♂): 26.8 (24.2–28.9) mm, n = 46*

GWS (♀♀): 25.4 (23.6–28.9) mm, n = 47*

C–M² (♂♂): 16.6 (15.2–18.2) mm, n = 48*

C–M² (♀♀): 16.1 (14.4–17.4) mm, n = 47*

Throughout African geographic range (NMK and literature)

*Bergmans 1994

Key References Bergmans 1994; Herzig-Straschil & Robinson 1978; Jacobsen & Du Plessis 1976; Kulzer 1969a, b, 1979; Kwiecinski & Griffiths 1999; Mutere 1968.

Meredith Happold

Rousettus lanosus LONG-HAIRED ROUSETTE

Fr. Roussette laineuse; Ger. Gebirgs-Höhlenflughund

Rousettus lanosus Thomas, 1906. Ann. Mag. Nat. Hist., ser. 7, 18: 137. Mubuku Valley, Rwenzori East, Uganda.

Taxonomy Subgenus *Stenonycteris*. The taxonomy of *lanosus* is controversial: analyses based on morphological, molecular and behavioural data have sometimes placed this taxon in *Rousettus* (with no subgenera recognized), sometimes in *R. (Stenonycteris)*, and sometimes *Stenonycteris* is given full generic status (see profile Genus *Rousettus*). Based on a combination of morphological and molecular data, Giannini & Simmons (2003) and Simmons (2005) concluded that *Stenonycteris* is a subgenus of *Rousettus*, and pending resolution of all incongruencies, this view is held here. Synonyms: *kempi*. Subspecies: two of dubious validity. Chromosome number: not known.

Description Small to medium-sized, brown fruit bat with no white markings; no epaulettes; no ruff of coarse hair around the throat; no webbing between the toes; pelage long and shaggy; wing-membranes usually attaching to second toe. Sexes similar. Pelage shaggy, slightly coarse, underfur woolly; dorsal pelage extending along each upper arm and half-way along each forearm, over the interfemoral membrane, and also over the tibiae (cf. *R. aegyptiacus*); mid-dorsal length of underfur hairs 7–8 mm interspersed with hairs of 16–18 mm. Dorsal pelage medium to dark greyish-brown to dark rusty-brown, sometimes with scattered paler hairs; hairs unicoloured. Ventral pelage slightly paler, sometimes with more scattered paler hairs. Adult ♂♂ with longer, slightly stiffer hairs on neck and throat, but no conspicuous ruff of coarse hairs (cf. *Lissonycteris*, *Myonycteris*). Head without markings; muzzle long; lips and cheeks not very expansible. Ears naked, dark brown; antitragal lobe vestigial and indistinct. Palate usually with four undivided ridges, three divided ridges and one very thin ridge at the posterior end of the palate (Figure 53b), but some individuals have four undivided ridges (Bergmans 1994). Eyes blackish. Wing-membranes dark brown, attaching to second toe (Figure 53d) or occasionally between first and second toes. Dorsal surface of tibiae

well furred (cf. *R. aegyptiacus*). Tail protruding up to 16 mm beyond interfemoral membrane.

Skull medium-sized for an African fruit bat but delicate. Zygomatic arches extremely slender (cf. *R. aegyptiacus*). Rostrum of medium relative length. Premaxillae not fused (cf. *Lissonycteris*). Braincase strongly deflected ventrally; upper alveolar line straight (Figure 53f). Upper cheekteeth comparatively narrow in occlusal view (Figure 53h), breadth of large premolars and molars equal to half their lengths or slightly more (cf. *R. aegyptiacus*); posterior upper molar (M²) not greatly reduced (cf. *Myonycteris*). Lower cheekteeth also narrow. Dental formula $2^{132}/_{2133} = 34$.

Geographic Variation Bergmans (1994) preferred not to distinguish subspecies until the distribution and geographic variation are better known, but two subspecies are recognized by some authors including Hayman & Hill (1971), Aggundey & Schlitter (1984) and Koopman (1994):

R. l. lanosus: E DR Congo, Burundi, Rwanda and W Uganda.

R. l. kempi: E Uganda, Tanzania, Kenya, SW Sudan, Ethiopia.

Similar Species Four other African mainland species of fruit bats are small to medium-sized (FA: 56–107 mm) with no basal ear-patches and no other white or pale markings on the head:

Rousettus aegyptiacus. Dorsal pelage shorter, sleek; antitragus distinct; wing usually attaching to first toe (occasionally between first and second toes); tibiae dorsally practically naked. Skull not delicate; braincase only slightly deflected; cheekteeth comparatively broad. *Lissonycteris angolensis*. Usually smaller (FA: 68–90 mm). Ruff of coarse hairs in adult ♂♂; antitragus distinct; toes partly webbed. Upper

alveolar line with weak angle between 3rd and 4th premolars; cheekteeth broad and squarish. Does not orientate acoustically. *Myonycteris* spp. Smaller (FA: 56–75 mm). Adult ♂♂ with ruff of coarse hairs.

Distribution Endemic to Africa. Occurs mainly in the Afromontane–Afroalpine BZ in S Sudan, SW Ethiopia, E DR Congo, Rwanda, Uganda, Kenya, Tanzania and Malawi. Also occurs in Burundi according to Koopman (1994), but this locality has not been traced or mapped. Map based on Bergmans (1994).

Habitat Mostly recorded in, or on the borders of, undifferentiated afromontane vegetation, but also recorded in mosaics of East African evergreen bushland and secondary *Acacia* woodland, and occasionally in drier lowland rainforest, wetter and drier miombo woodland, East African evergreen and semi-evergreen bushland and thicket, and *Acacia–Combretum* deciduous bushland and thicket (Bergmans 1994; terminology from White 1983). Occurs from 500 to 4000 m, but most locality records (72%) are between 1500–2500 m, indicating that this species is mainly, but not strictly, montane (Bergmans 1994).

Abundance Uncertain. Sometimes abundant near caves in suitable habitat (Kingdon 1974), but there are few records.

Adaptations Wing morphology and flight characteristics: no information. By day, roosts in dark, damp caves and mine-adits, sometimes in the twilight zone and sometimes in total darkness (Kingdon 1974). Since the roosts are mostly at high altitudes, these bats are often exposed to sub-zero temperatures at night, and low temperatures in their caves: they are probably obliged to roost in clusters (see below) to conserve heat and a comparison of temperature regulation in this species and in *R. aegyptiacus* would be most interesting. Sometimes shares caves with *R. aegyptiacus* and/or *Lissonycteris angolensis*. When flying in total darkness, *R. lanosus* produces a series of clicks similar, although more ‘musical’, to the echolocation clicks produced by *R. aegyptiacus* (Kingdon 1974). It is probable that *R. lanosus* echolocates, but this is not yet confirmed.

Foraging and Food The fragility of the skull, and comparative weakness of the dentition, suggests that the diet of *R. lanosus* is very soft fruits, nectar and perhaps pollen. In Rwanda, a bat believed to be *R. lanosus* was seen feeding on a flower of *Lobelia gibberosa* at ca. 2900 m (Hutson & Wilson 1992).

Social and Reproductive Behaviour Roosts in groups (colonies) of up to several hundred individuals. Like *R. aegyptiacus*, individuals hang huddled together in clusters. Kingdon (1974) observed that, in one mine-adit, pregnant and lactating ♀♀ with young clustered in the twilight zone while the rest of the colony roosted deeper inside. He suggested that, within single day-roosts, the sexes separate and maternity colonies are established, but this needs confirmation. Sometimes, sexually active ♂♂ were observed in the ‘maternity’ cluster. The number of ♀♀ and young in the ‘maternity’ cluster varied from month to month.

Reproduction and Population Structure Litter-size: one (n = 1). Reproductive chronology uncertain. In W Uganda, Kingdon



Rousettus lanosus

(1974) collected one lactating ♀ with her uterus filled with semen, and he also reported that ‘some of the females that were still nursing were already pregnant again’. This indicates polyoestry in at least some females, but further observations are needed to elucidate the chronology in detail. Not known when young are born.

Predators, Parasites and Diseases Ectoparasites include fleas *Thaumapsylla breviceps*, *T. dina* (Siphonaptera: Ischnopsyllidae); bat-flies *Phthiridium scissum*, *Dipseliopoda setosa* (Diptera: Nycteribiidae), *Brachytarsina bequaerti* (Diptera: Streblidae); and a mite *Macronyssus granulosus* (Acari: Macronyssidae) (Anciaux de Faveaux 1984).

Conservation IUCN Category: Least Concern.

Major threats: loss of habitat and hunting by humans.

Measurements

Rousettus lanosus

FA: 90.0 (85–95) mm, n = 71*

WS (d): 606 (580–644) mm, n = 8

HB: 145.0 (114–173) mm, n = 6

T: 19.7 (9–25) mm, n = 30

E: 21.7 (19–25) mm, n = 33

Tib: n. d.

HF: n. d.

WT: 118.8 (94–162) g, n = 31*

GLS: 42.3 (39.4–44.8) mm, n = 62*

GWS: 24.3 (22.3–26.6) mm, n = 57*

C–M²: 14.7 (13.5–15.7) mm, n = 55*

Throughout geographic range (BMNH, NMK, ROM)

*Bergmans 1994

Key References Bergmans 1994; Kingdon 1974.

Meredith Happold

GENUS *Scotonycteris*

Tear-drop Fruit Bats

Scotonycteris Matschie, 1894. Sitzb. Ges. Naturf. Fr. Berlin, p. 202. Type species: *Scotonycteris zenkeri* Matschie, 1894.

Scotonycteris is a polytypic genus with two species, endemic to Africa, found mainly in the Rainforest BZ from Guinea and Liberia to E DR Congo. Diagnostic characters: white markings on the nose and behind the eyes and usually a more or less conspicuous white border to the upper lip; one species with inconspicuous or without white basal ear-patches, one species without ear-patches; dorsal hairs tricoloured; adult ♂ without epaulettes; FA: 47–87 mm; postdental bony palate extending posteriorly well beyond the teeth, its lateral margins converging posteriorly; rostrum (viewed laterally) not slightly upturned; canines long to very long; three upper and five lower cheekteeth. The palatal ridges of *Scotonycteris zenkeri* are shown in Figure 54a. The skull of *Scotonycteris zenkeri* (Figure 54b) illustrates the basic characters of the genus, but there are substantial inter-specific differences in size and dentition (see below and Figure 54c, f and g). Similar to *Casinycteris* but see Table 11, p. 228.

Scotonycteris was placed in the epomophorine section of Andersen (1912a). He considered this genus to be closely related to *Casinycteris* and, more distantly, to *Nanonycteris*. Hence Andersen (1912a) grouped

these genera in the ‘*Nanonycteris* branch’. In recent phylogenetic analyses, *Scotonycteris* grouped with *Casinycteris*, and this clade grouped together with an epomophorine clade including *Epomophorus*, *Epomops*, *Hypsignathus*, *Micropteropus* and *Nanonycteris* (Springer *et al.* 1995, Jones *et al.* 2002). Consequently, *Scotonycteris* was placed with *Casinycteris* in the tribe Scotonycterini (subfamily Epomophorinae) by Bergmans (1997). According to the data by Romagnoli & Springer (2000), however, *Scotonycteris* and *Casinycteris* would group as a derived clade together with *Micropteropus* and within the other epomophorine fruit bats. The karyotype of *Scotonycteris ophiodon* is very distinct from other investigated African species of fruit bats, i.e. *Micropteropus*, *Epomops*, *Hypsignathus*, *Megaloglossus*, *Myonycteris*, *Lissonycteris* and *Rousettus* (Haiduk *et al.* 1980, 1981; but note that neither *S. zenkeri* nor *Casinycteris argynnis* was examined in these studies). Novick (1958a) suggested that the peculiar dental features of *S. ophiodon* merit subgeneric recognition.

The two species are:

S. ophiodon. FA: 73–87 mm; GLS: 35.3–42.9 mm; WT: 60–95 g.

S. zenkeri. FA: 47–55 mm; GLS: 24.0–27.4 mm; WT: 16–24 g.

Jakob Fahr

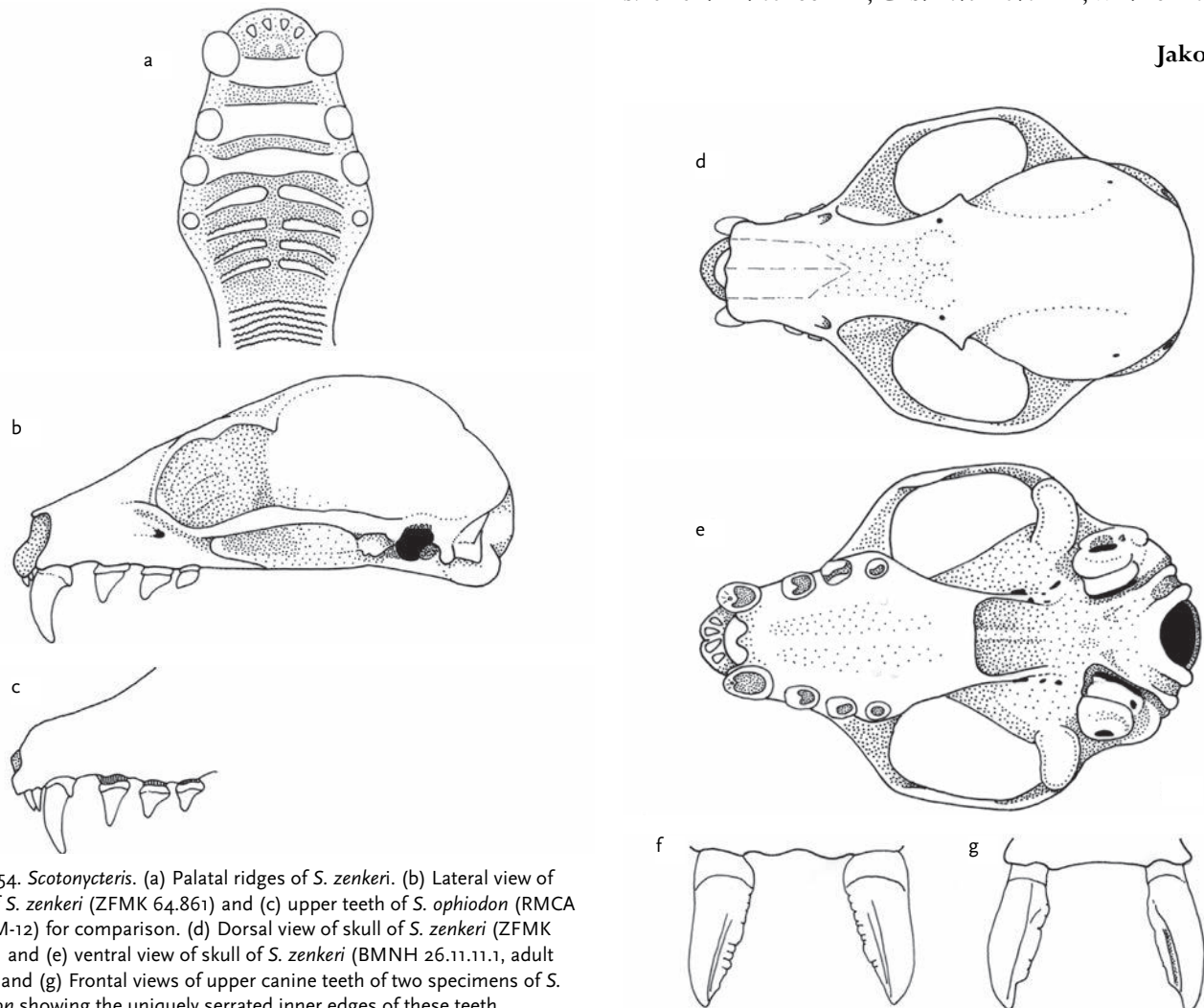


Figure 54. *Scotonycteris*. (a) Palatal ridges of *S. zenkeri*. (b) Lateral view of skull of *S. zenkeri* (ZFMK 64.861) and (c) upper teeth of *S. ophiodon* (RMCA 80-43-M-12) for comparison. (d) Dorsal view of skull of *S. zenkeri* (ZFMK 64.861) and (e) ventral view of skull of *S. zenkeri* (BMNH 26.11.11.1, adult ♂). (f) and (g) Frontal views of upper canine teeth of two specimens of *S. ophiodon* showing the uniquely serrated inner edges of these teeth.

***Scotonycteris ophiodon* POHLE'S FRUIT BAT (SNAKE-TOOTHED FRUIT BAT)**

Fr. Scotonyctère à dents de serpent; Ger. Schlangenzähniger Harlekin-Flughund (Pohles Harlekin-Flughund)

Scotonycteris ophiodon Pohle, 1943. Sitzb. Ges. Naturf. Fr. Berlin 1942: p. 78 [publ. 1943]. Bipindi, Kribi District, Cameroon.

Taxonomy Synonyms: *cansdalei*. Subspecies: none (but see Geographic Variation). Novick (1958a) suggested that the peculiar dental features of *S. ophiodon* merit subgeneric recognition. Chromosome number (Cameroon): $2n = 34$; $aFN = 62$; very distinct from other African pteropodid karyotypes (Haiduk *et al.* 1980, 1981, but these authors did not examine *S. zenkeri* and *Casinycteris argynnis*).

Description Very small to small fruit bat with face-markings (white patch on forehead, white posterior eye-spots, broad white band around lips); no conspicuous basal ear-patches; no epaulettes; snout and finger-joints yellowish; forehead region of skull weakly concave; bony palate extending well beyond last teeth; premolars and molars with distinct cusps; FA: 73–87 mm. Sexes similar in colour, ♀♀ on average with slightly longer forearms. Pelage dense, soft and woolly dorsally; much shorter and sparser ventrally with very short and stiff hairs on chest and belly; mid-dorsal hairs 9–10 mm. Dorsal pelage medium brown to rusty-brown, mottled; hairs tricoloured, whitish to very pale grey with dark brown or blackish base and brown tip. Ventral pelage with chin, throat, breast and central belly white or whitish-grey; flanks medium to dark brown, contrasting with paler areas. No epaulettes or white markings on shoulders. Head brown with three conspicuous white patches (one on forehead between anterior corners of eyes, and one at posterior corner of each eye); skin of upper lip and front of muzzle greenish-yellow; lips bordered by broad band of white hair, conspicuously white except under nostrils; anterior basal ear-patches indistinct or absent. Muzzle broad, fairly short; cheeks of adult ♂♂ strikingly wide and capacious; upper lip moderately expansible, internally fringed with conspicuous papillae. Ears dark brown with yellowish rim (paler near base), naked, oval, somewhat pointed at tip. Eyes large, greenish-brown. Palate usually with six thick, undivided interdental ridges and 10–13 narrow, serrated postdental ridges. Wing-membranes brown with marked yellowish-green reticulation (in subadults, more or less uniformly medium to dark brown); attaching to first toe. Finger-joints of adults yellowish to bright greenish-yellow. Thumb comparatively long. Penis and scrotum of (? sexually active) ♂♂ also bright greenish-yellow. No visible tail.

Skull with braincase rounded; rostrum of medium relative length (33–37% of GLS), not upturned. Profile of forehead region (viewed laterally) weakly concave (cf. *Casinycteris*). Zygomatic width relatively narrow (62–64% of GLS) and zygomatic arches comparatively lightly built with lower margin level with infraorbital foramen (cf. *Casinycteris*). Bony palate extending well beyond last teeth. Canines comparatively long and with well-developed secondary cusps on inner edges. Upper canines strongly backward curved (*ophiodon* means snake-toothed); inner edges markedly serrated (Figure 54f and g) (cf. *S. zenkeri*, *Casinycteris* and all other fruit bats). Premolars and molars (except anterior premolar and posterior molar of lower tooththrow) with two distinct cusps on inner and outer side of each tooth, giving a bifurcated appearance. Dental formula usually $2121/_{2132} = 28$.

Geographic Variation Not yet adequately assessed because sample sizes are too small. Specimens from Liberia, Côte d'Ivoire and Ghana seem to be similar in measurements but specimens from Cameroon are slightly larger. Two ♀♀ from Dimonika, Congo (one subadult) are larger than any specimens from elsewhere (FA: 87, 82 mm, GLS: 42.9, 38.0 mm, GWS: 27.3, 23.1 mm, C–M¹: 15.1, 13.8 mm) (Bergmans 1973, 1979, 1990). A very small, adult ♂ from Goumina, Congo (FA: 68 mm; GLS: 29.6 mm, GWS: 22.0 mm, C–M¹: 10.2 mm) with different palatal ridges and peculiar dental characters was published by Dowsett *et al.* (1991) as *S. ophiodon*. This specimen represents an undescribed species and is not included here (J. Fahr unpubl.).

Similar Species Only two other species of African fruit bats have white markings on the nose, upper lips and near the eyes:

Scotonycteris zenkeri. Much smaller (FA: 47–55 mm). Finger-joints not yellowish.

Casinycteris argynnis. Much smaller (FA: 50–62 mm; GLS: 22.2–28.4 mm). Rostrum upturned; bony palate barely extending beyond last teeth.

Distribution Endemic to Africa. Rainforest BZ (Western and West Central Regions). Known from only 15 localities, in Liberia, Côte d'Ivoire, Ghana, Cameroon and Congo. Known range very small and apparently disjunct (12,600 km² in E Liberia and SW Côte d'Ivoire, 14,700 km² in S Ghana, 7500 km² in Cameroon), and a single locality in Congo. Mt Nimba, ca. 250 km inland, is the locality



Scotonycteris ophiodon

furthest from the coast; absent from the central Congo Basin. The distribution partly resembles the assumed distribution of Pleistocene rainforest refugia. Gaps in the distribution are likely to be real because this species has never been found in some intensely surveyed areas between the regions of distribution, e.g. NE Gabon. Mostly recorded with *S. zenkeri*, except at Dugbe R. near Jaoudi in Liberia. In contrast, *S. zenkeri* is known from many regions from which *S. ophiodon* has not been recorded (e.g. East Central Region of the Rainforest BZ and the lowland forest and foothills along the western slope of the mountains flanking the Albertine Rift).

Habitat One of the few African fruit bats that seems to be restricted to the Rainforest BZ. Within this biotic zone, it has been recorded from lowland rainforest, montane forest and coastal forest vegetation zones. In Côte d'Ivoire, Ghana, Cameroon and Congo, seems to prefer lowland rainforest up to 600 m (Eisentraut 1973a, Bergmans 1990, J. Fahr unpubl.). In Liberia, it has been caught fairly frequently on Mt Nimba up to 1200 m where it seems most abundant in montane forest dominated by *Parinari excelsa* (Wolton *et al.* 1982). However, it is not confined to the immediate vicinity of Mt Nimba but also occurs in the lowland rainforests of SE Liberia and adjacent Côte d'Ivoire. In Congo, recorded from degraded rainforest in an area with low mountains (Bergmans 1973).

Abundance Locally rare to very rare. In Tai N. P., Côte d'Ivoire, comprised 6.5% of the fruit bat catch ($n = 1216$ individuals) and was the fifth most abundant species in a community of eight species of fruit bats (J. Fahr & S. Pettersson unpubl.). At Mt Nimba, Liberia, comprised 1.0% of the fruit bat catch ($n = 979$; Wolton *et al.* 1982) and was the seventh most abundant species in a community of nine species of fruit bats.

Adaptations Probably roosts in vegetation; one individual was found hanging from a forest tree (Hayman 1945). Recapture-rate in Tai N. P. 17.1% ($n = 41$); most recaptures up to half a year later; three recaptured one year later. All (including subadults and young-adults) were recaptured less than 400 m from initial site (most less than 250 m) suggesting that home-ranges are very small (several ha) and site-fidelity is unusually high (J. Fahr unpubl.). Frequency of captures varied throughout night, with three distinct peaks: 19:30–20:30h, 23:30–02:30 h, and 03:30 h to dawn. In captivity, the 1.5 hours before dawn were spent extensively grooming the body (Wolton *et al.* 1982).

Foraging and Food Frugivorous. Eisentraut (1959) caught three individuals in elevated nets and concluded that this bat might forage in the upper forest strata. Data from Tai N. P. partly support this (median capture height 18.4 m, $n = 40$) but also indicate foraging from ground to canopy level (min–max: 1.1–23.6 m) (J. Fahr unpubl.). Captive bats fed more or less continuously from ca. 21:00h to 06:00h, but usually rested for ca. 20 minutes, two or three times per night (Wolton *et al.* 1982). The unique dentition suggests a specialized diet or way of feeding. While most other fruit bats hang vertically (from one foot) and hold fruit in the other foot while eating it, *S. ophiodon* hangs horizontally (with both feet and thumbs gripping a branch), and keeps its food on its chest: pieces are bitten off and slowly masticated until the fibrous parts are spat out as pellets. Diet mostly unknown.

Eisentraut (1959) found *Ficus* seeds in stomach. In Tai N. P., most captured individuals had *Ficus* seeds in faeces and some were caught with entire figs in mist nets. Captive bats at Tai N. P. ate fruits of *Parinari excelsa* (J. Fahr unpubl.), and those at Mt Nimba ate fruits of *Ongokea gore*, bananas, plantains and guavas (Wolton *et al.* 1982). In captivity, the mean \pm S.D. nightly fruit consumption was 49.6 ± 8.5 g ($n = 7$); the dry weight assimilated was 81%; and the mean consumption per unit body weight was lower (0.79 g/g^{bwt}) than in five other species of fruit bats (0.92 – 1.18 g/g^{bwt}) (Wolton *et al.* 1982). The ratio between body length and intestine length is 1 : 5.4 (5.1–5.7), which is typical for (mainly) frugivorous fruit bats (Eisentraut 1959).

Social and Reproductive Behaviour No information.

Reproduction and Population Structure Litter-size: one ($n = 6$). Reproductive chronology uncertain. At $05^{\circ}50'N$ (Tai N. P., Côte d'Ivoire), 9 adult ♀♀ were neither pregnant nor lactating in Jan–Feb; 3 of 11 were lactating in Mar, 1 of 5 was pregnant in May, 1 of 4 was pregnant in Aug, 12 of 15 were pregnant in Sep, 1 of 1 was pregnant in Oct, and 2 of 7 were pregnant and one was lactating in Dec; none of the ♀♀ was simultaneously lactating and pregnant; no data for other months (J. Fahr unpubl.). At $07^{\circ}32'N$ (Mt Nimba, Liberia), one ♀ was not palpably pregnant in Jul, 2 of 2 were pregnant in late Aug, 1 of 1 was pregnant in early Sep and 1 of 1 was pregnant (CR: 33 mm) in mid-Nov; no data for other months (Wolton *et al.* 1982). At $04^{\circ}20'N$ (Malende, Cameroon), a pregnant ♀ (CR: 23 mm) was recorded in mid-Dec (Eisentraut 1959). At $05^{\circ}55'N$ (Oda, Ghana), a lactating ♀ was found in Dec (Hayman 1945). These data suggest that in West Africa and Cameroon most ♀♀ are pregnant between Aug–Dec, that most births occur at end of wet season (ca. Nov–Dec), and that most ♀♀ lactate during the dry season (between Dec–Mar). The data are compatible with extended seasonal monoestry, but more data are needed to confirm the chronology. Data from four marked and recaptured ♀♀ is also indicative of monoestry: one was pregnant in two consecutive Septembers and reproductively inactive in the intervening Mar; one was pregnant in two consecutive Septembers and reproductively inactive the following Mar, and one was reproductively inactive in Feb and pregnant the following Aug.

The ratio of ♂♂ to ♀♀ in 73 individuals captured at Tai N. P. was 1 : 1.9. In museum collections, the ratio in 22 specimens was 1 : 1.

Predators, Parasites and Diseases Ectoparasites include a mite *Binuncus* (*Binuncus*) *scotonycteris* (Acari: Myobiidae) (Uchikawa 1986).

Conservation IUCN Category: Near Threatened.

Close to qualifying as Vulnerable because of its small and disjunct area of occupancy (see Distribution), its low abundance and strong dependency on forest habitat. Major threats: agriculture, mining, selective logging and deforestation. Human activities in historic times have reduced the area of forests in West Africa by at least 88.5%. Several of the sites where this species is known to occur, e.g. Mt Nimba, forest sites in Ghana, and Mt Cameroon, are under heavy pressure from mining, logging and encroachment by farmers. Population size unknown, population trend inferred as strongly declining (>50%) due to loss of habitat.

Measurements

Scotonycteris ophiodon

FA (♂♂): 76.5 (74–79) mm, n = 19

FA (♀♀): 77.5 (73–81) mm, n = 38

WS (c): 523 (469–548) mm, n = 10

HB: 117.1 (115–122) mm, n = 9

T: 0 mm

E: 22.6 (20–25) mm, n = 14

Tib: 29.1 (26–32) mm, n = 10

HF: 18.1 (17–19) mm, n = 15

WT (♂♂): 67.2 (60–77) g, n = 12

WT (♀♀): 74.4 (64–95) g, n = 30

GLS: 37.8 (35.3–40.0) mm, n = 8

GWS: 23.3 (22.3–24.3) mm, n = 14

C–M¹: 12.5 (12.0–13.4) mm, n = 17

Liberia, Côte d'Ivoire, Ghana, Cameroon (BMNH [incl. holotype *cansdalei*], FC, SMF, SMNS, USNM, ZFMK)

For specimens from Congo, see Geographic Variation

Key References Bergmans 1973, 1990; Eisentraut 1959; Hayman 1945; Novick 1958a; Wolton *et al.* 1982.

Jakob Fahr

Scotonycteris zenkeri ZENKER'S FRUIT BAT

Fr. Scotonyctère de Zenker; Ger. Zenkers Harlekin-Flughund

Scotonycteris zenkeri Matschie, 1894. Sitzb. Ges. Naturf. Fr. Berlin 1894: p. 202. Yaunde [=Yaoundé], Cameroon.

Taxonomy Synonyms: *bedfordi*, *occidentalis*. Subspecies: three, but limits uncertain (see Geographic Variation). Chromosome number (Gabon): 2n = 32 (Primus *et al.* 2006); as a result of conventional staining, no detailed comparison could be made with the banded karyotype of *S. ophiodon*, which is very distinct from other African fruit bats.

Description Very small fruit bat with face-markings (white patch on forehead, white posterior eye-spots, partly white or pale lips); no conspicuous basal ear-patches; no epaulettes; snout and finger-joints not yellowish; forehead region of skull almost straight; bony palate extending well beyond last teeth; cusps of premolars and molars relatively weak; FA: 47–55 mm. Sexes similar in colour; ♀♀ on average with slightly longer forearms. Pelage dense, soft and woolly dorsally; shorter and sparser ventrally with stiff hairs on chest and belly; mid-dorsal hairs 9–10 mm. Dorsal pelage medium sepia brown to rusty-brown, mottled; hairs tricoloured, white or whitish with dark brown at base and sepia brown to rusty-brown at tip. Ventral pelage with lower breast and central belly whitish to pale grey, flanks medium to dark brown or greyish-brown, contrasting with the paler areas. No epaulettes or white markings on shoulders. Head with three conspicuous white patches, one on forehead (between anterior corners of eyes) and one at posterior corner of each eye; anterior basal ear-patches indistinct or absent; no posterior basal ear-patches; lips usually bordered by a narrow and indistinct band of white or pale hairs around each corner. Muzzle short, slender; lips only moderately expansible. Ears dark brown (paler near base), naked; oval with broadly rounded tip. Eyes large, dark brown. Palate with four thick and smooth ridges (the first three undivided, the fourth sometimes medially divided) and 6–9 very thin, serrated and irregular ridges (Figure 54a). Wing-membranes dark greenish-brown or brown, reticulated; attaching to first toe; finger-joints not yellowish (cf. *S. ophiodon*). No visible tail.

Skull short and delicate for an African fruit bat. Braincase rounded; rostrum relatively short (30.4–34.6% of GLS), not upturned. Profile of forehead region (viewed laterally) almost straight (cf. *Casinonycteris*). Zygomatic width relatively narrow (62–69% of GLS) and zygomatic arches comparatively lightly built and with lower

margin level with infraorbital foramen (cf. *Casinonycteris*). Bony palate extending well beyond last teeth. Upper incisors comparatively short. Upper canines only moderately long, with faint inner groove, not conspicuously curved, and without secondary cusps or serrated inner edges (cf. *S. ophiodon*). Premolars and molars rounded to slightly oval in transverse section, with moderate outer cusps but only faint inner cusps (cf. *S. ophiodon*, *Casinonycteris argyannis*). Dental formula usually $^{2121}_{2132} = 28$ (variations known).

Geographic Variation Three subspecies are tentatively recognized here with the following distributions:

S. z. zenkeri: E Nigeria, Cameroon, Gabon and mainland Equatorial Guinea.

S. z. bedfordi: Bioko I.

S. z. occidentalis: Liberia, Guinea, Côte d'Ivoire, Ghana.

Andersen (1912a), Eisentraut (1959) and Kuhn (1961) questioned subspecific differences. However, Bergmans (1990) demonstrated morphological differentiation between five disjunct populations in (1) Liberia, Côte d'Ivoire, Ghana, (2) W Nigeria, (3) Cameroon, mainland Equatorial Guinea and probably E Nigeria, (4) Bioko I. and (5) E DR Congo, which differ in size and/or cranial and dental morphology. This is not adequately reflected in the above subspecific classification. Furthermore, there are isolated records from Congo and Central African Republic and it is not yet clear if these should be assigned to one or more of the above populations or if they represent additional independent and disjunct enclaves. Apart from cranial and dental differences, the population from W Nigeria seems to average largest in measurements while that from Bioko I. is smallest (Bergmans 1990).

Similar Species Only two other species of African fruit bats have white markings on the nose, upper lips and/or near the eyes:

Casinonycteris argyannis. Forearm often longer (50–62 mm). Finger-joints pale yellowish. Forehead region of skull strongly concave; rostrum upturned; bony palate barely extending beyond last teeth.

Scotonycteris ophiodon. Much larger (FA: 73–87 mm). Finger-joints yellowish.

Distribution Endemic to Africa. Mainly found in the Rainforest BZ (Western, West Central and East Central Regions) and marginally in the Afromontane–Afroalpine BZ. Recorded, disjunctly, from Guinea, Liberia, Côte d'Ivoire, Ghana, Nigeria, Cameroon, Equatorial Guinea (including Bioko I.), Gabon, Central African Republic, Congo and DR Congo. Not yet recorded from Dahomey Gap. A gap between records from W Nigeria and E Nigeria mentioned by Bergmans (1990) has been partly bridged by a record from Orashi, Niger Delta (Angelici *et al.* 2000). The records from Central African Republic, E DR Congo and Congo appear isolated. This species has been found at almost all localities where *S. ophiodon* occurs but is much more widely distributed than the latter.

Habitat Recorded in lowland rainforest, coastal forest, montane forest, swamp forest, mangroves and marginally in forest–savanna mosaic vegetation zones. Recorded up to 1000 m on Mt Nimba (Verschuren 1976) and up to 1100 m on Mt Kupé and Rumpi Hills, Cameroon (Eisentraut 1973a). However, seems to prefer lowland rainforests and usually is not found higher than 500–800 m (Eisentraut 1973a, Coe 1975, Wolton *et al.* 1982, Fedden & Macleod 1986). On Bioko I., only found below 400 m (Juste & Perez del Val 1995). Occurs in both pristine and disturbed rainforest and has been mist-netted frequently near forest fringes, in gardens and forest gaps but never in extensively cleared areas or far from closed forest (Eisentraut 1959, Brosset 1966, Jeffrey 1975, Happold & Happold 1978, Wolton *et al.* 1982, J. Fahr unpubl.). On Bioko I., mist-netted significantly more often in cultivated clearings than in lowland rainforest (Juste & Perez del Val 1995). The habitats in Congo are described as degraded rainforest in an area with low mountains (Bergmans 1973) and heavily disturbed low-altitude forest dominated in the understorey by *Haumania liebrechtsiana* (Marantaceae) (Dowsett *et al.* 1991).

Abundance Locally rare to very rare. In Tãï N. P., comprised 3.6% of fruit bat catch ($n = 1216$ individuals); sixth most abundant species in community of eight species of fruit bats (J. Fahr & S. Pettersson unpubl.). At Mt Nimba, comprised 2.7% of the fruit bat catch ($n = 979$) and was the sixth most abundant species in a community of nine species of fruit bats (Wolton *et al.* 1982). On Bioko I., between 0 and 400 m, represented 13.0% of the catch of four sub-canopy species of fruit bats ($n = 332$) (Juste & Perez del Val 1995).

Adaptations By day, usually roosts hanging from vegetation; has been found between plantain leaves and in trees or bushes, sometimes at the forest edge (Hayman 1946a, Kuhn 1961, Rosevear 1965). Recapture rate in Tãï N. P. was 23.8% ($n = 21$); much higher than in most other fruit bats at this locality. Most were recaptured from six months to one year later; two were recaptured 1.7 and 2.1 years later. All individuals (including subadults and young-adults) were recaptured less than 400 m from the initial site; most less than 250 m away. This suggests that home-ranges are very small (several hectares) and site-fidelity is unusually high for a fruit bat (J. Fahr unpubl.).



Scotonycteris zenkeri

Frequencies of captures had two distinct peaks (21:00–23:00h and 02:00–04:30h), with very few captures between midnight and 02:00h. In contrast, almost the inverse pattern was shown by *S. ophiodon* at the same locality. Captive *S. zenkeri* were active for only ca. six hours per night (Wolton *et al.* 1982). The activity was either broken up into two 3-hour periods with a 2–3 hour rest commencing around midnight, or continuous for ca. six hours. Kuhn (1968) studied the innervation of the larynx of *S. zenkeri* and concluded that the pattern in this species is basal but derived in *Epomophorus labiatus*, *Epomops buettikoferi* and *Hypsignathus monstrosus*.

Foraging and Food Frugivorous. Data regarding vertical preference are equivocal. Eisentraut (1959) and Fedden & Macleod (1986) caught *S. zenkeri* mainly in elevated mist-nets. Cosson (1995) and Happold & Happold (1978), using only mist-nets at ground-level, caught *S. zenkeri* in the understorey. The latter authors suggested that foraging is more likely to occur in the upper strata and canopy. However, captures in mist-nets set from 0 to 25 m above ground in Tãï N. P. suggest that foraging occurs from ground to canopy level (median capture height 15.4 [1.5–23.6] m, $n = 21$) (J. Fahr unpubl.). Diet almost unknown. Eisentraut (1959) noted a honey-like smell when examining the stomach of a specimen but could not identify the ingested food. At Mt Nimba, this bat fed extensively on *Solanum torvum* and *S. erianthum* between Jul and Sep (Wolton *et al.* 1982). Captive individuals (in Gabon) refused various fruits, honey-water and flowers (Brosset 1966). Captive individuals (in Liberia) spent 2–2.5 h/night feeding; the mean \pm S.D. nightly fruit consumption was 20.3 ± 9.7 g ($n = 11$); the dry weight assimilated was 90%; the mean consumption per unit body weight was $0.99 \text{ g/g}^{\text{bw}}$ and the through-put time was 24 ± 8 min (Wolton *et al.* 1982). The ratio between body and intestine length is 1 : 3.6 and the intestine is rather short compared to that of other (mainly) frugivorous pteropodids (Eisentraut 1959).

Social and Reproductive Behaviour Usually roosts singly. In Gabon, Brosset (1966) caught three ♀♀, each accompanied by volant young, which were almost the same size as their mothers; later, in captivity, these young huddled with their mothers. According to Wolton *et al.* (1982), captive ♀♀ appear to be more active and more vocal than ♂♂. They emitted an abrupt high-pitched whistle throughout the night, with maximum frequency just before dawn. Adult ♂♂ in Tai N. P. had a remarkably strong and spicy scent.

Reproduction and Population Structure Litter-size: one (n = 7), two (n = 1) (Jeffrey 1975, Wolton *et al.* 1982, J. Fahr unpubl.). Embryos are implanted in both uterine horns. In West Africa (E Liberia, Côte d'Ivoire, SW Ghana) the reproductive chronology is probably seasonal bimodal monoestry: out of 70 adult ♀♀, pregnancies have been recorded for Jan and Feb (n = 7) and from Jul to Nov (n = 12), with peaks in Feb (37.5% of 16 ♀♀) and between Sep (60% of 5 ♀♀) and Oct (83.3% of 5 ♀♀). In the same region, lactating ♀♀ were found from Feb to Apr (n = 5) and from Oct to Dec (n = 5); notably, none of 10 ♀♀ was lactating in Jan (Kuhn 1961, Wolton *et al.* 1982, J. Fahr unpubl., IRSN, SMF, SMNS, USNM). None of the 29 reproductively active ♀♀ was simultaneously palpably pregnant and lactating, which suggests that the chronology is not polyoestry. In the rainforest region of West Africa, the first lactation period (Feb–Apr) would correspond to the onset of the wet season while the second period (Oct–Dec) would be at the end of the wet and start of the dry season, possibly coinciding with peaks in fruit production. Data from central Africa are inconclusive: in SW Cameroon, a ♀ was pregnant with a pea-sized embryo in Feb, and another ♀ was pregnant in Oct on Bioko I. (Eisentraut 1973a). In the Ituri region of DR Congo (near Epulu: 01° 23' N) a ♀ had an embryo (CR: 15 mm) in Jun (FMNH).

The ratio of ♂♂ to ♀♀ in 75 bats captured at Tai N. P. was 1 : 0.8 (J. Fahr unpubl.); the ratio in 16 bats captured on Bioko I. was 1 : 0.8 (Eisentraut 1973a), and the ratio in 22 museum specimens was 1 : 1.

Predators, Parasites and Diseases Two specimens were recovered from green mambas (*Dendroaspis jamesoni*) in Niger Delta, Nigeria (Luiselli *et al.* 2000). No other information.

Conservation IUCN Category: Least Concern.

Although this species probably depends on undisturbed forest to a lesser degree than *S. ophiodon*, it is most likely to be lost from areas with extensive clearings and land conversion. Population size unknown but decline inferred from loss of habitat, degradation and fragmentation. Recent records are mostly from undisturbed sites.

Measurements

Scotonycteris zenkeri

FA (♂♂): 50.3 (47–55) mm, n = 25

FA (♀♀): 52.2 (47–55) mm, n = 21

WS (c): 346 (330–372) mm, n = 10

HB: 77.5 (65–85) mm, n = 37

T: 0 mm

E: 14.4 (12–17) mm, n = 38

Tib: 20.5 (18–24) mm, n = 11

HF: 12.7 (11–14) mm, n = 33

WT: 20.3 (16–24) g, n = 59

GLS: 25.9 (24.0–27.4) mm, n = 16

GWS: 16.9 (15.9–17.8) mm, n = 17

C–M¹: 8.4 (7.9–9.0) mm, n = 18

Liberia, Côte d'Ivoire, Ghana, Cameroon, Equatorial Guinea, Central African Republic, Congo, DR Congo (BMNH [including holotypes *bedfordi* and *occidentalis*], FC, FMNH, IRSN, MNHN, RMCA, ROM, SMF, USNM, ZMB [including holotype *zenkeri*])

Key References Bergmans 1990; Eisentraut 1959; Hayman 1946a; Wolton *et al.* 1982.

Jakob Fahr

Family RHINOLOPHIDAE

HORSESHOE BATS

Rhinolophidae Gray, 1825. Zool. Journ., 2 (6): 242.

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|---------------------------------|----------------|--------|
| <i>Rhinolophus</i> (27 species) | Horseshoe Bats | p. 303 |
|---------------------------------|----------------|--------|

This is a monotypic family, which is widely distributed in the tropical and sub-tropical regions of the Old World, with some species extending into temperate regions. All rhinolophids belong to the genus *Rhinolophus*. Currently, 77 extant species are recognized, of which 27 occur in Africa (Simmons 2005). Some of these contain subspecies that almost certainly should have specific rank. Rhinolophids have a large, complex noseleaf, the anterior component of which roughly resembles the underside of a horse's hoof and is referred to as the horseshoe (Figure 49b). The posterior part of the noseleaf has a single, erect, pointed tip. Rhinolophids have large leaf-shaped ears without a tragus, toes with three phalanges, and a medium-length tail that is completely enclosed by an interfemoral membrane (Figures 33b and 55). Rhinolophids resemble hipposiderids (which are closely related) but differ externally in the form of the noseleaf and the number of phalanges in the toes. None are considered to be pests.

Rhinolophids are small to medium-sized microbats with long, soft, dense fluffy pelage. Most African rhinolophids are greyish-fawn or greyish-brown in their grey-phase, and have an orange-phase. They have a small compact body and a rounded head with a short blunt muzzle. The ears are almost as broad as they are long and are well separated; the antitragus is conspicuous and there is no tragus. The eyes are very small. The noseleaf is very prominent and is comprised of an anterior horseshoe-shaped component (the horseshoe), a central component, which has a transverse projection (the sella)

and a longitudinal connecting process, and a subtriangular posterior component with an erect tip referred to as the lancet (Figure 56). Many species of rhinolophids are distinguished by the shape of the lancet, sella and connecting process. The wings are large and broad with rounded tips; the second finger has a long metacarpal but no bony phalanges. The hindlimbs are moderately long with small soles and relatively long toes, each (except the hallux) having three phalanges (cf. two in hipposiderids). The tail is relatively short to medium (30–37% of TL), and is completely enclosed by the interfemoral membrane; calcars are present. Females have one pair of pectoral nipples and one pair of pubic nipples; the ♂♂ of some species have a false nipple and tuft of stiff hairs (axillary tuft) in each armpit. The skull (Figure 57) has nasal swellings (sometimes called rostral swellings or rostral inflations), a low sagittal crest (usually more prominent anteriorly than posteriorly) and no postorbital processes. Supraorbital ridges vary from weak to prominent. The nasal branches of the premaxillae are lost. The palatal branches are reduced, partly cartilaginous, not fused with each other and not fused with the maxillary; they are usually lost when skulls are cleaned. Because of this, greatest length of skull (GLS) of rhinolophid bats is replaced by CrnC (the distance from the anterior of the upper canine to the most posterior part of the skull). The palate has a very deep, wide, roughly U-shaped anterior palatal emargination, and also a U-shaped posterior emargination, and is shorter than it is broad. The length of the palate between the two emarginations is referred to as the length of the palatal bridge. The tympanic bullae are relatively small

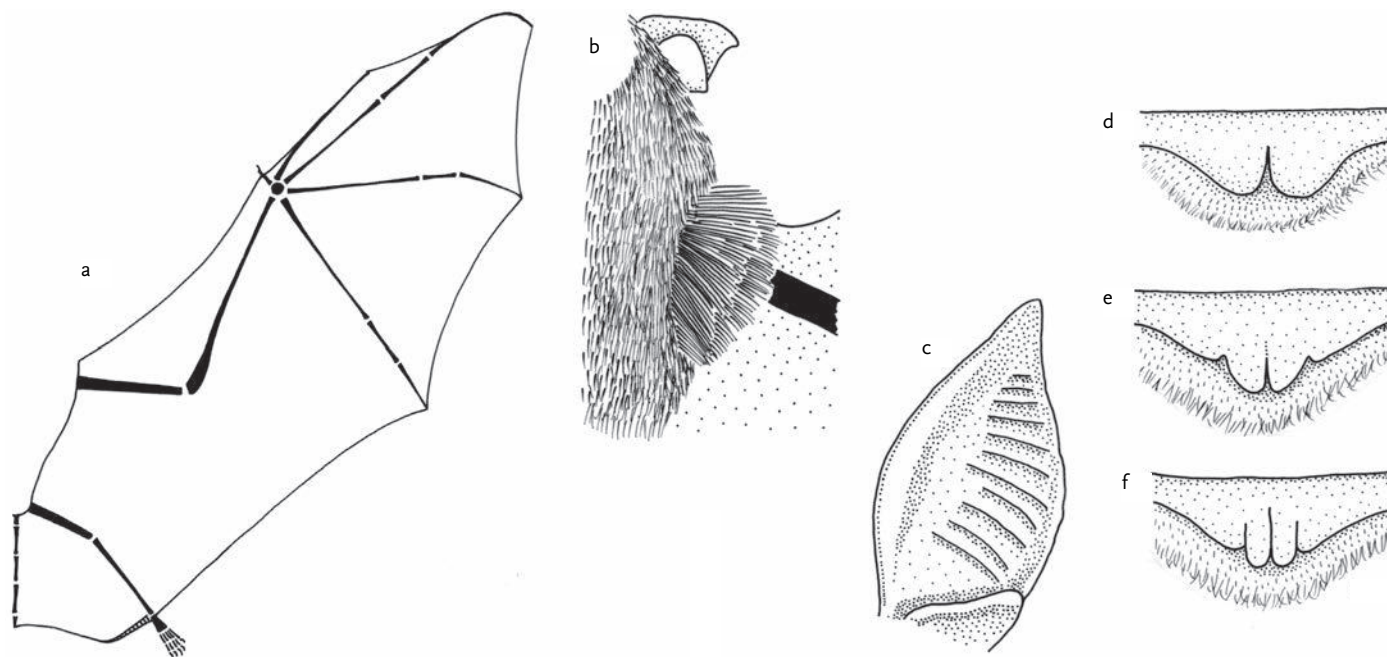
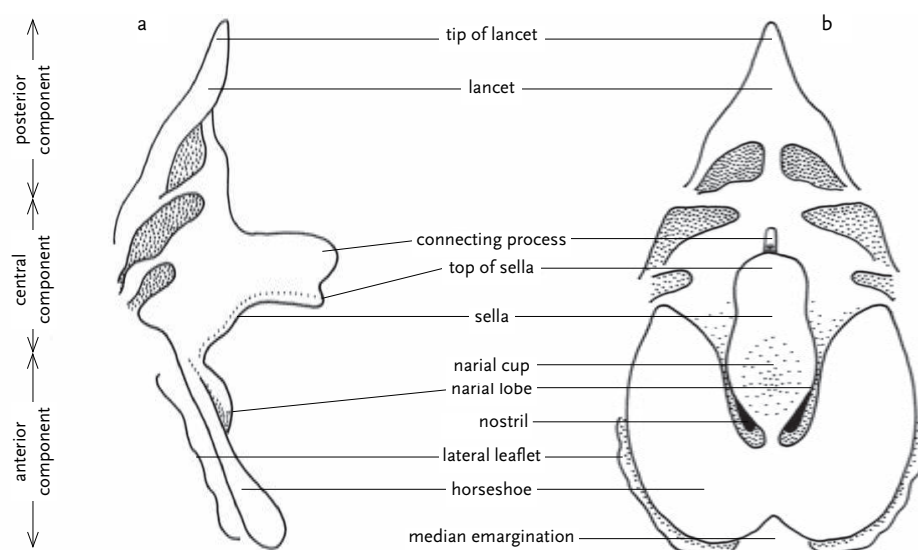


Figure 55. Characters of African bats in the family Rhinolophidae. (a) Flight membranes and bones of wing, hindlimb and tail (e.g. *Rhinolophus blasii*). (b) Ventral view of armpit showing axillary tuft (e.g. *R. alcyone*; based on Rosevear 1965). (c) Ear with 11 internal folds, a large antitragus but no tragus (e.g. *R. ziama*; based on photo by T. Vierhaus). Grooves in the lower lip: (d) one well-defined median groove and no lateral grooves (e.g. *R. eloquens*, (e) one well-defined median groove and one poorly-defined lateral groove on each side (e.g. *R. alcyone*) and (f) three well-defined grooves (e.g. *R. simulator*).

Figure 56. (a) Lateral and (b) frontal views of a noseleaf of *Rhinolophus* showing the components as defined and referred to in the profiles below (some components are defined differently by some other authors).



but the cochleae are well developed. The dental formula is variable, usually $^{1123}/_{2133} = 32$. However, the anterior upper premolar and/or the posterior middle premolar may be missing. In some species, the anterior upper premolar lies within the toothrow (albeit sometimes slightly displaced) and separates the canine from the posterior premolar: in other species, this tooth is fully displaced labially and the canine and posterior premolar are in contact. Similarly, the middle lower premolar may be within the toothrow or partly or fully displaced labially, or it may be absent, and the anterior and posterior

lower premolars may be separated or in contact accordingly. The upper incisors are very small; the lower incisors are tricuspid. The molariform teeth do not show any particular modification; M^3 almost always has three ridges (Csorba *et al.* 2003).

Most African rhinolophids have low to very low aspect ratios and low to very low wing-loadings; only one species is known to have medium wing-loading. They fly slowly with considerable manoeuvrability. They can hover briefly and take off from the ground. Rhinolophids are insectivorous: several feed mainly on moths and/or small beetles, at least during some seasons. Some forage by slow-hawking, and some are predominantly fly-catchers and/or gleaners that often forage within 6 m of the ground, often close to foliage and tree-trunks, in cluttered environments. At least one species catches flying insects in the tip of one wing, bending the phalanges to hold the prey before rapidly transferring it to the mouth (Webster & Griffin 1962). Rhinolophids do not 'pouch' their prey in the interfemoral membrane (cf. vespertilionids). They sometimes fly into lighted rooms in search of prey. Most forage alone. Their echolocation calls are typically FM/CF/FM calls with a sustained CF component and maximum energy in the second harmonic: some (perhaps all) species in Africa can be distinguished by the CF-frequency of their calls (Figure 58). The echolocation calls of rhinolophids are adapted to facilitate the detection of flutter (by exploiting Doppler-shifted echoes reflected from the fluttering wings of insects), and are particularly suitable for densely cluttered environments (Neuweiler 1989). Harmonics are of particular value to bats that emit long CF calls. The calls, which initially include the fundamental harmonic, are produced in the larynx, and the nasal swellings (swellings in the skull beneath the noseleaf) facilitate the production of harmonics and suppress the fundamental harmonic in the emitted sound (Suthers *et al.* 1988). Tracheal chambers suppress the fundamental harmonic in internally reflected sound, and this may enable rhinolophids to rely on the tissue-conducted fundamental as a reference or marker of their own laryngeal generated sound, which could be useful in processing sonar information (Suthers *et al.* 1988). Rhinolophids emit their echolocation calls through the nostrils and the noseleaf acts as a parabolic reflector to direct a beam of sound in front of the bat and shield the ears, to some extent, from the emitted sounds

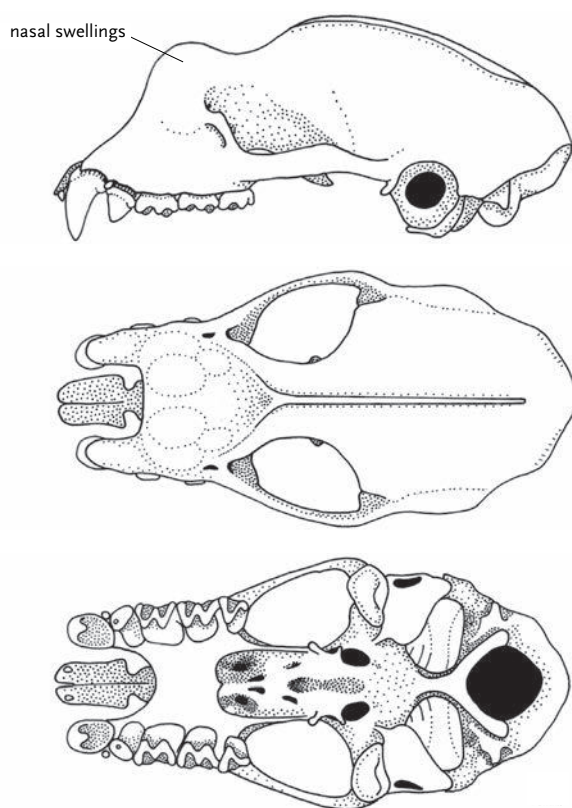


Figure 57. *Rhinolophus hildebrandtii*. Skull (RMCA RG 23816).

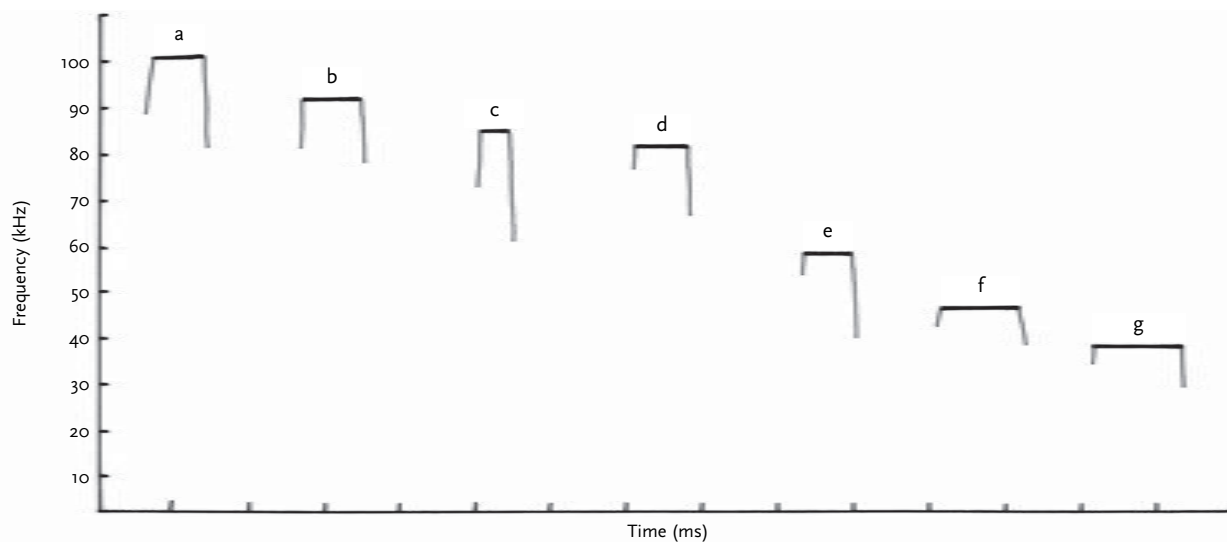


Figure 58. Sonograms of the FM/CF/FM echolocation calls of seven species of *Rhinolophus* from Malawi, presented in order of decreasing CF frequency: all bats hand-held (M. Happold unpubl.). (a) *R. swinnyi*, (b) *R. blasii*, (c) *R. simulator*, (d) *R. clivosus*, (e) *R. fumigatus*, (f) *R. ? eloquens* and (g) *R. hildebrandtii*. Time axis marked at intervals of 50 ms.

(Möhres 1953). While echolocating, the ears move independently with a very characteristic flickering movement, and the head moves up and down and from side to side to beam the sound in different directions.

Rhinolophids are unable to scuttle over the ground, and they cannot climb. During the day, most roost in dark caves or cave-like day-roosts such as mine-adits, hollow trees and dark places in buildings. They hang freely from ceilings or hang in contact with vertical walls. When hanging, the tail and interfemoral membrane fold up over the back and the wings fold around the chest so the body is either mostly or fully enclosed by the flight-membranes. Rhinolophids roost singly or in small to very large groups. Very little is known about the social behaviour of African species. Maternity colonies are established by many species. When ♂ and ♀ *R. ferrumequinum* begin to roost together at the end of summer, the ♂♂ become territorial and establish small harems (see profile); the mating systems of other species in Africa are apparently not known. All of the seven African rhinolophids for which data are available are monotocous and seasonally monoestrous. Delayed fertilization and sperm storage has been documented for *R. capensis*, *R. clivosus*, *R. ferrumequinum* and *R. hipposideros*, delayed implantation for *R. landeri* and retarded embryonic development for *R. ferrumequinum* (in Europe) (see species profiles). In temperate regions, rhinolophids mate in autumn, sperm storage and hibernation occur during winter, and ovulation followed by uninterrupted gestation occurs in spring. In the tropics, young are born at the end of the dry season or in the wet season (data available for five species). It is thought that the young cling to the pubic nipples with their toes and to the pectoral nipples with their teeth. Females carry their young while flying from perch to perch within a day-roost, and will carry the young away from a disturbed day-roost, but they probably do not carry their young while routinely foraging for food.

The geological range of the Rhinolophidae is late Eocene to Recent in Europe, Miocene to Recent in Africa, early Miocene to Recent in Asia, middle Miocene to Recent in Australia and Recent in other regions now occupied (Bogdanowicz & Owen 1992, Corbet & Hill 1992, Csorba *et al.* 2003). The Rhinolophidae had probably diverged

from the Hipposideridae by the late Eocene (Csorba *et al.* 2003). According to Bogdanowicz & Owen (1992), the family probably originated in the Old World tropics, perhaps in Africa or perhaps in southern Asia. Maree & Grant (1997) also agree that morphological analyses indicate that the family probably originated in South-East Asia. In contrast, a European origin for the family, and monophyly for the African and Palaearctic species is proposed by Csorba *et al.* (2003). Based on genetic evidence, Csorba *et al.* (2003) suggest that there was an early emergence of a clade containing *R. trifoliatum* and *R. hipposideros* (of which only *R. hipposideros* occurs in Africa), and a clade containing, amongst others, an African clade, which probably contains all of the other African species. Within this African clade, the clade representing the most basal lineage comprises species linked to rainforest habitat (*R. alcyone*, *R. landeri* and probably *R. guineensis*). Subsequently, there seems to have been a series of radiations into dry environments. The first of these radiations seems to have given rise to a Mediterranean group (*R. blasii*, *R. euryale* and *R. mehelyi*) and *R. blasii* appears to have migrated southwards as far as southern Africa more recently. Subsequently, there appear to have been at least two radiations in arid areas of eastern and southern Africa, one giving rise to a lineage including *R. capensis*, *R. denti*, *R. simulator* and *R. swinnyi* (Maree & Grant 1997) and probably also *R. adami* and *R. maendeleo* (Csorba *et al.* 2003), and another giving rise to a lineage containing *R. clivosus*, *R. darlingi*, *R. fumigatus* and *R. hildebrandtii* (Maree & Grant 1997) and also *R. ferrumequinum*, *R. maclaudi* and *R. eloquens* (Csorba *et al.* 2003).

Rhinolophids have radiated into forests, woodlands and semi-desert habitats at both high and low altitudes. The majority of species are tropical or sub-tropical and a few occur in temperate regions. Of the 27 species that occur in Africa, 14 are found only in the tropics, four are found only in temperate regions and seven are in tropical, sub-tropical and temperate regions. Seven species are only or mainly found in forest habitats, nine occur in both forests and savannas, four occur only in savannas, one occurs in both savanna and arid habitats, three occur in all of these habitats, and three which are found in the Mediterranean Coastal BZ extend marginally into the arid habitats of the Sahara Arid BZ. Thirteen species (48%) have been found in montane habitats but,

of these, only *R. ruwenzorii* and the very closely related *R. hilli* are found only in montane habitats. It is not uncommon to find two species at any one locality, but the occurrence of three or more species seems to be very rare (except in Malawi where 3–5 species have been recorded at six localities Happold & Happold 1997). Some examples are:

Misserghin, Algeria (garrigue): *R. blasii*, *R. ferrumequinum*, *R. hipposideros* and *R. mehelyi* (Kowalski & Rzebik-Kowalska 1991).

Shimoni, Kenya (coastal forest mosaic): *R. fumigatus*, *R. deckenii* and *R. landeri* (Aggundey & Schlitter 1984).

Liwonde N. P., Malawi (miombo woodland): *R. blasii*, *R. clivosus*, *R. fumigatus*, *R. hildebrandtii* and *R. simulator* (Happold & Happold 1997).

Based on morphological data, the family Rhinolophidae was placed in the superfamily Rhinolophoidea with the families Nycteridae, Megadermatidae and the very closely related Hipposideridae

(Simmons 1998, Simmons & Geisler 1998), but more recent molecular studies have contradicted many groupings based on morphological data and, pending resolution of the controversies, no chiropteran superfamilies are recognized by Simmons (2005). Some authors, including Koopman (1984, 1993, 1994) and Simmons (1998), follow Tate (1941) in considering the Rhinolophidae to include the Hipposideridae as a subfamily. However, the familial status of the Hipposideridae has been retained by Maree & Grant (1997), Csorba *et al.* (2003), Simmons (2005) and in the majority of books about African mammals and is retained here. For further comment, see Family Hipposideridae.

The Rhinolophidae have been comprehensively reviewed by Csorba *et al.* (2003). All rhinolophids belong to the genus *Rhinolophus*.

Meredith Happold & F. P. D. Cotterill

GENUS *Rhinolophus*

Horseshoe Bats

Rhinolophus Lacépède, 1799. Tabl. Div. Subd. Orders Genres Mammifères, p. 15. Type species: *Vespertilio ferrum-equinum* Schreber, 1774.

This genus currently has 77 species of which 27 occur in Africa (Simmons 2005). There are no other genera in the family Rhinolophidae and the characters of this genus are given in the family profile.

This genus is divided into 15 species-groups following Csorba *et al.* (2003) (see also Bogdanowicz 1992, Bogdanowicz & Owen 1992, Maree & Grant 1997, Fahr *et al.* 2002). Of these groups, eight are represented in Africa:

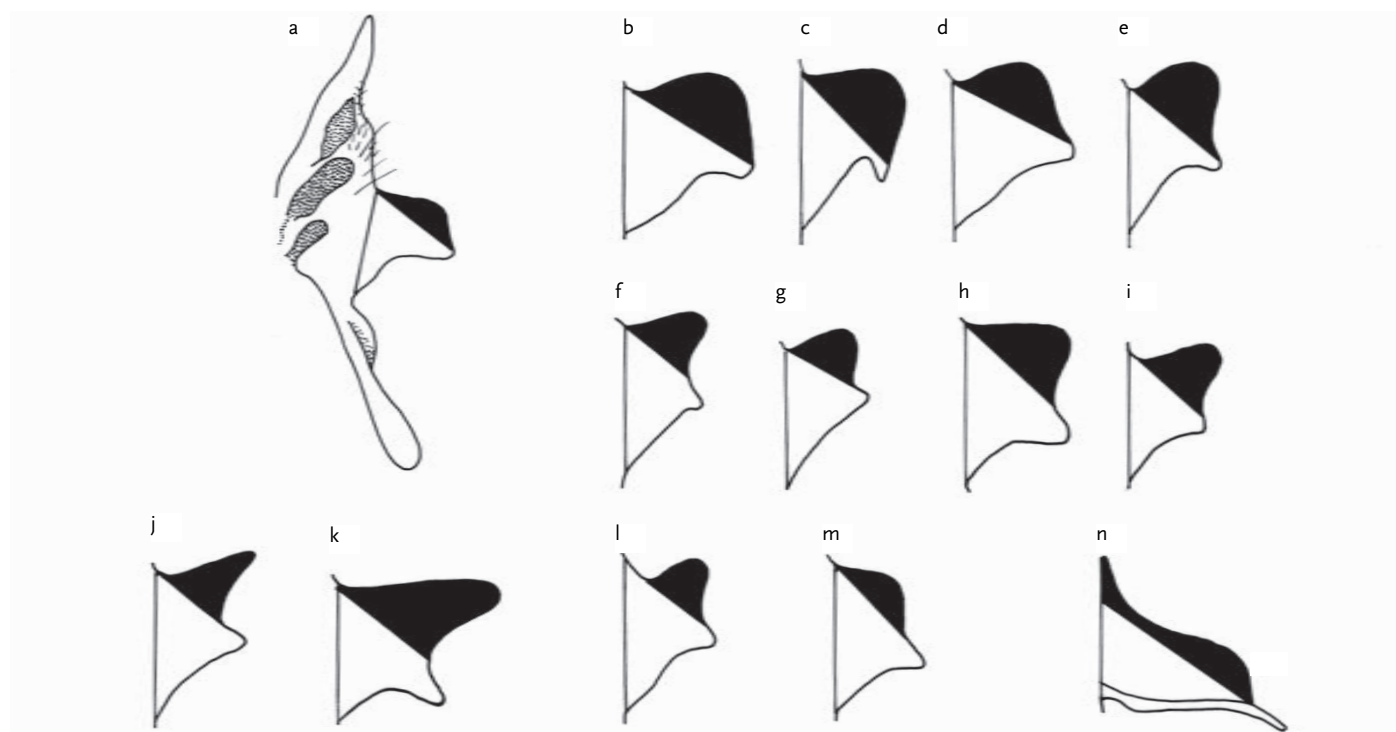


Figure 59. Variations in the shape of the connecting process of the noseleaf of African *Rhinolophus*. (a) Noseleaf showing (black) that part of the connecting process that is described by the following terms. Rounded as in (b) *R. maendeleo* (based on Kock *et al.* 2000), (c) *R. adami* (based on Kock *et al.* 2000), (d) *R. simulator* (M. Happold, Malawi) and (e) *R. clivosus* (M. Happold, Malawi). Subtriangular as in (f) *R. landeri* (based on Csorba *et al.* 2003), (g) *R. guineensis* (based on Csorba *et al.* 2003), (h) *R. alcyone* (based on Csorba *et al.* 2003) and (i) *R. mehelyi* (based on Csorba *et al.* 2003). Rising to a high horn as in (j) *R. blasii* (M. Happold, Malawi) and (k) *R. euryale* (based on Gaisler 2001a). Rounded but rising to a high peak as in (l) *R. sakejiensis* (based on Csorba *et al.* 2003). Very low, slightly rounded or flat as in (m) *R. hipposideros* (based on Csorba *et al.* 2003). Greatly reduced, very low and concave as in (n) *R. ziama* (from photo in Fahr *et al.* 2002).

*Rhinolophus hildebrandtii*.

adami group: two species – *R. adami*, and *R. maendeleo*.

capensis group: four species – *R. capensis*, *R. denti*, *R. simulator* and *R. swinnyi*.

euryle group: two species – *R. euryle* and *R. mehelyi*.

ferrumequinum group: eight species including *R. clivosus*, *R. darlingi*, *R. deckenii*, *R. ferrumequinum*, *R. hillorum*, *R. sakejiensis* and *R. silvestris*.

fumigatus group: three species – *R. eloquens*, *R. fumigatus* and *R. hildebrandtii*.

hipposideros group: one species – *R. hipposideros*.

landeri group: four species – *R. alcyone*, *R. blasii*, *R. guineensis* and *R. landeri*.

maclaudi group: four species – *R. hilli*, *R. maclaudi*, *R. ruwenzorii* and *R. ziama*.

The African species are distinguished mainly on the basis of the following characters (Table 14):

Table 14. Key to the African species in the family Rhinolophidae. Information from African material, mostly from species profiles. Sample sizes of *R. adami*, *R. hilli*, *R. maendeleo*, *R. sakejiensis*, *R. silvestris* and *R. ziama* are less than six. Distinguishing species that are morphologically very similar from the information below is not easy, and identifications should be confirmed using the additional information in the Description, Similar Species and Distribution sections of the species profiles.

| Connecting process | Position of anterior upper premolar ^a
(Proximity of canine and posterior premolar) | Sella ^b
Hairiness and shape | Lancet | Horseshoe mean (range) (mm) | |
|--------------------|---|--|---|-----------------------------|--|
| Rounded | Within toothrow
(Well separated) | Naked
Sides slightly concave | Subtriangular, sides slightly convex
Tip broad and rounded | 8.5, 9.0 | |
| Rounded | Within toothrow
(Well separated) | Naked
Sides concave | Subtriangular, sides slightly concave
Tip bluntly pointed | 8.2, 8.4 | |
| Rounded | Within toothrow
(Well separated) | Naked
Almost parallel-sided or slightly concave | Subtriangular, sides slightly concave
Tip bluntly pointed | 7.1 (6.8–7.5) | |
| Rounded | Within toothrow
(Well separated) | Naked
Sides slightly concave | Subtriangular, almost hastate, sides concave
Tip bluntly pointed | 6.8 (6.0–7.4) | |
| Rounded | Within toothrow
(Well separated) | Naked
Sides slightly concave | Subtriangular or hastate
Tip somewhat rounded | 7.4 (6.7–9.0) | |
| Rounded | Usually partly displaced, sometimes fully displaced
(Typically well separated, never in contact) | Naked
Sides parallel or slightly concave | Hastate
Tip bluntly pointed | 7.7 (7.3–8.1) | |
| Rounded | Usually fully displaced or absent
(Separated by very narrow gap) | Naked
Sides parallel or slightly concave | Subtriangular, sides almost straight
Tip bluntly pointed | 10.3 (9.1–11.5) | |
| Rounded | Fully displaced
(In contact or almost so) | Naked
Sides concave | Subtriangular, sides slightly concave
Tip bluntly pointed | 9.5, 10 | |
| Rounded | Fully displaced or absent
(In contact) | Naked
Sides concave | Subtriangular, sides slightly concave
Tip bluntly pointed | 8.0 (7.1–8.7) | |
| Rounded | Fully displaced or absent
(In contact) | Naked
Sides slightly concave | Hastate
Tip bluntly pointed | 8.1 (7.0–9.0) | |
| Rounded | Fully displaced or absent
(In contact) | Naked
Sides concave | Hastate
Tip rounded | 7.8 (6.6–9.6) | |

Connecting process. Can be rounded (with variable height relative to the height of the sella), rounded but rising to a high peak, rising to a high horn (not rounded), subtriangular, or greatly reduced (Figure 59).

Position of the anterior upper premolar. Can be within the toothrow (so canine and posterior premolar are well separated), or fully displaced labially (so canine and posterior premolar are in contact) or partly displaced labially (so canine and posterior premolar are almost in contact). It is only the cingula of the canine and premolar that are ever in contact. The anterior upper premolar is, or can be, absent in some species (Figure 62).

Sella. Can be hairy (well covered by longish, moderately conspicuous hairs) or naked (sparsely covered by inconspicuous short hairs). The shape of the sella is variable (Figure 60).

Lancet. Can be subtriangular, subtriangular with slightly convex sides, subtriangular with slightly concave sides, hastate (having a broad base, markedly concave sides and narrow tip), or short, very narrow and almost parallel-sided (Figure 61). The tip of the lancet can be bluntly pointed or broader and more rounded.

Greatest breadth of horseshoe.

Relative length of first phalanx of the fourth finger to the metacarpal of the fourth finger. Said to be relatively short if its mean relative length is less than 22% of the metacarpal, medium if its mean relative length is 22–25% of the metacarpal, and long if its mean relative length is >25%.

Length of forearm, tibia and ear.

Relative length of palatal bridge. This is the distance from anterior emargination to posterior emargination along mid-line of the bony palate, excluding the median spike projecting from the posterior margin (Figure 23g); expressed as a percentage of $C-M^3$. Said to be short if less than 30%, medium if 31–37%, and long if >37% (all data from Csorba *et al.* 2003).

Axillary tuft. Present (Figure 55b) or absent.

Ear folds. This is the number of internal folds in the outer side of the pinna (Figure 55c). Particularly relevant to species in the *maclaudi* group.

| | First phalanx of fourth finger as % of 4th metacarpal: category ^c , mean (range) | FA mean (range) (mm) | Tib mean (range) (mm) | E mean (range) (mm) | Miscellaneous | Species |
|--|---|----------------------|-----------------------|---------------------|--|-------------------------|
| | Medium 23 | 46–50 ^d | 20, 20 | 25, 26 | Palatal bridge 42–44% of $C-M^3$
Congo | <i>R. adami</i> |
| | Medium 21, 23 | 48, 49 | 19, 19 | 24, 25 | Palatal bridge 37, 39% of $C-M^3$
Tanzania | <i>R. maendeleo</i> |
| | Medium 24 (21–27) | 42.0 (37–44) | 16.7 (15–18) | 18.0 (14–21) | Sella breadth not known
CrnC: 16.5 (15.8–17.3) mm
See Distribution | <i>R. denti</i> |
| | Medium 22 (21–25) | 41.7 (40–44) | 18.4 (17–21) | 17 (15–20) | Sella comparatively narrow (1.2–1.3 mm prior to preservation)
CrnC: 17.4 (17.0–18.2) mm
See Distribution | <i>R. swinnyi</i> |
| | Long 23 (20–25) | 45.2 (42–49) | 18.3 (18–20) | 21 (18–23) | Sella comparatively broad (1.5–1.7 mm after preservation)
CrnC: 18.4 (17.3–19.3) mm
See Distribution | <i>R. simulator</i> |
| | Long 26 (24–30) | 48.8 (47–51) | 18.7 (17–21) | 23.8 (21–25) | Western and Eastern Cape Provinces, South Africa | <i>R. capensis</i> |
| | Long 27 (24–30) | 53.1 (48–56) | 25.0 (24–28) | 22.6 (18–27) | Uganda, Kenya, Tanzania, Pemba I., Mafia I. and Zanzibar I.
Mainly in coastal forests | <i>R. deckenii</i> |
| | Long ca. 31 | 53.6 (50–56) | 23 (23–24) | 22, 23 | Gabon and Congo
CrnC: 23.1 (22.3–23.7) mm | <i>R. silvestris</i> |
| | Long 27 (24–30) | 46.9 (42–51) | 20.9 (20–22) | 20.1 (15–23) | Angola to Tanzania and southwards to South Africa
CrnC: 19.3 (18.4–20.5) mm | <i>R. darlingi</i> |
| | Long 28 (24–31) | 55.4 (51–59) | 24.0 (23–25) | 22.8 (19–25) | North-West Africa | <i>R. ferrumequinum</i> |
| | Long 28 (25–31) | 51.5 (42–59) | 21.9 (16–27) | 20.1 (16–24) | Widespread but not north-west Africa and not West Africa | <i>R. clivus</i> |

Table 14. *continued.*

| Connecting process | Position of anterior upper premolar ^a
(Proximity of canine and posterior premolar) | Sella ^b
Hairiness and shape | Lancet | Horseshoe mean (range) (mm) | |
|--|--|--|--|-----------------------------|--|
| Rounded | Absent
(In contact) | Naked
Sides almost parallel | Short, mostly very narrow and almost parallel-sided
Tip hairy and rounded | 8.8 (8.4–9.1) | |
| Rounded | Fully displaced or absent
(In contact or almost so) | Hairy
Sides concave near base, parallel above | Subtriangular, sides straight or slightly concave
Tip rounded | 13.0 (11.0–15.0) | |
| Rounded | Fully displaced or absent
(In contact or almost so) | Hairy
Upper two-thirds parallel-sided | Subtriangular, sides slightly concave
Tip rounded | 11.6 (11.1–12.3) | |
| Rounded | Fully displaced or absent
(In contact) | Hairy
Sides parallel or slightly concave | Subtriangular, sides slightly concave
Tip rounded | 10.3 (9.6–11.5) | |
| Rounded but rising to high narrow peak | Absent (n = 3)
(In contact) | Naked
Sides slightly concave | Hastate
Tip long, narrow, bluntly pointed | ca. 10–11 | |
| Rising to high horn | Within tooththrow
(Well separated) | Naked
Wedge-shaped, top narrow | Subtriangular or hastate
Tip rounded | 8.1 (7.2–9.0) | |
| Rising to high horn | Within tooththrow
(Well separated) | Naked
Parallel-sided, top broad, rounded | Subtriangular
Tip bluntly pointed | 7.2 (6.5–7.5) | |
| Subtriangular | Somewhat displaced
(Separated) | Naked
Parallel-sided | Hastate, upper half narrow and almost parallel-sided
Tip bluntly pointed | 6.4 (4.9–7.5) | |
| Subtriangular | Within tooththrow
(Well separated) | Naked
Sides slightly concave | Hastate
Tip bluntly pointed | 7.2 (6.0–8.0) | |
| Subtriangular | Within tooththrow
(Well separated) | Naked
Parallel-sided | Hastate
Tip bluntly pointed | 8.6 (8.3–9.3) | |
| Subtriangular | Within tooththrow
(Well separated) | Naked
Parallel-sided | Subtriangular, sides straight or slightly concave
Tip bluntly pointed | 10.0 (8.3–11.2) | |
| Very low, slightly rounded or flat | Within tooththrow
(Well separated) | Naked
Long, narrow, wedge-shaped | Subtriangular, sides slightly concave
Tip bluntly pointed | 6.6 (6.1–7.1) | |
| Greatly reduced, very low, concave | Within tooththrow or slightly displaced
(Separated) | Naked
Inclined forward, sides almost parallel, basal lobes very large | Subtriangular, moderately tall
Tip pointed | 15.0, 16.0
– | |
| Greatly reduced, very low, concave | Within tooththrow
(Separated) | Hairiness not known
Inclined forward, sides almost parallel, basal lobes very large | Almost parallel-sided, moderately tall
Tip moderately broad and rounded | ca. 11.5 | |
| Greatly reduced, very low, concave | Within tooththrow or slightly displaced
(Separated) | Naked
Upright, sides concave, basal lobes very large | Subtriangular, moderately tall
Tip truncated | 11.9 (10.8–12.6) | |
| Greatly reduced, very low, concave | Displaced
(Almost in contact) | Naked
Upright, sides concave, basal lobes very large | Subtriangular, tall
Tip bluntly pointed | 12 | |

^aThe anterior upper premolar is said to be ‘within tooththrow’ if it lies in the middle of the tooththrow or is only slightly displaced labially, causing the canine and posterior upper premolar to be distinctly separated.

^bThe sella is said to be naked unless it is well covered by longish and fairly conspicuous hairs (as opposed to inconspicuous short hairs).

^cThe first phalanx of the fourth finger varies in its length relative to that of the fourth metacarpal: it is said to be ‘short’ if its mean relative length is less than 22% of the metacarpal, ‘medium’ if its mean relative length is 22–25% of the metacarpal, and ‘long’ if its mean relative length is >25%.

^dNo mean given; sample size not known.

| | First phalanx of fourth finger as % of 4th metacarpal: category ^c , mean (range) | FA mean (range) (mm) | Tib mean (range) (mm) | E mean (range) (mm) | Miscellaneous | Species |
|--|---|----------------------|-----------------------|---------------------|---|-------------------------|
| | Long
28 (27–31) | 54.5 (52–57) | 23.6 (22–25) | 22.4 (21–24) | West Africa, perhaps Sudan | <i>R. hillorum</i> |
| | Long
27 (24–29) | 63.9 (60–67) | 27.9 (26–31) | 33.2 (26–36) | CrnC: 27.4 (26.1–28.7) mm | <i>R. hildebrandtii</i> |
| | Long
26 (23–28) | 58.4 (53–63) | 23.9 (22–25) | 27.5 (21–38) | CrnC: 25.4 (24.8–26.2) mm | <i>R. eloquens</i> |
| | Long
26 (24–28) | 50.9 (47–60) | 21.4 (19–24) | 22.9 (19–28) | CrnC: 22.7 (21.6–24.3) mm | <i>R. fumigatus</i> |
| | Long
27 | 53, 55, 55 | 25 | 20, 22, 22 | As yet, only NW Zambia
No axillary tufts (♂ ♂) | <i>R. sakejiensis</i> |
| | Long
26 (24–28) | 46.0 (43–48) | 19.3 (18–21) | 18.0 (16–21) | No marked contrast between crown areas of anterior and posterior lower premolars
North-West Africa, and eastern Africa to South Africa | <i>R. blasii</i> |
| | Short
20 (17–22) | 48.2 (46–50) | 21.2 (21–22) | 20.1 (19–22) | Marked contrast between crown areas of anterior and posterior lower premolars
North-West Africa | <i>R. euryale</i> |
| | Short
21 (19–23) | 50.1 (48–53) | 20.9 (19–23) | 20.9 (19–23) | Marked contrast between crown areas of anterior and posterior lower premolars
Axillary tufts: n. d.
Morocco to N Egypt, north of Sahara | <i>R. mehelyi</i> |
| | Short
21 (19–23) | 43.3 (35–49) | 18.7 (17–21) | 16.6 (13–20) | Widely distributed S of Sahara (but not Cape Provinces, South Africa)
Axillary tufts (♂ ♂) reddish-brown | <i>R. landeri</i> |
| | Short
20 (17–21) | 46.3 (44–50) | 21.1 (21–22) | 19.1 (17–22) | Senegal, Guinea, Sierra Leone
Axillary tufts (♂ ♂) usually white | <i>R. guineensis</i> |
| | Short
21 (19–22) | 52.3 (48–56) | 24.2 (21–27) | 22.2 (19–25) | Rainforest. Senegal to Uganda
Axillary tufts (♂ ♂) orange-red | <i>R. alcyone</i> |
| | Long
26 (24–28) | 36.8 (35–40) | 17.2 (15–18) | 16.1 (15–17) | North-West Africa, Sudan, Ethiopia, Eritrea, Djibouti, Sinai | <i>R. hipposideros</i> |
| | Long
26 (25–29) | 65.8 (64–69) | 29.0 (28–31) | 41.4 (40–46) | Horseshoe without lateral leaflets, median emargination very small or absent
Each ear with 10–12 folds
Guinea | <i>R. macclaudi</i> |
| | Long
26, 29 | 60, 60 | 26, 27 | 35, 36 | Horseshoe without lateral leaflets, without median emargination
Each ear with 11 or 12 folds | <i>R. ziama</i> |
| | Long
27 (26–28) | 57.6 (55–62) | 23.6 (22–26) | 34.7 (32–38) | Horseshoe with lateral leaflets and median emargination
Each ear with eight folds
Rwenzori Mts (DR Congo, Uganda), Rwanda | <i>R. ruwenzorii</i> |
| | Long
26, 27 | 54, 54 | 24 | 29 | Horseshoe with lateral leaflets and median emargination
Each ear with nine folds
SW Rwanda | <i>R. hilli</i> |

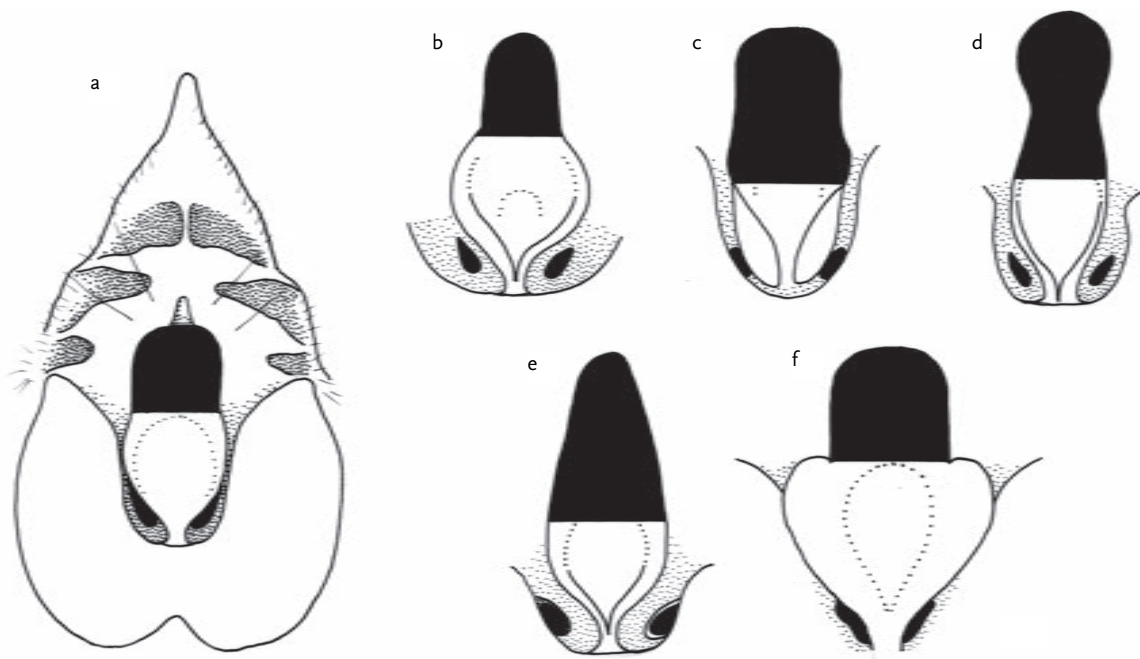


Figure 60. Variations in the shape of the sella in African *Rhinolophus*. (a) Frontal view of the noseleaf showing the relevant part of the sella (shaded). The sella can be described as (b) almost parallel-sided (e.g. *R. alcyone*; based on Rosevear 1965), (c) with upper two-thirds parallel-sided (e.g. *R. hildebrandtii*; M. Happold, Malawi), (d) concave sided (e.g. *R. clivosus*; M. Happold, Malawi), (e) wedge-shaped (e.g. *R. blasii empusa*; M. Happold, Malawi) or (f) parallel-sided with greatly expanded narial lobes (e.g. *R. ziama*; based on Fahr *et al.* 2002). Sellas which curve forwards have been pushed back to flatten the anterior surface and reveal its outline.

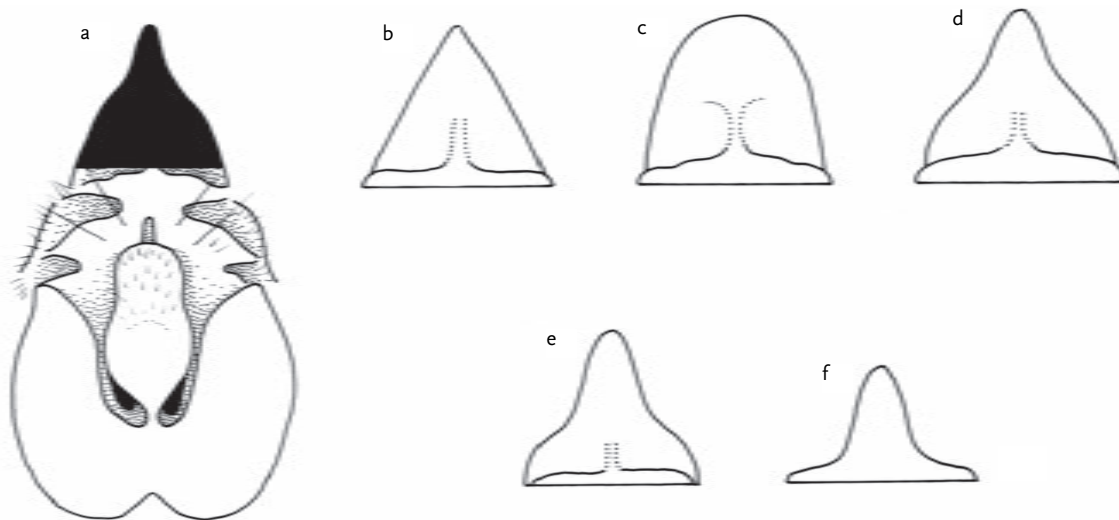


Figure 61. Variations in the shape of the lancet in African *Rhinolophus*. (a) Frontal view of the noseleaf showing the lancet (shaded). The lancet can be (b) subtriangular (e.g. *R. deckenii*; based on Csorba *et al.* 2003), (c) subtriangular with slightly convex sides (e.g. *R. adami*; based on Kock *et al.* 2000), (d) subtriangular with slightly concave sides (e.g. *R. maendeleo*; based on Kock *et al.* 2000), (e) hastate (e.g. *R. ferrumequinum*; based on Csorba *et al.* 2003), or (f) short, very narrow and almost parallel-sided (e.g. *R. hillorum*).

Distribution. Some species are extremely similar morphometrically, and are best distinguished by their distributions. The validity of the specific status of some of these species is uncertain.

Additional diagnostic characters include:

Cranio-canine length (CrnC). For *Rhinolophus*, the distance from the anterior of the upper canine to the most posterior part of the skull (Figure 23f) is used instead of GLS. This is because the nasal branches

of the premaxillae are absent and the palatal branches are frequently lost during preparation of the skulls of these bats.

Zygomatic width relative to mastoid width. Zygomatic width ranges from much greater than mastoid width to much narrower than mastoid width (see Figure 63b and c for same character in Hipposideridae).

Lateral leaflets (on each side of horseshoe). Can be present, rudimentary (inconspicuous) or absent.

Number of grooves in the chin region of the lower lip. There is invariably a well-defined median groove. Lateral grooves (one on each side of the median groove) can be well defined, indistinct or absent (Figure 55d–f).

Median emargination in horseshoe. Can be present (deep to shallow) or absent.

Frontal and lateral views of the noseleaf, lateral views of the rostral part of the skull, and occlusal views of the upper canine and premolars, are given for almost all African species in Csorba *et al.* (2003).

The species are presented in alphabetical order irrespective of the species-group to which they belong.

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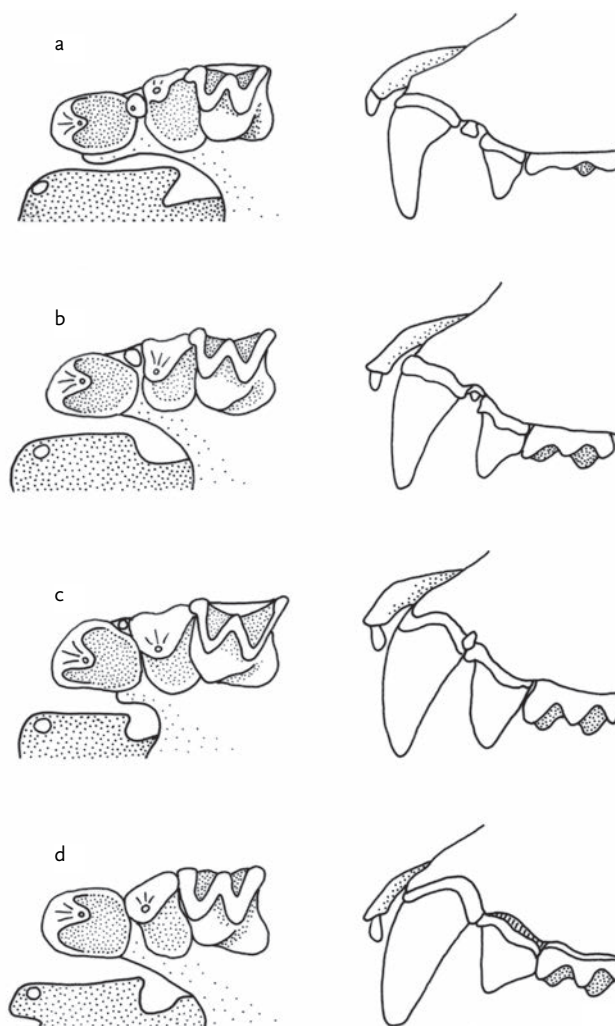


Figure 62. Variations in the size and position of the upper premolars in African *Rhinolophus*. *Left*: occlusal views of teeth on left side of upper jaw. *Right*: lateral views of labial side of the same teeth. The anterior upper premolar can be (a) within the toothrow so canine and posterior premolar are well separated (e.g. *R. denti*), (b) partly displaced labially so canine and posterior premolar are almost in contact (e.g. *R. hilli*), (c) fully displaced labially so canine and posterior premolar are in contact (e.g. this specimen of *R. fumigatus*), or (d) absent (e.g. this specimen of *R. hildebrandtii*).

Rhinolophus adami ADAM'S HORSESHOE BAT

Fr. Rhinolophe du Congo; Ger. Adams Hufeisennase

Rhinolophus adami Aellen and Brosset, 1968. Rev. Suisse Zool. 75: 443. Grotte de Kimanika, Kouilou, Congo.

Taxonomy Species-group: *adami* (with *R. maendeleo*). Appears closely related to *R. maendeleo* (Kock *et al.* 2000). Synonyms: none. Chromosome number: not known.

Description Small microbat with noseleaf (posterior component subtriangular with erect tip); medium-sized for an African rhinolophid; anterior upper premolar within toothrow; connecting process rounded and comparatively high; lancet subtriangular with slightly convex sides; sella with slightly concave sides and top which curves acutely forward and slightly downward; horseshoe breadth 8.5–9.0 mm. Sexual dimorphism: no information. Dorsal pelage brownish. Ventral pelage brownish-grey, sometimes becoming whitish on lower abdomen. Orange-phase: no information. Axillary tufts: no information. Ears comparatively and relatively of medium length (25–26 mm, 51–53% of FA), brown with darker rims. Noseleaf with lancet long, subtriangular with rounded tip, sides convex (Figure 61c) or almost so (cf. *R. maendeleo*). Connecting

process well developed, smoothly rounded, rising higher than sella. Sella naked, large and broad, sides slightly concave, top curving acutely forward and slightly downward. Basal lobes of sella poorly developed but surrounding a well-developed narial cup. Horseshoe narrow (8.5, 9.0 mm); almost covering muzzle; no lateral leaflets; median emargination well defined. Lower lip with three grooves. Wings dark brown; first phalanx of fourth finger of medium relative length (23% of fourth metacarpal, $n = 2$). Tibia 38–40% of FA ($n = 2$). Baculum with basal cone short with shallow dorsal and ventral invaginations (cf. *R. maendeleo*); shaft becoming dorsoventrally flattened distally; tip not expanded (Kock *et al.* 2000).

Skull narrow; zygomatic width much less than mastoid width. Rostrum with anterior median swellings well developed, posterior swellings reduced (Csorba *et al.* 2003). Frontal depression moderately deep. Sagittal crest low. Infraorbital foramen covered by bony bar (cf. *R. maendeleo*). Palatal bridge 2.8–3.0 mm, 42–44% of $C-M^3$. Anterior upper premolar small, within toothrow; canine and

posterior premolar well separated. Middle lower premolar slightly displaced labially; anterior and posterior lower premolars separated. Dental formula $^{1123}/_{2133} = 32$.

Geographic Variation None known.

Similar Species Five other *Rhinolophus* in Africa have the anterior upper premolar in the toothrow and a rounded connecting process, but none are known to be sympatric with *R. adami*:

Rhinolophus maendeleo. Lancet subtriangular with slightly concave sides; connecting process rising only just above sella; sella with markedly concave sides, top of sella curving obtusely forward; horseshoe narrower (8.2, 8.4 mm). Skull with infraorbital foramen open; palatal bridge 37–39% of C–M³.

R. simulator simulator. Ears shorter (18–23 mm). Lancet hastate, horseshoe narrower (6.7–8.3 mm). Palatal bridge relatively short (29–34% of C–M³).

R. swinnyi. Smaller (FA: 40–44 mm). Lancet hastate, horseshoe narrower (6.8–7.4 mm).

R. denti. Smaller (FA: 37–44 mm). Horseshoe narrower (6.8–7.5 mm).

R. capensis. Horseshoe narrower (7.3–8.1 mm).

Distribution Endemic to Africa. Known only from the type locality, Kouilou, Congo, in the Rainforest–Savanna Mosaic very near the Rainforest BZ.

Habitat The vegetation of the Kouilou region is a mosaic of lowland rainforest and secondary grassland, and limestone caves are present.

Abundance Only four specimens were described by Aellen & Brosset (1968): these, and an additional seven specimens (six in

MNHN, one in HNHM) recognized by Kock *et al.* (2000), appear to be the only known specimens. Probably very rare (see Conservation).

Remarks The holotype, an adult ♀, and two subadult ♀♀ were collected on the same day in a limestone cave (Grotte de Kimanika) for which no details are available (Aellen & Brosset 1968). A fourth specimen, an adult ♂, was collected in another limestone cave (Grotte de Meya-Nzouari), parts of which were dry and ‘dead’ with respect to the growth of limestone formations, and parts of which were still ‘living’ and very humid, with water seeping over the formations and trickling into underground streams (Adam & Le Pont 1974). This cave was also inhabited by *Rousettus aegyptiacus*, *Rhinolophus silvestris*, *Hipposideros ruber*, *H. gigas*, *Triaenops afer* and *Miniopterus minor*.

Predators, Parasites and Diseases Ectoparasites include a bat-fly *Penicillidia penicillidia* (Diptera: Nycteribiidae) (Anciaux de Faveaux 1984).

Conservation IUCN Category: Data Deficient.

Known from only four specimens from only two of 45 caves investigated for the presence of bats over a period of ca. seven years (Adam & Le Pont 1974), and an additional seven specimens from the type locality (Kock *et al.* 2000). Furthermore, not recorded from ten localities in nearby Mayombe and Lower Kouilou regions of Congo, where 80 specimens (14 species) were collected by Dowsett *et al.* (1991). Also, not recorded from Haut-Ivindo region of Gabon where 1732 individuals belonging to 27 species were captured from caves and by mist-netting by Brosset (1966), nor from Kikwit (05° 13'S, 18° 49'E, DR Congo) where 538 bats belonging to 18 species were collected in 1995 (Van Cakenberghe *et al.* 1999). As indicated by Dowsett *et al.* (1991), this species is potentially at risk because it roosts in caves occupied by the fruit bat *Rousettus aegyptiacus*, which is sometimes hunted for food.

Measurements

Rhinolophus adami

FA: 46–50 mm, n = ?*

WS: n. d.

TL: n. d.

T: 28, 27 mm

E: 25, 26 mm

NL (breadth): 9.0, 8.5 mm

Tib: 20, 20 mm

HF: 9, 9 mm

WT: n. d.

CrnC: 20.1 (19.8–20.6) mm, n = 7*

GWS: 9.8 (9.5–9.9) mm, n = 7*

C–M³: 7.3 (7.1–7.6) mm, n = 7*

Congo (holotype ♂ and one adult ♀ respectively; Aellen & Brosset 1968)

*Csorba *et al.* 2003

Key Reference Aellen & Brosset 1968.

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Rhinolophus adami

Rhinolophus alcyone HALCYON HORSESHOE BAT

Fr. *Rhinolophe alcyon*; Ger. Temmincks Hufeisennase

Rhinolophus alcyone Temminck, 1852. Esquisses Zool. sur la Côte de Guinée, p. 80. Boutry River, Ghana.

Taxonomy Species-group: *landeri*. Synonyms: none. Chromosome number: not known.

Description Small microbat with noseleaf (posterior component subtriangular with erect tip); medium-sized for an African rhinolophid; anterior upper premolar within tooththrow; connecting process triangular; lancet subtriangular; sella parallel-sided; first phalanx of fourth finger relatively short; axillary tufts orange-red (if present); tibia 24 (21–27) mm. Sexes similar. Pelage dense, soft, fluffy; mid-dorsal hairs ca. 9 mm. Dorsal pelage dark to medium brown; hairs yellowish-beige with brown at tip. Ventral pelage slightly paler. Orange-phase: dorsal pelage pale brown to bright orange-red. Adult ♂♂ often with orange-red or brown axillary tufts. Ears comparatively and relatively short (19–25 mm, 36–49% of FA); each with 8–9 internal folds. Noseleaf with lancet subtriangular (margins straight or slightly concave), tip bluntly pointed. Sella with extremely short white hairs, narrow, with straight, almost parallel sides (Figure 60b); top rounded, curved forward. Connecting process well developed, subtriangular, with bluntly to sharply pointed tip. Horseshoe of medium breadth (8.3–11.2 mm) almost covering muzzle; lateral leaflets present, median emargination present. Lower lip with a well-defined median groove and two poorly defined lateral grooves. Wings medium to blackish-brown; first phalanx of fourth finger relatively short (20.8 [19–22]% of fourth metacarpal, $n = 20$). Interfemoral membrane paler. In one specimen (possibly abnormal) the flight-membranes are cream with dark brown reticulation (BMNH 66.6242). Tibia 46.1 (38–52)% of FA ($n = 22$).

Skull robust; zygomatic arches moderately robust; zygomatic width greater than mastoid width. Nasal swellings relatively high, anterior median swellings globular and prominent, lateral and posterior swellings medium (Csorba *et al.* 2003). Frontal depression very shallow; supraorbital ridges weak. Sagittal crest variable – low to well developed. Palatal bridge 29–35% of C–M³. Anterior upper premolar within tooththrow or only slightly displaced labially; canine and posterior premolar well separated. Middle lower premolar either within tooththrow or displaced labially; anterior and posterior lower premolars separated. Anterior lower premolar at least two-thirds the height of the posterior premolar. Dental formula $^{1123}/_{2133} = 32$.

Geographic Variation No subspecies. Eisentraut (1964) reported that six specimens from Bioko I. are larger than those from the mainland (especially ear length). However, the differences are small. For example:

Bioko I.: FA: 53.5 (51–56) mm; T: 31.3 (26–38) mm; E: 24.0 (23–25) ($n = 6$).

Cameroon: FA: 52.4 (49–56) mm; T: 26.1 (22–32) mm; E: 22.0 (20–24) mm, $n = 26$.

Similar Species Only two other *Rhinolophus* in sub-Saharan Africa have the following combination of characters: anterior upper

premolar within tooththrow; connecting process triangular and pointed; first phalanx of fourth finger relatively short:

Rhinolophus landeri. Body measurements almost always smaller (FA: 35–49 mm, Tib: 17–21 mm). Skull smaller (CrnC: 16.9–19.1 mm).

R. guineensis. Body measurements usually smaller (FA: 44–50 mm, Tib: 21–22 mm). Skull smaller (CrnC: 19.2–20.6 mm). Sagittal crest less developed. Axillary tufts in ♂♂ usually white.

Distribution Endemic to Africa. Mainly recorded from the Rainforest BZ and surrounding Rainforest–Savanna Mosaics, from Guinea to Ghana, from Nigeria to Central African Republic and southwards to S Congo and Bioko I., with some apparently isolated records in NE DR Congo, S Sudan and Uganda. Also recorded from the Sudan Savanna BZ in Senegal, and the Guinea Savanna BZ in Côte d’Ivoire and Ghana. Records are scattered but this probably reflects insufficient collecting. Predicted to occur throughout the Rainforest BZ. Mapped from country checklists (see order Chiroptera), other literature and museum records.

Habitat Predominantly lowland rainforest, but also dense relict and riverine forests north of the Rainforest BZ.

Abundance Uncertain: rarely collected.

Remarks Day-roosts include caves, hollow trees and hollow logs, a mine-shaft and in the roof of a hut (Eisentraut 1956, Verschuren 1957, Rosevear 1965, Brosset 1966). Reported roosting singly and



Rhinolophus alcyone

in small groups of unknown composition (Rosevear 1965). Has been seen flying over water, swampy areas and along forest paths. Diet not known. Echolocation call-shape FM/CF/FM; CF-frequency (Uganda) 87 kHz (Pye & Roberts 1970, Roberts 1972). Litter-size: one (n = 5). Reproductive chronology not known. At ca. 6°N in Côte d'Ivoire, 4 of 4 ♀♀ were pregnant in mid-Feb (CR: 19–26 mm) (Lim & Van Coeverden de Groot 1997). Ectoparasites include bat-flies *Phthiridium inopinatum* (Diptera: Nycteribiidae), *Raymondia allisoni* (Diptera: Streblidae) (Anciaux de Faveaux 1984).

Conservation IUCN Category: Least Concern.

Measurements

Rhinolophus alcyone

FA: 52.3 (48–56) mm, n = 100

WS (a): 342.4 (320–355) mm, n = 9

TL: 87.4 (75–100) mm, n = 49

T: 27.0 (18–32) mm, n = 57

E: 22.2 (19–25) mm, n = 74

NL (breadth): 10.0 (8.3–11.2) mm, n = 26

Tib: 24.2 (21–27) mm, n = 35

HF: 12.2 (11–13) mm, n = 25

WT: 15.4 (14–23) g, n = 23

CrnC: 22.3 (21.0–23.3) mm, n = 30*

GWS: 11.8 (11.2–12.7) mm, n = 24

C–M³: 8.7 (7.9–9.2) mm, n = 32

Throughout geographic range (BMNH, HZM, ROM and literature)

*Csorba *et al.* 2003

Key References Rosevear 1965; Csorba *et al.* 2003.

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Rhinolophus blasii BLASIUS'S HORSESHOE BAT (PEAK-SADDLE HORSESHOE BAT)

Fr. Rhinolophe de Blasius; Ger. Blasius Hufeisennase

Rhinolophus blasii Peters, 1867. Monatsber. K. Preuss. Akad. Wiss. Berlin 1866: 17 [publ. 1867].

SE Europe; restricted to Italy by Ellerman *et al.* (1953: 59).

Taxonomy Species-group: *landeri*. Synonyms: *andreinii*, *blasiusi*, *brockmani*, *clivus* Blasius, 1857, *empusa*, *meyeroehmi*. Subspecies: four; three in Africa. Chromosome number (South Africa): 2n = 58; aFN = 60. Two pairs biarmed chromosomes, 26 pairs acrocentric chromosomes; X = large submetacentric; Y = small metacentric (Rautenbach 1986).

Description Small microbat with noseleaf (posterior component subtriangular with erect tip); small for an African rhinolophid; anterior upper premolar within tooththrow; connecting process rising to high, narrow, forward-curving pointed horn; sella wedge-shaped; horseshoe breadth 7.2–9.0 mm; no axillary tufts; first phalanx of fourth finger relatively long; no marked contrast between crown areas of anterior and posterior lower premolars. Sexes similar. Pelage dense, soft, fluffy; mid-dorsal hairs 8–9 mm. Dorsal pelage greyish-fawn to brownish-grey; hairs pale greyish-fawn or pale brownish-grey, with darker tip. Ventral pelage considerably paler. Only one individual in orange-phase has been recorded (Ansell 1974). No axillary tufts on adult ♂♂. Ears comparatively and relatively short (16–21 mm, 33–44% of FA), dark greyish-brown. Noseleaf with lancet subtriangular with slightly concave sides (sometimes hastate), tip rounded. Connecting process well developed, rising to high, narrow, pointed horn (Figure 59j). Sella naked, wedge-shaped with sides converging towards top; top narrow and tilted forward (Figure 60e). Horseshoe narrow (7.2–9.0 mm), not covering whole muzzle but on average broader than in *R. euryale*; lateral leaflets absent, rudimentary or well developed (probably depending on subspecies); median emargination present but indistinct. Lower lip with three grooves: the two lateral grooves are poorly defined in *R. b. empusa*. Wings and interfemoral membrane dark greyish-brown. First phalanx of fourth finger relatively long (25.8 [24–28]% of fourth metacarpal, n = 30) and usually >50% of second phalanx (cf. *R. euryale* and *R. mehelyi*). Tibia 42.1 (39–45)% of FA (n = 31).

Skull delicate; zygomatic arches narrow; zygomatic width = mastoid width. Nasal swellings relatively low. Frontal depression shallow to very shallow; supraorbital ridges poorly developed (Csorba *et al.* 2003). Sagittal crest usually low. Palatal bridge 32–35% of C–M³. Upper incisors weakly bilobed. Upper canine with weak anterior and posterior cusps. Anterior upper premolar small (but moderate to relatively large for a rhinolophid), within tooththrow; canine and posterior premolar well separated. Molar width more than half width of palate between molars (cf. *R. landeri*). Middle lower premolar minute and either within tooththrow or displaced labially, or absent; anterior and posterior lower premolars usually well separated. Crown area of anterior lower premolar equal to or only slightly less than that of posterior lower premolar. Dental formula $^{1123}/_{2133} = 32$ or $^{1123}/_{2123} = 30$.

Geographic Variation Koopman (1994) recognizes three subspecies in Africa.

R. b. blasii: NW Africa (and extraliminally southern Europe and SW Asia).

R. b. andreinii: Ethiopia and Somalia.

R. b. empusa: S DR Congo to the former Transvaal.

Similar Species Only one other *Rhinolophus* in Africa has a connecting process which rises to a high narrow pointed horn:

Rhinolophus euryale. Sella parallel-sided, horseshoe usually narrower (6.5–7.5 mm). First phalanx of fourth finger relatively short (17–22% of fourth metacarpal). Marked contrast between crown areas of anterior and posterior lower premolars. NW Africa.

Two potentially sympatric species (with anterior upper premolar within tooththrow) have triangular connecting processes, which, although lower, also rise to a point:

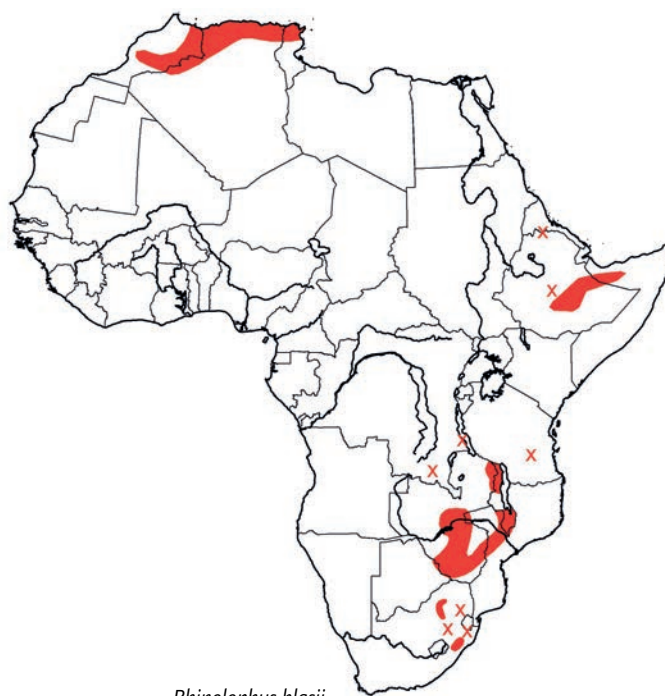
- R. mehelyi*. Usually larger (FA: 48–53 mm). Sella parallel-sided; horseshoe usually narrower (4.9–7.5 mm). First phalanx of fourth finger relatively short (19–23% of metacarpal). Marked contrast between crown areas of anterior and posterior premolars. N Africa.
- R. landeri*. Horseshoe narrower (6.0–8.0 mm). First phalanx of fourth finger relatively short (19–23% of metacarpal). Axillary tufts present in ♂♂. South of Sahara.

Distribution In Africa, occurs in three isolated regions, each occupied by a different subspecies. In NW Africa, found in the Mediterranean Coastal BZ (and marginally in the Sahara Arid BZ). In Ethiopia and Somalia, found in the Afroalpine–Afroalpine BZ (and marginally in the Somalia–Masai Bushland BZ). In south-central and southern Africa, found in the Zambezian Woodland, Afroalpine–Afroalpine and Coastal Forest Mosaic BZs. Two specimens in BMNH, recorded from ‘Cape of Good Hope’, probably came from Mozambique or KwaZulu–Natal (Roberts 1951). Extraliminally: Southern Europe and SW Asia. Mapped from country checklists (see order Chiroptera), other literature and museum records.

Habitat In NW Africa, recorded from Mediterranean sclerophyllous forests, sub-Mediterranean semi-desert grassland and shrubland, and in stone or gravel desert habitats with wadis (but perhaps only where water is available). In Algeria, most localities are near caves and/or streams (Kowalski & Rzebiak-Kowalska 1991). In Ethiopia and Somalia, most localities are in montane vegetation, evergreen and semi-evergreen bushland and thicket, and *Acacia–Commiphora* bushland and thicket. In Malawi and Zambia, found between 500–2300 m, in miombo woodland and montane forests (Ansell 1978, Happold *et al.* 1987). In KwaZulu–Natal, South Africa, most records are from major river valleys in Lowveld, Valley Bushveld and Mistbelt bioregions (Taylor, P. 1998).

Abundance Uncertain. Appears common at least in some parts of geographic range (e.g. very commonly recorded in Malawi; Happold & Happold 1997).

Adaptations Aspect ratio low; wing-loading low; wing-tip rounded (M. Happold unpubl.). Sometimes flies slowly with shallow wing-beats and some gliding and dipping, but can also put on bursts of fast flying with sudden turns. Can take off from ground, hover briefly; flies with great manoeuvrability; turns by banking (minimum radius <25 cm) and by stalling-and-twisting; individuals sustained flight within a 1 × 1 × 1 m enclosure for up to 13 circuits/flight (9 bats, 10 flights each; M. Happold unpubl.). By day, sometimes hangs freely in caves, mine-adits and in cave-like spaces under piles of boulders (Aellen 1955, Smithers 1983), but not found in caves at Zomba, Malawi (Happold *et al.* 1987) and rarely encountered in caves in Algeria (Kowalski *et al.* 1986). Possibly, caves are not utilized except during winter in temperate regions (?). In Algeria, there are some winter records, some individuals being active, others torpid (Kowalski *et al.* 1986). At ambient temperatures of 21–24 °C in Malawi, becomes torpid during the day. Hibernates in caves during winter in the former Transvaal, South Africa (Taylor, P. 1998) and Iran (Lay 1967). Individuals kept in the room of a house and fed winged termites drank ca. five times/night, either by landing and lapping or sucking water from a dish, or by scooping mouthfuls from a tray of water while in flight; predicted mean maximum urine



Rhinolophus blasii

concentration is comparatively low (3116 mOsmol/kg) (Happold & Happold 1988). Undoubtedly very dependent on water in the wild.

Foraging and Food Forages by slow-hawking, fly-catching and both foliage- and ground-gleaning. In Malawi, often forages along hedges and banks of vegetation at the edges of patches of forest, along pathways through dense vegetation, under tree-canopies in relatively uncluttered spaces and within canopies in dense clutter, close to buildings and sometimes over grassy clearings. Foraging is often within 1–2 m of the ground, but can be at least as high as ca. 6 m (M. Happold pers. obs.). In Zambia, analysis of stomach contents indicated that the dry season diet was 100% moths and the wet season diet was 96.5% moths with some termites, flies, beetles and other insects (Whitaker & Black 1976).

Echolocation Call-shape FM/CF/FM; CF-frequency (Malawi) 91–95 kHz, but usually 92–93 kHz (16 ♂♂ and 9 ♀♀ hand-held, 2 ♂♂ flying in open; M. Happold unpubl.). There was no significant difference between the CF-frequencies of ♂♂ and ♀♀. In Swaziland, CF-frequency 85.9 kHz (1 bat; Monadjem 2005). In Europe, mean CF-frequency 94 kHz (Heller & von Helversen 1989).

Social and Reproductive Behaviour Very little is known. In southern Africa, roosts singly or in small groups, never more than three or four together, with individuals hanging apart (Roberts 1951, Rautenbach 1979). In Malawi, often forages in groups of ca. five. Group composition variable; no evidence of harem-formation from these data. In caves in Arabia and the Middle East, has been found roosting singly, in pairs and once in a group of ca. 30 (Harrison & Bates 1991). In Iran, several colonies of 100–500 individuals have been found hibernating in caves (Lay 1967).

Reproduction and Population Structure Litter-size: one. At 15° 23' S (Zomba, Malawi), the reproductive chronology is extended

seasonal monoestry with births in wet season (Nov–Jan) (Happold & Happold 1990a). Extraliminally, in Pakistan, the chronology is restricted seasonal monoestry (Roberts 1977).

Predators, Parasites and Diseases Ectoparasites include a bed-bug *Adroctenes horthvathi* (Hemiptera: Polyctenidae) (Kock *et al.* 1998b); a flea *Rhinolophopsylla unipectinata* (Siphonaptera: Ischnopsyllidae); bat-flies *Phthiridium integrum*, *P. ovale* (Diptera: Nycteribiidae), *Brachytarsina africana*, *Raymondia alulata*, *R. hardyi* (Diptera: Streblidae); mites *Neomyobia africanoides* (Acari: Myobiidae), *Nycteridocoptes eyndhoveni* (Acari: Sarcoptidae) (Anciaux de Faveaux 1984, Beaucournu & Kowalski 1985).

Conservation IUCN Category: Least Concern.

This assessment is based on the global population, which is large, and populations in some areas are stable although others are declining.

Measurements

Rhinolophus blasii

FA: 46.0 (43–48) mm, n = 71

WS (a): 287.0 (271–297) mm, n = 8*

TL: 80.6 (75–89) mm, n = 48

T: 26.9 (20–31) mm, n = 59

E: 18.0 (16–21) mm, n = 77

NL (breadth): 8.1 (7.2–9.0) mm, n = 50†

Tib: 19.3 (18–21) mm, n = 41

HF: 9.4 (8–11) mm, n = 81

WT: 9.0 (7–13) g, n = 44

CrnC: 19.0 (17.9–20.0) mm, n = 50

GWS: 9.0 (8.5–9.8) mm, n = 47

C–M³: 6.5 (6.0–7.7) mm, n = 56

Throughout African geographic range (BMNH, HC, NMZB, SMNS, ZFMK and literature)

**R. b. empusa* from Malawi only

†Mostly *R. b. empusa* from Malawi

Key References Csorba *et al.* 2003; Harrison & Bates 1991; Kowalski & Rzebik-Kowalska 1991.

Meredith Happold

Rhinolophus capensis CAPE HORSESHOE BAT

Fr. Rhinolophe du Cap; Ger. Kap-Hufeisennase

Rhinolophus capensis Lichtenstein, 1823. Verz. Doblet. Mus. Univ. Berlin, p. 4. Cape of Good Hope, Cape Province, South Africa.

Taxonomy Species-group: *capensis*. Synonyms: *auritus*. Chromosome number (South Africa): 2n = 58; aFN = 60 (Rautenbach 1986).

Description A small microbat with noseleaf (posterior component subtriangular with erect tip); medium-sized for an African rhinolophid; anterior upper premolar usually slightly displaced labially, canine and posterior premolar never in contact; connecting process rounded and higher than sella; lancet hastate; sella with parallel or slightly concave sides; no axillary tufts. Sexes similar. Pelage soft, fluffy; mid-dorsal hairs 8–9 mm. Dorsal pelage (grey-phase) pale to medium brown; hairs pale grey, beige or cream, with brown tip. Ventral pelage paler, sometimes more greyish. In orange-phase, dorsal pelage orange-red. No axillary tufts on adult ♂♂. Ears comparatively short (21–25 mm) but of medium relative length (50 [46–52]% of FA). Noseleaf with lancet hastate; tip bluntly pointed. Sella naked, sides parallel or slightly concave; top rounded. Connecting process rounded, sometimes almost triangular but with the top rounded; higher than the sella. Horseshoe narrow (7.3–8.1 mm), not covering whole muzzle; lateral leaflets present but rudimentary; anterior emargination deep. Lower lip with one well-defined groove. Wings and interfemoral membrane brown. First phalanx of fourth finger relatively long (26.4 [24–30]% of fourth metacarpal, n = 29). Mean tibia 41% of mean FA.

Skull robust; zygomatic arches broad; zygomatic width greater than mastoid width. Nasal swellings of medium relative height. Frontal depression shallow; supraorbital ridges weak. Sagittal crest well developed anteriorly, absent posteriorly. Palatal bridge 33–39% of C–M³ (Csorba *et al.* 2003). Interpterygoid groove distinct. Anterior upper premolar small to medium-sized, usually slightly

displaced labially but sometimes almost fully displaced; canine and posterior premolar never in contact, typically well separated (Csorba *et al.* 2003). Middle lower premolar small, partly or fully displaced labially. Dental formula $^{1123}/_{2133} = 32$.

Geographic Variation None recorded.

Similar Species Five other *Rhinolophus* in Africa (those in *capensis* group) have the anterior upper premolar within toothrow and the connecting process rounded, but only three occur in southern Africa (Table 14, p. 304):

Rhinolophus simulator. Connecting process not higher than sella. Body measurements smaller on average (FA: 45.2 [43–47] mm). Skull smaller (CrnC: 17.4–19.4 mm; C–M³: 6.1–6.9 mm). Frontal depression moderately deep; supraorbital ridges prominent. Not known from Eastern and Western Cape Provinces of South Africa.

R. swinnyi. Connecting process not higher than sella. Smaller (FA: 40–45 mm). Skull smaller (CrnC: 17.4–18.0 mm; C–M³: 6.1–6.6 mm).

R. denti denti. Lancet subtriangular. Smaller (FA: 37–44 mm; Tib: 15–18 mm). Skull shorter (CrnC: 15.8–17.0 mm). Semi-arid savannas and deserts.

Because the anterior upper premolar is sometimes displaced labially in *R. capensis*, this species can also be confused with:

R. clivosus. Upper canine and posterior premolar in contact; anterior upper premolar, if present, is small or minute and invariably fully displaced labially. Dorsal pelage darker. Nasal swellings relatively

low. In South Africa, FA, on average, longer (53.6 [49–57] mm, $n = 105$).

Distribution Endemic to Africa. Apparently restricted to a coastal belt (100–200 km wide), mainly in the South-West Cape BZ but extending marginally into the Karoo, Highveld, Coastal Forest Mosaic and Afromontane–Afroalpine BZs, in the Western and Eastern Cape Provinces of South Africa. Herselman & Norton (1985) and Smithers (1983) show the distribution extending along the west coast of South Africa as far north as the Orange R. but, because they found it difficult to distinguish *R. capensis* from *R. darlingi* and *R. clivosus*, records of *R. capensis* north of 32° S, where *R. capensis* might be replaced by *R. darlingi* or *R. clivosus*, need confirmation and have not been mapped here. Records from Zambia and Malawi are erroneous (Koopman 1993); records from Zimbabwe (Hayman & Hill 1971) and one from the NE Eastern Cape Province of South Africa (Lynch 1989) are probably erroneous (Smithers 1983, R. T. F. Bernard pers. obs.).

Habitat Savanna, Afromontane Forest, Coastal Forest and South-West Cape fynbos.

Abundance Common throughout geographic range.

Adaptations Not much known. By day, hangs freely or in contact from the ceilings and walls of caves and disused mine tunnels, but apparently avoids houses. Often shares caves with *R. clivosus*: the two species sometimes hang in separate clusters (Herselman & Norton 1985) and sometimes in clusters comprised of ♂♂ and ♀♀ of both species (McDonald *et al.* 1990b). Sometimes also shares caves with *Miniopterus natalensis*. Sometimes hibernates in winter, but torpor not as deep as in *R. clivosus* (R. T. F. Bernard pers. obs.). Small-scale migrations of 10 km have been noted (Taylor 2000).

Foraging and Food On basis of wing morphology, predicted to forage by flying slowly through vegetation and gleaning from the ground or foliage (McDonald *et al.* 1990a). The number of individuals emerging from a cave, and activity outside the cave (both assessed from the number of captures/minute in a harp-trap set at the entrance), was found to be maximal during the first two hours after sunset; this presumably indicates that foraging activity is greatest during this time although some of the measured activity was probably associated with bats returning to the cave to roost in between bouts of foraging (McDonald *et al.* 1990a). At Algeria Forest station, Western Cape, individuals were seen regularly using the eaves of buildings at night, and culled parts of insects and faeces found in the morning suggests they used the eaves as night roosts (Seamark 2005). Diet is mainly beetles (McDonald *et al.* 1990a, Taylor 2000).

Echolocation Call-shape FM/CF/FM. CF-frequency 85–90 kHz (McDonald *et al.* 1990a).

Social and Reproductive Behaviour Roosts in colonies, which seldom contain more than 500 (R. T. F. Bernard pers. obs.) but sometimes contain more than a thousand individuals (Herselman & Norton 1985). Both sexes roost together. Individuals roost in clusters, but tend not to be in contact with each other.



Rhinolophus capensis

Reproduction and Population Structure Litter-size: one ($n = 27$). At 33–34° S in South Africa, the reproductive chronology is restricted seasonal monoestry, with spermatogenesis between Oct–May; sperm storage in the cauda epididymides throughout winter (which is unusual for a rhinolophid); copulation at end of winter (Aug–Sep); and births in summer (Nov–Dec) after 3–4 month gestation (Bernard 1985, 1988). Although ♀♀ are in oestrus or submaximal oestrus in May, cornified epithelial cells block the vagina and prevent copulation throughout the winter hibernation period. In contrast, most hibernating species of *Rhinolophus* copulate before hibernating and ♀♀ store the sperm until they ovulate in the spring. Females do not become reproductively active in their first year. Testes of ♂♂ are active after 11–12 months, but first matings occur in the second year.

Predators, Parasites and Diseases Ectoparasites include fleas *Rhinolophopsylla ashworthi*, *R. capensis* (Siphonaptera: Ischnopsyllidae); bat-flies *Nycteribia schmidli*, *Phthiridium scissum* (Diptera: Nycteribiidae), *Brachytarsina africana* (Diptera: Streblidae), mites *Neomyobia jacksoni*, *N. africanoides* (Acari: Myobiidae), *Labidocarpus rollinatti*, *Alabidocarpus diceratops* (Acari: Chirodiscidae), *Opsonyssus zumpti* (Acari: Gastronyssidae) (Anciaux de Faveaux 1984).

Conservation IUCN Category: Least Concern.

The extent of occurrence is >20,000 km², but it is known from only ca. 15 locations and there is a decline in the extent and quality of habitat.

Measurements

Rhinolophus capensis

FA: 48.8 (47–51) mm, $n = 25$

WS (d): 310, 325 mm, $n = 2$

TL: 87.7 (80–98) mm, $n = 14$

T: 27.7 (24–32) mm, $n = 10$

E: 23.8 (21–25) mm, n = 17
 NL (breadth): 7.7 (7.3–8.1) mm, n = 10
 Tib: 18.7 (17–21) mm, n = 50
 HF: n. d.
 WT (♂♂): 11.6 (9–13) g, n = 99*
 WT (♀♀): 12.3 (10.4–14.6) g, n = 83*
 CrnC: 20.5 (20.0–21.1) mm, n = 20†
 GWS: 10.4 (10.0–11.2) mm, n = 27
 C–M³: 7.5 (7.2–7.8) mm, n = 26

Throughout geographic range (AM, BMNH, HZM, TM)

*R. T. F. Bernard pers. obs.

†Csorba *et al.* 2003

Key References Bernard 1985; McDonald *et al.* 1990a, b; Smithers 1983.

Ric T. F. Bernard

Rhinolophus clivosus GEOFFROY'S HORSESHOE BAT (CRETZSCHMAR'S HORSESHOE BAT)

Fr. Rhinolophe de Cretzschmar; Ger. Geoffroys Hufeisennase

Rhinolophus clivosus Cretzschmar, 1828. In: Rüppell, Atlas Reise Nordl. Afr., Säugeth., p. 47. Mohila, Saudi Arabia.

Taxonomy Species-group: *ferrumequinum*. Synonyms: *acrotis* Heuglin, 1861, *andersoni*, *augur*, *brachygnathus*, *keniensis*, *schwarzi*, *zambesiensis*, *zuluensis*. Subspecies: seven, six in Africa. Variability in measurements, bacular morphology, colour, habitat, echolocation calls and reproduction strongly suggest *R. clivosus* includes more than one species. Chromosome number (East Africa): 2n = 58; aFN = 62 (Dulić & Mutere 1974). In South Africa, 2n = 58; aFN = 60 or 62 and X and Y are large submetacentrics (Rautenbach 1986).

Description Small microbat with noseleaf (posterior component subtriangular with erect tip); medium-sized for an African rhinolophid; anterior upper premolar displaced labially or absent; upper canine and posterior premolar always in contact; connecting process rounded and high; sella naked with concave sides; horseshoe breadth 6.6–9.6 mm; nasal swellings very low; no axillary tufts. Sexes similar. Pelage soft, fluffy; mid-dorsal hairs ca. 8 mm. Dorsal pelage variable: cream, grey, brownish-grey, greyish-fawn or reddish-brown; hairs pale, usually with darker-coloured tip. Ventral pelage beige, pale brown or grey. Individuals in orange-phase have been recorded. No axillary tufts on adult ♂♂. Ears comparatively and relatively short (16–24 mm, 39 [30–47]% of FA). Noseleaf with lancet hastate; tip rounded. Connecting process rounded but sometimes smoothly curved and sometimes slightly angular; slightly to clearly higher than sella. Sella naked, narrow, with concave sides; top broad and rounded (Figure 60d). Horseshoe narrow–medium (6.6–9.6 mm depending on subspecies), not covering whole muzzle; lateral leaflets present but sometimes rudimentary; median emargination is a shallow to moderately deep notch. Lower lip with a well-defined median groove; lateral grooves distinct, indistinct or absent. Wings and interfemoral membrane dark grey. First phalanx of fourth finger relatively long (28.4 [25–31]% of fourth metacarpal, n = 50). Tibia 42.1 (33–49)% of FA, n = 64. Baculum: basal cone with shallow dorsal invagination and deep ventral invagination; shaft dorsoventrally flattened without expanded tip in *R. c. zuluensis*, but with slightly expanded tip in *R. c. augur*, length 4.7 (4.5–5.2) mm, n = 3 in *R. c. augur*, 3.6 (3.2–4.0) mm, n = 21 in *R. c. zuluensis* (based on Cotterill 2002a). No data for other subspecies.

Skull robust; zygomatic width greater than mastoid width. Nasal swellings relatively low. Frontal depression very shallow; supraorbital ridges weak. Sagittal crest low anteriorly, absent posteriorly. Palatal bridge relatively short (25–31% of C–M³; Csorba *et al.* 2003). Interpterygoid groove absent or very indistinct. Anterior upper

premolar minute and fully displaced labially, or absent; upper canine and posterior in contact. Middle lower premolar minute and fully displaced labially, or absent; anterior and posterior lower premolars in contact. Dental formula $^{1123}/_{2133} = 32$, $^{1113}/_{2133} = 30$, $^{1123}/_{2123} = 30$ or $^{1113}/_{2123} = 28$.

Geographic Variation Seven subspecies are currently recognized (Thomas 1997, Csorba *et al.* 2003) of which six are represented in Africa:

R. c. schwarzi: SE Algeria and SW Libya.

R. c. brachygnathus: NE Libya, Egypt, N Sudan (and extraliminally Israel).

R. c. acrotis: most of C and S Sudan, and Ethiopia. Comparatively small.

R. c. keniensis: SE Sudan, Uganda, Kenya and N Tanzania. Intermediate in size.

R. c. augur: S Tanzania, Malawi, Zimbabwe, Botswana and N South Africa. Largest.

R. c. zuluensis: coastal South Africa. Intermediate in size.

The bacular morphologies of *R. c. augur* and *R. c. zuluensis* are very different (Cotterill 2002a, F. P. D. Cotterill unpubl.).

Similar Species Six other *Rhinolophus* in Africa have the following combination of characters – anterior upper premolar fully displaced labially or absent; connecting process rounded; sella naked (or with sparse short hairs only) (Table 14, p. 304):

Rhinolophus darlingi. FA often shorter (47 [42–51] mm). Dorsal pelage greyer. Nasal swellings of medium relative height. Interpterygoid groove distinct. Palatal bridge relatively longer (30–35% of C–M³).

R. silvestris. Lancet subtriangular. Horseshoe broader (9.5, 10.3 mm), as broad as muzzle. Connecting process lower. Nasal swellings of medium relative height. Frontal depression moderately deep; supraorbital ridges prominent. Interpterygoid groove shallow but distinct. Rainforest BZ; Gabon and Congo.

R. deckenii. Lancet subtriangular. Horseshoe broader (9.1–11.5 mm), as broad as muzzle. Connecting process lower (ca. same height as sella). Nasal swellings of medium relative height. Frontal depression moderately deep; supraorbital ridges prominent.

Interpterygoid groove shallow but distinct. Upper canine and posterior premolar usually separated by narrow gap. East Africa. Furthermore, the tibia is longer (24–28 mm), the horseshoe is broader and the skull is longer (CrnC: 22.6–24.1 mm) than in sympatric *R. c. keniensis*.

R. sakejensis. Connecting process rising to high, rounded peak, much higher than sella. Horseshoe breadth 10.3 mm, $n = 1$. Skull larger (CrnC: 24.3–25.3 mm; C–M³: 9.4–9.7 mm).

R. hillorum. Connecting process higher and narrower in profile. Skull larger and more robust (CrnC: 23.3–24.4 mm; C–M³: 8.9–9.5 mm). Anterior upper premolar absent. Rainforest BZ from Guinea and Liberia to Cameroon, and possibly, S Sudan.

R. ferrumequinum. Forearm, on average, longer (55.4 [51–59] mm). As yet, African records are only in the Maghreb (NW Africa).

Distribution In Africa, mainly recorded from the Sahara Arid, Somalia–Masai Bushland, Zambezian Woodland, South-West Arid, Highveld, South-West Cape and Afromontane–Afroalpine BZs, with some records in the Eastern and Southern Rainforest–Savanna Mosaics and the Coastal Forest Mosaic BZ. Not recorded from the Rainforest BZ. Distributed, apparently very disjunctly, from Algeria to Egypt and southwards through most countries on the eastern side of Africa to South Africa. Also recorded from W Namibia and S Angola, and at an isolated locality in SW DR Congo. Not recorded from Tanzania (where previous records are now considered to represent *R. deckenii* and *R. fumigatus* (F. P. D. Cotterill pers. comm.)). Records from Kitale, Kenya (HZM, USNM) also possibly represent *R. deckenii*. Extralimittally: Israel, Jordan and Arabian Peninsula (Simmons 2005). Mapped from country checklists (see order Chiroptera), other literature and museum records.

Habitat Woodland savannas, montane forests, open grasslands, semi-desert and desert habitats. In Algeria, probably restricted to mountains in the Sahara Desert region (Kowalski & Rzebik-Kowalska 1991). In NE Africa, occurs in sub-desert and savanna habitats (Qumsiyeh 1985). Mainly associated with mountainous and hilly areas in Sudan and Kenya (Koopman 1975), Zambia (Ansell 1978), Zimbabwe (Hutton 1986) and also in Rwanda and DR Congo. In Malawi, recorded from montane forest, miombo woodland and thicket-clump savanna, from 100 to 2300 m (Happold *et al.* 1987). In southern Africa, occurs mainly in woodland savannas, but extends into deserts in the west, and grasslands in the Drakensberg Mts (Taylor 2000). Throughout geographic range, its occurrence probably depends on availability of caves and/or cave-like day-roosts.

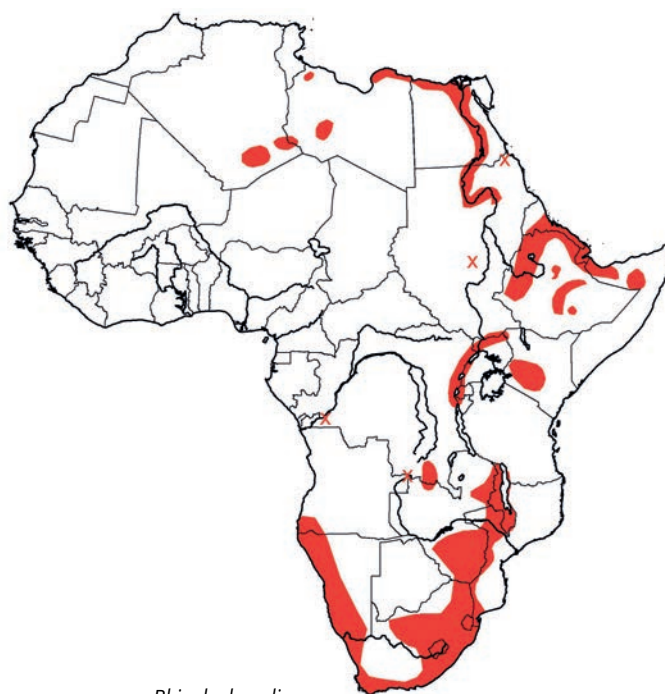
Abundance Uncertain throughout most of geographic range. Reported ‘rarely recorded’ in Malawi (Happold & Happold 1997), common in southern Africa (Taylor 2000), and locally abundant in vicinity of caves in Rwanda (Baeten *et al.* 1984) and South Africa (Herselman & Norton 1985).

Adaptations Aspect ratio low; wing-loading very low; wing-tip rounded (M. Happold unpubl.). Flight very variable in speed and highly manoeuvrable. Can take off from ground and almost hover. Turns by banking (minimum radius <25 cm), and by stalling-and-twisting; individuals sustained flight within a 1 × 1 × 1 m enclosure for up to eight circuits/flight (4 bats, 10 flights each; M. Happold unpubl.).

By day, hangs freely from ceilings or in contact with walls, in caves, rock crevices, abandoned mine tunnels, catacombs, stone huts and other cave-like places in abandoned buildings. Also roosts in hollow baobabs *Adansonia*. Inter-cave movements of up to 10 km (Herselman 1980, Rautenbach 1982, McDonald *et al.* 1990b), and prolonged periods of hibernation (R. T. F. Bernard unpubl.), occur in South Africa. In Malawi, at ambient temperatures of 21–24 °C, becomes torpid during day (Happold & Happold 1988). Considered more arid-adapted than *R. ferrumequinum* (Harrison & Bates 1991; Thomas 1997). Captive individuals, feeding on winged termites, drank regularly. Predicted mean maximum urine concentration is comparatively low (2981 mOsmol/kg); therefore probably very dependent on water for drinking in the wild (Happold & Happold 1988).

Foraging and Food In Malawi and southern Africa, forages under canopies of trees and along banks of vegetation, in areas of moderate clutter. Foraging begins ca. half an hour after sunset (Smithers 1983). Forages by slow-hawking and fly-catching, and predictably by gleaning. Individuals eat while hanging from branches, and sometimes from perches in verandas, and these perches are marked by accumulations of discarded fragments of insects. In South Africa, fragments under perches included moths and small beetles (Rautenbach 1979). In Zimbabwe, faecal pellets of two individuals contained only beetles (Fenton *et al.* 1977). Captive bats ate mantises (Dictyoptera: *Miomantis* sp.) that were thrown into the air near perching bats; the bats responded by taking flight and capturing the prey in mid-air (as in typical fly-catching) (Cumming 1996). The mantises responded to the echolocation calls of approaching bats by swerving and diving sharply to the ground; deafened mantises did not respond in this way.

Echolocation Call-shape FM/CF/FM. CF-frequency (Malawi) 79–84 kHz (usually 82–84 kHz) (M. Happold unpubl.). In South Africa, 90–100 kHz (McDonald *et al.* 1990a), 80–85 kHz (Cumming



Rhinolophus clivus

1996); 94 kHz (Taylor 1999a). In Swaziland, 90.9 kHz (1 bat; Monadjem 2005). This variation in CF-frequency strongly suggests that the South African and Swaziland bats represent two different species, one of which also occurs in Malawi.

Social and Reproductive Behaviour In Algeria, roosts singly or in groups of up to 50 individuals (Kowalski & Rzebik-Kowalska 1991). In Malawi and southern Africa, roosts singly, in small groups (M. Happold unpubl., R. T. F. Bernard unpubl.) and in colonies of up to 10,000 individuals (Herselman & Norton 1985). Bats roosting in a small group hang slightly apart within a cluster. In very large colonies, there are many small clusters. Roosts usually contain individuals of both sexes, even when young and subadults are present.

Reproduction and Population Structure Litter-size: one. In Zimbabwe, the reproductive chronology is restricted seasonal monoestry with copulation in the dry season (Jun–Jul) and parturition at the beginning of the unimodal wet season (mid-Nov) (R. T. F. Bernard & F. P. D. Cotterill unpubl.). At ca. 29° S (KwaZulu–Natal, South Africa), the reproductive chronology is also restricted seasonal monoestry with copulation in autumn (Apr), sperm-storage by the ♀♀ until late winter (Aug) when ovulation and fertilization occur, and parturition in summer (Nov–Dec) (Bernard 1983, 1988). Gestation 3.5 months; lactation approximately 2 months. In contrast, at ca. 25° S (Gauteng Highveld, South Africa), ♀♀ do not uniformly store spermatozoa for prolonged periods and sperm-storage seems to take place in the ♂♂ (Wessels & van der Merwe 1997). The differences in reproduction lend weight to the probability that *R. clivosus* contains more than one species. Approximately 20% of ♀♀ are sexually mature after 18 months, 80% after 18 months and the remainder after 42 months or more (Wingate 1986).

Predators, Parasites and Diseases Ectoparasites include fleas *Xenopsylla nubica* (Siphonaptera: Pulicidae), *Oxyparius isomalus*,

Rhinolophopsylla ashworthi, *R. capensis* (Siphonaptera: Ischnopsyllidae); 13 species of bat-flies (Diptera: Nycteribiidae, Streblidae); four species of ticks (Acari: Argasidae, Ixodidae); 14 species of mites (Acari: Amblyomidae, Spinturnicidae, Macronyssidae, Myobiidae, Trombiculidae, Psorergatidae, Chirodiscidae, Sarcoptidae and Gastronyssidae) (Anciaux de Faveaux 1984).

Conservation IUCN Category: Least Concern.

On the Zimbabwe plateau (>1000 m) its occurrence has been augmented by the increased density of abandoned mines.

Measurements

Rhinolophus clivosus

FA: 51.5 (42–59) mm, n = 251

WS (c): 348 (341–355) mm, n = 4

TL: 92.3 (68–112) mm, n = 197

T: 31.4 (22–40) mm, n = 140

E: 20.1 (16–24) mm, n = 119

NL (breadth): 7.8 (6.6–9.6) mm, n = 37

Tib: 21.9 (16–27) mm, n = 64

HF: 10.4 (11–13) mm, n = 25

WT: 16.0 (10–25) g, n = 67

CrnC: 20.7 (18.1–22.8) mm, n = 57*

GWS: 10.5 (9.2–12.2) mm, n = 46

C–M³: 7.3 (6.7–8.9) mm, n = 46

Throughout geographic range (AM, BMNH, HC, ZFMK and literature)

*Csorba *et al.* 2003

Key References Bernard 1983, 1988; Smithers 1983; Taylor 2000.

Ric T. F. Bernard & Meredith Happold

Rhinolophus darlingi DARLING'S HORSESHOE BAT

Fr. Rhinolophe de Darling; Ger. Darlings Hufeisennase

Rhinolophus darlingi K. Andersen, 1905. Ann. Mag. Nat. Hist., ser. 7, 15: 70. Upper Mazoe Valley, Mashonaland, Zimbabwe.

Taxonomy Species-group: *ferrumequinum*. Synonyms: *barbertonensis*, *damarensis*. Subspecies: two. The taxonomic status of a population in Nigeria is unclear (Hill *et al.* 1988; Csorba *et al.* 2003). Chromosome number (South Africa): 2n = 58; aFN = 60. X = large subtelocentric, Y = small metacentric (Rautenbach 1986).

Description Small microbat with noseleaf (posterior component subtriangular with erect tip); medium-sized for an African rhinolophid; anterior upper premolar displaced labially or absent; connecting process rounded; lancet subtriangular; sella with concave sides; no axillary tufts. Sexes similar. Pelage soft, fluffy; mid-dorsal hairs 8–10 mm. Dorsal pelage grey, brownish-grey or greyish-brown; hairs cream or pale greyish-brown with grey, brownish-grey or greyish-brown tip. Ventral pelage paler, often pale grey. Apparently no orange-phase. No axillary tufts on adult ♂♂. Ears comparatively and relatively short (15–23 mm, 42 [40–47]% of FA).

Noseleaf with lancet large, subtriangular, sides slightly concave: tip bluntly pointed. Connecting process smoothly rounded, ca. same height as sella or slightly lower. Sella naked, sides concave, top broad and rounded. Horseshoe narrow (7.1–8.7 mm) but almost covering muzzle; lateral leaflets present; median emargination deep. Lower lip with one groove. Wings and interfemoral membrane translucent grey to black. First phalanx of fourth finger relatively long (27.3 [24–30]% of fourth metacarpal, n = 52). Tibia 42.0 (41–47)% of FA, n = 17. Baculum trumpet-shaped with round, relatively short shaft (total length <2 mm).

Skull robust; zygomatic arches sturdy; zygomatic width greater than mastoid width. Nasal swellings of medium relative height. Frontal depression shallow to moderately deep; supraorbital ridges pronounced. Sagittal crest moderately well developed anteriorly, weak to absent posteriorly. Palatal bridge of medium relative length 30–35% of C–M³ (Csorba *et al.* 2003). Interpterygoid groove well

defined. Anterior upper premolar small and fully displaced labially, or absent; canine and posterior premolar in contact. Middle lower premolar minute and fully displaced labially, or absent; anterior and posterior lower premolar in contact. Dental formula $^{1123}/_{2133} = 32$, $^{1113}/_{2133} = 30$, $^{1123}/_{2123} = 30$ or $^{1113}/_{2123} = 28$.

Geographical Variation Two subspecies are recognized by Meester *et al.* (1986) and Koopman (1994):

R. d. darlingi: Angola, Tanzania, Malawi, Mozambique, Zimbabwe, E and N Botswana, NE South Africa.

R. d. damarensis: Namibia and South-West Arid Zone in neighbouring countries.

Measurements of specimens from Nigeria (Hill *et al.* 1988) fall almost entirely within the range of *R. d. darlingi*, but more material is needed to establish the subspecific status of the West African population (Csorba *et al.* 2003). Furthermore, the true pattern of variation of *R. darlingi* in Tanzania, Malawi and Mozambique is unclear.

Similar Species Four other African *Rhinolophus* occurring south of the Equator have the following combination of characters – anterior upper premolar fully displaced labially or absent; connecting process rounded; sella naked (or with sparse short hairs only) (Table 14, p. 304):

Rhinolophus clivosus. FA often longer (51.5 [42–59] mm). Dorsal pelage browner. Nasal swellings low. Interpterygoid groove absent or indistinct. Palatal bridge relatively shorter (25–31% of C–M³).

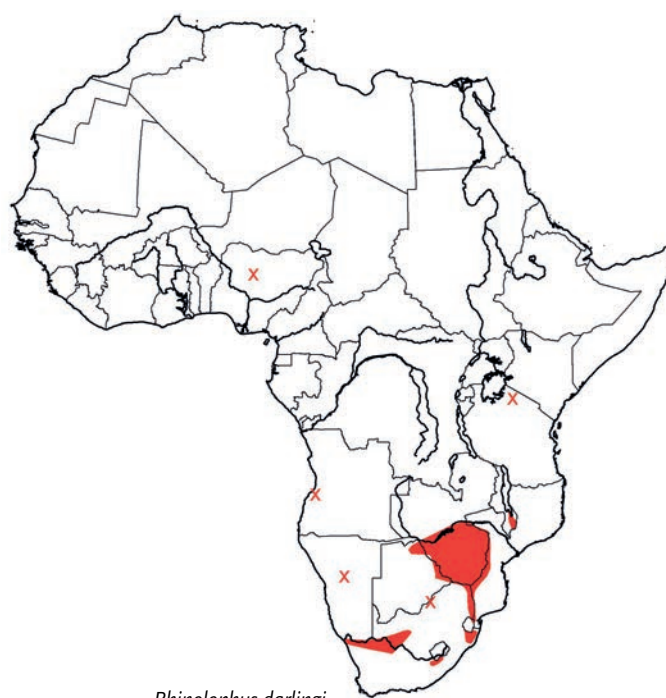
R. deckenii. Horseshoe broader (9.1–11.5 mm). FA usually longer (53 [48–56] mm). Skull larger (CrnC: 22.6–24.1 mm; C–M³: 8.2–9.4 mm).

R. sakejensis. Larger (FA: 53–55 mm; CrnC: 24.3–25.3 mm). All three known specimens are in orange-phase. Horseshoe broader (10.3 mm). Nasal swellings low. Frontal depression extremely shallow; supraorbital ridges indistinct. Anterior upper premolar absent in the three known specimens; canine and posterior premolar in contact.

R. silvestris. Horseshoe broader (9.5, 10 mm). FA longer (50–56 mm). Skull larger (CrnC: 22.3–23.7 mm; C–M³: 8.7–9.3 mm).

Distribution Endemic to Africa. Mainly recorded from parts of the Zambezian Woodland, Highveld, South-West Arid, Afromontane–Afroalpine and Coastal Forest Mosaic BZs in south-central Africa and southern Africa, with outlying records in the Guinea Savanna BZ in West Africa, and in the Afromontane–Afroalpine BZ in Tanzania. Recorded very disjunctly from Nigeria and N Tanzania, and from Angola to Malawi and southwards to South Africa. Occurs throughout Zimbabwe (F. P. D. Cotterill unpubl.); records in other countries are scarce and scattered (Andersen 1905a, Smithers & Lobão Tello 1976, Smithers 1983, Hill *et al.* 1988, Taylor 2000, Csorba *et al.* 2003 and others).

Habitat Mesic and semi-arid woodland savannas where suitable day-roosts (including caves and abandoned mines) are present. In southern part of its geographic range, particularly associated with broken, rocky terrain (Smithers 1983). Absent from deserts.



Rhinolophus darlingi

Abundance Rarely recorded in Malawi (Happold & Happold 1997), and apparently rare elsewhere north of the Zambezi R. Locally common in vicinity of day-roosts in Zimbabwe, Namibia and South Africa.

Adaptations Aspect ratio low; wing-loading very low (F. P. D. Cotterill unpubl.). Flight predicted to be slow and very manoeuvrable. Day-roosts include caves, abandoned mine-adits, cavities and fissures in rock or in piles of boulders, large hollow trees, disused buildings (including under the floors of disused houses in Kruger N. P. [Pienaar *et al.* 1980]); hangs freely from ceilings (Rautenbach 1982, Smithers 1983). Complete darkness not essential: at least some roosts are dimly lit. In Namibia, three caves used as day-roosts varied greatly in humidity but the temperature remained almost constant (24–24.5 °C) (Churchill *et al.* 1997). In Zimbabwe, *R. darlingi* enters torpor daily during the cool-dry season (F. P. D. Cotterill unpubl.).

Food and Foraging No information. Based on wing morphology and echolocation, predicted to forage in cluttered habitats (Aldridge & Rautenbach 1987). Diet not known.

Echolocation Call-shape FM/CF/FM. CF-frequency (Swaziland) 86 kHz; maximum duration 35.2 ms (10 bats; Taylor 1999a).

Social and Reproductive Behaviour Usually roosts in groups of 'dozens of individuals' (Smithers 1983); a group of ca. 20 individuals is reported from KwaZulu–Natal (South Africa) by Taylor, P. (1998), and one of ca. 160 individuals from Namibia by Churchill *et al.* (1997). In the former Transvaal (South Africa), groups of 2–15 were recorded by Rautenbach (1982). Group members hang in clusters but with each individual slightly separated from its neighbours.

Reproduction Litter-size: normally one; twinned foetuses near full term, one in each uterine horn, were observed once in

Zimbabwe (Smithers & Wilson 1979). Reproductive chronology uncertain. In Zimbabwe, ♀♀ with young were recorded in Oct, and one pregnant ♀ in Dec (Smithers & Wilson 1979). No pregnant or lactating ♀♀ have been found during the cool-dry season (F. P. D. Cotterill unpubl.). In the former Transvaal (South Africa) one pregnant ♀ was recorded in Oct (Rautenbach 1982). The data are consistent with monoestry, but this needs confirmation.

Predators, Parasites and Diseases Ectoparasites include a flea *Echidnophaga aethiops* (Pulicidae); bat-flies *Phthiridium scissum*, *P. tectum* (Diptera: Nycteribiidae) and *Brachytarsina africana* (Diptera: Streblidae) (Anciaux de Faveaux 1984).

Conservation IUCN Category: Least Concern.

Measurements

Rhinolophus darlingi

FA: 46.9 (42–51) mm, n = 94

WS (d): 288 (229–320) mm, n = 13

TL: 92.6 (70–99) mm, n = 93

T: 29.1 (20–37) mm, n = 105

E: 20.1 (15–23) mm, n = 106

NL (breadth): 8.0 (7.1–8.7) mm, n = 20*

Tib: 20.9 (20–22) mm, n = 17

HF: 9.4 (8–11) mm, n = 50

WT: 9.2 (6–13) g, n = 105

CrnC: 19.3 (18.4–20.5) mm, n = 15†

GWS: 9.8 (9.1–10.4) mm, n = 40

C–M³: 7.0 (6.7–7.3) mm, n = 41

Zimbabwe and South Africa (NMZB, TM)

*Nigeria and Zimbabwe only (ROM)

†Throughout geographic range (Csorba *et al.* 2003)

Key References Churchill *et al.* 1997; Csorba *et al.* 2003; Hill *et al.* 1988; Smithers 1983.

F. P. D. Cotterill & Meredith Happold

Rhinolophus deckenii DECKEN'S HORSESHOE BAT

Fr. Rhinolophe de Decken; Ger. Deckens Hufeisennase

Rhinolophus deckenii Peters, 1868. Monatsber. K. Preuss. Akad. Wiss. Berlin 1867: 705 (publ. 1868). 'Zanzibar Coast'
[= mainland opposite Zanzibar I.], Tanzania.

Taxonomy Species-group: *ferrumequinum*. Treated as a subspecies of *R. clivosus* by Hayman & Hill (1971), but considered to be a distinct species by Koopman (1975, 1993, 1994) and subsequently by many authors including Csorba *et al.* (2003) and Simmons (2005). Synonyms: currently none. Subspecies: currently none, but some authors, including Aellen (1959) and Csorba *et al.* (2003), suggest that *silvestris* (tentatively treated here as a distinct species) is probably a western subspecies of *R. deckenii*. Chromosome number: no information.

Description Small microbat with noseleaf (posterior component subtriangular with erect tip); medium-sized for an African rhinolophid; anterior upper premolar displaced labially or absent; connecting process rounded; lancet subtriangular; sella with slightly concave sides; no axillary tufts; dorsal pelage greyish-brown, apparently no orange-phase (cf. *R. sakejensis*); baculum with flattened, spatulate shaft (cf. *R. silvestris*). Difficult to distinguish from *R. silvestris* except by distribution and baculum morphology (see Similar Species). Sexes similar. Pelage soft, fluffy; mid-dorsal hairs 8–10 mm. Dorsal pelage medium greyish-brown; hairs greyish-fawn with medium greyish-brown at tip. Ventral pelage slightly paler. Apparently no orange-phase. No axillary tufts on adult ♂♂. Ears comparatively and relatively medium-short (18–27 mm, 39–49% of FA). Noseleaf with lancet high, subtriangular (Figure 61b), sides straight or slightly concave, tip bluntly pointed. Connecting process rounded, ca. same height as sella. Sella naked, sides parallel or slightly concave, top broad and rounded. Horseshoe of medium breadth (9.1–11.5 mm), covering whole muzzle; lateral leaflets present; median emargination distinct. Lower lip with a well-defined median groove and two poorly-defined lateral grooves.

Wings brown, semi-translucent; interfemoral membrane slightly paler and more translucent (museum material). First phalanx of fourth finger relatively long (27.1 [24–30]% of fourth metacarpal, n = 25). Tibia 46.7 (44–50)% of FA, n = 24. Baculum with dorsal and ventral parts of basal cone deeply invaginated so sides of cone form two long wings; shaft spatulate and dorsoventrally flattened; tip not expanded; length 3.8 (3.6–4.2) mm, n = 7 (Cotterill 2002a).

Skull robust; zygomatic arches sturdy; zygomatic width much greater than mastoid width. Nasal swellings of medium relative height, lateral profile smoothly rounded. Frontal depression moderately deep; supraorbital ridges prominent. Sagittal crest well developed anteriorly, absent posteriorly. Palatal bridge 29–34% of C–M³ (Csorba *et al.* 2003). Interpterygoid groove shallow but distinct. Anterior upper premolar minute, fully displaced labially (or rarely only half-way displaced), or absent; upper canine and posterior premolar usually separated by a very narrow gap (Csorba *et al.* 2003). Middle lower premolar absent; anterior and posterior lower premolars in close contact. Anterior lower premolar ≤ half height, and ≤ half of the crown area, of the posterior premolar. Dental formula $^{1123}/_{2123} = 30$ or $^{1113}/_{2123} = 28$.

Geographic Variation None currently recognized, but see Taxonomy.

Similar Species Only three other *Rhinolophus* occurring in eastern Africa (or perhaps likely to occur there) have the following combination of characters: anterior upper premolar displaced labially or absent; connecting process rounded; sella naked (or with sparse short hairs only):

Rhinolophus clivosus. Lancet hastate; horseshoe narrower (6.6–9.6 mm), not covering whole muzzle; connecting process higher, lateral profile smoothly curved. Nasal swellings very low. Interpterygoid groove absent or very indistinct. Upper canine and posterior premolar always in contact. Where sympatric, tibia usually shorter (21–24 mm) and skull shorter (CrnC: 19.8–20.9 mm).

R. darlingi. Horseshoe narrower (7.1–8.7 mm). FA usually shorter (47 [42–51] mm). Skull smaller (CrnC: 18.4–20.5 mm, C–M³: 6.7–7.3 mm).

R. hillorum. Horseshoe narrower (8.6, 8.7 mm, n = 2). Skull with nasal swellings low. Frontal depression very shallow, supraorbital ridges indistinct. Anterior upper premolar absent in all known specimens; canine and posterior premolar in contact. Rainforest BZ, Guinea and Liberia to Cameroon (and possibly Sudan).

Rhinolophus silvestris, known only from the Rainforest BZ in Gabon and Congo, is almost indistinguishable morphometrically from *R. deckenii* but has higher nasal swellings and the baculum has a rounded shaft. *Rhinolophus sakejensis*, as yet known only from Zambia, has all three known specimens in orange-phase and the connecting process rises to high rounded peak. *Rhinolophus fumigatus*, *R. eloquens* and *R. hildebrandtii*, which also occur in East Africa and have the anterior upper premolar displaced labially, the connecting process rounded and the horseshoe broader than 10 mm, differ from *R. deckenii* in having hairy sellas (Table 14, p. 304).

Distribution Endemic to Africa. Mainly recorded from the Coastal Forest Mosaic BZ of Kenya, Tanzania, Mafia I. (Kock & Stanley 2009), Pemba I. and Zanzibar I. (Kulzer 1959, Aggundey & Schlitter 1984, Pakenham 1984, Cockle *et al.* 1998, BMNH, HZM), but there are isolated records from the Afromontane–Afroalpine BZ and Zambezi Woodland BZ in inland Tanzania (HZM), and from the Eastern Rainforest–Savanna Mosaic in Uganda (LACM, W. Bogdanowicz pers. comm.). According to Thorn & Kerbis Peterhans (2009), the Ugandan records represent *R. clivosus* or *R. alcyone* (not *R. deckenii*). One specimen was reported from Chinizua Forest, C Mozambique, but without further information (Monadjem *et al.* 2010) (not mapped).

Habitat Mainly known from the small coastal forests that are part of the East African coastal forest mosaic. Bat assemblages in the Tanzanian coastal forests are documented by Cockle *et al.* (1998). The inland records are in drier miombo woodland at 650 m, and in afromontane vegetation on the slopes of Kilimanjaro: no information for Uganda.

Abundance Uncertain. Numerous in at least two Tanzanian coastal forests (Cockle *et al.* 1998).

Remarks Day-roosts on Zanzibar I. include underground caverns and deep caves in coral-rock country, the dark interior of a ruined Marahubi Palace, and within ruined Persian Baths (Pakenham 1984). Also found roosting in an empty mud house on Pemba I. (Pakenham 1984). Collections of bats taken from these day-roosts comprised (a) 2 ♂♂ and 14 ♀♀ of which 11 carried advanced foetuses in Oct, (b) 1 ♂ and 1 ♀ with large foetus in Oct, (c) 2 ♂♂ in Nov, (d) 2 ♂♂ and one non-pregnant ♀ in Mar, (e) 1 ♂ in Jan, (f) 1 ♂ in Jan

and (g) 3 ♂♂ and 5 ♀♀ (of which two had very early embryos) in Aug. However, it is not stated that all occupants of these roosts were captured. Two roosts were shared with *Hipposideros caffer*, and another with *Nycteris macrotis* and *N. thebaica*. Ectoparasites on *R. deckenii* from these two roosts included bat-flies (Diptera: Streblidae), lice and ticks (Pakenham 1984).

Conservation IUCN Category: Near Threatened.

Population probably significantly declining because of deforestation: close to qualifying for Vulnerable. The coastal forests of East Africa are on the verge of eradication because they lie inside a rapidly developing area with high population density (Cockle *et al.* 1998).

Measurements

Rhinolophus deckenii

FA: 53.1 (48–56) mm, n = 39

WS (d): 344 mm, n = 1

TL: 88.3 (76–100) mm, n = 20

T: 28.6 (25–33) mm, n = 12

E: 22.6 (18–27) mm, n = 37

NL (breadth): 10.3 (9.1–11.5) mm, n = 18

Tib: 25.0 (24–28) mm, n = 29

HF: 12.1 (11–13) mm, n = 17

CrnC: 23.4 (22.6–24.1) mm, n = 19*

GWS: 12.0 (10.6–12.6) mm, n = 19

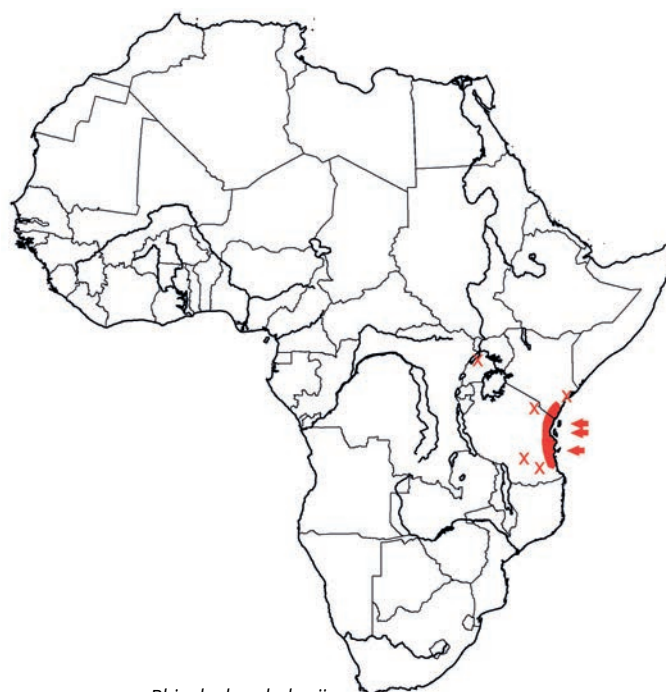
C–M³: 8.8 (8.2–9.4) mm, n = 22

Throughout geographic range (BMNH, HZM, ROM)

*Csorba *et al.* 2003

Key Reference Csorba *et al.* 2003.

Meredith Happold



Rhinolophus deckenii

Rhinolophus denti DENT'S HORSESHOE BAT

Fr. Rhinolophe de Dent; Ger. Dents Hufeisennase

Rhinolophus denti Thomas, 1904. Ann. Mag. Nat. Hist., ser. 7, 13: 386. Kuruman, Cape Province, South Africa.

Taxonomy Species-group: *landeri*. Groups phenetically with *swinyi* and *simulator* (Bogdanowicz 1992, Bogdanowicz & Owen 1992). Synonyms: *knorri*. Subspecies: two. Csorba *et al.* (2003) suggest *R. denti* might include *swinyi*. Many literature references to *R. denti*, notably those in Zimbabwe, actually refer to *R. swinyi*. Chromosome number (South Africa): $2n = 58$; $aFN = 62$; $X =$ large subtelocentric, $Y =$ small metacentric (Rautenbach 1986).

Description Small to very small microbat with noseleaf (posterior component subtriangular with erect tip); small for an African rhinolophid; anterior upper premolar within tooththrow; connecting process rounded; lancet subtriangular with slightly convex sides; sella parallel-sided or with slightly concave sides; no axillary tufts; ears 18 (14–21) mm. Sexes similar. Pelage soft; mid-dorsal hairs 6–7 mm. Dorsal pelage (grey-phase) pale brown (buff) to pale grey or cream; hairs nearly unicoloured, or very pale with brown or grey near the tip. Ventral pelage white, off-white or pale grey. In orange-phase, dorsal pelage bright orange, ventral pelage slightly paler. No axillary tufts on adult ♂♂. Ears comparatively and relatively short (14–21 mm, 44 [38–48]% of FA). Noseleaf with lancet relatively short, well covered with fine pelage, subtriangular with sides slightly concave; tip bluntly pointed. Connecting process rounded, ca. same height as sella. Sella naked with sides almost parallel or slightly concave; top broad and rounded. Lobes at base of sella comparatively low (cf. *R. simulator*). Horseshoe narrow (6.8–7.5 mm) but almost covering muzzle; no lateral leaflets; anterior emargination a distinct notch. Lower lip with three grooves. Wings and interfemoral membrane greyish-black or brown. First phalanx of fourth finger of medium relative length (23.9 [21–27]% of fourth metacarpal, $n = 44$). Tibia 40.5 (40–43)% of FA, $n = 17$.

Skull delicate; zygomatic arches thin; zygomatic width equal or slightly greater than mastoid width. Nasal swellings rounded; relative height medium–low. Frontal depression shallow; supraorbital ridges weak. Sagittal crest very low anteriorly, absent posteriorly. Palatal bridge of medium relative length (30–35% of $C-M^3$). Anterior upper premolar small, within tooththrow; canine and posterior premolar well separated. Lower canines distinctly smaller and shorter than upper canines (cf. *R. landeri*). Middle lower premolar minute, fully displaced labially; anterior and posterior lower premolars in contact. Anterior lower premolar (*R. d. denti*) one half the height of the posterior lower premolar (Kock *et al.* 2002). Dental formula $1123/2133 = 32$.

Geographic Variation Two subspecies are recognized (Koopman 1994):

R. d. knorri: West Africa (details below). Body measurements on average smaller (FA: 38–41 mm; E: 14–17 mm; Tib: 15–16 mm) (Rosevear 1965). Skull longer (CrnC: 17.0–17.6 mm) (Rosevear 1965). Darker, ventral pelage pale grey; ears, wings and interfemoral membrane greyish-black.

R. d. denti: southern Africa. Body measurements on average larger (FA: 40–44 mm; E: 18–21 mm; Tib: 17–18 mm) (Smithers 1983). Skull shorter (GLS: 15.8–17.0 mm) (Rautenbach 1986). Paler, ventral pelage white or off-white; ears, wings and interfemoral membrane brown.

Similar Species Five other African *Rhinolophus* have the anterior upper premolar within tooththrow and the connecting process rounded (Table 14, p. 304):

Rhinolophus simulator simulator. Lancet hastate. Often larger (FA: 43–47 mm; E: 21 [18–23] mm; CrnC: 18.5 [17.4–19.4] mm). Lobes at base of sella higher. Skull with frontal depression moderately deep; supraorbital ridges prominent. Rostrum longer and broader. Mesic woodland savannas. In southern Africa, not recorded west of 25° E.

R. swinyi. Lancet hastate. Top of sella broad and rounded. Tibia often longer (17–21 mm). Cranially indistinguishable except CrnC usually longer. Montane forests and woodland savannas. In southern Africa, not recorded west of 24° E.

R. capensis. Lancet hastate. Larger (FA: 47–51 mm). Skull longer (CrnC: 20.0–21.1 mm). Known only from Cape Province of South Africa.

R. adami. Larger (FA: 46–50 mm). Known only from DR Congo.

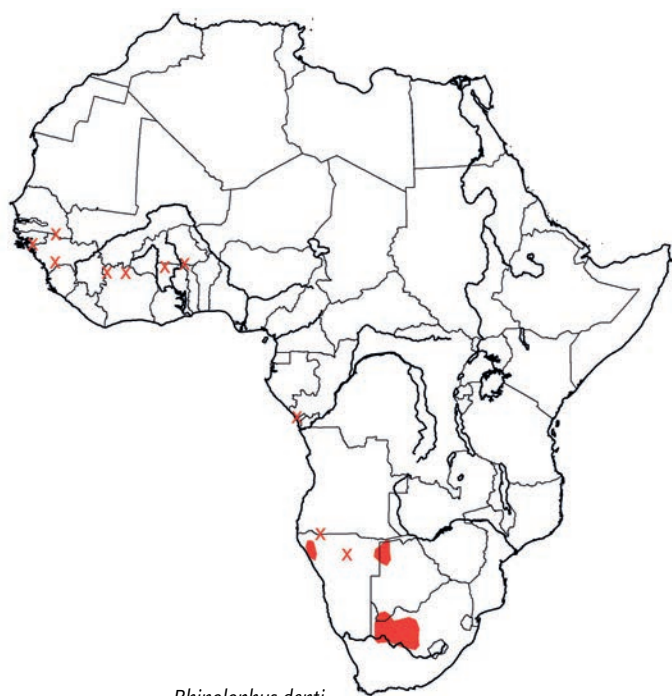
R. maendeleo. Larger (FA: 48, 49 mm). Known only from coastal forests of Tanzania.

Distribution Endemic to Africa. *Rhinolophus d. knorri* is known from the Sudan Savanna and Guinea Savanna BZs (with one record in the Rainforest–Savanna Mosaic) in West Africa: recorded from Guinea-Bissau, Guinea, Côte d'Ivoire and Ghana (Rosevear 1965; Csorba *et al.* 2003, Simmons 2005). Subsequently also recorded from Sierra Leone (Decher *et al.* 2010); not mapped. *Rhinolophus d. denti* is known from the South-West Arid BZ: recorded from S Angola, Namibia, NW and C Botswana, and Northern Cape Province of South Africa (Smithers 1971, Crawford-Cabral 1986, Taylor 2000). Records from Zambia and Mozambique in Csorba *et al.* (2003) are considered here to represent *R. swinyi*.

Habitat In West Africa, recorded from undifferentiated woodland, *Isobrerlinia* woodland and rainforest–savanna mosaic, with caves present at least at one locality. In southern Africa, recorded from semi-arid and desert vegetation zones including Bushy Karoo–Namib shrubland, Kalahari *Acacia* wooded grassland and the Namib Desert (terminology: White 1983). According to Smithers (1983), the availability of caves or rock crevices is probably more important than the type of vegetation.

Abundance Uncertain. Locally common in caves in Botswana and Namibia (Smithers 1971, Churchill *et al.* 1997).

Adaptations Not much information. *Rhinolophus d. knorri* has been found roosting by day in caves, under a bridge, and in a



Rhinolophus denti

hollow Kapok tree *Ceiba pentandra* (Eisentraut 1960, Grubb *et al.* 1998). *Rhinolophus d. denti* has been found roosting in caves, under the thatch roof of a house and in a culvert under a road (Shortridge 1934). In Drotsky's Caves (Botswana), found hanging freely from sides of stalactites; one colony in semi-darkness 90 m from entrance, another colony in pitch-darkness deep inside the cave (Smithers 1971). Roosts in these caves throughout the year. In Namibia, selects humid microclimates in caves (mean relative humidity 90.4%) and comparatively low temperatures (mean 24.4 °C) and enters torpor daily (Churchill *et al.* 1997). One was found roosting with a group of *Nycteris* (Shortridge 1934).

Foraging and Food No information. Observations made by Fenton (1985) refer to *R. swinnyi* (F. P. D. Cotterill unpubl.).

Echolocation No information. Echolocation calls attributed to *R.*

denti by Fenton (1975, 1985), Fenton & Bell (1981), Taylor (1999a) and Csorba *et al.* (2003) refer to *R. swinnyi* (F. P. D. Cotterill unpubl.).

Social and Reproductive Behaviour *Rhinolophus d. denti* has been found roosting singly, in twos and in small to large groups; two groups, each comprised of 'dozens' of individuals were located in Drotsky's Caves (Botswana); individuals were hanging in open clusters (Shortridge 1934, Smithers 1983).

Reproduction No information.

Predators, Parasites and Diseases Ectoparasites include bat-flies *Brachytarsina africana*, *Raymondia aspera* (Diptera: Streblidae) (Anciaux de Faveaux 1984).

Conservation IUCN Category: Least Concern.

Measurements

Rhinolophus denti

FA: 42.0 (37–44) mm, n = 141

WS: n. d.

TL: 71.2 (61–84) mm, n = 31

T: 21.2 (17–24) mm, n = 38

E: 18.0 (14–21) mm, n = 38

NL: (breadth): 7.1 (6.8–7.5) mm, n = 6

Tib: 16.7 (15–18) mm, n = 17

HF: 9–10 mm, n = 20

WT: 6.2 (4–9) g, n = 83

CrnC: 16.5 (15.8–17.3) mm, n = 112

GWS: 8.4 (7.7–8.8) mm, n = 109

C-M³: 5.7 (5.5–6.1) mm, n = 111

Guinea, Nigeria (*R. d. knorri*, n = 9), Botswana, South Africa (*R. d. denti*) (BMNH, ROM, TM, ZFMK, Rosevear 1965, Smithers 1971, Rautenbach 1986)

Key References Churchill *et al.* 1997; Csorba *et al.* 2003; Rautenbach 1986; Rosevear 1965; Smithers 1971.

F. P. D. Cotterill

Rhinolophus eloquens ELOQUENT HORSESHOE BAT

Fr. Rhinolophe éloquent; Ger. Andersens Hufeisennase

Rhinolophus eloquens K. Andersen, 1905. Ann. Mag. Nat. Hist., ser. 7, 15: 74. Entebbe, Uganda.

Taxonomy Species-group: *fumigatus*. Synonyms: *perauritus*. Subspecies: two. Described as subspecies of *R. hildebrandtii*, but subsequently considered to be a distinct species by Andersen (1907), Allen (1939), Koopman (1975, 1994) and Csorba *et al.* (2003) although not by Hayman & Hill (1971), who treated *eloquens* as a subspecies of *R. fumigatus*. Chromosome number: not known.

Description Medium-small microbat with noseleaf (posterior component subtriangular with erect tip); medium-large for an African rhinolophid; anterior upper premolar displaced labially or absent; connecting process rounded; lancet subtriangular; sella

hairy with upper two-thirds parallel-sided; no axillary tufts; FA: 53–63 mm. Sexes similar. Pelage soft, fluffy; mid-dorsal hairs 7–9 mm. Dorsal pelage usually pale brown; hairs with dark grey at base. Ventral pelage paler than dorsal pelage. No orange-phase. No axillary tufts on adult ♂♂. Ears comparatively and relatively medium-short (21–38 mm, 47 [44–51]% of FA). Noseleaf with lancet long, subtriangular with sides slightly concave; tip rounded. Connecting process large, rounded, not higher than sella. Sella liberally covered with longish hairs, broad, upper two-thirds parallel-sided, top rounded. Horseshoe of medium breadth (11.1–12.3 mm), covering muzzle; lateral leaflets present, median emargination deep. Lower lip

with one groove. Wings and interfemoral membrane brown to dark greyish-brown. First phalanx of fourth finger relatively long (26.1 [23–28]% of fourth metacarpal, $n = 22$). Tibia 41.2 (37–44)% of FA, $n = 17$. Baculum trumpet-shaped with straight, cylindrical shaft, length 3.0 (2.8–3.2) mm, $n = 5$ (Cotterill 2002a).

Skull robust; zygomatic arches sturdy; zygomatic width much greater than mastoid width. Nasal swellings relatively high, longer than they are broad. Frontal depression shallow to moderately deep. Sagittal crest comparatively prominent anteriorly and usually extends some distance across parietals. Palatal bridge of medium relative length (32–37% of C–M³; Csorba *et al.* 2003). Anterior upper premolar minute and fully displaced labially, or absent; canine and posterior premolar in contact or almost so. Middle lower premolar usually absent; if present, fully displaced labially and lies under cingula of the anterior and posterior premolars, which overlap; anterior and posterior lower premolars in contact. Dental formula usually $^{1123}/_{2123} = 30$ or $^{1113}/_{2123} = 28$, rarely $^{1123}/_{2133} = 32$ or $^{1113}/_{2133} = 30$.

Geographical Variation Koopman (1975, 1994), followed by Csorba *et al.* (2003) and Simmons (2005), recognizes two subspecies:

R. e. eloquens: S Sudan, E DR Congo, Uganda and N Tanzania, Pemba I. and Zanzibar I.

R. e. perauritus: S Somalia.

Similar Species Only two other *Rhinolophus* in Africa have the following combination of characters: anterior upper premolar displaced labially or absent; connecting process rounded and lower than the sella; sella hairy; horseshoe usually broader than 10 mm and as broad as the muzzle or almost so (Table 14, p. 304):

Rhinolophus fumigatus. Body measurements usually smaller, especially in areas of sympatry (Koopman 1975), (FA: 51 [47–60] mm). Skull smaller (CrnC: 22.7 [21.6–24.3] mm; C–M³: 8.0 [7.3–8.7] mm).

R. hildebrandtii. Usually larger (FA: 64 [60–67] mm; Tib: 26–31 mm; CrnC: 27.4 [26.1–28.7] mm). Baculum longer (>3.0 mm).

Distribution Endemic to Africa. Recorded mainly from the Somalia–Masai Bushland, Afromontane–Afroalpine and Coastal Forest Mosaic BZs in E DR Congo, Rwanda, E Uganda, Kenya, Somalia, N Tanzania, Pemba I., Zanzibar I. and Kirue I., with some records in the Sudan Savanna and Guinea Savanna BZs and the Rainforest–Savanna Mosaics in S Sudan and NE DR Congo (Koopman 1975, Aggundey & Schlitter 1984, Csorba *et al.* 2003). Specimens collected from Ntchisi F. R. and Liwonde N. P. (Malawi) by Happold & Happold (1997) include one specimen from each locality, which, based on echolocation CF-frequencies, probably represent *R. eloquens* (M. Happold pers. comm.); pending confirmation, neither locality has been mapped. Southern extent of distribution might also reach Zambia, Zimbabwe and N Mozambique (F. P. D. Cotterill & P. J. Taylor unpubl.). A specimen from Chano, S Ethiopia (not mapped), might represent *R. eloquens* (D. Kock in Yalden *et al.* 1996). Subsequently recorded from W, SW and S Uganda (Thorn & Kerbis Peterhans 2009) (not mapped): some of these records were previously considered to represent *R. hildebrandtii*.

Habitat Semi-arid savannas (including *Acacia–Commiphora* bushland and thicket, and mosaics of evergreen bushland and secondary



Rhinolophus eloquens

Acacia wooded grassland), mesic woodland savannas and montane forests. Both of the Malawian bats mentioned above were captured in miombo woodland at altitudes of 1500 m and 500 m, respectively.

Abundance Based on numbers in museum collections, locally common in E Uganda and Kenya; apparently scarcer elsewhere. Apparently less common than the sympatric *R. hildebrandtii*.

Adaptations Very little is known about this species. The literature almost certainly contains information about specimens that have been misidentified as *R. hildebrandtii* or *R. fumigatus*. One specimen from Malawi, provisionally identified as *R. eloquens* because it echolocated with CF-frequency 47.5 kHz (see Echolocation), had a low aspect ratio and low wing-loading (M. Happold pers. comm.).

Echolocation Echolocation call-shape FM/CF/FM. Echolocation calls from bats previously identified as *R. hildebrandtii* have CF-frequencies of 35–38 kHz (1 ♀, 7 ♂♂, hand-held) and 47–48 kHz (2 ♀, hand-held) (Malawi; M. Happold pers. comm.); 37 kHz and 46 kHz ($n = 2$, flying in open) (Zimbabwe, Fenton & Bell 1981), and ca. 40 kHz ($n = 9$, flying in room or in open) (Kruger N. P., South Africa, Aldridge & Rautenbach 1987). It is probable that the lower-frequency calls are made by the larger *R. hildebrandtii*, and that the higher-frequency calls are made by the smaller *R. eloquens* or a closely related form (F. P. D. Cotterill, M. Happold & P. J. Taylor unpubl.). The acoustics of the vocal tract, and the role of the tracheal chambers and nasal cavities, of bats from Zimbabwe identified as *R. hildebrandtii* (but with CF-frequency ca. 48 kHz), were investigated by Suthers *et al.* (1988) and Hartley & Suthers (1988) (see Family Rhinolophidae).

Social and Reproductive Behaviour No information.

Reproduction and Population Structure No information.

Predators, Parasites and Diseases Ectoparasites include a flea *Rhinolophopsylla ectopa* (Siphonaptera: Ischnopsyllidae) (Beaucournu & Kock 1996). Some of the ectoparasites listed as hosted by *R. hildebrandtii* by Anciaux de Faveaux (1984) were hosted by *R. eloquens* (see profile of *R. hildebrandtii*). Mt Elgon bat virus was isolated from salivary glands (Metselaar *et al.* 1969).

Conservation IUCN Category: Least Concern.

Measurements

Rhinolophus eloquens

FA: 58.4 (53–63) mm, n = 220

WS (d): 373 (364–384) mm, n = 3

TL: 101.0 (88–117) mm, n = 231

T: 31.5 (20–45) mm, n = 234

Tib: 23.9 (22–25) mm, n = 6

HF: 13.5 (12–14) mm, n = 23

E: 27.5 (21–38) mm, n = 233

NL (breadth): 11.6 (11.1–12.3) mm, n = 10

WT: 21.3 (13–40) g, n = 196

CrnC: 25.4 (24.8–26.2) mm, n = 36*

GWS: 12.9 (12.1–13.9) mm, n = 68

C–M³: 9.2 (8.7–9.6) mm, n = 68

Throughout geographic range (BMNH, HZM, NMZB, ROM)

*Csorba *et al.* 2003

Key References Andersen 1905b; Csorba *et al.* 2003; Koopman 1975.

F. P. D. Cotterill

Rhinolophus euryale MEDITERRANEAN HORSESHOE BAT

Fr. Rhinolophe euryale; Ger. Mittelmeer-Hufeisennase

Rhinolophus euryale Blasius, 1853. Arch. Naturgesch. 19 (1): 49. Milan, Italy.

Taxonomy Species-group: *euryale*. Synonyms in Africa: *algirus*, *barbarus*, *meridionalis* (extralimitally: *atlanticus*, *cabreræ*, *judaicus*, *nordmanni*, *toscanus*). The form *tuneti* from Tunisia is currently included in *R. mehelyi*. Subspecies: possibly two of which only the nominate occurs in Africa (see Geographic Variation). Chromosome number (Europe): 2n = 58; aFN = 60 (Manfredi Romanini *et al.* 1975). There are four metacentric and 52 acrocentric autosomes, X = large metacentric, Y = very small metacentric, acrocentric or dot-like (Zima 1982, Zima *et al.* 1992).

Description Small microbat with noseleaf (posterior component subtriangular with erect tip); medium-sized for an African rhinolophid; anterior upper premolar within tooththrow; connecting process rising to high horn; sella parallel-sided; no axillary tufts; first phalanx of fourth finger relatively short; marked contrast between the crown areas of the anterior and posterior lower premolars (cf. *R. blasii*); faint spectacles around eyes (cf. *R. mehelyi*). Not easily distinguished from *R. mehelyi*. Sexes similar. Pelage soft, fluffy; mid-dorsal hairs 7–9 mm. Dorsal pelage greyish-brown with slight reddish, lilac or yellowish tinge (juveniles grey); hairs of adults whitish with greyish-brown at tip. Ventral pelage paler to considerably paler (but never almost white); boundary with dorsal pelage indistinct. Usually some brown hairs around eyes, but ‘spectacles’ comparatively faint (cf. *R. mehelyi*). No orange-phase. No axillary tufts on adult ♂♂. Ears comparatively and relatively short (19–22 mm, mean E ca. 42% of mean FA). Noseleaf with lancet subtriangular, tip bluntly pointed. Connecting process rising to high, narrow, forward-curving, pointed horn (Figure 59k). Sella naked, almost parallel-sided, top broad, rounded and tilted forward. Horseshoe narrow (6.5–7.5 mm), not covering whole muzzle; no lateral leaflets; median emargination shallow. Lower lip with three grooves. Wings and inter-femoral membrane pale brown. First phalanx of fourth finger relatively short (20.0 [17–22]% of fourth metacarpal, n = 22), and <50% of second phalanx (cf. most *R. blasii*). Tibia 43 (41–45)% of FA, n = 4.

Skull delicate; zygomatic and mastoid widths usually nearly equal but sometimes one or the other is the widest. Rostrum narrow; nasal

swellings relatively low. Frontal depression shallow; supraorbital crests poorly developed. Sagittal crest absent or very low. Bar between infraorbital foramen and orbit short and broad, infraorbital foramen small (cf. *R. mehelyi*). Palatal bridge of medium relative length (31–35% of C–M³; Csorba *et al.* 2003). Anterior upper premolar small, within tooththrow; canine and posterior premolar well separated. Middle lower premolar very small, somewhat displaced labially; anterior and posterior lower premolars separated. Crown area of lower anterior premolar 50% or less of that of the posterior premolar. Dental formula ¹¹²³/₂₁₃₃ = 32.

Geographic Variation Currently, only the nominate subspecies is considered to occur in Africa (Kowalski & Rzebiak-Kowalska 1991, Horáček *et al.* 2000, Csorba *et al.* 2003). Extralimitally, *R. e. judaicus* (E Mediterranean) is considered to be the only other valid subspecies by Csorba *et al.* (2003) and Simmons (2005), but its validity is questioned by Harrison & Bates (1991).

Similar Species Only one other *Rhinolophus* in Africa has a connecting process which rises to a high narrow pointed horn (Table 14, p. 304):

Rhinolophus blasii. Sella wedge-shaped; horseshoe usually broader (7.2–9.0 mm). First phalanx of fourth finger relatively long (24–28% of fourth metacarpal). No marked contrast between crown areas of anterior and posterior lower premolars.

One sympatric species has a triangular connecting process that, although lower, also rises to a point:

R. mehelyi. Lancet hastate with distal half narrow, almost parallel-sided but slightly tapering to a thin apex. Eyes usually with dark spectacles or a dark patch under each eye; dorsal hairs with pale greyish-beige bases; ventral pelage almost white or pure white. Craniodental characters almost indistinguishable.

Distribution In Africa, recorded from the Mediterranean Coastal BZ (and marginally from the Sahara Arid BZ) in NW Africa, from Morocco through Algeria to Tunisia. Extends southwards to ca. 32°N in Morocco (Aulagnier & Thévenot 1986) and 34° 25'N in Tunisia (Aellen & Strinati 1969) but as yet recorded from only three localities close to the coast in Algeria (Kowalski & Rzebik-Kowalska 1991) although likely to occur further inland in some areas. Extraliminally: France and Portugal to Turkmenistan and Iran, and also Arabian Peninsula (Horáček *et al.* 2000, Hutson *et al.* 2001).

Habitat In NW Africa, recorded from Mediterranean sclerophyllous forest, sub-Mediterranean semi-desert grassland and shrubland, and transitional zones (terminology: White 1983). Prefers limestone areas with numerous caves and water nearby.

Abundance Rare in Algeria and Tunisia, common in certain areas of N Morocco.

Adaptations Aspect ratio low; wing-loading low (Gaisler 1959). Flight slow, fluttering, very manoeuvrable. Can hover. In NW Africa, apparently roosts by day only in caves but, in Europe, also roosts in buildings. Usually does not wrap the wings completely around the body, even during hibernation. In summer, roosts deep inside caves at ambient temperature of 22 °C (Morocco), 20–26 °C (Algeria); sometimes shares roosts with *Rhinolophus blasii*, *Myotis emarginatus*, *M. punicus* and/or *Miniopterus schreibersii*. In winter, hibernates at roosts near the entrances of caves at ambient temperatures of 10–12.5 °C (Morocco) (Aulagnier & Thévenot 1986, Gaisler 2001a). In Lebanon, hibernating individuals hang singly (Atallah 1977). In Europe, usually sedentary; greatest recorded movement 134 km (Schober & Grimmberger 1989).

Foraging and Food No data from Africa. In Europe, leaves day-roosts in late dusk; forages low over ground; preys on moths and

other insects (Schober & Grimmberger 1989, Gaisler 2001a). Often takes prey to a night-roost where it is consumed.

Echolocation Call-shape FM/CF/FM. CF-frequency 101–108 kHz; duration ca. 20–30 ms (Schober & Grimmberger 1989).

Social and Reproductive Behaviour Roosts in groups (colonies) of varying size and composition depending on season. Extraliminally, roosts in colonies of up to 2000 individuals of both sexes during winter; and forms maternity colonies of 50–400 ♀♀ in summer; ♂♂ sometimes present in the maternity colonies. In Algeria, assemblages of up to 200 individuals of both sexes were recorded at one cave in spring and also in autumn but, in mid-winter, this cave was not inhabited by *R. euryale*, and in summer it was only inhabited sporadically by ♂♂ (Kowalski *et al.* 1986). Individuals roosted singly if torpid, or in associations, often in contact with neighbours, if they were active. In Morocco, colonies comprised of several dozens of ♀♀ were noted at the time of 'reproduction' (Brosset 1955 in Aulagnier & Thévenot 1986).

Reproduction and Population Structure Litter-size: probably one (as in Europe). In Europe, births occur in summer (Jun–Jul); no detailed information. Sexual maturity: ♂♂ at 15 months to 2¼ years; ♀♀ at 2–3 years (Gaisler 2001a).

Predators, Parasites and Diseases Ectoparasites (North Africa) include a flea *Rhinolophopsylla unipunctinata arabs* (Siphonaptera: Ischnopsyllidae); bat-flies *Nycteribia latreillei*, *N. vexata*, *Penicillidia dufouri*, *Phthiridium biarticulatum* (Diptera: Nycteribiidae) and *Brachytarsina africana* (Diptera: Streblidae) (Anciaux de Faveaux 1984).

Conservation IUCN Category: Near Threatened.

The global population appears stable and/or even increasing in some areas.

Measurements

Rhinolophus euryale euryale

FA: 48.2 (46–50) mm, n = 13

WS (d): 300–320 mm*

TL: 77.7 (72–82) mm, n = 13

T: 26.0 (22–28) mm, n = 13

E: 20.1 (19–22) mm, n = 13

NL (breadth): 7.2 (6.5–7.5) mm, n = 16

Tib: 21.2 (21–22) mm, n = 4

HF: 9.9 (9–11) mm, n = 13

WT: 9.3 (7.5–10.5) g, n = 11

CrnC: 18.4 (17.6–18.8) mm, n = 7

GWS: 9.1 (8.5–9.4) mm, n = 7

C–M³: 6.1 (5.7–6.4) mm, n = 7

Algeria (BMNH, Gaisler 1983, Kowalski & Rzebik-Kowalska 1991)

*Europe (Schober & Grimmberger 1989); sample size not recorded

Key References Csorba *et al.* 2003; Gaisler 2001a; Harrison & Bates 1991; Horáček *et al.* 2000; Kowalski & Rzebik-Kowalska 1991.



Rhinolophus euryale

Jiří Gaisler

Rhinolophus ferrumequinum GREATER HORSESHOE BAT

Fr. Grand rhinolophe; Ger. Große Hufeisennase

Rhinolophus ferrumequinum (Schreber, 1774). Die Säugethiere 1: 174, pl. 62. France.

Taxonomy Originally *Vespertilio ferrum-equinum*. Species-group: *ferrumequinum*. Synonyms in Africa: one (extraliminally 33 others listed by Simmons [2005]). Subspecies: only the nominate subspecies occurs in Africa; extraliminally, six others recognized by Simmons (2005) but subspecies limits are unclear, the validities of some are dubious, and more than one species might be represented (Horáček *et al.* 2000, Csorba *et al.* 2003). Chromosome number (Tunisia): $2n = 58$; $aFN = 60$ (Baker *et al.* 1975). There are usually 4–6 metacentric and 50–52 acrocentric autosomes, $X =$ large, metacentric or submetacentric, $Y =$ very small, acrocentric, metacentric or dot-like (Zima 1982, Zima *et al.* 1992).

Description Small microbat with noseleaf (posterior component subtriangular with erect tip); medium-sized for an African rhinolophid; anterior upper premolar displaced labially or absent; connecting process rounded; lancet hastate; sella with concave sides; no axillary tufts. Sexes similar. Pelage soft, fluffy; mid-dorsal hairs 9–11 mm. Dorsal pelage greyish-brown or brown, more or less tinged with red (juveniles ashy-grey); hairs of adults beige with greyish-brown or brown at tip. Ventral pelage greyish-white to yellowish-white. No orange-phase. No axillary tufts on adult ♂♂. Ears comparatively medium-short (19–25 mm) and relatively short (mean E 41% of mean FA). Noseleaf with lancet hastate (Figure 61e) or subtriangular becoming slightly concave near tip, tip bluntly pointed. Connecting process rounded, much higher than sella. Sella naked, relatively small and curved forward so front surface is strongly concave, sides slightly concave, top broad and rounded. Horseshoe narrow (7.0–9.0 mm in Africa), not covering whole muzzle; lateral leaflets present but sometimes inconspicuous; median emargination deep. Lower lip with one or three grooves (lateral grooves sometimes inconspicuous). Wings and interfemoral membrane pale brown or greyish-brown. First phalanx of fourth finger relatively long (27.6 [24–31]% of fourth metacarpal, $n = 39$) and <50% of second phalanx (cf. *R. blasii*). Tibia 44.8 (44–46)% of FA, $n = 6$.

Skull robust; zygomatic arches sturdy; zygomatic width greater than mastoid width. Nasal swellings of medium-low relative height. Frontal depression shallow; supraorbital crests weak. Sagittal crest well developed anteriorly, absent posteriorly. Palatal bridge 28–35% of $C-M^3$ (Csorba *et al.* 2003). Anterior upper premolar minute and fully displaced labially, or absent; canine and posterior premolar in contact. Middle lower premolar minute and fully displaced labially, or absent; anterior and posterior lower premolars in contact. Dental formula $^{1123}/_{2133} = 32$, $^{1113}/_{2133} = 30$, $^{1123}/_{2123} = 30$ or $^{1113}/_{2123} = 28$.

Geographic Variation *Rhinolophus f. ferrumequinum* is the only subspecies in Africa (Aulagnier & Thévenot 1986, Csorba *et al.* 2003, Simmons 2005). No variation has been recorded in Africa, but a clinal trend in size is manifested by populations of this subspecies in Europe: size increases from west to east in the Mediterranean region (including the Maghreb in NW Africa), and from north-west to south-east in Eastern Europe (Kryštufek 1993, de Paz 1995).

Similar Species Only one other *Rhinolophus* found in North Africa has the anterior upper premolar fully displaced labially or absent, and the connecting process rounded (Table 14, p. 304):

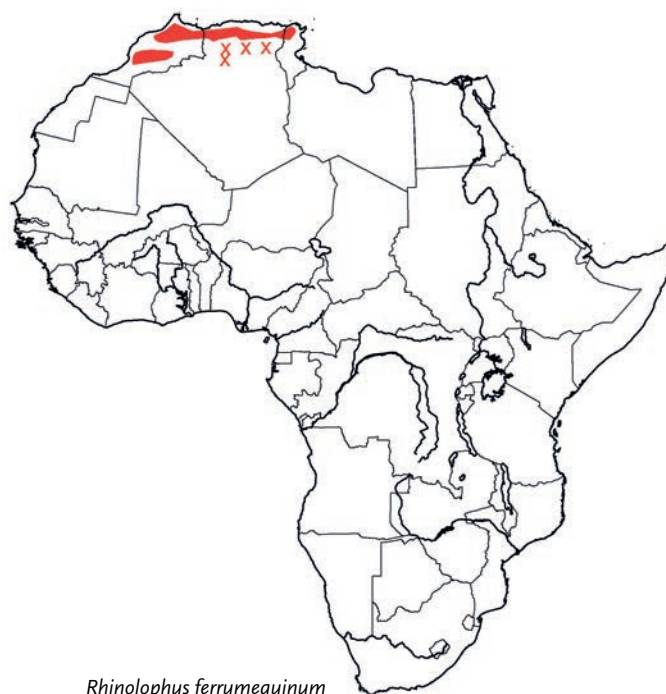
Rhinolophus clivosus. Not recorded from NW Africa, therefore not sympatric. In S Algeria, Libya and Egypt, forearm shorter (46.1 [43–49] mm).

Distribution In Africa, found in the Mediterranean Coastal and Afromontane–Afroalpine BZs (and very marginally in the Sahara Arid BZ) in the Maghreb (NW Africa). Recorded from Morocco (coast to Anti Atlas at 31°N), Algeria (coast to southern border of Saharan Atlas at 33°N) and Tunisia (coast to northern border of Sahara). Possibly occurs in Mediterranean Libya (but not yet recorded). Subsequently recorded as far south as 32° 55'N in Tunisia (Dalhoumi *et al.* 2011); not mapped. Extraliminally: Western Europe to China, Korea and Japan, also Arabian Peninsula and Indian sub-continent.

Habitat In Africa, these cave-roosting bats inhabit rocky regions with sparse vegetation, either primary or secondary (macchia or garrigue), from sea level to at least 1500 m (Brezina, Saharan Atlas, Algeria).

Abundance Common and widely distributed in the northern (Mediterranean) zone of Morocco, Algeria and Tunisia where caves and other underground spaces are abundant. Less common in the middle zone of the Hauts Plateaux.

Adaptations A particularly well-studied species extraliminally, but comparatively little information from Africa. Aspect ratio low; wing-



Rhinolophus ferrumequinum

loading medium; wing-tip rounded and short (Norberg & Rayner 1987). Flight slow, manoeuvrable, fluttering, with some glides; can hover briefly and take off from ground. Usually flies low (0.5–6 m above ground). Mean flight speed (indoors) 5.5 m/s (Norberg 1987). In Africa, roosts by day in caves and other subterranean spaces such as rhattaras (underground irrigation channels); hangs from walls or ceilings. Roosts in warmer galleries in summer; in contrast to Europe, African populations do not seem to use buildings in summer, and even maternity colonies are in caves. Males, and ♀♀ which are neither pregnant nor lactating, become torpid during the day when temperature is 22 °C or less. Summer-roosts that are not maternity roosts are often shared with other *Rhinolophus* spp., *Miniopterus schreibersii* or *Myotis* spp. and, in Morocco, also with *Asellia tridens* and *Plecotus gaisleri*. Maternity roosts are sometimes shared with other species. In winter, hibernates in cool parts of caves. Certain caves are inhabited all year round, others just in summer and others only in winter. Distance between summer- and winter-roosts does not exceed 35 km (Gaisler 2001b). Individuals wrap themselves completely in their wing-membranes during hibernation.

Foraging and Food Forages by slow-hawking, fly-catching and ground-gleaning (Norberg & Rayner 1987, Jones & Rayner 1989a, Schober & Grimmberger 1989, Duvergé & Jones 1994, Jones *et al.* 1995). Flying insects often caught by the tip of the bat's wing-membrane. Sometimes lands to take dung-beetles and other insects from cow dung. Some insects are eaten on wing; others are taken to a perch and eaten there. Forages in terrain with sparse tree cover, on hillsides, cliff faces, and in gardens (Europe). Supposedly foraging individuals were mist-netted at six localities in Algeria, mostly among bushes and close to rocks or water (Gaisler & Kowalski 1986). Activity is strictly nocturnal; individuals typically leave day-roosts 15–30 min after sunset, and begin foraging soon after. They usually linger close to their roosts before foraging further afield; foraging individuals stay outside the day-roost for the whole night, or return after 2–3 h and leave the day-roost again for 30–50 min before sunrise. Some rest in night-roosts close to their foraging areas. Extraliminally, Lepidoptera and Coleoptera were found to prevail in diet; Hymenoptera, Diptera and Araneae were rare.

Echolocation Call-shape usually FM/CF/FM. CF-frequency 80 (77–83) kHz; call-duration ca. 40 ms (Schober & Grimmberger 1989, Limpens & Roschen 1995; country not given, probably Southern Europe). In England, found to use harmonics other than the dominant second harmonic, and to modify the call-shape according to the bat's activity (Jones & Rayner 1989a). When flying (e.g. leaving the day-roost or foraging) call-shape is FM/CF/FM and the terminal descending FM sweep usually has the greater bandwidth. When perch-hunting, in ca. 49% of calls, the ascending and descending FM sweeps have roughly equal bandwidths, and ca. 35% have no discernible FM sweeps.

Social and Reproductive Behaviour Forages singly; juveniles forage independently of their mothers prior to weaning. Roosts singly, in small groups or in very large groups (colonies). Extraliminally, winter colonies contain up to 500 individuals of both sexes. In summer, pregnant ♀♀ form maternity colonies containing up to 400 ♀♀; some immature and non-breeding individuals of both sexes roost with these ♀♀; adult ♂♂ may be present initially, but usually depart when parturition begins, and subsequently roost in small, scattered groups. A colony of juveniles separated from adults, and an all-male colony, were

recorded in Algeria. In Europe, adult ♂♂ and ♀♀ begin roosting together in late summer; copulations take place at the day-roosts and occur until the end of October. During these times, ♂♂ are territorial and, as in many other cave-roosting bats, they establish small harems. Typically, a single cave contains many discrete mating-roosts, each occupied by one ♂ and up to eight ♀♀. Females not inseminated during this time can copulate later in winter or soon after the end of hibernation in spring (Gaisler 2001b).

Reproduction and Population Structure Litter-size: one. At 35–36°N in NW Algeria, the reproductive chronology is restricted seasonal monoestry, with births in summer (Jun), volant young appearing in late Aug, and lactation lasting until early Sep (Kowalski *et al.* 1986). In Europe, sperm-storage occurs in the epididymides of the ♂ and also in the ♀ oviducts until ovulation and fertilization take place in Mar–Apr. The interval between fertilization and birth varies from 2 to 3 months, depending on whether embryonic development is lengthened because of torpor in the pregnant ♀♀ (Ransome 1973). Females are 3–5 years old when they produce their first young. Pubic nipples are not fully developed until after first birth. Males mature when 2–4 years old. Extraliminally, longevity is up to 30 years 6 months (♂♂) and 27 years 8 months (♀♀).

Predators, Parasites and Diseases Predators in Africa not known. In Europe, preyed on, rarely, by owls *Tyto alba* and *Strix aluco*. Individuals emerging at dusk are sometimes taken by Sparrowhawks *Accipiter nisus* (Jones *et al.* 1995). Ectoparasites in Africa include fleas *Ischnopsylla octactena*, *Rhinolophopsylla unipectinata* (Siphonaptera: Ischnopsyllidae); bat-flies *Nycteribia schmidli*, *Penicillidia dufouri*, *Phthiridium biarticulatum* (Diptera: Nycteribiidae), *Brachytarsina kollari* (Diptera: Streblidae) and two species of mites (Anciaux de Faveaux 1984).

Conservation IUCN Category: Least Concern (assessed from extralimital as well as African data).

Measurements

Rhinolophus ferrumequinum ferrumequinum

FA: 55.4 (51–59) mm, n = 52

WS (d): 350–400 mm*

TL: 97.9 (90–113) mm, n = 53

T: 35.4 (30–42) mm, n = 53

E: 22.8 (19–25) mm, n = 53

NL (breadth): 8.1 (7.0–9.0) mm, n = 14

Tib: 24.0 (23–25) mm, n = 6

HF: 11.6 (10–14) mm, n = 53

WT: 17.2 (12.5–21.5) g, n = 32

CrnC: 22.1 (21.5–22.6) mm, n = 32

GWS: 11.8 (11.3–12.2) mm, n = 32

C–M³: 8.3 (7.6–8.7) mm, n = 32

Algeria (BMNH, Gaisler 1983, Kowalski & Rzebik-Kowalska 1991)

*Europe (Schober & Grimmberger 1989); sample number not given

Key References Aulagnier & Thévenot 1986; Gaisler 2001b; Jones & Rayner 1989a; Jones *et al.* 1995; Kowalski *et al.* 1986; Kowalski & Rzebik-Kowalska 1991.

Rhinolophus fumigatus RÜPPELL'S HORSESHOE BAT

Fr. Rhinolophe de Rüppell; Ger. Rüppells Hufeisennase

Rhinolophus fumigatus Rüppell, 1842. Mus. Senckenbergianum 3: 132, 155. Shoa, Ethiopia.

Taxonomy Species-group: *fumigatus*. Synonyms: *abae*, *acrotis* G. M. Allen, 1914, *aethiops*, *antinnorii*, *diversus*, *exsul*, *foxi*, *macrocephalus*. Subspecies: six. The status and geographic ranges of several of these taxa are uncertain (see Geographic Variation); revision needed. Variation (especially in size) suggests that more than one species is contained within *R. fumigatus* (Rosevear 1965, Csorba *et al.* 2003), possibly as many as four. However, it is not yet known to what extent variation in *R. fumigatus* reflects clinal variation and character displacement (see Geographic Variation). Chromosome number (*R. f. aethiops*: South Africa): $2n = 58$; $aFN = 62$. $X =$ large subtelocentric, $Y =$ small metacentric (Rautenbach 1986).

Description Small microbat with noseleaf (posterior component subtriangular with erect tip); medium to fairly large for an African rhinolophid; anterior upper premolar displaced labially or absent; connecting process rounded; lancet subtriangular; sella hairy; no axillary tufts. Sexes similar. Pelage dense, soft, fluffy; mid-dorsal hairs 8–9 mm. Dorsal pelage grey to greyish-brown; hairs greyish-fawn to pale greyish-brown, darker at tip. Ventral pelage slightly paler. Apparently no orange-phase. No axillary tufts on adult ♂♂. Ears comparatively and relatively medium–short (19–28 mm ♂♂, 46 [40–51]% of FA, $n = 27$). Noseleaf with lancet subtriangular, sides slightly concave, tip rounded. Connecting process large, rounded, not higher than sella. Sella liberally covered with longish hairs, broad, sides slightly concave or almost parallel; top broad and rounded. Horseshoe of medium breadth (9.6–11.5 mm); almost covering muzzle; lateral leaflets present; median emargination a distinct notch. Lower lip with one groove. Wings and interfemoral membrane dark grey to dark brown. First phalanx of fourth finger relatively long (25.8 [24–28]% of fourth metacarpal, $n = 18$). Tibia 42 (39–45)% of FA, $n = 35$. Baculum trumpet-shaped with round shaft, length 2.9 (2.7–3.1) mm, $n = 11$ (Cotterill 2002a).

Skull robust; zygomatic arches moderately slender; zygomatic width much greater than mastoid width. Rostrum sturdy. Nasal swellings of medium relative height; broader than they are long. Frontal depression shallow to moderately deep, supraorbital ridges pronounced. Sagittal crest well developed anteriorly, low or absent posteriorly. Interpterygoid groove distinct and narrowed medially. Palatal bridge relative length variable (28–37% of $C-M^3$; Csorba *et al.* 2003). Anterior upper premolar minute and fully displaced labially, or absent; canine and posterior premolar in contact. Middle lower premolar absent except rarely; anterior and posterior lower premolars in contact. Dental formula usually $^{1123}/_{2123} = 30$ or $^{1113}/_{2123} = 28$, rarely $^{1123}/_{2133} = 32$ or $^{1113}/_{2133} = 30$.

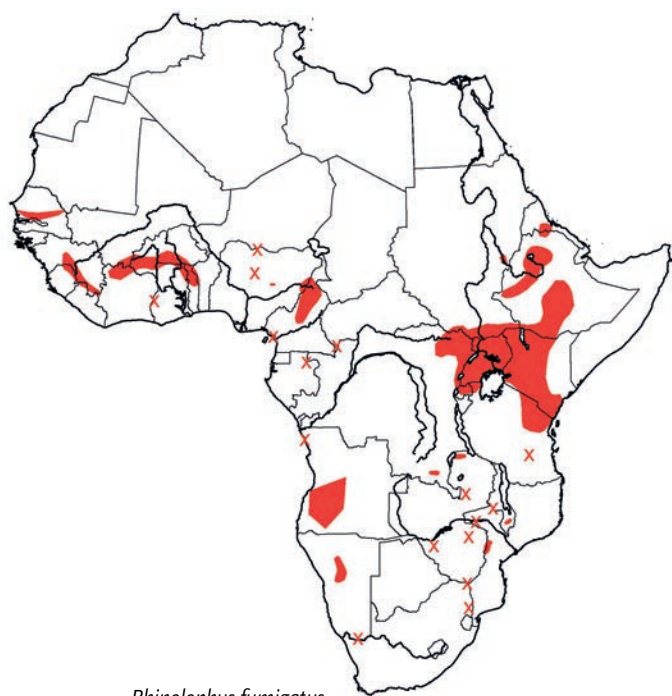
Geographic Variation Six forms are tentatively treated as subspecies (following Koopman 1975, 1994, Csorba *et al.* 2003, Simmons 2005), but their status, geographic ranges and the extent to which variation is clinal are uncertain (Rosevear 1965, Koopman 1994, Csorba *et al.* 2003):

- R. f. diversus*: West Africa: Senegal to Sierra Leone (Koopman 1994). FA: 53–55 mm; CrnC: 23–24 mm (Rosevear 1965). Possibly a distinct species, or a subspecies of *R. aethiops* (see below).
- R. f. foxi*: West Africa: Burkina (and perhaps Côte d'Ivoire) to Central African Republic (Koopman 1994). FA: 50.1 (47–54) mm, $n = 53$; CrnC: 22.5 (21.5–23.8) mm. Possibly a distinct species.
- R. f. fumigatus*: Eritrea and N and C Ethiopia. FA: 49–53 mm; CrnC: 21.5–22.6 mm (Rosevear 1965).
- R. f. abae*: NE DR Congo, W Uganda and extreme SW Sudan (F. P. D. Cotterill unpubl.). FA: 53 (50–54) mm, $n = 10$; CrnC 23 (21.9–23.6) mm, $n = 10$ (Allen 1917a). Very closely related to *exsul* (Koopman 1965) and both *abae* and *exsul* are closer to *fumigatus* than to *aethiops* (Koopman 1966). Possibly *abae* and *exsul* exhibit clinal variation across equatorial Africa from NE DR Congo to the east coast (F. P. D. Cotterill unpubl.).
- R. f. exsul*: eastern Africa from C Sudan, S Ethiopia, E Uganda, Kenya and Tanzania (Koopman 1994), and apparently Malawi as far southwards as Zomba (Happold *et al.* 1987, Ansell & Dowsett 1988). FA: 51.4 (48–55) mm, $n = 21$; CrnC: 22.8 (21.6–23.9) mm, $n = 31$.
- R. f. aethiops*: southern Africa from S Angola to C Mozambique and southwards to Cape Province of South Africa (Meester *et al.* 1986). FA: 55–60 mm, CrnC: 23–25.1 mm (Rosevear 1965). Possibly a distinct species; if distinct, perhaps contains *diversus* as subspecies (J. E. Hill in Grubb *et al.* 1998).

Similar Species Only two other *Rhinolophus* in Africa have the following combination of characters: anterior upper premolar displaced labially or absent; connecting process rounded and lower than the sella; sella hairy; horseshoe usually broader than 10 mm and as broad as the muzzle or almost so (Table 14, p. 304):

- Rhinolophus eloquens*. Body measurements usually larger, especially in areas of sympatry (Koopman 1975) (FA: 53–63 mm). Skull larger (CrnC: 23.8–26.2 mm; $C-M^3$: 9.2 [8.7–9.6] mm).
- R. hildebrandtii*. Larger (FA: 60–67 mm; Tib: 26–31 mm; CrnC: 26.1–28.7 mm). Anterior median nasal swellings longer than they are broad.

Distribution Endemic to Africa. Mainly recorded from the Sudan Savanna, Guinea Savanna, Afromontane–Afroalpine, Somalia–Masai Bushland, Coastal Forest Mosaic and Zambezian Woodland BZs, and from the Rainforest–Savanna Mosaics. Also a few records in the Rainforest BZ and South-West Arid BZ. In the west, there are scattered records from Senegal to Cameroon and N Congo and southwards to Angola and Namibia. In the east, recorded disjunctly from Eritrea, Ethiopia and EC and S Sudan to NE South Africa. Probably more widespread than records indicate; many of the gaps probably reflect insufficient sampling. Not yet recorded from NE Botswana but likely to occur there. Mapped from country checklists (see order Chiroptera), other literature and museum records.

*Rhinolophus fumigatus*

Habitat Savannas, including undifferentiated woodland and *Isoberlinia* woodland in West Africa, *Acacia*–*Commiphora* bushland and thicket in East Africa, and miombo and mopane woodlands in south-central Africa, where suitable day-roosts are available. Absent from true moist forest, and deserts.

Abundance Based on museum specimens, locally common in West Africa. Commonly recorded in Malawi (Happold & Happold 1997); rarer in Zimbabwe.

Adaptations Aspect ratio low; wing-loading low; wing-tip rounded (Malawi; M. Happold unpubl.). Flight variable in speed and highly manoeuvrable. Can take off from ground; probably cannot hover. Turns by banking (minimum radius <25 cm), and by stalling-and-twisting; individuals sustained flight within a 1×1×1 m enclosure for up to five circuits/flight (5 bats, 10 flights each; M. Happold unpubl.). Day roosts include caves, cavities and narrow crevices in piles of boulders, mine-adits, hollow baobab trees *Adansonia* and occasionally houses and tobacco barns (Rosevear 1965, Smithers & Wilson 1979, Smithers 1983). Hangs freely from ceilings; body completely enclosed by wings. Roosts in complete darkness or in dimly lit places. In Malawi, sometimes shares day-roosts with *R. simulator* and *Nycteris thebaica*. In Namibian caves, selects roost-sites where temperature (± 1 S.D.) is 25.6 ± 1.05 (24–27) °C and relative humidity is 69 ± 13 (55–94)%, and enters torpor during the day (Churchill *et al.* 1997). Captive bats in Malawi also were torpid during the day at ambient temperature 21–24 °C (Happold & Happold 1988). Predicted mean maximum urine concentration is comparatively low (3122 mOsmol/kg); captive bats drank several times each night (they landed beside water and drank by lapping and sucking) (Happold & Happold 1988).

Foraging and Food Forages by fly-catching and slow-hawking (Shortridge 1934, Grubb *et al.* 1998), and also predictably by gleaning. One fly-catching individual foraged for moths from a perch

at the end of a branch ca. 3 m above ground; same perch used the following night (Shortridge 1934). Diet includes small to medium-sized beetles, moths and other insects (Aldridge & Rautenbach 1987).

Echolocation Call-shape FM/CF/FM. In Malawi, CF-frequency 55–58 kHz ($n = 8$ ♀♀ and 1 ♂ hand-held, 1 ♀ released in the field, 2 ♀♀ tethered); maximum variation by a hand-held individual was 3 kHz. In the wild, CF-frequencies 55–59 kHz were emitted by 13 bats flying together in a cave, and 53–56 kHz were emitted by three bats flying in the open. The low values in the open suggest that the bats were using Doppler shift compensation in this situation. Call-duration 36–53 ms (nine hand-held bats; 699 calls), 59–67 ms (three bats flying low in the wild), 29–44 ms (many bats flying in a cave) (M. Happold unpubl.). In Kruger N. P. (South Africa), CF-frequency 55 kHz (Aldridge & Rautenbach 1987). CF-frequencies 45–50 kHz were recorded in Uganda by Pye & Roberts (1970), but these overlap the CF-frequencies of *R. hildebrandtii*, suggesting that the Ugandan specimens were misidentified.

Social and Reproductive Behaviour Roosts singly or in small to very large groups. Groups of ca. 10–50 seen in Malawi; rarely more than 10 in Zimbabwe; found singly and in groups of 25–500 in N Namibia (Churchill *et al.* 1997). Group-members hang in close contact with neighbours. Five individuals captured from a group of ca. 12 in Cameroon, were all ♀♀ (Aellen 1952) and some samples taken from groups in Malawi contained only pregnant and/or lactating ♀♀; this suggests that maternity colonies are established.

Reproduction and Population Structure Litter-size: one ($n = 14$). In Malawi and southern Africa, the reproductive chronology is probably restricted seasonal monoestry. At 14–15°S in Malawi, 1 of 1 ♀♀ was pregnant in Sep; 8 of 8 pregnant and in close reproductive synchrony in early Nov; 3 of 3 lactating in mid-Nov; 1 of 3 pregnant and 2 of 3 lactating in Dec; and 3 of 3 neither palpably pregnant, nor lactating, in Apr–May. Juveniles reported Dec–Mar. No data for other months. These data are consistent with restricted seasonal monoestry with births at beginning of wet season (Nov–Dec) (Happold & Happold 1990a, M. Happold unpubl.). In Zimbabwe, pregnant ♀♀ are reported in Sep–Oct (Smithers 1983) and (in NE Zimbabwe) lactation in Nov–Jan; ♀♀ found during cool-dry season were neither visibly pregnant nor lactating (F. P. D. Cotterill unpubl.); these data are also consistent with restricted seasonal monoestry with births in Nov–Dec.

Predators, Parasites and Diseases Predators include Spotted Eagle-owls *Bubo africanus* (Demeter 1982). Ectoparasites include a bug *Adroctenes horvathi* (Hemiptera: Polytectenidae), bat-flies *Penicillidia fulvida*, *P. pachymela*, *Phthiridium scissum*, *P. hoogstraali* (Diptera: Nycteribiidae), *Ascodipteron brevior*, *Brachytarsina africana*, *Raymondia intermedia*, *R. seminuda* (Diptera: Streblidae); two species of ticks (Argasidae, Ixodidae) and eight species of mites (Spinturnicidae, Macronyssidae, Leeuwenhoekidae, Psorergatidae, Chirodiscidae, Sarcopitidae) (Anciaux de Faveaux 1984, Kock *et al.* 1998b).

Conservation IUCN Category: Least Concern.

Measurements

Rhinolophus fumigatus

FA: 50.9 (47–60) mm, n = 119
 WS (a): 327 (313–342) mm, n = 6
 TL: 87.7 (60–113) mm, n = 100
 T: 27.6 (20–39) mm, n = 116
 E: 22.9 (19–28) mm, n = 121
 NL (breadth): 10.3 (9.6–11.5) mm, n = 30
 Tib: 21.4 (19–24) mm, n = 35
 HF: 10.9 (9–15) mm, n = 52
 WT: 14.4 (11.0–24.0) g, n = 60
 CrnC: 22.7 (21.6–24.3) mm, n = 60*

GWS: 11.4 (10.4–12.2) mm, n = 93

C–M³: 8.0 (7.3–8.7) mm, n = 86

Burkina, Cameroon, Côte d'Ivoire, Ghana, Togo, DR Congo, Malawi, Zambia, Zimbabwe (BMNH, HC, HZM, NMZB, ROM, USNM, Allen 1917a, Aellen 1952)

*Throughout geographic range (Csorba *et al.* 2003)

Key References Csorba *et al.* 2003; Rosevear 1965; Smithers 1983.

F. P. D. Cotterill & Meredith Happold

Rhinolophus guineensis GUINEAN HORSESHOE BAT

Fr. Rhinolophe de Guinée; Ger. Guinea-Hufeisennase

Rhinolophus guineensis Eisentraut, 1960. Stuttgarter Beitr. Naturk. (39): 1. Near Tahiré, base of Kelesi Plateau, 500 m, Guinea.

Taxonomy Originally *Rhinolophus landeri guineensis*. Species-group: *landeri*. Synonyms: none. Raised to species rank by Böhme & Hutterer (1978) based on sympatric occurrence in Sierra Leone (Rosevear 1965). Chromosome number: not known.

Description Small microbat with noseleaf (posterior component subtriangular with erect tip); medium-small for an African rhinolophid; anterior upper premolar within tooththrow; connecting process subtriangular; lancet hastate; sella parallel-sided; first phalanx of fourth finger relatively short; tibia 21–22 mm. Sexes similar in body measurements but ♂♂, on average, larger craniodentally. Pelage soft, fluffy; mid-dorsal hairs 7–8 mm. Dorsal pelage brown to greyish-brown, sepia brown, orange-brown or pale reddish-brown; hairs with tip darker than base. Ventral pelage slightly paler. No orange-phase known. Axillary tufts in ♂♂, when present, usually white although in one case reddish-brown (Eisentraut 1960, Böhme & Hutterer 1978). Ears comparatively and relatively short (17–22 mm, 41.3 [38–47]% of FA), each with 11–12 internal folds. Noseleaf with lancet hastate. Connecting process subtriangular in profile; tip pointed (Figure 59g). Sella naked and parallel-sided. Horseshoe narrow (8.3–9.3 mm); no lateral leaflets; median emargination present. Lower lip with one groove. Wings and interfemoral membrane dark grey. First phalanx of fourth finger relatively short (19.6 [17–21]% of fourth metacarpal, n = 11). Tibia 45.4 (42–48)% of FA, n = 12.

Skull of medium build, zygomatic arches moderately broad; zygomatic width slightly greater than mastoid width. Nasal swellings relatively narrow but high. Frontal depression shallow. Palatal bridge 26–31% of C–M³ (Csorba *et al.* 2003). Anterior upper premolar comparatively large, within tooththrow or only slightly displaced labially; canine and posterior premolar well separated. Middle lower premolar very small to vestigial, fully displaced labially; anterior and posterior lower premolars in contact. Anterior lower premolar smaller than posterior lower premolar and only ca. half of its height, or less (cf. *R. l. landeri*). Dental formula $^{1123}/_{2133} = 32$.

Geographic Variation None.

Similar Species Only two other *Rhinolophus* in sub-Saharan Africa have the following combination of characters: anterior upper premolar within tooththrow; connecting process triangular and pointed; first phalanx of fourth finger relatively short; axillary tufts in ♂♂ usually present (Table 14, p. 304):

Rhinolophus landeri. Usually smaller, especially in West Africa where FA: 39–45 mm, Tib: 17–21 mm, CrnC: 16.9–18.9 mm, C–M³: 6.3–7.0 mm. Anterior lower premolar larger, more than half and usually two-thirds of the height of the posterior premolar. Axillary tufts in ♂♂ usually reddish or reddish-brown. Horseshoe narrower (6.0–8.0 mm).

R. alcyone. Body measurements usually larger (FA: 48–56 mm, Tib: 21–27 mm). Skull larger (CrnC: 21.0–23.3 mm, C–M³: 7.9–9.2 mm). Sagittal crest more developed. Axillary tufts in ♂♂ usually orange-red or brown.

Distribution Endemic to Africa. Recorded mainly from the Afromontane–Afroalpine BZ, Rainforest BZ and Northern Rainforest–Savanna Mosaic (and very marginally from the Sudan Savanna BZ). Known from only 15 localities within an area of ca. 180,000 km². The distribution follows the highlands from the Man region in Côte d'Ivoire (Déoulé waterfall, FMNH; published by Csorba *et al.* 2003, as *R. landeri*) through Mt Nimba to Liberia, Sierra Leone and the Fouta Djallon in Guinea (Eisentraut & Knorr 1957, Eisentraut 1960, Brosset 1984, Koopman 1989, Koopman *et al.* 1995, J. Fahr unpubl.). There are also two fairly isolated records in S Senegal (Böhme & Hutterer 1978). Several records from Guinea (Darsalam, Nyembaro, Tahiré) and Sierra Leone (Makeni) referred to *R. landeri guineensis* by Rosevear (1965) are listed erroneously by Csorba *et al.* (2003) under *R. landeri*.

Habitat Sub-montane to montane forests in highlands of Guinea, Liberia and Côte d'Ivoire, and lowland rainforest and forest–savanna mosaic in Senegal and Guinea. On Mt Nimba (Liberia, Guinea), found in montane grasslands below 1400 m (Brosset 1984) and, at Makeni (Sierra Leone), recorded from 'degraded landscape with small relict patches of forest' (Rosevear

*Rhinolophus guineensis*

1965). Local presence and abundance probably determined by availability of suitable day-roosts.

Abundance Usually captured in small numbers in its day-roosts or with mist-nets. Apparently comparatively rare, although 38 individuals were collected during Mar 1990 near Ziggida in the Wonegizi Mts, Liberia (AMNH).

Remarks Day-roosts most often reported are caves and artificial substitutes such as mines (Eisentraut & Knorr 1957, Brosset 1984). Two individuals were found in the hollow trunk of a tree (Böhme & Hutterer 1978). Roosts are regularly shared with other bats including *Lissonycteris angolensis smithii*, *Nycteris macrotis*, *N. gambiensis*, *Rhinolophus simulator alticolus*, *R. denti knorri*, *R. hillorum*, *R. fumigatus*

diversus, *R. maclaudi*, *Hipposideros jonesi* and *H. ruber*. During the day at ca. 1400 m, *R. guineensis* and *R. hillorum* were torpid in their roosts while *R. simulator alticolus* was active (Brosset 1984). Echolocation call-shape FM/CF/FM; CF-frequency 85 kHz (significantly lower than in *R. landeri*; Fahr & Ebigo 2003). Reproduction: no conclusive information.

Conservation IUCN Category: Vulnerable.

Only 15 localities known; distribution small and patchy. Population size probably small; population trend not known but decline inferred because of loss and degradation of habitat. Dependent on caves; colonies small; hence potentially also threatened by exploitation as bushmeat. Ongoing and planned large-scale mining poses special threat in several areas (Fahr & Ebigo 2003).

Measurements

Rhinolophus guineensis

FA: 46.3 (44–50) mm, n = 14

WS: n. d.

TL: 77.8 (72–87) mm, n = 12

T: 25.8 (23–30) mm, n = 11

E: 19.1 (17–22) mm, n = 13

NL (breadth): 8.6 (8.3–9.3) mm, n = 8

Tib: 21.1 (21–22) mm, n = 12

HF: 9.8 (8–10) mm, n = 10

WT: 9.1 (8.0–11.0) g, n = 9

CrnC: 20.0 (19.2–20.6) mm, n = 10

GWS: 10.1 (9.5–10.6) mm, n = 10

C–M³: 7.5 (6.9–7.9) mm, n = 13

Senegal, Guinea, Sierra Leone, Côte d'Ivoire (BMNH, FMNH, MNHN, SMNS [incl. holotype], ZFMK, J. Fahr unpubl.)

Key References Böhme & Hutterer 1978; Csorba *et al.* 2003; Brosset 1984; Eisentraut 1960; Eisentraut & Knorr 1957.

Jakob Fahr

Rhinolophus hildebrandtii HILDEBRANDT'S HORSESHOE BAT

Fr. Rhinolophe d'Hildebrandt; Ger. Hildebrandts Hufeisennase

Rhinolophus hildebrandtii Peters, 1878. Monatsber. K. Preuss. Akad. Wiss. Berlin 1878: 195. Ndi, Taita Hills, Kenya.

Taxonomy Species-group: *fumigatus*. Synonyms: none. The identities of the large horseshoe bats that are currently called *R. hildebrandtii* in Zambia, Malawi and Zimbabwe are under review. In Zimbabwe, these bats separate into two groups, which differ in their bacular morphology and echolocation. Possibly the smaller form represents *eloquens* (F. P. D. Cotterill, M. Happold & P. J. Taylor unpubl.). Sometimes spelled *hildebranti* and *hildebrandti*, but *hildebrandtii* is the original and correct spelling. Chromosomes (Zimbabwe, South Africa): 2n = 58; aFN = 62. X = large subtelocentric, Y = small metacentric (Rautenbach 1986).

Description Medium-sized microbat with noseleaf (posterior component subtriangular with erect tip); large for an African

rhinolophid; anterior upper premolar displaced labially or absent; connecting process rounded; lancet subtriangular; sella hairy and parallel-sided; no axillary tufts; FA: 60–67 mm. Not easily distinguished from *R. eloquens*. Sexes similar. Pelage soft, dense, fluffy; mid-dorsal hairs 11–13 mm. Dorsal pelage grey to greyish-brown; hairs grey to greyish-brown, darker at tip. Ventral pelage slightly paler than dorsal. No orange-phase. No axillary tufts on adult ♂♂. Ears comparatively and relatively medium-long (26–36 mm, 48 [44–52]% of FA). Noseleaf with lancet long, subtriangular, sides straight or slightly concave; tip rounded. Connecting process rounded, not higher than sella. Sella liberally covered with longish hairs, sides concave near base, parallel above (Figure 60c), top broad and rounded. Horseshoe broad

(11.0–15.0 mm), covering muzzle; lateral leaflets present; median emargination is a deep notch. Lower lip with one groove. Wings and interfemoral membrane dark greyish-brown. First phalanx of fourth finger relatively long (26.5 [24–29]% of fourth metacarpal, $n = 42$). Tibia 44.2 (42–46)% of FA, $n = 116$. Baculum trumpet-shaped with cylindrical shaft, length >3 mm.

Skull robust and comparatively long (GLS: 27.3 [25.0–29.7] mm); zygomatic arches sturdy; zygomatic width much greater than mastoid width. Nasal swellings relatively high, longer than they are broad. Frontal depression deep; supraorbital ridges pronounced. Sagittal crest well developed anteriorly and to ca. half-way across parietals. Palatal bridge of medium to long relative length (32–38% of $C-M^3$; Csorba *et al.* 2003). Anterior upper premolar very small and fully displaced labially or absent; canine and posterior premolar in contact or nearly so. Middle lower premolar apparently always absent; anterior and posterior lower premolars in contact. Dental formula usually $^{1123}/_{2123} = 30$ or $^{1113}/_{2123} = 28$. Further anatomical information in Pearl (1994).

Geographic Variation None recorded.

Similar Species Only two other *Rhinolophus* in Africa have the following combination of characters: anterior upper premolar displaced labially or absent; connecting process rounded and lower than the sella; sella hairy; horseshoe usually broader than 10 mm and as broad as the muzzle or almost so (Table 14, p. 304):

Rhinolophus fumigatus. Smaller (FA: 47–60 mm; Tib: 19–24; CrnC: 22.7 [21.6–24.3] mm). Anterior median nasal swellings broader than they are long.

R. eloquens. Usually smaller (FA: 58 [53–63] mm, Tib: 22–25 mm, CrnC: 25.4 [24.8–26.2] mm). Baculum shorter (<3.0 mm).

Distribution Endemic to Africa. Known mainly from the Somalia–Masai Bushland, Afromontane–Afroalpine, Coastal Forest Mosaic and Zambezian Woodland BZs and from the Eastern Rainforest–Savanna Mosaics. Recorded from Ethiopia and S Sudan to N South Africa (Hayman & Hill 1971, Koopman 1975, 1993, Smithers & Lobão Tello 1976, Aggundey & Schlitter 1986, Cockle *et al.* 1998, Csorba *et al.* 2003). Not recorded from Angola (Crawford-Cabral 1986), but likely to occur in the E and S of that country. A specimen from Kagora in Nigeria, identified as *R. macclaudi* by M. Gartshore (in Happold 1987), has been re-identified as *R. hildebrandtii* by J. Eger (ROM), but this record is very isolated and deserves further investigation. The records from Uganda are considered to represent *R. eloquens* by Thorn & Kerbis Peterhans (2009).

Habitat Recorded from both semi-arid and mesic woodland savannas (including mopane and miombo woodlands) and riverine forests. Also recorded in montane areas in NE Zambia (Ansell & Ansell 1973). Absent from true moist forest, and deserts (Smithers 1983).

Abundance Common in Zimbabwe (F. P. D. Cotterill unpubl.); and locally common in Kenya, as judged from representation in collections (Aggundey & Schlitter 1986). Uncommonly recorded in Malawi (Happold & Happold 1997).



Rhinolophus hildebrandtii

Adaptations Aspect ratio low; wing-loading low; wing-tip rounded. Flight very variable in speed, highly manoeuvrable, looks weak and fluttering. Can take off from ground, and predictably can almost hover. Turns by banking (minimum radius <25 cm), and by stalling-and-twisting and, despite its size, individuals sustained flight within a $1 \times 1 \times 1$ m enclosure for up to four circuits/flight (4 bats, 10 flights each; M. Happold unpubl.). Climbs very short distances by moving hindfeet in alternation (wings not used); uses wings to 'row' itself, very awkwardly, for short distances over horizontal surfaces. Roosts by day in caves, fissures and cavities between and under rocks and boulders, disused mine-adits, abandoned aardvark-burrows and warthog-holes, large hollow trees, in shade under eaves of thatched houses, and in roofs of buildings. Roosts vary from completely dark to merely shaded. Hangs freely from ceilings or hangs in contact with walls. Becomes torpid during day at ambient temperature $21\text{--}24^\circ\text{C}$ (Happold & Happold 1988). Roosts during the night in foliage, usually 2–4 m above ground (Fenton & Rautenbach 1986). Predicted mean maximum urine concentration is medium (3610 mOsmol/kg); captive bats drank regularly every day (Happold & Happold 1988).

Foraging and Food Forages by perch-hunting and by slow-hawking under canopies of woodland or riverine trees (either just above open ground or just above understorey vegetation), close to the outsides of canopies, near and inside buildings, and along corridors of vegetation adjacent to creeks; rarely forages over open ground (Fenton & Rautenbach 1986, M. Happold unpubl.). Slow-hawking flights are characterized by zig-zagging with direction-changes ca. every five seconds; monitored flights lasted up to 53 minutes without an interval for perching (Fenton & Rautenbach 1986). Perch-hunting bats use perches 2–2.5 m above ground; eight observed flights from perches were always towards the ground (but it is not stated if the prey was on the ground or flying); increased repetition-rate of echolocation calls emitted prior to leaving the perch indicates prey was detected from the

perch. Radio-tracked individuals left the day-roost and flew directly for 200–1000 m before beginning to forage; periods of foraging were interspersed with periods of resting at night-roosts; most foraging occurs during first hour or so after emergence from day-roost. Attracted to insects flying around lights; quite often enters houses in search of prey (Smithers 1983). Faecal pellets from Zimbabwe and South Africa contained remains of beetles and moths (and very rarely Diptera) (Fenton *et al.* 1977, Fenton & Rautenbach 1986).

Echolocation Call-shape FM/CF/FM. Maximum energy in second harmonic; four harmonics usually present. In Malawi, CF-frequency 35–38 kHz (1 ♀ 7 ♂ hand-held, 1 ♂ released); maximum variation by a hand-held individual was 1 kHz; call-duration variable, up to 84 ms (M. Happold unpubl.). In Zimbabwe, CF-frequency 37 kHz (one bat, flying in open; Fenton & Bell 1981); 37.6 kHz (F. P. D. Cotterill & P. J. Taylor unpubl.). In South Africa, CF-frequency ca. 40 kHz (Aldridge & Rautenbach 1987). Bats, identified as *R. hildebrandtii*, which emitted CF-frequencies of 47–48 kHz (Malawi; M. Happold unpubl.) and 46 kHz (Zimbabwe; Fenton & Bell 1981) probably represent *R. eloquens* or a closely related form (see profile *R. eloquens*). The acoustics of the vocal tract, and the role of the tracheal chambers and nasal cavities, of bats from Zimbabwe identified as *R. hildebrandtii* (but with CF-frequency ca. 48 kHz therefore probably not this species), were investigated by Suthers *et al.* (1988) and Hartley & Suthers (1988) (see Family Rhinolophidae).

Social and Reproductive Behaviour Roosts singly, in small groups, or in clusters of up to ca. 50 individuals in caves containing several hundreds (Smithers 1983). Individuals in clusters hang apart, usually evenly separated from neighbours. All but three members of a group of 28 adults roosted in the same hollow tree for at least 21 consecutive days (Fenton & Rautenbach 1986). Establishes maternity roosts where each mother hangs separately from other mothers, with her neonate fastened to the pubic nipples. The foraging areas of radio-tracked bats from one day-roost overlapped with those of individuals from other roosts; no agonistic or territorial interactions were observed (Fenton & Rautenbach 1986).

Reproduction and Population Structure Litter-size (Zimbabwe): one (n = 5). Each of 12 ♀♀ had one neonate, which is further evidence that the litter-size is normally one. At 18° 18' S in C Zimbabwe,

the reproductive chronology is restricted seasonal monoestry, with conception and implantation inferred to occur in Jul, births at end of Oct, and lactation for more than three months (Cotterill 1998). Foetuses at limb-bud stage seen in late Aug. Juveniles volant when ca. ten weeks old. At 12° 47' S (Luangwa Valley, Zambia), two juveniles (incisors just erupting) were recorded in mid-Jun (no data for other months; Ansell 1967): this is unexpected in view of the Zimbabwe chronology, but possibly the date of this observation is incorrect.

Predators, Parasites and Diseases Bats leaving one day-roost in a hollow tree in South Africa were pursued by two Barn Owls *Tyto alba* (Fenton & Rautenbach 1986). Ectoparasites recorded by Anciaux de Faveaux (1984) include a bed-bug *Afrocinex leleupi* (Cimicidae), another bug *Adroctenes horvathi* (Polychtenidae); 15 species of bat-flies (Nycteribiidae, Streblidae); five species of mites (Ixodidae, Spinturnicidae, Trombiculidae, Chirodiscidae), but the hosts of at least some of these are *R. eloquens*.

Conservation IUCN Category: Least Concern.

Measurements

Rhinolophus hildebrandtii

FA: 63.9 (60–67) mm, n = 74

WS (a): 406 (402–415) mm, n = 4

TL: 116.7 (101–143) mm, n = 74

T: 39.5 (28–49) mm, n = 70

E: 33.2 (26–36) mm, n = 74

NL (breadth): 13.0 (11.0–15.0) mm, n = 28

Tib: 27.9 (26–31) mm, n = 16

HF: 14.8 (12–16) mm, n = 39

WT: 27.8 (21.5–34.9) g, n = 67

CrnC: 27.4 (26.1–28.7) mm, n = 44*

GWS: 13.5 (12.3–14.5) mm, n = 174

C–M³: 9.5 (8.7–12.1) mm, n = 188

Malawi and Zimbabwe (HC, NMZB, ROM, ZFMK, Happold *et al.* 1987)

*Throughout geographic range (Csorba *et al.* 2003)

Key References Cotterill 1998; Csorba *et al.* 2003; Fenton & Rautenbach 1986; Pearl 1994.

F. P. D. Cotterill & Meredith Happold

Rhinolophus hilli HILL'S HORSESHOE BAT

Fr. Rhinolophe de Hill; Ger. Hills Hufeisennase

Rhinolophus hilli Aellen, 1973. Period. Biol. Zagreb 75: 101. Uwinka, 2512 m, Parc National de Nyungwe, Préfecture de Cyangugu, Rwanda.

Taxonomy Species-group: *maclaudi* (Fahr *et al.* 2002). Synonyms: none. Smith & Hood (1980) synonymized *R. hilli* with *R. ruwenzorii* and classified the latter taxon as a subspecies of *R. maclaudi*. Csorba *et al.* (2003) considered *R. hilli* to be a subspecies of *R. ruwenzorii*. Fahr *et al.* (2002) showed that both *R. ruwenzorii* and *R. hilli* are clearly differentiated from *R. maclaudi* and re-instated their status as distinct species. Chromosome number: not known.

Description Small microbat with noseleaf (posterior component subtriangular with erect tip); large for an African rhinolophid (FA: ca. 54 mm); anterior upper premolar displaced labially; lancet subtriangular; connecting process greatly reduced, very low and concave; sella upright with concave sides and broadened tip and greatly enlarged basal lobes; horseshoe with lateral leaflets and deep median emargination; no axillary tufts.

Sexual dimorphism: no information. Pelage soft, woolly; mid-dorsal hairs 13–15 mm. Dorsal and ventral pelage dark brown. Orange-phase: not yet reported. No axillary tufts on adult ♂♂. Ears comparatively and relatively of medium length (29 mm, 53% of FA), pointed, each with nine internal folds; antitragus very large. Noseleaf with lancet subtriangular, height of lancet conspicuously exceeding height of sella (cf. *R. ruwenzorii*). Connecting process greatly reduced, low and concave, leaving a deep emargination between sella and lancet (Figure 59n). Sella naked, upright and more or less parallel to lancet (i.e. not inclined forward), sides concave, top distinctly broadened and rounded (spoon-shaped); narial lobes at base of sella greatly enlarged, forming an almost circular cup. Nostrils bordered by semi-circular, conspicuously raised rims that are parallel to the inner cup (therefore not reaching anterior margin of horseshoe). Horseshoe of medium breadth (12.0 mm); covering muzzle; lateral leaflets present; median emargination conspicuous. Lower lip with a well-defined median groove and two indistinct lateral grooves. Wings and interfemoral membranes dark grey. First phalanx of fourth finger relatively long (27% of fourth metacarpal). Tibia ca. 24 mm, 47% of FA.

Skull large and slender; zygomatic arches broad but comparatively weak, zygomatic width slightly less than mastoid width. Rostrum robust; rostral emargination squarish; premaxillae narrow. Nasal swellings high-domed; chambers (viewed dorsally) roughly circular (posterior indentation weak). Frontal depression very deep. Braincase (viewed dorsally) not conspicuously constricted behind mastoid process, but rather evenly rounded; (viewed laterally) the highest point is clearly behind the glenoid process (cf. *R. macclaudi*). Sagittal crest moderate anteriorly, poorly developed posteriorly. Infraorbital bridge very short and stout. Interpterygoid groove very deep. Anterior upper premolar small, clearly displaced labially; canine and posterior premolar almost in contact. Middle lower premolar small, slightly to clearly displaced labially; distance between anterior and posterior lower premolars variable. Lower molars comparatively large (cf. other species in *R. macclaudi* group). Dental formula $\frac{1123}{2133} = 32$. For detailed comparison of *R. hilli* with other species in *R. macclaudi* group, see Fahr *et al.* (2002).

Geographic Variation No information but, based on small distribution, probably negligible.

Similar Species Three other *Rhinolophus* in Africa have a greatly reduced, low and concave connecting process (Table 14, p. 304):

Rhinolophus ruwenzorii. Larger (FA: 55–62 mm, CrnC: 23.7–25.6 mm, GWS: 11.2–12.3 mm, C–M³: 8.2–8.9 mm). Height of lancet only moderately exceeding height of sella. Skull with braincase constricted behind mastoid process; infraorbital bridge longer and more slender; lower molars comparatively small. Nearly sympatric.

R. macclaudi. Larger (FA: 64–69 mm, CrnC: 29.0–30.1 mm, C–M³: 10.5–10.8 mm). Ears with 10–12 internal folds. Sella inclined forward. Horseshoe broader (15–16 mm), no lateral leaflets, median emargination small or absent, rims around nostrils more or less parallel. Skull with highest point at height of glenoid process; zygomatic width usually > mastoid width; infraorbital bridge much longer and slender. West Africa.

R. ziama. Larger (FA: 60 mm, CrnC: 26.1, 26.2 mm, C–M³: 8.9, 9.0 mm). Ears with 11, 12 internal folds. Sella inclined forward, sides parallel. Horseshoe narrower (11.5, 11.6 mm), no lateral leaflets, median emargination inconspicuous or absent, nostrils bordered laterally by more or less straight and parallel rims. Skull with zygomatic width ≥ mastoid width; infraorbital bridge longer and more slender. West Africa.

Distribution Endemic to Africa and only known from an extremely small area in the Afromontane–Afroalpine BZ flanking the Albertine Rift Valley. Known from only two localities in SW Rwanda (Uwinka and Ruta Bansugera, ca. 8 km apart, in Nyungwe N. P.). The distribution of the *Rhinolophus macclaudi* species-group is very disjunct and resembles that of the otter-shrews of the genus *Micropotamogale* (see species profile for *R. macclaudi*).

Habitat Montane forest, between 1750 and 2512 m.

Abundance Uncertain; apparently very localized and rare.

Remarks The holotype was mist-netted (Aellen 1973) and the day-roosts are not known. The echolocation call-shape is probably FM/CF/FM (as in other species of *Rhinolophus*) and, based on the comparatively large size of this bat, the CF-frequency is likely to be rather low for a *Rhinolophus*. The holotype is a ♀ that was pregnant with a 15 mm embryo in late Aug (Aellen 1973).

Conservation IUCN Category: Critically Endangered.

Distribution extremely small: known from only two specimens collected in 1964 and 1981 within Nyungwe N. P. Surrounding region seriously affected by civil wars; rural population density amongst highest in Africa. Surveys in region of Albertine Rift have not found this species elsewhere. Considered seriously threatened by destruction of its habitat and roosts, and by direct exploitation in its roosts.



Rhinolophus hilli

Measurements*Rhinolophus hilli*

FA: 54, 54 mm

WS: n. d.

TL: 92, – mm

T: 30, – mm

E: 29, – mm

NL (breadth): 12.0, – mm

Tib: 24, – mm

HF: 12, – mm

WT: –, 16.5 g

CrnC: 23.0, – mm

GWS (MW): 10.9, 11.2 mm

C–M³: 8.1, 7.9 mm

Rwanda (ZMUZ 126639 [holotype] and RMCA 82006-M-1 respectively; both ♀ ♀)

Key References Aellen 1973; Fahr *et al.* 2002; Smith & Hood 1980.**Jakob Fahr*****Rhinolophus hillorum* UPLAND HORSESHOE BAT**

Fr. Rhinolophe des collines; Ger. Hochland-Hufeisennase

Rhinolophus hillorum Koopman, 1989. Amer. Mus. Novit. 2946: 4. John Hegbe Farm, near Zozoma, 2 miles SW Voinjama, Lofa County, NW Liberia.**Taxonomy** Originally *Rhinolophus clivosus hillorum*. Species-group: *ferrumequinum*. Proposed as a subspecies of *Rhinolophus clivosus* by Hill (1968, 1982a) and described as such by Koopman (1989) but elevated to species rank by Cotterill (2002a). Synonyms: none. Chromosome number: not known.**Description** Small microbat with noseleaf (posterior component subtriangular with erect tip); medium-sized for an African rhinolophid; anterior upper premolar absent; connecting process high but rounded; lancet short, mostly narrow and almost parallel-sided; sella parallel-sided; no axillary tufts. Sexes similar. Pelage soft, fluffy; mid-dorsal hairs ca. 10 mm. Dorsal pelage medium brown to greyish-brown. Ventral pelage paler. Orange-phase not yet reported. No axillary tufts on adult ♂♂. Ears comparatively and relatively short (21–24 mm, 40.7 [37–44]% of FA); each with 11–12 internal folds. Noseleaf with lancet short and, except at base, very narrow and almost parallel-sided; tip hairy and slightly rounded (Figure 61f). Connecting process narrow and high but rounded, ellipsoid in profile and liberally furnished with hairs, much higher than sella. Sella naked, almost parallel-sided, diverging slightly towards the rounded top. Horseshoe narrow (8.4–9.1 mm); not completely covering muzzle; no lateral leaflets; median emargination distinct. Lower lip with one groove. Wings and interfemoral membrane blackish-brown. First phalanx of fourth finger relatively long (28.2 [27–31]% of fourth metacarpal, n = 10). Tibia 42.8 (41–44)% of FA, n = 10. Baculum trumpet-shaped, shaft dorsoventrally flattened, length 2.9–3.1 mm, n = 2 (Cotterill 2002a).Skull very robust; zygomatic arches thick and broad; zygomatic width much greater than mastoid width. Rostrum very broad. Nasal swellings very low, frontal depression very shallow. According to Csorba *et al.* (2003), supraorbital crests ill-defined. Sagittal crest anteriorly well developed, posteriorly moderately developed. Dentition robust. Anterior upper premolar absent; canine and posterior premolar in contact. Middle lower premolar absent; anterior and posterior lower premolars in contact. Anterior lower premolar half to two-thirds of the height, and half the crown area, of the posterior premolar. Dental formula $^{1113}/_{2123} = 28$.**Geographic Variation** Quite uniform throughout geographic range but data are limited. A specimen from Lotti Forest, Sudan, which perhaps represents *R. hillorum* (see Distribution), is somewhat smaller than other specimens (FA: 53 mm, CrnC: 23.0 mm, GWS: 12.4 mm, C–M³: 8.9 mm).**Similar Species** Only two other *Rhinolophus* occurring south of the Sahara and north of the Equator have the following combination of characters: anterior upper premolar fully displaced labially or absent; connecting process rounded; sella naked (or with sparse short hairs only) (Table 14, p. 304):*Rhinolophus clivosus*. Connecting process lower and broader in profile. Skull smaller and less robust (CrnC: 18.1–22.8 mm); dentition weaker, C–M³: 6.7–8.9 mm. Anterior upper premolar usually present. Not known in West Africa.*R. deckenii*. Horseshoe broader (9.1–11.5 mm). Skull with nasal swellings moderately high. Frontal depression moderately deep; supraorbital ridges prominent. Anterior upper premolar present or absent; canine and posterior premolar usually separated by narrow gap. East Africa.**Distribution** Endemic to Africa. Known only from three small areas within the Rainforest BZ (Western and West Central Regions) and Afromontane–Afroalpine BZ, and perhaps from one locality in the Eastern Rainforest–Savanna Mosaic. Recorded from 12 localities in Guinea, Liberia, Nigeria, Cameroon and possibly Sudan. Records from Mt Nimba, Guinea (MNHN, published as *R. fumigatus* by Brosset 1984) and from R. Peblei, Liberia (IRS, tentatively identified as *R. alcyone* by Verschuren 1976) represent *R. hillorum* (Fahr *et al.* 2006). Specimens from Tokadeh, Mt Nimba (BMNH) were erroneously listed by Csorba *et al.* (2003) from both Guinea and Liberia; Tokadeh is on the Liberian side of Mt Nimba. A record from Sapoba F. R., Nigeria (M. E. Gartshore in Fedden & Macleod 1986, Cotterill 2002a), is unusual because the locality is situated in lowland rainforest and therefore this specimen should be re-examined. A specimen from Lotti Forest in the Imatong Mts, Sudan (FMNH 67500, published as *R. clivosus keniensis* by Koopman

1975) has characters that indicate it might be referable to *R. hillorum* but the specimen needs re-examination.

Habitat Found in montane forests in the highlands of SE Guinea–NW Liberia and the Cameroon Highlands, and in lowland rainforests and coastal forests in the immediate vicinity of hilly or mountainous landscapes. Found up to 1400 m on Mt Nimba, up to 1950 m on Mt Kupé, Cameroon, and at 1800 m at L. Manenguba, Cameroon. The vegetation has been described as montane grassland (Brosset 1984), montane forest (Fedden & Macleod 1986), dense rainforest (Verschuren 1976), secondary forest with surrounding primary forest (Wolton *et al.* 1982) and gallery forest amidst savanna at the foot of a mountain. The specimen from Lotti Forest, Sudan, was taken in East African Montane Forest at an altitude of ca. 1500 m.

Abundance No detailed information but apparently very localized and rare.

Adaptations Has been recorded roosting by day in caves and artificial equivalents such as mines and bridges (Verschuren 1976, Brosset 1984, Fahr *et al.* 2006). Has been found sharing roosts with *Lissonycteris angolensis smithii*, *Rhinolophus simulator alticolus* and *R. guineensis* (Brosset 1984, as *R. fumigatus*). During the day at ca. 1400 m, *R. hillorum* and *R. guineensis* were torpid in their roosts while *R. simulator alticolus* was active (Brosset 1984).

Foraging and Food No information. Based on body size, probably forages, at least some of the time, by perch-hunting. The powerful skull and teeth suggest that this bat can feed on relatively large and hard-shelled insects.

Echolocation No information.

Social and Reproductive Behaviour There are three reports of these bats roosting in small groups. In Diécké Forest, Guinea, two colonies roosted under small concrete bridges; one colony comprised four ♂♂ and one ♀, and the other comprised one ♂ and three ♀♀ (Fahr *et al.* 2006). One specimen in Liberia was taken from a colony of 10 individuals (sexes not recorded) (Verschuren 1976).

Reproduction and Population Structure Litter-size: one ($n = 1$). Reproductive chronology not known. A ♀ from 07° 29' N (R. Peblei, Liberia) was pregnant in late Jan (Verschuren 1976).

Predators, Parasites and Diseases Ectoparasites include bat-flies *Brachytarsina africana* (Diptera: Streblidae) and a species of the *Raymondia intermedia*-group (Diptera: Streblidae) (Wolton *et al.* 1982).

Conservation IUCN Category: Near Threatened.

Close to qualifying for Vulnerable. Distribution small and disjunct



Rhinolophus hillorum

(five locations). Population size low; trend inferred to be declining as result of deforestation of montane forest within area of occupancy. Small colonies roosting in caves are potentially threatened by exploitation for bushmeat. Populations in the highlands of SE Guinea–NE Liberia are particularly at risk from on-going and planned large-scale mining (Fahr & Ebigo 2003).

Measurements

Rhinolophus hillorum

FA: 54.5 (52–57) mm, $n = 17$

WS: n. d.

TL: 101.5 (94–112) mm, $n = 9$

T: 36.4 (30–41) mm, $n = 9$

E: 22.4 (21–24) mm, $n = 7$

NL (breadth): 8.8 (8.4–9.1) mm, $n = 7$

Tib: 23.6 (22–25) mm, $n = 10$

HF: 13.2 (12–14) mm, $n = 6$

WT: 20.2 (16.5–25.0) g, $n = 9$

CrnC: 23.8 (23.3–24.4) mm, $n = 7$

GWS: 13.0 (12.3–13.5) mm, $n = 9$

C–M³: 9.2 (8.9–9.5) mm, $n = 13$

Guinea, Liberia, Cameroon (AMNH incl. holotype, BMNH, FC, IRSN, MNHN, SMNS)

Key References Cotterill 2002a; Hill 1968, 1982a; Koopman 1989; Koopman *et al.* 1995.

Jakob Fahr

Rhinolophus hipposideros LESSER HORSESHOE BAT

Fr. Petit rhinolophe; Ger. Kleine Hufeisennase

Rhinolophus hipposideros (Bechstein, 1800). In: Pennant, Allgemeine Uebers. Vierfüß. Thiere 2: 629. France.

Taxonomy Originally *Noctilio hipposideros*. Species-group: *hipposideros*. Synonyms in Africa: *escalerae*, *minimus* (extraliminally 21 others listed by Simmons [2005]). Subspecies: controversial (see Geographic Variation). Chromosome number (Europe and Asia): $2n = 54, 56, 58, 62$ (Zima *et al.* 1992, Horáček & Zima 1996, Benda & Horáček 1998). This is the only rhinolophid in which chromosomal polymorphism has been reported. However, the older 54 karyotype should be re-examined, and the 62 karyotype probably represents another species (Horáček *et al.* 2000). There are no data from Africa. In specimens from Europe and Asia, 4–10 metacentric and 44–52 acrocentric chromosomes are reported, X is metacentric or acrocentric, Y acrocentric or dot-like (Zima *et al.* 1992, Horáček & Zima 1996, Benda & Horáček 1998).

Description Very small microbat with noseleaf (posterior component subtriangular with erect tip); smaller than any other rhinolophid in Africa (FA: 35–40 mm in Africa); anterior upper premolar within toothrow; connecting process very low and either slightly rounded or flat; lancet long and wedge-shaped; sella wedge-shaped and backward-sloping with the top curving forward; no axillary tufts. Sexes similar. Pelage soft, fluffy; mid-dorsal hairs ca. 10 mm. Dorsal pelage greyish-brown to medium brown (dark grey in juveniles); hairs of adults pale beige with greyish-brown or brown tip. Ventral pelage paler or grey to greyish-white. Apparently no orange-phase. No axillary tufts on adult ♂♂. Ears comparatively short (15–17 mm) but of short–medium relative length (mean E ca. 47% of mean FA). Noseleaf with lancet subtriangular with slightly concave sides, tip bluntly pointed. Connecting process low (not rising above sella), slightly rounded (Figure 59m) or sometimes flat. Sella naked, long, narrow, wedge-shaped; top pointed and curves forward and downward. Horseshoe narrow (6.1–7.1 mm in Africa) but almost covering muzzle; no lateral leaflets; median emargination a distinct notch. Wings and interfemoral membrane medium to dark brown. First phalanx of fourth finger relatively long (26.0 [24–28]% of fourth metacarpal, $n = 31$). Tibia 45.4 (41–49)% of FA, $n = 10$.

Skull very delicate; zygomatic arches extremely slender; zygomatic width slightly greater or almost equal to mastoid width. Nasal swellings of medium relative height. Frontal depression shallow, supraorbital ridges weak. Sagittal crest low and extending part-way across parietals. Palatal bridge (African specimens) relatively short to medium (29–33% of $C-M^3$; G. Csorba pers. comm.). Anterior upper premolar relatively large (reaching one-third height of canine), within toothrow; canine and posterior premolar well separated. Middle lower premolar very small, usually fully displaced labially; anterior and posterior lower premolars in contact or nearly so. Dental formula $^{1123}/_{2133} = 32$.

Geographic Variation Controversial. Six subspecies are currently recognized by Csorba *et al.* (2003) and Simmons (2005), of which two occur in Africa:

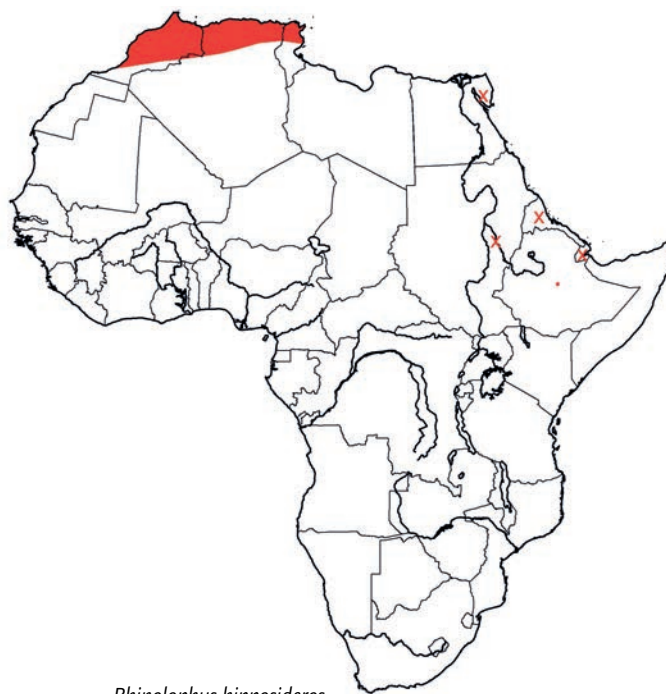
R. h. escalerae: NW Africa. Considered subspecifically distinct on basis of size and also the narrowness of the bar between the infraorbital foramen and the orbit (Gaisler 1983, Kowalski & Rzebiak-Kowalska 1991, Steiner & Gaisler 1994). FA: 35.8 (35–38) mm, $n = 9$.

R. h. minimus. Southern Europe to eastern end of Mediterranean, including several islands, and southwards to Sudan, Ethiopia and SW Arabia. Possibly represents a distinct species (see Zagorodniuk 1999). FA: 37.7 (36–40) mm, $n = 10$.

Extraliminally: *majori* (Corsica), *minutus* (Britain and Ireland), *hipposideros* (continental Europe to eastern end of Black Sea), *midas* (Transcaucasia and Iraq to Kazakhstan and Kashmir). In contrast, only *hipposideros* and *midas* have been recognized by majority of authors in the past (Horáček *et al.* 2000). Aulagnier & Thévenot (1986) included both *minimus* and *escalerae* in the nominate subspecies.

Similar Species No other *Rhinolophus* in Africa is so small, and none has the combination of a connecting process that is very low and either slightly rounded or flat and a sella that is wedge-shaped and backward-sloping with the top curving forward (Table 14, p. 304).

Distribution In Africa, recorded from almost all of the Mediterranean Coastal and Afromontane–Afroalpine BZs in NW Africa (Aellen & Strinati 1969, Aulagnier & Thévenot 1986, Kowalski & Rzebiak-Kowalska 1991), and from the Afromontane–Afroalpine BZ of the Ethiopian Highlands and adjacent Somalia–Masai Bushland BZ in Sudan, Ethiopia, Eritrea and Djibouti (Largen *et al.* 1974, Koopman

*Rhinolophus hipposideros*

1975, Pearch *et al.* 2001). Also one record from the Sahara Arid BZ in Sinai (Egypt) (Qumsiyeh 1985). Not known in Libya. In Morocco, recorded from the northern region south to Anti-Atlas and the pre-Saharan region (29°N); in Algeria from the coast to the southern limit of Saharan Atlas (33°N), and in N Tunisia to Kasserine (35°N) (Aellen & Strinati 1969, Aulagnier & Thévenot 1986, Kowalski & Rzebik-Kowalska 1991). Extraliminally: Ireland to Tajikistan, Kashmir and Arabian Peninsula (see Geographic Variation).

Habitat In NW Africa, this cave-roosting species seems to be rare and its foraging habitats are little known. In Algeria, recorded from sea level to ca. 1500 m; three ♂♂ mist-netted in a bushy forest with a permanent stream (Sebdour, Tlemcen Mts), one ♀ mist-netted over water in a desert environment (Brezina, Saharan Atlas [Gaisler & Kowalski 1986, Kowalski & Rzebik-Kowalska 1991]). One specimen was taken beside a lake in an area of grassland, thorn scrub, volcanic rubble and lava blister caves, at ca. 1000 m, in Awash N. P. (Hill & Morris 1971).

Abundance Common in N Morocco but rare in Algeria and Tunisia, even in coastal areas. Probably rare in Sudan, Ethiopia and Eritrea.

Adaptations Aspect ratio very low; wing-loading very low; wing-tip especially short and rounded (Norberg & Rayner 1987). Flight slow (possibly with some short bursts of speed), fluttering and butterfly-like with intermittent gliding; manoeuvrable. Can hover. Day-roosts in Africa include both natural and man-made underground spaces such as caves; individuals hang from ceilings or walls; when torpid and hibernating, they wrap themselves completely in the wing-membranes and draw close to the substrate by bending the legs. In winter in Algeria, they hibernate in the coolest places, usually close to openings (Kowalski *et al.* 1986); extraliminally, temperatures in hibernacula are 6–9 °C and humidity is high (Schober & Grimmberger 1989).

Foraging and Food No information for African populations except that three foraging ♂♂ were mist-netted in bushy areas and one ♀ above water in a desert environment in Algeria (Gaisler & Kowalski 1986, Kowalski & Rzebik-Kowalska 1991), and one individual was reported flying low over the muddy shore of a lake in Ethiopia (Hill & Morris 1971). In England and Eire, bats were observed foraging by gleaning (they usually picked non-volant prey [including larvae] from stones, rocks and vegetation without landing but sometimes pounced on prey on the ground) and by slow-hawking; not known to forage by fly-catching (Jones & Rayner 1989a). Foraged close to vegetation, either patrolling edges of river banks close to riverine vegetation, or close to walls. Some individuals regularly patrolled an ivy-covered bridge when ivy flowers were attracting moths. Apparently patrols well-defined beats. Foraging is strictly nocturnal; sometimes reported to continue for at least five hours after sunset. In Europe, diet is mainly small Lepidoptera and Diptera (Nematocera), and less often Neuroptera, Trichoptera, Coleoptera and Araneae.

Echolocation No data for African populations. In England and Europe, call-shape usually FM/CF/FM with the terminal FM component greater in bandwidth; some CF and CF/FM calls

are emitted during slow-hawking (Jones & Rayner 1989a). CF-frequency 105–113 kHz; call-duration 20–30 ms; maximum energy in second harmonic (but some in first harmonic); average terminal FM bandwidth 29.1 kHz suggesting *R. hipposideros* relies particularly heavily on FM information (Jones & Rayner 1989a). For hand-held bats, the CF-frequencies of calls emitted by bats more than one year old were higher than those emitted by younger bats, and ♀♀ emit higher frequencies than ♂♂ (Jones *et al.* 1992).

Social and Reproductive Behaviour In North Africa in winter, single individuals, mostly ♂♂, were sporadically seen roosting in caves (Kowalski *et al.* 1986); no other information. Extraliminally (Europe), during winter, hibernates singly or in colonies of up to 500 individuals, which hang apart, 25–50 cm from their neighbours (Macdonald & Barrett 1993). In summer, ♀♀ form maternity colonies of 10–800 individuals; immature ♂♂ sometimes present; ♀♀ hang apart except when heavily pregnant in cool weather, or when huddling with their young. Audible (to humans) vocalizations at roosts include chirping. Mating often takes place in autumn; preceded by chasing; ♂ hangs behind and over ♀ during brief copulation; sometimes copulates in hibernacula.

Reproduction and Population Structure Litter-size: no data for Africa. In Iran, ca. 65% of ♀♀ bear singletons, and 35% bear twins (DeBlase 1980 in Csorba *et al.* 2003); in Europe, litter-size is one. Reproductive chronology in Africa not known. In Europe, it is restricted seasonal monoestry with mating in autumn (Sep–Nov) or in hibernacula during winter; sperm-storage by ♀♀ until Mar–Apr when ovulation and fertilization occur; births in summer (mid-Jun to early Jul); lactation for 4–5 weeks (Gaisler 1966, Macdonald & Barrett 1993). A ♀ with vaginal plug was recorded in Jan at Sig, NW Algeria (Kowalski *et al.* 1986). Extraliminally, ♀♀ reach sexual maturity in first year, but most give birth for first time when two years old. Maximum life-span: 21 years 3 months.

Predators, Parasites and Diseases Preyed on, rarely, by Barn Owls *Tyto alba* (Cabrera 1932 in Aulagnier & Thévenot 1987). Ectoparasites include a bat-fly *Phthiridium biarticulatum* (Diptera: Nycteribiidae) for which *R. hipposideros* is the principal host (Corbet & Harris 1991).

Conservation IUCN Category: Least Concern (assessed from extralimital as well as African data).

Measurements

Rhinolophus hipposideros

FA: 36.8 (35–40) mm, n = 19

WS (d): 192–254 mm*

TL: 63.0 (60–68) mm, n = 10

T: 24.2 (21–26) mm, n = 11

E: 16.1 (15–17) mm, n = 11

NL (breadth): 6.6 (6.1–7.1) mm, n = 10

Tib: 17.2 (15–18) mm, n = 10

HF: 7.0 (6–8) mm, n = 7

WT: 3.8 (3.5–4.0) g, n = 4

CrnC: 14.9 (14.3–15.5) mm, n = 12

GWS: 7.2 (6.8–7.6) mm, n = 11

C–M³: 5.0 (4.8–5.3) mm, n = 13

Morocco, Algeria, Sudan, Ethiopia (BMNH, Gaisler 1983, Kowalski & Rzebik-Kowalska 1991). For NW Africa, n = 9–11; for Sudan and Ethiopia, n = 1–3 (except FA, NL and Tib)

*Europe (Schober & Grimmberger 1989)

Key References Aulagnier & Thévenot 1986; Csorba *et al.* 2003; Horáček *et al.* 2000; Jones & Rayner 1989a; Kowalski & Rzebik-Kowalska 1991.

Jiří Gaisler

Rhinolophus landeri LANDER'S HORSESHOE BAT

Fr. Rhinolophe de Lander; Ger. Landers Hufeisennase

Rhinolophus landeri Martin, 1838. Proc. Zool. Soc. Lond. 1837: 101 [publ. 1838]. Bioko I., Equatorial Guinea.

Taxonomy Species-group: *landeri*. Synonyms: *angolensis*, *axillaris*, *dobsoni*, *lobatus*. Subspecies: three. Chromosome number (South Africa): 2n = 58; aFN = 60. Two pairs biarmed chromosomes and 26 pairs acrocentric chromosomes. X = large submetacentric; Y = no data (Rautenbach 1986).

Description Small microbat with noseleaf (posterior component subtriangular with erect tip); small for an African rhinolophid; anterior upper premolar within toothrow; connecting process triangular; lancet hastate; sella parallel-sided; axillary tufts in adult ♂♂ reddish or reddish-brown; first phalanx of fourth finger relatively short; tibia 17–21 mm. Sexes similar. Pelage dense, soft, fluffy; mid-dorsal hairs 8–9 mm. Dorsal pelage greyish-fawn to brownish-grey; hairs pale greyish-fawn or pale brownish-grey with darker tip. Ventral pelage slightly paler. In orange-phase, dorsal pelage golden-brown, orange-cinnamon to bright rusty-red. Adult ♂♂ with reddish or reddish-brown axillary tufts, which are sometimes sticky with yellow secretion. Ears comparatively and relatively short (13–20 mm, 34–42% of FA). Noseleaf with lancet hastate, tip bluntly pointed. Connecting process subtriangular with tip either sharply or bluntly pointed. Sella naked, narrow with slightly concave sides, top broad and rounded. Horseshoe narrow (6.0–8.0 mm) but covering whole

muzzle; no lateral leaflets; median emargination a deep notch. Lower lip with a well-defined median groove and two very poorly defined lateral grooves. Wings and interfemoral membrane dark greyish-brown to blackish-brown (grey-phase) or brown (orange-phase). First phalanx of fourth finger relatively short (21.0 [19–23]% of fourth metacarpal, n = 52). Tibia 42.4 (38–45)% of FA, n = 18.

Skull of medium build; zygomatic arches of moderate breadth; zygomatic width slightly greater than mastoid width. Nasal swellings of medium relative height. Frontal depression usually shallow (Csorba *et al.* 2003). Sagittal crest low to moderately developed anteriorly, absent posteriorly. Palatal bridge 28–37% of C–M³ (Csorba *et al.* 2003). Anterior upper premolar small, within toothrow or only slightly displaced labially; canine and posterior premolar well separated. Molar width less than half width of palate between molars (cf. *R. blasii*). Lower canines not distinctly smaller than upper canines (cf. *R. denti*, *R. simulator*, *R. swinnyi*). Middle lower premolar small, slightly to fully displaced labially; anterior and posterior lower premolars separated by narrow gap or in contact. Anterior lower premolar (*R. l. landeri*) only a little smaller than posterior lower premolar; more than half and usually two-thirds of its height (Kock *et al.* 2002) (cf. *R. guineensis*). Dental formula $^{1123}/_{2133} = 32$.

Geographic Variation Three subspecies are recognized by Koopman (1994):

R. l. landeri: Gambia to Cameroon and south to mouth of Congo R.

R. l. lobatus: Sudan and Ethiopia, and south to former Transvaal; also Zanzibar I.

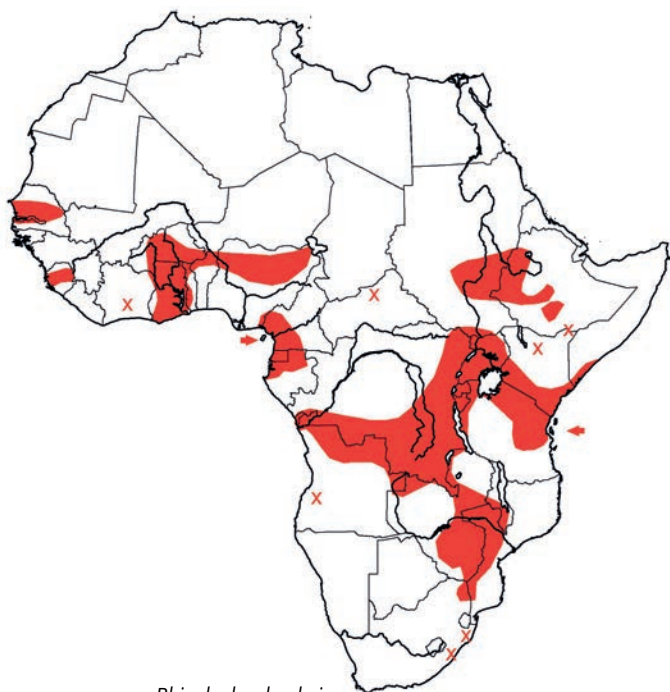
R. l. angolensis: W Angola.

Similar Species Only two other sub-Saharan *Rhinolophus* have the following combination of characters: anterior upper premolar within toothrow; connecting process triangular and pointed; first phalanx of fourth finger relatively short (Table 14, p. 304):

Rhinolophus guineensis. Body measurements usually larger (FA: 44–50 mm [cf. 39–45 in *R. landeri* from West Africa], Tib: 21–22 mm). Skull larger (CrnC: 19.2–20.6 mm [cf. <18.9 in *R. landeri* from West Africa]). Axillary tufts of ♂♂ white. Horseshoe broader (8.3–9.3 mm). Not known to occur east of 07° 30'W.

R. alcyone. Body measurements larger (FA: 48–56 mm, Tib: 21–27 mm). Skull larger (CrnC: 21.0–23.3 mm).

Distribution Endemic to Africa. Found in most sub-Saharan biotic zones, but apparently absent from large areas in each zone. No records



Rhinolophus landeri

from the arid Horn of Africa, nor from the South-West Arid, Highveld and South-West Cape BZs. Recorded (disjunctly) from Gambia and Senegal to Ethiopia, and south to the former Transvaal and KwaZulu-Natal in South Africa. Also Bioko I. A record from Namibia (Slater 1901) represents *R. darlingi*. Mapped from country checklists (see order Chiroptera), other literature and museum records. Subsequently recorded from Liberia (Monadjem & Fahr 2007): not mapped.

Habitat In West Africa, recorded mainly in lowland rainforest and degraded forest (Rosevear 1965). Also recorded in *Isoberlinia* woodland and occasionally in undifferentiated woodland, often near rivers and riverine woodland. Recorded in montane vegetation at 1400 m on Mt Cameroon, Cameroon, and in primary forest at 1000 m on Mt Bintamane, Sierra Leone (Rosevear 1965). Recorded from 515 to 1800 m in Ethiopia (Largen *et al.* 1974), and from sea level to 1981 m on Mt Elgon, in Kenya (Aggundey & Schlitter 1984). In Malawi and southern Africa, recorded mainly in woodland savannas, often near riverine woodland and well-watered areas (R. C. Wood in Kershaw 1922, Smithers 1983). In Zimbabwe, predominantly recorded below 1200 m and apparently absent from miombo and *Baikiaea*-dominated areas (Hutton 1986). Not recorded from arid zones. The presence of suitable day-roosts is possibly more important than vegetation (Smithers 1983).

Abundance No information.

Adaptations Aspect ratio low; wing-loading very low (Aldridge & Rautenbach 1987). Can fly slowly (minimum 3.5 m/s) with bursts of speed. Has great manoeuvrability; can take off from the ground and can hover briefly. By day, hangs freely in caves, caverns in rocky outcrops and piles of boulders, mine-adits, enclosed roofs, wells and other holes in ground, hollow baobabs *Adansonia*, and hangs from thatch inside thatched buildings. Both active and torpid individuals were found in a cave in Cameroon (Eisentraut 1940). In Nigeria, Menzies (1973) observed that young and newly moulted bats were in grey-phase, but became golden in colour later, possibly as result of high concentrations of ammonia (released from guano) in the cave where they roosted.

Foraging and Food Slow-hawking within 2 m of the ground has been observed in rainforest, well after daybreak (T. S. Jones in Grubb *et al.* 1998) and in savanna (O'Shea & Vaughan 1980). There are no records of fly-catching and gleaning, but both are predicted to occur (based on wing morphology). In Zimbabwe, the remains of ca. 66 insects found under a roost included 92% noctuid moths, one butterfly and several Orthoptera (Fenton 1975). In the Sudan, the diet is mainly small beetles (Kock 1969a).

Echolocation Call-shape FM/CF/FM. CF-frequency appears to vary: 101 kHz in Côte d'Ivoire (Fenton & Fullard 1979); 115–122 kHz in Nigeria (Pye & Roberts 1970); 55 kHz (presumably first harmonic) in Kenya (O'Shea & Vaughan 1980); 110 kHz in South Africa (Aldridge & Rautenbach 1987). According to Novick (1958b), 73–84 kHz in DR Congo, but this seems too low for the second harmonic, and too high for the first harmonic, for this species.

Social and Reproductive Behaviour Roosts singly or in groups. Group-size in southern Africa less than 12 (Taylor 2000);

20–50 in DR Congo; ca. 1000 in one cave in Nigeria (Menzies 1973). Individuals hang apart in clusters. In Nigeria, one cave was usually inhabited by both ♂♂ and ♀♀, but ♂♂ left prior to parturition and did not return until young were weaned (Menzies 1973). Often shares day-roosts with other species including *Lissonycteris angolensis*, *Coleura afra*, *Nycteris arge*, *N. macrotis*, *Rhinolophus fumigatus*, *R. simulator*, *Hipposideros cyclops*, *H. abae*, *H. caffer* and *H. jonesi*.

Reproduction and Population Structure Litter-size: one. Reproductive chronology is restricted seasonal monoestry, with delayed implantation in at least one locality. At 10° 20' N (Shagunu, Nigeria), copulation occurs in early dry season (Nov), ovulation in late Nov, implantation (after approximately two months' delayed implantation) in late dry season (early Feb), parturition in early wet season (ca. late Apr), and lactation during wet season (Apr–Jun) (Menzies 1973). Newborn bats may be carried for a short time by their mothers while foraging; young begin to fly when 4–5 weeks old. There is some evidence that ♂♂ and ♀♀ do not breed until their second year. Young are weaned when two months old (Anciaux de Faveaux 1972). Year-round observations have not been made elsewhere, but births have been recorded during the wettest month, in the short wet season (Nov) at 02° 18' S (Masalani, near Kibwezi, Kenya; records Oct–May only) (O'Shea & Vaughan 1980). For other records (inconclusive) see Brown & Dunlop (1997).

Predators, Parasites and Diseases Ectoparasites include a bug *Adroctenes horvathi* (Hemiptera: Polytentidae); fleas *Lagaropsylla setzeri*, *L. idae* (Siphonaptera: Ischnopsyllidae); ten species of bat-flies (Diptera: Nycteribiidae, Streblidae); ten species of mites (Acari: Spinturnicidae, Macronyssidae, Myobiidae, Leeuwenhoekidae, Chirodiscidae) (Anciaux de Faveaux 1984, Brown & Dunlop 1997, Kock *et al.* 1998b).

Conservation IUCN Category: Least Concern.

Measurements

Rhinolophus landeri

FA: 43.3 (35–49) mm, n = 128

WS (d): 280–307 mm*

TL: 77.2 (63–83) mm, n = 75

T: 25.6 (21–31) mm, n = 75

E: 16.6 (13–20) mm, n = 80

NL (breadth): 7.2 (6.0–8.0) mm, n = 27

Tib: 18.7 (17–21) mm, n = 50

HF: 8.1 (7–9) mm, n = 31

WT: 7.3 (5–10) g, n = 21

CrnC: 18.1 (16.9–19.1) mm, n = 41

GWS: 9.4 (8.7–10.0) mm, n = 35

C–M³: 6.7 (6.0–7.7) mm, n = 49

Throughout geographic range (BMNH, HC, HZM, SMNS and literature)

*Kock 1969a

Key References Brown & Dunlop 1997; Csorba *et al.* 2003; Menzies 1973; Rosevear 1965.

Meredith Happold

Rhinolophus macclaudi MACCLAUD'S HORSESHOE BAT

Fr. Rhinolophe de Macclaud; Ger. Macclauds Hufeisennase

Rhinolophus macclaudi Pousargues, 1898 [publ. 1897]. Bull. Mus. Natn. Hist. Nat. 3: 358. Conakry I., Guinea.

Taxonomy Species-group: *macclaudi* (Fahr *et al.* 2002). Synonyms: none. Smith & Hood (1980) classified *R. ruwenzorii* (including *R. hilli* as a synonym) as a subspecies of *R. macclaudi*. Fahr *et al.* (2002) showed that both *R. ruwenzorii* and *R. hilli* are clearly differentiated from *R. macclaudi* and re-instated their status as distinct species. Traditionally, *R. macclaudi* was placed in the otherwise Australasian *philippinensis*, *luctus* or *trifolius* species-groups (Andersen 1905c, d, Hill 1942, Aellen 1973, Koopman 1994). In contrast, Laurent (1940, 1941) concluded that *R. macclaudi* is not closely related to any Australasian form but instead represents an archaic African species. A closer affinity with African forms was partly supported by Bogdanowicz (1992) and Bogdanowicz & Owen (1992), who studied the phenetic and phylogenetic relationships of the genus *Rhinolophus*. Recently, Fahr *et al.* (2002) revised the taxa allied to *R. macclaudi* and established the *macclaudi* species-group to comprise *R. macclaudi*, *R. ziama*, *R. ruwenzorii* and *R. hilli*. Chromosome number: not known.

Description Medium-sized microbat with noseleaf (posterior component subtriangular with erect tip); on average the largest rhinolophid in Africa (FA: 64–69 mm); anterior upper premolar within tooththrow; connecting process greatly reduced, low and concave; lancet subtriangular; sella parallel-sided, inclined forward, with greatly enlarged basal lobes; horseshoe without lateral leaflets, median emargination small or absent. Sexual dimorphism: none apparent. Pelage soft, woolly; mid-dorsal hairs 13–14 mm. Dorsal pelage pale chestnut to greyish-brown; hairs with slightly paler base. Ventral pelage paler than dorsal pelage. Orange-phase: not yet reported. No axillary tufts on adult ♂♂. Ears comparatively and relatively long (40–46 mm, 63.7 [61–70]% of FA, *n* = 6), each with 10–12 internal folds. Noseleaf with lancet subtriangular, tip pointed; height of lancet conspicuously exceeding height of sella. Connecting process greatly reduced, low and concave, leaving a deep emargination between sella and lancet. Sella naked, inclined forward and therefore not parallel to lancet, almost parallel-sided; top not distinctly broadened; narial lobes at base of sella greatly enlarged, forming a roughly heart-shaped corolla-like cup. Nostrils laterally bordered by conspicuously raised, almost straight and more or less parallel rims, which almost reach anterior margin of horseshoe. Horseshoe broad (15.0, 16.0 mm); no lateral leaflets; median emargination very small or absent. Lower lip with one groove. Wings and interfemoral membrane dark grey. First phalanx of fourth finger relatively long (25.6 [25–29]% of fourth metacarpal, *n* = 6). Tibia 28–31 mm, 44.4 (43–46)% of FA, *n* = 6.

Skull large, slender; zygomatic arches broad but comparatively weak, dorsally notched; zygomatic width \geq mastoid width. Rostrum robust; rostral emargination U-shaped; premaxillae broad. Nasal swellings high-domed; chambers (viewed dorsally) roughly heart-shaped (with posterior indentation). Frontal depression very deep. Braincase (viewed dorsally) constricted behind mastoid process; viewed laterally, the highest point is directly above the glenoid process. Sagittal crest moderate anteriorly, low posteriorly. Infraorbital bridge

moderately long and slender. Interpterygoid groove very deep. Palatal bridge relatively long (45–48% of C–M³; Csorba *et al.* 2003). Anterior upper premolar small, within tooththrow or only slightly displaced labially; canine and posterior upper premolar separated. Middle lower premolar small, clearly displaced labially, anterior and posterior lower premolars either in contact or separated; anterior lower premolar ca. half to two-thirds of the height of the posterior premolar. Lower molars medium-sized (cf. *R. hilli* and *R. ruwenzorii*). Dental formula $^{1123}/_{2133} = 32$. For detailed comparison of *R. macclaudi* with other species in *R. macclaudi* group, see Fahr *et al.* (2002).

Geographic Variation None.

Similar Species Three other *Rhinolophus* in Africa have a greatly reduced, low and concave connecting process (Table 14, p. 304):

Rhinolophus ziama. Smaller (FA: 60 mm, CrnC: 26.1, 26.2 mm, C–M³: 8.9, 9.0 mm). Horseshoe narrower (11.5, 11.6 mm). Ears shorter (35, 36 mm). Skull with highest point clearly behind glenoid process; infraorbital bridge longer and more slender. West Africa.

R. ruwenzorii. Smaller (FA: 55–62 mm, CrnC: 23.7–25.6 mm, C–M³: 8.2–8.9 mm). Ears shorter (32–38 mm) with eight internal folds. Sella upright and more or less parallel to lancet. Horseshoe narrower (10.8–12.6 mm); lateral leaflets present, median emargination conspicuous, rims around nostrils semi-circular. Skull with highest point clearly behind glenoid process; zygomatic width < mastoid width; infraorbital bridge stouter and shorter. Mountains flanking Albertine Rift Valley.

R. hilli. Smaller (FA: 54 mm, CrnC: 23.0 mm, C–M³: 7.9, 8.1 mm). Ears with nine internal folds. Sella upright and more or less parallel to lancet. Horseshoe narrower (12 mm), lateral leaflets present, median emargination conspicuous, rims around nostrils semi-circular. Skull with highest point clearly behind glenoid process; zygomatic width < mastoid width; infraorbital bridge much shorter and stouter. Mountains flanking Albertine Rift Valley.

Distribution Endemic to Africa. Only known from ca. 360 km² in the Northern Rainforest–Savanna Mosaic in Guinea. The holotype is supposedly from Conakry I., but all other specimens are from three localities (ca. 150 km away) situated along the lower, SE slopes of the Fouta Djallon highlands between Kindia and Mamou near the border with Sierra Leone. Specimens from Kagoro, C Nigeria (M. E. Gartshore in Happold 1987, Koopman *et al.* 1995), have been re-identified as *R. hildebrandtii* (J. Eger in Fahr *et al.* 2002). Csorba *et al.* (2003) listed two separate localities from Guinea (Nyembaro; Salung Plateau), but these represent the same locality. A record from Liberia (Koopman 1994, Koopman *et al.* 1995, Csorba *et al.* 2003) was re-identified as *R. ziama* (Fahr *et al.* 2002). The distribution pattern of the *R. macclaudi* species-group strikingly resembles that of the otter-shrews *Micropotamogale lamottei* and *M. ruwenzorii* with a remarkable disjunction between the highlands of Guinea, N Liberia and W



Rhinolophus maclaudi

Côte d'Ivoire in the West and the mountains flanking the Albertine Rift Valley in the East. Both the *R. maclaudi* species-group and the two species of *Micropotamogale* apparently have a paramontane distribution (*sensu* Koopman 1983), i.e. their distribution is restricted to mountainous regions although their altitudinal range covers both lower and higher elevations.

Habitat Except for the holotype, all specimens are from a region where the predominant vegetation is bush-tree savanna intersected by forests along rivers and in topographically protected pockets.

Abundance Uncertain but probably extremely localized and rare. Only nine specimens known with gap of 58 years between captures of the holotype (1896) and the next specimen (1954). Not recorded since 1968.

Remarks Most specimens were taken from their day-roosts in caves (Aellen 1956a, Eisentraut & Knorr 1957); one was caught

in a house (Aellen 1973). Day-roosts were shared with small colonies of *Lissonycteris angolensis smithii*, *Nycteris macrotis*, *Rhinolophus guineensis*, *R. fumigatus diversus*, *R. denti knorri* and larger colonies of *Hipposideros ruber* and *H. jonesi* (Eisentraut & Knorr 1957, Fahr *et al.* 2002). Echolocation call-shape likely to be FM/CF/FM (as in other *Rhinolophus*) and, based on the comparatively large size of this bat, the CF-frequency is likely to be rather low for a *Rhinolophus*. Roosts singly or in small groups. Eisentraut & Knorr (1957) reported a group consisting of three ♂♂ and three ♀♀ in one cave, and two individuals (including 1 ♀) in another cave.

Predators, Parasites and Diseases Ectoparasites include some unidentified mites (Acari) (Aellen 1956a).

Conservation IUCN Category: Endangered.

Major threats: occurs in densely populated region affected by continuous destruction of habitat; highly dependent on caves, therefore vulnerable to disturbance at roosts and exploitation as bushmeat. See also Distribution and Abundance.

Measurements

Rhinolophus maclaudi

FA: 65.8 (64–69) mm, n = 7

WS: n. d.

TL: 117.7 (111–137) mm, n = 6

T: 40.6 (38–43) mm, n = 7

E: 41.4 (40–46) mm, n = 7

NL (breadth): 15, 16 mm, n = 2

Tib: 29.0 (28–31) mm, n = 7

HF: 15, 15 mm, n = 2

WT: 31.8 (30.0–33.0) g, n = 6

CrnC: 29.3 (29.0–30.1) mm, n = 7

GWS: 13.7 (13.4–13.9) mm, n = 7

C–M³: 10.6 (10.5–10.8) mm, n = 6

Guinea (IFAN, MNHN [holotype], SMNS, ZFMK, ZMA)

Key References Aellen 1956a; Eisentraut & Knorr 1957; Fahr *et al.* 2002; Laurent 1940, 1941; Smith & Hood 1980.

Jakob Fahr

Rhinolophus maendeleo MAENDELEO HORSESHOE BAT

Fr. Rhinolophe de Maendeleo; Ger. Maendeleo Hufeisennase

Rhinolophus maendeleo Kock, Csorba and Howell, 2000. Senckenbergiana Biol., 80: 234. Amboni Cave Forest, Mkulumuzi R. Gorge, 2.5 km west of Tanga, Tanga District, Tanzania.

Taxonomy Species-group: *adami*, with *R. adami* (Kock *et al.* 2000). Synonyms: none. Its closest known relative appears to be *R. adami*. Chromosome number: not known.

Description Small microbat with noseleaf (posterior component subtriangular with erect tip); medium-sized for an African rhinolophid; anterior upper premolar within tooththrow; connecting process rounded and comparatively high; lancet subtriangular with

slightly concave sides; sella with markedly concave sides and top, which is angled obtusely forward; horseshoe breadth 8.2, 8.5 mm. Sexual dimorphism: no information. Dorsal pelage medium brown; hairs medium brown. Ventral pelage beige merging into white on lower abdomen; darker brown collar around lower neck and upper chest. Orange-phase: no information. Axillary tufts: no information. Ears comparatively short (24, 25 mm) but of medium relative length (49–51% of FA), reaching beyond tip of nose when laid forward; tips

bluntly rounded. Noseleaf with lancet subtriangular, sides slightly concave (Figure 61d); tip bluntly pointed (cf. *R. adami*). Connecting process well developed, hairy, smoothly rounded (arched) and high. Sella naked, broad at base, sides markedly concave, top curving obtusely forward. Lobes at base of sella poorly developed but surrounding a well-developed narial cup. Horseshoe narrow (8.2, 8.4 mm) but almost covering muzzle; no lateral leaflets, median emargination well defined. Lower lip with three well-defined grooves. Wings brown; first phalanx of fourth finger of medium relative length (21, 23% of fourth metacarpal). Interfemoral membrane brown. Tibia 38, 40% of FA. Baculum with dorsal and ventral parts of basal cone deeply invaginated so sides of cone form two long wings, ventral invagination less deep; shaft becoming dorsoventrally flattened distally; tip slightly expanded; length 2.66 mm (Kock *et al.* 2000).

Skull narrow; zygomatic width equal to or slightly narrower than mastoid width. Nasal swellings relatively high. Anterior median swellings bulbous, broad and long; posterior swellings less developed (Csorba *et al.* 2003). Frontal depression moderately deep. Sagittal crest low. Infraorbital foramen open, not covered by bony bar (cf. *R. adami*). Palatal bridge 2.70, 2.78 mm, 37, 39% of C–M³. Anterior upper premolar small, within toothrow; canine and posterior premolar well separated. Middle lower premolar small, somewhat displaced labially; anterior and posterior lower premolars separated. Dental formula $^{1123}_{2133} = 32$.

Geographic Variation None recorded.

Similar Species Five other *Rhinolophus* in Africa have the anterior upper premolar in the toothrow and a rounded connecting process:

Rhinolophus adami. Lancet subtriangular with slightly convex sides; connecting process rising well above sella; sella with only slightly concave sides, top of sella curving acutely forward and slightly downward, horseshoe broader (8.5, 9.0 mm). Skull with infraorbital foramen closed by bony bar; palatal bridge 42, 44% of C–M³. Rainforest, Congo.

R. simulator. Ears shorter (18–23 mm). Lancet hastate, horseshoe almost always narrower (6.7–8.3 mm). FA shorter in area of sympatry (42–47 mm).

R. swinyi. Lancet hastate, horseshoe narrower (6.8–7.4 mm). FA shorter (40–44 mm).

R. denti. Horseshoe narrower (6.8–7.5 mm). FA shorter (37–44 mm).

R. capensis. Horseshoe narrower (7.2–8.1 mm). South Africa.

Distribution Known only from three localities in Tanzania: the type locality (Amboni Cave Forest, 05° 5'S, 39° 02'E), Mazumbai F. R. (04° 25'S, 38° 15'E) on the east ridge of West Usambara Mts (Kock *et al.* 2000), and Iringa (07° 48'S, 35° 43'E) (F. P. D. Cotterill pers. comm.). The first two localities are in relict forests in the Coastal Forest Mosaic BZ (and in the Swahili regional centre of endemism of Burgess *et al.* 1998). Iringa is in the Somalia–Masai Bushland BZ.

Habitat Amboni Cave Forest is a coastal forest of 350 ha, altitude 0–80 m, consisting of degraded forest and evergreen thicket in a limestone gorge. Masumbai Forest is a primeval lower montane rainforest of 450 ha, at altitude 1400–1900 m. The unique nature of these forests is described by Sheil (1992). The altitude of Iringa is ca. 1650 m; no other details available.

Abundance No information. Only four specimens known.

Remarks Nothing else is known about this species.

Conservation IUCN Category: Data Deficient.

Distribution, population size and trend not sufficiently known. The coastal forest localities from which this species has been recorded lie wholly within protected areas (Kock *et al.* 2000). Threats facing these forests and their inhabitants are described by Sheil (1992).

Measurements

Rhinolophus maendeleo

FA: 48, 49 mm

WS: n. d.

TL: 69, 75 mm

T: 23, 26 mm

E: 25, 24 mm

NL (breadth): 8.4, 8.2 mm

Tib: 19, 19 mm

HF: 8, 8 mm

WT: 6, – g

CrnC: 20.8, 20.6 mm

GWS: 9.4 (9.2–9.7) mm, n = 4*

C–M³: 7.1 (7.0–7.3) mm, n = 4*

Tanzania (holotype [adult ♂] and paratype [adult ♀]) from Kock *et al.* 2000

*As above with additional data for two specimens from Iringa, Tanzania (F. P. D. Cotterill pers. comm.)

Key Reference Kock *et al.* 2000.

Meredith Happold



Rhinolophus maendeleo

Rhinolophus mehelyi MÉHELY'S HORSESHOE BAT

Fr. Rhinolophe de Méhely; Ger. Méhely Hufeisennase

Rhinolophus mehelyi Matschie, 1901. Sitzb. Ges. Naturf. Fr. Berlin, p. 225. Bucharest, Romania.

Taxonomy Species-group: *euryale*. Synonyms: *carpetanus* and, following Cockrum (1976), *tuneti*. Subspecies: uncertain (see Geographic Variation). Chromosome number (Tunisia): $2n = 58$; $aFN = 60$ (Baker *et al.* 1974); 4–8 metacentric and 48–52 acrocentric autosomes, X = large metacentric, Y = small acrocentric. In Romania, $aFN = 64$ (Dulić & Soldatović 1969); in Azerbeidjan, $aFN = 64$ (Zima *et al.* 1992).

Description Small microbat with noseleaf (posterior component subtriangular with erect tip); medium–small for an African rhinolophid; anterior upper premolar somewhat displaced; connecting process triangular; lancet hastate with distal half narrow and almost parallel-sided; sella parallel-sided; first phalanx of fourth finger relatively short, and marked contrast between crown areas of anterior and posterior lower molars (cf. *R. blasii*); usually with dark spectacles around the eyes (cf. *R. euryale*). Not easily distinguished from *R. euryale*. Sexes similar. Pelage soft, dense, velvety; mid-dorsal hairs 8–9 mm. Dorsal pelage greyish-brown; hairs pale greyish-beige with greyish-brown at tip. Face paler, usually with dark brown hairs around eyes creating fairly conspicuous brown ‘spectacles’ (or a patch under each eye). Ventral pelage much paler, almost white to pure white; boundary with dorsal pelage fairly distinct. Apparently no orange-phase. Axillary tufts: no information. Ears comparatively and relatively short (19–23 mm, mean E ca. 42% of mean FA). Noseleaf with lancet hastate, with upper half narrow, almost parallel-sided but tapering slightly; tip bluntly pointed. Sella naked, parallel-sided with top broad, rounded and tilted forward. Connecting process subtriangular. Horseshoe narrow (4.9–7.5 mm), not covering whole muzzle; no lateral leaflets; median emargination slight. Grooves in lower lip: no information. Wings and interfemoral membrane greyish-brown; first phalanx of fourth finger relatively short (21.2 [19–23]% of fourth metacarpal, $n = 24$) and < 50% of second phalanx (cf. most *R. blasii*). Tibia 41.4 (40–44)% of FA ($n = 13$).

Skull of medium build; zygomatic arches slender; zygomatic width invariably greater than mastoid width. Nasal swellings low. Frontal depression shallow to almost flat; supraorbital ridges indistinct. Sagittal crest moderately developed. The bar between the infraorbital foramen and the orbit is narrow, and the infraorbital foramen is large (cf. *R. euryale*). Palatal bridge of medium relative length, 32–33% of $C-M^3$ (Csorba *et al.* 2003). Anterior upper premolar somewhat displaced labially but canine and posterior premolar not in contact. Middle lower premolar minute, fully displaced labially; anterior and posterior lower premolars in contact. Crown area of lower anterior premolar is 50% or less than that of the posterior lower premolar. Dental formula $^{1123}/_{2133} = 32$.

Geographic Variation Controversial. Two subspecies are recognized by Gaisler (1983), Koopman (1994), Csorba *et al.* (2003) and Simmons (2005):

R. m. mehelyi: Europe and W Asia.

R. m. tuneti: North Africa.

However, Aellen & Strinati (1970) and Felten *et al.* (1977) stated that the taxonomic position of *tuneti* cannot be determined. Furthermore, specimens from Morocco, Algeria and Tunisia were not considered to differ from those from elsewhere by Felten *et al.* (1977), Aulagnier & Thévenot (1986) and Kowalski & Rzebik-Kowalska (1991). Here, pending further studies, *tuneti* is not considered to be a valid subspecies.

Similar Species No other *Rhinolophus* in North Africa has a triangular connecting process. Two other rhinolophids in North Africa have pointed connecting processes but, in each of these species, the connecting process rises to a high, narrow, forward-curving horn (Table 14, p. 304):

Rhinolophus euryale. Lancet subtriangular (distal half not tapering to a thin apex). Eyes with faint spectacles; bases of dorsal hairs almost white; ventral pelage never white or almost white. Craniodental characters almost indistinguishable.

R. blasii. Sella wedge-shaped, horseshoe usually broader (7.2–9.0 mm). First phalanx of fourth finger relatively long (24–28% of fourth metacarpal). No marked contrast between crown areas of anterior and posterior lower premolars.

Most specimens of both *euryale* and *blasii* are a little smaller than *mehelyi*.

Distribution In Africa, known from the Mediterranean Coastal and Afromontane–Afroalpine BZs in the Maghreb (NW Africa) and



Rhinolophus mehelyi

from the northern edge of the Sahara Arid BZ in NE Libya (Cyrenaica) and the Nile Delta in NE Egypt. Recorded from N Morocco, Algeria (from coast to Saharan Atlas), N Tunisia, NE Libya (Cyrenaica) and N Egypt as far south as Saqqara (Hanák & Elgadi 1984, Qumsiyeh 1985, Aulagnier & Thévenot 1986, Kowalski & Rzebik-Kowalska 1991, Benda *et al.* 2004d). Extraliminally: Portugal to Caucasus, and Israel, Iran, Iraq and Afghanistan.

Habitat In Africa, this cave-roosting species inhabits regions rich in caves or man-made subterranean shelters. In the supra-Saharan region, has the widest distribution of all horseshoe bats and occurs in various dry Mediterranean habitats of the Maghreb, Cyrenaica and NE Egypt. Found in several places along the Atlantic coast of Morocco but apparently absent from coastal areas with high rainfall, such as the Mediterranean coast of the Algerian Kabylia. In Morocco and Algeria, recorded from sea level to ca. 2000 m in the High and Saharan Atlas (Aulagnier & Thévenot 1986, Kowalski & Rzebik-Kowalska 1991, Benda *et al.* 2004d). In Algeria, netted only once in a rocky ravine at Brezina (Gaisler & Kowalski 1986). Seems to occur in Mediterranean forests, woodlands and montane forests, and sub-Mediterranean semi-desert grassland and shrubland.

Abundance Common in N Morocco and NW Algeria, rare in remainder of geographic range in Africa.

Adaptations Flight slow, very manoeuvrable, with short glides. In Algeria (and elsewhere), roosts by day in caves; hangs from ceilings with body not completely enveloped by the wings. In Arabia, also observed half protruding from cracks and fissures in ceiling of a cave in which the temperature reached maximum of 31.5°C, and humidity was very high (Harrison & Bates 1991). No precise data on hibernation available; in Algerian caves, both active and torpid individuals were observed in winter (Kowalski & Rzebik-Kowalska 1991). At one cave, very fat ♀♀ and ♂♂, which were devoid of fat, roosted in the warm chambers in autumn; in winter they roosted near the entrance (Kowalski *et al.* 1986). Caves are often shared with *R. ferrumequinum*, *Myotis punicus* and/or *Miniopterus schreibersii*; in winter these species roost in inter-specific clusters, but in spring and summer they roost separately (Kowalski *et al.* 1986).

Foraging and Food No information from Africa. Lepidoptera were found in stomachs in Romania (n = 3) (Gaisler 2001c). In Iran, the food of a maternity colony was mainly Lepidoptera (68–97% by volume), followed by Coleoptera (3–29%) and Diptera (0.1–1.3%) (Sharifi & Hemmati 2001).

Echolocation Call shape: FM/CF/FM. CF-frequency (Europe) 109 (105–112) kHz; call-duration 20–30 ms (Heller & von Helversen 1989, Schober & Grimmberger 1989).

Social and Reproductive Behaviour Roosts singly, in groups or in very large colonies; extraliminally up to 3000 in summer and 5000 in winter. A maximum of ca. 1000 was recorded on one occasion at a regularly visited cave at Misserghin (Algeria) (Kowalski *et al.* 1986). Individuals, whether torpid or active, sometimes roost

in contact with their neighbours (unlike other *Rhinolophus* in North Africa), and sometimes hang apart in loose clusters. During winter, ♂♂ and ♀♀ roosted together; in the Misserghin cave, both ♂♂ and ♀♀ continued roosting together during spring, but ♂♂ departed prior to parturition, leaving ♀♀ in what became a maternity colony. Juveniles roosted with their mothers prior to weaning, and then roosted in separate associations. Extraliminally, vocalizations (audible to humans) include comparatively deep, loud, short chirping or squeaking (Macdonald & Barrett 1993).

Reproduction and Population Structure Litter-size (Algeria): one (n = 9); other ♀♀ seen with only one young attached. At 35–36°N in NW Algeria, the reproductive chronology is restricted seasonal monoestry, with births in May and early Jun (based on histology of reproductive organs and year-round observations by Kowalski *et al.* 1986). Females reach sexual maturity when three years old; ♂♂ when two years old. In a spring sample of both ♂♂ and ♀♀, immature and adult animals were discriminated histologically. Sex ratio at birth close to 1 : 1.

Predators, Parasites and Diseases Ectoparasites in North Africa include a flea *Rhinolophopsylla unipeptinata* (Siphonaptera: Ischnopsyllidae); bat-flies *Nycteribia latreillei*, *N. schmidli*, *Penicillidia dufouri*, *P. conspicua*, *Phthiridium biarticulatum* (Diptera: Nycteribiidae) and *Brachytarsina africana*, *B. kollari* (Diptera: Streblidae); and a tick *Carios boueti* (Acari: Argasidae) (Anciaux de Faveaux 1984). For more information, see Beaucournu & Kowalski (1985).

Conservation IUCN Category: Vulnerable (assessed from extralimital as well as African data).

Major threat: ongoing human-induced destruction and degradation of habitat.

Measurements

Rhinolophus mehelyi

FA: 50.1 (48–53) mm, n = 87

WS (d): 330–340 mm*

TL: 88.9 (75–96) mm, n = 81

T: 29.3 (25–37) mm, n = 81

E: 20.9 (19–23) mm, n = 88

NL (breadth): 6.4 (4.9–7.5) mm, n = 42

Tib: 20.9 (19–23) mm, n = 18

HF: 10.8 (9–12) mm, n = 81

WT: 13.6 (11.0–18.0) g, n = 58

CrnC: 19.5 (18.8–19.9) mm, n = 56

GWS: 10.5 (9.8–11.2) mm, n = 56

C–M³: 6.9 (6.5–7.1) mm, n = 56

Morocco, Algeria, Tunisia, Libya (BMNH, HZM, ZFMK, Gaisler 1983, Kowalski & Rzebik-Kowalska 1991)

*Europe (Schober & Grimmberger 1989)

Key References Aulagnier & Thévenot 1986; Benda *et al.* 2004d; Gaisler 1983; Kowalski & Rzebik-Kowalska 1991; Kowalski *et al.* 1986.

Rhinolophus ruwenzorii RWENZORI HORSESHOE BAT

Fr. Rhinolophe du Rwenzori; Ger. Ruwenzori-Hufeisennase

Rhinolophus ruwenzorii J. Eric Hill, 1942. Am. Mus. Novit., 1180: 1. South side of Butahu Valley, 2286 m, W slope of Rwenzori Mts, DR Congo.

Taxonomy Species-group: *maclaudi* (Fahr *et al.* 2002). Synonyms: none. Smith & Hood (1980) classified *R. ruwenzorii* (including *R. hilli* as a synonym) as a subspecies of *R. maclaudi*. Fahr *et al.* (2002) showed that both *R. ruwenzorii* and *R. hilli* are clearly differentiated from *R. maclaudi* and re-instated their status as distinct species. Chromosome number: not known.

Description Small microbat with noseleaf (posterior component subtriangular with erect tip); large for an African rhinolophid (FA: 55–62 mm); anterior upper premolar usually within toothrow; connecting process greatly reduced, very low and concave; lancet comparatively short and subtriangular; sella upright with concave sides, broadened tip and greatly enlarged basal lobes; horseshoe with lateral leaflets and median emargination; no axillary tufts. Sexes similar. Pelage soft, woolly; mid-dorsal hairs 13–14 mm. Dorsal pelage medium to dark brown or smoky-brown. Ventral pelage paler than dorsal pelage. Orange-phase: not yet reported. No axillary tufts on adult ♂♂. Ears comparatively medium-long (32–38 mm) and relatively long (60.3 [57–66]% of FA, $n = 19$), each with eight internal folds; antitragus very large. Noseleaf with lancet subtriangular, tip bluntly pointed, height of lancet only moderately exceeding height of sella. Connecting process greatly reduced, low and concave, leaving a deep emargination between sella and lancet. Sella naked, upright and more or less parallel to lancet (i.e. not inclined forward), sides concave, top distinctly broadened and rounded (spoon-shaped); narial lobes at base of sella greatly enlarged, forming an almost circular cup. Nostrils bordered by semi-circular, conspicuously raised rims that are parallel to the inner cup (therefore not reaching anterior margin of horseshoe). Horseshoe of medium breadth (10.8–12.6 mm); lateral leaflets present; median emargination conspicuous. Lower lip with a well-developed median groove and either two poorly-developed lateral grooves or no lateral grooves. Wings and interfemoral membranes dark grey. First phalanx of fourth finger relatively long (27.0 [26–28]% of fourth metacarpal, $n = 18$). Tibia 41.1 (38–46)% of FA, $n = 19$.

Skull large, slender; zygomatic arches broad but comparatively weak; zygomatic width < mastoid width. Rostrum robust; rostral emargination squarish; premaxillae broad. Nasal swellings high; chambers (viewed dorsally) roughly circular (posterior indentation weak). Frontal depression very deep. Braincase (viewed dorsally) constricted behind mastoid process; viewed laterally, the highest point is clearly behind the glenoid process (cf. *R. maclaudi*). Sagittal crest moderate anteriorly, poorly developed posteriorly. Infraorbital bridge moderately short and stout. Interpterygoid groove very deep. Palatal bridge relatively long (41–47% of C–M³; Csorba *et al.* 2003). Anterior upper premolar small, within toothrow or only slightly displaced labially; canine and posterior premolar separated. Middle lower premolar small, slightly to clearly displaced labially; distance between anterior and posterior lower premolars variable. Lower molars comparatively small (cf. other species in *R. maclaudi* group). Dental formula $^{1123}/_{2133} = 32$. For detailed comparison of

R. ruwenzorii with other species in *R. maclaudi* group, see Fahr *et al.* (2002).

Geographic Variation None.

Similar Species Three other *Rhinolophus* in Africa have a greatly reduced, low and concave connecting process (Table 14, p. 304):

Rhinolophus hilli. Height of lancet conspicuously exceeding height of sella. Smaller (FA: 54, 54 mm; CrnC: 23.0, – mm; GWS: 10.9, 11.2 mm; C–M³: 7.9, 8.1 mm). Skull with braincase not conspicuously constricted behind mastoid process; infraorbital bridge shorter and stouter; lower molars comparatively large. Nearly sympatric.

R. maclaudi. Larger (FA: 64–69 mm; CrnC: 29.0–30.1 mm). Ears longer (40–46 mm) with 10–12 internal folds. Sella inclined forward, lateral margins parallel-sided. Horseshoe broader (15–16 mm), no lateral leaflets, median emargination small or absent; nostrils bordered laterally by more or less straight and parallel rims. Skull with highest point at height of glenoid process; zygomatic width usually > mastoid width; infraorbital bridge slender and longer. West Africa.

R. ziamia. Ears with 11–12 internal folds. Skull larger (CrnC: 26.1–26.2 mm, C–M³: 8.9, 9.0 mm). Sella inclined forward. Horseshoe broader (11.5, 11.6 mm), no lateral leaflets, median emargination inconspicuous or absent; nostrils bordered laterally by more or less straight and parallel rims. Skull with zygomatic width ≥ mastoid width; infraorbital bridge much longer and more slender. West Africa.

Distribution Endemic to Africa. Apparently restricted to ca. 20,740 km² in the Afromontane–Afroalpine BZ flanking the Albertine Rift Valley. Known from 13 localities in the Rwenzori Mts (DR Congo and Uganda), Kivu and Kibali–Ituri Forests (DR Congo), Bwindi–Impenetrable Forest (Uganda) and Mutura (NW Rwanda) (Fahr *et al.* 2002). The distribution of the *Rhinolophus maclaudi* species-group is very disjunct and resembles that of the otter-shrews (genus *Micropotamogale*) (see profile of *R. maclaudi*).

Habitat Mostly recorded in (sub-) montane forests, but marginally also in lowland rainforests. Smith & Hood (1980) characterized the vegetation of the known localities as ‘Montane Evergreen/Bamboo forest’: they mist-netted one specimen in dense undergrowth near a dense bamboo forest. The known altitudinal range covers 1066–2667 m (median 1901 m, $n = 14$).

Abundance Uncertain; apparently very localized and rare. Only 36 specimens known.

Adaptations Most specimens have been captured in caves or artificial substitutes such as mines. Hayman (1960a) reported that the presence of *R. ruwenzorii* in a cave was indicated by rather loud squeaks

*Rhinolophus ruwenzorii*

as these bats took wing. Known to share day-roosts with *Rousettus lanosus*, *Rhinolophus clivosus* and *Hipposideros caffer* (Hill 1942, Smith & Hood 1980), the latter population probably representing *H. ruber*.

Foraging and Food Foraging behaviour not known. Stomachs and intestines of five adults contained remains of large moths (probably Noctuidae, Geometridae and Arctiidae), including their masticated wings and legs, which suggests that the prey is consumed whole with little culling of extremities (Smith & Hood 1980). The estimated body size of the insects was 8–12 mm with a wingspan of 25–35 mm (Smith & Hood 1980).

Echolocation No information. Call-shape probably FM/CF/FM (as in other *Rhinolophus*) and, based on the comparatively large size of this bat, the CF-frequency is likely to be rather low for a *Rhinolophus*.

Social and Reproductive Behaviour Roosts singly or in small groups of up to ten individuals (median = 3 individuals, $n = 7$) (Hayman 1960a, Smith & Hood 1980, unpublished museum data). One group consisted of three ♂♂ and four ♀♀, one of each sex being immature (Smith & Hood 1980). The majority of museum records are either single specimens or small series of one or two individuals.

Reproduction and Population Structure Litter-size: no information. Reproductive chronology not known. At ca. 1°S (Impenetrable Forest, Kigezi Highlands, SW Uganda), ten bats taken from mines in late Mar included four adult ♀♀ that had probably been lactating very recently, two large juveniles with unfused epiphyses, one ♂ with scrotal testes (4 mm in length) and three ♂♂ with abdominal testes (3 mm in length) (Smith & Hood 1980). These data indicate that at least some births occur in ca. early to mid-Feb and suggest reproductive synchrony, but there are no data for other months. The ♂ : ♀ sex ratio in museum collections is 1 : 0.6 ($n = 32$).

Predators, Parasites and Diseases No information.

Conservation IUCN Category: Vulnerable.

Major threats: loss and degradation of habitat (the region has one of the highest rural population densities in Africa and the protected areas are affected by recent civil wars); highly dependent on caves and mines and therefore vulnerable to disturbance at day-roosts and exploitation as bushmeat. Population trend not known but population size probably small. Most records are from 1926 to 1967 with a few additional records from 1982 to 1997. See also Distribution and Abundance.

Measurements

Rhinolophus ruwenzorii

FA: 57.6 (55–62) mm, $n = 21$

WS: n. d.

TL: 93.6 (83–104) mm, $n = 18$

T: 29.8 (25–34) mm, $n = 18$

E: 34.7 (32–38) mm, $n = 19$

NL (breadth): 11.9 (10.8–12.6) mm, $n = 14$

Tib: 23.6 (22–26) mm, $n = 19$

HF: 12.5 (11–15) mm, $n = 11$

WT: 17.6 (16.0–19.5) g, $n = 5$

CrnC: 24.5 (23.7–25.6) mm, $n = 12$

GWS: 12.0 (11.2–12.3) mm, $n = 18$

C–M³: 8.4 (8.2–8.9) mm, $n = 14$

DR Congo, Uganda, Rwanda (AMNH [holotype], BMNH, FMNH, IRSN, LACM, RMCA)

Key References Csorba *et al.* 2003; Fahr *et al.* 2002; Hayman 1960a; Hill 1942; Smith & Hood 1980.

Jakob Fahr

Rhinolophus sakejiensis SAKEJI HORSESHOE BAT

Fr. Rhinolophe de Sakeji; Ger. Sakeji-Hufeisennase

Rhinolophus sakejiensis Cotterill, 2002. J. Zool., 256: 166. Kavunda (11° 17' S; 24° 21' E), Ikelenge pedicle, Mwinilunga District, NW Zambia.

Taxonomy Species-group: *ferrumequinum*. Synonyms: none. Chromosome number: not known.

Description Small microbat with noseleaf (posterior component subtriangular with erect tip); medium-sized for an African rhinolophid;

anterior upper premolar absent; connecting process rising to a high rounded peak; lancet long and hastate; sella with slightly concave sides; no axillary tufts; first phalanx of fourth finger relatively long; dorsal pelage bright brownish-orange in all three known specimens (cf. *R. deckenii*). Sexual dimorphism: no information, only three ♂♂ known.

Pelage of medium length, soft, fluffy. Dorsal pelage bright brownish-orange; hairs orange with darker tip. Ventral pelage bright yellowish-orange. Eyes surrounded by darker, brown pelage. Grey-phase not known. No axillary tufts on adult ♂♂. Ears dark brown, comparatively and relatively short (20–22 mm, 39 [37–40]% of FA). Noseleaf with lancet hastate. Connecting process rising steeply to a high, narrow, rounded peak, much higher than sella (Figure 59l). Sella naked, sides slightly concave, top broad, rounded and angled forward. Horseshoe of medium breadth (ca. 10–11 mm), not covering whole muzzle; lateral leaflets present; median emargination wide and deep. Lower lip with a prominent median groove (lateral grooves faint). Wings and interfemoral membrane dark blackish-brown. First phalanx of fourth finger relatively long, 27% of fourth metacarpal, $n = 1$. Tibia 47% of FA, $n = 1$. Baculum trumpet-shaped with dorsoventrally flattened shaft, length 4.2 (3.9–4.5) mm, $n = 3$ (Cotterill 2002a).

Skull very robust; zygomatic arches sturdy; zygomatic width greater than mastoid width. Nasal swellings relatively low; not smoothly rounded. Frontal depression extremely shallow; supraorbital ridges indistinct. Sagittal crest well developed anteriorly, weak posteriorly. Interpterygoid groove shallow. Palatal bridge ca. 33% of $C-M^3$ (Csorba *et al.* 2003). Anterior upper premolar absent in all three known specimens; canine and posterior premolar in contact. Middle lower premolar also absent in these specimens; anterior and posterior lower premolars in contact. Anterior lower premolar ca. half size of posterior lower premolar. Dental formula $^{1113}/_{2123} = 28$.

Geographic Variation No information.

Similar Species Four other *Rhinolophus* occurring south of the Equator have the following combination of characters: anterior upper premolar fully displaced labially or absent, connecting process rounded, sella naked (or with sparse short hairs only) (Table 14, p. 304):

Rhinolophus clivosus. Connecting process rounded but sometimes smoothly curved and sometimes slightly angular; slightly to clearly higher than sella. Horseshoe breadth 6.6–9.6 mm. Skull smaller (CrnC: 18.1–22.8 mm, $C-M^3$: 6.7–8.9 mm).

R. darlingi. Smaller (FA: 42–50 mm, CrnC: 18.5–20.8). Apparently no orange-phase. Horseshoe narrower (7.1–8.7 mm). Skull with nasal swellings moderately high; frontal depression shallow to moderately deep; supraorbital ridges prominent. Anterior upper premolar present or absent; canine and posterior premolar usually separated by small gap.

R. deckenii. Dorsal pelage greyish-brown: apparently no orange-phase. Connecting process rounded. Known only from East Africa.

R. silvestris. Anterior upper premolar present, displaced labially. Connecting process smoothly rounded and lower. Lancet subtriangular with slightly concave sides. Skull with nasal swellings of medium relative height; frontal depression moderately deep; supraorbital ridges prominent.

Distribution Endemic to Africa. Known only from the type locality (in Zambia), which lies between the Sakeji and Zambezi Rivers, ca. 11 km north-north-east of the source of the Zambezi R., at 1388 m. This locality is in the Zambezian Woodland BZ.



Rhinolophus sakejiensis

Habitat Wetter miombo woodland mosaic, with evergreen forest along the drainage lines and tall, deciduous, closed-canopy miombo woodland (dominated by *Brachystegia floribunda*) on the higher ground. There are flooded caves formed from granitic boulders along the perennial rivers and streams of the region (Cotterill 2002a, b).

Abundance Not known. Only three specimens known.

Remarks The three specimens, two adult ♂♂ and a young ♂, belonged to a group of six found roosting during the day; they were hanging in evergreen foliage on the underside of a branch at the base of a large tree. This is an unusual day-roost for a rhinolophid and perhaps is atypical for this species. At the type locality, *R. sakejiensis* is sympatric with *R. clivosus zuluensis*, a very similar species.

Conservation IUCN Category: Data Deficient.

Probably threatened by loss of habitat, especially of mesic miombo woodland and gallery forest, in its area of occupancy (Cotterill 2002a).

Measurements

Rhinolophus sakejiensis

FA: 55, 53, 55 mm WS: n. d.

TL: 88, 87, 88 mm

T: 31, 29, 30 mm

E: 22, 20, 22 mm

NL (breadth): –, –, 10.3 mm

Tib: –, –, 25 mm

HF: 15, 14, 14 mm

WT: 23, 19, 24 g

CrnC: 25.3, 24.3, 25.1 mm

GWS: 13.2, 12.9, 13.5 mm

$C-M^3$: 9.7, 9.4, 9.7 mm

Zambia (NMZB holotype, NMZB paratype, HZM paratype, respectively, Cotterill 2002a). All ♂♂

Key References Cotterill 2002a; Csorba *et al.* 2003.

F. P. D. Cotterill

Rhinolophus silvestris FOREST HORSESHOE BAT

Fr. Rhinolophe sylvestre; Ger. Wald-Hufeisennase

Rhinolophus silvestris Aellen, 1959. Arch. Sci. Phys. Nat. Geneve 12: 228. N'Dumbu Cave, Latoursville, Gabon.

Taxonomy Taxonomy controversial. The first specimen was identified with *R. fumigatus* by Sanborn (1953). Aellen (1959) described *silvestris* as a species distinct from *fumigatus*, but suggested that it might prove to be a western forest subspecies of *R. deckenii*. Hayman & Hill (1971) treated both *deckenii* and *silvestris* as subspecies of *R. clivosus*. Koopman (1975) considered both *silvestris* and *deckenii* to be closely related but specifically distinct, and related to the *fumigatus*–*eloquens*–*hildebrandtii* complex. Aellen & Brosset (1968) considered *R. silvestris* and *R. deckenii* to have distinctly different characters, but suggested that there might be populations located between the geographic ranges of these species that could be intermediate in character. The phylogenetic analysis of Bogdanowicz & Owen (1992) indicated that *R. silvestris* is slightly more closely related to *R. alcyon* than to *R. deckenii*. In contrast, comparison of the bacula of *R. silvestris* and *R. deckenii* supports the hypothesis that these are sister species restricted to the W Congo Basin and the East African coast, respectively (Cotterill 2002a). Csorba *et al.* (2003) consider the differences between these two species to be very slight. Chromosome number: not known.

Description Small microbat with noseleaf (posterior component subtriangular with erect tip); medium-sized for an African rhinolophid; anterior upper premolar displaced labially; connecting process rounded; lancet subtriangular; sella with concave sides; baculum with rounded shaft (cf. *R. deckenii*). Difficult to distinguish from *R. deckenii* except by distribution and baculum morphology (see Similar Species). Sexes apparently similar. Pelage of medium length, soft, fluffy. Dorsal pelage rusty-brown. Ventral pelage paler. Orange-phase not yet known. Axillary tufts: no information. Ears comparatively medium–short (22, 23 mm) and relatively short (ca. 42% of mean FA). Noseleaf with lancet subtriangular, sides slightly concave, tip bluntly pointed. Connecting process smoothly rounded, higher than sella. Sella naked, sides concave, top broad and rounded. Horseshoe of medium breadth (9.5, 10 mm), covering muzzle; median emargination deep; no information about lateral leaflets. Lower lip with a well-defined median groove and two poorly defined lateral grooves. Wings and interfemoral membrane brown. First phalanx of fourth finger relatively long (ca. 31% of fourth metacarpal). Mean tibia 42.4% of mean FA. Baculum trumpet-shaped with rounded shaft, length 4.1 mm, $n = 1$ (Cotterill 2002a).

Skull robust; zygomatic arches sturdy; zygomatic width much greater than mastoid width. Nasal swellings of medium relative height; lateral profile smoothly rounded. Frontal depression moderately deep; supraorbital ridges prominent. Sagittal crest well developed. Palatal bridge of medium relative length (31–34% of C–M³; Csorba *et al.* 2003). Interpterygoid groove shallow but distinct. Anterior upper premolar minute, fully displaced labially; canine and posterior premolar in contact or almost so. Middle lower premolar minute

and fully displaced labially, or absent; anterior and posterior lower premolars in contact. Dental formula $^{1123}/_{2133} = 32$ or $^{1123}/_{2123} = 30$.

Geographic Variation None recorded.

Similar Species Four other African *Rhinolophus* occurring south of the Equator have the following combination of characters: anterior upper premolar fully displaced labially or absent; connecting process rounded; sella naked (or with sparse short hairs only) (Table 14, p. 304):

- Rhinolophus clivosus*. Lancet hastate. Horseshoe narrower (6.6–9.6 mm), narrower than muzzle. Connecting process higher. Skull with nasal swellings very low; frontal depression very shallow; supraorbital ridges weak. Interpterygoid groove absent or very indistinct. Upper canine and posterior premolar always in contact.
- R. darlingi*. Horseshoe narrower (7.1–8.7 mm). FA shorter (42–50 mm). Skull smaller (CrnC: 18.5–20.5, C–M³: 6.7–7.3 mm).
- R. deckenii*. Known only from East Africa. Morphometrically almost indistinguishable. Nasal swellings lower. Baculum with flattened, spatulate shaft.
- R. sakejensis*. Anterior upper premolar absent. Connecting process rising to high rounded peak. Lancet hastate. Skull with nasal swellings lower; frontal depression shallow; supraorbital ridges indistinct.

Distribution Endemic to Africa. Only known from the Rainforest BZ and from very nearby in the Southern Rainforest–Savanna Mosaic. Recorded only from Latoursville (Aellen 1959), Benga (Justine 1989) and Bélinga in Gabon, and from La Bamba and Meya-Nzouari in Congo (Csorba *et al.* 2003).

Habitat Dense rainforest in vicinity of caves.

Abundance Apparently rare; very few specimens known. See Conservation.

Remarks One of the most poorly known species of African bats. All specimens have been taken in caves, in which they roost by day. These caves include the Grotte de Maya-Nzouari in Congo, described in the profile of *R. adami*. From this limestone cave, one adult ♂ and five adult ♀♀ were collected on 26 July 1963, and three juveniles, two immature ♂♂ and one immature ♀ were collected on 25 November 1964, indicating that parturition occurs in this cave (Aellen & Brosset 1968): it is not known if other *R. silvestris* were present at the same time. This cave was also occupied by *Rousettus aegyptiacus*, *Rhinolophus adami*, *Hipposideros ruber*, *H. gigas*, *Triaenops afer* and *Miniopterus minor* (Adam & Le Pont 1974). Ectoparasites include bat-flies *Penicillidia fulvida* (Nycteribiidae) (Anciaux de Faveaux 1984).



Rhinolophus silvestris

Conservation IUCN Category: Data Deficient.

Only 12 specimens were collected (and none others reported) from only one of 45 caves investigated for the presence of bats over a period of ca. seven years (Adam & Le Pont 1974). Furthermore, it was not recorded from the nearby Mayombe and lower Kouilou regions of Congo, nor from the Haut-Ivindo region of Gabon, nor from Kikwit

(05° 13'S, 18° 49'E), DR Congo, during extensive investigations by other authors (for details, see profile of *R. adami*). As indicated by Dowsett *et al.* (1991), this species is potentially at risk because it roosts in caves occupied by fruit bats which may be hunted for food. Its status needs investigation.

Measurements

Rhinolophus silvestris

FA: 53.6 (50–56) mm, n = 6

WS: n. d.

TL: n. d.

T: 28, 32 mm, n = 2

E: 22, 23 mm, n = 2

NL (breadth): 9.5, 10 mm, n = 2

Tib: 23 (23–24), n = 5

HF: n. d.

WT: n. d.

CrnC: 23.1 (22.3–23.7) mm, n = 5*

GWS: 11.9 (11.7–12.1) mm, n = 5

C–M³: 9.0 (8.7–9.3) mm, n = 5

Gabon, Congo (Aellen 1959, Aellen & Brosset 1968, FMNH, MNHN)

*Csorba *et al.* 2003

Key References Aellen 1959; Aellen & Brosset 1968; Csorba *et al.* 2003.

F. P. D. Cotterill

Rhinolophus simulator BUSHVELD HORSESHOE BAT

Fr. Rhinolophe de brousse; Ger. Buschveld-Hufeisennase

Rhinolophus simulator K. Andersen, 1904. Ann. Mag. Nat. Hist., ser. 7, 14: 384. Upper Mazoe Valley, Mashonaland, Zimbabwe.

Taxonomy Species-group: *capensis*. Synonyms: *alticolus*, *bembanicus*. Subspecies: two of uncertain status. Aellen & Brosset (1968) treat *bembanicus* as a distinct species. However, the holotype of *bembanicus* no longer exists and until further specimens are available, its status remains uncertain (Ansell & Dowsett 1988). Possibly *alticolus* is also a distinct species (Csorba *et al.* 2003); for differences, see Geographic Variation. This form is considered distinct by Eisentraut (1963), Rosevear (1965), Hayman & Hill (1971) and others, but as conspecific with *R. simulator* by Koopman (1975), Hill & Morris (1971), Grubb *et al.* (1998) and Kock *et al.* (2000). Chromosome number (*R. s. simulator*, South Africa): 2n = 58; aFN = 60. X = large subtelocentric, Y = small submetacentric (Rautenbach 1986).

Description Small microbat with noseleaf (posterior component subtriangular with erect tip); medium–small for an African rhinolophid; anterior upper premolar within tooththrow; connecting process rounded; lancet triangular or hastate; sella with almost parallel or slightly concave sides, narrowest part of sella ca. 1.8 mm; no axillary tufts; E: 18–23 mm. Sexes similar. Pelage soft, fluffy; mid-dorsal hairs 8–9 mm. Dorsal pelage variable, dark sepia brown, medium brown, greyish-fawn, brownish-grey or grey; sometimes yellowish; hairs with

paler base. Ventral pelage notably paler, sometimes whitish. Orange-phase not known except, according to Kingdon (1974), in East Africa (but this needs confirmation). No axillary tufts on adult ♂♂. Ears comparatively and relatively short (18–23 mm, 45 [40–50]% of FA). Noseleaf with lancet subtriangular with sides straight or slightly concave (*R. s. alticolus*) or hastate (*R. s. simulator*). Connecting process rounded, higher than sella (*R. s. alticolus*) or ca. same height (*R. s. simulator*). Sella naked, sides almost parallel or slightly concave; narrowest part 1.5–1.7 mm (0.1–0.2 mm broader before preservation) (cf. *R. swinnyi*). Narial lobes at base of sella comparatively well developed (cf. *R. swinnyi*, *R. denti*). Horseshoe narrow (6.7–9.0 mm); lateral leaflets present in *R. s. alticolus*, very indistinct in *R. s. simulator*; anterior margination a deep notch. Lower lip with three grooves (lateral grooves occasionally indistinct). Wings dark brown to dark greyish-brown, darker near body; interfemoral membrane almost black. First phalanx of fourth finger of medium relative length in both subspecies (23.2 [20–25]% of metacarpal, n = 29). Tibia 40.0 (36–44)% of FA, n = 23 (including both subspecies).

Skull delicate; zygomatic arches thin; zygomatic width ≤ mastoid width. Nasal swellings relatively high, rounded. Frontal depression moderately deep; supraorbital ridges prominent. Sagittal crest very low.

Palatal bridge usually 29–34% of $C-M^3$, but up to 38% in *R. s. alticolus* (Csorba *et al.* 2003). Anterior upper premolar small to medium-sized, within toothrow; canine and posterior premolar well separated. Lower canines smaller than upper canines (cf. *R. landeri*). Middle lower premolar minute and fully displaced labially or (occasionally) absent; anterior and posterior lower premolars in contact. Anterior lower premolar less than half height of posterior premolar. Dental formula usually $^{1123}/_{2133} = 32$ or occasionally $^{1123}/_{2123} = 30$.

Geographic Variation Two subspecies are tentatively recognized here, but possibly *alticolus* is a distinct species (see Taxonomy):

R. s. alticolus: Guinea, Liberia, Nigeria, Cameroon. Rainforest and savanna. Dorsal pelage dark sepia brown. Lancet triangular, horseshoe broader, sella larger (Kock *et al.* 2000). Measurements and cranial morphology similar.

R. s. simulator: eastern Africa from Ethiopia to KwaZulu–Natal, South Africa. Mainly woodland savannas. Dorsal pelage medium brown to grey. Lancet hastate, horseshoe narrower, sella smaller (Kock *et al.* 2000).

Similar Species Five other *Rhinolophus* in Africa have the anterior upper premolar within the toothrow and the connecting process rounded (Table 14, p. 304):

Rhinolophus maendeleo. Lancet subtriangular, horseshoe probably almost always broader (8.2, 8.4 mm). FA longer (48, 49 mm), cf. 42–47 mm for *R. simulator* in area of sympatry.

R. swinnyi. Ears on average shorter (17 [15–20] mm). Sella narrower (narrowest part 1.2–1.3 mm); lobes at base of sella low. Skull with frontal depression very shallow, sometimes almost flat; supraorbital ridges weak.

R. d. denti. Lancet subtriangular. Often smaller (FA: 40–44 mm; E: 19 [18–21] mm; CrnC: 16.4 [15.8–17.0] mm). Lobes at base of sella low. Skull with frontal depression shallow; supraorbital ridges weak. Rostrum shorter and narrower. Semi-arid savanna and desert. In southern Africa, not recorded east of 25° E.

R. capensis. Connecting process higher than sella. Body measurements larger on average (FA: 48.8 [47–51] mm). Skull larger (CrnC: 20.0–21.1 mm; $C-M^3$: 7.2–7.8 mm). Frontal depression shallow; supraorbital ridges weak. As yet, known only from the Cape Province of South Africa.

R. adami. Ears longer (25, 26 mm). Lancet subtriangular with slightly convex sides, horseshoe broader (8.5, 9.0 mm). Palatal bridge relatively long (42, 44% of $C-M^3$). Rainforest of DR Congo and not known to be sympatric.

Distribution Endemic to Africa. Distribution very disjunct. In West Africa, *R. s. alticolus* is known from the Guinea Savanna BZ (Jos Plateau), the Northern Rainforest–Savanna Mosaic, marginally in the Rainforest BZ, and in the Afromontane–Afroalpine BZ of the Cameroon Mountains. Recorded from Guinea, Liberia, Nigeria, Cameroon. In the east, *R. s. simulator* is mainly recorded from the Somalia–Masai Bushland, Coastal Forest Mosaic and Zambezi Woodland BZs, and the Afromontane–Afroalpine BZ of the Ethiopian Highlands, but it extends marginally into the Eastern Rainforest–Savanna Mosaic and Sudan Savanna BZ. Recorded from S



Rhinolophus simulator

Sudan and Ethiopia southwards to Northern Province and KwaZulu–Natal in South Africa. Mapped from country checklists (see order Chiroptera), other literature and museum records.

Habitat In West Africa, habitats include montane forest (Mt Nimba, Cameroon Highlands), rainforest at 130 m (inland Cameroon), and the forest–savanna mosaic of the Jos Plateau (Nigeria). In eastern Africa, mainly found in wetter woodland savannas dominated by *Brachystegia*, with some records in montane habitats and coastal mosaics. In KwaZulu–Natal (South Africa), associated with Valley Bushveld along lower reaches of major, east-flowing rivers (Taylor, P. 1998). Distribution probably dependent on presence of caves and/or abandoned mines (Cotterill 1998, Taylor, P. 1998). Rare in semi-arid savanna; absent from deserts.

Abundance *Rhinolophus s. alticolus* ‘occurs in large numbers’ in Cameroon (Rosevear 1965). *Rhinolophus s. simulator* is ‘rarely recorded’ in Malawi (Happold & Happold 1997), but is locally common in Zimbabwe (colonies of hundreds recorded).

Adaptations *Rhinolophus s. alticolus* roosts by day in caves; sometimes shares roosts with *R. alcyone* (Rosevear 1965) and other rhinolophids. At ca. 1400 m, *R. s. alticolus* was active in its roost during the day whereas *R. hillorum* and *R. guineensis* (as *R. fumigatus*) in the same roost were torpid (Brosset 1985).

Rhinolophus s. simulator: aspect ratio low; wing-loading very low; wing-tip rounded. Flight very variable in speed and highly manoeuvrable. Can take off from ground, predictably can hover briefly. Turns by banking (minimum radius <25 cm), and by stalling-and-twisting; individuals sustained flight within a 1×1×1 m enclosure for up to 107 circuits/flight (3 bats, 10 flights each; M. Happold unpubl.). Roosts by day in both wet and dry caves and mine-adits (Rautenbach 1982); not known to roost by day elsewhere. Hangs freely from ceilings. In Malawi, shares caves with *R. fumigatus*

and *Nycteris thebaica* (M. Happold unpubl.); in Zimbabwe, shares caves with *Hipposideros vittatus* (but each species roosts in separate chambers), *R. hildebrandtii* and *Miniopterus natalensis* (Cotterill 1998). In Zimbabwe, becomes torpid by day in cool-dry season but not in hot-wet season (Cotterill 1998). Predicted mean maximum urine concentration is comparatively low (2904 mOsmol/kg) (Happold & Happold 1988). Captive bats drank several times each night; they landed beside water and drank by lapping and sucking.

Foraging and Food Forages by slow-hawking; predictably also by gleaning. *Rhinolophus s. alticolus* enters lighted rooms at night (Rosevear 1965); *R. s. simulator* takes insects near lights (Smithers 1983). In Zambia, in wet season, the stomachs of 34 individuals contained moths (73% by volume), beetles (13%), termites (8%), crickets (5%) and some other insects (Whitaker & Black 1976). In dry season, the stomachs of 18 individuals contained moths (87%) and midges (13%).

Echolocation Call-shape FM/CF/FM. For *R. s. simulator* in Malawi, CF-frequency 84–86 kHz (1 ♀, 3 ♂♂ hand-held, 1 ♀ tethered); maximum variation by a hand-held individual 1 kHz; call-duration 24–34 ms (M. Happold unpubl.). In Zimbabwe, CF-frequency 78 kHz (one bat flying in laboratory) (Fenton & Bell 1981). In South Africa, CF-frequency (mean \pm 1 S.D.) is 82.7 ± 0.4 kHz; maximum call-duration 17.7 ± 3.9 ms (Taylor 1999a). In Swaziland, CF-frequency 81.3, 82.0 kHz (two bats; Monadjem 2005). The low CF-frequency recorded by Fenton & Bell (1981) suggests that the recorded individual was misidentified.

Social and Reproductive Behaviour *Rhinolophus s. alticolus* has been found roosting singly and in groups of four ♂♂, 25–30 not sexed, ca. 250 (mostly ♀♀), and ‘hundreds’ (Rosevear 1965, Brosset 1984). *Rhinolophus s. simulator* usually roosts in colonies of several dozens, but colonies of ca. 150 and ca. 300 individuals have been recorded in South Africa (Rautenbach 1982, Wingate 1983). Group-members often hang in clusters but without touching their neighbours (Smithers 1983), but ♀♀ with young attached huddle very closely together (Cotterill 1998). Doornhoek Tunnel (near Pietermaritzburg, South Africa) was occupied by ca. 150 individuals of both sexes; in spring, the ♀♀ migrated to maternity roosts elsewhere and then returned in late summer; the ♂♂ remained throughout the year (Wingate 1983 in Taylor, P. 1998). Maternity colonies are also reported by Rautenbach (1982) and Cotterill (1998).

Reproduction *Rhinolophus s. alticolus* is reported to be seasonally monoestrous by Brosset (1984), but no conclusive evidence is given. For *Rhinolophus s. simulator*, litter-size (Malawi, Zimbabwe, South

Africa) one (n = 26). At 18–19°S (Zimbabwe), the reproductive chronology is restricted seasonal monoestry, with spermatogenesis in ca. May; sperm-storage in epididymides for at least three months (during cool-dry season); copulation beginning in late Jun; implantation beginning in Jul; births in the wet season (mid-Nov) after gestation periods of 90–130 days (depending on absence or occurrence of a period of retarded embryonic development); lactation not exceeding seven weeks (Cotterill 1998). Juveniles become volant when less than three weeks old. In Malawi and Zambia, births have been reported in Nov, but no data for other months (Happold & Happold 1990a). In South Africa, scrotal size increased from Apr–Jul indicating copulation probably occurs in winter (Wingate 1983); pregnant ♀♀ observed in Sep; lactating ♀♀ in Jan (Rautenbach 1982).

Predators, Parasites and Diseases Ectoparasites include a flea *Echidnophaga aethiops* (Pulicidae), bat-flies *Brachytarsina africana*, *Raymondia waterstoni*, *R. hardyi* (Streblidae) and a tick *Ixodes simplex* (Ixodidae) (Anciaux de Faveaux 1984).

Conservation IUCN Category: Least Concern.

Nevertheless, the breeding and maternity colonies are especially vulnerable to disturbance in their day-roosts (Cotterill 1998).

Measurements

Rhinolophus simulator

FA: 45.2 (42–49) mm, n = 60

WS (d): 292 (288–294) mm, n = 6*

TL: 74 (63–85) mm, n = 66

T: 25 (19–29) mm, n = 69

E: 21 (18–23) mm, n = 73

NL (breadth): 7.4 (6.7–9.0) mm, n = 15

Tib: 18.3 (18–20) mm, n = 25

HF: 8.3 (7–10) mm, n = 68

WT: 7.1 (5.1–11.2) g, n = 104*

CrnC: 18.4 (17.3–19.3) mm, n = 60†

GWS: 8.8 (7.6–9.5) mm, n = 39

C–M³: 6.4 (5.3–7.3) mm, n = 43

West Africa (n = 18), Malawi, Zimbabwe, South Africa (BMNH, HC, NMZB, ROM and literature)

*Southern Africa only

†Csorba *et al.* 2003

Key References Cotterill 1998; Csorba *et al.* 2003; Hill & Morris 1968; Kock *et al.* 2000; Smithers 1983.

F. P. D. Cotterill & Meredith Happold

Rhinolophus swinnyi SWINNY'S HORSESHOE BAT

Fr. *Rhinolophe de Swinnyi*; Ger. *Swinny's Hufeisennase*

Rhinolophus swinnyi Gough, 1908. Ann. Transvaal Mus. 1: 72. Ngqeleni District, Pondoland, South Africa.

Taxonomy Species-group: *capensis*. Synonyms: *piriensis*, *rhodesiae*. Subspecies: none. Considered closely related to *R. denti* and, based on close similarities in size, morphology and/or echolocation calls, it has often been suggested that *swinnyi* is a subspecies or synonym of *R.*

denti (e.g. Roberts 1914, Koopman 1966, Hayman & Hill 1971, Kock & Howell 1988, Bronner 1990). However, pending revision, *R. swinnyi* is tentatively retained here as a distinct species. Many references to *R. denti* in Zimbabwe actually refer to *R. swinnyi* (e.g. Fenton 1975, 1985,

Smithers & Wilson 1979, Fenton & Bell 1981, Taylor 1999a, Csorba *et al.* 2003). Chromosome number (South Africa): $2n = 58$; $aFN = 62$. $X =$ large subtelocentric, $Y =$ small metacentric (Rautenbach 1986).

Description Very small to small microbat with noseleaf (posterior component subtriangular with erect tip); small for an African rhinolophid; anterior upper premolar within tooththrow; connecting process rounded; lancet subtriangular with distinctly concave sides, or hastate; sella with slightly concave sides, narrowest part of sella 1.2–1.3 mm; no axillary tufts; ears 15–20 mm. Sexes similar. Pelage soft, fluffy; mid-dorsal hairs ca. 7 mm. Dorsal pelage pale grey to pale brown; hairs with pale cream at base. Ventral pelage paler, sometimes off-white or cream. In orange-phase, the dorsal pelage is bright orange. No axillary tufts on adult ♂♂. Ears comparatively and relatively short (15–20 mm, 35 [33–36]% of FA). Noseleaf with lancet subtriangular with markedly concave sides, sometimes almost hastate; tip bluntly pointed. Connecting process rounded, ca. same height as sella. Sella naked, sides slightly concave, narrowest point 1.2–1.3 mm, $n = 4$ (slightly narrower after preservation). Narial lobes at base of sella comparatively low (cf. *R. simulator*). Horseshoe narrow (6.0–7.4 mm), not covering whole muzzle; no lateral leaflets; median emargination a deep notch. Lower lip with three grooves but the lateral grooves are sometimes indistinct. Wings and interfemoral membrane brown. First phalanx of fourth finger of medium relative length (22.1 [21–25]% of fourth metacarpal, $n = 9$). Tibia 42.6 (39–47)% of FA, $n = 7$.

Skull delicate; zygomatic arches thin; zygomatic width = mastoid width. Nasal swellings rounded and of medium relative height. Frontal depression very shallow, sometimes almost flat; supraorbital ridges weak. Sagittal crest very low anteriorly, absent posteriorly. Palatal bridge of medium relative length, 30–34% of $C-M^3$ (Csorba *et al.* 2003). Anterior upper premolar small, within tooththrow; canine and posterior premolar well separated. Lower canines distinctly smaller than upper canines (cf. *R. landeri*). Middle lower premolar minute, fully displaced labially; anterior and posterior lower premolars in contact or almost so. Dental formula $^{1123}/_{2133} = 32$.

Geographic Variation No subspecies recognized. Csorba *et al.* (2003) report that the orange-phase appears to have become fixed in the topotypical population of *rhodesiae*.

Similar Species Five other African *Rhinolophus* have the anterior upper premolar within the tooththrow and the connecting process rounded (Table 14, p. 304):

- Rhinolophus simulator*. Ears on average longer (21 [18–23] mm). Sella broader (narrowest part 1.6–1.8 mm); lobes at base of sella higher. Skull with frontal depression moderately deep; supraorbital ridges prominent.
- R. denti*. Lancet subtriangular, sides slightly convex. Tibia often shorter (15–18 mm). Cranially indistinguishable except $CrnC$ usually shorter. Semi-arid savannas and deserts. In southern Africa, not recorded east of $25^\circ E$.
- R. capensis*. Connecting process higher than sella. Larger (FA: 47–51 mm). Skull larger ($CrnC$: 20.0–21.1 mm; $C-M^3$: 7.2–7.8 mm). Known only from the Cape Province of South Africa.
- R. adami*. Known only from rainforest in DR Congo.
- R. maendeleo*. Known only from coastal forests of Tanzania.

Distribution Endemic to Africa. Mainly recorded from the Zambezian Woodland BZ, with scattered records in the Afrotropical BZ (e.g. Uzungwa Mts in C Tanzania and Ntchisi F. R. in Malawi) and in the Coastal Forest Mosaic BZ (Zanzibar I. and South Africa), and a very isolated record in the Southern Rainforest–Savanna Mosaic at mouth of Congo R. There are scattered records in DR Congo, Tanzania, Zambia and Malawi, widespread records in Zimbabwe (Cotterill 1996a), and scattered records in E South Africa (Hayman *et al.* 1966, Anciaux de Faveaux 1978, Ansell 1978, Kock & Howell 1988, Bronner 1990, Happold & Happold 1997, Csorba *et al.* 2003).

Habitat In Tanzania, recorded from montane forest at 1350 m on the Uzungwa Mts (Kock & Howell 1988). In Malawi, known only from sub-montane seasonal rainforest at 1642 m on Ntchisi Mountain and adjacent open-canopy miombo woodland in Ntchisi F. R. (Happold & Happold 1997). In South Africa, recorded from montane forests (including *Podocarpus* mist forest) in KwaZulu–Natal and Cape Province (Bronner 1990). Recorded from savanna woodlands elsewhere in its geographic range (Cotterill 1996a).

Abundance Apparently rare south of Zambezi R.; widespread but scattered in Zimbabwe and only recorded singly or in small groups (Cotterill 1996a). Larger colonies recorded in SW Zambia (Ansell 1967), Katanga (DR Congo) and Zanzibar I. (Hayman & Hill 1971).

Adaptations Aspect ratio low; wing-loading very low; wing-tip rounded (M. Happold pers. comm.). Flight very variable in speed, and highly manoeuvrable. Can take off from ground; can almost hover. Turns by banking (minimum radius < 25 cm) and by stalling-and-twisting; individuals sustained flight within a $1 \times 1 \times 1$ m enclosure for up to seven circuits/flight (4 bats, 10 flights each). Roosts by day in totally dark positions in caves and old mines (Cotterill 1996a). Hangs from ceilings. In Zimbabwe, sometimes shares caves with much larger numbers of *R. simulator* (Cotterill 1996a).



Rhinolophus swinnyi

Food and Foraging Predicted to forage, by slow-hawking and possibly by gleaning, in cluttered places. In Zambia, in wet season, stomachs of 23 bats contained moths (55% by volume), beetles (26%), termites (6%) and also flies, midges, crickets, bugs and unidentified insects (Whitaker & Black 1976). In dry season, stomachs of nine bats contained moths (56%), midges (43%) and flies (1%).

Echolocation Call-shape FM/CF/FM. In Malawi, CF-frequency 102–104 kHz (3 ♀, 1 ♂ hand-held); maximum call-duration 37–74 ms (M. Happold pers. comm.). In Zimbabwe, CF-frequency 107 kHz, 110 kHz and 112 kHz (three bats; Fenton & Bell 1981, as *R. denti*): these bats have been confirmed as *R. swinnyi* (Monadjem *et al.* 2010). In Kruger N. P. (South Africa), CF-frequency 115 kHz (one bat flying in open) (Aldridge & Rautenbach 1987). The differences in CF-frequency at these different localities raise doubts about the identities of some of these bats (see Taxonomy).

Social and Reproductive Behaviour Single caves are occupied by 1–5 individuals, which roost singly or in twos scattered throughout the roost (Smithers 1983, Cotterill 1996a).

Reproduction Litter-size: one (n = 4). Reproductive chronology not known. At 13° 22' S (Ntchisi F. R., Malawi) 3 of 4 ♀ ♀ were heavily pregnant and one was lactating at beginning of wet season (early Nov); no data for other months (M. Happold pers. comm.). In C Zimbabwe, a ♀ had a full-term foetus on 14 Nov; no data for other months.

Predators, Parasites and Diseases Ectoparasites include bat-flies *Penicillidia pachymela*, *Phthiridium hoogstraali*, *P. ovale* (Diptera: Nycteribiidae), *Brachytarsina africana*, *Raymondia alulata*, *R. waterstoni* (Diptera: Streblidae) and mites *Eyndhovenia euryalis*, *Spinturnix walkerae*

(Acari: Spinturnicidae) and *Steatonyssus benoiti* (Acari: Macronyssidae) (Anciaux de Faveaux 1984).

Conservation IUCN Category: Least Concern.

Major threats: on-going, human-induced loss and degradation of habitat associated with agriculture and extraction of wood.

Measurements

Rhinolophus swinnyi

FA: 41.7 (40–44) mm, n = 24

WS (d): 257 (240–273) mm, n = 7

TL: 72 (60–95) mm, n = 24

T: 24 (16–30) mm, n = 24

E: 17 (15–20) mm, n = 22

NL (breadth): 6.8 (6.0–7.4) mm, n = 6

Tib: 18.4 (17–21) mm, n = 7

HF: 8.8 (8–9) mm, n = 19

WT: 6.1 (4.5–8.3) g, n = 17

CrnC: 17.4 (17.0–18.2) mm, n = 15*

GLS: 17.7 (17.4–18.0) mm, n = 9†

GWS: 8.5 (8.3–8.6) mm, n = 9

C-M³: 6.3 (6.1–6.6) mm, n = 10

Zambia, Zimbabwe and Malawi (BMNH, HC, NMZB)

*Csorba *et al.* 2003

†GLS measured to front of premaxillae

Key References Bronner 1990; Cotterill 1996a; Csorba *et al.* 2003; Smithers 1983; Whitaker & Black 1976.

F. P. D. Cotterill

Rhinolophus zياما ZIAMA HORSESHOE BAT

Fr. Rhinolophe de Zياما; Ger. Zياما-Hufeisennase

Rhinolophus zياما Fahr, Vierhaus, Hutterer and Kock, 2002. Myotis 40: 109. Western edge of Sérédou near park station, border of Réserve de la Biosphère du Massif du Zياما, Guinée Forestière, Guinea.

Taxonomy Species-group: *maclaudi* (Fahr *et al.* 2002). Synonyms: none. Chromosome number: not known.

Description Medium-sized microbat with noseleaf (posterior component subtriangular with erect tip); one of the largest rhinolophids in Africa (FA: 60 mm); anterior upper premolar within tooththrow; connecting process greatly reduced, very low and concave; lancet elongated, narrow with distal half almost parallel-sided; sella parallel-sided, inclined forward, with greatly enlarged narial lobes; horseshoe without lateral leaflets and a median emargination; no axillary tufts. Sexual dimorphism: no information. Pelage long, soft, woolly. Dorsal pelage buffy-brown; hairs with pale buff base and pale brown tip. Ventral pelage paler than dorsal pelage, dirty buff with pale brown sheen. Orange phase: not yet reported. No axillary tufts on adult ♂ ♂. Ears comparatively and relatively long (35, 36 mm, 59, 61% of FA), each with 11, 12 internal folds; antitragus very large. Noseleaf with lancet long and narrow, distal half with sides almost parallel, tip rounded, height of lancet conspicuously exceeding height of sella. Connecting process

greatly reduced, low and concave, leaving a deep emargination between sella and lancet (Figure 59n). Sella inclined forward and therefore not parallel to lancet, sides almost parallel, top not distinctly broadened; lobes at base of sella greatly enlarged, forming a roughly heart-shaped corolla-like cup (Figure 60f). Nostrils bordered laterally by conspicuously raised, nearly straight and more or less parallel rims, which almost reach anterior margin of horseshoe. Horseshoe of medium breadth (ca. 11.5 mm), almost covering muzzle; no lateral leaflets; median emargination inconspicuous or absent. Lower lip with one groove. Wings and interfemoral membranes dark grey. First phalanx of fourth finger relatively long (26, 29% of fourth metacarpal). Tibia 44, 45% of FA.

Skull large, slender; zygomatic arches broad but comparatively weak, dorsally notched; zygomatic width ca. = mastoid width. Rostrum robust; rostral emargination U-shaped; premaxillae broad. Nasal swellings high-domed; chambers (viewed dorsally) roughly heart-shaped (with posterior indentation). Frontal depression very deep. Braincase (viewed dorsally) constricted behind mastoid process; viewed laterally, the highest point is clearly behind the glenoid process (cf. *R. maclaudi*).

Sagittal crest moderate anteriorly, poorly developed posteriorly. Infraorbital bridge very long and very slender. Interpterygoid groove very deep. Palatal bridge: no data. Anterior upper premolar small, within toothrow; canine and posterior premolar separated. Middle lower premolar small, slightly to clearly displaced labially; anterior and posterior lower premolars sometimes in contact, sometimes separated. Lower molars medium-sized (cf. *R. hilli*, *R. ruwenzorii*). Dental formula $^{1123}/_{2133} = 32$. For detailed comparison of *R. ziama* with other species in *R. maclaudi* group, see Fahr *et al.* (2002).

Geographic Variation No information but, based on small distribution, probably negligible.

Similar Species Three other African *Rhinolophus* have a greatly reduced, low and concave connecting process (Table 14, p. 304):

Rhinolophus maclaudi. Larger (FA: 64–69 mm; CrnC: 29.0–30.1 mm; C–M³: 10.5–10.8 mm). Ears longer (40–46 mm). Horseshoe broader (15, 16 mm). Skull with highest point at height of glenoid process; infraorbital bridge stouter. West Africa.

R. ruwenzorii. Each ear with eight internal folds. Skull smaller (CrnC: 23.7–25.6 mm; C–M³: 8.2–8.9 mm). Sella upright and more or less parallel to lancet. Horseshoe narrower (10.8–12.6 mm); lateral leaflets present, median emargination conspicuous; nostrils bordered by semi-circular rims. Skull with zygomatic width < mastoid width; infraorbital bridge much shorter and stouter. Mountains flanking Albertine Rift Valley.

R. hilli. Smaller (FA: 54 mm; CrnC: 23.0 mm; C–M³: 7.9, 8.1 mm). Each ear with nine internal folds. Sella upright and more or less parallel to lancet, sides slightly concave. Horseshoe slightly broader (12 mm), lateral leaflets present, median emargination conspicuous, rims around nostrils semi-circular. Skull with zygomatic width slightly < mastoid width; infraorbital bridge very short and stout. Mountains flanking Albertine Rift Valley.



Rhinolophus ziama

Distribution Endemic to Africa. Apparently restricted to a very small area in the Rainforest BZ (Western Region) and Afromontane–Afroalpine BZ of SE Guinea and NW Liberia. Only known from two localities in the highlands of SE Guinea and NW Liberia (the Massif du Ziama near Sérédou in Guinea, and the Wonegizi Mts in Liberia). These localities are ca. 32 km apart. The record from Liberia was published as *R. maclaudi* (Koopman 1994, Koopman *et al.* 1995, Csorba *et al.* 2003). The distribution of the *Rhinolophus maclaudi* species-group is very disjunct and resembles that of the otter-shrews (genus *Micropotamogale*) (see profile of *R. maclaudi*).

Habitat The holotype and two additional individuals were mist-netted in degraded forest near the protected area of the Massif du Ziama in Guinea at ca. 600 m; this locality has a mean annual precipitation of 2400 mm. Close to the type locality, the vegetation is composed of wetter evergreen lowland rainforest and semi-deciduous lowland rainforest, with montane forest at higher altitudes. The specimen from Liberia was caught in ‘undisturbed High Forest’ (Koopman *et al.* 1995), also at ca. 600 m.

Abundance Not known but seems extremely localized and rare. Only four individuals have been reported. The surrounding areas have been surveyed recently but the species has not been found elsewhere.

Remarks Day-roosts not known but it seems likely that *R. ziama* is dependent on caves as are other members of the *R. maclaudi* species-group. The echolocation call-shape is likely to be FM/CF/FM (as in other *Rhinolophus*) and, based on the comparatively large size of this bat, the CF-frequency is likely to be rather low for a *Rhinolophus*.

Conservation IUCN Category: Endangered.

Major threats: extent of occurrence extremely small and within an area seriously affected by the civil war in Liberia and the adjacent region of Guinea; remaining forests are increasingly affected by logging, mining and agriculture. Possibly threatened by disturbance and direct exploitation in its day-roosts.

Measurements

Rhinolophus ziama

FA: 60, 60 mm

WS: n. d.

TL: –, 111 mm

T: 35, 37 mm

E: 36, 35 mm

NL (breadth): 11.5, 11.6 mm

Tib: 27, 26 mm

HF: 14, 14 mm

WT: 20.5, – g

CrnC: 26.1, 26.2 mm

GWS: 12.3, 12.5 mm

C–M³: 9.0, 8.9 mm

Guinea, Liberia (ZFMK [holotype] and AMNH [paratype], respectively); both ♂

Key Reference Fahr *et al.* 2002.

Jakob Fahr

Family HIPPOSIDERIDAE

OLD WORLD LEAF-NOSED BATS

Hipposideridae Lydekker, 1891. In: Flower & Lydekker, Mamm., Living and Extinct, p. 657.

| | | |
|----------------------------------|---------------------------|--------|
| <i>Asellia</i> (2 species) | Trident Leaf-nosed Bats | p. 360 |
| <i>Cloeotis</i> (1 species) | Short-eared Trident Bat | p. 364 |
| <i>Hipposideros</i> (14 species) | Old World Leaf-nosed Bats | p. 367 |
| <i>Triadenops</i> (1 species) | Trident Bat | p. 398 |

This is a polytypic family widely distributed in the tropical and sub-tropical regions of the Old World. Currently, the family contains nine extant genera (of which four are monotypic) and 81 extant species (Simmons 2005). In Africa, there are four genera and 18 currently recognized species, but some of these species probably contain cryptic species. The vast majority of species are in the genus *Hipposideros*. Hipposiderids have a complex noseleaf: the anterior component is usually very roughly horseshoe-shaped (as in Rhinolophidae) but there is no sella or connecting process, and the posterior component is either roughly elliptical, or 'trident-shaped' with three vertical projections (details below). Hipposiderids have roughly leaf-shaped ears with a minute tragus, toes with two phalanges, and a medium-length tail that is usually completely enclosed by the interfemoral membrane (but protrudes up to 3 mm in some African species of *Hipposideros* and up to 7 mm in *Asellia*). Hipposiderids resemble rhinolophids (which are closely related) but differ externally in the form of the noseleaf and the number of phalanges in the toes.

Hipposiderids (including African species) range in size from very small to very large. They have long soft dense pelage that is mostly brown, reddish-brown, grey or brownish-grey (in grey-phase), and most African species have an orange-phase. Most species have a small compact body and a rounded head with a short blunt muzzle, but some species are larger and more robustly built. The ears are mostly almost as broad as long and typically are well separated (but they are joined by a low band of skin in one species); the antitragus is conspicuous and the tragus is minute. The eyes are very small. The noseleaf is comprised of an anterior component that is roughly horseshoe-shaped in most species and often fringed with lateral leaflets, a central component that is little more than a thickened transverse pad, and an erect posterior component that is either low-arched or subtriangular in outline, or trident-shaped with three pointed projections. The central component has no sella or connecting process (cf. Rhinolophidae). Behind the posterior component, there is sometimes a frontal sac that opens through either a vertical or a horizontal slit. Many species of African hipposiderids are distinguished by the form of the noseleaf (see genus profiles). The wings are relatively large with short, rounded tips; the second finger has a long metacarpal but no bony phalanges. The hindlimbs are moderately long with small soles; the toes (excluding hallux) have two phalanges (cf. three in Rhinolophidae and other families). The tail is relatively short to medium (30–44% of TL); usually it is completely enclosed by the interfemoral membrane but it projects up to 7 mm beyond the membrane in *Asellia*, and up to 3 mm in some *Hipposideros*. Calcars are present. Females have one pair of pectoral nipples and one pair of pubic nipples. The skull is similar to that of the Rhinolophidae: for details of African species, see Hill (1963, 1982b). Because the nasal branches of the premaxillae are absent, and the palatal branches often lost during preparation of skulls, the greatest length of

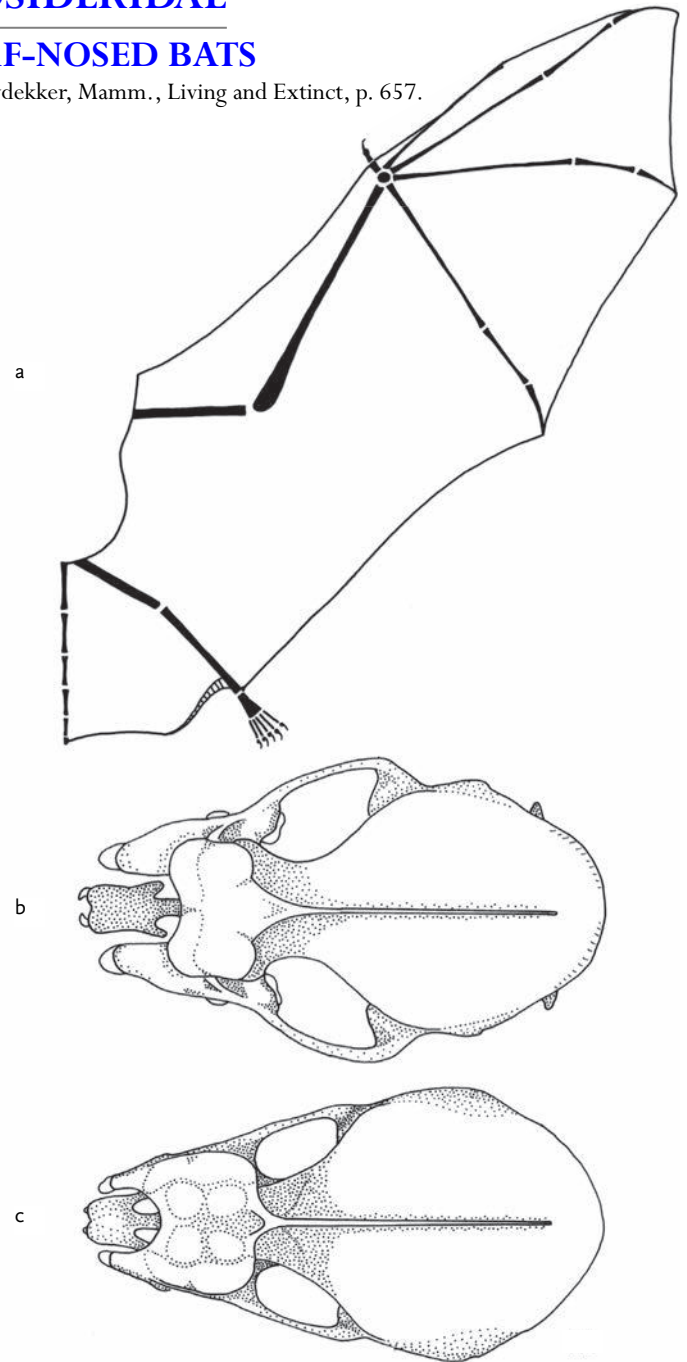


Figure 63. Characters of African bats in the family Hipposideridae. (a) Flight membranes and bones of wing, hindlimb and tail (e.g. *Hipposideros ruber*). (b) Dorsal view of a skull in which the zygomatic width is much greater than the mastoid width (e.g. *H. abae*; RMCA RG 36693). (c) Dorsal view of a skull in which the zygomatic width is much less than the mastoid width (e.g. *H. jonesi*; RMCA).

skull (GLS) of hipposiderids is replaced by CrnC – the distance from the anterior of the upper canine to the most posterior part of the skull. The greatest width of the skull (GWS) can be either the zygomatic width (ZW) or the mastoid width (MW) or it can be variable (Figure 63). The sagittal crest varies from low to greatly developed and usually extends over both frontal and parietal bones of the braincase (cf. many Rhinolophidae). Nasal swellings are present; the degree of inflation

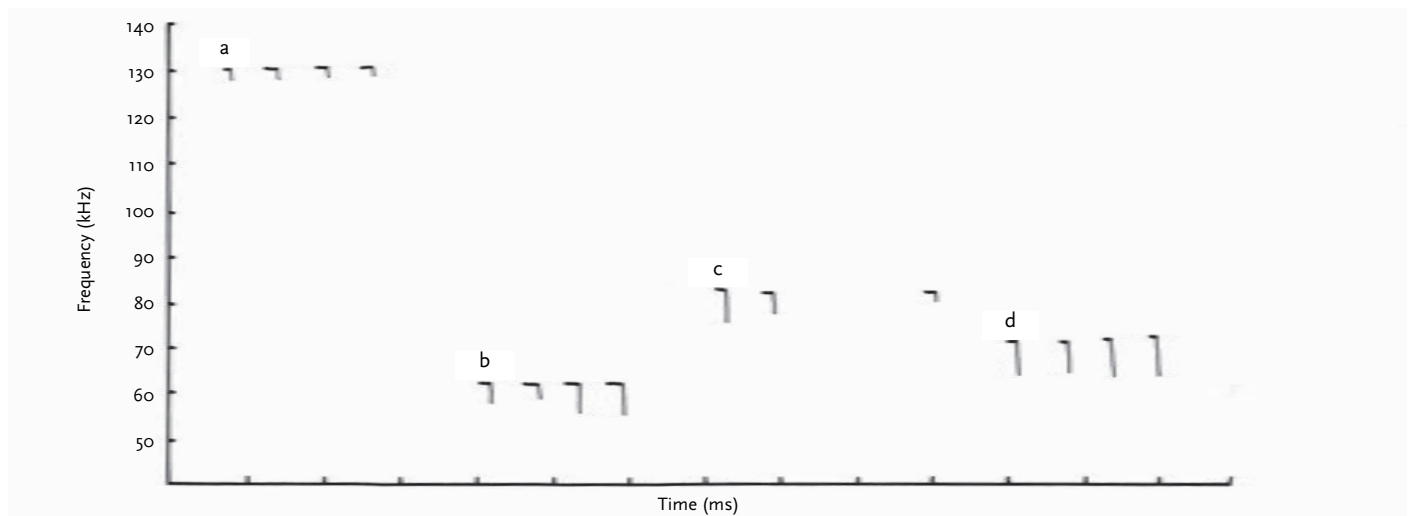


Figure 64. Sonograms of sequences of CF/FM echolocation calls emitted by four bats representing three species of Hipposideridae from Malawi (all hand-held) (M. Happold unpubl.). (a) Four calls by ♀ *Hipposideros ruber*, (b) four calls by ♂ *H. vittatus*, (c) three calls by ♀ *Triaenops afer* and (d) four calls by ♂ *T. persicus*. Time axis marked at intervals of 50 ms.

varies. Supraorbital ridges are usually low but definable, sometimes absent and sometimes prominent. In some species, the cochlea are expanded so the width of each one is equal to or greater than their distance apart. The dental formula is $^{1123}/_{2123} = 30$ except in *Asellia* and *Hipposideros megalotis*, which have only one upper premolar on each side. The upper incisor is usually weakly bicuspid, but the outer lobe may be greatly reduced or absent. The upper canine is longer than the other teeth and sometimes has anterior or posterior cusps. In *Hipposideros*, the length of the upper canine ranges from 38 to 54% of $C-M^3$, so 38–43% is relatively short, 44–49% is medium, and 50–54% is relatively long. The anterior upper premolar (P^2) is very small; it is often displaced labially so that the canine and posterior premolar (P^4) are in contact or nearly so, or it can be within the tooththrow or only slightly displaced, in which case the canine and posterior premolar are separated. The posterior upper premolar is long, sharp and somewhat similar to the canine in shape. The anterior lower premolar is typically lower than the posterior lower premolar, and has a smaller crown area.

Hipposiderids have very low to medium aspect ratios and very low to high wing-loadings. Their flight is variable: some fly slowly with considerable manoeuvrability; others fly more swiftly with greater agility but less manoeuvrability (Norberg & Rayner 1987). They can take off from the ground and some can hover briefly. Hipposiderids are insectivorous: the taxa and size of prey varies according to the size of the bat and the robustness of its teeth. Hipposiderids are often fly-catchers and gleaners but they also forage by slow-hawking, some to a greater extent than others. Unlike most rhinolophids, many hipposiderids forage in small groups. The echolocation calls are typically CF/FM in shape, with a sustained CF component and maximum energy in the second harmonic (Figure 64). Some (perhaps all) African hipposiderids can be recognized by the CF-frequency. The bimodal distribution of CF-frequencies recorded in a cave occupied by '*Hipposideros commersoni*' drew attention to the presence of two distinct species in this cave; they are now known as *H. gigas* and *H. vittatus*. Perhaps in some species, ♂♂ and ♀♀ use different frequencies (e.g. *Hipposideros caffer*, *Triaenops afer*) but this needs confirmation. The echolocation calls of hipposiderids are adapted to detect flutter (by exploiting Doppler-shifted echoes reflected from the fluttering wings of insects), and are particularly suitable for

densely cluttered environments (Neuweiler 1989). Hipposiderids, like rhinolophids, have nasal swellings (= rostral inflations, rostral swellings), which possibly facilitate the production of harmonics. Hipposiderids emit their echolocation calls through the nostrils, and the noseleaves direct a beam of sound in front of the bat and perhaps also modify the emitted sounds in other ways. While echolocating, the ears move independently with a rapid flickering movement, and the head moves up and down and from side to side to beam the sound in different directions. The rapid movements of the ears are correlated with the production of the echolocation calls, and the possible functions of the movements are discussed by Pye & Roberts (1970).

Hipposiderids are unable to scuttle over the ground, and apparently cannot climb. During the day, they roost in dark caves or cave-like day-roosts such as mines, tunnels, rock-crevices, hollow trees and dark places in buildings. They hang freely from footholds on horizontal ceilings or hang in contact from footholds on vertical surfaces. Some roost apart; some roost in contact with conspecifics. When roosting, the tail and interfemoral membrane folds up over the back and the wings fold around the chest so the body is almost enclosed by the flight-membranes. Some species hibernate, but hibernation is not known to occur in Africa although torpor for short periods during particularly cold weather has been reported for *Hipposideros caffer* in South Africa. Most African hipposiderids roost in large to very large colonies. The social organizations and mating systems of most species are not known, but a remarkable study of *H. beatus* by Brosset (1982) revealed that this species lives in monogamous family groups, and there is some evidence that the mating systems of *H. caffer* and *H. vittatus* are resource-based polygyny of some sort (see species profiles). Maternity colonies are established by some species. All African hipposiderids for which data are available are monotocous and seasonally monoestrous ($n = 6$ species). Species that occur both north and south of the Equator exemplify both boreal and austral chronologies. Reproductive delays have been documented for two species: delayed implantation in *Hipposideros caffer* at 10° N, and retarded embryonic development in *H. caffer* at 29° S, and in *H. ruber* at 7° S. Females carrying a juvenile have been mist-netted at night on two occasions, and I. L. Rautenbach observed that most of ca. 300 ♀♀ at a night-roost had young attached, indicating that the young

may be carried between day- and night-roosts and also on foraging flights (Ansell 1986a). Presumably the young cling to the pubic nipples as well as to the pectoral nipples while being carried.

The geological range of the family Hipposideridae is middle Eocene to Recent in Europe (but there are no hipposiderids in Europe at the present time), early Oligocene to Recent in Arabia, early Miocene to Recent in Africa, Pleistocene to Recent in Asia, late Oligocene to Recent in Australia (Hand & Kirsch 1998). Because they are predominantly cave-dwelling bats, their remains are frequently preserved in Cenozoic limestone sediments. The earliest known *Hipposideros* is from the early Miocene, and the subgenus *Syndesmotis* (into which *H. megalotis* is sometimes placed) appears to have separated from *Hipposideros* in the middle Miocene. Based on phylogenetic analyses, Bogdanowicz & Owen (1998) suggest that the Hipposideridae probably originated somewhere in the Oriental region. In contrast, based on evidence from fossils, Hand & Kirsch (1998) suggest that the family originated in Australia.

Hipposiderids have radiated into forests, savannas (especially woodland savannas) and arid habitats: the most extensive adaptive radiation has been within the genus *Hipposideros*. The majority of extant hipposiderids are found in the eastern half of the Old World tropics and sub-tropics: there are no temperate species (cf. Rhinolophidae). Of the 18 species in Africa, all species occur in the tropics but three species extend marginally either north (*Asellia tridens*) or south (*Cloeotis percivali*, *Hipposideros caffer*) of the tropics. Six species are found mainly or only in forests, six in both forest and savanna habitats, two mainly or only in savannas, two in both savanna and arid habitats, one only in arid habitats, and one (*H. caffer*) is found in all of these habitats. Nine species (50%) have been found in montane habitats, but none has been found only in montane habitats. Three or more species have been recorded at several localities, including:

Kagoro, Nigeria (Guinea savanna): *H. abae*, *H. jonesi*, *H. ruber* (Happold 1987).

Shimoni, Kenya (Coastal Forest mosaic with coral caves): *H. gigas*, *H. vittatus*, *T. afer* (Aggundey & Schlitter 1984).

Awash N. P., Ethiopia (grassland, thorn scrub with lava caves): *A. patrizii*, *A. tridens*, *H. vittatus*, *T. afer* (Largen *et al.* 1974).

Garamba N. P., DR Congo (Rainforest–Savanna mosaic with caves): *H. abae*, *H. beatus*, *H. caffer*, *H. cyclops*, *H. ruber* (Verschuren 1957).

Based on morphological data, the family Hipposideridae was placed in the superfamily Rhinolophoidea with the families Nycteridae, Megadermatidae and the very closely related Rhinolophidae (Simmons 1998, Simmons & Geisler 1998), but more recent molecular studies have contradicted many groupings based on morphological data (Simmons 2005). Some authors, including Koopman (1984, 1993, 1994) and Simmons (1998), follow Tate (1941) in considering the Hipposideridae to be a subfamily of the Rhinolophidae. However, the familial status of the Hipposideridae has been retained in the majority of books about African mammals and is tentatively retained here for several reasons. In addition to differences in the form of the noseleaves, the number of phalanges in the toes and the number of lower premolars, there are differences in the shoulder and pelvic regions. In the family Hipposideridae, the first and second ribs and corresponding vertebrae are fully fused, the lumbar vertebrae are frequently fused, and the pelvic girdle has a preacetabular foramen. In contrast, in the family Rhinolophidae, the first and second

ribs are only partially fused, there is no fusion of the lumbar vertebrae and no preacetabular foramen. Furthermore, the earliest fossil Hipposideridae (from the late Eocene and early Oligocene of France) were already distinct from the Rhinolophidae that occurred in the same deposits (Lekagul & McNeely 1977). However, the similarities between these taxa are greater than those between other families and they are evidently closely related. The family Hipposideridae has been reviewed by Hill (1963, 1982b) but not all of Hill's conclusions are supported by more recent phylogenetic studies. For example, it has been suggested that the genus *Hipposideros* is not monophyletic (see Genus *Hipposideros*). Furthermore, it has been indicated that the Hipposideridae is not monophyletic (Benda & Vallo 2009).

In Africa there are four genera:

Hipposideros. Posterior component of noseleaf roughly elliptical in outline (although the outline of upper margin varies from almost flat to low-arched or even subtriangular), without three projections (Figure 65a). Fourteen species currently recognized in Africa.

Asellia. Posterior component of noseleaf with three short, triangular projections (Figure 65b), tail protruding up to 7 mm beyond interfemoral membrane, only one upper premolar on each side, M³ greatly reduced (two ridges). Two species.

Cloeotis. Posterior component of noseleaf with three tall tapering projections (Figure 65c), tail completely enclosed by interfemoral membrane, FA: 31–39 mm, two upper premolars on each side, M³ not reduced (four ridges). One species.

Triaenops. Posterior component of noseleaf with three tall tapering projections (Figure 65d), tail completely enclosed by interfemoral membrane, FA: 49–61 mm, two upper premolars on each side, M³ not greatly reduced (three ridges). One species in Africa.

Meredith Happold

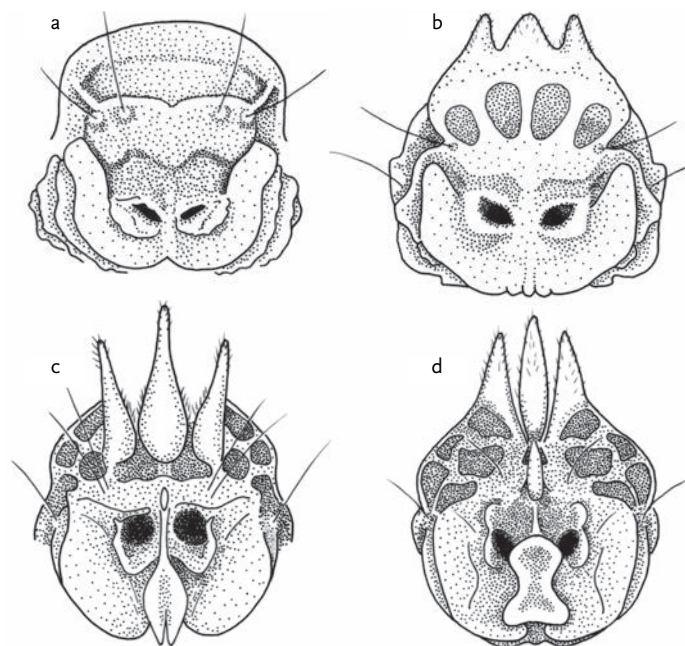


Figure 65. Noseleaves of representatives of the four genera of bats in the family Hipposideridae that are found in Africa. (a) *Hipposideros abae* (based on Rosevear 1965), (b) *Asellia tridens* (RMCA RG 31163), (c) *Cloeotis percivali* (based on Hill 1982b) and (d) *Triaenops afer* (based on Hill 1982b).

GENUS *Asellia*

Trident Leaf-nosed Bats

Asellia Gray, 1838. Mag. Zool. Bot. 2: 493. Type species: *Rhinolophus tridens* E. Geoffroy, 1813.

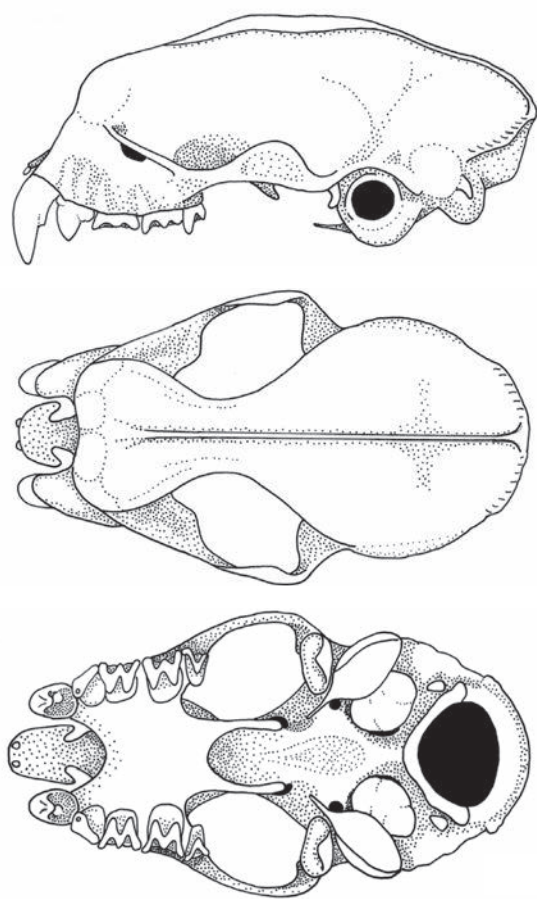


Figure 66. *Asellia tridens*. Skull (BMNH 1.5.5.17).

Asellia is a polytypic genus with only two species; neither is endemic to Africa. Distinguished from other African genera of hipposiderids by the following combination of characters: posterior component of

noseleaf with three subtriangular projections rising from the upper margin (i.e. somewhat trident-shaped – the central projection is pointed, the other two are blunt) (Figure 65b); tail projecting up to 7 mm beyond the interfemoral membrane. Furthermore, the posterior component of the noseleaf is not divided into deep cells by well-defined septa (cf. *Cloeotis* and *Triaenops*). Skull with sagittal crest greatly developed in the interorbital region; the deep rostrum and low braincase are of nearly equal height (Figure 66). Nasal swellings relatively small. Dental formula $^{1113}/_{2123} = 28$. The dentition is more modified than that of *Hipposideros*; the anterior upper premolar (P^2) is absent, the upper canine has a well-developed secondary cusp, and M^3 is considerably reduced, with only four cusps and two ridges. The species range in size from very small to small.

One species is widespread across most of Africa north of 12°N (extending further southwards in Ethiopia and Somalia) and extends extraliminally across Arabia to Pakistan. The other is confined to a small area in Ethiopia, Eritrea and offshore islands, extending extraliminally only as far as the nearby Saudi Arabian islands in the Red Sea. Both species are among the most desert-adapted bats; they are particularly tolerant of low relative humidities in their day-roosts (down to <30%).

Based on fossil evidence, Legendre (1982) noted that species of the extinct subgenus *Hipposideros* (*Pseudorhinolophus*) are morphologically similar to some recent taxa and could be ancestral to *Asellia*; this hypothesis is supported by the cladograms of Bogdanowicz & Owen (1998). The modern *Asellia* are reported from the Miocene of Europe (Astaratian) with *A. mariaetheresae* and Africa (Ternanian) with *A. vetus*. The karyotype of *Asellia tridens* is the nearest to the ancestral karyotype of the family.

The two species are:

A. patrizii. Smaller, FA: 38–43 mm, CrnC: 14.4–15.8 mm.

A. tridens. Larger, FA: 45–55 mm, CrnC: 16.5–19.3 mm.

Stéphane Aulagnier

Asellia patrizii PATRIZI'S TRIDENT LEAF-NOSED BAT

Fr. Trident de Patrizi; Ger. Patrizis Dreizackblattnase

Asellia patrizii De Beaux, 1931. Ann. Mus. Civ. Stor. Nat. Genova 55: 186. Gaarre [= Gahare], Dancalia, Ethiopia.

Taxonomy Synonyms: none. Chromosome number: not known.

Description Very small microbat with noseleaf (posterior component with three short projections); dorsally pale brownish-grey; tail projecting 3–5 mm beyond interfemoral membrane; FA: 38–43 mm. Sexual dimorphism: no information. Pelage soft, fluffy, dense; mid-dorsal hairs 6–7 mm. Dorsal pelage pale brownish-grey; hairs off-white or pale beige with brownish-grey at tip. Ventral pelage off-white. Ears well separated, naked, broad, height exceeding breadth; inner margin convex, outer margin convex with slight concavity below tip; tip shallowly pointed. Posterior component of

noseleaf with three short projections (the central one pointed, the outer two blunt), and with six cells arranged in a semi-circle below the projections – the outermost cells are open basally. Anterior component broad; two lateral leaflets on each side; no anterior median emargination; no hour-glass-shaped process. Wings and interfemoral membrane dark brown or sometimes paler; wing-membrane attaching to ankle. Third metacarpal long – slightly longer than fourth, much longer than fifth. Length of third metacarpal plus first phalanx is ca. 2–3 mm shorter than FA (cf. *A. tridens*). Interfemoral membrane small, rectangular, naked. Tail protruding 3–5 mm beyond interfemoral membrane.

Skull short, broad; zygomatic arches laterally flared with low jugal projection; zygomatic width > mastoid width. Nasal swellings well developed. Sagittal crest well developed and forming an evenly convex curve from the nasal swellings to the lambda. Upper incisor small, unicuspid. Upper canine powerful with well-developed secondary cusp at ca. half to two-thirds of its height. Anterior upper premolar absent; canine and large posterior premolar in contact. M³ greatly reduced and with only two ridges.

Geographical Variation No subspecies recognized.

Similar Species Three other hipposiderids in Africa have three vertical projections arising from the posterior component of the noseleaf:

Asellia tridens. Larger (FA: 45–55 mm; CrnC: 16.5–19.3 mm). Length of third metacarpal plus first phalanx is ca. 2 mm longer than FA.

Triaenops afer. Larger (FA: 49–60 mm; CrnC: 17.6–21.2). Tail fully enclosed by interfemoral membrane. Projections arising from posterior component of noseleaf are conspicuous, tall and tapering. Anterior component of noseleaf is broad with a conspicuous process (hour-glass shaped in outline) arising from the sides of a deep median emargination. Two upper premolars on each side; M³ not greatly reduced (three ridges).

Cloeotis percivali. Tail fully enclosed within interfemoral membrane. Ears shorter (7–11 mm). Projections arising from posterior component of noseleaf are tall and tapering. Two upper premolars

on each side; M³ not reduced (four ridges). Not known to be sympatric.

Distribution In Africa, known only from the Somalia–Masai Bushland and Afromontane–Afroalpine BZs in Ethiopia and Eritrea, including some small islands (Entedebir I., Nocra I.) in the Red Sea off the coast of Eritrea (Largen *et al.* 1974). Extraliminally: Saudi Arabian islands in the southern part of the Red Sea (Moeschler *et al.* 1990).

Habitat Recorded from very dry, open, rocky terrain, such as the semi-desert grassland, thorn scrub and volcanic rubble of the Awash N. P. in C Ethiopia (Hill & Morris 1971) and a lava field with scarce *Acacia* and other shrubs at Metahara, Shoa, Ethiopia (BMNH). Sea level (islands) to 1000 m in the Awash N. P.

Abundance Uncertain. Only small colonies have been observed, and few specimens have been collected. Populations are probably small and scarce.

Remarks Roosts by day in caves (including lava blister caves) and buildings, sometimes together with *A. tridens*. De Beaux (1931) observed *A. patrizii* leaving the roost and flying close to the ground while catching small insects. In Awash N. P., both sexes were observed in the same colony in Sep and Dec (Hill & Morris 1971).

Conservation IUCN Category: Least Concern.

Major threat: disturbance of roosts.

Measurements

Asellia patrizii

FA: 40.1 (38–43) mm, n = 22

WS (d): 240 (226–247) mm, n = 7

TL: 61.0 (55–66) mm, n = 10

T: 16.6 (13–20) mm, n = 21

E: 14.5 (12–16) mm, n = 22

NL (length): 6.5 (5.8–7.7) mm, n = 8

NL (breadth, including lateral leaflets): 6.7 (6.4–7.3) mm, n = 7

Tib: 16.6 (15–18) mm, n = 9*

HF: 6 mm, n = 1

WT: 3.9 (3.4–4.4) g, n = 9

CrnC: 15.0 (14.4–15.8) mm, n = 9

GWS: 8.0 (7.2–8.8) mm, n = 11

C–M³: 5.1 (4.9–5.2) mm, n = 11

Ethiopia and Entedebir I. (BMNH, de Beaux 1931)

*Ethiopia only

Key References De Beaux 1931; Hill & Morris 1971; Largen *et al.* 1974; Moeschler *et al.* 1990.

Stéphane Aulagnier



Asellia patrizii

Asellia tridens GEOFFROY'S TRIDENT LEAF-NOSED BAT

Fr. Trident du désert; Ger. Geoffroys Dreizackblattnase

Asellia tridens (E. Geoffroy, 1813). Ann. Mus. Natn. Hist. Nat. Paris 20: 265. Tombs of the Kings (Luxor) and Dadara (restricted to Luxor [= Thebes] by Kock 1969a), Egypt.

Taxonomy Originally *Rhinolophus tridens*. Synonyms: *diluta*, *italosomalica*, *murraiana*, *pallida*. Subspecies: four, three in Africa. Chromosome number (Tunisia): $2n = 50$; $aFN = 62$ (Baker *et al.* 1974).

Description Small microbat with noseleaf (posterior component with three short projections); dorsally pale brownish-grey with orange-phase; tail projecting up to 7 mm beyond interfemoral membrane; FA: 45–53 mm. Sexes alike in colour; based on forearm length, ♂♂ on average larger than ♀♀ in S Egypt but smaller than ♀♀ in Tunisia. Pelage soft, fluffy, dense; mid-dorsal hairs 5–9 mm. Dorsal pelage (grey-phase) pale brownish-grey; hairs off-white or pale beige with brownish-grey at tip. Ventral pelage (grey-phase) off-white. Orange-phase: dorsal and ventral pelage reddish to bright orange. Both colour phases and all intermediate colours have been observed in a single colony. Ears well separated, nearly naked, broad, height exceeding breadth; inner margin convex, outer margin convex with slight concavity below tip; tip shallowly pointed. Noseleaf as in Figure 65b. Posterior component with three short projections (the central one pointed, the outer two blunt), and with six cells arranged in a semi-circle below the projections – the outermost cells are open basally. Anterior component broad; two lateral leaflets on each side; no anterior median emargination; no hour-glass shaped process. Wings and interfemoral membrane with varying amounts of dark brown pigmentation – pale and translucent in some individuals. Wing-membrane attaching to ankle. Third metacarpal longer than fourth, much longer than fifth. Third metacarpal plus first phalanx ca. 2 mm longer than FA (cf. *A. patrizii*). Interfemoral membrane small, rectangular. Tail protruding up to 7 mm beyond interfemoral membrane.

Skull (Figure 66) short, broad; zygomatic arches laterally flared with low jugal projection; zygomatic width > mastoid width. Nasal swellings well developed. Sagittal crest well developed and forming an evenly convex curve from the nasal swellings to the lambda. Upper incisor small, unicuspid. Upper canine powerful with well-developed secondary cusp at ca. half to two-thirds of its height. Anterior upper premolar absent; canine and large posterior premolar in contact. M^3 greatly reduced and with only two ridges.

Geographic Variation Based on morphometric and colour variation, three main groups can be identified in Africa:

Large, dark animals: Morocco, Mauritania and N Egypt.

Small, pale animals: most of geographic range (Owen & Qumsiyeh 1987).

Smaller animals: Somalia and S Ethiopia (Koopman 1975).

The taxonomic status of these groups, whose differences could be local adaptations, needs confirming by genetic evidence.

Similar Species Three other hipposiderids in Africa have three vertical projections arising from the posterior component of the noseleaf:

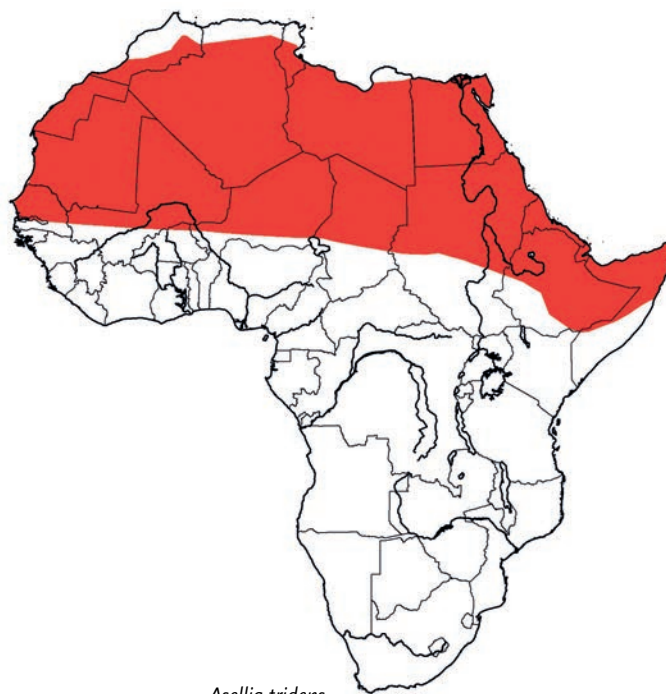
Asellia patrizii. Smaller (FA: 38–43 mm; CrnC: 14.4–15.8 mm).

Length of third metacarpal plus first phalanx is ca. 2–3 mm shorter than FA.

Triaenops afer. Tail fully enclosed by interfemoral membrane. Projections arising from posterior component of noseleaf are conspicuous, tall and tapering; central projection taller than outer ones. Anterior component of noseleaf broad with a conspicuous process (hour-glass-shaped in outline) arising from the sides of a deep median emargination. Two upper premolars on each side; M^3 not greatly reduced (three ridges).

Cloeotis percivali. Tail fully enclosed within interfemoral membrane. Smaller (FA: 31–39 mm; CrnC: 12.0–13.5 mm). Projections arising from posterior component of noseleaf are tall and tapering. Two upper premolars on each side; M^3 not reduced (four ridges). Not known to be sympatric.

Distribution In Africa, this desert species has been recorded from the Sahara Arid and Sahel Savanna BZs (and marginally in the Sudan Savanna BZ) and from the most arid parts of the Mediterranean Coastal and Somalia–Masai Bushland BZs. Recorded from very scattered localities in Morocco (south of Atlas Mts), Algeria, Tunisia, Libya and Egypt (but not in coastal belt), and southwards to Mauritania, Gambia, Senegal, Mali, Burkina, Niger,



Asellia tridens

N Chad, N Sudan, Ethiopia and N Somalia (Kock 1969a, Koch-Weser 1984, Qumsiyeh 1985, Aulagnier & Thévenot 1986, Kowalski & Rzebik-Kowalska 1991, Jones *et al.* 1993, Benda *et al.* 2004d). Extraliminally: through Arabia to Pakistan. A record from Zanzibar (Peters 1871) has never been confirmed (though often cited) and may be a mislabelled MNHN specimen (D. Kock pers. comm.).

Habitat Found in a wide variety of desert and semi-desert vegetation zones, mainly in oases or nearby. The extremely arid parts of the Sahara are avoided, and the distribution elsewhere is limited to areas with suitable day-roosts and supplies of insects.

Abundance Very common. The most commonly mist-netted bat in the Saharan Atlas and the Occidental Erg; also the most common bat in owl pellets in S Morocco and Algerian Sahara. Colonies number from ca. ten to several hundred individuals in Africa; up to 5000 extraliminally in Iran.

Adaptations Aspect ratio medium–low; wing-loading low (Jones *et al.* 1993). Flight predicted to be slow with great manoeuvrability; bats observed to make rapid twists and turns. By day, roosts in caves and mines (near the entrance), open wells and underground irrigation tunnels, old tombs, dark ruins and buildings. Clings in contact with walls. Surprisingly tolerant of light; roosts in lighted shelters and individuals were recorded flying in the daylight under palm trees in Morocco (Aulagnier & Thévenot 1986), and emerging from their day-roosts before dusk in Algeria (Kowalski & Rzebik-Kowalska 1991). Also very tolerant of low relative humidities in their day-roosts (down to <35%; Gaisler *et al.* 1972). Active all year round (Koch-Weser 1984). In Iraq, colonies are suspected to migrate in some parts of the geographic range; from winter to summer quarters in Apr–May, and back again from mid-Sep to mid-Nov (Al-Robaee 1966). Fat deposits have been observed during the wet season in Burkina (Koch-Weser 1984).

Foraging and Food Forages by slow-hawking and presumably by ground-gleaning; has been observed foraging around palm trees and buildings, and over water. Foraging flights are low with rapid twists and turns. Feeds mainly on large insects: Coleoptera, Hymenoptera, Orthoptera, Diptera and Lepidoptera (Jones *et al.* 1993, Whitaker *et al.* 1994, Feldman *et al.* 2000), and even on scorpions. There are important variations in diet, both locally and seasonally.

Echolocation Search-phase call-shape CF/FM. The CF-component is sometimes of very low amplitude, but is always present (Pye 1972): this is discussed in detail by Roberts (1972). For 11 Egyptian bats, the CF-frequency varied from 115 to 120 kHz; each individual emitted a narrow range of frequencies, and different individuals emitted different ranges of frequencies (Roberts 1972). For 18 Tunisian bats, resting, the CF-frequency was 111–124 kHz (the CF-frequency varied from bat to bat; individuals kept the frequency constant); bandwidth of terminal FM sweep 19–21 kHz; call-duration 7–10 ms; minimum intercall interval 27–215 ms (depending on degree of alertness) (Gustafson & Schnitzler 1979). Flying bats lowered their emission frequency to compensate for Doppler shifts caused by the flight movement; call-duration 9–11 ms; minimum inter-call interval 26 ms. For bats in a roost in

Gambia containing thousands of individuals, the CF-frequency was 108–122 kHz (frequency found to be negatively correlated with FA length within sexes); lowest frequency of the terminal FM sweep 97 kHz: call-duration 7.5–9 ms, inter-call interval 10–20 ms (Jones *et al.* 1993).

Social and Reproductive Behaviour Normally roosts in groups (colonies) containing, in Africa, ca. 10 to several hundred individuals (up to 500 in Egypt; Gaisler *et al.* 1972). In Morocco, sexes segregate in Mar when these bats move from their winter to their summer quarters. Pregnant ♀♀ establish maternity colonies; non-reproductive ♀♀ often roost with the ♂♂ (Brosset 1955, Brosset & Caubère 1960). Groups of subadults have been found in Egypt (Gaisler *et al.* 1972). In Burkina, ♂♂ and ♀♀ share the same roost throughout the year (Koch-Weser 1984), however sexual segregation perhaps occurs inside the roost, as in Iraq (Al-Robaee 1966).

Reproduction and Population Structure Litter-size (Mauritania, Tunisia and Egypt): one ($n = 32$). Reproductive chronology in Africa not known (data inconclusive); in Iraq, the reproductive chronology is restricted seasonal monoestry with mating in autumn, births in early Jun and lactation lasting ca. 40 days (Al-Robaee 1966). At 17°02'N in Mauritania, five pregnant ♀♀ were reported in mid-May (crown–rump length of embryos 7–13 mm); no data given for other months (Qumsiyeh & Schlitter 1981). In Egypt, 13 of 18 ♀♀ were pregnant, and five were adult but not pregnant, in late Apr to early May; no data for other months (Gaisler *et al.* 1972). In Burkina, young were observed in the wet season (mid-Jul); they were not yet independent and, based on their size, births were estimated to have occurred in late May to early Jun; adult-size attained in Nov (data collected Jun–Jan only; Koch-Weser 1984).

Predators and Diseases Regular, but minor, prey of Sooty Falcons *Falco concolor*, Lanner Falcons *Falco biarmicus*, Barn Owls *Tyto alba*, Pharaoh Eagle-owls *Bubo ascalaphus*, Spotted Eagle-owls *Bubo africanus* and Northern Long-eared Owls *Asio otus* (Booth 1961, Aulagnier 1989, Kowalski & Rzebik-Kowalska 1991, Benda *et al.* 2004d). Ectoparasites include a flea *Chiropteropsylla brockmani* (Siphonaptera: Ischnopsyllidae); bat-flies *Penicillidia senegalensis*, *Eucampsipoda hyrtlui* (Diptera: Nycteribiidae), *Brachytarsina kollari*, *Raymondia huberi*, *R. setosa* (Diptera: Streblidae); a tick *Carios boueti* (Acari: Argasidae); and mites *Hipposiderobia heteronycha* (Acari: Myobiidae) and *Opsonyssus striatus* (Acari: Gastronyssidae) (Anciaux de Faveaux 1984).

Conservation IUCN Category: Least Concern.

Measurements

Asellia tridens

FA: 49.8 (45–55) mm, $n = 153$

WS: n. d.

TL: 80.8 (66–89) mm, $n = 140$

T: 23.3 (18–28) mm, $n = 144$

E: 19.0 (15–21) mm, $n = 145$

NL (length): 8.7 (7.7–10.1) mm, $n = 12$

NL (breadth): 8.1 (7.1–9.1) mm, $n = 31$

Tib: 19.3 (17–21) mm, n = 19

HF: 9.1 (8–10) mm, n = 144

WT: 10.3 (6–13) g, n = 61

CrnC: 18.5 (16.5–19.3) mm, n = 66

GWS: 10.3 (9.4–10.8) mm, n = 66

C–M³: 6.7 (6.2–7.1) mm, n = 123

Morocco, Algeria, Tunisia (excluding skull measurements), Egypt, Sudan (BMNH, Panouse 1951, Gaisler *et al.* 1972 [weights], Baker *et*

al. 1974, Qumsiyeh 1985, Romero Zarco 1990, Kowalski & Rzebik-Kowalska 1991)

Key References Brosset & Caubère 1960; Kock 1969a; Koch-Weser 1984; Kowalski & Rzebik-Kowalska 1991; Qumsiyeh 1985.

Stéphane Aulagnier

GENUS *Cloeotis* Percival's Trident Bat

Cloeotis Thomas, 1901. Ann. Mag. Nat. Hist., ser. 7, 8: 28. Type species: *Cloeotis percivali* Thomas, 1901.



Cloeotis percivali.

Cloeotis is a monotypic genus endemic to Africa and known only from south-east Africa. Distinguished from other African genera of hipposiderids by the following combination of characters: posterior component of noseleaf with three tall, spear-like projections rising from the upper edge (i.e. trident-shaped) (Figure 65c); tail fully enclosed by interfemoral membrane, FA 32–39 mm. Furthermore, the posterior component of the noseleaf is pitted with deep cells (cf. *Asellia*) and the ears are short, very rounded and deep (Figure 67). Skull (Figure 67) with zygomatic arches not greatly expanded (c.f. *Triaenops*); rostrum very short with nasal swellings weakly developed; premaxillae not unusually thick; upper canine with secondary cusps. Dental formula $^{1123}/_{2123} = 30$.

The only species is *Cloeotis percivali*.

Meredith Happold

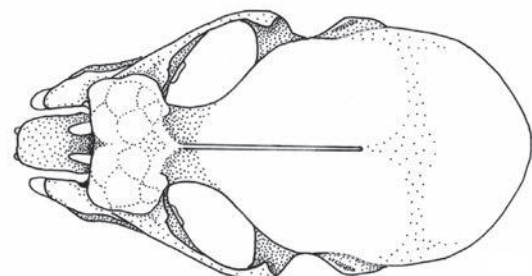
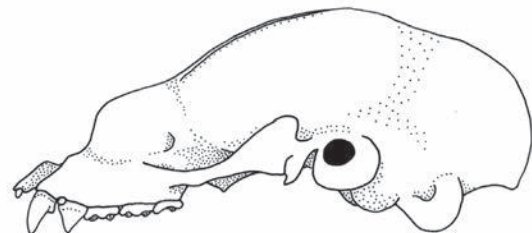
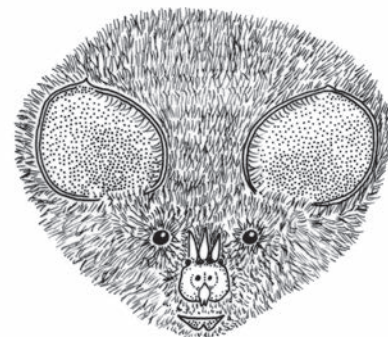
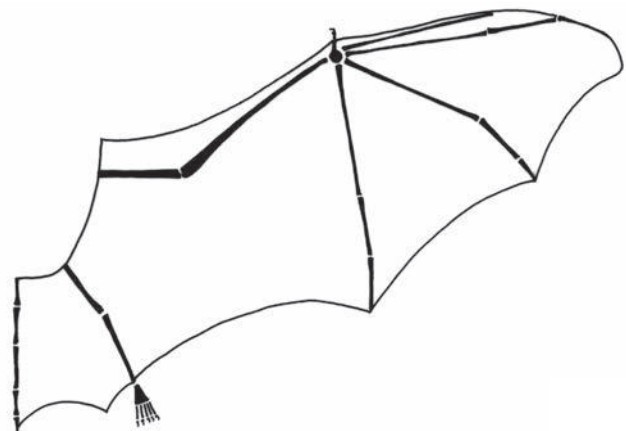


Figure 67. *Cloeotis percivali*. Flight membranes and bones of wing, hindlimb and tail. Dorso-frontal view of face showing the very deep, rounded ears (based on photo by N. Rautenbach in Mills & Hes 1997). Lateral view of skull (HZM 13.4765) and dorsal view of skull (RMCA RG 19243).

Cloeotis percivali PERCIVAL'S TRIDENT BAT (SHORT-EARED TRIDENT BAT)

Fr. Cléote de Percival; Ger. Percivals Kleinohr-Dreizackblattnase

Cloeotis percivali Thomas, 1901. Ann. Mag. Nat. Hist., ser. 8, 7: 28. Takaungu, north of Mombasa, Coast Province, Kenya.

Taxonomy Synonyms: *australis*. Subspecies: two of uncertain validity (see Geographic Variation). Chromosome number (South Africa): $2n = 40$; aFN not known (Rautenbach *et al.* 1993).

Description Very small microbat with noseleaf (posterior component with three tall projections); smallest African hipposiderid; dorsally grey to greyish-brown with orange-phase; tail almost fully enclosed by interfemoral membrane; FA: 31–39 mm. Sexes alike. Pelage soft, dense, silky; mid-dorsal hairs 7–8 mm. Dorsal pelage (grey-phase) slate-grey to medium or pale greyish-brown; hairs unicoloured. Face often paler (sometimes yellowish, sometimes off-white) with brown or grey around eyes, noseleaf and mouth. Ventral pelage white, off-white or yellowish-white; hairs dark brownish-grey or grey with white, off-white or yellowish tips. Orange-phase: dorsal pelage brown to bright brownish-orange becoming paler and more yellow on shoulders and head, with brown around eyes, noseleaf and mouth. Muzzle broad, short and rather flat. Ears separated, almost hidden by pelage, greyish-brown, comparatively and relatively short (25.4 [22–31]% of FA, $n = 46$), very rounded and deep with barely perceptible tip, giving each ear the appearance of a satellite dish. Noseleaf as in Figure 65c. Posterior component with a semi-circle of six cells (separated by moderately fleshy septa) around the outer margin, and four central cells arranged transversely across the middle. Each of the three projections arising from the posterior component is in line with one of the three septa separating the central cells: the three projections comprise the 'trident' referred to by the common name of this genus. Anterior component narrow, not concealing the broad, conspicuous lateral leaflets, anterior margin with deep, narrow median emargination. Nostrils deeply pocketed with well-defined lateral lappets. Wings and interfemoral membrane dark brown to greyish-brown. Calcar short, weak. Tail with last vertebra only protruding beyond interfemoral membrane; 64–91% of HB. Hindfoot small, delicate, with long claws. See also Hill (1982b).

Skull (Figure 67) very small and delicate; rostrum short and narrow; braincase relatively large. Zygomatic arches slender with a prominent jugal processes; zygomatic width > than mastoid breadth. No supraorbital ridges. Interorbital constriction very pronounced. Sagittal crest very low anteriorly, absent posteriorly. Cochlea slightly enlarged, their breadth ca. 1.5 times their distance apart. Upper incisor bicuspid. Upper canine slender with conspicuous posterior cusp and smaller anterior cusp. Anterior upper premolar fully displaced labially; canine and posterior premolar in contact or nearly so. M^3 not reduced, four ridges. Further craniodental details in Hill (1982b).

Geographic Variation Two subspecies are recognized by Koopman (1994) and Simmons (2005):

C. p. percivali: SE Kenya, NE Tanzania (but no localities given). FA: 31–32 mm, $n = 2$. Anterior lower premolar at least three-quarters the crown area of posterior premolar and more than half its height.



Cloeotis percivali

C. p. australis: S DR Congo to Botswana and Swaziland. FA: 32–39 mm, $n = 82$. Anterior lower premolar one half or less the crown area of posterior premolar and less than half its height.

These differences between the subspecies are slight, and the description of *australis* was based on only eight specimens. Hayman (1960b) noted an apparently constant colour difference between the northern and southern populations but at least one specimen from Zambia was the same colour as the holotype from Kenya (Hayman & Hill 1971). Therefore, subspecific distinction is probably not warranted.

Similar Species Four other hipposiderids in Africa have three vertical projections arising from the posterior component of the noseleaf:

Asellia tridens. Tail protruding up to 7 mm beyond interfemoral membrane. Larger (FA: 45–55 mm; CrnC: 16.5–19.3 mm). Only one upper premolar on each side; M^3 greatly reduced (only two ridges). Not sympatric.

A. patrizii. Tail protruding up to 5 mm beyond interfemoral membrane. Ears usually longer (12–16 mm). Only one upper premolar on each side; M^3 greatly reduced (only two ridges). In Africa, known only from Ethiopia and Eritrea.

Triaenops afer. Larger (FA: 49–60 mm; CrnC: 17.7–21.2 mm). Anterior component of noseleaf broad with a conspicuous process (hour-glass shaped in outline) arising from the sides of a deep median emargination. M^3 not greatly reduced (three ridges).

Distribution Endemic to Africa. Recorded mainly from the Zambezian Woodland BZ, but also found in some small parts of the Kalahari Desert, Highveld and Coastal Forest Mosaic BZs. In East Africa, known from the type locality just north of Mombasa in coastal Kenya and from Mafia I. (K. M. Howell pers. comm.). In south-central Africa and southern Africa, recorded disjunctly from SE DR Congo (Shinkolobwe, Katanga), Zambia (Kafue Gorge), SE Botswana (Kanye and Molopole areas), Mozambique (Tete District), Zimbabwe (six localities from the Kariba Dam in the north to Mutare in the east and Gwanda in the west), Swaziland (two localities) and South Africa (nine localities in the Northern, Mpumalanga and KwaZulu–Natal Provinces). References include Hayman 1960b, Koopman 1966, Smithers & Lobão Tello 1976, Smithers 1983, Monadjem 1998a.

Habitat Not much is known. Vegetation zones from which these bats have been recorded include undifferentiated woodland, wetter and drier miombo woodland and mopane woodland. In South Africa and Zimbabwe, many of the roosts are located in mixed woodland.

Abundance Uncertain. Since its description, only one other specimen has been taken from the type locality area (Kingdon 1974). Although the geographical range in south-central Africa and southern Africa is fairly wide, it is not known to occur there in great numbers.

Adaptations Aspect ratio very low; wing-loading very low. Based on wing morphology, probably capable of slow, manoeuvrable flight in dense vegetation. By day, recorded roosting in caves, service tunnels in dam walls, an underground irrigation canal in Zimbabwe, and disused mines; usually occupies the deepest, darkest parts where no light penetrates. Skull, lower jaw and dentition comparatively gracile; adapted for specializing on soft-bodied prey (Jacobs 2000).

Foraging and Food Foraging habits not known; wing morphology suggests foraging in dense vegetation (see Adaptations). Feeds almost exclusively on moths (Black 1979, Jacobs 2000).

Echolocation Call-shape CF/FM. CF-frequency 208–212 kHz; duty cycle high (Fenton & Fullard 1981, Taylor 1999a, Jacobs 2000). Fenton & Fullard (1981) and Jacobs (2000) suggest that the high frequency of its echolocation calls enables this species to prey more efficiently on moths. Moths respond to the sound of approaching bats by closing their wings and falling away from the bats' flight-path, but they hear best at frequencies between 20–50 kHz and are deaf to the high-frequency echolocation calls of *C. percivali*. Therefore this species can approach moths without eliciting their escape behaviour.

Social and Reproductive Behaviour Very little information. Roosts in groups (colonies) ranging in size from ca. 12 to a few hundred individuals. Hangs in loose groups in which adjacent individuals are

not in contact (i.e. not in tight clusters as indicated by Smithers 1983).

Reproduction and Population Structure Litter-size: one ($n = 6$). Reproductive chronology not known (data inconclusive). In Zimbabwe, pregnant ♀♀ were reported in Oct; no data published for other months (Smithers & Wilson 1979). At 27° 25' S (Jozini Dam, KwaZulu–Natal, South Africa), none of 3 adult ♀♀ was palpably pregnant in mid-Aug; 4 of 4 were pregnant or lactating in Nov (P. J. Taylor pers. comm.). At 25° 22' S (Sudwala, Mpumalanga Province, South Africa) 7 of 11 ♀♀ were pregnant and two were lactating in late Nov. These data indicate that some births occur in summer (Nov) and that adult ♀♀ are in reproductive synchrony, but it is not yet known if this species is monoestrous or polyestrous.

Predators, Parasites and Diseases Ectoparasites include a bug *Eoctenes intermedius* (Hemiptera: Polycetidae); bat-flies *Raymondia alulata*, *R. hardyi*, *R. seminuda* (Diptera: Streblidae); and mites *Eoctenes intermedius*, *Hipposiderobia cloeotis* (Acari: Myobiidae) (Anciaux de Faveaux 1984).

Conservation IUCN Category: Least Concern.

However, very sensitive to disturbance by humans. Classified as 'specially protected' under the KwaZulu–Natal Nature Conservation Service Conservation Ordinance of 1999.

Measurements

Cloeotis percivali australis

FA: 34.1 (32–39) mm, $n = 82$

WS (c): 211 (196–228) mm, $n = 18^*$

TL: 65.8 (60–76) mm, $n = 61$

T: 29.1 (24–36) mm, $n = 81$

E: 8.8 (7–11) mm, $n = 81$

NL (length): 4.9 (4.6–5.2) mm, $n = 5$

NL (breadth, including lateral leaflets): 4.4 mm, $n = 1$

Tib: n. d.

HF: 6.2 (5–8) mm, $n = 20$

WT: 4.1 (3–6) g, $n = 52$

CrnC: 13.0 (12.0–13.5) mm, $n = 51$

GWS: 7.3 (7.1–7.5) mm, $n = 28$

C–M³: 4.1 (3.9–4.3) mm, $n = 33$

Zambia, Zimbabwe, Mozambique, South Africa (BMNH, HZM, RMCA, TM and literature)

*South Africa only (D. S. Jacobs unpubl.)

Key References Hayman 1960b; Hill 1982b; Jacobs 2000; Smithers 1983.

David S. Jacobs

GENUS *Hipposideros*

Old World Leaf-nosed Bats

Hipposideros Gray, 1831. Zool. Misc. 1: 37. Type species: *Vespertilio speoris* Schneider, 1800.

Hipposideros cyclops.



Hipposideros gigas.



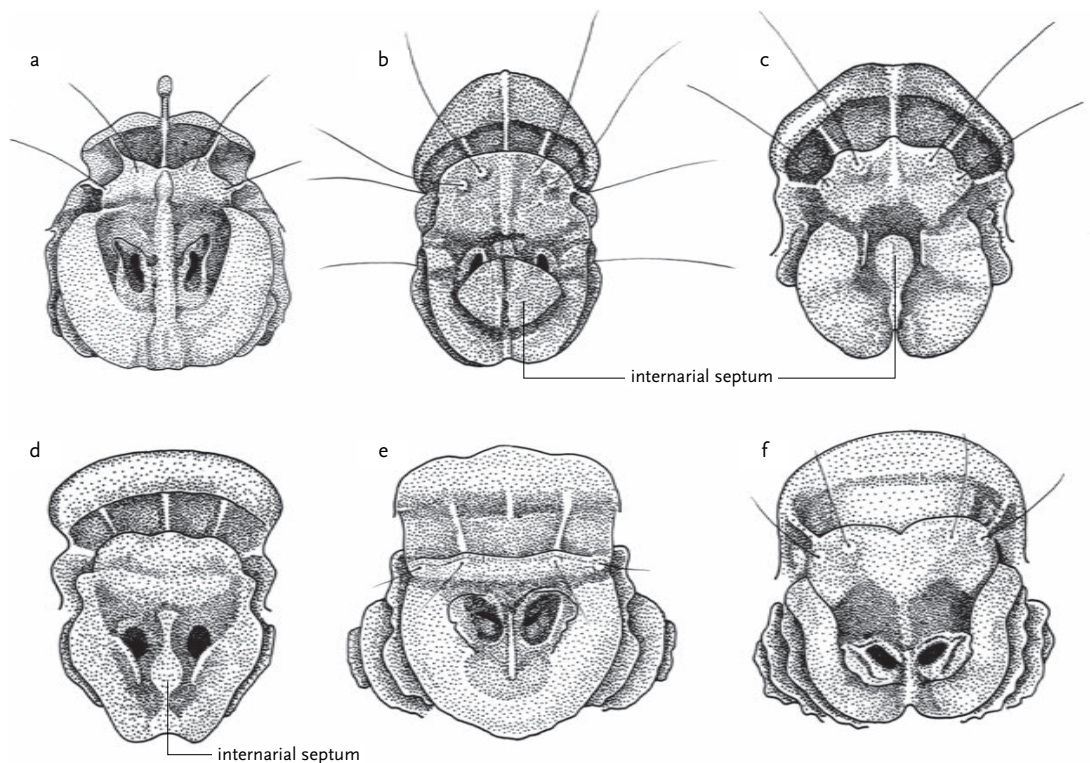
Hipposideros contains many more species than any other genus in the family Hipposideridae. Sixty-seven species are recognized by Simmons (2005), most of which occur in the eastern half of the Old World tropics and sub-tropics. Fourteen species occur in Africa. Distinguished from other genera of hipposiderids in Africa by the

following combination of characters. Posterior component of noseleaf roughly elliptical in shape and its upper margin is comparatively simple in outline (usually low-arched but subtriangular in one species) and does not have three triangular projections (although there is a club-shaped projection in some species) (Figure 68).

Tail more or less fully enclosed by interfemoral membrane (in some species, the last one or two vertebrae protrude). Skull with sagittal crest not developed primarily in the immediate postorbital region (cf. Rhinolophidae): the skull of *Hipposideros ruber* is illustrated as an example for the genus but there are some substantial inter-specific variations (Figure 69). Upper canine without enlarged secondary cusp. Dental formula $^{1123}/_{2123}$ in all African species except *H. megalotis* in which there is only one upper premolar on each side. African species range in size from very small to very large.

Figure 68. Noseleaves of selected African *Hipposideros* exemplifying the characters that are used to distinguish some of the species in this genus.

(a) Club-shaped process present (e.g. *H. cyclops*). (b) Outline of upper margin subtriangular; posterior component divided into four cells by three well-developed septa; internarial septum greatly enlarged into a prominent pad (e.g. *H. jonesi*). (c) Internarial septum moderately enlarged into a medium-sized pad; anterior component with deep median emargination (e.g. *H. curtus*). (d) Outline of upper margin low-arched; internarial septum moderately enlarged into comparatively small pad; two weakly-developed lateral leaflets present (e.g. *H. marisae*). (e) Posterior component divided into three cells by two well-defined septa; three well-developed lateral leaflets; anterior component without median emargination (e.g. *H. gigas*). (f) Posterior component not divided into cells by any well-developed vertical septa (e.g. *H. abae*). All noseleaves redrawn from Rosevear (1965).



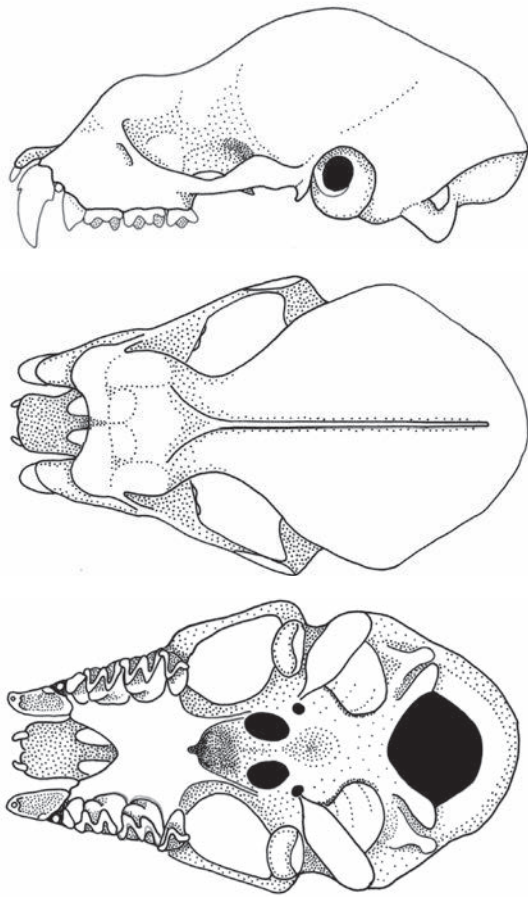


Figure 69. *Hipposideros ruber*. Skull (partly based on Rosevear 1965).

Species in the genus have been allocated to species-groups by Tate (1941) and Hill (1963). Based on morphometric characters, Hill (1963) recognized seven species-groups, and most of the more recent researchers (e.g. Koopman 1994) have either accepted Hill's species-groups, or have made only minor changes. Do these species-groups reflect the phylogenetic history of the genus or convergent evolution? Bogdanowicz & Owen (1998) concluded, on the basis of cladistic analyses of craniodental characters and some body measurements, that some groups need to be redefined and revised and they also indicated that the genus *Hipposideros* does not comprise all of the descendants of an ancestor and most probably should be treated as a paraphyletic group. Based on evidence from fossils, Hand & Kirsch (1998) also concluded that some of Hill's species-groups do not reflect the phylogenetic history of the genus, and they too concluded that *Hipposideros* is probably paraphyletic. However, these two investigations have led to different conclusions about the relationships between the species. Because of this, Simmons (2005) has retained the traditional contents of *Hipposideros* pending a thorough revision, and has provisionally retained the contents of the species-groups according to the classification of Hill (1963) with some modifications, including the separation of four of the species in Hill's *diadema* group into a new group, the *commersoni* group. Here, the species-groups are as given by Simmons (2005).

Of the eight species-groups provisionally retained by Simmons (2005), five are represented in Africa as listed below:

megalotis group: one species – *H. megalotis*.

bicolor group: 34 species including *H. beatus*, *H. caffer*, *H. curtus*, *H. fuliginosus*, *H. jonesi*, *H. lamottei*, *H. marisae* and *H. ruber*. Support for this group as a whole is weak, but *H. curtus*, *H. jonesi* and *H. marisae* are evidently closely related.

cyclops group: eight species including *H. cyclops* and *H. camerunensis*, which are very closely related.

speoris group: two species, including *H. abae*.

commersoni group: four species, including *H. gigas* and *H. vittatus*.

The genus is a very old one, as indicated by the very large number of species, their diversification into so many species-groups, and the extent to which members of some of the species-groups are spread over the geographic range of the genus as a whole. Furthermore, according to Hill (1963), there are three distinct evolutionary trends within the genus: (1) exemplified by the *megalotis* and *bicolor* groups, towards small size, large ears and (usually) more complex noseleaves; (2) exemplified by the *cyclops* group, towards greatly developed noseleaves and much modification of the ears and the auditory region of the skull; (3) exemplified by the *speoris* group (and other groups extraliminally) towards greater size without extensive increase in the size and complexity of the ears and noseleaf, but with corresponding broadening of the skull. The genus is mainly confined to the tropics and sub-tropics, but species, including those in Africa, are found in diverse habitats and from high to low altitudes. In Africa, six species are found mainly in forest, five in both forest and savanna, one mainly in savanna, one in both savanna and arid habitats, and one in all of these habitats. Eight species are found in montane habitats but none is known only from montane habitats.

The 14 African species are distinguished mainly by the following characters:

Ears. Either well separated or joined by a low, inconspicuous frontal band.

Club-shaped process on the noseleaf. Either present (Figure 68a) or absent.

Internarial septum. Either enlarged by some specified degree into a pad (Figure 68b–d), or not enlarged.

Number of lateral leaflets on each side. One to four.

Frontal sac above the noseleaf. It can be absent, or present in one or both sexes in which case it can open horizontally (= transversely) or vertically (= longitudinally).

Position of the anterior upper premolar. It can be within the toothrow (so canine and posterior premolar are well separated), or fully displaced labially (so canine and posterior premolar are in contact) or partly displaced labially (so canine and posterior premolar are almost in contact). It is only the cingula of the canine and premolar which are in contact). The anterior upper premolar is absent in some species (Figure 70).

Posterior component of the noseleaf. It can be divided into cells by well-defined vertical septa (Figure 68a–e), or not divided by well-defined septa (Figure 68f).

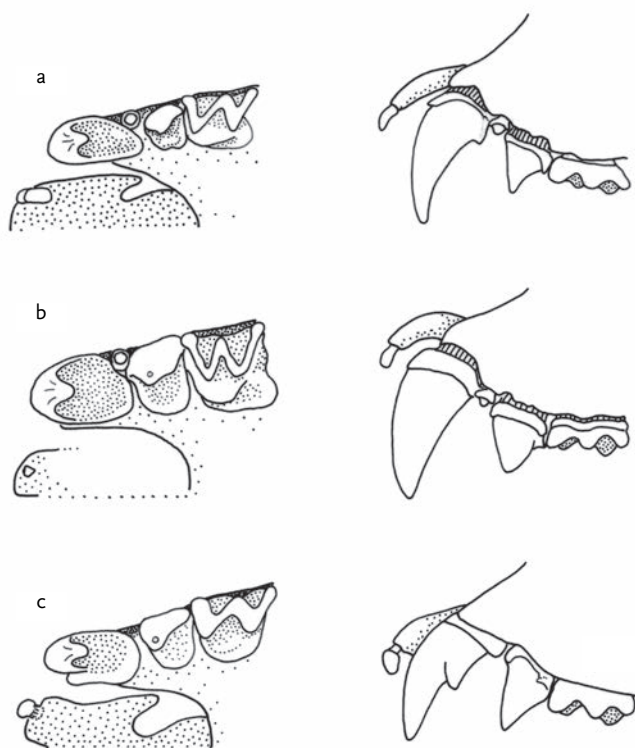


Figure 70. Variations in the sizes and positions of the upper premolars in *Hipposideros* occurring in Africa. *Left*: occlusal views of teeth on left side of upper jaw. *Right*: lateral views of labial side of the same teeth. The anterior upper premolar can be within the toothrow (e.g. *H. lamottei*: not illustrated), or (a) slightly displaced labially so canine and posterior premolar are well separated (e.g. *H. ruber*), (b) fully displaced labially so canine and posterior premolar are in contact (e.g. this specimen of *H. camerunensis*) or (c) absent, leaving a gap between the canine and the posterior premolar (e.g. *H. megalotis*). The outline of the premaxilla of the specimen of *H. camerunensis* was obscured by soft tissue.

Widest part of skull. It can be the zygomatic width (ZW) or the mastoid width (MW) or these dimensions can be equal (Figure 63). In some species (possibly those containing cryptic species) the widest part of the skull is variable.

Length of the forearm.

With these characters, all except seven species can be distinguished (see Table 15). Of these seven, the two largest species, *H. gigas* and *H. vittatus*, overlap in size but, where sympatric, *H. gigas* appears to be larger (see species profiles for further information). Some of the characters that enable the remaining five species (*H. beatus*, *H. caffer*, *H. ruber*, *H. fuliginosus* and *H. lamottei*) to be distinguished are given in the miscellaneous column of the table-key (Table 15) and additional characters are given in the Description and Similar Species sections of the species profiles. These include:

Length of the thumb claw. Measured from the top of the claw, where it emerges from the toe, to its tip, in a straight line (Figure 71).

Height of the thumb claw. Measured from the top to the bottom of the claw where it emerges from the toe (Figure 71).

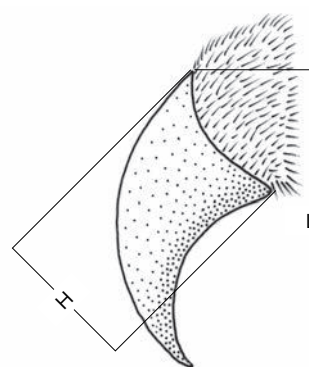


Figure 71. Measurements of thumb claw used in profiles of some *Hipposideros* spp. L = length, H = height.

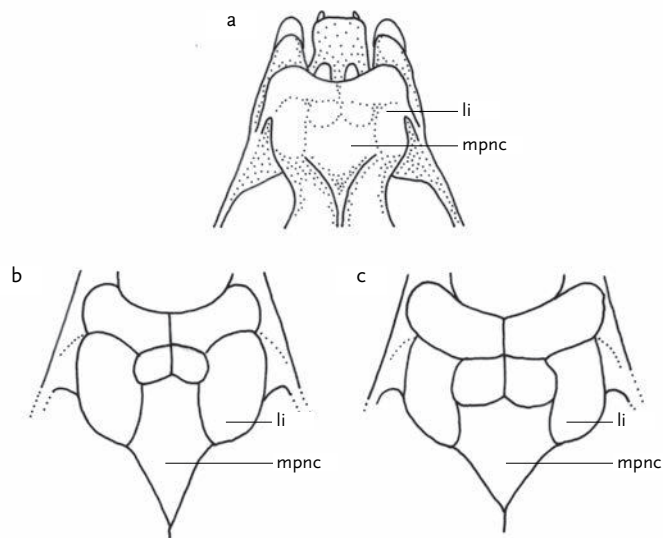


Figure 72. Differences in the rostral swellings of *Hipposideros caffer* and *H. ruber*. (a) Dorsal view, lit from above, of the anterior of the skull of *H. ruber* showing the position of the rostral swellings: li = lateral inflation; mpnc = median posterior nasal compartment. (b) Dorsal view of the rostral swellings of *H. caffer tephros*, backlit from below: the median posterior nasal compartment is narrow relative to the width of each of the lateral inflations (based on Kock 1969a). (c) Dorsal view of the rostral swellings of *H. ruber*, backlit from below: the median posterior nasal compartment (mpnc) is wide relative to the width of each of the lateral inflations (li) (based on Kock 1969).

Length of the phalanges of the third finger.

Length of the tibia (Tib).

Outline of the upper margin of the posterior component of the noseleaf. It can be low-arched (as in a flattened semi-circle, Figure 68a and c–e) or subtriangular (Figure 68b).

Width of the median posterior narial compartment of the nasal swelling relative to the width of each of the lateral inflations. This can be seen by back-lighting the skull (Figure 72).

Breadth of the cochleae relative to their distance apart (Figures 23 and 73).

The species are listed alphabetically, irrespective of the group to which they belong.

Table 15. Key to the African species in the genus *Hipposideros*. With these characters, all but seven species can be distinguished: the characters that enable *H. beatus*, *H. caffer*, *H. fuliginosus*, *H. lamottei* and *H. ruber* to be distinguished from each other are given in the profiles of these species. The widest part of the skull can be the zygomatic width (ZW) or the mastoid width (MW) or variable. Data taken from species profiles.

| Ears | Club-shaped processes | Internarial septum | Number of lateral leaflets | Frontal-sac (opening) | Position of anterior upper premolar (proximity of canine and posterior premolar) | |
|-----------|-----------------------|---------------------|----------------------------|---|--|--|
| Joined | Absent | Not enlarged | 0 | Absent | Absent
(In contact or separated) | |
| Separated | Present | Not enlarged | 2 | Both sexes
(Vertical) | Fully displaced
(In contact or almost so) | |
| Separated | Present | Not enlarged | 2 | Both sexes
(Vertical) | Fully displaced
(In contact or almost so) | |
| Separated | Absent | Greatly enlarged | 1 | Absent | Slightly displaced
(Well separated) | |
| Separated | Absent | Moderately enlarged | 2 (weakly developed) | Usually both sexes
(Horizontal) | Slightly displaced
(Well separated) | |
| Separated | Absent | Somewhat enlarged | 1 (rarely 2) | Both sexes
(Horizontal) | Slightly displaced
(Almost in contact) | |
| Separated | Absent | Not enlarged | 2 | Both sexes
(Horizontal) | Fully displaced
(In contact or almost so) | |
| Separated | Absent | Not enlarged | 2 | Both sexes, small in
♀ ♀
(Horizontal) | Slightly displaced
(Separated) | |
| Separated | Absent | Not enlarged | 2 | ♂ ♂ only
(Horizontal) | Slightly displaced
(Separated, usually well separated) | |
| Separated | Absent | Not enlarged | 2 | Both sexes
(n. d.) | Within tooththrow
(Well separated) | |
| Separated | Absent | Not enlarged | 2 | Absent | Somewhat displaced
(Almost in contact) | |
| Separated | Absent | Not enlarged | 3 | ♂ ♂ only
(Horizontal) | Fully displaced
(Almost in contact) | |
| Separated | Absent | Not enlarged | 3 | Both sexes
(Vertical) | Fully displaced
(In contact or almost so) | |
| Separated | Absent | Not enlarged | 3 or 4 | Both sexes
(Vertical) | Fully displaced
(In contact or almost so) | |

^aThe anterior upper premolar is said to be 'within tooththrow' if it lies in the middle of the tooththrow or is only slightly displaced labially, causing the canine and posterior upper premolar to be separated by a distinct gap.

^bPosterior component has three poorly defined septa.

^cThe median septum is comparatively weakly developed.

^dThe median septum is well defined, the lateral septa are very weak.

| | Posterior component divided into cells by well-defined septa (Number of septa) | FA mean (range) (mm) | Widest part of skull | Miscellaneous | Species |
|--|--|---|----------------------|--|------------------------|
| | No ^b | 36.8 (34–39) | MW | | <i>H. megalotis</i> |
| | Yes (3) | 75.9 (74–80) | ZW | Anteorbital foramen smaller; closed by narrow bar | <i>H. camerunensis</i> |
| | Yes (3) | ♂ ♂ 65.4 (61–75)
♀ ♀ 68.0 (59–74) | ZW | Anteorbital foramen larger; closed by moderately wide bar | <i>H. cyclops</i> |
| | Yes (3) ^c | 46.7 (44–50) | MW | Upper margin of posterior component of noseleaf subtriangular in outline | <i>H. jonesi</i> |
| | Yes (3) | 43.7 (42–47) | MW or equal | Upper margin of posterior component of noseleaf low-arched in outline | <i>H. curtus</i> |
| | Yes (3) | 40.6 (38–42) | Usually MW | Upper margin of posterior component of noseleaf low-arched in outline | <i>H. marisae</i> |
| | No | 43.7 (39–48) | ZW | Tib: 16.1 (15–19) mm | <i>H. beatus</i> |
| | No | 46.4 (42–52) | Variable | Tib: 20.0 (18–22) mm
Dorsal pelage greyish. Median posterior narial compartment of nasal swelling relatively narrow with wide lateral inflations | <i>H. caffer</i> |
| | No | 51.1 (47–55) | Variable | Tib: 21.4 (18–24) mm
Dorsal pelage brownish. Median posterior narial compartment of nasal swelling relatively wide with narrow lateral inflations | <i>H. ruber</i> |
| | No | 55.8 (55–57) | MW | Thumb claw length <2.5 mm
Third finger phalanges short, first: 12.5–14.3 mm, second: 10.5–12.1 mm | <i>H. lamottei</i> |
| | No | See profile for means (51–64) | ZW | Thumb claw length >3 mm
Third finger phalanges long, first: 14.3–18.7 mm, second: 17.8–21.9 mm | <i>H. fuliginosus</i> |
| | No | 59.3 (54–65) | ZW | No silver, white and brown markings | <i>H. abae</i> |
| | Yes (3) ^d | ♂ ♂ 101.5 (93–106)
♀ ♀ 93.9 (84–101) | ZW | Silver, white and brown markings. Smaller on average. Pelage shorter, not slightly woolly. Predominantly in savannas | <i>H. vittatus</i> |
| | Yes (3) ^d | ♂ ♂ 107.9 (100–124)
♀ ♀ 103.8 (95–116) | ZW | Silver, white and brown markings. Larger on average. Pelage longer, slightly woolly. Predominantly in forests | <i>H. gigas</i> |

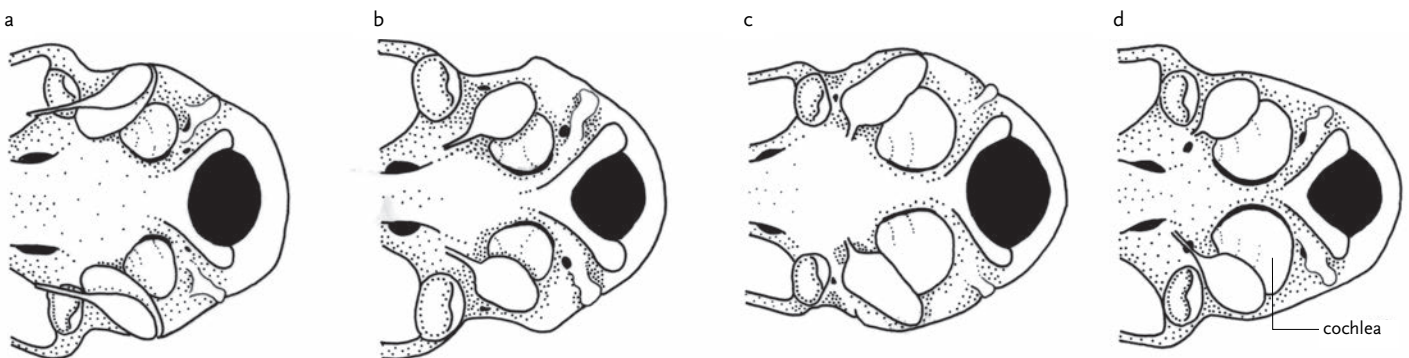


Figure 73. Ventral views of skulls showing variations in the relative sizes of the cochleae in African *Hipposideros*. The cochleae are said to be not enlarged if the breadth of each one ranges from (a) slightly less than their distance apart (e.g. *H. abae*) to (b) slightly more than their distance apart (e.g. *H. gigas*). They are said to be (c) moderately enlarged if their breadth is 2–3 times their distance apart (e.g. *H. jonesi*) and (d) greatly enlarged if their breadth is 3–4 times their distance apart (e.g. *H. cyclops*).

Hipposideros abae ABA LEAF-NOSED BAT

Fr. Phyllorhine d'Aba; Ger. Aba-Rundblattnase

Hipposideros abae J. A. Allen, 1917. Bull. Am. Mus. Nat. Hist. 37: 432. Aba, Orientale, DR Congo.

Taxonomy Species-group: *speoris*; the only African representative of this group. Synonyms: none. Chromosome number: not known.

Description Medium-small microbat with noseleaf (posterior component roughly elliptical); blackish-brown with orange-phase; ears separated; noseleaf with three lateral leaflets on each side, no club-shaped processes and nostrils not concealed by an enlarged internarial septum. Sexes similar. Pelage fine, dense; mid-dorsal hairs 7–9 mm. Dorsal pelage (grey-phase) blackish-brown, paler on shoulders; hairs pale greyish-brown or smoke-grey with dark grey at base and blackish-brown at tip. Ventral pelage pale greyish-brown. Orange-phase: dorsal pelage bright orange or cinnamon-brown darkening to rusty-brown on middle of back (hairs pale orange-grey with cinnamon or rusty-brown at base and tip); ventral pelage paler especially on throat. In orange-phase, in DR Congo, ♀♀ are brighter than ♂♂ (Allen 1917a). Ears separated, comparatively and relatively short (29–39% of FA); brown, subtriangular, very broad; tip pointed with marked concavity in outer margin just below tip. Antitragus shallow with thickening at antitragal lobe. Noseleaf as in Figure 68f. Posterior component with well-developed transverse serrated supplementary structure; not divided into cells by vertical septa. No median club-shaped processes. Internarial septum weakly developed, not concealing nostrils. Three lateral leaflets on each side. Males with frontal sac, with horizontal opening and anterior cutaneous lip, enclosing stiff dark hairs; ♀♀ with tuft of hairs but no frontal sac. No anal sac. Wings and interfemoral membrane dark brown. Fifth metacarpal 84–90% of third metacarpal. Thumb moderately robust; claw length 2.8 (2.4–3.1) mm, claw height 1.2 (1.0–1.5) mm. Tibia 39–45% of FA. Tail 48–64% of HB.

Skull with zygomatic arches slender; zygomatic width > mastoid width (Figure 63b). Rostrum narrow and flattened. Sagittal crest low to moderate. Cochleae not enlarged, their breadth equal to their distance apart or a little less (Figure 73a). Upper incisor large, slightly bicuspid. Upper canine of moderate relative length (49 [47–53]% of C–M³, n = 11). Anterior upper premolar minute, displaced labially; canine and posterior premolar almost in contact. Anterior lower premolar one half the length and height of posterior premolar or slightly less. For further craniodental information, see Hill (1963).

Geographic Variation None recorded.

Similar Species Only two other African *Hipposideros* have three lateral leaflets on each side (Table 15, p. 370).

Hipposideros gigas. Much larger (FA: 95–124 mm; CrnC: 33.3–42.7 mm).

H. vittatus. Much larger (FA: 84–106; CrnC: 29.9–33.2 mm).

(Note: *H. beatus*, *H. caffer*, *H. fuliginosus* and *H. ruber* are otherwise fairly similar externally, but have only two lateral leaflets on each side).

*Hipposideros abae*

Distribution Endemic to Africa. Found in the Guinea Savanna BZ and Rainforest–Savanna Mosaic and, in West Africa and Uganda, marginally in the Rainforest BZ. Recorded, disjunctly, from Guinea-Bissau to S Sudan and N Uganda (but not in all countries). Most records are in isolated clusters. Mapped from country checklists (see order Chiroptera), other literature and museum records.

Habitat Typically found in *Isoberlinia* woodland and in mosaics of *Isoberlinia* woodland, lowland rainforest and secondary grassland (Rosevear 1965). In Sierra Leone and Uganda, occurs in lowland rainforest, suggesting that this species may be expanding its geographic range into this habitat (Grubb *et al.* 1998). In Ghana, found in thicket-like dry forest on Accra Plains (Decher 1997) as well as in *Isoberlinia* woodland north of the rainforest. In Garamba N. P., DR Congo, found in riverine forests and in nearby savanna habitats. Throughout geographic range, probably limited to habitats with caves or rocky outcrops (see below).

Abundance Uncertain. Locally abundant in some areas where caves are present, but not often collected (Lang & Chapin 1917b, Verschuren 1957, Rosevear 1965). Considered comparatively rare by Decher *et al.* (1997).

Adaptations By day, hangs freely in humid, draught-free day-roosts including caves, crevices, spaces under piles of boulders, and burrows (Verschuren 1957, Rosevear 1965). Day-roosts range in size from the dark recesses of caves to shallow grottos, holes between rocks, burrows of large mammals and the undersides of boulders

as long as these give protection from bright light and draughts. Sometimes roosts close to ground. The use of a subterranean bunker in Burkina was reported by Koch-Weser (1984). However, apparently *H. abae* differs from many other cave-dwelling species by only very rarely using man-made day-roosts (e.g. mines, buildings) or hollow trees. Caves opening into both forest and savanna habitats were utilized in Garamba N. P. (Verschuren 1957). Often shares day-roosts with other bats, including *Lissonycteris angolensis*, *Rhinolophus landeri*, *R. guineensis*, *Hipposideros caffer*, *H. jonesi* and *H. ruber* (Verschuren 1957, Koch-Weser 1984). Does not become torpid by day (Verschuren 1957, Rosevear 1965).

Foraging and Food No information. Has been netted over waterholes (Koopman *et al.* 1978), and sometimes flies into houses at night.

Echolocation No information.

Social and Reproductive Behaviour Typically roosts in small to very large groups (several hundreds) (Lang & Chapin 1917b, Verschuren 1957, Rosevear 1965), but the social structure of these groups is not known. The number of bats that roost together perhaps depends on the size of the day-roost. Individuals hang apart but near others. In Garamba N. P., occasionally found singly or in twos in caves shared with small groups of *H. ruber*, and also found in very large numbers with very large numbers of *H. ruber* (total number more than 1000). Individuals of both species intermingle and hang together. In Garamba N. P., they remain active and alert throughout the day, make a continuous clatter of sharp cries, and often make spontaneous flights within the day-roost. Occupancy of one cave varied from month to month, suggesting roost-fidelity is not high. In a sample of 229 bats taken from one cave in Apr, adult ♀♀ outnumbered adult ♂♂ by 2.2 : 1. Of the ♀♀ in this sample, two-thirds were lactating and the remainder reproductively inactive. Verschuren (1957) suggested that these data imply polygamy, but pair-formation cannot be ruled out. Segregation of the sexes during parturition and lactation does not seem to occur. The presence of insects in the stomachs of non-volant young suggests that adults bring prey to their young.

Reproduction and Population Structure Litter-size and reproductive chronology: uncertain. Monotoccy and restricted seasonal monoestry, with births in Mar, was reported for Cameroon and Uganda (Anciaux de Faveaux 1972) but both need confirmation. At 04°40'N (Garamba N. P., NE DR Congo) non-volant juveniles were recorded in Apr implying births in Mar (Verschuren 1957), but there are no data for other months.

Predators, Parasites and Diseases Ectoparasites include a bat-fly *Ascoapteron jonesi* (Diptera: Streblidae) and a mite *Psorergatoides hipposideros* (Acari: Psorergatidae) (Anciaux de Faveaux 1984). Rift Valley Fever virus has been isolated from *H. abae* (Calisher *et al.* 2006).

Conservation IUCN Category: Least Concern.

However, population trends and major threats are not known.

Measurements

Hipposideros abae

FA: 59.3 (54–65) mm, n = 188

WS (d): 320 mm*

TL: 100.8 (87–107) mm, n = 51

T: 35.2 (28–40) mm, n = 52

E: 21.2 (18–24) mm, n = 59

NL (breadth): 8.8 (7.5–9.4) mm, n = 18

Tib: 25.7 (22–30) mm, n = 43

HF: 11.2 (7–13) mm, n = 39

WT: 17, 19 g, n = 2

CrnC: 23.1 (21.9–24.6) mm, n = 52

GWS: 13.4 (12.6–14.5) mm, n = 69

C-M³: 8.8 (8.1–9.4) mm, n = 24

Throughout geographic range (BMNH, RMCA, SMNS, ZFMK, Allen 1917a and other literature)

*Lang & Chapin 1917b, DR Congo (range and sample size not given)

Key References Allen 1917a; Decher *et al.* 1997; Hill 1963; Rosevear 1965; Verschuren 1957.

Meredith Happold

Hipposideros beatus BENITO LEAF-NOSED BAT

Fr. Phyllorhine naine; Ger. Benito-Rundblattnase

Hipposideros beatus K. Andersen, 1906. Ann. Mag. Nat. Hist., ser. 7, 17: 279. 15 miles (24 km) from Benito River, Rio Muni, Equatorial Guinea.

Taxonomy Species-group: *bicolor*. Considered closely related to *H. caffer* (Hill 1963). Synonyms: *maximus*. Subspecies: two. Chromosome number: not known.

Description Small to very small microbat with noseleaf (posterior component roughly elliptical); sepia brown, possibly without orange-phase; ears separated; noseleaf with two lateral leaflets on each side, no club-like processes and nostrils not concealed by internarial septum; frontal sac present in both sexes; thumb weakly developed; anterior upper premolar greatly reduced and fully displaced labially. Sexes similar. Pelage fine, fluffy; mid-dorsal hairs ca. 9 mm. Dorsal pelage

medium to dark sepia brown; hairs tricoloured, central third pale sepia brown, basal and terminal thirds medium to dark sepia brown. Orange-phase not known to occur. Ears separated, comparatively and relatively short (27–38% of FA), dark brown, triangular; tip shallowly pointed with concavity in outer margin just below tip. Antitragus with slight thickening at antitragal fold. Noseleaf approximately as in Figure 68f. Posterior component with well-developed transverse, serrated, supplementary structure on posterior face; not divided into cells by supporting septa; upper margin with low-arched outline. No club-like processes. Internarial septum not enlarged, not concealing nostrils. Two lateral leaflets on each side. Frontal sac present in both sexes; opening

through horizontal slit. Wings and interfemoral membrane dark brown. Thumb weakly developed (claw length 1.9 [1.4–2.3] mm, claw height 1.0 [0.9–1.2] mm). Tibia 36–44% of FA. Tail 47–72% of HB.

Skull short and broad; zygomatic arches slender; zygomatic width > mastoid width. Sagittal crest low. Cochleae not enlarged, their breadth equal to their distance apart or a little greater. Upper incisor slightly bicuspid. Upper canine relatively short (42 [38–48]% of C–M³, $n = 8$). Anterior upper premolar minute, fully displaced labially; canine and posterior premolar in contact or nearly so (Hill 1963). Anterior lower premolar a little more than half the length and height of the posterior lower premolar.

Geographic Variation Two subspecies are recognized by Hill (1963) and Koopman (1994):

H. b. beatus: Sierra Leone to Gabon. FA: 39–48 mm.

H. b. maximus: Central African Republic, extreme SW Sudan, NE DR Congo. FA: 43–48 mm.

Similar Species Four other African *Hipposideros* have the following combination of characters: ears separated; noseleaf with two lateral leaflets on each side, no club-shaped processes and nostrils not concealed by internarial septum (Table 15, p. 370):

Hipposideros caffer. Tibia usually longer (19.2 [18–22] mm). Anterior upper premolar small but not greatly reduced, only slightly displaced labially; canine and posterior premolar not in contact. Echolocation CF-frequency (Côte d'Ivoire) 161 kHz.

H. ruber. FA longer (51.1 [47–55] mm). Tibia usually longer (21.4 [18–24] mm). Anterior upper premolar small but not greatly reduced, only slightly displaced labially; canine and posterior premolar not in contact (usually well separated).

H. fuliginosus. Much larger (FA [western population]: 55.0 [51–60] mm, FA [eastern population]: 62.6 [60–64] mm; CrnC [western population]: 19.9 [19.2–21.5] mm, CrnC [eastern population]: 23.2 [22.8–23.4] mm).

H. lamottei. Much larger (FA: 55.8 [55–57] mm; CrnC: 19.2 [18.9–19.6] mm).

(Note: *H. abae*, which is otherwise fairly similar externally, has three lateral leaflets on each side).

Distribution Endemic to Africa. Mostly recorded disjunctly from the Rainforest BZ (with some records in the Northern Rainforest–Savanna Mosaic, and one marginally in the Guinea Savanna BZ). Recorded from Sierra Leone to northern half of DR Congo. Subsequently recorded east of L. Albert, Uganda, by Thorn & Kerbis Peterhans (2009): not mapped. Not recorded from the Dahomey Gap, nor Bioko I. A record from Guinea-Bissau is erroneous (J. Fahr in Simmons 2005). A record from N Central African Republic (Schlitter *et al.* 1982) is rejected because, based on other records, the habitat is inappropriate and some craniodontal measurements of the specimen fall below the range exemplified by other specimens. A record from Kango, Chad (MNHN) has not been confirmed and has not been mapped because the habitat seems inappropriate. Mapped from country checklists (see order Chiroptera), other literature and museum records.



Hipposideros beatus

Habitat In West Africa, found in closed forests, degraded areas within the lowland rainforest, coastal woodlands and coastal scrub, and mosaics of thickets and grasslands, usually (possibly always) near rivers or swamps. In Gabon, not found anywhere except near rivers and swamps (Brosset 1966, 1982). In Garamba N. P., NE DR Congo, found in dense, humid riverine forests in Guinea Savanna BZ, but not found further south where these forests were much degraded (Verschuren 1957).

Abundance Uncertain. Rare in collections.

Adaptations Flies fast and powerfully with unceasing changes of direction and considerable manoeuvrability. Frequently glides short distances. Adept at flying in dense vegetation. By day, hangs freely in small day-roosts near the ground, which include hollow logs, spaces between piles of logs, small holes in trees, cavities under rocks, caverns eroded by streams, sheltered areas under exposed tree roots over water, holes in the ground and road culverts (Verschuren 1957, Rosevear 1965). One was found hanging from a grass-thatched roof (Grubb *et al.* 1998). Three were found in the partly flooded galleries of a mine in Gabon (Brosset 1966). In Gabon, one population roosted in abandoned traps (see Social and Reproductive Behaviour). When disturbed, individuals immediately fly from the day-roost into vegetation where they hide amongst leaves (Brosset 1966): therefore presumably they do not become torpid by day. Not known to roost in large caves, or to share day-roosts with other species of bats (Rosevear 1965). In Garamba N. P., the same roosts were occupied for several consecutive months, suggesting roost-fidelity is high (Verschuren 1957).

Foraging and Food Very little information. Forages in dense vegetation. Flying-ants and bugs were found in the stomach of one individual from Garamba N. P. (Verschuren 1957).

Echolocation Call-shape CF/FM. CF-frequency (*H. b. beatus* from Côte d'Ivoire) 139–147 kHz (J. Fahr & N. Ebigbo pers. comm.). CF-frequency (*H. b. maximus* from DR Congo, hand-held) 108 kHz (Novick 1958b).

Social and Reproductive Behaviour An impressive study of the social organization of *H. beatus* was made by Brosset (1982). He found that, on a small island in the Ivindo R., Gabon, seven of 22 abandoned traps originally built for catching Water Chevrotains *Hyemoschus aquaticus* were occupied by groups of *H. beatus*, which evidently preferred the traps to all other roost-sites available on the island. The traps were 90×90×150 cm in size, and all bats roosting inside could be captured; they were marked and censused at four-monthly intervals for three years. The bats were found to live in monogamous family groups comprised of one pair of adults with their young and one yearling of the preceding breeding season. These groups were sedentary and occupied small territories that saturated the island. Pairs maintained their associations from the beginning of one mating-period to the beginning of the next (Jul–Jun), but at the beginning of each mating-period, new pairs were formed through an exchange of mates in the population. Consequently, yearlings sometimes associated with a pair of adults that were not its parents. According to a few observations, ♀♀ reach sexual maturity when six months old; ♂♂ when at least one year old. In Garamba N. P., *H. beatus* was usually found roosting singly, in pairs and in groups of 3–4 but, on one occasion, a group of 12 was observed (Verschuren 1957). Another group, taken from a hollow tree in DR Congo, included two ♂♂, two ♀♀ and one juvenile (BMNH).

Reproduction and Population Structure Litter-size: one (n = 6; Brosset 1982). At 00°04'N (Makokou, Gabon), the reproductive chronology is restricted seasonal monoestry with mating at end of first wet season (Jun–Jul) and parturition in middle of second

wet season (Oct–Nov) (Brosset 1966, 1988). In contrast, at ca. 5°N (Garamba N. P., NE DR Congo) one lactating ♀ was observed in Apr and another post-lactating in May (no data for other months; Verschuren 1957).

Predators, Parasites and Diseases No information.

Conservation IUCN Category: Least Concern.

Fairly widespread and no specific threats identified other than destruction of forest habitat.

Measurements

Hipposideros beatus

FA: 43.7 (39–48) mm, n = 50*

WS: n. d.

TL: 73.7 (66–83) mm, n = 11

T: 24.7 (20–31) mm, n = 28

E: 13.9 (12–16) mm, n = 23

NL (breadth): 7.0 (6.3–7.6) mm, n = 17

Tib: 16.1 (15–19) mm, n = 35

HF: 7, 9 mm, n = 2

WT: 7.2 (6.0–9.5) g, n = 11

CrnC: 16.8 (16.1–18.1) mm, n = 27*

GWS: 9.4 (8.5–10.1) mm, n = 15

C-M³: 5.9 (5.6–6.2) mm, n = 22

Throughout geographic range (BMNH, MNHN, RMCA, SMF, SMNS, ZFMK and literature)

*Mostly from J. Fahr pers. comm.

Key References Brosset 1966, 1982; Hill 1963; Rosevear 1965; Verschuren 1957.

Meredith Happold

Hipposideros caffer SUNDEVALL'S LEAF-NOSED BAT

Fr. Phyllorhine de Cafrerie; Ger. Sundevalls Rundblattnase

Hipposideros caffer (Sundevall, 1846). Öfv. Kongl. Svenska Vet.-Akad. Forhandl. Stockholm 3 (4): 118. Durban, South Africa.

Taxonomy Originally *Rhinolophus caffer*. Species-group: *bicolor*. Synonyms: *angolensis*, *aurantiaca*, *bicornis*, *braima*, *gracilis*, *nanus*, *tephrus*. Subspecies: four. Differences in skull morphology and echolocation calls suggest *H. caffer* includes more than one species. Since this profile was submitted, based on molecular evidence, *tephrus* Cabrera, 1906, has been restored to specific status by Vallo *et al.* (2007, 2008). Chromosome number (Kenya, Zimbabwe, South Africa): 2n = 32; aFN = 60 (Dulić & Mutere 1974, Peterson & Nagorsen 1975, Rautenbach *et al.* 1993).

Description Small microbat with noseleaf (posterior component roughly elliptical); greyish with orange-phase; ears separated; noseleaf with two lateral leaflets on each side, no club-shaped processes and nostrils not concealed by internarial septum; frontal sac present in both sexes; thumb weakly developed with comparatively small claw and basal pad. Sexes alike. Pelage fluffy, dense, silky; mid-dorsal hairs ca. 9 mm. Dorsal pelage (grey-phase) grey to brownish-

grey; hairs tricoloured – cream to off-white with basal quarter pale greyish-brown and terminal quarter grey to brownish-grey. Ventral pelage slightly paler; hairs with basal half (or more) pale to medium greyish-brown and terminal half paler and sometimes with darker tips. Orange phase: dorsal pelage ranging from bright rusty-orange to golden-yellow. Ears comparatively short but relatively short to medium (24–38% of FA); broad, inner margin convex, outer margin convex becoming concave near tip; tip pointed. Antitragus shallow with slight thickening at antitragal fold. Noseleaf approximately as in Figure 68f. Posterior component with well-developed transverse serrated supplementary structure; not divided into cells by vertical septa; no club-shaped processes; internarial septum not concealing nostrils; anterior component without median emargination; two lateral leaflets on each side. Frontal sac present in both sexes but very small in ♀♀; opening horizontally. No anal sac. Wings and interfemoral membrane blackish-brown in both phases. Fifth metacarpal 86–92% of third metacarpal. Thumb, including claw

and basal pad, weakly developed (cf. *H. fuliginosus*), claw length 2.0 (1.6–2.7) mm, claw height 1.1 (0.9–1.3) mm. Tibia 39–46% of FA. Tail 49–65% of HB.

Skull short, broad; zygomatic arches slender anteriorly with a high jugal projection set far back; zygomatic width =, > or < than mastoid width (regional differences not yet resolved). Median posterior nasal compartment of rostral swelling relatively narrow with wide lateral inflations (Figure 72b) (cf. *H. ruber*); this can be seen in backlit skulls. Sagittal crest low. Cochleae not enlarged, their breadth equal to their distance apart, or a little greater. Upper incisor weakly bicuspid, outer cusp very weakly developed. Upper canine of medium relative length (48 [43–50]% of $C-M^3$, $n = 7$). Anterior upper premolar small or minute, only slightly displaced labially; canine and posterior premolar not in contact. M^3-M^3 greater than $C-M^3$.

Geographical Variation Koopman (1994) recognizes four subspecies:

H. c. tephros: Morocco and dry sub-Saharan belt from Mauritania and Guinea to Sudan, but see Taxonomy.

H. c. angolensis: Ghana, Gabon, Angola, Namibia.

H. c. nanus: NE DR Congo.

H. c. caffer: Remainder of geographic range.

Similar Species Four other African *Hipposideros* have the following combination of characters: ears separated; noseleaf with two lateral leaflets on each side, no club-shaped processes and nostrils not concealed by internarial septum (Table 15, p. 370):

Hipposideros ruber. Usually larger, especially where sympatric (FA: 51.1 [47–55] mm; CrnC: 19.1 [17.8–20.3] mm). Median posterior nasal component of rostral swelling relatively wide with narrow lateral inflations. Dorsal pelage (grey-phase) usually more brown than grey.

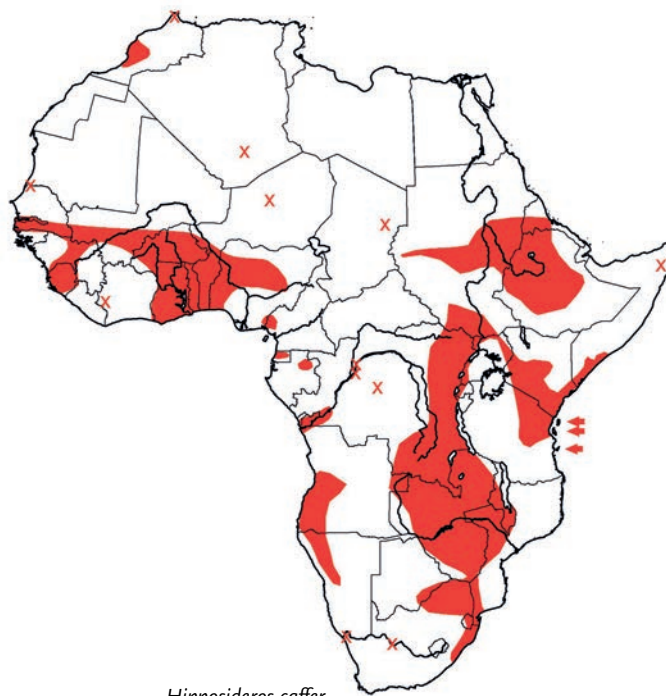
H. beatus. Tibia usually shorter (16.1 [15–19] mm). Anterior upper premolar greatly reduced and fully displaced labially; canine and posterior premolar in contact or almost so.

H. fuliginosus. Much larger (FA [western population]: 55.0 [51–60] mm, FA [eastern population]: 62.6 [60–64] mm; CrnC [western population]: 19.9 [19.2–21.5] mm, CrnC [eastern population]: 23.2 [22.8–23.4] mm).

H. lamottei. Much larger (FA: 55.8 [55–57] mm; CrnC: 19.2 [18.9–19.6] mm).

(Note: *H. abae*, which is otherwise fairly similar externally, has three lateral leaflets on each side.)

Distribution In Africa, widely but disjunctly distributed in all sub-Saharan biotic zones, except the Highveld and South-West Cape BZs, but not distributed in all parts of any of these biotic zones, and there are comparatively few records in the Rainforest and South-West Arid BZs and in the Horn of Africa. There are isolated populations in the Mediterranean Coastal BZ in NW Africa (Aulagnier & Thévenot 1986). Recorded from Morocco (Aulagnier & Thévenot 1986) and from most countries south of the Sahara; also Mafia I. (Kock & Stanley 2009), Pemba I. and Zanzibar I. There is a recent record (not mapped) from Terjît, Wilaya Adrar, Mauritania (20° 15.578' N,



Hipposideros caffer

13° 05.854' W) (Padial & Ibáñez 2005). Extraliminally: SW Arabian Peninsula.

Habitat Most records are in woodland savannas; less commonly recorded in more arid regions and in forests. In Mauritania, one specimen was recorded near a small relict stream in the Adrar Mts where some other plant and animal species of the Sahel have been found (Padial & Ibáñez 2005). In South Africa, Zimbabwe and Botswana the geographic range appears restricted to regions receiving more than 500 mm rain (Rautenbach 1982), and in the more arid parts of the range, they may be restricted to river courses (Taylor 2000).

Abundance Apparently common to very abundant in optimum habitats where day-roosts are available, but seldom mist-netted. One cave in Gabon contained ca. 500,000 (Brosset 1968) but possibly many represented *H. ruber*. One cave in Nigeria probably contained ca. 1000 (Menzies 1973). In Malawi, Zimbabwe and South Africa, colonies of several hundreds have been reported, but much smaller colonies also occur, at least in South Africa (Smithers & Wilson 1979, Rautenbach 1982, Taylor, P. 1998, R. T. F. Bernard pers. obs.).

Adaptations Aspect ratio low; wing-loading very low (Aldridge & Rautenbach 1987). Able to fly slowly or rapidly, and with agility and manoeuvrability. Can take off from ground and hover briefly. Turns by banking and by stalling-and-twisting. Day-roosts include caves, small rock cavities and fissures, mine-adits, culverts under roads, abandoned buildings, roofs of houses, wells and hollow trees (Smithers 1983). Hangs freely from ceilings or rafters. In KwaZulu-Natal (South Africa), roosts at back of mine-adits and caves where microclimate is most stable (R. T. F. Bernard unpubl.). Sometimes shares roosts with other species, including *Rhinolophus landeri*, *R. clivosus*, *Nycteris thebaica*, *Myotis tricolor* and *Miniopterus schreibersii*. Does not hibernate, but becomes torpid for short periods during particularly cold weather (Bernard & Meester 1982). In dry country,

often mist-netted over water and observed sipping water while in flight; suggests dependence on this resource (Smithers 1983).

Foraging and Food Forages by slow-hawking and by gleaning from branches and the ground. Commonly feeds on swarms of insects attracted to electric lights. A study of the foraging behaviour of free-living bats under controlled conditions (in Zimbabwe) in which the prey was either motionless, fluttering and flying, or fluttering but not flying, and in which the bats could use echolocation and/or visual cues or neither, indicated that they attack fluttering targets that are flying as well as those sitting on smooth or cluttered solid backgrounds, and that they use only Doppler-shifted echoes to detect their targets (Bell & Fenton 1984 as *H. ruber*). Some light-tagged individuals foraged by slow-hawking 1–10 m over water; others flew along the face of an escarpment and gleaned from rock surfaces and vegetation; one foraged ca. 1 m high over open ground and made frequent dives to the ground. Individuals attracted to swarms of insects around an electric ultraviolet light fed primarily on moths, and attacked and captured those of wingchord 5–60 mm (wingchord = length of leading edge of forewing). However, analysis of wings discarded by these bats showed that they fed mostly on moths of wingchord 10–25 mm, irrespective of species. The majority of insects attracted to the light were usually moths of this size and, although on certain nights beetles comprised ca. 80% of the total attracted insects, moths were still the chosen prey. Moths comprised 88% of insects identified in faeces. Bowie *et al.* (1999) also found that moths comprised most (80%) of the diet of *H. caffer* in South Africa. However, they occasionally feed on other insects including lacewings, caddis-flies, orthopterans, termites and beetles (Fenton *et al.* 1977, Findley & Black 1983, Bell & Fenton 1984 as *H. ruber*).

Echolocation Call-shape CF/FM. CF-frequency varies in different localities as follows:

Gambia: 138 ± 8.25 kHz (4 ♂♂) and 149 ± 4.35 kHz (2 ♀♀) (Jones *et al.* 1993).

Côte d'Ivoire (Taï N. P.): 161 kHz (Fahr *et al.* 2003).

E DR Congo (Irangi): 154–157 kHz (Heller 1992).

Uganda (Entebbe): 136.7–152.5 kHz (14 bats, not sexed) (Pye 1972).

Kenya (Shimoni): 146.5–159.7 kHz (12 bats not sexed) (Pye 1972).

Zimbabwe: 141.5 ± 2.7 kHz (Fenton 1986).

South Africa (Kruger N. P.): 138 kHz (25 bats, not sexed) (Aldridge & Rautenbach 1987); (Luvuvhu) 145.4 ± 2.5 kHz (Fenton 1986); (Jozini Dam) 145 ± 0.2 kHz (14 bats, not sexed) (Taylor 1999a).

(Note: mean \pm 1 S.D. in some cases).

The data suggest that the CF-frequency can vary by as much as ca. 16 kHz within a single population, and by as much as ca. 24 kHz across the continent. Pye (1972) found some evidence of a bimodal distribution of CF-frequency and a silent interval when bats were recorded in groups but not when isolated, and tentatively proposed a functional interpretation of the silent interval in terms of Doppler spreading. The data from Gambia (Jones *et al.* 1993) suggest that ♀♀ may use higher CF-frequency than ♂♂, but apparently this has not been investigated elsewhere. Another explanation for the variation between different localities is that more than one species is involved.

Social and Reproductive Behaviour Brosset (1966) and Kock (1969a) reported some foraging areas being used only by ♂♂, but the segregation of sexes during foraging needs further investigation. Roosts singly or in groups of two to several hundreds, possibly as many as 500,000 (see Abundance). Neighbours hang apart (separated by a few centimetres). Sex ratio in day-roosts changes seasonally as a consequence of the formation of maternity colonies (Menzies 1973, R. T. F. Bernard pers. obs.); at one cave in Nigeria, the ♂♂ apparently dispersed, leaving the ♀♀ behind to give birth and suckle (Menzies 1973). (Note: although Menzies [1973] identified his bats with *H. caffer guineensis* [now considered a subspecies of *H. ruber*], on basis of FA, GLS and habitat, they are more likely to represent *H. caffer*.) In Zimbabwe, a group of banded bats comprised of one adult ♂, seven lactating ♀♀ and their young, occupied a hollow baobab *Adansonia* from late Dec to late Jan (Bell 1987). The stability and composition of this group suggests a harem mating system. During this time, a large number of non-resident *H. caffer*, and other species, attempted to gain access to this roost, implying that the availability of day-roosts for *H. caffer* in this locality is limited, and suggesting that resource-defence (*sensu* Emlen & Oring 1977) is the basis for harem associations in this species, but more data are needed to confirm this and to show if harems are maintained in larger roosts where it may be more difficult to defend particular sites.

Reproduction and Population Structure Litter-size: one. Throughout Africa, the reproductive chronology is restricted seasonal monoestry (Menzies 1973, O'Shea & Vaughan 1980, Bernard & Meester 1982). At 10° 20' N (Shagunu, Nigeria), births occur at beginning of the unimodal wet season (ca. Apr) (Menzies 1973); in South Africa, births occur in early summer (early Dec). At equatorial latitudes, perhaps some populations exhibit a boreal cycle with births in Mar while other have an austral cycle with births in Oct (Brosset 1968), but the possibility that the different cycles were exemplified by different species (*H. caffer* and *H. ruber*) needs investigation. At equatorial latitudes (where the identification of material needs confirmation), gestation is ca. 100 days (Brosset 1968) and this increases to 150 days at 10° N (Shagunu, Nigeria; Menzies 1973) as a result of delayed implantation, and 210 days at 29° S (KwaZulu–Natal, South Africa; Bernard & Meester 1982) as a result of three months of retarded embryonic development during winter.

Predators, Parasites and Diseases Ectoparasites include a flea *Lagaropsylla consularis* (Siphonaptera: Ischnopsyllidae); 29 species of bat-flies (Diptera: Nycteribiidae, Streblidae); a tick *Carios vespertilionis* (Acari: Argasidae); and 25 species of mites (Acari: Spinturnicidae, Macronyssidae, Myobiidae, Trombiculidae, Leeuwenhoekidae, Psorergatidae, Chirodiscidae) (Anciaux de Faveaux 1984). Chikungunya and Rift Valley Fever viruses have been isolated from *H. caffer* (Bres & Chambon 1964, Calisher *et al.* 2006).

Conservation IUCN Category: Least Concern.

Measurements

Hipposideros caffer

FA: 46.4 (42–52) mm, $n = 187$

WS (d): 288 (277–297) mm, n = 15
 TL: 78.4 (66–96) mm, n = 78
 T: 30 (24–37) mm, n = 139
 E: 14 (10–18) mm, n = 135
 NL (breadth): 6.0 (5.3–7.5) mm, n = 22
 Tib: 20.0 (18–22) mm, n = 72
 HF: 8.0 (6–10) mm, n = 71
 WT: 7.7 (5–11) g, n = 76
 CrnC: 17.2 (16.1–18.3) mm, n = 195*
 GWS: 9.0 (8.0–9.8) mm, n = 70

C–M³: 5.6 (5.1–6.3) mm, n = 89

Throughout geographic range (AM, BMNH, HC, MMB, MNHN, ROM, SMNS and literature)

*J. Fahr pers. comm.

Key References Bell 1987; Bell & Fenton 1984; Bernard & Meester 1982; Menzies 1973; Smithers 1983.

Ric T. F. Bernard & Meredith Happold

Hipposideros camerunensis CAMEROON LEAF-NOSED BAT

Fr. Phyllorhine du Cameroun; Ger. Kamerun-Rundblattnase

Hipposideros camerunensis Eisentraut, 1956. Zool. Jahrb. Abt. Syst. Oekol. Geogr. Tiere 84: 526. Near Buea, Cameroon.

Taxonomy Species-group: *cyclops*. *Hipposideros camerunensis* and *H. cyclops* are closely related and considered the most primitive members of this group. The disjunction between the population in Cameroon and the population(s) in E DR Congo and W Kenya raises the possibility that these populations might be specifically, or subspecifically, distinct (see Conservation), but as yet there is no confirmatory evidence. Synonyms: none. Chromosome number: not known.

Description Medium-large microbat with noseleaf (posterior component roughly elliptical); blackish-brown; pelage woolly and frosted; noseleaf with two median club-shaped processes; FA: 75.9 (74–80) mm. Not easily distinguished from *H. cyclops*. Sexes apparently similar but data are limited. Pelage dense, soft, woolly; mid-dorsal hairs 13–15 mm. Dorsal pelage blackish-brown with pale creamy-brown frosting; hairs dark blackish-brown with curly, creamy-brown tip. Dorsal pelage extending along proximal half of forearm. Ventral pelage slightly paler; frosting less conspicuous. No orange-phase. Ears well separated, comparatively long but of medium relative length (40–50% of FA), narrow, dark brown, inner margin convex, outer margin convex becoming concave near tip, tip narrowly pointed. Antitragus smoothly convex. Noseleaf similar to that of *H. cyclops* (Figure 68a). Posterior component divided into four cells by three vertical septa, and with a club-like process arising from middle of posterior edge. A second median club-shaped process arises from the central component. Internarial septum weakly developed, not concealing nostrils. Two well-developed lateral leaflets on each side, the lower pair continuous with the posterior component. Frontal sac present and prominent in both sexes; opening vertically. Wings and interfemoral membrane slightly translucent dark brown; skin on forearm, digits and tibia much paler reddish-brown. Fifth metacarpal 93–99% of third metacarpal. Tibia 44–52% of FA. Hindfoot 18–22 mm. Tail 33–46% of HB. As in *H. cyclops*, ♂♂ have a (glandular?) sac between penis and anus, opening posteriorly just in front of anus. This anal sac can be everted to reveal a conspicuous tuft of stiff, reddish-brown hairs. Females lack this anal sac but have a patch of bare skin with scattered long and stiff hairs near the vagina.

Skull large, robust, elongate with broad rostrum and broadened braincase; zygomatic arches massive; zygomatic width > mastoid width. Rostrum broad. Sagittal crest low. Anteorbital foramen comparatively small (cf. *H. cyclops*), closed by narrow bar. Cochleae

greatly enlarged, their breadth 3–4 times their distance apart. Upper incisor slightly bicuspid. Upper canine massive but relatively short (42 [40–44]% of C–M³, n = 7). Anterior upper premolar small, fully displaced labially; canine and posterior premolar in contact or almost so. Anterior lower premolar ca. one-quarter the length and ca. half the height or slightly less of the posterior premolar. Further craniodental information in Hill (1963).

Geographic Variation None recorded.

Similar Species Only one other African *Hipposideros* has two median club-shaped processes on the noseleaf, and frosted blackish-brown woolly pelage (Table 15, p. 370):

Hipposideros cyclops. Usually smaller (FA ♂♂: 65.4 [61–75] mm, FA ♀♀: 68.0 [59–74]; CrnC: 28.2 [26.3–30.0] mm). Anteorbital foramen larger and closed by a moderately wide bar.



Hipposideros camerunensis

Distribution Endemic to Africa. Known only, very disjunctly, from the Afromontane–Afroalpine BZ (Cameroon) (Eisentraut 1956), the Rainforest BZ (E DR Congo) (Hayman *et al.* 1966), and from two localities in the Eastern Rainforest–Savanna Mosaic in W Kenya (Schlitter *et al.* 1986). Subsequently also recorded from Budongo (00°45'N, 31°36'E) and Itama (00°57'S, 29°42'E), Uganda, by Thorn & Kerbis Peterhans (2009): not mapped.

Habitat Afromontane forests at 1200–1400 m on Mt Cameroon; degraded afromontane forest with undergrowth of *Acanthus arboreus* and *Brillantaisia* in North Nandi Forest, Kenya; intermediate evergreen forest in Kakamega Forest, Kenya; and lowland rainforest at Shabunda, DR Congo.

Abundance Uncertain. Rare in collections.

Adaptations Based on measurements of a dried museum specimen, aspect ratio is low and wing-loading is high or very high, but this needs confirmation from unpreserved specimens. If correct, flight is predicted to be fast, agile and energetically expensive, and manoeuvrability is probably poor. Day-roosts include caves and hollow trees (Eisentraut 1973a). One individual was caught in the bottom shelf of a mist-net (Schlitter *et al.* 1986), suggesting that this species sometimes forages near the ground.

Foraging and Food Predictably forages by fly-catching, as does *H. cyclops* and *H. vittatus* (see species profiles). Diet not known, but the massiveness of the zygomatic arches suggests that *H. camerunensis* can eat hard-shelled insects.

Social and Reproductive Behaviour No information.

Reproduction and Population Structure Twelve ♀♀ were pregnant in Oct in Cameroon (Eisentraut 1963). No other information.

Conservation IUCN Category: Data Deficient.

The possibility that the records comprise more than one species has been debated by the IUCN assessors and evaluators: because of habitat loss, the Mt Cameroon population is possibly a threatened endemic species.

Measurements

Hipposideros camerunensis

FA: 75.9 (74–80) mm, n = 17

WS (c): ca. 340 mm, n = 1

TL: 127.7 (110–140) mm, n = 9

T: 31.8 (23–45) mm, n = 13

E: 33.6 (30–38) mm, n = 16

NL (breadth): 17.4 (14.8–18.7) mm, n = 5

Tib: 35.9 (35–39) mm, n = 21

HF: 19.0 (18–22) mm, n = 7

WT: 47.7 (39–53) g, n = 7

CrnC: 30.2 (29.2–31.5) mm, n = 14

GWS: 16.3 (15.7–16.9) mm, n = 16

C–M³: 10.7 (9.6–11.5) mm, n = 17

Cameroon, Kenya, DR Congo (BMNH, NMW, RMCA, SMNS, ZFMK and literature)

Key References Eisentraut 1973a; Hill 1963; Schlitter *et al.* 1986.

Meredith Happold

Hipposideros curtus SHORT-TAILED LEAF-NOSED BAT

Fr. Phyllorhine à queue courte; Ger. Kurzschnauz-Rundblattnase

Hipposideros curtus G. M. Allen, 1921. Rev. Zool. Bot. Afr. 9: 194. Sakbayeme, Cameroon.

Taxonomy Species-group: *bicolor*. Synonyms: *sandersoni*. Subspecies: none. Chromosome number: not known.

Description Small to very small microbat with noseleaf (posterior component roughly elliptical); sepia brown; ears large and separated; noseleaf with enlarged internarial septum, which partly conceals the nostrils, and two lateral leaflets on each side; frontal sac usually present in both sexes. Sexes similar. Pelage long, silky, fluffy. Dorsal pelage sepia brown; hairs buff with sepia brown at base and at tip. Ventral pelage same as dorsal pelage, or slightly paler. Orange-phase: no information. Ears separated, comparatively short but of medium relative length (35–49% of FA), rounded (length and breadth almost equal), tip bluntly pointed with sharp concavity in outer margin just below tip; each ear with 11 internal folds (n = 1). Antitragus well developed with small fold. Noseleaf as in Figure 68c. Posterior component not elongated; divided into four cells by three vertical septa; upper margin with low-arched outline. No club-like processes. Anterior component broad, almost covering muzzle. Internarial septum pad-like and moderately enlarged, forming a

longitudinally oval disc (longer than broad), which partly conceals the nostrils. Two weakly-developed lateral leaflets on each side. Frontal sac usually present in both sexes (sometimes absent in ♀♀); opening horizontally. Wings and interfemoral membrane blackish-brown. Fifth metacarpal 89–109% of third metacarpal. Tibia 37–49% of FA. Tail 35–51% of HB.

Skull delicate, short and broad; zygomatic arches moderate; zygomatic width = mastoid width or slightly less. Sagittal crest low. Cochleae not enlarged, their breadth ca. equal to their distance apart or a little greater. Upper incisor slightly bicuspid. Upper canine relatively short (42 [38–48]% of C–M³, n = 4). Anterior upper premolar small, slightly displaced labially, canine and posterior premolar well separated. Further details in Hill (1963).

Geographic Variation None recorded.

Similar Species Only two other African *Hipposideros* have a noseleaf with the internarial septum enlarged (Table 15, p. 370):

Hipposideros jonesi. Margin of posterior component elongated, subtriangular in outline; internarial septum larger, broader than long; one long, well-developed lateral leaflet on each side; no frontal sac. Ears usually larger (21–28 mm) and ca. 50% of FA.

H. marisae. Usually smaller (FA: 40.6 [38–42] mm; CrnC: 15.6 [15.4–15.8] mm). Ears 15–17 mm; no antitragal fold. Internarial septum less enlarged, oval disc smaller; usually only one, rudimentary, lateral leaflet on each side. Frontal sac present in both sexes.

Distribution Endemic to Africa. As yet, known only from the Rainforest BZ in Cameroon (where recorded from at least seven localities) and from Equatorial Guinea (both mainland and Bioko I.) (Allen 1921, Sanderson 1939, Aellen 1952, Perret & Aellen 1956, Eisentraut 1973a, J. Juste pers. comm.).

Habitat Apparently restricted to lowland rainforest.

Abundance Uncertain. Very rare in collections.

Remarks Very little is known about this species (Rosevear 1965). Its flight is described as sluggish in comparison with that of *H. caffer* (Sanderson 1939). One individual foraged with numerous *H. caffer* in the verandah of a house. One was caught over a stream (Sanderson 1939). A small colony, which varied in size according to season, roosted in a shelter formed by big rocks; others have been found under a boulder in a forest (Perret & Aellen 1956). Also roosts in caves (Eisentraut 1964).

Conservation IUCN Category: Vulnerable.

Some of the few known roosts have disappeared and habitat is being lost as a result of selective logging, clear-cutting and other human activities. Population trend: declining.

Measurements

Hipposideros curtus

FA: 43.7 (42–47) mm, n = 21

WS: n. d.

TL: 71.5 (69–75) mm, n = 11



Hipposideros curtus

T: 20.7 (18–23) mm, n = 16

E: 18.1 (15–22) mm, n = 18

NL (breadth): 5.7 (5.1–7.2) mm, n = 12

Tib: 18.8 (16–21) mm, n = 16

HF: 7.3 (7–8) mm, n = 3

WT: 7.1 g, n = 1

CrnC: 17.0 (16.3–17.5) mm, n = 13

GWS: 9.3 (8.4–10.2) mm, n = 15

C–M³: 5.6 (4.9–7.1) mm, n = 17

Côte d'Ivoire, Cameroon, Bioko I. (BMNH, RMCA, ROM, SMNS, ZFMK and literature)

Key References Hill 1963; Rosevear 1965; Sanderson 1939.

Meredith Happold

Hipposideros cyclops CYCLOPS LEAF-NOSED BAT

Fr. Phyllorhine cyclope; Ger. Zyklopen-Rundblattnase

Hipposideros cyclops (Temminck, 1853). Esquisses Zool. sur la Côte de Guinée, p. 75. Boutry River, Ghana.

Taxonomy Originally *Phyllorhina cyclops*. Species-group: *cyclops*. Synonyms: *langi*, *micaceus*. Subspecies: none recognized. Chromosome number: not known.

Description Medium-sized microbat with noseleaf (posterior component roughly elliptical); blackish-brown with woolly, frosted pelage; ears separated; noseleaf with two median club-shaped processes; FA: 66.6 (59–75) mm. Not easily distinguished from *H. camerunensis*. Females significantly larger and heavier than ♂♂ in most body measurements. Pelage dense, soft, woolly; extending along proximal half of forearm; mid-dorsal hairs 11–13 mm (18–

19 mm at high altitudes). Dorsal pelage blackish-brown with white or silvery frosting; hairs blackish-brown with curly, white or silvery tip. Head greyish-brown with darker eye-rings. Ventral pelage paler than dorsal pelage with less conspicuous frosting. No orange-phase. Ears separated, comparatively medium to long but of medium relative length (42–53% of FA), narrow, medium to dark brown, inner margin convex, outer margin convex becoming concave near tip, tip narrowly pointed. Eyes comparatively large. Noseleaf as in Figure 68a. Posterior component divided into four cells by three vertical septa, and with a club-shaped process arising from middle of posterior edge. A second median club-shaped process arises

from the central component above the nostrils. Internarial septum weakly developed, not concealing nostrils. Two well-developed lateral leaflets on each side, the lower pair continuous with the base of the posterior component. Frontal sac present and prominent in both sexes; opens vertically. It is lined with long, stiff, white hairs that form a conspicuous tuft when the sac is everted. At each side of the frontal sac there is a glandular patch or shallow sac. Wing and interfemoral membranes blackish-brown; skin on forearm, digits and tibia much paler reddish-brown. Fifth metacarpal 96 (92–100)% of third metacarpal. Tibia 42–52% of FA. Tail 45–49% of HB. Males have a (glandular?) sac lined with long, stiff, reddish-brown hairs, between penis and anus, opening posteriorly just in front of anus (Figure 74). Females lack this anal sac but have a patch of bare skin with scattered long and stiff hairs near the vagina.

Skull robust, elongate with broad rostrum and elongated braincase; zygomatic arches massive; zygomatic width much greater than mastoid width. Rostrum broad. Sagittal crest low. Infraorbital (= anteorbital) foramen large, rounded and closed by a moderately wide bar (cf. *H. camerunensis*). Cochleae greatly enlarged, their breadth four times their distance apart (Hill 1963) (Figure 73d). Upper incisor slightly bicuspid. Upper canine powerful, relatively short (42 [37–46]% of C–M³, n = 8). Anterior upper premolar very small, fully displaced labially; canine and posterior premolar in contact. Anterior lower premolar ca. one-third to half the length and half the height of the posterior premolar.

Geographic Variation Variable throughout geographic range although no subspecies are currently recognized. Populations from drier habitats have significantly longer forearms than those from wetter habitats as exemplified (in Côte d'Ivoire) by bats from the Guinea Savanna BZ (Comoé N. P.) with FA: 67.1 (62–72) mm (n = 45) compared to those from the Rainforest BZ (Taï N. P.) with FA: 65.2 (62–70) mm (n = 28). Specimens from E DR Congo, W Uganda and N Burundi seem to attain larger dimensions, but sample-size is limited.

Similar Species Only one other African *Hipposideros* has two median club-shaped processes on the noseleaf, and frosted blackish-brown woolly pelage (Table 15, p. 370):

Hipposideros camerunensis. Usually larger (FA: 75.9 [74–80] mm; CrnC: 30.2 [29.2–31.5] mm). Infraorbital foramen smaller and closed by a narrow bar. Not known west of 9° E, but geographical ranges overlap from Cameroon to Kenya.

Distribution Endemic to Africa. Recorded from the Rainforest BZ (Western, West Central and East Central Regions), the adjacent Northern and Eastern Rainforest–Savanna Mosaics and Afromontane–Afroalpine BZ, with an apparently isolated population in the Eastern Arc Mts and the Coastal Forest Mosaic BZ of Kenya and Tanzania. Recorded, somewhat disjunctly, from Senegal to coastal Kenya and Tanzania. Gaps in Guinea and Nigeria might reflect insufficient sampling. There are very few records from the central Congo Basin and it remains to be established if the species ranges throughout the entire Congolian rainforest zone. The record from Bamingui-Bangoran N. P., Central African Republic, appears to be very isolated.

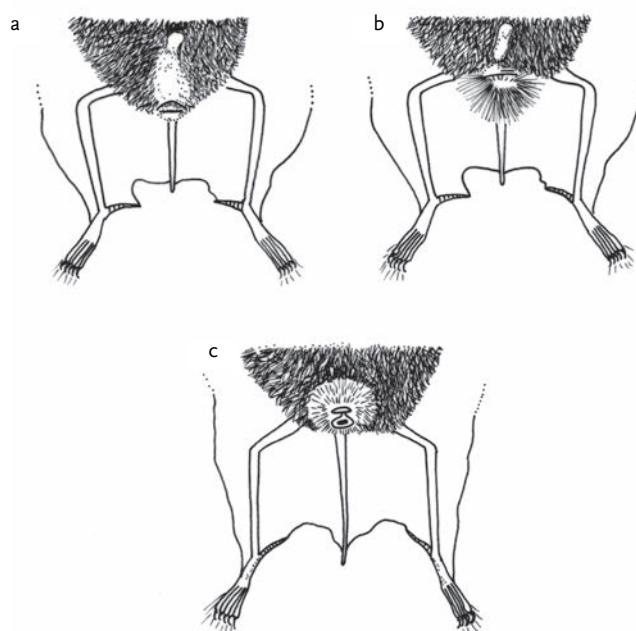


Figure 74. Pubic region of adult ♂ *Hipposideros cyclops* showing (a) the anal sac in its invaginated state and (b) in its everted state. (c) Pubic region of adult ♀ *H. cyclops* showing the patch of bare skin with scattered long, stiff hairs near the vagina. All based on Allen (1917a). The pubic region is the same in *H. camerunensis*.



Hipposideros cyclops

Habitat Recorded mainly from lowland rainforest but also from coastal forest, montane forest, swamp forest and mangroves vegetation zones. Also extends far into the Rainforest–Savanna Mosaic, and into the Guinea Savanna BZ where sufficiently large relict forests and gallery forests are present. Although mostly recorded in undisturbed forest, also found in secondary forest, highly degraded areas, and converted habitats such as cocoa and rubber plantations (Lang & Chapin 1917b, Jeffrey 1975, Fedden &

Macleod 1986, Schlitter *et al.* 1986, Juste & Ibáñez 1994, USNM records). Highest reported altitudes are 1000–1200 m on Mt Nimba (Liberia), 1100 m on Mt Kupé (Cameroon) (Hill 1968, Wolton *et al.* 1982) and 1950 m in Kibira N. P., Burundi (FMNH).

Abundance Widespread and comparatively abundant in suitable habitat. The most frequently captured hipposiderid in Comoé N. P., Côte d'Ivoire, and the second most frequently captured hipposiderid in Tai N. P. Local distribution and abundance is probably determined by the availability of suitable day-roosts.

Adaptations Flight moderately fast, manoeuvrability poor; energetic cost of flight probably high (J. Fahr & K. Soer unpubl.). By day, most often found roosting in spacious hollow trunks of standing trees, including *Borassus*-palms, *Ceiba pentandra*, *Cola cordifolia*, *Cordia* sp., *Hallea stipulosa*, *Klainedoxa gabonensis*, *Macaranga* sp., *Pseudospondias microcarpa*, *Ricnodendron heudelotii* and *Terminalia superba* (Decher & Fahr 2005a). Very occasionally found inside fallen logs, old wells and disused mines, and once found in a belfry. Never found in hollow *Cynometra megalophylla* in Comoé N. P. although this tree is very abundant in gallery forests and its hollow trunks seem suitable. Often shares day-roosts with other bats (*Lissonycteris angolensis*, *Nycteris arge*, *N. major*, *Rhinolophus alcyone*, *R. landeri*), anomalures (*Idiurus macrotis*, *Anomalurus* spp.), African Dormice (Gliridae) and Tullberg's Soft-furred Mouse *Praomys tullbergi* (Decher & Fahr 2005a). The recapture rate was 17% ($n = 35$) in Tai N. P. and 20% ($n = 59$) in Comoé N. P. (J. Fahr unpubl.). Most individuals were recaptured up to one year after marking, and two individuals were recaptured after three years. All were recaptured less than 400 m from the initial site, most less than 250 m, suggesting that home-ranges are very small (several ha) and that site-fidelity is unusually high. The eyes of *H. cyclops* are large in comparison with those of most other African hipposiderids, suggesting that vision plays a more important role in orientation than in other species of bats. Together with its sister species *H. camerunensis*, it is possibly the only African *Hipposideros* that does not have an orange-phase. The frosted pelage perhaps helps to camouflage these bats while they are exposed to predators during perch-hunting (see Foraging).

Foraging and Food Insectivorous. Forages by fly-catching and, very rarely, by slow-hawking. Usually forages not far from the ground or vegetation. Median foraging height in Côte d'Ivoire (as determined by captures in mist-nets set 0–25 m above ground) was 1.9 (0.4–23.6) m, $n = 91$, J. Fahr unpubl.). Most individuals were caught 1–8 m above ground, but six were caught between 13.5 and 23.6 m. They are specialized fly-catchers and rarely fly except when commuting from day-roosts to feeding areas, flying from one perch to another, or attacking prey. They emerge from their day-roosts comparatively early (18:00–18:30h) and fly to perches, such as tree trunks, branches and twigs, which are usually 2–6 m above ground. There they rotate from side to side while echolocating and scanning the surroundings for flying insects. Detected insects are captured in flight, and either carried back to the perch, or to the day-roost, where they are divested of their wings and other hard parts, and then consumed. Verschuren (1957) analysed discarded wings and other remains collected in Garamba N. P., NE DR Congo, and found predominantly hawk-moths (Sphingidae) and cicadas but also owl-flies (Neuroptera: Ascalaphidae),

flat-bugs (Heteroptera: Aradidae), wasps (Hymenoptera: Eumenidae) and beetles (Coleoptera: Scarabaeidae, Elateridae). Additionally, Verschuren (1957) found bark-lice (Psocoptera), moth-flies (Diptera: Psychodidae) and ants (Hymenoptera: Formicidae) in stomach contents. In Comoé N. P. these bats predominantly took hawk-moths, cicadas and beetles, but also ant-lions (Neuroptera: Myrmeleontidae), grasshoppers and crickets (Orthoptera: Acrididae, Gryllidae) and winged male driver-ants (Hymenoptera: Formicidae: *Dorylus* spp.) (K. Soer & J. Fahr unpubl.).

Echolocation Call-shape CF/FM. CF-frequency in resting bats (Côte d'Ivoire) 59.7 (58.4–60.8) kHz (J. Fahr & N. Ebigo unpubl.). The CF-frequency of 101–109 kHz given by Novick (1958b) is erroneous and possibly the result of the recording equipment at that time (J. Fahr unpubl.).

Social and Reproductive Behaviour Roosts singly or in small to medium-sized groups comprised of 1–3 ♂♂ and several ♀♀ (Aellen 1952, Verschuren 1957, Fedden & Macleod 1986, J. Fahr unpubl.). The largest group found in Comoé N. P. consisted of 18 individuals (not sexed). Lang & Chapin (1917b) and Eisentraut (1956) reported group-sizes of 12 individuals. The mean ratio of ♂♂ to ♀♀ in colonies was 1 : 1.8 in Garamba N. P. (Verschuren 1957). Individuals roosting singly are mostly ♂♂. The frontal sac in both sexes, and the anal sac in ♂♂, are likely to play an important role in olfactory communication although the specific function is not known. The anal sac, when everted, emits a very strong, almost pungent odour. Not yet known if the odour is produced by glands or by bacterial fermentation of excretions. Young are not left in day-roosts during the night but are carried by their mothers, even during perch-hunting (J. Fahr pers. obs.).

Reproduction and Population Structure Litter-size: one. Reproductive chronology uncertain. In the Northern Rainforest–Savanna Mosaic (Fintonia, NW Sierra Leone; Comoé N. P., NE Côte d'Ivoire; Garamba N. P., NE DR Congo), 11 of 14 adult ♀♀ were pregnant, two were lactating and one was neither pregnant nor lactating in Feb–Apr; 10 of 15 ♀♀ were lactating and five were neither pregnant nor lactating in May–Jun; none of 18 ♀♀ was pregnant or lactating in Oct–Nov; no data for other months (Verschuren 1957, J. Fahr unpubl., USNM). According to Verschuren (1957), in Garamba N. P., ♀♀ are in fairly close reproductive synchrony; births take place in mid-Mar, lactation ends in mid-May, and there is no evidence of a second parturition season; young are born with a FA ca. 25 mm. In the Rainforest BZ of Côte d'Ivoire, none of 18 adult ♀♀ was pregnant or lactating in Jan–Feb; 1 of 11 was pregnant, one was lactating and nine were neither pregnant nor lactating in Mar; none of 3 ♀♀ was pregnant or lactating in Jun; 8 of 14 ♀♀ were pregnant and six were neither pregnant nor lactating in Jul–Oct; 1 of 1 was lactating in Dec; no data for other months (J. Fahr unpubl., CM, MHNG, ROM, SMF, USNM). None of the females was found simultaneously lactating and pregnant ($n = 34$). These data are not conclusive but they are compatible with restricted seasonal monoestry in the Rainforest–Savanna Mosaic (with lactation coinciding with the onset of the wet season), and extended seasonal monoestry in the Rainforest BZ (with the majority of ♀♀ giving birth towards the end of the wet season).

The ratio of ♂♂ to ♀♀ as determined by captures with mist-nets (excluding recaptures) in Comoé N. P. was 1 : 0.6 (n = 55); in Taï N. P., it was 1 : 0.7 (n = 29; J. Fahr unpubl.).

Predators, Parasites and Diseases Remains of one individual were found in scats of an unidentified small carnivore (probably genet *Genetta* sp.) in Central African Republic (Hutterer & Ray 1997). Ectoparasites include bat-flies *Raymondia brachyphysa*, *R. intermedia* (Diptera: Streblidae) and a mite *Steatonyssus hipposideros* (Acari: Macronyssidae) (Jobling 1956). In Taï N. P., 23% of the individuals (n = 35) were heavily infested with unidentified, bright orange mites (J. Fahr unpubl.).

Conservation IUCN Category: Least Concern.

Probably most threatened by destruction of suitable day-roosts and direct exploitation therein.

Measurements

Hipposideros cyclops

FA (♂♂): 65.4 (61–75) mm, n = 54

FA (♀♀): 68.0 (59–74) mm, n = 47

WS (c): 400 (374–425) mm, n = 13

TL (♂♂): 109.6 (99.0–133.0) mm, n = 45

TL (♀♀): 113.1 (95.0–128.0) mm, n = 79

T: 83.6 (18–36) mm, n = 124

E: 33.5 (28–38) mm, n = 125

NL (breadth): 14.9 (12.9–15.7) mm, n = 8

Tib: 32.2 (29–35) mm, n = 20

HF: 20.1 (18–22) mm, n = 114

WT (♂♂): 29.2 (21–40) g, n = 81

WT (♀♀): 34.8 (24–45.5) g, n = 91*

CrnC: 28.2 (26.3–30.0) mm, n = 14

GWS: 15.3 (14.0–16.3) mm, n = 17

C–M³: 10.4 (9.9–10.8) mm, n = 12

Gambia, Guinea-Bissau, Liberia, Côte d'Ivoire, Ghana, Togo, Benin, Cameroon, DR Congo, Uganda, Burundi, Tanzania (FC, FMNH, IICT/CZ, MZUF, RMCA, ROM, SMF, SMNS, USNM)

*Non-pregnant ♀♀. Pregnant ♀♀ up to 58 g

Key References Decher & Fahr 2005a; Eisentraut 1956; Hill 1963; Lang & Chapin 1917b; Verschuren 1957.

Jakob Fahr

Hipposideros fuliginosus SOOTY LEAF-NOSED BAT (TEMMINCK'S LEAF-NOSED BAT)

Fr. Phyllorhine fuligineuse; Ger. Temmincks Rundblattnase

Hipposideros fuliginosus (Temminck, 1853). Esquisses Zool. sur la Côte de Guinée, p. 77. Ashanti Land, Ghana (type locality 'Côte de Guinée' restricted by Jentink 1887, 1888).

Taxonomy Originally *Phyllorhina fuliginosa*. Species-group: *bicolor*. Synonyms: currently none. Subspecies: currently none recognized (but see Geographic Variation). Often confused with *Hipposideros ruber*, *H. caffer*, *H. lamottei* and *H. abae*. Andersen (1906) recognized the confused taxonomy of this bat and pointed out some of the specific characters for a diagnosis of the species. The analyses of Koopman (1989) and Koopman *et al.* (1995) again confused the situation by focusing entirely on measurements of the skull while not considering external measurements, proportions and characters. The following account is therefore largely based on specimens examined by the author, disregarding most of the published records because of the difficulties in identifying this species. Chromosome number: not known.

Description Small to medium-sized microbat with noseleaf (posterior component roughly elliptical); dark brown with orange-phase; ears separated; noseleaf with two lateral leaflets on each side, no club-shaped processes and nostrils not concealed by internarial septum; no frontal sac; thumb well developed with comparatively large claw and basal pad. Sexes similar. Pelage slightly coarser than in *H. caffer* and *H. ruber*. Dorsal pelage (grey-phase) dark brown. Ventral pelage similar but paler. Ears separated; comparatively and relatively short (30–31% of FA), broad, triangular and pointed with slight concavity in outer margin just below tip: 11 internal folds. Antitragus with slight fold. Posterior component of noseleaf not divided into cells by vertical septa; upper margin with low-arched outline. Behind the upper margin, there is a low to well-developed transverse supplementary structure, which is sometimes smooth

(Hill 1963) and sometimes more or less serrated (Koopman *et al.* 1995); the variability renders this character of little value as a means of distinguishing *H. fuliginosus* from *H. ruber* and *H. caffer* in which the structure is serrated (Koopman *et al.* 1995). No club-shaped processes; internarial septum not concealing nostrils; two lateral leaflets on each side. Frontal sac absent in both sexes (but sometimes there is a patch of bare skin). No anal sac. Wings and interfemoral membrane blackish-brown. Thumb and claw comparatively long and powerful, claw length >3 mm, claw height >1.2 mm; pad at base of thumb well developed. Fifth metacarpal 84–92% of third metacarpal. Third finger with comparatively long phalanges (first phalanx 14.3–18.7 mm, 28–31% of FA; second phalanx 17.8–21.9 mm, 33–37% of FA) (cf. *H. lamottei*). Tibia comparatively short, and 38–39% of FA (cf. *H. lamottei*). Tail comparatively short, and 45–49% of HB.

Skull robust; zygomatic arches slender; zygomatic width > mastoid width. CrnC relatively long (36.3 [35–40]% of FA, n = 83) (cf. *H. lamottei*). Sagittal crest prominent in specimens from the eastern population, much less so in specimens from the western population (see below). Cochleae not enlarged, their breadth only a little greater than their distance apart. Upper incisor slightly bicuspid. Upper canine of medium relative length (48 [44–51]% of C–M³, n = 3). Anterior upper premolar small, somewhat displaced labially; canine and posterior premolar almost in contact. Anterior lower premolar ca. half the height and length of the posterior premolar.

Geographic Variation Although no subspecies have been described, there are two morphometrically distinct populations –

a western population in Guinea to Cameroon and Gabon, and an eastern population known from only a few specimens from DR Congo, Central African Republic and Uganda. Eastern specimens are much heavier, and larger in both body and craniodental measurements (see Measurements) and have proportionally broader zygomata. They probably represent an undescribed taxon closely related to *H. fuliginosus*.

Similar Species Four other African *Hipposideros* have the following combination of characters: ears separated; noseleaf with two lateral leaflets on each side, no club-shaped processes and nostrils not concealed by internarial septum (Table 15, p. 370):

Hipposideros ruber. Smaller on average in all measurements (FA: 51.1 [47–55] mm; CrnC: 19.1 [17.8–20.3] mm). Thumb, claw and basal pad smaller (claw length <3 mm). Frontal sac usually present in ♂♂ but not in ♀♀. Echolocation CF-frequency higher (132–144 kHz).

H. lamottei. Skull relatively smaller (CrnC: 34–35% of FA), and usually also comparatively smaller (CrnC: 19.2 [18.9–19.6] mm; C–M³: 6.6 [6.4–6.7] mm); zygomatic width < mastoid width; dentition much weaker. Frontal sac present in both sexes. Ears relatively shorter (25–29% of FA). Thumb, claw and basal pad much smaller and less powerful (claw length <2.5 mm). Third finger with shorter phalanges (first 12.5–14.3 mm; second 10.5–12.1 mm). Tibia relatively longer (41–42% of FA).

H. beatus. Much smaller (FA: 43.7 [39–48] mm; CrnC: 16.8 [16.1–18.1] mm).

H. caffer. Much smaller (FA: 46.4 [42–52] mm; CrnC: 17.2 [16.1–18.3] mm).

(Note: *H. abae*, which is otherwise fairly similar externally, has three lateral leaflets on each side.)



Distribution Endemic to Africa. Recorded, disjunctly, from the Rainforest BZ (Western, West Central and Eastern Regions), Afromontane–Afroalpine BZ and Northern and Eastern Rainforest–Savanna Mosaics. Known from ca. 25 localities in West Africa (Sierra Leone, Guinea, Liberia, Côte d'Ivoire, Ghana, SE Nigeria) and west-central Africa (Cameroon and Gabon). Also, five isolated records from the central Congo Basin, from the Ituri/Albertine Rift area in E DR Congo and W Uganda, and from S Central African Republic (Pépélou, MHNG). Two records from Gabon (Booué [00°06'S, 11°56'E], Kango [00°09'N, 10°08'E]) are included based on the description and measurements (FA: 54–57 mm) of the specimens (Malbrant & Maclatchy 1949). A record from Gaba R., Ethiopia, published as *H. fuliginosus* by Lagen *et al.* (1974), probably represents an unnamed species resembling *H. lamottei* (J. Fahr unpubl.). A record from Ngombe, DR Congo, by Hayman *et al.* (1966), needs to be re-examined and is not included here.

Habitat Largely restricted to Rainforest BZ and mostly recorded from wetter and drier types of lowland rainforest although also recorded from coastal forest and mangroves vegetation zones. In Guinea, recorded from ravine forests within montane grassland at 1350 m altitude (Fahr & Ebigo 2003) and in Kalinzu Forest, Uganda, from sub-montane forest at 1500 m altitude (LACM). Extends along riverine forests into drier areas such as Fintonia (Sierra Leone) and Comoé N. P. (Côte d'Ivoire) in the Northern Rainforest–Savanna Mosaic.

Abundance Widespread but localized and comparatively rare.

Adaptations Wings broad and rounded; flight very manoeuvrable. By day, has been found roosting in the hollow trunks of standing trees. Sometimes shares roosts with *H. ruber* (Hayman 1945, Aellen 1952 as *H. caffer*). Hayman (1945), when comparing *H. fuliginosus* with *H. abae*, suggested that the presence of the frontal sac in ♂♂ might be under seasonal influence and of little diagnostic value. However, the frontal sac was consistently absent in adult ♂♂ of *H. fuliginosus* taken throughout the year and therefore it is of diagnostic value.

Foraging and Food In contrast to larger hipposiderids, forages by slow-hawking and does not seem to forage by fly-catching. Median foraging height in Côte d'Ivoire (as determined by captures in mist-nets set 0–25 m above ground) was 1.7 (0.4–2.6) m (n = 22), indicating that this bat forages mainly in the understorey of the forest, in densely cluttered situations (J. Fahr unpubl.). Diet not known in detail, but likely to be medium- to large-sized flying insects such as moths and beetles.

Echolocation Call-shape CF/FM. CF-frequency in resting bats from Côte d'Ivoire: 113–121 kHz (18 bats; J. Fahr & N. Ebigo unpubl.). CF-frequency of six hand-held bats from Guinea was 120–123 kHz (Fahr & Ebigo 2003). CF-frequency can help to distinguish *H. fuliginosus* from *H. ruber*.

Social and Reproductive Behaviour Has been recorded roosting in groups of 2–39 individuals (Hayman 1945, Aellen 1952, USNM). In Cameroon, one group included two adult ♂♂, five adult ♀♀ and five young (Aellen 1952). A collection from Oda, Ghana,

apparently taken from the same hollow tree, comprised at least 30 ♂♂ and nine ♀♀ (USNM).

Reproduction and Population Structure Litter-size: not known. Reproductive chronology not known. At 05° 50' N (Taï N. P., Côte d'Ivoire), 1 of 1 ♀ was pregnant in Feb; 5 of 5 ♀♀ were lactating in Mar; 3 of 3 were neither lactating nor palpably pregnant in late Aug and Sep; no data for other months. At 08° 45' N (Comoé N. P., Côte d'Ivoire), 4 of 8 were lactating and four were neither lactating nor palpably pregnant in May, and 2 of 2 were neither lactating nor palpably pregnant in Oct; no data for other months. These data, although inconclusive, are compatible with seasonal monoestry.

Predators, Parasites and Diseases Ectoparasites include a bat fly *Raymondia seminuda* (Diptera: Streblidae) (Anciaux de Faveaux 1984).

Conservation IUCN Category: Least Concern.

Population trend inferred to be declining because of large-scale loss and degradation of habitats within the distribution of this species, particularly in West Africa.

Measurements

Hipposideros fuliginosus

Western population

FA: 55.0 (51–60) mm, n = 95

WS (c): 330 (317–344) mm, n = 11

TL: 120.1 (104–132) mm, n = 79

T: 27.3 (21–34) mm, n = 81

E: 17.0 (14–20) mm, n = 79

NL (breadth): 7.1, 8.4 mm, n = 2

Tib: 20.8 (18–24) mm, n = 64

HF: 10.4 (8–12) mm, n = 55

WT: 10.3 (8.0–15.0) g, n = 75

CrnC: 19.9 (19.2–21.5) mm, n = 87

GWS: 11.1 (10.6–12.3) mm, n = 88

C–M³: 7.4 (7.1–8.2) mm, n = 92

Sierra Leone, Liberia, Côte d'Ivoire, Ghana (incl. holotype), Nigeria, Cameroon (AMNH, BMNH, FC, FMNH, MCZ, MHNC, MHNG, MNHN, RMCA, SMF, USNM)

Eastern population

FA: 62.6 (60–64) mm, n = 6

WS: n. d.

TL: 139.4 (134–148) mm, n = 4

T: 34.7 (29–40) mm, n = 4

E: 18.2 (17–20) mm, n = 5

NL (breadth): 8.9, 9.4 mm, n = 2

Tib: 25.0 (23–26) mm, n = 5

HF: 11.8 (11–13) mm, n = 5

WT: 20.5 (18–23) g, n = 3

CrnC: 23.2 (22.8–23.4) mm, n = 7

GWS: 13.1 (12.9–13.5) mm, n = 6

C–M³: 8.7 (8.5–8.9) mm, n = 6

DR Congo, Central African Republic, Uganda (BMNH, LACM, MHNG, SMF, USNM)

Key References Aellen 1952; Andersen 1906; Hayman 1946; Hill 1963; Koopman 1989; Koopman *et al.* 1995.

Jakob Fahr

Hipposideros gigas GIANT LEAF-NOSED BAT

Fr. Phyllorhine géante; Ger. Riesen-Rundblattnase

Hipposideros gigas (Wagner, 1845). Arch. Naturgesch. 11 (1): 148. Benguela, Angola.

Taxonomy Originally *Rhinolophus gigas*. Species-group: *commersoni* with *H. vittatus* (Africa) and *H. thomensis* (São Tomé). Synonyms: *gambiensis*, *niangarae* and probably *viegasi*. Based on FA length (♂ 107 mm, ♀ 103 mm), *viegasi* is more likely to be a synonym of *H. gigas* than *H. vittatus* and therefore, following Hayman & Hill (1971) it is provisionally retained here in *H. gigas*. In contrast, Simmons (2005) has followed a suggestion by J. Fahr (pers. comm.) that *viegasi* is probably a synonym of *H. vittatus*. Subspecies: none currently recognized. Formerly often considered to be a subspecies of *H. commersoni* (e.g. Hill 1963, Koopman 1993) but differences in morphology and echolocation calls indicate *H. gigas* and also *H. vittatus* are distinct species (Pye 1972, McWilliam 1982) and *Hipposideros commersoni* is now considered restricted to Madagascar. In some parts of Africa, *H. gigas* is now known to occur sympatrically with *H. vittatus*, which, as *H. c. marungensis*, was also formerly considered a subspecies of *H. commersoni*. Consequently, the distributions of both *H. gigas* and *H. vittatus* are expected to be considerably more extensive than pre-2005 records indicate and, furthermore, it might be some time before pre-2005 information attributed to *H. commersoni* in Africa,



Hipposideros gigas

H. c. gigas and *H. c. marungensis* is reallocated to its correct species. Chromosome number: not known.

Description Very large microbat with noseleaf (posterior component roughly elliptical); the largest African hipposiderid and the largest African microbat; medium to dark brown with silver, white and brown markings and an orange-phase; ears separated; noseleaf with three or four lateral leaflets on each side, no club-shaped processes and nostrils not concealed by internarial septum. Not easily distinguished morphometrically from *H. vittatus*. Sexes similar in colour; ♂♂ on average larger than ♀♀. Pelage slightly woolly, not sparse on rump; mid-dorsal hairs ca. 8 mm. Dorsal pelage (grey-phase) ranging geographically from medium to dark brown, with silvery frosting on nape, rump and next to wings; head paler; hairs unicoloured or with silvery-grey at tip. Ventral pelage medium grey to pale brown, with silvery frosting. Armpits pure white or yellow, usually surrounded by dark brown. Orange-phase: dorsal pelage bright dark rusty-brown to bright orange; ventral pelage golden rusty-brown. Ears separated, comparatively medium to long but relatively short (23–37% of FA); brown; triangular, tapering to bluntly pointed tip with little or no concavity in outer margin below tip. Antitragus shallow. Noseleaf as in Figure 68e. Posterior component divided into four shallow cells by three weak, vertical septa. No club-shaped processes. Internarial septum not enlarged, not concealing nostrils. Three or four lateral leaflets on each side. Frontal sac present in both sexes; opening vertically. No anal sac. Wings and interfemoral membrane brown. Fifth metacarpal 95–100% of third metacarpal. Tibia 42 (39–44)% of FA. Tail 30 (23–37)% of HB.

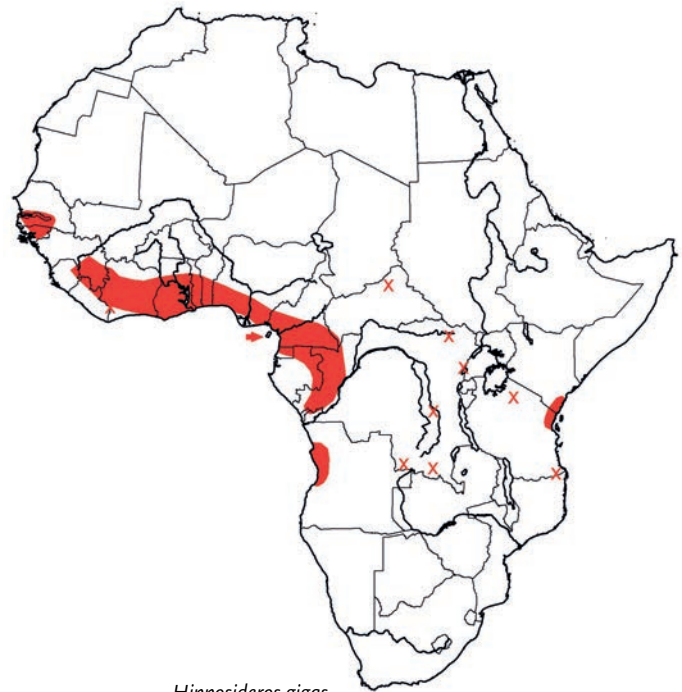
Skull large with broad rostrum; zygomatic arches massive; zygomatic width > mastoid width. Sagittal crest greatly developed (especially in ♂♂) and merging with the supraorbital ridges. Cochleae not enlarged, their breadth only a little greater than their distance apart. Upper incisor slightly bicuspid. Upper canine relatively long (53 [49–59]% of C–M³, n = 13). Anterior upper premolar very small, displaced labially; canine and posterior premolar in contact or nearly so. Anterior lower premolar half the length and height of posterior premolar or slightly less.

Geographic Variation Uncertain. No subspecies recognized by Simmons (2005).

Similar Species Only one other African *Hipposideros* has FA >79 mm, and no club-shaped processes on noseleaf (Table 15, p. 370):

Hipposideros vittatus. Smaller on average (FA [♂♂]: 101.5 [93–106] mm, FA [♀♀]: 93.9 [84–101] mm). Pelage shorter, not slightly woolly. Echolocation CF-frequency 61–66 kHz (depending on locality). Predominantly a savanna species. In at least some areas of sympatry, FA measurements of adults of same sex do not overlap – e.g. in coastal Kenya, *H. vittatus* FA (♂♂): 90–108 mm; FA (♀♀): 85–98 mm (cf. *H. gigas* FA [♂♂]: 109–122 mm; FA [♀♀]: 105–116 mm) (A. N. McWilliam pers. comm.).

Distribution Endemic to Africa. Recorded mainly from the Sudan Savanna, Guinea Savanna, Rainforest and Coastal Forest Mosaic BZs, the Rainforest–Savanna Mosaics and the Zambebian



Hipposideros gigas

Woodland BZ. Previously thought to occur only in western side of Africa, from Senegal to southern Central African Republic and southwards to Namibia (including Bioko I.) (Koopman 1994), but now known to occur in E DR Congo, Kenya and Tanzania, and perhaps occurs even further afield (see Taxonomy). Based on habitat, specimens referred to *gigas* from N Burkina (Koopman *et al.* 1978) and N Togo (De Vree *et al.* 1969) probably represent *H. vittatus* and are tentatively mapped for that species, but no measurements are available for these specimens. Based on FA length, specimens identified with *H. commersoni* from three localities in N Nigeria (BMNH, Bergmans 1977b), and one identified with *H. commersoni gigas* from Central African Republic (Schlitter *et al.* 1982), are more likely to represent *H. vittatus* and are mapped for that species. Currently not considered to occur in Namibia (Simmons 2005) or in S Angola (J. Fahr pers. comm.). Mapped from localities of museum and published specimens whose identification (if not already assigned to *gigas*) could be verified by FA and GLS measurements.

Habitat Lowland rainforest habitats, East African coastal forests and wetter types of woodland savanna. The presence of suitable caves and hollow trees in which to roost is likely to be more important than the type of vegetation (Grubb *et al.* 1998).

Abundance Uncertain; very common in some localities.

Adaptations Aspect ratio, wing-loading and flight characteristics not known but likely to be fairly similar to those of *H. vittatus*. By day, usually hangs, free or in contact, in caves and large hollow trees, but sometimes roosts singly in foliage (Rosevear 1965). Easily disturbed by humans, and may desert a day-roost after a single disturbance. Does not become torpid during the day, and does not hibernate (Brosset 1969). Heavy fat deposits have been reported in Guinea-Bissau by Monard (1939, as *H. gigas viegasi*) and at the end of the first wet season (Jun) in Gabon (Brosset 1966). In Kenya, *H. gigas*

migrates from the coast inland in Oct and again in Mar, to take advantage of the earlier and more predictable arrival inland of the two wet seasons (McWilliam 1982).

Foraging and Food Foraging: no information. Diet is mainly large beetles but individuals sometimes take large Orthoptera (Brosset 1969), and gorge themselves seasonally on winged termites (Lang & Chapin 1917b).

Echolocation Call-shape CF/FM. CF-frequency (Shimoni, Kenya) 54 (51–56) kHz (17 bats; A. N. McWilliam pers comm.). Pye (1972) observed a bimodal distribution of CF-frequencies in a colony of '*H. commersoni*' inhabiting caves at Shimoni: the CF-frequencies were ca. 56 kHz and ca. 66 kHz with a silent interval of 8 kHz. It is now known that *H. gigas* emits the 56 kHz calls, and that *H. vittatus* emits the ca. 66 kHz calls.

Social and Reproductive Behaviour In Gabon, roosts in colonies of 50–400 (Brosset 1966, Brosset & Saint Girons 1980). Parturient ♀♀ segregate for only a few days (Brosset 1969).

Reproduction and Population Structure Litter-size: one. At 0–1°N in NE Gabon the reproductive chronology is restricted seasonal monoestrus with copulation in May during the Apr–May peak in rainfall, and births in Oct during the Sep–Dec peak in rainfall (Brosset 1969). The young grow rapidly, fly at 30–35 days, reach adult-size at ca. two months and sexual maturity after two years. At 04° 39'S (Shimoni, coastal Kenya), copulation occurs in the long dry season (Jul–Aug), and births during the short wet season (Nov) (McWilliam 1982).

Predators, Parasites and Diseases Anciaux de Faveaux (1984) lists parasites of '*H. commersoni*' in Africa, but it is not certain which have been recorded from *H. gigas*, and which from *H. vittatus*.

Conservation IUCN Category: Least Concern.

In Gabon, colonies are periodically drastically reduced by humans who eat these bats (Brosset 1966), but overall population trend not known. Potentially also threatened by selective logging and clear cutting.

Measurements

Hipposideros gigas

FA (♂♂): 107.9 (100–124) mm, n = 39

FA (♀♀): 103.8 (95–116) mm, n = 39

WS (d): 611 mm, n = 1

TL (♂♂): 154 (128–167) mm, n = 18

TL (♀♀): 148 (123–175) mm, n = 14

T (♂♂): 37.9 (30–50) mm, n = 22

T (♀♀): 31.8 (25–39) mm, n = 13

E: 31.4 (24–36) mm, n = 34

NL (breadth): 14.7 (11–19) mm, n = 18

Tib: 43.9 (42–46) mm, n = 9

HF (♂♂): 24.8 (18–27) mm, n = 10

HF (♀♀): 22.9 (19–25) mm, n = 9

WT (♂♂): 130.2 (125–138) g, n = 6

WT (♀♀): 94.5 (85–105) g, n = 4

CrnC (♂♂): 38.8 (36.1–42.7) mm, n = 22

CrnC (♀♀): 36.2 (33.3–39.0) mm, n = 15

GWS (♂♂): 21.8 (17.5–23.8) mm, n = 46

GWS (♀♀): 20.1 (17.2–21.9) mm, n = 29

C-M³ (♂♂): 13.7 (10.7–14.5) mm, n = 26

C-M³ (♀♀): 13.2 (12.1–14.1) mm, n = 18

Throughout geographic range (BMNH, HZM, MNHN, RMCA, ROM, SMNS, ZFMK and literature)

Key References Brosset 1969; McWilliam 1982; Rosevear 1965.

Meredith Happold

Hipposideros jonesi JONES'S LEAF-NOSED BAT

Fr. Phyllorhine de Jones; Ger. Jones' Rundblattnase

Hipposideros jonesi Hayman, 1947. Ann. Mag. Nat. Hist. ser. 11, 14: 71. Makeni, Sierra Leone.

Taxonomy Species-group: *bicolor*. Synonyms: none. Chromosome number: not known.

Description Small microbat with noseleaf (posterior component very roughly elliptical but upper margin more angular than in other *Hipposideros*); greyish-brown with orange-phase; ears very large and separated; noseleaf with enlarged internarial septum, which partly conceals the nostrils, and one lateral leaflet on each side; frontal sac absent in both sexes. Sexes similar. Pelage fine, dense, silky; mid-dorsal hairs 10–11 mm. Dorsal pelage (grey-phase) greyish-brown to dirty-brown; hairs dark grey with grey at tip. Ventral pelage paler; hairs grey with pale grey or pale brown to whitish tip. Orange-phase: dorsal pelage tawny-orange to cinnamon. Ears separated; comparatively short to medium, but relatively medium to long (45–60% of FA), broad, subtriangular, pointed with only a

faint concavity in outer margin below tip; each ear with 11 internal folds. Antitragus with distinct fold. Noseleaf as in Figure 68b, longer than broad. Posterior component conspicuously elongated, divided into four cells by two prominent lateral septa and one weak middle septum. Upper margin strongly curved and subtriangular in outline. No club-like processes. Anterior component hairy and broad, covering muzzle. Internarial septum pad-like and greatly enlarged, forming a transversely oval disc (broader than long), which partly conceals the nostrils. One well-developed and long lateral leaflet on each side. No frontal sac. No anal sac. Wings and interfemoral membrane dark grey. Fifth metacarpal 96 (93–100)% of third metacarpal. Thumb comparatively weak. Tibia 46 (43–48)% of FA. Tail 48 (34–53)% of HB.

Skull delicate, elongated, with narrow, pointed rostrum and relatively broad, high braincase; zygomatic arches slender; zygomatic

width < mastoid width (Figure 63c). Sagittal crest low. Cochleae moderately enlarged, their breadth 2–3 times their distance apart (Figure 73c). Upper incisors slightly bicuspid. Upper canines relatively short (38 [34–42]% of C–M³). Anterior upper premolar small, slightly displaced labially; canine and posterior premolar well separated. Anterior lower premolar ca. half the length and height of posterior lower premolar.

Geographic Variation Hayman (1964) documented extensive geographic variation and ascribed this to a morphological cline, with western specimens (Sierra Leone) being significantly smaller than eastern specimens (Ghana). However, specimens from even further east (C Nigeria) are smaller than those from Ghana and populations from Côte d'Ivoire, Mali and Burkina also show considerable variation (Koch-Weser 1984, Fahr & Ebigo 2003). It seems that the exceptional geographic variability of *H. jonesi* is not simply clinal as proposed by Hayman (1964), but more likely to be linked to environmental factors such as seasonality and/or precipitation, with bats from more seasonal and/or drier regions (e.g. W Guinea, Mali, C Nigeria) smaller on average than those from less seasonal and/or wetter regions (e.g. SE Guinea, coastal Sierra Leone, Ghana). Available data indicate that specimens from Ghana attain the largest dimensions (Hayman 1964), e.g. FA: 52.4 (50–55) mm, n = 54; CrnC: 20.0 (19.0–20.6) mm, n = 15; C–M³: 6.7 (6.4–6.9) mm, n = 15.

Similar Species Only two other African *Hipposideros* have a noseleaf with the internarial septum enlarged (Table 15, p. 370):

Hipposideros curtus. Margin of posterior component low-arched in outline; internarial septum smaller, longer than broad; two weakly developed lateral leaflets on each side; frontal sac usually present (but sometimes lacking in ♀♀). Ears usually shorter (15–22 mm), less than 50% of FA.

H. marisae. Smaller (FA: 38–42 mm; CrnC: 15.4–15.8 mm). Ears shorter (15–17 mm), less than 50% of FA; no antitragal fold. Posterior component of noseleaf not elongated, low-arched in outline; internarial septum much less enlarged, oval disc longer than broad; one (rarely two) rudimentary lateral leaflet on each side; frontal sac present.

Distribution Endemic to Africa. Known only in West Africa, from 26 scattered localities in the Rainforest and Afromontane–Afroalpine BZs, the Northern Rainforest–Savanna Mosaic and the Guinea Savanna, Sudan Savanna and Sahel Savanna BZs. Recorded from Guinea, Sierra Leone, Liberia, Côte d'Ivoire, Mali, Burkina, Ghana and Nigeria (Hayman 1947, 1964, Eisentraut & Knorr 1957, Koch-Weser 1984, Happold 1987, Koopman *et al.* 1995, Fahr & Ebigo 2003).

Habitat Apparently strictly dependent on caves or artificial substitutes such as mines and, within the biotic zones exploited, the patchy distribution of this species seems determined by the availability of these roosts without apparent preference for any particular type of vegetation. Has been recorded from lowland rainforest, montane forest, dry forests in the Rainforest–Savanna Mosaic, and in savannas of the Sudan Savanna BZ and the southern part of the Sahel Savanna BZ up to 15°00'N (Douentza, Mali). A lack of records from the wettest parts of the rainforest in Sierra Leone, Liberia, Côte d'Ivoire



Hipposideros jonesi

and Ghana suggests that this habitat is avoided. Specimens have been caught over waterholes and creeks, in groves of oil-palms, tree-shrub savanna, farmed semi-deciduous forest and cutover rainforest. In Guinea, found at 1350 m on the Simandou Range, in montane grassland intersected by ravine forests (Fahr & Ebigo 2003).

Abundance Widespread in different vegetation zones but localized. The occurrence and abundance of this bat is probably determined by the availability of suitable day-roosts.

Adaptations Day-roosts include caves, disused mines, a bunker and cavities under rocks. Emergence from a day-roost in a bunker at 10°55'N in Burkina was observed at 19:00h in mid-Sep (Koch-Weser 1984). Reported to share its day-roosts with *Lissonycteris angolensis smithii*, *Nycteris macrotis*, *N. gambiensis*, *Rhinolophus denti knorri*, *R. fumigatus*, *R. landeri*, *R. guineensis*, *R. maclaudi*, *Hipposideros ruber* and *H. abae* (Eisentraut & Knorr 1957, Hayman 1964, Koch-Weser 1984, J. Fahr unpubl.). At dusk, observed drinking while flying along creeks in gallery forest (H. Knorr, SMNS). Six specimens from Djipologo, Burkina, were mist-netted over a waterhole (USNM).

Foraging and Food No information. The comparatively delicate skull and dentition suggests that this bat feeds on small to medium-sized moths and other soft-bodied, flying insects. The ears are relatively longer (i.e. in relation to the length of the forearm) than in any other African *Hipposideros* except *H. megalotis*, and are relatively much longer than the ears of the two other African species (*H. curtus* and *H. marisae*) that have noseleaves of similar shape. This suggests that *H. jonesi* has a special foraging strategy.

Echolocation Call-shape CF/FM. The CF-frequency (second harmonic) of one hand-held individual from Guinea was 48 kHz (N. Ebigo & J. Fahr unpubl.). This frequency is surprisingly low for a *Hipposideros* of its body size.

Social and Reproductive Behaviour Roosts in colonies. One colony, roosting in a disused mine in Ghana, was estimated to comprise 200–300 individuals; a sample of 54 contained 27 ♂♂ and 27 ♀♀ (Hayman 1964). Within the mine, the bats were hanging in large groups, with a few hanging singly that might have found temporary shelter after being disturbed. A group roosting in Burkina included three ♂♂ and one ♀ (Koch-Weser 1984). A group from Ghana included four ♂♂ and two ♀♀ (ROM).

Reproduction and Population Structure Litter-size and reproductive chronology not known. At 06° 30' N (near Nkawkaw, Ghana), one ♀ was lactating, and three ♂♂ had scrotal testes (5×3 mm), in early Aug (USNM).

Predators, Parasites and Diseases Ectoparasites include a bat-fly *Penicillidia allisoni* (Diptera: Nycteribiidae) (Theodor 1968).

Conservation IUCN Category: Near Threatened.

Dependent on caves and cave-like structures, therefore vulnerable to hunting by people, disturbance of roosts, and mining. Population trend unknown but possibly declining. Also vulnerable because of its patchy distribution and small area of occupancy.

Measurements

Hipposideros jonesi

FA: 46.7 (44–50) mm, n = 24

WS (c): 250, 270 mm, n = 2

TL: 72.0 (65–80) mm, n = 22

T: 22.7 (17–27) mm, n = 22

E: 24.5 (21–28) mm, n = 22

NL: 8.3 (8.1–9.1) mm, n = 7

Tib: 21.2 (20–23) mm, n = 22

HF: 7.9 (6–9) mm, n = 15

WT: 4.6 (3.0–8.0) g, n = 45

CrnC: 18.4 (17.6–19.1) mm, n = 16

GWS (MW): 10.0 (9.6–10.6) mm, n = 16

C–M³: 6.0 (5.7–6.3) mm, n = 20

Guinea, Sierra Leone, Liberia, Côte d'Ivoire, Mali, Burkina, Nigeria (AMNH, BMNH, FC, FMNH, HZM, MHNG, SMF, SMNS, ZFMK) This species shows pronounced variation in size of most parameters, and specimens from Ghana surpass some of the ranges given here (see Geographic Variation)

Key References Eisentraut & Knorr 1957; Hayman 1947, 1964; Koch-Weser 1984.

Jakob Fahr

Hipposideros lamottei LAMOTTE'S LEAF-NOSED BAT

Fr. Phyllorhine de Lamotte; Ger. Nimba Rundblattnase (Lamottes Rundblattnase)

Hipposideros lamottei Brosset, 1984 [publ. 1985]. Mammalia 48: 548. Pierré Richaud, Mt Nimba, 1450 m, Guinea.

Taxonomy Species-group: *bicolor*. Synonyms: none. An enigmatic species. Since its description in 1985, it was reported from various West African countries by Koopman (1989) and Koopman *et al.* (1995), although these authors considered the taxonomic status of *H. lamottei* as somewhat doubtful. However, most of the specimens on which these additional records were based have been re-examined and found to represent *H. caffer* (Decher & Fahr 2005b). Ethiopian specimens, reported as *H. fuliginosus* by Lagen *et al.* (1974), resemble *H. lamottei* more closely than *H. fuliginosus*. However, they differ from *H. lamottei* in overall size and wing shape (first and second phalanx of third digit much longer) and probably represent an undescribed species (see Geographic Variation). Chromosome number: not known.

Description Small microbat with noseleaf (posterior component roughly elliptical); brown, probably with orange-phase; ears separated; noseleaf with two lateral leaflets on each side, no club-shaped processes and nostrils not concealed by internarial septum; frontal sac present in both sexes; thumb weakly developed with comparatively small claw and basal pad; anterior upper premolar within tooththrow. A poorly known species. Pelage fine and dense. Pelage, so far as known, brown. Orange-phase: not yet reported but likely to occur. Ears separated, comparatively and relatively short (25–29% of FA) and broad. Posterior component of noseleaf not divided into cells by vertical septa; upper margin straight (horizontal), terminating with an almost right-angle at each end; breadth of posterior component equal to or greater than breadth

of anterior component (cf. *H. ruber*). No club-shaped processes. Internarial septum not concealing nostrils. Two well-developed lateral leaflets on each side. Frontal sac present in both sexes. No anal sac. Wings and interfemoral membrane blackish-brown. Thumb, claw and basal pad weakly developed, claw length <2.5 mm, claw height <1.2 mm (cf. *H. fuliginosus*). Third finger with comparatively short phalanges (first phalanx 12.5–14.3 mm, 23–25% of FA; second phalanx 10.5–12.1 mm, 19–21% of FA) (cf. *H. fuliginosus*). Fifth metacarpal 80–90% of third metacarpal. Tibia comparatively long, and 41–42% of FA (cf. *H. fuliginosus*).

Skull fairly delicate; zygomatic width < mastoid width. CrnC relatively short (34–35% of FA) (cf. *H. fuliginosus*). Dentition relatively weak. Anterior upper premolar small, within tooththrow; canine and posterior premolar well separated.

Geographic Variation None. Sixteen specimens from Ethiopia (SMF, partly published by Lagen *et al.* 1974 as *H. fuliginosus*) are slightly larger on average than the six specimens of the type series from Mt Nimba, Guinea. However, they clearly differ from *H. lamottei* in the length of the third digit (*H. lamottei*, first phalanx: 13.2 [12.5–14.3], second phalanx: 11.4 [10.5–12.1]; Ethiopian specimens, first phalanx: 17.6 [16.3–18.3], second phalanx: 19.5 [18.7–20.7]), and probably represent an unnamed species (J. Fahr unpubl.).

Similar Species Four other African *Hipposideros* have the following combination of characters: ears separated; noseleaf with

two lateral leaflets on each side, no club-shaped processes and nostrils not concealed by internarial septum (Table 15, p. 370):

Hipposideros ruber. Body measurements usually smaller (FA: 51.1 [47–55] mm), but skull relatively larger (CrnC 38.2 [35–41]% of FA, $n = 322$). In West Africa, zygomatic width greater than mastoid width. Dentition stronger. Frontal sac usually present in ♂♂ only.

H. fuliginosus. Skull (western population) relatively larger (CrnC 36.3 [35–40]% of FA, $n = 83$), and also usually comparatively larger (CrnC: 19.9 [19.2–21.5] mm, C–M³: 7.4 [7.1–8.2] mm); zygomatic width greater than mastoid width; dentition much stronger. Frontal sac absent in both sexes. Ears relatively longer (30–31% of FA). Thumb, claw and basal pad much larger and more powerful; claw length >3 mm. Third finger with longer phalanges, first 14.3–18.7 mm, second 17.8–21.9 mm. Tibia relatively shorter (38–39% of FA).

H. beatus. Much smaller (FA: 43.7 [39–48] mm; CrnC: 16.8 [16.1–18.1] mm).

H. caffer. Much smaller (FA: 46.4 [42–52] mm; CrnC: 17.2 [16.1–18.3] mm).

(Note: *H. abae*, which is otherwise fairly similar externally, has three lateral leaflets on each side.)

Distribution Endemic to Africa. As yet only known from the vicinity of Mt Nimba, Guinea: Pierré Richaud (07° 41'N, 08° 22'W, 1400 m, in the Afromontane–Afroalpine BZ), and Grotte de Blandé near Ziéla (07° 43'N, 08° 2'W, 500 m, in the Rainforest BZ). Specimens on which the records from Sierra Leone, Liberia, Côte d'Ivoire, Ghana and Cameroon were based by Koopman (1989) and Koopman *et al.* (1995) represent *H. caffer* (Decher & Fahr 2005b).

Habitat The holotype and four other specimens were collected from horizontal mine-adits opening onto afroalpine grassland at

1400 m, and another specimen was taken from a natural cave in degraded rainforest at 500 m (Brosset 1984).

Abundance No data available but apparently very rare.

Remarks The type series (five adult ♂♂ and one adult ♀) was taken from two day-roosts, ca. 4 km apart, on Mt Nimba (Brosset 1984). One was a cave located at the base of Mt Nimba (500 m) in a valley in degraded forest. It was known to shelter a colony of *H. ruber* (Aellen 1963). Four specimens were captured, of which three represented *H. ruber* and one represented *H. lamottei*. The entrance area of the cave was formerly occupied by a large colony of *Rousettus aegyptiacus*, which has been eliminated as a result of human disturbance and exploitation (Lamotte & Roy 1998). The second day-roost was the horizontal tunnel, ca. 100 m long, of an iron-ore mine near Pierré Richaud (1450 m) that opened over a steep slope devoid of bushy vegetation. In this mine, there was a colony of ca. 130 *Hipposideros*. Ten individuals (5 ♂♂ and 5 ♀♀) were captured in Dec; five were retained as the type series of *H. lamottei* and the others identified with *H. lamottei* on the basis of their external characters. There were no juveniles, and none of the ♀♀ was visibly pregnant. Four *Lissonycteris angolensis smithii* also roosted in this mine. Nothing else is known about the habits of *H. lamottei*. Its comparatively small skull and weak dentition suggest that it takes softer prey than similar-sized hipposiderids such as *H. ruber* and *H. fuliginosus*.

Conservation IUCN Category: Critically Endangered.

Only known from one location (two localities ca. 4 km apart) and six individuals. Known extent of occurrence extremely small and within a region seriously affected by civil war in adjacent Liberia. Population size not known but likely to be small; population trend inferred to be declining. Major threats: large-scale mining (past and present), logging and agriculture. Probably vulnerable to disturbance and direct exploitation in its day-roosts. Surrounding areas have been surveyed recently but the species has not been found elsewhere (Fahr & Ebigo 2003, Fahr *et al.* 2006).

Measurements

Hipposideros lamottei

FA: 55.8 (55–57) mm, $n = 6$

WS: n. d.

TL: n. d.

T: 37.2 (34.6–39.0) mm, $n = 6$

E: 15.2 (14.0–16.0) mm, $n = 6$

NL: n. d.

Tib: 23.7 (22.9–24.6) mm, $n = 6$

HF: 8.9 (8.2–9.6) mm, $n = 6$

WT: n. d.

CrnC: 19.2 (18.9–19.6) mm, $n = 6$

GWS: 10.2 (10.1–10.3) mm, $n = 3$

C–M³: 6.6 (6.4–6.7) mm, $n = 6$

Guinea: Mt Nimba (type series: MNHN, MHNG)

Key References Brosset 1984; Koopman 1989; Koopman *et al.* 1995.



Hipposideros lamottei

Jakob Fahr

Hipposideros marisae AELLEN'S LEAF-NOSED BAT

Fr. Phyllorhine d'Aellen; Ger. Marisas Rundblattnase

Hipposideros marisae Aellen, 1954. Rev. Suisse Zool. 61: 474. Rocher de la Panthère Blanche, Duékoué, Côte d'Ivoire.

Taxonomy Species-group: *bicolor*. Synonyms: none. Closely related to *H. jonesi* and *H. curtus*. Chromosome number: not known.

Description Very small microbat with noseleaf (posterior component roughly elliptical); greyish-brown with orange-phase; ears separated; noseleaf with a somewhat enlarged internarial septum, which partly conceals the nostrils and one (rarely two) very small lateral leaflet on each side; frontal sac present in both sexes. Sexual dimorphism: no information. Dorsal pelage (grey-phase) greyish-brown; hairs with dark grey bases and paler tip. Ventral pelage paler; hairs with grey or brown at base and pale grey or whitish at tip. Orange-phase: dorsal pelage tawny-orange to cinnamon; ventral pelage paler. Ears comparatively small but of medium relative length (39–43% of FA); broad, subtriangular, bluntly pointed with faint concavity in outer margin just below tip; each ear with 12–13 internal folds. Antitragus with no fold. Noseleaf longer than broad (Figure 68d). Posterior component divided into four cells by three vertical septa; upper margin low-arched in outline; internarial septum moderately enlarged, pad-like, forming a comparatively small, oval disc (longer than broad), which partly conceals the nostrils; usually only one rudimentary lateral leaflet on each side, rarely two (Liberia: SMNS 38563). Frontal sac present in both sexes; opening horizontally, lined with stiff, black hairs. No anal sac. Wings and interfemoral membrane dark grey. Fifth metacarpal 100–105% of third metacarpal. Tail 36–44% of HB.

Skull delicate with short, slender, pointed rostrum and relatively high braincase; zygomatic width usually < mastoid width (*contra* Aellen 1954). Sagittal crest weakly developed. Cochleae moderately enlarged, their breadth ca. 2.5 times their distance apart. Upper incisor unicuspid. Anterior upper premolar very small, slightly displaced labially; canine and posterior upper premolar almost in contact. Anterior lower premolar ca. half height of posterior lower premolar or slightly higher.

Geographic Variation None.

Similar Species Only two other African *Hipposideros* have a noseleaf with the internarial septum enlarged (Table 15, p. 370):

Hipposideros curtus. Usually larger (FA: 43.5 [42–47] mm; CrnC: 17.0 [16.3–17.5] mm). Ear: 15–22 mm. Antitragal fold small. Internarial septum more enlarged, oval disc larger; two weakly developed lateral leaflets on each side. Frontal sac sometimes absent in ♀♀.

H. jonesi. Larger (FA: 44–50 mm; CrnC: 17.6–19.1 mm). Ear longer (21–28 mm, 45–60% of FA). Antitragal fold distinct. Posterior component of noseleaf elongated, subtriangular in outline; internarial septum much more enlarged, disc broader than long; one long well-developed lateral leaflet on each side. No frontal sac.

Hipposideros beatus and *H. caffer* are somewhat similar, but do not have an enlarged internarial septum that partly conceals the nostrils.



Hipposideros marisae

Distribution Endemic to Africa. Apparently restricted to a very small region in the Rainforest BZ (Western Region). Known from only seven localities in the highlands of SE Guinea, N Liberia and W Côte d'Ivoire (Aellen 1954, 1963, Kuhn 1965, Roche 1971, Hill 1982a, Koopman *et al.* 1995, J. Fahr unpubl.), covering ca. 23,800 km² in an area to the north-west and south-east of Mt Nimba.

Habitat Most records are from drier and wetter types of lowland and sub-montane rainforest, up to 650 m. The type locality in Côte d'Ivoire was in a semi-deciduous forest (now destroyed). Most of the known individuals were found in caves (Aellen 1954, 1963, Wolton *et al.* 1982), suggesting that caves might be an essential component of the habitat of this species.

Abundance Uncertain; apparently extremely localized and rare. Since the description of this bat in 1954, only 15 specimens have been collected.

Remarks The holotype, a ♂, was roosting in a fissure of a cave. It shared the cave with a small colony of *H. ruber* (Aellen 1954, as *H. caffer guineensis*). A single adult ♀ was taken from a system of very small caves in a rocky outcrop; this roost was also shared with *H. ruber* (Wolton *et al.* 1982). One individual was caught when it flew into a room of a house in Guinea (Roche 1971). In late Oct, a group including four ♂♂ and five ♀♀ was caught in a cave situated near the bed of a torrential forest creek (Aellen 1963, MHNG, MNHN). Probably feeds on small, soft-bodied flying insects as it is one of the smallest African hipposiderids.

Conservation IUCN Category: Vulnerable.

Distribution very small; only seven localities known. Population size not known; trend inferred to be declining. Major threats: large-scale loss and degradation of habitat (caused by logging, agriculture and mining [past and future]), and disturbance and/or exploitation by humans in caves used as day-roosts. Occurs in region of high human population density that has been seriously affected by the recent civil conflict in Liberia and adjacent regions.

Measurements

Hipposideros marisae

FA: 40.6 (38–42) mm, n = 9

WS (d): 255 mm, n = 1

TL: 61, 66 mm, n = 2

T: 20.0 (19–22) mm, n = 6

E: 16.4 (15–17) mm, n = 7

NL (breadth): 5.1 mm, n = 1

Tib: 17.6 (17–18) mm, n = 6

HF: 7.2 (6–8) mm, n = 6

WT: n. d.

CrnC: 15.6 (15.4–15.8) mm, n = 7

GWS: 8.7 (8.6–8.7) mm, n = 7

C–M³: 5.0 (4.7–5.1) mm, n = 9

Guinea, Liberia, Côte d'Ivoire (AMNH, BMNH, MHNG, MNHN, SMNS)

Key References Aellen 1954, 1963.

Jakob Fahr

Hipposideros megalotis LARGE-EARED LEAF-NOSED BAT

Fr. Phyllorhine à grandes oreilles; Ger. Großohr-Rundblattnase

Hipposideros megalotis (Heuglin, 1862). Nova Acta Acad. Caes. Leop.-Carol., Halle 29 (8): 4, 8. Keren, Bogos Land, Eritrea.

Taxonomy Originally *Phyllorhina megalotis*. Synonyms: none. Sometimes placed in subgenus *Syndesmotis* Peters 1871 (e.g. Gaucher & Brosset 1990). Senna (1905) raised *Syndesmotis* to generic rank. This is rejected by Hill (1963), Koopman (1993) and Simmons (2005), but Legendre (1982) proposes its revalidation as a genus containing *megalotis* together with *vetis*, a fossil form. *Hipposideros megalotis* is considered to be the only extant member of the *megalotis* species-group, and it is considered the most primitive species in the genus *Hipposideros* (Hill 1963, Legendre 1982). The fossil record shows that hipposiderids belonging to the subgenus *Syndesmotis* were present in S France and Morocco during the early and middle Miocene (Legendre 1982). Chromosome number: not known.

Description Very small microbat with noseleaf (posterior component roughly elliptical); smallest African *Hipposideros*; sepia brown or bright cinnamon; ears large, rounded, joined by low frontal band; noseleaf with no lateral leaflets. Sexes similar in colour. Pelage fluffy; mid-dorsal hairs 8–9 mm. Dorsal pelage (grey-phase) sepia brown to dark rusty-brown; hairs beige to almost white with terminal quarter sepia-brown or dark rusty-brown. Ventral pelage (museum specimens) cream to yellowish-beige (perhaps white in living bats) becoming pale sepia-brown on chin and near flight-membranes. Orange-phase: dorsal pelage bright cinnamon with silky sheen; hairs pale cinnamon with terminal quarter cinnamon; ventral pelage pale cinnamon with bright cinnamon on chin. Ear length comparatively short to medium, but relatively long (51–68% of FA), broad, joined at base by a low, inconspicuous frontal band; inner and outer margins convex, tip rounded. Noseleaf small and simple. Posterior component divided into four cells by three weakly defined septa; upper margin sinuous and notched. No lateral leaflets. Frontal sac absent, but there are paired glandular bodies behind the noseleaf. Wings and interfemoral membrane brown in both phases. Tibia 40–42% of FA. Tail 40–42% of HB.

Skull small and elongated with narrow rostrum and inflated braincase; zygomatic arches moderate; zygomatic width < mastoid

width. Sagittal crest low. Cochleae moderately enlarged, their breadth ca. three times their distance apart. Upper incisor slightly bicuspid. Upper canine relatively short (41 [35–45]% of C–M³, n = 12). Anterior upper premolar absent; canine and posterior upper premolar either in contact, almost in contact or well separated. Anterior lower premolar ca. three-quarters the length and half the height of the posterior lower premolar.

Geographic Variation None recorded.

Similar Species None (Table 15, p. 370).



Hipposideros megalotis

Distribution In Africa, recorded from the Afromontane–Afroalpine and Somalia–Masai Bushland BZs in Eritrea, Ethiopia, Djibouti and Kenya (Largen *et al.* 1974, Legendre 1982, Aggundey & Schlitter 1984). According to Koopman (1993) and Nowak (1999), *H. megalotis* also occurs in Somalia, but their information originates from an erroneous indication by Gaucher & Brosset (1990). Extraliminally: one record from Jeddah in Saudi Arabia (Gaucher & Brosset 1990).

Habitat Mostly recorded from highlands and uplands in Ethiopia and Kenya. Localities are in undifferentiated afromontane vegetation, mosaic of East Africa evergreen bushland and secondary *Acacia* wooded grassland, Somalia–Masai semi-desert grassland and shrubland, Somalia–Masai *Acacia–Commiphora* deciduous bushland and thicket, and evergreen and semi-evergreen bushland and thicket (terminology: White 1983). Considered to be a relict species by Kingdon (1974).

Abundance Uncertain. Appears to be a rare species (Gaucher & Brosset 1990).

Remarks During the day, has been found in a farmhouse at Nakuru, Kenya (Hayman 1954) and in a lava tube ca. 200 m long, 2–3 m high with some lower portions, on Mt Suswa, Kenya (Kock & Hillman 1975). The entrance to the lava tube was a hole ca. 1 m in diameter at the base of a fig tree *Ficus* sp. The bats were roosting at the far end in a region ca. 2 m high; temperature 28–30 °C; humidity high. The bats, fewer than 100 and all adults, were hanging freely from the ceiling of the cave, in loose groups. A ♀ with one embryo of unrecorded size was taken near Nakuru in the short wet season (Dec).

Conservation IUCN Category: Least Concern.

Population trend: not known. Although seldom recorded, it exploits a range of habitats and its numbers are unlikely to be declining fast enough for qualifying as Near Threatened. The major threats are loss and degradation of habitat because of human activities (smallholder farming, agro-industry farming, tourism and other disturbances).

Measurements

Hipposideros megalotis

FA: 36.8 (34–39) mm, n = 26

WS: n. d.

TL: 64.5 (58–71) mm, n = 20

T: 24.3 (21–27) mm, n = 21

E: 21.9 (18–25) mm, n = 20

NL (breadth): 3.9 (3.0–4.5) mm, n = 5

Tib: 15.8 (15–18) mm, n = 10

HF: 5.6 (5–6) mm, n = 4

WT: n. d.

CrnC: 14.1 (11.0–15.5) mm, n = 16

GWS: 7.0 (6.0–7.7) mm, n = 16

C–M³: 4.6 (4.2–5.1) mm, n = 19

Throughout geographic range (BMNH, HZM, NMK, SMF, SMNS and literature)

Key References Hill 1963; Kock & Hillman 1975.

Meredith Happold

Hipposideros ruber NOACK'S LEAF-NOSED BAT

Fr. Phyllorhina rousse; Ger. Noacks Rundblattnase

Hipposideros ruber (Noack, 1893). Zool. Jahrb. Abt. Syst. Oekol. Geogr. Tiere 7: 586. Ngerengere River, Eastern Province, Tanzania.

Taxonomy Originally *Phyllorhina ruber*. Species-group: *bicolor*. Synonyms: *centralis*, *guineensis*, *naipu*. Subspecies: two. Closely related to *H. caffer*. Although *H. caffer* and *H. ruber* are distinctly different in most parts of their geographic ranges, they are not easily distinguished in Angola, which led Crawford-Cabral (1986) to question the specific status of *H. ruber*. Recently, Vallo *et al.* (2008) reported three genetic forms of *H. ruber* at least one of which probably represents a distinct species: all three may correspond to named taxa but their proper taxonomic assignment was not assessed in this publication. Chromosome number: not known.

Description Small microbat with noseleaf (posterior component roughly elliptical); greyish-brown with orange-phase; ears separated; noseleaf with two lateral leaflets on each side, no club-like processes and nostrils not concealed by internarial septum; frontal sac present in ♂♂; thumb weakly developed with comparatively small claw and basal pad. Sexes similar in colour; in Congo, ♀♀ on average a little larger than ♂♂ (Allen & Brosset 1968, as *H. caffer*). Pelage fluffy, fine, silky; mid-dorsal hairs ca. 9 mm. Dorsal pelage medium to dark greyish-brown, sometimes suffused with cinnamon; hairs fawn with brown at base and grey-brown at tip. Ventral pelage same

as dorsal pelage or paler. Orange-phase: dorsal pelage bright rusty-brown with golden sheen to pale gold (hairs unicoloured); ventral pelage similar. Bats moult into greyish-brown phase; pelage changes to orange-phase as oxidized by fumes within day-roost (Wolton *et al.* 1982). Ears comparatively short, but relatively short to medium (28–41% of FA); broad, inner margin convex, outer margin convex becoming concave near tip; tip pointed. Antitragus shallow, often with slight to distinct point resulting from thickening at the antitragal fold. Noseleaf approximately as in Figure 68f. Posterior component with transverse serrated supplementary structure behind the upper margin; not elongated, not divided into cells by well-defined vertical septa, upper margin with low-arched outline. No club-shaped processes. Internarial septum weakly developed, not concealing nostrils. Two lateral leaflets on each side. Frontal sac well developed in ♂♂ only, opening horizontally: ♀♀ with line of longer, darker hairs arising from a shallow horizontal groove. No anal sac. Wings and interfemoral membrane blackish-brown in both phases. Thumb, including claw and basal pad, weakly developed (cf. *H. fuliginosus*) (claw length 2.3 [1.8–2.7] mm, claw height 1.1 [0.9–1.4] mm). Fifth metacarpal 87–94% of third metacarpal. Tibia 35–48% of FA. Tail 24–38% of HB.

Skull short, broad; zygomatic width $>$ or $<$ mastoid width. In West Africa, zygomatic width $>$ mastoid width (cf. *H. lamottei*). Skull relatively large (CrnC: 38.2 [35–41]% of FA, $n = 322$; J. Fahr pers. comm.) (cf. *H. lamottei*). Median posterior nasal component of rostral swelling relatively wide with narrow lateral inflations (Figure 72c) (cf. *H. caffer*). Sagittal crest low. Cochleae not enlarged, their breadth equal to their distance apart or a little greater. Upper incisor weakly bicuspid, outer cusp very weakly developed. Upper canine of medium relative length (48 [43–50]% of C–M³, $n = 50$). Anterior upper premolar small or minute, slightly displaced labially; canine and posterior premolar not in contact (usually well separated). Anterior lower premolar one half the length and height of posterior premolar or more.

Geographic Variation Two subspecies are recognized by Koopman (1994); see also Taxonomy:

H. r. ruber (= *centralis*, *niapu*): Central African Republic and Angola to eastern Africa from Ethiopia to Malawi.

H. r. guineensis: Senegal to Gabon and Bioko I.

Similar Species Four other African *Hipposideros* have the following combination of characters: ears separated; noseleaf with two lateral leaflets on each side, no club-shaped processes, nostrils not concealed by internarial septum (Table 15, p. 370):

Hipposideros caffer. Usually smaller, especially where sympatric (FA: 46.8 [42–52] mm; CrnC: 17.2 [16.1–18.3] mm). Median posterior narial compartment of the rostral swelling relatively narrow with wide lateral inflations. Dorsal pelage (grey-phase) more grey than brown. Typically found in savanna woodlands and bushveld, less common in forests.

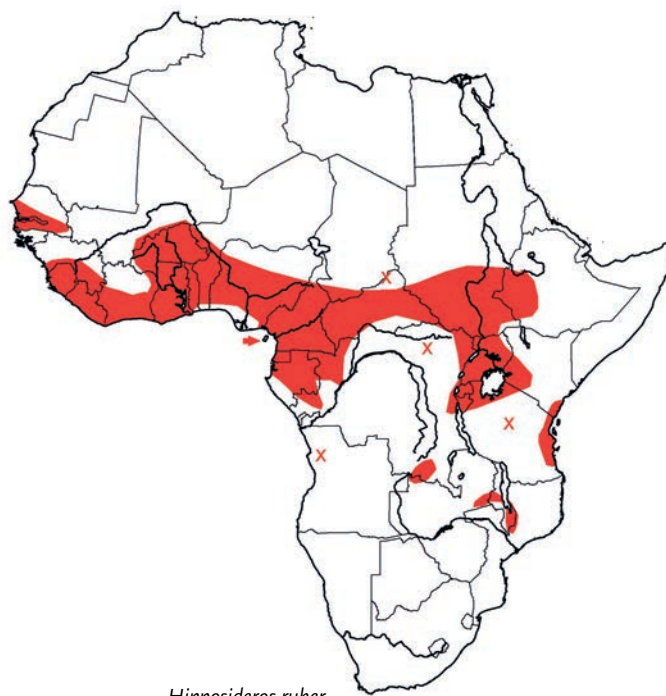
H. beatus. FA shorter (43.7 [39–48] mm). Tibia usually shorter (16.1 [15–19] mm). Anterior upper premolar greatly reduced and fully displaced labially; canine and posterior premolar in contact or almost so.

H. fuliginosus. Larger on average in all measurements (FA [western population]: 55.0 [51–60] mm, FA [eastern population]: 62.6 [60–64] mm; CrnC [western population]: 19.9 [19.2–21.5] mm, CrnC [eastern population]: 23.2 [22.8–23.4] mm). Thumb, claw and basal pad larger; claw length > 3 mm. Frontal sac absent in both sexes but sometimes there is a patch of bare skin. Echolocation CF-frequency (western population) lower (120–121 kHz).

H. lamottei. Body measurements usually larger (FA: 55.8 [55–57] mm) but skull relatively smaller (CrnC: 34–35% of FA). Zygomatic width $<$ mastoid width. Dentition weaker. Frontal sac present in both sexes.

(Note: *H. abae*, which is otherwise fairly similar externally, has three lateral leaflets on each side.)

Distribution Endemic to Africa, Príncipe and São Tomé. Widely distributed, mainly in the Sudan Savanna and Guinea Savanna BZs, Northern and Eastern Rainforest–Savanna Mosaics, Rainforest BZ, Afromontane–Afroalpine BZ of the Ethiopian Highlands, and Zambezian Woodland BZ. Extends marginally into the Sahel Savanna and Somalia–Masai Bushland BZs. Rarely reported from



Hipposideros ruber

eastern half of the Congolian rainforest. In Africa, recorded from Gambia and Senegal to Ethiopia and south to Angola, Malawi and Mozambique; also Bioko I. Not known south of Zambezi R. (Hutton 1986). Records from Zimbabwe in Fenton & Bell (1981), Bell & Fenton (1984) and Fenton (1985) refer to *H. caffer*. If material from Central African Republic and Angola to eastern Africa (from Ethiopia to Malawi) represents only one subspecies (Koopman 1994), gaps in the distribution south of the Equator perhaps reflect insufficient collecting. Mapped from country checklists (see order Chiroptera), other literature and museum records.

Habitat Typically found in lowland rainforest, and in or near wetter areas (including riverine, relict and montane forests) in woodland savanna zones. Probably typically a forest species (cf. *H. caffer*), but this needs further investigation.

Abundance Uncertain. Fairly common in collections; probably fairly common in suitable habitats.

Adaptations Aspect ratio low; wing-loading very low. Flies slowly with bursts of speed and with agility and considerable manoeuvrability. Frequently glides for short distances. Can take off from ground and hover briefly. Turns by banking (minimum radius < 25 cm) and by stalling-and-twisting. By day, has been found hanging, freely, in caves, crevices, mine-adits, enclosed roofs, abandoned buildings, under a bridge, in hollow trees and burrows of large mammals (Lang & Chapin 1917b, Verschuren 1957, Poché 1975, Schlitter *et al.* 1982, Wolton *et al.* 1982, Kityo & Kerbis 1996, Grubb *et al.* 1998). Humidity in day-roosts is very variable (Verschuren 1957). In Sierra Leone, sometimes roosts with *Rhinolophus guineensis*, *H. abae* and *H. jonesi* (Grubb *et al.* 1998), and in Cameroon, reported roosting with *H. fuliginosus* (Aellen 1952). Captive individuals in Malawi did not become torpid during day when ambient temperature was 21–24 °C. Captive bats offered water twice daily invariably drank every time, and the predicted mean

maximum urine concentration is comparatively low (3133 mOsmol/kg) (Happold & Happold 1988). Predicted to need to drink several times/night in the wild.

Foraging and Food Forages in cluttered environments and avoids open habitats (Jones *et al.* 1993). Foraging predicted to include slow-hawking and gleaning as in *H. caffer*. In Liberia, *H. ruber* emerged and began foraging just as it was getting dark; returned to day-roost with full stomachs after two hours; foraged again intermittently through night with peak just before dawn (Wolton *et al.* 1982). Diet, in West Africa in wet season, ca. 84% beetles with some moths, Diptera and Isoptera (Jones *et al.* 1993). Beetles were also found in stomachs of five bats from Garamba N. P., DR Congo (Verschuren 1957).

Echolocation Call-shape CF/FM. CF-frequency shows only a little variability in different localities:

Gambia: 134.13 ± 1.84 kHz (8 ♂♂); 131.85 ± 0.99 kHz (20 ♀♀); Jones *et al.* 1993).

Côte d'Ivoire: 132–144 kHz (J. Fahr & N. Ebigbo pers. comm.).

E DR Congo (Irangi): 136.2 (131.8–138.2) kHz (5 ♂♂), 132.8, 135.1 kHz (2 ♀♀; Heller 1992).

Malawi: 133–135 kHz (1 ♂, 30 calls), 140 kHz (1 ♀, 30 calls; M. Happold unpubl.) (Figure 64a).

(Note: mean \pm 1 S.D. in some cases.)

The possibility that there are inconsistent sex-related differences in CF-frequency calls for investigation.

Social and Reproductive Behaviour Very little known. Typically roosts in small to very large (several hundreds) groups; occasionally both ♂♂ and ♀♀ roost singly. Individuals hang apart but in close proximity to group-members. In Liberia, ♂♂ roost apart from ♀♀ at least during Jul–Sep (no data for Mar when births occur), suggesting formation of maternity colonies. In Garamba N. P., groups ranging in size from 5 to 71 were comprised of both ♂♂ and ♀♀; usually ♀♀ outnumbered ♂♂ by 2–3 to 1 (Verschuren 1957).

Reproduction and Population Structure Litter-size: one. Reproductive chronology is restricted seasonal monoestry; retarded embryonic development recorded at one locality. At 7°S in Tanzania, copulation, ovulation, fertilization in Jun–Jul, retarded development for ca. two months, parturition in Dec, lactation Dec–Feb (Howell

1976 in Bernard & Cumming 1997). At 07° 39' N (Mt Nimba, Liberia), births occur in Mar (Wolton *et al.* 1982). At 04° 40' N (Garamba N. P., NE DR Congo), births occur in late Mar to early Apr (Verschuren 1957). At 2–3° N in Equatorial Guinea, three ♀♀ with large embryos in Oct, lactating ♀♀ in Nov (Jones 1971, as *H. caffer*) and, at 9° N in Central African Republic, all of seven ♀♀ were lactating in late May (Schlitter *et al.* 1982). In Gabon, Brosset (1968) reported that within one population, some colonies had a boreal cycle with births in Mar, while others had an austral cycles with births in Oct: however it is not known if Brosset studied *H. ruber*, *H. caffer* or both.

Predators, Parasites and Diseases The remains of one individual were found in the scats of a mongoose *Herpestes naso* (Hutterer & Ray 1997). Ectoparasites include bat-flies *Penicillidia allisoni*, *P. fulvida*, *P. senegalensis* (Diptera: Nycteribiidae), *Brachytarsina longiarista* and *Raymondia seminuda* (Diptera: Streblidae) (Aellen 1952, Wolton *et al.* 1982).

Conservation IUCN Category: Least Concern.

Widely distributed, but population trend not known, and likely to be threatened by loss and degradation of forest habitat as result of wood extraction and shifting agriculture.

Measurements

Hipposideros ruber

FA: 51.1 (47–55) mm, n = 298

WS (a): 308, 320 mm, n = 2

TL: 87.5 (82–94) mm, n = 23

T: 31.2 (24–38) mm, n = 117

E: 15.4 (11–20) mm, n = 159

NL (breadth): 7.0 (5.6–8.1) mm, n = 23

Tib: 21.4 (18–24) mm, n = 69

HF: 10.2 (7–12) mm, n = 56

WT: 10.1 (7–12) g, n = 44

CrnC: 19.1 (17.8–20.3) mm, n = 178

GWS: 10.6 (9.6–11.4) mm, n = 181

C-M³: 6.8 (5.6–7.5) mm, n = 170

Throughout geographic range (BMNH, HZM, MNHN, SMNS and literature)

Key References Jones *et al.* 1993; Wolton *et al.* 1982.

Meredith Happold

Hipposideros vittatus STRIPED LEAF-NOSED BAT

Fr. Phyllorhine rayée; Ger. Gestreifte Rundblattnase

Hipposideros vittatus (Peters, 1852). Naturwiss. Reise Mossambique, Säugeth., p. 32. Ibo I., Cap Delgado group, Mozambique.

Taxonomy Originally *Phyllorhina vittata*. Species-group: *commersoni*. Synonyms: *marungensis*, *mostellum* and perhaps *viegasi*. The status of *viegasi* is uncertain (Simmons 2005) but is tentatively retained here in *H. gigas* following Hayman & Hill (1971). Subspecies: none currently recognized. The taxonomy of the *H. commersoni* group is problematical and in need of revision (see Genus *Hipposideros*). Hill (1963) considered *vittata* (Peters, 1852) to be a synonym of *H. commersoni gigas*.

Subsequently, although *vittata* was considered more likely to be a synonym of *marungensis* (Noack, 1887), most authors continued to refer to these forms by the better-known junior synonym, *H. c. marungensis* (e.g. Hayman & Hill 1971), possibly because they considered that the affinity of *vittata* was still uncertain. As *vittata* is currently considered synonymous with *marungensis*, the seniority of *vittata* is provisionally recognized here. As *H. c. marungensis*, *H. vittatus*

was formerly considered to be a subspecies of *H. commersoni* (e.g. Hill 1963, Koopman 1993) but differences in morphology and echolocation calls indicate that *H. vittatus*, and also *H. gigas*, are distinct species (Pye 1972, McWilliam 1982). *Hipposideros commersoni* is now considered restricted to Madagascar (Simmons 2005) and, in some parts of Africa, *H. vittatus* is now known to occur sympatrically with *H. gigas*. Consequently, the distributions of both *H. vittatus* and *H. gigas* are expected to be considerably more extensive than pre-2005 records indicate and, furthermore, it will be some time before pre-2005 information attributed to *H. commersoni* in Africa, *H. c. marungensis* and *H. c. gigas* is reallocated to its correct species. Chromosome number (South Africa): $2n = 52$ (Rautenbach *et al.* 1993).

Description Very large microbat with noseleaf (posterior component roughly elliptical); robustly built; pale to medium brown with silver, white and brown markings; second largest African hipposiderid; ears separated; noseleaf with three lateral leaflets on each side, no club-shaped processes and nostrils not concealed by an enlarged internarial septum; not easily distinguished morphometrically from *H. gigas*. Males on average larger than ♀♀. Pelage soft, not woolly, sparse on hindquarters; mid-dorsal hairs 5–8 mm. Dorsal pelage (grey-phase) medium to pale brown (fawn) or reddish-brown; paler and with silvery frosting on head, nape, rump and next to wings; hairs unicoloured or with darker base; some with silvery-grey at tip. Ventral pelage medium to pale brown, with silvery frosting; flanks white; armpits white or yellow, partly surrounded by C-shaped brown stripe that curves around the shoulder. In Zimbabwe, parous ♀♀ are rich reddish-brown whereas ♂♂ are greyish (Cotterill & Fergusson 1999). Orange-phase: no information. Ears comparatively medium to long but relatively short (26–33% of FA); brown; triangular, tapering to bluntly pointed tip with little or no concavity in outer margin below tip. Antitragus shallow. Noseleaf similar to that of *H. gigas* (Figure 68e). Posterior component divided into four shallow cells by three weak vertical septa. Three lateral leaflets on each side. Frontal sac present in both sexes but more prominent in reproductively active ♂♂; opening vertically. No anal sac. Wings and interfemoral membrane brown. Fifth metacarpal 92–99% of third metacarpal. Tibia 39.2 (32–45)% of FA, $n = 19$. Tail 31.0 (21–46)% of HB.

Skull large with broad rostrum; zygomatic arches massive; zygomatic width > mastoid width. Sagittal crest greatly developed (especially in ♂♂) and merging with the supraorbital ridges. Infraorbital foramen large, elongate and closed by narrow bar. Cochleae not enlarged, their breadth only a little greater than their distance apart (cf. *H. camerunensis*, *H. cyclops*). Upper incisor slightly bicuspid. Upper canine relatively long (54 [48–60]% of C–M³, $n = 10$). Anterior upper premolar very small, displaced labially; canine and posterior premolar in contact or nearly so. Anterior lower premolar half the length and height of posterior premolar or slightly less.

Geographic Variation Uncertain. No subspecies recognized by Simmons (2005).

Similar Species Only one other African *Hipposideros* has FA >79 mm and no club-shaped processes on noseleaf (Table 15, p. 370):

Hipposideros gigas. Larger on average (FA [♂♂]: 107.9 [100–124] mm, FA [♀♀]: 103.8 [95–116] mm). Pelage longer and

slightly woolly. Echolocation CF-frequency ca. 56 kHz (at least in Kenya). Predominantly a forest species. In at least some areas of sympatry, FA measurements of adults of same sex do not overlap – e.g. in coastal Kenya, *H. gigas*: FA ♂♂: 109–122 mm; FA ♀♀: 105–116 mm (cf. *H. vittatus*: FA ♂♂: 90–108 mm; FA ♀♀: 85–98 mm) (A. N. McWilliam pers. comm.).

Distribution Endemic to Africa. Recorded with reasonable certainty from the Zambezian Woodland and Coastal Forest Mosaic BZs, with marginal extensions into the Somalia–Masai Bushland BZ and the Kalahari Desert. Probably also exploits Sudan Savanna and Guinea Savanna BZs (e.g. in Central African Republic and Nigeria). Traditionally thought to occur only on the eastern side of Africa, from Ethiopia and Somalia to South Africa, but now considered to occur also in Angola and Namibia, and considered likely to occur much further afield, including Central African Republic and Nigeria (see Taxonomy). Mapped from localities of museum and published specimens whose identification (if not already assigned to *vittatus* or *marungensis*) could be verified by FA and GLS measurements. Specimens from three localities in Nigeria are tentatively considered to represent *H. vittatus* because all three specimens are ♂♂ of FA: 98–102 mm and because the habitat is not typical of *H. gigas* (see Bergmans 1977b). A specimen from Central African Republic, recorded as *H. commersoni gigas* (Schlitter *et al.* 1982), is a ♀ with FA: 94 mm and, based on FA and habitat, this specimen is also more likely to represent *H. vittatus*. Possibly, the specimens from Burkina (Koopman *et al.* 1978) and N Togo (De Vree *et al.* 1969) (mapped as *H. gigas*) also represent *H. vittatus*, but no measurements are available for these specimens. Since this profile was submitted, *H. vittatus* was shown to occur in Sierra Leone by Decher *et al.* (2010): not mapped.

Habitat Recorded mostly from woodland savannas and coastal forests. Extends into drier bushlands and (rarely) into Sahel savanna, but possibly only during wet seasons and/or near riverine woodlands



Hipposideros vittatus

and forests. Apparently absent from most of the Congolian rainforest, and not yet recorded from montane or arid habitats.

Abundance Uncertain; very common in some localities.

Adaptations Aspect ratio low; wing-loading high for an African microbat, very high for an African hipposiderid; flight-speed variable; manoeuvrability moderate. Can take off from ground. Turns by banking (minimum radius of turn just under 50 cm) and by stalling-and-twisting; despite its size, sustained flight in a 1×1×1 m enclosure for up to two circuits/flight (5 bats, 10 flights each; M. Happold unpubl.). By day, usually hangs, free or in contact, in caves, but has also been found roosting singly in foliage in inland Kenya (Vaughan 1977), in the roof of a traditional hut (R. C. Wood in Kershaw 1922) and under eaves of buildings (Taylor 2000). Fidelity to roosts in foliage was noted by Vaughan (1977). In Malawi (at 20–21 °C) and in Mabura Cave in Zimbabwe, *H. vittatus* does not become torpid during the day (Happold & Happold 1988, Cotterill & Fergusson 1999). Not known to hibernate. Heavy fat deposits have been recorded when insects are maximally abundant (Cotterill & Fergusson 1999). This species was present at Masalani (near Kibwezi, inland Kenya) only during the two annual wet seasons when insects are abundant, and Vaughan (1977) assumed they moved to and from the coastal forests, perhaps using riverine habitats as their route. Migration away from coastal Kenya in Oct and again in Mar, to take advantage of wet seasons that arrive earlier and more predictably inland than at the coast, was confirmed by McWilliam (1982).

Foraging and Food Near Masalani, *H. vittatus* foraged, mainly for large flying beetles, by fly-catching (Vaughan 1977). Individuals left their daytime roosts (in foliage of trees) ca. 30 minutes after sunset, and flew directly to habitually used perches 40–75 m away. They flew within 2 m of the ground, possibly to avoid Bat Hawks *Macheiramphus alcinus*. Perches were typically 6–7 m above ground (range 4–15 m), in riverine trees; each night, one individual used at least five perches along a 45 m line. Perches typically commanded views of unobstructed spaces beneath the tree's canopy. Perching bats scanned a 180 degree arc, and flew to intercept prey that came within a 10 m radius; this presumably being the maximum distance at which prey can be detected by their echolocation. The bats swooped down towards the prey, then carried it (apparently laboriously) to the perch where, for the next 3–8 min, it was chewed and eaten. An hour of intense foraging, with 1–2 flights/min, was followed by an hour or more with only ca. three flights per hour. Occasionally, the bats made seemingly reconnaissance flights around the tree containing the perch, and perhaps gleaned prey from the flowers or foliage. This behaviour tended to occur later in the night when fewer beetles were flying. Even during periods of intense fly-catching, the bats spent 4–5 times longer at the perch than in flight and it is assumed that, for these large, heavy bats, fly-catching and the selection of large prey optimizes energy return per unit of foraging time. Feeds mainly on large beetles (Vaughan 1977, Fenton 1985), but undoubtedly gorges seasonally on winged termites, and R. C. Wood (in Kershaw 1922) observed hundreds of *H. vittatus* feeding on large larvae of weevils found in wild figs in Malawi.

Echolocation Call-shape CF/FM. Pye (1972) observed a bimodal distribution of CF-frequencies in a colony of '*H. commersoni*' inhabiting caves in Kenya: the CF-frequencies were ca. 56 kHz and

ca. 66 kHz with a silent interval of 8 kHz. It is now known that *H. gigas* emits the 56 kHz calls, and that *H. vittatus* emits the ca. 66 kHz calls. CF-frequency (Malawi): 61–63 kHz (n = 4 bats identified by FA; Figure 64b; M. Happold unpubl.). CF-frequency in Zimbabwe (n = 3 bats) and in South Africa (n = 2 bats) is 62 kHz (Fenton & Bell 1981, Aldridge & Rautenbach 1987); bats identified with *H. vittatus* on basis of habitat.

Social and Reproductive Behaviour Apparently forages singly (Vaughan 1977, Smithers 1983), but typically roosts in groups (colonies) of 50–400 individuals, although colonies of more than 100,000 are known (Cotterill & Fergusson 1999). Occasionally roosts singly, usually in day-roosts other than caves (species not confirmed). A 15-month study at Mabura Cave, Zimbabwe, provided evidence that the mating system is a form of resource-defence polygyny (*sensu* Vehrencamp & Bradbury 1984) (Cotterill & Fergusson 1999). From Feb to Jun, breeding ♂♂ defended roost-site territories (marked by patches of urine ca. 30 cm apart) on the exposed walls and ceilings. During this time, subadult ♂♂ clustered into rock crevices within the cave, often alongside parous and subadult ♀♀. Copulation occurred in Jun–Jul, when a ♀ landed near a ♂ on his territory. Copulations are prolonged (ca. 30 minutes), ejaculates are large and copulatory plugs are formed in the vaginae, suggesting the occurrence of sperm competition. Territoriality ceased after the mating-season and, in Aug–Mar, the adult ♂♂ clustered together in crevices. After the mating-season, pregnant ♀♀ roosted elsewhere until late-Oct when they returned to Mabura Cave to give birth and lactate. They established maternity-roosts in extensive side chambers, which had high temperatures and humidities and high levels of CO₂ and ammonia. When flying within the cave, mothers carried their neonates, but did not carry them while foraging; when carried, neonates fasten their teeth around a pubic nipple and cling to the mother's fur with their hindfeet. Adult ♀♀ were again absent from Mabura Cave in Mar–Apr, and it seems likely that they migrate at this time, and also during mid-pregnancy, to remote areas that have rainfall and abundant insects during these months.

Reproduction and Population Structure Litter-size: one. The reproductive chronology appears to be restricted seasonal monoestry at both low and high latitudes. At 04°03'S in coastal Kenya, copulation occurs in the long dry season (Jul–Aug), and births during the long wet season (Mar–Apr) (McWilliam 1982). At 18°S in C Zimbabwe, copulation occurs in the cool dry season (mid-Jun to mid-Jul), parturition at beginning of wet season (late Oct to early Nov), and lactation continues for at least 13 weeks until mid-Mar (Cotterill & Fergusson 1999). Juveniles can make short gliding flights within the roost when ca. two weeks old but remain dependent on mothers' milk for at least 13 weeks. FA length almost doubles within first 34 days.

Predators, Parasites and Diseases Anciaux de Faveaux (1984) lists parasites of '*H. commersoni*' in Africa, but it is not certain which have been recorded from *H. vittatus* and which from *H. gigas*.

Conservation IUCN Category: Near Threatened.

Almost meets criteria for qualifying as threatened. Populations are severely fragmented. Major threats: loss of habitat and disturbance

of colonies in caves (by hunters, miners and recreational cavers). Mining of guano from caves threatens populations in Zimbabwe, especially where mining is permitted during the mating, parturition and lactation seasons (Cotterill & Fergusson 1999).

Measurements

Hipposideros vittatus

FA (♂♂): 101.5 (93–106) mm, n = 78
 FA (♀♀): 93.9 (84–101) mm, n = 58
 WS (d) (♂♂): 609 (515–660) mm, n = 43
 WS (d) (♀♀): 567.2 (523–590) mm, n = 10
 TL (♂♂): 142.6 (121–167) mm, n = 56
 TL (♀♀): 131.5 (116–151) mm, n = 26
 T (♂♂): 33.5 (25–39) mm, n = 59
 T (♀♀): 29.9 (22–37) mm, n = 35
 E: 29.5 (23–35) mm, n = 95
 NL (breadth): 13.9 (13–15) mm, n = 10

Tib: 38.7 (32–45) mm, n = 19
 HF: 21.3 (17–25) mm, n = 20
 WT (♂♂): 99.7 (70–180) g, n = 30
 WT (♀♀): 80.4 (51–138) g, n = 15
 CrnC (♂♂): 34.5 (31.6–37.3) mm, n = 22
 CrnC (♀♀): 31.8 (29.9–33.2) mm, n = 14
 GWS (♂♂): 19.5 (17.3–20.8) mm, n = 74
 GWS (♀♀): 16.9 (14.3–18.4) mm, n = 53
 C–M³ (♂♂): 12.1 (9.3–12.8) mm, n = 58
 C–M³ (♀♀): 11.2 (8.6–12.3) mm, n = 30
 Throughout geographic range (BMNH, HZM, TM, ZFMK and literature)

Key References Cotterill & Fergusson 1999; Vaughan 1977.

Meredith Happold

GENUS *Triaenops*

Trident Bats

Triaenops Dobson, 1871. J. Asiat. Soc. Bengal 40: 455. Type species: *Triaenops persicus* Dobson, 1871.

Triaenops is a polytypic genus that was previously considered to have four species, *T. persicus* (with *afer* and *majusculus* as subspecies) distributed from Pakistan, Iran and southern Arabia to Africa, and three other species confined to Madagascar and nearby islands (Simmons 2005). Recently, however, the genus has been revised (based on morphological and molecular evidence) by Benda & Vallo (2009), who split *T. persicus* into three species: *T. afer*, which is monotypic and endemic to Africa, and *T. persicus*, and a new species

(*T. parvus*), which occur in the Middle East. These authors have proposed a new genus, *Paratriaenops*, for four other species that were previously placed in *Triaenops*: three (*P. menemena*, *P. furculus* and *P. auritus*) that are endemic to Madagascar and a fourth (*P. pauliani*) that is endemic to the western Seychelles.

Triaenops is distinguished from other genera of hipposiderids in Africa by the following combination of characters: posterior component of noseleaf trident-shaped (i.e. with three tall, spear-

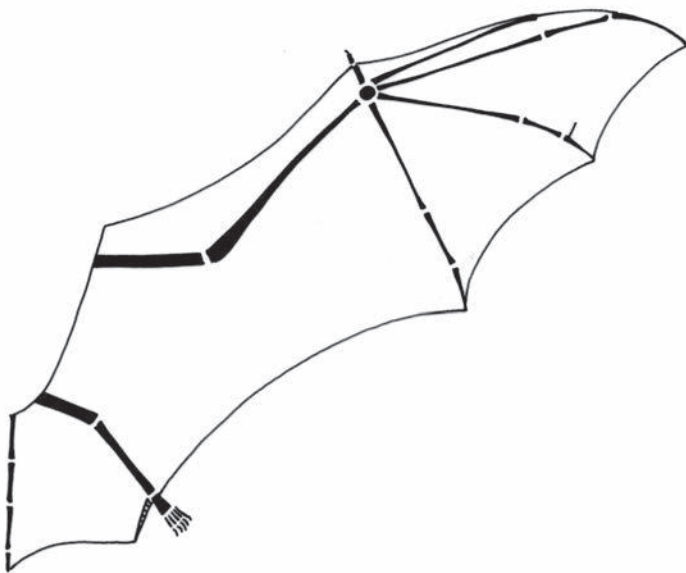
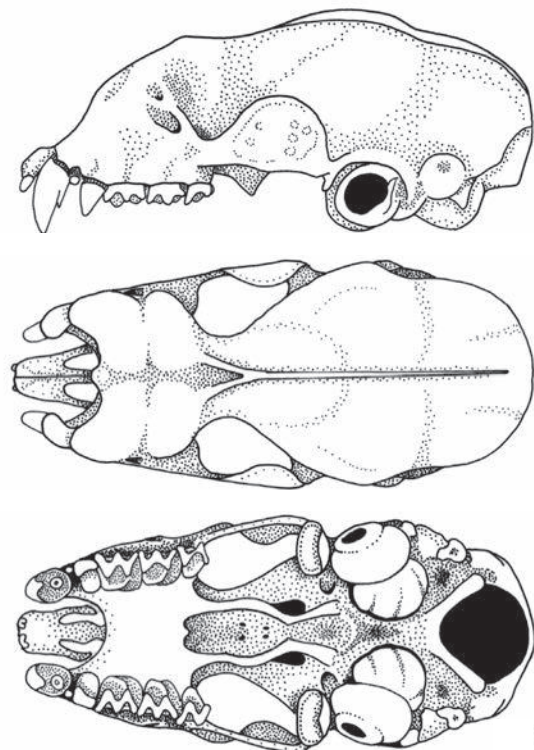


Figure 75. *Triaenops afer*. Flight membranes and bones of wing, hindlimb and tail. Skull (BMNH 79.11.12.1).



like projections arising from the upper edge) (Figure 65d), tail fully enclosed by interfemoral membrane (Figure 75) and FA: 49–60 mm (in Africa). Furthermore, the posterior component is divided into deep cells giving it a pitted appearance (cf. *Asellia*) (Figure 65). The skull (Figure 75) has each zygomatic arch expanded into a broad plate; braincase scarcely higher than rostrum; rostrum with

prominent nasal swellings; premaxillae unusually thick; upper canine with strong posterior secondary cusp. Dental formula $^{1123}/_{2123} = 30$.

The species occurring in Africa is *Triadenops afer*.

Meredith Happold

Triadenops afer AFRICAN TRIDENT BAT

Fr. Triénope d'Afrique; Ger. Afrikanische Dreizahnblattnase

Triadenops afer Peters, 1877. Mb. Kön. Preuß. Akad. Wissen. Berlin 1876: 913. Mombassa, Kenya.

Taxonomy Although described as a species, *afer* was subsequently considered to be a subspecies of *Triadenops persicus* Dobson, 1871 (e.g. Simmons 2005), but it was restored to specific status by Benda & Vallo (2009). These authors place all African forms of *Triadenops* in this species, and consider *T. persicus* to be extralimital to Africa. Furthermore, these authors restrict *afer* to Africa and place specimens from Yemen, that were referred to as *T. p. afer* by Hill (1982b) and Koopman (1994), in *T. persicus*. Synonym: *majusculus* (Simmons 2005, Benda & Vallo 2009). Subspecies: none recognized by Benda & Vallo (2009): see Geographic Variation. Chromosome number (Kenya): $2n = 36$; $aFN = 60$. X = medium-sized metacentric; Y = small subtelocentric (Dulić & Mutere 1977).

Description Small microbat with noseleaf (posterior component with three tall projections); greyish-brown to medium brown with orange-phase; tail fully enclosed by interfemoral membrane; FA: 49–60 mm. Sexes similar. Pelage soft, fine, dense, silky with conspicuous sheen; mid-dorsal hairs 6–7 mm. Dorsal pelage greyish-brown; hairs greyish-brown with browner tip. Ventral pelage pale greyish-brown to beige. Orange-phase: dorsal and ventral pelage a spectacular brilliant rusty-brown with golden sheen. Ears small, widely separated, funnel-shaped, acutely pointed; height and breadth ca. equal; inner margin with central step-like emargination. Eyes minute. Muzzle broad and flat. Noseleaf as in Figure 65d. Posterior component divided into 13 cells (of which five on each side are conspicuous although sometimes obscured by pelage) and with three very prominent, pointed projections resembling a trident – hence the vernacular name of this genus. Central component with one smaller pointed process. Anterior component broad with two lateral leaflets on each side, and a deep median emargination, the sides of which are flexed upwards and recurved to form a process resembling an hour-glass in outline. Wings dark brown, slightly translucent; second phalanx of fourth finger with unique transverse spicule of bone projecting 2.5–3 mm outwards from proximal end into membrane (Figure 75). Interfemoral membrane dark brown; pelage extending onto proximal quarter of both surfaces.

Skull (Figure 75) narrow, elongated; braincase scarcely higher than rostrum; zygomatic arches not outwardly flared, each expanded dorsally into a broad plate; zygomatic width slightly greater than mastoid width. Rostrum with prominent nasal swellings. Sagittal crest well developed; supraorbital ridges weakly developed. Premaxillae unusually thick, with distinct ridge along line of contact that terminates anteriorly in upward-directed point. Upper incisor bifid. Canine with strong posterior secondary cusp reaching half

height of main cusp. Anterior premolar small, within toothrow but slightly displaced labially; canine and posterior premolar not in contact. M^3 not reduced and has three ridges (cf. *Asellia*).

Geographic Variation Prior to the recognition of *afer* as a valid species, two forms were recognized as African subspecies of *T. persicus* by Hill (1982b), Koopman (1994) and Simmons (2005):

T. p. afer: eastern Africa to Mozambique and E Zimbabwe (and extraliminally Yemen). FA: 49–56 mm; condylobasal length: 16.6–18.3 mm (Aellen & Brosset 1968, Hill 1982b).

T. p. majusculus: Uganda, Congo and Angola. FA: 53–60 mm, condylobasal length: 16.9–18.7 mm (Aellen & Brosset 1968, Hill 1982b).

Hill (1982b) reported that a series from West Nile District, Uganda is intermediate in size, although closer to *T. p. majusculus*. This suggested that the variation in Africa is possibly clinal. Subsequently, Benda & Vallo (2009) found no evidence for subspecific variation in *T. afer* and therefore consider *majusculus* to be a synonym of *T. afer*.

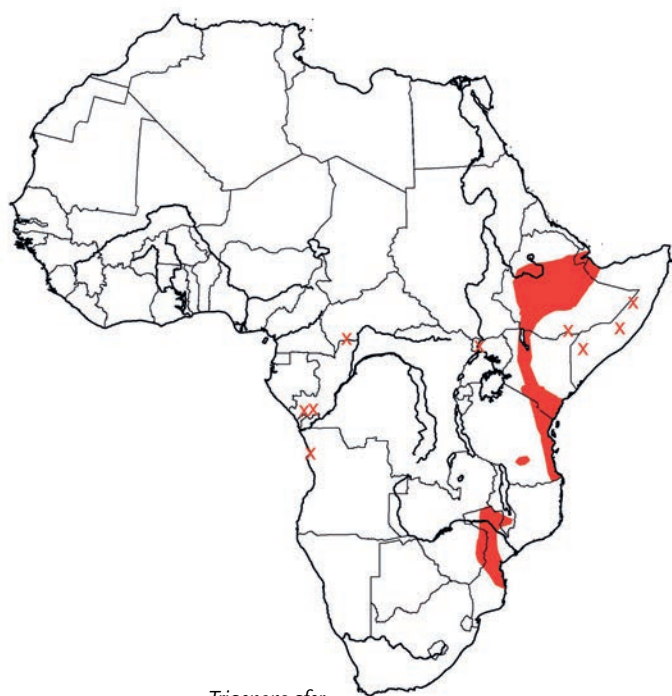
Similar Species Three other hipposiderids in Africa have three vertical projections arising from the posterior component of the noseleaf:

Asellia tridens. Tail protruding up to 7 mm beyond interfemoral membrane. Projections arising from posterior component of noseleaf short, triangular. Only one upper premolar on each side; M^3 greatly reduced (only two ridges).

Asellia patrizii. Smaller (FA: 38–43 mm; CrnC: 14.4–15.8 mm). Tail protruding up to 5 mm beyond interfemoral membrane. Projections from posterior component of noseleaf short, triangular. Only one upper premolar on each side; M^3 greatly reduced (only two ridges).

Cloeotis percivali. Smaller (FA: 31–39 mm; CrnC: 12.0–13.5 mm). Anterior component of noseleaf very narrow with deep median emargination; no process arising from sides of emargination. M^3 not reduced (four ridges).

Distribution *Triadenops afer* is endemic to Africa and is widespread in the Somalia–Masai Bushland, Afromontane–Afroalpine and Coastal Forest Mosaic BZs of Ethiopia, Djibouti and Somalia southwards to Zimbabwe and Mozambique, with separate populations in the Rainforest–Savanna Mosaics in Central African Republic (La

*Triaenops afer*

Maboké, MNHN 1198, 1199), Uganda, Congo and Angola (Funaioli 1971, Kock & Felten 1980, Aggundey & Schlitter 1984, Feiler 1986, Happold & Happold 1997, Pearch *et al.* 2001, BMNH, and other literature, all as *Triaenops persicus* or *T. p. afer*). Also Zanzibar I. (Hill 1982b).

Habitat Recorded in hundreds to thousands from coastal habitats in Kenya, Tanzania and Mozambique, and from numerous, widespread inland localities where, in contrast, only 1–12 individuals have been observed at a time. This suggests that *T. afer* is predominantly a coastal species, but this needs confirmation. Habitats include coastal forests of Tanzania (Cockle *et al.* 1998, as *T. p. afer*), dense trees and bush with maize cultivation near bank of Nile R. at Awash N. P., Ethiopia (Hill & Morris 1971, as *T. p. afer*), and farmlands with patches of miombo woodland, riverine forest and/or remnant rainforest, at 1000 m in Malawi (Happold & Happold 1997, as *T. persicus*). The presence of caves, mines or similar day-roosts is apparently essential.

Abundance Very common in some coastal localities where caves and mines are present (see Habitat).

Adaptations Has narrower wings than typical for hipposiderids; aspect ratio medium; wing-loading low. Flies slowly with fluttering, butterfly-like wing-beats and great manoeuvrability. Can take off from ground. Turns by banking (radius of turn <25 cm) and by stalling-and-twisting; sustained flight in a 1 × 1 × 1 m enclosure for up to four circuits/flight (3 bats, 10 flights each; M. Happold unpubl.). By day, hangs freely in caves and mines; one cave in Mozambique was humid and very warm (Dalquest 1965, as *T. p. afer*). Often shares caves with *Coleura afra*.

Foraging and Food Emerges from day-roost in evening, sometimes before dark. Forages low over ground and bushes (Harrison 1964, Hill & Morris 1971). Faecal material from 'a few'

individuals contained abundant scales of Lepidoptera (Matthews 1941).

Echolocation Call-shape CF/FM. CF-frequency appears to be very variable. Pye (1972) found CF-frequencies distributed bimodally with the following combinations: 77.0–80.5 kHz and 85.5–89 kHz (7 bats recorded in isolation), 75–77.5 kHz and approximately 85.5–88.5 kHz (bats foraging in wild). CF-frequencies of 72–75 kHz (2 ♂♂, hand-held) and 80–85 kHz (1 ♀, hand-held) were recorded in Malawi (Figure 64) (M. Happold unpubl.). The possibility that ♂♂ and ♀♀ emit different frequencies might explain the bimodal distribution of CF-frequencies, but this needs confirmation.

Social and Reproductive Behaviour In coastal habitats, roosts in very large groups (hundreds to thousands; possibly more) (Kulzer 1959, as *T. persicus*, Dalquest 1965, as *T. p. afer*). Hangs, apart, in clusters (Smithers 1983, as *T. persicus*).

Reproduction and Population Structure No conclusive data. In Tanzania, spermatogenesis was high in Jun–Oct, low in Dec–Jan (Mainoya 1979). At 05° 03' S (Amboni Cave, coastal Tanzania), 2 of 6 ♀♀ were pregnant in Dec; each had one foetus (Matthews 1941). Also in Tanzania, births were reported in Jan (Anciaux de Faveaux 1972).

Predators, Parasites and Diseases Ectoparasites include a flea *Araeopsylla scitula* (Siphonaptera: Ischnopsyllidae) (Beaucournu & Kock 1996, as *T. p. afer*); seven species of bat-flies (Diptera: Nycteribiidae, Streblidae); nine species of mites (Acari: Spinturnicidae, Macronyssidae, Myobiidae, Chirodiscidae, Sarcoptidae) (Radovsky & Yunker 1963, Anciaux de Faveaux 1984, as *T. persicus*).

Conservation IUCN Category for *Triaenops persicus* (*sensu* Simmons 2005): Least Concern.

Measurements

Triaenops afer

FA: 54.0 (49–60) mm, n = 50

WS (a): 322.3 (305–336) mm, n = 3*

TL: 90.1 (82–108) mm, n = 41

T: 31.5 (25–38) mm, n = 48

E: 12.8 (10–16) mm, n = 30

NL (length): 13.1 (12.3–14.5) mm, n = 12

Tib: 19.3 (18–21) mm, n = 17

HF: 9.5 (8–12) mm, n = 51

WT: 11.9 (8–15) g, n = 40

CrnC: 19.5 (17.6–21.2) mm, n = 22

GWS: 9.1 (8.4–9.7) mm, n = 30

C–M³: 6.9 (6.1–7.5) mm, n = 32

Throughout geographic range (BMNH, MNHN, RMCA, Matthews 1941, Aellen & Brosset 1968, Hill 1982b)

*Malawi only

Key References Benda & Vallo 2009, Hill 1982b; Kock & Felten 1980.

Meredith Happold

Family MEGADERMATIDAE

FALSE VAMPIRE BATS

Megadermatidae H. Allen, 1864. Monogr. Bats N. Am., pp. xxiii, 1.

| | | |
|--------------------------------|-------------------|--------|
| <i>Cardioderma</i> (1 species) | Heart-nosed Bat | p. 403 |
| <i>Lavia</i> (1 species) | Yellow-winged Bat | p. 406 |

The family Megadermatidae is polytypic and confined to the tropics of the Old World and Australasia. There are four extant genera and five species with two monotypic genera in Africa. They have enormous ears, which are partly joined together (Figure 32d). They also have a prominent noseleaf, a large interfemoral membrane and the tail is vestigial or absent (Figures 33d and 76a).

African megadermatids are small to medium-sized microbats with long grey or greyish pelage. The head is rounded, the muzzle short with a conspicuously long, erect noseleaf. The ears are longer than the length of head and are partly joined together for at least a third of their length by a membrane between their inner margins and the forehead. The tragus is long and uniquely bifid. The eyes are large for a microbat. The wings are large and broad; the second finger has a long metacarpal and one phalanx. The hindlimbs are long and the toes (except hallux) have three phalanges. The tail is vestigial or absent. The interfemoral membrane is large and broad, and is partly supported by calcars. Females have one pair of pectoral nipples and one pair of pubic nipples. The skull (Figure 76) is characterized by the loss or extreme reduction of the premaxillae and the concomitant loss of the incisors. Even if present, the minute remnants of the premaxillae are lost during preparation of skulls and therefore the greatest length of the skull (GLS) is taken to be the distance from the front of the maxilla to the most posterior part of skull. As in the family Nycteridae, there is a broad frontal plate formed by the fusion of flattened postorbital processes with the supraorbital ridges; this plate unites with a shallow sagittal crest. There is no lambdoid crest. The palate has a very deep-wide emargination between the canines, which sometimes reaches beyond the first premolars. The dental formula is $0^{113}/_{2123} = 26$ (except in one non-African species, which has two upper premolars).

Megadermatids have large wings, low to very low aspect ratios and medium to high wing-loadings. Their flight is slow and manoeuvrable; they can take off from the ground and can exploit cluttered environments. They are not adapted for cursorial locomotion or for climbing. Most megadermatids feed on insects and small vertebrates; an exception is the African *Lavia frons*, which seems to feed only on insects. The common name of the family, false vampire bats, stems from the old, erroneous belief that they fed on blood, as do the true vampire bats of the New World. There are no blood-sucking bats in Africa. Like nycterids, megadermatids sometimes forage and catch small prey by slow-hawking, but more often they are perch-hunting fly-catchers and gleaners, and carry larger prey back to the perch before eating it. Prey is detected visually and/or from sounds made by the prey, and also by echolocation. Like nycterids, megadermatids are 'whispering bats' whose echolocation calls are low intensity, multiharmonic CF calls of short duration, which provide detailed information about close objects, and are particularly well suited to densely cluttered environments (Möhres & Kulzer 1957, Möhres & Neuweiler 1966). The echolocation calls are probably emitted

through the nostrils and modified by the noseleaf. During the day, megadermatids roost in caves, crevices, hollow trees and buildings, or in the foliage of bushes or trees (Nowak 1999). Some roost singly, some in pairs, others in groups ranging in size from small to very large. *Lavia frons* establishes long-lasting monogamous pair-bonds and is territorial (Vaughan & Vaughan 1986). *Cardioderma cor* roosts in colonies and its mating system is not known, but individuals establish foraging territories, which are advertised by 'singing' (Vaughan 1976). Other megadermatids roost in groups of mixed composition throughout most or all of the year: ♀♀ of two species establish maternity colonies. The litter-size is typically one but is occasionally two in the case of one Asian species. Reproductive chronologies include restricted seasonal monoestry (in the Australian *Megaderma gigas*), seasonal bimodal polyoestry (in the African *C. cor*) and perhaps others.

The geological range of the family Megadermatidae is early Oligocene to Recent in Africa, early Oligocene to early Pliocene in Europe, middle Miocene to Recent in Australia and Pleistocene to Recent in Asia (Koopman 1984, Hand 1985, Koopman & Jones 1970). Apparently, there were many more species of megadermatids in the past, which may explain the diversity of the adaptations exemplified by the four extant genera. These genera are *Macroderma* (one species in Australia), *Cardioderma* (one species in Africa), *Megaderma* (two species in Asia) and *Lavia* (one species in Africa) (Koopman 1994). Based on hyoid morphology, *Macroderma* is considered phylogenetically primitive and somewhat removed from the other genera (Griffiths *et al.* 1992). *Macroderma gigas* (FA: 96–113 mm) and the African hipposiderid *Hipposideros gigas* (FA: 95–124) are the largest living microbats.

Megadermatids are almost entirely tropical but exploit habitats ranging from rainforest to semi-deserts. Both of the African species are tropical and both are mainly woodland savanna species that are also found in some forests (but not lowland rainforests). They are almost always found below 1000 m. At some localities, they have been recorded sympatrically.

Based on morphological data, the family Megadermatidae was placed in the superfamily Rhinolophoidea with the families Nycteridae, Rhinolophidae and Hipposideridae (Simmons 1998, Simmons & Geisler 1998), but more recent molecular studies have contradicted many groupings based on morphological data and therefore Simmons (2005) does not recognize any of the chiropteran superfamilies.

The genera in Africa are:

Cardioderma. Noseleaf 9–14 mm; pelage grey without yellow tinge; frontal shield of skull strongly concave, minimum breadth of shield 5.3–6.2 mm (see also Figure 76).

Lavia. Noseleaf 19–26 mm; pelage bluish-grey usually with yellowish tinge; frontal shield of skull comparatively flat, minimum breadth of shield 6.8–7.9 mm (see also Figure 76).

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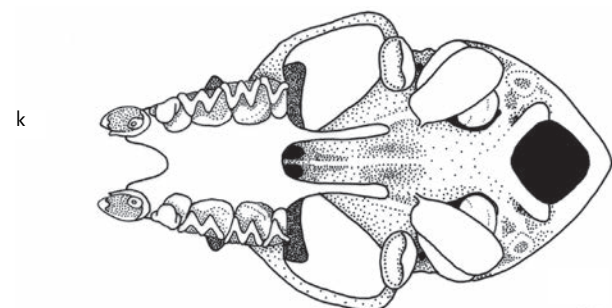
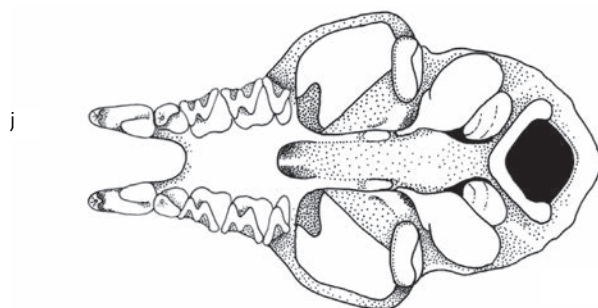
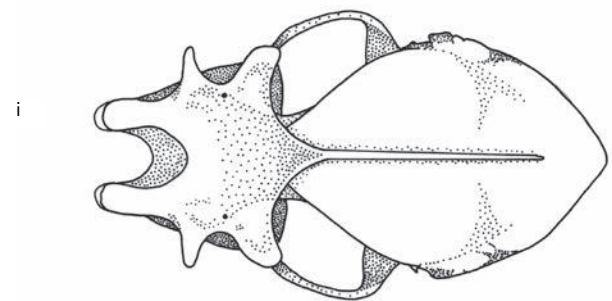
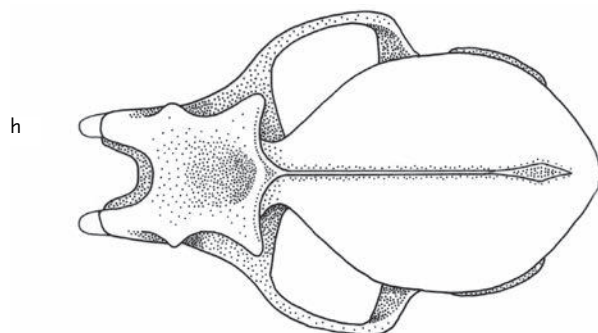
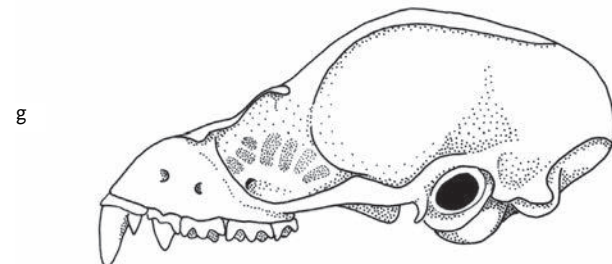
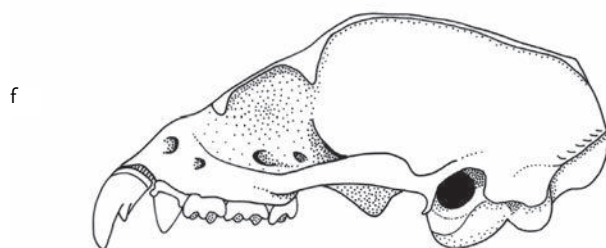
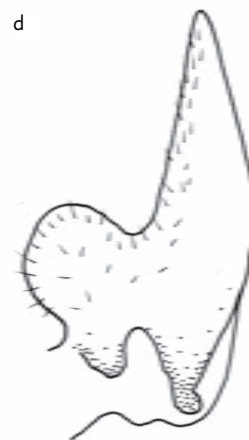
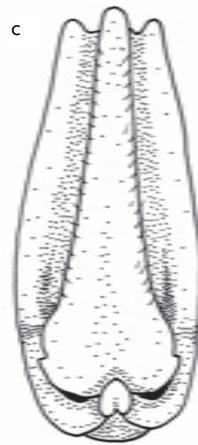
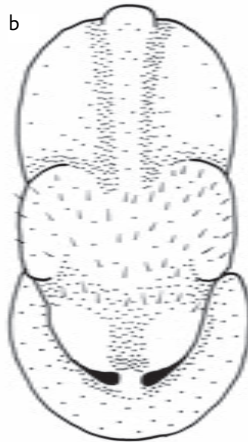
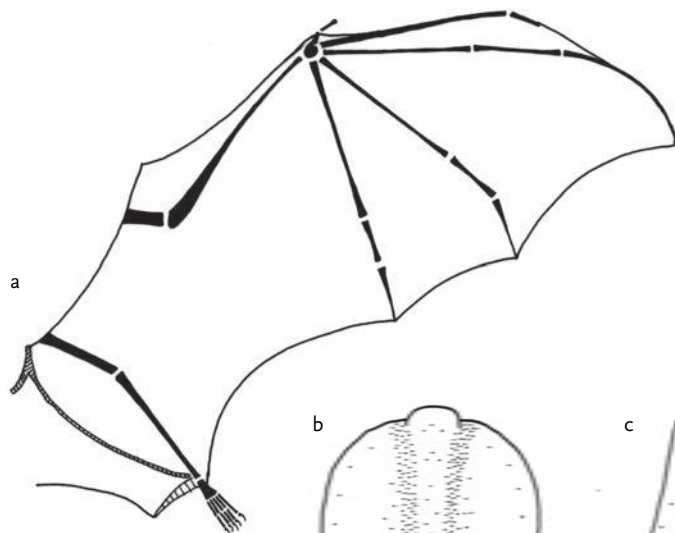


Figure 76. African bats in the family Megadermatidae: some of the distinguishing characters of *Cardioderma cor* and *Lavia frons*. (a) Flight membranes and bones of wing and hindlimb of *L. frons*. (b) Noseleaf of *C. cor* and (c) noseleaf of *L. frons* drawn to same length. (d) Left tragus of *C. cor* and (e) left tragus of *L. frons* drawn to same length. (f) Lateral view of skull of *C. cor* (RMCA RG 5116). (g) Lateral view of skull of *L. frons* (NMHN 1957-576). (h) Dorsal view of skull of *C. cor*. (i) Dorsal view of skull of *L. frons*. (j) Ventral view of skull of *C. cor*. (k) Ventral view of skull of *L. frons*.

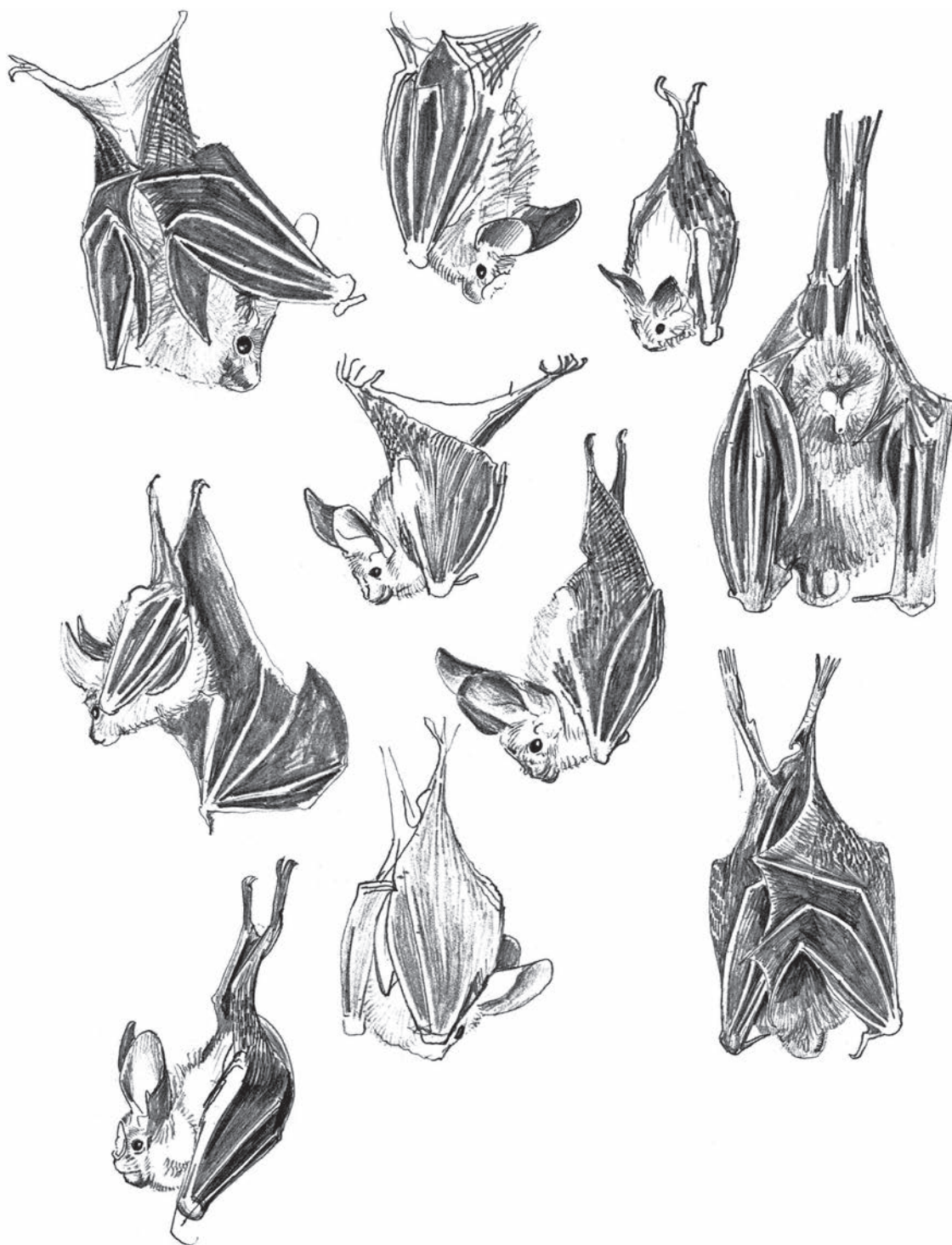
GENUS *Cardioderma***Heart-nosed Bat**

Cardioderma Peters, 1873. Monatsber. K. Preuss. Akad. Wiss. Berlin 1873: 488. Type species: *Megaderma cor* Peters, 1872.

Cardioderma is a monotypic genus confined to the northern half of eastern Africa. Distinguished from the other African genus in the family Megadermatidae by the comparatively shorter length of the noseleaf (9–14 mm), the absence of any yellowish tinge in the pelage, and the strong concavity of the frontal shield together with its

comparative narrowness (minimum breadth 5.3–6.2 mm) (see also Figure 76). The only species is *C. cor*.

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Cardioderma cor.

***Cardioderma cor* HEART-NOSED BAT (AFRICAN FALSE VAMPIRE BAT)**Fr. *Cardioderme à nez en coeur*; Ger. *Herznasen-Fledermaus**Cardioderma cor* (Peters, 1872). Monatsber. K. Preuss. Akad. Wiss. Berlin 1872: 194. Ethiopia.

Taxonomy Originally *Megaderma cor*. Synonyms: none. Chromosome number: not known.

Description Small microbat with noseleaf and very large interfemoral membrane but no tail; pale grey with brown wings and white digits; ears enormous and partly joined; tragus bifid; noseleaf erect and comparatively short (9–14 mm). Sexes similar. Pelage loose; mid-dorsal hairs 14–15 mm. Dorsal pelage pale grey, sometimes bluish, never suffused with yellow; hairs unicoloured. Ventral pelage slightly paler, never yellowish. Noseleaf as in Figure 76b; erect, somewhat heart-shaped, 9–14 mm (cf. 19–26 mm in *Lavia frons*). Ears pale brown, almost twice as long as head, basal halves joined by interaural membrane. Tragus bifid; outer lobe tapering to fine point; inner lobe less than half length of outer lobe, squarish or rounded (Figure 76d). Eyes very large for a microbat. Wings very broad, sepia brown, semi-translucent; skin over forearms and finger-bones white or whitish. Interfemoral membrane sepia brown. No tail.

Skull as in Figure 76f, h and j. Frontal shield strongly concave and relatively narrow (cf. *L. frons*); minimum breadth 5.8 (5.3–6.2) mm, $n = 15$. For additional data, see Csada (1996) but note that the photographed skull is that of *Coleura afra*, see p. 496.

Geographic Variation None.

Similar Species There is only one other megadermatid in Africa:

Lavia frons. Noseleaf longer (19–26 mm). Pelage bluish-grey with yellow tinge; skin over wing-bones not white. Frontal shield of skull comparatively flat; narrowest part broader (6.8–7.9 mm).

Distribution Endemic to Africa. Recorded mainly in the Sahel Savanna, Somalia–Masai Bushland and Coastal Forest Mosaic BZs, but extends marginally into the Afromontane–Afroalpine BZ of the Ethiopian Highlands along the Ethiopian Rift Valley. Recorded from Sudan, Eritrea, Djibouti, Ethiopia and Somalia to Uganda, Kenya and C Tanzania (including Zanzibar I.) (Swynnerton & Hayman 1951, Kulzer 1959, 1962, Funaioli 1971, Largen *et al.* 1974, Koopman 1975, Aggundey & Schlitter 1984, Varty & Hill 1988, Yalden *et al.* 1996, Cockle *et al.* 1998 and others). Possibly not distributed throughout Somalia as was indicated by Kingdon (1974) without supporting evidence, and Csada (1996). Reported to occur in N Zambia by Kingdon (1974) but not by Ansell (1978), and there are apparently no confirmed records from this region.

Habitat Recorded from both dry and moister habitats in *Acacia–Commiphora* deciduous bushland and thicket, semi-desert grassland and shrubland, and coastal forest mosaic vegetation zones. Also recorded from one of the coastal forests in Tanzania (Cockle *et al.* 1998), from riverine forest in Somalia in dry season (Varty & Hill 1988) and from open grassland and thorn scrub with volcanic rubble and lava blister caves, at ca. 1000 m, in Awash N. P., Ethiopia (Hill & Morris 1971).

*Cardioderma cor*

Abundance Uncertain. Moderately common in museum collections.

Adaptations Aspect ratio very low; wing-loading not known; wing-tip rather long. Flight slow and manoeuvrable. Can take off from ground; can hover briefly (Vaughan 1976, O'Shea & Vaughan 1980). By day, hangs free in caves, hollow baobabs *Adansonia* and abandoned Masai huts (Vaughan 1976). Seldom shares roosts with other species, but Kulzer (1962) found *C. cor* sharing one cave with *Rousettus aegyptiacus*, *Coleura afra*, *Taphozous hildegardeae*, *Rhinolophus* sp. and *Hipposideros* sp. While roosting, individuals are constantly vigilant and easily disturbed, suggesting *C. cor* does not become torpid.

Foraging and Food *Cardioderma cor* is a specialized perch-hunter, which forages by fly-catching and by ground-gleaning and leaf-gleaning, in feeding territories that are advertised by 'singing' (Vaughan 1976, McWilliam 1987a, Ryan & Tuttle 1987). No other African bat is known to do this. Ground-gleaning (mainly for large beetles but also for centipedes, scorpions and cockroaches) predominates during the dry seasons when grass-cover is reduced by termites. Perches are usually twigs of *Acacia* or *Commiphora*, 0.3–3.5 m above ground. Interlacing thorny or spiny branches above the perches provide protection from predators. Perching bats are also camouflaged by their wings, which resemble bunches of leaves, the white digits mimicking the veins of the leaves. For much of the year, individuals of both sexes occupy feeding territories, 0.1–1.01 ha ($n = 4$), each containing a series of habitually used perches (see Social

and Reproductive Behaviour). Perches are located over ground that is covered during the dry season by dead leaves and detritus, which produce characteristic sonic and ultrasonic sounds when disturbed by potential prey. These sounds (not vision or echolocation) indicate the position of potential prey. While listening for prey, individuals rotate through almost 360 degrees and, when perched 2 m above ground, scan an area ca. 4 m in diameter. They glide down, often snatch the prey without landing, sometimes land and immobilize the prey, sometimes hover after an initial unsuccessful attack, and finally carry the prey to the perch for eating. Flights to capture prey and to move between perches are usually of less than five seconds duration (details in Vaughan 1976). In wet seasons, when tall grass prevents ground-gleaning, and flying insects and leaf-eating insects are abundant, the bats switch to fly-catching (mainly for large flying beetles and hawk-moths; occasionally for small bats) and leaf-gleaning (mainly for Orthoptera). Although captive individuals eat frogs, there is no evidence that frogs are eaten in the wild (Ryan & Tuttle 1987). Changes in population density suggest that *C. cor* sometimes disperses seasonally from dry areas (where insects are scarce) to moist refugia such as riverine and coastal forests (Vaughan 1976, O'Shea & Vaughan 1980, Varty & Hill 1988). However, dry season ground-gleaning for large prey, with minimal expenditure of energy while searching for prey, and the exclusive utilization of previously established foraging territories, are highly adaptive to dry season conditions in dry habitats, and enable many individuals to exploit these habitats year-round.

Echolocation Although terrestrial prey is located by prey-generated sounds, *C. cor* uses both vision and echolocation to perceive its surroundings. The echolocation calls are FM sweeps (Pye 1980) with peak-frequency 42 kHz (O'Shea & Vaughan 1980) or 56.7 ± 11 kHz (Taylor *et al.* 2005). The calls are of low intensity, broad bandwidth (40–90 kHz) and short (2 ms) (Taylor *et al.* 2005). Four harmonics are present in at least some calls (Pye 1980).

Social and Reproductive Behaviour Roosts in groups (colonies); up to 80 found in hollow baobabs (Vaughan 1976). Wide spacing is maintained between individuals. Colony-composition and mating system not known. Despite roosting in colonies, individuals often forage singly. They establish foraging-territories, which, at least in the case of ♂♂, are advertised and delineated by singing, as in many passerine birds. In inland Kenya, each territory is held by a single individual or a mother–young couple. Territorial song consists of 4–9 (usually six) high-intensity pulses with fundamental frequency ca. 12 kHz (audible to humans), each song lasting ca. 1 sec. Singing occurs while ♂♂ are hanging from their foraging-perches. Inland, there is no singing during the short wet season, regular singing several times/min during the long wet season and early long dry season, and low-rate singing during the remaining dry periods. Thus territories are established when food is maximally abundant, but have their greatest survival value at the end of the long dry season when insects are most scarce (Vaughan 1976). In contrast, in coastal Kenya, there is pronounced territorial singing in the long dry season, and territories are sometimes occupied by male–female pairs that interact by sharing perches and flying together (McWilliam

1987a). Only ♂♂ were heard singing. Females make soft twittering vocalizations, possibly associated with mating. The differences in behaviour of inland and coastal individuals possibly reflect differences in reproductive chronology, lower inland population densities, and the dispersal of some inland individuals away from dry habitats during the long dry season. In addition to territorial singing, *C. cor* also makes a 'flight call' (a series of pulses more widely spaced than songs), which perhaps is a long-range location-call serving to inform individuals of each other's locations and directions of flight (Vaughan 1976).

Reproduction and Population Structure Litter-size: one. At ca. 2° S (near Kibwezi, inland Kenya), reproductive chronology is seasonal bimodal polyoestry with births during the wettest month in the short wet season (Nov) and at beginning of the long wet season (Mar–Apr) (Vaughan 1976). At ca. 4° S (Diani Beach, coastal Kenya [where rainfall is bimodal, insects most abundant in the wet seasons, less abundant in the short dry season and scarce in the long dry season]), very limited data suggest a different chronology (possibly aseasonal polyoestry with births peaking in the wet seasons but also occurring in the long dry season) (McWilliam 1987a). More data are needed from coastal habitats.

Predators, Parasites and Diseases Ectoparasites include bat-flies *Basilia daganiae* (Diptera: Nycteribiidae), *Raymondia huberi*, *R. planiceps*, *R. seminuda* (Diptera: Streblidae); a tick *Carios boueti* (Acari: Argasidae); and a mite *Megadermicolus yunkeri* (Acari: Chirodiscidae) (Anciaux de Faveaux 1984).

Conservation IUCN Category: Least Concern.

Measurements

Cardioderma cor

FA: 53.5 (50–58) mm, n = 52

WS (d): 333.9 (292–380) mm, n = 18

HB: 74.8 (66–85) mm, n = 35

T: 0 mm

Interfemoral membrane: n. d.

E: 37.9 (30–41) mm, n = 62

TR: 14.6 (12–20) mm, n = 12

NL (length): 11.7 (9–14) mm, n = 21

Tib: n. d.

HF: 17.3 (14–19) mm, n = 41*

WT: 24.3 (20–32) g, n = 36

GLS: 24.6 (23.0–26.0) mm, n = 65

GWS: 15.6 (14.8–16.4) mm, n = 46

C–M³: 10.0 (9.4–10.5) mm, n = 49

Throughout geographic range (BMNH, HZM, ROM, SMNS, Varty & Hill 1988)

*Somalia and East Africa only (Kulzer 1959, 1962, Varty & Hill 1988)

Key References Csada 1996; McWilliam 1987a; Ryan & Tuttle 1987; Vaughan 1976.

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GENUS *Lavia*

Yellow-winged Bat

Lavia Gray, 1838. Mag. Zool. Bot. 2: 490. Type species: *Megaderma frons* E. Geoffroy, 1810.

Lavia is a monotypic genus confined to Africa. Distinguished from the other African genus in the family Megadermatidae by the comparatively long length of the noseleaf (19–26 mm cf. 9–14 mm in *Cardioderma*) and a yellowish tinge in the pelage, the flatness of the frontal shield of the skull, which is also broader at its narrowest part

(minimum breadth 6.8–7.9 mm).

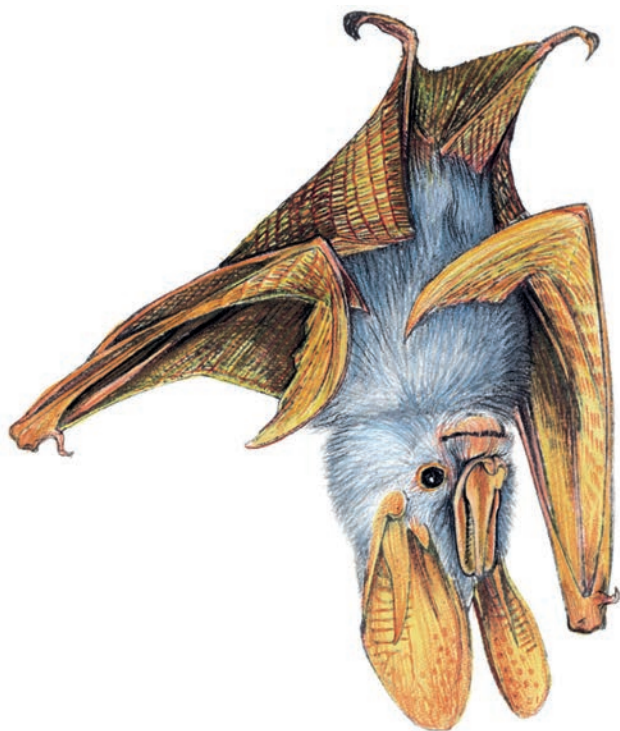
The only species is *Lavia frons*.

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Lavia frons YELLOW-WINGED BAT

Fr. Mégaderme à ailes orangées; Ger. Gelbflügel-Fledermaus

Lavia frons (E. Geoffroy, 1810). Ann. Mus. Natn. Hist. Nat. Paris 15: 192. Senegal.



Lavia frons.

Taxonomy Originally *Megaderma frons*. Synonyms: *affinis*, *rex*. Subspecies: three of very dubious validity. Chromosome number: not known.

Description Medium-small microbat with noseleaf and very large interfemoral membrane but no tail; brightly coloured (grey with orange–yellow wings); ears enormous and partly joined; tragus bifid; noseleaf erect and comparatively long (19–26 mm). Sexes similar in colour; ♀♀ slightly larger, on average, than ♂♂. Pelage slightly shaggy; mid-dorsal hairs ca. 15 mm. Dorsal pelage bluish-grey to slate-grey, suffused with greenish-yellow on lower back; hairs unicoloured. Ventral pelage greyish-fawn; sometimes yellowish. Males produce yellow secretion from glands on lower back (Lang & Chapin 1917b), but both sexes have yellowish pelage on lower back. Head appears very large because of the long ears and noseleaf. Noseleaf

very long and erect (Figure 76c), 19–26 mm long (cf. 9–14 mm in *Cardioderma cor*). Ears orange–yellow, almost twice as long as head; basal halves joined by interaural membrane. Tragus bifid; outer lobe long and tapering to fine point, inner lobe much shorter (Figure 76e). Eyes very large for a microbat. Wings very broad, variegated bright yellow, orange and pale brown; colour fades after death. Interfemoral membrane yellowish-orange. Hindlimbs long. No tail.

Skull as in Figure 76g, i and k. Frontal shield comparatively flat and wide (cf. *C. cor*); minimum breadth 7.3 (6.8–7.9) mm, *n* = 10. For more details, see Vohnhof & Kalcounis (1999).

Geographic Variation Koopman (1994) and Simmons (2005) list three poorly defined subspecies, but they are of dubious validity:

L.f. affinis: Sudan, Chad, N Uganda and extreme NW DR Congo. FA: 57.3 (49–61) mm, *n* = 44.

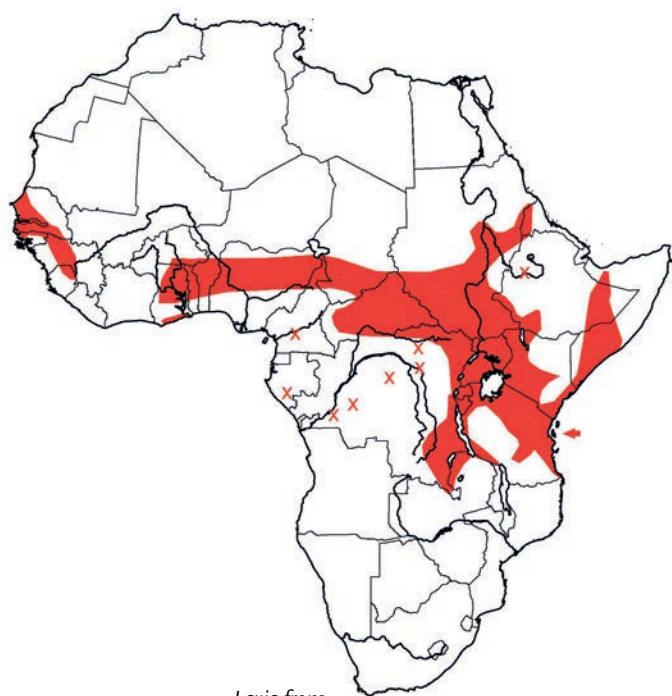
L.f. frons: western part of geographic range. FA: 59.3 (53–64) mm, *n* = 51.

L.f. rex: Ethiopia and southwards to N Malawi and westwards to E DR Congo. FA: 59.8 (56–65) mm, *n* = 25.

Similar Species There is only one other megadermatid in Africa:

Cardioderma cor. Noseleaf shorter (length 9–14 mm). Pelage grey or bluish-grey without yellow tinge. Frontal shield of skull strongly concave; minimum breadth narrower (5.3–6.2 mm).

Distribution Mainly Sudan Savanna, Guinea Savanna, Somalia–Masai, Coastal Forest Mosaic and Zambezi Woodland BZs, with some records in the Rainforest BZ and the Rainforest–Savanna Mosaics and two records in the Sahel Savanna BZ. Also recorded, but only very rarely, in Afromontane–Afroalpine BZ. Recorded disjunctly from Senegal to Eritrea and W Somalia (but absent from most of Ethiopia) and southwards to Gabon, DR Congo and Tanzania (including Zanzibar I.) with marginal records in C Zambia and N Malawi (Kock 1969a, Largen *et al.* 1974, Ansell 1978, Harrison 1982, Grubb *et al.* 1998 and others). The gap between 2°W and 11°W probably reflects insufficient collecting in that area. A record from Namibia (Andersen & Wroughton 1907 as *Vespertilio megalotis* Bechstein, 1800) is very dubious (D. Kock pers. comm.) and is not mapped.



Lavia frons

Habitat In the savanna zones from West Africa to eastern Africa, *L. frons* seems to occur mainly in woodland savannas with abundant acacias (Rosevear 1965, Verschuren 1966, Vaughan & Vaughan 1986). Also occurs in West African coastal mosaic, open degraded riverine forests in the Rainforest BZ of the central Congo Basin, East African Coastal Forest Mosaic and miombo woodland. In arid areas, *L. frons* is found in bush country surrounding lakes, marshes and along rivers (Lang & Chapin 1917a). Usually found below 1000 m. Apparently not found in closed rainforest, or at altitudes above 2000 m.

Abundance Uncertain; moderately common in museum collections.

Adaptations A well-known species. Wings very broad; aspect ratio very low; wing-loading medium; wing-tip rounded (Norberg & Rayner 1987). Flight fairly slow (mean speed 6.6 m/s), erratic and fluttering. Negotiates clutter with precise manoeuvrability. Roosts in foliage of trees throughout year. In Kenya, roosts in crowns of acacias, 5–10 m above ground. Basks in the sun on cool mornings and after rain, but usually roosts in shade and, during the day, moves from perch to perch, or into dense low shrubs, to find shadier positions (Vaughan 1987). To facilitate thermoregulation, at temperatures above 31 °C, blood vessels in the wings dilate and the wings are folded loosely and slightly away from the body (Vaughan 1987). Remains open-eyed and vigilant throughout the day, and flies to another perch if approached by hornbills (which prey on small vertebrates), other large birds and humans. Does not become torpid during day, and does not hibernate.

Foraging and Food Appears to be entirely insectivorous – unlike other megadermatids, *L. frons* is not known to include small vertebrates in its diet. Usually forages by opportunistic fly-catching, but occasionally flies from its perches to glean from the ground. Foraging is described in detail by Vaughan & Vaughan (1986).

Individuals hang from exposed perches, swivelling from side to side, flickering the ears, and raising the head up and down. Flying insects appear to be detected at long range by eyesight: the eyes have a tapetum lucidum, which implies enhanced night-vision, and it seems likely that *L. frons* can see insects silhouetted against the evening and night skies. The echolocation calls of *L. frons* (see below) would not allow long-range detection of prey, but may be used in the final stages of prey-catching. When prey is detected, individuals make a precise and very brief (typically three seconds) flight to intercept the prey, and then invariably returns to the perch before eating. There are no pursuits, and the energetic cost of foraging is minimal. During wet seasons, when insects are abundant, *L. frons* selects prey 1–2 cm long, which are searched for, and captured, near the perch and roughly on the same horizontal plane as the perch. When insects are scarce, individuals scan more than 90 degrees from ground level to high above, and attack any insect that will provide more energy than the cost of its capture. At such times, they will swoop down to take insects near the ground and also make towering flights into open spaces 20–30 m above the ground (perhaps to catch prey >2 cm in length). Throughout the year, foraging may occur during the day, but the main feeding period is after sundown. Most foraging is done from favoured perches along a particular route, which is exploited for several consecutive nights before a change is made. Individuals fly from perch to perch until a concentration of insects is located. In Kenya, *L. frons* occupies an exclusive feeding niche and exploits diurnal insects to a greater extent than other species of bat in the same area. In East Africa, this bat is closely associated with *Acacia tortilis*, which flowers and grows new leaves asynchronously in response to erratic dry-season rains: the trees attract insects that may be of crucial importance to *L. frons* during the dry seasons. In DR Congo, individuals have been observed at noon, perch-hunting insects in front of a grass fire, and they are often found roosting in trees and bushes fringing rivers, swamps and lakes where, perhaps, favoured insects are particularly common (Lang & Chapin 1917b). Feeds on a wide variety of very small to relatively large, soft and hard-shelled insects, including mosquitoes, flies, winged termites, butterflies, moths, grasshoppers and beetles.

Echolocation The echolocation calls are low-intensity broad bandwidth calls that provide detailed information about close objects, and are particularly suited to cluttered environments.

Social and Reproductive Behaviour Lives in monogamous pairs, in territories that are defended by the ♂ (Wickler & Uhrig 1969, Vaughan & Vaughan 1986). In Kenya, territories are 0.6–0.95 ha in area and contain 17–34 acacia trees (Vaughan & Vaughan 1986). Paired bats roost together, less than 1 m apart, and at least 20 m from the nearest neighbouring pair. Each pair has a primary roost (near the territorial boundary) where both bats spend most of the day and, although they may have moved to a shadier roost during the day, they return to the primary roost for a period of grooming, stretching and social interaction before beginning to forage. The ♂ leaves first, and patrols the territory for 10–15 min before the ♀ leaves. Evening patrols are stereotyped: the ♂ flies to sentinel posts in trees around the territorial boundary, each post being visited in a consistent sequence. Intruding conspecifics are attacked and driven away. Apparently, there is no territorial ‘song’

as in *C. cor*. Foraging begins after the evening patrol and is confined to the territory. When insects are abundant, the pair often forages together. When insects are scarce, they may forage apart but, if one finds a concentration of insects, the other may be attracted to the site. When this happens, the bats forage from separate perches and interference is avoided. More often than not, it is the ♀ which joins the ♂, probably because he locates concentrations of insects while making his territorial patrols. When the ♀ joins the ♂, he swoops close to her, which suggests close-range communication of some sort (possibly vocal). Ritualized interactions between the pair are conspicuous aspects of daily behaviour. There are at least three social vocalizations that are audible to humans; they are associated with aggression, mating and mother–young interactions (Wickler & Uhrig 1969).

During a study from mid-Dec to early Jul, courtship was observed in May and early Jun when rain was frequent and insects abundant (Vaughan & Vaughan 1986). Courtship includes brief (ca. 10 second) ‘aerial ballets’ during which the pair circle and chase each other, and longer displays during which the ♂ flies tight figure-eights close to his perching mate. Mating apparently occurs while the pair are hanging from a perch. The testes, which are unusually prominent and pendulous, have substantial deposits of melanin in the scrotal skin; as well as protecting developing spermatogonia from harmful ultraviolet radiation, this pigmentation may have a social/reproductive communication function (Kermott & Timms 1988). Parental behaviour has been described in detail by Vaughan & Vaughan (1987). The single young clings to its mother continuously until ca. one week before it first flies and forages. It grips a pubic nipple in the mouth, and holds the back of the mother’s neck with its feet. Periodically, it turns ‘upside down’ (i.e. head down) to suck. Older juveniles occasionally release their grip on the pubic nipple, turn ‘upside-down’, hold on by the feet only, and stretch, groom and flap their wings. Mothers lick the inguinal region of the young (perhaps to induce urination) and eat the faeces (perhaps to recycle water). Newly volant young forage with their parents and soon develop foraging strategies closely resembling those of the parents. They are weaned ca. 20 days after becoming volant. For at least 30 days more, they share the parents’ territory, synchronize grooming and foraging periods with those of the parents, and periodically huddle against the mother when roosting.

Monogamy, territoriality, division of labour, opportunistic foraging and long mother–young associations are probably adaptations to habitats with low carrying capacities and seasonal shortages of food (Vaughan & Vaughan 1986).

Reproduction and Population Structure Litter-size: one. Gestation ca. 3–3.5 months (Verschuren 1957, Anciaux de Faveaux 1972). Reproductive chronology uncertain. At 00° 36' N (near Kampi ya Samaki, Kenya), young were born in early Apr to all of five ♀♀ under observation, and courtship and attempted mating were observed in May and early Jun: no data from mid-Jul to early Dec (Vaughan & Vaughan 1986, 1987). These data suggest seasonal bimodal polyoestry (as in *C. cor*) but there are no data to confirm if or when other births occur in Kenya. In Sudan, a juvenile was recorded in Dec, and two ♀♀ with embryos 11.5 mm in Mar (Kock 1969a). At Faradje, NE DR Congo, Lang & Chapin (1917b) recorded ‘one large foetus in Mar and five young from Oct to Apr’ but these

data are inconclusive. In Garamba N. P., NE DR Congo, Verschuren (1957) recorded 4 of 4 ♀♀ pregnant in Mar, 1 of 1 near end of term in early Apr, and a juvenile in Apr, indicating births in early Apr with ♀♀ in synchrony: he found no evidence of births at other times of the year. Koopman *et al.* (1978) recorded that nine ♀♀ taken from Cella, Burkina in mid-Mar were pregnant; crown–rump lengths of embryos 13–33 mm, but they do not record if non-pregnant ♀♀ were caught at the same time, and there are no records for other months in Burkina. (These authors did not record pregnancies in May and Sep as stated by Nowak 1999.) In Tanzania, ♀♀ with well-developed embryos were recorded in late Jan, early Feb, early Apr and early Aug (Eisentraut 1958), and births have been reported during Jan, Apr, Aug and Nov (Anciaux de Faveaux 1972).

Predators, Parasites and Diseases Comparatively vulnerable to predation by diurnal birds of prey: they maintain constant vigilance and fly if approached by large birds. Captures by European Kestrels *Falco tinnunculus* have been observed (Vaughan & Vaughan 1986). One bat was found in the stomach of a Common Mamba *Dendroaspis angusticeps* (Allen & Lawrence 1936). Other predators include Bat Hawks *Macheiramphus alcinus*, and a Night Tree Viper *Boiga blandingii* (Wickler & Uhrig 1969 in Vohnhof & Kalcounis 1999). Ectoparasites include fleas *Echidnophaga aethiops* (Siphonaptera: Pulicidae), *Chiropteropsylla brockmani* (Siphonaptera: Ischnopsyllidae); a bat-fly *Raymondia planiceps* (Diptera: Streblidae); and mites *Ancystropus zebeborii* (Acari: Spinturnicidae), *Psorergatoides laviae* (Acari: Psorergatidae), *Lapidocarpus laviae*, *Olalidocarpus africanus*, *Alalidocarpus hilli*, *A. laviae* (Acari: Chirodiscidae), *Nycteriglyphus laviae* (Acari: Rosensteiniidae), *Rodhainyssus yunkeri* (Acari: Gastronyssidae) (Anciaux de Faveaux 1984).

Conservation IUCN Category: Least Concern.

Measurements

Lavia frons

FA: 58.4 (49–65) mm, n = 85

WS (d): 165, 181 mm, n = 2

HB: 70.1 (60–90) mm, n = 50

T: 0 mm

Interfemoral membrane: 48.7 (44–58) mm, n = 7

E: 41.7 (35–46) mm, n = 65

TR: 23.8 (21–26) mm, n = 20

NL (length): 20.0 (19–26) mm, n = 25

Tib: 32.2 (29–37) mm, n = 25

HF: 18.5 (16–20) mm, n = 25

WT: 24.6 (16–30) g, n = 12

GLS: 23.9 (22.1–26.2) mm, n = 57

GWS: 14.5 (13.5–15.9) mm, n = 35

C–M³: 8.8 (8.2–9.7) mm, n = 52

Throughout geographic range (BMNH, NMK, SMF, SMNS, ZFMK and literature)

Key References Kock 1969a; Lang & Chapin 1917b; Vaughan 1987; Vaughan & Vaughan 1986, 1987; Vohnhof & Kalcounis 1999; Wickler & Uhrig 1969.

Meredith Happold

Family RHINOPOMATIDAE

MOUSE-TAILED BATS

Rhinopomatidae Bonaparte, 1838. Syn. Vert. Syst. In: Nuovi Ann. Sci. Nat., Bologna, 2: 111.

| | | |
|------------------------------|-------------------|--------|
| <i>Rhinopoma</i> (3 species) | Mouse-tailed Bats | p. 410 |
|------------------------------|-------------------|--------|

This is a monotypic family distributed from Africa (north of the Equator) to southern Asia through Arabia, the Middle East and India, mainly in semi-arid and arid habitats. There are currently four species (Van Cakenberghe & De Vree 1994, Simmons 2005) of which three occur in Africa and one in Arabia and the Middle East (*Rhinopoma muscatellum*). These bats of primitive structure are characterized by a tail that is exceptionally long and has at least half of its length projecting beyond the narrow interfemoral membrane (Figure 77), slit-like valvular nostrils that can be closed, and a small triangular noseleaf surmounting a hog-shaped muzzle (that gave the name to the genus) (see Figure 32e). Miller (1907) proposed the name Rhinopomidae and this was adopted by several authors; however, the original name is most commonly used. The family was reviewed by Hill (1977a) and more recently by Van Cakenberghe & De Vree (1994).

Rhinopomatids are small to medium-sized microbats with moderately long pelage that is generally more or less sepia grey (but varying in colour and tone across the geographic range), and usually paler ventrally. The face, rump and posterior portion of the abdomen are naked and medium brown. Sexes similar in colour, and ♂♂ are often slightly larger than ♀♀. A thickened narial pad is present on the end of the muzzle, surmounted by a distinct ridge-like dermal outgrowth (a rudimentary noseleaf). The ears are more or less triangular and joined across the forehead by a connecting band of skin; each ear has a simple but moderately long and erect tragus. Eyes are relatively large for a microbat. Wings rather narrow; second finger with two bony phalanges (cf. all other African families); all of the fingers are shorter, relative to the length of the forearm, than in any other bats (Figure 77). The tip of the wing can be shortened by folding to facilitate cursorial locomotion, but not to the same extent as in the Emballonuridae and Molossidae. This is achieved by the terminal phalanx of the third finger bending round, but not fully, upon the ventral surface of the wing (Rosevear 1965). The hindlimbs are moderately long; the toes (except the hallux) have three phalanges. The tail has sensitive hairs at its distal end. The skull is relatively short and broad; there are no postorbital processes: the skull of *Rhinopoma microphyllum* is illustrated as an example for the genus (Figure 77). Separate nasal swellings are present on each side of the rostrum. The sagittal crest is low and sharp. The auditory bullae are rather large. The premaxillae are separate from each other and from the adjacent part of the skull. The upper incisor (I^2) is very small, barely emerging from the gum. The canines are conical and simple. The first and second upper molars are lacking distinct hypocones. Dental formula $^{1113}/_{2123} = 28$.

Rhinopomatids roost in dry caves, crevices, various underground structures and buildings including tombs and pyramids; their day-roosts are impregnated with a characteristic smell. An oily substance is secreted by the numerous glands of the facial region in response to stimuli (e.g. touch, fear, aggression) (Kulzer *et al.* 1985). Sometimes, they share day-roosts with other species of bats, including other

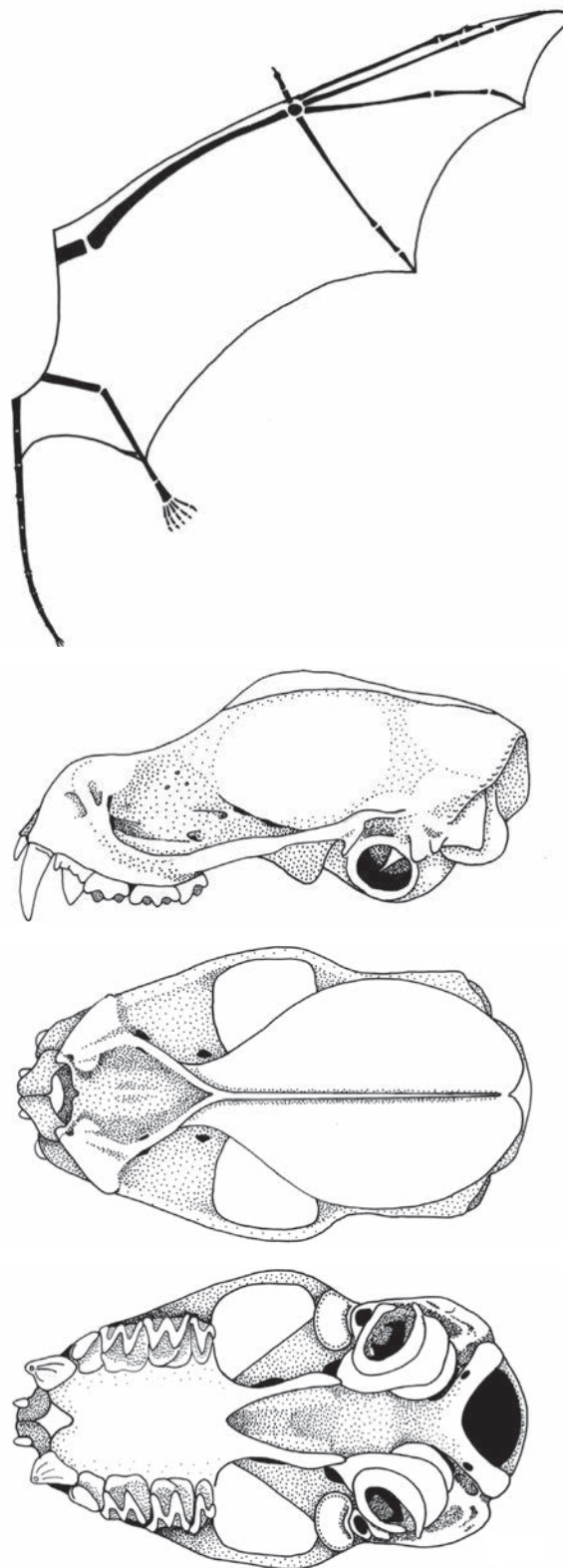


Figure 77. Characters of African bats in the family Rhinopomatidae. Flight membranes and bones of wing, hindlimb and tail (e.g. *Rhinopoma hardwickii*). Skull (e.g. *R. microphyllum*; BMNH 3.12.8.26)

species of rhinopomatids, but the different species do not roost in exactly the same places. Rhinopomatids sometimes roost in clusters numbering up to many thousands of individuals, but most of the groups are smaller (10–100 bats). The sexes segregate for at least part of the year. Little is known of their breeding habits in Africa.

These insect-eating bats are poor fliers and tire quickly. Their wings are adapted for fast flight in open areas, gliding or rapid wing-flapping. When echolocating, ultrasound pulses are emitted through the mouth; the echolocation calls are loud with little modulation of frequency when the bats are foraging (Figures 82 and 83), and become more frequency-modulated when the bats are approaching prey or when they are emerging from their day-roosts in groups (Schmidt & Joermann 1986). Rhinopomatids can accumulate fat in the lower abdominal region; this is metabolized when food is scarce. These bats do not hibernate, but they can remain torpid for several days. Their water metabolism reflects extreme adaptations to desert habitats; the concentration of urea in the blood is high, and the skin is poorly vascularized so that loss of water through evaporation is minimal, even

at high temperatures. Some populations are suspected to migrate.

No fossils referable to this family have been found; the oldest remains of rhinopomatids were collected from Egyptian tombs, which have been inhabited by these bats for ca. 3000 years.

All of the three species of rhinopomatids in Africa occur in the tropics; two also extend northwards into temperate habitats. In Africa, one species is found in semi-desert vegetation zones, and the other two are found in both desert and semi-desert vegetation zones. Two species have also been found in montane habitats (but not above ca. 1200 m).

Based on morphological data, the family Rhinopomatidae was placed in the superfamily Rhinopomatoidea by Simmons (1998) and Simmons & Geisler (1998), but more recent molecular studies have contradicted many groupings based on morphological data and, pending resolution of the controversies, Simmons (2005) does not recognize the chiropteran superfamilies.

All rhinopomatids belong to the genus *Rhinopoma*.

Stéphane Aulagnier

GENUS *Rhinopoma* Mouse-tailed Bats

Rhinopoma E. Geoffroy, 1818. Description de l’Egypte 2: 113. Type species: *Vespertilio microphyllus* Brünnich, 1782.

This genus contains four species of which three occur in Africa. As this is the only genus in the family Rhinopomatidae, its characters are given in the family profile.

Almost all authors recognize two main species that are widely distributed in Africa and Asia: the comparatively large *Rhinopoma microphyllum* and the smaller *R. hardwickii* (original spelling). Additionally, most authors agree to recognize a third species, smaller than the former ones – this is *R. muscatellum*, an extralimital species currently considered to occur from Arabia to SW India (Simmons 2005). Subsequently, based on a biometric study of 15 skull and 14 external measurements, and six morphological characters, Van Cakenberghe & De Vree (1994) confirmed the validity of *R. muscatellum* and, in addition, proposed specific status for *macinnesi*, a taxon first described from Kenya as a subspecies of *R. cystops* by Hayman (1937) and later considered a subspecies of *R. hardwickii* by Kock (1969a) and Hill (1977a). Small rhinopomatids have also been collected in Eritrea since Senna (1905). Lagen *et al.* (1974) and Demeter & Topal (1982) suspected that these represented *R. muscatellum*, but Van Cakenberghe & De Vree (1994) indicated that they represent *R. macinnesi*.

The three species that occur in Africa can be distinguished by their distributions and/or the combination of characters given in Table 16. These characters are as follows:

Forearm length (FA).

Greatest length of skull (GLS).

Relative length of tail. Expressed as percentage of FA.

Rostrum shape. The shape of the rostrum, viewed dorsally, can be triangular or pentagonal (Figure 78).

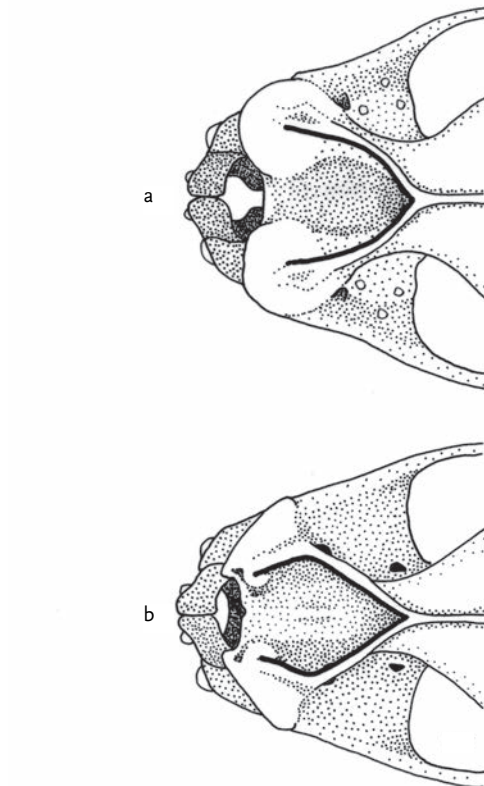
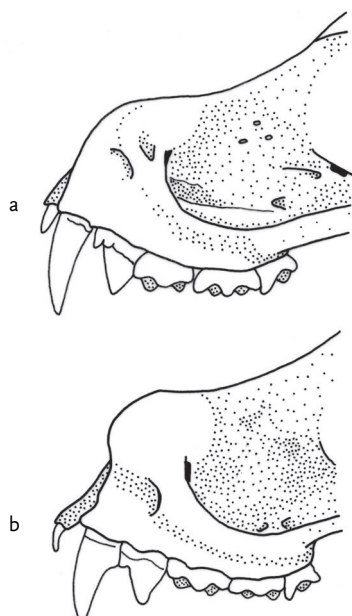


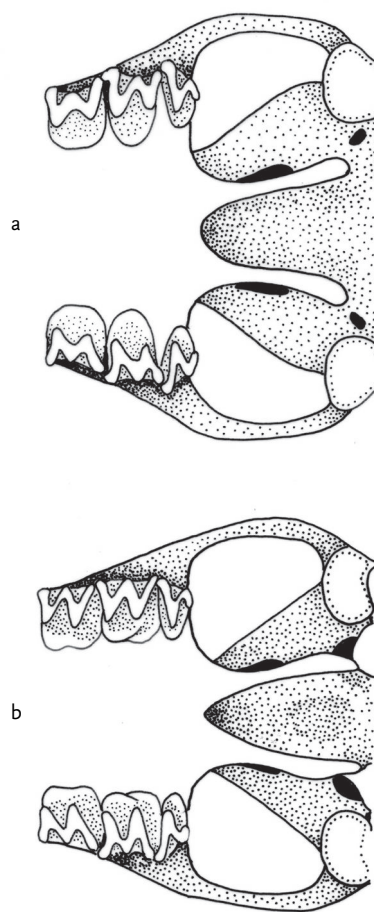
Figure 78. Variations in the outline of the rostrum (viewed dorsally) in African *Rhinopoma* (following Van Cakenberghe & De Vree 1994). (a) Rostrum of *Rhinopoma macinnesi* showing triangular outline. (b) Rostrum of *Rhinopoma microphyllum* showing pentagonal outline.

Sagittal crest. Can be inconspicuous and sometimes absent, or prominent.



ABOVE: Figure 79. Variations in the extent of development of the nasal swellings in African *Rhinopoma* (following Van Cakenberghe & De Vree 1994). (a) Weakly developed (e.g. *R. microphyllum*). (b) Moderately developed (e.g. *R. macinnesi*).

RIGHT: Figure 80. Variations in the shape of the posterior palatal emargination, and the extent to which it reaches forward, in African *Rhinopoma* (following Van Cakenberghe & De Vree 1994). (a) U-shaped and reaching as far forward as the line connecting the posterior edges of the third molars (e.g. *R. macinnesi*). (b) V-shaped and not reaching as far forward as the line connecting the posterior edges of the third molars (e.g. *R. microphyllum*).



Development of nasal swellings. Said to be weak for the genus if the most anterior point of the nasal bones (viewed laterally) is posterior to the upper canines (Figure 79a), moderate if the most anterior point is directly above the canines (Figure 79b), or strong if the most anterior point is anterior to the canines. The development is strong only in the extralimital species, *R. muscatellum*.

Another character, mentioned only in the species profiles is:

Posterior palatal emargination. Can be U-shaped or V-shaped, and can reach, or not reach, as far forward as the line connecting the posterior edges of the third molars (M^3 – M^3) (Figure 80).

Stéphane Aulagnier

Table 16. Key to the African species of *Rhinopoma*. For explanation of the characters, see Genus *Rhinopoma*. Measurements and distributions pertain only to Africa.

| Distribution | FA (mm) | GLS (mm) | T % of FA | Rostrum outline; sagittal crest; nasal swellings | Species |
|--|--------------|------------------|---------------|---|------------------------|
| Kenya, Somalia, Ethiopia in Somalia–Masai Bushland BZ | 48.6 (45–53) | 15.4 (14.2–16.2) | 136 (122–158) | Triangular
Inconspicuous or absent
Moderately developed | <i>R. macinnesi</i> |
| Widespread north of Equator in Mediterranean Coastal, Sahara Arid, Sahel Savanna and Sudan Savanna BZs | 56.0 (50–62) | 16.8 (15.4–18.0) | 118 (87–155) | Triangular
Inconspicuous
Usually weakly developed | <i>R. hardwickii</i> |
| Widespread north of Equator in Mediterranean Coastal, Sahara Arid, Sahel Savanna and Sudan Savanna BZs | 68.6 (62–74) | 20.4 (18.7–21.5) | 92 (73–126) | Pentagonal
Very prominent
Weakly developed | <i>R. microphyllum</i> |

***Rhinopoma hardwickii* LESSER MOUSE-TAILED BAT**

Fr. Petit rhinopome; Ger. Hardwickses Mausschwanz-Fledermaus

Rhinopoma hardwickii Gray, 1831. Zool. Misc. 1: 37. India, restricted to Bengal by Qumsiyeh *et al.* (1992).

Taxonomy Originally *Rhinopoma hardwickii*. Thomas (1903a) changed the name to *hardwickei* because the species was named after Major-General Hardwicke and subsequently both names have been used. Synonyms (excluding misspellings; African only): *arabium*, *brevicauda*, *brevicaudatum*, *cystops*, *ferox*, *longicaudatum*, *microphyllus* E. Geoffroy Saint-Hilaire, 1818, *sennaariense*, *sondaicum*. Subspecies: four; two in Africa. Chromosome number (Palestine): $2n = 36$; $aFN = 68$ (Qumsiyeh & Baker 1985). Since this profile was submitted, *cystops* has been restored to specific status by Hulva *et al.* (2007).

Description Small microbat with rudimentary 'noseleaf' and extremely long, mostly free tail; medium-sized for an African *Rhinopoma* (FA: 50–62 mm); tail considerably longer than FA; 'noseleaf' comparatively large; nasal swellings only sometimes reaching as far forward as upper canines. Sexes similar in colour; ♂♂ on average slightly larger than ♀♀. Pelage fine; mid-dorsal hairs 7–8 mm; rump and lower abdomen naked or only sparsely haired; face and ears naked. Dorsal pelage sepia grey; hairs with paler base, especially on the flanks. Ventral pelage paler and greyer, sometimes very pale to white posteriorly. Muzzle upturned; nostrils valvular; dermal ridge ('noseleaf') relatively large; upper margin triangular in ca. 75% of cases, or with a central papilla. Ears subtriangular, joined across forehead by connecting band of naked skin. Tragus sickle-shaped, conspicuous, erect, narrow, moderately long (just < half of ear length); tip bluntly rounded, usually with small, finger-like projection rising from anterior edge, which gives the tip a notched appearance (Figure 81a). Eyes large for a microbat. Wings and interfemoral membrane medium brown, naked, attaching to each tibia well above the ankle (at ca. two-thirds to three-quarters of distance from knee). Interfemoral membrane very narrow. Hindfeet comparatively small and delicate. Tail very slender, projecting well beyond interfemoral membrane, usually longer than forearm (118 [87–155]% of FA, $n = 338$; Van Cakenberghe & De Vree 1994).

Skull medium-sized for a *Rhinopoma*. Sagittal crest present but not conspicuous anteriorly, absent posteriorly; lambdoid crest well developed ventrally, absent dorsally. Rostrum (viewed dorsally) is triangular and relatively large. Nasal swellings usually weakly developed for the genus (the most anterior points of the nasal bones are usually posterior to the canines [as in *R. macinnesi*, Figure 79b], but are

sometimes level with them) (Figure 79). Posterior palatal emargination U-shaped, usually extending forward as far as the line connecting the posterior edges of the third molars (as in *R. macinnesi*, Figure 80a).

Geographic Variation Two subspecies occur in Africa (Hill 1977a, Van Cakenberghe & De Vree 1994):

R. h. cystops: central part of African geographic range (S Algeria, S Egypt, N Niger). On average smaller (FA: 53.0 [50–57] mm; GLS: 16.2 [15.4–16.7] mm, $n = 22$). Recently restored to specific status by Hulva *et al.* (2007).

R. h. arabium: remainder of African geographic range and, extraliminally, Arabia. On average larger (FA: 57.7 [53–62] mm; GLS: 17.2 [16.3–18.0] mm, $n = 38$).

Similar Species Only two other species of African bats have an extremely long tail protruding far beyond the interfemoral membrane:

Rhinopoma macinnesi. Often smaller (FA: 48.6 [45–53] mm; GLS: 15.4 [14.2–16.2] mm). Eritrea, Ethiopia, Somalia and N Kenya.

R. microphyllum. Larger (FA: 62–74 mm; GLS: 18.7–21.5 mm). Tail usually shorter than forearm.

Distribution In Africa, mainly recorded around the periphery of the Sahara Arid BZ, in arid inland parts of the Mediterranean Coastal BZ and in the Sahel Savanna, Sudan Savanna and Somalia–Masai Bushland BZs, but also found in mountainous areas of the Sahara and in the Afromontane–Afroalpine BZ in Ethiopia. Recorded from

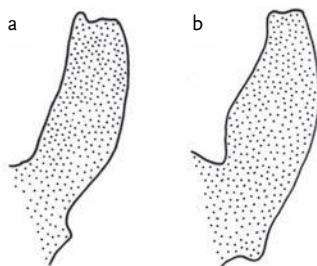
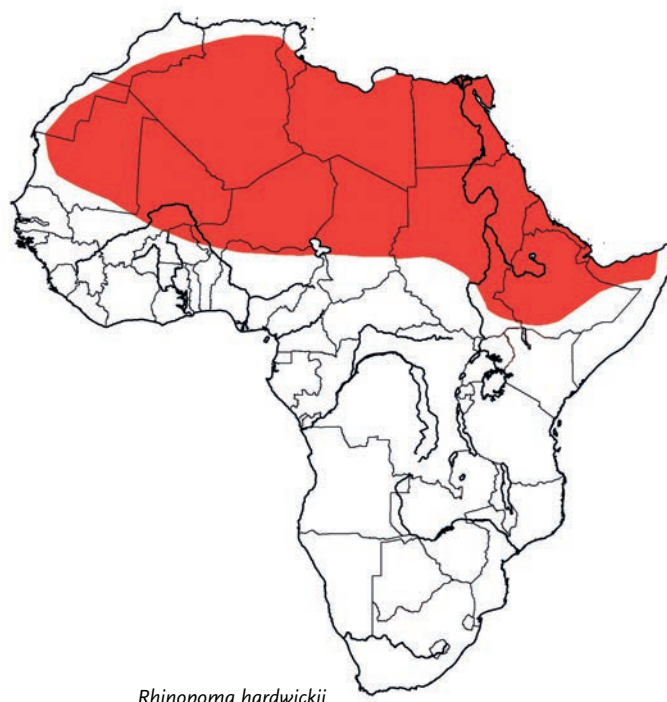


Figure 81. Variations in the shape of the tragus of (a) *Rhinopoma hardwickii* and (b) *Rhinopoma microphyllum*: left tragus illustrated; both drawn to same length.



Rhinopoma hardwickii

Morocco, Algeria (Saharan Atlas and Hoggar), Tunisia, Libya, Egypt and southwards to Mauritania, Senegal (locality not mapped), Mali, Burkina, Niger, N Nigeria, Chad (Tibesti), Sudan, Eritrea, Djibouti, Ethiopia, N Somalia (Hill 1977a, Van Cakenberghe & De Vree 1994, Benda *et al.* 2004a). The known specimens from Kenya refer to *R. macinnesi* according to Van Cakenberghe & De Vree (1994). Extraliminally: through Arabia to India, Myanmar and Sunda Is.

Habitat Inhabits arid and semi-desert vegetation zones where suitable day-roosts and food are available; penetrates the wooded steppe in some eastern areas. Absent from areas of high humidity. Ranges from sea level in Egypt to ca. 1100 m in Morocco and Algeria (Aulagnier & Destre 1985, Kowalski & Rzebik-Kowalska 1991). Recorded from bank of large river flanked by riverine forest and on slope of a dormant volcano in Awash N. P., Ethiopia, a region of semi-desert grassland with areas of *Acacia* scrub (Largen *et al.* 1974); along the Nile R. in Egypt (Gaisler *et al.* 1972); in an oasis with gardens and orchards surrounded by sandy desert and hamada in Libya (Benda *et al.* 2004a); and in gorges of wadis with some *Tamarix* *Tamarix* sp. and Oleanders *Nerium oleander* in Morocco (Aulagnier & Destre 1985).

Abundance Uncertain. More widely distributed and more often recorded than *R. microphyllum*. Seems to be particularly abundant near oases. However, both distribution and abundance are indubitably insufficiently investigated because the roosts and suitable habitats are very often unreachable.

Adaptations Aspect ratio low; wing-loading high; wing-tip extremely short: the short wings and absence of an interfemoral membrane contribute to the high wing-loading (Norberg & Rayner 1987). Flight fast and very distinctive – characterized by a series of alternating flutters and glides, and a rising and falling motion (Harrison & Bates 1991). This undulating pattern helps to save energy expended during flight (Rayner 1985). Cannot hover (Habersetzer 1986 in Norberg & Rayner 1987). Climbs and scuttles with agility; tail often held at stiff right-angle to body during these activities. Roosts by day in warm caves, underground tunnels, wells, ruins, catacombs, mosques and deserted buildings. Clings to ceilings (less often to walls), with tail

extended and limbs wide apart. When disturbed, escapes by climbing with agility (rather than by flying), with the tail often held at a stiff right-angle to body. Roost temperatures range from 21 to 34.5 °C and relative humidities can be as low as 35% (Kock 1969a, Gaisler *et al.* 1972) or even 20–25% (Poulet 1970). Surprisingly tolerant of light; in summer, sometimes roosts in fissures, small crevices and among boulders that are fully exposed to strong solar radiation (Kowalski & Rzebik-Kowalska 1991); also roosts in total darkness (Poulet 1970, Gaisler *et al.* 1972). Moves to underground day-roosts in winter. Stays active throughout most of winter but sometimes has periods of extended rest when it survives on accumulated deposits of fat (Kock 1969a, Poulet 1970, Vogel 1977, Aulagnier & Destre 1985, Kowalski & Rzebik-Kowalska 1991). Often roosts with *Asellia tridens*, *Rhinolophus blasii*, *R. clivus*, *R. ferrumequinum*, *R. hipposideros*, *Plecotus* spp. and *Miniopterus schreibersii* in the north of its African geographic range (Gaisler *et al.* 1982, Aulagnier & Destre 1985); and with *Rhinopoma microphyllum*, *Asellia tridens*, *Taphozous perforatus*, *Nycteris thebaica* and *Hipposideros ruber* in the south (Kock 1969a, Poulet 1970, Koch-Weser 1984). For more information, see Qumsiyeh & Jones 1986.

Foraging and Food Forages by slow-hawking. Emerges from day-roost early after sunset. Foraging sites in Africa not known: flies 10–15 m above ground when commuting to foraging sites. In India, usually forages in open spaces (above and around canopies and over clearings) ca. 6–9 m above ground (Neuweiler 1984); on bright moonlit nights foraging is suppressed and takes place under cover of canopies (Usman 1989). In Israel, feeds mainly on Coleoptera and Hymenoptera, but also on Homoptera and Heteroptera (Whitaker & Yom-Tov 2002).

Echolocation The echolocation of *Rhinopoma* spp. is considered acoustically primitive by Simmons (1979) because these bats use signals with four or more harmonics (usually with maximum energy in second harmonic) and little frequency modulation. Search-phase call-shape (India) usually CF but calls sometimes begin with a very narrow-bandwidth descending FM-component (Figure 82; Habersetzer 1981). CF-frequency (second harmonic) during pursuit of insects (Egypt) 36–40 kHz; call-duration 6–10 ms; call repetition-

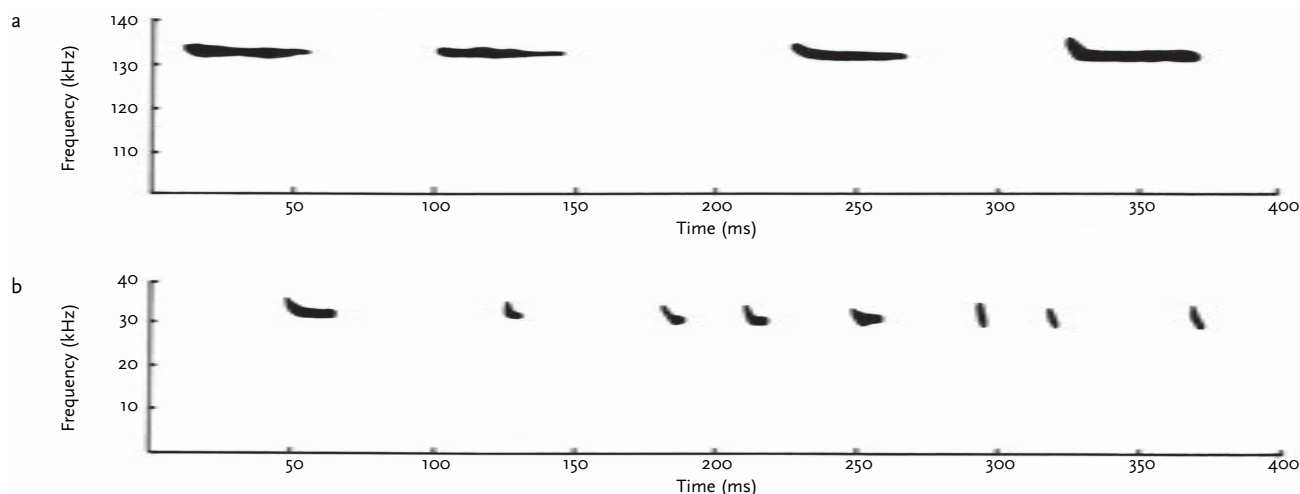


Figure 82. Echolocation calls of *Rhinopoma hardwickii*. (a) Sonogram of a sequence of search-phase calls: one bat flying in open prior to returning to its roost. (b) Calls emitted as this bat approached its roost (based on Habersetzer 1981). Only the dominant harmonic (second) is shown (for harmonics, see Habersetzer 1981). Note that the time-scale relative to the frequency scale is substantially different to that of most other sonograms in other profiles.

rate ca. 10 calls/sec. Darting flight is accompanied by shortening the signals to 1 ms or less and increasing the call repetition-rate to ca. 100 calls/sec; laboratory tests indicated that Doppler shift compensation is probably not used by this species (Simmons *et al.* 1984). When three individuals flew together in the laboratory, each used a different CF-frequency, suggesting that they regulated the CF-frequency to avoid jamming each other (Habersetzer 1981). After landing, CF calls of mean duration 74 ms are emitted and these have maximum energy in the fundamental harmonic; the purpose of these calls (echolocation and/or communication) is not known (Habersetzer 1981). The first harmonic frequencies (18–20 kHz; Simmons *et al.* 1984) of calls made in a roost in Morocco were audible to humans (Aulagnier & Destre 1985).

Social and Reproductive Behaviour Roosts singly or in groups ranging in size from a few individuals to several hundred (Poulet 1970, Gaisler *et al.* 1972). Group-members cling apart (i.e. without touching their neighbours). Facultative sexual segregation only occurs during summer (Panouse 1951, Kock 1969a, Poulet 1970).

Reproduction and Population Structure Litter-size: one. In India, absence of young from Oct to Apr, and sightings of neonates mainly in Jun, indicate that the reproductive chronology is restricted seasonal monoestry (Brosset 1962) with copulation from mid-Feb to early Mar; gestation 95–100 days; lactation for ca. two months (Bates & Harrison 1997). In Egypt, 27 of 30 adult ♀♀ were pregnant and all adult ♂♂ were sexually inactive in Apr; no data for other months (Gaisler *et al.* 1972), and in Sudan, early stages of pregnancy were recorded in late Mar (Kock 1969a); so births were expected from May to early Jun at these localities. In Israel, non-volant young were caught in late May and two ♀♀ were still pregnant at this time (Yom-Tov *et al.* 1992). In Burkina, ♀♀ carried half-grown young in the wet season (mid-Jul) (Koch-Weser 1984). These data are consistent with restricted seasonal monoestry.

Predators, Parasites and Diseases Ectoparasites in Africa include fleas *Chiropteropsylla aegyptia* (Siphonaptera: Ischnopsyllidae), *Xenopsylla ramesis* (Siphonaptera: Pulicidae); bat-flies *Phthiridium integrum*, *Eycampsipoda hyrtlui* (Diptera: Nycteribiidae), *Ascodipteron rhinopomatos*, *Brachytarsina diversa* (Diptera: Streblidae); and ticks *Argas transgaripepinus*, *Carios vespertilionis*, *C. boueti* (Acari: Argasidae) (Hastriter & Tipton 1975, Anciaux de Faveaux 1984).

Conservation IUCN Category: Least Concern.

Measurements

Rhinopoma hardwickii

FA: 56.0 (50–62) mm, n = 86

WS (d): 300–346 mm, n = ?*

HB: 58.1 (53–65) mm, n = 62

T: 65.8 (54–78) mm, n = 81

E: 18.2 (16–20) mm, n = 66

TR: 7.1 (5.5–8.5) mm, n = 66

Tib: n. d.

HF: 11.7 (10–13.5) mm, n = 73

WT: 9.0 (6.5–12.0) g, n = 66

GLS: 16.8 (15.4–18.0) mm, n = 66

GWS: 10.2 (9.5–11.8) mm, n = 81

C–M³: 5.9 (5.4–6.5) mm, n = 85

Egypt and Sudan (Kock 1969a, Gaisler *et al.* 1972, Van Cakenberghe & De Vree 1994)

*Mauritania (Poulet 1970)

Key References Hill 1977a; Kowalski & Rzebik-Kowalska 1991; Poulet 1970; Qumsiyeh & Jones 1986; Van Cakenberghe & De Vree 1994.

Stéphane Aulagnier

Rhinopoma macinnesi MACINNES'S MOUSE-TAILED BAT

Fr. Rhinopome de MacInnes; Ger. MacInnes' Mausschwanz-Fledermaus

Rhinopoma macinnesi Hayman, 1937. Ann. Mag. Nat. Hist., ser. 10, 19: 530. Bat I., near Central I., L. Rudolf [= L. Turkana], Kenya.

Taxonomy Originally *Rhinopoma cystops macinnesi*. Synonyms: none. Considered a subspecies of *R. hardwickii* by some authors (e.g. Kock 1969a, Koopman 1975, Hill 1977a, Aggundey & Schlitter 1984) and of *R. muscatellum* (a small Arabian species) by Largent *et al.* (1974), but considered to be a distinct species by Van Cakenberghe & De Vree (1994). Chromosome number: not known.

Description Small microbat with rudimentary 'noseleaf' and extremely long, mostly free tail; the smallest African *Rhinopoma* (FA: 45–53 mm); tail considerably longer than FA; nasal swellings reaching forward to level of upper canines. Sexual dimorphism: no information. Pelage fine; rump and lower abdomen naked or sparsely haired; mid-dorsal hairs ca. 7 mm. Dorsal pelage sepia grey. Ventral pelage essentially grey. Muzzle upturned; nostrils valvular, dermal ridge ('noseleaf') relatively large. Ears subtriangular, joined across forehead by connecting band of skin. Tragus: no information. Eyes

large for a microbat. Wings and interfemoral membrane medium brown, naked. Interfemoral membrane very narrow. Hindfeet comparatively small and delicate. Tail very slender, projecting well beyond interfemoral membrane, longer than forearm (136 [122–158]% of FA, n = 40; Van Cakenberghe & De Vree 1994).

Skull small for a *Rhinopoma*. Sagittal crest reduced (not conspicuous) or absent. Rostrum (viewed dorsally) is triangular. Nasal swellings moderately developed for this genus (the anterior-most points of the nasal bones are level with the upper canines) (Figure 79b). Posterior palatal emargination U-shaped; extending forward as far as the line connecting the posterior edges of the third molars (Figure 80a).

Geographic Variation None recorded.

Similar Species Only two other species of African bats have an extremely long tail protruding far beyond the interfemoral membrane:

Rhinopoma hardwickii. Often larger (FA: 56.0 [50–62] mm; GLS: 16.8 [15.4–18.0] mm). Widespread.

R. microphyllum. Larger (FA: 62–74 mm; GLS: 18.7–21.5 mm). Tail usually shorter than FA. The most anterior points of the nasal bones are posterior to the canines.

Distribution Endemic to Africa. As yet known only from the Somalia–Masai Bushland BZ. Recorded from Abbas on the S Eritrean coast; Galago Oasis in Somalia; and from Central I. and Bat I. in L. Turkana, Lesucut I. and Gibralter I. in L. Baringo, Kampi ya Samaki near L. Baringo, and Lodwar, in Kenya (Hayman 1937, Aggundey & Schlitter 1984, Van Cakenberghe & De Vree 1994). A specimen from Lokomarinyang in extreme SE Sudan (Koopman 1975) is no longer assigned to this species (Van Cakenberghe & De Vree 1994).

Habitat The known localities are in semi-desert vegetation zones including semi-desert grassland and shrubland, and *Acacia–Commiphora* deciduous bushland and thicket (terminology: White 1983). Ranges from sea level in Eritrea to ca. 500 m in Kenya. Three of the four Kenyan records are from islands in large lakes.

Abundance Probably a rare species as no specimens were collected during several expeditions into its geographic range.

Remarks Very little is known about the habits of this species. Climbs and scuttles with some agility; tail often held at stiff right-angle to body during these activities (Kingdon 1974 as *R. hardwickii*). Moves backwards into crevices with its tail waving in all directions; tip of tail has very fine hairs and these, and the tail itself, possibly have a sensory role (Kingdon 1974).

Conservation IUCN Category: Data Deficient.

Population very restricted in its area of occupancy – occurs in a small region of Kenya and only two other localities are known.

Measurements

Rhinopoma macinnesi

FA: 48.6 (45–53) mm, n = 42

WS: n. d.



Rhinopoma macinnesi

HB: n. d.

T: 66.3 (55–76) mm, n = 40

E: 16.0 (11–20) mm, n = 41

TR: n. d.

Tib: 22.1 (20–24) mm, n = 42

HF: n. d.

WT: 8.0 (5–11) g, n = 24

GLS: 15.4 (14.2–16.2) mm, n = 47

GWS: 8.9 (8.1–9.4) mm, n = 40

C–M³: 5.6 (4.9–6.1) mm, n = 52

Throughout geographic range (Van Cakenberghe & De Vree 1994)

Key References Hayman 1937; Hill 1977a; Kingdon 1974; Van Cakenberghe & De Vree 1994.

Stéphane Aulagnier

Rhinopoma microphyllum GREATER MOUSE-TAILED BAT

Fr. Grand rhinopome; Ger. Ägyptische Mausschwanz-Fledermaus

Rhinopoma microphyllum (Brünnich, 1782). Dyrenes Historie 1: 50. Giza, Egypt.

Taxonomy Originally *Vespertilio microphyllus*. Synonyms in Africa: *cordofanicum*, *lepsianum* and *tropicalis* (extralimitally, five others listed by Simmons [2005]). Subspecies: four; one in Africa (but see Geographic Variation). Chromosome number (Palestine): 2n = 42; aFN = 66 (Qumsiyeh & Baker 1985).

Description Medium-size microbat with rudimentary ‘noseleaf’ and very long, mostly free tail; the largest *Rhinopoma* in Africa (FA: 62–74 mm); tail usually shorter than FA; ‘noseleaf’ comparatively small; nasal swellings not reaching as far forward as the canines. Sexes similar. Pelage fine, silky; mid-dorsal hairs 5–7 mm; rump and

lower abdomen, face, ears and throat naked or almost so. Dorsal pelage greyish-brown, sometimes paler; hairs unicoloured. Ventral pelage paler to whitish. Muzzle upturned; nostrils valvular; dermal ridge (‘noseleaf’) relatively small with upper margin variable in shape. Ears subtriangular, joined across forehead by band of skin. Tragus sickle-shaped with small basal lobule; tip bluntly rounded, sometimes smooth, sometimes with projection from anterior margin giving the tip a notched appearance. Eyes large for a microbat. Wings and interfemoral membrane medium brown, naked; second finger with two phalanges. Hindfeet slender but, on average, longer than those of *R. hardwickii*. Interfemoral membrane very narrow. Wing

and interfemoral membranes attaching to each tibia well above the ankle (at ca. three-quarters of distance from knee). Tail very slender, projecting well beyond interfemoral membrane but usually shorter than forearm (92 [73–126]% of FA, $n = 139$; Van Cakenberghe & De Vree 1994) and usually shorter than HB.

Skull (Figure 77) large and robust for a *Rhinopoma*. Sagittal crest very prominent anteriorly and posteriorly; lambdoid crest comparatively well developed dorsally and ventrally. Rostrum (viewed dorsally) is pentagonal (Figure 78b) and relatively small. Nasal swellings weakly developed for the genus (the most anterior points of the nasal bones are posterior to the canines) (Figure 79a). Posterior palatal emargination sharply V-shaped and not extending as far forward as the line connecting the posterior edges of the third molars (Figure 80b). Complete cranial and postcranial osteology in Sinha (1982).

Geographic Variation Specimens from some areas (e.g. S Sudan and Wase Rock, Nigeria) are possibly larger on average than those from elsewhere in Africa and, based on this, Kock (1969a) and Hill (1977a) recognized two subspecies in Africa, *R. m. tropicalis* and *R. m. microphyllum*. However, the differences are not considered to justify the subspecific status of *tropicalis* by Van Cakenberghe & De Vree (1994).

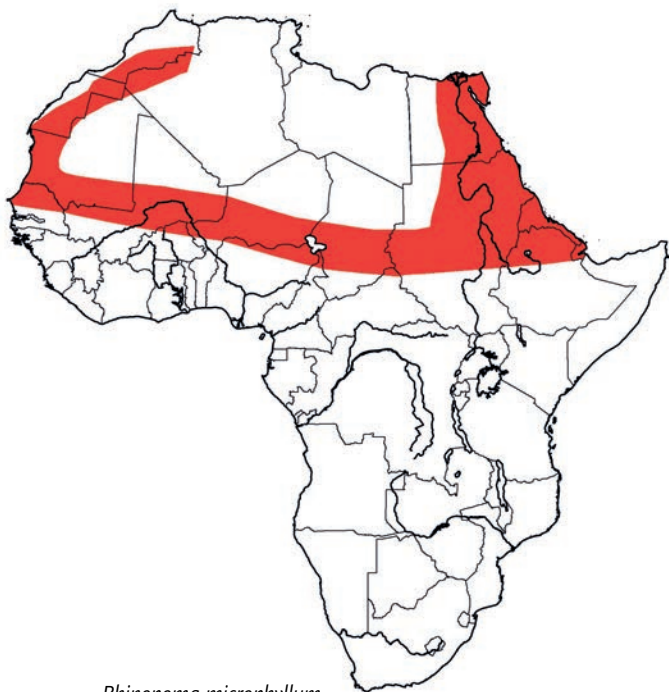
Similar Species Only two other species of African bats have an extremely long tail protruding far beyond the interfemoral membrane:

Rhinopoma hardwickii. Smaller (FA: 50–62 mm; GLS: 15.4–18.0 mm).

Tail almost always longer than FA.

R. macinnesi. Smaller (FA: 45–53 mm; GLS: 14.2–16.2 mm). Tail longer than FA. Most anterior points of nasal bones are level with the canines.

Distribution In Africa, mainly recorded in the arid regions of the Mediterranean Coastal BZ, the north-western and eastern regions



of the Sahara Arid BZ and the Sahel Savanna BZ, and marginally in the Sudan Savanna, Somalia–Masai Bushland and Afromontane–Afroalpine BZs. Possibly also occurs in scattered localities in the central Sahara Arid BZ. Recorded from SE Morocco, W Mauritania, Senegal, Burkina, Nigeria, N Cameroon, Sudan, Djibouti and Egypt (Kock 1969a, Qumsiyeh 1985, Aulagnier & Thévenot 1986, Le Berre 1990, Van Cakenberghe & De Vree 1994, Pearch *et al.* 2001, Benda *et al.* 2004d). Extraliminally: Arabia and Middle East to India and Sumatra.

Habitat Inhabits arid regions (rainfall <300 mm) with very sparse vegetation, ranging from sea level in Egypt (Qumsiyeh 1985) to ca. 1200 m in Morocco (Aulagnier & Destre 1985). Also exploits semi-arid habitats (rainfall 400–500 mm) in the southern part of the geographic range.

Abundance Uncertain; likely to be populations in regions not yet investigated, and known populations have not been adequately surveyed. Colonies of several thousands have been reported in Egypt and Mauritania (see Social and Reproductive Behaviour).

Adaptations Aspect ratio medium-high; wing-loading very high; wing-tip extremely short (Norberg & Rayner 1987). Flight fast; alternates fluttering with gliding so flight-path is undulating, as in *R. hardwickii* (Roberts 1977 in Norberg & Rayner 1987). Climbs and scuttles with agility. Roosts by day in more-or-less dark crevices, small caves, mines, underground tunnels, wells, old monuments and buildings; tolerates low relative humidities (20–25%) and light. Clings to ceilings and walls with its limbs spread out and the sensory tail looking like a fifth limb. If disturbed, climbs with agility across vertical cliffs instead of hiding in deep crevices (Aulagnier & Destre 1985). Sometimes shares day-roosts with *Taphozous perforatus*, but the roost-sites of each species are always far apart. At Khartoum, Sudan, found roosting in a cave shared with a colony of *Asellia tridens* (Happold 1967). In Mauritania and Burkina, commonly roosts with *R. hardwickii*, often in larger numbers (Poulet 1970, Koch-Weser 1984). In India, migrates on a seasonal basis (Gopalakrishna 1986). In Mauritania, by the end of autumn or the wet season, considerable amounts of fat are deposited in the thighs, the lower portion of the abdomen and the upper part of the interfemoral membrane, and used later as a source of energy (Poulet 1970). In Africa, remains active throughout the year. Adaptations to desert habitats include skin that is less vascularized and produces very little perspiration even when temperatures are high, and the ability to tolerate concentrations of urea in the blood that are 4–5 times higher than in humans (see Schlitter & Qumsiyeh 1996).

Foraging and Food Forages by slow-hawking. Foraging areas not known. In Mauritania in autumn, reported to forage for a comparatively short period (1–1.5 h); stomachs of three individuals contained mainly Coleoptera (Tenebrionidae, Scarabaeidae, Cucurionidae) and some Hemiptera (Poulet 1970). In Israel, feeds mainly on Coleoptera (80% of volume), and also on Lepidoptera, Hymenoptera and Homoptera (Whitaker & Yom-Tov 2002).

Echolocation Search-phase call-shape (Egyptian animals in laboratory) CF (multiharmonic) (see Figure 83; Schmidt & Joermann

1983). CF-frequency (second harmonic) 27–31 kHz (but each individual emits only one frequency); call-duration ‘long’. When flying in a flight-tunnel, this species emits shorter and slightly frequency-modulated calls (as does *R. hardwickii*). However, if three individuals fly together in the flight-tunnel, instead of avoiding jamming by changing to three different frequencies (see *R. hardwickii*), the main response of these bats is to greatly increase the intensity of their calls (Schmidt & Joermann 1983).

Social and Reproductive Behaviour Usually roosts in groups varying in size from a few individuals in crevices to colonies of several thousands in Egyptian monuments and underground sites in Mauritania (4000–5000 of both species of *Rhinopoma* were recorded in several wells near Akjoujt by Poulet 1970). Even in very large colonies, individuals never roost close to each other (Poulet 1970). The sexes segregate during part of the year but this is not related to parturition (at one roost in Morocco, only ♂♂ were present in Dec; both sexes were present in Jun; Heim de Balsac 1948).

Reproduction and Population Structure Litter-size: one. In India, the reproductive chronology is restricted seasonal monoestry (Brosset 1962), with spermatogenesis in winter (testes reach maximum size by late Jan), copulation around Mar; births in second half of Jun or early Jul; young weaned in Aug to early Sep after lactation period of four weeks (see Schlitter & Qumsiyeh 1996). Both sexes reach sexual maturity in 18–19 months (Schlitter & Qumsiyeh 1996).

Predators, Parasites and Diseases Occasionally preyed on by Pharaoh Eagle-owls *Bubo ascalaphus* (Aulagnier 1989, Aulagnier & Denys 2000). Ectoparasites (in Egypt) include fleas *Ischnopsylla consimilis*, *Chiropteropsylla aegyptia* (Siphonaptera: Ischnopsyllidae); bat-flies *Ascodipteron namrui*, *Brachytarsina africana*, *B. diversa*, *B. kollari* (Diptera: Streblidae); ticks *Carios vespertilionis*, *C. boueti*, *Alectorobius tholozani* (Acari: Argasidae); and mites *Meristaspis lateralis* (Acari: Spinturnicidae) and *Liponyssus lepidopeltis* (Acari: Macronyssidae) (Anciaux de Faveaux 1984).

Conservation IUCN Category: Least Concern.

Conservation should include monitoring of human disturbance of major roosts.

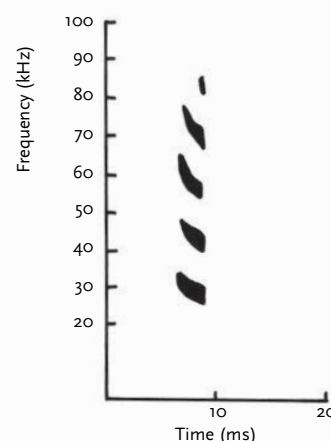


Figure 83. Sonogram of a search-phase call emitted by *Rhinopoma microphyllum*, showing all harmonics (based on Schmidt & Joermann 1986).

Measurements

Rhinopoma microphyllum

FA: 68.6 (62–74) mm, n = 34

WS (d): 330–380 mm, n = ?*

HB: 76.1 (72–81) mm, n = 19

T: 63.7 (52–85) mm, n = 32

E: 20.6 (19–22) mm, n = 19

TR: n. d.

Tib: n. d.

HF: 16.2 (13–17) mm, n = 19

WT: 26.8 (14–37) g, n = 32

GLS: 20.4 (18.7–21.5) mm, n = 19

GWS: 12.2 (11.2–13.1) mm, n = 25

C–M³: 7.3 (6.6–7.7) mm, n = 31

Egypt and Sudan (Kock 1969a, Qumsiyeh 1985, Van Cakenberghe & De Vree 1994, HZM)

*Mauritania (Poulet 1970)

Key References Hill 1977a; Kock 1969a; Poulet 1970; Schlitter & Qumsiyeh 1996; Van Cakenberghe & De Vree 1994.

Stéphane Aulagnier

Family EMBALLONURIDAE
SHEATH-TAILED BATS

Emballonuridae Gervais, 1855. In: F. Comte de Castelnau, Exped. Partes Cen. Am. Sud., Zool. (Sec. 7), Vol. 1, pt 2 (Mammifères), p. 62 footnote.

| | | |
|---------------------------------|--------------------|--------|
| Subfamily Emballonurinae | | p. 421 |
| <i>Coleura</i> (1 species) | Sheath-tailed Bats | p. 421 |
| Subfamily Taphozoinae | | p. 424 |
| <i>Saccolaimus</i> (1 species) | Pouched Bats | p. 424 |
| <i>Taphozous</i> (5 species) | Tomb Bats | p. 427 |

This is a polytypic family that is distributed widely in the tropical and sub-tropical regions of the world. There are 13 extant genera (of which four are monotypic) and 51 extant species, but only three genera and seven species occur in Africa (Simmons 2005). Emballonurids have short sleek pelage, a relatively long body, a triangular head with pointed muzzle, moderately large ears, small but conspicuous eyes, no noseleaf, long narrow wings and a unique tail that projects upwards through the centre of the interfemoral membrane into a sheath of skin (Figure 84e and f). None are considered to be pests.

African emballonurids range in size from small to very large (FA: 44–95 mm). *Saccolaimus peli*, the largest emballonurid in Africa, is the third largest insectivorous bat in Africa (FA: 87–95 mm). Males and ♀♀ are usually similar in size and colour. The pelage is short and sleek and does not extend onto the flight-membranes; the posterior of the body is naked in some species. The body is elongated and moderately robust. The head is slightly flattened, the cranial area is broad and the muzzle is conical. The lacrimal region is not swollen. The forehead is either slightly concave or there is a deep depression between the eyes. The nostrils are close together. The upper lip has a small bare patch below the nostrils; this is matched by a larger prominence on the lower lip, which is divided by a vertical groove in some genera. During echolocation, the lips open slightly and the prominences on the lips form a small O through which the sound is emitted. The ears are relatively short (ca. 26–33% of FA), widely separated, roughly triangular with rounded tips; they point backwards and lie flat against the head and neck when these bats rest. The outer margin has a large

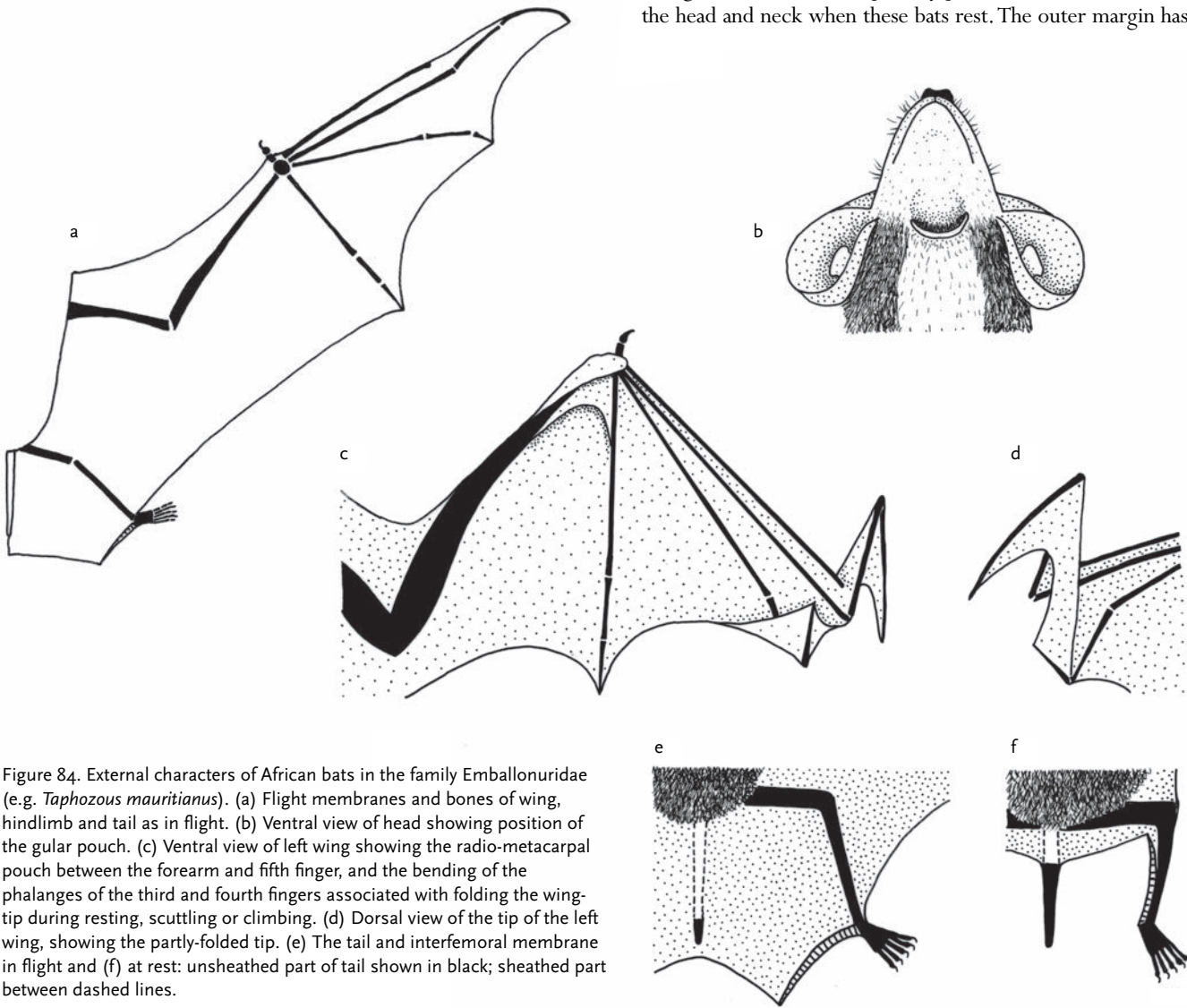


Figure 84. External characters of African bats in the family Emballonuridae (e.g. *Taphozous mauritanus*). (a) Flight membranes and bones of wing, hindlimb and tail as in flight. (b) Ventral view of head showing position of the gular pouch. (c) Ventral view of left wing showing the radio-metacarpal pouch between the forearm and fifth finger, and the bending of the phalanges of the third and fourth fingers associated with folding the wing-tip during resting, scuttling or climbing. (d) Dorsal view of the tip of the left wing, showing the partly-folded tip. (e) The tail and interfemoral membrane in flight and (f) at rest: unsheathed part of tail shown in black; sheathed part between dashed lines.

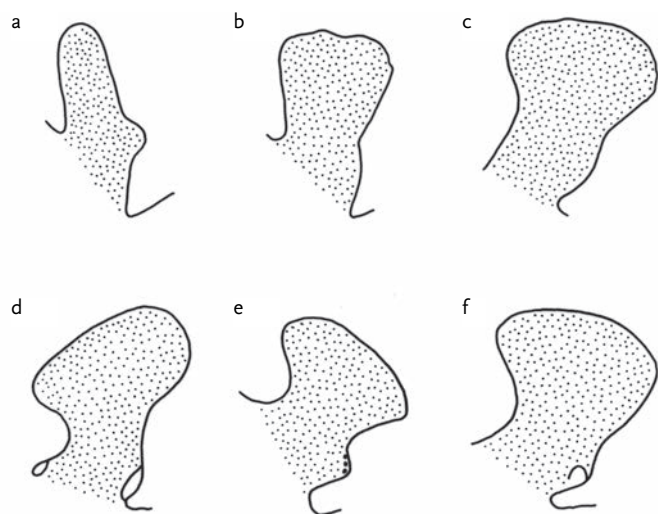


Figure 85. Variations in the shape of the tragus of some African Emballonuridae. (a) *Coleura afra*. (b) *Saccolaimus peli*. (c) *Taphozous hildegardeae*. (d) *T. mauritanus*. (e) *T. nudiventris*. (f) *T. perforatus*. Left tragus illustrated; all drawn to same length.

antitragus, which extends forwards almost to the mouth; the tragus is conspicuous and its shape is a means of distinguishing the African genera (Figure 85). The eyes are large for a microbat and, during the day, emballonurids watch for danger and sometimes fly away, without echolocating, if they are disturbed. In some species, there is a glandular region on the throat, which may range from a patch of bare skin (gular patch) to a deep pouch (gular pouch or sac) (Figure 84b). Gular patches and pouches are sometimes less developed, or absent, in ♀♀. Pelage in the gular area of the throat is sometimes black and referred to as a 'beard'. The wings are long and narrow; the second finger has a long metacarpal but no bony phalanges. In most species, a small flap of skin stretches between the forearm and the metacarpal of the fifth finger: this is the radio-metacarpal pouch and its function is not known. Except during flight, the tip of each wing folds back above the remainder of the wing in a way unique to this family: the first phalanx of the third finger folds upwards and backwards to lie against the metacarpal while the second phalanx folds downwards to lie against the first (Figure 84c and d). This shortens the wings and allows the membranes to be 'furled' tightly against the forearm. At the same time, the tail projects into its sheath allowing the elastic interfemoral membrane to contract and lie close against the body. These adaptations enable emballonurids to scuttle and climb very rapidly over horizontal and vertical surfaces without being impeded by the flight-membranes. The interfemoral membrane is supported by substantial calcars (Figure 84e and f). During flight, the hindlimbs and calcars can stretch outwards and backwards thereby increasing the area of the interfemoral membrane and causing the terminal half of the tail to slide into it. It is probable that the area and curvature of the interfemoral membrane is frequently adjusted during flight. The hindlimbs are moderately short; the toes (except hallux) have three phalanges. The tail is relatively short (21–26% of TL in African emballonurids). There are no pubic nipples.

The skull has long, slender postorbital processes, which curve outwards and downwards behind each orbit (Figure 86). These processes do not fuse with the supraorbital ridges to form a concave frontal plate (cf. Nycteridae and Megadermatidae), and no other microbats have postorbital processes. The profile of the forehead

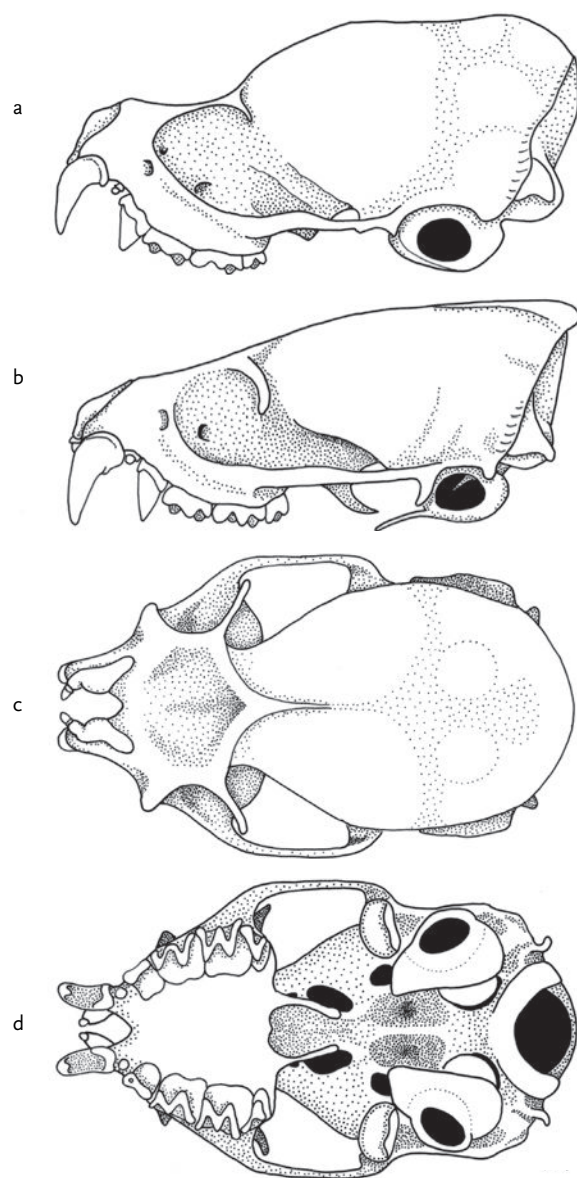


Figure 86. Craniodental characters of African bats in the family Emballonuridae. (a) Lateral view of skull showing strongly concave profile of forehead region (e.g. *Taphozous perforatus*, BMNH 3.12.8.24). (b) Lateral view of skull showing weakly concave profile of forehead region (e.g. *Taphozous nudiventris*, ZFMK 96.548). (c) Dorsal view of skull (e.g. *T. perforatus*). (d) Ventral view of skull (e.g. *T. perforatus*).

region (viewed laterally) can be strongly concave (Figure 86a) or very weakly concave (sometimes almost straight to very slightly convex) (Figure 86b). Supraorbital ridges are present. The sagittal crest is usually low but sometimes well developed. An occipital helmet is present in some species. The premaxillae are represented by nasal branches only; they are not fused with each other, not usually fused to other parts of skull, and do not meet dorsal to the nasal aperture. The palate has a very deep, wide, U-shaped or sometimes V-shaped anterior emargination (Figure 87). The tympanic bullae are either complete, or they are incomplete, i.e. having one or more lacunae (gaps or holes) in the inner face (Figure 88). Deep basisphenoid pits are present. For some species, the condylocanine length (CcL) of the skull is more useful diagnostically than the GLS: CcL = distance from the most posterior point of one exoccipital condyle to the front of the

canine on the same side (Figure 23). The dental formula is $^{1123}/_{3123} = 32$ or $^{1123}/_{2123} = 30$. The anterior upper premolar is very small; the posterior premolar is large and taller than the molars. The postcranial skeleton is, in general, primitive for microbats (Koopman 1994).

Emballonurids vary greatly in their wing morphology, flight and foraging strategies. The four African species for which data are available have medium to high aspect ratios and medium to extremely high wing-loadings and their flight is fast to very fast, and agile with poor manoeuvrability. They can take off from the ground but cannot hover.

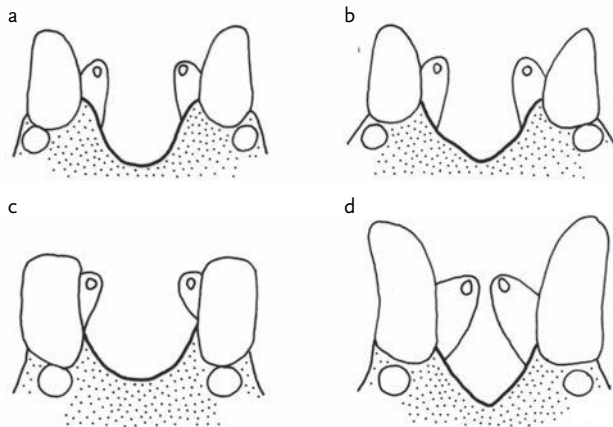


Figure 87. Variations in the shape of the anterior palatal emargination in African bats in the family Emballonuridae. (a) Comparatively wide and U-shaped (e.g. *Saccolaimus peli*). (b) Somewhat V-shaped (e.g. *S. peli*). (c) Comparatively wide and U-shaped (e.g. *Taphozous nudiventris*). (d) Comparatively narrow and more V-shaped (e.g. *T. perforatus*). Canine widths drawn to same size.

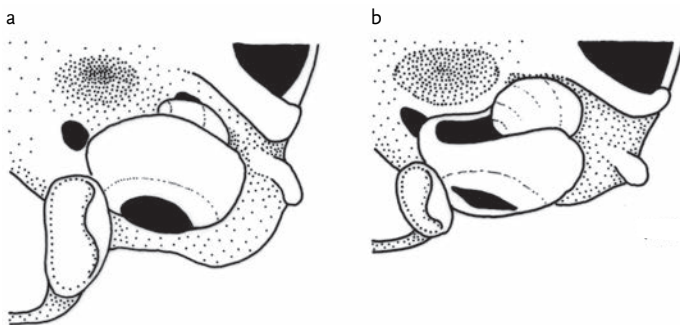


Figure 88. Differences in the auditory bullae of *Saccolaimus* and *Taphozous*. Each skull has been slightly rotated (right zygomatic arch lower than left) to expose the inner surface of the right bulla. The bullae are (a) complete in *Saccolaimus* and (b) incomplete in *Taphozous*.

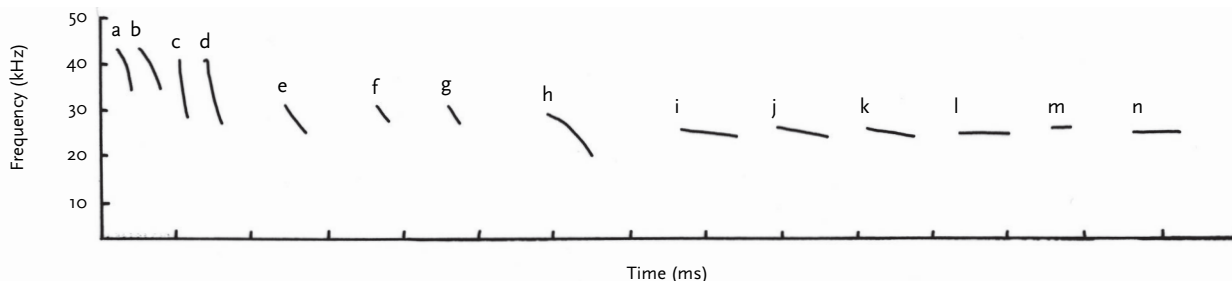


Figure 89. Sonograms of echolocation calls of an emballonurid (*Taphozous mauritanus*) showing the diversity of call-shapes associated with echolocation in different circumstances (M. Happold unpubl.). From left to right: calls (a) to (e), a sequence emitted as a bat was released and flew very close to the ground. Calls (f) and (g), two adjacent calls in a sequence emitted as this bat gained height. Call (h), one of a sequence emitted by a bat foraging in vicinity of trees and buildings. Calls (i) to (n), a sequence emitted by a bat foraging in open space, high above ground. Time axis marked at intervals of 10 ms.

The cost of flight is comparatively low, and they forage for long periods at a time in uncluttered open spaces, mainly high above the ground and trees, and they eat their prey while continuing to fly. They appear to be exclusively insectivorous. One African species, *Taphozous mauritanus*, has been recorded foraging up to 550 m above ground (Fenton & Griffin 1997). African emballonurids for which data are available echolocate with search-phase calls that are either multiharmonic CF calls, or shallow linear FM sweeps (Figure 89). In their wing morphology, flight and foraging, and also in some aspects of their echolocation calls, African emballonurids resemble free-tailed bats (*Tadarida*: Molossidae), probably as a result of convergent evolution.

Emballonurids are well adapted for cursorial locomotion. On vertical surfaces, *Taphozous* scuttle sideways like crabs, sometimes with incredible rapidity, and on horizontal surfaces they bounce forwards or sideways like clockwork toys, with the limbs in synchrony (no information for *Saccolaimus* and *Coleura*). During the day, African emballonurids roost in caves, rock crevices, mines, hollow trees and cavernous buildings and one species clings to shaded tree trunks and walls. They cling in contact, head facing down, to vertical or steeply sloping surfaces. Some species roost singly or in small groups; others in colonies of hundreds or thousands. None hibernates. The social and reproductive behaviour of two African species, *T. hildegardae* and *C. afra*, is well known (see profiles). African emballonurids invariably have one young/litter. The reproductive chronologies of African species include restricted seasonal monoestry (*T. hildegardae*, *T. nudiventris*) and bimodal polyoestry (*C. afra*, *T. mauritanus* and perhaps *T. perforatus*). Sperm storage with delayed fertilization has been documented for *T. nudiventris* in Iraq. Delayed implantation has been documented for *T. hildegardae*, and retarded embryonic development (under some circumstances) for *C. afra*. The reproductive biology of the other African species is poorly known.

The geological range of the family Emballonuridae is middle Eocene to early Miocene in Europe, early Miocene to Recent in Africa, Pliocene to Recent in Australia, Pleistocene to Recent in South America and Recent in other parts of the geographic range (Koopman 1984, Archer *et al.* 1991). Fossils from the late Eocene–early Oligocene of Europe are morphologically similar to species in the genera *Taphozous* and *Saccolaimus* (Barghoorn 1977 in Robbins & Sarich 1988).

Emballonurids are found mainly within the tropics, in both the Old and the New Worlds, including islands of the Indian and central Pacific oceans, the Malay archipelago and Australia. They have radiated into rainforests, open woodland savannas and more arid habitats. All of the seven African species occur in the tropics, but two extend northwards and one extends southwards into the temperate regions. Three are

found mainly in savannas, one in both forests and savannas, one in both savanna and arid habitats, one in rainforest, and one is found in all three habitats. No species appears to inhabit montane habitats. A preliminary survey suggests that there are few localities where more than one species has been recorded, but there are some localities where two species occur sympatrically, e.g. *S. peli* and *T. mauritanus* at Avakubi, DR Congo (Hayman *et al.* 1966) and Lagos, Nigeria (Happold 1987); *T. nudiventris* and *T. perforatus* at Luxor, Egypt (Gaisler *et al.* 1972). Three species occur sympatrically at Shimoni, Kenya (*C. afra*, *T. hildegardeae* and *T. mauritanus*). The radiation of emballonurids in Africa has not been as extensive as in South America where there are eight genera and 21 species (data from Simmons 2005).

Emballonurids are regarded as one of the most primitive groups of bats and have, in common with the Pteropodidae, well-developed eyes, long postorbital processes and unfused premaxillae. Cladistic analysis of morphological and molecular characters indicates that the Emballonuridae are a monophyletic family that is outside the clade containing all other microbats. For this reason, the family Emballonuridae is placed by itself in the superfamily Emballonuroidea (Simmons 1998, Simmons & Geisler 1998). Morphological characters analysed by Barghoorn (1977) and evidence from protein electrophoresis and immunology (Robbins & Sarich 1988) support the division of the family into two subfamilies: the Taphozoinae (with *Saccolaimus* and *Taphozous*) and the Emballonurinae (with *Coleura* and all other genera). The separation of *Taphozous* and *Saccolaimus* from the other

genera is supported by hyoid morphology (Griffiths & Smith 1991) and the morphometric analysis of Freeman & Leman (1991). Some taxonomists consider that two of the New World genera should be placed in a third subfamily (Corbet & Hill 1991, Freeman & Leman 1991, Jones & Hood 1993), but only two subfamilies are recognized by Simmons (2005). The subfamily Emballonurinae has been divided into two tribes by McKenna & Bell (1997) and Robbins & Sarich (1988), but the tribes (as defined by McKenna & Bell 1997) are possibly paraphyletic (Dunlop 1998 in Simmons 2005) and therefore no tribes are recognized by Simmons (2005) or here.

The three genera in Africa, and their distinguishing characters in Africa, are:

- Coleura*. FA: 44–53 mm; no radio-metacarpal pouch; tragus parallel-sided (Figure 85a); three lower incisors on each side. One species.
- Saccolaimus*. FA: 87–95 mm; no radio-metacarpal pouch; tragus not parallel-sided (Figure 85b); two lower incisors on each side. One species.
- Taphozous*. FA: 56–79 mm; radio-metacarpal pouch present; tragus not parallel-sided (Figure 85c–f); two lower incisors on each side. Five species.

The subfamilies and genera are presented alphabetically.

Meredith Happold

Subfamily EMBALLONURINAE – Sheath-tailed Bats, Sac-winged Bats, Ghost Bats and others

Emballonurinae Gervais, 1855. In: F. Comte de Castelnau, Exped. Partes Cen. Am. Sud., Zool. (Sec. 7), Vol. 1, pt 2 (Mammifères), p. 62 footnote.

This subfamily contains 11 extant genera of which one, *Coleura*, is represented by one species in Africa and another in the Seychelle Is. Of the ten other genera, seven occur mainly in Central and/or South America and the others are found mainly on the Malay Peninsula, the Malay Archipelago (including Philippines and New Guinea), Caroline

and Mariana Is., Solomon Is., Vanuatu, Fiji and Samoa. Two species of one genus, *Emballoneura*, occur on Madagascar. For further information, see Family Emballonuridae.

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GENUS *Coleura* African Sheath-tailed Bats

Coleura Peters, 1867. Monatsber. K. Preuss. Akad. Wiss. Berlin 1867: 479. Type species: *Emballonura afra* Peters, 1852.

Coleura is a polytypic genus with two species, one in Africa and Arabia, and one in the Seychelle Is. The latter has also been reported from Zanzibar I., but this record is extremely dubious (Koopman 1993). *Coleura* is distinguished from African members of the genera *Saccolaimus* and *Taphozous* by the following combination of characters: FA: 44–53 mm; no radio-metacarpal pouch; tragus parallel-sided; profile of forehead region of skull (viewed laterally) strongly concave; dental formula $\frac{1123}{3123} = 32$. Craniodental characters of *Coleura afra* are illustrated in Figure 90.

The only species in Africa is *Coleura afra*.

Meredith Happold *Coleura afra*.



Coleura afra AFRICAN SHEATH-TAILED BAT

Fr. Coléoure d'Afrique; Ger. Afrikanische Schiebeschwanz-Fledermaus

Coleura afra (Peters, 1852). Reise nach Mossambique, Säugeth., p. 51. Tete, Mozambique.

Taxonomy Originally *Emballonura afra*. Synonyms: *gallarum*, *kummeri*, *nilosa*. Subspecies: three of dubious validity. Chromosome number: not known.

Description Small microbat without noseleaf and with terminal portion of tail projecting freely from middle of dorsal surface of interfemoral membrane; smaller than any other African emballonurid (FA: 44–53 mm); three lower incisors on each side; tragus tall and almost parallel-sided; pelage covering all of body; dorsal pelage dark brown; wings brown. Sexes similar in colour; ♀♀ on average slightly larger than ♂♂. Pelage soft, dense; mid-dorsal hairs ca. 5–7 mm. Dorsal pelage medium to dark brown (not grizzled); hairs with paler base. Ventral pelage slightly paler. Head broad with pointed muzzle; sides of face appear swollen; nostrils protrude beyond lower jaw; prominence on lower lip not divided by median groove. Ears brown, subtriangular, tip rounded; antitragus shallow, long, almost reaching corner of mouth. Tragus tall, narrow, roughly parallel-sided with small lobule on posterior margin (Figure 85a). No gular pouch; no black beard. Wings long, narrow, translucent brown to blackish-brown; no radio-metacarpal pouch. Dorsal pelage extending over anterior quarter of interfemoral membrane. Calcars almost as long as tibiae.

Skull (Figure 90) small and delicate for an African emballonurid. Braincase ovoid, elevated above plane of rostrum so dorsal profile of skull (viewed laterally) is concave in forehead region. Postorbital process long, comparatively robust. Sagittal crest weak to well developed anteriorly, absent posteriorly; no occipital helmet. Six lower incisors (cf. four in *Saccolaimus* and *Taphozous*). Further anatomical information in Harrison & Bates (1991) and Dunlop (1997).

Geographic Variation The forms *nilosa* from N Sudan and *gallarum* from Somalia are smaller than *C. afra* from Mozambique, and the pelage is darker in the Nile Valley than in the arid regions to the east. Based on these observations, Koopman (1965, 1975) suggested that *gallarum* and *nilosa* might be subspecies of *C. afra*, but he indicated that the variation was apparently clinal and no subspecies are recognized by Koopman (1994) and Simmons (2005). See also Kock (1969a).

Similar Species Three other African emballonurids have pelage covering all of the body:

Taphozous mauritanus. Two lower incisors on each side. Prominence on lower lip divided by median groove. Wings whitish. Dorsal pelage grizzled. Ventral pelage white or stained yellowish.

Taphozous hildegardeae. Two lower incisors on each side. Prominence on lower lip divided by median groove. Wings mainly white but with brown pigmentation near body. Dorsal pelage pale brown. Throat with blackish beard (♂♂) or white (♀♀).

T. perforatus. Two lower incisors on each side. Prominence on lower lip divided by median groove. Wings white to pale brown. Ventral pelage pale grey, pale greyish-brown to dark greyish-brown; chin

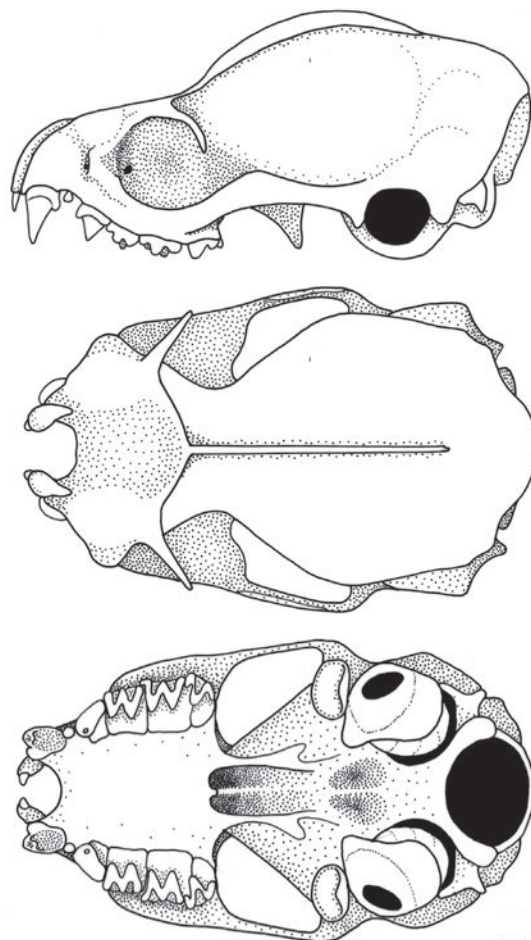
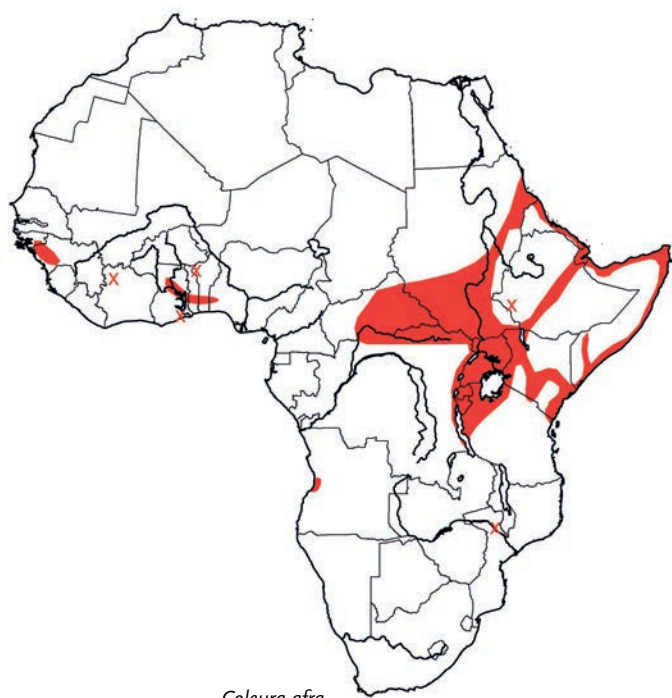


Figure 90. *Coleura afra*. Skull (lateral and dorsal views: BMNH 75.881; ventral view BMNH 15.1.18.3).

and throat usually darker. Adult ♂♂ and ♀♀ with a poorly-defined patch of longer darker hairs on the throat (perhaps not always present).

Distribution Mainly recorded from the Sahel Savanna, Sudan Savanna and Somalia–Masai Bushland and Coastal Forest Mosaic BZs and the Eastern Rainforest–Savanna Mosaic. Recorded from Central African Republic, Sudan, Ethiopia, Djibouti, Somalia, N and E DR Congo, Rwanda, Burundi and East Africa. There are also seemingly isolated populations in West Africa, mainly in the Guinea Savanna BZ and Northern Rainforest–Savanna Mosaic (Guinea-Bissau and Guinea, Côte d'Ivoire, Ghana to W Nigeria), and in the Zambezi Woodland BZ in Angola and Mozambique. Possibly occurs on Zanzibar I. (Kock 1969a): not mapped. A record from Pemba I. 'by Fischer' is rejected by Moreau & Pakenham (1940). Extralimittally: Arabia. Mapped mainly from Kock (1969a) and country checklists.

Habitat Coastal habitats from forests to arid steppes along the Red Sea and Indian Ocean in eastern Africa and the Atlantic in Angola,



Coleura afra

and inland habitats including woodland savannas, drier bushlands, thicket-scrubs and grassy steppes – usually near large lakes or large rivers. Caves, rocky outcrops or similar day-roosts required.

Abundance Common. Sometimes very abundant in vicinity of caves.

Adaptations Wing morphology and flight characteristics: no information. Locomotion over horizontal and sloping surfaces is very rapid, as in other emballonurids. By day, clings, head-down, to the walls of caves and cavities in rocky outcrops, deserted buildings and unused cellars (Rosevear 1965). Prefers dimly lit places (e.g. near entrances of caves). Roosts apart from other species, such as *Taphozous hildegardeae*, *Rhinopoma macinnesi*, *Asellia tridens*, *Triaenops afer* and *Hipposideros caffer*, that sometimes share the same caves.

Foraging and Food Forages by fast-hawking in open spaces. Near the Kenyan coast, feeds mainly on Coleoptera and Lepidoptera, lesser amounts of Hemiptera, Homoptera and Hymenoptera, and some Orthoptera, Isoptera, Neuroptera and Diptera (McWilliam 1987b). Feeds opportunistically on whatever insects are most abundant; consequently there are seasonal changes in diet.

Echolocation Echolocation calls were reported to be relatively long (>10 ms) shallow FM sweeps with the dominant harmonic ca. 28 kHz (Pye 1980, Neuweiler & Fenton 1988). Taylor *et al.* (2005), in Kenya, recorded QCF calls of three bats (one released in open habitat, one released in forest and one flying free), and found considerable variation between these individuals, and within single sequences emitted by each individual. Mean start-frequencies of the three bats, respectively: 32.2, 34.5, 35.3 kHz; mean end-frequencies: 30.7, 31.1, 33.1 kHz; mean peak-frequencies: 31.2 (30–34), 33.3 (30–36), 34.2 (31.5–36.4) kHz; mean call-durations: 7.7 (7.0–8.0), 3.8 (2.9–5.4), 10.7 (8.3–13.0) ms (n = 11, 25, 13 calls, respectively).

The second harmonic is dominant. The calls were often preceded by a short, ascending, vertical ‘spike’. The calls emitted by the bat released in open habitat had lower peak-frequencies and longer durations than those emitted by the bat released in forest.

Social and Reproductive Behaviour Well studied by McWilliam (1987b). Males defend individual feeding territories. Some (perhaps ♀♀) forage in groups. Roosts in very large groups (colonies); East African colonies sometimes exceed 50,000 individuals. During the cool dry season, colony members huddle in very large, homogeneous, mixed-sex aggregations; apparently to maximize thermoregulatory efficiency. In contrast, throughout most of the year, adult ♀♀ roost in discrete clusters together with their young. Adult ♂♂ compete for access to these clusters of ♀♀; usually each cluster has one ♂ but larger clusters may have a dominant ♂ and a satellite ♂ roosting on the periphery. Solitary ♂♂, and groups of bachelor ♂♂, roost at the periphery of the colony. The compositions of clusters of ♀♀ are stable, and their roost-fidelity is very high. Some young, especially ♀♀, remain in their natal clusters for at least a year and up to at least three years – this probably leads to the formation of clusters of related ♀♀. Clustering facilitates thermoregulation, and cluster-members take turns to roost in optimal positions. Competition by ♂♂ for access to clusters of ♀♀ peaks when the ♀♀ come synchronously into oestrus; synchrony favours mating access by the dominant ♂ in each cluster, and minimizes disturbance to the cluster by inter-male competition. This mating system is known as female-defence polygyny (Bradbury & Vehrencamp 1976), and is a type of harem mating system.

Reproduction and Population Structure Litter-size: one. At ca. 4° S (Diani Beach, coastal Kenya), where rainfall is bimodal (insects most abundant in the wet seasons, less abundant in the short dry season and scarce in the long dry season), the reproductive chronology is seasonal bimodal polyoestry without postpartum oestrus (McWilliam 1987b). Almost all ♀♀ give birth, in synchrony, at the beginning of the long wet season in early Apr, lactate through the wet season, and mate at the end of lactation. After this mating period, if the year is a good one, gestation proceeds in ca. 90% of cases, but foetal growth is slower and this gestation is ca. 122 days long – ca. eight days longer than the preceding gestation. In drought years, 40–60% ♀♀ terminate this pregnancy soon after conception. If gestation proceeds, the pregnant ♀♀ give birth in middle of the short wet season (mid-Nov), and lactation extends into the following dry season and is ca. two weeks shorter than the preceding lactation. Whether or not they are lactating, all adult ♀♀ come synchronously into oestrus and mate ca. 4 weeks after the mid-Nov births. Consequently, ♀♀ can be both pregnant and lactating during the short dry season, but insects are moderately abundant in this dry season. Perhaps unexpectedly, the smaller number of young born in the short wet season and suckled by their pregnant mothers throughout most of the short dry season have a better chance of survival than those born in the long wet season and weaned at the start of the long dry season. This reproductive strategy ensures that the most energetically expensive activities (spermatogenesis, competitive mating and lactation) occur when insects are most abundant. Furthermore, selection favours juvenile survival at the expense of female breeding success during the short wet season birth cycle, and vice versa for the other cycle. Also, the option to terminate the more stressful of the two possible pregnancies

when conditions are unfavourable, undoubtedly increases the life-time reproductive success of the ♀♀.

Predators, Parasites and Diseases Ectoparasites include a bug *Eothenes coleurae* (Hemiptera: Polytetidae); a flea *Chiropteropsylla brockmani* (Siphonaptera: Ischnopsyllidae); bat-flies *Penicillidia fulvida* (Diptera: Nycteribiidae), *Raymondia huberi*, *R. seminuda* (Diptera: Streblidae); a tick *Carios boueti* (Acari: Argasidae); and eight species of mites (Anciaux de Faveaux 1984).

Conservation IUCN Category: Least Concern.

Measurements

Coleura afra

FA: 48.3 (44–53) mm, n = 154

WS: n. d.

TL: 77.4 (70–92) mm, n = 19

T: 17.4 (10–24) mm, n = 115

E: 16.0 (11–19) mm, n = 120

Tr: 6 mm, n = 1

Tib: 18.2 (17–19) mm, n = 13

HF: 9.2 (8–11) mm, n = 114

WT: 8.3 (7–10) g, n = 3

GLS: 16.8 (15.7–18.1) mm, n = 28

GWS: 9.8 (8.9–10.4) mm, n = 58

C–M³: 6.9 (6.4–8.0) mm, n = 80

Throughout geographic range except for West Africa (BMNH and literature)

Key References Dunlop 1997; McWilliam 1987b.

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Subfamily TAPHOZOINAE – Pouched Bats and Tomb Bats

Taphozoinae Jerdon, 1867. Mammals of India, p. 30.

This subfamily contains four species of *Saccolaimus* and 14 species of *Taphozous*. The *Taphozous*–*Saccolaimus* group has been distinct at least since the Miocene (Robbins & Sarich 1988). See also Family Emballonuridae, Genus *Saccolaimus* and Genus *Taphozous*.

Meredith Happold

GENUS *Saccolaimus*

Pouched Bats

Saccolaimus Temminck, 1838. Tijdschr. Nat. Gesch. Physiol. 5: 14.



Saccolaimus peli.

Saccolaimus is a polytypic genus with four species: *S. peli* in Africa, *S. flaviventris* and *S. mixtus* in Australia and New Guinea only, and *S. saccolaimus*, which is widespread from Bangladesh, India and Sri Lanka through South-East Asia to the Philippines, Indonesia, New Guinea and Australia (Simmons 2005). The African species is distinguished from African species in other emballonurid genera by the following combination of characters: FA: 87–95 mm; no radio-metacarpal pouch, tragus not parallel-sided (Figure 85b); profile of forehead region of skull (viewed laterally) almost straight; tympanic bullae complete (Figure 88a); dental formula: $^{1123}/_{2123} = 30$. Other craniodental characters of the African *Saccolaimus* are illustrated in Figure 91.

Three species, including *S. peli*, are found mainly in tropical forests and woodlands. In contrast, one Australian species (*S. flaviventris*) occurs in almost all habitats from wet and dry sclerophyll forests and open woodlands to shrublands, grasslands and deserts, and extends from tropical to cool temperate regions (Churchill 1998). *Saccolaimus flaviventris* and *S. saccolaimus* (in Australia) are monotocous and seasonally monoestrous (Churchill 1998); the reproductive strategies of the other two species are not known.

The only species in Africa is *S. peli*.

Meredith Happold

***Saccolaimus peli* PEL'S POUCHED BAT (GIANT POUCHED BAT, BLACK-HAWK BAT)**

Fr. Saccolaime de Pel; Ger. Pels Taschenfledermaus

Saccolaimus peli (Temminck, 1853). Esquisses Zool. sur la Côte de Guinée, p. 82. Boutry River, Ghana.

Taxonomy Originally *Taphozous peli*. Synonyms: none. Chromosome number: not known.

Description Large to very large microbat without noseleaf and with terminal portion of tail projecting freely from middle of dorsal surface of interfemoral membrane; larger than any other African emballonurid (FA: 87–95 mm); two lower incisors on each side; pelage covering all of body except for a narrow band at the posterior of the rump; dorsal pelage usually dark chocolate brown to blackish; wings black; tympanic bullae complete. Males on average lighter and slightly smaller in body measurements than ♀♀. Pelage dense and silky or greasy; dorsal pelage extending laterally to the wing-membrane but posteriorly only to the level of the anus, leaving a narrow band naked; mid-dorsal hairs 6–7 mm. Dorsal pelage usually almost black with isolated pale-coloured hairs, some individuals

dark or reddish-brown, some with silvery-white frosting; hairs unicoloured or with white at tip. Ventral pelage somewhat paler, longer around chest. U-shaped gular pouch present in both sexes between chin and throat, opening anteriorly. Head moderately flat, subtriangular (viewed dorsally); no frontal depression between the eyes; muzzle conical, somewhat flattened, of naked appearance but actually covered with very short, thin hairs. Eyes very large for a microbat. Ears relatively short (26–28% of FA), thick and leathery, pointed; anterior margin almost straight with papillae inconspicuous or absent; posterior margin convex and almost reaching corner of mouth. Tragus broad and short, spatulate, with a pronounced constriction on posterior margin. Antitragus large. Wing and interfemoral membranes black, thick. No radio-metacarpal pouch. Thumb long and thick with a relatively weak claw.

Skull (Figure 91) very large and robust for an African microbat, and somewhat flattened. Profile of forehead region (viewed laterally) very weakly concave (almost straight). Dorsal profile of skull (viewed laterally) almost smoothly convex. Shield shallow but sharply angular. Postorbital processes thick, strongly curved downwards. Sagittal crest well developed; occipital helmet present. Anterior palatal emargination usually broad and U-shaped (occasionally more V-shaped – Figure 87a and b). Tympanic bullae complete (Figure 88a). Upper incisors simple and small. Anterior upper premolar very small, posterior premolar large and taller than the molars. Two lower incisors on each side.

Geographic Variation Apparently none.

Similar Species Only two other African emballonurids have a band of naked skin on the posterior of the rump adjacent to the interfemoral membrane:

Taphozous hamiltoni. Much smaller (FA: 61–71 mm; GLS: 20.9–25.5 mm).

T. nudiventris. Much smaller (FA: 67–79 mm; GLS: 23.2–28.5 mm). Naked area wider.

Distribution Endemic to Africa. Mainly found in the Rainforest BZ (Western, West Central, East Central and South Central Regions); marginally found in Eastern Rainforest–Savanna Mosaic, and one record in the Zambezian Woodland BZ. Known from more than 70 localities in Guinea (Ziama Forest, Diecké Forest; J. Fahr unpubl.), Liberia, Côte d'Ivoire, Ghana, Nigeria, Cameroon, Gabon, Equatorial Guinea, Congo, DR Congo, Uganda, Kenya and Angola. Conspicuously unrecorded from most of the central Congo Basin and it seems unlikely that this is solely a consequence of insufficient sampling in this region.

Habitat The only African emballonurid found mainly in the rainforest zone. Most of the known localities are in lowland, coastal or swamp forests. Also found in mangroves, montane forests, forest–

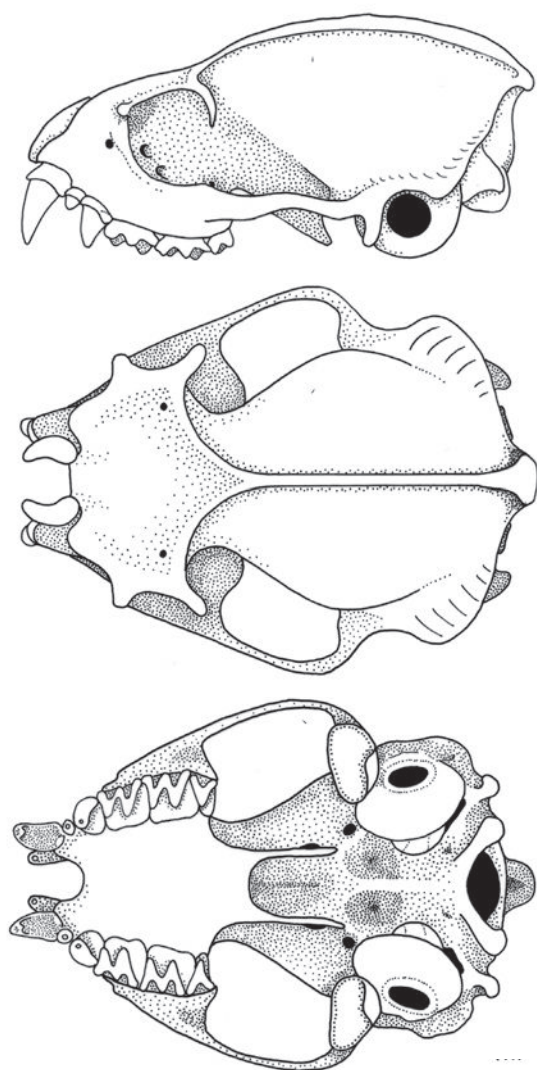


Figure 91. *Saccolaimus peli*. Skull (NMHN CG 1984-1274, BMNH 65.756).

*Saccolaimus peli*

savanna mosaic, and rarely in miombo woodland and *Isoberlinia* woodland. In the past, various authors stated that *S. peli* avoids the depths of undisturbed forest (e.g. Rosevear 1965, Happold 1987) but it seems more likely that this conclusion is a result of the difficulties associated with sampling high-flying bats in the rainforest zone. *Saccolaimus peli* extensively uses clearings in the forest – probably taking advantage of a higher insect-availability – but also forages above the canopy of closed forest (J. Fahr pers. obs.).

Abundance Widespread and locally common.

Adaptations Wings pointed and narrow; wingspan greater than in any other African microbat. Flies with strong, deliberate wing-strokes; sometimes glides between wing-beats; makes long, hawk-like swoops when pursuing prey. Eyes unusually large, suggesting that vision plays a more important role in orientation and/or capture of prey than in most other insectivorous bats. Roosts during the day in large, hollow trunks of trees and *Borassus* palms (Lang & Chapin 1917b, De Vree 1971, museum data). Clings to the walls of the roost in typical emballonurid fashion, with the belly flat against the surface and the head raised. Two ♂♂ were collected when emerging from a slit-like hole in the trunk of a silk cotton tree *Ceiba pentandra* ca. 27 m above the ground (Coe 1975). Not known to share day-roosts with other species of bats.

Foraging and Food Forages by fast-hawking in open spaces. Early in the evening, individuals are easily observed foraging 5–15 m above ground in forest clearings, above villages and along river valleys through forests; later at night they fly much higher and forage well above the canopy of closed forest (Lang & Chapin 1917b, J. Fahr pers. obs.). The reverse pattern, with high-level foraging at dusk and lower-level foraging later, has also been observed (Kingdon 1974, Coe 1975). Maximum foraging height above ground not known; it is certainly in the range of several dozen or possibly even hundreds

of metres (compare Fenton & Griffin 1997 for data on *Taphozous* sp.). Activity apparently not reduced by moonlight (Lang & Chapin 1917b). Brosset (1966) proposed that individuals do not have fixed home-ranges but forage opportunistically over large areas. Foraging seems to be very efficient – one specimen had its stomach gorged with small insects half an hour after arrival at the foraging area (Lang & Chapin 1917b). Diet largely unknown but small beetles and swarming termites have been documented (Kingdon 1974, USNM).

Echolocation Search-phase calls are multiharmonic, shallow linear FM sweeps. The lower frequencies of the calls are audible to the human ear and have been mistaken for social or contact calls (J. Fahr unpubl.).

Social and Reproductive Behaviour Usually forages in small groups (2–4), although sometimes singly or in aggregations of 12–30 individuals (Lang & Chapin 1917b, Kingdon 1974, J. Fahr pers. obs.). Two ♂♂ were found roosting in one hollow tree (Coe 1975); apparently nothing else is documented about the size and composition of groups that share day-roosts. Adult members of groups roost apart without huddling or forming clusters. Captive bats are not aggressive towards each other. Males scratch their gular pouch with the hindclaws and, in subsequent grooming, transfer the gular secretion to other parts of the body (Kingdon 1974). The yellow secretion was more copious in a ♂ with enlarged testes.

Reproduction and Population Structure Litter-size: one (n = 8). Reproductive chronology not known. North of the Equator in West Africa, pregnancies have been observed in Jul (n = 3) and Dec (n = 3) (USNM, J. Fahr unpubl.). Brosset (1966) reported a ♂ from Gabon (Makokou, 00° 34' N) that was sexually active in Aug (epididymis filled with spermatozooids), and Kingdon (1974) reported ♀♀ from Uganda (without specifying locality) that were just fertilized or had just copulated (uterus distended with semen) in Mar. However, the total number of bats examined during these months, and information for other months, is not available. In DR Congo, pregnant ♀♀ were observed in Jun and Dec (3 out of 10 adult ♀♀) (Lang & Chapin 1917b). Apparently there have been no year-round observations at any one locality and, although the data seem compatible with two seasons of parturition per year (as in some other emballonurids), there is as yet no evidence of polyoestry, and the data also fit alternative chronologies. Lengths of gestation and lactation not known.

Predators, Parasites and Diseases Ectoparasites include bat-flies *Brachytarsina alluaudi* (Diptera: Streblidae), *Basilia aequisetosa* (Diptera: Nycteribiidae) and mites *Carios vespertilionis* (Acari: Argasidae), *Ugandobia taphozous* (Acari: Myobiidae), *Olabidocarpus taphozous* (Acari: Chirodiscidae) and *Rodhainyssus taphozous* (Acari: Gastronyssidae) (Anciaux de Faveaux 1984).

Conservation IUCN Category: Least Concern.

Although mainly found in the rainforest zone, which is increasingly being degraded or destroyed, this species can cope with secondary forests and plantations and consequently is probably less adversely affected by deforestation than other rainforest bats. It has been observed in large numbers even where the surrounding area was heavily degraded (J. Fahr pers. obs.). Major threats: loss and fragmentation of habitat, and destruction of roosts.

Measurements*Saccolaimus peli*

FA (♂ ♂): 89.2 (87–90) mm, n = 6

FA (♀ ♀): 91.8 (88–95) mm, n = 8

WS (a): 685 mm, n = 1

TL (♂ ♂): 143.1 (132–161) mm, n = 21

TL (♀ ♀): 150.3 (138–165) mm, n = 24

T (♂ ♂): 32.7 (26–40) mm, n = 20

T (♀ ♀): 35.0 (27–42) mm, n = 24

E: 24.3 (22–27) mm, n = 42

Tr: 8.8 (6.8–10.0) mm, n = 6

Tib: 37, 37 mm, n = 2

HF: 24.4 (21–27) mm, n = 25

WT (♂ ♂): 88.6 (80–101) g, n = 12

WT (♀ ♀): 94.9 (77–114) g, n = 14

GLS: 29.5 (28.0–31.6) mm, n = 22

GWS: 21.5 (20.8–21.9) mm, n = 19

C–M³: 12.4 (11.9–13.5) mm, n = 23

Liberia, Côte d'Ivoire, Ghana, Nigeria, Cameroon, Gabon, Equatorial Guinea, DR Congo, Kenya (BMNH, FC, FMNH, RMCA, USNM)

Key References Brosset 1966; Kingdon 1974; Lang & Chapin 1917b.**Jakob Fahr****GENUS *Taphozous*****Tomb Bats***Taphozous* E. Geoffroy, 1818. Descript. de L'Egypte 2: 113. Type species: *Taphozous perforatus* E. Geoffroy, 1818.

A polytypic genus with 14 species found only in the Old World. Five species occur in Africa. Of these, two are endemic to Africa, one extends westwards from Africa to islands in the Gulf of Guinea and eastwards to islands in the Indian Ocean, and two extend from Africa across Arabia to NW India or Myanmar (Burma). The other eight species occur in the Oriental and Australasian Regions. *Taphozous* is considered the most highly evolved genus in the family. In Africa, members of this genus are distinguished from African species in other emballonurid genera by the following combination of characters: FA: 56–79 mm; radio-metacarpal pouch present, tragus not parallel-sided; profile of forehead region of skull (viewed laterally) either very weakly concave (almost straight) or strongly concave; tympanic bullae incomplete; dental formula: $^{1123}/_{2123} = 30$. The upper incisors are minute and often absent. Selected craniodental characters of two representatives of the genus are illustrated in Figure 86.

*Taphozous mauritanus*.**Table 17. Key to the African species in the genus *Taphozous*.**

| Pelage coverage
Profile of forehead region of skull | Colour of dorsal pelage | Colour of ventral pelage | Miscellaneous | Species |
|--|--|--|--|-----------------------|
| Rump and lower belly naked
Almost straight | Not grizzled
Dark sepia or rusty-brown | Belly brown
Throat brown | Condylocanine length 20–22 mm
Occipital helmet weakly developed
Naked area less extensive | <i>T. hamiltoni</i> |
| Rump and lower belly naked
Almost straight | Not grizzled
Sepia brown, dark
rusty-brown or
greyish-brown | Belly brown
Throat brown | Condylocanine length
23.0–25.2 mm
Occipital helmet well developed
Naked area more extensive | <i>T. nudiventris</i> |
| Body entirely covered by pelage
Strongly concave | Grizzled
Greyish (sometime
suffused with pale-
brown) | Belly pure white
(or stained yellowish)
Throat white | Very widespread
Roosts on tree trunks, rockfaces,
exterior walls of buildings | <i>T. mauritanus</i> |
| Body entirely covered by pelage
Strongly concave | Not grizzled
Pale greyish-brown | Belly pure white (or stained
yellowish-brown)
Throat black (♂ ♂) or white
(♀ ♀) | Kenya and Tanzania
Roosts in caves | <i>T. hildegardae</i> |
| Body entirely covered by pelage
Strongly concave | Not grizzled
Brown or greyish-brown | Belly pale grey to dark
greyish-brown
Throat usually sepia brown;
darker than belly | Very widespread
Roosts in caves, inside buildings,
in rock crevasses and similar
places | <i>T. perforatus</i> |

Species of *Taphozous* are called tomb bats because some of them often roost in cavernous buildings – including the tombs and temples of Ancient Egypt where they were first discovered – as well as in caves, rock crevices and mine-adits. There is also a tomb bat that roosts on shaded tree trunks and walls. Tomb bats often scuttle out of sight if disturbed, and some of those that roost in cave-like day-roosts sometimes scuttle short distances between their landing (and take-off) sites, and the crevices or other sites in which they roost. Tomb bats occur in most parts of Africa, in woodland savannas, in oases and riverine habitats in arid and desert regions, and marginally in the rainforests.

Two subgenera are recognized:

Taphozous. Body entirely covered by pelage; forehead with deep depression between the eyes; forehead region of skull (viewed laterally) strongly concave; no occipital helmet (Figure 86a). Three species in Africa: *T. hildegardae*, *T. mauritanus* and *T. perforatus*.

Liponycteris. Rump and lower belly naked; forehead without depression; forehead region of skull (viewed laterally) very weakly concave (almost straight); occipital helmet present (Figure 86b).

Two species in Africa: *T. hamiltoni*, *T. nudiventris*.

African species in the genus *Taphozous* can be distinguished by the characters given in Table 17. The species are presented in alphabetical order, irrespective of the subgenus to which they belong.

Meredith Happold

Taphozous hamiltoni HAMILTON'S TOMB BAT

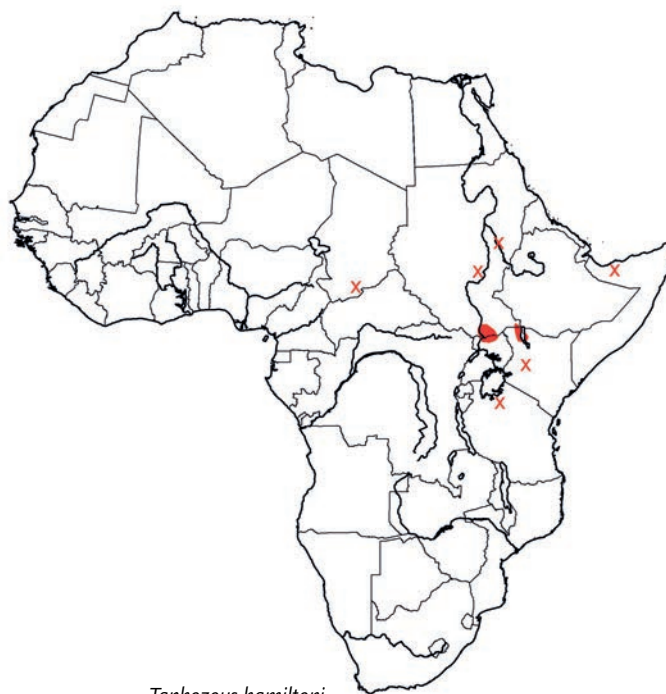
Fr. Taphien de Hamilton; Ger. Hamiltons Grabfledermaus

Taphozous hamiltoni Thomas, 1920. Ann. Mag. Nat. Hist., ser. 9, 5: 142. Mongalla, Equatoria, Sudan.

Taxonomy Synonyms: none. Formerly in subgenus *Taphozous*, but now considered a primitive species of the subgenus *Liponycteris* (Koopman 1975). Chromosome number: not known.

Description Medium-sized microbat without noseleaf and with terminal portion of tail projecting freely from middle of dorsal surface of interfemoral membrane; two lower incisors on each side; rump and lower belly naked; dorsal pelage dark brown; ventral pelage brown; wings dark brown; condylocanine length: 20–22 mm (cf. *Taphozous nudiventris*). Sexes similar. Pelage sleek; mid-dorsal hairs ca. 6 mm. Dorsal pelage uniformly dark sepia brown to dark rusty-brown (not grizzled); hairs unicoloured or with basal half much paler than terminal half. Rump and flanks naked with clear demarcation between furred and naked areas; naked area ca. 10–20 mm wide mid-dorsally. Ventral pelage paler than dorsal pelage; longer and paler on flanks than mid-ventrally; posterior quarter of ventral surface naked. Gular pouch well developed in both sexes; no black beard. Head moderately flat, subtriangular (viewed dorsally), with long pointed muzzle and a very shallow depression between the eyes. Lower lip with conspicuous grooved prominence. Eyes large for a microbat. Ears subtriangular, backward-pointing, with papillae along the lower inner margin. Tragus broad, axe-head-shaped with pronounced lobule at base of posterior margin; antitragus large, almost reaching corner of mouth. Wings and interfemoral membrane very dark brown; radio-metacarpal pouch present. Hindlimbs naked.

Skull very broad and heavily built for an African emballonurid. Frontal depression shallow. Dorsal profile of skull (viewed laterally) almost smoothly convex; profile of forehead region very weakly concave (almost straight). Postorbital processes long, slender, curved downwards behind orbit. Sagittal crest low; occipital helmet present but weakly developed. Anterior palatal emargination wide and U-shaped. Inner face of tympanic bulla incomplete. Condylocanine length: 20–22 mm.



Taphozous hamiltoni

Geographic Variation None recorded.

Similar Species Only two other African emballonurids have a band of naked skin on the posterior of the rump adjacent to the interfemoral membrane:

Taphozous nudiventris. Naked area usually more extensive. Gular pouch of ♀♀ less developed. Skull with occipital helmet well developed. Condylocanine length: 23.0–25.2 mm.

Saccolaimus peli. Much larger (FA: 87–95 mm, GLS: 28.0–31.6 mm).

Distribution Endemic to Africa. Known only from the Sudan Savanna and Somalia–Masai Bushland BZs. Recorded from Sudan (Koopman 1975), Uganda (BMNH) and Kenya (Kock 1981, BMNH), with isolated records from Sarh (Fort Archambault) in Chad (NMW), Lower Sheikh in Somalia (BMNH 34.9.14.5) and Shanwa in Tanzania (BMNH 21.1.1.14).

Habitat Very poorly known except for the general vegetation zones from which specimens have been collected. These include undifferentiated woodland in Chad, *Acacia* wooded grassland and deciduous bushland near the Blue Nile R. at Sennar, Sudan and *Acacia*–*Commiphora* deciduous bushland and thicket, and semi-desert grassland and shrubland, in the vicinity of L. Turkana, Kenya (terminology: White 1983).

Abundance Not known. Very poorly represented in collections.

Remarks One specimen was ‘found in cracks among rocks’ where the species was reported ‘common’ (BMNH 36.11.4.8 from Lodwar, Turkwell R., Kenya). No other information.

Conservation IUCN Category: Data Deficient.

There are very few records and significant loss of habitat is predicted in the near future, mainly because of farming. Population trend: not known.

Measurements

Taphozous hamiltoni

FA: 65.5 (61–71) mm, n = 20

WS (d): 379 (369–405) mm, n = 4

TL: 104.2 (100–119) mm, n = 11

T: 25.1 (20–35) mm, n = 9

E: 19 (15–22) mm, n = 8

Tr: 7 mm, n = 1

Tib: 25, 26 mm, n = 2

HF: 15 (15–15) mm, n = 3

WT: 19.4, 22 g, n = 2

GLS: 23.5 (20.9–25.5) mm, n = 12

GWS: 14.8 (13.1–16.4) mm, n = 12

C–M³: 9.7 (8.8–10.6) mm, n = 18

Throughout geographic range (BMNH, NMK, NMW and literature)

Key References Kock 1981; Koopman 1975.

Meredith Happold

Taphozous hildegardeae HILDEGARDE’S TOMB BAT

Fr. Taphien de Hildegarde; Ger. Hildegardes Grabfledermaus

Taphozous hildegardeae Thomas, 1909. Ann. Mag. Nat. Hist., ser. 8, 4: 98. Rabai (near Mombasa, Coast Province, Kenya).

Taxonomy Subgenus *Taphozous*. Synonyms: currently none. Subspecies: none currently recognized but the taxonomic status of a population that migrates annually into SE Kenya requires elucidation (see Geographic Variation). Chromosome number: not known.

Description Medium-sized microbat without noseleaf and with terminal portion of tail projecting freely from middle of dorsal surface of interfemoral membrane; two lower incisors on each side; pelage covering all of body; dorsal pelage pale brown; ventral pelage white; wings mainly white; no gular pouch; adult ♂♂ with blackish throat-patch. Sexes similar in appearance (except for ventral pelage); skulls of ♂♂ reported to be ‘distinctly larger’ than those of ♀♀ (Thomas 1915a) but this needs confirmation. Pelage dense, covering all of body; mid-dorsal hairs 7–9 mm. Dorsal pelage uniformly pale greyish-brown (not grizzled); hairs with white base and brown tip. Ventral pelage of ♀♀ pure white. Adult ♂♂ with a prominent blackish throat-patch or ‘beard’ over a glandular area on the throat; glandular secretions frequently stain the white ventral pelage yellowish-brown. No gular pouch in either sex. Head subtriangular (viewed dorsally) with long pointed muzzle and deep depression between the eyes. Lower lip with conspicuous grooved prominence. Eyes comparatively large for a microbat. Ears subtriangular, backward-pointing, with small papillae along inner margin. Tragus roughly axe-head-shaped with weakly developed lobule at base of posterior margin (Figure 85c). Wings long and narrow, pale with brown pigmentation close to body on dorsal side; radio-metacarpal pouch present in both sexes.

Skull small for an African emballonurid. Frontal depression deep. Dorsal profile of forehead region of skull (viewed laterally) strongly concave. Postorbital processes long and slender. Sagittal crest absent; lambdoid crests low; occipital helmet absent. Anterior palatal emargination wide and U-shaped. Inner face of tympanic bulla incomplete. Two lower incisors on each side.

Geographic Variation Uncertain. A taxonomically distinguishable population immigrates annually (in Nov) to a coastal cave in SE Kenya (in which it establishes a maternity colony), and emigrates in May for an unknown destination (A. N. McWilliam unpubl.). These bats (several hundred adult ♀♀ and a few adult ♂♂) are larger than the non-migrating resident population (FA: 68.2 [67–71] mm, cf. 65.1 [61–67] mm), are heavier with darker dorsal pelage, and the ♂♂ lack yellow tinges on the chest and abdomen. The distribution and taxonomic status of this population (possibly a sibling species) need further investigation.

Similar Species Three other African emballonurids have pelage covering all of the body:

Taphozous mauritanus. Dorsal pelage grizzled; belly and throat pure white (sometimes stained yellowish); no blackish beard.

T. perforatus. Dorsal pelage uniformly dark chocolate brown, sepia brown, greyish-brown or ashy-brown. Belly pale grey, pale greyish-brown to dark greyish-brown; chin and throat usually

*Taphozous hildegardeae*

darker. Adult ♂♂ and ♀♀ with poorly defined patch of longer, darker hairs on the throat (perhaps not always present).

Coleura afra. Three lower incisors on each side. Prominence on lower lip not divided by median groove. FA: 44–53 mm. Wings brown to blackish-brown. Ventral pelage brown.

Distribution Probably restricted to the Coastal Forest Mosaic BZ along the coasts of Kenya and Tanzania (Thomas 1909, Kulzer 1959, Kock 1974a, McWilliam 1982, 1988a, Aggundey & Schlitter 1984, Cockle *et al.* 1998; localities listed by Colket & Wilson 1998). Reported on Zanzibar I. by Kingdon (1974) but not recorded there by Moreau & Pakenham (1940) or Pakenham (1984). Also recorded from two inland localities in Kenya (Harrison 1960; specimens in NMK) but, because these are the only inland records and occur within geographic range and habitat of *T. perforatus*, the identity of the relevant specimens needs confirmation (Kock 1974a). Alternatively, these specimens perhaps represent the migratory population of uncertain taxonomic status (see Geographic Variation); these localities are mapped as question marks.

Habitat Recorded in vicinity of coral-caves in remnant coastal forests, but probably forages in adjacent scrublands and plantations near these caves.

Abundance Populations in caves are encountered infrequently. Populations in two large Kenyan coral-cave systems were estimated at ca. 1000 and 2000 bats (McWilliam 1980), although a viable breeding population in a smaller cave fluctuated between 200 and 400 bats (McWilliam 1982).

Adaptations Aspect ratio not known; wing-loading medium (dry season) to very high (wet season); flight fast and agile; manoeuvrability poor; hovering impossible; can take off from ground with difficulty but, when inside caves, scuttles over floors and climbs walls instead

of attempting to take off from the ground. In vicinity of coast, roosts by day in caves in a narrow band of uplifted Pleistocene coral reef that extends along the East African coast. Prefers to roost in darker recesses of more open chambers. Roosts apart from other species but, in larger cave systems, sometimes roosts adjacent to colonies of *Coleura afra* and *Miniopterus minor*. In smaller caves, very occasionally roosts adjacent to colonies of *Cardioderma cor.* The large, darker chambers of these coral-caves are occupied by *Hipposideros (gigas and/or vittatus)* and *Rousettus aegyptiacus*, and the narrower, deeper recesses by *Trienops afer*, *Hipposideros caffer* and *Rhinolophus landeri* (A. N. McWilliam pers. obs.). Although local movements of banded *T. hildegardeae* were recorded by McWilliam (1982), with the exception of the taxonomically distinguishable immigrant population, this species was resident year round and there were no differences between adult ♂♂ and ♀♀ in the distribution of recaptures between seasons. Does not enter pronounced torpor but, during the cold dry season, solitary ♂♂ were noticeably colder to touch and inactive.

Foraging and Food Limited observations, in degraded forest surrounding a cave used as a day-roost, suggest that foraging is by fast-hawking above treetops or in open spaces, at high levels, between well-spaced trees (A. N. McWilliam pers. obs.). However, foraging locations and behaviour remain poorly known. Although these bats forage throughout the night, their caves also function as night-roosts and ♂♂, in particular, return to diurnal territories (see below). As many as a quarter of the diurnal population can be present during what appears to be a main rest from foraging during the middle of the night. Prey consists mainly of Lepidoptera and Orthoptera, with traces of Homoptera, Coleoptera and Hymenoptera. However, there are seasonal differences and Lepidoptera comprise the major part of the diet during both of the annual wet seasons. Analysis of faecal pellets revealed that, during the wet seasons, 52% of the pellets contained only Lepidoptera, 19% contained only Orthoptera and 29% contained both Lepidoptera and Orthoptera ($n = 165$ pellets). In contrast, during the dry season, 26% of the pellets contained only Lepidoptera, 22% contained only Orthoptera, and 52% contained both Lepidoptera and Orthoptera ($n = 153$; A. N. McWilliam unpubl.). Insects are most abundant during the two periods of peak rainfall (Oct–Dec and Apr–Jun), and ♂♂ accumulate substantial deposits of fat at these times (ca. 30% of body weight between Apr–Jul). These reserves of energy are depleted during competitive mating and the dry seasons when insects are comparatively scarce. With the exception of pregnancy, the weight cycles of ♀♀ are less pronounced than those of ♂♂ because of the energy demands associated with lactation, which normally lasts from Dec to beginning of May. Insects first appear in the diet of juveniles in Mar.

Echolocation No information.

Social and Reproductive Behaviour Roosts in very large groups (colonies) of 100–2000 individuals of both sexes. A study of behaviour and social structure at a day-roost revealed that this species has a polygynous mating system based on the monopolization of favoured roosting sites and also of ♀♀ by successful ♂♂ (McWilliam 1982, 1988a). Consequently, the colony dispersion-pattern is highly structured, with separate areas used as crèches for young bats and roost-sites for ‘bachelor’ ♂♂. The most protected and favoured

sites are retained year round as territories by successful ♂♂, which they mark with scents from glands under their beards, and from the anogenital region. Other ♂♂ are repelled by wing-flicks, 'tcheek tcheek' vocalizations, scent-marking, visual displays, posture changes and attacks with extended forearm and claw. Territorial activities increase during Apr–Jun (including the scent-marking of ♀♀ prior to mating in late Jul), and again during Oct–Dec after the long dry season (for concomitant reproductive data, see below). Most harem ♂♂ roost year-round with up to seven adult ♀♀, although some form multimale groups (including up to four 'satellite' ♂♂) with between 7 and 15 ♀♀. Harems appear generally stable in composition, and there is no consistent segregation of the sexes during parturition and early lactation. Active 'herding' of ♀♀ and young into compact groups, involving forearm attacks and nipping, was a behaviour only carried out by those ♂♂ associated with large clusters of ♀♀, and therefore was more commonly observed in multimale groups. However, some ♀♀ (possibly from smaller territories) move to maternity groups in a warmer outer chamber about a fortnight after parturition while still carrying their young. A second similar move, probably also temperature-induced, occurs at the end of the cold dry season in Sep when rapid growth of foetuses is initiated.

Reproduction and Population Structure Litter-size: one. At ca. 4°S (coastal Kenya), the reproductive chronology is restricted seasonal monoestry with copulation and ovulation (from right ovary) when rainfall is lowest (late Jul to early Aug); gestation normally ca. 140 days; and parturition during the second wet-season (mid- to late Dec). A pronounced delay in the timing of parturition (some still pregnant late Jan to early Feb), following a severe dry season when body condition in ♀♀ was very poor, was linked to a delay in implantation of the blastocyst of some 49 days. Unusually for a mammal, the diapause occurred in the oviduct, where histology showed morulae at the same stage in late Aug and mid-Oct (McWilliam 1982). Testicular regeneration occurs during both wet seasons; weight increase of testes in Apr–Jun and peak

epididymal weights in Jul culminated in copulation; in contrast, the increase in Oct–Dec did not result in reproduction but suggests that *T. hildegardae* was polyoestrous in the past (McWilliam 1988a). Possibly, the maintenance of year-round harems is also linked to vestigial polyoestry. The present monoestrous strategy ensures that both spermatogenesis in the ♂♂, and late-pregnancy and lactation in the ♀♀, coincide with peaks in abundance of insects.

Predators, Parasites and Diseases Ectoparasites include a bed-bug *Loxaspis miranda* (Hemiptera: Cimicidae) and a bat-fly *Brachytarsina alluaudi* (Diptera: Streblidae) (Anciaux de Faveaux 1984).

Conservation IUCN Category: Vulnerable.

Has a very small geographic range and is threatened by destruction of habitat along the coastal strip and other human activities, including tourism, recreation and disturbing colonies within coastal caves.

Measurements

Taphozous hildegardae

FA: 65.1 (63–68) mm, n = 9

WS: n. d.

TL: 105.9 (101–113) mm, n = 9

T: 24.9 (20–29) mm, n = 9

E: 20.0 (18–22) mm, n = 9

Tr: 6.2 (5–8) mm, n = 4

Tib: 23.8 (23–25) mm, n = 4

HF: 12.4 (11–14) mm, n = 10

GLS: 19.8 (19.4–21.0) mm, n = 8

GWS: 12.6 (12.3–12.7) mm, n = 8

C–M³: 8.8 (8.7–9.0) mm, n = 4

Kenya (BMNH, HZM, ROM)

Key References Colket & Wilson 1998; McWilliam 1988a.

Andrew McWilliam & Meredith Happold

Taphozous mauritanus MAURITIAN TOMB BAT

Fr. Taphien de Maurice; Ger. Mauritius-Grabfledermaus

Taphozous mauritanus E. Geoffroy, 1818. Descrip. de L'Egypte 2: 127. Mauritius (Indian Ocean).

Taxonomy Subgenus *Taphozous*. Synonyms: *cinerascens*, *dobsoni*, *leucopterus*. Subspecies: none currently recognized. Chromosome number (South Africa): 2n = 42; aFN = 64 (Rautenbach *et al.* 1993).

Description Medium-sized microbat without noseleaf and with terminal portion of tail projecting freely from middle of dorsal surface of interfemoral membrane; two lower incisors on each side; pelage covering all of body; dorsal pelage grizzled, ventral pelage white; wings white. Sexes similar in colour and size. Pelage sleek, soft and dense, covering all parts of body; mid-dorsal hairs 5–7 mm. Dorsal pelage grizzled dark and pale grey, suffused with pale-brown (fawn) in some individuals, which can make the grizzling indistinct; hairs pale grey or pale greyish-brown at base with band of dark grey across terminal half and pale grey tip. Ventral pelage pure white (sometimes stained yellow). Gular pouch present in ♂♂, present or

absent in ♀♀. No black beard. Head moderately flat, subtriangular (viewed dorsally) with a long, pointed muzzle and a deep depression between the eyes. Lower lip with conspicuous grooved prominence. Eyes comparatively large. Ears subtriangular, backward-pointing, with no papillae on inner margins; antitragus long, shallow, almost reaching corner of mouth. Tragus very broad with terminal half subrectangular and a small lobule at base of posterior margin (Figure 85d). Wings long and narrow; wing-membranes translucent and white with some colourless areas; radio-metacarpal pouch present in both sexes.

Skull small to medium-sized for an African emballonurid. Frontal depression deep. Profile of forehead region of skull (viewed laterally) strongly concave. Postorbital processes long and slender. Sagittal crest usually absent, sometimes poorly developed; no occipital helmet. Anterior palatal emargination U-shaped. Inner face of

tympanic bulla incomplete. Upper incisors minute and sometimes absent. Two lower incisors on each side.

Geographic Variation Uncertain. There appears to be some geographical variation in size (Dengis 1996), but this needs confirmation.

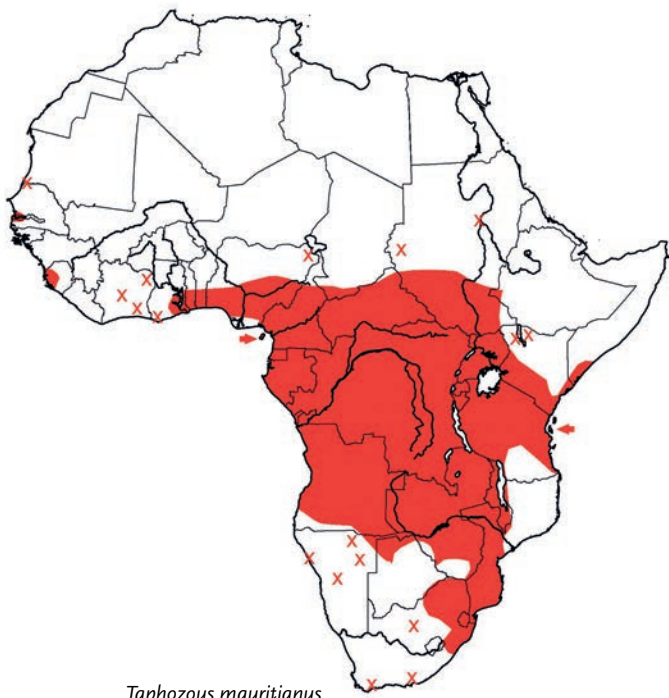
Similar Species Three other African emballonurids have pelage covering all of the body:

Taphozous hildegardeae. Dorsal pelage uniformly pale greyish-brown (not grizzled). Adult ♂♂ with blackish 'beard' on throat, ventral pelage white stained yellowish-brown.

T. perforatus. Dorsal pelage uniformly dark chocolate brown, sepia brown, greyish-brown or ashy-brown (not grizzled). Belly pale grey, pale greyish-brown to dark greyish-brown; chin and throat usually darker. Adult ♂♂ and ♀♀ with poorly defined patch of longer, darker hairs on the throat (perhaps not always present).

Coleura afra. Three lower incisors on each side. Prominence on lower lip not divided by median groove. FA: 44–53 mm. Wings brown to blackish-brown. Ventral pelage brown.

Distribution In Africa, very widely but patchily distributed, mainly in the Guinea Savanna BZ, Rainforest–Savanna Mosaics, Rainforest BZ, southern part of Somalia–Masai Bushland BZ, Coastal Forest Mosaic BZ, Zambezan Woodland BZ and South-West Cape BZ; also a few records in the Sudan Savanna and Sahel Savanna BZs. Distributed from Senegal to Somalia (but not recorded from all countries) and extending southwards to Namibia on the western side of the continent, and to the Cape Province of South Africa on the eastern and southern sides. Extraliminally: islands in Gulf of Guinea (Annobón, São Tomé and Príncipe), and islands of Indian Ocean (Madagascar, Mauritius, Réunion, Aldabra and Assumption). Mapped from country checklists (see order Chiroptera), other literature and museum records.



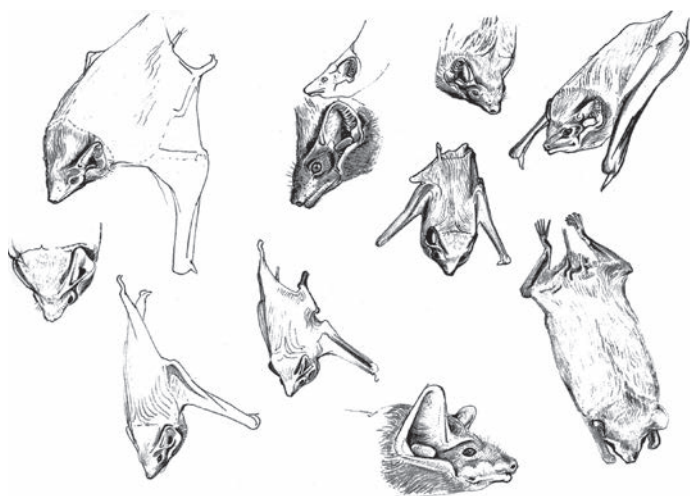
Taphozous mauritanus

Habitat Woodland savannas and large open areas within rainforests (e.g. Lang & Chapin 1917b), and scattered localities in the Sahel Savanna BZ. Distribution correlates with areas receiving at least 500 mm annual rainfall or, in drier areas, near rivers or swamps (Dengis 1996). Apparently avoids dense forests (e.g. Malbrant & Maclatchy 1949) and montane habitats. Distribution is patchy throughout most of geographic range; records especially sparse around periphery of range. Exploits suburban environments in KwaZulu–Natal (Taylor, P. 1998). Has a wider distribution, and appears to have a wider habitat tolerance, than any other African emballonurid, but its habitat requirements need further investigation.

Abundance Uncertain. Moderately common in collections but population numbers appear low throughout much of its geographic range (see Adaptations). Reported 'very numerous' in the bushveld region north of NE DR Congo (Lang & Chapin 1917b) but no recent reports are available.

Adaptations Aspect ratio medium; wing-loading medium; wing-tip pointed. Flight fast and very agile, manoeuvrability poor, hovering impossible. Usually turns by banking with minimum radius of turn usually >50 cm; stall-and-twist turns possible but rare; able to fly across a 1×1×1 m enclosure, but a complete circuit was observed only once (4 bats, 10 flights each, M. Happold unpubl.). Although able to take off from ground, prefers to dive to gain initial speed for flight and roost sites are selected accordingly. Whirring sound made during flight – perhaps caused by vibration of radio-metacarpal pouch (Lang & Chapin 1917b). By day, clings to tree trunks, rockfaces and exterior walls of buildings, two or more metres above ground, where overhanging branches, rocks or eaves create shade. Often roosts on or near buildings occupied by humans; surprisingly tolerant of humans provided they ignore the bats and do not come too close. Holds on with hindfeet and thumbs; head facing downwards but raised, chest seldom in contact; grizzled pelage provides camouflage on some natural surfaces. Reported to roost with *Coleura afra* in coastal caves (Kingdon 1974) but this observation almost certainly refers to *T. hildegardeae* (see profile); apparently there are no other published records of cave-roosting in *T. mauritanus*. Individuals return to the same roosts each day, and these sites become stained (? urine and/or glandular secretions). In wet weather, they move temporarily leeward and, if possible, shelter under branches, leaves or eaves. In Malawi, does not become torpid (even at 21 °C); instead, remains vigilant using the eyes and seldom echolocating. If large birds fly overhead, or if humans come too close, moves out of sight by scuttling sideways around corners or under branches and eaves at great speed. Only flies to nearby sites if danger comes very close. The importance of constant daytime vigilance to avoid predators, and the concomitant need to avoid torpor, probably limits this species to warm environments. Three captive bats, eating winged termites and seldom flying, did not drink (Happold & Happold 1988). Kidneys well adapted for conservation of water; predicted mean maximum urine concentration is comparatively high (3921 mOsmol/kg) (Happold & Happold 1988). Perceives surroundings during day mainly visually (even in flight), but echolocates at night.

Foraging and Food Forages mainly by fast-hawking in open spaces (Fenton *et al.* 1980, M. Happold unpubl.); wing morphology



Taphozous mauritanus.

and echolocation are primarily adapted for this. However, also forages by chasing insects over walls (Grubb *et al.* 1998), and by taking off and catching butterflies passing their roosts during the day (D. Rushworth in Smithers 1983). Fast-hawking occurs above treetops, between well-spaced trees, over clearings, along cliff-faces and over rivers (5–40 m above the water) (Smithers 1971, Fenton *et al.* 1980, M. Happold unpubl.). Sometimes forages up to 550 m above ground (Fenton & Griffin 1997). Kingdon (1974) reports three hours of intensive activity beginning after dark, followed by long rests (at favoured night roosts) interspersed with short flights. However, foraging sometimes begins at sunset (M. Happold unpubl.). Foraging is characterized by steep dives, up to 10 m, assumed to be pursuits of moths diving evasively in response to the bat's echolocation calls (Fenton *et al.* 1980). Feeds mainly on moths (based on stomach contents examined by Lang & Chapin 1917b), but captive bats also eat beetles, winged termites, flies and many other insects, suggesting that opportunistic feeding would occur if moths were comparatively scarce.

Echolocation In Zimbabwe, one foraging bat emitted multiharmonic CF search-phase calls (second harmonic ca. 25 kHz) followed by shorter, multiharmonic shallow linear FM approach-phase calls and then even shorter, angular shallow/steep FM terminal-phase calls. There were four harmonics – the second was dominant but the first and third contained appreciable energy, especially in the approach- and terminal-phases, and therefore these calls are audible to humans (Fenton *et al.* 1980). Search-phase call-shape (Malawi): typically short, multiharmonic CF or very shallow linear FM; intensity high; bandwidth 0–2 kHz; start-frequency 26–29 kHz (second harmonic); end-frequency 24–27 kHz; call-duration 5–13 ms (five bats foraging or flying in open, 50 calls; M. Happold unpubl.) (Figure 89). While orientating in clutter (near ground, trees, buildings), the calls are steep quasi-linear FM sweeps falling from ca. 30 to 24 kHz (second harmonic); mean duration 2.3–3.9 ms; call repetition-rate 10–27 calls/sec. As bats gain height, calls become narrower in bandwidth, longer in duration and sequences may contain some angular shallow/steep FM sweeps (M. Happold unpubl.). See Taylor (1999a) for data from South Africa and Swaziland.

Social and Reproductive Behaviour Roosts singly (? adult ♂♂ only) or in groups typically of 2–6 (but up to 12) of mixed composition, apparently including several adult ♂♂ and ♀♀ (with or without unweaned juveniles or subadults), but group composition and distance between neighbouring groups need further investigation. Group-members (except ♀♀ with young) roost at least 10 cm apart, and up to several metres apart. They make brief contacts, including climbing-over, but then immediately move apart. Vocalizations include (a) single loud 'ping' emitted in contexts of threat and/or alarm to repel conspecifics that come too close, (b) a three-syllable call emitted at 2–3 second intervals when a group-member returns to the roost area, (c) 'twittering' emitted by mothers and young (sustained if they are kept apart) and (d) several other vocalizations of unknown meaning (Happold *et al.* 1987). Individuals sometimes pursue each other in flight, and fight on the roosts, and they screech in these contexts (Lang & Chapin 1917b). Mating system not known, but fragmentary evidence suggests territoriality with defence of foraging areas, day-roosts and perhaps ♀♀, but the possibility that this indicates resource-defence polygyny and/or female-defence polygyny needs confirmation. Resource-defence polygyny is exemplified by the South American emballonurid *Saccopteryx bilineata* (Bradbury & Vehrencamp 1977). Female *T. mauritanus* fly with their young attached to their underparts until the young are volant (D. Rushworth in Smithers 1971). Juveniles often roost on their mothers' backs.

Reproduction and Population Structure Litter-size: one. Reproductive chronology probably bimodal polyoestry throughout geographic range. At ca. 4°N (DR Congo), limited data (Lang & Chapin 1917b, Verschuren 1957) suggest bimodal polyoestry with births ca. Nov–Dec and ca. Apr–May (perhaps less synchronized than in Kenya and Malawi). No conclusive data for more northern latitudes. At ca. 02°18'S (Masalani, near Kibwezi, Kenya), births occur in Nov (peak of main wet season) and Mar–Apr (little wet season) (O'Shea & Vaughan 1980): polyoestry probable but not confirmed at this locality. At ca. 15°S (Liwonde N. P., Malawi), ♀♀ bimodally polyoestrous with births in early wet season (Nov–Dec) and end of wet season (Mar–Apr) (Happold & Happold 1990a). At ca. 30°S (Durban area, South Africa), ♀♀ are polyoestrous with births in Oct–Dec and Feb or Mar (F. Mackenzie in Taylor, P. 1998). Happold & Happold (1990a) did not state that *T. mauritanus* may be monoestrous in some regions of Africa (as erroneously reported by Dengis 1996); monoestry has not been confirmed in this species.

Predators, Parasites and Diseases Predators include owls (Demeter 1981, Taylor, P. 1998). Roosting behaviour implies danger of predation by hawks, other raptors, snakes and perhaps genets *Genetta* spp. Ectoparasites include bat-flies *Basilia blainvillii*, *Phthiridium integrum* (Diptera: Nycteribiidae) and a mite *Olabidocarpus taphozous* (Acari: Chirodiscidae) (Aellen 1952, Anciaux de Faveaux 1984).

Conservation IUCN Category: Least Concern.

Measurements

Taphozous mauritanus

FA: 61.4 (58–65) mm, n = 103

WS (a): 420.8 (409–443) mm, n = 5*

TL: 105 (91–116) mm, n = 55
 T: 22.5 (15–28) mm, n = 55
 E: 17.6 (13–22) mm, n = 63
 Tr: 6.1 (5–7) mm, n = 7
 Tib: 24.8 (19–27) mm, n = 19
 HF: 13.4 (11–18) mm, n = 93
 WT: 26.4 (20–36) g, n = 39
 GLS: 21.0 (19.5–22.5) mm, n = 27
 GWS: 12.9 (12.2–13.4) mm, n = 19

C–M³: 8.8 (7.7–9.4) mm, n = 25

Throughout geographic range except West Africa (SMNS, ZFMK and literature)

*Malawi only

Key References Dengis 1996; Fenton *et al.* 1980; Smithers, 1971, 1983.

Meredith Happold

Taphozous nudiventris NAKED-RUMPED TOMB BAT

Fr. Taphien à ventre nu; Ger. Nacktbauch-Grabfledermaus

Taphozous nudiventris Cretzschmar, 1830. In: Rüppell, Atlas Reise Nordl. Afr., Zool. Säugeth., p. 70. Giza, Egypt.

Taxonomy Subgenus *Liponycteris*. Synonyms (Africa only): *assabensis*, possibly *serratus*. Subspecies: five; one in Africa. Chromosome number (Egypt): 2n = 42; aFN = 64 (Hood & Baker 1986).

Description Medium-sized microbat without noseleaf and with terminal portion of tail projecting freely from middle of dorsal surface of interfemoral membrane; two lower incisors on each side; rump, lower belly and hindlimbs naked; dorsal pelage greyish-brown or dark brown; ventral pelage brown; wings dark brown; condylocanine length 23.0–25.2 mm (cf. *Taphozous hamiltoni*). Sexes similar in colour; ♂♂ on average slightly larger than ♀♀. Pelage sleek; mid-dorsal hairs 6–7 mm. Dorsal pelage uniformly sepia brown, dark rusty-brown or ashy greyish-brown (not grizzled); hairs with basal half cream. Rump and flanks naked with clear demarcation between furred and naked areas; up to one-third of the dorsal surface of the body is naked. Ventral pelage paler than dorsal pelage; posterior third of ventral surface of body is naked. Gular pouch well developed in ♂♂, less so in ♀♀. No black beard. Head moderately flat, subtriangular (viewed dorsally) with long conical muzzle and very shallow depression between the eyes. Lower lip with conspicuous grooved prominence. Eyes comparatively large. Ears subtriangular, backward-pointing, with papillae along the lower inner margin. Tragus axe-head-shaped with pronounced lobule at base of posterior margin (Figure 85e); antitragus large, almost reaching corner of mouth. Wings and interfemoral membrane very dark brown; radio-metacarpal pouch present. Hindlimbs naked.

Skull (Figure 86b) medium-large for an African emballonurid, very broad and heavily built. Frontal depression shallow. Dorsal profile of skull (viewed laterally) almost smoothly convex; profile of forehead region very weakly concave (almost straight). Postorbital processes long, slender. Sagittal crest low; occipital helmet well developed. Anterior palatal emargination wide and U-shaped (Figure 87c). Tympanic bulla with inner face incomplete. Condylocanine length: 23.0–25.2 mm. Two lower incisors on each side.

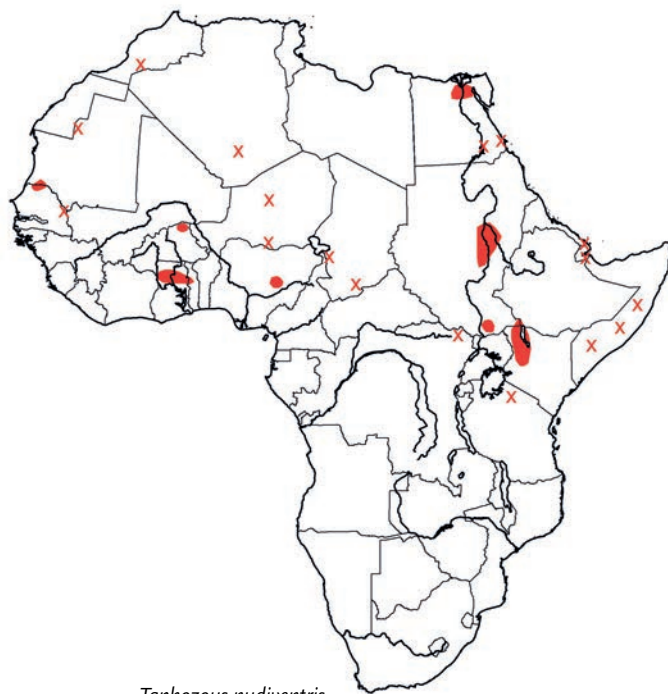
Geographic Variation None recorded in Africa, where only the nominate subspecies is recognized (Koopman 1994).

Similar Species Only two other African emballonurids have a band of naked skin on the posterior of the rump adjacent to the interfemoral membrane:

Taphozous hamiltoni. Naked area usually less extensive. Gular pouch of ♀♀ well developed. Skull with occipital helmet poorly developed; condylocanine length: 20–22 mm.

Saccolaimus peli. Much larger (FA: 87–95 mm; GLS: 28.0–31.6 mm).

Distribution In Africa, recorded from the Sahara Arid, Sudan Savanna, Guinea Savanna and Somalia–Masai Bushland BZs. Distributed from Morocco, Mauritania and Senegal, to Egypt, Eritrea, Djibouti and Somalia, with a narrow southward extension through S Sudan, NE DR Congo and Kenya to Tanzania. Recorded from Guinea-Bissau by Seabra (1900) and Veiga-Ferreira (1949); however, Seabra's identification has not been confirmed and Veiga-Ferreira's record refers to *T. perforatus* (Lopes & Crawford-Cabral 1990). Its occurrence in Gambia is unproven although plausible (Grubb *et al.* 1998). The African distribution appears very disjunct: there are some clusters of localities and many isolated localities. Not known to what extent this reflects insufficient sampling and/or the isolated nature of suitable habitats. Extraliminally: eastwards across



Taphozous nudiventris

Arabian Peninsula, Iran, Afghanistan, Pakistan and India to Myanmar. Mapped from country checklists (see order Chiroptera), Kock 1969a, other literature and museum records.

Habitat Woodland savannas including undifferentiated woodland, *Isoberlinia* woodland, *Acacia–Commiphora* bushland and thicket, and more arid habitats including semi-desert grasslands and shrublands, and deserts. Very little known about habitat requirements, but the distribution is probably restricted by the availability of both flying insects and day-roosts (see below): possibly this species was more abundant and widespread when northern Africa was less arid.

Abundance No information.

Adaptations Aspect ratio high; wing-loading extremely high; wing-tip pointed; flies very fast with great agility but poor manoeuvrability (Rosevear 1965, Norberg & Rayner 1987). Roosts by day in crevices and narrow fissures between rocks or stone blocks, in caves, inselbergs, sandstone hills, wells, old ruins, mosques and the ancient Egyptian temples and tombs of the Nile Valley, including Karnak (Hoogstraal 1962, Gaisler *et al.* 1972, Qumsiyeh 1985, Happold 1987). Day-roosts may have an unpleasant, pungent smell (to humans). Tolerates quite bright light in roosts. April temperatures recorded near roosting bats in Egypt ranged from 23 °C in a mosque to 35 °C in an occupied crevice at Karnak (cf. 37 °C outside in shade) (Gaisler *et al.* 1972). *Rhinopoma hardwickii*, *Asellia tridens*, *Nycteris thebaica* and *Rousettus aegyptiacus* also roosted in the temple complex at Karnak, but each species in a different place. In Iraq, spends summer in cool buildings and caves: moves to old buildings with wooden or rush roofs for hibernation during winter (Al-Robaae 1968). Accumulates fat prior to hibernation. In Pakistan, makes seasonal migrations between summer and winter day-roosts, accumulates fat towards end of monsoon and spends winter in torpor (Roberts 1977). In India and East Africa, fat also accumulates seasonally despite lack of hibernation there (Kingdon 1974). No further information for Africa, where this species has received little attention.

Foraging and Food Forages by fast-hawking in open spaces. Foraging more than 100 m above ground has been inferred from erratic flight paths by *T. nudiventris* in India (Siefer & Kringer 1991 in Fenton & Griffin 1997). Prey includes beetles, moths, grasshoppers, cockroaches, crickets and winged-ants (Pearch *et al.* 1999). Becomes particularly numerous in Gharbiya Province, Palestine during Jul–Aug when Cotton Leaf-worm moths invade cotton fields, and large quantities of moth scales are found in the bats' stomachs at this time (Madkour 1977 in Qumsiyeh 1985).

Echolocation No information for this species in Africa.

Social and Reproductive Behaviour Roosts gregariously; becomes very active ca. 30 minutes before sunset and emerges from the roost ca. 15 minutes after sunset. One colony in Egypt comprised ca. 50 individuals (Gaisler *et al.* 1972); 2000 recorded in Pakistan (Roberts 1977). In Iraq, colonies are of mixed composition throughout most of year. When ♀♀ approach time of parturition, ♂♂ leave or are driven away (sometimes to roosts 100–300 m away) where they are found in groups of 5–10. The ♂♂ rejoin the ♀♀ after the young become volant

(Al-Robaae 1968). Maternity colonies contain 200–1000 ♀♀. Large nuclear colonies with small colonies nearby have also been recorded in Pakistan (Roberts 1977). According to Al-Robaae (1968), the young bat clings to its mother's back for two weeks, then roosts beside her and remains with other young while she forages. According to Roberts (1977), the young remains attached to a nipple for 3–4 weeks, then clings to its mother's flank or back while she forages until eight weeks old. Young begin flying within and near the day-roost when five weeks old. Weaning occurs during sixth week. When foraging away from day-roost, young stay close to mother even after weaning.

Reproduction and Population Structure Litter-size: one. In Iraq, the reproductive chronology is restricted seasonal monoestry, with sperm storage and delayed fertilization (Al-Robaae 1968); no conclusive data for Africa. In Iraq, copulation occurs in Sep–Oct shortly before hibernation. Sperm are stored in the ♀ until late Mar when hibernation ends and ovulation and fertilization take place. Young are born nine weeks later. All young are born during a ten-day period in late May: they are blind, naked, FA: 25–30 mm, HB: 45–50 mm. Eyes open after one week. Growth rapid. Insects in stomach by seven weeks. Reproductive chronology in Pakistan is also restricted seasonal monoestry with copulation in Sep, emergence from winter-roosts at beginning of Mar, birth of young in mid-Apr (Roberts 1977).

Predators, Parasites and Diseases Predators include Barn Owls *Tyto alba* in Palestine (Dor 1947 in Qumsiyeh 1985) and hawks that capture the bats as they leave their roosts in Pakistan (Roberts 1977). Ectoparasites in Africa include bed-bugs *Leptocimex vespertilionis*, *L. duplicatus*, *Stricticimex puylaerti* (Hemiptera: Cimicidae); a flea *Xenopsylla conformis* (Siphonaptera: Ischnopsyllidae); ticks *Carios vespertilionis*, *C. boueti*, *C. confusus* (Acari: Argasidae); and a mite *Steatonyssus sudanensis* (Acari: Macronyssidae) (Anciaux de Faveaux 1984).

Conservation IUCN Category: Least Concern.

Measurements

Taphozous nudiventris

FA: 71.8 (67–79) mm, n = 103

WS: n. d.

TL: 120.0 (110–132) mm, n = 37

T: 31.0 (20–37) mm, n = 64

E: 20.4 (16–25) mm, n = 62

Tr: 6.6 (6–7) mm, n = 26

Tib: 29.1 (27–31) mm, n = 24

HF: 16.3 (11–18) mm, n = 50

WT: n. d.

GLS: 25.7 (23.2–28.5) mm, n = 69

GWS: 15.5 (14.5–16.6) mm, n = 72

C–M³: 10.9 (10.1–11.6) mm, n = 72

Burkina, Mali, Egypt, Sudan, Ethiopia (BMNH, SMNS, ZFMK and literature)

Key References Al-Robaae 1968; Gaisler *et al.* 1972; Kock 1969a; Qumsiyeh 1985.

Meredith Happold

Taphozous perforatus EGYPTIAN TOMB BAT

Fr. Taphien perforé; Ger. Ägyptische Grabfledermaus

Taphozous perforatus E. Geoffroy, 1818. Descrip. de L'Egypte 2: 126. Kom Ombo, between Edfu and Aswan, Upper Egypt.

Taxonomy Subgenus *Taphozous*. Synonyms in Africa: *haedinus*, *maritimus*, *rhodesiae*, *senegalensis*, *sudani*, *swirae*. Extraliminally: *maritimus*. Subspecies: four (three in Africa); boundaries unclear. Harrison (1958, 1962) considered *sudani* to be a distinct species, a view not shared by more recent authors (Rosevear 1965, Kock 1969a, Hayman & Hill 1971, Koopman 1975, Simmons 2005). Chromosome number (Egypt): $2n = 42$; $aFN = 64$ (Yaseen *et al.* 1994).

Description Medium-sized microbat without noseleaf and with terminal portion of tail projecting freely from middle of dorsal surface of interfemoral membrane; two lower incisors on each side; pelage covering all of body; dorsal pelage not grizzled; ventral pelage pale grey to dark greyish-brown; wings almost white to pale brown. Sexes similar. Pelage soft, fine, silky; covering all parts of body; mid-dorsal hairs 6–7 mm. Dorsal pelage uniformly dark chocolate brown, sepia brown, greyish-brown or ashy-brown; hairs white at base. Ventral pelage pale grey, pale greyish-brown to dark greyish-brown; chin and throat usually sepia brown and darker than dorsal or ventral pelage. Adult ♂♂ and ♀♀ with a poorly defined patch of longer darker hairs on the throat (perhaps not always present). No gular pouch in either sex according to Rosevear (1965), Hayman & Hill (1971) and Harrison & Bates (1991), but Rosevear mentions that a shallow fold of skin or merely a crescentic mark may be present. In contrast, Koopman (1975) implies that a gular pouch is present in some ♂♂ (see Geographic Variation). Head moderately flat, subtriangular (viewed dorsally) with long pointed muzzle and deep depression between the eyes. Eyes comparatively large for a microbat. Lower lip with conspicuous grooved prominence. Ears subtriangular, backward-pointing, with small papillae on lower inner margin. Tragus axe-head-shaped with poorly developed lobule at base of posterior margin (Figure 85f). Wings variable: almost white in individuals with darker brown dorsal pelage, to pale brown in individuals with paler ashy-brown dorsal pelage. Radio-carpal pouch present in both sexes. Interfemoral membrane pale brownish.

Skull (Figure 86) small for an African emballonurid. Frontal depression deep. Profile of forehead region of skull (viewed laterally) strongly concave. Postorbital processes long and slender. Sagittal crest absent, no occipital helmet. Anterior palatal emargination comparatively narrow, and more angular and more V-shaped than in other African *Taphozous* (Figure 87d). Inner face of tympanic bulla incomplete. Two lower incisors on each side.

Geographical Variation Four subspecies are recognized in Africa by Simmons (2005), but their boundaries (based on Koopman 1994) and diagnostic characters are not clear.

T. p. senegalensis: West Africa.

T. p. perforatus: Egypt and N Sudan.

T. p. sudani: C and S Sudan, E DR Congo, Botswana and Zimbabwe.

T. p. haedinus: Tanzania to Ethiopia and, extraliminally, across S Asia to India.

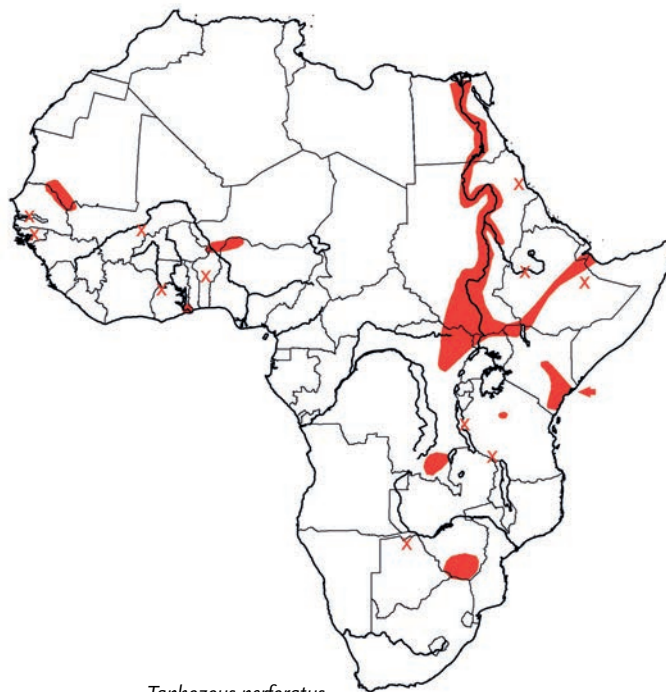
Similar Species Three other African emballonurids have pelage covering all of the body:

Taphozous mauritanus. Dorsal pelage grizzled (salt and pepper effect); ventral pelage pure white (sometimes stained yellowish).

T. hildegardeae. Dorsal pelage uniformly pale greyish-brown. Adult ♂♂ with blackish 'beard' on throat, ventral pelage white stained yellowish-brown. Adult ♀♀ with throat and belly pure white.

Coleura afra. Three lower incisors on each side. Prominence on lower lip not divided by median groove. FA: 44–53 mm. Wings brown to blackish-brown. Ventral pelage brown.

Distribution In Africa, found along Nile Valley in the Sahara Arid BZ and in some parts of the Sahel Savanna, Sudan Savanna, Guinea Savanna, Somalia–Masai Bushland, Coastal Forest Mosaic and Zambezi Woodland BZs, and in the Northern and Eastern Rainforest–Savanna Mosaics. Not recorded from the Rainforest BZ except in NE DR Congo. Except along the Nile Valley, the distribution appears very disjunct (possibly because of insufficient sampling and/or the absence of suitable day-roosts). In West Africa, recorded from Mauritania, Senegal, Mali, Ghana and E Burkina to NW Nigeria. On eastern side of Africa, recorded contiguously from Egypt, Sudan, NE DR Congo, Uganda, NW Kenya and the Ethiopian Rift Valley to the Red Sea in Djibouti and NW Somalia, and there are apparently isolated populations in E Sudan, the Ethiopian Highlands, C to SE Kenya, Tanzania, S DR Congo to N Zambia, the Okavango Swamp of N Botswana, and the low-lying area of S Zimbabwe and E Botswana. Over much of its wide distribution in Africa, records are



Taphozous perforatus

extremely sparse. Extraliminally: S Arabia, Jordan, S Iran, Pakistan and NW India.

Habitat Mainly open woodland savannas, including *Acacia* woodland, *Isoberrinia* woodland, *Acacia–Commiphora* bushland and thicket, and miombo and mopane woodlands, where suitable day-roosts are present. Also recorded from flooded savanna in the Nile Delta, in seasonally moist habitats along the Nile Valley, in rainforest–savanna mosaic, in East African coastal forest mosaic, and in the Okavango Swamp, Botswana. There are some records within the rainforest zone in NE DR Congo, but no details are available. Near the confluence of the Shashi and Limpopo Rivers in Zimbabwe, *T. perforatus* was found near a range of sandstone hills with *Acacia* woodland on the flat country, and well-developed riverine woodland along the seasonally dry river bed (Smithers 1983). Evidently avoids forests, montane habitats, semi-deserts and deserts.

Abundance Uncertain. Over much of its wide distribution, records are extremely sparse, e.g. in East Africa, only one specimen published from Uganda (Kock 1974b), two from Tanzania (Allen & Loveridge 1933, Harrison 1961) and seven from Kenya (Aggundey & Schlitter 1984). Also, comparatively poorly represented in museum collections. In contrast, large numbers (e.g. ca. 200) have been reported from day-roosts in the Nile Valley in Egypt (Gaisler *et al.* 1972, Qumsiyeh 1985) and Hoogstraal (1962) reports it as one of the most common bats in Egypt. Also, a colony of 150–200 was found in NE DR Congo (Lang & Chapin 1917b) and one of >100 in S DR Congo (Anciaux de Faveaux 1978).

Adaptations Aspect ratio medium; wing-loading medium-high. Based on wing morphology, flight-speed estimated to be ca. 8.0 m/sec (Rydell & Yalden 1997), which is medium for bats. By day, roosts in caves, crevices in rocky outcrops and old buildings, including Egyptian pyramids, tombs and other ancient monuments, gaining access by scuttling and climbing as well as by flying. Unlike *T. mauritanus* which roosts in the open, *T. perforatus* roosts tucked away in darkened narrow crevices in rocks or brickwork. Sometimes roosts quite close to the ground (Hoogstraal 1962).

Foraging and Food Forages by fast-hawking. Based on analysis of faeces (Rydell & Yalden 1997), the diet comprises predominantly, in order of priority, moths (56% by volume), termites (14%), beetles (10%) and, to a lesser extent, crickets and katydids (8%), bugs (3%), lacewings (2%), ants (1%) and flies (1%).

Echolocation No information.

Social and Reproductive Behaviour Unlike the less gregarious *T. mauritanus*, *T. perforatus* roosts in groups of several individuals to at least 200 (see Abundance), with individuals huddled together in dense associations (Lang & Chapin 1917b, Hoogstraal 1962). Group-members scuttle and crawl about, but Lang & Chapin (1917b) noted that they never crawled over each other.

Reproduction and Population Structure Litter-size (Egypt, Nigeria, Zimbabwe): one ($n = 19$). Reproductive chronology uncertain. At 25°41'N (Luxor, Egypt), 16 of 16 ♀♀ were in advanced pregnancy in Apr (no data for other months) (Gaisler *et al.* 1972). At 13°04'N (Sokoto, N Nigeria), 6 of 6 adult ♀♀ were lactating in mid-Jun (wet season) and, of these, one was examined histologically and found to be in early pregnancy (no data for other months) (Harrison 1958). This suggests that the chronology in N Nigeria is seasonal polyoestry with postpartum oestrus, but the number of litters/year, the timing of other births and the proportion of ♀♀ that have more than one litter/year, are not known. In Zimbabwe, two pregnant ♀♀ were reported in Nov (Smithers & Wilson 1979). The data from Nigeria and Zimbabwe indicate that at least some births occur at the beginning of the unimodal wet seasons, and that there are boreal and austral cycles. Data from elsewhere, summarized by Anciaux de Faveaux (1978), are not conclusive.

Predators, Parasites and Diseases Predators include Spotted Eagle-owls *Bubo africanus* (Demeter 1982), and probably Lanner Falcons *Falco biarmicus*, which have been observed feeding on bats emerging from a quarry where *T. perforatus* was known to roost (Butler 1905, D. Kock pers. comm.). Ectoparasites include fleas *Xenopsylla cheopis* (Siphonaptera: Pulicidae), *Araeopsylla wassiffi*, *Chiropteropsylla aegyptia*, *C. brockmani* (Siphonaptera: Ischnopsyllidae); bat-flies *Phthiridium integrum* (Diptera: Nycteribiidae), *Brachytarsina diversa*, *B. alluaudi* (Diptera: Streblidae); ticks *Carios vespertilionis*, *C. boueti*, *C. confusus*, *Alectorobius salahi* (Acari: Argasidae); and mites *Steatonyssus* sp. (Acari: Macronyssidae), *Ugandobia barnleyi* (Acari: Myobiidae), *Alabidocarpus taphozous* (Acari: Chirodiscidae) (Anciaux de Faveaux 1984). Dakar bat 249 virus has been isolated from *T. perforatus* (Anciaux de Faveaux 1984).

Conservation IUCN Category: Least Concern.

Measurements

Taphozous perforatus

FA: 62.6 (56–67) mm, $n = 129$

WS: n. d.

TL: 101.6 (90–112) mm, $n = 46$

T: 26.2 (19–32) mm, $n = 92$

E: 17.7 (15–21) mm, $n = 94$

Tr: 6.2 (4.9–7.5) mm, $n = 47$

Tib: 23.0 (21–24) mm, $n = 18$

HF: 12.4 (10–14) mm, $n = 21$

WT: 29.6 (20–39) g, $n = 13^*$

GLS: 19.7 (18.1–21.7) mm, $n = 70$

GWS: 11.7 (11.3–13.0) mm, $n = 70$

C–M³: 8.5 (7.8–9.0) mm, $n = 13$

Throughout geographic range (HZM, MNHN and literature)

*Zimbabwe (Smithers & Wilson 1979)

Key References Harrison 1958, 1962; Rosevear 1965; Rydell & Yalden 1997; Taylor 2000.

Family NYCTERIDAE
SLIT-FACED BATS

Nycteridae Van der Hoeven, 1855. Handb. Dierkunde, 2nd edn., 2: 1028.

| | | |
|-----------------------|-----------------|--------|
| Nycteris (13 species) | Slit-faced Bats | p. 440 |
|-----------------------|-----------------|--------|

All nycterids belong to the genus *Nycteris*. There are 16 extant species: 13 occur in Africa, one in Madagascar and two in South-East Asia (Simmons 2005). They are found mainly in rainforests and woodland savannas, but some species inhabit semi-arid habitats. Nycterids are unique in having a deep longitudinal cleft on the head (from the forehead to the nostrils), which is bordered by fleshy outgrowths whose outlines are usually obscured by the pelage (Figure 32g). Like the noseleaves on the muzzles of bats in the families Rhinolophidae, Hipposideridae, Megadermatidae and Rhinopomatidae, these outgrowths play a role in echolocation. Nycterids are also distinguished by a long tail that is completely enclosed by a very large interfemoral membrane and which terminates in a uniquely Y-shaped or T-shaped cartilaginous process (Figure 33g). None are considered to be pests.

African nycterids are very small to medium-sized microbats with moderately long, soft, loose, fluffy pelage, usually brown or grey, occasionally orange. Males and ♀♀ are similar in size and colour. The body is small and compact; the shape of the head is obscured by

pelage. The muzzle has a deep longitudinal cleft; the nostrils are located in the anterior end of this cleft, and the cleft expands into a deep pit on the forehead. The noseleaf is comprised of fleshy outgrowths along the margins of the cleft; its shape is not used diagnostically. The ears are enormous! They are longer than the length of the head, rounded and are united at the base by an inconspicuous low membrane. The tragus is well developed and its shape is an important diagnostic character. The eyes are minute. The wings are large and broad; the second finger has a long metacarpal but no phalanges. The hindlimbs are relatively long with small soles, short toes and small claws; the toes (except hallux) have three phalanges. The tail is relatively long (44–52% of TL), and is completely enclosed by a very large interfemoral membrane, which is supported and manipulated by long calcars and the Y-shaped or T-shaped terminal process of the tail. There are no pubic nipples. The interfemoral membrane is reinforced by numerous strands of collagen fibres, which form patterns of broken and/or unbroken but dotted transverse lines across the membrane. The skull is long and narrow, with a deeply concave frontal shield in the interorbital region; the shield is formed by the fusion of the postorbital processes

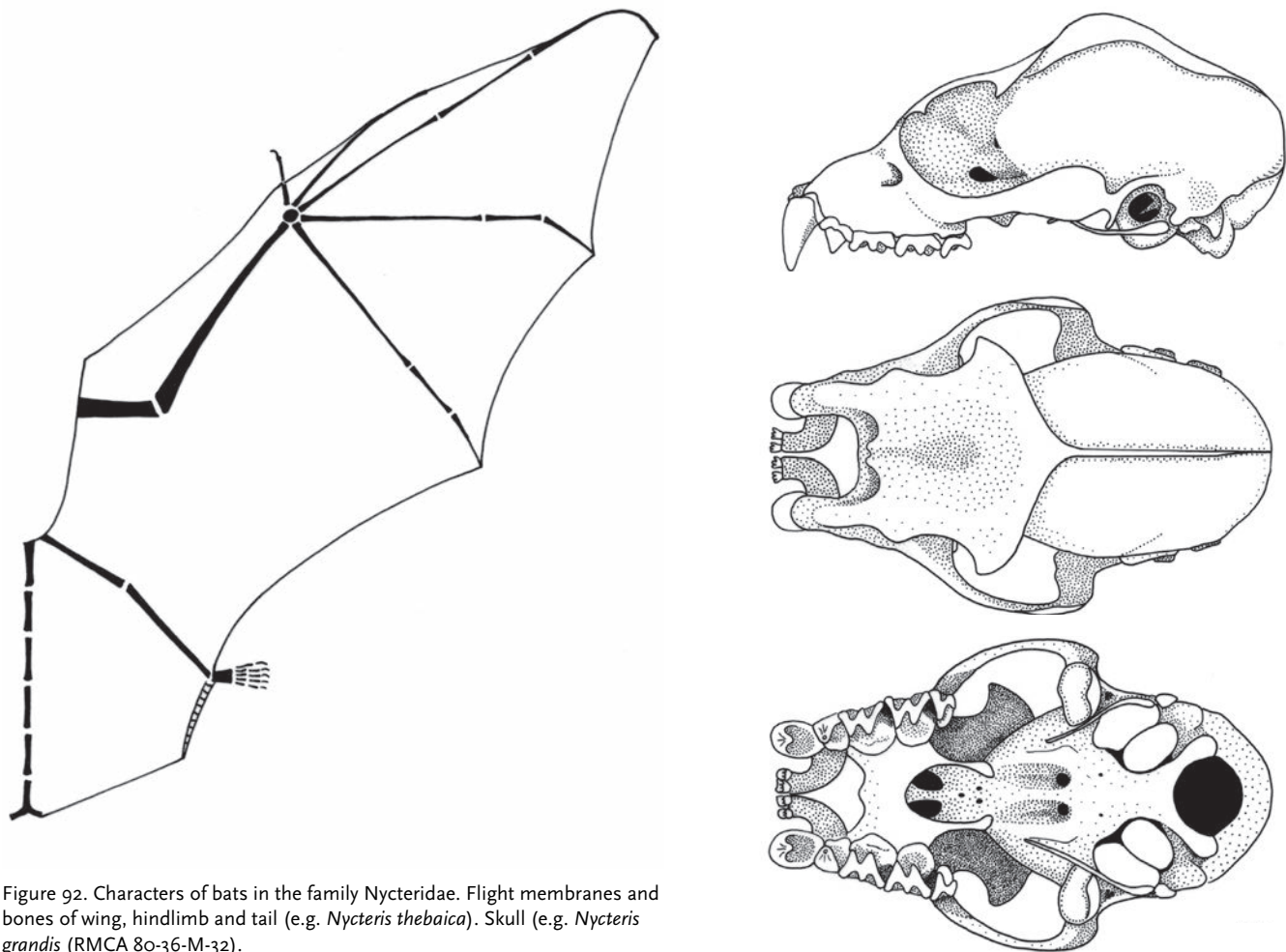


Figure 92. Characters of bats in the family Nycteridae. Flight membranes and bones of wing, hindlimb and tail (e.g. *Nycteris thebaica*). Skull (e.g. *Nycteris grandis* (RMCA 80-36-M-32).

with broad supraorbital ridges. Selected external and craniodental characters of representatives of the genus are illustrated in Figure 92 but there are important inter-specific variations in dentition (see below). Posteriorly, the frontal shield rises to the most elevated part of the skull where it merges with the sagittal crest. The cleft or 'slit' in the face leads into a large chamber supported by the frontal shield. The sagittal crest is usually low or absent (but well developed in two species) and there are no lambdoid crests. The nasal branches of the premaxillae are lost; the palatal branches are partly developed and not fused to each other but are lightly fused to the maxillae and other bones of the palate; they may fill, or only partly fill, the space between the maxillae. Skull characters are not as useful as external characters and dental characters for distinguishing between species of *Nycteris*, and therefore skulls are not described in the species profiles. The dental formula is $2^{113}/_{3123} = 32$. The karyotypes of nycterids are characterized by high fundamental numbers (aFN) compared to other families of bats (Lee *et al.* 1989).

The five species of African nycterids for which data are available have very low aspect ratios and low to very low wing-loadings (very low in all but one species). They can fly slowly with great manoeuvrability, hover, take off from the ground (even when carrying a young bat or heavy prey) and they can turn around in very confined spaces. These adaptations enable nycterids to forage close to the ground and in dense vegetation. Because of their wing morphology, flight is energetically expensive, so they spend minimal time in flight. Although they sometimes forage by slow-hawking, they are usually fly-catchers and perch-hunting gleaners and often carry larger prey back to the perch before eating it. Most species are insectivorous, feeding on a wide variety of taxa, but one African species (*Nycteris grandis*) also eats small vertebrates. Prey is detected from sounds made by the prey as well as by echolocation. Nycterids are referred to as 'whispering' bats because they emit multiharmonic CF echolocation calls of short duration and low intensity (Griffin 1958, Neuweiler 1989). These calls are particularly suited for densely cluttered environments. Nycterids can hover and glean prey from vegetation and other surfaces and, because they can take off from the ground, they can land to attack non-volant prey. However, they are unable to scuttle over the ground and they cannot climb. During the day, nycterids roost in hollow trees, caves, mines, buildings, road culverts, hollow logs, abandoned burrows and similar semi-dark places. They hang freely from footholds on horizontal ceilings, and maintain a space between adult individuals. Their exceptional manoeuvrability enables them to fly into confined spaces to find roosts inaccessible to other bats. They perform an aerobatic somersault in mid-air in order to gain a holdfast from which to hang. Nycterids do not hibernate.

The social behaviour and mating systems of nycterids are not well known. Bats of one species appear to be mainly solitary; some apparently form monogamous family groups (Hill & Smith 1984), and it seems likely, from the very limited data, that some might establish harems (but this needs confirmation). All nycterids for which data are available are monotocous. Surprisingly, the reproductive chronology of only one African species (*N. thebaica*) has been ascertained with

certainty, and only in South Africa where it exemplifies restricted seasonal monoestry. Polyestry has been reported for two species (*N. hispida* and *N. macrotis*) in Tanzania, but the chronologies of these species are not known in detail. Bernard (1982a) and Bernard & Cumming (1997) suggest that polyestry is the ancestral strategy for nycterids and that monoestry evolved as an adaptation to higher latitudes where conditions are optimal only once per year.

The geological range of the family Nycteridae is not known (Koopman 1984). It has been suggested that there have been at least two major dispersals of the genus in the Old World tropics (Thomas *et al.* 1994). First, the *arge* group (see below) dispersed from Africa, during a Miocene or Pliocene pluvial period, across forests that spread uninterrupted from Africa to eastern Asia and later, when drier conditions prevailed, two South-East Asian species became isolated from the remainder in Africa. Secondly, *N. thebaica*, which is adapted to xeric conditions, dispersed from Africa into Israel and Arabia. In Africa, adaptive radiation has been extensive: three species are found mainly in rainforest, six occur in both forests (including rainforest) and woodland savannas, three occur mainly in woodland savannas, and one (*N. thebaica*) occurs in diverse habitats including clearings in rainforest, woodland and grassland savannas, and oases and riverine habitats in arid regions. Four species (31%) have been found in montane habitats, but no species are mountain specialists. It is not uncommon to find more than one species at any one place, and 4–5 species have been recorded at several localities. For example:

- Comoé N. P., Côte d'Ivoire (Sudan Savanna BZ): *N. arge*, *N. intermedia*, *N. hispida*, *N. macrotis*, *N. nana* (Fahr & Kalko 2010).
 Ituri Forest, E DR Congo (Rainforest BZ): *N. arge*, *N. grandis*, *N. hispida*, *N. intermedia*, *N. nana* (Van Cakenberghe & De Vree 1985, 1993).
 Taï N. P., Côte d'Ivoire (Rainforest BZ): *N. arge*, *N. grandis*, *N. intermedia*, *N. major*, (Fahr & Kalko 2010).
 Adiopodoumé, Côte d'Ivoire (Rainforest BZ): *N. arge*, *N. hispida*, *N. intermedia*, *N. macrotis* (Van Cakenberghe & De Vree 1985, 1993).
 Avakubi, NE DR Congo (Rainforest BZ): *N. arge*, *N. hispida*, *N. intermedia*, *N. major* (Van Cakenberghe & De Vree 1985, 1993).
 Liwonde N. P., Malawi (Zambezian Woodland BZ): *N. grandis*, *N. hispida*, *N. macrotis*, *N. thebaica* (Happold & Happold 1997).

Based on morphological data, the family Nycteridae was placed in the superfamily Rhinolophoidea together with the families Rhinolophidae, Hipposideridae and Megadermatidae (Simmons 1998, Simmons & Geisler 1998), but more recent molecular studies have contradicted many groupings based on morphological data and, pending resolution of the controversies, no chiropteran superfamilies are recognized by Simmons (2005). The systematics of African nycterids has been revised by Van Cakenberghe & De Vree (1985, 1993, 1998).

All nycterids belong to the genus *Nycteris*.

Meredith Happold

GENUS *Nycteris*

Slit-faced Bats

Nycteris G. Cuvier & E. Geoffroy, 1795. Mag. Encyclop. 2: 186. Type species: *Vespertilio hispidus* Schreber, 1774 (*nomen nudum*, validated by Opinion 111 of the International Commission on Zoological Nomenclature).



Nycteris thebaica.

This genus has 16 extant species of which 13 occur in Africa. There are no other genera in the family Nycteridae and the characters of the genus *Nycteris* are given in the family profile.

African species of *Nycteris* can be distinguished by the combinations of characters given in Table 18, but see also additional information under Similar Species. Characters of particular diagnostic value are:

Shape of upper incisors. Bicuspid (Figure 93a) or tricuspid (Figure 93b).

Relative size of the posterior lower premolar. Can be large (reaching at least half the height of the anterior lower premolar Figure 93c) or small (reaching less than half height of anterior lower premolar (Figure 93d and e).

Shape of posterior margin of the tragus in conjunction with the shape of the tragus. The posterior margin can be smoothly convex and the shape semi-lunate (Figure 93f) or smoothly convex and the shape narrow (not semi-lunate) (Figure 93g); or the posterior margin can be deeply notched and the tragus inverted pear-shaped (Figure 93h), or the posterior margin can be concave or slightly concave (Figure 93i).

FA (length of forearm). Mean \pm 1 S.D. is given for some species.

E (length of ear). In African species, mean length ranges from 21.1–32.0 mm, so 21.1–24.7 mm is comparatively short, 24.8–28.3 mm is medium, and 28.4–32.0 mm is comparatively long.

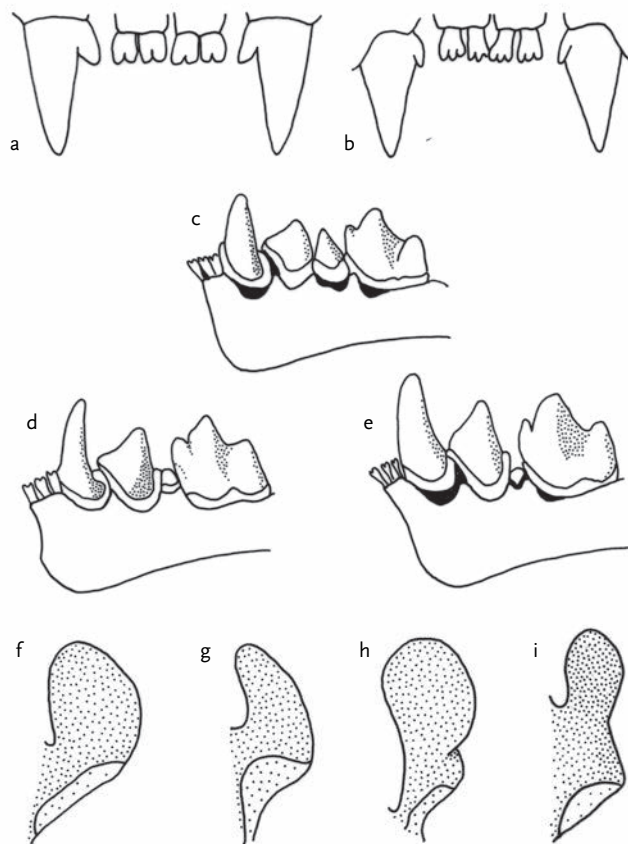


Figure 93. Diagnostic characters of species of *Nycteris*. (a) Upper incisors bifid (e.g. *N. capensis*). (b) Upper incisors trifid (e.g. *N. hispida*). (c) Posterior lower premolar relatively large (e.g. *N. intermedia*). (d) and (e) Posterior lower premolar relatively small (e.g. *N. macrotis*, *N. thebaica*). (f) Tragus broad with posterior margin smoothly convex; shape semi-lunate (e.g. *N. macrotis*). (g) Tragus narrow with posterior margin smoothly convex; shape not semi-lunate (e.g. *N. hispida*). (h) Tragus inverted pear-shaped with posterior margin deeply notched (e.g. *N. thebaica*). (i) Tragus with posterior margin concave or slightly concave (with 'kink' at centre) (e.g. *N. arge*; after Rosevear 1965). Left tragus illustrated; all drawn to same length.

Relative length of ear. In African species, ears range in relative length from 52–80% of FA, so 52–61% of FA is relatively short, 62–71% of FA is medium, and 72–80% of FA is relatively long.

Tib (length of tibia). In African species, mean length ranges from 15–30 mm, so 15–20 mm is comparatively short, 21–25 mm is medium, and 26–30 mm is comparatively long.

Relative length of tibia. In African species, mean relative length ranges from 44–56% of FA, so 44–48% is relatively short, 49–52% is medium and 53–56% is relatively long.

Shape of the baculum. The tip can be simple (Figure 94a–d), ventrally hooked (Figure 94e–h) or trifid (Figure 94i–k); for minor intra-specific variations, see Thomas *et al.* 1994.

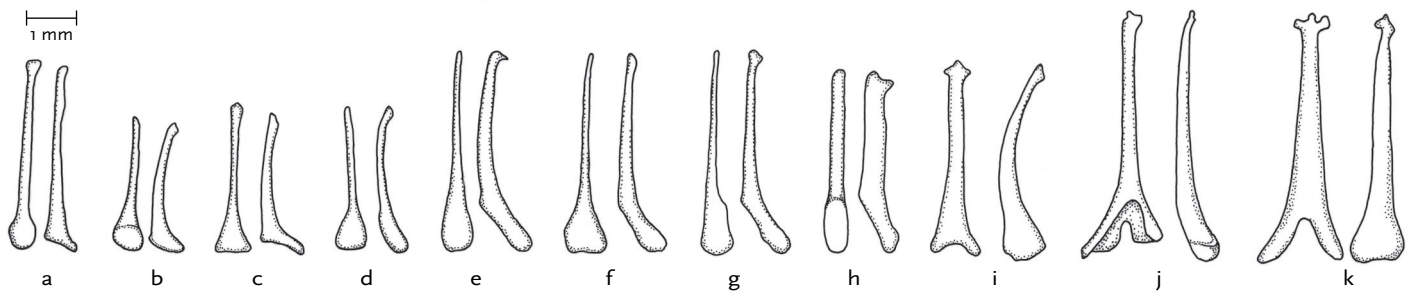


Figure 94. Bacular morphology in *Nycteris*. Bacula tips simple: (a) *N. arge*, (b) *N. nana*, (c) *N. gambiensis* (specimen 1) and (d) *N. gambiensis* (specimen 2). Bacula tips ventrally hooked: (e) *N. hispida* (specimen 1), (f) *N. hispida* (specimen 2), (g) *N. hispida* (specimen 3) and (h) *N. grandis*. Bacula trifid-tipped: (i) *N. macrotis* (specimen 1), (j) *N. macrotis* (specimen 2) and (k) *N. macrotis* (specimen 3). For each species, left illustration is the dorsal view with tip uppermost; right illustration is the lateral view of the right side with tip uppermost. Bacula for up to three different specimens are included to indicate intra-specific variation. All bacula traced from Thomas *et al.* (1994).

Table 18. Key to the African species in the genus *Nycteris*. Forearm lengths for *N. arge*, *N. intermedia*, *N. major* and *N. nana* from J. Fahr (see profiles), all others from Van Cakenberghe & DeVree (1985, 1993, 1998).

| Upper incisors | Posterior lower premolar | Posterior margin of tragus (Tragus shape) | FA mean \pm 1 S.D. (mm) | E (mm) | Tib (mm) | Miscellaneous | Species |
|----------------|--------------------------|--|-----------------------------|-----------------|-----------------|---|--------------------------------|
| Tricuspid | Small | Smoothly convex
Narrow | 58.25 \pm 2.6
(52–65) | 31.6
(24–35) | 30.1
(25–35) | Baculum tip ventrally hooked | <i>N. grandis</i> |
| Tricuspid | Small | Smoothly convex
Narrow | 38.72 \pm 1.65
(34–44) | 22.3
(16–24) | 18.1
(14–24) | Baculum tip ventrally hooked | <i>N. hispida</i> |
| Tricuspid | Small | Smoothly convex
Narrow | 41.63 \pm 1.72
(37–45) | 27.8
(25–31) | 20.3
(18–22) | Baculum: no data | <i>N. aurita</i> |
| Bicuspid | Small | Smoothly convex
(Semi-lunate) | 40.0
(38–41) | 21.8
(20–23) | 20.7
(18–23) | Baculum tip trifid
Ventral pelage dark grey (few specimens)
Ears 54.4 (51–56)% of FA (n = 3)
Cameroon, Ethiopia, Somalia | <i>N. parisi</i> |
| Bicuspid | Small | Smoothly convex
(Very narrowly semi-lunate) | 39.26 \pm 1.91
(35–42) | 31.7
(28–35) | 19.5
(16–22) | Baculum tip simple
Ventral pelage not dark grey
Ears 79.5 (74–89)% of FA
Tanzania, Zambia, Malawi, Mozambique | <i>N. woodi</i> |
| Bicuspid | Small | Smoothly convex
(Semi-lunate) | 48.19 \pm 2.03
(40–55) | 31.4
(27–35) | 22.7
(18–26) | Baculum tip trifid
Ears 65.0 (54–80)% of FA | <i>N. macrotis</i> |
| Bicuspid | Small | Deeply notched
(Pear-shaped) | 40.15 \pm 1.44
(35–44) | 27.3
(24–30) | 19.9
(17–22) | Baculum tip simple
W Africa and Cameroon | <i>N. gambiensis</i> |
| Bicuspid | Small | Deeply notched
(Pear-shaped) | 44.52 \pm 2.32
(34–52) | 31.7
(26–37) | 22.0
(17–27) | Baculum tip simple
Widespread S of Sahara | <i>N. thebaica</i> |
| Bicuspid | Small | ? Deeply notched
(? Pear-shaped) | 51 | 22 | 25 | Baculum: no data
As yet, only Mozambique | <i>N. vinsoni</i> ^a |
| Bicuspid | Large | Concave with 'kink' | 34.4 \pm 1.7
(32–37) | 21.1
(19–23) | 15.3
(14–17) | Baculum tip simple
Tibia 44 (40–47)% of FA
Concavity of tragus well defined | <i>N. nana</i> |
| Bicuspid | Large | Concave with 'kink' | 36.8 \pm 0.5
(36–38) | 22.7
(20–24) | 19.8
(18–21) | Baculum: no data
Tibia 54 (50–58)% of FA
Concavity of tragus well defined | <i>N. intermedia</i> |
| Bicuspid | Large | Slightly concave with ill-defined 'kink' | 42.1 \pm 1.0
(39–46) | 27.9
(25–34) | 22.0
(19–26) | Baculum tip simple
Tibia 52 (48–58)% of FA
Concavity of tragus poorly defined | <i>N. arge</i> |
| Bicuspid | Large | Concave with 'kink' | 47.5 \pm 1.0
(45–49) | 29.2
(27–31) | 26.3
(24–28) | Baculum: no data
Tibia 56 (53–59)% of FA
Concavity of tragus well defined | <i>N. major</i> |

^aThe taxonomic status of *N. vinsoni* is uncertain: the tragi of the only two specimens are damaged and their shape uncertain. If deeply notched and pear-shaped, the specific status is probably valid, but if smoothly convex and semi-lunate, *vinsoni* is probably as synonym of *N. macrotis* (see profile *N. vinsoni*).

Andersen (1912b) divided the African species of *Nycteris* (as *Petalia*) into four species-groups on the basis of morphological characters, including the size of the lower premolar, the shape of the upper incisors and the shape of the tragus. Using multivariate statistical analyses of morphological characters, Van Cakenberghe & De Vree (1985, 1993, 1998) confirmed that four African species-groups can be recognized. So too did Griffiths (1994) based on hyoid and other morphology. We follow the species and species-group compositions suggested by Van Cakenberghe & De Vree, with the exception that *N. parisi* is considered distinct from *N. woodi* on the basis of bacular morphology (Thomas *et al.* 1994) and the relative size of the ears (see profiles). The African species-groups, their characters and species are:

arge group. Posterior lower premolar large; upper incisors bicuspid; tragus with posterior margin concave. *N. arge*, *N. intermedia*, *N. major* and *N. nana*.

macrotis group. Posterior lower premolar small; upper incisors bicuspid; tragus semi-lunate, posterior margin smoothly convex. *N. macrotis*, *N. parisi* and *N. woodi*.

hispidia group. Posterior lower premolar small; upper incisors tricuspid; tragus not semi-lunate, posterior margin smoothly convex. *N. aurita*, *N. grandis* and *N. hispidia*.

thebaica group. Posterior lower premolar small; upper incisors bicuspid; tragus pear-shaped, posterior margin deeply notched. *N. gambiensis*, *N. thebaica* and ? *N. vinsoni*.

The species are presented in alphabetical order, irrespective of the species-group to which they belong.

Meredith Happold

Nycteris arge BATES'S SLIT-FACED BAT

Fr. Nyctère de Bates; Ger. Bates' Schlitznasen-Fledermaus

Nycteris arge Thomas, 1903. Ann. Mag. Nat. Hist., ser. 7, 12: 633. Efulen [= Efulan], SW Cameroon.

Taxonomy Species-group: *arge*. Synonyms: none. Some authors considered *N. intermedia* as a synonym. Chromosome number: not known.

Description Small to very small microbat with noseleaf comprised of a longitudinal cleft bordered by fleshy outgrowths; medium-small for a *Nycteris* (FA: 39–46 mm, GLS: 19.2–20.4 mm); upper incisors bicuspid; posterior lower premolar large; tragus with posterior margin slightly concave; E: 25–34 mm; Tib: 19–26 mm, 48–58% of FA. Not easily distinguished from *N. major*. Sexes similar. Pelage loose, fluffy; mid-dorsal hairs 9–10 mm. Dorsal pelage medium brown, rusty-brown or dark brown, sometimes straw-coloured on forehead between ears and along their outer margin. Ventral pelage similar but paler; some individuals with irregular whitish or pale brown patches. (One albino individual was found in Tâi N. P., Côte d'Ivoire; J. Fahr unpubl.) Ears broad, rounded, of medium length for a *Nycteris* and also of medium relative length (67 [60–79]% of FA); uniformly blackish-brown. Tragus with slight and ill-defined concavity ('kink') at centre of posterior margin (Figure 93i). Muzzle of naked appearance and pink. Wings and interfemoral membrane blackish-brown. Tibia of medium length for a *Nycteris* (22.0 [19–26] mm) and of medium relative length (52 [48–58]% of FA). Baculum tip simple (Figure 94a; Thomas *et al.* 1994).

Skull with sagittal crest low. Upper incisors bicuspid. Posterior lower premolar comparatively large (rising well above cingula of adjacent teeth and equal or almost equal to height of anterior cusp of first molar) and within toothrow.

Geographic Variation None.

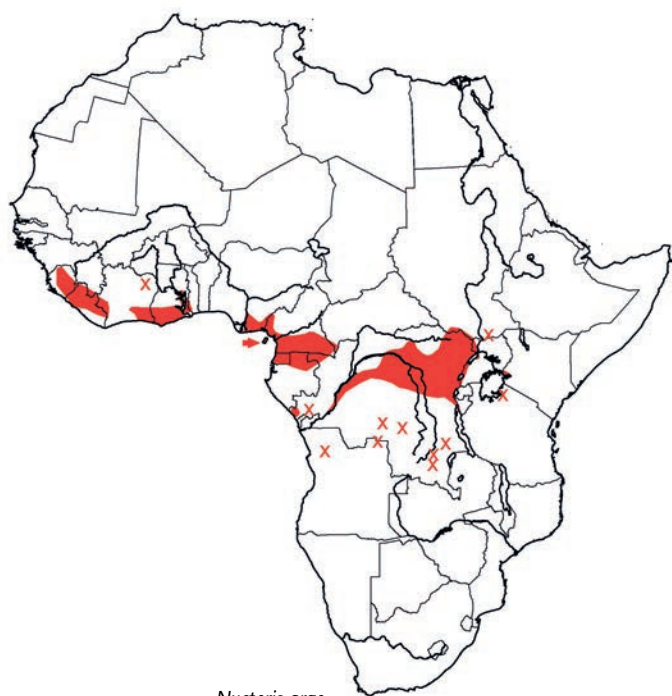
Similar Species Three other African *Nycteris* have the following combination of characters: upper incisors bicuspid; posterior lower premolar large; tragus with posterior margin concave (Table 18, p. 441):

Nycteris nana. Much smaller (FA: 32–37 mm; GLS: 15.6–17.0 mm). Tibia <47% of FA. Ears shorter (19–23 mm). Concavity in posterior margin of tragus well defined.

N. intermedia. Smaller (FA: 36–38 mm; GLS: 17.5–18.7 mm). Ears shorter (20–24 mm). Concavity in posterior margin of tragus well defined.

N. major. Almost always larger (FA: 47.5 ± 1.0 [45–49] mm; GLS: 21.0 [20.4–22.4] mm). According to Eisentraut (1956), the claws are broader, much stouter and blunter than in *N. arge*, but this was questioned by Rosevear (1965) and Van Cakenberghe & De Vree (1985). In some specimens there is overlap in univariate measurements between *N. arge* and *N. major*, and multivariate analysis is needed to distinguish between them (Van Cakenberghe & De Vree 1985).

Distribution Endemic to Africa. Mainly recorded from the Rainforest BZ (Western, West Central, East Central and South Central Regions) and the Rainforest–Savanna Mosaics. Frequently recorded, therefore gaps in the distribution are unlikely to reflect insufficient sampling in these areas. Recorded from Sierra Leone, Liberia, Côte d'Ivoire, Ghana, Togo, Nigeria, Cameroon, Equatorial Guinea (incl. Bioko I.), Gabon, Congo, DR Congo, Central African Republic, Sudan, Uganda, Burundi (Bururi F. R., Ruhinga Hill; FMNH), Kenya, Tanzania and Angola. Nigerian records from Afon and Kudu (Happold 1987) based on specimens in the USNM were probably misidentified – no specimens of *N. arge* from these localities are currently in the USNM and the habitat is not likely to be suitable. A record from Somalia (De Beaux 1923b) is based on misidentified specimens of *N. macrotis* (Koopman 1975). Based on their measurements, some of the specimens from Bioko I. published by Juste & Ibáñez (1994) as *N. arge* probably also include *N. intermedia* and *N. major* and should be re-examined.



Nycteris arge

Habitat Mainly recorded in lowland rainforest, coastal forest and forest–savanna mosaic, but also found in montane forest and swamp forest, and occasionally in or near relict forests and gallery forests in the Guinea Savanna BZ, and in *Acacia–Commiphora* bushland and miombo woodland. Most records are from undisturbed forests but this species is apparently able to cope with degraded and secondary forests and even cocoa plantations (e.g. Juste & Ibáñez 1994).

Abundance *Nycteris arge* is the most common species in the *N. arge* group and the most abundant nycterid in forest habitats.

Adaptations The preferred day-roosts are standing, hollow trees with an opening near the base of the trunk. Verschuren (1957) found this bat in Garamba N. P., NE DR Congo, in hollow trunks of *Alstonia congensis*, *Cordia* sp., *Hallea stipulosa*, *Klainedoxa gabonensis* and *Macaranga* sp. trees. Other day-roosts include fallen logs, small caves, culverts under roads, uninhabited buildings and a belfry. Day-roosts are sometimes shared with *Hipposideros cyclops* and *Rhinolophus landeri* (Lang & Chapin 1917b, Aellen 1952, Eisentraut 1956, 1973a, Rosevear 1965, Wolton *et al.* 1982, Juste & Ibáñez 1994).

Foraging and Food Forages by gleaning close to the ground in the understorey of the forest. In Côte d'Ivoire (Taï N. P. and Comoé N. P.), flight height (as determined by captures in mist-nets set 0–25 m above ground) was 0.7 (0.4–2.6) m ($n = 34$, J. Fahr unpubl.). Rosevear (1965) stated that these bats hunt mainly in clearings in forest but this could not be substantiated (J. Fahr pers. obs.). They glean from vegetation and probably also from the ground. Diet not known but likely to consist of rather soft-bodied arthropods.

Echolocation As in other nycterids, the echolocation calls consist of multiharmonic, steep FM sweeps, according to Novick (1958b) with 3–5 harmonics, a frequency range of 16–107 kHz and a call-duration of 0.4–1.4 ms. The sound is emitted through the nostrils.

Social and Reproductive Behaviour Roosts singly or in groups of 2–3 (rarely four) individuals. Groups are frequently composed of a pair with one young, and sometimes composed of two ♂♂ (Verschuren 1957, J. Fahr unpubl.).

Reproduction and Population Structure Litter-size: one. Reproductive chronology not known. In Côte d'Ivoire, pregnant ♀♀ were recorded in Mar (1 of 3), Sep (1 of 4) and Oct (1 of 1) (Taï N. P., 05° 50' N); Jul and Aug ($n = 2$) (Adiopodoumé: 05° 20' N) and May ($n = 1$) (Comoé N. P., 08° 45' N) (J. Fahr unpubl., MHNG). One lactating ♀ was found in May (Comoé N. P.) and another in late Aug (Ghana, near Anum: 06° 30' N), the latter with an attached juvenile 70 mm long (J. Fahr unpubl., USNM). These observations indicate that births are not restricted to one season per year, but as yet there is no evidence of polyoestry. Testis size varies in ♂♂ between 3.2×2.7 mm and 4.1×2.9 mm but the seasonal pattern is inconclusive. In Côte d'Ivoire, the ratio of ♂♂ to ♀♀ in marked bats captured in mist-nets set in standardized transects was 1 : 0.5 ($n = 33$) in Taï N. P., and 1 : 1 ($n = 10$) in Comoé N. P.

Predators, Parasites and Diseases Remains of one individual were found in the scats of an unidentified small carnivore in Dzanga-Sangha N. P., Central African Republic (Hutterer & Ray 1997). Ectoparasites include a bug *Eothenes nycteridis* (Hemiptera: Polyctenidae) and mites *Paraperiglischrus nycteris* (Acari: Spinturnicidae), *Nycterimyobia camerounensis* and *N. nycteris* (Acari: Myobiidae) (Anciaux de Faveaux 1984, Uchikawa 1988).

Conservation IUCN Category: Least Concern.

Measurements

Nycteris arge

FA: 42.1 (39–46) mm, $n = 57$

WS (c): 274 (255–302) mm, $n = 12$

TL: 107.3 (96–125) mm, $n = 39$

T: 52.6 (44–62) mm, $n = 39$

E: 27.9 (25–34) mm, $n = 39$

Tib: 22.0 (19–26) mm, $n = 51$

HF: 9.9 (9–11) mm, $n = 37$

WT: 9.3 (6.0–11.5) g, $n = 27$

GLS: 19.9 (19.2–20.4) mm, $n = 34$

GWS: 11.7 (10.7–12.4) mm, $n = 51$

C–M³: 7.0 (6.4–7.5) mm, $n = 40^*$

Sierra Leone, Liberia, Côte d'Ivoire, Ghana, Nigeria, Cameroon, DR Congo, Burundi, Angola (BMNH, FMNH, MHNG, RMCA, ROM, SMF, USNM)

*Not measured at level of alveoli (cf. most other *Nycteris* profiles). The minimum FA length (33.7 mm) given by Van Cakenberghe & De Vree (1985) would be very small for this bat and it seems likely that this is based on immature individual(s) or that the value was mistyped

Key References Rosevear 1965; Van Cakenberghe & De Vree 1985; Verschuren 1957.

Jakob Fahr

Nycteris aurita ANDERSEN'S SLIT-FACED BAT

Fr. Nyctère à longues oreilles; Ger. Andersens Schlitznasen-Fledermaus

Nycteris aurita (K. Andersen, 1912). Ann. Mag. Nat. Hist., ser. 8, 10: 547. Kitui, Kenya.

Taxonomy Originally: *Petalia aurita*. Species-group: *hispidia*. Synonyms: none. Considered a synonym or subspecies of *N. hispidia* by several authors including Harrison (1957b), Kock (1969a) and Ansell (1978), but considered to be a distinct species by Koopman (1975) and (on the basis of multivariate analysis of skull measurements) by Van Cakenberghe & De Vree (1993). Although Koopman (1994) listed *aurita* as a subspecies of *N. hispidia*, he remarked that both *aurita* and *hispidia* occur in E Kenya and 'may act as separate species'. Chromosome number: not known.

Description Small to very small microbat with noseleaf comprised of a longitudinal slit bordered by fleshy outgrowths; medium-small for a *Nycteris* (FA: 37–45 mm); upper incisors tricuspid, posterior lower premolar small, posterior margin of tragus smoothly convex; E: 25–31 mm; Tib: 18–22 mm, 51 (48–54)% of FA. Sexes similar. Pelage of medium length, loose and fluffy. Dorsal pelage usually dark beige to dark brown, sometimes paler; hairs unicoloured or with central portion paler. Ventral pelage paler. Ears of medium length for a *Nycteris* and of medium relative length (62 [52–71]% of FA). Tragus narrow (not semi-lunate), posterior margin smoothly convex without notch (as in *N. hispidia*; Figure 93g). Eyes minute. Wings and interfemoral membrane blackish-brown. Hindlimbs long and slender; soles, toes and claws very small. Tibia of medium length for a *Nycteris* (20.3 [18–22] mm) and of medium relative length (49 [46–53]% of FA). Bacular morphology not known.

Skull with sagittal crest very low or absent. Upper incisors tricuspid. Posterior lower premolar small (not reaching height of anterior cusp on first molar), within toothrow.

Geographic Variation None recorded. If the distribution is as restricted as current records indicate, geographic variation is unlikely.

Similar Species Only two other African *Nycteris* have tricuspid upper incisors (Table 18, p. 441):

Nycteris hispidia. Ears smaller (16–24 mm), other measurements on average smaller (FA: 38.7 ± 1.65 mm; GLS: 16.5 [15.3–18.4] mm; C–M³: 5.3 [4.6–6.7] mm; M³–M³: 5.9 [5.1–7.6] mm; C–M₃: 5.9 [5.1–7.6] mm). Best distinguished from *N. hispidia* by multivariate analysis of skull measurements (Van Cakenberghe & De Vree 1993).

N. grandis. Much larger (FA: 52–65 mm; GLS: 23.3–27.5 mm).

Distribution Endemic to Africa. Most records are from the Somalia–Masai Bushland BZ, but the geographic range extends marginally into the Sudan Savanna and Zambezian Woodland BZs. Recorded from Ethiopia, Somalia, Kenya and Tanzania. Specimens from Zambia and DR Congo, referred to as *N. h. aurita* by Ansell (1978), are considered to represent *N. hispidia* by Van Cakenberghe & De Vree (1993).

*Nycteris aurita*

Habitat Most localities appear to be in *Acacia–Commiphora* deciduous bushland and thicket, sometimes near rivers and riverine forests. Recorded, in Tanzania, from two coastal forests (Ruvu South and Somanga) (Cockle *et al.* 1998), from a coconut plantation at Msala, and from a thatched house in grassland near coastal mangroves on Ras Dima I. (Eisentraut 1958). Probably often occurs in more arid habitats than *N. hispidia*.

Abundance Uncertain.

Remarks Very little appears to be known about this species. Some information recorded for *N. hispidia* might pertain to *N. aurita* (e.g. Kingdon 1974). Matthews (1941) examined 12 individuals collected at ca. 4°S in Tanzania in late Dec: they included two lactating ♀♀, one non-lactating parous ♀ showing signs of approaching oestrus, and three 'sexually active' ♂♂. Although Matthews referred to these as *N. hispidia*, the length of their ears indicates that they probably represent *N. aurita*. Also, at ca. 8°S in Tanzania, a lactating ♀ was recorded in early May (Ras Dima I.) and a subadult in mid-Apr (Msala) (Eisentraut 1958).

Conservation IUCN Category: Least Concern.

Population trend not known.

Measurements

Nycteris aurita

FA: 41.5 (37–45) mm, n = 35*

WS: n. d.

TL: 97.1 (86–106) mm, n = 14[†]
 T: 50.4 (45–56) mm, n = 14[†]
 E: 27.8 (25–31) mm, n = 14[†]
 Tr: n. d.
 Tib: 20.3 (18–22) mm, n = 20*
 HF: 10.2 (10–11) mm, n = 12
 WT: 9.4 (6.2–12.3) g, n = 12
 GLS: 17.9 (17.2–18.3) mm, n = 13*
 GWS: 10.7 (10.1–11.1) mm, n = 14*
 C–M³ (alv.): 5.9 (5.7–6.2) mm, n = 22*

Throughout geographic range (BMNH, MZUF, ROM, SMF, USNM, ZFMK, ZMUC)

*Van Cakenberghe & De Vree 1993

[†]Hollister 1918, Matthews 1941

Key References Harrison 1957b; Van Cakenberghe & De Vree 1993.

Victor Van Cakenberghe & Meredith Happold

Nycteris gambiensis GAMBIAN SLIT-FACED BAT

Fr. Nyctère de Gambie; Ger. Gambia Schlitznasen-Fledermaus

Nycteris gambiensis (K. Andersen, 1912). Ann. Mag. Nat. Hist., ser. 8, 10: 548. Dialakoto, Senegal.

Taxonomy Originally *Petalia gambiensis*. Species-group: *thebaica*. Synonyms: none. Considered a subspecies of *N. thebaica* by Aellen (1956b), Kock (1969a) and Koopman (1975), but given specific status by Adam & Hubert (1976), Koopman (1993, 1994) and Van Cakenberghe & De Vree (1998). Chromosome number: not known.

Description Small microbat with noseleaf comprised of a longitudinal slit bordered by fleshy outgrowths; medium-small for a *Nycteris*; upper incisors bicuspid; posterior lower premolar small; tragus pear-shaped with posterior margin deeply notched; FA: 40.15 ± 1.44 (35–44) mm; E: 24–30 mm; Tib: 19.87 ± 0.99 (17–22) mm, 48.9 (46–53)% of FA; GLS: 17.58 ± 0.36 mm (mean \pm 1 S.D.). Not easily distinguished from *N. thebaica* but *N. gambiensis* is on average smaller than *N. thebaica* from West Africa where the two species are sympatric (see Similar Species). Sexes similar. Pelage loose and fluffy; mid-dorsal hairs 9–10 mm. Dorsal pelage dark beige, greyish-brown or sepia brown; hairs unicoloured or with basal half darker than terminal half. Ventral pelage slightly paler than dorsal pelage (cf. *N. thebaica*); hairs sepia brown with paler tips. Ears of medium length for a *Nycteris* and of medium relative length (67 [61–71]% of FA). Tragus inverted pear-shaped with notch in posterior margin (similar to *N. thebaica*, Figure 93h). Eyes minute. Wings blackish-brown; interfemoral membrane brown. Tibia short for a *Nycteris* but of medium relative length (49 [42–53]% of FA). Baculum tip simple (Figure 94c and d; Thomas *et al.* 1994).

Skull with sagittal crest very low. Upper incisors bicuspid. Posterior lower premolar minute (not rising above cingula of adjacent teeth and sometimes not visible above gum), displaced lingually to a greater or lesser extent; anterior premolar in contact with first molar or nearly so (cf. *N. thebaica*).

Geographic Variation None recorded.

Similar Species Only one other African *Nycteris* has the following combination of characters: upper incisors bicuspid; posterior lower premolar small; tragus (without doubt) pear-shaped with posterior margin deeply notched (Table 18, p. 441):

Nycteris thebaica. Ventral pelage paler to much paler than dorsal pelage.

In West Africa, on average larger (FA: 43.98 ± 1.31 mm; Tib:



Nycteris gambiensis

22.24 ± 1.06 mm; GLS: 18.68 ± 0.43 mm) (Van Cakenberghe & De Vree 1998). Anterior upper premolar and first molar usually separated by pronounced gap.

Nycteris vinsoni, if proved to have a pear-shaped tragus with a notch in the posterior margin, is probably a valid species (see profile) that also resembles *N. gambiensis* but it is probably larger (FA: 51 mm).

Distribution Endemic to Africa. Mainly recorded from the Sudan Savanna and Guinea Savanna BZs, but also recorded from the Northern Rainforest–Savanna Mosaic and Rainforest BZ. Distributed somewhat disjunctly from Senegal to W Nigeria, with one specimen from Cameroon (Van Cakenberghe & De Vree 1998). The apparent gaps in the distribution are unexplained: possibly they are artefacts resulting from inconsistent collecting.

Habitat Mainly found in undifferentiated woodland and *Isoperlinia* woodland, but with some records from (or near) grasslands and cleared areas in the Rainforest BZ (Grubb *et al.* 1998).

Abundance Uncertain: moderately common in collections.

Remarks By day, has been found roosting in a hollow tree, caves, derelict buildings, traditional houses and huts, and in roofs (Rosevear 1965, Grubb *et al.* 1998). A colony of ca. 50 occupied clefts in one cave in Guinea (Eisentraut & Knorr 1957). Lagos Bat virus has been isolated from this bat (Calisher *et al.* 2006).

Conservation IUCN Category: Least Concern.

Measurements

Nycteris gambiensis

FA: 40.1 (35–44) mm, n = 479*

WS: n. d.

TL: 98.9 (92–103) mm, n = 14

T: 50.8 (45–55) mm, n = 14

E: 27.3 (24–30) mm, n = 11

Tr: n. d.

Tib: 19.9 (17–22) mm, n = 90*

HF: 11–13 mm, n = 18

WT: 8.1 (7–9) g, n = 16

GLS: 17.6 (16.6–18.5) mm, n = 321*

GWS: 10.2 (9.2–11.0) mm, n = 290*

C–M³ (alv.): 5.7 (5.2–6.2) mm, n = 376*

Throughout geographic range (SMNS, SMF and literature)

*Van Cakenberghe & De Vree 1998

Key References Rosevear 1965; Van Cakenberghe & De Vree 1998.

Meredith Happold

Nycteris grandis LARGE SLIT-FACED BAT

Fr. Grande nyctère; Ger. Große Schlitznasen-Fledermaus

Nycteris grandis Peters, 1865. Monatsber. K. Preuss. Akad. Wiss. Berlin 1865: 358. 'Guinea'.

Taxonomy Species-group: *hispidus*. Synonyms: *baikii*, *marica*, *proxima*. Subspecies: none recognized by Van Cakenberghe & De Vree (1993), but see Geographic Variation. Chromosome number: not known.

Description Small to medium-sized microbat with noseleaf (longitudinal slit bordered by fleshy outgrowths); the largest *Nycteris* (FA: 52–65 mm); upper incisors tricuspid. Sexes similar. Pelage loose and fluffy; mid-dorsal hairs 11–12 mm. Dorsal pelage ranging from dark brown to reddish-brown (in forests) to greyish-brown or dark beige (in savannas); hairs paler at base. Ventral pelage slightly paler. Ears large for a *Nycteris* (24–35 mm), but relatively short (52 [46–59]% of FA). Tragus very narrow, not semi-lunate; posterior margin smoothly convex without notch (similar to *N. hispidus*, Figure 93g). Eyes minute. Wings and interfemoral membrane blackish-brown. Tibia long for a *Nycteris* and also relatively long (53 [49–55]% of FA). Baculum tip ventrally hooked (Figure 94h) (Thomas *et al.* 1994).

Skull (Figure 92) with sagittal crest well developed (see photographs in Hickey & Dunlop 2000). Upper incisors tricuspid. Posterior premolar small (usually rising just above cingula of adjacent teeth but well below height of anterior cusp on first molar) and within toothrow; anterior premolar and first molar well separated.

Geographic Variation Morphometrically, *N. grandis* is uniform throughout its geographic range and therefore no subspecies are recognized by Van Cakenberghe & De Vree (1993). However, this species has a disjunct distribution with darker and usually solitary individuals in rainforest habitats, and paler usually group-living individuals in savanna habitats (Tanzania, Zambia, Malawi and Zimbabwe). The latter possibly, but not necessarily, represent another subspecies, *N. g. marica* (Ansell 1978, Kock 1981). (For similar scenario, see *N. macrotis*.)

Similar Species Only two other African *Nycteris* have tricuspid upper incisors (Table 18, p. 441):

Nycteris aurita. Much smaller (FA: 37–45 mm).

N. hispidus. Much smaller (FA: 33–44 mm).

Distribution Endemic to Africa. Mainly recorded from the Rainforest BZ (and marginally from the Rainforest–Savanna Mosaics) from Senegal to NE DR Congo, with a seemingly separate population



Nycteris grandis

in the Coastal Forest Mosaic BZ of Kenya, Tanzania, Pemba I. and Zanzibar I., and scattered populations in the Zambezian Woodland BZ in Zambia, Malawi, Zimbabwe and Mozambique. Map based on Van Cakenberghe & De Vree (1993). Recently, a specimen from Gashora in SE Rwanda (02° 11'S, 30° 14'E) was published by Kityo *et al.* (2009); this first record from Rwanda has not been mapped.

Habitat In West and central Africa, predominantly rainforest habitats including swamp forest and secondary forest, with some records in dense humid riverine and relict forests outside the rainforest zone. In East Africa, known only in the coastal forests. In south-central Africa and southern Africa, seemingly isolated populations have been found in woodlands (including miombo and *Acacia albida* woodlands) and riverine forests, in the vicinity of large rivers such as the Zambezi, Luangwa, Shire and Buzi. Often found where there are baobabs *Adansonia*; these trees often have large hollow trunks in which *N. grandis* roosts.

Abundance Uncertain. Only moderately common in collections, but these bats are difficult to find, detect and capture.

Adaptations Aspect ratio very low; wing-loading low. Can take off from the ground, can almost hover, turns by banking (minimum radius <25 cm) and by stalling-and-twisting. Individuals sustained flight within a 1×1×1 m enclosure for up to seven circuits/flight (4 bats, 10 flights each; M. Happold unpubl.). Often reported roosting by day, hanging apart, in large hollows within standing trees (including baobabs, *Mitragyna stipulosa*, *Ceiba pentandra* and *Acacia albida*); occasionally found roosting in hollow logs, holes in ground and between rocks, and similar man-made sites such as dark abandoned rooms, water towers, culverts and mine-adits (Verschuren 1957, Rosevear 1965, Brosset 1966, Adam & Hubert 1976, Fenton *et al.* 1990, Happold & Happold 1997). One adult ♀ was collected from a flower of *Kigelia africana* (Kityo *et al.* 2009). Emerges between 19:00h and 21:00h; individuals vary from day to day (Fenton *et al.* 1990). Roost-fidelity has been observed and is probably normal; disturbed roosts may be abandoned but sometimes the occupants return after a few days. Does not become torpid by day under natural temperature regimes. Predicted mean maximum urine concentration is comparatively very low (2581 mOsmol/kg) (Happold & Happold 1988), implying that this species is highly dependent on water for drinking. Bats in captivity for four days did not drink but might have died of dehydration if kept longer. Fenton *et al.* (1983) kept seven in captivity, on a natural diet, but all died between 8–17 days; it was not reported whether they drank or not.

Foraging and Food Feeds on flying and non-flying insects and other arthropods, and small vertebrates including frogs, fish, birds and small bats; its diet and foraging have been well studied (Fenton *et al.* 1981, 1983, 1987, 1990, 1993). Forages by slow-hawking and perch-hunting (including both fly-catching and ground-gleaning), usually close to the ground, in forests, near edges of clearings, woodlands, over streams, rivers and marshes, and near lights where flying insects have aggregated. While perch-hunting, hangs from the perch by one foot and scans the surroundings by rotating the body through 180 degrees, elevating and twisting the head, and tilting the ears to and fro. Prey is detected by echolocation, and also by prey-generated

sounds including the low-frequency sounds of fluttering insects and prey moving on the ground, and the low frequency vocalizations of bats. Does not respond to the echolocation calls of bats, the calls of male frogs, or to prey that is silent and immobile. Captive individuals respond to chewing sounds made by conspecifics, and often attempt to steal their food. When perch-hunting, *N. grandis* swoops down on prey on the ground, envelopes it in the wings and immobilizes it by biting the head. Flying insects and bats are tracked and intercepted (not followed from behind), grasped in the mouth and immobilized by biting the head. Prey is carried to the perch where it is eaten slowly, sometimes as much as an hour later. Uses its wings to position the prey; frogs and bats are cupped in the wrist area of one wing and held to the mouth. Legs of insects and frogs, wings of moths and bats, skin and fur are discarded. Small bones are chewed and swallowed. Capture of fish has apparently not been observed, but Smithers (1983) suggests that stranded fish might be taken from drying pools.

Nycteris grandis is the only African bat that routinely feeds on small vertebrates as well as insects and other arthropods. Remains of arthropod prey, under feeding-perches in Zimbabwe, included Lepidoptera (moths), Orthoptera (katydids, grasshoppers, locusts, praying mantids), Coleoptera (beetles), Neuroptera (lace-wings, ant-lions) and Solifugidae (camel spiders, sun spiders). Remains of small vertebrates included small bats (at least six species including nycterids, rhinolophids, hipposiderids and vespertilionids), birds, frogs (seven species) and fish (three species). Captive bats also ate skinned mice (Happold & Happold 1988). In the wild, small vertebrates comprised ca. 80% of the diet by weight. Frogs were the most common prey (total numbers) in Mar–May, Aug and Sep; bats in Jun–Jul; and arthropods in Dec–Feb. As well as seasonal changes, diets varied from year to year, suggesting opportunism albeit with preferences for some foods. Captive bats preferred katydids and beetles to moths.

Echolocation Early approach-phase echolocation calls are short (1 ms or less), low intensity, multiharmonic calls with a complex overlay of harmonics, 17–104 kHz. Later, when the prey is closer, the calls become less complex and much narrower in bandwidth and, when prey is attacked, the calls become steep FM sweeps from 110 to 61 kHz. Call repetition-rate increases dramatically as prey is approached and attacked (Fenton *et al.* 1983).

Social and Reproductive Behaviour In the rainforest zone, 'seems to be solitary except at breeding times' (Rosevear 1965). In Zimbabwe, Malawi and Zambia, it has been found roosting singly, in twos and in small groups. Adults do not roost in contact with each other. Young are left in the day-roost while mothers forage, and mothers often use their day-roosts as feeding-perches at this time (Fenton *et al.* 1987). Records of occupants of day-roosts include (a) 1 adult ♂, (b) 2 post-lactating ♀♀, 1 subadult ♀, 4 others, (c) 5 ♀♀ with young and 1 reproductively inactive ♀, (d) 2 ♀♀ with young, (e) 1 adult ♂, 2 lactating ♀♀ and their young, (f) 1 adult ♂ and 7 pregnant ♀♀ (Ansell 1986b, Fenton *et al.* 1987, M. Happold unpubl.).

Reproduction and Population Structure Litter-size: one (n = 10) (Brosset 1966, Verschuren 1976, Ansell 1986b). Reproductive chronology not known (no year-round data from any one locality). At 7–8°N (Mt Nimba, Liberia), a single ♀ had a 5 mm embryo in Dec (Verschuren 1976), and lactating ♀♀ were recorded

in Jul and Aug (Wolton *et al.* 1982). At 0–1° N (Bélinga-Makokou, Gabon), newborn young (n = 3) were recorded in Apr and Aug, and a ♀ with large foetus in Nov (Brosset 1966). At 13° S in Zambia, 8 of 8 ♀♀ had large fetuses (CR: 20–27 mm) in mid-Sep (Ansell 1986b). At 15° S (Liwonde N. P., Malawi), 2 of 2 ♀♀ were lactating in Mar, and 2 of 2 were post-lactating in Jun. At ca. 16° S (Mana Pools N. P., Zimbabwe), 4 of 5 ♀♀ had 1–7 days old young in early Dec; the other was neither pregnant nor lactating (Fenton *et al.* 1987).

Predators, Parasites and Diseases Ectoparasites include a bug *Eothenes nycteridis* (Hemiptera: Polyctenidae); a flea *Echidnophaga aethiops* (Siphonaptera: Pulicidae); and a mite *Alabidocarpus nycteris* (Acari: Chirodiscidae) (Anciaux de Faveaux 1984).

Conservation IUCN Category: Least Concern.

Measurements

Nycteris grandis

FA: 58.3 (52–65) mm, n = 85*

WS (a): 425 (417–436) mm, n = 5†

TL: 145.8 (132–169) mm, n = 48

T: 69.9 (53–84) mm, n = 54

E: 31.6 (24–35) mm, n = 56

Tr: 7.4 (6–10) mm, n = 5†

Tib: 30.1 (25–35) mm, n = 33*

HF: 15.4 (14–17) mm, n = 9

WT: 26.9 (21–43) g, n = 31

GLS: 25.2 (23.3–27.5) mm, n = 70*

GWS: 16.2 (11.5–17.4) mm, n = 64*

C–M³ (alv.): 8.8 (7.9–9.7) mm, n = 79*

Throughout geographic range (BMNH, HC, MMB and literature)

*Van Cakenberghe & De Vree 1993

†Malawi only

Key References Fenton *et al.* 1981, 1983, 1987, 1990, 1993; Hickey & Dunlop 2000; Van Cakenberghe & De Vree 1993.

Meredith Happold

Nycteris hispida HAIRY SLIT-FACED BAT

Fr. Nyctère hérissé; Ger. Gemeine Schlitznasen-Fledermaus

Nycteris hispida (Schreber, 1775). Die Säugethiere 1: 169, 188. Senegal.

Taxonomy Originally *Vespertilio hispidus*. Species-group: *hispida*. Synonyms: *daubentoni*, *martini*, *pallida*, *pilosa*, *poensis* and *villosa*. *Nycteris aurita*, sometimes considered a subspecies of *N. hispida*, is considered here to be a distinct species following Van Cakenberghe & De Vree (1993). Chromosome number (Somalia): 2n = 42; aFN = 78 (Lee *et al.* 1989).

Description Small to very small microbat with noseleaf comprised of a longitudinal slit bordered by fleshy outgrowths; one of the five smallest and most gracile species of *Nycteris* (FA: 34–44 mm); upper incisors tricuspid; posterior lower premolar small; posterior margin of tragus smoothly convex; E: 16–24 mm; Tib: 14–24 mm, 46.2 (36–56)% of FA. Sexes similar in colour; ♀♀ slightly larger on average than ♂♂. Pelage loose and fluffy; mid-dorsal hairs ca. 10 mm. Dorsal pelage variable: uniformly dark beige, greyish-brown or sepia brown; hairs unicoloured or with central portion paler. Ventral pelage paler to markedly paler than dorsal pelage; hairs darker at base. Ears short for a *Nycteris* and also relatively short (58 [50–71]% of FA). Tragus (Figure 93g) narrow (not semi-lunate); posterior margin smoothly convex without notch, upper margin rounded (cf. flattened in *N. woodi*). Eyes minute. Wings and interfemoral membrane blackish-brown. Tibia short for a *Nycteris* and also relatively short (46 [36–56]% of FA). Baculum tip ventrally hooked (Figure 94e, f and g) (Thomas *et al.* 1994).

Skull with sagittal crest very low or absent. Upper incisors tricuspid. Posterior lower premolar small (sometimes rising just above cingula of adjacent teeth but well below height of anterior cusp on first molar) and within tooththrow; anterior premolar and first molar well separated.

Geographic Variation Koopman (1994) considers *villosa* to be a valid subspecies, but Van Cakenberghe & De Vree (1993) found *N. hispida* to be very uniform throughout its entire geographic range.

Similar Species Only two other African *Nycteris* have tricuspid upper incisors (Table 18, p. 441):

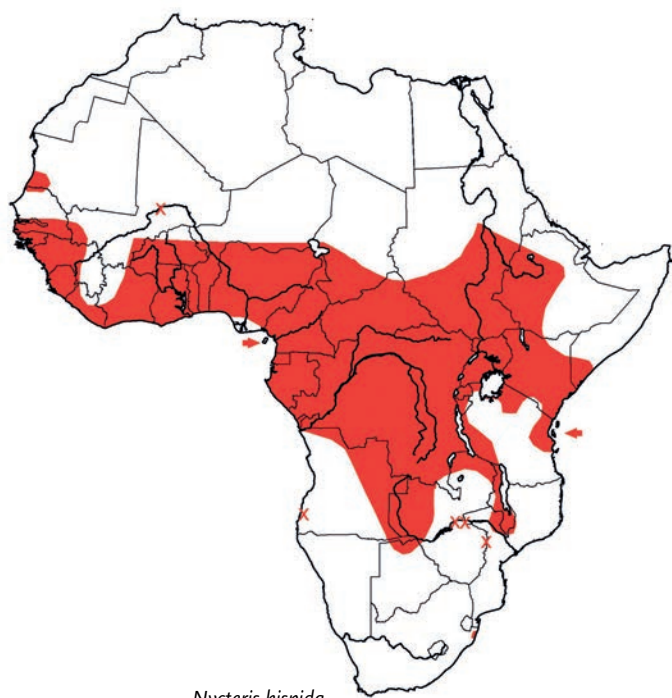
Nycteris aurita. Ears larger (24–31 mm), other measurements on average larger (FA: 41.6 ± 1.72 mm; GLS: 17.9 [17.2–18.3] mm; C–M³ (alv.): 5.9 [5.7–6.2] mm, M³–M³: 6.79 [6.2–7.2] mm; C–M₃ (alv.): 6.7 [6.4–7.5] mm). Best distinguished from *N. aurita* by multivariate analysis of skull measurements (Van Cakenberghe & De Vree 1993).

N. grandis: much larger (FA: 52–65 mm; GLS: 23.3–27.5 mm).

If the upper incisors are worn, *N. hispida* can be confused with *N. woodi* but, in the latter, the upper margin of the tragus is flattened (cf. rounded in *N. hispida*).

Distribution Endemic to Africa. Widely distributed in the Sudan and Guinea Savanna BZs (and marginally in Sahel Savanna Zone) and in the Rainforest BZ, Rainforest–Savanna Mosaics, Somalia–Masai Bushland BZ, Afromontane–Afroalpine BZ, Coastal Forest Mosaic BZ and Zambezian Woodland BZ. Recorded from Mauritania to Sudan, Ethiopia and Somalia, and southwards to Angola, Botswana and KwaZulu–Natal in South Africa. Also Bioko I. and Zanzibar I. Records from Cape of Good Hope are probably erroneous (Cotterill 1996a). Map based on Van Cakenberghe & De Vree (1993).

Habitat Can exploit a wide range of vegetation types, possibly because its roosting habits are comparatively unspecialized (Rosevear 1965). These include undifferentiated woodland and *Isobertinia* woodland, lowland rainforest and rainforest–savanna mosaics, miombo woodland and drier woodlands. Probably avoids grassland, montane and semi-arid habitats.



Nycteris hispida

Abundance Very common north of 10°S. One of the most common nycterids.

Adaptations Aspect ratio very low; wing-loading very low; wing-tip very rounded (M. Happold unpubl.). Flies slowly with very great manoeuvrability. Can take off from the ground, can hover briefly, turns by banking (minimum radius <25 cm) and by stalling-and-twisting. Individuals sustained flight within a 1×1×1 m enclosure for up to 93 circuits/flight (3 bats, 10 flights each; M. Happold unpubl.). Well known for its ability to dodge objects, moving and otherwise: rarely caught in mist-nets and extremely difficult to catch in butterfly nets, even if confined in small rooms (e.g. Lang & Chapin 1917b). By day, hangs freely from twigs of low bushes and trees, always in dense cover and complete shade (Verschuren 1957, Rosevear 1965). Also hangs under open banana leaves, from ridge-poles of grass- or mat-roofed houses, in hollow trees, dark cavities under exposed roots of trees in erosion gullies and ravines, disused huts, burrows (? Aardvark burrows), caves, road culverts, deep holes in the ground and in termitaria (Verschuren 1957, Rosevear 1965, Brosset 1966, Kock 1969a, Smithers & Wilson 1979, Kityo & Kerbis 1996, Grubb *et al.* 1998). In the Okavango Swamp, Botswana, roosts in dense beds of papyrus *Cyperus papyrus* (Archer 1977).

Foraging and Food Feeds on small moths and other insects (including praying mantises), which are caught by slow-hawking and gleaning from foliage and walls (and probably from the ground). In the Okavango Swamp, foraged along narrow channels through papyrus (Archer 1977). Often attracted to lighted rooms and verandas, and other lights, where insects are abundant, and sometimes returns regularly to such places (e.g. Grubb *et al.* 1998).

Social and Reproductive Behaviour Often found roosting singly, and less often in pairs and groups of 3–6. In Garamba N. P.,

NE DR Congo, Verschuren (1957) frequently observed pairs, and family groups comprised of an adult ♂ and ♀, a juvenile and a reproductively inactive adult. He also observed ca. 20 individuals in an extended patch of vegetation near the Garamba R. but it is not clear if this was one social unit or several separate small groups. In the Okavango, normally seen foraging singly; three seen together on one occasion (Archer 1977).

Reproduction and Population Structure Litter-size: one. Reproductive chronology uncertain. At ca. 4°N (Garamba N. P., NE DR Congo) Verschuren (1957) collected 2–6 ♀/month from Jan–Jul in 1951 and 1952: reproductively active ♀♀ were in synchrony with pregnancies in Jan–Mar, births in Apr and lactation until late Jun. The percentage of captured ♀♀ which were breeding in 1951 was 100%, and 84% in 1952. Verschuren (1957) also recorded one birth in Sep 1951, and one lactating ♀ in Nov 1951, but he obtained no other data for Aug–Dec 1951. The data are consistent with seasonal bimodal polyoestry. Furthermore, at 03°22'S (Mto-wa-mbo, Tanzania), Matthews (1941) reported signs of approaching oestrus in one recently lactating ♀ in Dec, and suggested ♀♀ have two litters/year with no overlap of pregnancy and lactation. Data from elsewhere are fragmentary and inconclusive. Neonates are naked; FA: ca. 15 mm. Carried by mother until at least half-grown. Reach adult-size in less than two months.

Predators, Parasites and Diseases Predators include a tree snake *Boiga blandingii* (Jones 1961). Ectoparasites include a flea *Lagaropsyllida idae* (Siphonaptera: Ischnopsyllidae); a bat-fly *Raymondia alulata* (Diptera: Streblidae); a tick *Amblyomma nuttalli* (Acari: Ixodidae); and ten species of mites (Acari: Macronyssidae, Demodicidae, Myobiidae, Trombiculidae, Erythetidae, Psorergatidae, Chirodiscidae, Gastronyssidae) (Anciaux de Faveaux 1984).

Conservation IUCN Category: Least Concern.

Measurements

Nycteris hispida

FA: 38.7 (34–44) mm, n = 742*

WS (d): 271.3 (265–280) mm, n = 4†

TL: 96.4 (89–106) mm, n = 49

T: 46.6 (41.0–56.5) mm, n = 55

E: 22.3 (16–24) mm, n = 58

Tr: n. d.

Tib: 18.1 (14–24) mm, n = 258*

HF: 9.4 (9–10) mm, n = 16

WT: 8.7 (6–12.3) g, n = 18

GLS: 16.5 (15.3–18.4) mm, n = 748*

GWS: 10.1 (8.8–12.0) mm, n = 678*

C–M³ (alv.): 5.3 (4.6–6.7) mm, n = 870*

Throughout geographic range (literature)

*Van Cakenberghe & De Vree 1993

†BMNH specimen labels

Key References Van Cakenberghe & De Vree 1993; Verschuren 1957.

Meredith Happold

Nycteris intermedia INTERMEDIATE SLIT-FACED BAT

Fr. Nyctère d'Aellen; Ger. Intermediäre Schlitznasen-Fledermaus

Nycteris intermedia Aellen, 1959. Archs. Sci. Genève 12: 218: Adiopodoumé, ca. 15 km WNW of Abidjan, Côte d'Ivoire.

Taxonomy Species-group: *arge*. Synonyms: none. Considered a synonym of *N. arge* by some authors (e.g. Rosevear 1965, Hayman & Hill 1971) but Eisentraut (1973a) and Van Cakenberghe & De Vree (1985) confirmed the species rank attributed by Aellen (1959). Chromosome number: not known.

Description Very small microbat with noseleaf comprised of a longitudinal slit bordered by fleshy outgrowths; one of the smallest and most gracile species of *Nycteris* (FA: 36–38 mm, GLS: 17.5–18.7); upper incisors bicuspid; posterior lower premolar large; tragus with marked concavity ('kink') in posterior margin; E: 20–24 mm; Tib: 18–21 mm, 50–58% of FA. Pelage loose and fluffy; mid-dorsal hairs ca. 9 mm. Dorsal pelage variable: medium brown, rusty-brown, reddish-brown to dark brown. Ventral pelage similar but paler. Ears broad and rounded, short for a *Nycteris* but of medium relative length, 63 (60–66)% of FA; dark brown or blackish with the basal third of the inner side much paler. Tragus with a well-defined concavity ('kink') at centre of posterior margin. Muzzle of naked appearance and pink. Wing-membranes dark brown or blackish-brown. Tibia comparatively short for a *Nycteris* but relatively long (54 [50–58]% of FA). Bacular morphology not known.

Upper incisors bicuspid. Posterior lower premolar comparatively large (rising well above cingula of adjacent teeth and equal or almost equal to height of anterior cusp of the first molar) and within toothrow.

Geographic Variation None.

Similar Species Three other African *Nycteris* have the following combination of characters: upper incisors bicuspid; posterior lower premolar large; tragus with posterior margin concave (Table 18, p. 441):

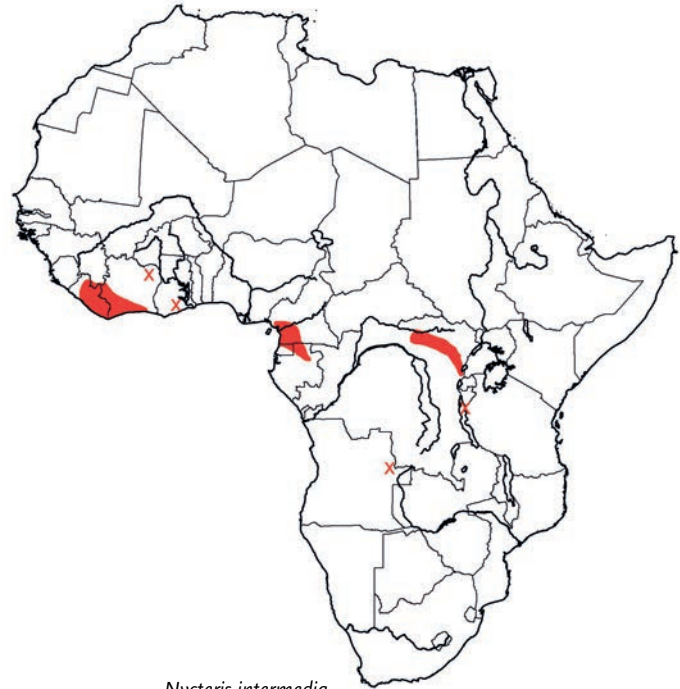
Nycteris nana. Smaller (FA: 32–37 mm; GLS: 15.6–17.0 mm). Tibia <47% of FA.

N. arge. Larger (FA: 39–46 mm; GLS: 19.2–20.4 mm). Ears comparatively longer, 25–34 mm. Concavity in posterior margin of tragus poorly defined.

N. major. Much larger (FA: 45–49 mm; GLS: 20.4–22.4 mm).

Distribution Endemic to Africa. Mainly recorded from the Rainforest BZ (Western, West Central, East Central and South Central Regions) and adjacent Rainforest–Savanna Mosaics, with two isolated records from the Zambezian Woodland BZ. Known from 27 localities in Guinea (Ziéla, Mt Nimba; MNHN), Liberia, Côte d'Ivoire, Ghana, Cameroon, Gabon (Brosset 1966 as *N. nana*), DR Congo, Tanzania (Howell & Wrangham 1974 as *N. nana*) and Angola.

Habitat Mainly recorded from lowland rainforest and coastal forest vegetation zones. Also recorded from Albert N. P., DR Congo,

*Nycteris intermedia*

which is situated in a transition zone between forest–savanna mosaic and the montane forests flanking the Albertine Rift, and from two localities in miombo woodland (Lucano, Angola; Gombe Stream N. P., Tanzania). The habitat at Gombe Stream N. P. was described as mixed deciduous woodland near gallery forest (Howell & Wrangham 1974). Where gallery and relict forests provide suitable habitat, these bats also penetrate into the southern Sudan savanna (Comoé N. P., Côte d'Ivoire).

Abundance Uncertain but appears to be quite rare. Within the *arge* species-group, rarer than *N. nana* and *N. arge* but more common than *N. major*.

Adaptations Day-roosts have rarely been reported. One bat was found in a cave leading vertically into the ground, another in an abandoned house (Brosset 1966 as *N. nana*; Eisentraut 1973a).

Foraging and Food Forages, by gleaning, close to the ground in the understorey of the forest. In Tai N. P. and Comoé N. P. (Côte d'Ivoire), the flight height (as determined by captures in mist-nets set 0–25 m above ground) was 1.4 (1.1–1.9) m, $n = 3$ (J. Fahr unpubl.). Sometimes flies into lighted rooms (Howell & Wrangham 1974). Probably gleans insects from the vegetation and probably also from the ground. Diet not known but likely to consist of rather soft-bodied arthropods.

Social and Reproductive Behaviour A pair was reported from an abandoned house in Gabon (Brosset 1966).

Reproduction and Population Structure Litter-size: not known but probably one. Reproductive chronology not known. At 05° 50' N (Taï N. P., Côte d'Ivoire) a pregnant ♀ was caught in early Mar. Two ♂♂ from Taï N. P. and Comoé N. P. (08° 45' N), caught in Aug and May respectively, had scrotal testes.

Predators, Parasites and Diseases No information.

Conservation IUCN Category: Least Concern.

Much more restricted to true rainforest than is *N. arge* and threatened by habitat loss in known localities.

Measurements

Nycteris intermedia

FA: 36.8 (36–38) mm, n = 16

WS (c): 244 (235–254) mm, n = 3

TL: 95.8 (84–105) mm, n = 8

T: 48.6 (41–53) mm, n = 13

E: 22.7 (20–24) mm, n = 13

Tib: 19.8 (18–21) mm, n = 16

HF: 8.6 (7–10) mm, n = 13

WT: 7.5 (6–9) g, n = 5

GLS: 18.1 (17.5–18.7) mm, n = 13

GWS: 10.6 (10.1–11.0) mm, n = 13

C–M³: 6.2 (6.0–6.4) mm, n = 13*

Guinea, Liberia, Côte d'Ivoire, Ghana, Cameroon (BMNH, CM, MHNG [type series], SMF, USNM)

The minimum FA length (33.7 mm) given by Van Cakenberghe & De Vree (1985) seems very small

*Not measured at level of alveoli (cf. most other *Nycteris* profiles).

Key References Aellen 1959; Van Cakenberghe & De Vree 1985.

Jakob Fahr

Nycteris macrotis LARGE-EARED SLIT-FACED BAT

Fr. Nyctère de Dobson; Ger. Großohrige Schlitznasen-Fledermaus

Nycteris macrotis Dobson, 1876. Monogr. Asiat. Chiroptera, p. 80. Sierra Leone.

Taxonomy Species-group: *macrotis*. Synonyms: *aethiopica*, *aurantiaca*, *guineensis*, *luteola*, *oriana*. Previously included *madagascariensis* as a synonym, but Peterson *et al.* (1995) consider this Madagascan form to be a distinct species. Hayman & Hill (1971) tentatively suggested that *aethiopica* (including *luteola*) might be a distinct species, but this view is not accepted by most authors, including Van Cakenberghe & De Vree (1985) and Simmons (2005). Sometimes considered to include *N. vinsoni* (but see species profile). Subspecies: uncertain (see Geographic Variation). Chromosome number (Somalia): 2n = 40; aFN = 74; this karyotype is unique for nycterids as a result of a chromosomal translocation involving the largest autosome (Lee *et al.* 1989).

Description Small microbat with noseleaf comprised of a longitudinal slit bordered by fleshy outgrowths; medium-sized for a *Nycteris*; upper incisors bicuspid, posterior lower premolar small; tragus semi-lunate with posterior margin smoothly convex, usually larger than other species in the *macrotis* group (FA: 48.2 ± 2.03 [40–55] mm). Sexes similar in colour; ♀♀ on average slightly larger than ♂♂. Pelage loose, fluffy; mid-dorsal hairs 9–12 mm. Dorsal pelage (grey-phase) sepia brown, reddish-brown, brownish-grey to grey; hairs with basal half paler than terminal half. Ventral pelage paler; most often pale grey. Orange-phase: dorsal pelage brownish-orange to bright orange; some grey-phase individuals exhibit an infusion of orange or rufous in the brownish pelage, especially on head and around neck. Ears long for a *Nycteris* but of medium relative length (65 [54–80]% of FA, n = 62). Tragus semi-lunate (half-moon shaped) with posterior margin smoothly convex (Figure 93f). Eyes small. Wings and interfemoral membrane greyish-brown to dark grey. Tibia of medium length for a *Nycteris* but relatively short (47 [37–53]% of FA). Baculum comparatively very long (3.84–5.12 mm); shaft long, parallel-sided, usually straight, thickening towards base; base with two basal lobes of varying development, in lateral view sometimes angled ventrally; tip expanded and trifold (Figure 94i, j and k; Thomas *et al.* 1994).

Skull with sagittal crest low but sharply defined anteriorly, absent posteriorly. Upper incisors bicuspid. Posterior lower premolar very small (not reaching above cingula of adjacent teeth), within toothrow or slightly displaced lingually.

Geographic Variation Uncertain. Van Cakenberghe & De Vree (1985) do not recognize any subspecies. In contrast, four African subspecies are recognized by Koopman (1994) and Simmons (2005):

N. m. macrotis: mainly in forest habitats from Gambia to Uganda and southwards to N Angola and S DR Congo.

N. m. aethiopica: mainly in savanna habitats from Senegal to Ethiopia.

N. m. luteola: NE DR Congo and S Somalia to Tanzania, including Zanzibar I.

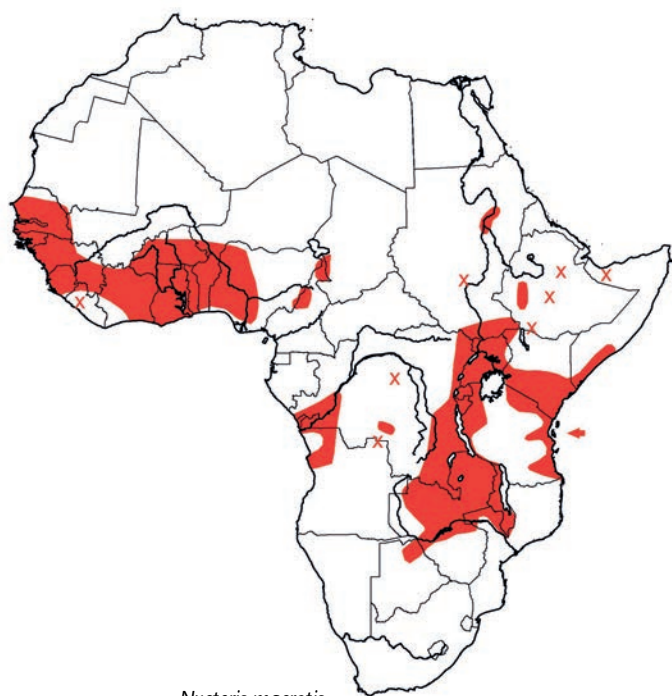
N. m. oriana: Tanzania, Malawi, Zambia, Zimbabwe.

Alternatively, it is possible that there are only two valid subspecies: *N. m. macrotis* in the Rainforest Zone and *N. m. aethiopica* (including *luteola* and *oriana*) in the savanna zones. It is also plausible that variation in *N. macrotis* is attributable solely to climate-related differences between forest and savanna habitats, and that subspeciation has not occurred at all (for a similar scenario, see *N. grandis*). Clearly, a pan-African investigation, using both morphological and genetic characters, is needed to elucidate the status of these forms.

Similar Species Only two other African *Nycteris* have the following combination of characters: upper incisors bicuspid; lower posterior premolar small; tragus with posterior margin convex (Table 18, p. 441):

Nycteris parisii. Usually smaller (FA: 40.0 [38–41] mm, n = 3).

Ventral pelage dark grey in the very few specimens for which there is information.

*Nycteris macrotis*

N. woodi. Usually smaller and less robustly built (FA: 39.3 ± 1.9 [36–42] mm). Ears usually relatively longer (79.5 [74–89]% of FA). Baculum tip simple and unexpanded.

Distribution Endemic to Africa. Recorded, disjunctly, from parts of the Sudan Savanna, Guinea Savanna, Rainforest, Afromontane–Afroalpine, Somalia–Masai Bushland, Coastal Forest Mosaic and Zambezian Woodland BZs, and from the Rainforest–Savanna Mosaics. Recorded from Senegal to Cameroon and SW Chad, from Congo, Angola and DR Congo, and from Sudan, Ethiopia and Somalia southwards to NE Botswana, the middle Zambezi valley in Zimbabwe, and Malawi. Also Zanzibar I. Map based on Van Cakenberghe & De Vree (1985) with some additional records (e.g. Cotterill 1996a). Gaps in the distribution, especially in Mozambique, probably reflect insufficient sampling.

Habitat In West Africa, mostly recorded from lowland rainforest and adjacent rainforest–savanna mosaic habitats, but also recorded in *Isoberlinia* woodland and undifferentiated woodland. In NE DR Congo, only recorded in savanna habitats and not in forests (Lang & Chapin [1917a] as *N. major*, but these specimens were re-identified as *N. macrotis* by Koopman [1965]). In Ethiopia, recorded from 515 to 2200 m (Largen *et al.* 1974). In Tanzania, recorded from a coastal forest (Cockle *et al.* 1998) as well as other habitats. In Malawi, recorded from miombo and mopane woodlands, riverine woodland and mosaics of thicket-clump, woodland and grassland savannas; 100–900 m (Happold *et al.* 1987). In southern Africa, mostly recorded below 1000 m, from riverine forests and riverine woodlands along permanent rivers and also seasonally dry waterways, in semi-arid savanna areas.

Abundance Uncertain. Comparatively uncommon in collections. Not common in West Africa according to Rosevear (1965), although ‘reasonably common’ in Senegal (T. S. Jones in Grubb *et al.* 1998).

Rarely encountered at the periphery of its geographic range in south-central Africa and southern Africa (Smithers 1983, Cotterill 1996a, P. D. F. Cotterill unpubl.). Widespread in Malawi, but uncommonly encountered (Happold & Happold 1997) except in Liwonde N. P. where 8 of 12 culverts investigated were occupied as day-roosts in April 1985 (Happold *et al.* 1987).

Adaptations Aspect ratio very low; wing-loading very low; wing-tip very rounded. Flight slow with great manoeuvrability. Can take off from the ground; probably able to hover briefly. Turns by banking (minimum radius <25 cm) and by stalling-and-twisting; individuals sustained flight within a 1×1×1 m enclosure for up to seven circuits/flight (4 bats, 10 flights each; M. Happold unpubl.). Day-roosts include hollow trees and logs, caves, abandoned mines and burrows, dry wells, dimly lit culverts under roads, dark cellars and human dwellings (Rosevear 1965, Poché 1975, Smithers 1983, Grubb *et al.* 1998). Hangs freely from ceilings. Sometimes roosts with *Hipposideros caffer* and *H. ruber*. At ambient temperatures of 20–24 °C, captive bats did not become torpid by day, and wild bats found in culverts during the cool-dry season in Malawi were active. Predicted mean maximum urine concentration is comparatively low (3257 mOsmol/kg), implying that *N. macrotis* is dependent on water for drinking (Happold & Happold 1988).

Foraging and Food Based on wing morphology, predicted to forage by hovering and gleaning, and its prey includes insects that are probably gleaned rather than taken in aerial pursuit (Whitaker & Black 1976, Findley & Black 1983). Stomach contents of five individuals from C Zambia contained predominantly large orthopterans (51% by volume), scarab beetles (27%) and termites (17%) (Whitaker & Black 1976).

Echolocation No information.

Social and Reproductive Behaviour Usually reported roosting singly or in small groups, but a colony of ca. 100 was found in a hollow baobab *Adansonia* in Senegal (Verschuren 1982). In 12 culverts in Liwonde N. P. (Malawi) in Apr, adult ♂♂ (with abdominal testes) were found roosting singly (n = 3); one group comprised one adult ♂ with scrotal testes, one ♀ with neonate, one adult ♀ (not palpably pregnant nor lactating) and three subadult ♀♀; a second group included one adult ♂ (testes scrotal), four adult ♀♀ (not palpably pregnant nor lactating) and two escapees; and a third group included an adult ♂ (testes scrotal) and one escapee. Nine years later, the same culverts contained only adult ♂♂ roosting singly (two with abdominal testes in Jan; one with abdominal testes and one with scrotal testes in Dec) (M. Happold unpubl.). The mating system cannot be determined from this limited data. Adults hang without touching neighbouring adults. In captivity, when a mother is resting, her baby hangs head-downwards with its feet hooked into the mother’s interfemoral membrane. If disturbed, the position of the young is rapidly adjusted before the mother flies away with the baby very firmly attached: the baby faces the mother’s head and holds on with its mouth attached to a nipple or pelage, its thumbs gripping the mother’s pelage or wing-membrane, and its toes gripping her pelage or interfemoral membrane. The thumbs and feet are very well developed, even in neonates.

Reproduction and Population Structure Litter-size: one. Reproductive chronology not known in detail. At 03° 22' S (Mto-wambo, Tanzania) in Dec, 2 of 13 adult ♀♀ were pregnant for the first time, two were lactating and also in oestrus, and nine were lactating and also pregnant (with foetuses up to 12 mm in length), indicating postpartum oestrus (Matthews 1939, 1941). The ovaries of these bats contained ripening follicles indicating the likelihood of a third oestrus cycle during the forthcoming lactation period, but the total number of litters/♀/year is not yet known. At ca. 15° S (Liwonde N. P., Malawi), 1 of 2 ♀♀ was post-lactating in Feb (the other subadult or inactive); 1 of 6 ♀♀ lactating and five post-lactating (also one neonate and one non-volant juvenile) in Apr; 1 of 1 lactating in Jun; no useful data for other months. These data are inconclusive, but indicate some births in wet season (ca. Dec) and early dry season (ca. Apr, May) and lack of close synchrony in ♀♀ (including those in same colony); no evidence to prove or disprove polyoestry in this population (Happold & Happold 1990a, M. Happold unpubl.).

Predators, Parasites and Diseases Ectoparasites include a bug *Eothenes nycteridis* (Hemiptera: Polyctenidae); bat-flies *Penicillidia pachymela*, *P. allisoni* (Diptera: Nycteribiidae), *Raymondia alulata*, *R. scopigera* (Diptera: Streblidae); and mites *Ancystropus zeleborii*, *Paraperiglischrus rhinolophinus*, *P. moucheti* (Acari: Spinturnicidae), *Bewsiella aelleni*, *Steatonyssus afer* (Acari: Macronyssidae), *Microtrombicula nycteris* (Acari: Trombiculidae), *Whartonia atracheata* (Acari: Leeuwenhoeekiidae), *Psorergatoides nycteris* (Acari: Psorergatidae) (Anciaux de Faveaux 1984).

Conservation IUCN Category: Least Concern.

Probably threatened by destruction of habitat by elephants and humans, in parts of its savanna range.

Measurements

Nycteris macrotis

FA: 48.2 (40–55) mm, n = 712*

WS (a): 341.8 (331–350) mm, n = 5†

TL: 116.0 (104–132) mm, n = 39

T: 55.0 (45–65) mm, n = 40

E: 31.4 (27–35) mm, n = 81

Tr: 10 mm, n = 1†

Tib: 22.7 (18–26) mm, n = 195*

HF: 12.3 (10–14) mm, n = 35

WT: 15.2 (11–18) g, n = 17

GLS: 20.5 (19.0–22.2) mm, n = 649*

GWS: 12.5 (10.4–13.8) mm, n = 649*

C–M³ (alv.): 7.0 (5.6–7.9) mm, n = 748*

Throughout geographic range (BMNH, HC, HZM, NMZB and literature)

*Van Cakenberghe & De Vree 1985

†Malawi only (M. Happold unpubl.)

Key References Rosevear 1965; Van Cakenberghe & De Vree 1985.

F. P. D. Cotterill & Meredith Happold

Nycteris major DJA SLIT-FACED BAT (JA SLIT-FACED BAT)

Fr. Nyctère du Dja; Ger. Dja Schlitznasen-Fledermaus

Nycteris major (K. Andersen, 1912). Ann. Mag. Nat. Hist., ser. 8, 10: 547. Dja River, Cameroon.

Taxonomy Originally *Petalia major*. Species-group: *arge*. Synonyms: *avakubia*. Considered a subspecies of *N. arge* by some authors, but Van Cakenberghe & De Vree (1985) and unpublished data (J. Fahr) show that it is a distinct species found in sympatry with *N. arge* at several localities (see Distribution). Chromosome number: not known.

Description Small microbat with noseleaf comprised of a longitudinal slit bordered by fleshy outgrowths; medium-sized for a *Nycteris* (FA: 47.5 ± 1.0 [45–49] mm, GLS: 20.4–22.4); upper incisors apparently bicuspid; posterior lower premolar large; tragus with marked concavity in posterior margin; E: 27–31 mm, Tib: 24–28 mm, 53–59% of FA. Not easily distinguished from *N. arge*. Pelage, loose, fluffy. Dorsal pelage variable: medium brown, rusty-brown to dark brown. Ventral pelage similar but paler. Ears broad and rounded; long for a *Nycteris* but of medium relative length (62 [58–65]% of FA). Tragus with well-defined concavity ('kink') at centre of posterior margin. Muzzle of naked appearance and pink. Wing-membranes blackish-brown. Tibia long for a *Nycteris* and also relatively long (56 [53–59]% of FA). Bacular morphology not known.

Skull with sagittal crest moderately to well developed. Upper incisors apparently usually bicuspid, but one specimen from Cameroon had unicuspid inner upper incisors (Perret & Aellen

1956). Posterior lower premolar comparatively large (reaching well above cingula of adjacent teeth and equal or almost equal to height of anterior cusp of first molar) and within tooththrow.

Geographic Variation Uncertain. Specimens from central Africa might average somewhat larger.

Similar Species Three other African *Nycteris* have the following combination of characters: upper incisors bicuspid; posterior lower premolar large; tragus with posterior margin concave (Table 18, p. 441):

Nycteris nana. Much smaller (FA: 32–37 mm; GLS: 15.6–17.0 mm).

N. intermedia: Much smaller (FA: 36–38 mm; GLS: 17.5–18.7 mm).

N. arge. Almost always smaller (FA: 42.1 ± 1.0 [39–46] mm; GLS: 19.9 [19.2–20.4] mm). Concavity in posterior margin of tragus poorly defined. According to Eisentraut (1956) the claws of thumbs and feet are more pointed and slender in *N. arge* than in *N. major*, but this was questioned by Rosevear (1965) and Van Cakenberghe & De Vree (1985). In some specimens there is overlap in univariate measurements between *N. arge* and *N. major* and multivariate analysis is needed to distinguish between them (Van Cakenberghe & De Vree 1985).



Distribution Endemic to Africa. Apparently restricted to the Rainforest BZ (Western, West Central, East Central and South Central Regions). Known from only 12 localities in Guinea (Ziéla, Mt Nimba; MNHN), Liberia, Côte d'Ivoire, Cameroon, DR Congo and Zambia (Van Cakenberghe & De Vree 1985, J. Fahr unpubl.). A record from Bimbereke (Benin) by Robbins (1980) was based on a misidentified *N. macrotis* (J. Fahr unpubl.). Specimens from Boma and Macaco (DR Congo), originally published as *N. major* by Kershaw (1923) and Schouteden (1947), have been re-identified as *N. macrotis* by Hayman *et al.* (1966) and Van Cakenberghe & De Vree (1985). A record from Yankari G. R., Nigeria, based on teeth and bones from owl pellets (Demeter 1981) is excluded here as it is more likely to be that of *N. macrotis* – it seems difficult at best to distinguish *N. major* and *N. macrotis* with certainty from bones and teeth alone, and the habitat (Sudan Savanna BZ, 09° 45'N) is almost certainly unsuitable for *N. major*. *Nycteris major* has been found sympatrically with *N. arge* near Mt Nimba (Liberia, Guinea), in Taï N. P. (Côte d'Ivoire), near Dja R. (Cameroon) and Avakubi (DR Congo).

Habitat Mainly recorded in lowland rainforest and coastal forest, but also recorded from one locality in flooded grassland with areas of Itigi thicket and woodland (Mweru Wantipa, Zambia; Ansell 1978).

Abundance One of the rarest nycterids and by far the rarest species in the *N. arge* group.

Adaptations Has been found by day in large, hollow, standing trees with holes near the base. A single specimen was found in a house (Lang & Chapin 1917b, as *N. avakubia*). The roosts are commonly shared with *Hipposideros cyclops* and, in one case, also with the mouse *Praomys tullbergi* (Eisentraut 1956, Verschuren 1976, Fedden & Macleod 1986).

Foraging and Food Forages close to the ground in the understorey of the forest. In Taï N. P., Côte d'Ivoire, a single individual was captured at a height of 1.9 m. Presumably gleans its prey from the vegetation and probably also from the ground. Details of diet not known: presumably arthropods, and, based on this bat's size, might also include small vertebrates.

Social and Reproductive Behaviour Found singly or in small groups. One non-reproductive group consisted of one adult ♂ and two adult ♀♀ (Cameroon; Eisentraut 1956). In Liberia, Verschuren (1976) found a pair in one hollow tree and a single ♂ in another. One pregnant ♀ roosted singly (Fedden & Macleod 1986).

Reproduction and Population Structure Litter-size: one. Reproductive chronology: not known. At 04° 38'N in Cameroon, a pregnant ♀ was reported in Jan (Fedden & Macleod 1986), and at 07° 30'N (near Mt Nimba, Liberia), another (with a 4 g foetus) was reported in mid-Feb (Verschuren 1976). At 06° 54'N in Côte d'Ivoire, a ♀ with a juvenile was captured in early Mar (USNM). For all of these localities, there are no data for other months, and therefore the limited observations are inconclusive.

Predators, Parasites and Diseases No information.

Conservation IUCN Category: Data Deficient.

Its population trend, the extent of its occurrence in central Africa, and its natural history and major threats are not known, but this species is probably threatened by fragmentation and decline of suitable habitat. Known from only 12 localities and ca. 16 specimens. Apparently largely dependent on forest habitat and might be much more affected by degradation and logging than any other nycterid.

Measurements

Nycteris major

FA: 47.5 (45–49) mm, n = 12

WS (c): 311, 314 mm, n = 2

TL: 122.9 (106–137) mm, n = 6

T: 60.3 (55–64) mm, n = 7

E: 29.2 (27–31) mm, n = 8

Tib: 26.3 (24–28) mm, n = 12

HF: 10.3 (10–12) mm, n = 8

WT: 12.6 (8.0–16.0) g, n = 6

GLS: 21.0 (20.4–22.4) mm, n = 9

GWS: 12.5 (12.0–12.9) mm, n = 9

C–M³: 7.3 (7.0–7.8) mm, n = 11*

Guinea, Liberia, Côte d'Ivoire, Cameroon (IRSN, MHNG, MNHN, SMF, SMNS, USNM)

*Not measured at level of alveoli (cf. most other *Nycteris* profiles)

Key References Eisentraut 1956; Van Cakenberghe & De Vree 1985

Jakob Fahr

Nycteris nana DWARF SLIT-FACED BAT

Fr. Nyctère naine; Ger. Kleinste Schlitznasen-Fledermaus

Nycteris nana (K. Andersen, 1912). Ann. Mag. Nat. Hist., ser. 8, 10: 547. Benito River, Equatorial Guinea.

Taxonomy Originally *Petalia nana*. Species-group: *arge*. Synonyms: *tristis*. Subspecies: none. Chromosome number: not known.

Description Very small microbat with noseleaf comprised of a longitudinal slit bordered by fleshy outgrowths; marginally the smallest species of *Nycteris* (FA: 32–37 mm, GLS: 15.6–17.0 mm); upper incisors bicuspid; posterior lower premolar large; tragus with marked concavity in posterior margin; E: 19–23 mm; Tib: 14–17 mm, 40–47% of FA. Sexes similar. Pelage loose, fluffy; mid-dorsal hairs 7–11 mm. Dorsal pelage variable: medium to dark brown. Ventral pelage similar but paler. Verschuren (1957) reported an albino from Garamba N. P., DR Congo. Ears broad and rounded, short for a *Nycteris* and also relatively short (60 [53–66]% of FA); dark brown or blackish with basal third of inner side much paler. Tragus with a well-defined concavity ('kink') at centre of the posterior margin. Muzzle of naked appearance and pink. Noseleaf, tragus and chin usually whitish or cream. Wings and interfemoral membrane dark brown or blackish-brown. Tibia short for a *Nycteris* and also relatively short (44 [40–47]% of FA). Baculum tip simple (Figure 94b; Thomas *et al.* 1994).

Skull with sagittal crest absent or consisting merely of an anterior rudiment. Upper incisors bicuspid. Posterior lower premolar comparatively large (reaching well above cingula of adjacent teeth and equal or almost equal to height of anterior cusp of first molar) and in toothrow.

Geographic Variation None.

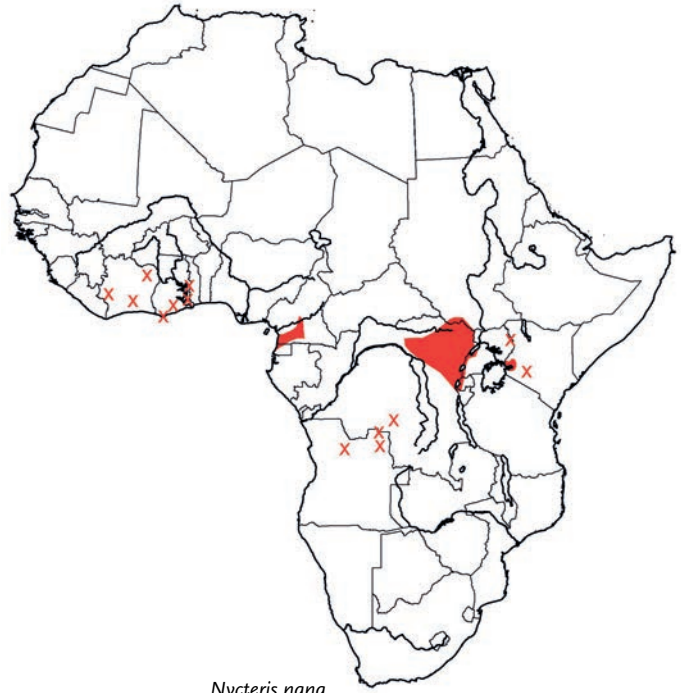
Similar Species Three other African *Nycteris* have the following combination of characters: upper incisors bicuspid; posterior lower premolar large; tragus with posterior margin concave (Table 18, p. 441):

Nycteris intermedia. Larger (FA: 36–38 mm; GLS: 17.5–18.7 mm). Tibia >50% of FA.

N. arge. Much larger (FA: 39–46 mm; GLS: 19.2–20.4 mm). Tibia >48% of FA. Ears comparatively longer (25–34 mm). Concavity in posterior margin of tragus poorly defined.

N. major. Much larger (FA: 45–49 mm; GLS: 20.4–22.4 mm).

Distribution Endemic to Africa. Apparently restricted to the Rainforest BZ (Western, West Central, East Central and South Central Regions), the Rainforest–Savanna Mosaics, and Afromontane–Afroalpine BZ within or near these zones. Known from Côte d'Ivoire, Ghana, Cameroon, Equatorial Guinea (excluding Bioko I.), Sudan, DR Congo, Uganda, Burundi (Bukinyanya, Kibira N. P., FMNH), Kenya and Angola. The distribution is patchy but this species is regularly recorded and therefore the gaps are not likely to only reflect insufficient sampling. Records from Gombe Stream N. P., Tanzania (Howell & Wrangham 1974) and Bengoué, Gabon (Brosset 1966) have been re-identified as *N. intermedia* (Van Cakenberghe & De Vree 1985).

*Nycteris nana*

Habitat In contrast to other members of the *arge* species-group, *N. nana* is often recorded from drier types of forest and seems to avoid the wettest parts of West Africa in Sierra Leone, Liberia, Côte d'Ivoire and Ghana. About half of the locality records are in rainforest–savanna mosaic, and most other localities are in lowland rainforest (both wetter and drier types), and montane forests flanking the Albertine Rift. Less often recorded in coastal forest, *Acacia–Commiphora* bushland and thicket, and *Isoberlinia* woodland.

Abundance Uncertain. Within the *arge* species-group, much rarer than *N. arge* but much more common than either *N. intermedia* or *N. major*.

Adaptations Occupies a wide variety of day-roosts and has been found in standing hollow trees, in caves, mines, culverts, in a hole of a Giant Pangolin, and under a bridge (in a narrow gap near the pier) (Verschuren 1957, Kingdon 1974, Heller *et al.* 1994, J. Fahr unpubl., MHNG, ROM). In NE DR Congo, found regularly in the upper parts of hollow trunks of *Canarium schweinfurthii*, *Halea stipulosa*, *Macaranga* sp., *Pseudospondia microcarpa*, *Randia* sp., *Spondianthus preussii* and *Syzygium guineense* (Verschuren 1957). Rosevear (1965) noticed that most of these trees are typical of younger secondary regrowth rather than mature forest. However, Rosevear (1965) concluded that the actual species of tree is unlikely to be of importance, provided a suitable cavity is present. When disturbed at their roosts during the day, individuals readily take flight (Verschuren 1957, Kingdon 1974, J. Fahr unpubl.). One ♀ roosted in a hollow tree (*Randia* sp.) that was also occupied by a Barn Owl *Tyto alba* (Verschuren 1957).

Foraging and Food Forages close to the ground in the understorey of the forest. In Comoé N. P. (Côte d'Ivoire), two individuals were captured 1.1 m above ground, in mist-nets set 0–25 m above ground (J. Fahr unpubl.). Gleans insects from vegetation and probably also from the ground. Diet not known but likely to consist of rather soft-bodied arthropods.

Social and Reproductive Behaviour Usually found in small groups or pairs, either with or without young (Verschuren 1957, Heller *et al.* 1994). Kingdon (1974) found a pair inhabiting a hole dug by a Giant Pangolin *Smutsia gigantea* over a period of eight years, although he could not determine if they were the same individuals.

Reproduction and Population Structure Litter-size: one (n = 4) (Verschuren 1957). According to Verschuren (1957), the reproductive chronology at 04° 10' N (Garamba N. P., NE DR Congo) is seasonal monoestry, but this needs confirmation. Verschuren (1957) reported pregnant ♀♀ in Jan–Apr (n = 4), lactating ♀♀ from Mar–May (n = 5) and a post-lactating ♀ with a juvenile in May (but he did not give data for other months and did not mention if ♀♀ in other reproductive states were captured during this period). The young are suckled for 45–60 days (Verschuren 1957). Data from other localities are inconclusive.

Predators, Parasites and Diseases No information.

Conservation IUCN Category: Least Concern.

Measurements

Nycteris nana

FA: 34.4 (32–37) mm, n = 14

WS (c): 217 (215–220) mm, n = 3

TL: 87.4 (80–93) mm, n = 10

T: 43.1 (37–49) mm, n = 10

E: 21.1 (19–23) mm, n = 10

Tib: 15.3 (14–17) mm, n = 14

HF: 8.4 (7–10) mm, n = 10

WT: 5.5 (4.5–7.0) g, n = 7

GLS: 16.2 (15.6–17.0) mm, n = 11

GWS: 8.8 (8.5–9.4) mm, n = 11

C–M³: 5.4 (5.1–5.7) mm, n = 12*

Côte d'Ivoire, Ghana, Equatorial Guinea (holotype), Cameroon, DR Congo, Sudan, Burundi, Kenya, Angola (BMNH, FMNH, MHNG, SMF, USNM)

*Not measured at level of alveoli (cf. most other *Nycteris* profiles)

Key References Van Cakenberghe & De Vree 1985; Verschuren 1957.

Jakob Fahr

Nycteris parisii PARISI'S SLIT-FACED BAT

Fr. Nyctère de Parisi; Ger. Parisis Schlitznasen-Fledermaus

Nycteris parisii (De Beaux, 1923, [publ. 1924]). Atti. Soc. Ital. Sci. Nat. 42: 254. Ballei Uen, lower Uebi Scebeli, Somalia (see Hill 1975: 507).

Taxonomy Originally *Petalia parisii*. Species-group: *macrotis*. Synonyms: *benuensis*. Subspecies: none. Based on similarities in craniodental measurements, considered a synonym of *N. woodi* by Van Cakenberghe & De Vree (1985), Koopman (1993) and Griffiths (1994), but considered to be a distinct species by Rosevear (1965), Hayman & Hill (1971), Thomas *et al.* (1994) and Simmons (2005). Although *N. parisii* is very similar to *N. woodi* in craniodental proportions (notably widths and lengths of maxillary and mandibular tooththrows; Van Cakenberghe & De Vree 1985), the baculum of *parisii* is most similar in morphology to that of *N. macrotis* (Thomas *et al.* 1994). Chromosome number: not known.

Description Very small microbat with noseleaf comprised of a longitudinal slit bordered by fleshy outgrowths; one of the five smallest and most gracile species of *Nycteris* (FA: 38–41 mm); upper incisors bicuspid; posterior lower premolar small; tragus semi-lunate with posterior margin usually smoothly convex; E: 20–23 mm, 54.4 (51–56)% of FA. Not easily distinguished from *N. woodi*. A very poorly known species. Sexual dimorphism: no information. Pelage soft, loose and fluffy; mid-dorsal hairs ca. 10 mm. Dorsal pelage brownish-grey; hairs slightly paler at base. Ventral pelage dark grey. Ears short for a *Nycteris* (20–23 mm), and relatively short (54.4 [51–56]% of FA, n = 3) (cf. *N. woodi*). Tragus semi-lunate; posterior margin smoothly convex (similar to *N. macrotis*, Figure 93f); lobe at base of posterior margin comparatively large and laterally orientated (cf. *N. woodi*). Eyes

small. Wings and interfemoral membrane brown. Tibia of medium length for a *Nycteris* and also of medium relative length (52 [48–56]% of FA, n = 3). Baculum comparatively large (4.30 mm, n = 1); shaft long, parallel-sided, essentially straight, thickening towards base; base expanded, in lateral profile angled ventrally; tip expanded, trifid with three variably developed processes (Thomas *et al.* 1994).

Upper incisors bicuspid. Lower posterior premolar very small (not rising above cingula of adjacent teeth) and in tooththrow.

Geographic Variation None recorded.

Similar Species Only two other African *Nycteris* have the following combination of characters: upper incisors bicuspid; lower posterior premolar small; tragus with posterior margin convex (Table 18, p. 441):

Nycteris macrotis. Usually larger (FA: 48.1 [40–55] mm). Ventral pelage not dark grey (most often pale grey).

N. woodi. Ears comparatively longer (28–35 mm) and relatively longer (79.5 [73–89]% of FA). Baculum shorter (2.5–2.7 mm), with tip unexpanded and simple. Ventral pelage paler to much paler than dorsal pelage (sometimes almost white).

Distribution Endemic to Africa. Only known from the Sudan Savanna BZ in N Cameroon, and from the Somalia–Masai Bushland



Nycteris parisii

BZ and Coastal Forest Mosaic BZ in Ethiopia and Somalia. Recorded from Lower Shabeelle and the Jubba Valley in Somalia (De Beaux 1923b, Varty & Hill 1988), NE of L. Stephanie, Gemu Gofa in Ethiopia at 500 m (Hill 1975), and Rei Bouba on a tributary of the Benue R. in N Cameroon (Aellen 1952, as *N. benuensis*). A specimen from S Tanzania (BMNH 64.1473), provisionally identified as *N. p. benuensis* by Hayman & Hill (1971), is considered here to represent *N. woodi*.

Habitat The type locality is believed to be near a well or waterhole where there was a temporary marsh in the wet season (Zammarano 1930, in Hill 1975). The specimen from Jubba Valley was taken in riverine forest on bank of Jubba R. At this locality, many of the trees and shrubs are evergreen, individual trees reach 30 m but the

overstorey is typically only 10–15 m high, and the rainfall is bimodal (Apr–Jun and Oct–Dec) (Varty & Hill 1988). The N Cameroon specimens were collected from an area of degraded savanna and woodland near the river, where swamps or marshes were important (Aellen 1952).

Abundance Uncertain. Presumably rare as apparently only five specimens have been collected.

Remarks One of the most poorly known African bats. Nothing else is known of its biology.

Conservation IUCN Category: Data Deficient.

Measurements

Nycteris parisii

FA: 40.0 (38–41) mm, n = 3

WS: n. d.

TL: 90, 97 mm, n = 2

T: 44, 50 mm, n = 2

E: 21.8 (20–23) mm, n = 3*

Tr: n. d.

Tib: 20.7 (18–23) mm, n = 3

HF: 9, 9 mm, n = 2

WT: 7.2 g, n = 1

GLS: 17.1 (16.4–17.4) mm, n = 3

GWS: 10.1 (10.1–10.2) mm, n = 3

C–M³ (alv.): 5.4 (5.2–5.6) mm, n = 3

Cameroon and Somalia (Rosevear 1965, Hill 1975, V. Van Cakenberghe pers. comm., Varty & Hill 1988)

*Ear length for the Somali specimen (given as 30 mm by Varty & Hill 1988) was remeasured and found to be 23 mm

Key References Hill 1975; Rosevear 1965; Thomas *et al.* 1994; Van Cakenberghe & De Vree 1985; Varty & Hill 1988.

F. P. D. Cotterill

Nycteris thebaica EGYPTIAN SLIT-FACED BAT

Fr. Nyctère de la Thébaïde; Ger. Ägyptische Schlitznasen-Fledermaus

Nycteris thebaica E. Geoffroy, 1818 (1813 in some publications). Descrip. de l’Egypte 2: 119. Thebes (near Luxor), Egypt.

Taxonomy Species-group: *thebaica*. Synonyms in Africa: *adana*, *affinis*, *albiventer*, *angolensis*, *aurantiaca*, *brockmani*, *capensis*, *damarensis*, *discolor*, *fuliginosa*, *geoffroyi*, *labiata*, *media*, *revoilii*, *senegalensis*. Also *aethiopicus* (*nomen nudum*). Subspecies: seven; six in Africa. Chromosome number (Zimbabwe, Namibia, South Africa): 2n = 42; aFN = 78 (Peterson & Nagorsen 1975, Rautenbach *et al.* 1993).

Description Small microbat with noseleaf comprised of a longitudinal slit bordered by fleshy outgrowths; medium-small for a *Nycteris*; upper incisors bicuspid; posterior lower premolar very small; tragus pear-shaped with posterior margin deeply notched; E: 28–39 mm. Not easily distinguished from *N. gambiensis* but, in West Africa where the two species are sympatric, *N. thebaica* is on average

the larger species (FA: 44.0 ± 1.31 mm; Tib: 22.24 ± 1.06 ; GLS: 18.68 ± 0.43 ; Van Cakenberghe & De Vree 1998). Sexes similar in colour; ♀♀ slightly larger on average than ♂♂ in some series. Pelage soft, fluffy; mid-dorsal hairs ca. 10 mm. Dorsal pelage pale grey, beige, reddish-brown to dark brown; individuals from drier areas paler; hairs unicoloured or grey at base. Ventral pelage paler to much paler than dorsal, often greyish-white, sometimes almost white. Some individuals have a reddish ruff. In orange-phase, dorsal pelage bright orange. Ears long for a *Nycteris*, but of medium relative length (70 [56–88]% of FA). Tragus inverted pear-shaped with deep notch in posterior margin, tip hairy (Figure 93h). Eyes minute. Wings and interfemoral membrane dark grey or greyish-brown. Tibia of medium length for a *Nycteris* (24.0 [21–26] mm), and of

medium relative length (49 [38–61]% of FA). Baculum tip simple (Thomas *et al.* 1994).

Skull with sagittal crest low. Upper incisors bicuspid. Anterior lower premolar minute (not rising above cingula of adjacent teeth), sometimes within toothrow, sometimes displaced lingually to a greater or lesser extent, but anterior lower premolar and first molar usually separated by pronounced gap.

Geographical Variation Gray *et al.* (1999) list and map six African subspecies, but comment that the subspecific classification is uncertain:

N. t. brockmani: S Somalia, Djibouti, NE Ethiopia.

N. t. thebaica: Egypt and N Sudan to Senegal, and also Morocco.

N. t. labiata: N Ethiopia and C Sudan to N Tanzania and Uganda.

N. t. capensis: S Tanzania, SE DR Congo and Zambia to Cape of Good Hope.

N. t. angolensis: Coastal SW Angola.

N. t. damarensis: SC Angola, Namibia and Botswana.

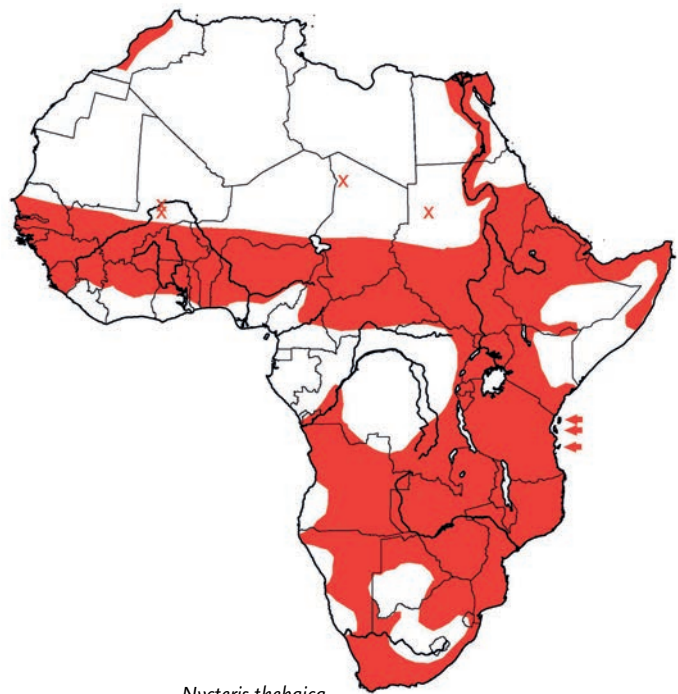
The subspecies differ in body and skull measurements; colour variation does not follow a geographic pattern (Van Cakenberghe & De Vree 1998) although individuals from drier habitats are sometimes paler.

Similar Species Only one other African *Nycteris* has the following combination of characters: upper incisors bicuspid; posterior lower premolar small; tragus (without doubt) pear-shaped with posterior margin deeply notched (Table 18, p. 441):

Nycteris gambiensis: ventral pelage only slightly paler than dorsal pelage; on average smaller (FA: 40.1 ± 1.4 mm; Tib: 19.9 ± 0.99 mm; GLS: 17.58 ± 0.36 mm); for comparison, see Similar Species of *N. gambiensis* for measurements of West African *N. thebaica*. Anterior lower premolar and anterior molar in contact or almost so. West Africa and Cameroon only.

Nycteris vinsoni, if proved to have a pear-shaped tragus with a notch in the outer margin, is probably a valid species (see profile), which also resembles *N. thebaica* but is probably, on average, larger (FA: 51 mm). Mozambique.

Distribution In Africa, known from the Mediterranean Coastal BZ in Morocco (eight localities), and from the Nile Valley in the Sahara Arid BZ. South of the Sahara, very widespread and recorded from all biotic zones although only very marginally in the Rainforest BZ and apparently absent throughout much of the Somalia–Masai Bushland BZ. The apparent gap between Morocco and Senegal possibly reflects insufficient sampling (Van Cakenberghe & De Vree 1998). Occurs on Mafia I. (Kock & Stanley 2009) as well as on Pemba I. and Zanzibar I. Extraliminally: Israel, Sinai, central Arabia. Has the largest distribution of any nycterid. Map based on Van Cakenberghe & De Vree (1998). Maps drawn by Kingdon (1974), Smithers (1983) and Gray *et al.* (1999) indicate occurrence in several regions for which there are apparently no records (e.g. Algeria, Tunisia, Libya, most of C and S Somalia, large parts of the South-West Arid BZ and much of the Highveld Grassland BZ).



Nycteris thebaica

Habitat In NE Africa, found in riverine habitats near Nile R. In West, north-central and eastern Africa, mostly open woodland savannas, and riverine or oasis habitats in more arid regions; also montane habitats in Ethiopian Highlands and occasionally clearings in lowland rainforest. In Zambia and Malawi, widespread in woodland savannas but not yet recorded from montane habitats (Ansell 1978, Happold *et al.* 1987). In southern Africa, mainly found in woodland savannas but also found in dense coastal and riverine forests; possibly limited to riverine habitats in arid regions; not known from colder Highland, Montane and Mistbelt bioregions (Smithers 1983, Taylor 2000, R. T. F. Bernard unpubl.).

Adaptations Aspect ratio very low; wing-loading very low; wing-tip very rounded (Figure 92). Flies slowly with great manoeuvrability. Can take off from ground and hover briefly; turns by banking (minimum radius <25 cm) and by stalling-and-twisting. Individuals sustained flight within a 1×1×1 m enclosure for up to seven circuits/flight (5 bats, 10 flights each; M. Happold unpubl.). By day, hangs freely from ceilings of caves and cave-like places (including mines, tombs, military bunkers, thatched huts and other buildings), rock crevasses, hollow trees, cavities under roots, Aardvark burrows, holes in termitaria, road culverts, wells, pit-latrines and fireplaces. Great manoeuvrability allows it to fly to roost-sites inaccessible to bats belonging to other families, but it sometimes shares more accessible day-roosts with other bats, including species of *Rousettus*, *Taphozous*, *Rhinolophus*, *Asellia*, *Myotis* and *Miniopterus*. Some switching between different roosts was observed during an 8-day study by Aldridge *et al.* (1990); sometimes this is a response to the presence of predatory *Nycteris grandis*. Migration occurs in South Africa, possibly in response to fluctuations in availability of food and the need for more food while reproducing (Bernard 1980a). In KwaZulu–Natal (South Africa), coastal roosts are occupied year-round but inland roosts are occupied only in winter (Bernard 1982a). Does not become

torpid during day under natural temperature regimes (Happold & Happold 1988), and does not hibernate (Bernard 1982a). Predicted mean maximum urine concentration is comparatively low (2886 mOsmol/kg), implying dependence on water for drinking (Happold & Happold 1988). In captivity, feeds well but often refuses to drink and dies after 4–5 days. For information published since this profile was submitted, see Monadjem (2006a, 2006b) and Monadjem *et al.* (2009, 2010).

Abundance Uncertain, but common in collections and thought to be common (at least locally) throughout much of geographic range.

Foraging and Food Forages for volant and non-volant arthropods by slow-hawking, fly-catching, foliage-gleaning and ground-gleaning, in places of moderate to dense clutter including in, under and just above tree canopies, in undergrowth, over streams, near lights and buildings (e.g. Fenton *et al.* 1983, Lindeque 1987, Aldridge *et al.* 1990, Seamark & Bogdanowicz 2002). Often forages very near ground; based on wing morphology, probably forages within short distance of day-roost. While fly-catching or ground-gleaning from a perch, hangs by one foot, rotates the body and turns the head while listening for prey-generated sounds. In response to sounds, directs the head towards the source, moves the ears rapidly to and fro, and then attacks – possibly using vision (in spite of its minute eyes) as well as echolocation to locate the prey's exact position. Volant prey taken in flight. Non-volant prey taken by hovering and gleaning from leaves, branches, walls, rockfaces and other surfaces. Alternatively, lands on ground, envelops the prey with the wings and uses the interfemoral membrane to transfer it to the mouth. Small insects (<14 mm) are consumed immediately; larger prey is taken back to the perch. Wings and legs of prey are usually discarded and accumulate under regularly used perches. Feeds opportunistically on wide variety of insects including Orthoptera, Coleoptera, Hemiptera and Lepidoptera (primary prey), and Homoptera, Isoptera, Neuroptera, Hymenoptera and Diptera, and possibly prefers hard-shelled prey (e.g. Fenton & Thomas 1980, LaVal & LaVal 1980, Seamark & Bogdanowicz 2002). Wings of the African bollworm *Helicoverpa armigera*, which is an agricultural pest, have been found under a feeding-perch on the coast of the Eastern Cape Province of South Africa (R. T. F. Bernard pers. obs.). Also eats scorpions (Scorpiones) and sun-spiders (Solifugae) (Felten 1956). Geckos, a frog and a small fish were reported in the diet by Seamark & Bogdanowicz (2002), but vertebrates are probably eaten only rarely (cf. *N. grandis*). Diet is influenced by seasonal changes in both absolute and relative abundance of different insects, geographical area and the condition of the bat (reviewed by Seamark & Bogdanowicz 2002). However, a year-round investigation in KwaZulu–Natal showed that prey varied significantly by order but not by season, although a significant interaction between prey-category and season suggested that these two factors are not independent from each other (Seamark & Bogdanowicz 2002). These authors conclude that dietary flexibility combined with versatile foraging behaviour has allowed this species to inhabit a variety of habitats over a wide geographic range.

Echolocation Echolocation calls (phase unspecified) are very low intensity, short duration (<2 ms), multi-harmonic, broad bandwidth,

steep FM sweeps. Data and sonogram in Taylor (2000) indicate that the fundamental frequency falls from ca. 27 to 20 kHz and that much energy is also placed in the second and third harmonics. The calls can only be picked up within 50 cm of bat-detectors.

Social and Reproductive Behaviour Usually roosts in groups of three to several hundred; occasionally roosts singly or in pairs. Adults hang apart in loose aggregations. In Swaziland, where roosts are occupied throughout the year, the ratio of ♂♂ to ♀♀ is 1 : 0.4 (A. Monadjem pers. comm.). Thirteen of 15 culverts under a 3 km long road were occupied by six groups of ♀♀; ♀♀ tended to show fidelity to one culvert but occasionally roosted in adjacent culverts. Males also roosted in these culverts, but probably moved between non-adjacent culverts more often than the ♀♀ (A. Monadjem pers. comm.). Bats at day-roosts, and also when hanging within 2 m of each other at night-roosts, emit a comparatively long and high intensity, tonal, narrow-bandwidth vocalization (audible to humans), which sometimes attracts other conspecifics (Aldridge *et al.* 1990). A comparatively long and high intensity, broad bandwidth call (also audible to humans) is emitted by bats leaving the roost. Courtship behaviour includes 'frenzied' flying, head-butting in flight and neck-biting; copulation occurs while the bats hover, and is repeated several times (Lindeque 1987). At dusk, mothers carry their young, attached to a nipple, away from the day-roost, possibly to avoid predation by *N. grandis* (Aldridge *et al.* 1990).

Reproduction and Population Structure Litter-size: one. At ca. 29°S (KwaZulu–Natal, South Africa), the reproductive chronology is restricted seasonal monoestry, with copulation and fertilization in Jun; gestation (without any delays) lasting five months; parturition in early Nov; lactation lasting ca. two months; and a period of anoestrus between termination of lactation and onset of pro-oestrus in Apr (Bernard 1982a). Ovarian and vaginal activity peaks in Apr–early Jun, and again in Jul–Aug, the second peak possibly being a relict from polyoestrous ancestors. At 02°18'S (Masalani, near Kibwezi, inland Kenya; O'Shea & Vaughan 1980), at 7°S in coastal Tanzania (Howell 1976) and at 15–16°S in Malawi (Happold & Happold 1990a), the reproductive chronology is also restricted seasonal monoestry with births in Nov, Nov, and Oct–Nov, respectively. Based on limited data combined from widespread and diverse localities, Anciaux de Faveaux (1978) invalidly suggests that *N. thebaica* exemplifies 'continuous polyoestry' and has a gestation of three months, and this has been widely quoted, especially in the context of reproduction of *N. thebaica* in the tropics. However, for specific localities, his published data are either inconclusive or indicative of monoestry, contain no evidence of polyoestry, and do not indicate length of gestation. Clearly, the reproductive chronology in wet tropical habitats needs investigation.

The ratio of ♂♂ to ♀♀ at birth is 1 : 1. Based on recaptures of bats roosting in 13 culverts along 3 km of one road in Swaziland, survival during first year appears low, but increases thereafter; ca. 15% of ♀♀ and 10% of ♂♂ banded as juveniles were alive three years later (Monadjem 2006a). Of 39 ♀♀ banded as adults, 23% were alive in the same culverts 4.5 years later, whereas only one of 28 ♂♂ was re-captured after four years. Female values probably reflect true survival; dispersal might account for the apparent loss of ♂♂.

Predators, Parasites and Diseases Predators include owls *Bubo africanus* and *Tyto alba* (Demeter 1982, Perrin 1982), and probably the bat *N. grandis* (see species profile). Ectoparasites include a bug *Eothenes nycteridis* (Hemiptera: Polyctenidae); four species of fleas (Siphonaptera: Pulicidae, Ischnopsyllidae); 12 species of batflies (Diptera: Nycteribiidae, Streblidae); five species of ticks (Acari: Argasidae); and 11 species of mites (Acari) (Anciaux de Faveaux 1984). Duvenhage virus has been isolated from *N. thebaica* (Calisher *et al.* 2006).

Conservation IUCN Category: Least Concern.

Measurements

Nycteris thebaica

FA: 44.4 (34–52) mm, n = 1276*

WS (a): 287.9 (276–302) mm, n = 8†

TL: 103 (82–130) mm, n = 148

T: 52 (43–59) mm, n = 244

E: 31.7 (26–37), n = 242

Tr: 7.8 (6–10), n = 24‡

Tib: 22.0 (17–27) mm, n = 627*

HF: 11.0 (8–14) mm, n = 125

WT: 10 (6–14) g, n = 88

GLS: 19.1 (17.0–21.2) mm, n = 871*

GWS: 11.1 (9.8–12.9) mm, n = 824*

C–M³ (alv.): 6.3 (5.0–7.5) mm, n = 1019*

Throughout geographic range (AM, BMNH, CM, HC, HZM, IRSN, KU, MCZ, MHNG, MNHN, MSNM, MZUF, OSU, RMCA, SMF, SMND, SMNS, TM, USNM, ZFMK, ZMB, ZMUC and literature)

*Van Cakenberghe & De Vree 1998

†Malawi only

‡Egypt and Malawi only

Key References Aldridge *et al.* 1990; Bernard 1982a; Gray *et al.* 1999; Seamark & Bogdanowicz 2002; Van Cakenberghe & De Vree 1998.

Ric T. F. Bernard & Meredith Happold

Nycteris vinsoni VINSON'S SLIT-FACED BAT

Fr. Nyctère de Vinson; Ger. Vinsons Schlitznasen-Fledermaus

Nycteris vinsoni Dalquest, 1965. J. Mammal. 46: 256. Zinave, Mozambique.

Taxonomy Species-group: *thebaica* (if *vinsoni* is a valid species). Synonyms: none. Considered to be a synonym of *Nycteris macrotis luteola* by Kock (1969a), but this was rejected by Koopman (1975), who placed it as a species in the *thebaica* group based on his opinion, at that time, that the tragus was pear-shaped. Koopman (1994) was still of this opinion but, subsequently, he considered it a subspecies of *Nycteris thebaica* (Koopman 1993). Koopman's 1994 publication was actually written earlier than his 1993 publication. Based on data from the literature, Van Cakenberghe & De Vree (1998) treat *N. vinsoni* as a distinct species in the *N. thebaica* group. Here, the status of *vinsoni* is considered to be uncertain because the shape of the tragus is uncertain and this is a crucial character. The ears and tragi of both the holotype and the single paratype were singed and shrivelled by smoke and heat at the time of capture, and their shape has been distorted. The tragi were described as semi-lunate by Kock (1969a) and Koopman (1992), but pyriform (pear-shaped) by Koopman (1975, 1994). If the tragus is semi-lunate (i.e. *N. macrotis*-like), *vinsoni* is probably a synonym of *N. macrotis* because its measurements and tooth characteristics are similar to those of *N. macrotis*. On the other hand, if the tragus is pyriform (i.e. *N. thebaica*-like), *vinsoni* is probably a valid species because its skull dimensions exceed the maxima for *N. thebaica*. Chromosome number: not known.

Description A small microbat with noseleaf comprised of a longitudinal slit bordered by fleshy outgrowths; medium-sized for a *Nycteris* (FA: ca. 51 mm); upper incisors bicuspid; posterior lower premolar small; tragus of uncertain shape; E: uncertain; Tib: 25 mm. Known only from two specimens. Described as similar in general proportions to *N. thebaica*, but larger and stouter. Two colour-phases, grey and orange. Ears apparently short for a *Nycteris* (ca. 22 mm, cf. 26–40 mm in *N. thebaica* and 26–35 mm in *N. macrotis*). However,

because the ears and tragi were shrivelled by smoke and heat, the ear measurements are unlikely to be accurate. Tragus shape uncertain: has been described as both pyriform and as semi-lunate (see Taxonomy); according to Koopman (1994) it apparently lacks a notch or concavity in the outer margin. The FA of the holotype is given as 50.6 mm, which lies only just outside the standard deviation for *N. macrotis* and well within its range. In contrast, it is at the upper limit of the range for *N. thebaica*. The tibia is of medium length for a *Nycteris* (25 mm) and of medium relative length (49% of FA). Bacular morphology not known.

All skull dimensions lie comfortably within range for *N. macrotis*, but some dimensions are larger than the maxima for *N. thebaica*. The posterior lower premolar is minute and displaced lingually, which suggests affinity with the *macrotis* group but, in *N. thebaica*, the position of this premolar in the tooththrow is very variable (Van Cakenberghe & De Vree 1998).

Geographic Variation No information.

Similar Species

Nycteris thebaica and *N. macrotis*: see Description.

Distribution Endemic to Africa. Known only from the type locality, Zinave on the Save R. in Mozambique, in the Zambezi Woodland BZ.

Habitat The Save R. runs through mopane woodland in this area.

Remarks Nothing else is known about the biology of this species except that the two specimens, an adult ♂ and ♀, were roosting together in a hollow, 15 cm diameter, near the base of a large baobab tree *Adansonia* (Dalquest 1965).



Nycteris vinsoni

Conservation IUCN Category: Data Deficient.

Because the status of this taxon is uncertain, its conservation status cannot be evaluated realistically.

Measurements

Nycteris vinsoni

FA: 51, – mm

WS: n. d.

TL: 125, – mm

T: 55, – mm

E: ? 22, ? 22 mm

Tr: n. d.

Tib: –, 25 mm

HF: 13, – mm

WT: n. d.

GLS: 21.9, 22.1 mm

GWS: 13.3, 13.5 mm

C–M³: 7.8, 7.6 mm*

Mozambique (holotype [Dalquest 1965] and paratype [Kock 1969a], respectively)

*Not measured at level of alveoli (cf. most other *Nycteris* profiles)

Key References Dalquest 1965; Kock 1969a; Koopman 1992; Van Cakenberghe & De Vree 1998.

Meredith Happold

Nycteris woodi WOOD'S SLIT-FACED BAT

Fr. Nyctère de Wood; Ger. Woods Schlitznasen-Fledermaus

Nycteris woodi K. Andersen, 1914. Ann. Mag. Nat. Hist., ser. 8, 13: 563. Chilanga, Zambia.

Taxonomy Species-group: *macrotis*. Synonyms: *sabiensis*. Following Hayman & Hill (1971) and Thomas *et al.* (1994), not considered to include *N. parisii* although this form is considered to be a subspecies of *N. woodi* by Van Cakenberghe & De Vree (1985) and Koopman (1993). Subspecies: none. Chromosome number (South Africa): 2n = 42; aFN = 78. Nineteen pairs of biarmed autosomes and one pair of small acrocentric autosomes. X = medium-sized metacentric, Y = small acrocentric (Rautenbach *et al.* 1993).

Description Very small microbat with noseleaf comprised of a longitudinal slit bordered by fleshy outgrowths; one of the five smallest and most gracile species of *Nycteris* (FA: 35–42 mm); upper incisors bicuspid; posterior lower premolar small; tragus semi-lunate with posterior margin smoothly convex; E: 20–23 mm; 80 (74–89)% of FA. Not easily distinguished from *N. parisii*. Sexes similar. Pelage loose, fluffy; mid-dorsal hairs ca. 10 mm. Dorsal pelage pale silvery-grey, grey, rusty-brown or brown, sometimes with paler pelage on back of head and shoulders and sometimes with darker patches on sides of muzzle and at bases of ears; hairs (in paler specimens) paler with terminal quarter same as dorsal colour; in brown specimens, hairs are brown with dark brown at base. Ventral pelage paler to much paler, sometimes almost off-white. Ears grey, long for a *Nycteris* (31.7 [28–35] mm) and relatively long (80 [74–89]% of FA, n = 16) (cf. *N.*

parisii). Tragus very narrowly semi-lunate; posterior margin smoothly convex, upper margin flattened (cf. rounded in *N. hispida*); lobe at base of posterior margin comparatively small (cf. *N. parisii*). Eyes minute. Wing-membranes of grey-furred individuals are translucent grey. Those of brown-furred individuals are correspondingly light reddish-brown (Ansell 1967). Tibia short for a *Nycteris* (19.5 [16–22] mm), but of medium relative length (50 [41–54]% of FA). Baculum comparatively short (2.49–2.73 mm); shaft straight, parallel-sided; base expanded, in lateral view angled ventrally; tip simple, unexpanded (Thomas *et al.* 1994).

Skull with sagittal crest low. Upper incisors bicuspid. Posterior lower premolar small (not rising above cingula of adjacent teeth), within tooththrow or slightly to fully displaced lingually.

Geographic Variation None recorded.

Similar Species Only two other African *Nycteris* have the following combination of characters: upper incisors bicuspid; lower posterior premolar small; tragus with posterior margin convex (Table 18, p. 441):

N. macrotis. Usually larger and more robustly built (FA: 48.2 ± 2.0 [40–55] mm). Ears usually relatively shorter (65 [55–80]% of FA). Baculum with tip expanded and trifid.

*Nycteris woodi*

N. parisi. Ears comparatively shorter (20–23 mm) and relatively shorter (51–56% of FA, $n = 3$). Baculum longer (>4 mm), with tip expanded and trifid. Ventral pelage dark grey in the very few known specimens. Cameroon, Ethiopia, Somalia.

Distribution Endemic to Africa. Zambezian Woodland BZ. Recorded from C and E Zambia, S and N Zimbabwe at lower altitudes (<1100 m), S and C Malawi, and marginally in northern South Africa in the Limpopo valley (Ansell 1967, 1978; Van Cakenberghe & De Vree 1985; Cotterill 1996a). In Mozambique, one specimen is known from Chicoa (USNM), but *N. woodi* is probably more widespread along the Limpopo, Save and Zambezi valleys. A specimen (BMNH 64.1473) collected by C. J. P. Ionides from S Tanzania (? Liwale, not mapped) was identified provisionally as *N. parisi* by Hayman & Hill (1971), but subsequently considered to represent *N. woodi* by K. Koopman and J. E. Hill (Hill 1975). Smithers (1983) mentions a series collected from Rwanda (without further information), but this record is not mentioned by Van Cakenberghe & De Vree (1985).

Habitat Woodland savannas (including miombo and mopane woodlands) where suitable day-roosts are available.

Abundance Uncertain. Locally common in Zimbabwe, especially in the low-lying valleys of the Limpopo, Save and Zambezi rivers and their tributaries, including the Sebungwe Basin of N Zimbabwe (Cotterill 1996a). Rarely recorded in Malawi (Happold & Happold 1997), where known from only two localities: Chiromo (three specimens; R. C. Wood in Kershaw 1922, as *N. hispida*) and Kota Kota (= Nkotakota, one specimen; Van Cakenberghe & De Vree 1985). Known from only three localities in Zambia (Ansell 1978). Considered one of the rarest African nycterids by Van Cakenberghe & De Vree (1985).

Adaptations Aspect ratio very low; wing-loading very low (F.

P. D. Cotterill unpubl.). Flight slow and highly manoeuvrable; adept at flying through very cluttered habitats. Day-roosts include large hollows in trees (including *Kigelia africana* and *Adansonia digitata*), caves, rock-fissures, disused mine-workings, human dwellings and a culvert under a railway. Individuals hang freely. Uses night-roosts (including in open corridors in buildings in Sengwa Wildlife Research Area, Zimbabwe) underneath which discarded remains of prey have been found.

Foraging and Food Based on wing morphology, diet and captures in mist-nets and harp-traps, this species forages in highly cluttered habitats by gleaning; perhaps also uses other foraging strategies but this needs confirmation. Stomach contents of five individuals from C Zambia in wet season contained predominantly adult Lepidoptera (46% by volume), adult Coleoptera (scarab beetles) (20%), Lepidoptera larvae (17%) and unidentified larvae (1%), Isoptera (termites – 10%), Orthoptera (3%) and flies and spiders (3%) (Whitaker & Black 1976). Discarded remains of prey found beneath day-roost sites and feeding-perches in the Sengwa Wildlife Research Area (SWRA; Zimbabwe) included predominantly Lepidoptera and Orthoptera; in early Jan 1989, the most abundant remains were those of tettigoniids (bush katydids) *Plangia graminea* and *Melidia brunneri*. Lepidopteran prey were predominantly moths, but some butterflies (including *Charaxes brutus natalensis*, a large nymphalid) were also eaten (F. P. D. Cotterill unpubl.).

Echolocation Call-shape multiharmonic, steep FM. Lowest frequency 35 kHz; highest frequency 55 kHz; peak-frequency 43 kHz; intensity low (Fenton & Bell 1981, Fenton 1985); but, based on frequency-time structure as illustrated by Fenton & Bell (1981), the minimum and maximum frequencies are those of different harmonics and the bandwidth of each harmonic appears to be ca. 10 kHz.

Social and Reproductive Behaviour Roosts in small or large groups (colonies) (Cotterill 1996a). One group, comprised of one adult ♂ and four ♀♀, was found in a mine-adit in Zimbabwe. A colony of more than 40 individuals roosted in a store-room at SWRA. Four other colonies, each containing ca. 50 individuals, have been found in Zimbabwe (F. P. D. Cotterill unpubl.).

Reproduction and Population Structure Litter-size: one ($n = 3$). Reproductive chronology uncertain. In Zimbabwe, three ♀♀ were in early pregnancy in mid-Aug; ♀♀ with single neonates were observed in mid-Nov; volant young in mid-Dec; post-lactating ♀♀ and volant young in early Jan; and ♀♀ found during cool-dry season were neither visibly pregnant nor lactating (F. P. D. Cotterill unpubl.). These data are consistent with restricted seasonal monoestry, but this needs confirmation.

Predators, Parasites and Diseases No information.

Conservation IUCN Category: Least Concern.

However, threatened by loss of habitat in S Malawi (Happold & Happold 1997) and parts of Zimbabwe (F. P. D. Cotterill unpubl.). Pesticides and destruction of hollow baobabs used as roosts are likely to cause population numbers to decline.

Measurements*Nycteris woodi*

FA: 39.1 (35–42) mm, n = 30

WS (d): 278 (272–283) mm, n = 3

TL: 93.2 (86–103) mm, n = 26

T: 47.5 (40–55) mm, n = 26

E: 31.7 (28–35) mm, n = 26

Tr: n. d.

Tib: 19.5 (16–22) mm, n = 32*

HF: 9 (8–10) mm, n = 12[†]

WT: 7.1 (6.5–9.0) g, n = 11

GLS: 17.4 (16.4–18.2) mm, n = 29*

GWS: 9.9 (9.2–10.5) mm, n = 28*

C–M³ (alv.): 5.5 (5.0–6.0) mm, n = 33*

Throughout geographic range (BMNH, NMZB, USNM)

*V. Van Cakenberghe (pers. comm.)

[†]Zimbabwe (Smithers & Wilson 1979)**Key References** Hill 1975; Van Cakenberghe & De Vree 1985.**F. P. D. Cotterill**

Family MOLOSSIDAE
FREE-TAILED BATS

Molossidae Gervais, 1856. In: Comte de Castelnau, Exped. Partes Cen. Am. Sud., Zool. (Sec. 7), Vol. 1, pt 2 (Mammifères): 53 footnote.

| | | |
|-------------------------------------|---------------------------|--------|
| <i>Mormopterus</i> (1 or 2 species) | Little Mastiff Bats | p. 472 |
| <i>Myopterus</i> (2 species) | Winged-mouse Bats | p. 475 |
| <i>Otomops</i> (1 species) | Giant Mastiff Bat | p. 479 |
| <i>Platymops</i> (1 species) | Flat-headed Bat | p. 483 |
| <i>Sauromys</i> (1 species) | Flat-headed Bat | p. 485 |
| <i>Tadarida</i> (28 species) | Tadarine Free-tailed Bats | p. 487 |

This is a polytypic family that is distributed throughout most of the tropical, sub-tropical and warm temperate regions of the world, in habitats ranging from rainforests to woodland savannas, dry bushlands, semi-deserts and deserts. There are 16 extant genera (of which three are monotypic) and 100 extant species: eight genera and ca. 33 species are found in Africa according to Simmons (2005). However, the taxonomy of this family is controversial (see below) and, here, the African species are provisionally placed in only six genera. Molossids have a mastiff-like face (Figure 32h), often with very wrinkled lips, sometimes with complexly folded ears, no noseleaf, and a long tail that projects through the posterior margin of the interfemoral membrane when these bats are not flying (Figure 33h). Most molossids fly very fast and high and are the nocturnal counterparts of swifts. Some of the African molossids are considered to be pests because they roost in large numbers in roofs and are very noisy and smelly. On the other hand, some of these bats feed mainly on moths and probably play a very important role in controlling moths that damage cotton and other crops.

African molossids are very small to medium-sized microbats with short, velvety pelage, which is sometimes greasy. Most species are dark brown or reddish-brown with a paler belly. Often they have a strong musky odour from secretions from glands in the skin. Many have a broad band of near-naked, wrinkled skin across their shoulders. The body is elongated and robust. The head is broad, flattish to very flat, and usually heavily jowled; the upper lips are often expansible and wrinkled into vertical folds; the lips and snout have long sensory hairs and short spoon-shaped bristles; the snout usually projects beyond the lower lip. When the mouth is wide open, the lips probably spread outwards to increase the gape and facilitate capture of prey (Vaughan 1966). The ears are forward-pointing; usually broad relative to their length; usually very large but often with creases enabling them to fold up in a somewhat fan-like manner. The margins are usually thickened with connective tissue and these strongly brace the ears during flight. The inner margins of the ears are thick and may be separated or joined in various ways, which are of diagnostic value (see below). In some species, this band, or the skin just behind or below it, carries a tuft of hairs that can be erected into an interaural crest (Figure 95f and g); in some species (but not all) the hairs of the crest appear to be scent-dispersing osmetrichia and probably arise from glandular tissue (Hickey & Fenton 1987). The tragus is small to minute. The eyes are moderately large for a microbat. The wings are typically very long and narrow; the thumb has a pad at its base; the second finger has a metacarpal and one vestigial phalanx (Figure 95a). The wing-membranes either have blackish-brown or white pigmentation, or are almost transparent. The hindlimbs are short and muscular, the soles are broad and

sometimes have a well-developed plantar pad, and the toes are short (Figure 95h). The outer toes are stout and have long bristles and short spoon-shaped bristles of uncertain function – perhaps they are used for grooming (Nowak 1999), or sexual stimulation (Rosevear 1965), or for feeling for toe-holds and obstacles especially when scuttling backwards. The toes (except first toe [hallux]) have three phalanges. Long sensory hairs project from the rumps of many species. There are no pubic nipples. The tail is relatively short to medium (27–44% of TL in African species) and, except during flight, it extends well beyond the somewhat shortened interfemoral membrane. During flight, the interfemoral membrane slides backwards so the tail is more or less fully enclosed, and the hindlimbs and calcars are able to alter the trim of this flight membrane. The tip of the tail can be waved around and is used to feel the walls and ceilings of confined spaces into which many species scuttle backwards to roost.

Molossid skulls have no striking features (such as nasal swellings and frontal shields) by which they can be recognized immediately. The rostrum ranges from moderately long to short, and the braincase is rather broad and either slightly flattened or very conspicuously flattened. There are no postorbital processes and no pronounced supraorbital ridges. The sagittal and lambdoid crests range from slightly developed to well developed. The nasal branches of the premaxillae are present; the palatal branches are sometimes present and sometimes absent. Consequently, the anterior palatal emargination can be open or closed and this is an important diagnostic character (see below). The basisphenoid bone, on the ventral surface of the braincase, has pits, which are also of diagnostic importance. The dental formula for African species is variable: $^{1123}/_{2123} = 30$, $^{1123}/_{1123} = 28$, $^{1123}/_{3123} = 32$, $^{1113}/_{3123} = 30$, or $^{1113}/_{1123} = 26$. Selected external characters of the molossids are illustrated in Figure 95. Characteristics of the dentition that are of diagnostic importance are listed below (pp. 467–471).

Molossids are widely considered to be the most highly adapted bats. The articulation of the bones in the shoulder represents an advanced condition (Vaughan 1966). The majority have high to very high aspect ratios, medium to very high wing-loadings, and wing-tips that are larger than average and slightly rounded. Consequently, these bats must fly fast and, although they have considerable agility, they have poor manoeuvrability and can only forage in open spaces (Norberg & Rayner 1987). During flight, the ears arch dorsally and resemble an aerofoil of high camber; they probably develop lift, which helps support the head during flight (Vaughan 1966). Molossids typically cannot hover or take off from the ground. They are insectivorous and, as a family, feed on many different night-flying insects. They fly high, and some species prey on nocturnal insects that migrate at high altitudes, or become concentrated in the warmer upper layers by atmospheric conditions such as temperature inversions and pressure fronts (Drake & Farrow 1988, Cotterill & Fergusson 1993b, Griffin 1995). For example, flocks of molossids in the southern USA forage as high as 3000 m (Williams *et al.* 1973), and molossids have been recorded foraging to 500 m in Zimbabwe (Fenton & Griffin 1997); no attempts have been made, as yet, to detect their presence at higher altitudes in Africa. Some molossids

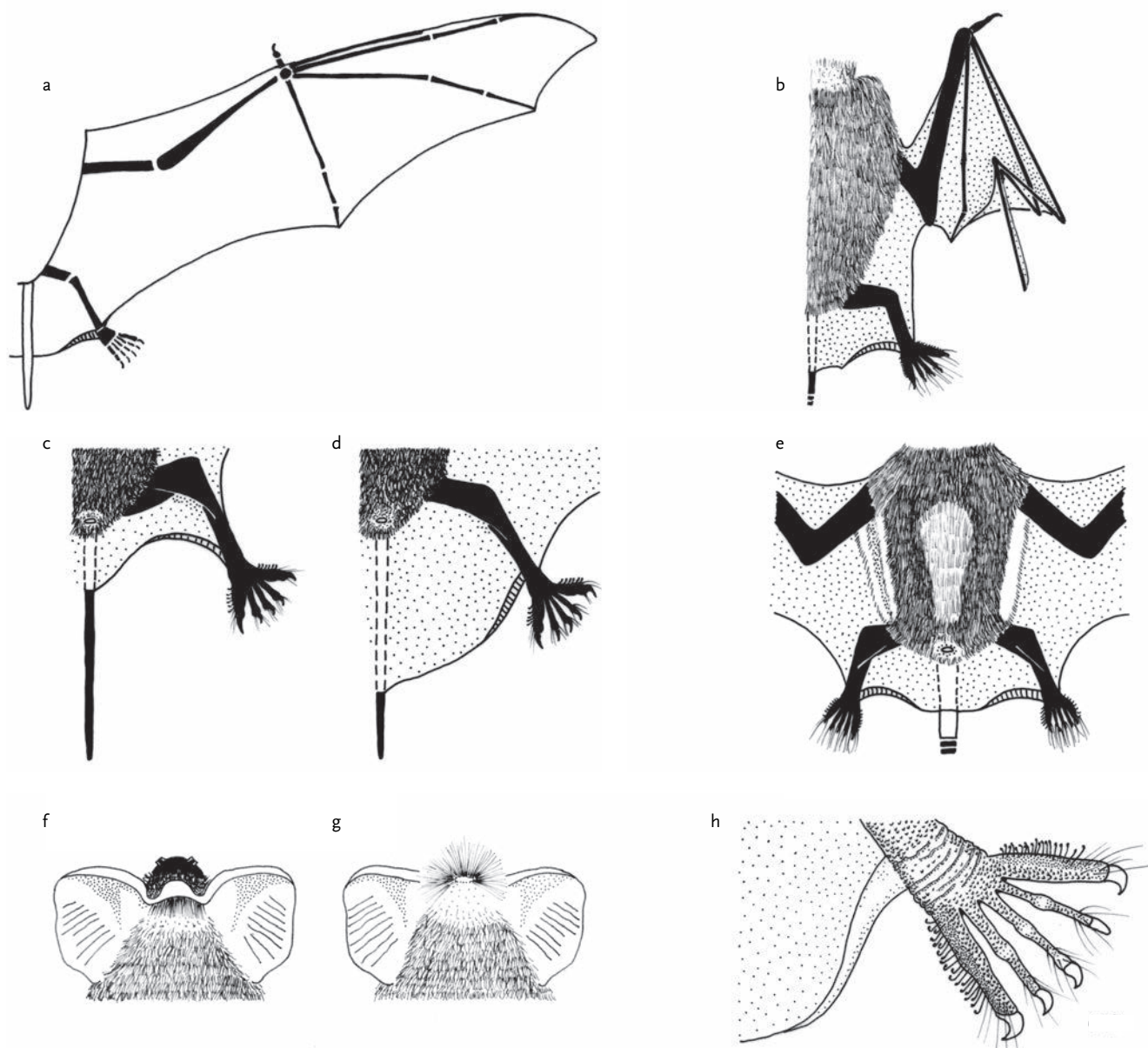


Figure 95. External characters of African bats in the family Molossidae. (a) Flight membranes and bones of wing, hindlimb and tail (e.g. *Tadarida condylura*). (b) Dorsal view of partly folded right wing showing the first phalanges of the third and fourth fingers flexing dorsally: the second finger lies against the ventral surface of the third finger and is not visible in this view. Ventral views showing the interfemoral membrane and calcar (c) during cursorial locomotion or rest, and (d) during flight. (e) Ventral view of a hypothetical molossid showing an example of a mid-ventral marking and two examples of ventral flank-stripes: one showing the pelage of the stripe more or less confined to the flank; the other showing the pelage of the stripe extending onto the wing-membrane with a narrow gap between the pelage on the wing and that on the flank. Dorsal views of the head of a *Tadarida* showing (f) an interaural crest retracted into the pocket-like invagination in the interaural band, and (g) erected. (h) Dorsal view of the right hindfoot showing long sensory hairs on all toes, and spoon-hairs on the outer sides of the thicker first and fifth toes.

eat hard-shelled beetles and have thick jaws, well-developed cranial crests and fewer but bigger teeth: others eat soft-bodied insects and have correspondingly thinner jaws, lower cranial crests and more but smaller teeth (Freeman 1979, 1981). Flight for these long-and-narrow winged bats is energetically cheap, so they forage and feed by fast-hawking, and foraging flights are usually of many hours' duration. Their foraging flights are characterized by agile diving, swerving and side-slipping. The echolocation calls of molossids (at least *Tadarida* spp.) are more varied and adaptable than those of most other African bats (see order Chiroptera). While cruising and foraging, the majority of calls are short to long CF calls or shallow

linear and shallow quasi-linear FM sweeps, with maximum energy in the fundamental harmonic (Figure 96a). As a bat approaches a target, its calls become progressively broader in bandwidth, shorter and more frequent (Figure 96c and d) and may be followed by a feeding-buzz (Figure 96e and f). These sequential changes in call-shape enable bats in Africa to be recognized as molossids, but it is not yet possible to recognize (with certainty) any species of African molossid from isolated calls because there are no data for many species, and the full repertoire of calls for most species is not yet known. For some species at least, calls emitted in cluttered surroundings (e.g. near day-roosts and close to ground) are steep linear FM sweeps (Figure 96g and h)

that are very different to the search-phase calls. Echolocation calls are emitted through the mouth. The calls of some species are audible to people with unimpaired hearing of higher frequencies.

Molossids are well adapted for cursorial locomotion: they can walk slowly or scuttle as fast as a mouse over horizontal to vertical surfaces, and they can move backwards or sideways for short distances. Molossids often scuttle forwards over distances of many metres between their roosts and landing-sites, and juveniles of at least one species, *Tadarida pumila*, apparently forage by chasing non-volant insects such as cockroaches inside their day-roosts (Marshall & Corbet 1959). Like emballonurids (and to a less extent like rhinopomatids), molossids can furl their flight-membranes so the forearms and legs can move freely. When a wing is furred, the first phalanx of the third and fourth finger flexes dorsally to lie against the metacarpals, and the metacarpals (which are never longer than the radius) flex to lie snugly against the forearm. Pads on the wrists and soles, and stout muscular legs, are additional adaptations associated with regular and sustained cursorial locomotion. During the day, molossids roost in caves and cave-like day-roosts, usually tucking themselves backwards into narrow nooks and crannies. Some roost in similar confined spaces under exfoliating rocks and bark and several species also roost in the roofs of all sorts of buildings, occupied by humans or otherwise. Bats in the African genera *Platymops* and *Sauromys* are dorsoventrally flattened and can squeeze into particularly narrow spaces. Molossids cling in contact with the horizontal and/or vertical surfaces of their roost-sites. Because of their wing morphology, they need to dive to gain sufficient speed for flight, and they need to swoop upwards and stall before landing. Consequently, they can only use day-roosts with landing and take-off sites at least 1.5 m above open ground, and they must be able to scuttle from there to a suitable roost-site. Bats diving very steeply from the roof of a house are almost always molossids. Molossids are particularly vulnerable to predation from bat hawks *Macheiramphus alcinus* and other birds of prey, which learn when and where the emerging bats make their dives. Small carnivores such as genets *Genetta* can catch these bats if they have to scuttle across a roof before diving. Some molossids seem to prefer roosts with high temperatures and are found under roofs of corrugated iron where temperatures may range from 16 to 54 °C, and relative humidities from 35 to 90% (Mutere 1973a). There is no definite evidence of true hibernation in this family although some species spend short periods (e.g. up to eight days in *T. teniotis*) in a state of torpor during winter. In

some localities, molossids remain active while some of the sympatric species in other families hibernate. Most African molossids roost in small to very large groups although some individuals of some species roost singly. Little is known about their social behaviour with the exceptions of *Otomops martiensseni* and *T. pumila*, which sometimes establish harems. Molossids have many vocalizations, apparently associated with intra-specific communication, which are audible to people as squeaking and twittering. Colonies of roof-dwelling molossids become very noisy for about an hour before the bats emerge. Molossids (except extremely rarely) are monogamous. The reproductive chronologies of African species include seasonal monoestry (*Tadarida aegyptiaca*, *Otomops martiensseni*), bimodal polyoestry with postpartum oestrus (*Tadarida condylura*, *T. fulminans*), bimodal polyoestry without postpartum oestrus (*T. condylura*, *T. thersites*) and multimodal polyoestry with postpartum oestrus (*T. pumila*). There is a trend (exemplified even intra-specifically by *T. pumila*) towards bimodal polyoestry or multimodal polyoestry and extended or well-separated parturition seasons in equatorial regions, with fewer litters/year crowded into progressively shorter reproductive seasons at higher latitudes (Happold & Happold 1990b, Bernard & Cumming 1997). Reproductive delays are not known to occur in African molossids. Neonates (for which data are available) are naked, relatively large and they develop rapidly. They are left in crèches while their mothers forage.

The geological range of the family Molossidae is late Eocene to Recent in Europe and North America, late Oligocene to Recent in South America, middle Miocene to Recent in Africa and Australia, and Pleistocene to Recent in Asia and the East and West Indies (Koopman 1984, Hand 1990). The late Eocene molossids from Europe are slightly younger than those from North America. Three different areas of origin have been suggested for this family: the Neotropics, Africa and the Indo-Australian region (Freeman 1981). Simmons (1998) concluded, from cladistic analysis of 192 morphological and molecular characters, that they most likely originated in the Neotropics.

Molossids have radiated into forests, savannas and bushlands, semi-deserts and deserts. Of the 34 species in Africa, 26 are found almost entirely in the tropics. Seven other species are mainly tropical but also extend southwards into temperate habitats (and one of these also extends northward into temperate habitats). There is also one Palearctic species, which, in Africa, is found only in temperate habitats in North Africa. Of the 32 species for which data are available, 13 are found

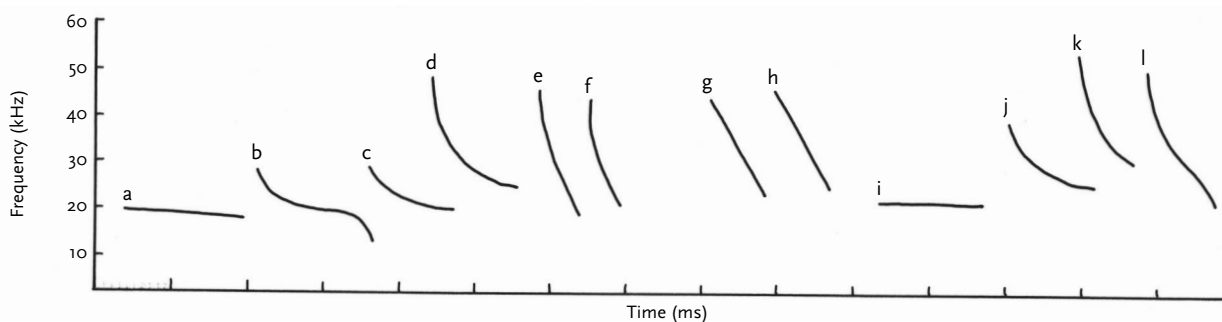


Figure 96. Sonograms of echolocation calls of two molossids from Malawi, showing the diversity of calls made in different situations (M. Happold unpubl.). (a) and (b) Search-phase calls of *Tadarida condylura*, emitted during foraging or cruising in open space high above ground. (c) and (d) Approach-phase calls of *T. condylura*, emitted during foraging high above the ground. (e) and (f) Consecutive calls from a 'feeding buzz' emitted by *T. condylura*. (g) and (h) Consecutive calls emitted by a bat, *Tadarida pumila*, as it dived to gain sufficient speed for flight after taking off from about 3 m above ground. (i) Search-phase call emitted by another individual, *T. pumila*, while foraging/cruising in open space far above ground. (j), (k) and (l) Non-consecutive approach-phase calls from a sequence (see Figure 27) emitted by *T. pumila*. Time axis marked at intervals of 10 ms.

mainly in woodland savannas, five are found in woodland savannas and extend into arid grassland savannas (and one of these also extends into desert habitats in the South-West Arid BZ), six are found mainly in rainforest, six in forest–savanna mosaics near the northern edge of the rainforest, one (*Tadarida bemmeleni*) is found in rainforest (*T. b. bemmeleni*) and in savannas and rainforest–savanna mosaics (*T. b. cistura*), and one is found in Mediterranean habitats. Only one species (*Sauromys petrophilus*) seems close to being a desert specialist. Only 12 species (36%) have been collected in montane habitats (although this might reflect inadequate sampling) but others possibly forage over montane habitats without roosting there. Most localities are probably exploited by more than one species, for example:

Kikwit, DR Congo (rainforest): *Myopterus whitleyi*, *Tadarida ansorgei*, *T. condylura*, *T. nanula*, *T. niveiventer*, *T. pumila* and *T. thersites* (Van Cakenberghe *et al.* 1999).

Sengwa Wildlife Research Area, Zimbabwe (miombo and mopane woodland): *Otomops martiensseni*, *Tadarida aegyptiaca*, *T. ansorgei*, *T. chapini*, *T. fulminans* and *T. nigeriae* (Fenton 1985).

Because molossids are difficult to capture, there are undoubtedly immense gaps in our knowledge of their habitat preferences and distributions.

The taxonomy of the family Molossidae is controversial. Based on morphological data, Simmons (1998) placed the Molossidae in the superfamily Molossoidea together with the New World family Antrozoidae, and she recognized two subfamilies, the Tomopeatinae in the New World and the Molossinae, which has representatives in Africa. Koopman (1993, 1994) placed the Tomopeatinae in the Vespertilionidae, and consequently does not recognize any subfamilies in the Molossidae. Recent studies, based on molecular data, contradict some of the groupings based on morphological data and therefore, pending further studies, no chiropteran superfamilies are recognized by Simmons (2005). The subfamilies Tomopeatinae and Molossinae are recognized by Simmons (2005); the subfamily Tomopeatinae is represented by only one species *Tomopeus ravs* that is found in Peru, and the subfamily Molossinae includes all other molossids. Based on dental morphology, Legendre (1984) divided the family Molossidae (not including *Tomopeus*) into three subfamilies: the Molossinae (including *Myopterus* from Africa and six genera from the New World), the subfamily Cheiromelinae (including one genus from South-East Asia) and the subfamily Tadarinae (including *Tadarida* [including *Chaerephon* and *Mops*], *Mormopterus* [including *Platymops* and *Sauromys*] and *Otomops*), all of which are represented in Africa, and also *Nyctinomops* (from the New World) and *Rhizomops* (treated as a synonym of *Tadarida* by Simmons 2005). Pending resolution of inter-generic relationships, no divisions of the family Molossidae are recognized by Simmons (2005), or here, except for the subfamilies Molossinae and Tomopeatinae. Neither subfamily is profiled below because differences between them are not relevant to this account, which is restricted to African molossids in the subfamily Molossinae.

Opinions also differ (and change) about the generic versus subgeneric status of several taxa including *Chaerephon*, *Mops*, *Xiphonycteris*, *Platymops* and *Sauromys*, which are represented in Africa. Pending further studies, *Platymops* and *Sauromys* are recognized here as distinct genera (although they are considered subgenera of *Mormopterus* by some authors). It seems probable that *Chaerephon* and *Mops* are not

monophyletic and, pending revision, these taxa and *Xiphonycteris* are retained here in *Tadarida* (*contra* Simmons 2005). For further details, see genus and species profiles.

The six genera recognized here, which occur in Africa, can be distinguished by the combination of characters given in Table 19, p. 472. The characters that are most useful as the means of distinguishing the genera, and also species within the genus *Tadarida sensu lato*, include the following:

Inner margins of ears. Can be (a) well separated, (b) meeting to form a V-shaped valley (as a result of the bases being close but not joined or only just joined), (c) forward-projecting and joined to forehead and muzzle, or (d) wide apart but well joined across forehead by a broad band of skin and cartilage (Figure 97).

Folding of ears. The ears can be with or without complex folding, or with moderate folding (Figure 97).

Relative size of ears. Described as small (extending about half-way along muzzle when laid forward) to large (extending well beyond snout when laid forward).

Interaural crest. Can be present or absent, long and bicoloured (Figure 112) or short and unicoloured (Figure 95).

Dorsal pelage. Varies in colour; can be striped, spotted, flecked or uniform in colour. Dorsal hairs can be unicoloured or bicoloured.

Mid-ventral markings. Can be present or absent. Markings include a stripe or a patch or several patches, in contrasting pale colour (Figure 95e).

Ventral flank-stripe in contrasting colour. Can be present or absent. Refers to the narrow band of pelage running along the ventral boundary between the wing-membrane and the body and sometimes extending marginally onto the wing-membrane; its hairs are sometimes longer than hairs of the adjacent ventral pelage (Figure 95e). This band of pelage can be the same colour as the adjacent ventral pelage (and therefore a ventral flank-stripe in contrasting colour is absent), or its colour can contrast with the adjacent ventral pelage, in which case it is usually much paler or white, but it is sometimes black and much darker.

Colour of wing-membranes. Can be black, white, various shades of brown or grey, or almost colourless and transparent. In some species, the dorsal and ventral surfaces differ in colour.

Upper lip. Can be smooth, or with fine microscopic wrinkles, or with a number of conspicuous vertical wrinkles. The number of wrinkles is the number of raised ridges (not the number of valleys). The upper lip can have many short, thick, spatulate hairs known as spoon-hairs, or few spoon-hairs, or no spoon-hairs.

Gular gland (sometimes in gular sac). Can be present or absent.

Plantar pad. A raised pad on the sole of the foot, which can be present or absent.

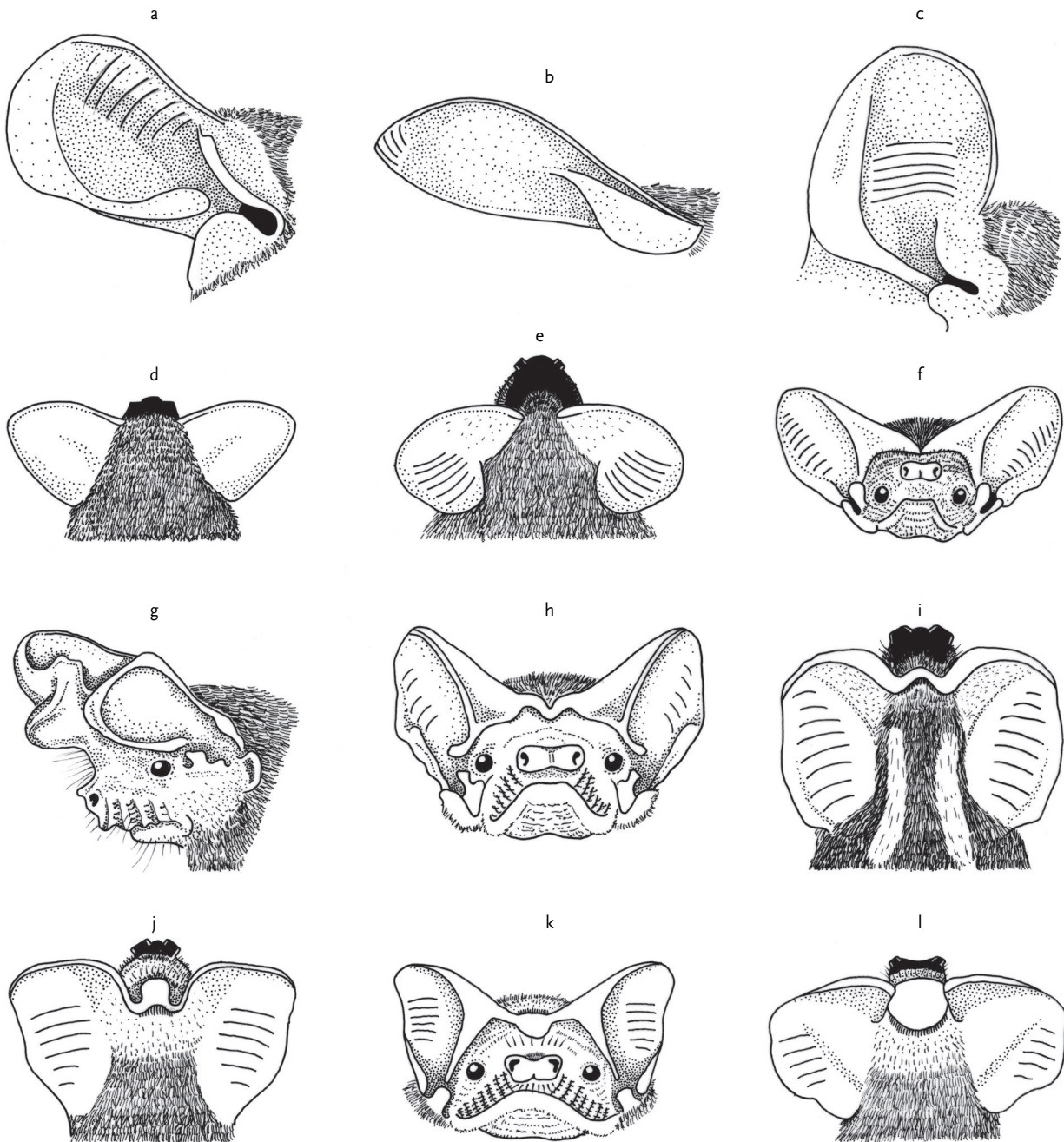


Figure 97. Variations in the ears of African bats in the family Molossidae. Ears that (a) have complex folding (e.g. *Tadarida aloysiisabaudiae*; based on photo by J. Fahr), (b) have moderate folding (*Otomops martiensseni*; after Smithers 1983) and (c) do not have complex folding (e.g. *Myopterus daubentoni*; based on photo by J. Fahr). Ears that are (d) well separated (e.g. *Platymops setiger*; based on photo in Harrison & Fleetwood 1960), (e) separated by narrow gap (*Sauromys petrophilus*; based on photo in Mills & Hes 1997), (f) meeting to form a V-shaped valley (e.g. *Tadarida lobata*; based on Peterson & Harrison 1970), (g) forward-projecting and joined to forehead and muzzle (*T. gallagheri*; based on Harrison 1975), (h) and (i) wide apart but well joined across forehead by an interaural band with V-shaped fold (e.g. *T. bivittata*; based on Eger & Peterson 1979), (j) and (k) joined by interaural fold with backward-opening pocket-like invagination in middle (e.g. *T. condylura*), (l) lappet-eared (*T. major*). Within most of these categories, there are considerable inter-specific variations.

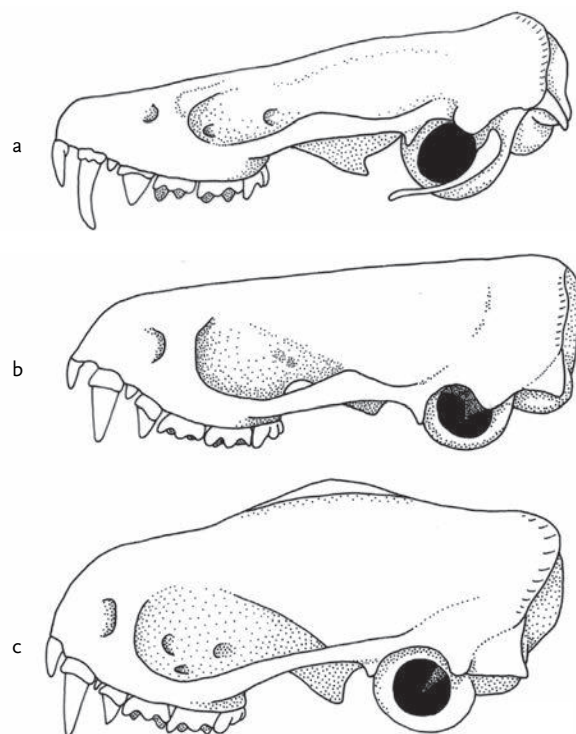
Degree of flattening of the skull. The skull (and head) can be extremely flattened dorsoventrally or not extremely flattened. In the latter category, the skull can be low but not extremely flattened in some species (Figure 98).

Anterior of braincase. Can be not noticeably elevated, slightly elevated, moderately elevated or prominently elevated above the plane of the rostrum (Figure 99).

Sagittal and lambdoid crests. Can be absent, or poorly developed to well developed.

Anterior palatal emargination. Can be closed (non-existent), or deep (reaching to mid-canine level or a little further posteriorly), very narrow, narrow or wide, and can be U-shaped or bulb-shaped (Figure 100). When the palatal emargination is closed, a pair of palatal foramina is usually present.

Figure 98. Skulls of African Molossidae showing different degrees of dorsoventral flattening: (a) extremely flattened (e.g. *Sauromys petrophilus*; ZFMK 77.489), (b) not extremely flattened but low (e.g. *Tadarida aegyptiaca bocagei*; BMNH 23.5.9.27), (c) not extremely flattened (e.g. *T. brachyptera leonis*; BMNH 92.10.6.3).



BELOW: Figure 99. Skulls of African *Tadarida* showing inter-specific differences in the elevation of the braincase above the plane of the rostrum. Braincase prominently elevated, as in (a) *Tadarida gallagheri* (holotype; after Harrison 1975) and (b) *Tadarida petersoni* (holotype; based on El-Rayah 1981). Braincase moderately elevated, as in (c) *Tadarida midas* (BMNH 22.12.17.99) and (d) *Tadarida bivittata* (BMNH 75.2674). Braincase slightly elevated, as in (e) *Tadarida ansorgei* (BMNH 66.3613) and (f) *Tadarida pumila* (RMCA 97-21-M-731). Braincase very slightly elevated or flat as in (g) *Tadarida nanula* (RMCA RG 19839) and (h) *Tadarida aegyptiaca* (BMNH 23.5.9.27).



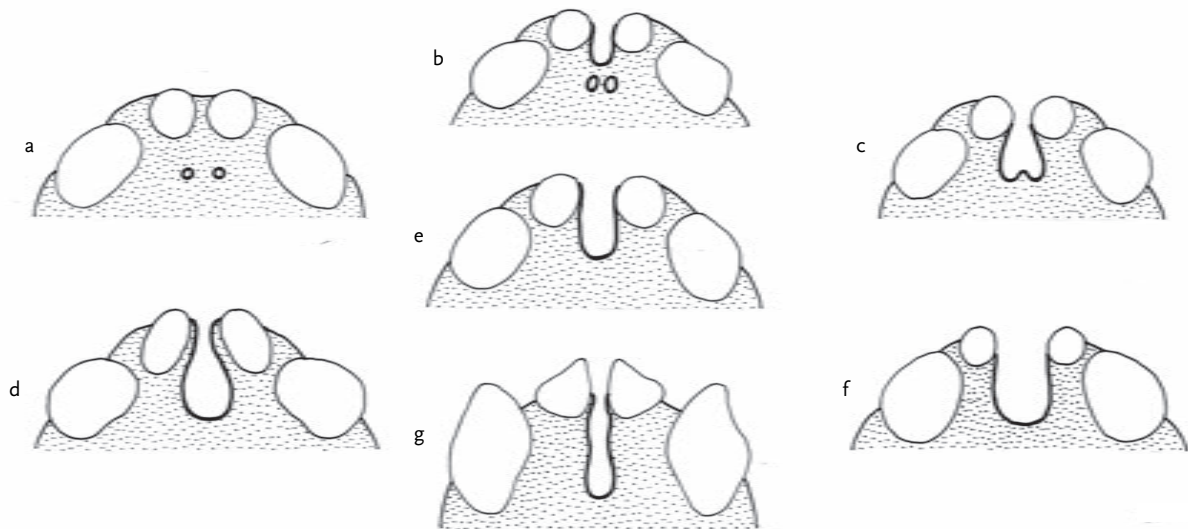


Figure 100. Shapes of the anterior palatal emargination found in African Molossidae. (a) Closed with incisive foramina visible (e.g. *Tadarida niveiventris*). (b) Narrow and separated from incisive foramina by bony bar (e.g. *T. pumila*). (c) Narrow and not separated from incisive foramina, which retain only a remnant of the bony septa between them (e.g. *T. pumila*). (d) Bulb-shaped (e.g. *T. bivittata*). (e) Narrow (e.g. *T. thersites*). (f) Wide (e.g. *T. fulminans*). (g) Very narrow and deep (*Otomops martiensseni*).

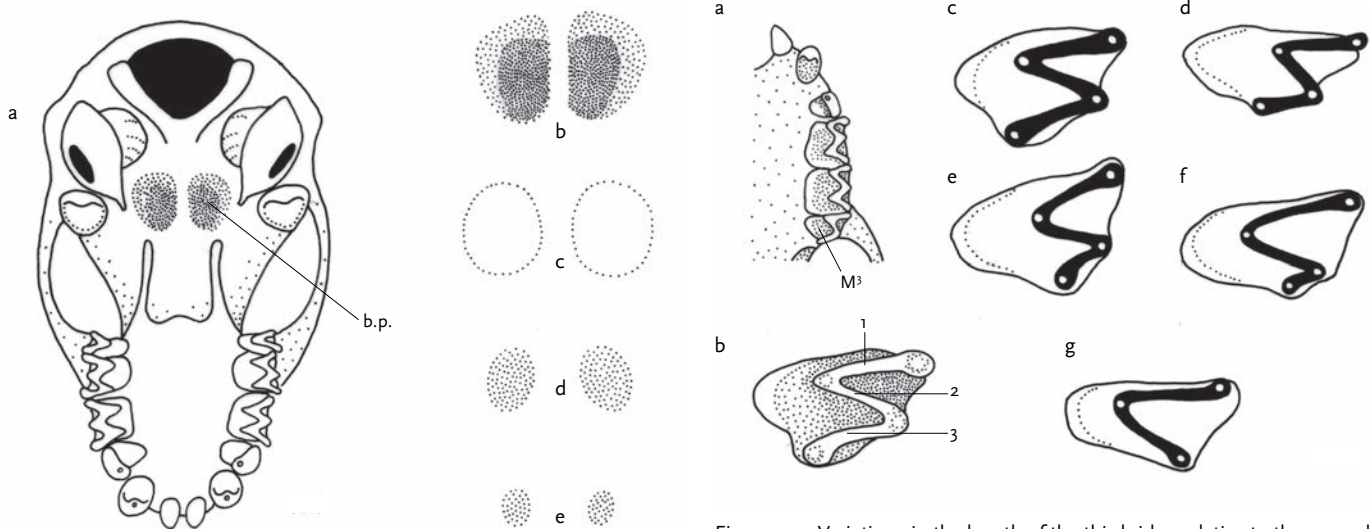


Figure 101. Variations in the depth and relative size of the basisphenoid pits of African Molossidae. (a) Ventral view of skull showing position of basisphenoid pits (b.p.). (b) Pits very deep and relatively large – width of each pit much greater than distance between pits (e.g. *Myotis whitleyi*). (c) Pits shallow and relatively large (e.g. *Mormopterus francoismoutoui*). (d) Pits moderately deep and of medium relative size – width of each pit about same as distance between pits (e.g. *Tadarida lobata*). (e) Pits moderately deep and relatively small – width of each pit noticeably less than distance between pits (e.g. *Tadarida petersoni*). The skulls from which each pair of pits was drawn were enlarged to the same mastoid width.

Basisphenoid pits. These are a pair of pits (one on each side) located in the basisphenoid bone on the ventral surface of the braincase (Figure 101a); they can be absent, shallow, moderate, deep or very deep (assessed qualitatively; most data from Freeman 1981) and they can be relatively large (width of pit noticeably > distance [septum] between pits), medium (width of pit ca. = distance between pits), or

Figure 102. Variations in the length of the third ridge relative to the second ridge of M^3 , the third upper molar, in *Tadarida*. (a) Left upper tooththrow showing M^3 . (b) Left M^3 with ridges one, two and three labelled. (c) Third ridge > second ridge. (d) Third ridge = second ridge. (e) Third ridge > half of second ridge. (f) Third ridge < half of second ridge. (g) Third ridge absent.

small (width of pit noticeably < distance between pits) (Figure 101c, d and e, respectively).

Length of third ridge relative to length of second ridge of M^3 , the posterior upper molar. The third ridge (the most posterior ridge) can be (a) equal in length or slightly longer than the second, (b) equal to the second, (c) more than half of the second but never equal to it, (d) less than half of the second but not completely absent or (e) absent (Figures 102c–g, respectively).

Anterior upper premolar. Can be distinctly shorter than the cingulum of the posterior premolar, and either displaced labially or in tooththrow,

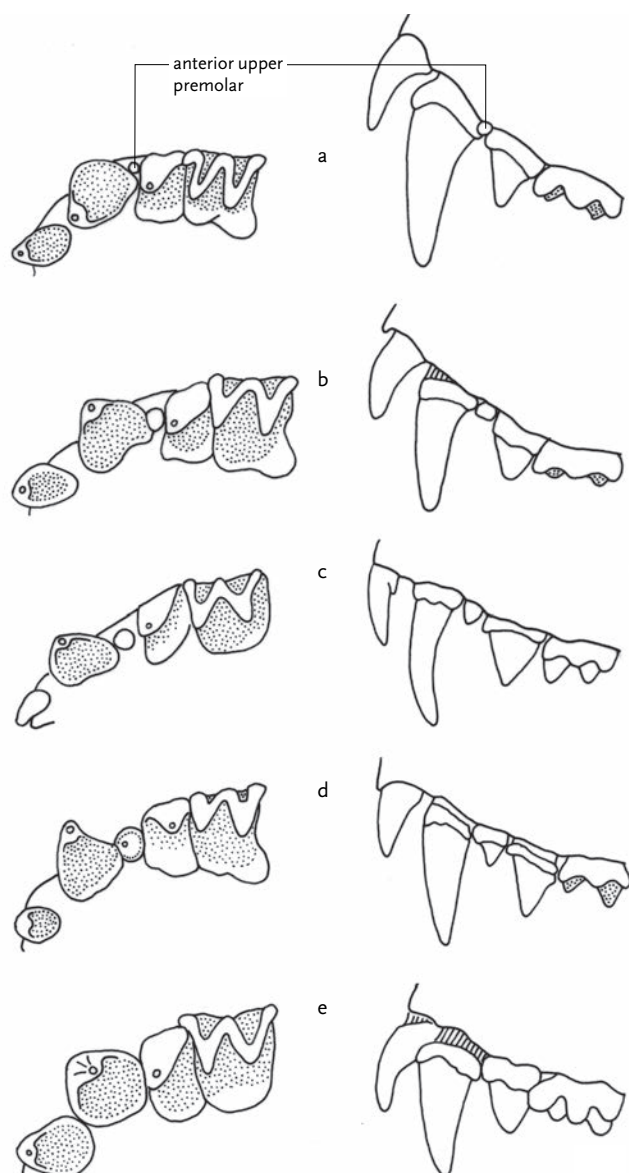


Figure 103. Sizes of the anterior upper premolar relative to the height of the cingulum of the posterior premolar, and its position. *Left*: occlusal views of teeth on left side of upper jaw. *Right*: lateral views of labial side of the same teeth. (a) Anterior upper premolar distinctly shorter than the cingulum of the posterior premolar and displaced labially (e.g. *Tadarida condylura*). (b) Anterior upper premolar distinctly shorter than cingulum of posterior premolar and in tooththrow (e.g. *T. major*). (c) Anterior upper premolar approximately same height as cingulum of posterior premolar and in tooththrow (e.g. *Sauromys petrophilus*). (d) Anterior upper premolar distinctly taller than cingulum of posterior premolar and in tooththrow (e.g. *T. aloysiisabaudiae*). (e) Anterior upper premolar absent (e.g. *Myopterus whitleyi*).

ca. same height as cingulum of posterior premolar, distinctly taller than cingulum of posterior premolar, or absent (Figures 103a–e, respectively).

Upper incisors. Can be procumbent (angled forward), or not procumbent (pointing downwards and/or somewhat inwards) (Figures 104a and b, respectively).

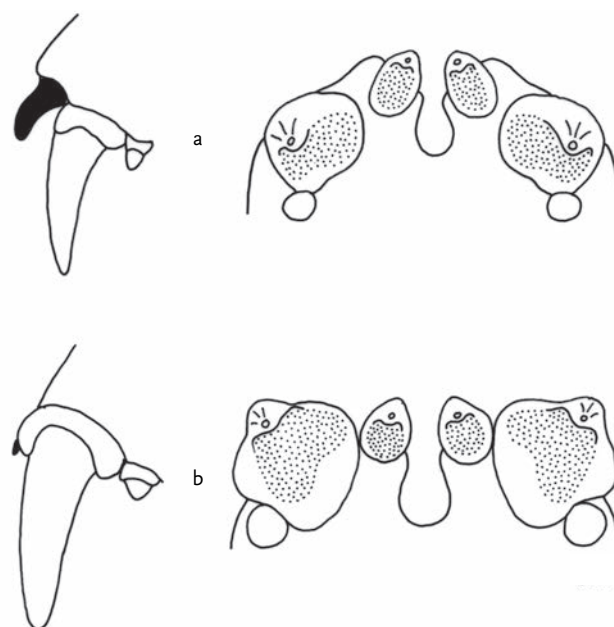


Figure 104. The upper incisors of *Tadarida* can be procumbent or not procumbent. (a) Lateral and occlusal views of the procumbent upper incisor in *Tadarida nanula* that is not obscured by the canine cingula. (b) Lateral and occlusal views of the non-procumbent upper incisor in *T. spurrelli* that is, in this specimen, almost entirely obscured by the canine cingula. Incisors shown in solid black; both specimens are ♂♂.

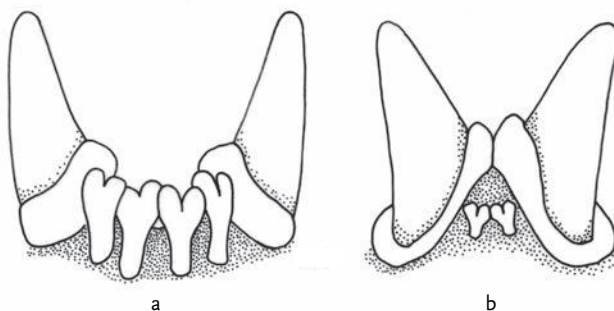


Figure 105. Lower incisors and canines of African *Tadarida*. (a) Canine cingula not greatly enlarged and not in contact; incisors crowded (e.g. *T. aegyptiaca*). (b) Canine cingula greatly enlarged and in contact; incisors reduced in number and crowded (*T. spurrelli* ♂).

Lower incisors. There can be one, two or three on each side, and they can be crowded by the cingula of the lower canines, or not crowded (Figure 105).

Lower canines. The cingula are always large and conspicuous compared with bats in other families but, in some species of molossids, they are greatly enlarged (Figure 105). The cingula are often larger in ♂♂ than in ♀♀ of the same species.

The six genera represented in Africa are presented in alphabetical order.

Meredith Happold & F. P. D. Cotterill

Table 19. Key to the African genera in the family Molossidae (based on African species only). For details of the differences in these characters, see Family Molossidae.

| Head and skull | Inner margins of ears
(Folding of ears) | Length of
third ridge (3)
in relation to
second ridge
(2) of posterior
upper molar
(M ³) | Miscellaneous | Genus |
|---|---|--|---|--|
| Extremely flattened | Widely separated
(Without complex folding) | $3 = 2$ | Forearm with warty granulations
FA: 27–36 mm
Upper lip with many fine wrinkles and many stiff bristles | <i>Platymops</i>
(1 species) |
| Extremely flattened | Meeting to form V-shaped valley
(Without complex folding) | $3 = 2$ | Forearm without warty granulations
FA: 37–50 mm
Upper lip smooth with only a few stiff bristles | <i>Sauromys</i>
(1 species) |
| Low but not extremely flattened | Distinctly separated or almost touching
(Without complex folding) | $3 \geq 2$ | Forearm without warty granulations
FA: 38–43 mm
Ears never white or translucent
Upper lip with many well-defined wrinkles but few spoon-hairs | <i>Mormopterus</i>
(1 or 2 species) |
| Not extremely flattened but sometimes low | Meeting (or almost meeting) to form V-shaped valley
or
Joined by band
(With complex folding) | Varied:
$3 = 2$
$3 > \text{half } 2$
$3 < \text{half } 2$
3 absent | FA: 27–67 mm
Ears never white or translucent
Ears 10–33 mm
Sometimes with yoke of almost naked, pale skin across nape of neck
Upper lip usually with well-defined wrinkles and many spoon-hairs | <i>Tadarida</i>
(27 species) |
| Low but not extremely flattened | Widely separated
or
Meeting to form V-shaped valley
(Without complex folding) | 3 absent | FA: 35–54 mm
Ears whitish or translucent
Ears 14–22 mm
Upper lip smooth with many spoon-hairs | <i>Myopterus</i>
(2 species) |
| Low but not extremely flattened | Forward-projecting and joined to forehead and along extended muzzle
(With moderate folding) | $3 \leq 2$ | FA: 61–74 mm
Band of dense white or pale pelage across top of shoulders and along flanks
Dorsal hairs conspicuously bicoloured
Ears very long (31–42 mm)
Upper lip with fine, microscopic wrinkles and no spoon-hairs | <i>Otomops</i>
(1 species) |

GENUS *Mormopterus*

Little Mastiff Bats and others

Mormopterus Peters, 1865. Monatsber. K. Preuss. Akad. Wiss. Berlin 1865: 258. Type species: *Nyctinomus (Mormopterus) jugularis* Peters, 1865.

Mormopterus was considered to contain ten species (Simmons 2005) but another species, *M. francoismoutoui*, has been described by Goodman *et al.* (2008). Species of *Mormopterus* include *M. acetabulosus* from Mauritius and *M. francoismoutoui* from Réunion, at least one of which has been recorded in Africa (but probably only as vagrants), and *M. jugularis* from Madagascar, which presumably has the potential to reach Africa as a vagrant although it has not yet been recorded there. The other species occur in the Malay archipelago, South America, Cuba or Australia. There are about seven more undescribed species in Australia (Churchill 1998). *Mormopterus* is included in *Tadarida* by some authors including Freeman (1981), but considered distinct by Legendre (1984), Meester *et al.* (1986), Corbet & Hill (1991, 1992) and others. *Mormopterus* is sometimes considered to include *Platymops* and *Sauromys* (e.g. Koopman 1993, 1994) but these genera are currently considered

distinct (Corbet & Hill 1992, Peterson *et al.* 1995, Simmons 2005). The only three species of *Mormopterus* likely to be recorded in Africa are distinguished from species in other molossid genera in Africa by the following combination of characters: head, body and skull low but not extremely flattened (cf. *Platymops* and *Sauromys*); ears black and not translucent (cf. whitish or translucent in *Myopterus*); inner margins of ears distinctly separated although close; third ridge of posterior upper molar (M³) equal in length or longer than second ridge; anterior palatal emargination wide; four upper cheekteeth on each side (cf. five in *Tadarida* except rarely); three lower incisors on each side (cf. one in *T. spurrelli*, two in all other African *Tadarida* except *T. teniotis*, which also has three; see also Table 19, p. 472). Dental formula (*M. acetabulosus*, *M. francoismoutoui*, *M. jugularis*): $\frac{1113}{3123} = 30$. Craniodental characters of *Mormopterus* are illustrated in Figure 106.

When the *Mormopterus* profiles were submitted, only two specimens of one species – *M. acetabulosus* – were said to have been recorded from Africa; one from Ethiopia and one from South Africa. Now, the Ethiopian specimen has been re-identified as *M. francoismoutoui* but the identity of the South African specimen could not be confirmed because its skull is missing: it could represent either *M. acetabulosus* or *M. francoismoutoui* (Goodman *et al.* 2008). Information about both species and the two African specimens is included in the following profile.

Meredith Happold

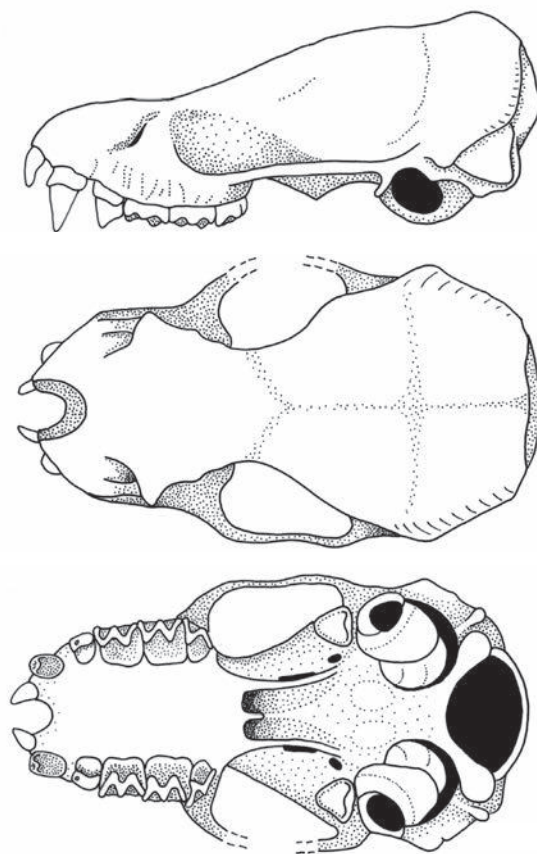


Figure 106. Skull of *Mormopterus francoismoutoui* (BMNH 6.11.1.9 from Ethiopia). This specimen was previously considered to represent *M. acetabulosus* (Goodman *et al.* 2008).

***Mormopterus acetabulosus* and *M. francoismoutoui* MAURITIAN LITTLE MASTIFF BAT AND RÉUNION LITTLE MASTIFF BAT**

Fr. Mormoptère à lèvres ridées; Ger. Mauritius Mastino-Fledermaus, Réunion Mastino-Fledermaus

Mormopterus acetabulosus (Hermann, 1804). Observ. Zool. p. 19. Port Louis, Mauritius. For several reasons, Goodman *et al.* (2008) designated FMNH 1984.368, from Palma Cave, Palma, Black River District, Mauritius, 20° 16.405' S, 57° 27.147' E, as the neotype of this species.

Mormopterus francoismoutoui Goodman, van Vuuren, Ratrimomonarivo, Probst & Bowie, 2008. J. Mammal. 89: 1318. Commune de La Possession, Pont de Balthazar, 2.2 km SSW La Possession, La Réunion, 20° 56.732' S, 55° 19.484' E, 40 m.

Taxonomy *Mormopterus acetabulosus* was originally described as *Vespertilio acetabulosus*. Until recently, it was thought to occur mainly on Mauritius and Réunion, but with two specimens (probably vagrants) recorded from Africa. However, based on both molecular and morphological evidence, specimens from Mauritius and Réunion are now considered specifically distinct and the Réunion bats have been described as a new species, *Mormopterus francoismoutoui* (Goodman *et al.* 2008) (details in Appendix). Of the two specimens from Africa, one (BM 6.11.1.9 from Ethiopia) is considered by these authors to represent *M. francoismoutoui*. The other (MNHN 1984-201 from 'Port Natal' [now Durban]) is in poor condition and its skull could not be located: consequently Goodman *et al.* (2008) could not ascertain if it represents *M. acetabulosus* or *M. francoismoutoui*. Synonyms: *natalensis*. Subspecies: none. Chromosome number: not known.

Description Very small microbats without noseleaf and with terminal portion of tail projecting freely from posterior margin of interfemoral membrane; small for an African molossid; head and body not extremely flattened; ears separated and without complex folds, upper

lip with many well-developed wrinkles; wings dark; forearms without warty granulations; anterior upper premolar absent. Sexes similar. Pelage short (mid-dorsal hairs 3–4 mm). Dorsal pelage uniformly dark brown; hairs unicoloured. Ventral pelage dark brown becoming slightly paler on abdomen. Head somewhat (but not extremely) flattened. Upper lip with many (>7) well-developed wrinkles, a few spoon-hairs and many fine hairs. Ears relatively short, erect, widely separated (by 2–4 mm) in *M. acetabulosus*, almost touching and joined by a slender band of skin in *M. francoismoutoui*, subtriangular with slight emargination below tip, without complex folds (cf. *Tadarida*). Tragus small but not concealed by antitragus. Antitragus low, indistinct. No interaural crest. Gular gland present in ♂♂. Wings and interfemoral membrane dark brown. No wart-like granulations on forearm. Hindfeet relatively large; toes with long hairs and many short, stout bristles.

Skull (Figure 106) low but not extremely dorsoventrally flattened (cf. *Platymops* and *Sauromys*) (maximum height ca. 41% of GLS as in *Tadarida pumila*). Rostrum relatively narrow (cf. *Platymops*). Zygomatic arches slender. Anterior of braincase rising above plane of rostrum; forehead slightly concave. Sagittal crest low or absent; lambdoid crest

low or absent. Lachrymal ridges indistinct and forming a comparatively small tubercle on each side of rostrum (cf. *Platymops*). Anterior palatal emargination wide. Basisphenoid pits shallow, much wider than their distance apart. Upper incisors well separated. Anterior upper premolar absent. M^3 with third ridge \geq second ridge (Figure 102c and d). Three lower incisors on each side. Lower canines with cingula not greatly enlarged and not in contact. Dental formula: $1^{113}/_{3123} = 30$.

Geographic Variation None recorded for either *M. acetabulosus* *sensu* Goodman *et al.* (2008) or *M. francoismoutoui*.

Similar Species Four other African molossids have ears without complex folds:

Myopterus daubentonii. Much larger (FA: 48–56 mm; GLS: 21.3–25.7 mm). Dorsal pelage with contrasting lateral bands of paler colour. Wings with arm-wing white, hand-wing transparent. M^3 with third ridge absent.

M. whitleyi. Forearm shorter (35–37 mm); skull larger (GLS: 16.6–18.5 mm). Arm-wing yellowish-white, hand-wing transparent. M^3 with third ridge absent.

Platymops setiger. Head extremely flattened. Forearms with warty granulations. Skull with very prominent lachrymal ridges.

Sauromys petrophilus. Inner margins of ears separated by narrow gap. Head extremely flattened. Anterior upper premolar present.

Distribution One specimen (of uncertain identity according to Goodman *et al.* 2008) was recorded in 1933 from Durban, KwaZulu–Natal, South Africa in the Coastal Forest Mosaic BZ, and one specimen (identified with *M. francoismoutoui* by Goodman *et al.* 2008) was recorded in 1905 from Ethiopia (between L. Turkana and Shewa Province), presumably in the Afromontane–Afroalpine BZ of the Ethiopian Highlands. Extraliminally: Mauritius and Réunion (but see Taxonomy). *Mormopterus acetabulosus* was said to occur

on Madagascar (e.g. Hayman & Hill 1971, Kingdon 1974, 1997, Koopman 1993) but no valid specimen appears to be available and the inclusion in Madagascar apparently arises from the confusion of names listed in synonymy dating back to Peters (1865), who proposed that the subgenus *Mormopterus* includes taxa from South Africa, Madagascar and the Mascarene Is. (Peterson *et al.* 1995). The lack of further records from Africa suggests that the African records are those of vagrants and that *Mormopterus* does not normally occur on the mainland. A specimen of ‘*Mormopterus* sp.’ (FA: 32 mm) from Meru N. P. (Webala *et al.* 2004) does not represent *M. acetabulosus* or *M. francoismoutoui* (M. Happold pers. obs.).

Habitat Recorded from the edge of a forest near Durban (Smithers 1983); no data for the Ethiopian locality. On Réunion, *M. francoismoutoui* is widespread and found from sea level to ca. 2000 m.

Abundance Only two specimens recorded in Africa. *Mormopterus francoismoutoui* appears common on Réunion.

Remarks On Réunion, *M. francoismoutoui* roosts in caves, crevices in rockfaces, and similar sites in bridges and buildings (Goodman *et al.* 2008). Anciaux de Faveaux (1984) catalogued a mite (*Ewingana lamoralis* [Acari: Myobiidae]) from a Kenyan specimen said to represent *M. acetabulosus*, but the identity of the specimen has not been confirmed. Apparently nothing else is known about *Mormopterus* in Africa.

Conservation IUCN Category (*M. acetabulosus*): Vulnerable (based on data from Mauritius and Réunion).

Measurements

Mormopterus acetabulosus

FA: 40.2 (38–43) mm, n = 35
 WS: (d) 242.5 (240–245) mm, n = 4*
 TL: 98.2 (92–102) mm, n = 34
 T: 44.9 (43–50) mm, n = 34
 E: 17.0 (15–18) mm, n = 34
 Tr: 3.6 (3.3–3.8) mm, n = 4*
 Tib: n. d.
 HF: 6.8 (6–7) mm, n = 34
 WT: 7.3 (6.0–8.2) mm, n = 34
 GLS: 15.1 (14.6–15.7) mm, n = 34
 GWS: 8.8 (8.5–9.1) mm, n = 30
 C– M^3 : 5.6 (5.3–5.9) mm, n = 36
 Mauritius (NMW, Goodman *et al.* 2008)
 *NMW

Mormopterus francoismoutoui

FA: 39.6 (38–42) mm, n = 33
 WS: n. d.
 TL: 93.4 (89–97) mm, n = 33
 T: 40.2 (38–45) mm, n = 33
 E: 16.7 (15–18) mm, n = 33
 Tr: n. d.
 Tib: n. d.
 HF: 6.1 (5–6.5) mm, n = 33
 WT: 6.0 (5.0–7.2) mm, n = 33
 GLS: 14.8 (14.1–15.3) mm, n = 35



GWS: 8.5 (8.1–8.9) mm, n = 33

C–M³: 5.5 (5.2–5.8) mm, n = 33

Réunion (Goodman *et al.* 2008)

Key References Goodman *et al.* 2008; Peterson *et al.* 1995.

Meredith Happold

GENUS *Myopterus* Winged-mouse Bats

Myopterus Oken, 1816. Lehrbuch der Naturgeschichte, pt 3 sect. 2: 932. Type species: *Myopterus senegalensis* Oken, 1816 (not available).

Myopterus E. Geoffroy, 1818. Description de l’Egypte 2: 113. Type species: *Myopterus senegalensis* Oken, 1816
(not available = *Myopterus daubentonii* Desmarest, 1820).

Myopterus (including *Eomops* as a synonym) is a polytypic genus with two species, endemic to tropical Africa from Senegal in the West to DR Congo and Uganda in the East, occurring in both rainforests and moist savannas. Distinguished from other genera of molossids in Africa by the following combination of characters: head, body and skull low but not extremely flattened dorsoventrally (cf. *Platymops* and *Sauromys*), wings translucent or whitish, ears whitish or translucent, without complex folding, either widely separated or meeting medially to form V-shaped valley; upper lip smooth with many spoon-hairs; third ridge of posterior M³ absent; dental formula: $^{1113}/_{1123} = 26$ (see also Table 19, p. 472). Bats in this genus also have white ventral pelage;

relatively short, narrow and erect ears; a large tragus (not concealed by the antitragus); upper incisors in contact; only one upper premolar on each side; one pair of lower incisors; anterior palatal emargination closed; and deep basisphenoid pits (distinct hole >1 mm in depth). Selected characters of a representative of the genus are illustrated in Figure 107, but there are some inter-specific differences. The savanna-dwelling species *M. daubentonii* is much larger than *M. whitleyi*, which is restricted to the rainforest zone. The latter species is one of the smallest molossids in Africa. In collections, both species are among the rarest African molossids. Almost nothing is known about their biology. They have been rarely captured except from their day-roosts,

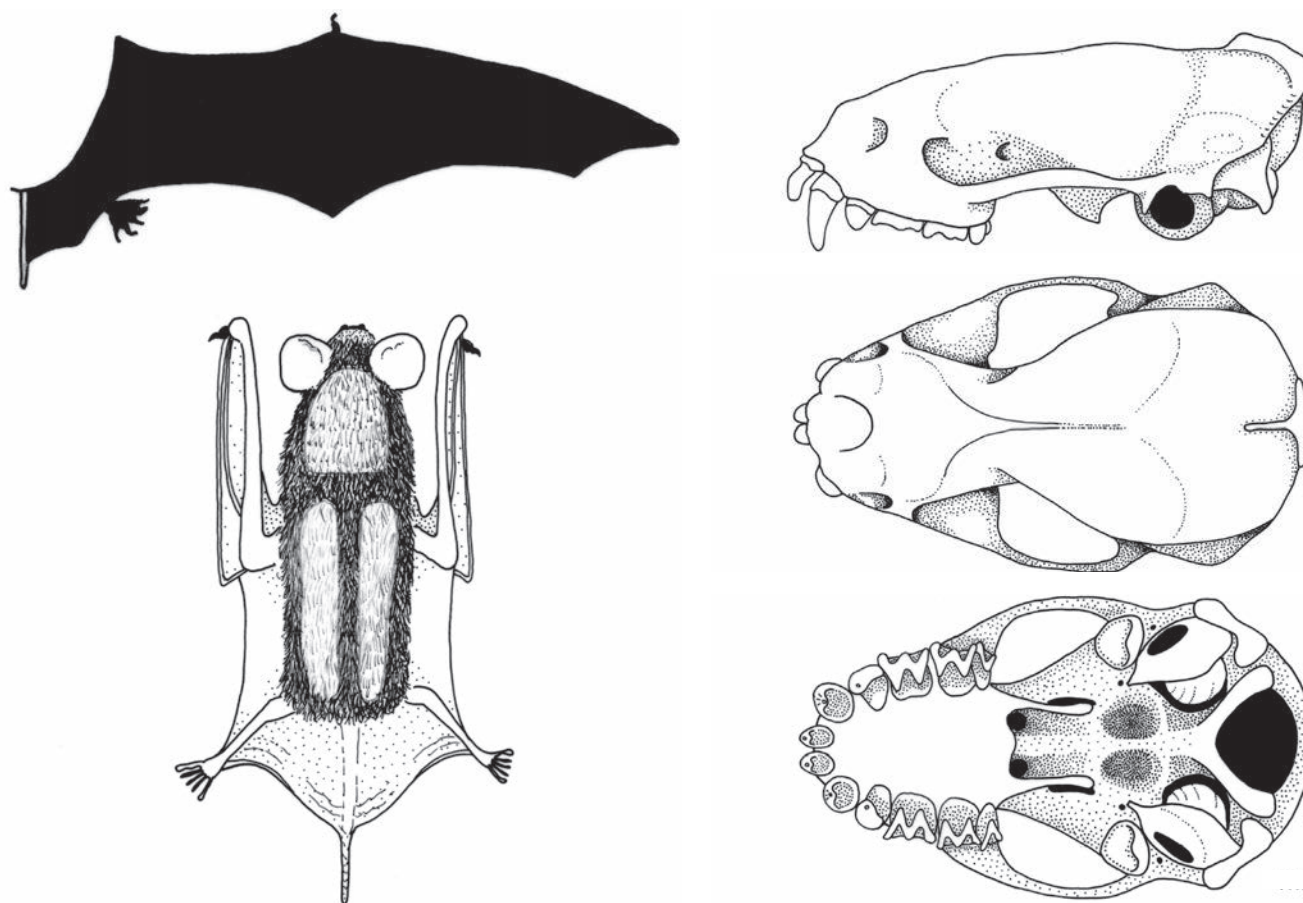


Figure 107. *Myopterus*. Flight membranes of *M. daubentonii*. Unique dorsal pelage markings of *M. daubentonii*. Skull of *M. whitleyi* (RMCA 97-021-M-0825).

which are sometimes rather unusual for molossids as *M. whiteyi* has been found roosting, unconcealed, in vegetation.

In her study of the family Molossidae, Freeman (1981) found phenetic similarity between *Myotis* and the Neotropical genera *Molossops*, *Neoplatymops* and *Cynomops*. According to her study, *Myotis* is one of the most derived molossid genera and the most derived of all African molossids. Freeman (1981) speculated that *Myotis* has no extant relative in the Old World but rather a Neotropical origin, with *Molossops* and *Cynomops* being the most closely related genera. Likewise, based on dental characters, Legendre (1984) would place *Myotis* in the subfamily Molossinae, which in his arrangement

comprises otherwise New World genera, whereas all other molossid genera occurring in Africa would be included in the subfamily Tadaridinae. In a recent cladistic analysis by Jones *et al.* (2002), *Myotis* grouped with the Asian *Cheiromeles* and Neotropical *Molossops*, again without any close relationship to African molossids.

The two species are:

M. daubentonii. FA: 48–56 mm; GLS: 21.3–25.7 mm; WT: 20–22 g.

M. whiteyi. FA: 35–37 mm; GLS: 16.6–18.5 mm; WT: 10–12.0 g.

Jakob Fahr

Myotis daubentonii DAUBENTON'S WINGED-MOUSE BAT

Fr. Myoptère de Daubenton; Ger. Daubentons Pergamentflügel-Fledermaus

Myotis daubentonii Desmarest, 1820. Encyclopédie Méthodique Mammalogie 1: 132. Senegal (no specified locality).

Taxonomy Synonyms: *albatus*. Subspecies: two. The taxonomic identity of this bat has been debated for a long time (Rosevear 1965). A specimen from Senegal was described by Daubenton (1765) and named 'rat-volant', which is not a proper binomial name. Based on the description of Daubenton, it was renamed *Myotis senegalensis* by Oken (1816) and the specimen was examined by Peters (1869). The holotype was subsequently lost and therefore Brosset & Vuattoux (1968) designated a new 'type' and 'cotype' based on specimens from Côte d'Ivoire. Hill (1969) pointed out that the name *senegalensis* was not available and referred the specimens from Côte d'Ivoire to *M. albatus* Thomas, 1915, at that time known from two localities in DR Congo. Finally, Adam *et al.* (1993) designated one neotype and four neoparatypes for *M. daubentonii* Desmarest, 1820, a name that was also based on the 'rat-volant' of Daubenton, from a series collected in Senegal. They synonymized *M. albatus* as a subspecies of *M. daubentonii*, referring specimens from Côte d'Ivoire and Central African Republic to *M. d. albatus*, while restricting the nominate form, *M. d. daubentonii*, to the Senegal population (but see Geographic Variation). Chromosome number: not known.

Description Small microbat without noseleaf and with terminal portion of tail projecting freely from posterior margin of interfemoral membrane; medium-sized for an African molossid (FA: 48–54 mm); head not flattened; ears meeting on forehead to form V-shaped valley and without complex folds, inner side whitish; upper lip smooth; dorsal pelage usually with longitudinal banding, wings partly white and partly colourless and transparent. Sexes similar in colour; ♀♀ on average slightly larger than ♂♂. Pelage short (mid-dorsal hairs 4–5 mm). Dorsal pelage dark cream, reddish-brown or greyish-brown usually with two lateral bands of whitish or pale yellowish-fawn on each side of the mid-dorsal line (Figure 107); hairs (except those of bands) whitish or cream-coloured with darker tip. Crown and nape with large patch of same colour as the lateral bands. Ventral pelage uniformly dirty- or creamy-white to pure white, much paler than, and conspicuously contrasting with, the dorsal pelage; no mid-ventral markings; ventral flank-stripe same colour as flanks. Head not dorsoventrally flattened; muzzle subcylindrical, smooth and rounded, almost naked except for dense

patch of spoon-hairs on upper lip below nostrils; upper lip smooth. Ears erect (without complex folds), narrow, with outer side partly pigmented and inner side whitish; bases of inner margins meeting on forehead to form V-shaped valley. Tragus relatively very large for a molossid, simple, anterior and posterior margins nearly parallel, tip rounded; not concealed by antitragus. Antitragus semi-circular, ca. same size as tragus. No interaural crest. No gular gland. Wings with arm-wing membranes white and hand-wing membranes strikingly transparent and showing red veining and some enclosed white spots of fat. Wing-membranes of living bats feel moist and somewhat sticky. Interfemoral membrane dorsally pale brown, ventrally white. Skin of forearm, tibia, fingers and tail pink.

Skull large and robust; not extremely dorsoventrally flattened. Sagittal and lambdoid crests absent or weakly developed. Anterior palatal emargination closed. Basisphenoid pits very deep, large, their width much greater than their distance apart. Upper incisors in contact. Anterior upper premolar absent. M³ with third ridge absent. Only one lower incisor on each side, bicuspid (inner cusp distinctly higher than outer cusp), not crowded. Lower canines with cingula not greatly enlarged, well separated. Dental formula $\frac{1113}{1123} = 26$.

Geographic Variation Two subspecies are recognized (Adam *et al.* 1993), but variability seems to be high in this species:

M. d. daubentonii. Originally considered to be restricted to Senegal (Adam *et al.* 1993), but a re-examination and comparison of published data with data from new specimens from Côte d'Ivoire show that the dimensions of specimens from Senegal, Côte d'Ivoire and Central African Republic overlap sufficiently to justify assigning all of them to the nominate subspecies. FA: 50.4 (48–54) mm; TL: 110.9 (104–120) mm; GLS: 22.5 (21.3–24.9) mm; GWS: 13.4 (13.0–14.5) mm (see Measurements).

M. d. albatus. Considered to include all populations east of Senegal by Adam *et al.* (1993), but considered here to include only specimens from DR Congo, which are clearly larger than those from Senegal to Central African Republic. For five ♀♀ from Niangara, DR Congo, FA: 53.7 (52–56) mm; TL: 126.0 (123–132) mm; GLS: 25.2 (24.2–25.7) mm; GWS: 14.5 (14.1–14.7) mm (Allen 1917a, Hill 1969).



Myotis daubentonii

Similar Species Four other African molossids have ears without complex folds:

Myotis whiteleyi. Much smaller (FA: 35–37 mm; GLS: 16.6–18.5 mm). Dorsal pelage without lateral bands.

Mormopterus spp. Much smaller (FA: 38–43 mm; GLS: 14.1–15.7 mm). Dorsal pelage without lateral bands. Wings dark brown. M³ with third ridge \geq second ridge.

Sauromys petrophilus. Dorsal pelage uniformly dark brown. Wings blackish-brown, brown or semi-translucent greyish-brown. M³ with third ridge present. South of 15° S.

Platymops setiger. Much smaller (FA: 27–36 mm; GLS: 14.7–17.0 mm). Dorsal pelage uniformly coloured.

Distribution Endemic to Africa. Mainly found in the Guinea Savanna BZ and the Northern Rainforest–Savanna Mosaic, but extending into the Sudan Savanna BZ in Senegal. Known from only eight localities in Senegal, Côte d'Ivoire, Central African Republic and DR Congo (Lang & Chapin 1917b, Hayman *et al.* 1966, Adam *et al.* 1993, J. Fahr unpubl.).

Habitat Predominantly a savanna species recorded in the following vegetation zones: Sudanian undifferentiated woodland savanna in Senegal, *Isobrerlinia* woodland (e.g. N'Délé in Central African Republic) and Rainforest–Savanna Mosaic (e.g. Lamto and Comoé N. P. in Côte d'Ivoire). Also recorded at 1250 m in montane grassland (Bunia, DR Congo). Specimens from Lamto were found roosting in a palm in grassland ca. 100 m from gallery forest (Brosset & Vuattoux 1968).

Abundance Uncertain. Only 23 specimens known. Apparently quite localized and rare.

Adaptations Most of the known specimens were taken in their day-roosts in hollow trees. These include the hollow trunk of a dead Palmyra Palm *Borassus aethiopum* in which the bats roosted at a height of ca. 12 m (Brosset & Vuattoux 1968). According to Freeman (1981), species of *Myotis* are characterized by broad wing-tips. She concluded that these species are probably more manoeuvrable than most other molossids and possibly fly more slowly. In contrast, preliminary flight-cage experiments indicate that *M. daubentonii* is less manoeuvrable than 16 other species of molossids tested (J. Fahr unpubl.). Individuals from Comoé N. P., Côte d'Ivoire, had a strong, spicy and almost pungent smell.

Foraging and Food Foraging strategy: fast-hawking. In Comoé N. P., in mist-nets set 0–25 m above ground, one ♂ and two ♀♀ were caught at the same time, at heights of 9, 14 and 20 m (J. Fahr unpubl.). Possibly these individuals were foraging together as group-foraging seems to be common in molossid bats. The mist-nets were set between two large trees in woodland savanna not far from gallery forest. The teeth and mandibles are very robust and powerful; from this, Freeman (1981) deduced that this bat is probably able to consume large and hard-shelled prey.

Social and Reproductive Behaviour Very little is known. One group in a hollow tree included a subadult ♂ and six ♀♀, but not all group-members were captured (Lang & Chapin 1917b). Another group included an adult ♂ and four adult ♀♀ (not stated if all group-members were captured) (Brosset & Vuattoux 1968), and a third group included three adult ♂♂, one subadult ♂ and one subadult ♀ (Adam *et al.* 1993).

Reproduction and Population Structure No information.

Predators, Parasites and Diseases No information.

Conservation IUCN Category: Data Deficient.

Distribution rather broad, but only eight localities known. Population trend inferred to be declining, in both past and future. Major threats: loss and degradation of habitat, particularly as result of logging and agriculture.

Measurements

Myotis daubentonii daubentonii

FA: 50.4 (48–54) mm, n = 14

WS (c): 368 (350–380) mm, n = 4

TL: 110.9 (104–120) mm, n = 14

T: 40.8 (37–44) mm, n = 14

E: 20.1 (18–22) mm, n = 14

Tr: 4.7 (4.6–5.0) mm, n = 3

Tib: 14.9 (14–17) mm, n = 13

HF: 11.2 (9–13) mm, n = 9

WT: 21.3 (20.0–22.0) g, n = 4

GLS: 22.5 (21.3–24.9) mm, n = 11

GWS: 13.4 (13.0–14.5) mm, n = 10

C–M³: 8.5 (8.0–9.2) mm, n = 11

Senegal, Côte d'Ivoire, Central African Republic (FC, MHNG, MNHN, SMF, USNM)

Specimens from DR Congo (*M. d. albatu*s) are on average larger (see Geographic Variation)

Key References Adam *et al.* 1993; Allen 1917a; Brosset & Vuattoux 1968; Hill 1969; Lang & Chapin 1917b; Rosevear 1965.

Jakob Fahr

Myotis whitleyi **BINI WINGED-MOUSE BAT (WHITLEY'S WINGED-MOUSE BAT)**

Fr. Myoptère de Whitley; Ger. Bini Pergamentflügel-Fledermaus

Myotis whitleyi (Scharff, 1900). Ann. Mag. Nat. Hist., ser. 7, 6: 569. Benin City, Nigeria.

Taxonomy Originally *Mormopterus whitleyi*. Synonyms: none. Chromosome number: not known.

Description Very small microbat without noseleaf and with terminal portion of tail projecting freely from posterior margin of interfemoral membrane; small for an African molossid (FA: 35–37 mm); head not flattened; ears well separated and without complex folds, whitish; upper lip smooth; wings partly white and partly transparent, contrasting with uniformly dark brown dorsal pelage. Sexes similar in colour, ♀♀ on average slightly larger than ♂♂. Pelage short (mid-dorsal hairs 4–5 mm). Dorsal pelage dark brown without stripes; hairs whitish with medium to dark brown at tip. Ventral pelage uniformly dirty-white, cream or pure white, in marked contrast to dorsal pelage; no mid-ventral markings; ventral flank-stripe white. Head not dorsoventrally flattened; muzzle smooth and rounded; almost naked except for dense patch of very stiff spoon-hairs on upper lip below nostrils, and fringe of stiff hairs along edge of upper lip; upper lip smooth. Ears erect (without complex folds), narrow and pointed, with apex unpigmented; bases of inner margins widely separated. Tragus large, squarish, not concealed by antitragus. No interaural crest. Gular gland in ♂♂. Wings with arm-wing membranes yellowish-white, hand-wing membranes transparent. Interfemoral membrane dorsally grey or pale brown, ventrally whitish. Skin on forearm, tibia and third finger dark pink.

Skull (Figure 107) low but not extremely dorsoventrally flattened. Sagittal crest absent or very indistinct except at the very back of the braincase where, in fully mature adults, it rises gradually or abruptly to form a small wing ca. 4 mm long. Lambdoid crest absent or weakly developed. Anterior palatal emargination closed. Basisphenoid pits deep. Upper incisors in contact. Anterior upper premolar absent. M³ with third ridge absent. Only one lower incisor on each side; bicuspid, not crowded. Lower canines with cingula not greatly enlarged, well separated. Dental formula: $\frac{1113}{1123} = 26$.

Geographic Variation None recorded, but data are limited.

Similar Species Four other African molossids have ears without complex folds:

Myotis daubentonii. Much larger (FA: 48–56 mm; GLS: 21.3–25.7 mm).

Dorsal pelage with contrasting lateral bands of paler colour.

Mormopterus spp. Forearm longer (38–43 mm); skull smaller (GLS: 14.1–15.7 mm). Wings and interfemoral membrane dark brown.

M³ with third ridge ≥ second ridge.

Sauromys petrophilus. Inner margins of ears meet to form V-shaped valley. Head extremely flattened. Wings blackish-brown, brown or semi-translucent greyish-brown. South of 15° S.

Platymops setiger. Head extremely flattened. Forearms with warty granulations. M³ with second and third ridges equal in length.

Distribution Endemic to Africa. Known only from the Rainforest BZ (Western, West Central, South Central and East Central Regions) and margins of the Eastern and Southern Rainforest–Savanna Mosaics. Known only from 20 localities in Ghana, Nigeria, Cameroon, Central African Republic, Gabon, DR Congo and Uganda (Hayman *et al.* 1966, Happold 1987, Adam *et al.* 1993, Van Cakenberghe *et al.* 1999, Barrière *et al.* 2002, J. Fahr unpubl.). Although based on rather few records, it seems that the distribution pattern is patchy or even disjunct. Conspicuously absent from central Congo Basin but its distribution in DR Congo is not confined to the Kasai River System as proposed by Hayman & Hill (1971) because it has also been found along the lower stretches of the Congo R. A record from Eala (Schouteden 1944, 1948, mentioned by Aellen [1952] as from



Myotis whitleyi

Coquilhatville) was based on a specimen (RMCA RG 5392) that Hayman *et al.* (1966) re-identified as *Tadarida pumila*.

Habitat Mainly recorded in rainforest–savanna mosaic, lowland rainforest and coastal forest vegetation zones, but also found in swamp forest and mangroves. Most of the localities are situated along the periphery of the Rainforest BZ. A single record from Kasenye near L. Albert, DR Congo, is from *Isoberlinia* woodland. Specimens from Calabar, Nigeria, were caught in a garden (ROM).

Abundance No information, but localized.

Remarks Day-roosts of *M. whitleyi* are variable and in some cases unusual for a molossid: specimens have been taken among the leaves of plantains, clinging to the outside of a *Cola* tree and in houses (Rosevear 1965). Surprisingly, a single, uninjured individual was captured on the ground in a bucket in a pitfall-trap line (Barrière *et al.* 2002).

Predators, Parasites and Diseases Ectoparasites include fleas *Lagarosylla obliqua*, *Allopsylla hetera* and *A. lobayensis* (Siphonaptera: Ischnopsyllidae) and a mite *Dentocarpus tenuis* (Acari: Chirodiscidae) (Beaucournu & Fain 1982, Anciaux de Faveaux 1984, Barrière *et al.* 2002).

Conservation IUCN Category: Least Concern.

Measurements

Myopterus whitleyi

FA: 35.8 (35–37) mm, n = 7

WS: n. d.

TL: 81.7 (78–87) mm, n = 7

T: 27.7 (25–31) mm, n = 7

E: 14.8 (14–16) mm, n = 7

Tr: 4.6, n = 1

Tib: 10.2 (9–12) mm, n = 6

HF: 7.0 (5.0–8.3) mm, n = 7

WT: 10.7 (10.0–12.0) g, n = 3

GLS: 17.6 (16.6–18.5) mm, n = 8

GWS: 10.5 (10.2–10.8) mm, n = 8

C–M³: 6.5 (6.1–6.9) mm, n = 8

Ghana, Nigeria, Cameroon, Gabon, Uganda, DR Congo (BMNH, HZM, MHNS, MNHN, USNM, Van Cakenberghe *et al.* 1999)

Key References Adam *et al.* 1993; Rosevear 1965; Thomas 1905.

Jakob Fahr

GENUS *Otomops* Giant Mastiff Bats

Otomops Thomas, 1913. J. Bombay Nat. Hist. Soc., 22: 91. Type species: *Nyctinomus wroughtoni* Thomas, 1913.



Otomops martiensseni.

Otomops currently contains seven species of which only one occurs in Africa; the others occur in Madagascar, S India, Java, Lesser Sundas Is. or New Guinea (Simmons 2005). Distinguished from other genera of molossids in Africa by the following combination of characters: head, body and skull low but not extremely flattened dorsoventrally; ears uniquely shaped with only moderate folding, forward-projecting and joined to the long muzzle (Figure 97b); no tragus; no antitragus; dorsal hairs bicoloured; a band of pale or white pelage across shoulders and along each flank above the wings; upper lip with fine, microscopic wrinkles and no spoon-hairs; basisphenoid pits very deep; third ridge of posterior upper molar (M³) as long or almost as long as the second ridge; dental formula: $\frac{1123}{2123} = 30$ (see also Table 19, p. 472). Selected characters of *Otomops martiensseni* are illustrated in Figure 108.



Otomops martiensseni showing ear flap folded down (upper) and open (lower).

The genus was reviewed by Peterson *et al.* (1995). Based on non-metric multidimensional scaling, these authors recognized all previously named forms of *Otomops* as distinct species (with the exception of

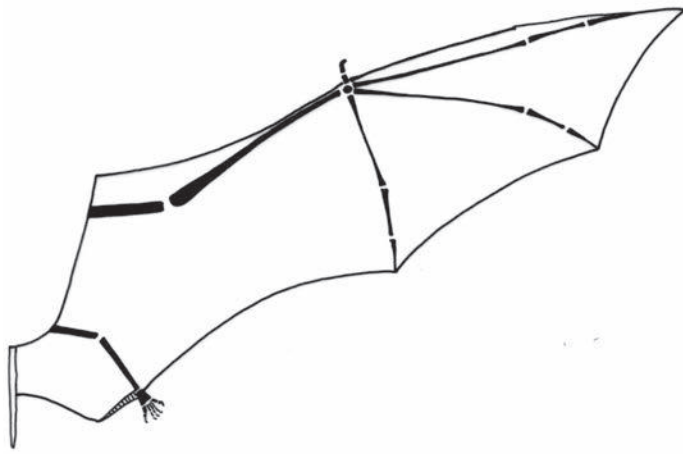
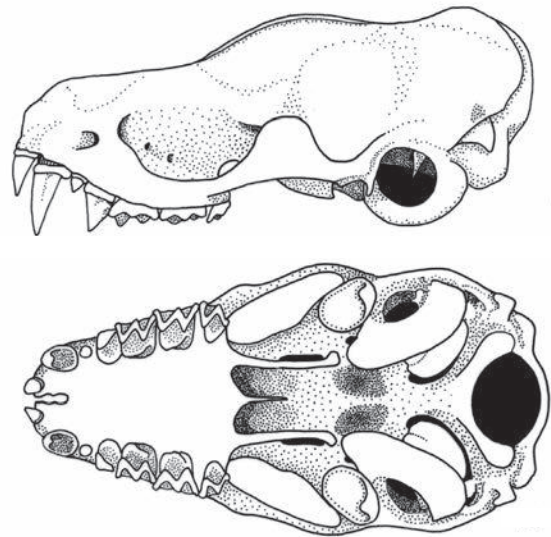


Figure 108. African *Otomops*. Flight membranes, and bones of wing, hindlimb and tail of *O. martiensseni* (BMNH 1975-914).



O. johnstonei from Indonesia, which was not described until 1992 and not included in their study), but they considered *O. icarus* very similar to *O. martiensseni*, and were uncertain of its specific status. This form is now considered to be a subspecies of *O. martiensseni* (see species profile). Peterson *et al.* (1995) found *O. madagascariensis* from Madagascar to be morphologically quite different from the African

O. martiensseni, and more closely related to *O. formosus* from Java, Indonesia than to any other species.

The species found in Africa is *O. martiensseni*.

Meredith Happold

Otomops martiensseni LARGE-EARED GIANT MASTIFF BAT

Fr. Grand molosse oreillard; Ger. Großohrige Riesen-Bulldoggfledermaus

Otomops martiensseni (Matschie, 1897). Arch. Naturgesch. 63 (1): 84. Magrotto Plantation, near Tanga, SE Usambara Mts, Tanzania.

Taxonomy Originally *Nyctinomus martiensseni*. Synonyms: *icarus*. Subspecies: two. A Madagascan form, *madagascariensis*, is considered to be a distinct species by Peterson *et al.* (1995) and Goodman (2011) although often considered a subspecies of *O. martiensseni* (e.g. Harrison 1957a, Koopman 1993, 1994). Chromosome number (Kenya): $2n = 48$; $aFN = 56$ (Dulić & Mutere 1973b) or 58 (Warner *et al.* 1973).

Description Medium-sized microbat without noseleaf and with terminal portion of tail projecting freely from posterior margin of interfemoral membrane; the largest African molossid (FA: 61–74 mm); ears very large, forward-projecting with inner margins joined together and to muzzle; dorsal pelage with band of pale pelage across shoulders and along flanks; dorsal hairs bicoloured. Sexes similar in colour; ♂♂ on average larger than ♀♀. Pelage soft, dense; mid-dorsal hairs 6–7 mm. Dorsal pelage dark brown with dark rusty-brown tinge, or blackish-brown, darker on head and body, with pale brown or white band across shoulders, and a thin band of pale brown separating the dark dorsal pelage from the dark wing-membrane on each side; mid-dorsal hairs dark brown with whitish base. Ventral pelage dark brown, throat paler. Head not flattened; face pink; snout ‘pig-like’. Upper lip expansible with many fine wrinkles, no spoon-hairs. Ears rounded, fairly stiff, projecting forward well beyond snout; inner margins joined together and to muzzle (Figure 97b). Tragus minute; antitragus absent. A semi-circular flap extends forward from base of ear;

can be folded down to seal auditory meatus. No interaural crest. Gular sac (gular gland) present in both sexes; well developed in adult ♂♂ (Harrison 1957b). Wings and interfemoral membrane blackish-brown.

Skull (Figure 108) not extremely dorsoventrally flattened. Anterior of braincase moderately elevated above plane of rostrum. Each zygomatic arch with a very prominent vertical projection. Sagittal crest moderate; lambdoid crest low or absent; no helmet. Anterior palatal emargination very narrow and deep. Basisphenoid pits very deep and much wider than the very narrow septum between them (as in Figure 101b). Dentition weak. Anterior upper premolar small but rising well above cingulum of posterior premolar. M^3 with third ridge equal or just a little shorter than second. Two lower incisors on each side, bicuspid, not crowded. Lower canines with cingula weakly developed (cf. *Tadarida*) and well separated. Dental formula: $^{1123}/_{2123} = 30$.

Similar Species None.

Geographic Variation Koopman (1994) lists two African subspecies:

O. m. icarus: Angola and Malawi to KwaZulu–Natal. Smaller (FA [KwaZulu–Natal]: 62–68 mm).

O. m. martiensseni: remainder of African geographic range. Larger (FA [Ethiopia]: 69–74 mm).



Otomops martiensseni

The validity of *icarus* as a subspecies, and its distribution, have been questioned (Hill & Carter 1941, Meester *et al.* 1986). The possibilities of a clinal decrease in size with increasing latitude within one species, or the existence of two distinct species, need investigation. See also Lamb *et al.* (2006, 2008) and Monadjem *et al.* (2010).

Distribution In Africa, widely but apparently disjunctly distributed in the Somalia–Masai Bushland, Coastal Forest Mosaic, Zambezan Woodland and Afromontane–Afroalpine BZs in the eastern side of Africa from Djibouti to KwaZulu–Natal, South Africa. Also three isolated records in the Guinea Savanna BZ (Côte d’Ivoire, Ghana, Central African Republic), one record from the Rainforest BZ (DR Congo), and one isolated record from the Zambezan Woodland BZ (Angola). This bat is difficult to catch (except at day-roosts), therefore the disjunctions probably reflect insufficient sampling. Extraliminally: Yemen.

Habitat Found in a wide range of habitats, from semi-arid scrub to montane forests, from urban and agricultural areas to undisturbed areas, and from sea level to 2000 m.

Abundance Uncertain. Seldom recorded throughout most of geographic range, but two colonies numbering >300 and several thousand were reported in 1960s by Mutere (1973b). Kock *et al.* (2005) provides further evidence that the two breeding colonies in Kenya may fluctuate in numbers (possibly due to migration) but can number tens of thousands. Common in certain residential suburbs in and around Durban, KwaZulu–Natal (Fenton *et al.* 2002).

Adaptations Aspect ratio very high; wing-loading high to very high; wing-tips broad; flight fast (9.5 m/sec for bat flying 20 m above ground); agile with poor manoeuvrability; uses side-slips to decrease altitude rapidly (Norberg 1976, Norberg & Rayner 1987, Rydell & Yalden 1997, Fenton *et al.* 2002). During flight, the somewhat rigid

ears project forward; the flap behind the antitragus can either open or close the auditory meatus – Kingdon (1974) suggests that the flap closes to increase streamlining; Valdivieso *et al.* (1979) suggest that it closes to protect the ear from intense noises. In Kenya, roosts by day on ceilings of caves including lava tunnels, preferring darker, poorly ventilated positions (Mutere 1973b). Becomes torpid during day (Mutere 1973b, D. W. Yalden pers. obs.). Emerges well after dark. Sometimes shares caves with *Rhinolophus* sp., *Miniopterus* sp. and *Triaenops afer*. In KwaZulu–Natal, roosts by day under roofs of houses and apartments in built-up areas, preferring old 2–3 storey houses, some of which have been occupied by bats for at least nine years (Taylor, P. 1998, Fenton *et al.* 2002). Entrances are high to allow diving to gain sufficient speed for flight, and so small that the bats have to scuttle in and out of them. Individuals hang or cling, face downwards, with their bellies in contact with vertical surfaces, or cling to horizontal surfaces. They huddle together and do not appear to become torpid during the day. Radio-tracking revealed that ♂♂ and also ♀♀ in different reproductive conditions used at least two day-roosts and up to four different day-roosts over a 12-day period (Fenton *et al.* 2002). Bats begin to emerge 15–30 min after sunset. *Otomops martiensseni* is docile to handle and, despite its pugnacious appearance, makes no attempt to bite handlers. For further adaptations, see Long (1995).

Foraging and Food Forages by fast-hawking in open spaces, probably at fairly high altitudes (see below). Because food resources near caves sheltering thousands of individuals are likely to be limited, these bats presumably travel long distances from their day-roosts while foraging. Local fluctuations in populations suggest that some individuals migrate seasonally at times of food-shortage (Mutere 1973b), but this needs confirmation. Radio-tracked bats in the Durban area, South Africa, covered considerable distances while foraging; most bats foraged more than 3 km from their day-roosts for most of the night; one ♂ night-roosted 6.8 km from his day-roost, and two ♀♀ night-roosted at least 10 km away (Fenton *et al.* 2002). Analysis of faecal pellets from Kenya and Rwanda indicated that moths comprise 97–100% by volume of the diet (Rydell & Yalden 1997) and, as in other molossid moth-specialists, the jaws are slender and the dentition weak (Freeman 1981).

Echolocation Search-phase call-shapes (South Africa): (a) very shallow linear or quasi-linear FM; start-frequency ca. 18 kHz; end-frequency ca. 9 kHz; peak-frequency 10–12 kHz; call-duration 5–50 ms; maximum energy in fundamental harmonic, other harmonics uncommon; and (b) lilt calls – as above but end with a shallow upward sweep (lilt), and include the second harmonic (Fenton *et al.* 2002). Lilt calls are most common in calls lasting over 25 ms. In cluttered surroundings (e.g. when emerging from day-roosts) individuals emit pairs of multiharmonic calls (7–16 kHz, peak-frequency 11 kHz), which are audible to humans (Taylor 2000). No feeding-buzzes were heard during more than 20 h of monitoring. Calls with frequencies 10–13 kHz, recorded 500–550 m above ground, were assumed to have been emitted by *O. martiensseni* by Fenton & Griffin (1997) because they resembled the low frequency calls of a light-tagged individual (Fenton & Bell 1981). These audible calls are lower in frequency than those detected by species of moths that can hear ca. 20–40 kHz and dive to avoid capture by bats echolocating at these frequencies.

Social and Reproductive Behaviour In Kenya, *O. m. martiensseni* roosts in very large groups (colonies) of several hundred to several thousand individuals of both sexes; social organization not known. In KwaZulu–Natal, *O. m. icarus* roosts singly, or in groups of up to 29 individuals that are typically comprised of one adult ♂, several adult ♀♀ and young: this suggests a harem mating system (Taylor, P. 1998, Fenton *et al.* 2002). Discounting four records of single bats, and two records of only two bats, 24 colonies averaged 11.2 ± 6.7 individuals (mean \pm S.D.). Males with well-developed gular sacs (gular glands) were found with ♀♀ and young outside the mating season, suggesting that the harem associations are not just related to mating, and year-round maintenance of harems is suggested by Fenton *et al.* (2004). Radio-tagged bats from different colonies were never observed roosting in the same houses. Roosting group-members usually hang in physical contact with each other, and make social vocalizations, which are audible to humans. Group-members emerge from a roost singly, at 3–10 min intervals, but remain in the vicinity and emit FM sweeps that have individual signatures permitting individuals to be recognized; these seem to have a communication function and perhaps are not used in echolocation (Fenton *et al.* 2004). This behaviour continues for ca. 5–30 min, apparently until other bats from the roost join those calling in flight. Because, on any one day, group-members are sometimes in different buildings, their signature-calls perhaps play an important role in synchronizing group activities away from the roosts (Fenton *et al.* 2004).

Reproduction and Population Structure Litter-size: one. Left ovary non-functional; implantation always in right horn. At 1–3°S (Ithundu and Mt Suswa, inland Kenya), the reproductive chronology is mainly restricted seasonal monoestry with 86% of 153 ♀♀ pregnant in Nov and most births at beginning of wet season (Nov–Dec) (Mutere 1973b). Gestation suggested to be ca. three months. A few pregnant ♀♀ were recorded in Jan (4%), Feb (1%) and May (2%) but no evidence of polyoestry was recorded. Testes size maximum in Aug, low Dec–May; gular sac of ♂♂ shows similar cycle. Neonates naked and pink; seldom cling to their mothers; form clusters often apparently surrounded by their mothers. Sex ratio of juveniles usually 1 : 1, but the ratio of ♂♂ : ♀♀ in adults apparently varies from 1 : 2 to 3 : 1 in different sites and years.

At 29–30°S (KwaZulu–Natal, South Africa) the chronology appears to be extended seasonal monoestry, with juveniles recorded Oct–Jan and in May and Jun; but data are limited and it is not yet known if some ♀♀ are polyoestrous (Taylor, P. 1998, Fenton *et al.* 2002). The ratio of adult ♂♂ : ♀♀ in colonies was skewed towards ♀♀ and, in five colonies, ranged from 1 : 2 to 1 : 11 (Fenton *et al.* 2002). The sex ratios at birth and in the adult population as a whole are not known.

Predators, Parasites and Diseases Ectoparasites include a flea *Araeopsylla scitula* (Siphonaptera: Ischnopsyllidae); a tick *Carios boueti* (Acari: Argasidae); and mites *Chiroptella suswaensis* (Acari: Trombiculidae), *Olavidocarpus otomops*, *Labidocarpellus abyssinicus* (Acari: Chirodiscidae) (Anciaux de Faveaux 1984, Beaucornu & Kock 1996). Bat fleas parasitizing *O. martiensseni* increase to tremendous numbers at certain periods of the year; e.g. 662 *A. scitula* on one juvenile (Beaucornu & Kock 1996).

Conservation IUCN Category: Near Threatened.

Guano collection from one breeding-cave was thought to be the cause of variation in apparent reproductive success there from year to year (Mutere 1973b). This thinly distributed and highly colonial species would be very vulnerable to disturbance of this sort. In and around Durban, South Africa, where *O. martiensseni* roosts in houses and is one of the most commonly encountered bats, the bats themselves, and the amateur and professional people studying them, have received wide positive local publicity and this has made many of the human residents of the area more interested in the bats and more tolerant of them as co-inhabitants (Fenton *et al.* 2002). In this area, *O. martiensseni* is clearly able to find and exploit roosts in urban areas and thrive in areas of intensive agricultural operations, and could have a role as a flagship species representing the resilience of nature (Fenton *et al.* 2002).

Measurements

Otomops martiensseni

FA: 66.8 (61–74) mm, n = 93

WS (d): 489.7 (432–549) mm, n = 38

TL: 148.7 (127–163) mm, n = 37

T: 48.9 (39–54) mm, n = 48

E: 39.0 (31–42) mm, n = 38

Tr: n. d.

Tib: 21.2 (20–23) mm, n = 11

HF: 13.6 (12–15) mm, n = 12

WT: 34.4 (26–47) g, n = 80

GLS: 26.3 (24.5–28.3) mm, n = 38

GWS: 13.8 (12.9–14.7) mm, n = 49

C–M³: 10.2 (9.4–11.3) mm, n = 40

Ethiopia, Kenya, Uganda, South Africa (BMNH, RMCA, ROM, TM, Fenton *et al.* 2002, D. W. Yalden unpubl.)

Key References Fenton *et al.* 2002, 2004; Freeman 1981; Long 1995; Mutere 1973b; Rydell & Yalden 1997

D. W. Yalden & Meredith Happold

GENUS *Platymops* Peters's Flat-headed Bat

Platymops Thomas, 1906. Ann. Mag. Nat. Hist., ser. 7, 17: 499. Type species: *Platymops macmillani* Thomas, 1906 (= *Platymops setiger* Peters, 1878).

Platymops is a monotypic genus known only from S Sudan, Ethiopia and Kenya. Distinguished from other genera of molossids in Africa by the following combination of characters: head and body extremely flattened (as in *Sauromys*); ears widely separated and without complex folding; wart-like granulations on FA (unlike all other African genera); gular sac (gular gland) well developed; upper lip with many fine wrinkles and many stiff bristles; dental formula probably $^{1123}/_{2123} = 30$ but with some variations (see species profile; see also Table 19, p. 472). Selected characters of *Platymops setiger* are illustrated in Figure 109. *Platymops* was elevated to generic status (distinct from *Mormopterus*) by Thomas (1906c), but subsequently considered a subgenus of *Mormopterus* by some authors including Freeman (1981), Legendre (1984) and Koopman (1993, 1994). Considered here as distinct following Harrison & Fleetwood 1960, Peterson (1965, 1985), Meester *et al.* (1986), Peterson *et al.* (1995) and Simmons (2005).

The only species currently recognized is *P. setiger*.



Meredith Happold *Platymops setiger*.

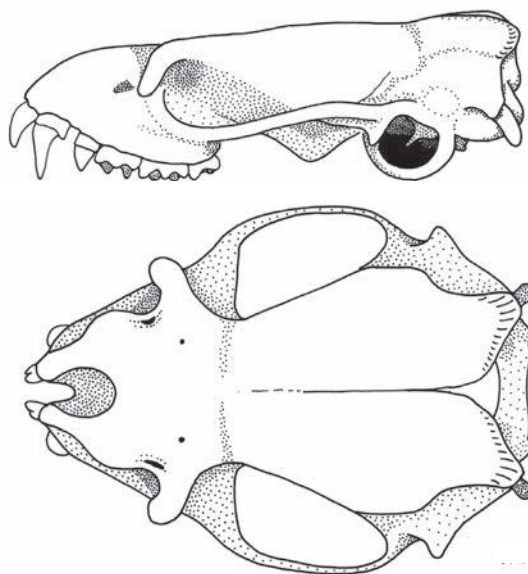


Figure 109. *Platymops setiger*. Flight membranes (traced from photo of dried skin in Harrison & Fleetwood 1960), and bones of wing and hindlimbs. Skull (HZM 6.3776): the anterior premolar is missing in this specimen.

Platymops setiger PETERS'S FLAT-HEADED BAT

Fr. Molosse à tête plate de Peters; Ger. Peters' Flachkopf-Bulldoggfledermaus

Platymops setiger (Peters, 1878). Monatsber. K. Preuss. Akad. Wiss. Berlin 1878: 196. Taita, Kenya.

Taxonomy Originally *Mormopterus setiger* but see Genus *Platymops*. Synonyms: *barbatogularis*, *macmillani*, *parkeri*. Subspecies: none currently recognized. Reviewed by Peterson (1965). Chromosome number (Kenya): $2n = 48$; $aFN = 54$ (Warner *et al.* 1974).

Description Very small microbat without noseleaf and with terminal portion of tail projecting freely from posterior margin of interfemoral membrane; small for an African molossid; head and body extremely flattened; ears well separated and without complex folds; upper lip without well-developed wrinkles; dorsal pelage without stripes; wart-like granulations on forearms and elsewhere; anterior

upper premolar minute or absent. Sexes similar. Pelage short (mid-dorsal hairs 3–4 mm). Dorsal pelage pale sepia brown, rusty-brown, brownish-grey or blackish; hairs with basal half dark cream. Ventral pelage rusty-yellow or creamy-white; sometimes with a darker to much darker lateral stripe beginning on neck and extending a variable distance along each flank, with a narrow band of brownish, rusty-yellow or creamy-white pelage between the lateral stripe and the wing-membrane. Head flattened dorsoventrally. Upper lip thick, relatively rigid, with many very fine microscopic wrinkles (giving lip a skirt-like appearance), and many dense, stiff bristles. Ears dark brown, well separated, without complex folds (cf. *Tadarida*). No interaural crest. Both sexes with small gular sac (gular gland) containing tuft of coarse, brownish hairs in the form *barbatogularis*, untufted in other forms (details in Harrison & Fleetwood 1960). Wings long, narrow, semi-translucent, lightly pigmented with dark brown, especially over bones; wart-like granulations on forearm, thumb and third metacarpal, and also on tail. Toes with long bristles (up to 8 mm).

Skull (Figure 109) extremely dorsoventrally flattened (maximum height 28–34% of GLS). Anterior of braincase not elevated above plane of rostrum. Sagittal crest low or absent anteriorly, moderate or absent posteriorly; lambdoid crests moderate to well developed (especially in adult ♂♂). Lachrymal ridges well developed and forming a prominent tubercle on each side of rostrum (cf. *Mormopterus* and *Sauromys*). Anterior palatal emargination narrow. No basisphenoid pits. Upper incisors bicuspid, well separated; tall, curved, deciduous milk incisors may be retained in immature specimens. Anterior upper premolar absent in adults but sometimes there is a minute spicule (probably a deciduous milk tooth) in younger animals, displaced labially; canine and posterior premolar in contact or almost so. M^3 with second and third ridges equal in length. Usually two lower incisors on each side, bicuspid, crowded. Lower canines with cingula not greatly enlarged and not in contact. Dental formula: probably $1^{123}/_{2123} = 30$ (but see above).

Geographic Variation Uncertain. Peterson (1965) recognized two subspecies on the basis of size: *P. s. setiger* in S Kenya, and a smaller form, *P. s. macmillani*, in the remaining geographic range. However, Peterson's samples were very small (eight adult *setiger*, 11 adult *macmillani*). Furthermore, as the distribution of this species is apparently contiguous, the variation is possibly clinal. In *barbatogularis* from Sudan (described as a species but now considered a synonym of *macmillani* by Simmons 2005), the gular sac contains a prominent tuft of brownish hairs (cf. *macmillani*) (Harrison 1956).

Similar Species Four other African molossids have ears without complex folds:

Sauromys petrophilus. Ears meeting to form V-shaped valley. Forearms without warty granulations. Upper lip smooth. No gular gland. Skull with lachrymal ridges indistinct. Anterior upper premolar present and about same height as cingulum of posterior premolar; canine and posterior premolar well separated.

Mormopterus spp. Head not extremely flattened. Forearms without warty granulations. Skull without very prominent lachrymal ridges.

Myopterus daubentonii. Much larger (FA: 48–56 mm; GLS: 21.3–25.7 mm). Dorsal pelage usually with contrasting lateral bands of paler colour.



Platymops setiger

Myopterus whitleyi. Head not extremely flattened. Forearms without warty granulations. M^3 with third ridge absent.

Distribution Endemic to Africa. Apparently confined to a narrow belt through the Somalia–Masai Bushland BZ (and marginally into the Sudan Savanna BZ) from SE Sudan and SW Ethiopia to SE Kenya (Largen *et al.* 1974, Koopman 1975, Aggundey & Schlitter 1984). Not known to extend into the Horn of Africa (*contra* Kingdon 1974).

Habitat At Masalani, near Kibwezi in inland Kenya, recorded from dense thorn scrub (*Combretum*, *Grewia*, *Premna*) with scattered patches of grassland (O'Shea & Vaughan 1980). Elsewhere, recorded from dry stony areas, and areas with rocky hills, in Ethiopian undifferentiated woodland, Somalia–Masai *Acacia–Commiphora* bushland and thicket, and mosaics of East African evergreen bushland and secondary *Acacia* wooded grassland (terminology: White 1983).

Abundance Uncertain.

Adaptations Wings short for an African molossid; metacarpal of third finger only ca. one-third longer than metacarpal of fifth finger (Thomas 1906c). Flight described as fast, direct or erratic. Roosts by day in very narrow crevices under stones or rocks lying on the ground, and in fissures in granite hills: sometimes found cohabiting with scorpions (Harrison & Fleetwood 1960). Able to squeeze into these confined spaces because head and body are flattened. Tactile hairs on feet and muzzle (as in other molossids) also facilitate movement into the day-roosts. According to Kingdon (1974), the tip of the tail is held aloft to gauge heights of crevasses, and the ears and raised phalanges of third and fourth fingers are also used for this purpose. Roosts have strong smell. Emergence is at dusk (Williams 1967).

Foraging and Food Forages by fast-hawking (O'Shea & Vaughan 1980). Has been observed flying over waterholes and marshes, at

heights of 9 m and less (Nowak 1999). Small beetles recorded in diet.

Social and Reproductive Behaviour Recorded roosting singly and in groups of up to five (Nowak 1999). No other information.

Reproduction and Population Structure Litter-size: one ($n = 4$; Anciaux de Faveaux 1972, O'Shea & Vaughan 1980). Reproductive chronology not known.

Predators, Parasites and Diseases No information.

Conservation IUCN Category: Least Concern.

Measurements

Platymops setiger

FA: 32.6 (27–36) mm, $n = 36$

WS (a): 257.4 (227–280) mm, $n = 20$

TL: 91.3 (72–114) mm, $n = 31$

T: 29.9 (22–36) mm, $n = 31$

E: 15.0 (11–17) mm, $n = 33$

Tr: 3.8 (3.2–4.2) mm, $n = 6$

Tib: n. d.

HF: 7.3 (7–8) mm, $n = 10$

WT: 12.6 (7–18) g, $n = 20$

GLS: 16.0 (14.7–17.0) mm, $n = 13$

GWS: 11.9 (11.2–12.3) mm, $n = 8$

C–M³: 5.9 (5.0–6.4) mm, $n = 27$

Throughout geographic range (BMNH, NMK, ROM, SMF, SMNS, Peterson 1965, Koopman 1975)

Key References Harrison 1956; Harrison & Fleetwood 1960; Nowak 1999; Peterson 1965.

Meredith Happold

GENUS *Sauromys* Roberts's Flat-headed Bat

Sauromys Roberts, 1917. Ann. Transvaal Mus., 6: 5. Type species: *Platymops petrophilus* Roberts, 1917.

Sauromys is a monotypic genus almost certainly found only in southern Africa. Simmons (2005) lists Ghana as a possible locality, and Meester *et al.* (1986) refer to an immature specimen from that country in the USNM collection. However, D. E. Wilson (pers. comm. in Jacobs & Fenton 2001) found that the USNM collection contained no specimens other than 38, all of which came from southern Africa. No records from Ghana are reported by Grubb *et al.* (1998). *Sauromys* is distinguished from other genera of molossids in Africa by the following combination

of characters: head, body and skull extremely flattened (as in *Platymops*); ears without complex folding and with inner margins separated by narrow gap (cf. ears widely separated in *Platymops*); no wart-like granulations on forearm; no gular sac (gular gland); upper lip smooth with few coarse bristles; third ridge of posterior upper molar (M³) equal in length to second ridge; dental formula: $^{1123}/_{2123} = 30$. The flight membranes, and bones of wing, hindlimb and tail, and the lateral, dorsal and ventral views of the skull are illustrated in Figure 110.

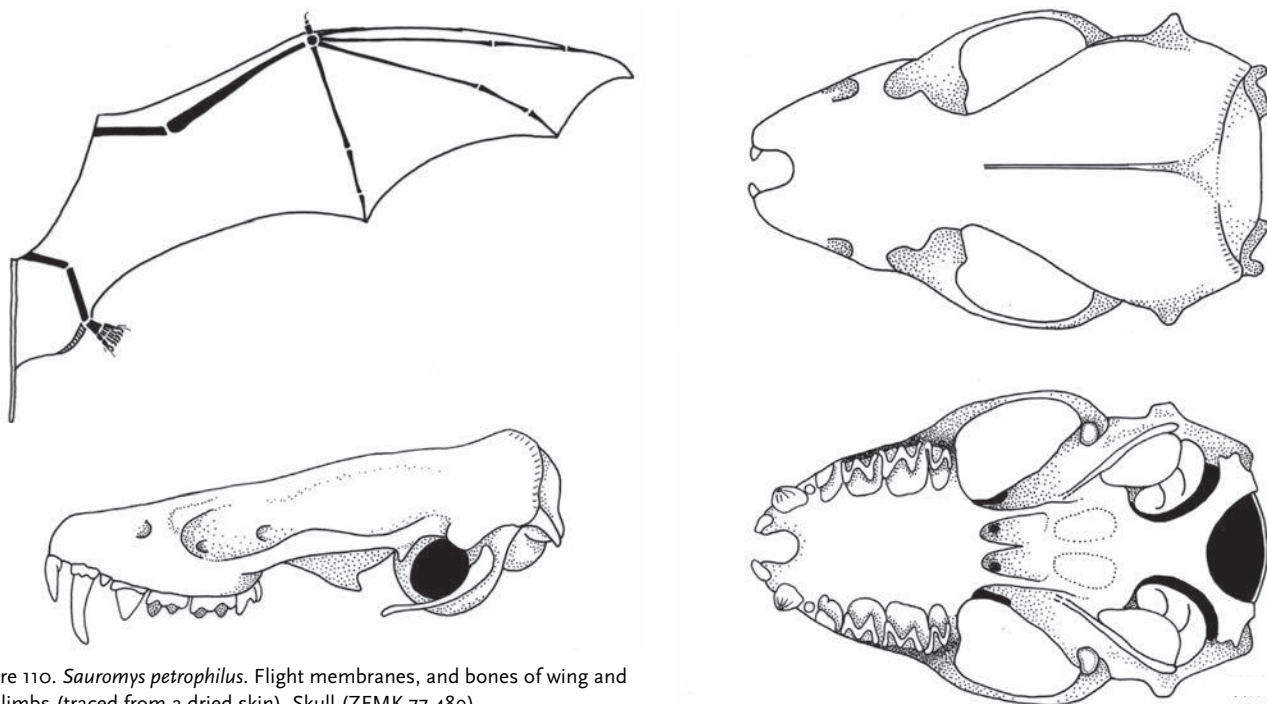


Figure 110. *Sauromys petrophilus*. Flight membranes, and bones of wing and hindlimbs (traced from a dried skin). Skull (ZFMK 77.489).

Sauromys was described as a subgenus of *Platymops*, then raised to generic status by Peterson (1965). Subsequently, it has been considered a subgenus of *Mormopterus* by Freeman (1981) and others including Legendre (1984) and Koopman (1993, 1994). It is considered a distinct genus here, following Peterson (1965), Meester

et al. (1986), Corbet & Hill (1992), Peterson *et al.* (1995) and Simmons (2005).

The only species is *S. petrophilus*.

Meredith Happold

Sauromys petrophilus ROBERTS'S FLAT-HEADED BAT

Fr. Molosse à tête plate de Roberts; Ger. Roberts Flachkopf-Bulldogfledermaus

Sauromys petrophilus (Roberts, 1917). Ann. Transvaal. Mus. 6: 4. Bleskop, near Rustenburg, Northwest Province, South Africa.

Taxonomy Originally *Platymops* (*Sauromys*) *petrophilus*. Synonyms: *erongensis*, *fitzsimonsi*, *haagneri*, *umbratus*. Subspecies: five of uncertain validity. Chromosome number (Namibia, South Africa): $2n = 48$; $aFN = 62$. X = medium-sized submetacentric; Y = small acrocentric (Rautenbach *et al.* 1993).

Description Very small microbat without noseleaf and with terminal portion of tail projecting freely from posterior margin of interfemoral membrane; medium-small for an African molossid; head and body extremely flattened; ears separated and without complex folds; dorsal pelage without stripes; forearms without wart-like granulations; anterior upper premolar well developed. Sexes similar in colour; ♀♀ on average slightly larger than ♂♂. Pelage soft and dense; mid-dorsal hairs 5–6 mm. Dorsal pelage dark brown, medium yellowish-brown, greyish-brown, dark grey to pale grey; hairs brown with the various shades of brown or grey at tip. Ventral pelage fairly dark greyish-brown, pale grey to whitish; flanks sometimes darker than throat and abdomen; chin naked. Head extremely dorsoventrally flattened. Upper lip smooth and with comparatively few coarse bristles (not spoon-hairs). Ears moderately large but not extending beyond muzzle when laid forward, broad, without complex folds; inner margins separated by narrow gap (Figure 97e) (cf. *Tadarida pumila* with which it has been confused [Jacobs & Fenton 2002]). Antitragus indistinct. Tragus very small. No interaural crest. No gular gland. Wings long, narrow, blackish-brown, brown to semi-translucent greyish-brown.

Skull (Figure 110) extremely dorsoventrally flattened (maximum height 32 [24–37]% of GLS, $n = 22$). Zygomatic arches slender. Anterior of braincase not elevated above plane of rostrum. Sagittal crest indistinct and depressed in shallow parietal groove; lambdoid crest moderate. Lachrymal ridges indistinct and forming a comparatively small tubercle on each side of rostrum (cf. *Platymops setiger*). Anterior palatal emargination wide; upper incisors well separated. Basisphenoid pits shallow (indistinct), large, their width much greater than their distance apart. Upper incisors with small secondary cusp on lateral side, just below gum. Anterior upper premolar about same height as cingulum of posterior premolar, within tooththrow; canine and posterior premolar well separated (Figure 103c). M^3 with second and third ridges equal in length. Two lower incisors on each side. Lower canines with cingula not greatly enlarged and not in contact. Dental formula: $^{1123}/_{2123} = 30$.

Geographic Variation Five subspecies (which were provisionally retained by Peterson 1965) are recognized by Koopman (1994) and Simmons (2005): *S. p. petrophilus*, *S. p. erongensis*, *S. p. fitzsimonsi*, *S. p. haagneri*, *S. p. umbratus*. However, they are based on colour differences

and their validity is uncertain (Smithers 1983, Meester *et al.* 1986). No subspecies are recognized by Jacobs & Fenton (2002).

Similar Species Four other African molossids have ears without complex folds:

Platymops setiger. Ears well separated. Forearm with warty granulations. Upper lip with many wrinkles. Gular sac (gland) present, albeit small, in both sexes. Skull with lachrymal ridges very well developed and prominent. Anterior upper premolar absent (but sometimes a minute spicule, probably a milk tooth, is present in younger animals); canine and posterior premolar in contact or almost so.

Mormopterus spp. Inner margins of ears widely separated in *M. acetabulosus* (but almost touching and joined by a slender band of skin in *M. francoismoutoui*). Head not extremely flattened. Anterior upper premolar absent.

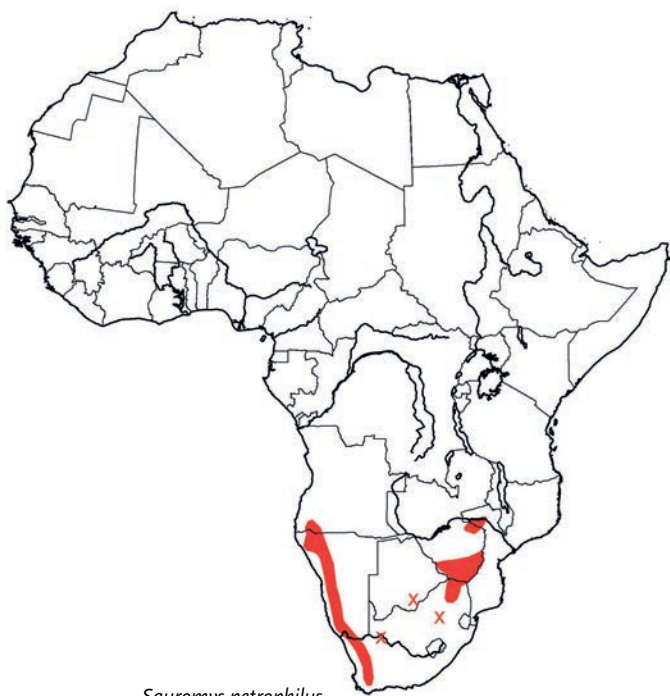
Myopterus daubentonii. Dorsal pelage usually with contrasting lateral bands of paler colour. Wings with arm-wing white, hand-wing transparent. M^3 with third ridge absent. North of Equator.

M. whiteleyi. Inner margins of ears widely separated. Head not extremely flattened. Arm-wing yellowish-white; hand-wing transparent. North of 10° S.

Distribution Endemic to Africa. Found in the Zambezi Woodland BZ south of Zambezi R., the South-West Arid BZ and the South-West Cape BZ. Recorded marginally in SW Angola (Crawford-Cabral 1986), and in Botswana, Zimbabwe, W Mozambique and South Africa (Smithers 1983). In Zimbabwe, widespread across the S, E and NE regions below 1300 m, but inexplicably absent from large areas of semi-arid savanna woodland in N and W Zimbabwe where suitable day-roosts in granitic and Karoo sandstone outcrops appear abundant (F. P. D. Cotterill unpubl.). Meester *et al.* (1986) reported an immature specimen from Ghana (USNM) tentatively assigned to *S. petrophilus*, but subsequently this could not be traced (Jacobs & Fenton 2002). Specimens from Cederberg in South-West Cape BZ listed as *Tadarida pumila* by Meester *et al.* (1986) have been re-identified as *S. petrophilus* (Jacobs & Fenton 2001).

Habitat Wetter and drier woodland savannas (including miombo, mopane and undifferentiated woodlands), shrublands, *Acacia*-wooded grasslands and deserts; always in areas with rocky outcrops and hills, principally of Karoo sandstones and granitic intrusions.

Abundance Locally abundant in areas where roosts are abundant, notably Mutoko district (NE Zimbabwe), Matobo Hills, Limpopo

*Sauromys petrophilus*

valley (SW Zimbabwe) and Cederberg (South-West Cape, South Africa). Elsewhere scarce.

Adaptations Aspect ratio high; wing-loading medium (Jacobs & Fenton 2002). Based on wing morphology, predicted to fly fast with poor manoeuvrability. Scuttles and climbs very efficiently. By day, roosts under slabs of exfoliated granite or sandstone, and in narrow fissures; roosts located near ground level in precipices. One roost was shared with 18 lizards *Platysaurus* sp. (Rautenbach 1982). The extreme flattening of the head, and the ability to fold-down the ears, enables *S. petrophilus* to squeeze into very narrow cracks and crevices. In Namibia, captive bats did not need to drink regularly (Roer 1970).

Foraging and Food Based on wing morphology, predicted to forage by fast-hawking. Reported flying as high as 37 m (Irwin & O'Donnelly 1962 in Freeman 1981). Most often captured over open water (Jacobs & Fenton 2002), but possibly because individuals come down to drink. Based on craniodental morphology, Freeman (1981) predicted that this species would feed mainly on small, soft-bodied insects, but the stomachs of 11 individuals contained both moths, beetles and other insects (Freeman 1981). Analysis of faecal pellets

from 14 individuals indicated that the diet was predominantly hard-shelled insects: Coleoptera (43%), Hemiptera (29%), Hymenoptera (18%). Soft-bodied prey (Lepidoptera, Diptera and Neuroptera) comprised ca. 10% of the diet (Jacobs & Fenton 2002).

Echolocation Search-phase call-shape: shallow FM (no details available). Start-frequency 31.4–43.5 kHz; end-frequency 26.7–30.9 kHz; bandwidth 3.9–14.7 kHz; call-duration 5.0–10.2 ms; peak-frequency 28.0–37.5 kHz (eight bats, 30 calls; Jacobs & Fenton 2002).

Social and Reproductive Behaviour Mostly found roosting singly, in pairs or in groups of up to four (Smithers 1971, 1983). Group-members huddle closely together, but scatter if disturbed.

Reproduction and Population Structure No conclusive information. In NE Zimbabwe, pregnant and lactating ♀♀ have been mist-netted in mid-Nov; ♀♀ examined during cool-dry season were neither visibly pregnant nor lactating.

Predators, Parasites and Diseases No information.

Conservation IUCN Category: Least Concern.

Measurements

Sauromys petrophilus

FA: 40.8 (37–50) mm, n = 76

WS (d): 251–275 mm, n = 4*

TL: 104.2 (89–131) mm, n = 58

T: 38.4 (29–49) mm, n = 66

E: 16.8 (13–22) mm, n = 64

Tr: 3.3 (2–6) mm, n = 10

Tib: 11.6 (10–12) mm, n = 11

HF: 7.8 (6–10) mm, n = 24

WT: 10.7 (6–22) g, n = 55

GLS: 17.1 (16.0–17.8) mm, n = 53

GWS: 11.2 (10.5–11.7) mm, n = 33

C-M³: 6.3 (5.9–7.9) mm, n = 44

Throughout geographic range (NMZB, TM, ZFMK, Smithers 1971, Smithers & Wilson 1979, Jacobs & Fenton 2001)

*Jacobs & Fenton 2002

Key References Jacobs & Fenton 2002; Smithers 1983.

F. P. D. Cotterill

GENUS *Tadarida*

Tadarine Free-tailed Bats

Tadarida Rafinesque, 1814. *Precis. Som.*, p. 55. Type species: *Cephalotes teniotis* Rafinesque, 1814.

Tadarida (*sensu lato*) contains 43 species (Simmons 2005), of which ca. 27 species occur in Africa; the remainder are found in Madagascar, Mauritius, Aldabra, São Tomé, Príncipe, S Europe, India to Japan, Malay Archipelago to Philippines, Australia, some Pacific islands and the New World. Some African species recognized as distinct by

Simmons (2005) are considered here to have subspecific status, and some species listed by Simmons (2005), and profiled here, probably contain more than one species. Since this profile was submitted, a new species has been described (as *Mops* [*Xiphonycteris*] *bakarii*) by Stanley (2008) (see *Tadarida brachyptera* for more information). This species is

not included in tables and maps. African *Tadarida* are distinguished from other genera of molossids in Africa by the following combination of characters: head, body and skull not extremely flattened although low in some species; ears complexly folded, never whitish or translucent, inner margins meeting (or almost meeting) to form V-shaped valley or joined by band of skin (never widely separated or separated by a narrow gap); upper lip thick, usually with prominent vertical wrinkles and many spoon-hairs; forearms never with warty granulations; dental formula: $^{1113}/_{2123} = 28$, $^{1123}/_{2123} = 30$, or $^{1123}/_{3123} = 32$. The length of the third ridge of posterior M^3 relative to the second ridge is highly variable within *Tadarida*.

Of the 28 species found in Africa, one is a Palearctic species found in North Africa, five are found mainly in forests, 11 mainly in savannas, seven in both forest and savanna habitats, three in savanna and arid habitats, and one only on Mafia I. Five species, *T. brachyptera*, *T. condylura*,

T. nigeriae, *T. pumila* and *T. thersites* often roost under the corrugated iron roofs of houses occupied by humans, and may well have become more abundant as a result of this adaptation. Although sometimes noisy and smelly, they probably play an important role in controlling insects including some that damage crops.

The taxonomy and systematics of *Tadarida* is controversial. Many authors, mainly following Freeman (1981), consider the forms *Chaerephon* and *Mops* to be distinct genera, and *Xiphonycteris* a subgenus of *Mops* (e.g. Koopman 1993, 1994, Simmons 2005). Many others, including Legendre (1984), Meester *et al.* (1986), Corbet & Hill (1992) and Peterson *et al.* (1995) recognize these forms as subgenera of *Tadarida*. It is currently considered probable that *Chaerephon*, *Mops* and *Tadarida* (*sensu stricto*) are not monophyletic. Furthermore, the affinities of some species are unclear and their placement in these taxa depends on what diagnostic characters are

Table 20. Key to the African species in the genus *Tadarida* (*sensu lato*). The traditional subgenera to which the species have been allocated are given, but the monophyly of these taxa, and their taxonomic status is uncertain. Ventral flank-stripe in contrasting colour = band of ventral pelage adjacent to wing membrane (sometimes extending onto wing) the colour of which contrasts with that of the flanks adjacent to the flank-stripe. Ears can be small (extending about half-way along muzzle when laid forward) or large (extending well beyond snout when laid forward). Plantar pad = raised pad on sole of foot. Depth of basisphenoid pits in *Tadarida* may be shallow, moderate or deep, and the relative size of the pits (i.e. width relative to width of septum between pits) may be small (pit noticeably narrower than septum), medium (pit about as wide as septum) or large (pit noticeably wider than septum). For additional characters, see similar species listed in species profiles.

| Inner margins of ears | Upper M^3 : size of ridge 3 in relation to ridge 2 | Number of lower incisors on each side | Anterior palatal emargination | Ventral flank-stripe in contrasting colour (colour) | |
|---|--|---------------------------------------|-------------------------------|---|--|
| Almost meeting to form V-shaped valley | $3 = 2$ | 2 | Wide | Present or absent (Whitish) | |
| Meeting to form V-shaped valley. | $3 = 2$ | 3 | Wide | Absent | |
| Meeting to form V-shaped valley | $3 > \text{half } 2$ | 2 | Wide | Present (White) | |
| Meeting to form V-shaped valley | $3 > \text{half } 2$ | 2 | Wide | Present (White, cream or yellowish) | |
| Meeting to form V-shaped valley | $3 > \text{half } 2$ | 2 | Wide | Absent | |
| Separated by a large bulbous lobe projecting well over the forehead | $3 > \text{half } 2$ | 2 | Closed | Absent | |
| Separated by a flat lappet over a small, backward-opening pocket | $3 \geq \text{half } 2$ | 2 | Closed in adults | Present (White or whitish) | |
| Joined by band | $3 > \text{half } 2$ | 2 | Narrow | Present (Whitish) | |
| Joined by band | $3 > \text{half } 2$ | 2 | Narrow | Absent | |
| Joined by band | $3 > \text{half } 2$ | 2 | Narrow | Absent | |
| Joined by band | $3 > \text{half } 2$ | 1 or 2 | Closed or narrow | Present or absent (White or whitish) | |
| Joined by band | $3 > \text{half } 2$ | 1 or 2 | Closed or narrow | Present or absent (White or whitish) | |

given precedence. Pending revision and redefining of these taxa, we present all of the African species as members of *Tadarida* but give their traditional 'subgeneric' affinities in each profile. African members of the 'subgenera', as traditionally defined, can usually be distinguished by the following combinations of characters:

subgenus *Tadarida*: inner margins of ears meeting or almost meeting to form a V-shaped valley; third ridge of posterior upper molar (M^3) more than half length of second or equal in length; anterior palatal emargination wide.

subgenus *Chaerephon*: inner margins of ears joined by band of skin (except in *T. (C.) gallagheri* and *T. (C.) major*); third ridge of posterior upper molar (M^3) more than half length of second or equal in length; anterior palatal emargination closed (except *T. (C.) ansorgei*, *T. (C.) bemmeleni* and *T. (C.) bivittata* in which it is narrow).

subgenus *Mops*: inner margins of ears joined by band of skin (except perhaps *T. (M.) niangarae*); third ridge of posterior upper molar (M^3) less than half length of second or absent (except sometimes equal in *T. (M.) condylura*); anterior palatal emargination closed.

subgenus *Xiphonycteris*: inner margins of ears joined by band of skin; third ridge of posterior upper molar (M^3) less than half length of second or absent; anterior palatal emargination narrow.

The African species of *Tadarida* (*sensu lato*) can be distinguished by the combination of characters in Table 20, but additional information under Similar Species in all profiles should be consulted in conjunction with this table-key. Many African molossids are very difficult to distinguish, and it is important to use cranial and dental characters as well as external characters. Many of the relevant diagnostic characters are illustrated in the profile of the family Molossidae.

In the text, the species of *Tadarida* (*sensu lato*) are presented in alphabetical order irrespective of the traditional subgenera to which they have been allocated by some authors.

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Tadarida condylura.

| | FA
(mm) | Wing membrane
dorsal side
(ventral side if
different) | Depth of
basisphenoid pits
(relative size of
pits) | Miscellaneous | Species |
|--|------------|--|---|--|---------------------------|
| | 42–55 | Brown or blackish-brown | Moderate
(Medium) | Ears small; inner margins meeting on forehead
No white spot between shoulder-blades
Plantar pad present | <i>T. (T.) aegyptiaca</i> |
| | 56–64 | Blackish | Moderate
(Large) | Three lower incisors on each side is unique | <i>T. (T.) teniotis</i> |
| | 55–62 | Greyish
(Whitish) | Shallow to moderate
(Medium) | Ears large; inner margins meeting near snout
White spot between shoulder-blades of fully mature adults
Plantar pad present | <i>T. (T.) lobata</i> |
| | 56–61 | Brown
(Whitish) | Deep
(Large) | Ears small; inner margins meeting at base of forehead
No white spot between shoulder-blades
Plantar pad present | <i>T. (T.) fulminans</i> |
| | 60–67 | Dark brown to almost
black | Deep
(Medium) | Ears small; inner margins meeting on forehead
No white spot between shoulder-blades
Plantar pad absent | <i>T. (T.) ventralis</i> |
| | 38 | Greyish-black | Deep
(Large) | Ears large
Rostrum uniquely with prominent nasal swellings | <i>T. (C.) gallagheri</i> |
| | 39–46 | Dark brown to blackish | Shallow to moderate
(Small to medium) | | <i>T. (C.) major</i> |
| | 41–48 | Pale grey | Shallow
(Medium) | Uniquely with pair of tail-glands opening ventrally as a slit on each side of
base of tail | <i>T. (C.) bemmeleni</i> |
| | 43–48 | Light reddish-brown or
light grey | Moderate
(Small) | Dorsal pelage somewhat frosted, occasionally with white spots | <i>T. (C.) ansorgei</i> |
| | 46–51 | Dark brown or light
reddish-brown | Moderate
(Small to medium) | White or whitish stripes and/or rows of spots on crown of most
individuals, and sometimes on shoulders and flanks | <i>T. (C.) bivittata</i> |
| | 34–40 | Usually white, sometimes
pale brown or greyish-
brown | Moderate
(Large) | Dorsal pelage pale grey, pale rusty-brown or medium greyish-brown
♂ ♂ with long bicoloured interaural crest | <i>T. (C.) chapini</i> |
| | 32–39 | White or blackish-brown | Moderate or shallow
(Medium or small) | Dorsal pelage almost black, brown, greyish-brown or reddish-brown
♂ ♂ with short unicoloured interaural crest | <i>T. (C.) pumila</i> |

continued overleaf

Table 20. *continued.*

| Inner margins of ears | Upper M ³ :
size of ridge 3
in relation to
ridge 2 | Number
of lower
incisors on
each side | Anterior palatal
emargination | Ventral flank-stripe
in contrasting
colour
(colour) | |
|-----------------------------|--|--|----------------------------------|--|--|
| Joined by band | 3 > half 2 | 2 | Closed | Absent | |
| Joined by band | 3 > half 2 | 2 | Closed | Absent | |
| Joined by band | 3 > half 2 | 2 | Closed | Present
(White) | |
| Joined by band | 3 ≤ half 2 | 2 | Closed | Present or absent
(White) | |
| Joined by band | 3 < half 2 | 2 | Narrow | Absent | |
| Joined by band | 3 < half 2 | 2 | Narrow | Absent | |
| Joined by band | 3 < half 2 | 2 | Narrow | Present but contrast
slight
(Black) | |
| Joined by band | 3 < half 2 | 2 | Closed | Absent | |
| Joined by band | 3 absent
or vestigial | 2 | Closed | Absent | |
| Joined by band | 3 absent | Usually 1,
rarely 2 | Narrow | Absent | |
| Joined by band | 3 absent | 2 | Narrow | Absent | |
| Joined by band | 3 absent | 2 | Closed | Absent | |
| Joined by band | 3 absent | 2 | Closed | Present but faint
(Whitish or pale grey) | |
| Joined by band | 3 absent | 2 | Closed | Present
(White or pale) | |
| Uncertain, ? well separated | 3 < half 2 | 2 | Closed | Probably absent | |

***Tadarida aegyptiaca* EGYPTIAN FREE-TAILED BAT**

Fr. Tadaride d'Égypte; Ger. Ägyptische Bulldoggfledermaus

Tadarida aegyptiaca (E. Geoffroy, 1818). Descrip. de L'Égypte 2: 128. Giza, Egypt.

Taxonomy Originally *Nyctinomus aegyptiacus*. Subgenus *Tadarida*. Synonyms in Africa: *anchietae*, *bocagei*, *brunneus*, *geoffroyi*, *talpinus*, *tongaensis*. Subspecies in Africa: two. Chromosome number (Kenya): 2n = 48; aFN = 54 (Nagorsen *et al.* 1976); (South Africa) 2n = 68 (Rautenbach *et al.* 1993).

Description Small microbat without noseleaf and with terminal portion of tail projecting freely from posterior margin of interfemoral

membrane; medium-sized for an African molossid; ears of medium relative size, with inner margins almost meeting to form V-shaped valley; M³ with second and third ridges equal in length, anterior palatal emargination wide; wings dark; ventral flank-stripe in contrasting colour sometimes present; two lower incisors on each side. Sexes similar. Pelage short (mid-dorsal hairs 5–6 mm), sometimes glossy. Dorsal pelage grey, greyish-brown, reddish-brown, blackish-brown or black, often darker on head and flanks; no spots; hairs mostly

| | FA
(mm) | Wing membrane
dorsal side
(ventral side if
different) | Depth of
basisphenoid pits
(relative size of
pits) | Miscellaneous | Species |
|--|------------|--|---|---|------------------------------------|
| | 48–53 | Blackish-brown | Deep
(Large) | Sometimes with greyish spots dorsally | <i>T. (C.)
aloyisiabaudiae</i> |
| | 42–46 | Mostly dark brown,
lighter towards tip | Moderate
(Large) | No spots or stripes | <i>T. (C.) russata</i> |
| | 41–51 | Whitish or blackish
(Whitish) | Shallow to moderate
(Small to medium) | | <i>T. (C.) nigeriae</i> |
| | 45–51 | Pale greyish-brown, paler
towards tip | Shallow
(Small) | Males without scent-glands between penis and anus
Ventral pelage with little or no white
Crown same colour as back
Phalanges of 3rd and 4th fingers long (see profile) | <i>T. (M.) condylura</i> |
| | 32–35 | Blackish-brown | Moderate
(Small) | Ventral pelage pale
Occipital helmet slight | <i>T. (X.) petersoni</i> |
| | 34–41 | Various shades of brown | Moderate or shallow
(Medium to large) | Ventral pelage pale
Occipital helmet moderately prominent
Wing insertion lower on body | <i>T. (X.)
brachyptera</i> |
| | 35–42 | Blackish | Moderate
(Small to medium) | Ventral pelage dark
Occipital helmet prominent
Wing insertion higher on body | <i>T. (X.) thersites</i> |
| | 51–55 | Dark brown | Deep
(Large) | Dorsal pelage medium sepia or yellowish-brown, or pale rusty-brown
Crown same colour as back | <i>T. (M.) trevori</i> |
| | 54–58 | Blackish-brown | Deep
(Large) | Dorsal pelage dark brown to almost black; not frosted or flecked | <i>T. (M.) congica</i> |
| | 27–30 | Blackish | Shallow
(Small) | Lower canines with greatly enlarged cingula, especially in ♂♂ | <i>T. (X.) spurrelli</i> |
| | 27–31 | Blackish-brown, pale
brown to whitish
(Paler) | Shallow
(Small) | Lower canines without greatly enlarged cingula
Upper incisors procumbent | <i>T. (X.) nanula</i> |
| | 44–48 | Blackish-brown to pale
grey | Moderate
(Medium to large) | Males without scent-glands between penis and anus
Ventral pelage predominantly white or cream
Crown darker than back
Phalanges of 3rd and 4th fingers of medium length (see profile) | <i>T. (M.)
niveiventer</i> |
| | 41–46 | Medium brown to dark
grey | Deep
(Large) | Males with paired glands between penis and anus
Ventral pelage white or very pale
Crown darker than back
Phalanges of 3rd and 4th fingers short (see profile) | <i>T. (M.)
demonstrator</i> |
| | 59–67 | Dark brown | Moderate
(Medium to large) | Dorsal pelage colour variable; frosted and flecked | <i>T. (M.) midas</i> |
| | ca. 52 | Dark brown | Deep
(Large) | This combination of characters appears to be unique | <i>T. (M.) niangarae</i> |

unicoloured but some have a slightly paler tip giving pelage a silvered or frosted appearance in some individuals. Ventral pelage slightly paler mid-ventrally, becoming same as dorsal colour on flanks, sometimes grizzled; no mid-ventral markings; ventral flank-stripe same as dorsal colour or distinctly paler or, exceptionally, white. Orange-phase not known. Head not extremely flattened. Upper lip with ca. five well-defined wrinkles on each side and comparatively few spoon-hairs. Ears blackish-brown, of medium relative length (just reaching tip of snout when laid forward); inner margins almost meeting on muzzle to form V-shaped valley. Tragus large, subrectangular, not concealed by antitragus. Antitragus ca. twice size of tragus, roughly semi-circular. No interaural crest. Gular gland present in both sexes. Wings and interfemoral membrane brown and semi-translucent, or blackish-

brown. Ventral sides of forearms and legs naked and whitish. Foot with raised pad on sole (plantar pad).

Skull low but not extremely dorsoventrally flattened. Anterior of braincase not elevated (or only very slightly elevated) above plane of rostrum (as in Figure 99h). Sagittal crest absent or poorly developed; lambdoid crest poorly developed. Anterior palatal emargination wide. Interdental palate tapering slightly but evenly towards incisors. Basisphenoid pits moderate in depth, their width ca. equal to their distance apart. Anterior upper premolar ca. same height as cingulum of posterior premolar or lower; within toothrow. M³ with second and third ridges equal in length. Two lower incisors on each side, bicuspid, crowded. Lower canines with cingula not greatly enlarged, not in contact. Dental formula: $^{1123}/_{2123} = 30$.

Geographic Variation Two subspecies occur in Africa (Koopman 1994):

T. a. aegyptiaca: African range excluding W Zambia, Angola, Namibia. Slightly larger; paler.

T. a. bocagei: W Zambia to Angola and Namibia. Slightly smaller; darker.

Similar Species Four other *Tadarida* in Africa have ears with inner margins meeting, or almost meeting, to form a V-shaped valley:

Tadarida fulminans. Larger (FA: 56–61 mm; GLS: 21.6–24.4 mm).

Wings ventrally whitish. Ventral pelage with a white, cream or yellowish mid-ventral band and ventral flank-stripe.

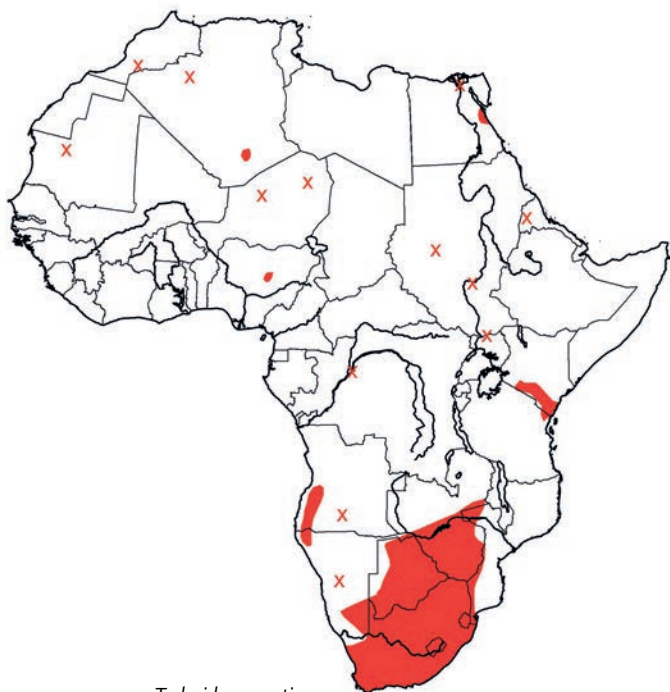
T. lobata. Usually larger (FA: 55–62 mm; GLS: 22.3–23.6 mm).

Inner margins of ears meeting close to snout; ears extending well beyond snout when laid forward. White spot between shoulder-blades of adults.

T. teniotis. Three lower incisors on each side. Larger (FA: 58–64 mm; GLS: 22.5–24.8 mm). North Africa.

T. ventralis. Much larger (FA: 60–67 mm; GLS: 23.4–26.1 mm).

Distribution In Africa, recorded disjunctly from Nile Delta, Red Sea coast and scattered inland localities in the Sahara Arid BZ, from a few scattered localities in the Sudan Savanna BZ, and from one locality in the Rainforest BZ, but mostly recorded from Somalia–Masai Bushland, Coastal Forest Mosaic, Zambezan Woodland, Highveld, South-West Arid, South-West Cape and Afromontane–Afroalpine BZs. Recorded from Morocco, Algeria, Egypt, Niger, Nigeria, Sudan, Ethiopia, DR Congo and Kenya, and all countries southwards except, as yet, Malawi. Extralimitally: Saudi Arabia, Yemen and Oman and beyond to Afghanistan, India and Sri Lanka. Mapped from country checklists (see order Chiroptera), other literature and museum records. Subsequently recorded from E Uganda (Thorn & Kerbis Peterhans 2009): not mapped.



Habitat In Africa, mostly recorded from open woodland and bushland savannas (including undifferentiated woodlands, *Acacia–Commiphora* bushland, miombo and mopane woodlands), arid scrublands, open grasslands and forest-dominated valley bushveld (Smithers 1983, Taylor, P. 1998). Also found in some very arid areas but probably only where drinking water, insects and suitable day-roosts are available; e.g. in arid Botswana, associated with waterholes, bore-holes, reservoirs and temporary pools (Smithers 1983). Frequently occupies built-up areas (Taylor, P. 1998, R. T. F. Bernard pers. obs.). The record in rainforest is probably that of a vagrant.

Abundance Abundant in some parts of geographic range, particularly in southern Africa where day-roosts may contain thousands of individuals (R. T. F. Bernard pers. obs.). Apparently restricted to a very limited range of localities in Angola and Zambia (Smithers 1983).

Adaptations Aspect ratio very high; wing-loading medium, lower than in most molossids (Norberg & Rayner 1987). Predicted to fly more slowly than most molossids (Norberg & Rayner 1987). Scuttles and climbs very adeptly over horizontal to vertical surfaces. Day-roosts include narrow horizontal and vertical crevices in rockfaces and buildings, cracks under exfoliating rocks, behind bark of *Acacia* trees, cracks in tree-trunks, hollow trees, roofs of houses and churches (often between tiles and insulation or between tiles and rafters), crevices and crannies within caves (Shortridge 1934, Rautenbach 1982, Smithers 1983, Taylor, P. 1998). Clings in contact with substrate, usually tucked into narrow cracks and crevices. Occasionally reported roosting with *T. pumila*, once with both *T. pumila* and *Otomops martiensseni*, and once with *Pipistrellus capensis* (Herselman & Norton 1985, Taylor, P. 1998). Can tolerate extreme roost temperatures, e.g. under corrugated iron roof in South Africa, below zero in winter to above 45 °C in summer (R. T. F. Bernard unpubl.). There is no evidence, from observations in laboratory and field, that this species enters torpor or hibernation (Bernard unpubl.). Specimens from Western Cape, South Africa, captured late Jan to early Feb, had yellow fat at base of ribs and hips, suggesting an increase in body fats before winter (Seamark 2005).

Foraging and Food Forages by fast-hawking. Observed flying high, and also skimming over water to pick up water-beetles and other aquatic insects or to sip water (Shortridge 1934, Smithers 1971). Based on remains in faeces, diet includes beetles and moths (Fenton & Thomas 1980, Fenton 1985).

Echolocation Call-shape variable. Search-phase call-shape: quasi-linear shallow FM. Search-phase (Zimbabwe): start-frequency 26 kHz; end-frequency 15 kHz; peak-frequency 18 kHz; maximum call-duration 15 ms; intensity high (five bats, flying in open; Fenton & Bell 1981). Search-phase (South Africa): start-frequency (mean \pm S.D.) 23.2 ± 1.9 kHz; end-frequency 18.7 ± 1.3 kHz; call-duration 7.0 ± 2.6 ms, sometimes up to 12 ms; energy mainly in fundamental harmonic but up to three harmonics may be present (three bats, flying in open; Taylor 1999a, 2000). When scuttling, call-shape similar but steeper; start-frequency ca. 29 kHz; end-frequency ca. 18.6 kHz; duration ca. 5.5 ms (Taylor 1999a).

Social and Reproductive Behaviour Occasionally roosts singly or in pairs, more often in groups of up to 50 or more, and sometimes in colonies of several hundreds (Shortridge 1934, Rautenbach 1982, Taylor, P. 1998) and even thousands (R. T. F. Bernard pers. obs.). Much noisy squeaking and chirping (audible to humans) occurs in the roosts prior to emergence of these bats at dusk. Maternity colonies are formed in summer in South Africa (Taylor 2000, R. T. F. Bernard pers. obs.).

Reproduction and Population Structure Litter-size: one. At ca. 33°S in South Africa, the reproductive chronology is restricted seasonal monoestry with copulation in Aug and parturition in early summer (Nov–Dec) after 4-month gestation (Bernard & Tsita 1995). Right ovary and right uterine horn significantly larger than on left; corpora lutea in right ovary only; pregnancies in right uterine horn only. Climate of study area is strongly seasonal, with a single hot and typically wetter season from Oct–Apr, and a cool, drier season from May–Sep. Monoestry at this high latitude is probably explained by the comparatively long gestation and the relatively short period during which temperatures are high enough to ensure abundant insects. In contrast, at 24°S where temperatures are higher for longer, *T. pumila* and *T. condylura* have shorter gestations and are polyoestrous (see profiles). There appear to be no conclusive data for *T. aegyptiaca* elsewhere in Africa. In Zimbabwe, pregnant ♀♀ were caught in Nov and lactating ♀♀ in Dec (no data given for other months) (Smithers & Wilson 1979). In South Africa, ♂♂ apparently reach sexual maturity in second year; ♀♀ in first year.

Predators, Parasites and Diseases Remains have been found in pellets of Barn Owls *Tyto alba* in the West Coast N. P., South Africa (Avery 1992). Ectoparasites include bed-bugs *Striticimex transversus*,

S. namru (Hemiptera: Cimicidae); fleas *Araeopsylla gestroi*, *A. scitula*, *A. wassifi*, *Chiropteropsylla brockmani* (Siphonaptera: Ischnopsyllidae); ticks *Carios vespertilionis*, *C. boueti*, *C. confusus* (Acari: Argasidae); and mites *Parasteatonyssus nyctinomi*, *P. cornutus* (Acari: Macronyssidae), *Microtrombicula kanyei* (Acari: Trombiculidae) (Anciaux de Faveaux 1984).

Conservation IUCN Category: Least Concern.

Measurements

Tadarida aegyptiaca

FA: 47.6 (42–55) mm, n = 97

WS: n. d.

TL: 109.8 (91–131) mm, n = 85

T: 39.7 (30–50) mm, n = 83

E: 19.4 (16–26) mm, n = 78

Tr: n. d.

Tib: 13, 14 mm, n = 2

HF: 9.5 (7–12) mm, n = 77

WT: 14.7 (9–22) g, n = 53

GLS: 18.7 (17.1–21.9) mm, n = 68

GWS: 11.4 (10.7–13.5) mm, n = 60

C–M³: 6.7 (6.0–8.2) mm, n = 62

Egypt, Sudan, Angola, Namibia, Botswana, Zimbabwe, Swaziland, South Africa (AM, TM, ZFMK and literature)

Key References Bernard & Tsita 1995; Smithers 1971; Taylor, P. 1998.

Ric T. F. Bernard & Meredith Happold

Tadarida aloysiisabaudiae DUKE OF ABRUZZI'S FREE-TAILED BAT

Fr. Tadaride d'Aloys Sabaud; Ger. Fürst von Abruzzen Bulldoggfledermaus

Tadarida aloysiisabaudiae (Festa, 1907). Boll. Mus. Zool. Anat. Comp. Univ. Torino 22 (546): 1. Toro, W Uganda.

Taxonomy Originally *Nyctinomus Aloysii-Sabaudiae*. Subgenus *Chaerephon*. Synonyms: *cyclotis*. Subspecies: none recognized here (see Geographic Variation). Chromosome number (Cameroon): 2n = 48; aFN = 66 (Smith *et al.* 1986). The name *aloyisabaudiae* is a latinization of one of the names and titles (Luigi di Savoia) of the Duke of the Abruzzi who led the Italian Rwenzori expedition during which this bat was first collected. Savoy was known to the Romans as Sabaudia (Hayman & Hill 1971). Considered to be closely related to *T. russata* by Peterson (1967, 1969, 1971a) and Fenton & Peterson (1972). Possibly also closely related to *T. bivittata* and *T. ansorgei* (Freeman 1981).

Description Small microbat without noseleaf and with terminal portion of tail projecting freely from posterior margin of interfemoral membrane; medium-sized for an African molossid; ears joined by interaural band; M³ with third ridge > half length of second ridge; anterior palatal emargination closed; wings blackish-brown; ventral flank-stripe not in contrasting colour; no tail-glands; rostrum uniquely narrow and elongated; FA: 48–53 mm. Sexes similar.

Pelage short (mid-dorsal hairs ca. 4 mm), sparse on nape; dorsal pelage extending over rump and onto interfemoral membrane. Dorsal pelage chocolate brown to dark rusty-brown (orange-phase: bright rusty-orange), sometimes with small, diffuse whitish spots or scattered whitish hairs; all dorsal hairs pale at base. Ventral pelage with flanks dark brown, belly similar to dorsal pelage but paler and suffused with greyish-fawn; no mid-ventral markings; ventral flank-stripe same colour as flanks. Head not extremely flattened; dorsal surface of snout inconspicuously covered with short, stiff bristle-like hairs. Upper lip with 8–9 well-defined wrinkles on each side and many spoon-hairs. Ears blackish-brown, broad, not quite reaching snout when laid forward; inner margins joined by interaural band across forehead, which projects forward as a knob-like protuberance (containing a backward-opening interaural pocket) that almost covers the snout. Tragus small, tip bluntly pointed, concealed by antitragus. Antitragus well developed, roughly semi-circular. Interaural crest of dark brown hairs arising from interaural pocket in both sexes. No gular gland. Wings and interfemoral membrane blackish-brown. For additional information, see Lanza & Harrison (1963).

Skull large and elongated with a long, narrow rostrum; not extremely dorsoventrally flattened. Anterior of braincase slightly but distinctly elevated above plane of rostrum. Sagittal and lambdoid crests weakly developed or absent. Anterior palatal emargination closed; two foramina, and usually also a third, median foramen behind the incisors. Basisphenoid pits deep, large, their width more than twice their distance apart. Anterior upper premolar distinctly taller than cingulum of posterior premolar, within toothrow; canine and posterior upper premolar well separated. M^3 with third ridge almost as long as second ridge. Two lower incisors on each side; bicuspid, crowded. Lower canines with cingula not greatly enlarged, not in contact. Anterior lower premolar ca. equal in size to posterior premolar in ♂♂, but smaller than posterior premolar in ♀♀. Dental formula: $^{1123}/_{2123} = 30$.

Geographic Variation None recorded but data are limited. Grubb *et al.* (1998) provisionally listed *cyclotis* Brosset, 1966 as a subspecies, but this view is not held by Hayman & Hill (1971), Fenton & Peterson (1972) and Simmons (2005), and is not held here.

Similar Species Four other African *Tadarida* have the following combination of characters: ears joined by interaural band; M^3 with third ridge > half length of second; wings neither white nor whitish; no ventral flank-stripe in contrasting colour; no tail-glands (Table 20, p. 488):

Tadarida ansorgei. Smaller (FA: 43–48 mm; GLS: 18.6–20.5 mm).

Wings semi-translucent light reddish-brown to light grey. Interaural band comparatively less prominent and with V-shaped fold in middle. Skull with anterior palatal emargination narrow (bulb-shaped). Basisphenoid pits moderate in depth, small, their width less than their distance apart.

T. bivittata. Often with white spots and sometimes short stripes on head and neck; dorsal pelage not extending on to interfemoral membrane. Ears on average smaller; not reaching snout when laid forward. Interaural band comparatively less prominent and with V-shaped fold in middle. Skull with anterior palatal emargination narrow (bulb-shaped). Basisphenoid pits moderate in depth, small to medium-sized, their width \leq their distance apart.

T. russata. Smaller (FA: 42–46 mm). Skull shorter (GLS: 17.8–19.4 mm) and narrower (GWS: 10.5–11.4 mm). Otherwise very similar in pelage pattern and colour as well as in external characters.

T. pumila (sometimes). Much smaller (FA: 32–39 mm; GLS: 14.2–17.6 mm).

Distribution Endemic to Africa. Recorded mainly from Rainforest BZ (Western, West Central and East Central Regions) and adjacent Northern and Eastern Rainforest–Savanna Mosaics, with one record very marginally in Sudan Savanna BZ on the upper Mountain Nile R. (Bahr al Jabal) in S Sudan. Known from 16 localities in Côte d'Ivoire, Ghana, Cameroon, Gabon, Central African Republic (Boukoko, MNHN), DR Congo, Sudan (Juba, SMNS) and Uganda (Brosset 1966, Peterson 1967, 1969, 1972, Fenton & Peterson 1972, Smith *et al.* 1986, Beaucournu & Fahr 2003, J. Fahr unpubl.).

Habitat Mainly recorded from lowland rainforest, montane forest flanking the Albertine Rift Valley, swamp forest, and rainforest–



Tadarida aloysiisabaudiae

savanna mosaic adjacent to rainforest; also from one locality in flooded grassland (Juba, Sudan). One specimen was taken in a clearing within forest in Gabon, one from cutover rainforest in Ghana, others from 'Guinea woodland' in Ghana and Uganda, and others appear to have been taken in forested areas but without further details (Fenton & Peterson 1972). Fenton & Peterson (1972) suggested that this species 'may be associated with a forest-edge or semi-open forest habitat rather than with either dense high forest or with open forest or savannas', but this needs confirmation because it has now been captured within closed primary rainforest (J. Fahr unpubl.). Mainly recorded from lower altitudes, with 1200 m as the known maximum (Fenton & Peterson 1972). Individuals were mostly captured with mist-nets set over water or in forest clearings (Brosset 1966, Fenton & Peterson 1972, J. Fahr unpubl.).

Abundance Not known. Appears to be quite rare but surveys with elevated mist-nets are needed to determine accurately both the abundance and distribution of this species.

Remarks In Garamba N. P., NE DR Congo, one ♂ was taken from a fissure in the trunk of an *Isoberlinia doka* tree that was also inhabited by a colony of ca. 150 *T. condylura* (Verschuren 1957 as *T. (Mops) trevori* but re-identified by Peterson 1972). Like most other molossids, mainly forages by fast-hawking in open spaces above the vegetation. In forest-savanna vegetation in Comoé N. P., Côte d'Ivoire, the median height of captures (in mist-nets set 0–25 m above ground) was 17.0 (12.4–19.6) m ($n = 5$). In rainforest in Taï N. P., Côte d'Ivoire, two individuals were mist-netted between 1–3 m over small creeks, but they had probably descended to drink.

Predators, Parasites and Diseases Ectoparasites include a flea *Lagaropsylla senckenbergiana* (Siphonaptera: Ischnopsyllidae) (Beaucournu & Fahr 2003).

Conservation IUCN Category: Least Concern.

Only 16 localities; seems comparatively rare. Major threats: loss and degradation of habitat mainly because of logging and agriculture. Population trend inferred to be declining.

Measurements

Tadarida alysiisabaudiae

FA: 51.5 (48–53) mm, n = 18

WS (c): 383 (343–401) mm, n = 6

TL: 118.8 (108–132) mm, n = 19

T: 40.1 (34–46) mm, n = 19

E: 22.0 (19–25) mm, n = 17

Tr: 1.5, 1.8 mm, n = 2

Tib: 18.1 (16–20) mm, n = 13

HF: 12.3 (10–14) mm, n = 17

WT: 26.1 (18–38) g, n = 13

GLS: 21.4 (20.0–22.3) mm, n = 18

GWS: 12.5 (11.7–13.1) mm, n = 18

C–M³: 7.8 (7.5–8.2) mm, n = 17

Côte d'Ivoire, Ghana, Gabon, DR Congo, Uganda (AMNH, FC, IRSN, LACM, MNHN [holotype *cyclotis*], MZUT [holotype *alysiisabaudiae*], ROM, SMF, USNM)

Key References Brosset 1966; Fenton & Peterson 1972; Lanza & Harrison 1963; Peterson 1967, 1969.

Jakob Fahr

Tadarida ansorgei ANSORGE'S FREE-TAILED BAT

Fr. Tadaride d'Ansorge; Ger. Ansorges Bulldoggfledermaus

Tadarida ansorgei (Thomas, 1913). Ann. Mag. Nat. Hist., ser. 8, 11: 318. Malanje [= Malange], Angola.

Taxonomy Originally *Nyctinomus ansorgei*. Subgenus: placed in *Chaerephon* (e.g. by Koopman 1994 and Simmons 2005) but previously placed in subgenus *Tadarida* by some authors (e.g. Hayman & Hill 1971). Synonyms: *rhodesiae*. Subspecies: none. Appears closely related to the often sympatric *T. bivittata* (Eger & Peterson 1979), but the *ansorgei/bivittata* complex needs further revision (see profile of *T. bivittata*). *Tadarida bivittata* currently appears to contain a form that resembles *T. ansorgei*, and some information in the literature attributed to *T. bivittata* probably refers to *T. ansorgei*, and vice versa. Furthermore, museum collections probably contain misidentified specimens. Chromosome number (Cameroon): 2n = 48; aFN = 66. X = medium-sized subtelocentric, Y = small acrocentric (Smith *et al.* 1986). In South Africa: 2n = 48; aFN = 68. X = medium metacentric, Y = small acrocentric (Rautenbach *et al.* 1993).

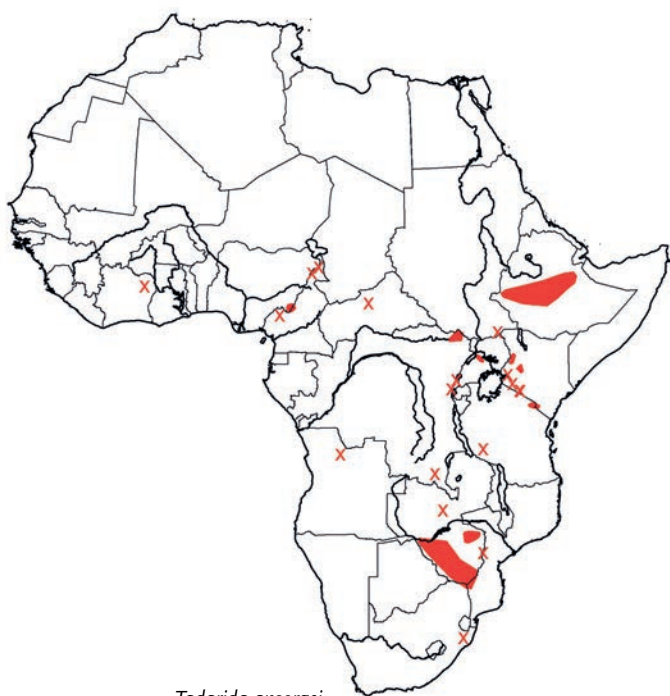
Description Small microbat without noseleaf and with terminal portion of tail projecting freely from posterior margin of interfemoral membrane; medium-sized for an African molossid; ears joined by interaural band; M³ with third ridge > half length of second ridge; anterior palatal emargination narrow; dorsal pelage dark greyish-brown to reddish-brown (occasionally spotted); wings light grey or reddish-brown; no ventral flank-stripe in contrasting colour; no tail-glands. Not easily distinguished from *T. bivittata*. Sexes similar in colour; ♂♂ slightly larger on average than ♀♀. Pelage short (mid-dorsal hairs ca. 4 mm), soft, dense, sparse on crown behind junction of ears and sometimes sparse on nape; terminates abruptly on rump. Dorsal pelage dark greyish-brown to chocolate brown or reddish-brown, somewhat frosted and occasionally with white spots; hairs unicoloured or with pale grey at tip. Based on museum specimens, greyish-brown individuals more common (cf. *T. bivittata*). Ventral pelage paler than dorsal pelage except on throat, which is blackish to brown, conspicuously darker and denser than elsewhere, especially in ♂♂. Chin naked, in marked contrast with dense pelage on throat. No mid-ventral markings; no ventral flank-stripe in contrasting colour; pelage not extending onto wing-

membrane. Head not extremely flattened. Upper lip with 6–7 well-defined wrinkles on each side and many spoon-hairs. Ears pale-grey to reddish-brown, reaching ca. half-way along muzzle when laid forward; inner margins joined by interaural band with V-shaped fold in middle. Tragus very small, subquadrangular; antitragus much larger and roughly trapezoid (widest at base). Interaural crest of dark hairs (ca. 2 mm) in shallow pouch, in both sexes; denser and more conspicuous in ♂♂. Gular gland: no information. Wings semi-translucent light reddish-brown to light grey dorsally and ventrally; interfemoral membrane slightly darker.

Skull not extremely dorsoventrally flattened. Anterior of braincase only slightly elevated above plane of rostrum (frontals inflated dorsally into a very shallow dome, Figure 99e) (cf. *T. bivittata*). Mastoid width: 10.8 (10.2–11.2) mm, n = 139 (sexes alike) (cf. *T. bivittata*) (Eger & Peterson 1979). Sagittal crest distinct although very low, and usually complete (extending unbroken across whole braincase), but in 7% of 60 specimens from DR Congo (RMCA) the crest does not extend across the posterior third of the cranium, and in 3%, it is very indistinct over this section. Lambdoid crests moderate. Anterior palatal emargination narrow, bulb-shaped (narrowest between incisors). Basisphenoid pits moderate in depth, small, their width less than their distance apart. Anterior upper premolar ca. same height as cingulum of posterior premolar, within toothrow; canine and posterior premolar separated. M³ with third ridge almost as long as second ridge. Two lower incisors on each side, bicuspid, crowded. Lower canines with cingula not greatly enlarged, usually almost in contact, occasionally in contact. Dental formula: $^{1123}/_{2123} = 30$.

Geographic Variation None recorded.

Similar Species Four other African *Tadarida* have the following combination of characters: ears joined by interaural band; M³ with third ridge > half length of second; wings neither white nor whitish, no ventral flank-stripe in contrasting colour; no tail-glands (Table 20, p. 488):

*Tadarida ansorgei*

Tadarida aloysiisabaudiae. Larger (FA: 48–53 mm; GLS: 20.0–22.3 mm). Wings blackish-brown. Interaural band comparatively prominent, with knob-like projection almost covering snout. Skull with anterior palatal emargination closed. Basisphenoid pits deep, large, their width more than twice their distance apart.

T. russata. Dorsal pelage uniformly dark rusty-brown to sepia brown; no grizzling, no white flecks or spots; hairs with paler bases. Skull with anterior of braincase moderately elevated above plane of rostrum. Anterior palatal emargination closed. Basisphenoid pits moderate in depth, separated by narrow bony ridge (< half breadth of one pit).

T. bivittata. Dorsal pelage often (but not always) with white stripes or rows of spots on head and neck. Wings dark brown or reddish-brown. Ears broader and dorsally browner. More robustly built (see weights). Skull with anterior of braincase moderately elevated above plane of rostrum. Mastoid width greater. Sagittal crest sometimes incomplete. A classification coefficient for distinguishing *T. bivittata* is given by Eger & Peterson (1979).

T. pumila (sometimes). Much smaller (FA: 32–39 mm; GLS: 14.2–17.6 mm).

Distribution Endemic to Africa. Mainly recorded from Eastern Rainforest–Savanna Mosaic, Somalia–Masai Bushland BZ and Afromontane–Afroalpine BZs in NE DR Congo, S Sudan, Ethiopia and East Africa, and from the Zambezian Woodland BZ from SE DR Congo through Zambia and Zimbabwe to KwaZulu–Natal (South Africa). There is also an apparently isolated record from Guinea Savanna BZ in Côte d’Ivoire and another in Southern Rainforest–Savanna Mosaic in N Angola (Eger & Peterson 1979, Hill 1983, Nikolaus & Dowsett 1989, Bouchard 2001).

Habitat Mainly woodland savannas (including *Isoberlinia* woodland, *Acacia*–*Commiphora* bushland and miombo woodland), and montane habitats (no details available). In Zimbabwe, recorded from dry

woodland savanna in the vicinity of rugged hills and mountain ranges with rock cliffs and precipices.

Abundance Locally common in Zimbabwe; some roosts accommodate hundreds of individuals.

Adaptations Aspect ratio high to very high; wing-loading medium. Flight fast and agile. Scuttles rapidly; scrambles backwards into small crevices. Most often roosts by day in small crevices that are high up in cracks and clefts in cliffs and rocky hills; also roosts in crevices inside caves, mine-adits and occasionally buildings, and in expansion joints high up in concrete bridges. Near Faradje, NE DR Congo, a colony roosted, in total darkness, in a crack in a hill rising ca. 60 m above the surrounding bushveld (Lang & Chapin 1917b). The accumulation of 30 cm of guano in this day-roost indicated long-term residence. However, day-roosts in Zimbabwe are sometimes temporarily abandoned; departures do not appear related to seasonal changes, and it is not known if the bats move into nearby day-roosts, or migrate further afield (F. P. D. Cotterill unpubl.). In NE DR Congo, sometimes shares roosts with *T. major* (Verschuren 1957). In Zimbabwe, sometimes shares roosts with *T. bivittata* (flocks of both species emerge together) and *T. fulminans* (Cotterill & Fergusson 1993a).

Foraging and Food Forages by fast-hawking. Flocks were observed leaving roost at dusk and flying fast to a considerable altitude (R. A. Fergusson pers. comm.). Stomachs of two individuals from DR Congo contained legs of beetles, wings of Formicidae (?) and antennae of Hymenoptera (?) (Verschuren 1957).

Echolocation Search-phase call-shape (Zimbabwe): shallow FM. Start-frequency 28 kHz; end-frequency 16 kHz; bandwidth 16–28 kHz; peak-frequency 17.8 kHz; maximum call-duration 15 ms (five bats flying in open; Fenton & Bell 1981).

Social and Reproductive Behaviour In NE DR Congo, found roosting in groups (colonies) of no more than 30–40 individuals; ♂♂ and ♀♀ in approximately equal numbers; no segregation of sexes observed (Verschuren 1957). In Zimbabwe, usually roosts in colonies of up to many hundreds. Within roosts, groups of bats huddle tightly together in nooks and crannies, but are often restless and can be heard squeaking and jostling. Samples of bats taken from roosts in Zimbabwe contained more ♂♂ than ♀♀.

Reproduction and Population Structure Litter-size: one ($n = 10$). At 16–18°S in Zimbabwe, the reproductive chronology appears to be seasonal bimodal polyoestry without postpartum oestrus, with births at beginning of hot-wet season (Nov) and at end of hot-wet season (Apr), but this needs confirmation. This is based on the following observations: ten ♀♀ pregnant and near term in Oct (crown–rump length of embryos 25 [21–29] mm); lactating ♀♀ found in Nov–Dec and also in Apr (no data for other months) (F. P. D. Cotterill unpubl.). Polyoestry is indicated by lactating ♀♀ collected in late Dec and mid-Jan, each of which had a fully developed Graafian follicle in the right ovary.

Predators, Parasites and Diseases Skulls have been recovered from pellets of Barn Owls *Tyto alba*, and Mackinder’s Eagle-owls *Bubo*

capensis have been observed hawking molossidids emerging from their roosts in Zimbabwe (Cotterill 1992). *Tadarida ansorgei* is collected from its day-roosts and eaten by people in DR Congo (Lang & Chapin 1917b). Ectoparasites include a flea *Lagaropsylla anciauxi* (Siphonaptera: Ischnopsyllidae) and mites *Chelanyssus spiniferus* (Acari: Macronyssidae), *Alabidocarpus molossicola* (Acari: Chirodiscidae) (Anciaux de Faveaux 1984).

Conservation IUCN Category: Least Concern.

Measurements

Tadarida ansorgei

FA: 45.9 (43–48) mm, n = 199*

WS (d): 342 (318–364) mm, n = 82

TL: 106 (99–119) mm, n = 87

T: 37 (32–46) mm, n = 86

E: 20.5 (15–23) mm, n = 87

Tr: n. d.

Tib: 16.2 (15–17) mm, n = 12

HF: n. d.

WT: 14.6 (10.5–24.5) g, n = 87

GLS: 19.6 (18.6–20.5) mm, n = 139*

GWS: 11.6 (11.0–12.2) mm, n = 139*

C–M³: 7.7 (7.3–8.2) mm, n = 139*

Throughout geographic range (ROM)

*Eger & Peterson 1979

Key References Bouchard 2001; Eger & Peterson 1979.

F. P. D. Cotterill

Tadarida bemmeleni GLAND-TAILED FREE-TAILED BAT

Fr. Tadaride à glande caudale; Ger. Schwanzdrüsen-Bulldoggfledermaus

Tadarida bemmeleni (Jentink, 1879). Notes Leiden Mus. 1: 125. Liberia (no specified locality).

Taxonomy Originally *Nyctinomus bemmeleni*. Sometimes incorrectly spelled *bemmelini*. Subgenus *Chaerephon*. Synonyms: *cistura*. Subspecies: two currently recognized (but see Geographic Variation). Possibly includes more than one species. The species was described from a specimen from Liberia. Later, Jentink (1888) stated that the specimen had been received in 1875 through the Zoological Garden Rotterdam, which led subsequent authors to question Liberia as the type locality. However, recent specimens from Liberia, Sierra Leone and Côte d'Ivoire support the Liberian origin of the holotype. According to Freeman (1981), *T. bemmeleni* is rather distinct and basal within *Chaerephon* and, together with *T. ansorgei* and *T. bivittata*, connects this subgenus with the subgenus *Tadarida*. Seems to be most closely related to *T. bivittata* (Peterson 1971b, Freeman 1981). Chromosome number (Kenya): 2n = 48; aFN = 54 (Nagorsen *et al.* 1976).

Description Small microbat without noseleaf and with terminal portion of tail projecting freely from posterior margin of interfemoral membrane; medium-sized for an African molossid; ears joined by low interaural band, M³ with third ridge > half length of second; anterior palatal emargination narrow; wings pale grey, ventral flank-stripe whitish; distinguished from other molossidids by conspicuous tail-glands that open ventrally, one on each side of the base of the tail. Sexual dimorphism slight: on average, ♂♂ with longer second phalanx of third and fourth finger, longer skull and longer canines. Pelage short (mid-dorsal hairs ca. 4 mm); covering rump but not extending onto interfemoral membrane, which is clad only with very short, thin hairs. Dorsal pelage dark brown with slight frosting but no spots or stripes; hairs bicoloured with pale tip. Head same colour as dorsal pelage. Ventral pelage paler, flanks darker than belly; hairs pale brown with whitish or greyish tips; no mid-ventral markings; ventral flank-stripe whitish, contrasting with dark flanks. No black or darker pelage on throat. Head not extremely flattened. Upper lip with 6–8 well-defined wrinkles on each side and comparatively few spoon-hairs. Ears blackish-brown, very broad and squarish in

outline, reaching snout when laid forward; inner margins joined by low interaural band with V-shaped fold in middle. Tragus small and concealed by antitragus. Antitragus large. Interaural band without distinct crest, sometimes with dense hairs, sometimes almost naked. No gular gland. Wings and interfemoral membrane pale grey. Forearm and third metacarpal dorsally clad with very short, fine hairs, giving a velvety appearance. Both sexes with longitudinal sac-like tail-glands that open ventrally on either side of the tail just posterior to its junction with the body (Figure 111). Sometimes these glands are also dorsally visible as paired swellings, one on each side of the base of the tail.

Skull not extremely dorsoventrally flattened. Anterior of braincase slightly to moderately raised above plane of rostrum. Sagittal crest weakly developed; lambdoid crest moderate. Anterior palatal emargination narrow. Basisphenoid pits shallow, their width ca. equal to their distance apart. Anterior upper premolar slightly higher than cingulum of posterior premolar, within tooththrow. M³ with third ridge ca. three-quarters to almost same length as second. Two lower incisors on each side, slightly to clearly crowded. Lower canines with cingula not greatly enlarged, not in contact. Dental formula: $1^{123}/_{2123} = 30$.

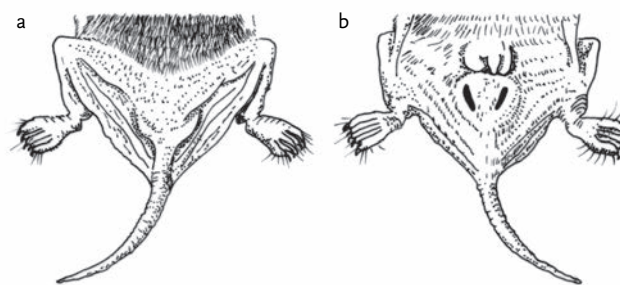


Figure 111. The unique tail-glands of *Tadarida bemmeleni*. (a) Dorsal view showing paired swellings associated with the glands, one on each side of the base of the tail. (b) Ventral view showing the two longitudinal openings of the glands. Based on Peterson (1971b).

Geographic Variation Two subspecies are currently recognized (e.g. Peterson 1971b, Koopman 1975, Simmons 2005):

T. b. bemmeleni: Guinea, Sierra Leone, Liberia, Côte d'Ivoire and Cameroon. On average smaller (FA: 43.8 [41–46] mm, $n = 34$; Tib: 13.3 [12–15] mm, $n = 34$; GLS: 17.3 [16.6–18.1] mm, $n = 24$).

T. b. cistura: E DR Congo, S Sudan, SW Kenya and N Tanzania. On average larger (FA: 46.0 [43–48] mm, $n = 9$; Tib: 13.9 [13–15] mm, $n = 6$; GLS: 18.3 [17.8–18.9] mm, $n = 8$).

The apparent disjunction between the distributions of these taxa, together with differences in size (especially in FA, tibia and craniodental measurements), skull morphology (braincase higher, lachrymal breadth of rostrum greater and width across upper canines greater in *T. b. cistura*; see Peterson 1971b) and habitat preferences, suggest that these taxa might be distinct species, but further material, especially from West Africa, is needed to resolve this question.

Similar Species No other African molossid has conspicuous sac-like tail-glands that open ventrally, one on each side of the base of the tail (sometimes also visible dorsally as paired swellings).

Distribution Endemic to Africa. *Tadarida b. bemmeleni* is known from only five localities in Rainforest BZ (Western and West Central Regions), Afromontane–Afroalpine BZ and Northern Rainforest–Savanna Mosaic. Recorded from Sierra Leone, Liberia, Côte d'Ivoire (Duékoué; Taï N. P.) and Cameroon (Peterson 1971b, J. Fahr unpubl.). A record from Marshall Territory near Harbel, Liberia, published by Bray (1958) as *T. bemmeleni*, was later referred to *T. brachyptera* by Koopman (1989). *Tadarida b. cistura* is more widely known from ca. 17 localities in Eastern Rainforest–Savanna Mosaic and Somalia–Masai Bushland BZ in S Sudan, E DR Congo, Uganda, SW Kenya and N Tanzania (Peterson 1971b, J. Fahr unpubl.).

Habitat *Tadarida b. bemmeleni* has been found in lowland rainforest and semi-deciduous forest (Liberia, Côte d'Ivoire), forest–savanna mosaic (Cameroon) and montane grassland (Mt Nimba). Recorded from lowlands to ca. 1600 m (Mt Nimba, Liberia; SMF). In Cameroon, individuals were mist-netted over a fast-running stream where it emerged from a forested area into a cleared area adjacent to a banana plantation (Peterson 1971b). One ♂ and one ♀ were captured on consecutive nights, at 13.6 and 10.8 m above the ground, in elevated mist-nets set over the clearing of a research station within Taï N. P., Côte d'Ivoire (S. Pettersson pers. comm.). *Tadarida b. cistura* has been recorded from drier vegetation zones such as *Acacia–Commiphora* bushland, *Isoberlinia* woodland and forest–savanna mosaic. Most specimens have been caught in mist-nets over rivers and streams. One from Budongo Forest, Uganda, was mist-netted over a dam at the edge of a forest; another was taken from a hole in some rocks on the side of a gorge at 1600 m near Kampala, Uganda, and another from the slopes of Mt Kilimanjaro, Tanzania. Possibly rocky outcrops are required for roosting (Peterson 1971b).

Abundance Uncertain. Apparently localized and probably fairly rare (especially the western subspecies), but data are not sufficient for accurate assessment.



Tadarida bemmeleni

Remarks Body mass appears to be relatively low for the size of this bat, possibly indicating a particular foraging strategy. Start (1969) found four individuals exhausted in a swimming pool: probably they became trapped after descending to drink from the pool. No other molossid in Africa has tail-glands: the cellular structure and function of these glands is not known. In Tanzania, one specimen was recovered from pellets of a Barn Owl *Tyto alba* (SMF). Ectoparasites include a mite *Ewingana hispinosa* (Acari: Myobiidae) (Anciaux de Faveaux 1984).

Conservation IUCN Category: Least Concern.

If *T. b. bemmeleni* and *T. b. cistura* are found to be distinct species (see Geographic Variation), the appropriate IUCN Category for *T. bemmeleni* would be 'Near Threatened' or 'Data Deficient' based on its limited area of occupancy, which is very fragmented and degraded. For *T. cistura*, 'Least Concern'.

Measurements

Tadarida bemmeleni

FA: 44.3 (41–48) mm, $n = 43$
 WS (d): 330.3 (320–338) mm, $n = 23^*$
 TL: 103.1 (94–110) mm, $n = 39$
 T: 36.3 (34–40) mm, $n = 41$
 E: 18.7 (14–20) mm, $n = 41$
 Tr: n. d.
 Tib: 13.4 (12–15) mm, $n = 40$
 HF: 11.1 (9–13) mm, $n = 40$
 WT: 12.7 (11–14) g, $n = 27$
 GLS: 17.5 (16.6–18.9) mm, $n = 32$
 GWS: 10.4 (9.8–11.3) mm, $n = 32$
 C–M³: 6.3 (6.0–6.8) mm, $n = 36$

Sierra Leone, Liberia, Côte d'Ivoire, Cameroon, Sudan, Kenya, Tanzania, Uganda (AMNH, BMNH, FC, HZM, MHNG, RMNH [holotype *T. b. bemmeleni*], ROM, SMF, USNM, Peterson 1971b)

Samples include only 6–9 specimens of *T. b. cistura* (see also Geographic Variation)

**T. b. bemmeleni* only

Key Reference Peterson 1971b.

Jakob Fahr

Tadarida bivittata SPOTTED FREE-TAILED BAT

Fr. Tadaride tachetée; Ger. Gefleckte Bulldoggfledermaus

Tadarida bivittata (Heuglin, 1861). Nouv. Act. Acad. Caes. Leop.-Carol., Halle 29 (8): 4, 13. Keren, Ethiopia.

Taxonomy Originally *Nyctinomus bivittatus*. Subgenus *Chaerephon*. Synonyms: none. Appears closely related to *T. ansorgei* (Eger & Peterson 1979). Contains more than one form. Heuglin described *T. bivittata* (on p. 13) from three umber brown specimens that have white markings (spots and/or stripes on head and neck) and dark brown wings and dark throats. As Heuglin did not designate a holotype, these specimens are considered to be syntypes (Hayman & Harrison 1966). Later (on p. 18), Heuglin referred to further specimens some of which are reddish-brown with almost no white markings (Hayman & Harrison 1966). In Zimbabwe, there appears to be a smaller, dark-throated form with lightly pigmented wings, and a larger, browner form, with more white markings and darker wings, which is not dark-throated; both are found in the same day-roosts, and both are sympatric with *T. ansorgei* in some areas (F. P. D. Cotterill pers. obs.). Although the relationship between *T. bivittata* and *T. ansorgei* was examined by Eger & Peterson (1979), it seems that the *ansorgei* / *bivittata* complex is in need of further revision to clarify the diagnostic characters of *T. ansorgei* and *T. bivittata*, and to ascertain if *T. bivittata* is polymorphic and/or contains cryptic species. Pending revision, some of the information below needs confirmation. Furthermore, museum collections probably contain some misidentified material, and the literature probably contains references to misidentified material. Chromosome number: $2n = 48$; $aFN = 54$. $X =$ subtelocentric; $Y =$ acrocentric (Peterson & Nagorsen 1975), but these authors reported difficulty in distinguishing between subtelocentric and acrocentric chromosomes.

Description Information not applicable to the syntypes is in brackets and marked with *. A small microbat without noseleaf and with terminal portion of tail projecting freely from posterior margin of interfemoral membrane; medium-sized for an African molossid; ears joined by interaural band; M^3 with third ridge $>$ length of second ridge; anterior palatal emargination narrow; dorsal pelage brownish (or reddish*), with white spots or stripes on head and neck (sometimes absent*); wings dark brown (or light reddish-brown*); no ventral flank-stripe in contrasting colour; no tail-glands. Not easily distinguished from *T. ansorgei*. Males slightly larger on average than ♀♀. Pelage short (mid-dorsal hairs 3–4 mm), soft, dense; sparse on crown; dorsal pelage covering rump but not extending on to interfemoral membrane (cf. *T. aloysiisabaudiae*). Dorsal pelage umber brown (or dark reddish-brown, greyish-brown to blackish-brown*), with rows of white spots and sometimes short stripes on crown, neck and back (or with almost no such markings*). Based on museum

specimens, reddish-brown individuals appear to be more common (cf. *T. ansorgei*) (Eger & Peterson 1979). It is not yet clear if these variations in colour and markings indicate polymorphism or cryptic species or perhaps both (see Taxonomy). Ventral pelage brown, often slightly frosted (especially on belly) and with or without pale speckling; no mid-ventral markings; ventral flank-stripe same colour as flanks and not extending onto the wing-membrane. Throat much darker than chest and belly (or similar in colour*). (Dark-throated specimens sometimes have, and sometimes lack, white spots and/or stripes*.) Head not extremely flattened. (Upper lip with 5–8 well-defined wrinkles on each side and many spoon-hairs [Freeman 1981, BMNH]*.) (Ears light reddish-brown, reaching about half-way along muzzle; inner margins joined by interaural band with V-shaped fold in middle*.) (Tragus very small, concealed by antitragus*.) (Antitragus large, roughly rectangular*.) Males with interaural crest of very short (ca. 2 mm) dark hairs. (No gular gland*.) Wings and interfemoral membrane dark brown (or wings light reddish-brown and interfemoral membrane slightly darker*).

Skull not extremely dorsoventrally flattened. Anterior of braincase moderately elevated above plane of rostrum (frontals inflated dorsally into a shallow dome, Figure 99d) (cf. *T. ansorgei*). (Mastoid width ♂♂: 11.7 [11.3–12.2] mm, $n = 71$; mastoid width ♀♀: 11.5 [11.0–11.9] mm, $n = 57$ [cf. *T. ansorgei*] [Eger & Peterson 1979]*.) Sagittal crest very low (and sometimes incomplete [i.e. with gap near middle of braincase]*). (Lambdoid crests moderate*.) Palate with small anterior vacuities (Hayman & Harrison 1966). (Anterior palatal emargination narrow, bulb-shaped [narrowest between incisors]*.) Basisphenoid pits moderate in depth, small to medium-sized, their width \leq their distance apart. Anterior upper premolar small (usually ca. same height as cingulum of posterior premolar but sometimes rising higher*), within toothrow; canine and posterior premolar well separated. M^3 with third ridge almost as long as second ridge. (Two lower incisors on each side, bicuspid, crowded*.) (Lower canines with cingula not greatly enlarged, well separated to almost in contact*.) Dental formula: $^{1123}/_{2123} = 30$.

Geographic Variation None reported.

Similar Species Four other African *Tadarida* have the following combination of characters: ears joined by interaural band; M^3 with third ridge $>$ half length of second; wings neither white nor whitish; no ventral flank-stripe in contrasting colour; no tail-glands (Table 20, p. 488):

Tadarida aloysiisabaudiae. Dorsal pelage only sometimes spotted; extending on to interfemoral membrane. Ears on average larger; almost reaching snout when laid forward. Interaural band comparatively prominent, with knob-like projection almost covering snout. Skull with anterior palatal emargination closed. Basisphenoid pits deep, large, their width more than twice their distance apart.

T. russata. Smaller (FA: 42–46 mm; GLS: 17.8–19.4 mm). Skull with anterior palatal emargination closed, pair of incisive foramina visible. Basisphenoid pits moderate in depth, separated by narrow bony ridge (< half breadth of one pit).

T. ansorgei. Dorsal pelage occasionally spotted, sometimes frosted, but not with rows of spots or stripes on head and neck. Wings semi-translucent light reddish-brown to light grey. Ears narrower and pale grey to off-white. Less robustly built (see weights). Anterior of braincase less obviously elevated above plain of rostrum. Mastoid width smaller. Sagittal crest complete. A classification coefficient for distinguishing *T. ansorgei* is given by Eger & Peterson (1979).

T. pumila (sometimes). Much smaller (FA: 32–39 mm; GLS: 14.2–17.6 mm).

Distribution Endemic to Africa. Mainly recorded from Afromontane–Afroalpine, Somalia–Masai Bushland, Coastal Forest Mosaic and Zambezian Woodland BZs, with marginal records in Sahel Savanna and Sudan Savanna BZs and in Eastern Rainforest–Savanna Mosaic. Known from scattered localities on eastern side of Africa, from Eritrea and Ethiopia to Zimbabwe (*contra* Hutton 1986) and SW Mozambique (Koopman 1975, Eger & Peterson 1979, Smithers 1983, F. P. D. Cotterill unpubl.).

Habitat Mainly savanna woodlands (including dry *Acacia*–*Commiphora* bushland, and *Acacia* woodland in East Africa, and

miombo woodland in the south), and montane habitats in Eritrea, Ethiopia and Kenya. Occurs peripherally to the Congo Basin, but evidently not within it. At least in Zimbabwe, typically found near exposed rocky outcrops of granite, basalt and sandstone, which provide day-roosts.

Abundance Uncertain. In Zimbabwe, locally common in vicinity of day-roosts. At roosts shared with *T. ansorgei* and *T. bivittata*, *T. bivittata* is always captured in smaller numbers.

Remarks Very little is known, and some information in literature refers to *T. ansorgei*. Wings long and narrow. Flight and cursorial locomotion as in other *Tadarida*. By day, roosts high up in rock crevices and occasionally in buildings. Not known to roost in mines (*contra* Smithers 1983 whose record refers to *T. ansorgei*). Roosts in small groups or colonies; individuals huddle together in nooks and crannies. In Zimbabwe, shares roosts with *T. ansorgei*, but samples captured as these bats emerged always contained fewer *T. bivittata*. In these samples, ♂♂ outnumbered ♀♀ but the reason for this is not known – perhaps ♂♂ emerge earlier than ♀♀. Litter-size: no information. In Zimbabwe, pregnant ♀♀ have been reported in Oct and Nov, and reproductively inactive parous ♀♀ have been reported in late Mar. Skulls have been recovered from pellets of Barn Owls *Tyto alba* found below the day-roosts of the bats, and Mackinder's Eagle-owls *Bubo capensis* have been observed hawking molossids emerging from these day-roosts in Zimbabwe (Cotterill 1992). Ectoparasites include a flea (*Lagaropsylla anciauxi* [Siphonaptera: Ischnopsyllidae]) (Beaucournu & Kock 1996).

Conservation IUCN Category: Least Concern.

Measurements

Tadarida bivittata

FA: 49.4 (46–51) mm, n = 131*

WS (d): 363.2 (316–392) mm, n = 116

TL: 114.7 (106–129) mm, n = 136*

T: 40 (32–48) mm, n = 134

E: 19.0 (15–22) mm, n = 130

Tr: n. d.

Tib: n. d.

HF: 10.6 (9–13) mm, n = 39†

WT: 18.1 (15–32) g, n = 104

GLS: 20.5 (19.5–21.3) mm, n = 128*

GWS: 12.4 (11.7–13.1) mm, n = 117*

C–M³: 7.5 (7.0–8.0) mm, n = 128*

Throughout geographic range (ROM)

*Derived from Eger & Peterson 1979

†Hayman & Harrison 1966, Smithers & Wilson 1979

Key References Eger & Peterson 1979; Hayman & Harrison 1966.

F. P. D. Cotterill



Tadarida brachyptera SHORT-WINGED FREE-TAILED BAT

Fr. Tadaride à ailes courtes; Ger. Kurzflügel-Bulldoggfledermaus

Tadarida brachyptera (Peters, 1852). Reise nach Mossambique, Säugeth., p. 59. Mozambique I. (15° S, 40° E), Mozambique.

Taxonomy Originally *Dysopes brachypterus*. Subgenus: *Xiphonycteris*. Synonyms: *leonis*, *ochraceus*. Subspecies: two of uncertain validity. Apparently closely related to *T. thersites* and some authors suggest that these forms might be conspecific (e.g. Rosevear 1965, Hayman & Hill 1971). Some authors (e.g. Freeman 1981) consider *leonis* (including *ochraceus*) to be a distinct species, but El-Rayah (1980, 1981) and Simmons (2005) treat *leonis* as conspecific. Chromosome number (Cameroon): $2n = 48$; $aFN = 54$; one pair large and three pairs medium metacentric and 19 pairs medium-small acrocentric autosomes (Smith *et al.* 1986).

Since this profile was submitted, a molossid from Pemba I. Tanzania, was described as *Mops (Xiphonycteris) bakarii* (Stanley 2008). This new species resembles *T. b. brachyptera* in size (FA: 35.9 [34–38] mm, $n = 21$; GSL: 19.3 [18.0–21.1] mm, $n = 13$), but differs mainly in that the basisphenoid pits are essentially absent and the anterior upper premolar barely extends above the cingulum of the canine. The new species is larger than *T. nanulus*, *T. petersoni* and *T. spurrelli*. It differs from *T. thersites* in lacking basisphenoid pits and having a much more reduced anterior upper premolar. There is no profile for this species and it is not mentioned in other profiles or tables. Further details in Appendix.

Description Very small microbat without noseleaf and with terminal portion of tail projecting freely from posterior margin of interfemoral membrane; small for an African molossid (FA: 34–41 mm); ears joined by interaural band; M^3 with third ridge present but $<$ half length of second; anterior palatal emargination narrow, usually bulb-shaped; wings dark brown to black; ventral pelage pale, no ventral flank-stripe in contrasting colour; canines without greatly enlarged cingula. Not easily distinguished from *T. thersites*. Sexes similar. Pelage short (mid-dorsal hairs 3–4 mm), sometimes sparse on nape; dorsally there is either no band of naked skin, or only an inconspicuous narrow band of naked skin, adjacent to the flight-membranes (cf. wide band in *T. thersites*). Rump with two tufts of long hairs (as in several other species of *Tadarida*). Dorsal pelage blackish-brown, dark rusty-brown, sepia brown, or greyish-brown; no grizzling, no white flecks or spots; hairs dark brown with paler base. Orange-phase: bright orange-red specimens known from Cameroon. Ventral pelage pale brownish-grey, very pale grey, orange, yellowish-cream or white; mid-ventral marking inconspicuous or absent; ventral flank-stripe sepia brown or brownish-orange not contrasting with colour of flanks. Head not extremely flattened. Upper lip with 5–7 well-defined wrinkles on each side and many spoon-hairs. Ears blackish-brown, relatively small (not extending as far as snout when laid forward); inner margins joined by interaural band with V-shaped fold in middle. Tragus small. Antitragus large, subrectangular sometimes with corners very rounded. Interaural crest probably absent, but the posterior base of the interaural band often supports a tuft of dark brown, longer hairs. Gular gland: no information. Wings slightly translucent with heavy to light amounts of dark brown or black pigmentation. Wings inserting lower on body than in *T. thersites*. Interfemoral membrane dark brown.

Skull not extremely dorsoventrally flattened. Anterior of braincase elevated above plane of rostrum (more so in *T. b. leonis* than in *T. b. brachyptera*; Freeman 1981). Sagittal crest absent, weakly developed or moderate depending on age. Lambdoid crest very well developed in both subspecies; helmet not quite so prominent as in *T. thersites* but more prominent than in *T. nanula*, *T. petersoni* and *T. spurrelli*. Anterior palatal emargination narrow, usually bulb-shaped (narrowest between incisors). Basisphenoid pits of moderate depth (*T. b. brachyptera*) or shallow (*T. b. leonis*) (Freeman 1981); their width slightly greater to much greater than their distance apart. Upper incisor not procumbent. Upper canines with cingula not enlarged; viewed laterally, incisor not obscured by canine (cf. *T. spurrelli*). Anterior upper premolar distinctly taller than cingulum of posterior premolar, within toothrow or slightly displaced labially. M^3 with third ridge much less than half length of second. Two lower incisors on each side, strongly bicuspid, crowded between canines. Lower canines long and robust; cingula not greatly enlarged, well separated. Dental formula: $^{1123}/_{2123} = 30$.

Geographic Variation Two subspecies are recognized by Koopman (1994) and Simmons (2005). Koopman (1994) proposed the following distributions for these subspecies:

T. b. leonis: Sierra Leone to E DR Congo.

T. b. brachyptera: Uganda to Mozambique; Zanzibar I.

The two widest gaps in the distribution of the species (see Map), especially that between the rainforest and coastal populations which is unlikely to be an artefact, do not seem to support the subspecific distributions proposed by Koopman (1994). If environmental factors (such as climate changes) have caused these two gaps, and if the gaps have resulted in subspeciation, it is more likely that there are three subspecies; *leonis* in the west, *ochraceus* in NE DR Congo and Uganda, and *brachyptera* in the Coastal Forest Mosaic BZ. However, this proposal needs further investigation.

Similar Species Five other African *Tadarida* have the following combination of characters: ears joined by interaural band; M^3 with third ridge absent or present but $<$ half length of second; palatal emargination narrow; FA almost always < 40 mm (Table 20, p. 488):

Tadarida nanula. Forearm shorter (27–31 mm). M^3 with third ridge absent. Upper incisors procumbent (projecting in front of anterior faces of the canine cingula) (Figure 121).

T. petersoni. Usually smaller (FA: 32–35 mm; GLS: 15.8–17.4 mm). Skull without well-developed lambdoid crest. Canines shorter.

T. spurrelli. Forearm shorter (27–30 mm). M^3 with third ridge absent. Canines with greatly enlarged cingula; in lateral view, upper incisors obscured by upper canines (Figures 121 and 122).

T. thersites. Ventral pelage medium brown becoming very dark brown on flanks; ventral flank-stripe black. Dorsally, there



is a conspicuous, wide band of naked skin adjacent to flight-membranes. Wing insertion higher on body. Also, *T. bakarii* mentioned above in Taxonomy.

Distribution Endemic to Africa. Recorded, disjunctly, from Rainforest BZ and marginally from the Northern Rainforest–Savanna Mosaic, from Sierra Leone to SW Central African Republic (except in Dahomey Gap) and from NE DR Congo to Uganda (Budongo and Bugala I.: not mapped). An apparently separate population occurs in the Coastal Forest Mosaic BZ from Kenya to Mozambique, including Zanzibar I. (Neumann 1900) and Mozambique I. Said to occur on Mafia I. by Simmons (2005), but not recorded there by Moreau & Pakenham (1940), Cockle *et al.* (1998) or Kock & Stanley (2009). Said to occur in Gambia by Koopman (1993), but not recorded west of Sierra Leone according to Grubb *et al.* (1998). Reports of this species on Bioko I. (e.g. Koopman 1994) are considered erroneous by Eisentraut (1973) and J. Juste (pers. comm.). Mapped from country checklists (see order Chiroptera), other literature and museum records.

Habitat Considered mainly a lowland rainforest species in West Africa (Rosevear 1965, Koopman *et al.* 1995), but also occurs along the rainforest–savanna ecotone and in the mosaic of lowland rainforest and secondary grassland. Not observed in primary rainforest in Gabon (Brosset 1966) and possibly occurs mainly in clearings and areas of invasive woodland savanna in and around

the Congolian rainforest, although a series from Budongo Forest, Uganda was collected when this was primary forest (ROM, J. Eger pers. comm.). Also occurs in the East African coastal forest mosaic, but was not found in any of the coastal forests investigated by Cockle *et al.* (1998) except Kiwengoma Forest.

Abundance Uncertain, but apparently common in some parts of geographic range.

Remarks Roosts by day in large hollow tree-trunks and hollow branches, deserted holes of barbets (Capitonidae) in dead trees, cracks in fabric of buildings and, very commonly, under corrugated iron roofs of houses. Large colonies are noisy and (to humans) pungently smelly; consequently regarded as pests. Sometimes roosts with *T. thersites*; less often with *T. condylura*. Recorded flying over water (Jones 1971). Known to eat winged termites (Lang & Chapin 1917b) but no other data available. Roosts in groups of 10–20 and in much larger colonies. Colonies reported to contain more ♀♀ than ♂♂ (Lang & Chapin 1917b). At 2–3°N in DR Congo, 14 of 18 ♀♀ had one medium-sized embryo (implanted in right uterine horn) in March (Lang & Chapin 1917b). Predators include Bat Hawks *Macheiramphus alcinus* (Chapin 1932).

Conservation IUCN Category: Least Concern.

If *leonis* is a distinct species, and even if it is retained as a subspecies, its conservation status should be assessed separately from that of *T. brachyptera* as it is probably much less common and widespread.

Measurements

Tadarida brachyptera

FA: 37.3 (34–41) mm, n = 69

WS (d): 250 mm, n = 1

TL: 88.1 (78–100) mm, n = 64

T: 28.9 (25–35) mm, n = 66

E: 17.0 (14–19) mm, n = 65

Tr: n. d.

Tib: n. d.

HF: 11, 11 mm, n = 2

WT: 15.3 (12–18) g, n = 3

GLS: 17.9 (16.2–19.9) mm, n = 41

GWS: 11.3 (10.1–12.3) mm, n = 44

C–M³: 6.6 (6.1–7.7) mm, n = 49

Throughout geographic range (BMNH, HZM, RMCA, SMF, SMNS and literature)

Key References Allen 1917a; El-Rayah 1980, 1981; Lang & Chapin 1917b; Rosevear 1965.

Meredith Happold

***Tadarida chapini* PALE FREE-TAILED BAT (CHAPIN'S FREE-TAILED BAT, LONG-CRESTED FREE-TAILED BAT)**

Fr. Tadaride de Chapin; Ger. Chapins Bulldoggfledermaus

Tadarida chapini (J. A. Allen, 1917). Bull. Amer. Mus. Nat. Hist. 37: 461. Faradje, Orientale, DR Congo.

Taxonomy Originally *Chaerephon* (*Lophomops*) *chapini*. Subgenus *Chaerephon*. Synonyms: *lancasteri*, *shortridgei*. Subspecies: three. Some authors consider *shortridgei* to be a distinct species (e.g. Peterson *et al.* 1995, Simmons 2005) but this view is not followed by Fenton & Eger (2002) and is not followed here. Chromosome number (Namibia, Zimbabwe): $2n = 48$; $aFN = 64$ (Rautenbach *et al.* 1993).

Description Very small microbat without noseleaf and with terminal portion of tail projecting freely from posterior margin of interfemoral membrane; small for an African molossid (FA: 34–40 mm); ears joined by interaural band; M^3 with third ridge $>$ half length of second ridge; anterior palatal emargination closed or slightly open; wings white (tinged with yellow) with minute black spots; ventral pelage pure white or pale greyish-brown; ventral flank-stripe white; ♂♂ with a long, bicoloured interaural crest. Sexes similar except for crest. Pelage short (mid-dorsal hairs 4–5 mm), soft; covering rump but not extending onto interfemoral membrane. Dorsal pelage pale grey, pale rusty-brown or medium greyish-brown; no grizzling, no white spots; patch of whitish hairs on crown; mid-dorsal hairs pale rusty-brown with off-white at base. Ventral pelage pure white or pale greyish-brown; mid-ventral markings absent or white, usually a broad band; ventral flank-stripe white, only sometimes contrasting with ventral pelage. Head not extremely flattened; forehead slightly elevated. Upper lip with 5–6 wrinkles on each side and many spoon-hairs. Ears brown; of

medium relative size (just reaching snout when laid forward); inner margins joined by interaural band with deep, backward-opening, pocket-like invagination in middle. Tragus minute, partly concealed by antitragus. Antitragus moderately large, roughly trapezoid with front-side and base widest. Adult ♂♂ with conspicuous long bicoloured interaural crest arising from interaural pocket (Figure 112); hairs 12–15 mm with basal half rusty-red or grey, terminal half white (Allen 1917a). Adult ♀♀ with short tuft of white hairs. No gular gland. Wings usually white becoming yellowish near body or almost transparent with little white pigmentation; arm-wing with many minute black specks; dorsal skin over bones dark brown. A few specimens from Kenya have pale brown to greyish-brown wings (Fenton & Eger 2002). Interfemoral membrane medium brown.

Skull not extremely dorsoventrally flattened. Anterior of braincase slightly elevated above plane of rostrum. Sagittal crest weakly developed. Lambdoid crests weakly developed or absent dorsally, moderately developed laterally. Anterior palatal emargination variable, can be closed or slightly open and narrow. Basisphenoid pits, moderate in depth, large, their width ca. twice their distance apart. Anterior upper premolar distinctly taller than cingulum of posterior premolar, within toothrow; canine and posterior premolar separated. M^3 with third ridge from just over half to ca. three-quarters the length of the second ridge. M^3-M^3 : 43.1 (41–44)% of GLS, $n = 11$ (cf. *T. pumila*). One or two lower incisors on each side (depending on locality); bicuspid, sometimes crowded. Lower canines slender and relatively short, with cingula not greatly enlarged and not in contact. Dental formula: $^{1123}/_{2123} = 30$ or (rarely) $^{1123}/_{1123} = 28$. For additional information see Fenton & Eger (2002).

Geographic Variation Three subspecies are recognized by Koopman (1994):

T. c. chapini: Ethiopia to DR Congo. Ventral pelage greyish-brown.

T. c. lancasteri: NE Angola to Botswana and Zimbabwe. Ventral pelage pure white.

T. c. shortridgei: SW Angola, NW Namibia. Ventral pelage greyish-brown.

The West African material has not been allocated.

Similar Species Only one other African *Tadarida* has the following combination of characters: ears joined by interaural band; M^3 with third ridge $>$ half length of second; no paired tail-glands at base of tail; FA: <40 mm (Table 20, p. 488):

Tadarida pumila. Dorsal pelage not pale brown; arm-wing dark or white without black specks; ♂♂ with short unicoloured interaural crest. M^3-M^3 relatively wider (45.5 [44–48]% of GLS, $n = 27$).

Distribution Endemic to Africa. Recorded from Guinea Savanna BZ in Côte d'Ivoire (J. Fahr pers. comm.), Ghana and S Sudan, from

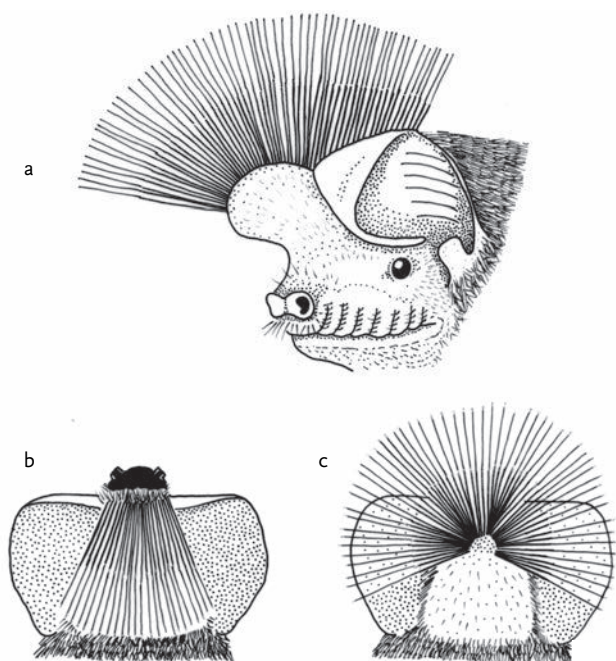


Figure 112. The long, bicoloured interaural crest of *Tadarida chapini*. (a) Lateral view based on photo in which details of face and ear are obscure. (b) Dorsal view (BMNH 52.1505, *T. c. lancasteri*, Zambia). (c) Dorsal view showing crest erected (BMNH 66.6036, *T. c. lancasteri* incorrectly labelled *T. pumila*, Zambia).

*Tadarida chapini*

Rainforest–Savanna Mosaic in NE DR Congo and Uganda, from Somalia–Masai Bushland BZ in Ethiopia and Kenya, and from the Southern Rainforest–Savanna Mosaic and Zambezian Woodland BZ in Angola, SW DR Congo, Zambia, Namibia, Botswana and Zimbabwe. Records are very disjunct, but the gaps probably reflect insufficient collecting. Mapped from country checklists (see order Chiroptera), other literature and museum records.

Habitat Recorded from woodland savannas including *Isobertinia* woodland, *Acacia–Commiphora* bushland, miombo woodland and mopane woodland. Also recorded in mosaic of rainforest and secondary grassland. Often recorded near and over rivers, streams and pools.

Abundance Uncertain. Seldom collected and relatively uncommon in collections, but probably far more abundant than records indicate. Often the most commonly captured molossid over the Sengwa R. (Zimbabwe) during periods of low or no water (Jun, Oct, Nov) (Fenton & Eger 2002).

Adaptations Aspect ratio high; wing-loading low; wing-tip relatively broad; flight predictably moderately fast, agile and marginally more manoeuvrable than that of many molossids. By day, has been found in a horizontal crack in a branch in the crown of a tall mopane tree *Colophospermum mopane* and in a hole in a tree. The interaural crest of ♂♂ can be erected conspicuously or laid back almost out of sight (Lang & Chapin 1917b). The hairs of the crest resemble body hairs: i.e. they are not osmetrichia adapted for the dispersal of scent (Hickey & Fenton 1987). Apparently not known whether or not the crest arises from glandular tissue – possibly its main function is to provide visual cues but the circumstances eliciting erection of the crest are not known. *Tadarida chapini* has been recorded flying over water with *T. ansorgei* in NW Zimbabwe, and with *T. condylura*, *T. nigeriae*, *T. niveiventer* and *T. pumila* in W Zambia.

Foraging and Food Forages by fast-hawking in open spaces. Recorded over water, but not known if it forages over water or comes to drink, or both. Echolocation calls, including feeding-buzzes, assumed to have been emitted by *T. chapini*, have been recorded from 0 to 450 m above ground in Zimbabwe (Fenton & Griffin 1997). Analysis of faeces of 15 individuals collected in dry season in Zimbabwe contained mainly Coleoptera with some Lepidoptera, Diptera and other insects (Fenton & Thomas 1980).

Echolocation Search-phase call-shape: shallow FM (details not available). Start-frequency 27 kHz; end-frequency 19 kHz; maximum call-duration 10 ms (five bats; Fenton & Bell 1981).

Social and Reproductive Behaviour There are several records of an adult ♂ and ♀ being mist-netted together, suggesting that *T. chapini* possibly lives in pairs (Grubb *et al.* 1998), but this needs confirmation. Four pregnant ♀♀ were mist-netted together at dawn: when released in succession at dusk the next day, all four flew to one crack in a mopane tree (see above), suggesting that they roosted together. Not known if other individuals also used this day-roost.

Reproduction and Population Structure Litter-size: no information. Reproductive chronology uncertain. At ca. 15°S in W Zambia, 1 of 5 ♀♀ was pregnant at full term and four were lactating in early Nov (F. P. D. Cotterill unpubl.). At ca. 19°S (near Xugana, Botswana), 5 of 6 ♀♀ were lactating at beginning of wet season (6 Dec); no data for other months (Archer 1977). At ca. 18°S (Sengwa Wildlife Research Area, Zimbabwe), three ♀♀ were heavily pregnant and also lactating in mid-Jan, indicating polyoestrus with postpartum oestrus (F. P. D. Cotterill unpubl.). The data are consistent with seasonal polyoestrus, but the details are not yet known.

Predators, Parasites and Diseases Predators include Bat Hawks *Macheiramphus alcinus* (Allen 1917a). Ectoparasites: no information.

Conservation IUCN Category: Least Concern.

Measurements

Tadarida chapini

FA: 36.7 (34–40) mm, n = 24

WS (a): 258.6 (247–276) mm, n = 10

TL: 86.4 (77–104) mm, n = 21

T: 32.5 (27–44) mm, n = 39

E: 15.8 (12–19) mm, n = 22

Tr: 3.7 (3.0–4.2) mm, n = 6

Tib: 12.2 (11–13) mm, n = 5

HF: 7.4 (6–9) mm, n = 18

WT: 8.8 (5–11) g, n = 32

GLS: 15.6 (14.2–17.2) mm, n = 16

GWS: 9.5 (9.1–10.2) mm, n = 14

C–M³: 5.6 (5.4–5.9) mm, n = 11

Throughout geographic range (BMNH, ROM, TM, Allen 1917a, Hill & Carter 1941)

Key References Allen 1917a; Fenton & Eger 2002.

Meredith Happold & F. P. D. Cotterill

Tadarida condylura ANGOLAN FREE-TAILED BAT

Fr. Tadaride à queue libre; Ger. Angola-Bulldoggfledermaus

Tadarida condylura (A. Smith, 1833). S. Afr. Quart. J. 1: 54. Durban, KwaZulu–Natal, South Africa.

Taxonomy Originally *Nyctinomus condylurus*. Subgenus *Mops*. Synonyms: *angolensis*, *fulva*, *occidentalis*, *orientis*, *osborni*, *wonderi*. Often includes *leucostigma*, but Peterson *et al.* (1995) and Goodman (2011) consider this Madagascan form to be a distinct species. Subspecies: four (excluding *leucostigma*). Chromosome number (Uganda): $2n = 48$; $aFN = 56$ (Dulić & Mutere 1973b). In Somalia and South Africa, $2n = 48$; $aFN = 66$; one pair large metacentric, three pairs small metacentric, four pairs medium subtelocentric, two pairs small subtelocentric and 13 pairs medium-small acrocentric autosomes (Smith *et al.* 1986, Rautenbach *et al.* 1993).

Description Small microbat without noseleaf and with terminal portion of tail projecting freely from posterior margin of interfemoral membrane; medium-sized for an African molossid; ears joined by interaural band; M^3 with third ridge present but $<$ half length of second ridge; anterior palatal emargination closed; wings pale greyish-brown; ventral pelage greyish-brown to whitish, ventral flank-stripe white; crown not darker than back; first phalanx of third and fourth finger comparatively long (cf. *T. demonstrator*, *T. niveiventer*). Sexes almost similar. Pelage short (mid-dorsal hairs 4–5 mm), sparse; covering rump but not extending onto interfemoral membrane; nape almost naked. Dorsal pelage blackish-brown, greyish-brown, pale grey or pale greyish-brown, sometimes with white flecks; hairs pale at base. Crown same colour as rest of dorsal pelage (cf. *T. niveiventer*). Ventral pelage greyish-brown, pale fawn, yellowish-white or whitish; mid-ventral markings white, varied in shape, sometimes absent; ventral flank-stripe white. The full range of dorsal and ventral colours can be found in a single colony. Neonates with dark skin (cf. *T. niveiventer*) (F. P. D. Cotterill pers. comm.). Head not extremely flattened. Upper lip with ca. seven well-defined wrinkles and many spoon-hairs. Ears blackish-brown; relatively short (reaching ca. half-way along muzzle when laid forward); inner margins joined by interaural band with backward-opening pocket-like invagination in middle. Tragus small, squarish, concealed by antitragus. Antitragus large, subrectangular with upper side convex with rounded corners, and thick. Males and ♀♀ with interaural crest of short, brown feathery hairs (osmetrichia) arising from the interaural pocket (Hickey & Fenton 1987). No gular gland. Wings semi-translucent, greyish-brown near body becoming paler towards tip. First phalanx of third finger 22.0 (20–24) mm, $n = 31$; first phalanx of fourth finger 18.3 (17–20) mm, $n = 21$ (cf. *T. niveiventer*, *T. demonstrator*). Interfemoral membrane dark greyish-brown.

Skull not extremely dorsoventrally flattened. Anterior of braincase usually elevated slightly above plane of rostrum. Sagittal crest usually well developed; lambdoid crest usually very well developed; occipital helmet present, usually prominent, sometimes poorly developed. Anterior palatal emargination closed; incisive foramina visible. Basisphenoid pits shallow and often indistinct, small, their width ca. half their distance apart. Anterior upper premolar absent or distinctly shorter than cingulum of posterior premolar and usually displaced labially but sometimes within toothrow; canine

and posterior premolar in contact or nearly so. M^3 with third ridge present but variable in length – usually just a little less than half the length of second ridge but sometimes equal to, and sometimes much less than, half the length of the second. Two lower incisors on each side, bicuspid, crowded. Lower canines relatively short with cingula sometimes well separated, sometimes somewhat enlarged and almost in contact. Dental formula: $^{1123}/_{2123} = 30$ or $^{1113}/_{2123} = 28$.

Geographic Variation Four African subspecies are recognized by Koopman (1994), but not all populations are allocated to subspecies:

T. c. wonderi: Mauritania and Guinea-Bissau at least to Mali.

T. c. orientis: Tanzania.

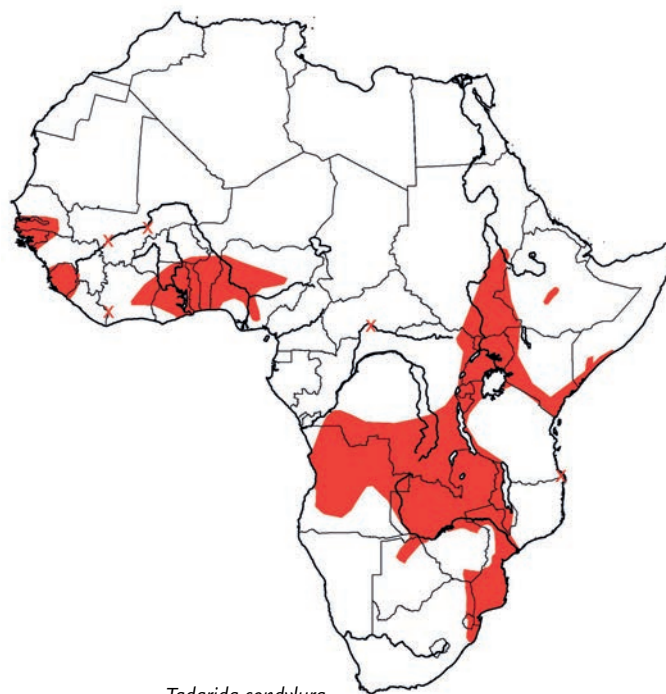
T. c. osborni: Congo and SW DR Congo.

T. c. condylura: Angola and SE DR Congo to Natal.

Similar Species Five other African *Tadarida* have the following combination of characters: ears joined by interaural band; M^3 with third ridge present (but $<$ half length of second ridge) or absent; anterior palatal emargination closed; FA: >40 mm (Table 20, p. 488):

Tadarida niveiventer. Ventral pelage mostly white or cream; ventral flank-stripe same colour. Crown and neck darker than back. First phalanx of fourth finger almost always shorter (15.4 [15–17] mm). Skull with sagittal crest only moderately developed. Basisphenoid pits moderate in depth, medium-sized. M^3 with third ridge absent.

T. demonstrator. First phalanx of third finger shorter (17.7 [16–19] mm). Males with pair of glands between penis and anus.



Tadarida condylura

Ventral pelage white or very pale. Crown usually black, always darker than back. Tibia usually shorter (15–16 mm). Skull with sagittal crest weakly developed, basisphenoid pits deep. Dentition more robust; M^3 with third ridge absent.

T. congica. Larger and heavier (FA: 54–58 mm; WT: 42–64 g).

T. midas. Much larger and heavier (FA: 59–67 mm; WT: 38–69 g).

T. trevori. Forearm almost always longer (51–55 mm). Wings dark brown. No ventral flank-stripe in contrasting colour. Skull with basisphenoid pits deep and large.

Distribution Endemic to Africa. Very widespread south of the Sahara. Mainly recorded from the Sudan Savanna, Guinea Savanna and Coastal Forest Mosaic BZs, the Rainforest–Savanna Mosaic, and the Zambezi Woodland BZ from Senegal to Somalia and south to Angola, Botswana and KwaZulu–Natal (South Africa). Also recorded from some parts of the Rainforest BZ in the Western Region, but not from any other region. Mapped from country checklists (see order Chiroptera), other literature and museum records.

Habitat Recorded mainly in woodland savannas including undifferentiated woodlands, *Isobertia* woodland, mosaics of rainforest and secondary grassland, wetter and drier miombo woodlands, coastal mosaics, *Acacia–Commiphora* bushland and thicket, and other thicket bushlands. Not recorded in undisturbed rainforest habitats, montane areas (except possibly in Ethiopia) and arid areas (except near large rivers in S Somalia). Not dependent on rocky, hilly or mountainous terrain for its roosts.

Abundance Common.

Adaptations Aspect ratio high; wing-loading high to very high. Flight fast, agile with very poor manoeuvrability; turns by banking (radius of turn >1.5 m) but not by stalling-and-twisting; cannot hover or take off from ground; must dive to gain sufficient speed for flight, and swoops upwards to reduce speed prior to landing. Unable to fly in a 1×1×1 m enclosure (M. Happold unpubl.). Scuttling and climbing are fast and efficient. Often roosts by day, clinging or crouching, under corrugated iron roofs; also roosts in nooks and crannies within hollow trees and palms, caves, mines and in the fabric of various buildings. Under roofs, microclimatic temperatures and relative humidities vary daily and seasonally, and reach challenging extremes: 17–39°C and 39–94% in Uganda (Mutere 1969), >40°C during summer days to <10°C during winter nights in South Africa (Bronner *et al.* 1999). Individuals under hot roofs often move from place to place as temperatures change. If possible, they choose 35–42°C (and 30–40%), presumably to minimize cost of thermoregulation without compromising reproductive activity or the ability to avoid predators (Bronner *et al.* 1999). Can survive at 40°C for 11 hours; panting and localized sweating (but not wing-fanning) sometimes occur after prolonged exposure to high temperatures. Becomes torpid at temperatures below thermal neutrality. Sometimes shares roosts with *T. pumila*. Because it is necessary to dive to gain flight speed, entrances are always at least 1.5 m above ground; landing-sites are often stained; individuals often scuttle several metres from landing-sites to roost-sites. Large colonies have a pungent smell (to humans), are noisy and produce much guano; therefore *T. condylura* is often regarded as

a pest. Starts emerging 15–60 min after sunset; time not correlated with season or weather. In Swaziland, sometimes does not emerge on cold wet nights (Monadjem 1998a). Predicted mean maximum urine concentration is comparatively very low (2634 mOsmol/kg). Despite this, non-flying captive bats, even when pregnant, did not drink, but independence of drinking water in the wild is very unlikely because of the high evaporative water loss from the wings during flight (Happold & Happold 1988). The ability of *T. condylura* to utilize thermo-challenging roosts reflects, in part, its tolerance of dehydration rather than its ability to maintain water balance (Buffenstein *et al.* 1999).

Foraging and Food Forages by fast-hawking in open spaces above tree canopies, over clearings and open water, and along fairly open waterways. Often seen foraging between 10–100 m above ground, but also as low as 2–3 m above open ground. Combines circling (sometimes gaining height) with long, straight flights; swerves and dives in pursuit of prey. Often forages in twos, the following bat flying lower than the leader, perhaps to catch moths that close their wings and fall, in response to the echolocation calls of the leader (M. Happold unpubl.). Captive bats foraged while scuttling around their cages/enclosures, and faeces of wild bats contained cockroaches (not necessarily flightless species), which were abundant in their day-roosts: this suggests that opportunistic foraging by chasing occurs in the day-roosts. Feeds opportunistically on very hard-shelled beetles as well as soft-bodied insects. Sometimes feeds mainly on beetles but also takes Hemiptera, Lepidoptera, Odonata, Homoptera and other insects (Verschuren 1957, Whitaker & Mumford 1978).

Echolocation Search-phase calls (Malawi) are mostly shallow linear FM or shallow sigmoid FM sweeps of very narrow bandwidth; end-frequency variable (18–30 kHz); call-duration 5–15 ms. About 7–30% of the calls are shallow linear FM sweeps (cf. 90–100% in *T. pumila*) with end-frequencies 21–24 kHz, bandwidths from 1 to 4 kHz and durations of 5–15 ms (eight light-tagged bats foraging, one flying high after release; M. Happold unpubl.). Individuals often insert a single, shallow linear FM or shallow quasi-linear FM call, with very narrow bandwidth and relatively low start- and end-frequencies, between sequences of 1–3 calls with wider bandwidths and higher start- and end-frequencies (Figure 113). This distinct alternation can be heard with a bat-detector (M. Happold unpubl.). Alternation between calls of different frequencies has been recorded

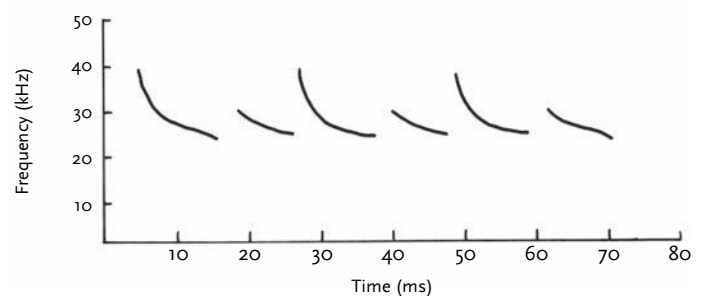


Figure 113. Sonograms of a sequence of search-phase echolocation calls with alternating broad bandwidth and narrow bandwidth calls, emitted by one *Tadarida condylura* while foraging in open space high above the ground (M. Happold unpubl.).

in the non-African molossid *Cheiromeles torquatus*, but not, as yet, for other African species. In cluttered environments (near day-roosts and/or the ground), and also when flying with flocks of conspecifics, *T. condylura* emits steep linear and steep quasi-linear FM sweeps with start-frequencies 28–50 kHz and end-frequencies 18–34 kHz. As individuals fly from cluttered to open spaces, their calls change gradually from broad to narrow bandwidth, and vice versa when approaching prey or returning to cluttered environments.

Social and Reproductive Behaviour Forages singly, in twos or in large groups. Roosts in groups of 10–20 in small natural day-roosts, but in groups of several hundred in buildings. Huddles, sometimes three deep, with much jostling, climbing-over, pushing-under, twittering and squeaking prior to settling down. There is also much movement and vocalizing for 1–2 hours prior to emergence. A colony in Malawi was noisiest in Oct: no apparent correlation between noise level and reproductive state. Composition of colonies and social organization not yet known. The ratio of ♂♂ to ♀♀ in a colony of 369 in Uganda was 1 : 0.7 (Mutere 1969). Mutere found that ♂♂ emerged earlier than ♀♀, which explains why samples of emerging bats taken soon after sunset often contain more ♂♂ than ♀♀. Verschuren (1957) suggested temporary segregation of sexes might occur, but no evidence of sexual segregation has been reported in other studies. On two occasions, in Mar and Jun in Malawi, several hundreds of *T. condylura* were seen flying anticlockwise in a circle 100–200 m in diameter, 10–15 m above ground over open ground near their day-roost. This flight was sustained for more than two hours; its significance is not known (Happold *et al.* 1987).

Reproduction and Population Structure Litter-size: one. Right ovary dominant; implantation in right uterine horn. Reproductive chronology apparently seasonal bimodal polyoestry throughout geographic range, but the interval between consecutive births decreases with increasing latitude so that births coincide with peaks in rainfall. At 0–1° N in Uganda, births occurred in Feb–Mar and Jul–Aug, just before each peak in rainfall (Mutere 1973a). At 02° 18' S (Masalani, inland Kenya), births occur in each of the two wet seasons (Nov, and Mar–Apr) (O'Shea & Vaughan 1980). At 14–16° S in Malawi, births occur in Nov–Dec and Feb–Mar; there is a postpartum oestrus and gestation is ca. 90 days (Happold & Happold 1989b). At 24–26° S (former eastern Transvaal, South Africa), births occur in mid-Dec and early Apr; there is a postpartum oestrus and conception within 18 days of first birth; gestation 85 days, lactation 50–60 days; reproductive quiescence May–Aug (Vivier & van der

Merwe 1997). In ♂♂, spermatogenic activity peaks in Aug to early Sep and Nov to early Dec (Vivier & van der Merwe 1996).

Predators, Parasites and Diseases Individuals scuttling over a roof prior to taking off from its edge were taken by a Central African Large-spotted Genet *Genetta maculata* in Malawi. Often taken by Bat Hawks *Macheiramphus alcinus*, and sometimes by other raptors, as the bats dive away from their day-roosts. Ectoparasites include a bed-bug *Loxapsis miranda* (Hemiptera: Cimicidae); fleas *Lagaropsylla consularis*, *L. duodecima*, *L. incerta*, *L. idae*, *L. leleupi*, *L. obliqua* (Siphonaptera: Ischnopsyllidae); a bat-fly *Nycteribia schmidli* (Diptera: Nycteribiidae); a tick *Lepidixodes kopsteini* (Acari: Ixodidae); and nine species of mites (Acari: Spinturnicidae, Macronyssidae, Trombiculidae, Chirodiscidae, Sarcoptidae) (Anciaux de Faveaux 1984, Beaucournu & Kock 1996). Viruses isolated from *T. condylura* include Bunyamwera, Yellow Fever, Chikungunya, West Nile and Zika, which can cause illness in humans, and Bukalasa Bat, Dakar Bat and Entebbe Bat viruses, which are not known to cause illness in humans (Metselaar *et al.* 1966, Anciaux de Faveaux 1984, C. Calisher pers. comm.).

Conservation IUCN Category: Least Concern.

Well adapted to semi-urban and agricultural areas.

Measurements

Tadarida condylura

FA: 46.9 (45–51) mm, n = 297

WS (a): 361 (348–368) mm, n = 6

TL: 110.7 (96–127) mm, n = 114

T: 40.5 (32–52) mm, n = 113

E: 16.1 (12–21) mm, n = 79

Tr: n. d.

Tib: 17.5 (14–20) mm, n = 151

HF: 13.0 (11–19), n = 96

WT: 23.9 (16–39) g, n = 350

GLS: 20.4 (18.8–22.0) mm, n = 52

GWS: 13.2 (12.2–14.1) mm, n = 65

C-M³: 7.5 (7.0–7.9) mm, n = 59

Throughout geographic range (BMNH, HC, RMCA and literature)

Key References Happold & Happold 1989b; Vivier & van der Merwe 1996, 1997.

Meredith Happold

Tadarida congica CONGO FREE-TAILED BAT

Fr. Tadaride du Congo; Ger. Kongo-Bulldoggfledermaus

Tadarida congica (J. A. Allen, 1917). Amer. Mus. Nat. Hist. 37: 467. Medje, Orientale, NE DR Congo.

Taxonomy Originally *Mops congicus*. Subgenus *Mops*. Synonyms: none. Does not include *T. trevori*, which was considered a subspecies of *T. congica* by Koopman (1965) and Hayman & Hill (1971) but subsequently shown to be a distinct species (Peterson 1972, Freeman 1981). Chromosome number: not known.

Description Small microbat without noseleaf and with terminal portion of tail projecting freely from posterior margin of interfemoral membrane; medium-sized for an African molossid (FA: 54–58 mm; WT: 42–66 g); ears joined by interaural band; M³ with third ridge absent or weakly developed; anterior palatal emargination closed; wings blackish-brown; ventral pelage variable but not white or

whitish, no ventral flank-stripe in contrasting colour; dorsal pelage dark brown to almost black; crown not darker than back. Males on average larger than ♀♀ in skull dimensions. Pelage short, moderately sparse on nape; flanks and posterior of rump naked. Dorsal pelage dark brown to almost black, often with isolated, pale hairs but no spots or flecking; hairs medium brown with dark brown or black at tip. There is a pronounced and well-defined dark patch behind and below the ear (cf. smaller and poorly defined in *T. trevori*). Ventral pelage variable, with a strong wash of grey, brown or rusty colour, resulting in a mottled appearance; no mid-ventral markings; ventral flank-stripe same colour as flanks. Head not extremely flattened. Upper lip with 7–8 well-defined wrinkles on each side and many spoon-hairs. Ears blackish, thick and leathery; not reaching snout when laid forward. Inner margins of ears joined across forehead by a thick interaural band with strong cartilaginous pocket-like support. Tragus minute, concealed by antitragus. Antitragus large, rounded dorsally with a rather straight anterior edge. Interaural crest: no information. No gular gland. Wings blackish-brown. Third metacarpal: 53–60 mm, $n = 38$; fourth metacarpal: 51–58 mm, $n = 28$ (cf. *T. trevori*).

Skull large and robust, not extremely dorsoventrally flattened. Anterior of braincase slightly elevated above plane of rostrum. Sagittal crest comparatively well developed anteriorly, lower posteriorly. Lambdoid crest moderate to well developed. Anterior palatal emargination closed. Basisphenoid pits deep, large, their width greater than their distance apart. Anterior upper premolar usually lower than cingulum of posterior premolar, within toothrow; canine and posterior upper premolar separated. M^3 with third ridge absent or weakly developed. Upper and lower canines in ♂♂ much larger than in ♀♀. Two lower incisors on each side, bicuspid, crowded. Lower canines with cingula not greatly enlarged and not in contact. Dental formula: $1^{123}/_{2123} = 30$.

Geographic Variation None recorded, but data are limited.

Similar Species Five other African *Tadarida* have the following combination of characters: ears joined by interaural band; M^3 with third ridge present (but usually* < half length of second ridge) or absent; anterior palatal emargination closed; FA: >40 mm (Table 20, p. 488). *In *T. condylura*, the length of the third ridge is variable and can be up to half length of second ridge.

Tadarida midas. Forearm longer (59–67 mm). Pelage more variable and generally paler, usually greyish, with frosted appearance and some whitish flecking. Skull of similar length but more robust and often wider (GWS: 15.2–18.1 mm).

T. trevori. FA usually shorter (51–55 mm), third and fourth metacarpals usually shorter (see Description). Dorsal pelage not dark brown to almost black. Interaural band much thinner. Skull usually smaller (GLS: 23.1–25.1 mm).

T. condylura. Smaller and lighter (FA: 45–51 mm; WT: 16–39 g).

T. niveiventer. Smaller and lighter (FA: 44–48 mm; WT: 20–30 g).

Ventral pelage mostly white or cream.

T. demonstrator. Much smaller and lighter (FA: 41–46 mm; WT: 20–24 g).

Distribution Endemic to Africa. Recorded in Rainforest BZ (West Central and East Central Regions) and marginally in Northern and



Tadarida congica

Eastern Rainforest–Savanna Mosaics. Known from seven localities in Cameroon, DR Congo and Uganda (Peterson 1972, Freeman 1981, Breman *et al.* 1999, RMCA, USNM). Records from Pampramase, Ghana (Jeffrey 1975) and Agege, Nigeria (Bergmans 1977b) are referable to *T. trevori* (Fahr *et al.* 2006). Based on habitat, a record from Guinea savanna in Bamingui-Bangoran N. P., Central African Republic (Spinage 1988) might also represent *T. trevori* but specimens need checking. An unspecified record for Gambia by Koopman (1993) is erroneous and probably refers to *T. demonstrator*, which is listed for Senegambia & Mauritania by Koopman *et al.* (1995); see also Koopman (1989).

Habitat Recorded from lowland rainforest, coastal forest and rainforest–savanna mosaic vegetation zones. Seems to be more closely associated with rainforest than its sister species, *T. trevori*, which is mainly found in the forest–savanna mosaic and woodland savannas north and east of the Rainforest BZ.

Abundance Appears to be very rare and localized, but this might reflect insufficient sampling, in suitable habitat, using elevated mist-nets.

Remarks One ♂ and 12 ♀♀ (the type series) roosted by day in the hollow trunk of a tree, and were captured when the tree was felled by a violent storm; this roost was shared by a colony of *T. russata* (see profile) (Lang & Chapin 1917b). In W Uganda, Kingdon (1974) observed individuals foraging just before dark, and coming down to drink at 19:30h in early Mar; he shot and mist-netted a 'large series' of which 'almost all' of the adult ♀♀ were 'very recently pregnant'. Three subsequent efforts to collect, at different times of the year and in the same locality, did not reveal any other bats of this species. This, together with a record by Lang & Chapin (1917b) that five of 12 ♀♀ were pregnant (each with one large embryo) in Sep, 60 years earlier and 200 km to the north-west, led Kingdon (1974) to suggest that these bats have a 'biannual breeding season' and that

they may migrate or undergo seasonal movements, but all of these suggestions need confirmation. The host of the ectoparasite *Allopyssa alloides* (Siphonaptera: Ischnopsyllidae) was published as *T. congica* by Smit (1977) but is here re-identified as *T. trevori*.

Conservation IUCN Category: Near Threatened.

Based on its patchy distribution and tight association with forest, a decline can be expected in future. Major threats: loss and degradation of habitat caused by logging and agriculture. Population trend not known.

Measurements

Tadarida congica

FA: 56.7 (54–58) mm, n = 32

WS (d): 436.4 (425–450) mm, n = 14

TL: 140.5 (130–152) mm, n = 32

T: 47.9 (39–58) mm, n = 32

E: 22.8 (21–28) mm, n = 32

Tr: n. d.

Tib: 19.2 (18–21) mm, n = 22

HF: 15.3 (13–17) mm, n = 32

WT: 56.5 (42–64) g, n = 32

GLS (♂♂): 26.8 (26.0–27.4) mm, n = 7

GLS (♀♀): 25.7 (24.9–26.2) mm, n = 21

GWS (♂♂): 15.8 (15.4–16.3) mm, n = 8

GWS (♀♀): 15.3 (14.8–15.7) mm, n = 23

C-M³ (♂♂): 10.0 (9.7–10.2) mm, n = 8

C-M³ (♀♀): 9.6 (9.1–10.0) mm, n = 22

Cameroon, DR Congo, Uganda (AMNH, FMNH, SMF, USNM, Peterson 1972)

Key References Allen 1917a; Freeman 1981; Kingdon 1974; Lang & Chapin 1917b; Peterson 1972.

Jakob Fahr

Tadarida demonstrator MONGALLA FREE-TAILED BAT

Fr. Tadaride de Mongalla; Ger. Mongalla-Bulldogfledermaus

Tadarida demonstrator (Thomas, 1903). Ann. Mag. Nat. Hist., ser. 7, 12: 504. Mangala [= Mongalla], Bahr el Jebel, Equatoria Prov., S Sudan.

Taxonomy Originally *Nyctinomus demonstrator*. Subgenus *Mops*. Synonyms: *faradjius*. Subspecies: none currently recognized. Koopman considered (1994) or discussed (1993) the possibility that *niveiventer* is a subspecies of *T. demonstrator*, but Freeman (1981) treated *niveiventer* as a separate species although most closely related to *T. demonstrator*. Chromosome number (Cameroon): 2n = 48; aFN = 54 (Smith *et al.* 1986).

Description Small microbat without noseleaf and with terminal portion of tail projecting freely from posterior margin of interfemoral membrane; medium-sized for an African molossid (FA: 41–46 mm); ears joined by interaural band; M³ with third ridge absent; anterior palatal emargination closed; wings medium to dark grey; ventral pelage white or very pale; no ventral flank-stripe in conspicuously contrasting colour; crown usually black, always darker than back; ♂♂ with paired glands near base of penis; first phalanges of third and fourth fingers comparatively short (cf. only *T. niveiventer*, *T. condylura*). Sexes almost similar. Pelage short (mid-dorsal hairs 2–5 mm), moderately sparse on nape. Dorsal pelage medium brown to slaty-grey, often suffused with pale grey or silvery-white giving frosted appearance; no distinct spots but slight to moderate flecking in some specimens; hairs white to pale grey with tip darker (greyish-brown to dark slaty-grey). Crown of head darker than back, usually black (as in *T. niveiventer*). Ventral pelage pure or creamy white to very pale grey; darker towards the flanks; hairs unicoloured; no mid-ventral markings; ventral flank-stripe whitish or pale grey, paler than flanks but not contrasting with mid-ventral colour. Head not extremely flattened; muzzle comparatively short, rounded and sturdy. Upper lip with 7–8 well-defined wrinkles on each side; very few spoon-hairs. Ears dark grey, relatively short (not reaching muzzle when laid forward); inner margins joined across forehead by a relatively

low interaural band with a forward-pointing, V-shaped fold in middle or forward-pointing, pocket-like invagination in middle. Tragus minute, concealed by antitragus. Antitragus large, rounded above with broad base. Posterior side of interaural band supporting longer and stronger black hairs, but not a distinct interaural crest. No gular gland. Wings medium to dark grey. First phalanx of third finger 17.7 (16–19) mm, n = 15; first phalanx of fourth finger 14.2 (13–16) mm, n = 15. Males with paired glands near base of penis, opening towards tail.

Skull large and robust relative to the size of the bat; not extremely dorsoventrally flattened. Anterior of braincase not noticeably rising above plane of rostrum. Sagittal crest well developed to weakly developed anteriorly, weakly developed posteriorly; lambdoid crests moderately developed, usually forming a weakly-developed helmet in older individuals, especially ♂♂. Anterior palatal emargination closed; incisive foramina present. Basisphenoid pits deep, large, their width > their distance apart. Anterior upper premolar distinctly shorter than cingulum of posterior premolar and usually displaced labially, sometimes absent; canine and posterior upper premolar in contact or almost so. M³ with third ridge absent. Two lower incisors on each side, bicuspid, crowded. Lower canines with cingula not greatly enlarged, separated by narrow gap. Dental formula: $\frac{1^{123}}{2_{123}} = 30$.

Geographic Variation Apparently none.

Similar Species Five other African *Tadarida* have the following combination of characters: ears joined by interaural band; M³ with third ridge present (but usually* < half length of second ridge) or absent; anterior palatal emargination closed; FA: >40 mm (Table 20, p. 488). *In *T. condylura*, the length of the third ridge is variable and can be up to half length of second ridge.

*Tadarida demonstrator*

Tadarida condylura. First phalanx of third finger longer 22.0 (20–24) mm. Males without scent-glands between penis and anus. Ventral pelage often with little or no white. Crown and neck same colour as back. Tibia usually longer (16–20 mm). Skull with sagittal crest usually well developed; basisphenoid pits shallow. Dentition less robust; M^3 with third ridge present (usually half to < half length of second ridge).

T. niveiventer. First phalanx of third finger almost always longer (19.4 [19–21] mm). Males without scent-glands between penis and anus. Wings pale grey. Basisphenoid pits moderate.

T. trevori. Larger (FA: 51–55 mm). Males without scent-glands between penis and anus. Dorsal pelage not frosted.

T. congica. Much larger and heavier (FA: 54–58 mm; WT: 42–64 g).

T. midas. Much larger and heavier (FA: 59–67 mm; WT: 38–69 g).

Distribution Endemic to Africa. Recorded from Sahel Savanna (but only in Blue Nile Valley), Sudan Savanna and Guinea Savanna BZs and the Northern and Eastern Rainforest–Savanna Mosaics. Known from 26 localities in N Côte d'Ivoire (Comoé N. P., Mt Sangbé N. P.; J. Fahr unpubl.), Burkina, Ghana, N Cameroon, Sudan, NE DR Congo and NW Uganda. A record from Kwabenya (Legon, Ghana) by Koopman *et al.* (1995) and cited by Grubb *et al.* (1998) does not represent *T. demonstrator*. A BMNH specimen taken 'at sea off Gambia' and mentioned by Koopman (1989) is disregarded by Grubb *et al.* (1998).

Habitat Prefers relatively open and dry savanna vegetation zones (such as *Isobelinia* woodland) as well as forest–savanna mosaic but, based on the known records, it seems that the distribution of this bat often follows larger rivers, especially in the north-eastern and drier parts of its geographic range. In Sudan, found along the Blue Nile R. where it runs through Sahel *Acacia* wooded grassland, and along the White Nile R. where it flows through *Acacia* wooded grassland and also through the Sudd with its seasonally flooded grasslands and semi-aquatic vegetation.

Abundance Uncertain. Appears to be localized and comparatively rare, but this might reflect insufficient sampling in suitable habitat using elevated mist-nets.

Adaptations In Garamba N. P., NE DR Congo, found roosting only in natural roosts, usually 3–4 m above ground: these included under bark, and in very narrow fissures and cracks in the trunks or branches of trees including *Terminalia*, *Vitex doniana* and *Parinari* sp. (Verschuren 1957, as *faradjius*). One roost was located in the same tree in which an owl had its nest with a young. In Garamba N. P., both *T. condylura* and *T. midas* roosted in the same sorts of places, but *T. demonstrator* was seldom found roosting with these molossids; on one occasion only, a group was found roosting with two *T. midas* and one *Nycticeinops schlieffeni* (Verschuren 1957). Unlike *T. condylura*, not found roosting under the roofs of houses in this locality. In Sudan, however, one individual was caught (together with 12 *T. pumila*) as it emerged from the thatch of a house (Kock 1969a).

Foraging and Food Forages by fast-hawking, high above the ground and vegetation. In Comoé N. P., Côte d'Ivoire, in mist-nets set 0–25 m above ground, captured at median height of 16.4 (8.4–19.6) m, $n = 4$ (J. Fahr unpubl.). In W Uganda, Kingdon (1974) mist-netted this bat early in the evening. Diet not known but likely to consist of comparatively hard-shelled, flying insects.

Social and Reproductive Behaviour In Garamba N. P., both ♂♂ and ♀♀ were found roosting singly or in small groups comprised of 2–10 individuals (Verschuren 1957). The groups included all-female groups of 2–7 ♀♀, and groups containing at least one ♂ with at least two ♀♀ (but sexes of some group-members not determined). One group included three ♂♂ and two ♀♀ and four others not sexed. In a collection of 35 sexed bats taken from 11 day-roosts occupied by a total of 42 bats, the ratio of ♂♂ to ♀♀ was 1 : 4.8. According to Verschuren (1957) this sex ratio reflects the social structure in the day-roosts (1 ♂ to ca. 5 ♀♀), but the group-compositions (which he tabulated) show that the compositions of groups are actually very variable. Verschuren (1957) also suggested that perhaps ♀♀ roost separately from ♂♂ during the parturition season, but this needs confirmation.

Reproduction and Population Structure Litter-size: not known (probably one). Reproductive chronology not known. At 03°55'N (Garamba N. P., NE DR Congo), pregnant ♀♀ (near term) were recorded in Apr and Jun, and one with a very small embryo in Sep; one lactating ♀ in Jun; juveniles in May, Jun and Sep (no data given for other months) (Verschuren 1957, as *faradjius*). In one all-female colony, 4 of 5 adults were pregnant (near term) and the other lactating, suggesting synchrony at least between ♀♀ roosting together. The data suggest polyoestry (as in several other African molossids), but this needs confirmation.

Predators, Parasites and Diseases The holotype of *faradjius* was taken from the crop of an African Bat Hawk *Macheiramphus alcinus* at Faradje, DR Congo, together with *Tadarida chapini*, *Pipistrellus nanus* and *P. tenuipinnis* (Lang & Chapin 1917b). Ectoparasites include a flea *Lagaropsylla hoogstraali* (Siphonaptera: Ischnopsyllidae) (Anciaux de Faveaux 1984).

Conservation IUCN Category: Least Concern.

Major threats: destruction of roost sites (mature trees) in savanna habitats, loss and degradation of habitat especially as result of wood extraction including selective logging. Population trend inferred to be declining.

Measurements

Tadarida demonstrator

FA: 44.4 (41–46) mm, n = 12

WS (c): 334 (326–344) mm, n = 5

TL: 108.8 (103–119) mm, n = 8

T: 32.3 (27–37) mm, n = 8

E: 17.1 (16–18) mm, n = 9

Tib: 15.9 (15–16) mm, n = 6

HF: 9.4 (8.1–10.8) mm, n = 8

WT: 22.3 (20–24) g, n = 6

GLS: 20.5 (19.2–22.2) mm, n = 11

GWS: 13.0 (12.3–13.3) mm, n = 12

C–M³: 8.0 (7.6–8.3) mm, n = 9

Côte d'Ivoire, Ghana, DR Congo, Sudan, Uganda (AMNH, FC, IRSN, RMCA, SMF, USNM)

Key References Lang & Chapin 1917b; Verschuren 1957.

Jakob Fahr

Tadarida fulminans MADAGASCAN FREE-TAILED BAT (MALAGASY FREE-TAILED BAT)

Fr. Tadaride de Thomas; Ger. Madagassische Bulldoggfledermaus

Tadarida fulminans (Thomas, 1903). Ann. Mag. Nat. Hist., ser. 7, 12: 501. Fianarantsoa, eastern Betsileo, Madagascar.

Taxonomy Originally *Nyctinomus fulminans*. Subgenus *Tadarida*. Synonyms: *mastersoni*. Subspecies: two. Chromosome number (South Africa): 2n = 48; aFN = 66. X = medium metacentric, Y = small acrocentric (Rautenbach *et al.* 1993).

Description Medium-small microbat without noseleaf and with terminal portion of tail projecting freely from posterior margin of interfemoral membrane; large for an African molossid; ears relatively short, meeting to form a V-shaped valley; wings brown dorsally, whitish ventrally; ventral flank-stripe white, cream or yellowish; two lower incisors on each side; M³ with third ridge > half length of second ridge. Sexes different in colour, similar in size. Pelage velvety; mid-dorsal hairs 6–7 mm. Dorsal pelage (♀ ♀) dark chocolate brown; no spots or flecking; hairs pale greyish-brown with dark chocolate brown tips. Ventral pelage (♀ ♀) dark chocolate brown on flanks, paler on abdomen with white or cream mid-ventral band; ventral flank-stripe white or cream. Dorsal pelage (adult ♂ ♂) reddish-brown; no spots or flecking; hairs with basal half pale greyish-brown or creamy-fawn. Ventral pelage (adult ♂ ♂) reddish-brown on flanks, paler on abdomen with cream or yellowish mid-ventral band; ventral flank-stripe yellowish. Subadults same as adult ♀ ♀. Head not extremely flattened. Upper lip without well-defined wrinkles; comparatively few spoon-hairs. Ears dark brown, comparatively small (not reaching snout when laid forward); with inner margins meeting at base of forehead to form a V-shaped valley. Tragus large, roughly rectangular, not concealed by antitragus. Antitragus low, triangular, only slightly larger than tragus. No interaural crest. Gular gland naked, conspicuous especially in ♂ ♂ in which it is often ringed by greenish hairs. Wing-membranes brown dorsally (paler over phalanges), whitish ventrally becoming browner towards tips. Interfemoral membrane dorsally brown, ventrally whitish, darkening towards margins. Ventral sides of forearms and legs naked and white. Foot with raised pad on sole (plantar pad).

Skull not extremely dorsoventrally flattened. Anterior of braincase elevated above plane of rostrum, but sometimes only slightly. Sagittal crest very weakly developed in ♂ ♂, absent in ♀ ♀; lambdoid crests

well developed in both sexes. Anterior palatal emargination wide. Interdental palate broad posteriorly, narrowing smoothly towards canines with only a slight constriction at level of posterior premolars (cf. *T. lobata*). Basisphenoid pits deep, large, their width greater than their distance apart. Upper incisors short and close together. Anterior upper premolar ca. same height as cingulum of posterior premolar, slightly displaced labially but canine and posterior premolar not in contact although sometimes nearly so. M³ with third ridge > half second ridge. Two lower incisors on each side, bicuspid and crowded. Lower canines well developed; cingula not greatly enlarged but nearly in contact. Dental formula: $\frac{1123}{2123} = 30$.

Geographic Variation None recorded.

Similar Species Four other *Tadarida* in Africa have ears with inner margins meeting, or almost meeting, to form a V-shaped valley:

Tadarida aegyptiaca. Almost always smaller (FA: 42–55 mm; GLS: 17.1–21.9 mm). Wings brown or blackish ventrally and dorsally. Ventral pelage with no mid-ventral markings and usually no ventral flank-stripe in contrasting colour.

T. lobata. Inner margins of ears meeting close to snout; ears extending well beyond snout when laid forward. White spot between shoulder-blades of adults. Skull with interorbital constriction slight; interdental palate markedly constricted at level of posterior premolar. Lower canines with cingula separated by the incisors.

T. teniotis. Three lower incisors on each side. Wings blackish. North Africa.

T. ventralis. No ventral flank-stripe in contrasting colour. Foot usually without plantar pad. Skull usually larger and more robust (GLS: 23.4–26.1 mm). Upper incisor longer.

Distribution In Africa, recorded mainly from Somalia–Masai Bushland, Zambezian Woodland and Afromontane–Afroalpine BZs, but probably extends into Eastern Rainforest–Savanna Mosaic near mountainous areas. Recorded from E DR Congo, Uganda, Rwanda, Kenya and Tanzania and southwards to NE South Africa



(Harrison 1971, Hayman & Hill 1971, Ansell 1978, Baeten *et al.* 1984, Happold *et al.* 1987, Cotterill 1996b, 2001c). Extraliminally: Madagascar (two specimens – the holotype collected in late nineteenth century and a melanistic topotype [FMNH 166074] collected in 1999).

Habitat Apparently prefers woodland savannas where steep rocky terrain provides suitable day-roosts. No details for the northern records except many appear to be near mountains. In Malawi, recorded in miombo woodland at base of Mulanje Mountain, which is a great, granite-syenite massif with precipitous, bare sides. In SW Zambia and NW Zimbabwe, recorded from the precipitous basalt gorges of the Upper Zambezi R. (Victoria Falls and Kalomo). In S and E Zimbabwe, recorded from a range of habitats including miombo and mopane woodlands, but mostly recorded in miombo woodland on the granitic shield, especially in rugged granite country where there are high, steep-sided inselbergs (Cotterill 2001c). Also recorded from day-roosts in a dolomite cave and in Karoo sandstone in the Sebungwe and Limpopo basins.

Abundance Locally common, but patchily distributed (based on a series collected in Rwanda, and observations and captures at roosts in NE and S Zimbabwe). Distribution and abundance is probably determined by the availability of suitable day-roosts (Cotterill 2001c). Rarely collected because it flies high and roosts in inaccessible places.

Adaptations Aspect ratio very high; wing-loading very high to exceptionally high (F. P. D. Cotterill unpubl.); this species, and *T. ventralis*, have the narrowest wing-tips found in any African *Tadarida* (Freeman 1981). Flight fast, agile, usually direct (Smithers 1983); manoeuvrability very poor; the agile swooping flight as a bat returns to its day-roost, with air rushing over its wings, is very reminiscent of the flight of swifts (Apodidae). Adept at rapid scuttling forwards,

backwards and sideways. Cannot take off from ground, and needs to dive to gain sufficient speed for flight. Roosts by day in narrow, horizontal rock-crevices located either high up in vertical cliffs or under overhangings. In Zimbabwe, most known roosts are in granite inselbergs; one colony roosted in cracks in the ceiling of a dolomite cave. Scuttles around roost-sites; scuttles backwards into crevices, using tip of tail to feel the way. In Zimbabwe, sometimes shares roosts with *T. ansorgei* and *T. bivittata* (Cotterill & Fergusson 1993a). Often mist-netted over water, suggesting dependence on accessible water for drinking.

Foraging and Food Forages by fast-hawking. Emerges at dusk, remains active all night and does not return to the day-roost until just before first light (Smithers 1983, F. P. D. Cotterill pers. obs.). Feeds on flying insects; details not known.

Echolocation Search-phase call-shape shallow FM. In Zimbabwe, start-frequency 27 kHz; end-frequency 14 kHz; peak-frequency 17 kHz; maximum duration 20 ms (1 bat, flying free; Fenton & Bell 1981). In South Africa, start frequency 27 kHz; end-frequency 14 kHz; intensity high (one bat in flight-cage; Aldridge & Rautenbach 1987).

Social and Reproductive Behaviour Roosts singly or in groups. No more than 20 individuals have been taken from any one day-roost but, in some cases, not all group-members were taken (Smithers 1983, F. P. D. Cotterill pers. obs.). Four captive adult ♂♂ roosted separately, suggesting that they are territorial; adult ♂♂ have also been observed roosting singly in rock-crevices. In contrast, captive ♀♀ huddled tightly together (F. P. D. Cotterill & N. C. Bennett unpubl.). Within day-roosts, there is much jostling and squeaking (audible to humans). Group-members emerge from the roost together, and make shrill squeaks as they dive away.

Reproduction and Population Structure Litter-size: one ($n = 10$); only right ovary is functional. Based on small samples of ♀♀ collected at 17° 30'S in NE Zimbabwe at ca. monthly intervals from Jul 1988 to Sep 1989 (Cotterill & Fergusson 1993b), the reproductive chronology appears to be seasonal polyoestrus, but further data are needed to elucidate the details. Births followed by postpartum oestrus are inferred to have occurred in ca. Mar–May at beginning of dry season (evidence: in late Jul, 3 of 5 ♀♀ were simultaneously lactating and in very early pregnancy and two were lactating with sperm *in uteri* and *in vaginae*; and in late Aug, 4 of 4 ♀♀ were post-lactating and in early pregnancy). In mid-Oct, 3 of 3 ♀♀ were pregnant. In mid-Nov, 5 of 5 ♀♀ were lactating and also pregnant with full-term foetuses; this indicates births from ca. late Oct to Nov (beginning of hot-wet season) and suggests either that the lactation period after the Mar–May births is exceptionally long, or that these bats had had a previous litter in ca. Aug at some other locality. There was no evidence of postpartum oestrus after the Oct–Nov births (8 of 8 ♀♀ in Dec, 5 of 5 in Feb and 2 of 2 in Apr were lactating but not pregnant), therefore this study did not indicate when the ♀♀ that gave birth in Mar–May became pregnant. Perhaps only some ♀♀ have a postpartum oestrus following births in Oct–Nov, or perhaps births in May–Jun do not occur every year. Perhaps this species migrates, and

its reproductive chronology cannot be elucidated from studies at only one locality. Considered overall, the unusual reproductive chronology of *T. fulminans* suggests that the pattern of annual fluctuation in the availability of its prey differs from those of the prey exploited by other Chiroptera.

Predators, Parasites and Diseases Predators include Mackinder's Eagle-owl *Bubo capensis*, which has been observed capturing this bat in NE Zimbabwe (Cotterill 1992). Ectoparasites include a bed-bug *Crassimex sexualis* (Hemiptera: Cimicidae), another bug *Hypoctenes faini* (Hemiptera: Polycetidae) and mites *Microtrombicula intranasalis* (Acari: Trombiculidae), *Notoedres* spp. (Acari: Sarcopidae) (Anciaux de Faveaux 1984). All examined *T. fulminans* carried one or more interstitial nematodes (ca. 10 mm overall length), clearly visible under skin on underside of wing-membrane along anterior edge of the forearm. (Note: internal parasites are not mentioned in other profiles.)

Conservation IUCN Category: Least Concern.

Measurements

Tadarida fulminans

FA: 58.5 (56–61) mm, n = 50

WS (d): 428 (400–510) mm, n = 21

TL: 144 (132–161) mm, n = 24

T: 57.5 (53–66) mm, n = 24

E: 23.5 (19–25) mm, n = 23

Tr: n. d.

Tib: 21.2 (20–22) mm, n = 18

HF: 13.0 (11–15) g, n = 14*

WT: 34.6 (23–49) g, n = 58

GLS: 23.0 (21.6–24.4) mm, n = 39

GWS: 13.6 (12.9–14.2) mm, n = 36

C-M³: 8.5 (7.8–9.2) mm, n = 40

Throughout African geographic range (BMNH, FMNH, HZM, NMZB, RMCA, ROM, USNM)

*Zimbabwe (Smithers & Wilson 1979)

Key References Cotterill 1996b, 2001c; Cotterill & Fergusson 1993b.

F. P. D. Cotterill

Tadarida gallagheri GALLAGHER'S FREE-TAILED BAT

Fr. Tadaride de Gallagher; Ger. Gallaghers Bulldoggfledermaus

Tadarida gallagheri Harrison, 1975. Mammalia 39: 313. Scierie Forest, 30 km south-west of Kindu, DR Congo.

Taxonomy Currently in subgenus *Chaerephon*. Synonyms: none. At the time of its discovery, the uniqueness of this little molossid, especially its nasal swellings and interaural membrane morphology, suggested that it might represent a distinct genus (Harrison 1975). Subsequently, *T. tomensis*, another species with very similar nasal swellings and interaural membrane morphology, was described from São Tomé (Juste & Ibáñez 1993b). Both of these species bear some resemblance to *Tadarida* (*Chaerephon*) *johorensis* from Asia. Chromosome number: not known.

Description Very small microbat without noseleaf and with terminal portion of tail projecting freely from posterior margin of interfemoral membrane; small for an African molossid; with inner margins of ears joined by an interaural membrane and a large, bulbous, interaural lobe, which projects well forward over the muzzle and dominates the lateral profile of the head (Figure 97g): no other mainland species resembles this bat. Sexual dimorphism: no information (only one ♂ specimen known). Pelage short (mid-dorsal hairs 5–6 mm). Dorsal pelage uniformly umber brown; no spots or flecking. Ventral pelage uniformly umber brown; no mid-ventral markings; ventral flank-stripe umber brown. Head not extremely flattened; muzzle blunt with transverse ridge above snout. Upper lip with five well-defined wrinkles on each side and few spoon-hairs except in front of the snout. Ears relatively large, extending beyond snout when laid forward; inner margins joined by a naked interaural membrane that rises centrally to form a flat-topped, truncated triangle with convex sides. Below this, there is a large bulbous lobe, which projects forward over the muzzle

and extends beyond the snout. This lobe is penetrated by a deep, backward-opening pocket. The pocket is bordered by two vertical hairless folds of skin, which extend backwards out of the pocket and unite on the crown of the head. Arising from the smooth floor of the pocket is an interaural crest of dark brown hairs, ca. 9 mm long, and presumably the pocket can be partly everted to display this crest. Tragus small but not concealed by antitragus. Antitragus well developed, roughly rectangular. No gular gland. Wings and interfemoral membrane greyish-black.

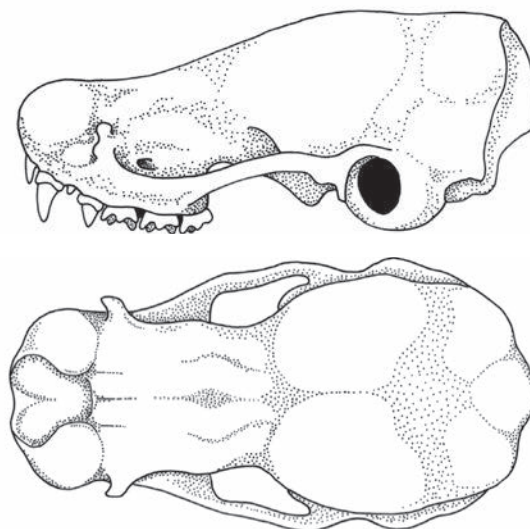


Figure 114. *Tadarida gallagheri*. Skull (holotype; based on Harrison 1975).

Skull (Figure 114) not extremely dorsoventrally flattened. Rostrum relatively very long for a *Tadarida*, with prominent paired nasal swellings surrounding the nasal aperture. Anterior of braincase prominently elevated above plane of rostrum (Figure 99a). Sagittal crest absent; lambdoid crest weakly developed. Anterior palatal emargination closed, incisive foramina not visible in holotype. Basisphenoid pits deep, large, much wider than the narrow septum separating them. Dentition not robust. Upper incisors comparatively large, well separated. Anterior upper premolar ca. same height as cingulum of posterior premolar, within toothrow but lateral to cingulum of the canine; canine and posterior premolar well separated. M^3 with third ridge > half length of second. Two lower incisors on each side; not crowded; inner incisor larger and faintly bicuspid; outer incisor narrower and unicuspid. Lower canines slender; cingula not greatly enlarged and not in contact. Dental formula: $^{1123}/_{2123} = 30$.

Geographic Variation No information.

Similar Species Only one other *Tadarida* in the African region (and *T. johorensis* from Asia) has a bulbous lobe containing an interaural pocket projecting over the muzzle, and a rostrum with nasal swellings:

Tadarida tomensis. Known only from São Tomé I, in Gulf of Guinea (and therefore not profiled), but occurrence on mainland is possible. Bulbous lobe similar but not projecting quite as far forward. No folds of skin extending backwards out of the pocket and uniting on crown of head. Swellings surrounding nasal aperture smaller; nasal aperture longer (Juste & Ibáñez 1993b).

Distribution Known only from type locality in Rainforest BZ (South Central Region).



Habitat The only known specimen was collected in the vicinity of the village of Scierie (03° 10' S; 25° 49' E) near the west bank of the Congo R. It was mist-netted in a clearing within the thick, evergreen undergrowth of a partly deciduous forest, in which the secondary regrowth was well advanced. The forest had been heavily logged and only a few giant trees remained (Gallagher & Harrison 1977).

Remarks Wings long and narrow, therefore flight predictably fast and agile, but with poor manoeuvrability, as in other molossids. The extraordinary nasal swellings, which are reminiscent of those of *Rhinopoma*, are so distinctive that generic status should be considered for this bat (Harrison 1975). In most features, however, it represents a highly specialized *Chaerephon*, a swift-flying species that has developed some special modification of the nasal region for echolocation (Harrison 1975). The discovery of a ♀ is awaited with great interest as the structure of its ears may differ from that of the ♂. It is not inconceivable that the three female bats from São Tomé, described as *Tadarida tomensis* by Juste & Ibáñez (1993b), represent *T. gallagheri* but, if so, the species exhibits a marked and very unmolossid-like degree of sexual dimorphism, especially in the extent to which the interaural pouch and the nasal swellings are developed. Furthermore, the skulls and teeth of the two forms differ in other ways, for example the extent of the interorbital constriction, the sizes and shapes of the upper incisors and canines, and the size and depth of the basisphenoid pits (Juste & Ibáñez 1993b), and these differences are more likely to occur in different species than in different sexes of the same species.

Conservation IUCN Category: Data Deficient.

Known from only one location, and population reduction is predicted to occur based on decline in area of occupancy, extent of occurrence or quality of habitat (Hutson *et al.* 2001). Other collections in area have not found this species. Major threat: loss of habitat because of logging, clear-cutting and farming. However, possibly more widespread than presently believed.

Measurements

Tadarida gallagheri

FA: 38 mm

WS: n. d.

TL: 77 mm

T: 28 mm

E: 19 mm

Tr: n. d.

Tib: 13 mm

HF: 8.4 mm

WT: n. d.

GLS: 16.0 mm

GWS: 8.9 mm

C-M³: 5.8 mm

DR Congo (holotype, adult ♂, Harrison 1975, Juste & Ibáñez 1993b)

Key References Gallagher & Harrison 1977; Harrison 1975.

F. P. D. Cotterill

Tadarida lobata BIG-EARED FREE-TAILED BAT

Fr. Tadaride du Kenya; Ger. Großohr-Bulldoggfledermaus

Tadarida lobata (Thomas, 1891). Ann. Mag. Nat. Hist., ser. 6, 7: 303. Turkwell Gorge, West Pokot, Kenya.

Taxonomy Originally *Nyctinomus lobatus*. Subgenus *Tadarida*. Synonyms: none. Chromosome number: not known.

Description Medium-small microbat without noseleaf and with terminal portion of tail projecting freely from posterior margin of interfemoral membrane; large for an African molossid; ears very large, meeting to form a V-shaped valley; wings greyish; ventral flank-stripe white; two lower incisors on each side; M³ with third ridge > half length of second ridge. Sexes almost similar; ♂ larger in some skull dimensions including C–M³. Pelage short, velvety. Dorsal pelage dark brown (various shades) with conspicuous white spot between shoulder-blades in all known fully mature adults, and variable amounts of white or pale pelage behind the junction of the ears; hairs bicoloured, base white, tip dark brown. Ventral pelage brown on flanks, very much paler (sometimes white) mid-ventrally; no mid-ventral markings; ventral flank-stripe fluffy, white, contrasting with flanks. Orange-phase: not known. Head not extremely flattened. Upper lip without well-defined wrinkles; comparatively few spoon-hairs (Freeman 1981). Ears semi-translucent pale greyish-brown; relatively large (extending well beyond snout when laid forward); inner margins meeting to form a V-shaped valley. Uniquely, the bases of the inner margins meet well forward on the muzzle where they join to form a membrane extending along muzzle almost as far as the snout (Figure 115). Tragus large, roughly rectangular, not concealed by antitragus. Antitragus moderate, roughly twice as big as tragus. No interaural crest. Gular gland present, equally developed in both sexes. Wings and interfemoral membrane semi-translucent, greyish dorsally, whitish ventrally. Ventral sides of forearms and legs naked and white. Foot with raised pad on sole (plantar pad).

Skull not extremely dorsoventrally flattened. Anterior of braincase only slightly elevated above plane of rostrum (Freeman 1981). Sagittal crest weakly developed in ♂♂, inconspicuous in ♀♀; lambdoid crests distinct in both sexes. Anterior palatal emargination wide. Interdental palate broad posteriorly, narrowing towards canines but not smoothly

– there is a marked constriction at level of posterior premolars (cf. *T. fulminans*). Basisphenoid pits shallow to moderate in depth, medium-sized, their width slightly greater to slightly less than their distance apart. Upper incisors moderate in length and close together. Anterior upper premolar distinctly taller than cingulum of posterior premolar, within tooththrow; canine and posterior premolar well separated. M³ with third ridge > half length of second ridge. Two lower incisors on each side; minute. Lower canines slender; cingula not enlarged, separated by the incisors. Dental formula: $^{1123}/_{2123} = 30$.

Geographic Variation None recorded.

Similar Species Four other *Tadarida* in Africa have ears with inner margins meeting, or almost meeting, to form a V-shaped valley (Table 20, p. 488):

Tadarida aegyptiaca. Usually smaller (FA: 42–55 mm; GLS: 17.1–21.9 mm). Inner margins of ears almost meeting on forehead; ears not extending beyond snout when laid forward. No white spot between shoulder-blades.

T. fulminans. Inner margins of ears meeting on forehead; ears not extending beyond snout when laid forward. No white spot between shoulder-blades. Skull with interorbital constriction moderate; interdental palate only slightly constricted at level of posterior premolar. Lower canines with cingula nearly in contact.

T. teniotis. Three lower incisors on each side. Inner margins of ears meeting on forehead; ears not extending beyond snout when laid forward. Interdental palate not markedly constricted at level of posterior premolar. North Africa.

T. ventralis. Inner margins of ears meeting on forehead; ears not extending beyond snout when laid forward. No white spot between shoulder-blades. Skull with interorbital constriction pronounced. Anterior upper premolar minute; canine and posterior premolar nearly in contact. Lower canines well developed; cingula in contact.

Distribution Endemic to Africa. As yet, only recorded from Afromontane–Afroalpine and Somalia–Masai Bushland BZs in Kenya, and Zambezian Woodland BZ in Zimbabwe. In Kenya, recorded from four localities (including type locality) in the north-west, and Maungu Hill in the south-east. In Zimbabwe, recorded from the Sengwa Gorge, Siabuwa District in the north-west, from two localities (Borrowdale Brook & Hatfield) on outskirts of Harare (Cotterill 1996b), and recently from the Mutoko District, where specimens were mist-netted in 1997 and 1999 (Cotterill 2001c).

Habitat Woodland savannas with suitable sites for day-roosts. In Kenya, 19 individuals were taken on a large flat plain of open thorn scrub with scattered rocky hills including Maungu Hill, a high rock outcrop with deep crevices along its cliff face (A. Williams in Peterson 1974). In Zimbabwe, one was mist-netted on the wall of a dam near



Figure 115. Left ear of *Tadarida lobata* (based on Peterson & Harrison 1970).

*Tadarida lobata*

precipitous sandstone cliffs of the 10 km-long Sengwa Gorge; the vegetation is semi-arid, mainly *Combretum/Commiphora* scrub and mopane woodland (Cotterill 2001c). The Harare specimens were taken in miombo woodland within 20 km of small granite outcrops, and the Mutoko specimens from a mosaic of farmlands with miombo woodland in terrain dominated by large granitic inselbergs, many with precipitous sides. The Mutoko specimens were mist-netted over, or very near, open water.

Abundance Uncertain. *Tadarida lobata* is one of Africa's rarest and most enigmatic molossids. Despite its description in 1891, it remained known only by the holotype until single specimens were collected from Kenya and Zimbabwe in 1964 and 1969, respectively (Peterson & Harrison 1970). Two larger series of specimens were collected from these two countries subsequently. This species appears to be locally common (based on a series of 19 specimens shot at Maungu Hill, Kenya, by Peterson [1974]; and eight specimens mist-netted in the Mutoko District of Zimbabwe in 1997 and 1998 [Cotterill 2001c]).

Remarks Wings very long and very narrow, as in *T. fulminans* and *T. ventralis*. Flight fast, agile, with poor manoeuvrability. Flies fast and straight, or circles more slowly (Peterson 1974). Bats converging on the areas around two water tanks (? dams) in Kenya, uttered a distinctive single- or double-noted loud squeak, audible to humans; no more than 2–3 individuals were seen or heard at a time. Although obviously attracted to the water, none of the bats was seen to descend to drink, and none was caught in mist-nets set over the tank. Two specimens from Harare (Zimbabwe) were found dead in suburban gardens; eight others were mist-netted near open water in the Mutoko District (Zimbabwe) in association with *Sauromys petrophilus*, *T. ansorgei* and *T. fulminans*. Three of these were mist-netted within the first hour of darkness in Nov 1997 and Nov 1999. All eight were lactating ♀♀, suggesting parturitions had occurred in late Oct or early Nov.

Conservation IUCN Category: Least Concern.

New records in Zimbabwe suggest that *T. lobata* is more widespread and perhaps more abundant than estimated by Hutson *et al.* (2001).

Measurements

Tadarida lobata

FA: 58.0 (55–62) mm, n = 38

WS (d): 407 (370–425) mm, n = 38

TL: 131.8 (124–146) mm, n = 40

T: 52.2 (46–60) mm, n = 40

E: 28.2 (25–32) mm, n = 40

Tr: n. d.

Tib: 19.5 (19–21) mm, n = 13*

HF: 12.9 (12–14) mm, n = 13*

WT: 25.0 (20–33) g, n = 30

GLS: 22.8 (22.3–23.6) mm, n = 20

GWS: 13.4 (13.0–14.0) mm, n = 20

C-M³ (♀ ♀): 8.7 (8.6–8.8) mm, n = 8*

C-M³ (♂ ♂): 9.0 (8.9–9.1) mm, n = 5*

Kenya and Zimbabwe (BMNH, HZM, ROM, NMZB, Peterson 1974)

*Kenya only (Peterson 1974)

Key References Cotterill 1996b, 2001c; Peterson 1974

F. P. D. Cotterill

Tadarida major LAPPET-EARED FREE-TAILED BAT

Fr. Tadaride à oreillettes; Ger. Stirnlappen-Bulldoggfledermaus

Tadarida major (Trouessart, 1897). Cat. Mamm. Viv. Foss. 1: 146. 5th Cataract of the Nile, N Sudan.

Taxonomy Originally *Nyctinomus pumilus* var. *major*. Subgenus *Chaerephon*. Synonyms: *abae*, *emini*. Subspecies: none. Similarities between the comparatively simple lappet between the ears of *T. major*, and the highly developed, forward-projecting lobe between the ears of *T. gallagheri* from DR Congo and *T. tomensis* from São Tomé, indicate a need to re-examine the relationships between these species, and between these species and other *Tadarida*. Chromosome number: not known.

Description Small to very small microbat without noseleaf and with terminal portion of tail projecting freely from posterior margin of interfemoral membrane; medium-small for an African molossid; ears separated by a distinctive lappet over an interaural pocket, which, in adult ♂♂, contains an interaural crest; M³ with third ridge > half second ridge; wings usually dark (rarely white or pale), ventral flank-stripe white or whitish. Sexes almost similar. Pelage short (mid-dorsal hairs ca. 3 mm), covering rump but not extending

onto interfemoral membrane. Dorsal pelage dark sepia brown, yellowish-brown, greyish-brown or dull rusty-brown; sometimes slightly grizzled but no white flecks or spots; hairs unicoloured, sometimes with white at tip. Ventral pelage similar becoming paler mid-ventrally; mid-ventral markings white, highly varied in size and shape; ventral flank-stripe white or whitish. Head not extremely flattened. Upper lip with 6–7 well-defined wrinkles on each side and many spoon-hairs. Ears dark brown or blackish; just reaching snout when laid forward; inner margins meeting to form V-shaped valley but, unlike other African *Tadarida*, there is a conspicuous, flat, subtriangular or roughly semi-circular flap (= lappet or lobe) projecting backwards between the inner margins of the ears: this forms a lid over a small pocket that opens posteriorly (Figure 97). In adult ♂♂, the pocket under the lappet is lined by short (7 mm) rusty-brown hairs, which form an interaural crest. Tragus small, squarish, concealed by antitragus. Antitragus large, tall, almost rectangular but with top corners rounded. No gular gland. Wings semi-translucent, with varying degrees of dark brown or black pigmentation in most individuals – the holotype, however, has white wings (Rosevear 1965). Interfemoral membrane dark brown.

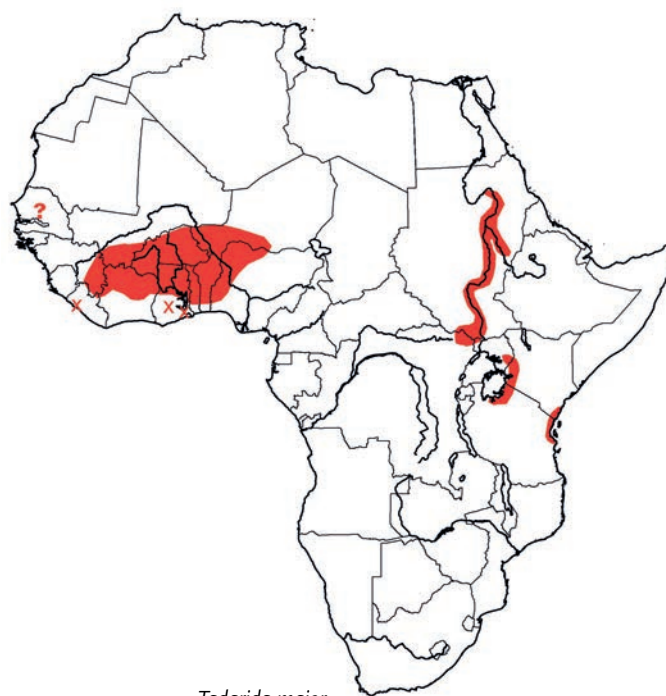
Skull not extremely dorsoventrally flattened. Anterior of braincase not noticeably elevated above plane of rostrum. Sagittal crest low or absent; lambdoid crest moderate. Anterior palatal emargination slightly open (in young adults) or closed. Basisphenoid pits shallow to moderately deep, variable in size – sometimes elongated and ca. half as wide as their distance apart, sometimes oval and as wide as their distance apart. Anterior upper premolar ca. same height as cingulum of posterior premolar or lower or higher, within toothrow; canine and posterior premolar separated. M³ with third ridge equal to, or just over, half length of second. Two lower incisors on each side; bicuspid, somewhat crowded. Lower canines with cingula not greatly enlarged and either in contact or not in contact. Dental formula: $^{1123}/_{2123} = 30$.

Geographic Variation None recorded.

Similar Species No other African *Tadarida* has a flat lappet over an interaural pocket between the ears.

Distribution Endemic to Africa. Distribution appears disjunct. Recorded from Sahel Savanna, Sudan Savanna and Guinea Savanna BZs and the Northern Rainforest–Savanna Mosaic, and from one locality in the Rainforest BZ (Western Region), from W Liberia to S Niger and Nigeria. Also occurs in these biotic zones, and also in the Sahara Arid BZ, in the valleys of the Nile R. and its tributaries in Sudan, in the Rainforest–Savanna Mosaics in NE DR Congo, Uganda, Kenya and Tanzania, and in the Coastal Forest Mosaic BZ in Kenya and Tanzania. It is not known if the apparent gap between ca. 10°E and 33°E reflects insufficient collecting or the absence of the species from this area for some unknown reason. Simmons (2005) indicates the occurrence of *T. major* in Senegal but without details. Mapped from country checklists (see order Chiroptera), other literature and museum records. Subsequently recorded widely in the south-western half of Uganda (Thorn & Kerbis Peterhans 2009): not mapped.

Habitat Recorded mainly from woodland and grassland savanna vegetation zones including undifferentiated woodland, *Isoberlinia*



Tadarida major

woodland, Sahel *Acacia* wooded grassland and deciduous bushland, and *Acacia–Commiphora* deciduous bushland and thicket, and from riverine habitats along the Nile R. and its tributaries (terminology: White 1983). Also recorded from areas of invasive grassland in the mosaic of rainforest and secondary grassland in West Africa and NE DR Congo, and from the Coastal Forest Mosaic BZ (but not within the coastal forests).

Abundance Uncertain.

Adaptations The wings are long and narrow implying flight characteristics similar to those of other species of *Tadarida*. By day, roosts in dark crannies within rocky clefts in hills, in hollows formed by aggregations of boulders, in hollow trees, lofts of houses and holes in walls of buildings (Lang & Chapin 1917b, Rosevear 1965). Roosts are sometimes revealed by their musty smell and the incessant squeaking of their occupants. Lang & Chapin (1917b) noted that disturbed bats seemed intent on returning to their habitual roosts, suggesting that roost-fidelity is high. Emergence occurs well before nightfall (Rosevear 1965). The triangular lappet between the ears is usually laid backwards and, in the ♀, covers a hairless spot. In the ♂, it can be erected to expose the interaural crest. The hairs of the crest are thicker than those of the body, and structurally resemble scent-dispersing hairs (osmetrichia) (Hickey & Fenton 1987), which suggests that they might arise from glandular tissue, but the contexts in which the crest is erected are not yet known.

Foraging and Food No information. Predictably forages by fast-hawking.

Social and Reproductive Behaviour Roosts in groups of ca. four to more than 100. Rosevear (1965) suggests size of groups depends on available accommodation. Only two of many more than 30 individuals captured together were ♂♂ (Lang & Chapin 1917b),

but the reproductive condition of these bats was not published and the social organization of this species is not known.

Reproduction and Population Structure No information.

Predators, Parasites and Diseases Ectoparasites include fleas *Lagaropsylla anciauxi*, *L. taeniolae* (Siphonaptera: Ischnopsyllidae); a tick *Carios confusus* (Acari: Argasidae); and a mite *Chelanyssus aethiopicus* (Acari: Macronyssidae) (Anciaux de Faveaux 1984, Beaucournu & Kock 1996).

Conservation IUCN Category: Least Concern.

Measurements

Tadarida major

FA: 42.4 (39–46) mm, n = 120

WS (d): 323.3 (311–335) mm, n = 11

TL: 100.1 (85–113) mm, n = 107

T: 33.8 (27–42) mm, n = 108

E: 16.8 (12–21) mm, n = 105

Tr: 4.3 (3.2–5.3) mm, n = 12

Tib: 14.2 (13–15) mm, n = 11

HF: 8.0 (7–11) mm, n = 43

WT: 15.3 (10–28) g, n = 55

GLS: 18.0 (17.0–19.3) mm, n = 45

GWS: 11.4 (10.6–12.3) mm, n = 50

C–M³: 6.9 (6.3–7.3) mm, n = 47

Throughout geographic range (BMNH, NMK, SMNS, ZFMK and literature)

Key Reference Rosevear 1965.

Meredith Happold

Tadarida midas MIDAS FREE-TAILED BAT

Fr. Tadaride midas; Ger. Midas-Bulldogfledermaus

Tadarida midas (Sundevall, 1843). Kongl. Svenska Vet.-Akad. Handl. Stockholm 1842: 207 [publ. 1843]. Jebel el Funj, White Nile River, West Bank, Blue Nile [= Bahr-el-Abiad Prov.], Sudan.

Taxonomy Originally *Dysopes midas*. Subgenus *Mops*. Synonyms: *unicolor*, *miarensis*. Subspecies: two; only one in Africa (but see Geographic Variation). Chromosome number (Somalia, Namibia, South Africa): 2n = 48; aFN = 66 (Smith *et al.* 1986; Rautenbach *et al.* 1993).

Description Medium-sized microbat without noseleaf and with terminal portion of tail projecting freely from posterior margin of interfemoral membrane; large, robustly built and particularly heavy for an African molossid (FA: 59–67 mm; WT: 38–69 g); ears joined by interaural band; M³ with third ridge absent; anterior palatal emargination closed; wings dark brown; ventral pelage greyish-brown to silvery-grey; ventral flank-stripe white or pale. Sexes almost similar. Pelage short (mid-dorsal hairs 5–6 mm), silky, sparse; nape almost naked. Dorsal pelage (grey-phase) dark brown, medium sepia brown, pale brown or pale grey with pale grey or white frosting and flecking; hairs with paler base and mostly with white or pale grey tip. Crown same colour as back. Ventral pelage greyish-brown, pinkish-brown to silvery-grey, frosted (subadults almost white); no mid-ventral markings; ventral flank-stripe white or paler than ventral pelage. Orange-phase: dorsal pelage reddish to almost orange. Pelage colouration apparently uniform within colonies, but Verschuren (1957) found two colonies roosting in the same tree, whose members had distinctly different colours. Head not extremely flattened. Upper lip with 5–6 well-defined wrinkles on each side and many spoon-hairs. Ears blackish-brown, relatively large (extending just beyond snout when laid forward); inner margins joined over muzzle by interaural band with a V-shaped fold and a forward-projecting pocket-like invagination, which protrudes ca. half-way along muzzle. Tragus small, squarish or hatchet-shaped; concealed by antitragus. Antitragus large, semi-circular. Males and ♀♀ with interaural crest of longer, brown hairs arising from the interaural

pocket. No gular gland. Wings and interfemoral membrane dark brown.

Skull not extremely dorsoventrally flattened. Anterior of braincase moderately to prominently elevated above plane of rostrum (Figure 99c). Sagittal crest moderately to well developed in both sexes; lambdoid crests well developed and forming a prominent helmet in adult ♂♂, weakly to moderately developed in ♀♀. Anterior palatal emargination closed; incisive foramina visible. Basisphenoid pits moderately deep, medium-large, their width varying from equal to their distance apart to almost twice their distance apart. Anterior upper premolar variable in size (lower to taller than the cingulum of the posterior premolar), within tooththrow. M³ with third ridge absent. Two lower incisors on each side, bicuspid, crowded or not crowded. Lower canines with cingula not greatly enlarged, sometimes well separated, sometimes almost in contact. Dental formula: $^{1123}/_{2123} = 30$.

Geographic Variation Two subspecies are recognized by Koopman (1994):

T. m. midas. Throughout African geographic range.

T. m. miarensis. Madagascar.

However, based on molecular genetics, the Madagascan and African populations are not distinct (Goodman 2011).

Similar Species Five other African *Tadarida* have the following combination of characters: ears joined by interaural band; M³ with third ridge present (but usually* < half length of second ridge) or absent; anterior palatal emargination closed; FA: >40 mm (Table 20, p. 488). *In *T. condylura*, the length of the third ridge is variable and can be up to half length of second ridge.

T. condylura. Much smaller and lighter (FA: 45–51 mm; WT: 16–39 g).

Tadarida congica. Forearm shorter (54–58 mm). Dorsal pelage less variable, dark brown to black; not frosted and without whitish flecking. Skull of similar length but less robust and often narrower (GWS: 14.8–16.3 mm).

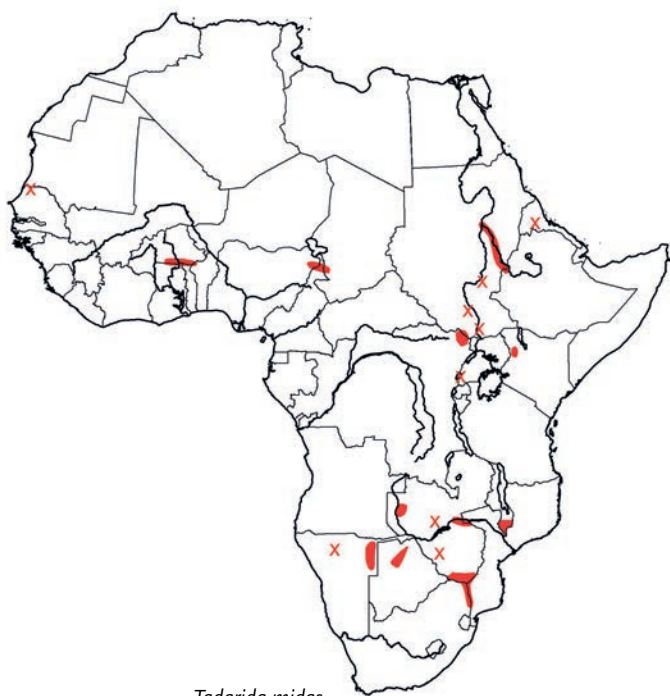
T. demonstrator. Much smaller and lighter (FA: 41–46 mm; WT: 20–24 g).

T. niveiventer. Much smaller and lighter (FA: 44–48; WT: 20–30 g).

T. trevori. Smaller (FA: 51–55 mm; GLS: 23.1–25.1 mm). M^3 with third ridge present (but < half length of second ridge).

Distribution In Africa, recorded from very scattered localities mainly in Sudan Savanna, Guinea Savanna and Zambezan Woodland BZs, with some records marginally in Sahel Savanna, Somalia–Masai Bushland and South-West Arid BZs, and the Rainforest–Savanna Mosaic in NE DR Congo. Recorded from Senegal to Eritrea and Ethiopia (but not from all countries) and southwards through S Sudan, NE DR Congo and W Kenya, and further southwards in N Namibia, SW Zambia, Botswana, Zimbabwe, S Malawi and NE South Africa. Distribution often follows major rivers and rift valleys including the Blue Nile R. in Sudan, the upper reaches of the White Nile R. and the East African Rift Valley, the Shire Valley in Malawi, and the valleys of the Zambezi R. and its tributaries, and the Limpopo R. in southern Africa. Gaps in distribution probably reflect insufficient sampling. Map based only on published records including Dorst (1959), Hayman *et al.* (1966), Smithers (1971), Vielliard (1974), Koopman (1975), Bergmans (1977b), Koopman *et al.* (1978), Ansell (1978), Cotterill (1996b) and others, and some museum records. Kingdon (1974), Smithers (1983) and Dunlop (1999) mapped vast areas (especially north of Equator) for which there appear to be no records. Extraliminally: Saudi Arabia, Madagascar.

Habitat Open woodland savannas (including Sudanian undifferentiated woodland, *Isoberlinia* woodland and drier miombo



woodland), grassland savannas and, in the Kalahari Desert, the transition zone from undifferentiated woodland to *Acacia* bushland and wooded grassland. Almost always found near major rivers and wetlands including the Sudd in Sudan, the Okavango Swamp in Botswana and the Shire R. and its marshes in S Malawi. Evidently avoids closed forests. Not dependent on rocky, hilly or mountainous terrain for its day-roosts.

Abundance Uncertain. Not very plentiful in collections (Rosevear 1965). Rarely recorded in Malawi (Happold & Happold 1997). Common, locally, in NE Botswana and Limpopo Valley (Zimbabwe) (Cotterill 1996b). Elsewhere: no information.

Adaptations Wings long and narrow. Flight fast, agile with poor manoeuvrability. Roosts by day in pitch-dark attics, in hollow cement bricks of the walls of buildings, in dimly lit expansion joints of bridges, under corrugated-iron roofs and, in DR Congo, in very long, narrow fissures penetrating deeply into the trunks or large branches of trees (particularly *Vitex* and *Parinari*) (Verschuren 1957, Smithers 1971, Smithers & Wilson 1979, Rautenbach 1982, Fenton & Rautenbach 1986). In DR Congo, not found roosting in rock-crevices that were available (Verschuren 1957). Entrances must be accessible by direct flight, and high enough to allow the bats to dive when they leave the roost. Apparently not reported to share roosts with other species of bats except in Kruger N. P., South Africa, where a roost was shared with *T. condylura* and *T. pumila*. At Faradje, NE DR Congo, only present for a short period at end of dry season: small beetles (prey) were common at that time (Lang & Chapin 1917b).

Foraging and Food Forages by fast-hawking in open spaces including over canopies, open water (rivers, swamps, flooded pans) and open plains. In DR Congo, individuals emerged at dusk and did not return to the day-roost until just before sunrise (Verschuren 1957). In Mar, ca. 12 were observed arriving about dusk to forage 15–30 m above the Dungu R.; they flew at high speed, and dodged and dived after small hard-shelled beetles, which were then common; stomachs of some of these bats contained remains of these beetles that had been masticated in flight (Lang & Chapin 1917b). In Botswana, observed flying 30–40 m above ground, and swooping down to a waterhole to take insects (Smithers 1971, 1983). In Kruger N. P., South Africa, radio-tracked individuals seemed to move at least 10 km from their day-roost; of 15 foraging flights observed, five (in immediate vicinity of roost) lasted <10 min, ten lasted 51.7 ± 41.1 min; there was no evidence that foraging behaviour changed according to moonlight (Fenton & Rautenbach 1986). The stomach of one individual from Botswana contained fragments of beetles (Archer 1977).

Echolocation Search-phase call-shape (South Africa): shallow FM. Start frequency 30 kHz; end-frequency not known (Aldridge & Rautenbach 1987).

Social and Reproductive Behaviour In DR Congo, has been observed foraging in groups of ca. 12 individuals (Lang & Chapin 1917b), and groups roosting together emerge together at dusk and also return within a minute of each other very shortly before sunrise (Verschuren 1957). Roosts in medium-sized to very large colonies; in DR Congo, colonies of 20–30 were reported by Verschuren (1957);

in southern Africa, colonies of 'dozens' and 'several hundreds' were reported by Smithers (1971) and Smithers & Wilson (1979). In DR Congo, the ratio of ♂♂ to ♀♀ in colonies taken from roosts was 1 : 3.6; in contrast, samples taken as bats emerged from a roost in Botswana contained ca. equal numbers of both sexes (Smithers 1971). In roosts, these bats are restless and utter squeaks (audible to humans) at all hours of the day. Verschuren (1957) noted that some trees housed more than one colony, each occupying a separate site and using a separate entrance.

Reproduction and Population Structure Litter-size (Malawi, Botswana): one ($n = 16$). Reproductive chronology not known. Near the Equator in S Uganda, 5 of 5 ♀♀ were in early pregnancy in Jan, 1 of 1 was lactating in Mar, 1 of 1 was post-lactating in Jun, and 1 of 1 had recently given birth in Oct: these data suggest that births occur during two seasons in this locality (Kingdon 1974), but this needs confirmation. At 20° 00' S (Okavango Swamp, Botswana), samples of 3, 3, 14 and 5 ♀♀, taken from an attic in Mar, Apr, Jun and Sep, respectively, contained only non-pregnant ♀♀; in Dec, 1 of 16 was pregnant, in Jan, 6 of 13 were pregnant and in Feb, 7 of 18 were pregnant (all others 'non-gravid') (Smithers & Wilson 1971). Additional records from Okavango Swamp, W Zambia and S Zimbabwe include four early pregnancies in Oct, four late pregnancies in mid-Nov, two ♀♀ lactating (and four non-volant juveniles) in Dec, and one lactating ♀ and one naked but volant juvenile in Apr. These data suggest that, in Botswana and nearby, births only occur in Dec–Mar, but whether the chronology is extended seasonal monoestry, or polyoestry, remains to be determined.

Predators, Parasites and Diseases Ectoparasites include fleas *Lagaropsylla hoogstraali*, *L. idae* (Siphonaptera: Ischnopsyllidae) and

mites *Chelanyssus aethiopicus* (Acari: Macronyssidae), *Ewingana nanula* (Acari: Myobiidae) and *Nycteriglyphus tadaridae* (Acari: Rosensteiniidae) (Anciaux de Faveaux 1984, Segerman & Braack 1988).

Conservation IUCN Category: Least Concern.

Probably threatened by destruction of woodland in parts of its geographic range.

Measurements

Tadarida midas

FA: 61.3 (59–67) mm, $n = 164$

WS: n. d.

TL: 141.4 (126–150) mm, $n = 168$

T: 46.0 (37–56) mm, $n = 170$

E: 26.5 (23–32) mm, $n = 167$

Tr: n. d.

Tib: 22.2 (20–24) mm, $n = 23$

HF: 13.0 (11–15) mm, $n = 38$

WT: 51.4 (38–69) g, $n = 84$

GLS: 27.4 (25.8–29.5) mm, $n = 71$

GWS: 16.8 (15.2–18.1) mm, $n = 75$

C–M³: 10.2 (9.2–10.9) mm, $n = 76$

West Africa, Botswana, DR Congo, Malawi, Zimbabwe (NMZB, USNM, Rosevear 1965, Smithers 1971, Smithers & Wilson 1979, Happold *et al.* 1987)

Key References Dunlop 1999; Fenton & Rautenbach 1986; Rosevear 1965; Smithers 1983; Verschuren 1957.

F. P. D. Cotterill & Meredith Happold

Tadarida nanula DWARF FREE-TAILED BAT

Fr. Tadaride naine d'Afrique; Ger. Zwerg-Bulldoggfledermaus

Tadarida nanula (J. A. Allen, 1917). Bull. Am. Mus. Nat. Hist. 37: 477. Niangara, Orientale, DR Congo.

Taxonomy Originally *Mops (Allomops) nanulus*. Subgenus *Xiphonycteris*. According to Koopman (1989), the distinction between *nanulus* and *spurrelli* is far from certain and depends largely on the greater degree of sexual dimorphism in dental characters in adult *T. spurrelli* compared with that in *T. nanula*. In contrast, El-Rayah (1980, 1981) demonstrated that *T. nanula* is distinct. Synonym: *calabarensis*. Subspecies: none. Chromosome number (Cameroon): $2n = 48$; $aFN = 54$; one pair large metacentric, two pairs small metacentric, one pair medium subtelocentric and 19 pairs medium-small acrocentric autosomes (Smith *et al.* 1986).

Description Very small microbat without noseleaf and with terminal portion of tail projecting freely from posterior margin of interfemoral membrane; one of the two smallest African *Tadarida* (FA: 27–31 mm); ears joined by interaural band; M³ with third ridge absent; anterior palatal emargination narrow; wings semi-translucent, whitish or brownish; ventral pelage moderately pale; no ventral flank-stripe in contrasting colour; canines without greatly enlarged cingula. Females not easily distinguished from female *T. spurrelli*. Sexes almost similar.

Pelage short (mid-dorsal hairs ca. 2 mm); dorsal pelage extending over most of rump but not quite reaching interfemoral membrane. Dorsal pelage varying from bright orange-brown to blackish-brown (Rosevear 1965), no grizzling, no spots; hairs cream with orange-brown to blackish-brown at tip. Rump with two tufts of long hairs (as in several other *Tadarida*). Ventral pelage with flanks brown, belly pale reddish-brown, yellowish-brown or brownish-grey; mid-ventral markings white, pale yellowish-brown or pale grey, variable in shape, not sharply delineated but merging with flank colour, sometimes covering most of ventral surface, sometimes absent; no ventral flank-stripe in contrasting colour. Head not extremely flattened. Upper lip with 5–6 well-defined wrinkles on each side and many spoon-hairs. Ears blackish becoming paler near base, reaching just over half-way along muzzle when laid forward; inner margins joined by interaural band with forward and downward-pointing V-shaped fold in middle. Tragus very small, pointed, concealed by antitragus. Antitragus large; roughly trapezoid. Interaural band supporting dense, dark brown hairs that are slightly coarser than body hairs and are longer in ♂♂ than in ♀♀. Gular gland: no information. Wings semi-translucent,

sometimes with light to moderate white pigmentation, sometimes pale brown, sometimes blackish-brown with varying amounts of pigmentation. Interfemoral membrane brown.

Skull not extremely dorsoventrally flattened. Anterior of braincase only very slightly elevated above plane of rostrum (Figure 99g). Sagittal crest low or absent; lambdoid crest low to well developed and forming a helmet, especially (but not solely) in old ♂♂ (Rosevear 1965). Anterior palatal emargination narrow, bulb-shaped (narrowest between incisors). Basisphenoid pits shallow, small, their width less to much less than their distance apart. Upper incisors (Figure 104a) are procumbent (angled slightly forward). They occupy the most anterior edge of the premaxillae and therefore are not in same plane as the canines (cf. *T. spurrelli*) (El-Rayah 1980). Upper canines with cingula not enlarged: when viewed laterally, the upper incisors are visible – not hidden by the canine cingula (cf. ♂ *T. spurrelli*). Anterior upper premolar distinctly taller than cingulum of posterior premolar, within toothrow or somewhat displaced lingually. M³ with third ridge absent. Two minute lower incisors on each side. Lower canines long and robust; cingula not greatly enlarged and not in contact. Anterior lower premolar larger than posterior premolar in ♂♂; smaller than posterior premolar in ♀♀ (Allen 1917a). Dental formula: $^{1123}/_{2123} = 30$.

Geographic Variation None recorded. Possibly wing colour varies geographically (whitish in West Africa, brown to dark brown in DR Congo and East Africa) but this needs confirmation.

Similar Species Five other African *Tadarida* have the following combination of characters: ears joined by interaural band; M³ with third ridge absent or present but < half length of second; palatal emargination narrow; FA almost always less than 40 mm (Table 20, p. 488):

Tadarida brachyptera. Forearm longer (35–38 mm). M³ with third ridge present but < half length of second. Upper incisors not procumbent.

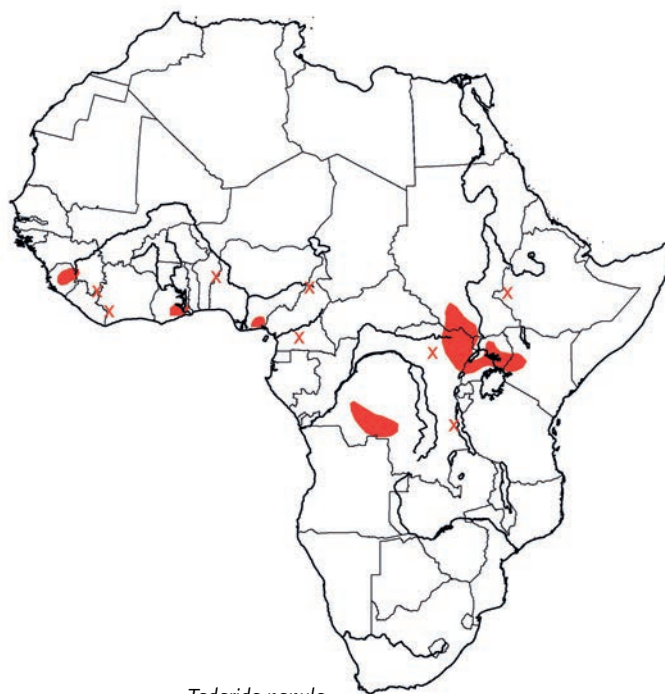
T. petersoni. Forearm longer (34–41 mm). M³ with third ridge present but < half length of second. Basisphenoid pits moderate in depth, larger and closer together.

T. spurrelli. Wings dark brown or blackish. Ventral pelage white merging into brown on flanks. Upper canines with enlarged cingula: when viewed laterally the upper incisors are hidden by the canine cingula in ♂♂, but partly visible in ♀♀. In adult ♂♂ and some adult ♀♀, cingula of lower canines greatly enlarged and in contact, forming an arch over the minute incisors. Usually one lower incisor on each side.

T. thersites. Forearm longer (35–42 mm). Ventral pelage very dark. M³ with third ridge present but < half length of second ridge.

See also *T. bakarii* in profile of *T. brachyptera*.

Distribution Endemic to Africa. Recorded disjunctly from Rainforest BZ and Rainforest–Savanna Mosaics from Sierra Leone to E DR Congo and Uganda, and in S DR Congo (but not recorded from all countries), and from the Afromontane–Afroalpine BZ in Ethiopia and W Kenya. Erroneously recorded from Gambia (J. Fahr in Simmons 2005). Mapped from country checklists (see order Chiroptera), other literature and museum records.



Tadarida nanula

Habitat Recorded mainly from various habitats near edges of lowland rainforest (Rosevear 1965). Often recorded near large rivers (perhaps because, in the past, they could be captured over water more easily than in other places). Occasionally recorded in woodland savannas (often near rivers). For example, recorded in *Combretum–Terminalia* woodland near riverine forest on Baro R., at 515 m in Ethiopia (Largen *et al.* 1974), and in light riverine forest by Wei Wei R. in 'dry grassy *Acacia* country' in Kenya (Start 1969).

Abundance Uncertain.

Remarks Has been found roosting by day in hollow trees, in thatch and inside buildings, but not under corrugated iron roofs (Lang & Chapin 1917b, T. S. Jones in Rosevear 1965, Grubb *et al.* 1998). One was found 'hanging down' in a clump of bamboo (T. S. Jones in Rosevear 1965) but this is unlikely to be normal roosting behaviour. Has been found singly, but more often in groups, usually of uncertain size and composition. One group included three adult ♂♂ and three ♀♀ and others (Lang & Chapin 1917b). A group of nine taken from a crack in a tree were all ♀♀ with very large embryos or neonates, suggesting that *T. nanula* might establish maternity colonies (T. S. Jones in Rosevear 1965). At 1–2°N in Kenya, 5 of 6 ♀♀ were heavily pregnant and one was lactating and also pregnant (with one embryo) in late Aug (Start 1969 and BMNH). In Uganda, this species appears to have two birth seasons a year, with births in late Mar–Apr, and Sep (Kingdon 1974), but no evidence is given and this suggestion needs confirmation.

Predators, Parasites and Diseases Ectoparasites include fleas *Lagaropsylla obliqua*, *L. convexa* (Siphonaptera: Ischnopsyllidae) and a mite *Ewingana nanula* (Acari: Myobiidae) (Anciaux de Faveaux 1984).

Conservation IUCN Category: Least Concern.

Threatened, however, by loss of habitat in the western part of the geographic range.

Measurements*Tadarida nanula*

FA: 29.6 (27–31) mm, n = 62

WS (d): 230.0 (220–241) mm, n = 33

TL: 81.6 (75–88) mm, n = 52

T: 23.9 (19–29) mm, n = 52

E: 13.3 (11–18) mm, n = 19

Tr: n. d.

Tib: 9.6 (8–12) mm, n = 15

HF: 7.5 (6–10) mm, n = 12

WT: 8.2 (6–11) g, n = 46

GLS: 16.2 (15.0–17.5) mm, n = 62

GWS: 10.3 (9.6–11) mm, n = 61

C–M³: 6.0 (5.6–6.2) mm, n = 55Throughout geographic range (ROM, Allen 1917a, El-Rayah 1981, Start 1969, Van Cakenberghe *et al.* 1999)**Key References** Allen 1917a; El-Rayah 1980; Lang & Chapin 1917b.**Meredith Happold*****Tadarida niangarae* NIANGARA FREE-TAILED BAT**

Fr. Tadaride de Niangara; Ger. Niangara-Bulldoggfledermaus

Tadarida niangarae (J. A. Allen, 1917). Bull. Am. Mus. Nat. Hist. 37: 468. Niangara, DR Congo.

Taxonomy Originally *Mops niangarae*. Placed in subgenus *Mops*. Synonyms: none. The specific status of *T. niangarae* is uncertain. Considered to be a subspecies of *T. congica* by Hayman & Hill (1971). Included in *Tadarida trevori* by Peterson (1972) (for reasons, see Description) and Koopman (1994). Tentatively considered to be a distinct species (pending examination of further specimens and a more formal revision of the *trevori/congica* complex) by Freeman (1981) and Simmons (2005). Chromosome number: not known.

Description Small microbat without noseleaf and with terminal portion of tail projecting freely from posterior margin of interfemoral membrane; medium-sized for an African molossid; ears originally described as well separated (but see below); M³ with third ridge present but < half second ridge; anterior palatal emargination closed; wings dark; probably no ventral flank-stripe in contrasting colour. Known only from the holotype (♂, skin and skull). Pelage short. Dorsal pelage uniform rusty-brown, no grizzling, no spots; hairs much paler at base. Ventral pelage yellowish-brown, paler and more yellowish on chest; mid-ventral markings and ventral flank-stripe in contrasting colour are not mentioned in type description and therefore are probably absent. Head not extremely flattened. Upper lip with more than seven wrinkles on each side and many spoon-hairs. Ears dark brown, described as well separated by Allen (1917a), but Peterson (1972) concluded that the apparent lack of an interaural band between the inner margins is an artefact of preparation. He concluded that there is an interaural band and that it is a fold of skin lacking cartilaginous support (as in *T. trevori*). The holotype appears to have a broad, low interaural crest of lengthened hairs, similar in colour and texture to those of dorsal pelage, but the shape has possibly been distorted in preparation. Tragus minute. Antitragus small, low. Gular gland: no information. Wings and interfemoral membrane dark brown.

Skull not extremely dorsoventrally flattened. Anterior of braincase slightly elevated above plane of rostrum. Sagittal crest moderate; lambdoid crest very well developed and forming a helmet (Peterson 1972). Anterior palatal emargination closed; incisive foramina visible. Basisphenoid pits deep, large, their width ca. twice their distance apart. Anterior upper premolar almost as high as cingulum of posterior premolar, within toothrow; canine and posterior premolar well

separated. M³ with third ridge present but < half length of second ridge. Two minute lower incisors on each side. Lower canines not specially modified, cingula not enlarged. Dental formula: $^{1123}/_{2123} = 30$.

Geographic Variation No information.

Similar Species This species of *Tadarida* would be unique if it has well-separated ears (i.e. inner margins not joined by interaural band) together with M³ with third ridge < half second, and anterior palatal emargination closed. However, if the inner margins of the ears are joined by a fold of skin lacking cartilaginous support, it is very similar to, and possibly conspecific with, *T. trevori*.

Distribution Known only from Niangara, DR Congo, which is in the Northern Rainforest–Savanna Mosaic very close to the Rainforest BZ.

*Tadarida niangarae*

Habitat Mosaic of lowland rainforest and secondary grassland.

Abundance No information.

Remarks Lang & Chapin (1917b) reported: 'It is one of many species that live in hollow trees and probably will be found to occur elsewhere in the more open country of the northern Uele.'

Conservation IUCN Category: Data Deficient.

Only one specimen known, but it is not certain that it represents a valid species.

Measurements

Tadarida niangarae

FA (from skin): ca. 52 mm

WS (d): 426 mm

TL: 125 mm

Tr: 34 mm

E: 22 mm

Tr: n. d.

Tib: n. d.

HF: n. d.

GLS: 23.2 mm

GWS: 14.4 mm

C-M³: 8.2 mm

DR Congo (holotype; AMNH, Allen 1917a, Lang & Chapin 1917b)

Key References Allen 1917a; Freeman 1981; Peterson 1972.

Meredith Happold

Tadarida nigeriae NIGERIAN FREE-TAILED BAT

Fr. Tadaride du Nigeria; Ger. Nigeria-Bulldoggfledermaus

Tadarida nigeriae (Thomas, 1913). Ann. Mag. Nat. Hist., ser. 8, 11: 319. Zaria Province, Northern Region, Nigeria.

Taxonomy Originally *Chaerephon nigeriae*. Subgenus *Chaerephon*. Synonym: *spillmani* (described as a distinct species, but considered conspecific by Koopman [1965, 1975], Simmons [2005] and others). Subspecies: two. Chromosome number (Zimbabwe, Namibia): 2n = 48; aFN = 68; and described as karyotypically similar to *Sauromys petrophilus* (Rautenbach *et al.* 1993).

Description Small microbat without noseleaf and with terminal portion of tail projecting freely from posterior margin of interfemoral membrane; medium-sized for an African molossid (FA: 41–51 mm); ears joined by interaural band; M³ with third ridge > half length of second; wings pale or dark; ventral flank-stripe white in marked contrast to ventral pelage; ♂♂ with short unicoloured interaural crest. Sexes similar. Pelage short (mid-dorsal hairs ca. 4 mm), dense; sparse between shoulder-blades. Dorsal pelage blackish-brown; no spots, rarely flecking; hairs unicoloured. Ventral pelage blackish-brown; no mid-ventral markings; ventral flank-stripe white, very conspicuous. Head not extremely flattened. Upper lip with 5–7 (*T. n. spillmani*) or 7–8 (*T. n. nigeriae*) well-defined wrinkles on each side and many spoon-hairs. Ears blackish, relatively medium-sized (almost reach snout when laid forward); inner margins joined by interaural band with backward-opening pocket-like invagination in middle. Tragus small, rectangular with top side straight or markedly concave, almost fully concealed by antitragus. Antitragus much larger than tragus, roughly trapezoid but top corners sometimes rounded. In adult ♂♂, the pocket in the interaural band contains an interaural crest of dark brown or dark rusty-brown hairs ca. 6 mm long. No gular gland. In *T. n. nigeriae*, wing-membranes blackish-brown dorsally, whitish ventrally especially close to body; interfemoral membrane blackish-brown. In *T. n. spillmani*, wings whitish and semi-translucent dorsally and ventrally, or blackish (Ansell 1960b); interfemoral membrane dark brown dorsally, paler ventrally. Skin on forearm dark brown dorsally extending narrowly onto wing-membrane as faint dark stripe. Further information in Willis *et al.* (2002).

Skull low but not extremely dorsoventrally flattened. Anterior of braincase not elevated above plane of rostrum. Sagittal crest very weakly developed; lambdoid crest well developed. Anterior palatal emargination closed. Basisphenoid pits shallow to moderate in depth, small to medium-sized, their width equal to, or less than, their distance apart (n = 9; BMNH). Anterior upper premolar usually rising higher than cingulum of posterior premolar, within tooth-row or somewhat displaced; canine and posterior premolar well separated. M³ with third ridge > half length of second. Two lower incisors on each side, bicuspid, sometimes crowded. Lower canines with cingula not greatly enlarged, not in contact but sometimes nearly so. Dental formula: $^{1123}/_{2123} = 30$.

Geographic Variation Two subspecies (similar in size) are recognized (Koopman 1965, 1994, Hayman & Hill 1971):

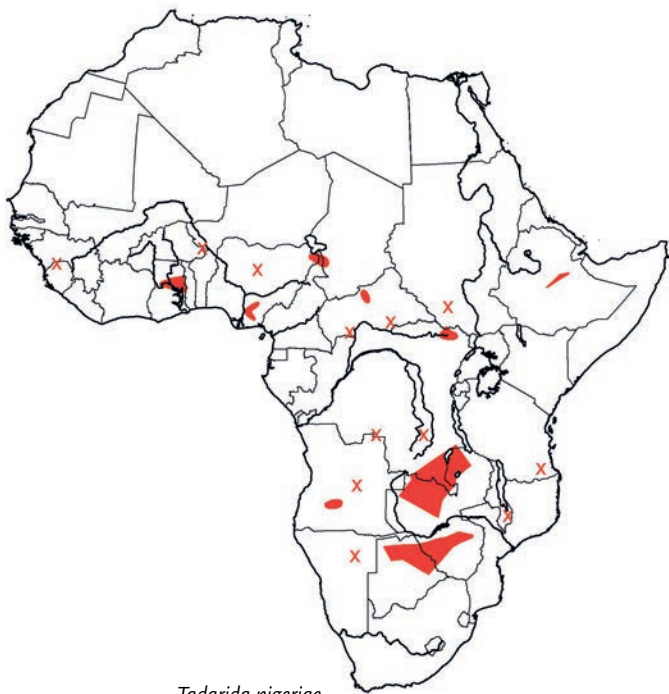
T. n. nigeriae: Sierra Leone to Ethiopia (extraliminally SW Arabia).

Wings dark brown.

T. n. spillmani: Angola to Tanzania and southwards to N Namibia and N Botswana. Wings whitish or blackish.

Similar Species None. No other African *Tadarida* has the following combination of characters: ears joined by interaural band; M³ with third ridge > half length of second; ventral flank-stripe white and in marked contrast with dark brown ventral pelage; no tail-glands; FA: 44–51 mm.

Distribution In Africa, *Tadarida n. nigeriae* is recorded from scattered localities in Sudan Savanna and Guinea Savanna BZs, Northern Rainforest–Savanna Mosaic and marginally in Rainforest BZ, from Sierra Leone to NE DR Congo and S Sudan (but not all countries), and in Somalia–Masai Bushland BZ and marginally in Afromontane–Afroalpine BZ, of the Ethiopian Rift Valley and Ethiopian Highlands. Extraliminally: Saudi Arabia (Harrison & Bates 1991). *Tadarida n. spillmani* is endemic to Africa. Recorded mainly

*Tadarida nigeriae*

from Zambezian Woodland BZ and marginally from Southern Rainforest–Savanna Mosaic and Kalahari Desert. Recorded from Angola, S DR Congo, Zambia, S Tanzania, N Namibia, N Botswana, Zimbabwe and S Malawi. Mapped from country checklists (see order Chiroptera), other literature and museum records.

Habitat *Tadarida n. nigeriae* is mostly recorded from savanna woodlands and from areas where lowland rainforest has been partly or completely degraded to Guinea woodland (Rosevear 1965). *Tadarida n. spillmani* has been recorded in *Acacia*, mopane and miombo woodlands, often in association with permanent water.

Abundance *Tadarida n. nigeriae*: Appears comparatively rare: poorly represented in collections. However, it was the species most commonly found roosting in bungalows in Umuahia (Nigeria) (Cozens & Marchant 1952).

Tadarida n. spillmani: Locally common in NE Botswana, Namibia and Zambia, but remains poorly represented in collections.

Adaptations Aspect ratio very high; wing-loading high ($n = 1$, Malawi). Flight predicted to be fast and agile with poor manoeuvrability. In West Africa, day-roosts include roofs (permanent and thatched) and eaves (Rosevear 1965). In southern Africa, it has been found by day under exfoliating bark of dead trees (including trees standing in water); the moderately flattened skull of this species, and other *Tadarida*, facilitates roosting in such places. Also reported roosting in a small cave (Smithers 1971). In Botswana, one roost under bark (see below) was shared with five adult *Pipistrellus* sp.

Foraging and Food Based on wing morphology, predicted to forage by fast-hawking and to feed on flying insects. Has been mist-netted over muddy pools and on the bank of a farm dam in Malawi (Happold & Happold 1997); not known if coming down to drink or to forage.

Echolocation Search-phase call-shape (Zimbabwe): shallow FM. Start-frequency 26 kHz; end-frequency 16 kHz; peak-frequency 17 kHz; intensity high; maximum duration 10 ms (three bats, flying free; Fenton & Bell 1981).

Social and Reproductive Behaviour *Tadarida n. nigeriae* roosts in colonies (no details available) (Rosevear 1965). Bats roosting in the roof of a house in Nigeria started rustling and squeaking ca. half an hour before dark, and ca. 10 min later most left the roost together; later they would return and after dark some would hunt near the house; some kept up a round-the-eaves circuit (Cozens & Marchant 1952). *Tadarida n. spillmani* also roosts in groups or colonies; in Zimbabwe, a group of six emerged from a roost under bark (Smithers 1983); in Botswana, a colony roosting under bark included more than 25 adults (of which at least 13 were lactating ♀♀) and neonates and furred juveniles (FA: 29–35 mm) (P. J. Wright & M. Jarvis pers. comm.). In Zambia, sometimes found in large colonies (by definition 30–100 individuals) (Ansell 1960b).

Reproduction and Population Structure Litter-size (Namibia): one ($n = 8$) (ZFMK). Reproductive chronology: not known. In southern Africa, pregnant ♀♀ have been recorded in late Oct (Zimbabwe), lactating ♀♀ in mid-Nov (W Zambia) and in mid-Dec (Okavango Swamp, Botswana) and 8 of 10 ♀♀ pregnant (near term) in late Jan (NW Namibia) (F. P. D. Cotterill unpubl., ZFMK). The data suggest births in wet season, but data for other months are not available.

Predators, Parasites and Diseases Ectoparasites include fleas *Lagaropsylla lipsi*, *L. idae* (Siphonaptera: Siphonopsyllidae) and mites *Spinturnix walkeri* (Acari: Spinturnicidae), *Chelanyssus longisetosus*, *Steatonyssus crassisetosus* (Acari: Macronyssidae) (Anciaux de Faveaux 1984).

Conservation IUCN Category: Least Concern.

In West Africa, the ability of this species to roost in buildings and to exploit cleared rainforest suggests that it may be comparatively resistant to anthropogenic impacts (Willis *et al.* 2002). In southern Africa, however, populations of this tree-roosting microbat are likely to be threatened by destruction of woodland in parts of its geographic range.

Measurements

Tadarida nigeriae

FA: 47.2 (41–51) mm, $n = 77$

WS: n. d.

TL: 111.0 (99–130) mm, $n = 41$

T: 39.4 (31–52) mm, $n = 52$

E: 19.6 (15–23) mm, $n = 51$

Tr: n. d.

Tib: 16.4 (14–19) mm, $n = 11$

HF: 11.1 (9–13) mm, $n = 21$

WT: 18.3 (10–26) g, $n = 64$

GLS: 19.6 (18.6–20.5) mm, $n = 49$

GWS: 12.3 (11.7–13.2) mm, $n = 53$

C–M³: 7.4 (7.0–7.8) mm, $n = 54$

Nigeria, Central African Republic, Ethiopia, Tanzania, Namibia,

Botswana, Zimbabwe (BMNH, NMZB, ROM, ZFMK, Rosevear 1965, Smithers 1971)

Key Reference Willis *et al.* 2002.

F. P. D. Cotterill & Meredith Happold

***Tadarida niveiventer* WHITE-BELLIED FREE-TAILED BAT**

Fr. Tadaride à ventre blanc; Ger. Weißbauch-Bulldoggfledermaus

Tadarida niveiventer (Cabrera and Ruxton, 1926). Ann. Mag. Nat. Hist., ser. 9, 17: 594. Luluabourg, Kasai Occidental Province, DR Congo.

Taxonomy Originally *Mops angolensis niveiventer*. Subgenus *Mops*. Synonym: *chitauensis*. Subspecies: none. Long considered a synonym or subspecies of *T. condylura*, until its specific status was confirmed by Koopman (1966) and Ansell (1967). Koopman (1975, 1993) suggests that *niveiventer* is 'probably a subspecies of *demonstrator*'. Considered to be a distinct species by Van Cakenberghe *et al.* (1999) and Simmons (2005). Chromosome number: not known.

Description Small microbat without noseleaf and with terminal portion of tail projecting freely from posterior margin of interfemoral membrane; medium-sized for an African molossid (FA: 44–48 mm); ears joined by interaural band; M³ with third ridge absent; anterior palatal emargination closed; wings pale; ventral pelage predominantly pure white or cream; no ventral flank-stripe in contrasting colour; crown darker than back; first phalanx of third and fourth finger intermediate in length (cf. only *T. demonstrator*, *T. condylura*). Not easily distinguished from *T. demonstrator*. Sexual dimorphism: uncertain. Pelage short (mid-dorsal hairs ca. 4 mm), glossy. Dorsal pelage dark brown or paler chocolate brown, often frosted (especially in dark brown individuals), sometimes flecked (especially in chocolate brown individuals); hairs dark brown or chocolate brown, sometimes with whitish tip. Crown and neck black or very dark brown – distinctly darker than back (as in *T. demonstrator*). Ventral pelage usually cream to pure white; no mid-ventral markings; ventral flank-stripe cream or white. Neonates with pale skin (cf. *T. condylura* at least in south-central Africa where sympatric with *T. niveiventer*). Head not extremely flattened. Upper lip with 5–6 well-defined wrinkles and many spoon-hairs. Ears brown (paler than dorsal pelage); relatively short (reaching ca. half-way along muzzle when laid forward); inner margins joined by interaural band with V-shaped fold in middle (Baeten *et al.* 1984). Tragus small, hatchet-shaped with bend in posterior margin and tip pointed; concealed by antitragus. Antitragus large, nearly semi-circular with upper margin pale and thick. Posterior side of interaural band supporting inconspicuous crest of slightly longer (3.5–4 mm) and slightly coarser black hairs. No gular gland. Wings semi-translucent, blackish-brown to pale grey (depending on amount of blackish-brown pigmentation); interfemoral membrane dark brown dorsally, whitish ventrally. First phalanx of third finger 19.4 (19–21) mm, n = 17; first phalanx of fourth finger: 15.4 (15–17) mm, n = 10 (cf. *T. demonstrator*, *T. condylura*).

Skull not extremely dorsoventrally flattened. Anterior of braincase not noticeably elevated above plane of rostrum. Sagittal crest only moderately developed (both anteriorly and posteriorly);

lambdoid crest weakly to well developed, forming a low to moderate helmet in ♀♀ and a moderate to well-developed helmet in ♂♂. Anterior palatal emargination closed; incisive foramina visible (Figure 100a). Basisphenoid pits moderate in depth, medium to large, their width ranging from equal to almost twice their distance apart. Anterior upper premolar distinctly shorter than cingulum of posterior premolar, within toothrow or slightly displaced labially; canine and posterior premolar separated or in contact. M³ with third ridge absent. Two lower incisors on each side, bicuspid, crowded. Lower canines with cingula not greatly enlarged, sometimes almost in contact. Dental formula: $^{1123}/_{2123} = 30$.

Geographic Variation None recorded.

Similar Species Five other African *Tadarida* have the following combination of characters: ears joined by interaural band, M³ with third ridge present (but usually* < half length of second ridge) or absent; anterior palatal emargination closed; FA: > 40 mm. *In *T. condylura*, the length of the third ridge is variable and can be up to half length of second ridge.

Tadarida condylura. Ventral pelage with little or no white areas; ventral flank-stripe white. Crown and neck same colour as back. First phalanx of fourth finger almost always longer (18.3 [17–20] mm). Neonates dark. Skull with sagittal crest usually well developed. Basisphenoid pits shallow, small. M³ with third ridge present (but usually < half length of second ridge).

T. congica. Larger and heavier (FA: 54–58 mm; WT: 42–64 g). Ventral pelage not mainly white or cream.

T. demonstrator. First phalanx of third finger almost always longer (17.7 [16–19] mm). Males with pair of glands between penis and anus. Wings medium to dark grey. Basisphenoid pits deep.

T. midas. Much larger and heavier (FA: 59–67 mm; WT: 38–69 g).

T. trevori. Forearm longer (51–55 mm). Ventral pelage pale but not mostly white or cream. Skull with basisphenoid pits deep and large.

Distribution Endemic to Africa. Only known from Southern Rainforest–Savanna Mosaic and Zambeian Woodland BZ. Recorded from Rwanda, Burundi, DR Congo, SW Tanzania, C Angola, Zambia and W Mozambique (Harrison 1968, Smithers & Lobão Tello 1976, Ansell 1978, Baeten *et al.* 1984, Van Cakenberghe *et al.* 1999). Gaps in the distribution, especially in E Angola, might reflect insufficient collecting.

*Tadarida niveiventer*

Habitat Poorly known. In south-central Africa, found in wetter woodland savannas, particularly miombo woodland. The presence of suitable day-roosts in tall miombo woodland may be an important determinant of their occurrence.

Abundance Uncertain. Less commonly mist-netted than *T. condylura* at Kikwit, DR Congo (Van Cakenberghe *et al.* 1999), at Nyamata and Rukira in Rwanda (Baeten *et al.* 1984) and in W Zambia (Cotterill 2002b).

Remarks In the Ikkelenge Pedicle, NW Zambia, a colony of seven adults (one ♂ and six ♀♀) roosted high up in a hollow tree *Brachystegia* sp. (Cotterill 2002b). Colonies have also been found in attics and in cracks in walls of buildings (Ansell 1967). Litter-size

(Zambia): one (n = 7). Reproductive chronology not known. In W Zambia, pregnant ♀♀ (near full-term) were recorded in Oct 1990 and Nov 1998; 4 of 6 ♀♀ had well-developed fetuses in Jan 1952, and lactating ♀♀ and/or juveniles have been collected in Jan, Feb and Mar (Ansell 1967, Cotterill 2000, 2002b). Although this limited evidence suggests births from ca. Nov to Feb (hot-wet season) as in *T. condylura* in Malawi (Happold & Happold 1989b), it is not known if the ♀♀ are monoestrous or polyoestrous, and there are no data for other months. Ectoparasites include mites *Spinturnix semilunaris* (Acari: Spinturnicidae) and *Chelanyssus aethiopicus* (Acari: Macronyssidae) (Anciaux de Faveaux 1984).

Conservation IUCN Category: Least Concern.

Measurements

Tadarida niveiventer

FA: 45.7 (44–48) mm, n = 14

WS: n. d.

TL: 110 (104–116) mm, n = 4

T: 34.6 (32–37) mm, n = 4

E: 18.9 (18–20) mm, n = 8

Tr: n. d.

Tib: 14–15 mm, n = 3

HF: 9–11 mm, n = 3

WT: 25.1 (20–30) g, n = 9

GLS: 21.6 (20.2–23.6) mm, n = 63

GWS: 13.3 (12.4–14.5) mm, n = 69

C–M³: 7.7 (7.2–8.6) mm, n = 71

Throughout geographic range (FA and craniodental measurements) or Zimbabwe only (BMNH, HZM, NMZB, RMCA, ROM, Van Cakenberghe *et al.* 1999)

Key References Ansell 1967; Baeten *et al.* 1984; Cotterill 2000, 2002b; Van Cakenberghe *et al.* 1999.

F. P. D. Cotterill

Tadarida petersoni PETERSON'S FREE-TAILED BAT

Fr. Tadaride de Peterson; Ger. Petersons Bulldoggfledermaus

Tadarida petersoni El-Rayah, 1981. R. Ontario Mus. Life Sci. Occas. Pap. 36: 3. 15 km S Kumba (04° 39' N, 09° 26' E), Cameroon.

Taxonomy Subgenus *Xiphonycteris*. Synonyms: none. Chromosome number (Cameroon): 2n = 48; aFN = 54; one pair large and three pairs medium metacentric and 19 pairs medium-small acrocentric autosomes (Smith *et al.* 1986).

Description Very small microbat without noseleaf and with terminal portion of tail projecting freely from posterior margin of interfemoral membrane; small for an African molossid (FA: 32–35 mm); ears joined by interaural band; M³ with third ridge present but < half length of second ridge; anterior palatal emargination narrow; wings blackish-brown; ventral pelage pale, no ventral flank-stripe in contrasting colour; canines without enlarged cingula. Sexes similar in colour; ♂♂ on average slightly larger than ♀♀. Pelage

short, sparse; covering rump but not extending onto interfemoral membrane. Dorsal pelage dark sepia brown; no grizzling, no spots; hairs with pale brown at base and sometimes with whitish tip. Ventral pelage pale brown to dark beige becoming paler mid-ventrally; no mid-ventral markings, no ventral flank-stripe in contrasting colour. Head not extremely flattened. Upper lip with five well-defined wrinkles and many spoon-hairs. Ears blackish-brown; relatively small (not reaching snout by 2–3 mm when laid forward); inner margins joined on muzzle by an interaural band with a forward-projecting knob-like protuberance (containing a backward-opening interaural pocket). Tragus small, subrectangular, concealed by antitragus. Antitragus large, roughly rectangular. No interaural crest. Wings and interfemoral membrane blackish-brown.

Skull not extremely dorsoventrally flattened. Anterior of braincase prominently elevated above plane of rostrum (Figure 99b). Sagittal crest low, lambdoid crest low, occipital helmet slight. Anterior palatal emargination narrow. Basisphenoid pits moderate in depth, small, their width much less than their distance apart. Upper incisor not procumbent. Upper canine with cingula not greatly enlarged; viewed laterally, incisor not obscured by canine (cf. *T. spurrelli*). Anterior upper premolar slightly taller than cingulum of posterior premolar, within tooththrow; canine and posterior premolar well separated. M³ with third ridge present but < half length of second ridge. Two lower incisors on each side; small, bicuspid and crowded. Lower canines unmodified; cingula not greatly enlarged and not in contact. Dental formula: $^{1123}/_{2123} = 30$.

Geographic Variation None recorded.

Similar Species Five other African *Tadarida* have the following combination of characters: ears joined by interaural band; M³ with third ridge absent or present but < half length of second; anterior palatal emargination narrow; FA almost always < 40 mm (Table 20, p. 488):

T. brachyptera. Usually larger (FA: 35–38 mm; GLS: 16.2–19.9 mm).

Skull with lambdoid crest very well developed.

T. nanula. Forearm shorter (27–31 mm). M³ with third ridge absent.

Basisphenoid pits shallow, smaller and further apart.

T. spurrelli. Forearm shorter (27–30 mm). M³ with third ridge absent.

Upper and lower canines with greatly enlarged cingula, especially in ♂♂; in lateral view, upper incisor obscured by canine. Usually one minute lower incisor on each side. Braincase lower but occipital helmet prominent, especially in ♂♂. Basisphenoid pits shallow.

T. thersites. Forearm usually longer (35–42 mm).

T. bakarii. See in profile of *T. brachyptera*.

Distribution Endemic to Africa. Known only from Rainforest BZ, at one locality in Ghana and five in Cameroon (El-Rayah 1981, Smith *et al.* 1986), but likely to occur elsewhere in the Rainforest BZ where suitable habitat exists, and likely to extend into the Northern Rainforest–Savanna Mosaic. A specimen from Sierra Leone, formerly identified as *T. petersoni* and referred to by Koopman (1989), is now considered to represent *T. brachyptera* (Grubb *et al.* 1998).

Habitat At most localities from which *T. petersoni* has been recorded up until now, the rainforest has been modified by forestry and agriculture and is more open than the undisturbed or climax forests found in less populated areas nearer the Equator (ROM, El-Rayah 1981). Other specimens (AMNH) appear to have been collected in or near the invasive Guinea woodland savanna (El-Rayah 1981). Has been recorded sympatrically with *T. spurrelli*, *T. thersites* and *T. brachyptera*.

Abundance Uncertain.



Tadarida petersoni

Remarks Apparently nothing else is known about the habits of this species.

Conservation IUCN Category: Near Threatened.

Close to qualifying as Vulnerable. Population trend not known, but recorded from only two locations in highly fragmented habitats undergoing further degradation as a result of shifting agriculture and small- and large-scale extraction of wood.

Measurements

Tadarida petersoni

FA: 33.6 (32–35) mm, n = 37

WS: n. d.

TL: 93 mm*

T: 27 mm*

E: 19 mm*

Tr: n. d.

Tib: 13 mm*

HF: 9 mm*

WT: n. d.

GLS: 16.8 (15.8–17.4) mm, n = 37

GWS: 10.7 (10.1–11.2) mm, n = 37

C–M³: 5.9 (5.7–6.2) mm, n = 37

Cameroon and Ghana (El-Rayah 1981)

*Holotype (adult ♂)

Key Reference El-Rayah 1981.

Meredith Happold

Tadarida pumila LITTLE FREE-TAILED BAT

Fr. Petite tadaride; Ger. Kleine Bulldoggfledermaus

Tadarida pumila (Cretzschmar, 1830–1831). In: Rüppell, Atlas Reise Nordl. Afr., Zool. Säugeth. 1: 69. Massawa, Eritrea.

Taxonomy Originally *Dysopes pumilus*. Synonyms: *cristatus*, *elphicki*, *faini*, *frater*, *gambianus*, *hindei*, *langi*, *leucogaster*, *limbata*, *naivashae*, *nigri*, *pusillus*, *websteri*. Contains dark- and light-winged forms, and possibly contains several species (for details see Meester *et al.* 1986). Peterson *et al.* (1995) consider *leucogaster* (including *cristatus*, *nigri* and *websteri*), *naivashae* and *limbata* to be distinct species: Goodman (2011) also considers *leucogaster* to be distinct. Taylor (1999b) suggests there is a cryptic species in South Africa and Swaziland. However, Jacobs *et al.* (2004) concluded, on the basis of genetic similarity between phenotypically diverse specimens (including both pale- and dark-winged forms), that there is no evidence of cryptic species in southern Africa. Pending revision, we retain the forms listed above as synonyms of *T. pumila* but warn that diversity and discrepancies in the information given below (and in literature) might reflect the presence of several species. Subspecies: pending revision, recognition of subspecies is not useful. Chromosome number (Uganda, Cameroon, Somalia): 2n = 48; aFN = 58; one pair large metacentric, two pairs medium metacentric, three pairs medium subtelocentric and 17 pairs acrocentric (Dulić & Mutere 1973b, Smith *et al.* 1986). In contrast, Rautenbach *et al.* (1993) reported aFN = 66 and ten pairs of biarmed autosomes in specimens from Namibia and South Africa.

Description Very small microbat without noseleaf and with terminal portion of tail projecting freely from posterior margin of interfemoral membrane; small for an African molossid (FA: 32–39 mm); ears joined by interaural band; M³ with third ridge > half length of second ridge; wings white or dark; ventral flank-stripe white, off-white or absent; dorsal pelage not pale brown; ♂♂ with short, unicoloured interaural crest. Sexes almost similar. Pelage velvety, sometimes oily, covering rump but not extending onto interfemoral membrane; mid-dorsal hairs 3–4 mm. Dorsal pelage almost black, brown, greyish-brown or reddish-brown, no grizzling, no white flecks or spots; hairs with paler base. Ventral pelage similar or paler; mid-ventral markings very variable or absent; ventral flank-stripe white, off-white or absent. Head not extremely flattened. Upper lip with 5–7 well-defined wrinkles (Kenya, Malawi), or > 7 (Freeman 1981), and many spoon-hairs. Ears black or dark brown; comparatively small (not reaching snout when laid forward), inner margins joined by interaural band with a backward-opening pocket-like invagination in middle, not separated as erroneously reported by Bouchard (1998). Tragus very small, squarish or sometimes with small lobe at top of posterior margin; concealed by antitragus. Antitragus much larger than tragus, roughly semi-circular. Adult ♂♂ with interaural crest of short, brown hairs (osmetrichia) arising from the interaural pocket. No gular gland. Wings with white or blackish-brown pigmentation (intermediate forms in some localities), and often semi-translucent. Interfemoral membrane blackish-brown.

Skull not extremely dorsoventrally flattened. Anterior of braincase slightly elevated above plane of rostrum (Figure 99f). Sagittal crest moderate anteriorly, low or absent posteriorly; lambdoid crest poorly to moderately developed. Anterior palatal emargination variable:

can be (a) closed and separated from incisive foramina by bony bar, (b) narrow but still separated from incisive foramina (Figure 100b) or (c) narrow and not separated from the incisive foramina, which retain only a remnant of the bony septa between them (Figure 100c). Basisphenoid pits moderate in depth and medium-sized (their width ≥ their distance apart), or shallow and small (their width much less than their distance apart) as, for example, in *leucogaster* (Peterson *et al.* 1995). Anterior upper premolar ca. same height as cingulum of posterior premolar or shorter, within toothrow or displaced labially; canine and posterior premolar separated or in contact. M³ with third ridge nearly as long as second. M³–M³ 45.5 (44–48)% of GLS, n = 27 (cf. *T. chapini*). One or two lower incisors on each side, small, bicuspid, crowded. Lower canines slender and relatively short, cingula not greatly enlarged and not in contact. Dental formula: $\frac{1^{123}}{2^{123}} = 30$ or $\frac{1^{123}}{1^{123}} = 28$.

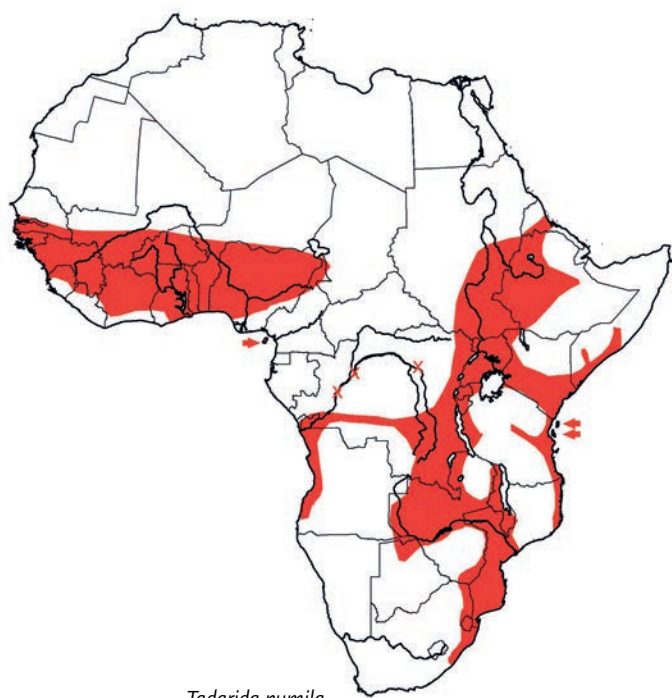
Geographic Variation *Tadarida pumila* currently includes forms with white wings, white ventral flank-stripe and pale mid-ventral markings (sometimes referred to as *T. limbata*), and forms with uniformly dark pelage and dark wings. These forms have identical cranial and dental characters and, in Uganda and DR Congo, dark and pale forms, and every intermediate form, exist sympatrically, which suggests a high degree of colour polymorphism. Alternatively, perhaps there might be two or more species that hybridize, given some circumstance(s), when sympatric. This variation in colour calls for investigation.

Similar Species Only one other African *Tadarida* has the following combination of characters: ears joined by interaural band; M³ with third ridge > half length of second; no paired tail-glands at base of tail; FA: <40 mm (Table 20, p. 488):

Tadarida chapini. Dorsal pelage pale brown; arm-wing yellowish-white with black specks; ♂♂ with long bicoloured interaural crest. M³–M³ relatively narrower (42.7 [41–44]% of GLS, n = 11).

Distribution Widespread south of the Sahara. Most often recorded in the Sudan Savanna and Guinea Savanna BZs, Rainforest–Savanna Mosaics, Coastal Forest Mosaic BZ and Zambezian Woodland BZ, but there are a few records in Rainforest BZ. Recorded, disjunctly, from Senegal to Eritrea, Ethiopia and Somalia, and south-westwards and southwards to Angola, Botswana and KwaZulu–Natal, South Africa. Also Bioko I., Pemba I. and Zanzibar I. Extraliminally: Yemen, Madagascar, Aldabra I. Records from Cape Province, South Africa, have been re-identified as *Sauromys petrophilus* (Jacobs & Fenton 2001). Mapped from country checklists (see order Chiroptera), other literature and museum records.

Habitat Mainly savannas including undifferentiated woodlands, *Isoblerlinia* woodland, mosaic of lowland rainforest and secondary grassland (Guinea savanna), wetter and drier miombo woodlands, coastal mosaics, *Acacia–Commiphora* bushland and thicket, and



Tadarida pumila

other thicket bushlands. Seldom recorded in West African lowland rainforest, but found in swampy gallery forests in DR Congo. Not found in montane areas except possibly in Ethiopia; not found above 1000 m south of ca. 10° S. Probably absent in arid areas except near rivers. Not dependent on rocky, hilly or mountainous terrain for its roosts.

Abundance Common to very common throughout geographic range, especially in built-up areas where buildings provide abundant day-roosts.

Adaptations Aspect ratio high; wing-loading medium. Flight fast, agile with very poor manoeuvrability; turns by banking (radius of turn >1.7 m) but not by stalling-and-twisting; cannot hover, cannot take off from ground, must dive at least 1.5 m to gain sufficient speed for flight; must swoop upwards to reduce speed prior to landing. Unable to fly in a 1×1×1 m enclosure. Scuttling and climbing are fast and very efficient, forwards and backwards. Often roosts by day under corrugated iron roofs; temperatures 17–39°C and relative humidities 39–94% were recorded where bats roosted in Uganda (Mutere 1969). Also roosts in hollow trees and palms, gaps in thatch and narrow cracks in tree trunks and brickwork; not known to roost in caves. In Kruger N. P., South Africa, 'found in rocky environments with an abundance of crevices in which colonies can take refuge in large numbers' (Pienaar *et al.* 1987 as quoted by Bouchard 1998), but this comment is ambiguous and also there are no other records of *T. pumila* roosting in lithophilic day-roosts – therefore this habit needs confirmation. Because it is necessary to dive to gain the requisite speed for flight, entrances are always at least 1.5 m above ground; landing-sites are often stained; bats often scuttle several metres from landing-sites to roost-sites. This species clings or crouches in contact against both horizontal and sloping surfaces, and prefers to tuck into small nooks and crannies into which it scuttles backwards using tactile hairs on rump and feet (and probably tail) for guidance.

Emerges soon after dusk (earlier in overcast weather than on clear or moonlit nights); harem ♂♂ emerge first (McWilliam 1989). Roost-fidelity variable. Of 350 bats released 43 km from their day-roost, 16% returned within one night (some within one hour) and others returned subsequently (Mutere 1969). Sometimes roosts with *T. condylura*. Becomes torpid during day at temperatures below 24 °C. Predicted mean maximum urine concentration is comparatively low (3251 mOsmol/kg); non-flying captive bats (including a lactating ♀) fed on flying-termites did not drink but, because evaporative water loss is very high during flight, independence of drinking water in the wild is highly unlikely (Happold & Happold 1988). Further information in Bouchard (1998).

Foraging and Food Forages by fast-hawking high above tree canopies, over clearings and open water, and sometimes between well-spaced tree trunks and along fairly open waterways. Combines circling (often gaining height) with long straight flights; and swerves and dives in pursuit of prey. Often seen foraging ca. 50–70 m above ground, and sometimes within 2–3 m of open ground. Foraging occurs throughout night, with maximum activity during first hour of darkness and between 04:00 and 05:00h (Mutere 1969). Captive adults, while scuttling around their cages, find and eat live and dead insects, and Marshall & Corbet (1959) found cockroaches in stomachs of non-volant juveniles (but not adults): this suggests opportunistic foraging by chasing but perhaps only in the day-roosts. Subsequently, Aspöberger *et al.* (2003) observed that cockroaches comprised more than 60% of the diet of *T. pumila* at Amani N. R., Tanzania; cockroaches shared the roost of these bats and it was suggested that the bats chased this prey in the roost and probably used vision to do so. Adults feed opportunistically, mainly on soft-bodied insects; diet includes Lepidoptera, Diptera, Coleoptera, Hymenoptera, Hemiptera, Orthoptera, Neuroptera and others (Whitaker & Mumford 1978). Probably does cotton growers much good by feeding on Cotton Bollworm moths (R. C. Wood in Kershaw 1922).

Echolocation Search-phase calls (Malawi) are mostly (90–100%) shallow linear FM sweeps (cf. 7–30% in *T. condylura*) with start-frequencies in the range 21–31 kHz and end-frequencies 20–27 kHz, call-duration 13–20 ms (five light-tagged bats foraging high above ground; M. Happold unpubl.). Sequences of shallow linear FM calls are occasionally punctuated by one or more shallow sigmoid or shallow quasi-linear FM sweeps, but regular alternation between calls of different frequencies (as in *T. condylura*) has not been recorded. In cluttered environments (near day-roosts or ground) *T. pumila* emits steep linear FM sweeps with start-frequencies 28–50 kHz and end-frequencies 19–38 kHz, and there is a gradual transition to narrow bandwidth calls as the bat flies into open spaces (12 bats, as released). Similarly, there is a gradual transition from narrow bandwidth search-phase calls to broad bandwidth calls as prey is approached (Figure 96i–l). In South Africa, calls emitted by three individuals flying in open were shallow FM with similar frequencies (Taylor 1999a).

Social and Reproductive Behaviour Forages singly but roosts in groups of ca. five to several hundreds of individuals. The social organization of a population in Ghana was based on female-defence polygyny (harem formation) with elements of resource-defence polygyny (McWilliam 1988b). Harems comprised an adult ♂ with

up to 21 adult ♀♀ and their young; composition stable during a 16-month study; heaviest ♂♂ had largest harems. Harems roosted in separate day-roosts; roost-fidelity very high. Some young ♀♀ were recruited into their natal harems, thereby replacing annual loss of harem ♀♀ and suggesting harem ♀♀ might often be related, but most young dispersed. In contrast, one day-roost in Malawi contained 20–30 individuals at any one time during a nine-month study, but the composition of the colony was labile and the ratio of adult ♂♂ to ♀♀ in monthly captures of bats emerging at dusk was 1 : 3.7 (n = 71) (Happold & Happold 1989b). Furthermore, a captive group (4 ♂♂, 6 ♀♀) from South Africa roosted in clusters that often included more than one ♂, and the dominant ♂ did not exclude subordinate ♂♂ from access to clusters of ♀♀, suggesting that these bats did not form harems (Somers & Bouchard 2000). Possibly, these studies were on different species.

Reproduction and Population Structure Litter-size: normally one throughout geographic range, very rarely two. Implantation usually in right horn. Reproductive chronology seasonal multimodal polyoestry, sometimes with postpartum oestrus, and potentially up to five litters/year although two or three are the norm in most localities. Gestation ca. 60 days (Malawi and South Africa), 67–72 days (N Ghana); reproductive delays not known to occur. The number of litters/year, the timing of births and the first oestrus after parturition vary with latitude and rainfall. At 9–10° N (Mole N. P., N Ghana), there are three consecutive, synchronized births (at least two followed by postpartum oestrus) during the wet season May–Oct and, for at least some ♀♀, two more births with postpartum oestrus in the dry season. Data from Niger, Burkina, Nigeria and Sudan are consistent with this boreal cycle. At 0–1° N in Uganda, there appear to be three peaks in births at 4-month intervals with less synchrony and without postpartum oestrus. At 02° 18' S (Masalani, near Kibwezi, Kenya) one litter is born in each of the two wet seasons (Nov and Mar–Apr); no postpartum oestrus. At 15° 16' S in Malawi and 25° S in South Africa, most ♀♀ have three litters during the wet season (Nov–Mar), with postpartum oestrus after births 1 and 2, and occasionally after birth 3. (References: Mutere 1973a, McWilliam 1976, 1987c, O'Shea & Vaughan 1980, van der Merwe *et al.* 1986, 1987, Happold & Happold 1989b, Monadjem 1998b).

Neonates are naked except for long tactile hairs, and are ca. 33% adult weight and 56% adult total length; eyes and auditory meatus closed (Happold & Happold 1989b). Growth rate, and attainment of sexual maturity, vary geographically. In Ghana, growth rate is very rapid; young reach 85% of adult-size and 75% of adult-weight

and become volant by ca. 19 days; are weaned between 21–28 days; attain adult-size and adult-weight at ca. three months; attain sexual maturity at ca. three months in ♀♀, and ca. five months in ♂♂ (McWilliam 1976, 1987c). In Malawi and southern Africa, ♀♀ attain sexual maturity in the breeding season following their birth.

Predators, Parasites and Diseases Emerging bats are commonly taken by Bat Hawks, *Macheiramphus alcinus*; and are also taken by other raptors *Accipiter tachiro* (1–5 bats/bird/night), *Falco subbuteo*, *Milvus migrans* and *Aquila wahlbergi* (McWilliam 1989, Rautenbach *et al.* 1990, Fenton *et al.* 1994). Ectoparasites include six species of bed-bugs and their allies (Hemiptera: Cimicidae, Polyctenidae); seven species of fleas (Siphonaptera: Ischnopsyllidae); four species of bat-flies (Diptera: Nycteribiidae, Streblidae), a tick *Lepidixodes kopsteini* (Acari: Ixodidae) and 13 species of mites (Acari: Laelapidae, Spinturnicidae, Macronyssidae, Myobiidae, Trombiculidae, Ereynetidae, Chirodiscidae, Sarcoptidae) (Anciaux de Faveaux 1984). Viruses isolated from *T. pumila* include Chikungunya, Dakar Bat, Yellow Fever, West Nile and Zika viruses, and others (such as Bukalassa Bat and Entebbe Bat viruses), which are not known to cause illness in humans (Anciaux de Faveaux 1984, C. Calisher pers. comm.).

Conservation IUCN Category: Least Concern.

Measurements

Tadarida pumila

FA: 36.7 (32–39) mm, n = 457

WS (a): 278 (270–290) mm, n = 6

TL: 86.7 (70–102) mm, n = 457

T: 31.5 (25–41) mm, n = 350

E: 13.4 (10–17) mm, n = 238

Tr: n. d.

Tib: 12.3 (10–15) mm, n = 68

HF: 8.0 (5–10) mm, n = 142

WT: 9.5 (7–17) g, n = 500

GLS: 16.1 (14.2–17.6) mm, n = 262

GWS: 9.8 (9.1–10.8) mm, n = 262

C–M³: 5.8 (5.0–6.6) mm, n = 274

Throughout geographic range (BMNH, SMNS and literature)

Key References Bouchard 1998; Happold & Happold 1989b; McWilliam 1987c, 1988b; van der Merwe *et al.* 1986, 1987.

Meredith Happold

Tadarida russata RUSSET FREE-TAILED BAT

Fr. Tadaride roussâtre; Ger. Rostfarbene Bulldoggfledermaus

Tadarida russata (J. A. Allen, 1917). Bull. Am. Mus. Nat. Hist. 37: 458. Medje, Orientale, DR Congo.

Taxonomy Originally *Chaerephon russatus*. Synonyms: none. Considered closely related to *T. aloysiisabaudiae* (Fenton & Peterson 1972). Chromosome number: not known.

Description Small microbat without noseleaf and with terminal portion of tail projecting freely from posterior margin of interfemoral

membrane; medium-sized for an African molossid (FA: 42–46 mm); ears joined by interaural band; M³ with third ridge > half length of second ridge, anterior emargination closed; wings mostly dark brown; ventral pelage moderately dark; no ventral flank-stripe in contrasting colour; no tail-glands. Sexes almost similar. Pelage short (mid-dorsal hairs 3–4 mm), nape nearly naked. Dorsal pelage dark rusty-brown to sepia

brown; sometimes with single, whitish hairs or small pale spots; dorsal hairs with paler base. Ventral pelage slightly paler and greyer, sometimes becoming even paler mid-ventrally; no mid-ventral markings, ventral flank-stripe same colour as flanks. Head not extremely flattened. Upper lip with 7–8 well-defined wrinkles on each side and many spoon-hairs. Ears blackish-brown; of medium relative length (reaching snout when laid forward); inner margins joined across forehead by an interaural band with a forward-projecting knob-like protuberance containing a backward-opening interaural pocket. Tragus minute, narrow, concealed by antitragus. Antitragus small, rounded. Interaural crest of short black hairs arising from interaural pocket of ♂♂. Gular gland absent. Wings dark brown from body to fourth finger, outer part semi-translucent and paler. Interfemoral membrane brown.

Skull not extremely dorsoventrally flattened. Anterior of braincase slightly elevated above plane of rostrum. Sagittal crest low or absent; lambdoid crest moderate. Anterior palatal emargination closed; incisive foramina visible. Basisphenoid pits moderate in depth, large, their width more than twice their distance apart. Anterior upper premolar rising distinctly above cingulum of posterior premolar, within toothrow; canine and posterior premolar well separated. M^3 with third ridge just over half length of second. Two lower incisors on each side; minute, bicuspid and not crowded. Lower canines with cingula not greatly enlarged, well separated. Canines of ♂♂ on average larger than those of ♀♀. Anterior lower premolar larger in ♂♂ than in ♀♀. Dental formula: $^{1123}/_{2123} = 30$.

Geographic Variation Three specimens from Kenya are larger than three from Cameroon with which they were compared, suggesting that the Kenyan population may prove significantly larger and worthy of subspecific recognition (Schlitter *et al.* 1986).

Similar Species Four other African *Tadarida* have the following combination of characters: M^3 with third ridge > half length of second; wings neither white nor whitish; no ventral flank-stripe in contrasting colour; no tail-glands (Table 20, p. 488):

Tadarida aloysiisabaudiae. Larger (FA: 48–53 mm; GLS: 20.0–22.3 mm; GWS: 11.7–13.1 mm). Otherwise very similar in pelage pattern and colour as well as in external characters.

T. ansorgei. Dorsal pelage dark greyish-brown to chocolate brown or reddish-brown, somewhat frosted, occasionally with white spots; hairs with paler tips. Skull with anterior of braincase not noticeably elevated above plane of rostrum. Anterior palatal emargination narrow (bulb-shaped). Basisphenoid pits moderate in depth, small, their width less than their distance apart.

T. bivittata. Larger (FA: 46–51 mm; GLS: 19.5–21.3 mm). Skull with anterior palatal emargination narrow (bulb-shaped). Basisphenoid pits moderate in depth, small, their width ≤ their distance apart.

T. pumila (sometimes). Smaller (FA: 32–39 mm; GLS: 14.2–17.6 mm). Skull with basisphenoid pits moderate in depth, small, their width ≤ their distance apart.

Distribution Endemic to Africa. Currently only known from four widely separated areas in Rainforest BZ; in SW Côte d'Ivoire (J. Fahr pers. comm.), Ghana, Cameroon and NE DR Congo (Allen 1917a, Fenton & Peterson 1972), and unexpectedly from Somalia–Masai Bushland BZ at Hell's Gate in Kenya (Schlitter *et al.* 1986).



Tadarida russata

Habitat Recorded along edge of Rainforest BZ in the belt of invasive Guinea woodland (type 11a of White 1983), which extends from NE DR Congo to Ghana and further westwards to Guinea (Fenton & Peterson 1972). Sympatric with *T. spurrelli* and *T. thesites*. Also recorded from Hell's Gate Canyon in the mosaic of East African evergreen bushland and secondary *Acacia* wooded grassland (type 45 of White 1983) in Kenya (Schlitter *et al.* 1986).

Abundance Uncertain; very rarely recorded.

Remarks Twenty-seven (4 ♂♂, 20 ♀♀, 3 not adult) were taken at Medje, DR Congo, on 8 Sep 1910, when a huge hollow tree housing a large colony of *T. russata* and *T. congica* fell during a storm (Lang & Chapin 1917b). No further specimens were obtained until 1970 when five were taken in Cameroon (Peterson 1971a), one in Ghana in 1971 (Fenton & Peterson 1972) and three in Kenya in 1985 (Schlitter *et al.* 1986). The Cameroon specimens were mist-netted over a river and forest streams. In captivity, the *T. russata* from Medje huddled together up to six deep, and regrouped with much squeaking and fighting if disturbed. They scuttled and climbed with speed and agility (as typical of *Tadarida*). Six of the 20 ♀♀ captured were pregnant, each with one embryo. Bat flies (Nycteribiidae) were found in the bats' pelage. A flea, *Lagaropsylla senckenbergiana* (Siphonaptera: Ischnopsyllidae) was found on *T. russata* from Côte d'Ivoire (Beaucournu & Fahr 2003).

Conservation IUCN Category: Data Deficient.

Population trend not known, but the known records are in threatened habitats (highly threatened in West Africa) and it appears to be rare throughout its geographic range. Major threats: extraction of wood (subsistence, selective logging and clear-cutting).

Measurements

Tadarida russata

FA: 44.6 (42–46) mm, n = 36

WS: n. d.
 TL: 100.6 (93–110) mm, n = 31
 T: 33.2 (29–37) mm, n = 30
 E: 20.4 (19–23) mm, n = 31
 Tr: n. d.
 Tib: 14 (14–14) mm, n = 7
 HF: 10.6 (9–12) mm, n = 5
 WT: 17.3 (16–19) g, n = 6
 GLS: 18.6 (17.8–19.4) mm, n = 31

GWS: 11.0 (10.5–11.4) mm, n = 32
 C–M³: 6.6 (6.3–6.7) mm, n = 8
 Throughout geographic range (BMNH, RMCA, Allen 1917a, Peterson 1971a, Fenton & Peterson 1972, Schlitter *et al.* 1986)

Key References Allen 1917a; Fenton & Peterson 1972; Peterson 1971a.

Meredith Happold

Tadarida spurrelli SPURRELL'S FREE-TAILED BAT

Fr. Tadaride de Spurrell; Ger. Spurrells Bulldoggfledermaus

Tadarida spurrelli (Dollman, 1911). Ann. Mag. Nat. Hist. ser. 8, 7: 211. Bibianaha, Ghana.

Taxonomy Originally *Xiphonycteris spurrelli*. Subgenus *Xiphonycteris*. Probably closely related to *T. nanula*. Synonyms: none. Chromosome number (Cameroon): 2n = 48; aFN = 64; one pair large metacentric, three pairs small metacentric, four pairs medium subtelocentric, one pair small subtelocentric and 14 pairs medium-small acrocentric autosomes (Smith *et al.* 1986).

Description Very small microbat without noseleaf and with terminal portion of tail projecting freely from posterior margin of interfemoral membrane; one of the two smallest African *Tadarida* (FA: 27–30 mm); ears joined by interaural band; M³ with third ridge absent; anterior palatal emargination narrow; wings blackish; ventral pelage mostly pale; no ventral flank-stripe in contrasting colour; usually only one lower incisor on each side; canines with greatly enlarged cingula especially in ♂♂. Females not easily distinguished from *T. nanula*. Sexes similar in colour; some morphological differences; ♀♀ smaller on average than ♂♂, especially craniodentally. Pelage short (mid-dorsal hairs 2–3 mm). Dorsal pelage uniformly dark reddish-brown, sometimes with scattered white hairs and (possibly only in ♂♂) scattered dark brown hairs, but no flecks or spots; hairs mostly reddish-brown with whitish base. Ventral pelage white merging into greyish-white on chest and throat and into brown on flanks; apparently no mid-ventral markings; ventral flank-stripe same colour as flanks. Head not extremely flattened. Upper lip with 6–7 well-defined wrinkles on each side and few spoon-hairs. Ears blackish-brown, relatively small (not reaching snout when laid forward); inner margins joined by interaural band with forward- and downward-pointing V-shaped fold in middle. Tragus minute, concealed by antitragus. Antitragus large, tall, with rounded top and broad base. In ♂♂, interaural band has darker and longer hairs on the posterior margin, but no distinct crest; no information for ♀♀. Wings and interfemoral membrane blackish.

Skull not extremely dorsoventrally flattened. Anterior of braincase slightly elevated above plane of rostrum (Freeman 1981). Sagittal crest moderate; lambdoid crest very well developed, especially in ♂♂; helmet prominent, especially in ♂♂. Anterior palatal emargination narrow, sometimes somewhat bulb-shaped (narrowest between incisors). Basisphenoid pits shallow, small, their width < distance apart (sometimes half their distance apart). Upper incisors and canines almost in same plane. Upper incisors widely separated at their bases, and with cutting edges apically sharper than in *T. nanula* (El-Rayah 1980). Upper canines with enlarged cingula, especially in ♂♂: when

viewed laterally, upper incisor obscured by the canine cingulum in ♂♂ (Figure 104b) (cf. *T. nanula*), but partly visible in ♀♀. Anterior upper premolar distinctly taller than cingulum of posterior premolar and within toothrow in ♂♂, smaller and slightly displaced lingually in ♀♀; canine and posterior premolar separated. M³ with third ridge absent. Usually one lower incisor on each side, bicuspid and minute, but occasionally the outer incisor is retained in both sexes (Koopman 1989). Lower canines (Figure 105b) also large with greatly enlarged cingula (especially in ♂♂); in ♂♂ (and some ♀♀), the cingula meet centrally and form an arch over the minute incisors (cf. *T. nanula*) (Rosevear 1965, De Vree 1969, Kock 1969b). In ♂♂, the first lower premolar is larger at base than the second, whereas in ♀♀ the first is smaller than the second (De Vree 1969, El-Rayah 1980). Dental formula: usually $^{1123}/_{1123} = 28$, occasionally $^{1123}/_{2123} = 30$.

Geographic Variation None recorded.

Similar Species Five other African *Tadarida* have the following combination of characters: ears joined by interaural band; M³ with third ridge absent or present but < half length of second; palatal emargination narrow; FA almost always < 40 mm (Table 20, p. 488):

Tadarida brachyptera. Forearm longer (34–41 mm). M³ with third ridge present but < half length of second. Lower canines without greatly enlarged cingula.

T. nanula. Wing-membranes semi-translucent, sometimes brownish, sometimes with light to moderate white pigmentation. Upper canines without enlarged cingula; when viewed laterally, upper incisors are visible – not hidden by the canine cingula. Cingula of lower canines not greatly enlarged and never in contact (cf. in contact in adult ♂♂ and some ♀♀ in *T. spurrelli*). Usually two lower incisors on each side.

T. petersoni. Forearm longer (32–35 mm). M³ with third ridge present but < half length of second ridge. Upper and lower canines without enlarged cingula. Usually two lower incisors on each side. Skull with braincase higher but occipital helmet poorly developed. Basisphenoid pits moderate in depth.

T. thersites. Forearm much longer (35–42 mm). Ventral pelage very dark. Lower canines without greatly enlarged cingula. Two lower incisors on each side.

T. bakarii. See in profile of *T. brachyptera*.



Tadarida spurrelli

Distribution Endemic to Africa. Recorded disjunctly from Rainforest BZ and Rainforest–Savanna Mosaics, from Sierra Leone, Liberia, Guinea, Côte d'Ivoire, Ghana, Togo, Cameroon, perhaps Central African Republic, Equatorial Guinea including Bioko I. and NE DR Congo (De Vree 1969, Kock 1969b, Jones 1971, El-Rayah 1981, Schlitter *et al.* 1982, Smith *et al.* 1986, Koopman 1989, Juste & Ibáñez 1994, Koopman *et al.* 1995, Grubb *et al.* 1998, RMCA). The lack of records from most of the Congolian rainforest in DR Congo might reflect insufficient collecting.

Habitat Found in wetter and drier types of lowland rainforest, secondary forest and areas of invasive Guinea woodland savanna

close to the rainforest. Has been recorded along streams and rivers (e.g. Schlitter *et al.* 1982, Juste & Ibáñez 1994).

Abundance Uncertain; considered rare but possibly more common and widespread than records indicate. Seems to be the most common molossid on Bioko I. (Juste & Ibáñez 1994).

Remarks Nothing else appears to be known about this species.

Conservation IUCN Category: Least Concern.

Measurements

Tadarida spurrelli

FA: 28.3 (27–30) mm, n = 49

WS: n. d.

TL: 83.8 (78–91) mm, n = 10

T: 23.3 (20–25) mm, n = 12

E: 12.6 (11–14) mm, n = 8

Tr: n. d.

Tib: 10 mm, n = 1

HF: 8.0 (7–10) mm, n = 6

WT: 10.6, 11 g, n = 2

GLS (♂♂): 16.7 (14.8–17.6) mm, n = 12

GLS (♀♀): 15.4 (14.6–16.3) mm, n = 25

GWS (♂♂): 10.2 (10.0–10.5) mm, n = 12

GWS (♀♀): 9.6 (9.3–10.0) mm, n = 25

C–M³ (♂♂): 6.2 (5.7–6.8) mm, n = 12

C–M³ (♀♀): 5.9 (5.6–6.3) mm, n = 12

Throughout geographic range (BMNH, RMCA and literature including Juste & Ibáñez 1994)

Key References De Vree 1969; Freeman 1981; Kock 1969b; Rosevear 1965.

Meredith Happold

Tadarida teniotis EUROPEAN FREE-TAILED BAT

Fr. Tadaride de Cestoni; Ger. Europäische Bulldoggfledermaus

Tadarida teniotis (Rafinesque, 1814). Précis. Som., p. 12. Sicily, Italy.

Taxonomy Originally *Cephalotes teniotis*. Subgenus *Tadarida*. Synonyms: *cestoni*, *nigrogriseus*, *savii*, *rueppelli* (see Simmons 2005), but only *rueppelli* and *teniotis* occur in Africa. Subspecies: two, both in Africa. Chromosome number (Croatia): 2n = 48; aFN = 76 (Dulić & Mrakovčić 1980).

Description Medium-sized microbat without noseleaf and with terminal portion of tail projecting freely from posterior margin of interfemoral membrane; large for an African molossid; ears relatively large, meeting to form a V-shaped valley; wings blackish; no ventral flank-stripe in contrasting colour; three lower incisors on each side (cf. two in other *Tadarida*); M³ with third ridge = second ridge. Sexes similar in colour; ♀♀ on average with larger body dimensions. Pelage fine, soft, dense; mid-dorsal hairs ca. 7 mm. Dorsal pelage ashy-grey or brownish-grey; no spots, flecking or frosting; hairs grey

with whitish base. Ventral pelage paler; no mid-ventral markings; no ventral flank-stripe in contrasting colour. No orange-phase. Head not extremely flattened. Upper lip with four well-defined wrinkles on each side and comparatively few spoon-hairs. Ears blackish, relatively large (extending well beyond snout when laid forward); inner margins only just meeting on forehead to form V-shaped valley. Tragus short, concealed by antitragus. Antitragus large, subrectangular. No interaural crest. No gular gland. Wings and interfemoral membrane blackish. Ventral sides of forearms and legs naked and blackish. Foot with raised pad on sole (plantar pad).

Skull not extremely dorsoventrally flattened. Anterior of braincase not elevated above plane of rostrum. Sagittal crest absent or weakly developed; lambdoid crest poorly to moderately developed. Anterior palatal emargination wide. Interdental palate broad, narrowing only very slightly towards canines, not constricted at level of posterior

premolar. Basisphenoid pits moderate in depth, large, their width greater than their distance apart. Anterior upper premolar rising distinctly above level of cingulum of posterior premolar, within toothrow; canine and posterior premolar well separated. M^3 with third ridge equal in length to second. Three lower incisors on each side (cf. two in all other African species in subgenus *Tadarida*), bicuspid, crowded. Lower canines with cingula not greatly enlarged and not in contact. Dental formula: $^{1123}/_{3123} = 32$.

Geographic Variation Two subspecies are currently recognized (Simmons 2005):

T. t. teniotis: Morocco to Libya (and extraliminally Canary Is., W Mediterranean Europe to Central Asia). Dorsal pelage brownish-grey.

T. t. rueppelli: Egypt (and extraliminally Arabia *sensu* Harrison & Bates 1991). Dorsal pelage paler, ashy-grey.

Similar Species Four other *Tadarida* in Africa have ears with inner margins meeting, or almost meeting, to form a V-shaped valley:

Tadarida aegyptiaca. Two lower incisors on each side. Smaller (FA: 42–55 mm; GLS: 17.1–21.9 mm).

T. fulminans. Two lower incisors on each side. Wings brown dorsally, whitish ventrally. Not known north of 5° N.

T. lobata. Two lower incisors on each side. Inner margins of ears meeting close to snout; ears extending well beyond snout when laid forward. White spot between shoulder-blades. Interdental palate markedly constricted at level of posterior premolar. Kenya and Zimbabwe.

T. ventralis. Two lower incisors on each side. Upper lip without well-defined wrinkles. Anterior upper premolar minute; canine and posterior premolar nearly in contact. Not known north of 18° N.



Distribution In Africa, this Palearctic species is found in the Mediterranean Coastal and Afromontane–Afroalpine BZs, in Morocco, Algeria, Tunisia, the Cyrenaica region of Libya, and the Cairo and Giza areas of N Egypt. One doubtful record, based on a mummified specimen with small FA (55 mm), from the Sahara Arid BZ in Algeria (Dorst & Petter 1959), is in very unusual habitat and needs confirmation; it could represent *T. aegyptiaca* (Kowalski & Rzebik-Kowalska 1991). Extraliminally: the Canary Is. and Mediterranean Europe to Central Asia.

Habitat Mainly found in areas with Mediterranean-like vegetation; absent in drier areas. Its presence is locally linked to suitable day-roosts, which include narrow crevices in rocky cliffs or human constructions. In the Aures Mts, Algeria, specimens were mist-netted over a stream (Kowalski & Rzebik-Kowalska 1991). The locality in Cyrenaica is Wadi el Kuff, a limestone mountain area with numerous caves and cracks. The vegetation is shrubland (a type of Maquis) with trees in protected areas; rainfall 300–600 mm per year, mostly in Nov–Feb (Qumsiyeh & Schlitter 1982). In Kyrgyzstan, recorded from sea level to 3100 m (Rybin *et al.* 1989).

Abundance Throughout its distribution, never abundant but, based on hearings of the very low-frequency echolocation calls of this species, which are audible to humans, it is more common than originally estimated from captures.

Adaptations Aspect ratio very high; wing-loading very high. Flight fast and agile with poor manoeuvrability; median speed 50 km/h (Marques *et al.* 2004) (= 13.9 m/sec). Roosts by day in crevices, 2–4 cm wide and variable in depth (15 cm up to several metres), in cliffs or similar human-made structures; sometimes with several entrances (Arlettaz 1990, 1993, Ibáñez & Pérez-Jordá 1998). In Egypt, roosts by day in small caves (Qumsiyeh 1985). The free part of the tail is used as a tactile sensor when moving backwards within crevices (Arlettaz 1993). Although summer-roosts are usually in superficial crevices parallel to the main rocky mass, winter-roosts are deeper and typically located within cracks perpendicular to the cliff face; this allows a deeper positioning in thermally more stable environments. This species is able to live at higher latitudes than any other molossid. In Switzerland, it can stay in torpor as long as eight consecutive days (mean in Jan 3.4 days) (Arlettaz *et al.* 2000). When in torpor, it is able to adjust its body temperature to the environment as long as the ambient roost-temperature does not drop below a threshold situated around 6.5–10°C. Colder roost temperatures induce costly thermogenesis.

Foraging and Food Forages by fast-hawking in open areas, from 10 m to at least 100 m above ground. In Europe, activity starts later than in other species (39–65 min after sunset) and lasts for 10 h without periods of rest (Arlettaz 1990, Marques *et al.* 2004). Foraging areas extend up to 30 km or even farther from the day-roost, although most of the foraging activity takes place between 5 and 15 km from the day-roost (Marques *et al.* 2004). In the European Alps, seems to ascend to passes in the mountains to feed on migratory insects (Arlettaz 1990). In France, Kyrgyzstan and Israel, the diet is mainly moths (65% and 88% by volume), beetles (up to 27%), neuropterans (up to 24%) and hemipterans (up to 12%) according to the locality (Rydell & Arlettaz 1994, Whitaker *et al.* 1994). A diet

comprised largely of tympanate insects (moths and neuropterans) is only possible because the low-frequency echolocation calls emitted by this bat are largely inaudible to these insects and therefore they do not take evasive action to avoid capture (Rydell & Arlettaz 1994).

Echolocation Search-phase call-shape (Switzerland): shallow linear FM. Start-frequency 13 kHz; end-frequency 10.7 kHz; peak-frequency 11.6 kHz; call-duration ca. 15 ms; call repetition rate 1.3–4 per second ($n > 100$ calls; Zbinden & Zingg 1986). These calls, which are audible to humans, are described as a characteristic ‘Tsick’.

Social and Reproductive Behaviour Forages singly or in groups (Arlettaz 1990). In Europe, generally roosts by day in groups of a few dozens, although varying from solitary individuals (normally ♂♂) to maternity colonies of up to 160 bats. Inside the day-roost, usually avoids physical contact with other roost-mates, and rarely forms clusters. Huddling to conserve body-heat occurs only when roost temperature drops below ca. 6.5 °C (Arlettaz *et al.* 2000). In communal roosts, each individual usually defends a small territory against intruders by making loud vocalizations (Arlettaz 1990). These vocalizations are particularly intense when the bats return to the day-roost at sunrise (Arlettaz 1990). Typical social calls are an undulating trill, which alternates up and down in frequency (Ahlén 1990). The mating system, and the mating season, of this species are not well documented. One of six ♂♂ captured in Mar–Apr had scrotal testes in Libya (Qumsiyeh & Schlitter 1982), although ♂♂ display courtship behaviour in mid-Aug and Sep in Kyrgyzstan (Rybin *et al.* 1989) and in the European Alps.

Reproduction and Population Structure Litter-size (Europe): one. In southern Europe and Lebanon, the reproductive chronology is restricted seasonal monoestry, with births in Jun. At ca. 35°N (Aures Mts, Algeria), 3 of 4 ♀♀ were lactating in early Aug (Kowalski & Rzebik-Kowalska 1991). Despite being a Palaearctic species, it is not known whether this species follows a typically temperate zone chronology (with sperm storage or delayed implantation during hibernation). The maximum known longevity record is 13 years (at least) from a ♂ in S Iberia (Ibáñez & Pérez-Jordá 1998).

Predators, Parasites and Diseases Bone remains were found in pellets of Peregrines *Falco peregrinus* and owls *Tyto alba* and *Strix aluco* (Aymerich & García de Castro 1982, Brunet-Lecomte & Delibes 1982, Kock & Nader 1984). Ectoparasites include a flea *Araeopsylla wassifi* (Siphonaptera: Ischnopsyllidae) (Beaucournu & Kowalski 1985); ticks *Carios vespertilionis*, *C. boueti* (Acari: Argasidae); and a mite *Parasteatonyssus hoogstraali* (Acari: Macronyssidae) (Anciaux de Faveaux 1984).

Conservation IUCN Category: Least Concern (assessed from extralimital as well as African data).

Likely to be threatened by decrease in abundance of its main prey, e.g. moths.

Measurements

Tadarida teniotis

FA (♂♂): 61.0 (58–64) mm, $n = 24$

FA (♀♀): 58.9 (56–61) mm, $n = 9$

WS (d): mean 410 mm, $n = 9^*$

TL (♂♂): 127.5 (119–139) mm, $n = 9$

TL (♀♀): 135 (129–142) mm, $n = 12$

T (♂♂): 42.8 (37–52) mm, $n = 9$

T (♀♀): 50.2 (46–57) mm, $n = 12$

E: 30.0 (25–33) mm, $n = 20$

Tr: n. d.

Tib: 19 mm, $n = 1$

HF: 12.1 (10–14) mm, $n = 21$

WT: 29.5 (20–40) g, $n = 60$

GLS: 23.8 (22.5–24.8) mm, $n = 23$

GWS: 14.1 (13.4–15.1) mm, $n = 27$

C-M³: 8.8 (8.5–9.1) mm, $n = 29$

Morocco, Algeria, Libya, Egypt (BMNH, Qumsiyeh & Schlitter 1982, Kock & Nader 1984, Kowalski & Rzebik-Kowalska 1991)

*Portugal (Marques *et al.* 2004)

Key References Arlettaz 1990; Arlettaz *et al.* 2000.

Carlos Ibáñez & R. Arlettaz

Tadarida thersites RAILER FREE-TAILED BAT (RAILER BAT)

Fr. Tadaride railleuse; Ger. Thersites Bulldoggfledermaus

Tadarida thersites (Thomas, 1903). Ann. Mag. Nat. Hist., ser. 7, 12: 634. Efulen, Cameroon.

Taxonomy Originally *Nyctinomus thersites*. Subgenus *Xiphonycteris*. Synonyms: *occipitalis*. Subspecies: none. Chromosome number (Cameroon): $2n = 48$; $aFN = 62$; one pair large metacentric, three pairs small metacentric, three pairs medium subtelocentric, one pair small subtelocentric and 15 pairs medium-small acrocentric autosomes (Smith *et al.* 1986).

Description Small to very small microbat without noseleaf and with terminal portion of tail projecting freely from posterior margin of interfemoral membrane; small for an African molossid (FA: 35–42 mm); ears joined by interaural band; M³ with third ridge present

but < half length of second ridge; anterior palatal emargination narrow; wings blackish, ventral pelage dark; ventral flank-stripe black. Not easily distinguished from *T. brachyptera*. Sexes apparently similar. Pelage short (mid-dorsal hairs ca. 2 mm), sleek; dorsally with a conspicuous wide band of naked skin adjacent to the flight-membranes (cf. absent or very narrow in *T. brachyptera*). Dorsal pelage blackish-brown to dark reddish-brown; no grizzling, no spots; hairs with paler, yellowish base. Flanks naked, black. Rump naked, with two tufts of long hairs (as in several other species of *Tadarida* but not often so conspicuous). Ventral pelage medium brown becoming almost black on flanks; mid-ventral markings absent; ventral flank-stripe black and mainly

on the wing. Head not extremely flattened. Upper lip with 5–6 well-defined wrinkles on each side and many spoon-hairs. Ears blackish; relatively small (reaching no more than half-way along muzzle when laid forward); inner margins joined by interaural band with forward-pointing, V-shaped fold in middle. Tragus very small, concealed by antitragus. Antitragus large, trapezoid with rounded corners and broad base. Apparently no interaural crest although hairs are longer and very dense at back of interaural band. Wings blackish, arm bones ventrally pale. Wings inserting higher on body than in *T. brachyptera*. Interfemoral membrane dark brown or blackish.

Skull not extremely dorsoventrally flattened. Anterior of braincase not noticeably elevated above plane of rostrum. Sagittal crest moderate; lambdoid crest very well developed and forming a very prominent, up-turned helmet. Anterior palatal emargination narrow, sometimes U-shaped, sometimes bulb-shaped (narrowest between incisors). Basisphenoid pits moderately deep, small to medium-sized, their width varying from ca. half to equal their distance apart. Upper incisor slightly procumbent; when viewed laterally, not obscured by canine. Upper canines with cingula not enlarged. Anterior upper premolar distinctly taller than cingula of posterior premolar, within toothrow; canine and posterior premolar well separated. M^3 with third ridge present but $<$ half length of second ridge. Two lower incisors on each side, bicuspid, crowded or not crowded. Lower canines with cingula not greatly enlarged, sometimes in contact and sometimes separated. Dental formula: $^{1123}/_{2123} = 30$.

Geographic Variation None recorded.

Similar Species Five other African *Tadarida* have the following combination of characters: ears joined by interaural band; M^3 with third ridge present (but $<$ half length of second ridge) or absent; palatal emargination narrow; FA almost always less than 40 mm (Table 20, p. 488):

Tadarida brachyptera. Ventral pelage (including flanks) pale; no ventral flank-stripe in contrasting colour. Dorsally, the band of naked skin adjacent to flight-membranes is narrow and inconspicuous. Wing inserting lower on body.

T. nanula. Forearm shorter (27–31 mm). Ventral pelage moderately pale. Upper incisor procumbent. M^3 with third ridge absent.

T. petersoni. Forearm usually shorter (33–35 mm). Ventral pelage pale.

T. spurrelli. Forearm much shorter (27–30 mm). Ventral pelage white merging into brown on flanks. In lateral view, upper incisor obscured by upper canine. In adult ♂♂ and some adult ♀♀, cingula of lower canines greatly enlarged and in contact, forming arch over minute incisors. Usually one lower incisor on each side.

T. bakarii. See in profile of *T. brachyptera*.

Distribution Endemic to Africa. Recorded, somewhat disjunctly, from Rainforest BZ and Rainforest–Savanna Mosaic from Sierra Leone to Cameroon (excluding Togo and Benin), and from Cameroon to NE DR Congo, Uganda and Rwanda, and also from Cameroon to SC DR Congo. Not yet recorded from much of the Congolian rainforest in central Africa. There are uncertain records from the Coastal Forest Mosaic BZ on Zanzibar I. (questioned by Koopman



Tadarida thersites

1993) and Mozambique I. (questioned by Smithers & Lobão Tello 1976 and Koopman 1993), which are not mapped. Mapped from country checklists (see order Chiroptera), Smith *et al.* (1986), Van Cakenberghe *et al.* (1999) and other literature (mentioned below) and museum records.

Habitat Recorded from lowland rainforest, secondary forest, areas of invasive Guinea savanna woodland, and mosaics of rainforest and secondary grassland.

Abundance Uncertain. Common on Bioko I. at least in lowland areas and cities (Juste & Ibáñez 1994) and at some localities in mainland Equatorial Guinea (formerly Rio Muni) (Jones 1971). Based on museum collections and literature, probably fairly common elsewhere.

Adaptations Roosts by day in hollow trees, under corrugated iron roofs, in cracks in fabric of buildings, and in road culverts and drains (Lang & Chapin 1917b, Rosevear 1965, Happold 1987). Sometimes roosts with *T. brachyptera* and *T. congica*. Has been recorded flying over water (Jones 1971).

Foraging and Food No information.

Social and Reproductive Behaviour Has been found roosting singly, but more often in small groups of unspecified size and composition (Rosevear 1965). Catch size and sex ratios in catches of *T. thersites* mist-netted over a pool in Uganda varied from month to month; ♀♀ were caught more often than ♂♂ except in Jan and Jul when numbers of ♂♂ and ♀♀ were equal (Kingdon 1974). However, no details of mist-netting times or durations are given and it is not known if the results reflect changes in the local abundance of this species, differences in the behaviour of ♂♂ and ♀♀, or differences in the mist-netting procedures.

Reproduction and Population Structure Litter-size: no published records. At 0–1°N in Uganda, the reproductive chronology appears to be seasonal bimodal polyoestry with births in Mar and Sep (Kingdon 1974). Based on the relative numbers of ♂♂ and ♀♀ mist-netted each month over a pool, and whether or not the ♀♀ were pregnant, Kingdon concluded that mating occurs in Jan and Jul, that gestation is ca. 2.5 months and that the lactation period is ca. 3.5 months, but no details of this study are given, no voucher specimens are mentioned and, although these conclusions are plausible, they need confirmation.

Predators, Parasites and Diseases Ectoparasites include fleas *Lagaropsylla incerta*, *L. obliqua*, *L. convexa* (Siphonaptera: Ischnopsyllidae) (Anciaux de Faveaux 1984).

Conservation IUCN Category: Least Concern.

Measurements

Tadarida thersites

FA: 38.2 (35–42) mm, n = 66

WS (a): 294.9 (272–305) mm, n = 15

TL: 101.7 (91–113) mm, n = 38

T: 31.2 (25–36) mm, n = 40

E: 16.8 (13–22) mm, n = 37

Tr: n. d.

Tib: 14.7 (13–16) mm, n = 7

HF: 9.6 (8–10) mm, n = 16

WT: 20.3 (10–34) g, n = 20

GLS: 18.8 (16.8–21.5) mm, n = 64

GWS: 12.0 (11.1–12.9) mm, n = 64

C-M³: 6.8 (6.2–7.3) mm, n = 39

Cameroon, Equatorial Guinea (mainland and Bioko I.), DR Congo (ROM, Allen 1917a, Jones 1971, Juste & Ibáñez 1994)

Key Reference Rosevear 1965.

Meredith Happold

Tadarida trevori TREVOR'S FREE-TAILED BAT

Fr. Tadaride de Trevor; Ger. Trevors' Bulldoggfledermaus

Tadarida trevori (J. A. Allen, 1917). Bull. Am. Mus. Nat. Hist. 37: 468. Faradje, Orientale, DR Congo.

Taxonomy Originally *Mops trevori*. Subgenus *Mops*. Treated as subspecies of *T. congica* by Koopman (1965), but considered to be a distinct species by Peterson (1972), Freeman (1981) and Koopman (1993, 1994). Synonyms: none. Tentatively not considered to include *T. niangarae* (but see profile of *T. niangarae*). Chromosome number: not known.

Description Small microbat without noseleaf and with terminal portion of tail projecting freely from posterior margin of interfemoral membrane; medium-large for an African molossid (FA: 51–55 mm); ears joined by interaural band; M³ with third ridge present but < half length of second ridge; anterior palatal emargination closed; wings dark brown; ventral pelage pale brown, darker on flanks; no ventral flank-stripe in contrasting colour; dorsal pelage not dark brown to almost black; crown not darker than back. Sexes apparently similar in most parameters, but data are available for only three ♂♂. Pelage sleek; nape naked or nearly so; mid-dorsal hairs ca. 6 mm. Dorsal pelage (grey-phase) medium sepia brown or yellowish-brown; no grizzling, no spots; hairs unicoloured or with paler base. There is a poorly defined patch of dark pelage behind and below the ear. Ventral pelage pale greyish-brown, pale pinkish-grey or pale yellowish-brown, becoming darker on flanks; mid-ventral markings absent; no ventral flank-stripe in contrasting colour. Orange-phase, dorsal pelage pale rusty-brown; ventral pelage pinkish-buff. Head not extremely flattened. Upper lip with 8–9 well-defined wrinkles on each side and many spoon-hairs. Ears dark brown, relative length medium (almost reaching snout when laid forward); inner margins joined across forehead by a thin, flexible interaural band with a forward-pointing, V-shaped fold in the middle. Tragus very small,

concealed by antitragus. Antitragus large, trapezoid. Interaural crest probably absent although, in both sexes, the posterior side of the interaural band supports dense, dark brown hairs. Gular gland: no information. Wings semi-translucent, lightly to heavily pigmented with dark brown. Third metacarpal (both sexes): 53–56 mm, n = 16; fourth metacarpal: 51–54 mm, n = 16 (cf. *T. congica*). Interfemoral membrane dark brown.

Skull not extremely dorsoventrally flattened. Anterior of braincase slightly elevated above plane of rostrum. Sagittal crest moderate; lambdoid crest well developed. Anterior palatal emargination closed; incisive foramina visible. Basisphenoid pits deep, large, their width much greater than their distance apart. Anterior upper premolar ca. same height as cingulum of posterior premolar; within tooththrow. M³ with third ridge present but < half length of second. Two lower incisors on each side, bicuspid, crowded. Lower canines fairly long and robust; cingula not greatly enlarged, usually separated. Dental formula: $1^{123}/_{2123} = 30$.

Geographic Variation None recorded.

Similar Species Five other African *Tadarida* have the following combination of characters: ears joined by interaural band; M³ with third ridge present (but usually* < half length of second ridge) or absent; anterior palatal emargination closed; FA: >40 mm (Table 20, p. 488). *In *T. condylura*, the length of the third ridge is variable and can be up to half length of second ridge.

Tadarida demonstrator. Smaller (FA: 41–46 mm). Males with pair of glands between penis and anus. Dorsal pelage hoary. No dark patch behind and below each ear.

T. condylura. Forearm almost always shorter (45–51 mm). Wings semi-translucent pale greyish-brown. Ventral flank-stripe white or whitish, contrasting with darker flanks. Skull with basisphenoid pits shallow and small.

T. niveiventer. Forearm shorter (44–48 mm). Skull with basisphenoid pits moderate in depth and size. Ventral pelage mostly white or cream.

T. congica. FA usually longer (54–58 mm); 3rd and 4th metacarpals usually longer (see Description). Dorsal pelage dark brown to black. Interaural band much thicker. Skull usually larger (GLS: 24.9–27.4 mm). M^3 with third ridge absent.

T. midas. Larger (FA: 59–67 mm; GLS: 25.8–29.5 mm). M^3 with third ridge absent.

Distribution Endemic to Africa. Mostly recorded disjunctly from the Northern and Eastern Rainforest–Savanna Mosaics, from Guinea to W Ghana, from SW Nigeria, possibly from Central African Republic, and from NE DR Congo, S Sudan and Uganda (Peterson 1972, J. Fahr pers. comm.). Also recorded from the Guinea Savanna BZ in Côte d'Ivoire. Records from Mt Bero, Guinea and Côte d'Ivoire are from J. Fahr (pers. comm.). Specimens, previously identified as *T. congica*, from Nigeria (Bergmans 1977b) and Ghana (Jeffrey 1975, Koopman *et al.* 1995, Grubb *et al.* 1998) are considered to represent *T. trevori* by Fahr *et al.* (2006). A record of *T. congica* from Bamingui-Bangoran N. P., Central African Republic (Spinage 1988) is likely to represent *T. trevori* (inferred from its distribution in Guinea woodland savanna by J. Fahr pers. comm.).



Habitat Primarily recorded from forest edges and areas of invasive Guinea woodland savanna in the Rainforest–Savanna Mosaic, but extending into undifferentiated woodland and *Isobertinia* woodland. Recorded from 'rocky hill country covered with savanna bush or open woodland', 'over a shallow stream with riverine forest on one side and open savanna on the other', and over ponds and streams in open areas within forest or at edges of forest, which suggests that *T. trevori* does not usually inhabit closed rainforest (Peterson 1972). Possibly it sometimes commutes from open habitats to forage above the canopy of closed forest, but this needs confirmation.

Abundance Uncertain. Poorly represented in museum collections, which suggests that *T. trevori* is uncommon or rare; however, it is not easy to catch and may be more abundant than records indicate.

Remarks The holotype, from 03° 50' N (Faradje, NE DR Congo), had fed on good-sized Coleoptera and contained one large embryo in late Sep (Lang & Chapin 1917b). Ectoparasites include a flea *Lagaropsylla alloides* (Siphonaptera: Ischnopsyllidae) described by Smit (1977) (host given as *T. congica* but specimen re-identified by J. Fahr pers. comm.).

Conservation IUCN Category: Data Deficient.

Apparently rare. Inhabits rainforest–savanna mosaic in very heavily populated areas where shifting agriculture and extraction of wood are ongoing threats, and apparently does not roost in buildings.

Measurements

Tadarida trevori

FA: 53.0 (51–55) mm, n = 8

WS (d): 384 mm, n = 1

TL: 126 (121–130) mm, n = 12

T: 39.8 (34–44) mm, n = 16

Tib: 16.7 (15–18) mm, n = 9

HF: 13.3 (11–15) mm, n = 16

E: 20.6 (18–25) mm, n = 15

Tr: 1.8 (1.6–1.8) mm, n = 4

WT: n. d.

GLS: 23.9 (23.1–25.1) mm, n = 8

GWS: 14.7 (14.4–15.1) mm, n = 8

C– M^3 : 9.0 (8.8–9.2) mm, n = 10

Throughout geographic range (Peterson [1972] except maximum FA and minimum GLS [J. Fahr pers. comm.], wingspan [Lang & Chapin 1917b] and tragus [BMNH])

Key References Lang & Chapin 1917b; Peterson 1972.

Meredith Happold

Tadarida ventralis GIANT FREE-TAILED BAT

Fr. Grande tadaride africaine; Ger. Große Bulldoggfledermaus

Tadarida ventralis (Heuglin, 1861). Nova. Acta. Acad. Caes. Leop.-Carol. 29 (8): 4, 11. Keren, Eritrea.

Taxonomy Originally *Nyctinomus* (*Dysopes*) *ventralis*. Subgenus *Tadarida*. Synonyms: *africana*. History of synonymy of *ventralis* and *africana* is summarized by Kock (1975). Chromosome number: not known.

Description Medium-sized microbat without noseleaf and with terminal portion of tail projecting freely from posterior margin of interfemoral membrane; large for an African molossid and the largest African *Tadarida*; ears relatively small, inner margins meet to form V-shaped valley; M^3 with third ridge > half length of second ridge; palatal emargination wide; wings dark brown; no ventral flank-stripe in contrasting colour; two lower incisors on each side. Sexes similar except ♂♂ on average heavier than ♀♀. Pelage velvety, sometimes glossy; mid-dorsal hairs 4–5 mm. Dorsal pelage (grey-phase) chocolate brown, rusty-brown or dark brown without spots or flecking; hairs with beige or cream at base. Ventral pelage paler with white or cream mid-ventral stripe; ventral flank-stripe same colour as flank but with longer hairs. Orange-phase: dorsal pelage orange-brown, ventral pelage yellowish. Head not extremely flattened. Upper lip without well-defined wrinkles; comparatively few spoon-hairs. Ears brown, relatively small (extending to ca. middle of muzzle when laid forward); inner margins meeting on forehead to form a V-shaped valley. Tragus large, roughly rectangular, not concealed by antitragus. Antitragus low, triangular, not much larger than tragus. No interaural crest. Gular gland naked, conspicuous (especially in ♂♂), and often ringed by grey hairs. Wings and interfemoral membrane semi-translucent, dark brown to almost black. Ventral sides of forearms naked and whitish; ventral sides of legs naked and brownish. Foot without raised plantar pad on sole.

Skull not extremely dorsoventrally flattened. Anterior of braincase not noticeably elevated above plane of rostrum. Sagittal crest very weakly developed; lambdoid crest well developed laterally but absent dorsally. Anterior palatal emargination wide. Interdental palate broad, narrowing smoothly (but slightly) to canines. Basisphenoid pits deep, medium-sized, their width slightly greater than their distance apart to almost twice their distance apart. Upper incisors long and close together. Anterior upper premolar variable (it can be lower, level with, or taller than the cingulum of posterior premolar); in tooththrow or slightly displaced labially; canine and posterior premolar nearly in contact, sometimes in contact. M^3 with third ridge > half length of second ridge. Two lower incisors on each side, bicuspid and crowded. Lower canines well developed; cingula enlarged and in contact or almost so, or separated. Dental formula: $^{1123}/_{2123} = 30$.

Geographical Variation No information.

Similar Species Four other *Tadarida* in Africa have ears with inner margins meeting, or almost meeting, to form a V-shaped valley:

Tadarida aegyptiaca. Much smaller (FA: 42–55 mm; GLS: 17.1–21.9 mm).

*Tadarida ventralis*

T. fulminans. Ventral flank-stripe white, cream or yellowish. Foot with plantar pad. Skull usually smaller and less robust (GLS: 21.6–24.4 mm). Upper incisor shorter.

T. lobata. Inner margins of ears meeting close to snout; ears extending well beyond snout when laid forward. White spot between shoulder-blades. Skull with interorbital constriction slight. Anterior upper premolar large; canine and posterior premolar well separated. Lower canines slender; cingula separated by incisors.

T. teniotis. Three lower incisors on each side. Upper lip with five well-defined wrinkles. Anterior upper premolar large; canine and posterior premolar well separated. North Africa.

Distribution Endemic to Africa. Recorded from scattered localities in Afromontane–Afroalpine, Somalia–Masai Bushland and Zambezian Woodland BZs, and Eastern Rainforest–Savanna Mosaic. Recorded from Eritrea and Ethiopia, S Sudan, E DR Congo, Kenya, Tanzania, Malawi, Zimbabwe, Mozambique and from somewhere unspecified in the former Transvaal (South Africa) (Harrison 1971, Hill & Morris 1971, Lagen *et al.* 1974, Koopman 1975, Cotterill 1996b, 2001c). Most records are from Kenya (Cotterill 2001c). Voucher specimens (USNM) for two localities in Mozambique (Chiuta and Vila Gouveia) mapped by Smithers & Lobão Tello (1976) as *T. africana* actually represent *T. fulminans*.

Habitat Mostly recorded from dry woodland savannas (including *Acacia–Commiphora* bushland, drier types of miombo woodland and mopane woodland), but also recorded from montane habitats (including Keren, Eritrea, at 1400 m, Fatam R. [= Blue Nile Gorge]

at Great Abbai, Ethiopia at 1900 m, and the Kenyan Highlands), and from semi-desert grassland and shrubland near L. Turkana, Kenya. The availability of rock crevices in which to roost appears to be a major determinant of their occurrence in these vegetation zones (Cotterill 2001c).

Abundance Not known.

Remarks Only five specimens were known until 1971 (Hayman & Hill 1971) but more have been collected since, especially from Kenya (Cotterill 2001c). Nevertheless, all aspects of the biology of *T. ventralis* remain barely known. A pregnant ♀ with one foetus (CR = 30 mm) was collected from a rock crevice in E Zambia in mid-Nov (Ansell 1986b), and a skull was recovered from an owl pellet underneath crevices in a large granitic overhang in S Zimbabwe. This site was occupied as day-roosts by *T. fulminans* and large numbers of *T. ansorgei* (Cotterill 1996b). Two specimens from Kenya were collected as they emerged from the roofs of houses (Start 1966, Cotterill 1996b). *Tadarida ventralis* occurs sympatrically with *T. lobata* at Maungu Hill, Kenya (Cotterill 2001c).

Conservation IUCN Category: Data Deficient.

Remains poorly known despite intensive sampling effort. Most records are historical. Has a wide geographic range, but is inferred to be threatened by pesticides and loss of habitat.

Measurements

Tadarida ventralis

FA: 63.7 (60–67) mm, n = 49

WS (d): 459.7 (440–485) mm, n = 12

TL: 153.3 (142–168) mm, n = 36

T: 58.3 (51–66) mm, n = 58.3

E: 24.7 (18–29) mm, n = 36

Tr: n. d.

Tib: n. d.

HF: n. d.

WT (♂ ♂): 45 (38–55) g, n = 23

WT (♀ ♀): 39 (31–46) g, n = 10

GLS: 23.8 (23.4–26.1) mm, n = 51

GWS: 15.2 (14.0–15.8) mm, n = 50

C–M³: 9.5 (8.9–10.0) mm, n = 53

Throughout geographic range (BMNH, FMNH, HZM, LACM, NMZB, ROM)

Key References Cotterill 1996b, 2001c; Harrison 1971.

F. P. D. Cotterill

Family VESPERTILIONIDAE

VESPER BATS

Vespertilionidae Gray, 1821. London Med. Repos., 15: 299.

| Subfamily Vespertilioninae | | p. 545 |
|---|-------------------------|--------|
| <i>Barbastella</i> (2 species) | Barbastelles | p. 546 |
| <i>Eptesicus</i> (5 species) | Serotines | p. 550 |
| <i>Glauconycteris</i> (12 species) | Butterfly Bats | p. 560 |
| <i>Laephotis</i> (4 species) | African Long-eared Bats | p. 578 |
| <i>Mimetillus</i> (1 species) | Mimic Bat | p. 585 |
| <i>Nyctalus</i> (2 species) | Noctules | p. 589 |
| <i>Nycticeinops</i> (1 species) | Twilight Bat | p. 594 |
| <i>Otonycteris</i> (1 species) | Desert Bat | p. 597 |
| <i>Pipistrellus sensu lato</i> (28 species) | Pipistrelles | p. 600 |
| <i>Plecotus</i> (3 species) | Long-eared Bats | p. 660 |
| <i>Scotoecus</i> (2 species) | Lesser House Bats | p. 666 |
| <i>Scotophilus</i> (6 species) | House Bats | p. 672 |
| Subfamily Myotinae | | p. 684 |
| <i>Cistugo</i> (2 species)* | Wing-gland Bats | p. 685 |
| <i>Myotis</i> (11 species) | Myotis | p. 688 |
| Subfamily Miniopterinae* | | p. 710 |
| <i>Miniopterus</i> (5 species) | Long-fingered Bats | p. 711 |
| Subfamily Kerivoulinae | | p. 723 |
| <i>Kerivoula</i> (7 species) | Woolly Bats | p. 724 |
| <i>Phoniscus</i> (? 1 species) | Trumpet-eared Bats | p. 734 |

* Since this profile was submitted, it has been indicated that two of these taxa should be raised to family status: the genus *Cistugo* to Cistugidae (Lack *et al.* 2010), and the subfamily Miniopterinae to Miniopteridae (Miller-Butterworth *et al.* 2007). As major updating was not possible, both are still presented here as vespertilionids.

This is a very large polytypic family that is distributed throughout the world wherever there are enough insects to eat and day-roosts of some sort: only the polar regions, the highest mountains and the most arid deserts are uninhabited by vespertilionids. Having 48 extant genera and 407 extant species (Simmons 2005), this is the largest family of bats and, among mammals, it is second in size only to the rodent family Muridae. The family Vespertilionidae is also one of the most widely dispersed families of mammals. In Africa, there are ca. 93 species (some 'species' almost certainly contain two or more cryptic species, and two species, *Pipistrellus permixtus* and *Phoniscus aerea*, are unlikely to be genuine African species). Simmons (2005) recognizes 19 genera which have African representatives: here, partly because their species contents are uncertain, two genera (*Neoromicia* and *Hypsugo*) are included in *Pipistrellus sensu lato*. Vespertilionids have a simple muzzle without a noseleaf (Figure 32i), and the tail is completely enclosed by the interfemoral membrane (except for part of the terminal vertebra in some species) (Figure 33i). Most are brown, grey or blackish-brown with paler bellies and are often dubbed 'little brown bats'. However, some vespertilionids are unexpectedly colourful, with delicate to spectacular markings, and are among the most beautiful of all mammals. For example, the Pied Butterfly Bat *Glauconycteris superba* has a striking pattern of white patches and lines on a black background, and black wings. Welwitsch's Bat *Myotis welwitschii* is rufous and cream with spectacular wings that are black with bright orange-red markings. The Variegated Butterfly Bat *Glauconycteris variegata* is often creamy-

fawn with yellowish wings patterned with fine brown 'veins' so that they resemble dry leaves, and the Rufous Myotis *Myotis bocagii* has a subspecies that is bright rufous dorsally and cream ventrally with very dark brown ears, snout and wings.

African vespertilionids include *Pipistrellus musculus* (FA: 25, WT: 3–4 g), which is one of the smallest of all mammals, and *Scotophilus nigrita* (FA: 77–88 mm, WT: 88–91 g), which is one of the largest microbats. Most, however, are small to very small; some medium-sized. Most have pelage that is shortish and dense, or woolly, and most have slightly elongated bodies. In other characters, vespertilionids are very varied. The head can be rounded to very flat; the muzzle conical, and short to long. The ears (Figure 116) are comparatively simple, usually widely separated but joined in two genera, often relatively short (means 23–48% of FA), sometimes relatively long (means 72–97% of FA). The tragus is well developed and its shape is often used to identify genera and species (Figure 116). The eyes are small and sometimes hidden by pelage. The wings are very varied in shape and colour; the second finger has a metacarpal and one short phalanx (Figure 117). The hindlimbs vary in relative length and, in some species, are modified for climbing over slippery leaves. The toes (except the first [hallux]) have three phalanges. The interfemoral membrane is broad and long. Usually it fully encloses

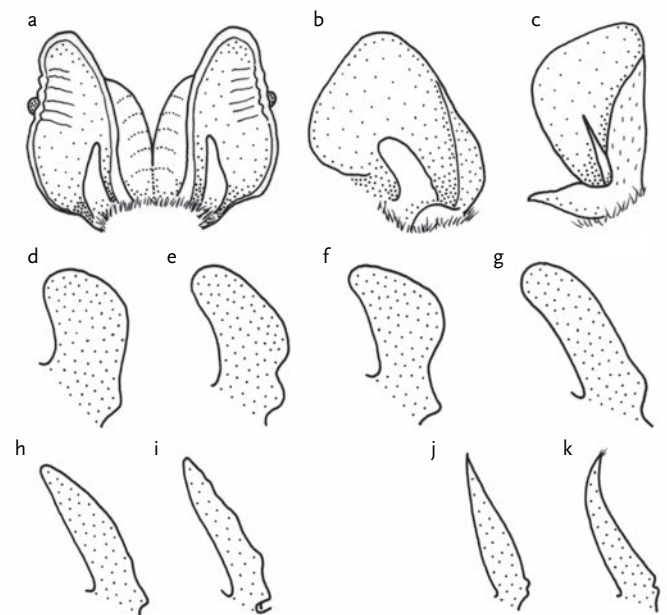


Figure 116. Ears and tragi of African bats in the family Vespertilionidae to show differences between subfamilies. (a) Ears joined (e.g. *Barbastella*, Vespertilioninae). (b) Ear not funnel-shaped; widely separated from other ear (e.g. *Miniopterus*, Miniopterinae). (c) Ear funnel-shaped; widely separated from other ear (e.g. *Kerivoula*, Kerivoulinae). (d) Tragus short and blunt as in (d) *Scotoecus*, Vespertilioninae; (e) *Laephotis*, Vespertilioninae; (f) *Glauconycteris*, Vespertilioninae and (g) *Miniopterus*, Miniopterinae. Tragus long and narrow but not sharply pointed as in (h) *Otonycteris*, Vespertilioninae and (i) *Myotis*, Myotinae. Tragus long, narrow and sharply pointed as in (j) and (k) *Kerivoula* spp., Kerivoulinae.

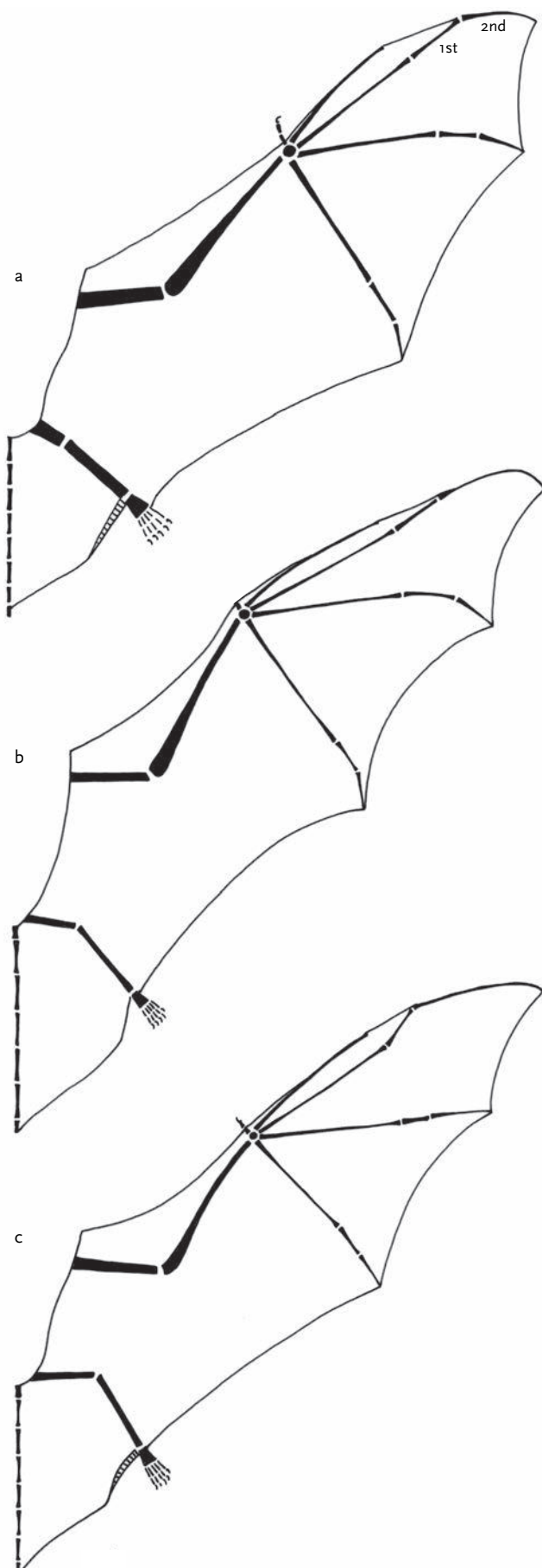


Figure 117. Variations in the length of the second phalanx of the third finger in relation to length of the first phalanx of third finger, in African Vespertilionidae. (a) Second phalanx ca. as long as first (most Vespertilioninae). (b) Second phalanx ca. twice as long as first (*Glauconycteris*, Vespertilioninae). (c) Second phalanx about three times as long as first (*Miniopterus*, Miniopterinae).

the tail, which extends to the membrane's V-shaped posterior border although, in some species, the terminal vertebra protrudes beyond the interfemoral membrane. Relative tail length varies from short to long (27–54% of TL). Females usually have one pair of nipples in the pectoral region; some species (but only *Otonycteris hemprichii* in Africa) have two pairs. There are no pubic nipples. The skull has a rostrum that varies from short to moderately long, and the cranial region varies from flat to highly domed. There are no postorbital processes and no enlarged supraorbital ridges. The sagittal and lambdoid crests are usually low but may combine to form a helmet in the largest members of some genera. The premaxillae have nasal branches that are usually widely separated; the palatal branches are absent and consequently the palate has a deep to very deep, wide anterior emargination. Within this family, there is a trend towards shortening of the jaws and a concomitant loss of incisor and premolar teeth: there may be a total of 38 teeth, or as few as 28. Consequently the dental formula varies from genus to genus and is used diagnostically (Figure 119).

There is greater diversity in the adaptations of the vespertilionids than in any other family of bats in Africa. In African species (excluding *Cistugo* and *Miniopterus*), aspect ratios range from low to medium, and wing-loadings range from very low to extremely high (the majority have low aspect ratios and low or very low wing-loadings). Tip shapes range from short and rounded to long and pointed. In *Miniopterus*, aspect ratios range from medium to very high, and wing-loadings from low to medium. Most vespertilionids, including all African species, are insectivorous (a few species from elsewhere eat fish), but *Nyctalus lasiopterus* also preys on small birds migrating during the night (see profile). The flying abilities, foraging strategies and diets of vespertilionids are as varied as their wing morphology. Foraging behaviour includes fast-hawking (e.g. *Nyctalus*, *Pipistrellus savii*), moderately fast-hawking (e.g. *Miniopterus*, *Pipistrellus tenuipinnis*, *Scotophilus*, *Scotoecus* and at least one *Glauconycteris*), slow-hawking (most other species), gleaning (e.g. *Eptesicus serotinus*, *Kerivoula* spp., some *Myotis* spp., *Otonycteris hemprichii* and *Plecotus christii*) and trawling (e.g. *Myotis bocagii*, *M. capaccinii*). Some species exemplify more than one strategy. There are species of vespertilionids in almost all environments, from open to densely cluttered. Many vespertilionids use their wings to flick a flying insect into a temporary pouch created between the legs by the interfemoral membrane, and then tuck the head down to remove the insect and eat it. Their aerial acrobatics, associated with the pursuit, capture and manipulation of prey, are spectacular to watch and, as their name implies, vesper bats often forage in the evening and can be watched with ease. They often forage in groups. The adaptive radiation within this family has been so extensive that there are many examples of convergent evolution. In Africa, for example, the wing morphology and foraging habits of vespertilionids in the genus *Kerivoula* are similar to those of nycterids while, at the other end of the continuum, vespertilionids such as *Scotophilus* and *Scotoecus* have converged towards the emballonurids and molossids. This convergence also embraces echolocation. The majority of African vespertilionids for which data are available, emit high intensity steep FM/QCF calls (Figure 118), but

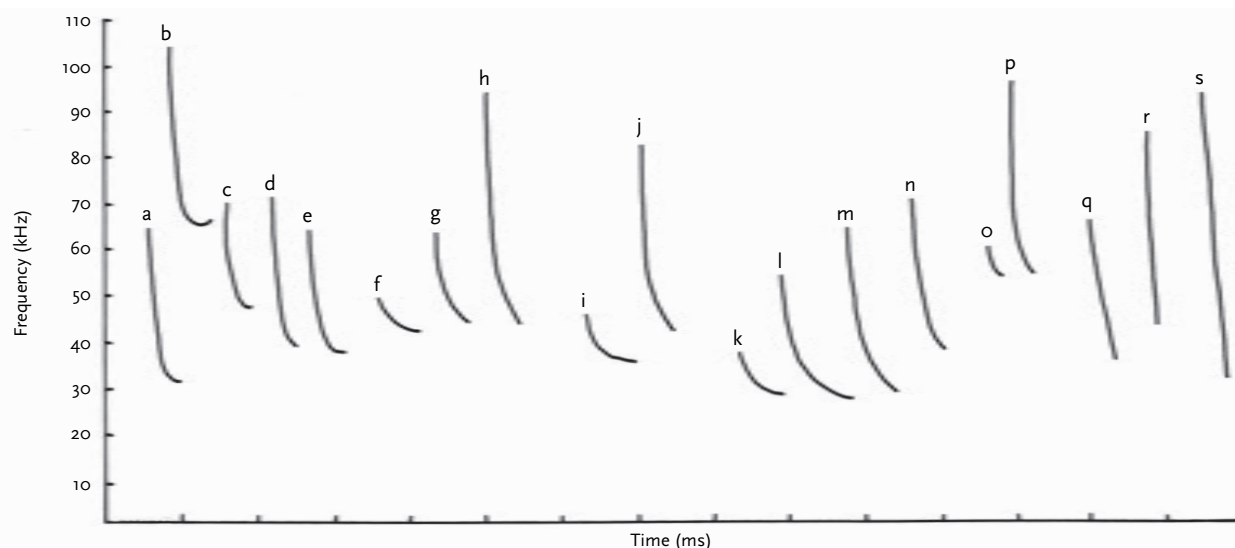


Figure 118. Sonograms of individual echolocation calls emitted by 13 species of vespertilionids from Malawi to indicate differences between species and, in some cases, differences associated with echolocating in different situations: all bats flying < 3 m above ground except where indicated (M. Happold unpubl.). (a) *Laephotis botswanae*; (b) *Pipistrellus nanus*; (c) *P. zuluensis*; (d) *P. capensis*; (e) *P. cf. melckorum*; (f), (g) and (h) *P. rueppellii*; (i) *Nycticeinops schlieffeni* (well above ground); (j) *N. schlieffeni* (< 3 m above ground); (k) *Scotophilus dinganii* (search-phase); (l) and (m) *S. dinganii* (approach-phase); (n) *S. viridis*; (o) and (p) *Miniopterus fraterculus*; (q) *Myotis bocagii* (flying near ground); (r) *Myotis tricolor* (flying near ground) and (s) *Myotis welwitschii* (flying near ground). See also Figure 27.

there are 'whispering' bats in the vespertilionid genus *Kerivoula* as there are in the Nycteridae and Megadermatidae, and some of the high-flying vespertilionids such as *Scotophilus* and *Scotoecus*, emit shallow to very shallow FM search-phase calls that are remarkably similar to those emitted by high-flying Molossidae (Figure 27). A less obvious example concerns the use of Doppler shift to distinguish targets that are fluttering from those that are not. Rhinolophids and hipposiderids are well known to do this by perceiving Doppler-shifted changes in echoes of the CF-components of their calls when they are reflected from fluttering targets but, recently, it has been demonstrated that bats emitting FM calls may also be able to do this by detecting Doppler-shifted 'frequency smears' in echoes reflected from fluttering targets (Taylor 1990). Because many vespertilionids forage in groups, their high-intensity echolocation calls, when made audible to our ears by a bat-detector, make an almost deafening racket of harsh staccato noises not unlike machine-gunfire. These bats emit their echolocation calls through the mouth, so individuals with bared teeth and threatening grimaces are usually just having a good 'look' at you with no intention to bite at all! It is unfortunate that so many artists make bats look savage and repulsive when, in fact, they are usually gentle and attractive. Most vespertilionids make vocalizations, in the contexts of communication and the expression of pain and/or fear, which are audible to humans as sounds such as squeaking, twittering, buzzing and nickering.

Vespertilionids are moderately adapted for cursorial locomotion and are able to move over horizontal, sloping and vertical surfaces. However, with the exception of *Miniopterus*, they cannot furl their flight-membranes as effectively as emballonurids and molossids, and they do not normally scuttle or climb except when moving very short distances between a landing place and a roost-site. Some species have pads on the wrists and heels to facilitate climbing slippery banana leaves. Vespertilionids, as a family, exploit the full range of day-roosts known to be used by bats (but with limitations on where they roost within some of these day-roosts), and some utilize day-roosts that are not used or seldom used by bats of other families in Africa.

These include inside the furred leaves of banana plants (exploited by *Pipistrellus nanus* and *Myotis bocagii*), weaver-bird and sunbird nests (*Kerivoula*), holes in trees made by nesting woodpeckers and barbets (*Scotophilus* but also some molossids), and crevices in bark and spaces under loose sheets of bark (*Barbastella*, *Mimetillus*, and some species of *Laephotis*, *Myotis*, *Nyctalus* and *Pipistrellus* [and also some molossids]). With few exceptions, vespertilionids cling in contact with the sloping or horizontal surfaces of their day-roosts: very few ever roost hanging freely. Consequently, vespertilionids rarely compete with bats of other families that hang freely from ceilings. Vespertilionids roost singly or in small to very large groups, and group-members typically roost in close contact with each other. Many African vespertilionids go into torpor during the day, even in the tropics, but true hibernation is rare. Some exceptions include *Barbastella barbastellus*, *Nyctalus leisleri*, *Pipistrellus pipistrellus*, *Myotis* spp. and *Miniopterus schreibersii*, which hibernate in North Africa, and *Myotis tricolor*, *Miniopterus fraterculus* and *M. natalensis*, which hibernate in South Africa. The social behaviour and mating systems of African vespertilionids have received little attention: exceptions are *Myotis bocagii* and *Pipistrellus nanus*. Some appear to have solitary organizations, some establish pairs and harems and many live in small to very large groups of various compositions. Maternity colonies are established by many species. The reproductive strategies of African vespertilionids are not as diverse as might be expected, except in litter size. Most vespertilionids are monotocous but there are many species in Africa (and elsewhere) that have litters of 1–2, usually two, or 2–3 (and one non-African species, *Lasiurus borealis*, regularly has four, and occasionally five, young). All African vespertilionids (and the vast majority elsewhere) for which data are available, are seasonally monoestrous with the exceptions in Africa of *Myotis bocagii*, which is polyoestrous in Gabon, and *Pipistrellus nanus*, which is perhaps aseasonally monoestrous in some equatorial localities (assuming the data are not from several cryptic or misidentified species). Polyoestrous individuals have also been reported for *Mimetillus molonyi* and *Pipistrellus rendalli* (see species profiles), although the reproductive chronologies of

these species are not yet fully understood. The advantages of timing spermatogenesis and lactation to coincide with seasons of maximum abundance of insects and/or optimal temperatures has led to the evolution of delays between copulation and parturition. These delays, which usually occur during the cold dry season or winter, include sperm storage and delayed fertilization (*Myotis tricolor*, *Pipistrellus capensis*, *P. nanus*), delayed implantation (*Scotophilus leucogaster*, *Miniopterus fraterculus*, *M. natalensis*, *M. schreibersii* and probably *M. minor*) and retarded embryonic development (*M. schreibersii*, *Scotophilus viridis* and perhaps *P. rusticus*) (see species profiles). The ♀♀ of some species carry their neonates while foraging but leave them in the roost when they become larger and heavier.

The geological range of the family Vespertilionidae is middle Eocene to Recent in Europe, late Oligocene to Recent in North America, middle Miocene to Recent in Africa and Asia, Pleistocene to Recent in the West Indies, South America and Australasia, and Recent over the remainder of the present geographic range (Koopman 1984).

Of the 91 species definitely known to occur in Africa, 48 species are only or mainly found in the tropics, 26 species occur in both tropical and temperate regions and 17 species (of which 16 are Palearctic species) occur only in temperate regions. Of the 90 species for which data are available, 23 are only or mainly found in savannas, 22 only or mainly in forests, 20 in both forests and savannas, 15 in Mediterranean habitats, six in arid regions, and four in both savanna and arid regions. Thirty-eight species (42%) are found in montane habitats, but only five of these species have been found only in montane habitats. Because vespertilionids are very diverse in their wing morphology and flight, and in their feeding and roosting habits, it is not surprising that there are considerably more than one species at most localities (except localities in some arid regions), for example: four species along the Nile R. at or near Khartoum, six at Kikwit, DR Congo (rainforest), six at Luluabourg, DR Congo (rainforest–savanna mosaic), six on Zomba Plateau, Malawi (montane forest and grassland, 1500–1800 m), 12 in Taï N. P., Côte d'Ivoire (rainforest), 13 in Liwonde N. P., Malawi (miombo woodland) and 17 in Comoe N. P., Côte d'Ivoire (forest–savanna mosaic) (refs. Hayman *et al.* 1966, Koopman 1975, Happold & Happold 1997, Van Cakenberghe *et al.* 1999, Fahr & Kalko 2011).

The family Vespertilionidae was placed by itself in the superfamily Vespertilionoidae by Simmons (1998) although some authors, including Teeling *et al.* (2005), also include the Molossidae in this superfamily. However, recent studies based on molecular data contradict some of the groupings based on morphological data and, pending resolution of the controversies, no chiropteran superfamilies are recognized by Simmons (2005). There is also some uncertainty about the monophyly of the Vespertilionidae: *Miniopterus* (currently in subfamily Miniopterinae) may represent a distinct family. Indeed, since this profile was submitted, Miller-Butterworth *et al.* (2007) have confirmed that *Miniopterus* does represent a distinct family (Miniopteridae) and, furthermore, Lack *et al.* (2010) concluded that *Cistugo* (placed here in the Vespertilionidae, subfamily Myotinae) also represents a distinct family (Cistugidae). The Vespertilionidae are divided into subfamilies but the number, composition and affinities of the subfamilies is perhaps not yet fully understood. However, Simmons (2005) recognizes six subfamilies of which four are represented in Africa, and they are profiled here because it was not possible to incorporate the recent recognition of the families Cistugidae and Miniopteridae (see above).

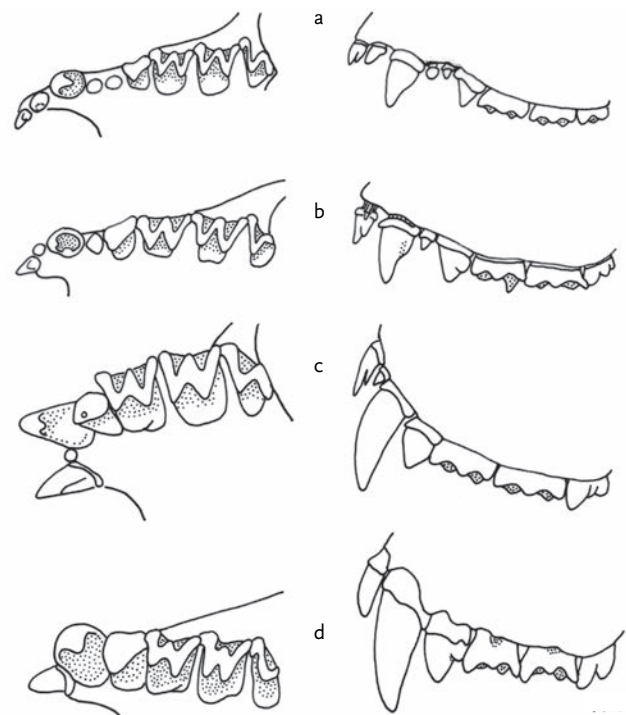


Figure 119. Variations in the number of upper incisors and cheekteeth on each side in African Vespertilionidae. *Left*: occlusal views of teeth on left side of upper jaw. *Right*: lateral views of labial sides of the same teeth. (a) Two incisors and six cheekteeth (e.g. *Myotis*). (b) Two incisors and five cheekteeth (e.g. *Plecotus*). (c) Two incisors and four cheekteeth (e.g. *Glauconycteris*). (d) One incisor and four cheekteeth (e.g. *Scotophilus*).

The characters by which the four subfamilies (*sensu* Simmons 2005) can be distinguished in Africa, and the African genera in each subfamily, are listed below and illustrated in Figures 116, 117 and 119.

Vespertilioninae. Second phalanx of third finger ca. as long as the first phalanx or longer but not more than twice as long as the first; ears not funnel-shaped; tragus short and blunt or long and narrow but not sharply pointed; pelage not frizzled; four or five upper cheekteeth; baculum present. All genera except those listed below.

Myotinae. Second phalanx of third finger ca. as long as the first; ears not funnel-shaped; tragus long and narrow but not sharply pointed; pelage not frizzled; six upper cheekteeth; baculum present. *Cistugo*, *Myotis*.

Miniopterinae. Second phalanx of third finger ca. three times longer than the first; braincase high and rounded; ears not funnel-shaped; tragus short and blunt; pelage not frizzled; five upper cheekteeth; baculum absent. *Miniopterus*.

Kerivoulinae. Second phalanx of third finger ca. as long as the first; braincase high and rounded; ears funnel-shaped with deep emargination below tip; tragus long, narrow and sharply pointed; pelage frizzled; six upper cheekteeth; baculum: no information. *Kerivoula* and (very dubiously) *Phoniscus*.

Following Simmons (2005), the subfamilies are presented in the above order. The African genera in each subfamily are presented in alphabetical order irrespective of any relationships between them.

Meredith Happold

Subfamily VESPERTILIONINAE – Barbastelles, Serotines, Butterfly Bats, Long-eared Bats, Noctules, Pipistrelles, House Bats and others

Vespertilioninae Gray, 1821. London Med. Repos. 15: 229.

Diagnostic combination of characters: second phalanx of third finger ca. as long the first or longer but not more than twice as long as the first (Figure 117); ears not funnel-shaped (Figure 116); tragus short and blunt, or long and narrow, but not sharply pointed (Figure 116); less than six upper cheekteeth (Figure 119). This subfamily includes 37 genera (Simmons 2005) of which 14 occur in Africa (Simmons 2005) but, of the latter, only 12 are presented here (*Hypsugo* and *Neoromicia*

being provisionally treated as *Pipistrellus* [*sensu lato*] for reasons given below – see genus *Pipistrellus*). The phylogenetic relationships of the genera in this subfamily have been investigated many times, numerous hypotheses have been advanced, and various tribes have been described (e.g. Hill & Harrison 1987, Menu 1987, Koopman 1994, Volleth & Heller 1994, Hooper & Van Den Bussche 2001 and many others). Simmons (2005) recognizes seven tribes of which five are represented

Table 21. Key to the African genera in the subfamily Vespertilioninae. Ears are said to be relatively short if 23–48% of FA, medium if 49–72% of FA and long if 73–97% of FA. Measurements and distributions pertain only to Africa.

| Number of lower cheek-teeth | Number of upper incisors | Number of upper cheek-teeth | Ears joined at base | Ear length (mm) (relative length) | FA (mm) | Miscellaneous | Genus |
|-----------------------------|--------------------------|-----------------------------|---------------------|-----------------------------------|---------|--|---------------------------------------|
| 6 | 2 | 5 | Yes | 32–40 (Long) | 36–42 | North Africa, Sudan, Eritrea, Ethiopia | <i>Plecotus</i>
(3 species) |
| 5 | 2 | 5 | Yes | 13–18 (Short) | 36–44 | North Africa | <i>Barbastella</i>
(2 species) |
| 5 | 2 | 5 | No | 13–23 (Short) | 41–64 | Fifth finger shortened (about = 4th metacarpal)
North Africa | <i>Nyctalus</i>
(2 species) |
| 5 | 2 | 4 or 5 | No | 5–16 (Short) | 23–39 | Fifth finger not shortened (> 4th metacarpal)
Head not flattened
No body pattern; wings not reticulated
Outer margin of ear not reaching mouth | <i>Pipistrellus</i>
(28 species) |
| 5 | 2 | 4 | No | 15–25 (Medium) | 30–41 | Head slightly flattened
No body pattern; wings not reticulated
Outer margin of ear not reaching mouth | <i>Laephotis</i>
(4 species) |
| 5 | 2 | 4 | No | 9–14 (Short) | 27–31 | Head conspicuously flattened
No body pattern; wings not reticulated
Outer margin of ear not reaching mouth | <i>Mimetillus</i>
(1 species) |
| 5 | 2 | 4 | No | 6–16 (Short) | 32–48 | Head not flattened
Most with body pattern of spots and/or lines, or reticulated wings
Outer margin of ear reaching mouth
Lower lip with lobe at posterior angle | <i>Glauconycteris</i>
(12 species) |
| 5 | 2 | 4 | No | 10–20 (Short) | 34–54 | Head not flattened
No body pattern; wings not reticulated
Outer margin of ear not reaching mouth
Lower lip without lobe at posterior angle | <i>Eptesicus</i>
(5 species) |
| 5 | 1 | 4 | No | 30–41 (Long) | 50–65 | | <i>Otonycteris</i>
(1 species) |
| 5 | 1 | 4 | No | 11–24 (Short) | 41–88 | Penis relatively short
Tragus relatively moderately long
Posterior upper molar with two ridges | <i>Scotophilus</i>
(6 species) |
| 5 | 1 | 4 | No | 9–13 (Short) | 28–35 | Penis short (5.6–6.2 mm)
Upper canine with anterior surface rounded not grooved
Posterior upper molar with three ridges
Anterior lower premolar ca. half height of posterior premolar | <i>Nycticeinops</i>
(1 species) |
| 5 | 1 | 4 or 5 | No | 9–15 (Short) | 28–40 | Penis extremely long (ca. 9–16 mm)
Upper canine with anterior surface flat and grooved
Posterior upper molar with three ridges
Anterior lower premolar at least two-thirds height of posterior premolar, usually subequal | <i>Scotoecus</i>
(2 species) |

in Africa: the total number of genera in these tribes is given in brackets, and the named genera are those represented in Africa.

Eptesicini (3 genera): *Eptesicus*.

Nycticeiini (8 genera): *Nycticeinops*, *Scotoecus*, *Scotophilus*.

Pipistrellini (4 genera): *Nyctalus*, *Pipistrellus* (*sensu stricto*).

Plectotini (6 genera): *Barbastella*, *Otonycteris*, *Plecotus*.

Vespertilionini (13 genera): *Glauconycteris*, *Hypsugo*, *Laephotis*, *Mimetillus*, *Neoromicia*.

However, because it is unlikely that relationships between genera are fully understood, tribal affinities are not included in most species profiles here.

The status of some genera is also controversial and there have been many changes of opinion since Koopman (1993), including the following examples. (a) Following Hill & Harrison (1987) and others, *Glauconycteris* is recognized as a distinct genus instead of a subgenus of *Chalinolobus*. (b) Following Horáček & Hanák (1986), Hill & Harrison (1987) and others, *Nycticeinops* is recognized as a distinct genus instead of a subgenus of *Nycticeus*. (c) Following Hill & Harrison (1987), Menu (1987), Volleth & Tidemann (1991), Volleth *et al.* (2001) and others, many species traditionally in *Eptesicus* have been removed, with the result that, in Africa, *Eptesicus* is now considered to be represented by only five species (details in Genus *Eptesicus*). The species which have been removed from *Eptesicus* (*brunneus*, *capensis*,

grandidieri [as *flavescens*], *guineensis*, cf. *melckorum*, *rendalli*, *somaticus*, *tenuipinnis* and *zuluensis*), have been placed in *Neoromicia* by several authors, including Simmons (2005), but the placement of some of these species in *Neoromicia* is controversial (e.g. Hooper & Van Den Bussche 2001), and so too is the placement of *nanus* in *Neoromicia* by (Simmons 2005). (d) Following Horáček & Hanák (1986) and others, *savii*, which was previously in *Pipistrellus*, is considered to belong to the genus *Hypsugo*, and this, and the generic status of *Hypsugo*, is well supported by morphological, chromosomal and molecular evidence. However, often in the absence of evidence other than morphology, many other species formerly in *Pipistrellus* have now been placed in *Hypsugo* (see Simmons 2005) and this also is controversial. Therefore, pending resolution of the species contents of *Neoromicia* and *Hypsugo*, and also for convenience, all of the *Pipistrellus*-like species in Africa are presented here as species of *Pipistrellus* (*sensu lato*). With this exception, the African species in the subfamily Vespertilioninae are placed in the genera recognized by Simmons (2005), but some genera (*Plecotus*, *Pipistrellus*) contain new species, and some forms given specific status by Simmons (2005) are considered here to be subspecies.

The 12 genera of Vespertilioninae represented in Africa can be distinguished by the characters given in Table 21. In the text, they are presented in alphabetical order irrespective of any relationships that might exist between them.

Meredith Happold

GENUS *Barbastella*

Barbastelles

Barbastella Gray, 1821. London Med. Repos. 15: 300. Type species: *Vespertilio barbastellus* Schreber, 1774.



Barbastella barbastellus.

A polytypic genus with two species, both found in North Africa. Diagnostic combination of characters: five upper and five lower cheekteeth and two upper incisors on each side; ears joined at base (as in *Plecotus*) but short (cf. *Plecotus*); tympanic bullae small (cf. large in *Plecotus*). Dental formula $2^{123}/_{3123} = 34$ (as in *Nyctalus* and most African *Pipistrellus*). Selected characters of *Barbastella* are illustrated in Figure 120.

Morphologic, bacular and karyotypic data suggest close affinity with *Plecotus*, *Otonycteris* and about three other non-African genera (e.g. Hill & Harrison 1987, Frost & Timm 1992, Tumlison & Douglas 1992, Qumsiyeh & Bickham 1993). Mitochondrial ribosomal sequences

support the relationship with *Plecotus*, but not with *Otonycteris* (Hooper & Van Den Bussche 2001). Simmons (2005) places *Barbastella* in the tribe Plectotini (with both *Otonycteris* and *Plecotus*, and three non-African genera). Some authors consider that *Barbastella* is monotypic (but see profile of *B. leucomelas*). *Barbastella* is distributed from North Africa through Europe, SW Asia, N India to W China and also Japan (Koopman 1994). In Africa, both species have been found in semi-desert habitats but *B. barbastella* is also found in cool montane habitats in NW Africa, whereas *B. leucomelas* has been found only at low altitudes (and probably the only records in Africa are those of vagrants).

The two species are:

B. barbastellus. Pelage, wings and interfemoral membrane pale; ventral pelage pale fawn to off-white; condylobasal length 13–14 mm; tympanic bullae smaller; auditory meati smaller; mastoid region less inflated and without a prominent projecting flange (Figure 121a); outer margin of ear usually with a prominent projecting lobe (Figure 120).

B. leucomelas. Pelage, wings and interfemoral membrane dark, ventral pelage dark grey; condylobasal length 14–15 mm; tympanic bullae larger; auditory meati larger; mastoid region noticeably inflated and with a prominent projecting flange (Figure 121b); outer margin of ear normally without projecting lobe.

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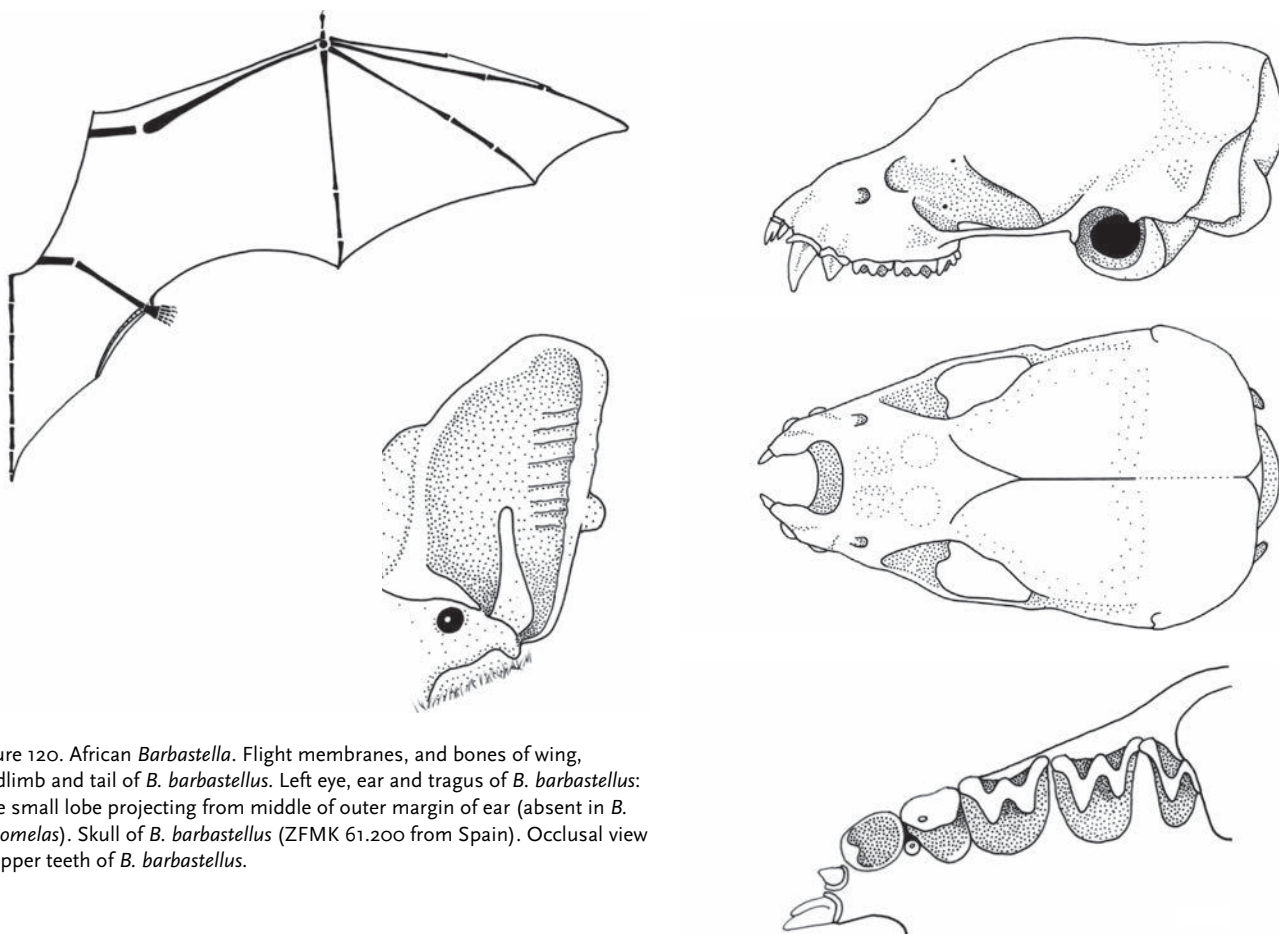
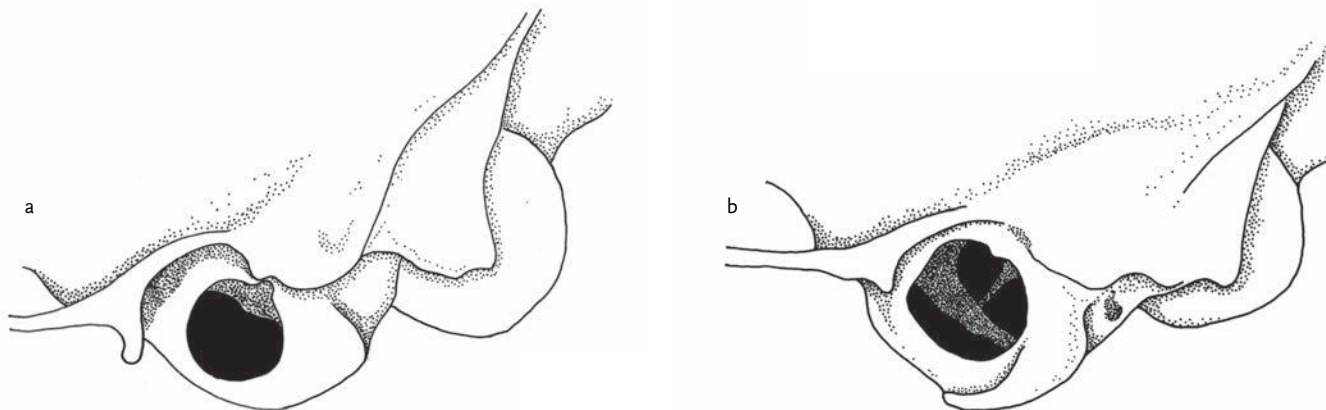


Figure 120. African *Barbastella*. Flight membranes, and bones of wing, hindlimb and tail of *B. barbastellus*. Left eye, ear and tragus of *B. barbastellus*: note small lobe projecting from middle of outer margin of ear (absent in *B. leucomelas*). Skull of *B. barbastellus* (ZFMK 61.200 from Spain). Occlusal view of upper teeth of *B. barbastellus*.

BELOW: Figure 121. The tympanic regions (left side) of (a) *Barbastella barbastellus* and (b) *B. leucomelas* (after Harrison & Makin 1988).



Barbastella barbastellus WESTERN BARBASTELLE

Fr. Barbastelle d'Europe; Ger. Mopsfledermaus

Barbastella barbastellus (Schreber, 1774). Die Säugethiere 1: 168. Burgundy, France.

Taxonomy Originally *Vespertilio barbastellus*. Synonyms: *barbastelle*, *communis*, *daubentonii*. Subspecies: none. Possibly includes *leucomelas* but, pending further information, *B. leucomelas* is treated as a distinct species here (see profile for *B. leucomelas*). Chromosome number (Turkey): $2n = 32$; $aFN = 50$ (Volleth 1985).

Description Very small microbat without noseleaf and with tail more or less fully enclosed in interfemoral membrane; five upper and five lower cheekteeth and two upper incisors on each side; dorsal pelage silvery-black; wings blackish-brown to black; ears joined at base, short for a vespertilionid (13–14 mm), normally with projecting lobe on

outer margin. Pelage silky, dense; mid-dorsal hairs ca. 10 mm. Dorsal pelage dark blackish-brown to black with silvery sheen; hairs dark blackish-brown or black with whitish or yellowish tip. Ventral pelage dark grey; hairs dark blackish-brown with greyish-white to beige tip. Chin, throat and chest darker than belly and flanks. Dorsal pelage of young up to 12 months old is black without silvery sheen. Muzzle short, flat and broad; nostrils opening upwards and outwards between two high, lateral glandular swellings and behind prominent median pad. Ears (Figure 120) blackish, relatively short for a vespertilionid (40.1 [36–46]% of FA, $n = 12$) (cf. relatively long in *Plecotus* and moderately long in *Otonycteris*); forward-facing, inner margins joined at base by low frontal band, outer margin conspicuously notched near base and usually with a small lobe projecting from the middle of the margin (cf. *B. leucomelas*). Ears fold back close to head when bat rests. Tragus reaching just over half height of ear, triangular with long rounded tip, covered with fine hairs. Wings and interfemoral membrane dark brown to black (cf. *B. leucomelas*). Tail 91.6 (70–110)% of HB (Europe).

Skull (Figure 120) with rostrum narrow and weak; braincase elongated and rounded; zygomatic arches slender and without marked dorsal curvature; zygomatic width < mastoid width. Sagittal crest absent or very low; lambdoid crest weakly developed. Tympanic bullae comparatively small (cf. *Plecotus*); smaller than in *B. leucomelas* (Harrison & Makin 1988). Auditory meati comparatively small (cf. *B. leucomelas*); mastoid region less inflated and without a prominent projecting flange (Figure 121a). Inner incisor bicuspid; outer incisor smaller, not reaching level of secondary cusp of inner incisor. Upper canines slender. Two upper premolars on each side; anterior premolar minute (shorter than cingulum of canine), displaced lingually; canine and posterior premolar in contact. Lower incisors (three on each side) tricuspid, arranged in a V-shape with the outer pair the largest. Two lower premolars and three lower molars on each side.

Geographic Variation Uncertain. If new evidence shows *B. leucomelas* is conspecific, it might be considered a subspecies of *B. barbastellus*.

Similar Species The only other African vespertilionids that have ears with inner margins joined are:

Barbastella leucomelas. Outer margin of ear normally without small projecting lobe; ear longer (15–18 mm) and narrower. Pelage, wings and interfemoral membrane pale; ventral pelage pale fawn to off-white. Tympanic bullae and especially the auditory meati larger; mastoid region more inflated and with a prominent projecting flange; lambdoid crest less evident.

Plecotus spp. Ears much longer (32–40 mm). Six lower cheekteeth on each side.

Distribution In Africa, this Palearctic species occurs only in the mountains of the Mediterranean Coastal and Afromontane–Afroalpine BZs in Morocco (Rif, Middle Atlas, High Atlas) (Panouse 1955, Ibáñez 1988, Fonderflick *et al.* 1998). Extralimittally: England and W Europe to Caucasus, also Canary Is. and larger islands in Mediterranean (Simmons 2005).

Habitat In Africa, inhabits cool mountains and semi-desert areas. Associated with forested areas in Europe.



Barbastella barbastellus

Abundance Uncommon throughout much of the African geographic range.

Adaptations Aspect ratio low; wing-loading low (Norberg & Rayner 1987). Based on wing morphology, flight predicted to be slow with great manoeuvrability. In Europe, roosts by day in summer in roof-spaces and cracks in buildings, behind wooden window-shutters, holes in trees and behind bark. Hibernates in winter in caves, mines and fissures. Tolerates low ambient temperatures (ca. –5 to +5 °C) and low as well as high relative humidities (40–96%) (Bogdanowicz & Urbanczyk 1983, Weidner 2000). Migratory movements as far as 290 km were reported by Kepka (1960). For more information, see Rydell & Bogdanowicz (1997).

Echolocation The echolocation calls of *B. barbastellus* are unique among Palearctic bats (Ahlén 1981, 1990). Search-phase calls are of two types – one loud and one weak. (a) Call-shape short CF/FM; calls beginning with a short (1–1.5 ms) CF or narrow bandwidth component, and ending with a short downward FM sweep; start-frequency 35 kHz, end-frequency 28 kHz; call-duration 4 ms; intensity high. (b) Call-shape short CF/FM as above or FM; start-frequency 43 kHz; end-frequency 33 kHz; call-duration 5.2 ms; intensity low. Highest call intensity at 30–35 kHz or 40–43 kHz (Schober & Grimmberger 1987, Ahlén 1990). It is suggested that the bat alternates between the loud and weak calls (Jones 1993). Call repetition-rate: 8–9 calls per second. Calls are emitted through the nose as well as through the mouth.

Foraging and Food No information from Africa. In Europe, forages by slow-hawking above the canopy in forested areas and low over water. Has been reported to glean from foliage but this is doubtful. Small moths make up 70–99% of prey by volume (based on analysis of faeces from Europe and C Asia; Beck 1995, Rydell *et al.* 1996, Sierro & Arlettaz 1997). Has a small gape and weak dentition, therefore its diet does not include large, hard-shelled prey.

Social and Reproductive Behaviour In Europe, hibernates singly, or in clusters in colonies of up to 1000 individuals. In summer, sexes segregate; ♀♀ form maternity colonies of 5–80 individuals; ♂♂ roost in small groups (Schober & Grimmberger 1987, Richarz 1989). Mating takes place in autumn, when the bats return to the hibernacula.

Reproduction and Population Structure Litter-size: normally one, rarely two. Reproductive chronology in Africa not known; in Europe, it is seasonal monoestry with mating in autumn (and sometimes in hibernacula); births from mid-Jun (Schober & Grimmberger 1987). Maximum life-span 23 years. In many hibernacula, there is a predominance of ♂♂ (Schober & Grimmberger 1987).

Predators, Parasites and Diseases Predators in Europe include owls *Asio otus*, *Tyto alba*, *Strix aluco*, *Bubo bubo* and the Beech Marten *Martes foina* (Abeijentsev *et al.* 1956, Urbanczyk 1981). Ectoparasites in Europe include fleas (Siphonaptera) and bat-flies (Diptera), both of which are found occasionally, and mites (Acari), which heavily infest this bat.

Conservation IUCN Category: Near Threatened.

Population fragmented and predicted to decline significantly within next 15 years. Has specific habitat requirements and its habitats are declining.

Measurements

Barbastella barbastellus

FA: 38.1 (36–40) mm, n = 6

WS: n. d.

TL: 102.1 (97–107) mm, n = 8*

T: 50.1 (45–56) mm, n = 8*

E: 13.5 (13–14) mm, n = 4

E: 15.7 (15–18) mm, n = 8*

Tr: n. d.

Tib: n. d.

HF: n. d.

WT: 7.5, 8 g, n = 2

GLS: 15, 15 mm, n = 2

GWS: n. d.

ZW: 7.6, 7.6 mm, n = 2

C–M³: 4.6 mm, n = 1

Morocco (Panouse 1955, Ibáñez 1988, Fonderflick *et al.* 1998)

*Spain (ZFMK)

Key References Rydell & Bogdanowicz 1997; Sierro 1999; Sierro & Arlettaz 1997.

Antoine Sierro

Barbastella leucomelas EASTERN BARBASTELLE

Fr. Barbastelle asiatique; Ger. Östliche Mopsfledermaus

Barbastella leucomelas (Cretzschmar, 1826). In: Rüppell, Atlas Reise Nordl. Afr., Zool. Säugeth., p. 73. Sinai, Egypt.

Taxonomy Originally *Vespertilio leucomelas*. Synonyms: *blanfordi*, *caspica*, *darjelingensis*, *walteri*. Subspecies: two, of which probably only the nominate occurs in Africa. Considered a subspecies of *Barbastella barbastellus* by Qumsiyeh (1985), but not by Corbet (1978), Harrison & Makin (1988), Harrison & Bates (1991) and Corbet & Hill (1991) and, pending further study, Horáček *et al.* (2000) and Simmons (2005). Chromosome number (Japan): 2n = 32; aFN = 50 (Andō *et al.* 1977).

Description Very small microbat without noseleaf and with tail more or less fully enclosed in interfemoral membrane; five upper and five lower cheekteeth and two upper incisors on each side; dorsal pelage silvery-fawn over dark brown; wings pale; ears joined at base, medium-short for a vespertilionid (15–18 mm), without projecting lobe on outer margin. Sexes similar. Pelage silky, dense; mid-dorsal hairs ca. 10 mm. Dorsal pelage dark brown with conspicuous silvery-fawn to golden-beige sheen; hairs dark chocolate brown with fawn to beige at tip. Ventral pelage: pale fawn to off-white (throat occasionally appears darker); hairs dark brown with terminal third pale fawn to off-white. Muzzle short, flat and broad; nostrils opening upwards and outwards between two high, lateral glandular swellings and behind prominent median pad. Ears relatively short (40.2 [36–46]% of FA, n = 4) (cf. relatively long in *Plecotus* and moderately long in *Otonycteris*), forward-facing, joined at base by low frontal band; outer margin conspicuously notched near base and without small projecting lobe (cf. *B. barbastella*). Ears fold back close to head when bat rests. Tragus long with covering of fine hairs; tip rounded.

Wings and interfemoral membrane pale brown, semi-translucent (cf. *B. barbastellus*). Tibia 47.8 (46–51)% of FA, n = 4. Tail 105 (96–119)% of HB, n = 4. Baculum (Turkmenistan) lanceolate in dorsal view; proximal part comparatively wide, stout and with well-marked furrow (cf. *B. barbastella* from Europe) (Strelkov 1987).

Skull with rostrum narrow and weak; braincase elongated and rounded; zygomatic arches slender and without marked dorsal curvature; zygomatic width < mastoid width. Supraorbital ridges poorly developed; sagittal crest very low or absent; lambdoid crest very weakly developed and less evident than in *B. barbastella*. Tympanic bullae comparatively small (cf. *Plecotus*), but larger than in *B. barbastella* (Harrison & Makin 1988). Auditory meati comparatively large (cf. *B. barbastella*); mastoid region inflated and with a prominent projecting flange (Figure 121b). Dentition as in *B. barbastella*.

Geographic Variation None in Africa.

Similar Species The only other vespertilionids in Africa that have ears with inner margins joined are:

Barbastella barbastellus. Outer margin of ear normally with small projecting lobe ca. half-way between base and tip; ear shorter (13–14 mm) and broader. Pelage, wings and interfemoral membrane dark, ventral pelage dark grey. Tympanic bullae and especially the auditory meati smaller; mastoid region less inflated and without projecting flange; lambdoid crest more evident.

*Barbastella leucomelas*

Plecotus spp. Ears much longer (32–40 mm). Six lower cheekteeth on each side.

Distribution In Africa, the nominate subspecies has been recorded from Sinai (Egypt) and from the Somalia–Masai Bushland BZ in Eritrea, but the reports are few and far between and it seems probable that they are records of vagrants. Von Heuglin (1862, 1877) listed this species from Massawa, Eritrea, and there is a specimen from ‘Erythrea’ in the MCZ, and the holotype is from Sinai. *Barbastella leucomelas* was also recorded from Senegal by de Rochebrune (1883), but there have been no further records of any *Barbastellus* from Senegal (Hayman & Hill 1971): furthermore, this record is more likely to refer to *B. barbastella* than *B. leucomelas*. Extraliminally: the nominate subspecies is known from Arabia and Iran, and *B. l. darjelingensis* is known from S Israel and Iran to N India, Nepal, W China and Japan.

Habitat No details available for the African records other than that Massawa is near the coast and in the semi-desert grassland and shrubland vegetation zone (terminology: White 1983).

Abundance Very rarely recorded in Africa. Has not been recorded in Sinai since the species was described (Corbet 1978).

Remarks Nothing is known about the biology of this species in Africa and there is very little information from elsewhere. Flight heavy and fluttering; sometimes close to ground, sometimes high (Roberts 1977). In Pakistan, roosts by day in crevices under bark and in tree hollows during summer (Roberts 1977). Also roosts in caves, tunnels, mine-shafts and old deserted houses (Cretzschmar 1826, Ognev 1928, Lay 1967). Roosts and forages singly (Roberts 1977). Litter-size (Eastern Europe and northern Asia): one or two (Ognev 1928).

Conservation IUCN Category: Least Concern (assessment based mainly on extralimital data).

Measurements

Barbastella leucomelas

FA: 39 (37–44) mm, n = 10

WS: n. d.

TL: 100 (92–107) mm, n = 4

T: 46 (33–58) mm, n = 8

E: 16 (15–18) mm, n = 4

Tr: 9.1, 14 mm, n = 2

Tib: 18.2 (17–20) mm, n = 4

HF: 6.6 (6–7) mm, n = 4

WT: n. d.

GLS: 15.3 (14.6–16.0) mm, n = 5

GWS: 8.3 (8.0–8.5) mm, n = 5

ZW: 7.7 (7.4–8.1) mm, n = 3

C–M³: 4.6 (4.3–4.9) mm, n = 8

Arabia, Israel, Iran (BMNH, HZM, SMF, Kock 1969a, Harrison & Makin 1988)

Key Reference Harrison & Bates 1991.

Meredith Happold

GENUS *Eptesicus*

Serotines

Eptesicus Rafinesque, 1820. Ann. Nature, p. 2. Type species: *Eptesicus melanops* Rafinesque, 1820 (= *Vespertilio fuscus* Beauvois, 1796).

A polytypic genus, considered by Hill & Harrison (1987) to contain 19 species, and by Simmons (2005) to contain 23 species of which five occur in Africa (see subfamily Vespertilioninae). Diagnostic combination of characters for African members: invariably four upper and five lower cheekteeth and two upper incisors on each side; ears comparatively and relatively short and not joined at base; 5th finger not shortened (considerably longer than metacarpals of 3rd and 4th fingers) (cf. *Nyctalus*); no body pattern; wings dark coloured, not reticulated; outer margin of ear not reaching mouth;

lower lip without lobe near posterior angle (cf. *Glauconycteris*); FA: >37.8 mm (except *E. floweri*); GLS: >15.0 mm. Dental formula: $\frac{2^{113}}{3_{123}} = 32$. Selected characters of African *Eptesicus* are illustrated in Figure 122. Species of *Pipistrellus* (*sensu lato*) sometimes share most of these characters but African *Eptesicus* (except *E. floweri*) are almost always larger (FA: 38–51 mm; GLS: 15.3–21.3 mm) than African *Pipistrellus* (FA: 23–39 mm; GLS: 10.0–15.4 mm). Furthermore, species of *Eptesicus* invariably have only one upper premolar on each side whereas, in contrast, 20 of the 28 African species of *Pipistrellus*

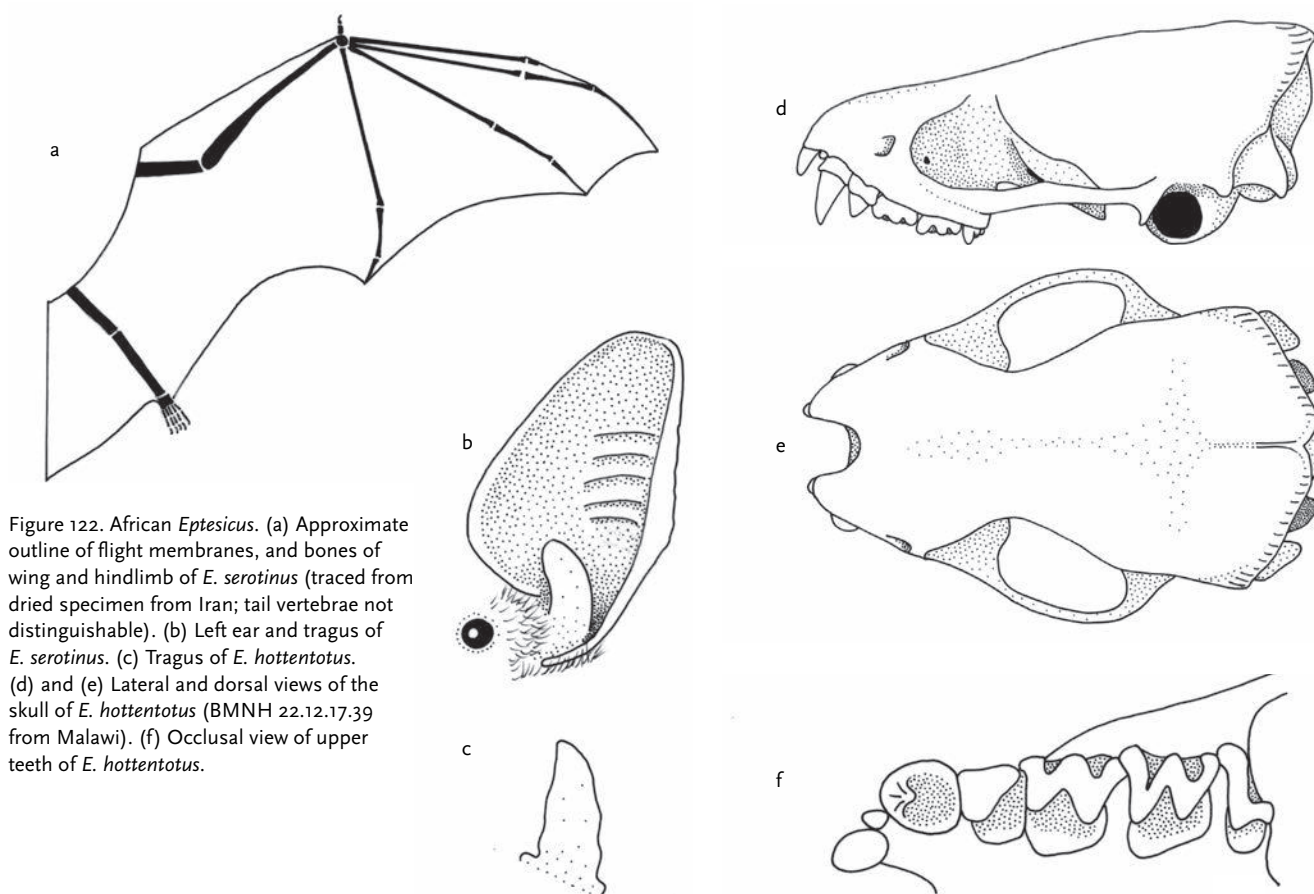


Figure 122. African *Eptesicus*. (a) Approximate outline of flight membranes, and bones of wing and hindlimb of *E. serotinus* (traced from dried specimen from Iran; tail vertebrae not distinguishable). (b) Left ear and tragus of *E. serotinus*. (c) Tragus of *E. hottentotus*. (d) and (e) Lateral and dorsal views of the skull of *E. hottentotus* (BMNH 22.12.17.39 from Malawi). (f) Occlusal view of upper teeth of *E. hottentotus*.

have two upper premolars on each side (although the anterior upper premolar is often minute and therefore sometimes not visible above the gum, and can be absent in some individuals). Also, in *Eptesicus*, the baculum (Figure 123) is more-or-less triangular (cf. variable but not triangular in *Pipistrellus*), and the chromosome number ($2n$) is 50 (cf. variable but always less than 50 in *Pipistrellus*).

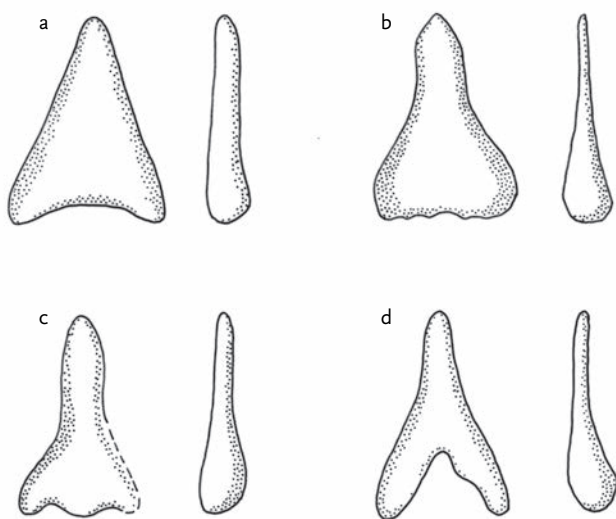


Figure 123. Bacula of African *Eptesicus*: dorsal views on left, lateral views of right side on right, tips uppermost. (a) *Eptesicus bottae innesi* from Cairo. (b) *E. hottentotus* from KwaZulu Natal. (c) *E. floweri lowei* from Sudan. (d) *E. serotinus isabellinus* from Morocco. All based on Hill & Harrison (1987). All drawn to same size (for scale drawings, see Hill & Harrison 1987).

Eptesicus was traditionally considered to contain ca. 33 species world-wide (Koopman 1993) and, traditionally, the generic distinction between *Eptesicus* and *Pipistrellus* was based on the absence or presence, respectively, of a second upper premolar (the anterior upper premolar). However, this proved unreliable because tooth reduction appears to have taken place independently in several lineages of the Vespertilionidae. Based on bacular morphology, Hill & Harrison (1987) retained only 19 species in *Eptesicus*, and placed the remaining species into *Neoromicia* (nine species; Africa only) and *Vespadelus* (five species; Australia only), both of which were considered to be subgenera of *Pipistrellus*. This rearrangement is supported by dental morphology (Menu 1987) and chromosomes (Heller & Volleth 1984, Volleth & Tidemann 1991, Volleth *et al.* 2001, Kearney *et al.* 2002). For further details, see genus *Pipistrellus*.

Of the species that remain in *Eptesicus*, five occur in Africa: *E. bottae*, *E. floweri*, *E. hottentotus*, *E. platyops* and *E. serotinus*. The relationships between these taxa are uncertain (Rosevear 1962, Kock 1969a, Ibáñez & Valverde 1985, Schlitter & Aggundey 1986) but, pending revision of the genus, we follow Koopman (1993) and Simmons (2005), and tentatively recognize all of these taxa as distinct species.

Eptesicus – as currently conceived – is distributed almost world-wide (with the exception of the islands of South-East Asia and Australia), in a wide variety of tropical, sub-tropical and temperate forests, woodlands, savannas and deserts. In Africa, one species is found mainly in the Rainforest BZ (Western Nigerian sub-region and Bioko I.), two mainly in savannas, one in the Sahara Arid BZ and one mainly in the Mediterranean Coastal BZ. No members of this genus are known from the Congolian rainforest.

Table 22. Key to the African species in the genus *Eptesicus*. Relative heights of the braincase are based on height as a percentage of GLS (details in Genus *Pipistrellus* and in *Eptesicus* species profiles). Measurements and distributions pertain only to Africa.

| Inner upper incisor | Ventral hairs | FA (mm) | GSL (mm) | Miscellaneous | Species |
|---------------------|---------------|--------------|------------|---|-----------------------|
| Unicuspid | Bicoloured | 48.2 (45–54) | 16.9–21.5 | Braincase relatively low
Savannas of southern and eastern Africa | <i>E. hottentotus</i> |
| Bicuspid | Bicoloured | 45, 50 | 18.8 | Braincase relatively high
Nigeria, Bioko I. and ? Senegal | <i>E. platyops</i> |
| Bicuspid | Bicoloured | 42.2 (38–47) | 15.3–18.0 | Braincase relatively high
Egypt (Cairo district) | <i>E. bottae</i> |
| Bicuspid | Unicoloured | 48.7 (45–52) | 18.1–20.1 | Braincase of medium relative height
Morocco, Algeria and Tunisia (except deep Sahara), to NW Libya | <i>E. serotinus</i> |
| Bicuspid | Unicoloured | 36.5 (34–38) | 12.0, 13.5 | Unique horny warts on forearms, legs and tail
Braincase relatively high
Sudan south of Sahara | <i>E. floweri</i> |

The species occurring in Africa can be distinguished by the characters and distributions given in Table 22. Further information is given in the Similar Species sections in which comparisons are made only between species of *Eptesicus* and *Pipistrellus* that occur in Africa.

For other characters and explanations of terminology, see genus *Pipistrellus*.

Victor Van Cakenberghe & Meredith Happold

Eptesicus bottae **BOTTA’S SEROTINE**

Fr. Sérotine de Botta; Ger. Bottas Breitflügelfledermaus

Eptesicus bottae (Peters, 1869). Monatsber. K. Preuss. Akad. Wiss. Berlin 1869: 406. Yemen. Nader & Kock (1990) limit the type locality to the area between Hodeida, Hays, Ta’izz and Al Muhka in SW Yemen.

Taxonomy Originally *Vesperus bottae*. Sometimes considered to belong to *E. serotinus* or *E. hottentotus*, but Harrison (1964) corrected this misconception. Synonyms: *innesi* and others extralimitally (Koopman 1993). Subspecies: six of which only one, *E. b. innesi*, occurs in Africa (Koopman 1994). Chromosome number (Soviet Central Asia, Greece): 2n = 50; aFN = 48 (Zima & Horáček 1981, Volleth *et al.* 2001).

Description Small to very small microbat without noseleaf and with tail more or less fully enclosed in interfemoral membrane; four upper and five lower cheekteeth and two upper incisors on each side; ears separated and short (13–18 mm); medium-sized for an African *Eptesicus* (FA: 38–47 mm); ventral hairs bicoloured; inner upper incisor bicuspid. Sexes similar in colour; ♀♀ on average slightly larger than ♂♂. Pelage soft, dense; mid-dorsal hairs 7–10 mm. Dorsal pelage dark cream; hairs with dark grey at base. Ventral pelage much paler; hairs whitish with pale greyish-brown bases. Ears brown to blackish-brown, relatively short, subtriangular with tip rounded. Tragus length ca. half of E; breadth almost constant over the entire length, tip blunt. Eyes very small. Wings and interfemoral membrane dark brown to blackish, semi-translucent; wings without white hind-border but sometimes with very narrow pale border. Tail protruding ca. 3.5 mm beyond membrane. Postcalcareal lobe well developed. Baculum short, flat, stout, triangular with rounded corners (Figure 123a; Hill & Harrison 1987) and see also Spitzenberger (1994).

Skull medium-sized for an African *Eptesicus*. Braincase relatively high (43% of GLS, n = 1) and broad (47% of GLS, n = 1). Rostrum fairly broad, flattened dorsally. Profile of forehead region (viewed laterally) weakly concave (for definition, see genus *Pipistrellus*). Occipital helmet present, sagittal and lambdoid crests moderately developed for this genus. Inner upper incisor large, bicuspid. Outer upper incisor very small (only just reaching above cingulum of inner incisor). Anterior upper premolar absent; canine and posterior premolar in contact. Lower molars myotodont (Menu 1987).

Geographic Variation None in Africa.

Similar Species Six other vespertilionids in North Africa have (on each side) two upper incisors, five lower cheekteeth and only one upper premolar or (at least sometimes) only one that is clearly visible above the gum:

Eptesicus serotinus. Ventral hairs unicoloured. Usually larger (FA: 48.7 [45–52] mm; GLS: 18.1–20.1 mm). Morocco to NW Libya.
Pipistrellus (5 spp.). Smaller (FA: 24–38 mm; GLS: 10.8–14.6 mm). Anterior upper premolar usually present although not always visible above gum.

For other African *Eptesicus*, see Table 22, p. 552.



Eptesicus bottae

Distribution In Africa, known only from the Sahara Arid BZ in the Cairo area of Egypt. Extralimittally: the subspecies in Egypt (*E. b. innesi*) occurs in Israel and Jordan (Harrison & Bates 1991); the other subspecies are recorded from Rhodes (Greece), Turkey, SW and SE Arabia, and from Iraq, Iran and Pakistan north-eastwards to NW China and Mongolia (Gaisler 1970, Harrison & Bates 1991, Simmons 2005). Le Berre (1990) mentions the presence of *E. bottae* in Morocco based on a record of *E. isabellinus* from Heim de Balsac (1948), but this record probably represents *E. serotinus isabellinus*, which occurs in NW Africa.

Habitat In SW Asia, apparently restricted to the deserts and semi-desert regions, but probably only occurs in localized areas, such as farmlands near water, where insects and suitable day-roosts are available. In Israel, has been observed 'flying over cultivated fields lined by eucalyptus and tamarisk trees, surrounded by desert' (Harrison & Bates 1991). Feldman *et al.* (2000) mention edges of vegetation and cliffs as the preferred habitat in Israel. In Iraq, found in gardens and date-groves near rivers, but not encountered in desert localities (Harrison & Bates 1991). In Oman, recorded flying over rocky mountain slopes at 1880–2100 m (Harrison & Bates 1991).

Abundance Apparently not very common anywhere. Based on museum records and the literature, the African subspecies is probably rare or very rare.

Adaptations No information for Africa. In Arabia, *E. bottae* is reported to fly strongly and to be noisy in flight (Harrison & Bates 1991). In Israel, flight-speed of 5.70 m/sec was recorded by Holderied *et al.* (2005). In Iraq, has been found roosting by day in buildings, including in crevices beneath the corrugated iron roofing of verandahs (Holderied *et al.* 2005).

Foraging and Food No information for Africa. Elsewhere, *E. bottae* forages by slow-hawking, rather high above ground (Harrison & Bates 1991). Begins foraging at dusk in some localities, but at some time after dusk at others. In Kurdistan, has been seen feeding on numerous insects gathered around an electric light (Harrison & Bates 1991). In Jordan, recorded flying over a pool, but it is not clear if the bats were foraging or coming to drink. In Israel, feeds mainly on Hymenoptera and Lepidoptera (Feldman *et al.* 2000).

Echolocation Search-phase call-shape (Israel) QCF. Start-frequency ca. 41 kHz; end-frequency and peak-frequency (mean \pm S.D.) 32.5 ± 0.87 kHz; call-duration 6.9 ± 1.32 ms; intercall-interval 155.6 ± 61 ms (134–143 calls, Holderied *et al.* 2005). The loudest calls emitted had an intensity of 121 ± 7.8 dB at 10 cm, and it was calculated from this that *E. bottae* would be able to detect large prey and conspecifics up to a distance of 21 m.

Social and Reproductive Behaviour No information.

Reproduction and Population Structure No information for Africa. From Israel, there are records of two ♀♀, each with twin embryos (crown–rump length ca. 14 mm), in Apr (Harrison & Bates 1991).

Predators, Parasites and Diseases Nader & Kock (1989) were unable to find ectoparasites and, although they do not exclude the possible loss of parasites during transport, they suggest that the lack of parasites might be the result of specific nesting sites or habits. This invites investigation.

Conservation IUCN Category: Least Concern (Africa and also extralimittally).

Measurements

Eptesicus bottae

FA: 42.2 (38–47) mm, n = 54

WS: 281.6 ± 7 mm, n = 6*

TL: n. d.

T: 39.5 (27–50) mm, n = 43

E: 15.6 (13–18) mm, n = 60

Tr: 6.5 (3.9–8.8) mm, n = 50

Tib: 16.7 (13–20) mm, n = 51

HF: 8.8 (7–10) mm, n = 24

WT: 14.0 (14.0–14.0) g, n = 3

GLS: 16.6 (15.3–18.0) mm, n = 46

GWS: 10.9 (10.0–12.7) mm, n = 43

C–M³ (alv.): 6.1 (5.6–6.8) mm, n = 47

Throughout geographic range (BMNH, ZMB)

*Mean \pm S.D.; Israel (Holderied *et al.* 2005)

Key References Feldman *et al.* 2000; Harrison & Bates 1991; Nader & Kock 1989.

Victor Van Cakenberghe & Meredith Happold

Eptesicus floweri HORN-SKINNED SEROTINE

Fr. Sérotine de Flower; Ger. Warzen-Breitflügelfledermaus

Eptesicus floweri (de Winton, 1901). Ann. Mag. Nat. Hist., ser. 7, 7: 46. Wad Marium, Khartoum, Sudan.

Taxonomy Originally *Glauconycteris floweri*. This species has unique horny warts on the forearms and consequently has been placed in a separate subgenus, *Rhinopterus*, by some authors, including Hayman & Hill (1971), Hill & Harrison (1987) and Koopman (1993, 1994). Synonyms: *lowei*. Subspecies: none recognized but see Geographic Variation. Chromosome number: not known.

Description Very small microbat without noseleaf and with tail more or less fully enclosed in interfemoral membrane; four upper and five lower cheekteeth and two upper incisors on each side; ears separated and short (ca. 10 mm); the smallest African *Eptesicus* (FA: 34–38 mm); ventral hairs unicoloured; inner upper incisor bicuspid; unique horny warts on forearms, legs and tail. A poorly known species. Dorsal pelage yellowish-fawn to pale rusty-brown; hairs unicoloured. Ventral pelage yellowish-brown on throat, becoming paler or pure white on abdomen; hairs unicoloured. Muzzle and cheeks, naked, dark brown. Ears dark brown, relatively short, subtriangular with tip rounded. Tragus length ca. 40% of E; anterior margin straight; posterior margin convex with lobe at base; broadest at mid-height. Wings and interfemoral membrane pale brown, wings of holotype of *floweri* (and one other specimen) with very faint pale hind-border, a third specimen with a conspicuous white hind-border (no other information); horny warts (denticles) on arm-wings and anterior three-quarters of interfemoral membrane give the membranes a spotted appearance. The horny warts on the dorsal surfaces of the forearms, tibiae and tail are characteristic of the monotypic subgenus *Rhinopterus*. Postcalcareal lobe fairly well developed. Tail ca. 76% of HB. Baculum short, flat, roughly triangular (Figure 123c, Hill & Harrison 1987).

Skull small for an African *Eptesicus*. Braincase relatively high (42, 43% of GLS, $n = 2$) and broad (47, 50% of GLS, $n = 2$). Rostrum short and broad; dorsal surface almost completely flat with angular margins (therefore clearly distinguishable from the lateral surfaces). Profile of forehead region (viewed laterally) almost straight. No occipital helmet; sagittal crest moderate, low or absent; lambdoid crests moderate to weakly developed. Inner upper incisor bicuspid. Outer upper incisor very small, barely exceeding cingulum of inner incisor. Anterior upper premolar absent; canine and posterior premolar in contact. Lower molars myotodont (G. Bennell pers. comm.).

Geographic Variation No subspecies recognized by Koopman (1994) and Simmons (2005). Braestrup (1935) regarded *E. floweri* as a variable species, there being a smaller form with ventral pelage buff (*floweri*) and a larger form with ventral pelage whitish (formerly *lowei*). Both forms occur sympatrically in some parts of Sudan, so the variation is apparently not geographic. See also Distribution.

Similar Species No other African vespertilionid has horny warts. The South African *notius* was described as a bat with warts and referred to *Rhinopterus*, but it is probable that the warts of this individual were caused by nematodes and this form is now considered a subspecies of *Pipistrellus capensis* (Koopman 1975).

*Eptesicus floweri*

Distribution Endemic to Africa. Known with certainty only from the Sahel Savanna and Sudan Savanna BZs in Sudan (Kock 1969a, Koopman 1975). A specimen from Timbuktu, Mali, is either a small representative of *E. floweri* or a separate form (Braestrup 1935). In this Malinese specimen, the inner upper incisor is unicuspid and the outer upper incisor is two-thirds of the height of the inner (cf. the Sudanese *E. floweri* described above), suggesting this specimen represents a separate form (E. Thorn pers. comm.). Recently, two specimens (EBD 26179-80) were reported from Mahmûdê L., Wilaya Hodh Ech, Mauritania (16° 29.969'N, 07° 42.911'W) by Padial & Ibáñez (2005); not mapped. The FA lengths of these specimens are 33.5 mm (♀) and 33.2 mm (♂); therefore they are slightly smaller than specimens from Sudan and Mali (see Measurements).

Habitat Recorded from *Acacia* wooded grassland and deciduous bushland, semi-desert grassland and shrubland, and mosaics of edaphic grassland with *Acacia* wooded grassland (terminology: White 1983). Two were shot beside a pool in Sudan (NMW). Possibly limited to habitats with *Acacia* spp. (Koopman 1975). The recent specimens from Mauritania were also found in 'Acacia formations of the Sahel' (Padial & Ibáñez 2005).

Abundance Uncertain. De Winton (1901) reported it common at Shendi in N Sudan. Rarely collected.

Remarks Flies slowly and apparently forages near the ground amongst the dense and thorny *Acacia* bushes. Has also been observed flying low over ponds (von Wettstein 1917). Roosts by day in *Acacia*

thickets – low down near the roots of these trees (de Winton 1901). At dusk, individuals crawl up the branches and take flight, uttering a very characteristic squeak, which they continue to make during flight. The horny warts on the wings are also characteristic of the African molossid *Platymops setiger*, and the non-African *Eptesicus nasutus*, suggesting an ecological parallel with these species (E. Thorn pers. comm.).

Conservation IUCN Category: Least Concern.

Acacia senegalensis, the widely distributed tree that provides the roosting sites of this species in Sudan, is a valuable source of Gum Arabic, but the extent to which harvesting of Gum Arabic has affected the abundance of *E. floweri* is not known (D. Kock pers. comm.).

Measurements

Eptesicus floweri

FA: 36.5 (34–38) mm, n = 5

WS: n. d.

TL: 79 or 83*

T: 34 or 36*

E: 10 mm, n = 1

Tr: 4.1 mm, n = 1

Tib: 12 mm, n = 1

HF: n. d.

WT: n. d.

GLS: 12.0, 13.5 mm, n = 2

GWS: 8.4 mm, n = 1

C–M³ (alv.): 4.4, 4.9 mm, n = 2

Sudan (AMNH, BMNH and literature)

*de Winton 1901 and Thomas 1915b

Key References de Winton 1901; Kock 1969a; Padial & Ibáñez 2005; Thomas 1915b.

Victor Van Cakenberghe & Meredith Happold

Eptesicus hottentotus LONG-TAILED SEROTINE

Fr. Sérotine hottentote; Ger. Hottentotten-Breitflügelfledermaus

Eptesicus hottentotus (A. Smith, 1833). S. Afr. Quart. J. 2: 59. Uitenhage, Cape Province, South Africa.

Taxonomy Originally *Vespertilio hottentota*. Synonyms: *augusticeps*, *bensoni*, *megalurus*, *pallidior*, *portavernus*, *smithi*. Subspecies: three or four (see Geographic Variation). Chromosome number (Zimbabwe, South Africa): 2n = 50; aFN = 48; X is a medium-sized submetacentric and Y a small acrocentric (Peterson & Nagorsen 1975, Rautenbach *et al.* 1993, Kearney *et al.* 2002).

Description Small microbat without noseleaf and with tail more or less fully enclosed in interfemoral membrane; four upper and five lower cheekteeth and two upper incisors on each side; ears separated and short for a vespertilionid (14–20 mm); one of the three large African *Eptesicus* (FA: 45–54 mm); ventral hairs bicoloured; inner upper incisor unicuspid (cf. bicuspid in other African *Eptesicus*). Males on average with slightly shorter FA than ♀♀, at least in some parts of geographic range (Namibia). Pelage sleek, soft and dense; mid-dorsal hairs 7–9 mm. Dorsal pelage varying geographically from pale brown to almost black, often with silky sheen; hairs dark at base with paler tips. Ventral pelage paler, often with creamy sheen; hairs with basal two-thirds blackish-brown, terminal third pale greyish-brown with cream or whitish tips. Ears dark brown to blackish, relatively short, tip rounded. Tragus length ca. one-third of E; broadest at base; posterior margin mostly straight but smoothly convex near tip; tip rounded (Figure 122c). Wings and interfemoral membrane brown (when pelage is comparatively pale) to blackish-brown; no white hind-border. Tail 73 (58–84)% of HB, therefore (on average) not relatively longer than in other African *Eptesicus*. Tail with terminal vertebra slightly protruding beyond interfemoral membrane. Postcalcaneal lobe well developed. Baculum short, roughly triangular but with concave sides, flat but with proximal end thicker than distal end (Figure 123b) (Hill & Harrison 1987).

Skull (Figure 122d and e) large for an African *Eptesicus*. Braincase relatively low (38.8 [37–42]% of GLS, n = 19) and narrow (45.7

[42–49]% of GLS, n = 43). Rostrum broad. Profile of forehead region (viewed laterally) straight. Occipital helmet present; sagittal crest slight; lambdoid crest well developed. Inner upper incisor large, unicuspid. Outer upper incisor minute. Anterior upper premolar absent; canine and posterior premolar in contact (Figure 122f). Lower molars myotodont.

Geographic Variation Based on measurements and/or pelage colouration, the following taxa have been given subspecific status by some authors, but more information and material are needed to confirm their status:

E. h. portavernus: SW Kenya. According to Schlitter & Aggundey (1986), this subspecies is larger and heavier than the other subspecies, and has a shorter palate and deeper braincase. Dorsal pelage pale brown; ventral pelage pale tan. However, only two specimens are known.

E. h. bensoni: E Zambia, Malawi and NW Mozambique and across Zimbabwe to E South Africa (Rautenbach *et al.* 1984, Schlitter & Aggundey 1986, Koopman 1994). Dorsal pelage dark brown to almost black; ventral pelage buff.

E. h. pallidior: Namibia to NW Cape Province (Meester *et al.* 1986). Dorsal pelage pale brown to fawn; ventral pelage whitish-buff with irregular darker patches. Considered a synonym of *hottentotus* by Schlitter & Aggundey (1986).

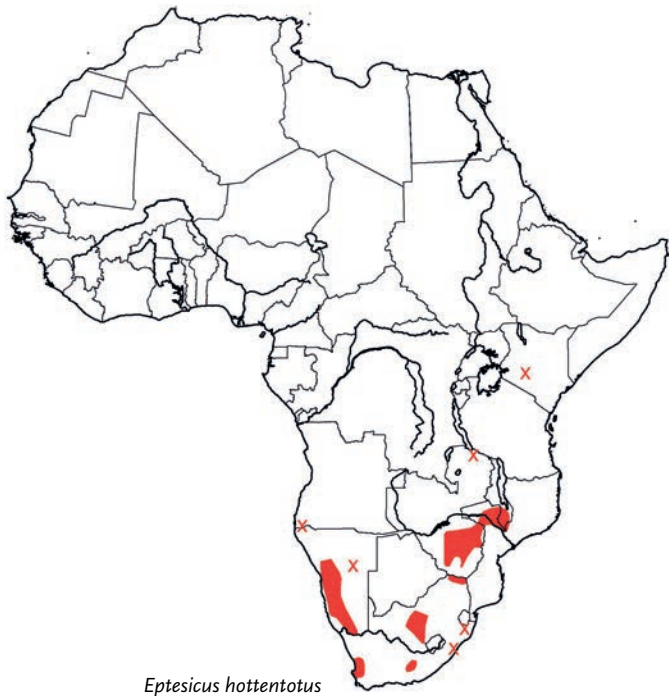
E. h. hottentotus: S and SW Cape Province (Meester *et al.* 1986), not extending far inland. Dorsal pelage deep reddish-brown (Smith 1833) or brown, sometimes with yellowish tinge (specimens from Algeria State Forest; T. Kearney pers. comm.).

Similar Species

Eptesicus serotinus. Inner upper incisor bicuspid. North Africa.

E. bottae. Inner upper incisor bicuspid. Egypt.

E. platyops. Inner upper incisor bicuspid. Senegal, Nigeria and Bioko I.



E. floweri. Much smaller (FA: 34–38 mm; GLS: 12.0, 13.5 mm).

Horny warts on forearms, legs and tail. Sudan.

Pipistrellus (28 African spp.). All much smaller (FA: <40 mm).

Distribution Endemic to Africa. Recorded from the Somalia–Masai Bushland in Naivasha District, Kenya, and from all of the biotic zones in south-central and southern Africa. Recorded from scattered localities in NE Zambia, SW Angola, Zimbabwe, Malawi, NW Mozambique, Namibia and South Africa (Smithers & Lobão Tello 1976, Smithers 1983, Schlitter & Aggundey 1986, Ansell & Dowsett 1988, Crawford-Cabral 1986, Lynch 1994, Watson 1998, Taylor 2000, T. Kearney pers. comm.). Map based on above sources and data from V. Van Cakenberghe (pers. comm.).

Habitat Woodland savannas, and along rivers with permanent water in deserts (e.g. along the Kuiseb R. in the Namib Desert). In Kenya, two were mist-netted in rocky gorges near water. In Malawi, recorded from the rocky escarpment of the Central Plateau (Ntcheu) and from flat country with riverine forest, marshlands and farmlands at the confluence of Shire and Ruwara Rivers (Chiromo). In Zimbabwe, most records are in miombo woodland in the vicinity of gorges and granitic hills (Cotterill 1996a, unpubl.). In South Africa, all records are from the vicinity of cliffs (T. Kearney pers. comm.).

Abundance Locally abundant in NE Zimbabwe (Mutoko District) with repeated records from Bvumba (eastern highlands) and Marondera over the past three decades (Cotterill 1996a). Locally abundant at Cederberg, Western Cape Province, South Africa (T. Kearney pers. comm.). Rarely recorded in Malawi (Happold & Happold 1997).

Adaptations Aspect ratio medium; wing-loading high (Aldridge & Rautenbach 1987). Flight predicted to be slow and manoeuvrable

in clutter, faster while foraging in semi-open areas (Norberg & Rayner 1987). Day-roosts include dry caves, one very wet cave, abandoned mines, a small hollow in rocks at the entrance of an old mine inhabited by *Miniopterus natalensis*, and the outside wall of a building (Smithers 1983, Herselman & Norton 1985). Individuals hang from the walls in very loose formations. Has been mist-netted over water.

Foraging and Food No information. Based on wing morphology, predicted to forage by slow-hawking in both moderately cluttered areas and open spaces. One was mist-netted flying low over a marsh (Herselman & Norton 1985). Six were captured in mist-nets set partly over water and partly over land at the edge of the water; all were caught over the land (Seamark 2005). Diet not known.

Echolocation Calls of one individual (flying in a room) were broad bandwidth calls (20–54 kHz) of short duration (2–4 ms), with peak-frequency 28–32 kHz and usually a strong harmonic component (Taylor 2000). See also Monadjem *et al.* (2010).

Social and Reproductive Behaviour Roosts singly or in small groups. Smithers (1983) did not find more than 3–4 roosting together and noted that they hung together in loose clusters; five were taken from a small hollow in rocks (not known if any escaped) (Herselman & Norton 1985).

Reproduction Litter-size: no information. Reproductive chronology not known. At ca. 17°S (near Mutoko District, NE Zimbabwe), 9 of 9 ♀♀ were either heavily pregnant or lactating at beginning of hot wet season (mid-Nov) (F. P. D. Cotterill unpubl.).

Predators, Parasites and Diseases Ectoparasites include a mite *Pteracarus pusillus* (Acari: Myobiidae) (Anciaux de Faveaux 1984).

Conservation IUCN Category: Least Concern.

Considered threatened in Malawi (Happold & Happold 1997).

Measurements

Eptesicus hottentotus

FA: 48.2 (45–54) mm, n = 68

WS (d): 353.3 (340–363) mm, n = 4

TL: 116.0 (100–135) mm, n = 30

T: 49.1 (38–58) mm, n = 40

E: 16.9 (14–20) mm, n = 40

Tr: 6 mm, n = 3

Tib: 19.0 (17–21) mm, n = 4

HF: 10.1 (9–11) mm, n = 30

WT: 15.9 (10.8–24.5) g, n = 27

GLS: 19.6 (16.9–21.5) mm, n = 77

GWS: 12.9 (11.7–14.1) mm, n = 74

C–M³: 7.0 (6.5–7.7) mm, n = 48

Throughout geographic range (AM, BMNH, HZM, NMZB, TM, USNM, Schlitter & Aggundey 1986)

Key References Schlitter & Aggundey 1986; Smithers 1983.

F. P. D. Cotterill & Meredith Happold

Eptesicus platyops LAGOS SEROTINE

Fr. Sérotine à grands yeux; Ger. Lagos-Breitflügelfledermaus

Eptesicus platyops (Thomas, 1901). Ann. Mag. Nat. Hist., ser. 7, 8: 31. Lagos, Western Region, Nigeria.

Taxonomy Originally *Vespertilio platyops*. The taxonomic position of *Eptesicus platyops* is uncertain. Sometimes considered to be a subspecies of *Eptesicus hottentotus* (e.g. Rosevear 1962) or *Eptesicus serotinus* (Ibáñez & Valverde 1985). Kock (1969a) indicates that affinity with *Eptesicus bottae* is another possibility. Koopman (1975) suggests that *platyops*, *loveni* (Granvik, 1924) from Kenya and *hottentotus* might be subspecies of *E. serotinus*, but concludes that all should be retained as separate species until the genus has been thoroughly revised. Schlitter & Aggundey (1986) concluded that the holotype from Lagos was smaller in size than *E. hottentotus portavernus*, and therefore not identical with either *E. hottentotus* or *E. serotinus*. They also showed that the holotype of *loveni* is actually a young *Myotis tricolor*. Synonyms: none. Chromosome number: not known.

Description Small microbat without noseleaf and with tail more or less fully enclosed in interfemoral membrane; four upper and five lower cheekteeth and two upper incisors on each side; ears separated and short (ca. 16 mm); one of the three large African *Eptesicus* (FA: 45, 50 mm); ventral hairs bicoloured; inner upper incisor bicuspid. Pelage silky. Dorsal pelage pale to medium fawn; hairs with basal half brown. Ventral pelage paler (cream to whitish); hairs with fawn at base. Ears brown, relatively short; inner margin convex with maximum curvature around basal third; outer margin mainly convex with 1–2 concave sections and a low rounded lobe at the base; tip very rounded. Tragus broad and blunt; broadest part mid-way along length; anterior margin straight; posterior margin convex (without abrupt angle) and with small triangular lobe at base. Wings brown with narrow white hind-border. Interfemoral membrane brown; tail with terminal vertebra protruding beyond membrane; postcalcareal lobe small. Tail ca. 65% of HB. Bacular morphology not known.

Skull large and robust for an African *Eptesicus*. Braincase relatively high (44% of GLS, $n = 1$) and broad (47% of GLS, $n = 1$) although Thomas (1901) described this species as having a very flat skull. Profile of forehead region (viewed laterally) concave (holotype) or straight (IRSN 12426 from Senegal). No occipital helmet; sagittal crest very weak posteriorly, lambdoid crest even weaker. Inner upper incisor large, broad, flattened, bicuspid. Outer upper incisor very small, barely exceeding cingulum of inner incisor. Anterior upper premolar absent. Lower molars myotodont (G. Bennell pers. comm.).

Geographic Variation None.

Similar Species

Eptesicus hottentotus. Inner upper incisor unicuspid. Braincase relatively low. East Africa, south-central Africa and southern Africa.

E. floweri. Much smaller (FA: 34–38 mm). Horny warts on forearms, legs and tail.

E. serotinus. North Africa (see Table 22, p. 552).

E. bottae. North Africa (see Table 22).

Pipistrellus (28 African spp.). Smaller (FA: <40 mm).

*Eptesicus platyops*

Distribution Endemic to Africa. The only records are those of the holotype from Lagos (Nigeria) and three subadult specimens from Bioko I. (all in the Rainforest BZ), and another specimen (IRSN 12426) reputedly from Senegal (biotic zone not known).

Habitat Uncertain. No details are available for the type locality. On Bioko I., the bats were recorded in a cocoa plantation (Ibáñez & Valverde 1985). The specimen reputedly from Senegal presumably came from dry open-woodland country but localities were seldom recorded accurately when these records were made (Rosevear 1965).

Abundance Uncertain. Very rarely collected; probably rare to extremely rare, but the record of three subadult specimens from Bioko I. suggests that it might be more abundant at this locality than elsewhere.

Remarks Nothing else is known about this species.

Conservation IUCN Category: Data Deficient.

Measurements

Eptesicus platyops

FA: 45, 50 mm

WS (c): ca. 240 mm*

TL: n. d.

HB: ca. 60–75 mm*

T: 40, 49 mm*

E: 16, – mm

Tr: 3.7, – mm

Tib: 18, 20 mm
 HF: n. d.
 WT: n. d.
 GLS: 18.8, – mm
 GWS: 13.4, – mm
 C–M³ (alv.): 6.8, 7.0 mm

Nigeria (holotype BMNH 1888.5.17.3) and Senegal (IRSN 12426)
 *Rosevear 1965

Key References Ibáñez & Valverde 1985; Rosevear 1962, 1965; Thomas 1901.

Victor Van Cakenberghe & Meredith Happold

Eptesicus serotinus **COMMON SEROTINE**

Fr. Séroline commune; Ger. Breitflügel-Fledermaus

Eptesicus serotinus (Schreber, 1774). Die Säugethiere, 1: 167. France.

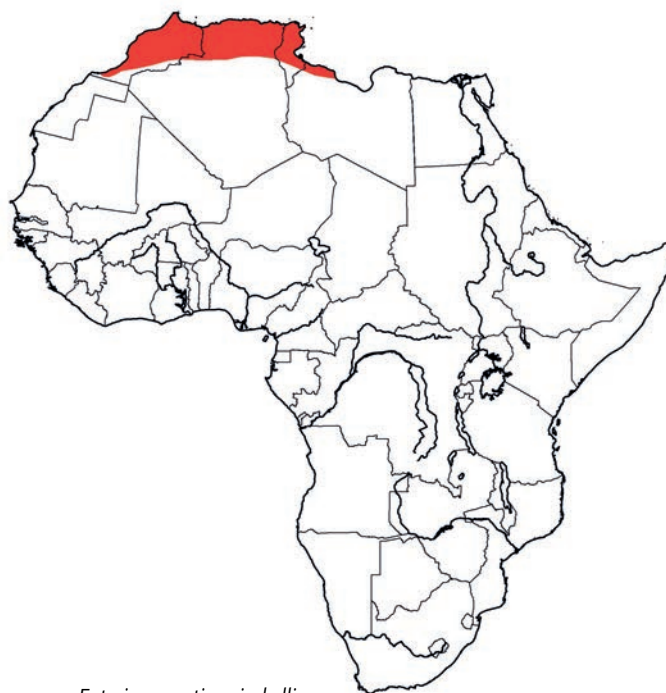
Taxonomy Originally *Vespertilio serotinus*. Synonyms: *isabellinus* in Africa, 22 others extraliminally (Simmons 2005). Subspecies: nine; one in Africa. Chromosome number (Tunisia): $2n = 50$; $aFN = 48$ (Baker *et al.* 1974). Since this profile was written, the specific status of *isabellinus* has been restored by Benda *et al.* (2004d), Mayer *et al.* (2007), Artyushin *et al.* (2009) and Juste *et al.* (2009): see Appendix. Consequently, this profile contains some data for *E. serotinus* that does not apply to *E. isabellinus*.

Description Small microbat without noseleaf and with tail more or less fully enclosed in interfemoral membrane; four upper and five lower cheekteeth and two upper incisors on each side; ears separated and short for a vespertilionid (12–18 mm); one of the three large African *Eptesicus* (FA: 45–52 mm); ventral hairs unicoloured; inner upper incisor bicuspid. Females slightly larger than ♂. Pelage soft, sleek with silky sheen; mid-dorsal hairs ca. 7–9 mm. Dorsal pelage pale yellowish-brown with creamy sheen; hairs with slightly darker bases. Ventral pelage paler, no distinct boundary with dorsal pelage; hairs unicoloured. Muzzle and cheeks naked, dark brown. Ears dark brown, subtriangular; outer margin with five transverse folds. Tragus length ca. one-third of E; posterior margin smoothly convex; tip bluntly pointed. Wings and interfemoral membrane dark brown; wings without white hind-border. Calcars robust, reaching one-third to half-way to tip of tail. Tail protruding 2–3 mm beyond margin of interfemoral membrane (ca. 1.5 vertebrae). Baculum Y-shaped, flattish but proximal end thicker than distal end (Figure 123d) (Hill & Harrison 1987).

Skull large and robust for an African *Eptesicus*. Braincase of medium relative height (ca. 42% of GLS, $n = 2$) and broad (48–49% of GLS, $n = 3$). Rostrum broad and flat; lachrymal ridges prominent. Profile of forehead region (viewed laterally) straight. No occipital helmet; sagittal crest low but distinct in adults; lambdoid crest moderately developed. Inner upper incisor bicuspid (secondary cusp clearly present in unworn teeth). Outer upper incisor small, slightly higher than cingulum of inner incisor. Anterior upper premolar absent; canine and posterior premolar in contact. Lower molars myotodont.

Geographic Variation None recorded in Africa. Only one of nine subspecies recognized by Simmons (2005) occurs in Africa:

E. s. isabellinus: North Africa (extraliminally Iberian Peninsula). Paler than nominate subspecies (Europe to Caucasus), but similar in cranial dimensions and external characters (Harrison 1963a).



Eptesicus serotinus isabellinus

Similar Species Five other vespertilionids in North Africa have (on each side) two upper incisors, five lower cheekteeth, and only one upper premolar or (at least sometimes) only one which is clearly visible above the gum:

Eptesicus bottae. Ventral hairs bicoloured. Usually smaller (FA: 42.2 [38–47] mm; GLS: 15.3–18.0 mm). Egypt.

Pipistrellus spp. Smaller (FA: 24–38 mm; GLS: 10.8–14.6 mm). Anterior upper premolar usually present although not always visible above gum.

For distinguishing characters and distributions of other African *Eptesicus*, see Table 22, p. 552.

Distribution In Africa, *E. s. isabellinus* is recorded from the Mediterranean Coastal and Afromontane–Afroalpine BZs, and marginally from the adjacent Sahara Arid BZ, in North Africa. Widely distributed in Morocco, Algeria, Tunisia and NW Libya, except in the deep Saharan regions of these countries (Hanák & Elgadi 1984). Extraliminally: *E. s. isabellinus* occurs in Iberian Peninsula. *Eptesicus*

serotinus (excluding *isabellinus*) is widespread from England, Europe and eastwards to Himalayas, Thailand, China and Korea. Also, most islands in the Mediterranean and Lanzarote (Canary Is.). See Taxonomy for new information.

Habitat *Eptesicus s. isabellinus* inhabits lowlands as well as mountains. Has been mist-netted among trees in the coastal zone of Algeria, and over a stream and among rocks in almost treeless regions of the Aures Mts and Saharan Atlas (Kowalski & Rzebik-Kowalska 1991). Well adapted to living in areas occupied by people.

Abundance Common. Although not a cave-dwelling species, records in Africa are numerous and it is the most common species in mist-net sampling from the coastal Oranais to Aures Mts in Algeria.

Adaptations Aspect ratio low; wing-loading medium; wing-tip short and rounded (*E. serotinus*: Norberg & Rayner 1987). Flight fairly slow; mean flight speed in open 9.8 m/s (Norberg 1987). In summer, commonly roosts in buildings, occasionally in hollow trees (especially palm trees in the south). In winter, roosts in buildings and occasionally in underground sites and in cracks in rocks. Sometimes uses night-roosts. Generally stays within 5 km of roosts, but movements of up to 300 km have been recorded between summer- and winter-roosts in Europe. In England, individual home ranges varied from 0.16 to 47.58 km² (Robinson & Stebbings 1997). In North Africa, active on warm nights during winter (Gaisler & Kowalski 1986).

Foraging and Food Mostly forages by slow-hawking, occasionally by gleaning (lands on foliage with wings outstretched). Forages in parklands, along hedges and edges of woodlands (and sometimes within woodlands), over pastures and streams, and around street lights. Flies slowly in large loops above groves and open terrain; often in groups of 2–3 individuals. Foraging is bimodal with main peak at beginning of night and a second lower peak before dawn (Gaisler & Kowalski 1986). In western Europe, *E. serotinus* feeds on large Coleoptera (mainly Scarabaeoideae) and Lepidoptera, also Tipulidae and other small Diptera, Hemiptera and Hymenoptera (Robinson & Stebbings 1993, Beck 1995, Catto *et al.* 1996, Vaughan 1997).

Echolocation No data for Africa. In Europe, search-phase call-shape (5–10 m from obstacles): steep FM/QCF. Intensity high; start-frequency 53 kHz; end-frequency (CF-component) and peak-frequency 24–27 kHz; call-duration 15–20 ms; inter-call interval 150–250 ms (Jones 1993, Tupinier 1996). For variation with height of flight, see Jensen & Miller (1999).

Social and Reproductive Behaviour In Europe, adult ♀♀ establish maternity colonies of ca. 20–60 individuals, which show

high fidelity to their day-roost; at this time, ♂♂ roost singly or in small groups. Mating occurs in early autumn. In winter, both sexes are mainly found singly in cracks and crevices (Arthur & Lemaire 1999).

Reproduction and Population Structure Litter-size (Algeria): 1 (n = 1) or 2 (n = 5) (Kowalski & Rzebik-Kowalska 1991). Reproductive chronology in Africa not known. At 35°41'N (near Oran, Algeria), the majority of ♀♀ mist-netted in late May and mid-Jun were pregnant (most embryos 10–15 mm long); 4 of 4 were lactating in mid-Jul; no data for other months (Kowalski & Rzebik-Kowalska 1991). In Tunisia, 4 of 4 ♀♀ were lactating in early Jun; no data for other months (Baker *et al.* 1974). Weaning age: 6–7 weeks. Maximum life-span: 19.5 years.

Predators, Parasites and Diseases Occasionally preyed on by Barn Owls *Tyto alba*, Pharaoh Eagle-owls *Bubo ascalaphus* and Tawny Owls *Strix aluco* (Aulagnier 1989). Ectoparasites include a flea *Ischnopsylla intermedia* (Siphonaptera: Ischnopsyllidae) and a tick *Argas transgaripepinus* (Acari: Argasidae) (Anciaux de Faveaux 1984). In western Europe, this bat is a principal reservoir for rabies, EBL1; this Lyssavirus is suspected to originate from North Africa (Amengual *et al.* 1997).

Conservation IUCN Category: Least Concern.

In North Africa and Europe, populations are likely to remain stable provided that pesticides do not reduce the numbers of dung beetles and other large insects on which these bats feed.

Measurements

Eptesicus serotinus isabellinus

FA: 48.7 (45–52) mm, n = 52

WS: n. d.

TL: 116.6 (105–132) mm, n = 52

T: 49.7 (43–56) mm, n = 52

E: 16.6 (12–18) mm, n = 52

Tr: n. d.

Tib: 19, 21 mm, n = 2*

HF: 11.0 (8.5–13) mm, n = 52

WT: 20.6 (15–27) g, n = 20

GLS: 19.0 (18.1–20.1) mm, n = 45

GWS: 13.3 (12.6–14.2) mm, n = 45

C–M³: 7.0 (6.5–7.3) mm, n = 45

Algeria (Kowalski & Rzebik-Kowalska 1991)

*BMNH

Key References Gaisler & Kowalski 1986; Hanák & Elgadi 1984; Harrison 1963a; Kowalski & Rzebik-Kowalska 1991.

Stéphane Aulagnier

GENUS *Glauconycteris*

Butterfly Bats

Glauconycteris Dobson, 1875. Proc. Zool. Soc. Lond. 1875: 383. Type species: *Kerivoula poensis* Gray, 1842.



Glauconycteris argentata.

A polytypic genus with 12 species recognized by Simmons (2005). Another species is referred to as *G. cf. poensis* by Fahr & Kalko (2011). Endemic to Africa south of the Sahara. Diagnostic combination of characters: four upper and five lower cheekteeth and two upper incisors on each side; ears short and not joined at base; outer margin of ear reaches mouth, head not flattened; lower lip with lobe at corner of mouth; fifth finger not shortened (considerably longer than metacarpal of fourth finger); six species with body pattern of lines and/or spots, two other species with reticulated wings (dark lines on pale background) and two species without body patterns or reticulated wings. Second phalanx of third finger ca. twice as long as first phalanx (cf. about three times as long as the first in *Miniopterus*, and about equal to the first in most other vespertilionids). Dental formula: $2^{113}/_{3123} = 32$. The flight-membranes, bones of wing, hindlimb and tail of a representative of the genus are shown in Figure 117b, and the ear and tragus, and craniodental characters in Figure 124.

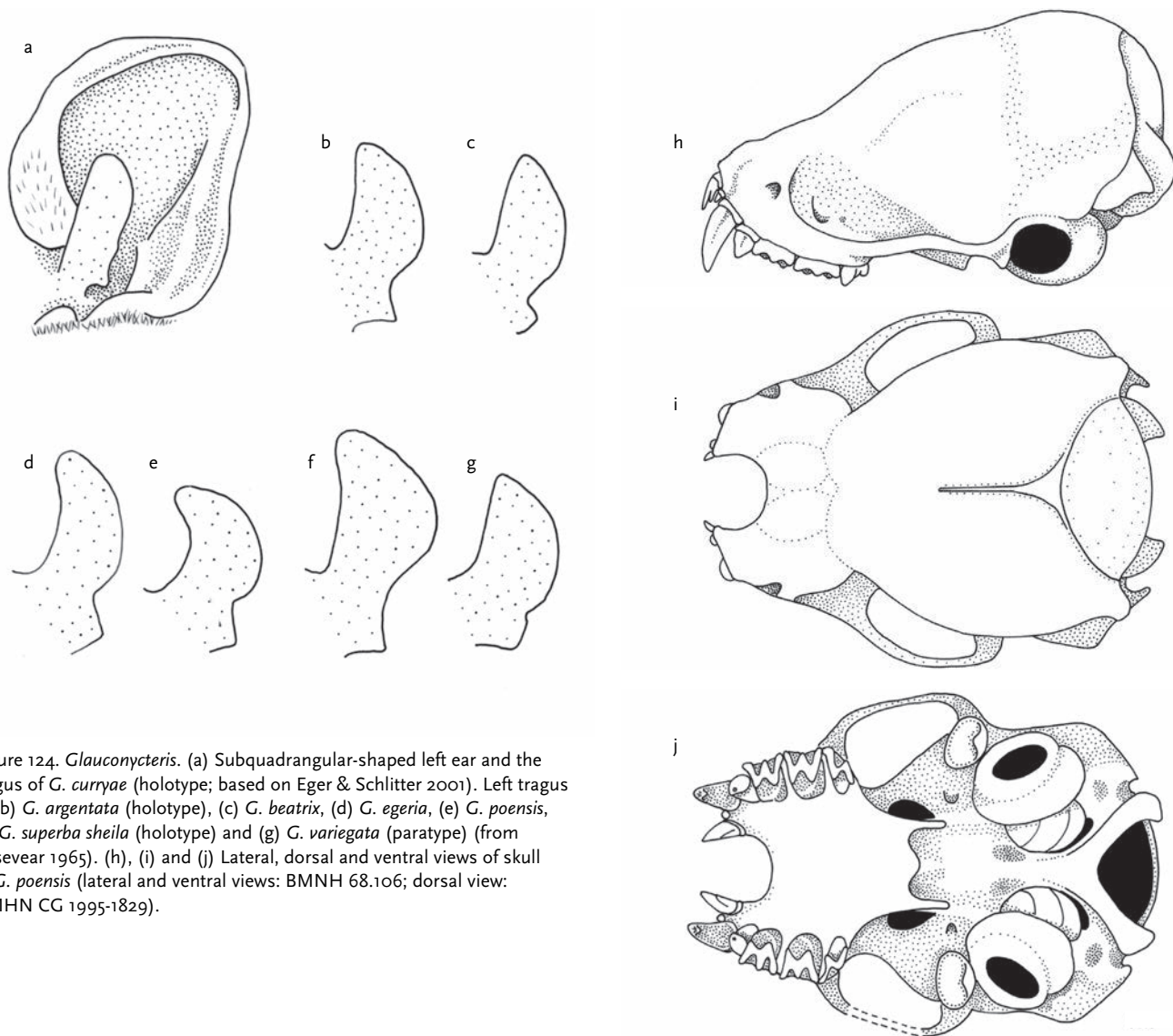


Figure 124. *Glauconycteris*. (a) Subquadrangular-shaped left ear and the tragus of *G. curryae* (holotype; based on Eger & Schlitter 2001). Left tragus of (b) *G. argentata* (holotype), (c) *G. beatrix*, (d) *G. egeria*, (e) *G. poensis*, (f) *G. superba sheila* (holotype) and (g) *G. variegata* (paratype) (from Rosevear 1965). (h), (i) and (j) Lateral, dorsal and ventral views of skull of *G. poensis* (lateral and ventral views: BMNH 68.106; dorsal view: NMNH CG 1995-1829).

Glauconycteris was created as a subgenus of *Chalinolobus*, then raised to generic status by de Winton (1901). Subsequently still sometimes considered a subgenus of *Chalinolobus* (e.g. Smithers 1983, Koopman 1993, 1994) but considered to have generic status by Ellerman *et al.* (1953), Hayman & Hill (1971), Peterson & Smith (1973) and Peterson (1982). *Glauconycteris* is endemic to Africa, whereas *Chalinolobus* occurs in Australia, New Guinea, New Zealand, Norfolk I. and New Caledonia. In *Glauconycteris*, the upper premolar is absent (cf. usually present although very small in *Chalinolobus*). In *Glauconycteris*, but not in *Chalinolobus*, there has been shortening and broadening of the rostrum, elevation of the braincase and (in some species) the evolution of reticulated wings and conspicuous colour patterns. These differences, together with the long isolation of the two taxa, led Hayman & Hill (1971) to retain the generic status of *Glauconycteris*. Bacular morphology (Hill & Harrison 1987) strongly supports the generic status of *Glauconycteris*. In *Glauconycteris*, the baculum is small and somewhat variable, but mostly more or less triangular, with some modification (usually reduction) to a

deeply lobed base with a short distal portion. In some species, the base is slightly or considerably expanded and the distal portion lengthened to a shaft. In contrast, in *Chalinolobus*, the baculum is long, with clearly defined basal lobes, a long cylindrical shaft and an expanded tip. The molecular evidence of Hooper & Van Den Bussche (2003) not only supports the generic status of *Glauconycteris*, but indicates the separation of *Glauconycteris* into the tribe Nycticeiini, and *Chalinolobus* into the tribe Vespertilionini. Simmons (2005), however, places both genera in tribe Vespertilionini. In view of the geographic distributions of *Glauconycteris* and *Chalinolobus*, it is likely that many of the similarities have arisen from convergent evolution (F. P. D. Cotterill pers. comm.).

The taxonomy of some of the African forms is controversial (see *G. beatrix*).

Eight species of *Glauconycteris* are found only in forest habitats (seven mainly or only in rainforest, one in coastal forest mosaic), one in both rainforest and woodland savanna, and two only in woodland savanna.

The species of *Glauconycteris* are distinguished by the characters in Table 23, p. 562, which are:

Wing colour and reticulation. Can be pale or dark. In some species, the venation stands out in a contrasting darker colour creating a net-like pattern, in which case the wings are described as reticulated (Figure 125).

Colour and pattern of dorsal pelage. Of particular importance is the presence or absence of a shoulder-spot (= patch of white or pale dorsal pelage where upper arm joins body) and/or a dorsal flank-stripe (= line of white or pale pelage along the flank above the wing) (Figure 126). The dorsal flank-stripe is sometimes conjoined with the shoulder-spot.

Length and characters of the ears. Characters include outline (rounded or subquadrangular); the shape of the fleshy lobe on the lower lip with which the outer margin of the ear connects; and the shape of a lobule at the base of the inner margin of the ear.

Length of tibia. Mean length ranges from 14.7 to 20.0 mm for this genus, therefore 14.7–16.5 = comparatively short, 16.6–18.2 = medium, 18.3–20.0 = comparatively long.

Forehead region of skull. The dorsal profile (viewed laterally) of the region around the junction of the rostrum and frontal bones can be strongly, moderately or weakly concave (Figure 127).

Inner upper incisor. Can be unicuspid, weakly bicuspid or strongly bicuspid.

Bacular morphology can also be used to distinguish some of the species of *Glauconycteris* (Figure 128).

Meredith Happold

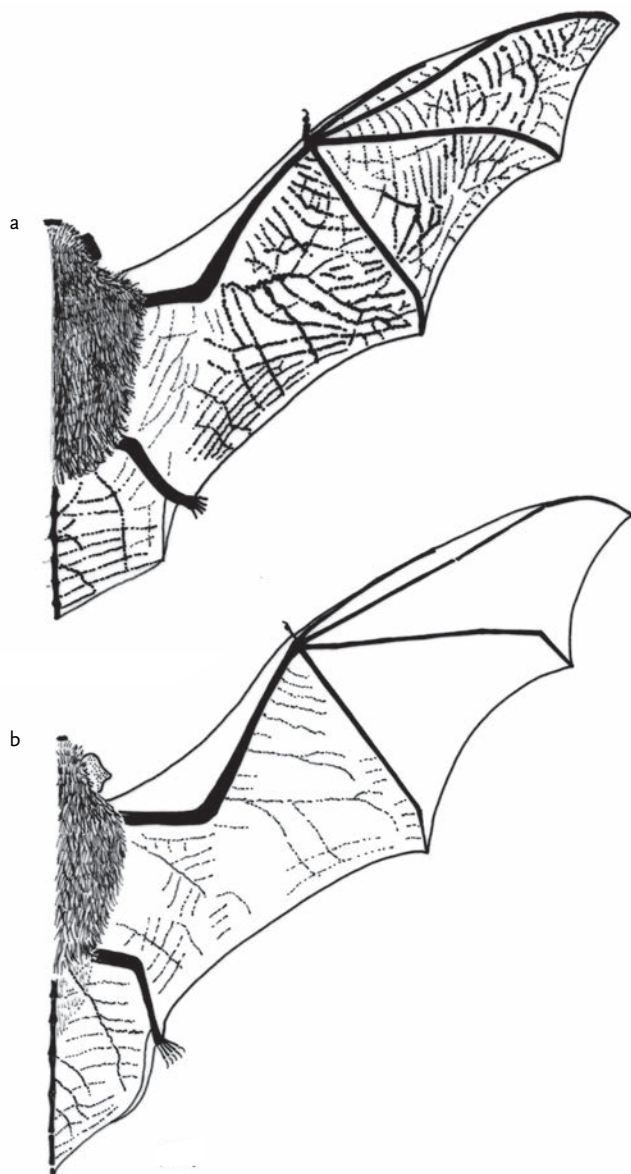


Figure 125. Reticulated wings of (a) *Glauconycteris variegata* and (b) *G. gleni*.

Table 23. Key to the species in the genus *Glauconycteris*.

| Wings conspicuously reticulated | Colour of wings | Body pattern | Colour of dorsal pelage (Dorsal hairs) ^a | FA (mm) | Tib (mm) | Ears: outline (E, mm) | |
|---------------------------------|-----------------|---|---|---------|----------|-------------------------|--|
| Yes (fully) | Pale | None | Creamy-buff to yellowish-fawn (Tricoloured or inconspicuously bicoloured) | 38–45 | 18–21 | Rounded (11–14) | |
| Yes (fully) | Medium | None | Medium-dark brown (Inconspicuously bicoloured) | 46 | 20 | Rounded (13) | |
| Yes (partly) | Pale | None | Pale greyish-fawn (Inconspicuously tricoloured) | 38–42 | 15–17 | Bluntly pointed (13–16) | |
| No (faint) | Pale | Whitish markings on nose and around base of each ear | Sepia brown (Inconspicuously bicoloured) | 41 | 20 | Moderately rounded (13) | |
| No (faint) | Pale | Flank-stripe (sometimes indistinct) | Pale golden-fawn or darker and greyer (Tricoloured) | 39–44 | 17–20 | Rounded (8–14) | |
| No | Dark | 5–7 dorsal markings (spots, patches and stripes) | Black and white (Bicoloured or white) | 45–48 | 21 | Subquadrangular (13) | |
| No | Dark | Flank-stripe and shoulder-spot | Dark sepia brown (Tricoloured) | 38–42 | 16–18 | Rounded (12–14) | |
| No (faint) | Dark | Flank-stripe and shoulder-spot (one or both sometimes absent) | Medium to dark greyish or brownish (Tricoloured) | 32–41 | 16–19 | Rounded (9–13) | |
| No | Dark | White shoulder-spot (except perhaps rarely) | Dark sepia brown (Bicoloured) | 35–41 | 16–20 | Rounded (6–12) | |
| No | Dark | Usually none (perhaps rarely a white shoulder-spot) | Dark sepia brown (Bicoloured) | 35–42 | 18–21 | Rounded (7–12) | |
| No | Dark | Flank-stripe and shoulder-spot | Dark brown or black (Bicoloured) | 37–39 | 16–18 | Subquadrangular (12–19) | |
| No | Dark | None | Umber-, sepia- or reddish-brown (Tricoloured) | 34–38 | 14–16 | Rounded (11–12) | |

^aDorsal hairs are described as inconspicuously bicoloured if the two colours merge.
^bThe degree of concavity of the profile (viewed laterally) of the forehead region of the skull is graded weak to strong in comparison only with other *Glauconycteris* (see Figure 144).

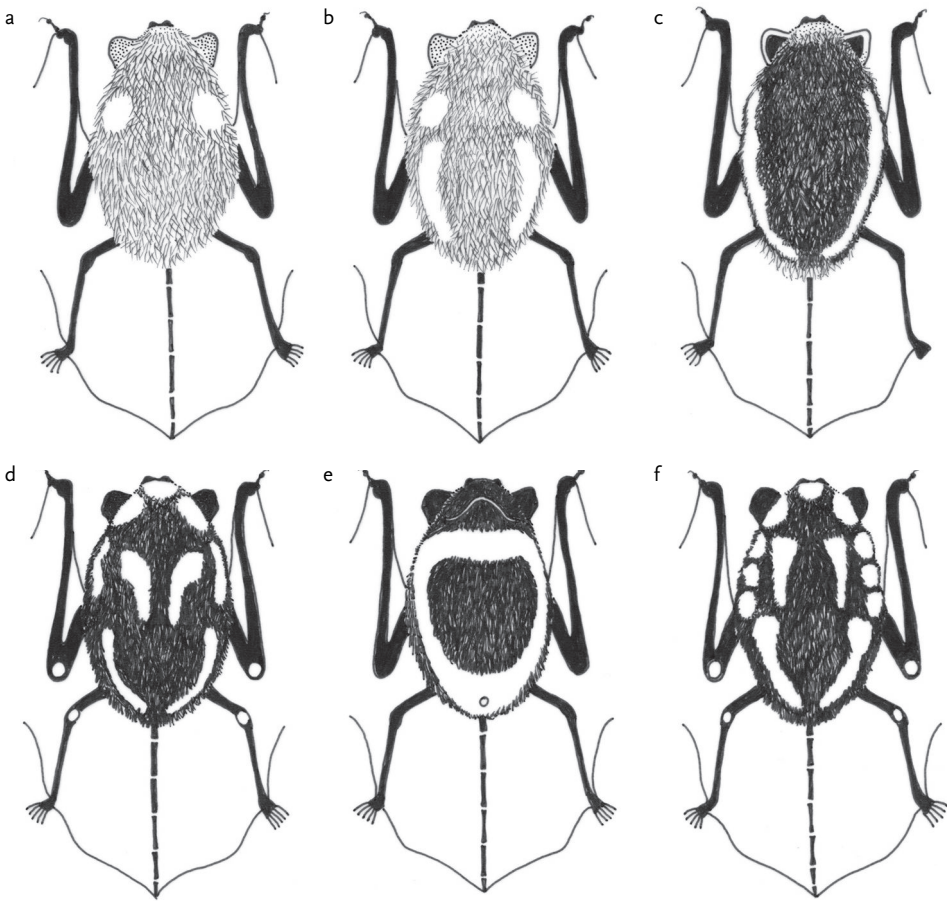
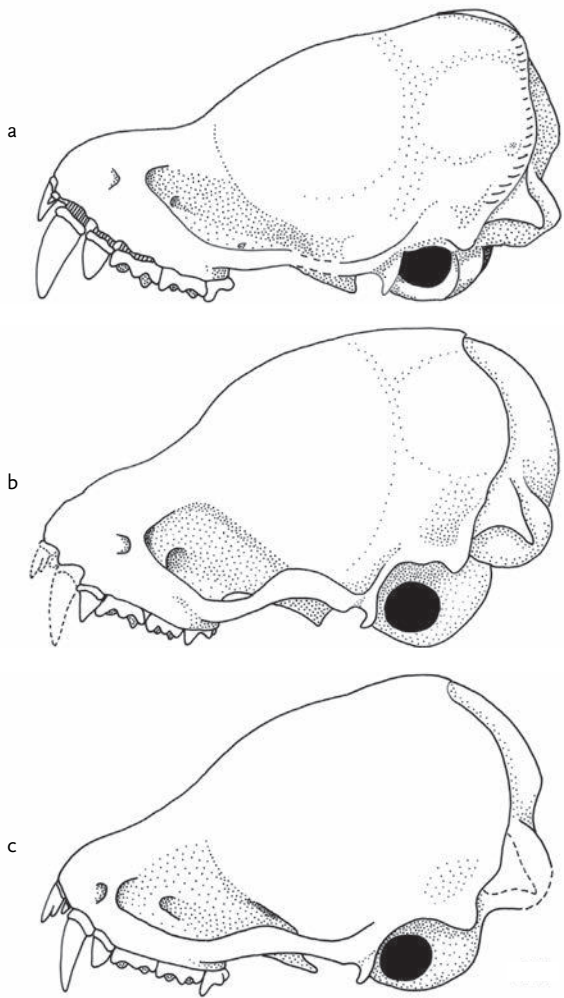
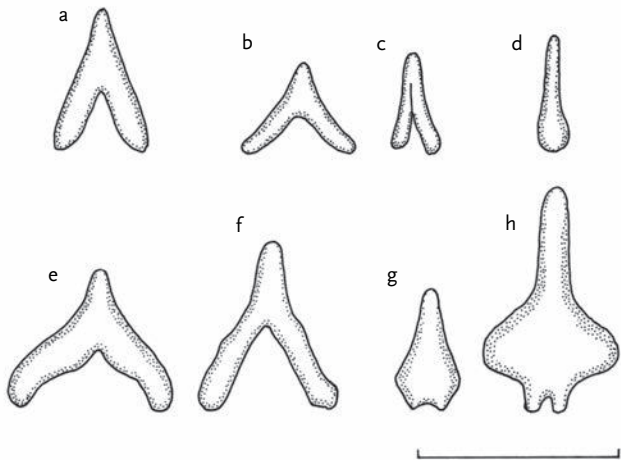


Figure 126. Pelage markings of some species of *Glauconycteris*.
(a) *G. humeralis*.
(b) *G. alboguttata*.
(c) *G. egeria*.
(d) *G. superba superba*.
(e) *G. superba superba* (ventral view).
(f) *G. superba sheila*.

All are dorsal views except (e).

| | Inner upper incisor | Forehead region of skull ^b | Species |
|--|--|---------------------------------------|--------------------------------|
| | Unicuspid to bicuspid with unequal cusps | Weakly concave | <i>G. variegata</i> |
| | n. d. | Weakly concave | <i>G. machadoi</i> |
| | Usually weakly bicuspid; sometimes unicuspid | Weakly concave | <i>G. gleni</i> |
| | Unicuspid | Weakly concave | <i>G. kenyacola</i> (holotype) |
| | Unicuspid or weakly to strongly bicuspid | Weakly concave | <i>G. argentata</i> |
| | Unicuspid | Strongly concave | <i>G. superba</i> |
| | Weakly bicuspid with unequal cusps | n. d. | <i>G. alboguttata</i> |
| | Weakly bicuspid with unequal cusps | Strongly concave | <i>G. poensis</i> |
| | Strongly bicuspid with subequal or unequal cusps | Moderately concave | <i>G. humeralis</i> |
| | Strongly bicuspid with subequal or unequal cusps | Weakly concave | <i>G. beatrix</i> |
| | Strongly bicuspid with subequal cusps | Weakly concave | <i>G. egeria</i> |
| | Strongly bicuspid with unequal cusps | Strongly concave | <i>G. curryae</i> |



ABOVE: Figure 127. The range of variation in the degree of concavity of the dorsal profile of the forehead region (viewed laterally) in *Glauconycteris*. (a) Strongly concave (e.g. *G. superba*; holotype, RMCA RG 14765). (b) Moderately concave (e.g. *G. humeralis*; BMNH 30.11.11.175). (c) Weakly concave (e.g. *G. argentata*; BMNH 71.7.10.5).

LEFT: Figure 128. Bacula of some *Glauconycteris*. (a) *G. argentata* (BMNH 59.510, Zaire). (b) *G. beatrix* (BMNH 48.713, Cameroon). (c) *G. beatrix* (SMF 79439, Zaire). (d) *G. humeralis* (BMNH 1930.11.11.173, Uganda). (e) *G. poensis* (BMNH 69.26, Côte d'Ivoire). (f) *G. poensis* (SMF 64987, Zaire). (g) *G. variegata* (BMNH 76.780, Ghana). (h) *G. variegata* (form *papilio*) (BMNH 55.409, Mozambique). Figs (c) and (f) from Heller *et al.* (1994); all others from Hill & Harrison (1987). All are dorsal views with tip uppermost. Scale = 1 mm.

Glauconycteris alboguttata **STRIPED BUTTERFLY BAT**

Fr. Glauconyctère à gorge blanche; Ger. Gestreifte Schmetterlingsfledermaus

Glauconycteris alboguttata J. A. Allen, 1917. Bull. Am. Mus. Nat. Hist., 37: 449. Medje, Orientale, DR Congo.

Taxonomy Originally *Glauconycteris alboguttatus* but in this name the gender is incorrect. Synonyms: none. Chromosome number: not known.

Description Small microbat without noseleaf and with tail more or less fully enclosed in interfemoral membrane; four upper and five

lower cheekteeth and two upper incisors on each side; ears separated, short for a vespertilionid (13 mm) and rounded; wings uniformly dark brown (not conspicuously reticulated); dorsal pelage sepia brown with shoulder-spot and dorsal flank-stripe on each side; inner upper incisor weakly bicuspid with cusps unequal in size. Sexes similar. Pelage soft; mid-dorsal hairs 7–8 mm. Dorsal pelage sepia brown, sometimes paler

on face; hairs pale sepia brown with blackish-brown at base and sepia brown at tip. White shoulder-spot and narrow white dorsal flank-stripe: joined in some individuals, pale and faint in other individuals. Ventral pelage slightly paler than dorsal pelage. Head high-domed; muzzle short, broad, flattish. Ears pale brown with paler rim, rounded; inner margin semi-circular with backwardly projecting, long, subtriangular lobe; outer margin with semi-circular antitragus and connecting with fleshy lobe on lower lip near corner of mouth. Eyes very small. Wings and interfemoral membrane uniformly dark brown. Tibia of medium length for this genus. Tail shorter than HB ($n = 1$).

Skull moderately large for a *Glauconycteris*. Profile of forehead region (viewed laterally) concave (no details available). Inner upper incisors weakly bicuspid with secondary cusp small although clearly visible. Lower incisors tricuspid, not crowded.

Geographic Variation None recorded.

Similar Species Two other *Glauconycteris* have dark wings and a dorsal flank-stripe:

Glauconycteris egeria. Dorsal pelage dark brown or almost black with conspicuous whitish dorsal flank-stripe but no shoulder-spot. Ears subquadangular, dark brown with conspicuous pale rim. Inner upper incisor strongly bicuspid with cusps ca. equal in size.

G. poensis (sometimes). Dorsal pelage greyish-brown or brownish-grey; hairs bicoloured. Shoulder-spot and/or dorsal flank-stripe either conspicuous, faint or absent.

Distribution Endemic to Africa. Known only from the Rainforest BZ, from four localities in Cameroon (Eger & Schlitter 2001) and four localities in DR Congo (Allen 1917a, Hayman *et al.* 1966, Eger & Schlitter 2001).

Habitat Rainforest.

Abundance Uncertain. Very rarely collected.

Remarks Apparently nothing else is known about the biology of this species.

Conservation IUCN Category: Least Concern.

Population trend not known. Distribution likely to be wider than is currently known.



Glauconycteris alboguttata

Measurements

Glauconycteris alboguttata

FA: 39.9 (38–42) mm, $n = 8$

WS: n. d.

TL: 95.1 (93–101) mm, $n = 8$

T: 43.1 (42–46) mm, $n = 8$

E: 13.1 (12–14) mm, $n = 8$

Tr: 5 mm, $n = 1$

Tib: 17.2 (16–18) mm, $n = 8$

HF: 8.5 (8–9) mm, $n = 8$

WT: 7.4 (6.0–9.5) g, $n = 8$

GLS: 13.2 (13.0–13.5) mm, $n = 8$

GWS: 9.8 (9.4–10.1) mm, $n = 8$

C–M³: 4.6 (4.4–4.7) mm, $n = 8$

Throughout geographic range (Eger & Schlitter 2001)

Key References Allen 1917a; Eger & Schlitter 2001.

Meredith Happold

Glauconycteris argentata COMMON BUTTERFLY BAT

Fr. Glauconyctère argentée; Ger. Silberne Schmetterlingsfledermaus

Glauconycteris argentata (Dobson, 1875). Proc. Zool. Soc. Lond., 1875: 385. Mont Cameroun, Cameroon.

Taxonomy Originally *Chalinolobus argentatus*. Synonyms: none. Chromosome number: not known.

Description Small to very small microbat without noseleaf and with tail more or less fully enclosed in interfemoral membrane; four upper and five lower cheekteeth and two upper incisors on each side; ears separated, short for a vespertilionid (9–14 mm); wings pale

(sometimes faintly, but never conspicuously, reticulated); dorsal pelage golden-fawn to pale greyish-brown with pale (sometimes indistinct) dorsal flank-stripe; inner upper incisor unicuspid or weakly bicuspid. Sexes apparently similar in colour and size. Pelage dense; mid-dorsal hairs ca. 7 mm. Dorsal pelage (in savanna habitats) pale golden-fawn, pale cinnamon or pale greyish-brown; paler on head; hairs tricoloured – beige with brown at base and golden-fawn to greyish-brown at tip. In

Rainforest BZ, dorsal pelage darker and greyer, sometimes with silvery sheen (Rosevear 1965). There is a paler dorsal flank-stripe, which is indistinct in some individuals. Ventral pelage darker and greyer than dorsal pelage. Head high-domed; muzzle short, broad, flattish. Ears rounded, brown; inner margin with moderately long, rounded, backward-pointing lobe at base; outer margin with rectangular antitragus and connecting with a smooth, broad, rounded, fleshy lobe on lower lip near corner of mouth. Tragus as in Figure 124b. Eyes very small. Wings and interfemoral membranes translucent, pale brown; faintly reticulated near body; dorsal pelage extending over anterior quarter of interfemoral membrane. Tibia long for this genus, 17–20 mm. Tail a little shorter than HB.

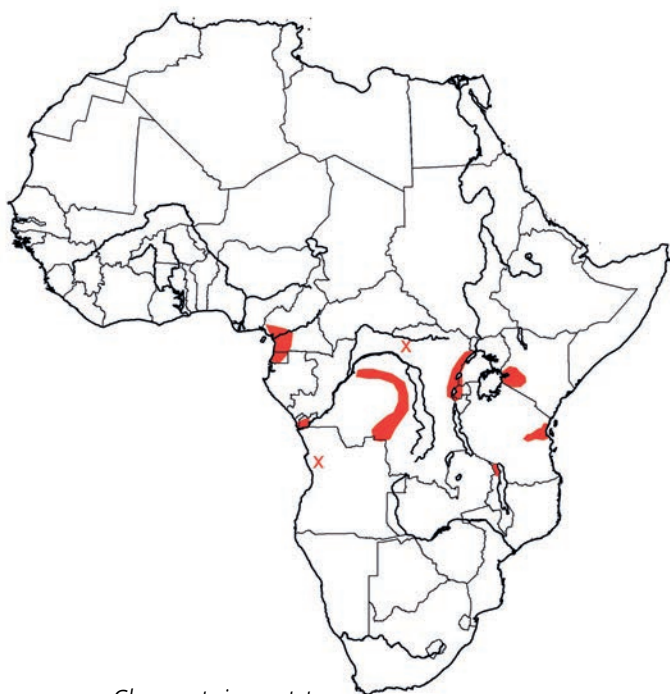
Skull small and profile of forehead region (viewed laterally) weakly concave for a *Glauconycteris* (Figure 127c). Inner upper incisor very long, slender, unicuspid, weakly bicuspid or strongly bicuspid. Lower incisors tricuspid or sometimes with four cusps; not crowded.

Geographic Variation Individuals from rainforest habitats are darker and more grey than those from woodlands (Rosevear 1965), but no subspecies have been described.

Similar Species Only one other *Glauconycteris* has pale wings without any conspicuous reticulation:

Glauconycteris kenyacola. Dorsal pelage dark brown; no shoulder-spot or dorsal flank-stripe. Whitish markings on nose and base of each ear.

Distribution Endemic to Africa. Mostly recorded from the Rainforest BZ and Eastern and Southern Rainforest–Savanna Mosaics, but with some records in the Zambezian Woodland BZ and Coastal Forest Mosaic BZ. Recorded disjunctly (and not in all countries) from Cameroon and Equatorial Guinea (excluding Bioko I.), to Kenya (south of 5°N) and southwards to ca. 10°S in Angola and the Misuku Hills in N Malawi. Mapped from country checklists (see order



Chiroptera), Allen & Loveridge 1933, Cockle *et al.* 1998, BMNH, IRSN.

Habitat Recorded from rainforest habitats at both high and low altitudes (Kingdon 1974), the rainforest–Guinea woodland boundary (Rosevear 1965), bamboo forest (ROM), miombo woodland and the coastal forests of Tanzania (Cockle *et al.* 1998). In East Africa, not found in areas with less than 900 mm annual rainfall (Kingdon 1974). Often recorded over streams, rivers, pools and fish-ponds.

Abundance Uncertain. Fairly common in collections and, based on specimens, this appears to be the most common species in the genus *Glauconycteris* (Rosevear 1965).

Adaptations By day, clings to undersides of fronds of palms including Doum, Coconut and Oil Palms, and *Dracaena* (Rosevear 1965, BMNH). One such day-roost was ca. 7 m above ground.

Foraging and Food No information.

Social and Reproductive Behaviour One palm frond (where these bats roost) may carry more than 30 bats. ‘They cling to the “leaves” near the midrib in groups, only 2–4 on each leaf; they do not hang clear with heads down, but cling to the leaf with their tails towards the midrib, the head of the one nearest the midrib rests upon the back of the next bat in front of him’ (Loveridge 1922 in Rosevear 1965). One roosting group of ca. 25 included four ♂♂ and three ♀♀ of which two were lactating and one was neither pregnant nor lactating. Another group included at least one ♂ and two ♀♀ (BMNH).

Reproduction and Population Structure Loveridge (1937 in Kingdon 1974) recorded that 4 of 8 ♀♀ collected in the Kenya uplands in Mar ‘were carrying young’. At 1–2°S in Kenya, two lactating ♀♀ were recorded on 25 Jun; at the same time, another ♀ was neither pregnant nor lactating (BMNH).

Predators, Parasites and Diseases Ectoparasites include mites *Spinturnix walkeri* (Acari: Spinturnicidae) and *Alabidocarpus glauconycteris* (Acari: Chirodiscidae) (Anciaux de Faveaux 1984). Rift Valley fever virus has been isolated from *G. argentata* (Addy *et al.* 1978).

Conservation IUCN Category: Least Concern.

Measurements

Glauconycteris argentata

FA: 41.7 (39–44) mm, n = 67
 WS (d): 312.5 (290–333) mm, n = 57
 TL: 100.5 (94–114) mm, n = 62
 T: 46.5 (41–53) mm, n = 63
 E: 11.6 (8–14) mm, n = 63
 Tr: 4.3 (3–5) mm, n = 4*
 Tib: 18.3 (17–20) mm, n = 61
 HF: 7.5 (5–10) mm, n = 63
 WT: 9.2 (6.0–12.0) g, n = 44
 GLS: 12.9 (12.1–13.3) mm, n = 61
 GWS: 9.3 (8.8–9.7) mm, n = 48
 C–M³: 4.2 (4.0–4.5) mm, n = 63

Throughout geographic range (Peterson & Smith 1973)

*BMNH

Key Reference Rosevear 1965.

Meredith Happold

Glauconycteris beatrix **BEATRIX BUTTERFLY BAT**

Fr. Glauconyctère de Beatrix; Ger. Kleine Schmetterlingsfledermaus

Glauconycteris beatrix Thomas, 1901. Ann. Mag. Nat. Hist., ser. 7, 8: 256. 15 mi (24 km) from mouth of Benito River, Rio Muni, Equatorial Africa.

Taxonomy Synonyms: none. Rosevear (1965) expressed doubt about the distinction of *beatrix* from *poensis*, but the specific status of *beatrix* has been accepted by many, including Peterson & Smith (1973), Hill & Harrison (1987) and Koopman (1989, 1994). Considered to include *humeralis* by some authors but, pending revision, *humeralis* is tentatively treated here as a distinct species. *Glauconycteris humeralis* usually has a white shoulder-spot whereas most specimens of *G. beatrix* have no markings. The holotype, however, has a white shoulder-spot, which led Hayman & Hill (1971) to point out that it remains to be seen whether the shoulder-spot is exceptional in *beatrix*, or whether *beatrix* is an earlier name for *humeralis*, in which case the unspotted 'beatrix' specimens represent either an unnamed form or a variant. Chromosome number (DR Congo): $2n = 22$; $aFN = 40$ (M. Volleth pers. comm.).

Description Very small microbat without noseleaf and with tail more or less fully enclosed in interfemoral membrane; four upper and five lower cheekteeth and two upper incisors on each side; ears separated, short for a vespertilionid (7–12 mm) and rounded; wings dark brown (not conspicuously reticulated); dorsal pelage dark brown, no shoulder-spot (except rarely), no dorsal flank-stripe; tibia long (18–21 mm); inner upper incisor strongly bicuspid. Sexes apparently similar. Pelage dense; mid-dorsal hairs 8–9 mm. Dorsal pelage uniformly dark sepia brown; hairs bicoloured (cf. *G. curryae*) with basal half blackish-brown, terminal half dark sepia brown. White shoulder-spot present in holotype but apparently usually absent (see Taxonomy). Ventral pelage same as dorsal pelage. Head high-domed; muzzle short, broad and flattish. Ears comparatively short for a *Glauconycteris*, very rounded; inner margin with rounded lobe at base; outer margin connecting with well-developed, fleshy lobe on lower lip near corner of mouth. Tragus as in Figure 124c. Wings and interfemoral membrane dark brown, not reticulated. Tibia long for this genus (18–21 mm). Tail either longer, equal to, or shorter than HB. Baculum (dorsal view) triangular with basal portion deeply lobed and distal portion short and blunt (cf. *G. humeralis*) (Figure 128b; Hill & Harrison 1987, Heller *et al.* 1994). Heller *et al.* (1994) suggest that the baculum of SMF 79439 (Figure 128c) is intermediate in shape between that of *G. beatrix* and *G. humeralis* (Figure 128d) (see profile of *G. humeralis*). Skull small; profile of forehead region (viewed laterally) weakly concave for a *Glauconycteris*. Inner upper incisor bicuspid with cusps ca. equal in size or with outer cusp smaller than inner cusp. Lower incisors tricuspid or sometimes 4-cuspid; not crowded.

Geographic Variation None recorded.

Similar Species Three other *Glauconycteris* have dark wings and no dorsal flank-stripe:

Glauconycteris curryae. Dorsal pelage blackish-brown, sepia brown or reddish-brown; head and shoulders slightly paler than rump; hairs conspicuously tricoloured. No dorsal markings. Tibia shorter (14–16 mm). Profile of forehead region of skull strongly concave.

G. humeralis. Dorsal pelage dark brown with shoulder-spot (except rarely).

G. poensis (sometimes). Dorsal pelage medium to dark greyish sepia brown or brownish-grey; hairs tricoloured. Shoulder-spot and/or dorsal flank-stripe either conspicuous, faint or absent. Tibia often shorter (18.0 [16–19] mm). Inner upper incisor weakly bicuspid.

Distribution Endemic to Africa. Recorded from the Rainforest BZ and Southern Rainforest–Savanna Mosaic, from Côte d'Ivoire, Ghana, Nigeria and Cameroon, and southwards to Equatorial Guinea (including Bioko I.), Gabon and N Angola. Probably also extends across the Rainforest BZ to Irangi, E DR Congo (Heller *et al.* 1994), where it is sympatric with *G. humeralis*. Mapped from country checklists (see



Glauconycteris beatrix

order Chiroptera) with some exclusions, Sanderson 1939, Adam & Aellen 1975, Eger & Schlitter 2001, BMNH, SMF.

Habitat Predominantly lowland rainforest, but also forest habitats just outside the rainforest zone. In Nigeria, one was found by a waterhole in secondary forest (Happold 1987). On Bioko I., recorded from forests and cocoa plantations (Juste & Ibáñez 1994). One was found in swamp forest in Taï N. P., Côte d'Ivoire (Fahr & Kalko 2011).

Abundance Uncertain. Rarely recorded throughout geographic range.

Remarks Sanderson (1939) reported that 'these bats were often mistaken for swallows, amongst which they fly in broad daylight from ca. 4 o'clock onwards, high above the forest trees', which were over 30 m high.

Conservation IUCN Category: Least Concern.

Major threats: loss and degradation of lowland rainforest. Population trend: not known. Recorded from only a few scattered localities but

probably very difficult to sample even if common. However, could be more threatened than this assessment suggests.

Measurements

Glauconycteris beatrix

FA: 38.3 (35–42) mm, n = 25

WS: n. d.

TL: 89.9 (71–101) mm, n = 10

T: 42.8 (35–51) mm, n = 10

E: 10.0 (7–12) mm, n = 11

Tr: 3 mm, n = 1

Tib: 19.4 (18–21) mm, n = 6

HF: 7.0 (6.8–7.5) mm, n = 4

WT: 5.4 (4–9) g, n = 5

GLS: 11.6 (10.6–12.0) mm, n = 17

GWS: 8.5 (7.9–9.0) mm, n = 12

C–M³: 4.1 (3.6–4.6) mm, n = 11

Throughout geographic range (BMNH, SMF and literature)

Key References Eger & Schlitter 2001; Rosevear 1965.

Meredith Happold

Glauconycteris curryae CURRY'S BUTTERFLY BAT

Fr. *Glauconyctère de Curry*; Ger. *Currys Schmetterlingsfledermaus*

Glauconycteris curryae Eger and Schlitter, 2001. Acta Chiropterologica 3: 2. 10 km W Bipindi (03° 05' N, 10° 25' E), at ca. 300 m, Cameroon.

Taxonomy Originally *Glauconycteris curryi* but the spelling was emended to *curryae* (Eger 2001). Synonyms: none. Chromosome number: not known.

Description Very small microbat without noseleaf and with tail more or less fully enclosed in interfemoral membrane; four upper and five lower cheekteeth and two upper incisors on each side; ears separated, short for a vespertilionid (11–12 mm) and rounded; wings dark brown (not conspicuously reticulated); dorsal pelage medium to dark brown, no shoulder-spot, no dorsal flank-stripe; tibia 14–16 mm; inner upper incisor strongly bicuspid. Sexes similar. Pelage dense; length at shoulder 7 mm. Dorsal pelage umber brown to sepia brown or reddish-brown; head and shoulders slightly paler than rump; hairs conspicuously tricoloured (cf. *G. beatrix*), basal half blackish-brown, followed by a narrow band of pinkish-buff, and a narrow terminal band of umber brown, sepia brown or reddish-brown. Ventral pelage paler. Head high-domed; muzzle short, broad and flattish. Ears of medium length for a *Glauconycteris*; inner margin semi-circular with rounded lobe at base; outer margin flattened, connecting with well-developed fleshy lobe on lower lip near corner of mouth. Tragus with tip rounded, inner margin straight, posterior margin straight with triangular lobe at base (Figure 124a). Wings and interfemoral membrane dark brown, not reticulated. Tibia short for this genus (14–16 mm). Tail length ca. equal to HB or slightly shorter.

Skull small and profile of forehead region (viewed laterally) strongly concave for a *Glauconycteris*. Inner upper incisor strongly bicuspid with secondary cusp ca. one-third to half the height of the main cusp. Lower incisors typically tricuspid, not crowded.



Glauconycteris curryae

Geographic Variation None.

Similar Species Three other *Glauconycteris* have dark wings and no dorsal flank-stripe:

Glauconycteris beatrix. Dorsal pelage dark sepia brown; hairs bicoloured. No dorsal markings (except shoulder-spot very rarely). Tibia longer (18–21 mm). Frontal region of skull weakly concave.

G. humeralis. Dorsal pelage dark brown; hairs bicoloured. Shoulder-spot present (except rarely). Ears rounded. Tibia almost always longer (16–20 mm).

G. poensis (sometimes). Dorsal pelage medium to dark greyish-sepia brown or brownish-grey. Shoulder-spot and/or dorsal flank-stripe either conspicuous, faint or absent. Tibia usually longer (16–19 mm). Inner upper incisor weakly bicuspid.

Distribution Endemic to Africa. Known only from five localities in Cameroon (10 km W Bipindi, Kumba, Njombo R. [67 km W Ayos], 13 km S and 8 km E Amban, and Eseka) and one in DR Congo (Bumba Zone, Yalosemba) (Eger & Schlitter 2001). All are in the Rainforest BZ.

Habitat Rainforest. Has been recorded over a pool in a vast stand of bamboo near a river. Also recorded over pools and forest streams, and on the shore of a lake, in Rainforest BZ.

Abundance Uncertain. Only seven specimens and six localities known.

Remarks Nothing else is known about the biology of this species.

Conservation IUCN Category: Data Deficient.

Major threat thought to be destruction of forest habitat.

Measurements

Glauconycteris curryae

FA: 35.9 (34–38) mm, n = 6

WS (d): 272.3 (260–282) mm, n = 3

TL: 80.7 (75–85) mm, n = 6

T: 38.8 (35–41) mm, n = 6

E: 11.2 (11–12) mm, n = 6

Tr: 7 mm, n = 1

Tib: 14.7 (14–16) mm, n = 6

HF: 7.0 (6–8) mm, n = 6

WT: 4.4 (4–5) g, n = 6

GLS: 12.1 (11.7–12.3) mm, n = 6

GWS: 8.7 (8.4–9.0) mm, n = 6

C–M³: 4.1 (4.0–4.2) mm, n = 6

Throughout geographic range (Eger & Schlitter 2001)

Key Reference Eger & Schlitter 2001.

Judith Eger

Glauconycteris egeria BIBUNDI BUTTERFLY BAT

Fr. Glauconyctère de Bibundi; Ger. Bibundi Schmetterlingsfledermaus

Glauconycteris egeria Thomas, 1913. Ann. Mag. Nat. Hist., ser. 8, 11: 44. Bibundi, Western Province, Cameroon.

Taxonomy Synonyms: none. Chromosome number: not known.

Description A beautiful, very small microbat without noseleaf and with tail more or less fully enclosed in interfemoral membrane; four upper and five lower cheekteeth and two upper incisors on each side; ears separated, short for a vespertilionid (12–19 mm) and subquadrangular; wings dark brown (not conspicuously reticulated); dorsal pelage dark brown to almost black with conspicuous whitish dorsal flank-stripe; inner upper incisor strongly bicuspid. Sexes apparently similar in colour. Pelage soft, dense. Dorsal pelage dark brown to almost black; hairs blackish-brown with terminal third dark brown, or black. Thomas (1913a) did not describe any markings (but the pelage of the holotype is in very poor condition); however, conspicuous shoulder-spots and dorsal flank-stripes are present in eight specimens (AMNH, ROM), with skull characters matching those of the holotype of *G. egeria*. Ventral pelage same as dorsal pelage. Head comparatively large, high-domed; muzzle short, broad and flattish. Ears comparatively long and broad for a *Glauconycteris*, subquadrangular in outline (cf. rounded in other dark-winged *Glauconycteris*), dark brown with a conspicuously pale rim. Inner margin of ear with long, backward-pointing lobe at base; outer margin connecting with rather small fleshy lobe on lower lip near corner of mouth. Tragus as in Figure 124d. Eyes very small. Wings and interfemoral membrane dark brown without reticulation. Tibia short for this genus. Tail ca. equal in length to HB.

Skull small and profile of forehead region (viewed laterally) weakly concave for a *Glauconycteris*. Inner upper incisor long, strongly bicuspid with cusps ca. equal in size; the secondary cusp is near tip in holotype (Thomas 1913a). Inner upper incisor minute. Lower incisors tricuspid, not markedly crowded.

Geographic Variation No subspecies recognized. Dorsal pelage almost pure black in Uganda, but sepia brown in Cameroon (J. Eger pers. comm.).

Similar Species Two other *Glauconycteris* have dark wings and a dorsal flank-stripe:

Glauconycteris alboguttata. Dorsal pelage sepia brown with shoulder-spot as well as dorsal flank-stripe. Ears rounded, pale brown with paler rim. Inner upper incisors weakly bicuspid but secondary cusp small although clearly visible.

G. poensis (sometimes). Dorsal pelage medium to dark greyish sepia brown or brownish-grey; shoulder-spot and/or dorsal flank-stripe either conspicuous, faint or absent. Ears rounded. Inner upper incisor weakly bicuspid, cusps unequal in size.

Distribution Endemic to Africa. Known only from two areas in the Rainforest BZ (Bibundi and Buea in Cameroon [Thomas 1913a, ROM] and Dzanga-Sangha in Central African Republic [Lunde *et al.* 2001]), and one in the Eastern Rainforest–Savanna Mosaic (Budongo



Glauconycteris egeria

Forest, Uganda [ROM]). The identity of the specimens from Central African Republic reported as *Glauconycteris* cf. *egeria*, has since been confirmed by J. Eger (pers. comm.).

Habitat Rainforest. In Uganda, recorded over a swamp in rainforest, at ca. 1200 m.

Abundance Uncertain. Very rare in collections (four from Cameroon, three from Central African Republic, four from Uganda).

Remarks In Dzanga-Sangha forest reserve in Central African Republic, two adult ♀♀ were mist-netted within a metre of each other at the edge of a clearing in dense forest, and a ♂ was mist-netted along a road through the forest (Lunde *et al.* 2001). Kingdon's sketches labelled *G. superba* from Budongo Forest, Uganda (Kingdon 1974) do not resemble *G. superba*; instead they resemble *G. egeria*, which has been recorded and confirmed from this locality.

Conservation IUCN Category: Data Deficient.

Measurements

Glauconycteris egeria

FA: 38.0 (37–39) mm, n = 8

WS (a): 274.8 (270–291) mm, n = 5

TL: 88.3 (85–94) mm, n = 7

T: 40.6 (35–48) mm, n = 8

E: 14.4 (12–19) mm, n = 8

Tr: 6.4 (6–8) mm, n = 5

Tib: 16.8 (16–18) mm, n = 6

HF: n. d.

WT: 6.3 (5.5–7.5) g, n = 6

GLS: 12.6 (12.0–13.0) mm, n = 7

GWS: 9.2 (9.1–9.3) mm, n = 7

C–M³: 4.3 (4.1–4.5) mm, n = 7

Throughout geographic range (AMNH, ROM, Thomas 1913a, Lunde *et al.* 2001)

Key References Lunde *et al.* 2001; Thomas 1913a.

Meredith Happold

Glauconycteris gleni GLEN'S BUTTERFLY BAT

Fr. Glauconyctère de Glen; Ger. Glens Schmetterlingsfledermaus

Glauconycteris gleni Peterson and Smith, 1973. R. Ont. Mus. Life Sci. Occas. Pap. 22: 3. Near Lomie, Cameroon.

Taxonomy Synonyms: none. Chromosome number: not known.

Description Very small microbat without noseleaf and with tail more or less fully enclosed in interfemoral membrane; four upper and five lower cheekteeth and two upper incisors on each side; ears separated, short for a vespertilionid (13–16 mm); wings white with dark brown reticulation on inner part of arm-wing and transverse lines across interfemoral membrane; dorsal pelage pale greyish-fawn without markings; inner upper incisors usually weakly bicuspid. Females on average slightly larger than ♂♂ in most body measurements. Pelage soft; extending over proximal third of interfemoral membrane; mid-dorsal hairs 7–9 mm. Dorsal pelage pale greyish-fawn with creamy sheen; hairs pale greyish-fawn or cream (both present) with dark brownish-grey base, an inconspicuous dark brown subterminal band and greyish-fawn or cream tip. No shoulder-spot or dorsal flank-stripe. Ventral pelage white to creamy-fawn; hairs pure white or creamy-fawn, with grey at base. Head high-domed; muzzle short, broad, flattish. Ears small for a vespertilionid but comparatively long for a *Glauconycteris*;

very pale brown, bluntly pointed; outer margin concave becoming convex near tip; inner margin convex. Wings semi-translucent white with dark brown pigmentation over wing-bones, hindlimbs and tail, and dark brown reticulation lines on arm-wing (sometimes only between elbow and ankle). Interfemoral membrane with dark brown transverse lines (Figure 125b). Tibia short for this genus (15–17 mm). Tail shorter than HB.

Skull moderately large and profile of forehead region (viewed laterally) weakly concave for a *Glauconycteris*. Inner upper incisors usually weakly bicuspid; sometimes unicuspid. Lower incisors tricuspid or sometimes with four cusps; not crowded.

Geographic Variation None.

Similar Species Two other *Glauconycteris* have conspicuously reticulated wings:

Glauconycteris variegata. Dorsal pelage creamy-fawn. Flight-membranes

*Glauconycteris gleni*

pale yellowish-orange with dark brown reticulation on arm-wing, finger-wing and interfemoral membrane. Tibia longer, 18–21 mm.

G. machadoi. Dorsal pelage dark brown. Flight-membranes pale brown (? orange) with very dark reddish-brown reticulation on arm-wing, finger-wing and interfemoral membrane. Tibia longer, 20 mm.

Three other vespertilionids have white wings:

Pipistrellus rendalli and *P. tenuipinnis*. No brown reticulation lines on arm-wing. Outer margin of ear not reaching mouth; lower lip without lobe at posterior corner.

Scotoecus albofuscus. Only one upper incisor on each side. No brown reticulation lines on arm-wing. Penis long (ca. 9 mm).

Distribution Endemic to Africa. As yet, only known from the Rainforest BZ near Lomie, Cameroon and from the Eastern Rainforest–Savanna Mosaic at Malabigambo Forest in the Masaka District of Uganda (Peterson & Smith 1973).

Habitat Rainforest. No details recorded.

Abundance Uncertain. Very rarely recorded; only 18 specimens known when this species was described in 1973.

Remarks Nothing else appears to be known about the biology of this species.

Conservation IUCN Category: Data Deficient.

Only known with certainty from two localities but *Glauconycteris* are difficult to sample and this species might be more widely distributed than the records indicate. Population trend and threats not known.

Measurements

Glauconycteris gleni

FA: 40.5 (38–42) mm, n = 15

WS (d): 301.4 (290–310) mm, n = 13

TL: 100.4 (96–106) mm, n = 15

T: 45.8 (44–50) mm, n = 15

E: 14.3 (13–16) mm, n = 6

Tr: 8 mm, n = 1

Tib: 16.2 (15–17) mm, n = 15

HF: 8.9 (8–10) mm, n = 15

WT: 10.8 (8.5–15.0) g, n = 15

GLS: 14.1 (13.9–14.6) mm, n = 13

GWS: 9.9 (9.4–10.1) mm, n = 13

C–M³: 4.7 (4.5–4.9) mm, n = 15

Throughout geographic range (Peterson & Smith 1973)

Key Reference Peterson & Smith 1973.

Meredith Happold

Glauconycteris humeralis SPOTTED BUTTERFLY BAT

Fr. Glauconyctère tachetée; Ger. Gefleckte Schmetterlingsfledermaus

Glauconycteris humeralis J. A. Allen, 1917. Bull. Am. Mus. Nat. Hist. 37: 448. Medje, Orientale, DR Congo.

Taxonomy Synonyms: none. Considered to be a distinct species by Hayman *et al.* (1966) and Hayman & Hill (1971), but considered to be a subspecies of *G. beatrix* by some authors, including Koopman (1971, 1993), Peterson & Smith (1973) and Eger & Schlitter (2001). Differences in bacular morphology (Hill & Harrison 1987) indicate that *humeralis* probably is distinct (Heller *et al.* 1994). However, Heller *et al.* (1994) found that the baculum of a specimen from Irangi, DR Congo, is intermediate in shape and suggested that *humeralis* might merely represent a spotted form of *beatrix*. Tentatively treated here as a distinct species pending revision. Chromosome number: not known.

Description Very small microbat without noseleaf and with tail more or less fully enclosed in interfemoral membrane; four upper

and five lower cheekteeth and two upper incisors on each side; ears separated, short for a vespertilionid (6–12 mm) and rounded; wings dark brown (not conspicuously reticulated); dorsal pelage dark brown with a white shoulder-spot but no dorsal flank-stripe; tibia 16–20 mm; inner upper incisor strongly bicuspid with cusps ca. equal in size or with outer cusp smaller than inner cusp. Sexes apparently similar in colour and size. Pelage dense. Dorsal pelage dark sepia brown; hairs bicoloured (cf. *G. curryae*) with basal half blackish-brown, terminal half dark sepia brown. White shoulder-spot present (except perhaps rarely); hairs sometimes pure white, sometimes brown with white or yellowish-white at tip (Allen 1917a). Ventral pelage same as dorsal pelage. Head high-domed; muzzle short, broad and flattish. Ears yellowish-brown, medium-short for a *Glauconycteris*, very rounded;

inner margin with rounded lobe at base; outer margin connecting with well-developed, fleshy lobe on lower lip near corner of mouth. Tragus short, broad, anterior margin straight, posterior margin convex. Wings and interfemoral membrane dark brown, not reticulated; wing-bones pale brown dorsally and ventrally. Tibia of medium length for this genus (16–20 mm). Tail length greater than HB. Baculum (dorsal view) with basal portion unexpanded and unilobed, and distal portion lengthened to a short shaft (cf. *G. beatrix*) (Figure 128d; Hill & Harrison 1987).

Skull small and profile of forehead region (viewed laterally) moderately concave for a *Glauconycteris* (Figure 127b). Inner upper incisor described above. Lower incisors tricuspid or sometimes with four cusps; not crowded.

Geographic Variation None recorded.

Similar Species Three other *Glauconycteris* have dark wings and no dorsal flank-stripe:

Glauconycteris beatrix. Dorsal pelage dark brown without shoulder-spot (except rarely).

G. curryae. Dorsal pelage blackish-brown, sepia brown or reddish-brown; hairs conspicuously tricoloured. No shoulder-spot. Tibia usually shorter (14–16 mm).

G. poensis (sometimes). Dorsal pelage medium to dark greyish sepia brown or brownish-grey; hairs tricoloured. Shoulder-spot and/or dorsal flank-stripe either conspicuous, faint or absent. Inner upper incisor weakly bicuspid.

Distribution Endemic to Africa. Recorded from a part of the Rainforest BZ in DR Congo and extending into the Eastern Rainforest–Savanna Mosaic in Uganda and W Kenya (Rahm 1966, Heller *et al.* 1994, Eger & Schlitter 2001).

Habitat Rainforest. Recorded from Kakamega Forest in W Kenya, which has numerous grassy glades in extensive stands of tall evergreen forest.

Abundance Uncertain; seldom collected.

Remarks The holotype, an adult ♀, was one of four individuals ‘captured together in a bush’ (Lang & Chapin 1917b). A pregnant ♀ was recorded at 1–2° N (Avakubi) in DR Congo in Feb (Lang & Chapin 1917b).

Conservation IUCN Category: Data Deficient.



Glauconycteris humeralis

Measurements

Glauconycteris humeralis

FA: 37.7 (35–41) mm, n = 32

WS (a): 275.3 (255–298) mm, n = 9

TL: 90.8 (82–98) mm, n = 27

T: 47.8 (37–59) mm, n = 31

E: 9.9 (6–12) mm, n = 26

Tr: 6, 8 mm, n = 2

Tib: 17.9 (16–20) mm, n = 25

HF: n. d.

WT: 5.3 (4–7) g, n = 30

GLS: 11.5 (10.8–12.0) mm, n = 30

GWS: 8.3 (7.9–8.8) mm, n = 26

C–M³: 3.9 (3.6–4.2) mm, n = 28

Throughout geographic range (BMNH, SMF and literature [especially Eger & Schlitter 2001])

Key References Allen 1917a; Eger & Schlitter 2001.

Meredith Happold

Glauconycteris kenyacola KENYACOLA BUTTERFLY BAT

Fr. Glauconyctère du Kenya; Ger. Kenya-Schmetterlingsfledermaus

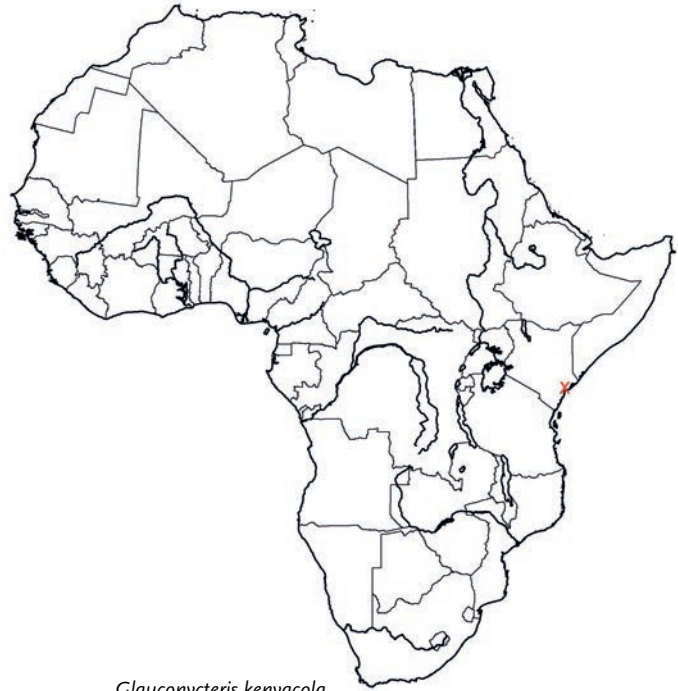
Glauconycteris kenyacola Peterson, 1982. Canadian J. Zool. 60: 2521. 8.5 km N Garsen, Coast Province, Kenya.**Taxonomy** Synonyms: none. Chromosome number: not known.

Description Very small microbat without noseleaf and with tail more or less fully enclosed in interfemoral membrane; four upper and five lower cheekteeth and two upper incisors on each side; ears separated, short for a vespertilionid (ca. 13 mm), moderately rounded; wings pale and faintly reticulated; dorsal pelage sepia brown with unique whitish markings on nose and around the bases of ears; inner upper incisor unicuspid. Pelage soft, dense. Dorsal pelage sepia brown, head and nape paler; hairs pale sepia brown merging into sepia brown at tip. No shoulder-spot or flank-line. Ventral pelage paler than dorsal pelage. Head with tuft of whitish hairs on nose, a thick band of white hairs extending from antitragus to base of ear, and whitish patches behind each ear. Ears of medium length for this genus, moderately rounded; inner margin with small subtriangular lobe at base; outer margin connecting with fleshy lobe on lower lip near corner of mouth. Eyes very small. Wings pale brownish-yellow with faint venation lines; dorsal surface with blackish-brown skin over bones of wing, legs and tail. Interfemoral membrane slightly darker than wings. Tibia long for this genus (20 mm). Tail equal in length to HB.

Skull small and profile of forehead region (viewed laterally) weakly concave for a *Glauconycteris*. Four upper and five lower cheekteeth and two upper incisors on each side. Inner upper incisors unicuspid but with slight, posterior, blade-like ridge. Lower incisors tricuspid, not markedly crowded.

Geographic Variation None.**Similar Species** Only one other *Glauconycteris* has pale wings without conspicuous reticulation:

Glauconycteris argentata. Dorsal pelage pale golden-fawn or darker and greyer; no shoulder-spot; dorsal flank-stripe present but sometimes indistinct. No whitish markings on nose or base of each ear.

Distribution Endemic to Africa. Known only from the type locality in the Coastal Forest Mosaic BZ, in E Kenya.**Habitat** Peterson (1982) speculates that *G. kenyacola* may be restricted to the lower coastal plains of Kenya and adjacent regions. No other details are available.**Abundance** Uncertain. Only one individual known.**Remarks** Nothing else appears to be known about this species.*Glauconycteris kenyacola***Conservation** IUCN Category: Data Deficient.**Measurements***Glauconycteris kenyacola*

FA: 41 mm

WS (d): 296 mm

TL: 98 mm

T: 49 mm

E: 13 mm

Tr: 5 mm

Tib: 20 mm

HF: 10 mm

WT: 7.0 g

GLS: 12.8 mm

GWS: ca. 9.4 mm

C-M³: 4.2 mm

Kenya (holotype; ♀, Peterson 1982)

Key Reference Peterson 1982.

Meredith Happold

***Glauconycteris machadoi* MACHADO'S BUTTERFLY BAT**

Fr. Glauconyctère de Machado; Ger. Machados Schmetterlingsfledermaus

Glauconycteris machadoi Hayman, 1963. Comp. Diamantes de Angola, Ser. Cult. 1963: 107. Lac Calundo, Angola.

Taxonomy Synonyms: none. Often considered to be a subspecies of *G. variegata*, but given specific status by Crawford-Cabral (1986), Hayman & Hill (1971) and Peterson & Smith (1973). Koopman (1971) suggested that the only known specimen might be a melanistic mutant of *G. variegata*, or a representative of a localized melanistic population almost surrounded by the typical pale form. Tentatively treated here as a distinct species, pending further information, including the extent of normal variation in colour of *G. variegata*, molecular information for both forms, and whether or not there is an extant population of the dark coloured form that differs from *G. variegata* in other ways besides colour. Chromosome number: not known.

Description Small microbat without noseleaf and with tail more or less fully enclosed in interfemoral membrane; four upper and five lower cheekteeth and two upper incisors on each side; ears separated, short for a vespertilionid (ca. 13 mm), rounded; all flight-membranes conspicuously reticulated; dorsal pelage brown without markings. Pelage fluffy, silky; mid-dorsal hairs ca. 8 mm. Dorsal pelage medium-dark brown, becoming slightly paler on the neck, and distinctly darker on top of head and face; changes colour, like shot-silk, depending on angle of view; hairs dark brown with slightly paler base. Ventral pelage pale greyish-cream; chin, lips and throat suffused with pale greyish-brown. Ears rounded; outer margin connecting with fleshy lobe near corner of mouth; inner margin – no data. Tragus as in *G. variegata*. Eyes very small. Wings and interfemoral membrane translucent, pale brown with very dark reddish-brown pigment outlining the wing-bones and venation (i.e. conspicuously reticulated), but the specimen is preserved as a dry skin and, in life, the flight-membranes may have been orange. Tibia long for this genus (20 mm). Skull and dentition as in *G. variegata*.

Geographic Variation None.

Similar Species Two other *Glauconycteris* have conspicuously reticulated wings:

Glauconycteris variegata. Dorsal pelage creamy-fawn. Flight-membranes pale yellowish-orange with dark brown reticulation on arm-wing, finger-wing and interfemoral membrane. Otherwise similar.

G. gleni. Dorsal pelage pale brown. Wings semi-translucent white with dark brown reticulation on inner part of arm-wing, and dark brown transverse lines across interfemoral membrane. Tibia shorter (15–17 mm).

Distribution Endemic to Africa. Known only from type locality in the Zambezian Woodland BZ in Angola.

Habitat The type locality is in wetter miombo woodland dominated by *Brachystegia* and *Julbernardia*.



Glauconycteris machadoi

Abundance Known from only one specimen.

Remarks The holotype was collected in a house. Nothing else is known about this species.

Conservation IUCN Category: Data Deficient.

Measurements

Glauconycteris machadoi

FA: 46 mm

WS: n. d.

TL: 105 mm

T: 48 mm

E: 13 mm

Tr: n. d.

Tib: 20 mm

HF: 8.5 mm

WT: n. d.

GLS: 14 mm

GWS: 10.5 mm

C–M³: 5.2 mm

Angola (holotype; ♀, Hayman 1963)

Key Reference Hayman 1963.

Meredith Happold

Glauconycteris poensis ABO BUTTERFLY BAT

Fr. Glauconyctère d'Abo; Ger. Abo Schmetterlingsfledermaus

Glauconycteris poensis (Gray, 1842). Ann. Mag. Nat. Hist., ser. 1, 10: 258. Abo (lower Niger R.), Nigeria.

Taxonomy Originally *Kerivoula poensis*. Synonyms: *kraussii*. Subspecies: none. Chromosome number: not known.

Description Very small microbat without noseleaf and with tail more or less fully enclosed in interfemoral membrane; four upper and five lower cheekteeth and two upper incisors on each side; ears separated; short for a vespertilionid (9–13 mm), rounded; wings dark brown (not conspicuously reticulated); dorsal pelage greyish-brown or brownish-grey with or without shoulder-spot and/or dorsal flank-stripe; tibia 16–19 mm; inner upper incisors weakly bicuspid. Sexes similar in colour; ♀♀ on average slightly larger in body measurements than ♂♂. Pelage dense, soft; mid-dorsal hairs 5–7 mm. Dorsal pelage medium to dark greyish-sepia brown or brownish-grey; hairs tricoloured with basal third dark grey, middle third pale greyish-brown and terminal third medium to dark greyish-sepia or brownish-grey, sometimes with sandy tip. Head and shoulders sometimes paler. Shoulder-spot and dorsal flank-stripe markings very variable: one or both may be present, on one or both sides and, if present, they may be conspicuous to very faint. Shoulder-spot and flank-stripe may be separate or joined. Ventral pelage same as dorsal pelage; sometimes paler on throat. Pattern variation in individuals from Sierra Leone is described by Hayman & Jones (1950). Head high-domed; muzzle short, broad, flattish. Ears rounded; inner margin with moderately long, backward-pointing lobe at base; outer margin connecting with fleshy lobe on lower lip near corner of mouth. Eyes very small. Wings and interfemoral membrane dark brown with faint venation lines, especially near body. Postcalcareal lobe: no information. Tibia of medium length for this genus. Tail shorter than HB.

*Glauconycteris poensis*

Skull (Figure 124) small and profile of forehead region (viewed laterally) strongly concave for a *Glauconycteris*. Upper inner incisor weakly bicuspid with unequal cusps. Lower incisors tricuspid, sometimes slightly crowded.

Geographic Variation No subspecies recognized (Koopman 1994). No other information.

Similar Species Two other *Glauconycteris* have dark wings and a dorsal flank-stripe:

Glauconycteris albofasciata. Dorsal pelage sepia brown; hairs tricoloured. Shoulder-spot and dorsal flank-stripe present but sometimes faint.

G. egeria. Dorsal pelage dark brown or almost black with conspicuous whitish dorsal flank-stripe but no shoulder-spot. Ears subquadrangular, dark brown with conspicuously pale rim. Inner upper incisor strongly bicuspid, cusps ca. equal in size.

Three other species are similar to individuals of *G. poensis* which lack a dorsal flank-stripe:

G. beatrix. Dorsal pelage dark sepia brown; hairs bicoloured. No dorsal markings (except shoulder-spot very rarely). Tibia often longer (19.4 [18–21] mm). Inner upper incisor strongly bicuspid.

G. humeralis. Dorsal pelage dark sepia brown; hairs bicoloured. Shoulder-spot present (except rarely). Inner upper incisor strongly bicuspid.

G. curryae. Dorsal pelage blackish-brown, sepia brown or reddish-brown; head and shoulders slightly paler than rump. No dorsal markings. Tibia almost always shorter (14–16 mm). Inner upper incisor strongly bicuspid.

Distribution Endemic to Africa. Recorded from the Rainforest BZ and marginally from the Northern Rainforest–Savanna Mosaic from Sierra Leone to Cameroon and Bioko I., with isolated records near the boundary of the Sudan Savanna and Guinea Savanna BZs of Senegal (Adam & Hubert 1972), from the Rainforest BZ in DR Congo (Hayman *et al.* 1966) and perhaps from the Somalia–Masai Bushland BZ in Tanzania. Koopman (1971) refers to a specimen from Tanzania in BMNH (presumably 1902.11.5.3 from Guni R., Kilimanjaro): the identity of this specimen has not been confirmed and, because the locality is remote from other records, it is mapped as a question mark. A record from Marangu, Kilimanjaro, Tanzania (Uchikawa 1991) is most likely to represent *G. variegata* (Grimshaw *et al.* 1997). Mapped from country checklists (see order Chiroptera), other literature and museum records.

Habitat Rainforest except for one record in Saboya Forest Reserve, near the Guinea and Sudan Savanna boundary in Senegal (Adam & Hubert 1972), and the dubious records from Tanzania (see Distribution). Recorded from primary forest in a sacred grove

surrounded by farmland on the Accra Plain of Ghana (Decher 1997). Found in rainforests and cocoa plantations, up to 1300 m on Bioko I. (Juste & Ibáñez 1994). Found in swamp forest in Taï N. P., Côte d'Ivoire (Fahr & Kalko 2011).

Abundance Uncertain. Uncommon in collections. Apparently common on Bioko I. (Juste & Ibáñez 1994).

Remarks By day, has been found, singly, in small holes in trees and clinging to stems of banana plants. Also found in groups of up to nine, clinging in a row, head to tail, along the leaflets of the fronds of Coconut Palms and Oil Palms in Sierra Leone (T. S. Jones in Grubb *et al.* 1998), and some were found in buildings (Rosevear 1965). A pair (♂ and ♀) were found inside a dead Cottonwood *Ceiba pentandra* (Jeffrey 1975).

Predators, Parasites and Diseases Ectoparasites include a flea *Lagaropsylla duodecima* (Siphonaptera: Ischnopsyllidae) (Beaucournu & Kock 1989).

Conservation IUCN Category: Least Concern.

Measurements

Glauconycteris poensis

FA (♂ ♂): 37.6 (32–40) mm, n = 24

FA (♀ ♀): 38.9 (36–41) mm, n = 34

WS (d): 276–277 mm, n = 3

TL: 91.0 (77–99) mm, n = 25

T: 42.0 (34–46) mm, n = 26

E: 10.5 (9–13) mm, n = 25

Tr: 4.4 (4.0–4.9) mm, n = 19

Tib: 18.0 (16–19) mm, n = 30

HF: n. d.

WT: 17.4 (15.7–18.9) g, n = 7

GLS: 12.0 (10.8–13.0) mm, n = 37

GWS: 9.1 (8.1–9.7) mm, n = 26

C–M³: 4.3 (4.0–4.8) mm, n = 28

Mainly Bioko I., also Sierra Leone and Togo (BMNH, RMCA, Juste & Ibáñez 1994)

Key Reference Rosevear 1965.

Meredith Happold

Glauconycteris superba PIED BUTTERFLY BAT (SUPERB BUTTERFLY BAT)

Fr. Glauconyctère pie; Ger. Schwarzweiße Schmetterlingsfledermaus

Glauconycteris superba Hayman, 1939. Ann. Mag. Nat. Hist., ser. 11, 3: 219. Pawa, ca. 45 km ENE Medje, Ituri District, DR Congo.

Taxonomy Synonyms: *sheila*. Subspecies: none. Chromosome number: not known.

Description Small microbat (spectacularly black and white) without noseleaf and with tail more or less fully enclosed in interfemoral membrane; four upper and five lower cheekteeth and two upper incisors on each side; ears separated, short for a vespertilionid (ca. 13 mm), subquadrangular; wings blackish (not conspicuously reticulated); dorsal pelage black, strikingly marked with white spots and stripes including three spots on the head; rostrum elongated and flattened (cf. other *Glauconycteris*). Medium-sized for a vespertilionid and the largest *Glauconycteris*. Sexual dimorphism: no information. Pelage dense, soft; mid-dorsal hairs 6–7 mm. Dorsal pelage black with white markings comprising one spot on the nose and two on forehead next to each ear, a backward-pointing subtriangular band on each side of mid-dorsal line (from shoulder-blade to mid-back), a narrow dorsal flank-stripe on each side, and either three spots in a row or one short line on each shoulder (Figure 126d–f). Ventral pelage with broad white band across throat, extending laterally to shoulders and then along each side of belly to anal region, leaving chin, flanks and mid-ventral area black. Dorsal and ventral hairs reddish to dark brown with black tip, or pure white. Ears long for the genus, subquadrangular. Tragus very broad, posterior margin distinctly curved with small basal lobule (Figure 124f). Wing-membranes dorsally blackish and without reticulation, ventrally with pale reticulation. Interfemoral membrane dorsally blackish, ventrally pale grey. Elbows, knees and ankles either black or pale. Tibia long for this genus (21 mm). Tail ca. 79% of HB.

Skull comparatively very large and robust for a *Glauconycteris*; profile of forehead region (viewed laterally) strongly concave (Figure

127a). Braincase high; sagittal crest weakly developed; lambdoid crest moderately developed. Rostrum conspicuously flattened and (viewed laterally) forming a sharp angle with braincase in frontal region. Inner upper incisor unicuspid. Lower incisors tricuspid (some with trace of fourth cusp) and crowded.

Geographic Variation Based on differences in colour pattern, Hayman (1946b) described *sheila* as a subspecies, but Rosevear (1965) suggested that pattern is possibly as variable in *G. superba* as in other *Glauconycteris* species, that the pattern described for *sheila* is not necessarily restricted to West Africa, and that the validity of *sheila* as a subspecies is dubious.

Similar Species None. No other *Glauconycteris* has conspicuous white markings on its head and ventral pelage.

Distribution Endemic to Africa. Known from only three localities in the Rainforest BZ (Western and East Central Regions). The record from Côte d'Ivoire, examined by Peterson & Smith (1973), is based on a single specimen from Matonguiné supposedly in the RMCA collection (J. Eger pers. comm.), which could not be found upon request (W. Van Neer pers. comm.). The record by Kingdon (1974) from Budongo Forest, Uganda, is disregarded here as the specimen illustrated by the author apparently does not represent *G. superba*.

Habitat The records from Matonguiné, Côte d'Ivoire (07° 18' N, 08° 04' W) and Oda, Ghana (05° 55' N, 00° 59' W) are located in the region of semi-deciduous forest at the periphery of evergreen lowland rainforest at ca. 360 m and 190 m, respectively. The type

*Glauconycteris superba*

locality – Pawa, DR Congo (02° 32' N, 27° 42' E) – is situated in the NE Congolian lowland rainforest at ca. 700 m.

Abundance Apparently very rare and local; only one specimen known from each of three localities.

Remarks The specimen from Ghana was found on the ground but still alive by G. S. Cansdale. No other information.

Conservation IUCN Category: Least Concern.

Apparently very rare, only three localities and specimens known; area of occupancy very restricted. The specimens originated from areas that are nowadays heavily degraded and fragmented, especially in West Africa. Major threat: loss of habitat as result of logging and agriculture. Population size unknown but population trend inferred to be declining. Based on this information, categorization as Least Concern seems very misleading: a threatened category or Data Deficient would be more appropriate.

Measurements

Glauconycteris superba

FA: 46.1 (45–48) mm, n = 3

WS: n. d.

TL: 88, 112 mm, n = 2

T: 39, 49 mm, n = 2

E: 13 mm, n = 1

Tr: 7.5 mm, n = 1

Tib: 21, 21 mm, n = 2

HF: 8.3 mm, n = 1

WT: n. d.

GLS: 16.4 (16.2–16.5) mm, n = 3

GWS: 11.3 (11.0–11.9) mm, n = 3

C–M³: 6.0 (5.8–6.2) mm, n = 3

Côte d'Ivoire, Ghana, DR Congo (BMNH [holotype *sheila*], RMCA [incl. holotype *superba*], J. Eger pers. comm.)

Key References Hayman 1939, 1946b; Rosevear 1965.

Jakob Fahr

Glauconycteris variegata VARIEGATED BUTTERFLY BAT

Fr. Glauconyctère papillon; Ger. Genetzte Schmetterlingsfledermaus

Glauconycteris variegata (Tomes, 1861). Proc. Zool. Soc. Lond. 1861: 36. Otjoro, Namibia.

Taxonomy Originally *Scotophilus variegata*. Synonyms: *papilio*, *phalaena*. Subspecies: two currently recognized. *Glauconycteris machadoi*, which is sometimes considered to be a melanistic subspecies or mutant of *G. variegata*, is tentatively treated here as a distinct species. Chromosome number (South Africa): 2n = 18; aFN = 32 (Rautenbach *et al.* 1993).

Description Beautiful, small to very small microbat without noseleaf and with tail more or less fully enclosed in interfemoral membrane; four upper and five lower cheekteeth and two upper incisors on each side; ears separated, short for a vespertilionid (11–14 mm); all flight-membranes conspicuously reticulated; dorsal pelage pale without markings. Sexes similar. Pelage dense, soft; mid-dorsal hairs 7–10 mm. Dorsal pelage pale creamy-buff to yellowish-fawn, sometimes becoming paler on head and neck; hairs pale creamy-buff or yellowish-fawn with paler base, or creamy-white with brown base and yellowish-fawn tip. Ventral pelage yellowish-cream to pure white, sometimes suffused with pale grey especially

on throat. Head high-domed; muzzle short, broad and flattish. Ears light brown; outer margin connecting with fleshy lobe near corner of mouth; inner margin with moderately long, backward-pointing lobe at base. Tragus with anterior margin straight, posterior margin convex with inconspicuous lobe at base (Figure 124g). Eyes very small. Wings and interfemoral membrane pale yellowish-orange with dark brown pigment outlining bones and venation (i.e. conspicuously reticulated) (Figure 125a). Tibia long for this genus (18–21 mm). Tail shorter than HB.

Skull moderately large and profile of forehead region (viewed laterally) weakly concave for a *Glauconycteris*. Upper incisor variable (unicuspid to strongly bicuspid with unequal cusps). Lower incisors tricuspid, crowded, at right-angles to line of jaw.

Geographic Variation Two subspecies are currently recognized (Hayman & Hill 1971, Koopman 1975, Simmons 2005), but their validity is uncertain:

- G. v. phalaena*: SC Sudan, Somalia. Dentition comparatively less massive. Dorsal pelage paler (Thomas 1915b).
G. v. variegata: remainder of geographic range (including NE Ethiopia according to Hill & Morris [1971]). Canines, premolars and molars comparatively massive.

Koopman (1975) commented that the distribution of *G. variegata* and the subspecies *phalaena* (if valid) in the region of the Sudan is imperfectly known.

Similar Species Two other *Glauconycteris* have conspicuously reticulated wings:

- Glauconycteris machadoi*. Dorsal pelage dark brown. Flight-membranes pale brown (? orange) with very dark reddish-brown reticulation on arm-wing, finger-wing and interfemoral membrane. Otherwise similar.
G. gleni. Dorsal pelage pale brown. Wings semi-translucent white with dark brown reticulation on inner part of arm-wing, and dark brown transverse lines across interfemoral membrane. Tibia shorter (15–17 mm).

Distribution Endemic to Africa. Widespread south of the Sahara, mainly in the Sudan Savanna and Guinea Savanna BZs, the Rainforest–Savanna Mosaics and the Somalia–Masai Bushland, Coastal Forest Mosaic and Zambezian Woodland BZs. Also recorded in the Afromontane–Afroalpine BZ in some localities, and there is one record in the Rainforest BZ. Senegal to Ethiopia and Somalia, and southwards to N Namibia, N Botswana and N South Africa (but not yet recorded from all countries within this area). Mapped from country checklists (see order Chiroptera), other literature and museum records.

Habitat Mainly savanna habitats including open woodland savannas and open bush country (e.g. Lang & Chapin 1917b, Smithers 1983,

Happold & Happold 1987, Obrist *et al.* 1989, Grubb *et al.* 1998). Has been recorded within the rainforest zone, but probably where the forest has been destroyed (Rosevear 1965). In dry country in Zimbabwe and Malawi, often associated with riverine woodland. Has been recorded over streams and pools. In southern Africa, not found in forests according to Smithers (1983), but more recently a specimen was mist-netted in a public picnic ground within dense forest in KwaZulu–Natal (Taylor, P. 1998).

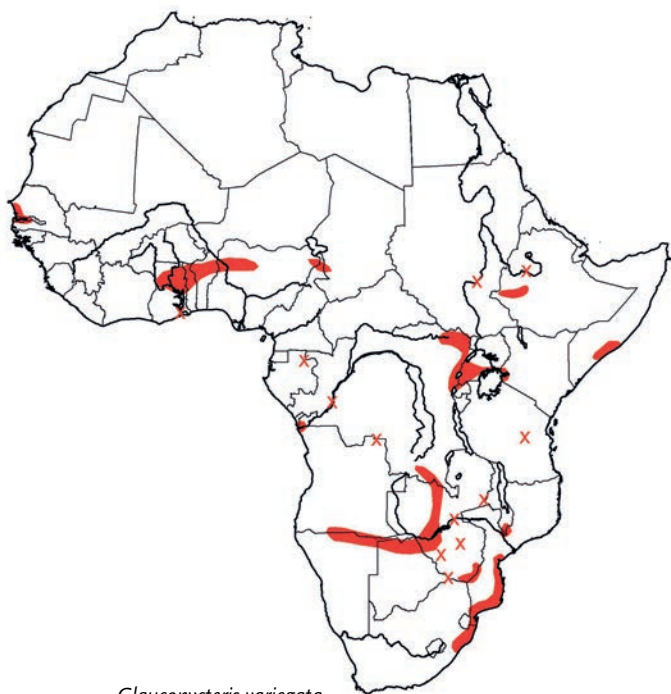
Abundance Rarely collected and considered rare throughout its geographic range, but its habits make this species difficult to find and capture.

Adaptations Aspect ratio low; wing-loading low to very low; wing-tip comparatively long and pointed (Obrist *et al.* 1989, M. Happold unpubl.). These data imply efficient low-speed flight as well as being able to fly moderately fast. Manoeuvrability moderate. Turns by banking (minimum radius just under 50 cm) and sometimes by stalling-and-twisting; individuals could fly across a 1×1×1 m enclosure but were unable to fly more than one circuit/flight (2 bats, 10 flights each). Can take off from ground. By day, roosts mainly in trees, hanging within dense clusters of leaves (Lang & Chapin 1917b, Pienaar *et al.* 1980, McLellan 1986, Obrist *et al.* 1989). Because the reticulated wings resemble dead leaves, roosting bats are very difficult to see unless they move. Has also been found hiding in the thatch of abandoned huts (Lang & Chapin 1917b). In Zimbabwe, one group returned to roost in the same cluster of leaves for several consecutive days, despite being disturbed every day (Obrist *et al.* 1989); this roost was in the underside of the canopy of a *Trichilia emetica* tree, ca. 7.5 m above ground. On overcast days, individuals sometimes leave their roosts up to two hours before sunset (Lang & Chapin 1917b).

Foraging and Food Forages, by moderately fast-hawking, high above the ground (e.g. 18 m) in uncluttered environments (Lang & Chapin 1917b), but can also forage close to clutter, such as between trees (Taylor 2000, M. Happold unpubl.). Lang & Chapin (1917b) wrote: ‘They fluttered swiftly, now and then increasing their speed with such spontaneous ease that one hardly noticed the quickened beating of their wings as they gathered their tiny insect prey.’ Stomach contents and faeces of perhaps no more than three bats contained moths (Kingdon 1974, Fenton *et al.* 1977).

Echolocation Search-phase call-shape (Zimbabwe) smooth steep–shallow FM. Start-frequency (mean ± S.D.) 53.4 ± 7.7 kHz; end-frequency 33.7 ± 1.7 kHz; peak-frequency 37.7 ± 1.6 kHz; bandwidth 19.7 ± 7.7 kHz; call-duration 5.3 ± 1.4 ms (211 calls, two bats foraging; Obrist *et al.* 1989). Approach-phase calls are shorter and broader in bandwidth.

Social and Reproductive Behaviour Has been found roosting singly, in pairs and in small groups of three to ca. 12. One group of six adults comprised four ♀♀ with neonates and two not sexed (Obrist *et al.* 1989). A group of eight adults, found roosting on a low branch of a mango tree in Sudan, included a ♂ and two ♀♀ (others not sexed) (McLellan 1986).



Glauconycteris variegata

Reproduction and Population Structure Litter-size: one or two; single foetuses ($n = 5$), twin foetuses ($n = 1$), ♀ ♀ with one neonate ($n = 4$) (Lang & Chapin 1917b, Smithers & Wilson 1979, Obrist *et al.* 1989, BMNH). Reproductive chronology: not known. At 3–4°N in NE DR Congo, 3 of 10 ♀ ♀ were pregnant in Mar; parturition predicted to occur in Mar–Apr at which time the young could take refuge in low bushes and vegetation newly in leaf after the annual dry season fires in Dec and Jan had left them completely bare (Lang & Chapin 1917b). At 01° 17'S (Nairobi, Kenya), a lactating ♀ was recorded in Apr (ROM). At 16–20°S in Zimbabwe, pregnancies were recorded in Aug (Smithers & Wilson 1979) and births in Nov (Obrist *et al.* 1989), but there are no data for other months. The reproductive chronology cannot be determined from these data because there are no year-round observations at any of these localities.

Predators, Parasites and Diseases No information.

Conservation IUCN Category: Least Concern.

Measurements

Glauconycteris variegata

FA: 42.2 (38–45) mm, $n = 32$

WS (a): 314.3 (300–324) mm, $n = 8$

TL: 102.6 (88–115) mm, $n = 27$

T: 46.6 (40–53) mm, $n = 26$ E: 12.6 (11–14) mm, $n = 24$

Tr: 5.5, 6.0 mm, $n = 2$

Tib: 19.4 (18–21) mm, $n = 28$

HF: 8.9 (7–10) mm, $n = 18$

WT: 11.1 (5–14) g, $n = 15$

GLS: 14.0 (13.6–14.5) mm, $n = 23$

GWS: 10.4 (9.9–10.7) mm, $n = 16$

C–M³: 4.9 (4.7–5.2) mm, $n = 25$

Throughout geographic range (Peterson & Smith 1973, M. Happold unpubl.)

Key References Lang & Chapin 1917b; Obrist *et al.* 1989; Smithers 1983.

Meredith Happold

GENUS *Laephotis* African Long-eared Bats

Laephotis Thomas, 1901. Ann. Mag. Nat. Hist., ser. 7, 7: 460. Type species: *Laephotis wintoni* Thomas, 1901.



Laephotis wintoni with ears fully erect.

A small genus with four species, endemic to Africa south of the Sahara. Diagnostic combination of characters: four upper and five lower cheekteeth and two upper incisors on each side; ears moderately long and wide for an African vespertilionid (15–25 mm) but relatively larger than in any other sub-Saharan genus (ca. half length of FA or a little longer); ears not joined at base (cf. *Plecotus*); outer margin of ear not reaching mouth; no body pattern; wings not reticulated; head slightly flattened; dental formula: $^{2113}/_{3123} = 32$ (cf. *Otonycteris* but as in *Glauconycteris*, *Eptesicus*, some *Pipistrellus* and *Mimetillus*); see Table 21, p. 545. The upper and lower premolars are tall teeth, almost the same height as the canines, and this, together with toothwear on the canines, might account for the suggestion that the canines are

extremely reduced (Hayman & Hill 1971, Kingdon 1974). Selected characters of *Laephotis* are illustrated in Figure 129. Placed in tribe Vespertilionini by Hill & Harrison (1987) on basis of baculum morphology, and retained in that tribe by Simmons (2005).

Prior to Peterson's (1971c) and Setzer's (1971) revisions, this genus was considered monotypic with two subspecies. Peterson (1971c) introduced *wintoni* and *angolensis* as distinct species, while Setzer (1971) described two further species, *namibensis* and *botswanae*. However, inter-specific relations remain unresolved largely because specimens are few and in scattered collections (Kock & Howell 1988, Stanley & Kock 2004). Several specimens from South Africa were assigned to *L. wintoni* and *L. cf. wintoni* on the basis of multivariate analyses (Rautenbach & Nel 1978, Watson 1990a, Kearney & Taylor 1997). Given the distance of South African localities from other populations of *L. wintoni* in Kenya and Ethiopia, this identification was considered with some scepticism and not followed by Honacki *et al.* (1982) or Corbet & Hill (1991). Specimens described by Rautenbach & Nel (1978) were subsequently provisionally placed with *L. namibensis* (Skinner & Smithers 1990). Kock & Howell (1988) and Stanley & Kock (2004) identified several cases where specimens identified as *L. angolensis* have been re-identified as *L. botswanae* or *L. cf. angolensis*. Morphometric analyses that included palatal and post-palatal measurements (Kearney & Seamark 2005) allowed the distinction of *L. botswanae* and *L. cf. angolensis* from other species of *Laephotis*, and suggested the assignment of specimens from KwaZulu–Natal previously identified as *L. cf. wintoni* to *L. botswanae*. However, the distinction between *L. wintoni* and *L. namibensis* was not confirmed and still remains to be clarified (Kearney & Seamark 2005).

In his initial description of the genus *Laephotis*, Thomas (1901) suggested the genus was most closely allied to *Vespertilio*. Tate (1942)

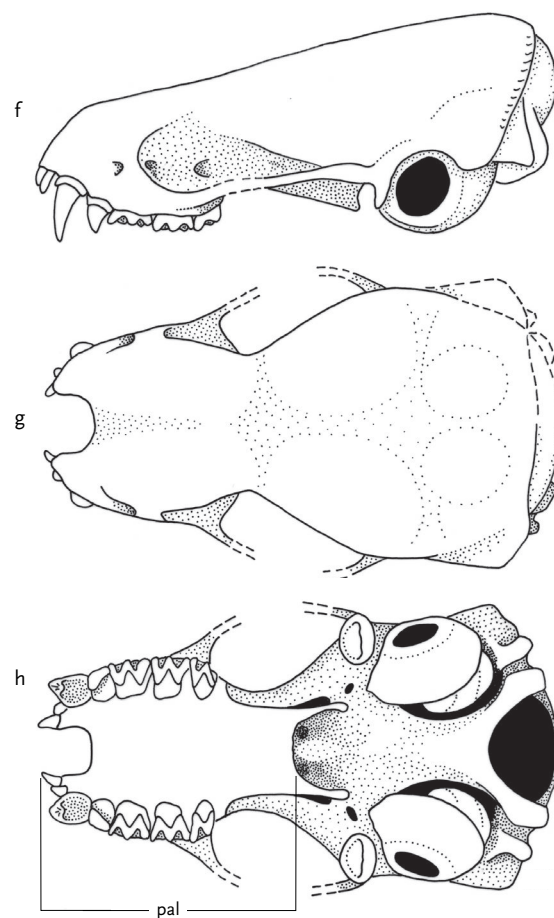
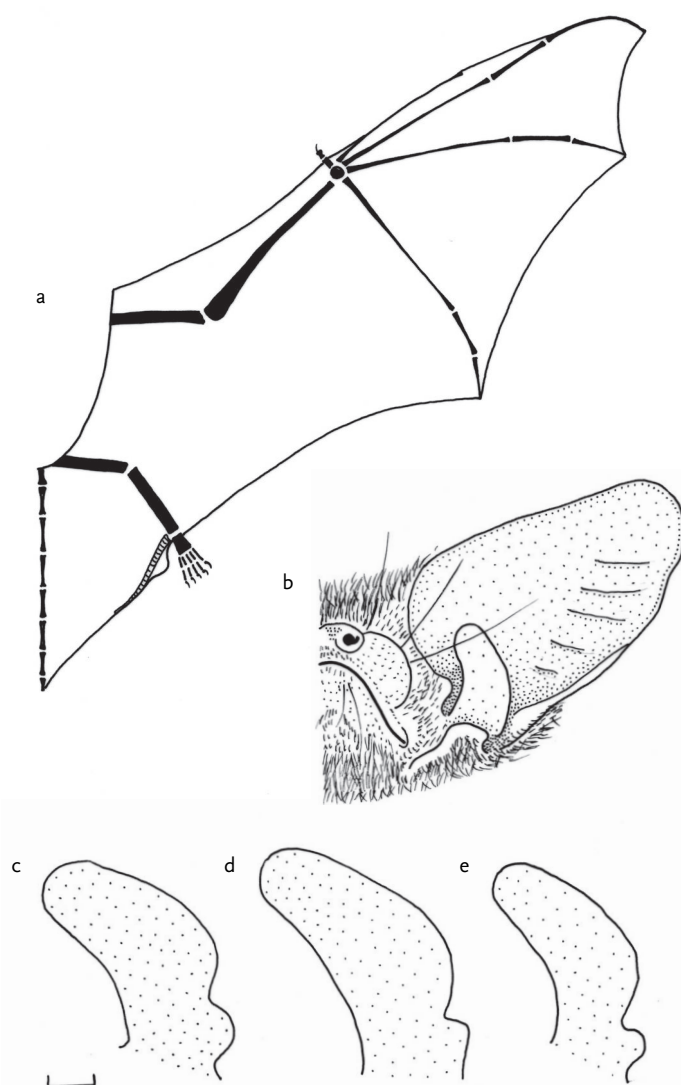


Figure 129. *Laephotis*. (a) Flight membranes, and bones of wing, hindlimb and tail of *L. botswanae*. (b) Left ear of *L. botswanae* (frontal view). Tragi of (c) *L. botswanae*, (d) *L. namibensis* and (e) *L. wintoni* (scale = 2mm). (f), (g) and (h) Lateral, dorsal and ventral views of skull of *L. wintoni* (holotype, BMNH 1.5.6.5). pal = palatal length as defined by Kearney & Seamark (2005), see Table 24.

considered *Laephotis* the closest relative of the Neotropical big-eared genus, *Histiotus*, which in turn was considered an offshoot of *Eptesicus*. However, the ears in *Laephotis* are not as greatly enlarged as in *Histiotus*, nor are they connected across the forehead (Hayman & Hill 1971). On geographic grounds, Williams & Mares (1978) doubted the association with *Histiotus*. Hill (1974a) considered *Laephotis* an independent offshoot of *Eptesicus*.

A fairly wide range of biotic zones and habitats are exploited by this genus: the Somalia–Masai Bushland, Zambezi Woodland, the Southern Rainforest–Savanna Mosaic (marginally), Afromontane–Afroalpine, Highveld, South-West Arid and South-West Cape BZs.

The four species can be identified from the information in Table 24.

Teresa Kearney

Table 24. Key to the species in the genus *Laephotis*. Palatal length = distance from anterior edge of incisors to anterior edge of mesopterygoid fossa.

| Palatal length (mm) | FA (mm) | E (mm) | GLS (mm) | Distribution | Species |
|---------------------|--------------|--------------|------------------|---|----------------------|
| 6.1, 6.2 | 34.3 (32–36) | 16.2 (15–18) | 13.7 (13.7–13.8) | Angola, DR Congo
South of 11°S | <i>L. angolensis</i> |
| 6.7 (6.2–7.3) | 36.3 (30–39) | 19.2 (17–22) | 14.6 (14.1–15.5) | Angola, DR Congo, Tanzania, Zambia, Malawi
Botswana, Zimbabwe, South Africa
South of 11°S | <i>L. botswanae</i> |
| 8.0 (7.6–8.7) | 37.8 (36–40) | 22.8 (22–25) | 16.4 (16.1–17.0) | Namibia, SW South Africa
West of 20°E | <i>L. namibensis</i> |
| 8.1 (7.9–8.5) | 39.6 (37–41) | 22.0 (21–24) | 16.0 (15.6–16.3) | Ethiopia, Kenya, Tanzania, E South Africa, Lesotho
East of 25°E | <i>L. wintoni</i> |

Laephotis angolensis ANGOLAN LONG-EARED BAT

Fr. Oreillard d'Angola; Ger. Angola-Langohrfledermaus

Laephotis angolensis Monard, 1935. Archos. Mus. Bocage 6: 45. Tyihumbwe, 15 km west of Dala, Angola.

Taxonomy Synonyms: none. Described, as a distinct species, from a single specimen, ♀ with damaged skull, but subsequently considered a subspecies of *L. wintoni* (Ellerman *et al.* 1953, Hayman & Hill 1971). Although currently treated as a distinct species, the relationship between *L. angolensis* and *L. botswanae* is obscure, partly because specimens of *L. angolensis* are so scarce that variation within this form cannot be assessed. Peterson (1973) suggests that *L. botswanae* may prove to be a larger, southern race of *L. angolensis*. However, both species occur together in S DR Congo (Setzer 1971). Several specimens originally considered to represent *L. w. angolensis* were later reassigned to *L. botswanae* (Smithers 1971, Hill 1974a). Chromosome number: not known.

Description Very small microbat without noseleaf and with tail more or less fully enclosed in interfemoral membrane; four upper and five lower cheekteeth and two upper incisors on each side; ears separated, of medium length for a vespertilionid (15–18 mm) and of medium relative length (45–46% of FA, $n = 2$), not joined at base; GLS: 13.7–13.8 mm. A very poorly known species. Sexual dimorphism: no information. Mid-dorsal hairs ca. 7 mm. Dorsal pelage yellowish-brown to reddish-brown; hairs distinctly bicoloured, basal 5 mm blackish-brown, terminal 2 mm yellowish-brown or reddish-brown. Ventral pelage pale grey on chin, paler on throat, becoming cream or white in pelvic region; hairs (except pelvic region) blackish-brown with pale grey, cream or white tip. Ventral hairs in pelvic region pure white. The naked skin on muzzle and around eyes is dark brown. Ears dark brown, roughly triangular but very elongated; tip rounded; inner margins almost meeting on forehead but not joined. Ears may be held erect above head or (when resting) held sideways at right-angles to head. Tragus with notch at base of posterior margin as in *L. botswanae*, but diagnostic differences between the tragi of these species, if present, are not known. Wings dark brown; arm-wing with whitish hind-border. Interfemoral membrane medium-brown, more translucent.

Skull (as in all *Laephotis* spp.) with braincase slightly flattened; rostrum rather narrow; zygomatic arches slender; no sagittal crest; lambdoid crest weakly developed. Skull apparently shorter and usually narrower than in other *Laephotis* but data very limited (GLS: 13.7–13.8 mm; GWS: 6.7, 8.1 mm, $n = 2$). Palatal length 6.1, 6.2 mm ($n = 2$) (cf. >6.4 mm in *L. botswanae* and *L. wintoni*) (Hill 1974a).

Geographic Variation None.

Similar Species Not easily distinguished from other *Laephotis*, and relationship with *L. botswanae* is uncertain.

Laephotis botswanae. Ventral pelage paler. Tragus broader; posterior margin more angular. Skull longer (GLS: 14.1–15.5 mm) and usually broader (GWS: 8.0–8.8 mm). Rostrum slightly longer and broader, palate longer (Hill 1974a).

*Laephotis angolensis*

L. wintoni. Forearm longer (37–41 mm). Ears longer (21–24 mm) and broader. Skull longer and broader (GLS: 15.6–16.3 mm, GWS: 8.8–9.5 mm, C–M³: 5.1–5.3 mm).

L. namibensis. Forearm usually longer 37.8 (36–40 mm). Ears longer (22–25 mm). Skull larger (GLS: 16.1–17.0 mm, GWS: 8.4–9.2 mm, C–M³: 4.8–5.4 mm).

Distribution Endemic to Africa. Apparently restricted to the Zambezian Woodland BZ and the southern fringe of the Southern Rainforest–Savanna Mosaic. Recorded from Angola and SE DR Congo (Peterson 1971c, Setzer 1971, Hill 1974a).

Habitat No details available.

Abundance Rare.

Remarks Nothing else is known about the habits of this species. **Predators, Parasites and Diseases** Ectoparasites recorded include a bed-bug *Cacodmus villosus* (Hemiptera: Cimicidae), a tick *Rhipicephalus simus* (Acari: Ixodidae) and mites *Spinturnix walkeri* (Acari: Spinturnicidae), *Steatonyssus* sp. (Acari: Macronyssidae) (Anciaux de Faveaux 1984), although the information is uncertain because the identity of the host still needs to be confirmed.

Conservation IUCN Category: Data Deficient.

Measurements

Laephotis angolensis

FA: 34.3 (32–36) mm, n = 4

WS: n. d.

TL: n. d.

HB: 46, 50 mm, n = 2

T: 36, 38 mm, n = 2

E: 16.2 (15–18) mm, n = 4

Tr: n. d.

Tib: n. d.

HF: 6.0 mm, n = 1

WT: n. d.

GLS: 13.7 (13.7–13.8) mm, n = 3

GWS: 6.7, 8.1 mm, n = 2

C–M³: 4.3, 4.3 mm, n = 2

Angola and DR Congo (Monard 1935, Setzer 1971, Hill 1974a)

Key Reference Hill 1974a.

Teresa Kearney

Laephotis botswanae BOTSWANAN LONG-EARED BAT

Fr. Oreillard du Botswana; Ger. Botswana-Langohrfledermaus

Laephotis botswanae Setzer, 1971. Proc. Biol. Soc. Washington 84: 260, 263. 80 km west and 19 km south of Shakawe, Botswana.

Taxonomy Synonyms: none. The distinction between *L. botswanae* and *L. angolensis* remains obscure and many specimens originally described as *L. angolensis* have been reassigned to *L. botswanae* (Hill 1974a, Ansell 1978) or remain of unsettled identity (Fenton & Bell 1981, Fenton 1985). Both species occur together in S DR Congo (Setzer 1971), and Kock & Howell (1988) question the validity of the species status of *botswanae* because of this. Chromosome number (South Africa): 2n = 34; aFN = 50 (as in *L. namibensis* and *L. wintoni* [Rautenbach *et al.* 1993]).

Description Very small microbat without noseleaf and with tail more or less fully enclosed in interfemoral membrane; four upper and five lower cheekteeth and two upper incisors on each side; ears separated, of medium length for a vespertilionid (17–22 mm) and of medium relative length (44–64% of FA, n = 22); GLS: 14.1–15.5 mm. A poorly known species. Sexes similar. Pelage soft, slightly shaggy on rump; mid-dorsal hairs ca. 8 mm. Dorsal pelage reddish-brown, chocolate brown or pale brown; hairs distinctly bicoloured, basal 6 mm blackish-brown, terminal 2 mm reddish-brown, chocolate brown or pale brown. Ventral pelage creamy-brown on chin, paler on throat, becoming cream or white in pelvic region; hairs (except in pelvic region) with basal 4 mm blackish-brown, terminal 4 mm creamy-brown, cream or white. Hairs in pelvic region pure white. The naked skin on muzzle and around eyes is brown. Ears pale to medium brown, roughly triangular with broad base and rounded tip; reaching well beyond snout when laid forward; inner margins almost meeting on forehead, but not joined. Ears may be held erect above the head or (when resting) held horizontally at right-angles to head. Tragus as in Figure 129c. Wings dark brown; arm-wing usually with whitish hind-border; interfemoral membrane paler and more translucent.

Skull (as in all *Laephotis* spp.) with braincase slightly flattened; rostrum rather narrow; zygomatic arches slender; no sagittal crest; lambdoid crest weakly developed. Skull on average medium-short and of medium width for the genus (GLS: 14.4–15.5 mm; GWS: 8.0–8.8 mm). Palatal length 6.7 (6.2–7.3) mm, n = 21 (Kearney & Seamark 2005).

Geographic Variation No subspecies recognized. Pelage colour varies according to locality – the dorsal pelage of TM specimens from South Africa are reddish-brown, those from Zimbabwe are paler brown.

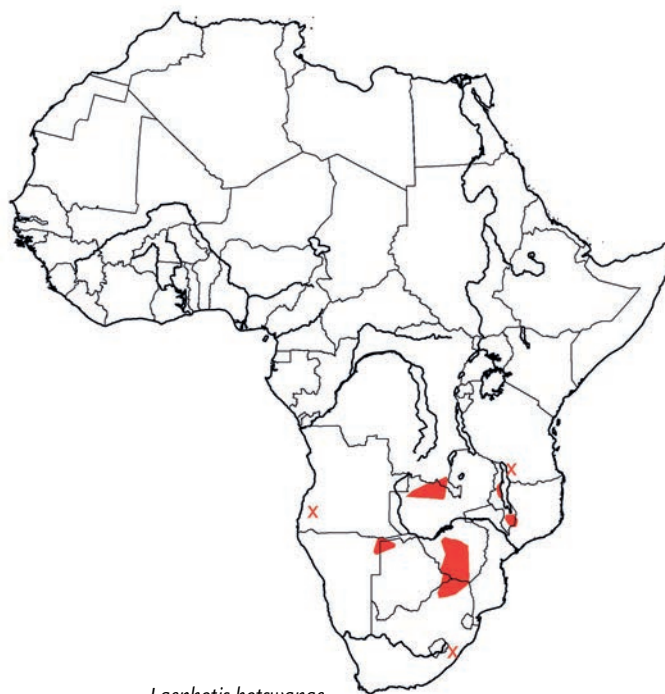
Similar Species Not easily distinguished from other *Laephotis*, and relationship with *L. angolensis* is uncertain.

Laephotis angolensis. Ventral pelage darker. Tragus narrower, posterior margin less angular. Skull shorter (GLS: 13.7–13.8 mm) and usually narrower (GWS: 6.7, 8.1 mm), but data very limited. Rostrum slightly shorter and narrower; palate shorter (Hill 1974a).

L. wintoni. Forearm on average longer (39.6 [37–41] mm). Skull usually larger (GLS: 16.0 [15.6–16.3] mm; C–M³: 5.2 [5.1–5.3] mm).

L. namibensis. Skull longer (GLS: 16.1–17.0 mm).

Distribution Endemic to Africa. Known from scattered localities in the Zambezian Woodland BZ and marginally in one part of the Kalahari Desert area in the South-West Arid BZ. Recorded from Angola, S DR Congo, S Tanzania, Zambia, Malawi, N Botswana, Zimbabwe, South Africa. The most southern record (see map) is



Laephotis botswanae

based on re-identified specimens from Hella-Hella (KwaZulu–Natal, South Africa): it extends the geographic range by ca. 658 km further south (Kearney & Seamark 2005).

Habitat Most specimens have been caught in mist-nets, usually over or close to water, in riverine woodland or woodland savanna. Their association with rocky outcrops has been noted in some localities (Herholdt 1989, Cotterill 1996a). In Malawi, recorded near streams, and lakes in montane and sub-montane evergreen forest at 1520–1700 m, from miombo woodland near sub-montane rainforest at 1350–1500 m, from mosaic of miombo woodland, farmland and riverine woodland near rocky hills, dams, streams and marshes at 1000 m, and in ornamental gardens in the town of Zomba (800–900 m), with rocky hills nearby (Happold & Happold 1997).

Abundance Rare in some parts of their distribution, although Herholdt (1989) and Happold & Happold (1997) have suggested it is not uncommon, but seldom caught at other localities. There was a marked change in numbers recorded in Malawi between a survey in 1984–85 with three specimens (Happold *et al.* 1987), and 1993–94 with 17 specimens (Happold & Happold 1997). Herholdt (1989) suggested that their being caught singly might indicate they are not easily captured in mist-nets. Numbers in museum collections are growing.

Adaptations Aspect ratio low; wing-loading very low (Malawi; M. Happold pers. comm.). Flight highly manoeuvrable; turns by banking (minimum radius <25 cm) and by stalling-and-twisting; individuals were able to sustain flight in a 1×1×1 m enclosure for up to three circuits/flight (6 bats, 10 flights each; M. Happold pers. comm.). Can take off from ground. Not easily able to climb or scuttle. A pair was found roosting under the bark of a broken limb of a tree (HSM specimen label written by W. F. H. Ansell); no other roosts known. Becomes torpid during day at ambient temperatures 21–24 °C. Predicted mean maximum urine concentration is medium (3745 mOsmol/kg); captive bats drank regularly every night (Happold & Happold 1980).

Foraging and Food Forages by slow-hawking. A light-tagged individual, released in an area with marshland, a large dam, some woodland and farmland, observed for 53 min, foraged mainly between 1–3 m over the marsh, making straight level traverses to and fro with some jerky zig-zagging and some wide circling, but no diving or swooping upwards or any other aerobatic manoeuvres; also foraged over tall grass in spaces between trees, and flew over a banana plantation; did not fly above other trees and did not forage over the open water (M. Happold pers. comm.). Fenton (1985) reported Coleoptera, Lepidoptera and Trichoptera in cool season diet of *Laephotis* in Zimbabwe, and Lepidoptera only in wet season; however, he was not sure if the bats represented *L. botswanae* or *L. angolensis* and this is still unresolved.

Echolocation Search-phase call-shape (Malawi) (a) steep FM/QCF (Figure 118a) and (b) smooth steep/shallow FM (six bats recorded as released, one tethered; M. Happold pers. comm.). (a) Start-frequency 60–72 kHz; end-frequency 29–33 kHz; peak-frequency 29–33 kHz; call-duration ca. 3–5 ms (155 calls). (b) Start-frequency 47–49 kHz; end-frequency 32–33 kHz; call-duration

7–8 ms (12 calls). Fenton & Bell (1981) reported calls from *Laephotis* of uncertain identity from Zimbabwe (see above) for which call-shape (based on one illustrated call) was angular steep/shallow FM; start-frequency 55 kHz; end-frequency 32 kHz; peak-frequency 33 kHz; maximum call-duration 5 ms. Although call-shapes differed, the peak-frequency was the same in calls from Malawi and Zimbabwe, suggesting that the bats in both localities represent *L. botswanae*.

Social and Reproductive Behaviour Very little information. Of 20 individuals sampled in Malawi, one post-lactating ♀ and one subadult ♂ were mist-netted together; one reproductively inactive ♀, one lactating ♀ and one ♂ with abdominal testes were caught in one mist-net at intervals of 15 min and 5 min respectively; and all others were caught singly on different dates and at different localities (M. Happold pers. comm.). All of four individuals mist-netted by Herholdt (1989) in the Waterberg area in the Limpopo Province of South Africa were caught singly.

Reproduction and Population Structure Litter-size: not known. Reproductive chronology not known (data inconclusive). At 15° 31' S (near Namadzi, Malawi), 2 of 3 adult ♀♀ were lactating and one was reproductively inactive in Dec; 2 of 2 were reproductively inactive in Jan; 2 of 2 were post-lactating in Feb; no data for other months (M. Happold pers. comm.). Two subadults were captured in Jan and Feb. These data suggest that ♀♀ might not reach sexual maturity until second year.

Predators, Parasites and Diseases A bed-bug *Cacodmus villosus* (Hemiptera: Cimicidae) has been recorded on *L. botswanae* from Huila, Angola, and found on *Laephotis* from S DR Congo, of which most of the host series have been identified as *L. botswanae*, although two specimens are considered to represent *L. cf. angolensis* (Stanley & Kock 2004).

Conservation IUCN Category: Least Concern.

Measurements

Laephotis botswanae

FA: 36.3 (30–39) mm, n = 31

WS (a): 262.8 (255–274) mm, n = 6*

TL: 93.2 (88–97) mm, n = 11*

HB: 51.5 (47–55) mm, n = 13

T: 42.2 (39–47) mm, n = 14

E: 19.2 (17–22) mm, n = 14

Tr: 9.1 (8.5–9.5) mm, n = 4*

Tib: 15.3 (14–16) mm, n = 10*

HF: 7.4 (7–8) mm, n = 9

WT: 6.6 (5.0–8.0) g, n = 14

GLS: 14.6 (14.1–15.5) mm, n = 22

GWS: 8.4 (8.0–8.8) mm, n = 17

C–M³: 4.7 (4.5–4.9) mm, n = 25

Throughout geographic range (HC, NMZB, TM, Hill 1974a)

*Malawi only (M. Happold unpubl.)

Key References Herholdt 1989; Hill 1974a; Setzer 1971.

Teresa Kearney

***Laephotis namibensis* NAMIBIAN LONG-EARED BAT**

Fr. Oreillard de Namibie; Ger. Namibia-Langohrfledermaus

Laephotis namibensis Setzer, 1971. Proc. Biol. Soc. Washington 84: 259. Kuiseb River, Gobabeb, Namibia.

Taxonomy Synonyms: none. Two specimens from Algeria Forest, Cederberg, in the Western Cape of South Africa were identified as *L. wintoni* (on basis of multivariate statistics) by Rautenbach & Nel (1978), but they were subsequently re-identified as *L. namibensis* in Skinner & Smithers (1990). Three additional specimens caught at Algeria, two of which are in the South African Museum collection, confirm the occurrence of *L. namibensis* in South Africa. Chromosome number (Namibia): $2n = 34$; $aFN = 50$ (as in *L. botswanae* and *L. wintoni*) (Rautenbach *et al.* 1993).

Description Very small microbat without noseleaf and with tail more or less fully enclosed in interfemoral membrane; four upper and five lower cheekteeth and two upper incisors on each side; ears separated, of medium length for a vespertilionid (22–25 mm) and of medium relative length (54–65% of FA, $n = 11$); GLS: 16.1–17.0 mm. A poorly known species. Sexes similar. Pelage soft, slightly shaggy on rump; mid-dorsal hairs ca. 7 mm. Dorsal pelage creamy-brown or yellowish-brown; hairs distinctly bicoloured, basal 4 mm dark brown, terminal 3 mm creamy-brown or yellowish-brown. Ventral pelage (except in pelvic region) pale cream to whitish; hairs with basal 4 mm blackish-brown, terminal 3 mm pale cream or white. Hairs in pelvic region pure white. The naked skin on muzzle and around eyes is pale brown. Ears pale to medium-brown, roughly triangular but elongated; tip rounded; inner margins almost meeting on forehead but not joined. Ears may be held erect above the head or (when resting) held horizontally at right-angles to head. Tragus shape much like that of *L. botswanae* except that in *L. namibensis* the bulge above the basal, posterior notch extends further out, making the tragus much wider at that point (Figure 129d). Wings pale creamy-brown (when dorsal pelage is pale) or dark brown (when dorsal pelage is yellowish-brown); arm-wing usually with whitish hind-border. Interfemoral membrane paler and more translucent.

Skull (as in all *Laephotis* spp.) with braincase slightly flattened; rostrum rather narrow; zygomatic arches slender; no sagittal crest; lambdoid crest weakly developed. Skull on average long and wide for the genus (GLS: 16.1–17.0 mm; GWS: 8.4–9.2 mm). Palatal length: 8.0 (7.6–8.7) mm, $n = 10$ (Kearney & Seamark 2005).

Geographic Variation No subspecies are currently recognized. Specimens from Namibia have much paler pelage and flight-membranes than those from South Africa.

Similar Species Not easily distinguished from other *Laephotis*:

Laephotis angolensis. FA shorter (34.3 [32–36] mm). Ears shorter (15–18 mm) and narrower. Skull smaller (GLS: 13.7–13.8 mm; GWS: 6.7, 8.1 mm; C–M³: 4.3 mm).

L. botswanae. Skull shorter (GLS: 14.1–15.5 mm).

L. wintoni. Skull usually shorter (GLS: 15.6–16.3 mm). Dorsal pelage and wings apparently never creamy-brown (as far as is known).



Laephotis namibensis

Distribution Endemic to Africa. Found in the South-West Arid BZ (Namib Desert) and in the South-West Cape BZ. Recorded from Namibia (Gobabeb, Zwartmodder, Klein Aus, Helmeringshausen) and South Africa (Algeria Forest) (Setzer 1971, TM).

Habitat Arid, mountainous habitat, in close proximity to open water.

Abundance Rare.

Remarks Very little is known about this species. One individual was found under exfoliating rock (TM). The holotype and paratype were mist-netted over a waterhole in the bed of the Kuiseb R. near Namib Desert Research Station (Setzer 1971). Individuals from Algeria Forest were mist-netted as they flew along a water-course, close to the water surface, between 20:30 and 21:00h.

Conservation IUCN Category: Least Concern.

Categorized as such because most of its known range is within well-protected areas, there are no significant threats and its population is unlikely to be declining fast enough to qualify for listing in a more threatened category. Type locality (Gobabeb) is close to Namib Naukluft Park, which includes some of the Naukluftberge where this species probably roosts.

Measurements

Laephotis namibensis

FA: 37.8 (36–40) mm, $n = 10$

WS: n. d.
 TL: 100.3 (91–111) mm, n = 4
 HB: 55.8 (49–65) mm, n = 4
 T: 44.5 (38–47) mm, n = 4
 E: 22.8 (22–25) mm, n = 4
 Tr: 11.5 (10.0–13.6) mm, n = 3
 Tib: n. d.
 HF: 7.7 (7–8) mm, n = 3
 WT: 8.9 (7.8–11.0) g, n = 3

GLS: 16.4 (16.1–17.0) mm, n = 10
 GWS: 8.9 (8.4–9.2) mm, n = 10
 C–M³: 5.1 (4.8–5.4) mm, n = 10
 Namibia and South Africa (SAM, TM)

Key Reference Setzer 1971.

Teresa Kearney

Laephotis wintoni DE WINTON'S LONG-EARED BAT

Fr. Oreillard de De Winton; Ger. De Wintons Langohrfledermaus

Laephotis wintoni Thomas, 1901. Ann. Mag. Nat. Hist., ser. 7, 7: 460. Kitui, 1150 m, Kenya.

Taxonomy Synonyms: none. South African specimens were assigned to *L. wintoni* on the basis of multivariate analysis of external and cranial measurements (Rautenbach & Nel 1978, Watson 1990a, Kearney & Taylor 1997). However, on the basis of post-palatal measurements and morphometric analyses of cranial characters including palatal measurements by Hill (1974a), the specimens assigned to *L. wintoni* by Kearney & Taylor (1997) have now been re-identified as *L. botswanae* (Kearney & Seamark 2005). Specimens from Algeria Forest in the Western Cape (South Africa) originally described by Rautenbach & Nel (1978) as *L. wintoni* were subsequently re-identified as *L. namibensis* in Skinner & Smithers (1990). However, new specimens from Algeria have been referred to as *L. wintoni* (based on Rautenbach & Nel 1978) by Jacobs *et al.* (2005). On the basis of morphometric analyses of cranial characters, including palatal measurements, the distinction between *L. wintoni* and *L. namibensis* could not be confirmed by Kearney & Seamark (2005); therefore, pending clarification of the status of *namibensis*, information from Jacobs *et al.* (2005) is mentioned in the profile for *L. namibensis*. Chromosome number (South Africa): 2n = 34; aFN = 50 (as in *L. botswanae* and *L. namibensis*) (Rautenbach *et al.* 1993).

Description Very small microbat without noseleaf and with tail more or less fully enclosed in interfemoral membrane; four upper and five lower cheekteeth and two upper incisors on each side; ears separated, of medium length for a vespertilionid (21–24 mm) and of medium relative length (53–60% of FA, n = 12); GLS 15.6–16.3 mm. A poorly known species. Sexes similar. Mid-dorsal hairs ca. 8 mm. Dorsal pelage yellowish-brown to reddish-brown; hairs distinctly bicoloured, basal 6 mm dark brown, terminal 2 mm yellowish-brown or reddish-brown. Ventral pelage with chin yellowish-orange, reddish-brown or pale brown, throat paler, pelvic region cream or white. Hairs (except in pelvic region) blackish-brown with yellowish-orange, reddish-brown, cream or white tips. Hairs in pelvic region pure white. Head fairly flat; naked skin on muzzle and around eyes is dark brown. Buccal pads observed in one ♂. Ears dark brown, roughly triangular but very elongated; tip rounded; inner margins almost meeting on forehead but not joined. Ears may be held erect above the head or (when resting) held horizontally at right-angles to head. Tragus as in Figure 129e. Wings dark brown or blackish-brown; presence or absence of hind-border is not known. Interfemoral membrane paler and more translucent.

Skull (as in all *Laephotis* spp.) with braincase slightly flattened; rostrum rather narrow; zygomatic arches slender; no sagittal crest; lambdoid crest weakly developed. Skull on average medium-long and wide for the genus (GLS: 15.6–16.3 mm; GWS: 8.8–9.5 mm). Palatal length: 8.1 (7.9–8.5) mm, n = 15.

Geographic Variation None recorded.

Similar Species Not easily distinguished from other *Laephotis*:

Laephotis angolensis. FA shorter (32–36 mm). Ears shorter (15–18 mm) and narrower. Skull shorter and broader (GLS: 13.7–13.8 mm; GWS: 6.7, 8.1 mm; C–M³: 4.3 mm).

L. botswanae. Forearm on average shorter (36.3 [30–39] mm). Skull usually smaller (GLS: 14.6 [14.1–15.5] mm; C–M³: 4.7 [4.5–4.9] mm).

L. namibensis. Skull usually longer (GLS: 16.1–17.0 mm). Dorsal pelage and wings sometimes creamy-brown (see Geographic Variation).

Distribution Endemic to Africa. Distribution disjunct. There are scattered records in the Afromontane–Afroalpine and Somalia–Masai BZs of Ethiopia and East Africa, and records much further south in the Afromontane–Afroalpine and Highveld BZs of South Africa. Recorded from Ethiopia (Koka, Shoa Province), Kenya (Kitui, Namanga, Nyeri, Nanyuki), Tanzania (West Usambara Mts and near Iringa), South Africa (Free State) and E Lesotho (Setzer 1971, Hill 1974a, Kock & Howell 1988, Watson 1990a, Kearney & Taylor 1997, Stanley & Kock 2004).

Habitat In Ethiopia, found at 1700 m, near a large Rift Valley reservoir on the Awash R. surrounded by *Acacia* woodland that has been extensively degraded to provide open farmland (Largen *et al.* 1974). In East Africa, recorded from highland and mountainous areas with mosaics of evergreen bushland, secondary *Acacia* wooded grasslands and farmlands, and forests on the mountains: caught in forests, near forests and in woodlands. In the Free State Province of South Africa, recorded amongst large exotic trees in a drainage line flanked by sandstone cliffs (Watson 1990a). In Lesotho, recorded from the vicinity of a dam surrounded by a vlei overgrown with medium-height (600 mm) vegetation in Sehlabathebe N. P. (Lynch & Watson 1990). In this N. P., there is no significant cover of tall grass,

*Laephotis wintoni*

forbs or woody vegetation; the climate is harsh; the topographical relief is fairly uniform, and the altitude is 2300–2650 m.

Abundance Rare, but numbers in museum collections are increasing.

Remarks Roosts not known, but the association of this bat with cliffs (in South Africa) indicates that it might roost in cracks and crevices of cliff-faces. In South Africa, active later than *Cistugo lesueuri* (Lynch & Watson 1990). Specimens have been caught while foraging for insects from early to mid-evening (18:30–21:40h). In Lesotho, one of three ♀♀ was pregnant (with one embryo) in Nov (Lynch & Watson 1990).

Conservation IUCN Category: Least Concern.

Measurements

Laephotis wintoni

FA: 39.6 (37–41) mm, n = 13

WS: n. d.

HB: 57.8 (53–64) mm, n = 8

T: 45.6 (38–50) mm, n = 9

E: 22.0 (21–24) mm, n = 12

Tr: n. d.

Tib: n. d.

HF: 8.5 (6–9) mm, n = 9

WT: 8.7 (7.7–10.0) g, n = 6*

GLS: 16.0 (15.6–16.3) mm, n = 12

GWS: 9.1 (8.8–9.5) mm, n = 11

C–M³: 5.2 (5.1–5.3) mm, n = 13

Ethiopia, Kenya, Tanzania, Lesotho, South Africa (BMNH, FMNH, NMB, SMF)

*South Africa only (NMB)

Key References Hill 1974a; Kearney & Taylor 1997.

Teresa Kearney

GENUS *Mimetillus* Moloney's Mimic Bat

Mimetillus Thomas, 1904. Abstr. Proc. Zool. Soc. Lond. 1904 (10): 12. Type species: *Vesperugo (Vesperus) moloneyi* Thomas, 1891.

*Mimetillus moloneyi*.

Pending revision, considered here to be a monotypic genus endemic to tropical Africa including Bioko I. (but see Cotterill [2001d] and Monadjem *et al.* [2010]). Diagnostic combination of characters: four upper and five lower cheekteeth and two upper incisors on each side; head conspicuously flattened; ears relatively short and not joined at base; outer margin of ear not reaching mouth; phalanges of third, fourth and fifth fingers very short (third finger shorter than HB); no body pattern; wings not reticulated. Dental formula: $2^{113}/_{3123} = 32$. Selected characters of *Mimetillus moloneyi* are illustrated in Figure 130. Placed in tribe Vespertilionini (Simmons 2005).

The only species is *Mimetillus moloneyi*.

Meredith Happold

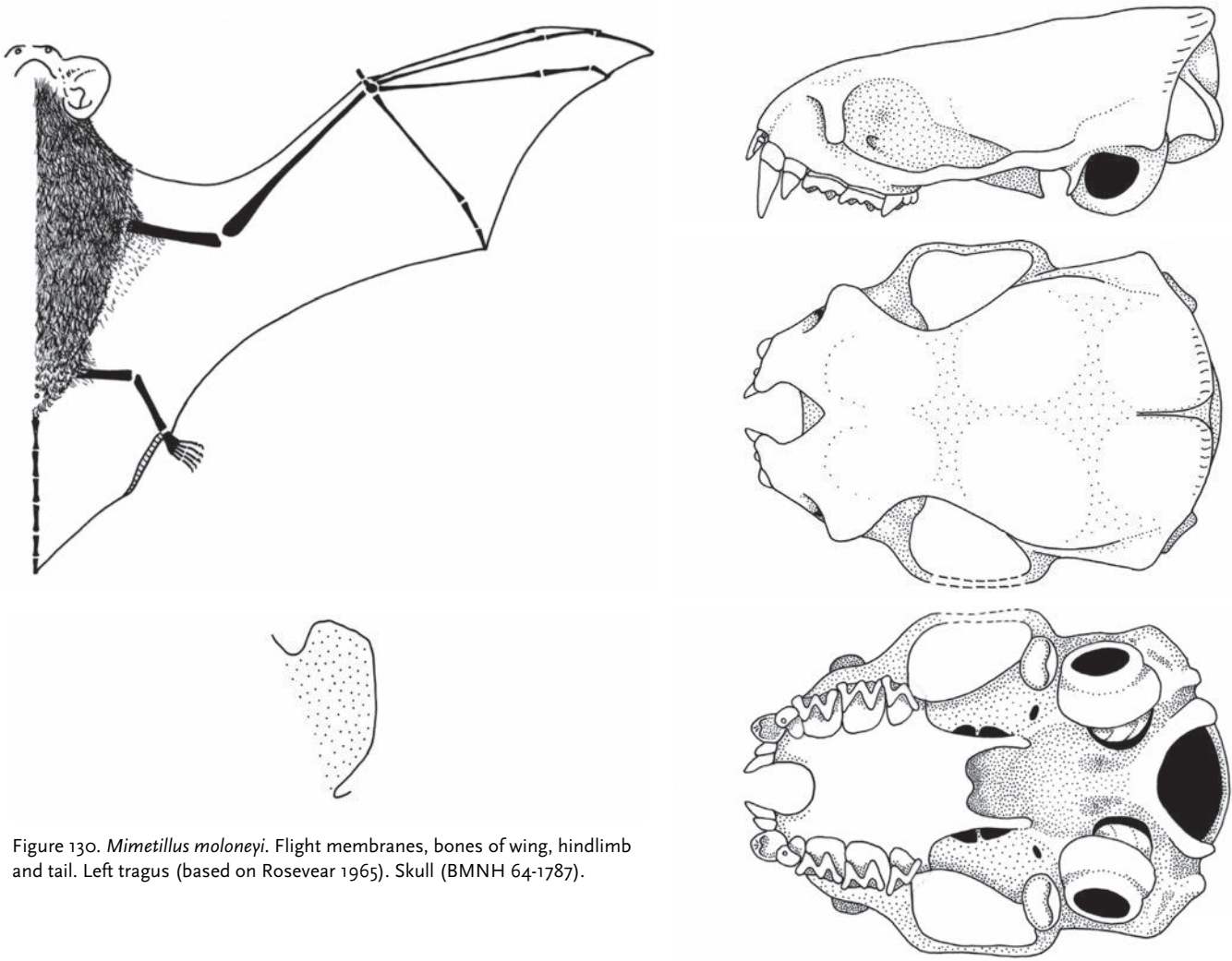


Figure 130. *Mimetillus moloneyi*. Flight membranes, bones of wing, hindlimb and tail. Left tragus (based on Rosevear 1965). Skull (BMNH 64-1787).

***Mimetillus moloneyi* MOLONEY'S MIMIC BAT (MOLONEY'S FLAT-HEADED BAT)**

Fr. Mimétille de Moloney; Ger. Moloneys Schmalflügel-Fledermaus (Moloneys Flachkopf-Fledermaus)

Mimetillus moloneyi (Thomas, 1891). Ann. Mag. Nat. Hist., ser. 6, 7: 528. Lagos, Nigeria.

Taxonomy Originally *Vesperugo* (*Vesperus*) *moloneyi*. Synonyms: *berneri*, *thomasi*. Subspecies: two recognized by Hayman & Hill (1971) and Simmons (2005), three by Koopman (1994) and, pending revision, three are tentatively recognized here. Cotterill (2001d) considers *thomasi* to be a distinct savanna species, which is larger than the forest-dwelling nominate subspecies, but additional locality records and morphometric data (see Geographic Variation) indicate a more complex pattern and, pending further evidence, only one species of *Mimetillus* is recognized here. Chromosome number: not known.

Description Very small microbat without noseleaf and with tail more or less fully enclosed in interfemoral membrane; four upper and five lower cheekteeth and two upper incisors on each side; ears separated, short for a vespertilionid (9–14 mm); tragus mushroom-shaped; wings extremely short and narrow; head conspicuously flattened and with broad muzzle. No apparent sexual dimorphism.

Pelage velvety; mid-dorsal hairs 2–3 mm. Dorsal and ventral pelage dark chocolate brown to almost black; hairs unicoloured. Head uniquely flattened for an African vespertilionid; muzzle with very large glands in sexually active animals. Ears blackish, naked, short, pointed. Tragus very short, mushroom-shaped. Wings dark brown to black with finger-wing translucent; extremely narrow, short and pointed (at first glance of juvenile appearance). Phalanges of third, fourth and fifth fingers relatively very short, third finger shorter than HB. Legs very short and stout. Tail 44–49% of HB. Penis remarkably long (12.8 mm; Gallagher & Harrison 1977), possibly without baculum (Hill & Harrison 1987).

Skull (Figure 130) with braincase greatly flattened (viewed laterally, profile of rostrum and braincase is a straight line). Rostrum shortened, very broad, with well-developed supraorbital tubercles (ante-orbital inflation of the maxillary bones). Postorbital constriction very pronounced. Skull (viewed dorsally) almost circular in outline. Sagittal crest negligible; lambdoid crest fairly well developed. Outer

upper incisors comparatively long and lateral to the inner upper incisor. Upper canine without secondary cusp. Upper premolar exceeding height of molars.

Geographic Variation Koopman (1994) recognizes three subspecies. Simmons (2005) recognizes only two, *moloneyi* and *thomasi*, and considers a third form, *berneri*, to be a synonym of *thomasi*. The status of *thomasi* and *berneri*, and their affinities, are controversial and therefore, solely for convenience, they are both listed here as subspecies:

M. m. moloneyi. SE Guinea and Sierra Leone to W Ethiopia, Kenya and NE Tanzania, and southwards to NW Angola (Cabinda enclave) and W DR Congo. Forest, forest–savanna mosaic and savanna habitats. FA: 28.9 (27–31) mm, $n = 16$; GLS: 13.8 (13.0–15.1) mm, $n = 64$; C–M³: 4.8 (4.1–5.3) mm, $n = 65$. Considered by Cotterill (2001d) to be smaller and darker than the other forms, but there is considerable overlap in measurements, and bats from humid forest habitats are often darker than those from drier habitats and therefore colour can be unreliable as an indicator of taxonomic status.

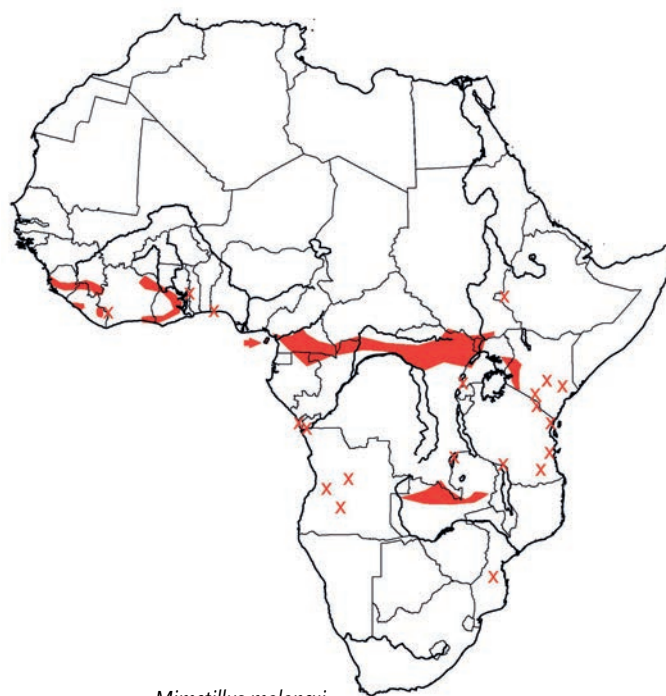
M. m. thomasi. SE DR Congo, S Tanzania, Zambia and Mozambique. Mostly savanna habitats. FA: no information; GLS: 14.4 (14.0–14.9) mm, $n = 11$; C–M³: 5.1 (4.8–5.4) mm, $n = 13$ (Cotterill 2001d). Considered by Cotterill (2001d) to be larger and paler than *M. m. moloneyi*, and to be a distinct species.

M. m. berneri. WC Angola. Savanna habitats. Body measurements similar to those of *M. m. moloneyi*, but craniodentally on average larger. FA: 30.6 (29–31) mm, $n = 5$; GLS: 14.2 (13.6–14.7) mm, $n = 5$; C–M³ (alv.): 5.0 (4.6–5.4) mm, $n = 4$. Considered a subspecies endemic to the Angolan Plateau by Crawford-Cabral (1986). Considered to be a synonym of *thomasi* by Cotterill (2001d) and Simmons (2005). The type locality, Cubango Mission (Vila da Ponte; Monard 1933), was incorrectly given as Chitau by Cotterill (2001d).

Similar Species None. Distinct from any other African bat and one of the most unusual vespertilionids.

Distribution Endemic to Africa. Recorded mainly from the northern fringe of the Rainforest BZ (Western, West Central and East Central Regions), the Rainforest–Savanna Mosaics, the Somalia–Masai Bushland, Coastal Forest Mosaic and Zambezan Woodland BZs, with marginal extensions into the Sudan Savanna BZ in Ethiopia, and the Guinea Savanna BZ in N Côte d'Ivoire and S Sudan. Recorded from Guinea (Ziéla, Mt Nimba; MNHN) and Sierra Leone to W Ethiopia and S Kenya, and southwards (avoiding most of the central Congo Basin), to Angola, Zambia and Mozambique. Also Bioko I. (but not mainland Equatorial Guinea). Not yet recorded from Dahomey Gap in West Africa (a single record from Odomi Jongu is situated in the partly forested Volta Highlands of Ghana) and the southern rainforest–savanna mosaic in DR Congo. For subspecific distributions, see Geographic Variation.

Habitat *Mimetillus m. moloneyi* was generally assumed to prefer rainforest, but most of the records within this zone are in a very narrow band along the northern border of the Rainforest BZ, and this bat is conspicuously absent from most of the interior of the (formerly) closed rainforest zone of the Western Region, and from



Mimetillus moloneyi

most of the central Congo Basin. Furthermore, it extends well outside the Rainforest BZ. Recorded in lowland rainforest (mostly drier types), coastal forest, montane forests, mangroves, forest–savanna mosaics, *Acacia–Commiphora* bushland and thicket, and *Isoberlinia* woodland. The distribution and habitats suggest that this bat prefers the edge of the rainforest from which it penetrates into the adjacent forest–savanna mosaic and woodlands. In East Africa, found up to 2300 m (Kingdon 1974).

The southern subspecies seem to prefer drier vegetation types: *M. m. thomasi* has been recorded from mopane and miombo woodlands, *Cryptosepalum* dry forest, and the Coastal Forest Mosaic at Rufiji River, S Tanzania. The subspecies *M. m. berneri* is known from miombo woodland and montane forest–grassland mosaic on the Angolan Plateau.

Abundance Probably not uncommon but, because it flies high and is not easily captured at its roosts, it is comparatively rarely encountered.

Adaptations Aspect ratio low; wing-loading exceptionally high (higher than in any other vespertilionid for which data are available except *Nyctalus leisleri*); wing-tip unusually pointed; wing morphology the most extreme of all bats examined and the characteristics of its flight are hard to predict – presumably fast with poor agility and poor manoeuvrability (Norberg & Rayner 1987). Flies fast, either straight or in wide shallow arcs, without sudden turns; wing-beat unusually rapid (whirring of wings can be heard as bat flies overhead); cannot take off from ground and needs to dive from its roost to gain sufficient speed for flight (Lang & Chapin 1917b, Brosset 1966, Kingdon 1974). However, an individual hunting under the roof of an open and spacious dining hall was observed making narrow and abrupt turns as well as flying in straight or shallowly curved lines (N. Ebigo & K. Soer pers. comm.). This individual clung to one of the ceiling beams and repeatedly flew off in direct lines with narrow and

abrupt curves at the turning points before returning to the starting point. Climbs well; scuttles over ground in fast, jerky manner with body held well clear of substrate; when resting, the body is flattened and the ears folded down (Kingdon 1974). By day, roosts under bark of dead trees in forest clearings, at 8–12 m above ground (Brosset 1966), also roosts in native houses and roofs (BMNH, ROM), and one was found in a hollow baobab tree *Adansonia digitata* (Cotterill 2001d). The flattened skull and body, and the very short pelage, are probably adaptations facilitating roosting under bark, in narrow cracks and fissures. Compared to other vespertilionids, the mammae are positioned far back along the abdomen (Ansell 1967); possibly their position is related to the way ♀♀ carry their young in flight or in the roost.

Foraging and Food Usually forages at medium height in clearings or above vegetation; foraging strategy likely to be variable. In Comoé N. P., Côte d'Ivoire, four individuals were captured at heights of 9.3–11.1 m, in mist-nets set 0–25 m above ground. In Taï N. P., two individuals were caught at heights of 1.1 and 1.9 m in mist-nets set over a small forest stream, but possibly these bats, as well as others caught over ponds and streams elsewhere, were descending to drink (J. Fahr unpubl). Foraging commences at dusk. Evidently the early hunt can be very successful: bats were observed to return to their day-roost after short foraging bouts of 10–15 min; at Double R. (Liberia), one individual with a full stomach was captured at 19:15h (Brosset 1966; Verschuren 1976 as *Eptesicus capensis*). Diet includes small winged termites (Lang & Chapin 1917b), and presumably other small to medium-sized flying insects. Kingdon (1974) caught a bat that had the head of a large-jawed ant attached to the corner of the mouth.

Social and Reproductive Behaviour Two colonies in Gabon, checked time and again, comprised 9–12 individuals (Brosset 1966).

Reproduction and Population Structure Litter-size: one ($n = 4$). Reproductive chronology uncertain; the limited data are consistent with seasonal bimodal polyoestrus with postpartum oestrus and births six months apart, but the gestation period is not known and the possibility of asynchronous breeding and/or more than two births per year cannot be ruled out. At 07° 54' N (near Lalehun, Sierra Leone), two pregnant ♀♀ (crown–rump length of embryos 7 and 8 mm) and one ♂ with large testes, were found in late Jan, and one of the ♀♀ was also lactating (USNM), indicating polyoestrus with postpartum oestrus at least in that ♀. Observations of a pregnant ♀ at end of Mar (05° 50' N, Taï N. P., Côte d'Ivoire), a lactating ♀ in mid-May (08° 45' N, Comoé N. P., Côte d'Ivoire) and a pregnant ♀ in mid-Oct (06° 27' N, Lagos, Nigeria) are also consistent with polyoestrus in West Africa (BMNH, FMNH, USNM, J. Fahr unpubl.). At 01° 08' N (Bélinga, Gabon) one ♀ was pregnant close to term in late Feb (Brosset 1966). In Uganda (locality not

given), 4 of 4 ♀♀ were pregnant (and a ♂ had large testes) in Jan, 1 of 1 was lactating in Mar, 2 of 2 were pregnant and one of these was also lactating (and a ♂ had large testes) in Jun, suggesting seasonal bimodal polyoestrus with births in Feb or Mar and again in Aug (Kingdon 1974). Furthermore, nearby at 01° 35' N (Wei-Wei R., W Kenya), a ♀ with an embryo 22 mm in length was found in late Jul (FMNH).

Predators, Parasites and Diseases Predators include the Bat Hawk *Macheiramphus alcinus* (Lang & Chapin 1917b). Kingdon (1974) reasoned that larger hornbills (Bucerotidae) might be important predators as they spend much time probing loose bark. Ectoparasites include mites *Carios vespertilionis* (Acari: Argasidae), *Acanthophthirus mimetilli* (Acari: Myobiidae), *Pteracarus mimetillius* (Acari: Myobiidae) and *Notoedres mimetilli* (Acari: Sarcoptidae) (Anciaux de Faveaux 1984, Uchikawa 1989).

Conservation IUCN Category: Least Concern.

If this species prefers forest-edge habitats (see Habitat), it is likely to be favoured by moderate degradation of the rainforest and the creation of clearings within what was formerly closed forest. In this case, its area of occupancy is likely to increase.

Measurements

Mimetillus moloneyi

FA: 29.3 (27–31) mm, $n = 21$
 WS (c): 186 (180–193) mm, $n = 4^*$
 TL: 83.1 (74–95) mm, $n = 19$
 T: 28.3 (23–32) mm, $n = 20$
 E: 12.1 (9–14) mm, $n = 18$
 Tr: 3.6, 3.7 mm, $n = 2^*$
 Tib: 9.9 (9–10) mm, $n = 13$
 HF: 7.2 (5–9) mm, $n = 18$
 WT: 7.6 (5.5–10.0) g, $n = 27^*$
 GLS: 13.9 (13.0–15.1) mm, $n = 80$
 GWS: 10.1 (9.1–11.4) mm, $n = 61$
 C–M³: 4.9 (4.1–5.4) mm, $n = 82$
 Sierra Leone, Liberia, Côte d'Ivoire, Ghana, Nigeria (incl. holotype *moloneyi*), Cameroon, Equatorial Guinea (Bioko I.), Gabon, DR Congo, Central African Republic, Sudan, Ethiopia, Uganda, Kenya, Tanzania, Angola (incl. holotype *berneri*), Zambia (incl. holotype *thomasi*) (BMNH, CM, FC, FMNH, IRSN, MNHN, ROM, SMF, USNM, ZFMK, Hill & Carter 1941, Cotterill 2001d)
 **Mimetillus m. moloneyi* only (see Geographic Variation)

Key References Brosset 1966; Cotterill 2001d; Kingdon 1974; Lang & Chapin 1917b.

Jakob Fahr

GENUS *Nyctalus*

Noctules

Nyctalus Bowdich, 1825. Excursions in Madeira and Porto Santo, 36, footnote. Type species: *Nyctalus verrucosus* Bowditch, 1825 (= *Vespertilio leisleri* Kuhl, 1817).

This widespread Palearctic genus has six species, of which at least two occur in NW Africa. Diagnostic combination of characters (African species): five upper and five lower cheekteeth and two upper incisors on each side; FA: 41–64 mm, wings particularly narrow (fifth finger shortened [ca. equal third and fourth metacarpals]); ventral pelage extending onto arm-wing and marginally onto hand-wing. Wings dark, leathery and opaque. Muzzle short and somewhat flattened. Ears relatively short and rounded; tragus short and kidney-shaped. Dorsal profile of skull is a smooth convex curve from front to back; rostrum broad and robust; rostral emargination unusually large (extending back half-way to the interorbital constriction) (Figure 131). Dental formula: $\frac{2123}{3123} = 34$. Second upper incisor deeply concave, with a large anterior and a small posterior secondary cusp. Anterior upper premolar extremely small and often not visible from outside. The first and second upper molars have a small but rather distinct hypocone. Selected characters of *Nyctalus* are illustrated in Figure 131.

Not surprisingly, the two species found in Africa are the most southern of the European species, one of them extending its geographic



Nyctalus leisleri.

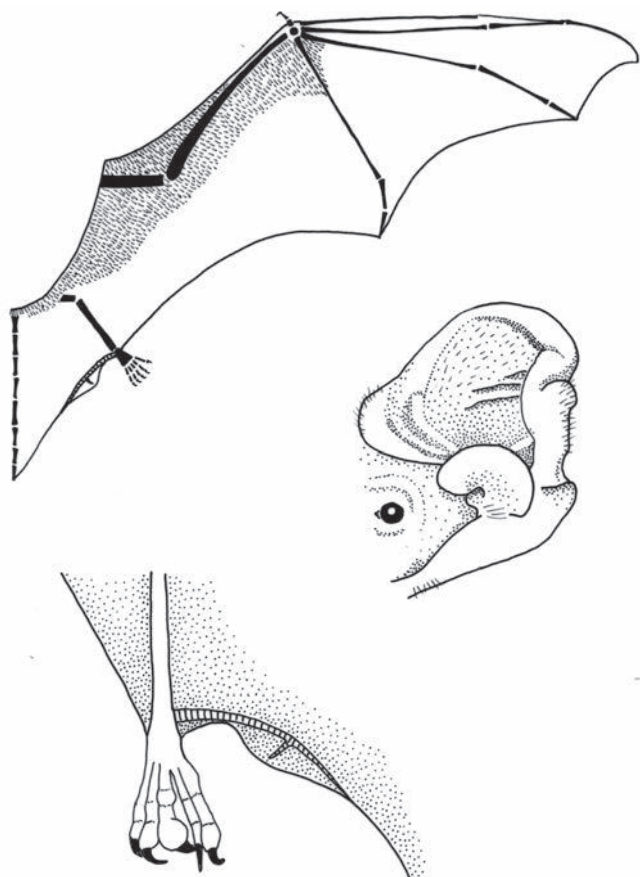


Figure 131. African *Nyctalus*. Ventral view of flight membranes showing areas covered by pelage, and bones of wing, hindlimb and tail (e.g. *N. lasiopterus*). Left ear and tragus of *N. lasiopterus* (based on Ibáñez *et al.* 2004). Postcalcaneal lobe with T-shaped cartilage (e.g. *N. leisleri*). Skull (e.g. *N. lasiopterus*; ZFMK 46.297, partly based on Ibáñez *et al.* 2004).

range also to Madeira and Canary Is. Noctules are migratory and, until recently, their occurrence in North Africa was suspected to reflect occasional crossings of the Mediterranean Sea. However, the finding of breeding colonies clearly indicates that *N. leisleri* is fully part of the African fauna. Possibly, *N. noctula* also occurs in North Africa, but this needs confirmation. There is only one reliable record in Algeria (Loche 1858) – two specimens (one ♂ and one ♀) collected in a hollow tree in Cheliff plain, which were lost with the rest of Loche's collection. According to Palmeirim (1982), possibly they belonged to *N. lasiopterus*, this species being considered as conspecific by earlier zoologists. There are some doubts as to the place of origin of the specimens of *N. noctula* in the BMNH (Palmeirim 1982) and in the RMNH (Jentink 1888): one was mentioned by Dobson (1878) as having been bought in Algiers, and Kowalski & Rzebik-Kowalska (1991) suggest that all were bought from professional dealers in zoological specimens. Hayman & Hill (1971) also expressed doubts as to the true provenance of Peters's specimens of *N. macuanus*, reported from Mozambique and later included in the synonymy of *N. noctula*.

Because its occurrence in Africa is uncertain, there is no profile for *N. noctula* here.

Noctules are tree-dwelling species. Although they are found in buildings in some parts of their range, they mainly roost in hollow trees in deciduous forests and parks, so they are restricted to the Mediterranean habitats of the Maghreb and Cyrenaica. Noctules in flight resemble pipistrelles and both leave their roosts before or just after sunset.

The two species known to occur in North Africa, and *N. noctula* which might occur there, can be identified by the following combination of characters:

N. lasiopterus. FA: 59–69 mm throughout geographic range.

N. leisleri. FA: 35–46 mm throughout geographic range; dorsal hairs dark brown at base becoming golden-brown towards tip.

N. noctula. FA: 45–57 mm; dorsal pelage unicoloured.

Stéphane Aulagnier

Nyctalus lasiopterus GIANT NOCTULE

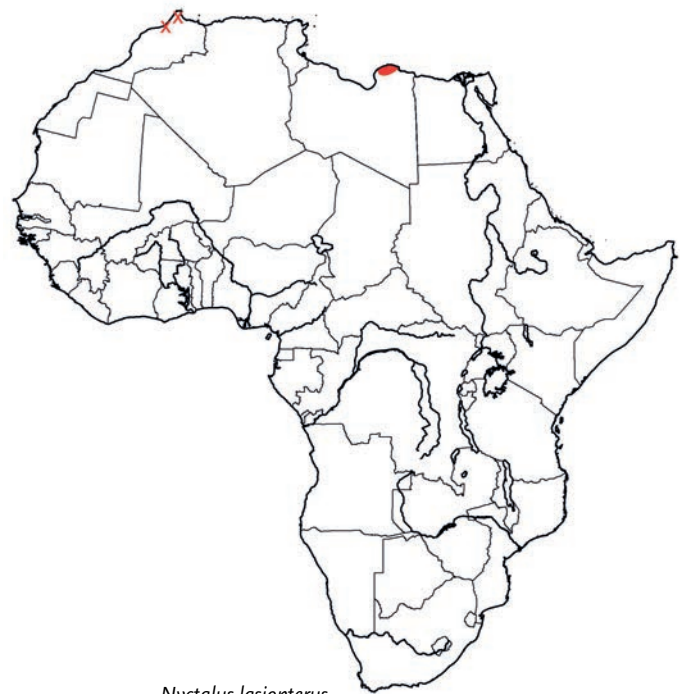
Fr. Grand noctule; Ger. Riesenabendsegler

Nyctalus lasiopterus (Schreber, 1780). In: Zimmermann, Geogr. Gesch. Mensch. Vierf. Thiere 2:412. ? Pisa (uncertain), northern Italy.

Taxonomy Originally *Vespertilio lasiopterus*. Synonyms: *ferrugineus*, *maxima*, *sicula*. Subspecies: none. Chromosome number (Europe): $2n = 42$; $aFN = 50$ (Volleth 1992).

Description Medium-sized microbat without noseleaf and with tail more or less fully enclosed in interfemoral membrane; five upper and five lower cheekteeth and two upper incisors on each side; ears separated, of medium length for a vespertilionid (19–23 mm) but relatively short (33–35% of FA); fifth metacarpal notably shorter than third and fourth (cf. *Pipistrellus*); FA: 59–64 mm. Sexes similar. Pelage dense, glossy in spring, summer and autumn; ventral pelage extending on to wings and interfemoral membrane as in Figure 131; mid-dorsal pelage 10–13 mm. Dorsal pelage rufous-brown; hairs unicoloured. Ventral pelage paler. Muzzle dark brown. Ears dark brown, widely separated, relatively short (33.9 [33–35]% of FA, $n = 4$ from southern Spain), broad, roughly triangular but tip very rounded; outer margin with four folds. Tragus kidney-shaped. Wings dark brown, long and narrow, fifth metacarpal notably shorter than third and fourth. Wing-membrane attaching to side of hindfoot (metatarsus). Interfemoral membrane dark brown with ventral pelage extending over proximal quarter. Calcar reaching half-way towards tip of tail. Postcalcareal lobe wide with visible T-shaped piece of cartilage. Hindfoot less than half length of tibia.

Skull (Figure 131) large and robust (cf. *N. leisleri*); rostrum broad; viewed laterally, the dorsal profile is a smooth convex curve from front to base of helmet. Sagittal crest weakly developed; lambdoid crest moderately developed forming a low occipital helmet. Dentition massive. Anterior upper premolar small (ca. level with cingulum of posterior premolar), fully displaced lingually; canine and posterior premolar in contact (therefore anterior premolar not visible from the outside).



Nyctalus lasiopterus

Geographic Variation None recorded in Africa. African specimens seem to have shorter forearms than specimens from Eastern Europe, but sample sizes are small (Ibáñez *et al.* 2004).

Similar Species Only two other vespertilionids occurring (or perhaps occurring) in North Africa have five upper and five lower cheekteeth and two upper incisors on each side; ears not joined at base; FA: >40 mm:

Nyctalus leisleri. Much smaller (FA: 35–46 mm throughout geographic range).

N. noctula Smaller (FA: 45–57 mm). Occurrence in Africa uncertain.

Distribution In Africa, recorded in the Mediterranean Coastal BZ of North Africa, from two widely separated regions: in the Rabat area and Rif mountains of Morocco (Laurent 1937, Palmeirim 1982, Ibáñez 1988), and in the mountains of Cyrenaica, Libya (Qumsiyeh & Schlitter 1982, Spitzenberger 1982). These African populations are considered to be sedentary. Possibly also recorded from Algeria (see genus *Noctula*). Extralimittally: this Palearctic species occurs from Mediterranean Europe to Iran and Kazakhstan.

Habitat Associated with well-preserved Mediterranean forests of cork oak *Quercus suber* and semi-deciduous oak *Q. canariensis* in Morocco, and with forest of cypress *Cupressus sempervirens* and juniper *Juniperus excelsior* in Libya. African specimens were captured at altitudes 0–800 m. In southern Iberia, also found in city-parks with old-grown trees.

Abundance Rare in Africa. Only two specimens known from Morocco and nine from Libya.

Adaptations Aspect ratio medium; wing-loading high (Ibáñez *et al.* 2001). Can take off from ground (with difficulty); when leaving day-roost, dives for up to 3 m to gain sufficient speed for flight. Sometimes scuttles and climbs around inside its roosts. Roosts by day in holes in mature trees, and under old, dry leaves of tall palms *Washingtonia filirifera*; also roosts in bat-boxes (Dondini & Vergari 2000, Ibáñez *et al.* 2004). One individual from Cyrenaica, Libya, was captured in a little cave (Spitzenberger 1982). In southern Iberia, active all year around except from Dec to Feb (Ibáñez *et al.* 2001); probably hibernates in Dec–Feb but this has not been confirmed.

Foraging and Food Based on wing morphology, echolocation and visual observations, forages by fast-hawking in open spaces (e.g. above canopies and over marshes) more than 50 m above ground (Ibáñez *et al.* 2004). The occasional presence, in faeces, of non-flying prey (e.g. Opiliones), and other prey which is inactive at night, suggests that this bat also gleans or captures prey inside its day-roosts (Dondini & Vergari 2000). Moves daily more than 25 km from roosts to foraging areas (Ibáñez *et al.* 2004). Diet (in Europe) includes a wide range of invertebrates and also small birds. Analysis of more than 14,000 faecal pellets indicated that birds comprised up to 50% of the diet (both in frequency and volume) during the nocturnal migration of small passerines in autumn and spring (Ibáñez *et al.* 2001).

Echolocation Search-phase call-shape >50 m above ground (Iberia): steep/shallow FM; fundamental harmonic only (Figure 132a). Start-frequency 25.1 kHz; end-frequency 17.6 kHz; bandwidth 7.5 kHz; peak-frequency 18.8 kHz; call-duration 12.3 ms; inter-call interval 319.7 ms (Ibáñez *et al.* 2001). Uses consecutive calls of alternate frequency as does *Nyctalus noctula* (not found in Africa) although more rarely and only during flights at low altitude (<20 m) (Ibáñez *et al.* 2004). At low altitude, call-shape is steep FM/QCF and the second harmonic is present (Figure 132b).

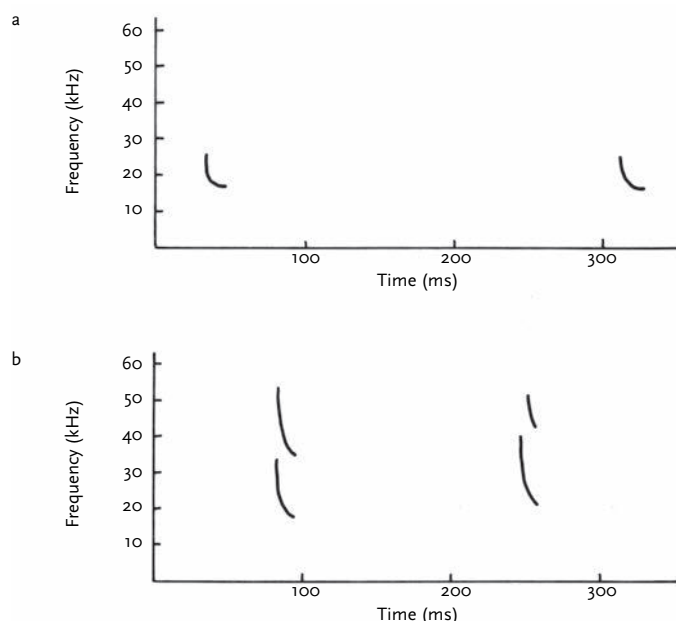


Figure 132. Sonograms of search-phase echolocation calls of *Nyctalus lasiopterus* from Seville, Spain. (a) In flight at high altitude (> 50 m): successive calls have same frequency; only the fundamental harmonic is present; bandwidth comparatively narrow; inter-call interval comparatively long. (b) In flight at low altitude (< 20 m) a few minutes after leaving roost: successive calls differ in frequency; second harmonic present; bandwidth wider; inter-call interval shorter.

Social and Reproductive Behaviour Very little information. Establishes maternity colonies of up to 80 ♀♀ (no ♂♂). Vocalizations in the maternity colonies are frequent even during the day. These social calls have high intensities; each sequence comprises 25 calls with tonal structure, which are slightly modulated with end-frequencies between 9 and 15 kHz; therefore they are audible to humans and have a characteristic metallic tone (Ibáñez *et al.* 2004). As yet, there is no information about the roosting behaviour of ♂♂.

Reproduction and Population Structure Litter-size (Europe): one or two (frequencies not known). Extralimittally, in southern Iberia, the reproductive chronology is restricted seasonal monoestry with ♂♂ showing well-developed scrotal testes from early Aug to Oct (mid-summer to mid-autumn), and ♀♀ giving birth at end of May or early Jun (late spring) and lactating until early Aug (Ibáñez *et al.* 2004). A neonate born in captivity weighed 9.9 g and had forearm 26.5 mm (Topál 1976). Young are volant by ca. 40 days (Aleksseva 1988).

Predators, Parasites and Diseases Several cases of predation by the Barn Owl *Tyto alba* are known in Europe. A predation by Beech Marten *Martes foina* is reported from Crimea (Ibáñez *et al.* 2004).

Conservation IUCN Category: Near Threatened (assessed mainly from extralimittal data).

Ongoing reduction of Mediterranean forests in North Africa as result of human activities and desertification is likely to severely reduce population numbers. Almost qualifies for Vulnerable.

Measurements*Nyctalus lasiopterus*

FA: 61.4 (59–64) mm, n = 6

WS: n. d.

TL: 145.2 (138–152) mm, n = 6

T: 55.2 (48–62) mm, n = 6

E: 21.0 (19–23) mm, n = 6

Tr: n. d.

Tib: n. d.

HF: 14.2 (13–16) mm, n = 6

WT: 48.8 (37.3–58.5) g, n = 60*

GLS: 22.4 (22.1–22.7) mm, n = 6

GWS: 15.5 (15.1–16.0) mm, n = 6

C–M³: 8.8 (8.6–9.0) mm, n = 6

Libya (Qumsiyeh & Schlitter 1982)

*Southern Iberia (C. Ibáñez unpubl.)

Key Reference Ibáñez *et al.* 2004.

C. Ibáñez

***Nyctalus leisleri* LEISLER'S NOCTULE (LEISLER'S BAT)**

Fr. Noctule de Leisler; Ger. Kleinabendsegler

Nyctalus leisleri (Kuhl, 1817). Die Deutschen Fledermäuse. Hanau, pp. 14, 46. Hanau, Hessen, Germany.

Taxonomy Originally *Vespertilio leisleri*. Synonyms: four; none in Africa. Subspecies: two; only the nominate occurs in Africa. Chromosome number (Poland, Czechoslovakia): 2n = 46; aFN = 50 (Fedyk & Fedyk 1970, Zima 1978).

Description Small to very small microbat without noseleaf and with tail more or less fully enclosed in interfemoral membrane; five upper and five lower cheekteeth and two upper incisors on each side; ears separated, short for a vespertilionid (13–16 mm) and also relatively short; fifth metacarpal notably shorter than third and fourth (cf. *Pipistrellus*); FA: 41–44 mm. Sexes similar. Pelage soft, sleek, dense; mid-dorsal hairs 7–9 mm; ventral pelage extending on to wings and interfemoral membrane. Dorsal pelage golden-brown; hairs dark brown at base becoming golden-brown towards tip. Ventral pelage slightly paler (yellowish); hairs blackish-brown with brown tip. Muzzle dark brown. Ears dark brown, widely separated, relatively short, subtriangular but with very rounded tip; outer margin with 4–5 folds. Tragus kidney-shaped, short, blunt. Wings dark brown, long and narrow; fifth metacarpal notably shorter than third and fourth metacarpals (ca. 80–85% of third metacarpal, n = 3). Wing-membranes attaching to ankle. Interfemoral membrane dark brown. Calcar reaching half-way to tip of tail. Postcalcareal lobe wide with visible T-shaped piece of cartilage (Figure 131).

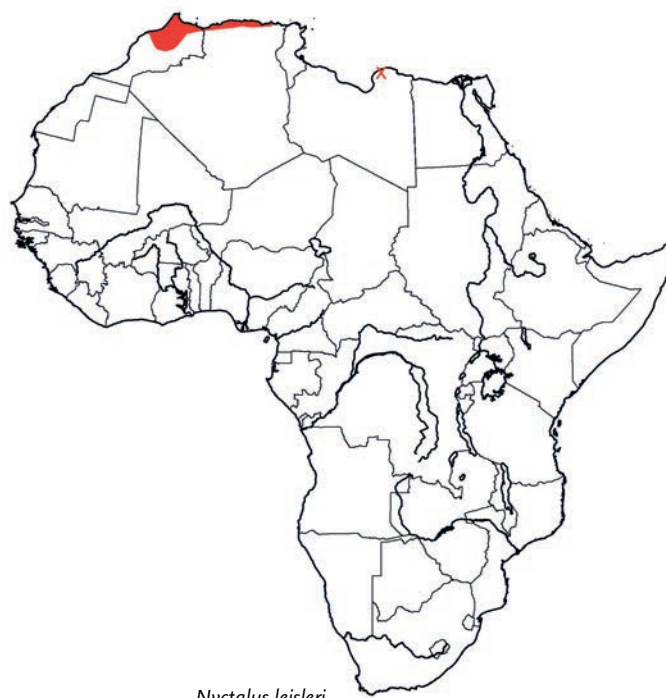
Skull small (cf. *N. lasiopterus*); rostrum broad; viewed laterally, the dorsal profile is a smooth convex curve from front to back. No sagittal crest; lambdoid crest weakly developed; no occipital helmet. Dentition moderately weak. Incisors relatively small. Anterior upper premolar visible from the outside. Height of mandibular ramus: 2.9–3.6 mm.

Geographic Variation None recorded in Africa.

Similar Species Only two other vespertilionids occurring (or perhaps occurring) in North Africa have five upper and five lower cheekteeth and two upper incisors on each side; ears not joined at base; FA: >40 mm:

Nyctalus lasiopterus. Much larger (FA: 59–69 mm throughout geographic range). Height of mandibular ramus >5.0 mm.

N. noctula. Larger (FA: 45–57 mm). Height of mandibular ramus 4.3–4.8 mm. Pelage unicoloured. Occurrence in Africa uncertain.

*Nyctalus leisleri*

Distribution In Africa, recorded in the Mediterranean Coastal and Afromontane-Afroalpine BZs from the mountains of Morocco (Rif, High Atlas), Algeria (Tell Atlas) and Libya (Cyrenaica) (Hanák & Gaisler 1983, Ibáñez 1988, Kowalski & Rzebik-Kowalska 1991, Benda *et al.* 2004d). Presumably also occurs in N Tunisia although not yet recorded there. Extraliminally: this Palearctic species ranges from western Europe (and Madeira I.) through Urals and Caucasus to the W Himalayas.

Habitat All of the North African specimens were mist-netted in, or near, forests at 400–900 m; mainly oak forests (*Quercus suber*, *Q. ilex*, *Q. faginea*, *Q. canariensis*), and also juniper-cypress forest (*Juniperus excelsa*, *Cupressus sempervirens*), where they often foraged over streams (Hanák & Gaisler 1983, Gaisler & Kowalski 1986, Ibáñez 1988, Benda *et al.* 2004d).

Abundance Uncertain. As for nearly all the tree-dwelling species that require specific surveys, most of the records in North Africa are recent. Particularly abundant in mist-net captures in Djurdjura (NE Algeria) (Gaisler & Kowalski 1986). Population size limited by the reduced distribution of suitable habitats.

Adaptations Aspect ratio medium; wing-loading very high (Norberg & Rayner 1987). Flight fast; manoeuvrability predicted to be poor. In summer, roosts by day mainly in tree-holes, under bark (including for breeding colonies) and occasionally in buildings. In winter, hibernates in hollow trees and sometimes in rock-crevices (Schober & Grimmberger 1987). Hibernation period in Africa shorter than in Europe – in Algeria, ♂♂ were active in mid-Oct (Gaisler & Kowalski 1986). Migrates: longest recorded movement 1567 km, from Germany to Spain (Ohlendorf *et al.* 2000).

Foraging and Food Forages by fast-hawking over open areas and above canopies; foraging flights fast, straight, often with dives. Foraging mainly occurs during two periods, the first after dusk and the second ending ca. 30 min before dawn. Occasionally flies during the day. Foraging areas average 7.4 km², but are up to 18.4 km² in southern Britain (Waters *et al.* 1999). Diet: no information for Africa. In Ireland and England, Diptera (Nematocera and Cyclorrhapha) are the predominant prey, but Coleoptera, Trichoptera and Lepidoptera are also important (Sullivan *et al.* 1993, Waters *et al.* 1995, 1999, Vaughan 1997). In Germany and Switzerland, Lepidoptera, Nematocera and Neuroptera may, at least locally, be important items of food (Beck 1995, Shiel *et al.* 1998).

Echolocation Search-phase calls (above level of treetops) are of two types. (a) Call-shape QCF; start-frequency 26–28 kHz; end-frequency 22–24 kHz; peak-frequency 22–24 kHz; call-duration 15–25 ms. (b) Call-shape shallow FM; start-frequency 26–30 kHz; end-frequency 25–26 kHz; peak-frequency 25–26 kHz; call-duration 7–15 ms; intercall-interval 220–550 ms (Waters *et al.* 1995, Tupinier 1996).

Social and Reproductive Behaviour Mating takes place in late summer. Males are very territorial at this time; each ♂ is assumed to attract ♀♀ by means of an ‘advertisement song’ (von Helversen & von Helversen 1994) and occupies a mating-roost with a harem of up to nine ♀♀. During winter, ♂♂ and ♀♀ hibernate together in large groups. In summer, ♀♀ form maternity colonies of 10–50 individuals (exceptionally several hundred in attics in Ireland; Shiel &

Fairley 1999); adult ♂♂ and immature bats roost elsewhere. In Poland, maternity colonies in trees comprised 20.7 (7–38) individuals; roost-fidelity was low (Ruczynski & Ruczynska 1999). Maternity roosts are vacated by late Aug to early Sep.

Reproduction and Population Structure Litter-size (Western Europe): usually two. In Europe, the reproductive chronology is restricted seasonal monoestry with mating in late summer (late Aug–Sep); births in mid-summer (Jun–Jul); young are volant one month later (Pottier 1993, Shiel & Fairley 1999). In Morocco, births occur in May and by mid-Jul juveniles are almost the same size as adults (Ibáñez 1988). Maximum life-span: nine years (Schober & Grimmberger 1987).

Predators, Parasites and Diseases No information.

Conservation IUCN Category: Least Concern (assessed mainly from extralimital data).

Loss of habitat because of logging and overgrazing is the main threat in North Africa.

Measurements

Nyctalus leisleri

FA: 42.4 (41–44) mm, n = 14

WS (d): 279.2 (267–286) mm, n = 5

TL: 101, 104 mm, n = 2

T: 40.9 (38–44) mm, n = 7

E: 14.1 (13–16) mm, n = 7

Tr: 6.6 (5.5–7.5) mm, n = 10

Tib: 15.3 (15–16) mm, n = 5

HF: 9.2 (9–10) mm, n = 6

WT: 12.1 (11–15) g, n = 11

GLS: 15.2 (14.8–15.7) mm, n = 27

GWS: 10.3 (10.0–10.8) mm, n = 24

C–M³: 5.8 (5.6–6.1) mm, n = 24

Morocco, Algeria, Libya (Hanák & Gaisler 1983, Ibáñez 1988, Romero Zarco 1990, Kowalski & Rzebik-Kowalska 1991, Benda *et al.* 2004d)

Key References Benda *et al.* 2004d; Gaisler & Kowalski 1986; Hanák & Gaisler 1983; Ibáñez 1988; Kowalski & Rzebik-Kowalska 1991.

Stéphane Aulagnier

GENUS *Nycticeinops*

Schlieffen's Twilight Bat

Nycticeinops Hill & Harrison, 1987. Bull. Br. Mus. Nat. Hist. 52: 254. Type species: *Nycticeius schlieffeni* Peters, 1859.



Nycticeinops schlieffeni.

A monotypic genus endemic to Africa south of the Sahara. Diagnostic combination of characters: four upper and five lower cheekteeth and one upper incisor on each side (as in *Otonycteris*, *Scotoecus* and *Scotophilus*); ears relatively short (cf. *Otonycteris*); penis short (cf. *Scotoecus*); FA: 28–35 mm (cf. 41–88 mm in *Scotophilus*); dental

formula: $^{1113}_{3123} = 30$. Selected characters of *Nycticeinops* are illustrated in Figure 133.

Based on bacular morphology, Hill & Harrison (1987) removed *schlieffeni* (the only African member of the genus *Nycticeus*) into a new genus, *Nycticeinops*. *Nycticeinops* is considered a subgenus of *Nycticeus* by Koopman (1994), but chromosomal evidence from one specimen from Somalia provides additional support for the generic status of *Nycticeinops* (Ruedas *et al.* 1990): the chromosome numbers for the Somali specimen are $2n = 34$, $aFN = 52$ compared with $2n = 46$, $aFN = 48$ for *Nycticeus humeralis*, a species from North America. This difference would represent one of the largest intra-generic differences in diploid number within the Vespertilionidae, which strongly indicates that *Nycticeinops* and *Nycticeus* are not congeneric. Mitochondrial ribosomal sequences provide further support for the generic distinction between *Nycticeus* and *Nycticeinops* (Hoofe & Van Den Bussche 2001). However, Rautenbach *et al.* (1993) found the karyotypes of 22 specimens of *N. schlieffeni* from southern Africa to be $2n = 42$, $aFN = 50$ (i.e. different from that of the specimen from Somalia). The difference between the karyotype of these southern African specimens and that of *Nycticeus humeralis* is not so marked and therefore Rautenbach *et al.* (1993) retained *schlieffeni* in *Nycticeus*. It is possible that the material from Somalia and that from South Africa represents two distinct species (G. N. Bronner pers. comm.). Alternatively, the identity of the Somali specimen

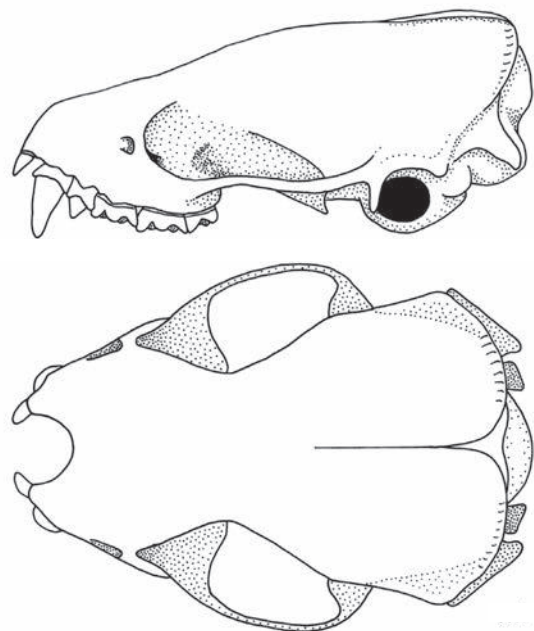
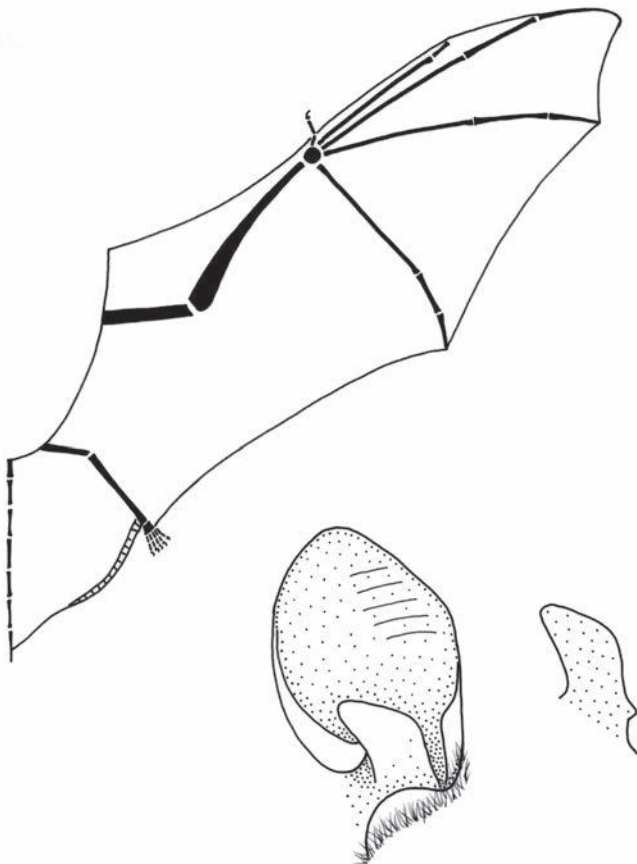


Figure 133. *Nycticeinops schlieffeni*. Flight membranes, and bones of wing, hindlimb and tail. Left ear and tragus. Details of tragus. Skull (MNHN CG 1997-2104).

might be erroneous. *Nycticeinops* is placed in the tribe Vespertilionini by Hooper & Van Den Bussche (2001) and in tribe Nycticeiini (with *Scotoecus* and *Scotophilus*) by Simmons (2005).

The only described species is *Nycticeinops schlieffeni*.

Meredith Happold

Nycticeinops schlieffeni SCHLIEFFEN'S TWILIGHT BAT (SCHLIEFFEN'S BAT)

Fr. Nycticinope de Schlieffen; Ger. Schlieffens Abendfledermaus

Nycticeinops schlieffeni (Peters, 1859). Monatsber. K. Preuss. Akad. Wiss. Berlin 1859: 223. Cairo, Egypt.

Taxonomy Originally *Nycticejus schlieffeni*. Synonyms: *adovanus*, *africanus*, *albiventer*, *australis*, *bedouin*, *cinnamomeus*, *fitzsimonsi*, *minimus*. Subspecies: uncertain (see Geographic Variation). Chromosome number (South Africa): $2n = 42$; $aFN = 50$ (Rautenbach *et al.* 1993). This differs markedly from the $2n = 34$; $aFN = 52$ karyotype reported for a specimen from Somalia (Ruedas *et al.* 1990) (see Genus *Nycticeinops*).

Description Very small microbat without noseleaf and with tail more or less fully enclosed in interfemoral membrane; four upper and five lower cheekteeth and only one upper incisor on each side; ears well separated, short for a vespertilionid (9–13 mm); FA: 28–35 mm; wings dark brown; penis 5.6–6.2 mm; anterior lower premolar ca. half height and half crown area of posterior premolar. Sexes similar in colour and size. Pelage dense, soft, slightly fluffy, with no sheen; mid-dorsal hairs 4–6 mm. There is considerable variation in colour. Dorsal pelage cinnamon, fawn or greyish-fawn; hairs unicoloured. Ventral pelage slightly to considerably paler, whitish or pure white. Head slightly flattened; muzzle short with prominent lateral glandular swellings. Ears dark brown; comparatively and relatively short for a vespertilionid (36.1 [31–42]% of FA); inner margin slightly convex, outer margin slightly concave; tip rounded. Tragus length 43.7 (40–50)% of E; shape as in Figure 133. Eyes very small. Wings and interfemoral membrane dark brown with blackish-brown venation. Free edge of interfemoral membrane with faint white border in some individuals. Penis comparatively short (5.6–6.2 mm, $n = 9$) (cf. *Scotoecus albobfuscus*, *S. hirundo*). Baculum with expanded bifid base and long fluted shaft with pointed tip (Hill & Harrison 1987).

Skull (Figure 133) somewhat flattened and fairly broad; dorsal profile (viewed laterally) rising at gentle slope from incisors to lambdoid crest; frontal area slightly concave. Zygomatic arches slender and weak but seldom lost during preparation of skulls (cf. *Scotoecus*). Sagittal crest absent or very low and only over posterior of braincase; lambdoid crest weakly developed; no occipital helmet. Upper incisor fairly long, unicuspid. Canines (upper and lower) robust; upper canine with anterior surface rounded and not grooved. Upper premolar sharply pointed, reaching to two-thirds to three-quarters height of canine. Posterior upper molar with three ridges (cf. *Scotophilus*). Lower incisors tricuspid. Anterior lower premolar ca. half height and half crown area of posterior lower premolar (cf. *Scotoecus*).

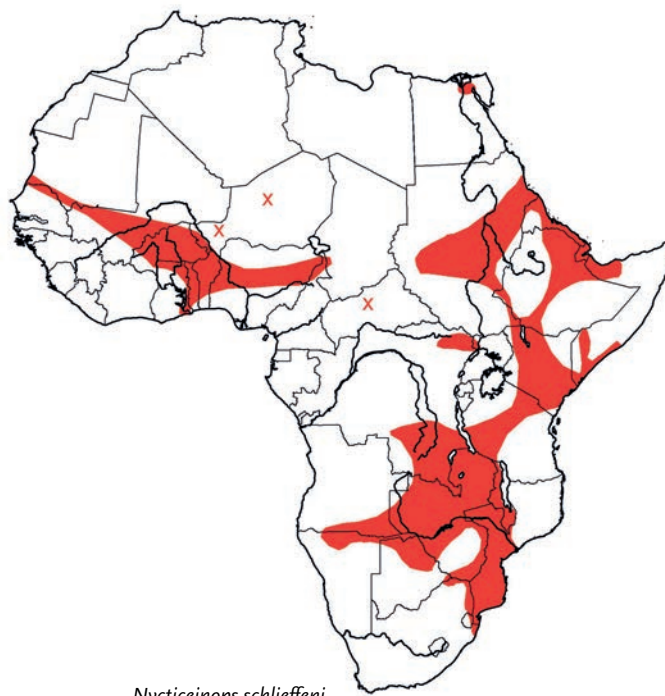
Geographic Variation Four subspecies (*albiventer*, *australis*, *fitzsimonsi* and *schlieffeni*) were recognized by Hayman & Hill (1971), but they are based largely on colour and are of dubious validity

(Rosevear 1965, Koopman 1994) and are not recognized by Simmons (2005). Specimens from Mozambique and KwaZulu–Natal, South Africa (the form *australis*) are darker than those from elsewhere.

Similar Species Only one other dark-winged vespertilionid in Africa has only one upper incisor on each side and FA <41 mm:

Scotoecus hirundo. Usually heavier (10.2 [8–15] g). FA sometimes longer (28–40 mm). Dorsal pelage chocolate brown, or medium to pale sepia brown; ventral pelage grey, beige, greyish-white or pale beige. Tragus less pointed (Figure 144b). Penis extremely long (14–16 mm). Upper canine with anterior surface flat and shallowly grooved. Anterior lower premolar at least two-thirds height of posterior premolar, usually only slightly shorter.

Distribution In Africa, recorded from the Sahara Arid BZ near the Nile R. in N Egypt, and in almost all biotic zones and mosaics south of the Sahara except the Rainforest, South-West Arid and Highveld BZs. Recorded disjunctly from Mauritania to Sudan, Eritrea, Djibouti and Somalia (with outlying localities near the Nile R. in N Egypt), and southwards (mainly on the eastern side of the



Nycticeinops schlieffeni

continent) to N Namibia and KwaZulu–Natal. Extraliminally: SW Arabia. Mapped from country checklists (see order Chiroptera), Kock (1969a), other literature and museum records.

Habitat North of the Equator and south of the Sahara, found mainly in Sudanian woodlands (including woodlands dominated by *Isoberlinia* in West Africa); penetrates into more arid areas where local conditions are favourable (e.g. near rivers). South of the Equator, found in semi-desert grassland and shrubland, *Acacia–Commiphora* bushland, in wetter and drier miombo woodlands and mopane woodland, and in some coastal habitats, but not found in the most arid areas. Occurs at 1000 m on Central African Plateau in Malawi, but usually found below 900 m in southern part of its geographic range. Throughout Africa, apparently avoids forest habitats, with the exception of some riverine forests.

Abundance Uncertain. Assessed as ‘numerous in collections although not many examples from West Africa’ by Rosevear (1965), uncommon in Nigeria (Happold 1987) and ‘uncommonly recorded’ in Malawi (Happold & Happold 1997).

Adaptations Aspect ratio low; wing-loading very low. Flight fast or slow with great manoeuvrability; can take off from ground; cannot hover. Turns usually by banking (minimum radius <25 cm); occasionally by stalling-and-twisting; individuals sustained flight within a 1×1×1 m enclosure for up to three circuits/flight (4 bats, 10 flights each; M. Happold unpubl.). Cursorial locomotion slow and awkward. Roosts by day in hollow branches, rock crevices and in cracks and crevices inside hollow trees, roofs and cellars (Rosevear 1965, Pienaar *et al.* 1980, Happold *et al.* 1987). Has been found roosting in a cellar with *Coleura afra* (Anderson in Rosevear 1965) and, once, in a narrow crevice in a branch together with 12 *Tadarida demonstrator* and two *T. midas* (Verschuren 1957). Becomes torpid during day at ambient temperatures 21–24°C. In Sudan, drinks from small expanses of water soon after sundown (Kock 1969a). Captive bats, fed on winged termites, did not drink; predicted mean maximum urine concentration comparatively very high (4562 mOsmol/kg) (Happold & Happold 1988).

Foraging and Food Forages by slow-hawking, mostly 2–6 m above ground, in moderately cluttered spaces between tree trunks and between canopies, and in more open spaces in clearings, over flood-plains and over water (Fenton & Thomas 1980, Pienaar *et al.* 1980, M. Happold unpubl.). Occasionally enters houses while foraging (Rosevear 1965). Apparently feeds opportunistically on a wide variety of small insects. In Sudan, mainly small Lepidoptera and Coleoptera (Kock 1969a). In Zimbabwe (wet season), mainly Coleoptera; also Diptera, Lepidoptera and Hemiptera (dry season), Coleoptera (50% by weight); also Trichoptera and Lepidoptera (Fenton & Thomas 1980). In Kruger N. P., South Africa, mainly Coleoptera but also Diptera, Hymenoptera and Trichoptera (Aldridge & Rautenbach 1987).

Echolocation Search-phase call-shape (Malawi) smooth steep/shallow FM (Figure 118i). Intensity high; start-frequency 46–64 kHz; end-frequency 38–43 kHz; peak-frequency 38–41 kHz; call-duration mostly 7–9 ms (two tethered bats flying in open; M.

Happold unpubl.). When flying closer to ground, call-shape becomes steep FM/QCF (Figure 118j); start-frequency up to 76 kHz; end-frequency 38–42 kHz, call-duration mostly ca. 5–6 ms (two other bats, tethered; M. Happold unpubl.). In Zimbabwe, call-shape steep FM/QCF; start-frequency 78 kHz; end-frequency 33 kHz, peak-frequency 42 kHz (three bats; Fenton & Bell 1981). In Kruger N. P., South Africa, the calls of 20 released and light-tagged bats were the same as the bats from Zimbabwe (Aldridge & Rautenbach 1987). In Swaziland, call-shape steep FM; start-frequency (mean ± S.D.) 45.5 ± 0.7 kHz; end-frequency 39.5 ± 0.2 kHz, peak-frequency 41.0 ± 1.0 kHz; call-duration 3.7 ± 0.6 ms (three bats, flying in open; Taylor 1999a).

Social and Reproductive Behaviour Numbers occasionally congregate to forage (Smithers 1983). Reported to roost singly, in pairs or in small groups (Rosevear 1965, Smithers & Lobão Tello 1976), and in large numbers (Rautenbach 1982). A maternity colony containing at least 40 post-lactating ♀♀ and their young was found in the roof of a house in Malawi (Happold *et al.* 1987).

Reproduction and Population Structure Litter-size: 1–3 (details below). Reproductive chronology at 02°18'S (Masalani, Kenya): restricted seasonal monoestry; births in short wet season (Nov); litter-size 2, 3 (n = 2) (O'Shea & Vaughan 1980). At 15–16°S in Malawi: restricted seasonal monoestry with births in wet season (Nov–Dec); litter-size 2.4 (2–3), n = 5 (Happold & Happold 1990a). At 22°25'S (Kruger N. P., South Africa): restricted seasonal monoestry; births in summer (Nov–Dec [mainly Nov]) (van der Merwe & Rautenbach 1987). Spermatogenesis extends over 10 months; spermatozoa in epididymides from end Apr to early Sep. Copulation begins in early winter (Jun). Females store spermatozoa in uterine horns from then until ovulation occurs at end Aug. Gestation ca. 11 weeks. Up to five conceptuses but some reabsorbed; litter-size 2.8 (1–3), n = 11 (van der Merwe & Rautenbach 1986).

Predators, Parasites and Diseases Predators include Bat Hawks *Macheiramphus alcinus* (Fenton *et al.* 1978). Ectoparasites include a bed-bug *Aphrania elongata* (Hemiptera: Cimicidae); fleas *Lagaropsylla consularis*, *L. idae* (Siphonaptera: Ischnopsyllidae); a bat-fly *Basilia robusta* (Diptera: Nycteribiidae); and a mite *Chelanyssus aethiopicus* (Acari: Macronyssidae) (Anciaux de Faveaux 1984).

Conservation IUCN Category: Least Concern.

Measurements

Nycticeinops schlieffeni

FA: 30.7 (28–35) mm, n = 142

WS (a): 228 (218–245) mm, n = 6*

HB: 44.4 (37–48) mm, n = 81

TL: 74.6 (64–80) mm, n = 81

T: 30.4 (24–34) mm, n = 81

E: 10.8 (9–13) mm, n = 80

Tr: 5.03 (5.0–5.5) mm, n = 16*

Tib: 12.8 (12–14) mm, n = 23*

HF: 7.3 (7–8) mm, n = 20*

WT: 5.5 (4–9) g, n = 37

GLS: 12.7 (11.9–13.6) mm, n = 35

GWS: 8.8 (8.1–9.3) mm, n = 26

C–M³: 4.5 (4.1–4.9) mm, n = 40

Throughout geographic range (BMNH, HC, IRSN, SMNS and literature)

*Malawi only (HC, Happold *et al.* 1987)

Key References Smithers 1983; van der Merwe & Rautenbach 1986, 1987.

Meredith Happold

GENUS *Otonycteris* Hemprich's Desert Bat

Otonycteris Peters, 1859. Monatsb. K. Preuss. Akad. Wiss. Berlin 1859: 223. Type species: *Otonycteris hemprichii* Peters, 1859.

Until 2010, considered to be a monotypic genus distributed in deserts from North Africa to Arabia, SW Asia and Central Asia (but see below). Diagnostic combination of characters: four upper and five lower cheekteeth and one upper incisor on each side (cf. *Laephotis*); ears very long (30–41 mm) but not joined at base (cf. *Plecotus*); dental formula $\frac{1113}{3123} = 30$. Selected characters of *Otonycteris hemprichii* are illustrated in Figure 134. Placed in tribe Plecotini, with *Plecotus* and *Barbastella*, on basis of bacular morphology (Hill & Harrison 1987) and chromosomal characters (Horáček 1991, Qumsiyeh & Bickham 1993). In contrast, Koopman (1994) places *Otonycteris* in tribe Nycticeini. Hooper & Van Den Bussche (2003) keep the position of the genus within the Vespertilioninae uncertain



Otonycteris hemprichii.

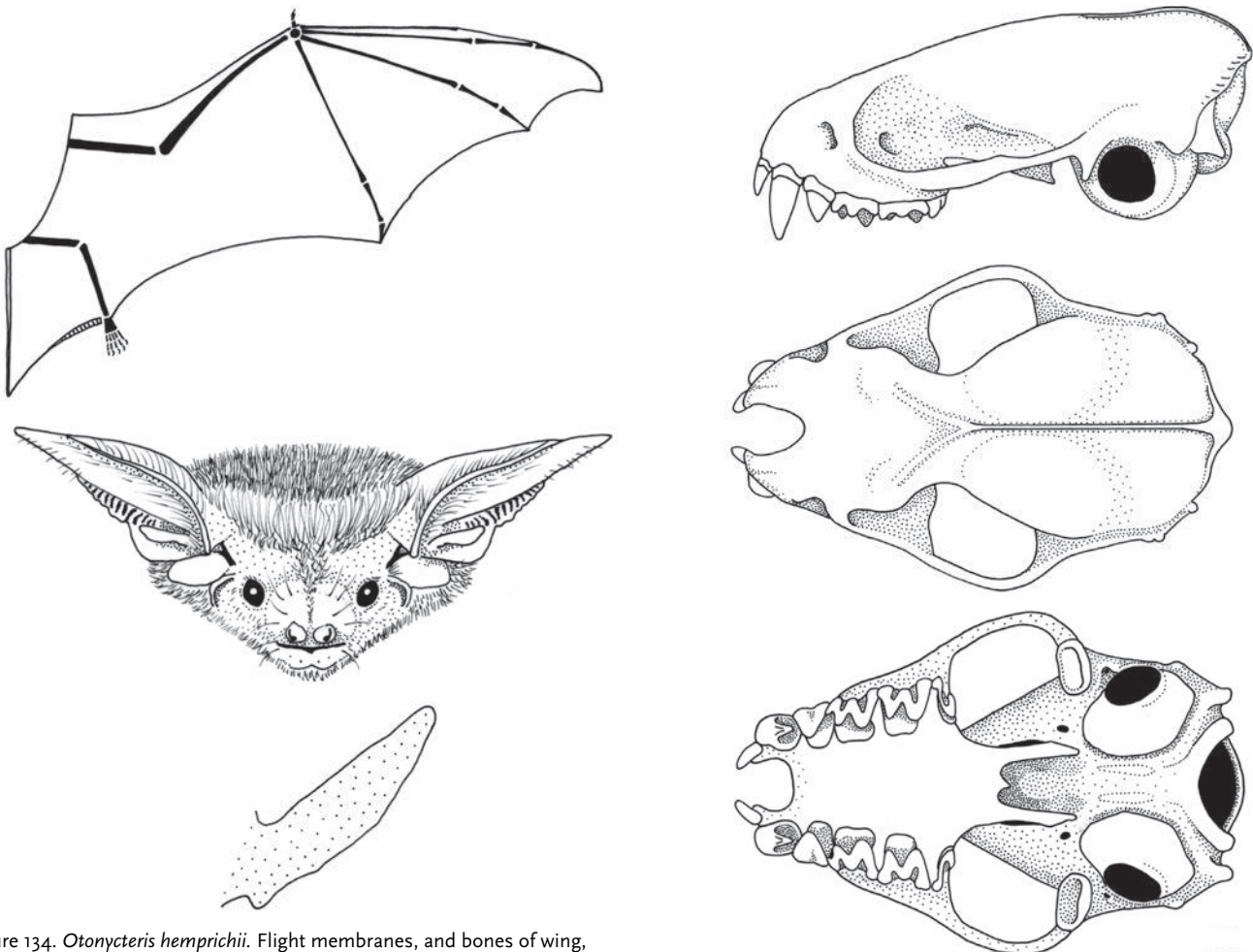


Figure 134. *Otonycteris hemprichii*. Flight membranes, and bones of wing, hindlimb and tail. Frontal view of head showing long, widely-separated ears. Left tragus. Skull (ZFMK 97.148).

suggesting possible relations to *Antrozoini*. Nevertheless, Simmons (2005) placed it in tribe *Plecotini*, the solution recently supported also by strong molecular evidence (Roehrs *et al.* 2010). Placed in tribe *Plecotini* by Simmons (2005). In most characters, *Otonycteris* is quite unique among the extant *Vespertilioninae*.

Since this profile and the following species profile were submitted, Benda & Gvozdk (2010) concluded that *Otonycteris* contained three

subspecies: *O. h. hemprichii* in North Africa and extralimally in Levant and Mesopotamia, *O. h. cinerea* and *O. h. jin* both extralimally only, and an additional species, *O. leucophaea* (Severcov, 1873), found extralimally in Asia.

The only species in Africa is *Otonycteris hemprichii*.

Meredith Happold

Otonycteris hemprichii HEMPRICH'S DESERT BAT

Fr. Oreillard d'Hemprich; Ger. Hempriches Wüstengroßohr

Otonycteris hemprichii Peters, 1859. Monatsber. K. Preuss. Akad. Wiss. Berlin 1859: 233. Type locality: not stated; most probably Nile Valley south of Aswan, Egypt (Kock 1969a).

Taxonomy In Africa, monotypic with the nominate subspecies (but see Geographic Variation). Synonyms in Africa: *saharae*, *ustus*. Chromosome number (Israel): $2n = 28$; $aFN = 46$ (Qumsiyeh & Bickham 1993). For molecular data (cyt b, ND 1) and variation in morphometric characters, see Benda and Gvoždík (2010).

Description Medium-small, robustly built microbat without noseleaf and with tail more or less fully enclosed in interfemoral membrane; four upper and five lower cheekteeth and one upper incisor on each side; ears separated, long for a vespertilionid (30–41 mm). Sexes similar. Pelage loose, soft; ventral pelage less dense; mid-dorsal hairs 9–12 mm. Dorsal pelage pale beige; hairs off-white with beige to pale beige at tip. Ventral pelage whitish to pure white. Muzzle fairly long and narrow. Ears yellowish-brown, long for a vespertilionid (30–41 mm) and of medium relative length (55.7 [52–60]% of FA); well separated; inner and outer margins smoothly convex; tip rounded (Figure 134). Antitragus very small. Tragus long, tapering to blunt point. Eyes fairly large for a microbat. Two pairs of pectoral nipples (cf. one pair in all other African bats). Wings very broad; fifth finger longer than fourth. Wings and interfemoral membrane thick and leathery, semi-translucent, pale yellowish-brown near body, becoming pale greyish-brown and then whitish around wing-tips and posterior edges. Tail moderately long (72.7 [66–86]% of HB, $n = 27$). Interfemoral membrane broad; calcar reaching less than half-way to tip of tail. Tibia 38.6 (35–43)% of FA, $n = 5$. Penis very unusual in form – the glans is expanded dorsoventrally and protrudes through two lateral swellings, and there is a third swelling on the dorsal surface of the penis.

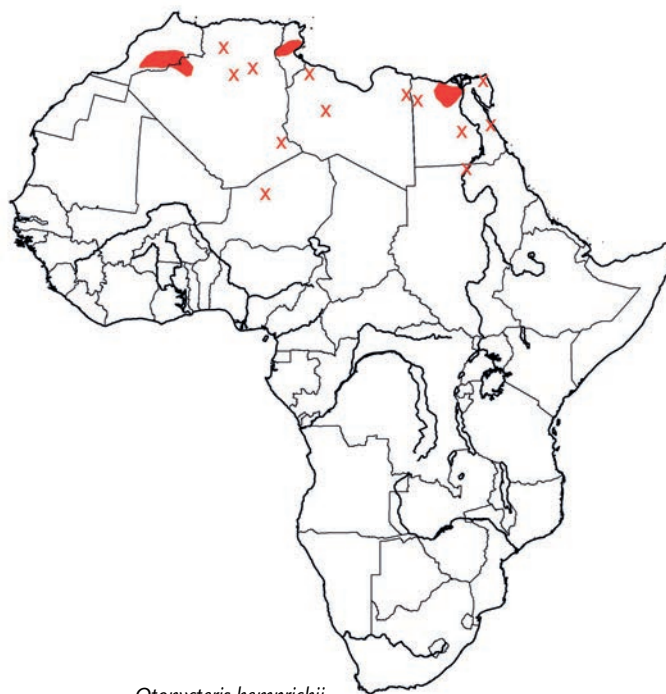
Skull (Figure 134) robust with braincase elongated; rostrum broad and high; interorbital constriction narrow. Dentition robust and long. Upper incisor unicuspid, sharp and caniniform. Canine large, round in transverse section. Upper premolar large and caniniform, comparatively higher than the molars. M^3 and talonid of M_3 extremely reduced in comparison with other bats. Lower incisors small, bicuspid, compressed and partly overlapping; outer lower incisors (I_3) with small cusp on lingual side. Anterior lower premolar small, within toothrow; lower canine and posterior premolar not in contact. Lower molars myotodont.

Geographic Variation In Africa, there is clinal variation in size and colouration from west to east; individuals from north-west are on average slightly smaller and are paler (dorsal pelage

almost white). Some authors (e.g. Koopman 1994) recognize up to five subspecies, of which only *O. h. hemprichii* occurs in Africa. However, the overall pattern of geographical variation seems to be clinal rather than categorical, and therefore the species is currently considered monotypic (Kock 1969a, Horáček 1991, Kowalski & Rzebik-Kowalska 1991). Nevertheless, Benda & Gvoždík (2010) demonstrated that the latitudinal W–E cline is associated with strong phylogeographic substructures suggesting a categorical variation. Consequently, besides the nominate subspecies (Morocco to Levant) they distinguish two eastern subspecies of *O. hemprichii* (*cinerea* in C Iran and Oman, *jin* in SE Iran) and separate the Central Asiatic populations into a distinct species *O. leucophaea* (Severcov, 1873).

Similar Species Only three other vespertilionids in Africa have ears that are long for an African vespertilionid (>28 mm):

Plecotus (3 spp). Much smaller (FA: <43 mm; GLS: <18 mm). Ears with inner margins joined at base by low frontal band. Five upper and six lower cheekteeth and two upper incisors on each side.



Otonycteris hemprichii

Distribution In Africa, recorded from the Sahara Arid BZ and marginally in the southern fringe of the Mediterranean Coastal BZ, from W Morocco to Egypt and southwards to N Niger and N Sudan. Extraliminally: Arabia and SW Asia to Tajikistan, N Pakistan and Kashmir.

Habitat Rocky deserts covered with a sparse xeric herbaceous vegetation.

Abundance Among the rarest and the least known species in almost all parts of its geographic range, although may be found quite regularly in some localities (e.g. where rocky cliffs are present).

Adaptations Aspect ratio low; wing-loading low. Flight slow and 'floppy' (Nowak 1999). By day, has been found roosting in rock-fissures and similar places in buildings, e.g. cracks in the stone walls of deserted buildings (Harrison & Bates 1991, Gharaibeh & Qumsiyeh 1995). Apparently well adapted to desert habitats, heterothermic and capable of hibernating (evident in C Asia). Daniel *et al.* (2010) observed in Negev Desert, Israel, that ♀♀ often used both deep and shallow daily torpor during the first two trimesters of pregnancy, with body temperature frequently dropping as low as 15 °C. During the last trimester of pregnancy and during nursing, the bats used only shallow torpor, with body temperature always >29 °C.

Foraging and Food Apparently feeds opportunistically on non-flying prey, which is gleaned from the ground. In Sep in C Asia, feeds mainly on grasshoppers and crickets (Orthoptera), scorpions and spiders (Solifugidae) (Arlettaz *et al.* 1995). In Israel, the diet is mainly Coleoptera, Heteroptera and Diptera (Fenton *et al.* 1999); sometimes only Coleoptera of the family Scarabaeidae (Whitaker *et al.* 1994). Based on wing morphology, Norberg & Fenton (1988) predict that this species also feeds on small vertebrates but, although geckos have been eaten by captive bats, there is no evidence that vertebrate prey is taken in the wild. Typically, these bats emerge ca. 40 minutes after sunset (Fenton *et al.* 1999) and fly slowly over rocky terrain, staying within 40–100 cm of the ground (Arlettaz *et al.* 1995). When prey is detected, the bat lands briefly to attack and collect its prey, and then eats on the wing while flying and mainly gliding slowly in wide circles 3–7 m above ground. These bats do not forage from perches. When foraging close to the ground, echolocating sometimes ceases, suggesting that non-flying prey can be located by alternative methods (perhaps visually or by detecting sounds made by the prey). Daniel (2005) found in Negev Desert, Israel, that the diet was composed of Coleoptera, Chilopoda, Scorpiones, Aranae and Soliphugae with certain seasonal variation. Feeding on scorpions (up to more than 70% of the diet in August) was analysed in detail by Holderied *et al.* (2011). The scorpions are located by passive listening. No evidence of risk-sensitive prey selection was found, bats were frequently stung during predatory action without any change in the bats' behaviour and also without any signs of poisoning. In the Negev Desert, Israel, the distance between roosts and foraging sites varied from 0.5 to 9 km; daily foraging time, mean daily foraging bout length, and first daily foraging bout length were all significantly and positively correlated with distance between the roost and the foraging site, which support the prediction that *O. hemprichii* is a 'central-place forager' (Daniel *et al.* 2008).

Echolocation Search-phase call-shape shallow FM. Intensity high; start-frequency 40 kHz; end-frequency 18 kHz; peak-frequency 30–32 kHz; second harmonic with half intensity of first; third harmonic weak; call repetition rate comparatively slow and regular (Horáček 1991). Holderied *et al.* (2011) reports that during a searching flight (with average speed 3.52 m/s) *O. hemprichii* emits multiharmonic calls of a low intensity with peak frequency of upper harmonic 54.45 kHz and peak frequency of lower harmonics 29.96 kHz. Average pulse duration was 2.46 ms with 131 ms pulse interval.

Social and Reproductive Behaviour Little is known. Males appear to roost singly. Maternity colonies of 3–18 ♀♀ were recorded by Bogdanov (1953). Radio-tracking revealed frequent changes in day-roosts (Fenton *et al.* 1999).

Reproduction and Population Structure Litter-size (extraliminally): 2 (n = 9) (Attalah 1977, Horáček 1991). Reproductive chronology not known in Africa or extraliminally. In Niger, 2 of 3 ♀♀ were lactating in mid-Jun (Fairon 1980). For extralimital records, see Gharaibeh & Qumsiyeh (1995).

Predators, Parasites and Diseases Remains have been found in pellets of Pharaoh Eagle-owl *Bubo ascalaphus* in Morocco (Aulagnier 1989) and Barn Owl *Tyto alba* in Algeria (Kowalski & Rzebiak-Kowalska 1991). Ectoparasites include ticks *Argas hermanni*, *A. transgarepinus*, *Carios vespertilionis*, *C. boueti*, *C. confusus* (Acari: Argasidae) and a mite *Rodhainyssus myotis* (Acari: Gastronyssidae) (Anciaux de Faveaux 1984).

Conservation IUCN Category: Least Concern (assessed from African and extralimital data).

Little is known about populations of these bats and their potential threats remain unclear.

Measurements

Otonycteris hemprichii

FA: 59.7 (50–65) mm, n = 24

WS: n. d.

TL: 119.7 (112–132) mm, n = 20

T: 51.8 (45–60) mm, n = 20

E: 36.6 (30–41) mm, n = 20

Tr: 16.7 (15–19) mm, n = 7

Tib: 23.3 (21–25) mm, n = 8

HF: 11.8 (9–14) mm, n = 7

WT: 18.3 (18–19) g, n = 3

GLS: 22.6 (21.9–24.0) mm, n = 33

GWS: 14.6 (13.6–15.8) mm, n = 32

C-M³: 8.3 (7.6–9.0) mm, n = 31

Algeria, Tunisia, Libya and Egypt (Kock 1969a, Gaisler *et al.* 1972, Qumsiyeh 1985, Kowalski & Rzebiak-Kowalska 1991)

Key References Arlettaz *et al.* 1995; Fenton *et al.* 1999; Gharaibeh & Qumsiyeh 1995; Harrison & Bates 1991; Horáček 1991.

Ivan Horáček

GENUS *Pipistrellus*

Pipistrelles

Pipistrellus Kaup, 1829. Skizz. Entwickel.-Gesch. Nat. Syst. Europ. Thierwelt 1: 98. Type species: *Vesperilio pipistrellus* Schreber, 1774.

As defined by Hill & Harrison (1987), *Pipistrellus* is a large genus with ca. 79 species of which 28 occur in Africa (at least two of these probably contain more than one species). In contrast, Simmons (2005) recognizes only 31 species in *Pipistrellus*, the remainder having been placed in five other genera, of which two (*Neoromicia* and *Hypsugo*) are represented in Africa. For reasons given below, this treatment is not followed here. Diagnostic combination of characters for species found in Africa: four or five upper cheekteeth, five lower cheekteeth and two upper incisors on each side; ears short and not joined at base; fifth finger not shortened (considerably longer than metacarpals of third and fourth fingers) (cf. *Nyctalus*); no body pattern; wings not reticulated but sometimes with white or pale margin along the posterior edge, which is referred to as a hind-border; outer margin of ear not reaching mouth; lower lip without lobe near posterior angle (cf. *Glauconycteris*); FA: <40 mm. Most species (possibly all) have a glandular swelling on each side of the muzzle and a buccal gland (= buccal pad) on the inside of each corner of the mouth; these glands change in size and prominence probably in conjunction with reproductive condition. Most species of *Pipistrellus* have five upper cheekteeth of which two are premolars. However, in some species, the anterior upper premolar (P^2) is minute and often not visible above the gum, or it can be absent. Although those species of *Pipistrellus* with only four visible upper cheekteeth strongly resemble species of *Eptesicus*, all African *Pipistrellus* are smaller (FA: 23–39 mm; GLS: 10.0–15.0 mm) than all African *Eptesicus* (FA: 38–54 mm; GLS: 15.3–21.5 mm) with the exception of *E. floweri* (FA: 34–38 mm; GLS: 12.0–13.5 mm). Selected external and craniodental characters of *Pipistrellus* are illustrated in Figure 135, and bacula of most species are illustrated in Figures 139, 140 and 141.

Traditionally, *Pipistrellus* and *Eptesicus* were distinguished by the presence or absence, respectively, of the anterior upper premolar. However, this proved unsatisfactory and phylogenetically invalid, mainly because reduction in teeth apparently occurred independently in several lineages of the Vespertilionidae. The baculum is considered to be a more conservative character than teeth and, based on bacular morphology, Hill & Harrison (1987) removed many species from *Eptesicus* to *Pipistrellus*. At the same time, they divided *Pipistrellus* into seven subgenera of which three, *P. (Pipistrellus)*, *P. (Hypsugo)* and *P. (Neoromicia)*, are represented in Africa. Subsequently, there have been other investigations based on chromosomes and DNA. Unfortunately, the systematics of many of the species in *Pipistrellus*, as defined above, is controversial – studies based on different criteria lead to different conclusions. A brief summary of some of the major proposals is as follows. (1) Based mainly on cranial characters, Koopman (1993) considered *Neoromicia* to be a subgenus of *Eptesicus* rather than *Pipistrellus*. (2) Based on morphological characters, *Hypsugo* was raised to generic status by Horáček & Hanák (1986), and this is supported by the biochemistry of the type species *H. savii* (Ruedi & Arlettaz 1991), by chromosomal characteristics (e.g. Volleth & Heller 1994) and by mitochondrial DNA characters (Hoofer & Van Den Bussche 2003). (3) Based on dental morphology of both extant and fossil forms, Menu (1987) placed the African species examined by him into three genera (*Pipistrellus*, *Hypsugo* and

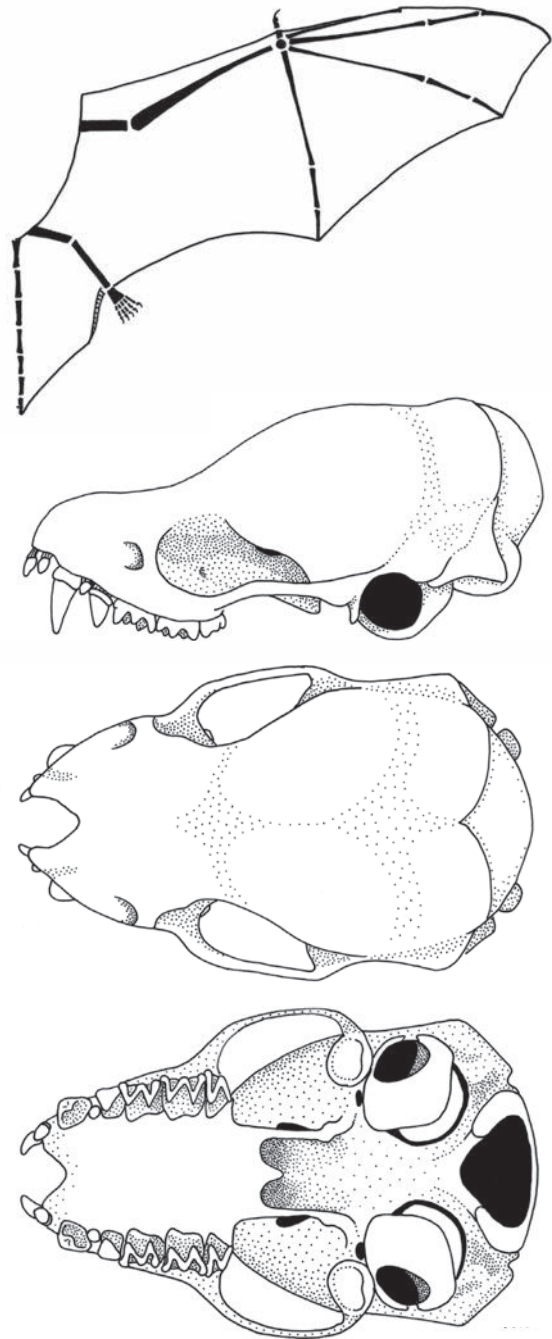


Figure 135. African *Pipistrellus* (*sensu lato*). Flight membranes, and bones of wing, hindlimb and tail (e.g. *Pipistrellus nanus* from Malawi). Skull of *Pipistrellus nanus* (HC 2870, Malawi).

Nycterikaupius) and a collective group referred to as *Attalepharca*. (4) On the basis of chromosomal characters, *Neoromicia* was raised to generic status by Volleth *et al.* (2001), and the African species, for which chromosomal data were available, were reclassified into the genera *Pipistrellus*, *Hypsugo* and *Neoromicia* (Heller *et al.* 1994, Volleth *et al.* 2001, Kearney *et al.* 2002, M. Volleth pers. comm.). (5) On

the basis of mitochondrial DNA, Hofer & Van Den Bussche (2003) questioned the definitions of *Hypsugo* and *Neoromicia* and, pending further studies, restricted *Hypsugo* to the type species, *H. savii*, and restricted *Neoromicia* to the type species, *N. somalicus*.

Although the generic status of *Hypsugo* and *Neoromicia* appears to be justified, it is not possible to distinguish these genera from each other, and from *Pipistrellus* (*sensu stricto*), on the basis of external characters that can be checked by examining living or whole specimens. Furthermore, these genera cannot, as yet, be diagnosed consistently by morphological, bacular, dental, chromosomal or molecular characters and, consequently, the species compositions of these taxa are very controversial. Also, it has not yet been possible to investigate the chromosomes, biochemistry and DNA of several species, so that their placement in *Neoromicia* or *Hypsugo* is largely guesswork based on morphological criteria. To avoid complications arising from these controversies, and pending a thorough revision of these species, we tentatively follow Hill & Harrison (1987) – and also Koopman (1994) and Nowak (1999) – in considering all of the African pipistrelle-like species to be members of the genus *Pipistrellus*. However, the traditional classification and subsequent alternative possibilities are given in the profiles of each of these species. As conventional, subgenus names are given in brackets, e.g. *Pipistrellus* (*Neoromicia*) *capensis* or *P. (Neoromicia) capensis*.

Pipistrellus, as defined by Hill & Harrison (1987), is very widely distributed in the tropical, sub-tropical and temperate regions of Africa, Europe, Asia, the South-East Asian islands, Australia and North America as far south as Honduras. In Africa, four species are found mainly or only in rainforest, eight mainly in savanna habitats, nine in both forest and savanna habitats, two in both savanna and arid habitats, and four mainly in the Mediterranean Coastal BZ. The true habitat of one species, *P. permixtus*, is not known.

Distinguishing the African species in the genus *Pipistrellus* is not easy and seldom possible without examining skull and dental characters. Some of the most useful distinguishing characters are:

Wing colour: can be white, pale (various shades of pale brown) or dark (various shades of dark brown to almost black).

Hind-border: said to be present when part or all of the posterior edge of the wing-membrane is white or pale; it can be broad or narrow.

Hairs of dorsal and ventral pelage: can be unicoloured, bicoloured or tricoloured.

Tragus: the following characters are often useful: (a) level of broadest part (can be above, at, or below mid-height, 'mid-height' being half-way along the length of the posterior margin of the tragus), (b) anterior margin (straight or concave), (c) posterior margin (said to be 'smoothly convex' when it is smoothly convex either for its entire length or between the tip of the tragus and the top of the basal lobe, or 'with abrupt angle' when there is a distinct, obtuse angle in the margin [excluding any angles associated with a basal lobe]), (e) tip (rounded, angular, or bluntly pointed) (Figure 136). The approximate length of the tragus relative to the length of the ear is mentioned in most profiles but, because this ratio may be distorted in preserved specimens, accurate estimates of relative length are seldom available. Tragi of 16 species are illustrated in Figure 136.

Skull: skulls vary (amongst other things) in size, robustness, the extent to which the braincase is elevated and broadened, the extent to which the rostrum is lengthened, broadened and/or flattened, and the extent to which the lambdoid and/or posterior sagittal crests are developed to form a low occipital helmet. In African *Pipistrellus*, mean GLS ranges from 11.0 to 14.5 mm, so 11.0–12.2 mm is small, 12.3–13.3 mm is medium and 13.4–14.5 mm is large. Five aspects of skull shape are covered in the *Pipistrellus* species profiles:

Braincase height as percentage of GLS (height measured over the bullae) (Table 25): means (excluding that of *P. pipistrellus* for which there are no African data) range from 39.2 to 48.1%, therefore 39.2–42.2% is relatively low, 42.3–45.1% is medium, and 45.2–48.1% is relatively high. Data in all profiles are from V. Van Cakenbergh (unpubl.).

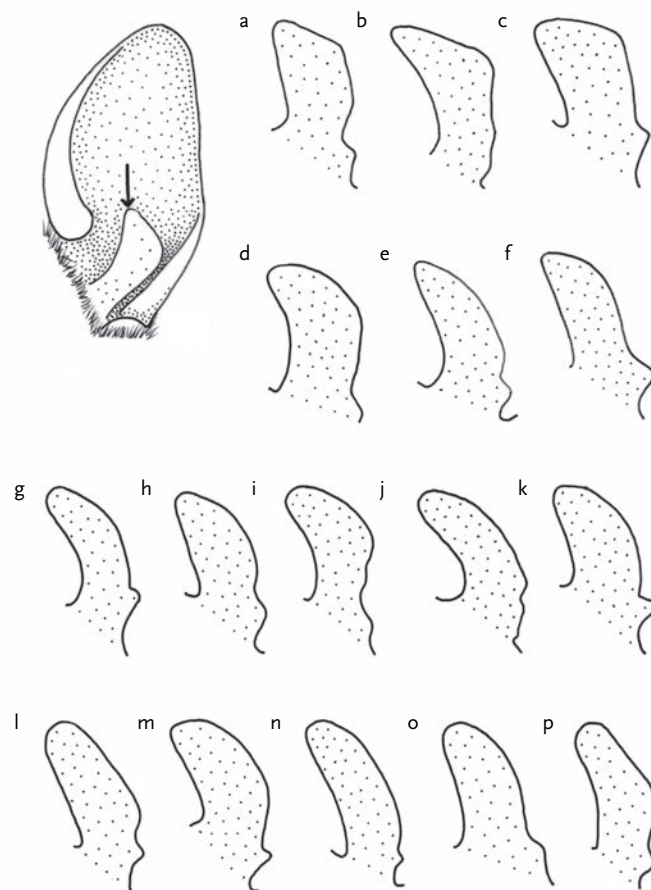


Figure 136. Left ear and tragus of *Pipistrellus nanus* and tragi of some other African species of *Pipistrellus* (*sensu lato*). The posterior margin of the tragus, above the basal notch, is described as 'having an abrupt angle' in (a) *P. brunneus* (holotype), (b) the 'hatchet-shaped' tragus of *P. nanus* (syntype), (c) the tragus of *P. tenuipinnis* (and also that of *P. cf. helios* [not illustrated]). The posterior margin, above the basal notch, is described as 'smoothly convex' in (d) *P. ariel*, (e) *P. capensis*, (f) *P. crassulus bellieri*, (g) *P. guineensis*, (h) *P. hesperidus*, (i) *P. inexpectatus*, (j) *P. cf. melckorum*, (k) *P. nanulus* (holotype), (l) *P. pipistrellus*, (m) *P. rendalli* (holotype), (n) *P. rueppellii*, (o) *P. rusticus*, (p) *P. somalicus* and other species. Arrow points to tip of tragus. (d) based on Makin & Harrison (1988); (b), (i), (k) and (m), based on Rosevear (1965); (o) based on photo by T. Kearney; (e), (h), (j) and (n) based on camera lucida drawings of fresh specimens: all others based on camera lucida drawings of well-preserved specimens in alcohol. All tragi drawn to same size.

| Species | Relative braincase height
mean (range)
(mm) | | Relative braincase breadth
mean (range)
(mm) | | Relative interorbital breadth
mean (range)
(mm) | | |
|-------------------------------|---|---------------------------|--|---------------------------|---|---------------------------|--|
| <i>P. aero</i> | H | 46
(n = 1) | M | 50, 52 | N | 28, 28 | |
| <i>P. anchietae</i> | M | 43, 44
(n = 2) | M | 49.5 (48–52)
(n = 25) | M | 28.9 (27–31)
(n = 24) | |
| <i>P. ariel</i> | M | 44, 44
(n = 2) | N | 46, 48 | N | 26, 27 | |
| <i>P. brunneus</i> | H | 45.3 (43–47)
(n = 6) | M | 49.6 (46–54)
(n = 48) | N | 28.1 (26–30)
(n = 48) | |
| <i>P. capensis</i> | L | 40.6 (32–48)
(n = 67) | M | 49.3 (43–57)
(n = 222) | N | 26.8 (23–33)
(n = 228) | |
| <i>P. crassulus crassulus</i> | L | 41.5 (36–45)
(n = 16) | B | 53.5 (51–56)
(n = 19) | B | 30.0 (28–33)
(n = 9) | |
| <i>P. crassulus bellieri</i> | H | 45.3 (44–47)
(n = 3) | B | 51.5 (50–52)
(n = 5) | B | 33.7 (33–35)
(n = 6) | |
| <i>P. deserti</i> | H | 45.2 (39–47)
(n = 12) | M | 50.9 (47–54)
(n = 19) | M | 29.5 (28–32)
(n = 19) | |
| <i>P. eisentrauti</i> | M | 43.9
(n = 1) | M | 50.4 (48–52)
(n = 3) | N | 28.6 (26–30)
(n = 3) | |
| <i>P. grandidieri</i> | M | 42.6 (39–47)
(n = 5) | M | 50.8 (48–53)
(n = 6) | M | 28.8 (28–31)
(n = 6) | |
| <i>P. guineensis</i> | M | 44.9 (41–49)
(n = 21) | M | 51.3 (47–58)
(n = 40) | M | 29.5 (24–34)
(n = 38) | |
| <i>P. hanaki</i> | H | 46.2 (45–48)
(n = 12) | N | 49.0 (47–51)
(n = 40) | N | 28.3 (26–30)
(n = 12) | |
| <i>P. cf. helios</i> | H | 47.6 (42–52)
(n = 53) | M | 50.6 (47–54)
(n = 91) | M | 28.9 (27–32)
(n = 91) | |
| <i>P. hesperidus</i> | H | 45.5 (41–50)
(n = 60) | M | 50.7 (47–56)
(n = 88) | M | 29.2 (26–32)
(n = 88) | |
| <i>P. inexpectatus</i> | L | 41.7 (39–44)
(n = 5) | M | 49.4 (48–51)
(n = 6) | N | 28.5 (27–30)
(n = 6) | |
| <i>P. kuhlii</i> | M | 44.4 (38–48)
(n = 17) | N | 48.4 (46–53)
(n = 68) | N | 27.3 (24–30)
(n = 69) | |
| <i>P. cf. melckorum</i> | L | 39.2 (36–42)
(n = 14) | N | 48.7 (46–51)
(n = 26) | N | 26.1 (23–33)
(n = 26) | |
| <i>P. muscivulus</i> | H | 48.1 (43–53)
(n = 11) | M | 51.5 (50–55)
(n = 13) | B | 31.1 (29–34)
(n = 14) | |
| <i>P. nanulus</i> | H | 47.4 (43–51)
(n = 12) | B | 52.0 (49–56)
(n = 49) | B | 31.6 (29–36)
(n = 50) | |
| <i>P. nanus</i> | H | 45.4 (27–50)
(n = 335) | M | 51.2 (44–61)
(n = 526) | M | 30.2 (26–37)
(n = 550) | |
| <i>P. pipistrellus</i> | | n. d. | N | 48.2 (46–50)
(n = 3) | M | 29.2 (28–31)
(n = 3) | |
| <i>P. rendalli</i> | M | 43.1 (40–47)
(n = 35) | M | 51.1 (47–56)
(n = 96) | M | 29.9 (27–34)
(n = 96) | |
| <i>P. rueppellii</i> | H | 47.6 (44–52)
(n = 47) | M | 51.0 (47–56)
(n = 70) | M | 30.8 (27–36)
(n = 74) | |
| <i>P. rusticus</i> | M | 44.3 (41–48)
(n = 21) | M | 51.3 (47–60)
(n = 64) | M | 30.3 (25–36)
(n = 65) | |
| <i>P. savii</i> | M | 43.7 (40–46)
(n = 45)* | N | 48.9 (47–50)
(n = 8)* | N | 27.6 (26–29)
(n = 8)* | |
| <i>P. somalicus</i> | M | 44.3 (41–48)
(n = 29) | M | 49.3 (45–57)
(n = 126) | N | 28.1 (25–33)
(n = 126) | |
| <i>P. tenuipinnis</i> | H | 45.3 (40–50)
(n = 28) | M | 50.1 (47–60)
(n = 98) | M | 29.5 (26–34)
(n = 101) | |
| <i>P. zuluensis</i> | H | 45.3 (41–49)
(n = 55) | N | 49.1 (46–55)
(n = 67) | N | 28.3 (25–31)
(n = 67) | |

| | Relative rostral length
mean (range)
(mm) | | Relative rostral breadth
mean (range)
(mm) | |
|--|---|---------------------------|--|---------------------------|
| | L | 36, 37 | B | 34, 34 |
| | M | 35.6 (32–37)
(n = 24) | N | 31.2 (28–34)
(n = 23) |
| | M | 35, 37 | N | 29, 31 |
| | M | 36.0 (34–40)
(n = 48) | M | 32.1 (29–35)
(n = 47) |
| | M | 35.8 (32–40)
(n = 228) | M | 32.6 (28–37)
(n = 227) |
| | M | 35.5 (34–39)
(n = 19) | B | 33.2 (31–36)
(n = 19) |
| | M | 35.4 (34–36)
(n = 5) | B | 33.7 (33–36)
(n = 6) |
| | M | 35.6 (34–41)
(n = 20) | M | 32.1 (28–35)
(n = 20) |
| | L | 36.4 (35–38)
(n = 3) | B | 33.1 (32–34)
(n = 3) |
| | M | 35.8 (34–37)
(n = 6) | B | 34.5 (33–37)
(n = 6) |
| | S | 34.6 (32–39)
(n = 40) | N | 30.7 (27–35)
(n = 40) |
| | M | 35.8 (34–38)
(n = 12) | M | 31.8 (30–33)
(n = 12) |
| | S | 34.5 (31–39)
(n = 90) | N | 31.2 (27–36)
(n = 90) |
| | L | 36.4 (33–39)
(n = 88) | M | 32.7 (29–37)
(n = 87) |
| | M | 36.0 (35–37)
(n = 6) | M | 32.8 (32–34)
(n = 6) |
| | L | 37.0 (35–39)
(n = 68) | M | 32.8 (30–36)
(n = 68) |
| | L | 36.2 (34–39)
(n = 25) | M | 32.5 (30–36)
(n = 25) |
| | S | 34.4 (33–37)
(n = 14) | M | 32.2 (29–36)
(n = 14) |
| | S | 35.3 (32–38)
(n = 50) | B | 33.5 (29–37)
(n = 50) |
| | S | 34.7 (31–41)
(n = 530) | N | 30.7 (27–43)
(n = 516) |
| | S | 35.0 (35–35)
(n = 3) | N | 30.7 (27–34)
(n = 3) |
| | S | 35.0 (32–39)
(n = 96) | M | 32.7 (29–36)
(n = 97) |
| | M | 35.6 (31–39)
(n = 73) | N | 31.4 (28–35)
(n = 65) |
| | M | 35.5 (33–39)
(n = 65) | B | 33.4 (30–36)
(n = 65) |
| | M | 35.8 (35–38)
(n = 8)* | B | 33.1 (32–34)
(n = 8)* |
| | M | 35.6 (33–42)
(n = 126) | M | 31.7 (26–35)
(n = 126) |
| | S | 34.4 (31–37)
(n = 101) | B | 33.1 (28–37)
(n = 102) |
| | S | 34.9 (31–38)
(n = 67) | N | 30.4 (26–33)
(n = 66) |

Table 25. Relative heights and breadths of braincase, relative breadth of interorbital constriction and relative lengths and breadths of rostrum for African *Pipistrellus*. For each species, relative braincase height (measured over bullae) and breadth (measured at onset of zygomatic arches) are given as percentages of greatest length of skull (GLS). Interorbital breadth is given as percentage of GLS. Relative rostral length is estimated from C–M³ (alveolar) as percentage of GLS. Relative rostral breadth is estimated from the width across the canines (C¹–C¹) as percentage of GLS. H = high, M = medium, L = low or long, S = short, B = broad, N = narrow (these terms referring to relative parameters in all cases; for definitions see genus *Pipistrellus*). All data from V. Van Cakenberghe (unpubl.). All data are from African specimens except where indicated by asterisk. No data are available for the only known specimen of *P. permixtus*.

Braincase breadth as percentage of GLS (breadth measured at onset of zygomatic arches) (Table 25): means range from 47.0 to 53.5%, therefore 47.0–49.2% is relatively narrow, 49.3–51.3% is medium, and 51.4–53.5% is relatively broad. Data in all profiles from V. Van Cakenberghe (unpubl.).

Interorbital breadth as percentage of GLS: means range from 26.1 to 33.7%, therefore 26.1–28.6% is relatively narrow, 28.7–31.2% is medium, and 31.3–33.7% is relatively broad. Data in all profiles from V. Van Cakenberghe (unpubl.).

Rostral shape: varies in relative breadth and length. Relative length has been estimated from C–M³ as percentage of GLS: means range from 34.4 to 37.0%, therefore 34.4–34.9% is relatively short, 35.0–35.8% is medium, and 35.9–37.0% is relatively long. Relative breadth has been estimated from C¹–C¹ (distance across the upper canines, measured from the outer side of each canine at alveolar level) as percentage of GLS: means range from 29.9 to 34.5%, therefore 29.9–31.4% is relatively narrow, 31.5–33.0% is medium, and 33.1–34.5% is relatively broad. Data in all profiles from V. Van Cakenberghe (unpubl.).

Forehead region of skull: the profile (viewed laterally) of the forehead region (i.e. that part of the profile encompassing most of the rostrum and the anterior part of the braincase) can be strongly concave, moderately concave, weakly concave, or straight (or almost straight) depending on the extent to which the frontal region is inflated and raised above the plane of the rostrum (Figure 137); the variation is gradual and the boundaries between these categories are not clearly demarcated. Note that, in *Pipistrellus*, the concavity, even when maximal as in ‘strongly concave’, is not as strongly concave as, for example, in *Kerivoula* and *Miniopterus*.

Anterior upper premolar: present or absent; well developed, medium or minute relative to the size of the posterior premolar (assessed

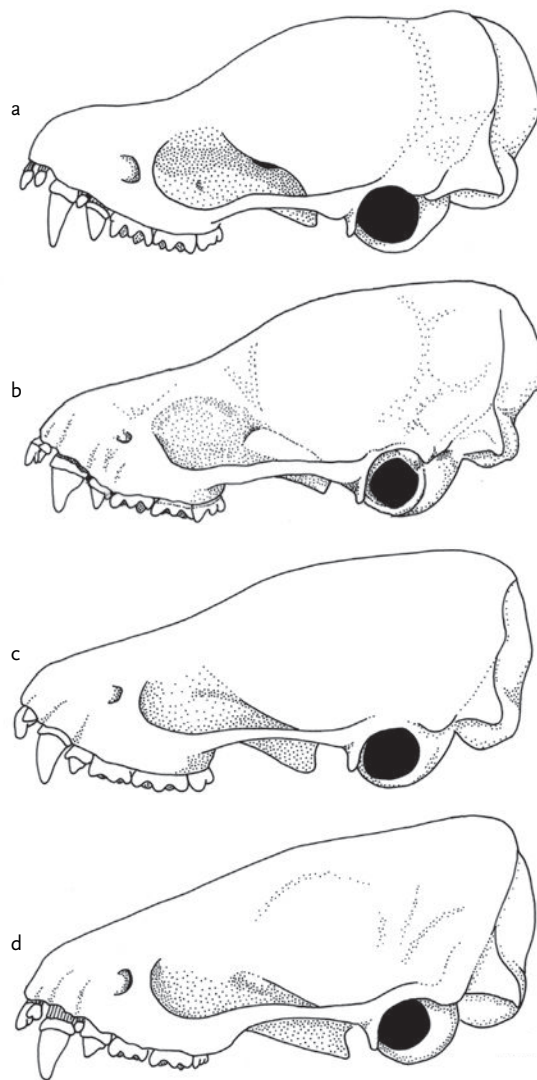


Figure 137. Range of variation in the degree of concavity of the dorsal profile of the forehead region (viewed laterally) in African *Eptesicus* and *Pipistrellus* (*sensu lato*). (a) Strongly concave (e.g. *P. nanus*; HC 2870). (b) Moderately concave (e.g. *P. hanaki*, based on Benda *et al.* 2004b). (c) Weakly concave (e.g. *P. guineensis*; ZFMK 73.23). (d) Straight (or almost straight) (e.g. *P. crassulus bellieri*; holotype, RMCA RG 35686).

qualitatively); visible or not visible above gum; in tooththrow or displaced lingually. Note that the anterior upper premolar is always much smaller than the posterior upper premolar and that the above size categories have been established solely to enable the relative sizes of the anterior premolars of African species of *Pipistrellus* to be compared with each other.

Inner upper incisor: may be unicuspid or bicuspid. However, weakly bicuspid teeth may appear unicuspid after wearing.

Lower molars: may be myotodont or nyctalodont (Figure 138). Myotodont lower molars are characterized by the path of the postcristid ridge, which directly connects the hypoconid cusp with the entoconid cusp, leaving the hypoconulid isolated. Nyctalodont lower molars are characterized by the path of the postcristid ridge, which connects the hypoconid cusp with the hypoconulid without reaching the entoconid cusp, or which runs into the gap between the

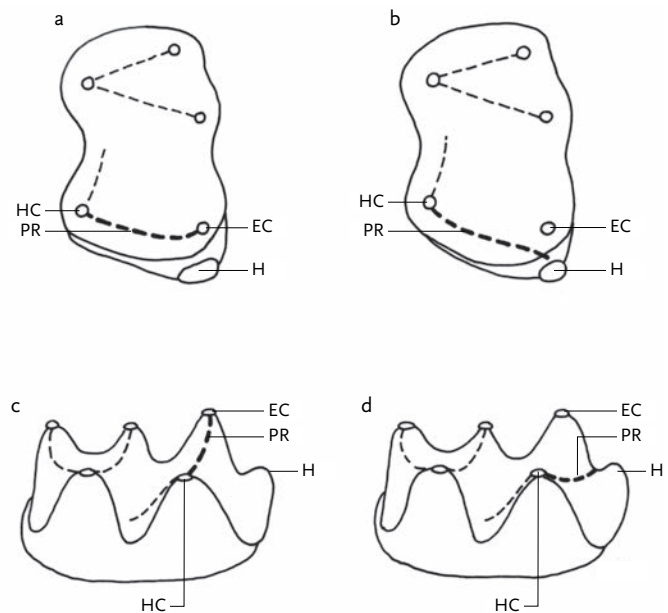


Figure 138. Myotodont and nyctalodont lower molars of vespertilionid bats: these are distinguished by differences in the path of the postcristid ridge (broad dashed line) in relation to the entoconid cusp and the hypoconulid. (a) Occlusal view of a myotodont lower molar, with anterior side uppermost and labial side on left, showing the postcristid ridge connecting the hypoconid cusp and entoconid cusp, leaving the hypoconulid isolated. (b) Occlusal view of a nyctalodont lower molar, showing the postcristid ridge connecting the hypoconid cusp with the hypoconulid or running into the gap between the hypoconulid and the side of the molar. (c) Myotodont lower molar viewed from the labial (outer) side (with anterior side on left). (d) Nyctalodont lower molar viewed from the labial side showing (in this case) the postcristid ridge running into the gap between the hypoconulid and the molar. Cusps indicated by open circles; ridges by narrow or broad dashed lines. PR = postcristid ridge, HC = hypoconid cusp, EC = entoconid cusp, H = hypoconulid.

hypoconulid and the side of the molar. A high-quality binocular microscope is necessary to distinguish myotodont and nyctalodont molars accurately, especially for small species.

Bacular morphology: also useful diagnostically (Figures 139, 140 and 141).

Based on the shape of the lower molars, African *Pipistrellus* can be divided into the myotodont group and nyctalodont group, and then the species within each group can usually be distinguished by the characters given in Tables 26 and 27, respectively. These are not necessarily species-groups in the systematic sense, but it is noteworthy that all African species placed in *Neoromicia* and *Hypsugo* by Simmons (2005) have myotodont lower molars with the exception of *P. nanus*, and all African species placed in *Pipistrellus* by Simmons (2005) have nyctalodont lower molars. Because of this, we have strong doubts about the assignment of *P. nanus* to either *Hypsugo* or *Neoromicia*, and retain it in *Pipistrellus* (*sensu stricto*). Where the tabulated information fails to distinguish very similar species, see 'Similar Species' in the relevant profiles. In the Similar Species sections, comparisons are made only between species of *Pipistrellus* and *Eptesicus* that occur in Africa (with very few exceptions).

The species are presented in alphabetical order irrespective of any relationships between them.

Victor Van Cakenberghe & Meredith Happold

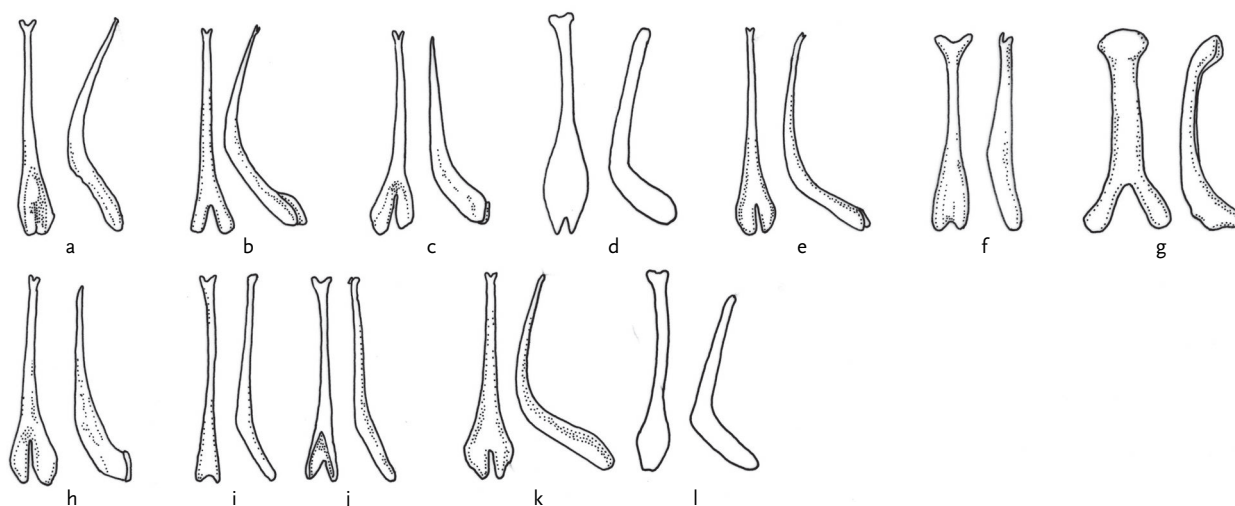


Figure 139. Bacula of ten species of *Pipistrellus* (*sensu stricto*) occurring in Africa. (a) *P. aero* (lateral view is of left side reversed). (b) *P. deserti*. (c) *P. hanaki* (lateral view is of left side reversed). (d) *P. hesperidus*. (e) *P. kuhlii* from Greece. (f) *P. nanulus*. (g) *P. nanus*. (h) *P. pipistrellus* (lateral view is of left side reversed). (i) *P. rueppellii* from Uganda. (j) *P. rueppellii pulcher* (holotype) from Zanzibar. (k) *P. rusticus*. (l) *P. rusticus*. Based on bacular morphology, *P. nanus* was placed *P. (Hypsugo)* by Hill & Harrison (1987), but is retained in *Pipistrellus* (*sensu stricto*) here (see profile). For each species, left illustration is dorsal view with tip uppermost, right illustration is lateral view of the right side unless stated otherwise. Figs: (a) based on Lavrenchenko *et al.* (2004), (c) and (h) based on Benda *et al.* (2004b), (d) and (l) adapted from Kearney *et al.* (2002); all others based on Hill & Harrison (1987). Bacula drawn to same size (for scale drawings, see sources cited above).

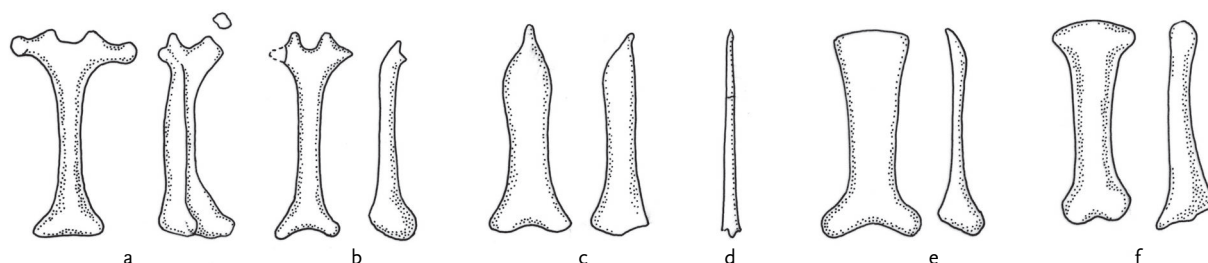


Figure 140. Bacula of four species of *Pipistrellus* (*sensu lato*), occurring in Africa, that are placed in *P. (Hypsugo)* by Hill & Harrison (1987) on basis of bacula morphology, and *P. crassulus*, which was placed in *P. (Pipistrellus)* by Hill & Harrison (1987) but subsequently placed in *Hypsugo* by Heller *et al.* (1994) and others (see profile). (a) *P. anchietae* (views: dorsal and left ventro-lateral reversed). (b) *P. anchietae* (syntype of *Vesperus bicolor*). (c) *P. ariel* (based on Makin & Harrison 1988). (d) *P. crassulus* (dorsal view only). (e) *P. eisentrauti* (BMNH 84.1686 from Mt Cameroun). (f) *P. savii*. For each species except (a), left illustration is dorsal view with tip uppermost, right illustration is lateral view of right side. (c) based on Makin & Harrison 1988; all others based on Hill & Harrison (1987). Bacula drawn to same size (for scale drawings, see sources cited above).

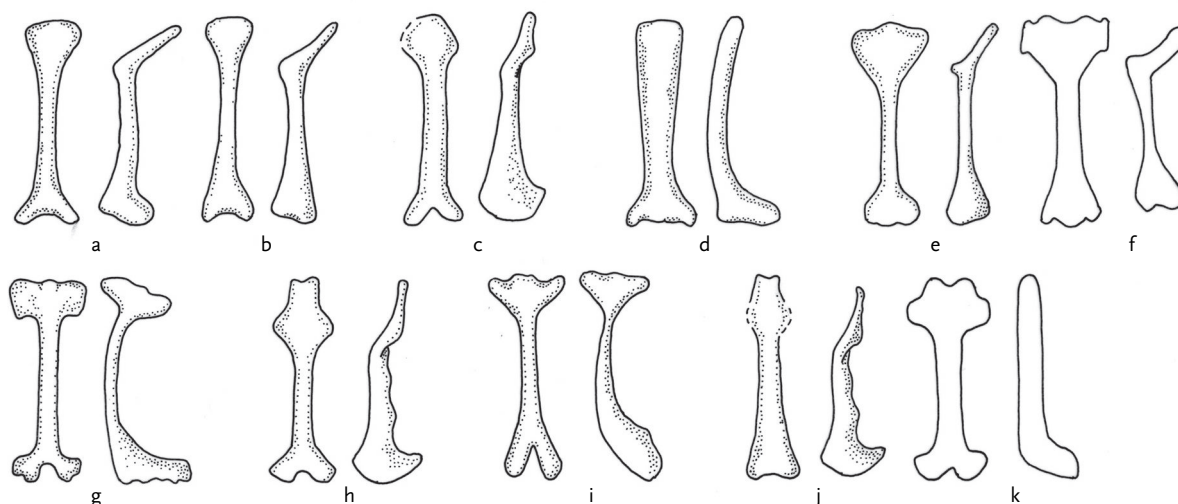


Figure 141. Bacula of seven species of *Pipistrellus* (*sensu lato*) that are placed in *P. (Neoromicia)* by Hill & Harrison (1987) on basis of bacula morphology, and also *P. cf. helios* which is placed in *P. (Hypsugo)* by Hill & Harrison (1987) but in *Neoromicia* by Simmons (2005, as *N. helios*). (a) *P. capensis* from Ghana. (b) *P. capensis* from Ethiopia. (c) *P. guineensis*. (d) *P. cf. helios*. (e) *P. cf. melckorum* from Zimbabwe (Hill & Harrison 1987 as *P. melckorum*). (f) *P. cf. melckorum* (adapted from Kearney *et al.* 2002 as *Neoromicia cf. melckorum*). (g) *P. rendalli*. (h) *P. somalicus*. (i) *P. tenuipinnis*. (j) *P. zuluensis*. (k) *P. zuluensis* (adapted from Kearney *et al.* 2002 as *Neoromicia zuluensis*). All except (f) and (k) are based on Hill & Harrison (1987).

Table 26. Key to the African species of the genus *Pipistrellus* (*sensu lato*) that have myotodont lower molars. Most of these species have only one upper premolar, the anterior premolar being absent. In some species, the anterior upper premolar may be present, but small or minute, difficult to see because it is displaced lingually from the toothrow (sometimes resulting in the canine and posterior premolar being in contact), or not visible because it has not erupted through the gum. Measurements and distributions pertain only to Africa.

| Wing colour | Inner upper incisor | Dorsal hairs (Ventral hairs) | FA (mm) | Mid-ventral pelage | Anterior upper premolar
If present, size and visibility above gum | |
|-------------|---------------------------------------|---|---------------------------|---|---|--|
| White | Unicuspid | Bicoloured or tricoloured (Bicoloured) | 33.7 (29–37) | Cream, whitish or pale grey | Absent | |
| White | Weakly bicuspid | Usually unicoloured (Bicoloured) | 29.8 (28–33) | Whitish or cream | Sometimes present
If present: minute, usually visible | |
| Dark | Unicuspid | Unicoloured (Bicoloured) | 34.9 (33–38) | Pale greyish-brown to medium brown | Absent | |
| Dark | Unicuspid | Bicoloured (Bicoloured) | 29.1 (30–31) | Greyish-cream | Minute, sometimes not visible | |
| Dark | Unicuspid or weakly bicuspid | Bicoloured (Bicoloured) | 37.1 (36–39) ^b | Brownish-cream | Absent | |
| Dark | Weakly bicuspid (unicuspid when worn) | Bicoloured (Bicoloured) | 31.9 (28–38) | White, whitish, cream or buff | Absent except extremely rarely, in which case, minute, not visible | |
| Dark | Usually unicuspid | Bicoloured or tricoloured (Bicoloured) | 29.9 (27–33) | Pale greyish-brown or brown | Absent except extremely rarely, in which case, minute, hardly visible | |
| Dark | Usually unicuspid | Faintly bicoloured (Faintly bicoloured) | 28.8 (22–32) | Pale brown or brown | Usually absent | |
| Dark | Bicuspid | Unicoloured (Unicoloured) | 35.4 (33–38) | Pale brown, usually yellowish | Minute, sometimes not visible, sometimes absent | |
| Dark | Bicuspid | Unicoloured (Unicoloured) | 30.2 (28–32) | Dark brown or reddish-brown | Minute, barely visible or not visible | |
| Dark | Bicuspid | Unicoloured (Unicoloured) | 24.9 (23–26) | Dark umber-brown | Minute and often not visible; sometimes absent | |
| Dark | Bicuspid | Unicoloured (Bicoloured) | 30.5 (28–33) | Pale brown | Small to medium-sized, visible | |
| Dark | Bicuspid | Bicoloured (Unicoloured) | 32.0 (31–33) | Reddish-cream | Minute, usually not visible | |
| Dark | Bicuspid | Bicoloured (Bicoloured) | 34.0 (32–36) | Slightly reddish-brown tinged with beige | Minute to medium-sized, usually visible, occasionally absent | |
| Dark | Bicuspid | Bicoloured (Bicoloured) | 35.5 (34–38) | Yellowish-white or greyish-white | Minute, not visible, sometimes absent | |
| Dark | Bicuspid | Bicoloured (Bicoloured) | 31.3 (29–34) | Pale brown, cream or white | Minute, not visible | |
| Dark | Bicuspid | Bicoloured (Bicoloured) | 27.7 (23–35) | Dark to medium rust-brown, sometimes speckled | Absent | |
| Dark | Bicuspid | Tricoloured (Bicoloured) | 28.0 (26–30) | Pale brown to pale yellowish-brown | Well developed, visible | |

^a Sample less than six.

^b Data for five specimens of *P. cf. melkorum* identified from their chromosomes; for other specimens, FA: 35.3 (32–38) mm, n = 35; GLS: 14.6 (13.7–15.5) mm, n = 26 (V. Van Cakenberghe, pers. comm.).

| | Forehead region of skull | Relative height of braincase (relative breadth of braincase) | GLS (mm) | Miscellaneous | Species |
|--|-----------------------------------|--|-------------------------------|--|-------------------------|
| | Straight | Medium (Medium) | 13.3 (12.3–14.4) | Dorsal pelage pale brown, not contrasting strongly with pale wings | <i>P. rendalli</i> |
| | Weakly concave | High (Medium) | 12.3 (11.6–13.0) | Dorsal pelage blackish-brown in strong contrast to pale wings | <i>P. tenuipinnis</i> |
| | Weakly concave | High (Medium) | 13.5 (13.0–14.1) | Rainforest habitats | <i>P. brunneus</i> |
| | Strongly concave | Medium (Narrow) | 11.1, 11.3 ^a | Sahara Arid and Sahel BZs; only known from Sudan | <i>P. ariel</i> |
| | Straight to weakly concave | Low (Narrow) | 14.5 (13.8–14.9) ^b | Zambezian Woodland BZ
Tail: 39.6 (35–44) mm ^b
Occipital helmet weakly developed
Molars more massive than in <i>P. capensis</i> | <i>P. cf. melckorum</i> |
| | Straight to weakly concave | Low (Medium) | 13.5 (12.0–15.4) | Widespread south of Sahara
Tail: 30.6 (25–38) mm
Occipital helmet usually well developed
Molars less massive than in <i>P. cf. melckorum</i> | <i>P. capensis</i> |
| | Weakly to moderately concave | High (Narrow) | 12.2 (11.3–12.9) | Widespread south of 9° S, and also Kenya
Occipital helmet absent | <i>P. zuluensis</i> |
| | Weakly concave to almost straight | Medium (Medium) | 12.2 (11.3–12.9) | Widespread south of Sahara to 5° S (but seldom in Rainforest BZ); occurrence further south uncertain
Occipital helmet absent | <i>P. somalicus</i> |
| | Weakly concave to almost straight | Medium (Medium) | 14.2 (13.8–14.7) | Various BZs and Mosaics; Cameroon, Uganda, Burundi, Somalia, Angola and Malawi | <i>P. grandidieri</i> |
| | Weakly concave to almost straight | Low (Broad) | 12.8 (12.5–13.2) | Rainforest and Afroalpine–Afromontane BZs and Rainforest–Savanna Mosaics; east of 10° E | <i>P. c. crassulus</i> |
| | Weakly concave | High (Medium) | 11.0 (10.3–11.4) | Rainforest BZ and Northern Rainforest–Savanna Mosaic; West and central Africa | <i>P. musciculus</i> |
| | Straight to weakly concave | High (Broad) | 12.9 (12.1–13.6) | Rainforest BZ and Northern Rainforest–Savanna Mosaic; Guinea, Liberia, Côte d'Ivoire | <i>P. c. bellieri</i> |
| | Weakly concave to almost straight | Low (Medium) | 12.6 (12.5–12.6) ^a | Guinea Savanna BZ and Northern Rainforest–Savanna Mosaic
Wings with white hind-border | <i>P. inexpectatus</i> |
| | Very weakly concave | Medium (Medium) | 13.9 (13.7–14.1) | Afroalpine–Afromontane BZ; Cameroon
Wings without white hind-border | <i>P. eisentrauti</i> |
| | Weakly concave to almost straight | Medium (Narrow) | 14.0 (12.8–14.6) | North-west Africa; no overlap with geographic ranges of other species | <i>P. savii</i> |
| | Weakly concave | Medium (Medium) | 12.5 (11.2–13.7) | Mainly Zambezian Woodland BZ; Angola, S DR Congo, Zambia, Zimbabwe, South Africa
Wings with or without white hind-border | <i>P. anchietae</i> |
| | Weakly concave | Medium (Medium) | 11.3 (10.7–11.8) | Mainly Guinea and Sudan Savanna BZs and Rainforest–Savanna Mosaics
Wings with or without white hind-border | <i>P. guineensis</i> |
| | Strongly concave | High (Medium) | 11.0 (10.4–11.4) | Mainly Somalia–Masai Bushland BZ and Coastal Forest Mosaic; Kenya and marginally in some adjacent countries
Tragus hatchet-shaped
Usually paired glands on interfemoral membrane | <i>P. cf. helios</i> |

Table 27. Key to the African species of the genus *Pipistrellus* that have nyctalodont lower molars. All of these species (except *P. rusticus*) have two upper premolars on each side, but the anterior upper premolar is often minute and difficult to see because it is displaced lingually from the toothrow (sometimes resulting in the canine and posterior premolar being in contact), or not visible because it has not erupted through the gum (see genus *Pipistrellus* for explanation of the size categories). In *P. rusticus*, one or both anterior upper premolars is sometimes absent. Measurements and distributions pertain only to Africa.

| Ventral pelage pure white | Tragus with sharp angle on posterior border | Inner upper incisor | Dorsal hairs (Ventral hairs) | White hind-border on wing | Colour of dorsal pelage | |
|---------------------------|---|---------------------|-----------------------------------|---|--|--|
| Yes | No | Bicuspid | Bicoloured (Unicoloured) | Sometimes present | Grey to sepia brown | |
| No | Yes | Usually bicuspid | Bicoloured (Bicoloured) | Absent | Chocolate brown or sepia brown, sometimes with gold sheen | |
| No | No | Bicuspid | Unicoloured (Usually unicoloured) | Usually absent | Reddish-brown | |
| No | No | Bicuspid | Bicoloured (Bicoloured) | Absent | Brown to rusty-brown | |
| No | No | Bicuspid | Bicoloured (Bicoloured) | Absent (pale hind-border sometimes present) | Pale brownish to greyish-brown | |
| No | No | Bicuspid | Bicoloured (Not known) | No data | Not known | |
| No | No | Unicuspid | Bicoloured (Bicoloured) | Present | Pale sepia brown to pale yellowish-brown, sometimes with greenish tint | |
| No | No | Unicuspid | Bicoloured (Bicoloured) | Present | Sepia brown, dark rusty-brown to pale yellowish-brown | |
| No | No | Unicuspid | Bicoloured (Bicoloured) | Absent | Dark, slightly reddish-brown | |
| No | No | Unicuspid | Bicoloured (Bicoloured) | Sometimes present | Reddish-brown, orange-brown, greyish-orange or medium brown | |
| No | No | Unicuspid | Bicoloured (Bicoloured) | Absent | Greyish-brown, reddish-brown, dark brown or blackish | |

***Pipistrellus aero* Mt GARGUES PIPISTRELLE**

Fr. Pipistrelle du Kenya; Ger. Luftige Zwergfledermaus

Pipistrellus aero Heller, 1912. Smithson. Misc. Coll. 60 (12): 3. Mt Gargues, Matthews Range, Kenya.

Taxonomy Traditionally *Pipistrellus aero*, but subsequently classified as *P. (Pipistrellus) aero* by Hill & Harrison (1987), Koopman (1993, 1994) and Simmons (2005). Allen (1917a) mistakenly assumed that *P. aero* was near *P. nanus*. Koopman (1975) suggested that *P. aero* is possibly a subspecies of *P. kuhlii* or *P. deserti*; the relationships between these forms are still uncertain. Specimens from Ethiopia, mentioned by Hayman (1967), are considered to represent *Pipistrellus kuhlii fuscatus* (Hill 1968, Hayman & Hill 1971). Synonyms: none. Chromosome number: not known.

Description Very small microbat without noseleaf and with tail more or less fully enclosed in interfemoral membrane; five upper cheekteeth (but sometimes only four visible above gum), five lower cheekteeth and two upper incisors on each side; ears separated and short (ca. 8–10 mm); FA: 31–34 mm; wings dark without white

hind-border; dorsal pelage dark; dorsal and ventral hairs bicoloured; lower molars nyctalodont; inner upper incisor unicuspid; profile of forehead region of skull moderately concave. A poorly known species. Pelage dense, silky; mid-dorsal hairs ca. 7 mm. Dorsal pelage dark, slightly reddish-brown; hairs blackish-brown at base. Ventral pelage slightly paler; hairs pale reddish-brown with blackish-brown at base. Ears black, relatively short. Tragus length ca. one-third of E; narrow; breadth constant for most of length; breadth much less than length of anterior margin; anterior margin concave; posterior margin smoothly convex; tip rounded. Wings uniformly very dark brown; no white hind-border. Interfemoral membrane very dark brown. Baculum strongly curved with bifurcations both distally and proximally (Figure 139a; Lavrenchenko *et al.* 2004).

Skull medium-sized for an African *Pipistrellus*. Braincase relatively high but of medium relative breadth; interorbital region relatively

| | Anterior upper premolar
(size, visibility above gum, position in toothrow) | FA
(mm) | Miscellaneous | Species |
|--|--|------------|---|------------------------|
| | Medium-sized, conspicuous, within toothrow or slightly displaced | 29–37 | Widespread but disjunct (see map) | <i>P. rueppellii</i> |
| | Medium-sized, visible, slightly displaced linguallly | 25–35 | Sub-Sahara, rainforest and savannas
Day-roosts include furred banana leaves
Rarely any glands on tail | <i>P. nanus</i> |
| | Medium-sized to well-developed, visible, in toothrow or slightly displaced linguallly | 24–29 | Mainly rainforest | <i>P. nanulus</i> |
| | Well-developed, visible, displaced linguallly | 31–33 | NE Libya (Cyrenaica) | <i>P. hanaki</i> |
| | Medium-sized, visible, slightly displaced linguallly | 28–33 | North-west Africa (Maghreb) | <i>P. pipistrellus</i> |
| | Well-developed, visible, uncertain | 34 | Tanzania
Forehead region of skull moderately concave
Only the holotype is known | <i>P. permixtus</i> |
| | Minute, usually not visible, displaced linguallly | 25–34 | North Africa to Equator
Forehead region of skull moderately concave
GLS: 11.7 (10.8–12.4) mm | <i>P. deserti</i> |
| | Minute, hardly visible, usually displaced linguallly | 29–37 | North Africa only
Forehead region of skull moderately to weakly concave
GLS: 13.2 (12.3–13.8) mm | <i>P. kuhlii</i> |
| | Minute, often not visible, displaced linguallly | 31–34 | Kenya, Ethiopia
Forehead region of skull moderately concave | <i>P. aero</i> |
| | Minute, seldom visible, displaced linguallly, sometimes absent | 24–31 | Sub-Saharan savanna, woodland and bushland zones
Forehead region of skull straight to weakly concave | <i>P. rusticus</i> |
| | Medium-sized to minute, usually visible, within toothrow to fully displaced linguallly | 29–38 | Forehead region of skull moderately concave | <i>P. hesperidus</i> |

narrow; rostrum relatively long and broad (Table 25, p. 603). Profile of forehead region (viewed laterally) moderately concave. No occipital helmet. Upper incisors conical, unicuspid. Outer incisor less than half height of inner incisor. Anterior upper premolar present, but minute, displaced linguallly and often not visible above gum. Lower molars nyctalodont (M. D. Carleton pers. comm.). Dental formula: $\frac{2123}{3123} = 34$.

Geographic Variation None recorded.

Similar Species Three other sub-Saharan *Pipistrellus* have lower molars nyctalodont; inner upper incisors unicuspid (Table 27, p. 608):

Pipistrellus rusticus. Dorsal pelage reddish-brown to medium brown. Forearm usually shorter (24–31 mm). Profile of forehead region of skull straight or almost straight. Widespread.

P. deserti. Dorsal pelage pale sepia brown to pale yellowish-brown (sometimes with greenish tint); wings with white hind-border. Algeria to Egypt, West Africa, Sudan, Somalia.

P. hesperidus. Interfemoral membrane paler and more translucent than wing-membranes. Comparatively widespread.

Distribution Endemic to Africa. Known only from the Afromontane–Afroalpine BZ at Mt Gargues, Kenya (Heller 1912) and at three localities in Ethiopia (see below), and from the Somalia–Masai BZ at L. Marsabit and Ngong (Aggundey & Schlitter 1984). Specimens from south of L. Tana, Ethiopia, mentioned by Hayman & Hill (1971) do not seem to represent *P. aero* and this locality is questioned. However, recently acquired specimens (now in ZMMU) from three other localities in Ethiopia do represent this species (Lavrenchenko *et al.* 2004). These Ethiopian localities (not mapped) are the tributary of Beko R. (07° 07'N, 35° 25'E, 1300 m), Godare Forest, Dushi Area, Yamboshi R. (07° 21'N, 35° 13'E, 1200 m) and Chercher Mts, between Hirna and Deder (09° 20'N, 41° 16'E, 2700 m). The distance between these localities, and the differences in altitude, suggest that *P. aero* is probably widely distributed in Ethiopia.

Habitat Heller (1912) reported this species from ‘heavy forest’ (= montane forest) on the summit of Mt Uarguess (= Mt Gargues, Mathews Range, Kenya). The other Kenyan localities are in a vegetation zone described as a mosaic of evergreen bushland and secondary *Acacia* wooded grassland but, at L. Marsabit, there is afromontane vegetation in the area.

*Pipistrellus aereo*

Conservation IUCN Category: Data Deficient.

Geographic range restricted.

Measurements

Pipistrellus aereo

FA: 31.6 (31–34) mm, n = 7

WS (d): 220 mm, n = 1

TL: n. d.

HB: 45.0 (40–49) mm, n = 8*

T: 32.7 (32–34) mm, n = 4

E: 11.5 (10–15) mm, n = 5

Tr: 4.1 (3–5) mm, n = 5

Tib: 10.9 (8–13) mm, n = 6

HF: 7.0 (5–10) mm, n = 8*

WT: 4.5 (4.0–5.0) g, n = 8*

GLS: 12.6 (12.2–13.0) mm, n = 4

GWS: 8.3 (8.1–8.6) mm, n = 4

C–M³ (alv.): 4.5 (4.4–4.6) mm, n = 5

Throughout geographic range (BMNH, USNM [including holotype], ZMMU)

*Lavrenchenko *et al.* (2004)

Abundance Uncertain. Very rarely recorded.

Remarks Nothing more is known about this species.

Key References Heller 1912; Lavrenchenko *et al.* 2004.

Victor Van Cakenberghe & Meredith Happold

Pipistrellus anchietae ANCHIETA'S PIPISTRELLE

Fr. Pipistrelle d'Anchieta; Ger. Anchieta's Zwergfledermaus

Pipistrellus anchietae (Seabra, 1900). J. Sci. Math. Phys. Nat. Lisboa, ser. 2, 6: 26, 120. Cahata, Angola.

Taxonomy Originally *Vesperugo anchieta*. The emendation to *anchietae* is justified; *anchietai* is incorrect (Kock 2001a). Traditionally *Pipistrellus anchietae*. Subsequently classified as *P. (Hypsugo) anchietae* by Hill & Harrison (1987) and Koopman (1993) and as *Hypsugo anchietae* by Kearney *et al.* (2002) and Simmons (2005). In contrast, Hoofer & Van Den Bussche (2003) question the placement of *anchietae* in *Hypsugo*. Placed in collective group *Attalepharca* by Menu (1987). Identification of *P. anchietae* using chromosomes and bacula has shown that keys, using tooth shape and height characters (e.g. Meester *et al.* 1986) are problematic (Kearney & Taylor 1997). It is possible that more *P. anchietae* exist in collections, misidentified as *P. kuhlii* (Hill & Carter 1941, Kearney & Taylor 1997). Synonyms: tentatively none. Koopman (1975, 1993) considered *anchietae* a synonym of *Pipistrellus bicolor*, which is the prior name. However, *bicolor* is tentatively treated here as a synonym of *P. tenuipinnis* (see profile of *P. tenuipinnis*). Subspecies: none. Chromosome number (South Africa): 2n = 26; aFN = 32 (Rautenbach *et al.* 1993).

Description Very small microbat without noseleaf and with tail more or less fully enclosed in interfemoral membrane; five upper cheekteeth (but only four visible above gum), five lower cheekteeth and two upper incisors on each side; ears separated and short (10–23 mm); FA: 29–34 mm; dorsal pelage brown; dorsal and ventral hairs bicoloured; wings dark with or without white hind-border;

lower molars myotodont; inner upper incisors bicuspid; profile of forehead region of skull weakly concave. Sexes similar. Pelage soft, dense; mid-dorsal hairs ca. 6 mm. Dorsal pelage yellowish-brown, reddish-brown, medium brown or dark brown; hairs with basal two-thirds blackish-brown. Ventral pelage pale brown, cream or white; palest in pelvic region; hairs mostly with basal two-thirds blackish-brown but some all-white hairs in pelvic region. Bare skin on muzzle and around eyes medium or dark brown. Buccal glands have been observed in one ♀. Ears medium-brown, subtriangular with rounded tip. Tragus length ca. half of E; posterior margin smoothly convex with basal lobe; tip rounded. Wing-membranes dark brown or blackish-brown, sometimes without white hind-border, sometimes with very narrow white hind-border. Interfemoral membrane paler (medium or dark brown). Baculum as in Figure 140a, b (Hill & Harrison 1987) (but see Kearney *et al.* 2002 for variation).

Skull medium-small and gracile for an African *Pipistrellus*. Braincase of medium relative height and breadth; interorbital region of medium relative breadth; rostrum of medium relative length but relatively narrow (Table 25, p. 603). Profile of forehead region (viewed laterally) weakly concave. Rostrum with well-developed lateral depressions just above the infraorbital foramina (J. E. Hill in Rautenbach *et al.* 1985) as in *P. inexpectatus* and some *P. capensis*. No occipital helmet. Inner upper incisor bicuspid. Outer upper incisor minute. Anterior upper premolar minute, not visible above gum, displaced lingually

but canine and posterior premolar not in contact. Lower molars myotodont (Menu 1987). Dental formula: $^{2123}/_{3123} = 34$.

Geographic Variation None recorded.

Similar Species One African *Eptesicus* and four other African *Pipistrellus* also have dark wings; bicoloured dorsal hairs; myotodont lower molars; and have (or might have) distributions overlapping that of *P. anchietae* (Table 26, p. 606):

Pipistrellus capensis. Inner upper incisor weakly bicuspid before tooth is worn, then unicuspid. Anterior upper premolar absent. Occipital helmet well developed.

P. somalicus. Hairs faintly bicoloured. Inner upper incisor unicuspid or weakly bicuspid. Anterior upper premolar absent. Widespread south of Sahara.

P. zuluensis. Dorsal hairs bicoloured or tricoloured. Inner upper incisor usually unicuspid. Anterior upper premolar absent.

P. cf. melckorum. Inner upper incisor bicuspid. Anterior upper premolar absent. Skull longer (GLS: 13.7–15.5 mm).

Eptesicus hottentotus. Much larger (FA: 45–54 mm; GLS: 16.9–21.5 mm).

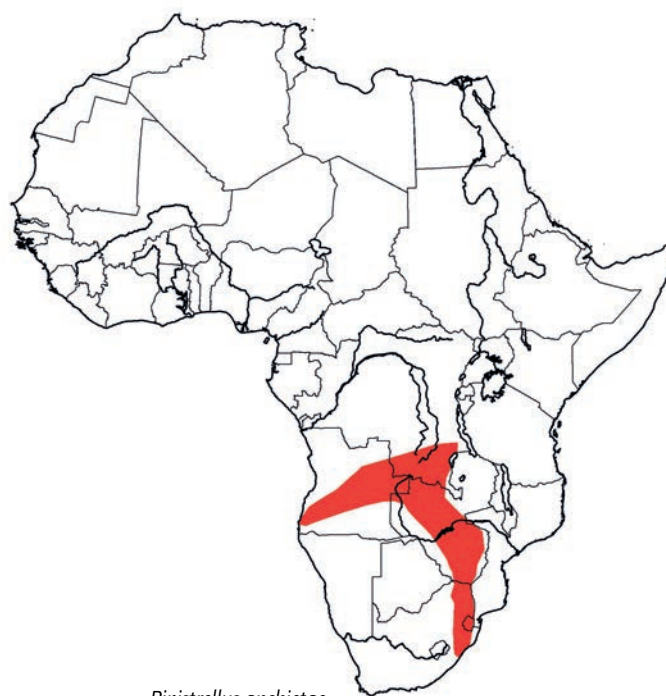
Distribution Endemic to Africa. Mainly found in the Zambezan Woodland BZ, but extends marginally into the South-West Arid BZ in S Angola and into the Coastal Forest Mosaic BZ in South Africa. Recorded from Angola, S DR Congo, Zambia, Zimbabwe and South Africa.

Habitat Found in riverine, coastal and scrub forests as well as bushveld, often in vicinity of open water.

Abundance Rare, but possibly more specimens exist, misidentified as *P. hesperidus*.

Remarks Has been caught while flying over or near water, along dirt roads with thick bush on either side and along dry river beds. One was found roosting in a tree in woodland at the edge of a riverine forest in Zambia (HZM). In KwaZulu–Natal (South Africa), 3 of 3 ♀♀ were reproductively inactive in Apr–May; 1 of 1 was pregnant with two foetuses in Nov (Kearney & Taylor 1997).

Conservation IUCN Category: Least Concern.



Pipistrellus anchietae

Measurements

Pipistrellus anchietae

FA: 31.3 (29–34) mm, n = 24*

WS: n. d.

TL: 81.8 (78–87) mm, n = 6

T: 35.3 (32–39) mm, n = 6

E: 11.2 (10–13) mm, n = 6

Tr: 5.7 (4.9–6.0) mm, n = 8

Tib: 12.1 (11–14) mm, n = 9*

HF: 5.5 (5.0–6.0) mm, n = 8

WT: 4.8 (4.2–5.6) g, n = 6

GLS: 12.5 (11.2–13.7) mm, n = 25*

GWS: 8.1 (7.0–8.9) mm, n = 18*

C–M³ (alv.): 4.5 (4.1–5.6) mm, n = 27*

Zimbabwe and South Africa (DM, NMZB)

*Throughout geographic range (V. Van Cakenberghe pers. comm.)

Key Reference Kearney & Taylor 1997.

Teresa Kearney

Pipistrellus ariel FAIRY PIPISTRELLE

Fr. Pipistrelle ariel; Ger. Elfen-Zwergfledermaus

Pipistrellus ariel Thomas, 1904. Ann. Mag. Nat. Hist., ser. 7, 14: 157. Wadi Alagi, (22°N, 35°E, 610 m), Kassala Province, Sudan.

Taxonomy Traditionally *Pipistrellus ariel*. Subsequently classified as *P. (Hypsugo) ariel* by Hill & Harrison (1987) and Koopman (1993) and as *Hypsugo ariel* by Simmons (2005). The closest ally of this species appears to be the South-West Asian *Pipistrellus bodenheimeri* Harrison, 1960, with which it might be conspecific (Yom-Tov *et al.* 1992). Synonyms: none. Chromosome number: not known.

Description Very small microbat without noseleaf and with tail more or less fully enclosed in interfemoral membrane; five upper cheekteeth (but often only four visible above gum), five lower cheekteeth and two upper incisors on each side; ears separated and short (ca. 9–11 mm); FA: 30–31 mm; dorsal pelage pale; dorsal and ventral hairs bicoloured; wings dark without white hind-border; lower molars myotodont; inner upper incisor unicuspid; profile of

forehead region of skull strongly concave. A poorly known species. Pelage not dense; mid-dorsal hairs 5–6 mm. Dorsal pelage pale pinkish-brown to pale greyish-cream, with underlying colour showing through; hairs blackish-brown at base. Ventral pelage slightly paler; hairs blackish-brown with pale greyish-cream at tip. Ears relatively short; inner margin convex; outer margin concave; tip rounded. Tragus length ca. one-third of E ($n = 1$); maximum breadth only a little less than length of anterior margin; anterior margin straight; posterior margin smoothly convex with distinct lobule at base; tip rounded (Figure 136d). Wings pale brown; no white hind-border. Interfemoral membrane pale brown; postcalcarea lobe very narrow; tail projecting slightly beyond edge of membrane. Penis relatively short. Baculum as in Figure 140c (Makin & Harrison 1988).

Skull small and gracile for an African *Pipistrellus*. Braincase of medium relative height and relatively narrow; interorbital region relatively narrow; rostrum flattened, of medium relative length and relatively narrow (Table 25, p. 603). Profile of forehead region (viewed laterally) strongly concave. No occipital helmet. Inner upper incisor unicuspid. Outer upper incisor about two-thirds length of inner upper incisor. Anterior upper premolar minute, sometimes not visible above gum, displaced lingually; canine and posterior upper premolar in contact. Lower molars myotodont. Dental formula: $\frac{2123}{3123} = 34$.

Geographic Variation None recorded.

Similar Species In Sudan and S Egypt, three other dark-winged *Pipistrellus* and one *Eptesicus* have lower molars myotodont; dorsal hairs bicoloured (Table 26, p. 606):

Pipistrellus capensis. Skull apparently larger (GLS: 12.0–15.4 mm; C–M³: 3.6–5.6 mm). Profile of forehead region of skull almost straight. Inner upper incisor weakly bicuspid before wearing. Anterior upper premolar absent. Widespread south of Sahara.

P. somalicus. Pelage only faintly bicoloured. Ventral pelage brown. Profile of forehead region of skull weakly concave. Outer upper incisor hardly higher than cingulum of inner incisor. Anterior upper premolar absent. More widely distributed (see Map).

P. guineensis. Ventral pelage dark rusty-brown. Inner upper incisor bicuspid. Anterior upper premolar absent.

Eptesicus bottae. Much larger (FA: 38–47 mm; GLS: 15.3–18.0 mm). Anterior upper premolar always absent.

Distribution In Africa, known with certainty only from two localities in Sudan (Koopman 1975, Qumsiyeh 1985), one in the Sahara Arid BZ and the other in the Sahel Savanna BZ. There is an unconfirmed sight record from Bir Kansisrob, Egypt (Sanborn & Hoogstraal 1955), which is not mapped. An Egyptian record mentioned by Gaisler *et al.* (1972) was found to represent *P. deserti* (Hill & Harrison 1987, Kock 1999). Extralimittally: Israel (Makin & Harrison 1988) and Jordan (Qumsiyeh *et al.* 1992).

Habitat The type locality is a valley (wadi) at ca. 670 m, in an area of gravel and stony desert incised by wadis that are dry except after heavy rain. The most southern record is from Rahad in Sudan



Pipistrellus ariel

(12° 45' N, 30° 40' E), in *Acacia* wooded grassland and deciduous bushland.

Abundance Apparently extremely rare (Harrison & Bates 1991).

Remarks Nothing else is known about this species.

Conservation IUCN Category: Data Deficient.

Measurements

Pipistrellus ariel

FA: 29.1 (30–31) mm, $n = 3$

WS: n. d.

TL: 69 (68–71) mm, $n = 3^*$

T: 32.3 (30–34) mm, $n = 3^*$

E: 9, 11 mm, $n = 2$

Tr: 3.8 mm, $n = 1$

Tib: 10, 15 mm, $n = 2$

HF: 5.2 (5–6) mm, $n = 3^*$

WT: n. d.

GLS: 11.1, 11.3 mm, $n = 2$

GWS: 6.8 mm, $n = 1^*$

C–M³ (alv.): 3.8, 4.1 mm, $n = 2$

Throughout geographic range in Africa (BMNH)

Specimens include the holotype and paratype, and one specimen from Rahad, Sudan

*Qumsiyeh 1985

Key References Hill & Harrison 1987; Qumsiyeh 1985; Thomas 1904a.

Victor Van Cakenberghe & Meredith Happold

Pipistrellus brunneus DARK-BROWN PIPISTRELLE

Fr. Pipistrelle brune; Ger. Dunkelbraune Zwergfledermaus

Pipistrellus brunneus (Thomas, 1880). Ann. Mag. Nat. Hist., ser. 5, 6: 165. Calabar, SE Nigeria.

Taxonomy Originally *Vesperugo* (*Vesperus*) *brunneus*. Traditionally *Eptesicus brunneus*. Subsequently classified as *P. (Neoromicia) brunneus* by Hill & Harrison (1987), *Nycterikaupius brunneus* by Menu (1987), *E. (Neoromicia) brunneus* by Koopman (1993), *P. (Neoromicia) brunneus* by Koopman (1994) and *Neoromicia brunneus* by Simmons (2005). Hoofer & Van Den Bussche (2003) allocated *brunneus* together with *rendalli* and *nanus* to a yet unnamed genus. Synonyms: none. Chromosome number (Cameroon): $2n = 36$; $aFN = 50$ (McBee *et al.* 1987). The karyotype does not fit the general *Eptesicus*-pattern, which is very conservative, but agrees with the more variable '*Pipistrellus*'-pattern, supporting an arrangement within *Neoromicia* (Hill & Harrison 1987, McBee *et al.* 1987).

Description Very small microbat without noseleaf and with tail more or less fully enclosed in interfemoral membrane; four upper cheekteeth, five lower cheekteeth and two upper incisors on each side; ears separated and short (9–15 mm); FA: 33–38 mm; wings blackish-brown without white hind-border; dorsal pelage dark; dorsal hairs unicoloured, ventral hairs bicoloured; lower molars myotodont; inner upper incisor unicuspid; profile of forehead region of skull weakly concave; posterior margin of tragus sharply angular. Sexes similar. Pelage dense, soft. Dorsal pelage varying from medium brown, reddish-brown to dark chocolate brown; hairs unicoloured. Ventral pelage shorter and paler; hairs blackish-brown with pale greyish-brown tips or medium-brown tips. Buccal glands sometimes very prominent. Ears blackish, subtriangular with rounded tip. Tragus length ca. 40% of E and broad; anterior margin short and straight; posterior margin with sharp angle giving tragus a diagonally truncated appearance (Figure 136a). Thumb comparatively long and slender for a *Pipistrellus*. Wing-membranes blackish-brown without white hind-border. Because wing colour was not mentioned in the type description, and because the wings of the holotype were bleached by preservative, *P. brunneus* was grouped with the pale-winged species (*P. rendalli*, *P. tenuipinnis*) (e.g. Rosevear 1965), but Koopman (1965) and De Vree (1971) showed that it is dark-winged. Bacular morphology: no information.

Skull large and robust for an African *Pipistrellus*. Braincase domed, relatively high but of medium relative breadth; interorbital region relatively narrow; rostrum of medium relative length and breadth (Table 25, p. 603). Profile of forehead region (viewed laterally) weakly concave. Sagittal and lambdoid crests very weakly developed; no occipital helmet. Inner upper incisor unicuspid (without accessory cusp at posterior base of tooth (cf. *P. rendalli*)). Outer upper incisor ca. one-quarter to one-third height of inner incisor (usually reaching only slightly above cingulum of inner incisor). Anterior upper premolar absent. Lower molars myotodont. Dental formula: usually $2^{113}/_{3123} = 32$.

Geographic Variation Apparently none.

Similar Species Five other African *Pipistrellus* have dark wings; unicoloured dorsal hairs; myotodont lower molars (Table 26, p. 606):

Pipistrellus grandidieri. Dorsal pelage pale brown. Ventral hairs unicoloured, yellowish. Posterior margin of tragus smoothly convex for most of its length. Inner upper incisor bicuspid. Anterior upper premolar sometimes present although not always visible above gum.
P. crassulus crassulus. Ventral pelage dark brown or reddish-brown; hairs unicoloured. Posterior margin of tragus smoothly convex for most of its length. Inner upper incisor bicuspid. Anterior upper premolar present although not always visible above gum.
P. crassulus bellieri. Posterior margin of tragus smoothly convex for most of its length. Inner upper incisor bicuspid. Anterior upper premolar present and visible above gum.
P. musciculus. Much smaller (FA: 23–26 mm; GLS: 10.3–11.4 mm). Posterior margin of tragus smoothly convex for most of its length. Inner upper incisor bicuspid.

Distribution Endemic to Africa. Recorded mainly from the Rainforest BZ (Western and West Central regions), but also recorded marginally from the Rainforest–Savanna Mosaic and, in Côte d'Ivoire, from the Guinea Savanna BZ. There are ca. 22 records from Sierra Leone, Liberia, Côte d'Ivoire, Ghana, SE Nigeria, Cameroon, Equatorial Guinea, Gabon (Cape Esterias; V. Van Cakenberghe pers. comm.) and DR Congo. Specimens from Nko, Nigeria in BMNH, published as *Eptesicus brunneus* by Sanderson (1939), Rosevear (1965), Hayman & Hill (1971) and Happold (1987), represent *P. rendalli* (De Vree 1973a, Hill & Harrison 1987). The only known specimen from the central Congo Basin (Lukolela, AMNH) was identified as *P. brunneus* by Koopman (1965). This record appears to be rather isolated and the specimen should be re-examined.

*Pipistrellus brunneus*

Habitat Apparently one of the most specialized rainforest vespertilionids, known almost exclusively from localities in undisturbed to slightly disturbed lowland rainforests. Within the Rainforest BZ, has been recorded mainly from both evergreen and semi-deciduous lowland rainforests, but also from swamp forest, and mangroves. Two other records are from riverine forest within the Rainforest–Savanna Mosaic (near Fintona, Sierra Leone) and from a relict forest within the Guinea Savanna BZ (Comoé N. P., Côte d'Ivoire). Although mostly found at low altitudes, a record from Bake River bridge, Cameroon, is located at ca. 1470 m in sub-montane forest.

Abundance Localized but apparently not rare in suitable habitat.

Adaptations No information.

Foraging and Food No detailed information. Presumably forages by slow-hawking (as in other *Pipistrellus*). In Tai N. P. and Comoé N. P., Côte d'Ivoire, mostly caught in harp-traps or mist-nets near small forest creeks and in elevated mist-nets 0–25 m above ground, in tree-fall gaps within the forest. Individuals were caught at a median height of 9 (1–21) m ($n = 9$) (J. Fahr unpubl.). Diet not known.

Echolocation No information.

Social and Reproductive Behaviour No information.

Reproduction and Population Structure Litter-size: one ($n = 1$). Reproductive chronology not known (data inconclusive). At 05° 50' N (Tai N. P., Côte d'Ivoire), 4 of 5 ♂♂ had scrotal testes between Feb and Mar; 1 of 1 ♀ was pregnant in late Sep; 1 of 1 was lactating in late Feb and one was lactating in early Mar, and 1 of 1 was neither lactating nor pregnant in late Aug (Lim & Van Coeverden de Groot 1997, J. Fahr unpubl.). At 05° 22' N (Banco N. P., Côte d'Ivoire) 1 of 2 ♀♀ was pregnant, the other was neither lactating nor palpably pregnant, and 2 of 2 ♂♂ had scrotal testes in mid-Sep. At 09° 40' N (near Fintonia, Sierra Leone), two lactating ♀♀ were collected in late Apr (total number of captured ♀♀ not known)

(USNM). In a sample of eight bats from Tai N. P., the ratio of ♂♂ to ♀♀ was 1 : 1.7, and in 15 museum specimens from West Africa, the ratio was 1 : 1.5.

Predators, Parasites and Diseases Ectoparasites include a bat-fly *Basilia echinata* (Diptera: Nycteribiidae) (Anciaux de Faveaux 1984).

Conservation IUCN Category: Near Threatened.

Apparently rare and only known from ca. 22 localities, mostly in the rainforest zone that is already, and to a large extent, degraded or destroyed. Major threats: loss and degradation of habitat as result of deforestation and agriculture. Population trend inferred to be declining.

Measurements

Pipistrellus brunneus

FA: 34.9 (33–38) mm, $n = 29$

WS (c): 237 (225–256) mm, $n = 5$

TL: 84.5 (76–94) mm, $n = 18$

T: 37.9 (33–46) mm, $n = 18$

E: 12.7 (9–15) mm, $n = 18$

Tr: 5.1 (4.8–5.5) mm, $n = 7$

Tib: 13.2 (12–15) mm, $n = 21$

HF: 8.0 (7.0–9.5) mm, $n = 22$

WT: 5.9 (4.0–9.0) g, $n = 22$

GLS: 13.5 (13.0–14.1) mm, $n = 25$

GWS: 8.9 (8.6–9.2) mm, $n = 21$

C–M³: 4.9 (4.6–5.3) mm, $n = 27$

C–M³ (alv.): 4.9 (4.4–5.5) mm, $n = 36^*$

Sierra Leone, Côte d'Ivoire, Ghana, Nigeria (incl. holotype), Cameroon, Equatorial Guinea (Rio Muni) (BMNH, FC, CM, RMCA, ROM, SMF, USNM, De Vree 1973a)

*Throughout geographic range (V. Van Cakenberghe pers. comm.)

Key References De Vree 1973a; McBee *et al.* 1987.

Jakob Fahr

Pipistrellus capensis CAPE PIPISTRELLE

Fr. Pipistrelle du Cap; Ger. Kap-Zwergfledermaus

Pipistrellus capensis (A. Smith, 1829). Zool. J. 4: 435. Grahamstown, Cape Province, South Africa.

Taxonomy Originally *Vespertilio capensis*. Traditionally *Eptesicus capensis*. Subsequently classified as *P. (Neoromicia) capensis* by Hill & Harrison (1987), *Nycterikaupius capensis* by Menu (1987), *E. (Neoromicia) capensis* by Koopman (1993), *P. (Neoromicia) capensis* by Koopman (1994) and *Neoromicia capensis* by Volleth *et al.* (2001), Kearney *et al.* (2002) and Simmons (2005). In contrast, Hooper & Van Den Bussche (2003), pending further study, restrict *Neoromicia* to *N. somalicus*. Synonyms: *damarensis*, *garambae*, *gracilior*, *nkatiensis*, *notius* and probably *melckorum* Roberts, 1919 (but not all material, see profile of *P. cf. melckorum*). Subspecies: none recognized here (see Geographic Variation). *Pipistrellus capensis* has long been a taxonomic problem. It has a very wide geographic range and shows considerable variation in colour and size. Whether this variation is indicative of different

species or races, or is ecologically induced, remains to be answered. Chromosome number (Zimbabwe, South Africa): $2n = 32$; $aFN = 50$ (Volleth *et al.* 2001, Kearney *et al.* 2002).

Description Very small microbat without noseleaf and with tail more or less fully enclosed in interfemoral membrane; usually with four upper cheekteeth (sometimes five but only four visible above gum), five lower cheekteeth and two upper incisors on each side; ears separated and short (8–15 mm); FA: 28–38 mm; wings dark, occasionally with narrow white hind-border; dorsal pelage pale to dark; dorsal and ventral hairs bicoloured; lower molars myotodont; inner upper incisor weakly bicuspid when not worn; profile of forehead region of skull straight to weakly concave. Sexes alike in colour; in

some localities, ♀♀ on average larger than ♂♂ e.g. in South Africa, FA (♀♀): 34.9 (32–38) mm, $n = 24$, FA (♂♂): 32.1 (30–35) mm, $n = 16$; GLS (♀♀): 14.1 (12.8–15.0) mm, $n = 24$, GLS (♂♂): 13.3 (12.2–14.5) mm, $n = 16$. Pelage soft, dense; mid-dorsal hairs 5–6 mm. Dorsal pelage very variable – pale yellowish-brown, pale greyish-brown, reddish-brown, and all shades of brown (from pale to dark brown); hairs with basal two-thirds dark brown or black. Some individuals paler around eyes and mouth; others with white-tipped hairs scattered through dorsal pelage. Ventral pelage white, whitish, cream or buff; hairs mostly bicoloured with basal three-fifths brownish-black or black, but some all-white hairs in pelvic region and adjacent to flight-membranes. Ears subtriangular with rounded tip. Tragus length ca. 45% of E; widest at middle or a little below; posterior margin smoothly convex for most of its length; tip rounded (Figure 136e). Wing-membranes yellowish-brown, greyish-brown or blackish-brown, occasionally with narrow white hind-border; dorsal pelage and membrane colours similar. Interfemoral membrane paler, more translucent, sometimes with yellowish border; transverse lines dark (cf. *Cistugo*). Tail 65–66% of HB (cf. *Cistugo* spp.). Baculum as in Figure 141a (Harrison & Hill 1987); variation in Kearney *et al.* (2002).

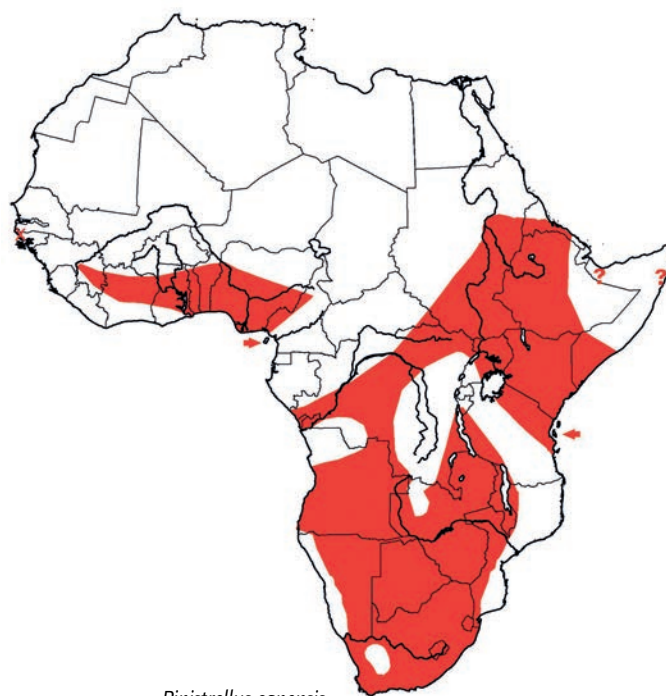
Skull comparatively large and robust for a *Pipistrellus*. Braincase relatively low but of medium relative breadth; interorbital region relatively narrow; rostrum of medium relative length and breadth (Table 25, p. 603). Rostrum sometimes with well-developed lateral depressions just above the infraorbital foramina as in *P. anchietae* and *P. inexpectatus*. Profile of forehead region (viewed laterally) straight to weakly concave. Occipital helmet (formed when the backward-pointing lambdoid crest and the posterior end of the sagittal crest are well developed) usually present, but specimens with little tooth-wear do not always have a helmet. With experience, the straight forehead and occipital helmet (if present) can be felt (without extracting skull) by stroking the head from rostrum to back of neck. Inner upper incisor almost always appears unicuspid, but is weakly bicuspid in specimens with very little tooth-wear. Outer upper incisor less than half height of inner incisor but reaching above its cingulum. Anterior upper premolar usually absent: reported present but minute, on one or both sides, in some specimens in northern part of distribution, but this condition is extremely unusual. Lower molars myotodont. Dental formula: usually $2^{113}/_{3123} = 32$.

Geographic Variation Koopman (1994) lists seven subspecies, of which one, *matroka* from Madagascar, is no longer included in *P. capensis* (Peterson *et al.* 1995), and another, *grandidieri*, is now considered a distinct species:

- P. c. capensis*: Eastern Cape Province.
- P. c. damarensis*: Angola and Zambia to Namibia and Botswana.
- P. c. garambae*: S Sudan and NE DR Congo.
- P. c. gracilior*: Mozambique to KwaZulu–Natal, South Africa.
- P. c. notius*: Western Cape Province.

Simmons (2005) also lists *P. c. nkatiensis* Roberts 1932 as a subspecies, without giving its distribution. Koopman (1994) points out that most West African populations have not been allocated to subspecies.

Similar Species One African *Eptesicus* and eight other African *Pipistrellus* also have dark wings; bicoloured dorsal hairs; myotodont



Pipistrellus capensis

lower molars; and have (or might have) distributions overlapping that of *P. capensis* (Table 26, p. 606):

- Pipistrellus ariel*. Skull apparently smaller (GLS: 11.1, 11.3 mm: C–M³: 3.8, 4.1 mm, $n = 2$). Profile of forehead region of skull strongly concave. Inner upper incisor always unicuspid; anterior upper premolar present but minute and sometimes not visible. Sahara Arid and Sahel Savanna BZs of Sudan and perhaps Egypt.
- P. cf. melckorum*. Forearm on average longer (37.1 [36–39] mm in karyotypically confirmed material, 35.3 [32–38] mm in non-confirmed material). Tail on average longer (39.6 [35–44] mm), $n = 5$). Inner upper incisor always unicuspid; molars more massive. Zambezi Woodland BZ.
- P. somalicus*. Hairs only inconspicuously bicoloured. Ventral pelage brown. Dorsal hairs often longer (5–8 mm). FA not >32 mm. No sagittal crest. In older animals with some tooth-wear, an occipital helmet is present but comparatively weakly developed. Profile of forehead region of skull weakly concave.
- P. zuluensis*. Dorsal hairs bicoloured or tricoloured. Ventral pelage pale greyish-brown. Braincase more inflated and globular; rostrum shorter and narrower; profile of forehead region weakly to moderately concave. Occipital helmet absent, therefore braincase smoothly rounded posteriorly. With experience, the globular braincase, concave forehead and lack of helmet can be felt without extracting the skull. Outer upper incisor ca. half height of inner incisor.
- P. anchietae*. Inner upper incisor bicuspid. Anterior upper premolar present but not visible above gum. No occipital helmet.
- P. inexpectatus*. Inner upper incisor bicuspid. Anterior upper premolar present although not visible above gum. Ventral pelage reddish-cream.
- P. guineensis*. Ventral pelage dark rusty-brown. Inner upper incisor bicuspid. Skull shorter, GLS: 10.7–11.8 mm.
- P. eisentrauti*. Inner upper incisor bicuspid. Anterior upper premolar usually present.

Eptesicus hottentotus. Much larger (FA: 45–54 mm; GLS: 16.9–21.5 mm).

Distribution Endemic to Africa. Recorded in at least some parts of all biotic zones south of the Sahara, from Guinea-Bissau to Ethiopia and southwards to South Africa; also Bioko I. and Zanzibar I. Not recorded from Western Region of Rainforest BZ and from much of West Central region, and probably absent from the arid Horn of Africa and most of the Namib Desert. Two unconfirmed reports from E Somalia are plotted as question marks. The gap in NE Angola, and the gap from C DR Congo through Tanzania to Mozambique, probably reflect insufficient sampling. Map based on data from V. Van Cakenbergh (pers. comm.).

Habitat Recorded in most vegetation zones south of Sahara, except large deserts and some coastal habitats. Often associated with human settlements.

Abundance Common; their success being assisted in more recent history by their use of man-made roosts.

Adaptations Aspect ratio low; wing-loading very low (M. Happold pers. comm.). Flight can be fairly slow and fluttering or sometimes faster; moderately manoeuvrable; turns by banking (minimum radius just under 50 cm) and only rarely by stalling-and-twisting; individuals could fly across a 1×1×1 m enclosure but could not fly more than one complete circuit/flight (8 bats, 10 flights each; M. Happold pers. comm.). Can take off from ground; cannot hover. Climbs and scuttles moderately well. Roosts by day in restricted cavities: e.g. under bark of trees, among leaves of aloes, in cracks or holes in plants and rocks, in ceilings, under roofs (including between sheets of corrugated iron) and in walls of buildings (Rosevear 1965, Smithers 1983). Sometimes roosts with *Scotophilus dinganii*. In South Africa, frequently active during winter and apparently does not enter prolonged periods of torpor (van der Merwe 1994a) although becomes torpid during day (even at 21–24 °C; Happold & Happold 1988) and sometimes remains torpid for a few days. Predicted mean maximum urine concentration comparatively high (4427 mOsmol/kg); captive bats, fed winged termites, sometimes did not drink for up to 3.5 days (Happold & Happold 1988). There are several glands on the face, above the eye, in the corner of the mouth, on either side of the muzzle and under the chin. In South Africa, these glands change seasonally, becoming more conspicuous and in some cases excreting a clear fluid, in Mar and Apr, which is the same time as mating occurs.

Foraging and Food Forages by slow-hawking in moderately clutter-free spaces including between trunks of trees, around and over canopies (but not at high altitudes) and clearings fairly close to vegetation; sometimes forages within a metre of canopy foliage (M. Happold pers. comm.). Attracted to concentrations of insects around vegetation, over water, over termite mounds when winged termites are emerging, and around lights. In such situations, flight characterized by swerving and jinking and some direct pursuits. Emerges at dusk; has several bouts of foraging per night, with peak activity at dusk and just before dawn. Activity reduced by moonlight, probably to reduce risk of predation. Tends not to fly in heavy rain and strong wind. Faeces, in wet/dry seasons in Zimbabwe, contained Coleoptera

(68/26%), Lepidoptera (18.5/7.4%), Hemiptera (6/0%), Diptera (6/5.4%) and Trichoptera (0/45%) (n = 40/13 bats) (Fenton *et al.* 1977, Fenton & Thomas 1980). Fenton & Thomas (1980) noted that *P. capensis* and *Nycticeinops schlieffeni* took more caddis-flies (Trichoptera) than other bats in the study area, and suggested this was related to their early emergence and canopy-associated foraging behaviour.

Echolocation Search-phase call-shape (Malawi) steep FM/QCF (QCF 'heel' sometimes missing, sometimes replaced by short shallow FM sweep) (Figure 118d). Intensity high; start-frequency 65–84 kHz; end-frequency 38–44 kHz (ten bats, 332 calls; M. Happold pers. comm.). In Zimbabwe, end-frequency 35 kHz (five bats; Fenton & Bell 1981). In South Africa, end-frequency 35–37 kHz (four bats in flight cage, 20 light-tagged; Aldridge & Rautenbach 1987, one bat in room, one bat in open; Taylor 1999a). In contrast, peak-frequency is similar in all three localities: 38–44 kHz (usually 39–41 kHz) (Malawi), 40 kHz (Zimbabwe), 38–40 kHz (South Africa). Call-duration: 3.5–8 ms.

Social and Reproductive Behaviour Earlier accounts indicated that this species roosts singly, which appears to be the case in natural roosts. Now, however, often found in buildings, roosting in mixed-sex groups of ca. 20 individuals.

Reproduction and Population Structure Litter-size (southern Africa, based on embryo counts): usually two, often three, occasionally one or four (van der Merwe 1994a). At 24° S (former Transvaal, South Africa), the reproductive chronology is usually restricted seasonal monoestry with spermatogenesis peaking in Mar–May; the first copulations in late Mar to early Apr; sperm storage by the ♀♀ and also additional copulations until ovulation and fertilization occur in second half of Aug; and parturition in late Oct to early Nov after gestation of ca. 12 weeks (van der Merwe 1994a). Rarely, pregnant ♀♀ have been found in Mar (Lynch 1989).

A ♂ and ♀ born in captivity were born hairless with eyes closed. Eyes started opening on Day 8 and were fully open by Day 11; bodies furred by Day 12. Born with forearms 36.0% (♀) and 36.8% (♂) of the adult length; forearms reached 87.5% (♂) and 85.8% (♀) of adult length by Day 38.

Predators, Parasites and Diseases Predators include Barn Owls *Tyto alba* (Dean 1975, Avery 1992), Pied Crows *Corvus albus* (Smithers 1983) and probably Bat Hawks *Macheiramphus alcinus* (Fenton *et al.* 1977). One of these bats was found in a spider's (*Nephila* sp.) web in Serengeti N. P., Tanzania (Verschuren 1965b). Ectoparasites include a bed-bug *Cacodmus villosus* (Hemiptera: Cimicidae); fleas *Echidnophaga gallinacea* (Siphonaptera: Pulicidae), *Araeopsylla scitula*, *Damfia grahamsi*, *Ischnopsylla emmina* (Siphonaptera: Ischnopsyllidae); bat-flies *Nycteribia schmidli*, *Basilia robusta* (Diptera: Nycteribiidae); ticks *Carios vespertilionis*, *C. confusus* (Acari: Argasidae); and a mite *Acanthophthirus capensis* (Acari: Myobiidae) (Anciaux de Faveaux 1984, Beaucournu & Kock 1996).

Conservation IUCN Category: Least Concern.

Measurements

Pipistrellus capensis

FA: 31.9 (28–38) mm, n = 268

TL: 85.1 (69–115) mm, n = 114
 T: 30.6 (25–38) mm, n = 63
 E: 11.3 (8–15) mm, n = 180
 Tr: 5.2 (3.3–7.2) mm, n = 176
 Tib: 11.6 (9–15) mm, n = 235
 HF: 7.1 (7–9) mm, n = 106
 WT: 6.0 (4.0–9.0) g, n = 69
 GLS: 13.5 (12.0–15.4) mm, n = 229

GWS: 8.9 (7.8–10.0) mm, n = 162
 C–M³ (alv.): 4.8 (3.6–5.6), n = 244
 Throughout geographic range (V. Van Cakenberghe pers. comm.)

Key References Fenton *et al.* 1977; Rosevear 1965; Smithers 1983.

Teresa Kearney

Pipistrellus crassulus BROAD-HEADED PIPISTRELLE

Fr. Pipistrelle à grosse tête; Ger. Breitköpfige Zwergfledermaus

Pipistrellus crassulus Thomas, 1904. Ann. Mag. Nat. Hist., ser. 7, 13: 206. Efulen [= Efulan], SW Cameroon.

Taxonomy Traditionally *Pipistrellus crassulus*. Subsequently classified as *P. (Pipistrellus) crassulus* by Hill & Harrison (1987) and Koopman (1993) and as *P. (Vansonia) crassulus* by Koopman (1994). Placed in collective group *Attalepharca* by Menu (1987), in *Hypsugo* by Heller *et al.* (1994), Volleth *et al.* (2001) and Simmons (2005), and in *Nycticeinops* by Hooper & Van Den Bussche (2003; as *eisentrauti*). Synonyms: possibly *bellieri*. This taxon was described as a subspecies of *P. eisentrauti* by De Vree (1972), then transferred to *P. crassulus* by Heller *et al.* (1994) (but see Koopman 1993, Koopman *et al.* 1995). It might be a valid subspecies (and is treated as such here), but it is probably a distinct species. For this reason, the descriptions, distributions, habitats and biology of the two taxa are given separately in each section of this profile. Chromosome number (*P. c. crassulus*, DR Congo): 2n = 30; aFN = 56 (Volleth *et al.* 2001). Chromosome number (*P. c. bellieri*): not known.

Description *Pipistrellus c. crassulus* is a very small microbat without noseleaf and with tail more or less fully enclosed in interfemoral membrane; five upper cheekteeth (but often only four visible above gum), five lower cheekteeth and two upper incisors on each side; ears separated and short (9–12 mm); FA: 28–32 mm; wings blackish-brown without white hind-border; dorsal and ventral hairs unicoloured; lower molars myotodont; inner upper incisor bicuspid; skull conspicuously broad and flattened, dorsal profile almost straight. Sexes similar. Pelage soft, dense; mid-dorsal hairs ca. 4–5 mm. Dorsal pelage dark brown or reddish-brown; hairs unicoloured. Ventral pelage same as dorsal; hairs unicoloured. Throat same colour as rest of ventral pelage. Ears blackish, rounded; 29–39% of FA (cf. *P. c. bellieri*). Tragus length ca. 35–45% of E; broadest at base of anterior margin; anterior margin straight, posterior margin smoothly convex with small basal lobe. Tail relatively longer than in *P. c. bellieri* (63 [57–67]% of HB). Wing- and interfemoral membranes dark blackish-brown, no white hind-border. Penis unusually long for a *Pipistrellus*. Baculum very long and slender, tip not bifid but simple, very small basal lobes in line with the extended bacular shaft in the vertical plane (Figure 140d; Hill & Harrison 1987); for variation see Heller *et al.* (1994).

Skull medium-sized and moderately robust for an African *Pipistrellus*. Braincase relatively low, broad and rounded; interorbital region relatively broad; rostrum low, of medium relative length but relatively broad (Table 25, p. 603). Profile of forehead region (viewed laterally) almost straight to weakly concave. Zygomatic arches slender (cf. *P. eisentrauti*). Sagittal and lambdoid crests weakly

developed; no occipital helmet. Inner upper incisor deeply bicuspid, very broad and robust. Outer upper incisor unicuspid, slender, ca. one-third to half height of inner incisor (cf. *P. c. bellieri*). Anterior upper premolar present but either not visible or only barely visible above gum, displaced lingually in recess between canine and posterior premolar, which are usually in contact or almost so. M³–M³: 5.8 (5.6–5.9) mm (cf. *P. c. bellieri*). Lower incisors trifold (not bifid as stated by Thomas 1904b and Aellen 1959). Lower molars myotodont. Dental formula: $^{2123}/_{3123} = 34$.

Pipistrellus c. bellieri is a very small microbat without noseleaf and with tail more or less fully enclosed in interfemoral membrane; five upper cheekteeth (usually all visible above gum), five lower cheekteeth and two upper incisors on each side; ears separated and short (E: 11–13 mm); FA: 28–33 mm; wings dark without white hind-border; dorsal pelage medium to dark brown; dorsal hairs unicoloured, ventral hairs bicoloured; lower molars myotodont; inner upper incisor bicuspid; profile of forehead region of skull straight to weakly concave. Sexes similar. Pelage mid-dorsal hairs ca. 3–4 mm. Dorsal pelage medium to dark (chocolate) brown; hairs unicoloured. Ventral pelage various shades of pale brown (including pale fawn, pale greyish-fawn); hairs bicoloured (*contra* De Vree 1972, Heller *et al.* 1994), bases medium to dark brown with pale tips. Colour of throat variable but usually paler and contrasting with rest of ventral pelage. Ears dark brown, broadly rounded, 41 (35–46)% of FA (cf. *P. c. crassulus*). Tragus length ca. 43–47% of E; broadest at mid-point; anterior margin straight or slightly convex; posterior margin smoothly convex with small basal lobe; tip rounded. Wing- and interfemoral membranes dark brown; wings without white hind-border. Tail relatively shorter than in *P. c. crassulus* (56 [52–65]% of HB). Penis unusually long for a *Pipistrellus*; dark grey with whitish tip and long, dark hairs. Bacular morphology not known.

Skull medium-sized and moderately robust for an African *Pipistrellus*. Braincase relatively high, rounded and broad; interorbital region relatively broad; rostrum of medium relative length but relatively broad (Table 25, p. 603). Rostrum comparatively larger and higher than in *P. c. crassulus*. Forehead elevated, inflated and profile (viewed laterally) is weakly concave to straight (Figure 137d). Sagittal and lambdoid crests weakly developed forming a weak occipital helmet. Inner upper incisor bicuspid. Outer upper incisor unicuspid, ca. half to two-thirds height of inner incisor. Anterior upper premolar medium-sized to small (but larger than in *P. c. crassulus*), visible above gum, displaced lingually but canine and posterior premolar usually

separated. M^3-M^3 : 6.1 (5.8–6.3) mm (cf. *P. c. crassulus*). Lower molars myotodont. Dental formula: $^{2123}/_{3123} = 34$.

Geographic Variation No subspecies are recognized by Koopman (1994) and Simmons (2005). However, *P. crassulus* contains two populations that are disjunct and sufficiently different in several characters and morphometrically to suggest that they represent distinct species. Pending confirmation of this, they are treated here as subspecies. For diagnostic characters, see Description.

P. c. crassulus: Cameroon, Congo, DR Congo, Sudan, Uganda, Kenya, Angola.

P. c. bellieri: Guinea, Liberia, Côte d'Ivoire.

Similar Species Three other African *Pipistrellus* have dark wings; unicoloured dorsal hairs; myotodont lower molars (Table 26, p. 606):

Pipistrellus grandidieri. Larger (FA: 33–38 mm; GLS: 14.2 [13.8–14.7] mm).

P. musculus. Smaller (FA: 23–26 mm; GLS: 10.3–11.4 mm). Ventral pelage dark umber brown; hairs unicoloured. Anterior upper premolar minute, often not visible.

P. brunneus. Ventral pelage paler, greyish-brown to medium brown; hairs bicoloured. Posterior margin of tragus angular so tragus appears truncated (Figure 136f). Inner upper incisor unicuspid; anterior upper premolar absent.

Distribution Endemic to Africa. Apparently restricted to the Rainforest BZ (Western, West Central, South Central and East Central regions), the adjacent Rainforest–Savanna Mosaic and the Afromontane–Afroalpine BZ. *Pipistrellus c. crassulus* is known from 11 localities in SW Cameroon, Congo (Majumba; MNHN, V. Van Cakenberghe pers. comm.), DR Congo, S Sudan, Uganda, W Kenya and NW Angola. Rosevear (1953) and Rahm (1966) listed this

species for the Cross R. region, Nigeria, but without specific locality or reference to specimens. A doubtful record from Niokolo-Koba N. P., Senegal (Verschuren 1986) needs confirmation and is not mapped here. *Pipistrellus c. bellieri* is known from only seven localities (within 54,000 km²) in the Rainforest BZ and Northern Rainforest–Savanna Mosaic of Guinea, Liberia and Côte d'Ivoire (Roche 1971 [as *P. nanulus*], De Vree 1972, Koopman 1989 [as *P. eisentrauti bellieri*], Lim & Van Coeverden de Groot 1997 [as *P. eisentrauti*], Hoofer & Van Den Bussche 2003 [as *Hypsugo eisentrauti*], J. Fahr unpubl.).

Habitat *Pipistrellus c. crassulus* has been recorded from lowland rainforest, swamp forest, coastal forest and montane forest, and from rainforest in the Rainforest–Savanna Mosaic such as Budongo, Bwamba and Sango Bay Forests in Uganda (LACM, ROM), and Kakamega and Rondo Forests in W Kenya (CM, ROM) (localities from V. Van Cakenberghe pers. comm.). Altitude of known localities 300–1600 m; majority of records between 800–1600 m. *Pipistrellus c. bellieri* is known only from rainforests between 70–600 m.

Abundance No detailed information. Seems to be rather localized but not uncommon in suitable habitat. In Tâi N. P. (Côte d'Ivoire), *P. c. bellieri* was the most frequently caught pipistrelle (J. Fahr unpubl.).

Adaptations One of the few African pipistrelles adapted for foraging in cluttered habitats (see below).

Foraging and Food Forages by slow-hawking, in cluttered habitats such as the understorey of forests. In Tâi N. P., 17 individuals were caught at heights of 1.5–3.4 m in mist-nets set 0–25 m above ground or in harp-traps set across or near small forest creeks. One was caught 20 m above ground in an elevated mist-net set in a tree-fall gap (J. Fahr unpubl.). According to these data, this bat seems to forage mostly in the understorey of the forest and along creeks. Diet not known.

Social and Reproductive Behaviour No information.

Reproduction and Population Structure Litter-size: one ($n = 7$). Reproductive chronology not known (data inconclusive). At 05° 50' N (Tâi N. P., Côte d'Ivoire), 6 of 7 ♀♀ were pregnant and 1 was lactating between late Feb and late Mar, 4 of 4 ♀♀ were nulliparous between late Aug and late Sep, and 1 of 1 ♀ was pregnant in early Oct; 4 of 5 ♂♂ had scrotal testes between late Feb and late Mar and 1 of 1 ♂ had scrotal testes in late Aug (no data for other months) (J. Fahr unpubl.). At 06° 56' N (Mt Peko N. P., Côte d'Ivoire), 1 of 2 ♂♂ had scrotal testes (4×2 mm) and the other had abdominal testes (2×1 mm) in Feb (ROM, Lim & Van Coeverden de Groot 1997). In a sample of 18 bats from Tâi N. P., the ratio of ♂♂ to ♀♀ was 1 : 2.

Predators, Parasites and Diseases Ectoparasites include a mite *Adentocarpus pipistrelli* (Acari: Chirodiscidae) on *P. c. crassulus* (Anciaux de Faveaux 1984).

Conservation IUCN Category: Least Concern.

The current assessment is based on a monotypic species. If the western population (*P. c. bellieri*) should be confirmed as a separate species, its restricted distribution within the already highly fragmented



and degraded rainforest region of Guinea, Liberia and Côte d'Ivoire would call for concern. The area of occupancy appears to be very small and the population trend can be inferred to be declining due to past and ongoing loss of habitat. Pending the taxonomic status of the species, a ranking as Vulnerable is proposed.

Measurements

Pipistrellus crassulus crassulus

FA: 30.2 (28–32) mm, n = 9
 WS (a): 199 mm, n = 1
 TL: 74.0 (70–81) mm, n = 7
 T: 28.6 (27–31) mm, n = 8
 E: 10.4 (9–12) mm, n = 8
 Tr: 4.1 (3.5–4.9) mm, n = 4
 Tib: 11.9 (11–13) mm, n = 5
 HF: 6.4 (5.9–7.0) mm, n = 9
 WT: 5.3 (4.0–7.0) g, n = 7
 GLS: 12.8 (12.5–13.2) mm, n = 5
 GWS: 9.1 (8.9–9.2) mm, n = 3
 C–M³: 4.5 (4.4–4.6) mm, n = 6
 C–M³ (alv.): 4.4 (4.2–4.7) mm, n = 20*
 Cameroon, Sudan, DR Congo, Uganda, Angola (BMNH [holotype], FMNH, LACM, SMF)
 *V. Van Cakenberghe (pers. comm.)

P. c. bellieri

FA: 30.5 (28–33) mm, n = 25
 WS (a): 209 (199–220) mm, n = 10
 TL: 79.0 (72–84) mm, n = 15
 T: 28.4 (25–32) mm, n = 15
 E: 12.4 (11–13) mm, n = 14
 Tr: 6.4 (5.6–7.0) mm, n = 4
 Tib: 11.9 (11–13) mm, n = 16
 HF: 6.4 (5.3–7.5) mm, n = 15
 WT: 6.0 (4.0–8.0) g, n = 23
 GLS: 12.9 (12.1–13.6) mm, n = 18
 GWS: 9.0 (8.4–9.5) mm, n = 17
 C–M³: 4.7 (4.5–5.0) mm, n = 19
 C–M³ (alv.): 4.6 (4.2–4.8) mm, n = 6*
 Guinea, Liberia, Côte d'Ivoire (AMNH, FC, MNHN, RMCA [holotype], ROM, SMF, USNM)
 *V. Van Cakenberghe pers. comm.

Key References De Vree 1972; Heller *et al.* 1994; Thomas 1904b.

Jakob Fahr

Pipistrellus deserti DESERT PIPISTRELLE

Fr. Pipistrelle du désert; Ger. Wüsten-Zwergfledermaus

Pipistrellus deserti Thomas, 1902. Proc. Zool. Soc. Lond. 2: 4. Mursuk [= Murzuq], Tripoli, Libya.

Taxonomy Traditionally *Pipistrellus deserti* (= *aegyptius*). Subsequently classified in the subgenus *Pipistrellus* by Hill & Harrison (1987), Koopman (1993, 1994) and Simmons (2005). Qumsiyeh (1985) suggested that *aegyptius* was the senior synonym of *P. deserti* and many authors, including Koopman (1993, 1994), used this name. However, Kock (1999) showed that *Vespertilio pipistrellus* var. *aegyptius* Fischer, 1829 should be considered a '*nomen dubium*', and he reinstated the name *Pipistrellus deserti*. Koopman (1975) indicated that the closely related *P. aero* Heller, 1912 might be conspecific with *deserti*, or that both *aero* and *deserti* might be dwarf forms of *P. kuhlii*. Molecular data suggest that *deserti* is probably a subspecies of *P. kuhlii* although both forms differ in size (P. Benda & M. Ruedi unpubl.) but, pending confirmation from further studies, it is retained here as a distinct species. Synonyms: probably *minuta* Loche, 1867 (which is considered a synonym of *P. kuhlii* by Simmons 2005 and a '*nomen dubium*' by Kowalski & Rzebik-Kowalska 1991) according to the rather uncertain description details given by Loche (1867). Subspecies: none currently recognized. Chromosome number: not known.

Description Very small microbat without noseleaf and with tail more or less fully enclosed in interfemoral membrane; five upper cheekteeth (but usually only four visible above gum), five lower cheekteeth and two upper incisors on each side; ears separated and short (7–13 mm); FA: 25–34 mm; dorsal pelage pale; dorsal and ventral hairs bicoloured; wings dark with white hind-border; lower molars nyctalodont; inner upper incisor unicuspid; forehead

region of skull moderately concave; outer upper incisor very small. A poorly known species. Sexes apparently similar in colour; ♀♀ on average slightly larger than ♂♂ in some body dimensions. Pelage texture and length: no information. Dorsal pelage varying from pale sepia brown (= olive-brown) to pale yellowish-brown, sometimes with greenish tint; hairs darker to almost black at base. Ventral pelage greyish or creamy-grey; hairs with dark grey at base. Ears pale buff, translucent, relatively short. Tragus length probably just under half of E, but very variable in preserved material; sickle-shaped; breadth constant for most of length; maximum breadth less than half the length of anterior margin; anterior margin concave (cf. *P. savii*); posterior margin smoothly convex; tip rounded. Wings dark brown with distinct white hind-border. Interfemoral membrane dark brown. Penis short. Baculum thin and long, arched dorsally in the median plane, with proximal bifurcation (Figure 139b; Hill & Harrison 1987).

Skull small but moderately robust for an African *Pipistrellus*. Braincase relatively high but of medium relative breadth; interorbital region of medium relative breadth; rostrum of medium relative length and breadth (Table 25, p. 603). Profile of forehead region (viewed laterally) moderately concave. No occipital helmet. Inner upper incisor unicuspid. Outer upper incisor usually less than half height of inner incisor, sometimes barely reaching above cingulum of inner incisor. Anterior upper premolar minute, usually not visible above gum; canine and posterior premolar usually in contact. Lower molars nyctalodont. Dental formula: $2^{123}/_{3123} = 34$.

Geographic Variation No subspecies currently recognized (e.g. Simmons 2005). Possibly, individuals from desert habitats in Algeria, Libya, Somalia and Sudan are larger on average than those from non-desert habitats in West Africa (Burkina, Ghana, Nigeria and Senegal), but data from West Africa are very limited.

Desert specimens. FA: 29.5 (25–34) mm, $n = 21$; GLS: 11.6 (10.8–12.4) mm, $n = 9$.

West African specimens. FA: 27.4 (25–30) mm, $n = 3$; GLS: 11.4 (11.1–11.7) mm, $n = 3$.

Similar Species Eight other *Pipistrellus* and *Eptesicus* occur in North Africa:

Pipistrellus ariel. Wings without white hind-border. Lower molars myotodont. Outer upper incisor about two-thirds length of inner upper incisor. S Egypt and Sudan.

P. savii. Larger (FA: 34–38 mm; GLS: 12.8–14.6 mm). Ears broader than their length. Wings without white hind-border. Lower molars myotodont.

P. kuhlii. Dorsal pelage dark sepia brown or dark brown. Forearm sometimes longer (32.8 [29–37] mm). Skull dimensions usually greater (GLS: 13.2 [12.3–13.8] mm; GWS: 8.5 [8.0–8.9] mm; C–M³: 4.8 [4.4–5.2] mm). Anterior lower premolar less reduced. Relative skull dimensions different (Table 25, p. 603).

P. pipistrellus. Wings without distinct white hind-border. Inner upper incisor bicuspid.

P. hanaki. Dorsal pelage brown to rusty-brown. Wings without distinct white hind-border. Inner upper incisor bicuspid. Outer upper incisor almost as high as inner incisor.

P. rueppellii. Mid-ventral pelage pure white; face and ears dark; throat sometimes pale rusty-brown.

Eptesicus (2 spp.). Larger (FA: 38–52 mm; GLS: 15.3–20.1 mm). Anterior upper premolar always absent. Lower molars myotodont.

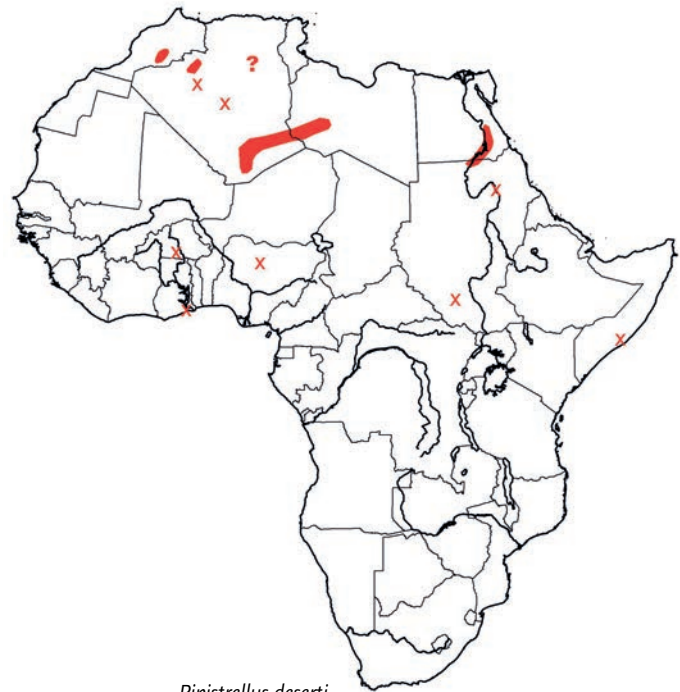
South of the Sahara, three other *Pipistrellus* also have lower molars nyctalodont and inner upper incisors unicuspid (see also Table 27, pp. 608):

P. aero. Dorsal pelage dark brown. Wings without white hind-border. Kenya and possibly Ethiopia.

P. hesperidus. Dorsal pelage greyish-brown, reddish-brown, dark brown or blackish. Wings without white hind-border. Very little overlap in distribution.

P. rusticus. Dorsal pelage reddish-brown to medium brown. Wings sometimes without white hind-border. Forehead region of skull straight to weakly concave. Distribution possibly only overlapping in West Africa, Sudan and Kenya.

Distribution Endemic to Africa. Appears to have a disjunct distribution with long-standing records in northern part of the Sahara Arid BZ in S Morocco, C and S Algeria, S Libya and in the Nile Valley in Egypt and N Sudan (Gaisler *et al.* 1972, Benda *et al.* 2004d), and a more recent record from the Somalia–Masai BZ in Somalia (unpublished museum record). Recently, specimens from non-desert habitats (mainly in the Sudan Savanna and Guinea Savanna BZs) in Burkina (Koopman *et al.* 1978), Ghana (Decher *et*



Pipistrellus deserti

al. 1997), Nigeria, S Sudan and possibly Senegal, have been identified as *P. deserti* (unpublished museum records). There are also records from the Somalia–Masai BZ in Kenya and Uganda (not mapped), but Koopman (1975) suggests these are probably erroneous and might represent *Pipistrellus nanus helios* (= *P. helios* or *P. cf. helios*) or *Pipistrellus somalicus*.

Habitat Mostly recorded from isolated localities in the most arid regions of the Sahara, where local conditions (e.g. oases) provide day-roosts and an adequate supply of insects (Happold 1984, P. Benda unpubl.). In Egypt and N Sudan, all records have been near the Nile R. where palm trees are present (Qumsiyeh 1985 as *P. aegyptius*). Qumsiyeh also reported that, elsewhere, it has been collected only in areas where palm trees occur, but possibly this is because both *P. deserti* and palms are species that inhabit desert oases. The more recent southern records (see above) indicate that *P. deserti* also occurs in Sudanian woodland including areas with abundant *Isoberlinia*, and perhaps in *Acacia–Commiphora* deciduous bushland and thicket. On the Accra Plains of Ghana, it was recorded in a mosaic of grassland and *Zanthoxylum–Capparis* thicket (Decher 1997, Decher *et al.* 1997).

Abundance Uncertain: probably rare. However, *P. deserti* was recorded as the most common species of bat in oases in S Libya (P. Benda unpubl.).

Adaptations Little is known. In Fezzan, Libya, roosts by day in abandoned buildings (P. Benda unpubl.). One colony, in an old mosque in the Gabroon oasis, occupied a narrow fissure between a wooden ceiling joist and a wall, and in other oases, it was found in fissures in a mud wall and between ceiling joists. There is an unconfirmed report that this species was also found in a tomb in Sudan (Hufnagl 1972). In Algeria, local people said that it roosts in hollow palm trees (Qumsiyeh 1985).

Foraging and Food In Egypt, ca. 100 individuals gradually appeared in a garden in Luxor during the evening while it was still light. They foraged for insects by slow-hawking 0.5–3 m above the ground. In Fezzan, S Libya, they were observed foraging from near ground level up to 10 m above ground in several surveyed oases (P. Benda unpubl.).

Echolocation Search-phase call-shape steep FM/QCF. Intensity high; start-frequency not known; end-frequency and peak-frequency 42–43 kHz (P. Benda pers. comm.). Very similar to echolocation calls of *P. kuhlii*.

Social and Reproductive Behaviour In Gabroon Oasis (see above), 15 members of a colony of ca. 30 individuals were adult or subadult ♀♀, suggesting they belonged to a maternity colony (P. Benda unpubl.). Several other roosts in Fezzan, S Libya, were occupied by single ♂♂. A sample of 16 from the aggregation in Luxor, comprised one ♂ and 15 ♀♀, of which 12 were lactating (Gaisler *et al.* 1972). This supports the suggestion that *P. deserti* forms maternity colonies.

Reproduction and Population Structure Litter-size and reproductive chronology not known. At 24°41'N (Luxor, Egypt) 12 of 15 ♀♀ captured between 26 Apr and 3 May were lactating (Gaisler *et al.* 1972).

Predators, Parasites and Diseases No information.

Conservation IUCN Category: Least Concern.

Measurements

Pipistrellus deserti

FA: 30.1 (25–34) mm, n = 40

WS: n. d.

TL: n. d.

HB: 43 (35–47) mm, n = 36

T: 34 (23–40) mm, n = 27

E: 10.8 (7–13) mm, n = 31

Tr: 4.6 (3.3–5.7) mm, n = 36

Tib: 10.2 (8–12) mm, n = 23

HF: 6.5 (6–8) mm, n = 27

WT (♂♂): 3.5 (2.0–4.0) g, n = 7

WT (♀♀): 3.7 (3.0–4.6) g, n = 15

GLS: 11.7 (10.8–12.4) mm, n = 37

GWS: 7.8 (7.4–8.2) mm, n = 27

C–M³ (alv.): 4.2 (3.7–4.6) mm, n = 37

Throughout geographic range (BMNH, CM, MHNG, NMP, ROM, USNM)

Key References Decher *et al.* 1997; Gaisler *et al.* 1972; Qumsiyeh 1985.

Victor Van Cakenberghe & Petr Benda

Pipistrellus eisentrauti EISENTRAUT'S PIPISTRELLE

Fr. Pipistrelle d'Eisentraut; Ger. Eisentrauts Zwergfledermaus

Pipistrellus eisentrauti Hill, 1968. Bonn. Zool. Beitr. 19: 45. Dikume-Balue, Rumpi Highlands, Western Province, Cameroon.

Taxonomy Traditionally *Pipistrellus eisentrauti*. Subsequently classified as *P. (Hypsugo) eisentrauti* by Hill & Harrison (1987) and Koopman (1993), *Pipistrellus eisentrauti* by Menu (1987), *P. (Pipistrellus) eisentrauti* by Koopman (1994). Based on the karyotype of one specimen from Rwanda (SMF 79444; 2n = 42; aFN = 58), *eisentrauti* was placed in *Hypsugo* by Volleth & Heller (1994), Heller *et al.* (1994), Volleth *et al.* (2001) and Simmons (2005). However, the Rwandan specimen is larger than any other known specimen of *P. eisentrauti* and is not considered here to represent *P. eisentrauti*. *Pipistrellus eisentrauti* formerly included *bellieri* (e.g. Koopman 1993, Koopman *et al.* 1995) but, following Heller *et al.* (1994), *bellieri* is provisionally included here in *P. crassulus* pending further investigation of its status. Based on mitochondrial DNA of one specimen from Côte d'Ivoire (ROM 100532), *eisentrauti* is tentatively placed in *Nycticeinops* by Hofer & Van Den Bussche (2003), but this specimen is considered here to represent *P. crassulus bellieri*. Chromosome number: not known.

Description Very small microbat without noseleaf and with tail more or less fully enclosed in interfemoral membrane; five upper cheekteeth (usually all visible above gum), five lower cheekteeth and two upper incisors on each side; small and short-eared for a vespertilionid (FA: 33–36 mm; E: 10–13 mm); wings dark without white hind-border; dorsal pelage dark; dorsal and ventral hairs bicoloured; lower molars myotodont; inner upper incisor bicuspid; posterior margin of tragus without sharp angle. Sexual dimorphism: no data. Pelage soft,

dense; mid-dorsal hairs 6–7 mm. Dorsal pelage dark, slightly reddish, brown; hairs described as unicoloured by Hill (1968), but the holotype (ZFMK 68.5) and one paratype (ZFMK 68.6) are bicoloured (J. Fahr pers. comm.), and a further five specimens (BMNH 84.1684–88) are also bicoloured. Another paratype (BMNH 67.2129) does have unicoloured dorsal pelage, but this specimen is not considered here to represent *P. eisentrauti* (see below). Ventral pelage slightly paler and more beige; hairs with blackish-brown at base. Ears blackish-brown, 34 (24–39)% of FA, n = 17; inner margin convex with small basal lobe, outer margin almost straight; tip rounded. Tragus length probably just under half of E but very variable in preserved material; broadest at mid-point; anterior margin almost straight except for slight basal concavity; posterior margin slightly and smoothly convex for most of its length; tip rounded. Wings and interfemoral membrane dark blackish-brown; wings without white hind-border. Baculum short and stout, base bilobed and tip widened, shaft broad and flattened dorsoventrally (Figure 140e, BMNH 84.1684; Hill & Harrison 1987).

Skull large and robust for an African *Pipistrellus*. Braincase of medium relative height and breadth; interorbital region relatively narrow; rostrum massive, deep, relatively long and broad (Table 25, p. 603). Supraorbital region expanded so dorsal surface of rostrum is roughly pentagonal in outline (cf. *P. inexpectatus*, *P. permixtus*). Braincase inflated frontally; profile of forehead region (viewed laterally) very weakly concave (almost straight). Sagittal crest very weakly developed; lambdoid crests weakly developed; no distinct

occipital helmet. Inner upper incisor long, bicuspid. Outer upper incisor unicuspid (but with a low lateral cingulum cusp), slender and small, ca. half to two-thirds the height of inner incisor (reaching almost the height of the posterior cusp of the inner incisor). Anterior upper premolar usually present, comparatively minute to medium-sized, usually visible above gum, displaced lingually into recess between canine and posterior premolar, which are almost in contact. Lower molars of the holotype and one paratype (ZFMK 68-5, 68-6), and two other specimens (BMNH 84.1684, 84.1686) are myotodont (no data for the other specimens in this series). Another paratype (BMNH 67.2129) is nyctalodont but, based on its more concave forehead and unicoloured dorsal pelage, it is not considered here to represent *P. eisenrauti*. Dental formula: $^{2123}/_{3123} = 34$.

Geographic Variation Apparently none.

Similar Species Five other African *Pipistrellus* have dark wings; bicoloured dorsal hairs; myotodont lower molars; and have (or might have) distributions overlapping that of *P. eisenrauti* (Table 26, p. 606):

Pipistrellus capensis. Inner upper incisor weakly bicuspid before tooth is worn, then unicuspid. Anterior upper premolar absent. Forehead region of skull usually straighter, although sometimes also weakly concave.

P. guineensis. Ventral pelage dark rusty-brown, sometimes speckled. Anterior upper premolar absent.

P. crassulus crassulus. Ventral hairs unicoloured. Forearm shorter (28–32 mm, $n = 9$). Skull notably flattened, braincase usually low, rostrum lower and less massive. Zygomatic arches comparatively slender; zygomatic width almost always less (9.1 [8.9–9.2] mm, $n = 3$).

P. musculus. Smaller (FA: 23–26 mm; GLS: 10.3–11.4 mm).

P. brunneus. Inner upper incisor unicuspid. Anterior upper premolar absent.

Distribution Endemic to Africa. Known (with certainty) only from the Afromontane–Afroalpine BZ of Cameroon. Records from DR Congo (Lukolela; AMNH 86916), Uganda (Kampala, BMNH 66.1171), Kenya (Kirono Forest, BMNH 78.951), Kenya (AMNH, CM) and Somalia (Varty & Hill 1988) do not sufficiently resemble the holotype and paratype of *P. eisenrauti* to be considered representatives of this species (V. Van Cakenberghe unpubl.).

Habitat The holotype was found in montane forest at 1100 m in the Rumpi Highlands, and the paratype (ZFMK 68.6) in montane forest at 1100 m on Mt Kupé. Also in the Cameroon Highlands, Fedden & Macleod (1986) mist-netted 26 individuals (including BMNH 84.1684–88 mentioned above). Of these, one was netted at 750 m, and nine were netted at 850 m, over stagnant pools in the dried-up beds of water-courses that flow torrentially only in the wet season and create natural flyways through the forest. Another two were netted over a running stream in an area of disturbed forest and cultivated land. Twelve others were netted over stagnant pools in montane forest (two at 1100 m and ten at 1500 m), another was netted over a stream running through forest at 1950, and one was mist-netted at 2235 m over the shore of a lake surrounded by forests that showed signs of disturbance. At this site, many bats were seen



Pipistrellus eisenrauti

flitting through the vegetation overhanging the lake and flying over the lake, but the only species netted were *P. eisenrauti* and *Miniopterus* sp. (referred to as *M. schreibersii*, but not likely to be this species).

Abundance Uncertain.

Remarks Some observations of reproductive condition were published by Fedden & Macleod (1986) but they are hard to interpret and are not conclusive. Apparently nothing else is known about the biology of this species.

Conservation IUCN Category: Data Deficient.

If restricted to Cameroon Highlands, the geographic range is very restricted and this species is probably threatened.

Measurements

Pipistrellus eisenrauti

FA: 34.0 (33–36) mm, $n = 11$

WS: n. d.

TL: n. d.

T: 32.6 (29–37) mm, $n = 10$

E: 11.6 (10–13) mm, $n = 10$

Tr: 4.0 (2.9–4.8) mm, $n = 10$

Tib: 12.5 (12–14) mm, $n = 11$

HF: n. d.

WT: 7.0, 8.3 g, $n = 2$

GLS: 13.9 (13.7–14.1) mm, $n = 3$

GWS: 9.4, 9.5 mm, $n = 2$

C–M³: 5.1 (4.8–5.3) mm, $n = 3$

Cameroon (BMNH, ZFMK)

Key References Fedden & Macleod 1986; Hill 1968.

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Pipistrellus grandidieri YELLOW PIPISTRELLE

Fr. Pipistrelle jaune; Ger. Gelbe Zwergfledermaus

Pipistrellus grandidieri (Dobson, 1876). Ann. Mag. Nat. Hist., ser. 4, 18: 500. Zanzibar.

Taxonomy Previously *Vesperugo* (*Vesperus*) *flavescens* Seabra, 1900. Traditionally *Eptesicus flavescens*. Subsequently classified as *P. (Neoromicia) flavescens* by Hill & Harrison (1987) and Koopman (1994), as *E. (Neoromicia) flavescens* by Koopman (1993) and as *Neoromicia flavescens* by Simmons (2005). Placed in collective group *Attalepharca* (Menu 1987). Hayman & Hill (1971) suggested that *P. flavescens* might be conspecific with *Pipistrellus melckorum*, but Koopman (1975, 1993, 1994) considers it to be a valid species. The holotype of *flavescens* was destroyed in a fire and subsequently many authors disregarded the original description of *flavescens* and relied on 'topotypes' at MNHN. However, these do not seem to represent the original *flavescens*: instead they appear to represent *P. capensis angolensis* (Hill & Carter 1941) and *flavescens* appears to be a *nomen dubium* and should be replaced by *grandidieri* (Thorn *et al.* 2007). Following Thorn *et al.* (2007), *grandidieri* is also the sole member of a newly created subgenus of *Pipistrellus*, *Afropipistrellus*. Synonyms: *angolensis*. Subspecies: two. Chromosome number: not known.

Description Very small microbat without noseleaf and with tail more or less fully enclosed in interfemoral membrane; four or five upper cheekteeth (but often only four visible above gum), five lower cheekteeth and two upper incisors on each side; ears separated and short (8–13 mm); FA: 33–38 mm; dorsal pelage pale; dorsal and ventral hairs unicoloured; wings dark, usually without white hind-border; lower molars myotodont, inner upper incisor bicuspid; profile of forehead region of skull almost straight. A poorly known species. Pelage silky with slight sheen; mid-dorsal hairs ca. 5–6 mm. Dorsal pelage pale brown; hairs unicoloured. Ventral pelage very slightly paler and usually yellowish; hairs unicoloured. Head with muzzle short, broad. Ears brown, subtriangular, relatively short. Tragus length ca. 60% of E in one freshly killed specimen but very variable in preserved material; broadest at mid-height; anterior margin straight; posterior margin smoothly convex with conspicuous basal lobe; tip rounded. Wings blackish-brown, slightly translucent, usually without white hind-border. Interfemoral membrane blackish-brown; tail fully enclosed by membrane. Baculum fairly straight, tapering to a slender distal tip, basally bifurcated, and the margins somewhat bent ventrally to form a half-pipe covering the urethra for the basal two-thirds. Laterally the shaft decreases apically in its diameter (Thorn *et al.* 2007).

Skull comparatively large and robust for an African *Pipistrellus*. Braincase of medium relative height and breadth; interorbital region of medium relative breadth; rostrum of medium relative length but relatively broad (Table 25, p. 603). Profile of forehead region (viewed laterally) weakly concave to almost straight. Occipital helmet sometimes present. Inner upper incisor bicuspid. Outer upper incisor almost as high as inner upper incisor. Anterior upper premolar minute, displaced lingually and sometimes not visible above gum, or absent; canine and posterior upper premolar in contact. Lower molars myotodont. Dental formula: $^{2113}/_{3123} = 32$ or $^{2123}/_{3123} = 34$.

Geographic Variation Two subspecies of *P. grandidieri* are recognized by Thorn *et al.* (2007).

Pipistrellus g. angolensis. Cameroon, Angola and Malawi.

P. g. grandidieri. East Africa and Burundi (and presumably Somalia and Zanzibar I., see below).

Similar Species Four other African *Pipistrellus* have dark wings; unicoloured dorsal hairs; myotodont lower molars (Table 26, p. 606):

Pipistrellus c. crassulus. Smaller (FA: 28–32 mm; GLS: 12.5–13.2 mm).

P. c. bellieri. Almost always smaller (FA: 28–33 mm; GLS: 12.1–13.6 mm). Ventral hairs bicoloured, various shades of pale brown. Guinea, Liberia, Côte d'Ivoire.

P. muscivulus. Much smaller (FA: 23–26 mm; GLS: 10.3–11.4 mm).

P. brunneus. Dorsal pelage reddish-brown to dark chocolate brown. Ventral hairs bicoloured. Posterior margin of tragus angular so tragus appears truncated. Inner upper incisor unicuspid. Anterior upper premolar absent.

Distribution Endemic to Africa. Known only from mostly isolated localities in the Rainforest BZ, Eastern Rainforest–Savanna Mosaic, Afromontane–Afroalpine BZ, Coastal Forest Mosaic BZ and Zambezian Woodland BZ. Recorded from Cameroon, Uganda, Burundi, Somalia, Zanzibar I., Angola and Malawi. According to Thorn *et al.* (2007), *P. grandidieri* has also been recorded from 04° 20' S, 39° 32' E on the southern coast of Kenya, and from 10 localities on or near the NE coast of Tanzania.



Pipistrellus grandidieri

Habitat Three specimens from Malawi were mist-netted over a pool in montane evergreen forest at the foot of Mulanje Mt and one was mist-netted over a stream in remnant riverine forest in a mosaic of farmland and wetter Zambezian miombo woodland on the Shire Highlands (Happold & Happold 1997). In Somalia, recorded in riverine forest in the Jubba Valley (Varty & Hill 1988 as *P. eisentrauti*). In Tanzania, recorded from lowland forest, secondary forest, undifferentiated riverine forest, forest edge and sub-montane forest at altitudes of 120–800 m: often netted near and over streams and a pond, and once netted in forest near a rocky outcrop (Thorn *et al.* 2007). The two localities in Angola are in the wetter miombo woodland zone, the Cameroon localities in the lowland rainforest zone and the Burundi locality in undifferentiated afromontane vegetation, but no habitat details are available for these records. Known altitudinal range: 120–1633 m.

Abundance Apparently rare to extremely rare throughout its range, but the taxonomy of this species is controversial and it might be more abundant than the records indicate.

Remarks One individual from Malawi had low aspect ratio and low wing-loading. It was only moderately manoeuvrable in flight; minimum radius of banked turns >50 cm; able to fly across a 1×1×1 m enclosure, but not able to fly a complete circuit. Able to take off from ground.

Pipistrellus guineensis GUINEAN PIPISTRELLE

Fr. Pipistrelle de Guinée; Ger. Guinea-Zwergfledermaus

Pipistrellus guineensis (Bocage, 1889). J. Sci. Math. Phys. Nat. Lisboa, ser.2, 1: 6. Bissau, Guinea-Bissau.

Taxonomy Originally *Vesperugo guineensis*. Traditionally *Eptesicus guineensis*. Subsequently classified as *Pipistrellus* (*Neoromicia*) *guineensis* by Hill & Harrison (1987) and Koopman (1993, 1994), and as *Neoromicia guineensis* by Simmons (2005). Horáček & Hanák (1986) indicate that *guineensis* might belong to *Hypsugo*. This species was called *pusillus* by Hayman & Hill (1971), but specimens of *P. somalicus* have also been identified as *pusillus* (Koopman 1975). The specific status of *guineensis* has been discussed by Rosevear (1962), Koopman (1965), Kock (1969a) and Lagen *et al.* (1974), but it is currently regarded as a valid species, closely related to *P. capensis* and *P. somalicus*. Synonyms: *rectitragus*. Subspecies: two. Chromosome number: not known.

Description Very small microbat without noseleaf and with tail more or less fully enclosed in interfemoral membrane; four upper and five lower cheekteeth and two upper incisors on each side; ears separated and short (6–12 mm); FA: 23–35 mm; dorsal pelage dark; dorsal and ventral hairs bicoloured; wings dark, sometimes with white hind-border; lower molars myotodont, inner upper incisor bicuspid; profile of forehead region of skull weakly concave. Sexes similar in colour: ♀♀ reported larger than ♂♂ by Koch-Weser (1984), but this was not evident from our data (unpublished museum material). Pelage soft and dense; mid-dorsal hairs 6–8 mm. Dorsal pelage dark rusty-brown; hairs much darker at base. Ventral pelage similar or slightly paler than dorsal pelage, sometimes speckled;

Conservation IUCN Category (as *P. flavescens*): Data Deficient.

Measurements

Pipistrellus grandidieri

FA: 35.4 (33–38) mm, n = 24

WS (a): 252 mm, n = 1

TL: 84.7 (81–90) mm, n = 13*

T: 31.7 (30–34) mm, n = 3

E: 10.8 (8–13) mm, n = 6

Tr: 4.4 (3.6–5.0) mm, n = 6

Tib: 13.4 (11–14) mm, n = 7

HF: 8, 10 mm, n = 2

WT: 7.4 (7.0–8.0) g, n = 3

GLS: 14.2 (13.8–14.7) mm, n = 7

GWS: 10.0 (9.7–10.1) mm, n = 4

C–M³ (alv.): 5.0 (4.7–5.2) mm, n = 10

Throughout geographic range (AMNH, CM, HC, MNHN, ROM, SMF, TM)

*Seabra (1900)

Key References Hill & Carter 1941; Thorn *et al.* 2007.

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hairs bicoloured. Rostrum short and slender. Ears dark greyish-brown, subtriangular, rounded at base, relatively short. Tragus length ca. 40% of E; broadest at mid-height; anterior margin concave; posterior margin without abrupt angle, but with small triangular lobe at base; tip rounded (Figure 136g). Wings dark greyish-brown, sometimes with narrow white hind-border. Interfemoral membrane dark greyish-brown; tail almost completely enclosed by membrane; postcalcareal lobe with convex border. Baculum as in Figure 141c (Hill & Harrison 1987).

Skull small and gracile for an African *Pipistrellus*. Braincase of medium relative height and breadth; interorbital region of medium relative breadth; rostrum low, relatively short and narrow (Table 25, p. 603). Profile of forehead region (viewed laterally) weakly concave (Figure 137c). No occipital helmet. Inner upper incisor large, bicuspid or conspicuously stepped. Outer upper incisor small, less than half height of inner incisor. Anterior upper premolar absent. Lower molars myotodont (M. D. Carleton pers. comm.).

Geographic Variation Two subspecies are recognized by Kock (1969a), Koopman (1994) and Simmons (2005):

P. g. guineensis: Senegal to Central African Republic. FA: 24–30 mm, n = 280; GLS: 10.7–11.8 mm, n = 22.

P. g. rectitragus: Ethiopia, S Sudan, NE DR Congo. FA: 26–31 mm, n = 26; GLS: 10.9–11.6 mm, n = 17.

Similar Species Six other African *Pipistrellus* also have dark wings; bicoloured dorsal hairs; myotodont lower molars; and have (or might have) distributions overlapping that of *P. guineensis* (Table 26, p. 606):

Pipistrellus capensis. Ventral pelage white, whitish or cream. Inner upper incisor weakly bicuspid before tooth is worn, then unicuspid. Skull longer (GLS: 12.0–15.4 mm).

P. inexpectatus. Ventral pelage reddish-cream; hairs unicoloured. Anterior upper premolar present although not visible above gum.

P. zuluensis. Dorsal hairs bicoloured or tricoloured. Ventral pelage pale greyish-brown. Inner upper incisor usually unicuspid. Geographic range might overlap in Uganda, S Sudan and Ethiopia.

P. ariel. Ventral pelage greyish-cream. Inner upper incisor unicuspid. Anterior upper premolar present although not always visible above gum.

P. somalicus. Mid-ventral pelage brown; hairs only faintly bicoloured. Inner upper incisor unicuspid or weakly bicuspid.

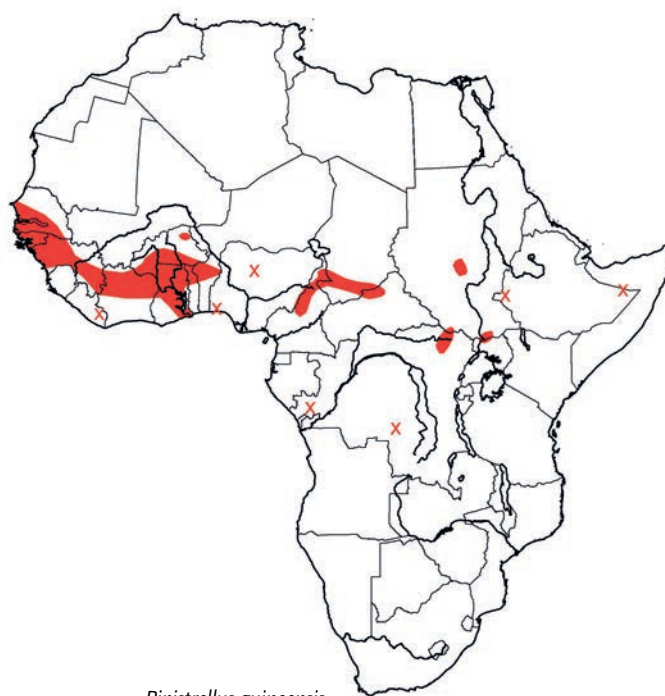
P. eisentrauti. Ventral pelage palish brown. Anterior upper premolar usually present and visible above gum.

Distribution Endemic to Africa. Recorded disjunctly mainly from the Sudan Savanna and Guinea Savanna BZs and the Rainforest–Savanna Mosaics, with some very marginal records in the Rainforest BZ and one isolated record in the Somalia–Masai Bushland BZ. Recorded from most countries from Senegal to Ethiopia and Somalia, and from Congo and DR Congo. Recently recorded from Ghana (Kock *et al.* 2002). Reports of *P. guineensis* (as *Eptesicus pusillus* and/or *E. guineensis*) in Angola (Hayman 1963, Feiler 1990) and Tanzania (Swynnerton & Hayman 1951) are more likely to refer to *P. somalicus* (Koopman 1975). Subsequently recorded for first time in Liberia by Monadjem & Fahr (2007).

Habitat In West Africa, apparently inhabits the various woodland savannas, reaching the coast where climate and vegetation permit, as on the Accra Plains (Ghana) and at Conakry (Guinea) (Decher *et al.* 1997). On the Accra Plains, two individuals were recorded near an artificial waterhole in a mosaic of grassland and thicket, and one was recorded amongst savanna trees near rocky cliffs. Others have been recorded in gardens (Koch-Weser 1984, Decher 1997). Thirty specimens for which data are available were recorded between 420 and 2166 m.

Abundance Uncertain. Rarely recorded.

Remarks Based on morphometric data, Fenton & Bogdanowicz (2002) suggest that this species forages by slow-hawking, possibly over water. Two lactating ♀♀ were recorded on 2 Nov 1991 at Yendi in the Northern Region of Ghana (Decher *et al.* 1997).



Pipistrellus guineensis

Conservation IUCN Category: Least Concern.
Geographic range comparatively large.

Measurements

Pipistrellus guineensis

FA: 27.7 (23–35) mm, n = 46

WS: n. d.

TL: 65.9 (60–72) mm, n = 5*

T: 27.8 (21–34) mm, n = 19

E: 9.2 (6–12) mm, n = 26

Tr: 3.8 (2.6–5.2) mm, n = 24

Tib: n. d.

HF: 7.7 (6–11) mm, n = 13

WT: 3.2 (2.0–5.0) g, n = 17

GLS: 11.3 (10.7–11.8) mm, n = 34

GWS: 7.3 (6.7–7.8) mm, n = 14

C–M³ (alv.): 3.8 (3.4–4.3) mm, n = 35

Throughout geographic range (AMNH, CM, FMNH, MHNG, MNHN, RMCA, SMF, USNM, ZFMK)

*Burkina (Koch-Weser 1984)

Key References Barboza du Bocage 1889; Decher *et al.* 1997; Koch-Weser 1984.

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Pipistrellus hanaki HANÁK'S PIPISTRELLE

Fr. Pipistrelle de Hanák; Ger. Hanáks Zwergfledermaus

Pipistrellus hanaki Hulva & Benda, 2004. Acta Chiropterologica 6: 207. Upper part of the Wadi Al Kuf (Jabal Akhdar Mts.), ca. 5 km south-west of Al Bayda, Al Jabal Al Akhdar District, 32° 44' N, 21° 41' E; ca. 495 m. Cyrenaica, Libya.

Taxonomy Formerly considered to represent *Pipistrellus pipistrellus* until recognized as a distinct species, belonging to the *Pipistrellus pygmaeus* genetic lineage, by Benda *et al.* (2004b) on the basis of morphology and genetics. Synonyms: *pipistrellus* of Hürka, 1982, Qumsiyeh & Schlitter 1982, Hanák & Elgadi 1984, Le Berre 1990, Amr & Qumsiyeh 1993 and others: see Benda *et al.* 2004b for complete list. Chromosome number: not known.

Description Very small microbat without noseleaf and with tail more or less fully enclosed in interfemoral membrane; five upper cheekteeth (all visible above gum), five lower cheekteeth and two upper incisors on each side; ears separated and short (11–13 mm); FA: 31–33 mm; wings dark with pale or translucent hind-border; dorsal pelage brown to rusty-brown; dorsal and ventral hairs bicoloured; lower molars nyctalodont; inner upper incisor bicuspid; profile of forehead region of skull moderately concave; posterior margin of tragus without sharp angle. Sexes similar. Pelage dense, soft; mid-dorsal hairs ca. 5 mm. Dorsal pelage brown to rusty-brown: hairs with basal half dark rusty-brown, terminal half pale brown to rusty-brown. Ventral pelage pale brown, moderately paler than dorsal pelage: hairs dark rusty-brown with terminal third umber brown. Naked skin of muzzle and around eyes dark brown. Ears dark brown, subtriangular with rounded tip. Tragus length ca. half of E; almost equally broad along most of its length; anterior margin rather straight, posterior margin smoothly convex with basal lobe; tip rounded. Wing and interfemoral membranes dark brown; wings with no hind-border or with a pale or translucent hind-border, but never with a distinct white hind-border (cf. *P. kuhlii*, *P. deserti*). Penis uniformly pale greyish-brown with a short, pale median stripe only on the most distal part of the foreskin (cf. *P. pipistrellus*). Baculum long, thin, bifurcated at both ends, ca. 1.8 mm long (Figure 139c; Benda *et al.* 2004b).

Skull medium-sized and moderately robust for an African *Pipistrellus*. Braincase relatively high and narrow; interorbital region relatively narrow; rostrum of medium relative length and breadth (Table 25, p. 603). Profile of forehead region (viewed laterally) moderately concave (Figure 137b). Occipital helmet almost absent; sagittal crest almost absent. Inner upper incisor bicuspid (posterior cusp ca. two-thirds height of main cusp). Outer upper incisor almost as high as inner incisor. Canines comparatively massive (cf. *P. pipistrellus*). Anterior upper premolar present, well developed, visible above gum, displaced linguallly; canine and posterior premolar not in contact. Lower molars nyctalodont. Dental formula $^{2123}/_{3123} = 34$.

Geographic Variation None.

Similar Species Seven other *Eptesicus* and *Pipistrellus* occur in North Africa (excluding *P. ariel* in S Egypt) (see also Table 26, p. 606):

Pipistrellus rueppellii. Mid-ventral pelage pure white; throat sometimes pale rusty-brown.



Pipistrellus hanaki

P. pipistrellus. Skull shorter (GLS: 11.5 [11.0–11.9] mm). Forearm on average shorter (FA: 29.6 [28–33] mm). Dorsal pelage darker and with greyish tinge. NW Africa (the Maghreb).

P. kuhlii. Wings with distinct white hind-border. Inner upper incisor unicuspid. Outer upper incisor much smaller than inner incisor.

P. deserti. Dorsal pelage pale sepia brown to pale yellowish-brown (sometimes with greenish tint). Wings with broad white hind-border. Inner upper incisor unicuspid. Outer upper incisor much smaller than inner incisor.

P. savii. Larger (FA: 34–38 mm; GLS: 12.8–14.6 mm). Anterior upper premolar minute, not visible above gum, sometimes absent. Lower molars myotodont.

Eptesicus (2 spp.). Larger (FA: 38–52 mm; GLS: 15.3–20.1 mm). Anterior upper premolar always absent. Dorsal pelage very pale brown.

Distribution Endemic to Africa. Known only from the Mediterranean Coastal BZ in the Cyrenaica region of Libya. Recorded from at least eight localities within this region (Benda *et al.* 2004b).

Habitat Recorded from Mediterranean shrubland from sea level to ca. 500 m, and from mosaics of shrubland and agricultural land (including pastures and fields). Has been found in wadis (ravines or valleys with flowing water in wet season) and highlands.

Abundance No information.

Remarks As yet, very little is known about the habits of this species. Its search-phase echolocation calls are steep FM/QCF sweeps with end-frequency (QCF component) and peak-frequency 45 kHz (as in *P. pipistrellus* from NW Africa).

Reproduction and Population Structure Litter-size: 2 ($n = 7$). Reproductive chronology not known. At 32–33°N (Cyrenaica, Libya), 7 of 8 ♀♀ were pregnant (near term) in late May, suggesting reproductive synchrony; no data for other months. The testes of seven adult ♂♂ captured between early Mar and early Apr ranged in size from 1.5 to 3.5 mm in length and 1.2 to 2.5 mm in width (Qumsiyeh & Schlitter 1982).

Predators, Parasites and Diseases Ectoparasites include bat-flies *Basilina mediterranea* and *B. daganiae* (Diptera: Nycteribiidae) (Hürka 1982, Amr & Qumsiyeh 1993).

Conservation IUCN Category: Data Deficient.

Distribution apparently restricted to ca. 3000–5000 km², which implies need for extreme conservation priorities. Consequently, Benda *et al.* (2004b) suggest that the IUCN Category should be Vulnerable.

Measurements

Pipistrellus hanaki

FA: 32.4 (31–33) mm, $n = 13^*$

WS: n. d.

TL: 44.7 (41–49) mm, $n = 11$

T: 36.9 (33–39) mm, $n = 11$

E: 12.0 (11–13) mm, $n = 11$

Tr: 5.2 (4.8–5.9) mm, $n = 11$

Tib: n. d.

HF: n. d.

WT: n. d.

GLS: 12.4 (12.1–12.7) mm, $n = 12^*$

GWS: 8.1 mm, $n = 1$

C–M³ (alv.): 4.4 (4.2–4.5), $n = 12^\dagger$

Throughout geographic range (NMP). GWS: holotype

*Benda *et al.* (2004b)

†V. Van Cakenberghe (pers. comm.)

Key Reference Benda *et al.* 2004b.

Stéphane Aulagnier & Petr Benda

Pipistrellus cf. helios SAMBURU PIPISTRELLE

Fr. Pipistrelle du Saburu; Ger. Samburu-Zwergfledermaus

Pipistrellus cf. helios auctorum non Heller, 1912. Smiths. Misc. Coll. 60 (12): 3. Merelle Water, 30 miles south Mt Marsabit, Kenya.

Taxonomy Formerly considered a subspecies of *P. nanus* (e.g. Koopman 1975, 1993). However, Hill & Harrison (1987) raised *helios* to specific status on the basis of its bacular morphology, and Peterson (1987) also indicated that *helios* is a distinct species. Behavioural differences between *P. helios* (O'Shea 1980, as *P. nanus*) and *P. nanus* (Happold & Happold 1990b, 1996) support this conclusion. Furthermore, the lower molars of specimens studied by Harrison & Hill (1987) are myotodont (unlike those of *P. nanus*, which are nyctalodont) and these specimens have glands on the interfemoral membrane (which are not present in *P. nanus*) (see details below). *Pipistrellus helios* was placed in *P. (Hypsugo)* by Hill & Harrison (1987) and, as a subspecies of *P. nanus*, was placed in *P. (Pipistrellus)* by Koopman (1993, 1994). It is placed in *Neoromicia* by Simmons (2005), as is *nanus* (as *Neoromicia nana*). Synonyms: none. Chromosome number: not known.

Since this profile was written, D. E. Wilson examined the holotype of *helios* and reported to Teresa Kearney (pers. comm.) that its lower molars are nyctalodont (as in *P. nanus*), and there were no glands on its interfemoral membrane. This indicates that the material on which this profile is based applies to another taxon that is referred to here as *P. cf. helios*. Specimens BMNH 69.207 and HZM 2.4086, referred to as *helios* by Hill & Harrison (1987), have myotodont lower molars and glands on the interfemoral membrane, and therefore are considered here to represent *P. cf. helios*: the lower molars of the third specimen referred to as *P. helios* by Harrison & Hill (1987) have not been examined. Voucher specimens for the studies by O'Shea (1980) have glands on the interfemoral membrane but it is not known if the lower molars are myotodont or not. Other specimens labelled *helios* in the BMNH (presumably identified by J. Edwards Hill) have myotodont

lower molars and most (but not BMNH 69.207) have glands on the interfemoral membrane (see below), and are therefore considered here to represent *P. cf. helios*. Based on lower molars, it is unlikely that both *cf. helios* and *nanus* belong to *Neoromicia*.

Description Very small microbat without noseleaf and with tail more or less fully enclosed in interfemoral membrane; five upper cheekteeth (usually all visible above gum), five lower cheekteeth and two upper incisors on each side; ears separated and short (5–11 mm); FA: 26–30 mm; dorsal pelage pale; dorsal hairs tricoloured; ventral hairs bicoloured; wings dark with white hind-border; lower molars myotodont; inner upper incisor bicuspid; profile of forehead region of skull strongly concave; posterior margin of tragus with abrupt angle; glands usually present on interfemoral membrane. Sexes similar in colour; ♂♂ on average larger than ♀♀. Pelage soft, dense; mid-dorsal hairs 5–7 mm. Dorsal pelage pale brown to pale yellowish-brown; hairs tricoloured with basal quarter blackish-brown, central half pale creamy-fawn, terminal quarter pale brown. Ventral pelage paler; hairs dark blackish-brown with pale brown at tip. Ears naked, pale brown with rounded tip; relatively short. Tragus length probably ca. half of E but very variable in preserved material; broadest above mid-height; hatchet-shaped (anterior margin slightly to distinctly concave, posterior margin with abrupt, obtuse angle above mid-height, tip rounded) (as in *P. tenuipinnis*, Figure 136c). Wings very dark brown to blackish with very narrow to moderate white hind-border. Interfemoral membrane semi-translucent and markedly paler than wings (cf. *P. nanus*). Most adults of both sexes have a pair of glands, 1.2–3.8 mm in diameter, one on each side of

the tail, on the proximal quarter of the interfemoral membrane; glands best seen when backlit and magnified. Baculum as in Figure 139c (Hill & Harrison 1987).

Skull small and gracile for an African *Pipistrellus*. Braincase relatively high but of medium relative breadth; interorbital region of medium relative breadth; rostrum relatively short and narrow (Table 25, p. 603). Profile of forehead region (viewed laterally) strongly concave. No occipital helmet. Inner upper incisor bicuspid and broad. Outer upper incisor reaching the posterior cusp of the inner incisor. Anterior upper premolar well developed, displaced lingually (occasionally only somewhat displaced), visible above gum; in some specimens this tooth is missing on one side. Lower molars myotodont. Dental formula: $^{2123}/_{3123} = 34$.

Geographic Variation No definite information. Thomas O'Shea (pers. comm.) observed *P. nanus*-like thatch-roosting bats with tail-glands, and leaf-roosting *P. nanus* without tail-glands living sympatrically in Côte d'Ivoire, which suggests that a form very similar to *P. cf. helios* occurs in West Africa. Furthermore, specimens of a myotodont *Pipistrellus* with hatchet-shaped tragus and glands on the tail (but bicoloured dorsal hairs) (BMNH 3.2.3.62 [Côte d'Ivoire], 11.1.22.5, 65.757, 65.758 [Ghana], 5.12.1.2-4 [Nigeria], labelled as *P. nanus*) might also indicate geographical variation and a much wider distribution for *P. cf. helios*, but this needs confirmation.

Similar Species None. Although some other African species of *Pipistrellus* have myotodont lower molars and bicuspid inner upper incisors (Table 26, p. 606), none of these have tricoloured dorsal hairs, hatchet-shaped tragus and paired glands on the interfemoral membrane.

Distribution Endemic to Africa. *Pipistrellus cf. helios* is mainly found in the Somalia–Masai Bushland BZ and Coastal Forest Mosaic BZ. Primarily distributed in Kenya (except NW corner and much of

the NE side), with an extension along the coast to Somalia and along the Jubba and Webi Shabeelle rivers in S Somalia. The type locality for true *P. helios* lies in this area. The range for *P. cf. helios* also extends westward into E and NE Uganda and extreme S Sudan, and as far as L. Victoria in Tanzania. There is an isolated record from Djibouti (Funaioli & Lanza 1968), which needs confirmation. The possibility that *P. cf. helios* (or a closely related form) occurs in West Africa is mentioned above. It is also possible that *P. cf. helios* (or a closely related form) occurs in the Kruger N. P., South Africa (see profile *P. nanus*).

Habitat In eastern Africa, widely recorded in dry habitats (*Acacia*–*Commiphora* deciduous bushland, mosaic of East African evergreen bushland and secondary *Acacia* wooded grassland, and semi-desert grassland and shrubland), but also recorded from East African coastal forest mosaic, *Isoberlinia* woodland, undifferentiated montane vegetation and mosaics of lowland rainforest and secondary grassland. Sixty-five specimens for which data are available were found between 400 and 1333 m.

Abundance Uncertain.

Adaptations At Masalani, near Kibwezi, Kenya, the roosting, foraging, social and reproductive behaviour and reproduction of *P. cf. helios* were studied by O'Shea (1980, as *P. nanus*) and O'Shea & Vaughan (1980, as *P. nanus*). Aspect ratio low; flight characteristics not known. Roosts by day, and also intermittently at night, between overlapping, vertically hanging fronds of palms *Phoenix reclinata*, in small crevices around the edges of roofs thatched with bundles of palm fronds, and in crevices in vertical sections of thatch used to cover walls. Becomes torpid during the day. The function of the glands on the interfemoral membranes of adults of both sexes is not known; in adult ♂♂, there was no correlation with testes size.

Foraging and Food Forages for small insects by slow-hawking 2–5 m above ground, frequently within 1 m of vegetation.

Echolocation Search-phase call-shape steep FM/QCF. Intensity high; start-frequency ca. 115 kHz; end-frequency 65 kHz (as in *P. nanus*) (n = ?; O'Shea & Vaughan 1980, as *P. nanus*).

Social and Reproductive Behaviour At Masalani, *P. cf. helios* roosted singly or in groups of 2–12; group-composition highly labile (O'Shea 1980). Prior to parturition in Nov, all ♀♀ left the study area, presumably to establish a maternity colony elsewhere. At other times, most adult ♂♂ roosted singly; others usually roosted with one ♀ or, less frequently, with two or more ♀♀. Adult ♀♀ usually roosted with one ♂; occasionally with other ♀♀ without a ♂. Adult ♂♂ almost never roosted with other ♂♂. Prime roost sites (large enough to accommodate a ♂ and one or more ♀♀) were scarce; ♂♂ showed roost-fidelity, competed aggressively for prime roosts and defended them by fighting intruders and by chasing them in flight. Males often carried scars and bite wounds. Activities in and near roosts occurred throughout the night: some bats rested; territorial ♂♂ patrolled outside their roosts and chased other ♂♂ away; ♀♀ flew along the roof, stopping to circle at roosts of ♂♂ and apparently choosing where to spend the day. Males vocalized at their roosts and ♀♀ were attracted to the most vocal ♂♂. Although



♀ ♀ roosted with several ♂ ♂ sequentially, they avoided roosting with most ♂ ♂ more than once, and roosted more frequently with certain others. These observations suggest that the mating system resembles one based on resource-defence polygyny.

Reproduction and Population Structure Litter-size: 2 (n = 16). At 02°18'S (Masalani, inland Kenya), reproductive chronology is restricted seasonal monoestry, with births in Nov, lactation until late Dec or early Jan. No evidence of testicular activity until Mar, when testes descended; they remained descended (scrotal) from Apr through Sep. Copulation not observed but assumed to occur from May to Aug (when ♂ ♂ were most vocal at their roosts). Ovulation and fertilization assumed to occur in late Aug (O'Shea 1980).

Sex ratio at birth not known (cf. *P. nanus*). Overall ratio of ♂ ♂ to ♀ ♀ in the resident population at Masalani was 2 : 1. A seasonal phase of dispersal occurred in late May to mid-Jun, when some adult bats left and others joined the population.

Predators, Parasites and Diseases Predators include Heart-nosed Bats *Cardiaderma cor* and probably arboreal snakes (especially *Psammodphis* sp.), which were found in thatch near the roost sites (O'Shea 1980). Ectoparasites include a bat-fly *Basilia ansifera* (Diptera: Nycteribiidae) (Theodor 1956).

Conservation IUCN Category: Data Deficient.

Measurements

Pipistrellus cf. *helios*

FA: 28.0 (26–30), n = 75

WS (c): 196.0 (180–210) mm, n = 6

TL: 69.3 (60–75) mm, n = 29

T: 30.1 (26–34) mm, n = 41

E: 8.1 (5–11) mm, n = 57

Tr: 3.6 (2.4–5.5) mm, n = 71

Tib: 9.9 (8–12) mm, n = 72

HF: n. d.

WT: 3.4 (2.0–6.0) g, n = 38

GLS: 11.0 (10.4–11.4) mm, n = 73

GWS: 7.0 (6.6–7.4) mm, n = 32

C-M³ (alv.): 3.8 (3.5–4.5) mm, n = 73

Throughout geographic range (AMNH, BMNH, CM, HZM, MZUF, NAU, ROM, USNM, ZFMK). Includes measurements of some *P. helios* as well as *P. cf. helios*

Key References Heller 1912; Hill & Harrison 1987; O'Shea 1980; O'Shea & Vaughan 1980.

Meredith Happold & Victor Van Cakenberghe

Pipistrellus hesperidus DUSK PIPISTRELLE

Fr. Pipistrelle hespéride; Ger. Abendstern-Zwergfledermaus

Pipistrellus hesperidus (Temminck, 1840). Monographies de Mammalogie ou description de quelques genres de mammifères, dont les espèces ont été observées dans les différents Musées de l'Europe, 2: 211. Type locality given by Temminck (1840) as 'the shores of the Red Sea towards the coasts (or at the side of) Abyssinia', a topographic description not definitely identifiable (Kock 2001) but likely to be the coast of Eritrea (not the coast of Ethiopia, and not Shewa province as indicated by Simmons 2005).

Taxonomy Originally *Vespertilio hesperida*. Synonyms: *broomi*, *fuscatus*, *subtilis*. Subspecies: uncertain (see Geographic Variation). Until recently, this species was considered as *Pipistrellus kuhlii*, although Göpfert *et al.* (1995) and Volleth *et al.* (2001) had shown that specimens from Europe and North Africa have a different chromosome number (2n = 44) to specimens from southern Africa and Madagascar (2n = 42). Awaiting further description, southern African and Malagasy specimens were called *P. 'cf. kuhlii'* as a way of distinguishing this taxon from Palearctic *P. kuhlii*. Kock (2001b) reinstated the name *Pipistrellus hesperidus* for sub-Saharan populations, which he identified as a species distinct from *P. kuhlii* on morphological and parasitological characters.

Description Very small microbat without noseleaf and with tail more or less fully enclosed in interfemoral membrane; five upper cheekteeth (usually all visible above gum), five lower cheekteeth and two upper incisors on each side; ears separated and short (9–15 mm); FA: 29–38 mm; wings palish or dark without white hind-border; dorsal pelage various shades of brown but not rusty-brown; dorsal and ventral hairs bicoloured; lower molars nyctalodont, inner upper incisor unicuspid; profile of forehead region of skull moderately concave; posterior margin of tragus without sharp angle. Not easily distinguished from *P. rusticus*. Sexes similar. Pelage dense, soft; mid-

dorsal hairs ca. 5 mm. Dorsal pelage variable – some individuals paler (greyish-brown or reddish-brown), others darker (dark brown to almost black); hairs with basal three-fifths blackish-brown or black, therefore either faintly or conspicuously bicoloured. Ventral pelage cream, creamy-orange, orangey-red, reddish-brown or dark brown (pale when dorsal colour is pale and vice versa); hairs with basal three-fifths dark brown or blackish-brown. Ventral pelage not noticeably paler in pelvic region; no all-white hairs there. Naked skin of muzzle and around eyes is dark brown. Ears dark reddish-brown, subtriangular with rounded tip. Tragus length ca. half of E; widest just below mid-height; anterior margin almost straight; posterior margin smoothly convex with small basal lobe; tip rounded. Wing-membrane colour pale brown (when pelage is pale) to blackish-brown (when pelage is dark); no white hind-border. Interfemoral membrane paler than wing-membranes. Baculum as in Figure 139d (Kearney *et al.* 2002).

Skull medium-sized and moderately robust for an African *Pipistrellus*. Braincase relatively high but of medium relative breadth; interorbital region of medium relative breadth; rostrum relatively long but of medium relative breadth (Table 25, p. 603). Dorsal margin of orbit slightly but obviously inflated – viewed dorsally, the upper rim of the orbit bulges outwards (cf. straight in *P. kuhlii*). Profile of forehead region (viewed laterally) moderately concave. Rostral emargination

comparatively wide and U-shaped (cf. *P. kuhlii*). Inner upper incisor unicuspid, without posterior basal cusp (Kock 2001b). Outer upper incisor less than half height of inner incisor but reaching above its cingulum. Anterior upper premolar present, medium-sized to minute, usually visible above gum, within tooththrow to fully displaced lingually; canine and posterior premolar well separated or in contact. Posterior upper molar large, comparatively broad with a long third ridge and a wide gap between protocone and metacone (cf. *P. kuhlii*) (Kock, 2001b). Lower molars nyctalodont. Dental formula: $^{2123}_{3123} = 34$.

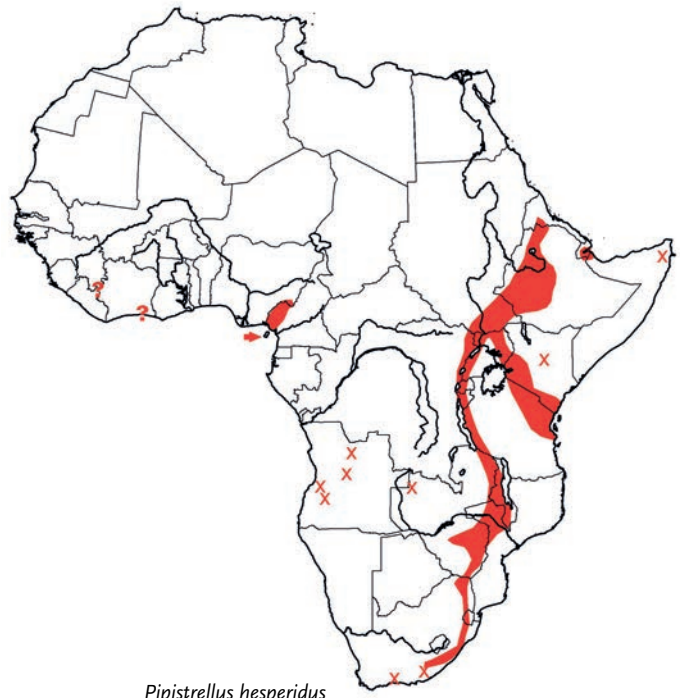
Geographic Variation The distinction of subspecies and allocation of many populations to subspecies still remains uncertain and requires further investigation (Koopman 1994, Kock 2001b). Koopman (1994) tentatively recognized two subspecies within the geographic range of *P. hesperidus*: *fuscatus* (East Africa) and *subtilis* (south-east Africa); Simmons (2005) also recognizes these subspecies. In contrast, Kock (2001b) tentatively recognized *fuscatus* (East Africa) and *broomi* (south-east Africa). Kock (2001b) did not examine or identify any *subtilis* but he indicates that the definition and differentiation of *subtilis* from other species in the group containing *P. hesperidus* and *P. kuhlii* is still uncertain. Differences in size between specimens from East Africa and those from elsewhere in the geographic range of *P. hesperidus* are very slight.

Similar Species South of the Sahara, three other *Pipistrellus* also have lower molars nyctalodont and inner upper incisors unicuspid (Table 27, p. 608):

- Pipistrellus. aero.* Interfemoral membrane and wings alike in colour and translucency. Kenya and possibly Ethiopia.
- P. deserti.* Dorsal pelage pale sepia brown to pale yellowish-brown (sometimes with greenish tint). Wings with white hind-border. Distribution possibly only overlapping in West Africa, Sudan and Kenya.
- P. rusticus.* Dorsal pelage paler, more orange, and shorter. Profile of forehead region of skull straight to weakly concave. Wings sometimes with white hind-border.

Distribution Endemic to Africa. Recorded mainly from the eastern side of Africa, and mainly in the Somalia–Masai Bushland, Afromontane–Afroalpine, Coastal Forest Mosaic and Zambeian Woodland BZs, with one record in the South-West Cape BZ. Also recorded from the Zambeian Woodland BZ in Angola and W Zambia, and from the Rainforest BZ (Western and West Central Regions) in West Africa (although at least some of the specimens from West Africa might represent *P. crassulus bellieri*; J. Fahr pers. comm.).

Habitat Found in diverse habitats including lowland rainforest, montane forests, mosaics of montane forest and grassland and other montane vegetation, coastal forests, *Acacia–Commiphora* bushland and miombo woodland; never far from open water, and often in association with human settlements. In the north-east of its geographic range, recorded at sea level in Djibouti (Pearch *et al.* 2001) but also from 1800 to 3000 m in the Ethiopian Highlands (Largen *et al.* 1974). In Malawi, recorded mainly in montane forests, miombo woodland, farmlands with riverine and/or relict rainforests: from 800 to 2300 m; not recorded below 500 m (Happold & Happold 1997). In South Africa,



Pipistrellus hesperidus

recorded from most bioregions (although largely absent from Drier and Moist upland, Highland and Montane regions; Taylor, P. 1998).

Abundance Common in certain areas, while uncommon and localized at others.

Adaptations Aspect ratio low; wing-loading very low (M. Happold pers. comm.). Flight slow but acrobatic. Roosts by day in cracks in rock (including narrow cracks in exfoliating granite), behind loose bark of dead trees, in hollow trees, under roofs, and in crevices of buildings (Smithers & Wilson 1979, Rautenbach 1982, Happold *et al.* 1987). In Malawi, becomes torpid during day at ambient temperatures 21–24 °C (Happold & Happold 1988). Predicted mean maximum urine concentration comparatively high (4168 mOsmol/kg) (Happold & Happold 1988).

Foraging and Food Forages by slow-hawking in moderately cluttered spaces including between tree trunks, around and over canopies, over grass or dirt roads, in clearings, around houses (probably to pursue insects attracted to lights) and near water. Flight very acrobatic especially when pursuing insects that are concentrated in swarms or near lights. Emerges and begins foraging at dusk and remains active for several hours after sunset, with a smaller peak in activity at dawn (Rautenbach 1982).

Echolocation Search-phase call-shape (Malawi) steep FM/QCF (QCF 'heel' varies in duration). Intensity high; start-frequency 63–86 kHz; end-frequency 44–50 kHz; peak-frequency 45–50 kHz (usually 46–48 kHz); call-duration 2–7 ms (depending on duration of QCF 'heel') (26 bats, free-flying or tethered, 956 calls; M. Happold pers. comm.). In Zimbabwe, frequencies from 85 to 45 kHz were emitted by four bats flying in lighted room or veranda (Fenton 1975 as *P. kuhlii*). In South Africa, start-frequency (mean \pm S.D.) 65.7 \pm 5.3 kHz; end-frequency 48.7 \pm 0.4 kHz; peak-frequency

50.3 ± 0.4 kHz; call-duration 3.5 ± 0.5 ms (six bats, free-flying; Taylor 1999a).

Social and Reproductive Behaviour Roosts in groups of up to 12 individuals. Observed foraging in groups (Kingdon 1974, Rautenbach 1982, T. Kearney unpubl.). Mixed-sex groups of 2–10 have been mist-netted – the audible (to humans) calls of the first one caught would bring the others buzzing around the mist-net, in which case they were sometimes also caught (Kingdon 1974, T. Kearney unpubl.).

Reproduction and Population Structure Litter-size (Malawi, South Africa): usually two, rarely one (Rautenbach 1982, T. Kearney unpubl., M. Happold pers. comm.). Reproductive chronology uncertain. At 15–16°S in Malawi, 9 of 9 adult ♀♀ were not palpably pregnant, lactating or post-lactating in May–Jun; no data Jul–Sep; 14 of 17 were pregnant, two were lactating and one was reproductively inactive in Oct–Nov; 8 of 8 were lactating in Dec; no data Jan–Feb; 2 of 3 were post-lactating and one reproductively inactive in Mar–Apr. Volant young in Dec–Mar. These data are consistent with restricted seasonal monoestry with births in Nov–Dec at the beginning of the wet season (M. Happold pers. comm.). In South Africa, 4 of 4 ♀♀ were pregnant in Oct–Nov; 13 of 13 were not pregnant in Dec, Mar and May. Scrotal ♂♂ recorded only from Feb–Jun.

Predators, Parasites and Diseases Predators include Fiscal Shrikes *Lanius collaris* in Kenya (Schwan & Hikes 1979) and Little Sparrowhawks *Accipiter minullus* in South Africa (Kemp & Rautenbach 1987). Ectoparasites include bed-bugs *Cacodmus villosus* and *C. sparsilis* (Hemiptera: Cimicidae); a flea *Ischnopsyllus emminus* (Siphonaptera:

Ischnopsyllidae); and a bat-fly *Basilia robusta* (Diptera: Nycteribiidae) (Anciaux de Faveaux 1984, Kock *et al.* 1998b, Kock 2001b [host given as *P. rusticus*, re-identified as *P. hesperidus* by V. Van Cakenberghe]). In *P. kuhlii*, the bed-bug is replaced by *Cacodmus vicinus* and the flea by *Ischnopsyllus octactenus* (Kock 2001b).

Conservation IUCN Category: Least Concern.

Measurements

Pipistrellus hesperidus

FA: 32.5 (29–38) mm, n = 248

WS (a): 232.0 (217–262) mm, n = 31*

TL: 78.0 (70–87) mm, n = 47*

T: 32.0 (24–40) mm, n = 90

E: 11.4 (9–15) mm, n = 110

Tr: 4.8 (2.8–6.3) mm, n = 106

Tib: 11.7 (10–14) mm, n = 122

HF: 6.8 (5–9) mm, n = 80

WT: 5.7 (3.5–8.0) g, n = 50

GLS: 12.8 (11.6–13.7) mm, n = 87

GWS: 8.5 (7.7–9.2) mm, n = 72

C–M³: 4.6 (4.2–5.1) mm, n = 95

Throughout geographic range (AMNH, BMNH, CM, FMNH, HC, HZM, MNHN, RMCA, SMF, TM, USNM, YPM, ZFMK, ZMUC, ZMMU, V. Van Cakenberghe pers. comm.)

*Malawi only (M. Happold pers. comm.)

†Malawi and South Africa only

Key References Kock 2001b; Rautenbach 1982.

Teresa Kearney

Pipistrellus inexpectatus AELLEN'S PIPISTRELLE

Fr. Pipistrelle d'Aellen; Ger. Unerwartete Zwergfledermaus

Pipistrellus inexpectatus Aellen, 1959. Arch. Sci. Phys. Nat. Genève 12: 226. Ngaouyanga, Upper Benoue [= Benue] Valley, Cameroon.

Taxonomy Traditionally *Pipistrellus inexpectatus*. Subsequently classified as *P. (Pipistrellus) inexpectatus* by Hill & Harrison (1987), *Nycterikaupius inexpectatus* by Menu (1987), *P. (Hypsugo) inexpectatus* by Koopman (1993) and *P. (Pipistrellus) inexpectatus* by Simmons (2005). Hill & Harrison (1987) placed *inexpectatus* in the *kuhlii* group of the subgenus *Pipistrellus*, implying close relationship between *inexpectatus* and *kuhlii*. Furthermore, the holotype of *inexpectatus* was originally considered to represent *P. marginatus*, a name now considered to be a synonym of *P. kuhlii*. Often spelled *inexpectatus*, but this is incorrect. Synonyms: none. Chromosome number: not known.

Description Very small microbat without noseleaf and with tail more or less fully enclosed in interfemoral membrane; five upper cheekteeth (but only four visible above gum), five lower cheekteeth and two upper incisors on each side; ears separated and short (10–13 mm); FA: 31–33 mm; dorsal pelage dark; dorsal hairs bicoloured, ventral hairs unicoloured; wings dark with white hind-border; lower molars myotodont, inner upper incisor bicuspid; profile of forehead region of skull weakly concave to almost straight. A poorly known

species. Dorsal pelage bright reddish-brown to dark brown; hairs with basal half blackish-brown. Ventral pelage reddish-cream; hairs darker at base. Ears brown, tip rounded; relatively short. Tragus length probably just under half of E but very variable in preserved material; broadest above mid-height; maximum breadth ca. one-third length of anterior margin; anterior margin concave as in Figure 136i (Rosevear 1965) or straight; posterior margin more or less smoothly convex with pronounced basal lobule; tip broadly rounded. Wings brown with distinct white hind-border. Interfemoral membrane paler than wings; tail extending slightly beyond membrane; postcalcarea lobe present but hardly visible. Bacular morphology not known.

Skull medium-sized but robust for an African *Pipistrellus*. Braincase relatively low but of medium relative breadth; interorbital region relatively narrow; rostrum of medium relative length and breadth (Table 25, p. 603). The rostrum has a well-developed lateral depression just above the infraorbital foramina (De Vree 1972) as in *P. anchietae* (J. E. Hill in Rautenbach *et al.* 1985) and some *P. capensis* (T. Kearney pers. comm): this character has not been checked in other species. Supraorbital region not so expanded that the dorsal

surface of the rostrum assumes a pentagonal outline (cf. *P. eisenrauti*). Profile of forehead region (viewed laterally) weakly concave to almost straight. No occipital helmet. Inner upper incisor long, bicuspid and straight; outer upper incisor small, approximately half the height of the inner incisor. Anterior upper premolar minute, almost always not visible above gum; canine and posterior premolar in contact. Lower molars myotodont. Dental formula: $^{2123}/_{3123} = 34$.

Geographic Variation None recorded.

Similar Species Four other African *Pipistrellus* also have dark wings, bicoloured dorsal hairs and myotodont lower molars, and have (or might have) distributions overlapping that of *P. inexpectatus* (Table 26, p. 606):

Pipistrellus capensis. Inner upper incisor weakly bicuspid before tooth is worn, then unicuspid. Anterior upper premolar absent. Ventral pelage white, whitish or cream.

P. guineensis. Ventral pelage dark rusty-brown, sometimes speckled; hairs bicoloured. Anterior upper premolar absent.

P. somalicus. Dorsal and ventral hairs only faintly bicoloured; ventral pelage brown with darker brown bases. Inner upper incisor unicuspid or weakly bicuspid. Outer upper incisor hardly higher than cingulum of inner incisor. Anterior upper premolar absent.

P. eisenrauti. Ventral pelage palish brown. Wings without white hind-border. Dorsal surface of rostrum roughly pentagonal in outline.

Distribution Endemic to Africa. Known from the Guinea Savanna BZ and the Northern Rainforest–Savanna Mosaic in Sierra Leone, Ghana, Benin, Nigeria and Cameroon. There are some specimens from elsewhere that have, at some time, been identified with *P. inexpectatus* (and sometimes with *P. eisenrauti*), but their identities are still controversial and provisionally they are not considered here to represent *P. inexpectatus*. These include specimens from DR Congo (Lukolela; AMNH 86916), Uganda (Kampala, BMNH 66.1171), Kenya (Kirono Forest, BMNH 78.951), Kenya (AMNH, CM). A specimen from Sudan, recorded as *P. inexpectatus* by Aellen (1959), is too young to be identified (Koopman 1975). According to E. Thorn, D. Kock & J. Cuisin (pers. comm.), specimens from Kenya in the CM belong to another species, altogether different from both *P. inexpectatus* and *P. eisenrauti*.

Habitat The type locality is Guinea woodland (Rosevear 1965), in a valley of the Upper Benue R. in Cameroon. No detailed descriptions of habitat seem to be available.

Remarks Very little is known about this species. The only reproductive data available refer to a single lactating ♀ recorded in September at ca. 1° S in Uganda (Bwindi Forest) (Kityo & Kerbis 1996). However, no voucher specimen was referenced or any



Pipistrellus inexpectatus

information on identifying characters. In view of the erroneous identifications from that area (see Distribution), the animal's identity could not be confirmed and therefore its locality is not mapped.

Conservation IUCN Category: Data Deficient.

Measurements

Pipistrellus inexpectatus

FA: 32.0 (31–33) mm, n = 6

WS: n. d.

TL: 83 mm*

T: 31.1 (30–33) mm, n = 3

E: 11.0 (10–13) mm, n = 5

Tr: 4.8 (4.5–5.1) mm, n = 5

Tib: 12.4 (11–14) mm, n = 6

HF: 6 mm, n = 1*

WT: 3.8 (3.0–4.0) g, n = 4

GLS: 12.6 (12.5–12.6) mm, n = 5

GWS: 8.0 (7.7–8.3) mm, n = 5

C–M³ (alv.): 4.5 (4.4–4.6) mm, n = 5

Throughout geographic range (ROM, USNM)

*Aellen 1952 (as *P. marginatus*)

Key References Aellen 1959; Hill & Harrison 1987; Koopman 1993; Koopman *et al.* 1995.

Victor Van Cakenberghe & Meredith Happold

***Pipistrellus kuhlii* KUHL'S PIPISTRELLE**
Fr. Pipistrelle de Kuhl; Ger. Weißbrandfledermaus

Pipistrellus kuhlii (Kuhl, 1817). Die Deutschen Fledermäuse. Hanau, p. 14. Trieste, Italy.

Taxonomy Originally *Vespertilio kuhlii*. Traditionally *Pipistrellus kuhlii*. Subsequently classified as *P. (Pipistrellus) kuhlii* by Hill & Harrison (1987), Koopman (1993, 1994) and Simmons (2005), and *Pipistrellus kuhlii* by Menu (1987) and Volleth *et al.* (2001). Until recently, *P. kuhlii* was considered to be a very stable and well-defined species, represented in North Africa by the form *kuhlii* and south of the Sahara by several forms, including *fuscatus* and *broomi*, which differed in a number of small details (e.g. wings without white hind-border). Then specimens from North Africa and Europe were found to have a different chromosome number ($2n = 44$) to that of specimens from southern Africa and Madagascar ($2n = 42$) (Rautenbach *et al.* 1993, Göpfert *et al.* 1995, Volleth *et al.* 2001), and the latter were sometimes referred to as *P. cf. kuhlii*. Kock (2001b) reinstated the name *Pipistrellus hesperidus* for most of the sub-Saharan forms (see species profile). Consequently, this profile deals only with *P. kuhlii* in North Africa. The specific name is sometimes spelled *kuhli*, *kühli* or *kühlii*, but *kuhlii* is the original spelling (Bogdanowicz & Kock 1998). Synonyms in Africa: *marginatus*, *pallidus* and possibly *minuta* (but *minuta* is considered here more likely to be a synonym of *P. deserti*). Subspecies: pending further analysis, none recognized here (see Geographic Variation). *Pipistrellus deserti* is considered to be a subspecies of *P. kuhlii* by P. Benda & M. Ruedi (unpubl.) but, pending confirmation, *deserti* is tentatively retained here as a distinct species. Chromosome number: $2n = 44$, aFN = 50 (Volleth *et al.* 2001).

Description Very small microbat without noseleaf and with tail more or less fully enclosed in interfemoral membrane; five upper cheekteeth (but sometimes only four clearly visible above gum), five lower cheekteeth and two upper incisors on each side; ears separated and short (8–15 mm); FA: 29–37 mm; wings dark with white hind-border; dorsal pelage dark to pale; dorsal and ventral hairs bicoloured; lower molars nyctalodont; inner upper incisor unicuspid; profile of forehead region of skull moderately to weakly concave; posterior margin of tragus without sharp angle; outer upper incisor very small. Not easily distinguished from *P. deserti*. Sexes similar. Pelage soft, dense, fairly fluffy; mid-dorsal hairs 5–7 mm. Dorsal pelage varying from pale yellowish-brown, sepia brown (= olive brown) to dark rusty-brown; hairs bicoloured, dark brown or dark greyish-brown at base. Ventral pelage same as dorsal pelage or paler and greyer; hairs blackish-brown at base. Ears brown to blackish-brown, subtriangular; tip rounded. Tragus length ca. half of E but very variable in preserved material; broadest just below mid-height; anterior margin almost straight, posterior margin smoothly convex; tip rounded. Wings blackish-brown with white or pale hind-border, which varies in width (see Geographic Variation). Interfemoral membrane blackish-brown, brown or pale brown. Baculum strongly curved with bifurcations both distally and proximally (Figure 139e; Hill & Harrison 1987).

Skull medium-sized and moderately robust for an African *Pipistrellus*. Braincase of medium relative height but relatively narrow; interorbital region relatively narrow; rostrum relatively long but of medium relative breadth (Table 25, p. 603). Profile of forehead

region (viewed laterally) moderately to weakly concave. Dorsal margin of orbit not inflated, therefore, viewed dorsally, upper rim of orbit is straight (cf. *P. hesperidus*). No occipital helmet. Rostral emargination comparatively narrow and V-shaped (cf. *P. hesperidus*). Inner upper incisor large, unicuspid but with a posterior basal cusp. Outer upper incisor very small, less than half height of inner incisor but reaching above its cingulum. Anterior upper premolar extremely small, hardly visible above gum, usually displaced lingually; canine and posterior premolar in contact. Posterior upper molar large, comparatively narrow with a short third ridge and a short distance between protocone and metacone (cf. *P. hesperidus*) (Kock, 2001b). Lower molars nyctalodont. Dental formula: $^{2123}/_{3123} = 34$.

Geographic Variation Based on pelage colour and the width and colour of the hind-border on the wing, three 'colour forms' (not taxa) can be recognized in North Africa (P. Benda pers. obs.):

Desert populations from oases of C Algeria and Libya (ca. 100–300 km inland). Dorsal pelage pale yellowish-brown; hind-border white, very broad (6–8 mm) and restricted to arm-wing.

Coastal populations widespread in North Africa from Egypt to Algeria (at least) and extraliminally in the eastern Mediterranean (Syria, Lebanon, Turkey, Greece). Dorsal pelage sepia brown (= olive brown); hind-border white, narrower (1 mm) and extending along entire posterior edge of the wing.

Populations in N Morocco (and extraliminally Spain). Dorsal pelage dark rusty-brown (as in *P. pipistrellus*); hind-border pale (not white), extremely narrow (maximum 0.3 mm) and restricted to arm-wing.

According to Lewis & Harrison (1962), colour variation is clinal in the extralimital E Mediterranean region, and also varies according to habitat, desert-living populations being much paler than those from along the Mediterranean coast. Gaisler *et al.* (1972) found both dark and pale individuals in the same locality (Abu Rawash, Egypt), but this variation might represent age differences – young animals being darker than adults.

Similar Species Seven other *Pipistrellus* and *Eptesicus* occur in North Africa (excluding *P. ariel* in S Egypt):

Pipistrellus deserti. Dorsal pelage pale sepia brown to pale yellowish-brown, sometimes with greenish tint (i.e. similar to *P. kuhlii* in geographically close desert populations but not similar to *P. kuhlii* from elsewhere); FA sometimes shorter (30.1 [25–34] mm). Skull dimensions usually smaller (GLS: 11.7 [10.8–12.4] mm; GWS: 7.8 [7.4–8.2] mm, C–M³: 4.2 [3.7–4.6] mm). Anterior upper premolar more reduced.

P. savii. Ears broader than their length. Wings without white hind-border. Inner upper incisor bicuspid. Anterior upper premolar not visible above gum or absent. Lower molars myotodont.

P. pipistrellus. Wings without distinct white hind-border. Skull shorter (GLS: 11.0–11.9 mm). Inner upper incisor bicuspid. Outer upper incisor almost same height as inner incisor (or at least as high as its secondary cusp).

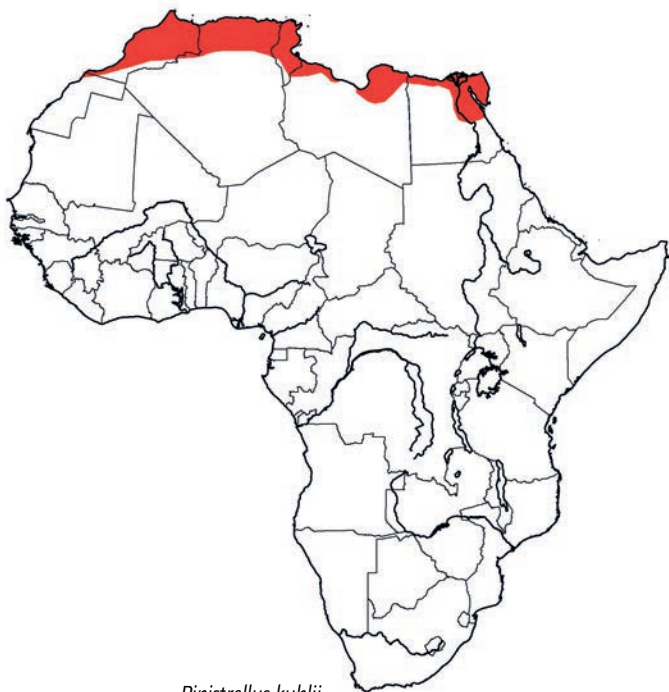
P. hanaki. Wings without distinct white hind-border. Inner upper incisor bicuspid. Outer upper incisor almost same height as inner upper incisor.

P. rueppellii. Mid-ventral pelage pure white; face and ears dark; throat sometimes pale rusty-brown.

Eptesicus (2 spp.). Larger (FA: 38–52 mm; GLS: 15.3–20.1 mm). Anterior upper premolar always absent.

Distribution In Africa, now considered to occur only in the Mediterranean Coastal and Afromontane–Afroalpine BZs and in the northern fringes of the Sahara Arid BZ, from Morocco to Egypt. Most records are north of 30°N. Records from Sahara Arid BZ south of 30°N in Algeria, and along the Nile Valley from C Egypt to N Sudan, are considered here to represent *P. deserti*. These include records from S Algeria, which Kowalski & Rzebik-Kowalska (1991) suggested might represent *P. deserti*. Previously thought to occur over a large part of Africa, but sub-Saharan specimens are now considered to represent *P. hesperidus* (Kock 2001b): so too are specimens from the Red Sea coast to Djibouti. Extralimittally: Mediterranean and Central Europe, S and C Ukraine as far north as Kiev, through Near East (including Arabian Peninsula) and through Caucasus to Kazakhstan, Afghanistan, Pakistan and SW Asia.

Habitat Widespread in the northern African vegetation zones bordering the Mediterranean Sea, and extending southwards to the northern fringes of the Sahara; recorded from sea level to 1500 m (in the Anti-Atlas Mts). In Algeria, often seen flying in towns and villages, often mist-netted (usually over water) in forests (including those in Atlas Mts) and in sparser vegetation, and common in oases in the northern Sahara (Kowalski & Rzebik-Kowalska 1991). Similarly,



very common in Mediterranean region of Morocco, Tunisia and Libya, and the most common species (and sometimes the only species) in the northern Saharan oases and in the Nile Delta in Egypt (P. Benda pers. obs.). In Egypt, occurs in deserts near cultivated areas, but not in Egyptian oases (Gaisler *et al.* 1972), and is commonly found around populated areas in N Egypt (Qumsiyeh 1985).

Abundance *Pipistrellus kuhlii* is one of the most common species of bats in the most northern parts of North Africa – possibly the most common.

Adaptations Flight speed of hunting bats (Eastern Europe) 4.0–4.5 m/sec (Schnitzler *et al.* 1987). The two colour types found in Abu Rawash (Egypt) by Gaisler *et al.* (1972) indicated to these authors that *P. kuhlii* might be a migratory species. However, this has not been confirmed – the different colours might be the result of age variation, and the records might include two age cohorts. Day-roosts include cracks and crevices in buildings (Anderson 1902).

Foraging and Food Forages by slow-hawking in comparatively open habitats (Barak & Yom-Tov 1989). At Oran in Algeria, activity is bimodal. The first peak begins soon after the bats emerge from their day-roosts (usually a little before sunset) and ends soon after sunset. A second, less marked, peak occurs around sunrise and the last individuals return to their roosts in full morning light (Kowalski & Rzebik-Kowalska 1991). In Israel, *P. kuhlii* hunts insects attracted to street lights but, unlike the insects, the bats never fly closer than 1.5 m to the lights (for unknown reasons). Some individuals hunt singly or in groups of 2–3, but the majority hunt in groups of 4–5, possibly because the echolocation calls of this number of bats disturb the insects sufficiently to cause them to disperse away from the lights – which makes them easier to catch (Barak & Yom-Tov 1989). On several occasions in North Africa, groups of *P. kuhlii* were observed flying together at sunset, but it was not clear if this represented group-hunting or swarming after emergence from the day-roosts (P. Benda pers. obs.). Faeces, collected in Israel, contained Lepidoptera, Coleoptera (Scarabaeidae, Dytiscidae and Curculionidae), Diptera (Chironomidae and Tipulidae), Hymenoptera (Formicidae), Hemiptera (Lygaeidae), Homoptera (Delphacidae and Cicadellidae) and Neuroptera (Feldman *et al.* 2000).

Echolocation For *P. kuhlii* from Eastern Europe, flying high in open (probably above 8 m) search-phase call-shape shallow FM. Intensity high; bandwidth 3–6 kHz; end-frequency 35–40 kHz; peak-frequency ca. 42 kHz; call-duration 8–12 ms. When these bats come closer to obstacles, search-phase call-shape becomes steep FM/QCF; intensity high; bandwidth ca. 35 kHz; end-frequency 35–40 kHz; call-duration shortened to 8–6 ms (Schnitzler *et al.* 1987). In sequences of calls, the end-frequency of search-phase calls is kept rather constant; the range of end-frequencies (35–40 kHz) reflects variation between different individuals.

Social and Reproductive Behaviour In a fort near Biskra, Algeria, and in old ruined tombs at Oaurgla, Algeria, generally only one individual was found in each occupied hole (Anderson 1902).

Reproduction and Population Structure Litter-size (Tunisia, Libya): one ($n = 3$) or 2 ($n = 18$) (Baker *et al.* 1974, P. Benda pers.

obs.). Reproductive chronology in Africa not known (data inconclusive). In Tunisia, 15 of 15 ♀♀ were pregnant on 25 Apr (crown–rump length of embryos 5–11 mm); 1 of 3 was lactating and the other two neither pregnant nor lactating on 5 Jun; and 1 of 1 was not pregnant on 19 Nov (Baker *et al.* 1974). At 36° 09' N (Sétif, Algeria), a pregnant ♀ was reported on 8 May, and two subadult ♀♀ on 16 Dec; and nearby, at Djemila, a colony included two lactating ♀♀, five juveniles and an adult ♀ on 11 Sep (Gaisler 1983). At 31° 02' N (Sinawan oasis, Libya), a colony comprised of three pregnant and five lactating ♀♀ was found on 8 May; whereas at 32° 43' N (Cyrenaica, Libya), one lactating and three pregnant ♀♀ were found on 22 May, and at 32° 28' N and 31° 47' N (Tripolitania, Libya), five lactating ♀♀ were found on 27 May and four on 28 May (P. Benda pers. obs.): this indicates that, in Libya, births occur earlier in the S desert populations than in the Mediterranean populations. In Egypt, 'parturition occurs in May' (Anderson 1902) but no year-round data are given, and in the Nile Delta, three non-lactating adult ♀♀ were found in Sep (P. Benda pers. obs.).

Predators, Parasites and Diseases Predators, in Morocco, include owls *Bubo ascalaphus*, *Strix aluco* and *Asio capensis* (Aulagnier 1989). Remains of *P. kuhlii* were also found in pellets of Barn Owls *Tyto alba* in Israel, Iran and Syria (J. Obuch pers. comm.), as well as in pellets of the owls *Asio otus* in Israel and Syria, *Athene noctua* in Syria and Iran, and *Strix aluco* in Turkey. Ectoparasites in Africa include bed-bugs *Cacodmus tunetanus*, *C. vicinus*, *Cimex pipistrelli* (Hemiptera: Cimicidae); fleas *Ischnopsylla octactena*, *I. consimilis*, *Nycteridopsylla ancyluris* (Siphonaptera: Ischnopsyllidae); bat-flies *Basilia daganiae*, *B. robusta* (Diptera: Nycteribiidae); ticks *Ixodes vespertilionis*, *Peplonyssus*

cruciplica (Acari: Ixodidae); and four species of mites (Theodor 1956, Hoogstraal & Traub 1963, Anciaux de Faveaux 1984, Kock 2001b).

Conservation IUCN Category: Least Concern (based on African and extralimital data).

Measurements

Pipistrellus kuhlii

FA: 32.8 (29–37) mm, n = 111

WS (d): 222–235 mm*

TL: 85.1 (77–94) mm, n = 52*

T: 34.2 (29–39) mm, n = 36

E: 11.7 (8–15) mm, n = 59

Tr: 5.0 (2.4–6.6) mm, n = 64

Tib: 11.6 (9–14) mm, n = 94

HF: 6.8 (5–9) mm, n = 69

WT: 6.2 (4.2–8.0) g, n = 18*

GLS: 13.2 (12.3–13.8) mm, n = 84

GWS: 8.5 (8.0–8.9) mm, n = 53

C–M³: 4.8 (4.4–5.2) mm, n = 84

Throughout North African range (CM, FMNH, HZM, IRSN, MHNG, MNHN, NRM, RMCA, SMF, USNM, ZFMK)

*Algeria only (Kowalski & Rzebik-Kowalska 1991)

Key References Kock 2001b; Kowalski & Rzebik-Kowalska 1991; Qumsiyeh 1985.

Victor Van Cakenberghe & Petr Benda

Pipistrellus cf. melckorum MELCK'S PIPISTRELLE

Fr. Pipistrelle des Melcks; Ger. Melcks Zwergfledermaus

Pipistrellus cf. melckorum (auctorum non Roberts, 1919). Ann. Transvaal Mus. 6: 113. Kersfontein, Berg River, Cape Province, South Africa.

Taxonomy Specimens from the Cape, South Africa, described by Roberts as *Eptesicus melckorum*, are now considered synonymous with *P. capensis* (Thorn 1988). Recent chromosome GTG-banding and morphometric analyses support this conclusion (Rautenbach *et al.* 1993); furthermore, specimens from the type locality of *melckorum* have the same chromosome number as *capensis*, 2n = 32 (T. Kearney unpubl.). There is, however, a more northerly distributed species fitting the description of *melckorum*, which is distinct from *capensis* on basis of chromosome number, 2n = 40; aFN = 50 (Rautenbach *et al.* 1993), and which has unusually heavy molars (Koopman 1994). Specimens of this species have been called cf. *melckorum* pending renaming. Specimens from the northern population have been referred to as *Eptesicus (Neoromicia) melckorum* by Koopman (1993), *Pipistrellus (Neoromicia) melckorum* by Hill & Harrison (1987), and as *Neoromicia melckorum* by Simmons (2005). Its placement in *Neoromicia* is questioned by Hoofer & Van Den Bussche (2003). Subspecies: none. Chromosome number: see above.

Description Very small microbat without noseleaf and with tail more or less fully enclosed in interfemoral membrane; four upper

and five lower cheekteeth and two upper incisors on each side; ears separated and short (10–16 mm); FA: 32–39 mm; wings dark with or without white hind-border; dorsal pelage pale to dark; dorsal and ventral hairs bicoloured; lower molars myotodont; inner upper incisor unicuspid or weakly bicuspid; profile of forehead region of skull straight to weakly concave. Sexes similar. Pelage soft, dense; mid-dorsal hairs ca. 6 mm. Dorsal pelage pale brown to dark brown, often with slight silvery or golden sheen; hairs with basal two-thirds dark brown to blackish-brown. Ventral pelage chocolate brown to silvery-brown on chin and throat, becoming brownish-cream on chest and belly, and cream or greyish-white in pelvic region; hairs mostly dark brown with paler tips; pelvic hairs all-cream or greyish-white except, according to Ansell (1967), in Zambian specimens. Naked skin of muzzle and around eyes brown. Ears brown, subtriangular with rounded tip. Tragus length just over half of E; breadth nearly constant for most of length; anterior margin concave; posterior margin smoothly convex with shallow, folded basal lobe; tip rounded (Figure 136j). Wing-membranes brown, dark brown or blackish-brown, slightly translucent; usually with narrow white hind-border, sometimes with no hind-border, rarely with conspicuous

hind-border. Interfemoral membrane paler and more translucent. Baculum as in Figure 141e and f (Kearney *et al.* 2002).

Skull large and robust for an African *Pipistrellus*. Braincase relatively low and narrow; interorbital region relatively narrow; rostrum relatively long but of medium relative breadth (Table 25, p. 603; material not confirmed by its chromosomes). Profile of forehead region (viewed laterally) straight to weakly concave. Occipital helmet weakly developed. Inner upper incisor unicuspid or weakly bicuspid. Outer upper incisor reaching above cingulum of inner incisor (ca. one-third height of inner incisor). Anterior upper premolar absent. Molars unusually heavy. Lower molars myotodont. Dental formula $2^{113}/_{3123} = 32$.

Geographic Variation No information. No subspecies recognized because the true extent of the species is not yet clearly identified.

Similar Species One African *Eptesicus* and four other African *Pipistrellus* also have dark wings; bicoloured dorsal hairs; myotodont lower molars; and have (or might have) overlapping geographic ranges (Table 26, p. 606):

Pipistrellus capensis. Forearm on average shorter (31.9 [28–38] mm).

Tail on average shorter (30.5 [25–38] mm). Inner upper incisor weakly bicuspid before wearing. Molars not as massive. Widespread south of Sahara.

P. somalicus. Smaller (FA: 22–31 mm; GLS: 11.3–12.9 mm). Braincase relatively high; profile of forehead region weakly concave.

P. zuluensis. Skull shorter (GLS: 11.3–12.9 mm). Forearm usually shorter (27–33 mm). Braincase relatively high; profile of forehead region weakly to moderately concave; no occipital helmet. Inner upper incisor sometimes bicuspid.

P. anchietae. Inner upper incisor unicuspid. Anterior upper premolar present although not visible above gum. Skull shorter (GLS: 11.2–13.7 mm).

Eptesicus hottentotus. Much larger (FA: 45–54 mm; GLS: 16.9–21.5 mm).

Distribution Endemic to Africa. Recorded from scattered localities in the Zambezian Woodland BZ and marginally in the Somalia–Masai Bushland BZ, from Tanzania, Zambia, Malawi, Zimbabwe, Mozambique and South Africa (Ansell 1960a, 1967, 1978, Smithers & Lobão Tello 1976, Happold *et al.* 1987, Hill & Harrison 1987, Rautenbach *et al.* 1993, Cotterill 1996a).

Habitat Poorly known but includes woodlands and riverine forests. In Malawi, recorded from miombo woodland at 1000 m (Kasungu N. P.) and from open areas between houses in the Administration Camp, in miombo woodland at 500 m (Liwonde N. P.); not recorded from montane areas, or from the more arid habitats of the Lower Shire Valley (100 m) (Happold *et al.* 1987).

Abundance Uncertain, but appears uncommon. Rarely recorded in Malawi (Happold & Happold 1997).

Remarks Aspect ratio low; wing-loading very low ($n = 1$; M. Happold pers. comm.). Flies with great manoeuvrability; turns



Pipistrellus cf. melckorum

by banking (minimum radius <25 cm) and by stalling-and-twisting; sustained flight in a 1×1×1 m enclosure for up to two circuits/flight (1 bat, 10 flights; M. Happold pers. comm.). Day-roosts not known. Ansell (1960a) indicated that '*Eptesicus melckorum*' roosts inside buildings but he cites Roberts (1951) as the source of this information, and therefore it probably pertains to *P. capensis* (see Taxonomy). Echolocation search-phase call-shape near obstacles (Malawi) steep FM/QCF (Figure 118e); intensity high; start-frequency 56–72 kHz; end-frequency 37–39 kHz; peak-frequency 39–41 kHz; call-duration 2–6.5 ms (1 bat, tethered, 31 calls; M. Happold pers. comm.). Data for bats tentatively identified as '*melckorum*' by Taylor (1999a) are now known to pertain to *P. capensis*. Ectoparasites include a bed-bug *Aphranzia cf. barys* (Diptera: Cimicidae) (Kock *et al.* 1998b).

Conservation IUCN Category (as *Pipistrellus melckorum*): Data Deficient.

Measurements

Pipistrellus cf. melckorum

FA: 37.1 (36–39) mm, $n = 5$

FA: 35.3 (32–38) mm, $n = 35^*$

WS (a): 260 mm, $n = 1^\dagger$

TL: 93.8 (78–101) mm, $n = 5$

T: 39.6 (35–44), $n = 5$

E: 12.8 (10–16) mm, $n = 5$

Tr: 5.6 (4.3–7.5) mm, $n = 25^*$

Tib: 12.4 (9–14) mm, $n = 28^*$

HF: 8 mm, $n = 3^\dagger$

WT: 6.2 (5.6–6.7) g, $n = 3$

WT: 8.2 (5.6–10.5) g, $n = 9^*$

GLS: 14.5 (13.8–14.9) mm, $n = 5$

GLS: 14.6 (13.7–15.5) mm, $n = 26^*$

GWS: 9.6 (9.2–10.0) mm, $n = 16^*$

C–M³ (alv.): 5.3 (4.7–5.7) mm, $n = 5$

Zambia, Zimbabwe (NMZB and TM specimens identified from their chromosomes)

*Throughout geographic range (material not identified from chromosomes; V. Van Cakenberghe pers. comm.)

†Malawi (material not identified from chromosomes; HC)

Key Reference Ansell 1967.

Teresa Kearney

Pipistrellus musculus MOUSE-LIKE PIPISTRELLE

Fr. Pipistrelle murine; Ger. Mäuschen-Zwergfledermaus

Pipistrellus musculus Thomas, 1913. Ann. Mag. Nat. Hist., ser. 8, 11: 316. Dja River, Bitye, 2000 ft (610 m), Cameroon.

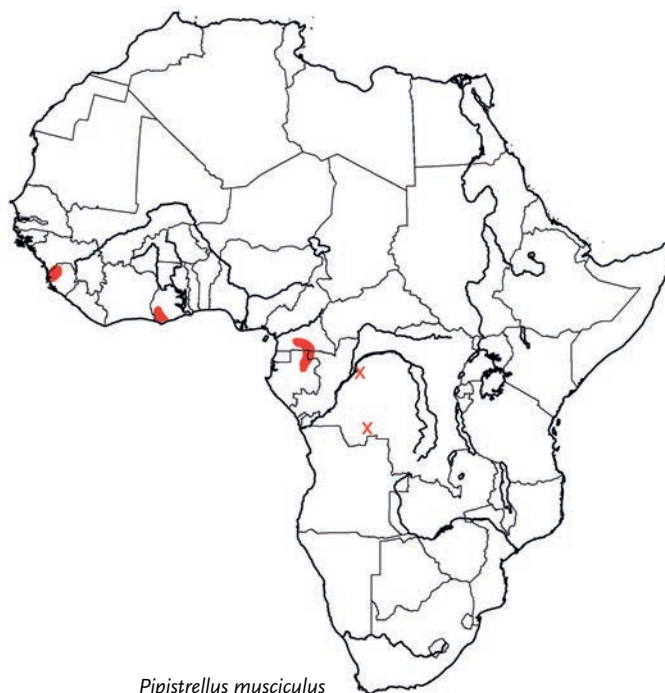
Taxonomy Traditionally *Pipistrellus musculus*. Subsequently classified as *P. (Hypsugo) musculus* by Hill & Harrison (1987) and Koopman (1993) and as *Hypsugo musculus* by Simmons (2005). Placed in collective group *Attalepharca* by Menu (1987), and in *Pipistrellus* by Heller *et al.* (1994). Placed in *Pipistrellus*, in the *hesperus* group by Koopman (1994) – *Pipistrellus hesperus* is a North American pipistrelle. Based on its incisors and premolars, Hill & Harrison (1987) speculated that *P. musculus* might be closely related to *P. nanus* but, based on other characters, including cuspidation of lower molars, this opinion is not held here. Synonyms: none. Chromosome number: not known.

Description Very small microbat without noseleaf and with tail more or less fully enclosed in interfemoral membrane; four or five upper cheekteeth (but only four visible above gum), five lower cheekteeth and two upper incisors on each side; ears separated and short (8–11 mm); FA: 23–26 mm; pelage dark; dorsal and ventral hairs unicoloured; wings dark without white hind-border; lower molars myotodont; inner upper incisor bicuspid; profile of forehead region of skull weakly concave. A poorly known species. Sexes similar in colour. Pelage soft, dense; mid-dorsal hairs 3–4 mm. Both dorsal pelage and ventral pelage dark umber-brown; hairs unicoloured. Ears very dark blackish-brown; inner margin strongly convex at base, then straight. Tragus length ca. one-third of E; narrow, anterior margin straight; posterior margin smoothly convex; tip rounded. Wings dark blackish-brown; no white hind-border (Thomas 1913b). Interfemoral membrane dark blackish-brown; postcalcareal lobe well developed. Penis relatively short. Bacular morphology not known.

Skull small and gracile for an African *Pipistrellus*. Braincase relatively high but of medium relative breadth; interorbital region relatively broad; rostrum relatively short but of medium relative breadth (Table 25, p. 603). Profile of forehead region (viewed laterally) weakly concave. No occipital helmet. Inner upper incisor bicuspid; outer and inner upper incisors almost equal in size. Anterior upper premolar minute, often not visible above gum, displaced lingually, sometimes absent. Lower molars myotodont. Dental formula: $2^{113}/_{3123} = 32$ or $2^{123}/_{3123} = 34$.

Geographic Variation None recorded.

Similar Species Four other African *Pipistrellus* have dark wings; unicoloured dorsal hairs; myotodont lower molars (Table 26, p. 606):



Pipistrellus musculus

Pipistrellus grandidieri. Much larger (FA: 33–38 mm; GLS: 13.8–14.7 mm).

P. crassulus bellieri. Larger (FA: 28–33 mm; GLS: 12.1–13.6 mm). Ventral pelage various shades of pale brown; ventral hairs bicoloured. Anterior upper small, visible.

P. crassulus crassulus. Larger (FA: 28–32 mm; GLS: 12.5–13.2 mm). Ventral pelage dark brown or reddish-brown.

P. brunneus. Much larger (FA: 33–38 mm; GLS: 13.0–14.1 mm). Inner upper incisor unicuspid.

Distribution Endemic to Africa. Found in the Rainforest BZ and the Northern Rainforest–Savanna Mosaic in West Africa and central Africa. As yet, only recorded from Sierra Leone, Ghana, Cameroon, Gabon and DR Congo. Gaps in the distribution are likely to be the result of insufficient sampling.

Habitat Mainly rainforest habitats, but recorded from Guinea savanna in Sierra Leone, and on the coast as well as in the rainforest zone in Ghana (Grubb *et al.* 1998).

Remarks Flight very rapid. An adult ♂ and ♀ and two young were taken from the hollow stem of a Raphia Palm *Raphia vinifera* in Jun (BMNH). Another adult ♀ was caught in the hollow stem of another Raphia Palm (BMNH). Perret & Aellen (1956) captured some flying in the town of Foulassi in Cameroon, and Brosset (1966) observed some foraging in groups of 4–5, near the ground in the vicinity of buildings in Gabon. At 9–10° N in Sierra Leone, a lactating ♀ was collected in mid-May (USNM 547020).

Conservation IUCN Category: Data Deficient.

Measurements

Pipistrellus musciculus

FA: 24.9 (23–26) mm, n = 13

WS: n. d.

TL: n. d.

T: 23.6 (21–26) mm, n = 4

E: 9.3 (8–11) mm, n = 11

Tr: 3.3 (2.5–4.2) mm, n = 9

Tib: 9.6 (8–11) mm, n = 12

HF: n. d.

WT: 3.8 g, n = 1

GLS: 11.0 (10.3–11.4) mm, n = 13

GWS: 7.4 (7.1–7.6) mm, n = 4

C–M³ (alv.): 3.7 (3.5–3.9) mm, n = 13

Throughout geographic range (AMNH, BMNH, MHNG, MNHN, RMCA, ROM, USNM)

Key Reference Thomas 1913b.

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Pipistrellus nanulus TINY PIPISTRELLE

Fr. Pipistrelle miniscule; Ger. Kleine Zwergfledermaus

Pipistrellus nanulus Thomas, 1904. Ann. Mag. Nat. Hist., ser. 7, 14: 189. Efulen, Cameroon.

Taxonomy Traditionally *Pipistrellus nanulus*. Subsequently classified as *P. (Pipistrellus) nanulus* by Hill & Harrison (1987), Koopman (1993) and Simmons (2005), *Pipistrellus nanulus* by Menu (1987) and Heller *et al.* (1994), and *P. (Vansonia) nanulus* by Koopman (1994). Dieter Kock (pers. comm.) doubts the assignment to *Vansonia*. Placed in the *rueppellii* group by Hill & Harrison (1987). Synonyms: none. Chromosome number: not known.

Description Very small microbat without noseleaf and with tail more or less fully enclosed in interfemoral membrane; five upper cheekteeth (all visible above gum), five lower cheekteeth and two upper incisors on each side; ears separated and short (7–11 mm); FA: 24–29 mm; dorsal pelage reddish-brown; dorsal hairs unicoloured, ventral hairs sometimes bicoloured; wings dark, usually without white hind-border; lower molars nyctalodont; inner upper incisor bicuspid; profile of forehead region of skull moderately concave; posterior margin of tragus without abrupt angle. Sexes similar. Pelage dense; mid-dorsal hairs 4–5 mm. Dorsal pelage reddish-brown; hairs unicoloured. Ventral pelage usually pale brown; hairs usually unicoloured but sometimes bicoloured, pale brown with darker base. Ears rather short and rounded. Tragus length ca. half of E but variable in preserved material, anterior margin almost straight; posterior margin smoothly convex with pronounced basal lobe; tip rounded (Figure 136k). Wings reddish-brown (similar to dorsal pelage); usually without white hind-border although a clear (translucent) hind-border is sometimes present. Interfemoral membrane reddish-brown; tail protruding slightly beyond membrane; postcalcarea lobe narrow. Penis enlarged; prepuce hairy. Baculum as in Figure 139f (Hill & Harrison 1987).

Skull small and gracile for an African *Pipistrellus*. Braincase relatively high and broad; interorbital region relatively broad; rostrum relatively short and broad (Table 25, p. 603). Profile of forehead region (viewed laterally) moderately concave. No occipital helmet. Inner upper incisor bicuspid. Outer upper incisor bicuspid, well developed, attaining

almost the height of the inner incisor. Anterior upper premolar comparatively medium to large, almost within toothrow or slightly displaced lingually, visible above gum and from the outside; canine and posterior premolar not in contact. Lower molars nyctalodont. Dental formula: $2^{123}/_{3123} = 34$.

Geographic Variation None recorded.

Similar Species Three other sub-Saharan *Pipistrellus* have nyctalodont lower molars and bicuspid inner upper incisors (Table 27, p. 608):

Pipistrellus rueppellii. Mid-ventral pelage pure white; throat sometimes pale rusty-brown.

P. nanus. Dorsal pelage not reddish-brown; hairs bicoloured. Tragus hatchet-shaped (posterior margin with abrupt angle). FA sometimes >29 mm.

P. permixtus. Dorsal hairs bicoloured. Only known from Dar-es-Salaam, Tanzania.

Distribution Endemic to Africa. Primarily known from the Sudan Savanna, Guinea Savanna and Rainforest BZs and the Northern Rainforest–Savanna Mosaic in West Africa, and recorded in most countries from Senegal to Cameroon, Gabon and Bioko I. There are some additional records from the Rainforest BZ and Eastern Rainforest–Savanna Mosaic in E DR Congo, Uganda and W Kenya.

Habitat No details available for most records. Occurs mainly in the rainforest zone but extends northwards into derived and Guinea savannas and riverine forests; 15 specimens for which data are available were recorded between 50 and 1833 m. Recorded flying over small streams and pools (Happold 1987, Decher *et al.* 1997). Recorded in a cocoa plantation on Bioko I. (Eisentraut 1964).

Abundance Uncertain.

Adaptations One individual flew into a hollow branch that was also occupied by a hive of wild bees (Lang & Chapin 1917b, as *P. musculus* but the specimen was re-identified as *P. nanulus* by Koopman 1965). Perret & Aellen (1956) captured some flying around in the town of Foulassi, Cameroon.

Foraging and Food Two were seen foraging at daybreak for insects swarming over a damp wallow (Lang & Chapin 1917b, as *P. musculus*).

Reproductive and Social Behaviour An 'enormous' colony was found in the roof of a European-style house in a cocoa plantation on Bioko I. (Eisentraut 1964).

Reproduction and Population Structure Litter-size: one or 2 ($n = 2$; Decher *et al.* 1997). Reproductive chronology not known. Two pregnant ♀♀ were recorded in Ghana in Jan (Decher *et al.* 1997). One lactating ♀, one non-pregnant and non-lactating ♀, and four ♂♂ with abdominal testes, were recorded in Côte d'Ivoire in Jan (Lim & Van Coeverden de Groot 1997).

Predators, Parasites and Diseases Ectoparasites include bed-bugs (Hemiptera: Cimicidae), which were found on the wings (Lang & Chapin 1917b, as *P. musculus*).

Conservation IUCN Category: Least Concern.

Widespread, comparatively common, no known threats.

Measurements

Pipistrellus nanulus

FA: 26.6 (24–29) mm, $n = 55$

WS (c): 162 mm, $n = 1^\dagger$

TL: 66–74 mm, $n = 8^*$

T: 27.5 (26–32) mm, $n = 13$

E: 8.8 (7–11) mm, $n = 20$

Tr: 3.9 (2.9–6.1) mm, $n = 16$

Tib: 9.0 (8–12) mm, $n = 33$



Pipistrellus nanulus

HF: 5.5 (5–7) mm, $n = 11$

WT: 4.0 (2–7) g, $n = 22$

GLS: 11.1 (10.4–11.7) mm, $n = 54$

GWS: 7.5 (6.9–8.0) mm, $n = 29$

C–M³ (alv.): 3.9 (3.6–4.3) mm, $n = 55$

Throughout geographic range (AMNH, BMNH, CM, MHNG, MNHN, RMCA, ROM, USNM, ZFMK and literature)

*Thomas 1904c, Eisentraut 1964, Lim & Van Coeverden de Groot 1997

†DR Congo only (Lang & Chapin 1917b, as *P. musculus*)

Key References Decher *et al.* 1997; Eisentraut 1964; Happold 1987; Lang & Chapin 1917b; Lim & Van Coeverden de Groot 1997.

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Pipistrellus nanus BANANA PIPISTRELLE (BANANA BAT)

Fr. Pipistrelle naine; Ger. Bananenfledermaus

Pipistrellus nanus (Peters, 1852). Reise nach Mossambique, Säugeth., p. 63. Inhambane, Mozambique.

Taxonomy Originally *Vespertilio pipistrellus* var. *africanus*. Traditionally *Pipistrellus nanus*. Subsequently classified as *P. (Hypsugo) nanus* by Hill & Harrison (1987), *Pipistrellus nanus* by Menu (1987), *P. (Pipistrellus) nanus* by Koopman (1993) and *Neoromicia nana* by Volleth *et al.* (2001), Kearney *et al.* (2002) and Simmons (2005). Unlike all other pipistrelles placed in *Neoromicia* by Simmons (2005) and also unlike all African species placed in *Hypsugo* (Simmons 2005), *P. nanus* has nyctalodont lower molars, as have all African species in *Pipistrellus* (*sensu stricto*): therefore (based on this and other craniodental characters) the assignment of *P. nanus* to either *Hypsugo* or *Neoromicia* is dubious and, pending further investigation, it is retained here in *Pipistrellus* (*sensu stricto*). Koopman (1975) indicated that *africanus* Rüppell, 1842 is the senior synonym of *nanus* Peters, 1852.

However, *africanus* is seldom used and the International Commission on Zoological Nomenclature, Opinion 2120, has ruled that the name *nanus* is given precedence over the name *africanus* whenever the two are considered to be synonyms (Anonymous 2005). Synonyms, pending revision: *abaensis*, *africanus*, *culex*, *fouriei*, *meesteri*, *minusculus*, *pagenstecheri*, *pusillulus* and *stampflii*. Formerly included *helios* but, based on bacular and dental and/or behavioural data, *helios* was considered to be a distinct species by Hill & Harrison (1987) and (following M. Happold) by Simmons (2005) and others. However, it is now known that the above data refer to another form – profiled here as *P. cf. helios* – and therefore the status of *helios* and its relationship to *P. nanus* needs to be reassessed. Several other forms also have been considered specifically

distinct, or perhaps specifically distinct, by some authors; e.g. Perret & Aellen (1956) indicated that *culex* is a distinct species occurring in the Sudan and Sahel savanna zones. Peterson (1987), without including reasons, indicated that *australis* (now *meesteri*) is a distinct species, and that *minusculus* (including *fouriei* and *culex*) might be a distinct species. Koopman (1965) suggested that *stampflii* (= *minusculus*) might be a distinct species. The taxon *P. nanus* clearly needs revision. Subspecies: seven of uncertain status. Chromosome number (Zimbabwe, South Africa): $2n = 36$; $aFN = 50$ (Peterson & Nagorsen 1975, Rautenbach *et al.* 1993, Kearney *et al.* 2002).

Description Very small microbat without noseleaf and with tail more or less fully enclosed in interfemoral membrane; five upper cheekteeth (all visible above gum), five lower cheekteeth and two upper incisors on each side; ears separated and short (7–13 mm); FA: 25–35 mm; dorsal pelage dark; dorsal and ventral hairs bicoloured; wings dark without white hind-border; lower molars nyctalodont, inner upper incisor bicuspid; profile of forehead region of skull strongly concave; posterior margin of tragus sharply angular; usually no glands on interfemoral membrane. Sexes similar in colour; ♀ on average larger than ♂. Pelage soft, dense, fairly fluffy, with silky sheen; mid-dorsal hairs ca. 5 mm. Dorsal pelage chocolate brown or sepia brown, usually with golden sheen; hairs bicoloured, basal half blackish-brown, terminal half chocolate or sepia brown usually merging into golden-brown towards tip. Ventral pelage dark greyish-buff; hairs bicoloured, blackish-brown with greyish-buff at tip. Ears blackish-brown, relatively short, subtriangular; tip rounded; outer margin with lobule at base inconspicuous or absent. Tragus length ca. half E; broadest well above mid-height; hatchet-shaped (anterior margin slightly to distinctly concave, posterior margin making an obtuse-angle bend just above mid-height; no basal lobe); tip narrow and rounded (Figure 136b). Wings blackish-brown; no white hind-border. Thumb very small with friction pad on wrist. Hindfeet very small with friction pad on sole. Interfemoral membrane blackish-brown; sometimes with the posterior margin pale or white. No glands on interfemoral membranes of specimens from Kenya and DR Congo (cf. *P. cf. helios*), but 13 of 93 specimens from Malawi and South Africa had one, rarely two, small opaque disks of unknown significance, usually near the body. Baculum as in Figure 139g (Hill & Harrison 1987).

Skull small and gracile for an African *Pipistrellus*. Braincase on average relatively high and of medium relative breadth (but very variable); interorbital region of medium relative breadth; rostrum on average relatively short and narrow (but again very variable) (Table 25, p. 603). Profile of forehead region (viewed laterally) strongly concave (Figure 137a). No occipital helmet. Inner upper incisor usually bicuspid, sometimes unicuspid. Outer upper incisor at least half height of inner upper incisor (often reaching posterior cusp of inner incisor). Anterior upper premolar medium-sized, somewhat displaced lingually; canine and posterior premolar not in contact. Lower molars nyctalodont. The lower molars of holotypes of *nanus* and *culex* are very worn and some are missing, but they appear to be nyctalodont; those of lectotype of *africanus* are nyctalodont. Dental formula: $2^{123}/_{3123} = 34$.

Geographic Variation The following subspecies of *P. nanus* (as *P. africanus*) were recognized by Koopman (1994) and/or Kock (2001c), but their status and geographic ranges are uncertain (see Taxonomy):

P. n. stampflii: Sierra Leone to Côte d'Ivoire.

P. n. culex: Nigeria, Ghana.

P. n. africanus: DR Congo to Ethiopia, mostly in highlands.

P. n. nanus: DR Congo, Kenya and Tanzania to South Africa, also Cameroon (Rosevear 1965).

P. n. fouriei: S Angola, W Zambia, N Namibia.

P. n. meesteri: Transkei, South Africa.

P. n. minusculus: Liberia.

The subspecific assignment of specimens from C and S Sudan and S Somalia is uncertain. Rosevear (1965) found a clinal increase in size from Sierra Leone to Cameroon and was unable to find lines of demarcation between the subspecies *stampflii*, *culex* and *nanus*. No subspecies were recognized by Hayman & Hill (1971).

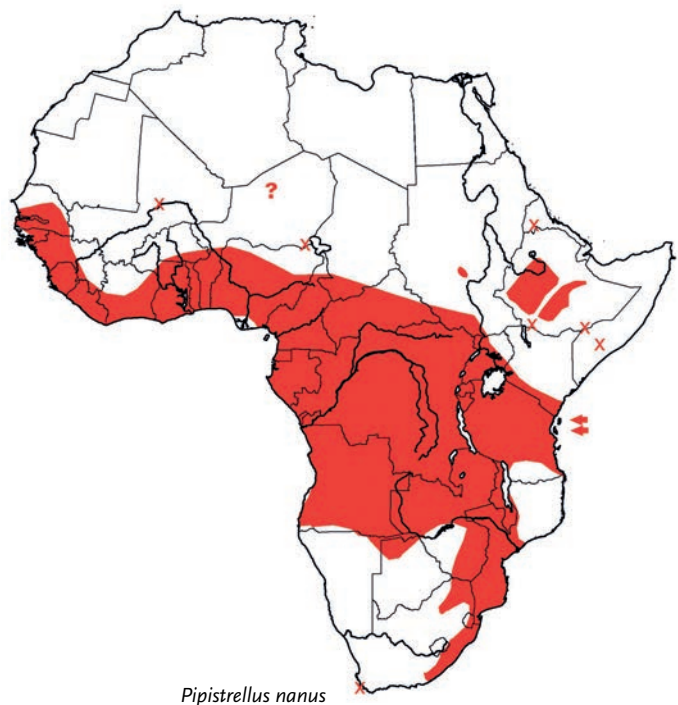
Similar Species Three other sub-Saharan *Pipistrellus* have nyctalodont lower molars and bicuspid inner upper incisors (Table 27, p. 608):

Pipistrellus rueppellii. Mid-ventral pelage pure white; throat sometimes pale rusty-brown.

P. permixtus. Tragus sickle-shaped (posterior margin without abrupt angle).

P. nanulus. Dorsal pelage reddish-brown; hairs unicoloured. Tragus not hatchet-shaped (no abrupt angle on posterior margin). Forearm not known to exceed 29 mm.

Distribution Endemic to Africa. Very widespread in most sub-Saharan biotic zones (except in the South-West Arid and South-West Cape BZs and in the Horn of Africa) but possibly only where banana plants and/or other musaceous plants are found (see Habitat). There are records at oases in Niger (at Air and just south of Air at Tchin-n-Tajet kori) which have not been confirmed (see question mark on map).



Pipistrellus nanus

Habitat Diverse forest and savanna habitats and sometimes sub-desert steppe; sea level to 2500 m. Possibly dependent on musaceous plants for roosts and restricted to habitats moist and warm enough for these plants to grow, either wild or cultivated. There are records in habitats devoid of musaceous plants, but some of these refer to *P. cf. helios* and others possibly refer to cryptic species (see Taxonomy).

Abundance Apparently common wherever banana plants are abundant. On any single day during a ten-month study with sampling at fortnightly intervals, 27–49 individuals roosted by day in a 40×50 m plantation of bananas in Malawi (Happold & Happold 1996).

Adaptations Aspect ratio low; wing-loading very low; flight slow and highly manoeuvrable in confined spaces, faster and very agile in open spaces. Turns by banking (minimum radius <25 cm) and by stalling-and-twisting; can take off from ground; cannot hover; individuals sustained flight in a 1×1×1 m enclosure for up to 23 circuits/flight (10 bats, 10 flights each). Cursorial locomotion on ground, and climbing on sloping surfaces, are moderately efficient; friction pads on wrists and hindfeet facilitate climbing on banana leaves.

Roosts by day in furled leaves of domestic banana and plantain plants *Musa* spp., wild bananas *Ensete* and strelitzias *Strelitzia nicolai* (Musaceae) (e.g. LaVal & LaVal 1977, Baagøe 1978, Happold & Happold 1990b, 1996). Occasionally recorded roosting elsewhere, including in bunches of banana fruits, skirts of dead banana leaves, crevices in thatch, under rafters, in culverts and in a cave (e.g. Fenton *et al.* 1977, LaVal & LaVal 1977, Baagøe 1978, O'Shea & Vaughan 1980), but at least some of these records refer to other species (e.g. *P. cf. helios*). *Ensete* and *Strelitzia* are indigenous to Africa, and bananas were introduced to West Africa 2500 years ago, and to East Africa at least 1000 years ago (Coghlan 2001): consequently, the leaf-roosting form has had time to specialize and adapt to the peculiarities of this roost. It has very little inter-specific competition for roosts – only *Myotis bocagii*, *M. scotti* (and very rarely *M. welwitschii*) sometimes roost in furled leaves in some localities. Furled leaves are only occupied by *P. nanus* if the entrance diameter is 7–24 cm (optimally 19–24 cm). Banana leaves unfurl rapidly and are suitable for only 1–3 days, but they are produced throughout the year. Roost-fidelity (*sensu stricto*) is not possible, but almost half of the ♂♂ in one study showed fidelity to a small number (<5) of clumps of 'reliable' plants growing close together, which invariably had one or more suitable leaves at all times (Happold & Happold 1996). Females did not show such fidelity and their roost-ranges were much larger. In localities where separate banana plantations may be one or more kilometres apart, some individuals apparently maintain at least two separate roost-ranges and alternate between them.

Temperatures inside and outside leaves are similar, but relative humidities inside are 80–100%, even when as low as 35% outside. During the cool dry season, all individuals become torpid during the day; in the hot wet season, only some do. In Malawi, *P. nanus* occurs at some localities where night temperatures are sometimes too low for flying insects to be active, and perhaps the ability to reduce urinary water loss enables these bats to remain torpid for several days at such times. The kidneys have a long papilla and thick medulla; the predicted mean maximum urine concentration is comparatively high (4004 mOsmol/kg) (Happold & Happold 1988). Nevertheless, captives, fed winged termites and offered water twice daily, took 1–2 drinks/day.

Foraging and Food In Malawi, forages by slow-hawking in moderately uncluttered places such as clearings, gaps between trees, and around canopies of trees. Foraging is characterized by acrobatic swerving as small insects are pursued. Foraging begins at dusk and individuals do not return to their furled leaves until just before sunrise, but bouts of foraging appear to be interspersed with periods of inactivity. Small beetles and moths appear to be main components of the diet, with some Diptera also (Fenton & Thomas 1980).

Echolocation Search-phase call-shape (Malawi) steep FM/QCF (Figure 118b). Intensity high; start-frequency up to 111 kHz; end-frequency and peak-frequency 59–67 kHz (usually 63–65 kHz); call-duration 2.5–6.0 ms (depending on duration of the QCF 'heel') (24 bats, foraging, 300 calls; M. Happold unpubl.). Calls with similar end-frequencies were recorded in Zimbabwe (62 kHz, 3 bats, flying in open; Fenton & Bell 1981) and South Africa (67.4 ± 1.4 kHz, 1 bat, flying in open, 4 calls; Taylor 1999a). Taylor also recorded end-frequencies of 42.4 kHz (1 bat, 2 calls), but this bat is not likely to represent *P. nanus*.

Social and Reproductive Behaviour Frequently aggregates to forage, but the composition of aggregations is not known. LaVal & LaVal (1977) observed that in leaf-roosting *P. nanus* in South Africa, adult ♂♂ roost singly or in labile groups comprised of 1–6 adult ♂♂ and 1–8 adult ♀♀ without young, and that adult ♀♀ with young roosted singly or with up to nine other adult ♀♀ with their young. About one-third of 101 banded bats were recaptured at least once, indicating that some are comparatively sedentary.

To obtain further information, the social organization of *P. nanus* roosting in a banana plantation containing 138 clumps of banana plants arranged in a 40×50 m grid was studied by Happold & Happold (1996) in Malawi. Roosting behaviour was fairly similar in both localities – during parturition and lactation, ♀♀ with young roosted separately from ♂♂, and ♂♂ roosted singly. At other times, adult ♂♂ roosted singly, or in groups comprised of one (very rarely two) ♂♂ and 1–10 ♀♀. Formation of groups is not attributable to shortage of leaves. There were invariably more habitable clumps of banana plants (i.e. with two or more suitable leaves) than adult ♂♂, so competition for clumps by ♂♂ was unlikely. On most occasions, each ♂ was found with a different group of ♀♀, and each ♀ with a different ♂, showing that group-membership is highly labile and suggesting that the mating system is promiscuous. Some ♂♂ attracted more ♀♀ than others, but what makes a ♂ attractive to ♀♀, especially during the mating season, is not understood. Males were not heard vocalizing to attract ♀♀ to their roosts (cf. *P. cf. helios*). Bats do not return to their roosts before dawn, there is no evidence that ♂♂ are territorial and they did not have injuries attributable to fighting (cf. *P. cf. helios*). It might be that ♂♂ are selected for the quality of the clumps of banana plants that they roost in, although this did not appear to be the case. Alternatively, each ♀ might mate with many ♂♂ and rely on sperm competition to obtain the best sire for her progeny.

LaVal & LaVal (1977) recorded what appeared to be a maternity colony of 150 bats roosting tightly grouped in a thatched roof in Kruger N. P., South Africa. They were identified as *P. nanus*, but this behaviour is different to that of leaf-roosting *P. nanus*, suggesting that this record refers to a cryptic species or perhaps *P. cf. helios*.

Reproduction and Population Structure Litter-size (Zimbabwe, Malawi, Zambia): invariably two. Elsewhere, embryo counts are rare, but ♀♀ with one or two young have been recorded from South Africa, Namibia, DR Congo, Gabon, Ghana and Liberia: however, ♀♀ with only one young might have given birth to twins and subsequently lost one. There appear to be no records of ♀♀ with single embryos, but 'no cases of twin births' were reported from DR Congo (Verschuren 1966) and Rwanda (Verschuren 1965a). The reproductive chronology in Malawi (15–16°S) is restricted seasonal monoestry, with spermatogenesis in hot wet season (Feb–Apr), mating in cool dry season (mid-Jun to early Jul), sperm storage by the ♀♀ until ovulation in Aug, sperm storage in the ♂ until at least Sep, parturition in mid-Nov ca. 10 weeks after fertilization and 20 weeks after copulation (Bernard *et al.* 1997). This chronology ensures that both spermatogenesis and lactation occur during the hot wet season when insects are maximally abundant. In South Africa, the chronology is also restricted seasonal monoestry (LaVal & LaVal 1977) but, at 25°S, frequent copulations occur between May and beginning of Aug when ovulation and fertilization occur, and there is not strong evidence to support sperm storage at this locality (Stirnermann & van der Merwe 2005). In DR Congo, Gabon and Rwanda, parturition is aseasonal (Lang & Chapin 1917a, Verschuren 1957, 1966, Brosset 1966) but it is not possible to tell, from the available data, whether the chronology is aseasonal monoestry with highly unsynchronized parturition, or aseasonal polyoestry. Furthermore, these data possibly include records from cryptic species.

Neonates are naked, eyes closed, weight ca. 1 g (M. Happold unpubl.). They cling tenaciously to the nipples and to the ventral pelage; they are enclosed by the mother's wings when she rests, and carried when she flies. Neonates groom themselves with rapid combing movements of the hindfeet. Detached neonates make vocalizations (audible to humans) but do not appear to echolocate. By week 3, cursorial scuttling over horizontal and sloping surfaces is efficient, and they echolocate. By week 7, deciduous dentition begins to be replaced. By week 9, the diet includes insects as well as milk and the young are just volant. Weaning occurs at 8–9 weeks.

Sex ratio at birth is 1 : 1. In the banana plantation in Malawi, adult ♂♂ were outnumbered by adult ♀♀ (1 : 1.7) during the hot wet season when ♀♀ were pregnant, but more ♀♀ were lost during the wet season, when they were lactating and post-lactating, and the ratio reversed (1 : 0.8). Seasonal fluctuations in the sex ratio possibly explain the differently biased sex ratios reported for DR Congo and Senegal by Verschuren (1957, 1966, 1982).

Predators, Parasites and Diseases Predators include Bat Hawks *Macheiramphus alcinus* (Lang & Chapin 1917a). A Grey-headed Bush-shrike *Malaconotus blanchoti* was observed opening furred banana leaves and, on one occasion, removing a bat (Van Jaarsveld 1988). Ectoparasites include a bed-bug *Cacodmus villosus* (Hemiptera: Cimicidae); bat-flies *Nycteribia schmidli*, *N. styliidiopsis*, *Basilia daganiae*, *B. ansifera*, *B. robusta*, *B. tarda* (Diptera: Nycteribiidae); a tick *Carios vespertilionis* (Acari: Argasidae); and mites *Spinturnix walkerae*, *Meristaspis kenyaensis* (Acari: Spinturnicidae), *Chelanyssus aethiopicus*, *Steatonyssus eos*, *S. brucei*, *S. afer* (Acari: Macronyssidae), *Acanthophthirus radfordi* (Acari: Myobiidae), *Alabidocarpus eptesicus* (Acari: Chirodiscidae), *Notoedres miniopteri* (Acari: Sarcopidae) (Anciaux de Faveaux 1984).

Conservation IUCN Category: Least Concern.

Because it roosts in banana leaves, this is one of the few species that benefit from the conversion of natural habitats to subsistence farms and villages.

Measurements

Pipistrellus nanus

FA: 30.1 (25–35) mm, n = 1376

WS (a): 222 (214–231) mm, n = 11*

TL: 75.0 (64–84) mm, n = 203

T: 33.0 (24–40) mm, n = 135

E: 10.0 (7–13) mm, n = 1048

Tr: 4.9 (3.5–5.5) mm, n = 22

Tib: 11.2 (7–15) mm, n = 1232

HF: 6.2 (5–9) mm, n = 155

WT: 3.6 (2.5–6.5) g, n = 237

GLS: 11.4 (10.0–12.6) mm, n = 497

GWS: 7.1 (6.6–7.7) mm, n = 143

C–M³ (alv.): 3.8 (3.2–4.8) mm, n = 494

Throughout geographic range (AMNH, BMNH, CAS, CM, CZL, FMNH, HC, HZM, IRSN, MHNG, MNHN, MZUF, NMZB, NRM, RMCA, RMNH, ROM, SMF, TM, USNM, YMP, ZFMK, ZMA, ZMB, ZMMU, ZMUZ, from V. Van Cakenberghe pers. comm.)

*Malawi only

Key References Baagøe 1978; Bernard *et al.* 1997; Happold & Happold 1990b, 1996; LaVal & LaVal 1977.

Meredith Happold

Pipistrellus permixtus DAR-ES-SALAAM PIPISTRELLE

Fr. Pipistrelle de Tanzanie; Ger. Verwechselte Zwergfledermaus

Pipistrellus permixtus Aellen, 1957. Rev. Suisse Zool. 64: 200. Dar-es-Salaam, Tanzania.

Taxonomy Traditionally *Pipistrellus permixtus*. Subsequently classified as *P. (Pipistrellus) permixtus* by Hill & Harrison (1987), Koopman (1993, 1994) and Simmons (2005). According to Aellen (1957), *Pipistrellus permixtus* is more closely related to Palearctic or Oriental members of the genus such as *P. pipistrellus* and *P. nathusii* (Keyserling & Blasius, 1839) than to the other African pipistrelles. Synonyms: none. Chromosome number: not known.

Description Very small microbat without noseleaf and with tail more or less fully enclosed in interfemoral membrane; five upper cheekteeth (all visible above gum), five lower cheekteeth and two upper incisors on each side; ears separated and short (ca. 13 mm); FA: ca. 34 mm; dorsal hairs bicoloured; lower molars nyctalodont, inner upper incisor bicuspid; profile of forehead region of skull moderately concave; posterior margin of tragus smoothly convex.

Only known from holotype. Sexual dimorphism: no information. Dorsal pelage colour not known (colour lost before species was described [Aellen 1957]); hairs bicoloured. Pelage extending on to proximal fifth of interfemoral membrane on the dorsal side. Ventral pelage not pure white (no other information). Ears relatively short; tip rounded. Tragus length ca. one-third of E; broadest just above middle of anterior margin; sickle-shaped (anterior margin concave, posterior margin smoothly convex; tip rounded). Wing-membrane: no information. Thumb relatively long. Tail not projecting beyond interfemoral membrane. Postcalcaneal lobe large, well developed. Bacular morphology not known.

Skull medium-sized for an African *Pipistrellus*. Supraorbital region not so expanded that the dorsal surface of the rostrum assumes a pentagonal outline (cf. *P. eisenrauti*). Profile of forehead region (viewed laterally) moderately concave. Inner upper incisor bicuspid. Outer upper incisor about two-thirds height of inner incisor (i.e. as high as the posterior cusp of the inner incisor). Anterior upper premolar well developed and clearly visible above gum; displaced lingually according to Aellen (1957) although Koopman (1994) found it to be in the toothrow. Lower canines relatively robust. Lower molars nyctalodont (Menu 1987). Dental formula: $\frac{2123}{3123} = 34$.

Geographic Variation No information.

Similar Species Three other sub-Saharan *Pipistrellus* have nyctalodont lower molars and bicuspid inner upper incisors (Table 27, p. 608):

Pipistrellus rueppellii. Mid-ventral pelage pure white; throat sometimes pale rusty-brown.

P. nanulus. Dorsal hairs unicoloured. No known overlap in distribution.

P. nanus. Tragus hatchet-shaped (posterior margin with abrupt angle).

Distribution Known only from Dar-es-Salaam in Tanzania. Because this bat appears to be related to Palaearctic pipistrelles, Kingdon (1974) suggests that it might have come to the port of Dar-es-Salaam as a stowaway.

Remarks Nothing more is known about the biology of this bat.

Conservation IUCN Category: Data Deficient.



Pipistrellus permixtus

Measurements

Pipistrellus permixtus

FA: 34 mm

WS: n. d.

TL: ca. 75 mm

T: ca. 33 mm

E: ca. 13 mm

Tr: 3.5 mm

Tib: 13 mm

HF: 6 mm

WT: n. d.

GLS: 12.6 mm

GWS: 8.4 mm

C-M³: 4.8 mm

Dar-es-Salaam, Tanzania (holotype, Aellen 1957)

Key Reference Aellen 1957.

Victor Van Cakenberghe & Meredith Happold

Pipistrellus pipistrellus COMMON PIPISTRELLE

Fr. Pipistrelle commune; Ger. Zwergfledermaus

Pipistrellus pipistrellus (Schreber, 1774). Die Säugethiere 1: 167. France.

Taxonomy Originally *Vespertilio pipistrellus*. Traditionally *Pipistrellus pipistrellus*. Subsequently classified as *Pipistrellus pipistrellus* by Menu (1987), and as *P. (Pipistrellus) pipistrellus* by Hill & Harrison (1987), Koopman (1993, 1994) and Simmons (2005). Synonyms: none in Africa. Does not include *Pipistrellus hanaki*, a recently discovered cryptic species (see profile) distinguished by differences in its echolocation and genetic (DNA) characteristics (Benda *et al.* 2004b, Hulva *et al.* 2004). Subspecies: meristic and genetic information

support that *P. pipistrellus*, the 45 kHz phonic type, occurs in North Africa but it should represent a distinct subspecies (Barratt *et al.* 1995, 1997). Chromosome number (Europe): 2n = 44; aFN = 50 as in all European *Pipistrellus* spp. (Volleth *et al.* 2001).

Description Very small microbat without noseleaf and with tail more or less fully enclosed in interfemoral membrane; five upper cheekteeth (all visible above gum), five lower cheekteeth and two

upper incisors on each side; ears separated and short (7–11 mm); FA: 28–33 mm; wings dark, sometimes with pale hind-border; dorsal pelage pale brownish to greyish-brown; dorsal and ventral hairs bicoloured; lower molars nyctalodont; inner upper incisor bicuspid; profile of forehead region of skull moderately concave; posterior margin of tragus without sharp angle. The smallest bat in North Africa. Sexes similar. Pelage dense, soft; mid-dorsal hairs ca. 5 mm. Dorsal pelage pale brownish to greyish-brown; hairs distinctly bicoloured with basal two-thirds to three-quarters dark brown. Ventral pelage paler; hairs with basal two-thirds to three-quarters dark brown. Naked skin of muzzle and around eyes dark brown. Ears dark brown, subtriangular with rounded tip. Tragus length ca. half of E; widest at mid-height; anterior margin slightly concave; posterior margin smoothly convex; tip rounded. Wing and interfemoral membranes dark brown; wings usually without a hind-border but sometimes with a pale hind-border. Penis typically very pale grey (almost unpigmented) with a long, pale median band on dorsal side of glans penis (cf. *P. hanaki*). Baculum long, thin, bifurcated at both ends, ca. 1.8 mm long (Figure 139h; Benda *et al.* 2004b).

Skull small and gracile for an African *Pipistrellus*. Braincase relatively narrow; interorbital region of medium relative breadth; rostrum relatively short and narrow (Table 25, p. 603). In European specimens, the braincase is relatively high (no data for African specimens). Profile of forehead region (viewed laterally) moderately concave. Occipital helmet almost absent; sagittal crest almost absent. Inner upper incisor bicuspid (posterior cusp ca. two-thirds height of main cusp). Outer upper incisor almost as high as inner incisor. Canines comparatively weak (cf. *P. hanaki*). Anterior upper premolar present, visible above gum, slightly displaced lingually; canine and posterior premolar not in contact. Lower molars nyctalodont. Dental formula: $\frac{2^{123}}{3^{123}} = 34$.

Geographic Variation None in Africa (Benda *et al.* 2004b).

Similar Species Seven other *Eptesicus* and *Pipistrellus* occur in North Africa (excluding *P. ariel* in S Egypt):

Pipistrellus rueppellii. Mid-ventral pelage pure white; throat sometimes pale rusty-brown.

P. hanaki. Forearm on average larger (32.4 [31–33] mm). Skull longer (GLS: 12.4 [12.1–12.7] mm). Dorsal pelage paler and with rusty tinge. NE Libya (Cyrenaica).

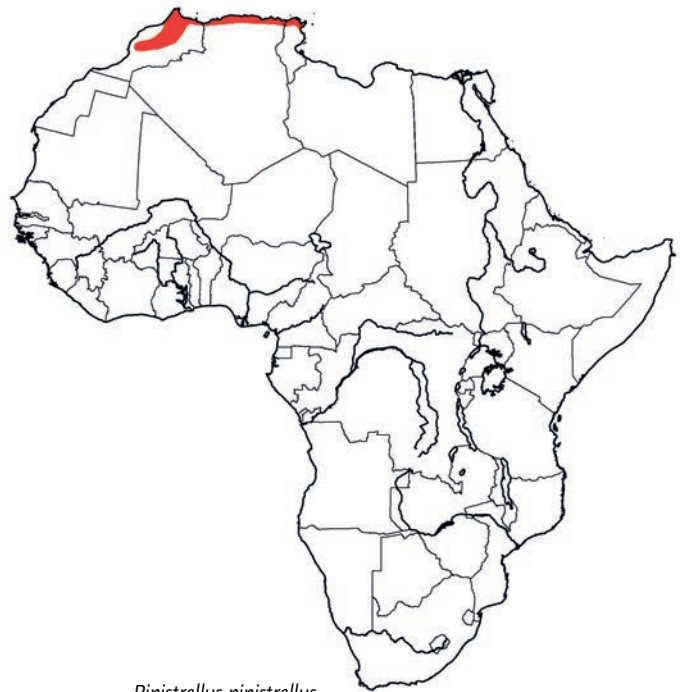
P. kuhlii. Wings with white hind-border. Inner upper incisor unicuspid. Outer upper incisor much smaller than inner incisor.

P. deserti. Wings with white hind-border. Inner upper incisor unicuspid.

P. savii. Larger (FA: 34–38 mm; GLS: 12.8–14.6 mm). Dorsal hairs conspicuously bicoloured. Anterior upper premolar minute, not visible above gum, sometimes absent. Lower molars myotodont.

Eptesicus (2 spp.). Larger (FA: 38–52 mm; GLS: 15.3–20.1 mm). Anterior upper premolar always absent.

Distribution In Africa, only known from mountainous areas in the Mediterranean Coastal and Afromontane–Afroalpine BZs of NW Africa (the Maghreb). Recorded from Morocco (Rif, Middle Atlas, High Atlas), Algeria (Tell Atlas, Hauts Plateaux and Aures Mts) and Tunisia (Panouse 1951, Vaughan *et al.* 1977, Aulagnier & Thévenot 1986, Kowalski & Rzebiak-Kowalska 1991, Fonderflick *et al.* 1998,



Pipistrellus pipistrellus

Beneš & Hanák 2003, Benda *et al.* 2004d). Extralimitally: widely distributed in Europe (including British Isles and south Scandinavia), Asia Minor to Kashmir and Sinkiang (China).

Habitat In Algeria, specimens have been mist-netted in a park in the town of Setif, over irrigation basins and a permanent stream among orchards, and in forests including Cork Oak *Quercus suber* forests with other broadleaved trees (Gaisler & Kowalski 1986). In N Morocco, recorded in Cedar *Cedrus atlantica* and Green Oak *Q. ilex* forests. Some individuals were also captured near an oasis in a semi-desert environment in the Aures Mts (Gaisler & Kowalski 1986), and on the southern slope of the High Atlas, where vegetation was restricted to rare palm trees *Phoenix dactylifera* along rivers running through rocks and cliffs (Fonderflick *et al.* 1998). Recorded up to 2650 m (Benda *et al.* 2004d).

Abundance Common (in mountainous areas). In Algeria, the most frequently captured species during mist-netting sessions in Tlemcen and Djurdjura Mts; abundance decreases toward the coastal zone where *P. kuhlii* is more abundant.

Adaptations Aspect ratio low to very low (Great Britain; Jones & Van Parijs 1993); wing-loading not known. Flight-speeds of 4.3 m/sec (Baagoe 1987) and 4.5 m/sec (Jones & Rayner 1989b) have been recorded. By day, roosts mainly in buildings, ruins and also in trees (Morales Agacino 1933, Brosset 1960a, Gaisler 1983, Benda *et al.* 2004d); probably also roosts in caves and mines as it was mist-netted at the entrance of an abandoned lead mine in Tunisia (Vaughan *et al.* 1977). In Europe, most populations are sedentary but some large movements have been recorded in Germany (up to 770 km; Schöber & Grimmberger 1987). In Algeria, activity decreases from Dec–Feb when some time is probably spent in hibernation, but one individual was mist-netted in Jan when temperature was 6.5 °C, although no other bats were observed (Gaisler 1984).

Foraging and Food Forages by slow-hawking in various habitats including fields, steppes and forests. Usually emerges early in evening and is most active during first half of night (Gaisler & Kowalski 1986). Diet in Africa not known. In Switzerland and Britain, feeds on small insects, mainly Diptera, and also Lepidoptera and Hemiptera (Beck 1995, Barlow 1997).

Echolocation Search-phase call-shape (2–5 m from obstacles) steep FM/QCF. Start-frequency ca. 70–85 kHz; end-frequency (QCF component) 44–48 kHz; call-duration 5–7 ms (Tupinier 1996); inter-call interval 82.3 ± 10.5 ms (Jones & Van Parijs 1993). When flying in clutter, uses only steep linear FM calls (Jones & Van Parijs 1993).

Social and Reproductive Behaviour Usually roosts in groups (colonies). In Europe, ♀♀ begin to establish maternity colonies in Apr–May and leave them in early Aug, at least 15–20 days before their young leave them. Maternity colonies contain 20–200 ♀♀ and subadults (Barlow & Jones 1999). Males establish individually occupied territories from late Aug to late Sep, vocalizing and emitting a strong smell during display flights close to the roosts where mating occurs (Schober & Grimmberger 1987); they have harems of 2–3 ♀♀ (Park *et al.* 1996). In winter they roost either isolated or in clusters up to 2000 individuals (and even 100,000 in one Romanian cave; Decu *et al.* 2003).

Reproduction and Population Structure Litter-size: one in SW Europe, two in NE Europe. In Europe, the reproductive chronology is restricted seasonal monoestry with parturition from mid-Jun to early Jul; young become volant when 3–4 weeks old (Schober & Grimmberger 1987). In Algeria, one ♀ with one embryo was recorded in early Jun (Gaisler 1983). Maximum longevity: 16 years and 7 months (Schober & Grimmberger 1987).

Predators, Parasites and Diseases Ectoparasites include fleas *Ischnopsyllus intermedius*, *I. octactenus* and *Nycteridopsylla longiceps* (Siphonaptera; Ischnopsyllidae) (Anciaux de Faveaux 1976, Beaucournu & Kowalski 1985).

Conservation IUCN Category: Least Concern (based largely on extralimital data).

Measurements

Pipistrellus pipistrellus

FA: 29.6 (28–33) mm, n = 23

WS: n. d.

TL: 72.7 (69–78) mm, n = 15

T: 32.3 (29–34) mm, n = 24

E: 9.2 (7–11) mm, n = 24

Tr: 4.9 (4.5–5.5) mm, n = 9

Tib: n. d.

HF: 6.3 (6–7) mm, n = 10

WT: 4.2 (3.5–5.5) g, n = 20

GLS: 11.5 (11.0–11.9) mm, n = 32

GWS: 7.2 (6.8–7.5) mm, n = 13

C–M³ (alv.): 4.1 (4.0–4.1) mm, n = 3*

Algeria and Morocco (Gaisler 1983, Kowalski & RzebiK-Kowalska 1991, Benda *et al.* 2004b)

*V. Van Cakenberghe (pers. comm.)

Key References Aulagnier & Thévenot 1986; Benda *et al.* 2004d; Gaisler & Kowalski 1986; Kowalski & RzebiK-Kowalska 1991; Panouse 1951.

Stéphane Aulagnier

Pipistrellus rendalli RENDALL'S PIPISTRELLE

Fr. Pipistrelle de Rendall; Ger. Rendalls Zwergfledermaus

Pipistrellus rendalli (Thomas, 1889). Ann. Mag. Nat. Hist., ser. 6, 3: 362. Bathurst, Gambia.

Taxonomy Originally *Vesperugo* (*Vesperus*) *rendalli*. Traditionally *Eptesicus rendalli*. Subsequently classified as *P.* (*Neoromicia*) *rendalli* by Hill & Harrison (1987) and Koopman (1993, 1994), *Nycterikaupius rendalli* by Menu (1987) and *Neoromicia rendalli* by Kearney *et al.* (2002) and Simmons (2005). Synonyms: *faradjius*, *phasma*. Subspecies: two. Chromosome number (Somalia, Zimbabwe, South Africa): 2n = 38; aFN = 50 (McBee *et al.* 1987, Rautenbach & Fenton 1992, Kearney *et al.* 2002).

Description Very small microbat without noseleaf and with tail more or less fully enclosed in interfemoral membrane; four upper and five lower cheekteeth and two upper incisors on each side; ears separated and short (8–14 mm); FA: 29–37 mm; dorsal pelage pale; wings white and not contrasting markedly with dorsal pelage; lower molars myotodont, inner upper incisors unicuspid; profile of forehead region of skull straight. Sexes similar in colour; ♀♀ on average with slightly larger body measurements. Pelage fluffy, without sheen; mid-dorsal hairs 5–6 mm. Dorsal pelage pale to medium-pale brown, not

strongly contrasting with colour of wings; hairs fawn with dark brown at base (sometimes reddish at tip) or with basal third dark greyish-brown, middle third beige, terminal third fawn. Ventral pelage cream, whitish or pale grey (flanks and anal region sometimes pure white); hairs with basal half dark greyish-brown, or pure white. Ears pale brown, subtriangular; tip rounded. Tragus length ca. half of E; broadest above mid-height; anterior margin straight for most of its length (slightly concave near tip); posterior margin smoothly convex with triangular basal lobe; tip rounded (Figure 136m). Wings and interfemoral membrane creamy-white; skin over bones brownish-pink; venation lines cream. Wing-membranes translucent. Interfemoral membrane more heavily pigmented; tail completely enclosed by membrane; postcalcarea lobe present. Baculum as in Figure 141g (Hill & Harrison 1987).

Skull medium-sized and moderately robust for an African *Pipistrellus*. Braincase of medium relative height and breadth; interorbital region of medium breadth; rostrum relatively short but of medium relative breadth (Table 25, p. 603). Profile of forehead region (viewed laterally) straight. Occipital helmet present but low.

Inner upper incisor unicuspid with small basal cusp (not always visible). Outer upper incisor half height of inner incisor; triangular in transverse section and sometimes with a small basal cusp at one or both angles. Anterior upper premolar absent. Lower molars myotodont. Dental formula $\frac{2^{113}}{3123} = 32$.

Geographic Variation Two subspecies are recognized by Koopman (1994) and Simmons (2005), but considered dubious by Kock *et al.* (2002):

P. r. rendalli: Gambia to Chad.

P. r. phasma: Sudan and Somalia to Botswana and Mozambique.

Ansell (1978) and Ansell & Dowsett (1988) indicate that the southern populations of *Pipistrellus rendalli* have a shorter tail and longer ears than populations from other parts of the distribution, but this is incorrect (see Kock *et al.* 2002 for details).

Similar Species Three other African vespertilionids have white wings:

Pipistrellus tenuipinnis. Dorsal pelage blackish-brown, contrasting conspicuously with the white wings. Sometimes smaller (FA: 29.8 [28–33] mm). Inner upper incisor weakly bicuspid. Mostly in wetter habitats.

Scotoecus albobfuscus. Only one upper incisor on each side; penis very long.

Glauconycteris gleni. Dark brown pigment over wing-bones; brown reticulation lines on arm-wing. Outer margin of ear reaching mouth. Lower lip with lobe at posterior corner.

Distribution Endemic to Africa. Widespread in most biotic zones and mosaics south of the Sahara, but recorded only marginally in the Rainforest BZ and not recorded from the Sahel Savanna, South-West

Arid and South-West Cape BZs, nor from the Horn of Africa. Recorded disjunctly, and not in all countries, from Senegal to Sudan and Somalia and southwards to Mozambique, Botswana and E South Africa.

Habitat Mainly woodland savannas from West Africa to Sudan and Somalia, but also degraded lowland rainforest habitats on border of rainforest zone. Known altitudinal range: sea level (Tanga, Tanzania) to 1480 m (Katana, DR Congo). In Mali, frequently reported over ditches and small ponds (Meinig 2000) and, in Burkina, netted over the Mékrou R. and Niger R. (Poché 1975). In Abuko N. P., Gambia, recorded flying over permanent freshwater pools within gallery forests (Kock *et al.* 2002). In Malawi, recorded over a swamp in the Lower Shire Valley. In southern Africa, recorded from well-watered habitats including Mana Pools in Zimbabwe, the Okavango Swamp in Botswana, and a pan within the Zululand Palm Veld in KwaZulu-Natal, South Africa (Kearney & Taylor 1997).

Abundance Not often recorded and considered to be rare throughout range (Smithers 1983, Happold & Happold 1997), but possibly not uncommon in some localities (Rosevear 1965).

Adaptations Aspect ratio low; wing-loading low. Flight slow with bursts of speed; manoeuvrability poor; turns by banking (minimum radius of turn >50 cm) and by stalling-and-twisting. Able to fly across a 1×1×1 m enclosure, but not able to complete a full circuit (3 bats, 10 flights each; M. Happold unpubl.). Wings make distinct whirring noise during flight (Lang & Chapin 1917b). Roosts by day in dense foliage of low bushes and trees, and in huts and houses (especially after dry-season fires when bushes and trees are leafless) (Lang & Chapin 1917b). In Faradje, DR Congo, 'they clung to the brick walls or to the rafters or even to a single grass stalk hanging from the thatch' and preferred the more secluded and darker places (Lang & Chapin 1917b). When disturbed, they moved quickly out of sight, climbing over the brick walls or deeper into the recesses of the thatch. Also recorded roosting among leaves of *Hyphaene* palms in Sudan (BMNH) and S Malawi (Thomas 1896), and in a cotton plant (R. C. Wood, field notes in Kershaw 1922). Does not become torpid during day in DR Congo (Lang & Chapin 1917b). In S Mali, observed drinking from ditches and small ponds shortly after dawn (Meinig 2000).

Foraging and Food Forages for small insects by slow-hawking, usually within 2 m of the ground (Lang & Chapin 1917b). Foraging begins early in the evening. Sometimes forages in vicinity of houses, but rarely enters lighted houses. Also forages low over swamps, pools, pans and rivers (Taylor, P. 1998, M. Happold unpubl.). In Kenya, stomach contents (n = 9) in dry season contained mainly moths, beetles and bugs, with some Orthoptera and other insects (Whitaker & Mumford 1978).

Echolocation Search-phase call-shapes (Malawi): include CF, shallow linear FM and steep/shallow FM. Intensity high; start-frequency up to 76 kHz; end-frequency 42–44 kHz (four tethered bats and others foraging; M. Happold unpubl.).

Social and Reproductive Behaviour Observed roosting in groups of up to six individuals (Lang & Chapin 1917b).



Pipistrellus rendalli

Reproduction and Population Structure Litter-size: 2 (n = 1). Reproductive chronology not known. The record of one ♀ simultaneously lactating and pregnant with two embryos in Dec in KwaZulu–Natal (Taylor, P. 1998), suggests polyoestry with postpartum oestrus, but it is not yet known if polyoestry is normal in this species. At ca. 4°N (Garamba N. P., NE DR Congo), a ♀ with two juveniles was recorded at end of Apr (Verschuren 1957); no data for other months. At ca. 16°S in Malawi, 1 of 2 ♀♀ was lactating and the other post-lactating in Apr: neither was pregnant (M. Happold unpubl.).

Predators, Parasites and Diseases Ectoparasites include bed-bugs *Cacodmus ignotus*, *Aphrania recta* (Hemiptera: Cimicidae) (Ueshima 1968); bat-flies *Basilina ansifera*, *B. bouvieri* (Diptera: Nycteribiidae); and mites *Spinturnix walkerae*, *Spinturnix faini* (Acari: Spinturnicidae); and *Rodhainyssus eptesicus* (Acari: Gastronyssidae) (Anciaux de Faveaux 1984).

Conservation IUCN Category: Least Concern.
Widespread; no known threats.

Measurements

Pipistrellus rendalli

FA (♂♂): 32.7 (29–36) mm, n = 65

FA (♀♀): 34.6 (31–37) mm, n = 70

WS (a): 254 (227–271) mm, n = 4

TL: 89.9 (70–102) mm, n = 21

T (♂♂): 33.4 (30–37) mm, n = 7

T (♀♀): 35.8 (33–41) mm, n = 10

E (♂♂): 11.1 (8–14) mm, n = 39

E (♀♀): 11.7 (10–14) mm, n = 39

Tr: 4.7 (2.7–5.9) mm, n = 37

Tib (♂♂): 11.0 (9–13) mm, n = 56

Tib (♀♀): 11.7 (9–14) mm, n = 58

HF: 8.2 (7–10) mm, n = 14

WT (♂♂): 5.5 (4–9) g, n = 21

WT (♀♀): 6.5 (5–9) g, n = 19

GLS: 13.3 (12.3–14.4) mm, n = 90

GWS: 8.9 (8.3–9.7) mm, n = 55

C–M³ (alv.): 4.7 (4.1–5.2) mm, n = 94

Throughout geographic range (AMNH, BMNH, CAS, CM, FMNH, HC, HZM, IRSN, MHNG, MNHN, RMCA, USNM, ZFMK, ZMA and literature)

Key References Lang & Chapin 1917b; Rautenbach & Fenton 1992; Rosevear 1965.

Victor Van Cakenberghe & Meredith Happold

Pipistrellus rueppellii RÜPPEL'S PIPISTRELLE

Fr. Pipistrelle de Rüppell; Ger. Rüppells Zwergfledermaus

Pipistrellus rueppellii (J. Fischer, 1829). Synopsis Mammalium, p. 109. Dongola, Northern Province, Sudan.

Taxonomy Originally *Vespertilio temminckii* Cretzschmar, 1827; renamed *Vespertilio Rüppellii*. Traditionally *Pipistrellus rueppellii*. Subsequently classified as *P. (Pipistrellus) rueppellii* by Hill & Harrison (1987), Koopman (1993) and Simmons (2005), *P. (Vansonia) rueppellii* by Koopman (1994), and *Pipistrellus rueppelli* by Menu (1987). The specific name is sometimes spelled without the first *e* and with *ü*, and/or with one *p*, one *l* or one *i*: of these, *rueppellii* (although not the original spelling) is used most commonly, and is retained here in the interests of stability and because the species is named after Rüppell. Synonyms: *coxi*, *fuscipes*, *hypoleucus*, *leucomelas*, *pulcher*, *senegalensis*, *vernayi*. Subspecies: uncertain (see Geographic Variation). Chromosome number (South Africa): 2n = 36; aFN = 54 (Rautenbach *et al.* 1993).

Description Very small (and very beautiful) microbat without noseleaf and with tail more or less fully enclosed in interfemoral membrane; five upper cheekteeth (all visible above gum), five lower cheekteeth and two upper incisors on each side; ears separated and short (6–14 mm); FA: 29–37 mm; lower molars nyctalodont; mid-ventral pelage uniquely pure white (cf. all other African *Pipistrellus*). Sexes similar in colour and size. Pelage soft, dense, sleek; mid-dorsal hairs 5–6 mm. Dorsal pelage grey, pale greyish-brown or sepia brown, sometimes with silvery sheen; hairs dark sepia brown or dark grey with either sepia brown or pale grey at tip. Ventral pelage (except throat) pure white; hairs pure white. Throat pure white or pale rusty-brown. Ears relatively long for this genus; subtriangular, rounded at

tip; outer margin with semi-circular lobule at base. Tragus length ca. half of E; breadth constant for most of length; anterior margin slightly concave; posterior margin slightly and smoothly convex with small lobule at base; tip rounded (Figure 136n). Wings usually translucent pale grey but varying from whitish to medium brown; pale hind-border present in at least some specimens. Interfemoral membrane pale grey. Penis relatively long (12–13 mm). Baculum as in Figure 139i, j (Hill & Harrison 1987); variation in Kearney *et al.* (2002).

Skull medium-sized and moderately robust for an African *Pipistrellus*. Braincase relatively high but of medium relative breadth; interorbital region of medium relative breadth; rostrum of medium relative length but relatively narrow (Table 25, p. 603). Profile of forehead region (viewed laterally) weakly concave to almost straight. No occipital helmet. Inner upper incisor very long, very deeply bicuspid and grooved. Outer upper incisor small (not more than half height of inner incisor) to minute (ca. same height as cingulum of inner incisor), sometimes tucked close against inner incisor. Anterior upper premolar medium-sized, clearly visible above gum, within tooththrow but sometimes slightly displaced linguallly; canine and posterior premolar not in contact. Lower molars nyctalodont. Dental formula: $^{2123}_{3123} = 34$.

Geographic Variation Five African and one extralimital subspecies are recognized by Koopman (1994), but their validity is uncertain. The African subspecies are:

- P. r. senegalensis*: Algeria to Senegal.
P. r. rueppellii: Egypt to Nigeria and C Sudan.
P. r. fuscipes: Ethiopia to N Angola.
P. r. pulcher: NE Tanzania.
P. r. leucomelas: Malawi to the former Transvaal and S Angola.

In contrast, Smithers (1983), Meester *et al.* (1986) and Simmons (2005) recognize *vernayi* as a subspecies but not *leucomelas*. The status of *leucomelas* is controversial; it is considered a synonym of *P. r. rueppellii* by Meester *et al.* (1986) and a synonym of *P. r. vernayi* by Simmons (2005).

Similar Species No other African *Eptesicus* or *Pipistrellus* has ventral pelage (excluding throat) pure white.

Distribution In Africa, recorded very disjunctly in almost all biotic zones (a notable exception being the Somalia–Masai Bushland BZ), but not widely recorded in any zone except the Eastern Rainforest–Savanna Mosaic. Occurs along the Nile R. and its tributaries in Egypt and Sudan, then Ethiopia to W coast of DR Congo and southwards to Angola, Botswana and extreme N of South Africa; also Zanzibar I. There are seemingly isolated records in NE Nigeria, Chad, Morocco and Algeria, and on the N Senegal–Mauritania border. Furthermore, there is a recent record (not mapped) at 16° 29' 969 N, 07° 42' 911 W in SE Mauritania (Padial & Ibáñez 2005). Extralimittally: Arabia, Israel, Bahrain and Iraq.

Habitat Mainly woodland and grassland savannas, but occasionally found in desert habitats and montane forests and along some river systems in the rainforest zone in DR Congo. In Mauritania, found in Sahel savannas; the most recent record being from 'temporary wetland surrounded by Sahel savannas composed mainly by *Acacia* spp. formations' (Padial & Ibáñez 2005). In Egypt, Zambia, Botswana and Zimbabwe, associated with rivers or swamps (Smithers 1983). In Malawi, common near streams, ponds and lakes in montane

forests. Probably dependent on rivers, lakes or large pools over which to forage. Forest areas are largely avoided according to Koopman (1994), but possibly this only applies to forests without suitable foraging areas over water. Has been recorded from sea level (Tanzania) to 1700 m (Malawi).

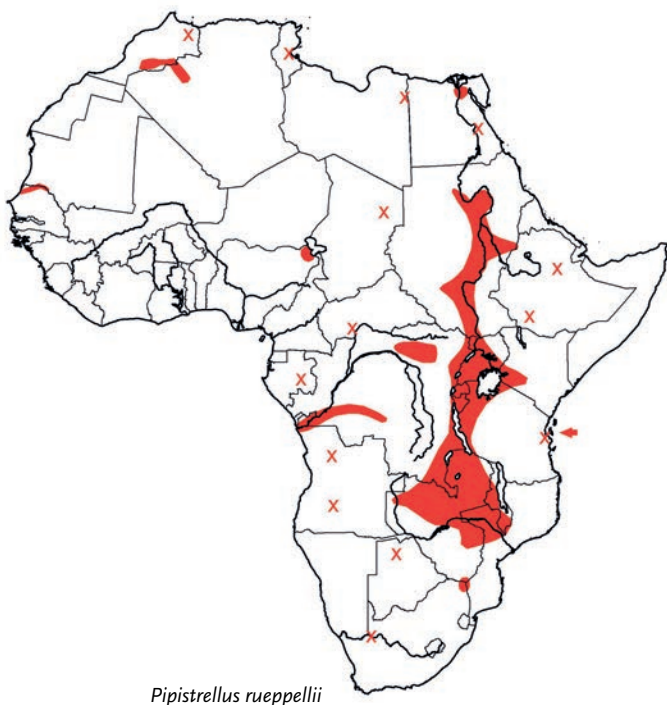
Abundance Uncertain. Moderately common in some localized areas near open water. Rare in Morocco and considered to be a remnant population there (Arlettaz & Aulagnier 1988).

Adaptations Aspect ratio low; wing-loading very low. Flight slow and highly manoeuvrable in confined spaces, faster and very agile in open spaces. Turns by banking (minimum radius <25 cm) and by stalling-and-twisting; can take off from ground; cannot hover. Individuals sustained flight within a 1×1×1 m enclosure for up to three circuits/flight (7 bats, 10 flights each). Cursorial locomotion on ground and climbing on sloping surfaces are moderately efficient. By day, has been found under plaster on the wall of a ruin (Allen & Loveridge 1933), behind a notice board against a wall (Ansell 1960a) and under rocks in desert and semi-desert areas in Egypt (Hoogstraal 1962). In Malawi, individuals sometimes became torpid during the day at 21–24 °C. Kidneys with short papilla; predicted mean maximum urine concentration comparatively low (3045 mOsmol/kg) (Happold & Happold 1988).

Foraging and Food Often (perhaps almost always) forages by slow-hawking over open water and its surrounding grassy or marshy areas. Foraging individuals fly straight and fast with frequent interruptions to swerve, dive or swoop upwards in pursuit of prey – such manoeuvres are very acrobatic (M. Happold unpubl.). They often fly within a metre of the surface, but intermittently fly higher, up to ca. 10 m. They occasionally make contact with water, sometimes up to seven contacts in very quick succession; this might be to obtain water but the frequency of contacts suggests that they probably take prey from the water surface. Foraging has been observed over lakes, dams, ponds, rivers and open stretches along streams (Archer 1977, M. Happold unpubl.). Faecal pellets of one individual contained remains of Coleoptera only (Aldridge & Rautenbach 1987).

Echolocation Search-phase call-shape (Malawi): steep FM/QCF and curvilinear steep/shallow FM (Figure 118f–h). Intensity high; start-frequency up to 100 kHz; end-frequency and peak-frequency 41–48 kHz (usually 46–48 kHz); maximum duration 7.3 ms (eight bats, flying in open; M. Happold unpubl.). In Zimbabwe, call-shape steep-shallow FM; start-frequency 70 kHz; end-frequency 40 kHz; peak-frequency 45 kHz; maximum duration 8 ms (one bat, flying in open; Fenton & Bell 1981). In South Africa, call-shape FM (no details); start-frequency 70 kHz; end-frequency 40 kHz (five bats in flight-cage; Aldridge & Rautenbach 1987).

Social and Reproductive Behaviour Congregates in small numbers (up to several dozens) over water and sometimes individuals follow each other. Found singly or in pairs under rocks in Egypt (Hoogstraal 1962). One was found behind a notice board against a wall, and another in the same place several days later (Ansell 1960a). Sometimes said to be 'solitary' (e.g. Ansell 1960a), but observations are too few to be conclusive.



Reproduction and Population Structure Litter-size and reproductive chronology not known. Juveniles have been reported in Sep and Nov in Zambia (Ansell 1960a, 1986), and very young subadults in Dec in Malawi (Happold & Happold 1990a), but year-round data are not available.

Predators, Parasites and Diseases Ectoparasites include a flea *Ischnopsyllus emminus* (Siphonaptera: Ischnopsyllidae) (Beaucournu & Kock 1996).

Conservation IUCN Category: Least Concern.
Widespread; no known threats.

Measurements

Pipistrellus rueppellii

FA: 32.7 (29–37) mm, n = 106

WS (a): 262.8 (254–282) mm, n = 6*

TL: 83.1 (69–89) mm, n = 47

T: 32.4 (25–41) mm, n = 47

E: 11.9 (6–14) mm, n = 82

Tr: 5.8 (4.5–7.0) mm, n = 17

Tib: 9.8 (10–15) mm, n = 98

HF: 8.9 (6–10) mm, n = 27

WT: 6.3 (4–9) g, n = 36

GLS: 13.3 (12.1–15.0) mm, n = 72

GWS: 8.7 (7.8–9.2) mm, n = 40

C–M³ (alv.): 4.7 (4.1–5.4) mm, n = 74

Throughout geographic range (AMNH, BMNH, CAS, CM, FMNH, HC, HZM, MHNG, MNHN, RMCA, SMF, TM, USNM, ZFMK, ZMA, ZMB, from Van Cakenberghe, pers. comm.)

*Malawi (M. Happold unpubl.)

Key Reference Smithers 1983.

Meredith Happold

Pipistrellus rusticus RUSTIC PIPISTRELLE (RUSTY PIPISTRELLE)

Fr. Pipistrelle rustique; Ger. Rustikale Zwergfledermaus

Pipistrellus rusticus (Tomes, 1861). Proc. Zool. Soc. Lond. 1861: 35. 'Damaraland'. Limited to Olifants Vlei, Damaraland, Namibia by Thomas (1926).

Taxonomy Originally *Scotophilus rusticus*. Traditionally *Pipistrellus rusticus*. Subsequently classified as *P. (Pipistrellus) rusticus* by Hill & Harrison (1987), Koopman (1993, 1994) and Simmons (2005), and *Pipistrellus rusticus* by Menu (1987) and Kearney *et al.* (2002). Synonyms: *marrensis*. Subspecies: two. Chromosome number (South Africa): 2n = 42; aFN = 50 (Rautenbach *et al.* 1993). This species shares the Robertsonian fusion chromosome 11/12 with *P. hesperidus* (Kearney *et al.* 2002).

Description Very small microbat without noseleaf, tail more or less fully enclosed in interfemoral membrane; five upper cheekteeth (all visible above gum), five lower cheekteeth and two upper incisors on each side; ears separated and short (10–12 mm); FA: 24–31 mm; wings dark, sometimes with white hind-border; dorsal pelage variable; dorsal and ventral hairs bicoloured; lower molars nyctalodont; inner upper incisor unicuspid; profile of forehead region of skull straight to weakly concave; posterior margin of tragus without sharp angle. Sexes similar. Pelage soft, dense; mid-dorsal hairs ca. 4 mm. Dorsal pelage reddish-brown, orange-brown, greyish-orange, greyish-brown or medium brown; hairs with basal half medium brown, dark brown or blackish-brown. Both paler and darker individuals are sometimes found at the same localities. Ventral pelage orange, yellowish-orange, creamy-orange, yellow, or cream; darkest under chin, palest in pelvic region; hairs with basal half blackish-brown. Naked skin on muzzle and around eyes pale or medium brown. Ears pale or medium reddish-brown, triangular with rounded tip. Tragus length just under half of E; widest near mid-height, anterior margin straight; posterior margin smoothly convex for most of its length but with wide, deep notch above a basal lobe at base; tip rounded (Figure 136o). Wing-membranes pale brown, dark brown or reddish-black; sometimes

with narrow white hind-border. Interfemoral membrane medium brown or reddish-brown, paler than wing-membranes; sometimes with cream border. Baculum as in Figure 139k, l (Hill & Harrison 1987, Kearney *et al.* 2002).

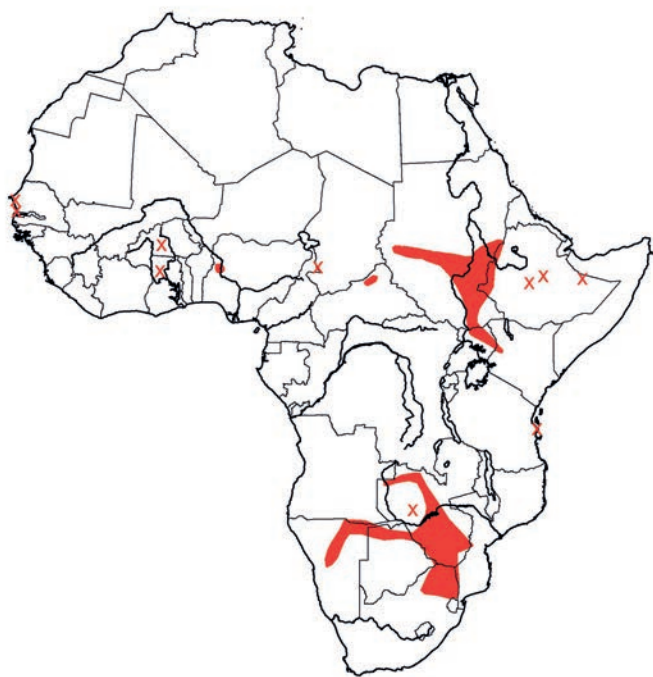
Skull small and gracile for an African *Pipistrellus*. Braincase of medium relative height and breadth; interorbital region of medium relative breadth; rostrum of medium relative length but relatively broad (Table 25, p. 603). Profile of forehead region (viewed laterally) straight to weakly concave. No occipital helmet. Inner upper incisor unicuspid. Outer upper incisor minute, reaching only slightly above cingulum of inner incisor. Anterior upper premolar usually present, minute, seldom visible above gum, displaced lingually; canine and posterior premolar in contact. Lower molars nyctalodont. Dental formula: $2^{123}/_{3123} = 34$.

Geographic Variation Two subspecies are recognized (Koopman 1994, Simmons 2005):

P. r. marrensis: Senegal to Ethiopia and NW Kenya. On average slightly smaller (FA: 26.8 [25–31] mm, n = 39; GLS: 11.3 [10.8–12.3] mm, n = 25; C–M³: 4.0 [3.6–4.4] mm, n = 26; V. Van Cakenberghe pers. comm.). Skull with narrower rostrum.

P. r. rusticus: Zambia, NE Namibia, N Botswana, Zimbabwe and NE South Africa. On average slightly larger (FA: 27.8 [24–31] mm, n = 58; GLS: 11.7 [11.0–12.6] mm, n = 43; C–M³: 4.2 [3.8–4.6] mm, n = 43; V. Van Cakenberghe pers. comm.). Skull with broader rostrum.

Similar Species Three other sub-Saharan *Pipistrellus* have lower molars nyctalodont; inner upper incisors unicuspid (Table 27, p. 608):

*Pipistrellus rusticus*

Pipistrellus aero. Dorsal pelage dark brown. Forearm usually longer (31–34 mm). Profile of forehead region of skull moderately concave. Kenya, Ethiopia.

P. deserti. Dorsal pelage pale sepia brown to pale yellowish-brown (sometimes with greenish tint). Wings with white hind-border. Profile of forehead region of skull moderately concave. Distribution possibly only overlapping in West Africa, Sudan and Kenya.

P. hesperidus. Dorsal pelage darker, less orange and longer. Wings without white hind-border.

Distribution Endemic to Africa. Distribution disjunct. Recorded from scattered localities in the Sudan Savanna, Guinea Savanna and Somalia–Masai Bushland BZs, from Senegal and Gambia to Ethiopia (but not in all countries). A record from Niumi N. P., Sine Saloum Delta in Gambia (13° 35'N, 16° 32'W) by Kock *et al.* (2002) is not mapped. Also recorded from one locality in the Coastal Forest Mosaic BZ in E Tanzania, and from several localities in the Zambezian Woodland BZ and northern fringe of the South-West Arid BZ. The southern records are from W Zambia, Namibia, N Botswana, Zimbabwe and South Africa. The occurrence of *P. rusticus* in Malawi is uncertain (M. Happold & V. Van Cakenberghe pers. comm.) and, pending re-examination of material assigned to both *P. rusticus* and *P. kuhlii* (now *P. hesperidus*) by Happold *et al.* (1987) and Happold & Happold (1997), no Malawi records have been mapped.

Habitat Inhabits montane and riverine forests, woodland and dry savanna, at high and low altitudes, and coastal forests and scrub. Often mist-netted over water.

Abundance Rare across distribution, but observed in comparatively large numbers at certain localities. At Messina (Limpopo Province, South Africa), *P. rusticus* comprised 22% of 60 bats (seven species) caught over three mist-net-nights in 1996 (*Nycticeinops schlieffeni*, the predominant species netted, comprised

50% of this catch). In the Waterberg region (Limpopo Province, South Africa), *P. rusticus* was the predominant species mist-netted; in 2001, it comprised 79% of 14 bats (three species) caught over three mist-net-nights; in 2004, using a larger macro mist-net, it comprised 90% of 31 bats (three species) caught over two mist-net-nights (E. Seamark & T. Kearney unpubl.).

Adaptations Aspect ratio low; wing-loading very low (Aldridge & Rautenbach 1987). Day-roosts include hollow trees (HZM). In South Africa, does not enter hibernation or prolonged periods of torpor during winter (van der Merwe & Rautenbach 1990).

Foraging and Food Forages by slow-hawking; recorded foraging between 3–18 m over a dry river bed (Smithers & Wilson 1979) and over open water (where it is most often encountered) (Rautenbach 1982). Also mist-netted in riverine forest and at dams in dry mopane veld (Rautenbach 1982), but not necessarily while foraging. Flies lower and less erratically than *P. capensis* (Shortridge 1934). Begins foraging at dusk. Insectivorous, details not known.

Echolocation Search-phase call-shape (South Africa): steep FM/QCF. Intensity high; start frequency (mean \pm S.D.) 77.8 ± 5.2 kHz; end-frequency 46.8 ± 2.4 kHz; peak-frequency 53 ± 1.8 kHz; call-duration 2.8 ± 0.6 ms (15 calls; Taylor 1999a).

Social and Reproductive Behaviour No information. A group of three was found roosting together in a tree in Zambia (HZM, Taylor 2000).

Reproduction and Population Structure Litter-size: normally two (one from each uterine horn), occasionally one; up to five conceptuses but no more than two implantations were observed (van der Merwe & Rautenbach 1990). At ca. 24° S (near Vaalwater, South Africa), the reproductive chronology is restricted seasonal monoestry, with spermatogenesis from Oct–Feb; sperm storage in ♂♂ for at least five months; copulation beginning in Apr; sperm storage in ♀♀ (Apr–Aug); ovulation and fertilization in second half of Aug; implantation in Sep; gestation estimated to be 11–12 weeks (possibly with an interval of retarded early embryonic development) and births in Nov (van der Merwe & Rautenbach 1990). Contrary to most other species of bats, in which the amnion is formed by folding, it is formed by cavitation in *P. rusticus* (van der Merwe 1994b).

Predators, Parasites and Diseases No information. Bats identified as *P. rusticus* and said to be hosts of bed-bugs *Cacodmus villosus* and *C. sparsilis* (Hemiptera: Cimicidae) by Kock *et al.* (1998b), need re-examination to confirm their identity (M. Happold pers. comm.).

Conservation IUCN Category: Least Concern.

Measurements

Pipistrellus rusticus

FA: 27.4 (24–31) mm, n = 97*

WS: n. d.

TL: 74.4 (65–85) mm, n = 17

T: 30.0 (19–32) mm, n = 33

E: 10.4 (10–12) mm, n = 30
 Tr: 4.6 (3.2–5.0) mm, n = 37
 Tib: 9.4 (6–12) mm, n = 86*
 HF: 5.4 (4–6) mm, n = 22
 WT: 4.0 (3.4–4.0) g, n = 12
 GLS: 11.5 (10.5–12.4) mm, n = 65*
 GWS: 7.8 (6.7–8.5) mm, n = 35*
 C–M³: 4.1 (3.6–4.6) mm, n = 66*

Namibia, Botswana, Zimbabwe, South Africa (AM, DM, TM)

*Throughout geographic range (V. Van Cakenberghe pers. comm.)

Key References Rautenbach 1982; Smithers & Wilson 1979; van der Merwe & Rautenbach 1990.

Teresa Kearney

Pipistrellus savii SAVI'S PIPISTRELLE

Fr. Vespère de Savi (Pipistrelle de Savi); Ger. Alpenfledermaus

Pipistrellus savii (Bonaparte, 1837). Fauna Ital. 1, fasc. 20. Pisa, Italy.

Taxonomy Originally *Vespertilio savii*. Traditionally *Pipistrellus savii*. Subsequently classified as *P. (Hypsugo) savii* by Hill & Harrison (1987) and Koopman (1993), *P. (Pipistrellus) savii* by Koopman (1994), and *Hypsugo savii* by Horáček & Hanák (1986), Menu (1987), Ruedi & Arlettaz (1991), Volleth & Heller (1994), Volleth *et al.* (2001), Hofer & Van Den Bussche (2003), Benda *et al.* (2004d) and Simmons (2005). Chromosomal and molecular evidence supports the generic status of *Hypsugo* but, although *savii* is the type species, it is treated here as a species of *Pipistrellus* solely for convenience (see Genus *Pipistrellus*). Synonyms: 13; none in Africa. Subspecies: four; only one in Africa. Chromosome number (Italy): 2n = 44; aFN = 50 (Capanna & Civitelli 1967).

Description Very small microbat without noseleaf and with tail more or less fully enclosed in interfemoral membrane; four or five upper cheekteeth (but only four visible above gum), five lower cheekteeth and two upper incisors on each side; ears separated and short (12–15 mm); FA: 34–38 mm; wings dark without white hind-border; pelage pale; dorsal and ventral pelage bicoloured; lower molars myotodont; inner upper incisor bicuspid; profile of forehead region of skull weakly concave to almost straight. Sexes similar. Pelage dense, soft, glossy; mid-dorsal hairs 7–8 mm. Dorsal pelage pale yellowish-brown with glossy golden sheen; hairs distinctly bicoloured with basal half to two-thirds dark brown. Ventral pelage distinctly paler; hairs yellowish-white or greyish-white with basal half blackish-brown. Naked skin of muzzle and around eyes dark brown or black. Ears dark brown or black; broader and rounder than in other North African pipistrelles. Tragus length ca. 42% of E; maximum breadth only a little less than length of anterior margin; posterior margin smoothly convex with basal lobe; tip rounded. Wing and interfemoral membranes dark brown; wings without white hind-border. Baculum as in Figure 140e (Hill & Harrison 1987).

Skull large and moderately robust for an African *Pipistrellus*. Braincase of medium relative height but relatively narrow, interorbital region relatively narrow; rostrum of medium relative length but broad (Table 25, p. 603). Profile of forehead region (viewed laterally) weakly concave to almost straight. No occipital helmet. Inner upper incisor bicuspid, the posterior cusp just a little shorter than the main cusp. Outer upper incisor at least as high as the posterior cusp of the inner incisor. Anterior upper premolar absent in 10–40% of animals; if present it is minute, not visible above gum, displaced lingually;

canine and posterior premolar in contact. Lower molars myotodont. Dental formula: $2^{113}/_{3123} = 32$ or $2^{123}/_{3123} = 34$.

Geographic Variation Four subspecies recognized (Simmons 2005); only one, *P. s. ochromixtus*, in Africa.

Similar Species Two *Eptesicus* and five other *Pipistrellus* occur in North Africa (excluding *P. ariel* in S Egypt):

Pipistrellus rueppellii. Mid-ventral pelage pure white; throat sometimes pale rusty-brown.

P. deserti. Smaller (FA: 25–34 mm; GLS: 10.8–12.4 mm). Ears longer than their breadth. Wings with white hind-border. Lower molars nyctalodont.

P. kuhlii. Ears longer than their breadth. Wings with white hind-border. Inner upper incisor unicuspid. Anterior upper premolar minute, displaced lingually but usually visible. Lower molars nyctalodont.

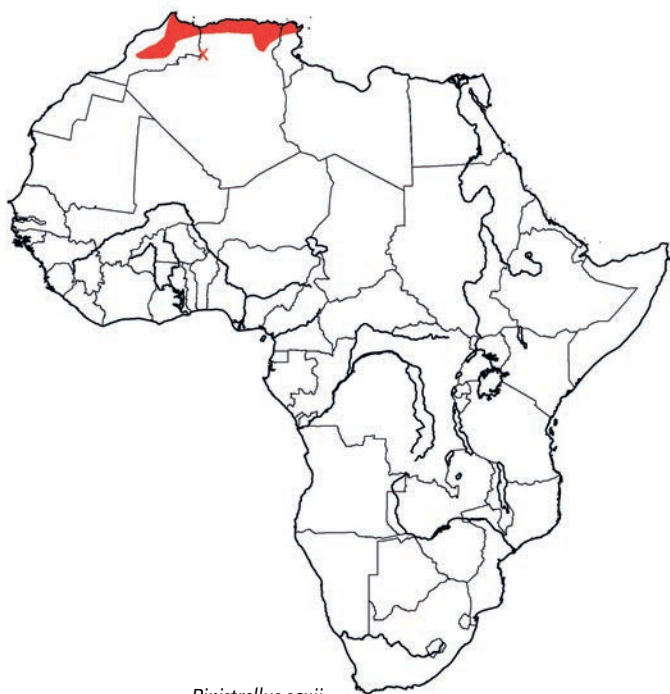
P. pipistrellus. Smaller (FA: 28–33 mm; GLS: 11.0–11.9 mm). Ears longer than their breadth. Anterior upper premolar visible above gum. Lower molars nyctalodont.

P. hanaki. Smaller (FA: 31–33 mm; GLS: 12.1–12.7 mm). Anterior upper premolar visible above gum. Lower molars nyctalodont.

Eptesicus (2 spp.). Larger (FA: 38–52 mm; GLS: 15.3–20.1 mm). Anterior upper premolar always absent.

Distribution In Africa, mainly found in the upland and mountainous areas of the Mediterranean Coastal and Afrotropical Afroalpine BZs of NW Africa, and marginally from the adjacent Sahara Arid BZ. Recorded from Morocco (Rif, Beni Snassen, Middle Atlas, High Atlas), Algeria (Tell Atlas, Central Plateau) and Tunisia (Djebel Zaghouan) (Panouse 1955, Hill 1964, Vaughan *et al.* 1977, Aulagnier & Thévenot 1986, Kowalski & Rzebik-Kowalska 1991, Benda *et al.* 2004d). Extraliminally: southern Europe (palaeo-xeromontane element), the Canary and Cape Verde Is. and most of temperate Asia.

Habitat As in Europe (where it ranges up to 3300 m in the Sierra Nevada, Spain), inhabits rocky uplands and mountains (500–2004 m in Jbel Babor), deep valleys, cliffs and limestone areas; has also been found in a park in a town and in buildings (Gaisler 1983, Gaisler & Kowalski 1986). Several captures were recorded in sparsely vegetated

*Pipistrellus savii*

places, e.g. over water on montane grasslands surrounded by forests of Cork Oak *Quercus suber*, Green Oak *Q. ilex* or Atlas Cedar *Cedrus atlantica* (Gaisler 1983, Gaisler & Kowalski 1986). On the southern slope of the High Atlas, restricted to rare localities where palm trees *Phoenix dactylifera* grow along rivers running through rocky canyons (Fonderflick *et al.* 1988, Benda *et al.* 2004d).

Abundance Uncertain in Africa. There are few records from North Africa but this probably reflects inappropriate census methods (acoustic detection should be used). Suitable mountain habitat is widespread.

Adaptations Wing morphology not known. Flight described as quick, with wide swingings, 10–50 m above the ground (Barataud 1992). By day, roosts in holes in trees, behind bark, in rock fissures and in crevices in walls (Kowalski & Rzebik-Kowalska 1991). Migratory movements are suspected in Europe where the longest recorded movement is 250 km. In Europe, hibernates in winter; no information for Africa.

Foraging and Food Forages by fast-hawking in open spaces, sometimes above houses and treetops. Emerges shortly after sunset and forages almost all night. Feeds on small flying insects; in Switzerland, the diet was Lepidoptera, Diptera (mainly Tipulidae), Hymenoptera, Neuroptera and Hemiptera (Beck 1995).

Echolocation Search-phase call-shape (Switzerland; above canopies of trees): QCF. Start-frequency 35–38 kHz; end-frequency 30–33 kHz; call-duration 10–15 ms; inter-call interval 190 ms (Zingg 1988, Tupinier 1996).

Social and Reproductive Behaviour Very little information from Africa. In Europe, roosts singly while hibernating; maternity colonies of 20–70 ♀♀ are established in spring (Schober & Grimmberger 1987).

Reproduction and Population Structure Litter-size (SW Europe): usually two. In Europe, the reproductive chronology is restricted seasonal monoestry with mating in late Aug–Sep and births in mid-Jun to early Jul (Schober & Grimmberger 1987). No conclusive data for Africa; mating observed in Nov in Algeria.

Predators, Parasites and Diseases Ectoparasites include a flea *Ischnopsyllus octactenus* (Siphonaptera: Ischnopsyllidae) (Beaucournu & Kowalski 1985) and a tick *Argas transgaripepinus* (Acarina, Argasidae) (Médard *et al.* 1997).

Conservation IUCN Category: Least Concern (based mainly on extralimital data).

Measurements

Pipistrellus savii

FA: 35.5 (34–38) mm, n = 22

WS (c): 220–225 mm[†]

TL: 92.7 (89–101) mm, n = 6

T: 39.4 (37–42) mm, n = 8

E: 13.5 (12–15) mm, n = 8

Tr: 5.7 (5.0–6.0) mm, n = 3

Tib: 13.6 (11–15) mm, n = 9*

HF: 7.7 (7–9) mm, n = 9

WT: 7.1 (5.5–9.5) g, n = 8

GLS: 14.0 (12.8–14.6) mm, n = 9

GWS: 9.0 (8.3–9.5) mm, n = 9

C–M³ (alv.): 4.8 (4.5–5.0) mm, n = 7*

Morocco and Algeria (Hill 1964, Gaisler 1983, Kowalski & Rzebik-Kowalska 1991, Fonderflick *et al.* 1998)

*V. Van Cakenberghe (pers. comm.)

[†]Europe (Schober & Grimmberger 1987)

Key References Aulagnier & Thévenot 1986; Benda *et al.* 2004d; Gaisler 1983; Kowalski & Rzebik-Kowalska 1991; Panouse 1955.

Stéphane Aulagnier

Pipistrellus somalicus SOMALI PIPISTRELLE (SOMALI SEROTINE)

Fr. Pipistrelle de Somalie; Ger. Somalia-Zwergfledermaus

Pipistrellus somalicus (Thomas, 1901). Ann. Mag. Nat. Hist., ser. 7, 8: 32. Hargeisa, Northwest Province, Somalia.

Taxonomy Originally *Vespertilio minutus somalicus*. Traditionally *Eptesicus somalicus*. Subsequently classified as *P. (Neoromicia) somalicus* by Hill & Harrison (1987) and Koopman (1994), *Nycterikaupius somalicus* by Menu (1987), *E. (Neoromicia) somalicus* by Koopman (1993) and *Neoromicia somalicus* by Simmons (2005). Synonyms: *humbloti*, *malagasyensis*, *ugandae*. Subspecies: uncertain (see Geographic Variation). The taxonomy of *P. somalicus* is problematical and its position within the *capensis*, cf. *melckorum*, *zuluensis* group is still unclear. Besides being attributed to *minutus*, it has also been considered a subspecies of *pusillus* Leconte, 1857 and of *capensis* A. Smith, 1829, but it was indicated to be a distinct species by several authors, including Matschie (1907), Rosevear (1965) and Kock (1969a). Previously, when *P. zuluensis* was thought to occur only in southern Africa, it was often considered to be a subspecies of *somalicus*, but differences in karyotype (diploid number) and the shape of the cranium support the specific status of *zuluensis*, and most of the southern African records were transferred to this species by Rautenbach *et al.* (1993). However, there are some strong indications that both *somalicus* and *zuluensis* occur in the southern part of the continent and that *zuluensis* also occurs in eastern Africa (Peterson *et al.* 1995). In West Africa, the relationship with *P. guineensis* also remains unclear. Chromosome number (Somalia): $2n = 26$; $aFN = 48$ (McBee *et al.* 1987) although there is now some uncertainty about the identity of the specimens used.

Description Very small microbat without noseleaf and with tail more or less fully enclosed in interfemoral membrane; four or five upper cheekteeth (but only four visible above gum), five lower cheekteeth and two upper incisors on each side; ears separated and short (7–14 mm); FA: 22–32 mm; dorsal pelage brownish; dorsal and ventral hairs faintly bicoloured; wings dark, occasionally with narrow white hind-border; lower molars myotodont, inner upper incisor unicuspid or weakly bicuspid, profile of forehead region of skull weakly concave to almost straight. Sexes similar in colour; ♀♀ with forearms and metacarpals 1 mm longer on average than those of ♂♂. Pelage soft, dense, fairly fluffy; mid-dorsal hairs ca. 5–8 mm. Dorsal pelage brownish; hairs dark brown with brownish tip. Ventral pelage slightly paler; hairs brown with paler tip. In a very small number of specimens, a pale to whitish spot can be found on the throat. Ears dark brown, relatively short; outer margin convex at base, then slightly concave and then straight; tip rounded. Tragus length ca. half of E but very variable in preserved material; broadest near mid-height; anterior margin almost straight; posterior margin smoothly convex for most of its length (sometimes slightly angular just above the basal lobe); basal lobe triangular, prominent; tip rounded (Figure 136p). Wings dark brown; interfemoral membrane slightly lighter. A conspicuous white hind-border has been reported regularly in the literature but, in a sample of 102 specimens, only ca. 10% had a conspicuous hind-border, ca. 50% had a very narrow hind-border, and the remainder had no hind-border. Baculum as in Figure 141h (Hill & Harrison 1987).

Skull small and gracile for an African *Pipistrellus*. Braincase of medium relative height and breadth; interorbital region relatively narrow; rostrum of medium relative length and breadth. (Table 25, p. 603). Profile of forehead region (viewed laterally) weakly concave to almost straight. No occipital helmet. Inner upper incisor usually unicuspid, occasionally weakly bicuspid; outer upper incisor very small, hardly higher than the cingulum of the inner incisor. Anterior upper premolar usually absent; if present, not visible or barely visible above gum; canine and posterior premolar in contact. Lower molars myotodont. Dental formula: usually $2^{113}/_{3123} = 32$.

Geographic Variation Uncertain. Simmons (2005) recognizes *humbloti*, *malagasyensis* and *ugandae* as subspecies. However, pending revision, no subspecies are recognized here.

Similar Species One African *Eptesicus* and seven other African *Pipistrellus* also have dark wings; bicoloured dorsal hairs; myotodont lower molars; and have (or might have) geographic ranges overlapping that of *P. somalicus* (Table 26, p. 606):

Pipistrellus capensis. Pelage conspicuously bicoloured. Ventral pelage white, whitish or cream. Dorsal hairs often shorter (5–6 mm). Forearm sometimes >32 mm. Posterior end of sagittal crest present in adults. Occipital helmet conspicuous except in young animals with unworn teeth (indicated by weakly bicuspid inner incisors). Profile of forehead region of skull almost straight.

Pipistrellus cf. *melckorum*. Larger (FA: 32–39 mm; GLS: 13.7–15.5 mm). Braincase relatively low, profile of forehead region straight to weakly concave. Tanzania to South Africa.

P. zuluensis. Dorsal pelage conspicuously bicoloured or sometimes tricoloured. Ventral pelage pale greyish-brown; hairs conspicuously bicoloured. Braincase more inflated and globular, so profile of forehead region is weakly to moderately concave.

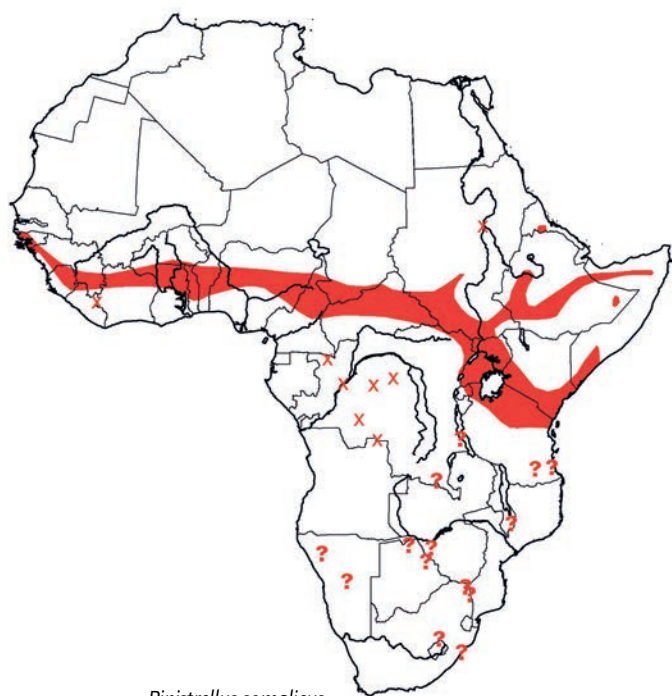
P. ariel. Pelage conspicuously bicoloured. Ventral pelage greyish-cream. Profile of forehead region of skull distinctly concave. Outer upper incisor about two-thirds length of inner incisor. Anterior upper premolar present but minute, sometimes not visible. Sahara Arid and Sahel Savanna BZs of Sudan and perhaps Egypt.

P. inexpectatus. Dorsal hairs bicoloured; ventral pelage reddish-cream, hairs unicoloured. Inner upper incisor bicuspid; outer cusp ca. three-quarters height of main cusp. Outer upper incisor ca. half height of inner incisor. Anterior upper premolar present but not visible above gum.

P. anchietae. Pelage distinctly bicoloured. Inner upper incisor bicuspid. Anterior upper premolar present although not visible above gum. Zambezian Woodland BZ and its margins.

P. guineensis. Mid-ventral pelage dark rusty-brown, sometimes speckled; hairs bicoloured. Inner upper incisor bicuspid.

Eptesicus hottentotus. Much larger (FA: 45–54 mm; GLS: 16.9–21.5 mm).

*Pipistrellus somalicus*

Distribution Endemic to Africa. Considered to occur mainly in the Sudan and Guinea BZs from Gambia to Sudan, and in the Somali–Masai Bushland BZ in Somalia, Kenya and Tanzania. Seldom recorded in the Rainforest BZ but penetrates into all of the Rainforest–Savanna Mosaics and the Coastal Forest Mosaic BZ. Possibly extends southwards to Mozambique, Botswana, South Africa and Namibia but, because of the confusion with *Pipistrellus zuluensis* in south-central Africa and southern Africa, its occurrence south of ca. 5°S is uncertain.

Habitat Recorded as an inhabitant of ‘comparatively dry conditions’ and as having been ‘caught among trees’ (Rosevear 1965). One was mist-netted in Pandam, Nigeria, over a track through riverine forest, just where it bordered Guinea savanna (Bergmans 1977a). Aellen (1952) found one specimen in Guinea savanna in Cameroon, but considered this record surprising as it was more than 2000 km from the usual habitat of this species. Found year-round at Masalani, near Kibwezi in inland Kenya, in area of dense thorn scrub dominated by *Combretum* shrubs and stands of *Commiphora* and *Acacia* trees, with scattered patches of grassland, and riverine woodland along the Athi R. (O’Shea & Vaughan 1980). Recorded in three coastal forests in the East African Coastal Forest Mosaic (Cockle *et al.* 1998). Known altitudinal range: 380–2150 m.

Abundance Uncertain. Considered rare in West Africa (Grubb *et al.* 1998). Apparently common at some localities (e.g. Masalani, Kenya).

Adaptations Aspect ratio low (O’Shea & Vaughan 1980); wing-loading not known. Flight characteristics probably very similar to those of *P. capensis* and *P. zuluensis*. Day-roosts uncertain: an hour after sunset, Kock (1969a) observed what appeared to be one individual coming and going several times from a hole between the wall and

roof-beam of a house, suggesting that its day-roost was somewhere under the roof. Each time it came and went, it followed a fixed flight-path.

Foraging and Food At Masalani, Kenya, forages for small, flying insects by slow-hawking 2–6 m above ground (mean height 4 m) in open spaces and more than 1 m from vegetation (O’Shea & Vaughan 1980). In contrast, *P. cf. helios* (which echolocates at higher frequencies) often forages within a metre of vegetation, and these differences probably contribute to the ability of these similar species to live sympatrically (O’Shea & Vaughan 1980). Details of diet not known.

Echolocation Search-phase call-shape (Masalani, Kenya): FM sweep (no details); intensity high; start-frequency 70 kHz; end-frequency 35 kHz (n = ?; O’Shea & Vaughan 1980).

Social and Reproductive Behaviour No information.

Reproduction and Population Structure Litter-size: 2 (n = 15; O’Shea & Vaughan 1980). At 02° 19’S (Masalani, Kenya), the reproductive chronology is restricted seasonal monoestry, with parturition in the wettest month of the short wet season (Nov) (O’Shea & Vaughan 1980).

Predators, Parasites and Diseases No information.

Conservation IUCN Category: Least Concern.

Measurements

Pipistrellus somalicus

FA (♂♂): 28.1 (22–31) mm, n = 72

FA (♀♀): 29.1 (26–32) mm, n = 80

WS: n. d.

TL: n. d.

HB: 46.0 (39–53) mm, n = 4*

T: 28.2 (24–33) mm, n = 37

E: 10.8 (7–14) mm, n = 78

Tr: 4.6 (3.2–6.8) mm, n = 77

Tib: 10.5 (8–13) mm, n = 93

HF: n. d.

WT: n. d.

GLS: 12.2 (11.3–12.9) mm, n = 96

GWS: 7.8 (7.0–8.7) mm, n = 71

C–M³ (alv.): 4.3 (3.5–4.9) mm, n = 101

Northern geographic range (AMNH, BMNH, CM, CZL, FMNH, HZM, MHNG, MNHN, MZUF, RMCA, ROM, SMF, TM, USNM, ZMA)

Measurements restricted to northern range because identity of southern specimens is uncertain

*J. Fahr (pers. comm.)

Key References Bergmans 1977a; McBee *et al.* 1987; O’Shea & Vaughan 1980; Peterson *et al.* 1995.

Victor Van Cakenberghe & Meredith Happold

Pipistrellus tenuipinnis WHITE-WINGED PIPISTRELLE (SLENDER-WINGED PIPISTRELLE)

Fr. Pipistrelle à ailes blanches; Ger. Weißflügel-Zwergfledermaus

Pipistrellus tenuipinnis (Peters, 1872). Monatsber. K. Preuss. Akad. Wiss. Berlin 1872: 263. 'Guinea', no specified locality.The type locality was incorrectly restricted to Kouilou River, Congo (Ellerman *et al.* [1953], based on Noack [1889]; see Kock [1969a]).

Taxonomy Originally *Vesperus tenuipinnis*. Traditionally *Eptesicus tenuipinnis*. Subsequently classified as *Pipistrellus* (*Neoromicia*) *tenuipinnis* by Hill & Harrison (1987), Koopman (1994) and Barratt *et al.* (1995), *Nycterikaupius tenuipinnis* by Menu (1987), *E.* (*Neoromicia*) *tenuipinnis* by Koopman (1993) and *Neoromicia tenuipinnis* by Simmons (2005). Synonyms: *ater* and possibly *bicolor*. The taxonomy of *bicolor* is problematic: it was tentatively considered a synonym of *tenuipinnis* by Hayman & Hill (1971), a view followed by Simmons (2005), while Crawford-Cabral (1986) suggested the possibility that it might represent a distinct species. However, Koopman (1975) and Hill & Harrison (1987) suggested that *bicolor* might be a prior synonym of *P. anchietae* based on respective syntypes in the BMNH, which they considered essentially similar. Unfortunately, the syntypes of both *bicolor* and *anchietae* in the Lisbon Museum were destroyed by a fire in 1978 (Crawford-Cabral 1986). Furthermore, discrepancies between the original description of *bicolor* and the remaining syntype at the BMNH (Hill & Harrison 1987: 249) raise doubts about the true identity of *bicolor* (Kock 2001b). The action by Koopman (1994) to list *anchietae* as a synonym of *bicolor* was rejected by Kock (2001) as premature. Pending further evidence, *bicolor* is tentatively retained here as a synonym of *P. tenuipinnis*, and *P. anchietae* is tentatively retained as a valid species. Subspecies: uncertain (see Geographic Variation). Chromosome number (Cameroon): $2n = 36$; $aFN = 52$ (McBee *et al.* 1987). Karyotypic data support the inclusion of *tenuipinnis* within *Neoromicia* (McBee *et al.* 1987).

Description Very small microbat without noseleaf and with tail more or less fully enclosed in interfemoral membrane; four or five upper cheekteeth; ears separated and short (10–14 mm); FA: 28–33 mm; wings pale, contrasting strongly with dark dorsal pelage (cf. *P. rendalli*); dorsal hairs usually unicoloured, ventral hairs bicoloured; lower molars myotodont; inner upper incisor weakly bicuspid; profile of forehead region of skull weakly concave. Sexes similar. Pelage silky, dense; mid-dorsal hairs ca. 6 mm. Dorsal pelage blackish-brown; hairs usually unicoloured, sometimes slightly paler at tip. Ventral pelage whitish or cream, throat and upper chest darker; hairs blackish-brown at base with silvery-white or cream at tip. Ears pale grey to pale brown, subtriangular; anterior margin straight, posterior margin slightly concave, tip rounded; 35–47% of FA. Tragus length 32–50% of E; relatively broad, widest above mid-point; anterior margin almost straight; posterior margin with sharp angle ca. one-quarter distance from tip, giving tragus a truncated appearance; tip rounded (Figure 136c). Wing-membranes white to pale yellow when folded, transparent when stretched out. Interfemoral membrane usually pigmented, thus darker than wing-membranes. Tibia, hind-foot and forearm reddish-brown, the latter in strong contrast to the unpigmented wing-membranes. Penis fairly long (5.5 mm). Baculum as in Figure 141i (Hill & Harrison 1987); tip expanded into an almost vertical, lobed, plate-like structure.

Skull medium-small and gracile for an African *Pipistrellus*. Braincase relatively high but of medium relative breadth; interorbital region of medium relative breadth; rostrum relatively short but broad (Table 25, p. 603). Profile of forehead region (viewed laterally) weakly concave; skull sloping almost uniformly from muzzle to occiput. No occipital helmet. Inner upper incisor broad to very broad, weakly bicuspid. Outer upper incisor unicuspid, variable in length (one-third to two-thirds height of inner incisor). Anterior upper premolar either absent or present (sometimes only on one side), if present, almost always visible above gum and displaced lingually into recess between canine and posterior premolar; canine and posterior premolar in contact. Lower molars myotodont. Dental formula: $2^{113}/_{3123} = 32$ or $2^{123}/_{3123} = 34$.

Geographic Variation Little variation in size but, even within populations, there is some variability in colour. Koopman (1994) recognized two subspecies, *P. t. tenuipinnis* (Senegal to DR Congo) and *P. t. ater* (NE DR Congo and Kenya to Angola). However, the distribution of *P. tenuipinnis* is contiguous throughout DR Congo to Uganda and specimens from Angola, allocated by Koopman to *P. t. ater*, do not appear to be geographically separated from those in SW DR Congo, which belong to the nominate form according to Koopman. Pending a revision of this species, which should include the critical examination of *bicolor* (see Taxonomy), no subspecies are recognized here.

Similar Species Three other African vespertilionids have white wings:

Pipistrellus rendalli. Dorsal pelage pale to medium-pale brown, not in strong contrast with the pale wings. On average larger (FA: 32.7 [29–36] mm). Inner upper incisor unicuspid with small basal cusp (the latter not always visible). Mostly in drier habitats.

Scotoecus albobfuscus. Only one upper incisor on each side. Penis extremely long.

Glauconycteris gleni. Dark brown pigment over wing bones; brown reticulation lines on arm-wing. Outer margin of ear reaching mouth; lower lip with lobe at posterior corner.

Distribution Endemic to Africa. Recorded from the Rainforest BZ (Western, West Central, East Central and South Central Regions) and the adjacent Rainforest–Savanna Mosaics, Afromontane–Afroalpine BZ and marginally from the Guinea Savanna BZ. Recorded disjunctly from Guinea and Sierra Leone to SW Kenya and southwards to N Angola, S DR Congo and N Tanzania, with rather isolated records from Senegal, Guinea-Bissau and SW Ethiopia. Apparently absent from most of the Dahomey Gap in West Africa (only known from Bismarckburg in Togo and not yet recorded from Benin). Also, not yet recorded from mainland Equatorial Guinea. Most of the localities in Kenya, Tanzania and Ethiopia have been

*Pipistrellus tenuipinnis*

recorded from riverine forests, montane forests, or near lakes along the Rift Valley.

Habitat Mostly recorded in lowland rainforest, swamp forest and coastal forest; also recorded from montane forest, mangroves, forest–savanna mosaic, *Isberlinia* woodland, *Acacia–Commiphora* bushland and thicket and miombo woodland. Within the Rainforest BZ, seems to prefer drier types of forest along the periphery of the rainforest. In West Africa, apparently restricted to lower altitudes, but reported at 3000 m in Rwanda (Rwankwi; Hayman *et al.* 1966). Also recorded from degraded forests as well as orchards and plantations; on Bioko I., primarily caught in cocoa plantations (Schlitter *et al.* 1982, Juste & Ibáñez 1994, USNM). In drier areas, it is associated with riverine and relict forests, and is commonly caught in nets set over rivers and pools (Duckworth *et al.* 1993, ROM, USNM).

Abundance No detailed information but comparatively abundant.

Adaptations Day-roosts very varied: this species has been found roosting in hollow standing trees, under boulders, in roofs and under eaves of huts and houses, and also in thatch and in crevices in walls and around windows (Lang & Chapin 1917b, Novick 1958b, Aellen 1963, Rosevear 1965, Roche 1972, Grubb *et al.* 1998, MHNG, USNM).

Foraging and Food Forages by slow- to moderately fast-hawking in spaces with background clutter and in open spaces. In Comoé N. P., Côte d'Ivoire, five individuals were caught at a median height of 12 (4–23) m in mist-nets set from 0 to 25 m above ground. Frequently attracted to light, and often enters rooms (Eisentraut 1956, Rosevear 1965). Diet not known; based on body-size, likely to consume very small flying insects.

Echolocation Call-shape (DR Congo) steep FM/QCF. Novick (1958b) reported start-frequency 62 (39–83) kHz; end-frequency 37 (24–42) kHz; and call-duration 1.5 (0.9–1.9) ms. However, this needs confirmation using modern equipment.

Social and Reproductive Behaviour Roosts singly and in groups. One group (in a hollow tree), was comprised of two ♂♂, four ♀♀ and one unsexed (Allen 1917a, Lang & Chapin 1917b). Sometimes found 'in considerable numbers' in crevices in the structure of houses (Rosevear 1965). Has been found singly and in groups of up to six (T. S. Jones in Grubb *et al.* 1998).

Reproduction and Population Structure Litter-size: one ($n = 3$). Reproductive chronology not known. In Uganda, there are records of a pregnant ♀ in early Dec (01° 12' N, Bugoma Forest), three lactating ♀♀ in Jan (locality not specified), and a pregnant ♀ in late Feb (00° 5' S, Sango Bay Forest); no data for other months or for other ♀♀ captured in these months (Kingdon 1974, LACM). Males with very large testes were noted in Jun, Oct and Nov; the facial glands of these ♂♂ were very large and exuded a greasy orange secretion that tinted the entire animal, including its wings, with a pinkish colour, and the hair on the face seemed to be less dense at this time (Kingdon 1974). One ♀ from Sierra Leone (near Fintonia, 09° 40' N) was lactating in mid-May (USNM), and in Cameroon (Isongo, 04° 05' N) one ♀ was pregnant in early Mar (Eisentraut 1956). These data are inconclusive.

Predators, Parasites and Diseases Predators include Bat Hawks *Macheiramphus alcinus* (Lang & Chapin 1917b) and a tree snake *Toxicodryas blandingii* (Jones 1961). Ectoparasites include a bed-bug *Aphrania elongata* (Hemiptera: Cimicidae); bat-flies *Raymondia intermedia* (Diptera: Streblidae), *Basilia ansifera*, *B. robusta* (Diptera: Nycteribiidae); a tick *Carios boueti* (Acari: Argasidae); and mites *Spinturnix aelleni* (Acari: Spinturnicidae), *Steatonyssus afer*, *S. javensis* (Acari: Macronyssidae), *Pteracarus holubi* (Acari: Myobiidae), *Alabidocarpus eptesicus* (Acari: Chirodiscidae) and *Notoedres schoutedeni* (Acari: Sarcoptidae) (Anciaux de Faveaux 1984).

Conservation IUCN Category: Least Concern.

This species is apparently able to exploit altered and degraded habitats and seems to be less adversely affected by deforestation than other forest bats.

Measurements

Pipistrellus tenuipinnis

FA: 29.8 (28–33) mm, $n = 31$

WS (d): 212 (200–228) mm, $n = 13$

TL: 74.7 (62–82) mm, $n = 12$

T: 31.1 (28–34) mm, $n = 27$

E: 11.9 (10–14) mm, $n = 31$

Tr: 5.0 (4–6) mm, $n = 12$

Tib: 10.6 (9–12) mm, $n = 15$

HF: 6.9 (5.3–8.5) mm, $n = 35$

WT: 4.4 (3.0–7.0) g, $n = 49$

GLS: 12.3 (11.6–13.0) mm, $n = 17$

GWS: 7.9 (7.5–8.2) mm, $n = 12$

C–M³: 4.3 (4.0–4.7) mm, $n = 13$

C–M³ (alv.): 4.2 (3.7–4.7) mm, n = 106*

Senegal, Guinea-Bissau, 'Guinea' (holotype), Guinea, Sierra Leone, Liberia, Côte d'Ivoire, Ghana, Nigeria, Cameroon, DR Congo (incl. holotype *ater*), Uganda, Kenya, Ethiopia (AMNH, FMNH, HZM, ICN, LACM, MHNG, MNHN, RMCA, ROM, SMF, SMNS, ZMB)

*V. Van Cakenberghe (pers. comm.)

Key References Lang & Chapin 1917b; McBee *et al.* 1987.

Jakob Fahr

Pipistrellus zuluensis ZULU PIPISTRELLE (ALOE BAT)

Fr. Pipistrelle zouloue; Ger. Zulu-Zwergfledermaus

Pipistrellus zuluensis (Roberts, 1924). Ann. Transvaal Mus. 10: 60. White Umfolosi G. R., KwaZulu–Natal, South Africa.

Taxonomy Originally and traditionally *Eptesicus zuluensis*. Subsequently classified as *P. (Neoromicia) zuluensis* by Hill & Harrison (1987), *Nycterikaupius zuluensis* by Menu (1987), *E. (Neoromicia) zuluensis* (as a synonym of *E. (Neoromicia) somalicus*) by Koopman (1993), *P. (Neoromicia) somalicus zuluensis* by Koopman (1994) and *Neoromicia zuluensis* by Kearney *et al.* (2002) and Simmons (2005). Considered closely related to *P. somalicus*, and much of the literature on *zuluensis* is mentioned under *somalicus*. Synonyms: *vansoni*. Subspecies: uncertain (see Geographic Variation). Chromosome number (South Africa): 2n = 28; aFN = 48 (Morales *et al.* 1991, Rautenbach *et al.* 1993, Kearney *et al.* 2002). Based on chromosomal differences, Rautenbach *et al.* (1993) regard *zuluensis* as specifically distinct from *somalicus*.

Description Very small microbat without noseleaf and with tail more or less fully enclosed in interfemoral membrane; four or five upper cheekteeth (only four usually visible), five lower cheekteeth and two upper incisors on each side; dorsal pelage medium brown; dorsal hairs bicoloured or tricoloured, ventral hairs bicoloured; wings dark, usually without white hind-border; lower molars myotodont; inner upper incisor usually unicuspid; profile of forehead region of skull weakly to moderately concave. Sexes similar. Pelage soft, dense, without sheen; mid-dorsal hairs 6–7 mm (9–10 mm on rump). Dorsal pelage medium brown, sometimes paler on rump; some individuals have a slightly orange hue (but none reddish as in *P. rusticus*); hairs blackish-brown (sometimes with paler middle section) and medium to pale brown at tip. Ventral pelage paler and more greyish; hairs very dark grey with pale greyish-brown or grey at tip. Ventral pelage not noticeably paler in pelvic region although some all-white hairs are present. Forehead sometimes raised (cf. straight in *P. capensis*). Ears brown, relatively short, subtriangular; tip rounded. Tragus length ca. half of E but very variable in preserved material; anterior margin smoothly concave; posterior margin smoothly convex for most of length (but with shallow rounded angle just below mid-height) and with a prominent, folded, triangular basal lobe; tip rounded. Eyes very small. Wings dark brown, slightly translucent, usually without white hind-border but sometimes with very narrow hind-border. Interfemoral membrane dark brown, slightly translucent; tail fully enclosed except for part of last vertebra. Baculum as in Figure 141j, k, (Hill & Harrison 1987, Kearney *et al.* 2002).

Skull small and gracile for an African *Pipistrellus*. Braincase relatively high and narrow; interorbital region relatively narrow; rostrum relatively short and narrow (Table 25, p. 603). Profile of forehead region (viewed laterally) weakly to moderately concave. Occipital helmet absent, therefore braincase smoothly rounded

posteriorly (cf. *P. capensis*). With experience, the globular braincase, concave forehead and lack of helmet can be felt without removing the skull. Inner upper incisor large, usually unicuspid but sometimes bicuspid. Outer upper incisor small, ca. half height of inner incisor, higher than cingulum of inner incisor but lower than the secondary cusp, if present. Anterior upper premolar almost always absent: if present, it is extremely minute and hardly visible above gum. Lower molars myotodont. Dental formula: usually $2^{113}/_{3123} = 32$.

Geographic Variation Possibly *vansoni* Roberts, 1932, from NE Botswana, N Namibia and perhaps Angola, might represent a valid subspecies.

Similar Species One African *Eptesicus* and five other African *Pipistrellus* also have dark wings, bicoloured dorsal hairs and myotodont lower molars, and have (or might have) geographic ranges overlapping that of *P. zuluensis* (see also Table 26, p. 606):

Pipistrellus capensis. Dorsal hairs bicoloured. Ventral pelage white, whitish or cream. Braincase relatively low; rostrum relatively longer and broader; profile of forehead region straight to weakly concave. Occipital helmet usually present, therefore braincase not smoothly rounded posteriorly. Outer upper incisor usually less than half the height, but above the cingulum, of the first incisor.

P. cf. melckorum. Skull longer (GLS: 13.7–15.5 mm). Forearm usually longer (32–39 mm). Braincase relatively low, profile of forehead straight to weakly concave; occipital helmet present although weakly developed. Inner upper incisor always unicuspid.

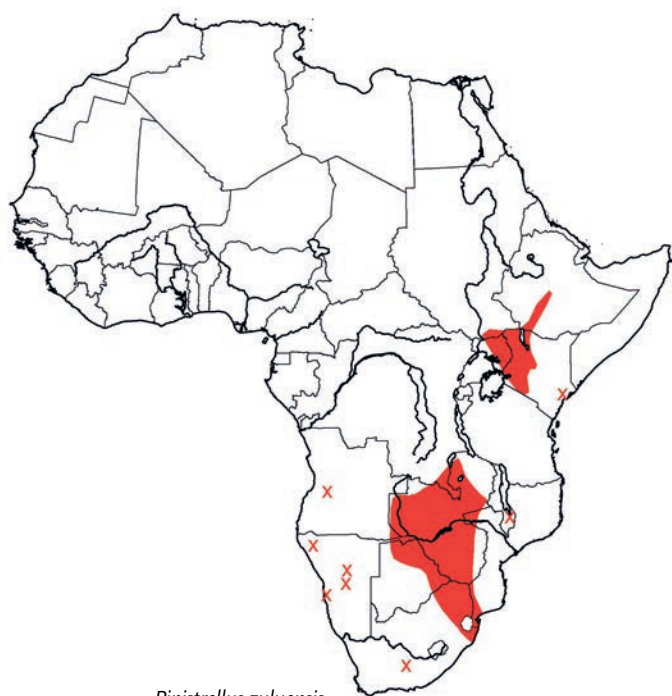
P. somalicus. Pelage only slightly bicoloured. Ventral pelage brown. Forehead only slightly raised – head feels flat. Braincase less inflated and less globular so profile of forehead region is only weakly concave. Outer upper incisor less than half the height, but above the cingulum, of the inner incisor.

P. anchietae. Dorsal hairs bicoloured (never tricoloured). Inner upper incisor bicuspid. Anterior upper premolar present but minute, not visible.

P. guineensis. Dorsal hairs bicoloured (never tricoloured). Ventral pelage dark rusty-brown, sometimes speckled. Inner upper incisor bicuspid. Geographic range might overlap in Uganda, S Sudan and Ethiopia.

Eptesicus hottentotus. Much larger (FA: 45–54 mm; GLS: 16.9–21.5 mm).

Distribution Endemic to Africa. Recorded mainly from the Somalia–Masai Bushland, Zambezian Woodland and South-West

*Pipistrellus zuluensis*

Arid BZs, with some records in some of the adjacent biotic zones. Recorded from scattered and sometimes apparently isolated localities in south-central Africa and southern Africa from Angola to Malawi and southwards through Namibia, Zambia, Zimbabwe, Botswana and South Africa, and recently found to occur also in Kenya (based on examination of material at ROM), Ethiopia (ZFMK) and Sudan (FMNH, SMF) (V. Van Cakenberghe unpubl.). Koopman (1975), who considered it highly probable that *zuluensis* was conspecific with *somalicus*, drew attention to an apparent gap in the distribution of these two forms, but the new data indicate that this gap is non-existent and that the distributions of *zuluensis* and *somalicus* overlap. Not yet recorded from Swaziland, but likely to occur there.

Habitat Records from Kenya, Ethiopia and Sudan are in semi-desert grassland and shrubland, and in *Acacia-Commiphora* deciduous bushland and thicket vegetation zones (terminology: White 1983). In south-central Africa and southern Africa, exploits woodland savanna habitats (including miombo woodland), and drier shrublands and bushlands in the South-West Arid Zone. Known altitudinal range: 500–2650 m.

Abundance Uncertain. Seldom recorded in Malawi (Happold & Happold 1997). Not as common as *P. capensis* in southern Africa (Taylor 2000).

Adaptations Aspect ratio low; wing-loading very low. Flight speed moderate; manoeuvrability high; can take off from ground. Turns by banking (minimum radius of turn <25 cm), and by stalling-and-twisting. Individuals could fly across a 1×1×1 m enclosure, but were not able to complete more than two circuits/flight (2 bats, 10 flights each). Scuttling over horizontal, sloping and vertical surfaces is fairly efficient although not fast. Day-roosts not known. Although Roberts (1924) used the name Aloe Bat in his description, it was

not *P. zuluensis* but *P. capensis* that he found roosting among the leaves of aloes (Smithers 1983). In Malawi, at 20–21 °C, becomes torpid during the day. A captive individual, fed winged termites and able to fly, drank water irregularly, the longest interval between drinks being 3.5 days in a 9-day trial. In the Namib Desert, captive bats exposed to prevailing desert conditions, but unable to fly, were able to rear young when deprived of water (Roer 1970, 1971). Predicted mean maximum urine concentration comparatively very high – 5010 mOsmol/kg in bats from the Namib Desert (Geluso 1980) and 4709 mOsmol/kg in bats from Malawi (Happold & Happold 1988). The predicted urine concentrating capacity of the bats from the Namib Desert is the highest known for bats. However, because of the high rate of evaporative water loss from the wings during flight, the species is unlikely to be independent of drinking water in the wild.

Because *P. zuluensis* and *P. somalicus* have often been confused and/or regarded as conspecifics, it is likely that further information about *P. zuluensis* has been recorded as pertaining to *P. somalicus*.

Foraging and Food In miombo woodland in Liwonde N. P., Malawi, forages by slow-hawking in spaces with moderate to high levels of clutter, including near canopies of trees, glades in woodland, open spaces between tree-trunks and lower branches, and clearings around buildings. Unlike many other species in this habitat, not recorded over a pool in the Likwenu R. on any of four occasions (M. Happold unpubl.), although one was caught over this river by David Harrison (pers. comm.). In contrast, T. Kearney (pers. obs.) caught some over a small man-made pond in dry mopane woodland and over a larger dam in the Waterberg, South Africa, but it is not known if they were foraging or coming to drink. Morphometric data suggest that this species does forage over water as well as in other places (Fenton & Bogdanowicz 2002). Diet includes moths and beetles (Fenton *et al.* 1998a, Taylor 2000).

Echolocation Search-phase call-shape (cluttered environment, Malawi) steep FM/QCF with the QCF ‘heels’ short (Figure 118c) to long. Intensity high; start-frequency up to 79 kHz; end-frequency and peak-frequency 48–50 kHz; maximum duration 5.5 ms (two bats, tethered, 175 calls; M. Happold unpubl.).

Social and Reproductive Behaviour No information.

Reproduction and Population Structure At 15°S (Liwonde N. P., Malawi), of a total of four adult ♀♀, one was pregnant with two embryos in Oct, one was lactating in Nov, one was post-lactating and another was reproductively inactive in Feb. A juvenile was recorded in Dec and two subadults in Apr. Two ♂♂ with abdominal testes were recorded in Nov, Dec; one with scrotal testes in Jun. Although inconclusive, these data are consistent with restricted seasonal monoestry with births early in wet season (Happold & Happold 1990a). At 22°23'S in South Africa, a lactating ♀ was recorded in Nov (T. Kearney pers. obs.).

Predators, Parasites and Diseases No information.

Conservation IUCN Category: Least Concern.

Measurements*Pipistrellus zuluensis*

FA: 29.9 (27–33) mm, n = 69

WS (a): 221 (219–228) mm, n = 4*

TL: 76 (72–80) mm, n = 12*

T: 33.5 (27–40) mm, n = 56

E: 9.5 (7–11) mm, n = 62

Tr: 4.3 (3.0–5.9) mm, n = 55

Tib: 11.2 (8–14) mm, n = 69

HF: 6.3 (5–8) mm, n = 18

WT: 4.2 (3.0–6.0) g, n = 23

GLS: 12.2 (11.3–12.9) mm, n = 66

GWS: 7.7 (7.3–8.2) mm, n = 50

C–M³ (alv.): 4.2 (3.8–4.8) mm, n = 67

Throughout geographic range (AMNH, CM, CZL, HC, FMNH, HZM, ROM, SMF, TM, ZFMK, ZMUZ and literature)

*Malawi only (HC)

Key Reference Smithers 1983.**Meredith Happold, Victor Van Cakenberghe &
Teresa Kearney**

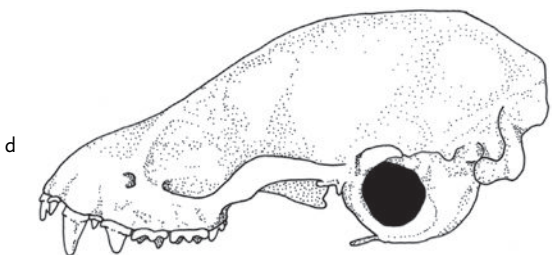
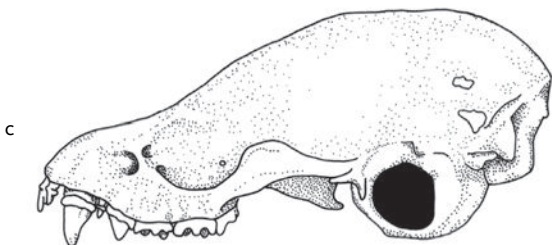
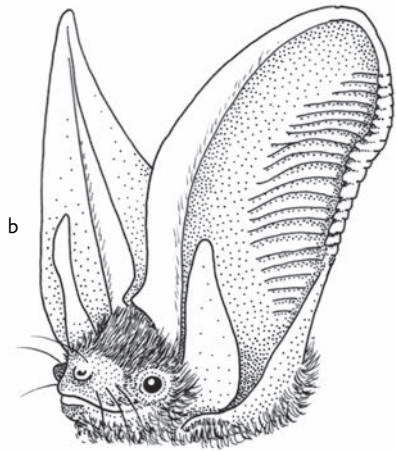
GENUS *Plecotus*

Long-eared Bats

Plecotus E. Geoffroy, 1818. Description de l'Égypte 2: 112. Type species: *Vesperilio auritus* Linnaeus, 1758.

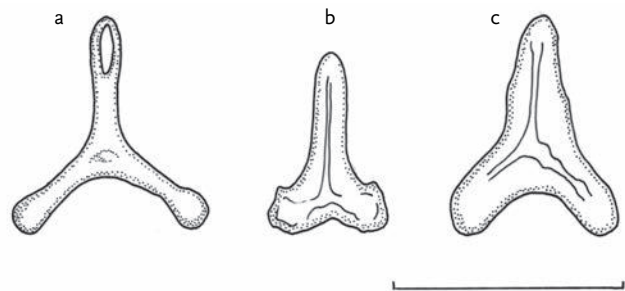


Plecotus christii.



This Old World genus currently contains at least 19 species of which three occur in Africa (Benda *et al.* 2004c), Spitzenberger *et al.* 2006). Diagnostic combination of characters: five upper and six lower cheekteeth and two upper incisors on each side; ears comparatively and relatively long (32–40 mm in African species; almost as long as forearm) and joined at base across the forehead (Figure 142). The tragus is long, reaching half the length of the ears; it remains erect when the ears are folded while the bats rest. The muzzle is coniform; the nostrils open upward with the orifices extending backward by a slit-like prolongation. The eyes are large for a microbat. The tail is long (ca. same as HB), and the terminal vertebra extends ca. 1.0–1.5 mm beyond the margin of the interfemoral membrane. The wings are short and broad. The distal part of the glans penis is broad (broadest part ca. 2.5–3.0 mm) and rounded. The bacula vary inter-specifically in shape (Figure 143). The skull has a large, elongate and rounded braincase, but the rostrum is slender and reduced (Figure 142). The supraorbital ridges are well developed and the tympanic bullae large. For African species, the profile of the forehead region (viewed laterally) varies from comparatively strongly concave (Figure 142c) to comparatively weakly concave (Figure 142d), but the variation is slight compared with that in other genera (e.g. *Glauconycteris*, *Pipistrellus*, *Myotis*). Dental formula: $2^{123}/_{3133} = 36$. The upper incisors are well developed, each with a distinct secondary cusp, the inner incisor is much smaller than the outer. The anterior upper premolar is very small, and is either situated in the tooththrow or displaced lingually. The upper molars are short on their lingual sides, and the spaces between their crowns are unusually large. Of the three lower premolars, the middle is the smallest.

Morphologic, bacular and karyotypic data suggest close affinity with *Barbastella*, *Otonycteris* and three other non-African genera (e.g.



LEFT: Figure 142. *Plecotus*. (a) Flight membranes, and bones of wing, hindlimb and tail of a non-African species (*P. austriacus*). (b) Head of *P. gaisleri* showing details of the left ear and tragus (based on photos in Benda *et al.* 2004c). (c) Lateral view of skull of *P. gaisleri* and (d) lateral view of skull of *P. christii* (both based on Benda *et al.* 2004c). For African *Plecotus*, the forehead region is comparatively strongly concave in *P. gaisleri* and weakly concave in *P. christii*.

ABOVE: Figure 143. Bacula of *Plecotus* occurring in Africa. (a) *P. balensis*, holotype (based on Kruskop & Lavrenchenko 2000). (b) *P. christii* (based on Lanza 1960 in Benda *et al.* 2004c). (c) *P. gaisleri* (based on Qumsiyeh 1985 as *P. austriacus austriacus*, in Benda *et al.* 2004c). For further examples, see Benda *et al.* 2004c). All are dorsal views with tip uppermost. Scale = 1 mm.

Hill & Harrison 1987, Frost & Timm 1992, Tumilson & Douglas 1992, Qumsiyeh & Bickham 1993); mitochondrial ribosomal sequences support the relationship with *Barbastella*, but not *Otonycteris* (Hoofer & Van Den Bussche 2001). Simmons (2005) places *Plecotus* in the tribe Plecotini, with both *Barbastella* and *Otonycteris* and three non-African genera. All *Plecotus* in Africa were formerly thought to represent *P. auritus* and then *P. austriacus*. Subsequently, *P. balensis* from Ethiopia was described as distinct from *P. austriacus* by Kruskop & Lavrenchenko (2000), *P. austriacus christii* from NE Africa and N Sudan was restored to specific status by Benda *et al.* (2004c), and these authors also found that specimens from Cyrenaica in NE Libya and the Maghreb in NW Africa represent two subspecies of *P. teneriffae*. Then Spitzenberger *et al.* (2006) revised the whole genus and concluded it contains at least 19 species, which are more or less cryptic. They also recognized three species in Africa but concluded that the populations in Cyrenaica and the Maghreb represent two subspecies of *P. kolombatovici* (*P. k. gaisleri* and an as yet unnamed subspecies, respectively). Subsequently, *gaisleri* was raised to specific status by Mayer *et al.* (2007) and the undescribed subspecies apparently belongs to this species. The *Plecotus* species profiles were updated in 2011 to embrace these changes in taxonomy.

Collectively, the African species inhabit a great variety of forests, semi-covered and open habitats; two species extend into desert regions but are found only near oases. Little is known about the habits of the African species but, as a general rule, *Plecotus* emerge from their roosts only after dark for intermittent periods of activity throughout the night. They appear to fly quite fast when they commute along hedges between roosts and feeding areas. When they forage, their flight is slow and fluttering, and they can hover briefly. Their prey is often gleaned from the foliage of trees or bushes, and from the walls of buildings. They feed mainly on Lepidoptera without using any echolocation. When the bats are travelling, they emit very

low FM calls that are only detectable over short distances. *Plecotus* are gregarious in summer, the usual number of individuals averaging 10–20 per colony. In winter they are more solitary, particularly the individuals that hibernate in deep cracks.

Fossil evidence of *Plecotus* has been recorded from the Miocene of Europe where it diversified during the Pliocene and Pleistocene (Sigé & Legendre 1983). No palaeontological record is available in Africa.

The three species in Africa are distinguished by their distributions and the following characters:

P. balensis. Dorsal pelage dark rusty-brown, hairs tricoloured with basal two-thirds dark. Ears dark brown or blackish-brown. Wings brown, heavily pigmented. Braincase breadth 50–53% of GLS. Profile of forehead region of skull (viewed laterally) comparatively weakly concave. Ethiopia.

P. christii. Dorsal pelage very pale brown or greyish-brown; hairs tricoloured with basal half dark. Ears unpigmented except around tip. Wings pale, semi-translucent. Braincase breadth 45–51% of GLS. Profile of forehead region comparatively weakly concave (Figure 142d). NE Sahara (Libya, Egypt, N Sudan).

P. gaisleri. Dorsal pelage greyish-brown; hairs tricoloured with basal half dark. Ears dark brown to dark greyish-brown. Wings dark brown to dark greyish-brown. Braincase breadth 47–51% of GLS. Profile of forehead region comparatively strongly concave for an African *Plecotus* (Figure 142c). The Maghreb and Cyrenaica.

Note that the concavity of the forehead region in all of these species is weak, and shows very little variability, in comparison with that in genera such as *Glauconycteris*, *Pipistrellus* and *Myotis*.

Stéphane Aulagnier

Plecotus balensis BALE LONG-EARED BAT

Fr. Oreillard d'Ethiopie; Ger. Bale-Langohr

Plecotus balensis Kruskop & Lavrenchenko, 2000. Myotis 38: 6. Hareenna Forest, Bale Mts, Ethiopia, ca. 06° 45' N, 39° 44' E, alt. 2760 m.

Taxonomy Synonyms: none. Multivariate analysis of morphological characters shows that *Plecotus* from Ethiopia (the southernmost part of the genus range) is clearly differentiated from *P. austriacus*, which was previously considered the only species of *Plecotus* in Africa. Species status confirmed by bacular morphology. Chromosome number (Ethiopia): 2n = 32 (Kruskop & Lavrenchenko 2000); aFN not known.

Description Very small microbat without noseleaf and with tail more or less fully enclosed in interfemoral membrane; five upper and six lower cheekteeth and two upper incisors on each side; ears joined at base, large for a vespertilionid (E: 37–40 mm) and relatively enormous (ca. 97% of FA); dorsal pelage dark rusty-brown, hairs with basal two-thirds dark; face, ears and wings dark; muzzle conspicuously inflated behind nostrils. Sexes apparently similar. Pelage moderately long, dense. Dorsal pelage dark rusty-brown; hairs tricoloured with basal two-thirds dark brown (cf. *P. christii*, *P. gaisleri*), terminal third grey with greyish-brown at tip. Ventral pelage whitish

or pale grey; hairs dark grey with whitish or pale grey tip. Muzzle narrow, conspicuously inflated behind nostrils; supraorbital gland comparatively small (ca. 1 mm in diameter). Naked parts of face brown. Ears dark brown or blackish-brown, relatively long (ca. 97% of FA and therefore look enormous); inner margins joined by low band across forehead. Tragus moderately long (ca. just under half of E), tapering to blunt point. Eyes relatively large for a microbat. Wing-membranes brown, heavily pigmented; skin over wing-bones and hindlimbs blackish-brown. Thumb comparatively short (5.74 [5.4–6.2] mm). Interfemoral membrane brown; calcar reaching ca. half-way to tip of tail. Baculum Y-shaped; lateral arms long, narrow, with obtuse angle between them (Figure 143a; Kruskop & Lavrenchenko 2000).

Skull medium-sized for a *Plecotus*, with braincase of medium relative height but very broad (braincase breadth 50–53% of GLS) (Benda *et al.* 2004c). Profile of forehead region (viewed laterally) weakly concave for an African *Plecotus* (cf. *P. gaisleri*). Rostrum relatively short (C–M³: 32–33% of GLS) and relatively narrow (width between canines 65–68% of C–M³). Tympanic bullae comparatively small (largest

vertical diameter 4.42 [4.28–4.53] mm, $n = 6$). Dentition weaker than in *P. gaisleri*. Anterior upper premolar medium-sized (length 0.46–0.49 mm; breadth 0.41–0.50 mm); displaced lingually but canine and posterior premolar well separated. For more information, see Kruskop & Lavrenchenko (2000) and Benda *et al.* (2004c).

Geographic Variation None.

Similar Species The only other vespertilionids in Africa that have ears with inner margins joined are:

Plecotus christii. Dorsal hairs with basal half dark rusty-brown; tip colour more prominent so pelage appears paler. Ears unpigmented except around tip. Wings pale, semi-translucent. Braincase and rostrum usually relatively narrower (details in Description). Baculum Y-shaped with acute angle between lateral arms. NE Sahara (Libya, Egypt, N Sudan).

P. gaisleri. Dorsal hairs with basal half dark rusty-brown. Skull with frontal region deeply concave. Rostrum usually relatively longer and broader (details in Description). Baculum Y-shaped with acute angle between lateral arms. Morocco to Libya.

Barbastella (2 spp.). Ears much shorter (13–18 mm). Only five lower cheekteeth and one upper incisor on each side.

Only one other vespertilionid in Africa has long ears (>28 mm):

Otonycteris hemprichii. Ears with inner margins not joined at base. Only four upper and five lower cheekteeth and one upper incisor on each side.

Distribution Endemic to Africa. Only known from the Afromontane–Afroalpine BZ of the Ethiopian Highlands on both sides of the Rift Valley. Recorded from the upper belt of the Harennā Forest on the Bale Mts, Ethiopia, from 2500–3000 m (Yalden 1988a, Kruskop & Lavrenchenko 2000), and from Abune Yosef (Benda *et al.* 2004c). There is also an early record from ‘Shoa’ (= Shewa), which probably came from the uplands N or NW of Addis Ababa (Kruskop & Lavrenchenko 2000).

Habitat In the Bale Mts, found in humid afromontane *Schefflera*–*Hagenia* and *Erica arborea* forest.

Abundance A relatively common bat in its habitat (according to sighting records).

Remarks Forages by slow-hawking and perch-hunting in open parts of the forest and near edges of clearings. Calls (? social) have been heard, but echolocation calls were not detectable with a QMC-mini narrow-band detector, suggesting that they are of very low intensity, as in *Plecotus auritus* (western Europe to Japan), which also forages in cluttered forest environments. It has been suggested that the ancestor of *P. balensis* came from comparatively arid habitats (now inhabited by *P. austriacus*), and that adaptation to the Ethiopian montane forest



Plecotus balensis

resulted in convergence with *P. auritus* (Kruskop & Lavrenchenko 2000, Lavrenchenko 2000). The convergent characters include darker colouration, the noticeably inflated muzzle behind the nostrils, smaller bullae and weaker dentition.

Conservation IUCN Category: Vulnerable.

Very small area of occupancy. Protected by Bale Mountains N. P.

Measurements

Plecotus balensis

FA: 39 (36–41) mm, $n = 7$

WS (d): 285 (272–295) mm, $n = 6$

HB: 49 (45–50) mm, $n = 7$

T: 50 (47–55) mm, $n = 7$

E: 38 (37–40) mm, $n = 7$

Tr: 16.5 (15.2–18.0) mm, $n = 5$

Tib: n. d.

HF: 8.5 (8–9) mm, $n = 7$

WT: 7.3 (6.5–8.5) g, $n = 6$

GLS: 17.1 (16.6–17.9) mm, $n = 6^*$

GWS: 8.8, 8.9 mm, $n = 2$

C–M³: 5.5 (5.4–5.7) mm, $n = 6^*$

Ethiopia (L. A. Lavrenchenko & D. W. Yalden unpubl.)

*Benda *et al.* (2004c)

Key References Benda *et al.* 2004c; Kruskop & Lavrenchenko 2000; Yalden 1988a.

Leonid A. Lavrenchenko

Plecotus christii CHRISTIE'S LONG-EARED BAT

Fr. Oreillard d'Egypte; Ger. Christies Langohr

Plecotus christii Gray, 1838. Mag. Zool. Bot. 2: 495. Nile Valley between Qena and Aswan, S Egypt (restricted by Qumsiyeh 1985).

Taxonomy Formerly identified as *P. auritus*, and more recently considered a subspecies of *P. austriacus* (e.g. Simmons 2005). However, a systematic revision of African populations of *Plecotus* indicates that it is a distinct species morphologically and genetically close to *P. balensis* (Benda *et al.* 2004c). Synonyms: *aegyptius*, *aegyptiacus*. Subspecies: none. Because it was named after Dr Turnbull Christie, the species name is often spelt *christiei*, but the original spelling is *christii*. Chromosome number (Jordan): $2n = 32$, $aFN = 50$ (Qumsiyeh & Bickham 1993).

Description Very small microbat without noseleaf and with tail more or less fully enclosed in interfemoral membrane; five upper and six lower cheekteeth and two upper incisors on each side; ears joined at base, large for a vespertilionid (E: 32–39 mm) and relatively enormous (ca. 97% of FA); dorsal pelage very pale brown or greyish-brown, hairs with basal half dark; face and ears pale; wings pale and semi-translucent; muzzle moderately inflated behind nostrils. Sexes similar. Pelage dense, soft, slightly woolly; mid-dorsal hairs ca. 7 mm. Dorsal pelage very pale umber brown or greyish-brown; hairs tricoloured with basal half rusty-brown, terminal half pale brownish-grey with umber brown or pale brown at tip (middle colour palest). Ventral pelage whitish; hairs dark rusty-brown with creamy or white tip. Face pinkish-grey to pale greyish-brown. Muzzle blunt, inflated behind nostrils; supraorbital gland comparatively small, ca. 0.9 mm diameter (cf. *P. gaisleri*); naked parts of face pale greyish-brown. Ears translucent, unpigmented except for pale brown tips; relatively long (97 [89–100]% of FA and therefore look enormous); inner margins joined by low band at base. Tragus mostly translucent but brownish around distal margins, moderately long (48 [46–50]% of E), 5 mm at widest, tapering to blunt point. Eyes relatively large for a microbat. Wings with arm-wing membrane creamy, hand-wing membrane translucent, pale grey; skin over wing-bones pale brown. Thumb comparatively short, on average 5.5 mm long (cf. *P. gaisleri*). Interfemoral membrane cream. Baculum Y-shaped; lateral arms short, broad, with acute angle between them (Figure 143b).

Skull small for a *Plecotus*, with braincase of medium relative height but long and narrow (braincase width 45–51% of GLS) (Benda *et al.* 2004c). Profile of forehead region (viewed laterally) comparatively weakly concave for an African *Plecotus* (Figure 142d) (cf. *P. gaisleri*). Rostrum relatively short ($C-M^3$: 32–33% of GLS), low and relatively very narrow (width between canines 62–65% of $C-M^3$). Tympanic bullae medium-sized (largest vertical diameter 4.47 [4.3–4.6] mm, $n = 6$). Dentition more gracile than in *P. balensis* and *P. gaisleri*. Anterior upper premolar comparatively small (length 0.37–0.44 mm, breadth 0.41–0.50 mm); within tooththrow; canine and posterior premolar well separated.

Geographic Variation No subspecies described, however individuals from Sinai and Palestine are larger on average than those from the Nile Valley and Siwa Basin (Qumsiyeh 1985, P. Benda unpubl.). Further research necessary, but the differences in size suggest subspecific status for the north-eastern populations.

Similar Species The only other vespertilionids in Africa which have ears with inner margins joined are:

Plecotus balensis. Dorsal hairs with basal two-thirds dark brown; tip colour less prominent so pelage appears darker. Ears dark brown or blackish-brown. Wings dark, heavily pigmented. Braincase and rostrum usually relatively broader (details in Description). Baculum Y-shaped with obtuse angle between lateral arms. Ethiopia, possibly Eritrea.

Plecotus gaisleri. Ears dark brown to greyish-brown. Wings dark, heavily pigmented. Muzzle not inflated behind nostrils. Skull with frontal region more strongly concave; rostrum relatively broader and usually relatively longer (details in Description). Baculum Y-shaped, robust, with comparatively long lateral arms. Morocco to Libya.

Barbastella (2 spp.). Ears much shorter (14–18 mm). Only five lower cheekteeth and one upper incisor on each side.

Only one other vespertilionid in Africa has long ears (>28 mm):

Otonycteris hemprichii. Ears with inner margins not joined at base. Only four upper and five lower cheekteeth and one upper incisor on each side.

Distribution In Africa, only known from the Sahara Arid BZ. Confirmed records are from the oases of Siwa and Al Jaghbub near the Libyan–Egyptian border, from the Nile Valley (from the Delta in Egypt to the Fifth Cataract in N Sudan), and from oases in Sinai

*Plecotus christii*

(Kock 1969a, Gaisler *et al.* 1972, Qumsiyeh 1985, P. Benda *et al.* unpubl.). Old records from Eritrea and Ethiopia are now assigned to *P. balensis*. Extraliminally: SW Jordan and S Palestine. Harrison & Bates (1991) provisionally identified specimens from the Arabian Peninsula as *P. austriacus christii*, but this bat lives only in the deserts along the Rift Valley (Jordan, Palestine); in N Arabia, only *Plecotus macrobullaris* has been confirmed (Benda *et al.* 2004c), and the population provisionally assigned to *P. christii* from Yemen and SW Saudi Arabia needs revision.

Habitat All records are from open areas of oases in very dry deserts, and from mesic habitats along the Nile R., where suitable day-roosts are available.

Abundance Probably rare. However, in Sinai, it was one of the bats that was recorded comparatively frequently.

Remarks Wings broad; this species is well adapted for hovering and forages by gleaning, often picking insects off leaves and blossoms. In Israel, feeds predominantly on medium-sized and large Lepidoptera (Noctuidae and Hepialidae) and occasionally on Coleoptera (Scarabaeidae), Diptera and Trichoptera (Whitaker *et al.* 1994, Feldman *et al.* 2000). By day, roosts mainly in rocky cavities, but also roosts in dark areas of pyramids, old monuments, ruins, caverns and abandoned mines where individuals hang from the walls. Sedentary; the home-range is restricted to the oasis. Usually found to be solitary. Males become territorial in autumn, when mating occurs. Litter-size: one ($n = 1$). Reproductive chronology not known. Extraliminally, in the Negev Desert (Israel), one ♀ in early pregnancy was reported at the beginning of Mar and, in the Dead Sea area, 50% of 48 ♀♀ were

lactating in mid-Apr, and one ♀ was still lactating in a cave nearby as late as mid-Jun (Yom-Tov *et al.* 1992).

Conservation IUCN Category: Data Deficient.

Population probably small; suitable habitat might be fragmented, but needs more research to be properly evaluated.

Measurements

Plecotus christii

FA: 38.4 (36–41) mm, $n = 17$

WS: n. d.

TL: 93.3 (92–96) mm, $n = 6$

HB: 48.5 (42–54) mm, $n = 9$

T: 45.0 (42–48) mm, $n = 6$

E: 36.0 (32–39) mm, $n = 10$

Tr: 17.8 (17.4–18.5) mm, $n = 4$

Tib: n. d.

HF: 8.3 (8–9) mm, $n = 7$

WT: 5.8, 7.8 g, $n = 2$

GLS: 16.6 (16.0–17.1) mm, $n = 15$

GWS: 8.6 (8.1–8.9) mm, $n = 14$

C–M³: 5.4 (5.2–5.7) mm, $n = 15$

Egypt and Libya (Gaisler *et al.* 1972, Qumsiyeh 1985, Benda *et al.* 2004c)

Key References Benda *et al.* 2004c; Gaisler *et al.* 1972; Kock 1969a; Qumsiyeh 1985.

Petr Benda & Stéphane Aulagnier

Plecotus gaisleri GAISLER'S LONG-EARED BAT

Fr. Oreillard du Maghreb; Ger. Libysches Langohr

Plecotus gaisleri Benda, Kiefer, Hanak and Veith, 2004. Folia Zool. 53, Monograph 1: 28. Wadi al Kuf, SW Massah, Cyrenaica, Libya.

Taxonomy Populations of *Plecotus* from the Maghreb in NW Africa and Cyrenaica in NE Libya were identified as *P. auritus* and then considered to represent a subspecies of *P. austriacus*. Subsequently, based on morphological evidence, Benda *et al.* (2004c) revised African populations of *Plecotus* and concluded that the Maghrebian and Cyrenaican populations represented subspecies of *P. teneriffae*. They described a new subspecies, *P. t. gaisleri*, based on specimens from Cyrenaica and, pending genetic evidence, tentatively included the Maghrebian population in *P. t. gaisleri* although some differences in colour were observed. In their Appendix 2, however, they referred to the Maghrebian population as *P. t. cf. gaisleri*. Genetic evidence confirmed that the Maghrebian and Cyrenaican populations are distinct (Juste *et al.* 2004). Subsequently, based on both morphological and genetic evidence, Spitzenberger *et al.* (2006) revised the genus *Plecotus*, and concluded that *P. kolombatovici* contained four subspecies of which two occurred in Africa: *P. k. gaisleri* in Cyrenaica and an as yet undescribed subspecies in the Maghreb. More recently, based only on material from Cyrenaica, Mayer *et al.* (2007) raised *gaisleri* to specific status, but did not discuss the relationship of *P. gaisleri* to the Maghrebian population. Therefore, for convenience and pending resolution of this relationship,

in this profile, both populations are treated as *P. gaisleri*, with presumably two subspecies. Synonyms: *aegyptius*, *christiei*. Chromosome number (Tunisia): $2n = 32$; $aFN = 50$ (Baker *et al.* 1974).

Description A very small microbat without noseleaf and with tail more or less fully enclosed in interfemoral membrane; five upper and six lower cheekteeth and two upper incisors on each side; ears joined at base, large for a vespertilionid (E: 33–40 mm) and relatively enormous (ca. 92% of FA); dorsal pelage greyish-brown, hairs with basal half dark; face, ears and wings dark; muzzle not inflated behind nostrils. Sexes similar. Pelage dense, soft, slightly woolly; mid-dorsal hairs 7–9 mm. Dorsal pelage greyish-brown; hairs tricoloured with basal half dark rusty-brown, terminal half pale or dark amber depending on humidity of habitat (animals from dry regions are paler) with brown or greyish-brown tip. Ventral pelage pale yellowish-brown or pale greyish-brown; hairs dark greyish-brown with pale yellowish-brown or pale greyish-brown at tip. Face dark brown to dark greyish-brown. Muzzle narrow, not inflated behind nostrils, protuberance above upper eyelid (supraorbital gland) comparatively large, ca. 1.2 mm in diameter (cf. *P. christii*). Ears dark brown to dark greyish-

brown, relatively long (94 [86–99]% of FA and therefore look enormous), inner margins joined by low band at base. Tragus opaque, of medium relative length (46 [42–50]% of E), 6 mm at widest, tapering to blunt point. Eyes relatively large for a microbat. Wing-membranes dark brown to dark greyish-brown; skin over wing-bones moderately darker. Thumb comparatively long (6.1 [5.2–6.8] mm) (cf. *P. christii*). Baculum Y-shaped; lateral arms long, broad, with acute angle between them (Figure 143c).

Skull medium-large for a *Plecotus*, with braincase relatively high, short and broad (braincase width 47–51% of GLS) (Benda *et al.* 2004c). Dorsal profile of forehead region strongly concave for an African *Plecotus* (Figure 142c) (cf. *P. balensis*, *P. christii*). Rostrum relatively long ($C-M^3$: 33–35% of GLS), medium in height and relatively broad (width between canines 68–71% of $C-M^3$). Dentition more robust than in *P. balensis* and *P. christii*. Anterior upper premolar comparatively large (length 0.44–0.54 mm; breadth 0.52–0.62 mm); within tooththrow; canine and posterior premolar well separated.

Geographic Variation There are no profound morphological differences between *P. g. gaisleri* from Cyrenaica and *P. g. cf. gaisleri* from the Maghreb (Benda *et al.* 2004c). These authors observed colour variation in the Maghrebian populations: specimens from more arid desert and semi-desert habitats are paler than those from coastal and montane habitats and, similarly, they are paler than *P. g. gaisleri* from Cyrenaica. Spitzenberger *et al.* (2006) also reported differences in colour but also observed differences in cranial characters. Mean CbL in ♂♂ and ♀♀ respectively: 15.8 and 16.0 mm in *P. gaisleri*; 15.9 and 16.2 mm in *P. g. cf. gaisleri*.

Similar Species The only other vespertilionids in Africa that have ears with inner margins joined are:

Plecotus balensis. Dorsal hairs with basal two-thirds dark brown. Skull with frontal region weakly concave. Rostrum usually relatively shorter and narrower (details in Description). Baculum Y-shaped with obtuse angle between lateral arms. Ethiopia, possibly Eritrea.

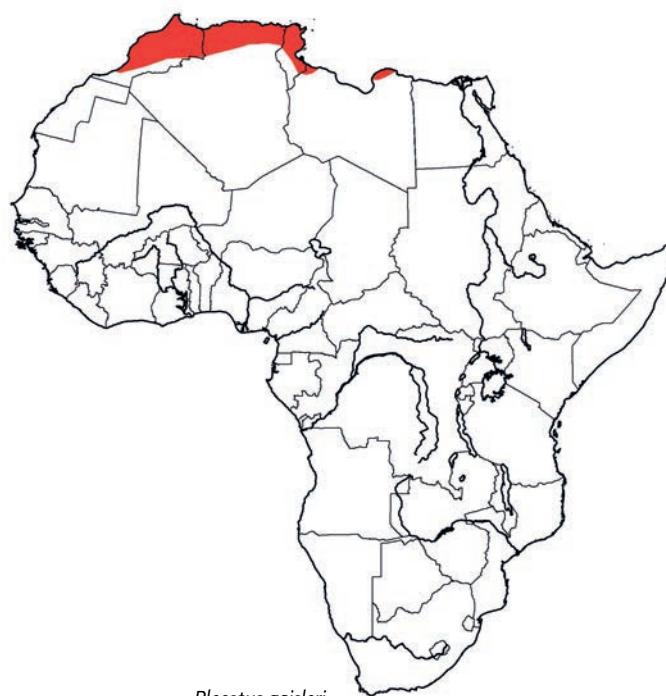
P. christii. Ears unpigmented except around tip. Wing-membranes pale, semi-translucent. Muzzle inflated behind nostrils. Skull with frontal region weakly concave; rostrum relatively narrower and usually relatively shorter (details in Description). Baculum Y-shaped with comparatively short lateral arms. NE Sahara (Libya, Egypt, N Sudan).

Barbastella (2 spp.). Ears much shorter (13–18 mm). Only five lower cheekteeth and one upper incisor on each side.

Only one other vespertilionid in Africa has long ears (>28 mm):

Otonycteris hemprichii. Ears with inner margins not joined at base. Only four upper and five lower cheekteeth and one upper incisor on each side.

Distribution In Africa, recorded from the Mediterranean Coastal and Afromontane–Afroalpine BZs in Morocco, Algeria, Tunisia and N Cyrenaica in Libya, and marginally from the Saharan Arid BZ in Morocco, Algeria, Tunisia and Tripolitania (NW Libya) (Aulagnier & Thévenot 1986, Kowalski & RzebiK-Kowalska 1991,



Plecotus gaisleri

Benda *et al.* 2004c, d). Extends from the coast to the NW border of the Sahara (Anti-Atlas, Saharan Atlas, Jebel Nafusa). Old records from Senegal require confirmation and have not been mapped (most probably they have been mislocated).

Habitat Inhabits a variety of open and semi-covered areas – mainly steppes but also agricultural landscapes, lowland basins and mountains. Recorded from sea level to 2630 m in the High Atlas. In the Maghreb, mostly recorded from Morocco and the geographic range covers all the mountain ridges of this country. In Algeria, recorded from the coast to the southern slopes of the Saharan Atlas Mts. In Tripolitania, recorded from three arid places on the Jebel Nafusa. In Cyrenaica, recorded from at least nine localities in an area of ca. 10,000 km² of coastal and montane vegetation.

Abundance Comparatively numerous, although only found in small colonies. Common in both small settlements and large towns.

Adaptations Wing morphology and flight characteristics similar to other *Plecotus*. In summer, roosts by day mainly in rocky cavities and caves, but also in dark areas of minarets, old monuments, ruins, caverns and old houses. Most frequently clings to sides of deep cracks, but also hangs from ceilings. In winter, roosts by day in various spaces in buildings, caves, mines, wells and holes in trees. Found in mixed colonies with *Rhinolophus blasii*. Active all year-round in Algeria, although daily torpor has often been recorded in summer, and undoubtedly occurs in all months.

Foraging and Food Forages at night (and even before sunset in autumn in Algeria; Kowalski & RzebiK-Kowalska 1991), by slow-hawking in parks, over meadows, among rocks with sparse sub-desert vegetation, and over water. Feeds predominantly on medium-sized and large Lepidoptera (mostly Noctuidae), and occasionally on Coleoptera and Diptera (Trujillo 2002).

Echolocation No information.

Social and Reproductive Behaviour In winter, roosts singly or in tight clusters of ca. ten individuals of both sexes. In summer, the sexes segregate; adult ♀♀ roost in maternity colonies of 10–30 adults; they hang separately or in small groups. Mating occurs in autumn; ♂♂ become territorial at this time.

Reproduction and Population Structure Litter-size: one (n = 2). Reproductive chronology not known, probably restricted seasonal monoestry as in *P. teneriffae* (Trujillo 2002). Births occur from end of Apr to mid-May in Cyrenaica, and from May to early Jun in Tunisia (Baker *et al.* 1974). In the Canary Is., 70% of ♀♀ give birth in the main known colony, and most of the young in this colony can fly by mid-Jul (Trujillo 2002). The size of testes is maximal in Sep, which is probably the main mating period.

Predators, Parasites and Diseases Predators occasionally include Barn Owls *Tyto alba* and Pharaoh Eagle-owls *Bubo ascalaphus* (Aulagnier 1989). Ectoparasites include a bat-fly *Nycteribia schmidli* (Diptera: Nycteribiidae), a flea *Nycteridopsylla pentactena* (Siphonaptera: Ischnopsyllidae) and a tick *Carios boueti* (Acari: Argasidae) (Anciaux de Faveaux 1984, Beaucournu & Kowalski 1985).

Conservation IUCN Category: Not Evaluated.
Pesticides threaten populations in agricultural areas.

Measurements

Plecotus gaisleri

FA: 39.5 (37–42) mm, n = 44

WS: n. d.

TL: n. d.

HB: 49.8 (45–55) mm, n = 24

T: 47.6 (44–52) mm, n = 24

E: 36.1 (33–40) mm, n = 28

Tr: 16.7 (14.9–18.5) mm, n = 25

Tib: n. d.

HF: 8.6 (8–9) mm, n = 14

WT: 8.1 (7.0–10.0) g, n = 24

GLS: 17.0 (16.2–17.4) mm, n = 43

GWS: 9.0 (8.6–9.2) mm, n = 39

C–M³: 5.8 (5.6–5.9) mm, n = 42

Morocco, Algeria, Tunisia, Libya (mainly from Benda *et al.* 2004c)

Key References Aulagnier & Thévenot 1986; Benda *et al.* 2004c; Gaisler 1984; Hanák & Elgadi 1984; Kowalski & Rzebik-Kowalska, 1991.

Petr Benda & Stéphane Aulagnier

GENUS *Scotoecus*

Lesser House Bats

Scotoecus Thomas, 1901. Ann. Mag. Nat. Hist., ser. 7, 7: 263. Type species: *Scotophilus albofuscus* Thomas, 1890.

A polytypic genus with, controversially, two, three or four species endemic to sub-Saharan Africa and one endemic to Pakistan and N India (Hill 1974b, Koopman 1994, Simmons 2005). Diagnostic combination of characters (African species only): four or five upper and five lower cheekteeth and one upper incisor on each side (as in *Nycticeinops*, *Otonycteris* and *Scotophilus*); ears relatively short; FA: 28–40 mm; penis very long (9–16 mm); upper canine with anterior surface flattened and grooved; posterior upper molar with three ridges; anterior lower premolar at least two-thirds height of posterior premolar, usually subequal. Skull somewhat flattened; braincase broad; rostrum very broad across lacrymals; dorsal profile (viewed laterally) rising at gentle slope from incisors to lambdoid crest; frontal area slightly convex. Interorbital region broad. Zygomatic arches very slender and weak; usually lost during preparation of skulls. Sagittal and lambdoid crests very weakly developed; helmet slight. Rostral and anterior palatal emarginations very deep. Selected characters of *Scotoecus* are illustrated in Figure 144.

Treated as subgenus of *Nycticeus* (e.g. Ellerman *et al.* 1953, Hayman & Hill 1971), reinstated to generic status by Rosevear (1965) and

retained as a genus by Hill (1974b), Koopman (1993, 1994) and Simmons (2005). In Africa, there are light-winged and dark-winged forms. All light-winged *Scotoecus* are placed in *S. albofuscus* (with *S. a. woodi* as a subspecies) and there are no taxonomical problems associated with this species. In contrast, five dark-winged forms have been named but their status is controversial. Simmons (2005) recognizes three dark-winged species. In contrast, pending resolution of the problems, all dark-winged forms are tentatively considered here to represent one species, *S. hirundo*. The controversies are discussed in the profile of this species.

Both African species are found in woodland savannas; *S. albofuscus* also occurs in some forest habitats.

The African species recognized here are:

S. albofuscus. Wings white, semi-translucent, becoming brownish around edges and near body.

S. hirundo. Wings dark-brown, slightly translucent.

Meredith Happold

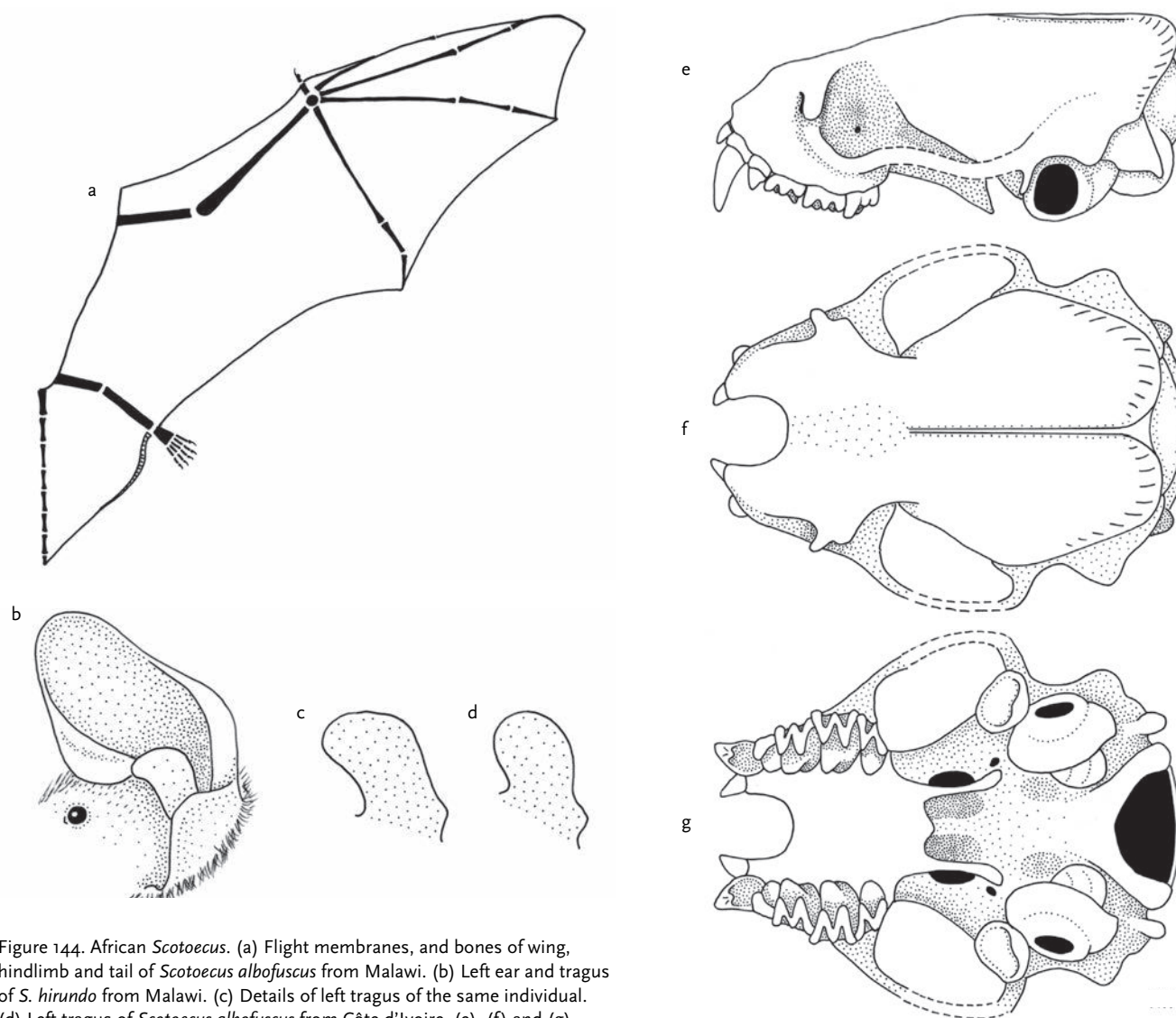


Figure 144. African *Scotoecus*. (a) Flight membranes, and bones of wing, hindlimb and tail of *Scotoecus albofuscus* from Malawi. (b) Left ear and tragus of *S. hirundo* from Malawi. (c) Details of left tragus of the same individual. (d) Left tragus of *Scotoecus albofuscus* from Côte d'Ivoire. (e), (f) and (g) Lateral, dorsal and ventral views of skull of *Scotoecus albofuscus woodi* (holotype, BMNH 17.2.1.1, from Malawi).

Scotoecus albofuscus LIGHT-WINGED LESSER HOUSE BAT (GAMBIAN LESSER HOUSE BAT)

Fr. Scotèce à ailes blanche; Ger. Weißflügel-Hausfledermaus

Scotoecus albofuscus (Thomas, 1890). Ann. Mus. Civ. Stor. Nat. Genova 29: 84. Bathurst, Gambia.

Taxonomy Originally *Scotophilus albofuscus*. Synonyms: *woodi*. Subspecies: two of dubious validity (see Geographic Variation). Chromosome number: not known.

Description Very small microbat without noseleaf and with tail more or less fully enclosed in interfemoral membrane; four upper and five lower cheekteeth and only one upper incisor on each side; ears well separated, short for a vespertilionid (9–15 mm); FA: 29–34 mm; wings white and semi-translucent; penis ca. 9 mm. Sexes apparently similar in colour and size, but data are limited. Pelage soft and dense; mid-dorsal hairs 4–6 mm. Dorsal pelage dark brown, golden-brown or fawn; hairs unicoloured. Ventral pelage slightly paler than dorsal pelage. Head somewhat flattened, muzzle broad, flat with

nostrils opening sideways from small transverse pad. Ears widely separated, comparatively and relatively short for a vespertilionid (40.8 [32–52]% of FA), oval; outer margin with semi-circular antitragus; tip rounded. Tragus short (just over one-third of E), rounded (Figure 144d). Eyes small. Wings white, semi-translucent, becoming brownish with brown venation around edges and close to body; forearms and first, second and third fingers brown, fourth and fifth fingers white. Interfemoral membrane blackish-brown. Calcars long but weak. Penis long (ca. 9 mm).

Skull (Figure 144) as described in Genus *Scotoecus*. Upper incisor fairly long, unicuspid, directed inwards. Upper canine with anterior face flat and conspicuously grooved. Only one upper premolar – anterior premolar apparently always absent (Hill 1974b, Taylor &

van der Merwe 1998). Posterior premolar pointed; in contact with canine; reaching two-thirds to three-quarters height of canine. Posterior upper molar with three ridges (cf. *Scotophilus*). Anterior lower premolar only slightly shorter, and slightly stouter, than the tall, slender posterior lower premolar (cf. *Nycticeinops*). Dental formula: $\frac{1113}{3123} = 30$.

Geographic Variation Two subspecies were recognized, mainly on basis of body and skull measurements, by Hill (1974b) and retained by Koopman (1994) and Simmons (2005). However, analysis of more data than Hill (1974b) had access to suggests that the morphometric differences are slight, but the geographic distributions of the two taxa appear to be very widely separated by the Rainforest BZ in the Congo Basin, and this supports their subspecific status:

S. a. albofuscus: West Africa. FA: 29.7 (29–31) mm, n = 7; GLS: 13.9 (13.1–14.6) mm, n = 4; C–M³: 4.9 (4.7–5.1) mm, n = 8.

S. a. woodi: eastern part of geographical range. FA: 30.1 (29–34) mm, n = 27; GLS: 13.6 (12.7–14.9) mm, n = 21; C–M³: 5.2 (4.9–5.6) mm, n = 21.

Similar Species Three other African vespertilionids have white wings:

Pipistrellus rendalli. Two upper incisors on each side. Penis not extremely long.

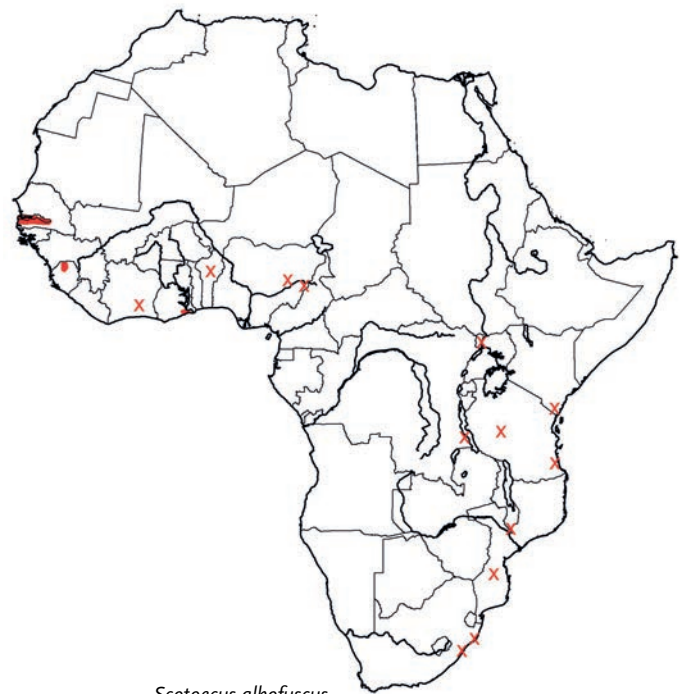
P. tenuipinnis. Two upper incisors on each side. Penis not extremely long.

Glauconycteris gleni. Two upper incisors on each side. Brown reticulation lines on arm-wing. Penis not extremely long.

Note: the wings of some other species, e.g. *Mimetillus moloneyi*, can become very pale after long preservation in alcohol, but these species have two upper incisors on each side.

Distribution Endemic to Africa. Known only from a few scattered localities, mainly in the Sudan Savanna, Guinea Savanna and Zambezian Woodland BZs but with some records in the Rainforest BZ and the Rainforest–Savanna Mosaic in West Africa, and in the Coastal Forest Mosaic BZ. Apparently absent from the Congolian rainforest. Distributed from Gambia to Cameroon, and from Uganda and Kenya to KwaZulu–Natal, but not yet recorded from all countries within this range. Mapped from country checklists (see order Chiroptera), Hill (1974b), Kearney & Taylor (1997), other literature (see below) and museum records.

Habitat In West Africa, recorded from Sudanian woodland savannas including those dominated by *Isoberlinia*; Yola Marsh in Nigeria; and mosaic of grassland and thicket in Shai Hills, Ghana (Rosevear 1965, Grubb *et al.* 1998). No evidence of occurrence in forests in West Africa. Elsewhere, recorded in Zoka Forest, Uganda (Kityo & Kerbis 1996); East African coastal mosaic in Kenya (Whitaker & Mumford 1978); riverine forest with *Hyphaene* palms in S Malawi (R. C. Wood, in Kershaw 1922) and remnants of this forest ca. 80 years later (Happold & Happold 1997); mopane woodland in Mozambique (Smithers & Lobão Tello 1976), and Dune Forest in KwaZulu–Natal (Kearney & Taylor 1997).



Scotoecus albofuscus

Abundance Very rarely collected and considered rare throughout its geographic range, but the use of elevated mist-nets might result in an increase in records (see below).

Adaptations Aspect ratio low; wing-loading medium. Flight fast with very poor manoeuvrability. One bat whose flying abilities were tested could not fly around a 3.5×3.5 m room by banking, and did not attempt to turn by stalling-and-twisting (M. Happold unpubl.). Mr R. C. Wood (in Kershaw 1922) noted that these bats roosted ‘among the leaves of low *Hyphaene* palms in forest, where they appear to be moderately numerous, though rarely seen’.

Foraging and Food Based on wing morphology and the flying characteristics of one individual, predicted to forage by moderately fast-hawking mainly in open spaces moderately high above ground and above canopies of trees. This, and the difficulty of catching this species at its day-roosts, might explain why *S. albofuscus* is rarely collected: it might be caught more often in elevated mist-nets in the future. The stomachs of three individuals in Kenya contained mainly Hemiptera and Coleoptera, with some Lepidoptera, Diptera and other insects (Whitaker & Mumford 1978).

Echolocation No comparable information available but one call is illustrated in Monadjem *et al.* (2010).

Social and Reproductive Behaviour Several may be taken together nestling down among the leaves (R. C. Wood in Kershaw 1922).

Reproduction and Population Structure At 16°32'S (Chiromo, Malawi), one ♀ was post-lactating in early Apr (M. Happold unpubl.). At 28°17'S (St Lucia, KwaZulu–Natal, South Africa), a newly caught ♀ gave birth to twins in late Nov (Kearney & Taylor 1997).

Predators, Parasites and Diseases Ectoparasites include a bat-fly *Basilia robusta* (Diptera: Nycteribiidae) and mites *Spinturnix walkeri* (Acari: Spinturnicidae) and *Notoedres* sp. (Acari: Sarcoptidae) (Anciaux de Faveaux 1984).

Conservation IUCN Category: Data Deficient.

Measurements

Scotoecus albofuscus

FA: 30.0 (29–34) mm, n = 35

WS (a): 228.6 (210–240) mm, n = 7

TL: 88.3 (76–95) mm, n = 29

T: 33.1 (27–41) mm, n = 30

E: 12.1 (9–15) mm, n = 29

Tr: 4.0, 4.4 mm, n = 2

Tib: 11.5 (10–13) mm, n = 3

HF: 8.5 (8–9) mm, n = 5

WT: 7.1 (5.0–9.5) g, n = 11

GLS: 13.6 (12.7–14.9) mm, n = 25

GWS: 10.5 (10.0–11.2) mm, n = 10

C–M³: 5.1 (4.7–5.8) mm, n = 30

Throughout geographic range (BMNH, HC, HZM, NMZB, ROM, SMF and literature)

Key References Hill 1974b; Kearney & Taylor 1997; R. C. Wood in Kershaw 1922.

Meredith Happold

Scotoecus hirundo DARK-WINGED LESSER HOUSE BAT (SWALLOW-LIKE LESSER HOUSE BAT)

Fr. Scotèce hironnelle; Ger. Schwarzflügel-Hausfledermaus

Scotoecus hirundo (de Winton, 1899). Ann. Mag. Nat. Hist., ser. 7, 4: 355. Gambaga, Ghana.

Taxonomy Originally *Scotophilus hirundo*. Synonyms: *albigula*, *artinii*, *falabae*, *hindei*. Subspecies: uncertain (see Geographic Variation). The taxonomy of dark-winged *Scotoecus* is controversial. Ellerman *et al.* (1953) placed all dark-winged *Scotoecus* in *S. hirundo*. Hill (1974b) revised the genus and divided African dark-winged forms into *S. hirundo* with no subspecies, and *S. hindei* with subspecies *S. h. hindei* and *S. h. albigula* (the latter having more massive canines and cheekteeth). A collection of one *S. h. hindei* and one *S. h. albigula* from Malawi (identified by J. E. Hill on basis of craniodental measurements) appeared to provide evidence of sympatry and, consequently, *albigula* was raised to specific status (Happold *et al.* 1987), a conclusion followed by Ansell & Dowsett (1988). However, a larger collection of eight ♂♂ and 11 ♀♀ from Malawi showed that differences in C–M³ and M³–M³ were correlated with sex, the ♂♂ having more massive teeth than the ♀♀: consequently, Happold & Happold (1997) followed Koopman (1965, 1975, 1993) and Robbins (1980) who placed all dark-winged *Scotoecus* in *S. hirundo*. Robbins (1980) recorded sexual dimorphism in dark-winged *Scotoecus* from Benin and Ghana (♂♂ larger than ♀♀), and also analysed Hill's measurements (Hill 1974b) to show that his sample of *S. hirundo* was comprised mostly of ♀♀ (14 of 17) and his sample of *S. hindei* was mostly ♂♂ (eight of nine). Taylor & van der Merwe (1998) conducted a principal component analysis of seven cranial characters of 19 dark-winged *Scotoecus* to test Koopman's (1993) hypothesis that *hindei*, *albigula* and *hirundo* are synonymous. They found that five *hirundo* from Cameroon, Uganda and Ethiopia, four *falabae* from Cameroon, four *hindei* from Ethiopia and Uganda plus one from Malawi, four other specimens referred to as *S. cf. hindei* from Malawi, and one *albigula* from Malawi, separated into five clusters, suggesting that *S. hirundo*, *S. hindei* and *S. albigula* merited specific status, and that the specimens referred to as *S. cf. hindei* could not be grouped with any of the above species. Sex was not taken into consideration in this study. Cotterill (2001e) measured FA and eight craniodental parameters of 11 female and two male dark-winged specimens from Zambia and, based on differences in skull proportions, concluded that one ♀ represented *S. hindei* and the

others *S. albigula*. The specimen he referred to *S. hindei* was larger and outside (albeit sometimes very marginally) the ranges of specimens referred to *S. albigula*, in the following measurements and ratios: C¹–C¹, C¹–C¹ as percentage of GLS, M³–M³, M³–M³ as percentage of GLS and C–M³. Although these differences indicate the possible presence of two species, the sample size is too small for statistical analysis. Pending a revision of dark-winged forms that takes sexual dimorphism into consideration, all dark-winged forms are provisionally treated here as *S. hirundo*. Chromosome number (Kenya, as *S. hindei*): 2n = 30; aFN = 50 (Nagorsen *et al.* 1976).

Description Very small microbat without noseleaf and with tail more or less fully enclosed in interfemoral membrane; four or five upper cheekteeth, five lower cheekteeth and only one upper incisor on each side; ears well separated and short for a vespertilionid (9–14 mm); FA: 28–40 mm; wings blackish-brown; penis extremely long (14–16 mm); anterior lower premolar at least two-thirds height of posterior premolar, usually only slightly shorter. Sexes similar in colour; ♂♂ on average slightly larger in some body measurements and with more massive teeth, longer upper tooththrow and wider M³–M³ (Robbins 1980, M. Happold unpubl.). Pelage soft, dense, with no sheen; mid-dorsal hairs 4–6 mm. Dorsal pelage chocolate brown, or medium to pale sepia brown; hairs unicoloured (Malawi) or with basal half off-white, terminal half sepia brown (West Africa). Ventral pelage grey, beige, greyish-white or pale beige: chest sometimes paler. Head somewhat flattened; muzzle broad, flat, dark brown, almost naked. Nostrils opening sideways from small transverse pad. Ears widely separated, comparatively and relatively short for a vespertilionid, oval; tip rounded. Tragus relatively short (41.9 [38–46]% of E); somewhat hatchet-shaped, anterior margin strongly concave; posterior margin with smooth, obtuse angle just above mid-height, tip rounded (Figure 144c; Malawi). Eyes very small. Wings and interfemoral membrane dark brown, slightly translucent. Penis extremely long, 14–16 mm, ca. 25–30% of HB.

Skull as described in Genus *Scotoecus*. Less flattened than in *S. albofuscus*. Upper canine with anterior surface flat and shallowly

grooved. Anterior upper premolar usually present (at least on one side) but minute, fully displaced lingually, sometimes loose and possibly easily lost. Posterior upper premolar pointed, in contact with canine and reaching two-thirds to three-quarters height of canine. Posterior upper molar with three ridges (cf. *Scotophilus*). Anterior lower premolar at least two-thirds height of posterior lower premolar, usually only slightly shorter (cf. *Nycticeinops*). Sexual dimorphism in craniodental characters is illustrated by differences in M^3-M^3 – in Benin and Ghana, ♂♂: 6.6 (6.3–6.8) mm, $n = 11$; ♀♀: 6.4 (5.8–6.6) mm, $n = 19$ (Hill 1974b in Robbins 1980). In Malawi, ♂♂ 7.7 (7.6–7.8) mm, $n = 6$; ♀♀ 7.3 (7.1–7.6) mm, $n = 10$ (M. Happold unpubl.). Dental formula: $\frac{1113}{3123} = 30$ or $\frac{1123}{3123} = 32$.

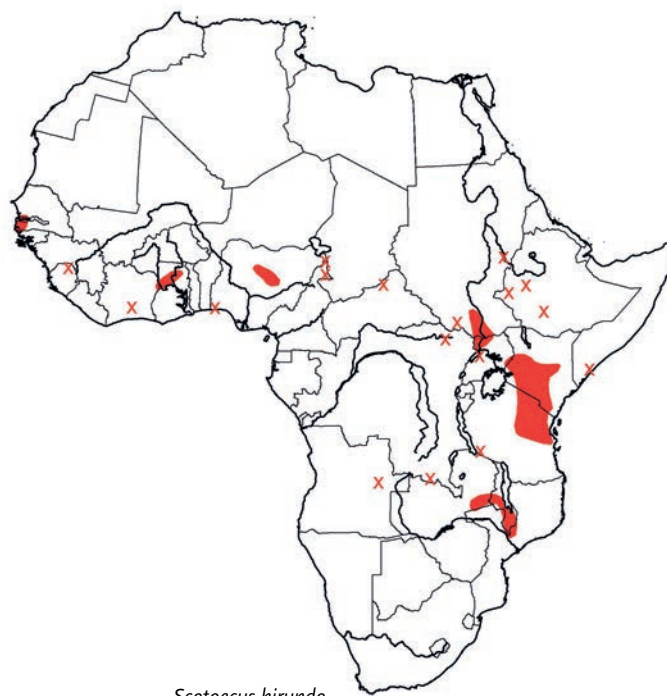
Geographic Variation Koopman (1994) recognized four subspecies, *S. h. hirundo* (Senegal to Benin, and possibly to Ethiopia), *S. h. falabae* (Nigeria and Cameroon), *S. h. hindei* (Southern Sudan and Somalia to SE DR Congo) and *S. h. albigula* (Kenya to Angola). However, the status and distribution of these forms is uncertain (see Taxonomy). A preliminary survey of FA, C– M^3 and M^3-M^3 measurements (made by different people) suggests that there is geographic variation, with an increase in size (in both sexes) from Ghana/Benin (Robbins 1980), to Sudan/Ethiopia, to Kenya/Tanzania, to Malawi. For example, in ♂♂, mean FA for these areas (in the above order) are 33.4 ($n = 11$); 33.6 ($n = 5$); n. d.; 35.4 ($n = 18$). Similarly, mean C– M^3 : 5.1 ($n = 11$); 5.2 ($n = 6$); 5.5 ($n = 9$), 6.0 ($n = 8$). Similarly, mean M^3-M^3 : 6.6 ($n = 11$), 6.6 ($n = 4$); Kenya/Tanzania n. d.; 7.7 ($n = 6$). West African specimens have bicoloured dorsal pelage, cf. unicoloured in Malawi.

Similar Species Only one other dark-winged vespertilionid has only one upper incisor on each side and FA: <41 mm:

Nycticeinops schlieffeni. Usually lighter (5.5 [4–9] g). FA: 28–35 mm. Dorsal pelage cinnamon, fawn or greyish-fawn; ventral pelage slightly to considerably paler, whitish or pure white. Tragus more pointed (Figure 144c). Penis 5.6–6.2 mm. Anterior lower premolar ca. half size of posterior premolar. Upper canine with anterior surface rounded and not grooved.

Note: *Mimetillus molonyi* also has an extremely long penis, but differs in having very short wings, a dorsoventrally flattened skull and two upper incisors on each side.

Distribution Endemic to Africa. Widespread south of the Sahara, mainly in the Sudan Savanna, Guinea Savanna, Somalia–Masai Bushland and Zambezi Woodland BZs, but with some records from the outer edges of the Rainforest–Savanna Mosaics and in the Coastal Forest Mosaic BZ. Recorded from most countries from Senegal to Sudan, Ethiopia and S Somalia, and southwards (mainly on eastern side of continent) to S Angola and S Malawi. Mapped from country checklists (see order Chiroptera), Hill (1974b), other literature and museum records. Apparently avoids the Congolian rainforest. In Angola, recorded from Lac Calundo and from the ‘Cunene Region’ in SW Angola (Crawford-Cabral 1989): the latter locality is not mapped. Subsequent records (Thorn & Kerbis Peterhans 2009) show that this species is more widespread in Uganda than the map



Scotoecus hirundo

indicates. Furthermore, Monadjem *et al.* (2010) have mapped five localities between ca. 19°S and ca. 25°S in S Mozambique that are not mapped here.

Habitat Found in open woodlands in West Africa (with one record from Lagos in the rainforest zone) (Rosevear 1965); woodlands and deciduous thicket and bushland in the east, and both wetter and drier miombo woodland vegetation zones in the south. In Malawi, has been found in miombo woodland, mosaic of farmland and woodland, relict rainforest, riverine woodland, gardens, villages and towns, at 100–1500 m (Happold & Happold 1987).

Abundance Uncertain. Rarely collected in West Africa (Grubb *et al.* 1998) and in most parts of its geographic range, but commonly recorded in Malawi (Happold & Happold 1997).

Adaptations Aspect ratio low; wing-loading medium. Flight fast to very fast, and agile with moderate manoeuvrability. Turns by banking (minimum radius of turn >25 and <50 cm; none of eight individuals carried out a stall-and-twist turn while under observation in captivity. Individuals could fly across a 1×1×1 m enclosure, but very rarely completed a full circuit (11 bats, 10 flights each; M. Happold unpubl.). By day, known to roost under the corrugated iron roofs of huts and houses, but natural day-roosts are not known. Becomes torpid during day at ambient temperatures of 21–24°C in Malawi. Predicted mean maximum urine concentration is comparatively very high (4550 mOsmol/kg). Captive bats, fed on winged termites and offered water twice/day, drank irregularly (mean drinks/day over a ten-day period, ranged from 0.1 to 0.5 in four individuals; Happold & Happold 1988). All of the above adaptations refer to bats from Malawi. At Masalani (02°18'S, 38°07'E) near Kibwezi in Kenya, numbers of *S. hirundo* were comparatively low during the long dry season (May–Oct), and there was a build-up of subcutaneous fat prior to this period. These

observations led O'Shea and Vaughan (1980) to suspect emigration from Masalani to places that receive rainfall during May–Oct (e.g. the highlands of W Kenya or the coast).

Foraging and Food Forages by moderately fast-hawking. Light-tagged bats ($n = 4$, Malawi) foraged in open spaces, above canopies of trees or over grassland, usually more than 5 m above ground, and often as high as ca. 25 m. They also came as low as 2 m to fly between the trunks of tall eucalyptus trees in a plantation. They foraged at high speed with long, level flights interspersed with spectacularly acrobatic swerving, up and down as well as sideways (M. Happold unpubl.). Diet not known.

Echolocation Search-phase call-shape (Malawi) in open spaces (a) very shallow linear FM and (b) curvilinear steep/shallow FM; these calls are sometimes emitted in alternation (7 bats, flying in open after release; M. Happold unpubl.) (Figure 145). For calls of type (a): intensity high; end-frequency 30–34 kHz; bandwidth 2–4 kHz; call-duration mostly 5–6 ms. End-frequencies of adjacent calls sometimes vary by ca. 2 kHz. For calls of type (b): intensity high, end-frequency 32–34 kHz; bandwidth ca. 6–7 kHz; call-duration mostly 5–6 ms. When calls alternate between types (a) and (b), the end-frequency of (a) is often 2–3 kHz lower than the end-frequency of (b). Approach-phase calls are firstly curvilinear steep/shallow FM sweeps of bandwidth up to ca. 15 kHz, and then steep FM/QCF of greater bandwidth. Calls emitted while close to ground in cluttered environments are steep FM/QCF sweeps; intensity high start-frequency up to 70 kHz; end-frequency 33–40 kHz (17 bats, tethered or as released). Characteristic frequencies (Anabat terminology, based on peak-frequencies) of sequences of steep FM/QCF sweeps emitted by ♀♀ were 37.6 (35–40) kHz (10 bats, 16 sequences), and by ♂♂ were 35.1 (35–37) kHz (6 bats, 10 sequences) with the exception of 39 kHz emitted by one ♂. The difference in characteristic frequency apparently largely reflects the sexual dimorphism in size exemplified by this species, with the larger ♂♂ echolocating at lower frequencies. A sequence including search-phase, approach-phase and 'feeding buzz' calls is shown in Figure 27 and a sequence of search-phase calls showing alternation between different call-shapes and frequencies is shown in Figure 145.

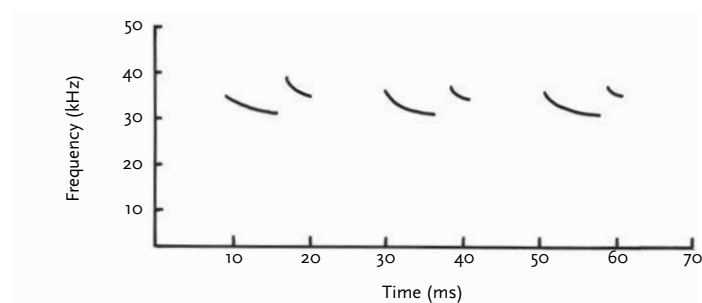


Figure 145. Sonogram of a sequence of search-phase calls emitted by *Scotoecus hirundo* from Malawi, showing alternation between calls of different call-shape and frequency (M. Happold unpubl.).

Social and Reproductive Behaviour No information.

Reproduction and Population Structure Litter-size: 2 ($n = 3$). At 02°18'S (Masalani, inland Kenya), the reproductive chronology is restricted seasonal monoestry with births in Nov (O'Shea & Vaughan 1980). At 15–16°S in Malawi, the chronology is also restricted seasonal monoestry with early pregnancy in Sep ($n = 1$); pregnancy in Oct ($n = 1$); birth in Nov ($n = 1$); 29 of 29 adult ♀♀ lactating Nov–Jan; volant young with unfused epiphyses Jan–Mar ($n = 28$); 4 of 4 adult ♀♀ post-lactating Feb–Mar; and 49 of 49 ♀♀ palpably not pregnant Apr–Jun. From Sep–Jan, 81% of 16 adult ♂♂ had abdominal testes. From Feb–May, 88% of 25 ♂♂ had large scrotal testes. These data suggest that mating may occur in ca. May, followed by sperm storage or reproductive delay until ca. late Aug, but this needs confirmation.

Predators, Parasites and Diseases Ectoparasites include a bed-bug *Cacodmus sparsilis* (Hemiptera: Cimicidae) (Kock *et al.* 1998b) and a flea *Echidnophaga aethiops* (Siphonaptera: Pulicidae) (Anciaux de Faveaux 1984).

Conservation IUCN Category: Least Concern.

Measurements

Scotoecus hirundo

FA (♂♂): 34.4 (31–40) mm, $n = 61$

FA (♀♀): 32.9 (28–37) mm, $n = 81$

WS (a): 245 (213–272) mm, $n = 18^*$

TL: 91.6 (77–105) mm, $n = 51$

T: 34.8 (28–40) mm, $n = 67$

E: 11.8 (9–14) mm, $n = 71$

Tr: 5.2 (4–6) mm, $n = 16$

Tib: 13.2 (12–14) mm, $n = 31^*$

HF: 8.5 (8–10) mm, $n = 32^*$

WT: 10.2 (8–15) g, $n = 36$

GLS: 14.1 (12.1–16.1) mm, $n = 89$

GWS (♂♂): 11.2 (9.6–12.4) mm, $n = 5$

GWS (♀♀): 10.5 (9.3–11.2) mm, $n = 8$

C-M³ (♂♂): 5.5 (4.7–6.4) mm, $n = 67$

C-M³ (♀♀): 5.3 (4.4–6.1) mm, $n = 76$

Throughout geographic range (BMNH, HC, HZM, NMZB, SMF, SMNS, ZFMK and literature)

*Malawi only (M. Happold unpubl.)

Dimensions vary geographically and, because some areas are better represented than others, the means are possibly biased

Key References Hill 1974b; Koopman 1965; Robbins 1980; Taylor & van der Merwe 1998.

Meredith Happold

GENUS *Scotophilus*

House Bats

Scotophilus Leach, 1821. Trans. Linn. Soc. Lond. 13: 69, 71. Type species: *Scotophilus kuhlii* Leach, 1821.

A polytypic genus with 12 species recognized by Simmons (2005) and two species described subsequently by Goodman *et al.* (2005, 2006). Of these 14 species, six occur in Africa, three on Madagascar and one on Réunion I. in the Indian Ocean, and four in Asia. Diagnostic combination characters (African species): four upper and five lower cheekteeth and one upper incisor on each side (as in *Otonycteris*, *Nycticeinops* and *Scotoecus*); ears relatively short; FA: 41–88 mm; penis relatively short; anterior upper molar with two ridges. *Scotophilus* are robust and heavy-bodied, with brown dorsal pelage and yellow, yellowish, white or whitish ventral pelage and dark wings. Tragus long and tapering. Thumb with swollen pad at base. Testes posterior to anus in at least three species. Adult ♀♀ of *S. dinganii*, *S. leucogaster* and *S. viridis* (the only species for which published data are available) have one pair of functional nipples. However, juvenile *S. dinganii* of both sexes have two pairs of rudimentary nipples, one of which disappears later (Verschuren 1957); no information for other species. Skull with well-developed sagittal crest and occipital helmet. Braincase not rising above plane of rostrum so dorsal profile of skull (viewed laterally) is mostly a gentle slope from front to back with a very shallow concavity in the forehead region. Jaws and dentition robust. Upper incisor long, unicuspid; upper canine long. Upper molars unusual – anterior and middle molars with concave surfaces, indistinct ridges and a worn appearance; posterior molar very short

with only two ridges (cf. three in *Nycticeinops* and *Scotoecus*). Dental formula: $^{1113}/_{3123} = 30$. Some external and craniodental characters of *Scotophilus* are shown in Figure 146.

The taxonomy of *Scotophilus* is very controversial and is undergoing further revision. Hayman & Hill (1971) recognized three species: *gigas*, *nigrita* (including *dinganii*, *nux* and other forms) and *leucogaster* (including *viridis* and other forms). Robbins (1978) showed that *nigrita* was the prior synonym of *gigas*, and that bats previously referred to as *nigrita* should be called *dinganii*. Based on multivariate analysis, Robbins *et al.* (1985) recognized six species in Africa: *S. dinganii*, *S. leucogaster*, *S. nigrita* (formerly known as *S. gigas*), *S. nucella*, *S. nux* and *S. viridis*, and restricted *S. borbonicus* and *S. robustus* to Réunion and Madagascar, respectively. Koopman (1994) recognized only three African species: *S. borbonicus* (including *viridis*), *S. leucogaster* (including *dinganii*, *nucella* and *nux*) and *S. nigrita*, but he subsequently recognized five African species: *S. dinganii*, *S. leucogaster* (including *nucella*), *S. nigrita*, *S. nux* and *S. viridis* (Koopman 1993). Additional taxonomic problems are discussed in the species profiles. Here we follow Robbins *et al.* (1985) as does Simmons (2005).

Since this profile was submitted, Jacobs *et al.* (2006) indicated that a cryptic sibling species of *S. dinganii* lives sympatrically with *S. dinganii* in KwaZulu–Natal and Zambia (see Appendix). The cryptic form, as yet not formally described but tentatively named *S. mhlangani* (Jacobs

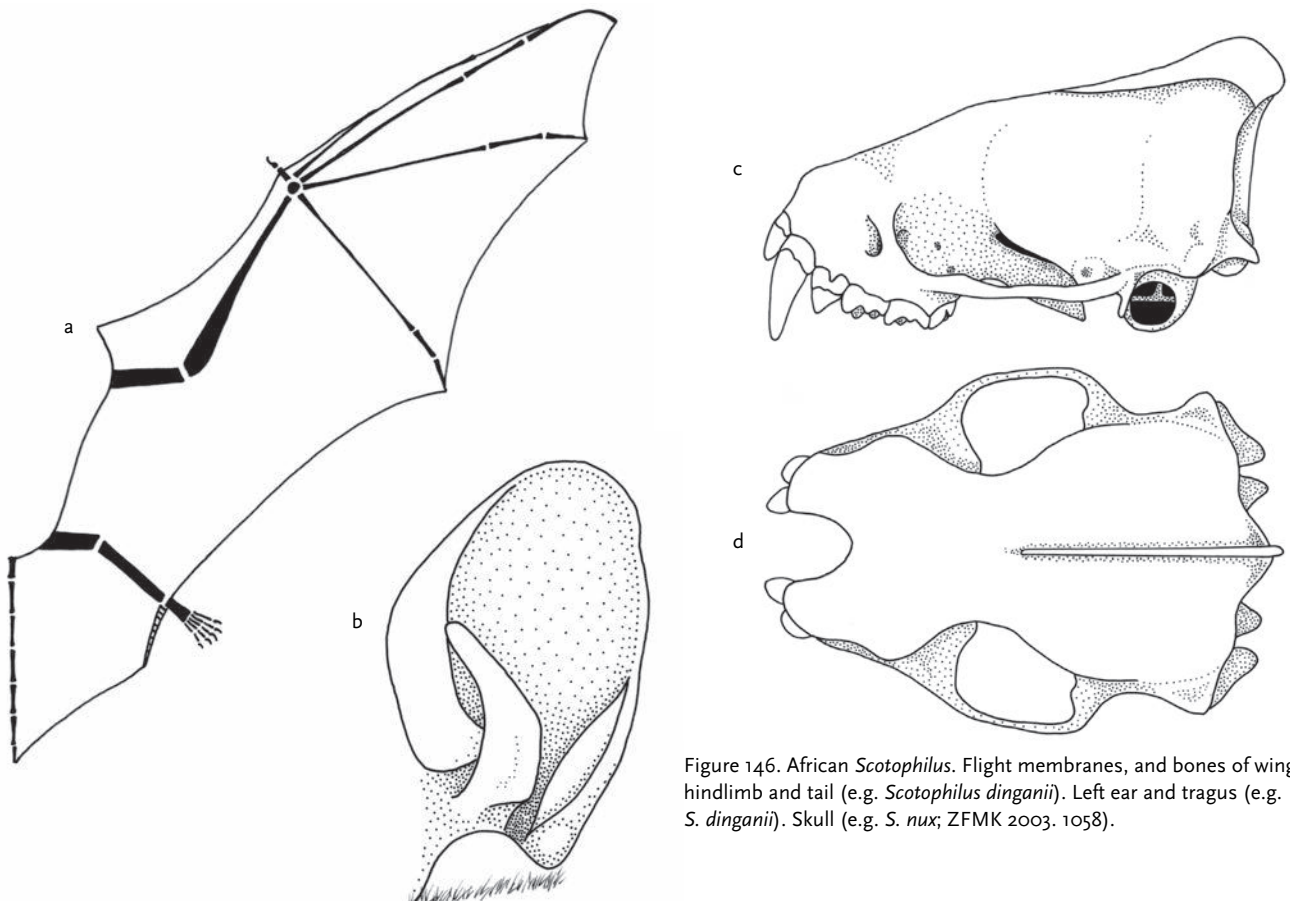


Figure 146. African *Scotophilus*. Flight membranes, and bones of wing, hindlimb and tail (e.g. *Scotophilus dinganii*). Left ear and tragus (e.g. *S. dinganii*). Skull (e.g. *S. nux*; ZFMK 2003. 1058).

et al. 2007), is said to echolocate with calls having peak frequencies 44.3 ± 0.9 kHz (according to Jacobs *et al.* 2007) or 42.6 ± 1.6 kHz (according to Jacobs & Barclay 2009). In contrast, *S. dinganii* in the same location emits lower frequencies (33.7 ± 1.8 kHz) (Jacobs & Barclay 2009). The cryptic species is smaller (FA: 48 [46–52] mm, $n = 17$), differs genetically (Jacobs *et al.* 2006) and karyotypically (Eick *et al.* 2007), and occupies a different ecological niche (Jacobs & Barclay 2009). However, Monadjem *et al.* (2010) consider that this form represents *S. viridis* (according to the original description of this species) and that the name *S. mhlangani* is a *nomen nudum*. *Scotophilus mhlangani* is undoubtedly a *nomen nudum*, but until further evidence clarifies the taxonomic status of this form and its relationships with *S. dinganii*, *S. viridis* and also *S. leucogaster*, it is not mentioned in any species profile here.

In Africa, two species are found only in rainforest, one in rainforest and savanna and three mainly or entirely in savanna habitats.

Some of the six African species can be recognized by their habitats and characters (see Table 28). However, *S. leucogaster* and *S. viridis* are best distinguished by the following discriminant functions in which $x > 0$ (positive) indicates *S. leucogaster*, $x < 0$ (negative) indicates *S. viridis* (V. Van Cakenberghe unpubl.).

North of Equator:

$$x = (0.226 \times \text{GLS}) + (1.235 \times \text{IoB}) + (0.608 \times \text{MW}) + (0.709 \times \text{C-M}_3) - 21.2$$

South of Equator:

$$x = (0.712 \times \text{GLS}) + (1.118 \times \text{IoB}) + (0.590 \times \text{MW}) + (2.802 \times \text{C-M}_3) - 43.3$$

Similarly, *S. leucogaster* and *S. dinganii* can be distinguished by the following discriminant function in which $x > 0$ (positive) indicates *S. dinganii*, $x < 0$ (negative) indicates *S. leucogaster*.

Throughout ranges of both species:

$$x = (0.484 \times \text{CbL}) - (0.741 \times \text{IoB}) - (0.455 \times \text{MW}) + (1.063 \times \text{C-C}) - 6.57$$

All measurements in mm. Abbreviations:

GLS = Greatest length of skull. Measured from most posterior part of skull to the base of the upper incisor.

CbL = Condylbasal length of skull. Measured from the posterior of an exoccipital condyle to the base of the upper incisor.

IoB = Interorbital breadth.

MW = Mastoid width.

C-M₃ = Length of lower toothrow. Measured from base of the lower canine to the base of the posterior lower molar.

C-C = Width across the upper canines. Measured at the base of the teeth.

The six species found in mainland Africa are presented in alphabetical order.

Victor Van Cakenberghe & Meredith Happold

Table 28. Key to the African mainland species in the genus *Scotophilus*. *Scotophilus dinganii*, *S. leucogaster* and *S. viridis* are best distinguished by the discriminant functions in Genus *Scotophilus*. Note separation of *S. leucogaster* and *S. viridis* into populations north and south of the Equator.

| FA (mm) | Ventral pelage | Dorsal pelage | Habitat | Species |
|--------------|---|---|---|---|
| 82.3 (78–88) | Yellow, yellowish or white | Various shades of dark brown suffused with yellow | Mainly Savannas; also Rainforest and Coastal Forest Mosaic | <i>S. nigrata</i> |
| 56.5 (53–61) | Dark brown to reddish-orange | Rusty-brown to blackish-brown | Rainforest | <i>S. nux</i> |
| 51.3 (49–53) | Dark brown to reddish-orange | Dark rusty-brown to blackish-brown | Rainforest | <i>S. nucella</i> |
| 53.3 (47–60) | Pale yellow, bright yellow or orange-yellow; not tinged with brown. In SW Arid zone, sometimes off-white (as in <i>S. leucogaster</i>) | Sepia brown, greenish-brown, greyish-brown or reddish-brown | Savannas and Rainforest–Savanna Mosaics; marginally in Rainforest | <i>S. dinganii</i> |
| 49.9 (44–58) | Pure white to medium brown; never yellowish | Pale to medium brown; never tinged with yellow or green | Savannas and Rainforest–Savanna Mosaics | <i>S. leucogaster</i>
North of Equator |
| 45.5 (41–50) | Always yellowish (pale to medium yellow), sometimes with brownish tinge | Yellowish-brown, greenish-brown to darker orange-brown | Savannas and Rainforest–Savanna Mosaics; marginally in rainforest | <i>S. viridis</i>
North of Equator |
| 47.5 (43–51) | Pure white to medium brown; perhaps sometimes yellowish | Pale to medium brown, not tinged with yellow or green | Not rainforest | <i>S. leucogaster</i>
South of Equator |
| 45.9 (42–50) | Pale grey or pale brown; perhaps sometimes yellowish | Greenish-brown to medium brown | Not rainforest | <i>S. viridis</i>
South of Equator |

Scotophilus dinganii YELLOW-BELLIED HOUSE BAT

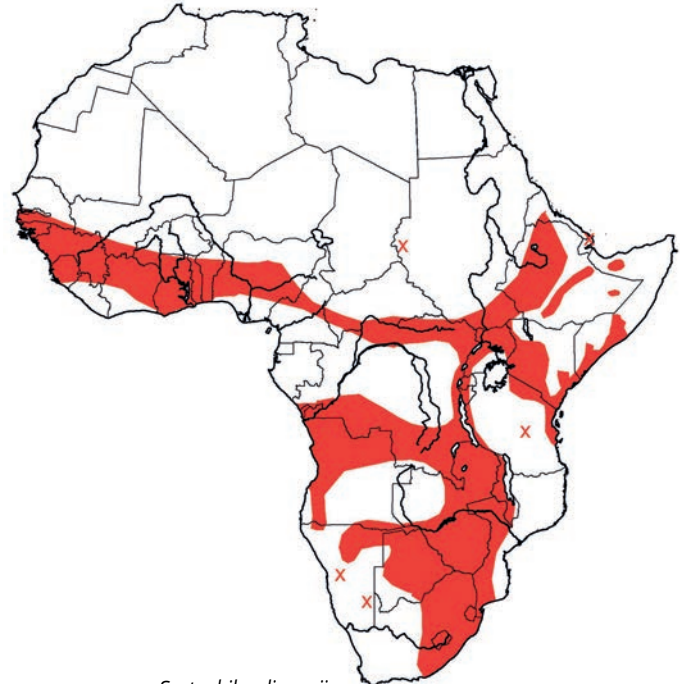
Fr. Scotophile à ventre jaune; Ger. Gelbbäuchige Hausfledermaus

Scotophilus dinganii (A. Smith, 1833). S. Afr. Quart. J. 2: 59. Between Port Natal [= Durban, South Africa] and Dalgoo Bay [= Maputo, Mozambique].

Taxonomy Originally *Vespertilio dinganii*. Synonyms: *colias*, *herero*, *planirostris*, *pondoensis*. Subspecies: uncertain (see Geographic Variation). This species was widely referred to as *S. nigrita* until Robbins (1978) showed that *S. nigrita* was a senior synonym of the very large *S. gigas* and that the next available name for the smaller species was *S. dinganii*. As *S. nigrita*, this species was considered to include *leucogaster* by Koopman (1975), but not by Rosevear (1965) nor (as *S. dinganii*) by Schlitter *et al.* (1980). The specific status of *S. dinganii* has been accepted without dispute since the review of African *Scotophilus*, based on multivariate analysis, by Robbins *et al.* (1985). Chromosome number (South Africa): $2n = 36$; $aFN = 52$. Four pairs metacentric, five pairs submetacentric and eight pairs acrocentric chromosomes. X = small acrocentric; Y = small metacentric (15 ♀♀; 16 ♂♂) (Schlitter *et al.* 1980). In specimens from Somalia, $aFN = 50$ and there are eight pairs metacentric and nine pairs acrocentric (the smallest with secondary constriction); X = medium submetacentric; Y = small telocentric (Ruedas *et al.* 1990).

Description Small, heavily built microbat without noseleaf and with tail more or less fully enclosed in interfemoral membrane; four upper and five lower cheekteeth and one upper incisor on each side; ears separated, short for a vespertilionid (11–22 mm); FA: 47–60; dorsal pelage greenish-brown, greyish-brown or reddish-brown; ventral pelage yellow to orange (never tinged with brown) or off-white in the South-West Arid BZ. Best distinguished from *S. leucogaster* by discriminant function (see Genus *Scotophilus*). Sexes similar in colour, ♀♀ on average slightly larger in body measurements. Pelage smooth, soft and sleek; mid-dorsal hairs 6–7 mm. Dorsal pelage sepia brown, greenish-brown, greyish-brown or reddish-brown; hairs paler at base. Ventral pelage pale yellow, bright yellow or orange-yellow, not tinged with brown; sometimes off-white in the South-West Arid BZ. Ears comparatively and relatively short for a vespertilionid (25–37% of FA), widely separated; inner margin strongly convex; outer margin almost straight. Tragus moderately long, tapering to bluntly rounded tip: anterior margin concave (Figure 146). Eyes small. Wings and interfemoral membrane uniformly dark brown, semi-translucent. Testes posterior to anus. Adult ♀♀ with one pair of functional nipples; juveniles of both sexes with two pairs of rudimentary nipples (one disappears later) (Verschuren 1957). Skull and dentition as described for the genus.

Geographic Variation Uncertain. No subspecies were recognized by Robbins *et al.* (1985), who tabulated means and standard variations of FA and seven cranial parameters for population samples from 13 widespread localities. In contrast, Koopman (1994) treats *colias*, *dinganii*, *herero* and *pondoensis* (and four other forms) as subspecies of *S. leucogaster*, and Simmons (2005) treats *colias*, *herero* and *pondoensis* as subspecies of *S. dinganii* but comments that subspecies are poorly defined. The form *herero*, which occurs in the South-West Arid BZ, has ventral pelage pale yellow to off-white with or without yellow on flanks.



Scotophilus dinganii

Similar Species Four other African *Scotophilus* have FA: <61 mm (Table 28, p. 673):

Scotophilus leucogaster. Best distinguished by discriminant functions, see Genus *Scotophilus*. North of Equator, ventral pelage white or whitish, sometimes tinged with brown, not tinged with yellow (south of Equator, pelage of both species is sometimes similar).

S. viridis. FA almost always shorter (45.5 [41–50] mm). Skull shorter (GLS: 17.0 [15.6–18.0] mm).

S. nucella. Dorsal pelage dark rusty-brown to blackish-brown; ventral pelage dark brown to reddish-orange. Rainforest.

S. nux. Dorsal pelage dark rusty-brown to blackish-brown; ventral pelage dark brown to reddish-orange. Rainforest.

Distribution Endemic to Africa. Widespread south of the Sahara and recorded from most biotic zones and most countries, from Gambia to Eritrea, Djibouti and Somalia and southwards to Namibia and South Africa. However, this species is known only around the edges of the Rainforest BZ, there are only a few records in the arid Horn of Africa and in the South-West Arid BZ, and there are no records from the South-West Cape BZ. The distribution gaps in the Somalia–Masai Bushland and Zambezian Woodland BZs are unexplained. Mapped mainly from Robbins *et al.* 1985.

Habitat Found in most habitats south of the Sahara. Most records are from woodland savannas (including Sudanian undifferentiated woodlands, *Isoberlinia* woodlands, miombo woodland)

and various bushland and thicket savannas. Also lives in rainforest habitats around the edges of the Rainforest BZ (but apparently not in the interior of the Congolian rainforest), in rainforest–savanna mosaics, and in riverine, coastal and montane forests. Thrives in farmlands and suburban areas.

Abundance Common in many areas; probably common throughout most of geographic range.

Adaptations Aspect ratio medium; wing-loading medium (M. Happold unpubl.). Flight fast and agile; cannot fly slowly; manoeuvrability poor; can take off from ground. Turns by banking (minimum radius of turn >50 cm), and by stalling-and-twisting (but not in confined spaces). Able to fly across a 1×1×1 m enclosure, but not able to complete a full circuit (6 bats, 10 flights each; M. Happold unpubl.). Scuttling, head first, up and down, over horizontal, sloping and vertical surfaces, is efficient although not as fast as in molossids. Roosts by day in small holes in trees and wooden lamp-posts (including nests of barbets [Capitonidae] and woodpeckers [Picidae]), and in crevices within hollow trees. Also commonly roosts in narrow crevices and crannies in buildings (both occupied and deserted), particularly under eaves and roofs of corrugated iron, and in crannies in thatch. This may largely explain the abundance of this species in farmlands and suburbia. Scuttles from landing and take-off sites to the nooks in which it roosts. Prefers to rest on sloping or horizontal surfaces, but sometimes clings to vertical surfaces. Tolerates high temperatures under iron roofs (Kingdon 1974). Not known to roost with other species of bats. In Malawi, at 20–21 °C, does not become torpid by day (Happold & Happold 1988). Seasonal fluctuations in abundance at particular localities were observed in Sudan (Thomas & Hinton 1923) and East Africa (Kingdon 1974). In the Shire Highlands, Malawi, captures/month were higher in the wet season (Nov–Feb) than in Mar–Jun and Sep–Oct (no data for Jul–Aug; M. Happold unpubl.). In Zimbabwe, absent from the plateau above 1200 m during the colder months (Smithers & Wilson 1979). Does not hibernate in South Africa (Rautenbach *et al.* 1988). Drinks, on the wing, from pools, streams and dams, and captive bats, fed winged termites, drank every day; predicted mean maximum urine concentration is comparatively low (2851 mOsmol/kg) (Happold & Happold 1988).

Foraging and Food Forages by moderately fast-hawking in moderately uncluttered spaces above canopies, in clearings and over fields (M. Happold unpubl.). Sometimes forages near lights, and sometimes comes into houses at night. Although individuals come to streams and dams to drink, there is no evidence, from echolocation calls, that they pursue insects flying near the surface. Not known to forage as high as some molossids and emballonurids, and often forages closer to trees and as low as ca. 2 m from the ground. Foraging is characterized by long, straight or gently banked flights (during which prey may be captured), and abrupt acrobatic swerves and spectacular dives in pursuit of prey (M. Happold unpubl.). Foraging begins soon after sunset and bats often have full stomachs before it is dark (Kingdon 1974). Foraging is not deterred by rain (M. Happold unpubl.). Apparently feeds mainly on beetles, but other flying insects are taken opportunistically (Kingdon 1974, Fenton 1985, Aldridge & Rautenbach

1987). In Kenya, three stomachs contained Coleoptera (65% by volume), Hemiptera (13%), Orthoptera (13%) and Lepidoptera (5%) (Whitaker & Mumford 1978).

Echolocation Search-phase calls (Malawi and South Africa) are high intensity, very shallow linear FM sweeps and smooth or angular steep/shallow FM sweeps of broader bandwidth, both with end-frequencies 28–35 kHz (Aldridge & Rautenbach 1987, Taylor 2000, M. Happold unpubl.) (Figure 118k, m). As prey is approached, the calls become broader in bandwidth, steeper and the shallow FM component becomes shorter and is lost just before the feeding-buzz commences. There are striking similarities between the calls of *S. dinganii* and those of the molossids *Tadarida pumila* and *T. condylura*, which also forage in uncluttered spaces.

Social and Reproductive Behaviour Very little known. Smithers & Wilson (1979) observed congregations of hundreds foraging where termites were swarming in Zimbabwe. Sightings of two individuals flying close together (tailing one another) have been reported, and it is common to capture a ♂ and ♀ side-by-side in a mist-net (E. C. J. Seamark pers. comm.). Of 93 bats mist-netted in Malawi (excluding those captured while emerging from day-roosts), 66 were netted singly, six were netted in pairs, 14 were netted with another of same sex, and six were netted in groups comprised of two ♂♂ and one ♀ (M. Happold pers. obs.). Occasionally roosts singly but usually roosts in groups of up to ca. 20; several groups sometimes roost under one roof but in different parts (Smithers 1983, M. Happold pers. obs.). In KwaZulu–Natal, South Africa, roosts singly or in groups of 2–10, and some roosts are occupied for at least eight years (Taylor, P. 1998). Group composition not known. Kingdon (1974) described the behaviour of a ♀ which gave birth, in captivity, to twins. During the first week, the ♀ licked the young, sheltered them with one wing, and sometimes squeaked. The young remained attached to the nipples until the third night, after which time they occasionally roosted beside her or climbed over her. When the young were a few days old, there were some prolonged bursts of squeaking in which both mother and young participated.

Reproduction and Population Structure Litter-size: usually two, sometimes one, occasionally three. Reproductive chronology at 15–16°S in Malawi is restricted seasonal monoestry with births in Nov–Dec, lactation Nov–Jan, post-lactation Jan–Feb (no data Jul–Sep) (Happold & Happold 1990a and unpubl.). Adult ♂♂ with enlarged scrotal testes and others with abdominal testes were present Oct–Mar (no data Apr–Sep). This chronology is also manifested at 22–31°S in South Africa (E. C. J. Seamark pers. comm.). In Uganda, 2 of 3 ♀♀ in Feb–Mar were pregnant and two young were recorded in May (Okia 1987), but Okia's suggestion that there are two breeding seasons is based on combined data from Zimbabwe, DR Congo and Uganda, which is not valid evidence of polyoestry. At 02°18'S (Masalani, near Kibwezi, Kenya), births were recorded during Nov and Mar–Apr during a year-round study on a resident population (O'Shea & Vaughan 1980), but it was not stated that these bats were polyoestrous, and the percentage of ♀♀ that gave birth during each of these periods was not given. Possibly *S. dinganii* is polyoestrous near the Equator, but this needs confirmation.

Predators, Parasites and Diseases In Zimbabwe, *Scotophilus* (species uncertain) are taken by Bat Hawks *Macheiramphus alcinus* (Fenton *et al.* 1978). Ectoparasites include bed-bugs *Cacodmus sparsilis* and *Aphrania* cf. *barys* (Hemiptera: Cimicidae); a flea *Chiropteropsylla brockmani* (Siphonaptera: Ischnopsyllidae); a bat-fly *Basilia glabra* (Diptera: Nycteribidae); and a mite *Spinturnix walkeri* (Acari: Spinturnicidae) (Whitaker & Mumford 1978, Wolton *et al.* 1982, Beaucournu & Kock 1989, 1996, Kock *et al.* 1998b).

Conservation IUCN Category: Least Concern.

Widespread and common; one of the species that roosts in occupied houses and has adapted well to semi-urban and agricultural environments.

Measurements

Scotophilus dinganii

FA: 53.3 (47–60) mm, n = 398

WS (a): 382 (373–391) mm, n = 7*

TL: 134 (120–155) mm, n = ca. 400

T: 52 (46–65) mm, n = ca. 400

E: 17.2 (11–22) mm, n = 121

Tr: 9.1 (6.7–10.5) mm, n = 43†

Tib: 21.6 (17–27) mm, n = 198

HF: 12 (10–14) mm, n = 398

WT: 23.9 (15–36) g, n = 98

GLS: 20.5 (18.3–23.5) mm, n = 366

GWS: 14.3 (12.0–17.3) mm, n = 397

C–M³: 6.9 (5.3–7.9) mm, n = 391

Throughout geographic range (Robbins *et al.* 1985, V. Van Cakenberghe pers. comm.)

*Malawi only

†Botswana, DR Congo, Kenya, Malawi, South Africa, Zambia, Zimbabwe (BMNH, HC, NMW and literature)

Key References Kingdon 1974; Robbins *et al.* 1985; Smithers 1983.

Meredith Happold

Scotophilus leucogaster WHITE-BELLIED HOUSE BAT

Fr. Scotophile à ventre blanc; Ger. Weißbäuchige Hausfledermaus

Scotophilus leucogaster (Cretzschmar, 1830). In: Rüppell, Atlas Reise Nördl. Afr., Zool. Säugeth., p. 71. Brunnen Nedger [Nedger Well, = Bir Nedger], Kordofan, Sudan.

Taxonomy Originally *Nycticejus leucogaster*. Synonyms: *altilis*, *damarensis*, *flavigaster*, *murinoflavus*. There are taxonomic problems, much controversy and much confusion associated with the names *leucogaster*, *borbonicus* and *viridis* and also *nigrita* and *dinganii* (see Genus *Scotophilus*). Here we follow Robbins *et al.* (1985) who, based on multivariate analysis, consider *leucogaster* to be specifically distinct from *viridis*, and include *damarensis* in *S. leucogaster* rather than in *S. viridis*. Because of the problems associated with the names, and also because *S. leucogaster* is not always easily distinguished from *S. viridis*, data in literature and museums pertaining to *S. leucogaster* is sometimes reported under other names (e.g. *S. borbonicus*, *S. nigrita* and *S. viridis*), and data pertaining to other species (e.g. *S. viridis*) is sometimes reported under *S. leucogaster*. Consequently it is difficult to assess the identity of the specimens reported in the literature. In this profile, information is restricted to material considered to represent *S. leucogaster* by Robbins *et al.* (1985), or by V. Van Cakenberghe or C. B. Robbins based on examination of new material and/or its distribution, or by re-examination of material mentioned in Robbins *et al.* (1985). Subspecies: two. Chromosome number (Namibia and Burkina): 2n = 36; aFN = 50 (Ruedas *et al.* 1990 and M. Volleth pers. comm., respectively).

Description Small, heavily-built microbat without noseleaf and with tail more or less fully enclosed in interfemoral membrane; four upper and five lower cheekteeth and one upper incisor on each side; ears separated, short for a vespertilionid (11–17 mm); FA: 43–58 mm; dorsal pelage sepia brown to pale brown; ventral pelage white to dirty medium brown (not tinged with yellow except perhaps sometimes in southern Africa). Best distinguished from *S. viridis* and *S. dinganii* by discriminant functions (see Genus *Scotophilus*). Sexes similar. Pelage smooth, soft and sleek; mid-dorsal hairs 6–8 mm.

Dorsal pelage medium sepia brown to pale brown (not tinged with green, orange or yellow); hairs unicoloured or becoming slightly paler towards base. Ventral pelage, north of Equator, white, off-white, very pale brown (beige) or dirty medium brown (not tinged with yellow); throat and chest sometimes paler than abdomen; chin sometimes almost naked and dark brown. Ventral pelage, south of Equator, might be tinged with yellow in some individuals, especially in the eastern part of the geographic range, but this needs confirmation. Pelage colouration can be faded by alcohol, rendering identification of preserved material, based on colour of ventral pelage, unreliable – originally yellowish *S. viridis* can look like whitish *S. leucogaster*. Ears comparatively and relatively short for a vespertilionid (24–37% of FA), widely separated; inner margin strongly convex; outer margin almost straight. Tragus tapering to bluntly rounded tip; anterior margin concave. Eyes small. Wings and interfemoral membrane uniformly dark brown, semi-translucent. Testes posterior to anus. Adult ♀♀ with one pair of functional nipples.

Skull and dentition as described for the genus. C–M³ slightly longer and more robust than in *S. viridis*. Posterior median projections of palate slightly more developed than in *S. viridis*, and projecting ventrally below the pterygoids. According to Robbins *et al.* (1985), the pterygoids are comparatively longer, and narrower between their posterior tips, than in *S. viridis*. However, these differences are very vague and might be the result of damage to the pterygoid bones during preparation of the skulls. Interorbital breadth: 4.9 (4.3–5.9) mm, n = 250; mastoid width: 11.6 (10.4–12.8) mm, n = 212; lower C–M₃: 7.0 (6.5–7.7), n = 254 (cf. *S. viridis*).

Geographic Variation Based on its discontinuous distribution, two subspecies are recognized by Robbins *et al.* (1985):

- S. l. leucogaster*. FA: 49.9 (44–58) mm; GLS: 18.3 (16.5–20.3) mm. North of Equator (Mauritania to Ethiopia and NW Kenya).
S. l. damarensis. FA: 47.5 (43–51) mm; GLS: 18.3 (17.3–19.9) mm. South of Equator (SW Kenya, Angola, W Zambia, S Malawi and southwards to Namibia, Botswana, S Mozambique and possibly NE South Africa).

Similar Species Four other African *Scotophilus* have FA: <61 mm (Table 28, p. 673):

- Scotophilus viridis*. Best distinguished by discriminant functions, see Genus *Scotophilus*.
S. dinganii. Best distinguished by discriminant function, see Genus *Scotophilus*. North of Equator, ventral pelage yellow to orange, not tinged with brown (south of Equator, pelage of both species is sometimes similar).
S. nucella. Dorsal pelage dark rusty-brown to blackish-brown; ventral pelage dark brown to reddish-orange. Rainforest.
S. nux. Dorsal pelage dark rusty-brown to blackish-brown; ventral pelage dark brown to reddish-orange. Skull longer (GLS: 19.6–23.0 mm). Rainforest.

Distribution Endemic to Africa. Recorded mainly from the Sudan Savanna, Guinea Savanna and Zambezian Woodland BZs, but with scattered records in the Sahel Savanna BZ, Northern and Eastern Rainforest–Savanna Mosaics, Somalia–Masai Bushland BZ, Coastal Forest Mosaic BZ and South-West Arid BZ (Namib Desert). Recorded from Mauritania, Senegal, Gambia, NW Guinea-Bissau and Sierra Leone (but not Liberia) to Sudan and NW Ethiopia, and southwards to Uganda and Kenya. Also recorded from Angola, Namibia, N Botswana, W Zambia, NW Zimbabwe, S Malawi, S Mozambique and possibly Kruger N. P., South Africa. Re-examination of specimens from Chiromo and Nsanje in S Malawi, identified as *S. viridis* by Robbins *et al.* (1985), indicates that they represent *S. leucogaster*. Specimens

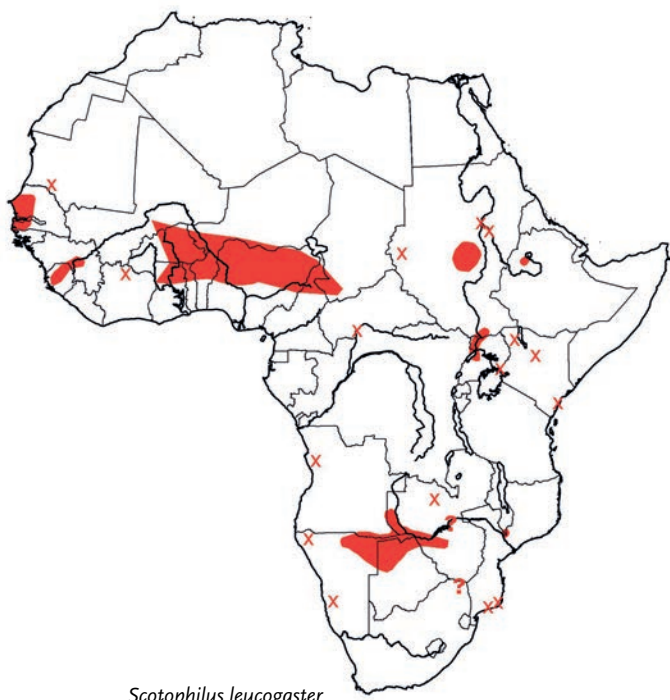
from Punda Milia in Kruger N. P. include large and small animals, and specimens without yellow in their ventral pelage as well as yellow-bellied specimens: this material needs re-examination to confirm if both *S. leucogaster* and *S. viridis* occur in Kruger N. P. Small *Scotophilus* with white bellies and yellow bellies occur in the Mana Pools N. P. of NW Zimbabwe, and are presumed to represent two species by Fenton *et al.* (1998b): skulls from this locality have not been analysed, but circumstantial evidence (including echolocation) suggests both forms represent *S. viridis*.

Habitat In West Africa, recorded from riverine woodland along rivers in shrub savanna in Park du W, Niger (Poché 1975), over grassland between riverine forest and Guinea savanna, and under mango trees in Nigeria (Bergmans 1977a). South of the Equator, recorded from mopane and miombo woodland, riverine forests and woodlands, open grasslands, flood-plains and pans, with many of the localities near rivers or marshes such as the Okavango Swamp in Botswana (Smithers 1971), the Cuanza R. in Angola, the Zambezi R. and its tributaries in Zambia (Ansell 1978) and the Sengwa, Lutope and Shana rivers in Zimbabwe (Barclay 1985). Seasonal fluctuations in abundance have been recorded in the Sahel Savanna BZ in Burkina (Koch-Weser 1984) and in S Mali (Meinig 2000), suggesting exploitation of drier areas in wet season and contraction or migration into wetter habitats in the dry season. In contrast, there is no evidence of migration in Sudan (Kock 1969a, as *S. nigrita*).

Abundance Uncertain. The most commonly mist-netted species at Sengwa (i.e. Sengwa Wildlife Research Area, Zimbabwe) (Barclay 1985).

Adaptations In Mali, roosts by day under dried leaves of *Borassus* palms (L. Granjon pers. comm.). In Sudan, roosts by day in holes in baobab trees *Adansonia* (Cretzschmar 1828–30), and under iron roofs of houses where mid-day temperatures can reach over 40 °C (Kock 1969a). At Sengwa, roosts by day in hollow mopane trees *Colophospermum mopane* (Fenton 1983, Barclay 1985). Roost-fidelity was observed in Sudan. In contrast, radio-tracked individuals regularly switched roosts at Sengwa (Fenton 1983). In Sudan, individuals were lethargic and flew clumsily unless the temperature was 34 °C or higher (Kock 1969a).

Foraging and Food Radio-tracked and light-tagged individuals foraged by moderately fast-hawking, 2–20 m above ground, in uncluttered open spaces above trees and over grasslands, and in moderately uncluttered spaces between tree trunks and tree-canopies (Fenton 1983, Barclay 1985). Foraging has been observed in mopane, miombo and riverine woodlands, and over flood-plains and the grassy edges of rivers. Foraging begins when the bats leave their roosts soon after dusk, and their stomachs are soon filled. Radio-tracked bats flew up to 3 km away from their roosts to find food and/or water. On bright moonlit nights, activity is reduced and the bats stay near or under trees. In Sudan, foraging begins soon after sunset and the bats often have full stomachs within an hour: subsequently, bouts of foraging are interspersed between pauses for digestion and rest. In contrast, at Sengwa, foraging only occurs during the first hour of the night, and the avoiding of open spaces on moonlit nights, are ways of reducing predation from aerial predators (Fenton *et al.* 1977,



Scotophilus leucogaster

Barclay 1985). At Sengwa, *S. leucogaster* feeds mainly on Coleoptera, Lepidoptera and Hemiptera, but also on Hymenoptera, Orthoptera, Homoptera, Neuroptera and Diptera (Barclay 1985, Fenton *et al.* 1977, as *S. viridis*). There is some evidence that Coleoptera and Hemiptera are particularly important in the wet season, and that Lepidoptera only comprise a major part of the diet in the dry season. Possibly, the bats are more selective in what they eat during the wet season when insects are more abundant. Captive bats ate geckoes and the carcasses of mice (Kock 1969a).

Echolocation Search-phase call-shape (Sengwa): steep/shallow FM. End-frequency 34 kHz; maximum call-duration: 10 ms (5 bats; Fenton & Bell 1981, as *S. viridis*).

Social and Reproductive Behaviour At Sengwa, day-roosts in hollow mopane trees contained 1–9 individuals of unrecorded age and sex (mean 4.6, $n = 15$ counts as the bats emerged; Fenton 1983).

Reproduction and Population Structure Litter-size: two (Barclay 1985). At ca. 18°S (Sengwa Wildlife Research Area, Zimbabwe), births were observed in Nov and Dec (Barclay 1985).

Predators, Parasites and Diseases In Mali, Barn Owls *Tyto alba* feed on *S. leucogaster* when mice *Mastomys huberti* are scarce: both *T. alba* and *S. leucogaster* roost among the leaves of palms *Borassus aethiopicus* (L. Granjon pers. comm.). At Sengwa, *Scotophilus* (species uncertain) are preyed on by Bat Hawks *Macheiramphus alcinus* (Fenton

et al. 1978). Ectoparasites (in Nigeria) include a mite *Spinturnix scotophili* (Acari: Spinturnicidae) (Dusbábek & Bergmans 1980).

Conservation IUCN Category: Least Concern.

Measurements

Scotophilus leucogaster

FA: 49.7 (43–58) mm, $n = 291$

WS: n. d.

TL: 120 (107–129) mm, $n = 78$

T: 45.9 (37–54) mm, $n = 63$

E: 15.2 (11–17) mm, $n = 81$

Tr: 10, 11 mm, $n = 2$

Tib: 19.1 (15–23) mm, $n = 237$

HF: n. d.

WT: 19.7 (12.0–27.0) g, $n = 75$

GLS: 18.3 (16.5–20.3) mm, $n = 228$

GWS: 13.2 (11.9–13.9) mm, $n = 199$

C–M³: 6.1 (5.5–6.6) mm, $n = 254$

Throughout geographic range (BMNH, FMNH, IRSN, MNHN, RMCA, RMNH, ROM, SMF, USNM, TM, ZMA)

Key References Barclay 1985; Fenton 1983; Fenton *et al.* 1977; Robbins *et al.* 1985.

Victor Van Cakenberghe & Meredith Happold

Scotophilus nigrita GIANT HOUSE BAT

Fr. Grand scotophile africain; Ger. Riesen-Hausfledermaus

Scotophilus nigrita (Schreber, 1774). Die Säugethiere 1: 171. Senegal.

Taxonomy Originally *Vespertilio nigrita*. Widely referred to as *S. gigas* until Robbins (1978) showed that *nigrita* was the senior synonym of *gigas*, and that bats previously referred to as *nigrita* should be called *dinganii*. Synonyms: *alvenslebeni*, *gigas*. Subspecies: two. Chromosome number: not known.

Description A large, heavily built microbat without noseleaf and with tail more or less fully enclosed in interfemoral membrane; four upper and five lower cheekteeth and one upper incisor on each side; ears separated, medium-sized for a vespertilionid (20–24 mm); FA: 78–83 mm; dorsal pelage brown; ventral pelage yellow, yellowish or white. Largest African vespertilionid. Sexes similar in colour; forearms of ♀♀ usually longer than those of ♂♂. Pelage mid-dorsal hairs 6–7 mm. Dorsal pelage blackish-brown, sepia brown, greenish-brown, rusty-brown or greyish-brown suffused with yellow; hairs unicoloured. Ventral pelage pale yellow to pale yellowish-grey (one individual white). Ears medium-sized but relatively short for a vespertilionid (28–31% of FA, $n = 4$), blackish-brown, widely separated; inner margin strongly convex with lobe at base; outer margin fairly straight with semi-circular fleshy antitragus. Tragus tapering to bluntly rounded tip; anterior margin concave. Wings and interfemoral membrane blackish-brown.

Skull with very well developed sagittal crest and occipital helmet. Canines particularly strong.

Geographic Variation Two subspecies are recognized (De Vree 1973b):

S. n. nigrita: Savannas of West Africa and Sudan. Almost always larger (FA: 85.9 [83–88] mm, $n = 5$; GLS: 30.7 [30.0–32.1] mm, $n = 6$).

S. n. alvenslebeni: Savannas of eastern and southern Africa. Almost always smaller (FA: 80.5 [77–84] mm, $n = 8$; GLS: 29.3 [28.5–30.4] mm, $n = 8$).

Similar Species None: all other African *Scotophilus* are much smaller (FA: <61 mm) (Table 28, p. 673):

Distribution Endemic to Africa. Known only from a few scattered localities, in the Sahel Savanna, Sudan Savanna, Guinea Savanna and Rainforest BZs (in Senegal, Côte d'Ivoire, Ghana, Togo, Nigeria), in the Sudan Savanna BZ (in Sudan), and in the Zambezian Woodland BZ and Coastal Forest Mosaic BZ (in SE DR Congo, Kenya, Tanzania, Malawi, Zimbabwe and Mozambique. A record from Botswana (Cotterill 1996a, Taylor 2000) is erroneous (F. P. D. Cotterill pers. comm.). Distribution appears disjunct, but this species is probably difficult to record and the gaps are likely to be artefacts. Mapped from Robbins *et al.* (1985), Cockle *et al.* (1998) and Grubb *et al.*



Scotophilus nigrita

(1998). According to Monadjem *et al.* (2010), also recorded from Komatipoort and Malelane in South Africa (not mapped here).

Habitat Recorded from relatively dry woodland savannas including Guinea, Sudan, Sahel and miombo woodland savannas, but often in the vicinity of rivers and riverine forests (R. C. Wood in Kershaw 1922, Dorst 1959, Smithers 1983). Also recorded from one locality in drier, semi-deciduous forest in Ghana (Grubb *et al.* 1998), from a woodland and riverine forest mosaic in Tanzania (Cockle *et al.* 1998), and from Lagos in the rainforest zone (Rosevear 1965), but precise details of this locality are not known.

Abundance Uncertain. Very rarely encountered and usually considered very rare.

Adaptations In Sudan, found under the corrugated iron roof of a house where mid-day temperatures sometimes reached over 40 °C (Kock 1969a); *Scotophilus leucogaster* was captured while emerging from the same roost several evenings earlier. In Malawi, near confluence of Ruw and Shire Rivers, one was found in a hollow, dead *Hyphaene* palm, one was shot over the bank of a river and another over a village (R. C. Wood's data with specimens in BMNH). In Zimbabwe, one was found in a house. One was mist-netted over an almost dry river in Togo (De Vree 1973b) and the Tanzanian specimen was mist-netted over a pool (Cockle *et al.* 1998).

Foraging and Food Foraging behaviour: no information but predicted to forage high above the ground (D. Kock pers. comm.). Kock (1969a) suggested these bats are carnivorous, but this was based on the observation that captive individuals of the smaller species, *S. leucogaster*, ate geckos and bodies of bats, and his observation that insects are scarce in Sudan during the dry season. Freeman (1984) notes that the occlusal cusp pattern of the molar teeth of *S. nigrita* is that of a strictly carnivorous bat but, on the other hand, other characters of the teeth suggest that their function is to crush rather than to slice, and therefore she suggests that *S. nigrita* is insectivorous.

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|--|-----------------|
| Social and Reproductive Behaviour | No information. |
|--|-----------------|

| | |
|--|-----------------|
| Reproduction and Population Structure | No information. |
|--|-----------------|

Predators, Parasites and Diseases Ectoparasites include a bedbug *Cacodmus villosus* (Hemiptera: Cimicidae) (Kock *et al.* 1998b) and a mite *Spinturnix scotophili* (Acari: Spinturnicidae) (Dusbábek & Bergmans 1980).

Conservation IUCN Category: Least Concern.

Measurements

Scotophilus nigrata

FA (♂♂): 80.4 (78–83) mm, n = 10*

FA (♀ ♀): 83.7 (80–88) mm, n = 12*

WS (d): 584 (575–600) mm, n = 3

TL: 191 (187–195) mm, n = 15†

T: 78 (64–92.3) mm, n = 15

E: 22 (20–24) mm, n = 15

Tr: n. d.

Tib: 34.4, 35.4 mm, n = 2

HF: 17 (17–19) mm, $n = 15^\dagger$

WT: 89 (88–91) g, n = 3*

GLS: 29.9 (27.8–32.1) mm, n = 22*

GWS: 20.6 (19.8–21.3) mm, n = 20*

C-M³: 10.2 (9.6–11.3) mm, n = 25*

Throughout geographic range (AMNH, BMNH, HZM, MNHN, RMCA, RMNH, SMF, USNM, ZMA and literature)

*V. Van Cakenberghe (pers. comm.)

†Robbins *et al.* (1985)

Key References De Vree 1973b; Kock 1969a; Robbins *et al.* 1985; Rosevear 1965; Smithers 1983.

Meredith Happold

Scotophilus nucella ROBBINS'S HOUSE BAT

Fr. Scotophile de Robbins; Ger. Robbins Hausfledermaus

Scotophilus nucella Robbins, 1983. Ann. Kon. Mus. Mid. Afr., Zool. Wetensch. and Mus. Roy. Afr. Centr. Sc. Zool., 237: 19.

[Publication has Dutch and French titles.] 1 mile N Nkawkaw, Eastern Region, Ghana.

Taxonomy Considered a subspecies of *S. leucogaster* by Koopman (1993, 1994), but considered distinct by Simmons (2005). Its status was not reviewed by Robbins *et al.* (1985). Synonyms: none. Chromosome number: not known.

Description Small, heavily built microbat without noseleaf and with tail more or less fully enclosed in interfemoral membrane; four upper and five lower cheekteeth and one upper incisor on each side; ears separated, short for a vespertilionid (15–16 mm); FA: 49–53 mm; dorsal pelage dark rusty-brown to blackish-brown; ventral pelage slightly paler to reddish-orange. Sexual dimorphism not apparent from limited data. Pelage soft, sleek. Dorsal pelage dark rusty-brown to blackish-brown; hairs unicoloured or with paler base. Ventral pelage slightly paler, dark brown to reddish-orange. Ears comparatively and relatively short for a vespertilionid (ca. 29% of FA), widely separated, dark brown; inner margin strongly convex with lobe at base; outer margin fairly straight with semi-circular, fleshy antitragus. Tragus tapering to pointed tip; anterior margin concave. Wings and interfemoral membrane sepia brown.

Skull typical of genus; braincase relatively inflated (cf. *S. leucogaster*); sagittal crest forming a conspicuous helmet.

Geographic Variation None recorded.

Similar Species Four other African *Scotophilus* have FA: <61 mm (Table 28, p. 673):

*Scotophilus nucella*

Scotophilus nux. Larger (FA: 56.4 [53–61] mm; GLS: 21.1 [19.6–23.0] mm, CbL: 19.0 [18.4–19.6] mm).

S. dinganii. Dorsal pelage (except in South-West Arid BZ) greenish-brown, greyish-brown or reddish-brown; ventral pelage pale yellow, yellow, orange, not tinged with brown. Savannas and rainforest-savanna mosaics; marginally in rainforest.

S. leucogaster. Dorsal pelage pale to medium brown; ventral pelage white, whitish, medium brown, sometimes yellowish. North of Equator in savannas and rainforest-savanna mosaics; south of Equator, various zones but not rainforest.

S. viridis. North of Equator, dorsal pelage yellowish-brown, greenish-brown or orange-brown; ventral pelage pale to medium yellow, sometimes tinged with brown. Savannas, riverine forests and coastal forests.

Distribution Endemic to Africa. Recorded from the Rainforest BZ in Côte d'Ivoire (J. Fahr pers. comm.) and Ghana, and from the Eastern Rainforest-Savanna Mosaic in Uganda (Robbins 1983). Predicted to occur in other rainforest areas of West, Central and East Africa (Robbins 1983). Occurs sympatrically with *S. nux* in Ghana and, based on their representation in collections made over a period of years, the two species occur in ca. equal numbers in the area of the type locality (Robbins 1983). *Scotophilus nucella* is sympatric with *S. nux* and *S. dinganii* in Uganda.

Habitat Rainforest.

Abundance Uncertain. When described, only ten specimens were known: two from each of three localities near Nkawkaw, Ghana, three from Oda, Ghana (collected on two occasions) and one from Budongo Forest, Uganda (Robbins 1983). Subsequently, apparently only collected from Côte d'Ivoire (J. Fahr pers. comm.; details not given).

Remarks After the description by Robbins (1983), hardly any references have been made to this species.

Conservation IUCN Category: Data Deficient.

Known from nine specimens from Ghana and one from Uganda, housed in three collections (CM, ROM, USNM) when described in 1984, and apparently rarely collected since. Consequently its range is poorly known and its population trend is not known.

Measurements

Scotophilus nucella

FA: 51.3 (49–53) mm, n = 7

WS: n. d.

TL: 121 (115–125) mm, n = 7

T: 44 (41–47) mm, n = 7

E: 15 (15–16) mm, n = 7

Tr: n. d.

Tib: n. d.
 HF: 11 (10–12) mm, n = 7
 WT: n. d.
 GLS: n. d.
 CbL: 17.3 (17.1–17.5) mm, n = 7
 GWS: 13.6 (13.1–14.0) mm, n = 7

C–M³: 6.5 (6.5–6.6) mm, n = 7
 Ghana (Robbins 1983)

Key Reference Robbins 1983.

Victor Van Cakenberghe & Meredith Happold

Scotophilus nux NUT-COLOURED HOUSE BAT

Fr. Scotophile noisettes; Ger. Nussfarbene Hausfledermaus

Scotophilus nux Thomas, 1904. Ann. Mag. Nat. Hist., ser. 7, 13: 208. Efulen, Cameroon.

Taxonomy Synonyms: none. Often considered to be a subspecies of *S. dinganii* (as *S. nigrita*) (e.g. Hayman & Hill 1971) and sometimes a subspecies of *S. leucogaster* (e.g. Koopman *et al.* 1978, Koopman 1994). Recognized as a distinct species by Robbins *et al.* (1985) on basis of multivariate analysis of FA and seven cranial parameters and, following these authors, recognized as distinct by Simmons (2005). Chromosome number (Cameroon): 2n = 36; aFN = 50. The non-differentially stained karyotype is identical with that of *S. dinganii* from Somalia except that in *S. nux* the autosomal pair bearing the secondary constriction is distinctly larger, the X is larger and the Y is smaller (Ruedas *et al.* 1990).

Description Small, heavily built microbat without noseleaf and with tail more or less fully enclosed in interfemoral membrane; four upper and five lower cheekteeth and one upper incisor on each side; ears separated, short for a vespertilionid (15–21 mm); FA: 53–60 mm; dorsal pelage rusty-brown to blackish-brown; ventral pelage slightly paler. Sexes similar. Pelage smooth, sleek and glossy; mid-dorsal hairs 6–7 mm. Dorsal pelage rusty-brown, dark rusty-brown or blackish-brown; hairs unicoloured. Ventral pelage slightly paler, dark brown to reddish-orange. Ears comparatively and relatively short for a vespertilionid (23–29% of FA), widely separated, dark brown; inner margin strongly convex with lobe at base; outer margin fairly straight with semi-circular fleshy antitragus. Tragus tapering to bluntly rounded tip; anterior margin concave. Wings and interfemoral membrane blackish-brown. Skull and dentition as in Figure 146.

Geographic Variation None recorded.

Similar Species Four other African *Scotophilus* have FA <61 mm (Table 28, p. 673):

Scotophilus nucella. Smaller (FA: 51.3 [49–53] mm; CbL: 17.3 [17.1–17.5] mm).

S. dinganii. Dorsal pelage (except in South-West Arid BZ) greenish-brown, greyish-brown or reddish-brown; ventral pelage pale yellow, yellow, orange, not tinged with brown. Savannas and rainforest–savanna mosaics; marginally in rainforest.

S. leucogaster. Dorsal pelage pale to medium brown; ventral pelage white, whitish, medium brown, sometimes yellowish. Skull shorter (GLS: 16.5–20.3 mm). North of Equator in savannas and rainforest–savanna mosaics; south of Equator, in various habitats but not rainforest.



Scotophilus nux

S. viridis. Smaller (FA: 45.9 [41–50] mm; GLS: 17.1 [15.6–18.3] mm). Dorsal and ventral pelage paler. Savannas and riverine and coastal forests.

Distribution Endemic to Africa. Recorded from the Rainforest BZ and the Northern and Eastern Rainforest–Savanna Mosaics from Sierra Leone, Côte d'Ivoire, Ghana, SE Nigeria and Cameroon, and from NW DR Congo to W Kenya. The gap between Cameroon and NW DR Congo probably reflects insufficient sampling in this area. The gap between SW Ghana and Calabar in Nigeria needs investigation. Map based on Robbins *et al.* (1985).

Habitat Lowland rainforest and clearings in the rainforest. Recorded in swamp forest in Tâi N. P., Côte d'Ivoire (Fahr & Kalko 2011).

Abundance Uncertain.

Remarks In Sierra Leone, roosts in small groups in roofs of houses; quite common in built-up areas; commonly has twins (Grubb *et al.* 1998). Also roosts in hollow trees. Two ♀♀, each with one large foetus, were recorded in Mar in DR Congo (Lang & Chapin 1917b).

Conservation IUCN Category: Least Concern.

Comparatively widespread; not known to be declining.

Measurements

Scotophilus nux

FA: 56.5 (53–61) mm, n = 57

WS: n. d.

TL: 121 (111–143) mm, n = 32

T: 50.5 (44–54) mm, n = 32

E: 17.2 (15–19) mm, n = 17

Tr: n. d.

Tib: 22.4 (19–25) mm, n = 20

HF: 14 (13–15) mm, n = 11

WT: 31.5 (24.7–37.0) g, n = 28

GLS: 21.0 (19.6–23.0) mm, n = 53

GWS: 14.9 (13.8–15.7) mm, n = 45

C–M³: 7.1 (6.6–7.7) mm, n = 57

Cameroon, Kenya, Nigeria (BMNH, IRSN, MNHN, NMW, RMCA, ROM, Robbins *et al.* 1985)

Key Reference Robbins *et al.* 1985.

Victor Van Cakenberghe & Meredith Happold

Scotophilus viridis GREEN HOUSE BAT

Fr. Petit scotophile africain; Ger. Grünliche Hausfledermaus

Scotophilus viridis (Peters, 1852). Reise nach Mossambique, Säugethiere, p. 67. Mozambique I., 15° S, Mozambique.

Taxonomy Originally *Nycticejus viridis*. Synonyms: *nigritellus*. There are taxonomic problems, much controversy and much confusion associated with the names *leucogaster*, *borbonicus* and *viridis*, and also *nigrita* and *dinganii* (see genus *Scotophilus*). Here we follow Robbins *et al.* (1985) who, based on multivariate analysis, consider *viridis* to be specifically distinct from *leucogaster*, and do not include *damarensis*, nor consider *viridis* to be a synonym of *borbonicus*. Because of the problems associated with the names, and also because *S. viridis* is not always easily distinguished from *S. leucogaster*, data in literature and museums pertaining to *S. viridis* is sometimes reported under other names (e.g. *S. borbonicus*, *S. leucogaster*), and data pertaining to other species (e.g. *S. leucogaster*, *S. dinganii*) is sometimes reported under *S. viridis*. Consequently it is very difficult to assess the identity of the specimens reported in the literature. In this profile, information is restricted to material considered to represent *S. viridis* by Robbins *et al.* (1985), or by V. Van Cakenberghe or C. B. Robbins based on examination of new material and/or its distribution, or by re-examination of material mentioned in Robbins *et al.* (1985), with the exception of some data for Malawian bats that have not been checked by these authors (see Distribution). Subspecies: possibly two. Chromosome number (South Africa): 2n = 36; aFN = 54 (Schlitter *et al.* 1980). Ruedas *et al.* (1990) report 2n = 36; aFN = 50 for *S. viridis* from Namibia but, based on distribution, these specimens represent *S. leucogaster*.

Description Small, heavily built microbat without noseleaf and with tail more or less fully enclosed in interfemoral membrane; four upper and five lower cheekteeth and one upper incisor on each side; ears separated, short for a vespertilionid (13–18 mm); FA: 41–50 mm; dorsal pelage variable shades of brown; ventral pelage always yellowish north of Equator (cf. *S. leucogaster*) and usually yellowish (but sometimes whitish or pale brown, without any yellow) south of the Equator. Best distinguished from *S. leucogaster* by discriminant functions (see Genus *Scotophilus*). Sexes similar. Pelage smooth, soft and sleek; mid-dorsal hairs ca. 6 mm. Dorsal pelage (north of Equator) yellowish-brown, greenish-brown to darker orange-brown; hairs with paler base. Ventral pelage (north of Equator) pale to medium-yellow, sometimes with brownish tinge, never whitish; hairs unicoloured. Dorsal pelage (south of Equator) greenish-brown to medium-brown; hairs with paler base. Ventral pelage (south of Equator) pale to medium yellow (unlike *S.*

leucogaster) or whitish, pale grey or pale brown (as in *S. leucogaster*). In alcohol, the yellow colour can be faded leading to confusion with *S. leucogaster*. Ears comparatively and relatively short for a vespertilionid (28–37% of FA), widely separated, dark brown; inner margin strongly convex; outer margin almost straight. Tragus moderately long, tapering to bluntly rounded tip; anterior margin concave. Eyes small. Wings and interfemoral membrane uniformly dark brown, semi-translucent. Testes posterior to anus. Adult ♀ ♀ with one pair of functional nipples.

Skull and dentition as described for the genus. According to Robbins *et al.* (1985), compared to *S. leucogaster*, the posterior median projections of the palate are not as well developed and do not project ventrally much below the pterygoids and, usually, the pterygoids are relatively shorter but wider between their posterior tips. These differences, however, are fairly vague or might be the result of damage to the pterygoid bones during preparation of the skulls. Interorbital breadth: 4.5 (3.9–5.0) mm, n = 150; mastoid width: 10.6 (9.6–11.4) mm, n = 141; C–M₃: 6.5 (5.9–7.2) mm, n = 149 (cf. *S. leucogaster*).

Geographic Variation No subspecies are recognized by Robbins *et al.* (1985) and Simmons (2005) but small differences in size suggest there might be two subspecies:

S. v. viridis: East Africa, south-central and southern Africa. FA: 46.8 (42–50) mm, n = 82; GLS: 17.2 (16.2–18.0) mm, n = 60; C–M³: 5.8 (5.4–6.6) mm, n = 60.

S. v. nigritellus: West Africa to Central African Republic, and probably Sudan and Ethiopia. FA: 45.0 (41–48) mm, n = 81; GLS 16.8 (15.6–17.8) mm, n = 69; C–M³: 5.7 (5.3–6.1) mm, n = 78.

However, the validity of these subspecies is not completely supported by biometrical data, and the affinities of specimens from Sudan and Ethiopia need further investigation.

Similar Species Four other African *Scotophilus* have FA: <61 mm (Table 28, p. 673):

Scotophilus leucogaster. Best distinguished by discriminant functions, see Genus *Scotophilus*.

S. dinganii. FA almost always longer (53.3 [47–60] mm). Skull longer (GLS: 20.5 [18.3–23.5] mm).

S. nucella. Dorsal pelage dark rusty-brown to blackish-brown; ventral pelage dark brown to reddish-orange. Rainforest.

S. nux. Larger (FA: 56.5 [53–61] mm; GLS: 21.1 [19.6–23.0] mm). Dorsal and ventral pelage darker. Rainforest.

Distribution Endemic to Africa. Although records are scattered, probably occurs throughout the Guinea Savanna BZ and wetter parts of the Sudan Savanna BZ from Gambia and Senegal to S Sudan and W Ethiopia (with some records in the Northern Rainforest–Savanna Mosaic). Also occurs in the Afromontane–Afroalpine BZ, Coastal Forest Mosaic BZ and Zambezian Woodland BZ in Kenya, Tanzania (including Mafia I.; Kock & Stanley 2009), Zambia, Malawi, Zimbabwe, Mozambique and South Africa. The identity of white-bellied and yellow-bellied bats from Mana Pools N. P., NW Zimbabwe, reported respectively as *S. borbonicus* and *S. 'viridis'* by Fenton *et al.* (1998b), has not been confirmed by analysis of skulls but circumstantial evidence (including echolocation) suggests that both forms represent *S. viridis*. Re-examination of specimens from Chiromo and Nsanje in S. Malawi, identified as *S. viridis* by Robbins *et al.* (1985), indicates they represent *S. leucogaster*. Yellow-bellied specimens from Lengwe N. P. and Chiromo, Malawi, identified as *S. viridis* by Happold *et al.* (1987) and Happold & Happold (1997), have not yet been re-examined to confirm their identity. Material from Mana Pools N. P. in NW Zimbabwe also needs re-examination to confirm the identification of *S. 'viridis'* reported by Fenton *et al.* (1998b). Many, possibly all, of the disjunctions in the distribution might reflect insufficient sampling.

Habitat Not well known. In the Shai Hills (Ghana), recorded mostly in mosaic of grassland and *Zanthoxylum*–*Capparis* thickets, but also amongst savanna trees, and near a waterhole in grassland (Decher 1997). In Central African Republic, captured near bank of river with interrupted strips of gallery forest (Schlitter *et al.* 1982). In Tanzania, reported from

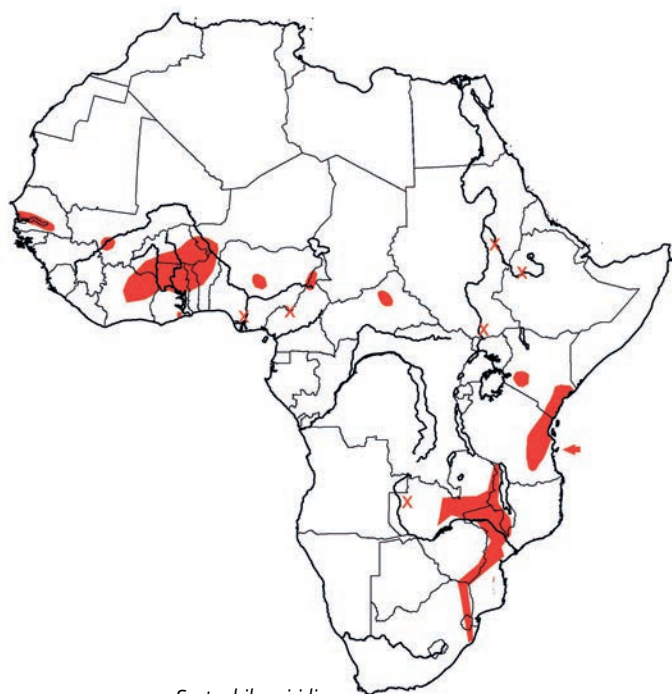
seven of 16 patches of coastal forest investigated by Cockle *et al.* (1998). In Malawi, recorded from miombo woodland dominated by *Brachystegia*, *Kirkia* and *Sterculia*, mostly near streams. Possibly also inhabits riverine woodland in the Lower Shire Valley but this needs confirmation (see Distribution). Appears to prefer wetter habitats than *S. leucogaster*.

Abundance Uncertain. Uncommonly recorded in Malawi (Happold & Happold 1997). Fairly common in some collections from elsewhere.

Adaptations Aspect ratio low; wing-loading medium (Aldridge & Rautenbach 1987, M. Happold unpubl.). Flight fast and agile; manoeuvrability moderate; able to take off from ground. Turns by banking (minimum radius ca. 50 cm) and by stalling-and-twisting. Able to fly across a 1×1×1 m enclosure, and occasionally to complete one full circuit (7 bats, 10 flights; M. Happold unpubl.). Cursorial locomotion efficient as in *S. dinganii*. In Kruger N. P. in South Africa, roosts by day in hollows in *Colophospermum mopane* trees (Fenton *et al.* 1985; bats identified as *S. viridis* by C. B. Robbins). Most (26 of 29) roosts were in living trees, and the selected trees were on the steep sides and tops of ridges – not in the riverine forests and adjacent mopane woodlands, although hollow mopane trees were present in both places (Fenton & Rautenbach 1986 as *S. borbonicus*). The bats often switched day-roosts, and moved from 100–1000 m between roosts. Radio-tracked individuals of both sexes used 2–6 (mean 4) roosts during 4–10 day observation periods, and did not use a single roost for more than 3–4 days. In Malawi, at 20–21 °C, does not become torpid during the day. Predicted mean maximum urine concentration comparatively low (3233 mOsmol/kg) (Happold & Happold 1988). Captive bats, fed winged termites, drank water every day.

Foraging and Food In Malawi, foraging by slow-hawking was observed in clearings and moderately uncluttered spaces between tree trunks: three light-tagged individuals foraged mainly 2–7 m above ground (M. Happold unpubl.). Foraging flights are characterized by swerving, diving and swooping upwards, and by the absence of acrobatic manoeuvring. In Kruger N. P., individuals moved, while foraging, towards the river and apparently drank before returning to their roosts within an hour (Fenton & Rautenbach 1986). Radio-tracked bats travelled up to 4 km from their roosts. In coastal Kenya in the dry season, the stomach contents of six individuals contained mainly Coleoptera (67% by volume) and Hemiptera (19%), with Orthoptera, Diptera, Homoptera and unidentified insects (14%) (Whitaker & Mumford 1978). In Kruger N. P., analysis of faeces of eight bats during the dry season showed that Coleoptera comprised ca. half of the consumed food, with Diptera, Lepidoptera, Hymenoptera and Hemiptera eaten less often (Fenton *et al.* 1985).

Echolocation In Malawi, calls recorded when seven bats were released, and while three others were tethered, were broad-bandwidth, high-intensity steep FM/QCF sweeps with start-frequencies up to 78 kHz and end-frequencies 37–45 kHz (usually 37–42 kHz) (Figure 118o, p; M. Happold unpubl.). At Mana Pools N. P. in NW Zimbabwe, the calls of two white-bellied bats had end-frequencies of 40.1 ± 0.9 kHz, and those of one yellow-bellied bat had end-frequencies of 37.9 ± 1.0 kHz (mean \pm S.D.; Fenton *et al.* 1998b). The echolocation data suggest that both forms represent *S. viridis*, although Fenton *et al.* (1998b) presumed that the white-bellied and yellow-bellied forms



Scotophilus viridis

represented different species. In Kruger N. P., calls with end-frequency 40 kHz were recorded by Aldridge & Rautenbach (1987, as *S. borbonicus*).

Social and Reproductive Behaviour No information for bats of confirmed identity.

Reproduction and Population Structure Litter-size: 2 ($n = 4$). At 22° 25' S (Pafuri, Kruger N. P., South Africa), where the presence of *S. viridis* has been confirmed from biometrical data, and the presence of *S. leucogaster* is uncertain, the reproductive chronology is restricted seasonal monoestry, with insemination, ovulation and fertilization in autumn (Apr). Early embryonic growth is retarded but not arrested: the embryo remains in the morula stage for 6–8 weeks, followed by a blastocyst stage of ca. two months. Implantation occurs after ca. three weeks. With the onset of warmer weather, embryogenesis accelerates and parturition occurs in Nov (van der Merwe *et al.* 1988, as *S. borbonicus*). At 15–17° S in Malawi, 8 of 8 adult ♀♀ were lactating in Dec, 1 of 1 was post-lactating in Feb and 7 of 7 in Apr–May were neither palpably pregnant nor lactating (M. Happold unpubl.). Volant young with unfused epiphyses were recorded in Oct–Jan. These data suggest seasonal monoestry with births at the end of the dry season and beginning of the wet season (Oct–Nov), but this needs confirmation from year-round observations.

Predators, Parasites and Diseases No information for bats of confirmed identity.

Conservation IUCN Category: Least Concern.

Widespread; probably fairly common; no known threats.

Measurements

Scotophilus viridis

FA: 45.9 (41–51) mm, $n = 167$

WS (a): 337 (328–350) mm, $n = 8^*$

TL: 122.6 (105–131) mm, $n = 30$

T: 41.3 (34–49) mm, $n = 18$

E: 14.8 (13–18) mm, $n = 20$

Tr: 8.3 (8–9) mm, $n = 6^*$

Tib: 17.3 (15–20) mm, $n = 60$

HF: 9.0 (8–10) mm, $n = 10^*$

WT: 16.5 (12.0–20.5) g, $n = 53$

GLS: 17.1 (15.6–18.3) mm, $n = 152$

GWS: 12.4 (11.2–13.7) mm, $n = 153$

C–M³: 5.8 (5.3–6.6) mm, $n = 161$

Throughout geographic range (BMNH, FMNH, IRSN, MNHN, RMCA, RMNH, SMF, TM, USNM, ZFMK, ZMA)

*Malawi (M. Happold unpubl.)

Key References Fenton *et al.* 1985; Fenton & Rautenbach 1986; Robbins *et al.* 1985; van der Merwe *et al.* 1988.

Victor Van Cakenberghe & Meredith Happold

Subfamily MYOTINAE – Wing-gland Bats and Myotis

Myotinae Tate, 1942. Bull. Amer. Mus. Nat. Hist., 80: 229.

Diagnostic combination of characters: second phalanx of third finger ca. as long the first; ears not funnel-shaped; tragus long and narrow but not as sharply pointed as in *Kerivoula* (Figure 116); six upper cheekteeth. Pelage dense, soft and fairly woolly (some species more so than others). Muzzle relatively long. There are three genera, of which two, *Cistugo* and *Myotis*, occur in Africa (but see updated information about *Cistugo* below).

Cistugo (2 species). Wing-glands present but not visible in dried skins (details in species profiles). Profile of forehead region (viewed laterally) moderately concave (see Figure 147 for definition). First two upper premolars greatly reduced and lying transversely to the toothrow (Figure 148).

Myotis (11 species in Africa). Wing-glands absent. Profile of forehead region (viewed laterally) weakly to strongly concave. First two upper premolars reduced but not greatly so, and not lying transversely to the toothrow.

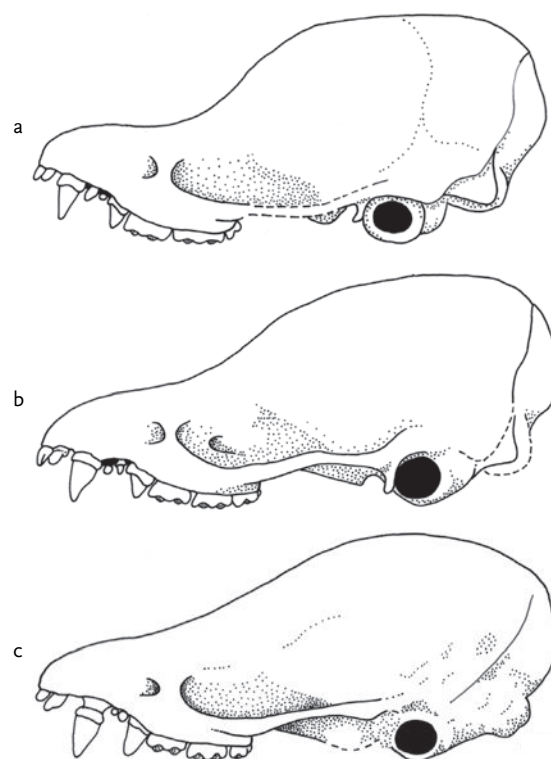


Figure 147. Range of variation in the degree of concavity of the dorsal profile of the forehead region (viewed laterally) in *Cistugo* and *Myotis* occurring in Africa. (a) Strongly concave (e.g. *M. scotti*; holotype, BMNH 27.3.4.1). (b) Moderately concave (e.g. *M. bocagii cupreolus*; BMNH 3.2.4.6). (c) Weakly concave (e.g. *M. dieteri*; holotype, NMHN CG 1985-1925). Cuspidation of inner incisors perhaps inaccurate.



Figure 148. *Cistugo*. Lateral view of skull of *Cistugo lesueuri* (holotype; based on photo by T. Kearney). Occlusal view of upper left teeth showing the anterior and middle premolars lying transversely to the toothrow; in some specimens, the angle of these premolars to the toothrow is sometimes greater and sometimes less than in the illustrated specimen (BMNH 27.4.1.3).

Since the *Myotis* profiles were submitted in 2006, Lack *et al.* (2010) concluded from analysis of mtDNA that *Cistugo* should constitute a distinct family (Cistugidae).

Meredith Happold

GENUS *Cistugo* Wing-gland Bats

Cistugo Thomas, 1912. Ann. Mag. Nat. Hist., ser. 8, 12: 205.

A polytypic genus with two species, both found only in the arid south-west corner of Africa. Diagnostic combination of characters: six upper cheekteeth (as in *Myotis*, *Kerivoula*, *Phoniscus*); ears not funnel-shaped, tragus long and narrow but not sharply pointed and pelage not frizzled (cf. *Kerivoula* and *Phoniscus*); first two upper premolars greatly reduced, and lying more-or-less transversely to the rest of the toothrow between the canine and the posterior (third) premolar; cranium less domed and muzzle less pinched in laterally than in some *Myotis* (including the sympatric species); glands present on the wings (cf. *Myotis*), but the glands are not visible when skins are dried; pelage not copper-red (cf. *Myotis* in southern Africa). Dental formula $2^{133}/_{3133} = 38$. Some craniodental characters of *Cistugo* are shown in Figure 148. For photographs of the wing-glands, see Seamark & Kearney (2006).

Cistugo was considered a subspecies of *Myotis* until Rautenbach *et al.* (1993) discovered that the karyotypes of *C. seabrae* and *C. lesueuri* ($2n = 50$; $aFN = 48$) differed from those of species of *Myotis* from the New and Old Worlds ($2n = 44$; $aFN = 52$). Molecular evidence supports the generic status of *Cistugo* (Bickham *et al.*

2004, Stadelmann *et al.* 2004). Then Lack *et al.* (2010) concluded that *Cistugo* should constitute a distinct family (Cistugidae). Given the similarity of *lesueuri* to *seabrae*, Corbet & Hill (1980) included *lesueuri* in *seabrae*. In contrast, Meester *et al.* (1986) retained *lesueuri* as a separate species but suggested that, in view of their allopatric distribution, *lesueuri* may best be treated as a subspecies of *seabrae*. Simmons (2005) also recognizes both taxa as distinct species. Here, the taxa are provisionally treated as distinct species, but their taxonomic relationship is in need of revision.

The species of *Cistugo* are:

Cistugo lesueuri. Dorsal pelage variable, yellowish-orange, yellowish-brown, pale brown, or reddish-brown; ventral pelage also variable, from medium brown to white. FA: 32–39 mm.

Cistugo seabrae. Dorsal pelage variable, yellowish-brown, orange-brown or greyish-brown; ventral pelage also variable, yellowish-orange, off-white or grey. FA: 33–35 mm.

Teresa Kearney

Cistugo lesueuri LESUEUR'S WING-GLAND BAT

Fr. Cistugine de Lesueur; Ger. Lesueurs Mausohr

Cistugo lesueuri Roberts, 1919. Ann. Transvaal Mus. 6: 112. L'Ormarins, Paarl District, Cape Province, South Africa.

Taxonomy Synonyms: none. The status of *lesueuri* is controversial (see Genus *Cistugo*). Pending further information, *C. lesueuri* is tentatively treated here as a distinct species (following Honacki *et al.* 1982, Simmons 2005). Chromosome number (South Africa): $2n = 50$; $aFN = 48$ (as in *C. seabrae*) (Rautenbach *et al.* 1993).

Description Very small microbat without noseleaf and with tail more or less fully enclosed in interfemoral membrane; six upper and six

lower cheekteeth on each side (but anterior upper premolar not always visible above gum); ears not funnel-shaped; pelage not frizzled; one or two glands on each wing but not close to forearm (not always present or visible). A very poorly known species, which is almost indistinguishable from *C. seabrae*. Sexes apparently similar. Pelage moderately dense, sleek (not woolly); mid-dorsal hairs ca. 5 mm. Dorsal pelage variable, yellowish-orange, yellowish-brown, pale brown or reddish-brown; hairs dark brown, dark greyish-brown or blackish-brown with tip



of dorsal colour. Ventral pelage colour also variable; individuals with darker dorsal pelage have darker ventral pelage; colour darkest under chin (pale brown or medium brown) becoming paler on neck (cream), and palest in pelvic region; hairs blackish-brown with pale tip or (in pelvic region) white. Muzzle with naked skin brownish-black. Ears blackish-brown, comparatively and relatively short for a vespertilionid (36.1 [28–40]% of FA); tip narrow and rounded. Tragus of medium relative length for a vespertilionid (ca. 54% of E), narrow, bluntly pointed with notch at base of posterior margin. Wings uniformly blackish-brown, possibly with less conspicuous paler reticulation than in *C. seabrae* (but this needs confirmation). The wing-glands are found in various positions on the wing-membrane, but never close to the forearm (cf. *C. seabrae*). Glands comparatively small (cf. *C. seabrae*) and not more than two on each wing. The number of glands per wing varies between wings and between individuals; sometimes absent; not visible on dry skins (Shortridge 1942, Herselman & Norton 1985). Tibiae dorsally and ventrally naked. Interfemoral membrane paler and more translucent than wings and with pale transverse lines in dried specimens (no data for living animals); distal third with fine, thinly scattered, cream hairs (1 mm) along veins on ventral surface only (cf. *C. seabrae*); posterior margin without projecting bristle-like hairs (cf. some *Kerivoula*). Tail 89.0 (78–100)% of HB (cf. *Pipistrellus capensis*). Length of calcar, the presence or absence of a postcalcareal lobe and the projection or otherwise of the terminal vertebrae of the tail, are not known.

Skull (Figure 148) small, delicate. Profile of forehead region (viewed laterally) moderately concave (see Figure 147 for definition). No sagittal crest. Anterior and middle premolars similar in size, both greatly reduced (not reaching cingulum of posterior premolar), crowded with anterior premolar displaced lingually and middle premolar displaced labially to such an extent that both lie more or less transversely across the toothrow (Figure 148) – the degree of transverse displacement is, however, very variable. Anterior upper premolar sometimes not visible above gum. No differences between the skulls and teeth of *C. lesueuri* and *C. seabrae* have been documented.

Geographic Variation None recorded.

Similar Species Three other vespertilionids in southern Africa have three upper premolars on each side and FA <42 mm:

Cistugo seabrae. Slightly paler and on average slightly smaller (FA: 34.4 [33–35] mm; GLS: 12.9 [12.2–13.2] mm). Usually two or three glands per wing; glands larger and usually close to forearm.

Myotis bocagii. Dorsal pelage rufous, dense, fairly woolly. Middle upper premolar ca. half to three-quarters height of anterior premolar; both visible above gum. Forearm on average longer: 38.6 (33–42) mm.

Kerivoula argentata. Ears funnel-shaped, tragus long, narrow, sharply pointed. Fringe of stiff hairs along posterior margin of interfemoral membrane. Dorsal pelage woolly, reddish-brown with silvery-white frosting.

If the anterior upper premolar is not visible, *C. lesueuri* is similar to:

Pipistrellus capensis. Tragus broad and rounded. Transverse lines on interfemoral membrane dark. Tail relatively shorter (65–66% of HB). Premolars not minute.

Distribution Endemic to Africa. Recorded, disjunctly, from the South-West Arid and South-West Cape BZs, and also from the Highveld BZ. The records are from South Africa (Cape and Orange Free State) and Lesotho (Roberts 1919, Herselman & Norton 1985, Lynch & Watson 1990, Lynch 1994, Watson 1998).

Habitat In Lesotho, mist-netted near water (dam, river, vlei) in open montane grassveld in mountainous terrain (Watson 1998). In the Western Cape Province of South Africa, netted over water in fynbos in mountainous terrain (TM).

Abundance Rare.

Remarks Day-roosts include rock-crevices close to water; one was a narrow horizontal crevice in an arid mountain cliff next to a river; another was a rock-crevice behind a waterfall (Lynch 1994, Watson 1998). Insectivorous. Emerges at dusk (Lynch & Watson 1990, Watson 1998). Roosts in mixed-sex groups (several to 40) (Lynch 1994, Watson 1998). Litter-size: 1 (1–2) foetus, n = 18 (Lynch 1994). Reproductive chronology not known; in Lesotho, pregnant ♀♀ were collected in Oct and Dec; no data for other months (Lynch 1994). Predators and ectoparasites not known. The possibility that this species is a reservoir host of Rift Valley Fever virus is indicated by Oelofsen & Van der Ryst (1999).

Conservation IUCN Classification: Least Concern.

However, surveys suggest that this species has a very small population.

Measurements

Cistugo lesueuri

FA: 35.6 (32–38) mm, n = 75

WS: n. d.

TL: 97 (88–107) mm, n = 70

HB: 49.8 (44–55) mm, n = 66

T: 44.0 (43–45) mm, n = 66
 E: 11.8 (11.0–14.0) mm, n = 66
 Tr: 6.4 (5.9–7.0) mm, n = 3
 Tib: 14.2 (14.0–14.5) mm, n = 3
 HF: 7.2 (6.0–8.0) mm, n = 66
 WT: 6.9 (5.5–8.0) g, n = 66
 GLS: 13.3 (12.9–13.8) mm, n = 8
 GWS: 8.6 (8.0–8.9) mm, n = 5

C–M³: 5.0 (4.9–5.2) mm, n = 9

Lesotho and South Africa (NMB, TM, Lynch 1994, Watson 1998, Seamark & Brand 2005)

Key References Lynch 1994; Watson 1998.

Teresa Kearney

Cistugo seabrae ANGOLAN WING-GLAND BAT

Fr. Cistugine d'Angola; Ger. Angola-Mausohr

Cistugo seabrae Thomas, 1912. Ann. Mag. Nat. Hist., ser. 8, 10: 205. Mossamedes, Angola.

Taxonomy Synonyms: none. Tentatively not considered to include *lesueuri* (but see Genus *Cistugo* and *C. lesueuri*). The specific name is commonly spelled *seabrai* but *seabrae* is the original spelling. Chromosome number (Namibia): 2n = 50; aFN = 48 (as in *C. lesueuri*) (Rautenbach *et al.* 1993).

Description Very small microbat without noseleaf and with tail more or less fully enclosed in interfemoral membrane; six upper and six lower cheekteeth on each side (but anterior upper premolar not always visible above gum); ears not funnel-shaped; pelage not frizzled; usually 2–3 glands close to forearm on each wing (but not always present or visible). A poorly known species almost indistinguishable from *C. lesueuri*. Sexes similar. Pelage moderately dense, sleek (not woolly); mid-dorsal hairs ca. 5 mm. Dorsal pelage yellowish-brown, orange-brown or greyish-brown; hairs medium to dark brown with tip of dorsal colour. Ventral pelage yellowish-orange (when dorsal pelage is orange-brown), off-white or beige; paler in pelvic region; hairs greyish-brown or blackish-brown with tip of ventral colour or (in pelvic region) white with grey base. Muzzle with naked skin dark brown. Ears medium brown, comparatively and relatively short for a vespertilionid (27.9 [25–37]% of FA); tip narrow, rounded. Tragus length not known. Wings medium to dark brown with paler reticulation lines (at least in dried specimens). Glands on wing usually found close to forearm; larger than in *C. lesueuri* and usually two or three on each wing (Thomas 1912a, Hill & Carter 1941, Shortridge 1942, Herselman & Norton 1985). Tibiae dorsally and ventrally naked. Interfemoral membrane paler and more translucent than wings and with pale transverse lines; distal third with fine, thinly scattered cream hairs along veins ventrally and dorsally (cf. *C. lesueuri*); posterior margin without projecting bristle-like hairs (cf. some *Kerivoula*). Tail 82.1 (71–91)% of HB (cf. *Pipistrellus capensis*). Calcar reaching half-way to tip of tail. No postcalcareal lobe. Not known if terminal vertebra protrudes beyond margin of interfemoral membrane.

No differences between the skulls and teeth of *C. lesueuri* and *C. seabrae* have been documented.

Geographic Variation None recorded for *C. seabrae* as defined here, but Meester *et al.* (1986) suggest that *C. lesueuri* might be a subspecies of *C. seabrae*.

Similar Species Three other vespertilionids in southern Africa have three upper premolars on each side and FA <42 mm:



Cistugo seabrae

Cistugo lesueuri. Slightly darker and on average slightly smaller (FA: 35.6 [32–38] mm, GLS: 13.3 [12.9–13.8] mm). No more than two glands per wing; glands smaller and not found near forearm.

Myotis bocagii. Dorsal pelage rufous, dense, fairly woolly. Middle upper premolar ca. half to three-quarters height of anterior premolar; both visible above gum. FA on average longer (38.6 [33–42] mm).

Kerivoula argentata. Ears funnel-shaped, tragus long, narrow, sharply pointed. Fringe of stiff hairs along posterior margin of interfemoral membrane. Dorsal pelage woolly, reddish-brown with silvery-white frosting.

If the anterior upper premolar is not visible, *C. seabrae* is similar to:

Pipistrellus capensis. Tragus broad and rounded. Transverse lines on interfemoral membrane dark. Tail relatively shorter (65–66% of HB). Premolars not minute.

Distribution Endemic to Africa. Apparently restricted to the Namib Desert region of the South-West Arid BZ. Recorded from SW Angola (Mossamedes), Namibia (Berseba, Huab River Mouth, Lüderitz District, 70 km W Maltahohe) and NW South Africa (Goegab, Steyerskraal, Goodhouse) (Thomas 1912a, Shortridge 1934, 1942, Herselman & Norton 1985). A new record (not mapped) on the Orange R. at 28° 39' S, 20° 26' E, extends the range eastwards by 216 km (Seamark & Kearney 2006).

Habitat Found in arid areas, in the vicinity of open water (Shortridge 1942, Herselman & Norton 1985).

Abundance Rare in collections, but plentiful at some localities where collected (Shortridge 1942, Herselman & Norton 1985).

Remarks Day-roosts not known – all specimens have been netted or shot. However, individuals found flying in a church were thought to have been roosting in the spire (Shortridge 1934). Insectivorous. Observed foraging a few metres off the ground, over vegetation and over or near water, shortly after sundown (Shortridge 1942, Herselman & Norton 1985). Shortridge (1942) observed that, on first appearing, its flight is comparatively steady and direct but, with approaching dusk, it descends and circles low around trees and bushes. At Goodhouse, *Cistugo* and *Sauromys* (as *Platymops*) have the same habit of fluttering in the deep shadow of orange trees and snapping small insects from the leaves.

Conservation IUCN Classification: Least Concern.

Populations small but not under any specific threat at present.

Measurements

Cistugo seabrae

FA: 34.4 (33.1–35.4) mm, n = 15

WS: n. d.

TL: n. d.

HB: 46.0 (40–54) mm, n = 12

T: 35.8 (32–40) mm, n = 6

E: 11.0 (10–11) mm, n = 4

Tr: 6.2 (5.6–7.4) mm, n = 11

Tib: n. d.

HF: 5.4 (5–6) mm, n = 14

WT: n. d.

GLS: 12.9 (12.2–13.2) mm, n = 14

GWS: 8.0 (7.5–8.2) mm, n = 8

C–M³: 4.9 (4.8–5.5) mm, n = 14

Namibia (TM). Body measurements made on dried skins

Key References Herselman & Norton 1985; Shortridge 1942.

Teresa Kearney

GENUS *Myotis*

Myotises (Mouse-eared Bats, Hairy Bats)

Myotis Kaup, 1829. Skizz. Entwickel.-Gesch. Nat. Syst. Europ. Thierwelt 1: 106. Type species: *Vespertilio myotis* Borkhausen, 1797.



Myotis welwitschii.

A polytypic genus with 104 species of which only ca. 20% occur in the southern hemisphere, and only 11 species occur in Africa. Diagnostic combination of characters: six upper cheekteeth (as in *Cistugo*, *Kerivoula*, *Phoniscus*) but sometimes the middle premolar is not visible from the outside lateral view although it is visible in the occlusal view; ears not funnel-shaped, tragus long and narrow

but not sharply pointed and pelage not frizzled (cf. *Kerivoula* and *Phoniscus*); anterior upper premolar and middle premolar not aligned transversely to the toothrow and no glands on the wings (cf. *Cistugo*). Pelage thick, soft, erect, often fairly woolly. Dental formula $2^{133}/_{3133} = 38$. Selected external characters of *Myotis* occurring in Africa are illustrated in Figure 149, and craniodental characters in Figure 150.

This genus is widely distributed over Africa, Eurasia and south-eastwards to Australia, and the Americas, but is sparsely distributed on oceanic islands. It has the widest distribution of any genus of bats and probably the widest natural distribution of any terrestrial mammal except *Homo* (Nowak 1999). Among mammals, the genus *Myotis* has had one of the most extensive adaptive radiations and, because the genus is so widespread, it appears that separate radiations have taken place in different localities with the result that convergent evolution has also occurred (see below). In Africa, there are 11 species and, of these, five occur in North Africa, mainly in the Mediterranean Coastal BZ but sometimes also in the Afromontane–Afroalpine BZ and in one case, also marginally in the Sahara Arid BZ. The remaining six species are sub-Saharan and, of these, two are known only from forest habitats, one only from savanna habitats and three occur in both. Altogether, eight of the species in Africa have been found in montane habitats; *M. scotti* is the only species that might be restricted to montane habitat, but most records of *M. welwitschii* are near mountainous regions although not restricted to high altitudes.

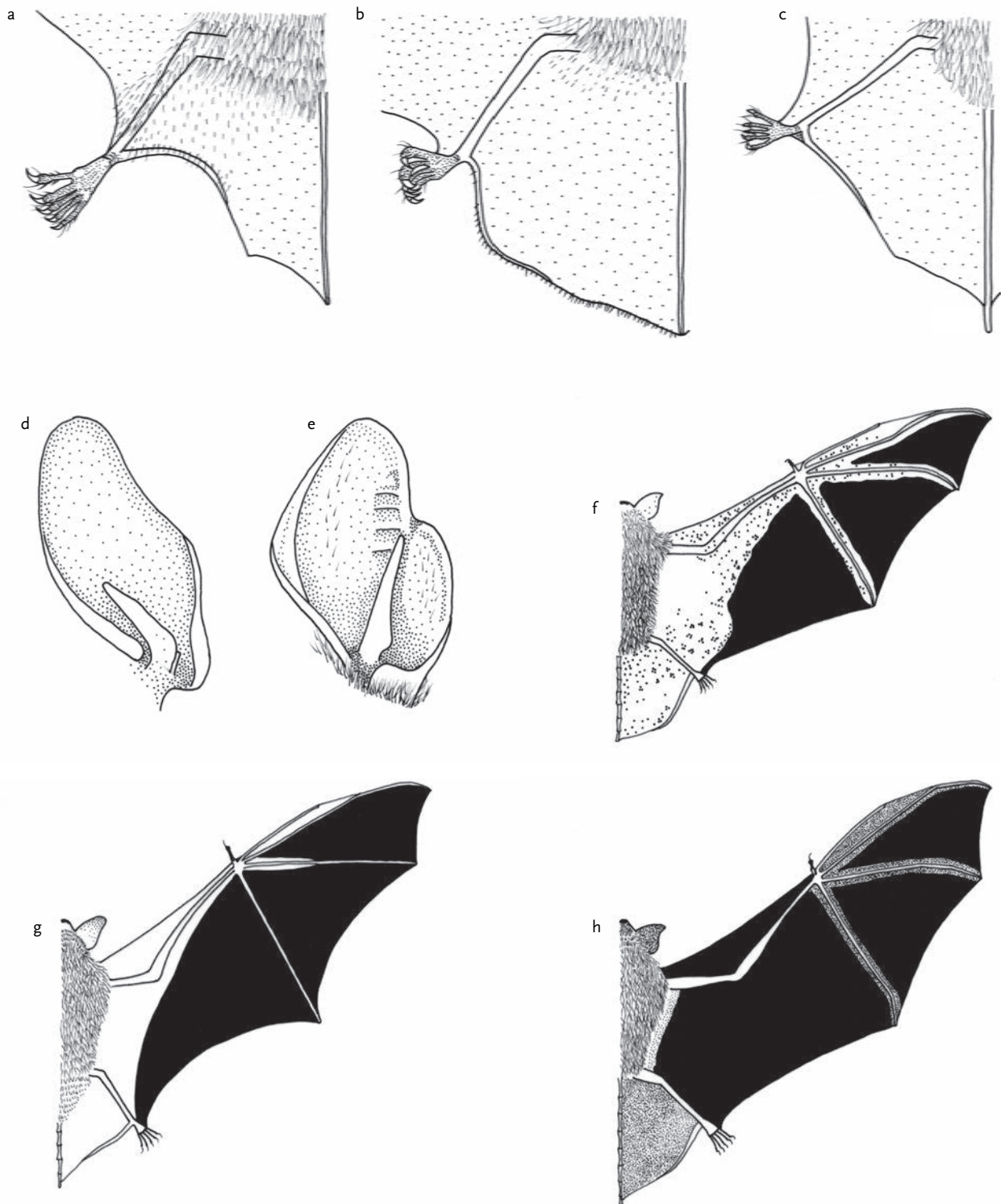


Figure 149. Some external characters of African *Myotis*. Ventral views of interfemoral membranes, tibiae, hindfeet and calcars of (a) *M. capaccinii*, (b) *M. nattereri* and (c) *M. mystacinus*; tibiae drawn to same size to show differences in sizes of hindfeet relative to lengths of tibiae; traced from photos of dried specimens. (d) Left ear and tragus of *M. bocagii*. (e) Left ear and tragus of *M. emarginatus* (based on Harrison & Bates 1991). Particoloured flight membranes of (f) *M. welwitschii*, (g) *M. morrisi* and (h) some specimens of *M. tricolor*.

The foraging strategies exemplified by *Myotis* are diverse and include slow-hawking, trawling, gleaning from foliage and walls, and perhaps ground-gleaning. The echolocation calls emitted by bats cruising in their main habitats are unlike those of other African vespertilionids; they are mainly very steep linear FM sweeps, which apparently have very

variable end-frequencies as well as variable start-frequencies. However, Barataud (2005) analysed the echolocation of seven species of *Myotis* (including four of those occurring in North Africa) and found that they emit several types of signals (up to six different types for one species) according to their flight behaviour and their distance from obstacles.

Some slow-hawking species of *Myotis* use the interfemoral membrane to catch and/or hold prey, and others use their hindfeet as grappling hooks to catch (gaff) prey on or near the surface of water in pools, lakes, streams and rivers. It was formerly thought that the suites of characters that reflect adaptation to the different foraging strategies were characteristic of the subgenera – namely, *Myotis* (gleaning off solid surfaces), *Selysius* (slow-hawking over land) and *Leuconoe* (trawling or slow-hawking over water) (e.g. Koopman 1994). However, it is now evident (from molecular systematics) that these subgenera are not monophyletic but instead represent ecomorphs whose distinguishing characters reflect convergent evolution (Ruedi & Mayer 2001, Stadelmann *et al.* 2004). Consequently, these subgenera are not recognized by Simmons (2005) or here.

The molecular evidence of Stadelmann *et al.* (2004) indicates the existence of an Ethiopian clade of *Myotis*, which includes the six sub-Saharan species, one species from Madagascar, one species from the Western Palearctic (*M. emarginatus*) and one from the Oriental region (*M. formosus*). The data suggest that the Ethiopian clade split from the other Old World *Myotis* in the middle Miocene, quite early in the *Myotis* radiation and therefore the comparative paucity of species in sub-Saharan Africa cannot be attributed to a late entry into this continent. The data also suggest that the Western Palearctic and Oriental regions were colonized secondarily from the Ethiopian region, probably at the end of the Miocene.

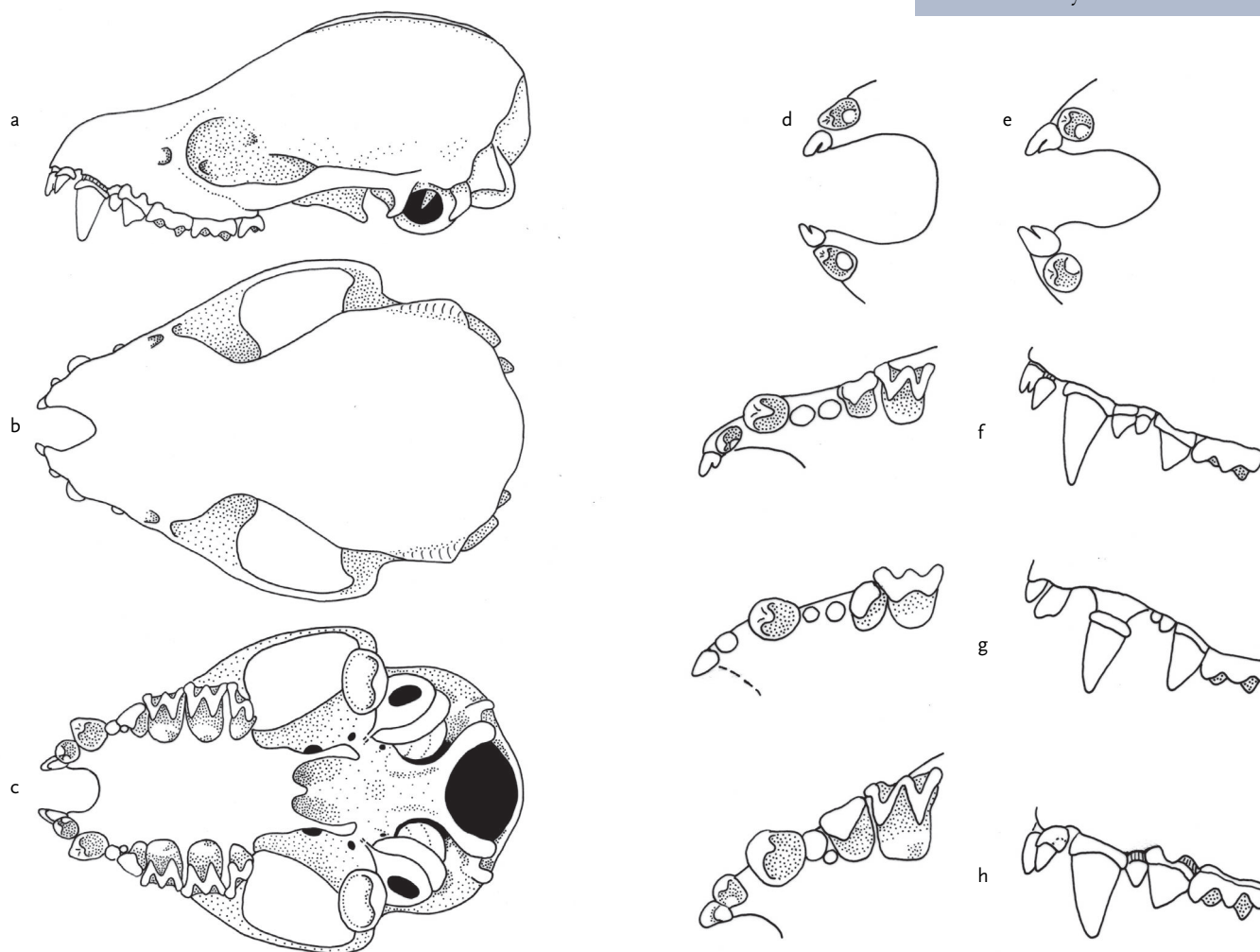
Because different foraging strategies are associated with different morphological characters, many of the diagnostic characters of the species in this genus reflect the manner in which they capture prey. These characters include the relative length of the tragus, the hairiness or otherwise of the tibiae; the relative length of the hindfeet, the

relative length, robustness and hairiness of the calcars and the development of postcalcarea lobes; the position of attachment of the wing to the hindlimb (i.e. attached to base [distal end] of tibia or to base [proximal end] of first toe), and the pilosity of the posterior margin of the interfemoral membrane (Figure 149; details below) (Fenton & Bogdanowicz 2002). Other diagnostic characters include the colour of the pelage and wings, the relative length and shape of the ears, and the presence or absence of a deep emargination in the outer margin of the ear (Figure 149). Diagnostic characters of the skull and dentition include skull size and robustness, the comparative height of the braincase and degree of concavity of the profile of the forehead region (viewed laterally), which ranges, in African *Myotis* and *Cistugo*, from strongly to weakly concave (Figure 147), and the relative size of the middle upper premolar (P^3) and its position in the toothrow.

The relative sizes of some characters, for African species, are as follows:

Mean length of ear as percentage of mean length of FA. For African *Myotis*, 27.0–34.7% is short, 34.8–38.3% is medium, 38.4–42.0% is long.

| Distribution in Africa | FA (mm) | Wings and interfemoral membrane | Relative length of hindfoot (Wing attachment) | Dorsal hairs (Dorsal pelage) | Ventral hairs | |
|--|---------|---|---|---|---------------|--|
| North-west Africa | 53–65 | Uniformly brown | Medium (Base of first toe) | Bicoloured (Medium to pale brown) | Bicoloured | |
| North-west Africa | 39–43 | Uniformly greyish-brown | Long (Tibia, well above heel) | Bicoloured (Pale brownish-grey) | Bicoloured | |
| North-west Africa | 39–43 | Uniformly greyish-brown | Short (Base of first toe) | Tricoloured (Greyish-brown to rusty-brown) | Bicoloured | |
| North-west Africa | 37–42 | Uniformly dark greyish-brown | Medium (Base of first toe) | Bicoloured (Greyish-brown) | Bicoloured | |
| North-west Africa | 33–37 | Uniformly dark brown | Short (Base of first toe) | Bicoloured (Greyish-brown) | Bicoloured | |
| Ethiopia to South Africa, and westwards to Angola. Also Guinea, Cameroon | 52–60 | Conspicuously parti-coloured, black and orange | Short (Base of first toe) | Tricoloured (Orange) | Bicoloured | |
| Ethiopia to South Africa | 47–53 | Uniformly dark or inconspicuously particoloured, black and dark red | Medium (Base of first toe) | Tricoloured (Rufous to coppery-brown) | Tricoloured | |
| Nigeria, Ethiopia | 45, 47 | Particoloured, black and yellowish | Short (Base of first toe) | Tricoloured (Orange-brown) | Unicoloured | |
| Congo | 37 | Uniformly blackish | Long (Base of tibia) | Bicoloured ('Pale auburn') | Bicoloured | |
| West Africa to Tanzania and southwards to Angola and NE South Africa | 33–42 | Uniformly blackish-brown | Medium (Base of first toe) | Bicoloured or tricoloured (Rufous, coppery-red or dark rusty-brown) | Bicoloured | |
| Ethiopia | 37–41 | Uniformly dark brown | Short (Base of first toe) | Bicoloured (Coppery-brown) | Bicoloured | |



| | Profile of forehead region | Miscellaneous | Species |
|--|--------------------------------|---|-----------------------|
| | Moderately concave | No fringe of bristle-like hairs along posterior edge of interfemoral membrane | <i>M. punicus</i> |
| | Strongly concave | Outer margin of ear slightly notched
Tragus ca. half length of ear
No fringe of bristle-like hairs along margin of interfemoral membrane | <i>M. capaccinii</i> |
| | Strongly concave | Outer margin of ear deeply notched
Tragus ca. half length of ear
No fringe of bristle-like hairs along margin of interfemoral membrane | <i>M. emarginatus</i> |
| | Strongly concave | Outer margin of ear slightly notched
Tragus notably > half length of ear
Dense fringe of bristle-like hairs along margin of interfemoral membrane | <i>M. nattereri</i> |
| | Strongly concave | Outer margin of ear with shallow notch
Tragus ca. half length of ear
No fringe of bristle-like hairs along margin of interfemoral membrane | <i>M. mystacinus</i> |
| | Moderately concave | Sparse fringe of bristle-like hairs along margin of interfemoral membrane between tips of calcars and tip of tail | <i>M. welwitschii</i> |
| | Strongly concave | No fringe of bristle-like hairs | <i>M. tricolor</i> |
| | Strongly concave | No fringe of bristle-like hairs along margin of interfemoral membrane | <i>M. morrisi</i> |
| | Weakly concave | Scattered short hairs along proximal two-thirds of margin of interfemoral membrane | <i>M. dieteri</i> |
| | Moderately to strongly concave | No fringe of hairs along margin of interfemoral membrane | <i>M. bocagii</i> |
| | Strongly concave | Numerous stiff hairs along margin of interfemoral membrane between tips of calcars and tip of tail | <i>M. scotti</i> |

Table 29. Key to the African species in the genus *Myotis*. Measurements and distributions pertain only to Africa.

Mean length of tragus relative to length of ear. About one-third of E is short, ca. half of E is medium, ca. two-thirds of E is long.

Mean length of hindfoot as percentage of mean length of tibia. For African *Myotis*, 36–49% is short, 49–62% is medium, 62–74% is long.

Relative length of calcar. Reaching ca. one-third of distance to tip of tail is short, ca. half of distance is medium, ca. two-thirds of distance is long.

Relative height of middle upper premolar. About same height as cingulum of anterior premolar is small, ca. half height of anterior premolar is medium, ca. two-thirds height of anterior premolar is large.

The species occurring in Africa can be distinguished from the information in Table 29. Additional diagnostic characters are given in the species profiles.

Meredith Happold

Myotis bocagii RUFOUS MYOTIS (RUFOUS MOUSE-EARED BAT)

Fr. Murin roux; Ger. Kupferfarbenes Mausohr

Myotis bocagii (Peters, 1870). J. Sci. Math. Phys. Nat. Lisboa, ser. 1, 3: 125. Duque de Bragança, Angola.

Taxonomy Originally *Vespertilio bocagii*. Because the species was named after J. V. Barboza du Bocage, some authors spell the name *bocagei*. Synonyms: *cupreolus*, *dogalensis*, *hildegardae*. Three subspecies: two in Africa. Chromosome number (South Africa): $2n = 44$; aFN = 50 (Rautenbach *et al.* 1993).

Description Small to very small, very beautiful microbat without noseleaf and with tail more or less fully enclosed in interfemoral membrane; six upper and six lower cheekteeth on each side; ears separated, not funnel-shaped; pelage not frizzled; FA: 33–42 mm; dorsal pelage rufous, coppery-red or dark rusty-brown; face sometimes with dark mask; wings uniformly blackish-brown, attaching to base of first toe; HF 47–60% of Tib; posterior margin of interfemoral membrane naked. Not easily distinguished from *M. scotti*. Sexes similar in colour and size. Pelage dense, fairly woolly; mid-dorsal hairs 5–6 mm. Dorsal pelage pale to bright rufous, bright coppery-red to dark rusty-brown; hairs vary geographically – tricoloured (cream with dark brown bases and rufous tip), or bicoloured (dark reddish-brown with rufous, coppery-red or dark rusty-brown tip). Ventral pelage cream or pale silvery-brown sometimes suffused with rufous; hairs bicoloured, blackish-brown with tip of ventral colour. Muzzle and naked skin around eyes dark brown. In some specimens of *M. b. bocagii*, pelage on cheeks and around eyes is also blackish or brown, creating a dark ‘mask’ across the face (similar to, but not as conspicuous as, that of *M. scotti*). Ears blackish-brown; of medium relative length for an African *Myotis* (37.1 [32–43]% of FA, $n = 31$); inner margin strongly convex, outer margin concave with no emargination. Tragus relatively short (43 [39–45]% of E). Wings uniformly dark blackish-brown without markings; attaching to base (proximal end) of first toe. Tibia hairless. Hindfoot of medium relative length (53 [47–60]% of Tib, $n = 23$). Calcar moderately robust, extending half to two-thirds of distance to tip of tail. Postcalcarea lobe poorly developed. Interfemoral membrane dark blackish-brown; posterior margin without fringe of hairs (cf. *M. scotti*). Tail with two vertebrae protruding beyond edge of interfemoral membrane.

Skull small and delicate. Braincase comparatively low; profile of forehead region (viewed laterally) moderately (Figure 147b) to strongly concave. No sagittal crest. Anterior palatal emargination comparatively wide (cf. *M. morrisi*) (Figure 150d). Upper canines (from top of cingula) 1.63 (1.5–1.8) mm, $n = 7$ (cf. *M. scotti*). Middle upper premolar comparatively large (half to three-quarters height of anterior upper premolar and much more than half crown area of anterior premolar);

usually displaced lingually but anterior and posterior premolars well separated (Figure 150f). Anterior upper premolar also somewhat displaced lingually. Anterior and middle lower incisors with four cusps.

Geographic Variation Following Koopman (1994) the African subspecies are:

Myotis b. bocagii: Ethiopia to Angola and the former Transvaal; woodland savanna. Dorsal pelage rufous, hairs tricoloured. Sometimes with dark mask.

M. b. cupreolus: Liberia to DR Congo; rainforest. Dorsal pelage coppery-red to dark rusty-brown (usually darker than nominate subspecies), hairs usually bicoloured. Some individuals in DR Congo are pale rufous. No mask.

Similar Species Four other sub-Saharan *Myotis* have uniformly coloured wings (Table 29, p. 691):

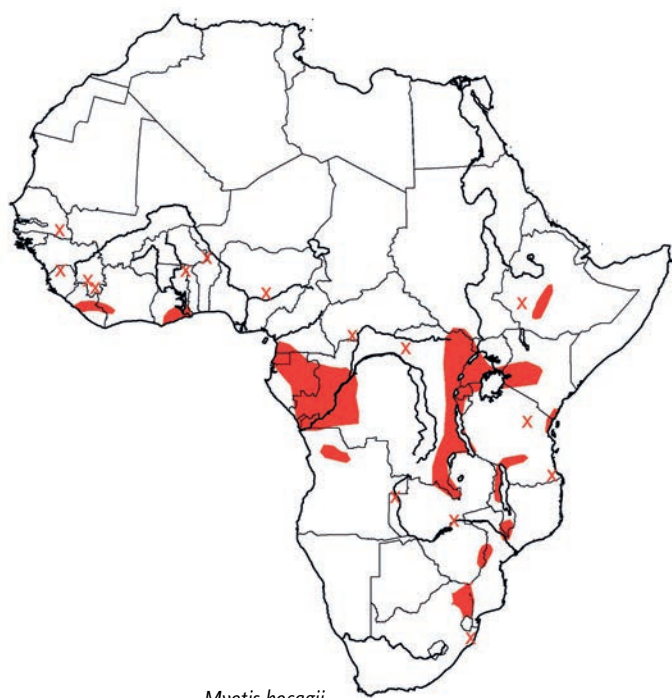
Myotis scotti. Dorsal pelage bicoloured. Posterior margin of interfemoral membrane with bristle-like hairs between ends of calcars and tip of tail. HF <50% of Tib. Braincase comparatively high; profile of forehead strongly concave. Upper canines shorter (ca. 1.2 mm). Middle upper premolar smaller (ca. half height of anterior premolar or less); within toothrow.

M. dieteri. Dorsal hairs dark brown with auburn tip. HF 65% of Tib. Skull with profile of forehead region weakly concave.

M. tricolor (sometimes). Larger (FA: 47–52 mm). Wings sometimes with faint black and dark reddish-brown pattern.

Distribution Widely distributed and recorded in Sudan Savanna BZ and most other biotic zones and mosaics south of the Sudan Savanna BZ, but not recorded from the Horn of Africa, nor from the South-West Arid, Highveld and South-West Cape BZs. Recorded from most countries from Senegal to N DR Congo, Uganda, Kenya and Ethiopia, and southwards to Angola and NE South Africa. According to Monadjem *et al.* (2010) more widely distributed in eastern half of Zimbabwe than mapped here, and also recorded further south in KwaZulu–Natal. Extraliminally: Yemen.

Habitat Recorded from riverine habitats in lowland rainforest and woodland savannas in West Africa, coastal forests in East Africa, and



Myotis bocagii

miombo woodland in the south. In savanna zones, probably limited to localities within or near remnant rainforest, riverine forest or afromontane forest, which are also within reach of open water such as rivers, large pools, dams and lakes. Often recorded where bananas are grown and sometimes apparently absent where musaceous plants are absent (see Adaptations). Appears to avoid villages.

Abundance Uncertain. Not often encountered and considered uncommon throughout most of its geographic range, but common in some localities where forest, banana plants and open water are present (Brosset 1976, Happold & Happold 1997).

Adaptations Aspect ratio low; wing-loading very low (M. Happold unpubl.). Flight fast or slow with great manoeuvrability; can take off from ground; cannot hover. Turns usually by banking (minimum radius <25 cm), occasionally by stalling-and-twisting; individuals sustained flight within a 1×1×1 m enclosure for up to four circuits/flight (6 bats, 10 flights each). Cursorial locomotion is slow and awkward. By day, roosts in the furled leaves of bananas and other musaceous plants; in bunches of bananas and under the dead leaves of bananas and plantains (Lang & Chapin 1917b). In DR Congo, the Mabudu people call it 'big red brother' of the Banana Pipistrelle *Pipistrellus nanus*. In Gabon, *M. bocagii* roosted 5–50 m from the Ivindo R. and was not found in rainforest along the river where there were no banana plants (Brosset 1976). Has also been found clinging to broad leaves in dank, dark vegetation of a thickly overgrown swamp and one pair, when disturbed, flew from the sheath of an Arum lily into the sheath of another lily some distance away (Sanborn 1949). Also roosts among leaves of *Hyphaene* palms (Rosevear 1965) and in hollow trees (R. C. Wood, in Kershaw 1922).

Foraging and Food Forages mainly by trawling and slow-hawking over water, taking prey from the surface and, less often, from above the surface. One light-tagged individual in Malawi foraged over a large

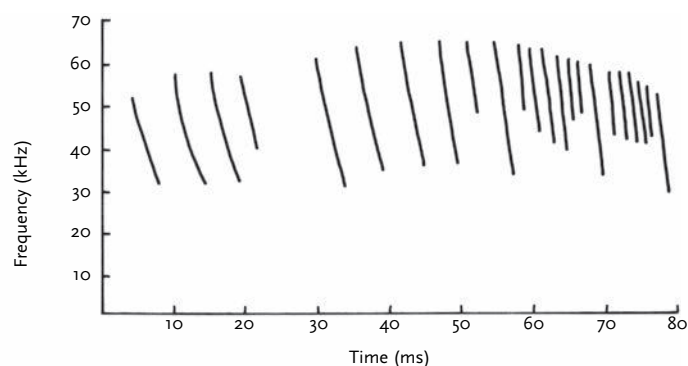


Figure 151. Sonogram of a sequence of search-phase and approach-phase echolocation calls emitted by a light-tagged *Myotis bocagii* while foraging low over a large farm dam and then approaching prey close to, or on, the surface of the water (M. Happold unpubl.).

farm dam for more than 1.5 hours with only one four-minute break after 55 minutes. This bat, and others, flew long straight or gently curving sweeps with occasional zig-zagging (usually within ca. 20 cm of the surface), with 5–6 dips/min to take prey from the surface, and occasional upward swoops in pursuit of insects flying 1–2 m (sometimes up to ca. 6 m) above the water. Most foraging was done more than 10 m from the edges (M. Happold unpubl.). Brosset (1966) suggests that prey on water surfaces, or just below, is gaffed by the hindfeet. Feeds on minute insects including moths, beetles, Diptera and Orthoptera (Lang & Chapin 1917b, Whitaker & Mumford 1978).

Echolocation Search-phase echolocation calls are very steep linear FM sweeps (Figures 118q and 151). Start-frequency 52–70 kHz; end-frequency 30–33 kHz; peak-frequency 34–35 kHz; band-width 26–40 kHz; call-duration ca. 3.5–5.5 ms (1 bat, light-tagged, foraging over open water; 78 calls; M. Happold unpubl.).

Social and Reproductive Behaviour The social organization of a marked population was studied over a period of 38 months at Makokou in NE Gabon (Brosset 1976). The bats roosted in furled banana leaves in plantations along the Ivindo R., over which they foraged at night. Banana leaves open after a few days and the bats must move into a new leaf, but clumps of bananas produce new leaves often enough to allow leaf-roosting bats to show roost-fidelity to particular clumps. The social organization of these bats is based on resource-defence polygyny. The bats lived in harems comprised of one adult ♂ and 2–7 adult ♀♀ and their young, the entire group roosting together in one furled leaf. Adult ♂♂ without harems roosted singly; sometimes near the roosts of harems, and sometimes at some distance away. In the main study area, there were four harems. Each occupied a distinct clump of bananas, and the distance between harems was 600–1000 m. Group-composition was stable with respect to the ♀♀, but turnover of the ♂♂ was quite rapid. Juveniles disappeared from the parental harem when 4–5 months old. Of nine juvenile ♂♂ marked in their parental harems, two returned when a year old and became 'harem-masters'. One took over a harem near his parental harem; the other took over his parental harem. Harem formation is often associated with adult ♀♀ outnumbering adult ♂♂. During this study, 61 adult ♀♀ were captured, but only 26 adult ♂♂, although the sex ratio at birth was balanced, suggesting that mortality is higher in ♂♂ than in ♀♀. Harem mating systems evolve when it is feasible for one ♂ to defend

a group of ♀♀ directly, or to defend some limited resource used by more than one ♀. In this case, roosts are not in short supply, but prime feeding territories over stretches of the river near roosting sites are perhaps limited and worth defending. Adult ♀♀ (whose roost-fidelity extends far beyond the tenure of the harem ♂♂) are probably attracted by the territory and/or the roost, rather than by a particular ♂. However, ♂♂ that can defend a roost occupied by ♀♀, presumably have unimpeded access to those ♀♀ when they are ready for mating.

Reproduction and Population Structure Litter-size: one (n = 10) or 2 (n = 1). At 00°40'N (Makokou, Gabon), the reproductive chronology is polyoestry with births in Dec–Feb and Jun. These are the two drier seasons when insects become concentrated in the vicinity of rivers and marshes, and provide optimal foraging for these bats. Evidence of polyoestry comes from a marked ♀ who gave birth in Jan and was heavily pregnant the following Jun, and three other marked ♀♀ who gave birth three times within two years (Brosset 1966, 1976). The extent to which ♀♀ are in reproductive synchrony is not known. There is other evidence of births in ca. Jan and ca. Jun in equatorial rainforest habitats: at 2–3°N in NE DR Congo, a heavily pregnant ♀ was recorded in early Jan and a birth in Jun (Lang & Chapin 1917b) and in Equatorial Guinea, a late pregnancy was recorded in early Jan and a young bat in late Jun (Jones 1971). At 15–16°S in Malawi, 1 of 3 adult ♀♀ was palpably pregnant (early) and two were not palpably pregnant in Sep, 1 of 1 was pregnant in Oct, 2 of 5 were pregnant, one was lactating, one was post-lactating and one was reproductively inactive in Jan, 1 of 1 was post-lactating in Feb, 2 of 8 were post-lactating and six reproductively inactive in Mar, and 6 of 6 were parous but reproductively inactive in May. This suggests that polyoestry at this latitude is unlikely unless two births occur within the Nov–Mar wet season.

Predators, Parasites and Diseases Ectoparasites include a flea *Lagaropsylla consularis* (Siphonaptera: Ischnopsyllidae); mites *Spinturnix walkeri* (Acari: Spinturnicidae), *Steatonyssus javensis* (Acari: Macronyssidae) (Dusbábek & Bergmans 1980, Anciaux de Faveaux 1984). Also mites *Psorergatoides kerivoulae* (Acari: Leeuwenhoeekiidae), *Alabidocarpus eptesicus*, *Olalidocarpus myoticola* and *O. squamosus* (Acari: Chirodiscidae), the hosts of these mites were erroneously identified as *Kerivoula smithii* by their describer, A. Fain (J. Fahr pers. comm.).

Conservation IUCN Category: Least Concern.

Widespread; no known threats.

Measurements

Myotis bocagii

FA: 38.6 (33–42) mm, n = 113

WS (a): 276 (267–285) mm, n = 6*

TL: 91.0 (80–103) mm, n = 55

T: 39.1 (30–50) mm, n = 52

E: 14.3 (12–16) mm, n = 33

Tr: 6.3 (4.9–7.4) mm, n = 17

Tib: 19.8 (18–21) mm, n = 13

HF: 11.2 (11–12) mm, n = 13

WT: 7.3 (5–10) g, n = 52

GLS: 14.8 (13.6–15.9) mm, n = 67

GWS: 9.1 (8.2–9.9) mm, n = 41

C–M³: 5.5 (4.9–6.0) mm, n = 61

Throughout geographic range (BMNH, HC and literature)

*Malawi only

Key References Brosset 1966, 1976; Rosevear 1965.

Meredith Happold

Myotis capaccinii LONG-FINGERED MYOTIS

Fr. Murin de Capaccini; Ger. Langfußfledermaus

Myotis capaccinii (Bonaparte, 1837). Fauna Ital. 1, fasc. 20. Sicily, Italy.

Taxonomy Originally *Vespertilio capaccinii*. Synonyms: six (none in Africa). Subspecies: none recognized by Simmons (2005). Chromosome number (Spain): 2n = 44; aFN = 52 (Pérez-Suárez *et al.* 1991). In Italy, 2n = 44; aFN = 50 (Capanna *et al.* 1968).

Description Small to very small microbat without noseleaf and with tail more or less fully enclosed in interfemoral membrane; six upper and six lower cheekteeth on each side; ears not funnel-shaped; pelage not frizzled; FA: 39–43 mm; dorsal hairs bicoloured; wings uniformly greyish-brown, attaching to tibia well above heel, HF 70–83% of Tib (cf. all other *Myotis* in North Africa); posterior margin of interfemoral membrane without fringe of bristle-like hairs (Figure 149a). Females on average slightly larger than ♂♂. Pelage soft, dense, silky; mid-dorsal hairs 6–7 mm. Dorsal pelage pale brownish-grey; hairs bicoloured, basal half dark blackish-brown, terminal half pale brownish-grey. Ventral pelage white to yellowish, sharply delineated from dorsal pelage especially between ear and shoulder; hairs bicoloured, blackish-brown with white to yellowish

tip. Juveniles dorsally darker and more brown than adults. Muzzle naked from prominent nostrils to eyes, rufous-brown to dark grey. Ears greyish-brown; relatively short for an African *Myotis* (27–37% of FA, n = 9); outer margin with slight notch. Tragus S-shaped with bluntly pointed tip; only ca. half of E. Wings uniformly greyish-brown without markings; attaching to distal end of tibia clearly above heel (Figure 149a) (cf. attaching to base of first toe in other North African species of *Myotis*). Tibiae hairy, especially on outer edge. Hindfeet relatively large (70–83% of tibia, n = 11); toes with long hairs and long claws. Calcars straight, extending ca. one-third of distance to tip of tail, and each with ‘false end’ two-thirds to three-quarters of the way down its length. Postcalcareal lobe poorly developed or absent. Interfemoral membrane greyish-brown, thickly covered by brown downy hairs especially near the body; posterior margin without any curved, bristle-like hairs (although soft, straight hairs project beyond the proximal half of the margin where membrane is supported by the calcars). Terminal vertebra protruding beyond interfemoral membrane (but not in all specimens).

Skull small and delicate. Braincase comparatively high, profile of forehead region (viewed laterally) strongly concave. No sagittal crest. Middle upper premolar slightly reduced (rising over half height of anterior premolar and ca. half of its crown area); within tooththrow.

Geographic Variation None recorded in Africa.

Similar Species Three other *Myotis* with FA <45 mm occur in NW Africa:

Myotis emarginatus. Dorsal pelage greyish-brown to rufous-brown, woolly; hairs tricoloured. Hindfoot almost always smaller (9–12 mm; 43–54% of Tib). Wing-membrane attaching to base of first toe. Interfemoral membrane naked. Outer edge of tibia not hairy. Notch in posterior margin of ear deep.

M. mystacinus. FA shorter (33–37 mm). Dorsal pelage dark greyish-brown. Hindfoot smaller (7–8 mm; 40–52% of Tib). Wing-membrane attaching to base of first toe. Interfemoral membrane naked.

M. nattereri. Dorsal pelage greyish-brown. Hindfoot smaller (8–10 mm; 46–60% of Tib). Wing-membrane attaching to base of first toe. Interfemoral membrane naked. Tragus longer (ca. 11–12 mm); notably more than half of E.

Distribution In Africa, only recorded from coastal fringe of the Mediterranean Coastal BZ in the northern Maghreb (N Morocco to N Tunisia) (Vaughan *et al.* 1977, Aulagnier & Thévenot 1986, Kowalski & Rzebik-Kowalska 1991). Extraliminally: found in the Mediterranean zone and islands of Europe and Asia Minor, extending east to Iran and Uzbekistan.

Habitat Recorded in the vicinity of rivers, mountain streams, ponds and lagoons, and often in the vicinity of caves, from the coast to mountainous areas. Mainly recorded from sea level to 600 m. At

Aokas in Algeria, some individuals roosted in a cave opening close to the sea and only slightly above its level; the cave is surrounded by mountain slopes overgrown with short Mediterranean shrubs (garrigue) (Kowalski *et al.* 1986).

Abundance Very scarce in NW Africa. Few specimens have been observed or mist-netted; only two locality records in Morocco, four in Algeria and one in Tunisia. None found during recent surveys of roosts in Morocco. Extraliminally, many colonies have disappeared in Spain and France, but the species is locally abundant in the eastern Mediterranean (with a colony of 10,000 ♀♀ in Albania [Chytil & Vlasin 1994]).

Adaptations Aspect ratio not known; wing-loading low (Norberg & Rayner 1987). Roosts by day in caves, mines and crevices that are not far from water; one Moroccan specimen roosted in a hole in a tree. Mainly in summer, often shares caves, and even clusters, with other bats, including *Miniopterus schreibersii*, *Myotis punicus*, *Rhinolophus ferrumequinum* and *R. euryale* (Laurent 1944, Brosset 1958, Vaughan *et al.* 1977). Hibernates during winter (Dec–Feb).

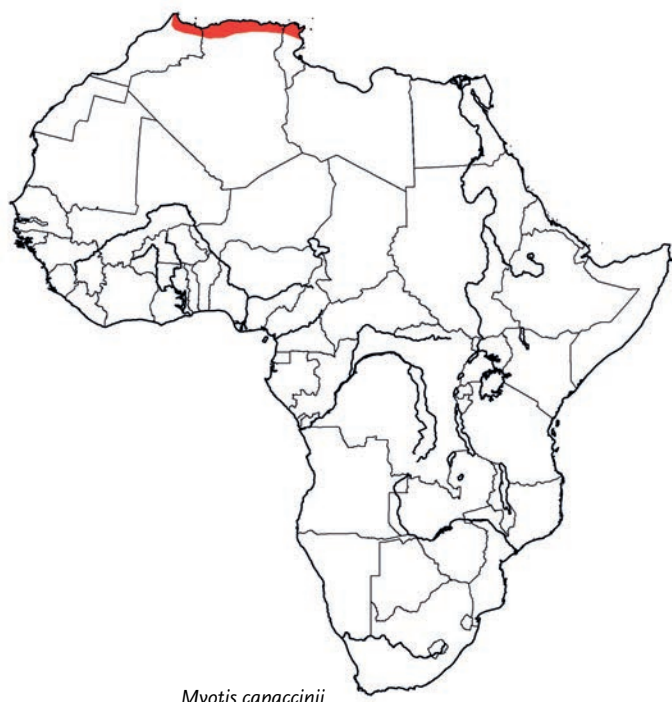
Foraging and Food Forages mainly by trawling and slow-hawking – using its large feet and/or interfemoral membrane to take small to medium-sized insects from the surface of water or flying just above the surface (Kalko 1990). Forages over mountain streams, rivers and ponds and even lagoons (where most Algerian specimens have been mist-netted). In S France, feeds mainly on Trichoptera and Diptera (Chironomidae and Culicidae) (Médard & Guibert 1993), and occasionally takes small fish (Aihartza *et al.* 2003).

Echolocation Highly variable depending on activity and habitat; these data refer to cruising calls in the main habitat. Search-phase call-shape (while hunting above water surface) hyperbolic FM. Start-frequency 43 kHz; end-frequency 22 kHz; peak-frequency 28–35 kHz; call-duration 6–9 ms, inter-call interval 145–165 ms (Barataud 2002, 2005).

Social and Reproductive Behaviour Mating takes place in the winter-roosts where this species gathers in small colonies (western part of the geographic range). Groups of up to 12 recorded in Algeria (Kowalski & Rzebik-Kowalska 1991). Sexes segregate from Mar to Jun when they migrate to summer-roosts. Some individuals roost singly. Pregnant ♀♀ establish maternity colonies in warm caves; they huddle together in dense clusters on the ceilings.

Reproduction and Population Structure Litter-size (Algeria): one ($n = 3$) (Brosset 1958, Kowalski & Rzebik-Kowalska 1991); extraliminally, usually one. In Europe, the reproductive chronology is restricted seasonal monoestry with births in mid- to late Jun. Young are volant after 3–4 weeks. In N Algeria, a pregnant ♀ was reported in early May, and a lactating ♀ in early Jun (Kowalski *et al.* 1986). In N Morocco, large young were observed in late May (Brosset 1958), indicating births in late Apr to early May.

Predators, Parasites and Diseases Predators poorly documented with only one report of predation in a hibernating group by an unidentified animal. Ectoparasites in Africa not known (Anciaux de Faveaux 1984).



Myotis capaccinii

Conservation IUCN Category: Vulnerable (based on African and extralimital data).

This species has specific habitat requirements and its remnant populations are threatened by the draining and polluting of waters over which it forages and by human disturbance in its scarce cave roosts.

Measurements

Myotis capaccinii

FA: 41.5 (39–43) mm, n = 66

WS (d): 251 mm, n = 1*

TL: 93.3 (81–98) mm, n = 61

T: 39.7 (37–45) mm, n = 66

E: 14.1 (11–16) mm, n = 66

Tr: 7.2 (5–9) mm, n = 58

Tib: 16.7 (16–17) mm, n = 11*

HF: 13.3 (12–15) mm, n = 66

WT: 8.3 (6–11) g, n = 65

GLS: 15.2 (14.8–15.4) mm, n = 11

GWS: 9.5 (9.4–9.5) mm, n = 5

C–M³: 5.6 (5.3–5.7) mm, n = 10

Body measurements from Tunisia (Vaughan *et al.* 1977, Kowalski & Rzebik-Kowalska 1991), skull measurements from Morocco and Algeria (Brosset 1958, Romero Zarco 1990, Kowalski & Rzebik-Kowalska 1991)

*Israel, Europe (HZM)

Key References Aulagnier & Thévenot 1986; Brosset 1958; Kowalski *et al.* 1986; Kowalski & Rzebik-Kowalska 1991; Vaughan *et al.* 1977.

Stéphane Aulagnier & Emmanuel Cosson

Myotis dieteri DIETER'S MYOTIS

Fr. Murin de Dieter; Ger. Dieters Mausohr

Myotis dieteri M. Happold, 2005. Acta Chiropterologica 7: 11. Grotte du Viaduc à Loudima, Congo (04° 15' S, 13° 00' E).

Taxonomy Synonyms: *megalopus* (not of Dobson, 1875). The holotype (only known specimen) was identified as *Myotis megalopus* (Dobson, 1875) by Aellen & Brosset (1968) who first reported the specimen, and by Adam & Le Pont (1974) who gave information relating to its capture in Congo by J.-P. Adam. Adam's specimen was identified as *M. megalopus* because some of its external characters (including long hindfeet) fitted the type description of *M. megalopus* originally thought to have come from nearby in Gabon. Subsequently, the holotype and one other specimen of *M. megalopus* were indicated to have come from Kashmir (Blanford 1888, 1891), and then Thomas (1915c) indicated that *megalopus* is a synonym of *M. longipes* (Dobson, 1873) from Kashmir and thereabouts. This conclusion is upheld by several authors, including Simmons (2005). Hayman & Hill (1971), Dowsett *et al.* (1991) and Grubb (2004) noted that Adam's specimen indicated that a long-footed *Myotis* occurred in Congo and that its identity needed investigation. It was found to represent a new species (Happold 2005). Subspecies: none. Chromosome number: not known.

Description Very small microbat without noseleaf and with tail more or less fully enclosed in interfemoral membrane; six upper and six lower cheekteeth on each side; ears separated, not funnel-shaped; pelage not frizzled; FA: 37 mm; dorsal pelage brown; wings uniformly blackish, attaching to base of tibia; HF 65% of Tib; posterior margin of interfemoral membrane with bristle-like hairs. Only one specimen known (adult ♀). Sexual dimorphism: no information. Pelage dense; mid-dorsal hairs ca. 5 mm. Dorsal pelage originally described by Aellen & Brosset (1968) as dark brown with pale auburn at tip; dried hairs are now very dark brown with paler tip. Ventral pelage, originally described as grey, is now greyish; hairs brown with greyish tip. Face uniformly brown. Muzzle with naked skin dark brown. Ears dark brown, subtriangular with rounded tip, relatively short for an African *Myotis* (27% of FA). Tragus narrow, relatively long (ca. 60% of E). Wings uniformly blackish (without markings); attaching to base (distal end) of tibia. Tibia dorsally and

ventrally naked. Hindfoot relatively long (65% of Tib); claws long and robust. Calcar probably extending only half-way to tip of tail, but this needs confirmation. Interfemoral membrane blackish, dorsally naked except for short, straight hairs that protrude slightly beyond the posterior margin from the heel to ca. three-quarters of distance to tip of tail. Tail with two vertebrae protruding beyond interfemoral membrane.

Skull small and delicate. Braincase comparatively low; profile of forehead region (viewed laterally) weakly concave (Figure 147c). Sagittal crest absent. Anterior palatal emargination wide. Anterior and middle upper premolars in toothrow, both very much smaller than the posterior upper premolar (Figure 150g). The anterior premolar, on each side, is apparently slightly lower than the middle premolar, and smaller in crown area. The mandibles are missing and there are no recorded data for the lower teeth.

Geographic Variation No information.

Similar Species Three other sub-Saharan *Myotis* have uniformly coloured wings (Table 29, p. 691):

Myotis bocagii. Dorsal pelage pale to bright rufous, coppery-red to dark rusty-brown; hairs tricoloured (*M. b. bocagii*) or bicoloured (*M. b. cupreolus*). Wings attaching to base of first toe. Hindfoot relatively shorter (47–60% of tibia). Skull with profile of forehead region moderately to strongly concave.

M. scotti. Dorsal pelage shiny coppery-brown; hairs dark brown with terminal third coppery-brown. Wings attaching to base of first toe. Hindfoot relatively short (36% length of tibia). Ethiopia.

M. tricolor (sometimes). Larger (FA: 47–53 mm).

Distribution Known only from the type locality at Loudima, Congo, in the Southern Rainforest–Savanna Mosaic very close to the Rainforest BZ.



Myotis dieteri

Habitat An area where the primary forest was degraded and partly replaced by patches of savanna, and where limestone caves and a river are present (Aellen & Brosset 1968).

Abundance Probably rare (see Conservation).

Remarks As Aellen & Brosset (1968) noted, *M. dieteri* has characters common to species of *Myotis* previously placed in the subgenus *Leuconoe*, which forage over water. These include the attachment of the wing higher up than the base of the first toe, the relatively large hindfoot and long claws, short calcar, short ear and narrow tragus (Fenton & Bogdanowicz 2002). The holotype was taken from a cave, which has its opening on the side of a hill, only ca. 100 m above the valley of the Loudima R. (Adam & Le Pont 1974). From the narrow opening of the cave, a steep slope leads inwards to a lenticular cavern ca. 10 m in diameter and 2 m high at its highest place. The cave was occupied by ca. 100 bats of which the majority were *Rhinolophus landeri landeri* as well as numerous *Nycteris macrotis macrotis*; the cave appeared to be a

permanent day-roost for *N. macrotis* and *R. landeri* because both species were present each time the cave was visited. Furthermore, young bats of both of these species had been observed in this cave. In contrast, there was only a small number of *M. dieteri* and the holotype was the only individual collected. *Myotis dieteri* was not found in the cave on other occasions, nor was it found in four other caves in the Loudima-Kimongo region, nor in 40 other caves in Congo, which were investigated by Adam & Le Pont (1974).

Conservation IUCN Category: Data Deficient.

Only one specimen known, and only a small number have ever been seen (on only one occasion), in only one of 45 caves investigated over a period of ca. seven years (Adam & Le Pont 1974). Furthermore, not recorded from ten localities in nearby Mayombe and lower Kouilou regions of Congo, where 80 specimens (of 14 other species) were collected by Dowsett *et al.* (1991). Also, not recorded from Haut-Ivindo region of Gabon where 1732 individuals (27 species) were captured, from caves and by mist-netting, by Brosset (1966), nor from Kikwit (05° 13'S, 18° 49'E, DR Congo) where 538 specimens (18 species) were collected in 1995 (Van Cakenberghe *et al.* 1999). Consequently, Happold (2005) suggested it should be classified as Critically Endangered.

Measurements

Myotis dieteri

FA: 37 mm

WS: n. d.

TL: 86 mm

T: 38 mm

Tib: 17 mm

HF: 11 mm

E: 10 mm

Tr: ca. 6 mm

GLS: 14.9 mm

GWS: 9.5 mm

C-M³: 5.3 mm

Congo (MNHN, holotype, adult ♀)

Key References Adam & Le Pont 1974; Aellen & Brosset 1968; Happold 2005.

Meredith Happold

Myotis emarginatus GEOFFROY'S MYOTIS

Fr. Murin à oreilles échancrées; Ger. Wimperfledermaus

Myotis emarginatus (E. Geoffroy, 1806). Ann. Mus. Natn. Hist. Nat. Paris 8: 198. Charlemenont, Givet, Ardennes, France.

Taxonomy Originally *Vespertilio emarginatus*. Synonyms: ten (none in Africa). Subspecies: three. Molecular evidence suggests *M. emarginatus* is closely related to *M. welwitschii* (Ruedi & Mayer 2001). Chromosome number (Spain): 2n = 44; aFN = 50 (Pérez-Suárez *et al.* 1991). In Czechoslovakia, 2n = 44; aFN = 52 (Zima 1978).

Description Very small microbat without noseleaf and with tail more or less fully enclosed in interfemoral membrane; six upper and six lower cheekteeth on each side; ears not funnel-shaped;

pelage not frizzled; FA: 39–43 mm; dorsal hairs tricoloured; wings uniformly greyish-brown without markings, attaching to base of first toe; HF 43–54% of Tib; posterior margin of interfemoral membrane without fringe of bristle-like hairs; ear with uniquely deep notch in outer margin. Sexes similar. Pelage dense, fairly woolly; mid-dorsal hairs 6–8 mm. Dorsal pelage greyish-brown to bright rusty-brown; hairs tricoloured, straw-yellow with grey base and tip of the dorsal colour. Ventral pelage slightly to considerably paler than dorsal pelage (yellowish-grey to pale rufous); hairs bicoloured,

basal half dark grey or dark greyish-brown. Juveniles darker and greyer; dorsal hairs less conspicuously tricoloured. Muzzle hairy, reddish-brown. Ears greyish-brown; relatively long for an African *Myotis* (ca. 40% of FA); outer margin with conspicuous angular notch ca. two-thirds from base (deeper than in other *Myotis* with notched ears) (Figure 149e). Tragus lancet-shaped, bluntly pointed; just over half of E (almost reaches notch). Wings uniformly greyish-brown without markings, naked; attaching to base of first toe. Tibia with dorsal surface hairy, ventral surface with sparse hairs. Hindfeet relatively short (43–54% of tibia, $n = 12$); toes with long claws and some long hairs. Calcars straight, extending ca. half-way to tip of tail. Interfemoral membrane greyish-brown; not covered by hairs; posterior margin with sparse, straight, soft hairs but no distinct fringe of curved bristle-like hairs. Terminal vertebra protruding beyond interfemoral membrane.

Skull of medium size for an African *Myotis*, fairly delicate. Braincase high; profile of forehead region (viewed laterally) strongly concave. Sagittal crest absent anteriorly, weakly developed posteriorly. Upper incisors subequal in crown area (cf. *M. nattereri*). Middle upper premolar reduced (slightly higher than cingulum of anterior premolar); within toothrow; anterior premolar not in contact with posterior premolar.

Geographic Variation None in Africa where only the nominate subspecies (*M. e. emarginatus*) occurs (Gaisler 1983).

Similar Species Three other *Myotis* with FA <45 mm occur in NW Africa (Table 29, p. 691):

Myotis capaccinii. Dorsal pelage medium to pale brownish-grey, silky; hairs bicoloured. Hindfoot larger (12–15 mm; 70–83% of tibia). Wing-membrane attaching to tibia well above heel. Interfemoral membrane covered by downy pelage. Outer edge of tibia hairy. Notch in posterior margin of ear shallow.



Myotis emarginatus

M. mystacinus. FA shorter (33–37 mm). Dorsal hairs bicoloured. Muzzle not hairy, naked skin blackish. Wings dark brown. Notch in posterior margin of ear shallow.

M. nattereri. Dorsal pelage greyish-brown; hairs bicoloured. Interfemoral membrane with dense fringe of bristle-like hairs between tip of each calcar and tail. Notch in posterior margin of ear comparatively shallow. Tragus longer (notably more than half of E).

Distribution In Africa, recorded mainly from the Mediterranean Coastal and Afromontane–Afroalpine BZs of the northern Maghreb in NW Africa. Recorded from the Middle Atlas, Rif Mts and Bni Snassen in Morocco, from the coastal zone and neighbouring part of the Tell Atlas in Algeria, extending into the northern mountains of Tunisia (Vaughan *et al.* 1977, Aulagnier & Thévenot 1986, Kowalski & Rzebik-Kowalska 1991). Extraliminally: S Europe northwards to the Netherlands and S Poland, and eastwards through Israel and Lebanon to Uzbekistan and E Iran.

Habitat Recorded from the coast to mountainous areas. In Europe, prefers limestone areas with caves as well as warm regions with woodlands, parks, gardens and water. No details available for Africa.

Abundance With few small colonies, NW African populations appear scarce by comparison with S Europe, where maternity colonies may comprise up to 1000 ♀♀.

Adaptations Aspect ratio low; wing-loading very low; wing-tip short and rounded (Norberg & Rayner 1987). Flight predicted to be slow with high manoeuvrability. Can hover, and does so while foraging. In winter, roosts in dark places in caves and mines with temperatures up to 12 °C and only rarely below 6 °C; individuals hang from ceilings or walls (and, rarely, disappear into crevices). In summer, also roosts in caves and mines; maternity roosts are warm, sometimes lighted and confined to elevations between 200–500 m. Avoids roosts in which temperature is likely to become too high. Predominantly sedentary; movements usually within 40 km (largest recorded 160 km). Breeding colonies have been found associated with *Rhinolophus ferrumequinum* in Tunisia (Vaughan *et al.* 1977), *R. euryale*, *R. blasii* and *Miniopterus schreibersii* in Algeria (Kowalski & Rzebik-Kowalska 1991), and *R. ferrumequinum*, *R. euryale*, *M. schreibersii* and *Myotis capaccinii* in Morocco (Brosset 1958). Torpid individuals were found in winter in Algeria (Kowalski & Rzebik-Kowalska 1991).

Foraging and Food Forages mainly by gleaning (from branches, foliage, walls and the ground), and less often by slow-hawking; occasionally hovers in front of foliage and walls (Krull *et al.* 1991). Forages late after dusk, in woodlands (mainly around the edges and in clearings) and often over water. Forages as far as 10 km from maternity roosts. Feeds mainly on spiders, and also on flies (Diptera: Muscoidea) moths and caterpillars (Lepidoptera) (Bauerova 1986, Krull *et al.* 1991, Beck 1995).

Echolocation Highly variable depending on activity and habitat; these data refer to cruising calls in the main habitat. Search-phase call-shape (close to foliage) steep linear FM. Start-frequency 110 kHz; end-frequency 39 kHz; peak-frequency 65 kHz; call-duration 2.6 ms; inter-call interval 26–32 ms (Barataud 2005).

Social and Reproductive Behaviour Roosts singly or in colonies; in Algeria, torpid ♂♂ and ♀♀ roosting singly were found in winter; and a colony of ca. 20 (of which five were non-pregnant ♀♀) was found in May (Kowalski *et al.* 1986). In Europe, mating starts in autumn. In winter, ♂♂ and ♀♀ roost together in colonies. The sexes segregate in Apr–May when pregnant ♀♀ establish maternity colonies; these may contain 20–200 adult ♀♀; up to 3000 in W France (Arthur & Lemaire 1999). In these colonies, ♀♀ huddle in very tight clusters. In summer, ♂♂ roost singly (Schober & Grimmberger 1987).

Reproduction and Population Structure Litter-size (Algeria): one (n = 2) (Brosset 1958, Kowalski *et al.* 1986). In Algeria, the reproductive chronology is assumed to be restricted seasonal monoestry (as in Europe); records of pregnant ♀♀ in mid-May, a ♀ with full-term foetus in early Jun, lactating ♀♀ and an almost-volant juvenile in early Jul, indicate that births probably occur in first half of Jun (Kowalski *et al.* 1986). Juveniles become volant in early Jul, but are weaned sometime later. Maximum life-span: 16 years.

Predators, Parasites and Diseases Ectoparasites include a flea *Rhinolophopsylla unipunctata* (Siphonaptera: Ischnopsyllidae) because *M. emarginatus* often roosts in tight association with rhinolophid bats, which are the principal hosts of this flea (Beaucournu & Kowalski 1985).

Conservation IUCN Category: Least Concern (based largely on extralimital data).

Because NW African populations are presumably numerically small, urgent conservation should focus on the main identified roosts and bodies of water nearby.

Measurements

Myotis emarginatus

FA: 40.5 (39–43) mm, n = 25

WS: n. d.

TL: 93.9 (88–101) mm, n = 16

T: 42.7 (32–46) mm, n = 25

E: 16.5 (14–18) mm, n = 23

Tr: 9.6 (9–10) mm, n = 8

Tib: 19.6 (18–21) mm, n = 12*

HF: 10.2 (9–12) mm, n = 23

WT: 8.0 (5–10.5) g, n = 17

GLS: 16.0 (15.5–16.5) mm, n = 9

GWS: 9.9 (9.5–10.0) mm, n = 9

C–M³: 6.2 (6.0–6.5) mm, n = 7

Morocco, Algeria, Tunisia (Brosset 1958, Vaughan *et al.* 1977, Gaisler 1983, Kowalski & Rzebik-Kowalska 1991)

*Oman, Saudi Arabia, France (HZM, MNHN)

Key References Aulagnier & Thévenot 1986; Brosset 1958; Gaisler 1983; Kowalski & Rzebik-Kowalska 1991; Vaughan *et al.* 1977.

Stéphane Aulagnier

Myotis morrisi MORRIS'S MYOTIS

Fr. Murin d'Éthiopie; Ger. Morris' Mausohr

Myotis morrisi Hill, 1971. Bull. Brit. Mus. (Nat. Hist.) Zool. 21: 43. Mouth of Didessa River, Walaga, Blue Nile Gorge, Ethiopia.

Taxonomy Synonyms: none. Chromosome number: not known.

Description Small microbat without noseleaf and with tail more or less fully enclosed in interfemoral membrane; six upper and six lower cheekteeth on each side; ears not funnel-shaped; pelage not frizzled; FA: 45, 47 mm; dorsal pelage orange-brown; wings blackish with yellow to orange markings (particoloured); ventral pelage unicoloured. Sexes similar. Pelage dense, fairly woolly; mid-dorsal hairs ca. 7 mm. Dorsal pelage bright orange-brown; hairs tricoloured, creamy-white with basal quarter dark brown and tip orange-brown. Ventral pelage dull creamy-white to orange-beige, chin and flanks slightly darker; hairs unicoloured (cf. all other *Myotis* from Africa). Muzzle pink. Ears pink basally shading to brown at tip; of medium relative length for an African *Myotis* (35–37% of FA, n = 2); outer margin with slight notch. Tragus pink, bluntly pointed, ca. half of E. Wings mainly dark blackish-brown but lightly pigmented with yellow along leading edge and in narrow band posterior to the forearm, and between the body and a line roughly joining the elbow and ankle (Figure 149g). Wings naked except for narrow band on dorsal surface adjacent to body; wing-membrane attaching to base of first toe. Tibia hairy. Hindfoot relatively short (45–49% of Tib, n = 2). Calcar extending half of distance to tip of tail. No postcalcareal lobe. Interfemoral membrane yellow; dorsal

pelage extending over distal half of membrane; no fringe of bristle-like hairs on posterior edge of membrane. Terminal vertebra may or may not protrude beyond membrane.

Skull of medium size for an African *Myotis*, fairly delicate. Braincase high, profile of forehead region (viewed laterally) strongly concave. No sagittal crest. Middle upper premolar reduced (reaching only slightly above cingulum of anterior premolar and slightly less than half crown area of anterior premolar); slightly to almost fully displaced labially but anterior and posterior premolars not in contact. Anterior and middle lower incisors with four cusps. Anterior palatal emargination very narrow (cf. *M. bocagii*) (Figure 150e).

Geographic Variation None recorded.

Similar Species Only two other *Myotis* in Africa have wings with a pattern in contrasting colour (Table 29, p. 691):

Myotis welwitschii. Larger (FA: 52–60 mm). Wing colours black and orange; pattern very conspicuous. Ventral hairs bicoloured.

M. tricolor (sometimes). Wing colours, if pattern is present, black and dark reddish-brown; pattern inconspicuous. Ventral hairs tricoloured.

Distribution Endemic to Africa. Only known from two specimens and two localities in the Sudan Savanna BZ: the type locality in the Blue Nile Gorge, Ethiopia, and Numan, Nigeria (Hill & Morris 1971, Hill *et al.* 1988). Presumably widespread across the Sudan Savanna BZ.

Habitat A lowland species of dry scrub. The holotype was found hunting over the Blue Nile R. in an area of riverine scrub and maize fields. The Nigerian specimen was taken near the Benue R., in a region of short grass and *Acacia* bush, with some silk-cotton trees (Hill *et al.* 1988).

Abundance Very rare?

Remarks Forages at moderate height (1–3 m). Nothing else is known about the habits of this species.

Conservation IUCN Category: Data Deficient.

Only two specimens and two widely separated locations known.

Measurements

Myotis morrissi

FA: 47, 45 mm

WS (d): 300, – mm

TL: 93, – mm

T: 45, – mm

E: 16, 17 mm

Tr: 8, – mm.

Tib: 22, 19 mm

HF: 10, 9.5 mm

WT: 8, – g

GLS: 17.5, 16.3 mm



Myotis morrissi

GWS: –, 10 mm

C–M³: 6.8, 6.6 mm

Ethiopia (holotype) and Nigeria respectively (BMNH, Hill & Morris 1972, Hill *et al.* 1988 and D. W. Yalden unpubl.)

Key References Hill & Morris 1971; Hill *et al.* 1988.

D. W. Yalden

Myotis mystacinus WHISKERED MYOTIS (WHISKERED BAT)

Fr. Murin à moustaches; Ger. Kleine Bartfledermaus

Myotis mystacinus (Kuhl, 1817). Die Deutschen Fledermäuse. Hanau, p. 15. Germany.

Taxonomy Originally *Vespertilio mystacinus*. Synonyms: 15 (none in Africa). Subspecies: four recognized by Benda & Tsytulina (2000) of which probably only one occurs in Africa. According to von Helversen *et al.* (2001), Moroccan specimens represent the nominate subspecies, *M. m. mystacinus*. However, they could represent the recently identified *M. m. occidentalis* from the Iberian Peninsula (Benda & Tsytulina 2000), but this needs confirmation. Chromosome number (Switzerland): 2n = 44; aFN = 50 (Bovey 1949).

Description Very small microbat without noseleaf and with tail more or less fully enclosed in interfemoral membrane; six upper and six lower cheekteeth on each side; ears not funnel-shaped; pelage not frizzled; FA: 33–37 mm; dorsal hairs bicoloured; wings uniformly dark brown, attaching to base of first toe; HF 40–52% of Tib; posterior margin of interfemoral membrane without fringe of bristle-like hairs. The smallest species of *Myotis* in Africa. Sexes similar. Pelage dense, somewhat shaggy, without sheen; mid-dorsal hairs 6–8 mm. Dorsal pelage greyish-brown; hairs bicoloured, black or blackish-brown with greyish-brown at tip. Ventral pelage grey to creamy-white; hairs

bicoloured, dark blackish-brown with grey to creamy-white at tip. Muzzle blackish; upper lip fringed with stiff hairs. Ears blackish-brown; relatively long for an African *Myotis* (34–45% of FA, n = 8); outer margin with shallow notch. Tragus sickle-shaped, bluntly pointed; ca. half of E. Eyes small, partly concealed by pelage. Wings uniformly dark brown without markings; naked; attaching to base of first toe. Tibia naked or almost naked dorsally and ventrally. Hindfoot relatively short (40–52% of Tib, n = 12); toes with some long hairs. Calcar extending less than half distance to tip of tail. Postcalcareal lobe absent or weakly developed. Interfemoral membrane dark brown; no fringe of bristle-like hairs on posterior margin (Figure 149c). Terminal vertebra of tail protruding beyond interfemoral membrane.

Skull small and delicate. Braincase high, profile of forehead region (viewed laterally) strongly concave. No sagittal crest. Middle upper premolar ca. half height and half crown area of anterior premolar; usually both in tooththrow, sometimes both slightly displaced lingually, anterior premolar not in contact with posterior premolar.

Geographic Variation None in Africa (see Taxonomy).



Myotis mystacinus

Similar Species Three other *Myotis* with FA <45 mm occur in NW Africa (Table 29, p. 691):

Myotis capaccinii. FA longer (39–43 mm). Dorsal pelage medium to pale brownish-grey. Hindfoot longer (12–15 mm; 70–83% of tibia). Wings attaching to tibia well above heel. Interfemoral membrane covered by downy pelage.

M. emarginatus. FA longer (39–43 mm). Dorsal hairs tricoloured. Muzzle hairy and reddish-brown. Wings greyish-brown. Notch in posterior margin of ear deep.

M. nattereri. FA longer (37–42 mm). Posterior margin of interfemoral membrane with dense fringe of bristle-like hairs between tip of each calcar and tail. Muzzle reddish-pink.

Distribution In Africa, only known from mountainous parts of the Mediterranean Coastal and Afromontane–Afroalpine BZs, and marginally from the adjacent Sahara Arid BZ, in N Morocco. Recorded from five localities: the Rif Mts, the Middle Atlas and the High Atlas (central northern slope and south-eastern piedmont) (Benda *et al.* 2004d). Extralimittally: widespread from Ireland and Scandinavia, through Iran and the Himalayas to China. Absent from the southern Iberian Peninsula.

Habitat Very little information for Africa. Several specimens were mist-netted over rivers in forests of sparse Cork Oak (*Quercus suber*), Green Oak (*Q. ilex*) or Atlas Cedar (*Cedrus atlantica*), up to 1780 m (Benda *et al.* 2004d). One record is from an oasis on the southern slope of the High Atlas Mts (Aulagnier & Destre 1985), and another is from an arid area (Panouse 1953). In Europe, found most often in forests, gardens, parks and riverine habitats (Schober & Grimmberger 1987). In former USSR, it favours deserts, semi-deserts and the lower and middle mountain zones (Strelkov 1983).

Abundance Apparently very rare in NW Africa (<25 specimens recorded); rare in S Europe but abundance increases further north.

Adaptations Aspect ratio low; wing-loading very low; wing-tip short and rounded (Norberg & Rayner 1987). Flight highly manoeuvrable; open-field flight estimated at ca. 4.4 m/sec (Baagøe 1987), which is comparatively very slow. In Morocco, day-roosts include behind bark of *Tamarix aphylla* in an oasis (Aulagnier & Destre 1985) and in little openings in the structure of a bridge (Ibáñez 1988). In Europe, roosts mainly in buildings in summer, and mainly in caves, mines and cellars in winter. Hangs from ceilings and walls and sometimes wedges itself in cracks and crevices. Hibernates from Oct–Mar in Europe; presumably for a shorter period in Morocco. Occasionally migrates; longest recorded movement 240 km (Schober & Grimmberger 1987).

Foraging and Food Forages by gleaning (from branches or from the ground) and by slow-hawking. In Britain, Jones (1993) has seen this species foraging around tops of fairly tall trees and sometimes flying into the foliage. In Switzerland and England, feeds mainly on Diptera (including Tipulidae, Chironomidae, Anisopodidae, Culicidae), spiders (Arachnida) and moths (Lepidoptera) (Vaughan 1977, Beck 1995).

Echolocation Echolocation calls (Europe) highly variable depending on activity and habitat; these data refer to cruising calls in the main habitat. Search-phase call-shape (close to foliage) steep linear FM. Start-frequency 105 kHz; end-frequency 33 kHz; peak-frequency 62 kHz; call-duration 2.7 ms; inter-call interval 50–80 ms (Jones 1993, Barataud 2005).

Social and Reproductive Behaviour Roosts singly or in groups. Hibernates in colonies, up to 600 individuals in France (Arthur & Lemaire 1999); ratio of ♂♂ : ♀♀ in hibernacula is male-biased. Sexes segregate in May; pregnant ♀♀ establish maternity colonies (10–70 individuals), which they occupy in summer; ♂♂ appear to be solitary in summer (Schober & Grimmberger 1987).

Reproduction and Population Structure Litter-size (Europe): one. In Europe, the reproductive chronology is restricted seasonal monoestry with mating from autumn to spring (sometimes in winter-roosts); births in Jun or early Jul; lactation for ca. six weeks. Juveniles begin foraging within six weeks. Females leave maternity colonies in late Aug (Schober & Grimmberger 1987). Maximum life-span: 23 years.

Predators, Parasites and Diseases Predators occasionally include Pharaoh Eagle-owls *Bubo ascalaphus* (Aulagnier 1989). Ectoparasites (Morocco) include a tick *Argas transgarepinus* (Acari: Argasidae) (Anciaux de Faveaux 1984).

Conservation IUCN Category: Least Concern (based mainly on extralimittal data).

NW African populations, however, are scarce and vulnerable. Pesticides and logging are presumably the main local threats.

Measurements*Myotis mystacinus*

FA: 34.3 (33–37) mm, n = 6

WS: n. d.

TL: 76 mm, n = 1

E: 34 mm, n = 1

E: 14.1 (12–15) mm, n = 8*

Tr: 7, 8 mm, n = 2*

Tib: 16.7 (15.5–17.7) mm, n = 10*

HF: 7 mm, n = 4

WT: n. d.

GLS: 13.5 (13–14) mm, n = 8

GWS: 8.2 (8.0–8.5) mm, n = 8

C–M³: 5.0 (4.7–5.3) mm, n = 8

Morocco (Romero Zarco 1990, pers. comm.)

*United Kingdom (HZM)

Key References Benda *et al.* 2004d; Ibáñez 1988; Panouse 1953; Romero Zarco 1990.

Stéphane Aulagnier

***Myotis nattereri* NATTERER'S MYOTIS (NATTERER'S BAT)**

Fr. Murin de Natterer; Ger. Fransenfledermaus

Myotis nattereri (Kuhl, 1817). Die Deutschen Fledermäuse. Hanau, pp. 14, 33. Hanau, Hessen, Germany.

Taxonomy Originally *Vespertilio nattereri*. Synonyms: five; none in Africa. Subspecies: two; only the nominate occurs in Africa (Koopman 1994). Chromosome number (Spain): $2n = 44$; $aFN = 50$ (Pérez-Suárez *et al.* 1991). Since this profile was submitted, *escalerai* Cabrera, 1904, formerly included in *M. nattereri*, was restored to specific status by Ibáñez *et al.* (2006), and García-Mudarra *et al.* (2009) conclude that a sister species is the only *Myotis* of the *nattereri* group in North Africa.

Description Very small microbat without noseleaf and with tail more or less fully enclosed in interfemoral membrane; six upper and six lower cheekteeth on each side; ears not funnel-shaped; pelage not frizzled; FA: 37–42 mm; dorsal hairs bicoloured; wings uniformly dark greyish-brown, attaching to base of first toe; HF 46–60% of Tib; margin of interfemoral membrane with fringe of bristle-like hairs; tragus just over two-thirds of E. Sexes similar. Pelage dense, silky; mid-dorsal hairs 6–8 mm. Dorsal pelage greyish-brown; hairs bicoloured, basal half blackish-brown, terminal half greyish-brown. Ventral pelage pale grey to off-white; hairs bicoloured, blackish-brown with whitish tip. Muzzle almost naked, reddish-pink; upper lip with long hairs. Ears dark greyish-brown; relatively long for an African *Myotis* (mean E ca. 40% of mean FA); outer margin with slight notch. Tragus long, slender, bluntly pointed; notably more than half of E (cf. ca. half in other North African species), reaching beyond notch in ear. Wings uniformly dark greyish-brown without markings; attaching to base of first toe. Tibia not hairy. Hindfoot of medium relative length (46–60% of Tib, $n = 22$); toes with long hairs. Calcar S-shaped, reaching half of distance to tip of tail. Interfemoral membrane dark greyish-brown; naked; posterior margin with dense fringe of bristle-like hairs (Figure 149b). Terminal vertebra of tail sometimes protruding beyond interfemoral membrane.

Skull small. Braincase high, profile of forehead region (viewed laterally) strongly concave. No sagittal crest. Outer upper incisor with crown area twice that of inner upper incisor (cf. *M. emarginatus*). Middle upper premolar more than half height of anterior premolar and ca. three-quarters of its crown area; within tooththrow.

Geographic Variation None in Africa.

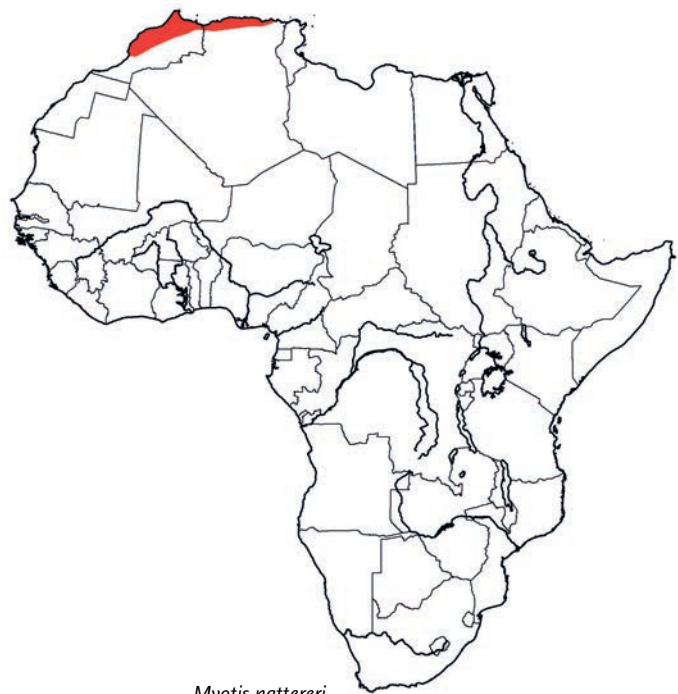
Similar Species Three other *Myotis* with FA <45 mm occur in NW Africa (Table 29, p. 691):

Myotis capaccinii. Dorsal pelage pale brownish-grey. Hindfoot longer (12–15 mm; 70–83% of tibia). Wings attaching to tibia well above heel. Interfemoral membrane covered by downy pelage; margin without fringe of bristle-like hairs. Tragus shorter (5–9 mm), ca. half of E.

M. emarginatus. Dorsal pelage reddish-brown; hairs tricoloured. Posterior margin of interfemoral membrane without dense fringe of bristle-like hairs. Notch in posterior margin of ear deep. Dorsal hairs tricoloured. Tragus shorter (less than half of E).

M. mystacinus. FA shorter (33–37 mm). Posterior margin of interfemoral membrane without dense fringe of bristle-like hairs. Muzzle blackish.

Distribution In Africa, recorded from the Mediterranean Coastal BZ of Morocco and Algeria, extending inland to the Afromontane–Afroalpine BZ (western High Atlas, Middle Atlas and Tell Atlas)

*Myotis nattereri*

(Brosset 1963, Aulagnier & Thévenot 1986, Ibáñez 1988, Kowalski & Rzebik-Kowalska 1991, Benda *et al.* 2004d). Extraliminally: Europe (except northern Scandinavia) through Turkey, Israel and Iraq to Turkmenistan.

Habitat Predominantly an open woodland bat, attracted by open water and marshland (some Algerian specimens were mist-netted over a stream in an oak forest [Gaisler & Kowalski 1986]). Also recorded in Mediterranean maquis and occasionally in towns. Recorded from sea level to 1200 m.

Abundance Based on paucity of records and limited area of suitable habitat, population numbers in NW Africa are probably low. However, one cave in Algeria contained a cluster of ca. 300 individuals (Kowalski *et al.* 1986).

Adaptations Aspect ratio low; wing-loading very low (Norberg & Rayner 1987). Flight predicted to be slow with high manoeuvrability; speed in open estimated to be ca. 4.5 m/sec (Baagøe 1987), which is comparatively very slow. In summer, roosts in hollow trees, behind bark, sometimes in cracks under bridges and cracks in buildings. In winter, hibernates in cool and damp caves, cellars and mines; hangs freely from ceilings or walls, or squeezes into small crevices. In Europe, hibernates in Oct–Apr. Sedentary; longest recorded movement is 90 km.

Foraging and Food Forages by slow-hawking and by gleaning (without landing) from vegetation (Arlettaz 1996b, Siemers & Schnitzler 2000). Emergence peaks one hour after sunset, and the last bats return to the roost half an hour before sunrise. Forages up to 3 km from the roost, in woodlands, near hedges and road-side vegetation, and over sheltered stretches of water. In Israel, feeds mainly on diurnal Diptera (Whitaker *et al.* 1994), but Coleoptera, Opilions, spiders and caterpillars are also important (Shiel *et al.* 1991, Beck 1995, Vaughan 1997).

Echolocation Echolocation calls highly variable depending on activity and habitat; these data refer to cruising calls in the main habitat. Search-phase call-shape (2–3 m from obstacles) steep linear FM. Start frequency 120 kHz; end-frequency 14 kHz; peak-frequency 55 kHz; call-duration 2–4 ms; inter-call interval 70–90 ms (Jones 1993, Siemens & Schnitzler 2000, Barataud 2005).

Social and Reproductive Behaviour Roosts singly or in groups or small colonies. Mating occurs in autumn. In winter, hibernates singly or in small groups; group-members roost in clusters. Sexes

segregate in spring when pregnant ♀♀ establish maternity colonies containing 20–70 individuals, rarely up to 300; summer colonies change their roosts quite often. In Algeria, a colony of ca. 300 individuals, huddled together in a dense cluster on the ceiling of a cave, was found in Apr; a sample contained 14 ♂♂ with small testes and eight ♀♀, each with a small foetus (Kowalski *et al.* 1986).

Reproduction and Population Structure Litter-size (Algeria): one (n = 8) (Kowalski *et al.* 1986). In Europe, the reproductive chronology is restricted seasonal monoestry with mating from autumn to spring; births in summer (Jun–Jul); lactation for six weeks. Juveniles volant and starting to forage at ca. three weeks. Maximum life-span: 20 years.

Predators, Parasites and Diseases Ectoparasites include a flea *Ischnopsylla hispanica* (Siphonaptera: Ischnopsyllidae) (Anciaux de Faveaux 1984).

Conservation IUCN Category: Least Concern (based mainly on extralimital data).

Status should be re-evaluated in NW Africa where populations are threatened by intense logging and pesticides.

Measurements

Myotis nattereri

FA: 39.8 (37–42) mm, n = 24

WS (d): ca. 260 mm, n = 1

TL: 93.0 (88–97) mm, n = 22

T: 43.9 (37–48) mm, n = 24

E: 15.9 (15–18) mm, n = 24

Tr: 11.0, 11.9 mm, n = 2

Tib: 16.4 (14–18) mm, n = 24*

HF: 9.2 (8–10) mm, n = 24

WT: 6 g, n = 1

GLS: 15.4 (14.9–16.0) mm, n = 19

GWS: 9.4 (9.1–9.8) mm, n = 17

C–M³: 5.5 (5.5–5.7) mm, n = 18

Morocco and Algeria (Brosset 1963, Gaisler 1983, Kowalski & Rzebik-Kowalska 1991)

*France (MNHN)

Key References Aulagnier & Thévenot 1986; Benda *et al.* 2004d; Brosset 1963; Gaisler & Kowalski 1986; Kowalski & Rzebik-Kowalska 1991.

Stéphane Aulagnier

Myotis punicus MAGHREB MYOTIS

Fr. Murin du Maghreb; Ger. Maghreb-Mausohr

Myotis punicus Felten, Spitzenberger and Storch, 1977. Senckenberg. Biol. 58: 39. Cap Bon, Tunisia.

Taxonomy Originally *Myotis blythii punicus*. Synonyms: none. *Myotis blythii* and *Myotis myotis* are two closely related, sibling species, which contain several forms of controversial taxonomic status. As these two species are essentially distinguished by size, several

intermediate forms have been alternatively attributed to either species (see reviews in Strelkov 1972, Felten *et al.* 1977, Arlettaz *et al.* 1997b, Topál & Ruedi 2001). The Maghreb Myotis illustrates this problem: it has been considered either as a smaller version of *M.*

myotis (Brosset 1960b, Arlettaz *et al.* 1997b) or as a larger subspecies of *M. blythii* (Bogan *et al.* 1978, Corbet & Hill 1991, Koopman 1994). However, recent molecular work based on microsatellite and mitochondrial DNA has shown that the North African taxon is genetically very distinct from both species, and therefore warrants specific status (Castella *et al.* 2000). These authors suggest that the current distribution of *M. punicus* does not overlap with that of *M. myotis* or *M. blythii*, possibly because of competitive exclusion. Chromosome number: not known.

Description Medium-small microbat without noseleaf and with tail more or less fully enclosed in interfemoral membrane; six upper and six lower cheekteeth on each side; ears not funnel-shaped; pelage not frizzled; FA: 54–62 mm; dorsal pelage bicoloured; wings uniformly brown, attaching to base of first toe; HF ca. 50% of Tib; posterior margin of interfemoral membrane naked. Females, on average, with slightly longer forearms than ♂♂. Pelage woolly, extending dorsally onto base of interfemoral membrane; mid-dorsal hairs 7–9 mm. Dorsal pelage medium to pale brown; hairs bicoloured, basal half dark grey. No distinctive white patch between the ears (cf. extralimital *M. blythii*; Arlettaz *et al.* 1991). Ventral pelage creamy-white; hairs bicoloured, basal half grey, terminal half creamy-white. Juveniles darker and greyer dorsally, white ventrally. Muzzle with naked area brownish-red. Ears brownish-red, relatively long for an African *Myotis* (42.5 [39–46]% of FA, $n = 116$). Tragus straight, narrow, of medium relative length (ca. 50% of E). Wings uniformly brown, attaching to base of first toe. Tibia naked. Hindfoot of medium relative length (50 [47–56]% of Tib). Calcar relatively short (reaching one-third of distance to tip of tail). Postcalcarea lobe vestigial or absent. Interfemoral membrane brownish-red; naked; posterior margin without fringe of bristle-like hairs. Tail almost completely enclosed by membrane.

Skull comparatively large, rostrum robust. Braincase comparatively low; profile of forehead region (viewed laterally) moderately concave. Sagittal crest strongly developed. Middle upper premolar ca. half height and crown area of anterior premolar or less; within toothrow or somewhat displaced lingually, anterior and posterior premolars separated.

Geographic Variation None recorded.

Similar Species None: all other *Myotis* known to occur in North Africa are much smaller (FA: <45 mm) and lighter (<13 g) (Table 29, p. 691).

Distribution In Africa, apparently only found in the Mediterranean Coastal and Afromontane–Afroalpine BZs in NW Africa (Morocco, Algeria and Tunisia) and very marginally from the Sahara Arid BZ in NW Libya. Its African distribution is limited to the south and to the east by the Saharan and Libyan deserts, respectively. Map based on Aulagnier & Th  venot (1986), Castella *et al.* (2000), Han  k & Elgadi (1984), Kowalski & Rzebik-Kowalska (1991) and Qumsiyeh (1983). Extraliminally: the Mediterranean islands of Corsica, Sardinia and Malta. That *M. punicus* is endemic to western North Africa and these adjacent islands is indicated by DNA data (Castella *et al.* 2000, Top  l & Ruedi 2001).



Myotis punicus

Habitat In Africa, widespread from the coastal zones to the high mountains in the Atlas and found from forested to more arid areas. Because of its foraging habits, probably prefers sparsely forested, semi-open and desert-like habitats.

Abundance Widespread and probably abundant throughout the Mediterranean Region of North Africa. The most numerous species of bat in the caves of N Algeria (Kowalski & Rzebik-Kowalska 1991 as *M. blythii*). Maternity colonies of several hundreds to thousands of ♀♀ not uncommon.

Adaptations Wing morphology: no information. Roosts by day in caves and abandoned mines. In the warmer months, often shares roosts with other cave-dwelling bats such as *Rhinolophus* spp. or *Miniopterus schreibersii*, but no mixed-species groups have been found in winter (Kowalski & Rzebik-Kowalska 1991). In winter, moves to more concealed quarters and enters into deep torpor. Extent of seasonal movements between winter and summer-roosts largely unknown.

Foraging and Food Rather adaptable; hunts probably mostly on bare grounds in forests without understorey, and in open, more arid habitats as well. Probably searches for prey by flying close to the ground, drops on it and eats it on the wing (Arlettaz 1996a, as *M. myotis*). In North Africa, its diet consists mainly of crickets, beetles, spiders; it also includes scorpions (Arlettaz *et al.* 1997a).

Social and Reproductive Behaviour Roosts singly, or in groups ranging from two to several thousands. During the mating period (Aug–Nov), ♂♂ establish small, individual territories in the ceilings of the caves to attract ♀♀ for copulation (Hor    ek & Gaisler 1985–86, as *M. blythii*). Each ♂ then maintains a small harem of 1–4 ♀♀. Several pairs were seen hanging together, the ♂ touching the ♀ with the ventral surface of his body (Kowalski & Rzebik-Kowalska 1991).

1991). In Nov, a colony of ca. 50 was observed, but none of the caves or mines under observation served as winter hibernacula; only a few individuals, roosting singly or in clusters of up to five individuals, were found during this time (Kowalski & Rzebik-Kowalska 1991). In summer, pregnant ♀♀ establish maternity colonies in the warmer caves and mines; these often contain hundreds or thousands of adult ♀♀. Nulliparous ♀♀ and a few ♂♂ also roost with these colonies; the adult ♂♂ usually roost away from the maternity colonies.

Reproduction and Population Structure Litter-size (Algeria): one (n = 5) (Kowalski *et al.* 1986, as *M. blythi*). In N Algeria, the reproductive chronology is restricted seasonal monoestry with spermatogenesis beginning in early Mar in mature ♂♂ and in Jun in ♂♂ breeding for the first time; mating from Aug to early Nov; births from mid-Apr to mid-May or sometimes early Jun (Kowalski *et al.* 1986). One banded ♀ mated in the year of her birth (Kowalski & Rzebik-Kowalska 1991).

Predators, Parasites and Diseases Predators include owls (Pharaoh Eagle-owl *Bubo ascalaphus*, Barn Owl *Tyto alba*, Tawny Owl *Strix aluco* and occasionally Little Owl *Athene noctua* [Aulagnier 1989]), small carnivores (e.g. *Martes foina*, *Genetta genetta*, *Felis libyca*) and a snake *Coluber hippocrepis* (Hammer & Arlettaz 1998). Ectoparasites include bat-flies (Diptera; Nycteriibidae) and mites *Spinturnix* sp. (Acari: Spinturnicidae). No known diseases have been reported for these bats.

Conservation IUCN Category: Near Threatened (based on African and extralimital data).

Although widespread and apparently abundant in North Africa, the area of occupancy is fairly restricted, and maternity colonies are very vulnerable to disturbance by humans. Throughout North Africa, dried bats are used in traditional medicine, and this species is sometimes heavily hunted to provision local markets. Almost meets criteria for Vulnerable.

Measurements

Myotis punicus

FA (♂♂): 58.6 (54–62) mm, n = 80
 FA (♀♀): 59.7 (53–65) mm, n = 118
 TL: 122.1 (107–139) mm, n = 63
 T: 54.6 (47–62) mm, n = 73*
 E: 25.2 (22–27), n = 73*
 Tr: 9.5 (8.4–10.2) mm, n = 12
 Tib: 25.9 (25–27) mm, n = 11
 HF: 13.2 (11–15) mm, n = 73*
 WT (♂♂): 21.9 (18–27) g, n = 19*
 WT (♀♀): 24.5 (18–33) g, n = 12*
 GLS: 22.3 (21.3–23.4) mm, n = 190
 GWS: 14.4 (12.8–15.0) mm, n = 172
 C–M³: 9.3 (8.2–9.7) mm, n = 194
 Tunisia, Algeria, Morocco (MHNG, Felten *et al.* 1977, Kowalski & Rzebik-Kowalska 1991)
 *Morocco only

Key References Felten *et al.* 1977; Horáček & Gaisler 1985–86; Kowalski & Rzebik-Kowalska 1991.

M. Ruedi & R. Arlettaz

Myotis scotti SCOTT'S MYOTIS

Fr. Murin de Scott; Ger. Scotts Mausohr

Myotis scotti Thomas, 1927. Ann. Mag. Nat. Hist., ser. 9, 19: 554. Djem-Djem Forest, 40 miles west of Addis Ababa, Ethiopia, 8000 ft (2438 m).

Taxonomy Synonyms: none. Chromosome number: not known.

Description Very small microbat without noseleaf and with tail more or less fully enclosed in interfemoral membrane; six upper and six lower cheekteeth on each side; ears separated, not funnel-shaped; pelage not frizzled; FA: 37–41 mm; dorsal pelage coppery-brown; face with conspicuous dark 'mask'; wings uniformly dark brown; HF 43 (39–47)% of Tib; posterior margin of interfemoral membrane with bristle-like hairs. Not easily distinguished from *M. bocagii*. Sexes similar. Pelage dense, slightly woolly with silky sheen; mid-dorsal hairs ca. 7 mm. Dorsal pelage shiny coppery-brown; hairs bicoloured, dark brown with terminal third coppery-brown. Ventral pelage beige to off-white; hairs bicoloured, dark brown with whitish tip. Face and naked skin of muzzle are dark brown, creating a dark 'mask'. Ears dark brown; of medium relative length for an African *Myotis* (ca. 37% of FA; n = 3); outer margin without notch. Tragus straight, relatively short, 34% of E (n = 1). Wings uniformly dark brown without markings; attaching to base of first toe. Tibia hairy dorsally and ventrally. Hindfoot relatively short (43 [39–47]% of Tib, n = 3); toes with long hairs. Calcar reaching half distance to tip

of tail. Interfemoral membrane dark brown; posterior margin with numerous bristle-like hairs between ends of calcars and tip of tail. Tail fully enclosed by interfemoral membrane, or slightly projecting.

Skull small and delicate. Braincase comparatively high, profile of forehead region (viewed laterally) strongly concave. No sagittal crest. Upper canines very short, ca. 1.2 mm from cingulum to tip (cf. *M. bocagii*). Middle upper premolar ca. half height of anterior premolar or less, and ca. two-thirds of its crown area; within toothrow.

Similar Species Three other sub-Saharan *Myotis* have uniformly coloured wings (Table 29, p. 691):

Myotis bocagii. Dorsal pelage tricoloured in area of sympatry. Posterior margin of interfemoral membrane naked. HF 53 (47–60)% of Tib. Braincase comparatively low; profile of forehead region moderately to strongly concave. Upper canines longer (1.5–1.8 mm). Middle upper premolar larger (ca. half to three-quarters height of anterior premolar); usually displaced lingually. *M. dieteri*. Dorsal hairs dark brown with auburn tip. No mask. HF 65% of Tib. Skull with profile of forehead region weakly concave.

M. tricolor (sometimes). Larger (FA: 47–53 mm). Wings sometimes with faint black and dark reddish-brown pattern.

Distribution Endemic to Africa. Apparently confined to the Afromontane–Afroalpine BZ of the Ethiopian Highlands; occurs both sides of the Rift Valley. Recorded from only seven sites in SC Ethiopia (Largen *et al.* 1974, Yalden & Largen 1992).

Habitat Found in moist forested locations, in a range of altitudes from 1300–2500 m.

Abundance Rare, only 11 specimens known. Collecting in Ethiopia, 1968–75, yielded only one in a sample of 305 bats.

Remarks Canines short compared with other African *Myotis*. The type series of six roosted colonially in furled leaves of banana plants (Thomas 1927a). Based on morphology, predicted to forage by slow-hawking at low to medium heights above ground, and to feed on small insects. Two specimens were captured with a hand-held flick-net, while they were foraging at 1–3 m above ground, over low bushes near water.

Conservation IUCN Category: Vulnerable.

Known from only seven locations in a very restricted area of occupancy. As a forest species, it must be threatened by continuing human population increase and consequent deforestation, but no specific information is available.

Measurements

Myotis scotti

FA: 38.9 (37–41) mm, n = 9

WS: n. d.

TL: 82, 90 mm, n = 2

T: 41 (40–44) mm, n = 3

E: 14.5 (14–15) mm, n = 3



Myotis scotti

Tr: n. d.

Tib: 17.4 (16–19) mm, n = 3

HF: 7.2 (7–8) mm, n = 4

WT: 4.6 g, n = 1

GLS: 13.8 (13.7–14.1) mm, n = 4

GWS: 8.4, 9.0 mm, n = 2

C–M³: 5.3 (5.2–5.4) mm, n = 4

Ethiopia (BMNH, D. W. Yalden unpubl.)

Key References Thomas 1927a; Yalden & Largen 1992.

D. W. Yalden

Myotis tricolor TEMMINCK'S MYOTIS (TEMMINCK'S HAIRY BAT)

Fr. Murin tricolore; Ger. Dreifarb-Mausohr

Myotis tricolor (Temminck, 1832). In: Smuts, Enumer. Mamm. Capensium, p. 106. Cape Town, Cape Province, South Africa.

Taxonomy Originally *Vespertilio tricolor*. Synonyms: *loveni*. Subspecies: none. Chromosome number (Zimbabwe, South Africa): 2n = 44; aFN = 50 (Rautenbach *et al.* 1993).

Description Small microbat without noseleaf and with tail more or less fully enclosed in interfemoral membrane; six upper and six lower cheekteeth on each side; ears not funnel-shaped; pelage not frizzled; medium-sized for an African *Myotis* (FA: 47–53 mm); dorsal pelage coppery-brown to rufous; wings blackish-brown, sometimes with inconspicuous reddish-brown markings (i.e. sometimes particoloured); ventral hairs tricoloured. Sexes similar. Pelage dense, fairly woolly; mid-dorsal hairs 7–8 mm. Dorsal pelage coppery-brown to rusty-brown; hairs tricoloured, cream with grey to dark blackish-brown at base and coppery-brown to rufous (rusty-brown) at tip. Ventral pelage paler; hairs tricoloured, creamy-fawn with dark blackish-

brown at base and pale brown at tip. Muzzle brown, almost naked. Ears brown; of medium relative length for an African *Myotis* (34.9 [32–48%] of FA, n = 20); tip rounded; outer margin with slight emargination mid-way. Tragus length on average 56% of ear length. Wings of living Malawian individuals are dark blackish-brown with reddish-brown over the finger-bones and adjacent to body (Figure 149h): these markings are faint (cf. the striking black and orange markings of *M. welwitschii*). Elsewhere, the wings are reported to be dark blackish-brown with no mention of markings. Wings naked; attaching to base of first toe. Tibia naked ventrally, some hairs dorsally. Hindfoot of medium relative length (51.6 [47–58%] of Tib). Calcar straight, extending half-way to tip of tail. Interfemoral membrane reddish-brown; naked; posterior margin without fringe of bristle-like hairs. Tail fully enclosed by membrane.

Skull comparatively large and robust. Braincase high, profile of forehead region (viewed laterally) strongly concave. Sagittal crest

weakly developed or absent. Middle upper premolar reduced (reaching only slightly above cingulum of anterior premolar and much less than half crown area of anterior premolar), partly to fully displaced lingually, anterior and posterior premolars separated or in contact.

Geographic Variation None recorded.

Similar Species Only two other *Myotis* in Africa have wings with a pattern in contrasting colour (Table 29, p. 691):

Myotis welwitschii. Almost always larger (FA: 52–60 mm). Wing colours black and orange; pattern very conspicuous. Ventral hairs bicoloured.
M. morrisi. Wing colours black and yellow; pattern moderately conspicuous. Ventral hairs unicoloured.

Note: individuals of *M. tricolor* that have unpatterned wings are distinguished from other sub-Saharan species with unpatterned wings by their larger size (FA: 47–52 mm cf. <42 mm in *M. bocagii*, *M. dieteri* and *M. scotti*).

Distribution Endemic to Africa. Recorded, very disjunctly, mainly from the Afromontane–Afroalpine, Somalia–Masai Bushland, Zambezan Woodland, Highveld and South-West Cape BZs and from some parts of the Coastal Forest Mosaic BZ, from Ethiopia to South Africa, with isolated records from the Rainforest BZ (Western Region) in Liberia, and from the Southern Rainforest–Savanna Mosaic in SW DR Congo. The specimen from Bomi Wood Concession, Liberia, agrees well with *M. tricolor* from the eastern side of Africa (Koopman 1989), but its isolation invites investigation. However, there are similarly isolated records of *M. welwitschii* in West Africa.

Habitat Very varied. Ethiopia: montane habitats from 1590–2600 m (Largen *et al.* 1974). Kenya: rainforests, montane forests and

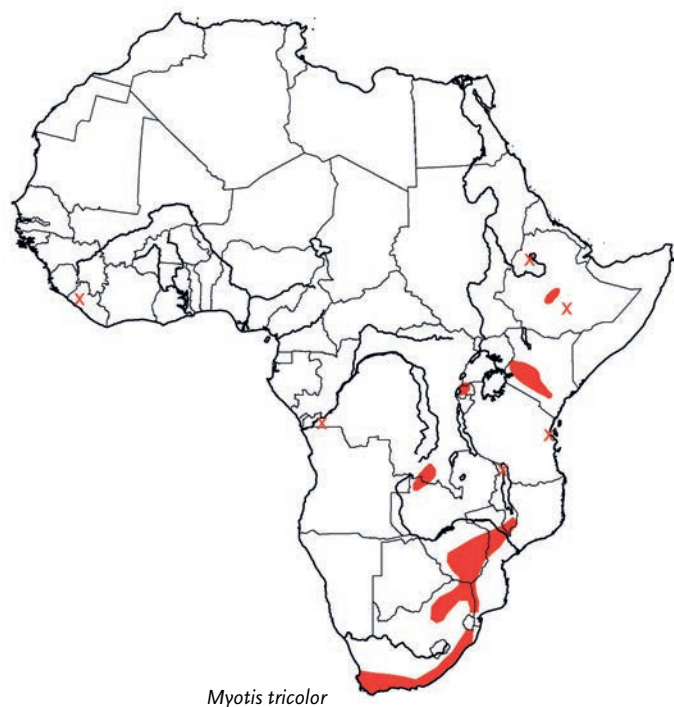
also much drier *Acacia–Commiphora* bushland and thicket. Tanzania: coastal forests (Cockle *et al.* 1998). Zambia: miombo woodland (Ansell 1978). Malawi: montane forest near large dam at 1450 m, miombo woodland at 480–500 m, and an ornamental garden with large trees and remnant riverine woodland near Shire and Ruvo rivers at 100 m (Harrison 1982, Happold & Happold 1997). South Africa: mainly woodland savanna habitats, but also drier grassland savannas, and montane habitats in the Drakensberg (Smithers 1983, Watson 1990b, Lynch 1994, Taylor 2000). All South African records are from regions with >500 mm annual rainfall (Rautenbach 1982) and the distribution is probably limited by rainfall and occurrence of suitably humid caves and mines (Smithers 1983, Bernard pers. obs.).

Abundance Uncertain. Appears to be uncommon or rare throughout geographic range (Koopman 1966, Happold & Happold 1997), except for South Africa where recorded from many localities in eastern parts, and in colonies of up to 2000 (Taylor, P. 1998, 2000).

Adaptations Aspect ratio low; wing-loading low (M. Happold pers. comm.). Flight very manoeuvrable; turns by banking (minimum radius of turn <25 cm) and by stalling-and-twisting; can take off from ground; not known to hover. Individuals in a 1×1×1 m enclosure were unable to complete more than two complete circuits/flight (3 bats, 10 flights each; M. Happold pers. comm.). Can scuttle over flat surfaces and climb well, moving wings and hindlimbs in alternation, sometimes with diagonal limb co-ordination. In South Africa, roosts by day in moist caves, mine-shafts and mine-adits; hangs freely from ceilings or clings in contact with walls. Often found in larger caves, usually ones containing pools of water, where disturbance is minimal (Roberts 1951, Herselman & Norton 1985). In parts of South Africa, migrates hundreds of kilometres between summer maternity caves and winter hibernation caves because different microclimatic conditions are required for these purposes (Herselman 1978 in McDonald *et al.* 1990b). In one maternity cave, the roost-site temperature was 21 °C and the relative humidity 85%. Often shares roosts with *Rhinolophus capensis* and *Miniopterus natalensis* (Smithers 1983, as *M. schreibersii*). Does not become torpid during day at 21–24 °C (Happold & Happold 1988) but, in South Africa, hibernates during winter (Laycock 1976, Bernard unpubl.). Predicted mean maximum urine concentration is medium (3686 mOsmol/kg), but captive bats drank regularly each day and are unlikely to be independent of drinking water in the wild except for some periods during the hibernation season (Happold & Happold 1988).

Foraging and Food Very little is known. Has been mist-netted in open spaces close to trees, and probably forages in such places for volant insects. Morphological features predict foraging by gleaning as well as slow-hawking (Fenton & Bogdanowicz 2002). Although sometimes found near open water with *M. bocagii* (M. Happold pers. obs.), and also mist-netted close to surface of running water (Seamark 2005), it possibly comes to water to drink and there is as yet no evidence, from morphology or field observations, that *M. tricolor* trawls for prey or forages over water (cf. *M. bocagii* and *M. capaccinii*). Diet insectivorous: details not known.

Echolocation In South Africa, Taylor (2000) recorded steep angular FM calls beginning around 86 kHz and falling to ca. 33 kHz;



call-duration 3 ms. In Malawi, one individual emitted steep linear FM calls as it was released (Figure 118r); start-frequency 56–101 kHz; end-frequency 43–49 kHz; mean peak-frequency 49 kHz; maximum call-duration 2.25 ms (19 calls; M. Happold pers. comm.). The significance of these differences needs investigating: probably they only reflect differences in the activities and environments of the bats at the time.

Social and Reproductive Behaviour In South Africa, apparently usually roosts huddled together in groups of a few dozen, but has also been observed in colonies of up to 1400 individuals in KwaZulu–Natal midlands (Laycock 1976) and 2000 individuals in Western Cape in summer (Taylor 2000). During winter, groups and colonies include both sexes. In summer, the sexes segregate and ♀♀ roost together, sometimes in very large numbers, in maternity caves while giving birth and lactating (Laycock 1976, Bernard 1982b). The roosting behaviour of ♂♂ during summer is not known: they are rarely seen but one record suggests that they possibly roost singly at this time (Taylor, P. 1998). In KwaZulu–Natal, ♀♀ and volant young leave the maternity colonies in late Jan. Most migrate to winter hibernacula where ♂♂ and ♀♀ reunite and mate prior to hibernating. At this time, most maternity caves are deserted but some are also used as hibernacula.

Reproduction and Population Structure Litter-size: one ($n = 19$). At ca. 29°S (KwaZulu–Natal, South Africa), the reproductive chronology is restricted seasonal monoestry with copulation in autumn (Apr); sperm storage by the ♀ through winter; ovulation and fertilization in Aug–Sep; parturition in Nov–Dec after gestation of ca. 63 days, and lactation for ca. six weeks (Bernard 1982b). Most ♀♀ become sexually mature when 4–5 months old, the remainder a year later (Wingate 1986).

Predators, Parasite and Diseases Predators include Spotted Eagle-owls *Bubo africanus* in Ethiopia (Demeter 1982). Ectoparasites include fleas *Rhinolophopsylla capensis*, *R. ectopa* (Siphonaptera: Ischnopsyllidae); bat-flies *Nycteribia capensis*, *N. latiterna*, *Penicillidia fulvida* (Diptera: Nycteribiidae), *Raymondia hardyi* (Diptera: Streblidae); ticks *Eschatocephalus vespertilionis*, *Ixodes simplex* (Acari: Ixodidae); and seven species of mites (Acari: Spinturnicidae, Macronyssidae, Myobiidae, Trombiculidae, Chirodiscidae) (Anciaux de Faveaux 1984).

Conservation IUCN Category: Least Concern.

In South Africa, winter hibernation caves and summer maternity caves are limited in availability, and human disturbance of bats in these caves could have a severe impact on populations.

Measurements

Myotis tricolor

FA: 50 (47–53) mm, $n = 67$

WS (a): 336 (329–342) mm, $n = 4$

TL: 105 (96–120) mm, $n = 22$

T: 47 (35–56) mm, $n = 57$

E: 17 (13–19) mm, $n = 55$

Tr: 10 (9–11) mm, $n = 9$

Tib: 22.0 (20–24) mm, $n = 24$

HF: 11.7 (10–13) mm, $n = 24$

WT: 12.0 (8–16) g, $n = 25$

GLS: 18.3 (16.9–19.1) mm, $n = 26$

GWS: 11.8 (11.0–12.3) mm, $n = 22$

C–M³: 7.2 (6.6–8.2) mm, $n = 26$

Throughout geographic range (AM, BMNH, HC, HZM and literature)

Key References Bernard 1982b; Smithers 1983; Taylor, P. 1998, 2000.

Ric T. F. Bernard

Myotis welwitschii WELWITSCH'S MYOTIS

Fr. Murin de Welwitsch; Ger. Welwitschs Mausohr

Myotis welwitschii (Gray, 1866). Proc. Zool. Soc. Lond. 1866: 211. NE Angola.

Taxonomy Originally *Scotophilus welwitschii*. Synonyms: *venustus*. Subspecies: none. Molecular evidence suggests *M. welwitschii* is closely related to *M. emarginatus* (Ruedi & Mayer 2001). Subsequently, *M. welwitschii* and the Oriental species, *M. formosus*, were found to be sister taxa by Bickham *et al.* (2004) and Stadelmann *et al.* (2004). Chromosome number (South Africa): $2n = 44$; aFN = 50 (Rautenbach *et al.* 1993).

Description Medium-small, very spectacular microbat without noseleaf and with tail more or less fully enclosed in interfemoral membrane; six upper and six lower cheekteeth on each side; ears not funnel-shaped; pelage not frizzled; FA: 52–60 mm; wings and interfemoral membrane with conspicuous pattern of black and orange; ventral hairs bicoloured. Sexes similar. Pelage dense, woolly, without sheen; mid-dorsal hairs 7–8 mm. Dorsal pelage orange; hairs tricoloured, cream with blackish-brown base and orange tip. Ventral

pelage cream slightly suffused with orange; hairs bicoloured, blackish-brown with cream tip. Muzzle naked, orange with black spots. Ears orange with small black spots and black edges; of medium relative length for an African *Myotis* (19–25 mm, 37.8 [32–48]% of FA, $n = 20$); outer margin with no notch. Tragus long, bluntly pointed, ca. half of E. Wings strikingly particoloured – outer arm-wing and hand-wing black with the bones outlined in orange; inner arm-wing orange with small black spots (Figure 149f). Wing-membranes naked; attaching to base of first toe. Tibia naked. Hindfoot relatively short (47.4 [37–56]% of Tib, $n = 14$). Calcar moderately robust, extending at least half-way to tip of tail. Postcalcereal lobe poorly developed or absent. Interfemoral membrane orange with small black spots; ventral surface with sparse backward-pointing hairs; posterior margin with sparse fringe of straight, bristle-like hairs between tips of calcars and tip of tail. Tail fully enclosed by interfemoral membrane or with part of last vertebra projecting beyond membrane.

Skull comparatively large and robust. Braincase comparatively low, profile of forehead region (viewed laterally) moderately concave. Sagittal crest low anteriorly, absent posteriorly. Middle upper premolar reduced (reaching only slightly above cingulum of anterior premolar or lower, and much less than half crown area of anterior premolar); partly to fully displaced lingually, anterior and posterior premolars separated or in contact. Anterior and middle lower incisors with three conspicuous cusps and a fourth, which is low and inconspicuous.

Geographic Variation No subspecies are currently recognized (Kock 1967, Simmons 2005).

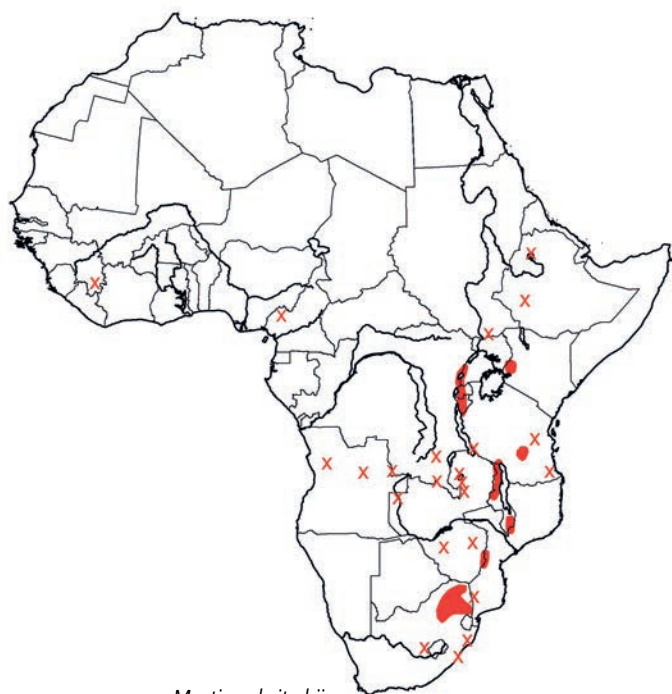
Similar Species Only two other *Myotis* in Africa have wings with a pattern in contrasting colour (Table 29, p. 691):

Myotis tricolor (sometimes). Almost always smaller (FA: 47–53 mm).

Wing colours, if pattern is present, black and dark reddish-brown; pattern inconspicuous. Ventral hairs tricoloured.

M. morrisi. Smaller (FA: 45, 47 mm). Wing colours black and pale yellow or pale orange; pattern moderately conspicuous. Ventral hairs unicoloured.

Distribution Endemic to Africa. Until recently, known only from the Sudan Savanna, Zambezi Woodland, Coastal Forest Mosaic, Highveld and Afromontane–Afroalpine BZs and the Eastern Rainforest–Savanna Mosaic in the eastern half of Africa south of the Sahara, from Ethiopia to E Angola and KwaZulu–Natal, South Africa. Now also known from three specimens from Simandou Range, Guinea (Fahr & Ebigo 2003) and from the Bamenda Highlands, Cameroon (06°05'27 N, 10°18'09 E) (Sedláček *et al.* 2006). This last record bridges the gap of 4400 km between the Simandou Range and the nearest known localities east of the rainforest, mentioned by Fahr & Ebigo (2003), and suggests that the remaining gaps in paramontane savanna areas probably reflect insufficient sampling.



Myotis welwitschii

Habitat Recorded from montane grassland near forest in Guinea, afromontane vegetation (2200 m) in Ethiopia, montane forests (2000–2100 m) in Uganda and Burundi (Stanley *et al.* 1996b), montane forests in Kenya, Tanzania, NE Zambia and N Malawi, wetter and drier miombo woodland and riverine woodland at 1000 m, 500 m and 100 m in Malawi (Happold *et al.* 1987, Happold & Happold 1997), woodland savannas elsewhere in south-central and southern Africa, and coastal forest surrounded by Thornveld in KwaZulu–Natal (Taylor, P. 1998). Koopman (1986) suggested that these bats remain close to mountains although not confined to high altitudes: many subsequent records support this (Fahr & Ebigo 2003) but not all (e.g. Chiromo in the Lower Shire Valley, Malawi).

Abundance Rarely encountered and considered rare throughout its geographic range.

Adaptations Aspect ratio low; wing-loading very low. Flight fast or slow with great manoeuvrability; can take off from ground; cannot hover. Turns usually by banking (minimum radius <25 cm), occasionally by stalling-and-twisting; individuals sustained flight within a 1×1×1 m enclosure for up to five circuits/flight (2 bats, 10 flights each; M. Happold unpubl.). Cursorial locomotion slow and awkward. By day, individuals hang in bushes and trees (Smithers & Wilson 1979, Pienaar *et al.* 1980, Rautenbach 1982) and are well camouflaged by their resemblance to dead leaves. One was found in a furred leaf of a banana plant at Livingstonia, Malawi (Ansell & Dowsett 1988) but no further records of banana leaves as day-roosts were obtained despite almost two years of intensive routine searching in Malawi – including in areas where *M. welwitschii* occurs – associated with studies of the leaf-roosting Banana Pipistrelle *Pipistrellus nanus* (Happold & Happold 1990b, 1996, Bernard *et al.* 1997). In Zimbabwe, some specimens were ‘taken in houses’ (Smithers & Wilson 1979) but Smithers (1983) reports that *M. welwitschii* enters houses at night while foraging, so it seems probable that the captured bats were not roosting in the houses. Stuart & Stuart (1988) state that *M. welwitschii* roosts in hollow trees, but the source of this information is not given and it needs confirmation. Not known to roost in deep caves (*contra* Ratcliffe 2002).

Foraging and Food There is no evidence that these bats forage by trawling over open water (cf. *M. bocagii*), but they have been recorded flying low over streams and a farm dam (e.g. Ansell & Ansell 1973, M. Happold unpubl.) as well as near the ground well away from water. They sometimes fly into houses while foraging. Diet in wild not known: observations in captivity suggest preference for soft-shelled insects, but faecal pellets from one individual contained remains of small beetles (M. Happold unpubl.).

Echolocation Search-phase calls of one individual (tethered) were steep linear FM sweeps; bandwidth 30–90 kHz; end-frequency 9–33 kHz; peak-frequency 35–55 kHz (usually 41–43 kHz. (Figure 118s; M. Happold unpubl.).

Social and Reproductive Behaviour As yet, only found roosting singly (Smithers & Wilson 1979, Pienaar *et al.* 1980), but data are limited.

Reproduction and Population Structure No information.

Predators, Parasites and Diseases No information.

Conservation IUCN Category: Least Concern.
Widespread.

Measurements

Myotis welwitschii

FA: 55.8 (52–60) mm, n = 31

WS (a): 380, 383 mm, n = 2

TL: 120.3 (112–132) mm, n = 25

T: 59.0 (55–65) mm, n = 16

E: 21.1 (19–25) mm, n = 22

Tr: 10.9 (10–11.5) mm, n = 4

Tib: 24.4 (22–29) mm, n = 15

HF: 11.4 (9.5–13) mm, n = 14

WT: 15.0 (14–19) g, n = 15

GLS: 19.4 (18.6–20.8) mm, n = 15

GWS: 13.2 (12.5–13.5) mm, n = 11

C–M³: 7.6 (7–7.9) mm, n = 16

Throughout geographic range (BMNH, HC, NMW, RMCA, SMF, SMNS and literature)

Key Reference Fahr & Ebigo 2003; Ratcliffe 2002.

Meredith Happold

Subfamily MINIOPTERINAE – Long-fingered Bats

Miniopterinae Dobson, 1875. Ann. Mag. Nat. Hist., ser. 4, 16: 349

Diagnostic combination of characters: second phalanx of third finger ca. three times longer than the first; ears not funnel-shaped, tragus short and blunt; braincase high and rounded; five upper cheekteeth; no baculum. The third finger has a characteristically bent appearance because the first phalanx is angled anteriorly towards the line of the second finger (Figure 117c), and *Miniopterus* are sometimes called ‘bent-winged’ bats. Pelage thick, short and velvety. Dental formula

$2^{123}/_{3133} = 36$. Some other external characters and craniodental characters of African *Miniopterus* are shown in Figure 152.

This subfamily contains only one genus, *Miniopterus*. Based on the presence of a vestigial anterior upper premolar in *Miniopterus schreibersii*, the absence of a baculum and the relative elongation of the second phalanx of the third finger, Mein & Tupinier (1977) proposed that this subfamily should be raised to family status. This is supported

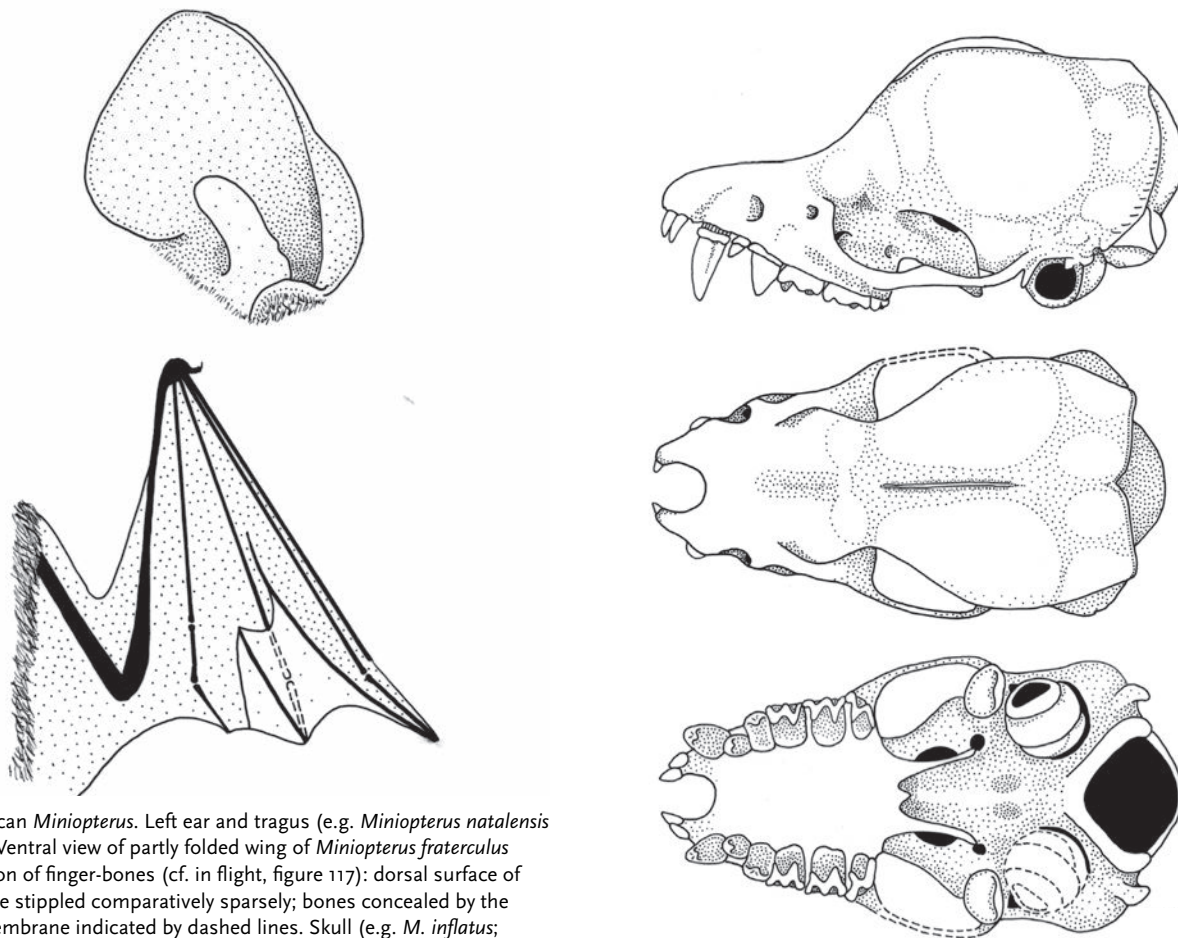


Figure 152. African *Miniopterus*. Left ear and tragus (e.g. *Miniopterus natalensis* from Malawi). Ventral view of partly folded wing of *Miniopterus fraterculus* showing position of finger-bones (cf. in flight, figure 117): dorsal surface of wing-membrane stippled comparatively sparsely; bones concealed by the folded wing-membrane indicated by dashed lines. Skull (e.g. *M. inflatus*; holotype, BMNH 3.2.4.8).

by the molecular evidence of Hofer & Van Den Bussche (2003), who indicate that this taxon represents an extremely divergent lineage relative to other vespertilionids and, in some analyses, is sister to the Molossidae and the New World family Natalidae. Pending further evidence, subfamilial status is retained here, following Simmons

(2005). However, since this profile was submitted, familial status has been confirmed by Miller-Butterworth *et al.* (2007).

Meredith Happold

GENUS *Miniopterus* Long-fingered Bats

Miniopterus Bonaparte, 1837. Fauna Ital. 1, fasc. 20. Type species: *Vespertilio ursinii* Bonaparte, 1837 [= *Vespertilio schreibersii* Kuhl, 1817].



Miniopterus schreibersii.

A polytypic genus with 19 species recognized by Simmons (2005), of which six occur in Africa, three in Madagascar (with one of these also in Comores), and the remainder collectively ranging from S Eurasia to Japan and through the Indo-Australian archipelago to New Caledonia, Vanuatu (New Hebrides) and Australia. One of the six African species recognized by Simmons (2005) is considered here to be a subspecies but its specific status has now been confirmed (see profile of *M. inflatus*). Also, since these profiles were submitted, based on levels of genetic variation, Juste *et al.* (2007) showed that a distinct, as yet undescribed species occurs in Zambia (FA: 44–45 mm, n = 2): not profiled or mapped. For diagnostic characters of *Miniopterus*, see subfamily Miniopterinae.

Members of this genus are cave-roosting bats, which are well adapted for cursorial locomotion: they can scuttle and climb with greater competence and speed than other African vespertilionids. Like emballonurids and molossids, which are very competent scuttlers and climbers, *Miniopterus* can 'furl' their wing-membranes. They do this by folding the very long second phalanx of the third finger, and the long second phalanx of the fourth finger, ventrally against the short first phalanges and metacarpals (Figure 152), and this enables the legs to move fairly freely. These bats have medium to very high aspect ratios and low to medium wing-loadings, and can fly slowly or rapidly with great manoeuvrability, and can therefore forage in both open and moderately cluttered places. At least some species are migratory, and

some hibernate. They roost mostly in small to very large groups, but little is known about their social behaviour and mating systems, except for *M. minor*, which appears to have a mating system based on lekking. All African species for which data are available are monogamous and seasonally monoestrous. Delayed implantation is exemplified by the species in temperate habitats, and intra-specific geographical differences in the timing of reproductive events have been documented for *M. natalensis*. *Miniopterus natalensis* is also capable of facultative retarded embryonic development. The reproductive biology of *M. minor* is particularly interesting because ♀♀ have a 'silent heat', which might trigger the lekking behaviour of the ♂♂.

All members of this genus show a remarkable degree of morphological uniformity, and this has made classification of the different forms difficult and controversial (e.g. Harrison 1953, Corbet & Hill 1992, Peterson *et al.* 1995). Juste & Ibáñez (1992) and Koopman (1993, 1994) recognize four species in Africa (*fraterculus*, *inflatus*, *minor* and *schreibersii*). Simmons (2005), following Peterson *et al.* (1995), recognizes *africanus* as distinct from *inflatus*, and *natalensis* as distinct from *schreibersii*. Here, *africanus* is treated as a subspecies of *M. inflatus* because, when these profiles were written, pelage colouration appeared to be the main difference between these forms and this might have reflected nothing more than a darkening of pelage associated with more humid habitats. The value of colour as a diagnostic character is also potentially unreliable because older pelage of one colour might be replaced by blacker pelage after moulting (as it is in *M. minor*). The separation of *M. natalensis* from *M. schreibersii* is supported by multivariate statistics (Peterson *et al.* 1995) and by differences in the DNA of *M. natalensis* from South Africa and that of *M. schreibersii* from Europe (Miller-Butterworth *et al.* 2005), and these taxa are treated as distinct here. Therefore, tentatively, five species are recognized here, but there is clearly a need for further investigation.

The relationship of several other forms to these five species is also very controversial. Of particular interest are the forms *vicinior*, *dasythrix*, *smitianus* and *villiersi*. Simmons (2005) considers *vicinior* to be a synonym of *M. natalensis*, but the discriminant function of Stoffberg *et al.* (2004), which distinguishes *M. natalensis* from *M. fraterculus* in southern Africa, also distinguishes *vicinior* from *M. natalensis* (M. Happold pers. obs.), suggesting *vicinior* is more likely to be a synonym of *M. fraterculus* (but this needs confirmation). The form *villiersi* (distributed from Guinea to DR Congo) is usually considered a synonym of *M. schreibersii* although it is isolated by the vast Sahara from populations of *M. s. schreibersii* in North Africa and Europe. In contrast, the forms *dasythrix* from Malawi to South Africa (Koopman 1994) and *smitianus* from Ethiopia to Namibia (Koopman 1994) have been placed in both *M. schreibersii* and *M. natalensis*. Peterson *et al.*

Table 30. Measurements of African species in the genus *Miniopterus*.

| Species | FA
mean \pm 1 S.D.
(range)
(mm) | GLS
mean (range)
(mm) | WT
mean (range)
(g) | HF
mean (range)
(mm) | Total length
mean \pm 1 S.D.
(range)
(mm) |
|---|--|--------------------------------|---------------------------|----------------------------|--|
| <i>M. inflatus</i> and
<i>M. africanus</i> | 48.3 \pm 1.3
(45–52) | 16.9
(16.4–17.8) | 13
(8–19) | 10
(7–11) | 111 \pm 7.6
(92–128) |
| <i>M. schreibersii</i> | 45.9 \pm 1.75
(44–49) | 15.8
(14.9–16.5) | 11.1
(9–16) | 9.9
(8–12) | 114.3 \pm 10
(104–124) |
| <i>M. natalensis</i> | 44.8 \pm 0.9
(43–46) | 14.3 \pm 0.31
(13.6–14.9) | 9.9
(7–12) | 9.5
(6–11) | 108.0 \pm 2.5
(104–115) |
| <i>M. fraterculus</i> | 43.3 \pm 1.1
(41–45) | 14.4 \pm 0.48
(13.3–15.5) | 7.9
(6–10) | 8.9
(7–11) | 97.6 \pm 3.5
(88–103) |
| <i>M. minor</i> | 39.8 \pm 1.0
(37–42) | 13.6
(11.1–14.5) | 6
(3–9) | 7.7
(5–10) | 91.3 \pm 3.0
(82–97) |

(1995) and Simmons (2005) place both forms in *M. schreibersii*, and this treatment is tentatively followed here. This, however, implies that three very similar species, *M. schreibersii*, *M. fraterculus* and *M. natalensis*, occur sympatrically in South Africa and this seems unlikely for ecological reasons. Furthermore, 305 *Miniopterus* from 13 colonies in South Africa, which were identified by DNA sequencing, contained only *M. fraterculus* and *M. natalensis*, both of which differ genetically from *M. schreibersii* from Europe (Miller-Butterworth *et al.* 2005). Unfortunately, it has not yet been possible to determine the DNA characteristics of the type specimens of *dasythrix* and *smitianus*, or any other of these controversial forms.

Because of the remarkable degree of morphological conformity in this genus, distinguishing the five African species is difficult and material should be sent to museum experts, or to laboratories

where molecular techniques are used, to confirm identification. Some species, however, can be distinguished from each other by the measurements given in Table 30 and, at least in southern Africa and Malawi, *M. fraterculus* and *M. natalensis* can be distinguished on the basis of the following discriminant function in which $x > 0$ (positive) indicates *M. fraterculus* and $x < 0$ (negative) indicates *M. natalensis* (Stoffberg *et al.* 2004):

$$x = (\text{HF} \times 0.279417) - (\text{TL} \times 0.989306) + 100$$

All measurements in mm. Abbreviations:

HF = length of hindfoot including claws.

TL = total length of the bat.

Meredith Happold

Miniopterus fraterculus LESSER LONG-FINGERED BAT

Fr. Minioptère d'Afrique australe; Ger. Kleine Langflügelfledermaus

Miniopterus fraterculus Thomas and Schwann, 1906. Proc. Zool. Soc. Lond. 1906: 162. Knysna, Western Cape Province, South Africa.

Taxonomy Synonyms: uncertain – pending further evidence, *vicinior* is considered here to be a synonym of *fraterculus* because, in the discriminant function of Stoffberg *et al.* (2004), x is positive, as in *fraterculus*. In contrast, Simmons (2005) considers *vicinior* a synonym of *M. natalensis*. Subspecies: pending revision, none recognized here. Koopman (1966) considered *fraterculus* to be a subspecies of *M. minor* but, later, *fraterculus* was again considered distinct (e.g. Hayman & Hill 1971, Meester *et al.* 1986, Koopman 1993, 1994, Peterson *et al.* 1995). Chromosome number (South Africa): $2n = 46$; $aFN = 50$; not karyologically distinct from *M. schreibersii* in South Africa (Rautenbach *et al.* 1993). In contrast, considered genetically distinct from *M. schreibersii* in South Africa by Miller-Butterworth (2001). The identities of the bats referred to as *M. schreibersii* in these last two studies have not been confirmed but they most probably represent *M. natalensis* (see Genus *Miniopterus*).

Description Small microbat without noseleaf and with tail more or less fully enclosed in interfemoral membrane; bent-winged; five upper and six lower cheekteeth on each side; medium-sized

for African *Miniopterus*, FA: 43.3 ± 1.1 mm; TL: 97.6 ± 3.5 mm; in the discriminant function of Stoffberg *et al.* (2004) (see Genus *Miniopterus*) x is positive (cf. negative in *M. natalensis*). Sexes similar. Pelage very soft, dense, velvety; mid-dorsal hairs ca. 9 mm; crown and forehead with thick, erect, velvety pelage concealing most of posterior surface of ears and dorsal surface of muzzle. Dorsal pelage (grey-phase) very dark brown (perhaps sometimes greyish-black) in southern Africa, or greyish-brown (Kenya); hairs unicoloured or with darker base. Holotype very dark brown. A rich reddish-brown orange-phase is known at some localities. Ventral pelage same as dorsal pelage or slightly paler. Head high-domed. Muzzle narrow; nostrils very small. Ears dark grey or blackish-brown, relatively short ($22.6 [18–30]\%$ of FA), roughly triangular, tip rounded. Tragus ca. half of E, but very variable in preserved material; narrow, basal two-thirds parallel-sided, posterior margin becoming convex near tip; tip rounded. Wings moderately long and narrow, very dark grey, dark brown or black; second phalanx of third finger ca. three times longer than the first; first phalanx of third finger angled forward so third finger appears bent. Interfemoral membrane large, very dark

grey or black; calcars stout. In Malawi and South Africa (at least), TL comparatively short (mean \pm 1 S.D: 97.6 ± 3.5 mm) and hindfeet comparatively long (8.9 ± 0.9 mm) (cf. *M. natalensis*).

Skull small for an African *Miniopterus*. Profile of forehead region (viewed laterally) very strongly concave; braincase elevated (as in all *Miniopterus*).

Geographic Variation Uncertain. Pending revision, no subspecies are recognized here.

Similar Species African *Miniopterus* are very difficult to distinguish (Table 30, p. 712):

Miniopterus minor. Forearm usually shorter (39.8 ± 1.0 [37–42] mm).

Skull sometimes smaller (GLS: 13.6 [11.1–14.5] mm).

M. natalensis. In the discriminant function of Stoffberg *et al.* (2004) (see Genus *Miniopterus*), x is negative.

M. schreibersii. On average, larger (FA: 45.9 [44–49] mm; GLS: 15.8 [14.9–16.5] mm).

M. inflatus. Forearm almost always longer (48.3 [45–52] mm). Skull longer (GLS: 16.9 [16.0–17.8] mm).

Distribution In Africa, traditionally considered to occur mainly in the Zambezian Woodland, Coastal Forest Mosaic, Afromontane–Afroalpine and South–West Cape BZs in Zambia, Malawi, S Mozambique, E Zimbabwe, South Africa and perhaps Angola. The identities of specimens from Malawi and South Africa have been confirmed by the discriminant function of Stoffberg *et al.* (2004). In addition, the form *vicinior* (see Taxonomy) occurs in the Rainforest BZ and Rainforest–Savanna Mosaic in NE DR Congo. According to Peterson *et al.* (1995), *M. fraterculus* also occurs in Nigeria, Cameroon, Kenya and Tanzania. Specimens identified by the discriminant function of Stoffberg *et al.* (2004) have been found in the Somalia–Masai and Zambezian Woodland BZs of Kenya and Tanzania. However, specimens from Cameroon and

Nigeria probably represent the form *villiersi*, which is treated here as a synonym of *M. schreibersii*. Because *M. fraterculus*, *M. natalensis* and *M. schreibersii* are difficult to distinguish, some records in the literature are probably erroneous. Extraliminally: Madagascar (Peterson *et al.* 1995).

Habitat In Malawi, recorded from montane evergreen forest, remnant lowland rainforest and wetter miombo woodland near forests of some kind, at 900–1680 m (Happold & Happold 1997). In South Africa, recorded from the coastal belt (rarely more than 300 km inland) in a variety of habitats including drier savanna bushveld to moister mistbelt, afromontane and coastal forests, where suitable day-roosts are present (Taylor, P. 1998, 2000). Absence from the interior suggests distribution is limited by rainfall. In KwaZulu–Natal, South Africa, most localities seem associated with major river valleys.

Abundance Uncertain. Uncommonly recorded throughout geographic range. In South Africa, apparently much less common than *M. natalensis* (Taylor 2000).

Adaptations Aspect ratio high; wing-loading low; wing-tip roughly triangular (M. Happold unpubl.). Flight fast to slow with great manoeuvrability; wing-beats shallow and irregular; frequently glides downwards at great speed. Can take off from ground; not known to hover. Turns by banking (minimum radius of turn <25 cm) or by stalling-and-twisting; individuals sustained flight in a $1 \times 1 \times 1$ m enclosure for up to four circuits/flight (6 bats, 10 flights each, M. Happold unpubl.). Can scuttle and climb competently and rapidly. By day, roosts in caves, rock fissures and overhangs, disused mine-adits and tunnels; clings in contact to walls, ceilings or other bats (Lang & Chapin 1917b, Smithers 1983, Taylor 2000). Often shares day-roosts with *M. natalensis*. Migrates between summer- and winter-roosts, and makes short-distance, inter-cave movements in winter (Bernard 1980b). Becomes torpid during day at 21 – 24 °C (Happold & Happold 1988). Hibernates in winter in South Africa but loses only 15% of body mass during first half of winter, suggesting that individuals periodically become active and feed during this period (cf. *M. natalensis*) (Bernard 1980b).

Foraging and Food Foraging: no information but, on basis of wing morphology, likely to be similar to *M. natalensis*. Bats (identified as *M. cf. fraterculus*) in Zimbabwe apparently ate mainly aquatic Diptera, but also took some Lepidoptera and Coleoptera (Fenton *et al.* 1977).

Echolocation Search-phase calls of seven Malawian individuals included steep FM/QCF calls with start-frequencies as high as 104 kHz, end-frequencies 50–56 kHz (usually 50–54 kHz), and maximum duration 3.5 ms, and also smooth steep/shallow FM sweeps with similar end-frequencies and maximum duration ca. 6 ms (Figure 118q; M. Happold unpubl.). In South Africa, search-phase calls have end-frequency 54.4 (44–57) kHz; peak-frequency 62.3 (59.8–65.8) kHz; call-duration 3.7 (2.6–4.5) ms (10 bats, Miller-Butterworth *et al.* 2005).

Social and Reproductive Behaviour In southern Africa, roosts in tightly packed groups of usually less than 100 individuals. Females congregate in maternity roosts to give birth and lactate. Hibernacula are occupied by both sexes (R. T. F. Bernard unpubl.).



Miniopterus fraterculus

Reproduction and Population Structure Litter-size: one. At 29–31° S (midlands of KwaZulu–Natal, South Africa), reproductive chronology is restricted seasonal monoestry with copulation, ovulation and fertilization in May and Jun, delayed implantation for ca. 2.5 months during winter, active foetal growth for ca. 4 months and parturition in Nov–Dec after gestation of 5.5–6 months (Bernard 1980b). The period of delayed implantation is 1.5–2 months shorter than in *M. natalensis* at the same locality, suggesting that *M. fraterculus* has had a shorter history at southern latitudes (Bernard 1980b). The right horn of the uterus is larger than the left and, in one study, 94% of ovulations originated in the left ovary and all implantations in the right horn (Bernard 1980c).

Predators, Parasites and Diseases Ectoparasites include a bat-fly (Diptera) (*M. Happold* unpubl.) and mites *Leptotrombidium lawrencei* (Acari: Trombiculidae) and *Macronyssus granulosus* (Acari: Macronyssidae) (Anciaux de Faveaux 1984; host given as subspecies of *M. minor*).

Conservation IUCN Category: Least Concern.

Measurements

Miniopterus fraterculus

FA: 43.3 (41–45) mm, n = 62

WS (a): 304 (293–315) mm, n = 11

TL: 97.6 (88–103) mm, n = 76

T: 47.2 (40–56) mm, n = 64

E: 9.8 (8–13) mm, n = 64

Tr: 5.8 (5–7) mm, n = 22

Tib: n. d.

HF: 8.9 (7–11) mm, n = 76

WT: 7.9 (6–10) g, n = 34

GLS: 14.4 (13.3–15.5) mm, n = 44

GWS: 8.2 (7.6–8.7) mm, n = 37

C–M³: 5.7 (5.1–6.1) mm, n = 44

Kenya, Tanzania, Zambia, Malawi, South Africa (HC, MCZ, ROM, SMNS, TM, Stoffberg *et al.* 2004)

For all of the measured specimens, $x > 0$ in the discriminant function of Stoffberg *et al.* (2004)

Key References Bernard 1980b, c; Miller-Butterworth *et al.* 2005; Smithers 1983; Stoffberg *et al.* 2004; Taylor, P. 1998, 2000.

Ric T. F. Bernard & Meredith Happold

Miniopterus inflatus GREATER LONG-FINGERED BAT

Fr. Grand minioptère africain; Ger. Aufgeblasene Langflügelfledermaus

Miniopterus inflatus Thomas, 1903. Ann. Mag. Nat. Hist., ser. 7, 12: 634. Efulen, Cameroon.

Taxonomy Synonyms following Koopman (1993): *africanus*, *rufus*. Juste & Ibáñez (1992) and Koopman (1993, 1994) included *africanus* and *rufus* in *M. inflatus*. In contrast, based on multivariate statistics, Peterson *et al.* (1995) considered *africanus* to be a distinct species (but without giving diagnostic characters) and they considered *rufus* to be a subspecies of *M. inflatus*. In Kenya, where *africanus* and *inflatus* have been found at localities ca. 75 km apart, *africanus* occurs in more arid habitats than *M. inflatus*, it is a grey form whereas *M. inflatus* is reddish-black, and there are subtle differences in the dorsal profile of its skull (viewed laterally) (J. Eger pers. comm.). Although these differences suggest that *africanus* is distinct, when this profile was written this possibility had not been confirmed by published evidence from other sources (e.g. chromosomes, genetics, echolocation). Furthermore, variation within *africanus* and *inflatus* had not been assessed, and it seemed plausible that the differences in colour reflected only the tendency for colours to be paler in drier habitats than they are in more humid habitats. However, since this profile was written, the specific status of *africanus* Sanborn, 1936 has been confirmed by Juste *et al.* (2007), but it was too late to profile *africanus* as a distinct species here. The form *rufus* is treated here as a synonym of *M. inflatus* although it might be a valid subspecies of *M. inflatus*. Because *M. inflatus* has been confused with *M. schreibersii* (especially with *M. s. villiersi*), references to *M. inflatus* in literature and museum records do not always pertain to this species. Data in this profile are, unless stated otherwise, from specimens identified as *M. inflatus* or *M. africanus* by R. Peterson, J. Eger (ROM), or from studies or collections that mention or include specimens having FA

>48 mm and/or GLS >16.5 mm. Chromosome number (Somalia): 2n = 46; aFN = 50. X = medium-sized metacentric; Y = small acrocentric (Ruedas *et al.* 1990).

Description Small microbat without noseleaf and with tail more or less fully enclosed in interfemoral membrane; bent-winged; five upper and six lower cheekteeth on each side; the largest African *Miniopterus* (FA: 48.3 ± 1.3 mm; TL: 111.2 ± 7.6 mm). Sexes similar. Pelage dense, silky; mid-dorsal hairs 5–7 mm. Dorsal pelage variable (see Geographic Variation), ranging from almost black with a reddish tint, through medium reddish-brown, sepia brown to greyish-brown; hairs unicoloured or with paler tip. Ventral pelage slightly to distinctly paler than dorsal pelage; hairs unicoloured or with paler tip. Head with high-domed forehead; muzzle fairly short and narrow. Ears relatively short (22.6 [18–30]% of FA), subtriangular; tip bluntly rounded. Tragus with anterior and posterior margins straight and parallel; tip rounded; ca. half of E (but very variable in preserved material). Wings long, narrow, greyish-brown, dark brown or almost black; second phalanx of third finger ca. three times longer than the first; first phalanx of third finger angled forward so third finger appears bent. Interfemoral membrane same colour as wings; anterior quarter to half of dorsal surface with downy hairs and sometimes with downy hairs extending further posteriorly close to tail.

Skull large for an African *Miniopterus*. Profile of forehead region (viewed laterally) very strongly concave; braincase elevated but varying in degree; sagittal crest present but varying in prominence (see Geographic Variation).

Geographic Variation Currently, the status of taxa that include the largest of the African *Miniopterus* is uncertain (see Taxonomy). The most distinctly different forms, tentatively treated here as subspecies, are:

M. i. africanus. Dorsal pelage greyish-brown with paler sheen; hairs greyish-brown with paler tip. Ventral pelage paler than dorsal pelage; hairs with more distinctly paler tip. Flight-membranes greyish-brown. Skull with braincase less elevated and less bulbous; muzzle area smaller; sagittal crest low (J. Eger pers. comm.). FA: 48.5 (45–52) mm; Tib: 20.5 (19–23) mm; GLS: 16.8 (16.0–17.4) mm; GWS: 9.2 (8.7–9.6) mm; C–M³: 6.4 (6.0–6.7) mm; n = 47 (Peterson *et al.* 1995).

M. i. inflatus (including *rufus*). Dorsal pelage ranging from very dark brown (holotype), very dark blackish-brown tinged with red (*rufus*), through reddish-brown, sepia brown to greyish-brown; hairs uncoloured or with slightly paler tip. Ventral pelage slightly paler. Flight-membranes dark brown to blackish-brown. Skull with braincase more highly elevated and more bulbous; muzzle area larger; sagittal crest prominent (J. Eger pers. comm.). FA: 48.2 (44–51) mm; Tib: 18.9 (18–21) mm; GLS: 17.0 (16.4–17.8) mm; GWS: 9.3 (8.9–9.8) mm; C–M³: 6.5 (6.3–6.9) mm; n = 162 (from Peterson *et al.* 1995).

Similar Species African *Miniopterus* are very difficult to distinguish (Table 30, p. 712):

Miniopterus minor. Smaller and lighter (FA: 39.8 [37–42] mm; GLS: 13.6 [11.1–14.5] mm; WT: 6 [3–9] g).

M. fraterculus. Forearm almost always shorter (43.3 [41–45] mm). Skull shorter (GLS: 14.4 [13.3–15.5] mm).

M. natalensis. Forearm almost always shorter (44.8 [43–46] mm). Skull shorter (GLS: 14.3 [13.6–14.9] mm).

M. schreibersii. On average, FA shorter (45.9 [44–49] mm). Skull

almost always smaller (GLS: 15.8 [14.9–16.5] mm; C–M³: 5.9 [5.4–6.3] mm).

Distribution Endemic to Africa. Recorded from widespread but mostly isolated localities south of the Sahara, in the Rainforest BZ, the Rainforest–Savanna Mosaics, the Somalia–Masai Bushland, Zambezian Woodland, Coastal Forest Mosaic and Afromontane–Afroalpine BZs. According to Peterson *et al.* (1995) and/or J. Eger (pers. comm.), *M. i. africanus* occurs in Eritrea, Ethiopia, Kenya, Tanzania, Botswana and Namibia, and *M. i. inflatus* occurs in Liberia, possibly Nigeria, Cameroon, Equatorial Guinea, Gabon, Central African Republic, DR Congo, Uganda, Burundi, Kenya and Mozambique (with specimens from DR Congo, Uganda, Burundi and Kenya representing the form *rufus*). *Miniopterus inflatus* has also been recorded recently from ca. 15° 57' S, 35° 29' E (Likabula Mission, Malawi) by Miller-Butterworth *et al.* (2005) and at 08° 08' N, 08° 34' W (Mt Béro, Guinea) by Fahr *et al.* (2006) (both not mapped).

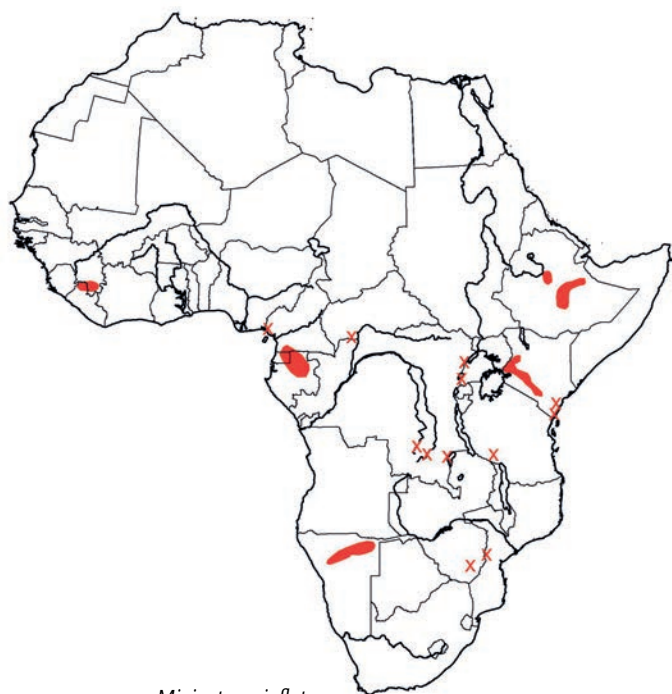
Habitat In Kenya, *M. i. africanus* occurs in the Rift Valley and comparatively dry savanna habitats. In Ethiopia, it has been recorded from open thorn scrub and grassland with scattered acacias, semi-desert grassland with areas of *Acacia* scrub and volcanic caves, and a gorge with *Acacia* and broadleaved scrub and limestone caves (Hill & Morris 1971, Largen *et al.* 1974). Other Ethiopian localities appear to be located in altimontane and afromontane vegetations (terminology: White 1983). In Kenya, *M. i. inflatus* occurs in comparatively moist forests associated with highlands. Elsewhere, it is recorded from lowland rainforest, caves in the rainforest zone and from caves in afromontane vegetation and drier miombo woodland. The presence of caves or mines seems essential.

Abundance Uncertain. Rare or uncommon in collections; probably uncommon throughout geographic range although large numbers sometimes become concentrated in a few maternity caves during the parturition season (see below).

Adaptations Aspect ratio high; wing-loading medium, wing-tips rounded (Norberg & Raynor 1987). Therefore this bat predictably flies fast or moderately slowly with great manoeuvrability (as does *M. fraterculus*). By day, roosts in caves (including volcanic and limestone caves, and those formed by granite boulders) and mine-adits. Individuals often tuck themselves into cracks and fissures, but sometimes hang from ceilings. Sometimes roosts with *Hipposideros caffer* and *H. gigas* in Gabon (Brosset 1969), *H. ruber* in Liberia (Wolton *et al.* 1982) and with *Miniopterus natalensis* in southern Africa (Smithers 1983, as *M. schreibersii*).

Foraging and Food Based on wing morphology, predictably forages for flying insects by moderately fast-hawking in open, uncluttered places including clearings, above trees and over water. One individual was observed flying high (6–8 m) among widely spaced *Acacia* trees in open scrub and grassland (Hill & Morris 1971). Jones (1971) caught ten flying under a bridge over a stream in lowland rainforest in Equatorial Guinea (as *M. schreibersii*).

Echolocation No information.



Miniopterus inflatus

Social and Reproductive Behaviour Sometimes roosts singly, sometimes in small groups (e.g. a group of eight immature ♀♀ was recorded at Mt Nimba, Liberia by Wolton *et al.* 1982). In NE Gabon, ♀♀ congregate to give birth and raise young in a maternity cave estimated to house ca. 40,000 individuals at this time (Brosset 1969). At other times, the numbers of *M. inflatus* in other caves in the area fluctuates from day to day, suggesting that individuals utilize many different caves and frequently move from cave to cave. The occurrence of *M. inflatus* in these Gabonese caves has been confirmed (M. Happold unpubl.).

Reproduction and Population Structure Litter-size: one (n = 3). At ca. 00° 40' N (NE Gabon), the reproductive chronology is restricted seasonal monoestry with copulation in Jul, births in Oct and lactation ending prior to Jan (Brosset 1969, Brosset & Saint Girons 1980). In Zimbabwe, three ♀♀, each with one embryo in the right uterine horn, were taken in Oct (Smithers & Wilson 1979).

Predators, Parasites and Diseases Ectoparasites include bat-flies *Nycteribia schmidli* and *Penicillidia allisoni* (Diptera: Nycteribiidae) (Wolton *et al.* 1982). A list of ectoparasites is given by Anciaux de Faveaux (1984) but the identities of the hosts have not been confirmed.

Conservation IUCN Category (including *africanus*): Least Concern.

Miniopterus minor LEAST LONG-FINGERED BAT

Fr. Petit minioptère africain; Ger. Zwerg-Langflügelfledermaus

Miniopterus minor Peters, 1867. Monatsber. K. Preuss. Akad. Wiss. Berlin 1866: 885 [publ. 1987]. Coast opposite Zanzibar I., Tanzania.

Taxonomy Synonyms: *newtoni*, *occidentalis*. Subspecies: three of uncertain status. Considered conspecific with *M. fraterculus* (Aellen & Brosset 1968) but later considered to be a distinct species on basis of differences in cranial proportions. For taxonomic review see Juste & Ibáñez (1992). Formerly included *manavi* and *griveaudi* of Madagascar and Comoro Is., but Peterson *et al.* (1995) considers these to be distinct species. See also Juste *et al.* (2007), who consider *newtoni* to be a valid species. Chromosome number: not known.

Description Small to very small microbat without noseleaf and with tail more or less fully enclosed in interfemoral membrane; bent-winged; five upper and six lower cheekteeth on each side; the smallest African *Miniopterus* (FA: 39.8 ± 1.0 mm; TL: 91.3 ± 3.0 mm); downy pelage on flight-membranes. Sexes similar. Pelage dense, velvety. Dorsal pelage very dark blackish-brown to almost black with slight greyish sheen; hairs dark blackish-brown (almost black) with slightly paler tip. Ventral pelage slightly paler and greyer. Head with high-domed forehead; muzzle short, narrow, with very small nostrils. Ears relatively short (23 [15–27]% of FA), subtriangular, partly concealed by pelage. Tragus moderately long (49.4 [30–70]% of E) with rounded tip. Wings long, narrow, dark brown; dorsal surface with sparse downy hairs; second phalanx of third finger ca. three times longer than the first; first phalanx of third finger angled forward so third finger appears bent. Dorsal surface of anterior half of interfemoral membrane with sparse, downy hairs, visible under microscope. Skull small for an African *Miniopterus*.

Measurements

Miniopterus inflatus and *M. africanus*

FA: 48.3 (45–52) mm, n = 295

WS (d): 344 (320–380) mm, n = 73

TL: 111 (92–128) mm, n = 210

T: 52 (40–62) mm, n = 232

E: 11 (8–14) mm, n = 236

Tr: 5.8 (4.0–7.5) mm, n = 132

Tib: 18.8 (18–27) mm, n = 209

HF: 10 (7–11), n = 75

WT: 13 (8–19) g, n = 142

GLS: 16.9 (16.4–17.8) mm, n = 209*

GWS: 9.3 (8.7–9.8) mm, n = 209*

C–M³: 6.5 (6.3–6.9) mm, n = 209*

Liberia, Cameroon, Gabon, Uganda, Kenya, Ethiopia, Tanzania, Botswana, Namibia (BMNH, RMCA, ROM, SMNS and literature)

Data include *africanus* and *rufus*

*Derived from Peterson *et al.* (1995)

Key Reference Brosset 1969.

Meredith Happold

Profile of forehead region (viewed laterally) very strongly concave; braincase elevated (as in all *Miniopterus*).

Geographic Variation Three subspecies are currently recognized but their status is uncertain. For some parameters, mean \pm S.D.

M. m. minor: Kenya and Tanzania. FA: 39.8 ± 0.65 mm; condylobasal length (CbL): 13.6 ± 0.22 mm.

M. m. occidentalis: lower reaches of Congo R. in Congo and DR Congo. FA: 38.2 ± 0.74 mm, CbL 13.1 ± 0.16 mm.

M. m. newtoni: extraliminally São Tomé. FA: 39.0 ± 0.66 ; CbL 13.3 ± 0.25 mm.

For other measurements see Juste & Ibáñez (1992). Considering the vast distance between the geographic ranges of the African subspecies, and the morphological uniformity of this genus, *minor* and *occidentalis* might be distinct species despite their similar morphological characters. *Miniopterus m. occidentalis* shows greater affinity with *M. m. newtoni* than with *M. m. minor* (Juste & Ibáñez 1992).

Similar Species African *Miniopterus* are very difficult to distinguish (Table 30, p. 712):

Miniopterus fraterculus. Forearm usually longer (43.3 ± 1.1 [41–45] mm). Skull sometimes larger (GLS: 14.4 [13.3–15.5] mm).



Miniopterus minor

M. natalensis. Forearm longer (44.8 [43–46] mm). Skull sometimes larger (GLS: 14.3 [13.6–14.9] mm; C–M³: 5.7 [5.5–6.0] mm).

M. schreibersii. Forearm longer (45.9 [44–49] mm). Skull almost always larger in some dimensions (GLS: 15.8 [14.9–16.5] mm; C–M³: 5.9 [5.4–6.3] mm).

M. inflatus. Larger and heavier (FA: 48.3 [45–52] mm; GLS: 16.9 [16.4–17.8] mm; WT: 13 [8–19] g).

Distribution Endemic to Africa. In Africa, there is a western population in the Southern Rainforest–Savanna Mosaic around the lower reaches of the Congo R. in Congo and DR Congo (apparently not reaching the coast), and an eastern population in the Coastal Forest Mosaic BZ on the Kenya–Tanzania coast.

Habitat All western records are near caves in woodland savanna habitats (Juste & Ibáñez 1992). The eastern population seems restricted to the coastal savanna and coastal forest mosaic, near caves: it has been recorded in one coastal forest but presumably exploits both forest and savanna components of the mosaic. For bat assemblages associated with *M. minor* in East Africa, see Cockle *et al.* (1998).

Abundance Uncertain. Rare in collections; the rarest African *Miniopterus*.

Adaptations By day, roosts in caves, including those in up-raised coral reefs along the Kenyan coast where *M. minor* was studied by McWilliam (1982, 1988c, 1990). Here, there is a short wet season in Nov–Dec followed by a short warm dry season, and a long wet season from late Mar to late Jun followed by a long cool dry season (McWilliam 1988c). Body weight fluctuates seasonally, with fat being deposited during each of the wet seasons; in ♂♂, weight peaks in Apr–May and again in Dec. During the cool dry season, when food is scarcest and body weight lowest, the bats become torpid during the day. McWilliam (1988c) suggests that this reversible hypothermia

evolved in the tropics as a response to colder dry seasons with concomitant food shortages, and that torpor, together with delayed implantation during these periods, pre-adapted *Miniopterus* for colonization of higher latitudes where winters are even more severe and hibernation occurs. Adults moult during Apr–May in conjunction with the improvement of body condition at the beginning of the long wet season: old browner pelage is replaced by blacker pelage.

Foraging and Food No details available. Like other *Miniopterus*, *M. minor* feeds on insects and predictably forages by moderately fast-hawking or slow-hawking.

Echolocation No information.

Social and Reproductive Behaviour The mating system of *M. minor* living in a cave near the Kenyan coast appears to be based on lekking (McWilliam 1990). During a three-year study, ♂♂ were found in this cave throughout the year, although numbers were usually <10 during the short dry season (Jan, Feb). At the start of the long rains (Apr), the cave population increased markedly as adults (accompanied by weaned young) returned from inland maternity colonies. In ♂♂, sexual regeneration and a marked increase in weight occurred during this wet season. In May, during the cool dry season, adult ♂♂ began to occupy the mating site – an erosion hollow situated in the outer coolest cave-chamber. This site was strategic in that the movements of bats, into or out of the cave, could be monitored from it. Adult ♂♂ competed for places in this site, suggesting that it functioned as a lek, but no copulations were seen and therefore it is possible (albeit unlikely) that mating was random. Successful occupants of the mating site were heavier than others and, having occupied this site during one year, they were more likely to gain access to it in subsequent years. These ♂♂, ca. 30 in number, continued to roost at this site throughout the entire mating season, and ca. 60% of them occupied it for at least two consecutive mating seasons. They produced a pungent odour associated with their urine, and their pelage became damp; possibly an odour plume was created enabling ♀♀ to orientate towards the mating site. Copulation occurred from late Jun to late Jul (see below), and a substantial loss in body weight of ♂♂ (16%) was coincident with their competitive mating activities. The mating site was abandoned at the conclusion of the mating season. Subsequently, colony size increased to a peak of ca. 200 as more adult ♀♀ arrived until, in Oct, ca. 80% of the bats were pregnant ♀♀. Then, in Oct–Nov, most of these ♀♀ migrated inland to maternity caves where, during the main food peak associated with the short inland wet season, they gave birth and suckled their young. The few bats (ca. ten) that remained in the coastal cave were mainly adult ♂♂. Although it not yet certain that *M. minor* exemplifies a mating system based on lekking, there is no evidence of harem-formation or the participation by ♂♂ in parental care.

Reproduction and Population Structure Litter-size: no published information but presumably one. At 04° 10'S (coastal Kenya), the reproductive chronology is restricted seasonal monoestry with reproductive events corresponding closely to the rainfall-induced seasonality of that area (see Adaptations) (McWilliam 1988c, 1990). Spermatogenesis occurs from Apr to Jul (mainly during the long wet season when insects are abundant and the ♂♂ are fat). Females have a 'silent heat' (ovulation without fertilization) in May,

with associated odour secretions that might trigger ♂ competition for occupancy of the 'lek' (see above). A second ovulation with copulation and fertilization occurs in late Jul to early Aug. There is probably a period of delayed implantation of up to three weeks with the result that the most energy-demanding stages of pregnancy are shifted to the beginning of the short wet season. Births and lactation occur during the short wet season when insects are maximally abundant. Males do not breed in their first year. Both sexes do not moult until their second year.

Predators, Parasites and Diseases Ectoparasites include bat-flies *Nycteribia schmidli*, *Penicillidia fulvida* (Diptera: Nycteribiidae), *Ascodipteron minor* (Diptera: Streblidae) and mites *Spinturnix semilunaris* (Acari: Spinturnicidae) and *Macronyssus granulatus* (Acari: Macronyssidae) (Anciaux de Faveaux 1984).

Conservation IUCN Category: Data Deficient.

The status of the subspecies requires re-evaluation. If any are distinct species, they are probably threatened. Caves used by this species should be protected.

Measurements

Miniopterus minor minor

FA: 39.8 (37–42) mm, n = 74

WS (d): 283 (264–293) mm, n = 41

TL: 91.3 (82–97) mm, n = 68

T: 40.6 (34–47) mm, n = 70

E: 9.2 (6–11) mm, n = 68

Tr: 4.7 (3–7) mm, n = 54

Tib: n. d.

HF: 7.7 (5–10) mm, n = 68

WT: 6.0 (3–9) g, n = 50

GLS: 13.6 (11.1–14.5) mm, n = 18

GWS: 8.0 (7.5–8.7) mm, n = 16

C–M³: 5.3 (4.1–5.6) mm, n = 18

Kenya (ROM).

For *M. m. occidentalis*, see Geographic Variation

Key Reference Juste 1992; McWilliam 1982, 1988c, 1990.

Meredith Happold

Miniopterus natalensis NATAL LONG-FINGERED BAT (NATAL CLINGING BAT)

Fr. Miniopière de Natal; Ger. Natal-Langflügel-Fledermaus

Miniopterus natalensis (A. Smith, 1834). S. Afr. Quart. J. 2: 59. Durban, KwaZulu–Natal, South Africa.

Taxonomy Originally *Vespertilio natalensis*. Synonyms: following Koopman (1994), Peterson *et al.* (1995) and Simmons (2005), *arenarius*, *breyeri*, *scotinus*. The status and relationships of *natalensis* and the above three forms (and also *dasythrix* and *smitianus*) are uncertain: revision is much needed. *Miniopterus natalensis* is often considered to be a subspecies of *M. schreibersii* (e.g. Meester *et al.* 1986, Koopman 1993). However, *natalensis* is considered to be a distinct species by Harrison (1953), O'Shea and Vaughan (1980) and Koopman (1994): multivariate statistics supports this conclusion (Peterson *et al.* 1995), and so too does genetic evidence (Miller-Butterworth *et al.* 2005). Following Koopman (1994) and Simmons (2005), *arenarius* is tentatively considered here to be a subspecies of *M. natalensis*, and *breyeri* and *scotinus* are treated as synonyms. Harrison (1953) and Meester *et al.* (1986) include *dasythrix* and *smitianus* as synonyms of *M. natalensis*, but Koopman (1994), Simmons (2005) and J. Eger (pers. comm.) consider these are subspecies of *M. schreibersii* and they are tentatively treated as such here. The geographic ranges of *dasythrix* and *smitianus* overlap with the range of *M. natalensis*, so it is possible that both *M. schreibersii* and *M. natalensis* occur sympatrically in southern Africa. It is also possible that *M. natalensis* and/or *M. schreibersii* include more than one species. The form *vicinior* is sometimes included in *M. natalensis* (e.g. Simmons 2005), but is tentatively considered here as a subspecies of *M. fraterculus*. Chromosome number in southern Africa: 2n = 46; aFN = 50 (Rautenbach *et al.* 1993 as *M. schreibersii*).

Description Small microbat without noseleaf and with tail more or less fully enclosed in interfemoral membrane; bent-winged; five upper and six lower cheekteeth on each side; medium-sized for African *Miniopterus* (FA: 44.8 ± 0.9 mm; TL: 108 ± 2.5 mm); in the discriminant function of Stoffberg *et al.* (2004) (see Genus *Miniopterus*)

x > 0 (positive). Sexes similar. Pelage very soft, dense, velvety; mid-dorsal hairs 7–9 mm. Dorsal pelage (grey-phase) very dark brown (holotype) to slate-grey or greyish-black (southern Africa), dark sepia brown (Kenya); hairs unicoloured or with darker base. Ventral pelage same as dorsal pelage, or slightly paler. Pelage may become rusty-red or rusty-brown (orange-phase) prior to being moulted: new pelage is in grey-phase. Head high-domed; crown and forehead with thick, erect velvety pelage, which conceals most of posterior surface of ears and dorsal surface of muzzle. Muzzle narrow; nostrils very small. Ears dark grey or blackish-brown; relatively short (24.5 [22–28]% of FA); roughly triangular, tip rounded. Tragus moderately long, 47.8 (33–60)% of E; basal two-thirds parallel-sided, posterior margin becoming convex near tip; tip rounded. Wings moderately long and narrow, very dark grey, blackish-brown or black; second phalanx of third finger ca. three times longer than the first; first phalanx of third finger angled forward so third finger appears bent. Interfemoral membrane large, very dark grey or black; calcars stout. In South Africa (at least), TL comparatively long (113.6 ± 3.5 mm) and hindfeet comparatively short (9.1 ± 0.6 mm) (cf. *M. fraterculus*). Skull small for an African *Miniopterus*. Profile of forehead region (viewed laterally) very strongly concave; braincase elevated (as in all *Miniopterus*).

Geographic Variation Two subspecies are recognized by Koopman (1994) and Simmons (2005), but they do not apparently vary in size:

M. n. arenarius: Sudan (and extraliminally Arabia) to Zimbabwe. FA: 45 (42–46) mm, n = 24; GLS: 14.4 (14.0–15.0) mm, n = 11.

M. n. natalensis: South Africa. FA: 45 (43–46) mm, n = 21; GLS: 14.3 (13.6–14.9) mm, n = 11.

Similar Species African *Miniopterus* are very difficult to distinguish (Table 30, p. 712):

Miniopterus minor. Forearm shorter (39.8 [37–42] mm). Skull sometimes smaller (GLS: 13.6 [11.1–14.5] mm; C–M³: 5.3 [4.1–5.6] mm).

M. fraterculus. In the discriminant function of Stoffberg *et al.* (2004) (see Genus *Miniopterus*), *x* is positive.

M. schreibersii. Possibly almost always larger in areas of sympatry (e.g. in Zimbabwe and Malawi, FA: 46.8 [46–49] mm; GLS: 16.2 [15.9–16.5] mm; C–M³: 6.11 [6.0–6.2], *n* = 18). Ear more rounded. Possibly very widely distributed, but this is controversial (see Genus *Miniopterus*).

M. inflatus. Forearm almost always longer (48.3 [45–52] mm). Skull longer (GLS: 16.9 [16.0–17.8] mm).

Distribution Endemic to Africa. Widespread, mainly in the Sudan Savanna, Afromontane–Afroalpine, Somalia–Masai Bushland, Coastal Forest Mosaic, Zambezian Woodland, Highveld, South-West Arid and South-West Cape BZs, from S Sudan and Ethiopia southwards through Uganda, Rwanda, Kenya and Tanzania, and in most of south-central and southern Africa from Angola to Malawi and southwards. Material from Ethiopia, Uganda and Rwanda needs confirmation using DNA technology (D. Jacobs pers. comm.). Records from Angola (Crawford-Cabral 1986) also need confirmation that they represent *M. natalensis* and not *M. schreibersii*.

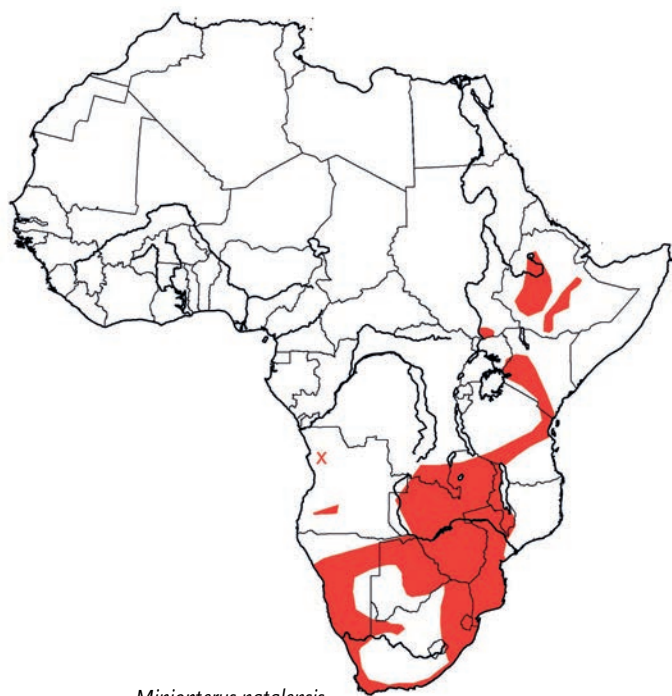
Habitat In Ethiopia, habitats include semi-desert grassland with *Acacia* scrub and volcanic caves, and areas of dense *Acacia* and broad-leaved scrub near limestone caves (Largen *et al.* 1974). In Kenya, recorded mainly from *Acacia–Commiphora* bushland and thicket; possibly also occurs in forest–savanna mosaics and afromontane vegetation but identity of specimens from these wetter habitats needs confirmation. In South Africa, occurs in a wide range of habitats including bushveld and grassland (Taylor, P. 1998). Tends to

avoid forests and, in more arid regions, is associated with standing or running water. Caves and/or similar underground day-roosts are apparently essential.

Abundance Uncertain. Sometimes very abundant in vicinity of suitable day-roosts, especially when numbers concentrate at maternity roosts. In South Africa, it is one of the most abundant cave-dwelling bats; apparently much more common than *M. fraterculus*.

Adaptations Aspect ratio very high; wing-loading low; flight characteristics similar to those of *M. fraterculus* (*n* = 1; M. Happold unpubl.). One individual sustained flight in a 1×1×1 m enclosure for up to three circuits/flight (10 flights). By day, roosts in dark caves or similar underground day-roosts including mine-adits and tunnels; clings or hangs freely to ceilings and walls and occasionally crawls into crevices. Also sometimes roosts by day in houses, rock crevices and hollow trees. At night, roosts in open buildings including verandas, pump-houses and garages (Rautenbach 1982). Selection of day-roosts is influenced by reproductive condition, and the microclimate and structure of the roosts (van der Merwe 1973a, Laycock 1976, Bernard 1980b, Bernard & Bester 1988, McDonald *et al.* 1990b, Brown & Bernard 1994). In South Africa, most ♂♂ and almost all ♀♀ migrate in autumn to higher altitude, inland caves with comparatively low temperatures (10.5–13 °C, sometimes 15.3 °C) in which they hibernate during May–Jul. These temperatures are higher than those generally accepted as suitable for hibernation (Brown 1999). In late winter, most migrate back to lower altitude caves, which are warmer (≥20 °C); migration distances of up to 260 km are known. Some hibernacula are occupied year-round. In summer-occupied caves, some individuals choose the coolest parts (20–24 °C) and become torpid during day, but most choose the warmest areas (around 30 °C) and remain alert and potentially active. Movements between summer-occupied caves are common. Some ♂♂ over-winter in these caves. A genetic study, using paternally inherited nuclear DNA markers and maternally inherited mitochondrial DNA markers, showed that both ♂♂ and ♀♀ of this migratory species tend to return consistently to the place where they were born, leading to constricted gene flow among subpopulations and hence to the existence of phenotypically distinct subspecific populations that are sympatric (Miller-Butterworth *et al.* 2003). In contrast, in most mammals (including other bats), ♂♂ disperse and only the ♀♀ are philopatric. For *M. natalensis*, the genetic structure of subpopulations is correlated with morphological differences between subpopulations and differences in the biomes they exploit, suggesting that each subpopulation has adapted to the particular conditions (including climate, availability of food) surrounding their roosts. Predicted mean maximum urine concentration is comparatively low (2937 mOsmol/kg), suggesting dependence on water for drinking (Happold & Happold 1988). Hibernacula sometimes have relative humidities fluctuating as low as 33%, so huddling to minimize evaporative water loss is probably obligatory. Furthermore, these bats often roost against moist surfaces.

Foraging and Food Forages opportunistically for flying insects by fast-hawking in open spaces, including over water, and also by slow-hawking in areas of moderate clutter: flexible flight (M. Happold unpubl.) and flexible echolocation make this diversity possible (Jacobs 1999). *Miniopterus natalensis* and/or *M. fraterculus* are attracted



Miniopterus natalensis

to swarms of insects over water and cattle enclosures. Diet includes mainly Coleoptera, Lepidoptera, Diptera and Isoptera (occasionally Homoptera, Orthoptera and others), with seasonal fluctuations in relative proportions of these insects in the diet (Fenton & Thomas 1980, Findley & Black 1983, Fenton 1985, McDonald *et al.* 1990a, as *M. schreibersii*). Where sympatric in South Africa, *M. natalensis* and *M. fraterculus* eat the same orders of arthropods, but the proportion of beetles in the diet is higher for *M. natalensis* (Miller-Butterworth *et al.* 2005).

Echolocation The calls of *M. n. arenarius* (identity not confirmed) in E DR Congo are broad bandwidth FM calls (shape not described) with end-frequencies 45–50 kHz (mean 48) (Novick 1958b). Calls with end-frequency 50 kHz were also recorded in Zimbabwe (Fenton & Thomas 1980, as *M. schreibersii*). At De Hoop Nature Reserve (Western Cape Province, South Africa), search-phase calls of bats identified as *M. schreibersii* (but currently considered to represent *M. natalensis*) were steep FM/QCF calls whose mean end-frequencies (minimum frequencies) and mean durations varied from cluttered to open habitats: 50.3 kHz and 2.2 ms in clutter, 43.3 kHz and 3.7 ms in open habitat near a cliff, and 37.5 kHz and 4.4 ms in more open habitat over a causeway (Jacobs 1999). The identity of these bats was confirmed genetically (Miller-Butterworth *et al.* 2003). At Knysna, South Africa, search-phase calls of *M. natalensis* have end-frequency 43.9 (43–47) kHz; peak-frequency 49.7 (47.6–50.9) kHz; call-duration 5.3 (3.9–6.1) ms (10 bats; Miller-Butterworth *et al.* 2005).

Social and Reproductive Behaviour Mostly roosts in very large groups (colonies); occasionally roosts singly or in smaller groups (van der Merwe 1973b, 1975; Laycock 1976). During autumn, ♂♂ and ♀♀ congregate in or near hibernacula, mate and then hibernate together, huddling in tightly packed clusters varying in size from a few individuals to ca. 4000. A few ♂♂ over-winter separately in summer-occupied roosts. In spring and summer, ♀♀ and ♂♂ roost together in great numbers in pre-maternity colonies, and then ♀♀ congregate in maternity colonies (sometimes but not always in the same roosts) where adult ♂♂ are absent or present only in very small numbers. Clusters of 50,000–100,000 have been observed in maternity colonies comprised of up to 260,000 individuals. Pregnant ♀♀, and lactating ♀♀ with neonates, tend to segregate into different clusters and, later, juveniles are left in separate clusters, which ♀♀ visit only briefly to suckle.

Reproduction and Population Structure Litter-size: one. Reproductive chronology is restricted seasonal monoestry with a period of delayed implantation, which varies from 2–4 months in duration depending on latitude and related differences in seasonal regimes (Bernard *et al.* 1996). At 24–26°S (former Transvaal, South Africa), copulation and conception peak in late Mar, implantation peaks in late Jul after a delay of ca. 4 months, and parturition peaks from mid-Nov to early Dec, i.e. ca. 8.5 months after fertilization (van der Merwe 1979, 1986). At 29–31°S (KwaZulu–Natal, South Africa), where summer ends a month later, copulation and conception occur in Apr, implantation occurs in Aug, and parturition occurs in Dec, i.e. 7.5 months after fertilization (Bernard 1980b). At 18–19°S in Zimbabwe, copulation occurs in mid-Apr to mid-May, implantation is delayed until early Jul, and parturition occurs between late Oct and

mid-Nov, i.e. 6–7 months after fertilization (Bernard *et al.* 1996). At 11°S (Shaba Province, SE DR Congo), copulation occurs in mid-Apr; implantation in late Jul after a three-month delay; parturition in Oct (Anciaux de Faveaux 1977). At 02° 18'S (Masalani, near Kibwezi, Kenya), births in Nov (O'Shea & Vaughan 1980). In South Africa, 90% of all ovulations are from the left ovary, and all implantations are in the right uterine horn (van der Merwe 1986). During the period of active foetal development (ca. 120 days) weight increase is exponential (van der Merwe 1979, 1981). One year, however, the rains failed during the last month of pregnancy (Nov), presumably causing a reduction in the abundance of insects, and this was correlated with slowing of foetal growth-rate, indicating that facultative retarded embryonic development can occur in this species (Bernard 1974). Mean birth mass is 2.7 g (27% of mother's mass), so young are proportionally heavier at birth than many other mammals (excluding other bats). Sex ratio at birth ca. 1 : 1 (van der Merwe 1973b).

Predators, Parasites and Diseases Predators include Barn Owls *Tyto alba* in South Africa (van der Merwe 1980). Ectoparasites of middle-sized *Miniopterus* spp. in Africa include bed-bugs *Afrocmex leleupi*, *Stricticmex anciauxi* (Hemiptera: Cimicidae); fleas *Oxypterus isomalus*, *Rhinolophopsylla capensis*, *R. ectopa* (Siphonaptera: Ischnopsyllidae); 23 species of bat-flies (Diptera: Nycteribiidae, Streblidae); five species of ticks (Acari: Ixodidae); and 14 species of mites (Acari: Spinturnicidae, Macronyssidae, Myobiidae, Trombiculidae, Chirodiscidae, Sarcoptidae, Gastronyssidae) (Anciaux de Faveaux 1984), but which of these parasites are hosted by *M. natalensis* is uncertain.

Conservation IUCN Category: Least Concern.

However, found in only a few sparse caves that are under threat from human disturbance (tourism).

Measurements

Miniopterus natalensis

FA: 44.8 (43–46) mm, n = 40
 WS (d): 323 (300–336) mm, n = 32*
 TL: 108.0 (104–115) mm, n = 51
 T: 51.5 (45–58) mm, n = 51
 E: 10.7 (10–12) mm, n = 51
 Tr: 5.2 (4–7) mm, n = 38
 Tib: n. d.
 HF: 9.5 (6–11) mm, n = 51
 WT: 9.9 (7–12) g, n = 33
 GLS: 14.3 (13.6–14.9) mm, n = 20
 GWS: 8.5 (8.3–8.8) mm, n = 20
 C–M³: 5.7 (5.5–6.0) mm, n = 20
 Kenya, Tanzania, South Africa (ROM)

*Kenya only

For all of the measured specimens, $x < 0$ in the discriminant function of Stoffberg *et al.* (2004)

Key References Bernard 1980b; Bernard & Bester 1988; Jacobs 1999; Miller-Butterworth *et al.* 2003, 2005; van der Merwe 1973a, b, 1979, 1981, 1986.

Ric T. F. Bernard & Meredith Happold

Miniopterus schreibersii SCHREIBERS'S LONG-FINGERED BAT

Fr. Miniopière de Schreibers; Ger. Schreibers Langflügelfledermaus

Miniopterus schreibersii (Kuhl, 1817). Die Deutschen Fledermäuse. Hanau, p. 14. Kolumbács Cave [= Kulmbazer Cave = Columbäza Cave], ca. 44° 37'N, 21° 40'E, Banat, near Coronini, Rumania.

Taxonomy Originally *Vespertilio schreibersii*. A polytypic species that probably comprises a complex of several species (Horáček *et al.* 2000). Information in the literature concerning this species is often questionable because of the confusion with identification. Synonyms in Africa: following Koopman (1994), Peterson *et al.* (1995) and Simmons (2005), *dasythrix*, *smitianus*, *villiersi*. Following these authors, *M. natalensis* (including *arenarius*, *breyeri* and *scotinus*) is excluded from *M. schreibersii*. The forms *dasythrix* and *smitianus* are sometimes considered synonyms of *natalensis* (e.g. Meester *et al.* 1986) but others (e.g. Koopman 1994, Peterson *et al.* 1995, Simmons 2005) include them in *schreibersii*. Based on morphological evidence, the form *villiersi* is usually considered a subspecies of *M. schreibersii* but this needs confirmation from genetic information. Subspecies: four currently recognized in Africa. The status of *M. schreibersii* subspecies in sub-Saharan Africa, as summarized here, can only be clarified by future genetic work. Chromosome number (Tunisia): 2n = 46; aFN = 50 (Baker *et al.* 1974). In Italy, 2n = 46; aFN = 50 (Capanna & Civitelli 1965). In Yugoslavia, 2n = 46; aFN = 52 (Bickham & Hafner 1978).

Description Small microbat without noseleaf and with tail more or less fully enclosed in interfemoral membrane; bent-winged; five upper and six lower cheekteeth on each side; medium-large for African *Miniopterus* (FA: 46.1 ± 1.75 mm; TL: 114.3 ± 10 mm). Sexes similar. Pelage very soft, dense, lying flat dorsally; mid-dorsal hairs 7–9 mm; pelage on crown and forehead thick, erect and velvety, concealing most of posterior surface of ears and dorsal surface of muzzle. Dorsal pelage greyish-brown, grey or brownish-black depending on subspecies (see below); hairs unicoloured. Ventral pelage paler; hairs bicoloured, dark with paler tip. Head high-domed; muzzle short and narrow; nostrils very small. Ears greyish-brown to brown; relatively short (26.1 [17–35]% of FA, n = 5); roughly triangular, tip rounded. Tragus moderately long, parallel-sided; tip rounded. Wings moderately long and narrow, greyish-brown; second phalanx of third finger ca. three times longer than the first; first phalanx of third finger angled forward so third finger appears bent. Interfemoral membrane large, greyish-brown; calcars reaching one-third distance to tip of tail. Skull medium-sized for an African *Miniopterus*. Profile of forehead region (viewed laterally) very strongly concave; braincase elevated (as in all *Miniopterus*).

Geographic Variation Subspecies in Africa, based on Koopman (1994), Peterson *et al.* (1995) and Simmons (2005) include:

- M. s. schreibersii*: Morocco, Algeria, Tunisia and Libya (and extraliminally Europe). Dorsal pelage greyish-brown to grey. FA: 45.1 (43–47) mm, n = 50; GLS: 14.9 (14.5–15.5) mm; upper C–M³: 5.7 (5.5–5.9) mm, n = 26 (Algeria, Libya; Qumsiyeh & Schlitter 1982, Kowalski & Rzebik-Kowalska 1991).
- M. s. villiersi*: Guinea to DR Congo (Koopman 1994). Dorsal pelage greyish-brown to brownish-black. FA: 45.2 (43–47) mm; GLS:

15.9 (15.5–16.2) mm; C–M³: 6.0 (5.7–6.2) mm, n = 14 (Guinea, DR Congo; Peterson *et al.* 1995).

M. s. smitianus: described from Namibia (Thomas 1927b); Ethiopia to Namibia (Koopman 1994); Peterson *et al.* (1995) found morphological differences between populations from Namibia and Kenya/Ethiopia. Dorsal pelage (Namibia) 'smokey grey near mouse grey' (Thomas 1927b); (Kenya/Ethiopia) greyish-brown to brownish-black. FA: 45.6 (45–46) mm, n = 8; GLS: 15.5 (14.9–15.8) mm; C–M³: 5.7 (5.6–5.9) mm, n = 8 (Namibia; Peterson *et al.* 1995).

M. s. dasythrix: described from Eastern Cape Province, South Africa (Temminck 1840). Malawi to South Africa (Koopman 1994). Dorsal pelage greyish-brown to brownish-black. FA: 46.4 (46–48) mm; GLS: 15.9 (15.4–16.1) mm; C–M³: 6.1 (6.0–6.3) mm, n = 6 (South Africa; Peterson *et al.* 1995).

Similar Species African *Miniopterus* are very difficult to distinguish (Table 30, p. 712):

Miniopterus minor. Forearm shorter (39.8 [37–42] mm). Skull almost always smaller in some dimensions (GLS: 13.6 [11.1–14.5] mm; C–M³: 5.3 [4.1–5.6] mm).

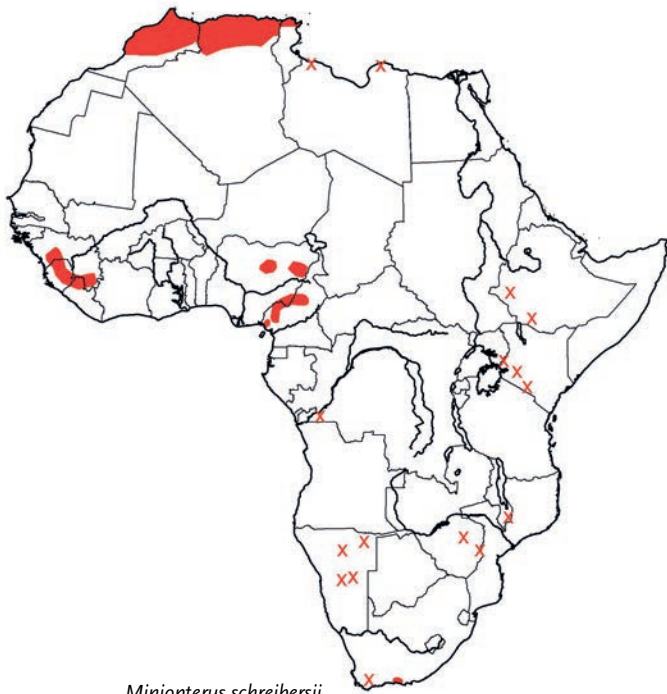
M. fraterculus. On average, smaller (FA: 43.3 [41–45] mm; GLS: 14.4 [13.3–15.5] mm).

M. natalensis. Possibly almost always smaller in areas of sympatry (e.g. in Zimbabwe and Malawi, FA: 44.5 [43–46] mm; GLS: 15.1 [14.7–15.5] mm; C–M³: 5.6 [5.3–6.0] mm). Ear less rounded. Distribution comparatively restricted.

M. inflatus. On average, FA shorter (48.3 [44–52] mm). Skull almost always larger (GLS: 16.9 [16.4–17.8] mm; C–M³: 6.5 [6.3–6.9] mm).

Distribution In Africa, the distribution appears very disjunct. Widespread in the Mediterranean Coastal and Afromontane–Afroalpine BZs of NW Africa (*M. s. schreibersii*). Also recorded in the Northern Rainforest–Savanna Mosaic in Guinea, Sierra Leone (USNM) and W Liberia, in the Sudan Savanna and Rainforest BZs in Nigeria, and in the Rainforest BZ and the Afromontane–Afroalpine BZ in Cameroon (*M. s. villiersi*). If *dasythrix* and *smitianus* are subspecies of *M. schreibersii*, this species also occurs in the Somalia–Masai Bushland, Zambezian Woodland, South-West Arid and South-West Cape BZs in eastern and southern Africa from Ethiopia to Namibia (Koopman 1994), but see Genus *Miniopterus* for further information. Extraliminally, *M. schreibersii* ranges from southern Europe eastwards to Afghanistan (Maeda 1982). Does not occur on Madagascar (Peterson *et al.* 1995). Subsequently recorded as far south as 34° 21'N in Tunisia (Dalhoumi *et al.* 2011): not mapped.

Habitat In NW Africa, *M. s. schreibersii* is recorded from sclerophyllous forests, semi-desert grasslands and steppes and from farmlands. In

*Miniopterus schreibersii*

Algeria, mist-netted over bushes and over water (Kowalski & Rzebik-Kowalska 1991). In sub-Saharan Africa, *M. s. villiersi* has been recorded from lowland rainforest and montane forest on Mt Cameroon from 1100 to 2100 m.

Abundance Uncertain. In Algeria (and presumably throughout geographic range in NW Africa), reported numerous in caves and other underground day-roosts (Kowalski & Rzebik-Kowalska 1991). Elsewhere in Africa, rarely recorded and probably uncommon or rare.

Adaptations Aspect ratio medium; wing-loading low; wing-tip roughly triangular (Norberg & Rayner 1987). Flight reminiscent of that of swallows; flight speed in open 50–55 km/h. Predictably can also fly slowly with great manoeuvrability. By day, roosts in caves and other underground day-roosts including mine-adits, cisterns, aqueducts and cellars. Hangs freely or clings in contact to ceilings, walls or conspecifics. Often shares roosts with *Rhinolophus* spp. and *Myotis* spp. In Algeria, becomes torpid during day in autumn (Kowalski & Rzebik-Kowalska 1991), and hibernates in winter (Weber 1912). In Europe, hibernates from Oct (?) to end of Mar; preferred temperatures 7–12 °C; sometimes moves to different hibernacula (Schober & Grimmberger 1989). Also hibernates in Lebanon (Lewis & Harrison 1962). Often migrates from hibernacula to summer-roosts; in Algeria, some caves are occupied year-round.

Foraging and Food In Europe, forages for flying insects by fast-hawking and slow-hawking, 5–20 m above ground, in open areas, often far from the day-roost (Macdonald & Barrett 1993). Food includes moths, gnats and beetles.

Echolocation No information for this species in Africa. In Italy, call-shapes include: (a) smooth steep/shallow FM (the shallow component becoming QCF); and (b) QCF (Russo & Jones 2002).

Social and Reproductive Behaviour In Algeria, roosts singly, in pairs or in small groups (Kowalski & Rzebik-Kowalska 1991); in Europe, sometimes roosts in colonies of up to 40,000 individuals. In Algeria, in autumn and winter, individuals huddle in tight all-male or male-female clusters, sometimes on top of each other. In summer, ♀♀ segregate and form maternity colonies in maternity roosts. Except when suckling their young, ♀♀ roost together in clusters, with most of the young in separate, peripheral clusters. Apparently, when the young become volant, they start roosting with the adult ♀♀. Towards the end of the lactation period, some adult ♂♂ begin roosting with ♀♀ and their young. At least two vocalizations, audible to humans, are known.

Reproduction and Population Structure Litter-size: one. At 36° 38' N (Aokas, N Algeria), reproductive chronology is restricted seasonal monoestry with parturition from mid-Apr to late Jun; earlier in west than in east (Kowalski *et al.* 1986). In Europe, copulation, ovulation and fertilization occur in autumn; implantation is delayed and gestation is 8–9 months (Schober & Grimmberger 1989).

Predators, Parasites and Diseases Found once in owl pellets in Algeria (Kowalski & Rzebik-Kowalska 1991). Ectoparasites in NW Africa include bat-flies *Nycteribia pedicularia*, *N. latreillei*, *N. schmidli*, *N. vexata*, *Penicillidia dufouri*, *P. conspicua*, *Phthiridium biarticulatum* (Diptera: Nycteriibidae), *Brachytarsina africana*, *B. kollari* (Diptera: Streblidae) (Anciaux de Faveaux 1984).

Conservation IUCN Category: Near Threatened (based on data from North Africa, West Africa and extraliminally).

Based on overall population declines and range contractions, this species almost qualifies as Vulnerable.

Measurements

Miniopterus schreibersii

FA: 45.9 (44–49) mm, n = 83

WS (d): 322 (305–344) mm, n = 15*

TL: 114.3 (104–124) mm, n = 68

T: 55.8 (50–61) mm, n = 68

E: 11.2 (9–13) mm, n = 67

Tr: 6.2 (6–7) mm, n = 16*

Tib: 19.1 (17–21) mm, n = 83

HF: 9.9 (8–12) mm, n = 67

WT: 11.1 (9–16) g, n = 47

GLS: 15.8 (14.9–16.5) mm, n = 83

GWS: 8.6 (8.3–9.0) mm, n = 83

C–M³: 5.9 (5.4–6.3) mm, n = 83

Throughout African geographic range (AMNH, MHNG, Qumsiyeh & Schlitter 1982, Kowalski & Rzebik-Kowalska 1991, Peterson *et al.* 1995)

*Zimbabwe and Malawi only

Key Reference Kowalski & Rzebik-Kowalska 1991.

Judith Eger

Subfamily KERIVOULINAE – Woolly Bats

Kerivoulinae Miller, 1907. Bull. U.S. Nat. Mus., 57: 232.

Diagnostic combination of characters: second phalanx of third finger ca. as long as the first; braincase high and rounded; ears funnel-shaped with deep emargination below tip (Figure 116c); tragus long, narrow and sharply pointed (Figure 116j, k); six upper cheekteeth. Pelage woolly. Partly reviewed by Hill (1965, 1977b) and Corbet & Hill (1992). There are two genera:

Kerivoula (7 species in Africa). Posterior margin of tragus without deep, parallel-sided notch near base, skull with interorbital region

markedly constricted (Figure 153), outer upper incisor small but comparatively well developed, upper canine not grooved or only faintly grooved (see also genus *Kerivoula*).

Phoniscus (?1 species in Africa). Posterior margin of tragus with deep, parallel-sided notch near base, skull with interorbital region not markedly constricted, outer upper incisor rudimentary, upper canine conspicuously grooved (see also genus *Phoniscus*). The only record of this genus in Africa, *P. aerea*, is very dubious.

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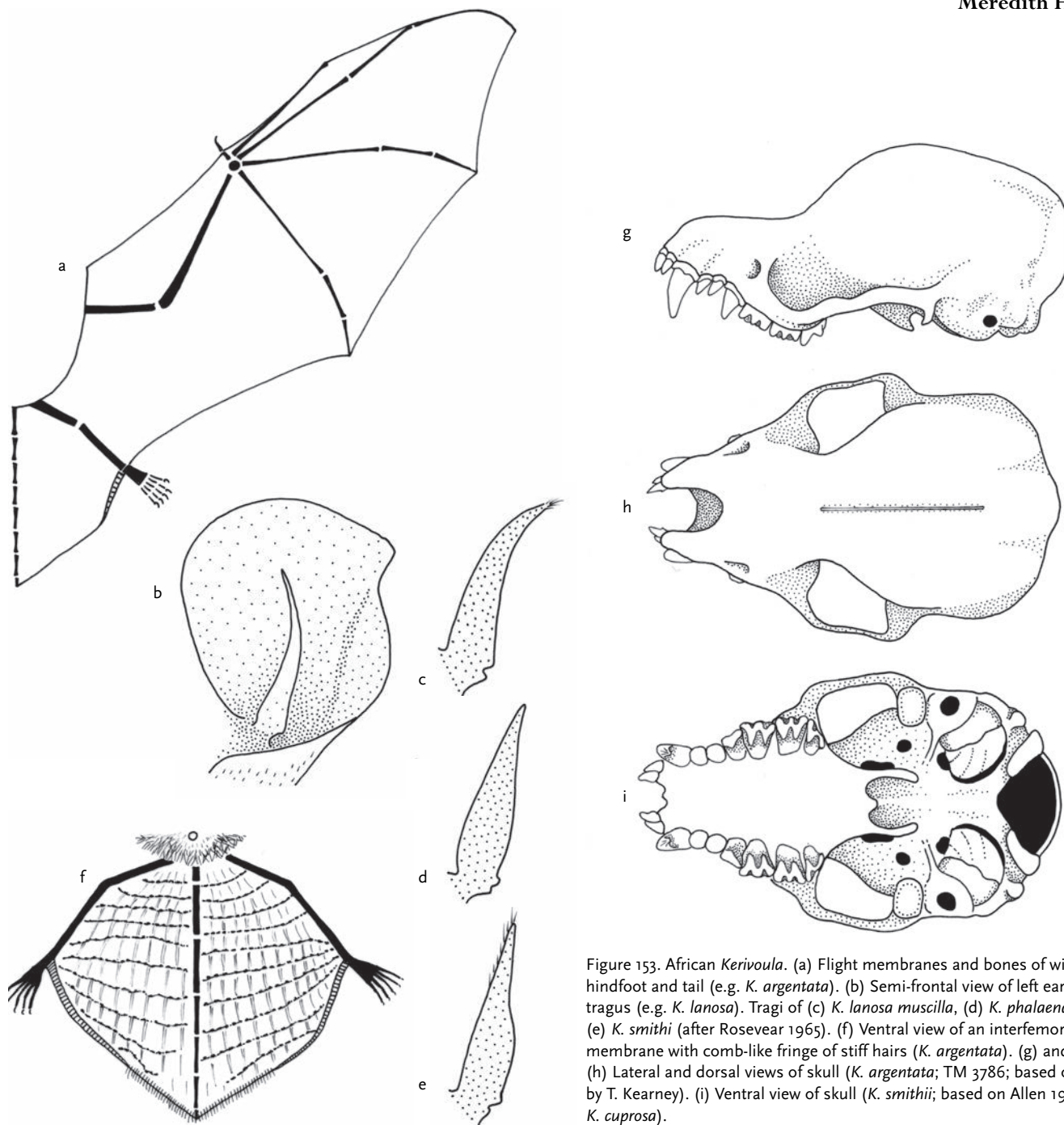


Figure 153. African *Kerivoula*. (a) Flight membranes and bones of wing, hindfoot and tail (e.g. *K. argentata*). (b) Semi-frontal view of left ear and tragus (e.g. *K. lanosa*). (c) Tragi of (c) *K. lanosa muscilla*, (d) *K. phalaena* and (e) *K. smithi* (after Rosevear 1965). (f) Ventral view of an interfemoral membrane with comb-like fringe of stiff hairs (*K. argentata*). (g) and (h) Lateral and dorsal views of skull (*K. argentata*; TM 3786; based on photos by T. Kearney). (i) Ventral view of skull (*K. smithii*; based on Allen 1917, as *K. cuprosa*).

GENUS *Kerivoula*

Woolly Bats

Kerivoula Gray, 1842. Ann. Mag. Nat. Hist., ser. 1, 10: 258. Type species: *Vespertilio pictus* Pallas, 1767.

A polytypic genus with 19 species, of which seven are endemic to Africa, and 11 occur in the Indo-New Guinea Region (Simmons 2005). Sometimes considered to include *Phoniscus* as a subgenus. Diagnostic combination of characters (African species): six upper cheekteeth (as in *Cistugo*, *Myotis* and *Phoniscus*), pelage woolly, frizzled, sometimes frosted; posterior margin of tragus with or without a shallow emargination near base (cf. *Phoniscus*); skull with rostral and anterior palatal emarginations long and narrow (cf. *Phoniscus*); interorbital region markedly constricted (narrower than posterior part of rostrum); outer upper incisor comparatively well developed albeit smaller than inner upper incisor; upper canine not grooved or only faintly grooved; dental formula: $2^{133}/_{3133} = 38$. Second phalanx of third finger not greatly elongated (cf. *Miniopterus*). Three species have a comb-like fringe of short, stiff, bristle-like hairs on or near the posterior margin of the interfemoral membrane. At least three (perhaps four) of the African species have frosted pelage, which, together with the underlying colour, provides very effective camouflage when these bats are roosting. The skull has a relatively long, narrow, flattened rostrum and a high-domed, rounded cranium, which rises at a sharp angle from the plane of the rostrum, giving the lateral profile a characteristic 'shoe shape' (Figure 153). Zygomatic arches slender; no sagittal crest; lambdoid crests very weakly developed. Auditory bullae prominent. Inner upper incisor larger than outer; inner incisor can be unicuspid, bicuspid or tricuspid, but the cuspidation of this tooth as a means of recognizing species is questioned by Rosevear (1965). Upper canines slender and small. Anterior and middle upper premolars equal in size and shape, both much smaller and simpler in form than the posterior upper premolar. Inner and middle lower incisors tricuspid or sometimes with four cusps. Outer lower incisor unicuspid, bicuspid, tricuspid

or occasionally with four cusps. Selected characters of African *Kerivoula* are illustrated in Figure 153.

The taxonomy of some African *Kerivoula* has been controversial, especially the status of forms with a comb-like fringe of hairs on the interfemoral membrane. These include *argentata*, *eriophora*, *harrisoni*, *lanosa* and *muscilla*, all of which have been given specific status fairly recently by some authors including Rosevear (1965), Hayman & Hill (1971), Ansell (1978), Smithers & Wilson (1979) and Happold *et al.* (1987). The status of *K. eriophora* is still uncertain, partly because the holotype has been lost and partly because there is no certain information about some of its characters (see profile), but its specific status is provisionally retained here, and by Simmons (2005). The specific status of *K. argentata* and *K. lanosa* are apparently unchallenged but, following Hill (1977b), both *harrisoni* and *muscilla* are currently placed in *K. lanosa*.

Kerivoula are rarely mist-netted but, in Cote d'Ivoire, *K. cuprosa* and *K. phalaena* have been harp-trapped but not mist-netted (see profiles). It is also very difficult to capture *Kerivoula* from their day-roosts. Consequently, the apparent rarity of *Kerivoula*, and the dearth of information about them, may be artefacts of sampling success.

The seven African species can be distinguished by a combination of characters including the presence or absence of a stiff comb-like fringe of hairs along the edge of the interfemoral membrane, FA length, the colour of the dorsal hairs and the extent to which the dorsal pelage is frosted or not frosted (Table 31). The cuspidation of the outer lower incisor and inner upper incisor is included in this table-key but the extent of variation is not yet known for some species (data available for <3 specimens), and might not yet be fully known for at least some of the other species.

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Table 31. Key to the African species in the genus *Kerivoula*.

| Comb-like fringe of hairs on interfemoral membrane | FA (mm) | Frosting on dorsal pelage | Colour of dorsal hairs (excluding hairs that are frosted) | Outer lower incisor | Inner upper incisor | Species |
|--|------------|---|--|--|----------------------------------|---------------------|
| Present | 28–39 | Conspicuous | Yellowish-fawn with dark brown at base and terminal quarter bright rusty-brown (perhaps occasionally pale sepia brown) | Usually tricuspid, sometimes with four cusps | Unicuspid, bicuspid or tricuspid | <i>K. argentata</i> |
| Present | 30–34 | Conspicuous or sometimes not very conspicuous | Dark sepia brown, golden-brown, greyish-brown or pale grey with dark brown at base | Bicuspid or tricuspid | Unicuspid or bicuspid | <i>K. lanosa</i> |
| Present | 28, ca. 32 | Probably absent | Pale 'earth-grey' with white tip | Bicuspid ^a | Tricuspid ^a | <i>K. eriophora</i> |
| Absent | 32–36 | Conspicuous | Blackish or dark brown | Unicuspid | Bicuspid | <i>K. smithii</i> |
| Absent | 30–33 | Conspicuous | Dark brown with terminal third bright rusty-brown or chocolate brown | Tricuspid | Bicuspid | <i>K. cuprosa</i> |
| Absent | 25–28 | Absent | Pale reddish-brown, fawn-brown or greyish-brown; usually darker at base | Unicuspid | Unicuspid or bicuspid | <i>K. phalaena</i> |
| Absent | 28 | Uncertain, if present, probably not conspicuous | Dark brown to black with greyish-brown tip | Unicuspid ^a | Bicuspid ^a | <i>K. africana</i> |

^a Based on samples of <3 specimens and therefore the variation is not known.

Kerivoula africana TANZANIAN WOOLLY BAT

Fr. Chauve-souris peinte de Tanzanie; Ger. Tansania-Wollfledermaus

Kerivoula africana Dobson, 1878. Cat. Chiroptera Brit. Mus., p. 335. Coast opposite Zanzibar I., Tanzania.**Taxonomy** Synonyms: none. Chromosome number: not known.

Description Very small microbat without noseleaf and with tail more or less fully enclosed in interfemoral membrane; six upper and six lower cheekteeth on each side; ears funnel-shaped; pelage frizzled; upper canine not grooved; FA: ca. 28 mm; dorsal pelage greyish-brown or brownish-grey, frosting uncertain; posterior margin of interfemoral membrane without comb-like fringe of bristle-like hairs. Pelage woolly and frizzled. Dorsal pelage greyish-brown to brownish-grey, sometimes with silvery-grey streaks (but probably without conspicuous frosting); hairs dark brown to black with greyish-brown tip (Dobson 1878). Ventral pelage slightly paler. Head with narrow muzzle and high-domed crown; face nearly naked between eyes; long hairs arising from glands on muzzle; upper lip with fringe of hairs. Ears widely separated, funnel-shaped, pale brown; relatively short (46% of FA) but reaching beyond snout when laid forward. Tragus long (ca. 58% of E), tapering, sharply pointed. Eyes minute. Wings dark brown. Interfemoral membrane dark brown; dorsal pelage extending onto membrane close to body; posterior margin with few fine hairs only. Skull with high-domed cranium; frontal region sharply angular to plane of rostrum as in all *Kerivoula*. Inner upper incisor bicuspid; outer upper incisor unicuspid or bicuspid (with small or large basal cusp), and almost reaching height of inner incisor. Anterior and middle upper premolars subequal; both smaller than posterior premolar. Outer lower incisor unicuspid. Lower premolars subequal.

Geographic Variation None.

Similar Species Three other African *Kerivoula* do not have a comb-like fringe of hooked, bristle-like hairs on posterior margin of interfemoral membrane (Table 31, p. 724):

Kerivoula smithii. Pelage conspicuously frosted. Forearm longer (32–36 mm). Outer lower incisor unicuspid.

K. cuprosa. Pelage conspicuously frosted. FA longer (30–33 mm).

K. phalaena. Dorsal hairs pale reddish-brown, fawn or greyish-brown, usually with darker base. Outer upper incisor ca. two-thirds height of inner incisor, and with only a minute secondary cusp at the internal base.

Distribution Endemic to Africa. Recorded from only three localities. Apparently endemic to the coastal forests and lowland Eastern Arc Mts of Tanzania (Cockle *et al.* 1998).

Habitat Wetter and drier evergreen and semi-evergreen coastal forests on hills near Tanzanian coast: four recorded in Genda Genda Forest in the north, and one in Tong'omba Forest in the south (Cockle *et al.* 1998). Also recorded from Morogoro (Swynnerton & Hayman 1951) without details of habitat.

Abundance Very rare in collections.

Remarks Very little is known about this species. A ♂ and three pregnant ♀ were found roosting together inside hanging epiphytes in thicket forest, ca. 2.5 m above ground (Cockle *et al.* 1998).

Conservation IUCN Category: Endangered.

Only known from two locations (three localities). Has a very small population in a well-surveyed area. The coastal forests, and those around Morogoro are being lost at a very rapid rate.

Measurements*Kerivoula africana*

FA: 28 mm

WS: n. d.

TL: 69 mm

T: 34 mm

E: 13 mm

Tr: 8 mm

Tib: 11 mm

HF: 6 mm

WT: n. d.

GLS: n. d.

GWS: n. d.

C–M³: n. d.

Tanzania (holotype; Dobson 1878). Original measurements in inches and, presumably, decimal fractions of one inch: e.g. T: 1".35

Key Reference Cockle *et al.* 1998.

Meredith Happold

*Kerivoula africana*

Kerivoula argentata DAMARA WOOLLY BAT

Fr. Chauve-souris peinte argentée; Ger. Bunte Wollfledermaus

Kerivoula argentata Tomes, 1861. Proc. Zool. Soc. Lond. 1861: 32. Otjoro, Namibia.

Taxonomy Synonyms: *nidicola*, *zuluensis*. Subspecies: three. Chromosome number: not known.

Description Very small microbat without noseleaf and with tail more or less fully enclosed in interfemoral membrane; six upper and six lower cheekteeth on each side; ears funnel-shaped; pelage frizzled; upper canine not grooved; FA: 35.1 (28–39) mm; dorsal pelage usually bright rusty-brown with conspicuous silvery frosting; posterior margin of interfemoral membrane with comb-like fringe of hairs. Sexes similar. Pelage woolly and frizzled (many hairs with hooked tips), extending onto dorsal surface of forearm and tibia; mid-dorsal hairs 7–9 mm, ventral pelage longer and fluffy. Dorsal pelage bright rusty-brown (possibly occasionally pale sepia brown) with conspicuous, almost iridescent, silvery frosting; hairs yellowish-fawn with dark brown at base and terminal quarter reddish-brown, often with silvery or white tip. Ventral pelage cream, dirty-white or white. Head high-domed; muzzle long, narrow, flattened, mostly hidden by facial pelage; snout prominent. Eyes minute. Ears widely separated, funnel-shaped with sharply pointed tip; outer margin with concavity below tip. Tragus long (ca. 60% of E), narrow, tapering to sharp point; base with shallow emargination below widest point. Wings and interfemoral membrane pale brown, translucent. Dorsal surface of proximal half of interfemoral membrane with sparse covering of hair; posterior margin (between tips of calcars) with comb-like fringe of bristle-like hairs that curve inwards like hooks (Figure 153f). Tail 92 (87–100)% of HB, $n = 9$.

Skull (Figure 153) delicate; braincase high-domed; rostrum narrow; frontal region sharply angular to plane of rostrum as in all *Kerivoula*. Inner upper incisor tall with 0–2 basal cusps; outer upper incisor shorter, with 1–2 basal cusps. Anterior and middle upper premolars subequal; ca. half height of posterior premolar. Outer lower incisor usually tricuspid but sometimes with four cusps (i.e. with two, or sometimes three, basal cusps arising from cup-shaped cingulum, which are less than half the height of the main cusp).

Geographic Variation Meester *et al.* (1986) (and others including Simmons 2005) recognize three subspecies:

K. a. argentata: SW Kenya, Tanzania, DR Congo (Katanga Province),

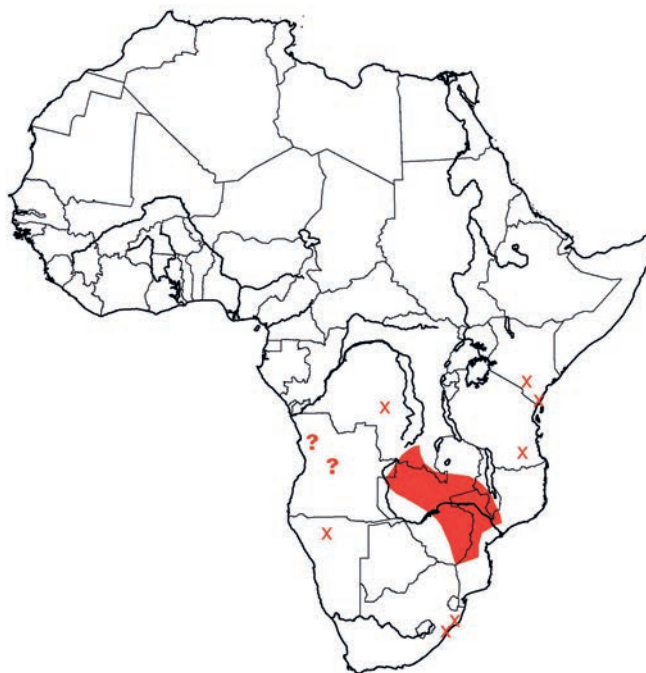
C Angola, N Namibia (Ovamboland), Zambia and Malawi.

K. a. nidicola: C Mozambique to Zambezi valley.

K. a. zuluensis: Zimbabwe, S Mozambique and KwaZulu–Natal.

Similar Species Only one other African *Kerivoula* (and possibly also *K. eriophora*) has a comb-like fringe of hairs on the posterior margin of the interfemoral membrane (Table 31, p. 724):

Kerivoula lanosa. Dorsal pelage dark brown to pale grey (with frosting), but not bright reddish-brown (with frosting). Ventral pelage sepia brown, grey to whitish. On average, FA shorter



Kerivoula argentata

(31.5 [30–34] mm). Skull shorter and more delicate (GLS: 12.6 [11.2–13.5] mm).

K. eriophora. Dorsal pelage frosted but not bright reddish-brown. Ethiopia.

Distribution Endemic to Africa. Recorded mainly from the Zambezian Woodland BZ, but also recorded from the Somalia–Masai Bushland BZ and the Southern Rainforest–Savanna Mosaic, and from the Coastal Forest Mosaic BZ in East Africa and in South Africa. Recorded from S DR Congo, SW Kenya, Tanzania, Zambia, Mozambique, Zimbabwe, Namibia and South Africa. Possibly recorded from Angola, but the records might represent *K. lanosa* (Crawford-Cabral 1986). Gaps in the distribution, especially in the Zambezian Woodland BZ, probably reflect insufficient sampling.

Habitat Evergreen forests, riverine forest and both mesic and dry woodland savannas. In southern Africa, tends to be confined to well-watered or riverine associations in dry country (Smithers 1983).

Abundance Uncertain. Although rarely encountered within its geographic range (e.g. Happold & Happold 1997), it may be more abundant than records indicate.

Adaptations Aspect ratio low; wing-loading very low (Aldridge & Rautenbach 1987, M. Happold unpubl.). Flight slow and fluttering, with very great manoeuvrability. Able to take off

from the ground; able to hover briefly; turns by banking (minimum radius <25 cm) and by stalling-and-twisting; one individual sustained flight within a 1×1×1 m enclosure for up to 32 circuits/flight (10 flights; M. Happold unpubl.). These abilities, together with efficient echolocation, probably enable *K. argentata* to avoid being captured in mist-nets. By day, has been found most often roosting in nests of weaver birds, including Masked Weaver *Ploceus velatus* and Spectacled Weaver *P. ocularis*, but has also been found roosting among clusters of dead leaves, on the rough bark of a tree, under the eaves of a hut, and on a wall sheltered by the eaves of a rondavel (Sclater 1901, Roberts 1951, Smithers & Wilson 1979). Frosted brown pelage provides roosting bats with effective camouflage: one cluster roosting under eaves resembled a mud-nest made by wasps (Shortridge 1934).

Foraging and Food No information. Based on wing morphology, flight characteristics and ‘whispering’ echolocation, this species is likely to forage near the ground in habitats cluttered by vegetation. The capture of one specimen ca. 1 m above ground (in a mist-net) supports this suggestion. Likely to forage by gleaning (as some Malaysian *Kerivoula* are predicted to do [Kingston *et al.* 1999]). Diet not known. The possibility that this species is a ‘spider specialist’ (as is *Phoniscus papuensis* in Australia [Schulz 2000, as *K. papuensis*]) invites investigation.

Echolocation Call-shape (flying in darkened laboratory) steep linear FM (Fenton & Bell 1981). Intensity very low; start-frequency ca. 120 kHz; end-frequency ca. 85 kHz; peak-frequency 90–118 kHz; maximum call-duration 2 ms. This species (and at least some other *Kerivoula* spp.) is a ‘whispering bat’, these being bats that echolocate with calls of very low intensity (<75 dB at 10 cm) (Fenton & Bell 1981). ‘Whispering’ echolocation is typical of nycterids, but *Kerivoula* spp. are the only African vespertilionids (for which information is available) that are whispering bats.

Social and Reproductive Behaviour Roosts singly, in pairs or in groups of up to five (Shortridge 1934, Smithers 1983). Up to three have been found, tightly huddled, in bird nests, and groups of 4–5 have been found hanging in tightly packed clusters, under eaves. One such group comprised five ♀♀.

Reproduction and Population Structure No information.

Predators, Parasites and Diseases No information.

Conservation IUCN Category: Least Concern.

This species is not well known but has a large geographic range and is difficult to sample. No specific threats identified.

Measurements

Kerivoula argentata

FA: 35.1 (28–39) mm, n = 23

WS (a): 284 mm, n = 1

TL: 88.2 (74–102) mm, n = 20

T: 43.2 (40–52) mm, n = 27

E: 13.2 (11–15) mm, n = 31

Tr: 6.9 (6.3–7.5) mm, n = 3

Tib: 15.6 (14–17) mm, n = 8

HF: 10.3 (10–11) mm, n = 8

WT: 7.4 (5.5–10.5) g, n = 23

GLS: 15.7 (14.7–16.5) mm, n = 15

GWS: 9.5 (9.1–10.8) mm, n = 13

C–M³: 6.2 (5.8–6.6) mm, n = 16

Angola, Malawi, Mozambique, Zimbabwe (BMNH, HC, NMZB, ROM, TM, Hill & Carter 1941, Smithers & Wilson 1979)

Key References Hayman & Hill 1971; Smithers 1993.

F. P. D. Cotterill

Kerivoula cuprosa COPPER WOOLLY BAT

Fr. Chauve-souris peinte cuivrée; Ger. Kupferfarbene Wollfledermaus

Kerivoula cuprosa Thomas, 1912. Ann. Mag. Nat. Hist., ser. 8, 10: 41. Bitye, Dja River, Cameroon.

Taxonomy Synonyms: none. *Kerivoula cuprosa* has frequently been confused with *K. smithii* and was incorrectly listed as a synonym of *K. smithii* by Anciaux de Faveaux (1984). Chromosome number: not known.

Description Very small microbat without noseleaf and with tail more or less fully enclosed in interfemoral membrane; six upper and six lower cheekteeth on each side; ears funnel-shaped; pelage frizzled; upper canine not grooved; FA: 31.7 (30–33) mm; dorsal pelage dark or chocolate brown with frosting; posterior margin of interfemoral membrane without comb-like fringe of bristle-like hairs; inner upper incisor bicuspid; outer lower incisor tricuspid. Sexual dimorphism: no information. Pelage dense, woolly, frizzled (many hairs with hooked tips); extending onto dorsal surface of forearm and tibia; mid-dorsal hairs ca. 7–8 mm. Dorsal pelage dark or chocolate brown, with golden sheen or singed appearance

depending on angle of view; hairs dark brown with terminal third bright rusty-brown or chocolate brown; many hairs with pale-brown hooked tip. Ventral pelage duller brown; hairs dark greyish-brown with terminal third paler; tip of some hairs whitish or cream. Head high-domed; muzzle long, pointed, hidden by facial pelage. Eyes minute. Ears brown, widely separated, comparatively and relatively short for a vespertilionid (42 [39–47]% of FA); anterior border strongly convex; posterior border with angular concavity just below the tip. Tragus moderately long (51 [46–56]% of E), narrow, tapering to sharp point, curved outwards, its base with a small lobule above which there is an emargination. Wings and interfemoral membrane dark brown. Posterior margin of interfemoral membrane with thinly scattered curled hairs but no comb-like fringe of hooked, bristle-like hairs; proximal third of dorsal surface sparsely covered with hairs. Tail 114 (100–133)% of HB.

Skull delicate; braincase high-domed; rostrum narrow; frontal region sharply angular to plane of rostrum as in all *Kerivoula*. Upper incisors comparatively short (cf. *K. phalaena*, *K. smithii*). Inner upper incisor bicuspid, the secondary cusp ca. half the length of the main cusp. Outer upper incisor ca. half to two-thirds the height of inner incisor, either unicuspid or weakly bicuspid, secondary cusp orientated postero-internally. Outer lower incisor tricuspid; outer cusps arising from cup-shaped cingulum (thereby creating tricuspid appearance) and ca. half height of main cusp. Lower premolars subequal in height but anterior premolar broader than both middle and posterior premolar.

Geographic Variation No information.

Similar Species Three other African *Kerivoula* have no comb-like fringe of hooked, bristle-like hairs on posterior margin of interfemoral membrane (Table 31, p. 724):

Kerivoula smithii. Outer lower incisor unicuspid (cingulum not distinctly raised on both sides of main cusp). Upper incisors comparatively long. Slightly larger (FA: 34.1 [32–36] mm; GLS: 13.1–14.1 mm) and heavier (5.9–7.0 g). Tragus longer (7.3–9.0 mm).

K. phalaena. Pelage not frosted. Outer lower incisor unicuspid. Almost always smaller (FA: 25–30 mm; GLS: 11.6–12.5 mm; GWS: 7.2 [6.6–7.4] mm).

K. africana. FA shorter (28 mm). Pelage probably not conspicuously frosted.

Distribution Endemic to Africa. Recorded mainly from the Rainforest BZ (Western, West Central, South Central and East Central regions) with one record in the Northern Rainforest–Savanna Mosaic in Guinea and another in the Guinea Savanna BZ in Côte d'Ivoire. Known from only seven localities: Pic de Fon, Guinea; Tâi N. P. and Comoé N. P., Côte d'Ivoire; Bitye (Dja R.), Cameroon; Eala, Koteli and Wafanya, DR Congo (Thomas 1912a, Schouteden 1944 [partim], J. Fahr unpubl., RMCA). A specimen from Ghana, originally identified as *K. cuprosa* (Koopman 1989), has been re-identified as *K. lanosa* (Koopman *et al.* 1995). Another record from Kenya (Fort Warwick, HZM 1.2066, Harrison 1957c) has been re-identified as *K. smithii* (J. Fahr unpubl.). Also many of the records from DR Congo, originally published as *K. cuprosa* (Allen 1917a, Dollman 1914, Schouteden 1944 [partim], Hayman *et al.* 1966 [partim], Anciaux de Faveaux 1984 [partim] and references therein) have been re-identified as *K. smithii* (Koopman 1965, J. Fahr unpubl.).

Habitat Recorded from lowland rainforest, swamp forest and forest–savanna mosaic in the Guinea Savanna BZ (Comoé N. P., Côte d'Ivoire).

Abundance Uncertain. Appears to be very rare, but probably very difficult to catch in mist-nets and by other methods used in the past; in Côte d'Ivoire, four individuals were captured with harp-traps, but none were caught in mist-nets (J. Fahr unpubl.).

Remarks Wings broad; flight highly manoeuvrable; can hover for short periods. Possibly roosts among leaves as do other members of the genus. All specimens in Côte d'Ivoire were caught in dense vegetation with harp-traps at height of 1.5 m (n = 4). Likely to forage in cluttered



Kerivoula cuprosa

spaces and likely to be a gleaner. Diet not known but delicate skull and dentition indicates that it probably consists of soft-bodied and rather small arthropods. Echolocation calls are steep, broad-band FM calls (details not known). Ectoparasites include a mite *Olabidocarpus belsorum* (Acari: Chirodiscidae) (Anciaux de Faveaux 1984, as *K. smithii*). Nothing else appears to be known about this species.

Conservation IUCN Category: Data Deficient.

Only seven localities known. Could become threatened under criterion A4c because of loss of forest. Population trend not known. Major threats: loss and degradation of habitat as result of logging and agriculture.

Measurements

Kerivoula cuprosa

FA: 31.7 (30–33) mm, n = 8

WS (d): 216 (201–223) mm, n = 4

TL: 78.3 (74–83) mm, n = 7

T: 42.2 (40–44) mm, n = 7

E: 13.3 (12–14) mm, n = 8

Tr: 6.5 (5.5–7.4) mm, n = 5

Tib: 14.0 (14–15) mm, n = 7

HF: 6.9 (5.8–7.5) mm, n = 7

WT: 4.1 (4.0–4.5) g, n = 4

GLS: 12.8 (12.3–13.1) mm, n = 5

GWS: 8.1 (7.9–8.4) mm, n = 5

C–M³: 5.1 (5.0–5.3) mm, n = 7

Guinea, Côte d'Ivoire, Cameroon (holotype), DR Congo (BMNH, FC, RMCA, SMF)

Key References Hayman *et al.* 1966; Koopman 1965; Schouteden 1944; Thomas 1912b.

Jakob Fahr

Kerivoula eriophora HEUGLIN'S WOOLLY BAT

Fr. Chauve-souris peinte d'Éthiopie; Ger. Heuglins Wollfledermaus

Kerivoula eriophora (Heuglin, 1877). Reise in Nordost-Afrika, 2: 34. Belegaz Valley, between Semian and Wogara, Ethiopia.

Taxonomy Originally *Nycticejus eriophorus*. Synonyms: none. A species of doubtful status. The holotype is lost, and presuming that this was the only information, Largen *et al.* (1974) referred it to *K. africana* from Tanzania, but Kock (1984) rediscovered a surviving syntype and concludes that it should be referred to *K. lanosa*. Yalden *et al.* (1996) also conclude that *eriophorus* is a junior synonym of *K. lanosa* and that it is a prior name for *K. l. harrisoni*. Chromosome number: not known.

Description Very small microbat without noseleaf and with tail more or less fully enclosed in interfemoral membrane; six upper and six lower cheekteeth on each side; ears funnel-shaped; pelage frizzled; upper canine not grooved; FA: ca. 28–32 mm; dorsal pelage pale grey probably without frosting; posterior margin of interfemoral membrane with comb-like fringe of hairs. Very poorly known. Based on the original description by Heuglin (1877), the pelage is frizzled; the dorsal pelage is pale 'earth-grey'; hairs with white tip, and the ventral pelage is dirty white becoming more greyish-brown on flanks. Wings and interfemoral membrane blackish-brown. Ears with pointed tip. Tragus long (almost as high as tip of ear), thin and 'lanceolate' (sharply pointed). No other information given. Heuglin's description of the pelage is ambiguous: 'hairs with white tip' could imply frosting but, if by 'tip' he meant the terminal third or terminal quarter of each hair, the pelage would look white or whitish without appearing to be frosted. The pelage of the syntype (NMW 24573) does not look frosted; the hairs are bicoloured, medium brown with rather long whitish tip (B. Herzig pers. comm.).

The skull of the syntype is damaged; its shape and measurements cannot be obtained. Inner upper incisor tricuspid with one small cusp arising from the cingulum and another minute one near the tip of the main cusp. Outer upper incisor distinctly more than half height of inner incisor (cf. *K. lanosa*). Anterior and middle upper premolars subequal. Outer lower incisor bicuspid, the second cusp being small. (Dentition described by B. Herzig pers. comm.)

Geographic Variation Not known.

Similar Species Uncertain (see Table 31, p. 724):

Distribution Endemic to Africa. If distinct, only known from the Afromontane–Afroalpine BZ of the Ethiopian Highlands, Ethiopia. Recorded from the Belegaz Valley between Semian and Wogara in Abyssinia (= Ethiopia) at 12° 50' N, 38° 20' E.

Habitat The Belegaz Valley is a high altitude (2300–3300 m) site in *Erica arborea*/*Hypericum revolutum* scrub. This habitat is now much degraded by the growing of cereals.

Abundance Uncertain. Known only from the three original specimens collected prior to 1877. It has not been collected in Ethiopia since then, despite moderately extensive collecting.

*Kerivoula eriophora*

Remarks The three bats were found in the hanging nest of a sparrow or species of weaverbird. If they do represent a distinct species, nothing else is known about their habits.

Conservation IUCN Category: Data Deficient.

Measurements

Kerivoula eriophora

FA: 28, ca. 32 mm

WS: n. d.

TL: ca. 85, – mm

T: 32, – mm

E: 13, – mm

Tr: n. d.

Tib: –, 13.6 mm

HF: –, 6.7 mm

GLS: n. d.

GWS: n. d.

C–M³: –, 5.0 mm

Ethiopia (holotype, Heuglin 1877, and syntype [NMW 24573]

Yalden *et al.* 1996, respectively)

Key References Heuglin 1877; Kock 1984; Yalden *et al.* 1996.

D. W. Yalden

Kerivoula lanosa LESSER WOOLLY BAT

Fr. Chauve-souris peinte laineuse; Ger. Kleine Wollfledermaus

Kerivoula lanosa (A. Smith, 1847). Illustr. Zool. S. Afr. Mamm., pl. 50. 322 km (200 miles) east of Cape Town, Cape Province, South Africa.

Taxonomy Originally *Vespertilio lanosus*. Synonyms: *bellula*, *brunnea*, *harrisoni*, *lucia* and *muscilla* (Hill 1977b), but the status of these forms needs further investigation. Possibly also includes *eriophora* (see profile *K. eriophora*). Its relationship to the poorly known *K. africana* awaits elucidation. Subspecies: four. Chromosome number (South Africa): $2n = 28$; $aFN = 50$. X = large metacentric, Y = small acrocentric (Rautenbach *et al.* 1993). Happold *et al.* (1987) treated *harrisoni* (Malawi and Zambia) as a distinct species, and *lucia* as a subspecies of *K. harrisoni*.

Description Very small microbat without noseleaf and with tail more or less fully enclosed in interfemoral membrane; six upper and six lower cheekteeth on each side; ears funnel-shaped; pelage frizzled; upper canine not grooved; FA: 31.5 (30–34) mm; dorsal pelage golden-brown, greyish-brown or pale grey, with frosting; posterior margin of interfemoral membrane with comb-like fringe of hairs; inner upper incisor unicuspid or bicuspid, outer lower incisor bicuspid. Sexes similar. Pelage fine, woolly and frizzled (many hairs with hooked tips); extending onto dorsal surface of forearm and tibia; mid-dorsal hairs 6–7 mm. Dorsal pelage variable, dark sepia brown, golden-brown, greyish-brown or pale grey; hairs with dark brown at base, many with a pale brown, cream, silvery or white tip giving pelage a frosted appearance (sometimes not very conspicuous). Ventral pelage similar or paler, sometimes whitish at least on chest and belly; hairs with basal half dark brown, medium greyish-brown or grey; some hairs with white tip. Head high-domed; muzzle long, pointed, hidden by facial pelage; snout prominent. Eyes minute. Ears widely separated, semi-translucent pale brown, comparatively and relatively short for a vespertilionid (37 [31–43]% of FA); funnel-shaped with pointed tips; outer margin with concavity below tip. Tragus long (68 (62–74)% of E, $n = 6$), narrow, tapering to sharp point, posterior margin with shallow notch below widest point; tip with a few short hairs (Figure 153b). Wings and interfemoral membrane semi-translucent, pale grey to pale brown; thumb long and slender. Dorsal surface of proximal half of interfemoral membrane with sparse covering of hair; posterior margin (between tips of calcars) with comb-like fringe of bristle-like hairs, which curve inwards like hooks. Tail 87 (70–100)% of HB, $n = 7$.

Skull delicate; braincase high-domed; rostrum narrow; frontal region sharply angular to plane of rostrum as in all *Kerivoula*. Inner upper incisors long, pointed, unicuspid or bicuspid (having a basal subsidiary cusp, which can be rudimentary to pronounced); outer upper incisor minute, usually unicuspid but sometimes with subsidiary cusp. Anterior and middle upper premolars subequal; both much smaller than posterior premolar. Outer lower incisor with a main cusp and cup-shaped cingulum, which gives tooth a bicuspid or tricuspid appearance.

Geographic Variation Four subspecies are recognized by Hill (1977b), Meester *et al.* (1986), Koopman (1994) and Simmons (2005):

K. l. muscilla: Liberia and Guinea to Ghana, Nigeria, Cameroon, Gabon, Central African Republic and N DR Congo. Inner and outer upper incisors usually unicuspid, but sometimes with a subsidiary cusp (J. Fahr pers. comm.).

K. l. harrisoni: Ethiopia to Kenya and Tanzania.

K. l. lucia: south-central Africa (S DR Congo [Katanga Province] to Malawi), southern Africa (Botswana, Zimbabwe and south to KwaZulu–Natal [South Africa]). Inner upper incisors bicuspid; outer upper incisors unicuspid (J. Fahr pers. comm.).

K. l. lanosa: S and E Cape Province, South Africa.

In contrast, Yalden *et al.* (1996) question the justification for recognizing subspecies and suggest variation in *K. lanosa* is clinal.

Similar Species Only one other African *Kerivoula* (and possibly also *K. eriophora*) has a comb-like fringe of hairs on the posterior margin of the interfemoral membrane (Table 31, p. 724):

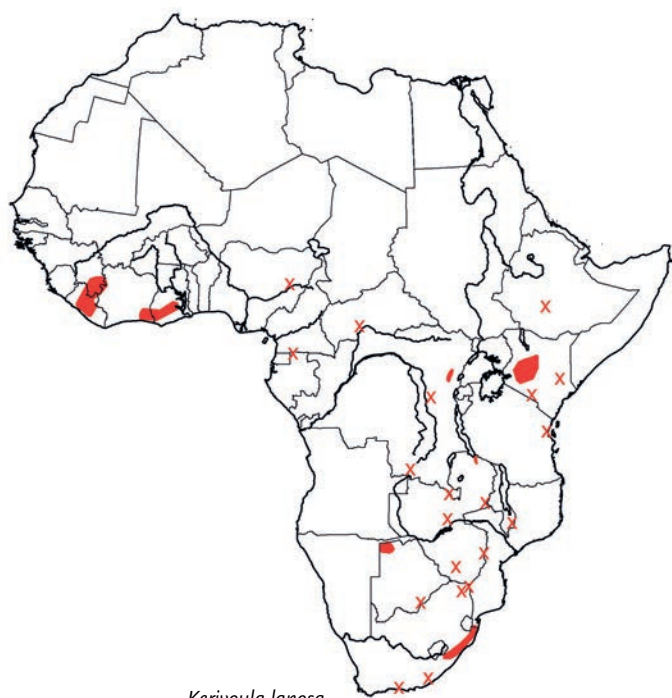
Kerivoula argentata. Dorsal pelage bright reddish-brown (with frosting). Ventral pelage cream, dirty-white or white. On average, FA longer (35.1 [28–39] mm). Skull longer and more robust (GLS: 15.7 [14.7–16.5] mm).

K. eriophora. Distinguishing characters (if any) not known: similar enough to be considered conspecific by Kock (1984). Presence of comb-like fringe of hairs on margin of interfemoral membrane is uncertain.

Distribution Endemic to Africa. Known from widespread, scattered records in the Rainforest BZ, the Northern Rainforest–Savanna Mosaic, Somalia–Masai Bushland, Coastal Forest Mosaic, Zambezian Woodland and South-West Cape BZs (with an outlying record in the Sudan Savanna BZ in Nigeria). Also occurs in or near the Afromontane–Afroalpine BZ of W Kenya (e.g. Nyeri and Cherangani Hills). Recorded from Liberia and Guinea to Ethiopia (but not in all countries), and southwards (on the eastern side of the continent) to South Africa (Hill 1997b and others).

Habitat Very varied. West Africa: apparently found mainly in rainforest (no details available); at Numan, Nigeria, found near the Benue R. in the Guinea Savanna BZ. Ethiopia: recorded between two of the lakes in the Rift Valley where the vegetation is predominantly *Acacia–Commiphora* bushland, at ca. 1300 m. Kenya: forests and *Acacia–Commiphora* bushland; no details available. Malawi: taken in a clump of bamboos in a forest full of bamboos at ca. 1000 m (R. C. Wood in Kershaw 1922). Southern Africa: evergreen forest, riverine forest and both wetter and drier woodland savannas (Cotterill 1996a). In drier areas, associated with riverine habitats.

Abundance Uncertain. Poorly represented in collections but this is possibly because their day-roosts are hard to find, they seem able to



Kerivoula lanosa

avoid being captured in mist-nets, and there have been comparatively few attempts to catch them in harp-traps.

Remarks Wings broad; based on wing morphology flight predicted to be slow and highly manoeuvrable as in *K. argentata*. The frosted pelage provides effective camouflage when this bat is roosting (e.g. Roberts 1951), and perhaps its woolly texture provides extra insulation from unfavourable temperatures likely to be experienced where these small bats roost in foliage. Most specimens have been taken from day-roosts in the woven-grass nests of weavers *Ploceus* spp.; some have been taken from nests made of cobwebs by sunbirds (Nectariniidae). A single ♀ was found in a sunbird nest, and a ♂ and two ♀♀ were found in a weaver nest (Smithers 1983). Two other nests contained two and

three individuals, respectively (not sexed) (Roberts 1951). Another nest contained a ♀ with two young, suggesting that she had given birth to twins. The echolocation calls of a ♂ (from Mberengwa, Zimbabwe) were steep linear FM in call-shape; start-frequency at least 170 kHz; end-frequency 100 kHz; intensity very low (F. P. D. Cotterill unpubl.). The calls are similar to those of Malaysian *Kerivoula* spp., which are predicted to forage by gleaning (Kingston *et al.* 1999). Diet not known; the possibility that this species is a 'spider specialist' (as is *Phoniscus papuensis* in Australia [Schulz 2000, as *K. papuensis*]) invites investigation.

Predators, Parasites and Diseases Ectoparasites include bat-flies *Basilia meridionalis*, *B. kerivoulae* (Nycteribiidae) (Anciaux de Faveaux 1984).

Conservation IUCN Category: Least Concern.

Measurements

Kerivoula lanosa

FA: 31.5 (30–34) mm, n = 23

WS (d): 253 (240–269) mm, n = 5

TL: 80.0 (74–90) mm, n = 16

T: 37.0 (30–42) mm, n = 22

E: 12.1 (10–14) mm, n = 22

Tr: 8.3 (7–9) mm, n = 6

Tib: 12.8 (12–15) mm, n = 15

HF: 6.8 (5–8) mm, n = 10

WT: 6.5 (4.5–8.0) g, n = 7

GLS: 12.6 (11.2–13.5) mm, n = 30

GWS: 8.0 (7.5–8.4) mm, n = 18

C–M³: 5.0 (4.6–5.8) mm, n = 29

Throughout geographic range (BMNH, NMZB, TM and literature)

Key References Cotterill 1996a; Hill 1977b; Smithers 1983.

F. P. D. Cotterill

Kerivoula phalaena SPURRELL'S WOOLLY BAT

Fr. Chauve-souris peinte phalène; Ger. Spurrells Wollfledermaus

Kerivoula phalaena Thomas, 1912. Ann. Mag. Nat. Hist., ser. 8, 10: 281. Bibianaha, 216 m (720 ft), inland of Denkwā, Ghana.

Taxonomy Synonyms: none. Chromosome number: not known.

Description Very small microbat without noseleaf and with tail more or less fully enclosed in interfemoral membrane; six upper and six lower cheekteeth on each side; ears funnel-shaped; pelage frizzled; upper canine not grooved; FA: 25–28 mm; dorsal pelage various shades of brown, without frosting; posterior margin of interfemoral membrane without comb-like fringe of bristle-like hairs; inner and outer upper incisors unicuspid or weakly bicuspid; outer lower incisor unicuspid. Females with on average slightly longer forearms; sexes otherwise similar. Pelage dense, woolly, frizzled (many hairs with hooked tips); mid-dorsal hairs 6–7 mm. Dorsal pelage pale reddish-brown, fawn-brown or greyish-brown; not frosted; hairs

usually darker at base. Ventral pelage paler, less reddish. Head high-domed; muzzle long, pointed, hidden by facial pelage. Eyes minute. Ears medium brown, widely separated, comparatively and relatively short for a vespertilionid (47 [39–56]% of FA). Tragus long (50 [43–57]% of E), narrow, tapering to fairly sharp point. Wings blackish brown; pelage not extending to dorsal surface of forearm and tibia. Interfemoral membrane blackish-brown; posterior margin with thinly scattered hairs but no comb-like fringe of hooked, bristle-like hairs; very few hairs on dorsal surface. Tail 115 (92–138)% of HB.

Skull delicate; braincase high-domed, rostrum narrow; frontal region sharply angular to plane of rostrum. Upper incisors comparatively long (cf. *K. cuprosa*). Inner upper incisor unicuspid or with small secondary cusp at posterior base. Outer upper incisor shorter (ca. two-

thirds height of inner incisor), with only a minute secondary cusp at the internal base. Inner and middle lower incisors tricuspid; outer lower incisor unicuspid. Lower premolars subequal in height and breadth.

Geographic Variation No information.

Similar Species Three other African *Kerivoula* do not have a comb-like fringe of hooked, bristle-like hairs on posterior margin of interfemoral membrane (Table 31, p. 724):

Kerivoula smithii. Pelage conspicuously frosted. Inner upper incisor bicuspid, secondary cusp reaching ca. half to two-thirds height of main cusp. Larger (FA: 32–36 mm; GLS: 13.1–14.1 mm) and heavier (5.9–7.0 g).

K. cuprosa. Pelage conspicuously frosted. Outer lower incisor tricuspid. Almost always larger (FA: 30–33 mm; GLS: 12.3–13.1 mm; GWS: 7.9–8.4 mm).

K. africana. Dorsal hairs dark brown to black with greyish-brown tip. Outer upper incisor almost reaching height of inner incisor; unicuspid or bicuspid (with small or large basal cusp).

Distribution Endemic to Africa. Recorded mainly from the Rainforest BZ (Western, West Central and East Central Regions) with outlying records from the Afromontane–Afroalpine BZ in NE DR Congo and W Uganda, and from the Guinea Savanna BZ in Côte d'Ivoire. Distribution disjunct. Known from 16 localities in Guinea (Fahr & Ebigo 2003), Liberia, Côte d'Ivoire, Ghana, Cameroon, DR Congo and Uganda (Thomas 1912c, Aellen 1952, Kuhn 1965, J. Fahr unpubl.).

Habitat Mostly reported from lowland rainforest and coastal forest (11 localities). Also found in the (sub-) montane forests on the mountains flanking the Albertine Rift Valley at 700–2400 m in W Uganda and NE DR Congo, and in gallery forest within the Guinea Savanna BZ at Comoé N. P., Côte d'Ivoire. Recorded from a ravine forest within montane grassland at 1350 m on the Simandou Range, Guinea (Fahr & Ebigo 2003).

Abundance No conclusive information but apparently quite rare.

Remarks A ♂ from Kayonza (Uganda, ROM) was taken from the nest of a warbler (*Apalis* sp.) (E. Thorn pers. comm.). In Côte d'Ivoire, caught with harp-traps at a height of 1.5 m (n = 4) (J. Fahr unpubl.). Probably forages by gleaning. Echolocation calls are steep, broad-band FM calls (details not known).

Conservation IUCN Category: Least Concern.

Known from 16 localities within an apparently disjunct distribution. Could become threatened under criterion A4c (inferred) because of



Kerivoula phalaena

its restricted geographic range and deforestation within its range. Population trend not known.

Measurements

Kerivoula phalaena

FA (♂ ♂): 27.0 (25–28) mm, n = 9

FA (♀ ♀): 28.5 (27–30) mm, n = 10

WS (c): 200 (185–208) mm, n = 5

TL: 72.3 (63–79) mm, n = 17

T: 38.2 (32–42) mm, n = 17

Tib: 12.5 (11–13) mm, n = 15

HF: 6.7 (6.0–7.2) mm, n = 14

E: 13.0 (11–14) mm, n = 16

Tr: 6.6 (6.0–6.7) mm, n = 9

WT: 3.5 (2.2–5.0) g, n = 7

GLS: 12.0 (11.6–12.5) mm, n = 15

GWS: 7.2 (6.6–7.4) mm, n = 8

C–M³: 4.8 (4.5–5.1) mm, n = 17

Liberia, Côte d'Ivoire, Ghana (incl. holotype), Cameroon, DR Congo, Uganda (BMNH, FC, LACM, MHNS, RMCA, SMF, USNM)

Key Reference Thomas 1912c.

Jakob Fahr

Kerivoula smithii SMITH'S WOOLLY BAT

Fr. Chauve-souris peinte de Smith; Ger. Smiths Wollfledermaus

Kerivoula smithii Thomas, 1880. Ann. Mag. Nat. Hist., ser. 5, 6: 166. Old Calabar, SE Nigeria.

Taxonomy Synonyms: none. Sometimes spelled *smithi* but original spelling is *smithii* and *smithi* is an invalid emendation. Frequently confused with *K. cuprosa* (see Distribution). Chromosome number: not known.

Description Very small microbat without noseleaf and with tail more or less fully enclosed in interfemoral membrane; six upper and six lower cheekteeth on each side; ears funnel-shaped; pelage frizzled; upper canine not grooved; FA: 34.1 (32–36) mm; dorsal pelage dark brown with conspicuous frosting; posterior margin of interfemoral membrane without comb-like fringe of bristle-like hairs; inner upper incisor bicuspid; outer lower incisor unicuspid. Sexes similar. Pelage dense, woolly, frizzled (many hairs with hooked tips); mid-dorsal pelage ca. 9 mm. Dorsal pelage greyish-brown to dark brown with silvery sheen and silvery or straw-coloured frosting; hairs blackish or dark brown, many with a silvery or straw-coloured tip. Ventral pelage paler brown; hairs greyish-brown or blackish-brown, usually with a pale brown or fawn tip but some with a whitish-silvery tip. Head high-domed; muzzle long, pointed, partly hidden by facial pelage. Eyes minute. Ears widely separated, dark brown or blackish, comparatively and relatively short for a vespertilionid (39 [33–44]% of FA); deeply emarginated below tips. Tragus long (58 [53–64]% of E), tapering, curved outwards; base with small triangular lobule over a shallow emargination (Figure 153e). Wings blackish or dark brown; pelage extending with scattered hairs to dorsal surface of forearm, third digit, thumb, tibia and tail. Interfemoral membrane dark brown; posterior margin with sparse hairs but no comb-like fringe of hooked, bristle-like hairs. Tail 107 (92–131)% of HB.

Skull delicate; braincase high-domed; rostrum narrow; frontal region sharply angular to plane of rostrum. Inner upper incisor comparatively long (cf. *K. cuprosa*), bicuspid (with secondary cusp reaching ca. half to two-thirds height of main cusp) and taller than outer incisor. Outer upper incisor unicuspid or weakly bicuspid, the main cusp attaining the height of secondary cusp of inner incisors. Anterior upper premolar slightly higher than middle premolar but both much smaller than the posterior premolar. Inner and middle lower incisors tricuspid. Outer lower incisor unicuspid, cingulum not distinctly raised on both sides of main cusp and therefore does not appear cup-shaped. Lower premolars subequal in size.

Geographic Variation None recorded but data are limited.

Similar Species Three other African *Kerivoula* do not have a comb-like fringe of hooked, bristle-like hairs on posterior margin of interfemoral membrane (Table 31, p. 724):

Kerivoula cuprosa. Outer lower incisor with tricuspid appearance (cingulum distinctly cup-shaped and forming a cusp on each side of the main cusp). Upper incisors comparatively short. Often smaller (FA: 31.7 [30–33] mm; GLS: 12.3–13.1 mm) and lighter (4.0–4.5 g). Tragus almost always shorter (5.5–7.4 mm).

K. phalaena. Pelage not frosted. Inner upper incisor unicuspid or with small secondary cusp at posterior base. Smaller (FA: 25–30 mm; GLS: 11.9–12.5 mm) and lighter (2.2–5.0 g).

K. africana. Pelage probably not conspicuously frosted. Forearm shorter (28 mm, $n = 1$). Outer lower incisor tricuspid.

Distribution Endemic to Africa. Mainly found in the Rainforest BZ (West Central, South Central and East Central Regions) with one fairly isolated record in the central Congo Basin and two isolated records from the Afromontane–Afroalpine and the Somalia–Masai Bushland BZs in Kenya. Distribution disjunct. Known from 12 localities in Nigeria, Cameroon, DR Congo, Uganda (Mwela [Bugoma Forest]; LACM) and Kenya (Thomas 1880, 1912b, Eisentraut 1956, Harrison 1963b, Koopman 1965, Hayman *et al.* 1966 [*partim*], Rahm 1966, J. Fahr unpubl.). Records from Liberia and Côte d'Ivoire (Happold 1987, Koopman 1993, Koopman *et al.* 1995) have not been confirmed and probably represent either *K. phalaena* or *K. lanosa*, which occur in both Liberia and Côte d'Ivoire (J. Fahr unpubl.). The record from Fort Warwick (Eastern Aberdare Mts), published as *K. cuprosa* by Harrison (1957c), has been re-identified as *K. smithii* (J. Fahr unpubl.). The same is true for many of the specimens from DR Congo that were published as *K. cuprosa* (e.g. Allen 1917a, Schouteden 1944) but later re-identified as *K. smithii* by Koopman (1965), Hayman *et al.* (1966) and J. Fahr (unpubl.).

Habitat Mostly recorded from lowland rainforest (seven localities), but also found in mangroves at Old Calabar, Nigeria, Congolian swamp forests at Mafanya, DR Congo and (sub-) montane forests in the

*Kerivoula smithii*

Cameroon Highlands (ca. 900 m), the Albertine Rift Mts east of L. Albert in Uganda (ca. 1200 m) and the Eastern Aberdare Mts (ca. 2700 m) in Kenya. Also recorded from Bura, near Garissa (Harrison 1963b) on the Tana R., which, in this area, runs through riverine forest within the Somalia–Masai Bushland BZ.

Abundance Unknown but apparently localized and fairly rare (see also *K. cuprosa*).

Adaptations Some specimens were captured when they flew into a house at night; others were taken in a hut, and some were found when saplings near a stream were felled during the day (Lang & Chapin 1917b, Eisentraut 1956, Harrison 1957c, Rahm 1966).

Foraging and Food No information but diet likely to consist of small and soft-bodied arthropods. Other species of *Kerivoula* (from Malaysia and Australia) are known to glean their prey (Schulz 1997, 2000, Kingston *et al.* 1999).

Social and Reproductive Behaviour No information.

Reproduction and Population Structure Litter-size: one ($n = 5$). Reproductive chronology not known (data inconclusive). At ca. 0–1°S in inland Kenya, a pregnant ♀ was reported in Sep from Bura, near Garissa, and another in Dec from Fort Warwick (Harrison 1957c, 1963b). At 01°12'N in Uganda (Bugoma Forest), two ♀♀ were pregnant in late Nov (LACM). At 1–3°N in NE DR Congo (Akenge and Avakubi), two ♀♀ each with an attached young were found in early Oct (Lang & Chapin 1917b, RMCA).

Predators, Parasites and Diseases Ectoparasites include a mite *Rodhainyssus myotis* (Acari: Gastronyssidae) (Anciaux de Faveaux 1984 as *K. smithii*).

Conservation IUCN Category: Least Concern.

Measurements

Kerivoula smithii

FA: 34.1 (32–36) mm, $n = 16$

WS (c): 257 (250–267) mm, $n = 4$

TL: 84.5 (79–93) mm, $n = 12$

T: 43.1 (40–49) mm, $n = 14$

E: 13.4 (11–15) mm, $n = 12$

Tr: 7.9 (7.3–9.0) mm, $n = 7$

Tib: 14.9 (14–16) mm, $n = 10$

HF: 7.3 (5.7–8.2) mm, $n = 14$

WT: 6.2 (5.9–7.0) g, $n = 5$

GLS: 13.7 (13.1–14.1) mm, $n = 14$

GWS: 8.7 (8.5–8.9) mm, $n = 6$

C–M³: 5.5 (5.1–5.8) mm, $n = 15$

Nigeria (holotype, ♂), Cameroon, DR Congo, Uganda, Kenya (AMNH, BMNH, HZM, LACM, NMW, RMCA, SMNS)

Key References Allen 1917a; Harrison 1957c, 1963b; Koopman 1965; Thomas 1880.

Jakob Fahr

GENUS *Phoniscus*

Trumpet-eared Bats

Phoniscus Miller, 1905. Proc. Biol. Soc. Washington 18: 229. Type species: *Phoniscus atrox* Miller, 1905.

A polytypic genus with three species in SE Asia and/or Australia and one very dubious species described, probably erroneously, from Africa. *Phoniscus* is sometimes considered to be a subgenus of *Kerivoula* (e.g. Koopman 1993, 1994), but is considered distinct from *Kerivoula* by Hill (1965), Corbet & Hill (1980, 1992) and Simmons (2005). Diagnostic combination of characters: six upper cheekteeth; pelage woolly and frizzled; ears funnel-shaped; posterior margin of tragus with deep,

nearly parallel-sided notch near base; skull with rostral and anterior palatal emarginations short and wide; interorbital region not constricted (nearly as wide as the posterior part of the rostrum); outer upper incisor rudimentary and difficult to see; upper canine conspicuously grooved. The dubiously African species is *P. aeresa*.

Meredith Happold

Phoniscus aeresa DUBIOUS TRUMPET-EARED BAT

Fr. Chauve-souris peinte rousse; Ger. Zweifelhafes Trompetenohr

Phoniscus aeresa (Tomes, 1858). Proc. Zool. Soc. Lond. 1858: 333. 'Eastern coast of South Africa'.

Taxonomy Originally *Kerivoula aeresa*. Synonyms: none. Occurrence in Africa is very dubious (see Distribution). Chromosome number: not known.

Description Very small microbat without noseleaf and with tail more or less fully enclosed in interfemoral membrane; six upper and six lower cheekteeth; ears funnel-shaped; pelage frizzled; posterior

margin of tragus deeply notched near base (details below); upper canine grooved; dorsal pelage dark brown with conspicuous golden-bronze frosting; posterior margin of interfemoral membrane without comb-like fringe of stiff hairs. Pelage thick, woolly. Dorsal pelage dark umber-brown with shiny golden-bronze frosting; hairs with basal half grey-brown, terminal half yellowish-brown merging into dark umber-brown with shining golden-bronze tip. Ventral pelage

dark sepia brown with brownish-bronze frosting. Head with narrow muzzle and highly domed crown; face moderately hairy with woolly moustache on upper lip, and bare area between each eye and ear. Chin nearly naked. Ears widely separated, brown with shallow indentation near tip; tip rounded. Tragus long, tapering, sharply pointed; posterior margin with deep notch near base – the upper and lower margins of the notch are parallel-sided and the apex is rounded (cf. *Kerivoula*). Eyes minute. Wings and interfemoral membrane brown, indistinctly marked with punctated lines. Posterior margin of interfemoral membrane sparsely furnished with short bristle-like hairs, which, however, do not resemble a comb-like fringe.

Skull with interorbital region less constricted than in *Kerivoula*. Inner upper incisors long and pointed, outer upper incisor rudimentary and difficult to see; upper canine long, strong, angular and conspicuously grooved (cf. smooth in all species of *Kerivoula*); anterior premolar also long and pointed. (Description from Tomes 1858, Roberts 1951, Hill 1965.)

Geographic Variation None.

Similar Species None. No other African member of the subfamily Kerivoulinae has a tragus with a deep, parallel-sided emargination near base and conspicuously grooved upper canines.

Distribution Not mapped. Known only from two specimens in BMNH labelled ‘South Africa, eastern coast’ (Tomes 1858) and thought to have come from Knysna District (Roberts 1951). Because this species belongs to the mainly South-East Asian genus *Phoniscus*, which has no other representatives in or near Africa, it has

been suggested that the specimens actually came from the Malay Archipelago – possibly Sulawesi because Tomes also identified a specimen from Sulawesi (Celebes) as the same species (Roberts 1951, Laurie & Hill 1954, Hill 1965, Hayman & Hill 1971).

Remarks There is no other information about this species.

Conservation IUCN Category: Data Deficient.

Measurements

Phoniscus aeresa

FA: 37, 37 mm

WS (d): 267, 267 mm

HB: ca. 44, 51 mm

T: 38, 42 mm

E: 12, 12 mm

Tr: n. d.

Tib: n. d.

WT: n. d.

GLS: n. d.

GWS: 9.0, 9.0 mm

‘Length dental series’: 6.4, 6.4 mm

‘Eastern coast of South Africa’ (syntypes 1 and 2 respectively, Tomes 1858). Original measurements in inches and lines (twelfths of inches)

Key References Hill 1965; Roberts 1951; Tomes 1858.

Meredith Happold

Appendix: New Taxa 2005–2010

Soricidae

Surdisorex schlitteri Kerbis Peterhans, Stanley, Hutterer, Demos & Agwanda, 2009. Bonner zool. Beitr. 56: 178. Distribution: Kenya, eastern flank of Mt Elgon, ericaceous zone at 3150m.

Myosorex gnoskei Kerbis Peterhans, Hutterer, Kaliba & Mzaibuko, 2008. J. East Afr. Nat. Hist. 97: 23. Distribution: Nyika National Park, Malawi. Remarks: The trapping station was 200 m north of Chilinda Guest House (10°34' 37" S, 33°48' 30" E), 2285 m.

Sylvisorex akaibei Mukinzi, Hutterer & Barriere, 2009. Mammalia 73: 130. Distribution: Masako Forest Reserve (00°36' 304"N, 25° 15' 389" E, 338 m), Kisangani area, Tshopo District, NW Democratic Republic of Congo. Remarks: Primary forest.

Sylvisorex corbeti Hutterer & Montermann, 2009. Bonner zool. Beitr. 56: 202. Distribution: Chappa Waddi, (07° 01' N, 11° 41' E), 1900 m a.s.l., Gotel Mountains, SE Nigeria. Remarks: forest swamp.

Sylvisorex silvanorum Hutterer, Riegert & Sedláček, 2009. Bonner zool. Beitr. 56: 151. Distribution: Near Lake Bambili, Mt Lefo, Bafut Ngemba F. R. (5° 55' N, 10° 14' E), 1800–1900 m a.s.l., Bamenda Highlands, North West Province, Cameroon.

Chiroptera

Hipposideridae

Hipposideros tephros Cabrera, 1906. Boln R. Soc. Esp. Hist. nat. 6: 358. Distribution: Mogador, Morocco. Also occurs elsewhere in NW Africa (the Maghreb), West Africa and Arabian Peninsula (Vallo *et al.* 2008). Recently considered a subspecies of *H. caffer* (Sundevall, 1846) but restored to specific status by Vallo *et al.* (2007).

Rhinopomatidae

Rhinopoma cystops Thomas, 1930. Annals and Magazine of Natural History, ser. 7, 11: 496. Distribution: Luxor, Egypt. Remarks: Recently considered a subspecies of *R. hardwickei* Gray, 1831 (e.g. Van Cakenberghe & De Vree 1994) but restored to specific status by Hulva *et al.* (2007).

Molossidae

Mops bakarii Stanley, 2008. Acta Chiropterologica 10: 184. Distribution: Kipangani village (4.96487°S, 39.71456°E, 12 m a.s.l.), Ngezi Forest, Kaskazini Region, Pemba Island, Tanzania. Remarks: Found in attic of hospital. For further information, see profile *Tadarida brachyptera*.

Vespertilionidae

Eptesicus isabellinus (Temminck, 1840). Distribution: NW Africa and extraliminally, Iberian Peninsula (Juste *et al.* 2007). Remarks: Recently considered a subspecies of *E. serotinus* (Schreber, 1774) but restored to specific status by Benda *et al.* (2004c), Mayer *et al.* (2007), Artyushin *et al.* (2009) and Juste *et al.* (2009).

Scotophilus mhlanganii A cryptic sibling species of *Scotophilus dinganii* (A. Smith, 1833) found sympatrically in St Lucia Wetland Park and Skukuza, Kruger N. P., KwaZulu–Natal, South Africa, and at Leopard's Hill Farm, Lusaka, Zambia (Jacobs *et al.* 2006). It is distinguished genetically and by its echolocation calls and smaller size (Jacobs *et al.* 2006), and karyotypically (Eick *et al.* 2007). It is not yet described but has been tentatively named *S. mhlanganii* (Jacobs *et al.* 2007) and has been referred to as such in several publications including Jacobs & Barclay (2009). Further information in profile of *S. dinganii*.

Miniopterus africanus Sanborn, 1936. Field Museum of Natural History, Publications, Zoological Series 20: 111. Distribution: Shoa, Ethiopia. Also occurs in Eritrea, elsewhere in Ethiopia, Kenya, Tanzania, Botswana and Namibia. Remarks: Recently often considered a subspecies of *M. inflatus* Thomas, 1903, but its specific status was confirmed by Juste *et al.* (2007).

Cistugidae

The genus *Cistugo*, containing two species, both in Africa, was raised to familial status by Lack *et al.* (2010).

Miniopteridae

The subfamily Miniopterinae, containing many species of *Miniopterus*, including seven in Africa, was considered to justify familial status by Mein & Tupinier (1977) (based on morphological evidence) and by Hoofer & Van Den Bussche (2003) (based on mitochondrial ribosomal sequences), but the taxonomic position of these bats remained controversial (e.g. Simmons 2005). The validity of the Miniopteridae is now confirmed by additional genetic information (Miller-Butterworth *et al.* 2007).

Glossary

abbrev. = abbreviation

adj. = adjective

cf. = *confer*, compare with; as opposed to

Lat. = Latin

pl. = plural

q.v. = *quod vide*, 'which see'

acrocentric: describes a chromosome that has the centromere (*q.v.*) very near one end and which therefore appears to have only one arm (= telocentric [*q.v.*] for practical purposes).

ad libitum: (*Lat.*) as much as one likes; having unrestricted access to a resource (e.g. water or food).

aestivate: state of torpor (*q.v.*) induced by cold or drought; usually associated with a reduced metabolic rate and inactivity.

aFN: the total number of chromosomal arms in the autosomal chromosome complement of a species (*cf.* fundamental number [FN], which includes the chromosomal arms of the sex chromosomes as well as those of the autosomal [*q.v.*] chromosomes). Each metacentric (*q.v.*), submetacentric (*q.v.*) or subtelocentric (*q.v.*) chromosome is given a value of 2; each acrocentric chromosome is given a value of 1. *See also* fundamental number.

afroalpine: describes habitats and/or vegetation occurring above the treeline on African mountains. Includes montane grassland and heathlands.

afromontane: refers to mountainous regions in Africa, e.g. afromontane forests and afromontane grasslands.

agility: in bats, the rate at which a turn can be initiated during flight.

agouti: having an even mixture of pale- and dark-tipped hairs on the pelage creating a grizzled, speckled or 'pepper and salt' appearance.

Albertine Rift Valley: *see* Rift Valley (*q.v.*).

alisphenoid: bone in the skull.

allele: an alternative form of a gene. A diploid organism carries two alleles (which may be same or different) for each gene locus. At any one locus, there may be several possible alleles (although only two are present in a single organism).

allopatry (*adj.* **allopatric**): the situation where populations of the same or different species have non-overlapping geographic ranges; refers also to populations of the same, or different, species that are geographically separated. *cf.* sympatry (*q.v.*); syntopy (*q.v.*).

allozyme: one of a number of forms of the same enzyme having different electrophoretic properties and which are encoded by alternate alleles at the same genetic locus.

altimontane: collective term for the belts of ericaceous and afroalpine vegetation on the high mountains of tropical East Africa (White 1983).

altricial: describes young born in an undeveloped state.

alv.: (*abbrev.*) *see* C–M³ (*alv.*).

alveolus (*pl.* **alveoli**, *adj.* **alveolar**): small cavity; socket that houses the root of a tooth.

angular process: process at the posterior lower corner of the mandible; situated ventral to the coronoid process (*q.v.*).

antebrachial: anterior to the arm (forelimb).

ante-orbital: in front of the orbit (*q.v.*).

anthropophilic: loving or thriving with humans; inhabiting domiciles or day-roosts in man-made structures and buildings (including mines); thriving in habitats substantially modified by humans (e.g. towns, farmlands). *cf.* lithophilic (*q.v.*); phytophilic (*q.v.*).

antitragus: in bats, the lobe near the base of the outer margin of the pinna or conch of the ear (Figure 22).

apomorphy (*adj.* **apomorphic**): situation in which a novel character evolves from a pre-existing character. In cladistics (*q.v.*), an apomorphic character shared among two or more species (synapomorphy [*q.v.*]) indicates shared descent from a common ancestor and hence monophyly (*q.v.*). *cf.* plesiomorphy (*q.v.*).

arboreal: living above the ground (in trees and shrubs). *cf.* scansorial (*q.v.*); terrestrial (*q.v.*).

arm-wing: that part of the wing between body, hindlimb and fifth finger (= propatagium, *q.v.* plus plagiopatagium, *q.v.*). *cf.* hand-wing (*q.v.*).

aspect ratio: describes the width of a wing relative to its length. Calculated by dividing the square of the wingspan by the wing area. Narrow wings have high aspect ratios.

attenuation: the reduction of the intensity of a sound (e.g. echolocation call), which occurs as the sound travels away from its source. High frequencies attenuate more rapidly than low frequencies, therefore low frequencies can be heard and/or recorded further away from the source.

auctorum: (*Lat.*) of various authors.

auditory bulla: *see* tympanic bulla.

auditory meatus (*pl.* **auditory meati**): the external opening of the ear; the passage leading from the tympanic membrane (ear drum) to the external ear.

autapomorphy: derived trait uniquely characteristic of a taxon.

autosomal: pertaining to any chromosome other than the sex chromosomes.

axillary tuft: in bats, a tuft of hair arising from the axilla (armpit) (Figure 55b).

baculum (*pl.* **bacula**, *adj.* **bacular**): the os penis, or penis bone, which supports the penis in some mammals.

bandwidth: the difference in frequency between the highest and lowest frequencies of a sound (e.g. an echolocation call).

banking: in bats, a method of changing direction during flight without losing much speed or height; achieved by altering the form of the flight membranes so one wing has more lift than the other and the bat rolls; radius of turn is proportional to speed so banked turns are of comparatively large radius. *cf.* stall-and-twist turning (*q.v.*).

baobab: a tree, *Adansonia digitata*, having a disproportionately wide trunk, which, in mature trees, is often hollow.

- basal metabolic rate:** metabolic rate required for survival in the thermal neutral zone (*q.v.*); a state that requires the lowest expenditure of energy when at rest.
- basicranial axis:** a line drawn in the lateral view of the skull indicating the position of the floor of the braincase, in the median line (Harrison & Bates 1991).
- basicranium:** the base of the skull.
- basisphenoid:** cranial bone in middle of base of skull; the median posterior part of the sphenoid bone, forming part of the floor of the braincase.
- basisphenoid pit:** in bats, one of a pair of pits in the basisphenoid bone (Figure 101).
- bent-winged:** having two marked bends in the alignment of the bones comprising the third finger in the wings of all species in the genus *Miniopterus* (*cf.* aligned in a smooth shallow curve) (Figure 117c).
- bicuspid:** having two points or cusps (particularly of teeth).
- bifid:** divided by a shallow notch.
- bipedal:** body supported by the two hindlimbs; movement not using the forelimbs.
- biserial:** arranged in pairs (as in the cusps of molar teeth in some mammals, e.g. some rodents).
- blastula:** a hollow ball of undifferentiated cells (derived from a fertilized ovum by cell division), which represents one of the earliest stages of embryonic development.
- brachydont:** describes a premolar or molar tooth with low crowns. *cf.* hypsodont (*q.v.*).
- braincase (= cranium):** that part of the skull housing the brain; the part of the skull posterior to the front line of the orbits. *cf.* rostrum (*q.v.*).
- bristle hairs:** in shrews, long stiff hairs on tail (*see also* pilosity [*q.v.*]).
- brown fat:** in bats, adipose tissue (fat) specifically used for the generation of heat during arousal after hibernation.
- buccal:** pertaining to the cavity of the mouth.
- buccal pad:** an oval epithelial structure containing lipoid (fatty) substances, situated in each angle of the mouth of some bats between the cheek and the posterior molars.
- bushmeat:** meat for human consumption derived from non-domesticated mammals, birds and reptiles taken from their natural habitats and domiciles.
- bushveld:** savanna vegetation type characterized by a grassy ground layer and a moderately dense upper layer of shrubs and scattered trees.
- BZ:** (*abbrev.*) Biotic Zone.
- C or c:** (*abbrev.*) canine tooth; upper case denotes adult dentition, lower case denotes deciduous dentition (milk teeth). *See also* canine.
- CF:** (*abbrev.*) constant frequency *cf.* FM (*q.v.*).
- c.u.:** (*abbrev.*) (*Lat. cum unguis* = with nail) measurement of the hindfoot when length of the nail on the claw is included in the measurement. Usually hindfoot is measured without the claw because claws may be broken or worn. When length of claw is included, it is conventional to record as 'HF c.u.'. *cf.* s.u. (*q.v.*).
- C–M¹, C–M², C–M³:** in golden-moles and bats, the length of the upper tooththrow, measured from the most anterior part of the canine to the most posterior part of the most posterior molar. For golden-moles, the most posterior molar is M² or M³. For microbats, the most posterior molar is M³; for megabats, M³ (and sometimes M²) is lost, and therefore the most posterior molar is either M² or M¹.
- C–M³ (alv.):** in bats, the length of the upper tooththrow measured at the level of the alveoli (*q.v.*), from the most anterior part of the canine to the most posterior part of the most posterior molar.
- calcar:** bony or cartilaginous spur arising from the ankle and, in bats, helping to support the hind margin of the interfemoral membrane (*q.v.*). Also called calcaneum.
- call-shape:** the way the frequency of a bat's echolocation call changes with time as shown on a sonogram (spectrogram).
- canine:** the most anterior tooth on the maxilla bone and in a similar position on the mandible; situated immediately posterior to the incisors; if incisors are absent, the most anterior tooth in the jaw. Unicuspid; tall and pointed in most mammals. Never more than one canine on each side of each upper and lower jaw; absent in some taxa.
- caniniform:** having shape and appearance of a canine tooth.
- caravanning:** in shrews, behaviour of young (fully furred and with the eyes open) when they form a line behind the mother, each young holding on to the rump of the individual in front. The young 'follow' the mother as she moves around outside the nest.
- cauda epididymides:** the ducts of the epididymides at the posterior end of the testes, which carry sperm from the testes to the vas deferens, which, in turn, carries sperm to the penis. Sometimes used to store sperm prior to copulation.
- CbL:** (*abbrev.*) *see* condylobasal length.
- CcL:** (*abbrev.*) *see* condylocanine length.
- Cenozoic (= Cenozoic Era):** geological era, ca. 65 mya to today, comprising the Quaternary and Tertiary Periods: the Age of Mammals.
- central Africa:** Cameroon (south of the Sanaga R.), Central African Republic (but only south of ca. 7°N), Equatorial Guinea, Gabon, DR Congo (except SE). Mainly rainforest habitats and rainforest–savanna mosaics.
- central parting:** in hedgehogs, a thin longitudinal area of spine-free skin in the centre of the forehead and bordered to left and right by normal spines; presence or absence is useful for identification (*see* Figure 5a).
- centromere:** the part of a chromosome where sister chromatids are linked together during mitosis.
- cf.** (in general usage): compare or compare with. In the context of descriptions, implies a difference or contrast: e.g. 'In *T. niveiventer*, ventral pelage white (*cf.* *T. thersites* in which the ventral pelage is dark brown).'
- cf.** (in taxonomy): precedes the specific name if there is uncertainty in the assignment.
- cheekteeth:** the premolar (*q.v.*) and molar (*q.v.*) teeth combined.
- choana (pl. choanae):** the openings of the internal nostrils on the skull, situated immediately posterior to the bony palate.
- chromosome:** one of the thread-like bodies within the nucleus of a cell, which carry the genes (genetic material) in linear order; each chromosome is composed of one long molecule of DNA (and two long molecules at cell division). Chromosomes occur in pairs (one from each parent) and are visible as rod-like bodies in cells that are dividing. The total number of chromosomes in a cell is expressed as the diploid number (2n).

- CI:** (*abbrev.*) condyloincisive length; in shrews, the length of the skull from the anterior end of the longest incisor tooth to the posterior end of the occipital condyles. *cf.* GLS.
- cingulum** (*pl.* **cingula**): ridge around the base of the crown of a tooth.
- clade:** branch of a phylogenetic tree containing the set of all organisms descended from a common ancestor.
- cladistic (analysis):** a methodology that provides a classification in which organisms are grouped in terms of the time when they had a common ancestor.
- cline** (*adj.* **clinal**): in context of geographic variation, a gradual and sequential change of a character(s) without a significant break such as would justify division into separate subspecies or species.
- CNL:** condylo-nasal length; measurement from the most anterior part of the nasal bone to the most posterior part of the occipital condyle (exoccipital) on the same side of the skull; a similar measurement to 'greatest length of skull'.
- cochlea** (*pl.* **cochleae**): in bats, a hollow structure, spirally coiled like a snail's shell, situated in the skull and containing the internal organ of hearing (Figure 23).
- Coleoptera:** taxonomic order containing the beetles (within the phylum Insecta).
- colony:** in bats, a group of individuals of the same species roosting together in close proximity (but not necessarily in contact). Applied here to groups of 15 or more individuals (*see* group size).
- comparatively:** used in the context of describing the size of one character compared with the size of the same character in a different species. Sizes described as small, medium or large (if range is divided into three) or very small, small, medium, large, very large (if range is divided into five). *cf.* relatively (*q.v.*).
- competitive exclusion:** the principle that two different species cannot indefinitely occupy the same ecological niche.
- concave:** having a curvature that curves inwards; having an outline or a surface curved like the interior of a circle or sphere. *cf.* convex (*q.v.*).
- concavity:** a concave depression in an outline or surface.
- conceptus:** embryo prior to implantation.
- conductance:** in thermal biology, the rate at which heat passes across a temperature gradient, e.g. the density and thickness of the pelage affects the rate at which body heat passes from the body to the outside. Thick pelage, which traps and holds air, results in low thermal conductance.
- condylar process:** process at the posterior upper corner of the mandible, which forms the lower hinge of the jaw articulation; fits into the glenoid fossa of the skull.
- condyle:** a rounded process on a bone, which articulates with a socket-like concavity in another bone.
- condylobasal length (CBL):** in bats, the length of skull from the most posterior point of one exoccipital condyle to the front of the premaxilla on the same side (Figure 23).
- condylocanine length (CCL):** in bats, the length of skull from the most posterior point of one exoccipital condyle to the front of the canine tooth on the same side (Figure 23).
- congeneric:** belonging to the same genus.
- connecting process:** the longitudinal structure arising from the central component of the noseleaf of bats in the family Rhinolophidae, that extends from the back of the sella (*q.v.*) to the base of the lancet (*q.v.*) (Figure 56). Its shape, viewed laterally, is a diagnostic character (Figure 59).
- conspecific:** belonging the same species.
- contiguous:** touching; sharing a boundary (as in geographic ranges).
- convex:** having a curvature that bulges outwards; having an outline or a surface curved like the exterior of a circle or sphere. *cf.* concave (*q.v.*).
- coprophagy:** the behavioural process of eating faeces as they are voided from the anus.
- copulatory plug:** plug formed in the vagina of the female after copulation; formed from seminal fluids of the male. Prevents or reduces the chance of sperm from another male(s) entering the female reproductive tract if the female copulates again soon after copulation with the first male.
- coronoid process:** angular pointed process on the upper margin of the mandible, situated anteriorly to the condylar process (*q.v.*); does not participate in the jaw articulation.
- corpus luteum** (*pl.* **corpora lutea**): a glandular mass of tissue on the surface of an ovary, that develops after the extrusion of an ovum from a Graafian follicle (*q.v.*); secretes the hormone progesterone.
- cotype:** originally synonymous with syntype but now used as synonym of paratype (*q.v.*).
- CR:** (*abbrev.*) *see* crown–rump length.
- cranial profile:** the shape of the cranium (that part of the skull which surrounds the brain) when viewed from the side.
- cranio-canine length (CrnC):** in bats, the distance from the most posterior part of the skull to the front of the upper canines (Figure 23). Often used instead of greatest length of skull (GLS) in bats of the families Rhinolophidae and Hipposideridae because, in these bats, the premaxillae are often lost during preparation of skulls.
- craniodental:** pertaining to the skull and teeth.
- cranium:** that part of the skull housing the brain. Also called braincase.
- crepuscular:** at, of, twilight, when light intensity is higher than at night but lower than during the day. *cf.* diurnal (*q.v.*); nocturnal (*q.v.*).
- CrnC:** (*abbrev.*) *see* cranio-canine length.
- crown area:** in bats, the area of the transverse section of a tooth just above the gum-line. For molars and premolars, can be assessed from their occlusal profiles.
- crown:** (1) top of head; (2) exposed part of a tooth (visible above gum), especially the grinding surface.
- crown–rump length (CR):** distance from the crown of head to the rump of a foetus (i.e. maximum length of a foetus in its natural form).
- cursorial:** pertaining to running. In bats, refers to scuttling or crawling in which the folded wings and hindlimbs are used for quadrupedal locomotion over a substrate (as opposed to flying, swimming or any other form of locomotion).
- cuspidate** (*adj.* **cuspidate**): a prominence or sharp point, such as on the occlusal surface of some teeth. *See also* t.
- Cyrenaica:** a region of north-east Libya. Includes the Cyrenaican Plateau and that part of the Mediterranean Coastal Biotic Zone between the plateau and the sea, as well as drier terrain south of the plateau.

cytochrome *b*: a protein involved in electron exchange in the mitochondria. It is the product of a gene in the mitochondrial genome. The sequence of this gene is often compared between species in phylogenetic studies to infer relatedness.

Dahomey Gap: the geographic region where savanna habitat extends southwards to the West African coast in E Ghana, Togo, Benin (formerly Dahomey) and extreme SW Nigeria. The presence of savanna forms a break (or gap) in the extensive Rainforest Biotic Zone, which extends along the West Africa coast from Sierra Leone to Cameroon. The Dahomey Gap is an important biogeographical barrier separating the faunas to the east and west of the Gap.

deciduous teeth: *see* milk teeth (*q.v.*).

Dega: Ethiopian word for the temperate agricultural/economic altitudinal zone, about 2300–3000 m, warm enough for cereal-based agriculture.

delayed implantation: a means of lengthening the interval between copulation and parturition by delaying the implantation of the blastula (*q.v.*), so that both copulation and parturition can occur in the most optimal seasons. Development to blastula stage is followed by a period of halted development lasting several weeks or months; then the blastula implants and embryonic development proceeds normally, usually without any further interruption, until the young is born.

dental formula: a simple numerical method of denoting the number of incisor (I), canine (C), premolar (P) and molar (M) teeth on one side of the upper jaw and lower jaw, and the total number of teeth. For example, the dental formula of a primitive mammal is $I^{3/3}, C^{1/1}, P^{4/4}, M^{3/3} = 44$, which means there are three incisors, one canine, four premolars and three molars on each side of the upper jaw and also the lower jaw, making a total of 44 teeth. The formula may also be expressed in the form $^{3143}_{3143} = 44$. Each incisor, premolar and molar is numbered according to its position in the tooth row; superscript numbers indicate upper jaw, subscript numbers indicate lower jaw (mandible), e.g. P^4 (upper fourth premolar), M_2 (lower second molar).

dichromatism: condition in which members of a species show one of only two distinct colours or colour-patterns.

dimorphism (*adj.* **dimorphic**): *see* sexual dimorphism.

diphyly: the derivation of a taxon from two separate lines of descent. *cf.* monophyly (*q.v.*)

diploid number (2n): total number of chromosomes (including sex chromosomes) in a somatic cell of an organism.

distal: the end of any structure furthest away from the mid-line of the body or furthest from the point of its attachment. *cf.* proximal (*q.v.*).

distichous: arranged in two rows; e.g. long hairs of the tail in some anomalurids and some dormice (as opposed to the hairs being evenly spread all around the tail).

diurnal: at, active in, daytime; when light intensity is high. *cf.* crepuscular (*q.v.*); nocturnal (*q.v.*).

DNA: (*abbrev.*) deoxyribonucleic acid; the very large self-replicating molecule which carries the genetic information of a chromosome; each molecule is composed of two complementary chains of DNA.

DNA hybridization: technique of comparing the similarity between two DNA molecules by reassociating single strands

from each molecule and determining the extent of double-helix formation. In phylogenetics, this technique is used to determine the relatedness of two or more taxa.

Doppler effect: variation in the pitch of a sound heard from a source of given frequency caused by any relative motion between the source and the observer.

Doppler shift: in bats, in context of echolocation, the change in pitch (frequency) of an echo resulting from the movement of the bat towards or away from the object reflecting the echolocation call, or from the movement of this object towards or away from the bat, or a combination of both.

dorsoventral (dorsoventrally): from dorsal to ventral surface; from back to belly of an animal.

duty cycle: in bats, in context of echolocation, the ratio of call duration to intercall interval; calculated by dividing the duration of a call by the time interval between the end of that call and the onset of the next call in the same sequence.

E: length of external ear or pinna (measured from tip of ear to the base of the ear conch nearest to the head). In bats, usually the length of ear from its tip to the notch in front of the orifice, but sometimes measured from the tip to the junction of the outer margin of the pinna (*q.v.*) with the head, or from the tip to the lower border of the external auditory meatus. This may account, in part, for wide ranges of ear measurements for some species when data are taken from diverse sources. For all mammals, length affected by preservation.

East Africa: Kenya, Uganda, Rwanda, Burundi and Tanzania.

eastern Africa: SE Sudan, Ethiopia, Eritrea, Djibouti, Somalia, Kenya, Uganda, Tanzania, Malawi (but only south of L. Malawi and east of the Shire R. Valley) and Mozambique (but only east of Malawi and north of the Zambezi R.).

echolocation: the use of reflected ultrasonic pulses of sound to perceive the surroundings (including obstacles, prey and other animals).

edaphic: influenced by conditions of soil or substratum.

emargination: a distinct notch or indentation.

embryo number: number of foetuses within the uterus or uteri of the female (as assessed by autopsy). Expressed as mean number (with range from minimum to maximum, and sample size). *cf.* litter-size (*q.v.*).

endemic: restricted to, peculiar to, or prevailing in, a specified country or region.

endoparasite: a parasite that lives in the interior of an organism (e.g., nematodes, cestodes, blood parasites). *cf.* ectoparasite (*q.v.*).

entoconid cusp: the posterior cusp on the lingual (inner) side of a lower molar tooth. In bats, one of the posterior cusps on the lingual side of a lower molar tooth, located just anterior to the hypoconulid (*q.v.*) (Figure 138).

Eocene: geological Epoch (within the Tertiary Period); 55–38 mya.

epigeal: in zoology, living close to the ground.

epiphysis (*pl.* **epiphyses**): any part of a long bone that is formed from a different centre of ossification and which later fuses with the bone to form its terminal part.

epomophorines: all fruit bats in the Epomophorine section of Andersen (1912), which includes *Epomophorus*, *Epomops*, *Hypsignathus*, *Micropteropus* and *Nanonycteris*, *Plerotes*, *Casinonycteris* and *Scotonycteris*.

- evaporative water loss:** the loss of water from the body through the skin and/or the lungs. A mechanism used by mammals to reduce Tb (*q.v.*) when Ta (*q.v.*) is high. Excessive evaporative water loss may lead to dehydration if free (drinking) water is unavailable.
- exfoliating:** shedding flakes (e.g. of bark), or breaking into relatively thin slabs (e.g. of granitic rock).
- exoccipital condyles:** a pair of projections from the occipital bone on either side of the foramen magnum (*q.v.*) that articulates with the first vertebra of the spine. Also called occipital condyles.
- extant:** living at the present time. *cf.* extinct.
- F. R.:** (*abbrev.*) Forest Reserve.
- FA:** (*abbrev.*) in bats, the length of the forearm from the elbow to the distal end of wrist when the wing is folded. *See also* forearm.
- face-mask:** in hedgehogs, the pattern of white-coloured pelage on the anterior part of the face in hedgehogs.
- facultative:** having the capacity to switch from one mode of life or action to another depending on conditions or circumstances. *cf.* obligate (*q.v.*).
- female-defence polygyny:** a mating system in which males control access to females directly, usually by virtue of female gregariousness (Emlen & Oring 1977). Sometimes called harem-defence polygyny.
- fingers:** in bats, the digits (metacarpals and phalanges) of the wings (forelimbs). The first finger is referred to as the thumb.
- first toe:** in bats, the toe furthest from the mid-line (= outer toe); this is because the hindlimbs of bats are rotated so that the knees point backwards instead of forwards. In contrast, the first toe of all other five-toed mammals is the toe nearest the mid-line.
- flank:** the side of the body of a mammal.
- flank-stripe:** in bats, a stripe, in contrasting colour, running lengthwise along the flank. A ventral flank-stripe is just under the wing; a dorsal flank-stripe is just above the wing.
- fly-catching:** the foraging behaviour of bats that hang from a perch while they are searching for flying insects, fly from the perch to catch the prey in mid-air, and then return to the perch to eat and/or to resume searching.
- FM:** (*abbrev.*) *see* frequency modulated *cf.* CF (*q.v.*).
- FN:** (*abbrev.*) *see* fundamental number.
- folivore** (*adj.* **folivorous**): an animal that eats leaves.
- foramen** (*pl.* **foramina**): an aperture (which is usually small, round or elliptical) in a bone, or between bones, for the passage of a nerve, blood vessel or muscle.
- foramen magnum:** the large opening at the posterior end of the skull through which the spinal cord passes.
- forearm:** in bats, the wing-bones between elbow and fingers, comprised of radius, ulna and carpals.
- forehead region of skull:** in bats, that part of the dorsal profile of the skull (viewed laterally) encompassing the posterior part of the rostrum and the anterior part of the braincase.
- forest island:** *see* relict forest.
- form:** a neutral term for a single individual or taxonomic unit which may be employed without reference to the formal taxonomic hierarchy of categories; one of the varieties found in a polymorphic species.
- fossorial:** adapted for digging; burrowing. *cf.* subterranean (*q.v.*).
- fovea:** small pit or depression.
- frequency modulation:** in bats, in context of echolocation, increasing or decreasing frequency (pitch) during the emission of a call so that the call-shape (*q.v.*) is not a straight, horizontal line.
- frizzled:** in bats, describes the texture of pelage in which many of the hairs have a hook-shaped tip.
- frontal bone:** one of a pair of bones forming the anterior part of the braincase.
- frontal depression:** in bats, the saddle between the rostrum and frontal bones of the skull.
- frugivorous:** fruit-eating.
- fundamental number (FN):** an ambiguous term sometimes defined as (1) the total number of chromosomal arms in the full chromosomal complement of an organism (i.e. including the sex chromosomes), or (2) the total number of chromosomal arms found in the autosomal chromosomes only (i.e. excluding the sex chromosomes). When only the autosomal chromosomes are included, some authors (but not all) use aFN instead of FN to avoid ambiguity. For further details, *see* aFN.
- fynbos:** the heath shrublands characteristic of the Cape Floristic Kingdom (within the South-West Cape Biotic Zone) of South Africa. Dominant plants are sclerophyllous, evergreen, low (<3 m), bushy and fine-leaved, but there are also scattered taller bushes and, less often, very widely spaced trees. Contains an exceptionally high number of endemic species of plants. The three main components on nutrient-poor sandy soils are species of Ericaceae, Restionaceae and Proteaceae. Also includes 'renosterveld' (dominated by species of Asteraceae) on nutrient-rich silt or clay soils.
- G. R.:** (*abbrev.*) Game Reserve.
- gallery forest:** type of forest outlier (in a savanna region) found in narrow sheltered valleys and ravines on hillsides, where soils are moist enough, and conditions humid enough, to support rainforest trees (Rosevear 1953).
- garrigue:** a type of short, Mediterranean shrubland (White 1983).
- genotype:** genetic term to describe the genetic constitution of an individual inherited from its parents. *cf.* phenotype (*q.v.*).
- gestation:** the development of embryo/foetus, which takes place in the uterus; the period during which this development takes place. The gestation period is defined as the interval between conception and parturition (birth). Strictly speaking, the gestation period is not the interval between copulation (mating) and parturition (birth), although many authors take it to be this interval.
- glans penis:** the bulbous tip of the penis.
- gleaning:** in bats, the taking of resting or non-flying prey from surfaces including foliage, tree trunks, walls and ground. Hover-gleaners glean while hovering or flying slowly. Foliage-gleaners specialize in taking prey from foliage and tree trunks and are usually hover-gleaners. Ground-gleaners often land to catch prey but may also take it while flying slowly.
- glenoid fossa (= glenoid):** the cavity (fossa) in the squamosal bone of the skull for the articulation of the condyle of the mandible (lower jaw) in mammals; visible on lateral and/or ventral views of skull depending on the taxon.
- glenoid process:** in bats, refers to the raised rim on the posterior edge of the glenoid fossa (*q.v.*) (Figure 23).

GLS: (*abbrev.*) greatest length of skull (measured from anterior end of incisor teeth or nasal bone (whichever is most anterior) to the posterior end of the skull (occiput, occipital condyles or auditory bullae, whichever is most posterior). *cf.* CI. In bats, as measured from its most posterior point (posterior of occipital bone) to the most anterior part (anterior edge of premaxilla). Replaced by CrnC (*q.v.*) for bats in families Rhinolophidae and Hipposideridae.

Gondwana (= Gondwanaland): the southernmost of the two Mesozoic (*q.v.*) supercontinents that later fragmented (as a result of continental drift) into the landmasses of Africa, Madagascar, Antarctica, Australia, South America, the Indian subcontinent and the Arabian peninsula.

Graafian follicle: the structure in the mammalian ovary that contains the developing ovum, and from which the ovum is released at the time of ovulation.

gracile: lightly built. *cf.* robust

granivore (*adj.* **granivorous**): an animal that eats grains and seeds.

gregarious: living together in groups, flocks, herds.

Gregorian Rift Valley: *see* Rift Valley.

group-size: in bats, in the context of groups roosting together, two = two of same sex, pair = two of different sex, small = 3–15, medium-sized = 15–30, large = 30–100, very large >100. Groups (usually medium to very large in size) are sometimes referred to as colonies, especially in context of maternity colonies (*see* maternity colony).

guard hair: long thin bristle-like hairs, mainly on the back and flanks, which project beyond the soft hairs of the pelage; when present, conspicuous but never as numerous as soft hairs; probably tactile in function.

gular: pertaining to the upper part of the throat (the gula) as in gular gland, gular pouch, gular region.

GWS: (*abbrev.*) greatest width of skull, usually measured across the widest point of the zygomatic arches (*q.v.*). In shrews, which do not have zygomatic arches, the GWS is across the widest part of the cranium. In bats, usually the zygomatic width (*q.v.*) but sometimes the mastoid width (*q.v.*).

hallux: the first digit of the hindlimb; the big toe. In bats, the hallux is the outermost toe.

hammada: flat plain covered with pebbles of various sizes on a hard substrate in an arid environment. Much of the Sahara Desert is formed of hammada.

hand-wing: in bats, that part of the wing between the second and fifth fingers. Also called dactylopatagium. *cf.* arm-wing (*q.v.*).

hard-shelled: describes insects (e.g. eaten by bats) that have hard cuticles, e.g. beetles. *cf.* soft-bodied (*q.v.*).

harem: in bats, a social group of several adult females that mate (and usually roost) with one male. May include their progeny.

harmonics: e.g. in echolocation calls of bats, usually considered to be the lowest frequency of sound produced by the vocal cords (= fundamental frequency or first harmonic) and any other component of the call that is a whole number multiple of the fundamental. In this context, the second harmonic is twice the frequency of the first, and so on. (Note: some authorities do not consider the fundamental to be a harmonic and therefore consider that the first harmonic is the component having twice the frequency of the fundamental.)

harp-trap: trap designed to catch bats without harming them. Comprised of one or more banks of vertically-strung 'wires' made of fine, nylon fishing-line, suspended over a deep trough (made of canvas or similar material) into which bats fall after flying into the banks of 'wires'. Bats are prevented from climbing out of the trough by flaps of over-hanging material under which the bats usually settle and rest.

hastate: shaped like an arrow-head or spear-head; having a wide base and relatively longer, concave sides that taper to a bluntly-pointed tip.

HB: (*abbrev.*) length of head and body (measured from the tip of the nose to the most posterior point of the pelvis (anterior to the first tail vertebra).

helmet: *see* occipital helmet.

heterothermic: condition when the body temperature fluctuates in relation to the ambient temperature T_a (*q.v.*).

HF: (*abbrev.*) length of hindfoot (measured from the 'ankle bone' to the tip of the longest digit usually without including the claw). In bats, measured from back of heel to tip of longest claw (unless stated otherwise). *See also* c.u.; s.u.

hibernaculum (*pl.* **hibernacula**): a place, domicile or roost where an animal hibernates.

hibernation: a state of inactivity accompanied by a reduction in metabolic rate (below basal metabolic rate [*q.v.*]), lower T_b , and slow breathing. Occurs when T_a is low and food is scarce; usually lasts for weeks or months; not common in African mammals (*cf.* torpor).

high forest: rainforest that has matured, stabilized and reached the climax stage of succession.

highveld: high plateaux characteristic of inland southern Africa, dominated by grasses.

hind-border: in bats, the posterior edge of the wing, a term used when the edge is white or pale, in contrast to rest of the wing membrane. May extend from wing-tip to ankle, or be limited to the arm-wing (*q.v.*) or hand-wing (*q.v.*).

Holocene: geological Epoch (within the Quaternary Period) (*q.v.*) following the Pleistocene Epoch (*q.v.*); ca.11,000 mya to today. Sometimes referred to as the 'Recent' Epoch.

holotype (= type): the single specimen designated or indicated by the original author of the original description of a new species or subspecies, to be the standard reference to the essential characters of the new taxon. *see also* cotype (*q.v.*), lectotype (*q.v.*), neoparatype (*q.v.*), neotype (*q.v.*), paratype (*q.v.*), syntype (*q.v.*), topotype (*q.v.*) and type locality (*q.v.*).

homeothermic: describes an organism having a body temperature that is maintained at a constant level (within limits), independently of the ambient temperature T_a (*q.v.*).

home-range: the area (expressed in square metres, or square kilometres) routinely used by an animal for its day-to-day activities and requirements, and which contains the resources required for survival and reproduction. Within the home-range there may be a 'core area' or 'centre of activity' that is utilized more frequently than other parts (e.g. 80% or 90% of known time-based observations). *cf.* territory (*q.v.*).

homoplasy: similarity between different organisms or taxa resulting from evolution along similar lines (e.g. convergent evolution) rather than descent from a common ancestor.

hyoid: a small bone or bones in the throat located at the base of the tongue and supporting the muscles of the tongue.

- hyperthermia:** elevation of body temperature above normal limits due to increase in $T\hat{a}$ (*q.v.*) or increase in metabolic rate. *cf.* hypothermia (*q.v.*).
- hypocone:** in bats, the cusp on the posterior lingual corner of an upper molar that has a W-pattern of ridges.
- hypoconid cusp:** the posterior cusp on the labial (outer) side of a lower molar tooth (Figure 138).
- hypoconulid:** in bats, the most posterior cusp on the lingual (inner) side of a lower molar tooth (Figure 138).
- hypogeal:** living or growing underground.
- hypothermia:** drop in body temperature below normal limits; occurs in some small mammals when $T\hat{a}$ (*q.v.*) falls, and is a means of conserving energy in cold weather. *cf.* hyperthermia (*q.v.*).
- hypsodont:** describes a premolar or molar tooth with high crowns; has short roots.
- I or i:** (*abbrev.*) incisor (*q.v.*) tooth or teeth; upper case denotes adult dentition, lower case denotes deciduous dentition (milk teeth). *See also* incisor.
- I. (pl. Is.):** (*abbrev.*) Island.
- I¹–M³:** the length of the tooththrow from the anterior end of the first upper incisor to the posterior end of the last molar. In taxa where the last molar is M¹ or M² (instead of M³), the measurement is I¹–M¹ or I¹–M².
- implantation:** the embedding of a blastula (*q.v.*) in the lining of the uterus.
- incertae sedis:** (*Lat.*) refers to a taxon of uncertain status and which may be taxonomically invalid.
- incisive foramen (pl. foramina):** in bats, paired foramina (sometimes three) located at the anterior end of the bony palate, just posterior to the incisor teeth.
- incisor:** tooth rooted in the premaxillary bone (most anterior bone of upper jaw) and in an equivalent position in the mandibular bone (lower jaw); always anterior to the canine teeth, if present. The number and form of the incisor teeth varies in different species. *See also* dental formula (*q.v.*).
- infraorbital foramen (pl. foramina):** foramen that connects the orbit (eye-socket) with the rostrum (premaxilla and maxilla bones); this foramen contains the masseter medialis muscle in some taxa. Also referred to as anteorbital foramen and antorbital foramen.
- inguinal:** situated in the groin, that is the area between the lower lateral part of the abdomen and the thigh.
- inner:** nearest to mid-line of body, e.g. inner incisor, inner margin of ear.
- insectivore (adj. insectivorous):** an animal that eats insects.
- inselberg:** isolated rocky hill; term used mainly in western Africa. *See also* jebel; kopje.
- interaual:** between the ears.
- interaual crest:** in bats, a tuft of erectile hairs posterior to the band connecting the ears of some species in the family Molossidae (Figure 95f, g).
- interfemoral membrane:** in bats, the flight membrane stretching from one hindleg to the other, sometimes enclosing or partly enclosing the tail, sometimes reduced to a very narrow flange around inside edge of legs (Figure 22). Also called uropatagium.
- interorbit (= interorbital constriction):** narrowest part of the skull between the orbits when viewed dorsally at the level of the frontal bones.
- interorbital breadth (IoB):** least breadth of the interorbital constriction (the narrowing of the skull [viewed dorsally] between the orbits) (Figure 23).
- interparietal:** bone (not paired) on dorsal surface of the skull, lying between and partly posterior to the parietal bones.
- interpterygoid:** the region between the two plate-like pterygoid bones (*q.v.*) that form part of the roof of the mouth.
- inter-specific:** between different species.
- intra-specific:** within one species; between members of the same species.
- invagination:** the formation of a cavity by the in-sinking of the outside wall or surface of a tissue or structure, thereby drawing an exterior layer into the interior of the structure to form the lining of the cavity; a cavity formed by the process of invagination.
- IoB:** (*abbrev.*) *see* interorbital breadth (*q.v.*).
- Isoptera:** taxonomic order containing the termites (within the phylum Insecta).
- isozyme:** any one of several different forms of an enzyme encoded by the same or different genes and which each differ in properties such as optimum pH or isoelectric point.
- iteroparous:** repeated reproduction throughout a season or a lifetime (*cf.* semelparous – reproduces once and then dies).
- Itigi thicket:** a type of vegetation found in Tanzania and Zambia, comprised of dense, deciduous, coppice-like, thornless shrubs, which interlace to form a continuous canopy, ca. 3–5 m in height, which is very dense when in leaf (White 1983). Occurs on specialized soils.
- jebel:** isolated rocky hill in savanna and arid habitats; term used mainly in northern Africa. *See also* inselberg (*q.v.*); kopje (*q.v.*).
- jugal:** bone of the skull, which forms the middle part of the zygomatic arch (*q.v.*); anteriorly joins the maxillary process (*q.v.*) of the maxilla bone and posteriorly joins the squamosal process of the squamosal bone.
- Kaokoveld:** area of sandstone and lava hills of the Namib Desert (Biotic Zone 11b) in NW Namibia, inland from the Skeleton Coast.
- Karoo:** southern African term for grassy dwarf shrubland on the semi-arid central plateau of the western half of South Africa at altitudes of 500–2000 m.
- karyogram:** a photographic representation of a karyotype (*q.v.*) as it appears at mitosis. Individual chromosomes are arranged in pairs from largest to smallest.
- karyological:** pertaining to the nucleus and chromosomes.
- karyotype:** the chromosomes in the cell of an animal. *See also* karyogram.
- kopje:** rocky hill with boulders, rock crevices and sparse vegetation; term used mainly in southern Africa. *See also* inselberg (*q.v.*); jebel (*q.v.*).
- K-selection:** selection for characteristics suitable in stable environments (slow development of young, small litter-size, relatively long time to maturity, relatively long life-span) *cf.* r-selection (*q.v.*).
- labial:** pertaining to the lips; situated near the lips; on the outer side of the teeth within the mouth. *cf.* lingual (*q.v.*).
- labially:** in the direction of the lips. *cf.* lingually (*q.v.*).
- lachrymal bone:** small bone in skull situated at the upper anterior margin of the orbit, near the lachrymal (tear) gland.
- lachrymal breadth:** in bats, the breadth across the rostrum dorsally at the lachrymal tubercles.

- lachrymal ridge:** in bats, a small ridge of bone, anterior to the orbit, on each side of the rostrum and sometimes forming a laterally-projecting lachrymal tubercle.
- lambdoid crest (= supraoccipital crest):** crest or ridge of bone running transversely across back of the skull at the junction of the dorsal (parietal) and posterior (occipital) bones of the braincase. May extend posteriorly above the occipital condyles (as in *Scutisorex*). In bats, can be absent, weakly developed, moderately developed or well developed in comparison with that of other species in the same family.
- lambdoid suture:** the line at the junction of the occipital and parietal bones of the skull. May be clearly defined in juveniles or obscured by complete fusion in adults, or by the formation of a lambdoid crest.
- lamina (pl. laminae):** in the context of premolar and molar teeth, a transverse row of cusps (e.g. t1, t2 and t3, or t4, t5 and t6, etc.), which, when worn, form a transverse ridge of bone and dentine across the tooth.
- lanceolate:** lance-shaped; slightly broad or tapering at base, and tapering towards a pointed tip.
- lancet:** the erect, subtriangular, posterior component of the noseleaf of bats in the family Rhinolophidae (Figure 56). Its shape (frontal view) is a diagnostic character (Figure 61).
- laryngeal echolocation:** echolocation using sounds produced by vocal chords in the larynx (as opposed to sounds produced in the mouth).
- lateral leaflets:** one or more pairs of leaflets, either rudimentary or well developed, situated below the anterior 'horseshoe' component of the noseleaf of bats in the families Rhinolophidae and Hipposideridae (Figure 56). Sometimes referred to as secondary leaflets (e.g. by Rosevear 1965, Csorba *et al.* 2003).
- Laurasia:** the northernmost of the two Mesozoic (*q.v.*) supercontinents that later fragmented (as a result of continental drift) into the landmasses of Europe, Asia (excluding the Indian subcontinent) and North America.
- lectotype:** a specimen chosen from syntypes (*q.v.*) to stand as 'the type' of a species or subspecies when no holotype (*q.v.*) was designated by the author who described the new species or subspecies.
- lek:** a traditional site where males gather for the sole purpose of attracting and courting females, and to which females come for the sole purpose of mating with the male of their choice.
- lenticular:** lens-shaped.
- Lepidoptera:** moths and butterflies and their larvae (caterpillars). In diets of bats, usually only refers to adult moths.
- limiting factor:** the principle that the growth or functioning of an organism is limited when any essential factor (or resource) is lacking or in short supply, regardless of the quantity available of any other factor (or resource). The principle may also be applied to the proliferation and/or distribution of a population or species.
- line (unit of measurement):** one-twelfth of an inch.
- lingual:** pertaining to the tongue; situated near the tongue; on the inner (tongue) side of the mouth. *cf.* labial (*q.v.*).
- lingually:** in the direction of the tongue. *cf.* labially (*q.v.*).
- lithophilic:** loving, or thriving amongst, stones, rocks; inhabiting domiciles or day-roosts in caves, on cliffs, or under or amongst rocks etc. *cf.* anthrophilic (*q.v.*); phytophilyc (*q.v.*).
- litter-size:** number of young born to a female. Expressed as mean number (with range from minimum to maximum, and sample size). *cf.* embryo number (*q.v.*).
- lobule:** small lobe.
- localized movements:** movements of an animal within part or all of its home-range within a single day or within a limited period of time. *cf.* migration (*q.v.*); nomadic movements (*q.v.*).
- longitudinal:** lengthwise; running in a head to tail direction. *cf.* transverse (*q.v.*).
- lowveld:** savanna at lower altitudes below the Great Escarpment of South Africa, with vegetation consisting of a grassy lower layer and a woody upper layer of shrubs and/or trees, at either high density (woodland) or intermediate density (bushveld, *q.v.*).
- M:** (*abbrev.*) molar tooth or teeth. *See also* molar (*q.v.*).
- macchia:** a type of Mediterranean shrubland, usually tall, often impenetrable (White 1983). Also called maquis.
- Maghreb:** *see* north-west Africa (*q.v.*).
- mandible:** lower jaw.
- mandibular ramus:** one of the two branches (sides) of the mandible (*q.v.*); the two rami are joined at the mandibular symphysis.
- manoeuvrability:** in bats, refers to the space required by an individual to alter its flight path while flying at a fixed speed; inversely proportional to minimum radius of turn that the bat can attain, and also to wing-loading (*q.v.*) (Norberg & Rayner 1987).
- mastoid:** one of a pair of bones, often with a prominent process, situated near the posterior end of the skull behind the auditory meatus (*q.v.*).
- mastoid width (MW):** greatest width across mastoid region of skull (Figure 23), measured just behind the auditory meatus (*q.v.*).
- maternity cave:** a cave that is particularly suitable for the rearing of young bats.
- maternity colony:** in bats, a congregation of females that are giving birth and/or caring for their young, from which adult males are excluded (or exclude themselves). Also called nursery colony.
- maternity roost:** in bats, a day-roost that is particularly suitable for the rearing of young.
- maxilla (pl. maxillae):** one of the pair of bones in the skull which forms that part of each upper jaw in which the canine (*q.v.*) (if present) and cheekteeth (premolars and molars) (*q.v.*) are rooted.
- maxillary:** pertaining to the maxilla (*q.v.*).
- maxillary process:** projection of bone from the maxilla, which forms the anterior portion of the zygomatic arch (*q.v.*); usually orientated vertically to the anterior-posterior line of the skull.
- meatus:** a passage or channel; the opening of a passage.
- medial:** situated in the middle.
- megabat:** originally the common name for bats in the suborder Megachiroptera. The Megachiroptera is currently not considered monophyletic, and therefore neither of the two traditional Chiropteran suborders (Megachiroptera, Microchiroptera) is recognized by Simmons (2005). However, the name megabat is retained here, in non-taxonomical contexts, where it is relevant to distinguish between megabats (= fruit bats, family Pteropodidae) and microbats (bats belonging to all other families).
- melanistic:** having an abnormally large amount of black or dark pigment in pelage and skin.
- mesa:** Ethiopian word for the micro-habitat (usually on slopes) within afroalpine moorlands and grasslands, where it is higher

- and drier than surroundings areas, so dominated by (usually) *Alchemilla*.
- mesopterygoid fossa:** in bats, the generally U- or V-shaped depression on the ventral aspect of the skull posterior to the palate and between the pterygoid processes (*q.v.*).
- metabolic rate:** see basal metabolic rate (*q.v.*).
- metabolic water:** water produced by oxidative processes within the body; an important source of water for arid-adapted mammals when free (drinking) water and water within the food is in short supply or unavailable.
- metacarpals:** the long bones of the hand, situated between the carpal bones of the wrist and the proximal phalanges of the fingers; the most proximal of the long bones that comprise the fingers in the wings of bats.
- metacentric:** describes a chromosome with the centromere (*q.v.*) at or very near the middle of its length, so there are two arms of equal or almost equal length (ratio not greater than 1 : 1.1). *cf.* submetacentric (*q.v.*).
- metacone:** the posterior labial (external) cusp of an upper molar tooth.
- metatarsals:** the long bones of the foot, situated between the tarsal bones of the ankle and the most proximal phalanges of the toes.
- microbat:** originally the common name for bats in the suborder Microchiroptera. Retained here as the common name of bats in all families except the family Pteropodidae (= megabats, = fruit-bats). *See also* megabat and see text, order Chiroptera.
- microcomplement fixation:** in molecular evolutionary studies, species can be compared by the extent to which antibodies to the proteins of one species cross-react to the proteins of another species. The extent of cross-reaction is indicative of the similarity of the proteins and, by inference, the evolutionary affinity of the two species. Albumin is a protein commonly used for these studies.
- migration:** movements of species that travel, predictably and more-or-less directly, from one habitat to another (and back again), along predetermined routes, in response to seasonal changes in climate, food supply or any other resource. *cf.* localized movements (*q.v.*); nomadic movements (*q.v.*).
- milk teeth:** teeth (usually simple) occurring in newborn mammals, or appearing soon after birth, and preceding the permanent teeth of the adult animal. Also called deciduous teeth. In bats, they are tiny, sharp-pointed spicules, shaped to enable neonates to cling very firmly to the nipples of the mother during flight.
- mine-adit:** horizontal or near-horizontal tunnel in a mine. *cf.* mine-shaft (*q.v.*).
- mine-shaft:** vertical or near-vertical tunnel in a mine. *cf.* mine-adit (*q.v.*).
- Miocene:** geological Epoch (within the Tertiary Period); ca. 23–5 mya.
- miombo:** a vernacular name applied to trees in the genus *Brachystegia*; a type of savanna woodland in the Zambezan region where *Brachystegia* spp. are the commonest trees or one of the commonest trees.
- Mistbelt:** foothills along the eastern Great Escarpment that experience regular fogs, with vegetation comprising mainly grasslands and patches of afro-montane forest in protected valleys and ravines.
- mist-net:** rectangular net made of fine netting (usually monofilament, sometimes two-ply), hung vertically between two upright poles. Several taut, horizontal strands of stronger thread ensure that the net hangs in such a way that a series of horizontal pockets is formed. Bats or birds flying into mist-nets usually fall into a pocket and become tangled. Mist-nets are usually 2.4 m wide and from 5.5 to at least 12.8 m long. They can be set at ground-level or elevated. Mist-nets need very frequent monitoring to prevent injury and stress to entangled animals.
- mitochondrial DNA:** the small amount of DNA contained within the mitochondria of a cell.
- molar:** grinding or cutting tooth rooted in the maxilla bone or the mandible; there are usually one, two or three molar teeth in each ramus of the jaw. Together with the premolars, if present, they form the “cheekteeth”. The number and form of the molar teeth varies in different species. Not preceded by deciduous (milk) teeth (*q.v.*).
- molariform:** similar in form to a molar tooth; used to describe the form of the premolar teeth in some taxa.
- monoestrous:** Generally, having a single oestrus cycle during a single reproductive season. *cf.* polyoestrous (*q.v.*). In bats, having one litter per year; for species and/or populations described as being monoestrous, each female has one litter/year. *cf.* polyoestrous (*q.v.*).
- monogamous:** having only one mate, usually for the whole of an animal's lifetime.
- monogamy (adj. monogamous):** a mating system in which one male mates with one female. Neither sex has the opportunity of monopolizing additional members of the opposite sex. Fitness often maximized through shared parental care (Emlen & Oring 1977). *cf.* polygyny (*q.v.*).
- monophyletic:** describes a taxonomic group descended from a common ancestor that was itself a member of that taxonomic group, and including *all* the descendants of that ancestor (Groves 2001). *cf.* paraphyletic (*q.v.*); polyphyletic (*q.v.*).
- monophyly:** derivation of taxa from a common ancestor. *cf.* diphyly (*q.v.*), polyphyly (*q.v.*).
- monotocous:** normally having only one young per litter (twinning, if it occurs, is very rare and abnormal). *cf.* polytocous (*q.v.*).
- monotypy (adj. monotypic):** describes a taxon containing only one immediately subordinate taxonomic unit, e.g. a monotypic family contains only one genus; a monotypic genus contains only one species. *cf.* polytypy (*q.v.*).
- mopane:** a vernacular name applied to the tree *Colophospermum mopane*; a type of savanna woodland in the Zambezan region in which *C. mopane* is the commonest species of trees.
- Mt:** (*abbrev.*) Mount.
- mtDNA:** (*abbrev.*) mitochondrial DNA (*q.v.*).
- Mts:** (*abbrev.*) Mountains.
- muzzle:** the snout; the nose and jaws of a mammal.
- MW:** (*abbrev.*) see mastoid width.
- mya:** (*abbrev.*) millions of years ago.
- myotodont:** lower molars of bats in the family Vespertilionidae are described as myotodont when the postcrisid ridge directly connects the hypoconid cusp with the entoconid cusp, leaving the hypoconulid isolated (Figure 138). *cf.* nyctalodont (*q.v.*).
- n. d.:** (*abbrev.*) no data.

- N. P.**: (*abbrev.*) National Park.
- narial**: pertaining to the nostrils.
- neonate**: a newly born animal.
- neoparatype**: any specimen described at the same time as the neotype (*q.v.*).
- neotype**: a specimen selected as the type in cases where the primary types are definitely known to be lost or destroyed.
- nipple**: external opening of mammary gland. Nipple number and position vary according to the taxon, but are consistent within a species. Nipples arranged in pairs, one of the pair on each side of body. Nipple number (if given) is: the number and the position of the nipples on one side of the body, and the total number for both sides. For example, in golden-moles, nipple number is: 1 (abominal) + 1 (inguinal) = 4. In some shrews, nipple number is 0 (pectoral) + 2 (inguinal) = 4 (total).
- nipple-clinging**: the behaviour of neonates and unweaned young that remain semi-permanently attached to the nipples of the mother (including while she is foraging) for a period of several days to several weeks. In some species there is a gap between the two deciduous upper incisor teeth, which assists in nipple-clinging.
- nipple-dragging**: situation when a mother drags her neonates and unweaned young, firmly attached to her nipples, when she is active outside her nest. *cf.* nipple-clinging.
- NL breadth**: in bats, the maximum breadth of the noseleaf. For bats in the family Rhinolophidae = breadth of horseshoe excluding lateral leaflets if present.
- NL length**: in bats, the length of the noseleaf.
- nocturnal**: at or active in the night; when light intensity is at its lowest; between sunset and sunrise. *cf.* crepuscular (*q.v.*); diurnal (*q.v.*).
- nomadic movements**: irregular and unpredictable movements, from one locality to another, made by species living in unpredictable habitats. *cf.* localized movements (*q.v.*); migration (*q.v.*).
- nomen dubium**: when the available evidence is not sufficient to permit the identification of a species, its name is considered to be a *nomen dubium* and therefore not available for taxonomic purposes.
- nomen nudum**: a name that is not valid because, when it was originally published, the organism to which it referred was not adequately described, defined or sketched. The name is therefore invalid because it is impossible to associate it indisputably with any specific organism.
- nominate subspecies**: the subspecies that bears the name of the species to which it belongs (e.g. *Myotis bocagii bocagii*), only brought into existence by the creation of one or more other subspecies in the same species (e.g. *Myotis bocagii cupreolus*).
- North Africa**: those parts of Mauritania, Morocco, Algeria, Tunisia, Libya and Egypt that are north of the Sahara Desert.
- north-central Africa**: southern Chad and southern Sudan, west of the Nile R. and south of the Sahara. Mainly savanna habitats.
- north-west Africa**: (= Mahgreb) those parts of Mauritania, Morocco, Algeria, Tunisia and NW Libya that are north of the Sahara Desert.
- noseleaf**: fleshy outgrowth on the dorsal surface of the muzzle of bats in some families, associated with the modification of their echolocation calls.
- nulliparous**: not having given birth.
- nursery colony**: *see* maternity colony.
- nyctalodont**: lower molars of bats in the family Vespertilionidae are described as nyctalodont when the postcristid ridge connects the hypoconid cusp with the hypoconulid without reaching the entoconid cusp (Figure 138). *cf.* myotodont (*q.v.*).
- obligate**: obligatory; limited to one mode of life or action irrespective of conditions or circumstances. *cf.* facultative (*q.v.*).
- occipital condyles**: the pair of smooth, rounded processes of the occipital bone at the posterior end of the skull on either side of the occipital foramen which acts as a hinge between the head and the neck.
- occipital helmet**: backward-pointing projection of the skull, formed either when the sagittal and lambdoid crests are well developed and united, or (in absence of sagittal crest) when the lambdoid crest is well developed and backward-pointing. Sometimes abbreviated to helmet.
- occiput**: the posterior part of the skull, above the foramen magnum (*q.v.*).
- occlusal**: pertaining to the biting surface of a tooth.
- Oligocene**: geological Epoch (within the Tertiary period), ca. 38–23 mya.
- omnivore** (*adj.* **omnivorous**): an animal that eats a wide range of foods.
- orbicularis**: one of the muscles under the skin of a hedgehog, which, when contracted, causes the hedgehog to roll up into a ball.
- orbit**: bony cavity (eye-socket) in which the eye is situated.
- osmetrichia**: hairs structurally specialized for the dispersal of scent.
- outer**: furthest from the mid-line of the body.
- outer margin of ear**: in bats, the margin that is furthest from the mid-line of the body; in most species, this is also the posterior margin.
- ovulation**: the release of female gametes (ova, eggs) from the ovary.
- ovum**: the female gamete or egg cell.
- owl pellets**: waste material, normally in an egg-like shape, regurgitated by owls, which contains undigested fragments of bone, hair, feathers and scales etc. from the prey; for mammalogists, useful in determining indirectly the species of small mammals in a habitat.
- P** or **p**: (*abbrev.*) premolar tooth or teeth; upper case denotes adult dentition, lower case denotes deciduous dentition (milk teeth). *See also* premolar.
- Palaearctic**: a zoogeographic region comprising temperate Europe, North Africa and the Arabian Peninsula.
- Palaeocene**: geological Epoch (within the Tertiary Period); 65–55 mya.
- palatal emargination**: the gap in the anterior of the bony palate associated with the loss or reduction of palatal branches of premaxillae. In bats, it can be closed (non-existent), shallow (barely reaching incisors), deep (reaching level of canines) or very deep (reaching level of premolars or beyond), narrow or wide, and can vary in shape (e.g. U-shaped, V-shaped, bulb-shaped) (Figure 24).
- palatal length**: the anterior–posterior length of the bony palate, taken at the mid-line (Figure 23). For *Rhinolophus* spp., data from Csorba *et al.* (2003) does not include the spike projecting from the posterior margin of the palate.

- palatal ridges:** fleshy ridges crossing the roof of the mouth from side to side.
- palatal shelf:** in hedgehogs, the bony palate of the skull; maximum width is a useful identification character; see also palate (*q.v.*)
- palate:** the roof of the mouth. The anterior part (hard palate) comprises the bony palate (formed by the premaxillae, maxillae and palatine bones), and a covering mucous membrane. The posterior part (soft palate) is composed only of muscular tissue covered by a mucous membrane.
- palpably pregnant:** describes a pregnant female whose pregnancy has been detected only by feeling the foetus(es), not by dissection. It is not possible to detect the early stages of pregnancy by palpation.
- panniculus:** in hedgehogs, one of the muscles under the skin which, when contracted, causes the hedgehog to roll up into a ball.
- papilla** (*pl. papillae, adj. papillate*): a small projection or protuberance.
- paramontane distribution:** *sensu* Koopman 1983, the geographical distribution of a species that is restricted to mountainous regions although the altitudinal range covers both lower and higher elevations.
- paraoccipital process:** narrow strut-like bone, which projects ventrally from the paraoccipital bone on the posterior part of the skull.
- parapatry** (*adj. parapatric*): the situation where two or more species have geographic ranges that are contiguous but do not overlap. This abutting may be along a line of habitat discontinuity, ecotone, or altitudinal/climatic contour, but may also arise from competitive exclusion of one (or both) by the other.
- paraphyletic:** describes a taxon containing units that have evolved from a single ancestral taxon but which do not contain all of the descendants of the most recent common ancestor.
- parastyle:** in shrews, small cusp on outer anterior margin (and labial to the paracone) of a molar tooth.
- paratype:** a specimen collected at the same time and place as the holotype (*q.v.*) and designated by the original authority as such. There may be one or more paratypes.
- parietal:** one of the pair of bones forming the vault of the braincase, situated between the frontal and the occipital bones.
- parous:** having given birth.
- particoloured:** partly of one colour and partly of another colour (as opposed to uniformly coloured).
- partim:** in taxonomy, used in context of taxon names and synonyms to indicate that not all material that has been referred to the name is currently considered to belong to that name. e.g. *auritus* (*partim*) is listed as a synonym of *Plecotus christii* because only some of the specimens that were earlier identified as *Plecotus auritus* are now considered to represent *P. christii*.
- parturition:** the act of giving birth.
- patagium:** flight membrane.
- pectoral:** pertaining to or situated on the chest.
- pelage:** the hairy, woolly or furry covering of the body in mammals. The pelage variously consists of hairs, guard hairs and underfur according to the species.
- perch-hunting:** in bats, any foraging behaviour in which the bat hangs from a perch while searching for its prey and then returns to the perch to eat and/or to resume searching. Includes fly-catching (*q.v.*) and some types of gleaning (*q.v.*).
- phalanx** (*pl. phalanges*): one of the bones in a finger.
- phenotype:** the visible characters of an individual resulting from the interaction between the genotype (*q.v.*) and the environment.
- philopatry:** the tendency to remain in or consistently return to the place where one was born.
- phylogenetics:** pertaining to the line of descent of a taxon; a method of classification which attempts to show the evolutionary relatedness of organisms.
- phylogeny** (*adj. phylogenetic*): the evolutionary history and line of descent of a species or higher taxonomic unit.
- phytophilic:** loving or thriving with plants; inhabiting domiciles or day-roosts in foliage, on tree trunks, in hollow trees, under bark etc. *cf.* anthropophilic (*q.v.*); lithophilic (*q.v.*).
- piloerection:** the erection of hairs which occurs as a means of conserving heat (*see* temperature regulation) and, in some mammals, as a threat display.
- pilosity:** in shrews, refers to the pale well-spaced long hairs on the tail of some species of shrews (mainly *Crocidura*); expressed as a percentage of length of the tail with long hairs (measured from base of tail to tip) to the total tail length. e.g. 0% = no long hairs, 30% = long hairs on basal 30% of tail, 100% = long hairs over whole length of tail, etc.
- pinna** (*pl. pinnae*): the external (outer) ear.
- placental scars:** scars on the inner surface of the uterus of a mammal; the site where a placenta was attached during pregnancy. The number of placental scars can give an indication of the number of litters that a female has had (when the average number of young/litter is known).
- plagiopatagium:** in bats, that part of the wing-membrane posterior to the forearm, i.e. between the body and the fifth finger.
- plantar:** of the sole of the foot.
- Pleistocene:** geological Epoch (within the Quaternary Period); ca. 1.7 mya to 10,000 year ago.
- plesiomorphy** (*adj. plesiomorphic*): in cladistics (*q.v.*), describes a pre-existing character state across a wide taxonomic grouping. Sharing of that state (symplesiomorphy [*q.v.*]) amongst a subset of taxa within the wider grouping is not indicative of monophyly (*q.v.*). *cf.* apomorphy (*q.v.*).
- Pliocene:** geological epoch (within the Tertiary period), ca. 2–5 mya.
- pollex:** digit 1 ('thumb') of forefoot ('hand').
- polygyny** (*adj. polygynous*): a mating system in which one male mates with several females. *See* resource-defence polygyny; female-defence polygyny. *cf.* monogamy (*q.v.*).
- polymorphism** (*adj. polymorphic*): the existence, within a species or population, of individuals having different forms (colour, size, shape etc.).
- polyoestrus:** generally, having a succession of oestrus cycles during a single reproductive season, *cf.* monoestrous (*q.v.*). In bats, having two or more litters/year; for species and/or populations that are described as polyoestrous, each female has two or more litters/year. *cf.* monoestrous (*q.v.*).
- polyphyletic:** describes a taxon derived from two or more ancestral sources; not of a single, immediate line of descent (Mayr *et al.* 1953). *cf.* monophyletic (*q.v.*).
- polyphyly:** derivation of a taxon from two or more ancestral sources. *cf.* monophyly (*q.v.*).

polytocus: normally or often having more than one young per litter. *cf.* monotocus (*q.v.*).

polytypy (*adj.* **polytypic**): a taxon that has several taxa in the next lower taxonomic category, e.g. a polytypic family contains two or more genera, a polytypic genus has two or more species. *cf.* monotypy (*q.v.*).

postauricular: behind the external ear (pinna).

postcalcareal lobe: a small lobe, situated behind the calcar of some bats, that forms a small projection of the interfemoral membrane (Figure 22).

postcristid ridge: in bats, the most posterior ridge (commissure) on a lower molar tooth (Figure 138).

postorbital: behind (posterior to) the orbit.

postorbital process: in bats, the bony projection arising from upper rim of orbit and projecting outwards and downwards around the posterior of the orbit (Figure 23); described as present, absent, long, slender and conspicuous, or concealed as result of merging with supraorbital ridge.

postpartum oestrus: an oestrus cycle immediately after (or very soon after) parturition and while lactating.

predicted mean maximum urine concentration: in microbats, an indicator of the urine-concentrating capacity of the kidney predicted from the ratio of the thickness of the renal cortex to the thickness of the medulla. Known range ca. 2300–5000 mOsmol/kg, therefore 2300–2840 is comparatively very low, 2841–3380 is low, 3381–3920 is medium, 3921–4460 is high and 4461–5000 mOsmol/kg is very high.

premaxilla (*pl.* **premaxillae**): one of a pair of bones at the anterior end of the skull, which bears the incisor teeth. In bats, comprised of a pair of nasal branches that form the anterior end of the rostrum, and a pair of palatal branches that carry the incisors and form the anterior end of the bony palate. Either or both branches may be present or absent, well-developed or reduced, independent or fused with other bones.

premolar: tooth (or teeth) on the maxilla bone; situated immediately anterior to the molar teeth; usually preceded in time by deciduous (milk) teeth. Number of premolars ranges from none to four according to species. Variable in structure and function.

preorbital: anterior to the eye.

procumbent: in context of teeth of bats, angled forward.

promiscuity: a mating system in which each male mates with several females and each female mates with several males.

protocone: The main inner (lingual) cusp of an upper molar tooth.

protopatagium: in bats, that part of wing-membrane anterior to the forearm (Figure 22).

proximal: nearest to the body or to the mid-line of the body; nearest to the point of attachment. *cf.* distal (*q.v.*).

pterygoid: one of a pair of cranial bones forming part of the roof of the mouth.

pterygoid process: one of a pair of narrow, ventrally projecting processes of the pterygoid bones situated immediately posterior to the bony palate and forming the walls of the mesopterygoid fossa (*q.v.*).

pubic nipples: pair of nipples found in the pubic region of bats in the families Rhinolophidae, Hipposideridae and Megadermatidae (and extralimitally Craseonycteridae), which provide holdfasts for the young and may have at least some lacteal function in many

species (Simmons 1993). Also known as false nipples, abdominal nipples and pelvic nipples.

pyriform: pear-shaped.

Quaternary Period: period within the Cenozoic Era; 2 mya to today, comprising two epochs: the Pleistocene and Holocene (Recent) (*q.v.*).

R.: (*abbrev.*) River.

radio-metacarpal pouch: in bats, a small flap of skin stretching between the forearm and the metacarpal of the fifth finger, ventrally to the wing-membrane, and forming a small, shallow pouch (Figure 84c).

radius: one of the two bones of the lower forelimb (the forearm of bats) between the humerus (upper arm) and the wrist.

ramus: one half (left or right) of the lower jaw or mandible.

range length: distance between the most distant captures (by live-trapping) of an individual; a rough method of assessing home-range (*q.v.*).

Recent: see Holocene (*q.v.*).

relatively: used in the context of describing the size of one character relative to the size of a different character in the same species. Usually expressed as a percentage. e.g. Tail 80–90% of HB. *cf.* comparatively (*q.v.*).

relict forest: a forest that persists where local conditions are favourable after the disappearance of forest from the surrounding area as a result of climate change or human activity. Relict forests include those at the base of inselbergs, which are watered by rainwater running off the inselberg, and forests growing in graveyards and sacred sites that are protected. Sometimes known as forest islands.

relict population: one that persists where local conditions are favourable after the extinction of the species from at least part of its former range.

reproductive capacity: number of young produced by a female during the breeding season.

reproductive chronology: the timing and duration of events, such as spermatogenesis, copulation, ovulation, gestation, parturition, lactation and reproductive inactivity, throughout the year.

resource-defence polygyny: a mating system in which a male controls access to several females indirectly, by monopolizing critical resources (Emlen & Oring 1977).

retarded embryonic development: a means of lengthening the interval between copulation and parturition so that both events can occur in the most optimal seasons. The implanted embryo enters a period of retarded (slowed) growth, which may last 4–8 months, after which development proceeds normally.

reticulation: having a net-like pattern.

rhinarium: area of naked moist skin surrounding the nostrils.

ridge (= commissure): in teeth, a ridge connecting two cusps.

Rift Valley: deep valley extending from the Red Sea through Ethiopia and East Africa to Malawi; formed ca. 12 mya by subsidence of the valley floor and uplifting of the edges to form mountains and highlands. Four parts: (1) Ethiopian Rift Valley dividing the Ethiopian plateau into two parts; (2) Albertine Rift Valley (Western Rift Valley) in Uganda, E DR Congo and W Tanzania; (3) Gregorian Rift Valley (Eastern Rift Valley) in N Kenya, C Kenya and N Tanzania; (4) Malawian Rift Valley – the extension of the Albertine Rift Valley in Malawi. The Rift Valleys are noted for their many deep and beautiful lakes.

- riparian:** growing on or living on the banks of streams or rivers.
- riverine forest:** forest growing along the banks of a river or stream where conditions are moister than in the surrounding area. Sometimes referred to as 'fringing forest'.
- Robertsonian fusion:** a chromosomal event involving the apparent fusion of non-homologous single armed (telocentric *q.v.*) chromosomes to form a bi-armed (metacentric *q.v.* or submetacentric *q.v.*) chromosome. Modern studies have revealed that all chromosomes have two arms, even if the smaller one is not detectable by light microscopy. Consequently, the term Robertsonian translocation is becoming more commonly used than Robertsonian fusion.
- roost-fidelity:** in bats, returning to roost at the same place, day after day.
- rostral:** pertaining to the rostrum.
- rostrum:** that portion of the skull anterior to the front line of the orbits and supporting the upper part of the muzzle, comprised of the nasals, premaxillae and maxillae bones.
- r-selection:** selection for characteristics suitable in unstable fluctuating environments (rapid development of young, large litter-size, relatively short time to maturity, relatively short life-span) *cf.* K-selection (*q.v.*).
- ruff (= collar):** in bats, a wide band of hairs, which differ in colour, length and/or texture from other hairs, extending from the shoulders across the throat and upper chest of some bats (Figure 34d), in some species, the ruffs arise from glandular skin and are sometimes stained by glandular secretions.
- rupicolous:** rock-living.
- s.u.:** (*abbrev.*) (*Lat. sans unguis* = without claw) sometimes added as a suffix to the hindfoot measurement to emphasize that HF has been measured without the claw. However, since this is the standard method of measurement, most authors write 'HF', not 'HF s.u.'. *cf.* c.u. (*q.v.*).
- sagittal crest:** longitudinal crest of raised bone on the mid-dorsal line of the cranium.
- scansorial:** climbs or scrambles over logs and in low vegetation close to the ground. *cf.* terrestrial (*q.v.*); arboreal (*q.v.*).
- sclerophyllous:** describes vegetation having hard leaves that are resistant to drought.
- scrotal:** pertaining to, or within, the scrotum (*q.v.*).
- scrotum:** an external sac containing the testes and epididymides in male mammals.
- scuttling:** rapid cursorial locomotion over the ground (or similar surfaces) in which the limbs move quickly; for bats and other small mammals, scuttling is quadrupedal.
- sella:** the transverse structure arising immediately above the horseshoe component of the noseleaf of bats in the family Rhinolophidae and sometimes overhanging the top of the horseshoe (Figure 56). The shape of the front face of the sella viewed from the front (Figure 60), and the pilosity of the front face, are diagnostic characters.
- semi-lunate:** half-moon shaped.
- Senegambia:** Senegal and Gambia.
- sensu:** (*Lat.*) in the sense of.
- sensu lato:** (*Lat.*) in a broad sense.
- sensu stricto:** (*Lat.*) in a strict sense.
- septum:** a dividing wall separating two cavities.
- sex ratio:** the number of males to the number of females, usually expressed as a proportion to one male, e.g. 1 : 1 (equal numbers of males and females), 1 : 0.5 (= twice as many males as females), 1 : 2 (= twice as many females as males).
- sexual dimorphism:** observable (phenotypic) difference(s) (e.g. in colour, size or form) between the males and females of a species or higher taxon.
- sibling species:** pairs or groups of true species that are reproductively isolated, but genetically closely related and so similar in appearance that they are difficult to separate solely on the basis of morphological characters.
- side-stripe:** longitudinal stripe(s) of contrasting colour on each flank, usually from shoulder to rump or upper part of hindlimbs. May be bordered by additional side-stripe above and below.
- singleton:** a neonate that is born singly as opposed to being one of a larger litter.
- sister species:** species that are thought to have arisen from a single dichotomous splitting event.
- soft-bodied:** describes insects (e.g. eaten by bats) that have soft cuticles (e.g. moths, flies). *cf.* hard-shelled (*q.v.*).
- south-central Africa:** Angola, SE DR Congo, Zambia and Malawi (but only west of L. Malawi and the Shire R. Valley).
- southern Africa:** South of the Cunene and Zambezi rivers (i.e. Namibia, Botswana, Zimbabwe, southern Mozambique and South Africa (after Smithers 1983).
- spatulate:** like a spatula, i.e. narrow at the base but wider, flat and parallel-sided distally.
- sperm storage:** storage of sperm in the cauda epididymides (*q.v.*) of males for some time before copulation, or in the reproductive tract of females for an extended period before ovulation takes place. A type of reproductive delay that, in females, lengthens the length of gestation (*q.v.*).
- sperm:** any male gamete; the male cell that fuses with a female gamete (ovum, egg cell) to produce a fertilized egg or zygote from which an embryo will develop.
- spermatogenesis:** the formation of sperm in the testes.
- spoon-hairs (= spatulate hairs):** short, spoon-shaped, bristle-like hairs with tips flattened and slightly curved; e.g. on lips and feet of some bats in the family Molossidae.
- stall-and-twist turning:** in bats, a method of turning during flight to minimize the radius of turn. Because radius of turn is proportional to speed, the bat swoops upwards until its speed is near zero before making the adjustments to the form of its flight membranes, which cause it to roll and turn. *cf.* banking (*q.v.*).
- sub, sub-:** prefix meaning under, signifying beneath or ventral to (as in anatomical features) or south of (as in sub-Saharan); less than (as in subsonic); not quite, nearly, almost, somewhat (as in subequal, subtriangular). In taxonomy, indicates a group just below the status of the taxa immediately following it (e.g. a genus may contain two or more subgenera).
- subauricular:** below the ear.
- subcaudal:** below the tail.
- submetacentric:** describes a chromosome with the centromere (*q.v.*) somewhat nearer one end than the other, so there are two arms of somewhat unequal length (ratio 1 : 1.2–1.9). *cf.* metacentric (*q.v.*); subtelocentric (*q.v.*).

- subspecies:** a geographically localized and isolated subdivision of a species, which differs genetically, morphologically and taxonomically from other subdivisions of the species.
- subtelocentric:** describes a chromosome with the centromere (*q.v.*) much nearer one end than the other, so there are two arms of very unequal length (ratio 1 : >2).
- subterminal:** just below the end or tip.
- subterranean:** living permanently below the ground; subterranean mammals show many adaptations for life underground, e.g. short limbs, thickset shoulder blades and forelimbs, reduced eyes, reduced ability to see, reduction (or absence) of ear pinnae, large extra-buccal incisors, sensory hairs over all the body, feet fringed with hairs, extensive subterranean burrows, etc. (e.g. species of Chrysochloridae). *cf.* fossorial (*q.v.*).
- suckling:** the act of a mother giving milk directly from her breast (mammary glands) to her young. Mothers suckle; their young suck.
- supraoccipital crest:** ridge of bone, orientated transversely across the back of the skull, at the junction of the parietal and/or supraoccipital bones and the occipital bone. Sometimes referred to as the lambdoid crest.
- supraorbital:** above (dorsal to) the orbit.
- supraorbital ridge:** ridge of bone along upper rim of orbit (eye-socket); can be well developed, low or absent.
- sympatry** (*adj.* **sympatric**): the situation where populations of two or more different species have overlapping geographic ranges; refers also to populations of two or more species whose geographic ranges are partly or wholly overlapping. They may or may not interact. *cf.* allopatry (*q.v.*); syntopy (*q.v.*).
- symplesiomorphy:** a primitive or ancestral character shared by two or more groups, which is inherited from ancestors older than the last common ancestor.
- synanthropic:** associated with humans and/or their houses and other buildings.
- synapomorphy** (*adj.* **synapomorphic**): situation in which a homologous character is present in two or more taxa and is thought to have originated in their most recent common ancestor. *See also* apomorphy.
- synonym:** one or more of different names for the same taxonomic unit. A synonym may be a 'senior synonym' (the oldest name), or a 'junior synonym' (a more recent name) that is no longer considered as valid. May be used to refer to all names that have been associated, at some time in the past, with the taxonomic unit as currently understood.
- syntopy** (*adj.* **syntopic**): describes the situation where two or more species use the same or similar habitats and activity times. They may or may not interact. *cf.* allopatry (*q.v.*); sympatry (*q.v.*).
- syntype:** any specimen, or one of a series of specimens, used to designate a species when a holotype (*q.v.*) and paratype(s) (*q.v.*) have either not been selected, or have been lost or destroyed.
- systematics:** the science of arranging organisms in a way that reflects their evolutionary relationships; such relationships may be expressed as a phylogeny (*q.v.*). Often defined (somewhat incorrectly) as a synonym of taxonomy (*q.v.*).
- t (= tubercle):** (*abbrev.*) as used to describe and number the cusps on premolar and molar teeth, e.g. t1, t3, t5.
- T:** (*abbrev.*) length of tail, measured from anterior of the first caudal vertebra to the posterior end of the last caudal vertebra (excluding any tufts, bristles etc. at tip of tail).
- T_a:** (*abbrev.*) ambient temperature; the temperature in which an animal is living. *cf.* T_b (*q.v.*).
- talonid:** heel at the posterior end of a lower molar tooth.
- tapetum lucidum:** light-reflecting layer behind or in the retina of the eyes of some vertebrates which reflects light back through the retina thereby increasing the sensitivity of the eye to dim light.
- taxon** (*pl.* **taxa**): any defined unit (e.g. family, genus, species, subspecies) in the classification of organisms.
- taxonomy:** the science of biological nomenclature; the study of the rules, principles and practice of naming and classifying species and other taxa. Sometimes considered as an integral part (and near synonym) of systematics (*q.v.*).
- T_b:** (*abbrev.*) body temperature; the temperature of the core (central) part of an animal. *cf.* T_a (*q.v.*).
- telocentric:** describes a chromosome that appears to have a terminal centromere (*q.v.*) and therefore only one arm. Modern studies have revealed that all chromosomes have two arms but the smaller arm of telocentric chromosomes is not visible under a light microscope.
- Tenebrionidae:** a family of beetles within the Order Coleoptera.
- termitarium** (*pl.* **termitaria**): a place where termites (Insecta: Isopoda) live. Often a large mound of modified hard soil. The shape and size of a termitarium is unique to each species of termite.
- terrestrial:** living on the ground. *cf.* arboreal (*q.v.*); scansorial (*q.v.*).
- territory:** an area defended by an individual against certain other members of the species, usually by overt aggression or advertisement; territory is marked by the urine, faeces or glandular secretions of the territory's owner. *cf.* home-range (*q.v.*).
- Tertiary Period:** geological period, 65–2 mya, comprising five epochs: Palaeocene, Eocene, Oligocene, Miocene and Pliocene (*q.v.*); followed by the Quaternary Period (*q.v.*).
- testes:** the male gonads, or testicles, in which spermatozoa are formed and in which the male hormone is produced.
- thermoneutral zone:** the range of body temperatures within which an animal does not have to increase its metabolic rate to increase T_b (*q.v.*) (when T_a (*q.v.*) is low) and reduce T_b (when T_a is high).
- thermoregulation:** regulation of body temperature, either by metabolic or behavioural means (or both simultaneously) so that T_b (*q.v.*) is kept more or less constant.
- thoracic:** pertaining to, or situated upon, the chest.
- through-put time:** time taken for food to pass through the digestive tract.
- Tib:** (*abbrev.*) in bats, the length of the hindleg from the knee to the distal end of ankle, usually measured from top of knee to base of ankle when both knee and ankle are flexed (bent).
- tibia** (*pl.* **tibiae**): one of the two bones forming the lower leg (the shin bone); part of hindlimb between knee and ankle.
- tip-shape:** in bats, refers to the length, area and pointedness of the hand-wing (between fingers 2 and 5) relative to the arm-wing (between the body, hindlimb and fifth finger) (see Norberg & Rayner 1987).
- TL:** (*abbrev.*) total length from tip of snout to posterior end of tail. Equivalent to the head and body length and tail length added together. *See also* HB (*q.v.*) and T (*q.v.*).

- toothrow:** Generally, the row of teeth from the most anterior incisor tooth to the most posterior molar. In bats, the row of teeth from the canine to the most posterior molar; also the line passing through the middle of the majority of these teeth (in occlusal view) indicating their alignment (used as reference line to determine if a tooth has become displaced to one side).
- topotype:** any specimen from the type locality (*q.v.*), i.e. the same locality as that from which the holotype (*q.v.*) was taken.
- topotypical:** pertaining to the type locality (e.g. a topotypical population is one found at the type locality).
- torpor** (*adj. torpid*): a state in which there is a (usually short-term) reduction of metabolic rate and a lowering of T_b (*q.v.*) when T_a (*q.v.*) declines; arousal from torpor occurs when T_a increases and without high energy costs to the individual. Torpor is associated with a state of inactivity and reduced responsiveness to stimuli. Torpor lasts for only short periods of time (hours or days) (*cf.* hibernation).
- Tr:** (*abbrev.*) in bats, length of tragus, usually from tip to junction of posterior margin with the ear. Different methods and effects of preservation contribute to the wide ranges given for some species.
- tragus:** a cartilaginous structure, usually small, projecting from the inner side of the external ear just anterior to the auditory meatus (*q.v.*). In bats, its shape and relative size is often of diagnostic importance.
- transverse:** in a direction across the body from side to side. *cf.* longitudinal (*q.v.*)
- Triassic Period:** period (within the Mesozoic Era); 248–208 mya. The first mammals appeared in this period.
- tricuspid:** having three points or cusps (particularly of teeth).
- tubercle:** a small rounded protuberance, e.g. a cusp of a tooth.
- tympanate:** having a tympanic membrane (e.g. ear drum) as a component of an organ of hearing.
- tympanic bulla** (*pl. tympanic bullae*): one of a pair of usually rounded bony capsules, on underside of skull (one on each side), housing structures of the middle and inner ear in many mammals. Also called auditory bulla (*q.v.*).
- type description:** the original description of a species; the original description of the holotype (and paratype[s] if included).
- type locality:** the locality from which a holotype (*q.v.*), lectotype (*q.v.*) or neotype (*q.v.*) was collected. Also called topotypical locality.
- type series:** the holotype and all specimens collected at the same place and time and used, together with the holotype, to describe a new species.
- type species:** usually the species that was the first to be described under the name of a new genus. Not all genera had a designated type species when they were first created; in such cases, other rules determine which species will be the type species.
- type specimen:** *see* holotype.
- underfur:** dense and often woolly layer of the pelage, situated close to the skin and below the soft hairs and guard hairs; usually short and present in those species that experience lower T_a .
- unicuspid:** having one cusp or point (particularly of teeth).
- urine concentration:** *see* predicted mean maximum urine concentration.
- vagrant:** an individual that has been found well outside the normal geographic range of its species, e.g. a bat or bird that has been wind-borne, or an animal that has been transported as a stowaway on a ship, to a distant locality.
- vascular foramen:** one of a pair of small foramina on the dorsal surface of the cranium (present in some genera of shrews).
- vascularized:** infiltrated with capillaries.
- vasoconstriction:** constriction of the capillaries of the blood system near the surface of the skin in order to reduce the rate of heat loss through the skin; a mechanism used by many mammals to conserve heat when T_a (*q.v.*) is low. *cf.* vasodilation (*q.v.*).
- vasodilation:** the dilation (or opening) of the capillaries of the blood system near the surface of the skin in order to increase the rate of heat loss through the skin; a mechanism used by many mammals to cool themselves when T_a (*q.v.*) is high. *cf.* vasoconstriction (*q.v.*).
- veld:** Africans word, used mainly by southern African biologists, to refer to a wide variety of grassland vegetation types typically used for grazing. *See also* bushveld, highveld, lowveld.
- vertebra** (*pl. vertebrae*): any of the bones that make up the backbone.
- vestigial:** small and imperfectly developed; a structure having a smaller and more simple form than the corresponding structure in an ancestral species.
- vibrissa** (*pl. vibrissae*): long stiff hairs on the face, especially around nostrils and lips; often associated with the perception of tactile sensation; 'whiskers'.
- vlei:** southern African term for a marsh or swamp, either permanent or seasonal.
- volant:** able to fly.
- wadi:** a desert valley, usually dry at the surface except after heavy rainfall.
- water turnover:** the rate at which water (fluids) is utilized and replaced in the body per unit time (normally expressed as ml/kg body weight/day); the amount of water an animal processes through its body each day. Water turnover is related to water availability, the urine concentrating ability of the kidney, amount of protein in the diet and T_a (*q.v.*). Water turnover rates are characteristically low in arid-adapted mammals when compared with non arid-adapted mammals.
- West Africa:** ca. south of 18°N from Senegal to the Sanaga R. in Cameroon, and Bioko I. (Equatorial Guinea) (Rosevear 1965).
- wing-loading:** in bats, the mass of the bat divided by its wing-area. For more details, and alternative methods of calculating wing-loading, *see* text, order Chiroptera.
- wingspan (WS):** in bats, the distance from wing-tip to wing-tip. Can be measured in several ways (*see* text, order Chiroptera).
- wrinkle:** in upper lips of some bats in the family Molossidae, a vertical ridge flanked by grooves; usually supporting spoon-hairs.
- WS:** (*abbrev.*) *see* wingspan.
- WT:** (*abbrev.*) weight of an individual, usually expressed in grams (g) or kilograms (kg).
- ZW:** (*abbrev.*) *see* zygomatic width.
- zygomatic arch:** one of a pair of cheekbones, formed of the maxillary process anteriorly, jugal bone medially and squamosal bone posteriorly. Ranges from massive, broad, widely flared and bony, to frail, slender and cartilaginous. When present, provides protection to the eyes and orbits. Also called zygoma.
- zygomatic width (ZW):** greatest width between the outer aspect of one zygomatic arch to the equivalent position on the opposite zygomatic arch (Figure 23). *See also* GWS.

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VOLUME V

CARNIVORES, PANGOLINS, EQUIDS
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B L O O M S B U R Y

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ILLUSTRATED BY JONATHAN KINGDON

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photograph by Jan Kalina

ABOVE LEFT: Jan Kalina.

ABOVE: From left to right: Jonathan Kingdon, Thomas Butynski, Meredith Happold, David Happold and Andrew Richford.
LEFT: Jonathan Kingdon (left) and Michael Hoffmann.

Acknowledgements for Volume V

It was more than a decade ago (mid-2000) that the first authors were contacted to write profiles for Volume V. As readers of earlier volumes will know (and certainly those intimately involved in this project), *Mammals of Africa* suffered a rather tumultuous period in its latter stages, but tenacity wins out, and we are immensely grateful to all those who have so faithfully supported this project over the years.

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Mammals of Africa:

An Introduction and Guide

David Happold, Michael Hoffmann, Thomas Butynski and Jonathan Kingdon

Mammals of Africa is a series of six volumes that describes, in detail, every extant species of African land mammal that was recognized at the time the profiles were written (Table 1). This is the first time that such an extensive coverage has been attempted; all previous books and field guides have either been regional in coverage, or have described a selection of mammal species – usually the larger species. These volumes demonstrate the diversity of Africa's mammals, summarize what is known about the distribution, ecology, behaviour and conservation status of each species, and serve as a guide to identification.

Africa has changed greatly in recent decades because of increases in human populations, exploitation of natural resources, agricultural development and urban expansion. Throughout the continent, extensive areas of forest have been destroyed and much of the forest that remains is degraded and fragmented. Savanna habitats have been altered by felling of trees and development for agriculture. Many of the drier areas are threatened with desertification. As a result, the abundance and geographic ranges of many species of mammals have declined – some marginally, some catastrophically, some to extinction. Hence, it seems appropriate that our knowledge of each

species is recorded now, on a pan-African basis, because the next few decades will see even more human-induced changes. How such changes will affect each mammalian species is uncertain, but this series of volumes will act as a baseline for assessing future change.

The study of African mammals has taken several stages. During the era of European exploration and colonization, the scientific study of African mammals was largely descriptive. Specimens that were sent to museums were described and named. As more specimens became available, and from different parts of the Continent, there was increasing interest in distribution and abundance, and in the ecological and behavioural attributes of species and communities. At first, it was the largest and most easily observed species that were the focus of most studies, but as new methodologies and equipment became available, the smaller and more cryptic and secretive species became better known. Many species were studied because of their suspected role in diseases of humans and livestock, and because they were proven or potential 'pests' in agricultural systems. During the past decade or so, there has been greater emphasis on the genetic and molecular characteristics of species. All these studies have produced a wealth of information, especially during the past 40 years or so. These volumes are not only a distillation of the huge literature that now exists on African mammals, but also of much unpublished information.

Readers will notice that there is a huge discrepancy among species in the amount of information available. Some species have been studied extensively for many years, especially the so-called 'game species', some species of primates and a few species that are widespread and/or easily observed. In contrast, other species are known only by one or a few specimens, and almost nothing is known about them. Likewise, some areas and countries have been well studied, while other areas and countries have been neglected. During the preparation of these volumes, the editors have often been surprised by the wealth of information about some species when little was anticipated, and by the paucity of information about others, some of which were assumed to be 'well known'. In addition to presenting information that is based on sound scientific evidence, the aims of these volumes are to point out where there are gaps in knowledge and to correct inaccurate information that has become embedded in the literature. For most taxa, the detail provided in the species profiles allows accurate identification.

Mammals of Africa comprises six volumes (Table 2). The volumes consist mainly of species profiles – each profile being a detailed

Table 1. The mammals of Africa.

| Order | Number of families | Number of genera | Number of species |
|-----------------|--------------------|------------------|-------------------------|
| Hyracoidea | 1 | 3 | 5 |
| Proboscidea | 1 | 1 | 2 |
| Sirenia | 2 | 2 | 2 |
| Afrosoricida | 2 | 11 | 24 |
| Macroscelidea | 1 | 4 | 15 |
| Tubulidentata | 1 | 1 | 1 |
| Primates | 4 | 25 | 93 |
| Rodentia | 15 | 98 | 395 ^a |
| Lagomorpha | 1 | 5 | 13 |
| Erinaceomorpha | 1 | 3 | 6 |
| Soricomorpha | 1 | 9 | 150 |
| Chiroptera | 9 | 49 | 224 |
| Carnivora | 9 | 38 | 83 |
| Pholidota | 1 | 3 | 4 |
| Perissodactyla | 2 | 3 | 6 |
| Cetartiodactyla | 6 | 41 | 93 |
| 16 | 57 | 296 | 1116^b |

^aIncluding five introduced species. ^bSpecies profiles in *Mammals of Africa*.

Table 2. The six volumes of *Mammals of Africa*.

| Volume | Contents | Number of species | Editors |
|--------|--|-------------------|--|
| I | Introductory chapters. Afrotheria (Hyraxes, Elephants, Dugong, Manatee, Otter-shrews, Golden-moles, Sengis and Aardvark) | 49 | Jonathan Kingdon, David C. D. Happold, Michael Hoffmann, Thomas M. Butynski, Meredith Happold and Jan Kalina |
| II | Primates | 93 | Thomas M. Butynski, Jonathan Kingdon and Jan Kalina |
| III | Rodents, Hares and Rabbits | 408 | David C. D. Happold |
| IV | Hedgehogs, Shrews and Bats | 380 | Meredith Happold and David C. D. Happold |
| V | Carnivores, Pangolins, Equids and Rhinoceroses | 93 | Jonathan Kingdon and Michael Hoffmann |
| VI | Pigs, Hippopotamuses, Chevrotain, Giraffes, Deer and Bovids | 93 | Jonathan Kingdon and Michael Hoffmann |

account of the species. They have been edited by six editors who distributed their work according to the orders with which they were most familiar. Each editor chose authors who had extensive knowledge of the species (or higher taxon) and, preferably, had experience with the species in the field. Each volume follows the same general format with respect to arrangement, subheadings and contents. Because *Mammals of Africa* has contributions from 356 authors (each with a different background and speciality), and each volume was edited by one or more editors (each with a different perspective), it has not been possible or even desirable to ensure exact consistency throughout. Species profiles are not intended to be exhaustive literature reviews, partly for reasons of space. None the less, they are written and edited to be as comprehensive as possible, and to lead the reader to the most important literature for each species. Inevitably, not all information available could be accommodated for the better-known species, and so such profiles are a précis of available knowledge. Extensive references in the text alert the reader to more detailed information.

In addition to the species profiles, there are profiles for the higher taxa (genera, families, orders and above). At the very least, there is a profile for each order, for each family within the order, for each genus within the family, and for each species within the genus. For some orders there are additional taxonomic levels, for example, subfamilies (e.g. Mustelinae). The taxonomy used in these volumes mostly follows that presented in the third edition of *Mammal Species of the World: A Geographic and Taxonomic Reference* (Wilson & Reeder 2005), although authors have employed alternative taxonomies when there were good reasons for doing so. Species are often presented alphabetically within genera. Volume I differs from the other volumes in that it contains a number of introductory chapters about Africa and its environment, and about African mammals in general.

The continent of Africa

For the purposes of this work, 'Africa' is defined as the continent of Africa (bounded by the Mediterranean Sea, the Atlantic Ocean, the Indian Ocean, the Red Sea and the Suez Canal) and the islands on the continental shelf, which, at some time in their history, have been joined to the African continent. The largest of the 'continental islands' are Zanzibar (Unguja), Mafia and Bioko (Fernando Po). All 'oceanic islands', e.g. São Tomé, Príncipe, Annobón (Pagulu), Madagascar, Comoros, Seychelles, Mauritius, Socotra, Canaries, Madeira and Cape Verde are excluded, with the exception of Pemba, which is included because of its close proximity (ca. 50 km) to the mainland.

The names of the countries of Africa are taken from the *Times Atlas* (2005). The Republic of Congo is referred to as 'Congo' and the Democratic Republic of Congo (former Zaire) as 'DR Congo'. Smaller geographical or administrative areas within countries are rarely referred to except for Provinces in South Africa, which are used extensively in the literature. A political map of Africa, and of the Provinces of South Africa, is given (Fig. 1), as well as a list of the 47 countries together with their previous names that are used in the older literature on African mammals (Table 3).

Africa is the second largest continent in the world (after Asia), but it differs from other continents (except Australia and Antarctica) in being essentially an island. At various times in the past, Africa has been joined to other continents – a situation that has had a strong influence on the fauna and flora of the continent. Africa is a vast continent (29,000,000 km², 11,200,000 mi²) that straddles the Equator, with about two-thirds of its area in the northern hemisphere and one-third in the southern hemisphere. As a result, Africa has many varied climates (with seasons in each hemisphere being six months out of phase), many habitats (including deserts, savannas, woodlands, swamps, rivers, lakes, moist forests, monsoon forests, mountains and glaciers), and altitudes ranging from 155 m (509 ft) below sea level at L. Assal, Djibouti, in the Danakil (Afar) Depression, to 5895 m (19,341 ft) on Mt Kilimanjaro, Tanzania. Africa is comprised of 47 countries, some of which are very large (e.g. Sudan [2,506,000 km²; 967,000 mi²], Algeria [2,382,000 km², 920,000 mi²], and Democratic Republic of Congo [2,345,000 km², 905,000 mi²]), and others that are relatively small (e.g. Djibouti [23,200 km², 9,000 sq miles], Swaziland [17,400 km², 6,700 mi²] and The Gambia [11,300 km², 4,400 mi²]). The human population of each country also varies greatly, from about 346/km² in Rwanda to only about 2.5/km² in Namibia. With its great size and varied habitats, Africa supports a high biodiversity, including a large number of species of mammals. Likewise, most countries have a high diversity of mammals (especially when compared with temperate countries).

Africa may also be categorized into Biotic Zones (Fig 2.). A biotic zone is defined as an area within which there is a similar environment (primarily rainfall and temperature) and vegetation, and which differs in these respects from other Biotic Zones. Africa can be divided into 13 Biotic Zones, two of which may be divided into smaller categories. The Biotic Zones concept provides a general assessment of the environmental conditions in which a species lives, as well as providing an assessment of the geographic distribution of the species. The Rainforest Biotic Zone and the South-West Arid Biotic Zone may be divided into regions and sub-regions that reflect the different biogeographical distributions of species, each region/



Figure 1. (a) Political map of Africa; (b) provinces of South Africa; (c) altitudes and major rivers of Africa. South Sudan and Somaliland are not identified as separate countries in the text.

Table 3. The countries of Africa: names, areas and human population density.

| Country name | Area
(km ²) '000 | Area
(miles ²) '000 | Human population
'000 (2006) | People per km ² |
|--|---------------------------------|------------------------------------|---------------------------------|----------------------------|
| Algeria | 2,382 | 920.0 | 33,500 | 14.1 |
| Angola (includes Cabinda) | 1,247 | 481.0 | 15,800 | 12.7 |
| Benin * [Dahomey] | 113 | 43.0 | 8,700 | 77.0 |
| Botswana [Bechuanaland] | 582 | 225.0 | 1,800 | 3.1 |
| Burkina Faso * [Upper Volta; Burkina] | 274 | 106.0 | 13,600 | 49.6 |
| Burundi [part of Ruanda-Urundi (= part of Belgian Congo)] | 27.8 | 10.7 | 7,800 | 280.5 |
| Cameroon [includes former French Cameroon, German Cameroon and part of Eastern Nigeria] | 475 | 184.0 | 17,300 | 36.2 |
| Central African Republic # | 623 | 241.0 | 4,300 | 6.9 |
| Chad [Tchad] | 1,284 | 496.0 | 10,000 | 5.8 |
| Congo [Republic of Congo] | 342 | 132.0 | 3,700 | 10.8 |
| Côte d'Ivoire * [Ivory Coast] | 322 | 125.0 | 19,700 | 61.2 |
| Democratic Republic of Congo [Belgian Congo; Congo (Kinshasa); Zaire] | 2,345 | 905.0 | 62,700 | 26.7 |
| Djibouti [French Somaliland] | 23.2 | 9.0 | 800 | 34.5 |
| Egypt | 1,001 | 387.0 | 75,400 | 75.3 |
| Equatorial Guinea # (includes Rio Muni [Spanish Guinea] and Bioko I. [Fernando Po]) | 28.1 | 10.8 | 500 | 17.8 |
| Eritrea (formerly part of Ethiopia) | 94 | 36.0 | 4,600 | 48.9 |
| Ethiopia [Abyssinia] | 1,128 | 436.0 | 74,800 | 66.3 |
| Gabon # | 268 | 103.0 | 1,400 | 5.2 |
| The Gambia | 11.3 | 4.4 | 1,500 | 132.7 |
| Ghana [Gold Coast] | 239 | 92.0 | 22,600 | 94.6 |
| Guinea * | 246 | 95.0 | 9,800 | 39.8 |
| Guinea-Bissau [Portuguese Guinea] | 36 | 13.9 | 1,400 | 38.9 |
| Kenya | 580 | 224.0 | 34,700 | 59.8 |
| Lesotho [Basutoland] | 30.4 | 11.7 | 1,800 | 59.2 |
| Liberia | 111 | 43.0 | 3,400 | 30.6 |
| Libya | 1,760 | 679.0 | 5,900 | 3.6 |
| Malawi [Nyasaland] | 118 | 46.0 | 12,800 | 108.5 |
| Mali * | 1,240 | 479.0 | 13,900 | 11.2 |
| Mauritania * | 1,030 | 412.0 | 3,200 | 3.1 |
| Morocco [includes former Spanish Morocco and French Morocco]; (now also includes Western Sahara = former Spanish Sahara) | 447 | 172.0 | 32,100 | 71.8 |
| Mozambique [Portuguese East Africa] | 802 | 309.0 | 19,900 | 24.8 |
| Namibia [South-west Africa] | 825 | 318.0 | 2,100 | 2.5 |
| Niger * | 1,267 | 489.0 | 14,400 | 11.3 |
| Nigeria | 924 | 357.0 | 134,500 | 145.6 |
| Rwanda [part of Ruanda-Urundi (= part of Belgian Congo)] | 26.3 | 10.2 | 9,100 | 346.0 |
| Senegal * | 197 | 76.0 | 11,900 | 60.4 |
| Sierra Leone | 71.7 | 27.7 | 5,700 | 79.5 |
| Somalia* [British Somaliland and Italian Somaliland; Somali Republic] | 638 | 246.0 | 8,900 | 13.9 |
| South Africa | 1,220 | 471.0 | 47,300 | 38.7 |
| Sudan § [Anglo-Egyptian Sudan] | 2,506 | 967.0 | 41,200 | 16.4 |
| Swaziland | 17.4 | 6.7 | 1,100 | 63.2 |
| Tanzania [German East Africa; Tanganyika] (now includes Zanzibar I., Mafia I. and Pemba I.) | 945 | 365.0 | 37,900 | 40.1 |
| Togo [Togoland] | 56.8 | 21.9 | 6,300 | 110.9 |
| Tunisia | 164 | 63.0 | 10,100 | 61.6 |
| Uganda | 236 | 91.0 | 27,700 | 117.4 |
| Zambia [Northern Rhodesia] | 753 | 291.0 | 11,900 | 15.8 |
| Zimbabwe [Southern Rhodesia] | 391 | 151.0 | 13,100 | 33.5 |
| Totals/mean density | 29,448 | 11,383 | 902,600 | 56.8 |

Former names are listed in chronological order in square brackets, with the oldest name listed first. Obsolete names are listed because much of the older literature refers to past colonial entities. * = formerly part of French West Africa. # = formerly part of French Equatorial Africa. § At the time of going to press, the country of Sudan had been divided into two: the Republic of Sudan in the north, and the Republic of South Sudan in the south. * The former British Somaliland is now a self-declared state under the name of the Republic of Somaliland, but remains internationally unrecognized.



Figure 2. The biotic zones of Africa. The numbers refer to the biotic zones as described in the text (from Happold & Lock, Volume I, *Mammals of Africa*).

sub-region having a community of mammals and other animals that is different to any other. Details of the Biotic Zones of Africa, and the regions and sub-regions of the Rainforest Biotic Zone and the South-West Arid Biotic Zone, are given in Volume I of *Mammals of Africa*.

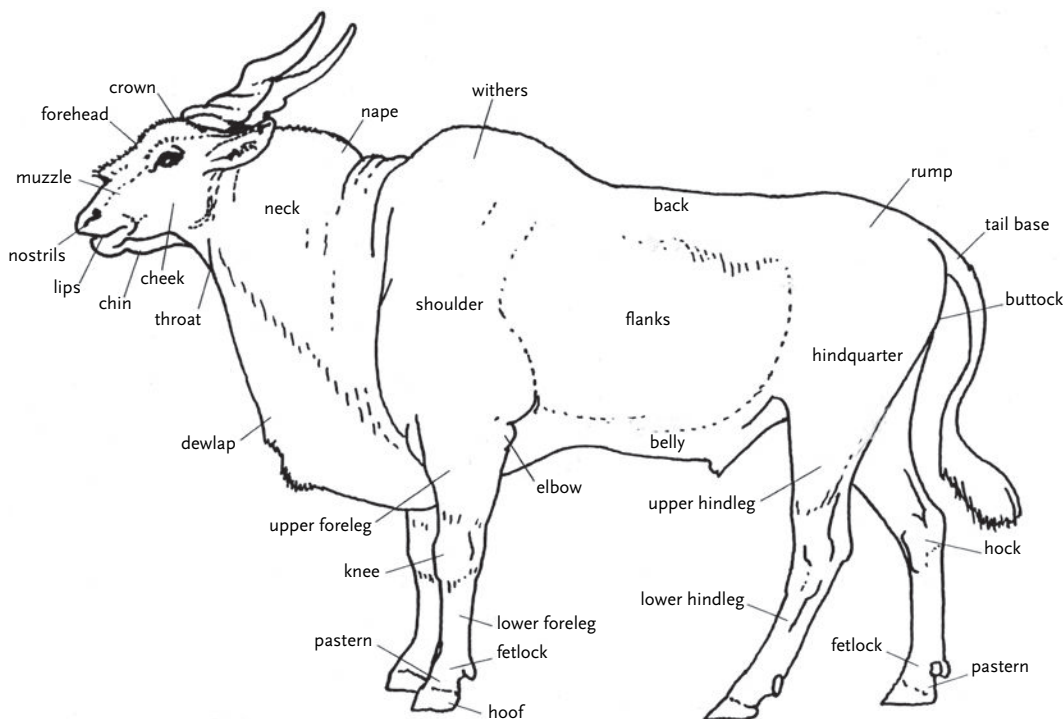


Figure 3. External features of a mammal: Common Eland *Tragelaphus oryx*.

The carnivores, pangolins, equids and rhinoceroses of Africa

This volume is devoted to the orders Carnivora (carnivores), Pholidota (pangolins) and Perissodactyla (equids and rhinoceroses). The most diverse is the carnivores (83 native species), ranging from iconic charismatic species like the Lion *Panthera leo* and African Wild Dog *Lycaon pictus* to the remarkable diversity of mongooses and genets. Carnivores show a close relationship with the pangolins (4 species) and, in turn, the carnivores and pangolins are allied with a clade that unites the perissodactyls with the cetartiodactyls (pigs, hippopotamuses, chevrotain, giraffes, deer and bovids; the subject of Volume VI). Note that introduced species are mentioned in the higher-level profiles (where relevant), but are not otherwise profiled.

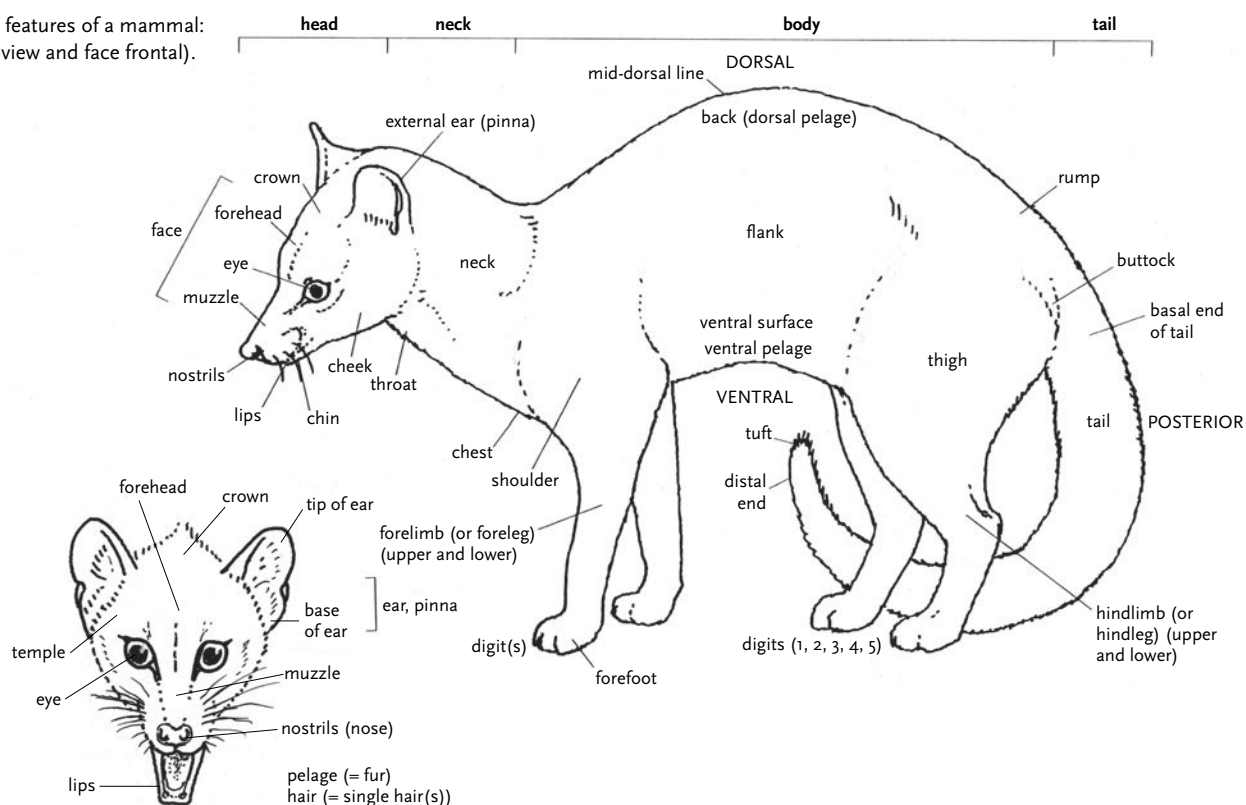
At the time of going to press, genetic research has suggested that a fifth species of the genus *Canis* occurs in Africa, namely the Grey Wolf *C. lupus* (Rueness *et al.* 2011; and see Gaubert *et al.* 2012). Further brief discussion is provided under the genus profile and species profile for the Golden Jackal *Canis aureus*, but the species is otherwise not separately profiled.

As *Mammals of Africa* was being finalized, a new work by Colin Groves and the late Peter Grubb, *Ungulate Taxonomy*, was published but it has not been possible to fully consider and evaluate the conclusions and classification presented in that work.

Species profiles

Information about each species is given under a series of subheadings. The amount of information under each of these subheadings varies greatly between species; where no information is available, this is recorded as 'No information available' or words to this effect. The sequence of subheadings is as follows:

Figure 4. External features of a mammal: *Genetta* sp. (side-view and face frontal).



Scientific name (genus and species) The currently accepted name of the species.

Common names English, French and German names are given, as available. The first given English name is the preferred common name for the species; alternative names are given in parentheses for some species. Wilson & Cole (2000) list proposed common names for all the world's mammals; most of these names were also given in the third edition of *Mammal Species of the World* (Wilson & Reeder 2005). Although these works have been consulted, the names used have not always been adopted in *Mammals of Africa*. French and German names were usually provided by authors.

Scientific Citation This provides the full scientific name of the species, i.e. genus name, species name, authority name, and date of authority. Parentheses around the authority's name and date indicate that the species was originally named in a different genus to its present generic allocation. The scientific name is followed by the publication where the species was described, and the location where the type specimen (or type series) was obtained. Most of this information is taken from Wilson & Reeder (2005).

Taxonomy This section contains information on taxonomic problems, if any, associated with the species, and its relationship with other species in the genus. For some species, there is considerable information about these topics; for others, there may be nothing. A list of synonyms (without the taxonomic authority for each) and the number of subspecies (if any) is presented, mostly taken from Wilson & Reeder (2005). The chromosome number is given if available, and in some cases this is followed by other information relevant to the chromosomes.

Description This section, together with the illustrations, provides the reader with adequate information to identify the species. The section begins with a brief overall description of the species, including an indication of size. This is followed by a detailed description of the external features of the species' head (and parts of the head), dorsal pelage, legs, feet, ventral pelage, and tail (in this order), as well as any special characteristics unique to the species. For some species, diagnostic characteristics of the skull and dentition are given. The characters described in this section are common to all subspecies of this species (unless otherwise noted). The mammary formula, i.e. the number and arrangement of nipples in adult females, is noted wherever this feature varies between the taxa being discussed.

Geographic Variation Variation within the species may be of two sorts: (a) clinal variation without subspecies, or (b) subspecific variation. If (a), there is a description of the character(s) that alter clinally across the geographic range of the species. If (b), each of the subspecies is listed with its geographic range and, where available, the characters that distinguish it from other subspecies of the species. For some species, subspecies have been described that are no longer considered to be valid; in some cases, such names may be listed but without further comment.

Similar Species Species that are sympatric or parapatric with the species under consideration, and with which it may be confused, are listed along with diagnostic characteristics (additionally, readers may refer to profiles of the similar species in question). In some instances, species that are allopatric in distribution are also included.

Distribution The first sentence 'Endemic to Africa' informs the reader that this is an African species and does not occur on any

other continent; if a species also occurs outside Africa, this is noted at the end of this section with a very brief synopsis of the extralimital range. For widespread species that generally remain so today (e.g. *Herpestes sanguineus*), the text provides a general idea of the range, highlighting only places or countries where the species may have been extirpated, recently newly recorded, or providing clarity on previously incorrectly attributed country records and range limits. In the case of widespread species that have undergone significant range contractions and declines (e.g. *Lycaon pictus*), the text generally differentiates between former and current ranges in an attempt to elucidate a clearer picture of where species do, or no longer, occur. Finally, for more range-restricted species (e.g. *Canis simensis*), the information provided may be quite precise, detailing even localized distribution within the confines of its small range. A distribution map (see below) augments the information given here.

Habitat This section provides a description of the range of habitats where the species lives. Details of plant communities, plant species, vegetation structure, soil type and/or structure and water availability, etc. (if available) are also recorded. Other information may include average annual rainfall, altitudinal limits and seasonal variation in habitat characteristics.

Abundance A general indication of abundance in the habitat. This may be unquantified, such as abundant, common, uncommon, rare, or phrases such as ‘rarely seen but frequently heard’, etc. For better-known species, abundance may be expressed as estimates of density (e.g. number/ha or number/km²), or relative abundance within the community (e.g. ‘comprised x% of carnivores captured’, ‘the second most numerous species’); for the better-known, rare species, actual numbers of individuals for the species may be given. Other information may include seasonal changes in density, frequency of observations, or the relative abundance of specimens in collections.

Adaptations This section describes morphological, physiological and behavioural characteristics that show how the species uniquely interacts with its environment, conspecifics and other animals. This section may also describe species-specific adaptations for feeding, locomotion, burrowing, mechanisms for orientation, production of sound, sensory mechanisms and activity patterns. In some instances comparison with related or convergent species allows the unique adaptations of the species under discussion to be detailed or highlighted.

Foraging and Food This section provides information on the diet and foraging habits of the species. The diet is described either by a list of the taxa of animals or plants consumed, or as a quantitative measure of the contents of the stomach or the faeces. This section can also include any of the following: location of food, foraging behaviour, times when foraging occurs and daily distance moved; hoarding; seasonal changes in diet and food availability; individual or co-operative behaviour used in foraging and hunting; sex and age differences in foraging and diet; and nomadic or migratory movements in relation to food availability.

Social and Reproductive Behaviour Topics in this section may include group structure (whether solitary, social, or colonial),

group size and composition; agonistic and amicable behaviour, comfort behaviour, etc.; home-range (including quantitative data), territorial behaviour, courtship and mating behaviour, behaviour of young, parental–young interactions; presence of helpers, vocalizations, and interactions with other species (mammals, birds, etc.).

Reproduction and Population Structure This section begins with an assessment of reproductive strategy (if known) and the times/seasons of the year when individuals are reproductively active (pregnancy and lactation in females, active spermatogenesis in males). Other information may include length of gestation, times/seasons of births, including peaks of births, litter-size, birth-weight and size, spacing of litters, growth and time to weaning, maturity, longevity, and mortality rates. Reproductive strategies, if known, are described with respect to locality, food availability, and population density. Population structure (sex ratio, adult/young ratio, abundance of different cohorts in the population at different times of the year) may be described, and related to seasonal variations in reproduction and environmental variables.

Predators, Parasites and Diseases The known predators, parasites and diseases are listed. Information on parasites and diseases is not intended to be exhaustive, but simply to provide an entry point into the literature on the topic. In some cases, information on diseases from captive animals is presented. Additional information is given if the species is a host to diseases that affect humans and domestic stock.

Remarks This subheading subsumes five of the above subheadings (Adaptations, Foraging and Food, Social and Reproductive Behaviour, Reproduction and Population Structure, and Predators, Parasites and Diseases) in those instances where there is little or no information available.

Conservation The conservation status of the species is stated, as given by the *IUCN Red List of Threatened Species* (version 2011.2). The IUCN Red List categories follow the definitions and criteria given in the *IUCN Red List Categories and Criteria Version 3.1* (Table 4). For those species classified as threatened (i.e. ‘Vulnerable’, ‘Endangered’, ‘Critically Endangered’), the criteria met are also indicated. Some species have changed status due to improved knowledge, taxonomic revision, or the impact of threatening processes or conservation actions. Readers can obtain detailed reasons for the past and present status of a species by going to the IUCN Red List website (www.iucnredlist.org). If a species was listed on Appendix I, II or III under CITES (Convention on International Trade in Endangered Species; www.cites.org; as of 22 December 2011) or Appendix I or II of CMS (Convention on Migratory Species; www.cms.int; as of 5 March 2009) this is also indicated. For some species, additional information is provided, such as presence in protected areas, major threats, and current or recommended conservation measures.

Measurements A series of morphological measurements is provided. For each species there is a standard set of measurements. The abbreviations for each measurement are given in the Glossary.

Table 4. Definitions for the IUCN Red List categories (from IUCN – Red List Categories, Version 3.1).

| Category | Description |
|-----------------------------------|--|
| Extinct (EX) | A taxon is Extinct when there is no reasonable doubt that the last individual has died. A taxon is presumed Extinct when exhaustive surveys in known and/or expected habitat, at appropriate times (diurnal, seasonal, annual), throughout its historic range have failed to record an individual. Surveys should be over a time-frame appropriate to the taxon's life-cycles and life-form. |
| Extinct in the Wild (EW) | A taxon is Extinct in the Wild when it is known only to survive in cultivation, in captivity or as a naturalized population (or populations) well outside the past range. A taxon is presumed Extinct in the Wild when exhaustive surveys in known and/or expected habitat, at appropriate times (diurnal, seasonal, annual), throughout its historic range have failed to record an individual. Surveys should be over a time-frame appropriate to the taxon's life-cycle and life-form. |
| Critically Endangered (CR) | A taxon is Critically Endangered when the best available evidence indicates that it meets any of the criteria A to E for Critically Endangered, and it is therefore considered to be facing an extremely high risk of extinction in the wild. |
| Endangered (EN) | A taxon is Endangered when the best available evidence indicates that it meets any of the criteria A to E for Endangered, and it is therefore considered to be facing a very high risk of extinction in the wild. |
| Vulnerable (VU) | A taxon is Vulnerable when the best available evidence indicates that it meets any of the criteria A to E for Vulnerable, and it is therefore considered to be facing a high risk of extinction in the wild. |
| Near Threatened (NT) | A taxon is Near Threatened when it has been evaluated against the criteria but does not qualify for Critically Endangered, Endangered or Vulnerable now, but is close to qualifying for (or is likely to qualify for) a threatened category in the near future. |
| Least Concern (LC) | A taxon is Least Concern when it has been evaluated against the criteria and does not qualify for the Critically Endangered, Endangered, Vulnerable or Near Threatened categories. Widespread and abundant taxa are included in this category. |
| Data Deficient (DD) | A taxon is Data Deficient when there is inadequate information to make a direct, or indirect, assessment of its risk of extinction based on its distribution and/or population status. Data Deficient is not a category of threat. Listing of taxa in this category indicates that more information is required and acknowledges the possibility that future research will show that a threatened classification is appropriate. |
| Not Evaluated (NE) | A taxon is Not Evaluated when it has not yet been evaluated against the criteria. |

A measurement is cited as the mean value (with minimum value to maximum value in parentheses) and sample size. For some, the standard deviation (mean \pm 1 S.D.) is given instead of the range. For most species, data for males and females are presented separately. In some cases, more than a single set of measurements is given; this is particularly the case for widespread species where geographic variation in size may be evident, and also for species with several well differentiated subspecies (in which case, we have endeavoured to present a set of measurements for each). Some

species have additional stand-alone measurements presented beneath the primary series. Skull measurements are generally not provided, with the exception of the small carnivores (Herpestidae, Mustelidae, Nandiniidae and Viverridae). The majority of measurements also contain the location(s) where the specimens were obtained, and the source of the data. Sources are either cited publications, or specimens in museums, or unpublished information from authors or others. The acronyms for museums where specimens were examined and measured are given in Table 5.

Table 5. Museum acronyms and abbreviations.

| Acronym | Museum name | Acronym | Museum name |
|---------|--|---------|--|
| AMNH | American Museum of Natural History, New York, USA | MZUF | Museo Zoologico de 'la Specola', Firenze, Italy |
| BMNH | Natural History Museum, London, UK [formerly British Museum (Natural History)] | NHMB | Naturhistorisches Museum, Berlin, Germany |
| CMNH | Cleveland Museum of Natural History, Ohio, USA | NMNH | Smithsonian National Museum of Natural History, Washington DC, USA |
| DM | Durban Natural Science Museum, Durban, South Africa | PCM | Powell-Cotton Museum, Birchington, UK |
| FMNH | Field Museum of Natural History, Chicago, USA | RMNH | Nationaal Natuurhistorisch Museum, Leiden, The Netherlands (formerly Rijksmuseum Natuurlijke Historie) |
| IRSN | Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium | SBP | Station Biologique de Paimpont, Université Rennes 1, France |
| JFBM | James Ford Bell Museum of Natural History, Minnesota, USA | SMF | Senckenberg Museum, Frankfurt, Germany |
| LACM | Los Angeles County Museum of Natural History, Los Angeles, USA | SMNK | Staatliches für Naturkunde, Karlsruhe, Germany |
| MCZ | Museum of Comparative Zoology, Harvard University, USA | SMNS | Staatliches Museum für Naturkunde, Stuttgart, Germany |
| MHNC | Musée d'Histoire Naturelle, La Chaux-de-Fonds, Switzerland | ZFMK | Zoologisches Forschungsmuseum, Alexander Koenig, Bonn, Germany |
| MNHN | Muséum National d'Histoire Naturelle, Paris, France | ZMA | Zoologisch Museum, Amsterdam, The Netherlands |
| MRAC | Musée Royal de l'Afrique Centrale, Tervuren, Belgium | ZMB | Zoologisches Museum der Alexander von Humboldt Universität, Berlin, Germany |
| MSUM | Michigan State University Museum, Michigan, USA | ZMMU | Zoological Museum, Moscow University, Moscow, Russia |
| | | ZSM | Zoologische Staatssammlungen München, Munich, Germany |

Key References A select list of references, which provides more general information on the species, or a work that is generally considered to be a key reference work on the species. Each reference is given in full in the Bibliography. Citations given in the text (but not cited in ‘Key References’) are also given in full in the Bibliography. In general, profiles account for all literature published up until the end of 2007. Authors and editors have endeavoured to keep the species profiles fully up-to-date throughout the long production schedule, and references published from 2008 onwards have been incorporated where possible. None the less, certain key recent papers will have been missed or omitted.

Author The name of the author, or authors, is given at the end of each profile. All profiles should be cited using the author name(s).

Tables With a few exceptions, the use of tables to present data has been avoided in Volume V of *Mammals of Africa*.

Higher taxon profiles

The profiles for orders, families and genera are much less structured than for the species profiles. Each profile usually begins with a listing of the taxa in the next lower taxon; for example, each family profile lists the genera in that family. An exception to this arrangement is where a taxon has only one lower taxon. Higher taxa profiles provide the characteristics common to all members of that taxon. Some of these characteristics (for example, number of nipples or dental formula) may not be repeated in lower taxon profiles (unless essential for identification), so readers are encouraged to consult also the higher-taxa profiles, e.g. the species profile for *Canis simensis* should be consulted in association with the genus *Canis* profile. Likewise, a generic profile, such as *Canis*, should be read in association with the family Canidae profile.

Distribution maps

Each species profile contains a pan-African map showing the geographic range of the species. The purpose of the maps is to show current known limits of distribution of the species within historical range, recognizing that within this mapped range a particular species’ distribution will not be homogeneous. Reintroductions within the former range of a species are included and mapped, but

introductions outside of the former known range are not. Note that due to the sensitivity around the location of rhinoceros populations in Africa, the maps for these species are degraded to the country level. Subspecies are only indicated in cases where the boundaries can be reasonably delineated.

Each map shows the boundaries of the 47 countries of Africa, some of the major rivers (Nile, Niger–Benue, Congo [with the tributaries Ubangi, Lualaba and Lomani], Zambezi and Orange), and Lakes Chad, Tana, Turkana (formerly Rudolf), Albert, Edward, Victoria, Kyoga, Kivu, Tanganyika, Malawi, Mweru, Bangwuela and Kariba. The map projection is Transverse Mercator, with the following parameters: False Easting: 0; False Northing: 0; Central Meridian: 20; Linear Unit: metre; Datum: Clarke 1866.

The geographic distribution of a species is indicated as:

- red shading = current range. Different colour shading denotes subspecies, where appropriate.
- × = isolated locations considered to be separate from the main geographic range(s); some locations indicated by × may include two or more closely spaced locations.
- ? = uncertain, but possible, presence.
- red arrow = recorded from the island indicated by the arrow.

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Cohort FEREUUNGULATA

Fereuungulata Waddell, Okada & Hasegawa, 1999. Syst. Biol. 48: 3.

Fereuungulata is a mammalian cohort that unites the carnivores and pangolins with what were traditionally and popularly dubbed 'Ungulates', a category that sometimes, but not always, has been thought to have a relationship with whales. Use of the taxon name Fereuungulata, instead of Ferungulata (*sensu* Simpson 1945, who included also paenungulates, but not pholidotes or cetaceans) follows Asher & Helgen (2010).

The orders Artiodactyla and Perissodactyla, or more commonly the even-toed and odd-toed 'ungulates', respectively, both made their first appearance in the fossil record in the earliest Eocene, around 55 mya. Members of both orders are known across the northern hemisphere at this time, but their origin is commonly assumed to be in Asia (Beard 1998). This time period coincides with a major fall in sea level and with dispersal events among many mammalian groups.

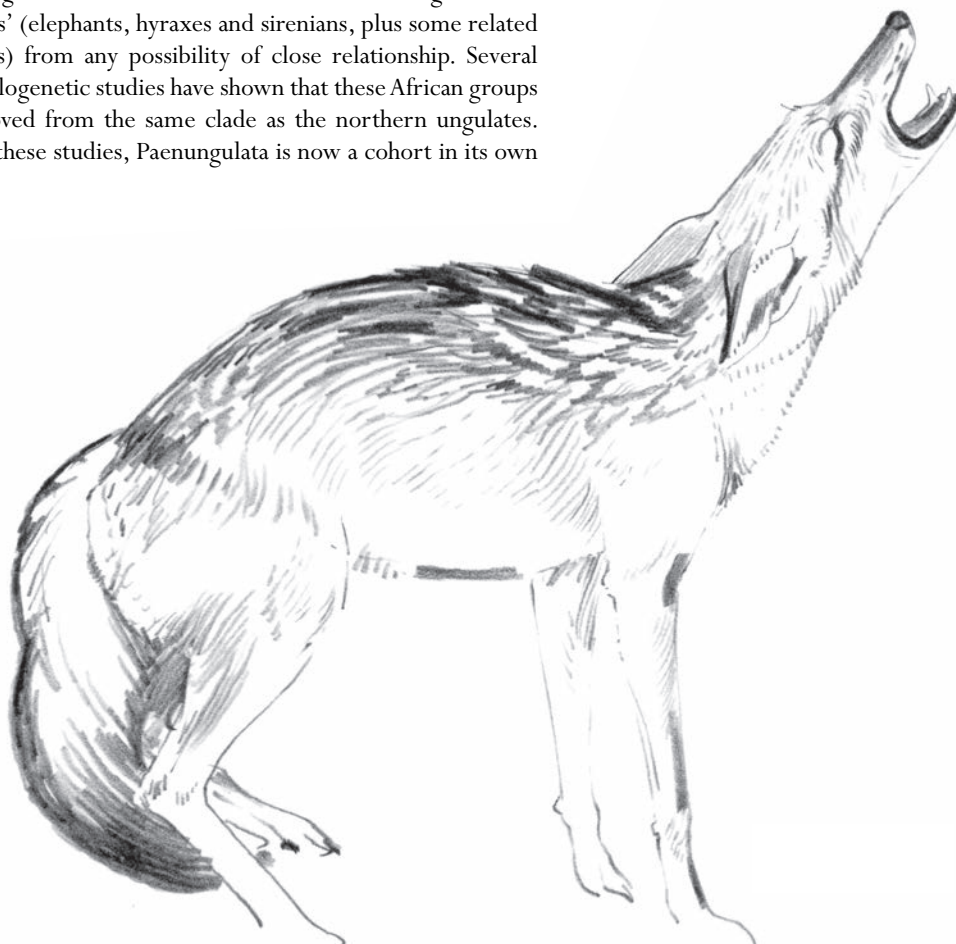
It has been commonly assumed that artiodactyls and perissodactyls had a common evolutionary origin, in part based on their dental and post-cranial similarities, and yet many of these features can be shown to have evolved convergently, including hooves (Prothero *et al.* 1988, Prothero & Shoch 2002). Recent molecular studies have further complicated traditional efforts to fathom the evolutionary history of 'Ungulates'.

Of major significance has been the excision of 'subungulates' or 'paenungulates' (elephants, hyraxes and sirenians, plus some related extinct groups) from any possibility of close relationship. Several molecular phylogenetic studies have shown that these African groups must be removed from the same clade as the northern ungulates. As a result of these studies, Paenungulata is now a cohort in its own

right within the new supercohort Afrotheria (see Springer *et al.* 2005; and Supercohort Afrotheria in *Mammals of Africa*, Volume 1).

Another complication has been the creation of a clade to embrace both whales and artiodactyls (see Springer *et al.* 2005 for a review of the molecular evidence for higher order mammalian clade relationships). For several decades cetaceans (whales and dolphins) were presumed to have a relationship to artiodactyls, but molecular studies now place them as a suborder *within* what used to be called the Artiodactyla (the two former orders now combined in order Cetartiodactyla). However, there is still much dissension between molecular biologists and morphologists as to exactly how whales are related to other artiodactyls.

It is also not clear whether artiodactyls (= cetartiodactyls) and perissodactyls form a monophyletic group. Molecular studies (e.g. Liu *et al.* 2001, Meredith *et al.* 2011) unite a clade of Carnivora plus Pholidota (pangolins) as the Ferae (see below), and in turn show a close relationship to these ungulates. But while some studies place the Ferae clade outside of the grouping of the two ungulate orders (thus making the ungulate grouping monophyletic), others group the Ferae as the sister taxon to Perissodactyla (e.g. Waddell *et al.* 1999), although the morphological support for this grouping is slender. Some molecular studies also place bats within this clustering of carnivores



Golden Jackal *Canis aureus*.

and ungulates (as related to perissodactyls), while others have bats as the sister taxon to ungulates plus carnivores (see Meredith *et al.* 2011). In spite of such uncertainties, this work has provisionally adopted a molecular taxonomy that aligns a monophyletic clade comprising the orders Cetartiodactyla and Perissodactyla (Euungulata, after Waddell *et al.* 2001) with a monophyletic Ferae (Carnivora + Pholidota) under the cohort 'Fereuungulata' (and see Zhou *et al.* 2012).

Modern Carnivora have, in general, modified their cranial anatomy less radically than have Cetartiodactyla (the most extreme, of course, being the whales). The diversification of carnivores is sketched out in the Carnivora profile. Modern Pholidotes (pangolins), totally toothless, have made their affinities particularly difficult to fathom so the discovery by geneticists of a molecular link with carnivores has, at last, provided some sort of a lead, however distant, into the remotest origins of this most enigmatic of mammal orders. None the less, by adopting such a specialized ant and termite diet, and evolving the equivalent of mediaeval armour, the pangolins are almost as different from their nearest affines as whales are from pigs and hippos.

Many phylogenies have positioned artiodactyls and perissodactyls as 'closely related'. Today, we may well see living artiodactyls and perissodactyls as being rather similar types of mammals: horses are not so dissimilar from cows (i.e. both are largish, long-legged grazing mammals) and rhinos are not superficially remote from hippos (but note there has never been a perissodactyl equivalent for the huge radiation of omnivorous pigs among the artiodactyls). It is, thus, important to remember that during the Eocene, when most of the northern hemisphere was covered by tropical-like forests and the earliest artiodactyls and perissodactyls had begun their radiation, each lineage represented emphatically different types of mammals (see Janis 2008).

Artiodactyls were mainly small forms, rather like present-day mouse deer (Tragulidae) in both size and ecology. Their dental morphology indicated omnivorous (or, at best, soft browsing diets that included berries, buds and non-fibrous leaves). The perissodactyl equivalent of these early artiodactyls would have been the early equids ('horses'). Perissodactyls also branched out into a number of different, and larger, ecological types, most with more specialized browsing diets. These included ceratomorphs (rhinos and true tapirs) and a diversity of extinct lineages: a diversity of small 'tapiroids', the rhino-like brontotheres, and the rather horse-like chalicotheres that substituted claws for hooves.

By the late middle Eocene, around 45 mya, the northern hemisphere climate commenced cooling and drying, a trend that characterized the rest of the Cenozoic (see Morley & Kingdon, *Mammals of Africa*, Volume 1, pp. 43–56). Tropical forests started to retreat, replaced by more temperate woodlands, and this period heralded a time of great evolutionary turnover among the ungulates, among which artiodactyls apparently pulled ahead of the perissodactyls in terms of 'evolutionary success'. The first fossil ruminants (still small, tragulid-like forms) are known from this time in Asia and North America.

This change in fossil diversity has long been interpreted as reflecting some evolutionary superiority of artiodactyls, presumed to relate to the rumen-based foregut method of fermentation of fibrous vegetation in at least some clades, in contrast to the less derived mode of hindgut fermentation in perissodactyls (see Hofmann & Kingdon, *Mammals of Africa*, Volume 6, p. 84). However, the fossil record does not support the notion of a blanket competitive replacement. Moreover, it is certainly not the case that rumen-based fermentation is inevitably superior to hindgut fermentation under *all*

ecological circumstances. The rise of the more folivorous clades of artiodactyls (Ruminantia and Tylopoda) during the late Eocene, and the decline of the perissodactyls, is best explained by changes that would have taken place in vegetational quantity, quality and seasonal availability that would favor these animals' mode of feeding selection (small amounts of high-quality food: see discussion in Janis 2008).

Among the later Eocene artiodactyls a clear division emerged. As presented in these volumes, this has taken the form of four modern suborders: Suiformes (pigs and peccaries), Tylopoda (camelids), Whippomorpha (hippos and whales) and Ruminantia (modern ruminant groups, including tragulids). There is considerable debate as to how the artiodactyl suborders are interrelated, and as to where extinct groups would fit in. Hippos, long supposed to have some sort of affinity with suids, have been declared as close whale relatives by molecular biologists (with Whippomorpha as a sister group of the Ruminantia by Price *et al.* 2005). Craniodental morphologies have linked tylopods and ruminants as sister taxa in the 'Neoselenodontia', but molecular biology has broken this grouping up, and placed camelids as basal to other artiodactyls (including whales) (see Price *et al.* 2005). In any event, the modern lineages of artiodactyls gained their first evolutionary foothold during the late Eocene (about 40–35 mya). At this time some clear divisions emerged and the contemporary descendants of these early radiations are provisionally presented in these volumes in the form of the aforementioned modern suborders.

The late early Miocene, around 20–18 mya, marks another critical point in the patterns of ungulate evolution. Out of the initial diversification of perissodactyls, only four families remained: rhinocerotids, tapirs, chalicotheres (which survived into the Pleistocene) and horses. At this time, the first of the more derived equids (subfamily Equinae) appeared in North America (first appearing in the Old World around 10.5 mya). These equids were of a larger body size (pony-sized) and larger than previous forms, with high crowned (hypsodont) cheekteeth indicative of a diet that included at least a good proportion of grass, and with limbs more adapted for locomotion in open habitats.

The radiation of equids in North America has long been a well-known example of evolution (although they subsequently became extinct on that continent). In the Old World there is today only a single genus of grazing equid (*Equus*, comprising some seven, mostly allopatric, species) in contrast with the broad diversity of antelopes (although only a minority of antelope species are specialized grazers). However, horses in the middle to late Miocene of North America, including both grazing and browsing forms, were equal in their taxonomic diversity to the present day African bovids. Their decline in the latest Miocene predated the entry of bovids to North America, and was likely related to climatic changes. The genus *Equus* only reached Africa in the Pleistocene (although there was a moderate African late Miocene/Pliocene radiation of immigrant equids of the three-toed genus *Hipparion*). When zebras today, in substantial numbers, share their African pastures with grazing bovids, their present-day ecological success echoes the success that horses achieved in North America, albeit now expressed outside of their continent of origin.

In spite of possessing different digestive systems, bovids and equids represent the evolution of specialized grazers on different continental land masses, rather than two competing adaptive types with clear 'winners' and 'losers'.

Christine Janis & Jonathan Kingdon

Superorder FERAЕ

Ferae Linnaeus, 1758. Syst. Nat., 10th edn, 1: 37.

The superorder Ferae describes the recognition of a very unexpected affiliation between Carnivora and the pangolins, Pholidota, a clade that is well supported in molecular studies (Liu *et al.* 2001, Murphy *et al.* 2001a, b, Springer *et al.* 2005, Meredith *et al.* 2011, Zhou *et al.* 2012). Use of the name Ferae follows Asher & Helgen (2010); alternatively, the name Ostentoria has been applied to this clade of pangolins plus carnivorans (e.g. Amrine-Madsen *et al.* 2003).

The later radiations of Carnivora are becoming better known, and these are outlined in the appropriate profiles, but what still earlier divergence could have led to pangolins? The multiplicity of extant carnivores includes many forms that are relatively conservative and some of these, such as the Two-spotted Palm Civet *Nandinia binotata*, are omnivorous (including insects), well-clawed and also arboreal. It is very likely that the earliest proto-pangolin was also a small, sharp-clawed, tropical Asiatic tree-climber with omnivorous or insectivorous tastes, and, given the crucial role of the tail in all pangolin species, that its long tail was prehensile and scaly. The beginnings of scales, which are cornified extrusions of outer skin, can be seen on the tails of various mammals such as rats, some insectivores and some afrotherians, while the most explicitly counter-abrasive tail-scales are found among anomalurid rodents. Carnivore-like proto-pangolins could, therefore, have been well-entrenched arboreal omnivores or insect-eaters with strongly prehensile and abrasion-resistant tails. Strong tails can also serve to mitigate accidents and predation in that it is harder for their owners to be dislodged. As a fifth limb, such tails also make it easier

for animals to engage in vigorous action while climbing, foraging or fighting.

Ants and termites have probably been a major component in the canopy of tropical rainforests for about as long as there have been rainforests and many species of arboreal ants and termites build nests in or on branches, or live in symbiosis with ‘ant-plants’, *Myrmecodia* and *Hylocophytum*, that have evolved chambers to accommodate the ants (Huxley 1978). Whereas many canopy resources are ephemeral, seasonal or unreliable, ants tend to be more predictably perennial inhabitants of the tropical canopy. Even in the Palaeocene, any arboreal predator that could penetrate the ants’ physical defences and also digest their chitinous, formic acid-protected bodies would have been assured of a reliable food supply. Once embarked on such a specific diet, the earliest pangolins, probably very small animals, must have progressively modified their teeth, tongues and digestions, and lost most of their fur as scales spread from the tail to body and limbs. Eventually some forms came to the ground and some became much larger (possible affinities between pangolins are discussed in the Manidae profile).

Modern pangolins no more resemble carnivores than whales do giraffes, yet fossils, genes and biological logic continue to reveal that such affinities, even when separated by many millions of years, can become comprehensible. As evidence accumulates we can expect that the intervening adaptive steps that have taken highly derived taxa ever further from their less-specialized origins can eventually be reconstructed with some confidence.

Jonathan Kingdon

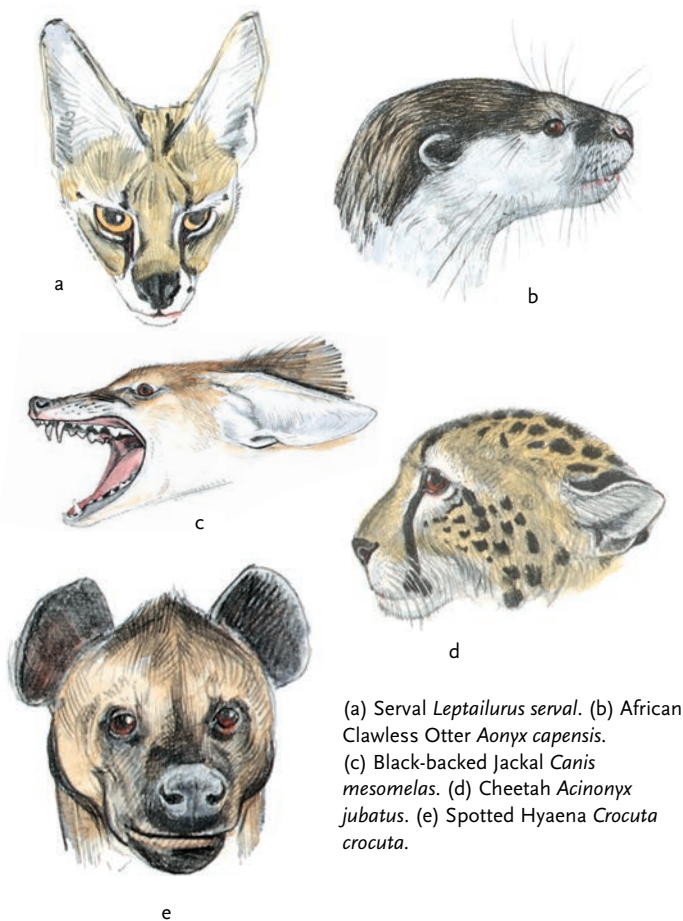
Order CARNIVORA – Carnivores

Carnivora Bowdich, 1821. An analysis of the natural classifications of Mammalia for the use of students and travellers. Paris, J. Smith, 115 + [31] pp., 16 plates.

| | | |
|-------------------------------------|---|--------|
| Caniformia | | |
| Canidae (4 genera, 12 species) | Foxes, Wolves, Jackals, Dogs | p. 28 |
| Mustelidae (8 genera, 11 species) | Weasels, Polecats, Otters, Ratel and allies | p. 82 |
| Otariidae (1 genus, 1 species) | Fur Seals | p. 126 |
| Phocidae (1 genus, 1 species) | True Seals | p. 132 |
| Feliformia | | |
| Nandiniidae (1 genus, 1 species) | Two-spotted Palm Civet | p. 138 |
| Felidae (6 genera, 10 species) | Cats | p. 144 |
| Viverridae (3 genera, 17 species) | Genets, Linsangs, Civets | p. 211 |
| Hyaenidae (3 genera, 4 species) | Hyaenas, Aardwolf | p. 260 |
| Herpestidae (14 genera, 26 species) | Mongoose | p. 293 |

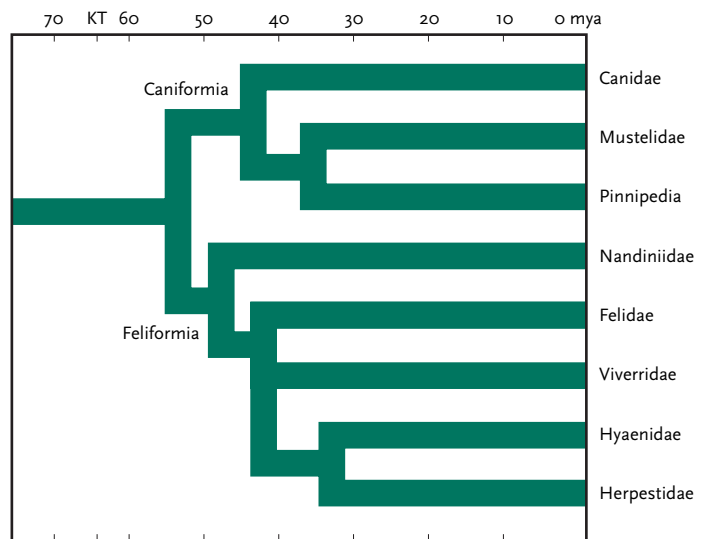
Carnivora are highly diverse in Africa. From Lions *Panthera leo*, Cheetahs *Acinonyx jubatus*, hyaenas and mongooses to clawless otters, polecats, Cape Fur Seals *Arctocephalus pusillus* and African Wild Dogs *Lycaon pictus*, this varied array of predators, scavengers, piscivores and omnivores play keystone roles in many African habitats, from the Serengeti Plains to the Congo rainforest. Yet, it is noteworthy that the key anatomical feature usually associated with Carnivora, elaborated and restricted carnassial shear in the dentition, predates its appearance in modern forms. The carnivory indicated by this primary dental adaptation has been substantially modified in the dietary specialization of many living carnivorans, with varying degrees of hypocarnivory to hypercarnivory, reflecting a wide range of specialized diets.

Even though many carnivorans retain a relatively generalized anatomy, diversity also marks virtually every aspect of their biology.



Carnivora are remarkably diverse taxonomically, being the fourth most speciose of modern mammalian orders with >280 species (see Wozencraft 2005 for a recent classification of the order). Species diversity varies markedly among the major extant clades, from the monospecific Nandiniidae, Ailuridae and Odobenidae to the dozens of mustelid species, and with terrestrial–freshwater taxa outnumbering the marine Pinnipedia by roughly 7 to 1. Carnivoran ecological diversity embraces diurnal, crepuscular and nocturnal forms; cursors, climbers, diggers, swimmers (freshwater and marine); and flesh eaters, herbivorous forms, insect eaters, piscivores and omnivores. The breadth of their geographic and environmental range spans land to water, all continents, from pole to pole, from deserts to high mountains to rainforests. An outstanding fossil record also makes Carnivora one of the most important and widely studied groups of mammals.

While ambling plantigrade forms are common, both speed and hunting range can be remarkable in cursorial carnivorans, with the Cheetah noteworthy as the fastest mammalian short-distance sprinter. Body size (correlated with many life history and physiological attributes) among living Carnivora ranges over more than four orders of magnitude, exceeding that observed in any other mammalian ‘order’, from the tiny Least Weasel *Mustela nivalis* at just 100 g to the gargantuan Southern Elephant Seal *Mirounga leonina* at up to 4000 kg. Delayed implantation of embryos is widespread among mammals, but is particularly common in mustelids and mephitids, representing almost half of the documented mammalian cases (Thom *et al.* 2004). Although it appears to be correlated with longevity, maximum latitude of geographic range and maternal investment (after correcting for phylogeny; Thom *et al.* 2004), the

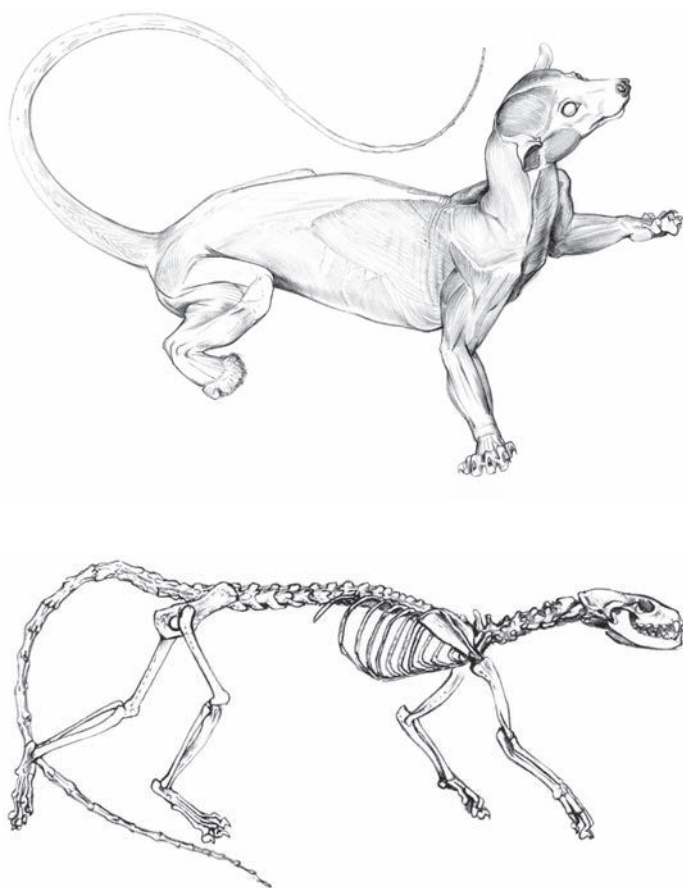


Tentative phylogenetic tree for extant African carnivora (after Flynn *et al.* 2005, Eizerik & Murphy 2009).

observation of delayed implantation in marine carnivorans (e.g. Ross Seals *Ommatophoca rossii*) and inference that it may occur in all pinnipeds, indicate that much remains to be learned about this important reproductive trait. Of course, the marine pinnipeds differ from their terrestrial relatives in many key features related to their specialized aquatic habitus, such as locomotor, metabolic and respiratory adaptations (e.g. the Weddell Seal *Leptonychotes weddellii* can remain submerged for 80 minutes during foraging dives to 700 m, while the champion diver is the Southern Elephant Seal, spending some 90% of its time submerged at depths up to 2150 m and for up to 120 minutes). Social systems also vary widely, from the many solitary species, to pair or small-group forming taxa, to the diverse array of social forms (e.g. Lion prides, colonial herpestids, or pack-hunting canids), all of which are found in Africa today.

The clade Carnivora is actually a relative latecomer to the African continent and the fossil record documents similar predator niches being first occupied by the now-extinct creodont clade Hyaenodontidae (first arriving in Africa during the late Eocene). Creodonts went extinct in Africa about 13 mya. The late arrival of Carnivora partially explains the uneven modern distribution of subclades in Africa. For example, many predominantly herbivorous forms that occur on other continents (e.g. Giant Panda *Ailuropoda melanoleuca*, Red Panda *Ailurus fulgens*) do not occur in Africa. In addition, members of the families Ailuridae, Procyonidae, Mephitidae, Eupleridae, Odobenidae and Ursidae do not occur in mainland Africa today. However, fossil bear (Ursidae) remains have been retrieved from north, north-east and southern Africa. Others, like Phocidae (one species) or Viverridae (two subfamilies), are much more diverse elsewhere. Several other entirely extinct higher-level clades also occurred in the past in Africa, such as various sabretooths and ‘false sabretooths’, Machairodontinae (Felidae) and Nimravidae, respectively, which flourished and diversified within Africa between the Miocene and about 1.5 mya, and the ‘bear-dogs’ of the family Amphicyonidae as well as the aforementioned creodonts.

Of living families, only one is found solely on mainland Africa: the monospecific Nandiniidae (recently raised to this rank based on strong genetic support for the Two-spotted Palm Civet *Nandinia binotata*



Two-spotted Palm Civet *Nandinia binotata* myology (above) and skeleton (below).

forming the outgroup to all other living feliform Carnivora, well outside of its traditional placement as a member of the Viverridae). In addition, the Eupleridae are now recognized to be a monophyletic array embracing all the carnivorans that are endemic to Madagascar (although they appear to have originated in Africa during the middle Cenozoic prior to their dispersal to the island; Yoder *et al.* 2003). Tectonic, environmental and biogeographic events and processes have profoundly influenced the global distributions of Carnivora (reviewed in Deméré *et al.* 2003, Hunt & Tedford 1993, Flynn & Wesley-Hunt 2005; for novel divergence times and biogeographic hypotheses in the Felidae, see Johnson *et al.* 2006).

Flynn & Wesley-Hunt (2005), Flynn *et al.* (2010) and Spaulding & Flynn (in press) have provided detailed overviews of higher-level phylogeny and taxonomy, temporal distributions and biogeography of modern Carnivora and their extinct relatives. Similarly, the higher-level phylogeny of living Carnivora has been investigated comprehensively by Flynn *et al.* (2005; using primary molecular data), while Bininda-Emonds *et al.* (1999) adopted a 'supertree' approach that derives from phylogenetic tree topologies from earlier studies. Several recent studies have begun expanding taxon or character sampling for living and fossil forms, such as the morphological studies of early fossil Carnivoramorpha (Spaulding *et al.* 2010, Spaulding & Flynn in press) and the molecular analyses of Eizirik *et al.* (2010; 14 nuclear loci for representatives of all extant families), Agnarsson *et al.* (2010; mitochondrial cyt b for about 80% of extant species), Yu *et al.* (2011; 22 new nuclear introns for 16

extant caniforms) and Meredith *et al.* (2011; 164 mammals, 26 loci, >35kb/11k amino acid sequences). Other authors in this volume provide in-depth treatments of current thinking about the phylogeny and evolution of the African Carnivora.

Recent analyses of, and controversies about, the higher-level phylogeny of Carnivora have centred on three hierarchical levels: (1) their closest relatives among the Eutheria (both living and fossil); (2) whether early Cenozoic fossils commonly assigned to the Miacidae and Viverravidae ('Miacoidae') are members of the crown-clade Carnivora or nearest outgroups to the living carnivorans (which together would be considered the Carnivoramorpha); and (3) the composition and positions of various subclades within Carnivora (especially the pinnipeds, Ailuridae, 'Mustelidae' and interrelationships among the modern feliform families).

Some of these problems now appear to have been resolved with significant molecular and palaeontological support, whereas others remain uncertain in spite of intense study and thus are the focus of continuing analysis. Carnivora have been among those living mammal orders that have remained difficult to ally to any others via morphological analyses (see Novacek 1992). These difficulties were often tied to the idea that the orders diversified extremely rapidly following the K/T boundary event (extinction of the dinosaurs). Among extinct forms, anatomical features that might associate Carnivora most closely with creodonts were noted by Wyss & Flynn (1993). Modifying an original conception of Linnaeus (1758), Simpson (1945) classed both as Ferae, a usage of the name accepted by the current author contra the broader definition used in the prior section of this volume. Among living forms, Wyss & Flynn (1993) also noted anatomical features shared by Carnivora and lipotyphlans, while initial molecular studies linked carnivorans to many other distinct lineages, from ungulates to bats, but the most comprehensive molecular samplings to date (e.g. Murphy *et al.* 2001) have suggested a surprising sister-group relationship between Carnivora and Pholidota (pangolins). Morphological support for this would come from an ossified tentorium in the braincase, which is shared by carnivorans, pangolins and creodonts (Wyss & Flynn 1993).

Monophyly of Carnivora is very strongly supported by both molecular and anatomical evidence. Likewise, a major split within the order of Caniformia ('dog-like') and Feliformia ('cat-like') is well supported. Within Caniformia, canids are outgroup to all the remaining forms (Arctoidea). Among arctoids there is sequential branching of ursids, pinnipeds and Musteloidea. Within musteloids there is a tritomy of Mephitidae (now removed from Mustelidae), Ailuridae and the clade of Mustelidae + Procyonidae. *Nandinia* has now been shown to be the outgroup to all other living feliforms. The monophyletic Malagasy Eupleridae is most closely related to Herpestidae, which together form a sister-group to Hyaenidae. Remaining ambiguity centres on the pattern of interrelationships among the Felidae, Viverridae and the HHE (or Hyaenidae–Herpestidae–Eupleridae) clades. In addition, recent documentation of the monophyly of all of Madagascar's Carnivora has resulted in a grouping of anatomically diverse forms that formerly had been placed in at least three separate families: Herpestidae, Viverridae, Felidae (Yoder *et al.* 2003). Furthermore, it has been proposed that prionodontine linsangs, formerly placed in Viverridae, might actually be allied with cats (Gaubert & Véron 2003, Gaubert *et al.*

2005a). These taxonomic upheavals suggest a much more complex pattern of behavioural and morphological transformations within the Feliformia than had previously been indicated.

The pre-Holocene fossil record for modern families is patchy (e.g. none for Eupleridae, extensive for Canidae), which partly reflects dominant habitats, geographic distributions and uneven palaeontological sampling. Entirely extinct clades have provided novel information about carnivoran history and the sabre-toothed nimravids, 'bear-dog' amphicyonids and the early fossil 'miacoids' are well represented. Anatomical data noted a century ago by Matthew (1909) suggested possible placement of the Miacidae and Viverravidae within a crown-clade Carnivora as basal caniforms and feliforms, respectively (Flynn & Galiano 1982). The most recent molecular and palaeontological studies now provide strong evidence for virtually all of these 'miacoids' being stem Carnivoramorpha lying outside the Carnivora (e.g. Wesley-Hunt & Flynn 2005, Spaulding & Flynn *in press*). It now appears that 'miacids' form a paraphyletic array of sequential outgroups to the Carnivora, with a monophyletic grouping of Viverravidae situated at the base of the Carnivoramorpha. This topology of fossil and living forms is highly significant for evolutionary and ecosystem studies because earlier results suggested that the origin of Carnivora and the split between caniforms and feliforms could have been as old as 65–60 mya, whereas the latest results suggest much younger ages for these events (minimum divergence estimate of 43 mya).

The 'order' Creodonta, named more than 125 years ago by Cope (1875), comprised an entirely extinct radiation of early to middle Cenozoic forms that resembled Carnivora in meat-eating specializations and in some locomotor features. In body form, creodonts were generally large-bodied, terrestrial predators or scavengers, with relatively large heads and plantigrade locomotion (Savage 1977). However, their relationship to the Carnivora has long been questioned and creodonts are of debatable monophyly themselves (see Flynn & Wesley-Hunt 2005).

A variety of craniodental and post-cranial features have been used to characterize living Carnivora, including reduction or loss of the clavicle, loss of the stapedial artery in the basicranium, fully ossified auditory bulla (except in *Nandinia*), thin lamina between the head and neck of the malleus, fusion of the scaphoid and lunar bones of the wrist (into a single scapholunar) and the specifically carnivoran P^4/M_1 carnassial pair. However, given that modern carnivorans are reasonably easy to identify, it is noteworthy that it has been difficult to rigorously diagnose the clade based on unique derived characters. There are a variety of potential reasons for this, notably their rapid divergence from other eutherians. Inferences of broader patterns of evolution across the entire Carnivora have been hindered by poor resolution of their higher-level interrelationships. Also, as mentioned above, the classical synapomorphy of Carnivora (P^4/M_1 carnassial shear) now appears to have much deeper roots in evolutionary ancestry, appearing first in early Cenozoic stem-Carnivoramorpha fossils (Palaeocene Viverravidae, ~63 mya) (for these and features cited below, see Wesley-Hunt & Flynn 2005). Similarly, a completely ossified bulla fused to the basicranium is not a synapomorphy of Carnivora, but rather evolved independently several times within the group, while the retractile claws found only in a few living clades

now appear to be a deep synapomorphy, with subsequent loss or reduction independently several times.

Carnivoramorpha are distinguished from all other Mammalia, including creodonts, by dental features such as P^4/M_1 carnassial shear (P^4 with anteriorly situated paracone), and a broad M_1 parastyle that is equal to or larger than the metastyle. Numerous advanced features of the crown-clade Carnivora were acquired sequentially, with Carnivora now uniquely diagnosed by a flange on the basioccipital (attachment for the entotympanic of the bulla), loss of M^3 , fusion of the scaphoid and lunar, and an expanded braincase (Wesley-Hunt & Flynn 2005).

Various features have been used to diagnose major subclades within the Carnivora ever since Turner's (1848) and Flower's (1869a) pioneering use of auditory bulla shape and bony internal partitions (see Ivanoff 2001, Wesley-Hunt & Flynn 2005). Those features that distinguish family and lower-level groups are summarized elsewhere in this volume but it should be remembered that many fossil Carnivora (and the living *Nandinia*) lack a fully ossified auditory bulla. 'The fully ossified entotympanic (wholly or partially fused to the basicranium) evolved independently within the Caniformia and Feliformia, although an increasingly strong attachment and incorporation of the bulla to the basicranium can be inferred along the phylogeny' (Wesley-Hunt & Flynn 2005: 14). Among interesting examples of anatomical specializations in these groups are the marked expansion of the maxilloturbinals in the Caniformia and a long and stylized baculum in Canoidea.

There have been many recent interesting studies of the comparative biology, ecology and evolution of carnivorans, including synthesis of evolutionary patterns through time (Van Valkenburgh 1999); palaeoecology, especially of large carnivorans (Turner 1990, Van Valkenburgh 1996); locomotion (Heinrich & Rose 1997); body size evolution or life history strategies (Gittleman 1993, 1994a, Meiri *et al.* 2004a, b, 2009); brain size (Gittleman 1991, 1994b, Gittleman & Van Valkenburgh 1997); social structure (Creel & Macdonald 1995, Geffen *et al.* 1996); and physiology, energetics or diet (Lee *et al.* 1991, McNab 1995, Carbone *et al.* 1999). Furthermore, the growing resolution and strength of support for the phylogeny of most major groups has brought greater precision to evolutionary analyses, adding genes and fossils to the study of living taxa and this synthesis from different disciplines will surely yield many more exciting results in the near future. Among selected relevant studies are: palaeoecology and ecomorphology (Werdelin 1996a, Van Valkenburgh *et al.* 2003, Werdelin & Lewis 2005, Wesley-Hunt 2005), locomotion (MacLeod & Rose 1993, Wang 1993, MacLeod 2001), body or brain size or correlated life history traits (Lindenfors *et al.* 2003, Webster *et al.* 2004, Finarelli & Flynn 2006, 2009, Flynn *et al.* 2010), biogeography (Hunt & Tedford 1993, Deméré *et al.* 2003) and novel approaches in genetics (Fondon & Garner 2004), modelling and comparative anatomy (Polly 2008) and developmental biology and morphological integration (e.g. relative influences of diet, brain size and phylogeny on cranial anatomy; Goswami 2006). In this thriving discipline are volumes that sample many other approaches and results, notably Gittleman (1989, 1996), Mazin & de Buffrénil (2001), Perrin *et al.* (2002) and Flynn (2003).

John J. Flynn

Table 6. Carnivore niches.

| Habitat | Fruits | Sessile or cryptic invertebrates and eggs | Active invertebrates | Aquatic or semi-aquatic fauna | Reptiles and amphibia | Small mammals and birds | Medium-sized mammals | Large mammals | Carrion |
|--------------------------------------|--------|--|----------------------|-------------------------------|--|---|----------------------|---------------|--------------------------------------|
| Forest | | <i>Nandinia</i>
<i>Crossarchus</i>
<i>Bdeogale nigripes</i>
<i>Genetta servalina</i>
<i>Genetta victoriae</i> | | | <i>Nandinia</i>
<i>Atilax*</i>
<i>Bdeogale nigripes</i>
<i>Genetta spp.</i>
<i>Genetta piscivora</i> | | | | <i>Nandinia</i> |
| Secondary growth | | <i>Dologale</i>
<i>Ichneumia*</i>
<i>Genetta tigrina*</i>
<i>Civettictis*</i>
<i>Rhynchogale</i> | | | <i>Ichneumia</i>
<i>Genetta tigrina</i>
<i>Civettictis*</i>
<i>Poecilogale*</i> | <i>Profelis aurata</i> | | | <i>Civettictis</i> |
| Moist savannas and woodlands | | <i>Bdeogale crassicauda</i>
<i>Mellivora*</i>
<i>Canis adustus*</i>
<i>Herpestes sanguineus*</i> | | | <i>B. crassicauda</i>
<i>Mellivora</i>
<i>Canis adustus</i>
<i>Herpestes sanguineus</i>
<i>Leptailurus serval</i> | <i>Panthera pardus</i> | | | <i>C. adustus</i> |
| Marshes and aquatic | | <i>Atilax*</i>
<i>Aonyx congicus</i> (forest swamps and rivers)
<i>Aonyx capensis</i> (swamps and rivers)
<i>Hydrictis</i> (rivers and lakes) | | | <i>Atilax</i> | | | | |
| Thickets, dry savannas and woodlands | | <i>Helogale*</i>
<i>Hyaena</i>
<i>Otocyon</i>
<i>Genetta genetta</i>
<i>Canis mesomelas</i> | | | <i>Helogale</i>
<i>Felis silvestris*</i>
<i>Otocyon</i>
<i>G. genetta</i>
<i>Canis mesomelas</i>
<i>Caracal caracal</i> | | | | <i>Hyaena</i>
<i>C. mesomelas</i> |
| (interzones) | | <i>Ictonyx*</i>
<i>Proteles*</i> | | | <i>Ictonyx</i> | <i>Lycaon*</i> | | | |
| Grasslands | | <i>Mungos*</i>
<i>H. ichneumon*</i>
<i>Canis aureus</i> | | | <i>Mungos</i>
<i>Herpestes ichneumon*</i>
<i>Canis aureus</i>
<i>P. leo</i> | <i>Crocuta</i>
<i>Acinonyx*</i>
<i>Panthera leo</i> | | | <i>C. aureus</i> |

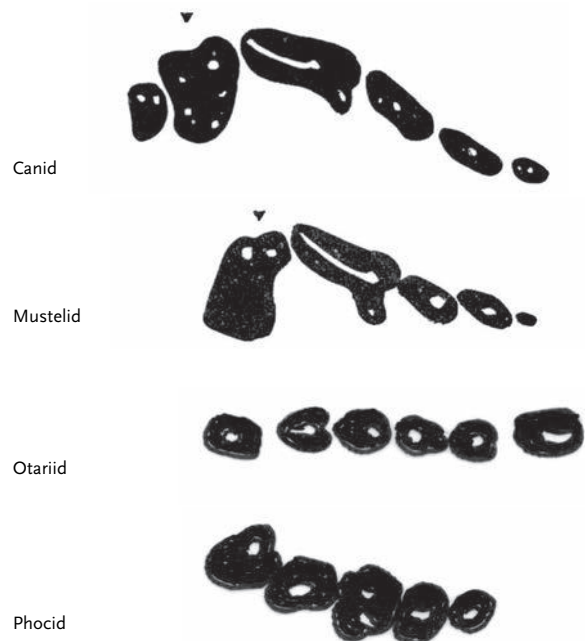
* Species thus marked occupy a wider range of habitats than can be suggested in a simplified table.

Suborder CANIFORMIA – Canids, Mustelids, Pinnipeds

Caniformia Kretzoi, 1943. Földtani Közlöny 73: 194.

Suborder Caniformia is traditionally subdivided into the Cynoidea, containing the family Canidae, and Arctoidea, represented by Ursidae (bears) (the most basal clade), Phocidae (true seals), Odobenidae (Walrus *Odobenus rosmarus*), Otariidae (fur seals and sea lions), Ailuridae (Red Panda *Ailurus fulgens*), Procyonidae (raccoons), Mustelidae (weasels, polecats, otters, ratel and allies) and Mephitidae (skunks). This taxonomic arrangement is consistently well supported both by morphological and molecular data (e.g. Flower 1869a, Flynn & Wesley-Hunt 2005, Eizirik *et al.* 2010, Meredith *et al.* 2011; but see Agnarsson *et al.* [2010] who suggest the possible placement of the Red Panda as sister to canids). In Africa, the suborder is represented by the Canidae (four genera and 12, and probably 13, species), Phocidae (one genus, one species), Otariidae (one genus, one species) and Mustelidae (eight genera and 11 species).

Michael Hoffmann



Carnivore molar teeth.

Family CANIDAE
FOXES, WOLVES, JACKALS, DOGS

Canidae Fischer, 1817. Mém. Soc. Imp. Nat. Moscow 5: 372.

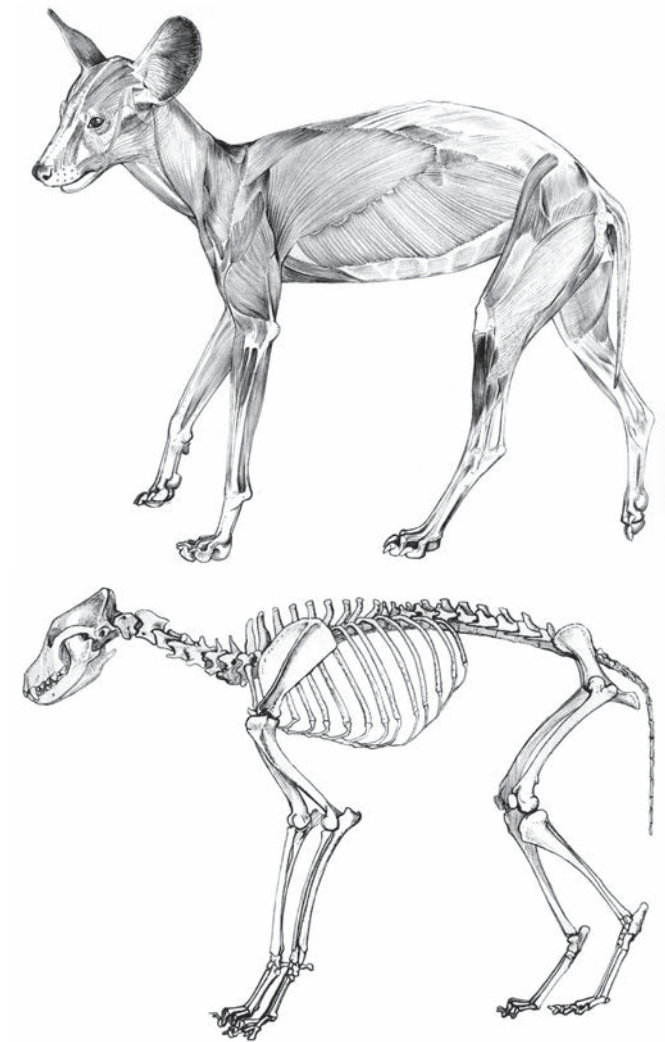
| | | |
|---------------------------------------|------------------|-------|
| <i>Canis</i> (4, probably 5, species) | Jackals, Wolves | p. 30 |
| <i>Lycaon</i> (1 species) | African Wild Dog | p. 50 |
| <i>Vulpes</i> (6 species) | Foxes | p. 59 |
| <i>Otocyon</i> (1 species) | Bat-eared Fox | p. 77 |

Canidae – the dog family – is morphologically a relatively homogeneous, polygeneric taxon, distributed widely in all continents with the exception of Antarctica (Macdonald & Sillero-Zubiri 2004). Although much of canid evolution was in open grasslands, their great adaptability has enabled them to flourish in arid habitats, the Arctic, mountains, woodlands and rainforests (and, indeed, cities). Their anatomy is adapted for the cursorial pursuit of prey in relatively open environments, with tall, lithe bodies, a bushy tail, long limbs and digitigrade, four-toed feet. They have triangular heads with long, pointed muzzles, well-developed jaws and prominent, roughly triangular pointed ears (which, in some desert species, are very large).

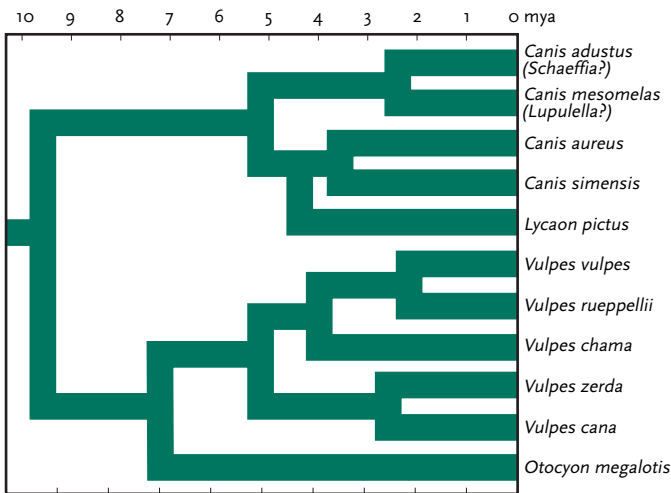
There are three major groups (subfamilies) in the family Canidae: Hesperocyoninae, Borophaginae and Caninae, the first two represented by fossil forms only. The Hesperocyoninae is the most ancient group of all canids, and its basal member, *Hesperocyon*, gave rise to the two more advanced subfamilies, Borophaginae and Caninae (Wang 1994). Canids originated in North America in the Eocene 56–34 mya and underwent extensive radiations from there before reaching the Old World towards the end of the Miocene (ca. 7 mya) (Wang 1994, Wang *et al.* 1999). The oldest records of canids in Africa are those of a small fox from Chad (de Bonis *et al.* 2007) at 7–6 mya, and Kenya, where remains of the genus *Eucyon* date to 6.1–5.6 mya (Morales *et al.* 2005). Prior to these discoveries, the oldest canid in Africa was known from the very earliest Pliocene of Langebaanweg, South Africa, probably referable to *Eucyon* and dated ca. 5.3–5 mya (Rook 1993, Tedford & Qiu 1996).

The genus *Canis* is first known in Africa from South Turkwel, Kenya at 3.5 mya (Werdelin & Lewis 2000), although material from Laetoli (if demonstrated as belonging to *Canis*) may be older (Werdelin & Dehghani 2011). Until the identification of *Canis ferox* from North America as the oldest member of the genus (Tedford *et al.* 2009), the record from South Turkwel – at the time, more than half a million years older than the oldest record of *Canis* elsewhere – suggested a possible African origin for the genus. Various fossils referred to different species of jackal have been recovered from Plio-Pleistocene deposits, but their relationship to modern jackals is uncertain (Werdelin & Lewis 2005). Interestingly, a primitive member of the racoon-dog lineage (no longer extant in Africa) is known from Laetoli in Tanzania at more than 3.8 mya (Barry 1987, Werdelin & Lewis 2005, Werdelin & Dehghani 2011) and younger members of the genus *Nyctereutes* are known from Morocco (Geraads 1997), South Africa (Ficcarelli *et al.* 1984) and Ethiopia (Geraads *et al.* 2010).

The Canidae can broadly be divided into two distinct lineages, the ‘wolf-like’ and ‘fox-like’ forms (e.g. Tedford *et al.* 1995), which diverged between 9 and 5 mya. Fox-like canids are generally small in size, have a low diploid chromosome number (2n = 36–66) and



African Wild Dog *Lycaon pictus* myology (top) and skeleton (bottom).



Tentative phylogenetic tree for African Canidae (after Lindblad-Toh *et al.* 2005, Wayne & Ostrander 2007).

are typically rodent hunters (Geffen *et al.* 1992d). Wolf-like canids (wolves, coyotes, jackals, dogs) are medium-sized to large and typically have a diploid chromosome number of $2n = 74-78$ (Wayne *et al.* 2004). The family blossomed in the Oligocene (19 genera) and exploded in the Miocene (42 genera), declining to the 13 genera recognized today. Bininda-Emonds *et al.* (1999) present a species-level phylogeny for the family, which indicates that some uncertainty remains, particularly among the monotypic canine genera (e.g. *Cuon*, *Speothos*, *Chrysocyon*).

For the most part, the taxonomy of wild canids is largely uncontroversial, although there is some disagreement regarding, for example, the use of the genus name *Pseudalopex* or *Lycalopex* for the South American genera, the validity of the Red Wolf *Canis rufus* as a distinct species, and the status of the Dingo and Guinean Singing Dog (Wang *et al.* 2004, Wozencraft 2005). Of the 13 extant genera and 35 species of Canidae, four genera and 12 species occur in Africa today: *Canis* (four, and probably five, species); *Lycaon* (one species); *Otocyon* (one species); and *Vulpes* (six species).

The Canidae range in size from the Fennec Fox *Vulpes zerda*, weighing less than 1 kg, to the Grey Wolf *Canis lupus*, which can weigh up to 62 kg (Mech & Boitani 2004). Most fox species weigh 1.5–9.0 kg, most other species 5–27 kg. Sexual dimorphism, when present at all, is minimal, with males slightly larger than females but similar in colour. Pelage is relatively short, with dense underfur mixed with longer guard hairs (colour is generally tawny brown or grey, but black, white and shades of ochre also occur). The underparts are usually paler than the rest of the body. The tail is generally bushy, often with a white tip and a darker, bristly patch covering the dorsal supracaudal scent gland near the root.

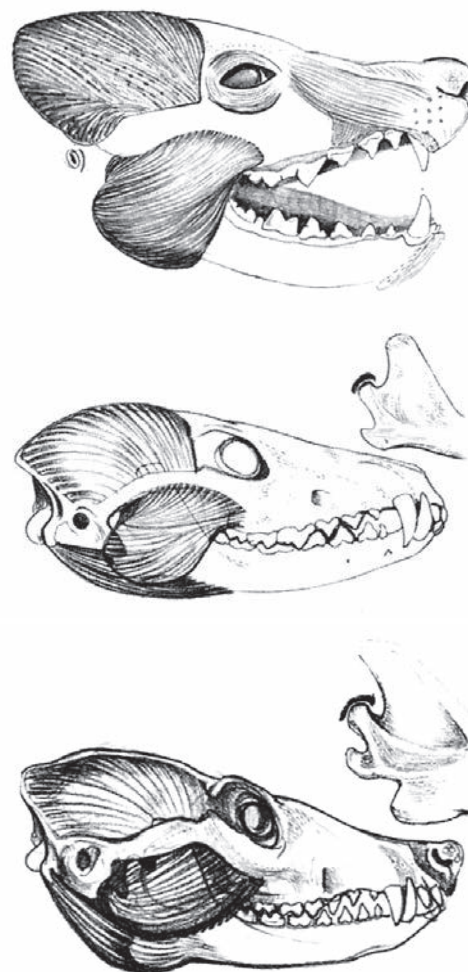
The facial region of the typical canid skull is elongated (although relatively shorter in *Canis* than in *Vulpes* and the South American *Pseudalopex*), with wide zygomatic arches and bony orbits that do not form a complete ring (Clutton-Brock *et al.* 1976). The temporal ridges are sometimes united in a sagittal crest. The auditory bullae are relatively large. Powerful jaw-closing muscles are adaptations for seizing, biting and holding prey. A complex cerebral cortex indicates that these carnivores are intelligent. The characteristic dental formula for the family is $I^{3/3}, C^{1/1}, P^{4/4}, M^{2/3} = 42$, although the Bat-eared Fox *Otocyon megalotis* departs from this pattern with 46–50 teeth. The shearing carnassial teeth (P^4/M_1) and crushing molars are well developed and the largest teeth in all species, except *Otocyon* (where they are molariform and no larger than the rest). The canine teeth are long and sharply pointed in all species. All canids have excellent senses of smell and hearing, with sight being less acute, although good.

The Canidae are cursorial, running on their toes or the small palmar pad (i.e. digitigrade), with long, slender limbs, compact feet with four functional toes and blunt, non-retractable, claws. A vestigial fifth toe (pollex or dew-claw) on the front feet occurs on all except the African Wild Dog *Lycaon pictus*. Other adaptations to running include fusion of scaphoid and lunar bones in the wrist, and locking of radius and ulna in the front leg to restrict rotation. Caecum always present, coiled into an S-shape.

Male canids have a well-developed grooved penis bone (baculum) and there is a copulatory tie during mating that can last up to an hour or more. This mechanism involves the pair facing away from each other, with the consequence that the blood trapped in the engorged

penis prevents withdrawal. Wild canids usually reach sexual maturity at one year old, and reproduce once annually (gestation lasts approximately nine weeks). However, social suppression of reproduction is common, so reproduction is often delayed and in larger species first reproduction is often after two years. Females have 6–16 nipples and have their young in underground dens. Litter-sizes typically range from 2 to 13; African Wild Dogs, for example, have very large litter-sizes, averaging 10–11, and occasionally as large as 21.

Although canids evolved in relatively open spaces, today they occur in all major African habitats, spanning tropical forests, woodland, savanna, deserts, mountains and afroalpine heathlands. The family is characterized by a great flexibility of diet, opportunistic and adaptable behaviour, and complex social organization with much within- and between-species variation. Most of the smaller species are opportunistic omnivores, eating anything from mammals to birds, reptiles, insects, fruit and carrion. Larger, group-living species may be more strictly carnivorous, preying on medium to large-sized mammals. All canids will feed on some carrion and vegetable matter. Several species – most notably in Africa, jackals and African Wild Dogs (although attitudes to the latter are changing) – are considered pests due to predation on livestock and game species.



Myology showing masticatory muscles and teeth in: African Wild Dog *Lycaon pictus* (wounding bite) (top); Side-striped Jackal *Canis adustus* (firm, puncturing grip) (centre); Bat-eared Fox *Otocyon megalotis* (rapid champing) (bottom).

From solitary to very social, most smaller canids live as territorial pairs (a relatively rare system amongst mammals as a whole) or small family groups, while the larger species are typically, but not invariably, pack hunters (Macdonald & Sillero-Zubiri 2004). Many of the smaller canids are nocturnal, whereas most of the social species are diurnal. Some species hunt in packs, whereas the Ethiopian Wolf *Canis simensis* hunts solitarily but also lives in groups. Benefits of living in groups besides pack hunting include cooperative defence of territories, monopoly of large carcasses and communal care and protection of offspring.

There is a tendency across the family for social system to vary with body size, such that where smaller species form groups these tend to include a dominant pair and female helpers and for dispersal to be male-biased, whereas amongst larger species the tendency is for dispersal to be female-biased and for groups to contain a preponderance of male helpers. In intermediate-sized canids, such as jackals, there is an approximately equal sex ratio of helpers. Scent-marking with both urine and faeces, often aloft visually conspicuous objects (such as tussocks of vegetation) and at trail junctions, is ubiquitous amongst canids – in the case of Ethiopian Wolves territorial border patrols are associated with intensive scent-marking.



African Wild Dog *Lycaon pictus* facial features.

Claudio Sillero-Zubiri & David W. Macdonald

GENUS *Canis* Jackals, Wolves

Canis Linnaeus, 1758. Syst. Nat., 10th edn, 1: 38.

Canis is a polytypic genus, comprising six or seven wild species depending on whether the Red Wolf *Canis rufus*, from North America, is considered a valid distinct species or not (Wozencraft 1993, 2005). Coyotes, jackals and wolves are distributed throughout North America, Europe, Asia and Africa, with the dingo (*Canis lupus dingo*) taken to Australasia by man during prehistoric times. Although canids typically favour open biotopes they occur in a wide range of habitats, adapting readily to forests, arid regions, high-altitude mountainous habitats and human-dominated environments.

The genus has generally been considered to include four species in Africa: Golden Jackal *Canis aureus*, Side-striped Jackal *C. adustus*, Black-backed Jackal *C. mesomelas* and Ethiopian Wolf *C. simensis*. The three species of jackals have wide distributions, utilizing most habitat types although absent from dense tropical forests. In contrast, the Ethiopian Wolf is confined to afroalpine grasslands and heathlands in the Ethiopian Highlands. The Grey Wolf is present in the Sinai Desert, Egypt, but has not typically been considered as a species occurring on the African continent. However, several authors have proposed that the taxon *C. aureus lupaster*, present in arid areas of Egypt and Libya (Osborn & Helmy 1980), may actually represent a small Grey Wolf rather than a large jackal (Ferguson 1981; and see Qumsiyeh 1996, Ferguson 2002). Recent genetic data also indicate that *C. a. lupaster* represents an ancient wolf lineage, which most likely colonized Africa prior to the northern hemisphere radiation (Rueness *et al.* 2011). The latter authors detected individuals at two localities in the Ethiopian Highlands, some 2500 km south of

the known distribution, an indication that the taxon may be more widely distributed. An observation in Eritrea may also represent a Grey Wolf (Tiwari & Sillero-Zubiri 2004). The current treatment is cognisant of these recent findings, but as this research became available at the time of going to press, only four species in the genus are profiled here.

Members of the genus *Canis* are medium-sized carnivores (HB varies from 65–140 cm, body mass 8–62 kg), well adapted to a cursorial way of life, with a relatively tall body and long limbs, and feet compact, with four functional toes. Members look alike, their heads being characteristically triangular with a conical muzzle and triangular ears. The pelage of all species is relatively short, with dense underfur mixed with longer guard hairs. The tail is bushy, broadest at its middle, and shorter than half of body length; a darker, bristly patch covers the supracaudal gland, of which the odour is, to the human nose, generally faint and somewhat sweet. They have interdigital glands whose function is unknown, as is that of the well-developed anal sacs, and all use urine and faeces for communication, including in the context of territoriality. Females have 8–10 nipples.

The dental formula is typically canid (although the lower third molar is sometimes absent in the Ethiopian Wolf), with short and heavy canines and upper carnassials highly developed; the upper incisors are predominantly lobed. The skull is heavy set with an elevated frontal region, large frontal sinuses and temporal ridges that are close together, united in a sagittal crest. The facial region of the

skull is relatively shorter than in *Vulpes* and *Pseudalopex*, except in the Ethiopian Wolf (Clutton-Brock *et al.* 1976). The latter had initially been placed in a separate genus or subgenus *Simenia* (Allen 1939), but morphological and genetic analysis places it unambiguously within *Canis* (Clutton-Brock *et al.* 1976, Gottelli *et al.* 1994). Hybridization has been recorded in the wild between Ethiopian Wolves and domestic dogs (Gottelli *et al.* 1994), suggesting a recent common ancestor for this group.

Reproduction in *Canis* is generally monopolized by dominant ♀♀, and non-breeding individuals of both sexes may act as helpers (although evidence that their contribution increases survival of the pups is surprisingly equivocal for the Ethiopian Wolf, although compelling for Black-backed and Golden Jackals). There is evidence of infanticide by dominant ♀♀, of allosuckling and of spontaneous lactation (associated with pseudopregnancy). The sociality in *Canis* species is conspicuously intricate, and variable between species, populations and individuals. The fundamental social unit is the

monogamous pair, but delayed dispersal of young (sometimes indefinitely) leads to the development of groups that, in some cases, become both large and structured. The most ubiquitous element of cooperation in these societies is in care of the young, but cooperative hunting and defence of resources are well documented, as is cooperative territorial defence.

While jackals have a generalist diet of medium and small-size mammals, invertebrates and fruits, Ethiopian Wolves have evolved into afroalpine specialists, existing almost exclusively on a diet of small mammals. The considerable similarity between all *Canis* species may underlie the intensity of intra-guild aggression between them: larger species tend to harass smaller ones throughout the family (and indeed throughout the order Carnivora), with the interesting exception that Black-backed Jackals have been reported as dominating the slightly larger sympatric Side-striped Jackal.

Claudio Sillero-Zubiri & David W. Macdonald

Canis adustus SIDE-STRIPED JACKAL

Fr. Chacal à flancs rayés; Ger. Streifenschakal

Canis adustus Sundevall, 1847. Ofv. K. Svenska Vet.-Akad. Forhandl. Stockholm 1846, 3: 121 [1847].
'Caffraria Interiore'; fixed by Sclater (1900) as 'Magaliesberg' [South Africa].

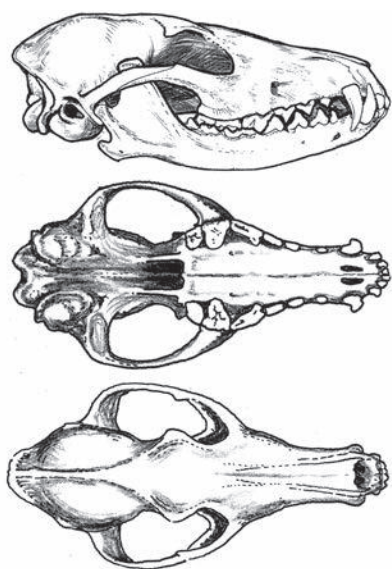


Side-striped Jackal *Canis adustus*.

Taxonomy Allen (1939) listed seven subspecies from the continent, Coetsee (1977) reduced this to five, while Kingdon (1997) recognizes only three (*C. a. adustus* from southern Africa, *C. a. lateralis* from Equatorial Africa and *C. a. kaffensis* from Ethiopia and Somalia) but without comment. Many authorities have pointed out that, as with Black-backed Jackal *C. mesomelas*, subspecies are hard to distinguish (e.g. Schouteden 1945), and the differences may be a consequence of individual variation (Ansell 1960a, Rosevear 1974, Kingdon 1997). None is recognized here, pending a revision of subspecies classification. Synonyms: *bweha*, *centralis*, *holubi*, *kaffensis*, *lateralis*, *notatus*, *studerii*, *wunderlichi*. Chromosome number: $2n = 78$ (Wayne 1993).

Description Medium-sized canid, grizzled, brown-grey to buff-grey, with white side-stripe half-way up the flanks, and distinctive white tip to tail (sometimes absent). Coat thick, long on back and neck and fluffy on chest, throat and underside. Underfur dark, overlaid by light beige or buff guard hairs. Head grizzled buff-grey; muzzle dark grey with black nose. Ears blackish-grey behind; considerably smaller in proportion to the head than those of other jackals. Back darker in colour (almost black in some animals) than underside and chest, while flanks are marked by white stripes running from elbow to hip with black lower margins. The boldness of markings, particularly flank-stripes, varies between individuals; those of juveniles less well defined than those of adults. Legs are tinged rufous-brown. Tail bushy and may be fluffed out when the animal is threatened or during intra-specific agonistic encounters; it is predominantly black and almost always bears the distinctive white tip (occasionally absent; see Rosevear 1974). Five digits on forefeet; four on hind. First digits on the front feet carry the dew-claw, and is situated far back on the plantar pad, not marking in the spoor. Claws between 15 and 20 mm long and dog-like (Skinner & Chimimba 2005). Two pairs of nipples.

Skull is similar to the Black-backed Jackal, but longer and less robust, with a noticeably narrower and longer rostrum. Elongation of rostrum is evident when the breadth at P^3 is considered relative to the distance from the back of this tooth to the incisors and is compared in the two species: in the Black-backed Jackal the ratio is about 31/42 or 74%, as opposed to about 28/55 or 51% in the Side-striped Jackal (Skinner & Chimimba 2005). Sagittal crest much better defined, and zygomatic arches of lighter build. Interparietal crest only slightly developed, and the bullae are smaller and flatter (Clutton-Brock *et al.* 1976). Canines are longer and more curved, but outer upper incisors not as large or robust as in the Black-



Lateral, palatal and dorsal views of skull of Side-striped Jackal *Canis adustus*.

backed Jackal. As a result of elongation of the rostrum, third upper premolar lies almost in line with the others and not at an angle as in the Black-backed Jackal (Skinner & Chimimba 2005). Permanent dentition starts erupting at 4–5 months. Relative pulp cavity width of the canine can be used to distinguish young adults from mature adults, but is of no value in determining age after one year (Bingham & Purchase 2003).

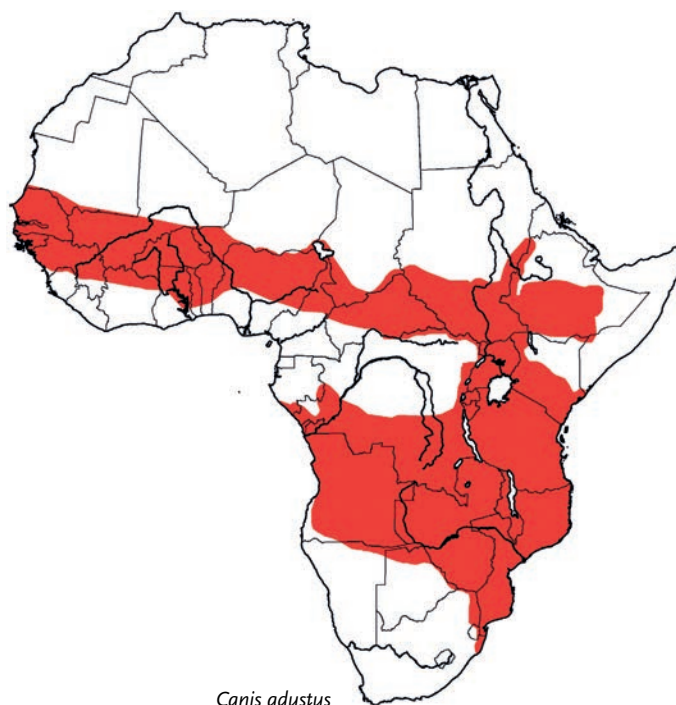
Geographic Variation Ansell (1960a) and Rosevear (1974) both commented on the great deal of individual variation in pelage colour within the species, and this has contributed to much confusion in apparent geographic variation; the form *centralis* from Cameroon and Central African Republic was apparently noteworthy for its very light ground colour.

Similar Species

Canis mesomelas. Sympatric in parts of eastern and southern Africa; in SW Angola, they appear to have a parapatric distribution (Crawford-Cabral 1993a). Characterized by a prominent dark 'saddle' and black-tipped tail, as well as reddish flanks and limbs; ears reddish-brown behind; lacks white-tipped tail characteristic of the Side-striped Jackal (and see Description above for notes on skull).

C. aureus. Sympatric in parts of East Africa and the Sahelian regions. Golden coat colour, and cream-coloured underparts; ears golden-brown behind; lacks white-tipped tail.

Distribution Endemic to Africa; distributed over much of sub-Saharan Africa, from Gambia and Senegal through the Sahelian regions of West Africa to the Central African Republic, Sudan, Ethiopia and Somalia, southwards into southern Africa, being absent or marginally distributed in the more arid westerly regions of southern Africa (Rosevear 1974, Kingdon 1977, Grubb *et al.* 1998, Skinner & Chimimba 2005). Distribution broadly coincides with broadleaved guinea woodland savannas, especially miombo (*Brachystegia*) woodland of central and southern Africa. In southern part of its range occurs marginally in NE KwaZulu–Natal (South Africa), at an altitude below 100 m, this marking its most southern



Canis adustus

occurrence on the continent (Rowe-Rowe 1992a). Also occurs occasionally in neighbouring lowveld regions of Swaziland, but is more common in the south (Monadjem 1998).

Habitat Found in a wide range of habitats. Distribution tends to coincide with the well-watered woodlands and woodland mosaics of central and West Africa (Coe & Skinner 1993, Skinner & Chimimba 2005). Tends to avoid areas of dry open savanna (areas often favoured by Black-backed Jackals), and is absent from the equatorial forest zone, but may enter in the wake of human cultivation (Kingdon 1997). Other habitats used include areas of abandoned cultivation, marshes and montane habitats up to 2700 m (Kingdon 1977, Estes 1991, Yalden *et al.* 1996). Side-striped Jackals frequently occur near rural dwellings and farm buildings, and penetrate peri-urban and urban areas (Skinner & Chimimba 2005).

Habitat use by the Side-striped Jackal varies considerably between different areas, dependent partly on habitat availability, but often more importantly, on the presence or absence of other jackal species. When allopatric, it occupies a wide range of habitats and appears especially to use grassland (as in Niokolo-Koba N. P., Senegal [C. Sillero-Zubiri pers. comm.], Rwenzori Mountains N. P., Uganda [Kingdon 1977] and NE KwaZulu–Natal [Rowe-Rowe 1992a]), but also savanna woodland on raised plateaux in Niokolo-Koba N. P. (Sillero-Zubiri *et al.* 1997). In Zambia it uses open woodland and grassland, avoiding forest (Ansell 1960a). Similarly, where this species is allopatric in N Zimbabwe, Atkinson (1997) found that grassland was used preferentially over woodland.

However, when it occurs in sympatry with other jackal species habitat is segregated. The Side-striped Jackal uses more thickly vegetated habitats, leaving open grassland and woodland to the other species. In Serengeti N. P., Tanzania it uses dense thicket and riverine habitats (Williams 1967, Wyman 1967, Kingdon 1977, Lamprecht 1978, Moehlman 1983, Estes 1991), with Black-backed Jackals using *Acacia* woodland and Golden Jackals using grassland; a similar

pattern occurred in Laikipia, Kenya (Fuller *et al.* 1989). In southern Africa, when occurring alongside the Black-backed Jackal, the Side-striped Jackal uses the dense vegetation of forest and river valleys and the Black-backed Jackal the open and lightly wooded areas (Pienaar 1969, Loveridge & Macdonald 2002, Skinner & Chimimba 2005). At least in W Zimbabwe, the mechanism for segregation between the two species is aggressive displacement of Side-striped Jackals by Black-backed Jackals (Loveridge & Macdonald 2002).

Abundance Generally common within its range in southern Africa. Rhodes *et al.* (1998) found that the resident population of territory-holding adults was 20–30 per 100 km² expanding to a breeding season peak of 80–120 jackals per 100 km² in N Zimbabwe. In W Zimbabwe (near Hwange N. P.) densities were approximately 54–79 per 100 km² expanding to as much as 97 per 100 km² in the breeding season (Macdonald *et al.* 2004). Ziegler *et al.* (2002) suggest that Side-striped Jackals are ‘rare in West Africa’, an observation that is borne out by the relatively low densities (7 per 100 km²) found in Niokolo-Koba N. P. (Galat *et al.* 1996, Sillero-Zubiri *et al.* 1997). The dietary flexibility of the Side-striped Jackal and its ability to co-exist with humans on the periphery of settlements and towns suggests that populations are only vulnerable in cases of extreme habitat modification, or intense disease epidemics.

Adaptations Like the Black-backed Jackal, this species is relatively unspecialized but well adapted anatomically and behaviourally for opportunism. Kingdon (1997) suggests that, in ecological terms, it is the tropical equivalent of the Red Fox *Vulpes vulpes*. The dentition is well suited to an omnivorous diet (Skinner & Chimimba 2005). The canines are long, curved and sharp-pointed, with a sharp ridge on their posterior surfaces. The upper outer incisors are canine-like, the carnassial shear well adapted for slicing, while the first and second upper molars are broad and developed for crushing. In comparison to the Black-backed Jackal, Side-striped Jackals have similar-shaped carnassials, and hence similar adaptation to carnivory; however, Side-striped Jackals have a larger grinding surface on their premolars and molars and are, therefore, better adapted to an omnivorous life-style (Van Valkenburgh 1991, Van Valkenburgh & Wayne 1994).

The Side-striped Jackal has smaller, more rounded ears than other jackals, which is the case with many forest-dwelling canid species,

such as the Bush Dog *Speothos venaticus* and the Small-eared Dog *Atelocynus microtus* of South America (Stains 1975). This suggests that the Side-striped Jackal is perhaps adapted to more mesic environments and the other jackal species to more arid regions.

The white tail tip of this species is possibly a ‘badge of nocturnal status’ (Kingdon 1977). The Red Fox and the White-tailed Mongoose *Ichneumia albicauda* also have white tail tips and correspondingly nocturnal habits. Macdonald (1987) suggests that a white tail flash may enhance tail signalling in nocturnal species. The white tail flash may also allow members of a foraging group to locate one another in the dark and avoid moving through areas from which food items have already been disturbed and gleaned by other group members (Loveridge 1999).

Foraging and Food Omnivorous, feeding on a wide array of items including small mammals, birds, reptiles, insects, carrion and vegetable matter (Smithers & Wilson 1979, Estes 1991, Atkinson *et al.* 2002a, Loveridge & Macdonald 2003). Their diet is very responsive to both seasonal and local variation in food availability. On commercial farmland in the Zimbabwe highveld, they eat mainly wild fruit (30%) and small (<1 kg) to medium-sized (>1 kg) mammals (27% and 23%, respectively), with the remainder of their diet comprising birds, invertebrates, cattle cake, grass and carrion (Atkinson *et al.* 2002a). In wildlife areas of W Zimbabwe, Side-striped Jackals feed largely on invertebrates during the wet season and small mammals up to the size of springhares *Pedetes* spp. during the dry months of the year.

Side-striped Jackals scavenge extensively from safari camp rubbish dumps and occasionally from large carnivore kills (although they are out-competed for this resource by Black-backed Jackals) (Loveridge & Macdonald 2003). In the Ngorongoro Crater, Estes (1991) recorded the species competing with Black-backed Jackals to catch Grant’s Gazelle *Nanger granti* fawns. Certain fruits (e.g. Mobola plum *Parinari curatelifolia*, wild fig *Ficus capensis* and waterberry *Syzygium guineense*) may be taken almost exclusively when in season (Smithers & Wilson 1979, Atkinson *et al.* 2002a).

As with Black-backed Jackals, this species is primarily nocturnal, with peaks in activity after sunset and before dawn (Loveridge & Macdonald 2003). Occasionally, they are seen active during the late afternoon in areas where they are not persecuted (Kingdon 1977). Side-striped Jackals feed solitarily, although in W Zimbabwe family groups have been observed foraging together on abundant invertebrate food resources (Loveridge 1999), and Estes (1991) mentions that as many as 12 have been counted at kills or scavenging offal outside towns. Similarly, groups have been observed scavenging from both Lion *Panthera leo* and Spotted Hyaena *Crocuta crocuta* kills in Liuwa Plains N. P., Zambia, with as many as 5–10 seen at any one time (G. Purchase pers. comm.).

As with other canids, this species exhibits extreme flexibility in its foraging strategies. Kingdon (1977) observed a captive, free-ranging individual bump vegetation with its body to dislodge invertebrates. A similar pattern of behaviour was observed in Hwange, Zimbabwe, where Side-striped Jackals ‘stamped’ the ground to disturb concealed grasshoppers (Loveridge 1999). Atkinson *et al.* (2002b) found that instead of searching for preferred foods, jackals in farmland tended to use the most seasonally abundant resources, moving through the agricultural landscape using an optimal foraging pathway (with fractal characteristics) for opportunistic use of spatially random



Side-striped Jackal *Canis adustus* facial details.



Side-striped Jackal *Canis adustus* action drawing.

and temporally variable resources. It is likely that this is a common foraging pattern in omnivorous medium-sized canids.

In all studies on the species, there is very little evidence for extensive predation on domestic stock (Shortridge 1934, Roberts 1951, Ansell 1960a, Smithers 1971, Smithers & Wilson 1979, Rowe-Rowe 1992a), or game larger than a baby antelope (Kingdon 1977, Estes 1991).

Social and Reproductive Behaviour Because their tendency to use wooded terrain makes it hard to confirm group sizes, Side-striped Jackals were at one time considered solitary; however, it is now known that they form social groups. As with other jackal species, the basis for the social system is the mated pair, which is known to be stable over several years. They may occasionally occur in family groups, or come together in feeding aggregations (though not as large as in Black-backed Jackals).

In game areas of W Zimbabwe, home-ranges varied from 0.2 km² in the hot dry season to 1.2 km² in the cold dry season, whereas in highveld farmland, they were seasonally stable and in excess of 4.0 km². In highveld farmland, territories are configured to encompass sufficient patches of grassland, where resources are most available, and the structure of the habitat mosaic appears an important factor. Pairs in N Zimbabwe used their home-range with a high degree of concordance, using the same areas with similar intensity and largely at the same times. The central core of each home-range is used exclusively by its occupants, but the peripheral third of the range may overlap widely with four or more neighbouring pairs; home-ranges overlapped by about 20% in highveld farmland and 33% in game areas (Atkinson 1997). In Hwange, Zimbabwe, at least four of five Side-striped Jackal territories included extra-pair members (up to five in one case, two of which were known to be between one and two years of age), and there is evidence for alloparental care in that young adults have been recorded returning to their natal home-ranges during the breeding season (Loveridge & Macdonald 2001).

Side-striped Jackals are not as vocal as other jackal species. The most obvious call is a series of staccato barks (an explosive 'bwaa'), which may be repeated for up to 10 minutes, usually in bouts of 13–17 barks over 30 seconds, with 4–5 seconds between bouts

(Loveridge 1999). These are often used as alarm/mobbing calls in the presence of Leopards *Panthera pardus*, and also during the breeding season where animals from neighbouring territories may answer calls. Side-striped Jackals do not howl, instead they have an 'owl-like hoot' (Kingdon 1977). This call was never heard in Hwange, Zimbabwe (A. Loveridge pers. obs.).

Pups are born in subterranean dens, often abandoned Aardvark *Orycteropus afer* holes or excavated termitaria that the ♀ modifies to her own requirements (Skinner & Chimimba 2005); the breeding chamber often has multiple entrances. Dens are sometimes used by the same pair over consecutive years (Kingdon 1977, A. Loveridge pers. obs.). During the early stages of pup growth, only the ♂ provisions the pups and the ♀, but after weaning both parents assist in rearing the young, returning at intervals of 2–3 hours through the night to feed the pups on food that is probably regurgitated (Moehlman 1979). The pups are aggressive towards each other, as evidenced by the degree of wounding seen.

Reproduction and Population Structure Reproduction can occur in the first year, with most mating occurring in July in Zimbabwe (Bingham & Purchase 2002, 2003). However, the breeding season is variable in different parts of Africa. In Zimbabwe pups are usually born in Sep and Oct, after a 57–60 day gestation period (Bingham & Purchase 2002, Skinner & Chimimba 2005); however, pups are born in Jun and Jul in Uganda, and Sep and Oct in S Kenya (Kingdon 1977) and Sep–Nov in Zambia (Ansell 1960a). Skinner & Chimimba (2005) report mean litter-sizes for Side-striped Jackals of 5.4 pups, and Bingham & Purchase (2002) give (from examination of foetuses and placental scars) a mean pre-birth litter-size of 5.8 (range 3–8). Perinatal litter loss is around 20% (Bingham & Purchase 2002) and Rhodes *et al.* (1998) estimate that only two per litter survive past six months. Lactation lasts about 10 weeks. Juveniles are probably independent before they are one year old and have been recorded dispersing up to 15 km (mean = 4.6 ± 3.51 km) (Loveridge & Macdonald 2001). As with Black-backed Jackals, longevity has been given as 10–13 years (Ginsberg & Macdonald 1990, Weigl 2005), but this is probably more representative of longevity in captivity, and Rhodes *et al.* (1998) suggest that the average life-span in the wild is probably closer to 3–4 years.

Predators, Parasites and Diseases Leopards are the only regular predator of the Side-striped Jackal, although it seems likely that other predators may take pups and young adults as they do with the other jackal species.

In Zimbabwe, seroprevalence of canine distemper virus, canine parvovirus and canine adenovirus (type 1) were 50%, 12.5% and 37.5%, respectively, in 22 free-ranging Side-striped Jackals sampled between 1990 and 1993 (Spencer *et al.* 1999); however, although jackals act as reservoirs for these diseases, susceptibility is not known. Side-striped Jackals, along with other jackal species, are vulnerable to rabies (Bingham & Foggin 1993, Bingham *et al.* 1999a, b), tick fever and sarcoptic mange (Kingdon 1977), for all of which they are known or suspected reservoirs and vectors for domestic dog infection. Computer simulations (Rhodes *et al.* 1998) suggest rabies can only persist in Side-striped Jackal populations where the density is very high – such as around towns – and that most rabies occurrence in Side-striped Jackals is a result of spillover from domestic dogs living on communally owned land. Side-striped Jackals can contract the disease from domestic dogs, conspecifics and other jackal species, although it appears that transmission of rabies cycles does not appear to occur from areas where Black-backed Jackals are the numerically dominant species to areas where Side-striped Jackals are prevalent (Bingham *et al.* 1999a).

Horak *et al.* (1987) collected the following parasites from a single Side-striped Jackal taken in Kruger N. P. in South Africa: *Amblyomma hebraeum*, *Haemaphysalis leachi* and *Rhipicephalus* spp. Ntiamoa-Baidu *et al.* (2005) recorded *Rhipicephalus sulcatus* and *Amblyomma variegatum* from jackals in Ghana.

Conservation IUCN Category: Least Concern. CITES: Not Listed.

Side-striped Jackals are persecuted primarily for their role in rabies transmission and their putative role as stock killers, which although unlikely to affect overall numbers may affect local abundance. In areas of high human population density, snaring may be the commonest cause of death in adults, and may account for as much as a third of adult deaths in such areas (Atkinson 1997, Atkinson & Loveridge 2004). Ziegler *et*

al. (2002) did not observe any Side-striped Jackals during a mammal survey in Upper Niger N. P., Guinea (where they have previously been recorded), perhaps because the level of illegal hunting is high. In towns and suburbs they may be run over by vehicles (Kingdon 1977). High reproductive productivity ensures this species is capable of rapid recovery following population crashes (Bingham & Purchase 2002). There may be some limited trade in jackal parts, because of their role in traditional practices and beliefs in parts of East Africa (Kingdon 1977), but this is not thought to be extensive. This species occurs in a number of well-managed protected areas throughout its range, including Niokolo-Koba N. P. (Senegal), Comoé N. P. (Côte d'Ivoire), Queen Elizabeth N. P. (Uganda), Serengeti N. P. (Tanzania), Hwange N. P. (Zimbabwe) and Kruger N. P. (South Africa), and seems well able to exploit semi-urban and urban habitats (Atkinson & Loveridge 2004).

Measurements

Canis adustus

TL (♂ ♂): 1082 (960–1165) mm, n = 50

TL (♀ ♀): 1075 (1000–1170) mm, n = 50

T (♂ ♂): 361 (305–390) mm, n = 50

T (♀ ♀): 354 (310–410) mm, n = 50

HF c.u. (♂ ♂): 172 (160–190) mm, n = 50

HF c.u. (♀ ♀): 168 (153–178) mm, n = 50

E (♂ ♂): 88 (80–97) mm, n = 50

E (♀ ♀): 86 (80–95) mm, n = 50

WT (♂ ♂): 9.4 (7.3–12.0) kg, n = 50

WT (♀ ♀): 8.3 (7.3–10.0) kg, n = 50

Zimbabwe (Smithers 1983)

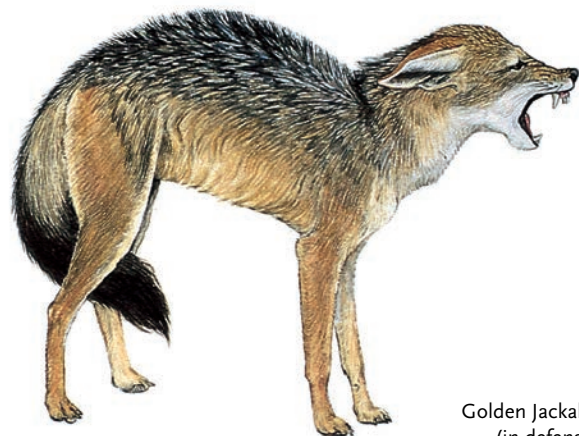
Key References Atkinson 1997; Bingham & Foggin 1993; Fuller *et al.* 1989; Kingdon 1977; Loveridge 1999; Loveridge & Macdonald 2001; Skinner & Chimimba 2005.

Andrew J. Loveridge & David W. Macdonald

Canis aureus GOLDEN JACKAL (ASIATIC JACKAL, COMMON JACKAL)

Fr. Le Chacal commun; Ger. Goldschakal

Canis aureus Linnaeus, 1758. Syst. Nat., 10th edn, 1: 40 'oriente';
restricted by Thomas (1911) to 'Benna Mountains, Laristan, Southern Persia' [Iran].

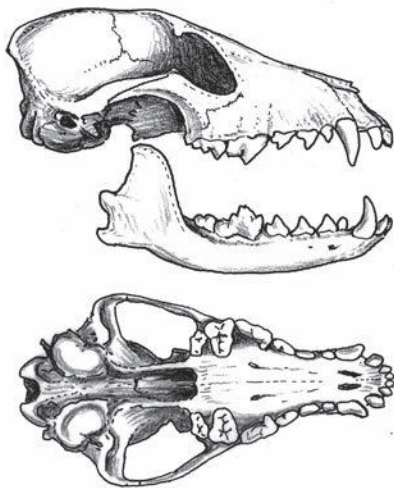


Golden Jackal *Canis aureus*
(in defensive posture).

Taxonomy Some 12 subspecies have been distinguished across the range (Allen 1939, Ellerman & Morrison-Scott 1951), and Coetzee (1977) listed seven for Africa, including the East African population, *C. aureus bea*, which is almost discrete (and see Heller 1914, Swynnerton & Hayman 1950). Ferguson (1981) has suggested that the taxon *C. aureus lupaster*, present in arid areas of Egypt and Libya (Osborn & Helmy 1980) may actually represent a small Grey Wolf *Canis lupus* rather than a large jackal. It is retained here as a form of the Golden Jackal following Wozencraft (2005) (see also Qumsiyeh 1996, Ferguson 2002). However, recent genetic data suggest that *C. a. lupaster* represents an ancient wolf lineage, which most likely colonized Africa prior to the northern hemisphere radiation (Rueness *et al.* 2011). The latter authors detected individuals at two localities in the Ethiopian Highlands, some 2500 km south of the known distribution, an indication that the taxon

may be more widely distributed than thought. Synonyms: *algirensis*, *anthus*, *bea*, *doederleini*, *grayi*, *hagenbacki*, *lamperti*, *lupaster*, *maroccanus*, *mengesi*, *nubianus*, *riparius*, *sacer*, *senegalensis*, *somalicus*, *soudanicus*, *studer*, *thooides*, *tripolitanus*, *variegatus*. Chromosome number: $2n = 78$ (Wurster & Benirschke 1968).

Description Considered to be the most typical representative of the genus *Canis*, without any outstanding features or specialization (Clutton-Brock *et al.* 1976), the Golden Jackal is medium-sized, with ears upright, legs relatively long and feet slender with small pads. Basic coat colour is golden but varies from pale creamy-yellow to a dark tawny hue on a seasonal basis. Pelage on the back is often a mixture of black, brown and white hairs, such that they can appear to have a dark saddle similar to the Black-backed Jackal *C. mesomelas*. Belly and underparts are a lighter pale ginger to cream. Unique lighter markings on throat and chest (Macdonald 1979a) and facial and body scars (Moehlman 1983) make it possible to differentiate individuals in a population. Tail is bushy with tan to black tip. Approximately 12% difference in body weight between sexes, with mean female body mass of 5.8 kg and mean male body mass 6.6 kg (Moehlman & Hofer 1997). Females have four pairs of nipples.



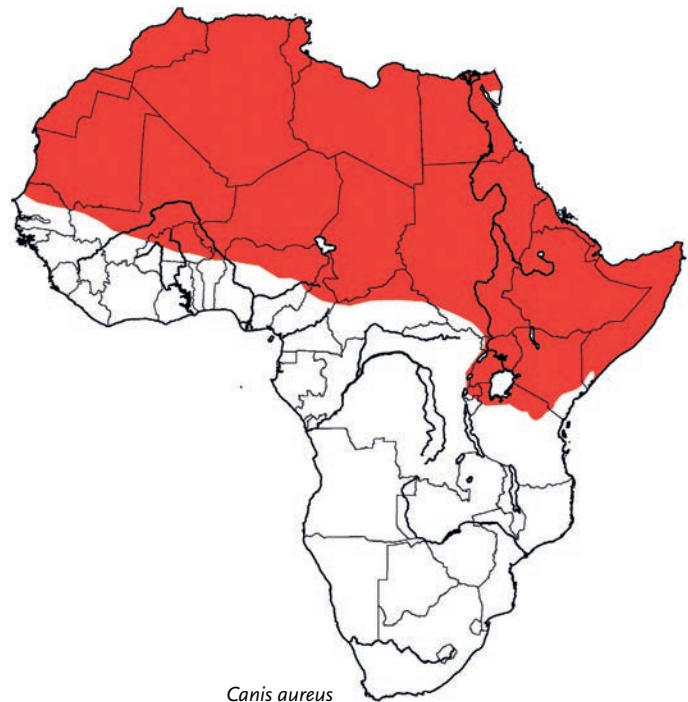
Lateral and palatal views of skull of Golden Jackal *Canis aureus*.

Skull has: well-developed, high-crowned teeth; interparietal crest present; facial region somewhat short; and often a well-marked cingulum on labial side of upper first molar. In these respects, skull is more similar to that of the Coyote *C. latrans* or a small Grey Wolf than that of the Black-backed Jackal, Side-striped Jackal *C. adustus*, or Ethiopian Wolf *C. simensis* (Clutton-Brock *et al.* 1976).

Geographic Variation Jackals inhabiting rocky, mountainous terrain may have a greyer coat shade (Sheldon 1992), and melanistic and piebald forms are sometimes reported (Muller-Using 1975, Jerdon 1984, P. Moehlman pers. obs.).

Similar Species

Canis mesomelas. Sympatric in East Africa. Distinguished by the smaller size and shape of its skull and, usually, a prominent dark saddle (the latter sometimes apparent in the Golden Jackal though usually not as prominent), and a distinct rufous tinge to flanks and legs.



Canis aureus

- C. adustus*. Sympatric in parts of East Africa and the Sahelian regions. Relatively shorter ears, a pale side stripe and a white-tipped tail; interparietal crest poorly developed; cheekteeth less high-crowned.
- C. simensis*. Ethiopian Highlands only. Larger, with longer legs; distinctive reddish coat, white underparts, throat, chest and tail markings.

Distribution Occurs across much of north-east and North Africa, from Senegal (though there is no confirmed record from Gambia; see Grubb *et al.* 1998), Mauritania, Morocco (including Western Sahara), and Algeria in the west through Libya, Niger, N Nigeria and Chad, to Egypt, the Horn of Africa (including Ethiopia, Djibouti, Eritrea and Somalia) and south to Kenya and N Tanzania. A record from Guinea-Bissau (Frade & Silva 1980) is the result of confusion with the Side-striped Jackal (Crawford-Cabral & Esteves 1989).

Extralimital to Africa, ranges from the Arabian Peninsula into western Europe to Austria and Bulgaria, and then continues eastwards into Turkey, Syria, Iraq, Iran, central Asia, the entire Indian sub-continent, then east and south to Sri Lanka, Myanmar, Thailand and parts of Indo-China (Jhala & Moehlman 2004).

Habitat Due to tolerance of dry habitats and omnivorous diet, the Golden Jackal can inhabit a wide variety of habitats, from the Sahara Desert (except the most hyper-arid parts) and Sahel to the evergreen forests of Myanmar and Thailand. In Africa, typically prefers semi-desert, short to medium grasslands and savannas, and has been recorded at 3800 m altitude in the Bale Mts of Ethiopia (Sillero-Zubiri 1996, Yalden *et al.* 1996).

Abundance Fairly common throughout its range. High densities are observed in areas with abundant food and cover. In Serengeti N. P. densities can be as high as two adults per km² (Moehlman 1983, 1986, 1989).

Adaptations The medium body size is energetically flexible and allows Golden Jackals to live off small prey items such as invertebrates, rodents, reptiles and even wild berries. They can trot for long distances in search of food, and are reported to have the ability to forego water, obtaining much of their moisture requirements from their food (Kingdon 1977); Golden Jackals have been observed on Pirotan I., in the Gulf of Kutch, India, where there is no fresh water (Y. Jhala pers. comm.).

Foraging and Food Golden Jackals are omnivorous and opportunistic foragers, and their diet varies according to season and habitat (Wyman 1967). In Serengeti N. P., although they consume invertebrates and fruit, over 60% of their diet is vertebrates and they will kill rodents (particularly gerbils; see Senzota 1990), lizards, snakes, birds (from quail to flamingos), hares, Thomson's Gazelle *Eudorcas thomsonii* and Grant's Gazelle *Nanger granti* (Wyman 1967, Moehlman 1983, 1986, 1989). They also scavenge the carcasses of larger herbivores, such as Common Wildebeest *Connochaetes taurinus*, Plains Zebra *Equus quagga* and African Buffalo *Syncerus caffer*. In C Niger, an analysis of scat samples ($n = 143$) showed that vegetable matter (including various species of grasses, *Acacia* seeds and *Cordia sinensis* and *Ziziphus mauritania* fruit) and invertebrates (ants, dung beetles, grasshoppers and scorpions) constituted the main identifiable items in the diet. Several rodent species, including gerbils, spiny mice and the Striped Ground Squirrel *Xerus erythropus*, were recorded, as were the remains of hares. Bird remains were recorded in 23.7% of scats, and in one sample, eggshell fragments were recovered. The remains of an unidentified snake were also found in one scat (McShane & Grettenberger 1984). Jackals have been recorded feeding on desert snails (*Eremica desertorum*) in Egypt, and digging freshwater snails (*Pila wernerei*) out of cracks in a mud pan in NE Sudan (Osborn & Helmy 1980 and references therein).

Single individuals typically hunt smaller prey such as rodents and birds, using their hearing to locate rodents in the grass and then pouncing on them by leaping through the air, or digging out gerbils from their burrows. However, individual animals will also hunt Thomson's Gazelle fawns. Golden Jackals have been observed to hunt young, old and infirm ungulates that are sometimes 4–5 times their own body weight (Van Lawick & Van Lawick-Goodall 1970, Eisenberg & Lockhart 1972). Admasu *et al.* (2004a) suggest that Golden Jackals in Bale may be more solitary than elsewhere in the range, with animals having been observed foraging alone on 87% of occasions. This is likely because food resources were widely dispersed and rarely concentrated enough for jackals to forage in groups (Admasu *et al.* 2004a). In Serengeti N. P., mated pairs will hunt cooperatively and regularly kill Thomson Gazelle fawns and occasionally adults; pairs have a higher kill rate than individuals (Wyman 1967, Kruuk 1972, Rosevear 1974). Indeed, cooperative hunting permits them to harvest much larger prey in areas where available. In some areas, particularly where food resources are clumped, aggregations of jackals may occur. Van Lawick & Van Lawick-Goodall (1970) reported 14 jackals on a carcass in Ngorongoro, and aggregations of between five and 18 jackals have been sighted scavenging on carcasses of large ungulates in India (Y. Jhala pers. obs.). Golden Jackals will cache excess food.

Golden Jackals are known to predate on domestic livestock. In C Niger, 17 of 37 herders reported losses of livestock to jackals, with an average of 1.7 goats and 0.24 sheep reported lost each year. Most



Golden Jackal *Canis aureus* facial detail.

predation was reported to occur during the day, when animals were unattended and away from camp, though some also occurred at night (McShane & Grettenberger 1984). In Egypt, jackals living near the Nile Valley and Delta are reputed to feed on various cultivated crops and fruit, as well as to prey upon domestic animals (Osborn & Helmy 1980).

Social and Reproductive Behaviour Social organization is extremely flexible depending on demography and food resources (Macdonald 1979a, Moehlman 1983, 1986, 1989, Fuller *et al.* 1989, Moehlman & Hofer 1997, Admasu *et al.* 2004a). The basic social unit is the breeding pair. Some offspring from the previous year's litter may remain with the parents and help to raise the current litter of pups (Moehlman 1983, 1986, 1989). In Tanzania, Golden Jackals usually form long-term pair bonds, both members of which mark and defend their territories, hunt together, share food and cooperatively rear the young (Moehlman 1983, 1986, 1989). Moehlman & Hofer (1997) give average group size as 2.5 (Serengeti N. P., Tanzania), similar to average group size (3; $n = 7$) in Velavadar N. P., India (Y. Jhala pers. obs.).

In Serengeti N. P., Golden Jackals (Moehlman 1983) maintain year-round exclusive territories of 0.5–7.0 km² in size (Moehlman 1983) and 2–5 km² in Ngorongoro (Van Lawick & Van Lawick-Goodall 1970), but will make excursions beyond these territorial boundaries to gain access to fresh carcasses. In Algeria, Khidas (1990) recorded seasonal territories as small as 0.39 km². Home-range size may depend on the age of individuals, demography and the distribution of food resources. For example, home-range size for an adult pair in *Acacia* woodland in Kenya was 2.4 km² and for two juvenile ♀♀, 5.6 and 21.7 km² (Fuller *et al.* 1989), while range size over a 16-month period in the Bale Mountains of Ethiopia varied from 7.9 to 48.2 km² for adults and from 24.2 to 64.8 km² for subadults (Admasu *et al.* 2004a). Home-ranges of individuals within a social group tend to overlap, as reported by Van Lawick & Van Lawick-Goodall (1970), Khidas (1990) and Admasu *et al.* (2004a).

In Serengeti N. P. only the territorial pair does raised-leg urinations. These urination scent-marks are done in tandem on the same spot as the pair forage in their territory. Such scent-marks are considered to play an important role in territorial defence (Rosevear 1974). Affiliative behaviours like greeting ceremonies, grooming and group vocalizations are common in jackal social interactions (Van Lawick & Van Lawick-Goodall 1970, Golani & Keller 1975). Vocalization consists of a complex howl repertoire beginning with 2–3 simple low-pitch howls and culminating in a high-pitched staccato of calls. In Serengeti N. P. individuals give reciprocal howls

to locate their mates and family members. Families also occasionally group howl in response to neighbouring family howls.

In the Serengeti mating typically occurs from Oct to Dec (Moehlman 1983, 1986), and involves a copulatory tie that lasts for several minutes (Golani & Mendelssohn 1971, Golani & Keller 1975). Young are born in dens, which can take the form of existing earthen burrows of Aardvark *Oryzomys afer* or warthogs *Phacochoerus* spp., or rivulets, gullies, road embankments, drainage pipes and other man-made structures. Earthen dens may have 1–3 openings and are typically about 2–3 m long and 0.5–1 m deep. Young pups could be moved from 2–4 dens during their first 14 weeks of life (Jhala & Moehlman 2004).

In the Serengeti both parents and ‘helpers’ – offspring from previous litters – provision and guard the new pups. The ♂ also feeds his mate during her pregnancy and both the ♂ and the ‘helpers’ provision the ♀ during the period of lactation (Moehlman 1983, 1986, 1989, Moehlman & Hofer 1997). The ‘helpers’ are the offspring of the same ‘behavioural’ parents and thus may be full siblings to the young pups that they are provisioning and guarding. However, the paternity of the pups has not been checked genetically. The presence of helpers correlates with a higher pup survival (Moehlman 1986).

Reproduction and Population Structure In the Serengeti, pups may be born in most months of the year, but usually from Dec to Mar, coinciding with the wet season and the arrival of the migrating herds of Common Wildebeest, Plains Zebra and Thomson’s Gazelle (Moehlman 1983, 1986, 1989). In Egypt, wild-born litters have been recorded in Mar, Apr and May (Flower 1932). Females are typically monoestrous, but there is evidence in Tanzania of multiple litters (P. Moehlman pers. obs.). Gestation lasts about 63 days (Sheldon 1992). Litter-size ranges from 1 to 9, and Moehlman & Hofer (1997) give mean litter-size as 5.7. In Tanzania, Wyman (1967) reported an average of two pups emerging from the den at three weeks of age. Pups are born blind and their eyes open at approximately nine days and their teeth erupt at 11 days after birth (Moehlman & Hofer 1997). Lactation usually lasts for 8–10 weeks. Maximum longevity recorded in Serengeti N. P. is about 14 years (Moehlman & Hofer 1997).

Predators, Parasites and Diseases In East Africa, Spotted Hyaenas *Crocuta crocuta* have been observed to kill and feed on Golden Jackals (Kruuk 1972, Kingdon 1977). In Serengeti N. P., Golden Jackals will give a ‘warning yowl’ when Spotted Hyaenas approach their dens. The adult jackals will then chase the hyaenas and bite them on the rump/genitals.

The co-existence of three sympatric species of jackals (Golden, Black-backed and Side-striped) in East Africa is possibly due to resource partitioning in terms of foraging ecology and spatial and temporal habitat utilization and the high relative diversity of prey and predators in Africa (Fuller *et al.* 1989, Wayne *et al.* 1989b). Jackals often scavenge off the kills of larger predators like Lions *Panthera leo*, Leopards *P. pardus*, and Spotted Hyaenas (Van Lawick & Van Lawick-Goodall 1970, Kruuk 1972, Moehlman 1986).

In Serengeti N. P. blood serology of three animals had positive titres to canine parvovirus ($n = 1$), canine adenovirus ($n = 2$), canine coronavirus ($n = 3$) and canine herpesvirus ($n = 2$). All three individuals had negative titres to rabies virus, canine distemper, canine brucellosis, leptospirosis, rinderpest, African horse sickness

and Rift Valley fever (W. B. Karesh pers. comm.). During the 1994–95 distemper outbreak in the Serengeti, a single jackal tested positive for canine distemper (Roelke-Parker *et al.* 1996).

Conservation IUCN Category: Least Concern. CITES: Not listed.

Although the Golden Jackal is present in a number of protected areas across its wide range, including the Serengeti–Masai Mara–Ngorongoro complex, there is evidence that some populations are undergoing declines, as traditional land use practices (such as livestock rearing and dry farming) that were conducive to the survival of jackals and other wildlife, are being steadily replaced by industrialization and intensive agriculture (Jhala & Moehlman 2004). As with other jackal species, they are sometimes killed in indiscriminate predator control programmes.

Measurements

Canis aureus

HB: 872 (822–893) mm, $n = 9$

T: 312 (290–347) mm, $n = 9$

HF c.u.: 200 (190–212) mm, $n = 19$

E: 112 (104–121) mm, $n = 9$

WT: 13 (10–15) kg, $n = 4$

Egypt (sexes combined; Osborn & Helmy 1980)

HB: 740, 785 mm, $n = 2$

T: 270, 280 mm, $n = 2$

E: 110, 110 mm, $n = 2$

WT: 6.3, 7.7 kg, $n = 2$

Tanzania (P. Moehlman pers. obs.)

Key References Fuller *et al.* 1989; Jhala & Moehlman 2004; MacDonald 1979a; Moehlman 1983, 1986, 1989; Moehlman & Hofer 1997.

Patricia D. Moehlman & Yadvendradev V. Jhala



Golden Jackal *Canis aureus*.

***Canis mesomelas* BLACK-BACKED JACKAL (SILVER-BACKED JACKAL)**

Fr. Chacal à chabraque; Ger. Schabrackenschakal

Canis mesomelas Schreber, 1775. Die Säugethiere 2 (14): pl. 95; text 1775, 3 (21): 370 [1976].

‘Vorgebirge der guten Hofnung’ [‘Cape of Good Hope’, South Africa].

Black-backed Jackal *Canis mesomelas*.

Taxonomy As many as six (Allen 1939) and five (Coetzee 1977) subspecies have been recognized. Meester *et al.* (1986) assigned all southern African material to the nominate subspecies. Considering the regional variation in the species, recognition of only two, geographically isolated, subspecies is followed here (and see Kingdon 1997, Walton & Joly 2003). Synonyms: *achrotes*, *arenarum*, *elgonae*, *mcmillani*, *schmidtii*, *variegatoides*. Chromosome number: $2n = 78$, with all but two chromosomes acrocentric (Wallace 1977).

Description Fox-like in appearance, weighing between 6 and 13 kg (see Measurements). Diagnostic features are dark saddle, black, bushy tail and reddish head, flanks and limbs. Muzzle pointed with black nose. In common with other arid-adapted carnivores, ears are relatively large and constantly mobile. Flanks, legs, ears and head tawny to rufous-brown, belly and front of neck pale brown to beige. A black stripe mid-way up each flank slopes up obliquely from behind shoulder to top of rump; dark saddle is broadest at shoulders and tapers to narrow point at base of the tail. Anterior to this stripe, behind the shoulder, is a small vertical stripe, diffuse in some individuals. Above side markings, the back is interspersed with black and white hairs giving an overall silver appearance in mature animals (hence the alternative name Silver-backed Jackal). Juveniles and subadults have similar markings but are drabber and only gain mature pelage at around two years of age. Tail dark brown to black with distinctive black subcaudal marking; tip of tail black. Markings, especially side- and shoulder-stripes, are unique to each individual and can be used as features for individual identification. In the drier west and Namib coast in southern Africa winter coat is deep reddish-brown (particularly so in ♂♂). Distinctive side markings are likely to be signals to conspecifics, flanks being a focus for behaviours such as side-slammings (a common behaviour between dominant and subordinate

canids). Albinism may occur. Five digits on front feet; the first carries the dew-claw and is set well back from the remainder, not marking in the spoor; the hindfoot has four digits. The claws are relatively short, measuring about 150 mm over the curve. Black-backed Jackals have 6–8 nipples (Smithers 1971). Little obvious sexual dimorphism when seen in the field (Moehlman 1983, A. J. Loveridge pers. obs.) although ♂ is in fact slightly larger and heavier than ♀ (Smithers 1971, Rowe-Rowe 1978a, Stuart 1981; and see Measurements).

Skull elongated, braincase pear-shaped, rostrum narrow, supraoccipital crest well developed, bullae rounded and paroccipital processes fused to back of bullae; zygomatic arches broad and well developed; postorbital bars incomplete represented by blunt processes on the zygoma and frontals. Overall, skull and dentition more robust than in Side-striped Jackal *C. adustus* and Golden Jackal *C. aureus*, with outer upper incisors larger, and more pointed and caniniform.

Geographic Variation*C. m. mesomelas*: southern Africa.*C. m. schmidtii*: East Africa and Horn of Africa.

In southern Africa, slight variation in body size and weight has been recorded, with jackals from the former Cape Province, for example, slightly larger than those collected from Zimbabwe (see Measurements). In addition, Rautenbach (1982) found evidence of a clinal increase southwards in mean greatest skull length and suggested this could apply throughout the range of the species in southern Africa. The data of Stuart (1981) from the former Cape Province lend support to this finding. According to Van Valkenburgh & Wayne (1994), skulls of jackals from East Africa are shorter in total length and wider than skulls from southern Africa, and, likewise, animals in East Africa have longer and narrower carnassials and smaller upper and lower molar grinding areas than do animals in southern Africa. Sexual dimorphism also appears less evident, at least in male : female skull length ratio. Van Valkenburgh & Wayne (1994) suggested this was evidence of significant character displacement in East Africa where the species' range overlaps with that of both the Golden and Side-striped Jackal, and that this species is less sexually dimorphic when sympatric with other jackal species than when allopatric (and see Loveridge 1999).

Similar Species

Canis adustus. Lacks dark saddle and rich reddish colour of the flanks and limbs; tail not uniformly black, and with a white tip; white stripe along side, from shoulder to top of rump. Sympatric in parts of East Africa (see also Yalden *et al.* 1980), NE Namibia, N Botswana, C and S Zimbabwe, Mozambique, NE Limpopo Province and E Mpumalanga (South Africa), Swaziland and NE KwaZulu-Natal (South Africa); apparently parapatric in SW Angola (Crawford-Cabral 1993a).

C. aureus. Slightly larger and taller; saddle not so prominent; body colour golden sand to fawn, not russet-red. Sympatric in parts of East Africa.

Distribution Endemic to Africa; occurs in two separate populations, one in north-east and East Africa, the other in southern Africa. Entirely absent from Zambia and through much of central and Equatorial Africa (Ansell 1978). The disjunct distribution of this species is similar to that of the Aardwolf *Proteles cristatus* and Bat-eared Fox *Otocyon megalotis*. The two populations are separated by as much as 1000 km and their discontinuous distribution suggests that regions of dry *Acacia* bush and savanna, the preferred habitat of this species, once connected south-west Africa with the Horn of Africa (Coe & Skinner 1993).

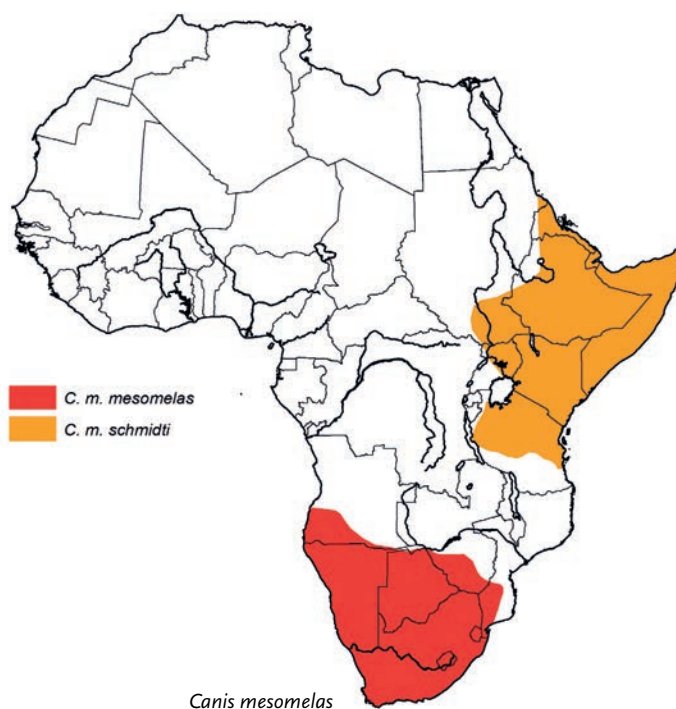
Historical Distribution Black-backed Jackal fossils are found in deposits in South Africa dating to at least 2 mya (Ewer 1956, Hendey 1974a), and there have been numerous palaeontological records in southern Africa over the past 30,000 years (Plug & Badenhorst 2001). Fossil remains have never been found north of Ethiopia, suggesting that they have always been restricted to sub-Saharan Africa. Commenting on remains of bones found in Bir Tarfawi and Bir Sahara, in the extreme south of Egypt, Gautier (1980) remarks 'The material should be certainly ascribed to Golden Jackal *Canis aureus*, although the presence of the small jackal *Canis mesomelas*, a species today found toward the south in the Sudan, cannot be ruled out *a priori*.'

Current Distribution In north-east and East Africa from Sudan through Eritrea, Djibouti and Ethiopia, south to Kenya, E Uganda and N Tanzania. Southern range extends from SW Angola and Namibia through Botswana and S Zimbabwe to S Mozambique, Swaziland, Lesotho and South Africa, where they are mostly widespread (Crawford-Cabral 1993a, Lynch 1994, Monadjem 1998, Skinner & Chimimba 2005).

Habitat Occurs in a wide variety of habitats, from the arid coastal desert of Namibia and W South Africa (Dreyer & Nel 1990) to areas receiving more than 2000 mm of rainfall (Rowe-Rowe 1982). Occurs in montane grassland in the South African Drakensberg and Lesotho Maluti's (above 3000 m) (Rowe-Rowe 1982, 1984, 1992a, Lynch 1994, N. Avenant pers. comm.) and in the alpine zone of Mt Kenya (3660 m; Young & Evans 1993), open savanna in Serengeti N. P., parts of Kenya, South Africa and Botswana (Kingdon 1977, Moehlman 1983, Fuller *et al.* 1989, Skinner & Chimimba 2005), woodland savanna mosaics in Zimbabwe and Mozambique (Smithers 1971, Loveridge & Macdonald 2002) and farmland. In most cases shows a preference for open habitats, tending to avoid dense vegetation. However, in Mokolodi G. R., Botswana, three radio-tracked Black-backed Jackals used bush savanna, mixed bushveld and agricultural land in preference to open grassland (Kaunda 2001).

Where more than one jackal species occurs in sympatry, the habitat is partitioned. Black-backed Jackals preferentially use either the grassland (when sympatric with the Side-striped Jackal, e.g. Hwange N. P., Zimbabwe), or *Acacia/Commiphora* woodland and long grassland (when sympatric with Golden and Side-striped Jackals, e.g. Laikipia and Serengeti; Kingdon 1977, Lamprecht 1978, Moehlman 1983, Estes 1991). In W Zimbabwe habitat partitioning is realized by aggressive encounters in which Black-backed Jackals displace Side-striped Jackals from grassland habitats into the less desirable woodland habitat (Loveridge & Macdonald 2002).

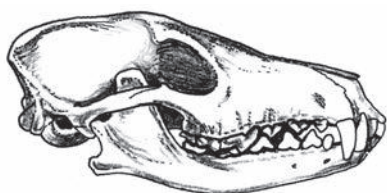
Abundance Generally common, especially in protected areas where suitable habitat occurs. In a wildlife area adjacent to Hwange N.



P. they occurred at densities of 53.9–79.1 per 100 km², expanding to 68.3–97.1 per 100 km² during the breeding season (A. Loveridge pers. obs.). Rowe-Rowe (1984, 1992a) recorded densities of 40/100 km² in Giants Castle G. R., KwaZulu–Natal, and 10–20/100 km² in other areas of the province (Rowe-Rowe 1982, 1992a). In dry river beds in the SW Kalahari strip counts yield densities that vary from 0.09 to 1.3/km² (mean = 0.62), extrapolated to 62/100 km² (mean = 9–130) (J. A. J. Nel unpubl.). In Serengeti N. P., East Africa, Waser (1980) found densities of 0.5/km². Densities of 22/km² have been reported at Cape Cross Seal Reserve, Namibia, perhaps because of superabundant resources there (Hiscocks & Perrin 1988). This density estimate for the Cape Cross population would only apply to the area in the immediate vicinity of the colony where the jackals aggregate at the seal colony to feed. In the surrounding West Coast Recreation Area where the jackals reside they are more dispersed (N. Jenner pers. comm.). Despite strenuous control measures (such as dog hunting, shooting, trapping and poisoning) in many farming areas of southern Africa this species has never been completely exterminated.

Adaptations Black-backed Jackals are relatively unspecialized canids and are well suited for an opportunistic life-style in a wide variety of habitats. They have a well-developed carnassial shear, with a longer premolar cutting blade than other jackal species, which suggests a greater tendency towards carnivory than other jackal species (Van Valkenburgh 1991, Van Valkenburgh & Koepfli 1993). Examination of kidney structure suggests that this species is well adapted to water deprivation (Loveridge 1999), which may explain its presence in the drier parts of the African continent. They apparently have a narrow thermoneutral zone (22.5–27.5 °C) above which thermal conductance – controlled by fur thickness, posture and piloerection – increases (Downs *et al.* 1991).

They show a high propensity for social learning (Nel 1999) and learn to avoid coyote getters (Brand & Nel 1997). Kingdon (1997) suggests that the Black-backed Jackal's brighter, more contrasting



Lateral view of skull of Black-backed Jackal *Canis mesomelas*.

colouration is indicative of its less cryptic behaviour. In addition, Black-backed Jackals are reputed to be more aggressive than other species of jackal (Kingdon 1977, Estes 1991, Skinner & Chimimba 2005). Wyman (1967) found that this species was much more common than Golden Jackals at large carnivore kills in the Ngorongoro Crater, Tanzania, despite being less numerous in the area. Estes (1991) notes that Black-backed Jackals are more likely to attempt to feed on Lion *Panthera leo* and Spotted Hyaena *Crocuta crocuta* kills than other jackal species and that pups of this species become 'quarrelsome and unsociable' and are more likely to emigrate than Golden Jackal pups. Greater tendency towards aggressive behaviour is an adaptation that allows this species to oust the Side-striped Jackal from favourable habitat (Loveridge & Macdonald 2002).

Foraging and Food Opportunistic, generalist feeders. Kok & Nel (2004) found Black-backed Jackals to be more opportunistic and less specialized than sympatric felids (Wildcat *Felis silvestris* and Caracal *Caracal caracal*), reflecting phylogenetic adaptations to prey acquisition, and less specialized than the sympatric Cape Fox *Vulpes chama*. Diet varies according to food availability (Loveridge & Macdonald 2003, Skinner & Chimimba 2005). Numerous studies of dietary preferences have been undertaken, with dietary items generally including small to medium-sized mammals (e.g. murids, springhares *Pedestes* spp., young ungulates), reptiles, birds and birds' eggs, carrion and human refuse, as well as invertebrates (e.g. termites, grasshoppers) and plant matter (Roberts 1922, Bothma 1966a, 1971a, Smithers 1971, Stuart 1976, 1981, 1987, Kingdon 1977, Lamprecht 1978, Rowe-Rowe 1978a, 1983, Ferguson 1980, Dreyer & Nel 1990, Kok 1996, Kaunda & Skinner 2003, Klare *et al.* 2009). They also will feed on beached marine mammals, seals, fish, sea birds (e.g. Cape Cormorant *Phalacrocorax capensis* and Kelp Gull *Larus dominicanus*) and mussels on coasts (Nel & Loutit 1986, Avery *et al.* 1987, Nel *et al.* 1997, Oosthuizen *et al.* 1997, Kolar 2005).

The main feature of this species' foraging behaviour is flexibility and opportunism. Black-backed Jackals are largely nocturnal, but activity periods are extended well into the daylight hours in areas where they are free from persecution. In Hwange N. P. (Zimbabwe), Mokolodi G. R. (Botswana) and the Kalahari of South Africa, Black-backed Jackals exhibited peaks of activity in the evening and early morning (Ferguson *et al.* 1988, Kaunda 2000, Loveridge & Macdonald 2003). The large, mobile ears are used to locate quails, invertebrates and small mammalian prey in long grass. A leap, followed by an accurate pounce is employed to capture prey, guided by the sound, after the manner of a Red Fox *Vulpes vulpes* (Kingdon 1977, A.J. Loveridge & J.A.J. Nel pers. obs.).

Rowe-Rowe (1983) showed that, in the Drakensberg (South Africa), occurrence of carrion, rodent and ungulate prey in the diet closely corresponded to availability within the environment. In Hwange N. P., the diet changed from seasonally abundant invertebrates in the wet season to mammalian prey and carrion in

the dry season. Seasonally, temporally or locally abundant patches of food are exploited wherever possible. Ferguson *et al.* (1988) found that their activity closely approximates the activity cycles of local rodent prey. Black-backed Jackals on the Namib Desert coast of southern Africa scavenge extensively in the seal colonies, where marine refuse provides a rich resource base (Dreyer & Nel 1990) and where they have been seen to kill and eat neonate seal pups (e.g. Kolar 2005). Jackals especially favour the rich afterbirth. Outside the seal birthing period, jackals actively kill yearling and adult seals (N. Jenner pers. comm.). In Serengeti N. P. Black-backed Jackals exploited temporally abundant African Arvicanthis *Arvicanthis nilotica* (Moehlman 1983). On game ranches in the Northern Cape, South Africa, medium-sized ungulates, particularly Springbok *Antidorcas marsupialis*, make up a large proportion (up to 78% of biomass ingested) of Black-backed Jackal diet, and jackals may have significant impact on Springbok numbers in this area (Klare *et al.* 2009).

Black-backed Jackals are quick to respond to prey distress calls and often investigate the activities of large carnivores such as Lions and Spotted Hyaenas (A. Loveridge pers. obs.). They are recorded hunting cooperatively with Cheetahs *Acinonyx jubatus* (Eaton 1969), and, in the Namib, frequently occur in association with Brown Hyaenas *Hyaena brunnea* and may benefit by occasionally scavenging food items from the larger carnivore. Weak or unwary prey items are quickly capitalized upon; for instance, a pair of Black-backed Jackals in Hwange N. P. was, on two occasions, observed snatching young Chacma Baboons *Papio ursinus* that had strayed too far from the protection of the troop (A. Loveridge pers. obs.).

Commonly, pairs and small family groups are seen foraging together; for example, in the Ukhahlamba Drakensberg Park, KwaZulu-Natal, 78% of sightings (n = 872) were of single animals, 19% of pairs and only 3% of groups of three or four (Rowe-Rowe 1984). Less often large aggregations have been observed at particularly rich food resources. Groups of between 8 and 12 aggregate at large carcasses of herbivores, and more than 80 have been recorded at seal colonies on the Namib Desert coast (Oosthuizen *et al.* 1997), with jackals commuting up to 20 km from their denning or resting sites to access this resource (Jenner *et al.* 2011). Such aggregations are accompanied by aggressive behaviour between territorial individuals. However, in the SW Kalahari, where antelope carcasses are uncommon, pairs or groups of up to 30 individuals congregated at Common Eland *Tragelaphus oryx* or Gemsbok *Oryx gazella* carcasses and fed in succession, without much overt aggression (J. A. J. Nel pers. obs.). Mated Black-backed Jackal pairs will often cooperate in the capture of prey resulting in a higher success rate (Lamprecht 1978, Macdonald *et al.* 2004.). In Botswana, McKenzie (1990) found that, on occasion, they form 'packs' in order to hunt adult Impala *Aepyceros melampus*, and other authors have recorded several jackals taking adult antelope (Pienaar 1969, Van Lawick & Van Lawick-Goodall 1970, Sleicher 1973, Lamprecht 1978, Krofel 2008). Kamler *et al.* (2010) report an observation of a single Black-backed Jackal chasing and killing, by means of a throat bite, an apparently healthy adult Impala.

Caching of food is common (Lamprecht 1978), while on the Namib Desert coast accumulations of prey remains result in 'middens' as a result of animals carrying prey to feeding sites (Avery *et al.* 1987, Dreyer & Nel 1990).

This species will prey on livestock (especially juvenile goats and sheep) and is thus considered vermin in many livestock-producing

regions (Van der Merwe 1953). In some sheep-farming areas of KwaZulu–Natal, Black-backed Jackal predation may account for 3% of newborn lambs (Lawson 1989), equating to 2% of the total flock per year (Rowe-Rowe 1975a). In the Graaff Reinet and Nuwe Roggeveld areas losses amount to 3.9% (De Villiers 1979) and 2.4% (Vorster 1988), respectively, and on some individual farms, as high as 15–18% (Brand 1993). In N Botswana, 77% of domestic livestock losses to wild carnivores were due to Black-backed Jackal predation (Gusset *et al.* 2009). By contrast, in S Namibia, where controlled herding is practised, losses due to predation amount to only 0.3–0.5% (Brown 1988). Likewise, in villages bordering Serengeti N. P., where households lose 4.5% of their livestock annually to predators, Black-backed Jackals accounted for < 1% of incidents (Holmern *et al.* 2007).

Social and Reproductive Behaviour The monogamous mated pair is the basis for social structure. The pair bond appears to be life-long in most cases, and if one member of a pair dies the other will often lose its territory (Moehlman 1978, 1986, Estes 1991). However, on one occasion an immigrant ♀ was observed to displace the established ♀ in a territory, subsequently mating with the original territorial ♂ and giving birth to a litter of pups (A. Loveridge pers. obs.). Black-backed Jackals are territorial, using faeces and urine to demarcate their territorial boundaries (Kingdon 1977, Ferguson *et al.* 1983). A mated pair will often scent-mark in tandem, and Moehlman (1983) reports that one foraging pair tandem marked on 76% of observed marking incidents. Tandem marking advertises the presence of both members of the pair, and the pair will aggressively expel intruders. Vocalization by the territorial pair advertises occupancy of the territory and thereby reduces the number of aggressive encounters. Territories are spatially and temporally stable, but may fluctuate in size with season (Loveridge & Macdonald 2001) or where resource levels are widely variable between years (Moehlman 1983). In Hwange N. P., a mated pair of Black-backed Jackals is known to have held the same territory for at least four years (A. J. Loveridge pers. obs.). In Cape Cross Seal Reserve, jackals actively defend a territory during the breeding season. One mated pair has been recorded in the same breeding territory for at least four years (N. Jenner pers. comm.).

Home-ranges differ between localities: in the Rift Valley in Kenya, home-ranges varied from 0.7 to 3.5 km², with a mean of 1.8 km² (Fuller *et al.* 1989). In Zimbabwe home-ranges were larger in the cold dry season (1.05–1.3 km²) and smaller in the hot dry season (0.32–0.62 km²) (Loveridge & Macdonald 2001). In South Africa, home-range size averaged 18.2 km² (n = 14) in Giants Castle G. R. in the Drakensberg (Rowe-Rowe 1982), and 17.8 km² in the Northern Cape Province (Kamler *et al.* 2012). In Gauteng and North West Province, home-range size was 3.4–21.5 km² (mean 10.6 km²; n = 8) (Ferguson *et al.* 1983). Ranges of subadults varied considerably, from 1.9 to 575 km² (mean 85.2 km², n = 11), with the largest ranges likely attained by dispersing individuals. In the more arid SW Kalahari, ranges were smaller, with adult ranges varying from 2.56 to 5.2 km² (mean 4.32 km²; n = 4) and subadult ranges from 4.04 to 8.8 km² (mean 6.32 km²; n = 4) (Ferguson *et al.* 1983). At Cape Cross Seal Reserve, average home-range size was 7.1 km² (range 3.2–13.2) or 24.9 km² (range 17.6–34) as calculated by the minimum area or modified minimum area methods (n = 4 in both cases). Here Black-backed Jackals did not defend their ranges, with home-ranges



Black-backed Jackal *Canis mesomelas* action drawing.

overlapping, and thus were not territorial (Hiscocks & Perrin 1988). At Cape Cross Seal Reserve home-range overlap is extensive around the seal colony. However, during the breeding season jackals actively defend and mark a territory (N. Jenner pers. comm.). In all other cases ranges were defended and mutually exclusive for pairs. Ferguson *et al.* (1983) reported that adults moved an average daily distance of 12 km.

In southern Africa the Black-backed Jackal is a very vocal species. A high-pitched, whining howl is used to communicate with group members and is often used to call the group together in the early evening. This may also function in territorial advertisement. Howling often stimulates the same behaviour in adjacent territories. A three- to five-syllable alarm call, consisting of an explosive yelp followed by a series of shorter high-pitched yelps, is used when disturbed and may be frantic and prolonged when mobbing a Leopard *Panthera pardus*. A low-pitched, gruff bark is used to warn pups of intruders near the den, and whines are used to call to pups. Kingdon (1997) notes the use of a 'clattering distress call' and a loud yelp when alarmed. Interestingly, Black-backed Jackals are much less vocal where they occur alongside the Golden Jackal in Serengeti N. P. in that they do not howl, and instead vocalize with yaps interspersed with howls. This is in contrast to their southern range where, in the absence of Golden Jackals, they howl in much the same way as Golden Jackals (Kingdon 1977, 1997, H. Kruuk pers. comm.). Elimination of the howl from the vocal repertoire of this species may serve to reduce the ambiguity of the signal, thereby limiting competition between these two species, and perhaps reducing instances of inter-specific territorial conflict.

Mating in this species is accompanied by increased vocalization and territoriality in both sexes (Skead 1973, Bernard & Stuart 1992, Loveridge & Macdonald 2001). The dominant individuals within the territory prevent same sex subordinates (usually offspring) from

mating by constant harassment. As with other canids, there is a copulatory tie after mating.

Pups are born in modified termitaria, disused burrows of Aardvark *Orycteropus afer* or other convenient burrows (less frequently caves or other crevices), often with multiple entrances. Jackals sometimes dig their own dens. At Cape Cross Seal Reserve jackals dig their own dens in salt-pans, dry river beds and under large boulders, but will also den in disused Brown Hyaena dens (N. Jenner pers. comm.). Jackals with pups will move dens several times during the first 4–5 months; the most likely explanation for this behaviour on the Namib coast is to reduce parasites (N. Jenner pers. comm.). The same den sites may be used from year to year. For the first three weeks the mother spends up to 90% of her time in the den with the pups; the ♂ and any helpers provision her during this time (Moehlman 1983). Parents and alloparents feed pups by regurgitation. Alloparental care is most fully documented for Black-backed Jackals in Serengeti N. P. (Moehlman 1978, 1983; but see also Ferguson *et al.* 1983). Alloparents guard the pups when the parents are foraging. One helper may increase the average number of pups surviving per mated pair from 1 to 3.3, and two helpers further increases survival to 4 pups (Moehlman 1979, 1983). Estes (1991) suggests that guarding of pups is more important in this species because they tend to den in thicker cover, allowing predators to approach the den more closely without detection. On the Namib coast, guarding helps protect pups from Brown Hyaena predation. Alloparents contribute to boundary defence and will actively protect young from intruding jackals (N. Jenner pers. comm.). Predators such as Spotted Hyaenas, approaching the den, are driven off by determined harassment, in some instances a pair of defending Black-backed Jackals will cooperate in this defence by alternately dashing in to nip the hindquarters of the intruder, before making a hasty escape (Moehlman 1983).

Juveniles disperse at one year of age, although some (24% in Serengeti; Moehlman 1983) may remain within their natal territory to act as helpers. In Hwange N. P., dispersal of five young Black-backed Jackals was documented (two ♀♀, three ♂♂). They dispersed over an average of 2.8 ± 2.05 km, the maximum distance being 20 km. Two (one ♀, one ♂) dispersed to neighbouring territories where a vacancy existed, two (one ♀, one ♂) dispersed to nearby territories using only the periphery of the territory until they were later integrated into the group, and one floated between the natal territory and adjacent territories (A. Loveridge pers. obs.). Elsewhere dispersal distances of more than 100 km have been recorded, in one instance a ♂ dispersing 126 km over a 15-month period (Bothma 1971b, Ferguson *et al.* 1983).

Reproduction and Population Structure Mating generally occurs from late May to Aug and, following a gestation period of about 60 days, births occur from around Jul (sometimes Jun) to Oct (Wyman 1967, Fairall 1968, Kingdon 1977, Stuart 1981, Moehlman 1983, Bernard & Stuart 1992, Bingham & Purchase 2002, N. Jenner pers. comm.); later births were recorded in the Rift Valley in Kenya (Sep–Jan; Fuller *et al.* 1989). In the KwaZulu–Natal Drakensberg, Rowe-Rowe (1978a) recorded a peak in births in Jul. Bernard & Stuart (1992) suggested that summer births are timed to coincide with the reproductive season of important prey like the Southern African Vlei Rat *Otomys irroratus* and Mesic Four-striped Grass Rat *Rhabdomys dilectus*, and winter births with an increase in the availability of ungulate carcasses at the end of the winter dry season.

Litter-size ranges between one and nine (Wyman 1967, Rowe-Rowe 1978a, Bingham & Purchase 2002, N. Jenner pers. comm.); Bingham & Purchase (2002) found mean prenatal litter-size to be 4.6 (range 1–8) pups based on examination of foetuses and placental scars. Pups are born blind, open their eyes at days 8–10, first emerge from the den at three weeks, are weaned at 8–9 weeks, and are completely independent of the den at 14 weeks (Moehlman 1978, A. Loveridge pers. obs.). Permanent teeth start erupting at around 14–16 weeks of age, and are usually fully erupted at one year (Lombaard 1971, Bingham & Purchase 2003). Pups are able to hunt on their own at six months of age, but parents continue to occasionally groom and feed them (Moehlman 1983). They reach sexual maturity at about 11 months (Ferguson *et al.* 1983), but they seldom reproduce in their first year (Ferguson *et al.* 1983, Bingham & Purchase 2002).

Most pup mortality occurs in pups younger than 14 weeks (Moehlman 1987). On the Namib coast, where jackals have few predators, risk of mortality may be greatest during dispersal (post six months) (N. Jenner pers. comm.). It is unlikely that Black-backed Jackals live much beyond about seven years of age in the wild (Rowe-Rowe 1986, 1992a), though captives have lived more than 14 years (Nowak 1999, Weigl 2005).

Predators, Parasites and Diseases Main predator of adults is the Leopard (Turnbull-Kemp 1967). Four of 11 radio-collared Black-backed Jackals were killed and eaten by Leopards in a study in Hwange N. P. (A. Loveridge pers. obs.) and Estes (1967) observed 11 jackals taken by a single Leopard over the course of three weeks, and they may be a favourite Leopard prey item in some areas (Kingdon 1977). Other large predators, such as Spotted Hyaenas and Brown Hyaenas, may prey on unprotected pups (Van Lawick & Van Lawick-Goodall 1970, N. Jenner pers. comm.), as will the Ratel *Mellivora capensis* (Begg *et al.* 2003a), and Kamler *et al.* (2007) document several instances of predation on Black-backed Jackals by African Wild Dogs *Lycaon pictus*. There is also a record of them being preyed upon by Caracals *Caracal caracal* (Melville *et al.* 2004). Other predators include birds of prey; Van Lawick & Van Lawick-Goodall (1970) observed a Martial Eagle *Polemaetus bellicosus* fly away carrying a subadult Black-backed Jackal.

In Zimbabwe, seroprevalence of canine distemper virus, canine parvovirus and canine adenovirus (type 1) were 63.6%, 18.5% and 9.1%, respectively, in 22 Black-backed Jackals sampled (Spencer *et al.* 1999). Although jackals act as reservoirs for these diseases, susceptibility is not known. However, in Serengeti N. P. distemper is believed to have been the cause of several epidemics affecting Black-backed Jackals (Moehlman 1983). Black-backed Jackals are extremely susceptible to rabies, succumbing to the disease after an incubation period of between 15 and 17 days (Foggin 1988, Bingham *et al.* 1995). They are significant vectors of rabies in C southern Africa and are responsible for transmission of the disease to domestic stock (Foggin 1988, Bingham & Foggin 1993, Swanepoel *et al.* 1993, Bingham *et al.* 1999a). Seasonal peaks in rabies cases correspond closely to the mating season and dispersal periods when social disturbance is high (Loveridge & Macdonald 2001). The loss of livestock and the expense of vaccination make rabies economically significant in southern Africa. In some areas rabies control is undertaken by culling of wildlife, especially jackals, and is thus a major cause of mortality. However, rabies spread may be more restricted in stable populations

than in those disturbed by culling regimes. Rabies is rare in national parks, which may be due to the absence of domestic dogs (Cumming 1982) or to intact ecological processes and low disturbance (Foggin 1988, McKenzie 1993). Rabies in jackals is probably better controlled by oral vaccination techniques (e.g. Bingham *et al.* 1995, 1999a) and immunization of domestic dogs (Rhodes *et al.* 1998, Bingham *et al.* 1999a) than by culling (Loveridge & Macdonald 2001). If, as in other sympatric canids, behavioural avoidance and spatial segregation between species occurs, the contact rate (and hence the opportunity for transmission) may be low and reduced overall when jackals occur in sympatry (Loveridge 1999).

Black-backed Jackals have been recorded infected with internal parasites, including the trematode *Athesmia* (Hammond 1972), various cestodes (see list in Walton & Joly 2003) and protozoan parasites such as *Babesia canis* (Van Heerden 1980), *Ehrlichia canis* (Price & Karstad 1980) and *Sarcocystis* spp. (Wesemeier *et al.* 1995). Black-backed Jackals have also succumbed to sarcoptic mange (Keep 1970, Van Heerden 1980), particularly on the Namib coast (N. Jenner pers. comm.). Ectoparasites recorded on Black-backed Jackals include numerous ixodid ticks: *Amblyomma hebraeum*, *A. marmoreum*, *A. variegatum*, *Boophilus decoloratus*, *Haemaphysalis leachi*, *H. silacea*, *H. spinulosa*, *Ixodes pilosus*, *I. rubicundus*, *Rhipicephalus appendiculatus*, *R. evertsi*, *R. nuttalli*, *R. simus* and *R. zambeziensis* (Hall-Martin & Botha 1980, Horak *et al.* 1987, 2000).

Conservation IUCN Category: Least Concern. CITES: Not Listed.

Black-backed Jackals are persecuted for their role as livestock killers and as rabies vectors. Such efforts at population control appear largely ineffective (Rowe-Rowe 1986) and probably only succeed in producing a temporary reduction in local numbers. Bingham & Purchase (2003) note that productivity in this species is sufficiently high for rapid recovery following population crashes or extermination campaigns. There is now no significant trade in jackal products, although hunting and trapping for skins occurs in some areas, and body parts are used in traditional African medicine and clothing (N. Avenant pers. comm.). Populations of the species occur in numerous well-managed protected areas across their range, including Masai Mara (Kenya), Serengeti N. P. and Selous G. R. (Tanzania), Skeleton Coast N. P., Cape Cross Seal Reserve and Etosha N. P. (Namibia), Kgalagadi Transfrontier Park (Botswana, South Africa), Hwange N. P. (Zimbabwe) and Ukhahlamba-Drakensberg Park and Kruger N. P. (South Africa) (Loveridge & Nel 2004). Black-backed Jackals have been maintained in captivity for use in experiments testing rabies vaccine (Bingham *et al.* 1995), but are usually not a common zoo species.

Measurements

Canis mesomelas

HB (♂ ♂): 721 (680–755) mm, n = 39
 HB (♀ ♀): 673 (640–725) mm, n = 52
 T (♂ ♂): 329 (280–365) mm, n = 39
 T (♀ ♀): 314 (250–370) mm, n = 52
 HF c.u. (♂ ♂): 161 (150–179) mm, n = 39
 HF c.u. (♀ ♀): 160 (140–180) mm, n = 52
 E (♂ ♂): 109 (90–115) mm, n = 39
 E (♀ ♀): 99 (80–115) mm, n = 52
 WT (♂ ♂): 7.9 (6.8–9.5) kg, n = 39

WT (♀ ♀): 6.6 (5.5–10.0) kg, n = 52
 Zimbabwe (Smithers 1983)

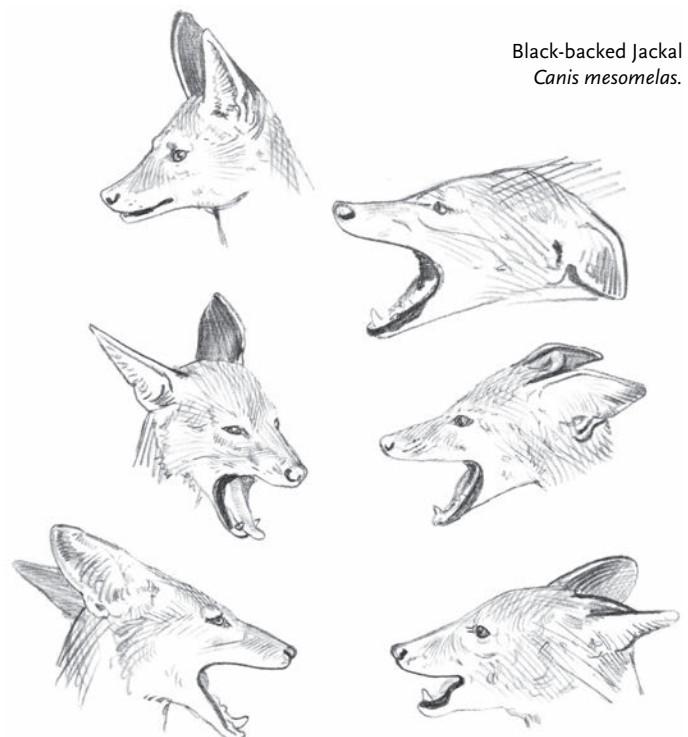
HB (♂ ♂): 785 (690–900) mm, n = 65
 HB (♀ ♀): 745 (650–850) mm, n = 42
 T (♂ ♂): 326 (270–395) mm, n = 70
 T (♀ ♀): 316 (260–381) mm, n = 45
 HF c.u. (♂ ♂): 160 (130–185) mm, n = 66
 HF c.u. (♀ ♀): 156 (140–180) mm, n = 43
 E (♂ ♂): 109 (90–132) mm, n = 68
 E (♀ ♀): 104 (80–120) mm, n = 41
 WT (♂ ♂): 8.2 (5.9–12.0) kg, n = 59
 WT (♀ ♀): 7.4 (6.2–9.9) kg, n = 42

Northern Cape, Western Cape and Eastern Cape, South Africa (Stuart 1981)

Other mean measurements recorded include: 8.4 kg for ♂ ♂ (range 6.4–11.4; n = 123) and 7.7 kg for ♀ ♀ (range 5.9–10.0; n = 84) in Ukhahlamba-Drakensberg Park, KwaZulu-Natal (Rowe-Rowe 1978a); and 8.2 kg for ♂ ♂ (range 5.0–9.3; n = 26) and 7.6 kg for ♀ ♀ (range 6.3–8.5; n = 19) in the former Transvaal (Rautenbach 1982). At Cape Cross Seal Reserve, jackals are slightly larger than in other parts of southern Africa and ♂ ♂ weigh 10.3 (7.5–13.3) kg, n = 28, and ♀ ♀ weigh on average 8.7 (7.0–10.7) kg, n = 29 (N. Jenner pers. comm.); Stutterheim (in litt.) recorded weights for ♂ ♂ of 9.7 (8.4–10.5) kg, n = 7, and for ♀ ♀ 8.7 (6.9–10) kg, n = 12. In East Africa, average weight of ♂ ♂ and ♀ ♀ is around 8.5 kg (7–13.5 kg) (Kingdon 1977).

Key References Dreyer & Nel 1990; Ferguson 1980; Loveridge 1999; Loveridge & Macdonald 2001, 2002, 2003; Moehlman 1979, 1983, 1986; Rowe-Rowe 1982; Skinner & Chimimba 2005.

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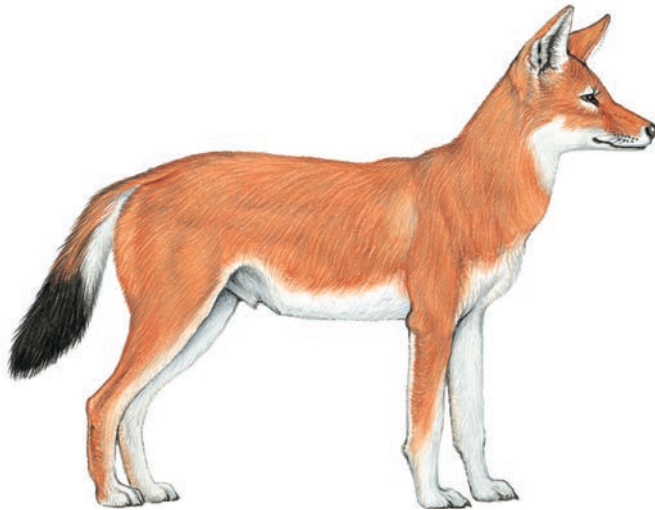


Black-backed Jackal
Canis mesomelas.

Canis simensis ETHIOPIAN WOLF (SIMIEN FOX)

Fr. Loup d'Abyssinie; Ger. Aethiopienfuchs

Canis simensis Rüppell, 1835. Neue Wirbelt. Fauna Abyssin. Gehörig. Säugeth.
1: 39, pl. 14. 'in der Bergen von Simen' [Simen Mountains, Ethiopia, ca. 13° 15' N, 38° 00' E].

Ethiopian Wolf *Canis simensis*.

Taxonomy The most distinct species in the genus *Canis*. Clutton-Brock *et al.* (1976) suggested close affinity with Side-striped Jackal *Canis adustus* and *Dusicyon* spp., and the species was placed in a separate genus *Simenia* by Gray (1868). Although it has been called the Simien or Simenian Fox, the Ethiopian Wolf is not closely linked to the *Vulpes* group (Clutton-Brock *et al.* 1976). Rook & Azzaroli Puccetti (1997) suggested a close relationship with jackals. Phylogenetic analysis using mitochondrial DNA sequencing suggested that *Canis simensis* is more closely related to the Grey Wolf *C. lupus* and the Coyote *C. latrans* than to any African canid (Gottelli *et al.* 1994). It may be an evolutionary relict of a grey wolf-like ancestor crossing to northern Africa from Eurasia (Gottelli *et al.* 1994), where fossils of wolf-like canids are known from the late Pleistocene (Kurtén 1968). Microsatellite and mitochondrial DNA variability is small relative to other canid species, suggesting small population sizes may have characterized its recent evolution (Gottelli *et al.* 2004). There is no fossil record of *C. simensis*. Two subspecies have been recognized (Coetzee 1977). Synonyms: *citernii*, *sinus*, *walgie*. Chromosome number: not known.

Description Medium-sized canid with reddish coat with distinctive white markings, long legs and elongate muzzle, resembling a large German Shepherd dog in conformation and size (Sillero-Zubiri & Gottelli 1994). Overall colour tawny-rufous (ochre to rusty-red), with dense whitish to pale ginger underfur. Throat, chest and underparts white. Distinctive white band around ventral part of neck; inner aspect of limbs white. Face, upper part of slender muzzle and dorsal surface of ears red. Ears broad and pointed, and directed forward; thickly fringed with long white hairs growing inward from the edge, whereas inside of pinnae is almost naked. Tail furry; anterior part white underneath. Rufous colour of coat continues in a short strip down back of tail, becoming a black strip connecting to

a thick black brush of guard hairs, which have black tips. No evident seasonal variation in coat colour, but contrast of white markings against the red coat increases with age and social rank in both sexes. Very long and slender legs. Forefoot has five toes; hindfoot has four toes. Limb posture is digitigrade. Male Ethiopian Wolves are larger than ♀♀ (20% larger in body mass). Female's coat generally paler than male's; during breeding and pregnancy coat turns pale yellow and becomes woolly, and tail turns brownish and loses much of its hair. There are eight nipples, but often only six are functional.

Skull elongated with a slender elongate nose. Facial length 58% of total skull length. Skull very flat in profile, with only a shallow angle between frontals and nasals. Neurocranium low and narrow, thick and almost cylindrical. Interparietal crest slightly developed. Teeth, especially premolars, small and widely spaced. Sharply pointed canines average 19 mm long (14–22 mm) and carnassials are relatively small (Sillero-Zubiri & Gottelli 1994). Lower third molar occasionally absent.

Geographic Variation

C. s. simensis: north-west of the Rift Valley. Nasal bones consistently shorter than those from the southern race.

C. s. citernii: south-east of the Rift Valley.

Dalton (2001) identified differences in the craniomorphology of wolves on both sides of the Rift Valley, but mtDNA analysis from a larger sample of individuals does not lend any support to subspecies recognition of northern and southern clades (Gottelli *et al.* 2004).

Similar Species

Canis aureus. Smaller, with relatively shorter legs; lacks distinctive reddish coat, white underparts, throat, chest, and tail markings of the Ethiopian Wolf. Other jackals (*C. mesomelas*, *C. adustus*) share same differences, but are not sympatric with Ethiopian Wolves.

Distribution Endemic to Africa; confined entirely to the Ethiopian Highlands, where species is restricted to a few mountain ranges of afroalpine grasslands and heathlands, between 6°N and 14°N.

Historical Distribution There are no recent records of the species at altitudes below 3000 m, although specimens were collected at 2500 m from Gojjam (where the species is now extinct – Marino 2003a) and north-western Shoa at the beginning of the century (Yalden *et al.* 1980). Its range restricted altitudinally by increasing agricultural pressure and small populations in Gosh Meda and Mt Guna recently became extinct (Marino 2003a, Marino *et al.* 2011). Reports from Chercher and North Sidamo are either erroneous or suggest further recent extinctions. There is no evidence that Ethiopian Wolves ever occurred in Eritrea.

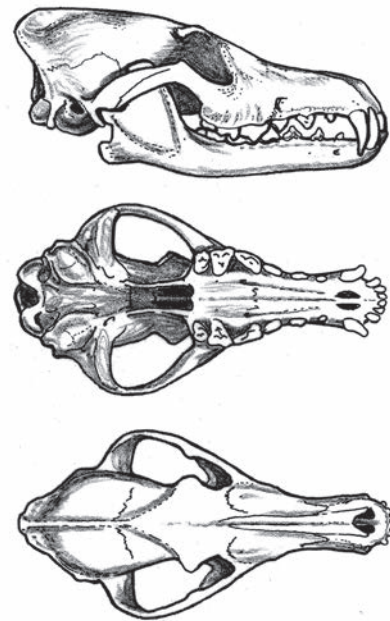


Current Distribution Confined to seven mountain ranges of the Ethiopian Highlands, at altitudes of 3000–4500 m (Gottelli & Sillero-Zubiri 1992, Marino 2003a). Wolf populations occur both sides of the Rift Valley: the Simen Mts, North and South Wollo highlands and Menz to the north; and Arsi Mts, Bale Mts and West Bale to the south.

Habitat A very localized endemic species, confined to isolated pockets of afroalpine grasslands and heathlands where they prey on afroalpine rodents. Suitable habitats extend from above the treeline at about 3200 m, up to 4500 m, with some montane grasslands at 3000 m. However, subsistence agriculture extends up to 3500–3800 m in many areas, restricting wolves to higher ranges (Marino 2003b). Rainfall at high altitude varies between 1000 and 2000 mm/year, with one pronounced dry period from Dec to Feb/Mar.

Ethiopian Wolves utilize all afroalpine habitats, but prefer open areas with short herbaceous and grassland communities where rodents are most abundant, along flat or gently sloping areas with deep soils and poor drainage in parts. Prime habitats in the Bale Mts are characterized by short herbs (*Alchemilla* spp.) and grasses and low vegetation cover, a community maintained in continuous succession as a result of Giant Root-rat *Tachyoryctes macrocephalus* burrowing activity. Other good habitats include tussock grasslands (*Festuca* spp., *Agrostis* spp.), high-altitude scrubs dominated by *Helichrysum* spp. and short grasslands in shallow soils. In northern parts of the range, plant communities characterized by a matrix of 'guassa' tussock grasses (*Festuca* spp.), 'cherenfi' bushes (*Euryops pinifolius*) and giant lobelias (*Lobelia rhynchopetalum*) sustain high rodent abundance and are preferred by Ethiopian Wolves. Ericaceous moorlands (*Erica* and *Phyllipia* spp.) at 3200–3600 m are of marginal value, with open moorlands with patches of herbs and grasses being relatively good habitat.

Abundance With only 400–450 individuals surviving (Gottelli & Sillero-Zubiri 1992, Marino 2003a, Marino *et al.* 2011), this distinctive carnivore is considered the rarest canid in the world (Sillero-Zubiri &



Lateral, palatal and dorsal views of skull of Ethiopian Wolf *Canis simensis*.

Marino 2004). More than half of the species' population (220–300) live in Bale Mts N. P., where density is positively correlated with density of rodent prey and negatively with vegetation height (Sillero-Zubiri & Gottelli 1995a, Marino 2003b). Not more than 110–150 Ethiopian Wolves persist north of the Rift Valley with less than 75 in Simien (Marino *et al.* 2011).

Highest densities are found in short afroalpine herbaceous communities (1.0–1.2 adults/km²); lower densities are found in *Helichrysum* dwarf-scrub (0.2/km²), and in ericaceous heathlands and barren peaks (0.1/km²). Ethiopian Wolves also are present at low density (0.1–0.2/km²) in montane grasslands at lower altitudes. Elsewhere, overall wolf density is relatively lower. In Menz, wolf density was estimated at 0.2 animals per km² (Tefera Ashenafi *et al.* 2005). Census data indicate higher abundance in North Wollo (0.20 ± 0.20 sightings per km), intermediate in Arsi and Guna (0.10 ± 0.11 and 0.10 ± 0.14, respectively), and lower in South Wollo and Simien (0.08 ± 0.13 and 0.06 ± 0.11, respectively) (Marino 2003b).

Adaptations The legs are strikingly long and slender, seemingly suitable for coursing in open country. The muzzle is long, and the small, well-spaced teeth suggest morphological adaptation to feeding on rodents. They have an unusually good sense of smell, and bolt more readily at scent than sight of man. The guard hairs are short and the underfur is thick, providing protection at temperatures as low as –15 °C. Ethiopian Wolves do not use dens to rest at night, and during the breeding season only pups and nursing ♀♀ use the den. Wolves sleep in the open, alone or in groups, curled up, with the nose beneath the tail. Several animals may sleep close together. During the cold nights in the dry season, a 'bed' is carefully prepared from a pile of vegetation debris, the product of Giant Root-rat activity. During the day they take frequent naps, usually resting on their sides. Occasionally, they seek shelter from the rain under overhanging rocks and behind boulders (Sillero-Zubiri 1994).

Foraging and Food Pack members forage and feed alone on small prey, contradicting the general trend in carnivores for grouping and

cooperative hunting. In the Bale Mts they are most active during the day feeding chiefly upon diurnal small mammals of the high-altitude afroalpine grassland community, such as the endemic Giant Root-rat (300–930 g), grass rats (*Arvicanthis blicki*, *Lophuromys melanonyx*, *L. flavopunctatus*, *Otomys typus*) and Starck's Hare *Lepus starcki*. Murid rodents accounted for 96% of all prey occurrences in faeces in Bale (Sillero-Zubiri & Gottelli 1995a). Elsewhere, Giant Root-rats are absent and the smaller African Root-rat *Tachyoryctes splendens* becomes an important component of the wolf diet (Malcolm 1997, Marino 2003b). Occasionally, Ethiopian Wolves were observed feeding on goslings and eggs, Rock Hyraxes *Procavia capensis*, and young of the Common Duiker *Sylvicapra grimmia*, Bohor Reedbuck *Redunca redunca* and Mountain Nyala *Tragelaphus buxtoni* (Sillero-Zubiri & Gottelli 1995a, Malcolm 1997, C. Sillero-Zubiri pers. obs.). Leaves of sedge (*Carex monostachya*) are occasionally ingested, probably to assist digestion or control parasites.

Ethiopian Wolves will take carrion or feed on carcasses; in fact a sheep carcass is the most successful bait for trapping. The local name 'Jeedala fardaa' – the horse's jackal – refers to the habit of following mares and cows about to deliver and eating the afterbirth. In areas of grazing in Bale Ethiopian Wolves were often seen foraging among herds of cattle, a tactic that may aid in ambushing rodents out of their holes, by using the herd as a mobile hide (Sillero-Zubiri 1994).

Ethiopian Wolves are mostly diurnal. Peaks of foraging activity in Bale suggest that they synchronize their activity with that of rodents above the ground (Sillero-Zubiri *et al.* 1995a, b). There is little nocturnal activity, with wolves seldom moving far from their evening resting site. They are more crepuscular and nocturnal where human interference is severe.

Digging out prey is common, mostly to catch Giant Root-rats, with the effort expended varying from a few scratches at a rat hole to the total destruction of a set of burrows. Sometimes digging serves to reach a nest of grass-rats. Kills often are cached and later retrieved. Rich food patches are carefully explored by wolves walking slowly, pausing frequently to investigate holes or to locate the rodents by hearing. Once a prey is located, the wolf moves stealthily towards it, taking short steps, and freezing, sometimes with its belly pressed flat to the ground. The quarry is grabbed with the mouth after a short dash. A stalk can last from seconds to up to one hour, in the case of a Giant Root-rat. Occasionally, wolves run in zig-zags across rat colonies picking up the rodents in passing.

Until recently, Ethiopian Wolves in Bale were unmolested by humans and did not appear to be regarded as a threat to sheep and goats, which are sometimes left unattended during the day (Gottelli & Sillero-Zubiri 1992). Only two instances of predation upon lambs were recorded during 1800 hours of foraging observation (Sillero-Zubiri & Gottelli 1994). Losses to wolves in the southern highlands were dismissed by herders as unimportant when compared with damage by Golden Jackals *Canis aureus* and Spotted Hyenas *Crocuta crocuta*. In N Ethiopia, Ethiopian Wolves have been persecuted in the past due to their reputation as predators of sheep and goats; livestock predation is reported as important in the heavily populated areas of Wollo and Simien (Marino 2003b).

Social and Reproductive Behaviour Ethiopian Wolves live in packs, a discrete and cohesive social unit that communally shares and defends an exclusive territory. Packs of 3–18 adults (mean 6)

congregate for social greetings and border patrols at dawn, noon and evenings, and to rest together at night, but break up to forage individually in the morning and early afternoon. Peaks of foraging activity suggest that wolves synchronize their activity with that of rodents above the ground. There is little nocturnal activity, with wolves seldom moving far from their evening resting site.

Annual home-ranges of eight packs monitored for four years averaged 6.0 km², with some overlap in home-ranges. Home-ranges in an area of lower prey biomass averaged 13.4 km² (n = 4) (Sillero-Zubiri & Gottelli 1995b). Overlap and aggressive encounters between packs were highest during the mating season. Dispersal movements are tightly constrained by the scarcity of suitable habitat. Males do not disperse and are recruited into multi-male philopatric packs; some ♀♀ disperse at two years of age and become 'floaters', occupying narrow ranges between pack territories until a breeding vacancy becomes available (Sillero-Zubiri *et al.* 2004b). Dead breeding ♀♀ typically are replaced by a resident daughter.

Adult Ethiopian Wolves hunt alone but travel in packs when patrolling to advertise and maintain their territories. All pack members, independent of social rank, regularly scent-mark territory boundaries, via urine posts, scratching and deposition of faeces on conspicuous sites (mounds, rocks, bushes) (Sillero-Zubiri & Macdonald 1998). More often only adults of both sexes take part, led by one of the dominant pair, usually the ♀. Vocalizations also play a role in territory defence. Aggressive interactions with neighbouring packs are common, highly vocal and always end with the smaller group fleeing from the larger (Sillero-Zubiri *et al.* 2004b).

Calls can be grouped into two categories: alarm calls, given at the scent or sight of man, dogs, or unfamiliar wolves, start with a 'huff' (rapid expulsion of air through mouth and nose), followed by a quick succession of high-pitched 'yelps' (a series of 4–5 'yeahp-yeahp-yeahp-yeahp') and 'barks'. 'Yelps' and 'barks' can be also given as contact calls, and often attract nearby pack mates. Greeting calls include a 'growl' of threat, a high-frequency 'whine' of submission, and intense 'group yip-howls', given at the reunion of pack members and advertise pack size, composition and position. A lone howl and a group howl are long-distance calls used to contact separate pack members and can be heard up to 5 km away. Howling by one pack of wolves may stimulate howling in adjacent packs. Communal calls mustered pack members before a border patrol (Sillero-Zubiri & Macdonald 1998).

Many postures and habits of the Ethiopian Wolf are typical of other social canids. It grooms itself by licking and nibbling and by reciprocating attention of others. It laps water with its tongue. Wolves often wade streams and swim across narrow rivers when necessary. Ethiopian Wolves remain playful throughout their lives, particularly male siblings.

Precopulatory behaviour by the dominant ♀ includes an increase in the scent-marking rate, play soliciting, food-begging towards the dominant ♂ and agonistic behaviour towards subordinate ♀♀. The receptive period is synchronized in sympatric ♀♀ to less than two weeks (Sillero-Zubiri *et al.* 1998). Courtship may take place between adult members of a pack or with members of neighbouring packs. After a short courtship, which primarily involves the dominant ♂ permanently accompanying the ♀, the pair copulate over a period of 3 to 5 days. Copulation involves a tie lasting up to 15 min. Other ♂♂ may stand by a tied pair with no signs of aggression. Mate



Ethiopian Wolf *Canis simensis* dominance display.

preference is shown, with the ♀ discouraging attempts from all but the pack's dominant ♂, by either defensive snarls or moving away; she is receptive to any visiting ♂ from neighbouring packs. Up to 70% of matings ($n = 30$) involved ♂♂ from outside the pack (Sillero-Zubiri *et al.* 1996a, 2004b).

During the breeding season social gatherings are more common and take place next to the den. Intense, energetic and noisy greetings that occur primarily when groups form or before tandem-marking patrols seem to be an important component in keeping cohesion and friendly relations within the pack. Other common interactions are food-sharing, allogrooming, nibbling and playing, which involves chasing, ambushing and mock fighting. Strong affiliative ties are developed between siblings during the first months of their life. Vicious play-fighting during the first weeks outside the den may determine the establishment of rank between siblings. Hierarchies among pack members are well established with frequent displays of dominance and subordination; a dominance rank develops among adults of each gender; shifts in rank may occasionally take place in ♂♂ but not among ♀♀ (Sillero-Zubiri *et al.* 2004b).

Reproduction and Population Structure The dominant ♀ of each pack gives birth once a year between Oct and Jan (Sillero-Zubiri *et al.* 1998, 2004b). Gestation, based on the time from last day of mating to parturition, lasts 60–62 days. Pups are born with their eyes closed and without teeth, in a den dug by the ♀ in open ground, under a boulder or inside a rocky crevice. Five and six placental scars were counted in the uteri of two ♀♀. A seven-week-old unborn litter comprised three female and two male foetuses, averaging 122 g. A ten-day-old female pup had a mass of 650 g. The natal coat is charcoal grey with a buff patch in chest and inguinal regions. Two to seven pups emerge from the den after three weeks. At this time, the dark natal coat begins to be replaced by the pelage typical of the species. Pups are regularly shifted between dens, up to 1300 m apart. In eight out of 18 natal dens watched, a subordinate ♀ assisted the mother in suckling the pups (Sillero-Zubiri *et al.* 2004b). At least 50% of extra nursing ♀♀ showed signs of pregnancy and may have lost or deserted their own offspring before joining the den of dominant ♀.

Development of the young is divisible into three stages: (1) early nesting (Week 1 to Week 4), when the young are entirely dependent on milk; (2) mixed nutritional dependency (Week 5 to Week 10), when milk is supplemented by solid foods regurgitated by all pack members until pups are completely weaned; and (3) postweaning dependency (Week 10 to Month 6), when the pups subsist almost entirely on solid foods supplied by helpers. Adults have been observed providing food to juveniles up to one year old. Juveniles will join adults in patrols as early as six months of age, but will not urinate with raised leg until 11 months if male or 18 months if female. Yearlings have 80–90% of adult body mass. Full adult appearance is attained at two years. Both sexes become sexually mature during their second year. Only about 60% of ♀♀ breed successfully each year (Sillero-Zubiri *et al.* 1996a). A ♂ in Bale lived to 15 years, but 8–10 is the norm (C. Sillero-Zubiri pers. obs.).

Adult sex ratio in packs is biased toward ♂♂ 1.8 : 1 ($n = 59$), with small family groups closer to 1 : 1 (Sillero-Zubiri & Gottelli 1995b).

Predators, Parasites and Diseases No known predators, but unattended young may be taken by Spotted Hyaenas or Verreaux's Eagles *Aquila verreauxi*. Attacks of the Tawny Eagle *Aquila rapax* directed at small pups result in swift defence by guarding adults. The high densities and diversity of raptors (12 recorded species in Bale), many of which have been observed to feed on small mammals, are likely to pose the greatest competitive threat to Ethiopian Wolves. In addition, free-ranging domestic dogs, Golden Jackals and Servals *Leptailurus serval* may also feed upon the same prey species, and, therefore, will compete when food resources are limited. There is interference competition with domestic dogs, which will actively chase away Ethiopian Wolves from large carcasses. The Ratel *Mellivora capensis* is also a possible competitor for food and burrows (Sillero-Zubiri 1996).

The most widespread disease to affect Ethiopian Wolves is rabies, and is the main cause of mortality, killing whole wolf packs and accounting for a major population decline in Bale Mts with losses of up to 77% in 1991–92 (Sillero-Zubiri *et al.* 1996b, Haydon *et al.* 2002, Randall *et al.* 2006). In 2003–2004 and 2008–2009, rabies epizootics had a similar impact; the outbreaks were contained through parental vaccination (Randall *et al.* 2004, 2006, Johnson *et al.* 2010). Elsewhere, rabies has been reported in domestic dogs, livestock, people and wolves (Marino 2003b). The level of rabies awareness amongst people in the highlands, and the frequency of the reports, suggests high incidence across the highlands. In Bale, dogs travel regularly with their owners in and out of wolf range, and are in contact with many other dogs that are attracted to garbage and carrion in villages, and they may provide the vehicle for pathogens such as rabies or distemper to reach their wild relatives (Haydon *et al.* 2002). The risk of transmission, however, will depend on the probability of contact between wolves and dogs, which varies with grazing regimes in high-altitude pastures, dog husbandry and the spatial distribution of wolf habitat in relationship to settlements. High-density populations of Ethiopian Wolves are particularly vulnerable to decline due to rabies (Marino *et al.* 2006). A population viability model indicates that disease-induced population fluctuations and extinction risks can be markedly reduced with the vaccination against rabies of a relatively small

proportion of wolves (Haydon *et al.* 2002). Randall *et al.* (2006) present an integrated management strategy for rabies in Ethiopian Wolves combining long-term population monitoring, disease surveillance, conventional and emergency vaccination programmes, and advanced modelling techniques.

Other causes of mortality in Ethiopian Wolves include starvation of juveniles between weaning and one year of age, road kills and shooting. At least four animals have been killed by vehicles in Bale since 1988. Two others have been shot from the road and another two were left with permanent limps from collisions with vehicles.

Ethiopian Wolves are free of ectoparasites, perhaps because of the cold mountain climate; none were found on any of over 300 animals handled (C. Sillero-Zubiri pers. obs.). Nematodes and trematodes were present in faeces and carcasses, including *Taenia pisiformis* (M. Anwar pers. comm.).

Conservation IUCN Category: Endangered B1ab(iii,v); C1+2a(i), D. CITES: Not listed.

The Ethiopian Wolf is less common and less widely distributed now than in the past (Yalden *et al.* 1980, Marino 2003a). The main causes of this decline are loss of habitat to agriculture and grazing, disease, hybridization with domestic dogs and human persecution.

The highlands of Ethiopia are among the most densely populated agricultural areas within Africa. Habitat destruction and soil degradation have steadily reduced the afroalpine ecosystems, which increasingly resemble islands. Sixty per cent of all land above 3200 m has been converted into farmland, and all populations below 3700 m are particularly vulnerable to further habitat loss, especially if the areas are small and of relatively flat relief (Marino 2003b). Extensive overgrazing by livestock probably depresses rodent populations significantly, and in some areas habitat is threatened by proposed development of commercial sheep farms.

Human persecution is currently less severe than in the past and associated with conflicts over livestock losses (Marino 2003a). Some Ethiopian Wolf populations have been exterminated due to their reputation as predators of sheep and goats. Local people in Simien regard them as a menace to sheep, and report that they would come near the pens at night. In many regions, people living close to wolves believe numbers are recovering through successive years of good breeding and less persecution. Still, the degree of conflict due to predation determines the negative attitudes to wolves in some regions and resulting persecution (Marino 2003a). In the past, sport hunters occasionally killed Ethiopian Wolves, but no hunting is currently permitted and the species is protected by national law. Most of the range of the two largest populations, i.e. Bale and Simien, is protected within National Parks. There are no reports of exploitation for fur or other purposes, although parts of wolf skins were seen used as saddle pads (C. Sillero-Zubiri pers. obs.). There are no animals in captivity.

In western areas of Bale some Ethiopian Wolves had pale-coloured coats, heavily built bodies and kinky tails (Gottelli *et al.* 1994). One melanistic ♀ was heavier than any other ♀ captured, did not belong to any pack, and gave birth outside the breeding season; she twice lost her offspring after birth. Mitochondrial DNA restriction fragments and microsatellite alleles concluded that hybridization

occurred in areas with sympatric dogs, and was due only to crosses between female Ethiopian Wolves and male domestic dogs (Gottelli *et al.* 1994). Although hybrids are confined to parts of Bale, they may threaten the genetic integrity of the wolf population. Following hybridization, a population may be affected by outbreeding depression, or reduction in fitness, although to date this does not seem to have taken place in Bale.

Ethiopian Wolves have been monitored since 1983. The IUCN SSC Canid Specialist Group produced an action plan for the Ethiopian Wolf (Sillero-Zubiri & Macdonald 1997), providing a detailed strategy for the conservation and management of remaining wolf populations. This plan advocated immediate action on three fronts – education, wolf population monitoring and rabies control in domestic dogs – to conserve the afroalpine ecosystem and its top predator. As a result, the Ethiopian Wolf Conservation Programme (EWCP) was established in 1995 by the University of Oxford with support from the Born Free Foundation, UK. Its overall aim is to protect the afroalpine ecosystem and many of its rare highland endemic plants and animals through better management in Bale and the establishment of other conservation areas in Arsi, Menz and Wollo. The EWCP has taken a number of important steps, including: (1) a dog vaccination campaign in Bale and north Ethiopia; (2) sterilization programme for domestic dogs and hybrids in Bale; (3) community and school education programme; (4) strengthening the capacity of protected areas – funding patrolling and infrastructure; (5) surveys to determine the persistence and status of all populations of wolves; (6) monitoring of all wolf populations; (7) wolf vaccination interventions to mitigate rabies epizootics in the Bale Mts; and (8) setting up the Ethiopian Wolf Conservation Committee within Ethiopia as a national steering committee for dealing with conservation issues (see Sillero-Zubiri & Marino 2004). A conservation strategy and National Action Plan for the conservation of Ethiopian Wolves is now in place (IUCN SSC Canid Specialist Group 2011).

Measurements

Canis simensis

HB (♂ ♂): 963 (928–1012) mm, n = 18

HB (♀ ♀): 919 (841–960) mm, n = 8

T (♂ ♂): 311 (290–396) mm, n = 18

T (♀ ♀): 287 (270–297) mm, n = 8

HF c.u. (♂ ♂): 199 (193–209) mm, n = 18

HF c.u. (♀ ♀): 187 (170–197) mm, n = 8

E (♂ ♂): 108 (100–119) mm, n = 18

E (♀ ♀): 104 (95–110) mm, n = 8

WT (♂ ♂): 16.2 (14.2–19.3) kg, n = 18

WT (♀ ♀): 12.8 (11.2–14.2) kg, n = 8

Bale Mts, Ethiopia (Sillero-Zubiri & Gottelli 1994)

Key References Gottelli & Sillero-Zubiri 1992; Gottelli *et al.* 1994, 2004; Haydon *et al.* 2002; IUCN SSC Canid Specialist Group 2011; Marino 2003a; Sillero-Zubiri & Gottelli 1994, 1995; Sillero-Zubiri & Macdonald 1997; Sillero-Zubiri & Marino 2004; Sillero-Zubiri *et al.* 1996a, b, 2004.

Claudio Sillero-Zubiri

GENUS *Lycaon* African Wild Dog

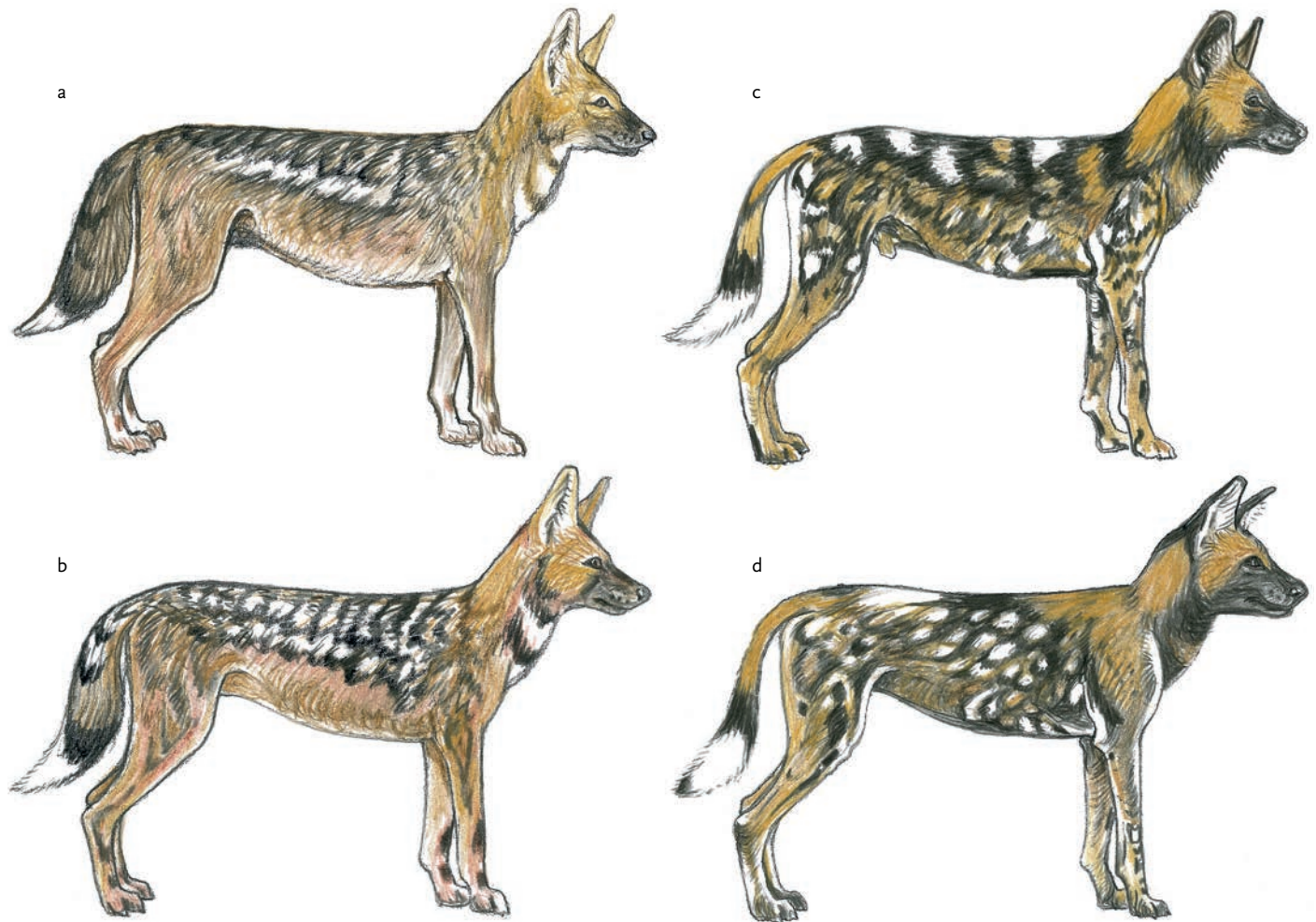
Lycaon Brookes, 1827. In: Griffith *et al.* Anim. Kingd. 5: 151.

The genus *Lycaon* was first identified by Brookes in 1827 after revising an earlier description by Temminck (1820) who identified a specimen as *Hyaena picta*. Extant *Lycaon* are known only from sub-Saharan Africa with fossil evidence of early forms of *Lycaon* identified in Africa from 3 to 2 mya. However, fossil evidence of *Lycaon* from the late middle Pleistocene also exists from localities outside of sub-Saharan Africa and includes a *Lycaon* specimen from Israel (Stiner *et al.* 2001) and possibly *Lycaon*-like fossils in Europe (Kurtén 1968; but see Stiner *et al.* 2001).

Studies by Matthew (1924, 1930) and Simpson (1945) placed *Lycaon* within the subfamily Simocyoninae. This was largely based on a modification of the carnassial tooth or blade-like lower molar with a unicuspid talonid (trenchant heel) possessed only by three extant canid genera (all monospecific); *Lycaon* (the African Wild Dog), *Cuon* (the Asian Dhole) and *Speothos* (the South American Bush

Dog). These hypercarnivorous canids have teeth specifically adapted for processing meat unlike other canid genera that are adapted more for omnivory (Van Valkenburgh 1989). More recent analyses of morphological and molecular genetic data reject the monophyly of the Simocyoninae. These data strongly support *Lycaon* as a distinct genus associated with the wolf-like canids, which include species in the genus *Canis* (wolves, coyotes, jackals, domestic dog) and *Cuon* (Clutton-Brock *et al.* 1976, Van Gelder 1978, Wayne & O'Brien 1987, Girman *et al.* 1993, Tedford *et al.* 1995, Wayne *et al.* 1997). The combination of molecular evidence (Wayne *et al.* 1997) and a review of palaeontological evidence (Rook 1994) suggests that *Lycaon* may be the sister taxon to the wolf-like canids and one of its most basal lineages.

Derek J. Girman



Pelage pattern formation in African Wild Dog *Lycaon pictus*. (a) Generalized, semi-cryptic formation in genus *Canis*, as expressed in various jackals and wolves. (b) Similar pattern becoming more conspicuous through enhanced tonal contrast. (c) *Lycaon* pelage in which *Canis*-like format has been dislocated but elements are still perceptible. (d) *Lycaon* pelage in which dislocation has generated typical 'marbling' (individual from Longido, N Tanzania).

Geographic Variation African Wild Dogs in East Africa are smaller than those in southern Africa and were originally believed to represent distinct subspecific populations. African Wild Dogs in north-east Africa also tend to be predominantly black with small white and yellow patches, while dogs in southern Africa are more brightly coloured with a mix of brown, black and white. However, on the basis of genetic analysis, no subspecies are currently recognized (Girman & Wayne 1997, Girman *et al.* 2001).

Similar Species Spotted Hyenas *Crocuta crocuta*, Striped Hyenas *Hyaena hyaena* and even jackals (*Canis* spp.) and feral domestic dogs are occasionally misidentified as African Wild Dogs, but all are only distantly related and morphologically distinct.

Distribution Endemic to Africa; formerly distributed throughout sub-Saharan Africa, from desert (Lhotse 1946) to mountain summits (Thesiger 1970). In North Africa occurred as disjunct populations in S and SW Algeria; there are no confirmed records from Libya, but they persisted (as vagrants) in Egypt until the late 1800s (Osborn & Osbornová 1998). Probably absent only from lowland rainforest and the most arid deserts (Schaller 1972).

Current Distribution African Wild Dogs have disappeared from much of their former range (Fanshawe *et al.* 1997, Woodroffe *et al.* 2004, IUCN SSC 2008, 2009). In North Africa, they may still survive in S Algeria, but there is no recent information; they were last recorded in the Tassili N. P. in 1996 (K. de Smet pers. comm.). The species is virtually eradicated from West Africa, where populations survive in Niokolo-Koba N. P. in Senegal and in the protected areas complex between Niger, Benin and Burkina Faso (Lamarque 2004, P. Chardonnet pers. comm.). African Wild Dogs are similarly greatly reduced in central Africa, where the only surviving populations are known in N Central African Republic and Chad. In north-east Africa they survive in good numbers only in parts of Ethiopia and S Sudan. The largest populations remain in southern Africa (especially N Botswana/W Zimbabwe/E Namibia) and parts of East Africa (particularly S Tanzania and N Mozambique). Important but relatively isolated populations, persist in C Zambia (Kafue N. P.), C Kenya (Laikipia and Samburu) and E South Africa (Kruger N. P.) (IUCN SSC 2008, 2009).

African Wild Dogs are known, or presumed, to be extinct, or near-extinct, in Burundi, Cameroon, Congo, Côte d'Ivoire, DR Congo, Eritrea, Gabon, Gambia, Ghana, Guinea, Guinea-Bissau, Mali, Nigeria, Rwanda, Sierra Leone, Swaziland, Togo and Uganda (updated from Fanshawe *et al.* 1997, Woodroffe *et al.* 2004).

Abundance Historical records indicate that African Wild Dog populations have always existed at relatively low densities, with very occasional historical reports of large aggregations (e.g. Cumming 1850). Today they are rarely seen even in the few protected areas where they are relatively common. Density estimates vary widely for the few populations comparatively unconstrained by fences or human population expansion. These range from a low of 0.5 adults/100 km² in some areas associated with the dry Kalahari Desert in C Botswana and NE Namibia, to a high of 3.5–4.6 adults/100 km² in NW Botswana and the Selous G. R. in Tanzania (Woodroffe *et al.* 2004). Relatively small and somewhat more fragmented populations persist in several additional parts of their former range with densities that vary between these extremes. The cur-

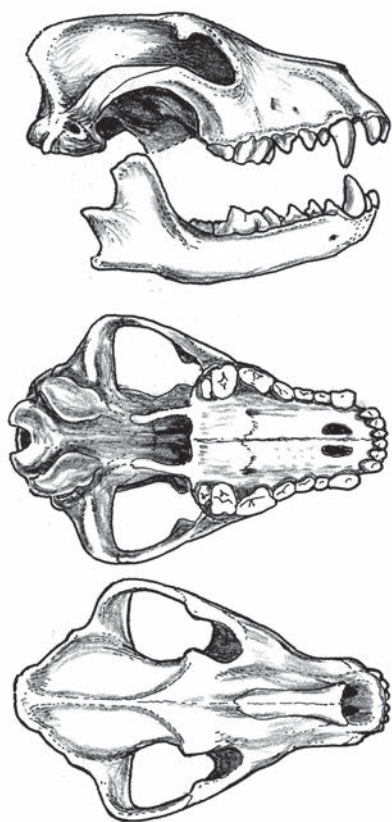


Lycaon pictus

rent population of free-ranging African Wild Dogs remaining in Africa has been estimated at less than 8000 individuals, in ~750 packs, with the largest populations in N Botswana/E Namibia/W Zimbabwe/S Angola (~2500) and in S Tanzania/N Mozambique (1300). These estimates are based primarily on density estimates from studied populations, on knowledge of presence elsewhere and on habitat characteristics.

Habitat African Wild Dogs occupy a range of habitats, including short-grass plains, semi-desert, bushy savannas, woodlands and upland forest. While early studies in Serengeti N. P., Tanzania, led to the belief that they were primarily an open plains species, more recent data indicate that they reach their highest densities in thick bush and woodland habitats (e.g. Selous G. R., Tanzania; Mana Pools N. P., Zimbabwe; and N Botswana). African Wild Dogs have been recorded in desert (Lhotse 1946), montane (Thesiger 1970) and coastal scrub and woodland habitats (Temminck 1820). Several relict populations occupy dense upland forest (e.g. Harenna Forest, Ethiopia; Ngare Ndare Forest, Kenya), and they are also the only mammal species, other than humans, known to have reached the summit of Kilimanjaro at 5895 m (Thesiger 1970, Grimshaw *et al.* 1995) and are recorded from 4250 m on Mt Kenya (Young & Evans 1993) and 4050 m on the Sanetti Plateau in Ethiopia (Dutson & Sillero-Zubiri 2005). It appears that their current distribution is limited primarily by human activities (which they avoid; Woodroffe 2011a), the availability of prey, and disease, rather than by the loss of a specific habitat type.

Adaptations The teeth are adapted to holding and slicing and show a much lesser function of grinding than in some other canids. The outer upper incisors are larger than the central ones, heavily built and recurved; they wear to sharp edges to assist the short, sharp-pointed canines in holding prey. The outer incisors in the lower jaw are less well developed. The back portion of the lower first molar is sectorial, adding to the slicing ability of the carnassial mechanism. The crushing function is performed by the second upper molar and



Lateral, palatal and dorsal views of skull of African Wild Dog *Lycaon pictus*.

the lower second and third molars that are less developed than the remainder of the teeth (Skinner & Chimimba 2005).

One of the most striking peculiarities of African Wild Dogs is their extraordinary tri-coloured mottle pattern, which is never the same in any two individuals and is almost without precedent in a wild mammal, although it does resemble the artificially selected polymorphisms of several domestic animal species. The conspicuous white tail-tip resembles a flag, and playing pups try to bite the white tip while chasing one another (Kuhme 1965a). Bold patterns have also been interpreted as helping scattered pack members to keep in visual contact and maintain group cohesion (Schaller 1972). Other authors have suggested that the main function of individual variation in colour is to aid recognition within the pack (Ewer 1973). Although it appears conspicuous to the human eye this type of patterning has been interpreted as camouflage by some observers because it breaks up the body's contours. Its adaptive value has also been linked to the social disciplines that maintain pack cohesion (Kingdon 1977).

African Wild Dogs can run at speeds of up to 60 km/h, and are specially adapted to deal with the heat stress that this involves (Taylor *et al.* 1971).

Foraging and Food African Wild Dogs are cursorial predators that opportunistically hunt medium-sized antelope. Many of the common prey species are more than twice their size, the average weighing around 50 kg, and may be as large as 200 kg (Creel & Creel 2002). In most areas where African Wild Dogs persist in relatively large numbers, their principal prey are Impala *Aepyceros melampus*, comprising, for example, around 54% of their prey in Selous G. R. (Creel & Creel 2002), more than 80% of their diet in Moremi G. R. in

N Botswana (McNutt 1996a) and as much as 94% of their diet in Kruger N. P. (Pienaar 1969, Reich 1981, Mills & Biggs 1993, Mills & Gorman 1997). In some habitats (and sometimes even in areas where Impala populations are not necessarily low), several other species take over as primary prey. These vary with habitat type and region but include in particular Greater Kudu *Tragelaphus strepsiceros* and Springbok *Antidorcas marsupialis* in southern Africa, and Thomson's Gazelle *Eudorcas thomsonii* and Common Wildebeest *Connochaetes taurinus* in East Africa (Estes & Goddard 1967, Schaller 1972, Fanshawe & FitzGibbon 1993, Creel & Creel 1995); for example, in Aitong, Kenya, Thomson's Gazelle made up 67% of prey compared with only 17% Impala (Fuller & Kat 1990). Similarly, in Kafue Valley, Zambia, Impala made up only 2% of kills whereas Common Duiker *Sylvicapra grimmia* and Common Reedbuck *Redunca arundinum* made up half their prey in about equal parts, with Lichtenstein's Hartebeest *Alcelaphus buselaphus lichtensteini* accounting for about 15% (Mitchell *et al.* 1965).

African Wild Dogs will chase, but rarely kill, larger species, such as Eland *Tragelaphus oryx*, Roan *Hippotragus equinus* and African Buffalo *Syncerus caffer*. More typically, calves of these species are targeted when encountered. Small antelopes, especially Common Duiker, dikdik *Madoqua* spp. and Steenbok *Raphicerus campestris*, are important in some areas. Warthogs *Phacochoerus* spp. are taken in some populations. In Samburu and Laikipia Districts, Kenya, dikdik made up 70% of the biomass consumed by African Wild Dogs, with Impala comprising 11% (Woodroffe *et al.* 2007b). African Wild dogs also opportunistically capture relatively smaller prey such as small carnivores like Bat-eared Foxes *Otocyon megalotis* (Rasmussen 1996), Black-backed Jackals *Canis mesomelas* (Kamler *et al.* 2007) or Banded Mongooses *Mungos mungo* (Creel & Creel 2002), hares, springhares *Pedetes* spp., francolins, lizards and even eggs, but these constitute a small proportion of their diet.

African Wild Dogs travel and hunt in packs. Hunts typically take place around the first and last hour of daylight and are preceded by a 'social rally' or 'greet' believed to alert and collect the pack in anticipation of departure (Kuhme 1964b, 1965a, Kingdon 1977). Occasionally, hunts can begin before dawn or extend after dusk. They commonly also hunt on moonlit nights. Typical capture is as follows: one dog bites and holds the quarry, usually at the flank, and other pack members help pull it to ground and quickly kill it by disembowelling. In some hunts, usually involving large prey, one pack member may effectively immobilize the prey by biting and holding its nose while others make the kill. Hunts can appear to be highly coordinated events, but in many areas, particularly typical woodland habitats with dense brush understorey, packs tend to split during hunts with individual dogs opportunistically chasing and often bringing down prey alone. In the Selous, successful chase distances varied from 50 m to as much as 4.6 km (n = 304, Creel & Creel 2002).

Although hunting is not necessarily cooperative, feeding at kills, in contrast, is highly coordinated and cooperative. In general, prey is consumed rapidly – Van Lawick & Van Lawick-Goodall (1970) recorded the consumption of a Thomson's Gazelle in 15 minutes – and quietly by the entire pack with several individuals pulling against others to facilitate the rending of the carcass. When pups are travelling with the pack a system of priority of access is given to the youngest first and reinforced by the dominant pair. Otherwise, all members of the pack eat together rapidly and leave a carcass after eating. If they have left pups somewhere, they return to the pups and regurgitate meat to them. Caching of food has also been recorded (Malcolm 1980).

Hunting success is relatively high in comparison with some other large carnivore species. In Serengeti N. P. 44% of hunts ($n = 666$) were successful (see Creel & Creel 2002, based on pooled data from studies of Schaller 1972, Malcolm & Van Lawick 1975, Fuller & Kat 1990, Fanshawe & FitzGibbon 1993), which is the same as hunting success of animals in Selous G. R. (Creel & Creel 2002). Hunting success also varies with prey; in their study in the Selous, Creel & Creel (2002) noted that Impala were not only hunted most often (40% of hunts) and killed most often (54%), but also yielded the highest hunting success (64%). Zebra, on the other hand, provided the most mass per kill, but were rarely killed, with a probability of killing (7%) far lower than other species (presumably because zebra are dangerous to hunt).

As a result of social hunting, each pack member has a higher foraging success (measured as kg killed per km chased) than it would if it hunted alone: hunting success increased from 42% in packs of three adults to 67% in packs of 20 adults while the mass of prey killed increased from 16 kg to 40 kg and the distance chased decreased from 1.1 km to 0.5 km, accordingly (Creel & Creel 1995). Small packs are more selective in their hunting decisions, likely because they are not as effective as larger packs in hunting larger prey (Creel & Creel 2002). Larger packs are able to utilize larger, more profitable prey species (e.g. Common Wildebeest; Creel & Creel 2002), and are better able to defend their kills against scavenging hyaenas (Fanshawe & FitzGibbon 1993; though see Carbone *et al.* 1997). African Wild Dogs themselves very rarely scavenge (Mills & Biggs 1993), although they have been observed appropriating kills of Leopards *Panthera pardus*, Lions *P. leo* and Spotted Hyaenas (Kruuk 1972, Creel & Creel 1995).

Consumption rates in the wild vary from 1.2 to 5.9 kg/dog/day. In East Africa, a pack of 17–43 African Wild Dogs killed an average of at least three animals per day (independent of size or composition of the pack), consuming 1.7 kg/dog/day (Fuller & Kat 1990), which compares favourably with the findings of Creel & Creel (2002) in the Selous (where food consumption averaged between 2.0 and 2.5 kg/dog/day). Observations in the Selous suggest an animal can consume 8–9 kg in one sitting (Creel & Creel 2002).

Social and Reproductive Behaviour African Wild Dogs are intensely social animals, spending virtually their entire lives in close association with other dogs (e.g. Kuhme 1965a, McCreery 2000). They are obligate social breeders that live in a close kin-related pack. A pack, then, rather than a pair of individuals, should be considered the basic reproductive unit within the population. A pack, defined by its potential for reproduction, is rarely static in membership for extended periods. Rather, pack membership typically changes throughout the year due to relatively high rates of mortality, dispersal and high variance in reproductive success. By definition a pack may be as small as a pair, but packs with fewer than four adults often dissolve or extinguish following unsuccessful attempts to rear pups through to one year. In Botswana, of 11 packs comprising fewer than four adults, only one (a pair) successfully raised pups to one year. Three had pups but lost them all to other predators before they were four months old. No pack of the 10 small packs that failed survived to attempt a second litter (J. W. McNutt pers. obs.). In contrast, in Kenya three packs of 3–4 adults all successfully raised pups and grew in size, although their reproductive success was lower than that of larger packs (Woodroffe 2011b). The low success of small packs provides empirical evidence of an Allee effect for African Wild Dogs that should

be incorporated into population viability estimates for all populations (Courchamp *et al.* 2000, 2002, Courchamp & Macdonald 2001; but see Buettner *et al.* 2007). Pack size varies between populations and also within populations over time (average range 5.9–13.2 from six studied populations), but the cumulative average pack falls roughly on the median: 9–10 adults, including yearlings ($n = 221$ pack-years) (Woodroffe *et al.* 2004). Packs greater than 30 adults and yearlings have been recorded in the comparatively large remaining populations in Botswana (max. = 36) and Tanzania (max. = 44). In the past, much larger, but very rare aggregations have been reported. In the nineteenth century packs of several hundred dogs were recorded in South Africa (Cumming 1850). In the 1920s an aggregation travelling across Masailand in S Kenya was estimated in the region of 500 dogs as described by Blixen (1937).

Both ♂♂ and ♀♀ emigrate from their natal packs in groups, with ♀♀ typically dispersing a year earlier than ♂♂. As with most mammals, ♂♂ disperse further than ♀♀, which often establish reproductive territories that incorporate part of their natal area (McNutt 1996a). Packs are formed when small same-sex subgroups (usually full siblings and litter-mates) leave their natal group and join subgroups of the opposite sex from other packs (McNutt 1996a, McCreery & Robbins 2001). In a new pack, therefore, the ♀♀ (mean = 2) are typically closely related to one another, but not to the ♂♂, and the ♂♂ (mean = 3–4) are closely related to one another, but not to the ♀♀. Offspring produced by the dominant pair are, therefore, typically related to all adults in the pack. In this sense most African Wild Dog packs represent an extended kin group, within which all dogs are closely related to others in the pack. However, it is not uncommon (25% of observed packs in Botswana) for packs to have an adult unrelated to any of the others as a consequence of stochastic events affecting subgroup membership among packs in transition, especially adoption of unrelated pups (McNutt 1996b, McNutt *et al.* 2008). As a result, inferences cannot be made safely about the kin relationships within any pack without a thorough knowledge of the history of the pack members. Occasionally, new packs form by fission of large packs, with some of the original founders of both sexes emigrating together in a secondary dispersal event. In such situations pups might remain with the natal pack or join the secondary dispersal group, irrespective of the whereabouts of their parents. The priority of access to meat in favour of the youngest animals (and reinforced by the dominant pair, as mentioned earlier) has implications for social structure. Older ♂♂ that had been designated as dominant have been recorded being replaced, after serious fighting, by young ♂♂ (Creel & Creel 2002). The susceptibility of adults to coercion (notably to regurgitate meat) by very young animals and a tendency for adult ♂♂ from the youngest cohorts to achieve dominant status has been called the 'youth first protocol' (Burrows 2004).

African Wild Dogs have large home-ranges for their body size and the mean is 606 km² ($n = 50$ packs) across habitats. However, these ranges vary widely between habitats (probably with prey density and availability) from 150 km² in the lowveld savanna woodlands of Kruger N. P. ($n = 20$ packs; Fuller *et al.* 1992a) to more than 2000 km² in the arid habitats of southern Africa, such as the Kahalari (J. W. McNutt pers. obs.), where prey populations live at comparatively low densities and are widely dispersed, and in Serengeti N. P. where migratory prey is only seasonally abundant. During the 3–4 months while feeding young pups at a den, packs are

confined to relatively small areas (50–200 km²), but the rest of the year a pack ranges widely within their much larger territory.

Although neighbouring African Wild Dog packs overlap along boundaries, African Wild Dogs should be considered territorial. They rarely enter other packs' core areas and they defend their ranges infrequently but aggressively, occasionally with fatal consequences, against intruders and unrelated neighbours. The large territories of packs translate into very low population densities typical for the species. Even packs that inhabit protected areas may travel extensively outside reserve borders, where they encounter conflict with human activities and threats such as roads, snares and livestock and game farmers likely to persecute them. African Wild Dogs of both sexes emigrating from their natal packs may range over extremely wide areas compared with territory sizes. Dispersing African Wild Dogs have been tracked over hundreds of kilometres (Fuller *et al.* 1992b), a characteristic that could account for the occasional reports of single animals, or single-sex groups from countries such as Uganda, DR Congo and Swaziland, where there have been no resident populations for several decades. It can also account for the occasional re-colonization of formerly occupied habitats such as the Serengeti ecosystem, Laikipia and Savé Valley in Zimbabwe.

African Wild Dogs have a complex communication system, including a number of unique vocalizations (Robbins 2000), as well as olfactory communication both within and between packs (Van Heerden 1981, M. Parker pers. comm.). Territory boundaries appear to be predominantly communicated through scent-marking with faecal and urine marks by the dominant pair. Semio-chemical communication is also important in maintaining pack cohesion during hunting in bush habitats. Most vocalizations are for intra-pack communication and are generally high frequency, and relatively low in volume and broadcast quality. Food-begging calls are typically twittering. Whines combine with body postures to suggest an appeasing function and yelps denote the anticipation of food. Broadcast inter-pack vocalizations such as the howls typical of other canids (e.g. wolves, coyotes, jackals) are rare in African Wild Dogs and only occur in the specific context of direct interactions between residents and intruders. This rare vocalization is a howl-like duet projected at the ground by the resident pack's dominant pair immediately following inter-pack encounters (J. W. McNutt pers. obs.). Even the commonly described intra-pack contact call, or 'hoo call' used to regroup a dispersed pack or a lost individual is only used conservatively, perhaps to minimize chances of alerting other large predators such as Lions and Spotted Hyaenas to their location (Webster *et al.* 2010).

In a pack larger than two adults the reproductive pair consists of the dominant ♂ and the dominant ♀ (Frame *et al.* 1979, Malcolm & Marten 1982). In most African Wild Dog packs, the dominant ♀ is the mother of all the pups, although two or even three ♀♀ may breed on some occasions. Similarly, the dominant ♂ fathers most of the pups but multiple paternity has been reported (Girman *et al.* 1997). All pack members are involved in caring for the pups and dominant ♂♂ are usually no more assiduous in caring for pups than are other ♂♂ in the pack (Malcolm & Marten 1982). There is some evidence to suggest that pup survival is higher in large packs where there are more helpers to assist with their care (Creel *et al.* 1997).

The advantages in terms of survival and reproduction associated with larger packs, including increased hunting success, appears to predispose African Wild Dogs to an unusual willingness to adopt pups irrespective of their relatedness. Adoption (provisioning and protection) of pups



African Wild Dogs *Lycaon pictus* action drawings. Note the solicitation-like postures during 'social rallies' (right foreground).

by free-ranging animals carries few costs to an average pack preying on medium-sized prey, and the predisposition has provided important management options for isolated populations and for African Wild Dogs living in conflict with domestic livestock (McNutt 1996b).

Pups are born in an underground den that they use for the first three months of life. Such dens are usually those of Aardvark *Oryzomys azer*, and are often enlarged and modified by Cape Porcupines *Hystrix africaeaustralis* or Spotted Hyaenas. Dens may also take the form of small caves or other suitable structures in rocky formations. The mother is confined to the den during early lactation, and is reliant on other pack members to provision her during this time. Pack members feed the mother, and, starting from about four weeks of age, the pups by regurgitating solid pieces of meat. Some pack members also 'baby-sit' the pups, and chase predators off while the remainder of the pack is away hunting. These adults sometimes join the pups in begging for food when the provisioners return.

Reproduction and Population Structure Births occur roughly annually. In southern Africa, pups are born between Apr and Sep, with a peak during the dry season in late May and early Jun. Following a gestation period of approximately 71–73 days (J. W. McNutt pers. obs.), ♀♀ whelp large litters for their body size, averaging 8–11 and occasionally as many as 21 pups (Fuller *et al.* 1992b). Birth-weight is approximately 300–350 g and pups are born blind. Pups are generally fully weaned by eight weeks but continue to use a den for refuge until 12–16 weeks of age. African Wild Dogs reach sexual maturity in their second year of life, and it is common for ♀♀ to first reproduce at this age though ♂♂ commonly delay another year (McNutt 1996a). However, reproductive suppression of subordinates of both sexes means that disproportionately few of those that live to reproductive age ever reproduce directly (Creel *et al.* 1997).

African Wild Dog populations have been widely reported to have male-biased sex ratios both at birth and among adult populations. Although some populations occasionally show deviations in favour of female pups (Fuller *et al.* 1992a), long-term observations (McNutt & Silk 2008) statistically support the male-biases first reported in Serengeti N. P. by Frame *et al.* (1979).

In Kruger N. P. and N Botswana, no African Wild Dog has survived more than 11 years, and most dogs studied in Selous lived six years or less (Creel & Creel 2002). In captivity, record longevity is 15 years (Weigl 2005). Annual age-specific adult mortality is generally quite high for African Wild Dogs compared with other large carnivore species (range 20–57%), but it varies with other demographic characteristics such as fecundity, litter-size and pup survival among populations. Pup mortality during the first year of life is relatively high, and averages around 50% in most populations. However, mean litter-size and variance in pup survivorship vary widely among populations. Juvenile survival has been shown to be an important variable in a population's long-term growth and stability (Creel *et al.* 2004), although adult mortality is also important. Buettner *et al.* (2007) investigated the influence of rainfall and pack size on juvenile survival from den emergence to 12 months of age in Kruger N. P. (based on data on 30 packs monitored over a period of 15 years), and found that past rainfall significantly influenced pup survival up to nine months of age, such that pups benefited from preceding dry periods. The positive effects of pack size on juvenile survival only became evident for pups older than nine months. Consequently, survival of juveniles as well as adults has been flagged as a focal point for assessing population status and conservation action.

Predators, Parasites and Diseases Competition with larger predators has a major impact on African Wild Dog behaviour and population biology (Creel & Creel 1996, 2002, Mills & Gorman 1997). There is a large degree of dietary overlap between African Wild Dogs and Spotted Hyaenas and Lions (see Creel & Creel 2002), and the latter two species will steal kills from African Wild Dogs, particularly in open areas, such as the Serengeti and Ngorongoro Crater, where such kills are easily located (Kruuk 1972, Fanshawe & FitzGibbon 1993). Loss of kills to other predators is much less common in well-wooded ecosystems (such as Kruger and the Selous). For example, Fanshawe & FitzGibbon (1993) found that Spotted Hyaenas were present at over 85% of all kills of Common Wildebeest and Thomson's Gazelle in Serengeti N. P. (24.5% of which were appropriated by hyaenas); on the other hand, Creel & Creel (1996), in the more densely vegetated Selous, reported their occurrence at only 18% of kills (of which only 2% were appropriated by hyaenas).

The high metabolic rate of African Wild Dogs means that prey loss to competitors has the potential to seriously impact their energy balance: a model based on data from Kruger suggested that dogs must spend about 3.5 hours/day hunting in order to meet their energy requirements but would need to increase this to some 12 hours if they lost 25% of their food (Gorman *et al.* 1998). Despite earlier suggestions (Fanshawe & FitzGibbon 1993), the benefits of increased group size for the purpose of defending the carcass against kleptoparasites such as Spotted Hyaenas might be countered by increasing intra-specific competition for food as pack size increases. Small groups would probably be particularly vulnerable to kleptoparasitism, because they would not be able to consume enough food before the hyaenas

appropriated the kill, and medium-sized groups may, therefore, be most effective to meet energy and nutritional demands (Carbone *et al.* 1997). As such African Wild Dogs seem to fare well where interference competition is minimal. However, where Spotted Hyaena density is high and visibility good, hyaenas can accumulate at kills in sufficient numbers to negatively impact foraging success (Creel & Creel 2002).

The degree of competition between African Wild Dogs and Lions is less clear, but predation by Lions (outside the context of kills) is a principal cause of natural mortality in African Wild Dogs. Lion predation accounted for 9% of 45 known-cause deaths in Selous (Creel & Creel 1996, 2002), 33% of 57 deaths in Kruger (Van Heerden *et al.* 1995), and 50% of 14 deaths in Moremi (McNutt 1995). An attempt to reintroduce African Wild Dogs to Etosha N. P. in Namibia failed because they were hunted out by a pride of Lions over a period of weeks (Scheepers & Venzke 1995). Away from kills, Spotted Hyaenas also occasionally kill dogs of all ages (Ginsberg *et al.* 1995, Creel & Creel 2002, J. W. McNutt & R. Woodroffe pers. obs.), and Leopards and African Rock Pythons *Python sebae* have also been recorded killing animals.

Competition with larger carnivores could help explain the ranging behaviour of African Wild Dogs. While larger predators tend to occur at higher densities where prey species are relatively abundant, African Wild Dogs (like Cheetahs *Acinonyx jubatus*) tend to avoid these areas. Because they range in areas of comparatively low prey densities, they tend to occupy ranges effectively requiring greater travel distances during hunting. Naturally wide-ranging behaviour, and a preference for areas with reduced large predator densities, can explain in part why African Wild Dogs are often found in habitats outside of protected areas. As a result of changes in Lion and Spotted Hyaena populations, some habitats with suitable prey populations can become marginal or completely unsuitable for African Wild Dogs.

In addition to inter-specific competition, adults and pups have been killed in inter-pack clashes. Intra-specific competition caused 69% of known-cause deaths in Selous through conflict within and between packs (Creel & Creel 1998).

Infectious disease can also play an important role in the dynamics of some African Wild Dog populations. Pups appear to be particularly susceptible, with 26% of pup deaths attributed to disease in some populations (Woodroffe *et al.* 2007a). Many of the pathogens infecting African Wild Dogs are common canine pathogens that also infect domestic dogs and other wild canids, such as jackals and foxes. Some, such as canine coronavirus, adenovirus and herpesvirus, probably have little effect on populations: a high proportion of healthy adults show evidence of past exposure to these infections (Woodroffe & Ginsberg 1997, Alexander *et al.* 2010). At the opposite extreme, rabies virus can have major population impacts, especially in small populations. Rabies has been implicated in the 'disappearance' (see Marsden *et al.* 2012) of the African Wild Dog population in the Serengeti ecosystem on the Kenya–Tanzania border in 1990–91 (Gascoyne *et al.* 1993, Burrows 1995, Kat *et al.* 1995) and has hindered the re-establishment of packs in Madikwe G. R., South Africa (Hofmeyr *et al.* 2000, 2004) as well as killing animals reintroduced to Etosha N. P. in Namibia (Scheepers & Venzke 1995). Evidence suggests that rabies similarly caused the deaths of several packs in N Botswana in 1995 and 1996 (J. W. McNutt pers. obs.) and in N Kenya in 2005 (R. Woodroffe pers. obs.).

African Wild Dog populations cannot maintain rabies infection: rates of contact between packs are so low that all pack members would

be expected to die before coming into contact with other packs to which infection could be transmitted (Woodroffe & Donnelly 2011). Instead, infection appears to spill over from other, more abundant, host species. Domestic dogs are likely to be an important reservoir of rabies infection (Woodroffe & Donnelly 2011, Woodroffe *et al.* 2012), but jackals (Hofmeyr *et al.* 2000), foxes and hyaenas may also be involved. Large African Wild Dog populations occupying extensive wildlife areas appear able to persist in the face of occasional rabies outbreaks that extirpate a few packs (Woodroffe 2011b), but small, isolated populations may be driven to extinction in a single outbreak. Vial *et al.* (2006) and Prager *et al.* (2011) developed population viability models, which predict that vaccination campaigns, using vaccines that provide two years of immunity, and targeting 30–40% of individuals within a population every 1–2 years would be successful in ensuring persistence of small populations.

The impact of some other diseases on African Wild Dog populations appears more variable. For example, canine distemper virus can be highly pathogenic for captive animals (van de Bildt *et al.* 2002) and has caused episodes of high mortality among free-ranging dogs in Botswana (Alexander *et al.* 1996) and Tanzania (Goller *et al.* 2010). However, some populations show high levels of exposure to this virus, without any observed ill-effects (Woodroffe & Ginsberg 1997, Alexander *et al.* 2010, K. C. Prager pers. comm.). Likewise, while Creel *et al.* (1995b) showed that adults can recover from anthrax infection, and the Kruger N. P. population increased during anthrax outbreaks in the early 1990s (M. G. L. Mills pers. comm.), the population in the Luangwa Valley, Zambia, declined dramatically in association with an anthrax epidemic (Turnbull *et al.* 1991). The reason for this variation is unknown, though it is not restricted to African Wild Dogs. For example, canine distemper has been shown to occasionally cause high mortality in Lions, but no detectable ill effects at other times (Packer *et al.* 1999), with mortality apparently reflecting exposure to concomitant infection with other pathogens (Munson *et al.* 2008). There is no evidence that canine parvovirus causes mortality in adult African Wild Dogs, although it may be a factor in some pup deaths.

African Wild Dogs are known to carry infections of *Hepatozoon* spp. (K. C. Prager pers. comm.), and there is some evidence that *Toxoplasma gondii* can have an important effect on pup survival; in Kruger N. P. an entire litter of 20 pups disappeared, and four of the pups were confirmed to have succumbed to *Toxoplasma* and/or *Neospora* (a related protozoan) (Van Heerden *et al.* 1995). In Selous, dogs were commonly infected with cestodes and trematodes (Creel & Creel 2002), and in Kruger *Taenia* and *Ancylostoma* hookworms were found in faecal samples (Van Heerden *et al.* 1995). Penzhorn *et al.* (1998a) recovered *Sarcocystis* oocysts from a free-ranging animal. In Kruger, Van Heerden *et al.* (1995) recorded a number of ticks, including *Haemaphysalis leachi*, *Amblyomma hebraeum*, *A. marmoreum*, *Boophilus decoloratus*, and a number of species of *Rhipicephalus* (and see Horak *et al.* 2000).

Conservation IUCN Category: Endangered C2a(i). CITES: Not listed. CMS: Appendix II.

Historically, African Wild Dogs have been perceived to have a negative impact on 'game' populations (e.g. Bere 1955), and they are still commonly reviled especially by game farmers who consider them a serious problem because they prey on valuable game species (Lindsey *et al.* 2005b). An average pack preying on medium-size antelope kills on average two prey every three days, or approximately

220 individuals of medium-sized prey per year (J. W. McNutt pers. obs.). Therefore, the health of a Wild Dog population is dependent on the size and health of those prey populations (see McNutt & Gusset 2012). In large intact ecosystems such as that found in N Botswana, the impact of the African Wild Dog population on Impala, their primary prey, is estimated to be approximately 10–20% of annual rate of reproduction (J. W. McNutt pers. obs.).

African Wild Dogs are a threat to livestock in some areas, but stock depredation is infrequent compared with the frequency of range overlap with domestic grazers. In and around Masai Mara National Reserve, Kenya, African Wild Dogs ignored livestock, and data from Samburu and Maasai areas of N Kenya indicate that they rarely caused problems unless wild prey was severely depleted (Woodroffe *et al.* 2005). A two-year study of African Wild Dog depredation of commercial livestock in Zimbabwe found that African Wild Dogs actually killed approximately half the number of cattle believed by farmers to have been lost (representing an actual annual loss of 0.4% of the regional herd; Rasmussen 1999). African Wild Dogs hunting in livestock areas outside Selous G. R., Tanzania, were never observed to kill livestock in six years of observation (Creel & Creel 2002). Nevertheless, African Wild Dogs can become a severe problem for small domestic stock (including calves), especially in areas where native prey species populations have been reduced by hunting (Woodroffe *et al.* 2005). Multiple kills of small stock have been reported from a single attack by packs of African Wild Dogs in Kenya, Botswana and Namibia.

While pups die almost exclusively from 'natural' causes (see Reproduction and Population Structure), a substantial proportion of known mortality recorded among adults in studied populations is caused directly by human activity such as road kills and snares, even in some of the largest and best-protected areas (summarized in Woodroffe *et al.* 2007a). In addition, African Wild Dogs originating in protected areas often range outside the boundaries where they encounter high-speed vehicles, guns, snares and poisons.

The occurrence of African Wild Dogs in protected areas is described in detail elsewhere (IUCN SSC 2008, 2009). The largest populations inside protected areas occur in Selous G. R. and Ruaha N. P. (Tanzania), Moremi G. R. and Chobe N. P. (Botswana), Kaudom N. P. (Namibia), Kruger N. P. (South Africa), Hwange N. P. (Zimbabwe) and Kafue N. P. (Zambia). Their presence outside protected areas especially where they overlap with commercial game and livestock interests is often viewed as undesirable by the people involved in these developments, although research in N Kenya suggests that coexistence with people and livestock is possible where wild prey remain and where traditional livestock husbandry methods are still practised (Woodroffe *et al.* 2007b).

The important role played by human-induced mortality has two long-term implications. First, it makes it likely that, outside protected areas, African Wild Dogs may well be unable to co-exist with increasing human populations unless better protection and local education programmes are implemented. Second, African Wild Dog ranging behaviour leads to a very substantial 'edge effect', even in large reserves. Simple geometry dictates that a reserve of 5000 km² contains no point more than 40 km from its borders – a distance well within the range of distances travelled by a pack of wild dogs in their usual ranging behaviour. Thus, a reserve of this size (fairly large by most standards) could be, from an African Wild Dog's perspective, all edge. As human populations increase around reserve borders, the risks to African Wild Dogs venturing outside are also likely to increase.

Under these conditions, only the very largest reserves, if they remain unfenced, will be able to provide adequate protection for African Wild Dogs. In South Africa, fencing around quite small reserves has proved moderately effective in keeping dogs confined to the reserve, although, of course, genetic interchange between sub-populations must then be managed artificially, contributing to the high cost of such intensive management (Lindsey *et al.* 2005a).

Even in large, well-protected reserves, or in stable populations persisting largely independent of protected areas (as in N Botswana/NE Namibia), African Wild Dogs live at low population densities. Predation by Lions, and, perhaps, competition with Spotted Hyenas, contribute to keeping African Wild Dog numbers below the level that their prey base could support. Such low population density brings its own problems. The largest areas contain only relatively small populations; for example, the Selous, with an area of 43,000 km² (about the size of Switzerland), is estimated to contain about 800 African Wild Dogs. Most reserves, and probably most African Wild Dog populations, are smaller: for example, the population in Niokolo-Koba N. P. and buffer zones (about 25,000 km², larger than the state of Israel) is likely to be not more than 50–100 dogs. ‘Catastrophic’ events such as outbreaks of epidemic disease may drive small populations to extinction when larger populations have a greater probability of recovery – such an event seems to have led to the extinction of the small population in the Serengeti. Problems of small population size will be exacerbated if, as seems likely, small populations occur in small reserves or habitat patches. As discussed above, animals inhabiting such areas suffer a strong ‘edge effect’. Thus, small populations might be expected to suffer disproportionately high mortality as a result of their contact with humans and human activity (Alexander & McNutt 2010).

African Wild Dogs are legally protected across much of their known former range. However, legal protection is rarely enforced where they still remain and they may have been exterminated in several countries despite stringent legal protection. Outside reserves, legal protection may have questionable value when it concerns a species that comes into conflict with people, often in remote areas with poor infrastructure. Under such circumstances, legal protection may serve only to alienate people from conservation activities.

Virtually no conservation measures have been implemented specifically for African Wild Dogs. The establishment of very large protected areas (e.g. Selous, Kruger) has ensured their persistence in parts of eastern and southern Africa, and maintenance of large wildlife areas remains the highest priority for their conservation. Conservation priorities include: (i) to maintain and expand connectivity of habitat available to African Wild Dogs, particularly in numerous transboundary areas in N Botswana/E Namibia/W Zimbabwe, South Africa/W Mozambique/SE Zimbabwe, N South Africa/SE Botswana/SW Zimbabwe and S Tanzania/N Mozambique; (ii) to work with local people to reduce deliberate killing of African Wild Dogs in and around these areas, and also in smaller populations elsewhere; (iii) to establish effective techniques for protecting small populations from serious infections such as rabies and distemper; (iv) to carry out surveys to establish the status of other potentially important populations, particularly in Algeria, Angola, Central African Republic, Ethiopia, Mozambique and Sudan; and (v) to continue long-term monitoring of ‘sentinel’ populations to identify emerging threats. Re-establishment of extirpated populations through reintroduction currently has a low

priority in most areas, although natural recolonizations should be encouraged (Woodroffe *et al.* 2004).

Measurements

Lycaon pictus

HB (♂ ♂): 1229 (1060–1385) mm, n = 16

HB (♀ ♀): 1265 (1090–1410) mm, n = 15

T (♂ ♂): 354 (320–420) mm, n = 15

T (♀ ♀): 326 (310–370) mm, n = 13

HF c.u. (♂ ♂): 250 (230–260) mm, n = 13

HF c.u. (♀ ♀): 241 (230–250) mm, n = 14

E (♂ ♂): 135 (125–148) mm, n = 15

E (♀ ♀): 130 (125–135) mm, n = 15

WT (♂ ♂): 28.0 (25.5–34.5) kg, n = 12

WT (♀ ♀): 24.0 (19.0–26.5) kg, n = 12

Kruger N. P., South Africa (M. G. L. Mills pers. comm.)

HB (♂ ♂): 981 (880–1068) mm, n = 19

HB (♀ ♀): 991 (930–1045) mm, n = 22

T (♂ ♂): 337 (270–390) mm, n = 19

T (♀ ♀): 330 (310–370) mm, n = 22

HF c.u. (♂ ♂): 221 (170–318) mm, n = 17

HF c.u. (♀ ♀): 216 (200–250) mm, n = 18

E (♂ ♂): 129 (110–145) mm, n = 19

E (♀ ♀): 129 (120–160) mm, n = 21

WT (♂ ♂): 22.7 (18.0–27.0) kg, n = 17

WT (♀ ♀): 22.7 (19.0–26.0) kg, n = 21

Laikipia and Samburu Districts, Kenya (R. Woodroffe pers. obs.)



African Wild Dog *Lycaon pictus*.

Key References Creel & Creel 1995, 1996, 2002; Creel *et al.* 1995b, 1997, 2004; Frame *et al.* 1979; Fuller *et al.* 1992a, b; Kuhme 1964a, b, 1965a, b; McNutt 1995, 1996a, b; Van Lawick & Van

Lawick-Goodall, 1970; Woodroffe *et al.* 1997, 2004.

J. Weldon McNutt & Rosie Woodroffe

GENUS *Vulpes*

Foxes

Vulpes Frisch, 1775. das Natur-System der Vierfüßigen Thiere, p. 15.

The genus *Vulpes* is present in North America, Europe, Africa and Asia, and was introduced to Australasia in the nineteenth century. It is represented by 11 species (Sillero-Zubiri *et al.* 2004a; although see Wozencraft 2005 who included the Arctic Fox *Alopex lagopus*), of which six occur in Africa: Cape Fox *Vulpes chama*, Rüppell's Fox *V. rueppellii*, Fennec Fox *V. zerda*, Pale Fox *V. pallida*, Blanford's Fox *V. cana* and Red Fox *V. vulpes*.

Each species occurs within communities that sometimes comprise several species of fox, and other canids, between which there is probably size-related competition. Cape Foxes are associated with open country and lightly wooded areas in southern Africa (where they may occur alongside the Black-backed Jackal *Canis mesomelas*, Bat-eared Fox *Otocyon megalotis* and African Wild Dog *Lycaon pictus*), particularly in the dry Karoo regions, the Kalahari and the fringes of the Namib Desert. Desert-dwelling foxes are widespread and present throughout their range in North Africa, but in most parts locally rare. The Pale Fox is one of the least-known canid species, typically inhabiting very dry sandy and stony sub-Saharan desert and semi-desert areas, but extending to some extent southwards into moister Guinean savannas where they may occur near human habitation. Well-developed molars suggest Pale Foxes are insectivorous and vegetarian, eating mainly arthropods, berries and wild fruit such as melons. The Rüppell's Fox is widespread in arid biotopes of desert and semi-desert regions of North Africa, the northern limit of which is the northern fringes of the Sahara Desert (and indeed into the Middle East), and are in many respects a scaled-down model of the Red Fox. They may occur alongside Red, Blanford's and Fennec Foxes, and jackals and wolves, and can survive without drinking water; they also live in coastal areas.

The Fennec Fox is the smallest canid (0.8–1.9 kg), although some Pale Fox and Blanford's Fox individuals are equally small. Fennecs have extremely large ears, the greatest ear to body ratio in the Canidae. They subsist in arid desert environments, preferring stable sand dunes. Blanford's Fox is a small fox with an exceptionally long and very bushy tail and, unlike the Fennec, naked foot pads for traction on steep terrain. Confined in Africa to the eastern fringes of the north-east (Peters & Rödel 1994) it is adapted to cliffs and steep, rocky slopes and canyons. Blanford's Fox is sufficiently elusive (and, like the other desert foxes, easily confused with other desert foxes) that its distribution is poorly known, so it may extend further south, into Sudan and Eritrea. It is primarily insectivorous and frugivorous and, in Israel (the only place where it has been studied in depth), eats mainly beetles and the fruits of caper bushes.

Although the most widespread extant canid, and very widely studied in the northern hemisphere, little is known of Red Foxes in North Africa. However, in the Middle East, where they have been studied, they are opportunistic foragers for small mammals, birds,

reptiles and invertebrates together with fruit. Although desert-dwelling Red Foxes are significantly smaller than their Palaearctic conspecifics, they are the largest members of the vulpine guild and hostile to their smaller congeners.

Vulpine foxes are characterized by a rather long, low body, relatively short legs, a long pointed muzzle, large triangular ears and bushy tails that are at least half as long as the head and body. The tail tip is often a different colour from the rest of the coat (e.g. black or white) but the presence of a white tail tag is not, as sometimes supposed, an indicator of the individual's sex; vulpine foxes have black, triangular face marks between eyes and nose. The pupils generally appear elliptical in strong light, and the vulpine skull is flattened in comparison with *Canis* species. Foxes have a pungent odour, characteristic particularly of their urine, while the odour of the Red Fox's supracaudal gland is sometimes characterized as reminiscent of violets. The odour of their anal sacs, in contrast, is strongly acrid, and these glands are evacuated when the animal is frightened, and their secretions probably also routinely coat faeces. Females usually have 6–8 nipples. Although once considered solitary, in some habitats vulpine foxes have territorial family groups of one ♂ and several related ♀♀, some of which may act as non-breeding helpers at the den. However, such groups are probably rare in the low carrying capacity of African arid habitats, although the poorly known Fennec Fox is thought sometimes to occur in larger social groups.

Vulpes has, in the past, been considered a subgenus of *Canis* (Van Gelder 1978), but is now widely regarded as generically distinct. Fennec Foxes have been placed in the genus *Fennecus* by some authors (Ellerman & Morrison-Scott 1951, Stains 1975, Coetzee 1977), but *Fennecus* is now generally included in the genus *Vulpes* (Clutton-Brock *et al.* 1976, Geffen *et al.* 1992d, Wozencraft 1993, 2005).

Thomas (1918) associated *Vulpes pallida* with Rüppell's Fox and the Fennec Fox. Clutton-Brock *et al.* (1976) support this grouping and suggest that these desert foxes are also closely related to the Indian Fox *V. bengalensis* and the Cape Fox. Blanford's Fox and Fennec Fox are an old radiation (3–4 million years) and are sister taxa, forming a monophyletic clade distinct from the other fox-like canids (Geffen *et al.* 1992d). This divergence of the Blanford's and Fennec from other vulpine foxes is thought to have coincided with the appearance of desert regions in the Middle East and North Africa (Wickens 1984). There is a second cluster of vulpine foxes – those that are Red Fox-like; the latter includes many of the Old World species as well as the Kit *V. macrotis*, Swift *V. velox* and Arctic Foxes (only recently evolved in the mid-Pleistocene; 0.5 mya).

Claudio Sillero-Zubiri & David W. Macdonald

Vulpes cana BLANFORD'S FOX (ROYAL FOX, HOARY FOX)

Fr. Renard royale; Ger. Afghanfuchs

Vulpes cana Blanford, 1877. J. Asiat. Soc. Bengal 46 (2): 321. Gwadar, Baluchistan, Pakistan.Blanford's Fox *Vulpes cana*.

The specific epithet *cana* (grey) refers to the colour of the species' pelage.

Taxonomy Monotypic. Genetic analysis has revealed that Blanford's Fox and the co-existing desert species, the Fennec Fox *Vulpes zerda*, are sister taxa forming a monophyletic clade distinct from the other fox-like canids (Geffen *et al.* 1992d). There is a single published record of this species' occurrence in Africa from Egypt (Peters & Rödel 1994), but its wider distribution on the continent is likely (Geffen *et al.* 1993, Peters & Rödel 1994). Accordingly, most data in this species account are based on studies of animals from its non-African populations, mainly from Israel. Synonyms: *nigricans*. Chromosome number: not known.

Description Small beige fox with slender face and pointed muzzle, and bushy and relatively long tail that almost equals its body length. Head orange-buff, especially in the winter coat, with black lacrimal stripe from the internal angle of the eye to the anteromedial part of the upper lip, extending over the muzzle to the chin. Iris almost as dark as the pupil. Ears pale brown on both sides, or grey on the back, with long white hairs along the anteromedial border. Pelage of body and tail brownish-grey, fading to pale yellow on belly, with dark mid-dorsal band on back and tail and distinctive dorsal black spot at base of tail, which usually has a black tip (in some individuals it is white). The fore- and hindfeet are dorsally pale yellowish-white, while posteriorly they are dark grey. Feet have blackish-naked pads, and claws are curved, sharp and semi-retractile. Winter coat is soft and woolly with dense, black underwool, dorsally sprinkled with white-tipped hair. Summer coat is less dense, fur is paler coloured and white-tipped hairs are less apparent. Juveniles have similar markings as adults, but coat is darker and more greyish. Slight sexual dimorphism in size, and some body measurements, but otherwise sexes are alike (Harrison & Bates 1991, Geffen 1994, Peters & Rödel 1994). Females have three pairs of nipples.

Skull is typically vulpine with noticeably slender rostrum and long and thin nasal bones. Postorbital processes well developed. Braincase is relatively narrow and weakly ridged; zygomatic width averages

*Vulpes cana*

about 50 mm. Tympanic bullae are relatively smaller than those of Rüppell's Fox *V. rueppellii*.

Geographic Variation The scarcity and scattered nature of records of Blanford's Fox from the species' large distribution range are insufficient for a sensible evaluation of possible causes of variation seen in some characters (size, pelage colour and markings) and their significance. Pelage colour of foxes from Iran and further eastward is predominantly grey, whereas in animals from the Arabian Peninsula, Israel and the one from Egypt the ground colour is beige. Animals from SW Arabia frequently have a white tail tip. Genetic data are necessary to clarify the situation.

Similar Species

Vulpes zerda. Smaller, with relatively shorter tail and larger ears. Sandy deserts and semi-deserts of North Africa from Morocco and Mauritania to Egypt and the Sudan.

V. rueppellii. Slightly larger, with relatively shorter tail and larger ears; long hair totally concealing the naked footpads. Widespread in desert and semi-desert regions of North Africa (north of 17° N) from Morocco and Mauritania to Egypt and Somalia.

V. vulpes. Larger, with relatively shorter tail and smaller ears. Coastal belt of North Africa from the hills of Morocco to Egypt and south along the Nile R. to N Sudan.

Distribution The only record of the species from Africa hitherto documented is an adult ♂ from Wadi Qiseib (29° 24' N, 32° 29' E), Governate Suez, Egypt (Peters & Rödel 1994), collected in 1988.

The closest records are from the S Sinai Peninsula (Jabal Umm Shawmar: 28° 22' N, 33° 55' E, Geffen *et al.* 1993; Jabal Sirbal: 28° 39' N, 33° 37' E, T. Wachter pers. comm.). A wider distribution than presently documented, along the western shore of the Red Sea, is likely (Geffen *et al.* 1993, Geffen 1994, Peters & Rödel 1994).

Main range is in arid mountainous regions from the Middle East eastward to Afghanistan and Pakistan and then north-eastward to Turkmenistan and Tajikistan (Geffen 1994, Peters & Rödel 1994, Geffen *et al.* 2004).

Habitat Mountainous desert ranges with steep, rocky slopes, canyons and cliffs but also occurs on various rock or gravel formations, irrespective of altitude (−400–3000 m). For example, in the United Arab Emirates (UAE) the southern Hajar, the Shimaliyya and the Rus Al Jibbal Mountains are the typical habitat of Blanford's Foxes.

Abundance Fairly common in SE Israel, the only region where the species has been studied in detail (Geffen 1994). An ongoing study in the UAE indicates that the species is fairly common in the eastern parts (Smith *et al.* 2003, C. Drew pers. comm). Abundance in other parts of the species' range is unknown. In Israel, 0.5–2 individuals/km² was recorded for the Judean and S Negev Deserts (Geffen 1994).

Adaptations Mendelssohn *et al.* (1987) described the jumping ability of Blanford's Fox as astonishing; captive individuals bounced from one wall to another or jumped to the highest ledges (2–3 m) in their cage with remarkable ease and as part of their normal movements. In the field, these foxes were observed climbing vertical, crumbling cliffs by a series of jumps up the vertical sections. Blanford's Fox has a relatively long, bushy tail, which is probably an important counter-balance during jumps and may function like a parachute (Geffen *et al.* 1992c). The small feet, naked pads and curved claws provide sure footing even on the narrow ledges of a vertical wall.

Blanford's Foxes in Israel are strictly nocturnal. Onset of activity is governed largely by light conditions, and closely follows sunset. Animals were active ca. 8–9 h/night, independent of duration of darkness (Geffen 1994).

Daily energy expenditure of free-ranging Blanford's Foxes near the Dead Sea was 0.63–0.65 kJ/g/day, with no significant seasonal difference (Geffen *et al.* 1992a). Mean rate of water intake is significantly higher in summer (0.11 mg/l/day) than in winter (0.08 mg/l/day). These foxes maintain water and energy balance on their diet of invertebrates and fruits, and forage more for water than for energy needs. In Israel these foxes consume more fruit during the hot summer, which compensates for deficiencies in body water (Geffen *et al.* 1992a, b).

Dens used by Blanford's Foxes in Israel usually were natural cavities under a large rock or boulder pile on a mountain slope, and the animals never dug burrows. Dens were used both for rearing young during spring and for day-time resting throughout the year. Frequent changes in location of den from day to day were more common in summer and autumn (Geffen & Macdonald 1992).

Foraging and Food Primarily insectivorous (mainly beetles, grasshoppers, ants, termites) and frugivorous (Ilani 1979, Geffen *et*



Lateral view of skull of Blanford's Fox *Vulpes cana*.

al. 1992b). Plant food in Israel consists mainly of the fruit of two caperbush species, *Capparis cartilaginea* and *Capparis spinosa*; fruits and plant material of *Phoenix dactylifera*, *Ochradenus baccatus*, *Fagonia mollis* and various species of Gramineae also were eaten. Remains of vertebrates were present in ca. 10% of faecal samples analysed. Diet differed significantly between two sites examined in Israel, but seasonal and individual differences were not detected (Geffen *et al.* 1992b).

Almost always forages solitarily (92% of 463 observations; Geffen *et al.* 1992b), only occasionally in pairs. Animals forage by searching between rocks in a small area, sniffing and looking under large stones and occasionally digging a shallow scrape; standing near a bush for a few seconds, alert with ears erect, prior to circling the bush or pouncing upon prey within it; or short, fast sprints after small terrestrial or low-flying prey. Average distance (\pm S.D.) travelled per night in Israel was 9.3 ± 2.7 km, and size of nightly home-range averages 1.1 ± 0.7 km² (Geffen & Macdonald 1992); there were no significant seasonal or sexual differences in duration of nightly distance travelled, or nightly home-range. Food caching is rare or absent, contrary to other fox species (Geffen *et al.* 1992b).

Social and Reproductive Behaviour Based on studies of Blanford's Foxes in Israel, the species lives in monogamous pairs in territories of ca. 1.6 km² with minimal overlap. During winter and spring, both members of a pair frequently occupy the same den, or adjacent dens at the same site, while during summer and autumn they often den in separate locations. Locations and configurations of home-ranges remained stable during a two-year study period. Shifts in the location of the home-range were observed only once following the death of a pair member. Three of five territories contained one, non-breeding yearling ♀ during the mating season, but there was no evidence of polygyny.

There are no specific data on details of social and reproductive behaviour and behaviour of young. Adult Blanford's Foxes have never been observed to carry food to the young and only one den was found with remains of prey at the entrance. Observations suggest that food is not regurgitated to the young, as in other small canids. There is no indication that the ♂ provides food either to the ♀ or to the cubs. Therefore, it appears that the direct contribution to survival of the young by any individual (other than the mother) probably is minimal. Young start to forage at about two months, accompanied by one of the parents, and at three months start to forage alone. Offspring often remain on their natal home-range until autumn (Oct–Nov) (Geffen & Macdonald 1992).

Two types of vocalizations have been recorded in adults: a high-pitched bark against intruders like Leopards *Panthera pardus* and humans and a greeting scream between pair members.



Blanford's Fox *Vulpes cana* action drawing of 'tail fluff'.

Reproduction and Population Structure Females are monoestrous and, in Israel, come into heat during Jan–Feb. Gestation period is ca. 50–60 days, and litter-size is one to three pups. Neonates are born with soft, black fur and weigh about 29 g at birth. Females have two to six active teats, and young are entirely dependent upon mother's milk until they begin to forage for themselves. Lactation period is 30–45 days. Based on repeated weighing of three young born in captivity, body mass of subadult (700–900 g) is reached in ca. 3–4 months. Sexual maturity is reached at 10–12 months of age (Mendelssohn *et al.* 1987, Geffen 1994).

Although they may live to four to five years in the wild, average longevity is 1.9 years; captives have lived to six years of age (Geffen 1994). Mortality rate, as likelihood of survival to the next month at two study sites in Israel, was 0.972 and 0.944.

Predators, Parasites and Diseases Primary causes of natural mortality are old age and rabies. Only a single known case of mortality

from predation was recorded, where the predator was suspected to be a Red Fox (Geffen 1994). Other likely predators include larger carnivores, such as Leopards. No other diseases have been documented (Geffen 1994). Individuals in poor body condition often have ticks.

Conservation IUCN Category: Least Concern. CITES: Appendix II.

In Africa, the known distribution range is not within any protected area and the species has no legal status. It is not trapped in Egypt, and no information is available on mortality causes or the status of this population. Elsewhere, the species is threatened by habitat loss.

Measurements

Vulpes cana

HB (♂ ♂): 427 (385–470) mm, n = 19

HB (♀ ♀): 411 (385–450) mm, n = 17

T (♂ ♂): 324 (260–355) mm, n = 19

T (♀ ♀): 317 (290–340) mm, n = 17

HF c.u. (♂ ♂): 92 (80–100) mm, n = 19

HF c.u. (♀ ♀): 93 (82–110) mm, n = 17

E (♂ ♂): 80 (72–85) mm, n = 19

E (♀ ♀): 78 (74–87) mm, n = 17

WT (♂ ♂): 1.1 (0.9–1.3) kg, n = 19

WT (♀ ♀): 1.0 (0.8–1.4) kg, n = 17

Ein Gedi and Eilat, Israel (Geffen *et al.* 1992c)

Measurements of the one adult ♂ specimen recorded from Africa (Peters & Rödel 1994) are within the ranges of the individuals from Israel.

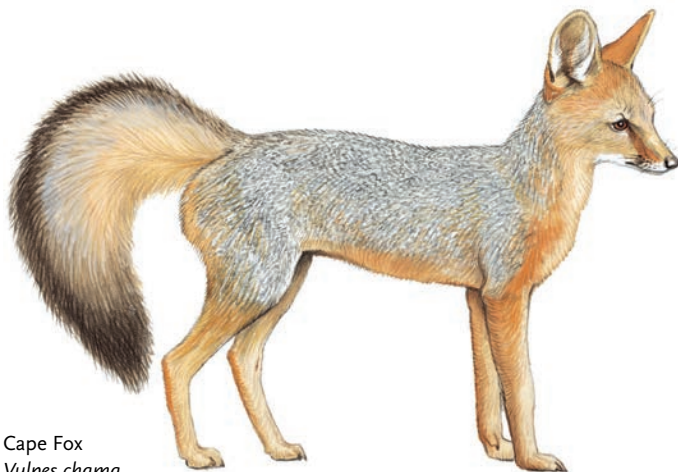
Key References Geffen 1994; Geffen & Macdonald 1992; Geffen *et al.* 1992a, b, c, d, 2004; Peters & Rödel 1994.

Eli Geffen & Gustav Peters

Vulpes chama CAPE FOX (SILVER FOX)

Fr. Le Renard du Cap; Ger. Kapfuchs

Vulpes chama (A. Smith, 1833). S. Afr. Quart. J. ser. 2, 2: 89. 'Namaqualand and the country on both sides of the Orange river', determined by Shortridge (1942: 41) as 'Port Nolloth, Little Namaqualand' [South Africa, ca. 29°15' N, 16°52' E].



Cape Fox
Vulpes chama.

Taxonomy Monotypic (Meester *et al.* 1986). Synonyms: *hodgsoni*, *variegatoides*. Chromosome number: not known.

Description The smallest canid and only true fox occurring in southern Africa. Slender build with bushy, black-tipped tail. Upper parts grizzled silver-grey, with lower limbs, face and back of ears reddish-brown to pale tawny-brown; upper chest fawny-red, with underparts off-white to pale fawn, often with a reddish-brown tinge. Head, and back of the long ears, reddish-fawn with some freckling of white hairs on face; front of ears also fringed with white hairs. Upper region of front legs reddish-yellow, paler towards paws, with a dark brown patch on backs of thighs of hindlegs. Overall, body pelage soft, with dense underfur of wavy hairs about 25 mm long. Hairs grey at base, buffy above. Underfur overlaid by thick guard coat, with individual hairs averaging 45 mm in length, predominantly black but with light-

coloured bases and banded silver. Slightly longer black tactile hairs scattered through the body coat. During the moulting period, from Oct to Dec, much of the guard coat is lost, giving the animals a rather dull and 'naked' appearance. Tail very bushy with individual hairs 55 mm long, with buffy-white bases and broadly black or dark brown towards the tips. Upper surfaces of paws pale fawn to reddish, with sharp curved claws, ca. 15 mm long on the curve, on the front feet. Pronounced hair growth between the foot-pads. Males slightly larger than ♀♀. Females have one pair inguinal and two pairs abdominal nipples.

Skull narrow and elongated (about 115 mm in length), with narrow rostrum and weak zygomatic arch. Mandible narrow and lightly built; bullae large relative to size of skull. Canines long, slender and strongly curved and the two upper molars are broad as an adaptation to crushing.

Geographic Variation None recorded.

Similar Species

Otocyon megalotis. Broadly sympatric in southern Africa. Similar in size, but more bushy silvery-grey to beige pelage; very large dark-backed ears; legs black; bushy tail black above and at tip.

Distribution Endemic to Africa, and largely restricted to southern Africa, being extralimital only in extreme SW Angola, to about 15° N (Crawford-Cabral 1989a). Widespread in arid and semi-arid C and W Namibia, Botswana and South Africa, but also occurs in areas with denser vegetation and receiving higher rainfall, such as fynbos biome of the Western Cape (Skinner & Chimimba 2005).

Current Distribution Has expanded its range over recent decades to the south-west, where it reaches the Atlantic and Indian Ocean coastlines (Stuart 1981). Expansion through the Eastern Cape of South Africa has been documented (Coetzee 1979). Status of the species in Swaziland is uncertain, but there are sight records from Nhlanguano and Mhlambanyatsi (Monadjem 1998); it occurs in adjacent regions of NW KwaZulu–Natal in South Africa (Rowe-Rowe 1992a). Not yet recorded from Lesotho, but may occur (Lynch 1994). Previous records of its occurrence in W Zimbabwe (Roberts 1951, Coetzee 1977) and Mozambique (Travassos Dias 1968) remain unsubstantiated, and it is unlikely that these records are valid.

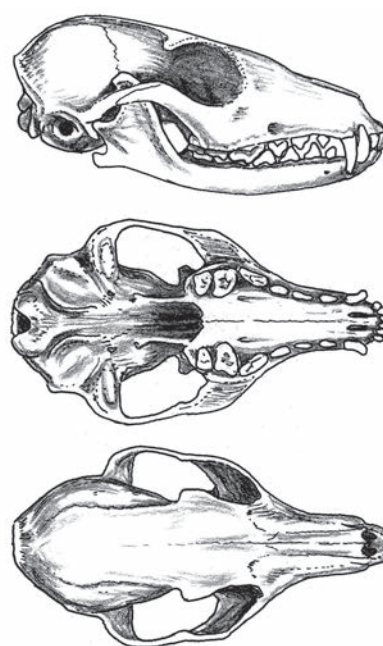
Habitat Mainly open country, including grassland, grassland with scattered thickets, arid scrub and lightly wooded areas in a precipitation range of between 100 and 500 mm per annum, although in KwaZulu–Natal they have been recorded between 1000 and 1500 m above sea level, where annual rainfall is roughly 720–760 mm (Rowe-Rowe 1992a). Prefer open scrub country and grassland, and are particularly associated with dry pans in arid Karoo, Kalahari and fringes of the Namib Desert. Also penetrates moderately dense scrub of Lowland Fynbos in SW South Africa, as well as agricultural lands (Stuart 1981), lying up in pockets of natural vegetation by day. Along the eastern flank of the Namib Desert and C South Africa they occupy rock outcroppings, inselbergs and kopjes, ranging out onto the plains at night (Stuart 1975, O. B. Kok & J. A. J. Nel unpubl.). In Botswana, they have been recorded from *Acacia*-scrubland, short grassland and especially on the fringes of shallow seasonal pans, as well as cleared and overgrazed areas (Smithers 1971).



Vulpes chama

Abundance Common to fairly abundant across most of its range, although problem animal control activities have resulted in population reductions in some areas. In the Free State, South Africa, an average density of 0.3 foxes/km² was estimated (total population of 31,000) (Bester 1982). Annual offtake from problem animal control operations averaged 16% up to 1985, with no obvious declines in overall populations (Bester 1982). Range and numbers have increased in SW and E South Africa (Stuart 1981).

Adaptations Large ears, bullae and auditory meatus suggest enhanced detection of prey and predators. Long rostrum and long,



Lateral, palatal and dorsal views of skull of Cape Fox *Vulpes chama*.

thin canines would aid capture of small prey, such as rodents. Molar teeth high cusped, facilitating crushing of insects. Thick coat aids thermoregulation in exposed habitats at low ambient temperatures during winter nocturnal foraging. Nocturnal activity could serve to reduce predation, especially by larger diurnal raptors, and coincides with the activity period of small rodents, an important prey. Changing dens could avoid accumulation of parasites and confuse predators (Bester 1982). The bushy tail serves as a counterbalance to the body when a fox makes sudden sharp turns during a hunt or when trying to evade predators. This accounts for the colloquial Afrikaans name *draaijakkals* (= 'jackal that makes turns').

Foraging and Food Omnivorous. Prey includes small rodents (murids), hares, reptiles, birds and invertebrates (e.g. arachnids, beetles and termites); Cape Foxes also eat some wild fruits (Bothma 1966b, 1971c, Lynch 1975, Stuart 1981, Bester 1982, Kok 1996, Kok & Nel 2004, Skinner & Chimimba 2005). In most studies, rodents are the most important mammal prey, with beetle larvae and adults, and grasshoppers predominating among the invertebrates. The largest wild prey species recorded include hares (*Lepus* spp.) and the Southern African Springhare *Pedetes capensis* (Lynch 1975) and Steenbok *Raphicerus campestris* (Kok & Nel 2004). Birds and reptiles are occasionally eaten. Where Cape Foxes coexist with possible competitors, such as Black-backed Jackals *Canis mesomelas*, some separation in prey use occurs (Bothma *et al.* 1984, Kok 1996, Kok & Nel 2004). Prey use seems to reflect prey availability, and seasonal and yearly variation in prey use occurs, with murids being common in spring and summer, while other mammals predominate in winter (Bester 1982). When six weeks old, cubs already hunt insects (Bester 1982).

Cape Foxes also scavenge, eat carrion and occasionally take young lambs and goat kids less than three months (Stuart 1981, Bester 1982), but not poultry. Although some authors (Roberts 1951, Bothma 1966b) recorded no evidence of stock killing by Cape Foxes in their particular study areas, the seasons when samples were taken could have influenced their conclusions, as the majority of sheep farmers follow fixed lambing times. The highest incidence of lamb losses to the Cape Fox has been documented from the Free State, where Bester (1982) recorded that they may take 4.5% of the lamb crop; lambs killed by the Cape Fox are seldom older than four months.

Food is located mainly by hearing and smell. Animals forage singly (Bester 1982, Mills 1997), but occasionally may gather in loose groups at an abundant food source (Stuart 1981). Foraging is almost exclusively nocturnal, with activity peaks shortly after sundown and just before dawn. Much prey is obtained by rapid digging with the front paws, often preceded by intensive listening bouts. Caching prey is common (Bester 1982).

Social and Reproductive Behaviour Cape Foxes live in monogamous pairs (Bester 1982), but forage singly. Interactions between adults are rare; only 2.5% of time is spent in social contact (Bester 1982). Home-ranges in the Free State vary from 1.0 to 4.6 km² and overlap widely in some parts of the range (Bester 1982), but the area around the den forms a territory. In some parts of the range, such as the SW Kalahari, group territories can occur.

A series of behaviours eliminates aggression, but allogrooming is absent. A submissive crouch and inguinal presentation occur

(Le Clus 1971). Cubs exhibit a range of play behaviour, including solitary play, eliciting play from siblings, and to express dominance and submission (Bester 1982). Vocalizations (a high-pitched howl and a bark) are more common during the breeding season and when cubs disperse (Bester 1982). Facial expressions, but not tail positions, play a prominent role in visual communication (Bester 1982).

Young are born in burrows, which the adults may excavate on their own, enlarge existing ones of other species (such as Southern African Springhare *P. capensis* or South African Ground Squirrel *Xerus inauris*) or use alternatives such as rock crevices or even dense vegetation (Stuart 1981, Bester 1982). M. G. L. Mills (pers. comm.) has recorded dens with two litters in the S Kalahari, and Bester (1982) recorded eight pups in one den in the Free State, which is perhaps an indication of a similar occurrence. The male can provision the ♀ just after birth of pups, and both parents – especially the ♀ – provision young. Both parents will defend the pups against potential predators. The ♀ may bark when a potential predator approaches a den occupied by pups (Bester 1982). Helpers are absent or rare.

Reproduction and Population Structure Breeding appears to be aseasonal in some areas, but strongly seasonal in others. The majority of births take place in spring and summer (Aug to Oct), towards the end of the dry season when insect and rodent numbers are low. Smithers (1971) recorded a gravid ♀ in Oct, while births have been recorded in Aug and Sep in W South Africa (Stuart 1981), and Aug–Oct, with a peak in Sep, in the Free State (Bester 1982). Gestation lasts 51–52 days (Brand 1963). Litter-size in the Free State and Kalahari is much the same, with a mean of 2.9 (range 1–6, n = 16) and 2.8 (range 2–4, n = 5), respectively (Bester 1982). One litter is born per year. Weaning takes place at about 16 weeks and pups disperse at around five months of age (Bester 1982). Longevity is unknown, but unlikely to exceed six or seven years in the wild.

Predators, Parasites and Diseases Predators include Black-backed Jackals, Lions *Panthera leo*, Leopards *Panthera pardus* (see Mills 1984), Caracals *Caracal caracal* and Ratels *Mellivora capensis*. Some of these predators, such as Black-backed Jackals, are also competitors, and some separation in prey use is evident where they co-exist with these species (Bothma *et al.* 1984, Kok 1996, Kok & Nel 2004).

The following parasites have been recorded from animals in South Africa: fleas (*Ctenocephalides conatus* and *Echidnophaga gallinacea*), ticks (*Haemaphysalis leachi*, *H. silacea*, *H. zumpti*, *Rhipicephalus capensis*, *R. evertsi*) and tapeworms (*Taenia endotheoracicus*, *Joyeuxiella* sp. and *Mesocestoides* sp.) (Stuart 1981, Horak *et al.* 2000). Cape Foxes have a very low incidence of rabies, compared with other southern African canids (Swanepoel *et al.* 1993).

Conservation IUCN Category: Least Concern. CITES: Not listed.

The Cape Fox suffers direct and indirect mortalities from problem animal control activities, particularly in South Africa and S Namibia. For example, in the Free State 4000 of these foxes were killed during organized control operations in 1974, and an average of 2000–3000 in each subsequent year (Bester 1978). However, direct and indirect problem animal control measures do not seem to have had a major impact on populations of the Cape Fox, even though they have resulted in declines in some areas. The illegal but widespread

and indiscriminate use of agricultural poisons on commercial farms poses the greatest threat. Cape Fox have several key populations in national parks and nature reserves, including Etosha and Skeleton Coast National Parks (Namibia), Central Kalahari G. R. (Botswana), Kgalagadi Transfrontier Park (South Africa and Botswana), and Addo, Augrabies Falls, Bontebok, Golden Gate, Karoo, Mountain Zebra and West Coast National Parks (South Africa) (Stuart & Stuart 2004). Expansion of semi-arid karroid vegetation has resulted in range extensions.

Measurements

Vulpes chama

HB (♂ ♂): 554 (450–610) mm, n = 21

HB (♀ ♀): 553 (510–620) mm, n = 15

T (♂ ♂): 348 (300–406) mm, n = 25

T (♀ ♀): 338 (250–390) mm, n = 17

HF c.u. (♂ ♂): 131 (123–140) mm, n = 20

HF c.u. (♀ ♀): 126 (115–140) mm, n = 17

E (♂ ♂): 98 (90–110) mm, n = 22

E (♀ ♀): 97 (87–105) mm, n = 17

WT (♂ ♂): 2.8 (2.0–4.2) kg, n = 17

WT (♀ ♀): 2.5 (2.0–4.0) kg, n = 11

Northern Cape, Western Cape and Eastern Cape, South Africa (Stuart 1981)

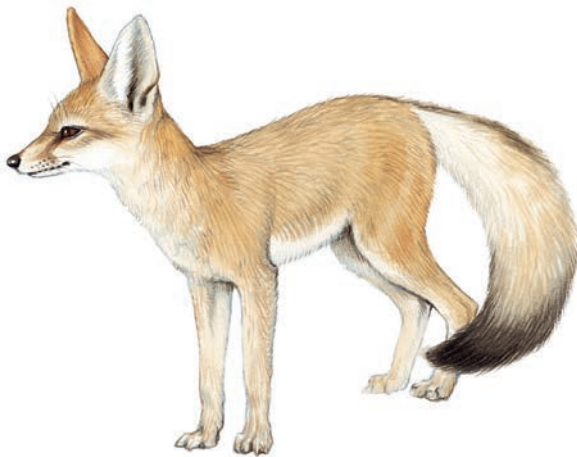
Key References Bester 1982; Bothma 1966b, 1971c; Skinner & Chimimba 2005; Stuart 1981.

Jan A. J. Nel, Chris Stuart & Tilde Stuart

Vulpes pallida PALE FOX (PALLID FOX, AFRICAN SAND FOX)

Fr. Renard pale; Ger. Blassfuchs

Vulpes pallida (Cretzschmar, 1827). In: Rüppell, Atlas Reise Nordl. Afr., Zool., Säugeth. (dated 1826), 1 (2): 33, pl. 11. 'Kordofan' [Sudan].



Pale Fox *Vulpes pallida*.

Taxonomy Thomas (1918) associated *V. pallida* with other desert foxes Rüppell's Fox *V. rueppellii* and Fennec Fox *V. zerda*, a grouping supported by Clutton-Brock *et al.* (1976), who suggest these desert foxes are also closely related to the Bengal Fox *V. bengalensis* and Cape Fox *V. chama*. Five races have been described, four of which are listed here, the subspecies *V. p. cyrenaica* being extralimital (following Coetzee 1977). However, there is insufficient specimen material available to assess the validity of the described forms, and according to Rosevear (1974) variation may be clinal. Synonyms: *cyrenaica*, *edwardsi*, *harterti*, *oertzeni*. Chromosome number: not known.

Description Small very pale fox with longish legs and large ears. Face pale with black eye-rings, relatively long whiskers and elongated muzzle. Large ears rounded at tip, white on inside and rufous-brown on outer surface. Creamy-white to sandy-fawn body, back sometimes flecked with black or rufous, darker mid-dorsal line. Flanks paler than dorsal pelage, merging into white or buffy-white undersides, rufous legs. Coat relatively thin and short. Tail long and



Vulpes pallida

bushy, at least half as long as body, reddish-brown with distinctive black tip and a dark patch above tail gland.

Small skull with a relatively short maxillary region, and well-developed upper molars (Clutton-Brock *et al.* 1976). Bullae are slightly larger, the nasals appreciably longer, and the carnassials 1–3 mm shorter than in Rüppell's Fox (Rosevear 1974).

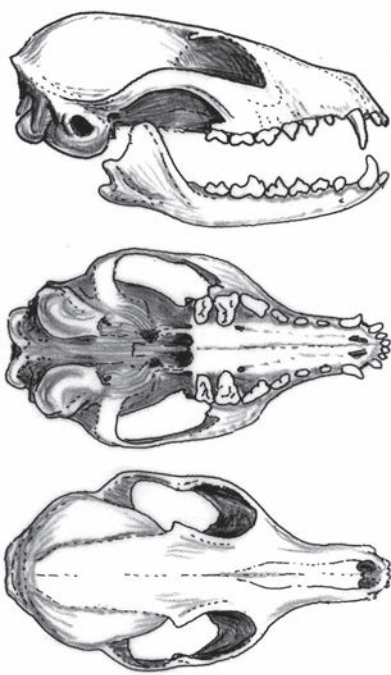
Geographic Variation

V. p. pallida: Sudan.

V. p. edwardsi: Mali, Senegal.

V. p. harterti: Burkina Faso, NW Nigeria.

V. p. oertzeni: Chad, Niger, NE Nigeria, N Cameroon.



Lateral, palatal and dorsal views of skull of Pale Fox *Vulpes pallida*.

Similar Species

Vulpes vulpes. Sympatric only in N Sudan. Larger, with shorter legs and ears dark backed and more pointed.

V. zerda. Saharan distribution, but sympatric in northern part of Pale Fox's range. Smaller with proportionately longer ears (but shares dark tail tip and dark patch above tail gland).

V. rueppellii. Northern limit in Africa is the northern fringes of the Sahara Desert. Tail lacks black tip (usually white), with larger ears.

Distribution Endemic to Africa; present in the semi-arid Sahel, south of the Sahara, reaching the northern Guinean savanna zones. Ranges from S Mauritania, Senegal and Gambia through Niger and N Nigeria to Sudan, Somalia and the Red Sea. Presence in Guinea remains to be confirmed (Barnett & Prangley 1997).

Habitat Typically inhabiting very dry country within an ecological band lying between true desert and the sub-Saharan savannas. Habitat includes sandy and stony marginal deserts, semi-deserts and savannas, and extending to some extent southwards into moister Guinean savanna areas. May occur near human habitation and cultivated fields where food is more readily available than in natural habitats (Rosevear 1974).

Abundance One of the least known African canids. Widespread, and may be locally common.

Adaptations Pale Foxes tolerate heat well, although they are unable to bear completely waterless conditions. They can survive lengthy hot, dry seasons, presumably on fruits and the residual moisture of their prey.

Foraging and Food Well-developed molars suggest Pale Foxes are essentially insectivorous and herbivorous, eating mainly arthropods,

berries, and wild fruit such as melons, but also vertebrates. In Niger, they consumed (in order of frequency of occurrence in faecal samples) arthropods (Coleoptera, Orthoptera, Scorpiones), small mammals (gerbils and jerboas), plants, reptiles and birds. Remains of agama lizards, and a Chestnut-backed Sparrow-Lark *Eremopterix leucotis* were found outside a burrow in Chad. Pale Foxes forage solitarily at night, moving between grass tussocks looking for insects (C. Sillero-Zubiri pers. obs.). Pairs at the burrow left in different directions to forage in separate areas of their home range.

Social and Reproductive Behaviour Active from dusk till dawn, resting during the day in extensive burrows. Little is known of their social organization, but they have been observed individually and in pairs and living gregariously at communal burrows (Rosevear 1974, Coetzee 1977, C. Sillero-Zubiri pers. obs.). A group of one ♀ and two ♂ got along amicably in captivity (Nowak 1999).

Reproduction and Population Structure Reproduction in Niger took place in spring (Apr–Jun), just before the rainy season (C. Sillero-Zubiri pers. obs.). A captive ♀ gave birth to a litter of four in Jun (Bueler 1973). Young are born in extensive self-dug burrows, 2–3 m deep and up to 15 m long, opening into inner chambers lined with dry vegetation. Burrows may be aggregated into 'towns', consisting of 15–20 openings in a 15 m x 15 m area (C. Sillero-Zubiri pers. obs.). Faecal latrines are located just outside these burrows. Burrow systems are often near villages or under tracks (Dorst & Dandelot 1970, Nowak 1999). Gestation period in captivity is 51–53 days. Three to six young are born, and weaning takes 6–8 weeks. A captive ♂ lived to 16 years of age (Weigl 2005).

Predators, Parasites and Diseases Uncertain, but may be susceptible to canid-related diseases such as rabies. Probably taken by birds of prey (skulls were found in the nest of a kite near Khartoum; Anderson 1902), particularly nocturnal species such as Pharaoh Eagle-owl *Bubo ascalaphus*.

Conservation IUCN Category: Data Deficient (will be moved to Least Concern in 2012). CITES: Not Listed.

No major threats known, although they may be persecuted locally, since they are known to kill domestic fowl (Rosevear 1974). Present in several protected areas, including Ouadi Rimé–Ouadi Achim Faunal Reserve in Chad. This is the least known of all the canids, and studies on distribution, status and ecological requirements are needed.

Measurements

Vulpes pallida

HB: 440 (415–475) mm, n = 7

T: 207 (170–230) mm, n = 7

E: 62 (55–71) mm, n = 5

WT: 1.2 (1.0–1.5) kg, n = 6

Niger (C. Sillero-Zubiri pers. obs.)

Key References Coetzee 1977; Dorst & Dandelot 1970; Happold 1987; Rosevear 1974; Sillero-Zubiri 2004.

Claudio Sillero-Zubiri

Vulpes rueppellii RÜPPEL'S FOX (SAND FOX, RÜPPEL'S SAND FOX)

Fr. Renard famélique (Renard de Rüppell); Ger. Rüppellfuchs (Sandfuchs)

Vulpes rueppellii (Schinz, 1825). In: G. Cuvier, Das Thierreich 4: 508. 'Vatherland Dongola' [Sudan].



Rüppell's Fox *Vulpes rueppellii*.

Taxonomy This species is closely related to the Red Fox *Vulpes vulpes* and the extralimital Bengal Fox *Vulpes bengalensis* and Arctic Fox *Alopex lagopus* (Geffen *et al.* 1992a). The specific name has been misspelled in various ways (e.g. *V. rüppelli*: Ellerman & Morrison-Scott 1951), and is most commonly cited as *V. rueppelli* (Coetsee 1977, Corbet 1978). The specific name *rueppellii* is the genitive form of 'rueppellius', the latinization of Rueppell's name (Grubb 2004a, P. Grubb pers. comm.). Many subspecies have been described (e.g. Allen 1939, Coetsee 1977), but the variability of specimens seems high (Hüfnagl 1972, Rosevear 1974) and the species has been considered monotypic (Larivière & Seddon 2001), which is the approach provisionally followed here. Synonyms: *caesia*, *cufrana*, *cyrenaica*, *famelicus*, *sabaea*, *sabbar*, *somaliae*, *zarudnyi*. Chromosome number: $2n = 40$, with X chromosome metacentric and Y chromosome very small (Matthey 1954).

Description A small fox, with broad ears, short legs and bushy tail. Head colour beige to pale sand. Ears and face usually pale, with most animals having black whisker patches running up to the eye (variations can occur). Lacks darker markings on the back of the ears. Colour of the back, flanks, upper thigh and tail (except tip) varying from pale sandy to greyish and even sometimes reddish, with a more or less silvery sheen due to black speckling. Flanks and ventral pelage usually paler. Legs beige to fawn in colour. Fur very fine and soft with a thicker, darker coat in winter and a lighter colour coat in summer. Plantar and digital pads almost completely covered by hairs. Tail full and bushy, tip usually white. Males larger than ♀♀. Females have three pairs of nipples.

Skull not unlike a small version of the Side-striped Jackal *Canis adustus*, but without such well-developed occipital crests. Braincase rounded, postorbital processes blunt and narrow, zygomatic arches strong and bullae relatively large (though not so expanded as in the Fennec Fox *Vulpes zerda*) (Rosevear 1974).

Geographic Variation Rosevear (1974) remarked on the considerable uniformity of appearance, despite the animal's wide east-westerly range, noting that it would be difficult to find any significant distinction between specimens from Afghanistan and the Hoggar Mountains in Algeria (with the possible exception of specimens from north-east Africa, which may prove to be slightly smaller).

Similar Species

Vulpes zerda. Much smaller, with shorter legs; paler and finer fur; very large ears; shorter and black-tipped tail; skull with larger tympanic bullae. Saharan distribution.

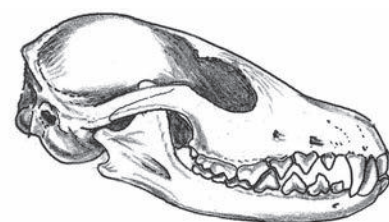
V. pallida. Size slightly smaller; tip of tail black. Confined to Sahelian regions, until the southern edge of Sahara.

V. vulpes. More robust and larger, with longer limbs and tail; ears shorter, with back of ears dark; white tail tip. Confined to North Africa, until the northern edge of Sahara, and Nile Valley.

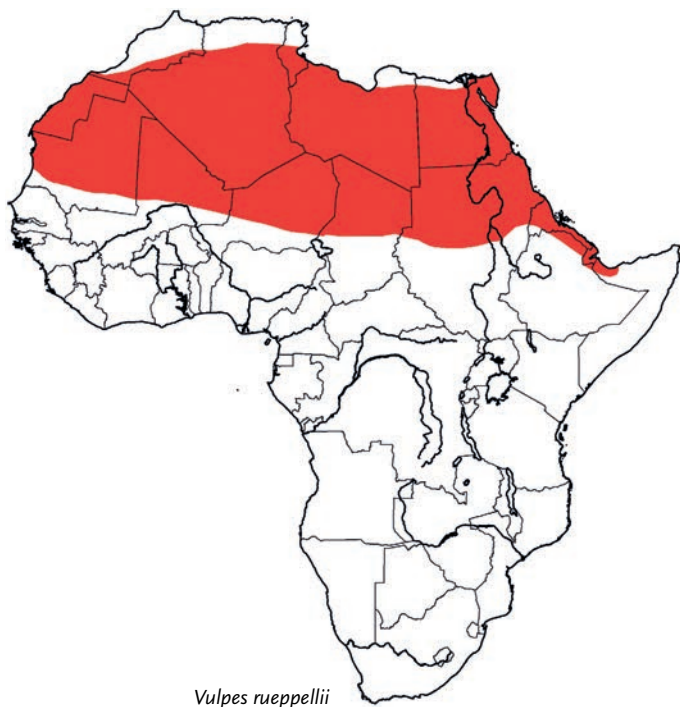
V. cana. Seems to prefer rocky and even precipitous mountain slopes; tail very bushy and long. Mostly Asiatic, but known in S Sinai and E Egypt (Saleh & Basuoni 1998).

Distribution Widespread in desert and semi-desert regions of North Africa (north of 17° N) from Morocco and Mauritania to Egypt (including Sinai) and north-east Africa, south to NW Somalia (Valverde 1957, Hüfnagl 1972, Rosevear 1974, Osborn & Helmy 1980, Aulagnier & Thévenot 1986, De Smet 1988, Kowalski & Rzebik-Kowalska 1991, Dragesco-Joffé 1993, Cuzin 1996). Northern limit is the northern fringes of the Sahara Desert. Also present in arid regions across the Arabian Peninsula eastwards to Pakistan and Afghanistan, and north-west to the Negev and Jordan (Larivière & Seddon 2001, Cuzin & Lenain 2004); a recent record for Syria is probably the first confirmation of their presence in this country (Serra *et al.* 2007). Suspected to have undergone an expansion of its historical distribution area due to desertification, offset by competition with the Red Fox due to expanding human settlements in the northern fringe of distribution area.

Habitat Typical habitat includes sand and stone deserts. The Rüppell's Fox seems to avoid the extreme arid regions in the middle of the Sahara, and, in Niger (Dragesco-Joffé 1993) and Morocco (F. Cuzin pers. obs.), this species is not found in large sand dune areas, where the Fennec Fox is the only other reported canid species; however, in Algeria, it occurs in large ergs (De Smet 1988). The species



Lateral view of skull of Rüppell's Fox *Vulpes rueppellii*.



is more abundant on the fringes of the Sahara, in mountain massifs and near oases. On the northern fringe of the Sahara, Rüppell's Fox may be found in areas with up to 150 mm annual rainfall. In Morocco (including Western Sahara), the general habitat comprises sparse to very sparse vegetation cover, dominated by small brushes (*Hammada scoparia*, *Panicum turgidum*, *Fagonia* spp.) mostly concentrated in wadis (with *Acacia* spp., *Balanites aegyptiaca*, *Maerua crassifolia* and *Capparis decidua* trees, and locally *Argania spinosa*). They also occur in coastal areas, with extremely sparse vegetation, and without any trees. It is able to survive in areas without any available water in Algeria (De Smet 1988) and in S Western Sahara (F. Cuzin pers. obs.), although animals were found only near water in Niger (up to 20 km) (Dragesco-Joffé 1993). In S Morocco, observations are inversely related to the distance of available water (Cuzin 2003), due to competition with the Red Fox.

Abundance Densities usually low, but higher in areas where food is more freely available, for example, near human settlements, or springs, when the Red Fox is absent (Valverde 1957, Osborn & Helmy 1980, K. De Smet pers. comm.). In the Air (Niger), Dragesco-Joffé (1993) suggests that the density of Rüppell's Foxes is higher in areas where other carnivores, such as the Golden Jackal *Canis aureus*, Caracal *Caracal caracal*, Sand Cat *Felis margarita*, Striped Hyaena *Hyaena hyaena* and Fennec Fox, are absent. In Saudi Arabia, in a large, fenced, protected area of 2244 km², recorded densities were 0.68/km², with lower population estimates outside the fenced reserve (Lenain 2000).

Adaptations Mainly crepuscular/nocturnal, although some animals are active during daytime in winter in Western Sahara (F. Cuzin pers. obs.) and in Tunisia (K. De Smet pers. comm.). In Saudi Arabia (Lenain 2000), this species leaves the den site usually within an hour following sunset. This is followed by alternating periods of activity and inactivity throughout the night, the latter usually taking place in the early hours of the morning. Foxes return to the den site often before sunrise and remain in the den throughout the day.

The ability to survive in extremely arid environments, where the opportunity to drink is extremely rare, appears to be facilitated by various ecological, behavioural and physiological adaptations (though not to the extent seen in the Fennec Fox). Behaviour of captive specimens is variable: some never drank (Petter 1952), while others did (Osborn & Helmy 1980). The diet, which includes plant material, fruits and roots (Rosevear 1974, Lenain 2000), likely provides much of their moisture requirements, and behavioural (in particular, activity patterns) and morphological adaptations (coat colour, presence of hair on feet, large ears) aid in thermoregulation. The role of physiological mechanisms (such as urinary concentrating ability) has yet to be established.

Two kinds of den are used: breeding dens, used by a pair for reproduction, and resting dens, used by a single animal for resting during daytime (Olfermann 1996). Dens are commonly located under slabs of rock or dug at the base of trees or bushes (Lindsay & Macdonald 1986, Harrison & Bates 1991, Kingdon 1997). In areas with few shelters (e.g. S Western Sahara), the species may use very exposed dens, often in the middle of plains (some of these burrows are dug by Ratels *Mellivora capensis*). In such areas, any disturbance induces the flight of the animal (F. Cuzin pers. obs.), and, in Niger, Dragesco-Joffé (1993) states that they often prefer to flee from their den in case of danger. In Oman, study animals changed den sites frequently (on average once every five days), likely as an anti-predator strategy or perhaps due to resource availability in other areas of a home-range (Lindsay & Macdonald 1986). Lenain (2000) recorded an instance where a shift occurred due to cooling: a male Rüppell's Fox used a shallow scrape in a sabkha-type substrate (packed silt), with a maximum depth of 70 cm. This type of substrate offers effective cooling, and midday temperatures may be 12–15° C lower inside the den than outside.

They are reportedly able to squirt the noxious contents of their anal glands at potential aggressors (Rosevear 1974).

Foraging and Food Rüppell's Fox is a generalist predator, the diet comprising a high invertebrate content as evidenced from scat and stomach analysis. Items consumed include a substantial insectivorous component (mostly Coleoptera and Orthoptera), as well as rodents, birds, lizards, snakes and occasional wild fruits, such as dates (Valverde 1957, Osborn & Helmy 1980, Kowalski 1988). In Saudi Arabia, small mammals are an important component of the diet and, in the absence of these, Rüppell's Foxes turn to Coleoptera (Lenain 2000). Their diet apparently is very opportunistic. In Saudi Arabia, scats contained remains of desert locusts (*Schistocera gregaria*), which were abundant during some study periods (Olfermann 1996, Lenain 2000). Frequent occurrence of plant material in scats may be a result of foraging for water (Lenain 2000). Local nomads report that Rüppell's Foxes prey on lambs and young goats in the Sahara in Egypt (Osborn & Helmy 1980), Niger (Dragesco-Joffé 1993) and in Hoggar (K. De Smet pers. comm.), and on chickens in Saudi Arabia (Lenain 2000). They are able to partially digest bones and teeth of prey (Denys *et al.* 1992).

Rüppell's Foxes are solitary foragers (Dragesco-Joffé 1993, F. Cuzin pers. obs.) and nocturnal visits to scavenge at temporary or permanent human settlements are common (Valverde 1957, Osborn & Helmy 1980, Kowalski 1988, F. Cuzin pers. obs.). Captive animals cached prey (Petter 1952). They are known to climb palms to obtain fruits (Osborn & Helmy 1980).

Social and Reproductive Behaviour Very little information available from Africa, but detailed studies have been conducted in Oman and Saudi Arabia. Adults are usually organized as monogamous pairs, but they may occur in groups (e.g. 3–15 in Arabia; I. Linn pers. comm.). The latter may represent extended family groups, and grouping may be incidental, caused by close aggregation of dens in the few areas where suitable sites are available.

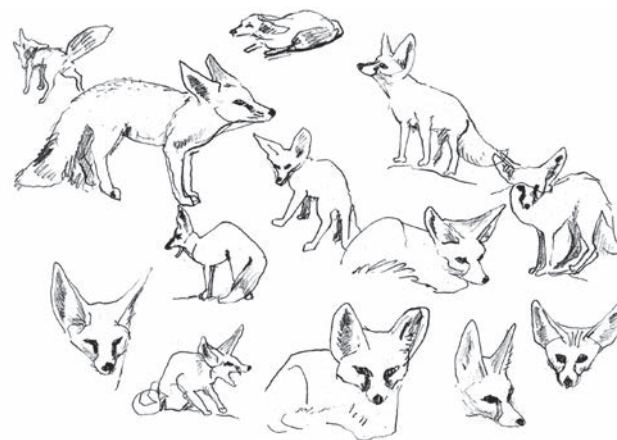
In Saudi Arabia, pairs have home-ranges that overlap extensively; there is no overlap between adults of the same sex (Olfermann 1996). Olfermann (1996) recorded mean annual home-range as 16.3 km², and Lenain (2000) recorded a home-range size of 10.2 km². In Oman, home-ranges are very expansive, covering some 69 km² and social units spatially separate (Lindsay & Macdonald 1986). Males have significantly larger seasonal home-ranges than ♀♀ (Lindsay & Macdonald 1986, Olfermann 1996). Vocalization mainly comprises a series of 6–10 high-pitched barks (Petter 1952, F. Cuzin pers. obs.); they may chatter and groan when content (Petter 1952, Haltenorth & Diller 1980).

Reproduction and Population Structure Tracks of two adult animals obviously engaged in a courtship display were found in S Morocco in Nov, a few days after heavy rainfall (F. Cuzin pers. obs.), whereas, in Saudi Arabia, mating takes place from Dec to Feb (Olfermann 1996, Lenain 2000), which usually coincides with the first rains after the harsh summer period. Captures of young cubs have been made in Mar in Western Sahara (Valverde 1957), and Petter (1952) recorded very young animals in the area of Beni Abbès (Algeria) in May. In Saudi Arabia, young cubs were caught as early as Mar, but peaks of captures were made from Jul to Aug following the dependency period (Lenain 2000). Gestation lasts 7–8 weeks and litter-size is 2–3 in the Mahazat as-Sayd protected area in Saudi Arabia, although ♀♀ have been recorded above ground with as many as six cubs (Olfermann 1996).

Young cubs remain dependent on their parents for an undefined period, after which they venture out from the den site area. Young disperse at 6–7 months of age, on average some 32 km; both sexes reach sexual maturity at around 9–10 months (Olfermann 1996). The maximum confirmed age in the wild is seven years, but it could be higher (Olfermann 1996); one captive specimen was still alive after 14.3 years (Weigl 2005).

In Saudi Arabia, sex ratio of juveniles favours ♂♂ (1.7 : 1 and 1.6 : 1 in two consecutive years) (Olfermann 1996), while, in Egypt, among 67 museum specimens, 58% were ♂♂ (corresponding to a sex ratio of 1.4 : 1) (Osborn & Helmy 1980).

Predators, Parasites and Diseases Fragments of the jaws of a young fox were found in pellets of a Pharaoh Eagle-owl *Bubo ascalaphus* in Mauritania by Heim de Balsac & Heim de Balsac (1954), and predation by Golden Eagle *Aquila chrysaetos* has been observed in Morocco (F. Cuzin pers. obs.). In Saudi Arabia, predation by avian predators such as the Steppe Eagle *Aquila nipalensis* and Pharaoh Eagle-owls was recorded by Olfermann (1996); Lenain & Ostrowski (1998) recorded the death of a Rüppell's Fox in a cage trap as a result of a Ratel, but this was probably opportunistic. Susceptibility to disease is poorly known. In Saudi Arabia, Lenain (2000) reported seroprevalence to canine distemper virus, canine parvovirus and canine rotavirus; this species is also infected by rabies (S. Ostrowski pers. comm.). They may be infested by the tick *Rhipicephalus sanguineus* and/or by different species of fleas (Olfermann 1996, Lenain 2000).



Rüppell's Fox *Vulpes rueppellii* action drawing.

Conservation IUCN Category: Least Concern. CITES: not listed.

Poisoned baits are used indiscriminately to control predators in Niger (Dragesco-Joffé 1993) and Morocco (Cuzin 1996) and some mortality of Rüppell's Fox is attributed to poisoning. Individuals also are accidentally killed by jaw-traps used against jackals (Dragesco-Joffé 1993). They are occasionally killed for food by nomads (Osborn & Helmy 1980, F. Cuzin pers. obs.), but rarely sold for fur. Impact of insecticides is unknown, but potentially harmful.

In the northern fringe of the Sahara, competitive exclusion by Red Foxes, which occur near new permanent human settlements, leads to local extirpation of Rüppell's Fox in very productive biotopes (Cuzin 2003). Rüppell's Foxes may only be able to compete in the harshest desert areas, where the Red Fox is not able to survive, or in protected areas where Red Fox control is taking place (Yom-Tov & Mendelssohn 1988, Cuzin 2003). Rüppell's Fox occurs in a number of protected areas throughout its range, including the Ahaggar and Tasili n'Ajjer National Parks (Algeria), Sidi Toui N. P. (Tunisia), Banc d'Arguin N. P. (Mauritania), Nefhusa N. P. (Libya), and Gebel Elba Conservation Area in Egypt (Cuzin & Lenain 2004).

Rüppell's Foxes are held in captivity. Attempts to breed them have not been very successful, although they have been successfully bred in the Hai Bar Breeding Centre, Eilat, Israel (E. Geffen pers. comm.).

Measurements

Vulpes rueppellii

HB (♂♂): 466 (419–519) mm, n = 28

HB (♀♀): 419 (411–559) mm, n = 16

T (♂♂): 341 (290–387) mm, n = 28

T (♀♀): 321 (273–363) mm, n = 16

HF c.u. (♂♂): 127 (115–138) mm, n = 29

HF c.u. (♀♀): 122 (110–131) mm, n = 16

E (♂♂): 98 (89–110) mm, n = 27

E (♀♀): 96 (88–110) mm, n = 16

WT (♂♂): 1.8 (1.4–2.3) kg, n = 13

WT (♀♀): 1.7 (1.4–1.8) kg, n = 6

Egypt (Osborn & Helmy 1980)

Key References Cuzin & Lenain 2004; Dragesco-Joffé 1993; Larivière & Seddon 2001; Lenain 2000; Lindsay & Macdonald 1986; Olfermann 1996; Osborn & Helmy 1980; Rosevear 1974.

Vulpes vulpes **RED FOX**

Fr. Renard roux; Ger. Rotfuchs.

Vulpes vulpes Linnaeus, 1758. Syst. Nat., 10th edn, 1: 40. 'Europe, Asia, Africa, antrafodiens'; restricted by O. Thomas (1911), to 'Sweden (Upsala)'.



Red Fox *Vulpes vulpes*.

Taxonomy Highly polymorphic species, with numerous described subspecies many of doubtful validity (see Larivière & Pasitschniak-Arts 1996). Synonyms (Africa only): *aegyptiaca*, *algeriensis*, *anubis*, *atlantica*, *barbarus*, *niloticus*, *vulpecula*. Chromosome number: $2n = 34$; the X chromosome is a submetacentric and the Y chromosome subtelocentric (Rausch & Rausch 1979).

Description Medium-sized canid, and the largest fox in the genus *Vulpes*. Sexes similar colour, ♂♂ about 15% heavier than ♀♀ (Macdonald 1987). Muzzle slender and pointed with white on upper lip. Ears large, pointed, erect and black-backed. Pupil of eye elongate vertically. Pelage reddish-brown but may vary from brown to russet-red to yellowish-grey (see Geographic Variation). Some individuals dark grey-black under throat and belly; underfur of ♀♀ during breeding season may appear pink-tinged. Throat and/or chest may have white markings. Legs long and slender. Lower legs black, may be splashed with white. Tail long, thick and bushy, sometimes with white tip. *Vulpes v. aegyptiaca* has dorsal stripe, reddish to reddish-brown, 50–80 mm wide, extending from eye to basal one-third of tail, broadest on shoulders (forming a cross) and on pelvis, darkened between ear and shoulder by black, and black-tipped, guard hairs (Osborn & Helmy 1980). Adult pelage generally paler in summer than in winter (Lloyd 1980, Osborn & Helmy 1980). Conspicuous moult in spring, sometimes giving piebald appearance. New hairs

grow first on lower legs, then spread upwards, to flanks by early Jul, back and tail by late Aug. Summer coat begins to thicken in early winter. Limbs plantigrade. There are five toes on the forefoot (although four show in the spoor); fur shows between pads; claws conspicuous (two front claws close together). Scent glands include: supracaudal (or violet) gland (upperside of tail, 70 mm from root); paired anal sacs (open via 2 mm diameter ducts either side of anus); facial glands around chin and angle of jaw; and interdigital glands between toes and pads of feet. Four pairs of nipples.

Skull long and slender, with a long, narrow rostrum (with a slight depression below the frontal region). The frontal sinuses are slightly inflated, the auditory bullae are prominent, and the paroccipital processes small. Canines are long and slender; the medial incisors show slight lobes (Larivière & Pasitschniak-Arts 1996).

Geographic Variation There are three main colour morphs: Red, Silver (black with variable amount of frosting due to silver tips on guard hairs) and Cross (greyish-brown with long black guard hairs forming a prominent stripe down back and another across shoulders) (Banfield 1987, Johnson & Hersteinsson 1993). The melanistic variants (Cross and Silver) are known to occur in some parts of North America, Russia and where the progeny of imported North American foxes have been released in Scandinavia (Lloyd 1980). Less common mutations include Samson fox (lacks guard

hairs entirely, thus appearing woolly), and Bastard fox (smoky-blue colour between red and black).

Across the species' wide distribution range, there is considerable geographic variation in size: adult head–body length may range from 455 to 900 mm, tail length from 300 to 555 mm and body weight from 3 to 14 kg (Nowak 1999). The species exhibits a temperature- and latitude-correlated size gradient in Palaearctic region, but there is little change in size apparent in the southern part of range, in the Saharo-Arabian region, where the species is sympatric with smaller Rüppell's Fox *Vulpes rueppellii* (Dayan *et al.* 1989). Individuals probably largest in Scotland, and smallest in remote Saudi Arabia. Skull measurements of specimens from N Algeria are much smaller than those from central Europe (Kowalski & Rzebik-Kowalska 1991), and the species is substantially smaller in Middle East deserts (Macdonald *et al.* 1999) than in Europe. Individuals from North America also smaller (Voigt 1987).

Many subspecies have been described (44 are listed by Larivière & Pasitschniak-Arts [1996]), on the basis of regional variation, but these have doubtful ecological significance as evidenced by successful introductions and re-introductions around the world. Indeed, Corbet (1978) wrote that 'the continuity of range is such that it is doubtful whether any discrete, definable sub-species can be recognized'. However, a recent review of North American Red Foxes indicated native subspecies are considerably distinct from introduced European Red Foxes, the latter having displaced the former in many areas (Kamler & Ballard 2002). Three subspecies have been recognized in Africa (and see Coetsee 1977): *V. v. aegyptiaca* (N Libya, Egypt and Sinai, and N Sudan), *V. v. atlantica* (Atlas Mts, Mitidja, wooded parts of Algeria) and *V. v. barbarus* (Barbary Coast, north-western Africa – Morocco, from Tangiers south-west to Mogador and Marrakech). The validity of these as distinct forms is doubtful.

Similar Species

Vulpes pallida. Similar body structure, but smaller with longer legs and ears; pale fawn body and ears, tail reddish-brown with black tip. Sympatric in N Sudan.

V. rueppellii. Smaller, with short legs and broad ears; pale sandy colour, back of ears pale brown, black patches on face, tail tip white. Sympatric in some parts of Africa, but better adapted to deserts, probably due to smaller size and ability to survive in waterless areas (Osborn & Helmy 1980).

V. cana. Smaller, with relatively longer tail. In Africa, recorded only from Wadi Qiseib in Egypt.

Distribution Has the widest geographical range of any member of the order Carnivora and indeed among any non-commensal mammal species, covering nearly 70 million km², being distributed from the Arctic Circle throughout Europe, greater part of Palaearctic Asia and North America. Absent from Iceland, the Arctic islands, some parts of Siberia, and extreme deserts. The European subspecies was introduced into E United States and Canada in the seventeenth century, and subsequently spread throughout most of North America, apparently displacing native subspecies in many areas (Kamler & Ballard 2002). Red Foxes were introduced to Australia in 1800s, and they have also been introduced to the Falkland Is. (Malvinas) and Isle of Man (UK), although the species may subsequently have disappeared there.

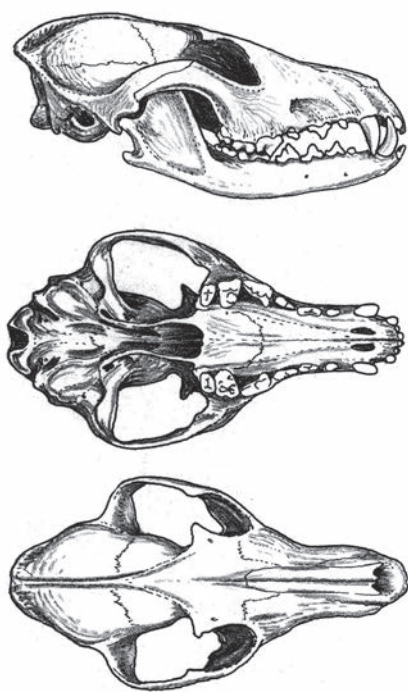


Vulpes vulpes

In Africa, the species is known from late Pleistocene and Holocene (Kowalski & Rzebik-Kowalska 1991), and today occurs throughout North Africa mainly in the coastal belt from the hills of Morocco through N Algeria, Tunisia, Libya, Egypt (from Sallum to Alexandria, in the Delta and the Nile Valley south to the Sudanese Border, in the Fayoum, and in Cairo and surrounds), and N Sudan towards Khartoum (Hufnagl 1972, Osborn & Helmy 1980, Aulagnier & Thévenot 1986, Kowalski & Rzebik-Kowalska 1991, Cuzin 2003, Hoath 2003).

Habitat In Africa, occurs in arid areas, bushes, steppe regions, stony deserts and river beds, cultivated and urban land, but not sand desert (Kowalski & Rzebik-Kowalska 1991). Elsewhere recorded in habitats as diverse as tundra, desert and forest. Natural habitat is dry, mixed landscape, with abundant 'edge' of scrub and woodland. Also abundant on moorlands, mountains (even above the treeline, known to cross alpine passes), deserts, sand dunes and farmland from sea level to 4500 m (Macdonald & Reynolds 2004). In parts of their range, they appear closely associated with humans, occurring in urban areas (including city centres, such as London and Paris), residential areas and intensive agricultural areas (e.g. North Dakota, USA) (Macdonald & Reynolds 2004). In Egypt, they are frequently encountered at major tourist sites, such as the Step Pyramid (Hoath 2003).

Abundance Densities highly variable. There are no recorded densities in Africa, but, in the United Kingdom, density varies with habitat quality; between one fox/40 km² in Scotland and 1.17/km² in Wales, but can be as high as 30 foxes/km² in some urban areas where food is superabundant (Harris 1977, Macdonald & Newdick 1982, Harris & Rayner 1986). Social group density is one family/km² on farmland, may vary between 0.2 and 5 families/km² in suburbs, may be as low as one family/10 km² in barren uplands (Macdonald 1981, Lindsay & Macdonald 1986). Fox density in mountainous rural areas of Switzerland is 3 foxes/km² (Meia 1994).



Lateral, palatal and dorsal views of skull of Red Fox *Vulpes vulpes*.

Adaptations Generalist conformation and lack of specialist adaptations make the Red Fox widely successful. Its weakest element, exploited by man and other predators, is the period of vulnerability for the young while they are tied to their breeding den. Red Foxes have great endurance, galloping for several kilometres if pursued, and have been recorded sprinting at 60 km/h; they also swim well (Haltenorth & Roth 1968, Macdonald & Barrett 1993). Can locate sounds to within one degree at 700–3000 Hz, although less accurate at higher frequencies. Adapted to pounce on prey with great precision, manipulating take-off angle to adjust length of jump and force of landing. Have relatively longer hindlegs than other members of the canid family, thereby increasing their propulsive force. Dense, but short, fur covers approximately one-third of body's surface area, particularly face, dorsal part of head, nose, ears, lower legs and paws; probably functions as major heat exchange surface for thermoregulation (Klir & Heath 1992). Nose is used for evaporative cooling and probably forms part of brain cooling mechanism as described in domestic dogs (Klir & Heath 1992). Physiology of their senses and physical size and agility mean foxes are well suited to preying on small rodents.

Underground dens are used to shelter cubs while very young. They dig their own dens or enlarge burrows of other species; dens usually have several openings. In Egypt, clay hills or *karms*, excavations from Roman cisterns, south of Burg el Arab are well-known burrowing sites. Foxes also burrow in palm groves, fields, gardens, quarries and beneath walls, stables, houses, ruins and tombs (Osborn & Helmy 1980). In a study of den use on Djerba I., SE Tunisia, dens were found in grassland, cultivated land (olive plantations and palm groves) and suburban areas (Dell'Arte & Leonardi 2008).

Foraging and Food Much of what is known of the ecology of the Red Fox comes from studies extralimital to Africa (but see Osborn & Helmy 1980, Dell'Arte & Leonard 2009), and much of

the information that follows is derived from those studies. Red Foxes are adaptable and opportunistic omnivores, feeding on vertebrates (lizards, rodents, hares, birds), carrion, invertebrates, fruit, eggs and plant material, as well as scavenged fish, crabs and refuse. They typically prey upon birds and mammals up to about 3.5 kg (equivalent to an adult brown hare) and require about 500 g of food per day, caching excess food and having a highly developed memory for location of hoards (Macdonald 1977a, 1981). In Egypt, stomachs of Red Foxes have contained green figs, various bird, plant and insect remains, and rodents (including *Gerbillus* sp. and *Dipodillus simoni*) (Osborn & Helmy 1980); Flower (1932) mentions one stomach full of mole crickets. Availability of water may be a factor limiting the distribution of Red Foxes in Egypt to the Nile Valley and Delta, the Western Mediterranean Coastal Desert, oases, and northern parts of the Eastern Desert and Sinai Peninsula (Osborn & Helmy 1980).

Mainly nocturnal and crepuscular; more diurnal where undisturbed. Independent and generally solitary foragers, although individuals may forage in close proximity where resources are clumped. Accounts of cooperative hunting, e.g. of young ungulates, have not been studied systematically (Macdonald 1980a). Often cache prey.

Considered a major predator of ground-nesting colonial birds, such as terns, and their effect on harvestable game-bird populations can be significant. Also prey upon hand-reared and released game-birds. Lambs may be taken but such losses typically constitute only a small percentage (<2%) of all lambs born (Macdonald *et al.* 2000).

Social and Reproductive Behaviour The basic social unit is a pair, but groups of up to six members (usually one adult ♂ and 2–5, probably related, ♀♀) may share a territory, depending on habitat. Pairs occupy large territories in impoverished habitats. Range size is habitat-dependent and can cover from <40 ha (e.g. urban foxes in Oxford, UK) to >4000 ha, depending on habitat (reviewed by Voigt & Macdonald 1984). One fox in an Omani desert had a range spanning 5000 ha (Lindsay & Macdonald 1986). There are reports of overlapping ranges in some urban (e.g. Harris 1979) and rural environments (Meia & Weber 1996), and of drifting territories in other urban settings (Doncaster & Macdonald 1991).

Red Foxes communicate using facial expressions, vocalizations and scent-marking. Twenty-eight categories of vocalization have been described; calls are used to communicate over long distances and also at close quarters. Individuals have characteristically different voices. Scent-marking involves urine and faeces (urine-marking is sometimes confined to dominant ♀♀ within a group), anal sac secretions, the supracaudal gland (more active in ♂♂ during breeding season) and glands around lips, in angle of jaw and between pads of feet. Faeces often deposited on prominent sites, e.g. stones, tussocks of grass and trail junctions. Faeces sometimes similar to those of domestic dogs, but darker, more tightly packed and smell differently; they often comprise visible clumps of undigested fur or feather, and, in season, traces of beetle elytra and fruit pips (Macdonald & Barrett 1993).

Mating behaviour highly variable; may include monogamous pairs, a single ♂ with two breeding ♀♀ (that may or may not share a communal den), or a single breeding ♀ with several non-breeding female helpers (probably related to breeding vixen). There is only ever one breeding ♂ in the group, although additional matings occur outside the group. Territorial ♂♂ make frequent excursions beyond



Red Fox *Vulpes vulpes* juvenile.

their territories during mating season, during which itinerant ♂♂ also make territorial incursions (Macdonald 1987).

In high-density populations where interactions with a dominant vixen are frequent, subordinate ♀♀ do not usually breed, although they may breed successfully in low-density populations (in the UK, usually only one or two ♀♀ in a group breed) (Macdonald 1980b, 1987). Both parents, and sometimes other ♀♀ in the group, care for young (Macdonald 1979b). The ♂ provides food to the lactating ♀, which is generally confined to the den prior to weaning. Both parents care for and provision young with weaned food. Non-breeding ♀♀ may also feed, groom and tend cubs and have been known to adopt them if orphaned (Macdonald 1979b). If two ♀♀ breed within a group, they may share a den and litters may be communally suckled.

There is socially mediated suppression of reproduction among ♀♀, lowest productivity occurring where fox density is high or food supply poor. Where food is not limited, social status itself can suppress reproduction, with only the dominant ♀ breeding. Behavioural mechanisms by which this occurs include harassment of subordinates, infanticide and cannibalism of subordinate vixens' cubs, and possibly dominant ♂ courting only dominant ♀♀ (Macdonald 1977b, 1980b). A hormonal mechanism whereby stress leads to lowered productivity through foetal reabsorption has also been identified (Hartley *et al.* 1994).

Reproduction and Population Structure There is limited information on reproduction in Red Foxes in Africa. Four pups were recorded in Mar in Egypt (Osborn & Helmy 1980), and Hufnagel (1972) mentions that the young are born in Feb or Mar in Libya. The information that follows is taken from Macdonald & Reynolds (2004). Males are seasonally fecund. In the UK, mating takes place from Dec to Feb; onset of breeding correlated with day length and so starts earlier at more southerly latitudes. Females are in oestrus for three weeks, but fertilization is possible over three days. Gestation period is 49–55 days. Births occur from Mar to May in UK. Litter-size varies with food availability, typically ranging between 3 and 12 (Voigt & Macdonald 1984). Birth-weight is around 100 g. Cubs are born blind, deaf and with dark brown fur. Eyes open at 11–14 days and are blue until about one month old, then brown to amber. Fur colour as adult by two months. Lactation lasts for four weeks, and cubs are fully weaned at Week 6–8. Sexual maturity is reached at 9–10 months. Fox populations that are dense relative to food

resources are generally less productive than those that are less dense. A single litter per year is the norm.

Juveniles may disperse at between six and 12 months of age, mostly between Oct and Jan. All or most ♂♂ disperse but proportion of each sex dispersing varies between habitats and may depend on extent of mortality. Males typically disperse further than ♀♀ (e.g. ♂♂ 13.7 km, ♀♀ 2.3 km in Welsh hills [Lloyd 1980, Trehwella *et al.* 1988]). Dispersal distance correlates positively with home-range size (Macdonald & Bacon 1982). In the UK, distances are generally between <5 km and >50 km, but distances up to 394 km have been recorded in the USA (Ables 1975).

Sex ratio in a sample of 174 museum specimens of *V. v. aegyptiaca* was 1 : 1 (Osborn & Helmy 1980). Foxes have been known to live up to nine years in the wild; a wild-caught ♀ was still living in captivity at an estimated 21.3 years of age (Weigl 2005).

Predators, Parasites and Diseases High juvenile and subordinate adult mortality, but lower adult mortality. Although mortality is variable between populations, roughly 75% die in their first year; adult mortality is approximately 50% per year. The Red Fox has few natural predators, although large birds of prey and large carnivores are known predators in some parts of the range.

Red Foxes are a widespread reservoir of rabies (Chomel 1993), especially in central Europe, SE Canada and NE USA (Larivière & Pasitschniak-Arts 1996). Populations are locally and periodically reduced by rabies epizootics (mortality estimated at 60–80% by simulation models; Voigt *et al.* 1985), although recovery appears swift (e.g. Western Europe, USA; Wandeler *et al.* 1974). Oral vaccination is regarded by the World Health Organization and European Union as an ongoing experiment; oral vaccines successfully used in some European countries (Kappeler *et al.* 1988), but the method has failed in some areas (Funk *et al.* 2001).

The Red Fox is host to a wide range of parasites (see Larivière & Pasitschniak-Arts 1966 for review). One of the most serious parasites is the skin-dwelling mite (*Sarcoptes scabiei* var. *vulpes*), which causes sarcoptic mange. This disease is locally and temporally prevalent. Mange appeared in Finland in 1967 and spread to Norway and Sweden in the 1970s and 1980s, where it reduced fox populations by over 70% (Holt & Berg 1990, Lindström 1992). Since then, mange has spread across most of Europe including England, wiping out over 90% of the fox population in Bristol, UK, in the early 1990s (McDonald *et al.* 1997), and south-west to Spain (Gortazar *et al.* 1998) and New York (Tullar *et al.* 1974). Mange may also have been responsible for population declines in Saqqara, Egypt in 1995/1996 (Hoath 2003). Several other diseases are recorded, including canine distemper, parvovirus, toxoplasmosis, bovine tuberculosis and paratuberculosis, but these do not appear to be major determinants of fox density (Little *et al.* 1982, Voigt 1987, Beard *et al.* 1999).

Conservation IUCN Category: Least Concern. CITES: Not listed.

Red Foxes are widely regarded as a pest and unprotected, except that most countries/states where trapping/hunting occurs have regulated closed and open seasons and restrictions on capture methods. As such, across much of their range, the major cause of mortality (particularly high among dispersers) is attempted pest control by people (through shooting, secondary poisoning etc.); in Morocco, 21,409 animals were destroyed between 1959 and 1972 at an annual average of

approximately 1600 animals, mainly through strychnine poisoning (Aulagnier 1990). Red Foxes are also hunted with dogs in France, Belgium, Portugal, Italy, Germany, Switzerland, Australia, USA and Canada, although this is not reported in any North African country.

Red Foxes have been extensively hunted and trapped for their fur. The worldwide trade of wild-caught foxes in 1985–86 was 1,543,995 pelts. In the USA, Red Fox made up 45% of this trade (worth \$50 million in 1983). Many individuals killed by vehicles in modern landscapes; juveniles and dispersers are particularly vulnerable (Macdonald & Reynolds 2004). Despite these and other potential threats, their versatility and eclectic diet are likely to ensure their persistence despite changes in landscape and prey base (Macdonald & Reynolds 2004).

Measurements

Vulpes vulpes

HB (♂ ♂): 602 (541–652) mm, n = 9*; 554 (533–592) mm, n = 8†
 HB (♀ ♀): 590 (552–634) mm, n = 24*; 513 (465–570) mm, n = 7†
 T (♂ ♂): 375 (343–401) mm, n = 9*; 350 (326–398) mm, n = 8†
 T (♀ ♀): 362 (307–391) mm, n = 23*; 321 (302–368) mm, n = 7†

HF c.u. (♂ ♂): 150 (136–165) mm, n = 9*; 138 (127–149) mm, n = 8†
 HF c.u. (♀ ♀): 149 (134–160) mm, n = 24*; 123 (105–134) mm, n = 6†
 E (♂ ♂): 99 (93–109) mm, n = 9*; 93 (91–106) mm, n = 8†
 E (♀ ♀): 98 (91–106) mm, n = 24*; 89 (70–104) mm, n = 7†
 WT (♂ ♂): 6.0 kg, n = 1
 WT (♀ ♀): 4.9 kg, n = 4
 Egypt: *Giza, †Bahig (Osborn & Helmy 1980)

HB (♂ ♂): 660 (590–720) mm, n = 11
 HB (♀ ♀): 630 (550–680) mm, n = 11
 T (♂ ♂): 400 (360–440) mm, n = 10
 T (♀ ♀): 370 (340–420) mm, n = 10
 WT (♂ ♂): 6.3 (4.4–7.6) kg, n = 19
 WT (♀ ♀): 5.3 (3.6–6.5) kg, n = 19
 Australia, Spain, Lebanon, Norway, UK and USA (Cavallini 1995)

Key References Kowalski & Rzebiak-Kowalska 1991; Macdonald 1987; Osborn & Helmy 1980.

David W. Macdonald

Vulpes zerda FENNEC FOX

Fr. Fennec; Ger. Fenek (Wüstenfuchs)

Vulpes zerda (Zimmermann, 1780). Geogr. Gesch. Mensch. Vierf. Thiere 2: 247. 'Es bewohnt die Soara und andere Theile von Nordafrika hinter des Atlas, der Ritter Bruce behautet, man Fände es auch in tripolitanischen' [Sahara].



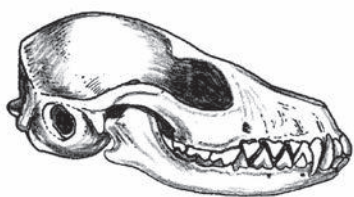
Fennec Fox *Vulpes zerda*.

al. 1992b). Synonyms: *arabicus*, *aurita*, *brucei*, *cerda*, *cerdo*, *denhamii*, *fennecus*, *saarensis*, *zaarensis*. Chromosome number: 2n = 64; the X chromosome is a large submetacentric and the Y chromosome is very small (Matthey 1954, Wurster & Benirschke 1968).

Description The Fennec Fox is the smallest canid, with extremely large ears that give it the greatest ear to body ratio in the family Canidae. The muzzle is slender and delicate. The large ears are darker on the back and white or nearly so inside; ear edges are white. Eyes large and dark, with dark streaks extending from the inner eye down and outward to either side of the muzzle. Pelage is typically sandy or cream-coloured, although it may have a light fawn, red or grey cast; the underfur is about 28 mm in length. Underparts are paler, almost white. Upper parts of slender limbs reportedly coloured reddish-sand in individuals from North Africa, whereas those from further south are nearly white in these areas. The coat is very thick, long and soft; dense fur on the feet extends to cover the pads (hairs up to 13 mm in length). The tail is short, rufous, well furred (tail hairs up to 35 mm) with a darker tip and a slightly darker spot covering the caudal gland. Females have three pairs of nipples.

Skull small, typically vulpine, but with very large tympanic bullae. Rostrum delicate, width less than 50% of braincase. Zygomatic arches widely flared anteriorly. Postorbital region wide, and postorbital process small. Sagittal crest only detectable as a low elevation in front of lambda, and temporal ridges small. The canines are small and slender, but sharp (Harrison 1968, Clutton-Brock *et al.* 1976).

Taxonomy Monotypic (Coetzee 1977). Included in the genus *Fennecus* by Ellerman & Morrison-Scott (1951), Stains (1975), Coetzee (1977) and Nowak (1999), although Wozencraft (1993, 2005) placed *Fennecus* in the genus *Vulpes*, an arrangement in agreement with other authorities (e.g. Clutton-Brock *et al.* 1976, Corbet 1978, Geffen *et al.* 1992b) and followed here. Genetic analysis confirms that Blanford's Fox *Vulpes cana* is the sister taxon to this species (Geffen *et*



Lateral view of skull of Fennec Fox *Vulpes zerda*.

Geographic Variation None recorded.

Similar Species

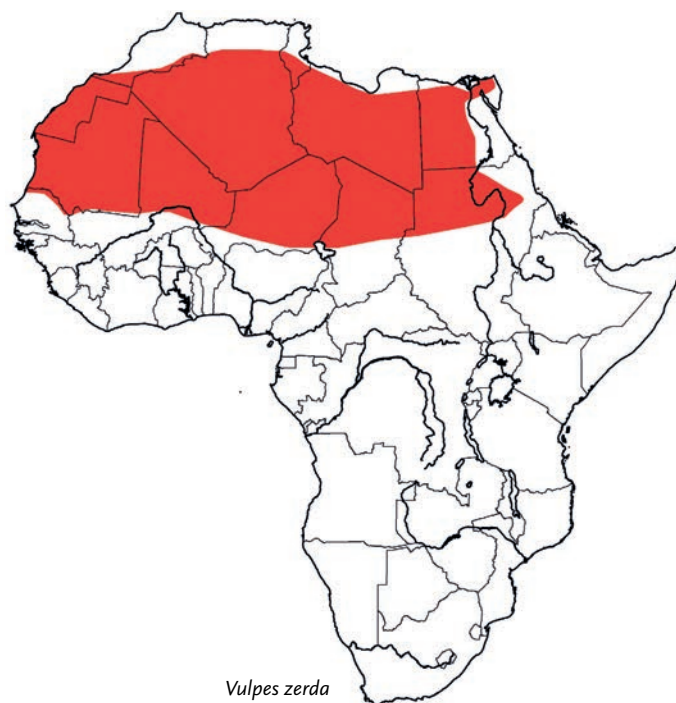
Vulpes rueppellii. Larger, but with smaller ears; upper parts silvery-grey, and the tip of the tail is white. Northern limit in Africa is the northern fringes of the Sahara Desert.

V. pallida. Larger; upper parts pale sandy-fawn suffused with black hairs (also has dark tail tip). Sympatric in southern parts of Fennec Fox range.

V. cana. Tail longer. In Africa, recorded only from Wadi Qiseib in Egypt.

Distribution Widespread in the sandy deserts and semi-deserts of North Africa from Morocco and Mauritania through Algeria, Tunisia, Libya and Egypt south to the Sudan; also in N Sinai (Saleh & Basuony 1998). Common throughout the Sahara, and may occur to the Sahelian areas in the south at around 14°N (Dragesco-Joffé 1993, Granjon *et al.* 1995). The distribution of Fennec Foxes extralimital to the African continent is unclear. Al-Robaee (1982) collected a specimen from near Jabal Sanam, south-west of Basrah in Iraq. References to Fennec Fox sightings in the United Arab Emirates were based on an animal in the Al Ain zoo (Al-Robaee 1982), which was, in fact, a Rüppell's Fox *V. rueppellii* (Gasparetti *et al.* 1985). A subadult Fennec Fox, apparently from Kuwait, is in the British Museum collection (Harrison & Bates 1991), but the true origin of this animal is in doubt. Thesiger (1949) reported Fennec Fox tracks in the region of Abu Dhabi, but whether the tracks were accurately identified is uncertain. Current distribution likely unchanged from historical range; the only documented regression concerns the northern Moroccan Sahara, where the Fennec Fox disappeared during the 1960s from four localities, which were restricted sandy areas close to permanent human settlements (F. Cuzin pers. obs.).

Habitat Subsists in arid desert environments. Stable sand dunes are believed to be ideal habitat (Dorst & Dandelot 1970, Coetzee 1977), presumably offering the ideal substrate for burrowing, although animals also live in very sparsely vegetated sand dunes near the Atlantic coast (Cuzin 2003). In the Sahara, sparse vegetation is usually dominated by *Aristida* spp., and *Ephedra alata* in large sand dunes. In small sand dunes, the vegetation is dominated by *Panicum turgidum*, *Zygophyllum* spp. and sometimes by trees such as *Acacia* spp. and *Capparis decidua* (F. Cuzin pers. obs.). Annual rainfall is less than 100 mm per year on the northern fringe of their distribution, but on the southern fringe they may be found up to the Sahelian areas that receive as much as 300 mm rainfall per year. They are able to live independently of water sources (Dekeyser & Derivot 1959, in Noll-Banhölzer 1979a, b, Cuzin 2003).



Vulpes zerda

Abundance Assumed to be locally common based on the observations that the Fennec Fox is still often trapped and sold in parts of North Africa. In S Morocco, they are commonly seen in all sandy areas away from permanent human settlements (F. Cuzin pers. obs.).

Adaptations Well adapted to desert living. Primarily nocturnal, although crepuscular activity is also reported (Gauthier-Pilters 1967). In S Morocco, animals were commonly active in winter until around mid-morning (F. Cuzin pers. obs.). The pale, sandy-coloured, dense fur presumably provides camouflage and serves to protect against cold night-time temperatures, whereas the well-furred feet facilitate walking on hot, sandy substrates and facilitate locomotion in loose sand. The exceptionally large ears likely help in heat dissipation, but may also aid in locating insects and small vertebrates (Ewer 1973) as Fennec Foxes have exceptional hearing ability (facilitated by their well-developed tympanic bullae) (Dragesco-Joffé 1993). Nocturnal activity patterns, the use of burrows during the day, and the moisture content of their prey probably contribute to their ability to go without drinking water (Schmidt-Nielsen 1964, Dragesco-Joffé 1993, F. Cuzin pers. obs.).

Dens in the wild are always dug in sand, in open areas or places sheltered by plants such as *Aristida pungens* and *Calligonum comosum* (Dragesco-Joffé 1993, Incorvaia 2005, F. Cuzin pers. obs.). Dens may be huge and labyrinthine, especially in the most compacted soils, covering up to 120 m², with as many as 15 different entrances (Dragesco-Joffé 1993). Bueler (1973) reports that dens may be close together or even interconnected. In soft sand, dens are usually small and simple, with just one entrance and one tunnel leading to a chamber (Dragesco-Joffé 1993). In case of danger, animals prefer to flee from this type of den. In captivity, Fennec Foxes often bury faeces by pushing loose substrate with their noses or hindfeet (Gauthier-Pilters 1962), presumably to conceal their presence. In the wild, finding fresh faeces is rare, probably because of this behaviour.

The Fennec Fox also shows some physiological adaptations to its extreme environment. In captive animals, both body temperature and heart rate decrease at mid-day and increase at night as animals become active. Body temperature of resting animals is ca. 37.6 °C, and heart rate ca. 100–115 beats/min; the thermoneutral zone ranges from 23 to 37.8 °C, and panting occurs above this range (Noll-Banholzer 1979a, Maloïy *et al.* 1982). Vasodilation occurs under heat stress and vasoconstriction in cold conditions. Under cold conditions (10–20.8 °C), piloerection and shivering were observed (Maloïy *et al.* 1982). Newborn animals are sensitive to cold, but seem incapable of thermoregulation. In addition, the kidneys filter extremely high concentrations of urea with little water loss (Noll-Banholzer 1979b, Gasperetti *et al.* 1985). When exposed to high heat stress, captives deprived of water decrease their activity and food intake and lose weight (Noll-Banholzer 1979b).

Foraging and Food Fennec Foxes are omnivorous, and are reported to consume insects (locusts, beetles) and other arthropods (scorpions), small rodents (e.g. *Jaculus jaculus*, *Gerbillus* spp. and *Meriones* spp.), lizards (e.g. *Acanthodactylus* spp.), geckos (e.g. *Stenodactylus* spp.), skinks (e.g. *Scincus albifasciatus*), eggs, small birds (e.g. larks and sandgrouse), various fruits and some tubers (Dragesco-Joffé 1993, Incorvaia 2005, F. Cuzin pers. obs.). They appear to be quite opportunistic: in the Moroccan Sahara, during an exceptionally cold morning in June, one Fennec Fox killed and ate at least four skinks, as the weather was too cold for the skinks to escape quickly (F. Cuzin pers. obs.). Captives have also been reported to capture and kill an adult rabbit (Gauthier-Pilters 1962).

Fennec Foxes hunt alone (Coetzee 1977), probably because solitary hunting of small prey is more efficient. They have not been seen using the ‘mouse jump’ hunting strategy typical of most fox species (Ewer 1973), but reportedly dig to find insects and small vertebrates. Because the jaw muscles are not very strong, killing relatively large prey (such as *Jaculus* or *Meriones*) may take up to five minutes (Dragesco-Joffé 1993). Like other foxes, they do cache food by burying. They are very opportunistic and commonly visit temporary human settlements during the night in search of food (Dragesco-Joffé 1993, F. Cuzin pers. obs.). In Niger, some individuals have been reported raiding poultry coops (Dragesco-Joffé 1993).

Social and Reproductive Behaviour Fennec Foxes are thought to be moderately social, but this evidence is based primarily on captive animals. The basic social unit is believed to be a mated pair and their offspring, and, like some other canids, the young of the previous year may remain in the family even when a new litter is born (Gauthier-Pilters 1967). Captive animals engage in high levels of affiliative behaviour, and typically rest in contact with each other. Play behaviour is common, even among adults, although ♂♂ begin to show more aggression and urine-marking when oestrus approaches. During the prooestrous and oestrous periods, members of a pair approach each other more frequently and spend more time in proximity. There is an increased frequency of mutual sniffing of each other’s muzzles and genitals, followed by mounting and copulation. Most remarkable is the exceptionally long copulatory tie lasting up to 165 min (Valdespino 2000, Valdespino *et al.* 2002). The ♂ becomes very aggressive and protective of the ♀ after mating and provisions her during pregnancy and lactation (Sowards 1981).

He is usually solicitous of the pups and may help guard and care for them. Vocalizations include barks, both soft and high-pitched, catlike purring, yapping and squeaking (Gauthier-Pilters 1967).

Reproduction and Population Structure In the wild, they are reported to mate in Jan and Feb and give birth in Mar and Apr (Gauthier-Pilters 1967), but these data are from only one site; captive Fennecs from Algeria bred in Feb, Mar and Apr, and gave birth in May and Jun (Saint Girons 1962). In captivity, births can occur year round, although most litters are born between Mar and Jul (Bauman 2002). Data from captivity are more extensive than those from the wild, but, because captive animals are maintained in a broad range of environmental conditions, inter-oestrous intervals vary considerably. Individual differences also likely contribute to this variability. Fennec Foxes most commonly have one litter per year, but a second litter is possible under some conditions (Koenig 1970, Valdespino *et al.* 2002).

The monoestrous cycle is characterized by a pro-oestrous phase of about six days and a one- to two-day oestrus, relatively short for a canid (Gauthier-Pilters 1967, Koenig 1970, Valdespino *et al.* 2002). There is no sanguineous discharge in association with oestrus or pro-oestrus. In non-fertile cycles, ovulation is followed by an approximately 50-day dioestrous period, also called pseudopregnancy because it is equivalent in hormonal pattern and duration to gestation (Asa & Valdespino 1998, Valdespino 2000).

Gestation lasts 50–52 days (Petter 1957, Volf 1957, Saint Girons 1962, Koenig 1970); however, 62- and 63-day gestations were reported for two animals at the Strasbourg Zoo (Gangloff 1972). Litter-size is 1–4 (Petter 1957, Gauthier-Pilters 1967, Koenig 1970, Gangloff 1972, Bauman 2002). Young are born blind and fully furred; eyes open at 8–11 days (Gangloff 1972) and weaning takes place at 61–70 days (Koenig 1970). First mating is reported at nine months (Bekoff *et al.* 1981) to one year (Gauthier-Pilters 1967) for both sexes. Longevity in the wild is unknown, but, in captivity the recorded longevity is 14 years for ♂♂ and 13 years for ♀♀ (Bauman 2002).

Predators, Parasites and Diseases In the wild, jackals, Striped Hyenas *Hyaena hyaena* and domestic dogs are reported to prey on Fennec Foxes (Gauthier-Pilters 1967), although this is anecdotal and possibly questionable. Fennec Foxes are fast and able to change direction very quickly, and nomads consider them very difficult to capture, even for the saluki, a local greyhound-like dog (Monteil 1951, Dragesco-Joffé 1993). However, Eagle-owls (*Bubo* spp.) may prey on young foxes (Dragesco-Joffé 1993). There is significant mortality of neonates in captivity, generally attributed to the sensitivity of the parents to disturbance (Petter 1957, Volf 1957, Gangloff 1972). The Fennec Fox is partly sympatric with, and thus may face competition from, Rüppell’s Fox (Lindsay & Macdonald 1986); in S Morocco encounters between these species are rare, as Rüppell’s Fox rarely goes into large sandy areas (F. Cuzin pers. obs.).

Fennecs are thought to be susceptible to pathogens and parasites that affect domestic dogs. There is some evidence that modified-live canine distemper vaccine may induce canine distemper in Fennec Foxes (Montali *et al.* 1994), but the newer sub-unit vaccines should not (R. Junge pers. comm.). Parasites recorded include trematodes (*Alaria alata*, *Joyeuxiella echinorhynchoides*, *Taenia crassiceps*) and nematodes (*Ancylostoma braziliense*, *A. caninum*, *A. duodenale*,

Cyathospirura seurati, *Oxyntema crassispiculum*, *Physaloptera cesticillata*, *Rictularia cahirensis*, *Spirocerca lupi*, *Spirura rytipleurites*, *Streptopharagus numidicus*, *Toxascaris*, *Toxocara masculior*, *Uncinaria stenocephala*) (see Larivière 2002a for references).

Conservation IUCN Category: Least Concern. CITES: Appendix II.

In Morocco, young foxes are captured in their burrows for sale to tourists, for photographic exhibition (Cuzin 2003), or even for meat (Schmidt-Nielsen 1964); adults may also be trapped for their fur. They occur in a number of protected areas throughout their range, including Ahaggar and Tassili n'Ajjer National Parks in Algeria, Banc d'Arguin and Diawling National Parks in Mauritania, Sidi Toui N. P. in Tunisia, Zellaf N. R. in Libya, and Bir El Abd Conservation Area in Egypt (Asa *et al.* 2004).

The North American Regional Studbook (Bauman 2002) lists 839 individuals held in captivity from 1900 to 2001. In 2001, there were 131 individuals in 51 institutions. The Australian Regional Studbook lists 81 historically, with only 12 in the captive population at present. Although Fennec Foxes occur in European zoos, there is no studbook or management plan. Fennec Foxes are also kept as pets and bred privately.

Measurements

Vulpes zerda

HB: 362 (333–395) mm, n = 9

T: 169 (125–187) mm, n = 9

HF c.u.: 93 (90–98) mm, n = 9

E: 91.3 (86–97) mm, n = 9

West Africa, Sudan, and northern Africa (Rosevear 1974)

HB: 368 (337–387) mm, n = 46

T: 207 (186–230) mm, n = 46

HF c.u.: 103 (93–111) mm, n = 46

E: 96 (88–104) mm, n = 46

WT: 1.1 (0.8–1.15) kg, n = 9

Egypt (Osborn & Helmy 1980)

HB (♂ ♂): 390, 395 mm, n = 2

HB (♀ ♀): 382 (345–395) mm, n = 5

T (♂ ♂): 225, 240 mm, n = 2

T (♀ ♀): 241 (230–250) mm, n = 5

HF c.u. (♂ ♂): 100, 110 mm, n = 2

HF c.u. (♀ ♀): 98 (92–100) mm, n = 5

E (♂): 100 mm, n = 1

E (♀ ♀): 93 (90–95) mm, n = 5

WT (♂ ♂): 1.3, 1.7 kg, n = 2

WT (♀ ♀): 1.4 (1.0–1.9) kg, n = 5

Saint Louis Zoo, St Louis, MO, USA

Key References Bauman 2002; Dragesco-Joffé 1993; Gangloff 1972; Gautier-Pilters 1962, 1967; Petter 1957; Valdespino 2000; Valdespino *et al.* 2002.

Cheryl S. Asa & Fabrice Cuzin

GENUS *Otocyon*

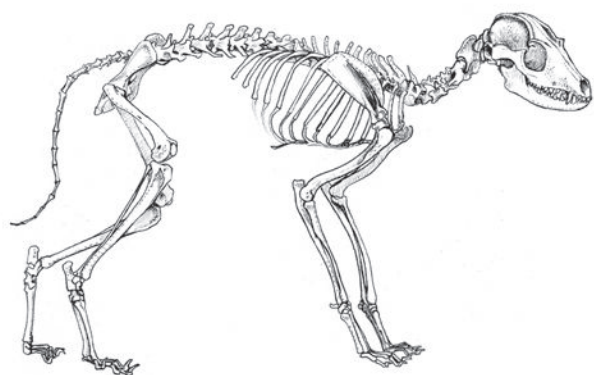
Bat-eared Fox

Otocyon Müller, 1836. Arch. Anat. Physiol., Jahresber. Fortschr. Wiss. 1835: [1836].

Otocyon is a monotypic genus, distributed in eastern and southern Africa in semi-arid and arid habitats, especially open grasslands, open scrub, *Acacia* savanna and shrublands. *Otocyon* was previously included in a separate subfamily, the Otocyoninae (Simpson 1945, Ellerman *et al.* 1953), on account of its unique dentition. Clutton-Brock *et al.* (1976), followed by other authors, have allied it with the typical canids,

although acknowledging its unique characters. Whereas typical canids have two upper and three lower molars, *Otocyon* typically have 3–4 upper and 4–5 lower molars, to yield a full dentition of 46–50, the highest amongst living eutherians, except odontocetes.

Jan A. J. Nel



Bat-eared Fox *Otocyon megalotis* skeleton.



Bat-eared Fox *Otocyon megalotis* myology.

Otocyon megalotis BAT-EARED FOX

Fr. L'Otocyon; Ger. Löffelhund

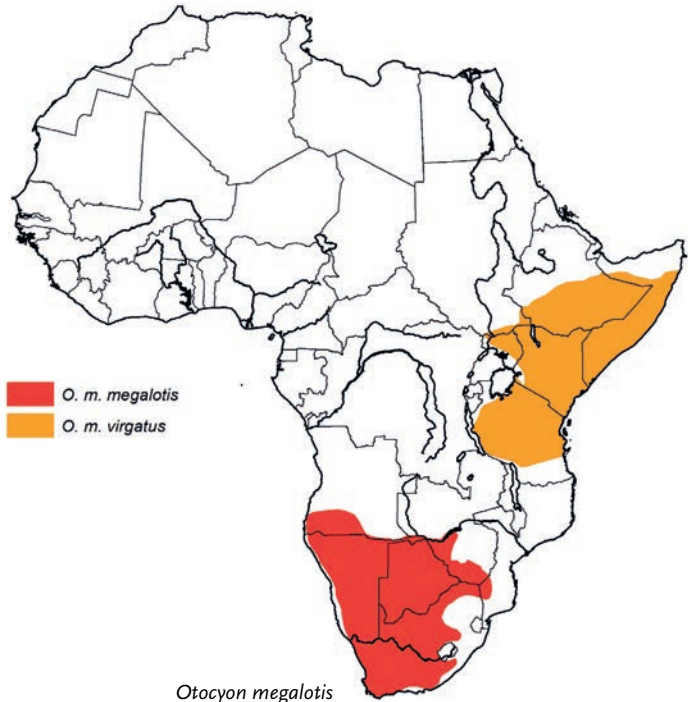
Otocyon megalotis (Desmarest, 1822). Mammalogie. In: Encyclop. Meth., 2 (Suppl.): 538.
'le Cap de Bonne-Espérance' [Cape of Good Hope, South Africa].

Bat-eared Fox *Otocyon megalotis*.

Taxonomy Two subspecies have been recognized (Coetzee 1977; and see Clarke 2005). Synonyms: *auritus*, *caffer*, *canescens*, *lalandii*, *steinhardti*. Chromosome number: $2n = 72$ (Wayne *et al.* 1987).

Description Small and slightly built with slender legs, but with fluffy pelage and a long bushy tail. Conspicuously large ears and short, sharp muzzle. Back of ears, front part of snout, face-mask, front legs and lower part of back legs, and tip and mid-dorsal part of tail black. A whitish band extends across the forehead to below and up the frontal rim of ears. Some individuals have a broad dark mid-dorsal band. Lower jaw, throat, chest and underparts buffy. Pelage paler in older individuals. Body and tail fur thick and soft; on upperparts with a black base and white tip, giving a grizzled or grey appearance; sides appear more buff. Underfur on the upper body about 30 mm long, while the dense over-layer of guard hairs measures about 55 mm. A sprinkling of tactile hairs up to 65 mm long occurs amongst guard hairs (Skinner & Chimimba 2005). They have an annual moult, which in southern Africa takes place between Aug and Sep and again between Jan and Feb (Smithers 1971). Females may weigh more than ♂♂ (see Smithers 1971). There are three pairs of abdominal nipples (Lynch 1983, Pauw 2000), although Skinner & Chimimba (2005) mention two pairs inguinal; the reasons for this discrepancy are unclear.

Skull elongated, narrowing evenly from the sides of the braincase to the front of the narrow muzzle. Supratemporal ridges well developed and extend backwards as a broad beading, to form a wide U-shape. Unique amongst living eutherians (except the odontocetes) in having 4–5 lower molars, and unique amongst living canids in having 3–4 upper molars (Guilday 1962). Supernumerary molars yield a dentition of $I^{3/3}$, $C^{1/1}$, $P^{4/4}$, $M^{3-4/4-5} = 46-50$ (unlike the

*Otocyon megalotis*

typically canid total of 42), the largest number for any non-marsupial land mammal. P^3 and P^4 are in contact in contrast to other canids (Roberts 1951).

Geographic Variation

O. m. megalotis: southern Africa, from Angola to Mozambique and South Africa

O. m. virgatus: East Africa, from S Sudan, Ethiopia and Somalia to Tanzania.

Similar Species

Vulpes chama. Sympatric in southern Africa. Somewhat smaller; silver-grey upperparts, underparts off-white to very pale fawn, head and back of ears reddish-fawn; tail very bushy with a black tip.

Distribution Endemic to Africa, occurring as two discrete populations, separated by about 1000 km, across the arid and semi-arid regions of eastern and southern Africa (Kingdon 1977, Skinner & Chimimba 2005). Occurs from S Sudan, Ethiopia and Somalia down through Uganda and Kenya to SW Tanzania, and then again from Angola through Namibia and Botswana to Mozambique and South Africa. No confirmed records from Zambia (Ansell 1978). The two ranges were probably connected during the Pleistocene (Coe & Skinner 1993). This disjunct distribution is similar to that of the Aardwolf *Proteles cristatus* and Black-backed Jackal *Canis mesomelas*. Range extensions linked to changing rainfall have occurred in southern Africa in recent years (e.g. Stuart 1981, Marais & Griffin 1993).

Habitat Mainly open grasslands, especially short-grass areas with bare patches, open arid or semi-arid *Acacia* savanna, open scrub and arid, semi-arid or winter rainfall (fynbos or Cape macchia) shrublands (Kingdon 1977, Nel & Mackie 1990, Skinner & Chimimba 2005). The range of both subspecies overlaps almost completely with that of *Hodotermes* and *Microhodotermes*, termite genera common in the diet (Mackie & Nel 1989, Maas 1993a). In Serengeti N. P. the species is common in open grassland and woodland boundaries, but not short-grass plains (Lamprecht 1979, Malcolm 1986).

Abundance Common in conservation areas in southern and eastern Africa, less common outside and in more arid areas in South Africa. Within a specific habitat, numbers can fluctuate dependent on rainfall, food availability (Nel *et al.* 1984), breeding stage or disease (Maas 1993a, b). In the SW Kalahari, regular counts along a 21 km stretch of dry river bed, with an area of ca. 10 km², recorded 7–140 individuals (or 0.7–14/km² (Nel *et al.* 1984, Nel 1996). In the Limpopo Province, South Africa, densities were 5.7 foxes/km², and in the nearby Mashatu G. R., Botswana, 9.2 foxes/km² in the breeding season and 2.3 foxes/km² at other times (Berry 1978). At Tussen-die-Riviere G. R., Free State, South Africa, Mackie (1988) recorded densities that varied from 0.3 to 0.5 foxes/km² over a three-year period, while Kuntzsch (1992) found densities that ranged from 1.1 to 2.0 foxes/km² in the central Karoo, Northern Cape, South Africa. Hendrichs (1972) recorded a density of 0.3–1.0 foxes/km² in Serengeti N. P.

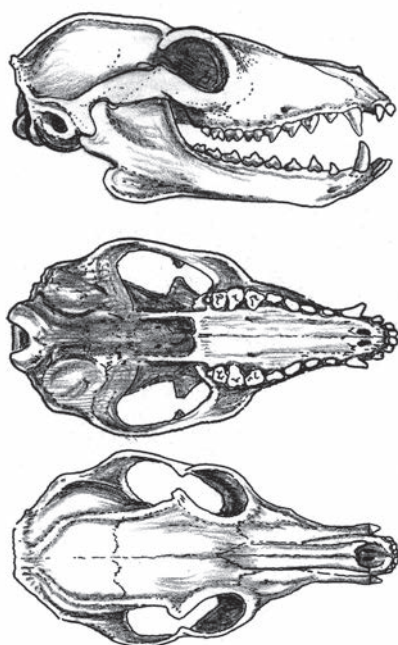
Adaptations Bat-eared Foxes show a number of morphological and behavioural adaptations to their insectivorous diet. Huge ears are used to locate insects and underground larvae (Smithers 1971) and may aid thermoregulation (Maas 1993b). Insectivory has not only affected the number of teeth (see Description), but also their shape; milk dentition is typically canid, with unreduced carnassials, but in adults the carnassial shear is lost and molars become the most

bunodont, verging on zalambdodont, of any canid (see Kieser 1995). A modification in the insertion point of the digastric muscle (in this case, in a flange situated vertically below or slightly in front of the glenoid) facilitates very rapid chewing (Kingdon 1977), up to five bites per second (Maas 1993b). In southern Africa, nocturnal foraging during summer changes to a diurnal pattern in winter, when subzero night temperatures are common (Nel 1990), mirroring similar changes in the activity of *Hodotermes mossambicus*; in eastern Africa, nocturnal foraging is the norm (Lamprecht 1979, Malcolm 1986, Maas 1993a, Wright 2004). By day, especially in winter, foraging peaks at the height of insect and termite activity (Nel 1990).

Group members huddle by night or in the early morning to escape the cold, or seek shade to escape the worst heat, or lie in the open, facing multiple directions, to ease predator detection. Dens are used for shelter and breeding and are excavated by breeding adults or adapted from disused dens of other mammals (e.g. springhares *Pedetes* spp., Aardvark *Orycteropus afer*, South African Ground Squirrel *Xerus inauris*, termite mounds and warthog holes *Phacochoerus* spp.; Lamprecht 1979, Maas 1993a). Dens have several entrances and chambers, and tunnels up to 3 m long (Smithers 1971, Berry 1978). Dens are carefully maintained throughout the year, although maintenance at breeding dens increases markedly in Aug (Smithers 1971) shortly before the birthing season. Apart from regular breeding dens, Bat-eared Foxes in Serengeti N. P. utilize 'foraging dens' for the protection of cubs in different parts of the territory (Maas 1993a). Breeding dens can be clustered: in the SW Kalahari, six dens were found in a 0.5 km² section of the river bed in 1976 (J. A. J. Nel pers. obs.); each den was occupied by an adult pair and 2–3 cubs (16 in total). Two further dens were nearby.

In some parts of the range, polygyny, allo-suckling and communal breeding occurs because insect prey has a high renewal rate, the cost of food sharing is low, and dispersal risk high amidst limited breeding territories (Maas 1993a). In Serengeti N. P., for example, allo-suckling and communal breeding occurs between closely related ♀♀ (Maas 1993a; and see Social and Reproductive Behaviour). In southern Africa, communal breeding is rare (Pauw 2000), but family groups can also coalesce, with up to ten non-suckling juveniles and three adults (J. A. J. Nel pers. obs.).

Foraging and Food Insectivorous. Food consists primarily of insects, with harvester termites *Hodotermes mossambicus* and *Microhodotermes viator* and beetles predominating and with smaller numbers of orthopterans, beetle larvae and ants (Berry 1978, Nel 1978, Lamprecht 1979, Stuart 1981, Koop & Velimirov 1982, Malcolm 1986, Mackie 1988, Maas 1993a, Skinner & Chimimba 2005). Other termite species are also taken, for example *Macrotermes* spp. in Botswana and Tanzania (Wright 2004, Skinner & Chimimba 2005). In open shrub savanna in Botswana other taxa such as arachnids can be more common, while fruit is taken seasonally (Nel 1978, Skinner & Chimimba 2005) but can be important in open shrub vegetation with scattered trees (Kuntzsch & Nel 1992). Small mammals, birds, eggs, reptiles and fruit are eaten sporadically in southern Africa (Nel 1978, Kok & Nel 1992, Kuntzsch & Nel 1992, Skinner & Chimimba 2005, Klare *et al.* 2011) but rarely in eastern Africa (Lamprecht 1979, Maas 1993a, Wright 2004). Seasonal changes in the proportion of particular taxa occur (Nel 1978, Nel & Mackie 1990, Maas 1993a, Klare *et al.* 2011). In Serengeti N. P. dung beetles are the main source of food during the wet season when termite activity is reduced (Waser 1980,



Lateral, palatal and dorsal views of skull of Bat-eared Fox *Otocyon megalotis*.



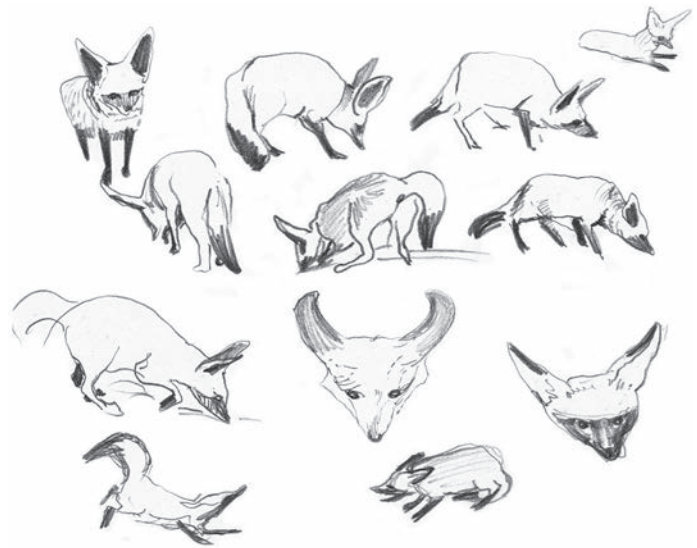
Bat-eared Fox *Otocyon megalotis* facial features.

Maas 1993a). When both are scarce, beetle larvae are often dug up from the ground (Maas 1993a). *Hodotermes mossambicus* is patchily distributed throughout the Serengeti and may constitute a limiting resource in this part of the species' range (Maas 1993a). Although the animals' water requirements may be met by the high water content of their insect prey or, in southern Africa, berries during the summer (Nel 1978, Kuntzsch & Nel 1992), water constitutes a critical resource during lactation (Maas 1993a).

Food is located primarily by sound (Nel 1978) but also by smell (Smithers 1971) while walking slowly with the nose close to the ground and the ears cocked forward. Foraging routes are mostly up- or crosswind (J. A. J. Nel pers. obs.). Foraging and feeding rates are higher when feeding on termites, concentrated in patches, than on other more dispersed insects (Nel 1990): they cover a mean of 1.3 km/h and have feeding bouts of 9.7 ± 8.5 sec/bout when feeding on termites, compared with 0.8 ± 0.3 km/h and 4.2 ± 1.7 sec/bout when feeding on dispersed insects. They also spend more of their foraging time ($69 \pm 11.7\%$) feeding when preying on termites than when preying on non-patch food ($4.3 \pm 2.4\%$) (Nel & Mackie 1990). When feeding on termite patches the foxes feed close together, but spread out to 200 m apart when feeding on other insects (Nel 1978, Maas 1993a).

Group members call each other to rich food patches with a low whistle. Males gradually initiate cubs into foraging, while ♀♀ forage independently (Nel 1978) till weaning (Maas 1993a). Social learning by cubs seems to be involved when first foraging (Nel 1999). Bat-eared Foxes do not cache food. They also do not take domestic stock, contrary to claims by farmers, or poultry. They do not scavenge or take carrion but will feed on maggots in carcasses. Stenkewitz & Kamler (2008) reported feeding associations between Bat-eared Foxes and at least four species of insectivorous birds, including the Southern Anteater-chat *Myrmecocichla formicivora*, Crowned Lapwing *Vanellus coronatus*, Double-banded Courser *Rhinoptilus africanus* and Northern Black Korhaan *Eupodotis afraoides*.

Social and Reproductive Behaviour Bat-eared Foxes in southern and East Africa live predominantly as monogamous pairs with cubs, with little extra-pair paternity (Nel *et al.* 1984, Wright *et al.* 2010; but see Pauw 2000), while those in eastern Africa have been reported living both in monogamous pairs (Wright *et al.* 2010) and in stable family groups that consist of a ♂ and up to three closely related ♀♀ with cubs (Maas 1993a). Group size varies with time of year, with a mean of 2.7 ($n = 623$) in the SW Kalahari. Average adult group size in Serengeti N. P. is 2.4 (± 0.1 , $n = 18$), and prior to dispersal of pups 6.0 (± 0.4 , $n = 18$; Maas 1993a). In Serengeti N. P., the



Bat-eared Fox *Otocyon megalotis*.

additional ♀♀ in the extended family groups are philopatric daughters, sometimes from several generations, which form a hierarchy based on age; all ♀♀ in such 'super families' breed (Maas 1993a).

Groups forage as a unit, and have home-ranges from less than 1 km² to more than 6 km². In southern Africa, home-ranges overlap widely (Nel 1978, Mackie & Nel 1989). In East Africa, they can either overlap (Malcolm 1986, Wright *et al.* 2010), changing little in size during the year, or, as in Serengeti, where they centre around harvester termite colonies, they can be defended as territories that are patrolled and urine-marked during part of the year (Lamprecht 1979, Maas 1993a). Group size determines the outcome of clashes during territorial conflict (Maas 1993). Territory inheritance is frequent in the Serengeti and neighbouring groups can be closely related, with animals visiting each other from time to time (Maas 1993a).

Bat-eared Foxes engage in frequent and extended allogrooming sessions, which serves to strengthen group cohesion (Maas 1993a). In the SW Kalahari it increases markedly (as does urine-marking) during courtship, when huddling, playing and mutual chasing are also more common than other times. Vigorous and extended social play is very common not only in cubs but also in adults even after the young have dispersed (B. Maas pers. comm.).

Communication is primarily visual, with a variety of ear and tail positions, emphasized by dark markings, used for displays (Nel & Bester 1983, B. Maas pers. obs.). The unique inverted U-position of the tail is indicative of a range of states of arousal including fear, play and alarm (Nel & Bester 1983). Vocalizations are mostly soft and sparingly used (Lamprecht 1979, Nel & Bester 1983), except when the animals are highly alarmed or excited during play (Maas 1993a). Urine marking is used on territory boundaries in East Africa (Maas 1993a) and for double marking during pair bonding (Nel & Bester 1983).

Pair-bonding and mating takes place from Jul to Sep in southern and East Africa with up to ten copulations per day for several days, and with a copulatory tie lasting ca. 4 minutes, followed by a peculiar post-copulatory play. Although the behaviour of partners is highly coordinated during the mating season, genetic data from a Kenyan population revealed that five of 44 cubs were sired by ♂♂ other than their social fathers (H. Wright pers. comm.). Small cubs nurse inside

the den, later outside, and first emerge for brief periods when they are 8–12 days old. Cubs are sometimes moved between dens (Maas 1993a, Pauw 2000).

Young cubs are initiated into foraging by the ♂ (Nel 1978), who spends more time close to the cubs than ♀♀, grooming, guarding and playing with them and defending them against predators (Wright 2006). Maternal investment during lactation is high in Bat-eared Foxes compared with other canids, but due to an insectivorous diet mothers and/or cubs cannot be provisioned directly (Maas 1993a; but see Pauw 2000). However, the high level of male parental care enables ♀♀ to maximize their foraging time. The importance of male care is illustrated by the fact that, in a Kenyan population, lactating ♀♀ spent >85% of the night actively foraging (Wright 2004), and the amount of time ♂♂ spent at breeding dens influenced cub survival to weaning (Wright 2006). The disparity in care between the sexes becomes less prominent after weaning (Berry 1978, Maas 1993a, Wright 2004), which in the SW Kalahari takes place after the first rains and subsequent flush of insects.

In eastern Africa, where there is more than one ♀, nursing effort per cub is higher in daughters than in ♂-females (Maas 1993a). The nuclear family group, consisting then of a mated pair and their cubs (in southern Africa), persists till the next Jun when cubs disperse and the pair, which mates for life, reaffirms their pair bond (Nel & Bester 1983).

Reproduction and Population Structure Bat-eared Foxes are sexually mature at 8–9 months. Births occur at the onset of the wet season, timed with the period of peak insect densities, from Sep to Dec in southern Africa (Smithers 1971, Lynch 1983, Nel *et al.* 1984) and Aug to Oct in East Africa (Malcolm 1986, Maas 1993a), after a gestation period of 60–75 days. They have a single litter per year. Litter-size is 1–6 (usually five); in Serengeti N. P. average litter-size is 2.6 (n = 90), although cubs raised per super-family averages 3.6 (n = 48) subject to annual variation potentially linked to food availability (Maas 1993a). The number of cubs to emerge from the den in ‘super-families’ is inversely related to the number of breeding ♀♀. Neonates weigh between 99 and 142 g. Lactation lasts 14–15 weeks (Lamprecht 1979). Longevity has been recorded at 17 years in captivity (Weigl 2005), and to nine years in the wild (Kamler & Macdonald 2006).

Predators, Parasites and Diseases Predators include raptors (e.g. Martial Eagle *Polemaetus bellicosus*, Spotted Eagle-owl *Bubo africanus*, Giant Eagle-owl *B. lacteus*), African Rock Python *Python sebae*, Spotted Hyaena *Crocuta crocuta*, Brown Hyaena *Hyaena brunnea*, Striped Hyaena *H. hyaena*, African Wild Dogs *Lycaon pictus* (see Rasmussen 1996) and Leopards *Panthera pardus* (see Bothma & Le Riche 1982). Pups may fall prey to Black-backed Jackals (Pauw 2000) and Ratels *Mellivora capensis* (Begg *et al.* 2003a). During droughts, or in the absence of suitable breeding territories (Maas 1993a), lack of food can cause starvation, or decrease ability to avoid predators. In southern Africa Bat-eared Foxes coexist widely with Black-backed Jackals and Cape Foxes with little overt aggression, perhaps due to food niche separation between the species. However, Bat-eared Foxes will displace Cape Foxes at dens or while feeding with cubs, and will mob and chase away Black-backed Jackals approaching breeding dens (J. A. J. Nel pers. obs.).

Little information on parasites, but Horak *et al.* (2000) recorded *Amblyomma marmoreum* (unusual on a wild carnivore smaller than a Lion *Panthera leo* and considered as evidence of stress in the host

animal) and *Haemaphysalis leachi/zumpti* from animals in the S Free State; *Haemaphysalis* spp. and *Ixodes pilosus* were also present on an animal taken in the Eastern Cape, South Africa (Horak *et al.* 1987).

Rabies (Maas 1993b, Nel 1993, Thomson & Meredith 1993) and canine distemper (Roelke-Parker *et al.* 1996) can cause drastic declines in populations. In Serengeti N. P. 90% of mortality in one population was caused by disease and 3% each by predation and road accidents (n = 94). Trichinellosis and canine parvovirus (CPV-2b) have been recorded (Pozio *et al.* 1997, Steinel *et al.* 2000).

Conservation IUCN Category: Least Concern. CITES: Not listed.

Primary threats include unwarranted persecution by farmers, and the effects of disease such as rabies and canine distemper. In addition, persistent drought can depress insect numbers leading to reproductive failure and precipitous drops in numbers. Unnatural mortality due to road kills can be numerous in South Africa, Namibia and Tanzania. Limited hunting and trapping for fur has taken place in some parts of their range, such as in Botswana, where treated pelts are sold as blankets (‘macloutsie’). Bat-eared Foxes are widespread and apart from healthy populations in farming areas enjoy protection in a number of national parks and other protected areas in their distribution areas, including Awash, Omo and Mago National Parks (Ethiopia), Masai Mara National Reserve (Kenya), Serengeti N. P. (Tanzania), Kidepo N. P. (Uganda), Etosha N. P. (Namibia), Kgalagadi Transfrontier Park (South Africa/Botswana), Hwange N. P. (Zimbabwe) and Augrabies Falls, Karoo, Namaqua, West Coast and Mountain Zebra National Parks (South Africa) as well as numerous smaller reserves (Nel & Maas 2004).

Measurements

Otocyon megalotis

HB (♂♂): 529 (462–607) mm, n = 25
 HB (♀♀): 536 (467–607) mm, n = 29
 T (♂♂): 298 (230–340) mm, n = 25
 T (♀♀): 303 (278–340) mm, n = 29
 HF c.u. (♂♂): 149 (140–161) mm, n = 25
 HF c.u. (♀♀): 150 (139–165) mm, n = 29
 E (♂♂): 124 (119–137) mm, n = 25
 E (♀♀): 124 (114–134) mm, n = 29
 WT (♂♂): 4.0 (3.4–4.9) kg, n = 22
 WT (♀♀): 4.1 (3.2–5.4) kg, n = 29
 Botswana (Smithers 1971)

HB (♂♂): 526 (470–570) mm, n = 22
 HB (♀♀): 515 (480–560) mm, n = 17
 HF c.u. (♂♂): 119 (110–130) mm, n = 22
 HF c.u. (♀♀): 118 (112–124) mm, n = 17
 E (♂♂): 111 (104–118) mm, n = 22
 E (♀♀): 109 (113–118) mm, n = 16
 WT (♂♂): 3.6 (3.1–4.1) kg, n = 22
 WT (♀♀): 3.5 (2.7–4.2) kg, n = 17
 Kenya (H. W. Y. Wright pers. comm.)

Key References Lamprecht 1979; Maas 1993a, b; Mackie 1988; Malcolm 1986; Nel 1978, 1990; Nel & Bester 1983; Nel *et al.* 1984; Skinner & Chimimba 2005; Wright 2004, 2006; Wright *et al.* 2010.

Jan A. J. Nel & Barbara Maas

Superfamily MUSTELOIDEA

MUSTELIDS

Musteloidea Fischer, 1817. Mém. Soc. Imp. Nat. Moscou 5: 372

Superfamily Musteloidea includes the families Mustelidae, Procyonidae, Ailuridae and Mephitidae. In Africa, it is represented only by the family Mustelidae, discussed below.

Family MUSTELIDAE

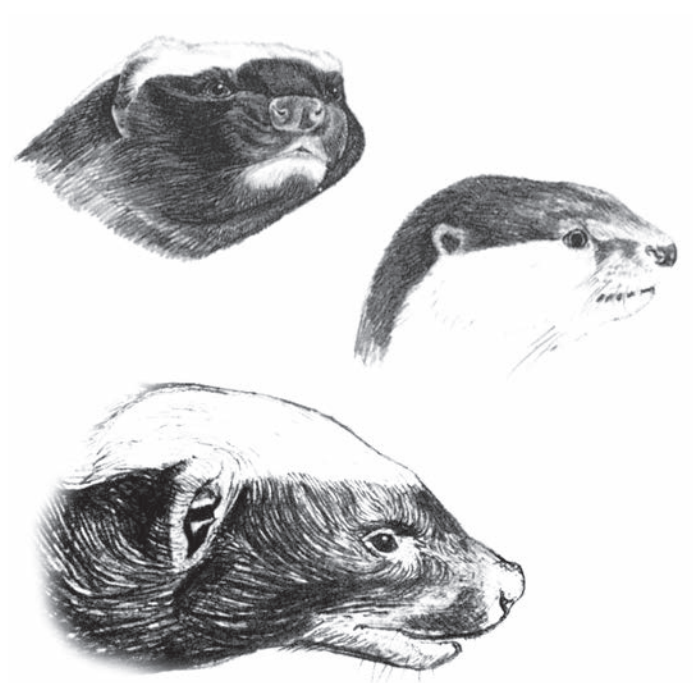
WEASELS, POLECATS, OTTERS, RATEL AND ALLIES

Mustelidae Fischer, 1817. Mém. Soc. Imp. Nat. Moscou 5: 372.

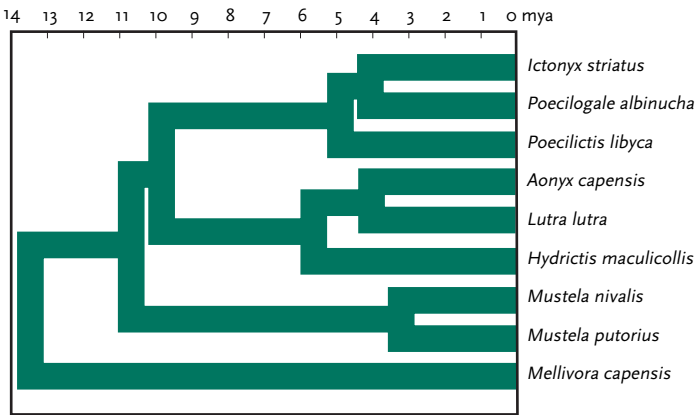
| | | |
|---------------------------------|------------------------|--------|
| Mustelinae | | |
| <i>Mustela</i> (3 species) | Weasels, Polecats | p. 85 |
| Ictonychinae | | |
| <i>Poeciliictis</i> (1 species) | Libyan Striped Weasel | p. 90 |
| <i>Ictonyx</i> (1 species) | Zorilla | p. 92 |
| <i>Poecilogale</i> (1 species) | African Striped Weasel | p. 98 |
| Lutrinae | | |
| <i>Aonyx</i> (2 species) | Clawless Otters | p. 103 |
| <i>Lutra</i> (1 species) | Common Otter | p. 111 |
| <i>Hydriictis</i> (1 species) | Spotted-necked Otter | p. 113 |
| Mellivorinae | | |
| <i>Mellivora</i> (1 species) | Ratel | p. 119 |

The Mustelidae (which contains weasels, polecats, minks, otters, martens, badgers and relatives) is a polygeneric family distributed throughout all continents except Antarctica and Australasia (though they have been introduced into New Zealand). The family Mustelidae is closely related to the Procyonidae (raccoons), Ailuridae (Red Panda *Ailurus fulgens*) and Mephitidae (skunks). These four families comprise the superfamily Musteloidea, which in turn is most closely related to the Pinnipedia (Fulton & Strobeck 2006, Sato *et al.* 2006, 2009). Mustelids occur in very varied habitats ranging from tropical rainforests to Arctic tundra and from deserts to inland waterways and coastal waters. This is the largest family of the order Carnivora. Wozencraft (2005) lists 22 genera and 59 species. As considered here, eight genera and 11 species occur in Africa.

A discussion of the classification of the Mustelidae, as currently understood, requires some elaboration on extralimital taxa. Until recently, five extant mustelid subfamilies in total have generally been recognized following Simpson (1945), namely Mustelinae, Lutrinae, Mellivorinae, Melinae and Mephitinae, although some have followed Pocock (1922) and recognized more subfamilies, including Ictonychinae, Guloninae, Helictidinae and Taxidiinae. There is now substantial evidence in support of a close relationship between the weasels, polecats and minks of the genera *Mustela* and *Neovison* (subfamily Mustelinae) and the otters (subfamily Lutrinae). Further, despite the treatment of Wozencraft (2005), who included taxa previously placed in Mellivorinae, Melinae, Ictonychinae, Guloninae, Helictidinae and Taxidiinae in Mustelinae, the distinctiveness of the subfamilies Mellivorinae (containing the Ratel *Mellivora capensis*),



Ictonychinae (African Striped Weasel) (top), Lutrinae (African Clawless Otter) (middle) and Mellivorinae (Ratel) (bottom).



Tentative phylogenetic tree of African Mustelidae (modified after Sato *et al.* 2012 and Wolsan & Sato 2010).

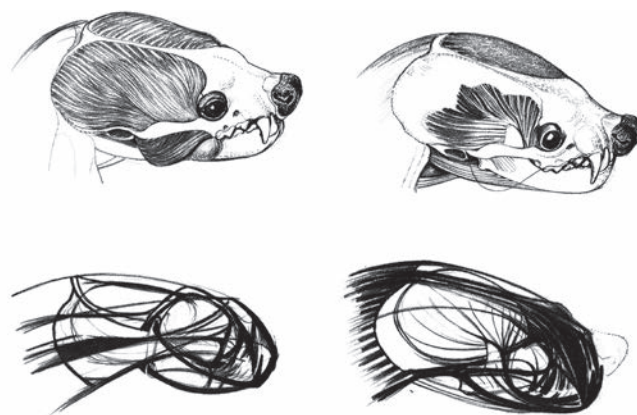


African Striped Weasel *Poecilogale albinucha* myology.

Melinae (containing the badgers of the genera *Meles* and *Arctonyx*), Ictonychinae (containing the polecats and weasels of the genera *Ictonyx*, *Poecilictis*, *Poecilogale*, *Vormela* and *Lyncodon*, and the grisons *Galictis*), Guloninae (containing the martens *Martes*, Fisher *Pekania pennanti*, Tayra *Eira barbara* and Wolverine *Gulo gulo*), Helictidinae (containing the ferret-badgers *Melogale*) and Taxidiinae (containing the American Badger *Taxidea taxus*) is also well evidenced at present (Koepfli *et al.* 2008, Wolsan & Sato 2010, Sato *et al.* 2012). The elevation of the skunks (including the stink badgers *Mydaus*) to the level of family agrees with Wozencraft (2005) and is now also well supported (Sato *et al.* 2009, 2012, Eizirik *et al.* 2010).

Mustelids are very small to medium-sized carnivorans, ranging in overall length and weight from 0.15 m and 0.025 kg (as in the Least Weasel *Mustela nivalis*, the smallest member of the order Carnivora) to 2.3 m (in the Giant Otter *Pteronura brasiliensis*) and 45 kg (in the Northern Pacific Sea Otter *Enhydra lutris*); sexual dimorphism in size (♂♂ larger than ♀♀) is pronounced in most species. Head and pinnae are usually small, neck and body long. Legs short, with five digits each; claws usually present, curved and non-retractile. In most otters, the minks and two species of South American weasels, the digits are webbed for swimming. Anal glands are usually present and well developed, with a large sac. The skull has a very short rostrum and long braincase (rostral length less than one-third of braincase length, as in the otters and mustelines) to a very long rostrum and short braincase (both about equal in length, as in the Hog Badger *Arctonyx collaris*). Other cranial features include: no alisphenoid canal; auditory bulla single-chambered; and middle ear with the mustelid suprameatal fossa (Wolsan 1993, 1999). Dental formula $I^{3/2-3}, C^{1/1}, P^{2-4/2-4} M^{1/1-2} = 28-38$; shearing blade of the upper carnassial without a slit-like notch; second lower molar, if present, small and single-rooted. Baculum (os penis) present in ♂♂.

Mustelids vary greatly in adaptations and biology. They are terrestrial, semi-arboreal (such as the martens and Tayra) or semi-aquatic (as the otters, minks and some South American weasels). They may be carnivorous or omnivorous, foraging both day and night or being either diurnal or nocturnal; in the northern part of their range, some remain inactive for several days, weeks or months during winter. Except during the mating season or when accompanied by young, most are solitary and territorial; some live in pairs and some in family or social groups. Secretion from the anal glands is used as a territory marker and, in species with striking, mostly black and white pelage patterning, in defence. Breeding is seasonal or non-seasonal. Copulation is vigorous, repeated and often very prolonged (which induces ovulation). Gestation lasts from four weeks to 12.5 months (as in the Stoat *Mustela erminea* and North American River Otter *Lontra canadensis*), including, in many species, a period of delayed implantation from a few days to 11



African Striped Weasel *Poecilogale albinucha*. Myology of skull musculature with diagrams of stress/reinforcement lines in the skull inserted.

months. There are 1–18 (usually 1–6) young per litter and between one and three (usually one) litters a year.

Four subfamilies are represented in Africa: Ictonychinae, Lutrinae, Mellivorinae and Mustelinae. The African ictonychines comprise three genera, each with a single species. They are adapted for terrestrial life, lightly built and skunk-like in appearance, with the tail length about two-thirds of head-and-body length. The pelage is black and white. In the skull, the pterygoid hamulus is fused with the auditory bulla. The upper dentition is characterized by the absence of a first premolar, with the second premolar being either present or absent; the carnassial is narrow relative to its length, with a small, antero-posteriorly short lingual wing; and the molar is short relative to its bucco-lingual width, with a small metacone. In the lower dentition, the second premolar is either present or absent; the carnassial is narrow relative to its length, with or without a metaconid and with a small talonid; and the second molar is either present or absent.

The African otters comprise three genera and four species (see genus accounts). These otters, like others in the subfamily, are adapted for aquatic life, with a streamlined body, and similarly broad head and neck; the tail is long (tail length exceeds the half of head-and-body length), thick and muscular to aid in swimming. A very dense underlayer of fur provides insulation in water. The pelage is largely brown to black. In the skull, the pterygoid hamulus is not fused with the auditory bulla. The upper dentition in all four species is characterized by the presence of the first and second premolars; the carnassial is broad relative to its length, with a large, antero-posteriorly long lingual wing; and the molar is long relative to its bucco-lingual width, with a large metacone. In the lower dentition, the second premolar is present; the carnassial is broad relative to its length, with both the metaconid and talonid large; and the second molar is present.

The Ratel *Mellivora capensis* is the single extant genus and species of the subfamily Mellivorinae. It is adapted for terrestrial life, heavily built and badger-like in appearance, with the tail length about one-third of head-and-body length. The pelage is largely black, dark grey and white. In the skull, the pterygoid hamulus is not fused with the auditory bulla. The upper dentition is characterized by the absence of a first premolar, with the second premolar being present; the carnassial is broad relative to its length, with a small, antero-posteriorly short lingual wing; and the molar is short relative to its bucco-lingual width, with a small metacone. In the lower dentition, the second premolar is present; the carnassial is narrow relative to its length,

without a metaconid and with a small talonid; and the second molar is absent.

The African mustelines comprise one genus containing three species. They are adapted for terrestrial life, lightly built and weasel-like in appearance, with the tail length about one-third of head-and-body length. The pelage is largely pale yellow to dark brown. In the skull, the pterygoid hamulus is not fused with the auditory bulla. The upper dentition is characterized by the absence of a first premolar, with the second premolar being present; the carnassial is narrow relative to its length, with a small, antero-posteriorly short lingual wing; and the molar is short relative to its bucco-lingual width, with a small metacone. In the lower dentition, the second premolar is present; the carnassial is narrow relative to its length, without a metaconid and with a small talonid; and the second molar is present.

The fossil record of Mustelidae (including stem mustelids) ranges from the late Oligocene onward in Europe, from the early Miocene onward in Africa, Asia and North America and from the late Pliocene onward in South America. The earliest known African mustelids are *Luogale rusingensis* from Kenya (Schmidt-Kittler 1987) and *Namibictis senuti* from Namibia (Morales *et al.* 1998), both dated between 20 and 17 mya. Although the earliest record of Mustelidae is from Europe, the family appears to have its origin in south-eastern Asia at the beginning of the late Oligocene, about 28.4 mya (Sato *et al.* 2009, 2012, Eizirik *et al.* 2010). The earliest mustelids (such as the

late Oligocene *Plesictis plesictis* and *Bathygale sicaulensis*) were small predators and the predatory mode of life has prevailed within the family during its history. This adaptation has only involved niches for small to medium-sized predators except for the late Miocene to Pliocene interval when the largest mustelids that ever lived shared the niche for large predators in Eurasia, North America and also Africa, from where the gigantic mellivorine *Ekorus ekakeran* and the gigantic lutrines of the genus *Enhydriodon* are known (Werdelin 2003a, Werdelin & Lewis 2005). The last are parts of the extensive late Miocene–Pliocene African radiation of the tribe Enhydriodontini (Werdelin & Lewis 2005, Pickford 2007). The largest African Enhydriodontini were the largest mustelids known, with a body mass of 250 kg or more (Lewis 2008). The earliest record of omnivory (represented by *Stromeriella depressa*) is from the early Miocene and since that time this adaptation has repeatedly been developed within the family. All subfamilies had diverged by the end of the Miocene (Sato *et al.* 2012). Although mustelids attain great diversity in the tropics, they are the most common carnivorans of the temperate regions. In Africa, the diversity of mustelids is lower than on any of the other continents, but the spectrum of their habitats is very wide, ranging from rainforests to deserts and including freshwater and coastal waters.

Mieczysław Wolsan

Subfamily MUSTELINAE – Weasels, Polecats

Mustelinae Fischer, 1817. Mém. Soc. Imp. Nat. Moscou 5: 372.

The Mustelinae (which contains weasels, polecats and minks) is widespread in Eurasia and North America and also occurs in North Africa and N South America (introduced into New Zealand), in habitats ranging from rainforests to tundra and from semi-deserts to freshwater and riparian areas. This is the most diverse subfamily of the family Mustelidae: there are currently two genera and 18 species (Wozencraft 2005). One genus (*Mustela*) and three species occur in Africa.

Mustelines are very small to small mustelids, ranging in overall length and weight from 0.15 m and 0.025 kg (as in the Least Weasel *Mustela nivalis*) to 0.75 m and 2 kg (as in the Steppe Polecat *Mustela eversmannii*). The head is small, flat-topped and roughly triangular, the vibrissae long, and the pinnae short and rounded. The neck and body are very long and slender, with legs very short and the tail length from one-fourth to two-thirds of the head-and-body-length; the elongated body shape is an adaptation that enables penetration of confined spaces (especially burrows) in search of prey. Sexual dimorphism in size is more pronounced in Mustelinae than in any other mustelid subfamily. This strong dimorphism appears to be an adaptation for the different roles of the two sexes in reproduction: large males being favoured by competitive mating and small females because of lower energetic requirements and greater efficiency in hunting small prey – vital advantages when rearing young (Erlinge 1979). In northern populations of the Stoat *Mustela erminea*, Long-

tailed Weasel *Neovison frenata* and the Least Weasel, the pelage turns white in winter.

The skull is long, narrow and dorso-ventrally flattened, with a short rostrum and long braincase (rostral length is about or less than one-third of braincase length); the middle-ear cavity is mostly filled with a spongy bone. Dental formula is $I^{3/3}, C^{1/1}, P^{3/3}, M^{1/2} = 34$. The upper and lower carnassials are long and narrow, with a long shearing blade; the lower carnassial lacks a metaconid and has a short, cutting talonid. The upper molar is elongated transversely and constricted antero-posteriorly, smaller than or about equal in size to the upper carnassial.

Most (including all African) mustelines are purely or largely terrestrial; the American Mink *Neovison vison*, European Mink *Mustela lutreola*, Amazon or Tropical Weasel *Neovison africana* and Colombian Weasel *N. felipei* are semi-aquatic. They are strictly or almost strictly carnivorous (including specialist and opportunistic hunters), promiscuous and, except during the mating season or with young, solitary and territorial. Gestation lasts from four weeks to 12.5 months (as in the Stoat), including, in some species, delayed implantation lasting up to 11 months. Litter-size is 1–18 (usually 1–8) with 1–3 (usually one) litters per year.

Mieczysław Wolsan

GENUS *Mustela*

Weasels, Polecats

Mustela Linnaeus, 1758. Syst. Nat., 10th edn, 1: 45.

Mustela is a polytypic genus distributed widely in North Africa, Eurasia, North America and N South America (introduced into New Zealand), in habitats ranging from rainforests to tundra and from semi-deserts to freshwater and riparian areas. This is the largest genus of the order Carnivora comprising 17 species (see Wozencraft 2005), of which three occur in Africa: the Least Weasel *M. nivalis* occurs in Morocco, Algeria and Tunisia; the Egyptian Weasel *M. subpalmata* is found only in Egypt; and the European Polecat *M. putorius* occurs only in Morocco.

In Africa, both the Least Weasel and Egyptian Weasel (both contained in the subgenus *Gale*) are characterized by small size; face without a dark mask across the eyes; tail not bushy; skull long and narrow, without noticeably projecting mastoid processes; and auditory bulla long, narrow and approximately rectangular. The European Polecat is contained in the subgenus *Putorius* and characterized by larger size; face with a dark mask across the eyes; tail bushy; skull short and broad, with noticeably projecting mastoid processes; and auditory bulla short, broad and approximately triangular.

Mieczysław Wolsan

Mustela nivalis LEAST WEASEL (COMMON WEASEL)

Fr. Belette; Ger. Wiesel (Mauswiesel)

Mustela nivalis Linnaeus, 1766. Syst. Nat., 12th edn, p. 69. Vesterbotten, Sweden.



Least Weasel *Mustela nivalis*.

The allopatric Least Weasel and Egyptian Weasel (below) have a relationship that is still uncertain. This issue and their common biology are discussed in the profile that follows.

Robbie A. McDonald

Mustela subpalmata EGYPTIAN WEASEL

Fr. Belette égyptienne; Ger. Ägyptischer Wiesel

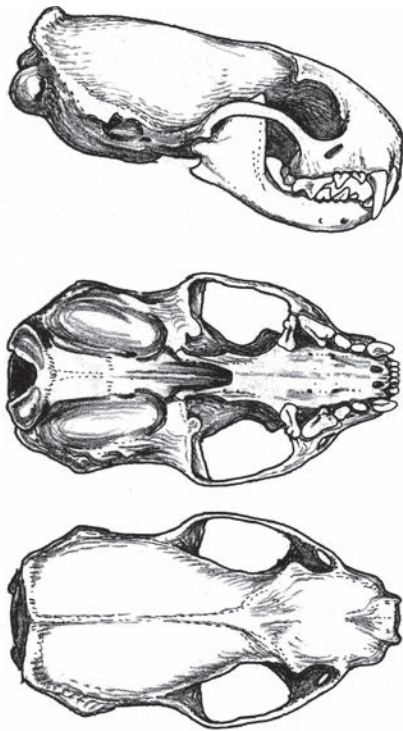
Mustela subpalmata Hemprich & Ehrenberg, 1833. Symb. Phys. Icon., Mamm. 3 (2).

In: 'Herpestes leucurus'; K verso. 'In domibus aegyptiacis Cahirae et Alexandriae murium vulgaris socius.'

Taxonomy The Least Weasel *M. nivalis* is a Holarctic species with a single African subspecies, *M. n. numidica*. This subspecies has been treated as a distinct species, of which the form *M. numidica subpalmata* from Egypt was considered a race on the grounds of its larger size (Allen 1939, Frechkop 1963). Subsequent authors have continued to recognize *numidica* as only a subspecies of *M. nivalis*, due to the general increase in the species' body size with decreasing latitude (Ellerman & Morrison-Scott 1951, Coetzee 1977). More recently, *numidica* has been thought to be sufficiently similar to southern European forms to be part of *M. n. vulgaris* (Van Zyll de Jong 1992). However, based on cranial morphology, the Egyptian Weasel *Mustela subpalmata* is a strong candidate for consideration as a distinct species (Van Zyll de Jong 1992, Reig 1997, Abramov & Baryshnikov 2000)



Egyptian Weasel *Mustela subpalmata*.



Lateral, palatal and dorsal views of skull of Least Weasel *Mustela nivalis*.

and was treated as such by Wozencraft (2005). This classification is followed here, but the two species are treated under *M. nivalis* for convenience; the information presented pertains to both species, unless indicated.

Synonyms (*nivalis*): *africana* Gray (not of Desmarest), *atlas*, *numidica*; (*subpalmata*): none.

Chromosome number for *M. n. nivalis* and *M. n. vulgaris*: $2n = 42$ (Zima & Král 1984). Chromosome number for *M. subpalmata*: not known.

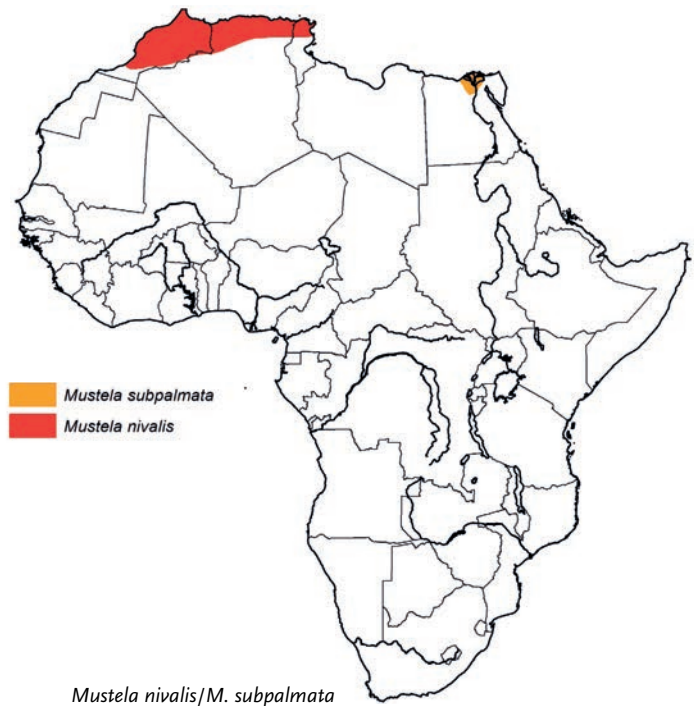
Description Small, elongated, slender body with pointed muzzle, short legs and short (one-quarter of body length, though slightly longer in *Mustela subpalmata* at approximately 30–40% of body length) furred tail. Conspicuous black eyes; rounded but flattened ears. Long, cat-like vibrissae. Dorsal pelage dull chestnut brown, ventral pelage white to creamy-yellow sometimes with spots of brown distributed in individually recognizable patterns. Irregular margin between dorsal brown and ventral pale fur. Distinct brown pads on paws. Males markedly larger than ♀♀. Usually four pairs nipples, visible only in adult ♀♀.

Skull flattened with broad, delicate zygomatic arch and large, rounded braincase. Sagittal and nuchal crests and postorbital constriction more pronounced in older animals than in younger animals. Small incisors, large canines, four premolars and molars in upper row, five on lower jaw. Molars have pronounced carnassial shear.

Geographic Variation None recorded.

Similar Species

Mustela putorius. In Africa, known from Morocco only. Larger, with marbled brown and cream pelage; face with a dark mask across the



eyes; skull short and broad, with noticeably projecting mastoid processes; auditory bulla short, broad and approximately triangular. *Poecilictis libyca*. Larger, stockier build, with characteristic striped black and white pelage.

Distribution Least Weasels are at the southernmost part of their Holarctic range in Africa and are confined to Morocco, Algeria and Tunisia; they may have been introduced by humans (Dobson 1998). The Egyptian Weasel is endemic to Africa and lives in the lower Nile Valley of Egypt, between Beni Suef in the south and Alexandria and the Delta in the north (Handwerk 1993). Morphology and biogeographical relationships with fossil record of the Middle East suggest Egyptian populations are a natural relict (Dayan & Tchernov 1988).

Habitat In north-west Africa, Least Weasels mostly inhabit regions with moderate rainfall (>500 mm), including coastal regions, irrigated farmland, forests and higher altitude zones up to 2600 m in the Moroccan High Atlas. In regions with lower rainfall (<500 mm), they are restricted to humid localities, including, for example, oases at the northern fringe of the Sahara (Aulagnier 1990, Kowalski & Rzebik-Kowalska 1991, Cuzin 1996, 2003).

Egyptian Weasels are largely commensal with humans. They are often trapped in underground larders and even in cars (Flower 1932, Osborn & Helmy 1980, Handwerk 1993, Hoath 2003).

Abundance In Morocco, Least Weasels are common outside of zones of intensive agriculture (Aulagnier 1990). Populations are stable or may have declined slightly between late 1980s and 1990s (Cuzin 1996). Information elsewhere is very scarce. Egyptian Weasels are considered common to abundant in parts of Cairo with densities of 0.5–1.0/ha estimated from trapping (Handwerk 1993). Populations volatile, and vary annually and seasonally in relation to prey availability.

Adaptations Specialized for pursuit of rodents, their elongated body-shape allowing entry to tunnels and narrow crevices.

Foraging and Food In north-west Africa, Least Weasels mainly eat small mammals (including *Apodemus*, *Gerbillus* and *Meriones*, possibly *Crociodura*) and birds, including hens (F. Cuzin pers. comm.).

Egyptian Weasels are opportunistic feeders, their diet comprising an unusually high percentage of fruit and vegetables, mainly grapes, dates and beans ($\approx 50\%$), as well as domestic hens and ducks ($\approx 20\%$) (Handwerk 1993). Rodents and domestic rabbits were less significant, as were invertebrates and fish (Osborn & Helmy 1980, Handwerk 1993). They also scavenge from waste heaps. Egyptian Weasels are active mainly at night and in the early evening, but also occasionally by day in seasonally variable bursts of activity alternated with prolonged rest periods (Handwerk 1993).

Social and Reproductive Behaviour Solitary and territorial. Larger male territories encompass a number of female territories, and territories are marked with faeces and urine. Mating is vigorous and prolonged, since ovulation is stimulated by the baculum (os penis) during copulation. Vocalizations include chattering and trilling during courtship and family play; they have a sharp, barking alarm call.

Reproduction and Population Structure There is direct implantation and gestation of approximately 4–5 weeks. When sufficient food is available there can be 2–3 litters a year, and young ♀♀ can breed in the year of birth. In Egypt, breeding occurs around Apr and Aug (Handwerk 1993). Litters have been recorded in Aug (four kits; Handwerk 1993) and early Dec (five kits; Flower 1932). Kits born naked and helpless, develop killing behaviour by approximately ten weeks and reach independence shortly afterwards. Few live more than one year.

Predators, Parasites and Diseases Likely predators include foxes, raptors and crows. A range of bacterial and viral diseases affects weasels and there are a few specific parasites. Two species of flea have been recorded, *Xenopsylla cheopis* from Rabat, Morocco (Jordan 1931) and *X. ramesis* from Mecharia, Algeria (Hopkins & Rothschild 1953).

Conservation IUCN Category: Least Concern (*Mustela nivalis*); Least Concern (*M. subpalmata*). CITES: Not listed.

Although issues of conflict with humans arise where predation of domestic animals is a problem, there is little cause for concern for either species, since they are both common and adaptable. In Morocco the species is commercially utilized for witchcraft purposes (F. Cuzin pers. comm.).

Measurements

Mustela nivalis numidica

GLS (♂♂): 42.9 mm, n = 4

North-west Africa (Van Zyll de Jong 1992)

Two further ♂♂ had GLS 43.2, 45.4 mm; one ♀ had GLS 39.0 mm (Alcover & Jaume 1983)

No other measurements available for Africa

Mustela subpalmata

HB (♂♂): 289 (252–301) mm, n = 9

HB (♀♀): 242 (232–259) mm, n = 5

T (♂♂): 117 (109–129) mm, n = 9

T (♀♀): 99 (94–110) mm, n = 5

HF c.u. (♂♂): 50 (45–55) mm, n = 9

HF c.u. (♀♀): 39 (34–42) mm, n = 5

E (♂♂): 21 (20–23) mm, n = 9

E (♀♀): 18 (15–20) mm, n = 5

WT (♂♂): 390 (355–425) g, n = 6*

WT (♀♀): 209 (190–230) g, n = 5*

GLS (♂♂): 50.0 (48.2–51.2) mm, n = 7

GLS (♀♀): 43.2 (41.8–43.9) mm, n = 5

Egypt (Osborn & Helmy 1980)

*Handwerk 1993

Other recorded mean GLS measurements include: 48.6 mm (n = 8) for ♂♂ and 43.6 mm (n = 8) for ♀♀ (Van Zyll de Jong 1992); 48.8 mm (n = 22) for ♂♂ and 42.5 mm (n = 13) for ♀♀ (Reig 1997)

Key References Cuzin 1996; Flower 1932; Handwerk 1993; Kowalski & Rzebik-Kowalska 1991; Osborn & Helmy 1980.

Robbie A. McDonald

Mustela putorius EUROPEAN POLECAT

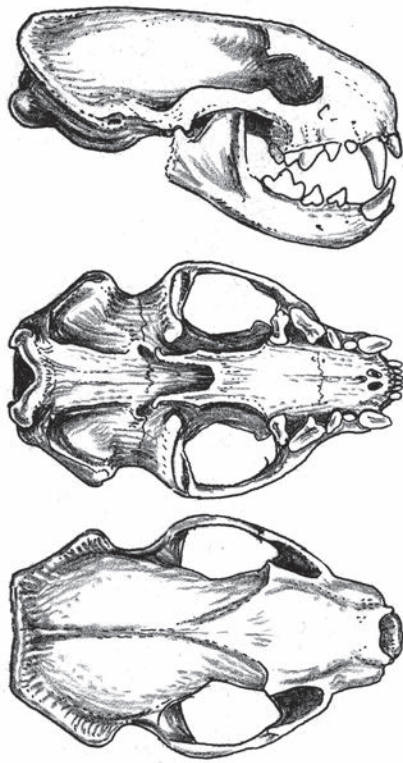
Fr. Furet; Ger. Frettchen

Mustela putorius Linnaeus, 1758. Syst. Nat., 10th edn, 1: 46. 'inter Europae rupes et lapidum acervos', restricted by Thomas (1911) to 'Scania, S Sweden'.



European Polecat *Mustela putorius*.

Taxonomy Monotypic. There has been some past debate over whether African populations (known only from Morocco) are true European Polecats or merely feral populations of their domesticated form (*furo*). Owen (1984) and Aulagnier & Thévenot (1986) are strongly of the opinion that Moroccan populations are ascribable to the latter. Owen (1984) even brought Moroccan ferrets to the United Kingdom and bred them for many years noting 'their colour and behaviour were similar to those of British specimens, except that no white specimens were bred'. However, while this animal could represent a feral exotic, recent fossil evidence suggests otherwise.



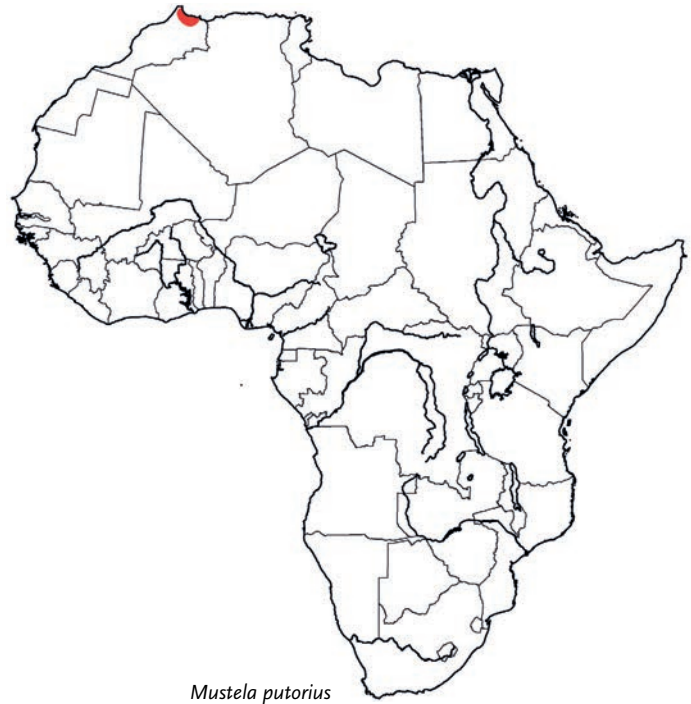
Lateral, palatal and dorsal views of skull of European Polecat *Mustela putorius*.

The only fossil record known is from El Harhoura I. (Temara), where two skulls and various post-cranial elements were ascribed to *M. putorius* by Aouraghe (2000). Dating for this site is poor, but the finds are ascribed to the late Pleistocene, and Aouraghe (2000) suggests that *M. putorius* may represent a relictual element within the fauna. Based on this evidence, we provisionally retain *M. putorius* as an African species (and see Wozencraft 2005). However, the possibility that Moroccan polecats are ancestral to ferrets cannot be excluded. The species is included in the subgenus *Putorius* (Abramov 2000).

Discrimination of feral ferrets from European Polecats is difficult because the two forms are closely related and a continuum of morphological variation may exist. For the purposes of discrimination, reliance upon the narrower postorbital constriction in ferrets is now questionable following work on British specimens (Kitchener *et al.* 1999). MtDNA markers apparently are also not considered reliable discriminants (Davison *et al.* 1999). Kitchener *et al.* (1999) developed a system of scoring pelage characteristics to discriminate between European Polecats and feral ferrets in Britain. Although free-living ferret populations occur on the British Isles, on some Mediterranean islands and New Zealand, few data are available on the species in the wild (King *et al.* 1996, Clapperton 2001).

Chromosome number: $2n = 40$ (FN = 68) (Fredga 1967), although animals from Morocco have not, to our knowledge, been karyotyped.

Description Slender, elongated body with short legs and tail; head with a short muzzle, small (normally light-coloured) ears, and small but pronounced brown eyes. Body colour of Moroccan populations is dark brown, with black guard hairs with lighter coloured underfur. Underbody, legs and tail are black to dark brown; face has a 'bandit mask' across the eyes (as is typical of other European



Mustela putorius

Polecat populations); albino forms are unknown in Morocco. Claws of fore- and hindfeet robust and moderately elongated. If similar to animals from elsewhere in the species' range, ♂♂ considerably larger than ♀♀ (about 50% heavier). Up to five pairs of nipples.

Skull typically mustelid, robust and rather flat, with marked postorbital constriction. Sagittal crest more developed in ♂♂ and older animals (Heráň 1974). Incisors small, canines large and almost straight.

Geographic Variation None recorded.

Similar Species

Mustela nivalis. Smaller, with ventral pelage white; face without dark mask across the eyes; skull long and narrow, without noticeably projecting mastoid processes; auditory bulla long, narrow and approximately rectangular.

Poecilectis libyca. Distinct black and white markings; lives in much drier habitat.

Distribution In Africa, there are records of European Polecats only from Morocco. Cabrera (1932) cites localities in Rif, between Chefchaouen and Oued Nekkour, and, further in the east, Brosset (1960) cites one locality in Beni Snassen. In 1986 and 1987, wild animals were seen in two localities of the area of Chefchaouen (western Rif) (Cuzin 1996). According to Cabrera (1932), wild animals were frequently caught for hunting rabbits, while Owen (1984) notes that the inhabitants of the Rif have bred these animals for the hunting of rabbits 'from time immemorial'; this was done in secret to avoid punitive Spanish game laws. Loche (1867) included this species on the list of mammals occurring in Algeria, but it has never been officially recorded (Kowalski & Rzebiak-Kowalska 1991).

Extralimittally, European Polecats are widespread in the western Palaearctic up to the Ural Mts in Russia, but are absent from Ireland, northern Scandinavia, and much of the Balkans and eastern Adriatic

coast. However, feral populations of the domesticated form (the ferret) have become established in a number of areas, including, for example, northern Britain, the Azores and New Zealand.

Habitat In Morocco the European Polecat lives in the most broken mountains of the Rif, and perhaps still in the Beni Snassen mountains. All these areas are comparatively wooded and rainy (from 400 mm up to more than 1100 mm of annual rainfall), compared with neighbouring areas. The altitudinal range of the area where animals may be found is from sea level up to 2400 m.

Abundance The European Polecat apparently inhabited the western and central Rif area in the eighteenth century (Shaw 1738, in Cabrera 1932) and, even though formal data are lacking, Cabrera (1932) suggested that populations were decreasing, and this trend was attributed by local people to the fact that ♀♀ rearing young were killed for catching the young. Presently, Cuzin (1996) suggests populations may be decreasing, although data are scarce.

Adaptations Slender body size is an obvious adaptation for entering the burrows of prey, and they can also enlarge burrows with their robust claws. The anal glands produce a noxious fluid that the animal sprays at potential predators.

Foraging and Food European polecats are solitary hunters that are active primarily at night (daytime activity tends to be underground). In Morocco they are said to eat small rodents, birds and their eggs (Aulagnier & Thévenot 1986) and probably rabbits. Little information is available from elsewhere, but in New Zealand ferrets take lagomorphs, rodents, birds, reptiles and invertebrates (King *et al.* 1996, Clapperton 2001). Feeding ecology is plastic, but some New Zealand studies suggest that ♂♂ may take more lagomorph and large rodent prey than ♀♀. In Britain both sexes prey heavily upon rabbits and rabbit burrows are commonly used as daytime resting sites (Birks & Kitchener 1999).

Social and Reproductive Behaviour No information available from the African part of the range, and little known from the wild elsewhere. Solitary, territorial and polygamous. Males have larger home-ranges than ♀♀, and scent-mark with anal gland secretions; home-range of ♂♂ may overlap those of ♀♀. The animal is active and alert, often standing erect on its hindlimbs when wary.

Reproduction and Population Structure Assuming reproductive biology is similar to that of other European polecats, Moroccan animals are likely to breed once a year without courtship. Spring mating vigorous, with ovulation stimulated by the os baculum, or possibly by the violent nature of mating, in which ♂ uses his teeth to grip back of neck of ♀ for many minutes, restraining her while copulation occurs (J. Birks pers. comm.). No delayed implantation and gestation is roughly 42 days. Young born May or Jun, wean at about three weeks, attain full adult dentition at 12 weeks and become independent from mother at three months of age.

In captivity can live more than ten years (Weigl 2005), although six is more usual. In New Zealand feral ferrets aged at least four years have been captured. Mortality of dispersing juveniles is high, especially from disease and starvation (Clapperton 2001).

Predators, Parasites and Diseases No information available on wild populations in Africa, but they are likely to be preyed upon by larger carnivores and birds of prey. Presumably subject to infection by wide range of viral and bacterial diseases, as well as protozoan, nematode, helminth and arthropod parasites.

Conservation IUCN Category: Least Concern. CITES: Not listed.

Not protected in Morocco. Possibly captured in some areas for rabbit hunting. There is a need for up-to-date information on the distribution and status of populations in North Africa.

Measurements

Mustela putorius

HB: 350–450 mm

T: 120 mm

Sh. ht: 45–60 mm

Morocco (Aulagnier & Thévenot 1986)

Sample sizes were not given, but presumably measurements are based on several animals in alcohol held in the Museum de l'Institut Scientifique, Rabat. There are no weight data from Morocco available; elsewhere, mean weight is 1.2 kg for ♂♂ and 0.8 kg for ♀♀ (Johnson *et al.* 2000)

Key References Aulagnier & Thévenot 1986; Cabrera 1932; Cuzin 1996.

Huw I. Griffiths & Fabrice Cuzin

Subfamily ICTONYCHINAE – Striped Weasels, Zorilla

Ictonychinae Pocock, 1922. Proc. Zool. Soc. Lond. 1921: 835.

The Ictonychinae (the polecats, weasels and grisons) is a polygeneric subfamily distributed widely in Africa and South America and also occurring in Eurasia and S North America, in a wide variety of habitats ranging from rainforests to deserts. As considered here, there are six genera (the African *Ictonyx*, *Poecilictis* and *Poecilogale*, Eurasian *Vormela*, South American *Lyncodon* and South and S North American *Galictis*) and seven species (Sato *et al.* 2012). Wozencraft (2005) included the Libyan Striped Weasel *Poecilictis libyca* in the genus *Ictonyx* (and see Rosevear 1974). However, evidence from DNA

sequences indicates that *Ictonyx* so circumscribed is paraphyletic with respect to *Poecilogale* (Koepfli *et al.* 2008, Sato *et al.* 2012).

Ictonychines are small to medium-sized mustelids, ranging in overall length and weight from 0.3 m and 0.20 kg (as in the Libyan Striped Weasel) to 0.76 m and 3.8 kg (as in the Greater Grison *Galictis vittata*). The pelage is contrastingly coloured black and white in the African species. Dental formula is $I^{3/3}, C^{1/1}, P^{2-3/2-3}, M^{1/1-2} = 28$ or 34.

Members of the subfamily are primarily terrestrial and carnivorous. Except during the mating season or with young, they

are mostly solitary, but occasionally travel or hunt in pairs or small groups. Gestation lasts from 30 days (as in the African Striped Weasel *Poecilogale albinucha*) to 11 months (as in the Marbled Polecat *Vormela peregusna*), including, in the latter species, delayed implantation. Litter-size is 1–8, with usually one litter born per year.

Three genera, each containing a single species, occur in Africa. *Ictonyx* and *Poecilictis* have the second upper and lower premolars

present; fourth lower premolar with a posterior accessory cusp; lower carnassial with the metaconid; and second lower molar present. *Poecilogale* has the second upper and lower premolars absent; fourth lower premolar without a posterior accessory cusp; lower carnassial without a metaconid; and second lower molar absent.

Mieczysław Wolsan

GENUS *Poecilictis* Libyan Striped Weasel

Poecilictis Thomas & Hinton, 1920. Ann. Mag. Nat. Hist. (9)5:367.

The genus *Poecilictis* is monotypic, represented by a single species, the Libyan Striped Weasel *P. libyca*, from North Africa. The species is often treated as congeneric with *Ictonyx* (see Rosevear 1974, Niethammer 1987, Wozencraft 1993, 2005), but is here included in its own genus based on recent molecular evidence (Koepfli *et al.* 2008, Sato *et al.* 2012), and in line with earlier authors (e.g. Thomas & Hinton 1920, Ellerman & Morrison-Scott 1951, Coetzee 1977,

Corbet 1978, Osborn & Helmy 1980, Baryshnikov & Abramov 1997, 1998). Compared with *Ictonyx*, the Libyan Striped Weasel is smaller, and shaggier in appearance, with four to five black stripes on back (cf. three in *Ictonyx*); the palms and soles of the feet are haired.

Michael Hoffmann and Mieczysław Wolsan

Poecilictis libyca LIBYAN STRIPED WEASEL

Fr. Zorille de Lybie; Ger. Streifenwiesel

Poecilictis libyca (Hemprich & Ehrenberg, 1833). Symb. Phys. Mamm. vol. 1, pt. 2, sig. K, verso. 'Libyae' [Libya].



Libyan Striped Weasel *Poecilictis libyca*.

Taxonomy Highly polytypic species, with as many as six described subspecies (Coetzee 1977, Corbet 1978). Rosevear (1974) suggested a strong possibility that two, if not three, species are really involved, namely *libyca*, *vaillantii* and *oralis*. Niethammer (1987) drew attention to the near absence of any overlap, at least in skull length, between populations north and south of the Sahara Desert. Synonyms: *alexandrae*, *frenata*, *multivittata*, *oralis*, *rothschildi*, *vaillantii*.

Chromosome number: not known.

Description Small, elongated, black-and-white-striped shaggy animal, with short legs and a long tail. Black head, with short ears, short muzzle and a white band encircling the head, passing between the eyes and ears. Back and flanks mostly buff to white (buff to orange in Egyptian animals; M. Saleh pers. comm.). Three black longitudinal stripes beginning behind the ears, the middle one subdividing into two to three additional stripes, all of them fusing on the rump (variations can occur, and pelage may seem spotted, while white long hairs may hide stripes). Black stripes produced by relatively short black under-hairs, and white stripes by long all-white guard hairs. Throat, belly and legs black to brownish. Palms and soles haired. Front claws elongated, with bevelled tips. Long, bushy black and white tail with long, bicoloured guard hairs. Tip of tail and underside darker. Anal glands produce a noxious fluid. One pair abdominal nipples, one pair inguinal.

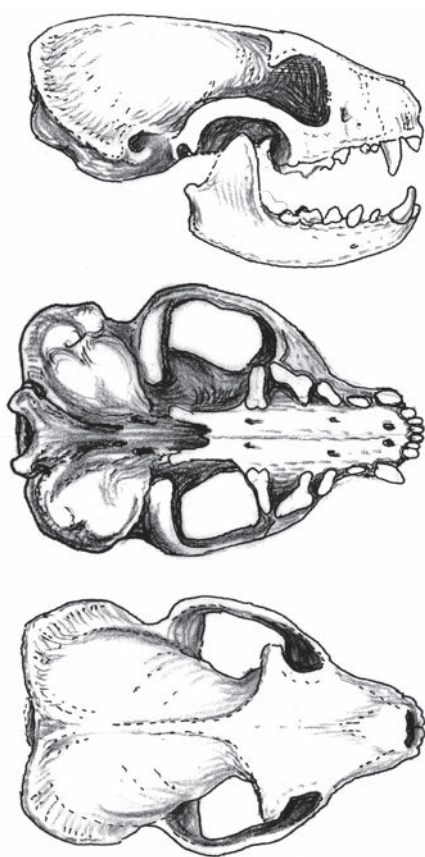
Skull short (up to 48 mm, cf. 72 mm in Zorilla *Ictonyx striatus*) and broad, triangular when seen from above. Mastoid and paroccipital processes obsolete; tympanic and mastoid bullae strongly inflated (Osborn & Helmy 1980). There is virtually no overlap in skull length between North African and Sahelian populations (Niethammer 1987). Dental formula is $I^{3/3}, C^{1/1}, P^{3/3}, M^{1/2} = 34$.

Geographic Variation

North Saharan populations:

P. l. libyca (including *alexandrae*, see Osborn & Helmy 1980): Egypt and Lybia.

P. l. vaillantii: Morocco, Algeria, Tunisia and Western Sahara.



Lateral, palatal and dorsal views of skull of Libyan Striped Weasel *Poecilictis libyca*.

South Saharan populations:

P. l. multivittata: C Sudan, and possibly E Chad.

P. l. oralis: coastal Sudan.

P. l. rothschildi: south-western Sahara to N Nigeria.

Similar Species

Ictonyx striatus. Restricted to sub-Saharan Africa, the most northerly observations being made in SE Egypt (Osborn & Helmy 1980, Saleh & Basuony 2005); apparently sympatric in parts of the Sahel. Larger (HB: 300–380 mm), with three long black stripes on the back, the medium one not subdivided in the lumbar region; palm and sole naked; postorbital swelling conspicuous.

Poecilogale albinucha. South of the Equator. Smaller, with much shorter legs, and shorter pelage; top of head and tail all white; pale dorsal stripes usually off-white to yellowish, seldom pure white.

Distribution Endemic to Africa, being found only in desert fringes, mountains and oases, and sub-deserts of the northern part of the continent from Morocco and Senegal to Egypt and Eritrea. Apparently absent in hyper-arid regions of central Sahara, except in Aïr (Niger), Murzuk and Jebel Uweinat (Libya). Their range apparently overlaps with that of the Zorilla in some regions, such as N Nigeria and in C and E Sudan (Niethammer 1987). Rosevear (1974) recorded Zorilla and Libyan Striped Weasel occurring in the same areas, but the former was generally more abundant; he mentions both species caught at Farniso (N Nigeria) and several other collection areas for Libyan Striped Weasel in Nigeria and Sudan



Poecilictis libyca

have records nearby for Zorilla. Although specimens and records are lacking, ranges could possibly overlap throughout the breadth of the Sahel belt (C. Stuart & T. Stuart pers. comm.).

Habitat Sand and stone deserts, sub-desert and cultivated land. General habitat is sparse to very sparse vegetation cover, dominated by small bushes, except in cultivated areas. In Morocco, mainly present in habitats with less than 150 mm of annual rainfall, except in coastal dunes, where annual rainfall may reach 250 mm (Cuzin 2003). Present in large ergs, and may live far from waterholes.

Abundance Limited information on the population status of this species. Not uncommon, and appears to be abundant in coastal dunes (Atlantic and also Mediterranean coastal zone). In S Morocco, in a Saharan habitat, after important rains, tracks of individual animals were found in every dry river bed (at an average distance of 0.6 km) (F. Cuzin pers. obs.). Given their dependence on highly unstable prey populations, they are probably subject to periodic fluctuations in numbers.

Adaptations As with the Zorilla, the anal glands produce a noxious, skunk-like fluid that the animal sprays at potential predators. Consequently, while it has been suggested that their colouring may act as a disruptive camouflage, the distinctive contrasting black and white colouration almost certainly acts as a warning to potential aggressors. They have long, well-developed claws for digging, and an elongated body shape probably enables this species to enter holes or burrows for catching rodents and other small prey. Their dentition is similar to the Zorilla, with a carnassial shear adapted to slicing, and a large I³ that probably aids the canine in holding larger prey. Basically ground-living, although they exhibit some climbing ability (Sitek 1996). Large bullae suggest good hearing. Niethammer (1987) has pointed out the likely role of competitive displacement in this species. In North Africa, the Libyan Striped Weasel has the Zorilla niche all to itself and its measurements overlap those of small

Zorillas. However, in the Sahelian zone, both species occur together, and in this part of their range Libyan Striped Weasels are substantially smaller, with no overlap in size with Zorillas.

This species digs single burrows into level surfaces or at the base of dunes, or in rocky or clay substrata, and hides in rock crevices or in the burrows of other animals (Kingdon 1997). In Niger, an excavated burrow in sand showed a unique narrow gallery, which was 3 m long, at 0.7 m under the ground surface, leading to a small chamber (Dragesco-Joffé 1993).

Foraging and Food Exclusively carnivorous, preying on small mammals (rodents, mainly *Gerbillus* spp.), birds resting or nesting on the ground, lizards and insects (Rosevear 1974, Dragesco-Joffé 1993). Local people report them taking poultry. They are solitary foragers, moving rather slowly, or with small jumps with the back arched. The kill is achieved by biting the occipital region of the prey's skull (Hufnagl 1972, Dragesco-Joffé 1993). Detailed comparisons in diet between northern and southern populations might help illuminate the nature of this species' accommodation to sympatry with the Zorilla in the southern, more ecologically diverse parts of its range.

Social and Reproductive Behaviour Nocturnal and predominantly solitary. Sitek (1996) noted that a captive pair would get on amicably (however, during pregnancy and rearing, animals were separated). This species is reportedly quite aggressive, and will spit and hiss when agitated. When threatened, it does not immediately flee, but faces its aggressor, bristles its hair, erects its tail and then turns its hindquarters toward the aggressor. An advancing predator will be squirted with the offensive smelling anal secretions. They may also feign death (Sitek 1996).

Reproduction and Population Structure Time of mating unknown, but probably very variable. In Algeria, one ♀ with two young cubs was found in Apr (Petter 1959). In Tunisia, two young were recorded in Aug (Hufnagl 1972). In Niger, cubs were found in Aug (wet season) and Nov (Dragesco-Joffé 1993). In Egypt, a ♀ contained advanced embryos in Sep (Hoogstraal 1964). In West Africa, parturition occurs from Jan to Mar (Rosevear 1974). Gestation is probably 37 days or slightly less (Petter 1959), although Rosevear (1974) quotes variable lengths between 37 and 77 days. There is no delayed implantation. Litters are usually 2–3 young (Petter 1959, Rosevear 1974, Dragesco-Joffé 1993, Sitek 1996) and birth-weight is 5 g (Sitek 1996). Young are born blind, although their ears are not sealed down, and they are covered with very short hair. Petter (1959) mentions some weasels covered with white hair, the skin being invisible. The dark patterning

develops at about three weeks, and the eyes open at about 3.5 weeks. Captive animals took solid food after five weeks, weighed 250 g at two months, and were separated from their mother at three months. An inter-litter interval of 40 days has been recorded for captive animals (Sitek 1996). No information on lactation or the age at which animals attain sexual maturity. Longevity is up to six years in captivity (Rosevear 1974, Haltenorth & Diller 1980, Weigl 2005).

Predators, Parasites and Diseases Probably very few predators. Pharaoh Eagle-owl *Bubo ascalaphus* seems to be the main predator: remains of animals killed by owls were found in Niger (Dragesco-Joffé 1993), and the skulls of these animals were found in owl pellets of eagle-owls in S Morocco (F. Cuzin pers. obs., M. Thévenot pers. comm.). Susceptibility to diseases unknown.

Conservation IUCN Category: Least Concern. CITES: Not listed.

Protected by law in Morocco, Algeria and Tunisia. There are no obvious major threats, but on the northern fringe of its distribution area they may suffer competition with Least Weasels *Mustela nivalis* in the most productive habitats (e.g. in Morocco). There is no evidence of them being utilized for food (Cuzin 2003), but in S Tunisia they are killed for witchcraft, in the belief that they are capable of increasing human male fertility, and there is even some limited international trade across the border into Libya (K. De Smet pers. comm.). Road kills have been recorded in Morocco, including Western Sahara (F. Cuzin pers. obs.) and in Tunisia (K. de Smet pers. comm.).

Measurements

Poecilictis libyca

HB: 256 (231–279) mm, n = 7

T: 174 (160–193) mm, n = 6

HF c.u.: 41 (38–46) mm, n = 7

E: 22 mm*

GLS: 47.1 (44.7–48.7) mm, n = 3†

GWS: 28.3 (28.0–29.0) mm, n = 3†

Egypt (Osborn & Helmy 1980)

*Sample size and range not given

†Sudan (Niethammer 1987)

Weight: three ♂ examined by Flower (1932) weighed 200, 200 and 250 g

Key References Cuzin 2003; Dragesco-Joffé 1993; Niethammer 1987; Osborn & Helmy 1980; Petter 1959; Rosevear 1974; Sitek 1996.

Fabrice Cuzin

GENUS *Ictonyx*

Zorilla

Ictonyx Kaup, 1835. Das Thierreich in Seinen Hauptformen 1: 352.

The genus *Ictonyx* includes a single species, the Zorilla or Striped Polecat *I. striatus*, which has a wide sub-Saharan range, but excludes true desert and tropical lowland forests. The Zorilla is one of the most easily recognized of all of Africa's small carnivores, particularly with its distinctive pitch black and white striped pelage; there is a

variable white blaze on the forehead between the eyes and a white spot at the base of each ear. As elaborated on elsewhere in this work, the Libyan Striped Weasel *Poecilictis libyca*, from North Africa, is not here included in *Ictonyx* because this would render *Ictonyx* paraphyletic (Koeppfli *et al.* 2008, Sato *et al.* 2012).

There has been considerable controversy and debate over the correct name for this genus (e.g. Ellerman & Morrison-Scott 1953, 1954, Hershkovitz 1953, 1955, 1963, China 1963, Holthuis 1963), eventually resolved once the observation was made that *Zorilla*, often used as the generic name for the Striped Polecat, was in fact based on a misidentified type, namely the Eastern Spotted Skunk *Spilogale*

putorius (see China 1966, Hershkovitz 1966, Van Gelder 1966). *Zorilla* was eventually suppressed under the plenary powers of the International Commission on Zoological Nomenclature in 1967 (for full discussion, see Grubb 2001, Wozencraft 2005).

Chris Stuart & Tilde Stuart

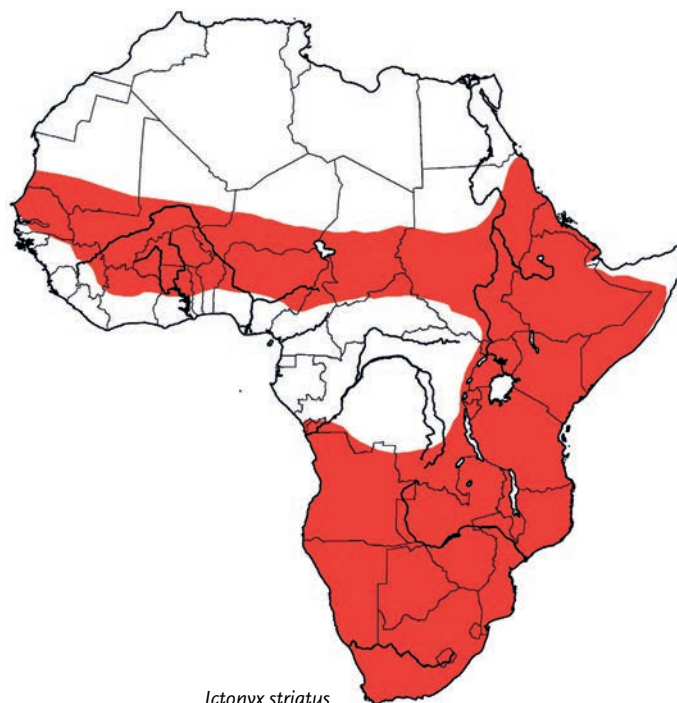
Ictonyx striatus ZORILLA

Fr. Zorille commun; Ger. Zorilla (Streifeniltis, Band-iltis)

Ictonyx striatus (Perry, 1810). Arcana, Mus. Nat. Hist., Signature Y, Fig. [41] [1810]. Type locality given as 'South America'. Obviously an error, and fixed by Hollister (1915) as 'Cape of Good Hope' [South Africa].



Zorilla *Ictonyx striatus*.



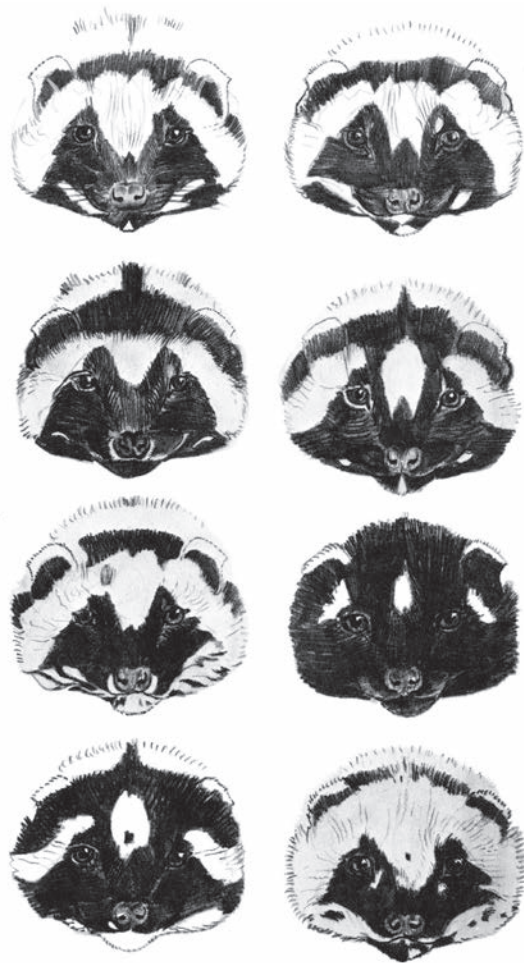
Ictonyx striatus

Taxonomy More than 20 subspecies have been described (Allen 1939), but the validity of most is questionable. The majority are based on variations in pelage colouration and markings but these vary considerably within any one population. Roberts (1951) listed four species of *Ictonyx* for southern Africa (*striatus*, *limpopoensis*, *orangiae* and *kalaharicus*), one monotypic and the rest comprising 11 subspecies; these species were all considered conspecific with *striatus* by Ellerman *et al.* (1953), who listed 12 subspecies. Coetzee (1977) listed ten subspecies from southern Africa (grouped under *I. s. striatus*), seven from north-eastern Africa (grouped under *I. s. erythrae*) and a single subspecies (*I. s. senegalensis*) from North and West Africa, but noted that they probably are invalid. Pending a revision, no subspecies are recognized here. Synonyms: *africana*, *albescens*, *arenarius*, *capensis*, *elgonis*, *erythrae*, *ghansiensis*, *giganteus*, *intermedius*, *kalaharicus*, *lancasteri*, *limpopoensis*, *maximus*, *mustelina*, *nigricaudus*, *obscuratus*, *orangiae*, *ovamboensis*, *pondoensis*, *pretoriae*, *senegalensis*, *shoae*, *shortridgei*, *sudanicus*, *variegata*, *zorilla*. Chromosome number: $2n = 38$ (Graphodatsky *et al.* 2002).

Description One of the most easily recognized small carnivores in Africa. A distinctly marked mustelid with long, shiny black body pelage broken by four, distinct, white dorsal stripes (making three prominent black stripes). Stripes extend from the top of the head and converge again at the base of the tail. Rhinarium small, muzzle bluntly pointed. On the forehead, between and extending above the eyes, is a white patch that varies greatly in size and shape. Another white patch is located above and between each eye and the base of the ear. In some individuals the white spots merge to form a continuous band.

Much variation in the size and shape of the white facial markings (Kingdon 1977). Tips of ears rimmed by short white hairs. Underparts, legs and feet black. Tail predominantly white but liberally flecked with black hairs. Hairs of the guard coat range from some 6 mm on the head, 50 mm on the hindquarters and up to 80 mm on the tail (Skinner & Chimimba 2005). Underfur fine and silky, being pure white on the white pelage and pure black on the black pelage. Albinos have been recorded (Shortridge 1934). Five digits on each foot, and claws on all front digits are long, curved and strong, up to 18 mm along the curve; claws on hindfeet average 10 mm and less curved (Skinner & Chimimba 2005). Palms and soles of feet naked. Anal glands are present, although Martinoli *et al.* (2006) report that anal glands were absent from all three animals (two adult ♂♂ and a subadult ♂) captured in Arusha N. P., Tanzania. In southern Africa, ♂♂ are larger and heavier than ♀♀ (Smithers 1971, Rowe-Rowe 1978a, Stuart 1981, Lynch 1983, 1989), which seems to be borne out from measurements of Egyptian animals (Saleh & Basuony 2005).

Typically mustelid skull, solid, and robustly structured (up to 72 mm in length). Braincase broad posteriorly, and rostrum short and blunt. Ear bullae very broad and flat, tapering to a point anteriorly.



Zorilla *Ictonyx striatus* individual variation in facial patterns.

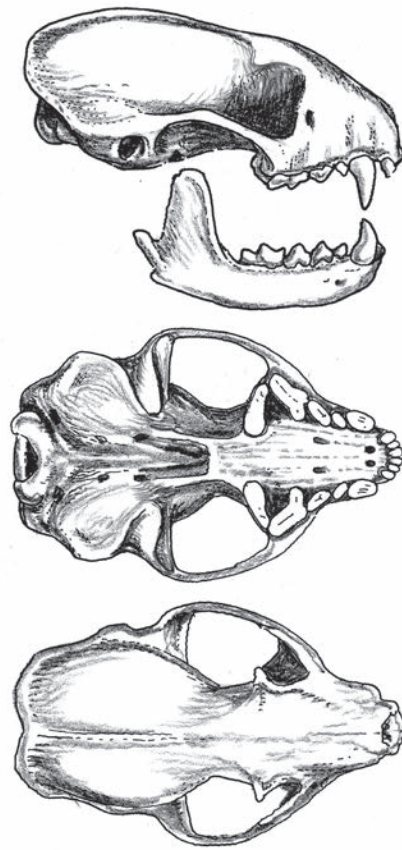
Mastoid and paroccipital processes prominent, zygomatic arches are thin and weak, and postorbital processes reduced to small knobs (Skinner & Chimimba 2005). Dental formula is $I^{3/3}, C^{1/1}, P^{3/3}, M^{1/2} = 34$. Outer upper incisor (I^3) much larger than others.

Geographic Variation An example of the confusion surrounding geographic variation and the recognition of subspecies is discussed by Smithers (1971) when comparing individuals from the same populations, stressing the great level of individual variation in hair length, breadth of dorsal striping and the extent of white hairs on the tail, not to mention variability in facial markings. Certainly, for southern Africa, and possibly throughout its range, individual variation is so great that at this stage recognition of any subspecies seems at best tenuous.

Similar Species

Poecilictis libyca. Possibly sympatric in extreme north-east and north-west of range, and perhaps in parts of the Sahel. Smaller; four to five black dorsal stripes; palms and soles haired; postorbital swellings inconspicuous.

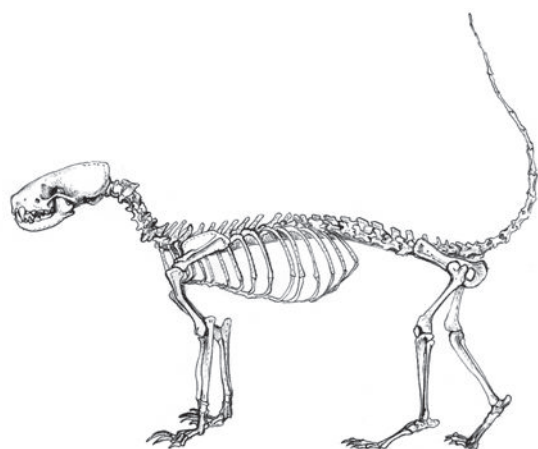
Poecilogale albinucha. Range overlaps south of Equator. Smaller, with shorter legs; body sinuous and elongated; shorter pelage; top of head and tail all white; pale dorsal stripes usually off-white to yellowish, seldom pure white; normally one lower molar, for a total of 28–30 teeth.



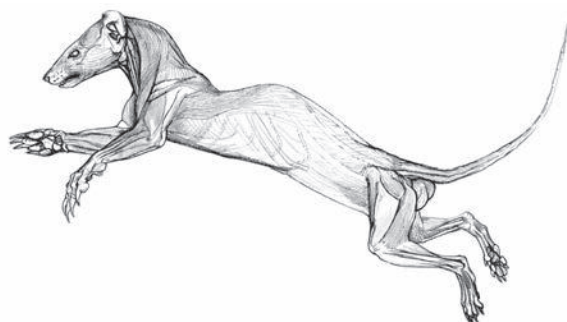
Lateral, palatal and dorsal views of skull of Zorilla *Ictonyx striatus*.

Distribution Endemic to Africa, south of the Sahara. Has a wide distribution, ranging from Mauritania and Senegal in the west to Sudan, Ethiopia and Djibouti in the east, and south to South Africa (Rosevear 1974, Kingdon 1977, Skinner & Chimimba 2005). Within this range, it is absent only from the equatorial forests of the Congo basin and West Africa, and certain regions of the Horn of Africa. Although present throughout the Sahel zone, the species is absent from the Sahara. The northernmost limit of distribution is extreme SE Egypt, from where the species has long been known from two specimens obtained in 1954 in Wadi Daraweena (see Osborn & Helmy 1980). Subsequently, Saleh & Basuony (2005) confirmed the presence of the species in open acacia forest of the Wadi Adaldeib north-east of Gebel Elba.

Habitat Has a wide habitat tolerance, being found in open grassland, savanna woodland, thornbush, rocky areas, forest and even desert (provided there is some scrub cover). Zorillas range from sea level to more than 4000 m (alpine zone of Mt Kenya; Coe 1969, Young & Evans 1993). In arid and semi-arid areas, they are commonly associated with drainage lines. In the south of their range they occur in the Namib and Kalahari Deserts, in the former penetrating even the driest areas along seasonal water-courses. They occur in many agricultural areas, including the wheatlands of SW South Africa, exotic plantations in KwaZulu–Natal (South Africa), and pastoral areas of the Kenyan highlands. According to Estes (1991), the species is most common on open rangeland where domestic or wild ungulates keep grass short by grazing.



Zorilla *Ictonyx striatus* skeleton.



Zorilla *Ictonyx striatus* myology.

Abundance Common over much of its extensive range, although locally uncommon. Easily overlooked as they are not trapped easily, but frequently seen as a road casualty. Hendrichs (1972) estimated density at one individual per 5–10 km² in East Africa.

Adaptations No sagittal crest, but two low ridges run from the centre of the supra-occipital crest, widening anteriorly to join the knoblike postorbital processes. These, together with the broadened braincase, provide a broad area of attachment for the powerful temporalis muscles that operate the robust lower jaws (Skinner & Chimimba 2005). Also has well-developed neck muscles, characteristic of efficient predators. The teeth of the Zorilla can deal with both cutting and crushing (presumably arthropod exoskeletons) although less sharp and pointed than those of the African Striped Weasel *Poecilogale albinucha*, suggesting their diet is less carnivorous; little evidence of competition between these two species, although where they co-occur African Striped Weasels may be less common (Kingdon 1977). Carnassial shear is adapted to slicing, while broad upper molar occludes with lower two molars to provide a surface for crushing. Outside incisor in upper jaw (I³) distinctly larger than the remainder and probably aids the canine in holding larger prey (Skinner & Chimimba 2005).

Long, strong curved claws on front feet are well adapted for digging. Although animals may excavate their own burrows in softer substrates, it is more common for them to use those abandoned by other species, lie up in rock piles or crevices, stone walls, hollow logs, amongst vegetation tangles and drift debris on river banks. In some areas, such as the South African central Karoo plain, they may take up residence under the floors of buildings and amongst scrap piles in farmyards. Almost exclusively terrestrial, but has been known to climb trees (Fitzsimmons

1919) and to swim well (Shortridge 1934). Nocturnal, only becoming active well after sunset and typically seeking shelter before sunrise (Smithers 1971, Rowe-Rowe 1975b, Rautenbach 1982).

The conspicuous pelage patterning and distinctive markings are presumed to serve as a warning to potential aggressors, as this carnivore can release a nauseating fluid from the anal glands. The excretion of the ♂ consists of a light, yellow oil and a colourless, translucent aqueous phase, with a strong and penetrating odour, as a result of the various sulphur compounds (Apps *et al.* 1988, Wheeler *et al.* 1997).

Foraging and Food Insects and small murids form the bulk of the diet but Zorillas also take a wide range of other invertebrates (including spiders, scorpions, hunting spiders, millipedes and centipedes), as well as reptiles, birds and amphibians (Smithers 1971, 1983, Rowe-Rowe 1975b, 1978a, Stuart 1981, Rautenbach 1982, Lynch 1983, 1989, Saleh & Basuony 2005). In all studies, insects dominate their diet – 62% and 61% occurrence in 21 and 36 stomachs from KwaZulu–Natal (Rowe-Rowe 1978b) and Zimbabwe/Botswana (Smithers 1983), respectively – especially beetle adults and larvae, grasshoppers and crickets. On the other hand, a single stomach from the Kalahari contained mostly reptile remains (Viljoen & Davis 1973).

There are regional as well as seasonal differences in diet but, as Zorillas are largely opportunistic foragers and hunters, diet is to a large extent a reflection of abundance and availability. The fact that many invertebrate and vertebrate prey items are subterranean dwellers for much, or all, of their time indicates that digging plays an important role in foraging. Captive animals showed similar dietary preferences, rejecting certain foods offered including snails, millipedes, toads and crabs; interestingly, they did consume shrews (Rowe-Rowe 1978b).

Zorillas are solitary and nocturnal foragers, and food is located mainly by smell and hearing (although some prey, such as large rodents, are located by sight). When foraging they move at a sustained trot with nose to the ground (Estes 1991, C. Stuart & T. Stuart pers. obs.). With few exceptions, foraging only begins well after sunset (Smithers 1971, C. Stuart pers. obs.). During foraging they move purposefully, stopping frequently to smell and listen, and insects, larvae and fossorial vertebrates are then dug out using front feet/claws (Rowe-Rowe 1978b). Slow-moving prey located on the surface are simply picked up with the mouth, whereas prey such as beetles or moths may be either bitten or pinned to the ground with a foot.

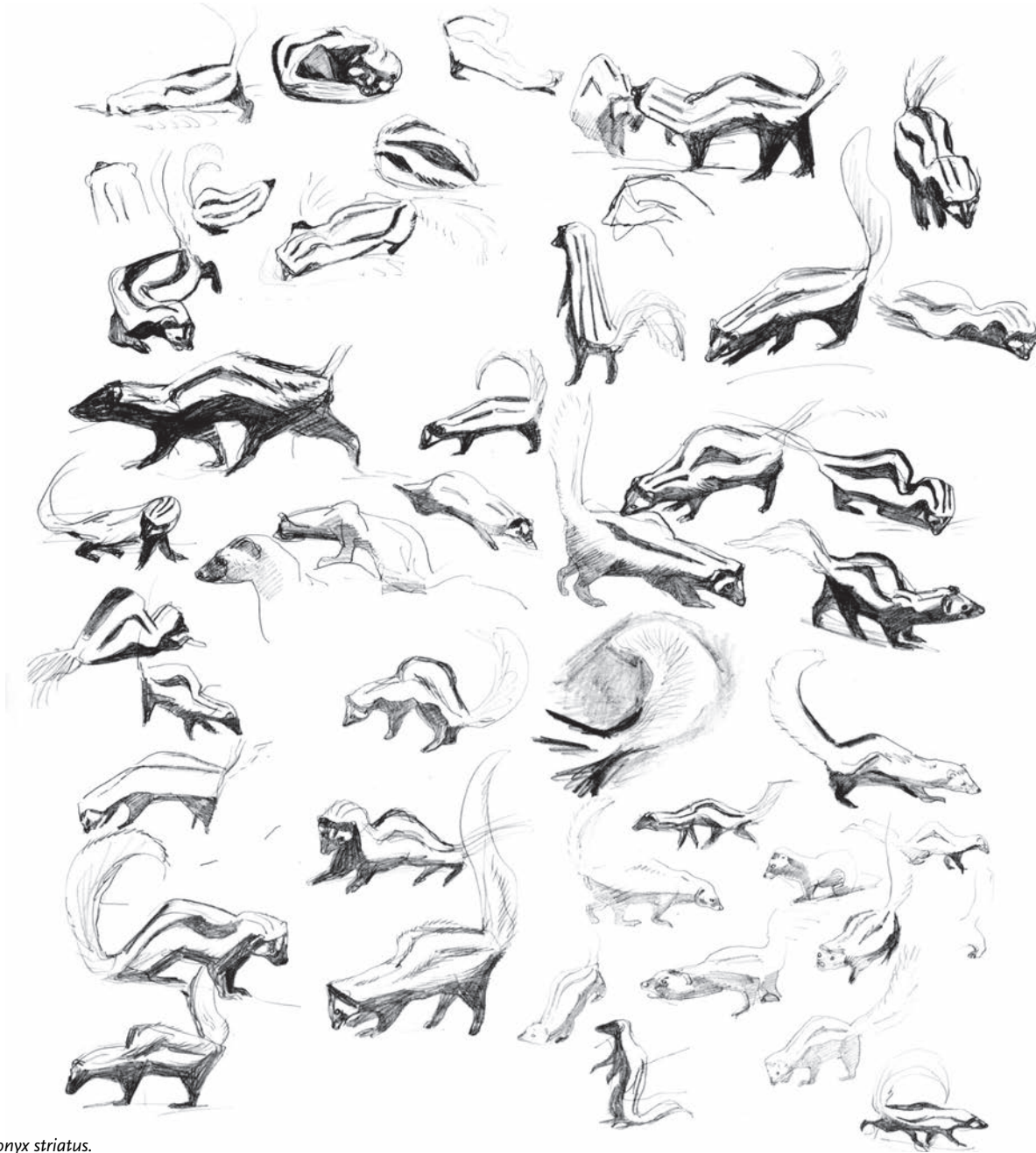
Larger prey, such as frogs and lizards, are stalked and bitten on the head, or initially held down by the front paws prior to biting; lizards and amphibians are eaten whole, lizards from the head first (Rowe-Rowe 1978b). Rowe-Rowe (1978b) describes how Zorillas kill snakes, which they usually consume head first (though sometimes tail or flanks are consumed first). Small rodents are initially bitten randomly and then usually killed with a bite to the neck (Rowe-Rowe 1978b, C. Stuart pers. obs.); larger rodents require more bites, and are then skinned and eaten, leaving the skull and other large bones too hard to crush (Rowe-Rowe 1978b). Birds are killed with a quick bite to the head; large birds are eaten from the head, and small birds are consumed whole. Captive animals offered eggs learned to break them open by biting or rolling the egg against a hard object (Rowe-Rowe 1978b). They have been recorded taking carrion (Shortridge 1934). Lautenbach (2005) records a rather remarkable instance of a Zorilla attacking a newborn Nyala *Tragelaphus angasi*.

Social and Reproductive Behaviour Solitary, although pairs are sometimes sighted and groups made up of a ♀ and her young are not uncommon (Rowe-Rowe 1975b, 1978a, Stuart 1981). Little information available on home-range sizes, or distances moved in the wild. Within their home-range Zorillas appear to have knowledge of the refuges available, for when disturbed, they make for these directly and quickly disappear into their shelter (Skinner & Chimimba 2005).

In threatening situations, the animal raises the body and tail hairs until erect, tail curved over the back, and turns rump to the perceived attacker. If the threat persists, a loud barking call accompanies the ejection of a foul-smelling fluid from the perineal glands (Rowe-Rowe 1975b, 1978a). Although the use of anal glands appears to be the ultimate defence in confrontation with larger enemies, when under extreme stress they may sham death for more than half an hour (Shortridge 1934, Kingdon 1977, C. Stuart pers. obs.).

In captivity ♂♂ were aggressive towards each other, culminating in fighting (Rowe-Rowe 1975b). During copulation, which lasts for between 25 and 106 minutes, ♀ calls frequently with loud yaps (Rowe-Rowe 1978c). Mating appears to induce ovulation (Irven 1993).

Six different adult vocalizations have been recognized, associated with greeting (one call), threat (two calls), defence (two calls) and mating (one call) (Channing & Rowe-Rowe 1977). Threat calls consist of a warning call emitted when another animal approaches either food or young, or when an intruder approaches. The warning call is followed by an aggression call, if the former fails to repel the intruder. Aggression calls may precede fighting. Defence calls are used as either submission or release calls. The former are emitted during early stages of displaying if an animal recognizes that the other animal is dominant, and non-receptive ♀♀ use it when ♂♂ attempt to copulate. Release calls are used by the losing ♂ at the end of a male–male fight. The mating call is



Zorilla *Ictonyx striatus*.

uttered by ♀ ♀ continually during copulation, and has three variations (Channing & Rowe-Rowe 1977). Juveniles also emit three calls: two types of distress calls, one each used before and after about 2.5 weeks of age, and a contact call (Channing & Rowe-Rowe 1977).

Reproduction and Population Structure In KwaZulu–Natal births are recorded in spring and summer (Oct and Nov; Rowe-Rowe 1978c), but elsewhere in South Africa pregnant ♀ ♀ and back-aged juveniles have been noted for Apr, Aug, Sep, Nov and Dec (Stuart 1981, Rautenbach 1982). Kingdon (1977) has recorded young in Feb, Jun, Sep and Oct in East Africa. A. J. Hopson (in Rosevear 1974) believed that in the L. Chad area the Zorilla may breed during the rains since young were observed from Sep to Nov. Saleh & Bsauony (2005) predicted births in early winter in SE Egypt, based on an observation of a mating pair in Aug. Rowe-Rowe (1978c) stated that if a captive ♀ successfully rears a litter, she will not produce a second litter until the following season; if, on the other hand, the young die at an early age, she will mate again.

Zorillas are probably polygamous and ♀ ♀ have their first litter from an age of ten months. The gestation period is 36 days ($n = 3$) (Rowe-Rowe 1975b) and litter size is one to three in wild-caught ♀ ♀, although litters of five are recorded from captivity (Rowe-Rowe 1978c). Young are born in an altricial state (birth mass 10–15 g) and at birth the dark stripes are apparent in the pink skin. The eyes open during the sixth week and the lower canines erupt at about 32 days, which is when they start to eat solid food. By Week 8 the young are fully mobile and capable of killing their own prey, and adult size is attained at about Week 20 (Rowe-Rowe 1978c). Longevity in captivity is about 14 years (Jones 1982, Weigl 2005), but in the wild this is unlikely to exceed five years.

Disparity in sex ratios has been recorded (Smithers 1971, Rowe-Rowe 1978a, Stuart 1981, Rautenbach 1982, Lynch 1983; and see summary in Larivière 2002b). Of a total of 183 sexed Zorillas from southern Africa, 68% were ♂ ♂ and 32% ♀ ♀. Rowe-Rowe (1975b) concluded that ♂ ♂ are more active than ♀ ♀, and appeared more willing to investigate unfamiliar objects. Perhaps this does explain the higher number of ♂ ♂ than ♀ ♀ killed on the roads, as ♂ ♂ are more mobile and most likely to be on roads and threaten oncoming vehicles (D.T. Rowe-Rowe pers. comm.).

Predators, Parasites and Diseases Known predators include Caracals *Caracal caracal*, Black-backed Jackals *Canis mesomelas*, Leopards *Panthera pardus* (Stuart 1981) and Brown Hyenas *Hyaena brunnea* (Mills 1978a), but direct predation, or scavenging, appears to be rare.

A malarial parasite was recorded from one of five specimens caught in traps in Senegal (Leger & Bedier 1923), and Round (1968) listed two nematode species, *Filaria martis* and *Hepaticofilaria pachycephalum*. Hill & Carter (1941) mention that most specimens are parasitized by worms that inhabit the frontal sinus and frequently erode the bone. Horak *et al.* (2000) recorded *Haemaphysalis leachi/zumpti* from an animal in the Free State, and *H. zumpti* from an animal in the Eastern Cape. There is no information on diseases, although they may carry rabies.

Conservation IUCN Category: Least Concern. CITES: Not listed.

Despite heavy mortality on roads, populations remain stable. Increasing rural human populations and the concomitant increase in numbers of dogs are a threat to its existence in many areas, and Zorillas are sometimes killed for preying on poultry (Rowe-Rowe 1992a,

Kingdon 1997). None the less, they remain common across their wide distribution, are present in numerous protected areas, and unlikely to be threatened in the near future.

Measurements

Ictonyx striatus

HB (♂ ♂): 340 (280–380) mm, $n = 30$

HB (♀ ♀): 331 (290–365) mm, $n = 8$

T (♂ ♂): 207 (165–255) mm, $n = 32$

T (♀ ♀): 191 (175–200) mm, $n = 10$

HF c.u. (♂ ♂): 54 (47–66) mm, $n = 28$

HF c.u. (♀ ♀): 49 (44–53) mm, $n = 10$

E (♂ ♂): 28 (22–34) mm, $n = 32$

E (♀ ♀): 25 (20–30) mm, $n = 10$

WT (♂ ♂): 793 (486–1200) g, $n = 21$

WT (♀ ♀): 576 (428–700) g, $n = 4$

Northern Cape, Western Cape and Eastern Cape, South Africa (Stuart 1981)

TL (♂ ♂): 627 (566–6703) mm, $n = 27$

TL (♀ ♀): 604 (565–630) mm, $n = 8$

T (♂ ♂): 261 (236–295) mm, $n = 27$

T (♀ ♀): 257 (248–263) mm, $n = 8$

HF c.u. (♂ ♂): 63 (56–70) mm, $n = 27$

HF c.u. (♀ ♀): 59 (50–64) mm, $n = 8$

E (♂ ♂): 30 (26–36) mm, $n = 27$

E (♀ ♀): 29 (26–31) mm, $n = 8$

WT (♂ ♂): 974 (681–1460) g, $n = 27$

WT (♀ ♀): 713 (596–880) g, $n = 8$

Zimbabwe and Botswana (Smithers 1983)

GLS: 71.7 (71.0–72.2) mm, $n = 4$

GWS: 32.5 (30.0–34.0) mm, $n = 4$

Botswana (Smithers 1971)

Key References Rowe-Rowe 1975b, 1978a, b, c; Smithers 1971; Stuart 1981.

Chris Stuart & Tilde Stuart



GENUS *Poecilogale*

African Striped Weasel

Poecilogale Thomas, 1883. Ann. Mag. Nat. Hist. 11: 370.

A monotypic genus that was originally assigned to *Zorilla* (Gray 1864), a designation followed by others (Bocage 1865, Peters 1865). However, Thomas (1883) reassigned the species to *Poecilogale* and this is now generally accepted. It has a wide, largely sub-equatorial, range

on the African continent and should not be mistaken for any other species within this region.

Chris Stuart & Tilde Stuart

Poecilogale albinucha AFRICAN STRIPED WEASEL

Fr. *Poecilogale* à nuque blanche; Ger. Weißnackenwiesel (Kappeniltis)

Poecilogale albinucha (Gray, 1864). Proc. Zool. Soc. Lond. 1864: 69, Plate X. 'It was without any habitat.'

Emended by Coetzee (1977) as 'Cape Colony', Zambia.



African Striped Weasel *Poecilogale albinucha*.

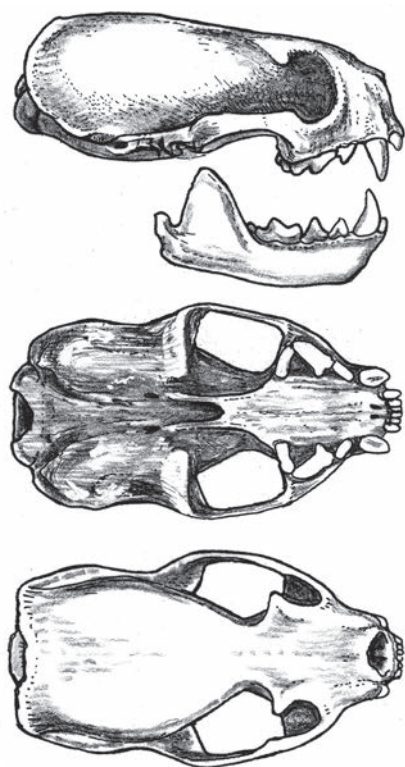
Taxonomy Six subspecies have been described, but Coetzee (1977) noted that their validity is probably questionable as they are based on minor and variable aspects of appearance (and see Meester *et al.* 1986). Synonyms: *africana*, *bechuanae*, *doggetti*, *flavistriata*, *lebombo*, *transvaalensis*. Chromosome number: not known.

Description The smallest African mustelid occurring south of the Sahara. Characterized by extremely slender form, very short legs and strongly contrasting black and white striping on dorsum. It is proportionally the longest African mammal (Estes 1991). Head typically mustelid, with short rounded ears and short snout. When walking or running the back is arched. Overall pelage colour is pitch black with four off-white to yellowish stripes that run from nape to base of tail, converging on neck into two broad bands and forming completely white cap on top of head. Overall dorsal stripe colouring and width are variable throughout their range and within any one population. Changes in colouration of pale dorsal stripes have been recorded (Ansell 1960b, Stuckberry 1967) but do not appear to be linked with factors such as age or season. Body hair short and coarse, and hairs of guard coat average

10 mm in length. Tail bushy with white hairs dominant; tail guard hairs average 30 mm in length, and are black at their base with predominantly white over much of length. There are five digits on each foot, with the claws on the front feet longer and more strongly curved than those on the hind. They are equipped with two perineal glands from which they can eject a yellowish fluid with a very heavy, sweet, pungent smell. One pair abdominal nipples, and one pair inguinal; occasionally extra pair inguinal (Rowe-Rowe 1972a). Males consistently larger than ♂♂, up to 50% greater in body weight (Rowe-Rowe 1978a).

Skull typically musteline, elongated, and the rostrum short and broad. Braincase ovoid, postorbital bars incomplete, orbits small and zygomatic arches weak (Skinner & Chimimba 2005). Dental formula is $I^{3/3}, C^{1/1}, P^{2/2}, M^{1/1} = 28$. Occasionally, there is an additional lower molar. The carnassials are sharp and the canines long.

Geographic Variation African Striped Weasels vary in size, width and colouration of the pale dorsal stripes throughout their range and within any given population. Rautenbach (1982), for example, besides pointing out that the ranges of three putative subspecies from the



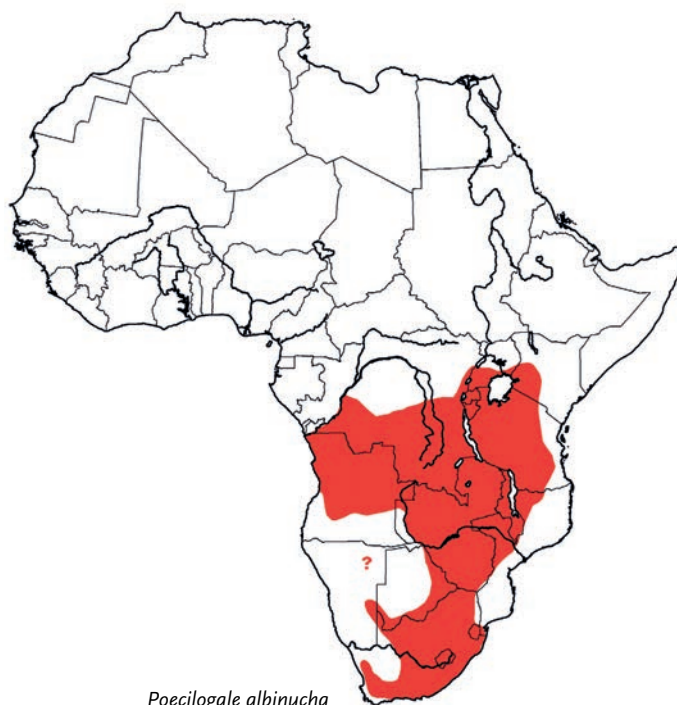
Lateral, palatal and dorsal views of skull of African Striped Weasel
Poecilogale albinucha.

former Transvaal in South Africa are largely unknown, also collected specimens of undescribed dorsal colouration phases. It seems unlikely that, with current knowledge, there is much geographic variation. Kingdon (1977) mentions that animals observed in W Uganda tend to be slightly larger than in other areas of East Africa; this observation is supported by data from L. Kivu (Rahm & Christiaensen 1963).

Similar Species

Ictonyx striatus. Sympatric south of the equator. Larger; shaggy and long pelage; black and white striping less clearly defined, lacks white cap on top of head and has variable white patches on face; tail more clearly mixed black and white; proportionally shorter in the body and longer in the leg; body not sinuous or elongated; normally two lower molars, 34 teeth.

Distribution Endemic to Africa. Restricted almost entirely to south of the Equator, from SW Uganda and Kenya to the Western Cape in South Africa (Kingdon 1977, Ansell 1978, Ansell & Dowsett 1988, Skinner & Chimimba 2005). The highest frequency of records comes from SE South Africa, where most research has been done. In the south-west of the same country, where this species was unknown until 1998, there have been three documented records based on road kills, suggesting range expansion (Stuart & Stuart 1998a). They are now also known to occur in the western extension of the Kalahari within the Kgaligadi Transfrontier Park (Stuart & Stuart 1990) and SE Namibia (C. Stuart & T. Stuart pers. obs.). Because of its secretive nature it has probably been overlooked in many areas, especially in light of the recent records from locations that were previously considered to be unsuitable. Its presence in the SW Kalahari indicates that it could well occur over large tracts of Botswana, as well as E Namibia.



Poecilogale albinucha

Habitat Although they probably have a wide habitat tolerance, they are mainly found in savanna associations, usually with a strong grass component. In N Angola and DR Congo they have been recorded from lowland rainforest. The few records from arid south-western Africa are associated with semi-desert grassland. In the south and south-west of their range they occupy areas of Cape fynbos (Stuart & Stuart 1998a). Road casualties recorded from the extreme south-west were in a mix of fynbos, cultivated fields and pastures, while road kills in Swaziland were also collected in commercially cultivated fields (Monadjem 1998). A sighting from Nyika N. P. was made in montane grasslands at approximately 2300 m (Medland & Dudley 1995). Rowe-Rowe (1990a) states that this mustelid is particularly associated with moist grassland areas experiencing an annual rainfall that exceeds 600 mm. It would seem to reach its highest densities in such areas, but in recent times it has been found in areas of the Kalahari that receive less than 500 mm per annum, as well as in the C Karoo with annual mean precipitation lower than 300 mm (Stuart & Stuart 1990).

Abundance Rare to uncommon throughout its range, although densities are considered to be higher in KwaZulu-Natal in South Africa (Rowe-Rowe 1975b). Highest densities appear to be reached in moist higher rainfall grasslands. It has been suggested that it is probably only common in habitats with perennially dense rodent populations (Estes 1991).

Adaptations The African Striped Weasel has an elongated cranium and relatively weak zygomatic arch, with broad attachments for the powerful temporalis muscles that operate the robust lower jaws. It also has well-developed neck muscles, characteristic of efficient predators. The carnassials are adapted to slicing predominantly murid prey. The long, slender body and short legs are ideally suited to entering small rodent burrows, which they frequently do, when hunting. They are terrestrial and apparently not good climbers, although Rowe-

Rowe (1972a) stated they would do so in captivity with some awkwardness.

Although individuals will make use of existing rodent burrows, which they may or may not modify, they have been shown to be active and efficient burrowers under captive conditions (Rowe-Rowe 1990a). Rowe-Rowe (1975b) described a burrow 50 mm in diameter, almost vertical for about 100 mm, then horizontal for up to about 200 mm, terminating in a chamber 100–150 mm in diameter. A captive kept by the authors (also recorded by Rowe-Rowe 1972a, 1975b) constructed shallow burrows in sand, digging the sand with its forepaws and sharp claws and then moving it back in 'caterpillar' fashion under the belly and out between the hindlegs. Rowe-Rowe (1972a) discussed how two together, in turn, would help to excavate a burrow.

The distinctive and contrasting black and white pelage probably serves as a warning to would-be attackers that they can expect to be sprayed with the unpleasantly smelling product of the perineal glands. This fluid, although rather unpleasant, does not have the pungency of that produced by the Zorilla *Ictonyx striatus*. Before ejection, the hair on the tail and on the lower part of the back is raised and the tail held vertically. Under stress the fluid can be ejected to a distance of up to 1 m but usually shorter distances are involved (Alexander & Ewer 1959). It has been suggested that the African Striped Weasel's similarity to the Zorilla may indicate a case of mimicry, but Kingdon (1977) holds that it is more likely to be a case of functional convergency in mustelids.

African Striped Weasels are predominantly nocturnal, but are occasionally seen in daylight. Rowe-Rowe (1978b) recorded six of 35 sightings during daylight. On two separate occasions he saw an adult (presumed ♀) with two well-grown young at 09:00h (KwaZulu-Natal) and 10:00h (Eastern Cape) (D. T. Rowe-Rowe pers. comm.).

Foraging and Food Mainly solitary, nocturnal hunter that feeds predominantly on small rodents that it may catch on the surface but frequently seeks out in their burrows. Mainly a small mammal hunter, with a predilection for rodents (but also shrews), but birds may also be taken (Rowe-Rowe 1978c). There are no reliable records of invertebrates, amphibians or reptiles being taken.

The African Striped Weasel is a specialized hunter that is capable of killing rodents up to its own size, but smaller species dominate

in its diet (Rowe-Rowe 1978c). Under captive conditions a weasel killed young domestic rabbits averaging 500 g on three occasions; the weasel apparently had no difficulty in handling and killing prey twice its own size (Stuart 1981). Rowe-Rowe (1978c) found that African Striped Weasels in captivity relied more on scent than sight to locate prey; Ansell (1960b) noted that a captive weasel used vision a great deal. Killing generally follows a set pattern in which the prey is taken using a well-directed bite to the back of the neck, followed by a lateral rolling action causing the prey to lose its footing. In the process the spine is broken by the vigorous kicking and treading against the prey with the hindfeet, which is referred to as 'curl, clasp, kick' (Rowe-Rowe 1990a). Neck bites are the most common killing technique, although bites to the throat have also been recorded when killing large prey. Small mammals are eaten head first, and usually entirely consumed (Rowe-Rowe 1978b). Birds are killed by a bite on the head without the use of the forefeet to hold the bird down, and are always eaten head first (Rowe-Rowe 1978b). After killing, prey was always carried or dragged to shelter. A single animal can consume 3–4 mice in a night, but surplus killing sometimes occurs. Captive animals offered eggs did not break them open and did not eat the contents of broken eggs. Hoarding of surplus prey has been recorded in captivity (Rowe-Rowe 1972a, 1978b).

Social and Reproductive Behaviour Normally solitary, but sightings of pairs and groups of up to four individuals are not unusual (typically a ♀ and her young). Individuals in these groups follow very close behind each other, giving the impression of a moving snake (Rowe-Rowe 1978b).

From observations in captivity it appears that the African Striped Weasel is strongly territorial but a ♂ and ♀ will share a burrow or shelter. In arranged encounters between ♂♂, three phases of intensity were recognized: immediate submission by one individual; a challenge followed by wrestling terminating when one released its hold uttering a release call; and high-intensity encounters with ritualized fighting and biting, inflicting no injury, and vocalization again important in termination (Rowe-Rowe 1996).

Marking with the faeces probably plays a territorial role, and according to Kingdon (1977) faeces are mainly situated around the den sites. Faeces may be used for scent-marking, as they are often deposited on vertical, or near vertical, surfaces and not infrequently spread during defecation (Ansell 1960b). In the wild, termitaries and the bases of trees are often used as marking locations with the faeces (Kingdon 1977). Apparently, this weasel does not mark objects with the anal gland secretions, but these are used purely as a self-defence mechanism (Rowe-Rowe 1972a). No information is available on home-range size but this will in large measure be dictated by prey abundance and availability.

Channing & Rowe-Rowe (1977) recognized a total of six different vocalizations by adults (three for threat, two for defence and one for greeting) and three by blind young. Threat calls include a warning call (very similar to that of the Zorilla) and an aggression call, while defence calls include submission and release calls. Males emit a greeting call to ♀♀, usually prior to mating. In both defensive and offensive threats, the short hair along the back is raised, also the tail hairs, with the effect amplified by bark-screaming and feigned attack. As a last resort the animal may spray the product of the anal glands at an attacker (Ansell 1960b).



African Striped Weasel *Poecilogale albinucha*.



African Striped Weasel *Poecilogale albinucha*.

Reproductive behaviour has not been recorded in the wild but captive observations showed that copulation only took place in the den or shelter (Rowe-Rowe 1978a). As African Striped Weasels may copulate for extended periods (62–78 minutes), the advantage of first retreating to shelter is that they would not be vulnerable to potential predators. Females tolerate ♂♂ when they are sexually receptive, and copulation may be preceded by a relatively lengthy courtship involving 'dancing' around each other, bouncing on the front feet, play wrestling, usually with tail erect and fluffed out (Rowe-Rowe 1975b). Females rear young without the help of ♂♂ (Rowe-Rowe 1996).

Reproduction and Population Structure In southern Africa most births are recorded from Nov to Mar, but nothing is recorded from elsewhere within its range. It seems likely that births will coincide with the wet season/s when their rodent prey is most abundant. Litters, normally with 2–3 young, are born after a gestation period of 31–33 days, the shortest of any carnivore without delayed implantation (Rowe-Rowe 1978a). In captivity ♀♀ that successfully raise a litter will not raise a second during the same season. Young are born in an altricial state, hairless, blind and deaf. Birth-weight is some 4 g (n = 6), with a total length averaging 70 mm. Canine teeth erupt at about 35 days, which is when young first eat solid food; eyes open at between 51 and 54 days after birth, and they make their first rodent kill at 13 weeks. Maturity is reached by Week 20 (Rowe-Rowe 1978c). Longevity is around 4–6 years (Rowe-Rowe 1992a, Weigl 2005).

Predators, Parasites and Diseases Little recorded on mortality, but probably vulnerable to predation by certain owls and other carnivores. A dead weasel found in the Drakensberg in South Africa appeared to have been killed, but not eaten, by a raptor. Perhaps the aposematic colouring also warns that they are distasteful (D. T. Rowe-Rowe pers. comm.). Over much of their range, they coexist with the Zorilla. Although the African Striped Weasel appears less common where their ranges overlap (Kingdon 1977), competition between the two species is likely avoided due to the Zorilla being more of a generalist predator, whereas the African Striped Weasel is a rodent specialist.

The only endoparasite recorded is the tapeworm *Taenia brachyacantha* (Round 1968). Some captive weasels have been recorded as dying from tuberculosis of the spleen (Ansell 1960b).

Conservation IUCN Category: Least Concern. CITES: Not listed.

Although thinly distributed and occurring at apparently low densities, the African Striped Weasel faces no known major threats, is present in several protected areas and does not require any special conservation action. However, Cunningham & Zondi (1991) found that pressure on weasel numbers had increased, and that they were becoming more scarce in E South Africa. They regarded the African Striped Weasel as highly threatened, being one of the most-used animals in traditional medicine. Indeed, in parts of its range the skins of this mustelid are commonly used by traditional healers and sangomas as a good luck charm. Rowe-Rowe (1990a, 1992a, 1996) stated that human population growth, predation by dogs, and loss of habitat owing to conversion of grasslands to monocultures, e.g. timber plantations, maize, sugarcane (KwaZulu–Natal), pineapples (Eastern Cape), as well as overgrazing with loss of suitable rodent habitat, is having an impact on weasel populations.

Measurements

Poecilogale albinucha

HB (♂♂): 290 (286–345) mm, n = 6
 HB (♀♀): 268 (264–299) mm, n = 11
 T (♂♂): 155 (128–163) mm, n = 6
 T (♀♀): 157 (136–166) mm, n = 11
 HF c. u. (♂♂): 36 (33–39) mm, n = 6
 HF c. u. (♀♀): 32 (30–36) mm, n = 11
 E (♂♂): 18 (15–19) mm, n = 6
 E (♀♀): 16 (14–18) mm, n = 11
 WT (♂♂): 263 (218–355) g, n = 6
 WT (♀♀): 173 (116–257) g, n = 11
 Zimbabwe (Skinner & Chimimba 2005)

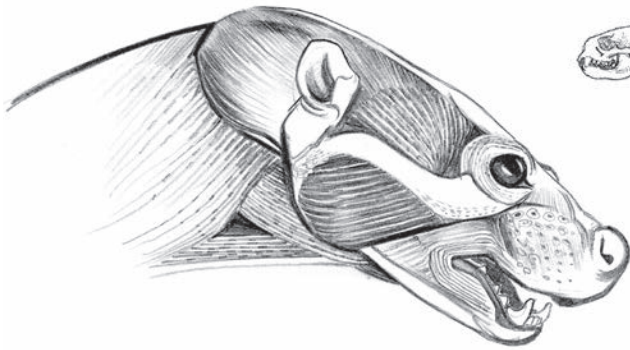
HB (♂♂): 313 (299–330) mm, n = 7
 HB (♀♀): 298 (275–320) mm, n = 3
 T (♂♂): 181 (163–200) mm, n = 6
 T (♀♀): 169 (162–180), n = 3
 WT (♂♂): 339 (283–380) g, n = 7
 WT (♀♀): 251 (230–290) g, n = 6
 GLS: 50.0, 52.5 mm, n = 2
 GWS: 23.6 (23.2–27.9) mm, n = 3
 KwaZulu–Natal, South Africa (Rowe-Rowe 1978a)
 Skull measurements: South Africa (Roberts 1951)
 In the former Cape Province, Stuart (1981) recorded HB as 314 mm (306–327 mm) for ♂♂ (n = 3) and 315 mm (280–350 mm) for ♀♀ (n = 2); and T as 176 mm (171–180 mm) for ♂♂ and 148 mm (145–150 mm) for ♀♀. In a series of seven ♂♂ from L. Kivu, body weight ranged from 255 to 390 g (with one animal apparently weighing 610 g), and in a series of eight ♀♀, from 214 to 350 g (Rahm & Christiaensen 1963)

Key References Ansell 1960b; Rowe-Rowe 1972a, 1975b, 1978a, b, c, 1992a, 1996.

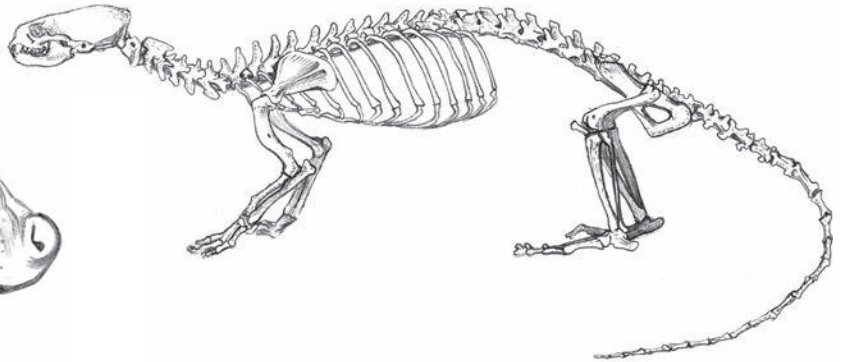
Chris Stuart & Tilde Stuart

Subfamily LUTRINAE – Otters

Lutrinae Bonaparte, 1838. Nuovi Ann. Sci. Nat. 2: 111.



Spotted-necked Otter *Hydrictis maculicollis* facial myology.



Spotted-necked Otter *Hydrictis maculicollis* skeleton.

The subfamily Lutrinae contains the Otters, with three genera (*Lutra*, *Hydrictis* and *Aonyx*) represented by four species in Africa. Worldwide, around 13 species are recognized in this subfamily, although there is some debate as to the validity of the Japanese Otter *Lutra nippon*, which has been considered a subspecies of the more widespread Common Otter *L. lutra*. Likewise, Wozencraft (2005) synonymized the two African forms of *Aonyx*, a view that has not been generally supported (see genus account). There is also uncertainty as regards the status of *Amblonyx* (for the Oriental Small-clawed Otter, *A. cinerea*), which is sometimes treated as congeneric with *Aonyx* (Ellerman & Morrison-Scott 1951, Koepfli & Wayne 1998, Wozencraft 2005), the separation of the New World otters (with the exception of *Pteronura*) in the genus *Lontra* (Van Zyll de Jong 1972, 1987, Koepfli & Wayne 1998, Wozencraft 2005), and the status of the Spotted-necked Otter *Hydrictis maculicollis*, which has variably been included in *Lutra* or in its own genus (e.g. Wozencraft 2005; and see genus account).

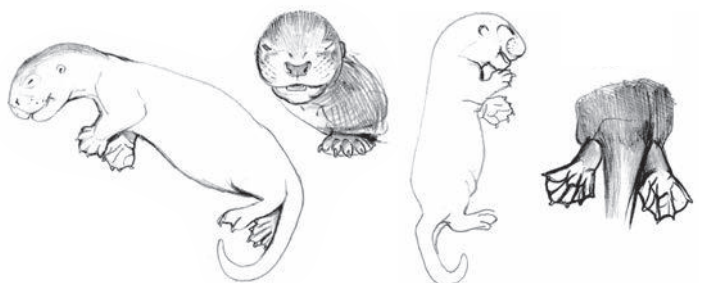
Otters are medium-sized, all rather similar in appearance, with an overall length of 1.0–1.5 m and a weight of 3.0–16.0 kg (up to 45 kg in the extralimital Northern Pacific Sea Otter *Enhydra lutra*); ♂♂ are up to 30% heavier than ♀♀. Their elongated body shape suggests adaptation to aquatic habitat, but this is probably incorrect, as such form is also found in related, non-aquatic mustelids. Thus, it is more likely that otters could take to an aquatic existence because of their overall shape, and this in itself is not an adaptation to water. Colour dark brown above, lighter underneath; guard hairs over very dense underfur provides insulation in water by holding air close to the skin. Otters differ from many other mammals by having little (<3%) body fat, and little of that is subcutaneous (to prevent buoyancy; Kruuk 1995, 2006). They are remarkably streamlined, and have a rather flat head with equally broad neck, short legs, small eyes and ears, and large prominent vibrissae. The thick tapering tail (dorso-ventrally flattened in some species) serves as a rudder, and is important especially to provide counterbalance when swimming: otters propel themselves underwater by kicking with both hindlegs simultaneously, whilst holding the frontlegs back along the body. For this mode of swimming, the centre of gravity needs to be close to the hindlegs. The heavy tail also helps with diving, and when swimming along the surface: otters flip forwards and down whilst lifting the tail out of water. Hindlegs with fully webbed digits, front legs partly webbed.

There are five upper cheekteeth, the upper first molar much enlarged, more or less square, as large or larger than the adjoining carnassial.

In *Aonyx*, the feet have rudimentary webs, nails are absent or small and blunt, the mastoid process projects prominently behind ear opening, the postorbital process is clearly developed, and the greatest skull length in adults is usually more than 115 mm. In *Lutra* and *Hydrictis* the feet are clearly webbed, with well-developed claws; the mastoid process is weak while the postorbital process is vestigial, and the skull is normally less than 110 mm (Coetzee 1977, Meester *et al.* 1986).

Otters are semi-aquatic carnivores, being highly dependent on water for feeding, with Common Otter and African Clawless Otter found along coastal areas as well as in freshwater habitat, while the others occur only in freshwater. Their movement on land is somewhat clumsy, though fast, and they cover long distances between water-courses. Feeding habits of different species vary widely, especially where two species co-occur: *Lutra* and *Hydrictis* specialize on fish and frogs, the African Clawless Otter specializes mostly on crustaceans (Rowe-Rowe & Somers 1998). Generally, all otters are nocturnal, but they are highly flexible and exceptions occur, particularly related to the availability of their main prey (Kruuk & Goudswaard 1990, Kruuk 1995, 2006, Perrin & d’Inzillo Carranza 2000). All species scent-mark frequently, with faeces (‘spraints’), urine and rubbing. Spraints have a strong, fishy smell detectable over long distances. All species are territorial, with single-sex territories; in some species, a territory may be inhabited by several individuals.

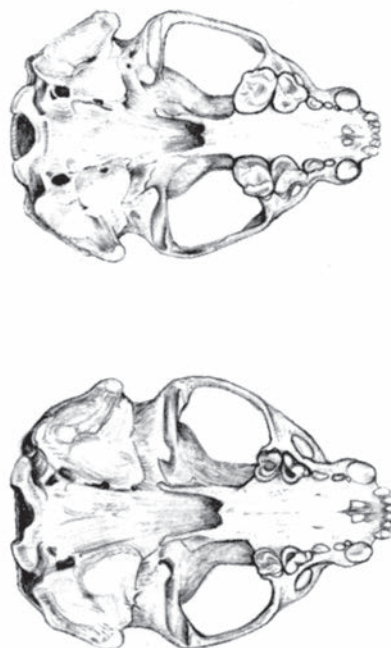
Hans Kruuk



Neonate Spotted-necked Otter *Hydrictis maculicollis* showing webbed feet.

GENUS *Aonyx* Clawless Otters

Aonyx Lesson, 1827. Manual de Mammalogie, p. 157.

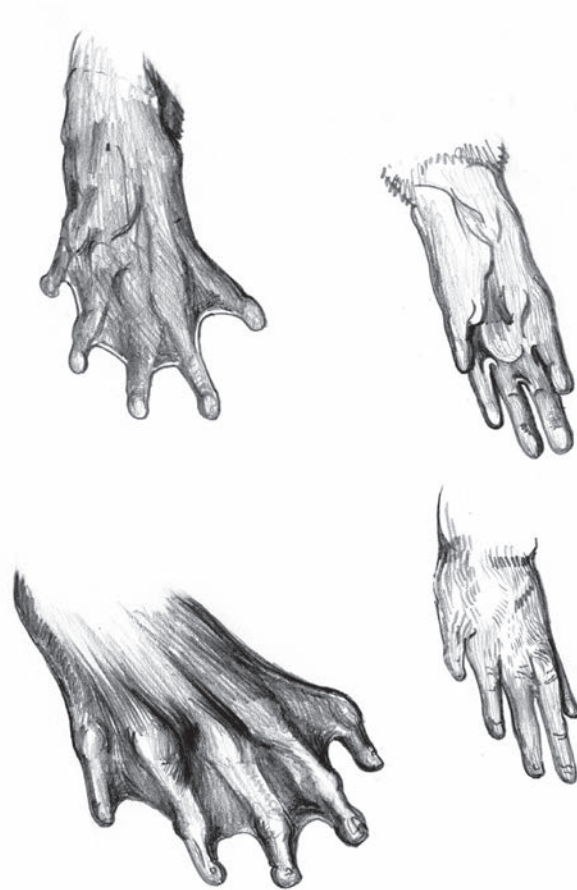


Palatal views of skulls of African Clawless Otter *Aonyx capensis* (top) and Congo Clawless Otter *A. congicus* (bottom).

This genus includes two species: the African Clawless Otter *A. capensis*, widely distributed in sub-Saharan Africa, except for the Congo basin, where it is replaced by the Congo Clawless Otter *A. congicus*. Allen (1924) and Davis (1978) stated that apparent differences in colour and molar size between the two species represent only geographic variations and that the Congo Clawless Otter does not represent a valid species. However, most authors have treated the two as separate species (e.g. Van Zyll de Jong 1972, Rosevear 1974, Coetzee 1977, Wozencraft 1993), although Wozencraft (2005) regarded them as conspecific.

Some authors, such as Ellerman & Morrison-Scott (1951), Coetzee (1977), Anderson & Jones (1984) and Koepfli & Wayne (1998), have considered the Asian Small-clawed Otter *Amblonyx cinerea* as congeneric, while Harris (1968), Medway (1978), and Van Zyll de Jong (1972, 1987) regarded it as a distinct genus (and see Bininda-Emonds *et al.* 1999). Marmi *et al.* (2004) suggested that all *Aonyx* and *Amblonyx* species could be included in the genus *Lutra*. Koepfli & Wayne (1998) found that although *Aonyx* (including *Amblonyx*) are linked to *Lutra* in a well-supported clade, these two genera last shared a common ancestor 8.0–6.3 mya. The Congo Clawless Otter also has been included in its own genus *Paraonyx* (Hinton 1921).

Characteristics of the genus include the unwebbed forefeet (unlike Spotted-necked Otter *Hydrictis maculicollis*), with blunt fingers lacking any nails or claws. Hindfeet are webbed to the second digit, but toes either lack nails or claws or have rudimentary nails. Postorbital bar present as a distinct process, and mastoid process projects behind the ear opening; rostrum short and broad. The dental formula is $I^{3/3}, C^{1/1}, P^{4/3}, M^{1/2} = 36$. The first upper premolar is sometimes



Congo Clawless Otter *Aonyx congicus* hands and feet.

absent, or present only on one side. Cheek teeth, especially P^4 and M^1 , as well as M_1 , are very robust and greatly enlarged, low cusped for a crushing function (rather less so in Congo Clawless Otter); those of the African Clawless Otter ca. 30% larger than in the Congo Clawless Otter (Jacques *et al.* 2004, 2009). Second lower molars occlude with upper molar for at least half their surface, and so assist with crushing function. Canines long and well developed; lower canines recurved. Outer upper incisors are enlarged.

Aonyx are specialized crab eaters, but they also include other items in their diet, including fish, small mammals, frogs and some invertebrate prey (Rowe-Rowe & Somers 1998). Otters of the genus *Aonyx* (meaning 'without nails') are well adapted to foraging with their fingers. The lack of webbing between the digits of their forepaws allows for considerable dexterity of individual fingers when feeling for prey in mud and murky water. Unlike other otter species, *Aonyx* use their forepaws to catch prey rather than their mouth (Duplaix 1982). They have larger somatic sensorial areas in their brain corresponding with increased forepaw use (Radinsky 1968). Both species are primarily solitary, although they may occur in small groups (Rowe-Rowe & Somers 1998).

Jan A. J. Nel & Michael J. Somers

Aonyx capensis AFRICAN CLAWLESS OTTER

Fr. Loutre à joues blanches; Ger. Fingerotter

Aonyx capensis (Schinz, 1821). In: G. Cuvier, Das Thierreich 1: 211. 'Capischer otter ... Afrika'
 ['Cape of Good Hope', Western Cape Province, South Africa].

African Clawless Otter *Aonyx capensis*.

Taxonomy Three subspecies have been recognized (Coetzee 1977): *A. c. capensis* (including *coombi* and *angolae*), from southern Africa, W Zambia, Angola, Gabon, Nigeria and throughout West Africa; *A. c. hindei* (including *helios*), from Uganda to E DR Congo as far south as N Zambia; and *A. c. meneleki*, from Ethiopia. Meester *et al.* (1986) only considered the nominate form to extend as far north as Angola and Zambia, noting that the case for including West African forms is unproven. Rosevear (1974) remarked that it was not possible to determine whether any forms might constitute valid West African races based on the study material available to him. Since variations in pelage are apparent from across the range of the species, subspecific delineation appears tenuous at best and no subspecies are recognized here. Synonyms: *angolae*, *calaboricus*, *coombi*, *delalandi*, *gambianus*, *helios*, *hindei*, *inunguis*, *lenoiri*, *meneleki*. Chromosome number: $2n = 38$ (Van Zyll de Jong 1987).

Description Medium-sized species, with streamlined body covered in short, dense fur. Head very broad at back, especially in ♂♂, narrowing to short, broad muzzle. Ears small, uniformly brown and adpressed to head. Top border of rhinarium rounded or lightly V-shaped. Colour varies from dark brown dorsally to creamy off-white on upper lips, side of face, throat, belly, edge of ears and neck. In some specimens, hair on forehead, across top of head and extending onto shoulders has silvery tips, giving the appearance of a mantle, somewhat like that found in the Congo Clawless Otter *A. congicus* (Skinner & Chimimba 2005). Coat has dense covering of guard hairs, from 10 mm in length on head and tail to 25 mm on mid-back (Skinner & Chimimba 2005). Underfur much finer, slightly shorter and white or off-white in colour, although it is obscured by the dense guard coat. Skin is thick. Vibrissae are white to grey (or sometimes with dark bases and white tips) and occur on both upper and lower jaws (Tayler 1970). Tail stout, long and dorsoventrally flattened. Legs short with hindfeet webbed for half their length while webs of the front feet are hardly noticeable. There are five digits. Forefeet clawless but rudimentary nails found on hindfeet (Skinner & Chimimba 2005). Both sexes have paired anal glands (Kingdon 1977). Females have two pairs of abdominal nipples.

Skull large and heavily built as brain size is large relative to body size (Sheppey & Bernard 1984). Eye orbits and ear bullae relatively

Lateral, palatal and dorsal views of skull of African Clawless Otter *Aonyx capensis*.

small compared with the size of the skull. Rostrum short and broad, the length from the front of the eye orbit to the incisors around one-fifth the total length of the skull. The zygomatic arch is thin and lightly built, as compared with the robust construction of the skull. This is a common feature in the mustelids, and reflects the development of the temporalis muscles at the expense of the masseters. The supra-occipital crest appears well developed. The lower jaw is thick and massive. Molars are broad and bunodont (Skinner & Chimimba 2005), highly suited for crushing crustaceans. The upper canines are formidable, round and sharp, the lower markedly recurved. The first upper premolar is not always present or, in some specimens, is present only on one side (Skinner & Chimimba 2005).

Geographic Variation See Taxonomy.

Similar Species

Aonyx congicus. Degree of sympatry with African Clawless Otter unknown. Similar size, but with posterior cheekteeth reduced in size (see Measurements and *Aonyx congicus* species profile) and more slender, especially in the head and neck region (Kingdon 1977); upper border of the rhinarium straight; head and neck extensively frosted, and throat, chin, side of head, nose and ears

creamy-white, with a prominent black patch between eyes and nostril (see species profile *Aonyx congicus*).

Hydricis maculicollis. See species profile for notes on sympatry.

Smaller in size with throat and neck with pale cream or white mottling, or the same colour as the rest of the body; webbed feet.

Distribution The African Clawless Otter is the most widely distributed otter species in Africa, occurring throughout most of the tropical and sub-tropical regions of sub-Saharan Africa, where there is permanent freshwater (Nel & Somers 2002). The range stretches from Senegal and Mali throughout most of West Africa to Sudan and Ethiopia then southwards throughout East Africa to the Western Cape of South Africa, being absent from the Congo basin (where they are replaced by the Congo Clawless Otter).

African Clawless Otters occur widely in seasonal rivers in arid and semi-arid areas of southern Africa, such as the Fish and Löwe Rivers in SC Namibia, and many seasonal or episodic rivers in the Karoo, such as the Sak, Vis, Riet and Gamka Rivers, as long as suitable-sized pools persist (Nel & Somers 2007). This suggests that this species could inhabit similar areas further north in Africa, albeit at probably lower densities than in more productive habitats. Skinner & Chimimba (2005) noted a tendency for the species to occur in the tributaries of some major rivers and not in the main rivers themselves, giving an example in Zimbabwe where they occur in the Mazoe R., which drains into the Zambezi R., from which they are absent downstream of the Victoria Falls. On the other hand, Somers & Nel (2004a) found that in the Western Cape they do often use main rivers and seldom use tributaries.

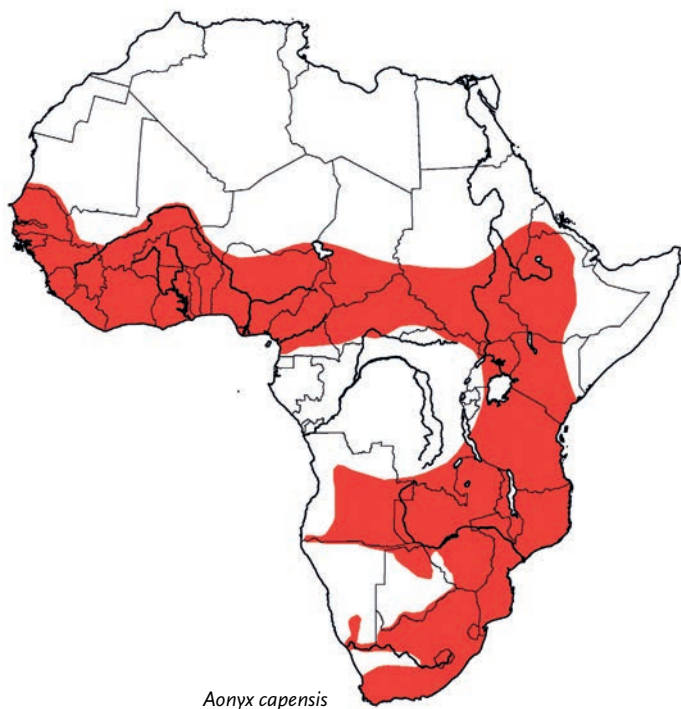
Habitat African Clawless Otters are predominantly aquatic and consequently are seldom found far from water. Freshwater is the essential habitat requirement (Van Niekerk *et al.* 1998), but they also occur in marine habitats provided there is access to freshwater (presumably to wash salt off coat and for drinking). In riparian habitats

the best habitats appear to be those with boulders and reed-beds (Somers & Nel 2004a). In marine habitats, rocky shores are preferred (Van Niekerk *et al.* 1998). Elsewhere, found in diverse habitats, from impoundments, estuaries, mangroves (Nel & Somers 2007, M.J. Somers pers. obs.) to the desert conditions of the upper Doring R. in the Western Cape and the Fish R. in S Namibia (Nel & Somers 2007). In general, their occurrence would appear to be independent of the surrounding terrain, providing the aquatic conditions are suitable and there is adequate cover. They have been recorded up to 2400 m in montane streams in the Drakensberg and Maluti Mts in South Africa and Lesotho (D.T. Rowe-Rowe & N. L. Avenant pers. comm.) and to 3000 m in Ethiopia (Yalden *et al.* 1996). African Clawless Otters have been found in towns (e.g. Stellenbosch) and cities (e.g. Port Elizabeth, Cape Town) (M. J. Somers & J. A. J. Nel pers. obs.), and can occupy rivers with high pollution and eutrophication levels (Heath & Claassen 1999, Somers 2001).

Abundance Throughout their range, African Clawless Otters are fairly common to rare, with populations thought to be stable in 29 of the 35 countries from which they have been recorded (Rowe-Rowe 1990b, 1995, Nel & Somers 2002). Abundance appears to be dependent on the availability of crabs (Rowe-Rowe & Somers 1998). For example, this species is the more abundant of the two otters in most of southern Africa, as crabs constitute the highest macro-invertebrate biomass in many rivers in the region (Hill & O’Keeffe 1992). Further north, however, where fishes are plentiful, the piscivorous Spotted-necked Otter is more abundant (Rowe-Rowe & Somers 1998).

Density estimates in Tsitsikamma Coastal N. P. in the Eastern Cape, South Africa, have been given as one otter per 1.9–2 km of coast (Van der Zee 1979, 1982, Arden-Clarke 1983, 1986). Verwoerd (1987) estimated one otter per 2 km of coast at Betty’s Bay in the Western Cape. As the otters rarely ventured further than 100 m from shore (Arden-Clarke 1983, 1986), these densities are equivalent to one per 20, 19 and 20 ha of water for the three studies, respectively. Using signs such as spoor, estimates of density in freshwater habitats are one otter per 1.25–2.5 km (Carugati 1995, Perrin & Carugati 2000b), one otter per 3–4 km (Rowe-Rowe 1992b) and one otter per 8–10 km of river (Butler & du Toit 1994). Somers (2001), using recovery of radioactive scats ($n = 55$), gives an estimate of 1.53 otters per km of river. Assuming there are two otters per km of river the estimate for the total population in South Africa alone is around 21,500 animals (M. J. Somers pers. obs.).

Adaptations The African Clawless Otter is highly adapted for an aquatic way of life. As with other otters, the guard hair and underfur are particularly dense to insulate the body when swimming. The hindfeet are webbed for half their length providing the main means of propulsion, while the tail serves as a rudder. Their many long vibrissae possibly assist in locating prey such as crabs (Rowe-Rowe 1977b). The front feet have no claws, the digits rather being adapted to feeling and grasping. The third and fourth, and in some cases the second, digits on the back feet have rudimentary nails. The undersides of the digits are rough to assist in holding slippery objects. The nasal apertures are set in slits in the rhinarium, which is small when compared with the size of the head; the edges of these slits can be brought together to close the nasal apertures when the individual is swimming under water (Skinner & Chimimba 2005).



Aonyx capensis

In an investigation of relative brain size (cranial volume in relation to body weight) among 30 South African carnivores, Sheppey & Bernard (1984) found that African Clawless Otters had the largest brain: 2.08 times the expected. These authors hypothesized that this accounted for their advanced dexterity. As in the Spotted-necked Otter, the structure of the glenoid cavity and glenoid processes is such that side-to-side movement of the lower mandible is limited. The dentition appears to be developed primarily for crushing. The development of P^4 and M^1 and M_1 is pronounced, being very heavy and broad; the outer edges can be used for cutting, but their main function is crushing hard-shelled prey such as crustaceans. The second lower molars, for at least half their surface, occlude on the first upper molars, and assist in this function (Skinner & Chimimba 2005).

In freshwater, otters are typically active from dawn for 2.6 h and from sunset for a mean of 2.3 h (Somers & Nel 2004b). In the coastal waters main periods of activity are from 20:00 to 22:00h (Arden-Clarke 1983). During the heat of the day they rest in dry places, in holes in the ground, under rocks, in sheltered places in erosion gullies or in dense reed-beds and shrubs adjacent to their habitat. Rowe-Rowe (1992b) found that they often excavate holts (dens) in river banks, the openings of which are elliptical (mean width, 361 ± 85 mm; mean height, 246 ± 32 mm; $n = 8$). The otters modify these resting places by lining them with vegetation, and indeed dense riparian vegetation (long grass, reeds, bushes) is essential to provide cover for holts and resting places (Rowe-Rowe 1992a, b). Some burrows have more than one entrance and tunnel lengths vary between 2 and 3 metres.

Foraging and Food African Clawless Otters are specialized crab eaters, but also feed on fish, frogs, insects and occasionally birds (waterfowl) and small mammals, such as shrews and rodents (Rowe-Rowe 1977a, Smithers & Wilson 1979, Kruuk & Goudswaard 1990, Butler & du Toit 1994, Ligthart *et al.* 1994, Purves *et al.* 1994, Carugati 1995, Somers & Purves 1996). The importance of different secondary items is probably related to local prey-availability (Rowe-Rowe & Somers 1998). For example, the highest percentage of crab and the lowest percentage of fish have been recorded from KwaZulu-Natal (South Africa). This study was done at mid-altitude (1060–1650 m) where fish faunas are poor and crabs abundant (Rowe-Rowe 1977a). It was at this wetland-rich locality, too, that the frog component was highest (23% relative occurrence) and constituted the most important supplement to crabs (65% relative occurrence). In Zimbabwe, where mountain catfish and eels were abundant, the percentage of fish was highest (23% relative occurrence; Butler & du Toit 1994; and see also Smithers & Wilson 1979). Purely aquatic prey comprised 87–97% relative occurrence at all localities (Rowe-Rowe & Somers 1998). In Groenvlei Lake, Western Cape, where freshwater crabs are absent, fish make up 69% of the diet, illustrating how otters adapt to local food abundance (Watson & Lang 2003).

In marine habitats they eat mostly fish followed first by crab, then by octopus or lobster (Van der Zee 1979, 1981, Arden-Clarke 1983, Verwoerd 1987, Somers 2000a, b). In Tsitsikamma N. P., Van der Zee (1979, 1981) recorded over 35 species of crabs, fish and octopus. Calculated on a relative frequency basis the Red Rock Crab *Plagusia chabrus* had the highest frequency at 28%, followed by Rocksucker *Chorisochismus dentex* at 17% and the Brown Rock Crab *Cyclograpsus punctatus* at 10%. At Betty's Bay, Verwoerd (1987) found that fish

constituted 59% of the biomass of the food, followed by octopus (15%), Red Rock Crab (13%) and rock lobster (10%).

Rowe-Rowe & Somers (1998) state that although African Clawless Otters may occur in groups, they usually forage singly. In shallow, stony bottomed water they walk, submerging the head occasionally, feeling with the forefeet under and between stones for prey (Rowe-Rowe 1977b, Somers 2000a). In deeper water the otter dives to the bottom and forages on the substrate, once again using the forefeet (Rowe-Rowe 1977b, Purves *et al.* 1994). In freshwater 1.5 m deep, dives had a mean duration of 17.4 sec (range 8–26 sec; Rowe-Rowe 1977b). Somers (2000a) found a mean dive time of 21 sec in the sea.

Somers (2000a) found they moved along the coast, while feeding, at a mean speed of 21.4 m per min. Almost all prey is captured using the forefeet (sometimes with the mouth), then bitten. Where larger prey is involved, such as large fish and frogs, the killing bite is directed at the head. Barbel *Barbus* spp., for example, are pinned to the bottom of the pool with the front feet and bitten behind the head. In experiments (Rowe-Rowe 1977c) it was found that slow-swimming fishes were more easily captured than fast-swimming species, as was the case with small fish versus larger specimens of the same species. Smaller fish and crabs may be consumed while treading water but are typically taken to the shallows (prey is usually carried in the forefeet, but sometimes in the mouth) and eaten there (Rowe-Rowe 1977b). Prey is fed into the mouth using the forefeet. Frogs and fish, except large *Clarias* spp. (which have a bony head structure), are eaten from the head first (in contrast to the Spotted-necked Otter *Hydricis maculicollis*, which eats fish from the tail first). Crabs of all sizes are consumed entirely (Rowe-Rowe 1977b), which is in contrast with the Marsh Mongoose *Atilax paludinosus*, which will leave the shell of the carapace in the case of crabs larger than about 40 mm across carapace (although the shells of smaller crabs [<30 mm] may be consumed; D. T. Rowe-Rowe pers. comm.). Rowe-Rowe (1977b) found that with large crabs, the otter usually ate the chelae and limbs first. No particular order was obvious with smaller crabs. In the case of frogs, the legs of the frog were grasped in a forefoot and pieces of the body torn off with the mouth by pulling the frog downwards and moving the head backwards, or by chewing pieces off with the cheekteeth (Rowe-Rowe 1977b).

In KwaZulu-Natal, most freshwater fishes eaten are small (less than 200 mm) (Rowe-Rowe 1977a). In the Okavango R., Botswana, much larger fish (up to 2 kg) were freely taken (Smithers 1983). Somers & Purves (1996) recorded that the mean carapace width of crabs eaten by African Clawless Otters in the Bushmans R., Eastern Cape, was 23.5 mm (range 3.1–65.5 mm; $n = 1365$) while a mean of 28.5 mm (range 4.3–61.0) was determined for the Olifants R., Western Cape (Purves *et al.* 1994). Nevertheless, African Clawless Otters will consume freshwater crabs of all sizes and capably handle even the largest crabs (D. T. Rowe-Rowe pers. comm.).

There is some trophic overlap between the African Clawless Otter, Spotted-necked Otter and Marsh Mongoose (Rowe-Rowe 1977a, Somers & Purves 1996, Rowe-Rowe & Somers 1998). Freshwater crabs feature prominently as shared food in the diets of the three species (Rowe-Rowe & Somers 1998). However, the diets of the two otters reflect a much greater dependence on aquatic prey than does that of the Marsh Mongoose. Comparisons of the diets of the two otters (Rowe-Rowe 1977a, Somers & Purves 1996) reflected a greater dependence on crabs by African Clawless Otters, and a higher amount of fish in the diet of Spotted-necked Otters (Rowe-Rowe & Somers 1998).

Social and Reproductive Behaviour African Clawless Otters are mainly solitary in all habitats, though occasionally they occur in pairs or small family parties (Arden-Clarke 1983, Somers 2000a, Somers & Nel 2004b). In KwaZulu–Natal, group size varied from one to five, with solitary individuals or pairs the most common (Rowe-Rowe 1978a), while in Tsitsikamma N. P., of 56 observations, 35 were of solitary individuals, five of two, eight of three, three of four and one group of five (Arden-Clarke 1986).

The pattern of female home-ranges is suggestive of territoriality. Males have overlapping home-ranges, both with other ♂♂ and ♀♀ (Somers & Nel 2004b). In freshwater, total home-range length varies from 4.9 to 54.1 km. The total area of water used ranges from 4.9 to 1063 ha (Somers & Nel 2004b).

Rowe-Rowe (1992b) found that latrines are usually in grass above river banks or oxbow lake shores or dams, on earth ledges in river banks, or on islands or rocks. African Clawless Otter defecated close to water (mean 4.2 m from water; range 1–15 m; $n = 135$), with most faeces (85%) found between 1 and 7 metres from water. There were between 1.4 and 2.6 faeces per km of river, with most found in spring. Latrines contain a large amount of crab shell remains and fish scales. Rowe-Rowe (1992b) found that, during late autumn, winter and early spring, when there was little rain, spraints remained intact, retaining their shape for 4–5 weeks. Spraints containing crab material bleached, changing colour from dark brown to cream. During summer, when rainfall was higher, spraints broke up after 15–21 days, although some remains were still visible. The spraints of African Clawless Otter can be distinguished from those of the Marsh Mongoose, because the latter contain rodent fur and other items normally not eaten by otters (although where both are feeding extensively on crabs alone, identification may be difficult).

The most common vocalizations of African Clawless Otters are squeaks but they also growl, whine, chirp and hiss. When alarmed they give a sudden *Hah!* sound after which they usually disappear underwater not to be seen again. They are very playful, especially after meals and even more so when kept as pets (Maxwell 1960, Eyre 1963). In the wild they often chase one another and slide down muddy banks, seemingly in a playful manner. When alone they may play with inanimate objects or play ‘cat and mouse’ with prey.



African Clawless Otter *Aonyx capensis*.

Reproduction and Population Structure One to three (though Rosevear [1974] suggests a possible five) young are born at widely divergent times throughout the year. At Betty's Bay, Verwoerd (1987) recorded five litters that he estimated were born between Apr and Jun. At Die Kelders in Walker Bay, ca. 100 km south-east of Cape Town, a ♀ suckled two very small cubs on land in late Dec; another ♀ and small cub was seen swimming at Scarborough on the Cape Peninsula beginning Jan (C. Boucher pers. comm.). The natal den at Die Kelders was situated in weathered calcrete and sandstone, near a freshwater seepage. Stuart (1981), also in the former Cape Province, recorded a foetus taken from a ♀ in Jul and a juvenile with its eyes still closed taken in Apr. In KwaZulu–Natal, Rowe-Rowe (1978a) recorded two one-week-old juveniles in the last week of Aug, and a single juvenile estimated to have been born in Nov. In Zimbabwe, Smithers (1971) recorded juveniles in Mar and Apr, while, in Zambia, Ansell (1960a) estimated births to occur in about Jul/Aug. Rosevear (1974) remarks on a very young animal that was probably still being suckled taken in early Oct in Sierra Leone.

Gestation is 60–64 days (Ewer 1973). Two young otters less than one week old weighed 260 g each (Rowe-Rowe 1978a) and the young are weaned at eight weeks (Verwoerd 1987). Kingdon (1977) noted that during the first months of life the young are hidden, opening their eyes at about four weeks, and then venturing out with the mother. Longevity in captivity is on the order of 14 years (Nowak 1999, Weigl 2005).

Predators, Parasites and Diseases No data available on natural predators. However, sharks are thought to be a possible predator in the sea (Somers 2000a) and Nile Crocodiles *Crocodylus niloticus* and birds of prey in freshwater (Kruuk & Goudswaard 1990). Endoparasites recorded from African Clawless Otters include trematodes (*Baschkirovitrema incrassatum*, *Clinostomum pyriforme* and *Prudhoella rhodesiensis*) and the nematode *Cloeoascaris spinicollis* (Round 1968). No information is available on possible diseases.

Conservation IUCN Category: Least Concern. CITES: Appendix II.

A rapidly increasing human population has been identified as the greatest threat to this species' existence (Rowe-Rowe 1990b, 1995), although the African Clawless Otter does not appear to have reduced its range (Nel & Somers 2002). Alteration of freshwater habitats and riparian vegetation, loss of habitat as a consequence of increased agricultural activity, unsound agricultural practices, overgrazing by livestock in rural areas, or lack of natural resource conservation are among the other main threats. They are sometimes killed when they prey upon waterfowl on farms, and as a competitor for a common food source, fish. Fisheries managers of the Kairezi River Protected Area in Zimbabwe blamed trout declines on otter predation and competition with trout for food, even though scat analysis revealed that only 1% of faeces ($n = 255$) contained the remains of trout and diets overlapped only 17% (Butler 1994, Butler & Marshall 1996). Occasionally, they are accidentally caught and drowned in gill nets and fish traps (Rowe-Rowe 1990b) and in peri-urban areas road kills can be significant (Verwoerd 1987). Although seldom killed for food, skins and other body parts are sought after for use in traditional medicine in various parts of

their range, including KwaZulu–Natal (Cunningham & Zondi 1991, White 2001), Lesotho (N. L. Avenant pers. comm.) and the Udzungwas (De Luca & Mpunga 2005). They are present in a number of protected areas across their range.

Measurements

Aonyx capensis

HB (♂♂): 1265 (1130–1380) mm, n = 13

HB (♀♀): 1233 (1140–1330) mm, n = 7

T (♂♂): 505 (445–570) mm, n = 13

T (♀♀): 483 (450–495) mm, n = 7

HF c.u. (♂♂): 159 (150–170) mm, n = 13

HF c.u. (♀♀): 147 (145–160) mm, n = 7

E (♂♂): 32 (30–36) mm, n = 7

E (♀♀): 30 (31–33) mm, n = 4

WT (♂♂): 14.1 (10.0–18.0) kg, n = 16

WT (♀♀): 11.7 (10.0–13.8) kg, n = 9

South Africa (Van der Zee 1979, Stuart 1981 [♀♀ only; excluding WT], Arden-Clarke 1983, Somers & Nel 2004)

Stuart (1981) recorded an average weight of 15.1 kg for ♂♂ in

the former Cape provinces of South Africa (11.5–21.0; n = 7) and 12.9 for ♀♀ (10.6–14.2; n = 3). The maximum weight recorded (34 kg) was a ♂ kept as a pet (Eyre 1963)

P⁺ (L × W): 12.9 × 14.1 mm, n = 26*

M¹ (L × W): 17.8 × 14.2 mm, n = 28*

M₁ (L × W): 17.6 × 10.7 mm, n = 23*

GLS ♂♂: 132.1 (119.6–142.7) mm, n = 24

GWS: 90.9 (72.0–99.1) mm, n = 22

Throughout range (Jacques *et al.* 2009)

*L = longest length, W = greatest width, at right-angles to the main longitudinal axis of the skull

Key References Arden-Clark 1983, 1986; Carugati 1995; Perrin & Carugati 2000a, b; Rowe-Rowe 1977a, b, c; Rowe-Rowe & Somers 1998; Skinner & Chimimba 2005; Somers 2000a, b, 2001; Somers & Nel 2004a, b; Van der Zee 1979, 1981, 1982; Verwoerd 1987.

Michael J. Somers & Jan A. J. Nel

Aonyx congicus CONGO CLAWLESS OTTER

Fr. Loutre à joues blanches du Congo; Ger. Kongootter (Kleinzahn Fingerotter)

Aonyx congicus Lönnerberg, 1910. Ark. Zool. 7 (9): 1. Lower Congo, Zaïre.



Congo Clawless Otter *Aonyx congicus*.

Taxonomy Originally described as, and sometimes included as, a subspecies of African Clawless Otter *Aonyx capensis* (see, most recently, Wozencraft 2005). Three subspecies have been recognized (Hinton 1921, Harris 1968, Coetzee 1977): *A. c. congicus*, from Gabon and Congo (DR Congo, except eastern highlands); *A. c. microdon*, from Cameroon and Nigerian border along the upper Cross R.; and *A. c. philippii*, from Rwanda, Burundi, the eastern highlands of DR Congo and SW Uganda. Kingdon (1997) added a fourth subspecies, *A. c. poensis*, known from a single specimen described by Waterhouse (1838) from Bioko I. This taxon has had a contentious past, including being considered as a synonym of *Aonyx capensis* (Wozencraft 1993) and as a subspecies of Spotted-necked Otter *Hydrictis maculicollis* (Rosevear 1974, Wozencraft 2005, and herein). Most authorities now consider *A. congicus* to be monotypic (e.g. Rosevear 1974, Larivière 2001), which is also the preferred

view followed here. Note that *Aonyx*, being of Greek origin and of masculine gender, requires the specific name to concur (Van Bree *et al.* 1999). Therefore, the correct name is *Aonyx congicus*, although *A. congica* is still often incorrectly used. Synonyms: *hindei*, *microdon*, *philippii*. Chromosome number: 2n = 38 (Van Zyll de Jong 1987).

Description A very large otter, similar in size to the African Clawless Otter. The species is characterized by a conspicuous dark patch between the eyes and the nostrils contrasting sharply with the surrounding whitish fur (Kingdon 1997, Jacques *et al.* 2002). Upper lips, top of the nose to the eyebrows white or yellowish-white. Head and shoulders conspicuously frosted (more so than in African Clawless Otter) by the silvery tips of most of the longer guard hairs, which are numerous on the head and shoulders, becoming rare on the back. Small round ears with a distinct white margin on

the border. Upper border of the rhinarium straight (rounded or V-shaped in African Clawless Otter). Sometimes a dusky cross-band behind the chin (Allen 1924, H. Jacques pers. obs.). Dorsal pelage dark chocolate to pale grey. Ventral pelage of a similar colour, except the cheeks, chin, throat and upper chest, which are white or light cream. Front digits naked, claws and webbing absent, toes webbed to the base of the second phalanx, rudiments of claws on the second, third and fourth toes only (rarely on the thumb and fifth). Tail long and heavily muscled, tapering towards the tip. There is little or no sexual dimorphism. Females have two pairs of abdominal nipples.

The skull of the Congo Clawless Otter resembles that of the African Clawless Otter in most respects. However, the cheekteeth (P^4 , M^1 , M_1 , M_2) are conspicuously smaller when compared with those of the African Clawless Otter (30% smaller; Rosevear 1974, Jacques *et al.* 2004, 2009) (see Measurements). Apart from the dentition, no important features distinguish mature skulls of the two species (Rosevear 1974, Jacques *et al.* 2004, 2009) (see Measurements).

Geographic Variation Both regional and individual variation appears to be minimal.

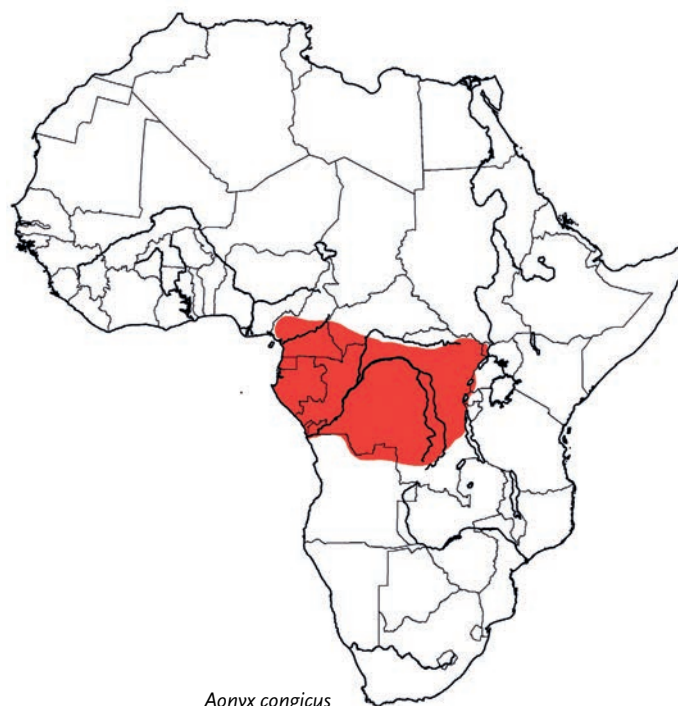
Similar Species

Aonyx capensis. Patch between eye and nostril is less conspicuous and blends with the colour of the darker upperparts; ears uniformly brown or may have a thin white edge; frosting reduced or absent on the head and shoulders (these differences are less conspicuous when the fur is wet); top border of rhinarium rounded or lightly V-shaped. Some individuals show intermediate patterns between Congo Clawless and African Clawless Otters. These intermediate forms seem to come from the limits of the distribution range of the former species (De Barros Machado 1969, H. Jacques pers. obs.). It is not yet known whether, or to what degree, the two species are sympatric.

Hydrictis maculicollis. See species profile for notes on sympatry. Smaller in size; throat and neck with pale cream or white mottling, or the same colour as the rest of the body; webbed feet.

Distribution Endemic to Africa, this species occurs in the rainforests of the Congo basin including Equatorial Guinea, Gabon, Congo, DR Congo, as well as S Cameroon, S Central African Republic, N Angola and extending eastward to the forests and the wetlands of Rwanda, Burundi and Uganda (Rowe-Rowe 1990b, Larivière 2001). The exact limits of the species' distribution range are still unclear (including the range east of the Rift), particularly due to the species' possible confusion with the African Clawless Otter. Older recorded localities of Congo Clawless Otter from Nigeria are now located in Cameroon due to international boundary changes (Harris 1968, relocated by Rosevear 1974). The African Clawless Otter is recorded in SE Nigeria (Eniang & Luiselli 2002), but Congo Clawless Otter probably are absent (L. Luiselli pers. comm.). Neither Happold (1987) nor Van Rompaey & Powell (1999) mention the species as occurring in Nigeria.

The 32 skins of Congo Clawless Otter examined in the Tervuren Royal Museum come mainly from the north and west of DR Congo. Due to hunting pressure the species is no longer found in the east of the country (J. P. Van de Weghe pers. comm.). In Angola, the species occurs only in the northern part of the Lunda district, north of the 10° parallel (De Barros Machado 1969, Crawford-Cabral 1989a), though interestingly Hayman (1963) does not mention the species.



Aonyx congicus

Habitat The prime habitat of this species is the tropical rainforest of the Congo basin. There is no evidence to suggest that they use shoreline habitats (as the African Clawless Otter does), although its presence further inland in coastal freshwater lagoons and mangrove swamps was reported in Gabon and Congo (Jacques 2002). Congo Clawless Otter can be readily observed in large and small rivers, and not only in swamps as one of its common names suggests. It is frequently observed in swampy forest clearings (bais) (e.g. Langoué Bai in C Gabon, and Mbeli Bai in Nouabalé-Ndoki N. P. in N Congo). Spotted-necked Otters are sympatric in parts of their range, such as at Mbeli, and both species have been observed feeding in proximity without conflict. Bai-use by Congo Clawless or Spotted-necked Otters seems to vary according to changes in aquatic vegetation, with the latter favouring more open water than the former (R. Parnell & E. Stokes pers. obs.). Recorded to 2200 m on the Kahuzi Massif (Rahm & Christiaensen 1963).

Abundance This is a very poorly known species, and there is limited information available. It may be common in certain undisturbed rainforest locations, though it is thought to be otherwise rare and perhaps even extirpated in parts of some countries. However, from 1998 to 2001 otters were observed in Mbeli Bai between 10 and 40% of days per month and appeared to be common (R. Parnell & E. Stokes pers. obs.).

Adaptations General adaptations are shared with African Clawless Otter. The smaller molars of the Congo Clawless Otter, compared with African Clawless Otter, probably reflect their selection of generally softer prey items (see Foraging and Food). Besides the Spotted-necked Otter, *A. congicus* is also sympatric with the Marsh Mongoose *Atilax paludinosus* and African Clawless Otter; segregation in diet presumably allows these species to co-exist (Rowe-Rowe & Somers 1998).

Foraging and Food Carnivorous. Food items include earthworms, molluscs, fish, frogs, crabs and other small vertebrates and invertebrates (see Jacques *et al.* 2009 and references therein). At Mbeli Bai, almost all observed feeding is on worms, though fish are sometimes caught (R. Parnell pers. obs.). Worms are located by pushing the forepaws deep into soft mud banks, and feeling through the mud with the fingers, gaze averted. After several seconds the forepaws are withdrawn and the worm transferred from the digits to the mouth. An average of three worms per minute are obtained in this manner. Parent otters have been observed feeding immatures, with worms passed from mouth to mouth. After feeding, otters at Mbeli were observed rolling in grass, self-grooming and further drying their fur by resting in the sun (R. Parnell pers. obs.). Defecation at rolling sites is common.

Social and Reproductive Behaviour Unknown, although 'family parties' have been observed in rivers in Cameroon (Kingdon 1997). At Mbeli Bai, up to four individuals have been seen together although most are seen alone or in pairs (frequently mother/offspring) (R. Parnell pers. obs.). Vocalizations, which are common when individuals meet, include barks, growls, snorts, hah!, coos, hums and whistles (Duplaix 1982). Serious fights are rare but squabbles and play fighting are frequently observed.

Reproduction and Population Structure Unknown. In DR Congo, there are records of cubs being born in Feb (R. Chapman pers. comm.) and Aug (J. Thompson pers. comm.) and three cubs were born in the beginning of Jan in SE Gabon (O. Bourry pers. comm.). At Mbeli Bai, subadults have been seen in most months of the year and cubs seen in Feb (R. Parnell pers. obs.). These meagre observations suggest that breeding may occur throughout the year. Other reproductive parameters are probably as for African Clawless Otter. Newborn cubs are pure white (J. Thompson & P. Charles-Dominique pers. comm.), although two-month-old cubs have the same colouration as adults.



Congo Clawless Otter *Aonyx congicus* face.

Predators, Parasites and Diseases Uncertain, but crocodiles, pythons, large raptors and Leopards *Panthera pardus* are likely predators, particularly of cubs. A single parasite has been reported, the nematode *Microfilaria aonycis* (van den Berghe *et al.* 1963); due to their aquatic way of life, otters in general have few ectoparasites. Distemper, parvovirus and leptospirosis have been reported in other otter species when in contact with infected domestic dogs.

Conservation IUCN Category: Least Concern. CITES: Appendix I (Cameroon, Nigeria); Appendix II (other populations).

Localized threats to the Congo Clawless Otter include hunting for bushmeat and skins, habitat loss and degradation, and overfishing. As with African Clawless Otters, this species is present in several protected areas across its range. Recent confirmed records include: Dja reserve in Cameroon (F. Alary pers. obs.); Dzanga-Sangha N. P. in Central African Republic (A. Turkalo, J. Ray pers. comm.); Ivindo N. P. (L. Davenport pers. comm.), Lopé N. P. (L. White pers. comm.) and Langoué Bai (WCS team pers. obs.) in Gabon; and Nouabalé-Ndoki (R. Parnell, H. Jaques, F. Alary pers. obs.) and Odzala (J.M. Froment pers. comm.) National Parks in Congo.

Measurements

Aonyx congicus

HB (♂ ♂): 692 mm, n = 3

HB (♀ ♀): 745 mm, n = 6

T (♂ ♂): 471 mm, n = 3

T (♀ ♀): 454 mm, n = 6

HF c.u. (♂ ♂): 147 mm, n = 3

HF c.u. (♀ ♀): 138 mm, n = 6

E (♂ ♂): 35 mm, n = 3

E (♀ ♀): 33 mm, n = 6

Allen 1924 (ranges not given)

Note that although Allen identifies his specimens as African Clawless Otter, the molar measurements given as well as the description and the locality of Faradje in DR Congo refer to Congo Clawless Otter instead (Schouteden 1942). Further, skins and skulls of the Lang & Chaplin expedition (examined in AMNH by the authors) are indeed Congo Clawless Otter. Lönnberg (1910) recorded weights of 13.6–18.1 kg from lower Congo, though Kingdon (1977, 1997) gives a range to 34 kg

P⁺ (L × W): 10.2 × 10.7 mm, n = 43*

M¹ (L × W): 13.0 × 10.0 mm, n = 44*

M₁ (L × W): 13.4 × 7.6 mm, n = 40*

GLS (♂ ♂): 129.9 (108.4–145.0) mm, n = 44

GWS: 89.7 (70.8–109.0) mm, n = 39

Throughout range (Jacques *et al.* 2009)

*L = longest length, W = greatest width, at right-angles to the main longitudinal axis of the skull

Key References Jacques *et al.* 2002, 2004, 2009; Kingdon 1977; Larivière 2001; Rosevear 1974.

Hélène Jacques, Richard Parnell & Franck Alary

GENUS *Lutra*

Common Otter

Lutra Brisson, 1762. Regnum Animale, Ed. 2.

The content of the genus is dependent upon whether the genera *Lontra* (four species of New World Otters, except the Giant Otter *Pteronura brasiliensis*) and *Hydrictis* (including the Spotted-necked Otter *H. maculicollis*) are considered distinct or synonymous with *Lutra*. Separation of New World Otters in *Lontra* appears well supported (Van Zyll de Jong 1972, 1987, Koepfli & Wayne 1998, Bininda-Emonds *et al.* 1999). However, whereas the genus *Hydrictis* has been recognized as distinct by some (e.g. Pocock 1921, Davis 1978, Davis *et al.* 1979, Grubb *et al.* 1998), it was not recognized as such by Harris (1968) or Van Zyll de Jong (1987) on morphological grounds. The molecular data of Marmi *et al.* (2004) also supported inclusion of all otters in the genus *Lutra*. None the less, inclusion of the Spotted-necked Otter in a separate genus appears warranted as the genus *Lutra* is paraphyletic, and the Spotted-necked Otter diverges before the clade that includes Common or Eurasian Otter *Lutra lutra* and the two clawless otter species, African Clawless Otter *Aonyx capensis* and Congo Clawless Otter *A. congicus* (Koepfli & Wayne 1998; and

see Bininda-Emonds *et al.* 1999). Consequently, Wozencraft (2005) recognized *Hydrictis* as distinct from *Lutra*, which now appears well supported (Koepfli *et al.* 2008, Sato *et al.* 2012).

Worldwide, then, three species of *Lutra* are recognized, of which one occurs in Africa: the Common or Eurasian Otter, which is found in North Africa and then extraliminally throughout much of Eurasia. The two extralimital *Lutra* species are the Japanese Otter *L. nippon* (which some authors consider synonymous with the Common Otter), and the Hairy-nosed Otter *L. sumatrana*, from South-East Asia. The Common Otter is considerably smaller than the two *Aonyx* species, and yet about twice the mass of the Spotted-necked Otter (which is the smallest of the African otters), though similar in appearance. In contrast to *Aonyx*, the Common Otter has webbed forefeet, strong claws on all feet and the tail is cylindrical, not flattened.

Hans Kruuk

Lutra lutra COMMON OTTER

Fr. Loutre; Ger. Fisch-Otter

Lutra lutra (Linnaeus, 1758). Syst. Nat., 10th edn, 1: 45. 'Euopae aquis dulcibus fluviis, flagnis, piscinis,' subsequently restricted by Thomas (1911) to 'Uppsala' [Sweden].

Common Otter *Lutra lutra*.



Taxonomy In North Africa originally described as a new species *Lutra angustifrons* Lataste, 1885, although the same author subsequently considered the species conspecific with European otters. Indeed, although African populations have been treated subspecifically as *L. l. angustifrons* (e.g. Allen 1939, Ellerman & Morrison-Scott 1951), Van Bree (1968) showed that otters from North Africa and the European populations are inseparable, Lataste having originally compared the skull of an adult otter from Algeria with that of a juvenile from France (Coetzee 1977). Synonyms (Africa only): *angustifrons*, *spendida*, *vulgaris*. Chromosome number: $2n = 38$ (Günter & Gebauer 1982).

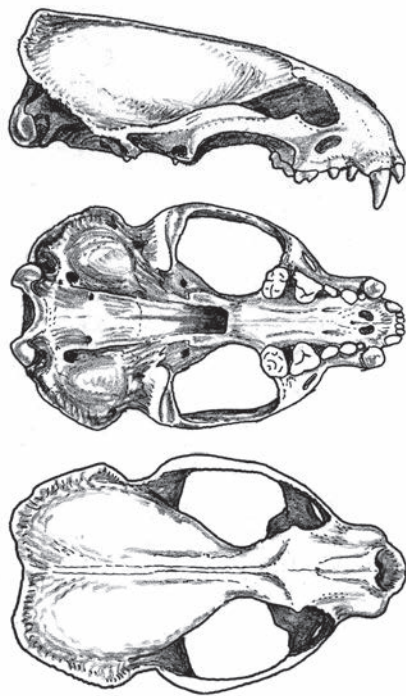
Description Medium-sized, with streamlined and elongated body, muzzle rather blunt with large whiskers, head somewhat flattened, short round ears, small eyes. Vibrissae can be rotated downward during diving, to create larger contact area when fishing. Head tapering into body, with head and neck of equal width. Pelage fairly short and extremely dense, hair length even over entire body, guard hairs overlying very compact undercoat (about 500 hairs per mm^2 , Kruuk 1995, 2006). Overall colour evenly dark brown, lighter underneath, throat usually the lightest part. Occasionally individuals have small, clear white patches on throat, but generally there is little variation in colour. Legs short, especially forelegs; also equipped with small vibrissae at the elbow. All feet have five toes and clear claws, not very sharp. Hindfeet fully webbed, forefeet partially so. Long, round tail, thick at base and tapering to end. Males are about one-third heavier than ♀♀. Two or three pairs abdominal nipples.

In the skull the postorbital constriction is uniquely narrow. Dental formula is $I^{3/3}, C^{1/1}, P^{4/3}, M^{1/2} = 36$; some incisors are often missing.

Geographic Variation None recorded within Africa.

Similar Species

Hydrictis maculicollis. Sub-Saharan Africa only. Darker brown and darker coloured underneath, with striking irregular white blotches on throat. Usually occurs in small groups and can be highly gregarious (e.g. in L. Victoria; Procter 1963).



Lateral, palatal and dorsal views of skull of Common Otter *Lutra lutra*.

Distribution The Common Otter is a Eurasian species, with the largest geographical distribution of all otters, ranging throughout much of the Palearctic (except the Siberian tundra), including the British Isles, Sri Lanka, Taiwan and Sumatra (Corbet 1978). Only a very small part of the range extends into North Africa, where it is found in rivers in the plains and in the Atlas Mts, in originally contiguous but now more fragmented populations. Widespread in the foothills of the Middle and High Atlas of N Morocco, where it seems to be limited by available water and rivers with suitable cover (Macdonald & Mason 1984, Broyer *et al.* 1988, Aulagnier 1990, Cuzin 1996, 2003, Delibes *et al.* 2012). In Algeria, Common Otters formerly inhabited larger rivers and lakes in the coastal region and Tell Atlas, and in W Algeria they were sporadically observed in seasonal rivers on the border of the Saharan Atlas and the desert (Kowalski & Rzebik-Kowalska 1991). Today, the Common Otter is limited to the Sebaou R. in Kabylie and the coastal eastern parts (Macdonald *et al.* 1985, Kowalski & Rzebik-Kowalska 1991), ranging into wetlands in N Tunisia, where they are common in and around L. Ichkeul, with the Oued Medjerde representing a southern limit for the species in the country (as rivers further south offer little shelter) (Macdonald & Mason 1983).

Habitat Totally dependent on water: edges of lakes, dams and rivers, extending into swamps and up the smallest of streams, including irrigation channels (Cuzin 2003). Forages in shallow water, mostly less than 2 m deep, but spends most of the time resting inside cover of reeds, shrubs and other dense vegetation. In Tunisia, otters would lie up in dense bankside cover, primarily provided by *Nerium oleander* (Macdonald & Mason 1983); the latter plant is evergreen and, being poisonous, is not grazed by livestock. In Africa, found up to 2295 m in Morocco (Cuzin 2003). Crosses watersheds overland, and dens may be used up to 1 km from water. May occur close to settlement and in tree plantations. In Europe, also occurs along rocky seashores, but only where freshwater is available (for otters to wash salt out of fur as well as for drinking; Kruuk



Lutra lutra

1995, 2006); in North Africa, they only very rarely are found in the sea (Piquet 1961) and in coastal lagoons (Cuzin 2003). In S Morocco, otters are found until the southern limit of permanent freshwater, reaching the northern Sahara. Habitat selection differs between ♂♂ and ♀♀: ♀♀ more often in small streams and lakes, ♂♂ in the larger rivers.

Abundance Locally relatively common, though declining throughout their African range. Rarely seen, so evidence for their presence is derived from field signs such as droppings ('spraints') and tracks (e.g. Macdonald *et al.* 1985, Delibes *et al.* 2012). Such evidence is not reliable for assessment of densities. Even in the best habitats, otters rarely reach densities of more than one animal per 10 km of bank, but spraints may be found in many places. There is a good correlation between fish biomass and otter density, suggesting that otter density in any area is limited by availability of prey (Kruuk 1995, 2006).

Adaptations Common Otters have remarkably sharp teeth (used for catching fish). Their eyesight is moderate, and used under and above water; hearing is not very acute, but their sense of smell is excellent, with an ability to detect other otters over hundreds of metres.

Foraging and Food Highly specialized fish eaters, but also taking amphibians, crustaceans and occasionally birds (as large as geese) and small mammals. They prefer slow, bottom-dwelling fish, preferably with a high fat content (e.g. eels, salmonids, silurids), and take fish upwards of about 4 cm in length, usually 12–20 cm long, and occasionally much larger. In Morocco, fish (*Salmo trutta* or *Barbus* spp.) predominate in the diet, but amphibians are the secondary main prey. Occasionally, birds, snakes and crustaceans are preyed upon; important seasonal variations have been observed, with predominance of amphibians and crustaceans (Broyer *et al.* 1988).

Common Otters forage for 4–6 hours per day. They rarely pursue their prey, but surprise it, often when the prey is non-active. Mostly nocturnal in areas where the main prey is diurnally active, and vice

versa. They often find underwater prey by touch (feet, vibrissae), but also use vision when there is sufficient light. In lakes they dive from the surface, remaining underwater for 10–25 sec (depending on water depth; rarely up to 60 sec), surfacing for 5–10 sec. When successful, they feed on small prey on the surface, but move to land with large prey. In streams, the amount of time spent underwater is much shorter. Because of heat loss in water, foraging is energetically very demanding and animals need to be highly successful. On average, Common Otters eat 1.2–1.5 kg per day (Kruuk 1995).

Social and Reproductive Behaviour Solitary, although cubs may accompany the ♀♀ for a year or more, even when fully grown. Females defend a territory against other ♀♀, though often there are large overlaps, and there may be several (related) ♀♀ in one territory, who avoid but tolerate each other. Males fight over territories larger than those of ♀♀, and overlap with several ♀♀. In Europe, individual home-ranges average about 21 km for ♀♀, and 40 km for ♂♂ (but up to 80 km; Kruuk 1995, 2006). Faeces ('spraints') are used for scent-marking, in small but strong fish-smelling quantities. There is no system of boundary-marking, but they spraint close to foraging sites and other resources, and more often when there is competition for food, so sprainting is often seasonal.

Cubs are born in dens, often far from water, or in a covered nest of reeds. After two months the mother forcefully carries the cubs into water, and they accompany the ♀ when foraging. In the first week outside the den ♀♀ may deliberately abandon one or more of the cubs, perhaps related to food availability (Kruuk 1995, 2006). Weaning takes place at 4–6 months, when cubs start to catch their own prey (usually close alongside the mother), but remain dependent on the mother for prey for another year. Cubs and mother keep in contact using a whistling call; when play-fighting they emit a high-pitched rattling call ('wickerling') or loud screams. Foraging and diving efficiency of cubs increases up to at least 18 months of age (Watt 1993). The ♂ is not involved in any aspect of rearing or defence.

Reproduction and Population Structure Most information available on breeding comes from the European part of its range. Females are polyoestrus, the cycle lasting 4–6 weeks, and with first litter at the age of 2–3 years. Young are born at any time of the year after a gestation period of about eight weeks (Wayre 1979). Litter-size is 1–4 and there is no delayed implantation. Longevity in captivity is around 18–20 years (Nowak 1999, Weigl 2005); in the wild average age at death is 4–5 years, and, with long cub dependence on mother, lifetime reproductive output is small (Kruuk 1995, 2006). Mortality rate increases with age, related to high rate of metabolism, and the main cause is probably food shortage.

Predators, Parasites and Diseases There are no known natural predators for this species in North Africa, with the exception of large raptors preying on cubs. Common Otters are susceptible to distemper and rabies, but the effects of these on populations is unknown.

Conservation IUCN Category: Near Threatened. CITES: Appendix I.

Legally fully protected in Morocco, Algeria and Tunisia. Common Otters are vulnerable to loss of habitat, especially in riparian vegetation. Their aquatic habitat is susceptible to pollution by organochlorines, such as DDT, dieldrin and heavy metals (Foster-Turley *et al.* 1990), and preferred prey species accumulate such pollutants. A large 1960s population crash in Europe was probably caused by dieldrin. Present-day effects on populations are often unclear (and probably over-rated). Macdonald *et al.* (1985) attributed a decline in Algeria to changing water levels in rivers (due to the destruction of forest), the disappearance of suitable habitat along water-banks and pollution (pollution of inland rivers in Algeria seems to contrast markedly with the situation elsewhere in parts of North Africa). In Morocco, pollution, mainly domestic but sometimes industrial, has increased dramatically in the major rivers, especially in the north, where otters have apparently disappeared from rivers in the lowland plains, and the use of domestic detergents has led to eutrophication, especially in the south, where water resources are scarce; dam building has also reduced available habitat and led to the fragmentation of populations. Compliance with international treaties, such as the Stockholm Convention, could see otters recolonize the plains from source populations in mountainous areas (Delibes *et al.* 2012). Usually, numbers are limited by fish biomass (Kruuk 1995, 2006), and the best way to promote otter numbers is to manage for high densities of fish. Illegal hunting is a problem in some areas, as otters are sometimes eaten and their pelts sold (F. Cuzin pers. comm.).

Measurements

Lutra lutra

HB (♂♂): 720 ± 33.2 mm, n = 18

HB (♀♀): 636 ± 25.9 mm, n = 24

T (♂♂): 446 ± 22.5 mm, n = 18

T (♀♀): 398 ± 20 mm, n = 24

WT (♂♂): 10.1 ± 1.37 kg, n = 433

WT (♀♀): 7.0 ± 1.03 kg, n = 220

Britain (Corbet & Harris 1991)

Key References Broyer *et al.* 1988; Kruuk 1995, 2006; Macdonald & Mason 1983, 1984; Macdonald *et al.* 1985.

Hans Kruuk

GENUS *Hydricis* Spotted-necked Otter

Hydricis Pocock, 1921. Proc. Zool. Soc. Lond, 1921: 543.

The genus *Hydricis* includes the Spotted-necked Otter, which occurs throughout most tropical and sub-tropical regions of sub-Saharan Africa. The species is often included in the genus *Lutra*; the classification here follows Wozencraft (2005), since inclusion in

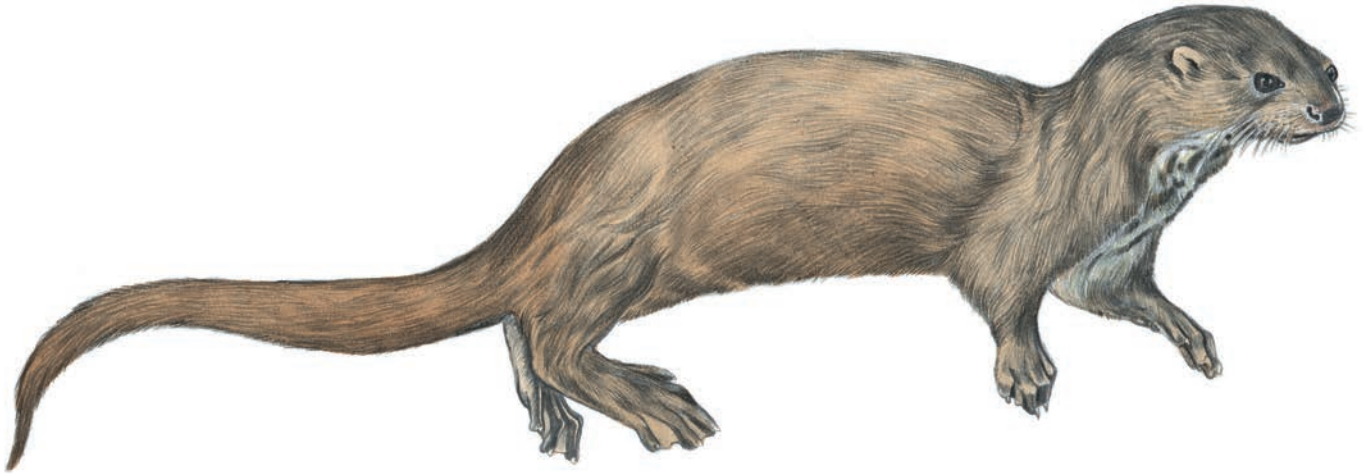
Lutra would render *Lutra* paraphyletic (Bininda-Emonds *et al.* 1999, Koepfli *et al.* 2008, Sato *et al.* 2012).

Michael Hoffmann

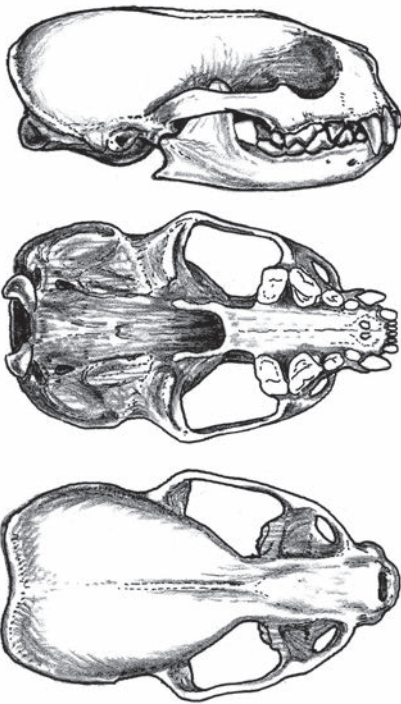
Hydriactis maculicollis SPOTTED-NECKED OTTER

Fr. Loutre à cou tacheté; Ger. Krallen-Otter

Hydriactis maculicollis (Lichtenstein, 1835). Archiv Naturgesch. 1 (1): 'Kafferlandes am ostlichen Abhange der Bambusberge' (Bamboesberge 31° 30' S 26° 20' E, near Sterkstroom, Eastern Cape Province, South Africa).



Spotted-necked Otter *Hydriactis maculicollis*.



Lateral, palatal and dorsal views of skull of Spotted-necked Otter *Hydriactis maculicollis*.

Taxonomy Nine forms have been described from Africa, mainly on the basis of size, colour or markings, with six subspecies listed by Allen (1939) and five by Coetzee (1977). The validity of these subspecies is questionable, and the listing of five subspecies here is provisional and follows Coetzee (1977) and Meester *et al.* (1986). Synonyms: *chobiensis*, *concolor*, *grayii*, *kivuana*, *malculicollis*, *matschiei*,

mutandae, *nilotica*, *poensis*, *tenuis*. Chromosome number: $2n = 40$, the only otter species with more than 38 chromosomes. Fundamental number is 66; X chromosome is submetacentric and Y chromosome is metacentric (Davis *et al.* 1979, Van Zyll de Jong 1987).

Description Spotted-necked Otters are the smallest of African otters. Medium-sized, with a streamlined body covered in short, dense fur (guard hairs 15–20 mm long) varying from chocolate brown to dark reddish in colour; underfur slightly shorter and white or off-white. Throat and neck with pale cream or white mottling, or, less commonly, same colour as rest of body. Underparts generally same colour as back and sides. Albinos or partial albinos have been recorded (Procter 1963). Head broad at back, narrows at short, broad muzzle. Ears small. Upper lips and area under nostrils pale pink. Tail long and dorsoventrally flattened. Legs short with five toes webbed to their tips, each possessing a creamy-white claw about 10 mm long. Anal glands present. Two pairs abdominal nipples.

The skull conforms to the typical mustelid shape but is lightly built, with rostrum short and broad. The postorbital bar is represented by a small knob-like process behind and above the eye and a slightly better developed process on the zygomatic arch. The eye sockets are proportionally larger than in the African Clawless Otter *Aonyx capensis* (Skinner & Chimimba 2005). Dental formula is $I^{3/3}, C^{1/1}, P^{4/3}, M^{1/2} = 36$.

Geographic Variation

H. m. maculicollis: South Africa, Mozambique, S Malawi.

H. m. chobiensis: N Botswana, Caprivi Strip, Cunene and Okavango Rivers of Namibia, Angola, W Zambia and lowland Congo basin.

H. m. kivuana (including *mutandae* and *tenuis*): L. Kivu area (DR Congo), Burundi, Rwanda, SW Uganda, L. Victoria, NW Tanzania and adjacent parts of Kenya.

H. m. matschiei: Gabon, Cameroon, Nigeria, S Niger. Western limit unclear.

H. m. nilotica: S Sudan and Ethiopia.

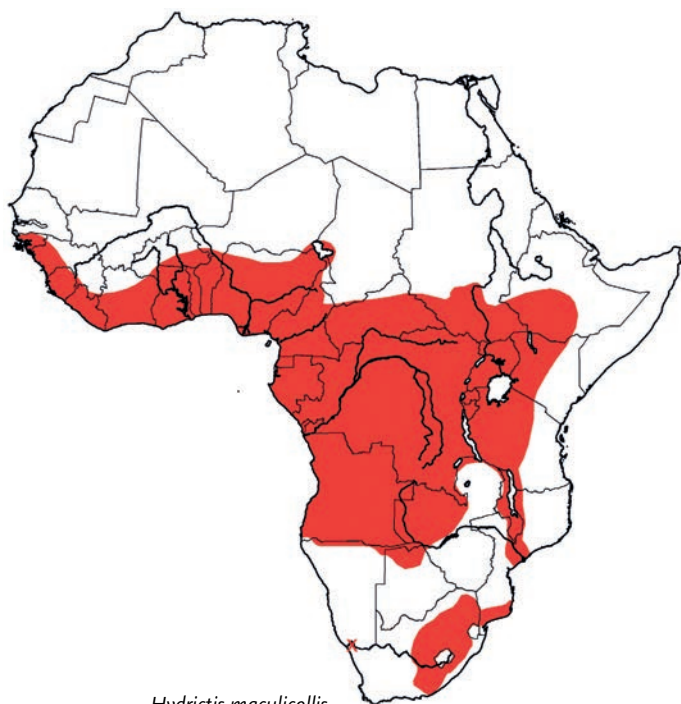
The subspecies status of *Hydrictis maculicollis* in West Africa is not clear, and none are currently named (see Rosevear 1977, Grubb *et al.* 1998). H.-J. Kuhn (in Coetzee 1977) thought that specimens from Liberia allied closely with the nominate form, even though he supported differentiating between *maculicollis* and *matschiei*, the form that might occur.

Similar Species

Lutra lutra. North Africa only and then extraliminally. Lacks white mottling on throat. Usually solitary.

Aonyx capensis and *A. congicus*. Both larger in size with unspotted off-white chin, throat, and upper chest; toes clawless and forefeet unwebbed; molars broad and robust for crushing crustaceans. The three species coexist in the Congo basin, SW Central African Republic and possibly in Rwanda, Burundi and W Uganda. The Congo Clawless Otter and the Spotted-necked Otter are both also found in Gabon. Clawless otters and Spotted-necked Otters coexist throughout most of the eastern and southern part of their range of distribution. Owing to behavioural and morphological differences and specific habitat use there does not appear to be competition between Spotted-necked Otters and the two clawless species (Rowe-Rowe 1977, Somers & Purves 1996, Rowe-Rowe & Somers 1998).

Distribution An African endemic, occurring throughout most of tropical and sub-tropical sub-Saharan Africa where there is permanent water containing small fishes. The range is given by Rowe-Rowe & Somers (1998) as Sierra Leone eastwards to L. Chad, then from S Central African Republic to SW Ethiopia. In the west, they range southwards to rivers forming the northern border of Namibia and swamps and rivers of NW Botswana. In the east,



Hydrictis maculicollis

they range southwards through W Kenya and Tanzania, Malawi, part of Mozambique, to E South Africa. Power & Slater-Jones (2010) recorded a sighting of a Spotted-necked Otter on the lower Orange R. at Senderling's Drift in the Ais/Ais Richtersveld Transfrontier Park, some 1200 km downstream from their known distribution.

Although usually reported as absent from Zimbabwe (Smithers & Wilson 1979), the species has recently been recorded from Zambezi N. P. and Matetsi Unit 7 in the far north-west (Purchase *et al.* 2007). They are otherwise absent from most of Zimbabwe, E Zambia and Swaziland, and apparently locally extinct in Burundi, Ghana, Togo and Lesotho (although it is not clear if they ever occurred in this country). That their range formerly extended further north at least along the Egyptian Nile is proven by the discovery of skeletal remains at late Palaeolithic fishing sites (Van Neer 2002).

In West Africa, the exact distribution range is unclear. According to Grubb *et al.* (1998) the farthest west the species has been reliably recorded is Guinea in the Kounounkan Massif (Barnett *et al.* 1996). Distribution is not continuous eastwards from Sierra Leone, and Grubb *et al.* (1998) state that 'west of Nigeria Harris (1968) recorded only Liberia, overlooking Sierra Leone and Côte d'Ivoire. But there is no confirmed record between the western part of Côte d'Ivoire and SW Niger where Poché (1976) listed it from 'W' N. P. (though this was not based on collected material) and Nigeria (Happold 1987). There is a real, though unexplained, absence of this species from many parts of eastern and southern Africa, as well as much of West Africa.' Their presence in the WAP Complex of protected areas at the confluence of the Benin, Niger and Burkina Faso borders is discussed by Lamarque (2004). The recent catch of a specimen, and findings from a field survey, have confirmed the presence of this species in Guinea-Bissau, moving its western boundary further west (Reuther *et al.* 2003).

Whether this species ever occurred on Bioko I. is unclear. Waterhouse (1838) described the form *poensis* (in the past also based on a single specimen) apparently collected from Bioko. However, Eisentraut (1973), reviewing earlier opinions on the matter, and who himself failed to record the species, contested the presence of the species on Bioko concluding that Waterhouse's specimen had mainland origins. The only other observations of an otter on Bioko are those reported by Kingsley (1897), who remarked on 'a very pretty otter (*Lutra poensis*) with yellow brown fur often quite golden underneath'. These observations provide some evidence that otters may once have existed on Bioko, although there is little doubt that the species is now extinct on the island (Harrington *et al.* 2002).

Habitat The Spotted-necked Otter inhabits freshwater habitats where water is unsilted, unpolluted and rich in small fishes; it does not occur in marine or estuarine waters. Most suitable habitat appears to be the large lakes of central and East Africa and open waters of areas such as the Okavango Delta (Rowe-Rowe & Somers 1998). Elsewhere, it is found in streams, rivers and impoundments up to altitudes of 2500 m (Yalden *et al.* 1996). Wherever it occurs, the Spotted-necked Otter prefers shallow to deep waters (Larivière 2002c). Adequate riparian vegetation in the form of long grass, reeds, or bushes is essential to provide cover during periods of inactivity. Resting places and dens are generally on stream or river banks, on ledges in banks, rock ledges, islands, or lake shores, wherever dense vegetation cover is present (Rowe-Rowe 1992b, Perrin & Carugati 2000b). A telemetry study conducted in KwaZulu-Natal, South Africa, revealed core areas

included a highland river and tributaries, natural oxbow lakes and some man-made lakes artificially stocked with alien trout (Perrin *et al.* 2000).

Abundance Common or fairly common in the fish-rich central African lakes. Throughout the rest of Africa, where fish faunas tend to be poor, the species is generally uncommon or rare (Rowe-Rowe 1990b, 1995). Abundance and density appear to be strictly dependent on the availability of fish. In the central and East African lakes, density was estimated at between one and two otters per kilometre of shoreline (Procter 1963, Kruuk & Goudswaard 1990, Lejeune & Frank 1990). In an area that included a highland stream and man-made lakes in South Africa, Perrin *et al.* (2000) estimated 1 otter/1–2 km of stream, while in less suitable habitat Rowe-Rowe (1992b) estimated 1 otter/6–11 km. In a survey conducted on four 5 km sections on three different rivers in Ukhahlamba-Drakensberg Park, Carugati (1995) estimated that the number of otters using each of the different sections ranged between one and five, depending on habitat suitability. In Sierra Leone, the species was found to be much rarer than the African Clawless Otter, and out of some 30 skins examined over a period of 15 years, only two were Spotted-necked Otters (Rosevear 1974, Grubb *et al.* 1998).

Adaptations The feet are fully webbed and clawed, unlike the clawless otters. This represents a substantial difference in the nature of the interface between otter and environment and, in spite of this species being quite dextrous with its forefeet, it can be described as ‘mouth-oriented’, rather than ‘finger-oriented’, as the clawless species are (Kingdon 1977). When swimming, all four feet are used for the initial thrust, and the hindfeet propel the otter onward. The forefeet steer the animal through water in combination with the very slightly flattened tail, which serves as a rudder and balancing organ (Mortimer 1963, Rowe-Rowe 1975b). The guard hair and underfur are particularly dense to insulate the body when swimming.

In the skull, the long glenoid process on the lower jaw fits into the groove of the upper part of the skull, inhibiting all sideways movement, unnecessary in an animal such as the Spotted-necked Otter where food does not need to be masticated thoroughly. The condyle is broad and high, allowing for a firm attachment of the temporalis muscles. However, the zygomatic arches are weak, the bone being broad and thin, suggesting that the function of the masseter muscles is reduced in favour of the temporalis (Skinner & Chimimba 2005). The upper canines are sharp and straight, lower canines recurved for holding prey. PM^4 and M_1 form carnassial shear for eating fish (Rowe-Rowe & Somers 1998). The perianal glands produce a secretion with a typical musty odour. The secretion appears as a gelatinous mass and it is always associated with spraints.

Dens are occasionally excavated by the otters where there is suitable alluvial soil (Rowe-Rowe 1992b). These excavated ‘holts’ have elliptical openings roughly 200 mm wide by 130 mm high ($n = 6$), with tunnel lengths between 0.9 and 1.0 m. Rowe-Rowe (1992b) noted that on a section of the Mooi R. in Ukhahlamba Drakensberg Park, the use of both dens and resting sites varied seasonally and ranged from 1 per 2 km to 1 per 3.5 km per season for dens and 1 per km to 1 per 1.7 km per season for resting sites. On three different rivers in the same park, Carugati (1995) found den density to be one den every 1–5 km.

Spotted-necked Otters have been described as diurnal, with activity peaks during early morning and late afternoon (Mortimer

1963, Procter 1963, Rowe-Rowe 1978a, Lejeune 1989). Using telemetry, d’Inzillo Carranza (1997) confirmed that they are most active between 06:00 and 09:00h, and then again between 15:00 and 18:00h. On bright moonlight nights activity was also recorded between 18:00 and 21:00h, occasionally continuing to 24:00h.

Foraging and Food The Spotted-necked Otter is a specialized fish eater, also feeding on crabs, frogs, insects and occasionally birds. In L. Muhazi (Rwanda) and L. Victoria (Tanzania) diet consists almost entirely of fish of the genus *Haplochromis*, followed by fish of the genus *Tilapia* (Procter 1963, Kruuk & Goudswaard 1990, Lejeune 1990). Kingdon (1977) in L. Bunyoni (Uganda/Rwanda) reported that the main prey before the introduction of *Tilapia* sp. was the clawed toad *Xenopus laevis*, and the otter population at that time was thriving.

In South Africa, where fish faunas of inland rivers are poor, Spotted-necked Otters appear to forage on almost equal amounts of fish, crabs and frogs, supplemented by small amounts of dragonfly (Odonata) larvae (Rowe-Rowe 1977a, Somers & Purves 1996, Perrin & Carugati 2000a). Where otters lived almost entirely on fish, no seasonal variation was obvious. In South Africa, the fish component was highest during autumn and winter while the crab component was highest during spring and summer (Rowe-Rowe 1977a, Perrin & Carugati 2000a). This could be related to the effects of water temperature on the prey: during the cold season crabs retreat into inaccessible places and at the same time the efficiency of locomotion of fishes is reduced by cold water (Rowe-Rowe 1977a).

In all studies to date, Spotted-necked Otters fed mainly on small fish, 80–90% being smaller than 100–150 mm fork length (Rowe-Rowe & Somers 1998). When preying on crabs, specimens with a carapace width <45 mm appear to be selected (Rowe-Rowe & Somers 1998) and Rowe-Rowe (1977b) found that most crabs with a carapace width >50 mm were avoided. Somers & Purves (1996) in the Bushman R. also found fish of the genus *Tilapia* to be the main component of its diet, and they did not find remains of any other species of fish. Rowe-Rowe (1977b) and Perrin & d’Inzillo Carranza (2000) suggested that they hunt mainly by sight. However, in the lakes where both small fishes and Spotted-necked Otters are most abundant, the water is very turbid (Lejeune & Frank 1990, H. Kruuk pers. comm.), suggesting that senses additional to sight are used. Foraging occurs mainly within 2–10 m of the shore (Procter 1963, Lejeune 1989, Kruuk & Goudswaard 1990). Foraging dives generally have a duration of 16–25 sec in deep water (Lejeune 1989) and shorter (5–20 sec) in shallower water (Rowe-Rowe 1977b). Surfacing periods between unsuccessful dives are brief (6–10 sec) as are those when small fish are caught and eaten in the water (11–16 sec) (Lejeune 1989). Larger prey is taken to the shore and eaten out of the water (Procter 1963, Rowe-Rowe 1977b). Prey appears to be always captured in the mouth. Very small fish (<60 mm) are eaten from the head, but all larger fish and frogs are eaten tail first, with the heads sometimes being discarded (Rowe-Rowe 1977b, Power & Slater-Jones 2010).

Foraging is mostly solitary, except in lakes where the otters fish in large groups (Procter 1963, Kruuk & Goudswaard 1990). In an impoundment stocked with alien trout, d’Inzillo Carranza (1997) occasionally observed groups of two or three individuals hunting together with synchronized dives, and on two occasions subsequently sharing the prey on the shore.

Social and Reproductive Behaviour Although territorial behaviour has never been observed, intra-specific relationships appear to vary in relation to food availability. In the fish-rich central African lakes Spotted-necked Otters generally occur in small groups, on average three, sometimes up to 10–20 individuals (Procter 1963, Lejeune 1989, Kruuk & Goudswaard 1990). In South Africa, where

fish faunas are poor, they are mainly solitary or in groups of up to five individuals (Rowe-Rowe 1978a, 1992a). As Rowe-Rowe & Somers (1998) hypothesized, larger aggregations seem to be associated with abundance of its favourite prey, such as small fishes. In the KwaZulu–Natal highlands a radio-telemetry study on six adult Spotted-necked Otters (three ♂♂ and three ♀♀) revealed a strict interrelation



Spotted-necked Otter *Hydrictis maculicollis*.

between social behaviour, group size and food availability: in an area that included several impoundments stocked with alien trout, 70% of all groups recorded ($n = 64$) comprised three otters or more, while in a nearby area comprising a natural stream and a few oxbow lakes, 77% ($n = 31$) of all groups seen consisted of two otters. No indication of territoriality was noted in either area (Perrin *et al.* 2000). Allo-grooming was often observed among individuals living around the impoundments, and activity and resting periods were mainly synchronized. Average sizes of home-range core areas were 8.7 km^2 for ♂♂ and 3.4 km^2 for ♀♀. Mean length of the river within the home-ranges was 14.8 km (Perrin *et al.* 2000).

Spraints are believed to be used for scent-marking as a means of communication. These latrines are similar to those of clawless otters (and sometimes even at the same site), and are located in grass above river banks or lake shores, on earth ledges in the river banks, on islands and less frequently on rocks (Rowe-Rowe 1992b). Most sites are found beside water at least 0.5–1 m deep, or in dense cover if water is very shallow. Distance from water was 1–6 m, mainly 2 m (Rowe-Rowe 1992b). Faeces have an average diameter of 15 mm (range 12–18 mm). If they contain a high proportion of crab remains they resemble clawless otter faeces in colour (dark brown when fresh fading gradually to cream). If mainly fish has been eaten they are dark grey and fade to light grey (Rowe-Rowe 1992b). Spraint sites are sometimes associated with rolling places, and spraint sites are spaced between 200 and 1000 m apart (Rowe-Rowe 1992b, Carugati 1995).

Vocalization as a form of communication among individuals was frequently noted (Procter 1963, d'Inzillo Carranza 1997). They occur mainly in the form of a high-pitched squeak. When alarmed, they emit a kind of a snort (Procter 1963, I. d'Inzillo Carranza pers. obs.). Mortimer (1963) observed in a captive specimen that a shrill trilling noise combined with neck stretching or lying on the back implies submission to another individual. Reliable information on other forms of communication is not available, neither is information on reproductive behaviour.

Reproduction and Population Structure In KwaZulu–Natal mating appears to take place during the dry season (May–Aug) (d'Inzillo Carranza 1997). On L. Victoria, Procter (1963) estimated that births occurred about Sep, while in Zambia Ansell (1960a) estimated Nov or Dec. Gestation is assumed to be 60–63 days (Rowe-Rowe 1992a), so young are born at the end of the dry season or early in the wet season. Delayed implantation likely does not occur (Procter 1963). Mean litter-size is not known, but adults with one or two young have been recorded (Rowe-Rowe 1978a, d'Inzillo Carranza 1997). Young may remain with the mother for up to one year (Kingdon 1997). No reliable information is available about where young are born and on growth. Davis (1978) suggested that longevity in the wild could reach eight years; in captivity, one animal lived to nearly 23 years (Weigl 2005).

Predators, Parasites and Diseases No meaningful data are available on natural predators, although crocodiles and pythons have been suggested (Lejeune & Frank 1990, Skinner & Chimimba 2005) and the young may be taken by African Fish-eagles *Haliaeetus vocifer* (Kruuk & Goudswaard 1990). Endoparasites recorded from Spotted-necked Otters include trematodes, such as *Baschkirovitrema incrasatum*, *Cynodiplostomum namrui* and *Prudhoella rhodesiensis* (Round

1968), and nematodes (Lejeune 1990). No information is available on possible diseases.

Conservation IUCN Category: Least Concern. CITES: Appendix II.

The Spotted-necked Otter is decreasing throughout its range. Rapidly increasing human populations are leading to the adverse alteration of freshwater habitats and riparian vegetation, exacerbated by the loss of habitat as a consequence of increased agricultural activity. Near urban areas expansion and industrialization have been responsible for both loss of habitat and pollution and sedimentation of streams and rivers, as too has acid pollution from coal mining (Stuart 1985, Rowe-Rowe 1990b, 1992a, 1995). Bioaccumulation of organochlorines and other biocontaminants has been recorded in Spotted-necked Otters: Mason & Rowe-Rowe (1992) examined four scats collected in KwaZulu–Natal and detected concentrations (mg/kg of extractable fat) of 0.02 for dieldrin (range 0.02–0.03), 0.04 for *O,p*-DDE (range 0.03–0.08) and 0.12 for total PCB (range 0.05–0.24).

Spotted-necked Otters are also killed for food or skins (see, for example, Lejeune & Frank 1990), as a perceived threat to poultry, or as a competitor for fish (Rowe-Rowe 1990b). Occasionally, they are accidentally caught and drowned in gill nets and fish traps (Stuart 1985, Rowe-Rowe 1990b). Introduction of alien fish species that out-compete the smaller indigenous fish was identified as a main threat for the L. Victoria population (Kruuk & Goudswaard 1990). Otter products are used in traditional medicine in KwaZulu–Natal (Cunningham & Zondi 1991). They are present in a number of protected areas across their range (in at least 28 of the 33 countries from which they have been recorded), though quality of protection obviously is not the same in all instances (Rowe-Rowe 1990b, 1995).

Measurements

Hydrictis maculicollis

HB (♂♂): 698 (650–760) mm, $n = 5$

HB (♀♀): 588 (570–606) mm, $n = 4$

T (♂♂): 397 (350–440) mm, $n = 5$

T (♀♀): 406 (335–440) mm, $n = 4$

HF c.u. (♂♂): 118 (113–122) mm, $n = 3$

HF c.u. (♀♀): 113 (111–115) mm, $n = 3$

E (♂♂): 18 (17–21) mm, $n = 4$

E (♀♀): 18 (15–20) mm, $n = 3$

WT (♂♂): 5.7 (4.5–6.6) kg, $n = 5$

WT (♀♀): 4.3 (3.8–4.7) kg, $n = 4$

GLS (♂♂): 107.1 (105–108.5) mm, $n = 3$

GLS (♀♀): 95.9 (94.2–97.5) mm, $n = 2$

GWS (♂♂): 63.8 (63.0–65.0) mm, $n = 3$

GWS (♀♀): 55.8 (52.0–59.5) mm, $n = 2$

KwaZulu–Natal, South Africa (Perrin & d'Inzillo Carranza 1999; and museum specimens: DM)

Skull measurements: South Africa (Roberts 1951)

Key References d'Inzillo Carranza 1997; Kruuk & Goudswaard 1990; Lejeune 1989, 1990; Perrin & d'Inzillo Carranza 1999, 2000; Perrin *et al.* 2000; Procter 1963; Rowe-Rowe 1977a; Rowe-Rowe & Somers 1998.

Ilaria d'Inzillo Carranza & David T. Rowe-Rowe

Subfamily MELLIVORINAE – Ratel

Mellivorinae Gray, 1865. Proc. Zool. Soc. London 1865: 103.

The Mellivorinae is a monogeneric subfamily. Recognition of the Mellivorinae here follows McKenna & Bell (1997), in line with recent molecular evidence (Koepfli *et al.* 2008, Wolsan & Sato 2010, Sato *et al.* 2012). Wozencraft (2005) provisionally retained *Mellivora* in the Mustelinae.

Mieczyslaw Wolsan & Michael Hoffmann

GENUS *Mellivora*

Ratel

Mellivora Storr 1780. Prodr. Meth. Mamm., p. 34, Tabl. A.

Mellivora is a monospecific genus, containing the single extant species, the Ratel *Mellivora capensis*, which is widely distributed in Africa and also in SW Asia. The oldest fossil *Mellivora* is from the earliest Pliocene of Langebaanweg, South Africa. The genus is also known from other sites of Plio-Pleistocene age in Africa and from the lower Pleistocene of the Indian sub-continent (Petter 1987). A possibly ancestral genus, *Erokomellivora*, is known from the late Miocene of Kenya (Werdelin 2003a).



Colleen Begg & Keith Begg Ratel *Mellivora capensis*.

Mellivora capensis RATER (HONEY BADGER)

Fr. Ratel; Ger. Honigdachs

Mellivora capensis (Schreber, 1776). Die Säugethiere 3 (18): pl. 125 [1776] + text in Vol. III (26) 450 [1777].

‘Vorgebirge der guten Hofnung’ [South Africa, Western Cape Prov., Cape of Good Hope].

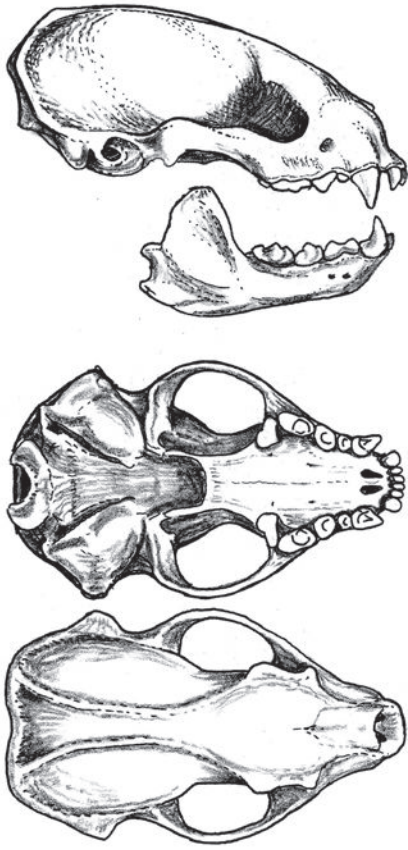
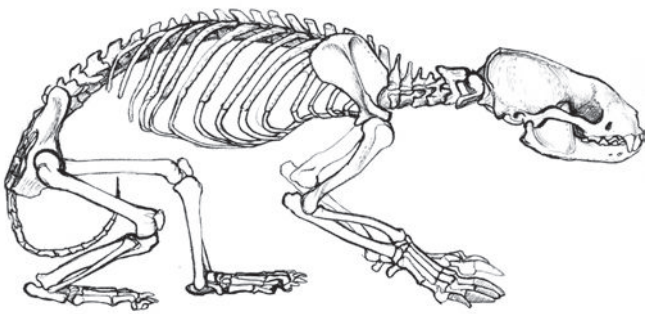
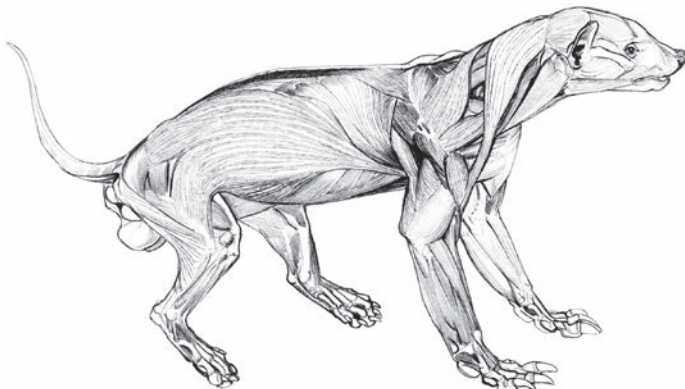


Ratel *Mellivora capensis*.

Taxonomy Ten subspecies have been described from Africa based primarily on size and pelage (mainly mantle) variation (Coetzee 1977). Since most type specimens appear to represent individual variants of a polymorphic species and the white mantle darkens with age, many (if not all) of these subspecies are of doubtful validity. Baryshnikov (1988,

2000) recognizes a total of ten subspecies from across the entire range of the species (i.e. including its distribution outside of the African continent) in two major subdivisions. The first, ‘*capensis*’ includes all the African subspecies together with *M. c. wilsoni* and *M. c. pumilio* from the Arabian peninsula and SW Asia. The second cluster, ‘*indica*’, comprises the other Asiatic forms. He distinguishes the two groupings on the basis of mantle colour (the presence of a whiter, border colour in the African subspecies) and skull morphometrics (the correlation of palatal length and condylobasal length). Ongoing research aims to determine the phylogeography of the Ratel and to investigate whether there is any genetic evidence to support the current subspecies descriptions. Preliminary analyses suggest a division between East African and southern African groups (J. Rhodes pers. comm.), but, pending the completion of such a revision, no subspecies are listed here (though see Vanderhaar & Hwang 2003). Synonyms (Africa only): *brockmani*, *buchanani*, *concisa*, *cottoni*, *leuconota*, *maxwelli*, *mellivorus*, *ratel*, *sagulata*, *signata*, *typicus*, *vernayi*. Chromosome number: 2n=40 (Wurster-Hill & Centerwall 1982).

Description Medium-sized, stocky, lumbering carnivore with distinctive black and white colouring. Forehead white, back mantle

Lateral, palatal and dorsal views of skull of Ratel *Mellivora capensis*.Ratel *Mellivora capensis* skeleton.Ratel *Mellivora capensis* myology.

greyish-white and underparts black. Some individuals with entire upper side white or near white, in others a white, narrow boundary line separates the greyish-white back from the black underparts. Occasional all-black animals have been recorded in central and West Africa (P. Henschel pers. comm.). Muzzle short, blunt and sparsely haired with rather few, slender vibrissae. Eyes are small and dark brown with black, nearly hairless lids set within dense, rather coarse black hair over the prominent cheek and brow. Cartilaginous pinnae of the ears are enclosed within the overall body sleeve of the skin and there is no obvious external ear. Muscular attachments at the back of the skull are well developed and there is little visible transition between the long head and short neck. Forehead white or off-white, bulbous, broad but elongated and sharply demarcated from the lower part of the head, which is black. The precise tone of the greyish-white mantle is the product of coarse hairs that are dispersed in variable ratios of white or black. The white mantle may extend to varying degrees onto the short, well-haired tail, which usually has a black tip. Pelage mainly composed of coarse guard hairs that are densest on the back and longest on the hindquarters; underside and inner surfaces of the limbs are more sparsely haired and the stomach and area around the genitalia and scent glands are bare. Underfur softer and shorter, individually variable in its density and occurrence (nearly absent in most animals).

In the S Kalahari 86% of adult male Ratels have a prominent scar or callus in the middle of the back (ca. 12×13 cm) that has not been observed in ♀♀ or young ♂♂. The scar develops over time and is thought to be the result of repeated bites in the same area by other Ratels (probably ♂♂). The callus has also been identified in male Ratels from Zimbabwe, Botswana and Namibia. Forelimbs long and flexible, well muscled along their entire length and forefeet robust and armed with sharp claws 3–4 cm in length. Hindlimbs less well developed and bearing conventional nails on small compact digits. Both fore- and hindfeet have five toes and tough dog-like pads. The different claw length and size of fore- and hindfeet show up well in spoor. Well-developed anal glands are under muscular control and can be extruded.

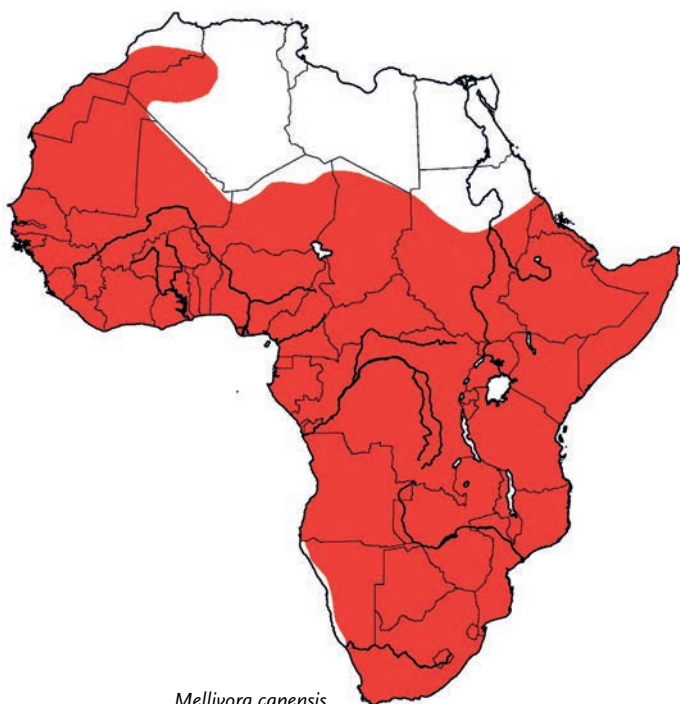
Sexes show marked sexual size dimorphism, with ♂♂ at least one-third heavier than ♀♀. There are no sexual differences in pelage colour. The testes of adult ♂♂ are disproportionately large for the animal's size. Baculum distinctive with the distal end of the shaft angulated sharply upwards, terminally expanded, and hollowed out above (Pocock 1920). Two pairs of inguinal nipples.

Strongly built skull with an undeveloped sagittal crest, broad braincase and well-developed zygomatic arches and mastoids. There is no second lower molar reducing the dental formula to $I^{3/3}, C^{1/1}, P^{3/3}, M^{1/1} = 32$. Teeth are robust but unspecialized; the two outer incisors are larger than the others, curved inwards and resemble canines but wear down rapidly.

Geographic Variation See Taxonomy.

Similar Species

Civettictis civetta. Sympatric through most of sub-Saharan Africa, but absent from parts of South Africa, most of Namibia, Eritrea and drier areas of the Horn where Ratels are present. Similar in size, but distinguished by its mottled pattern, gracile limbs, and long, well-haired tail.



Mellivora capensis

Distribution Widespread through most of the continent, particularly sub-Saharan Africa, but absent from some regions such as the Free State in South Africa, Lesotho, the Namib Desert, central Sahara Desert, Mediterranean littoral and the lower Nile Valley. Range extends outside of Africa through Arabia, Iran and western Asia to Turkmenistan and the Indian peninsula. Little information available on current distribution but it appears patchy due to persecution and habitat transformation.

Habitat Occurs in most habitat types, from sea level to above 4000 m (e.g. Sillero-Zubiri 1996) and can tolerate habitats with annual rainfall varying from 50 to 2000 mm, i.e. from desert to moist rainforest. Absent from the driest and sandiest parts of the Sahara and from the dunes of the Namib.

Abundance Ratels are considered rare or to exist at low densities throughout their range compared with other medium-sized carnivores. Their propensity to raid beehives has advertised their presence in certain areas, particularly *Brachystegia* woodland and the Cape fynbos, and this suggests that they may be more abundant than commonly thought. In some prime honey-producing areas beekeepers report them to be common, while nature conservation authorities suggest they are rare. Ratels are difficult to locate using conventional mammal surveys and, in the S Kalahari and Mana Pools N. P., in Zimbabwe, night counts and day transects were poor indicators of Ratel density due to their relatively small size, small eyes (poor eyeshine) and elusive nocturnal behaviour. Bearing this in mind, densities based on night counts have been estimated variously as 0.1 individuals/km² in Serengeti N. P., Tanzania (Waser 1980) and 0.07 ind/100 km (Sillero-Zubiri & Marino 1997) in Niokolo-Koba N. P., Senegal. The density of Ratels in the semi-arid Kgalagadi Transfrontier Park, South Africa, estimated from visual observations of marked and unmarked individuals, was 0.03 adults/km² (C. M. Begg 2001).

Adaptations The forelimbs are adapted for digging but their strength and manoeuvrability also serve to make them quite adequate for climbing. The long, massive claws are used to excavate hard termitaries, to dig for buried beetle larvae and to tear open bees' nests in tree trunks. In the latter activity the exceptionally robust jaws and teeth may also assist. The power of the claws may be augmented by leverage from muscular shoulders, neck and back, which are employed to dislodge hives or budge rocks that conceal prey. Indian Ratels have been filmed shifting rocks in this way to provide a platform from which to reach a previously inaccessible source of food. The thick but also loose skin around the neck area serves as some protection against the bites of larger carnivores and possibly the venom of snakes and bee stings. Enclosure of the external ear within the thickened body skin may also be an adaptation against bites, especially those of social insects. While the absence of external ears may attenuate longer-distance air-borne sounds, the Ratel is very sensitive to vibrations and sound within trees or underground.

The sense of smell is well developed and, while animals see well within their immediate vicinity, they appear not to register much from further afield. The anal glands are unusual among mustelids in being eversible (Pocock 1920). These glands are used for scent-marking and as a defence against predators. They also emit an aerosol that is repellant to humans and other predators and has been reported to deter or immobilize bees (Kingdon 1977). This behaviour and the chemistry of secretions needs further research.

Foraging and Food Opportunistic, generalized carnivores, which eat a wide variety of prey varying in size from small insect larvae to the young of ungulates. In the S Kalahari, 80% of their prey was caught through digging and their diet comprised more than 70 different species including insects, scorpions, reptiles, including the highly venomous Cape Cobra *Naja nivea* and Puff Adder *Bitis arietans*, rodents, particularly Paeba Hair-footed Gerbil *Gerbillurus paeba* and Highveld Gerbil *Gerbilliscus brantsii*, and the young of Cape Foxes *Vulpes chama*, Black-backed Jackals *Canis mesomelas*, Bat-eared Foxes *Otocyon megalotis* and Wildcats *Felis silvestris* (Begg *et al.* 2003a). In addition, Ratels climb up to Sociable Weaver *Philetairus socius* nests to feed on chicks, and remove raptor chicks from their nests (Marlow 1983).

In seven stomachs collected in Zimbabwe and Botswana scorpions had the highest occurrence (five stomachs), followed by spiders (4), murid rodents (4), lizards (3), insects (2), myriapods (2), birds (1), snakes (1), bee larvae and honey (1) (Skinner & Chimimba 2005). Ratels also eat young crocodiles (D. English pers. comm.), Mozambique Rain Frogs *Breviceps mossambicus* (Smithers & Lobão Tello 1976) and raid sea turtle nests (R. Penn Sawyers pers. comm.). They have been implicated in predation upon the Tent Tortoise *Psammobates tentorius* in a case in which more than 30 shells were found to be cleanly broken open and the body removed after forcibly pulling back the anterior projecting section of the plastron (Lloyd & Stadler 1998).

On the opposite side of the continent, in Aïr (Niger), the diet of Ratels includes small rodents (*Meriones* spp., *Gerbillus* spp.), Desert Hedgehogs *Hemiechinus aethiopicus*, terrestrial birds (hunted by night) and their clutches, African Spurred Tortoises *Geochelone sulcata*, lizards, skinks (Peters' Banded Skink *Scincopus fasciatus*), toads, human excrement and plants such as wild fruits (*Hyphaene thebaïca*, *Balanites aegyptiaca*, *Salvadora persica*, *Grewia tenax*, *Cordia rothii*), bark (*Maerua crassifolia*, *Boscia senegalensis*) and the grass Indian Sandbir *Cenchrus*

biflorus (Dragesco-Joffé 1993). In Western Sahara, they are well known for digging lizards (*Uromastix acanthinura*) out of their burrows, and eating roots of *Launaea arborescens* bushes (Valverde 1957). In S Morocco, they were seen actively digging out small rodents *Meriones* spp., searching for insects and small lizards under rocks, and eating dead animals; remains of *Uromastix* insects, and goat hairs were commonly found in their scats (F. Cuzin pers. comm.).

On occasion Ratels may pirate food from other carnivores (Kruuk & Mills 1983) and will also scavenge from the kills of larger animals although they are primarily hunters of their own food. Caching of food, notably honeycombs and dead animals, has been observed, with the animal returning to the cache during the next few days. Water does not appear to be essential and Ratels probably obtain sufficient moisture from their food. In the S Kalahari, the flesh of Tsama Melons *Citrullus lanatus* is regularly eaten, seemingly for its high water content.

There are strong regional, seasonal and individual differences in diet. For example, while small mammals (<100 g) and small reptiles (<100 g) were the most common prey items in all seasons in the S Kalahari, large snakes were particularly important in the hot-wet season and the cubs of jackals and foxes and raptor chicks were important prey items during their respective breeding seasons.

In areas where hives are uncommon, such as the S Kalahari, honey and bee larvae do not form a major part of the diet but are taken when available. In areas where beekeeping and hives are common, Ratels frequently break into traditional, commercial and natural hives. Dung examined in July in C Tanzania showed a very high incidence of bee remains (Kingdon 1977). Reports from beekeepers in Tanzania and the Western Cape of South Africa indicate a strong seasonality of attacks on hives (K. S. Begg 2001). In Tanzania attacks are negligible during the wet season (Dec–May) but numerous during the dry season, with a peak between Jul and Oct. The fact that attacks coincide with principal honey harvests suggests that Ratels respond opportunistically to the abundance of honey at that time.

While the buzzing of bees may be the Ratels' principal guide to hives during the day, there are fewer clues for nocturnal honey-hunting. The Ratel's legendary association with a small bird, the Greater Honeyguide *Indicator indicator*, was first reported in 1629, and has been extensively discussed but is still disputed. The Ratel is 'guided' by the bird to a bee's nest whereupon it tears open the nest in an untidy manner so that bees, larvae, wax and honey are available for the bird. Because the association is completely dependent upon diurnal foraging by the Ratel and has to be learned by both 'partners' it is fragile; none the less, once learned, it would seem to offer substantial rewards to both bird and mammal. Some ornithologists appear to have misrepresented the known and various interactions between honeyguides and Ratels as a 'co-evolved mutualistic behaviour' (Dean *et al.* 1990). That the interactions are likely to be opportunistic and learnt has been recognized by most observers of honeyguide, Ratel and human interactive behaviour (Kingdon 1977).

Foraging associations between the Pale Chanting-goshawk *Melierax canorus* and Ratels, and between Black-backed Jackals *Canis mesomelas* and Ratels are regularly seen in the arid, open areas of southern Africa (C. M. Begg 2001) and East Africa. In both cases, goshawks and jackals follow the badgers and catch rodents that escape while the Ratel is digging and this appears to be facultative commensalism with no benefits and few costs to the Ratel (C. M. Begg 2001). Other observations of Wildcats *Felis silvestris*, Barn Owls *Tyto alba*, Marsh

Owls *Asio capensis*, Spotted Eagle-owls *Bubo africanus*, Crimson-breasted Gonoleks *Laniarius atrococcineus* and the Southern Anteater-chat *Myrmecocichla formicivora* following foraging Ratels in the S Kalahari suggest that these inter-specific foraging associations may be common (Begg & Begg 2005). In other areas, a Dark Chanting-goshawk *Melierax metabates* has been observed following a Ratel in the lowveld of South Africa (Roche 2004, P. Chadwick pers. comm.), and a subadult male Ethiopian Wolf *Canis simensis* was observed following a Ratel in the Bale Mts of Ethiopia (Sillero-Zubiri 1996).

Both sexes are solitary foragers and foraging behaviour is characterized by a slow winding walk with systematic examination of holes and crevices. Foraging activity is primarily driven by scent; for example, individuals often stop to smell with their heads turned upwind and then change their foraging direction towards a prey item, but hearing is also important. On average, ♀♀ moved 8 km actual distance (2.4 km straight line) and ♂♂ moved 14 km actual distance (6.2 km straight line) during a single period of activity in the S Kalahari (C. M. Begg 2001). Males are capable of moving 40 km in a single day. In Air (Niger), tracks were followed for distances between 8 and 14 km from the burrow (Dragesco-Joffé 1993).

In the S Kalahari, activity patterns shift from being nocturnal in the hot-wet season, to primarily diurnal in the cold-dry season and seem to be driven primarily by temperature (C. M. Begg 2001). Ratels show a two-peaked activity pattern with two active periods of 2–8 hours during a 24-hour period and prolonged resting in burrows, or under bushes.

Social and Reproductive Behaviour Essentially solitary (no male involvement in parental care), with a non-territorial polygynous or promiscuous mating system. Detailed information on social and reproductive behaviour is available only from the S Kalahari (Begg *et al.* 2005a).

In the S Kalahari, adult male Ratels have average home-ranges of 541 km² (range 229–698 km²), which overlap extensively with other ♂♂ and encompass the smaller home-ranges of young ♂♂ (151 km²) and ♀♀ (126 km²; range 85–194 km²; Begg *et al.* 2005b). One adult ♂ had access to at least 12 ♀♀. The home-ranges of Ratels in more mesic environments are likely to be smaller although minimum home-range sizes of 150 km² and 480 km² have been recorded for young male Ratels on the Zambezi flood-plain and in Niassa Reserve, N Mozambique (primarily miombo woodland) (C. M. Begg & K. S. Begg pers. obs.).

Ratels do not have a fixed home site and rest in a different place each day. Females with cubs younger than three months old change dens every 2–5 days until, at three months old, they revert to the typical pattern of using a different hole each day. While Ratels usually dig their own resting burrows in the sandy Kalahari, they also used the burrows of Aardvark *Orycteropus afer* or Southern African Springhares *Pedetes capensis*. In the flood-plain habitat of Mana Pools N. P., Zimbabwe, they were not observed to dig their own burrows and utilized Aardvark and Cape Porcupine *Hystrix africae australis* burrows. Ratels in Niassa Reserve generally rest in hollow tree trunks, rocky caves, under bushes and in holes in termite mounds (C. M. Begg & K. S. Begg pers. obs.).

Males do not defend territories; rather adult ♂♂ adopt a roaming tactic to search the home-ranges of ♀♀ for receptive mates. Males compete with other ♂♂ for mating opportunities through a dominance hierarchy, which is maintained by direct interactions and scent-marking.



Ratel *Mellivora capensis*.

The dominance hierarchy is loosely correlated with age (older ♂♂ dominant over younger ♂♂), body weight and testes size. The hierarchy system is no guarantee that only the dominant ♂♂ will reproduce, as genetic analysis in the S Kalahari has revealed that the dominant ♂ was the most likely father of only 50% of the cubs within his home-range (Verwey *et al.* 2004). Most direct interactions are ritualized, being expressed through attack and retreat postures and through vocalizations. Overt aggression is rare but involves tumbling, biting and chasing.

In the Kalahari, ♂♂ of varying ages sometimes travel in groups of 2–5 individuals, searching for ♀♀ and scent-marking together. These ♂♂ have been seen in groups for up to 21 hours. Similar groups of five individuals have been seen in Zimbabwe. Of 34 Tanzanian beekeepers (who have extensive experience of Ratels), 23 had never seen more than two animals together while seven had only seen them singly and the remaining four observers had reported seeing 4, 6, 8 and 12, respectively (Kingdon 1977).

Scent-marking is the main form of communication in Ratels and both sexes have well-developed anal scent glands. Male Ratels regularly patrol latrines within their home-ranges and scent-marking behaviour at latrines involves anal dragging (Ratels assume a squatting position with the pelvis depressed so that the anus touches the ground and walk forward with the forelegs, dragging the anus along the substrate), squat-marking (repeatedly pressing anus to the ground on the same place whilst in a squatting position) and belly and neck rubbing on the ground as well as the deposition of faeces and urine. Latrines are commonly placed near prominent landmarks such as trees but are also located near productive food patches. Female Ratels only visit latrines when in oestrus but they routinely token-urinate in holes along their foraging path (Begg *et al.* 2003b). Token urination in ♀♀ is thought to mediate the spatio-temporal separation of neighbours because adult ♀♀ were never observed to interact although their home-ranges showed an average overlap of 13%.

Mating appears to occur in a burrow over the course of 2–4 days. During this period the ♂ physically restrains the ♀ from leaving the burrow and repeated matings are thought to occur. Once mating is complete, the pair separates. Young are born in a burrow, and for the first three months the cub does not accompany the mother foraging but remains in the den. Every 3–8 days the ♀ moves the cub to a new den with an average distance of 2.1 km recorded between dens in the Kalahari. At 2–3 months of age, ♀♀ begin to take prey to the den and it is assumed that weaning occurs during this period. Juveniles remain with their mothers for at least 12–18 months and are entirely dependent on their mothers for food during this first year, with a gradual increase in the proficiency of hunting, digging and climbing. In the S Kalahari, ♀♀ dispersed immediately on independence, while ♂♂ remained within their natal home-range for up to a year after independence before a sudden increase in home-range size occurs (Begg *et al.* 2005b). A female cub in the S Kalahari was located 53 km away from her natal home-range five months after dispersal. A similar dispersal of a young female Ratel was recorded in the Niassa Reserve.

During social interactions, vocalizations are common. Sikes (1964) described how the tongue modulated the common rasping call to generate a variety of calls at different frequencies and pitch in a captive Ratel. In free-living individuals vocalizations can be broadly divided into four types: a low, short rattle grunt used only by adult ♂♂ when interacting with ♀♀ and young ♂♂ accompanied by piloerection, head high, tail up and a stiff-legged posture; a high-pitched squeal-rattle

accompanied by a smacking or teeth-clapping sound used by young ♂♂ and ♀♀ when interacting with adult ♂♂ (accompanied by a side-on posture, with the head and tail held low); a short, high-pitched purr used as a contact call between mother and cub; and the threatening rattle-roar used in the anti-predator display (described later).

Reproduction and Population Structure There is no evidence for a distinct breeding season in South Africa (Fairall 1968, C. M. Begg 2001). Matings might be timed to coincide with the maximum availability of honey in Nigeria (Hancox 1992). Three litters were found after the summer rains between mid-Aug and Oct in Aïr, Niger (Dragesco-Joffé 1993).

Data from free-living Ratels in the S Kalahari (Begg *et al.* 2005a) and captive individuals in Israel (Mendelssohn & Yom-Tov 1999) suggest a gestation of 50–70 days and 62–72 days, respectively. In contrast, gestations of 153 and 162 days were recorded for two captive-bred individuals in Howletts Zoo, England (Johnstone-Scott 1981). This suggests that under some circumstances Ratels may show some form of delayed implantation or slowed foetal development, but this remains to be verified.

On all occasions only a single cub emerged from dens in the Kalahari ($n = 20$; Begg *et al.* 2005a). In captivity a litter of two was recorded on one occasion at Howletts Zoo, England (17%; $n = 6$ litters), but both died within a few days (Johnstone-Scott 1981), and once in Israel (20%; $n = 5$ litters; Y. Yom-Tov pers. comm.). An average birth-weight of 182 g was recorded for four female cubs in captivity (Johnstone-Scott 1981), but no data from wild individuals are available. Development is slow. Initially cubs are almost hairless and only attain the characteristic black and white pelage at 3–5 weeks old (Mendelssohn & Yom-Tov 1987). At the age of 6–8 months, male and female cubs already show marked sexual size dimorphism. As a result, adult ♀♀ are at least 2 kg lighter and noticeably smaller than male cubs during the final months of dependency. It seems likely that it is these mother–son pairs that have been confused with adult male–female pairs in the past, leading to the incorrect suggestion that Ratels are monogamous. The age of sexual maturity is unknown.

Cub mortality in the S Kalahari is at least 47% and the causes of death included starvation, infanticide (killed by adult ♂♂) and predation (Begg *et al.* 2003a). Ratels have been recorded to live for more than 30 years in captivity (Weigl 2005), although it is predicted that they do not live much longer than 6–8 years in the Kalahari (C. M. Begg & K. S. Begg pers. obs.).

Predators, Parasites and Diseases Adult Ratels are sometimes killed by Lions *Panthera leo* and Leopards *P. pardus*, though usually not without a fight; in one instance, it took six Lions some 15 minutes to kill a Ratel (Lautenbach & Vorster 2003). There is a record of an attempted predation by a Cheetah *Acinonyx jubatus* on a subadult from the Limpopo Province in South Africa (Retallack 2005). One cub was killed by two Golden Jackals *Canis aureus* in N Niger (Dragesco-Joffé 1993) and young are probably vulnerable to other large predators.

The conspicuousness of the Ratel's colouring is thought to provide a warning to predators of their strength and tenacity. Their impressive predator display consists of a rattling-roar vocalization, piloerection and the emission of a strong smelling evacuate from the anal scent glands, and is accompanied by rushing movements towards the predator. This display, aided by the Ratel's formidable strength,

powerful bite, loose skin and long claws, is well designed to intimidate and is frequently successful in driving predators away. Ratels do appear to have some immunity to snake and scorpion venom; for example, a male Ratel bitten on the face by the highly cytotoxic Puff Adder showed signs of severe pain, but recovered fully within five hours (C. M. Begg & K. S. Begg pers. obs.). Ratels are occasionally stung to death by bees, especially in commercial apiaries.

Srivastava (1964) recorded the trematode *Strongyloides akbari* and the nematode *Artyfechinostomum* in the intestine of an Indian Ratel. In South Africa, ixodid ticks of the species *Haemaphysalis aciculifer*, *H. zumpti*, *Rhipicephalus thelieri*, *R. appendiculatus*, *R. evertsi*, *R. simus*, *Boophilus decoloratus*, *Hyalomma truncatum* and *Amblyomma hebraeum* have been found on Ratels with old individuals particularly heavily infested (Horak *et al.* 2000). Horak *et al.* (2004) recovered the fleas *Ctenocephalides damarensis*, *Echidnophaga gallinacea* and *Synosternus caffer* from Ratels in South Africa, all likely infesting prey species. In addition, the biting louse *Trichodectes vosseleri* has been identified on Ratels from South Africa and Kenya (I. Horak pers. comm.).

Canine distemper has been implicated in Ratel deaths (A. Root pers. comm.), and while they are known to be carriers of rabies they do not appear to be vectors (J. Bingham pers. comm.). Ratels carrying rabies are usually associated with rabies outbreaks amongst Black-backed Jackals *Canis mesomelas*. A faecal sample from the Kalahari indicated infection with feline panleukopenia virus, a subgroup of feline parvovirus (Steinel *et al.* 2000).

Conservation IUCN Category: Least Concern. Appendix III: CITES (Botswana, Ghana).

Ratels are directly persecuted (through the use of, among others, steel-jawed traps and poisons) by apiculturists and small livestock farmers throughout their range, and are also indirectly killed by non-selective control programmes targeting other species (Stuart 1981, Dragesco-Joffé 1993, F. Cuzin pers. comm.). In the Western Cape of South Africa, where a permit is now required to move or kill a Ratel, half of 82 commercial beekeepers surveyed in 2001 admitted to killing Ratels despite their protected status; surveyed beekeepers destroyed a minimum of 248 Ratels, with 231 removals occurring within the previous 15 years (K. S. Begg 2001). Commercial hive damage can be simply and effectively reduced (26% to 1%) by securing the hive a metre or more above the ground on a stand or trestle (Begg & Begg 2002). Persecution of Ratels continues both due to ignorance of suitable hive protection measures and because of entrenched hostility towards Ratels and carnivores in general. Ratel body parts (particularly paws, skin and organs) are commonly used in traditional medicine because of the animals' reputation for fearlessness and tenacity. In some areas (W Zambia, Guinea), Ratels appear in the bushmeat trade due to the decline in other more favoured bushmeat species (C. M. Begg & K. S. Begg pers. obs., Colyn *et al.* 2004). As modern apiculture displaces the more fatalistic and tolerant practices of traditional beekeepers in East and central Africa, it is likely that the Ratel will suffer increasing persecution.

Since Ratels range over unusually large areas, many protected areas may be inadequate in conserving viable populations. Little information is available on their status, particularly from central and West Africa, but the number of areas in which Ratels are rare or absent appears to be increasing and populations may be becoming increasingly fragmented throughout their range. Their small litter-size

and long birth interval (14–16 months), and therefore slow recruitment to the population, may also make them particularly vulnerable to persecution. As Ratels are seldom seen, their populations could easily reach critically low levels without conservation authorities being aware of the problem. More information on the biology and status of Ratels is crucially needed, particularly in the northern and western parts of their range.

Measurements

Mellivora capensis

HB (♂ ♂): 686 (580–790) mm, n = 15
 HB (♀ ♀): 637 (580–690) mm, n = 12
 T (♂ ♂): 197 (160–230) mm, n = 19
 T (♀ ♀): 187 (180–220) mm, n = 14
 Sh. ht (♂ ♂): 394 (350–430) mm, n = 19
 Sh. ht (♀ ♀): 327 (320–370) mm, n = 14
 WT (♂ ♂): 9.3 (8.0–11.2) kg, n = 19
 WT (♀ ♀): 6.1 (5.2–7.1) kg, n = 14
 S Kalahari, South Africa (C. M. Begg 2001)

HB (♂ ♂): 715 (680–770) mm, n = 4
 HB (♀ ♀): 675 (630–720) mm, n = 2
 T (♂ ♂): 215 (160–220) mm, n = 4
 T (♀ ♀): 217 (190–245) mm, n = 2
 Namibia (Shortridge 1934)

TL (♂ ♂): 954 (902–1020) mm, n = 8
 TL (♀ ♀): 950, 960 mm, n = 2
 T (♂ ♂): 219 (200–240) mm, n = 8
 T (♀ ♀): 195, 220 mm, n = 2
 HF c.u. (♂ ♂): 133 (123–145) mm, n = 8
 HF c.u. (♀ ♀): 115, 120 mm, n = 2
 E (♂ ♂): 43 (40–48) mm, n = 8
 E (♀ ♀): 35, 47 mm, n = 2
 WT (♂ ♂): 11.7 (7.9–14.5) kg, n = 8
 WT (♀ ♀): 9.5, 13.6 kg, n = 2
 Zimbabwe (Smithers 1983)

Key References C. M. Begg *et al.* 2003a, b, 2005a, b; K. S. Begg 2001; Kingdon 1977; Pocock 1920.

Colleen Begg, Keith Begg & Jonathan Kingdon



Superfamily PINNIPEDIA

SEALS

Pinnipedia Illiger, 1811. Prodr. Syst. Mamm. Avium., p. 138.

The name pinniped is derived from the Latin *pinnipes*, for wing- or fin-footed, referring to the group’s modified fin-like appendages. The name refers to those mammals that are adapted to both terrestrial and aquatic conditions, have a fusiform body shape adapted to reduce turbulence and resistance (drag) while swimming and diving, possess a subcutaneous layer of fat (blubber) that provides stored energy, insulation and buoyancy, a coarse pelage of guard hairs, and relatively short, stout limbs (with limb bones enclosed inside the body) that are modified to form paddle-like flippers (Nowak 1999).

Members of this group range in size from, for example, small lake seals in Asia, the Baikal Seal *Pusa sibirica*, which reaches 1.5 m in length and 70 kg in weight, to the mammoth Southern Elephant Seals *Mirounga leonina*, bulls of which can reach masses of four tonnes and lengths of 4 m (Martin & Reeves 2002). Pinnipeds spend the majority of their lives at sea where they feed almost exclusively, but they are constrained by the need to return to land or stable ice substrates to give birth, to lactate and in some instances, to moult.

Pinnipeds are now thought to represent a monophyletic group, diagnosed by a suite of shared derived morphological characters (synapomorphies), including: enlarged orbits; large infraorbital foramen; a maxilla that uniquely contributes to the orbital wall; a lacrimal (absent or fused) that does not contact the jugal; enlarged humeral tuberosities and deltopectoral crest; short and robust humerus; and emphasized Digit I on both hand and foot, and Digit V on foot (Berta & Sumich 1999). Historically classified under a separate mammalian order, Pinnipedia, they are now contained within the order Carnivora, but still embrace the families Otariidae (sea lions and fur seals), Phocidae (‘true’ seals, or earless seals) and Odobenidae (walruses). Of the three extant families, only Odobenidae are not represented in African waters, with the single extant species, the Walrus *Odobenus rosmarus*, having a disjunct circumpolar Arctic distribution.

Pinnipeds have been believed to be most closely related to the bears (family Ursidae), although a possible diphyletic pinniped origin, with Phocidae arising from a mustelid ancestor instead, has caused some argument (see Heyning & Lento 2002, Flynn *et al.* 2005). Further controversy exists on the evolutionary relationships within the group, revolving around whether Odobenids are more closely related to the Otariidae (as historically proposed and

suggested by molecular evidence) or to the Phocidae (as suggested by morphological evidence) (see Berta & Sumich 1999, Deméré *et al.* 2003 for a discussion and suggestions for further reading). Recent molecular evidence not only strongly supports the monophyly of Pinnipedia, but also places Pinnipedia as the sister-group to the Musteloidea, a clade that includes Mustelidae + Procyonidae + Mephitidae + Ailuridae (i.e. leaving Ursidae as the most basal arctoid lineage) (Sato *et al.* 2009, Eizirik *et al.* 2010; although see Agnarrson *et al.* [2010] who found strong support for the traditional sister relationship between Ursidae and Pinnipedia). The latter study also strongly supports a sister-group relationship between Otariidae and Odobenidae (and see Arnason *et al.* 2006, Higdon *et al.* 2007).

Pinnipeds are believed to have had a northern Pacific centre of origin, evolving from a basal pinnipedimorph *Enaliarctos* sometime during the late Oligocene (27–25 million years ago), ‘true’ pinnipeds arising from this line some time before 18 mya, during the early Miocene (Berta & Sumich 1999, Deméré *et al.* 2003).

Phocids are the most widespread of the pinniped families, represented at most latitudes in both hemispheres, including both polar regions. Phocids consist of 19 species (one, the Caribbean Monk Seal *Monachus tropicalis* recently extinct) in 13 genera (Rice 1998, Wozencraft 2005). Originating in the North Pacific some time during the early Miocene, they are postulated to have dispersed to the North Atlantic some time before 16 mya, where they diverged into a northern group, the Phocinae, which includes temperate region, sub-Arctic and Arctic species, and a southern group, Monachinae, which embraces the warm-water monk seals, the Antarctic ice seals, as well as the wide-ranging elephant seals of the genus *Mirounga* (Heyning & Lento 2002, Deméré *et al.* 2003).

Otariids originated in the eastern North Pacific during the late Miocene, some time before 11 mya, migrated to the South Pacific during the Pliocene, around 6–5 mya, and from there radiated to most of the circum-Antarctic islands in association with the prevailing west wind drift (Berta & Sumich 1999, Deméré *et al.* 2003). Modern otariids are absent in the North Atlantic, but are widespread in the southern oceans, and occur in the Pacific as far north as the Bering Strait.

Marthán N. Bester & Paul N. Odendaal

Family OTARIIDAE

FUR SEALS

Otariidae Gray, 1825. Ann. Philos., n.s., 10: 340.

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|----------------------------------|-----------|-------|
| <i>Arctocephalus</i> (1 species) | Fur Seals | p.127 |
|----------------------------------|-----------|-------|

Worldwide, the family Otariidae has customarily been classified into seven genera and 16 species (Rice 1998, Wozencraft 2005), although various lines of evidence (Brunner 2000, 2003, Wynen *et al.* 2001), as well as observations of inter-specific, even inter-generic, hybridization

(see Brunner 2000, and references therein) have highlighted the taxonomic confusion present in this family. The otariids have been subdivided into two subfamilies, the Otariinae (sea lions – five genera and seven species: *Eumetopias*, *Neophoca*, *Otaria*, *Zalophus* and *Phocarctos*) and the Arctocephalinae (fur or eared seals – two genera and nine species: *Arctocephalus* and *Callorhinus*) (Berta & Sumich 1999). Sea lions

are characterized and readily distinguished from fur seals by their sparser pelage (fur seals have abundant underfur) and a tendency towards larger body size, and the separation is often maintained as a division of convenience. However, the validity of the subfamilial separation has long been questioned (Repenning & Tedford 1977). The monophyly of the Arctocephalinae, in particular, is not supported by fossil evidence, which suggests that *Callorhinus* diverged from the main line, *Arctocephalus* about 6 mya, about 3 million years before the divergence of sea lions (Bininda-Emonds *et al.* 1999). This is supported by recent morphological and molecular evidence (Brunner 2000, 2003, Wynen *et al.* 2001), and it has been argued that there should be no subdivision above the generic level within Otariidae (Bonner 1994, Bininda-Emonds *et al.* 1999, Higdon *et al.* 2007).

Sea lions do not occur on African coasts, the only otariid being the South African (Cape) Fur Seal *Arctocephalus pusillus pusillus* (conspecific with the Australian Fur Seal *A. pusillus doriferus*). One other species, the Subantarctic Fur Seal *A. tropicalis*, occasionally turns up on the southern African coastline as a vagrant.

Otariidae can be diagnosed as a monophyletic group by several osteological and soft anatomical characters that separate the family from the phocids (true, or earless seals) and odobenids (walruses). They have external ear pinnae, smooth vibrissae, a light coloured skin, a double layer of fur, partially hairless fore- and hind flippers, four nipples in females, and scrotal testes. Claws on the fore-flippers are vestigial or absent. Otariids swim primarily with fore-flipper strokes, the hindlimbs being used in steering when swimming. They can rotate the hindlimbs under the body and move on all fours on land. Eyes of otariids (as with the phocids) are relatively large and modified to focus underwater by means of greater corneal curvature and spherical eye lenses, and see effectively under conditions of reduced light. Physiological processes for diving are pronounced (see family Phocidae), but depths of dives are shallower for most otariids. Cranially they have large and shelf-like supra-orbital processes, their frontal bones penetrate between the nasals on the mid-line, a secondary spine subdivides the supraspinous fossa of the scapula, the trachea has an anterior bifurcation of the bronchi closer to the larynx, and they have uniformly spaced pelage units (Berta & Sumich 1999). As carnivores they typically have differentiated teeth, including incisors, canines and postcanines. Premolars and molars are not differentiated, neither are carnassial teeth. The characteristic dental formula is $I^{3/2}, C^{1/1}, PC^{5-6/5} = 34-36$. Some variation is

found in upper postcanine numbers especially (sea lions generally have five upper postcanines, and fur seals six, although sometimes one more or fewer is present). Their first two upper incisors are transversally grooved (Jefferson *et al.* 1993).

Pronounced sexual dimorphism in size is the rule in the otariids, ♂♂ being larger than ♀♀ roughly by a factor of five. Adult male fur seals reach masses of 60–350 kg and standard body lengths of 1.5–2.3 m, while the ♀♀ reach masses of approximately 22–80 kg and standard body lengths of 1.1–1.8 m (from Jefferson *et al.* 1993). They are all polygynous, ♂♂ using their large size and powerful forequarters for establishing and maintaining dominance on land during the breeding season (Boness *et al.* 2002). Mating generally takes place on land. Males defend onshore territories against other ♂♂, which results in access by relatively few dominant ♂♂ to numerous ♀♀. This social system represents rapid selection for very large, powerful ♂♂. Otariid ♂♂ gain condition at sea and then remain on land without feeding for the duration of the summer breeding season. The ♀♀, instead, alternate between periods of foraging at sea and suckling their pups on land. Male numbers ashore peak during the breeding season in spring and summer when ♀♀ give birth to single pups and become impregnated during a brief perinatal period. Otariids wean their pups after extended periods, from four months (as in the Antarctic Fur Seal *Arctocephalus gazella*) to ten months or sometimes longer. All otariids have an annual, gradual moult when the hairs fall out individually over periods of weeks or months, and hauling out is not a prerequisite for the gradual moult.

In general, while dives to 500 m are not uncommon, otariids are less capable divers and breath-holders than phocids. They feed variously on penguins (sometimes taking them also on land), fish, cephalopods, crustaceans, gastropods, jellyfish and occasionally on other marine birds, while sea lions take fur seal and elephant seal pups on occasion.

Several extinct otariids are known, the earliest being from the late Miocene (11 mya) of California. Amongst the southern fur seal genus *Arctocephalus*, the earliest known taxa are *A. pusillus* (South Africa) and *A. townsendi* (California) from the late Pleistocene. The widely accepted hypothesis is that primitive otariids entered the Southern Ocean from the North Pacific around 6–5 mya and radiated to most of the circum-Antarctic islands in association with the prevailing west wind drift (Berta & Sumich 1999, Deméré *et al.* 2003).

Marthán N. Bester & Paul N. Odendaal

GENUS *Arctocephalus*

Fur Seals

Arctocephalus E. Geoffroy Saint-Hilaire & F. Cuvier, 1826. In: F. Cuvier, Dict. Sci. Nat. 39: 554 [1826].

The genus *Arctocephalus* (from the Greek expression meaning ‘bear-headed’) is represented by eight species of fur seal, occurring from tropical to polar latitudes. The Cape Fur Seal *A. pusillus pusillus* and the Australian Fur Seal *A. p. doriferus* share subspecies status. The remaining seven species include: the South American Fur Seal *A. australis*; the Juan Fernández Fur Seal *A. philippii*; the Galapagos Fur Seal *A. galapagoensis*; the Guadalupe Fur Seal *A. townsendi*; the New Zealand or Australasian Fur Seal *A. forsteri*; the Subantarctic Fur Seal *A. tropicalis*; and the Antarctic Fur Seal *A. gazella*. With the exception

of *A. townsendi*, all occur in the southern hemisphere, hence the vernacular term ‘southern fur seals’ (Bonner 1981). Molecular studies show that *Arctocephalus* is not monophyletic (e.g. Arnason *et al.* 2006, Higdon *et al.* 2007), and the genus is in need of revision.

Arctocephalus and the only other genus of fur seal, the monotypic *Callorhinus* from the Northern Hemisphere, are distinguished on the basis of a few morphological traits, the most obvious of which are: the snout angle of *Arctocephalus* is more pointed than that of *Callorhinus*, which have a shorter, downwards curved rostrum;

and hair growth occurs on the dorsal surface of the fore-flipper of *Arctocephalus*, whereas hair growth terminates abruptly at the wrist of the fore-flipper in the case of *Callorhinus* (Bonner 1994).

In terms of appearance, social behaviour, reproduction and ecological role, *Arctocephalus* species are remarkably similar to each other (Gentry & Kooyman 1986). All are top carnivores, gregarious, sexually dimorphic in body size (σ σ outweigh φ φ by 2–4 times, depending on species), and have a polygynous mating system characterized by aggressive territoriality on the part of adult σ σ . Breeding is synchronous and φ φ give birth to a single pup (twin births are extremely rare). After birth, mothers alternate between foraging at sea and suckling on shore,

until weaning. Females are capable of producing a pup every year of their lives after first parturition. The natal fur of pups is nearly always black or very dark brown. Adults are typically coloured a grizzled dark-grey brown dorsally, shading to lighter beneath, with only the male *A. tropicalis* being clearly bi-coloured. Despite the similarities between *Arctocephalus* species, there are considerable underlying differences between them in details of their biology and ecology, including adult size, the duration of neonatal dependence and diet (Gentry *et al.* 1986, Wickens & York 1997).

Steve Kirkman & Herman Oosthuizen

Arctocephalus pusillus CAPE FUR SEAL

Fr. Phoque du Cap; Ger. Kapseehund

Arctocephalus pusillus (Schreber, 1776). Die Säugethiere 2 (13): pl. 85 [1775]; text, 3 (17): 314 [1776]. Unknown. 'Diese Gattung findet sich in den levantischen, und nach dem Herrn Grafen von Büffon, im indischen Meere'; see Allen (1880), Scheffer (1958).



Cape Fur Seal *Arctocephalus pusillus*.

Taxonomy Two subspecies are recognized, the Cape Fur Seal *A. p. pusillus* and the Australian Fur Seal *A. p. doriferus*, which occurs on the south-east coast of Australia and Tasmania (Repenning *et al.* 1971, Shaughnessy 1979, Warneke 1979, King 1983). The specific name *pusillus* means small, due to the fact that the type specimen was a pup. The information in this account relates only to the Cape Fur Seal. Synonyms (*A. p. pusillus* only): *antarctica*, *compressa*, *delalandii*, *nivosus*, *parva*, *peronii*, *schist-hyperves*. Chromosome number: $2n = 36$ (Arnason 1981).

Description The Cape Fur Seal is the only seal endemic to southern African waters. Cape Fur Seals look very similar to sea lions, to which they are closely related, the two major differences being the thick underfur of the fur seals, compared to very sparse underfur in sea lions, and the blunter nose of the latter (King 1983). At first glance the animals in a fur seal colony appear to be all dark grey, but closer inspection reveals variations in size and appearance between different age and sex classes. Coat colour in adults of both sexes is variable, but is mainly different shades of brown or grey, from light to very dark. Adult bulls are mostly dark grey, but φ φ can be lighter in colour and an occasional φ appears almost white. All seals appear black when they are wet. Pups are born with a jet-black velvety coat that changes to olive-grey during its first moult that takes place after about four months in Mar/Apr, and which then darkens noticeably towards the

end of the first year. A yellow strip round the jaws is prominent in yearlings. Juvenile σ σ are difficult to distinguish from φ φ as they are of similar size, but their neck, head and front flippers are proportionally larger than those of φ φ . Adult bulls are a conspicuous class, especially in summer during the breeding season, when their large size and noisy courting of φ φ set them apart. They have a prominent heavy mantle or wig of long hair on the nape of the neck and shoulders, which is an adaptation for protection during territorial disputes. Forelimbs have five rudimentary nails; hindlimbs are directed forwards and incised into flipper-like digits, the first without a claw, the three middle digits with large claws, and the fifth with a rudimentary claw (King 1983, Skinner & Chimimba 2005). Females have two pairs of inguinal nipples. Age determination in the Cape Fur Seal has been discussed in detail by Oosthuizen (1997) and Oosthuizen & Bester (1997).

Geographic Variation The Cape Fur Seal population is homogeneous (Matthee *et al.* 2006) and there is no discernible variation in colour or size of individuals throughout the subspecies' range. This is to be expected as there is continuous mingling of animals from different colonies as they move along the coast while foraging. Recaptures of tagged animals have demonstrated that even juveniles in their first year are capable of swimming from Seal I. in False Bay (near Cape Town) as far north as Cape Cross in Namibia, a distance of over 1500 km (David 1989, Oosthuizen 1991).

Similar Species All the fur seal species tend to be very similar in appearance and, with the exception of the Northern Fur Seal *Callorhinus ursinus*, which has a characteristic head shape, and the Subantarctic Fur Seal *Arctocephalus tropicalis*, which has a white chest and face, they are difficult to tell apart in the field (King 1983). In the skull, at least, *A. pusillus* is characterized by post-canine teeth with a small accessory cusp, and the ventral edge of the jugal arch lying dorsal to the dentary part of the maxilla (Coetzee 1977).

Distribution The Cape Fur Seal is widely distributed over the continental shelf. It is spread along over 3000 km of coastline and ranges from Baía dos Tigres in S Angola (16° S, 11° E) to about East London in SE South Africa (33° S, 27° E). It has been seen up to

220 km (120 nautical miles) from the coast (Rand 1959, Shaughnessy 1982, David 1987a). About 90% of the seal population occurs on the west coast of South Africa and Namibia, because of the high productivity of the Benguela Current marine ecosystem, which characterizes the region (Nelson & Hutchings 1983, Shannon 1985, 1989, David 1989). Cape Fur Seals do not undertake regular migrations, but there is a great deal of movement between the breeding colonies, particularly among juveniles (Rand 1956, Oosthuizen 1991). There are three confirmed records of vagrant Cape Fur Seals sighted outside southern African waters, two from West Africa, in Ghana (Thibault 1999) and Côte d'Ivoire (Marine and Coastal Management pers. comm.) (5°N) and one from Marion I. (46°S) (Kerley 1983).

Habitat The species occurs coastally in three marine zones, the highly productive cool Benguela system of southern Africa's west coast, the near-shore mixing area between warmer Agulhas water and cooler Atlantic water off South Africa's south coast, and the south-east coast inshore of the warm Agulhas system.

Breeding takes place at 25 colonies and there are another ten haul-out sites, classed as non-breeding colonies, where a few pups may be born annually (David 1987a, 1989, Oosthuizen & David 1988). Eighteen breeding colonies are on islands and seven are on the mainland. By preference, seals choose rocky near-shore islands for breeding, because they are cooler than the mainland and are free of terrestrial predators. It is thought that none of the mainland colonies, with the exception of Cape Cross in Namibia, existed before about 1940. The possible reasons for the establishment of mainland colonies include the fact that most of the islands are small, so that breeding space was limited and the disturbance caused by the annual seal harvests (see Conservation) would have caused some animals to flee to the nearby mainland. During the twentieth century the mainland became more suitable for colonization by seals, as all large land predators were eradicated and, in addition, large tracts of the west coast of South Africa and Namibia were declared security zones for diamond mining, thus prohibiting public access. Hence, the seals could breed undisturbed, with no space limitations. This has resulted in the development of some extremely large colonies (e.g. Kleinsee colony in South Africa, where over 70,000 pups are born per annum), so that currently over 75% of the population breeds on the mainland.

Abundance The Cape Fur Seal is possibly the most abundant of the fur seals worldwide, with a current population estimated to be about 1.5–2 million animals, based on regular aerial censuses of newly born black pups at all breeding colonies (Butterworth *et al.* 1995). The surveys are timed for the end of the breeding season (normally the period 18–23 December), when the black pups are on average about 2–4 weeks old, and cannot yet swim. The pups are counted on large monochrome or colour prints and the total population is then calculated from age-structured models (Butterworth *et al.* 1988, 1995). Some of the counts made are verified using tag-recapture estimates of pup population size at selected colonies.

Adaptations Cape Fur Seals are adapted for diving to catch prey, and while the majority of dives are shallow dives of no more than 50 m, results from the deployment of time-depth-recorders show that adult bulls can reach depths of 500 m and ♀♀ can dive to over 400 m (Marine and Coastal Management, pers. comm.). In addition,



the seals breed during summer (Nov/Dec) on the exposed coast of southern Africa where high day-time temperatures are common. Little shade is available at the colonies and adults are adapted to endure prolonged direct insolation. When body temperatures rise beyond a tolerable level, they retreat into the water to cool off. However, the young pups do not possess the same degree of heat tolerance and it is noticeable that on very hot days at mainland colonies pups less than about a month old may suffer heavy mortality due to heat stress, especially amongst pups occupying the sandy parts of the colonies.

Foraging and Food Cape Fur Seals are opportunistic feeders and prey on at least 34 species of fish, 18 species of cephalopods and a number of crustaceans such as swimming decapods, amphipods and isopods (Rand 1959, Lipinski & David 1990, Punt *et al.* 1995). The main prey of seals older than one year is teleost fish. Analysis of undigested stomach contents of seals collected at sea on the west coast of southern Africa, by reconstituting the mass of fish prey from measurement of the otoliths, shows that overall about 80–90% of the diet is teleost fish, with a range from about 50–100% depending on season and area, and that the next most important item is cephalopods (David 1987b, Punt *et al.* 1995). Crustacea constitute a minor fraction of the diet.

The importance of individual teleost species was determined from the otoliths occurring in seal stomachs. In South African waters anchovies (*Engraulis japonicus*), sardines (*Sardinops ocellatus*) and two species of hake (*Merluccius capensis* and *M. paradoxus*) are dominant, whereas in Namibia the Bearded Goby *Sufflogobius bibarbatus* and Horse Mackerel *Trachurus trachurus* are the most important fish prey. Castley *et al.* (1991), who analysed the stomach contents of 49 seals stranded on the south-east coast (mainly in the Algoa Bay area), concluded that regional differences in seal prey were worthy of further study.

Six time-depth-recorders were fitted to lactating ♀♀ at Kleinsee colony in 1977. Only two instruments with dive records were recovered, but analysis of these indicated that the animals dived much

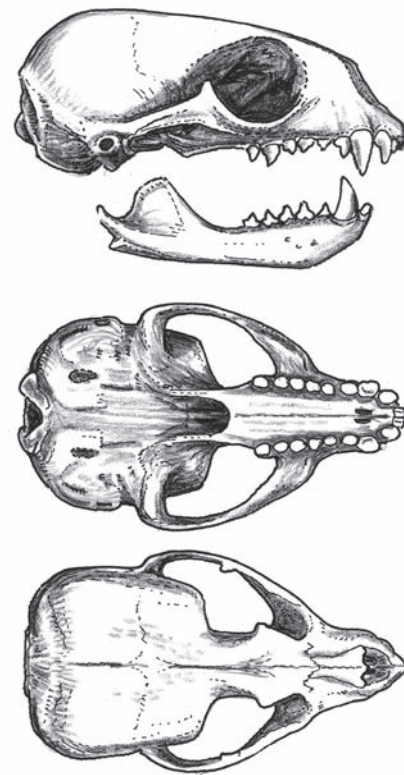
of the time they were at sea, which was presumed to reflect feeding activity (Kooyman & Gentry 1986). Feeding occurred in two peaks daily, but the timing of these peaks could not be determined. On average there were 12 bouts of diving of three hours' duration each during a feeding trip to sea. The dive rate was 16.5 dives per hour, but rates as great as 40 dives per hour were recorded. Most dives were of the continuous descent and ascent type, although on some dives seals spent some 1.5 minutes at the greatest depth reached. They descended rapidly, but the ascent was much slower, which would have facilitated searching for prey from below. It is suggested that seals were taking different prey at different times and depths. Dives lasted on average 2.1 minutes with a maximum of 7.5 minutes. The mean depth of all dives was 45 m and the maximum depth was 204 m. The most frequently attained depth was 50 m or less, but dives to 100 m were common (Kooyman & Gentry 1986).

The recovery of tagged animals at sea and the deployment of satellite-linked time-depth-recorders has also enabled some assessments to be made of the preferred foraging areas of seals from different colonies. Analysis of results indicates that seals from different coastal regions generally do not share the same feeding grounds, though there is some overlap. Tracking of seals fitted with satellite transmitters indicated that northern Namibian colonies feed north of Walvis Bay, the central Namibian colonies feed between Walvis Bay and Luderitz, the colonies south of Luderitz between just north of the Orange R. and Cape Agulhas and the Mossel Bay and Port Elizabeth colonies between Stilbaai and Cape St Frances (Marine and Coastal Management pers. comm.).

Lactating ♀♀ are likely to feed closer to their natal colonies immediately after pupping. They are thus more vulnerable to local fluctuations in food supply than seals with no ties to their colonies, which are free to forage more widely. The close proximity of colonies to abundant food sources is therefore a prerequisite for the colonies to function successfully as breeding units. Immature seals forage close inshore and progressively start to feed further offshore as they mature. Some juvenile and mature ♂♂ (but very few ♀♀) have learned to associate fishing vessels with easily obtainable food and will feed on the offal and trash fish discarded behind trawlers (David 1987b, 1989, Wickens *et al.* 1992, Punt *et al.* 1995, Miller *et al.* 1996).

Social and Reproductive Behaviour Most seals tend to return to their natal colony to breed and in many cases they occupy the same spot year after year. However, some seals do move between colonies and, in a growing population, new breeding colonies may be formed from time to time (e.g. Cape Frio in Namibia, which had been a non-breeding colony for years, became a breeding colony in 1994). Evidence for the movement of ♀♀ is provided by the results of aerial surveys, which sometimes show that there has been a sudden large increase in pup numbers at a particular colony. This can be attributed to the immigration of pregnant ♀♀.

Large bulls haul out and establish territories at the end of Oct and in early Nov, which they defend against all other ♂♂ including juveniles. This is achieved mainly through noisy ritualized displays at the common border between adjacent territories and seldom by actual fighting, although there are reports of bulls that have perished during severe skirmishes or as a result of wounds received (Rand 1956). If an interloping ♂ does not flee at the approach of the territory holder, he will be unceremoniously ousted through chest-



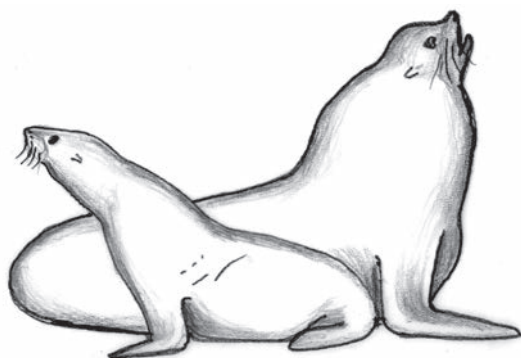
Lateral, palatal and dorsal views of skull of Cape Fur Seal *Arctocephalus pusillus*.

to-chest pushing by the dominant bull. Cows may fight over pups and there are frequent squabbles amongst themselves using a repertoire of threats and lunges. Territorial bulls usually prevent serious quarrels amongst ♀♀ by interposing themselves between the quarrelling pair. Juvenile and subordinate ♂♂ are scattered through the colony, and remain alert for an opportunity to mate with unattended ♀♀.

Females are gregarious and lie in close proximity to each other, except for ♀♀ with newly born pups, which are usually highly aggressive and defend the space around them against other ♀♀ and even pups. Females do not form groups of specific size, but form variable clumps with animals constantly joining or leaving throughout the day (David 1989).

Most ♀♀ arrive at the colonies from mid-Nov to mid-Dec, hauling out one or two days before they give birth to a single pup. After parturition, ♀♀ remain on average 4.3 days (range 0–13 days) with their pup, before they go to sea to feed, leaving the pup alone on the colony (David & Rand 1986). Pups older than about a week tend to congregate in large clumps or crèches for mutual warmth, comfort and protection. The mean duration of the feeding trips varied, but the average absence was 2.8 days during the first month, which increased progressively to 4 days by the third month. Females without pups spent approximately half as much time ashore as did mothers (David & Rand 1986). The mean interval from parturition to copulation was 6 days. At Van Reenen Bay colony in Namibia, 90% of births occurred from 22 Nov to 17 Dec, with a median pupping date of 4 Dec (David 1987a; and see Shaughnessy 1979).

On return to the colony, the ♀ finds her pup by going first to the precise spot where she left it. She recognizes her pup first by its call and when she reaches the pup she smells it carefully to confirm that



Sexual dimorphism in *Arctocephalus pusillus*.

it is indeed her own. If the pup wanders to a different part of the colony the mother may not be able to reunite with it and, because cows will only feed their own pups, lost pups will die of starvation.

Colonies of Cape Fur Seals are occupied all year round, but numbers fluctuate seasonally. The population peaks from mid-Nov to mid-Dec at the height of the breeding season and then declines slowly thereafter, as all bulls vacate the colony by early Jan. During the remainder of the year, the colonies are occupied by ♀♀ with dependent young, and by juveniles of both sexes. Bulls make sporadic brief visits throughout the year. The time of lowest numbers is during Oct, when most animals are at sea feeding in preparation for the coming breeding season.

A Cape Fur Seal colony is generally a noisy place, but this is especially true during the breeding season. The dominant noises are from the high-pitched bleating of the young pups, sounding much like domestic lambs, and the deeper, lowing calls of the ♀♀. The territorial bulls add their contribution through the staccato 'honking' or barking calls when courting ♀♀, and through explosive snorts when engaged in regular ritualized encounters with neighbouring ♂♂.

Reproduction and Population Structure Females give birth to a single pup after an apparent gestation period of almost a year. However, as implantation is delayed for about four months (taking place between Mar and Apr), the true gestation is about eight months. Females enter oestrus within a week of the birth of the pup (Rand 1955). Pups have a length of 0.6–0.7 m and a weight of 4.5–7.0 kg. Females suckle their pups for 8–10 months, though some continue to suckle into the second year. During this period the lactating ♀♀ make regular trips between the feeding grounds and the breeding colonies. Weaning is a gradual process, which starts in Jul and is normally complete by the end of Sep (with pups slowly supplementing their milk requirements with limited foraging bouts 3–4 months before weaning), so that the ♀ is free to spend Oct in foraging in preparation for the new birth (David 1987a).

Males reach puberty at the age of three years when most ♂♂ first exhibit spermatogenesis (De Villiers *et al.* 1997, Stewardson *et al.* 1998), but they are not socially mature until 8–10 years old, which coincides with a spurt in body and bacular growth (Oosthuizen & Miller 2000). At this age they may have attained a size large enough to challenge successfully for a territory during the breeding season (David 1989). Some ♀♀ become sexually mature at three years old, and give birth to their first pup at the age of four years, but most ♀♀ mature at the age of four or five, giving birth at age five or six (Shaughnessy 1982, David 1987a).

The sex ratio of full-term foetuses *in utero* is 1 : 1 ($n = 477$), but 57♂ : 43♀ for pups at an age of six weeks ($n = 68,980$). This ratio (57% male) was also found in a sample of adults and juveniles collected at sea ($n = 243$) (Oosthuizen 1991). This indicates that the initial natural mortality rate of ♀♀ is higher than for ♂♂ from birth to six weeks, but thereafter it is the same for both sexes. Males have a life expectancy of at least 20 years (Wickens 1993); one captive specimen lived to 32 years (Weigl 2005).

Predators, Parasites and Diseases Black-backed Jackals *Canis mesomelas* and Brown Hyenas *Hyaena brunnea* are the main terrestrial predators, preying mainly on pups at the Namibian mainland colonies. A study at Van Reenen Bay in S Namibia found that up to 36% of the pups born were preyed on by Black-backed Jackals (Oosthuizen *et al.* 1997). Marine predators include sharks and killer whales. White Sharks *Carcharodon carcharias* are common in the vicinity of seal colonies on the South African south and west coasts and many cases of predation on seals have been reported (see Stewardson & Brett 2000). Seal remains have been identified in the stomachs of seven-gill sharks in the vicinity of the Luderitz seal colonies.

Adult seals are sometimes infested with internal parasites, though generally the parasite load is quite moderate. Younger seals usually carry few parasites. Many animals have small numbers of mites in the nasal cavity (*Orthohalarachne attenuata*) and in the respiratory tract (*O. diminuta*) (Till 1955). Nematodes occur in the stomach (*Contracaecum osculatum* and *Anisakis simplex*), a cestode (*Diphyllobothrium atlanticum*) in the small and large intestine and an acanthocephalan (*Corynosoma australe*) in the small intestine (Rand 1956, Pansegrouw 1990). Larval cestodes (*Phyllobothrium tumidum*) are frequently found embedded in the abdominal blubber, especially of adult ♀♀ (Pansegrouw 1990), and a louse (*Proechinophthirus*), invisible to the naked eye, is a common ectoparasite (Rand 1956).

At the colonies one seldom sees sick animals. Known incidents of mass mortality, such as occurred in Namibia in 1994–95, were found to be due to starvation, not to disease (Roux 1998).

Conservation IUCN Category: Least Concern. CITES: Appendix II.

Uncontrolled exploitation by man over more than four centuries for meat, skins and oil has resulted in Cape Fur Seals disappearing from at least 23 island colonies around the South African and Namibian coastline, since sealing began late in the sixteenth century (Raven-Hart 1967, Shaughnessy 1984, David 1987a, 1989). The colonies were invaded at all times of year, even during the breeding season, and all age classes were taken, including pups and pregnant ♀♀, thus causing large-scale disturbance, and consequent abandonment of the colonies. As a result the seal population was reduced to very low levels by the end of the nineteenth century, which motivated the government of the Cape Colony to enact the first legislation protecting seals in 1893.

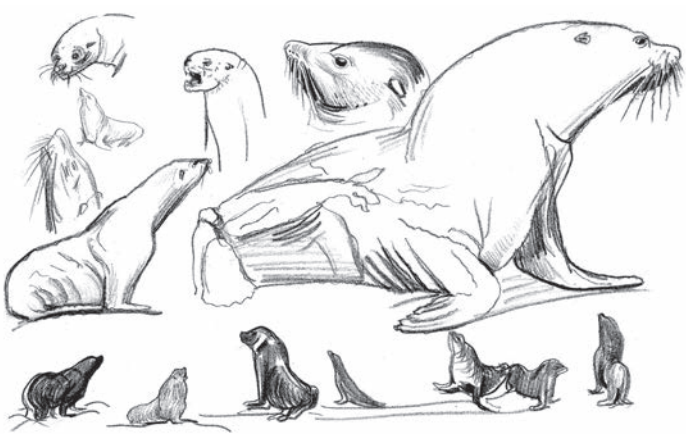
The proclamation of the Cape Fish Protection Act of 1893 stipulated that no seals might be harvested without a government permit. This was amended in 1909 and again in 1936 to prevent sealing during the breeding season. Sealing in Namibia (formerly the German colony of South West Africa, taken over by South Africa in 1920) was not controlled until 1922, when the Union Government passed the Sealing and Fisheries Proclamation. In 1949, this was replaced by the Sealing

and Fisheries Ordinance (Shaughnessy 1984, David 1989). All these measures were replaced by the Sea Birds and Seals Protection Act of 1973, which fully protected seals and sea birds in both countries until 1990, when Namibia gained its independence. The 1973 Act is still in force in South Africa, but is in process of being revised.

Despite the seal population being much reduced during the early years of the twentieth century, commercial harvesting of pups and bulls continued under government control in both countries up to 1990, when it was banned in South Africa for political reasons by the Minister of Environmental Affairs. However, seal harvesting in Namibia still continues under government licence at three mainland colonies. From 1900 to 1990 the total known harvest of pups in both countries was over 2.5 million and of bulls was over 200,000 (Wickens *et al.* 1991).

Despite this continuation of commercial exploitation, the Cape Fur Seal population has recovered in spectacular fashion, to stand currently at the previously mentioned total figure of 1.5–2 million animals. This is perhaps one of the outstanding success stories of conservation in the twentieth century. It is interesting that many of the extinct island seal colonies destroyed by the sealers were subsequently colonized by breeding sea birds. Only four extinct island colonies (three in Namibia and one in South Africa) are known to have been permanently recolonized by seals (Shaughnessy 1984).

Conflicts between the seal population and commercial fishing interests have led to the illegal shooting of seals at sea (Shaughnessy 1985, Wickens *et al.* 1992) and remain unresolved. Seals can be a nuisance around fishing vessels and may consume the catch and damage or become entangled in nets or lines. This is especially the case in the hand-line industry for the migratory Snoek *Thyrsites atun*, where the annual estimate of such damage is South African Rand 0.5–1 million (3.3–7% of the total landed annual value of Snoek; Wickens 1996). The conclusion that the seal population consumes roughly 2 million tonnes of food annually (Butterworth *et al.* 1995) has tended to confirm the fears of the fishing industry that seals are a major competitor for commercially important fish species. Close to sea bird breeding colonies there is concern that seals may kill and eat substantial numbers of fledgling and adult sea birds of threatened species such as Cape Gannets *Morus capensis* and African Penguins *Spheniscus demersus*



Cape Fur Seal *Arctocephalus pusillus*.

(Marks *et al.* 1997, David *et al.* 2003). However, the conclusion by Wickens *et al.* (1992) was that the overall losses to the fishing industry due to interference by seals in fishing operations, damage to gear and consumption of catch were minor compared with the wholesale value of the catches.

Measurements

Arctocephalus pusillus pusillus

TL (♂): 1900–2300 mm

TL (♀): 1200–1700 mm

WT (♂♂): 247.0 (200.0–350.0) kg, n = 53

WT (♀♀): 57.4 (40.0–80.0) kg, n = 206

Southern Africa (David 1987a)

Note: The weight of 700 kg given for ♂♂ in Shaughnessy (1979) is an error, as the weight in pounds was incorrectly published as kilograms, while the figures of TL 1800 mm and WT 122.0 kg for ♀♀, in the same publication, were undocumented estimates from Rand (1956).

Key References David 1987a, 1989; King 1983; Rand 1955, 1959; Shaughnessy 1982; Skinner & Chimimba 2005.

Jeremy H. M. David & Herman Oosthuizen

Family PHOCIDAE
TRUE SEALS

Phocidae Gray, 1821. London Med. Repos. 15: 297.

| | | |
|-----------------------------|------------|-------|
| <i>Monachus</i> (1 species) | Monk Seals | p.133 |
|-----------------------------|------------|-------|

The Phocidae (true seals or earless seals) form a monophyletic group, consisting of 19 species (one, the Caribbean Monk Seal *Monachus tropicalis* recently extinct) in 13 genera (Rice 1998, Wozencraft 2005). These are generally divided into two subgroupings, a northern group, Phocinae (containing, but not exclusively comprising, the tribe Phocini), which includes temperate region, sub-Arctic and Arctic species, and a southern group, Monachinae, which embraces the warm-water monk seals (tribe Monachini), the Antarctic ice seals (tribe Lobodontini), as well as the wide-ranging elephant seals of the genus *Mirounga* (Heyning & Lento 2002, Deméré *et al.* 2003, Fulton & Strobeck 2010).

Phocid seals can be recognized by the absence of external ear pinnae, a short muzzle, beaded vibrissae, a dark coloured skin, short fur, furred fore- and hind flippers, five claws on each fore-flipper, generally two nipples in ♀♀, internal testes, as well as a generally larger body size in comparison to otariids. Monophyly is supported by a pachyostic mastoid region, a greatly inflated entotympanic bone, the complete absence of supra-orbital processes, and strongly everted ilia (Berta & Sumich 1999). Also characteristic are the nasal bones that do not penetrate between the frontals on the mid-line and incisors that are not transversally grooved. Phocids typically have teeth differentiated into incisors, canines and postcanines. Premolars and molars are not differentiated, neither are carnassial teeth. The characteristic dental

formula is $I^{3/2}$, $C^{1/1}$, $PC^{5/5} = 34$, but with variations in both upper incisor ($I^{2/2}$ in *Monachus* and Antarctic phocids) and lower incisor ($I^{2/1}$ in hooded and elephant seals), but rarely in postcanine numbers (from Jefferson *et al.* 1993). Postcanine teeth may have multiple cusps in specialist krill feeders, and large canines and postcanines that allow some to hold and rend warm-blooded prey.

Sexual dimorphism in phocids is much less pronounced than in otariids, and may even be reversed, with ♀♀ being slightly larger than ♂♂, as in the lobodontine seals. An exception to this is found in elephant seals, the largest species of seal, which display the greatest disparity in size of all mammals. Southern Elephant Seal *Mirounga leonina* bulls reach masses of 2000–4000 kg, while ♀♀ only reach masses of 400–900 kg.

The earliest known fossil phocid is from the late Oligocene (29–25 mya) of South Carolina, the remainder from the middle Miocene (15 mya) when both phocine and monachine seals became distinct lineages in the North Atlantic. A fossil phocine seal from the late Miocene and early Pliocene has been discovered in South Africa (Hendey & Repenning 1972). Extant phocids are represented in Africa by only one genus and one species: the Mediterranean Monk Seal *Monachus monachus*. Three others, the Southern Elephant Seal, the Crabeater Seal *Lobodon carcinophaga* and the Leopard Seal *Hydrurga leptonyx*, turn up on the African coastline only as vagrants.

Phocids are adept swimmers, and, with the exception of the Leopard Seal (which swims with fore-flipper strokes like the otariids), propulsion is provided by the hindlegs. However, phocids are ungainly on land, moving with a characteristic humping locomotion on land or ice. Unlike otariids they are unable to rotate the hind flippers under the body because of a massively developed astragalar process and greatly reduced calcaneal tuber. Elephant seals and monk seals experience an annual catastrophic moult, with the skin sloughing away in large patches rather than the hairs falling out individually, as in all other species of phocids and all species of otariids.

The eyes are modified to focus underwater and see effectively under conditions of reduced light. Physiological adaptations for diving are especially well developed in several phocids, most remarkably so in the elephant seals and the Weddell Seal *Leptonychotes weddellii*. These include slowing of the heart rate (bradycardia), shunting blood from peripheral

areas to the brain and heart, high tolerance for carbon dioxide levels in the blood, a high concentration of haemoglobin in their red blood cells and myoglobin in their muscle tissue, a relatively large blood volume and the ability to withstand enormous pressures at depth. Upon rapid return to the surface they can avoid developing either nitrogen narcosis (an anaesthetic effect on the nervous system that may lead to unconsciousness and death) or the 'bends' (dissolved nitrogen coming out of solution, forming gas bubbles that may cause embolisms and also result in death). This ability is due to the absence of large gas-filled spaces and the exhalation of their lungs before diving deeply.

Phocids feed on a wide variety of species of open-water and benthic fish, cephalopods, crustaceans, marine birds (primarily penguins) and exceptionally (as in the case of Leopard Seals) other mammals, including otariids and phocids, and scavenging from carcasses of whales. Foraging behaviour depends on the area, season and species and generally takes place at depths of 50–450 m. Consummate divers such as Weddell Seals can make dives to depths of 700 m and of 82 min in duration, while Southern Elephant Seals can make dives to 2150 m (McIntyre *et al.* 2010) and up to 120 min, although foraging is believed to take place primarily between 300 and 400 m during shorter dives.

The breeding season for phocids is spring or summer, and sometimes the boreal autumn. A single pup is born after a gestation period of about one year, which includes a period of delayed implantation. Twinning is extremely rare, and twins have not been recorded to survive in the wild until weaning. Males do not care for the young. The mating systems vary from polygynous (e.g. Weddell Seals, Grey Seals *Halichoerus grypus* and elephant seals to serially monogamous (Crabeater Seals), with mating taking place on land or ice and/or at sea. Females of all phocid species are basically capital breeders, generally storing energy and nutrients in their subcutaneous blubber while foraging before the breeding season haul-out, then come ashore or haul out on ice to fast or feed very little while nursing their pups for between four (Hooded Seal *Cystophora cristata*) and 53 days (Weddell Seal). During the breeding season, polygynous species may haul out in large aggregations and ♀♀ generally come into oestrus from shortly before, to after their pups are weaned (Boness *et al.* 2002).

Marthán N. Bester & Paul N. Odendaal

GENUS *Monachus*

Monk Seals

Monachus Fleming, 1822. Philos. Zool. 2: 187.

The genus *Monachus*, considered to be the most primitive members of all phocids, contains three species: the Mediterranean Monk Seal *Monachus monachus*, the Caribbean Monk Seal *Monachus tropicalis* and the Hawaiian Monk Seal *Monachus schauinslandi* (King 1956, Scheffer 1958, Wozencraft 1993, 2005). With the exception of the California Sea Lion *Zalophus californianus*, monk seals are the only tropical pinnipeds. Unfortunately, the Caribbean Monk Seal is now extinct, with the last reliable observation dating to 1952 (Adam & Garcia 2003).

Differences among the species, which are geographically separated by at least 5000 km, are slight and based on characteristics of the skull and pelage. *Monachus monachus* has upper incisors without a marked cervical constriction; premolars 2–4 with a single cusp posterior to the main

cusp; antorbital process prominent; pterygoid processes poorly defined and not visible in dorsal view; anterior tips of nasals rounded; auditory bulla without distinct oblique ventral sulcus; and adult ♂♂ and pups with a conspicuous ventral white patch (Adam 2004). The structure of the bony parts of the ear indicates that *Monachus* is the least specialized genus of the living Monachinae seals (southern phocids).

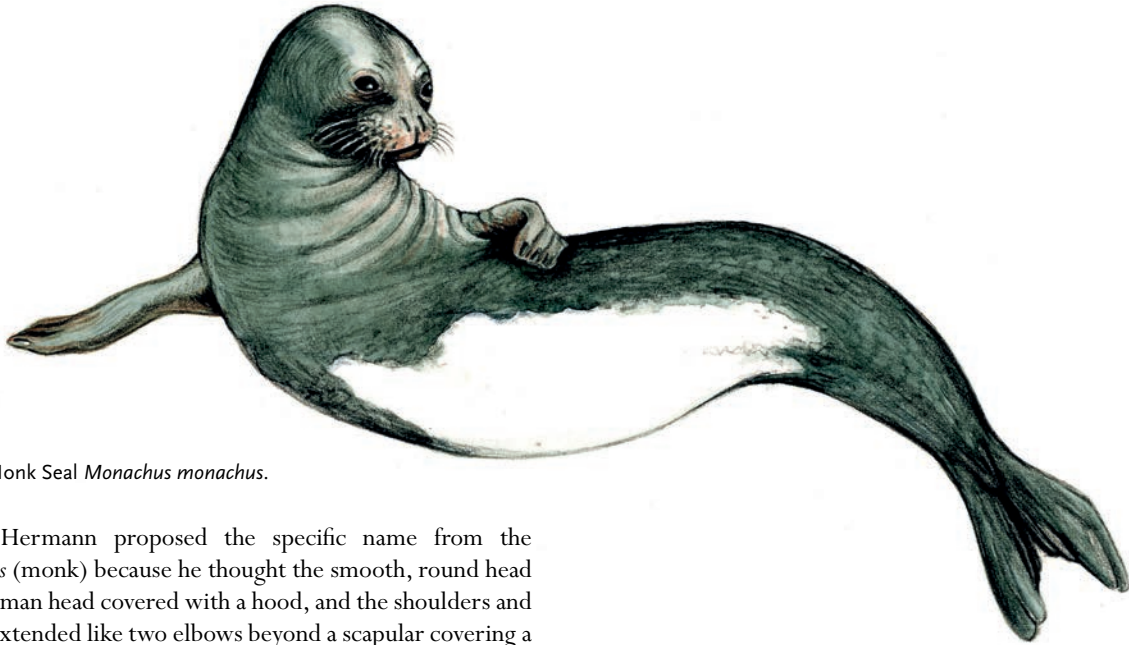
It has been suggested that the genus is paraphyletic, with *M. monachus* and *M. tropicalis* more closely related to other phocids than to *M. schauinslandi* (Wyss 1988), but see Bininda-Emonds *et al.* (1999) and Higdon *et al.* (2007).

Luis Mariano González

Monachus monachus MEDITERRANEAN MONK SEAL

Fr. Phoque moine de la Méditerranée; Ger. Mittelmeer-Mönschrobbe

Monachus monachus (Hermann, 1779). Beschäft. Berlin Ges. Naturforsch. Fr. 4: 501, pls. 12, 13. Ossero (now Osor), Cherso island (now Cres island), Croatia.



Mediterranean Monk Seal *Monachus monachus*.

Taxonomy Hermann proposed the specific name from the Greek *monakhos* (monk) because he thought the smooth, round head resembled a human head covered with a hood, and the shoulders and short flippers extended like two elbows beyond a scapular covering a frock. Individuals of the Atlantic were described as a distinct species *Heliophoca atlantica* (Gray 1854). Synonyms: *albiventer*, *atlantica*, *bicolor*, *byronii*, *crinita*, *hermannii*, *isidorei*, *leucogaster*, *mediterraneus*. Chromosome number: $2n = 34$ (Arnason 1974).

Description The Mediterranean Monk Seal is amongst the largest phocid species. Head rounded with a protruding muzzle. Face appears wide because of the flatness of the muzzle and the upper lips. Orbits and eyes large. Nostrils nearly on the dorsal surface of the snout and almost horizontal. Mystacial vibrissae light yellow to brown, oval in cross section and smooth. External ear pinnae absent, with small opening of the ear canal located just behind the eyes. Fusiform bodyshape, dark in colour dorsally and lighter ventrally. The body hair is the shortest of all the pinnipeds, only 5 mm in adults; secondary pelage absent. Unlike any other mammal, members of the tribe Monachini exhibit an unusual moult wherein the hairs are shed along with large sheets of cornified epidermis through which the club hairs penetrate. Moulting ♀♀ can be found throughout the year, with a peak in Mar. Moulting ♂♂ have been found from Apr to Oct, with a peak in Jun (Gazo *et al.* 1999). All individuals, except pups, present obvious marks and scars in the pelage due to the absence of hair pigmentation, caused by interaction between individuals and injuries inflicted by ♂♂ during mating. Adults exhibit marked sexual dimorphism in pelage colour (Samaranch & González 2000; and see below). Fore-flipper short and haired, with a claw on each of five digits. Nails present on both flippers, but very reduced in comparison with other pinnipeds. First digit of the fore-flipper about 25 mm long and the others decrease slightly in size towards the fifth digit. Hind-flippers oriented posteriorly and cannot be rotated forward. Testes not scrotal, but lie separately outside the body cavity in the hypodermal layer of the skin. Tail short and wide. Two pairs of nipples.

Six morphological age-classes have been described, all identifiable in the field (Badosa *et al.* 1998, Samaranch & González 2000):

Newborn/Pup: Pelage woolly. Nape, throat and back uniform black. Belly black interrupted by a yellowish-white patch, squarish in shape in which anterior edge coincides approximately with centre of body and ends caudally between umbilical scar and genital slit. In ♀♀ the caudal margin of the white patch is close to the tail and straight, with the umbilical slit falling within the patch. In contrast, in ♂♂ the caudal margin indents to reach, or almost reach, the umbilical slit. The penile opening falls outside the ventral patch. First moult of this pelage begins nearly 45 days after birth and lasts an average of 25 days.

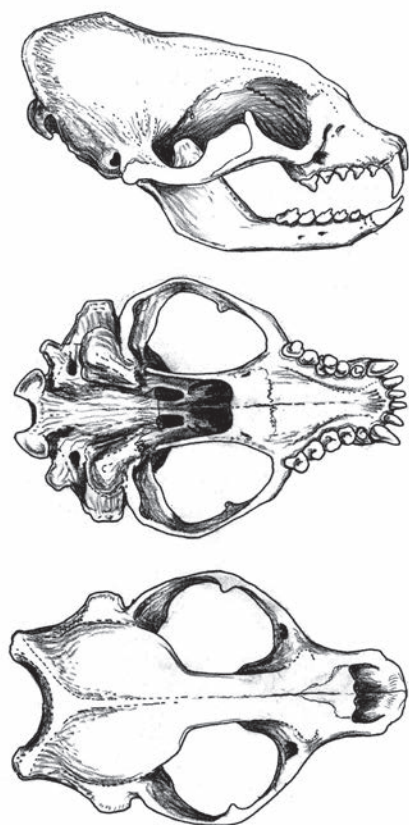
Youngster: Nape, throat, belly and back light grey. Upper part of head darker, extending to nostrils (hood), leaving 'mask' around eyes that stops above ear. Individuals with these characteristics appear from around 69 days until about nine months old.

Juvenile: Nape, throat, back and belly dark-grey, with hood and mask around eyes. Individuals with these characteristics appear from seven months until 23 months old.

Subadult: Nape, throat, back and belly medium-grey or dark-grey. Hood and 'mask' around eyes extends over outer ear, spreading in sideburn shape. Back interrupted with scars. Individuals with these characteristics appear from 18 months old, but class duration is unknown at present.

Adult female: Similar to subadult class, but with the back interrupted by scars in the form of a patch in the dorsal region.

Adult male: Distinctly black, except the throat is white and the belly presents a white patch similar to male pups'. Back interrupted by



Lateral, palatal and dorsal views of skull of Mediterranean Monk Seal *Monachus monachus*.

scars, without dorsal sash. This pelage appears at approximately four years old. The similarity in pelage pattern and colouring between pups and adult males is striking.

Skull broad in proportion to its length (mastoid width about 1/1.76 condylobasal length). The extension backwards of the zygomatic process of the maxilla is very much greater than in the Phocinae (King 1956).

Geographic Variation None recorded, although Van Bree (1979) reported on differences in skull morphology between Mediterranean Monk Seals from the Atlantic and the western Mediterranean based on a limited sample size.

Distribution Ranges from Cabo Blanco peninsula on the Atlantic Sahara coast (Morocco–Mauritania), at about 20° N, along the Atlantic coast and offshore islands of north-west Africa, and throughout the Mediterranean coasts (with individuals known to wander as far south as Gambia and Senegal) (Marchessaux 1989, Reijnders *et al.* 1997, Grubb *et al.* 1998, López-Jurado *et al.* 1998).

Historical Distribution Until the fourteenth century, this species also occurred on the Azores, Canary and Cape Verde Is., adjacent to the African continent. Present in the Mediterranean until the nineteenth century, and distributed along all the shores of the African coast (Monod 1948).

Current Distribution In the south-eastern North Atlantic, the species is confined to two small areas: Madeira (the main island, Porto Santo,



Monachus monachus

and the Desertas Is.; see Pires *et al.* 2008) and the Cabo Blanco Peninsula. There also are occasional records in the Canary Is. and the front coast of Morocco, the Cabo Barbas-Guerguerat region (Morocco), the Bay of Levrier and in the Banc d'Arguin (Mauritania).

Along the Mediterranean coast of Africa, populations have disappeared from Egypt, the majority of Libya, the western coast of Morocco and recently in E Algeria and Tunisia. The coast between Peñon de Vélez-Bokoyas and Chafarinas Is. (Morocco–Spain), and between Beni Saf and Mostaganem (Algeria), is still occupied by a few monk seals. Also there are sporadic sightings of individuals on La Gallite (Tunisia) and some individuals probably survive in Tolmeythia, along the Cyrenaic coast of Libya (Avellá & González 1984, Bayed & Beabrun 1987, Boutiba *et al.* 1988, Francour *et al.* 1990, Kowalski & Rzebiak-Kowalska 1991, González *et al.* 1997, Reijnders *et al.* 1997).

Otherwise, the stronghold for the species is in the eastern Mediterranean on islands in the Ionian and Aegean Seas, and along the coasts of Greece and W Turkey.

Habitat Predominantly coastal, although they have been observed as far as 80 nautical miles from shore (Maigret *et al.* 1976, Marchessaux 1989). This species prefers coastal waters, with sheltered beaches and caves along inaccessible rocky cliffs. Only two other pinnipeds use this type of habitat on land, the Guadalupe Sea Lion *Arctocephalus townsendi* and certain populations of Grey Seals *Halichoerus grypus* (Sergeant *et al.* 1978, Reijnders *et al.* 1997). Historically, in the Atlantic, Mediterranean Monk Seals also inhabited the beaches of islands and the sand banks and open beaches of the mainland, where there are records of large aggregations of seals (Monod 1948, Marchessaux 1989). Currently, Mediterranean Monk Seals are restricted to cliffs of very remote areas where disturbance by people is slight. Seals disappeared from these habitats due to human persecution, and only those populations that lived in caves or beaches protected by cliffs survived. It has been suggested that this habitat is sub-optimal for the monk seals due to the low survival rate of

pups (Sergeant *et al.* 1978, Francour *et al.* 1990). In the Cabo Blanco peninsula some adult males haul out on open beaches (Marchessaux 1989, González *et al.* 1997); recently, in Desertas, with no human disturbances, immature-size ♀♀ have reoccupied open beaches (abandoned a long time ago) to breed and this has improved the reproductive success of the colony (Costa Neves & Pires 2000).

Abundance The Mediterranean Monk Seal was common along the Atlantic Saharan coast in the Neolithic age, where it was consumed by human coast-dwellers (Marchessaux 1989). It certainly was abundant at least until the fifteenth century. Accounts left by the first Portuguese explorers to arrive on these coasts attest that the seals were sufficiently abundant to justify hunting expeditions for seal oil and skins. In the Mediterranean they also were common along the coast of Egypt, Libya and Algeria in the eighteenth and nineteenth centuries (King 1956, Marchessaux 1989, Kowalski & Rzebik-Kowalska 1991). However, since then, the world population of Mediterranean Monk Seals has undergone rapid decline – up to 80% in the last century – and now is highly fragmented (Reijnders *et al.* 1997). The global population currently is estimated at 300–400 individuals (Reijnders *et al.* 1997).

The largest known population currently occurs on the cliffs of ‘Costa de las Focas’ in the Cabo Blanco peninsula (González *et al.* 1997), with an estimated average population of 317 seals in the mid-1990s (Forcada *et al.* 1999). However, this population was affected by a severe mass mortality in 1997, which reduced its numbers to an estimated 103 individuals in 1998 (Forcada *et al.* 1999). The sub-population in Madeira was composed of about 50 animals in the late 1970s and has been severely reduced to date. Current numbers are around 20–30 animals (Pires *et al.* 2008). Along the Morocco–Algeria coast probably only a few individuals survive (Bayed & Beabrun 1987, Boutiba *et al.* 1988, F. Avella pers. comm.). Some 250–300 individuals survive in the eastern Mediterranean.

Adaptations The genus *Monachus* is considered the most primitive of living seals, due to the possession of some primitive anatomical features (structure of the skull, skeleton and vein system). Monk seals have very poor underwater hearing. The structure of the ear region of the skull offers little resistance to high pressure, and the Mediterranean Monk Seal is, in fact, a littoral species and a shallow diver. Internal temperature ranges between 35.9 and 37.5°C but the species is capable of tolerating solar thermal changes and high prevailing temperatures (36.3°C) without becoming hyperthermic. In this context, dark colouration of the pups could be an adaptive mechanism to intensive solar radiation because it can operate as a dispersant mechanism for the light energy (King 1956, Marchessaux 1989).

It has been suggested that in response to human persecution, the surviving individuals have modified important aspects of their biology and behavioural patterns. Breeding in caves is just one example, with most hauling out and pupping occurring today in caves or grottoes, some of which have underwater entrances. The Cabo Blanco colony occupies an area heavily affected by the action of large oceanic waves and the presence of storms. Individuals haul out and give birth on narrow sandy beaches that disappear during very high tides or when high swells reach the ends of caves. Consequently, pups are fatally injured against rock walls due to the impact of waves (Gazo *et al.* 2000a, Mozetich *et al.* 2002).

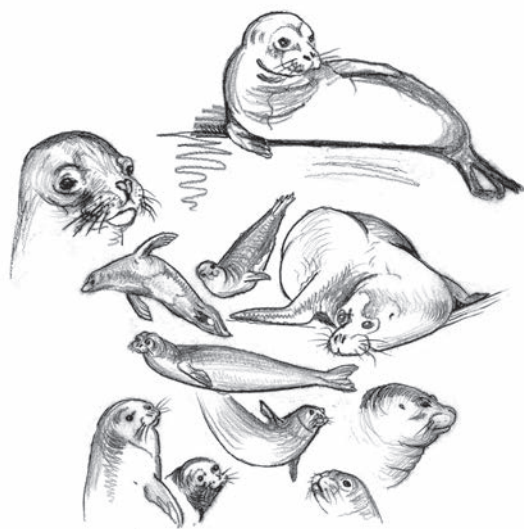
Foraging and Food Mediterranean Monk Seals are piscivorous and generally feed on demersal or pelagic fishes, such as those of the families Moronidae, Rynobathidae, Sparidae, Cupleidae, on crustaceans such as *Panulirus regius* and cephalopods of the genera *Octopus*, *Sepia* and *Loligo*. Daily food intake has been estimated at around 5–10% of their total body weight. They are opportunistic feeders, exploiting the resources that are most abundant at the time. Maximum diving depth has been recorded to 90 m (although dives rarely exceed 50 m); the recorded maximum duration of a dive is around eight minutes. They have been observed bringing large fishes (i.e. *Dicentrarchus* sp.) and *Octopus* to the surface, where they shake the prey vigorously before swallowing (Marchessaux 1989, M. Gazo pers. comm., P. Fernández pers. comm.).

Social and Reproductive Behaviour The biology and ecology of this species are not well known. Genetic studies in Cabo Blanco colony suggest that Mediterranean Monk Seals are polygynous, with ♂♂ mating with multiple ♀♀ (Pastor *et al.* 2004). In this colony, up to one hundred individuals have been seen hauled out at the same time. Adult ♂♂ defend aquatic territories at the entrance to their caves and surrounding areas (González *et al.* 1997). Tenure of aquatic territories extends throughout the year and, in some cases, for several years. Females and young regularly are found only in the breeding caves. They probably socialize more frequently in the water than out (Marchessaux 1989, ULPGC 1999).

There is no information regarding mating behaviour, and there are only a few observations that suggest that mating takes place underwater. Prior to parturition, ♀♀ look for isolated spots inside the caves far from other seals and where the beaches will not be covered during high tide and are protected from waves. They dig a hollow in the sand, probably with their fore-flippers and muzzle, and defend the site from any approaching seals (Layna *et al.* 1999). Newborns spend the majority of the time on beaches inside the caves. Pups are highly mobile and have been observed making trips in open waters up to 2.2 km unaccompanied by the mother. Females alternate nursing with feeding trips to open waters. Fostering and milk stealing occurs frequently. Sporadic sightings of juveniles in areas far away from the breeding colonies suggest juvenile dispersal over larger distances can occur (ULPGC 1999, CBD-Habitat pers. comm.).

Reproduction and Population Structure Females are sexually mature at three years of age by which stage they measure from 2.2 to 2.3 m in length (ULPGC 1999). A female at Cabo Blanco became pregnant at 2.5 years and gave birth at 3.7 years, the youngest age known for this species (Gazo *et al.* 2000b). The Mediterranean Monk Seal is the only phocid in which the pupping season extends throughout the whole year (Gazo *et al.* 1999, González *et al.* 2002). The gestation period is unknown, and it is not clear whether there is delayed implantation. Females give birth to a single pup weighing about 15–20 kg. Nursing extends over 120 days, almost doubling the maximum lactation periods observed in other phocids, and appears to end gradually. Average birth interval is about 375 days ($n = 8$) (CBD-Habitat pers. comm.).

In the Cabo Blanco colony, survival rates from known age classes were: 0.52 for pre-weaning pups (0–3 months), similar to rates recorded for pinnipeds breeding in caves, but lower than for those breeding on open beaches; 0.77 for post-weaning juveniles (3 months



Mediterranean Monk Seal *Monachus monachus*.

to 1 year); and 0.8 for juvenile/subadults (1–2.5 year). Only 32% of pups born in this colony reach sexual maturity (Gazo *et al.* 2000a, González *et al.* 2002). Average annual productivity in the Cabo Blanco colony was 60 pups prior to the mass-mortality, and 25–29 thereafter (Gazo *et al.* 1999, González *et al.* 2002). The average number of reproductive ♀♀ in the population that reproduce each year was estimated at 51.9% S. E. = 12.4%). The percentage of adult ♀♀ that successfully reproduce from year to year ranges from 30 to 70%. The massive die-off in 1997 in this colony area reduced the size of the adult ♀♀ population by over 50% (Harwood *et al.* 1998). Maximum recorded age is 44 years for an individual from the Aegean Sea (Reijnders *et al.* 1997).

Predators, Parasites and Diseases The mass-mortality episode in the Cabo Blanco colony was attributed to intoxication through the consumption of prey items contaminated with paralytic shellfish poison saxitoxins (PSPs) (Hernández *et al.* 1998, Reyero *et al.* 1999), caused by a bloom of toxic algae. A virus closely related to the dolphin morbillivirus was isolated from tissues of three individuals and serum antibodies to canine distemper virus were also detected in four individuals in the mass-mortality of 1997 (Osterhaus *et al.* 1997). One ectoparasite has been described, *Lepidophtrirus piriformis*, and eight cestodes and three nematodes, but only *Anisakis pegreffii* is host-specific (King 1956). There is no information regarding predators.

Conservation IUCN Category: Critically Endangered A2abc; C2a(i); E. CITES: Appendix I. CMS: Appendix I.

The Mediterranean Monk Seal is among the rarest and most threatened mammals in the world (Reijnders *et al.* 1993). The decline in population numbers is the result of adverse interactions with man, mostly through direct exploitation in the past, and now deliberate killing to prevent damage to fishing gear, incidental entanglement in fishing nets, destruction or alteration of coastal habitat, reduction of food, pollution, cave collapse and toxic algae blooms. Deliberate or incidental killing of seals by fishermen continues to take place along the Mediterranean shores and represents a significant source of adult mortality. The use of dynamite, driftnets and other illegal gear is frequent and causes sporadic mortality. In Madeira, dangerous

fishing activities have been eliminated from the Nature Reserve of the Desertas Is.; compensation was provided to fishermen forced to change their fishing practices (Costa Neves & Pires 2000).

Genetic studies in the Cabo Blanco colony indicated extremely low allelic variability in comparison with other pinniped populations (Pastor *et al.* 2004). Distances between the two Atlantic populations (some 2000 km between the Desertas and Cabo Blanco colony), and between the Atlantic and the Mediterranean populations, make regular mixing of individuals highly unlikely. Pastor *et al.* (2007) measured levels of nuclear genetic variation at 24 microsatellite loci in 12 seals from the eastern Mediterranean and 98 seals from the Western Sahara (Atlantic) population. The eastern Mediterranean population had 14 unique alleles and the Western Sahara had 18; highly significant differences in allele frequencies between the two populations were found for 14 out of 17 loci. These results suggest that each population may act as a source for introducing additional genetic variation into the other population.

Analysis of the tissues of Mediterranean Monk Seals from the Mediterranean populations has revealed extremely high concentrations of organochlorine compounds (PCBs, DDTs, etc.) and heavy metals (mercury, leads etc.), which may be having negative effects on reproduction and the immune system (Reijnders *et al.* 1993, 1997). This has raised considerable concern over the future of the species and has led to the drawing up of several action plans, including a 'Conservation Guidelines' (Johnson & Lavigne 1995) and two Action Plans, one for the Mediterranean under the Barcelona Convention and the other for the Atlantic under the Bonn Convention (González 2000), that proposed a series of conservation measures, including: (1) reduction in seal mortality; (2) enhancing the level of habitat protection; (3) management plans for protected areas; (4) regulatory measures to minimize the impact of fishing; (5) specific measures to avoid habitat deterioration; (6) reoccupation of beaches as breeding habitat; (7) rescue and rehabilitation of seals; (8) emergency plans for catastrophes; (9) awareness and socio-economic measures for the fishermen and local communities; and (10) research and monitoring of the species. These plans also identified a number of important areas for the protection of these seals, including: along the Mediterranean coasts of Spain and Morocco (the coast of Bokoyas [Peñon de Velez – Al-Hoceima] and Cabo Quilate – Cabo Tres Forcas – Chafarinas Is.); in Algeria (Maddagh – Habibas I. and Cap Ivi – Cap Tarsa – Cap Figalo – Ile Plane); Desertas Is. and Selvagens Is. (Madeira), Cap Tarfaya, Cap Barbas-Guerguerat and Cabo Blanco Peninsula (Morocco–Mauritania), and L'Etoile-Levrier Bay and National Park of Banc d'Arguin (Mauritania).

Measurements

Monachus monachus

HB (♂ ♂): 2520 (2100–2700) mm, n = 39

HB (♀ ♀): 2370 (2100–2620) mm, n = 50

T: 150–190 mm, n = 5

WT (♂): 335.0 kg, n = 1

WT (♀): 300.0 kg, n = 1

Cabo Blanco (ULPGC 1999, CBD-Habitat unpub. rep.).

Key References Costa Neves & Pires 2000; Forcada *et al.* 1999; González *et al.* 1997; Marchessaux 1989; ULPGC 1999.

Luis Mariano González

Suborder FELIFORMIA – Two-spotted Palm Civet, Cats, Viverrids, Hyaenids, Mongooses

Feliformia Kretzoi, 1945. Ann. Hist. Natur. Musei Natn. Hungar. 38: 62.

Suborder Feliformia has traditionally comprised four families (Felidae, Herpestidae, Hyaenidae and Viverridae). However, a much clearer understanding of the relationships within the suborder has developed in the past few decades. The Two-spotted Palm Civet *Nandinia binotata* is a basal feliform, and not included in the Viverridae (Hunt 1987, Flynn & Nedbal 1988). Asian linsangs (genus *Prionodon*) are included in the family Prionodontidae, and constitute the sister-group to felids (Gaubert & Veron 2003). Finally, Malagasy carnivores, once placed in the Herpestidae and Viverridae, form a separate feliform clade, the Eupleridae (Yoder *et al.* 2003). This revised classification of seven major clades now appears well supported (Eizirik *et al.* 2010,

Meredith *et al.* 2011), with Nandiniidae being the most basal lineage, followed by the Felidae + Prionodontidae clade; next to diverge was Viverridae, followed by Hyaenidae, leaving an internal clade composed of Eupleridae + Herpestidae.

In Africa, the Suborder is represented by the Nandiniidae (one genus and one species), Felidae (six genera, 10 species), Viverridae (three genera, 17 species), Hyaenidae (three genera, four species) and Herpestidae (14 genera and 26 species).

Michael Hoffmann

Family NANDINIIDAE TWO-SPOTTED PALM CIVET

Nandiniidae Pocock, 1929. Encyclopaedia Britannica, 14th Ed., IV: 898.

| | | |
|-----------------------------|------------------------|--------|
| <i>Nandinia</i> (1 species) | Two-spotted Palm Civet | p. 139 |
|-----------------------------|------------------------|--------|

The Nandiniidae is a monogeneric family, represented by a single species, the Two-spotted Palm Civet *Nandinia binotata* distributed in the inter-tropical and south-east African forests. The dorsal pelage is greyish-brown with small dark dorsal spots, and there is a pair of whitish-yellow spots on the shoulders. Both upper and lower canines are large, straight and relatively grooved (more so than in *Genetta*). *Nandinia* is the only extant species of Carnivora having the elements that constitute the bulla unfused in adults (although some specimens belonging to the Oriental Palm Civets [genus *Paradoxurus*] have been found with unfused bulla elements; R. M. Hunt pers. comm.). Moreover, the bulla is not divided by a septum, and a cartilaginous caudal entotympanic separates the rostral entotympanic from the tympanic (Hunt 1974). This plesiomorphic structural assembly and the rudimentary state of the cartilaginous caudal entotympanic, ectotympanic and rostral entotympanic are discussed in detail by Hunt (1987). The transpromontorial course of the internal carotid artery is rather small (Chapuis 1966), a characteristic that is supposed to represent the plesiomorphic aeluroid state (Hunt 1989).

There has been much controversy concerning which taxonomic group *Nandinia* should be assigned to. *Nandinia* was traditionally considered either a peculiar member of the Asiatic subfamily Paradoxurinae – it is commonly called the ‘African Palm Civet’ – (Pocock 1915, Simpson 1945, Meester *et al.* 1986) or the single genus constituting the subfamily Nandiniinae (Gregory & Hellman 1939, Coetzee 1977, Wozencraft 1993) in the family Viverridae. However, Gregory & Hellman (1939) themselves admitted that in *Nandinia* ‘carnassials ... are of nearly pure ‘trenchant’ type and directly derivable from those of the upper Eocene Viverrinae’, and assigned the taxon to a primitive branch antedating frugivorous



Two-spotted Palm Civet *Nandinia binotata*.

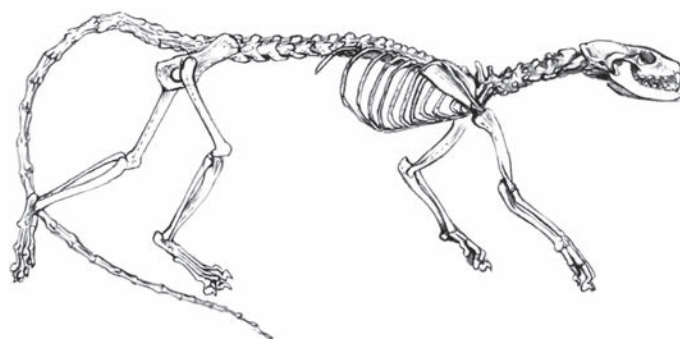
specializations in Paradoxurinae. Pocock (1929) erected the family Nandiniidae, on the basis of the presence/absence of perineal scent glands and both bullae and paroccipital characters. Important evidence for its very basal affinities within the Feliformia, and for plesiomorphic character states retained by the genus, are mainly based on the structure of the basicranium and auditory bullae. The data have been detailed by Hunt (1974, 1987), who suggested that the bulla of each current family of Feliformia could be derived from the bullar structure of *Nandinia*. Hunt (1989) also noticed that the shape of the petrosal bone is very similar to that of the oldest aeluroids, the stenoplesictines and proailurines from the Oligocene.



Plantar surfaces of hindfoot (*left*) and forefoot (*right*).

Some external characters also make *Nandinia* very different from Paradoxurinae and other subfamilies of viverrids. The area between the plantar and digital pads (digit 1 excepted) is hairy, and digital pads of the third and fourth digits are widely separated. The position of the scent gland (anterior to the penis/vulva), its flattened shape and very simple structure show no similarity at all with what is known among viverrids (Pocock 1915). In addition, other scent glands are located in the sole of the foot, chin area and also around the belly when females are lactating (Kingdon 1997).

The fossil record of *Nandinia* is limited to a single tooth (Morales *et al.* 2005), though African fossil viverrids (*sensu lato*) have been poorly studied. Some authors have suggested that this taxon belongs to a very primitive stock of aeluroids that evolved slowly in stable mesic forested biotopes of central Africa (Hunt 1974). On the other hand, the peculiar characters of the genus, together with the absence of a fossil record, could suggest that *Nandinia* is a very derived



Two-spotted Palm Civet *Nandinia binotata* skeleton.

genus within Viverridae (Pocock 1915, Gregory & Hellman 1939, Gaubert 2002b). However, the morphological phylogenetic analysis by Hunt (1987) placed *Nandinia* as a sister-taxon to the Feliformia; this clade in turn formed the sister-group to the extinct Nimravidae. Veron (1995), in a cladistic analysis, found the genus to be the most basal within Feliformia, with some affinities with the 'protoviverrid' *Paleoprionodon*. A combined molecular and morphological analysis by Flynn & Nedbal (1998) on the current families of Carnivora strongly supported *Nandinia* as being the sister-taxon of all other Feliformia. These results have been supported by subsequent molecular investigations (Gaubert & Veron 2003, Yoder *et al.* 2003, Flynn *et al.* 2005), with molecular estimates of divergence time suggesting an early Eocene split from the rest of extant feliformians (Gaubert & Cordeiro-Estrela 2006, Eizirik *et al.* 2010). Therefore, we follow the classification by Gaubert *et al.* (2005a) and Wozencraft (2005) in considering the family Nandiniidae as valid.

Philippe Gaubert

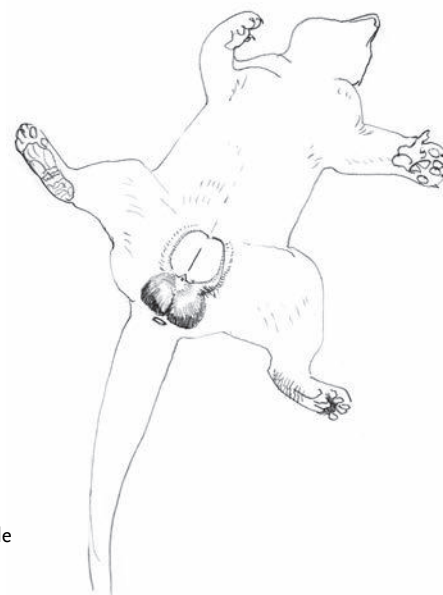
GENUS *Nandinia*

Two-spotted Palm Civet

Nandinia Gray, 1843. List Spec. Mamm. Coll. Brit. Mus. p. 54.

Nandinia is a monotypic genus, including a single species, the Two-spotted Palm Civet *Nandinia binotata*, which is found in various forest types throughout West and central Africa, and in a narrow belt of suitable forested habitats in East Africa southwards to S Mozambique. This genus is easily distinguished from other African carnivores by several external characteristics, including its short, thick legs and naked footpads, its exceptionally thick-muscled tail, and the twin yellow spots usually present on the shoulder blades. Unique cranial characters include an entirely cartilaginous posterior part of the auditory bulla, which is always lacking from prepared specimens and long, pointed, isolated paroccipital processes, more canoid than feloid in appearance (Rosevear 1974). Flower (1872) noted the absence of a caecum in *Nandinia*.

Harry Van Rompaey & Justina C. Ray



Genital region of adult male
Two-spotted Palm Civet
Nandinia binotata.

Nandinia binotata TWO-SPOTTED PALM CIVET (AFRICAN PALM CIVET, TREE CIVET)

Fr. Nandinie; Ger. Pardelroller

Nandinia binotata (Gray, 1830). Spicil. Zool. 2: 9. Africa, Ashantee (Ashanti region, approximately 06° 55' N, 00° 32' E, Ghana).Two-spotted Palm Civet *Nandinia binotata*.

Taxonomy Polytypic species with four subspecies described, but little consensus on their validity (Allen 1939, Schouteden 1945, Rosevear 1974, Coetzee 1977). Synonyms: *arborea*, *binotata*, *gerrardi*, *hamiltonii*, *intensa*. Chromosome number: $2n = 38$ (Todd 1967, Wurster & Benirschke 1967).

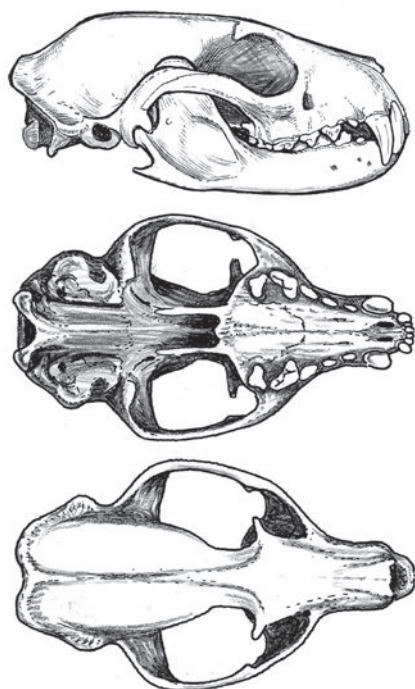
Description Similar to dark-brown-coloured genet in general appearance but more heavily built with shorter muzzle and longer tail. Pelage short, woolly and dense with pleasant musky smell. Dorsal pelage variable shades of greyish-brown with small irregular dark brown to black spots. Spots tend to coalesce into irregular black mid-line between the ears. Whitish-yellow spot on each shoulder. Three black lines on neck. Ventral pelage grey to yellowish and without spots. Rounded broad head with moderately pointed muzzle. Ears short, round, broad at base, single brown-black spot behind ear pinnae. Iris green to orange-brown. Limbs short, thickset, similar in colour to dorsal pelage but unspotted. Strongly textured underside of forepaws naked to wrist, hindpaws naked to ankle. Five claws sharp, curved and partially retractile. Tail long (110–120% of HB), densely furred and irregularly ringed with 9–15 brown to black rings, usually less well marked on the underside. Wide range of individual variation in both colour and markings (Allen 1924, Mertens 1925, Schouteden 1945, Rosevear 1974). Males may be slightly larger than ♀♀; considerable individual differences are noticeable in both sexes

but much more pronounced in ♂♂, who compete sexually. Both sexes with glandular abdominal pouch situated anterior of the vulva or penis; this glandular zone is ca. 55 mm long, 20 mm deep, 20–30 mm wide when open, and oozes yellowish liquid with an odour that is relatively faint to the human nose. Males have a penis bone (illustrated in detail by Didier [1948]). Two pairs of nipples.

Differs from all other carnivores in the persistence throughout life of the cartilaginous condition of the posterior chamber of the auditory bulla. Consequently, the paroccipital processes have no bone to attach to, making them conspicuous and a characteristic feature of the skull. The postorbital bars are incomplete, and represented by well-developed supraorbital processes and smaller processes on the zygomatic arches; the supraoccipital crest is well developed (Rosevear 1974, Skinner & Chimimba 2005). Dental formula: $I^{3/3}, C^{1/1}, P^{4/4}, M^{2/2} = 38$. Out of 121 specimens 91 had a normal dental formula, but ten missed both M^2 , four the right M^2 , two the left M^2 , one both M^2 , one both M^2 and right M^2 , one left P^1 , one both P^1 , three left P^1 , three right P^1 , two both P^1 , one both M^2 and both P^1 . One specimen missed the right M^2 but two had an extra P^1 .

Geographic Variation

N. b. binotata: from Gambia eastwards to Cameroon, Gabon, Congo, Central African Republic and DR Congo. See Description.



Lateral, palatal and dorsal views of skull of Two-spotted Palm Civet
Nandinia binotata.

N. b. gerrardi: S and E Tanzania, Mozambique, Malawi, NE Zambia (Nyika Plateau) and E Zimbabwe. Presumably also the form on Zanzibar. Three black stripes on neck absent; body more sparsely and finely spotted; light shoulder spots less distinct; dark rings on tail narrower, closer together and more sharply defined.

N. b. arborea: Uganda, Kenya and N Tanzania (Mts Kilimanjaro and Meru, and Eastern Arc Mts). Black stripes on neck narrower; absence of spots on the lower sides of the body; dark rings on tail narrower.

N. b. intensa: Angola, S DR Congo and NW Zambia (Mwinilunga District). Colour both dorsal and ventral much redder and brighter; spots intense black; light shoulder spots more conspicuous.

Schouteden (1945), after examining more than a hundred skins, was convinced that *intensa* and *gerrardi* had no systematic value and were synonyms of the nominate race. The boundaries between *gerrardi* and *arborea* are also poorly resolved: photos of specimens taken in the Udzungwa Mts show no white shoulder spots and also no white spots on the lower sides of the body, while others show relatively clear shoulder spots. The retention of four subspecies here is provisional.

Similar Species

Civettictis civetta. Wide distribution in sub-Saharan Africa. Substantially larger and terrestrial; black band across front of face and prominent neck stripes; tapered bushy tail half the length of head and body.

Genetta spp. Smaller, lighter and sleeker; no yellow spots on shoulders. Genet footpads fringed with hair; tail more distinctly annulated.

Distribution Endemic to Africa, ranging in the west and central African forest belt from Gambia to SW Sudan, Uganda and W Kenya south through the Congo basin to N Angola (southern limit ca. 9° S; Crawford-Cabral 1989a) and NW Zambia (Mwinilunga District; see Ansell 1978). They are more discontinuously distributed in eastern



Nandinia binotata.

and southern Africa in both montane and lowland forests of Tanzania, NE Zambia (Nyika Plateau region; see Ansell 1978), most of Malawi, E Zimbabwe and western parts of Mozambique (southern limit 20° 45' S; Smithers & Lobão Tello 1976). Occurrence on Bioko I. mentioned by several authors (Krumbiegel 1942, Basilio 1962, Eisentraut 1973). Recently observed on Zanzibar (Perkin 2004, 2005).

Habitat Deciduous forests, lowland rainforests and mountains up to 2500 m (2400 m in the Udzungwa Mts and up to 2500 m on the Mbeya range in Tanzania [D. De Luca pers. comm.]), gallery and riverine forests, savanna woodlands and logged and second-growth forests. Able to thrive in cultivation mosaic following forest clearing and known to visit cultivated fields bordering forest edge.

Abundance Widespread and locally abundant. Probably the most common African forest small carnivore, although few field censuses have been undertaken. In Gabon minimum average density estimated at ca. 5/km² with higher averages for inundated forests and river borders (8/km²) than for non-inundated primary forest (4/km²) where fruit yields were lower. Biomass estimated at close to 11 kg/km² – much higher than that of the more carnivorous sympatric carnivores, such as genets and linsangs (Charles-Dominique 1978). In Bwindi Impenetrable N. P., SW Uganda, average density was higher (3.3/km²) above 2000 m than below 1800 m (2.2/km²); higher density deeper into the park than in the periphery could mean they favour areas with minimal human presence (Andama 2000).

Adaptations Nocturnal and arboreal. Preference for heights between 5 and 35 m, possibly rarely going higher than 40 m. Usually uses larger branches and lianas (90% 1–30 cm diameter) with preference for those that are horizontal or obliquely inclined. Comes to the ground to cross deforested areas (Charles-Dominique 1978), or to forage, and is commonly captured in terrestrial traps. During the day, rests on thick horizontal branches or in dark and secluded



Two-spotted Palm Civet *Nandinia binotata*.

holes or crevices formed by vegetation 12–15 m in height. Sick or severely wounded animals sleep on the ground (Charles-Dominique 1978).

Both fore- and hindlimbs plantigrade. When walking on a branch the forefeet, when brought forward, are usually partially supinated. Adaptations to agile arboreal climbing are the large, soft and finely ridged palms on both fore- and hindfeet. The heels or tarsi of the hindfeet bear deeply carunculated, transversely ridged pads of thick skin that serve as friction pads. Able to climb a smooth post and descend head first by 'vertical looping', i.e. gripping the trunk, spread-eagled, with claws and hairless pads of forefeet, then bringing both hindfeet forward until they touch the forefeet (Taylor 1970a, 1974, 1976). Tail is used as a balancing rod when walking thin branches, and although not prehensile, can be wrapped around branches for support. Able to walk on steel wire (Van Rompaey 1997) and jump across gaps of about 1 m as well as jump as high as 1.8 m (Taylor 1970a; H. Van Rompaey pers. obs.). Thorneycroft (1958) observed an individual 'volplaning' several times from a high branch, with extended tail and legs stretched out, and making a perfect four-point landing.

Foraging and Food Predominantly frugivorous, although known to forage opportunistically for vertebrates and insects. In Gabon, 86% of 22 digestive tracts contained fruit and 32% yielded mammals, bird eggs, or insects. An average stomach contained ca. 75 g of fruit, while prey made up about 20% of fresh weight contents (Charles-Dominique 1978). In Zimbabwe, 60% of the stomachs ($n = 10$) contained vegetable matter, 30% bird remains, 10% murids and 10% Isoptera (Smithers 1983). In Central African Republic remains of eight scats contained ca. 44% fruit, 25% arthropods and 15% mammals (Ray & Sunquist 2001). In Uganda scats contained remains of bird's eggs (28.8%), wild fruits (24.3%), insects (20.3%) and rodents (20.2%) (Andama 2000). In the East Usambaras, scats had a high proportion of millipedes and fruit material of several plant species (N. Cordeiro pers. comm.).

Two-spotted Palm Civets are frequent raiders of crops and poultry (Naughton-Treves 1998, Skinner & Chimimba 2005). An individual in E Zimbabwe was killed after it had attacked and killed five full-grown turkeys; the stomach contained remains of a young turkey (J. M. Hutton pers. comm.). A captive killed a Potto *Perodicticus potto* and attacked a sleeping half-grown Mona Monkey *Cercopithecus mona* (Ewer

1973). In Cameroon a wild Potto was also attacked and eaten (Pimley 1999). Charles-Dominique (1977) observed on two occasions a fight between an adult Potto and a young Two-spotted Palm Civet; both times the carnivore gave up the struggle. Decher *et al.* (2010) observed an individual in Sierra Leone catching a small fruit bat, possibly Peter's Dwarf Epauletted Fruit Bat *Micropteropus pusillus* or Veldkamp's Bat *Nanonycteris veldkampii*. Also known to eat carrion (Bates 1905).

In attacking wild prey extensive use is made of the forefeet. Prey is usually taken with the forefeet and pressed to the substratum or held and bitten in quick succession all over the body until dead (Leyhausen 1965). Fruit is generally consumed in 5–10 min, after which the animal rests while stretched out on a branch 10–20 m away; such meals are taken about every two hours. Intestinal transit is fast and fruit is eliminated 2–3 h after it is eaten, its colour and aspect little changed (Charles-Dominique 1978). In Shimba Hills, Kenya, the Two-spotted Palm Civet probably assists the dispersal of at least 12 plant species (Engel 2000).

Captive specimens are reported to show a weakness for alcohol that may originate from consumption of fermented fallen fruit and tree exudates (Kingdon 1977). Widely reputed for drinking palm wine directly from vessels in palm trees in Sierra Leone and throughout the Niger Delta (Thompson 1858, Van Rompaey & Powell 1999).

Social and Reproductive Behaviour Predominantly solitary but young accompany the mother until approaching adult size. When in fruit, the groves of parasol trees *Musanga cecropioides* have been recorded attracting 12–15 individuals, sometimes several individuals into the same tree at the same time (Kingdon 1977). Usually they sleep alone but sometimes a ♂ and ♀ sleep in proximity to one another (Charles-Dominique 1978).

In Gabon Charles-Dominique (1978) recorded that ♂♂ have larger home-ranges than ♀♀: average 85 ha (34–153) vs. 45 ha (29–70). Male home-range size is related to number of available ♀♀ rather than nutritional needs. Although adult male home-ranges often overlap, broadly they consist of distinct sectors. Large ♂♂ will visit all sectors regularly while smaller ♂♂ tend to stay in their own sectors and away from dominant ♂♂. The home-range of a dominant ♂ can cover the home-ranges of several ♀♀. Adult ♀♀ have clearly delimited home-ranges with very narrow overlap zones along borders only a few metres wide where scent-marks are placed. Immature daughters remain with their mothers. Young ♂♂ seem to leave the maternal home-range as soon as they are weaned and inhabit a sector in the home-range of the dominant ♂. Their home-ranges being large, dominant ♂♂ seldom meet, but when they do fights can be very violent and the loser may die from his wounds. Such sexual competition appears to accentuate weight loss or gain, with dominant ♂♂ often becoming heavy while the surviving loser becomes thinner with smaller testicles and perineal glands, symptoms of social stress. Adult ♂♂ and ♀♀ and immature animals may feed at the same time at the same fruit tree, with ♀♀ having priority access to the food (Charles-Dominique 1978).

Scent-marking plays a role in communication and marking. The perineal gland is rubbed on branches while the hindlegs are flexed and the odour can persist for several months (Charles-Dominique 1978). Between the third and fourth toe of each foot there is a glandular pocket overlain with a patch of yellow fur, presumably also used to apply scent to trails and particularly to the scratch marks on bark (Vosseler 1928).

A dominant ♂ and neighbouring ♀ communicate with a loud cry, a plaintive 'hou' repeated five or six times, which can be heard over a distance of nearly 1 km. In Gabon such calls were at their maximum in Jun when one ♀ was found in oestrus (Charles-Dominique 1978). The same calls, called 'hooting' by Wemmer (1977), were made several times a night by two young captive ♂♂ up to the age of ca. one year (H. Van Rompaey pers. obs.). During courtship a captive pair produced apparently friendly close-range sounds, akin to coughing (Peters 1984).

Reproduction and Population Structure Births in Gabon occurred chiefly from Sep to Jan (long wet season and beginning of short dry season), occasionally in other months, but none was observed during Mar–Jun (Charles-Dominique 1978). In Côte d'Ivoire, a birth was noted in Oct (Bourlière *et al.* 1974). A ♀ captured in Zimbabwe in Jul had two foetuses (Smithers & Wilson 1979) while in Zambia Ansell (1960a) recorded a month-old juvenile in Oct.

Usually two young are born after a gestation of ca. 64 days; there are two litters per year (Rettig & Divers 1978). Weight ca. 56 g at birth, and young are born with eyes and ears closed. Will accompany mother to visit fruit trees as soon as able (Charles-Dominique 1978). Adult size and weight attained at 6–9 months (Happold 1987).

A captive specimen lived to 16 years and 5 months (Van Rompaey 1997) and a longevity survey listed a record of 21 years (Weigl 2005). Longevity in the wild is probably considerably less.

Predators, Parasites and Diseases Presumed to be preyed upon by larger carnivores, birds of prey and pythons. Preyed on by Leopards *Panthera pardus* in Gabon (Henschel *et al.* 2005) and Congo (Ososky 1998), and occasionally by the very arboreal African Golden Cat *Profelis aurata* in Cameroon (T. R. B. Davenport & G. Ngandjui, pers. comm.).

The following parasites have been recorded: a parasitic nematode *Kalichephalus* sp. in a captive specimen (Herman 1939); *Rictularia proni* and *R. dollfusi* in the intestines of specimens from Congo (Chabaud & Rousselot 1956, Vuylsteke 1956); *Cercopithifilaria corneti* in the subcutaneous tissues of a specimen from Central African Republic (Bain *et al.* 1987); and *Setaria* sp. in a stomach tumour (Walton 1927); nymphs of *Armillifer armillatus* in the coelomic cavity of a specimen from Cameroon (Heymons 1940); and *Trichinella britovi* from two (out of 45 examined) specimens in Guinea (Pozio *et al.* 2005). The louse *Felicola hopkinsi* (Werneck 1948) was recorded from an animal in Uganda. Ticks recorded include *Haemaphysalis (Rhipistoma) moreli* and *H. (R.) punctaleachi* in DR Congo (Camicas *et al.* 1972, 1973) and *Ixodes moreli*, *I. rarus* and *I. oldi* (Arthur 1965, Keirans *et al.* 1982).

Two-spotted Palm Civets inoculated with yellow fever virus either showed neutralizing antibodies for a while or developed a durable immunity (Dick 1952). The serum of a specimen from Kenya tested for complement-fixing antibodies reacted significantly to *Coxiella burnetii* (Heisch *et al.* 1962). Microfilariae are listed by Rewell (1948). Trypanosomes responsible for sleeping sickness, including *Trypanosoma brucei* non-gambiense group 1, *T. b. gambiense* group 1, and *T. vivax*, have been found in specimens from S Cameroon (Herder *et al.* 2002).

An old captive individual developed trophic ulcers of the tail, caudal cellulitis and died of septicaemia (Hamerton 1945); another suffered from rachitis and osteodystrophia and died of broncho-pneumonia (Hamerton 1941). Lovell (1930) described the lesions of an individual that died from tuberculosis; McKinney (1970) described lesions of hyaline arteriolosclerosis in a wild-caught specimen from East Africa.

Being arboreal the Two-spotted Palm Civet is prone to falls and fractures: a wild-caught individual had a clean break across its right femur and a fractured patella, both of which had healed (Taylor 1971b).

Conservation IUCN Category: Least Concern. CITES: Not listed. Although widely distributed, and present in many protected areas across its range, the close association of the Two-spotted Palm Civet with closed-canopy forest suggests vulnerability in the face of total deforestation, particularly in eastern and southern Africa, where the species' range is already fragmented. Two-spotted Palm Civets are commonly trapped, shot or persecuted by humans when raiding chicken coops or fields (see Campbell [2009] for results of a study of human reactions to the species in Ghana), as bushmeat, and for traditional medicine. They were the most common carnivore recorded (60% of 121 carcasses) in two markets in Rio Muni, Equatorial Guinea (Juste *et al.* 1995) as well as in Guinea (Colyn *et al.* 2004). In Kisangani region, DR Congo, they represented 10% of small carnivores trapped as bushmeat (Colyn *et al.* 1987), and in SE Cameroon 30.6% of carnivores trapped for bushmeat and 16.5% of trapped carnivore biomass (Ngandjui 1998, T. R. B. Davenport & G. Ngandjui pers. comm.). They are also hunted for meat in some parts of Uganda (Andama 2000). In Congo and Gabon, the fur is eagerly sought after to make ceremonial dresses (Malbrant & Maclatchy 1949) and in NE DR Congo to make wrist-bracelets, hats and to cover the bow (Carpaneto & Germe 1989).

Measurements
Nandinia binotata
HB (♂ ♂): 486 (398–625) mm, n = 34
HB (♀ ♀): 457 (370–610) mm, n = 38
T (♂ ♂): 538 (430–762) mm, n = 34
T (♀ ♀): 504 (340–701) mm, n = 38
HF c.u. (♂ ♂): 88 (76–100) mm, n = 29
HF c.u. (♀ ♀): 82 (66–95) mm, n = 36
E (♂ ♂): 39 (29–48) mm, n = 28
E (♀ ♀): 37 (27–43) mm, n = 35
WT (♂ ♂): 2.09 (1.30–3.00) kg, n = 18
WT (♀ ♀): 1.94 (1.20–2.70) kg, n = 19
GLS (♂ ♂): 100.6 (86.4–110.9) mm, n = 24
GLS (♀ ♀): 94.7 (84.4–103.2) mm, n = 30
GWS (♂ ♂): 57.2 (53.2–62.7) mm, n = 22
GWS (♀ ♀): 52.7 (47.3–58.4) mm, n = 29
Museum specimens (AMNH, BMNH, IRSN, FMNH, MNHN, NMNH, PCM, SBP, SMNS, MRAC, and ZMB)
Body measurements recorded by Smithers & Wilson (1979) are similar to the ranges given here

Key References Charles-Dominique 1978; Kingdon 1977; Rosevear 1974.

Harry Van Rompaey & Justina C. Ray

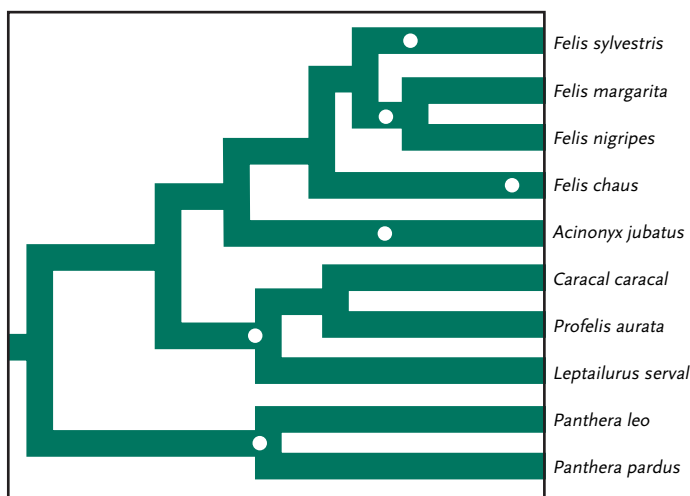
Family FELIDAE
CATS

Felidae Fischer de Waldheim, 1817. Mém. Soc. Imp. Nat. Moscou 5: 372.

| Felinae | | |
|--------------------------------|--------------------|--------|
| <i>Panthera</i> (2 species) | Roaring Cats | p. 148 |
| <i>Profelis</i> (1 species) | African Golden Cat | p. 168 |
| <i>Caracal</i> (1 species) | Caracal | p. 173 |
| <i>Leptailurus</i> (1 species) | Serval | p. 179 |
| <i>Acinonyx</i> (1 species) | Cheetah | p. 186 |
| <i>Felis</i> (4 species) | Small Cats | p. 196 |

The cat family, Felidae, is a morphologically highly uniform family of hypercarnivores, to the extent that if soft tissues are removed it is a specialist task to distinguish between such externally different species as the Lion *Panthera leo* and Tiger *P. tigris*. An important cause of this uniformity is the relatively young age of the subfamily Felinae, to which all living cats belong. This subfamily probably originated no more than about 11 mya (Johnson *et al.* 2006). As shown by the fossil record, however, felids are older and have been highly diverse: living cats are simply a restricted subset of this variation. The phylogeny and evolution of the Felidae has long been a contentious issue, especially as regards the living cats. Various ideas regarding the interrelationships of living cats were summarized in Werdelin (1996b). Johnson *et al.* (2006) carried out an extensive molecular study of cat phylogeny and have updated this issue. In their view, living cats can be subdivided into eight major clades (Panthera lineage, Bay Cat lineage, Caracal lineage, Ocelot lineage, Lynx lineage, Puma lineage, Leopard Cat lineage and domestic cat lineage). These

split off sequentially from the ancestral forms between ca. 11 and ca. 6 mya. Four of these clades have African representatives, the Panthera lineage (Lion and Leopard *P. pardus*), the Caracal lineage (Caracal *Caracal caracal*, Serval *Leptailurus serval*, African Golden Cat *Profelis aurata*), Puma lineage (Cheetah *Acinonyx jubatus*) and domestic cat lineage (Wildcat *Felis silvestris*, Sand Cat *F. margarita*, Swamp Cat *F. chaus*, Black-footed Cat *F. nigripes*). Of these, the Caracal lineage appears to be an endemic African group, with the Caracal only recently spreading to south-western Eurasia and the Indian sub-continent. This new, molecular perspective on cat phylogeny has also had an impact on taxonomy within the family, long a subject of dispute. In the primary taxonomic literature, genus-level names have proliferated (see summary in Werdelin 1996b), but it has been and still is common to see cats classified into only three genera: *Acinonyx* (the Cheetah), *Panthera* (the large 'roaring' cats) and *Felis* (all other cats). However, the study by Johnson *et al.* (2006) has shown, definitively, that this cannot be maintained. The Cheetah is related to the Puma *Puma concolor* and Jaguarundi *P. yagouaroundi* and is not distinct from other cats, and there are a number of lineages that despite the apparent morphological uniformity are as old as any lineages in other carnivore families and should therefore be accorded distinct generic names. Above the genus level, the taxonomy of cats has been equally contentious. Wozencraft (2005) has divided the family Felidae into two subfamilies, Pantherinae, including the large cats of the genera

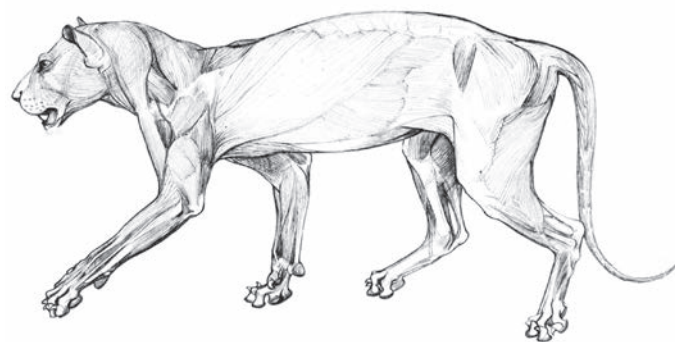


Tentative phylogenetic tree for African Felidae; at least 6 separate ancestral immigrations shown (O) (adapted from Johnson *et al.* 2006).

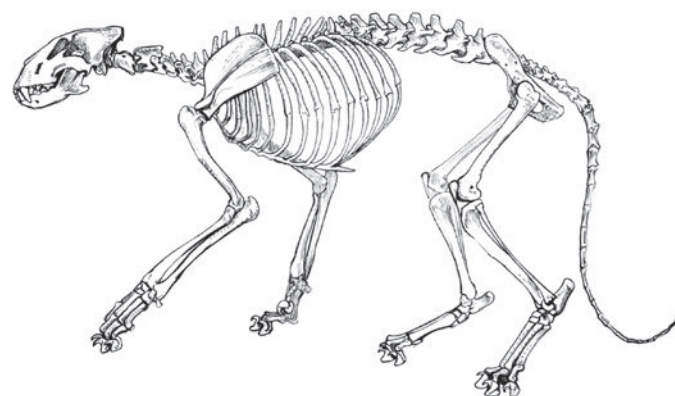
Panthera, *Uncia* and *Neofelis*, and Felinae, including all other living cats. Such a subdivision is compatible with the recent phylogeny of Johnson *et al.* (2006). However, as noted, fossils show that the modern radiation of cats is a subset of the full variation within the family and the same authors have shown the radiation of modern cats to be no older than late Miocene. Division at the subfamily level is, therefore, not tenable for modern cats as it would, among other difficulties, require raising various groups of sabre-tooth cats into separate families. A subdivision compatible with the fossil record is lowering the rank of the two above-mentioned groups to the tribes Pantherini and Felini, with all living cats placed in the subfamily Felinae.

In the African fossil record representatives of the living cats are relatively rare compared with sabre-toothed cats (of the subfamily Machairodontinae). The geologically oldest cat in Africa is *Asilifelis* from the late early Miocene site of Rusinga Island, Kenya (Werdelin 2012). This taxon is of unknown relationships and origin. The continuous record of cats in Africa begins in the late Miocene (ca. 10 mya), with the appearance of sabre-tooth cats with clear antecedents in Eurasia. Fossil Felinae appear at about the same time, but remain rare in the fossil record until the Pleistocene (last 1.5 my). Sabre-tooth cats are known from a number of late Miocene sites in Africa (e.g. Werdelin 2003a). In the Pliocene, all three major lineages occur: *Homotherium*, a large genus with some cursorial adaptations, is quite ubiquitous, being found from 4 mya until about 1.5 mya. The smaller, more forest adapted, *Megantereon* occurs in only a handful of sites between 3.5 and 1.5 mya. *Dinofelis*, the commonest sabre-tooth cat in Africa, made a substantial radiation, beginning about 6 mya (Werdelin & Lewis 2001). It might have been the last sabre-tooth cat to become extinct in Africa (with a last appearance at about 1 mya). Small cats belonging to the modern Felinae make their first appearance about 4.1 mya (Werdelin 2003b). Large cats of the genus *Panthera* first appear about 3.85 mya at Laetoli in Tanzania (Werdelin & Deghhani 2011), but are subsequently very rare in the fossil record until the end of the Pliocene, ca 1.8 mya, after which they become somewhat more common, possibly as a result of the extinction of large sabre-tooth cats.

Living cats vary greatly in size, from about 2–3 kg in the Black-footed Cat, the Kodkod *Leopardus guigna* and the Rusty-spotted Cat *Prionailurus rubiginosus* to about 300 kg in a large male Tiger. Sexual



Lion *Panthera leo* myology.



Lion *Panthera leo* skeleton.

dimorphism is limited but ubiquitous, with males in most species being about 5–10% larger than ♀♀ (although difference in mass between sexes is greater, as much as 25–100%; see Sunquist & Sunquist 2002). Body shape does not vary dramatically in cats, though differences can be noticeable when comparing, for example, the Cheetah with the lynxes. In general, however, differences between living cats in this respect are slight, while the difference in body shape between living cats and sabre-tooth cats is much greater (Martin 1980, Martin *et al.* 2000).

The karyotype of all cats is $2n = 38$, except in the Ocelot lineage (though the Kodkod and Andean Mountain Cat have not yet been karyotyped), where it is $2n = 36$ as the result of a fusion of two F group chromosomes into a metacentric C3 (Collier & O'Brien 1985). Cat evolution has been marked by a number of rare insertions and deletions of genes and gene families that help systematists to characterize the various cat lineages (summarized in Johnson *et al.* 2006).

All cats, living and extinct, are hypercarnivores, and this is reflected in their shared fundamental adaptations, some of which are outlined below. The basic dental formula of the living Felidae is $I^{3/3}, C^{1/1}, P^{3/2}, M^{1/1} = 30$ (although some species, notably the genus *Lynx*, retain only two premolars in the upper jaw; Russell *et al.* 1995). Primitive fossil cats had a fuller complement of teeth, but dental reduction went further in some sabre-tooth cats, with loss of the anterior premolar in the mandible as well as in the upper jaw (Turner & Antón 1997).

The skull in small cats is rounded, while in large cats it is more elongated, with a more extended muzzle. The orbital space in the skull is large and faces more or less forwards. It is normally open to

the side, though in many cases, especially in small cats, it can be closed by cartilage. The zygomatic arches flare, leaving room for large temporal muscles, which make up the main masticatory musculature. Small cats show only limited sagittal and nuchal crests, but these are much more prominent in the larger cats. The presence of extensive crests and elongated canines in the relatively small Clouded Leopard combine with its position at the base of the molecular tree to suggest that this species evolved from larger ancestors. By contrast, less extensive crests in the larger Puma suggests that it evolved from smaller ancestors (Werdelin 1983).

All cats are digitigrade and have five toes on the forefoot and four on the hindfoot. The forelimbs of cats have dual functions; they are, of course, part of locomotion, but they also function in prey capture. These two functions are often at odds with each other, since a forelimb that has optimal running ability cannot also have optimal grasping ability. While the forelimbs of other cats are primarily adapted to grasping and prey capture, the Cheetah forelimb has evolved specializations for high-speed locomotion (Andersson 2004). All cats have protractile claws (they are retracted in the resting position)

that are protected in a fleshy sheath when retracted. The sheaths are vestigial in the Cheetah (as well as in Fishing Cat *Prionailurus viverrinus* and Flat-headed Cat *P. planiceps*) such that the claws protrude visibly.

The tail is of variable length in cats. Some cats, such as the Leopard and Cheetah, have very long tails that serve an important function in counterbalancing the weight of the body when climbing or running. Other cats, such as the lynxes and the Caracal, have short tails. The functional basis for this reduction is not fully understood. The shortening of the tail is due to a combination of a (slight) reduction in the number of vertebrae in the tail and a (considerable) decrease in the size of the individual vertebrae.

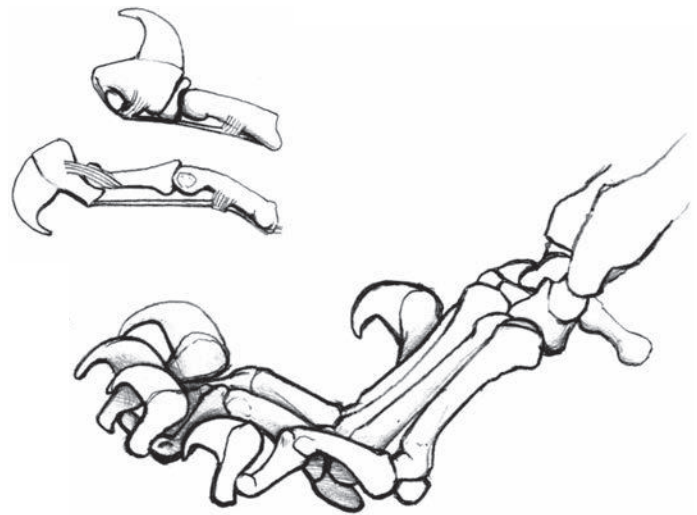
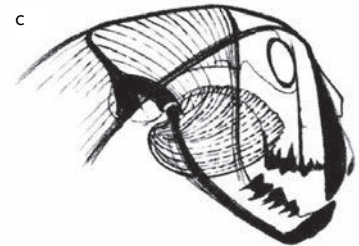
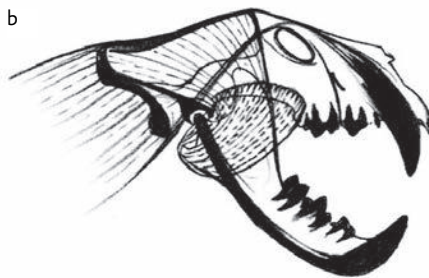
Though still important, the sense of smell is less important in cats than in other carnivores, as shown by the fact that the areas of the brain concerned with processing smell are smaller in cats than in most other carnivores (Radinsky 1975b). Further, the olfactory epithelium in cats has less surface area than in, for example, dogs. The relative reduction in the sense of smell in cats is to some degree compensated for by the whiskers or vibrissae. These are specialized sensory hairs with an important tactile function, which can be clearly seen in walking cats, which extend the whiskers on the muzzle forwards to feel the surroundings. This function is particularly important for cats that hunt at night: hence the Cheetah, which strictly hunts by day, has less developed whiskers than other cats.

Prominent features in the eyes of domestic cats are the pupils, which reduce to vertical slits in strong light. However, not all wild cats have vertical, slit-like pupils. Many species, especially among the larger cats, have round pupils. Exactly why some cats have one or the other is not well understood, but slit-like pupils possibly confer an advantage to animals that hunt in poor light, as this allows for a greater range of pupil



ABOVE: Skull and cranial musculature of Leopard *Panthera pardus*.

BELOW: Skull architecture in: (a) *Megantereon cultridens* (stabbing strike); (b) Lion *Panthera leo* (canine bite); (c) Cheetah *Acinonyx jubatus* (clamp stranglehold).



ABOVE: Mechanism for extension and retraction of felid claws.



Lion *Panthero leo* facial expression.

size, from extremely large by night to almost entirely closed in bright daylight. Preliminary study (Werdelin *et al.* 2010) shows that round pupils are never found in animals that are specialized for hunting in closed environments. The latter animals are more likely to hunt in poor light condition, lending some credence to the theory. This is only one of several adaptations in cats to activity in poor light conditions. Another is the pre-eminence of light-sensitive but colour-insensitive rods in the eye, which improves night vision but not sensitivity to colour. A third is the presence of a reflecting layer, the tapetum lucidum, in the back of the eye. Visual acuity varies in cats. Some have a relatively broad, rounded area of maximum visual acuity on the retina (the so-called visual streak). Species that hunt by sight, such as the Cheetah, often need to detect prey moving against the horizon, and their visual streak is a narrow line across the retina (Hughes 1977, 1985).

Hearing is an important sense in cats. They can hear a much wider range of sounds than humans, with the practical range being somewhere between 200 Hz and 65 kHz. The ability to hear very high frequency sounds is especially useful to small cats, as it allows them to detect the ultrasonic communication of small rodents. Since these sounds are of very low intensity, the external ear is large in some species, such as the Serval and Sand Cat. The large ear allows these cats not only to hear low-intensity ultrasounds, but also to detect the sound of small rodents running through the undergrowth. In the skull, the chamber surrounding the ear ossicles, the so-called

auditory bulla, is large in all cats. This is especially true of desert cats (and, indeed, of other desert animals). It is believed that such a large bulla enhances auditory acuity in the desert situation, where the ambient sound level is much lower than in other biotopes.

Members of the cat family are typically solitary, but they are sometimes found in pairs or larger groups, the most social species being the pride-living Lion. Communication is mainly by means of vocal, visual and chemical signals. Most species are nocturnal, but many also are active by day, and some, such as the Cheetah, do most of their hunting during the early hours of the morning and late afternoon, largely to avoid competition with other larger predators. Females are polyoestrus and although copulations are often brief, there may be repeated copulations over a short period of time (Lions, for example, have been recorded copulating 157 times over a 55-hour period; Schaller 1972). It is thought that repeated copulations may be necessary to induce ovulation, although male cats have a baculum and penile spines, suggesting a connection between sexual stimulation and ovulation (Sunquist & Sunquist 2002). Gestation length in felids varies greatly depending upon body size, with larger species having longer gestation periods, and litter-size is usually in the order of 2–3 young, although litter-sizes of as many as eight have been recorded in the Cheetah and the Sand Cat.

Lars Werdelin

Subfamily FELINAE – Cats

Felinae Fischer de Waldheim, 1817. Mém. Soc. Imp. Nat. Moscou 5: 372.

Contra the classification of Wozencraft (2005), the subfamily Felinae is here taken to include all living cats, comprising two tribes: Pantherini (for cats of the genera *Panthera* and *Neofelis*), and Felini (for the remaining members).

Tribe PANTHERINI – Roaring Cats

Pantherini Pocock, 1917. Ann. Mag. Nat. Hist., ser. 8, 20: 332.

Tribe Pantherini includes the larger-bodied cats of the genera *Panthera* and *Neofelis*. Only *Panthera* is represented in Africa (two species); *Neofelis* (clouded leopards) is Asian.

GENUS *Panthera*

Roaring Cats

Panthera Oken, 1816. Lehrb. Naturgesch. 3 (2): 1052.

The genus *Panthera*, often called the roaring cats, includes the largest members of the family. Two species, the Lion *Panthera leo* and Leopard *P. pardus*, occur in Africa; the other three species, Tiger *P. tigris*, Jaguar *P. onca* and Snow Leopard *P. uncia*, are extralimital. All species are united by the presence of an ossified hyoid bone, which gives them the ability to roar, hence the popular name (Pocock 1916d, Peters 1978, Peters & Hast 1994). The long-fanged Clouded Leopard is related to the aforementioned species, but is generally placed in a separate genus, *Neofelis*.

A recent molecular analysis by Johnson *et al.* (2006) has shown ancestral Clouded Leopards *Neofelis*, closely followed by an ancestor to the *Panthera* lineage, to be the first lineages to branch out from the main stem of emergent Felinae, some 11–10 mya. The inference that large cats emerged earlier than the smaller species has long had some support but apparently contradicts the fossil record because all known

Miocene Felinae fossils are small. However, the same study found that the radiation of modern species of *Panthera* is recent, mainly taking place in the late Pliocene, 3–2 mya. This accords well with the fossil record, as the oldest *Panthera* fossils come from Laetoli, Tanzania, with an age of 3.85–3.63 million years (Werdelin & Dehghani 2011).

The coat pattern of *Panthera* species is of spots characteristically placed into rosettes, the form and visual function of which have been analysed in some detail by Kingdon (1977), and see Volume I pp. 121–122, who suggested that this pattern type must have been developed in the common ancestral stock of Leopards, Lions and Tigers (the latter still exhibiting every graduation from lozenge-shaped rosettes to full stripes). Werdelin & Olsson (1997) have also suggested that the stripes of the Tiger may be very elongated rosettes.

Lars Werdelin



Leopard *Panthera pardus* spot patterns around eye and mouth.

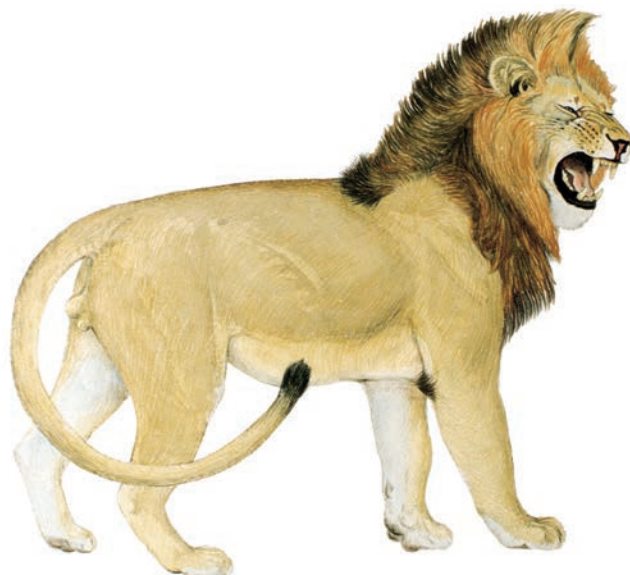


Lion *Panthera leo* skinfolds between nostrils and eyes during 'snarl'.

Panthera leo LION

Fr. Lion d'Afrique; Ger. Lowe

Panthera leo (Linnaeus, 1758). Syst. Nat., 10th edn, 1: 41. 'Africa', restricted by J. A. Allen (1924: 222) to 'the Barbary coast region of Africa, or, more explicitly, Constantine, Algeria'.



Lion *Panthera leo* male.

Taxonomy More than 20 subspecies have been described from parts of the African continent, many of which were based on specimens from zoological gardens. Since captive conditions influence skull shape (Hollister 1917), such specimens have little value for basing taxonomic descriptions. Many authorities have not recognized subspecies (Ellerman *et al.* 1953, Smithers 1975, Meester *et al.* 1986), although Hemmer (1974a) recognized seven subspecies in Africa, as did Nowell & Jackson (1996). Few quantitative data exist on the differences between the subspecies, and, in general, while isolation of Lion populations causes a loss of genetic heterozygosity in some areas (Wildt *et al.* 1987) and significant genetic differences between subspecies may exist (S. J. O'Brien pers. comm.), subspecies are morphologically indistinct. O'Brien *et al.* (1987) found that populations from the Serengeti and Kruger National Parks were so genetically similar as to warrant inclusion in a single African race, *P. leo leo*. Subsequent genetic evidence has supported distinction between an African – Asian subspecies (Dubach *et al.* 2005, Antunes *et al.* 2008). However, this seems less well supported by studies including better sampling from West and central Africa, which show a clear distinction between West and central African Lions (including India) on the one hand, and southern and East African lions on the other (Bertola *et al.* 2011). Synonyms (Africa only): *africana*, *azandica*, *barbara*, *barbarica*, *bleyenberghi*, *bleyenberghi*, *capensis*, *gambiana*, *hollisteri*, *kamptzi*, *krugeri*, *maculates*, *massaica*, *melanochaita*, *melanochaeta*, *nigra*, *nobilis*, *nubica*, *nyanzae*, *roosevelti*, *sabakiensis*, *senegalensis*, *somaliensis*, *vernayii*, *webbiensis*. Chromosome number: $2n = 38$ (Wurster & Benirschke 1968).

Description The largest of Africa's carnivores, and second largest member of the family Felidae (after the Tiger *Panthera tigris*), standing as much as 1.25 m at the shoulder. Body muscular and deep-chested;

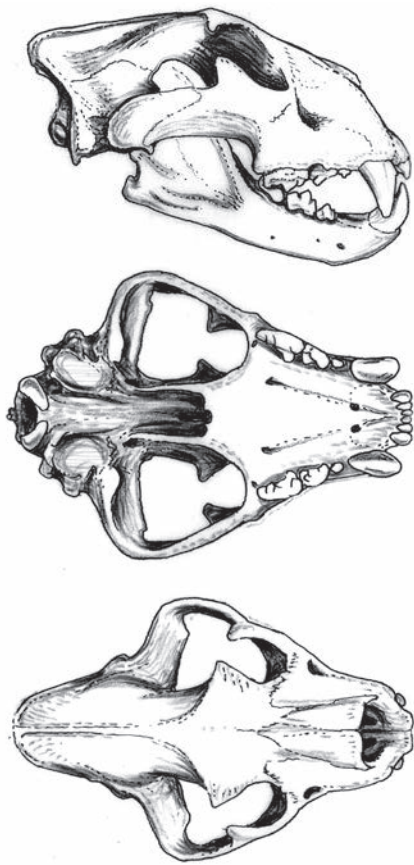
head relatively short-muzzled and round-faced with prominent whiskers and white chin. The base of each whisker, or vibrissa, is visible as a dark spot 1–2 mm wide and the majority of vibrissae are organized into 4–5 horizontal rows on either side of the muzzle. The random spots found above the top row of whiskers act as 'fingerprints' that distinguish individuals (Pennycuik & Rudnai 1970). Ears relatively small and round, and often scarred; backs of the ears black in sharp contrast to the remainder of the body. Eyes vary from pale yellow to dark brown.

Dorsal pelage ranges from pale gold to amber, with pale or white inner limbs and ventral surface. Young animals are spotted with rosettes that fade at maturity. Some adults retain vestigial spots on abdomen and legs. Dorsal pelage short and dense. A reversal in the direction of growth of the hair on the upper parts in the lumbar region forms a short transverse crest of upstanding hair when it meets the opposite-growing hair about the mid-dorsal region. Adult ♂♂ are distinguished by a mane of longer hair covering the head, neck, chest, elbows and occasionally belly. Considerable variation occurs in the extent of mane coverage with 'maneless' prime-aged ♂♂ common in some regions. Mane colour varies from platinum to black and is often patchy with lighter hair surrounding the face. Variation in mane characteristics occurs both within and between populations. Growth of mane begins in subadult ♂♂ at approximately 6–8 months in some habitats, but appears to be delayed in warmer climates (West & Packer 2002, Gnoske *et al.* 2006).

Limbs heavy and muscular, ending in large padded feet. Front feet with five digits of which the first is set well back, not marking in the spoor; hindfeet with four digits. All digits equipped with sharp, retractable claws. Tail thick, muscular and tapered, and just over half the length of head and body. Tail tip has tuft of long, dark or black hairs concealing a horny spur present in some animals (Schaller 1972). There are anal glands present, with ducts opening either side of the anus. Sexual dimorphism pronounced in size (perhaps more so than in any other terrestrial carnivore) as well as pelage; adult ♂♂ are typically 30–50% larger than adult ♀♀. Females have two pairs of nipples, very rarely three (Ewer 1973).

In profile, the skull is comparatively flat on top compared with that of the Leopard *Panthera pardus*. The highest point of the skull lies between the postorbital process from where it slopes off gradually forwards to the nasals and rather more abruptly to the supraoccipital crest. Postorbital processes broad and incomplete. Skull high and wide relative to overall length, and braincase small relative to size of skull (and lacks the pear-shaped outward bulge seen in the Leopard). Zygomatic arches broad and robust (providing upper attachment for masseter muscles) and swing outward at the back to allow room for the massive temporalis muscles. Sagittal crest is prominent, substantially deepening the upper attachment of the temporalis muscles. Mandible massive, its processes deeply hollowed out posteriorly to accommodate lower attachments for the masseter and temporalis muscles.

The upper outer incisors are rounded, heavily built and recurved; the lower outer incisors do not reach the same size as those in the



Lateral, palatal and dorsal views of skull of Lion *Panthera leo*.

upper jaw. The upper canines are sharp, slightly flattened on their inner sides, and have a fine longitudinal groove; they are as much as 50 mm in length, only slightly longer than the lower canines. The first lower molar has a sharp edge, which, occluding on the back half of the fourth upper premolar, serves to keep the edges of these two teeth continually sharpened. The small upper first molars, set at an angle to the cheekteeth, become worn on their front edges and while they may assist in keeping food from sliding backwards during the process of slicing, have little or no grinding ability (Ewer 1973, Rosevear 1974, Skinner & Chimimba 2005).

Geographic Variation Although genetic research and much individual variation argue for African Lions being monotypic, regional differences are perceptible and have given rise to an extensive, but not always consistent, nomenclature. The following subspecific names are those listed by Hemmer (1974a) and Nowell & Jackson (1996).

- P. l. azandica* (includes *massaica* partim and *somaliensis* partim): NE DR Congo.
- P. l. bleyenberghi* (includes *bleyenberghi*) (Angolan Lion): Shaba and Kasai woodland Savanna regions of S DRC, and presumably also neighbouring parts of Zambia and Angola.
- P. l. krugeri* (includes *vernayi*) (Transvaal Lion): Kalahari region east to E South Africa.
- P. l. leo* (includes *barbarica*, *barbarus* and *nigra*) (Barbary Lion): coastal woodlands of Morocco through Tunisia. Extinct in the wild.
- P. l. melanochaita* (includes *melanochæta*) (Cape Lion): Cape region of South Africa. Extinct.

P. l. nubicus (includes *hollisteri*, *massaica* partim, *nyanzæ*, *roosevelti*, *sabakiensis*, *somaliensis* partim, and *webbiensis*) (Nubian Lion): north-east and East Africa.

P. l. senegalensis (Senegalese Lion) (includes *gambianus*, *kamptzi* and *nobilis*): West Africa, east to the Central African Republic.

The Asiatic Lion *P. l. persica* is extralimital, and now confined entirely to the Gir Forest in India. The Asian subspecies is characterized by a longitudinal fold of skin running along the belly (Pocock 1930), although this fold is also sporadically present in African populations.

Melanistic forms of the Lion are extremely rare, but very pale ones are known from some regions, such as from Kaokoland, SW Botswana and the Pangani Valley in Tanzania. The 'white Lions' from Timbavati G. R. in the Limpopo Province of South Africa and from Kruger N. P. (McBride 1977, Robinson & de Vos 1982, Smuts 1982) are not albinos; the eyes retain the normal yellow pigment as opposed to the pink-red colour observed in albinos (Cruickshank & Robinson 1997). These Lions represent one of two possible mutations known as chinchilla or acromelanic albinism. Like albinism, these mutations arise from the same gene locus in the individual's chromosomes. The white-coat phenotype likely is inherited in an autosomal recessive manner (Cruickshank & Robinson 1997).

Similar Species

Panthera pardus. Broadly sympatric. Strongly spotted and more lightly built. Possibly immature, faintly spotted Lions could be confused with Leopards.

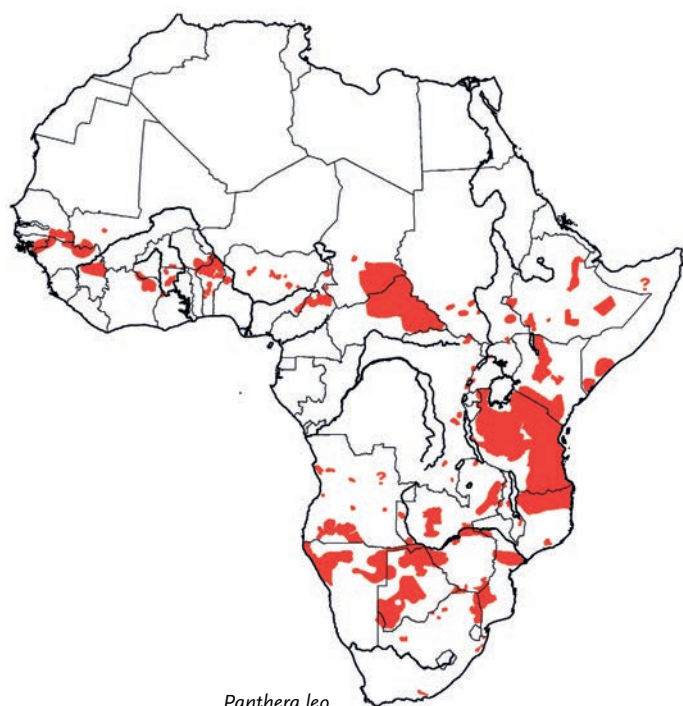
Distribution

Historical Distribution Lions formerly occurred across most of the African continent, except in equatorial forest and the inner regions of the Sahara. From North Africa, their range extended outside of the African continent, ranging through south-west Asia, west into Europe and east to India (Guggisberg 1961, Sunquist & Sunquist 2002, Schnitzler 2011). Based on fossil evidence, during the late Pleistocene, large Lion-like felids (generally considered to be *P. leo* or closely related to it) were distributed across most of Africa, Europe, Asia, North America and the northern part of South America; these Lions became extinct in the Americas and northern Eurasia ca. 10,000 years ago (Turner & Antón 1997; and see Yamaguchi *et al.* 2004a).

Lions were brought to extinction at various points in the Holocene: 3000 BC for temperate Europe; 1000 BC in the south of Greece; 12–13th century in the Near East, Arabian Peninsula, Trans-Caucasia or north of Afghanistan; and 19–20th century for North Africa and the Middle East (Schnitzler 2011).

Current Distribution Today, Lions are extinct in North Africa. They disappeared from the Moroccan coast by the mid-1800s, but may have survived in the High Atlas Mts up to the early 1940s (Cuzin 2003). The last-known Lion in Algeria was killed in 1893 near Batna, 97 km south of Constantine, while the last-known individual was killed in Tunisia in 1891 near Babouch, between Tabarka and Ain-Draham. Lions were extirpated from Tripolitania (N Libya) as early as 1700 (Guggisberg 1961, Nowell & Jackson 1996).

In general, Lions have undergone dramatic range retraction at the limits of the historical distribution: according to Ray *et al.* (2005) they have lost some 83% of their historical range in Africa. They



remain widespread in Africa from the southern Sahara to South Africa, excluding the equatorial rainforest belt, but many previously contiguous populations are now found in isolated enclaves. Populations today are largely restricted to protected areas and surrounding conservancies. There is strong evidence that no resident lion populations remain in Gabon, Congo, Côte d'Ivoire and Ghana (Henschel 2009, Henschel *et al.* 2010).

Extralimital to the African continent, Lions disappeared from Europe around AD 100 and in Palestine around the time of the Crusades (Guggisberg 1961). They remained widespread elsewhere until the mid-1800s when the advent of firearms led to the species' extinction over large areas. The last known Lion in Turkey was killed in 1870 near Birecik on the Euphrates (Üstay 1990), while the last reports from Iran and Iraq date to 1957 (see references in Schnitzler 2011) and 1918 (Hatt 1959), respectively. In India, the last report is of a sighting of a Lion in the Bolan Pass in 1935 (Guggisberg 1961). In India, Lions ranged east to the state of Bihar and Orissa, but by the turn of the century, the Asiatic Lion was confined to the Gir Forest, where it was protected by the Nawab of Junagadh in his private hunting grounds (Kinnear 1920). A detailed review of the former distribution of Lions in North Africa and extraliminally is given by Schnitzler (2011).

Habitat Lions display a wide habitat tolerance, persisting in virtually all habitats with the exception of rainforest and the interior of the Sahara Desert. They occur in semi-desert regions, as in parts of West Africa and in the Kalahari regions of South Africa and Botswana, and even formerly occurred in desert on the edge of Niger's Air Mountains (Rosevear 1974). Lions may range up to 3600 m on Mt Elgon and Mt Kenya (Young & Evans 1993), to 4200 m in the Bale Mts in Ethiopia (Yalden *et al.* 1996), and there is a record of one sighted at 4300 m on Mt Kilimanjaro (Grimshaw *et al.* 1995); formerly recorded to 3000 m in the Moroccan High Atlas (Cuzin 2003). Although they drink regularly if water is available, water is not an essential habitat requirement.

Abundance Data on the overall abundance of Lions are scarce. Two recent estimates put the total population at between 16,500 and 30,000 (Bauer & Van der Merwe 2004) and 29,000 and 47,000 (Chardonnet 2002): tallies from most of the range were 'informed guesses' or their equivalent in most cases (Bauer *et al.* 2005a, b) and should be treated cautiously. Lions are most abundant in East Africa (11,000–16,000) and southern Africa (10,000–20,000), with significantly smaller populations in central Africa (950–3000) and West Africa (850–1400) (Chardonnet 2002, Bauer & Van der Merwe 2004). According to the inventory of Bauer & Van der Merwe (2004), the largest populations in southern Africa occur in the Okavango Delta (1400), Kruger N. P. (2200), and Kafue N. P., Luangwa Valley and Lower Zambezi N. P. (1500); in East Africa, the largest populations occur in the Selous G. R. and surrounds (4500), the Serengeti ecosystem (2500; although, as of 2006, this estimate was revised to 3500, C. Packer pers. obs.) and Tsavo N. P. (675). No population in central Africa or West Africa numbers more than a few hundred individuals, the largest being that in the Benoue ecosystem (200) (Bauer & Van der Merwe 2004; but see Chardonnet 2002). The Asiatic Lion population in the Gir Forest currently stands at ~350 animals (Johnsingh *et al.* 2007).

Lion density is related to seasonal food availability with reported densities ranging from 0.17/100 km² in the Savute region of Botswana's Chobe N. P. (Viljoen 1993) to 1.5–2/100 km² (Kalahari Gemsbok N. P.: Mills *et al.* 1978; Etosha N. P.: Stander 1991), to 10/100 km² in Kruger N. P. (Smuts 1976, Funston *et al.* 2003) and the Serengeti Plains (Hanby *et al.* 1995), to as high as 40/100 km² in the Ngorongoro Crater (Hanby *et al.* 1995). Lions tend to live at densities higher than most other felids.

Adaptations As with all felids, Lions are highly specialized for a carnivorous life-style. Their tawny pelage renders them highly inconspicuous in dry grass and permits them to approach prey without being detected. Strong forearms and heavily muscled limbs enable short, powerful bursts of speed. Powerful jaws, huge canines and canine-like upper outer incisors facilitate the immobilization of prey by a strangling bite, while the remaining teeth are adapted to slicing meat. The greater size of ♂♂ assists them in capturing larger prey, as well as in monopolizing carcasses and imposing themselves upon ♀♀. As the largest of Africa's carnivores, Lions are well equipped to scavenge from other predators. Unpredictable prey availability and hunting success mean that Lions rarely capture prey every day. However, a distensible stomach enables them to gorge when meat is available and to wait several days before feeding again.

Lions prefer to drink water daily, but they can survive from the moisture obtained from fresh carcasses. Lions conserve energy and resources by spending a large proportion of each day asleep. Being sensitive to the heat of the day, they are primarily nocturnal. Panting is common only after exertion or a large meal (Schaller 1972). Other efforts to stay cool include lying on their backs and exposing their stomachs to the breeze. Tree climbing is not uncommon, especially in younger animals, and allows them to take advantage of breezes as well as to avoid flies (Fosbrooke 1963); in some situations it may also serve to keep Lions out of reach from dangerous animals (Makacha & Schaller 1969). Lions often rest on high points, including termite mounds and kopjes, and remain alert to feeding opportunities and intruding strangers.

Lions are the most social of all the felids and much of their sociality revolves around group territoriality. Both sexes are territorial,



Rooting of Lion *Panthera leo* tooththrow indicating slicing action during occlusion of upper and lower tooth rows.

marking their range with urine, roaring in chorus with pride-mates and expelling like-sexed strangers. Good territories complete with water, prey and hiding places for cubs are essential to raising offspring. Territories remain fairly constant over time with shifts in core areas coinciding with changes in water and prey availability. Males form coalitions with other ♂♂ thus increasing their ability to defeat other ♂♂ and to take over reluctant prides (Bygott *et al.* 1979). Female sociality derives from their need to exclude neighbouring ♀♀ from their territories as well as from the constant threat that incoming ♂♂ will kill their offspring. New ♂♂ accelerate the females' return to sexual receptivity by killing the cubs of the prior coalition (Bertram 1975), but groups of ♀♀ stand a chance of protecting their young from infanticidal ♂♂ whereas solo mothers are easily overpowered by the larger ♂♂ (Packer *et al.* 1990). An interesting adaptation, apparently unique among felids, is the ability of the ♀ to delay conception following the arrival of new ♂♂ to their pride. Females mate frequently with the new ♂♂, but fail to conceive over a period of approximately three months. The exact mechanism behind the delay is unclear, but it gives every appearance of allowing ♀♀ to evaluate new ♂♂ before committing to reproduction (Packer & Pusey 1983).

Physical adaptations are also related to the Lion's social system. The first Lions have been presumed to have been maneless, and maneless forms seem to have persisted in Europe, and possibly the New World, until around 10,000 years ago. It has been suggested that the maned form may have appeared between 320,000 and 190,000 years ago, and could have had a selective advantage that enabled it to expand to replace earlier maneless forms throughout Africa and western Eurasia (Yamaguchi *et al.* 2004a). The mane of the ♂ intimidates rivals and attracts ♀♀, but it also elevates surface temperatures and is associated with heat-related costs (West & Packer 2002), and manes may be reduced, or their development delayed, in hotter, moister climates (Selous 1908, West & Packer 2002, Gnoske *et al.* 2006). It has been hypothesized that the mane may also protect ♂♂ during fights with other Lions, but most attacks are directed away from the mane area and bites on the head and neck are often fatal regardless of mane characteristics (West *et al.* 2006). The possession of larger or darker manes also seems to indicate superior health and strength (West & Packer 2002). For example, in Ngorongoro Crater, a prolonged fight between a coalition of five ♂♂ and one of two ended in a draw; the smaller coalition was resident in the disputed pride and possessed much larger and darker manes. In fact, experiments using life-sized

models have revealed that both ♀♀ and ♂♂ are sensitive to variation in the characteristics of male manes; darker and longer manes seem to intimidate ♂♂ and to attract ♀♀ (West & Packer 2002). Thus, the mane appears to be a signal favoured by sexual selection occupying an important role in intra-specific communication. Spotted pelage on young animals may be the vestige of a time when Lion ancestors were restricted to forested environments, but it also renders the cubs inconspicuous while lying hidden in grassy, wooded or rocky nooks. The black ear and tail tips of adults aid in intra-specific communication, allowing Lions to follow each other through tall grass.

Roaring facilitates communication between pride members and serves as a warning to other prides (Schaller 1972, Grinnell 1994, McComb *et al.* 1994). Roaring is defined by low fundamental frequencies and lowered formant frequencies (Weissengruber *et al.* 2002) and is restricted, among the felids, to Lions, Tigers, Jaguars *Panthera onca*, Leopards and Snow Leopards *P. uncia* (sometimes called the 'roaring cats'). These species are unique among felids in having an incompletely ossified hyoid apparatus in which the epihyoideum is elastic rather than bony (Pocock 1916d, Weissengruber *et al.* 2002). This modification allows them to move the larynx from the palate and lengthen the pharyngeal passage (Hast 1989) allowing lower formant frequencies. Lower fundamental frequencies are probably produced by large, heavy vocal cords (Weissengruber *et al.* 2002). In Lions, the epihyoideum measures 150 mm when relaxed and 225 mm when stretched (Hast 1989). Although Schaller (1972) recorded several instances of purr-like vocalizations, it is generally agreed that a large pad in the vocal folds prevents Lions and the other roaring cats from true purring (Pocock 1916d, Weissengruber *et al.* 2002).

Foraging and Food Lions are generally thought of as predators of medium- and large-sized ungulates, but they are also known to eat rodents, hares, birds and reptiles (including tortoises), as well as to take down larger prey like Black Rhinoceroses *Diceros bicornis* (e.g. Brain *et al.* 1999, Matipano 2004). In a review of 32 studies from 48 different locations (all, except two, from Africa), Hayward & Kerley (2005) demonstrated a preference for prey species within a weight range of 190–550 kg irrespective of their availability, with an optimum weight of 350 kg. However, Lions often take prey substantially smaller than this range, reflecting their dietary opportunism. Species within the preferred weight range that are not significantly preferred generally have features that reduce predation either morphologically (e.g. horns of Sable Antelope *Hippotragus niger*), ecologically (e.g. Roan Antelope *H. equinus* and Sable occur at low density), or behaviourally (e.g. the large herd size and increased vigilance of Eland *Tragelaphus oryx*) (Hayward & Kerley 2005).

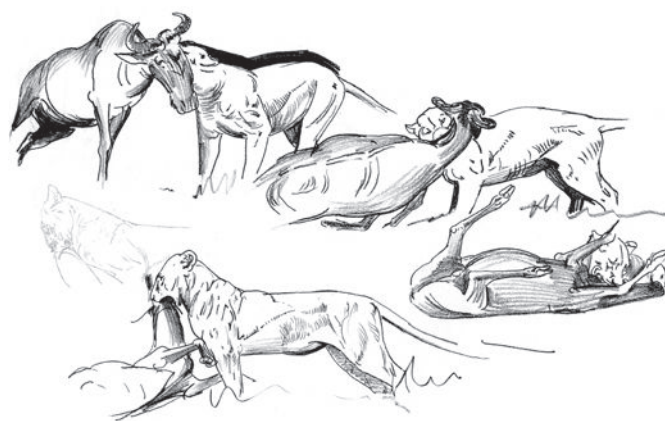
Most studies on foraging and feeding emanate from southern and East Africa. In Serengeti N. P., seven ungulate species account for 90% of all kills: African Buffalo *Syncerus caffer*, Common Wildebeest *Connochaetes taurinus*, Plains Zebra *Equus quagga*, Common Warthog *Phacochoerus africanus*, Thomson's Gazelle *Eudorcas thomsonii*, Hartbeest *Alcelaphus buselaphus* and Topi *Damaliscus lunatus*. During the wet season, Common Wildebeests are abundant on the plains and are then the most frequently killed prey; during the dry season, Thomson's Gazelles and Common Warthogs predominate. African Buffalo are mainstays when the migratory herds are absent (Scheel & Packer 1991). In Kafue N. P., Zambia, Giraffes *Giraffa camelopardalis*, made up 30% of kills (n = 410) followed by Impalas *Aepyceros melampus* and Common Elands

(Mitchell *et al.* 1965). In Hwange N. P., Zimbabwe, African Buffalo, Savanna Elephant *Loxodonta africana* calves, Giraffes, Common Wildebeests and Plains Zebras made up 83% of all kills (Loveridge *et al.* 2006). In Kruger N. P., Giraffes, Common Wildebeests, Plains Zebras, Impalas and African Buffalo had the highest relative frequency among prey items in stomach contents ($n = 257$) (Smuts 1979, 1982); Pienaar (1969) listed a total of 37 prey species from Kruger N. P. (and see Funston *et al.* 1998). In Lake Manyara N. P., Tanzania, African Buffalo make up more than half the diet (Prins & Iason 1989). At Phinda G. R. in KwaZulu-Natal (South Africa), Hunter (1998a) recorded Lions killing 28 different prey species, with Common Wildebeests, Common Warthogs and Nyalas *Tragelaphus angasii* the most frequent prey items accounting for 86% of estimated prey biomass (although Nyala were the most abundant prey item).

In Chobe N. P., Botswana, the majority (42%) of prey taken by Lions weighed less than 50 kg; medium-sized prey (50–300 kg) and large prey (>300 kg) constituted 30% and 29% of kills, respectively. During the wet season, Lions killed mainly medium- and large-sized prey (particularly African Buffalo and Plains Zebras), while during the dry season they killed significantly more smaller-sized prey (particularly Common Warthogs). In total, five prey species, Common Warthog (28%), African Buffalo (27%), Plains Zebra (15%), Impala (11%) and Tsesebe *Damaliscus lunatus* (9%), constituted just less than 90% of all recorded herbivores killed (Viljoen 1993). In Etosha, Lions also mainly killed prey weighing less than 50 kg (particularly Springboks *Antidorcas marsupialis*, which contributed about 73% of kills). Common Wildebeests contributed 12% of kills and 28% of edible biomass while zebras contributed 9% of kills and 24% of edible biomass (Stander 1992a). Similarly, in the Kalahari, small prey, including birds, small mammals (such as Cape Porcupines *Hystrix africaeaustralis*) and juvenile antelopes (Gemsboks *Oryx gazella* and Springboks) made up around two-thirds of the diet (Eloff 1973, 1984, 2002).

In the savannas of West Africa, scat analysis revealed that Lions in Comoé N. P. preyed predominantly upon small to medium-sized ungulates (with Buffon's Kobs *Kobus kob* and Bushbucks *Tragelaphus scriptus* the two most frequent prey species comprising a total of 44% of the biomass consumed), while large ungulates (such as Hartebeests, African Buffalo and Common Warthogs) made up only a small proportion of their diet (Bodendorfer *et al.* 2006). In a study in Faro N. P., N Cameroon, Lions preyed mainly on medium-sized antelopes, with Buffon's Kobs having the highest frequency occurrence (Breuer 2005).

Besides typical prey items, Lions have been recorded preying on other carnivores, including Spotted Hyenas *Crocuta crocuta*, Leopards, Cheetahs *Acinonyx jubatus*, Black-backed Jackals *Canis mesomelas*, Bat-eared Foxes *Otocyon megalotis*, Civets *Civettictis civetta*, Ratels *Mellivora capensis*, Caracals *Caracal caracal*, Banded Mongooses *Mungos mungo*, White-tailed Mongooses, *Ichneumia albicauda* and Zorillas *Ictonyx striatus* (Pienaar 1969, Eloff 1984, Stander 1992a, Hunter 1998a). Carnivores are typically left uneaten when killed. However, infanticidal ♂♂ and ♀♀ may eat cubs after killing them (Schaller 1972, Hunter 1998a) and Lions that find dead cubs sometimes eat them (Schaller 1972). Other recorded prey items include: Nile Crocodiles *Crocodylus niloticus*, Common Hippopotamus *Hippopotamus amphibius* and termites (Pienaar 1969), Chimpanzees *Pan troglodytes* (Tsukahara 1993) and other primates such as baboons *Papio* spp. and grivets *Chlorocebus/Cercopithecus* (e.g. Busse 1980, Bodendorfer *et al.* 2006), Cape Fur Seals *Arctocephalus pusillus* (Bridgeford 1985), pangolins (Manidae;



Lion *Panthera leo* seizing, throwing and strangling a zebra (from photographs).

e.g. Bodendorfer *et al.* 2006), Aardvark *Orycteropus afer* (Stander 1992, Bodendorfer *et al.* 2006), Ostrich *Struthio camelus* and Ostrich eggs (Schaller 1972, Stander 1992a), and even fish from shallow water. In the past, when Nile Crocodiles were widespread and common, they were a frequent prey, notably along the banks of the Rufiji R., where Common Hippopotamus were also regularly taken. Crocodiles were killed at the throat but eaten mainly around the base of the tail (Kingdon 1977). Lions have occasionally been recorded killing elephant calves (e.g. Schaller 1972, Ruggiero 1991), and they made up a considerable proportion of the diet (23% of kills) in Hwange N. P. (Loveridge *et al.* 2006); Joubert (2006) observed a total of 74 elephants killed by Lions during a four-year period with two-thirds of the kills in the age range of 4–15 years. Lions may occasionally actively feed on grass; Smuts (1979) recorded the stomach of a female containing 200 g of green grass.

Hunting is opportunistic, and occurs mostly at night (Schaller 1972, Stander 1992a, Mills & Biggs 1993) although ambushing prey at waterholes becomes more frequent during the day in dry seasons. In general, Lions hunt in areas where prey is easy to capture rather than areas where prey is more abundant (Hopcraft *et al.* 2005). Hunting typically involves a stealthy approach to within 15 m of the prey item; Lions quickly reach their top speed of 58 km/h, but as their prey is usually faster and has better stamina, most chases do not exceed 200 m. Stalking is followed by a swift charge then grabbing or slapping the quarry's flank and dragging the prey down; the prey is killed with a suffocating bite to the mouth or throat. Lions may leap on the backs of larger animals such as Gemsboks (Eloff 1973), Elands (P. M. West pers. obs.) and African Buffalo (C. Packer pers. obs.) in order to break the animal's back (Eloff 1973) or to bite the animal on the back and/or to knock it off-balance. Lions will also actively dig out prey such as Common Warthogs from shallow burrows (Guggisberg 1961, Kruuk & Turner 1967, Van Orsdol 1984).

Some evidence suggests links between pride size and foraging; for example, pride size is positively correlated with lean season prey abundance (Van Orsdol *et al.* 1985). However, while Lions enjoy the reputation of cooperative hunters, the prevalence of cooperative hunting is overestimated (Scheel & Packer 1991). Where prey is relatively easy to capture, Lions in a group often watch a companion as she begins to hunt, and only join her if and when the quarry is subdued. In mixed groups, ♀♀ older than about two years do most of the hunting (Schaller 1972, Scheel & Packer 1991); in Etosha N. P., ♂♂ only participated in 4% of hunting opportunities (Stander

1992a). Cooperative hunting is more common in harsh habitats, when the hunting success of a solitary animal is low, and when tackling large prey (Packer & Rutten 1988). In Etosha N. P., where Lions primarily prey upon Springboks, a species that is extremely difficult to catch, cooperation is not only frequent, but each Lion in a group repeatedly assumes a specific position in the hunt (Stander 1992b). Stander (1992b) classified hunting ♀♀ according to the position they assumed during the hunt, with some ♀♀ circling prey ('wings') while others ('centres') waited for prey to move towards them. The 'wings' usually initiated the attack while the 'centres' ambushed prey in flight. Hunts were most likely to succeed when ♀♀ occupied their preferred positions.

Lions throughout Africa will cooperate when hunting larger prey such as African Buffalo, first encircling the prey and then attempting to knock it down. Here the additional bulk of the ♂ is invaluable, and ♂♂ are frequent killers of African Buffalo (Funston *et al.* 1998, 2001). Females capture the majority of small- to mid-sized prey. Once the prey is subdued, ♂♂ dominate all other Lions at a kill, while ♀♀ tend to feed alongside the subadults and cubs. Feeding is a messy affair, and evidence of cooperation quickly disappears. Lions often emerge from a feeding bout bleeding at the face and ears from squabbling with companions. Prey is either consumed at the site of the kill or dragged to cover, with larger prey usually being consumed on the spot. The belly is ripped open, and the intestines, internal organs, muscle, bones and skin are consumed (Van Valkenburgh 1996).

Food consumption rates in Etosha N. P. in the dry season were around 8.7 kg/day/Lioness, while in the wet season average food intake was 14.1 kg/day/Lioness (Stander 1992a). In the Serengeti N. P., the estimated minimum daily food requirement is between 5.0 and 8.5 kg/day/Lion, with ♂♂ consuming twice as much as ♀♀ (Packer *et al.* 1990, Scheel & Packer 1991). Schaller (1972) recorded one ♂ in the Serengeti N. P. consuming 33 kg of meat in one night.

Hunting success rates vary among regions, presumably dictated by numerous ecological constraints (Sunquist & Sunquist 1989). In Etosha N. P., success rates were as low as 15% (one kill every 6.7 hunts; Stander 1992a), while in the Kalahari they were as high as 38% (Eloff 1984). In the Serengeti N. P., Schaller (1972) recorded hunting success at 23%. Van Orsdol (1984), working in Uganda, suggested that hunting behaviour varies with cover availability, prey availability and prey body size. In Etosha N. P., Stander & Albon (1993) found that hunting techniques employed by ♀♀, female group size, prey species, time of day/night, terrain, and interaction between terrain and day/night, all determined the likelihood of a hunt being successful. Hunts that involved coordinated stalking were most likely to succeed while an increase in female group size increased the success rate of hunting the five major prey species. Females also were more successful when hunting on moonless nights in undulating terrain. Stander & Albon (1993) attributed the social foraging habits of Lions in Etosha (where the solitary ♀♀ have very low hunting success, 2.5%; Stander 1992a) to their semi-arid, open habitat where there are long periods of food scarcity and where solitary hunters do not acquire the minimum food intake. In East Africa, where prey density is higher the success rates of solitary hunters is similar to groups. Funston *et al.* (2001) identified seven variables that they considered to have a significant independent influence on hunting success of male and female Lions in Kruger N. P. Those related to the Lions themselves, included the type of

hunt, wind orientation and number of adults, while those related to prey included prey species and herd size; the only two environment-related variables were moon brightness and grass height. The sex of the Lions had no effect on the overall probability of hunting success.

Lions primarily obtain their food by hunting, but scavenging can be a major source of food intake in habitats or at times when Lions can regularly find freshly dead animals. When large migratory herds are out on the treeless, open Serengeti Plains many die naturally, others are killed by Spotted Hyenas and every carcass is readily located by descending vultures or hyena calls; under these circumstances Schaller (1972) found that Lions scavenged as much as 53% of their food. In Etosha N. P. and Phinda G. R., Lions scavenged 5.5% and 8.8% of prey items, respectively (Stander 1992a, Hunter 1998a), but in the Serengeti N. P., the percentage of food scavenged was much higher (Packer *et al.* 1990). Lions scavenge opportunistically from all other predators including Spotted Hyenas, Cheetahs, Leopards and African Wild Dogs *Lycaon pictus* as well as from other Lions. Males are particularly persistent scavengers of Spotted Hyena kills. Lions locate scavenging opportunities by sight or sound (e.g. the squabbling of hyenas at a kill). Spotted Hyenas occasionally supplant Lions from their kills, particularly when they greatly outnumber Lions and when adult male Lions are absent, but typically wait until Lions abandon the carcass and then move in to consume the bones and scraps of skin that the Lions cannot eat. In Chobe N. P., hyenas located almost 80% of all kills made by Lions, usually arriving within 30 min of the kill having been made. Adult male Lions and their prides were never challenged by Spotted Hyenas, but female prides lost 20% of their food to hyenas, although hyenas had to outnumber ♀♀ by 4:1 to drive them off their kill (Cooper 1991). Cooper (1991) attributed this kleptoparasitism by Spotted Hyenas to a shortage of adult male Lions in the Savuti region (where the sex ratio was 1 ♂ to 5.7 ♀♀). In Kruger N. P., Spotted Hyenas only outnumbered ♀♀ at five out of 77 kills and never by more than 3:1 (Funston *et al.* 1998). In Etosha N. P., interactions between Lions and Spotted Hyenas are rare (Stander 1992a).

Social and Reproductive Behaviour The Lion's social organization is based on the pride, which in the Serengeti N. P. consists of 1–18 adult ♀♀, their dependent offspring and 1–9 adult ♂♂ (Packer *et al.* 1988, 2005a), although prides of 3–10 adult ♀♀ and 2–3 resident ♂♂ are more common. Prides tend to be smaller in southern Africa, particularly in arid environments where there are fewer prey species, such as Etosha N. P. (mean = 4.8 adult ♀♀; range 2–9; Stander 1991) and Kgalagadi Transfrontier Park (mean = 4.0; range 2–8; Funston 2001; and see Eloff 1998, 2002) (see also Van Orsdol *et al.* 1985).

The pride is a fission–fusion society (Schaller 1972, Packer *et al.* 1990) such that Lions spend most of their time in smaller subgroups or alone. The ♀♀ in a pride are always close genetic relatives with rare exceptions; two published cases of unrelated ♀♀ forming prides resulted from severe disturbance including prolonged drought in the Kalahari (M. Owens & D. Owens 1984) and extensive Lion culling in Kruger (Smuts 1978), and two apparently unrelated Serengeti ♀♀ formed a crèche with six cubs for at least six months although how long their association persisted is unknown (P. M. West & C. Packer pers. obs.). Resident ♂♂ are almost never related to pride ♀♀ (except in small, isolated populations) (Packer *et al.* 1991a). Females usually remain in their mothers' pride, but they will also disperse if their fathers are still resident when they reach sexual

maturity and incoming ♂♂ often evict subadult ♀♀ along with the subadult ♂♂ (Bertram 1973, Hanby & Bygott 1987, Stander 1991). In either case, dispersing ♀♀ may establish a new pride on the edge of their natal territory and neighbouring prides thus may also be closely related (Packer & Pusey 1987, Packer *et al.* 1991a, Spong *et al.* 2002). Relatedness between neighbouring prides may also result when a coalition of ♂♂ is resident with both or when young ♂♂ disperse to neighbouring prides, factors that may partially explain why the degree of relatedness does not appear to influence behaviour between neighbouring prides (Spong & Creel 2004).

In Serengeti N. P., young ♂♂ are either evicted by incoming adult ♂♂, or leave when they begin to reach maturity. While large coalitions often move directly into adjacent prides (Pusey & Packer 1987), leaving the pride can be the beginning of a long nomadic phase that can last in excess of two years. Nomadic male behaviour differs from that of residents; nomads abstain from roaring to evade detection by resident Lions (Grinnell & McComb 2001) and they rely largely on scavenging for food. Nomadic ♂♂ thus often display poor body condition, although they become more proficient at capturing large prey as they grow older and stronger. In areas dominated by migratory prey, ♂♂ may follow the migration far from their natal territory. In Kaudom G. R., nomadic ♂♂ moved over areas up to 5415 km² (Standar 1997a). Young ♂♂ from the same crèche leave the natal pride together, establishing a coalition that lasts throughout their lives; coalitions of more than three ♂♂ invariably consist of such related Lions. However, ♂♂ often end up alone either due to the lack of same-aged crèche-mates or to the death of their companions. These ♂♂ will team up with stranger Lions, and coalitions of 2–3 ♂♂ are often entirely unrelated. Such is the importance of male companionship that the behaviour of related and unrelated coalitions is virtually indistinguishable; male companions are demonstrably affectionate and highly cooperative (Grinnell *et al.* 1995).

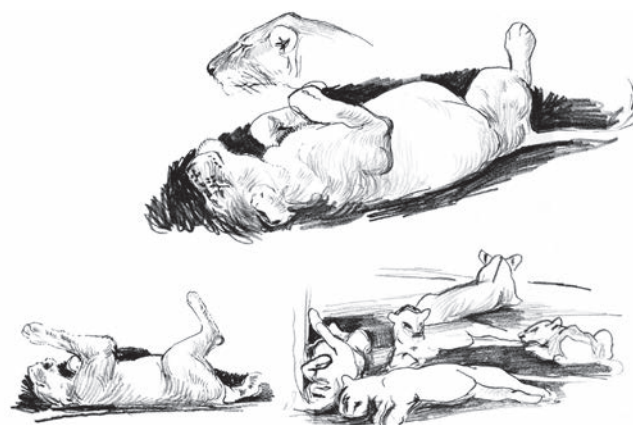
In contrast with Lions from 'plains-like' ecosystems where small coalitions of dispersing ♂♂ usually move far away from their natal pride's range and remain nomadic for extended periods of time, subadult male Lions in Kruger N. P. had a prolonged period of association with their natal pride regardless of coalition size, either directly or in a land tenure system that has not been described previously. After leaving the pride, most (80%) of young male coalitions, rather than becoming nomadic, remained close to their natal territory, either as non-territorial subadults, adults or even as territorial adults. Of the 20% of coalitions that did not stay close to their natal range, one acquired a territory 20 km away. However, the majority of holders acquired territories closer to their natal ranges (Funston *et al.* 2003). These authors hypothesized that dense bush and access to sufficient prey resources, particularly in the form of resident African Buffalo (which comprised the majority of male Lion kills; and see Funston *et al.* 1998) might have been important factors allowing extended residence close to the natal pride's territory.

The primary benefit of sociality in both ♂♂ and ♀♀ is to reproduction. Nomadic ♂♂ appear to be constantly on the lookout for vulnerable prides where they can defeat the resident ♂♂. Larger coalitions are more successful in such competitions, and solitary ♂♂ have very little hope of gaining access to ♀♀ (Bygott *et al.* 1979). In Kruger N. P., the minimum age at which ♂♂ become territorial is five years, and the oldest territorial ♂ recorded was 11 years; thus, ♂♂ have about six years in which to acquire and maintain a

territory and sire offspring (Funston *et al.* 2003). Once established, ♂♂ dispatch the offspring of their predecessors either through infanticide or eviction (Bertram 1975, Packer & Pusey 1984, Pusey & Packer 1994). While this improves the males' reproductive success, it represents a huge loss of investment for ♀♀. By living in groups and pooling their offspring, ♀♀ improve their chances of protecting their offspring from new ♂♂ (Packer *et al.* 1990). Sociality also enables ♀♀ to protect their territories from neighbouring prides (McComb *et al.* 1994). Solitary ♀♀, while consistently better fed than their social neighbours, rarely succeed in raising offspring or maintaining a satisfactory core territory, and constant conflict with neighbouring prides and strange ♂♂ is undoubtedly the primary factor in their increased mortality (Packer *et al.* 1990).

Pride ranges in Serengeti N. P. cover an area of 20–500 km² depending on the size of the pride, availability of water and prey abundance (Schaller 1972, Bertram 1978, Van Orsdol *et al.* 1985). In harsher habitats, average pride ranges can be much higher. For example, in areas of Kgalagadi Transfrontier Park, the home-ranges of 14 prides varied between 266 and 4532 km² (mean = 1462 km²; Funston 2001). Similarly, in Etosha N. P. the ranges of seven prides and two adult ♀♀ ranged from 150 to 2075 km² (Standar 1991), while pride ranges in Kaudom G. R. were between 1055 and 1745 km² (Standar 1997a). Van Orsdol *et al.* (1985) found a strong negative correlation between home-range size and the abundance of prey during the season of least abundance. Ranges often overlap with those of neighbouring prides, although each pride maintains a central area for its exclusive use, and ♂♂ may be resident with more than one pride. Both sexes defend the territory, with ♂♂ ranging more widely, and ♀♀ defending the core area against other groups of ♀♀ (including those with whom they may share resident ♂♂). Territory boundaries are maintained by roaring, urine-marking and patrolling. Roaring also allows Lions to locate distant pride-mates. Lions do make excursions beyond their ranges, with average recorded daily walking distances of up to 40 km per day (Eloff 2002).

Intruders usually retreat at the sight or sound of residents, and actual fights are rare. The lethal teeth and claws of opponents make it likely that even a successful competitor will not emerge unscathed, and consequently Lions have evolved a number of behavioural mechanisms that enable them to avoid fights. For example, when confronted with the recorded roars of like-sexed strangers, resident ♂♂ and ♀♀ are both sensitive to the odds. Females approach only



After feeding well Lions *Panthera leo* may lie around and sleep for several days at a time.

when they outnumber their opponents, and ♂♂ temper approaches with caution when outnumbered (McComb *et al.* 1994, Grinnell *et al.* 1995, Heinsohn & Packer 1995). Lions can also distinguish between individual roars allowing ♀♀ to avoid conflicts with potentially infanticidal ♂♂ (McComb *et al.* 1993). Some evidence suggests that ♂♂ alter their roars when repelling intruders; resident male roars recorded after playbacks of unfamiliar ♂♂ within their territory were shorter and louder than controls (Grinnell 1994).

When confronted with a challenge from a larger male group, outnumbered resident ♂♂ sometimes abandon their pride rather than fight, often fleeing the territory with their successors in hot pursuit. However, coalition numbers may not be the only factor in male success. Ownership of a pride probably confers an advantage, as does the possession of larger or darker manes, as indicated earlier (under 'Adaptations'; and see West & Packer 2002).

Male tenure length in prides is highly variable but generally increases with coalition size, and the average length of time ♂♂ spend with an individual pride is two years (Bygott *et al.* 1979, Packer & Pusey 1983; and see Funston *et al.* 2003). A pride 'takeover' by new ♂♂ can be chaotic. Roaring, chasing and fighting may precede the actual event, followed by an orgy of mating. After the loss of offspring, pride ♀♀ immediately begin to demonstrate sexual behaviour, which includes walking sinuously around ♂♂ and presenting themselves with low growls (Bertram 1975). A 'consorting' ♂ closely guards each receptive ♀, and his ownership is rarely challenged. Mating often continues throughout a period of four days at the rate of approximately three times per hour (Packer & Pusey 1983); one account reports 157 copulations over a 55-hour period (Schaller 1972). During copulation, a ♂ often licks or gently bites the female's nape while she emits a low growling noise. Copulation is generally brief and often ends with a growl or yelp from the ♂ and with the ♀ turning to snarl as the ♂ dismounts. After mating, ♀♀ often roll on to their sides or backs, a behaviour that may facilitate sperm retention (Schaller 1972).

Although the resident ♂♂ father all cubs born during their tenure, many coalitions show dominance relationships, and generally only two ♂♂ in a given coalition succeed in fathering offspring (Packer *et al.* 1991a). That mating is shared at all by ♂♂ may reflect the inability of a dominant ♂ to monopolize more than one oestrous ♀ while many more may be available simultaneously. Indirectly, ♀♀ may also exercise some choice over the paternity of their offspring in spite of established male dominance hierarchies (West & Packer 2002). Regardless of its cause, this reproductive skew probably helps explain why coalitions of more than three ♂♂ are never composed of unrelated ♂♂.

In contrast to ♂♂, female Lions exhibit no signs of dominance hierarchies and their reproduction is remarkable for its even distribution (Packer *et al.* 2001). The signs of pregnancy are subtle until a few weeks before birth, at which point the udder becomes distended and ♀♀ begin ranging alone. Birth typically occurs in a confined and protected spot, and the cubs remain hidden until approximately six weeks of age. At this point they can keep up with the pride and begin to eat meat, and they are pooled with other litters to form a 'crèche'. Such crèches can consist of more than 25 cubs (though 4–10 is more typical), and the mothers of the crèche spend most of their time together, remaining somewhat separate from other pride-mates. Cooperation becomes most pronounced at such times even to the point of nursing each other's offspring. However, the nursing of non-offspring is most common among the more closely related ♀♀, and by ♀♀ with only one cub

of their own; ♀♀ with large litters primarily nurse their own young (Pusey & Packer 1994). When prey is captured at a distance, mothers often return to their offspring and lead them to the kill, calling them with soft grunts (Schaller 1972). Although ♂♂ typically displace all other Lions from a kill, the rest of the pride respect each other's 'ownership' of a feeding site, and mothers often wait until their cubs have eaten their fill before feeding themselves. Older cubs compete with younger cubs for food, and the youngest cubs in a crèche have the highest mortality. Mothers with new cubs are thus less likely to join an extremely large crèche, or one with much older cubs.

Cubs are very playful, with play behaviour mimicking skills they will need as adults. Cubs will attempt to play with any adults in the vicinity but are usually met with bared teeth or a snarl. Fathers tend to remain at a slight distance when present with mothers and cubs, and ♀♀ may threaten them if they begin to move closer. Cubs begin to show signs of independence beginning around the age of 18 months, and can survive without the protection of the pride only from about two years. As early as one month of age, cubs display a vocal repertoire similar to that of adults although in modified form; the full roar is not seen until subadulthood (Schaller 1972).

Reproduction and Population Structure In Serengeti N. P., ♀♀ typically reach sexual maturity by the age of 30–38 months (Packer *et al.* 1988, 1998). Serengeti ♂♂ are probably sexually capable at the same age as ♀♀, but they typically fail to find mating opportunities until 48–54 months at which point they are large enough to challenge rival ♂♂ (Packer *et al.* 1988). By this age, the manes of young ♂♂ have usually reached their full size, while mane colour may continue to darken until age 9–10 years. Occasionally, manes will lighten over a male's life-span, and illness or injury may drastically reduce mane size at any age (West & Packer 2002); in fact, Lions will lose their mane entirely if castrated, so manes appear to be dependent on androgens (West 2005). The ages at which Lions reach full size and sexual maturity appears to vary between habitats with Lions in harsher habitats, such as Kruger N. P., trailing those of Serengeti N. P. by as much as a year. Funston & Mills (1997) gave the mean age at first conception in Kruger N. P. at 48 months, although at least 29% ($n = 14$) gave birth at 40 months; breeding was delayed until 54–60 months in certain individuals (and see Funston *et al.* 2003). Five known-aged males of 26–28 months sired cubs at Phinda G. R. in KwaZulu–Natal, but this opportunity for mating arose only because of the lack of mature ♂♂ (Hunter 1998a).



Male scrotum and backward facing penis.

Lions are polyoestrus; the oestrous cycle lasts 16 days and oestrus 4–7 days with a two-week interval and can occur at any time of year (Packer & Pusey 1983). It is not clear whether ovulation is induced by copulation or is spontaneous. Mating may take place at any time throughout the year, although Smuts (1982) recorded a large proportion of the cubs born between Feb and Apr in Kruger N. P. (timed to the period when prey species have their young) and Packer *et al.* (1990) recorded a peak in births between Mar and Jul in the Serengeti N. P.

Gestation is 15–16 weeks (Cooper 1942). Litter sizes in the wild vary from 1–6 (Schaller 1972, Rudnai 1973, Smuts *et al.* 1978b, Packer & Pusey 1995) with an average of 2–3 (Packer & Pusey 1995) and newborn cubs weigh less than 1% of adult weight (Schaller 1972). The sex ratio at birth is generally equal with a slight increase in favour of ♂♂ directly following a takeover (Packer & Pusey 1987). This may reflect the increased probability of synchronous litters directly following a takeover, and the benefits to ♂♂ of having same-aged and like-sexed companions. Cubs are born either with eyes open, or their eyes open very shortly after birth. Milk dentition erupts around three weeks. Cubs subsist exclusively on milk, which is very high in fat (De Waal *et al.* 2004), until approximately 4–6 weeks of age, and weaning is generally complete by eight months (Schaller 1972). However, weaned cubs can continue to steal milk from the lactating mothers of younger cubs (Pusey & Packer 1994). Mean inter-birth interval in Serengeti N. P., when raised to maturity, is 20 months (range 11–25; $n = 38$) and 4–6 months if the litter is lost (Packer & Pusey 1987). In two study prides in Kruger N. P., inter-birth intervals were extended with cohorts of cubs born on average every 40 months (Funston *et al.* 2003). These researchers found that yearly variations in the population size, with cubs comprising between 7% and 34% of the population, were due to this extended inter-birth interval (Funston *et al.* 2003).

Cub mortality is generally high: in the Serengeti N. P., in particularly harsh years, as many as 80% of cubs die before their first birthday (Packer & Pusey 1995). The overall average is closer to 60% with the primary causes being infanticide (or abandonment following a takeover by new ♂♂), starvation and disease. Once cubs reach one year of age, annual mortality declines to less than 20% (Packer *et al.* 2001). In Kruger N. P., the annual survival rate of cubs up to 12 months of age was higher (84%; $n = 55$), and the role of infanticide or predation by other carnivores appeared to be small; annual survival rates of large cubs (>12 months), and subadults still associating with the pride were also high (89% and 91%) (Funston *et al.* 2003). Few ♀♀ live past the age of 18 in the wild, and most cease to reproduce after age 15 (Packer *et al.* 1998). Males rarely reach the age of 16 years (Smuts *et al.* 1978a, Whyte & Smuts 1988). In captivity, longevity is extended, but anecdotal reports suggesting that Lions can live up to 30 years are probably incorrect. The record longevity in captivity is for a wild-born ♂ that died at Cologne Zoo at about 27 years of age (Weigl 2005).

In Ngorongoro Crater, the adult sex ratio is 2.1 ♀♀ to 1 ♂, and the adult : young ratio is 30 : 37. In the Serengeti N. P., the adult sex ratio is 2.7 : 1 (C. Packer pers. obs.). Similarly, Smuts *et al.* (1978b) determined a ratio of 2.1 ♀♀ to 1 ♂ in Kruger, while Funston *et al.* (2003) recorded a sex ratio of adult territorial Lions in Kruger of 2.5 ♀♀ to 1 ♂.

Predators, Parasites and Diseases As the largest of Africa's predators, the adult Lion has no actual predators of its own although

young are still vulnerable. Leopards, Spotted Hyaenas and African Wild Dogs will kill Lion cubs when the opportunity arises, but the greatest threat comes from other Lions. Infanticide by incoming ♂♂ is ubiquitous, and ♀♀ will also kill the cubs of unfamiliar Lions. Adult Lions can be severely injured while attempting to subdue prey, especially Common Wildebeests, Plains Zebras, Gemsboks, Common Warthogs and rhinoceroses. African Buffalo are a particular danger; in Ngorongoro Crater, African Buffalo even attack and kill non-hunting Lions, and are a significant factor in adult mortality (Kissui & Packer 2004).

The most important pathogens in Lions are probably canine distemper (CDV) and bovine tuberculosis (bTB). bTB is an emerging disease threat present in Serengeti and Kruger National Parks, and Hluhluwe–iMfolozi Park in KwaZulu–Natal, and is associated with morbidity in all three (Keet *et al.* 2000, Cleaveland *et al.* 2005), though the extent of this threat appears to be minor in East Africa. Lions are probably infected when they scavenge or kill infected African Buffalo in advanced stages of bTB (Keet *et al.* 2000). CDV is known to strike East African populations irregularly, and while some outbreaks caused minimal mortality, others have killed up to 40% of the population such as the outbreak in the Serengeti–Mara in 1993–94. The reservoir for the disease in this instance was the large domestic dog population inhabiting villages adjacent to the area (Roelke-Parker *et al.* 1996, Packer *et al.* 1999). The Serengeti N. P. population rapidly recovered, reaching its original size by 1997 (Packer *et al.* 1999). In contrast, a succession of disease outbreaks (including CDV) in the Ngorongoro Crater Lions has kept this population below its carrying capacity for over ten years (Kissui & Packer 2004). Feline immunodeficiency virus (FIV) infects close to 100% of adult Lions in the Serengeti N. P., Ngorongoro Crater and Kruger N. P. but is apparently absent in Etosha N. P. and Hluhluwe–iMfolozi Park (Brown *et al.* 1993, Packer *et al.* 1999). The health effects of FIV are unclear. Some infected Lions in captivity have been suggested to show FIV-related pathology, but Lions in natural FIV+ populations generally seem as healthy as those in FIV– populations. Lions in Tanzania are also infected with coronavirus, calicivirus, parvovirus, Rift Valley fever, anthrax and influenza, but the health effect of these pathogens appears to be minimal (Packer *et al.* 1999, C. Packer pers. obs.).

Boomker *et al.* (1997) listed a total of 31 helminths that infect Lions, including 21 nematode species (including members of the genera *Ancylostoma*, *Cylicospirura*, *Diriofilaria*, *Filaria*, *Gnathostoma*, *Physaloptera*, *Toxocara* and *Trichinella*), seven cestodes (such as *Echinococcus granulosus*, which causes hydatid cysts, and *Taenia* spp.), and a trematode (*Pharyngostomum cordatum*), as well as various protozoan parasites (*Babesia* sp., *Hepatozoon* sp., *Sarcocystis* sp. and *Trypanosoma* sp.); none of these appear to inflict life-threatening illness. Bjork *et al.* (2000) documented a further 12 previously undocumented parasites, including *Aelurostrongylus*, *Capillaria*, *Denodex*, *Eimeria*, *Habronema*, several *Isoospora* species and *Trichuris* in faecal samples from N Tanzania.

A very large number of ectoparasites have been recorded from Lions. Boomker *et al.* (1997) documented 32 species of ticks (18 of them in the genus *Rhipicephalus*), several of which are implicated in the transmission of protozoal and bacterial diseases, and two species of fleas (*Ctenocephalides felis* and *Echidnophaga larina*). Lions are also harassed by stable (*Stomoxys calcitrans*) and tsetse (*Glossina morsitans*) flies and other biting insects. The Ngorongoro population crashed

in 1962 following what appeared to be an exceptional outbreak of *Stomoxys* flies, resulting in widespread mortality (numbers collapsed from nearly 100 animals to 12 over the course of one year) (Packer *et al.* 1991b). The population eventually rebounded by 1975, only to decline again after 1983 possibly due to the effects of inbreeding (see Conservation). Sarcoptic mange *Sarcoptes scabiei* has also been recorded from Lions in Kruger N. P., which may result in mortality in severe cases (Young 1975).

Conservation IUCN Category: Vulnerable A2abcd. CITES: Appendix II.

While Lions are not immediately threatened with extinction, their long-term survival is far from assured. As noted already, current estimates suggest that the Lion's range declined by 80% during the twentieth century (Ray *et al.* 2005), with fewer than 50,000 Lions remaining continent-wide. Large areas of land are necessary to support Lions and their natural prey, and the most important remaining populations are restricted to eastern and southern Africa: the Serengeti–Mara ecosystem and the Maasai Steppe (both in Tanzania and S Kenya), the Selous–Niassa ecosystem (in Tanzania and N Mozambique), the greater Ruaha–Katavi–Moyowosi–Kigosi ecosystem (in W Tanzania), the greater Kruger ecosystem (in South Africa and Mozambique) and the Okavango–Chobe–Caprivi ecosystem (in Botswana and Namibia). There may also be a large viable population in S Sudan–Central African Republic–N DR Congo.

The main conservation threats are habitat conversion, loss of prey and conflict with local people. The severe declines witnessed in Lion populations in West Africa, in particular, are attributed primarily to the spread of human settlements and agriculture into Lion habitat (Bauer & Van der Merwe 2004). Most human population growth is in rural areas with attendant pressures to convert wildlife habitat to agriculture. Economic incentives for local communities to tolerate Lions have been provided by privately owned hunting companies in Tanzania, Mozambique, Zambia and Botswana and by community programmes in Kenya and Zimbabwe. However, there is an urgent need to improve and expand these activities owing to the recent emergence among rural communities of putting out poisoned carcasses that are capable of extirpating entire prides (Frank *et al.* 2006).

It can be argued that human–Lion conflict is linked with poverty: currently the highest incidence of man-eating occurs in S Tanzania and N Mozambique, where Lions have long been a threat and people are too poor to build safe houses, and rudimentary agricultural practices require long periods preparing and harvesting crops, leaving them vulnerable to attack (Packer *et al.* 2005b). Similarly, pastoralist herders cannot afford to buy fencing, and their herds are so susceptible to disease and drought that they are increasingly intolerant of Lion depredation (Patterson *et al.* 2004, Woodroffe & Frank 2005). Annual losses of cattle to Lions in areas adjacent to Waza N. P., Cameroon, comprised only about 3.1% of all livestock losses, but were estimated to represent more than 22% of financial losses amounting to some US\$112,000 or US\$370 per owner (Bauer 2003; and see Bauer & de Iongh 2005). Likewise, in communal lands bordering Sengwa Wildlife Research Area, Zimbabwe, Lions were responsible for 34% of recorded kills, representing 58% of financial losses (Butler 2000). Studies have shown that intensive monitoring of livestock and improved husbandry practices can reduce losses to Lions (Ogada *et al.* 2003, Patterson *et al.* 2004).

Trophy hunting, which is legally permitted in 13 countries in Africa, is not a significant threat to Lion populations, provided that hunters only remove ♂♂ that are at least six years of age. Shooting too many young ♂♂ (3–4 years of age) can result in elevated rates of male takeovers and infanticide. By restricting hunting to ♂♂ of 5–6 years of age or older, younger resident ♂♂ can rear their first set of offspring, thus minimizing the impact of infanticide on the population as a whole (Whitman *et al.* 2004). International legal trade for Lion products is mostly restricted to hunting trophies and skins by hunting companies. Local markets exist for Lion claws and Lion fat as talismans and traditional medicine. In Guinea and Guinea-Bissau, Lion skins are much sought after and are openly sold in front of international hotels. Hunting for skins is considered the chief threat to the species in some West African countries (Brugière *et al.* 2005).

Inbreeding could represent a potential threat in isolated populations. The population in Hluhluwe–iMfolozi Park, for example, grew to 120 animals from only three founders, and then steadily declined due to a host of factors thought to be allied with reduced heterogeneity (Maddock *et al.* 1996). Likewise, Lions in the Ngorongoro Crater have low levels of heterozygosity and ♂♂ had high levels of abnormal sperm (Packer *et al.* 1991b); consistent declines in this population may well be due to repeated outbreaks of disease owing to this low heterogeneity (Kissui & Packer 2004). It has been calculated that in order to sustain a large outbred population of Lions, a population of at least 50 prides with no limits to male dispersal is required (Bjorklund 2003). Lions are amenable to restoration: in South Africa, Lions have been reintroduced to at least 21 sites with a combined area of over 4560 km² (Hunter *et al.* 2004). However, the majority of sites are very small, enclosed by fencing and isolated from other populations, and their long-term contribution to conserving the species remains equivocal (Hunter *et al.* 2007b).

Although Lions are present in numerous captive-breeding programmes, Barbary Lions subsist only as a captive population (numbering fewer than 90 animals) in relatively isolated zoo collections (Black *et al.* 2010), although there have probably been multiple genetic hybridization events with sub-Saharan Lions (Burger & Hemmer 2006).

Measurements

Panthera leo

HB (♀♀): 1711 (1600–1840) mm, n = 38

HB (♂♂): 1938 (1840–2080) mm, n = 12

T (♀♀): 805 (720–895) mm, n = 37



Lion *Panthera leo* female.

T (♂♂): 882 (825–935) mm, n = 10
 HF c.u. (♀♀): 689 (633–775) mm, n = 36
 HF c.u. (♂♂): 804 (762–837) mm, n = 7
 WT (♀♀): 111.0 (90.5–138.0) kg, n = 4
 WT (♂♂): 155.5, 169.0 kg, n = 2

Serengeti N. P., Tanzania (L. Herbst & C. Packer pers. obs.)

Note: In a sample of 344 individuals weighed and measured in Kruger N. P., average mass was greater than in corresponding groups further north in Africa: the mass of the largest ♂ was 225 kg, the mean being 188 kg, while the largest ♀ weighed 152 kg, the mean being about

126 kg (Smuts 1982). A male Lion shot near Mt Kenya weighed 272 kg (Nowell & Jackson 1996).

Key References Bertram 1978; Funston *et al.* 1998, 2003; Packer & Pusey 1983, 1987, 1997; Packer *et al.* 1990, 2005a; Schaller 1972; Smuts 1982; Stander 1991, 1992a, b, 1997a; Van Orsdol *et al.* 1985; West & Packer 2002; Whitman *et al.* 2004.

Peyton M. West & Craig Packer

Panthera pardus LEOPARD

Fr. Panthère; Ger. Leopard

Panthera pardus (Linnaeus, 1758). Syst. Nat., 10th edn, I: 41. 'Indiis', fixed by Thomas (1911; Proc. Zool. Soc. London I: 135) as Egypt, and by Allen (1924: 249) as Algeria.

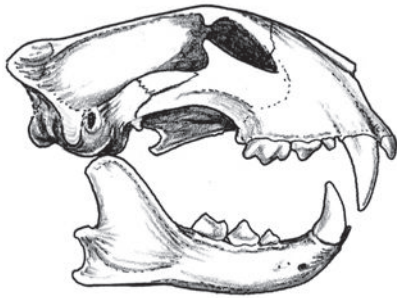


Leopard *Panthera pardus*.

Taxonomy Up to 15 African subspecies have been described (Allen 1939) based largely on pelage and cranial differences that vary widely within populations and are invalidated by recent molecular analyses. Variation in allozymes, mitochondrial DNA and feline-specific minisatellites suggests eight or nine subspecies worldwide, with all continental African Leopards classified as *P. p. pardus* (Miththapala *et al.* 1996, Uphyrkina *et al.* 2001). However, the limited sampling of African populations in both studies possibly underestimated phylogeographic population differences. The population on Zanzibar (now exterminated) is considered by some authors (e.g. Kingdon 1977) to represent a unique subspecies *P. p. adersi*.

Synonyms (Africa only): *adersi*, *adusta*, *antinorii*, *barbara*, *brockmani*, *centralis*, *chui*, *fortis*, *iturensis*, *leoparda*, *melanosticta*, *melanotica*, *minor*, *nanoparda*, *niger*, *palearia*, *panthera*, *poecilura*, *poliopardus*, *puella*, *reichenowi*, *ruwenzorii*, *shortridgei*, *suahelicus*, *varia*, *vulgaris*. Chromosome number: $2n = 36$ (Robinson 1979). In captivity, Leopards have hybridized with Lions *Panthera leo*, Tigers *P. tigris*, Jaguars *P. onca* and Pumas *P. concolor* (Gray 1972).

Description A large cat with robust, muscular forequarters, slender hindquarters, relatively short legs and a long tail around two-thirds of head and body length. Head and neck thickset, especially in ♂♂ where neck circumference may exceed head circumference by 40 mm (L.T.B. Hunter pers. obs.). Mature ♂♂ often develop a distinctive throat dewlap and, less often, an obvious belly fold. Pelage highly variable (see colour plate in Kingdon 1977: 350, and *Mammals of Africa* Volume I), ground colour ranges from pale cream, buff-grey, various shades of orange, tawny-brown or dark rufous graduating to white on belly, chest, throat, chin and underside of tail. Body is covered with rosettes, each a cluster of small, black spots surrounding a normally unspotted centre darker than the ground colour. Rosettes give way to large, solid black blotches on the distal half of limbs, belly, throat and tail. Tail tip is black with a white underside. Small, solid black spots cover the face and neck. Upper chest often has a distinctive yoke of connected or semi-connected elongated black blotches. Feet marked with small, black spots that typically thin out towards the digits but may aggregate in

Lateral view of skull of Leopard *Panthera pardus*.

dark individuals, giving a dark, almost black appearance (Henschel 2001). The pattern of rosettes and spots is unique to individuals and useful for individual identification. Guard hairs short and coarse on dorsal surfaces, shortest on head and face at 3–4 mm graduating to 15 mm on hindquarters. Ventral hair softer and longer, up to 30 mm on the belly (Skinner & Chimimba 2005). Vibrissae white. Back of the ears has prominent pale patch lighter than rest of the head, bounded by black. Cubs born with blue eyes that typically mature to yellow-green and rarely greenish-blue or rust-brown. Five digits on front feet and four on hind, all with extremely sharp, curved claws that are fully protractile. Front feet are longer and wider than hind. Forefoot's first digit rests above the ground and is not visible in the spoor, its claw, the dew claw, is the largest. Females have two pairs abdominal nipples. Sexual dimorphism is marked, with ♂ 30–100% heavier than ♀.

Skull is massively built with marked sexual dimorphism. Male skulls are larger and relatively longer with a distinct sagittal crest usually absent in ♀ (Sunquist & Sunquist 2002). In the ♂ postorbital constriction is narrower than the interorbital; the reverse applies for the ♀ (Skinner & Chimimba 2005). Dentition typically felid (though upper second premolars, absent in some smaller felids, are usually present), and is fully developed in some individuals by 12 months (L. T. B. Hunter & G. A. Balme pers. obs.), but usually at 18–24 months (Stander 1997b). Males have larger maxillary (mean = 33.2 mm) and mandibular (mean = 26.1 mm) canines than ♀ (mean = 27.2 and 22.5 mm; Stander 1997b). The canines are large, with sharp points and slightly flattened on the inner side; the cheekteeth are clearly adapted for slicing (Skinner & Chimimba 2005).

Geographic Variation Regional morphological variation is largely absent with the possible exception of Leopards from coastal mountain ranges in South Africa's Western Cape, which are apparently around half the mass of animals elsewhere in Africa (Stuart 1981). Extraliminally (e.g. Israel and Oman), individuals in some desert populations are very small but those from southern African deserts are comparable in size with Leopards from mesic areas (Bothma *et al.* 1997, Stander 1997b). Variation in pelage is extensive within populations, although Leopards inhabiting forests tend towards dark colouration while those in arid areas are pale (Pocock 1932, Kingdon 1977). Melanism is uncommon in Africa. Black individuals reputedly occur most often in humid, forested habitats and are reported from the Aberdare Mts, Mt Kenya, the Virunga Mts, Ethiopia, Zambia, Cameroon and Gabon (Turnbull-Kemp 1967, Guggisberg 1975, Kingdon 1977, Ansell 1978, Jackson 2002). D. Brugière (in litt., Jackson 2002) saw a melanistic Leopard in the Forêt des Abeilles, Gabon, but a three-year study in

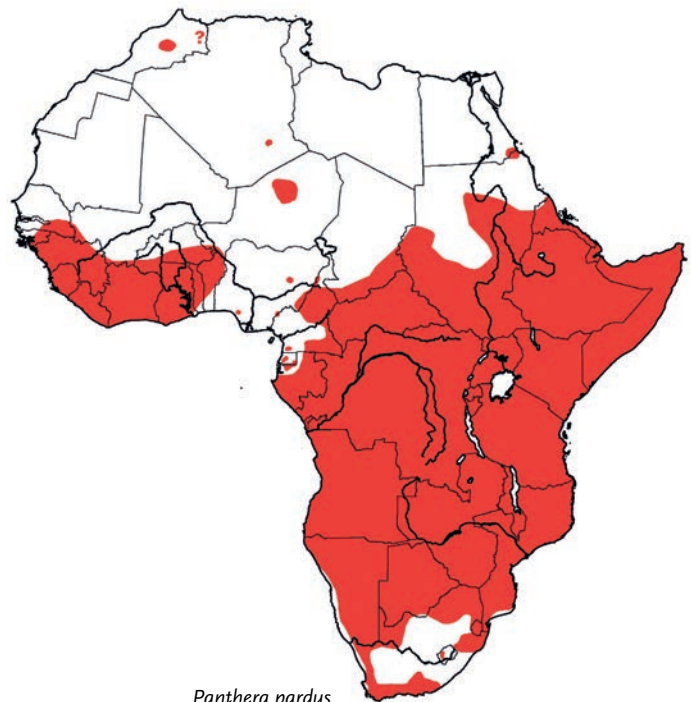
the Gabon rainforest using camera-traps recorded no melanism among at least 56 individuals (P. Henschel pers. obs.). Similarly, no melanistic individuals were found among 50 specimens collected from the Congo basin (Allen 1924). Occasional reports from savanna habitats such as near Masai Mara National Reserve (Scott & Scott 2003) and Lydenburg, South Africa (Jackson 2002) are unsubstantiated. Two aberrant individuals killed near Grahamstown, South Africa, had dark brown to black fur with lighter patches and contrasting spots on limbs and/or ventral surfaces (Günther 1885, 1886). Aberrantly marked individuals have been reported throughout the species' range (Allen 1924, Pocock 1932, Kingdon 1977).

Similar Species

Acinonyx jubatus. Sympatric. More slender, longer-legged build, uniformly marked with small, coin-shaped spots; facial tear streaks. *Profelis aurata*. Sympatric in West, Central and parts of East Africa. Smaller; ground colour dark golden to smoky-grey with variable spotting but always less distinct than Leopard; small, black-backed ears fading centrally to grey, less distinct than Leopard's unmistakable light patch; melanistic African Golden Cat might be confused for a young black Leopard.

Distribution Senegal eastwards to Sudan, Ethiopia and Somalia, south through most of Africa. Relict in North Africa. Also present in the Middle East, Turkey, throughout Central Asia into SW Russia, throughout tropical Asia into N China and Far Eastern Russia, and south to Sri Lanka, Peninsular Malaysia and Java (though naturally absent from Sumatra, Borneo and Bali) (Nowell & Jackson 1996, Sunquist & Sunquist 2002).

Historical Distribution Widespread throughout Africa in all habitats from rainforest to desert, reaching greatest densities in savanna woodlands. Naturally absent only from hyper-arid regions of the Sahara and Namib deserts.

*Panthera pardus*



Leopard *Panthera pardus* myology exposing powerful pectoral muscles.

Current Distribution Widely distributed within historical limits but with marked range retraction, especially in North Africa, West Africa, the Horn of Africa and South Africa (Nowell & Jackson 1996, Kingdon, 1997, Ray *et al.* 2005). Ray *et al.* (2005) estimated that Leopards have disappeared from at least 36.7% of their historical range in Africa. In North Africa, Leopards are relict in the Atlas Mts, Morocco; tracks of a ♀ and cubs were observed in 2002 in the eastern High Atlas (Cuzin 2003, Puroy *et al.* 2003) and there was a probable observation on the Morocco–Algerian border in Figuig in 2007 (F. Cuzin pers. comm.). Leopards have also recently been confirmed from the Ahaggar region of SE Algeria, the first record of Leopards from this region and the first direct evidence of this species in Algeria for over 50 years (Busby *et al.* 2006, 2009). Likely extinct in Egypt; five years of camera-trapping (1999–2004) failed to produce evidence of Leopards in S Sinai, where the last reliable report originates from 1963 (El-Alqamy *et al.* 2002, H. El-Alqamy pers. comm.). Leopards may be present in N Sinai and the Eastern Desert (H. El-Alqamy pers. comm.), but there are no confirmed records. Regular unconfirmed reports persist from the Gebel Elba region where a calling Leopard was heard and tracks photographed in 1994 (Hoath 2003).

In sub-Saharan Africa, they have been locally extirpated from areas densely populated with people or where habitat conversion is extreme. Leopards were extirpated from much of the West African coastal forest belt by 1945 (Bailey 2005; but see Brugière *et al.* 2005) and they have disappeared from much of the western Sahel (Anada in litt., Nowell & Jackson 1996). Leopards disappeared from Bwindi Impenetrable F. R., Uganda, in the 1960s (Andama 2000) and recent camera-trap surveys failed to find evidence of Leopards in Rwenzori Mts, Kibale N. P. and Kasyoha-Kitomi and Kalinzu Forest Reserves, Uganda (Treves *et al.* 2010). They disappeared from most forest reserves across SW Cameroon by the early 1980s (Maisels *et al.* 2001, Willcox 2002), and have been confirmed at only one site, Campo Ma'an N. P., since 2009 (Henschel 2009). In SE Nigeria, Leopard sign occurred in only two of 47 recently surveyed forest patches (Angelici *et al.* 1998). Leopards have naturally recolonized some areas in KwaZulu–Natal (South Africa), with the spread of game-farming (J. Anderson pers. comm.) and have reportedly increased in Eritrea since the cessation of human fighting in 1991 (Zinner *et al.* 2001). They are

likely extinct on Zanzibar, where there are no confirmed records since 1996 (Stuart & Stuart 1997b, Goldman & Walsh 2002).

Habitat The Leopard has a very wide habitat tolerance and is the only African felid occupying both rainforest and desert habitats. They are most successful in woodland, grassland savanna and forest but also occur widely in mountain habitats, coastal scrub, shrubland, semi-desert and desert. In central African rainforest, they inhabit all forest types including inundated forests, logged secondary forest and old-growth terra firma forest. Tracks are recorded in extensive swamp systems and Leopards are often observed crossing wide forest streams (P. Henschel & J. Ray pers. obs.). They occur in patches of mangrove and sub-humid forest in coastal West Africa (Brugière *et al.* 2005). Provided prey is available, they occur in areas where surface water is absent. They are absent from the open interiors of true desert but penetrate deeply into arid areas along water-courses and rocky massifs. Leopards rely on broken terrain and vegetation for hunting and for refuges but can occupy areas with minimal cover. They are tolerant of habitat conversion and, provided cover and prey is present, persist in reduced densities close to large human populations. A Leopard carcass was photographed on the rim of Mt Kilimanjaro's Kibo Crater at 5638 m in 1927 (Tilman 1937) and Leopards regularly traverse mountain ridges up to 4600 m on Mt Kenya (Rödel *et al.* 2004).

Abundance Continentally, Leopards are the most abundant large felid, but published total estimates are seriously flawed. Using rainfall data as a measure of productivity, Martin & de Meulenaer (1988) estimated over 700,000 Leopards in Africa though their model omitted prey availability and anthropogenic factors as explanatory variables, and is impossibly optimistic (Jackson 1989, Norton 1990, Marker & Dickman 2005a). Local Leopard densities correlate generally with prey availability (Stander *et al.* 1997a). Estimates vary from 0.5 Leopards/100 km² in Etosha N. P., Namibia (Stander *et al.* 1997a) to 30.3/100 km² for Kruger N. P., South Africa (Bailey 2005). Based on estimates from six studies, Marker & Dickman (2005a) estimated that mean density under protection (10.5 ± 4.0 Leopards/100 km²) was almost five times as high as outside protected areas (2.1 ± 1.6 Leopards/100 km²). Similarly, density estimates from camera-trap surveys in KwaZulu–Natal, South Africa, declined along a gradient associated with the level of protection. Density was 11.1 ± 1.3 Leopards/100 km² in a core protected area, 7.2 ± 1.1 Leopards/100 km² in a protected 'buffer' area suffering from strong edge effects, and 2.5 ± 0.9 Leopards/100 km² in non-protected farm land (Balme *et al.* 2010b).

Leopards reach their highest densities in protected East and southern African mesic woodland savannas. Including all individuals over one year old, Bailey (2005) estimated 30.3/100 km² for the Sabie R. area, in southern Kruger N. P., one of the most prey-rich areas of the park (Pienaar *et al.* 1966). The estimate for adults more than 3.5 years of age was 16.4/100 km². Lower densities (12 Leopards more than one year old/100 km², and 9.5 adults/100 km²) came from an adjoining area with marked seasonal absence of water. The estimate for adults across the entire park was 3.5/100 km². High estimates also come from Londolozi G. R. adjacent to western Kruger N. P. (23.8/100 km²; Le Roux & Skinner 1989) and Matopos Hills, Zimbabwe (23.6/100 km²; Smith 1977). In East African woodland savanna mosaics, estimates include 16/100 km² (Queen Elizabeth N.



Three-toned patterning on Leopards *Panthera pardus*.

Left: Two lighter toned areas balanced out by scattered clusters of small black spots. *Centre:* Rosettes consisting of black spots regularly dispersed around medium tone. *Right:* 2, 3 or 4 lesser rosettes sometimes coalesce to form larger, jaguar-like rosettes.

P., Uganda; van Ordsol 1981), 7.5/100 km² (Ngorongoro; Schaller 1972) and 5.6/100 km² (Serengeti N. P., Bertram 1982).

Few estimates exist for West and central Africa. Martin & de Meulenaer's (1988) rainfall/density regression produced inflated estimates as high as 40/100 km² but prey biomass is too low to support such numbers (Jenny 1996). In several protected Gabon rainforest sites, density estimates using mark-recapture models applied to camera-trap data varied from 4.6 to 12.1/100 km²; outside protected areas Leopards were either absent or occurred at reduced densities ranging from 0.9 to 2.7 Leopards/100 km², due chiefly to the intense demand for bushmeat (Henschel 2008, Henschel *et al.* 2011). Based on limited telemetry data from three animals, Jenny (1996) estimated densities in rainforest in Tâi N. P., Côte d'Ivoire, at 7.1–11.0/100 km² and J. Hart (in litt., Nowell & Jackson 1996) offered a preliminary estimate of 8.3–12.5/100 km² for the Ituri forest, DR Congo.

Lowest population estimates come from habitats with low prey biomass: 0.7/100 km² for Cape fynbos habitat in South Africa (Norton & Lawson 1985, Norton & Henley 1987), 1.3/100 km² for the S Kalahari, South Africa (Bothma & Le Riche 1984, Bothma *et al.* 1997), and 1.5/100 km² for NE Namibia (Stander *et al.* 1997a). Stander *et al.* (1997a) suggested 0.5/100 km² for Etosha N. P.

Adaptations The spotted pelage provides superb camouflage in a wide variety of habitats. Camouflage is important for concealment, mainly from prey but also from predators and competitors. Darker colouration in forests and paler in arid, open habitats probably enhances habitat-specific camouflage. Similarly, melanism may confer an adaptive advantage in dark, forested habitat but the rarity of specimens in Africa suggests any gain is insignificant. The bright white underside of the tail tip is held high by ♀♀ with young cubs as a signal to follow (Schaller 1972). The ears are flattened and the pale ear patch is displayed during aggressive or defensive interactions to emphasize warning.

The Leopard is a tremendous climber, with enormously powerful forequarters and an enlarged scapula with a wide, shallow attachment area for the levator scapulae and serratus magnus muscles to assist vertical lift (Hopwood 1947, Kingdon 1977, Turner & Antón 1997). Leopards retreat to a tree when threatened and haul kills to avoid kleptoparasitism. This behaviour, combined with a catholic diet and very wide habitat tolerance, enables them to successfully compete with larger carnivores (Mills & Biggs 1993). Sunquist & Sunquist (2002) suggest that the prominent sagittal crest in the skull of ♂♂ may be an adaptation for different food habits from ♀♀, but enlarged sagittal crests are common in the ♂♂ of many species, possibly as a result of sexual selection.

Free of disturbance, Leopards are often diurnal but are chiefly crepuscular or nocturnal, strictly so when hunted or harassed by humans. In Lopé N. P., Gabon, continuous camera-trapping showed that Leopard activity cycles vary with the amount of human disturbance. In sites with high hunting pressure, Leopards used trails only at night, and in an active logging concession where some hunting occurred, movements were restricted to between 18:00 and 06:00h. In an abandoned logging concession with minimal human disturbance for six years prior to the study, over 60% of activity occurred during daylight hours (Henschel & Ray 2003).

Foraging and Food Leopards have extremely catholic diets, including at least 92 species in sub-Saharan Africa ranging from arthropods to adult male Common Elands *Tragelaphus oryx* (Kingdon 1977, Bailey 2005). Reviewing datasets from 13 countries (11 in Africa), Hayward *et al.* (2006a) demonstrated a preference for prey species within a weight range of 10–40 kg, with an optimum weight of 23 kg. Within this weight range, preferred prey generally occurred in small herds, in dense habitat and incurred a low risk of injury during capture (Hayward *et al.* 2006a). In most well-studied populations, diet is dominated by one or two ungulate species weighing less than 80 kg, and typically reflecting availability. For example, Impalas *Aepyceros melampus* comprise 47.7–92.8% of kills in various southern African mesic savannas (Mills & Biggs 1993, Radloff & Du Toit 2004, Bailey 2005), Nyalas *Tragelaphus angasii* were 43% of 217 kills in KwaZulu–Natal (Balme *et al.* 2007) and Springboks *Antidorcas marsupialis* were 65% of 80 kills in the Kalahari (Mills 1984). Leopards in West African moist savannas similarly concentrate on ungulates but large rodents, specifically the Greater Cane Rat *Thryonomys swinderianus*, comprise a high percentage of kills. Estimating mass consumed from occurrence in scats, the two most important species to Leopards in Comoé N.P., Côte d'Ivoire, were Kob *Kobus kob* (24.4–31.6%, over two separate sampling periods) and Greater Cane Rat *Thryonomys swinderianus* (11.5–15.3%; Bodendorfer *et al.* 2006). In Marahoué N. P., also in Côte d'Ivoire, Greater Cane Rats (28.0%) and Hartebeests *Alcephalus buselaphus* (27%) were almost equally important. Overall, ungulates comprised 52.9% (Marahoué) to 58.9–67.6% (Comoé) of biomass consumed.

Where medium-sized ungulates are uncommon, Leopards switch to prey weighing less than 20 kg; Common Duikers *Sylvicapra grimmia* (32.8% of kills) and Steenboks *Raphicerus melanotis* (13%) in semi-arid NE Namibia (Stander *et al.* 1997a); Klipspringers *Oreotragus oreotragus*, Grey Rheboks *Pelea capreolus* and Cape Grysbocks *Raphicerus melanotis* in mountain habitat of the Western Cape (Norton *et al.* 1986, Stuart & Stuart 1993); and Rock Hyraxes *Procavia capensis* and Klipspringers in the Matopos Hills (Grobler & Wilson 1972). Rock Hyraxes comprised 65.9% by frequency and 79.8% by mass of prey items in scats of Leopards in the alpine zone of Mt Kenya, Kenya (Rödel *et al.* 2004).

Some 17–37 prey species are identified from West and central African rainforests (Hoppe-Dominik 1984, Hart *et al.* 1996, Ososky 1998, Ray & Sunquist 2001, Henschel *et al.* 2005, 2011). Duikers, Red River Hogs *Potamochoerus larvatus*, Water Chevrotains *Hyemoschus aquaticus*, African Buffalo *Syncerus caffer*, Okapis *Okapia johnstoni* and Sitatungas *Tragelaphus spekii* comprise 40–87% of prey consumed, followed by primates, rodents, pangolins and small carnivores. Mean prey weight varied from 7.3 kg (Ray & Sunquist 2001) to 31.6 kg

(Henschel *et al.* 2005, 2011). In sites with the highest recorded mean prey weight (Ituri, Lopé and Ivindo), Red River Hogs and larger duikers (Bay Duiker *Cephalophus dorsalis* and Yellow-backed Duiker *C. silvicultor*) were the most important prey species (Hart *et al.* 1996, Henschel *et al.* 2005, 2011). Blue Duikers *Philantomba monticola* were most important in all other studies, possibly because larger ungulates were uncommon and Leopards switched to smaller prey, or alternatively because of its abundance or profitability (Ray & Sunquist 2001). Blake (2004) provided evidence that Leopards may take young Forest Elephant *Loxodonta cycotis* calves.

Primates are prominent in rainforest Leopard diet. Up to 11 species occurred in 38–41% of Leopard scats in Tai N. P. (Hoppe-Dominik 1984, Zuberbühler & Jenny 2002), 34% in Ituri (Hart *et al.* 1996) and 26% in Dzanga-Sangha, Central African Republic (Ray & Sunquist 2001). Predation on Chimpanzees *Pan troglodytes* occurs (Hart *et al.* 1996, Ososky 1998, Zuberbühler & Jenny 2002, Henschel *et al.* 2005), and Leopards are believed to be the chief cause of mortality in a Chimpanzee population in Tai N. P. (Boesch 1991). Leopards occasionally attack Gorillas *Gorilla* spp. (Schaller 1963, Watson 1999), and Gorilla remains have been found in Leopard scats in Gabon (Henschel *et al.* 2005, 2011) and Central African Republic (Fay *et al.* 1995). A Leopard scat from Salonga N. P., DR Congo, contained Bonobo *Pan paniscus* remains (D'Amour *et al.* 2006). Primates are less important to savanna Leopards. East and southern African savanna Leopards regularly kill various *Papio* baboons and vervet monkeys but overall occurrence of primates in their diet rarely exceeds 5–6% (Norton *et al.* 1986, Radloff & Du Toit 2004). In West African moist savannas, where primate species diversity and biomass is higher, primates are eaten more often; six species comprised 14.2–15.3% of biomass consumed in Comoé N. P. (Bodendorfer *et al.* 2006).

Leopards readily kill other carnivores. Cheetahs *Acinonyx jubatus* and small carnivores (<14 kg) comprised 6.8% of kills consumed ($n = 9$) in semi-arid NE Namibia (Stander *et al.* 1997a) and 6.3% of kills ($n = 5$) in the Kalahari (Mills & Biggs 1993). Jackals *Canis* spp., African Civets *Civettictis civetta* and other felids were eaten in E Zambia where ungulate density was reduced due to tsetse fly control (Wilson 1976). In more productive habitats, individual preference apparently dictates how often other carnivores are consumed. A ♀ observed by Estes (1991) ate 11 jackals over a period of several weeks in Ngorongoro Crater, and a ♂ in Bailey's (2005) study ate at least two Spotted Hyaenas *Crocuta crocuta*. However, carnivores were rarely eaten in a sample of 1452 kills from Sabi Sands G. R., South Africa (Radloff & Du Toit 2004). Similarly, three adult Cheetahs killed by Leopards in Phinda G. R., KwaZulu–Natal, were left uneaten (Hunter 1998a) and no carnivores were recorded among 377 kills compiled by Walker (1999) at the same site. Leopards are occasionally cannibalistic, mostly of cubs. A ♂ ate three cubs he killed in Phinda G. R. (Balme & Hunter 2004) and ♀♀ sometimes eat their own cubs killed by other predators (Hes 1991). A fatal clash between two adults over a carcass ended in the victor partially consuming its rival (Charsley 1977) and Steyn & Funston (2006) documented a radio-collared ♀ in Botswana killed and entirely consumed by a ♂ in an apparent dispute over the female's kill. Henschel *et al.* (2005) found the remains of at least three adults in Leopard scats collected in Gabon.

Livestock losses to Leopards vary widely, depending on availability of natural prey and husbandry practices. Between 1996 and 1999, Leopards were not blamed for any of 433 livestock losses from a

690 km² ranch in S Kenya (Patterson *et al.* 2004) and were responsible for only 3% of depredations ($n = 4$) in Voi, Kenya, between 1994 and 1998 (Kerbis Peterhans & Gnoske 2002). Leopards on a 199 km² cattle ranch in N Kenya killed an average of 4.3 cattle and 10.5 sheep per annum, costing US\$0.25/ha/year and accounting for 16.4% of all depredation costs (Mizutani 1993, 1999). In arid areas, losses tend to be higher. From complaints made by pastoralists in the arid Kweneng District, Botswana, Leopards were the most injurious predator, causing 38.2% ($n = 976$) of depredations between 1999 and 2002 (M. Scheiss pers. comm.). Similarly, in NE Namibia, Leopards were the second most costly predator after Lions to rural Ju/Hoan San communities, accounting for 42% of cattle losses, all dog and 97% of chicken losses (Stander *et al.* 1997b). Leopards are rarely reported as livestock killers from rainforest, presumably because intensive pastoralism is exceptional and livestock is usually corralled in villages overnight. Three different ♂♂ that raided the same village in Ituri, DR Congo, were in poor condition, each having lost a front paw in a cable snare (A. Blom pers. comm.): two healthy ♂♂ that killed dogs and domestic fowl in Epulu, DR Congo, were young and possibly inexperienced hunters (J. Hart pers. comm.). A commercial ranch in SE Gabon lost 30 head to a healthy adult ♂ that probably turned to cattle because uncontrolled hunting had greatly reduced the availability of wild prey (Henschel 2003).

Leopards occasionally kill people as prey. Of 78 habitual man-eaters (African and Asiatic combined) listed by Turnbull-Kemp (1967), 62 (79.5%) were healthy adults in good condition. A man-eater from M'bigou, Gabon, killed about 20 people between 1947 and 1948 before it was destroyed (Malbrant & Maclatchy 1949). Thirty people were killed and 49 injured by Leopards in Tanzania between 1993 and 1999, although the proportion comprising unprovoked predation is not reported (Games & Severre 2002).

Leopards kill opportunistically around the clock but forage mainly at night, early morning and late afternoon. Continuously radio-tracked Leopards in Tai N. P. ($n = 2$) and Cederberg Mts ($n = 3$) hunted primarily during the day with crepuscular peaks, possibly reflecting the diurnal activity patterns of prey in those sites (Norton & Henley 1987, Zuberbühler & Jenny 2002). Leopards forage primarily on the ground, where they are widely supposed to prefer the densest habitats available for hunting (Hes 1991, Sunquist & Sunquist 2002, Bailey 2005, Hayward *et al.* 2006a). However, Balme *et al.* (2007) demonstrated avoidance of dense habitats in KwaZulu–Natal even though those habitats also had the highest densities of preferred prey, probably because the likelihood of detecting prey was reduced. Instead, Leopards preferred to hunt in habitats with the highest probability of making a kill, which were those with intermediate cover levels where prey densities were also intermediate. Hunting in trees is exceptional but they often climb after arboreal prey to flush it to the ground where it is killed (Kingdon 1977) or wait in ambush below trees for arboreal prey to descend (Jenny & Zuberbühler 2005). In rainforest, arboreal primates, pangolins and squirrels are killed mostly on the ground or enter the diet via scavenging (Henschel *et al.* 2005, Jenny & Zuberbühler 2005, J. Hart pers. comm.). Leopards seldom leap directly on terrestrial prey from a tree.

Leopards forage alone, including ♀♀ with large cubs that are usually left behind. Hunting strategy varies with prey species and habitat type. In open terrain in NE Namibia, 94% of hunts consisted of stalking (mean distance stalked = 29 m, $n = 94$) followed by a

short chase (mean distance = 4.4 m; Stander *et al.* 1997a). In the S Kalahari, Leopards stalked their quarry over distances of up to 3400 m (mean distance = 195.8 m, n = 117 stalks; Bothma & Le Riche 1989). Of 13 observed hunts in Kruger N. P., seven involved stalks, one was an opportunistic pursuit and five were ambushes with no stalk (Bailey 2005). G. A. Balme (pers. comm.) recorded extended pursuits of juvenile Impalas and Nyalas up to 150 m (mean = 77.4 m, n = 6). In dense habitats with limited visibility, long stalks and chases are rare and Leopards appear to wait where encounters with potential prey are likely. Hart *et al.* (1996) observed Leopards in Ituri rainforest waiting at fruiting trees that attract duikers and Red River Hogs. Based on signs at freshly killed carcasses, Leopards ambushed their prey from a few metres away. Gabonese Leopards were observed ambushing prey along well-used game trails (P. Henschel pers. obs.), and in N Congo, a Leopard took a Red River Hog from a herd moving along a game trail (D. Morgan pers. comm.). Zuberbühler & Jenny (2002) observed a female Leopard hide in dense vegetation near monkey groups (n = 91), presumably waiting for them to move close, which they did on 61.8% of occasions; one successful attack on a Sooty Mangabey *Cercocebus atys* was observed (Jenny & Zuberbühler 2005).

Most prey species, especially larger ungulates, are killed by asphyxiation with a bite to the throat. For oversized prey, a muzzle hold is sometimes used; a 14-month-old female Leopard weighing 20 kg suffocated a mature male Impala approximately three times her weight by this method, taking 14 minutes (G. A. Balme pers. comm.). Smaller prey is typically killed by biting the back of the skull or neck. Prey is often plucked of fur or feathers before eating, which usually begins at the rump or groin. Large carcasses are consumed over a number of days and often cached in trees, less so in kopjes, Aardvark *Orycteropus afer* burrows and caves (De Ruiter & Berger 2001). Stevenson-Hamilton (1947) estimated a young Giraffe *Giraffa camelopardalis* cached in a tree at no less than 91 kg and a Kenyan ♂ hauled a month-old Black Rhino *Diceros bicornis* calf it had killed (Scott & Scott 2003). In Matopos Hills, where competitors are largely absent, only one of 38 kills was found in a tree (Smith 1977) and kills are rarely hauled in rainforest where the Leopard is the only large predator (P. Henschel pers. obs.). Most kills made by NE Namibian Leopards are dragged for long distances (mean = 140 m, range 0–762 m) and hidden on the ground in dense vegetation even though Lions, Spotted Hyaenas and other competitors are present (Stander *et al.* 1997a). Similarly, at Phinda G. R. where there are Lions and Spotted Hyaenas, Leopards stored 91% (n = 198) of their kills in dense vegetation on the ground; the rest were cached in trees (Balme *et al.* 2007). Leopards cache multiple kills up to 2 km apart and generally utilize all over a number of days (Hes 1991).

Scavenging occurs; ♂♂ sometimes usurp kills from ♀♀ (G. A. Balme pers. obs.) and Leopards appropriate kills from competitively inferior carnivores such as Cheetahs, lone Spotted Hyaenas and jackals (Hunter 1998a, L. T. B. Hunter pers. obs.). Forest Leopards scavenge the remains of Crowned Hawk-eagle *Stephanoaetus coronatus* and Chimpanzee kills, and apparently appropriate carcasses from eagles feeding on the forest floor (J. Hart pers. comm.).

Hunting success in Leopards has been most accurately established by spoor tracking in semi-arid habitat or by continuous following in southern Africa. In KwaZulu–Natal savanna woodlands, 20.2% of observed hunts ($n = 129$) during continuous follows resulted in a



Leopard *Panthera pardus*.

kill (Balme *et al.* 2007). Based on spoor-tracking, Leopards in NE Namibia killed on average every 2.7 hunts, a success rate of 38.1% (Stander *et al.* 1997a). In the S Kalahari, mothers with cubs had the highest success rate (27.9%) compared with ♀♀ without cubs (14.5%) and ♂♂ (13.6%; Bothma & Coertze 2004). Kalahari mothers killed smaller prey than lone ♀♀ or ♂♂ but travelled less for each kill and killed more often. In contrast, Namibian mothers killed only slightly more frequently than lone ♀♀ but they killed larger prey resulting in higher per capita food acquired. Annually, Kalahari Leopards average 111 (♂♂) to 243 (♀♀) kills, the higher figure for ♀♀ reflecting smaller kills (Bothma & Le Riche 1986). Kruger N. P. Leopards make fewer but larger kills, estimated at one adult Impala per week (Bailey 2005). Namibian Leopards average 1.6 kg (♀♀) to 3.1 kg (♂♂) of meat per day while Kruger N. P. ♀♀ averaged 2.9 kg/day and two ♂♂ ate 4.4–4.7 kg/day (Bailey 2005).

Social and Reproductive Behaviour Leopards are solitary and territorial. Adults socialize mainly when mating but familiar non-mating pairs regularly meet and associate briefly (<24 hours) without aggression. Males are tolerant of cubs belonging to ♀♀ they have mated and interact with mothers and cubs more often than widely reported but never as long-term associations (L. T. B. Hunter pers. obs.).

Both sexes maintain enduring home-ranges in which ranges of ♂♂ are large and typically overlap one or more smaller ranges of ♀♀ (but see Marker & Dickman 2005a). Range size is broadly correlated with prey availability; where prey availability and hence Leopard density is high, ranges are small though high levels of human persecution possibly elevate range size above that predicted by prey availability alone (Marker & Dickman 2005a). Range size of adults estimated from radio-tracking varies from 5.6 to 2750.1 km². In Kenya, ranges were 14.4 km² for a ♀ and averaged 52.0 km² (17.9–63.9 km², *n* = 3) for ♂♂ in Tsavo N. P. (Hamilton 1981), and 16.9 km² (*n* = 2) for ♀♀ and 37.1 km² (*n* = 2) for ♂♂ on ranchlands (Mizutani & Jewell 1998). In a W Tanzanian hunting concession ranges for ♀♀

averaged 25.1 km² (17.7–36.6 km², *n* = 4) and 136.4 km² for ♂♂ (87.0–164.7 km², *n* = 3; Caso 2002). Southern Kruger N. P. ♀♀ had ranges averaging 16.4 km² (5.6–29.9 km², *n* = 5) while ♂♂ averaged 52.0 km² (16.4–96.1 km², *n* = 5; Bailey 2005). Range size for three ♂♂ in Cederberg Wilderness, South Africa, averaged 51.0 km² (40–69 km², Norton & Henley 1987). In rainforest, Jenny (1996) estimated range sizes of 22 km² and 29 km² for two ♀♀, and 86 km² for a ♂. Ranges are much larger in less productive habitats. NE Namibian ranges averaged 188.4 km² (182.9–194.4 km², *n* = 3) for ♀♀ and 451.2 km² (210–1163.5 km², *n* = 6) for ♂♂ (Stander *et al.* 1997a). This is comparable with range size on commercial Namibian farmlands (♀♀, 179.0 ± 148.2 km², *n* = 4; ♂♂ 229.0 ± 95.1 km², *n* = 3), though prey biomass was significantly higher and anthropogenic factors may have elevated range size (Marker & Dickman 2005a). In the Cape Fold Mts, South Africa, a female's range was 487 km² and a male's was 388 km² (Norton & Lawson 1985). In the S Kalahari, mean range size for ♀♀ was 488.7 km² (94.0–693.0 km², *n* = 5) and two males' ranges were 1893.0 and 2750.1 km² (Bothma *et al.* 1997). Marker & Dickman (2005a) found no difference between wet and dry season range size in NC Namibian leopards.

Although territorial adults curtail intrusion by same-sex conspecifics, overlap of home-ranges within sexes is often considerable. Leopards avoid conflict by temporally separating activity in overlapping areas (Stander *et al.* 1997a). Mean intra-sexual range overlap for two separate tenure periods in NE Namibian Leopards was 35.3–42.7% in ♀♀ and 29.3–46.0% in ♂♂ (Stander *et al.* 1997a). In NC Namibian farmlands, female Leopards overlapped by 22 ± 13% while ♂♂ overlapped by 24 ± 13% (Marker & Dickman 2005a). In Tai N. P. rainforest, a male's range encompassed the entire range of one ♀ and 73% of the second female's range while range overlap between both ♀♀ was about one-sixth of their respective ranges (Jenny 1996). Mizutani & Jewell (1998) observed no overlap between four Kenyan ♂♂ and little or no overlap between five ♀♀ except for an adult and subadult, probably mother and daughter. Average territorial tenure for male Leopards in Phinda was 2.4 years (*n* = 7, range 0.5–7.3 years), though four animals were replaced due to human-mediated mortality (Balme *et al.* 2010b).

Both sexes scent-mark by cheek-rubbing and spraying vegetation, and by depositing scats and scraping the ground with hindfeet. Scent marks are deposited along frequently used routes including roads, trails and game paths, and along range boundaries. Following a territorial male Leopard for 65 min, when he was never out of sight, G. A. Balme (pers. comm.) observed 17 sprays, six scrapes and five territorial calls. Both sexes in Tai N. P. carried out regular marking 'tours' along trails 1–3 times a week, placing scrapes at more or less regular distances averaging 3.6 scrapes per km (S.D. = 0.4, *n* = 471); defecation occurred on average every 2.1 km (Jenny 1996). In Gabon, camera traps placed along trails where Leopard scats and scrapes were abundant showed that male Leopards revisited sites every ten days on average (S.D. = 5.3, *n* = 25). The abundance of fresh Leopard sign suggested that renewing the markings was one of the chief purposes of these regular movements (P. Henschel pers. obs.).

Leopards have a limited vocal repertoire. The most distinctive call, sawing (also called coughing or rasping) carries up to 3 km and probably serves a dual function in advertising territorial occupancy and reproductive availability. Sawing is most frequent during peak activity periods at dawn and dusk. Bailey (2005) identified known

individuals by this call so Leopards probably make a similar distinction. Leopards also make a puffing sound through the nose and lips called chuffing, used as a close-range call during friendly encounters, appeasement or courtship. Leopards growl, snarl, spit and hiss during aggressive encounters and mothers call cubs with a soft grunt.

Scent-marking and vocalizations ensure Leopards usually avoid territorial confrontations. When they occur, encounters are largely demonstrative with typically ritualized feline aggression; lateral presentation, arched back, stiff-legged walk, bared teeth and flattened ears displaying the white patches. On rare occasions when encounters escalate, fights are sometimes fatal. A ♂ and a ♀ killed in separate same-sex territorial fights both died from a single nape bite in which one or both maxillary canines punctured the spinal column and/or a mandibular canine pierced the external jugular vein (Balme & Hunter 2004).

Oestrous ♀♀ show increased rates of vocalization and scent-marking (G. A. Balme pers. comm.), the latter likely associated with elevated sex hormones. Females sometimes wander far outside their territory during oestrous periods, presumably to locate ♂♂; G. A. Balme (pers. comm.) recorded such excursions measuring up to 4.7 km. Mating is typically feline. G. A. Balme (pers. comm.) recorded 215 copulations over a 48-hour period while continuously monitoring a mating pair. In 13 copulations observed by Laman & Knott (1997), all were initiated by the ♀ walking from side to side in front of the ♂, brushing against him and waving her tail in his face. Males usually bite the ♀ on the nape during mating and both sexes growl continually during copulation. Copulation averages 3.0 sec (range 2.0–4.0 sec, *n* = 7) and the average interval between 11 observed copulations was 6.5 min (2–17 min, Laman & Knott 1997). Mating reaches a peak around dawn and dusk when the interval between 452 recorded copulations was 5.4 min (G. A. Balme & L. T. B. Hunter pers. obs.); the interval was 14.7 min (52 copulations) at midnight, and 21.2 min (37 copulations) at midday. Mating associations are brief, averaging 2.8 days at Phinda (range 1–5 days; G. A. Balme pers. comm.), two days in Kruger N. P. (range 1–4; Bailey 2005) and no more than a day in Kalahari observations (Bothma & Le Riche 1984). Contrary to Laman & Knott's (1997) suggestion that one ♂ has exclusive mating access to one or more ♀♀, high overlap between female and male ranges as well as between male ranges facilitates oestrous ♀♀ meeting numerous ♂♂ (Stander *et al.* 1997a). A radio-collared ♀ in Phinda G. R. mated with at least three ♂♂ in three days (L. T. B. Hunter pers. obs.). As well as increasing chances of conception and male competition for mates, female promiscuity probably reduces the risk of infanticide by confusing paternity. Infanticide by non-sire ♂♂ occurs (Scott & Scott 2003, Balme & Hunter 2004).

Reproduction and Population Structure Leopards give birth year round. Bailey (2005) suggested a weak peak among six litters associated with the birth flush of Impalas in Kruger N. P. though 16 litters recorded in the neighbouring Londolozi G. R. showed no peak (Hes 1991). In captivity, oestrus lasts 7–14 days and the oestrous cycle averages 45 days (range 20–50 days; Sadlier 1966). Gestation lasts 90–106 days. Litters normally comprise 1–3 cubs, though up to six have been recorded in captivity. Mean litter-size at emergence was 1.7 at Phinda (range 1–3, *n* = 15; Balme *et al.* 2009), 1.8 at Londolozi G. R. (range 1–3, *n* = 13; Hes 1991) and 2.3 in Masai Mara National Reserve (range 1–3, *n* = 14; Scott & Scott 2003). Newborn cubs

weigh 430–1000 g (captivity) and open their eyes on Day 6–10 (Skinner & Chimimba 2005). Cubs are denned in thick vegetation, among rocks, tree roots, in caves or Aardvark burrows. The ♀ observed by Le Roux & Skinner (1989) moved her young cubs to new dens every 2–3 days. She first presented them with meat at day 65 and suckling ceased after 101 days. Cubs are led to kills from weaning.

Mean interval between successfully raised litters was 16.2 months at Phinda ($n = 6$, range 11–20 months; Balme *et al.* 2009), 16.6 months at Londolozi G. R. ($n = 11$; Hes 1991), 25 months for a Serengeti female's consecutive two litters (Schaller 1972), and ranged from 24 to 36 months for five Kruger N. P. ♀♀ (Bailey 2005). Females resume oestrus rapidly after losing a litter, giving birth again within 5–7 months (mean = 5.7, $n = 3$; Seymour 2004). Two ♀♀, in Kenya and South Africa, each had nine litters between 1979 and 1989; the South African ♀ raised at least one cub to independence in eight of her litters (Hes 1991, Scott & Scott 2003). Cub mortality in the first year varies from 50% (Kruger N. P.; Bailey 2005) to 90% (S Kalahari; Bothma & Walker 1999). The average proportion of ♀♀ producing cubs in Kruger N. P. was 27.7% (Bailey 2005). Stander *et al.* (1997a) calculated that NE Namibian ♀♀ spend about half of their adult lives with dependent cubs, though a South African ♀ intensively monitored between 1979 and 1991 (139 months) had dependent cubs for 108 months (78%; Hes 1991). Adoption of related cubs has been documented; for example, a 15-year-old ♀ adopted the 7-month-old male cub of her 9-year-old daughter and successfully raised him to independence (Balme *et al.* 2012).

Cubs reach independence at 7–18 months; mean at Phinda was 12.3 months ($n = 8$, range 7–15 months; Balme *et al.* 2009) and at Londolozi G. R. was 12.8 months (range 10–14 months, $n = 8$; Hes 1991). Dispersal of subadults is poorly known but ♀♀ sometimes inherit part of their mother's range while ♂♂ tend to disperse more widely (Le Roux & Skinner 1989, Hes 1991). Two subadult ♂♂ in Namibia stayed in their mother's range for 6–8 months before dispersing 25 km and 162 km, respectively (Stander *et al.* 1997a). One died in his new range six months later while the other (the further disperser) returned to his mother's range, which he occupied for five months before being killed for livestock raiding. A Kalahari subadult ♂ settled in a new range 112.6 km from its natal range (Bothma *et al.* 1997). Estimated annual mortality of subadults is 32% (Kruger N. P.) to 52.6% (Phinda G. R.) compared with adult mortality of 18.5% (Kruger N. P.; Bailey 2005) to 38.9% (Phinda G. R.; Balme & Hunter 2004). Stander *et al.* (1997a) suggest that mortality among subadults is high when the population is at ecological carrying capacity, supporting the notion that population regulation is density-dependent.

Leopards of both sexes are sexually mature at 24–28 months though wild ♀♀ rarely have their first litter before 33–36 months (Hes 1991, G. Balme & L. Hunter pers. obs.). Mean age at parturition for four known-age ♀♀ at Phinda was 43.3 months (range 36–48 months; Balme *et al.* 2009). Males are unlikely to win territory and access to ♀♀ until age 3.5 at earliest; a four-year-old immigrant ♂ in Phinda G. R. killed a resident ♂ about twice his age and mated numerous ♀♀ in the months immediately following (L. T. B. Hunter pers. obs.). Longevity in wild Leopards is poorly known; a Namibian ♀ of 15.4 years is recorded (Stander & Hanssen 2001) and a known-age female at Londolozi G. R. died aged 16.7 years (L. Hes pers. comm.). Adults can probably reproduce until death; the same Londolozi ♀ gave birth when she was 16.3 years old (Seymour 2004,

L. Hes pers. comm.) and captive animals of both sexes reproduce up until 19 years (Shoemaker in litt., Nowell & Jackson 1996). Sex ratio of adults in a protected population is 1 ♂ to 1.8 ♀♀ (Bailey 2005).

Predators, Parasites and Diseases The Lion is the only African carnivore in which a single aggressor is easily capable of killing a healthy adult Leopard. Lions exert considerable effort in pursuing Leopards even though they probably represent little competition; two Lionesses treed an adult male Leopard for over 30 hours before it slipped away while the Lions were sleeping (L. T. B. Hunter pers. obs.). Other large, group-living carnivores working in concert occasionally kill Leopards. Several Spotted Hyaenas can kill a Leopard, and a pack of 10 African Wild Dogs *Lycaon pictus* killed a young adult Leopard caught on open ground in N Botswana (K. Leo-Smith pers. comm.). Pairs or groups of adult male baboons have killed Leopards, usually in defence (Marais 1939, Cowlshaw 1994). At least one adult ♂ during Bailey's (2005) study was killed by a Nile Crocodile *Crocodylus niloticus* and Turnbull-Kemp (1967) reported an adult Leopard disgorged by an African Rock Python *Python sebae*.

Young animals are especially vulnerable to predation from Lions and, less so, Spotted Hyaenas, which account for most first-year mortality in protected populations. Unattended cubs could be killed by Brown Hyaenas *Hyaena brunnea*, Striped Hyaenas *H. hyaena*, Cheetahs, Caracals *Caracal caracal* and jackals though there are no reports and predation by these species is probably rare. An adult male Chimpanzee in Mahale N. P., Tanzania, snatched a very young cub from a cave with the mother Leopard present, eventually killing it but not eating it (Byrne & Byrne 1988). A 15-month-old independent ♂ weighing approximately 36 kg died of wounds inflicted by a single Spotted Hyaena (Balme & Hunter 2004). Intra-specific clashes account for significant mortality in some populations. Of 35 radio-collared Leopards monitored for 69 months in Phinda G. R., four adults and three cubs were killed by conspecifics (Balme *et al.* 2009). Seymour (2004) suggests infanticide is the chief cause of mortality in Londolozi cubs, but cause of death was inferred rather than observed.

Leopards test positive for numerous infectious diseases but known mortalities are restricted to individuals, and epidemics are unknown



Leopard *Panthera pardus*; black and white markings around mouth emphasize expression.

(Spong *et al.* 2000b). Four Leopards died of anthrax in northern Kruger N. P. after scavenging from infected carcasses (Pienaar 1969) but carnivores, including Leopards, are resistant and deaths are uncommon (Meltzer 1997). Rabies in Leopards has been confirmed from Botswana, Namibia and Zimbabwe at low incidences (van Vuuren *et al.* 1997). Canine distemper occurs widely in Leopard populations and bovine tuberculosis infection in African Buffalo has spilled over into Kruger N. P. Leopards but few deaths are known from either (Keet *et al.* 1996). Leopards have tested positive for feline immunodeficiency virus, feline calicivirus, feline panleukopenia, parvovirus and herpes virus, apparently without clinical signs or mortality though some of these diseases are occasionally fatal in captives. Southern African Leopards tested negative for feline leukaemia virus (van Vuuren *et al.* 1997).

Boomker *et al.* (1997) provide a comprehensive list of parasites, most with little zoonotic or disease significance. Leopards carry at least 32 species of ticks but grooming usually ensures infestations are moderate. The most common ticks on Kruger N. P. Leopards were *Rhipicephalus* spp. (Bailey 2005; and see Horak *et al.* 2000). The feline ear mite *Notoedres cati*, which gives rise to mange, affected 53% ($n = 16$) of Leopards in Bailey's study population in the Kruger N. P. Mange was worse in Leopards already in poor condition and probably contributed to mortality by secondary infections. There is no evidence that *Sarcoptes* mites, common in Lions, affect Leopards (Boomker *et al.* 1997). Walsh *et al.* (2004) provide anecdotal evidence from Lopé, Gabon, that stings of introduced Little Red Fire Ants *Wasmannia auropunctata* causes blindness in Leopards, but no data are available on survival or other impacts. At least two-dozen helminth parasites have been isolated from Leopards, the most important being *Trichinella*, various hookworms and ascarids (Boomker *et al.* 1997). Protozoan parasites include *Trypanosoma brucei rhodesiense* for which Leopards are a potential reservoir and were implicated in an outbreak of human sleeping sickness in Uganda (Kangwagye 1977). Leopards carry *Babesia* protozoans that are transmitted by the bites of ticks and give rise to potentially lethal babesiosis (Boomker *et al.* 1997, Bailey 2005).

Conservation IUCN Category: Near Threatened. CITES: Appendix I.

Although Leopards occur in numerous protected areas across their range, the majority of the population occurs outside of protected areas. Leopards are at risk mainly from habitat conversion and intense persecution, especially in retribution for real and perceived livestock loss (Ray *et al.* 2005). Estimates of removals by pastoralists are poorly reported; between 2001 and 2005, at least 41 Leopards were removed from 14 commercial Namibian farms with a combined size of 1484 km² (Stein 2005). Leopards are surprisingly resilient and persist where other large cats cannot, albeit at severely reduced densities estimated at 0.1–0.01 of normal (Martin & de Meulenaer 1988, Marker & Dickman 2005a, Henschel 2008). Outside protected areas, tourism can offset livestock losses to Leopards and foster their conservation; in a trial programme among a Ju/Hoan San community in Namibia, revenue generated by Leopard-viewing tourism exceeded losses to Leopards by 12-fold and all livestock losses by 2.6-fold (Stander *et al.* 1997a). In intact African rainforest, the chief threat to Leopards is probably competition with human hunters for prey (Henschel *et al.* 2011); the tremendous volume of

wild meat harvests denudes forests of prey and may drive localized extinctions (Wilkie *et al.* 2000, Ray 2001, Henschel 2009).

Legal international traffic is limited largely to exports of skins and hunting trophies by 13 countries (2011 CITES quota is 2648). The impact of trophy hunting on populations is unclear but it may constitute additive rather than compensatory mortality, especially when ♀♀ are shot (Spong *et al.* 2000a, Balme *et al.* 2010a). In Tanzania, which allows only ♂♂ to be hunted, ♀♀ comprised 28.6% of 77 trophies shot between 1995 and 1998 (Spong *et al.* 2000a). Overhunting (legal and illegal combined) of ♂♂ may diminish female reproductive output; preliminary evidence from 29 months of intensive monitoring at Phinda G. R. suggested that elevated turnover of ♂♂ due to human hunting gave rise to increased rates of infanticide and reduced rates of conception (Balme & Hunter 2004). Illegal killing of Leopards is poorly quantified, but occurs widely. Eight of 17 human-mediated deaths adjacent to Phinda were illegal (the rest were legal removals or accidents). Leopards were illegally shot on community land ($n = 1$), farmland ($n = 2$) and commercial game ranches ($n = 3$), and two adult ♂♂ were killed in poachers' snares. In the same population, one juvenile was hit by a vehicle on a public road, and two additional Leopards were hit by vehicles just prior to and immediately after the study (Balme *et al.* 2010b). Annual mortality rates in the same population dropped from 45% to 11% and population growth improved from 0.972 to 1.217 after the introduction of mitigation measures designed to improve the sustainability of legal anthropogenic mortality and reduce illegal persecution (Balme *et al.* 2009, 2010a).

Skins and teeth (canines) are still widely traded domestically in some central and West African countries where parts are used in traditional rituals and sold openly in villages and cities (Henschel & Ray 2003). In Guinea and Guinea-Bissau, Leopard skins are valued for traditional ceremonies, and as trophies by a wealthy urban middle class and tourists; skins are openly sold in front of international hotels in Conakry, Guinea, and hunting for skins is considered the chief threat to the species in the two countries (Brugière *et al.* 2005). In N Congo, 15 Leopard skins were seized from local hunters over a two-week period in 2000 (Ray & Quigley 2001) and skins are common in the large markets of Côte d'Ivoire where they fetch up to US\$250 (Gross 1998). In Ghana, Leopard parts have been recorded only six times since 1999 in urban bushmeat markets but hunter interviews suggest that most (perhaps 60–95%) of large carnivore parts are traded outside formal markets (J. Brashares pers. comm.). Djibouti is an important conduit for Leopard skins from East Africa, which are bought mainly by French military personnel and carried illegally to Europe. Künzel *et al.* (2000) counted 44 Leopard skins in tourist shops on one day in 1999. Leopard skins reportedly from Niger and Chad are freely available in markets in Morocco. Shipp (2002) counted 17 skins in a two-hour period in one Marrakech market and was offered a further 20, including courier delivery to the UK. Illegal traffic of skins was previously considered less common in southern Africa, but there is increasing evidence for organized trade; skins of at least 150 individuals were seized between 2004 and 2008 from a single supplier in KwaZulu-Natal where the demand is for Nazareth Baptist ('Shembe') Church religious attire. At least 1000 *amambatha* (shoulder capes) representing a minimum of 500 leopards were counted at one Shembe gathering in 2011 (T. Dickerson pers. comm.). With the rapid growth of the Shembe church in southern Africa, the demand for skins is expected to grow (Papini 2004, Tishken 2006).

Measurements*Panthera pardus*

HB (♂ ♂): 1380 (1350–1430) mm, n = 6

HB (♀ ♀): 1138 (1090–1180) mm, n = 4

T (♂ ♂): 852 (780–900) mm, n = 6

T (♀ ♀): 818 (800–850) mm, n = 4

WT (♂ ♂): 51.4 (45.0–61.0) kg, n = 6

WT (♀ ♀): 32.9 (27.5–38.0) kg, n = 4

Comoé N. P. (F. Fischer pers. comm.) and Taï N. P., Côte d'Ivoire (D. Jenny pers. comm.)

HB (♂ ♂): 1340 (1160–1830) mm, n = 59

HB (♀ ♀): 1143 (1050–1270) mm, n = 58

T (♂ ♂): 833 (710–930) mm, n = 59

T (♀ ♀): 764 (640–850) mm, n = 58

WT (♂ ♂): 53.0 (34.0–69.0) kg, n = 59

WT (♀ ♀): 30.5 (20.5–42.0) kg, n = 58

C Namibia (Conradie 2004, C. Conradie pers. comm.)

HB (♂ ♂): 1107 (920–1250) mm, n = 21

HB (♀ ♀): 1030 (950–1050) mm, n = 8

T (♂ ♂): 678 (510–800) mm, n = 20

T (♀ ♀): 677 (640–740) mm, n = 8

HF c.u. (♂ ♂): 219 (190–252) mm, n = 20

HF c.u. (♀ ♀): 206 (190–220) mm, n = 7

E (♂ ♂): 73 (65–100) mm, n = 20

E (♀ ♀): 70 (65–72) mm, n = 7

WT (♂ ♂): 30.9 (20.0–45.0) kg, n = 27

WT (♀ ♀): 21.2 (17.9–26.0) kg, n = 9

Northern Cape, Western Cape and Eastern Cape provinces, South Africa (Stuart 1981)

HB (♂ ♂): 1301 (1225–1370) mm, n = 11

HB (♀ ♀): 1054 (1010–1095) mm, n = 7

T (♂ ♂): 876 (785–935) mm, n = 10

T (♀ ♀): 783 (750–815) mm, n = 7

WT (♂ ♂): 64.5 (60.0–72.0) kg, n = 10

WT (♀ ♀): 35.0 (29.0–43.0) kg, n = 7

N KwaZulu–Natal (South Africa) (L. T. B. Hunter & G. A. Balme pers. obs.)

Key References Bailey 2005; Henschel & Ray 2003; Stander *et al.* 1997a; Sunquist & Sunquist 2002.**Luke Hunter, Philipp Henschel & Justina C. Ray****Tribe FELINI – Smaller Cats**

Felini Fischer de Waldheim, 1817. Mém. Soc. Imp. Nat. Moscow 5: 372

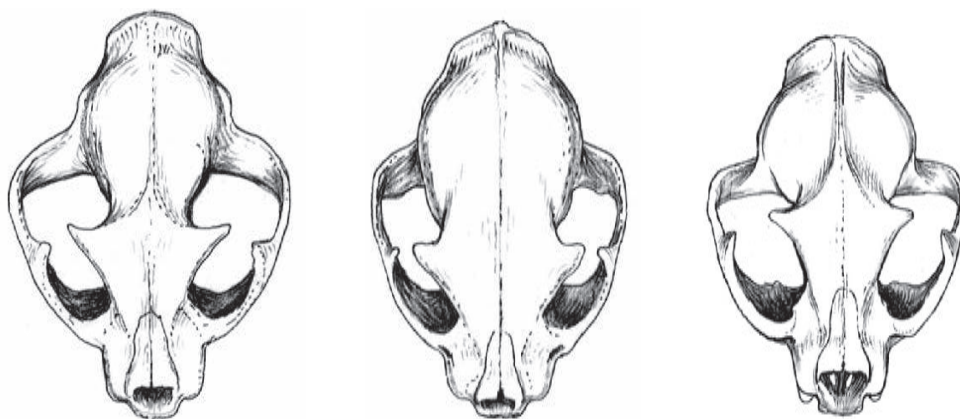
In Africa, tribe Felini is represented by five genera: *Felis*, comprising four species, and *Profelis*, *Caracal*, *Leptailurus* and *Acinonyx*, each includinga single species. Felini mostly radiated outside Africa; however, *Profelis*, *Caracal* and *Leptailurus* likely represent a single intra-African radiation.**GENUS *Profelis*****African Golden Cat***Profelis* Severtzov, 1858. Revue Mag. Zool. Paris (2), 10: 386.*Profelis* is a monotypic genus endemic to Africa. Although some authors have included its single representative, the African Golden Cat, in the genus *Felis* (e.g. Král & Zima 1980, McKenna & Bell 1997), many authors have followed Pocock (1917) in placing the species in the genus *Profelis* (e.g. Van Mensch & Van Bree 1969, Groves 1982, Wozencraft 1993, 2005). Despite studies that show affinity with *Catopuma* (which includes the Asian Golden Cat *C. temminckii*) (e.g.Weigel 1961, Bininda-Emonds *et al.* 1999), more recent molecular data unequivocally reveal that the Caracal *Caracal caracal* and the Serval *Leptailurus serval* are closely allied with the African Golden Cat, having diverged 8.5 mya (Janczewski *et al.* 1995, Johnson & O'Brien 1997, Mattern & McLennan 2000, Johnson *et al.* 2006).**Justina C. Ray & Thomas M. Butynski*****Profelis aurata* AFRICAN GOLDEN CAT**

Fr. Chat Doré Africain; Ger. Afrikanische Goldkatze

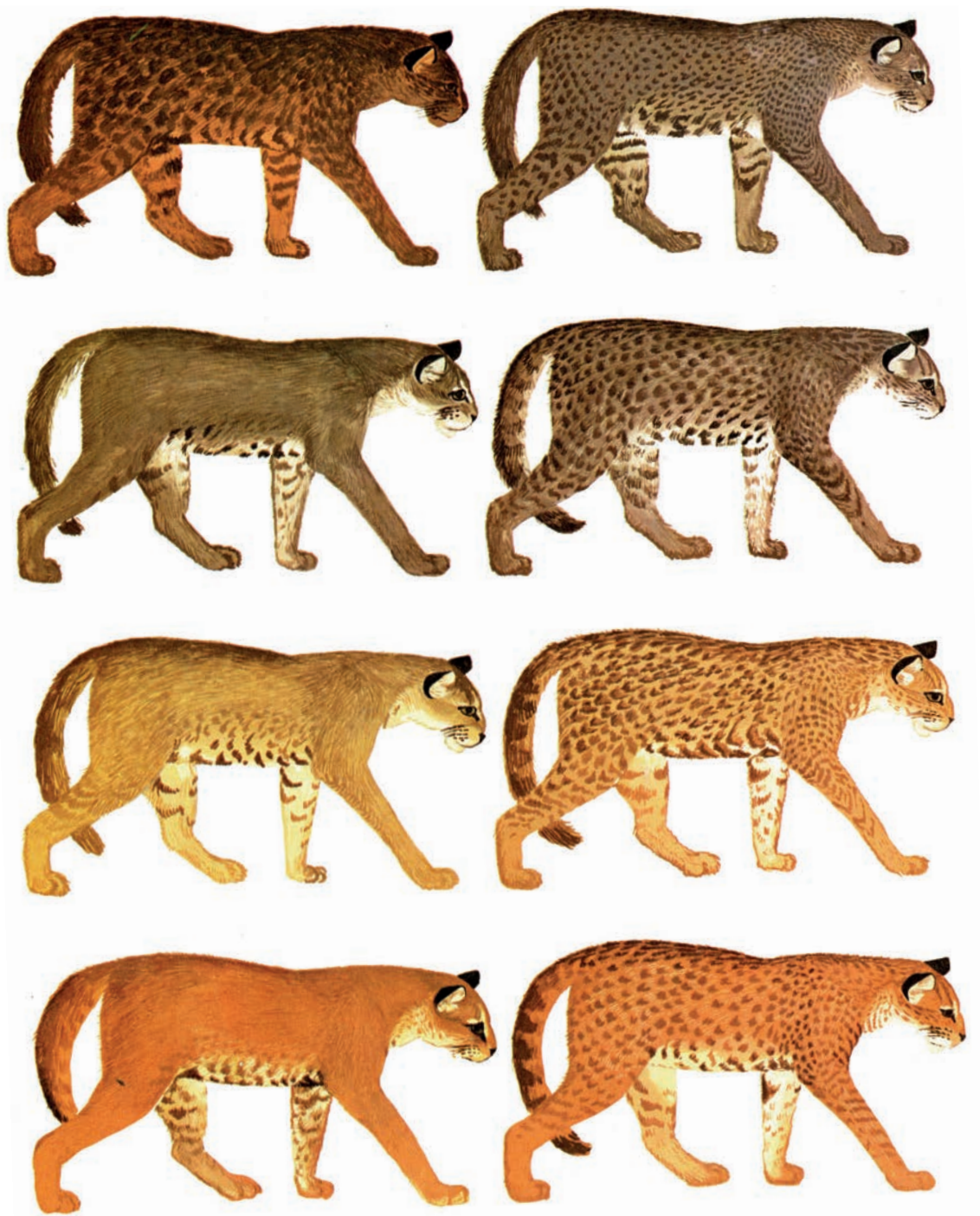
Profelis aurata (Temminck, 1827). Monogr. Mamm. 1: 120. 'Nous ne savons pas au juste dans quelle partie du globe a été trouvé'; fixed by Van Mensch & Van Bree (1969) to 'probably the coastal region of Lower Guinea (Between Cross River and River Congo ...)'.

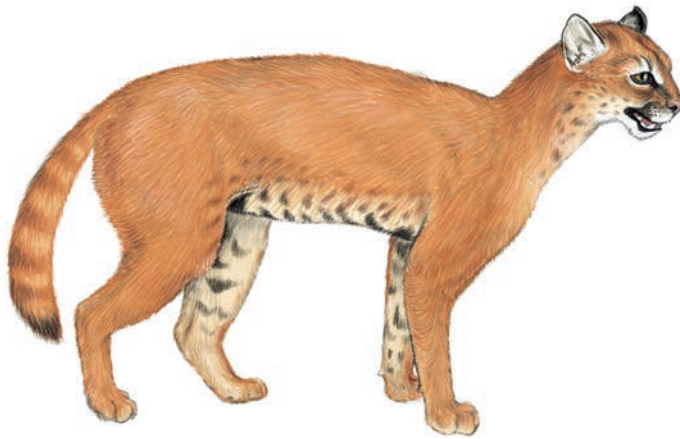
Taxonomy Marked variability across the range in pelage colour and pattern is responsible for a number of independent descriptions. Colour phases have been described as several species, but Pocock (1907), Van Mensch & Van Bree (1969) and others found pattern ofpelage more important for taxonomy than colour. Two subspecies are usually recognized (Smithers 1975). Synonyms: *celidogaster*, *chalybeata*, *chrysothrix*, *cottoni*, *maka*, *neglecta*, *rutila*. Chromosome number: 2n = 38 (Malouf & Schneier 1965).

Dorsal views of skulls of left to right,
Leptailurus, *Caracal* and *Profelis*.



BELOW: Polymorphic coat patterns in African
Golden Cat *Profelis aurata* (spotted morphs
more common in West Africa, unspotted
morphs more common in East Africa)



African Golden Cat *Profelis aurata*.

Description Medium-sized, solidly built cat with short face, heavy muzzle, small head, rather small black-backed ears and medium-length tail. Head round and small with distinctive light patches around eyes and above mouth. Chin, cheeks, throat, chest and belly off-white to pure white. Eyes green to golden-brown. Ears short, rounded, untufted and shiny black on the back. Hair on back of neck reverses direction, orienting forwards in one or two whorls and a low ridge. Pelage colour highly variable, ranging through pale sandy, reddish-brown, chestnut-red, chocolate-brown, greyish-brown, silver-grey, bluish-grey, to jet-black (melanistic) (see Geographic Variation). Pelage texture varies from short and rough to long and soft. Hairs on mid-dorsal line dark, tipped black or brown; may have distinct or obscure banding. Underhairs always grey; dark grey to dark brown spots nearly always visible on belly and inside limbs; spotting elsewhere ranging from absent to densely covering entire body. Spots vary from large and distinct circles or rosettes, to small and obscure freckles. Limbs short, stout and strong. Claws fully retractile, soles densely haired between pads. Tail 35–45% length of head and body. Sexes alike in colour, but ♂♂ have body measurements ca. 10% longer than ♀♀, and weigh about one-third more.

Skull relatively elongated; muzzle heavy and slightly enlarged. Sagittal crest well developed, and zygomatic arches more or less straight. Foramen large, narrow and elliptical. The auditory bullae are well developed. The carnassial teeth are relatively large, and the first premolar is reduced to a peg; third premolar with anterior cusp very small or absent.

Geographic Variation

P. a. celidogaster: west of Cross R. Usually with spotting all over body, with dark mid-line along back and tail banded, either distinctly or indistinctly.

P. a. aurata: east of Congo R. to Kenya. No spotting except on flanks and belly; dark mid-dorsal line absent; tail not banded or indistinctly banded.

East of the Cross R. and west of the Congo R. there is a large intermediate or clinal zone (Van Mensch & Van Bree 1969).

Pelage colour, and dorsal pelage spotting and texture are variable throughout the range (described and illustrated in detail by Van Mensch & Van Bree [1969] and Kingdon [1977]; and see Boy [2003]). Colour phases do not represent geographic races, as individuals of

*Profelis aurata*

different colours are present in the same areas (Van Mensch & Van Bree 1969, Rosevear 1974, T. Butynski pers. obs., T. Davenport, J. Hart, & P. Henschel pers. comm.). Captive individuals have reportedly changed colour from rufous to grey or vice-versa in a period of months (Pocock 1907, Brooks 1962, Boy 2003). In a study of incidence of colour phase among 186 skins, Van Mensch & Van Bree (1969) found no correlation between pelage colour and season, age, size, sex, locality, or climate. Of these 186 skins, 50% were russet/brownish, 46% grey/greyish and 4% black (melanistic); roughly the same percentages held when data from 68 additional individuals were combined (T. M. Butynski & J. C. Ray pers. obs.).

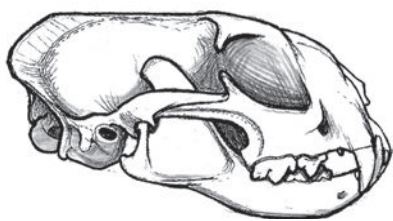
Similar Species

Leptailurus serval. In forest edge, savanna and woodland from S Senegal eastwards to Ethiopia and S Somalia south to South Africa and SW Angola. Build sligher; ears larger with white patch on backside; muzzle smaller; fur on neck does not change direction; limbs longer and thinner; parastyle of upper third premolar present. Van Mensch & Van Bree (1969) detail distinguishing characteristics between the skull of the African Golden Cat and Serval.

Caracal caracal. Largely allopatric, being absent from the forest zone of Equatorial Africa. Ears longer and triangular with long tufts; muzzle smaller and shorter; fur on neck does not change direction; hindquarters higher.

Panthera pardus. Broadly sympatric. Larger build, with distinct spotting including on face and neck; back of ears with prominent pale patch.

Distribution Endemic to the forest zone of Equatorial Africa, from S Senegal eastwards through Guinea, Sierra Leone, Côte d'Ivoire and Ghana, and again from E Nigeria and Cameroon through Gabon, Equatorial Guinea, Congo, SW Central African Republic, DR Congo, S Sudan to Uganda; the southern limit ranges from N Angola through DR Congo to Rwanda and Burundi (Rosevear 1974,



Lateral view of skull of African Golden Cat *Profelis aurata*.

Monfort 1992, Nowell & Jackson 1996). Also, in Omo N. P., Ethiopia (Schloeder & Jacobs 1996), and Mau Forest, Kenya (Toschi 1946). No other specimens known for Kenya, but reliable sightings reported for Mt Kenya (T. Archer pers. comm.; although not reported by Young & Evans [1993]), Aberdares Range (Hardy 1979, Watson 1980, Seth-Smith 1995), Ol Keju R. and Natron Swamp (Boy 2003) and Arabuko-Sokoke Forest (Virani 1993). Although suitable habitat exists in parts of Tanzania, there is no evidence for their presence to the east of L. Tanganyika.

Since most museum specimens of African Golden Cat were purchased by collectors from hunters or markets, the precise origin of many is in doubt (Rosevear 1974). A record from Chad (mapped in Boy 2003) was a captive zoo specimen (Van Mensch & Van Bree 1969). A record from Gambia (Van Mensch & Van Bree 1969) was rejected by Grubb *et al.* (1998); there also are no confirmed records from Guinea-Bissau, Togo and Benin (Van Mensch & Van Bree 1969, Sayer & Green 1984). Hapold (1987) noted there was no evidence that the species occurs in Nigeria as suggested by earlier authors, but the species definitely does occur at least in the Gashaka-Gumti N. P. on the Cameroon border (Nicholas 2004). A record from Mali (with locality given as Nioro; Bigourdan & Prunier 1937) is likely to be in error (Van Mensch & Van Bree 1969).

Habitat Africa's only forest-dependent felid, occurring in lowland and montane rainforest, swamp forest, bamboo forest, as well as alpine moorland (Rahm & Christiaensen 1963, Nowell & Jackson 1996, Andama 2000, Boy 2003). Penetrates drier regions by using gallery forest along major rivers (Van Mensch & Van Bree 1969, Kingdon 1977), wooded savannas (Brugière 2001), and savanna/forest mosaics (C. Tutin pers. comm.). Recorded from near sea level up to 3600 m in Uganda (Guggisberg 1975). Adapts well to selectively logged areas, presumably in response to increased prey abundance in dense secondary growth; also seen on roads, in banana plantations and near small villages (Kingdon 1977, Watson 1980, Virani 1993, Davenport 1996, C. Chapman, A. Gautier-Hion & J. Hart pers. comm.).

Abundance Thought to be very rare, based on the fact that African Golden Cats are so rarely observed in the field, even by field biologists who have spent many years within the species' range. However, the relatively high frequency at which skins are found among hunters, in bushmeat markets and in museums, may be an indication that they are more abundant than suggested by the low incidence of observations in the wild (Malbrant & Maclatchy 1949, Rosevear 1974, T. Davenport pers. comm.). In most localities, African Golden Cats seem to be more abundant in undisturbed and little-disturbed forest than in savanna woodland, highly disturbed, or fragmented forests (Nowell & Jackson 1996, Andama 2000, T. Davenport pers. comm.). By contrast, in Ituri Forest, NE DR Congo, African Golden Cat sign is more frequent in



Frontal, profile and dorsal views of African Golden Cat *Profelis aurata* head.

secondary areas and toward the savanna-forest ecotone (J. Hart pers. comm.).

Adaptations Generally considered to be crepuscular and nocturnal (Rosevear 1974, Guggisberg 1975, Andama 2000), but may also be active during the day (Kingdon 1977, Davenport 1996); in Lopé N. P., Gabon, 21 of 37 camera-trap captures were during daylight hours (Bahaa-el-Din *et al.* 2011). Almost all sightings are of animals on the ground, although occasional sightings are above ground (A. Gautier-Hion & J. Hart pers. comm.). Hart *et al.* (1996) found a nursing mother and one kitten in a den in a fallen hollow log in the Ituri Forest.

Foraging and Food Carnivorous. Principal prey are birds and small- and medium-sized mammals, especially rodents and duikers (Basilio 1962, Rahm & Christiaensen 1963). In the Ituri Forest, 60 scats (identified on the basis of diameter and bone fragment size) contained muroid rodents and squirrels (70%), Blue Duikers *Philantomba monticola* (25%), birds (18%), Giant Sengis *Rhynchocyon cirnei* (12%), Bates' Pygmy Antelopes *Neotragus batesi* (7%) and monkeys *Cercopithecus* spp. (5%). Modal prey weight was <1.5 kg, with only 1% of prey with adult weights greater than 5 kg (Hart *et al.* 1996). In Dzanga-Sangha, SW Central African Republic, 17 scats (identified by thin-layer chromatography) contained shrews, squirrels and other rodents (62% of 21 prey items), small- and medium-sized duikers (33%) and primates (5%). Mean adult weight of prey was 3.6 kg, and 17% of prey had adult weights greater than 5 kg (Ray & Sunquist 2001). Stomach



African Golden Cat *Profelis aurata*.

contents of one specimen from S Senegal contained bird remains, while a second held a frog cf. *Amnirana galamensis* (Gaillard 1969). Behavioural observations centred on primates indicate that African Golden Cats may be important predators of arboreal monkeys (Struhsaker 1981, A. Gautier-Hion pers. comm.). Seth-Smith (1996) observed a female with two kittens in S Sudan hunting bats as they swooped for insects feeding on fallen mangoes.

African Golden Cats probably catch most prey while on the ground, presumably by stalking and rushing, and by ambushing prey from low tree branches (Basilio 1962, Davenport 1996). Boy (2003) provides an eye-witness account of an African Golden Cat killing a Sykes's Monkey *Cercopithecus mitis* on the ground in riverine forest, south-east of Aberdare N. P., and Sheil (2011) observed an animal in Bwindi Impenetrable N. P. feeding on a long-tailed mouse on the ground while holding it between its front paws. Captive animals hook into prey with their claws and deliver a rapid bite to the back of the neck (Kingdon 1977). Hart *et al.* (1996) suggested that they scavenge the remains of eagle kills on the forest floor.

Several authors have reported African Golden Cats raiding poultry coops, and killing domestic goats and sheep (Van Mensch & Van Bree 1969, Kingdon 1977, Davenport 1996); however, many of these reports probably are due to misidentification with Servals *Leptailurus serval*.

Social and Reproductive Behaviour Solitary; almost all sightings are of single individuals. Tenure system probably like other felids, with core areas of home-range defended from same-sex adults

and overlap at edges. Exposed faeces on trails suggestive of marking behaviour (Kingdon 1977, J. C. Ray pers. obs.).

Vocal repertoire of captives described by Tonkin & Kohler (1978) as 'extensive'. Principal vocalization is a strong, abrupt and husky 'meow'. A female with kittens emits shrill meows accompanied by sequences of abundant trembling notes. Kittens often chirp (Jackson & Farrell Jackson 1996). During instances of friendly close contact (e.g. mother with young, courtship, mating), the most common vocalization is a 'gurgling' – a low-volume, short (0.5 s) rhythmical sound sequence (Peters 1984). Captives also give other common cat-like sounds: 'hisses', 'snarls' and 'growls' (Kingdon 1977).

Reproduction and Population Structure There is limited information on when young are born. A mother with one nursing kitten in Ituri Forest was found in Jun (Hart *et al.* 1996), and a ♀ in the final trimester of pregnancy was trapped in SW Uganda in early Sep (Kingdon 1977). Gestation period of a single animal in captivity was 75 days. Three captive litters each had two kittens (Tonkin & Kohler 1978). Birth-weights 180–235 g (n = 3). Two captive kittens had eyes completely open by Day 6, were walking by Day 13, taking meat by Day 40 and had permanent dentition erupting by 14 weeks (Tonkin & Kohler 1978). Compared with other small felids, there is more rapid development of physical agility. Weights of 2.5 kg (♀ ♀) and 2.9 kg (♂ ♂) are attained by 12 weeks. A captive ♀ reached sexual maturity at 11 months, and a captive ♂ at 18 months (Tonkin & Kohler 1978). A wild-caught animal could have been around 21 years old when it died in captivity (Weigl 2005).

Among those African Golden Cat specimens for which data on sex are available, 25 (74%) were male and nine (26%) female (T. M. Butynski & J. C. Ray pers. obs.). Of 13 animals found during a bushmeat survey in Lobeké Forest, SE Cameroon, 12 (92%) were male and 11 were adult (T. Davenport pers. comm.). The reason for the strong bias towards ♂♂ in these samples is unknown.

Predators, Parasites and Diseases African Golden Cat remains were recovered in five of 197 Leopard *Panthera pardus* scats from Lopé N. P. (Henschel 2001); a single carcass killed by a Leopard was found in Ituri Forest (Hart *et al.* 1996). Three individuals were found dead in an emaciated state from unknown causes in Lopé Reserve over 15 years (C. Tutin, pers. comm.). Three species of ectoparasites were collected by Gaillard (1969) from an adult ♂ in Senegal: *Dirofilaria granulosa*, *Taenia taeniformis* and a *Ligula* sp.

Conservation IUCN Category: Near Threatened. CITES: Appendix II.

The primary threats to African Golden Cats are habitat loss and hunting. Skins appear regularly in markets within the range of the species (Kingdon 1997), and in Yaoundé and Kampala these often are sold alongside medicinal herbs and fetishes (T. Davenport pers. comm.). Skins may be used during circumcision rites or to wrap valuable objects (Van Mensch & Van Bree 1969), or as good luck charms for hunting success (Guggisberg 1975). In a sample of 254 animals taken by hunters in NE Gabon, two (0.8%) were African Golden Cats (S. Lahm pers. comm.), while among 921 carnivore carcasses found in markets in E DR Congo, four (0.4%) were African Golden Cats (Colyn *et al.* 1987). Over the course of a three-month period at four sites in Lobeké Forest, 13 African Golden Cats were recorded killed by

wire snares (Davenport, in Ray *et al.* 2005). Bushmeat hunting heavily impacts many prey species, thereby posing a threat to the prey-base of African Golden Cats. Two of the four principal game species for hunters in Dzanga-Sangha, SW Central Africa Republic, are among the main prey of African Golden Cats (Ray 2001). About 47% of mammals in the bushmeat off-take in Lobeké Forest were prey species of African Golden Cats (T. Davenport pers. comm.). Hunting is prohibited or regulated in about half the range countries (Nowell & Jackson 1996), but there is little or no enforcement of laws.

Dependence on forest cover means that habitat loss is a threat particularly in West and East Africa. None the less, within their range, African Golden Cats occur in a number of key protected areas, including: Gola F. R. (Sierra Leone), Mount Nimba Strict N. R. (Liberia, Côte d'Ivoire, Guinea), National Park of Upper Niger (Guinea), Sapo N. P. (Liberia), Taï and Comoé National Parks (Côte d'Ivoire), Gashaka Gumti N. P. (Nigeria), Korup N. P. and Dja Faunal Reserve (Cameroon), Lopé and Ivindo National Parks (Gabon), Odzala and Nouabalé-Ndoki National Parks (Congo) and Dzanga-Ndoki National Parks (Central African Republic), Virunga N. P. (DR Congo), Queen Elizabeth and Bwindi Impenetrable National Parks (Uganda) and Aberdares N. P. (Kenya).

Measurements

Profelis aurata

HB (♂ ♂): 766 (616–935) mm, n = 18

HB (♀ ♀): 699 (630–750) mm, n = 8

T (♂ ♂): 319 (254–370) mm, n = 18

T (♀ ♀): 293 (280–300) mm, n = 7

HF c.u. (♂ ♂): 171 (155–193) mm, n = 9

HF c.u. (♀ ♀): 162 (140–170) mm, n = 6

E (♂ ♂): 56 (51–60) mm, n = 10

E (♀ ♀): 51 (44–55) mm, n = 4

WT (♂ ♂): 11.0 (8.0–14.0) kg, n = 6

WT (♀ ♀): 6.2, 8.2 kg, n = 2

Throughout range: museum data (AMNH, CMNH, FMNH, MCZ, NMNH), literature (especially Van Mensch & Van Bree 1969) and unpublished data (D. Brugière, T. Butynski, J. Kerbis, S. Lahm & E. Sarmiento pers. obs.)

Key References Boy 2003; Kingdon 1977; Nowell & Jackson 1996; Rosevear 1974; Van Mensch & Van Bree 1969.

Justina C. Ray & Thomas M. Butynski

GENUS *Caracal*

Caracal

Caracal Gray, 1843. List. Spec. Mamm. Coll. Brit. Mus. p. 46.

Once traditionally included in the genus *Felis* (e.g. Roberts 1951, Smithers 1975, Groves 1982, Meester *et al.* 1986), the Caracal *Caracal caracal* at one stage even saw its generic designation changed to *Lynx* (Roberts 1926) based primarily on superficial resemblances, although Werdelin (1981) could find no phylogenetic evidence to support such a relationship. Wozencraft (1993, 2005) placed the species in the monotypic *Caracal*, following others (Weigel 1961, Hemmer 1978, Werdelin 1981), a treatment that has since been widely accepted. Molecular data reveal that the Caracal is closely allied with the African Golden Cat *Profelis aurata* and Serval *Leptailurus serval*, having diverged around 8.5 mya (Janczewski *et al.* 1995, Johnson & O'Brien 1997, Johnson *et al.* 2006).

Lars Werdelin

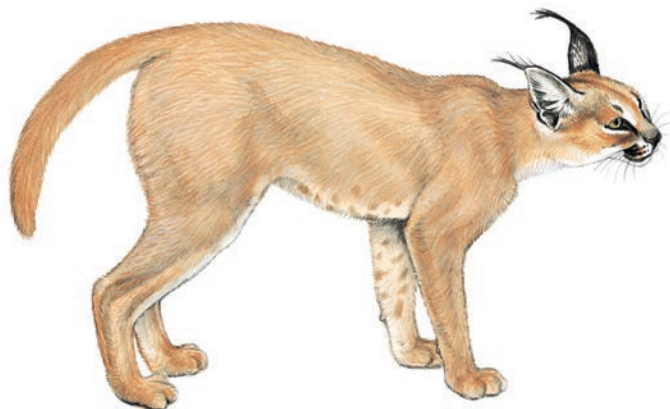


Caracal *Caracal caracal* facial expressions.

Caracal caracal CARACAL

Fr. Caracal; Ger. Karakal (Wüstenluchs)

Caracal caracal (Schreber, 1776). Die Säugethiere 3 (16): pl. 110 [1776]; text 3 (24): 413, 587 [1777].
 'Vorgebirge der guten Hofnung', restricted by J. A. Allen (1924: 281) to 'Table Mountain, near Cape Town, South Africa'.

Caracal *Caracal caracal*.

Taxonomy Seven subspecies have been recognized (Smithers 1975), but their validity seems questionable and they are perhaps best considered as geographical variants. Synonyms: *aharonii*, *algira*, *bengalensis*, *berberorum*, *coloniae*, *corylinus*, *damarensis*, *limpopoensis*, *lucani*, *medjerdae*, *melanotis*, *melanotix*, *michaelis*, *nubica*, *poecilotis*, *roothi*, *schmitzi*, *spatzi*. Chromosome number: $2n = 38$ (Hsu & Arrighi 1966).

Description Medium-sized, robustly built, uniformly coloured cat with dark-backed ears with distinct terminal tufts averaging 45 mm in length. Head typically cat-like with short face prominently marked with black and white patches, notably around eyes and mouth. Chin and throat are white, with variable extent of white on cheeks. The large ears pointed with a tuft of longish black hair at the tip. Back surfaces of the ears predominantly black but liberally sprinkled with white hairs; inner surfaces white. Hindquarters slightly higher than shoulders due to powerfully muscled and elongated hindlegs. Pelage thick but short and soft, the colour varying from pale reddish-fawn with a greyish infusion, to rich brick-red. Underparts, including inner leg surfaces, paler than rest of pelage and faint spotting or blotching may or may not be present. Extent of white on chest and belly very variable. Tail is similar in colour to the dorsal aspect and approximately one-third of head-body length. In temperate regions, guard hairs of the winter coat up to 30 mm long but usually less than 20 mm in the summer coat. Colour of guard hairs variable but pale at the base, with either broad annulations in off-white, dark brown or black. In temperate regions underfur in winter is thick but in summer greatly diminished. Paws proportionally large, with five digits on the forefeet and four on the hindfeet. The first digit on the forefoot is higher than the other four and does not make contact with the ground but is equipped with a substantial claw (dew claw). Claws of the forefeet are sharp, retractable and curved (about 25 mm along the upper curve). The claws on the hindfeet are less curved but larger (exceeding 30 mm). Males are consistently larger than ♀♀ in all respects (Stuart & Stuart 1992).

Skull high and rounded in profile, with particularly short, blunt rostrum. Supraoccipital crest well developed and in older animals

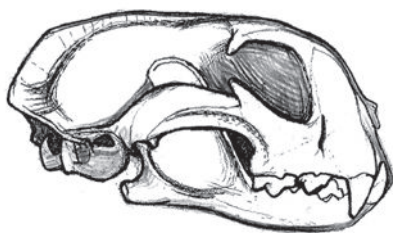
Caracal *Caracal caracal*.

joined at right-angles by sagittal crest. Ear bullae large and well developed. An overall heavily built skull, with stout mandible and tall, narrow coronoid process (Skinner & Chimimba 2005). Dentition is typically felid; the second upper premolar is usually absent (present in only eight of 100 skulls examined by Stuart & Stuart [1985]), unlike the Serval *Leptailurus serval* in which they are usually present.

Geographic Variation Separating the seven described subspecies occurring in Africa is based in most cases on small samples and minor differences in pelage colouration (Smithers 1975). Animals from arid low rainfall areas tend to be paler than those from higher rainfall regions. Within the southern African populations, from where the largest samples are available, there is considerable variation in overall pelage colour. Melanic individuals have been recorded from Kenya and Uganda (Rosevear 1974).

Similar Species

Leptailurus serval. Sympatric in most parts of the range, except, most notably, in the drier western and south-western parts of southern



Lateral view of skull of Caracal *Caracal caracal*.

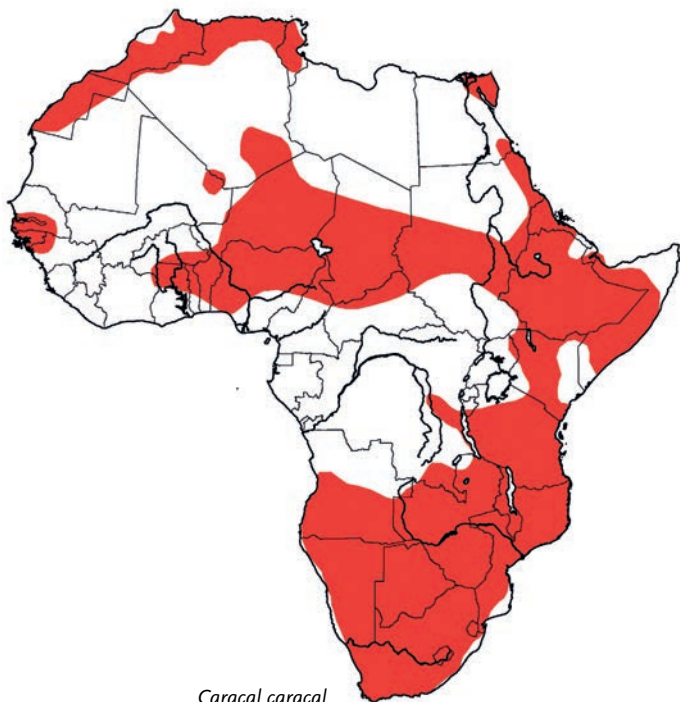
Africa. Distinctive spotting and barring, a ringed tail and a large white spot at back of each ear, with terminal tuft absent.

Profelis aurata. Largely allopatric, occurring in the forest zone of equatorial Africa. Dark-backed ears that lack a terminal hair tuft, have variably dark spotted upper- and underparts, the latter pelage being white to off-white.

Distribution The Caracal is widely distributed on the African continent, being absent only from the equatorial forest belt and from much of the central Sahara, but they are present in the montane massifs of that desert and its fringes, including the Adrar des Iforas in NE Mali (Sidiyène & Tranier 1990), Hoggar and Tassili mountains of SE Algeria and the Saharan Atlas (De Smet 1988, Kowalski & Rzebik-Kowalska 1991), the Aïr of Niger (Dragesco Joffé 1993), and edges of the great sand areas of the Eastern Great Erg.

The presence of Caracal in the savanna regions of the Congo basin, north of the Congo R., is equivocal. The form *lucani* is described from Landana, which is in Cabinda, Angola. Coetzee (1977) gave the range of this subspecies as N Angola, Gabon, and south-western DR Congo (it is also mentioned by Malbrant & Maclatchy 1949); however, the species is not mentioned in N Angola by Crawford-Cabral (1989a) or Hill & Carter (1941).

Extralimital to the African continent, the Caracal has a very wide distribution, occurring in suitable habitats to the Arabian Peninsula,



Caracal caracal

the Middle East and Turkey, and then eastwards to C India and northwards to Kazakhstan and Turkmenistan (Stuart 1984, Nowell & Jackson 1996, Sunquist & Sunquist 2002).

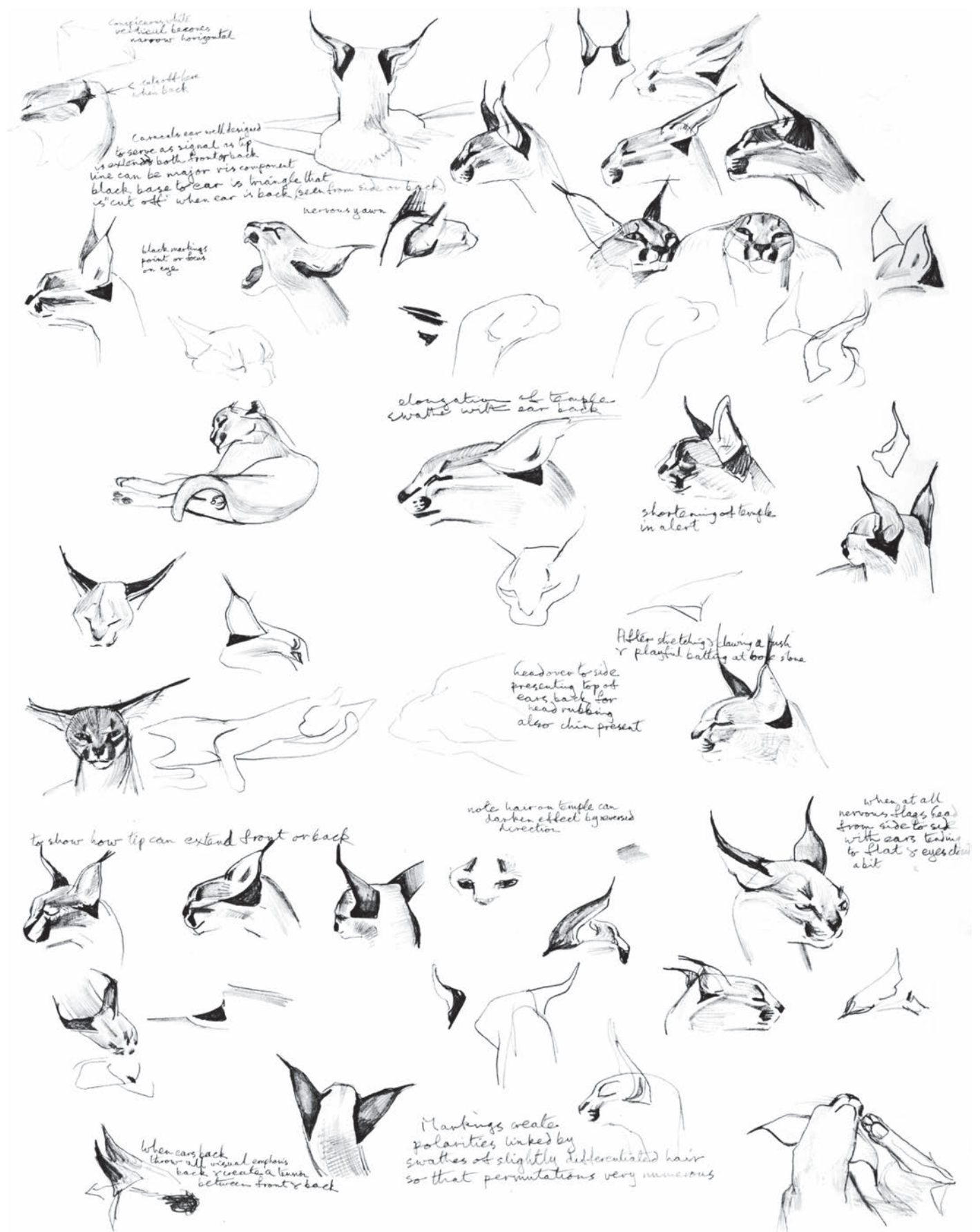
Habitat The Caracal occupies a wide variety of habitats from semi-desert to relatively open savanna and scrubland to moist woodland and thicket or evergreen/montane forest (as in the Western Cape of South Africa), but favours drier woodland and savanna regions with lower rainfall and some cover (Stuart & Wilson 1988). They range from sea level in many parts of their range, to 2,260 m in the Moroccan Atlas Mts (Cuzin 2003) and 3300 m in the Ethiopian Highlands (Yalden *et al.* 1996). In KwaZulu-Natal (South Africa), recorded in commercial forests (*Eucalyptus* spp. and *Pinus* spp.) (Rowe-Rowe 1992a), and in areas of intensive wheat cultivation in the Western Cape they hide up during the day in adjacent scrubland, moving at night on open fields. Particularly common in the Cape fynbos, an area of low and often dense scrub (Stuart 1981). On the Pro-Namib plains of Namibia Caracal are closely associated with lightly wooded dry river courses and rocky inselbergs, and on South Africa's central Karoo plains they are strongly associated with rugged mountain and hill ranges.

Abundance The Caracal is common in parts of its range, especially in South Africa and S Namibia where it is expanding into new, and recolonizing vacant, areas (Stuart 1984, Stuart & Wilson 1988). Found in all major national parks and many other conservation areas within their range (Stuart 1984, C. Stuart & T. Stuart pers. obs.). In central and West Africa, where they are largely absent, densities are apparently lower, possibly due to finer partitioning of resources in a more diverse carnivore community (Kingdon 1977, Stuart 1984, Nowell & Jackson 1996), while north of Sahara densities are very low, and Caracal could be on the verge of extinction at least in Morocco (F. Cuzin pers. comm.). In South Africa, Grobler (1981) estimated the population density of Caracal in Mountain Zebra N. P. in the Eastern Cape as 1/2.6 km², while Avenant & Nel (1998) recorded a density of 0.23–0.47/km² in West Coast N. P. in the Western Cape.

Adaptations Large pinnae and well-developed ear bullae reflect the important role played by hearing in hunting, but colouring and tufted tips appear to be elaborated to serve communication by means of frequent ritualized ear movements (Kingdon 1977). Skull and dentition (in particular the sharp canine teeth) are stoutly structured, an adaptation to taking relatively large prey in proportion to its size. The masseter and temporalis muscles are well developed to deliver the killing bite. As in other felids, the teeth of the carnassial shear are adapted to cutting, although the teeth in the lower jaw show no adaptation to crushing. Paws notably large and the well-developed claws also indicate an ability to take larger prey. Normally terrestrial, they are adept tree climbers, using their powerful dew claws in this pursuit.

Caracals are principally nocturnal, although in protected areas they may occasionally hunt during the day, especially in the early morning and late afternoon, and particularly on cooler days or if overcast.

Foraging and Food Caracal prey mainly on small- to medium-sized mammals, from small murids to antelope up to the size of around 50 kg, but they will also take birds, reptiles, invertebrates, fish and some plant matter. The most detailed studies of diet have



Caracal Caracal caracal.

been undertaken in South Africa (Grobler 1981, Moolman 1984, Palmer & Fairall 1988, Stuart & Hickman 1991, Avenant & Nel 1997, Melville *et al.* 2004); in these studies, the mammal component of the diet ranged from 86% to 100%. Small mammals in the form of rodents and springhares *Pedetes* spp. make up the bulk of the mammal component; the largest wild prey species recorded include Bushbuck *Tragelaphus scriptus* ewes, Mountain Reedbucks *Redunca fulvorufula*, Grey Rheboks *Pelea capreolus*, Springboks *Antidorcas marsupialis* and young Greater Kudus *Tragelaphus strepsiceros*. In the area to the north of L. Chad the local name for Caracal means 'gazelle cat' (Dragesco-Joffé 1993), where they are said to hunt Dorcas Gazelles *Gazella dorcas*. The same author records Barbary Sheep *Ammotragus lervia* ewes and lambs, Rock Hyraxes *Procavia capensis*, hares and birds (pigeons and doves, bustards) (Dragesco-Joffé 1993). The remains of small carnivores have been found in most studies, and have been noted as a prominent feature of the diet in Caracals in the Kalahari (Melville *et al.* 2004).

In most areas where Caracal diet has been studied, birds (ranging in size from Ostrich *Struthio camelus* to Cape Sparrows *Passer diffusus*) make up only a minor percentage of their prey. However, on South Africa's west coast, Avenant & Nel (2002) recorded average 23.3% bird occurrence, reaching more than 50% in some months. In the Kalahari, birds were an abundant prey resource, especially the larger ground-roosting species such as korhaans (Melville *et al.* 2004). Birds may be taken at night when roosting, ground birds such as francolin after stalking, or at waterholes (C. Stuart & T. Stuart pers. obs.). Avenant & Nel (2002) recorded 12.4% reptile occurrence in diet in West Coast N. P. and 17.4% on surrounding farms, but in other areas reptiles make up an insignificant contribution.

There appear to be regional and seasonal variations in diet but only limited information is available. Rodent remains were found to occur in 89% of the samples collected in West Coast N. P. (Avenant 1993), 39% in Karoo N. P. (Palmer & Fairall 1988), as low as 5.3% in Mountain Zebra N. P. (Grobler 1981, Moolman 1984), and over more extensive areas of South Africa 29% (Stuart & Hickman 1991).

In areas of sheep and goat farming Caracal are significant predators of these domestic animals. Percentage occurrence of domestic stock remains, as evidenced from scats and kills, ranged from a low of 3.6% (Avenant & Nel 2002) to a high of 55% (Pringle & Pringle 1979). Brand (1989) found that Caracals were responsible for the loss of up to 5.3 domestic stock per 100 km² per annum in the former Cape Province. Severity of depredation appears to be dependent on the availability of wild prey and husbandry techniques. Avenant & Nel (2002) demonstrated that predation on small stock and introduced Springboks was seasonal when alternative prey was scarce. Similarly, no remains of domestic livestock were found in 200 Caracal scats collected in Mountain Zebra N. P. (including boundary areas with farms) where wild prey was abundant (Grobler 1981). Comparative figures are not available from other regions of Africa. Surplus killing of domestic stock has been recorded in parts of South Africa (Skinner 1979, Stuart 1986) and on several occasions in Algeria (De Smet 1988). Although uncommon, eating of carrion has been recorded (Skinner 1979, Stuart 1982, Van Heezik & Seddon 1998, Avenant & Nel 2002); in coastal areas, scavenging of marine carrion (e.g. Cape Fur Seal *Arctocephalus pusillus*) is not uncommon (Stuart & Hickman 1991, N. Avenant pers. comm.).

Caracal are solitary hunters, except when a ♀ is accompanied by cubs (Stuart 1982). Prey is located mainly by hearing and sight.

Caracals are principally stalk and pounce, or stalk and short sprint hunters, and are considered to be amongst the fastest of most cats in short sprint situations. Use is effectively made of even minimal cover to allow close approach to intended prey. Avenant & Nel (2002) posited that Caracals are familiar with the areas of high prey availability within their home-ranges and that they select paths that maximize their encounter rates with prey. Melville & Bothma (2006) studied the foraging behaviour of Caracal relative to the dispersion of Brants' Whistling Rats *Parotomys brantsii* in the southern Kalahari, and found that foraging paths used by Caracal in the hot season did increase the likelihood of encountering colonies, but that in the cold season foraging appeared to be random.

Larger prey may be killed by a bite to the throat, to the nape, or initially to the nape and then switching to the throat (Grobler 1981, Stuart 1982, Moolman 1986). Medium-sized prey such as hyraxes and hares taken by captives were usually held by the throat, with the Caracal falling on its side and vigorously raking the belly and chest of the prey with the claws of the hind paws (Stuart 1982). Birds are taken from the ground or at roosts, but a number of authors have commented on their adeptness at hooking flying birds out of the air (Kingdon 1977, Stuart 1982, Skinner & Chimimba 2005). A hand-raised ♂ was observed hooking several bird species from the air at different times, including Cape Weavers *Ploceus capensis*, Cape Sparrows and on one occasion a Great Spotted Cuckoo *Clamator glandarius*. The same individual was seen on several occasions stalking feeding Laughing Doves *Streptopelia senegalensis* and Ring-necked Doves *S. capicola* and catching them on the ground, either swiping at them with a sideways action or occasionally with both front paws together (C. Stuart & T. Stuart pers. obs.).

Small prey is usually eaten at the site of capture but larger prey items may be dragged, or carried, to cover; in 27 of 28 kills recorded by Stuart & Hickman (1991) prey was eaten where it was killed and in only two cases was the prey dragged away to cover. Mills *et al.* (1984) report a Caracal caching the remains of a kill in a tree (and see Stuart & Hickman 1991). In the case of larger prey animals, such as antelope, the principal mode of eating is to open the skin in the buttock and inner thigh region and feed on muscle tissue. Grobler (1981) estimated the meat consumption of a free-ranging hand-raised Caracal to be 796 g per 24-hour period, whereas Stuart (1982) found consumption to average 536 g in ten captive Caracal held in large enclosures. In protected areas Caracals will frequently return to feed at larger kills (Grobler 1981, Avenant 1993) but this is rare on farmland where they are persecuted (Pringle & Pringle 1979, Stuart & Hickman 1991).

Social and Reproductive Behaviour Caracal are normally solitary, except when a pair briefly consort during the oestrous period, or when a ♀ is accompanied by cubs (Stuart 1981, Avenant & Nel 1998). Of 40 sightings in the wild, all were of solitary animals (Smithers 1983), and in a further 27 sightings on South Africa's central plain, 25 were lone individuals and the remainder ♀♀ accompanied by two and three cubs, respectively (C. T. Stuart pers. obs.).

On the African continent the only home-range studies have been undertaken in South Africa and Namibia. In the eastern Karoo three ♀♀ had slightly overlapping home-ranges from 11.8 to 26.7 km², with a ♀ on the coast occupying 11.9 km²; a ♂ in the Karoo had a home-range of 48 km² (Stuart 1982). In Mountain Zebra N. P., Moolman (1986) also found that female home-ranges, from 3.9 km² to

6.5 km² in extent (mean = 5.5 km²), overlapped each other slightly. In the same study it was found that male home-ranges showed considerable overlap, including over those of ♀♀, and varied from 5.1 km² to 30.6 km² (mean = 15.2 km²). In West Coast N.P., male home-ranges (26.9 ± 0.75 km²; $n = 2$) were much larger than those of ♀♀ (7.39 ± 1.68 km²; $n = 3$) and overlapped completely with them; those of ♀♀ overlapped as much as 19% (Avenant & Nel 1998). In Kgalagadi Transfrontier Park, Northern Cape, Bothma & Le Riche (1994) found the home-range of a single adult male to be 308.4 km², with a core area of 93.2 km², while in NC Namibian farmlands, mean home-range size for three ♂♂ was 312.6 km², with a mean range overlap of only 19.4%, which is considerably less than that noted in West Coast N. P. (Marker & Dickman 2005b). Considering the latter figure, and studies conducted in Arabia, home-range sizes in Sahara are probably much larger. In Saudi Arabia, a radio-tracked ♂ ranged over 270 km² to 1116 km² in different seasons (Van Heezik & Seddon 1998), while in an Israeli study, home-ranges of ♂♂ averaged 220.6 km² and 57.3 km² for ♀♀ (Weisbein & Mendelssohn 1990).

Males and females scent-mark by spraying urine on rocks, bushes and tree trunks (De La Fuente 1970, Stuart 1982). In captivity individuals sometimes follow urine spraying with vigorous claw scratching on logs (C. Stuart & T. Stuart pers. obs.). Scats appear to be dropped at random along pathways, with no indication of midden development.

Observations of sexual behaviour in the wild are unrecorded. A total of 12 copulations were observed in captive Caracal, ranging from 90 sec to 8 min (mean = 3.8 min) in duration (Bernard & Stuart 1987). The prelude to coitus followed a set pattern. When a ♂ was first introduced to an enclosure holding a receptive ♀ the first action was to smell at one or more of the female urine spray sites before approaching her (Bernard & Stuart 1987). Females made no attempt to approach ♂♂. Actual mating and copulation are very similar to that of the domestic cat. After copulation the ♂ rapidly disengages and moves away from the ♀. On two occasions the ♀ turned aggressively on the ♂ but without making contact. No calls were noted during copulations but snorting, growling and spitting were recorded before and after coitus. In most cases the ♂ proceeded to lick his genital area after copulation, but ♀♀ lay on their side or rolled in the sand (Stuart 1982). Cubs are born in abandoned Aardvark *Orycteropus afer* and porcupine burrows, in rock crevices and amongst dense vegetation tangles (Stuart 1982, Skinner & Chimimba 2005).

Vocalizations recorded in captive animals include miaowing, gurgling, growling, purring, spitting hisses, a 'wah-wah' call and loud coughing barks by both ♂ and ♀ before and after mating (Peters 1983, C. Stuart & T. Stuart pers. obs.).

Reproduction and Population Structure In the south of their range litters have been recorded in all months of the year but with a peak between Oct and Feb (Bernard & Stuart 1987, Stuart & Wilson 1988). Cade (1968), on the basis of captive and wild records, stated that the breeding season in Kenya was from Nov to May. Reproduction in Israel is apparently non-seasonal (Weisbein & Mendelssohn 1990). In captivity, the oestrous cycle has been recorded as 14 days ($n = 15$) and oestrus 1–3 days ($n = 7$) (Bernard & Stuart 1987). Bernard & Stuart (1987) give the gestation period



Caracal *Caracal caracal* yawning.

as 78–81 days, although shorter gestations are reported; litter-size averages 2.2 (range 1–4; $n = 37$) (Bernard & Stuart 1987), which is similar to the mean of 2.2 recorded by Avenant (1993).

In kittens the eyes open within ten days of birth but clear vision is only achieved several days after opening. At birth the ears are flattened against the head and only stand erect between the second and fourth week, but in most cases ($n = 12$) they are fully erect by the third week. The claws are non-retractable until the third week, but fully retractable by the fourth week. Full deciduous dentition is apparent at 50 days after birth, with permanent canines emerging at 4–5 months, displacing the deciduous canines at 5–6 months. Permanent dentition is complete at 10 months. The first recorded call is a bird-like chirrup emitted shortly after birth. This call was the only vocalization noted up to the age of 2.5 weeks, and persisted in a tame, house-trained Caracal to the age of one year. At 3.5–4 weeks the kittens start to wander around the den entrance. At 5–6 weeks curiosity and playfulness are well developed. Captive kittens were weaned between 15 and 24 weeks, with first solid food being taken at 3.5–8 weeks (Stuart & Stuart 1985).

Age at first reproduction in ♂♂ is 12.5–15 months and 14–16 months in ♀♀, but gametogenesis can occur earlier (Bernard & Stuart 1987). Females probably produce only one litter per year (Bernard & Stuart 1987). One ♀ is recorded as giving birth at 18 years, and longevity is up to 20 years in captivity (Nowell & Jackson 1996, Weigl 2005).

Predators, Parasites and Diseases Predation on Caracal by a number of carnivores has been recorded, including Lions *Panthera leo* (Pienaar 1969), Leopards *P. pardus* (Wilson 1976), Cheetahs *Acinonyx jubatus* (Frame 1986) and Black-backed Jackals *Canis mesomelas* (C.T. Stuart pers. obs.). In the latter case, remains of cubs were found in two stomachs. Several instances of cannibalism have been recorded, probably attributable to infanticide, with cub remains found in the stomach contents of adult ♂♂ (Stuart & Hickman 1991).

Various ecto- and endoparasites have been recorded from South Africa, including fleas (*Ctenocephalides felis*, *Echidnophaga gallinacea*, *Procatiopsylla divergens*), ticks (*Amblyomma marmoreum*, *Boophilus decoloratus*, *Haemaphysalis colesbergensis*, *H. elliptica*, *H. muhsamae*, *H. spinulosa*, *H. zumpti*, *Hyalomma marginatum*, *Ixodes pilosus*, *I. rubicundus*, *Margaropus winthemi*, *Rhipicentor bicornis*, *R. nuttalli*, *Rhipicephalus arnoldi*, *R. distinctus*, *R. evertsi*, *R. gertrudae*, *R. glabroscutatum*, *R. lounsburyi*) and cestodes (*Taenia hydatigena*, *Joyeuxiella* sp., *Mesocestoides* sp.) (Stuart 1981, Horak *et al.* 1987, 1991, 2004, 2010).

Conservation IUCN Category: Least Concern. CITES: Appendix II (the Asian population is listed on Appendix I).

Caracal are heavily persecuted in a number of countries throughout their range, including South Africa, Namibia, Niger and Morocco, during carnivore control activities (Stuart 1981, 1982, Avenant 1993, Dragesco-Joffé 1993, F. Cuzin pers. comm.). Stuart (1982) recorded that over the years 1931–52 an average of 2219 Caracals per year were killed in control operations in the Karoo, South Africa; Brand (1989) recorded 0.02–1.6 Caracals killed or captured per 10 km² a year in the former Cape Province. The Caracal has legal status as a ‘problem animal’ in South Africa and Namibia, and despite such heavy hunting pressure in these countries, it not only seems to be holding its own but in some areas is actually expanding its range and increasing in numbers. Elsewhere in its African range it is generally considered to be uncommon to rare and even threatened

over much of North Africa. In West Africa Caracals are increasingly seen in bushmeat markets, which could pose a serious long-term threat to its survival in that region.

Measurements

Caracal caracal

HB (♂ ♂): 868 (750–1080) mm, n = 97

HB (♀ ♀): 819 (710–1029) mm, n = 94

T (♂ ♂): 264 (210–340) mm, n = 99

T (♀ ♀): 252 (180–315) mm, n = 101

HF c.u. (♂ ♂): 193 (170–215) mm, n = 101

HF c.u. (♀ ♀): 180 (160–208) mm, n = 101

E (♂ ♂): 80 (65–92) mm, n = 98

E (♀ ♀): 76 (60–94) mm, n = 100

WT (♂ ♂): 12.9 (7.2–19.0) kg, n = 77

WT (♀ ♀): 10 (7.0–15.9) kg, n = 63

Northern Cape, Western Cape and Eastern Cape, South Africa (Stuart & Stuart 1992)

Key References Avenant 1993; Avenant & Nel 1997, 1998, 2002; Bernard & Stuart 1987; Nowell & Jackson 1996; Stuart 1981, 1982, 1984; Stuart & Hickman 1991; Stuart & Stuart 1985.

Chris Stuart & Tilde Stuart

GENUS *Leptailurus*

Serval

Leptailurus Severtzov, 1858. Rev. Mag. Zool. Paris (2), 10: 389.

A monotypic genus represented only by the Serval *Leptailurus serval*. Severtzov originally included it as a subgenus of *Felis*, but it was later elevated to generic rank (Roberts 1926: 248) based on gross morphological differences from other *Felis* species. Some authors subsequently reverted back to including it as a subgenus of *Felis* (e.g. Ellerman *et al.* 1953, Groves 1982, Meester *et al.* 1986, McKenna & Bell 1997). However, Wozenkraft (1993; and see 2005) reinstated *Leptailurus* as a monotypic genus following others (Weigel 1961, Hemmer 1978, Kratochvíl 1982) and this has since been widely accepted.

The relationship of the Serval to other felids has also been the matter of some debate, with the species variously allied with, for example, *Felis*, *Lynx* and *Caracal* (Weigel 1961, Bininda-Emonds *et al.* 1999) and with *Caracal* and *Profelis* (Johnson & O’Brien 1997, Mattern & McLennan 2000). A highly resolved molecular phylogeny has corroborated the later grouping (Johnson *et al.* 2006) as a lineage that diverged some 8.5 mya.

Luke Hunter



Serval *Leptailurus serval* male in mild threat posture.

Leptailurus serval SERVALFr. Chat-tigre (*Lynx tachete*); Ger. Serval*Leptailurus serval* (Schreber, 1776). Die Säugethiere 3 (16): pl. 108 [1776]; text 3 (23): 407 [1777].‘Ostindien und Tibet in gebirgigen Gegenden, vielleicht auch am Vorgebirge der guten Hoffnung und dem heissen Afrika’;
restricted by Allen (1924) to the ‘Cape region of South Africa’.Serval *Leptailurus serval*.

The name Serval is taken from the Portuguese name for the Iberian lynx *Lynx pardinus*, ‘lobo-cerval’. Forster, 1781 described the species as *Felis capensis*, using the colloquial name of ‘Tyger bosch katten’.

Taxonomy A speckled form, known as the servaline cat, was described as a separate species, *Felis servalina* Ogilby, 1839 or *Felis brachyura* Wagner, 1841. Pocock (1907) accepted that the two forms represent distinct species, but later (1917) considered them conspecific. Subsequent reports (e.g. Hollister 1918, Allen 1924, Pitman 1934) have illustrated the wide variability of maculation within populations and both forms have been recorded from the same litter (Kingdon 1977). Seventeen subspecies were listed by Allen (1939);

Smithers (1978) recognized six subspecies, while seven are listed by Nowell & Jackson (1996). The validity of subspecies has been brought into question by numerous authors because descriptions have been based on ground colour and size of spots, which, as noted above, are considerably variable. Synonyms: *algericus*, *beirae*, *brachyura*, *capensis*, *constantina*, *faradjus*, *ferrarii*, *galeopardus*, *hamiltoni*, *hindei*, *ingridi*, *kempi*, *kivuensis*, *larseni*, *limpopoensis*, *liposticta*, *lonnbergi*, *mababiensis*, *niger*, *ogilbyi*, *pantasticta*, *phillipsi*, *pococki*, *poliotricha*, *senegalensis*, *servalina*, *tanae*, *togoensis*. Chromosome number: $2n = 36$ (Wurster & Benirschke 1968). In captivity, Serval have hybridized with Caracal *Caracal caracal*, African and European Wildcats *Felis silvestris* and domestic cats.

Description A medium-sized cat with slender build, notably long legs, short tail and large ears. Overall ground colour varies from buffy to golden-yellow with black spots and stripes. Muzzle and chin whitish, blending into golden-yellow face, with small black spots on cheeks and above eyes, nose black occasionally with a pink mark or completely pink. Copper-brown or greenish eyes, rimmed with black. White vibrissae on muzzle and temples. Pinnae shaped like a domestic cat's ears though much larger relative to head size; very mobile, almost meeting at centre of crown when animal is focusing attention forwards. Long white hairs inside the ears, backs black with broad white band horizontally across middle. Three or four black stripes extend from back of head, along nape onto shoulders. Stripes break up into elongated spots along the back with smaller spots in rows on the shoulders, flanks and outer thighs. Throat whitish and chest buffy with small black spots in a full or broken 'necklace'. Outer limbs golden with horizontal black stripes or spots getting smaller distally. Inner legs whitish with greyish markings. Pelage on ventral surface soft and fluffy, white or buffy, with long guard hairs (5–10 cm), and dense wavy underfur. Neck, back and flank guard hair about 3 cm in length and facial hair about 1 cm long. Tail shortish, reaching about half-way to the ground when the animal is standing, golden-yellow with five or six black bands. Tail tip black. Feet, pads black, pelage on upper surface short, buffy. Five digits on forefoot and four on hindfoot. There are two pairs abdominal and one pair inguinal nipples. Males are more heavily built than females.

Skull is domed, rounded in profile, lightly built, and narrow compared with the similarly sized Caracal, with a more elongated rostrum and lacking well-developed sagittal and supraoccipital crests. The top of the skull is smooth and lacks well-defined muscle attachments. The coronoid process of the mandible is less developed than in the Caracal and lacks the central ridges seen in that species. Dentition is typically felid, and in contrast to most Caracal specimens, P^2 is always present (Skinner & Chimimba 2005).

Geographic Variation Wide variation occurs in the colouration of the pelage, ranging from differing numbers of stripes and rows of spots to the small spotted or servaline morph, which has a freckled appearance. The latter occurs more frequently in West Africa, and in the humid savanna at the ecotone of the equatorial rainforest belt; for example, 62% of skins from E DR Congo (Rahm & Christiaensen 1966). Melanistic forms occur, mainly in East Africa in the Aberdares, Kilimanjaro, Mt Kenya, Mkomazi, Tsavo and the Ethiopian Highlands (York 1973, Kingdon 1977, Grimshaw *et al.* 1995), although there are recent photographic records from the Bateke Plateau, SE Gabon (N. Bout, pers. comm.).

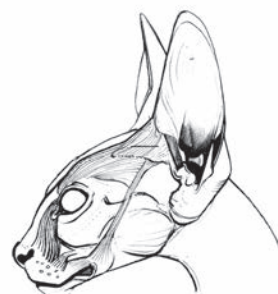
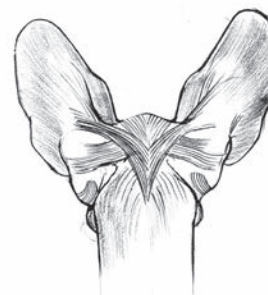
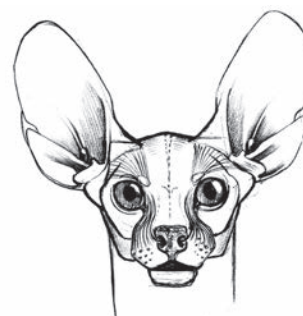
Similar Species

Caracal caracal. Sympatric across much of the range, except the western and south-western parts of southern Africa. Powerfully built, hindlimbs longer than forelimbs; largely unmarked red to fawn colour, with faint spots on underparts; black-backed ears with long terminal tuft.

Profelis aurata. Forest-dependent species, from Senegal through the Congo basin to Uganda, with isolated records from Kenya. Powerfully built, with limbs robust; small, black-backed ears lacking distinct white patch; ground colour dark golden to smoky-grey with variable spotting. Van Mensch & Van Bree (1969) detail



Serval *Leptailurus serval* myology.



Serval *Leptailurus serval*. Myology of ears.

distinguishing characteristics between the skull of the African Golden Cat and Serval.

Acinonyx jubatus. Sympatric across parts of Sub-Saharan range, with wide, but patchy, distribution from Senegal to Somalia and south to South Africa. Adult much larger, and with smaller ear pinnae; cubs uniformly marked with coin-shaped spots, facial tear streaks and have a silvery-grey mantle.

Distribution Endemic to Africa. Senegal eastwards in a narrow band of savanna-dominated habitat to S Sudan, Ethiopia and S Somalia, expanding into the mesic regions of East and southern Africa south to South Africa and SW Angola. Relict in North Africa.

Historical Distribution Widespread throughout Africa in two populations separated by the Sahara. Naturally absent from the Sahara, Congo basin, West African coastal rainforest, Horn of Africa and south-west Africa.

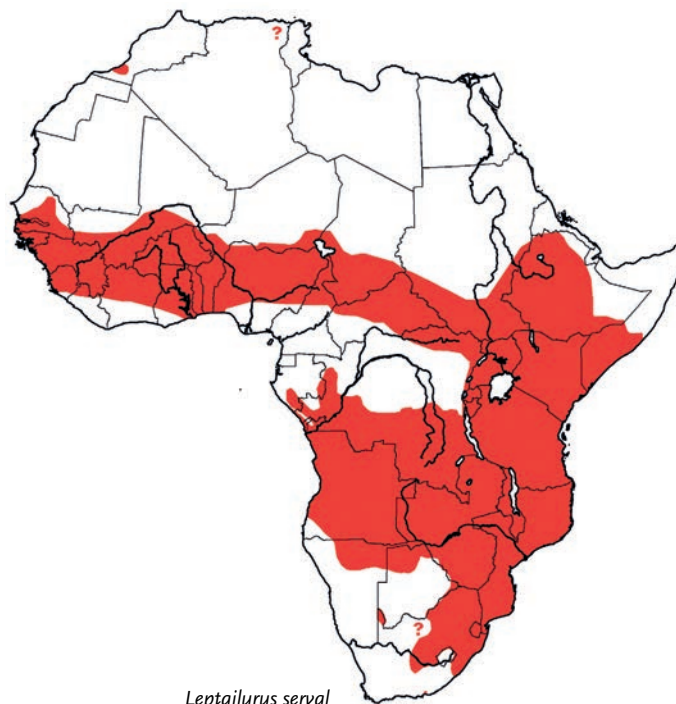
Current Distribution Widely distributed within historical limits, but localized in areas densely populated with people; they have suffered marked range loss, particularly at the north and extreme south of their range (Smithers 1978, Nowell & Jackson 1996).

In North Africa, an animal killed on the north-west coast of Algeria, east of Oran, in 1936 was said to be the last confirmed record from this country (Nowell & Jackson 1996), but they were recorded in El Kala N.P. in NE Algeria around 1992/93 (K. de Smet pers. comm.). Servals are also relict in SW Morocco in an arid littoral area (Cuzin 2003), and were reported from the Ifrane N. P. in the north in 2005 (F. Cuzin pers. comm.). In West Africa, in S Senegal's Casamance Province, they have increased in numbers due to the prolonged civil war and resulting human depopulation (O. Burnham pers. comm.); they still persist in N Senegal, as evidenced by a recent record from Ferlo North (Clément *et al.* 2007).

In South Africa, Serval probably occurred along the entire coastal belt and in water-courses from the Cape Peninsula to the former Transkei (Skead 1980, Stuart 1981, 1985). However, by the time of Stuart's survey, the species was on the verge of extinction in the then Cape Province, with only a single proven record of a specimen collected near Groenriver in Namaqualand in 1975 (Stuart 1981) as well as several unsubstantiated records. Lynch (1989) provided a few additional historical records from the Eastern Cape, while Lynch (1983) recorded the species from only three localities in the north-eastern Free State. Since these studies, there is evidence that, in a few regions, Serval have expanded their range; for example, they are known to be re-colonizing parts of the Free State (Herrmann *et al.* 2008, C. Stuart pers. comm.). There is also an interesting record of a Serval sighted in the dry river bed of the Nossob R. in Kgalagadi Transfrontier Park between South Africa and Botswana in 1990 (T. P. Jackson, in Skinner & Chimimba 2005, G. Mills pers. comm.), though this is well outside of historical range and ad hoc releases by private landowners cannot be ruled out. At least at the time of Stuart's survey Serval supposedly still occurred in what is today the western North West Province (P. Visser, in Stuart 1981). Serval are also possibly benefiting from forest clearance and resulting encroachment of savanna habitats around the fringes of the equatorial forest belt in central Africa (Ray 2001).

Captive-raised Servals of East Africa stock have been released in Feidja N. P. in Tunisia (K. De Smet & F. Cuzin pers. comm.), and 17 Servals of southern African origin have been reintroduced into Shamwari G. R. in the Eastern Cape, South Africa (L. T. B. Hunter pers. obs.).

Habitat The Serval is strongly associated with permanent water sources and it requires cover such as tall grass, reed-beds and underbrush for refuges and for rodent prey. Most common in savanna, grasslands and dry forest where it is typically associated with wetlands, rivers and flood-plains. Also favours alpine grasslands (to altitudes of



Leptailurus serval

3800 m in Kenya), moorland (to at least 3850 m near Mt Kilimanjaro; Grimshaw *et al.* 1995) and high-altitude bamboo forests (Andama 2000). In Somalia, Funaioli & Simonetta (1966) noted their occurrence along the rivers in the south of the country. Recorded from rainforest and coastal scrub in Sierra Leone (Grubb *et al.* 1998), in rainforest-savannah mosaic in SE Gabon (Bout 2011), in coastal and mountain fynbos (heath) in South Africa (Stuart 1981) and in riparian habitat in the Haremma Forest, Ethiopia (Yalden *et al.* 1996). Servals are able to tolerate agricultural areas provided cover is available. Rahm & Christiaensen (1966) recorded them from banana and coffee plantations in DR Congo, and Scaramella *et al.* (1974) stated that they are often killed around human habitations in Somalia. Short grassland or shrubland with few or no trees is considered marginal habitat (Nowell & Jackson 1996). The relict population in Morocco lives in arid dense shrubland, and wetlands (F. Cuzin pers. comm.), and elsewhere in North Africa, it inhabited scrubland and forest in more humid areas (Kowalski & Rzebik-Kowalska 1991). Absent from the Congo basin rainforest, semi-desert and desert.

Abundance Found in most major national parks and reserves within their range (Nowell & Jackson 1996), reaching their greatest abundance in protected areas in East and southern Africa. Considered fairly numerous in reserves throughout West Africa (I. Di Silvestre pers. comm., H. Bauer pers. comm.) though illegal hunting in Niokolo Koba N. P., Senegal and Badiar N. P., Guinea, has significantly reduced their numbers in the past ten years (O. Burnham pers. comm.). Status outside reserves uncertain, but they are inconspicuous and may be common in suitable habitat as they are tolerant of farming practices provided there is cover and food available. Minimum density of Servals in optimal habitat in Ngorongoro Crater during a good rainfall period was recorded as 0.42 animals/km² (Geertsema 1985). Andama (2000) calculated a density of 0.09 ± 0.08 animals per km² for Bwindi Impenetrable N. P., Uganda, where the extinction of the Leopard *Panthera pardus* may have resulted in predator release. Much



Lateral view of skull of Serval *Leptailurus serval*.

of Bwindi is rainforest where Serval density is very low and densities in more open habitat along the periphery of the park are comparable with the Ngorongoro figures (E. Andama pers. comm.). In Niokolo-Koba N. P., Servals were observed at a frequency of 0.6 individuals/100 km along road transects driven by vehicle (Sillero-Zubiri *et al.* 1997). No estimates exist for the Servals occupying arid shrublands in Morocco but densities there are probably very low.

Adaptations Well-developed ear bullae and large pinnae reflect this species' reliance on hearing for prey detection. The skull is lightly built, especially in comparison with the similarly sized Caracal, as it is adapted to small rodent and avian prey. Their long legs and slender build enable stealthy movement through long grass and allow high jumping to pounce upon its prey. The slender forelegs combined with long, loosely knit metatarsals and strongly curved claws are well suited to pinning rodents in long grass and also allow them to efficiently angle for prey in tree hollows and burrows, and hook fish from water (Kingdon 1977, Geertsema 1985). Although an efficient climber up to heights of at least 9 m (Smithers & Wilson 1979), they are predominantly terrestrial. Pelage colouration is probably more important for reducing visibility to predators than for concealment from prey. Darker toned Servals (melanistic and 'servaline') are associated with moister, equatorial regions; the selective advantages conferred are unclear though it may afford better camouflage in poorly lit habitats. Servals appear tolerant of low temperatures, possibly an adaptation for living at altitudes where they are often exposed to snow. They minimize heat loss at low temperatures by piloerection, curling up and remaining inactive, and can tolerate reductions in body temperature (e.g. to 35.2°C at ambient temperature of 15°C) before needing to increase oxygen consumption (Downs *et al.* 1991).

Servals are primarily crepuscular or nocturnal but often become diurnal in protected areas; for example, Servals in Serengeti N. P. were often diurnal (Geertsema 1976), Servals in Ngorongoro and Niokolo-Koba N. P. were largely crepuscular (Geertsema 1985, Di Silvestre & Novelli 1998), while Servals on farmland in Zimbabwe and South Africa were primarily active at night (Smithers 1978, Bowland 1990). Verheyen (1951) and Rowe-Rowe (1978a) recorded both nocturnal and diurnal activity in protected areas in DR Congo and KwaZulu-Natal (South Africa), respectively. Overcast conditions promote diurnal activity, and ♀♀ with litters devote proportionally more time to diurnal hunting than when they are without kittens. Servals rest in woody patches, ravines or clumps of long grass and seldom frequent the same resting site, probably to avoid attracting predators. When threatened, they crouch low in long grass remaining extremely well hidden until flushed when they flee using a 'zig-zag bouncing' gait that may confuse the pursuer (Geertsema 1985).

Foraging and Food Carnivorous. Servals prey mainly on small mammals, with murids particularly important. In Zimbabwe, analysis of 65 stomachs revealed that murids were present in 97% of stomachs (Smithers 1978), while scat analyses indicated that rodents and shrews accounted for over 80% of Serval diet in Uganda's Bwindi Impenetrable N. P. (Andama 2000) and 93.5% on farmland in the Drakensberg Mts of South Africa (Bowland & Perrin 1993). Small mammals accounted for 89% of direct observations of Serval feeding in the Ngorongoro Crater, Tanzania (Geertsema 1985). *Otomys* spp. (especially Angoni Vlei Rat *O. angoniensis* and Southern African Vlei Rat *O. irroratus*) are particularly common in the diet of Servals, reflecting both local abundance and their common association with rank grassland and wetlands. Other favoured rodent prey include multimammate mice *Mastomys* spp., Tiny Pygmy Mouse *Mus minutoides* and Nile Rat *Arvicanthis niloticus*. Shrews have been recorded from the diet of Servals in some parts of southern Africa (Smithers & Wilson 1979, Bowland & Perrin 1993); the latter are nocturnal and therefore likely prey where Servals are more active at night. Mole-rats *Tachyoryctes* spp. and *Cryptomys* spp., ground squirrels *Xerus* spp. and cane rats *Thryonomys* spp. have also been recorded (Verheyen 1951, Verschuren 1958, Rahm & Christiaensen 1963, York 1973, Kingdon 1977).

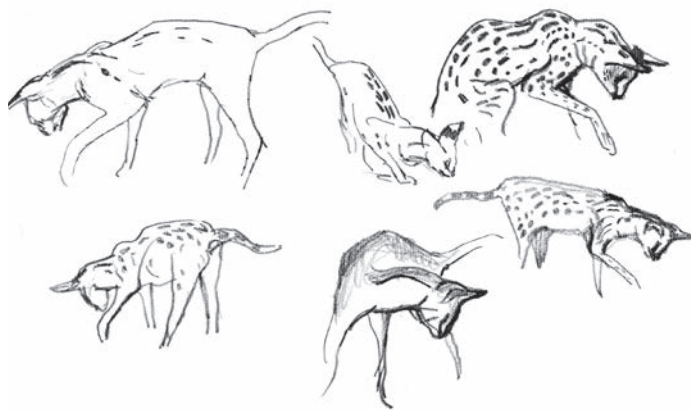
Birds are the second most common prey in the diet, mostly smaller birds such as weavers *Ploceus* spp., bishop and widow birds *Euplectes* spp. and flufftails *Sarothrura* spp., but significantly larger species including flamingos, herons and storks, are taken. Frogs comprise a significant proportion of the diet in Ngorongoro (77% occurrence), where Serval frequently hunt in shallow water (Geertsema 1985). Other prey includes reptiles, insects (notably termites and grasshoppers), crabs, eggs and fish. There are a few references to Servals taking larger prey such as the young of small antelope (Verheyen 1951, Pienaar 1969, York 1973), hares *Lepus* spp. (York 1973, Smithers & Wilson 1979) and Southern African Springhare *Pedetes capensis* (P. Viljoen pers. comm.). Small carnivores are occasionally killed: T. Dickerson (pers. comm.) saw a Serval consume an adult genet *Genetta* sp. in KwaZulu-Natal, and an adult Serval in Lower Zambezi N. P., Zambia, killed two Banded Mongooses *Mungos mungo* in quick succession and ate both (G. Cumming pers. comm.). Small quantities of grass are frequently eaten, possibly aiding digestion, and other vegetable matter such as bananas and avocados has been recorded (Rahm & Christiaensen 1966).

Servals locate prey in long grass by roaming around with frequent pauses to listen for potential targets. They often use established paths or roads to hunt or to commute to favoured hunting areas. Once prey is located they position themselves with a slow stalk, followed by a high pounce with forelegs tucked into the chest, descending on to the target with both forelegs extended. This technique possibly stuns the prey with a swift blow from one or both forefeet though vegetation usually impedes direct observation; it may be that the action simply secures the prey. Servals also flush prey using a series of high bounds on stiff legs with back straight and tail erect, a practice often employed for small birds and insects. They are exceptionally agile; a pounce may measure up to 3.6 m long and over 2 m high and they are able to change direction in mid-air when chasing prey (Smithers 1978, Estes 1991). They will leap high to grab fleeing birds and insects from the air. Large birds such as storks and herons are often stalked for some distance and captured after a sprinting charge and high leap as the quarry takes flight (Newman 1998). Servals sometimes excavate fossorial rodents from their burrows and Verheyen (1951) reported

individuals scratching at the plugged entrances of mole-rat burrows to draw them to the surface. Rarely, Servals hunt in trees, usually in pursuit of a fleeing terrestrial target such as rodents or lizards and seldom beyond 2 m high. Most prey is killed by an accurate bite to the head or neck; two Banded Mongooses were killed by a neck bite followed by violent shaking (G. Cumming pers. comm.). Snakes and lizards are often killed by repeated forceful slaps by one of the front paws (Geertsema 1976, 1985). Servals eat rodents head first, gulping them down with little chewing, often discarding the viscera (Geertsema 1976, J. Bowland pers. obs.). Feathers are plucked from larger birds prior to consumption and Kingdon (1977) recorded fur plucking from hares by captive Servals.

In Ngorongoro hunting success was about 50%, although it increased to 62% in an adult ♀ with kittens. Success did not differ between day and night hunts. They killed 15–16 times per 24-hour period, making 0.8 kills per hour during the day and 0.5 kills per hour at night. In terms of distance, this equates to 2.5 kills per km and 1.9 kills per km, respectively. Juveniles kill more frequently (4.2 kills/km) but hunt smaller prey with lower energy yields. Each Serval in Serengeti N. P. eats about 4000 rodents, 260 snakes and 130 birds per year (Geertsema 1985, Kitchener 1991). Maximum passage rate time is seven days for hair and the same prey item may appear in up to seven successive scats (Bowland & Bowland 1991). Caching by raking leaf litter and dead grass over large food items has been recorded in captivity (Kingdon 1977).

Scavenging appears to be very rare. Newman (1998) filmed a female Serval usurp a Black-backed Jackal *Canis mesomelas* from a juvenile Common Wildebeest *Connochaetes taurinus* carcass, and Geertsema (1985) observed two incidents of scavenging in more than 1300 hours of observation in Serengeti N. P.; in one of these cases, a young adult male Serval confronted an adult Spotted Hyaena *Crocuta crocuta* over a juvenile Common Hippopotamus *Hippopotamus amphibius* carcass. Conversely, York (1973) studied Servals in the Aberdares by drawing them to fresh carcasses laid along roads. Livestock predation is considered rare (Lawson 1987, Bowland 1990), though local people blamed Servals for 60 kills of sheep and goats between November 2001 and October 2002 in the Web Valley of Bale Mountains N. P., Ethiopia (Atickem 2003). Goats were most vulnerable, apparently because they foraged in mountainous areas away from villages where Servals were common (A. Atickem pers. comm.). All kills were juveniles except for one female goat.



Serval *Leptailurus serval* hunting mice.

Social and Reproductive Behaviour Servals are normally solitary, although during oestrus a ♂ and ♀ may hunt and rest together for several days (Geertsema 1976, 1985), and juveniles stay with their mothers for up to a year (Skinner & Chimimba 2005).

Home-range size varies considerably but female ranges are typically smaller than those of ♂♂. The home-ranges of two ♀♀ and one ♂ on farmland and an adjacent nature reserve in the KwaZulu–Natal Drakensberg were 19.8 km², 15.8 km² and 31.5 km², respectively (Bowland 1990). In Ngorongoro Crater, Tanzania, the home-range of an adult ♀ and adult ♂ was 9.5 km² and 11.5 km², respectively (Geertsema 1985). The home-ranges of two reintroduced, captive-bred adult ♂♂ observed by Van Aarde & Skinner (1986) were somewhat smaller at 2.0 and 2.7 km² and a reintroduced hand-reared ♀ had a home-range of 6.2 km² (Perrin 2002). The factors affecting home-range size have not been clearly delineated though the availability of prey and cover are certain to exert a strong effect. Geertsema (1985) suggests that disturbance such as fires, and human and livestock movements increase home-range sizes.

Home-ranges of Servals, especially ♀♀, overlap spatially but individuals normally avoid each other. In the KwaZulu–Natal Drakensberg, a mature ♂, a subadult ♂ and four ♀♀ were captured and radio-tracked for varying amounts of time within a period of seven months in a study area of about 30 km². However, only two of these, the mature ♂ and a ♀, were actually recorded within the study area at the same time. The subadult ♂ moved out of the study area within eight weeks of capture (Bowland 1990). In Ngorongoro, 17 different Servals were seen in an area of 30 km² over 2½ years. Some of the adult ♀♀ were probably related as female offspring are tolerated more than ♂♂, the latter being driven away by the mother and resident ♂ when almost fully grown at approximately one year old. Juveniles utilize their mothers' home-ranges intensively, gradually moving further afield as they mature. Young adults often wander quite widely, utilizing small areas for a few months before moving on and eventually settling in a permanent home-range. Local prey abundance such as rodent or insect irruptions may attract a few individuals to the same site.

Male and female Servals scent-mark along the paths they use by spraying (♂♂) or squirting (♂♂ and ♀♀) urine on grass clumps and bushes. Both sexes also rub their faces on the ground and grass stalks while salivating freely. Scats are dropped along pathways (Smithers 1978, Bowland 1990), in grass and occasionally on top of hyaena faeces (Geertsema 1985). Captive animals show a sexual difference in scat deposition, ♀♀ using the same site while ♂♂ scatter their faeces more randomly (Kingdon 1977). Latrines have not been observed in the wild. Resident adult ♂♂ spend more time than ♀♀ patrolling and marking their range (41 times per hour for ♂♂ cf. 20 times per hour for ♀♀), but do not regularly re-use the same marking site. Few direct aggressive or territorial confrontations have been observed as Servals seem to use a system of mutual avoidance rather than territorial defence (Geertsema 1985). Agonistic behaviour is largely demonstrative, with highly arched back, raised tail and hair, and lateral presentation. Heads are thrown up and down with bared teeth and flattened ears, which very effectively 'flags' the white patches on the ears (A. Geertsema pers. comm.). The action is usually accompanied by yowling while forefeet are raised and lowered (York 1973, Geertsema 1976, Leyhausen 1979).

Rosevear (1974) notes that Serval utter several different sounds, including a purr not unlike a domestic cat, only louder; a high-pitched,



Serval *Leptailurus serval* facial expressions.

slightly raucous miaow, expressed as a nasal 'mwa-mwa' slowly repeated six or eight times; and a complaining moan ending with a low purring growl, which becomes like a loud hiss. A swallowed mew signifies friendly recognition, often followed by an abrupt about-turn and distinctive shiver-display of the tail (Kingdon 1977).

Sexual behaviour is poorly known from the wild. A single mating filmed in Ngorongoro Conservation Area was preceded by numerous 'false alarms' in which the ♀ lay down and was circled repeatedly by the ♂ without mounting taking place (O. Newman & A. Barrett pers. comm.). After approximately an hour of this, the ♀ raised her rump and the ♂ immediately mounted and achieved intromission. In captivity, oestrous ♀ give repeated short, sharp miaows or bouts of yowling with constant pacing and frequent urine squirting. Occasionally, claws are raked down tree trunks. When approached by a ♂, she purrs and rubs the sides of her mouth and cheeks against him, salivating copiously and then walks along his length, leaning heavily against him. When the rump is reached, she turns sharply to repeat the action or presents for mating (Kingdon 1977). Copulation appears to be prolonged for felids; an observed copulation between wild Servals lasted for 30 sec (O. Newman & A. Barrett pers. comm.) and the copulation period may last for up to 10 days (Wackernagel 1968). The ♀ is often highly vocal during copulation, emitting screams and growls audible up to 200 m away (Stuart & Wilson 1988). The end of each copulation is typically feline; the ♂ leaps away from the ♀ who turns on him with momentary aggression, followed by her rolling from side to side. Kittens are well hidden in dense vegetation, disused Aardvark *Orycteropus afer* or porcupine holes, tree hollows or rocky outcrops, and they are moved frequently. Females' home-ranges and activity patterns alter radically when young are born. Far more time is spent hunting in the core area of the home-range and food is carried back to the kittens' hiding place (Geertsema 1985).

Reproduction and Population Structure In captivity oestrus lasts up to four days ($n = 4$), and the female may come into oestrus several times during the course of the month (Wackernagel 1968). Gestation lasts about 65–75 days (Geertsema 1976, Stuart & Wilson

1988) and litter-size ranges from 1–5, usually 2–3 (Smithers 1978, Stuart & Wilson 1988) and exceptionally 6 (Poonacha 1997). Sex ratio at birth in Johannesburg and Pretoria Zoological Gardens was recorded at 1 : 1 (Skinner & Chimimba 2005), not dissimilar from that recorded by Wackernagel (1968). Newborns weigh about 250 g and have a soft woolly grey coat, with indistinct markings. Eyes open between Day 7 and Day 10 (Stuart & Wilson 1988), and permanent dentition is fully erupted after six months; however, they take solid food as early as 2–3 weeks.

In the wild, birth peaks seem to be correlated with highest rodent densities, which are in turn correlated with rainfall and vegetation growth. In southern Africa, pregnant ♀♀ have been taken from Nov to Mar, with one record for Jul, indicating that the young are usually born during the middle or latter part of the warm, wet season (Smithers 1978, Skinner & Chimimba 2005). Geertsema (1985) suggests most births in the Ngorongoro Crater occur between late Aug and Nov, the mid- to late dry season. In Uganda and E DR Congo, births ($n = 8$) were clustered around the beginning and end of the wet season (Kingdon 1977). The ♀ brings prey to kittens in the den when they are about one month old and they accompany her when foraging from around three months of age (Geertsema 1985). Kittens are independent at 6–8 months, but juveniles may remain in their mother's range for over a year (Geertsema 1985). Individuals reach sexual maturity at 17–26 months (Farmer 1971, Bloxam 1973).

The shortest inter-litter interval with normal lactation recorded from captivity was 184 days (Wackernagel 1968) but wild litters are more widely spaced; a wild ♀ in Ngorongoro had two litters in 2½ years (Geertsema 1985). Longevity is around 22 years in captivity (Weigl 2005), and ♀♀ can breed until 14 years; a wild breeding female of 11 years is recorded (A. Geertsema pers. comm.).

Predators, Parasites and Diseases Servals are apparently very wary of Spotted Hyaenas (Estes 1991) though adult Servals sometimes do confront them (Geertsema 1985). Lions *Panthera leo* also will kill Servals (Lewis 1986, L. T. B. Hunter pers. obs.) and Leopards have been observed with cached Serval carcasses (L. T. B. Hunter pers. obs.). Turnbull-Kemp (1967) witnessed 'wild pigs' (presumably Bush Pig *Potamochoerus larvatus*) killing Servals. A Martial Eagle *Polemaetus bellicosus* in the Masai-Mara was observed taking a kitten despite its mother attempting to intervene (Butchart 2000). Black-backed Jackals (on kittens), Nile Crocodiles *Crocodylus niloticus* and African Rock Pythons *Python sebae* are probably occasional predators.

Cat fleas *Ctenophalides felis damarensis* and hard ticks *Haemaphysalis spinulosa* have been recorded from a South African ♂ (Hoffman 1987) and a single, unsexed, adult animal taken from Kruger N. P. was host to ixodid ticks *Amblyomma hebraeum*, *Rhipicephalus appendiculatus* and *R. simus* (Horak *et al.* 1987). Hookworms *Ancylostoma paradoudenale* were found in Servals from Somalia (Macchioni 1995). Two Servals (from a sample of eight) collected in S Sudan tested positive for leptospirosis (Sebek *et al.* 1989), while babesiosis was confirmed from a Serval in Lydenburg, South Africa, although the *Babesia* species involved was not established (B. Penzhorn pers. comm.).

Conservation IUCN Category: Least Concern. CITES: Appendix II.

Threatened mainly by wetland habitat loss and degradation. Degradation of grasslands through annual burning followed by over-

grazing by domestic livestock, thereby leading to reduced abundance of small mammals, is also a threat (Rowe-Rowe 1992a). Servals are also used in the local skin trade in West Africa (C. Stuart pers. comm.), East Africa and Sudan (Kingdon 1977), Somalia (Funaioli & Simonetta 1966), Uganda (Andama 2000), E DR Congo (J. Hart pers. comm.), South Africa (A. E. Bowland pers. obs.) and Morocco (F. Cuzin pers. comm.). Commercial trade is generally declining (Nowell & Jackson 1996), though skins are still traded in large quantities in some countries, such as Senegal, Gambia and Benin (O. Burnham & I. Di Silvestre pers. comm.). They are highly valued for traditional medicine in Nigeria: among markets surveyed in five SW Nigerian towns in 1994, they were the second most commonly offered mammalian species (Sodeinde & Soewu 1999). In rural areas throughout Africa, they are persecuted for taking poultry (Andama 2000) and indiscriminate predator control methods practised by pastoralists frequently kill them (L. T. B. Hunter pers. obs.).

Servals occur in a number of protected areas across their range, including: Ifrane N. P. (Morocco), possibly El Kala N. P. (Algeria), Feidja N. P. (Tunisia), Comoé N. P. (Côte d'Ivoire), 'W' N. P. (Burkina Faso, Benin, Niger), Zakouma N. P. (Chad), Simien and Bale Mountains National Parks (Ethiopia), Virunga N. P. (DR Congo), Queen Elizabeth N. P. (Uganda), Aberdare Mountains N. P. (Kenya), Serengeti and Selous National Parks (Tanzania), Moremi G. R. and Chobe N. P. (Botswana), and Kruger N. P. and Ukhahlamba-Drakensberg Park (South Africa).

Measurements

Leptailurus serval

TL (♂ ♂): 1111 (960–1205) mm, n = 23

TL (♀ ♀): 1097 (970–1230) mm, n = 23
 T (♂ ♂): 314 (280–380) mm, n = 23
 T (♀ ♀): 290 (254–330) mm, n = 23
 HF c.u. (♂ ♂): 193 (180–205) mm, n = 23
 HF c.u. (♀ ♀): 182 (165–194) mm, n = 23
 E (♂ ♂): 91 (83–97) mm, n = 23
 E (♀ ♀): 86 (80–97) mm, n = 23
 WT (♂ ♂): 11.1 (8.6–13.5) kg, n = 20
 WT (♀ ♀): 9.7 (8.6–11.8) kg, n = 23
 Zimbabwe (Smithers 1978)

TL (♂ ♂): 1122 (1010–1250) mm, n = 6
 TL (♀ ♀): 1026 (930–1090) mm, n = 8
 T (♂ ♂): 282 (250–330) mm, n = 6
 T (♀ ♀): 262 (230–290) mm, n = 9
 HF c.u. (♂ ♂): 186 (180–195) mm, n = 6
 HF c.u. (♀ ♀): 174 (160–190) mm, n = 9
 E (♂ ♂): 86 (82–90) mm, n = 6
 E (♀ ♀): 85 (79–90) mm, n = 9
 WT (♂ ♂): 10.7 (7.9–12.4) kg, n = 7
 WT (♀ ♀): 8.1 (6.0–9.8) kg, n = 9
 KwaZulu–Natal, South Africa (Bowland 1990)

Key References Bowland 1990; Bowland & Perrin 1993; Geertsema 1976, 1985; Kingdon 1977; Nowell & Jackson 1996; Smithers 1978; Stuart & Wilson 1988.

Luke Hunter & Jane Bowland

GENUS *Acinonyx*

Cheetah

Acinonyx Brookes, 1828. Cat. Anat. Zool. Mus. Joshua Brookes, London p. 16, 33.

Formerly included in a monophyletic group, the subfamily Acinonychinae (e.g. Wozencraft 1993), recent molecular evidence now clusters the Cheetah *Acinonyx jubatus* with the Puma *Puma concolor* and Jaguarundi *P. yagouaroundi*, which diverged some 6.7 mya (Johnson *et al.* 2006), in agreement with earlier studies (Johnson & O'Brien 1997, Bininda-Emonds *et al.* 1999, Mattern & McLennan 2000).

Cheetah-like felids once ranged across Asia, Africa and North America 10,000 years ago (Kurtén 1968). Two extinct species, the giant cheetah *A. pardinensis* and the smaller *A. intermedius*, have been found in the Pleistocene of Eurasia, as well as fragmentary remains of unknown species in Africa. In North America, two Cheetah-like species, *Miracinonyx studei* and *M. trumani*, have been described from the late Pleistocene. For many years it was uncertain whether similarities between *Acinonyx* and *Miracinonyx* were due to convergent evolution or common descent (if the latter, it would place the origin of *Acinonyx* in the New World, Adams 1979). Recent work involving ancient DNA indicates that *Puma* and *Miracinonyx* are more closely related than either is to *Acinonyx* (Barnett *et al.* 2005).

Tim Caro



Cheetah *Acinonyx jubatus*, alert and resting.

Acinonyx jubatus CHEETAH

Fr. Guepard; Ger. Gepard

Acinonyx jubatus (Schreber, 1775). Die Säugethiere 2 (15): pl. 105 [1775]; text 3 (22): 392 [1777]. 'südliche Afrika; man bekommt die Felle vom Vorgebirge der guten Hoffnung' [South Africa, Western Cape Province, Cape of Good Hope].

English name derived from the Hindi *chita*, meaning spotted one.

Taxonomy Previous generic names include *Cynilurus*, *Guepardus* and *Cynofelis*; *Acinonyx* derived from the Greek *akaina* (a thorn) and *onyx* (a claw), referring to the non-retractable claws. The species name, *jubatus* (Latin), refers to crest or mane seen in young and certain adults. Allen (1939) listed eight subspecies from Africa, while Smithers (1975) reduced the number to five (accepted by Krausman & Morales 2005). The subspecies *A. j. venaticus*, which formerly occurred in India, and throughout the Asiatic part of the range, but survives only in Iran, has generally been considered to be the subspecies occurring in North Africa (see Ellerman & Morrison-Scott 1951, Smithers 1975, Krausman & Morales 2005). However, Charruau *et al.* (2011) demonstrated the extant Iranian cheetahs are an autochthonous monophyletic population and the last representatives of the Asiatic subspecies *A. j. venaticus*. Consequently, North African cheetah may deserve independent subspecies status, although the population also may be genetically contiguous with those from West Africa, historically classified as *A. j. hecki*. Charruau *et al.* (2011) also confirmed the distinctiveness of *A. j. soemmerringi*. On the other hand, there was little genetic variation between two sub-Saharan subspecies, *A. j. jubatus* and *A. j. raineyi* (although minisatellite variation supports their separation; Menotti-Raymond & O'Brien 1993).

The so-called 'king cheetah', the form described as a new species of Cheetah, *Acinonyx rex*, from southern Africa (Pocock 1927, Hills & Smithers 1980) is synonymous with *A. j. jubatus* with a homozygous recessive gene for blotched coat pattern (Van Aarde & Van Dyk 1986); it is very rare in the wild.

Synonyms: *fearonii*, *fearonis*, *guttata*, *hecki*, *iubata*, *lanea*, *megabala*, *megabalica*, *ngorongorensis*, *obergi*, *raddei*, *raineyi*, *rex*, *senegalensis*, *soemmerringi*, *velox*, *venaticus*, *venator*, *wagneri*. Chromosome number: $2n = 38$; the X chromosome is a small metacentric, and the Y is acrocentric (Pathak & Wurster-Hill 1977).

Description Medium-sized, spotted felid, with a tall, slender build, long, thin legs, a deep, narrow chest, and a long tail measuring about half the head and body length. Head rounded, muzzle short, with small, rounded ears, set far apart and black when viewed from behind. A characteristic lachrymal or 'tear streak' extends from medial corner of eye to upper lip just behind canines. In profile, the back is slightly concave. Light brown or tan pelage covered with solid round or slightly oval black spots, the smaller of which are interspersed with larger ones. Chin, throat and upper lip white, as are the posterior parts of the belly, but the chest and anterior part of the belly is spotted. The tail is also spotted, the spots on the distal third coalescing into black rings; the tip of the tail is white. The spot patterning on the face and chest differs among individuals and is a useful feature for field identification; variations in coat patterns have been used to reveal



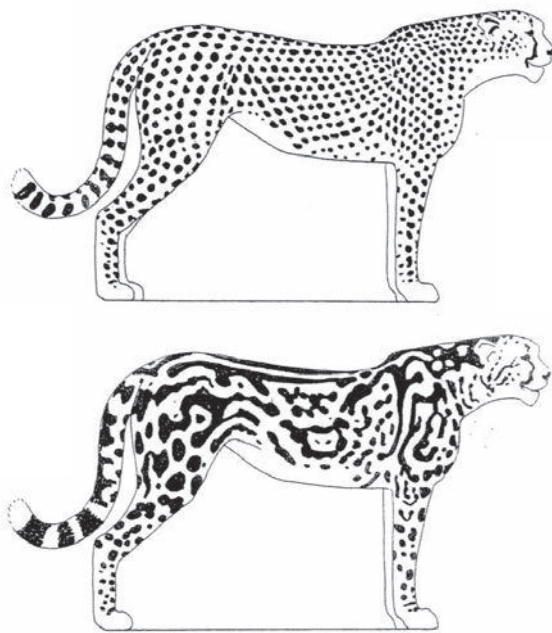
Cheetah *Acinonyx jubatus*.

family resemblances (Caro & Durant 1991). The fur is short and coarse, except for an erectile crest of greyish hair up to 80 mm long on the nape and shoulders, and which sometimes continues down the back, and that accentuates the height. Front feet with five digits, hindfeet with four. The first digit on the forefoot (the dew-claw) sits high and does not mark in the spoor. Claws are blunt and slightly curved, and slightly retractile; they are visible in the spoor due to the lack of claw-sheaths. Males heavier than ♀♀ and have larger chest girths. Females usually have six pairs of nipples, in contrast to the three or four pairs in other large cats.

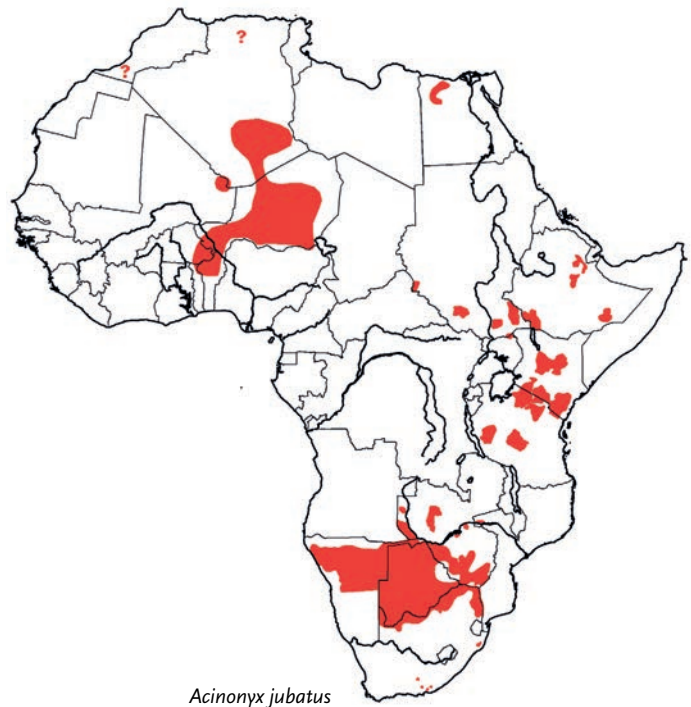
The skull is high domed, highest at the level of the middle of the orbits, then slopes abruptly forward to the nasals and back to the well-developed supra-occipital crest. The braincase is rounded, the poorly developed sagittal crest dividing into two low ridges to end on the postorbital processes (which are incomplete). The rostrum is short and wide, and the nasal openings are enlarged. The zygomatic arches are broad in the front, narrower behind and widen out posteriorly. Unlike other felids, they are distinctly upcurved when viewed from the side (Skinner & Chimimba 2005). The dental formula is typically felid, although P^2 is sometimes absent (and see Marker & Dickman 2004). The canines are short, sharp and rounded, not as long as in other felids where they are used for severing the spinal cord. The antero-internal cusp, which is well developed in other felids, is barely in evidence, represented by a small knob that occludes between the P^4 and M_1 . Its reduction allows the jaws to close tightly (Pocock 1916e, Ewer 1973, Skinner & Chimimba 2005).

Geographic Variation

A. j. hecki (includes *senegalensis*): West African Cheetah. Senegal, S Mauritania, Mali, Burkina Faso, Benin and Niger. Cheetahs from



Cheetah *Acinonyx jubatus*: (above) regular, even spotting; (below) typical 'King Cheetah' marbling.



Acinonyx jubatus

North Africa are provisionally included here pending further sampling to determine the phylogenetic position of this population.

- A. j. jubatus* (includes *rex*, *fearonii*, *guttata*, *lanea*, *obergi*): Southern African Cheetah. Angola, Zambia, S DR Congo, STanzania, Malawi, Mozambique and southwards.
- A. j. raineyi* (includes *velox* and *ngorongorensis*): East African Cheetah. Kenya, Uganda, N and C Tanzania and S Somalia. Genetic data indicate that there is very low genetic variation between this and the nominate subspecies.
- A. j. soemmeringi* (includes *megabalica* and *wagneri*): Central African Cheetah. N Somalia, Ethiopia, Sudan, N Central African Republic, N Cameroon, N Nigeria and S Niger. Intergradation with *hecki* not clear.
- A. j. venaticus* (includes *raddei* and *venator*): Asiatic Cheetah. Extralimittally in Iran. Formerly more widespread throughout the Arabian Peninsula, the Caspian to India.

A variant known as the 'king cheetah', characterized by a unique pattern of striped markings and slightly longer and distinctly silkier hair, was first described as a new species of Cheetah from skins (Pocock 1927), and first observed in the wild in 1928. Apart from one king skin recovered from Singou Faunal Reserve in Burkina Faso in 1992 (Frame 1992), all the skins and subsequent sightings come from a restricted area in E and SE Zimbabwe, E Botswana and South Africa's Limpopo Province and Mpumalanga (Hills & Smithers 1980, Skinner & Chimimba 2005). Research has confirmed that the king cheetah merely represents a colour variant and that the 'king' trait is inherited as an autosomal recessive allele, which probably arose as a mutation at the 'tabby' locus (Van Aarde & Van Dyk 1986). Melanistic and white Cheetahs are also known (Wrogemann 1975, Sunquist & Sunquist 2002). Cheetahs from the Sahara are considerably lighter in colour than those in sub-Saharan Africa (Dragesco-Joffé 1993), and Saleh *et al.* (2001) remark that skulls examined from Egypt and Libya are smaller than those from elsewhere.

Similar Species

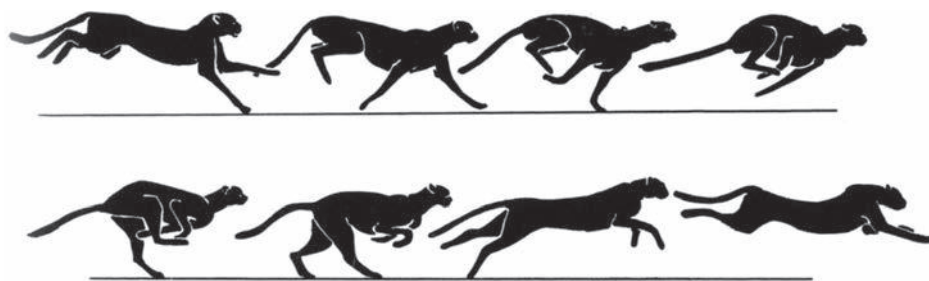
Panthera pardus. Shorter legged and marked with rosettes, not single spaced spots. Lacks distinctive 'tear-streak'.

Leptailurus serval. Savanna habitats from Senegal to Ethiopia and S Somalia and southwards to South Africa and SW Angola. Adults smaller in size; ear pinnae larger; lacks facial tear streaks; cubs lack bluish-grey mantle of dorsal fur.

Distribution Widely, but sparsely, distributed from Senegal to Somalia (both countries where their status is unclear) and south to South Africa, with small, isolated populations existing in Morocco, Algeria and Egypt (Myers 1975, Nowell & Jackson 1996, Sunquist & Sunquist 2002). Outside of the African continent, individuals survive only in extremely small fragmented populations in Iran and possibly Pakistan.

Historical Distribution At least until the nineteenth century Cheetahs had a wide range across much of Africa and south-west Asia. Their range extended through much of North Africa and the Saharan regions, through Arabia and the Middle East to the Caucasus and eastwards through Central Asia to about Kazakhstan and eastwards through Pakistan to India. In North Africa, the last record for the Cheetah in Western Sahara dates to 1976, when an animal was given to the Algiers Zoo, while the last known Cheetah in Tunisia was killed in 1960 near Bordj Bowrgiba in the extreme south. The last observation of a Cheetah in Libya was in 1980 in the south-western part of the country bordering Algeria (Nowell & Jackson 1996). In Saudi Arabia, the last record dates to 1973 (Nader 1989), in Yemen to 1963 (Harrison & Bates 1991), in Israel to 1959 (Ilani 1979, Shalmon 2004) and in India to 1947 (Nowell & Jackson 1996). In sub-Saharan Africa, they were widely distributed from Senegal to the Horn of Africa and then southwards at least as far south as about Beaufort West in the Western Cape and just north of Grahamstown in the Eastern Cape of South Africa (Skead 1980, 1987).

Serial silhouettes of running Cheetah
Acinonyx jubatus.



Current Distribution The current distribution of the Cheetah is much changed from its historical range; Ray *et al.* (2005) estimated that the Cheetah has disappeared from at least 76% of its historical range in Africa. In their once expansive range stretching from North Africa to India, populations remain only in a few isolated regions. In Egypt, the entire population has been reduced to a few nomadic individuals surviving in a highly inaccessible area in the northern and western parts of the Qattara Depression, in the northern section of the Western Egyptian Desert (Saleh *et al.* 2001). In Morocco, observations in the last 20 years come only from the contiguous areas of the Western Draa Mts, Bas Draa-Noun and the Aydar-Ouarkiz (Cuzin 1996, 2003) and the species may now be extinct (F. Cuzin pers. comm.). There is evidence for the persistence of the species in the Algerian high plateaux (Fellous 2007). In the southern Sahara, Cheetahs still persist in mountain ranges in SE Algeria, Mali and Niger, although they can range far out onto sandy plains where there is sufficient prey (Kowalski & Rzebik-Kowalska 1991, Dragesco-Joffé 1993, Nowell & Jackson 1996, Hamdine *et al.* 2003, Wachter *et al.* 2005, Busby *et al.* 2006, 2009).

In sub-Saharan Africa, they are now rare across most of their range in West Africa, and are considered regionally extinct in Nigeria and Cameroon (De Iongh *et al.* 2011). Likewise, they are now thinly distributed across the remaining parts of their range, and no longer occur in Djibouti, Eritrea, Rwanda or Burundi; a small resident population persists in NE Uganda. The indigenous population in Swaziland was also extirpated, but they have been reintroduced (Monadjem 1998), and widely so elsewhere, such as in South Africa's KwaZulu-Natal (Hluhluwe-iMfolozi Park, Mkhuze G. R., Ndumo G. R. and Phinda G. R.) (Rowe-Rowe 1992a). Their current status in eastern and southern Africa has been recently reviewed (IUCN SSC 2008, 2009), but their status in several countries, particularly Somalia and Angola, remains poorly known.

Extralimital to the continent, populations of Asiatic Cheetahs survive only in central Iran (Farhadinia 2004). The animals occur in the foothills and dry water-courses of desert massifs, where prey is more common than on the flats (Farhadinia & Hemami 2010).

Habitat Generally depicted as a species frequenting open plains, particularly the open grasslands of East Africa, but in much of their range also found in savanna woodlands, including the miombo and *Acacia* woodlands of southern and central Africa (Mills *et al.* 2004). They also are associated with the lowveld (and formerly highveld) of southern Africa, sparsely vegetated areas of the Sahel, and even semi-desert, as in the pro-Namib of Namibia. Some still survive in parts of the Sahara, where they lie up during the day in cover (Dragesco-Joffé 1993); the surviving population in Egypt inhabits uninhabited oasis depressions within the Qattara Depression, where large groves of

Acacia raddiana west and south-west of these habitats appear to be regularly visited by Cheetahs (Saleh *et al.* 2001). They are absent from rainforest and closed woodland. There are reports of Cheetah at altitudes of 4000 m on Mt Kenya (Young & Evans 1993), and in the central Sahara Cheetahs also occur in high mountainous habitat (K. De Smet pers. comm.).

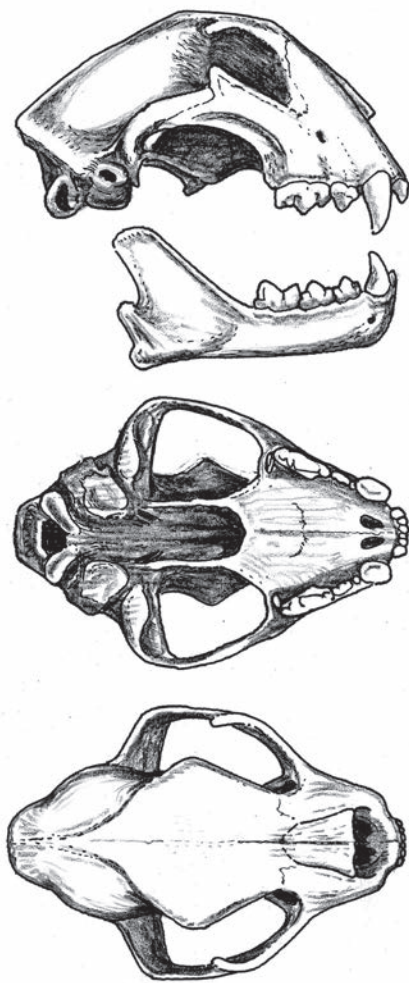
Abundance Surveys in the 1970s indicated that the total population of Cheetahs stood at between 7000 and 25,000 in 25 African countries (Myers 1975). Numbers certainly are considerably lower today, but reliable data estimates exist for only a few countries. National interview surveys conducted in the mid-1990s suggested that Tanzania contained 569–1007 individuals (Gros 2000, 2002), 40–295 in the Karamoja Region of Uganda (Gros & Rejmanek 1999), 793 in protected areas in Kenya (Gros 1998) and 15–30 in Malawi (Gros 1996). More recent figures put the total population of resident Cheetahs in eastern Africa at ~2570 adults in 15 populations, the largest of which is in the Serengeti/Mara/Tsavo (710) (IUCN SSC 2008).

In southern Africa, previous estimates have put the population at between 2000 and 3000 in Namibia, 1000 and 1500 in Botswana, less than 1000 in Zimbabwe and 500 in South Africa (with the largest population in Kruger N. P.) (Nowell & Jackson 1996, Marker 1998, 2003). Recent estimates cautiously put numbers in southern Africa at ~6260 adults in unfenced areas, although the overwhelming majority occurs in the transboundary population traversing Botswana, Namibia, South Africa, Zambia and Zimbabwe; in addition, around 200 adults occur in more than 20 fenced reserves (IUCN SSC 2009).

Reliable data regarding population status of the Cheetah in the Sahara are lacking, and summarized by Belbachir (2007). Dragesco-Joffé (1993) proposed approximately 300–500 individuals, while in Algeria, De Smet (1989) estimated 'several dozens' in the central Saharan massifs. Hamdine *et al.* (2003) suggested the population in the Ahaggar massif could be 30–40 individuals. Estimated at 200 animals in the 1970s, the last Asiatic Cheetahs are now thought to number around 60–100 animals (Hunter *et al.* 2007a).

Densities of Cheetah in protected areas are generally low (0.25–5.0/100 km²) but seasonally can reach 40/100 km² (Caro 1994). Sparse food supply outside protected areas in some parts of the range (though not, for example, outside protected areas in Namibia, where minimum density was 2.5 Cheetah/1000 km²; Marker 2003), human persecution, and high cub mortality from predation within protected areas, keep population densities relatively low (compared with Lions, for example).

Adaptations Cheetahs are designed for short, explosive sprints and are famed as the fastest animals on earth over short distances, able to



Lateral, palatal and dorsal views of skull of Cheetah *Acinonyx jubatus*.

attain a speed of at least 105 km/h when fully extended (Sharp 1997, and see Hildebrand 1959), although speeds of 85 km/h probably are more the norm (Frame & Frame 1980). To attain such speeds, Cheetahs have a number of important adaptations. The radius, ulna, tibia, fibula, metacarpals and metatarsals of the lower leg are elongated for increased stride length (Kitchener 1991). The tibia and fibula are firmly bound together with fibrous tissue that allows very little rotation about the lower leg, thereby providing much needed stability at top speeds, though at the same time hampering climbing ability (Ewer 1973). The spine is long and flexible, and flexing and straightening of the vertebral column while running increases stride length (Hildebrand 1961). At top speed, stride length approaches 7 m, and with three-and-a-half strides per second, the Cheetah can cover as much as 25 m per second (Hildebrand 1959, Ewer 1973, Taylor 1989b). The long, muscular tail functions as a counterbalance when turning or changing direction at high speeds (Kitchener 1991). Cheetahs also have a preponderance of fast-twitch fibres in their locomotor muscles (83% of the vastus lateralis and ca. 61% of the gastrocnemius), and the locomotor muscles are capable of anaerobically based exercise (Williams *et al.* 1997). Contrary to widely held belief, the Cheetah's claws are partially retractile, the modifications in the Cheetah's lower limbs resulting in somewhat diminished retractile function. The paws are small and compact, and reduced webbing between digits means the toes can be splayed more

widely. Furthermore, the absence of a protective sheath into which the claws can retract means that the claws protrude even when retracted, serving a function similar to running spikes to increase grip while pursuing prey (Kitchener 1991). Londei (2000) has remarked that the dew-claw in the Cheetah seems to have taken on the predatory function of the entire forepaw, as the other claws lost this function because of locomotory adaptation. Cheetahs also have very firm foot pads, with longitudinal ridges that act like the tread on car tyres running along the foot pads (Ewer 1973).

To facilitate rapid intake of air, the nasal passages are short and enlarged; reduction in the size of the teeth, particularly the canines, and root canals permits the enlarged nasal openings. The wide and large nasal passages help increase the concentration of oxygen in the blood during the sprint and during prey suffocation, allowing the Cheetah to regain its breath after capture. Furthermore, the respiratory tract has a wide cross-section, further facilitating rapid movement of air during breathing. During sprints, their respiratory rate climbs from 60 to 150 breaths per minute. In experimental trials, Cheetah refused to run when their core body temperature reached 40.5°C (Taylor & Rowntree 1973). As Cheetah store about 90% of the heat they produce while sprinting, their endurance is limited by the amount of heat they can store before body temperature reaches such a level.

An unusual, but important, dietary adaptation is the absence of a post-canine gap, present in other felids that kill with a neck bite where the canines need to gain maximum penetration in order to sever the spinal cord. In the Cheetah, the narrow upper and lower cheekteeth overlap such that there is no gap behind the canines; however, this arrangement does mean that the teeth are particularly well adapted to slicing and shearing (Ewer 1973).

The pelage of the Cheetah helps insulate the body from temperature changes, and the coat colour and spot patterning probably serve as camouflage. Young are born with a long mantle of dorsal fur, bluish-grey in colour, and forming a sharp boundary to dark fur below. The mantle gradually recedes as the cubs get older, until, at about four months of age, it is little more than a ruff of hair (and which is retained as the erectile crest or mane on the nape and shoulders). The adaptive significance of this mantle in young Cheetahs is still unknown. One suggestion is that the cubs' coat pattern mimics the colouring of the Ratel *Mellivora capensis* and therefore might deter predators (see Estes 1991), but the resemblance is poor. The very pale fluffy dorsal fur could also be seen as resembling dry grass, thereby assisting crypsis.

Foraging and Food Prey consists principally of small- to mid-sized ungulates, usually weighing less than 40 kg; however, body weights of prey have a large range, from the calves of African Buffalo *Syncerus caffer* and Giraffes *Giraffa camelopardalis* to ground-living birds and small mammals, including hares, porcupines, rats and guinea fowl (Pienaar 1969). Hayward *et al.* (2006b) used data from 21 published and two unpublished studies from six countries throughout the African distribution of the Cheetah to determine which prey species were preferred and which were avoided. Their results show that Cheetahs prefer to kill and actually kill the most available prey present at a site within a body mass range of 23–56 kg with a peak (mode) at 36 kg. Blesboks *Damaliscus pygargus*, Impalas *Aepyceros melampus*, Thomson's Gazelles *Eudorcas thomsonii* and Grant's Gazelles *Nanger granti*, and Springboks *Antidorcas marsupialis* are

significantly preferred, whereas prey outside this range are generally avoided. The preferred prey species offer minimal injury risk and their small size means Cheetahs can bolt down their meat before kleptoparasites arrive (as reflected by the speed with which they eat; see later), without risking losing too much food.

In the savanna woodlands of Kruger N. P., Impalas are the dominant prey item (68% of more than 2500 kills), although Cheetahs actually display a preference for Common Reedbucks *Redunca arundinum* in that region (Pienaar 1969). In Phinda G. R. in KwaZulu–Natal, where Cheetahs were reintroduced, the most common prey species taken was Nyala *Tragelaphus angasii* (the most abundant, medium-sized ungulate available), which constituted 39% of all kills, followed by Impala (34.5% of all kills) (Hunter 1998a). In the Kalahari, Springboks are the dominant prey (86.9% of kills; Mills 1984), while in Kafue N. P. in Zambia, Pukus *Kobus vardonii* were taken most frequently (Mitchell *et al.* 1965). In the Serengeti, Tanzania, Thomson's Gazelles were the most preferred prey (Kruuk & Turner 1967, Schaller 1968, Frame 1986, Caro 1994), while in Nairobi N. P., the three, favoured prey were Impalas (27% of 183 kills), Grant's Gazelles (25%) and Thomson's Gazelles (22%) (McLaughlin 1970). In the Sahara, the main prey includes Dorcas Gazelles *Gazella dorcas* and Dama Gazelles *Nanger dama*, bustards, ostriches, hares, hedgehogs, as well as camels and goats and sheep (Dragesco-Joffé 1993, Wacher *et al.* 2005).

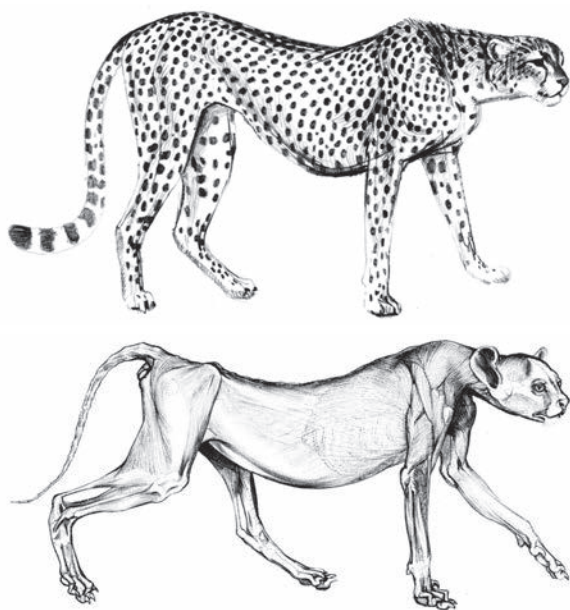
Throughout its range, young animals are taken in preference to adults, especially in the case of larger species such as Common Wildebeests *Connochaetes taurinus*. For example, in Serengeti N. P., Thomson's Gazelle fawns constituted 53.7% of Cheetah kills, but only 5.9% of the gazelle population (FitzGibbon & Fanshawe 1989). Success rates hunting neonates are high (McLaughlin 1970, Schaller 1972, Caro 1994). In addition, Cheetahs select ungulate prey that are alone or in small groups, in high vegetation, less vigilant, on the edge of the herd, and far from nearest neighbours. Such individuals are often ♂♂, although Cheetahs are actually more successful at capturing single female Thomson Gazelles than single ♂♂ (FitzGibbon 1990). Males take larger prey than ♀♀ by virtue of their larger size and

by hunting in coalitions. At Phinda G. R., over 20% of prey killed by male pairs and trios weighed more than 100 kg, whereas only one kill (<1% of total) taken by ♀♀ weighed more than 100 kg (Hunter 1998a). Hunter (1998a) observed male coalitions twice take juvenile Giraffes. However, adult ♂♂ are not necessarily more successful when hunting in groups than as individuals (Caro 1994). Cheetahs are sometimes injured during hunts, though fatal injuries are rare. On very rare occasions, Cheetahs will scavenge or return to abandoned kills (Pienaar 1969, Caro 1982, 1994, Stander 1990); Hunter (1998a) recorded ♀♀ with large cubs return to abandoned kills on 12 occasions after leaving them overnight.

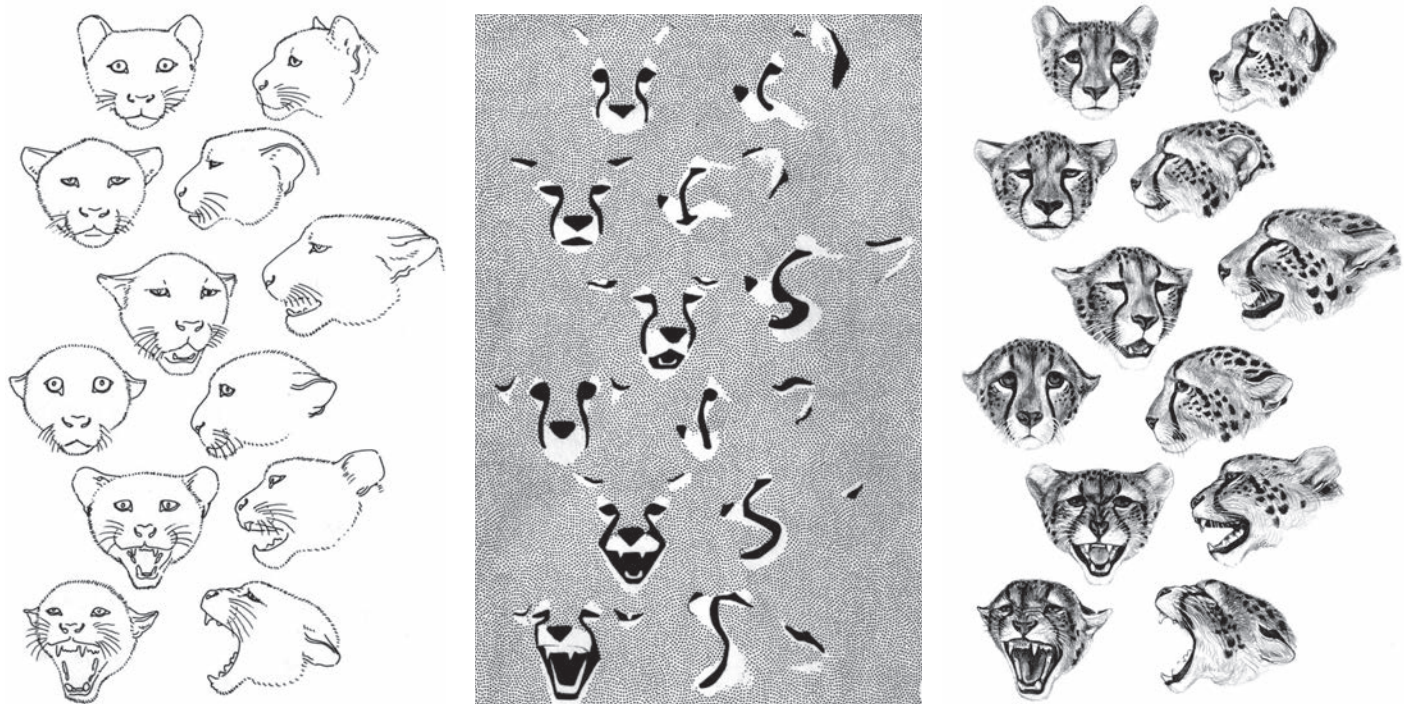
Cheetahs hunt by sight, and mainly by day, especially between 07:00 and 10:00h and 16:00 and 19:00h, which are the hours when competitors are less active (Schaller 1972, Cooper *et al.* 2007). In the Sahara, most hunting takes place during the cooler night-time hours, or shortly after dawn (Dragesco-Joffé 1993, Wacher *et al.* 2005); night-time hunting has also been recorded in Namibia (Standar 1990) and in the Serengeti (Schaller 1972). Five main hunting methods are employed (see Estes 1991): (i) crouch or sit as unsuspecting herd approaches; (ii) slow walk towards a herd in full view and break into a sprint from 60–70 m; (iii) start rush at 600 m if prey are oblivious or neonate ungulate prey stands up to nurse; (iv) approaching vigilant prey in semi-crouched stalk, freezing in mid-stride or dropping to a crouch if prey looks up, and interspersing these behaviours with trotting or sitting immobile until close enough to launch an attack; (v) flushing concealed prey from vegetation and pursuing it as soon as it runs off. On the Serengeti Plains, the last two mentioned methods are the main means of prey capture (FitzGibbon 1988). Cheetahs may take over two years to acquire some of these hunting methods, primarily relying on method (v) as juveniles.

Prey are pursued over short distances. Smaller prey are tripped or knocked over using a rapid swipe of the front paw. Medium- to large-sized prey is usually pulled off balance by hooking with the dew-claw and pulling backwards (see Londei 2000); larger prey may also be tackled by climbing onto the prey's haunches and toppling it. Large prey are suffocated or strangled by the Cheetah clamping the throat with its jaws, which takes time to achieve, with the Cheetah's large nasal passages allowing rapid inhalation to continue. Smaller prey are either grabbed by the muzzle, or killed with a bite to the skull or back of the neck. Prey are either eaten at the site of the kill, or dragged to nearby shelter. Cheetahs usually require time to recover following a chase, sometimes up to a full hour (Caro 1994). They feed rapidly, usually selecting the meat off the ventral surface first (although in 63% of more than 100 kills observed by L. T. B. Hunter [pers. comm.], Cheetahs began feeding on muscles of the hindlegs first), then the liver and the heart; however, bone consumption at kills has been recorded (Brain 1981, Phillips 1993). They are able to consume quite large quantities of food: in a feeding experiment, two Cheetahs consumed some 19 kg of food between them in a few hours of feeding (Phillips 1993).

Cheetahs make little attempt to defend their kills from larger predators and kleptoparasites such as Lions *Panthera leo* and Spotted Hyaenas *Crocuta crocuta*, and may lose up to 13% of their kills to kleptoparasites in Serengeti N. P. (Schaller 1972, Caro 1994). As a consequence, Cheetahs avoid hunting in areas where these predators are present (Durant 1998). Leopards *Panthera pardus*, African Wild Dogs *Lycaon pictus*, Brown Hyaenas *Hyaena brunnea* and even Striped



Cheetah *Acinonyx jubatus* external and myology views.



Cheetah *Acinonyx jubatus*. Far right: 12 heads with diverse facial expressions. The same 12 heads in outline (above left) and showing tonal contrast (centre).

Hyaenas *Hyaena hyaena*, Baboons *Papio* spp. and vultures have been recorded driving Cheetahs off their kills (J. S. Hunter *et al.* 2007a, b). There is one unusual record of a female Cheetah attempting to kill a subadult Ratel at Ngala Private G. R. in the Limpopo Province of South Africa; the tussle ended when a second Ratel, possibly the mother of the first, came to the rescue (Retallack 2005).

In Namibia, the Cheetah is an important predator of livestock on both commercial and communal farms: livestock depredation by Cheetahs on Namibian farmlands was calculated to account for at least 0.01 calves and 0.004 sheep per km², or 0.76 calves and 0.32 sheep annually on an averagely sized farm, and may be substantially more depending on estimates of Cheetah density (Marker 2003).

Social and Reproductive Behaviour All segments of the Cheetah population show variation in grouping patterns. Females live alone, unless they have dependent cubs (McLaughlin 1970, Frame 1984); ♂♂ live in small permanent coalitions of two or three (rarely four) animals throughout their lives, whereas others live alone. Most of these coalitions are composed entirely of littermates, but approximately 30% of Serengeti coalitions include an unrelated ♂ (Caro 1994). A ♂, or group of ♂♂, maintains close proximity to a single ♀, or to a mother and her cubs, when she is in oestrus. Such an association may last for as long as two days (although Hunter & Skinner [2003] observed ♂♂ associating with non-oestrous ♀♀ and their cubs for up to 18 days), and such associations may account for observations of larger documented group sizes (Graham 1966, Eaton 1970).

In the open plains habitats of Serengeti N. P., ♀♀ have enormous home-ranges of over 800 km² that follow the annual movements of Thomson's Gazelles (Durant *et al.* 1988, Caro 1994). Adult male Cheetahs, on the other hand, exhibit two distinct behavioural tactics. Resident or territorial ♂♂ hold and urine-mark small territories whereas non-resident (floater) ♂♂ roam over large

parts of the Serengeti Plains and rarely urine-mark. Non-residents are less relaxed than residents in that they sit up and lie alert more often; they exhibit signs of physiological stress, specifically elevated cortisol levels, and are in poor condition as determined from higher white blood cell counts, eosinophil levels, lower muscle mass and increased incidence of sarcoptic mange (Caro *et al.* 1989). Resident male territories are 37 km² (n = 22) on average whereas non-resident ranges are 777 km² (n = 9) on average, and overlap those of others. Males do not occupy territories continuously. All ♂♂ start out nomadic, but whereas some remain non-residents all their lives, others become territorial; yet others, first encountered as a resident, subsequently become nomads.

In contrast to the situation in Serengeti N. P., home-range sizes in woodland savannas vary from 24 km² in Matusadona N. P. in Zimbabwe to 320 km² in the Kalahari (Hunter 1998a, Mills 1998b, Purchase & du Toit 2000, Broomhall 2001). The nomadic nature of Springboks in the Kalahari (Mills 1998b), and the concentrated distribution of prey on grasslands in Matusadona N. P. (Purchase & du Toit 2000), likely influences home-range size of female Cheetahs in these areas. In Kruger N. P., where there are no migratory prey, home-range sizes were estimated at 126 km² for a three-male Cheetah coalition, 195 km² for a solitary ♂, and 150 km² and 171 km² for two female Cheetahs (Broomhall *et al.* 2003). Females used denser woodland habitat more frequently than ♂♂, as they seemed to be influenced by the distribution of their main prey, Impalas, which also preferred denser woodland habitat.

In opposition to the hypothesis that Cheetahs utilizing a migratory prey base have larger home-ranges than those using a sedentary one, very large home-ranges are reported in Namibia, where there also are no migratory prey, and where perturbation caused by extensive control is a factor: Stuart & Wilson (1988) mention 1500 km², not dissimilar to the study of Marker *et al.* (2008) who found that Namibian Cheetahs have a mean 95% kernel home-range of 1651 km² (± 1594 km²) over

calculations suggest that ♂♂ distribute themselves according to group size and territorial status in such a way that each encounters equivalent numbers of ♀♀ on the Serengeti Plains. In essence, for single ♂♂, reduced reproductive benefits of nomadism are balanced by not having to share matings with coalition partners. Conversely, there are also strong reasons for believing that nomad ♂♂ are disadvantaged in comparison with territory holders, such as being in poor condition, thus it is still not clear why some ♂♂ remain single (and nomadic) throughout their lives (Caro & Kelly 2001). Males form coalitions in other parts of the continent, such as in Namibia (Marker *et al.* 2003a) and KwaZulu–Natal (Hunter 1998a, b).

Cubs are born in the shelter of long grass, tall or thick vegetation, marshes, underbush, or among rocks or kopjes. Females eat the afterbirth. Mothers return to the lair to nurse cubs for 6–8 weeks, during which time they regularly carry cubs to new lairs (Frame & Frame 1980), before cubs accompany their mother on hunts from 3–4 months (Laurenson 1993). Mothers capture food for their cubs, and some of these prey items are then released again allowing cubs to pursue and subdue prey, which probably facilitates acquisition of hunting skills. Cubs engage in extensive locomotor, social and object play during development amounting to 3.4% of their day on average (Caro 1995). Although playful cubs sometimes spoil their mother's hunting attempts, overall effects on hunting success are thought to be minimal (Caro 1995). After leaving their mother, littermates remain as a sibling group mostly within their natal range for approximately six months, but ♀♀ split from the group at around time of first oestrus. Males disperse out of their natal range, probably to avoid inbreeding, while ♀♀ are the more philopatric sex, with their ranges overlapping those of their mothers by as much as 60% (Caro 1994). Infanticide has not been witnessed in Cheetahs (Hunter & Skinner 2003).

Cheetahs have few vocalizations. They growl during antagonistic interactions at kills, and when ♀♀ are approached too closely by ♂♂; spitting and hissing may accompany lunging during such encounters. Mothers and cubs yip, a high-pitched bleat, when trying to find each other (Caro 1994).

Reproduction and Population Structure Females are polyoestrus, and duration of the oestrous cycle is 13.6 ± 1.2 days



Cheetah *Acinonyx jubatus* cub.

(Brown *et al.* 1996; and see Bertschinger *et al.* 1984, Asa *et al.* 1992). Length of oestrus varies from 1 to 3 days (Bertschinger *et al.* 1984). Females breed throughout the year (Labuschagne 1979, Laurenson *et al.* 1992) and are induced ovulators (ovulation occurring after copulation; Wildt *et al.* 1981); non-mating induced ovulation appears rare (Brown *et al.* 1996). Young ♀♀ do not become sexually mature until 21–24 months old, and ♀♀ first give birth at approximately 2.4 years (Caro 1994, Kelly *et al.* 1998, Durant *et al.* 2004); ♀♀ are reported to be capable of reproduction at 13–16 months of age (Wrogemann 1975). Wild ♂♂ are capable of reproduction at approximately three years (Durant *et al.* 2004); captive ♂♂ have sired offspring in their third year of life, and all ♂♂ between 15 and 26 years in the study by Wildt *et al.* (1981) produced motile spermatozoa.

Gestation lasts approximately 93 days, and up to eight cubs are born in a litter, though six is normally the most that emerge from the lair in the wild (Caro 1994). Sex ratio does not differ from 1 : 1 at birth. In Serengeti N. P., cubs weigh 350 g at birth, though heavier weights are recorded from captivity (averaging 463 g; Wack *et al.* 1991), and are born altricial (Beekman *et al.* 1999). Young, up to the age of about three months, have a unique covering of long bluish-grey or smoky coloured hair, 70–80 mm in length, which conceals the tiny spots on the pelage underneath. Eyes open at Day 10–12, and the full set of milk teeth erupts by around six weeks; the permanent set is in place by about 8–9 months. Cubs in Serengeti N. P. grow at an average of 44.6 g/day in the lair (Laurenson 1995a, b), and were weaned at about four months, and independent between 13 and 20 months (average 17.1 months; Kelly *et al.* 1998), after which the mother begins to raise another litter (Schaller 1972). From data from animals measured in Namibia, ♂♂ and ♀♀ attain adult body mass after 49 months of age (Marker & Dickman 2003). Average inter-birth interval in Serengeti N. P. is 20.1 months (Kelly *et al.* 1998).

Serengeti ♀♀ continue to reproduce until 11.8 years of age, and can live as long as 13.6 years in the wild (Caro 1994, Kelly *et al.* 1998, Durant *et al.* 2004). Serengeti ♂♂ live for a maximum of 7.8 years, far shorter than ♀♀ (Durant *et al.* 2004; but see Oliver *et al.* 2011). Maximum longevity for a captive Cheetah has been given as 21 years, and in captivity a large number of animals have survived longer than 17 years (Marker-Kraus 1997); a captive ♀ of some 15 years of age still showed follicular activity (Wildt *et al.* 1981).

Mortality rates from emergence to independence may be high, partly due to high mortality between emergence and about age three months (Laurenson 1994, 1995c). Pienaar (1969) reported a 50% mortality rate in Kruger N. P., McLaughlin (1970) 43% in Nairobi N. P., and Hunter (1998a) 38% at Phinda G. R. Females will quickly resume oestrus and conceive again (on average, in 19 days) if a litter is lost prematurely; one ♀ mated and conceived two days after losing a litter (Laurenson *et al.* 1992).

In Serengeti N. P., average Cheetah litter-size at independence was 2.1 cubs; litter-size averaged 2.5 between 1969 and 1979 when Lion abundance was low on the Plains, but averaged 2.0 between 1980 and 1994 when Lion abundance increased by 60% (Kelly *et al.* 1998). Nevertheless, a population viability analysis shows that, in spite of increasing Lion density, on average, the Cheetah population in Serengeti N. P. is nearly self-replicating (i.e. $\lambda = 0.997$). Cheetah populations may be self-replicating because they move to areas where Lions are absent.

Certain matrilineal lines in Serengeti N. P. are far more successful than others (Kelly 2001, Pettorelli & Durant 2007), with five lineages contributing 45% of the Cheetah population. Why reproductively successful mothers produce reproductively successful daughters and granddaughters is unknown, but playbacks of Lion roars to Cheetahs demonstrate that the female Cheetahs that react most strongly to Lion roars by moving away from the speaker were those with the highest reproductive success (Durant 2000). Since Lion predation is so important in affecting reproductive success in this species, the finding raises the possibility that daughters inherit some aspects of their mothers' wariness or anti-predator tactics.

Predators, Parasites and Diseases Adult Cheetahs are relatively immune from predation although occasional cases of predation by Lions, Spotted Hyenas and Leopards have been reported. However, predation on cubs may be extremely high. In Serengeti N. P., 95% of cubs born fail to reach independence 14 months later, and 73% of these deaths are due to predation principally by Lions (Laurenson 1994). Cubs are sometimes killed when Lions take over a Cheetah kill (J. S. Hunter *et al.* 2007b) but they are also killed in their dens for unknown reasons; Cheetah mothers are unable to defend small cubs against Lions that are four times their weight. Groups of Cheetahs are less likely to be harassed by most predators than are single animals (Caro 1994).

There are no systematic surveys of diseases in wild Cheetah populations. In Namibia they have minimal to no disease (Munson *et al.* 2004a, 2005), although of seven telemetered Etosha Cheetahs, six died of anthrax (Lindeque *et al.* 1998; and see Jager *et al.* 1990). In Serengeti N. P., Cheetahs show high seroprevalence for feline coronavirus and herpesvirus (Evermann *et al.* 1993). Feline immunodeficiency virus is also present in high frequency (40%) in some Cheetah populations (e.g. Tanzania), but absent (0–2%) in others (e.g. Namibia) (Troyer *et al.* 2005). Lentivirus (Osofsky *et al.* 1996) and *Bartonella* (Molia *et al.* 2004) have also been reported in the wild. In captivity, infectious diseases are far more common: feline infectious peritonitis virus (FIPV)/feline enteric coronavirus and feline herpes virus are endemic. Indeed, an FIP outbreak dramatically reduced a captive collection in 1982 and 1983, but has not been a significant problem recently. In both the USA and South Africa, captive Cheetahs also suffer from gastritis associated with *Helicobacter* that account for up to 40% of adult mortality (Munson 1993, Terio *et al.* 2005). Chronic degenerative diseases, such as glomerulosclerosis, veno-occlusive disease and amyloidosis, are also major causes of mortality. Cheetahs under one year of age frequently die from pneumonia (Munson *et al.* 1999). Other diseases recorded in captivity include parvovirus (Steinel *et al.* 2000), spongiform encephalopathy (Kirkwood & Cunningham 1994), dermatitis (Munson *et al.* 2004b), leukoencephalopathy and hindlimb paralysis. Stress, as measured by elevated corticosteroid concentrations (Terio *et al.* 2004, Munson *et al.* 2005), and perhaps diet and low genetic variability, are both thought to be responsible for prevalence of degenerative disease in captive animals raising conservation and ethical concerns about keeping Cheetahs in captivity.

Marker & Dickman (2004) examined dental abnormalities in 208 wild cheetahs trapped on Namibian farmlands, and recorded three anomalies: erosion of the upper palate, crowding of lower incisors, and absence of one or both upper premolars. A little over 40% of Cheetahs showed evidence of deep palatine erosion (where the lower

molar penetrates the palatine mucosa), of which approximately 15% had perforated upper palates. Focal palatine erosion had previously only been recorded in captive Cheetahs (Fitch & Fagan 1982).

Penzhorn *et al.* (1998b; and see references therein) provided a detailed review of parasites recovered from both wild and captive Cheetahs at the time, including one rickettsia (*Eperythrozoon felis*, seen in blood smears from an animal in Nairobi N. P.), nine protozoa (including *Hepatozoon* sp., and *Theileria*-like piroplasms), 14 nematodes, four cestodes (including three species of *Taenia*), one trematode (*Pharyngostomum cordatum*), 21 ticks, two mites (*Notoedres cati* and *Sarcoptes scabiei*, the latter of which causes sarcoptic mange, an outbreak of which was recorded in the Masai Mara in Kenya), four flies (among which, lesions caused by *Stomoxys calcitrans* have been seen on the ears of Cheetahs at breeding centres in South Africa), four fleas and two lice (*Damalinia elongata*, usually associated with Impalas, and *Felicola* sp.). Some of these parasites normally are associated with the prey of Cheetahs, which presumably become infected while feeding.

Conservation IUCN Category: Vulnerable A2acd, C1 (*A. j. hecki* – Critically Endangered C2a(i), D; *A. j. venaticus* – Critically Endangered D). CITES: Appendix I. CMS: Appendix I (except populations in Botswana, Namibia and Zimbabwe).

An annual quota of 150 live animals or hunting trophies from Namibia, 50 from Zimbabwe and 5 from Botswana per annum was passed at 1992 CITES meeting. The international fur trade, prevalent in the 1960s, has all but halted, though domestic trade remains prevalent in some parts, such as north-east Africa.

Habitat encroachment and reduction in ungulate prey, stemming from cultivation and direct exploitation, are responsible for most of the massive reduction in range. Direct persecution still occurs in most areas where Cheetahs exist outside of protected areas, such as in Namibia, where the overwhelming majority of animals (more than 90%) live on farmland. In the past 20 years numbers in Namibia have declined from 6000 to ca. 2500 due to eradication and removal from farms because they are perceived as a threat to livestock (Marker *et al.* 2003b). Human-mediated mortality accounted for 79.4% (n = 50) of wild deaths reported, of which the majority involved prime adult animals, with a peak at around 5–6 years of age (Marker 2003, Marker *et al.* 2003b). None the less, between 1991 and 1999, annual tallies (informed by surveys) of Cheetahs killed by farmers significantly decreased, with an overall mean of 19 Cheetahs killed annually in an initial survey falling to 2.1 in the follow-up. These findings suggest that although Cheetahs on Namibian farmlands are still perceived as a problem, farmers' tolerance toward them might have improved. Management strategies that reduce livestock losses, such as the use of livestock guarding dogs, have proved successful and cost-effective at mitigating losses of livestock to Cheetahs outside protected areas (Marker 2003, Marker *et al.* 2003c).

The principal conservation tool for Cheetahs is enforced protection within fully protected areas such as national parks. However, mesopredators such as Cheetahs and African Wild Dogs suffer from competition with larger carnivores. For example, a stochastic model of the Serengeti Cheetah population demonstrates that Cheetah populations decline to extinction under high or average Lion abundances. That Cheetah juvenile survival is so strongly affected by Lion predation suggests that outside protected areas where Lions are hunted, Cheetahs

may have reasonably robust populations although evidence for this is controversial (Laurenson 1995c, Gros 1998). Important protected areas that represent strongholds for Cheetah populations include the Kgalagadi Transfrontier Park (South Africa, Botswana), Nxai Pan and Chobe National Parks, and Okavango Delta (Botswana), Etosha N. P. (Namibia), Liuwa Plains and Kafue National Parks (Zambia), Tsavo and Ruaha National Parks (Tanzania) and, of course, the Serengeti N. P. and Mara ecosystem (Tanzania, Kenya) (IUCN SSC 2008, 2009). In West Africa, the major remaining stronghold is the WAP protected areas complex between Benin, Niger and Burkina Faso (P. Chardonnet pers. comm.). An important population of desert-adapted Cheetah is still distributed widely through the Ahaggar National Park in Algeria (Hamdine *et al.* 2003, Wacher *et al.* 2005).

Allozyme work on wild and captive populations shows that the Cheetah lacks genetic variation in at least some portion of its genome; percentage polymorphism and average heterozygosity appear close to zero (O'Brien *et al.* 1983, Wayne *et al.* 1986). Reciprocal skin grafts between unrelated Cheetahs that fail to show rejection confirm absence of genetic variation (O'Brien *et al.* 1985). Nevertheless, mitochondrial DNA show more variation than previously supposed (Menotti-Raymond & O'Brien 1993), and more recent studies, including previously unsampled populations, have revealed higher genetic variation in the current global Cheetah population than previously described (Charruau *et al.* 2011). The causes of the genetic bottleneck are unknown but could possibly result from very low population sizes during the Pleistocene and breeding between relatives (Menotti-Raymond & O'Brien 1993, Hedrick 1996). In theory, genetic monomorphism raises two issues of conservation concern: (i) reduced juvenile survival because deleterious recessive alleles may not be masked by more dominant benign alleles if loci are not heterozygous, and (ii) populations are likely to be susceptible to disease because if a disease overcomes the immune system of one individual, it may overcome every member of the population. Both factors were thought to be involved in the Cheetahs' failure to breed well in captivity prior to the 1990s (O'Brien *et al.* 1985, Marker & O'Brien 1989), but chronic stress now seems far more probable (Munson *et al.* 2005; but see Wacher *et al.* 2011). In recent years, breeding success has improved (Marker & Grisham 1993) as problems with housing, maternal behaviour and feeding have been resolved suggesting poor management practice could have contributed to earlier problems (Wielebnowski 1996, Caro 2000). None the less, disease is viewed as a potential concern in both captivity and in the wild.

There are an estimated 1500 Cheetahs in captivity worldwide, maintained by importation of wild-caught animals (see Marker 2003).

Adult deaths in captivity account for 66% of mortalities in captivity and are principally due to renal failure and liver disease; juvenile mortality results from diverse causes but primarily pneumonia (Marker & Grisham 1993). Breeding is still limited to relatively few individuals so that effective population size is low (18.2% of the census population size). Causes of variation in captive breeding success include inbreeding (Wielebnowski 1996), inadequate social environment and housing (Wielebnowski *et al.* 2002), possible physiological problems associated with sperm abnormalities (Wildt *et al.* 1993), and disease (Munson 1993). In addition, individual temperament is an important predictor of reproduction with tense and fearful animals having low reproductive output (Wielebnowski 1999). Artificial insemination has been relatively successful and ♀♀ conceived through artificial insemination have also reproduced successfully. Furthermore sperm from Namibian Cheetahs has been used to produce litters in captivity. Sporadic reintroductions of captive-born individuals have been attempted in areas of South Africa but have largely failed due to inability to hunt wild ungulates and predation from Lions; in contrast, wild-to-wild translocations of Cheetahs in South Africa and Namibia have successfully re-established populations (Hofmeyr & Van Dyk 1998, Hunter 1998a, b).

Measurements

Acinonyx jubatus

HB (♂♂): 1225 (1130–1360) mm, n = 24

HB (♀♀): 1245 (1130–1400) mm, n = 16

T (♂♂): 680 (630–740) mm, n = 24

T (♀♀): 660 (600–730) mm, n = 19

WT (♂♂): 41.4 (28.5–51.0) kg, n = 23

WT (♀♀): 35.9 (21.0–43.0) kg, n = 19

Serengeti N. P. (Caro 1994)

HB (♂♂): 1255 (1080–1520) mm, n = 94

HB (♀♀): 1201 (1050–1350) mm, n = 38

T (♂♂): 767 (510–870) mm, n = 94

T (♀♀): 725 (570–790) mm, n = 39

WT (♂♂): 45.6 (31–64) kg, n = 99

WT (♀♀): 37.2 (26–51) kg, n = 38

Namibia (Marker & Dickman 2003)

Key References Caro 1989, 1994; Caro & Kelly 2001; Durant *et al.* 2004; Frame & Frame 1980; Kelly *et al.* 1998; Laurenson 1993, 1994, 1995; Marker 2003; Marker *et al.* 2003a, b, c; Wrogemann 1975.

Tim Caro

GENUS *Felis*

Small Cats

Felis Linnaeus, 1758. Syst. Nat., 10th edn, I: 41.

The genus *Felis* has, in the past, embraced a large part of the living felids, often only to the exclusion of the genera *Acinonyx* and *Panthera* (Simpson 1945, McKenna & Bell 1997). Such an arrangement, however, is not well supported by primary systematic studies (see Felidae for

further discussion), and following the most recent molecular analyses this genus is now restricted to members of the domestic cat lineage and includes some of the smallest species of the family: Black-footed Cat *Felis nigripes*, Sand Cat *Felis margarita*, Wildcat *Felis silvestris*, Swamp

or Jungle Cat *Felis chaus* and Chinese Desert Cat *Felis bieti* (Wozencraft 1993, 2005). However, *Felis bieti* has been reduced from a separate species to a subspecies of *Felis silvestris*, using mtDNA studies (Driscoll *et al.* 2007), having diverged about 0.23 mya from the European wildcats (*F. s. silvestris*). All wild species are distributed in the Old World and all occur on the African continent. Only one species, the Black-footed Cat, is endemic to Africa, the other species having wide distributions extending into Asia and Europe or just occurring on the fringes of north-east Africa. They inhabit all habitats, except for closed tropical forest.

Members of the genus are small or medium-sized felids (HB varies from 360–1120 mm, body mass 1–13 kg), displaying the classic felid body shape, with a strong elongate body, short to medium length legs, tail 38–60% of HB length, and small rounded paws with 4–5 functional toes (Haltcnorth 1953). The dental formula is $I^{3/3}, C^{1/1}, P^{3/2}, M^{1/1} = 30$. All but the Swamp Cat have relatively large and broad heads. The skull is lightly built compared with other Felidae lineages with slight zygomatic arches and large orbits and a large inflated skull capsule (Heptner & Sludskii 1972). The upper profile seen from the side is convex. A sagittal crest, if present, is only weakly expressed. The auditory bullae are strongly inflated especially in the Sand Cat and Black-footed Cat. The ears are narrowed towards the point, which is sometimes pencilled with a short tuft (Pocock 1951). The backsides of the ears are always uniformly coloured yellow-reddish, sometimes with black edge, but never with a conspicuous white spot. Shoulders are lower than sacral region. The forelegs have at least one stripe, the brachial, below the elbow on the inner side and the hindlegs are striped at least externally above the hocks. The tail may be banded above throughout and is always strongly striped in its distal half, and may have a black tip. The pelage of all African species is relatively short, with dense hair. The ground colour of the coat is brownish-buff to grey, and either of uniform colour or heavily marked. If spots are present there

is marked fusion on the flanks behind the shoulders, to form vertical stripes characteristic for *Felis* (Pocock 1951). Melanism is only rarely reported in the wild, as in the Swamp Cat in Pakistan (Roberts 1977).

Felis species are carnivores that usually prey on mammals and birds that are smaller than themselves (Sunquist & Sunquist 2002). Despite their relatively early scientific description, there is still little known about the ecology and social structure of several species. They are mostly solitary with their social organization generally following the typical felid pattern of little intra-sexual overlap, with the range of a territorial ♂ typically overlapping the smaller ranges of one or more ♀♀.

The genus *Felis* has a weakly represented fossil record, compared with *Panthera* (Turner & Antón 1997). The most likely fossil ancestor, *Felis attica*, is found throughout the late Miocene in Eurasia (Beaumont 1961). Further possible fossil ancestors were *Felis lunensis* of the late Pliocene/early European Pleistocene (Kurtén 1965, 1968). The recent analysis of Johnson *et al.* (2006) has shown that the *Felis* lineage split as one of the two most recently derived groups from the Asian Leopard Cat lineage, some 6.2 mya and is therefore the most recently evolved, and also the smallest in body sizes, of all felid lineages. The domestic cat lineage originated in Eurasia and then migrated to Africa probably in the late Pleistocene (Yamaguchi *et al.* 2004b, Johnson *et al.* 2006). The oldest African fossils pertaining to the genus *Felis* are from Kanapoi, Kenya, dated to ca. 4.1 mya (Werdelin 2003b). The genus appears sporadically in the African fossil record from that time onwards. Through climatic and geographic isolation events populations were cut off from each other by water, deserts and mountains and evolved also through adaptation to arid and mesic ecological conditions into the different species of *Felis*.

Alexander Sliwa

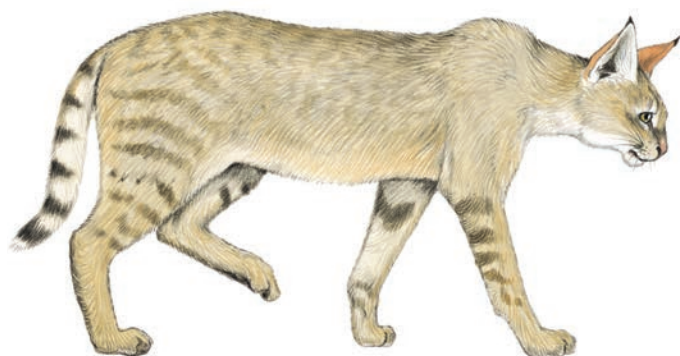
Felis chaus SWAMP CAT (JUNGLE CAT)

Fr. Chat des marais (Chat des jungle); Ger. Rohrkatze, Sumpfluchs

Felis chaus Schreber, 1777. Die Säugethiere 2 (13): pl. 110.B [1777]; text, 3 (24): 414 [1777]. 'wohnt in den sumpfigen mit Schilf bewachsenen oder bewaldeten Gegenden der Steppen um das Kaspische Meer, und die in selbiges fallenden Flüsse.

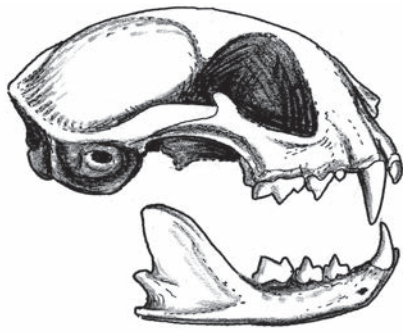
Auf der Nordseite des Terekflusses und der Festung Kislar ... desto häufiger aber bei der Mündung der Kur ... '.

Listed in Honacki *et al.* (1982) as 'U.S.S.R., Dagestan, Terek River, N. of the Caucasus'.



Swamp Cat *Felis chaus*.

Taxonomy The Swamp Cat was originally placed in a separate genus (*Catolynx*) due to its resemblance to the Eurasian Lynx *Lynx lynx*, but was later reassigned to the genus *Felis*. It has not yet been decisively decided whether the Swamp Cat played a role in the development of the domestic cat, with the Wildcat *Felis silvestris* typically considered as the progenitor of the domestic felid (Collier & O'Brien 1985, Driscoll *et al.* 2007). Although there is apparently no real evidence of this species ever having been fully domesticated, it is known that the Swamp Cat was tamed and trained by the ancient Egyptians to hunt wildfowl or to catch rodents, and they were also mummified and placed in tombs (Morrison-Scott 1952). Six subspecies are usually recognized (mainly reflecting morphological differences), but only one is currently listed from Africa, *F. c. nilotica*, in Egypt (Smithers 1975). Synonyms (Africa only): *nilotica*, *rüppelii*. Chromosome number: $2n = 38$ (Wurster-Hill & Gray 1973, C. Driscoll pers. comm.).



Lateral view of skull of Swamp Cat *Felis chaus*.

Description Large-bodied, long-legged cat with shortish, banded tail and large, pointed ears. Face long and slim. Long ears are rounded and set close together on the crown; backs reddish-buff with distinctive black apical tuft of hair (up to 15 mm in length). Muzzle and throat usually white or ochre; area around the eyes whitish with a dark line running from corner of eye down each side of nose. Pupil elliptical and iris yellow. The homogeneous unspotted coat can be sandy-brown, reddish, or grey in colour. Inside of forelegs bears 4–5 prominent black rings, and some individuals have faint stripes on the outside of the forelegs. Fur rough in the summer coat and individual hairs are dark tipped. Belly fur pale cream and comparatively long and soft in the winter coat. Melanistic individuals occur regularly in Pakistan and India (Roberts 1977, Chakraborty *et al.* 1988). Tail comparatively short, about one-third of body length (38% in Egypt; Osborn & Helmy 1980). Distal third of tail bears 2–3 blackish rings terminating in a black tip. Males larger than ♀♀. There are four pairs of nipples.

Rostrum and cranium somewhat elongate, and frontal and postorbital swellings are prominent. Postorbital width slightly more than rostral width. Anterior end of zygomatic process attenuate, and mastoid process large and protruding (Osborn & Helmy 1980).

Geographic Variation See Taxonomy.

Similar Species

Felis silvestris. In Egypt, found along margins of the Delta and the Nile Valley, including the Fayoum, in the Mediterranean coastal desert to Mersa Matruh, and in the Western Desert (Hoath 2003). Smaller, with body markings more conspicuous; cheek stripe present, and lacrimal stripe less prominent; tail longer; skull less elongate, and postorbital swellings absent; anterior end of zygomatic process rounded.

F. margarita. In Egypt, known only from the Sinai and rocky deserts of E Egypt. Lighter colour, with more conspicuous body markings; broader ears; pads of feet covered with hair; relatively longer tail; relatively longer nasals and larger bullae.

Distribution On the African continent, the Swamp Cat occurs only in Egypt, in the Nile Delta, and along the western Mediterranean coastal desert to Mersa Matruh. They are present in the Nile Valley south to Aswan, and in El Faiyum, Farafara, Dakhla and Kharga oases (Osborn & Helmy 1980, Hoath 2003). Meinertzhagen (1934) makes reference to this species from the Hoggar of Algeria, based on a skin purchased in Arak (and see Heim de Balsac 1936); however, Pocock (1944) identified this specimen as a Wildcat, and there is no



Felis chaus

evidence for the existence of this species in Algeria (Kowalski & Rzebik-Kowalska 1991).

Extraliminally, the Swamp Cat has a relatively wide distribution, ranging from Egypt eastwards throughout the Middle East from Israel to Asia Minor, Iraq, Iran, Afghanistan, Pakistan, India, Nepal, Sri Lanka, Myanmar, to mainland South-East Asia (Sunquist & Sunquist 2002).

Habitat The preferred habitat includes tangled stands of reeds and bushes, riverine swamps and tall grass. In Egypt, it is found in low cultivated or marshy ground, reed-beds, fields of sugarcane, bean fields or any similar thick cover (Osborn & Helmy 1980). They have been recorded around settlements in the El Faiyum. It usually avoids open spaces, and is commonly found below 1000 m altitude, although it ascends mountains up to 2400 m in the Himalaya (Sunquist & Sunquist 2002).

Abundance No available information for Egypt, although the Swamp Cat is the most common of the wild felids in Egypt. They appear fairly adaptable, but are only patchily distributed in suitable habitats (M. Saleh pers. comm.).

Adaptations The Swamp Cat is a very good swimmer, and can hunt in water. Its rough fur dries fast. It is also a very good tree climber. Its keen sense of hearing helps it locate its prey, particularly rodents. These cats often rest up in disused burrows of other species, such as porcupines and foxes, sometimes arranging a nest of dry reeds on the surface of the ground, under bushes or among reeds (Novikov 1956, Kitchener 1991, Alderton 1993, L. Glas pers. obs.); during the day they also rest up in dense cover or in rock crevices and tree cavities. They are primarily nocturnal, although cats have been observed hunting during daytime (when the weather is cool).

Foraging and Food Prey consists mainly of small mammals (rodents, gerbils and hares), birds (from the size of larks to various

waterfowl), and occasionally amphibians, reptiles and insects. Flower (1932) states that they would eagerly kill and eat live snakes of the genera *Coluber* and *Psammophis*. In Egypt, one cat collected from near Alexandria had its stomach full of fish (Osborn & Helmy 1980). Bonhote (1909) mentions that one killed an almost full-grown sheep, and 'after dragging it to the edge of the enclosure, devoured nearly a whole fore-quarter.' Flower (1932) found that average daily consumption of raw horse-meat was 0.49 kg per cat, and the maximum amount of meat that a cat would eat at one sitting was 1.87 kg.

Dietary studies from elsewhere in the species' range reveal similar dietary preferences (e.g. Ognev 1935, Ishunin 1965, Roberts 1977, Khan & Beg 1986, Mukherjee *et al.* 2004), and confirm that they are powerful enough to kill prey such as subadult gazelles. However, they are also known to supplement their diets with fruits; in Tajikistan, the fruits of the Russian olive made up 17% of the diet (Novikov 1956).

Swamp Cats will sit motionless, attentively listening for the sounds of their prey, and then leap vertically high in the air, landing and catching the prey. Similar leaps are also used to catch birds. When hunting in the water they seize the prey in their mouth, keeping their head in the water (Novikov 1956, Kitchener 1991, Alderton 1993, L. Glas pers. obs.).

Social and Reproductive Behaviour Swamp Cats are poorly studied, and there is limited information available on their social organization. They are solitary, and studies in Israel have shown that male territories overlap several female territories (L. Glas pers. obs.). The ♂ is vocal during oestrus, and will stalk a potential mate from a distance until she is ready to accept his attentions (Alderton 1993, L. Glas pers. obs.). The kittens are kept in a hidden reed-bed den, lined with fur and grass. Dens are concealed and located in inaccessible areas (Novikov 1956, Alderton 1993).

Reproduction and Population Structure Female Swamp Cats enter oestrus from Jan to Mar. Oestrus lasts five days (Sunquist & Sunquist 2002). In Egypt, the young are born from mid-Dec to Apr (Flower 1932, Osborn & Helmy 1980). Gestation period is 63–68 days (Sunquist & Sunquist 2002), and litter-size is 1–4 (usually 2–3), although Flower (1932) mentions a litter of six born in the Giza Zoological Gardens in mid-Apr. Birth-weight of neonates was 43–55 g in the wild (Heptner & Sludskii 1972), although captive kittens have been recorded with weights up to 160 g (Schauenberg 1979). Eyes first open at 10–13 days. The kittens differ significantly in appearance from adults as they have very distinctive black markings

on their coats. They are weaned around 15 weeks old (Schauenberg 1979). Both sexes reach sexual maturity at the age of about one year (Mendelssohn & Yom-Tov 1987), although other records put this much later at as much as 36 months of age (Eaton 1984). In captivity the Swamp Cat can live 15–20 years (Mendelssohn & Yom-Tov 1987, Weigl 2005), but in the wild longevity is probably less.

Predators, Parasites and Diseases Kittens are likely to fall prey to Golden Jackals *Canis aureus* and Leopards *Panthera pardus*. Recorded parasites in Egyptian animals include trematodes of the genus *Heterophyes* (Wells & Randall 1956) and the tick *Haemaphysalis leachi* (Hoogstraal 1958).

Conservation IUCN Category: Least Concern. CITES: Appendix II.

According to Hoath (2003), although protected by Egyptian law, the species is still persecuted in Egypt, with trapping recorded along the coast of the Delta, and pelts found on sale in the market at Kerdassa and the Khan al-Khalili. In other parts of its range, its generalist diet and adaptability, and ability to survive in a variety of habitats, make it the most common of the small felids (Sunquist & Sunquist 2002).

Measurements

Felis chaus

HB: 674.5 (595–760) mm, n = 12

T: 254.8 (210–280) mm, n = 12

HF c.u.: 168.4 (145–178) mm, n = 12

E: 71 (63–78) mm, n = 12

WT: 9.0 (7.0–11.2) kg, n = 5

Egypt (Osborn & Helmy 1980)

HB (♂ ♂): 1002 (890–1120) mm, n = 25

HB (♀ ♀): 911 (590–1020) mm, n = 20

T (♂ ♂): 298 (260–355) mm, n = 25

T (♀ ♀): 265 (190–310) mm, n = 20

WT (♂ ♂): 8.81 (5.0–13.2) kg, n = 27

WT (♀ ♀): 6.26 (2.5–8.9) kg, n = 21

Israel (L. Glas pers. obs.)

Key References Alderton 1993; Mendelssohn & Yom-Tov 1987; Novikov 1956; Osborn & Helmy 1980; Sunquist & Sunquist 2002.

Liora Glas

Felis margarita SAND CAT

Fr. Chat de Sables; Ger. Sandkatze

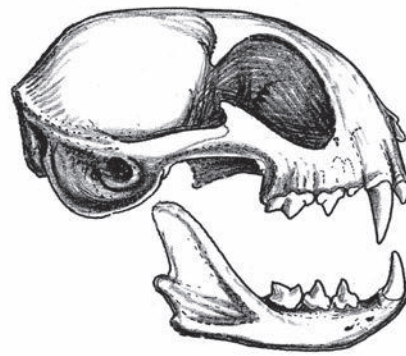
Felis margarita Loche, 1858. Revue Mag. Zool. Paris (2) 10: 49, p l. 1. 'environs de Négonca (Sahara)' [Algeria].

Taxonomy There are four recognized subspecies, including *F. m. harrisoni* from the Arabian Peninsula, *F. m. scheffeli* from the Nushki Desert of Pakistan (Hemmer 1974b) and *F. m. thinobia* from the sand deserts of Turkmenistan, Uzbekistan, Kazakhstan and possibly N Iran and NE Afghanistan; only the nominate form, *F. m. margarita*, occurs in Africa (Schauenberg 1974). The forms *airensis* and *meinertzhageni* were described from single specimens and were later considered

synonymous with the nominate form (Schauenberg 1974, Hemmer *et al.* 1976; but see Smithers 1975). The subspecies *F. m. thinobia*, called the Barchan Cat, was temporarily recognized as a separate species (Ognev 1926, Weigl 1961), but was later classified as a subspecies of the Sand Cat (Heptner & Sludskii 1972). Synonyms: *airensis*, *harrisoni*, *marginata*, *margarita*, *marquerittei*, *meinertzhageni*, *scheffeli*, *thinobia*. Chromosome number: 2n = 38 (Jotterand 1971).

Sand Cat *Felis margarita*.

Description A small cat, with size and build smaller than the Wildcat *Felis silvestris* (but ears outstandingly larger). Head flat and broad; ears broad and set low down on the sides of the head without apical tufts. Eyes yellow amber, greenish to yellow-bluish. Nose pad black. Vibrissae white, the supralabial group attaining about 80 mm. Pelage soft and dense, in winter up to 55 mm on the back, with abundant soft woolly underfur, giving the cat a solid appearance despite its small size. The colouration is strikingly pallid; the general tint of the back is pale sandy-isabelline to golden-sandy, finely speckled with black over the shoulders and with silvery-grey on the upper flanks. A poorly differentiated spinal band is present. Crown of the head pale sandy and marked with very faint ill-defined striations. Three to five dark, narrow, always obscure and sometimes indistinguishable, longitudinal lines on the back of the neck (Rosevear 1974). Face appears broad due to well-developed side-burns. Backs of the ears are rufous-tawny, each with an extensive apical black spot, extending for 15–25 mm about half the length of the external margin. Face is marked with a dark reddish-fulvous stripe from the anterior edge of each eye backwards, across the cheeks. Chest and belly are white, with an indistinct line of demarcation on lower flanks and very faint buffy wash on lower throat. Limbs white internally; externally marked by at least two pronounced black elbow-bar 'bracelets', extending round to the internal aspect. The outsides of the hindlimbs have from two to five dark, mostly brown-black, half-rings (Weigel 1961). The pattern of the flanks is composed of seven or eight indistinct reddish-brown vertical stripes, broken up into spots and lightly washed with black in places (Harrison & Bates 1991). The limbs are of medium length, with the paws broader than in the Wildcat; the palms and soles are distinctive, being covered with a dense mat of fine, long (15–30 mm, Heptner & Sludskii 1972), dark-brown to black wavy hair, completely concealing the pads. Front paw carries five digits, with the thumb carrying the sharp dew-claw higher up on the wrist; the ivory coloured claws touching the ground are somewhat blunt. Hind paw carries only four digits

Lateral view of skull of Sand Cat *Felis margarita*.

and claws are more blunt than those of the front paw. Tail is half the body length, tipped with black and has a varying number of subterminal tail rings (typically six in *F. m. margarita*). The baculum is very small, not exceeding 3 mm (Schauenberg 1974). Males on average larger and heavier than ♀♀. Four pairs of nipples.

Skull distinctive. Orbits large, more spherical and forward-facing than in the Wildcat and the interorbital region a little broader. Rostrum short and broad, with nasals almost parallel-sided throughout a great part of their length, only tapering abruptly posteriorly. Zygomatic arches wide and outwardly bowed. Sagittal crest strongly developed over the posterior braincase and lambdoid crests also pronounced and rather squarely truncated behind. Auditory bullae exceptionally large, in all directions peculiarly inflated (Harrison & Bates 1991), leaving only a space of 4–5 mm between them. Auditory orifice, like the bullae, also exceptionally large, complementing the broad external ears (Rosevear 1974).

Geographic Variation Sand Cats become gradually larger from west to east, with the smallest subspecies *F. m. margarita* in Africa (Schauenberg 1974). Probably the ancestral form most closely resembled *F. m. margarita*; from this a radiation of more specialized forms arose, with *F. m. thinobia* and *F. m. scheffeli* acquiring a more intensely eremial/psammophilic pattern of skin and *F. m. harrisoni* of skull (Hemmer *et al.* 1976). In *F. m. margarita*, specimens from Algeria and Niger tend to be brighter in colour and have more distinct markings than other recognized subspecies (Schauenberg 1974). Five specimens obtained from the N Sinai were assigned to the nominate form (Saleh & Basuony 1998) due to pelage colouration, but were intermediate in skull characters between the nominate form and *F. m. harrisoni* (Hemmer *et al.* 1976).

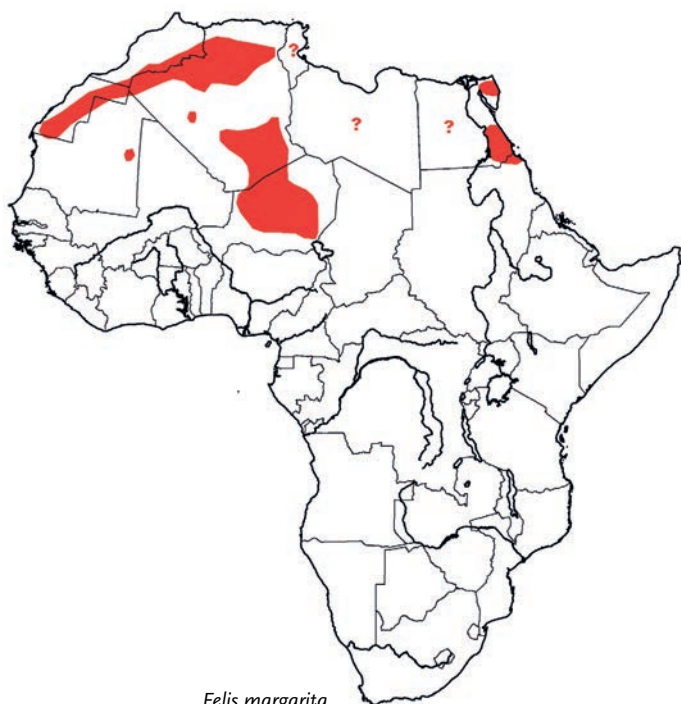
Similar Species

Felis silvestris. Wide, but discontinuous, distribution in North Africa.

Larger and darker, with longer legs, a relatively smaller and narrower head and more vertically oriented ears; plantar and digital pads not concealed by thick mat of long hair.

F. chaus. Restricted to vicinity of Nile R. and Mediterranean zone of Egypt. Overall sandy-brown pelage, without distinctive markings; reddish-brown hair on ear backs with short, black tufts of hair at tips.

Distribution In North Africa, the Sand Cat occurs marginally in W Morocco (Panouse 1957, Cuzin 2003) including Western Sahara



Felis margarita

(Valverde 1957, Hemmer *et al.* 1976, F. Cuzin pers. comm.), Algeria (De Smet 1988, Kowalski & Rzebik-Kowalska 1991), and from the Sinai to the rocky deserts of E Egypt (Mendelssohn, in Hemmer 1974c, Osborn & Helmy 1980, Goodman & Helmy 1986, Saleh & Basuony 1998, Hoath 2003). There are no confirmed records from Tunisia (Lataste 1887, and Blanc 1935, in LeBerre 1990), Libya (Hufnagl 1972) or Egypt, west of the Nile R. (Goodman & Helmy 1986, M. Saleh pers. comm.), but this distributional gap may close with future survey work.

There are both specimens and reliable sightings from Niger (Pocock 1938, Rosevear 1974, Schauenberg 1974, Dragesco-Joffé 1993, J. Newby & T. Wachter pers. comm.), and they are supposed to occur in the Majabat al Koubra (Lamarche 1980) in Mauritania. Since they are recorded from the Adrar Souttouf Mts in Western Sahara (Hemmer *et al.* 1976), they may well occur in adjacent parts of Mauritania. Sand Cats are thought to be present, although there are no confirmed records available, in Senegal, Mali, Chad (where spoor have been found; J. Newby & T. Wachter pers. comm.) and Sudan.

A presumed subfossil record from Tenerife, Canary Is. (Sarrion Montañana 1985) was later reassigned as a domestic cat (Hutterer 1990).

Extraliminally, the Sand Cat occurs in the Arabian Peninsula, Israel, Jordan, N Iran, Turkmenistan, Uzbekistan and the Baluchistan province in Pakistan (Harrison & Bates 1991, Sunquist & Sunquist 2002). A recent record for Syria is the first for this country (Serra *et al.* 2007).

Habitat A desert specialist inhabiting undulating stabilized dune areas, wadi beds and steppe with sparse grass and shrub cover (generally being absent from heavier vegetated valleys). Also found in shifting sand dunes and in rocky deserts ('hammada') (Abbadi 1991, Saleh & Basuony 1998) and coastal plains (M. Saleh pers. comm.). One cat was even seen sitting on a branch of a mangrove tree 2 m above ground (M. Saleh pers. comm.). Occurs to altitudes of about 2000 m.

Abundance Difficult to census and thus often reported as rare. Only density estimates come from a telemetry study in S Israel (Abbadi 1991, 1993), where 11 cats were caught in the study area of 15 × 25 km (375 km²) (M. Abbadi pers. comm.). In low-quality habitat, such as shifting sand dunes, densities may be very low.

Adaptations The palms and soles are covered by a dense mat of fine, long, wavy dark hair of about 1 cm length, completely concealing the pads. These tufts of hair may facilitate walking across shifting sands helping to spread the weight as it moves (Harrison 1968) and to make it more silent, or to protect the soles from hot ground. The claws are not very sharp, due to the lack of sharpening surfaces and the Sand Cat's digging habits – impressions are often visible in the spoor (Dragesco-Joffé 1993).

The ears are large, widely set apart and low on the sides of the head, flattening the Sand Cat's profile when hunting in open areas. This may aid detection of movements of subterranean prey and protect the inner ears from wind-blown sand (Kingdon 1990). The auditory bullae are exceptionally well developed, to increase hearing abilities in areas with little vegetation cover. While the area of the external ear's pinna flange is similar to that of the domestic cat, the dimensions of the ear canal are about twice those of the domestic cat, as is the volume of the middle air space (Huang *et al.* 2002). There is structural and functional evidence that Sand Cats have hearing sensitivity considerably greater than domestic cats for frequencies below 2 kHz. The placement of the Sand Cat's pinna flanges towards the side of the head together with the relatively long ear canals could increase the interaural time differences and thereby improve their accuracy in pinpointing the location of sound resources. This would be of habitat-specific survival value for pinpointing prey animals and danger from predators. The Sand Cat is considered the northern representative of the Black-footed Cat *Felis nigripes*, whose body and head is of similar shape. Sight is acute to allow for orientation during crepuscular and nocturnal hunting. The sand-coloured pelage is typical camouflage for sand-dwelling (eremial) species.

Dens are in disused fox *Vulpes* spp. warrens, and also in rodent and Desert Hedgehog *Paraechinus aethiopicus* burrows enlarged by the Sand Cats (Schauenberg 1974, Le Berre 1990). Several Sand Cats used burrows interchangeably (Abbadi 1993). The *thinobia* subspecies lives in shallow burrows in the sand, constructed amongst the roots of saltbushes or *Caligonum* plants (Heptner & Sludskii 1972). Sand Cats may also use the same burrows excavated by the Fennec Fox *Vulpes zerda*, which is ecologically similar (Dragesco-Joffé 1993). The latter author measured a den 150 cm in length, going down in a straight line 60 cm deep with a tunnel diameter of 15 cm. Le Berre (1990) described the den as 15–20 cm in diameter, 150 cm long, descending at an angle of 30–45°, generally with a single entrance. Scats are covered with sand.

Foraging and Food Carnivorous, feeding mainly on small desert rodents, including spiny mice (*Acomys* spp.), jirds (*Meriones* spp.), gerbils (*Gerbillus* spp.) and jerboas (*Jaculus* spp. and *Allactaga tetradactyla*), but also young of Cape Hare *Lepus capensis*. It will also hunt small birds like Greater Hoopoe Lark *Alaemon alaudipes*, Desert Lark *Ammomanes deserti*, and consume reptiles such as Desert Monitor *Varanus griseus*, fringe-toed lizards *Acanthodactylus* spp., Sandfish

Scincus scincus, short-fingered gecko *Stenodactylus* spp., and horned and sand vipers of the genus *Cerastes*, and insects (De Smet 1988, Abbadi 1993, Dragesco-Joffé 1993). They are capable of rapid digging to extract the latter prey items (Schauenberg 1974). Sand Cats may cover kills with sand and return later to feed. Sand Cats are independent of drinking water as they are capable of satisfying their moisture requirements from their prey, but drink readily if it is available.

Sand Cats are nocturnal, although during the winter they may be active during the day (Heptner 1970, Dragesco-Joffé 1993). Ambient temperatures may range from -25°C to 58°C . Sand Cats in the Aravah Valley, Israel, were active throughout the night and a ♂ hunted and travelled on average 5.4 km during nine nights (Abbadi 1993).

Social and Reproductive Behaviour Sand Cats are solitary, although during the reproductive season pairs share the same burrows (Schauenberg 1974). One ♂ in the Aravah Valley of Israel had a home-range of 16 km² (Abbadi 1993); the ranges of ♂♂ overlap. Home-range size is likely to vary between regions according to resources available to the animals, and possibly competition from other sympatric carnivores such as Red Fox *Vulpes vulpes* and Wildcat, which consume similar prey.

Males utter a distinctive sharp call, like a small dog (Hemmer 1974c). In captivity both sexes called upon first introduction (Mellen 1989). When it is surprised by a human observer the animal's reflex is to crouch immediately behind the nearest tuft of vegetation, chin on the sand, completely motionless. Some individuals are surprisingly placid when encountered (Goodman & Helmy 1986, Dragesco-Joffé 1993), and indeed they tame easily.

Reproduction and Population Structure In the Sahara, mating takes place from Nov to Feb. One ♀ had an oestrous cycle of 46 days, and oestrus lasts five days (Sunkuist & Sunkuist 2002). Gestation ranges from 59 to 67 days (Mellen 1989) and, in Niger, the young are born from Jan to Apr (Dragesco-Joffé 1993). Litter-size ranges from 2–8, but the norm is three. Birth mass has been given as 39 g (Scheffel 1974) and 50 g (Dragesco-Joffé 1993); four stillborn captive kittens weighed a mean of 72 g (range 70–75 g; G. Olbricht pers. comm.) and four surviving kittens averaged 71 g (range 56–84 g; K. Clark pers. comm.). Young grow rapidly: their eyes open at 15 days, they take solid food at five weeks, and may become independent possibly as early as four months (Dragesco-Joffé 1993). Sexual maturity is at 9–14 months (Mellen 1989, Dragesco-Joffé 1993, A. Sliwa pers. obs.). Captives may live up to 14 years (Sausman 2000, Weigl 2005).

Predators, Parasites and Diseases Kittens are probably vulnerable to predation from Red Fox and Eurasian Eagle-owls *Bubo bubo*. Adults fall victim to Golden Jackals *Canis aureus*, especially when they hunt in pairs (Dragesco-Joffé 1993), and probably domestic dogs. Eight species of helminth worms, four species of fleas and one species of tick were found on several individuals of *F. m. thinobia* in the former USSR (Heptner & Sludskii 1972). Little is known about

disease, but captive cats are highly susceptible to respiratory tract infections (Sausman 1997).

Conservation IUCN Category: Near Threatened. CITES: Appendix II.

On the African continent, Sand Cats are recorded from several protected areas, including Tassili n' Ajjer and Ahaggar National Parks (Algeria), and Air and Tenere National Reserve (Niger). The main threats include the expansion of human settlement, and the introduction of feral and domestic dogs and cats (which serve both as direct competitors and predators, as well as vectors for disease transmission) (Nowell & Jackson 1996). They may be killed in traps laid out by inhabitants of oases targeting foxes and jackals or in retaliation for killing their chickens (De Smet 1988, Dragesco-Joffé 1993). Most Sand Cats presently in captivity are *harrisoni* or represent hybrids (*harrisoni* × *sheffeli*) (Auckland 2001).

Measurements

F. m. margarita

HB (♂♂): 420, 455 mm, n = 2

HB (♀♀): 390, 420 mm, n = 2

T (♂♂): 270, 270 mm, n = 2

T (♀♀): 235, 245 mm, n = 2

HF c.u. (♂♂): 110, 112 mm, n = 2

HF c.u. (♀♀): 100, 105 mm, n = 2

E (♂): 70 mm, n = 1

E (♀): 52 mm, n = 1

WT (♀): 2.06 kg, n = 1

Algeria, Niger (Schauenberg 1974, Rosevear 1974)

F. m. margarita/harrisoni

HB (♂): 479 mm, n = 1

HB (♀♀): 463 (432–484) mm, n = 4

T (♂): 249 mm, n = 1

T (♀♀): 223 (221–229) mm, n = 4

HF c.u. (♂): 111 mm, n = 1

HF c.u. (♀♀): 103 (101–106) mm, n = 4

E (♂): 61 mm, n = 1

E (♀♀): 57 (54–59) mm, n = 4

Sinai, Egypt (Saleh & Basuony 1998)

F. m. harrisoni

HB (♂♂): 454 (440–452) mm, n = 3

T (♂♂): 270 (250–300) mm, n = 3

HF c.u. (♂♂): 110 (110–110) mm, n = 3

E (♂♂): 63 (57–68) mm, n = 3

Oman, U.A.E. & Saudi Arabia (Harrison & Bates 1991)

Key References Abbadi 1991, 1993; Dragesco-Joffé 1993; Hemmer *et al.* 1976; Schauenberg 1974.

Alexander Sliwa

Felis nigripes BLACK-FOOTED CAT

Fr. Chat à pieds noir; Ger. Schwarzfußkatze

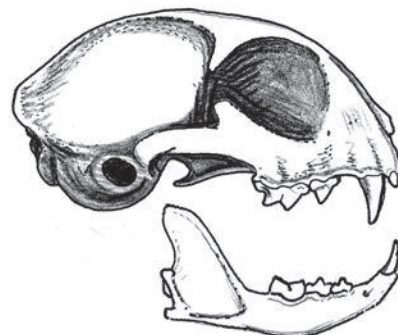
Felis nigripes Burchell, 1824. Travels in the Interior of Southern Africa, 2: 592. Burchell (1824: 509) implied the country of the 'Bachapins', presumably in the capital, 'the town of Litákun (Letárkoon) ... 27° 6' 44 [S] ... 24° 39' 27 [E]' [South Africa].



Black-footed Cat *Felis nigripes*.

Taxonomy Two subspecies have been described: the nominate form and *F. n. thomasi* (Meester *et al.* 1986). Smithers (1971) doubted the validity of the characters separating the two, and the current author believes they represent a geographical cline from the smaller, paler northern *F. n. nigripes*, with more bleached ground colour and less distinctive striping, to the larger more vividly coloured *F. n. thomasi* with jet black bands and spots in the Eastern Cape of South Africa described by Shortridge (1931). Specimens with characteristics of both subspecies are found close to Kimberley, C South Africa, where these distinctions break down (A. Sliwa pers. obs.). *Felis nigripes* may be polymorphic in the centre of its range and only differentiates into distinct ecotypes at the outer limits of its range. Synonyms: *thomasi*. Chromosome number: $2n = 38$ (Kráľ & Zima 1980).

Description The smallest felid in Africa. Stocky with broad head and large, widely spaced, rounded ears. Nose very small and varies from red to black in colour. Eyes coloured dark yellow to light greenish. Margins of eyes, ears and mouth white. Two black cheek stripes run from the corner of eyes and from below eyes to edge of face. Four black bands on nape of neck, two running along the back and on to the shoulder. Body colour varies from cinnamon-buff to tawny or off-white, hairs being 25–30 mm long. The soft fur grows longer and denser during winter. Bold black or rust-tinged bands or rings on shoulders and high on legs, up to five on back legs and two on front, and distinct spots of the same colour on the body. Throat has two or three black to reddish stripes, either solid or broken up. Underparts pale buff or white. Tail short (<40% length of the body and head) and narrowly black-tipped; backs of ears are the same colour as body (Skinner & Chimimba 2005). Hair on undersides of front paws and back legs black. Front paw carries five digits, with thumb or dew-claw higher up on wrist, each carrying a sharp claw. Hind paw carries only four digits and claws are somewhat more blunt. Body measurements suggest differences between the sexes, but these may be difficult or impossible to determine when seen at a distance, especially in the field. There are three pairs of nipples.



Lateral view of skull of Black-footed Cat *Felis nigripes*.

Skull is high and rounded, with a flatter section on top from the level of the eye orbits to the middle of the braincase, where it slopes off abruptly to the supraoccipital crest. Rostrum is very short and broad. Zygomatic arches are 75% of total skull length at their widest. Auditory bullae are exceptionally large, total length being 25% of total skull length and width at the widest point, 18% (Skinner & Chimimba 2005). Outer, upper incisors only very slightly larger than the remainder; canines very sharp and flattened on their inner sides. Upper second premolars are tiny, the fourth sectorial. Molars tiny.

Geographic Variation

F. n. nigripes: Kalahari of Botswana, Namibia, and Northern Cape (South Africa). Lighter in colour, being tawny or, in some specimens, off-white; the bands running from the nape of the neck are often broken into short stripes or spots; spots brownish-black or tawny; generally has a more bleached or washed out appearance than the southern specimens.

F. n. thomasi. Karoo of C and S South Africa. Background colour cinnamon-buff; the bands from the neck are often strongly developed and, originating from the forehead, the two central ones extend unbroken to the base of the tail; three distinctive throat rings, which are black, narrowly edged with rufous; the hairs of the spots and bars are satiny-black.

Similar Species

Felis silvestris. Sympatric. Almost threefold larger, with much longer legs and tail, and no clear spotting; reddish to rusty-brown tint to the hair on back of ears. Unlikely to be confused with Black-footed Cat, but also has black under feet.

Distribution Endemic to southern Africa. Black-footed Cats range from NE Namibia and SW Botswana, southwards through the Northern Cape and the Free State (Lynch 1983) of South Africa and over much of the interior to parts of the west coast of Namaqualand (Stuart 1981). Rautenbach (1982) took animals in North West Province and further east in what is now Gauteng, and it is likely that they occur eastwards in Mpumalanga, although they have yet to be recorded



from Swaziland or Mozambique. In South Africa they occur furthest south-east at the junction of the Fish and Kat Rivers (L. Wingate pers. comm.). They have a marginal occurrence into KwaZulu-Natal (Rowe-Rowe 1992a). During the latter part of the twentieth century it is quite possible that they may have expanded eastward with increasing desertification, i.e. due to livestock overgrazing, as confirmed by a recent record close to Warmbaths in the Limpopo Province, South Africa (Power 2000) and even further north-east in Ezemvelo Reserve on the highveld (J. Power pers. comm.) and close to Marble Hall (Skinner & Chimimba 2005). So far there is no confirmed record for Lesotho (Lynch 1994) and although they are likely absent from much of this country, especially the Lesotho highlands, they may occur in the lowlands adjacent to the Free State, South Africa (N. Avenant pers. comm.). They occur marginally into NW Zimbabwe (Hwange N. P.; V. Wilson pers. comm.) and, although not listed by Crawford-Cabral (1989a), almost certainly in SE Angola, since there is a specimen right across the border from Namibia in Cuando Cubango province (M. Griffin pers. comm.).

Habitat A specialist of open, short grass areas with an abundance of small rodents and ground-roosting birds. Inhabits dry, open savanna, grasslands and Karoo semi-desert with sparse shrub and tree cover and a mean annual rainfall of between 100 and 500 mm at altitudes of 0–2000 m. The presence of epigeal termitaria and burrowing rodents like the Southern African Springhare *Pedetes capensis* may be beneficial to the species. Absent from the driest and sandiest parts of the Namib and Kalahari Deserts.

Abundance Due to their shy and secretive nature, Black-footed Cats are very difficult to census, but are generally considered uncommon to rare throughout their range. The only density estimates come from C South Africa, near Kimberley, where ten adult cats roamed an area of 60 km² (Sliwa 2004). In low-quality habitat densities are probably very much lower.

Adaptations Its small size allows the Black-footed Cat to hunt and rest in open arid areas. Near Kimberley, South Africa, it uses and takes refuge in dens excavated by the Southern African Springhare. One study recorded 98% of 184 resting places used as being in abandoned springhare burrows (A. Sliwa pers. obs.). In some areas it frequently uses hollowed out, unused termite mounds (termitaria), hence the common name ‘anthill-tiger’ (the Afrikaans ‘miershoop tier’). Its auditory bullae are exceptionally well developed, benefiting hearing abilities in areas with little vegetation cover. Hearing is its most important sense. Sight is acute to allow for orientation during crepuscular and nocturnal hunting. It is considered to be the southern representative of the Sand Cat, *Felis margarita*, which has a body and head of similar shape. Black-footed Cats are nocturnal and crepuscular.

Foraging and Food Opportunistic carnivore, taking everything it can overpower. There are possibly strong regional, and certainly seasonal and sex-specific, differences in diet. Males kill on average larger prey while the smaller and more agile ♀♀ are more successful in catching small birds. In summer ♀♀ feed mainly on rodents while in winter a higher proportion of larger (>100 g) birds and mammals are taken, while ♂♂ show less seasonal variation in proportions of prey classes taken (Sliwa 2006). In seven stomachs collected in Botswana by Smithers (1971), muroid rodents were found in four, spiders in three and sengi, reptile, insect and bird remains in one each. A total of 43 vertebrate prey species were identified at the Kimberley study site (Sliwa 1994a, b, 2006, Olbricht & Sliwa 1997, 2006). There were 14 species of mammals comprising 72% of the total prey mass consumed, 21 species of birds (26%) with eggs of various species taken as well, and eight species of amphibians and reptiles. A minimum of ten invertebrate species was eaten, some as small as the alates of harvester termites. The most frequently taken prey species was the Large-eared Mouse *Malacothrix typica*, and average prey size was 24.1 ± 47.4 g (S.D.; $n = 1725$ prey captures) (Sliwa 2006). The largest prey they have been recorded taking successfully is Cape Hare *Lepus capensis*. They have also been recorded attempting to take resting Springbok *Antidorcas marsupialis* lambs, attempts that always failed when the lamb stood up (Sliwa 1994a).

Three different hunting styles have been identified. With the ‘fast-hunt’ technique, the cat moves in swift bounds at a speed of 1–2 km/h trying to flush prey from cover using the element of surprise and relying mostly on eyesight. The ‘slow-hunt’ involves a slow stalk, winding snake-like between the grass tufts, trying not to move any grass stalks in the process. The cat moves its head from side to side, looking and listening carefully, its ears moving constantly, alert to any movements or sounds. The average speed for this style is 0.5–0.8 km/h. When locating prey the cat stalks to within 1–2 m and tries to determine its exact position, catching it in a final rush. About 70% of the night is spent hunting. The ‘sit-down’ hunt involves the cat positioning itself at a rodent den system and waiting with drawn up front paws for up to two hours. The final rush consists of one, or several, fast jumps out of the crouch. Using this technique the cat moves at 0.1–0.4 km/h. Birds are sometimes snatched from the air.

Small mammals are killed with a neck bite and swallowed head first (Sliwa 1994a). Larger *Tatera* gerbils’ heads are sometimes bitten off, the stomach and intestines removed, and then the rest of the body is swallowed whole. Sometimes even the contents of the intestines are squeezed out by pulling them through the cat’s incisor

teeth and then swallowed. Cape Hares were killed by either a neck bite or by biting the forehead, and then left to die while kicking, while a Black Bustard *Eupodotis afra* was grabbed by the wing or neck and never released. Feeding started on the head, followed by the neck and back and only later the breast muscles were eaten. Little plucking takes place, as is the case with smaller birds (such as larks). Only the wing tips with primaries are always chewed off, sometimes the tail feathers, but the rest of the bird is eaten complete. Snakes were tired out by fast blows to their heads and then killed with a swift neck bite, then swallowed whole from the head first. Eggs are taken gently between the cat's jaws then cracked open to lap up the contents (Sliwa 1994a).

Black-footed Cats hunt throughout the night in all weather conditions and temperatures, ranging from -10°C to 35°C , with only brief resting periods. Hunting success is very high with about one vertebrate prey animal caught every 50 minutes and 10–14 rodents or small birds caught in a night. This represents about 250–300 g of food, about 20% of the cat's body weight, but record intakes can reach 450 g per night (Sliwa 1994a, b). Excess food is cached, usually in shallow Aardvark *Orycteropus afer* diggings or inside weathered, hollow termite mounds. Cats scavenge readily (even from antelope carcasses) (Sliwa 1994a). They are independent of water, but will drink occasionally when it is available, although this has never been seen in healthy cats in the wild (A. Sliwa pers. obs.). Black-footed Cats are occasionally shadowed by Marsh Owls *Asio capensis*, which catch birds that are flushed (Sliwa 1994c). Travelling distance is between 4.4 and 15 km (mean = 8.4 ± 2.1 km) per night as measured by a vehicle's odometer (Sliwa *et al.* 2010). When moving during daylight hours, they are mobbed by birds such as larks and Southern Ant-eating Chats *Myrmecocichla formicivora*.

Social and Reproductive Behaviour Black-footed Cats are solitary, except for ♀♀ with dependent kittens, and during mating. Males have larger annual home-ranges (20.7 km^2 ; $n = 5$) than ♀♀ (10.0 km^2 , $n = 7$) (Sliwa 2004). Male ranges overlap those of 1–4 ♀♀. Intra-sexual overlap varies from 12.9% for three ♂♂ to 40.4% for five ♀♀. Home-range size is likely to vary between regions according to resources available to the individuals.

Black-footed Cats communicate through olfaction predominantly using urine spray-marking. The frequency of spray-marking by a ♀ fluctuates strongly during the year, depending on the stage of her reproductive cycle. Marking frequency is high before mating, low when pregnant and ceases completely when rearing kittens (Molteno *et al.* 1998). Male scent-marking is most intensive prior to mating, when there are as many as 585 sprays per night (Sliwa *et al.* 2010). Scent-rubbing, and possibly claw-raking, may have some signalling function. Faeces are rarely covered and they do not use middens. Vocal communication, a loud meowing sound, repeated up to ten times in quick succession, is heard especially from ♂♂ looking for ♀♀ during the mating season. Females occasionally call loudly in oestrus. Soft calls are used when ♂♂ court ♀♀ and when ♀♀ call their kittens (Sliwa *et al.* 2010). Females with kittens have special alarm calls. During these calls the ears are depressed.

During winter up to ten copulations occur during oestrus (Sliwa *et al.* 2010). The resident ♂ guards the ♀ and chases intruding ♂♂, and fights ensue between competing ♂♂. Kittens are born in hollow termitaria, or springhare burrows (Olbricht & Sliwa 1997).

The mother leaves her kittens for several hours at night from the day of birth and resumes her hunting schedule after four days. She returns infrequently during the night to suckle the young (Sliwa 1995). Kittens are moved frequently after the first week. The mother carries prey items to the den to feed them and teaches the kittens to hunt using live prey (A. Sliwa pers. obs.). Kittens are independent after 3–4 months, but remain within the range of their mother for extended periods (A. Sliwa pers. obs.).

Reproduction and Population Structure Gestation is 63–68 days (Leyhausen & Tonkin 1966, Schürer 1988), and up to two litters are born per year from spring to autumn, coinciding with the rains and greater availability of food (Olbricht & Sliwa 1997). Litter-size is 1–4, but usually two, and birth-weight is 60–90 g (mean 77 ± 11 g, $n = 10$). Eyes open at 3–10 days, deciduous teeth erupt at 14–21 days and kittens take solid food within 30 days (Olbricht & Sliwa 1995). They are weaned in two months, and permanent teeth erupt at 148–158 days. Sexual maturity (in captivity) is seven months for ♀♀ and nine months for ♂♂ (Olbricht & Sliwa 1997). Females have an oestrous cycle of ca. 12 days (J. Herrick pers. comm.) and oestrus lasts about 36 hours (Leyhausen & Tonkin 1966).

The adult sex ratio in the wild was 4 ♂♂ to 6 ♀♀ or 1 : 1.5 (Sliwa 2004). Birth sex ratio is 1.16 : 1 in captivity (Olbricht & Sliwa 1997). Captive cats may live up to 16 years (Sliwa & Schürer 2000), although data from the wild indicate two ♀♀ were at least four years old and a ♂ about six years old before they died (A. Sliwa pers. obs.). Mortality of kittens is not known from the wild, although one kitten of a litter of two died in a hailstorm (A. Sliwa pers. obs.).

Predators, Parasites and Diseases Young, or sick, cats and kittens are vulnerable to predation by Black-backed Jackals *Canis mesomelas* and Caracals *Caracal caracal*. However, recently there were two cases of intraguild killing by Caracals and Black-backed Jackals of two adult radio-marked cats (B. Wilson & J. Kamler pers. comm.), as well as regular harassment of adult Black-footed Cats by Black-backed Jackals (Olbricht & Sliwa 1997, A. Sliwa pers. obs.). The presence and abundance of Black-footed Cats may be adversely affected by the density of meso-carnivores like Black-backed Jackals and Caracals as well as close competitors like the Wildcat *Felis silvestris*, which may explain the absence or rarity of the species in otherwise suitable habitat and protected areas (Sliwa *et al.* 2010). Kittens and possibly adults have been recorded falling victim to large nocturnal raptors such as eagle-owls (*Bubo* spp.). Cats also fall victim to domestic dogs, which are used to chase or dig out jackals during problem-animal control operations (Sliwa 1995). Little is known about disease, but both wild (A. Sliwa pers. obs.) and captive cats have succumbed to kidney failure (secondary AA amyloidosis) (Olbricht & Sliwa 1997), indicated by high urea concentrations and creatinin values in the blood (Sliwa & Schürer 2002).

In a study of cats caught for radio-collaring, fleas (*Pulex* sp.) and ticks (*Ixodes*) were common ectoparasites (A. Lawrenz pers. comm., A. Sliwa pers. obs.). Horak *et al.* (2010) recorded *Haemaphysalis zumpti* from five animals in the Northern Cape. Adult stages of *Toxascaris leonina* and the eggs of *Ancylostoma tubaeforme* and *Sarcocystes bovis* were found in faeces. Blood parasites of the complex *Babesia* have been recorded in the red blood cells of various individuals (A. Lawrenz pers. comm., A. Sliwa pers. obs.).

Conservation IUCN Category: Vulnerable C2a(i). CITES: Appendix I.

Black-footed Cats are present in several protected areas across their range in southern Africa, including Etosha N. P. (Namibia), Makgadikgadi Pan (Botswana), Hwange N. P. (Zimbabwe), albeit in low densities, and several reserves in South Africa, including Addo Elephant N. P. and Willem Pretorius G. R. Although not yet confirmed from the South African side of the Kgalagadi Transfrontier Park, there is a record from the Botswana side (Smithers 1971).

Threats to Black-footed Cats include the expansion of human settlement and arable agriculture, use of poison, desertification, overgrazing and bush encroachment. They may be susceptible to poisons used during locus-control campaigns. Farmers setting 'coyote-getters' and poisoning of carcasses during control operations targeting other predators may also affect Black-footed Cats since they readily scavenge (Visser 1978, Stuart & Wilson 1988, Sliwa 1994a, b). Night calling and shooting aimed at Black-backed Jackals as well as the use of free-roaming hunting dogs for predator control also impacts Black-footed Cats in the C Karoo (C. Stuart & T. Stuart pers. comm.).

Measurements

Felis nigripes (spp. *thomasi* or *nigripes*)

HB (♂ ♂): 453 (430–520) mm, n = 8

HB (♀ ♀): 397 (370–420) mm, n = 10

T (♂ ♂): 173 (160–200) mm, n = 8

T (♀ ♀): 151 (140–170) mm, n = 10

HF c.u. (♂ ♂): 95 (89–100) mm, n = 8

HF c.u. (♀ ♀): 88 (83–92) mm, n = 10

E (♂ ♂): 47 (40–50) mm, n = 8

E (♀ ♀): 44 (35–50) mm, n = 10

WT (♂ ♂): 1.93 (1.75–2.45) kg, n = 8

WT (♀ ♀): 1.30 (1.10–1.65) kg, n = 10

Kimberley, South Africa (A. Sliwa pers. obs.)

F. n. nigripes

HB (♂ ♂): 402 (376–433) mm, n = 5

HB (♀ ♀): 360 (369–360) mm, n = 3

T (♂ ♂): 177 (164–198) mm, n = 5

T (♀ ♀): 153 (126–170) mm, n = 3

HF c.u. (♂ ♂): 99 (94–104) mm, n = 5

HF c.u. (♀ ♀): 92 (89–94) mm, n = 3

E (♂ ♂): 54 (51–57) mm, n = 5

E (♀ ♀): 47 (45–50) mm, n = 3

WT (♂ ♂): 1.60 (1.50–1.70) kg, n = 5

WT (♀ ♀): 1.10 (1.00–1.40) kg, n = 3

Botswana (Smithers 1971)

Key References Olbricht & Sliwa 1997; Skinner & Chimimba 2005; Sliwa 1994a, b, 2004, 2006; Sliwa *et al.* 2010; Smithers 1971.

Alexander Sliwa

Felis silvestris WILDCAT

Fr. Chat ganté (Chat sauvage d'Afrique); Ger. Falbkatz

Felis silvestris Schreber, 1777. Die Säugethiere 2 (15): pl. 107 [1775]; text 3 (23): 397 [1777] Type locality not given.

Fixed by Haltenorth (1953) as 'vielleicht Nordfrankreich'. Listed by Pocock (1951) as Germany.

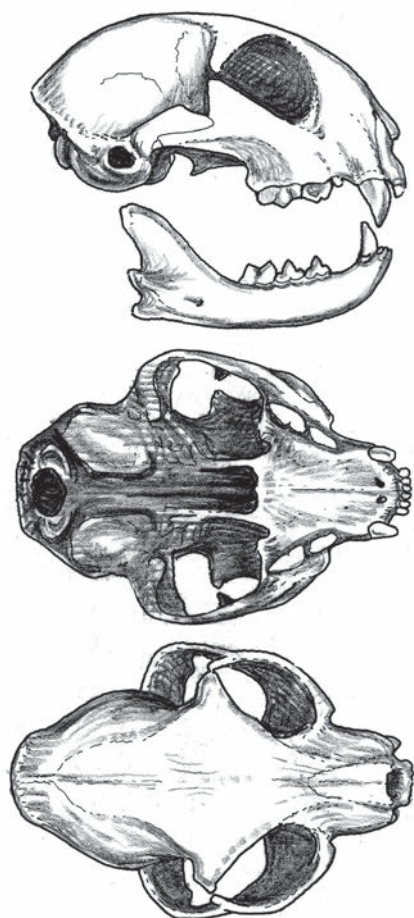


Wildcat *Felis silvestris*.

Taxonomy A problematic species from the taxonomic viewpoint, primarily due to differing views on the relationship of the African Wildcat to the European Wildcat, for many years considered two separate species, *Felis lybica* and *Felis silvestris*, respectively. Pocock (1951), in his massive synthesis of the species, held them to be

taxonomically distinct, while admitting a close relationship. On the other hand, Haltenorth (1953) considered *lybica* not as a separate species, but as a race of *silvestris*. Subsequent published classifications have either supported the idea of treating the two as conspecific (e.g. Ellerman *et al.* 1953, Haltenorth 1957, Corbet 1978, Wozencraft 1989a, 1993, 2005, Corbet & Hill 1991, Bronner *et al.* 2003) or assigned African representatives to *F. lybica* (Ellerman & Morrison-Scott 1951, Rosevear 1974, Smithers 1975, Ansell 1978, Swanepoel *et al.* 1980, Meester *et al.* 1986), usually not without reference to the domestic cat. A multivariate analysis of craniometric characters in the African Wildcat, European Wildcat and the domestic cat was unequivocal in considering *lybica* as conspecific with *silvestris* (Ragni & Randi 1986; but see Puzachenko 1996), and molecular studies have corroborated this viewpoint (Randi & Ragni 1991, Essop *et al.* 1997, Johnson & O'Brien 1997; but see Wiseman *et al.* 2000).

Nowell & Jackson (1996) recognized four groups of *F. silvestris*, following Weigel (1961) and Hemmer (1978): the forest cats (*silvestris* group) of Europe, the Caucasus and Asia Minor; the steppe cats (*ornata* group) of south and central Asia; the tawny cats (*lybica* group) of Africa and the Middle East; and the domestic cat (which several authors – most recently, Wozencraft [2005] – have treated as separate from the wildcat). In an attempt to investigate relationships among domestic cats, their indigenous wild progenitors, and



Lateral, palatal and dorsal views of skull of Wildcat *Felis silvestris*.

related species of the genus *Felis*, Driscoll *et al.* (2007) undertook a detailed genetic assessment and found that *F. s. silvestris* (European Wildcat), *F. s. lybica* (Near Eastern Wildcat), *F. s. ornata* (Central Asian Wildcat), *F. s. cafra* (Southern African Wildcat) and *F. s. bieti* (Chinese Desert Cat, usually considered a distinct species) each represents a distinctive subspecies of *Felis silvestris*. Wildcats from North Africa were attributable to *F. s. lybica*, but the boundaries between this form and the southern African *F. s. cafra* require further elucidation. The correct spelling of the specific name is *silvestris*, not *sylvestris*.

Synonyms (Africa only): *brockmani*, *bubastis*, *caligata*, *cafra*, *caffra*, *caligata*, *cristata*, *cyrenarum*, *foxi*, *griselda*, *guttata*, *haussa*, *hybrida*, *lowei*, *lybiensis*, *lybica*, *libyca*, *lynesi*, *maniculata* (Temminck, 1824 and Cretschmar, 1826), *mauritana*, *mellandi*, *namaquana*, *nandae*, *obscura*, *ocreata*, *pulchella*, *pyrrhus*, *rubida*, *rupellii*, *rusticana*, *sarda*, *savanicola*, *taitae*, *ugandae*, *vernayi*, *xanthella*. Chromosome number: $2n = 38$ (Jotterand 1971, Wurster-Hill & Gray 1973).

Description Similar in size and general appearance to domestic cat but tends to be heavier and longer in the leg. Can be difficult to distinguish the two in the field. A characteristic feature of the Wildcat is the reddish to rusty-brown tint to the hair on the backs of the subtriangularly pointed ears, which has been documented throughout its extensive African range (Rosevear 1974, Dragesco-Joffé 1993, Skinner & Chimimba 2005). Overall pelage colour ranges from dark grey, tawny-brown, reddish to sandy-yellow, marked with faint to fairly bold tabby spots, stripes and blotches. In general, populations in drier areas

are usually paler than those from higher rainfall regions. In the C Saharan mountains (Tassili) very dark cats have been observed (De Smet 1988). There is a wide zone of intergradation of colour in areas where different subspecies/colour forms come together. The length of the coat is extremely variable, and Pocock (1951) cites extremes of 22–44 mm on the flanks and 34–55 mm for the spinal crest. Tail tapers towards the tip, has variable dark ringing (normally two rings), is dark to black-tipped, and approximately 50–60% of the length of the head and body. Dark to black rings are often present on the legs, of variable intensity and distribution. The chin and throat are white and the underparts paler than the upper and often a fawn to reddish tinge. Undersurfaces of front and hindfeet very dark and most commonly black. The feet are entirely hairy below, except for the pads. Males are on average larger and heavier than ♀♀. Three pairs of nipples.

The skull is high, arched and comparatively lightly built, and with a short muzzle. The zygoma is rather thick and heavily constructed, thus providing substantial attachment for masseter muscles; there is also considerable space for powerful temporalis muscles. The supraoccipital crest is wide and strong. The postorbital processes do not join, although there may be a cartilagenous junction (Skinner & Chimimba 2005). Rosevear (1974) mentions aberrations in the typical dental formula: in some specimens, the upper second premolar is lacking on one or both sides having been shed and the alveolus closed over, an occurrence that apparently can be observed in process in some skulls.

Geographic Variation Differences in pelage colouration and patterning of museum skins has led to a proliferation of subspecies, most invalid. Pocock (1951) recognized 32 subspecies across the range of the species, of which 16 were African (one of them, *bubastis*, apparently extinct). Smithers (1975) recognized ten subspecies for the continent, and some 14 subspecies were listed in the *lybica* group by Nowell & Jackson (1996). The recognition of so many subspecies is doubtful, and based largely on minor differences in the pelage colouration and patterning of museum skins. For example, Dorst (1950) found a wide range of colour from red to grey in a series of 15 skins from a restricted collecting area just north of Lomé (Togo). The series also demonstrated the considerable range of size in a small population. Indeed, although there is variation in size within any Wildcat population there would appear to be few, if any, significant differences on the regional level. Rosevear (1974) gives head and body length ranges from 400 to 600 mm and weights of 4.5 to 5.5 kg for West Africa, with a possible low adult weight of 2.7 kg. Kingdon (1977) gives a head and body length range of 470–660 mm and weights of 3.0–6.5 kg for East Africa. In neither case is the number of specimens used to calculate these ranges given. The measurements for the former Cape Province (South Africa) presented in this account (see Measurements) also fall within this range.

A high degree of intergradation is evident between described forms, as evidenced in populations from southern Africa ascribed to the forms *cafra* and *griselda*. Differentiation is reportedly based on the darker colour of the former (from the better-watered southern and eastern areas) with the lighter sandier colour of the latter (from the drier western part of southern Africa). However, where their distributional ranges approach each other, it is almost impossible to assign the specimens to one subspecies or another. The issue is further complicated by the fact that this felid readily hybridizes with the domestic cat. The occurrence of hybridization seems to be uneven

across the species' range; in many areas, hybrids are common, and in some areas true Wildcats are at the best rare (as can be evidenced in some museum collections; C. Driscoll pers. comm.).

Similar Species

Felis nigripes. Sympatric in southern parts of range. About half the size and distinctly marked with dark to black spots and bars on body; tail and legs always distinctly ringed with dark brown or black; proportionally large head; backs of ears same as ground colour of body.

F. margarita. Sympatric in arid areas of North Africa. The smallest cat in Saharan belt restricted to sand desert; broad face with large, rounded ears; pelage more or less uniformly pale sandy-buff, with indistinct darker markings, dark edges to backs of ears; underparts white to off-white.

F. chaus. Restricted to vicinity of Nile R. and Mediterranean zone of Egypt. Larger (up to 12 kg), with overall sandy-brown pelage, without distinctive markings; reddish-brown hair on ear backs with short, black tufts of hair at tips.

Distribution Wildcats occur wholly, or in part, in nearly all African countries (Nowell & Jackson 1996). This extremely wide distributional range is accompanied by a very broad habitat tolerance, the species being apparently absent only from closed tropical forest. Although thinly distributed in true deserts such as the Sahara, Wildcats do occur, especially in association with hill and mountain country, such as the Hoggar. In North Africa they occur discontinuously from Morocco through Algeria, Tunisia, Libya and into Egypt. The species has an extensive distribution across the savannas of West Africa from Mauritania on the Atlantic seaboard, eastwards to the Horn of Africa, Sudan and Ethiopia; southwards, Wildcats are present in all East and southern African countries.

Extraliminally, Wildcats occur in the mountain ranges and on the desert fringes of the Arabian Peninsula, along the eastern border of

the Mediterranean Sea, then eastwards through Iran, Iraq, Pakistan, E Afghanistan and into W India. They also still occur throughout large parts of Europe, including N Scotland and the Mediterranean island of Sicily, and eastwards in Turkey, the Caucasus and from the Caspian Sea to S Mongolia and NW China (Sunquist & Sunquist 2002).

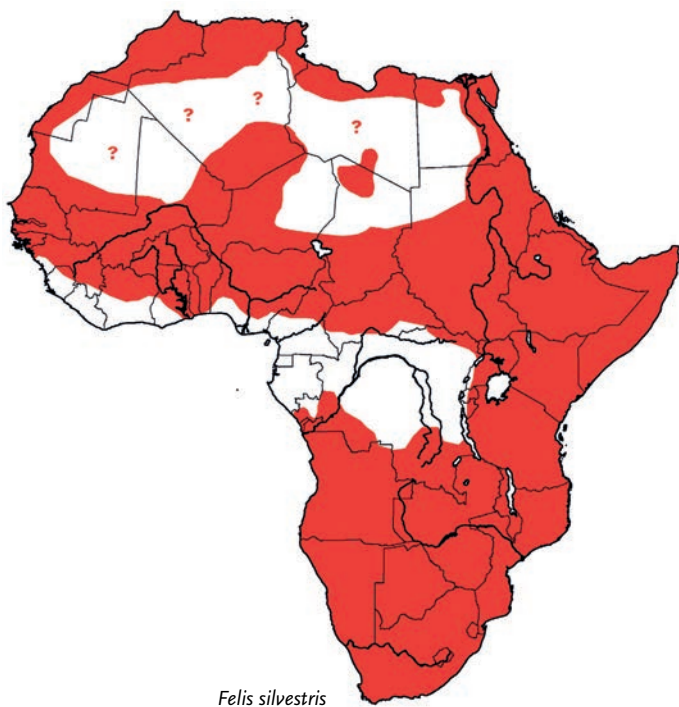
Habitat Very broad habitat tolerance, ranging from sea level to 2600 m in the Moroccan High Atlas (Cuzin 2003) and up to altitudes of more than 3800 m in the mountains of Kenya and Ethiopia (Young & Evans 1993, Yalden *et al.* 1996), but apparently absent from lowland tropical forest and open sand desert. Their distribution on a continental basis reportedly follows the 100 mm rainfall isohyet quite closely, below which they normally do not occur except where river courses serve as avenues into otherwise drier terrain, or where isolated mountains receive a slightly higher rainfall than the surrounding country (Skinner & Chimimba 2005).

Occurs around the fringes of the Sahara and in the massifs of Hoggar, Air and Tibesti in the central zone of that desert (De Smet 1988, Kowalski & Rzebik-Kowalska 1991). In the arid western and central areas of South Africa they are commonly associated with hill ranges and isolated rock outcroppings, penetrating the surrounding plains mainly along dry water-courses (C. Stuart & T. Stuart pers. obs.). Shows strong association with a variety of woodland types over much of its African range (Smithers 1971, Kingdon 1977). Throughout their range, adequate cover is required to rest up in during the day. Cover takes the form of rocky hillsides, reed-beds, riverine underbrush or stands of tall grass, holes or burrows excavated by other species, the exposed roots of trees, holes in termite mounds, and, in open semi-desert country such as the Kalahari, isolated stands of *Acacia* scrub or other bushes (Smithers 1971, Sliwa *et al.* 2010). The species is commonly found in and around cultivated areas and often in association with human settlements. In agriculturally developed areas, they use the shelter of standing crops such as maize and other high-standing grain crops.

Abundance Generally common despite human persecution, and high densities may be reached in suitable areas. In the broken hill country of the lower Orange R. basin of South Africa it is estimated that there is approximately one cat per 2 km² (C. Stuart & T. Stuart pers. obs.) while in East Africa density was estimated at 1/6–7 km² (Hendrichs 1972). Occurs at low densities in deserts such as the Nubian, Sahara and Namib. They are easily overlooked even when common, and difficult to trap.

Adaptations The thick and stoutly built zygoma provide substantial anchorage for the masseter muscles and are quite widely bowed to allow sufficient space for the well-developed temporalis muscles. The carnassial shear acts as an efficient cutting blade for slicing up prey. Cutting edges of the first lower molar lie at angles to each other and serve to hold prey firmly. Canines are somewhat flattened, sharp and quite long, adapted to delivering a killing bite by entering the neck vertebrae of their prey, prising them apart until the spinal chord is severed. The bullae are large and well developed, reflecting the keen sense of hearing (Skinner & Chimimba 2005). Terrestrial, but may climb trees.

Foraging and Food Detailed studies of diet have been made only in southern Africa (Smithers 1971, Stuart 1977, 1981, Rowe-



Felis silvestris

further than a few metres. The mother spent most of her time at the den and made short hunting trips. Initially, she hunted for herself and returned to the den to suckle the kittens. Later, the mother stayed away for longer periods, leaving the kittens in dense vegetation or in close proximity to trees. As the kittens approached five weeks of age she carried live prey back to them. The kittens played and practised their hunting skills on the stunned prey and either ate it or left the dead prey for the mother, who ate it or covered the remains. Males appeared to play no role in raising the young, although they visited ♀♀ with kittens. Kittens remained with the mother for 2–4 months after which they dispersed (Sliwa *et al.* 2010). Kittens from a previous litter have been observed playing with younger siblings (Herbst & Mills 2005).

Reproduction and Population Structure Breeding over much of its sub-Saharan range may occur throughout the year, but there are distinct peaks, and most births are recorded during warm summer months. In southern Africa births are mainly recorded from Sep to Mar (Skinner & Chimimba 2005) and in the Sahara and the Mediterranean coastal plain from Jan to Mar, the cooler months (De Smet 1988, Dragesco-Joffé 1993). In Kenya newborn young have been recorded in Mar (Allen & Lawrence 1937) and W Uganda in Dec (Kingdon 1977). One to five kittens (average 3; Smithers 1971, Sliwa *et al.* 2010) are born after a gestation period of 56–65 days (Green 1991).

Kittens are born blind, eyes opening at between 10 and 14 days, and accompany the mother hunting between the age of one and three months. Young mature rapidly and are independent at five months, allowing ♀♀ to have two litters in a year if conditions are optimal. Herbst & Mills (2005) recorded four litters in succession of three, two, two and three, although only a single kitten survived to five months in each case. Age at sexual maturity is 11 months. A wild-born Wildcat was about 19 years old when she died in captivity (Weigl 2005).

A captive-reared Wildcat crossed with a Serval *Leptailurus serval* producing several litters over a period of three years that reached maturity; in each case, the kittens were premature (Skinner & Chimimba 2005).

Predators, Parasites and Diseases Likely predators include larger carnivores, such as Lions *Panthera leo*, Leopards *P. pardus* and Spotted Hyaenas *Crocuta crocuta*, and raptors. On one occasion in the Kalahari, a male Ratel *Mellivora capensis* went into a Wildcat den, and a kitten escaped and was chased and caught above ground; another male Ratel was seen with a half-eaten adult although it was not seen how it was caught (C. Begg & K. Begg pers. comm.). In the same area, a Caracal *Caracal caracal* was seen with a half-eaten adult (M. Herbst pers. comm.). Sliwa *et al.* (2010) note that Giant Eagle Owl *Bubo lacteus* twice tried to grab a large adult male African Wildcat on the back, while the cat was crossing a clearing in the river bed. The owl was unable to lift the cat and the cat escaped into thick vegetation.

Parasites recorded from South Africa include fleas (*Ctenophalides connatus*, *Ctenocephalides felis*), ticks (*Haemaphysalis colesbergensis*, *H. zumpti*, *Ixodes rubicundus*, *I. pilosus*, *Rhipicephalus warburtoni*) and cestodes (*Diplopylidium acanthotetra*, *Joyeuxiella fuhrmanni*, *Mesocostoides lineatus*, *Taenia pisiformis* and *T. taeniaeformis*) (Horak *et al.* 1987, 2000, 2004, 2010). Johnson & Lester (1929) reported a specimen from West Africa infected with *Trypanosoma brucei*. Wildcats are susceptible to the same diseases as domestic cats, and feline panleukopenia may be a limiting factor in some areas (Mendelssohn 1989).

Conservation IUCN Category: Least Concern. CITES: Appendix II.

Found in most major, and many minor, conservation areas within its extensive range, the Wildcat is not threatened in the classical sense, although the threat of hybridization is real. Over wide areas of its range the Wildcat comes into contact with domestic and feral cats with which it readily interbreeds. Feral cats have been recorded far from human habitation, including arid areas such as the Kalahari, the Saharan Hoggar (De Smet 1988) and the deserts of Arabia. The main reported impacts of potential hybridization are from southern Africa (Stuart 1981, Wiseman *et al.* 2000, Skinner & Chimimba 2005) and North Africa (Hufnagl 1972, Kingdon 1977), although for southern Africa, at least, it is thought that the situation will not lead to species extinction in the foreseeable future (Wiseman *et al.* 2000). Especially in South Africa the Wildcat also is deliberately and incidentally targeted during ‘problem animal’ control exercises in sheep farming areas but this seems to have little impact on populations (C. Stuart & T. Stuart pers. obs.). Cunningham & Zondi (1991) report that there is a demand for the species in traditional medicine in KwaZulu–Natal (South Africa).

The Wildcat is frequently and accurately pictured in Egyptian temples and elsewhere, and it is generally held that cats were first domesticated in Ancient Egypt, at the latest by the twentieth to nineteenth centuries BC (Malek 1993). Ancient Egyptian ceremonies were held in Bubastis where cats were held sacred to the goddess of the hunt, of love and pleasure, Bast. Vast numbers of cats were mummified to please the goddess. An indication of this is of a shipment of mummified cats weighing 19 tons that was sent to England at the start of the twentieth century to be turned into fertilizer! However, several finds from Cyprus suggest that the origins of cat domestication were earlier, including the discovery of a cat buried in association with a human from the site of Shillourokambos, demonstrating that a close relationship had developed by 9500 years ago (Vigne *et al.* 2004). Recent genetic work suggests that cats were domesticated in the Near East (Driscoll *et al.* 2007). The Wildcat may have been attracted to human habitation by an abundance of small rodents that infested the grain stores of farmers and over time became habituated to man and his surroundings.

Measurements

Felis silvestris

HB (♂♂): 601 (545–665) mm, n = 21

HB (♀♀): 550 (460–620) mm, n = 15

T (♂♂): 305 (275–360) mm, n = 21

T (♀♀): 295 (250–355) mm, n = 16

HF c.u. (♂♂): 138 (120–150) mm, n = 21

HF c.u. (♀♀): 133 (120–150) mm, n = 14

E (♂♂): 62 (55–70) mm, n = 20

E (♀♀): 64 (55–72) mm, n = 15

WT (♂♂): 4.9 (4.0–6.2) kg, n = 10

WT (♀♀): 3.7 (2.4–5.0) kg, n = 10

Northern Cape, Western Cape and Eastern Cape, South Africa (Stuart 1981)

Key References Kingdon 1977; Skinner & Chimimba 2005; Sliwa *et al.* 2010; Smithers 1971; Stuart 1977, 1981.

Chris Stuart, Tilde Stuart & Koenraad J. De Smet

Family VIVERRIDAE

GENETS, LINSANGS, CIVETS

Viverridae Gray, 1821. London Med. Repos. 1821: 301.

| Genettinae | | |
|--------------------------------|---------------|--------|
| <i>Genetta</i> (14 species) | Genets | p. 214 |
| <i>Poiana</i> (2 species) | Linsangs | p. 251 |
| Viverrinae | | |
| <i>Civettictis</i> (1 species) | African Civet | p. 225 |

The Viverridae are distributed throughout the African and the Asiatic continents, with one species, the Common Genet *Genetta genetta*, also occurring in the Mediterranean ring. According to the classification presented by Wozencraft (2005), the family includes 15 extant genera and 35 species, although the systematics are debated. Its members occupy a large variety of habitats, from rainforest to woodland and more open milieus such as bushland, savanna and grassland. Some species may adapt to arid (*Genetta genetta*) and mountainous regions.

The Viverridae are small- to medium-sized carnivores, with head and body length ranging from 330 mm (*Poiana*) to 950 mm (*Civettictis*), and weight from 0.6 to 20 kg. Pelage is variable with striped, spotted or uniform patterns and the tail is either ringed or uniform. The body is long with short legs and a long tail, prehensile only in the genus *Arctictis*. The head is elongated with a pointed muzzle bearing long and mobile vibrissae. The feet and hands are variable, ranging from digitigrade to plantigrade paws with retractile, semi-retractile or non-retractile claws, and five toes in most of the genera. The sole of the feet bears wide and long metatarsal pads in the Paradoxurinae (palm civets), whereas the metatarsal pads are narrow in the Genettinae (genets), or very reduced (*Civettictis*) or absent (*Viverra*, *Viverricula*) in the Viverrinae (Veron 1999). Females have one to three pairs of nipples and males have a baculum. Most species have scent glands in the perineal region secreting a musky fluid. Sexual dimorphism is generally minimal.

The dental formula for the family is $I^{3/3}, C^{1/1}, P^{4/3-4}, M^{1-2/2} = 38-40$. The canines are elongated and straight, and the carnassials are developed in most species. The auditory bulla is characterized by a long, ovoid, well-inflated caudal entotympanic that forms a septum with the posterior wall of the ectotympanic (Hunt 1974). The viverrid bulla differs from those of most living feliforms in that the caudal entotympanic migrates anteriorly during ontogeny, which is similar to felids but with a caudal entotympanic more completely overgrowing the ectotympanic chamber of the bulla (Hunt 1987, Hunt & Tedford 1993).

Most of the viverrids are opportunistic omnivores with vertebrates (especially rodents) as the main source of prey. However, diet specializations occur in the Banded Palm Civet *Hemigalus derbyanus* (Hemigalinae) on invertebrates, in the palm civets on fruits, and in the semi-aquatic species (the Aquatic Genet *Genetta piscivora* and the Otter Civet *Cynogale bennettii*) on crustaceans and fishes. Their way of life ranges from wholly terrestrial (civets), semi-terrestrial (genets and Banded Palm Civets), to mostly arboreal (palm civets) or semi-aquatic (Otter Civet and Aquatic Genet). They are active at night and they usually spend the day in hollow trees, on large branches, in crevices or in burrows excavated by other animals (Nowak 1999).

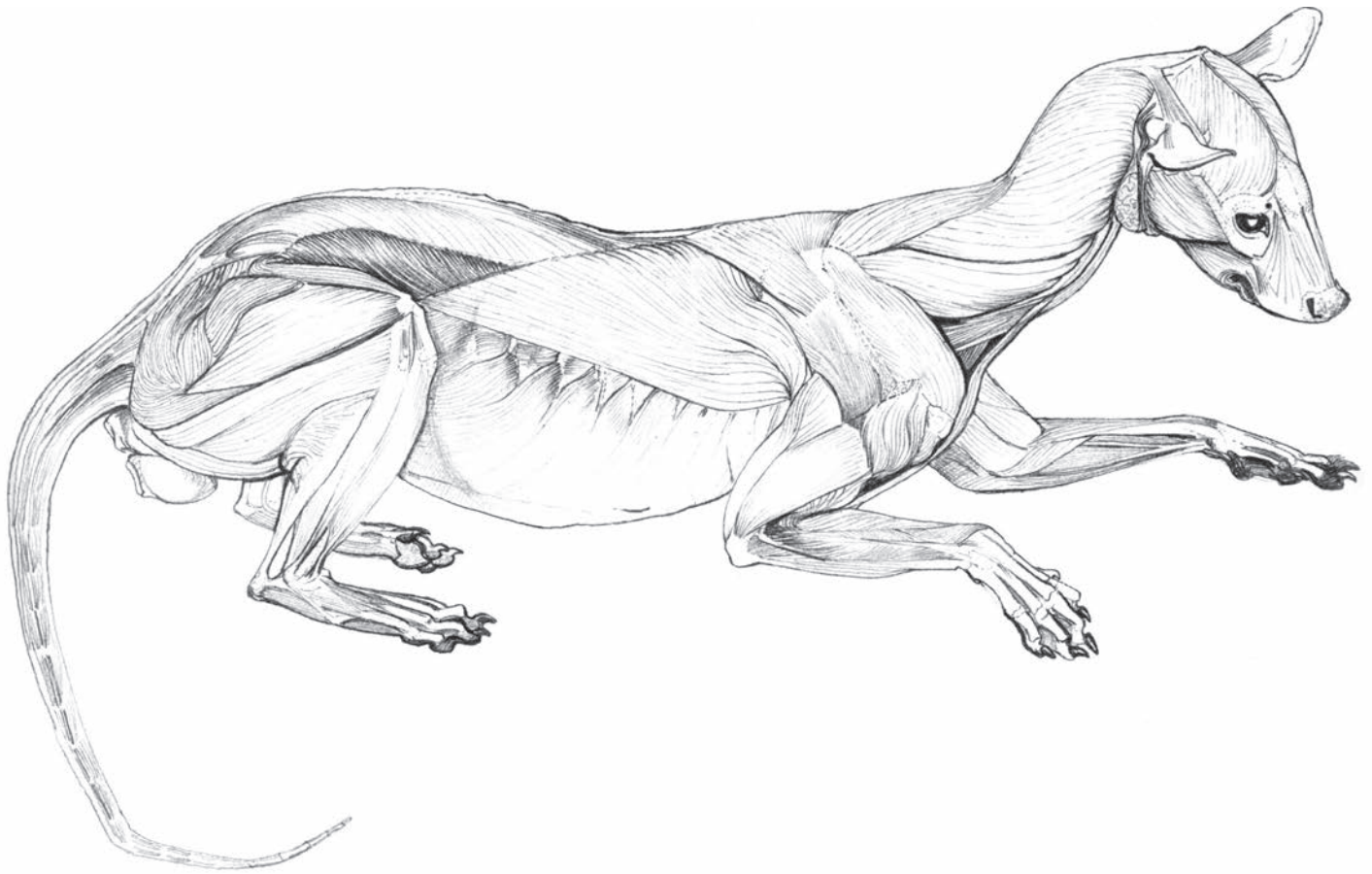


African Civet *Civettictis civetta*.

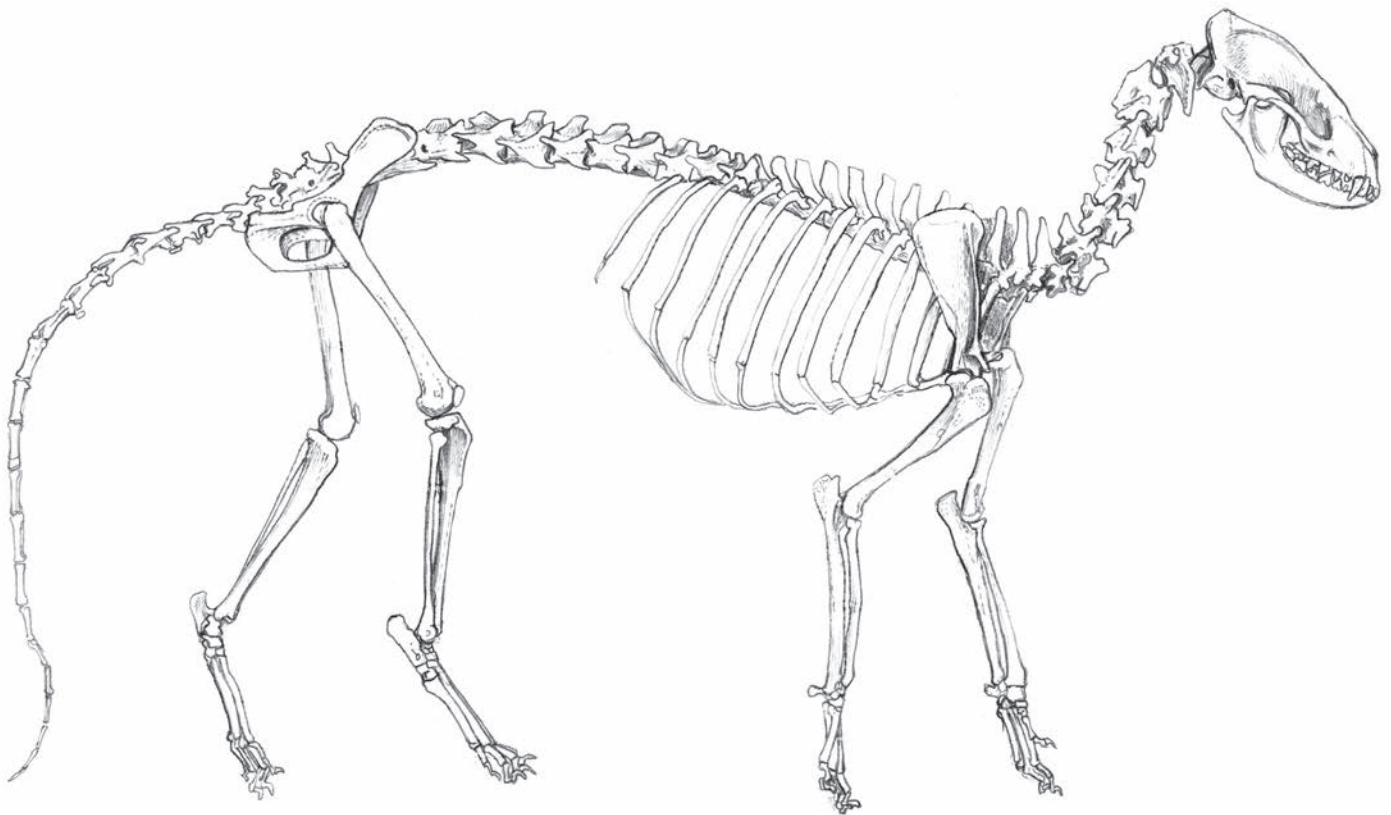
They are generally solitary but occasionally associate in pairs. The viverrids have a variety of visual, olfactory and auditory means of communication (Wemmer 1977, Nowak 1999). Locus-specific defecation is characteristic of some species of Viverridae (*Genetta*, *Civettictis*) (Wemmer 1977, Roeder 1980).

The first viverrids are found in the early Oligocene (34–30 mya) in Europe and Asia. The first possible African viverrids are from the early Miocene (20–18 mya), but the identifications are based on dental material only and not on the auditory bulla, the ontogenetic growth pattern and final adult form of which has been considered diagnostic of the family (but see Gaubert & Veron 2003). The first modern auditory region relatable to the Viverridae is found in *Herpestides* (23–21 mya, Aquitanian of France; Hunt 1991). The first African viverrid with a modern-type auditory bulla is *Kanuites* from the Middle Miocene (Dehghani & Werdelin 2008), while the earliest members of the modern clades *Civettictis*, *Viverra* and *Genetta* appear in the Late Miocene or early Pliocene (Werdelin & Peigné 2010). Most striking is the presence in the Plio-Pleistocene African record of several viverrids, belonging to the genera *Viverra*, *Sahelictis* and *Pseudocivetta* that were of considerably greater body size than any living viverrid.

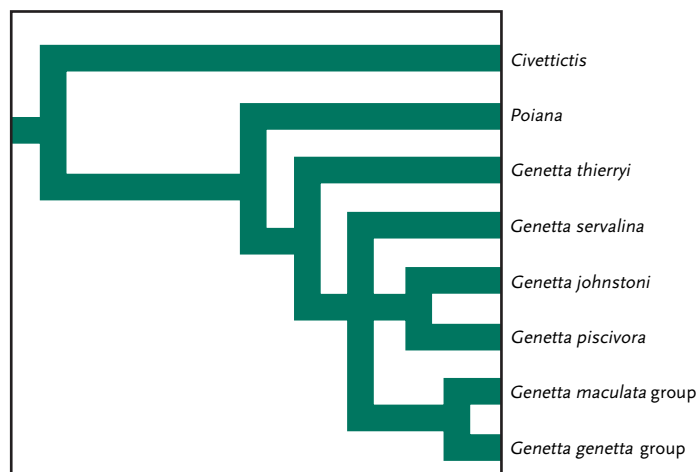
Using a fossil cross-validation method, Gaubert & Cordeiro-Estrela (2006) dated the emergence of Viverridae in the late Eocene–early Oligocene, with a split between the subfamilies Hemigalinae, Paradoxurinae and Viverrinae occurring in the late Oligocene–early Miocene; the terrestrial civets and the separation between (i) *Civettictis* and *Viverra*, and (ii) *Poiana* and *Genetta* were estimated to appear during the Middle Miocene. Ancestral area reconstructions recovered the Asian origin of Viverridae, Viverrinae, terrestrial civets and the clade (*Civettictis*, *Viverra*). Gaubert & Cordeiro-Estrela (2006) also identified two independent migration events from Asia to Africa, during the Middle Miocene (*Civettictis*) and between the



Myology of African Civet *Civettictis civetta*.



Skeleton of African Civet *Civettictis civetta*.



Tentative phylogenetic tree for African Viverridae (after Gaubert & Veron 2003).

late Oligocene and Middle Miocene (genets and oyans), most likely occurring via the Arabian microplate.

The Viverridae are included in the Feliformia as the sister-group of Hyaenidae (Herpestidae, Malagasy taxa) (Veron & Catzeflis 1993, Gaubert & Veron 2003, Yoder *et al.* 2003, Gaubert & Cordeiro-Estrela 2006, Eizirik *et al.* 2010). The monophyly of the Viverridae, as traditionally defined, has been questioned by many authors through both morphological and molecular studies (Hunt 1987, Wozencraft 1989b, Veron & Catzeflis 1993, Veron 1995, Flynn & Nedbal 1998, Veron & Heard 2000). As a consequence, *Nandinia* has been separated in the monotypic family Nandiniidae (Hunt 1987, Hunt & Tedford 1993, McKenna & Bell 1997, Flynn & Nedbal 1998; and see Nandiniidae profile), and the Malagasy taxa (*Cryptoprocta*, *Fossa*, *Eupleres* + Malagasy ‘mongooses’) represent the family Eupleridae, as sister-group to the Herpestidae (Yoder *et al.* 2003, Gaubert *et al.*

2005a; and see Wozencraft 2005). The Oriental Linsangs (*Prionodon*) also are now excluded from the Viverridae because they are sister-group of the Felidae (Gaubert & Veron 2003) and are included in the family Prionodontidae.

On the basis of molecular phylogenetic branching, morphological divergence and times of divergence, Gaubert & Cordeiro-Estrela (2006) proposed differentiating the remaining members of the Viverridae into two subfamilies: the Viverrinae *sensu stricto* (terrestrial civets of the genera *Civettictis*, *Viverra*, *Viverricula*) and the Genettinae (the genets and linsangs, represented by the genera *Genetta* and *Poiana*), with the clade (Viverrinae, Genettinae) forming the sister-group of the Asian clade (Hemigalinae, Paradoxurinae). Following this arrangement, two subfamilies comprising one and 16 species, respectively, occur in Africa: the Viverrinae, including *Civettictis* (monospecific), and the Genettinae, comprising *Genetta* (14 species, including former genus *Osbornictis*; after Gaubert *et al.* 2005b) and *Poiana* (two species). *Poiana* is strictly restricted to rainforest, while *Civettictis* and *Genetta* occur in both open and closed habitats. The African taxa are predominantly terrestrial, and most of them have an unspecialized post-cranial anatomy and dentition.

The Small Indian Civet *Viverricula indica*, which is widespread in South and South-East Asia, was introduced to Zanzibar and Pemba (Pakenham 1984) and to Mafia islands (see Kock & Stanley 2009), as well as Madagascar, the Comoros and Socotra. The species may have been introduced by Javanese traders as early as the twelfth century for extraction of the anal gland secretion that was used as perfume. Although clear tracks of this species were recorded in SE Zanzibar by Stuart & Stuart (1998c), it was not recorded at all during a camera-trapping survey (Goldman & Winther-Hansen 2003).

Philippe Gaubert & Géraldine Veron

Subfamily GENETTINAE – Genets, Linsangs

Genettinae Gray, 1864. Proc. Zool. Soc. Lond. 1864: 515.

Use of subfamily name follows Principle of Coordination of the International Commission on Zoological Nomenclature.

This subfamily was defined by Gaubert & Cordeiro-Estrela (2006), on the basis of both morphological grounds and molecular phylogenetics, to include the genera *Genetta* (type genus) and *Poiana*. The Genettinae have been subject to continuing taxonomic controversy over their numbers of species, especially within the genus *Genetta* (see Crawford-Cabral 1981a, Schlawe 1981, Wozencraft 1993, 2005, Gaubert *et al.* 2004b). In addition, *Poiana richardsonii* is either split into two distinct species, *P. richardsonii* and *P. leightoni*, or considered polytypic (see Beaufort 1965, Crawford-Cabral 1993b). Recent molecular phylogenetic analyses also include the Aquatic Genet (formerly *Osbornictis piscivora*) within *Genetta* (Gaubert & Veron 2003, Gaubert *et al.* 2004c), which is the approach followed here. The current treatment recognizes two genera in Africa: *Genetta* (14 species) are small to medium sized, with long tails, metatarsal pads well developed, and light dentition; and *Poiana* (two species), which are small sized, with very short fur, no distinct mid-dorsal line, and light dentition that lacks M2.

In general, the Genettinae are small and slender viverrids, with maxima of ca. 50 cm for head and body length and 3 kg in weight. The tail is longer and may equal the length of the body. Limbs are short compared with body length; members have short metacarpals and plantigrade forefeet, but long metatarsals with digitigrade hindfeet and slender but well-developed metatarsal pads (Taylor 1988). Semi-digitigrade feet (posterior feet digitigrade and anterior feet plantigrade) distinguish them from plantigrade Asiatic subfamilies (Paradoxurinae and Hemigalinae) and the digitigrade Viverrinae. The coat is spotted and the tail is clearly annulated with alternating bright and dark rings; the Aquatic Genet is an exception among Genettinae with its uniform brown-rufous coat colour. The facial mask has bright supra-orbital, and supra- and sub-labial pairs of spots. A well-marked and dark mid-dorsal line is usually present, often extending on the tail. The perineal glands are well developed (absent in *Poiana*), with a shallow interglandular pouch for musk storage in ♀♀.

The caudal entotympanic bone is weakly inflated, showing a globular shape; the paroccipital process covers the distal part of the bullae and is round and short without posterior prolongation. The dentition is weak

and sharp, with a reduced talonid in M1 and a well-marked lingual cusp in P3. The dentition of the Aquatic Genet is adapted to fish-eating.

General biology and adaptations are as in Viverridae (see family profile). The members of the group adapt to almost all terrestrial habitats throughout their range, with the exception of extremely arid regions and high-altitude mountain habitats. Foraging mainly occurs on the ground, although some species spend a large part of their time in trees and/or use them as refuges (*Poiana* and some genet species). *Genetta* and *Poiana* seem to have a more carnivorous diet than the omnivorous African Civet *Civettictis civetta* (subfamily Viverrinae), although many genet species are very opportunistic and adapt their diet according to seasonal and habitat variations. Births often coincide with the wet season (Jan–Mar), which might be correlated with the

peak of food abundance at this time. However, several species are reported to give birth throughout the year, and some species are known to have two litters in a year.

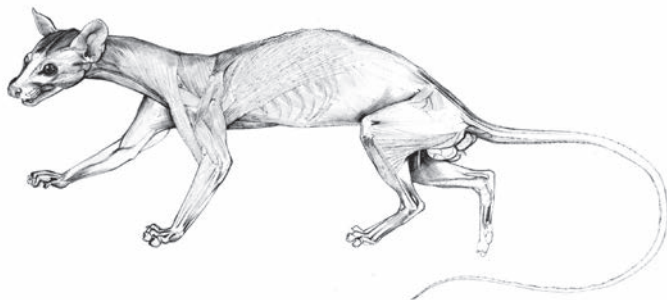
The earliest confirmed *Genetta* (an unnamed species) is early Pliocene (4 mya from Kanapoi in Kenya) (Werdelin & Manthi 2012). *Poiana* has no fossil records. Hunt (1996) suggested a possible phenomenon of *in situ* evolution in Africa following migrations from Eurasia, leading to diversification before taxa spread throughout the continent. The divergence between the genera *Genetta* and *Poiana* is estimated to have taken place at around 11 mya (Gaubert & Cordeiro-Estrela 2006).

Philippe Gaubert

GENUS *Genetta*

Genets

Genetta Cuvier, 1816. Le Règne animal 1: 156.



Servaline Genet *Genetta servalina* myology.

The origin of '*Genetta*' as a name is obscure. Borror (in Larivière & Calzada 2001) derived the name from the Greek prefix 'Gen', meaning 'bear' and the New Latin suffix 'etta', meaning 'small'. On the other hand, Lavauden (1926) suggested that '*genetta*' could be a derivative form of the French name for 'broom', i.e. 'genêt', the animal having been traditionally called 'broom cat' in German 'Geneth Katz', (nowadays rendered as 'Ginsterkatze' with similar affinities in the Portuguese name 'gato-ginete'; J. Crawford-Cabral, pers. comm.). Rosevear (1974) stated that it came from an Arabian word 'jarnait', which turned into 'genette' in Old French and was finally latinized into '*genetta*'. However, no evidence has been found about the use of such a word in Arab-speaking countries. *Genetta genetta* is 'namss' in Classic Arabic, 'el-zerdi' in Arabic dialects, and the Berber word is 'chbirdhou' (Algeria; W. Hamdine pers. comm.).

The taxonomy of the genus *Genetta* has been the focus of considerable debate. Inter-specific boundaries have sometimes been difficult to assess on the basis of morphological characters, especially due to the great variation in coat patterns and relatively low variability in skull characteristics. Wozencraft (1993) listed nine species grouped under three subgenera, namely: *G. johnstoni* (*Paragenetta*), *G. thierryi* and *G. abyssinica* (*Pseudogenetta*), *G. angolensis*, *G. genetta*, *G. maculata*, *G. servalina*, *G. tigrina* and *G. victoriae* (*Genetta*). However, other authors have recognized a larger number of species (e.g. Wenzel & Haltenorth 1972, Rosevear 1974, Crawford-Cabral 1981a, Schlawe 1981, Gaubert

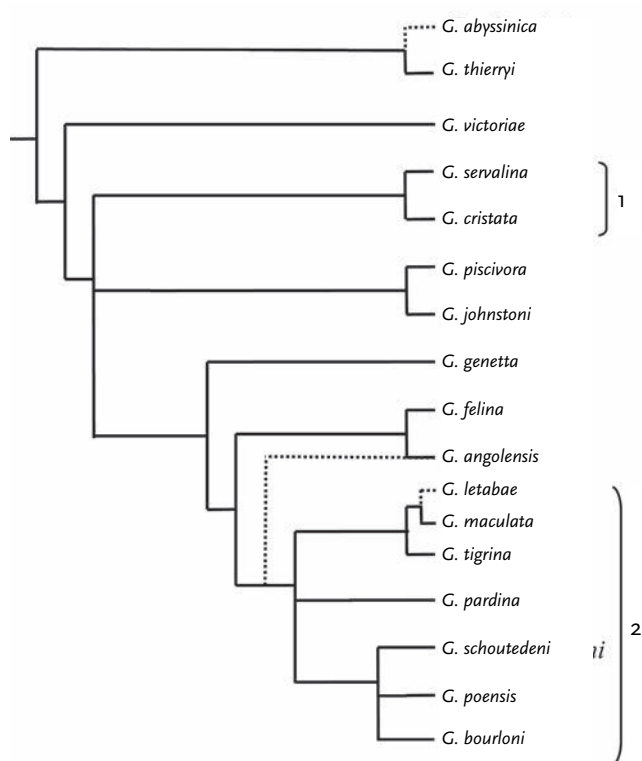
2003a, Gaubert *et al.* 2005b, Wozencraft 2005). This incongruence is primarily due to different opinions about the taxonomy of the morphologically similar large-spotted genets (see Table 7). Crawford-Cabral (1981a) suggested that populations of the large-spotted genets be divided into three geographical entities (which might correspond to valid species): *G. pardina*, west of the Volta R.; *G. 'rubiginosa'* (herein *G. maculata*, *sensu* Gaubert *et al.* 2003a, b), east of the Volta R.; and *G. tigrina*, along the coast of South Africa. This nomenclature only partly accords with Coetsee (1977), Kingdon (1977) and Wozencraft (1993). However, craniometrical analyses (Crawford-Cabral & Pacheco 1992), morphological observations (Schlawe 1981, Powell & Van Rompaey 1998, Gaubert 2003a, Gaubert *et al.* 2001, 2002b, 2005b), and analyses combining DNA and morphology (Gaubert *et al.* 2004b, 2005b), confirm the species status of these three taxa.

Although new methodologies have shed some light on species delimitations and phylogeny, the status of some taxa belonging to the large-spotted genet complex still need further clarification. For example, *G. maculata* appears to constitute a super-species comprising several valid species (Crawford-Cabral 1981a, Crawford-Cabral & Pacheco 1992, Crawford-Cabral & Fernandes 1999, 2001), such as the form *G. letabae* from south-east Africa (Gaubert *et al.* 2004a, 2005b). Further, recent investigations have also revealed that several forest 'forms' (*poensis*, *schoutedeni* and the newly described *bourloni*) constitute a distinct lineage of valid species (Gaubert 2003a, Gaubert *et al.* 2004b), although the status of the form *schoutedeni* requires further investigation and is not treated separately here.

Although the monophyly of the genus *Genetta* has been questioned by Gaubert *et al.* (2002b) on morphological grounds, DNA evidence (Gaubert & Veron 2003, Gaubert *et al.* 2004b, c) supports the inclusion of *G. johnstoni* with the other genets. Molecular analysis also supports the inclusion of the Aquatic Genet (formerly included in the genus *Osbornictis*) within the *Genetta* clade (Gaubert & Veron 2003, Gaubert *et al.* 2004c). The phylogenetic affinities of the Aquatic Genet have long been disputed. Gregory & Hellman (1939) considered the species to be a derived genet, and Wozencraft (1993) regarded it as the sister-taxon of *Genetta*. The new molecular evidence agrees with the morphological observations of Verheyen (1962) and Stains (1983), who felt that the

Table 7. Number of species and name usage in the main classifications of genus *Genetta* throughout ca. 150 years, with a focus on the taxonomy of the large-spotted genet complex.

| | Total number of species | Number of species and name usage within the large-spotted genet complex |
|------------------------------|---|---|
| Gray 1864 | 5 species – no subgenera | 2 species; <i>G. tigrina</i> ('South Africa; [...] Natal and East Africa; [...] Mozambique; [...] Abyssinia') and <i>G. pardina</i> ('Fernando Po; [...] Guinea; [...] Gaboon; [...] West Africa; [...] Interior of Senegal'; <i>G. poensis</i> and <i>G. genetoides</i> are junior synonyms)
Many erroneous synonymies with non Large-spotted Genets, including <i>G. maculata</i> with <i>G. vulgaris</i> (= <i>G. genetta</i>) |
| Matschie 1902 | 25 species – no subgenera | 10 species; <i>G. tigrina</i> (southern coast of South Africa), <i>G. rubiginosa</i> (Caconda, Angola; but erroneous attribution of type-locality), <i>G. schraderi</i> (Salomona, Eritrea), <i>G. zambesiana</i> (Mozambique), <i>G. gleimi</i> (Loanda, Angola), <i>G. stuhlmanni</i> (Uganda), <i>G. fieldiana</i> (Gabon), <i>G. dubia</i> (West Africa), <i>G. genetoides</i> (Ghana) and <i>G. pardina</i> (N Cameroon, Togo; <i>G. poensis</i> is a junior synonym) |
| Allen 1939 | 6 species – no subgenera | 2 species; <i>G. tigrina</i> (from Senegal to Ethiopia and Cape of Good Hope) and <i>G. maculata</i> (West Africa; <i>G. pardina</i> , <i>G. poensis</i> and <i>G. genetoides</i> are junior synonyms)
Many erroneous synonymies with non Large-spotted Genets |
| Coetzee 1977 | 7 species – subgenera
<i>Pseudogenetta</i> , <i>Paragenetta</i>
and <i>Genetta</i> | 1 species; <i>G. tigrina</i> 'sensu lato' (treated as a superspecies; includes <i>tigrina</i> – southern coast of South Africa – <i>rubiginosa</i> – from West Africa to Ethiopia and Natal – and <i>mossambica</i> – N Mozambique and S Tanzania) |
| Crawford-Cabral 1981a | 11 species, plus at least six taxa with debated status – subgenera <i>Pseudogenetta</i> , <i>Paragenetta</i> and <i>Genetta</i> | 5 species; <i>G. tigrina</i> (southern coast of South Africa; provisionally includes <i>G. methi</i> as a subspecies), <i>G. rubiginosa</i> ('from the Volta River eastwards to Abyssinia and southern Somalia and southwards to Zululand'), <i>Genetta</i> sp., aff. <i>G. rubiginosa</i> (S Sudan and SW Central African Republic; possibly corresponding to <i>G. aequatorialis</i> , but taxonomic status unclear), <i>G. pardina</i> (from Senegal to Volta River; <i>G. poensis</i> questionably considered a subspecies) |
| Schlawe 1981 | 10 species – no subgenera | 2 species; <i>G. tigrina</i> (southern coast of South Africa) and <i>G. maculata</i> (considered a polytypic species, with <i>G. pardina</i> , <i>G. poensis</i> and <i>G. genetoides</i> as junior synonyms and <i>G. rubiginosa</i> not valid) |
| Wozencraft 1993 | 9 species – subgenera
<i>Pseudogenetta</i> , <i>Paragenetta</i>
and <i>Genetta</i> | two species; <i>G. tigrina</i> (southern coast of Republic of South Africa) and <i>G. maculata</i> (all sub-Saharan Africa; <i>G. pardina</i> , <i>G. rubiginosa</i> , <i>G. poensis</i> and <i>G. genetoides</i> are junior synonyms) |
| Gaubert, Taylor & Veron 2005 | 17 species – no subgenera | 7 species; <i>G. tigrina</i> and <i>G. pardina</i> (same as Crawford-Cabral, 1981), <i>G. maculata</i> (from the Volta River to northern fringe of southern Africa), <i>G. letabae</i> (Mozambique to South Africa), <i>G. poensis</i> (West and central African rainforests), <i>G. burloni</i> (Upper Guinean Block) and possibly <i>G. schoutedeni</i> (central Africa; taxonomic status uncertain) |
| Wozencraft 2005 | 14 species – no subgenera | 5 species; <i>G. tigrina</i> , <i>G. pardina</i> , <i>G. poensis</i> , <i>G. burloni</i> and <i>G. maculata</i> (same as Gaubert <i>et al.</i> 2005a); <i>G. schoutedeni</i> considered <i>incertae sedis</i> |



morphological differences between *Osobornictis* and *Genetta* – in this case, skull and calcaneum characteristics – were too minor to justify generic status for the Aquatic Genet. Given the phylogenetic position of the Aquatic Genet within the genet phyletic tree, Gaubert (2004c) proposed that *Osobornictis* should be considered a junior synonym of *Genetta* (and see Wozencraft 2005).

According to the most recent phylogeny, *G. thierryi* is the most basal species and emerged ca. 8.5 mya (Gaubert & Veron 2003, Gaubert & Begg 2007). A paraphyletic group of rainforest species (*G. victoriae*, *G. johnstoni*, *G. piscivora* and *G. servalina*–*G. cristata*) then diverged during the late Miocene–early Pliocene (Gaubert & Begg 2007). Finally, *G. genetta* appears paraphyletic, since it is the sister-species of a clade grouping *G. angolensis*, *G. felina* (here included in *G. genetta*) and the large-spotted genets (*G. pardina*, *G. burloni*, *G. poensis*, *G. schoutedeni*, *G. maculata*, *G. tigrina*). The phylogenetic position of species in the aforementioned clade remains debated (Gaubert *et al.* 2004b, Gaubert

Tentative phylogenetic tree of the genets (adapted from Gaubert *et al.* 2004b, Gaubert & Begg 2007; *G. letabae*, *G. schoutedeni* and *G. felina* are not recognized here). Dashed branch leading to *G. abyssinica* and *G. letabae* represent assumptions based on morphological grounds (see Gaubert *et al.* 2002b, 2005c), whereas the alternative branching (plain and dashed lines) for *G. angolensis* reflects conflicting phylogenetic hypotheses (Gaubert *et al.* 2004b, Gaubert & Begg 2007). '1' represents the 'servaline genets' clade, and '2' includes the species of the 'large-spotted genet' complex.

& Begg 2007). Molecular studies have suggested that the large-spotted genets evolved from a recent common ancestor at the boundary of the late Pliocene–early Pleistocene (Gaubert & Begg 2007).

The genets are distributed throughout all sub-Saharan Africa, with one species (*Genetta genetta*) also occurring in the Arabian Peninsula, Maghreb and SW Europe (introduced in the latter region; see Morales 1994, Amigues 1999, Gaubert *et al.* 2009b, 2011). They occur in a wide range of habitats, from dense rainforest to open habitats, and may adapt to a diverse range of niches, including river streams (*G. piscivora*), arid regions (*G. genetta*), high-altitude plateaus and mountains (*G. abyssinica*, *G. maculata*, *G. servalina*) and human-disturbed environments (*G. genetta*, *G. maculata*, *G. pardina*). Remarkably, extant species of genets occupy most of the terrestrial habitats available in Africa. Although the genet morphotype has been conserved throughout the evolution of the genus, one important exception is the very derived, semi-aquatic Aquatic Genet (see below). Given the relatively recent time of divergence of this species (early–middle Pliocene; Gaubert & Begg 2007), accelerated morphological evolution seems likely. Johnston's Genet *Genetta johnstoni*, which arises at the same period and exhibits modified skull and dentition, supposedly adapted to insectivory (Lamotte & Tranier 1983), may also manifest accelerated evolution of morphological traits.

Genets are small- to medium-sized viverrids (HB roughly ranges from 420 to 570 mm) with a relatively long tail (ca. 70–100 % of HB). Coat pattern is distinctly spotted, with a dark mid-dorsal line, except in the Aquatic Genet, which has a uniform brown-rufous coat pattern. Coat patterns have been reported to play a role in individual recognition within genets (Wemmer 1977, Roeder 1984a). Drastic change in the phenotype of the Aquatic Genet, possibly adapted to hiding while fishing along stream borders, might involve modifications in recognition behaviour. Genet facial masks are characteristic, with upper labial, sub- and upper-orbital bright spots contrasting with the dark face. Limbs have semi-digitigrade paws, metatarsal pads are slender but well developed, and claws are felid-like but semi-retractile (Veron 1999, Gaubert *et al.* 2001). Skull characteristics are similar to those of *Poiana*. However, the general shape of the skull is more elongated and the interorbital constriction much more marked in *Genetta*. As additional diagnostic characters, the lingual cusp in P^3 is present (except in *G. tigrina* and *G. maculata* where it is reduced, and *G. piscivora* where it is absent), and the dental formula is $I^{3/3}, C^{1/1}, P^{4/4}, M^{2/2} = 40$, with a light and sharp dentition. Two species exhibit divergent dental characteristics adapted to particular feeding habits: *G. piscivora*, characterized by sharp-edged teeth adapted to piscivory, and *G. johnstoni*, which bears a weak dentition (especially jugal teeth) with proodontal inferior incisors that suggest an insectivorous diet.

Genets are opportunistic mesopredators mainly foraging on the ground, although the Aquatic Genet represents an exceptional case of specialization in hunting (Kingdon 1997). Although species differ markedly in how terrestrial they are, they all use trees as refuges and/or resting places. They also use latrines, possibly for territorial and communicational purposes. Latrines found in closed habitats do not form little hummocks unlike those from open places, but are, instead, more dispersed. Traces of scent-marking activity are found near latrines. Scent-marking relies on glandular secretions from perineal and anal glands presumably to communicate information pertaining to sexual, territorial, or social behaviour. Scent is deposited either through normal quadrupedal squatting, or the animal stands, with its head down and resting on its forefeet, in a reversed upright position. When fighting or stressed, genets may emit a musky scent from anal glands (Wemmer 1977). The number of nipples varies from one to two pairs and this difference may be correlated with habitats inasmuch as the rainforest-dwelling species *G. johnstoni*, *G. victoriae* and *G. servalina* bear only one pair of nipples. Fertile hybridizations have been recorded from captivity (between *G. genetta* and *G. pardina* or *G. maculata*; Gray 1972) and have been detected in the wild between (1) *G. maculata* and *G. tigrina* and (2) *G. tigrina* and *G. genetta* in South Africa (Gaubert *et al.* 2005b).

Fourteen species, including the Aquatic Genet *G. piscivora*, are described in this work, which takes account of several authors' opinions (Crawford-Cabral 1981a, Schlawe 1981, Heard & Van Rompaey 1990, Crawford-Cabral & Pacheco 1992, Wozencraft 1993, 2005, Gaubert 2003a, Gaubert *et al.* 2004a, b, 2005b, Gaubert & Begg 2007). Although the genets, as defined here, include a species characterized by high morphological divergence and niche adaptation (the Aquatic Genet), the genus *Genetta* is maintained without the traditional subgenera because: (1) some phylogenetic relationships within the genus are not well supported enough to accurately discriminate between the lineages; (2) the geological period during which major speciation events are thought to have occurred is relatively recent (Pliocene); and (3) a common genet morphotype (except in *G. piscivora*) has been generally conserved, including plesiomorphic lineages. Species can be distinguished by spot pattern, mid-dorsal line/crest, tail annulation, and colouration patterns on limbs. Gaubert *et al.* (2008) produced an interactive, web-based identification key for genets (and linsangs) that provides an updated diagnostic tool on the taxonomy of the genus *Genetta*.

Philippe Gaubert

Genetta abyssinica ETHIOPIAN GENET

Fr. Genette d'Abyssinie; Ger. Streifengenette.

Genetta abyssinica (Rüppell, 1836). Neue Wirbelt. Fauna Abyssin. Gehörig. Säugeth. 1: 33, pl. 11. 'In Abyssinien, wo es sehr häufig vorkommt, führt es beiden Landeseingebornen zu Gondar'; restricted to Gondar (12° 36' N, 37° 28' E), Ethiopia, by Schlawe (1981).

Taxonomy Described from a complete adult male specimen. Traditionally included in subgenus *Pseudogenetta* (see Crawford-Cabral 1980–81) with the similar Hausa Genet *G. thierryi* (but see genus profile). The sister-species relationship with the Hausa Genet was confirmed by morphological cladistic analysis (Gaubert 2002b).

Considered a primitive genet by Crawford-Cabral (1980–81) on the basis of its shared characters with the African Linsangs (*Poiana* spp.), such as having the central depression of the forefoot hairless and a smaller and less specialized skull. Synonyms: none. Chromosome number: not known.



Ethiopian Genet *Genetta abyssinica*.

Description One of the two smallest genet species (the other being the Hausa Genet). Sexes similar in colour and size. Dark facial mask well marked, contrasted by a pair of supra- and sub-ocular white spots. Forehead grey, with a thin dark vertical line on the muzzle. Ear slightly rounded. Hair short and straight. Pelage soft, with dorsal spots merged in two or three dark lines on each side of the mid-dorsal line. Ground colouration pale creamy-grey (lowland) to dirty yellow (highland plateaux of Ethiopia), with a widening of the dorsal spots and dark rings of the tail in forms from high altitudes (Diaz Behrens & Van Rompaey 2002); the general darkening of pelage in specimens from high plateaux is likely to be associated with higher annual rainfalls (Diaz Behrens & Van Rompaey 2002). Throat, chest and ventral pelage pale grey. Nuchal stripes well defined. Spots of both sides of the neck coalesced with spots of the shoulder, forming a pair of large dark stripes. Mid-dorsal line not contrasting with the rest of the dorsal markings, often starting from the neck between the pair of nuchal stripes and split longitudinally by a line of pale hairs (at least from the shoulder). Spots of the flank, thigh and shoulder rounded and not following a line. Hindlimbs and forelimbs pale grey with dark spots. Line bordering the outer side of the forefoot pads and inner side of the hindfoot pads brown. Forefeet and hindfeet unspotted and pale grey. Central depression of the forefoot hairless. Tail narrow and annulated with seven to nine pale rings to the tip (the tail tuft being black). As in the Hausa Genet, pale rings broken by dark hairs along the mid-dorsal line axis. The skull is reduced in size. The caudal entotympanic bone is rounded and weakly inflated in comparison with the ectotympanic bone (bullae).

Geographic Variation None recorded.

Similar Species

Genetta genetta. Sympatric. Taller; presence of dorsal crest; thick tail with long hairs, tuft whitish.

G. maculata. Sympatric. Taller; large dorsal spots squared or rounded and not coalesced; tip of the tail with a large dark ring.

Distribution Endemic to Africa. The collection-based work of Schlawe (1980) and the review by Yalden *et al.* (1996) restricted the species' range to high plateaux and dry lowlands of Ethiopia, N Somalia, Eritrea, Djibouti and SE Sudan. Records are scarce and patchily distributed: Annesley Bay (Zula–Massawa region, Eritrea), Bulhar (W



Genetta abyssinica

of Berbera, Somalia), Senaar (Sudan), Gondar, Awash and Simien Mountains National Parks, L. Metahara, Mt Albasso (Arsi province), Galu and Addis Ababa (Ethiopia) and Djibouti. The presence of the species was recently confirmed in the Abune Yosef massif, Ethiopia (Diaz Behrens & Van Rompaey 2002). A road-killed specimen from near Awash N. P. deposited in the Zoological Natural History Museum in Addis Ababa University, Ethiopia, initially identified as being this species (Balakrishnan & Bekele 2008) was subsequently shown to be a Common Genet *Genetta genetta* (Gaubert *et al.* 2009a). Künzel *et al.* (2000) stated that the existence of this genet in Djibouti was uncertain, although A. Laurent (pers. comm.) considered the species still present in the country.

Habitat Although the habitat requirements of this species are not well known, it appears to have a wide altitudinal and ecological range, from coastal plains and open dry lowlands to high plateaux (Yalden *et al.* 1996), with altitudes sometimes exceeding 3000 m (e.g. Mt Albasso: 3400 m). Diaz Behrens & Van Rompaey (2002) found evidence for, and directly observed, living specimens in montane heather moorlands and afroalpine grasslands up to 3750 m in the Abune Yosef massif, in the northern Highlands of Ethiopia. This is the first record of Ethiopian Genets in a forested habitat, namely the montane dry forest of Abi Jakula (dominant species include Tree Heath *Erica arborea*, Curry Bush *Hypericum revolutum* and Abyssinian Rose *Rosa abyssinica*). According to Haltenorth & Diller (1980), the Ethiopian Genet is sometimes found near urban areas, but this statement seems at odds with the fact that they are so poorly known.

Abundance The current population status of this species is unknown, but they are evidently rare. Rüppell (1835) found them to be rarer than the Common Genet *Genetta genetta* in Ethiopia, and Yalden *et al.* (1996) considered them 'remarkably uncommon'. Currently known from only a few museum specimens (Diaz Behrens & Van Rompaey [2002] listed 16 specimens).

Adaptations Mainly nocturnal, although Diaz Behrens & Van Rompaey (2002) reported diurnal activity, which they suggested was a response to the activity patterns of rodent prey at high altitudes.

Foraging and Food Little is known, but a comparative examination of scats collected from afroalpine latrines and savanna woodlands has suggested mainly carnivorous tendencies, with rodents (e.g. species of the genera *Arvicanthis* and *Lophuromys*), complemented by birds (passerines), insects (Coleoptera) and seeds. At higher altitudes, with a more impoverished fauna and flora, the relative percentage of insects varied, suggesting opportunistic consumption; likewise, fruits are rare but seeds resembling domestic lentils imply possible foraging in cultivated areas. On the other hand, in low-altitude savanna-woodland areas, scats contained more fruits and insect remains (Diaz Behrens & Van Rompaey 2002).

Social and Reproductive Behaviour Limited observations in the wild suggest a solitary life-style. Latrines are used as in genets inhabiting open habitats. Diaz Behrens & Van Rompaey (2002) indicated that each latrine contained about 30 droppings and was found on rocky edges and in rocky holes. Gotch (1979) suggested that it could be domesticated and was perhaps the original 'cat' of ancient Egypt, but probably confused the Ethiopian Genet with the Common Genet.

Reproduction and Population Structure Unknown, but likely to have similar, small litters as in other genet species. One specimen in captivity apparently lived to nearly 14 years of age (Weigl 2005), though the identity of this specimen is not confirmed.

Predators, Parasites and Diseases Nothing known. Probably susceptible to predation from the same predators as the Common Genet and Large-spotted Genet *G. maculata*. Stiles & Baker (1935) reported tapeworms *Dipylidium gervaisi* in intestines and *Hymenolepis*

liguloides as ectoparasites of the species.

Conservation IUCN Category: Least Concern. CITES: Not listed.

Yalden *et al.* (1996) mentioned habitat loss due to felling and cultivation in *Acacia* woodland and thornbush as a threat, together with pressures of herds of domestic stock in both arid lowlands and high plateaux. A recent niche modelling-based study suggested that the suitable range of the Abyssinian Genet was now highly fragmented by large mosaics of croplands (Papes & Gaubert 2007). In Ethiopia, only three National Parks are likely to support populations of the Ethiopian Genet: Yangudi-Rassa, Awash and Simien Mountains. To date only three Ethiopian Genets have ever been kept in captivity (at Frankfurt zoo from 1949 to 1958, and mentioned in Schreiber *et al.* 1989). After DNA analysis (cytochrome *b*) a specimen previously listed in ISIS and housed at the Miller Park Zoo (USA) proved to belong to the Pardine Genet *G. pardina*.

Measurements

Genetta abyssinica

HB: 408, 430 mm, n = 2

T: 380, 403 mm, n = 2

GLS: 81.3 (76.6–89.6), n = 6

GWS: 41.5 (38.8–46.4), n = 6

Body measurements: Djibouti and Ethiopia (museum specimens: BMNH and MNHN)

Skull measurements: museum specimens (BMNH, FMNH, NHMB, NMNH, SMF)

Haltenorth & Diller (1980) give weight as 1.3–2.0 kg

Key References Diaz Behrens & Van Rompaey 2002; Yalden *et al.* 1996.

Philippe Gaubert

Genetta angolensis MIOMBO GENET

Fr. Genette d'Angola; Ger. Bürstengenette

Genetta angolensis Bocage, 1882. J. Sci. Math. Phys. Nat. Lisboa, ser. 1, 9 (33): 29. Caconda, Angola (13°47' S; 15°08' E).



Miombo Genet *Genetta angolensis*.

Taxonomy The type material of the Miombo Genet, consisting of three adult specimens (one mounted and two stuffed skins) kept in the Lisbon Museum (Museu Bocage), was burned in a fire in

1978. Photographs of these specimens are all that remain. The type locality 'Calucimba' as given by some previous authors is actually the native name of this species, and indeed of all genets, in Angola. The specimens were sent from Caconda to Bocage. The collector, Mr Anchieta, had his headquarters in this town, and most probably all zoological specimens he sent from there were collected on the surroundings of Caconda or brought by natives from nearby.

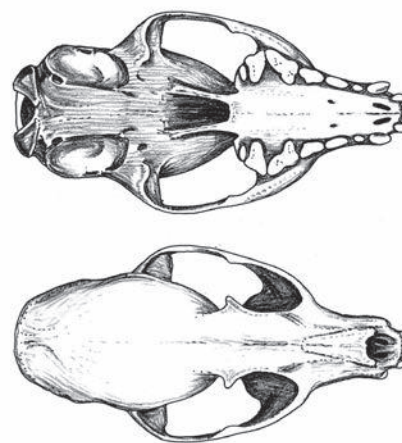
Synonyms: *hintoni*, *mossambica* (but see below). Of the two synonyms, *hintoni* was once regarded as a subspecies of the Common Genet *Genetta genetta* (e.g. Ellerman *et al.* 1953), but is now considered conspecific with *angolensis*. The second supposed synonym, *mossambica*, has been a source of taxonomic confusion. Originally described by Matschie in 1902, Moreau *et al.* (1946) fixed the type locality as 'Mossimboa (11°38' S, P. E. A)' (i.e. Portuguese East Africa, or Northern Mozambique). Later, Roberts (1914, 1951) identified three specimens in the Transvaal Museum collected in

Boror (Mozambique, between Lingungu and Lualua rivers in Zambezia Province) as *G. mossambica*. Crawford-Cabral (1980–81) considered *mossambica* a possible subspecies of *G. angolensis*, in spite of some differences in the skull, a treatment followed by others (e.g. Schlawe 1980, 1981, Wozencraft 1993). However, a study by Crawford-Cabral & Pacheco (1992) found that the specimens from Boror, identified by Roberts as *mossambica*, fell within the phenotypic profile of the large-spotted genet complex, and may constitute a separate species (Crawford-Cabral & Fernandes 2001). Consequently, the specimens from Boror have not been discussed in the present profile, but are provisionally allocated to the large-spotted genet complex (see section on Taxonomy under Large-spotted Genet *G. maculata*). The form described as *gleimi* is here also ascribed to the Large-spotted Genet. Finally, doubts about the validity of the name *mossambica* itself remain because the type specimen of the latter has since been identified as a potential hybrid between Large-spotted Genet and Miombo Genet (Gaubert *et al.* 2005b, c). The phylogenetic position of *G. angolensis* within *Genetta* and the monophyly of the species remain uncertain (Gaubert *et al.* 2004b, Gaubert & Begg 2007). Chromosome number: not known.

Description The Miombo Genet is medium sized, about the size of the Common Genet, but appearing bulkier, with a shorter, bushy tail (ca. 80–90% of HB) and relatively long feet (ca. 19% of HB). Hair very long, at least 30 mm on middle of tail, more than 40 mm on mid-dorsal line and up to 70 mm on rump. There is a great deal of individual variation in ground-colour and markings (stripes and spots), with ground-colour varying from light ochraceous to brownish or greyish tones or even to black. Melanic and half-melanic individuals are rather common (about 20% of the specimens in some museum series). Underparts creamy white to dirty white in non-melanic specimens. Stripes and spots vary from different hues of brown to black, except that the mid-dorsal stripe is always intensely black.

Muzzle black, chest and throat blackish, sub-ocular patch whitish. In parallel, two nuchal stripes run from the nape to the shoulders where they diverge and enlarge towards the elbows (although not so conspicuously marked as in other species). Below them, a pair of thinner stripes and small spots scatter on the shoulders and sides of the neck. Between the nuchal stripes another pair of thinner, parallel stripes runs down the neck and extends along about one-fourth of the mid-dorsal line, where the stripes vanish or break up into a first row of flank spots. A long-haired mid-dorsal stripe extends only over the terminal three-quarters of the mid-dorsum. Usually it is flanked on each side by four rows of oblong to squared spots, elliptically disposed, and, below, by a few small scattered spots. Tail black-tipped, with seven to nine black rings narrower than the intervening white spaces but becoming wider from the middle of the tail to the tip; the intervening white spaces graduate to a brownish tinge on the dorsal mid-line. Forelegs black, with pure white hairs on the upper surface of the extremities (metacarpals) and along a stripe to half-way up the legs. Hindlegs black, with only the upper surface of the extremities (metatarsals) marked with pure white, the black colouration extending to the thighs as a pair of stockings. Two pairs of nipples. In the skull, the caudal entotympanic bone is not ventrally inflated.

Geographic Variation Any geographic variation in this species seems to be obscured by the large amount of individual variation.



Palatal and dorsal views of skull of Miombo Genet *Genetta angolensis*.

Animals from the Angolan Plateau (C Angola) could constitute a nominate form attributable to *angolensis*. Likewise, animals from Shaba (SE DR Congo) and W Zambia (north of the Zambezi R.) could correspond with *hintoni*. However, specimens from Zambia and SE DR Congo do not seem to differ from those from Angola. The population in S and E Tanzania and the extreme north of Mozambique, between the coast and L. Nyasa, could be tentatively regarded as a separate subspecies. However, because of doubts about the validity over the name *mossambica* (Gaubert *et al.* 2005b, c; and see Taxonomy), no name is available for this eastern population.

Similar Species

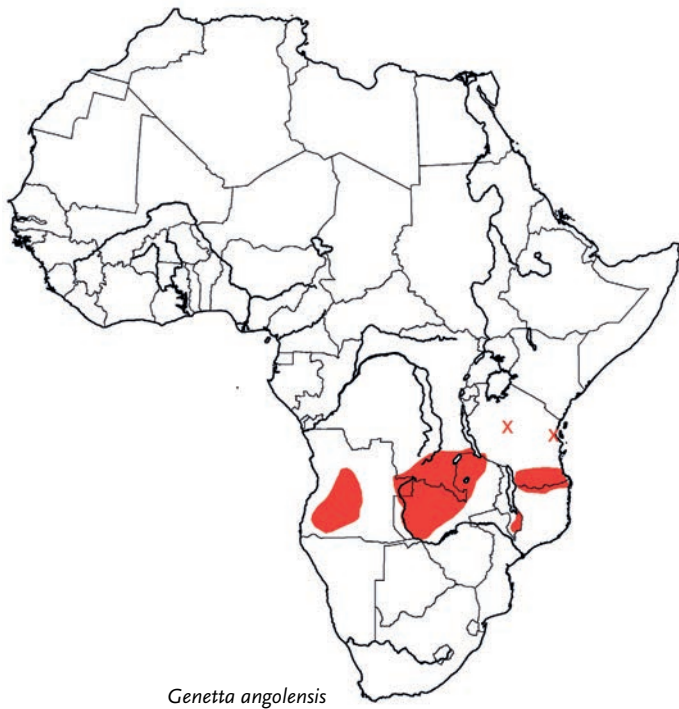
Genetta maculata. Sympatric. Hair much shorter, not exceeding 40 mm on the mid-dorsal stripe (even in *soror* Schwarz, a form characterized by relatively long and soft fur).

G. genetta. Only sympatric over parts of the range; paler ground-colour; smaller spots; longer, white-tipped tail, with a larger number of caudal rings.

Distribution Endemic to Africa. The Miombo Genet is recorded from Angola, DR Congo, N Mozambique, Tanzania and Zambia, and appears to have a disjunct range with two large gaps in its distribution, one in E Angola, the other between the Muchinga Escarpment (Zambia) and L. Malawi. The northernmost record is a skin in the Berlin Museum from 'Turu' (Singida area, C Tanzania) mentioned by Schlawe (1980). This identification was regarded as questionable by Schlawe himself, but has since been confirmed by P. Gaubert (pers. comm.). The species has also been recorded from Mandera, in NE Tanzania (Schlawe 1980), and from the Shire Highlands and Namwara, in S Malawi (Ansell 1985, Ansell & Dowsett 1988). Wozencraft (2005) lists Zimbabwe as a range country, but this cannot be substantiated.

Habitat As the common name suggests, a species of open miombo (*Brachystegia*) woodland interspersed with savannas, mainly from areas with ferrallitic soils and relatively high, but seasonal rainfall (more than 1000 mm per annum).

Abundance Although poorly known, the species was reported to be locally common on an open plain in the Luando Strict N.



R. (C Angola, north of Cuanza R.), characterized by *Cryptosepalum curtisiorum* and termitaria.

Adaptations The dentition, specifically the incisors, appears to show an adaptation for grasping, which suggests a high incidence of arthropods in the diet (Crawford-Cabral 1981b).

Foraging and Food Terrestrial and nocturnal, seen foraging on the ground at night. Stomach contents of a specimen from the Kafue N. P., Zambia, contained remains of grasshoppers, traces of chitinous insect remains, unidentified fruit and some grass (Ansell 1969), which lends support to the suggestion above that arthropods may be a favoured prey.

Social and Reproductive Behaviour There is a paucity of information relating to all aspects of the Miombo Genet's ecology and behaviour. Based on nocturnal observations of these animals, Crawford-Cabral (1967) suggested that they remain hidden during the day in old Aardvark *Orycteropus afer* burrows.

Reproduction and Population Structure No breeding records are currently available.

Predators, Parasites and Diseases Large carnivores and eagle owls are likely predators, and they are probably susceptible to many carnivore parasites and diseases but, currently, none has been specifically identified.

Conservation IUCN Category: Least Concern. CITES: Not listed.

At least as far as Angola is concerned, there are no apparent reasons why this species should be considered threatened. Its habitat has only

seen minor change and there is little hunting. None the less, there remains a need for further study of this poorly known species.

Measurements

Genetta angolensis

HB (♂ ♂): 465, 478 mm, n = 2

HB (♀ ♀): 440, 455 mm, n = 2

T (♂ ♂): 400, 430 mm, n = 2

T (♀ ♀): 380, 390 mm, n = 2

HF c.u. (♂ ♂): 87, 98 mm, n = 2

HF c.u. (♀ ♀): 80, 90 mm, n = 2

E (♂ ♂): 47, 54 mm, n = 2

E (♀ ♀): 51, 58 mm, n = 2

Angola (Hill & Carter 1941)

The type specimen from Caconda, Angola, had HB = 450 mm and T = 360 mm (Bocage 1882)

Skull measurements:

GLS: 89.9 (87.1–93.1) mm, n = 12

GWS: 46.4 (43.3–49.4) mm, n = 12

Angola (Crawford-Cabral 1981b)

GLS: 89.6 (87.6–94.0) mm, n = 8

GWS: 45.4 (42.0–46.5) mm, n = 8

DR Congo (Crawford-Cabral 1981b)

GLS: 90.0 (87.9–92.1) mm, n = 2

GWS: 46.0 (45.2–46.8) mm, n = 2

Liwale, Tanzania (Crawford-Cabral 1981b)

Key References Crawford-Cabral 1980–81, 1981b; Schlawe 1980, 1981.

João Crawford-Cabral



Genets from north Mozambique (as depicted here) and from S and E Tanzania could be tentatively regarded as a separate subspecies.

Genetta burloni BOURLON'S GENET

Fr. Genette de Bourlon; Ger. Bourlon-Genette

Genetta burloni Gaubert, 2003. Mammalia 67 (1): 95. 'GUINEA, Sérédou, Cercle de Macenta'.Bourlon's Genet *Genetta burloni*.*Genetta burloni*

Taxonomy Named in honour of Philippe Bourlon, keeper at the Vincennes Zoo, Paris, who lost his life in the course of his duties. The species belongs to what was commonly referred to as the large-spotted genet 'forest forms' of West Africa (with *poensis*, and the forms *schoutedeni* and *genettoides*; see Pocock 1908, Rosevear 1974, Crawford-Cabral 1980–81, Schlawe 1981 and Gaubert 2003a). Crawford-Cabral (1980–81), on the basis of a craniometrical study, isolated two specimens that he considered as potentially representing a species distinct from both Pardine Genet *G. pardina* and King Genet *G. poensis*. He suggested as a possible name *dubia*, but waited for further comparisons with type material. Gaubert (2003a), in a taxonomic revision of the forest forms based on discrete morphological characters, concluded that specimens attributable to this new species – including the material from Crawford-Cabral (1980–81) – had no available name, and thus erected *burloni*. Described from a complete specimen (skin and skull), its species status was further confirmed by DNA-based phylogenetic investigation (Gaubert *et al.* 2004b), and accepted by Wozencraft (2005). Synonyms none. Chromosome number: not known.

Description Similar to the Pardine Genet, but ground colouration 'dirtier', and spots completely dark and partly coalesced at the rump. Facial mask well marked, with a thin dark vertical line on the muzzle. Sub- and supra-ocular white spots contrasting with the dark muzzle. Ear broad-based and slightly rounded. Pelage relatively short and rough. Ground colouration generally pale yellowish-grey. Throat, chest and ventral pelage whitish-yellow to grey. Nuchal stripes well defined. Mid-dorsal line wide and dark without long crest hairs, beginning after the shoulder. Dorsal spots elongated and squared, completely dark and partly coalesced at the rump. Hindlimbs and

forelimbs dark and well spotted. Upper parts of the forefeet spotted; upper parts of the hindfeet unspotted. Underparts of feet dark. Tail thickly furred but hair relatively short, almost half completely dark, and annulated with five to seven pale rings. Sexes similar in colour and size.

The skull shows very large posterior extension of frontal bones, almost completely overlapping the dorsal region of interorbital constriction, and caudal entotympanic bone inflated.

Geographic Variation None recorded.

Similar Species

Genetta pardina. Sympatric. Dorsal spots not coalesced; tail annulated almost to the tip, which is covered by a large dark ring.

G. johnstoni. Sympatric. Dorsal spots rufous-red and coalesced; tail annulated with pale rings to the tip.

G. poensis. Sympatric. Dorsal spots greatly fused in various parts of body; nuchal stripes not clearly delimited.

Poiana leightoni. Sympatric. Smaller; ears large and rounded; spots smaller and dark, no mid-dorsal line.

Distribution Endemic to Africa. Collection localities suggest a distribution restricted to the Upper Guinean rainforests, including Sierra Leone (Tekea), Liberia (Fisherman Lake, New Camp, Monrovia, Bopulu, Grand Gedeh and Sinoe Counties), Guinea (Sérédou, Zياما Forest, Mt Nimba; also collected from Dieké forest; M. Colyn pers. comm.) and Côte d'Ivoire (Man; purchased specimen; and near Danane cuve) (Gaubert 2003a). A specimen in the Field Museum of

Natural History (FMNH54687), attributable to Bourlon's Genet, was collected from Oda in Ghana in 1946, but the true origin of this animal is in question.

Habitat Collection localities suggest restriction to rainforest (Gaubert 2003a).

Abundance The population status of this species in the wild is unknown. It is known from 29 museum specimens, several having been recovered from bushmeat markets in SE Guinea as recently as 2003.

Remarks There is no information available on the biology of this species. The coalesced spotted coat patterns suggest adaptation to more humid and closed habitats.

Conservation IUCN Category: Near Threatened. CITES: Not listed.

Several of the collecting localities in Guinea are Classified Forests (including Ziama and Diécké), and the species is also recorded from Mt Nimba. A field mission in 2001 in Taï N. P., adjacent to the species' current known range, failed to confirm the presence of the species, although other viverrids were sighted, including the rare Johnston's Genet *Genetta johnstoni* (see Gaubert *et al.* 2002a). Given its likely

restriction to rainforest, it is probably being affected by ongoing habitat loss in the region, although rates of forest loss in Liberia are nowhere near as high as, for example, in neighbouring Côte d'Ivoire (Christie *et al.* 2007). Hunting pressure is also probable, as skins were sighted in the bushmeat market of Man, Côte d'Ivoire (P. Gaubert & C. Crémère pers. obs.). This is a very poorly known species, and is urgently in need of survey work in order to assess the status of this species in the wild.

Measurements

Genetta bourloni

HB: 490, 500 mm, n = 2

T: 400, 420 mm, n = 2

GLS: 96.2 mm

GWS: 49.6 mm

Body measurements: Liberia and Guinea (museum specimens: MNHN, RMNH)

Skull measurements: type specimen, Sérédou, Cercle de Macenta, Guinea (Crawford-Cabral 1980–81, Gaubert 2003a)

Key References Gaubert 2003a.

Philippe Gaubert

Genetta cristata CRESTED GENET

Fr. Genette servaline à crête; Ger. Hauben-Ginsterkatze

Genetta cristata Hayman, in Sanborn 1940. Trans. Zool. Soc. Lond. 24: 686. Okoiyong, Mamfe Division, Cameroons (Nigeria, 05° 45' N, 08° 25' E).



Crested Genet *Genetta cristata*.

Taxonomy Monotypic. Originally described as a subspecies of the Servaline Genet *G. servalina* and recognized as such by Coetzee (1977) and Wozencraft (1993). Considered a distinct species by Rosevear (1974), Crawford-Cabral (1980–81) and Van Rompaey & Colyn (1998) on the basis of pelage characteristics and skull measurements. Studies involving morphology and molecular phylogenetics have confirmed its species status (Gaubert *et al.* 2004b, 2005b, 2006; and see Wozencraft 2005). Rosevear (1974) described *G. bini* from one skin collected from the Ohsu F. R., some 65 km north-west of Benin City, W Nigeria. The skin differs from typical *G. cristata* skins in the absence of a nuchal crest and in the size, shape and number of spots. Schlawe (1981) and Wozencraft (1993) consider it as synonymous with the Large-spotted Genet *G. maculata*. Powell & Van Rompaey (1998) considered it as a junior synonym of *G. cristata* as followed herein and by Gaubert (2003a) and Wozencraft (2005). Synonyms: *bini*. Chromosome number: not known.

Description Small, slender, long-legged genet with an elongated face and silky pelage. Ground-colour somewhat variable from grey over pale to rich ochraceous. Whole underside greyish with irregular, small, randomly spaced spots on the chest and throat; ventral pelage between hindlegs without spots. Hair covering the scrotum dark brown. Thin nuchal crest present composed of short hairs that run in the opposite direction to the surrounding hairs; discontinuous mid-dorsal line, with relatively long hairs, from just behind the shoulders to the base of the tail. Both nuchal crest and mid-dorsal line form an



erectile crest when the animal is excited. Body covered with numerous close-set, dark brown to black spots, which may form longitudinal rows, especially near the spine. Fore- and hindlegs spotted on the inner surface for two-thirds of their length. Fore- and hindfeet dark brown to black; there is often a distinct, pale, greyish patch over the metatarsal region above. Tail long, cylindrical with eight to ten dark rings, about three times as wide as the intervening light-coloured rings, and the tip grey. One pair of nipples. In the skull, the caudal entotympanic bone is ventrally inflated.

Geographic Variation Known to be present on both sides of the Niger R., but no geographic differences are currently known.

Similar Species

Genetta maculata. Sympatric. Spots larger, fewer, symmetrically arranged; black-tipped tail.

G. servalina. It is possible that this species may be sympatric and hybridize in Cameroon, Gabon and Congo (Gaubert *et al.* 2006). No nuchal or mid-dorsal crest.

Nandinia binotata. Sympatric. Heavier; more brownish coloured; two light-coloured shoulder spots; soles of fore- and hindfeet naked to wrist or ankle; tail not distinctly ringed.

Poiana richardsonii. Sympatric in Cameroon only. Smaller, more slender; spots smaller; lighter coloured.

Distribution Endemic to Africa. Confined to the lower Guinean rainforest of Nigeria and Cameroon. This species is recorded as ranging from the Niger R. eastwards probably to the Sanaga R. (Heard & Van Rompaey 1990, Powell 1995, Powell & Van Rompaey 1998). There are records of the species from west of the Niger Delta, including the type of *bini* from Ohosu F. R., and specimens from Odi (C. B. Powell pers. comm.), Tungbo (05° 07' N, 06° 10' E) (Powell & Van Rompaey 1998) and near Patani (05° 13' N, 06° 11' E) (Angelici & Luiselli 2005). Although the region between the Niger Delta and the Cross R. is

heavily populated with many villages interspersed by patches of forests and cultivated land, records do exist: one was recently bought at the roadside near Azumini (04° 57' N, 07° 29' E) (Angelici & Luiselli 2005). Gaubert *et al.* (2006) give records of the species that show it ranging more than 500 km south of the Sanaga R. to S Cameroon, Gabon and N Congo, as well as 180 km west of the type locality of the form *bini* in Nigeria between Oni and Epe (but these are not mapped here).

Habitat Inhabits scrub, low tangled vegetation and bare ground below trees in high deciduous forest. Occasionally, also present in secondary and montane forest up to more than 1000 m above sea level (Sanderson 1940, Heard & Van Rompaey 1990). In the Niger Delta, throughout the heavily forested parts, including the marsh forest zone but not the mangrove zone. In the largely deforested zone east of the Orashi R., there is no recent record but local hunters claimed the species was still present in 1997 (Powell & Van Rompaey 1998). Angelici & Luiselli (2005) found that the presence of Crested Genet was statistically correlated to the presence of primary dry forest and bush-mango plantations inside the forest, and to a lesser extent secondary dry forest, and primary flooded forest, but negatively influenced by the presence of suburban areas, pineapple plantations, bushlands and oil palm plantations.

Abundance In the Niger Delta area the Crested Genet seems common where it occurs (Powell 1995). There is no information on the abundance of the Crested Genet in its distribution area east of the Cross R.

Adaptations Crepuscular, and considered definitely terrestrial by Sanderson (1940), but probably semi-arboreal as most genet species (Heard & Van Rompaey 1990); captive specimens are agile climbers spending most of their time in high places.

Foraging and Food Examination of the stomachs of 11 specimens showed that insect remains were dominant in the diet (51.4%), with mammals accounting for 20%, reptiles 8.6% and vegetable matter 5.7% (Angelici & Luiselli 2005). Two semi-captive young pursued and ate small insects, frogs and lizards, the latter of which were a favourite prey (Heard & Van Rompaey 1990).

Social and Reproductive Behaviour Nothing is known about adult behaviour in the wild. Two young semi-captives groomed each other and slept, explored and hunted together. They defecated in one place and the older one appeared to scent-mark with perineal glands whilst urinating, slowly moving his pelvis from side to side. Both rolled and rubbed themselves in smells and substances to which they were attracted. They were quiet animals and did not vocalize often. Both had at least three easily recognizable vocalizations in addition to a purr and a growl: a long meow; a short squeak; and a combination of a short sneeze/cough/grunt with which they greeted each other after being apart and which they sometimes used to maintain contact when not in sight of each other (Heard & Van Rompaey 1990).

Reproduction and Population Structure One-week-old litters were recorded late Aug and mid-Oct in the Oban area of SE Nigeria (Heard & Van Rompaey 1990). Two embryos in a ♀ collected in Dec in the Niger Delta, Nigeria (C. B. Powell in litt.).

Predators, Parasites and Diseases Unknown, though probably similar to other genets.

Conservation IUCN Category: Vulnerable A2cd. CITES: Not listed.

Field surveys are needed to identify the exact distribution, habitat and conservation requirements of the species, especially since the Cross River State forests are rapidly being converted into farms or wastelands and the Niger Delta is exploited as an oil-production area. Indeed, there currently are no protected areas established in the Niger Delta. The Crested Genet is also believed to suffer from high hunting pressure, and in the Niger Delta (Nigeria) is a target of the bushmeat market (Angelici *et al.* 1999c).

Measurements

Genetta cristata

HB: 540 (495–622) mm, n = 13

T: 431 (431–432) mm, n = 3

E: 86, 95 mm, n = 2

GLS: 94.6 (87.5–99.2) mm, n = 14

GWS: 45.2 (42.7–48.9) mm, n = 14

Throughout range (museum specimens: BMNH, MRAC, SBP and ZMB)

Key References Angelici & Luiselli 2005; Heard & Van Rompaey 1990; Rosevear 1974; Sanderson 1940.

Harry Van Rompaey & Marc Colyn

Genetta genetta COMMON GENET (SMALL-SPOTTED GENET)

Fr. Genette commune; Ger. Ginsterkatze (Gemeinegenette, Kleinfleckgenette)

Genetta genetta (Linnaeus, 1758). Syst. Nat., 10th edn, 1: 45.

Spain [restricted to El Pardo, near Madrid (40° 32' N, 3° 46' W) by Cabrera (1914)].



Common Genet *Genetta genetta*.

Taxonomy High intra-specific variability within this species makes clear distinctions between populations difficult to assess. The main taxonomic groupings usually include genets from: (1) Europe and Maghreb (*genetta*); (2) West to East Africa, south of the Sahara (*senegalensis*); and (3) southern Africa (*felina*) (with *senegalensis* and *felina* sometimes being merged into one population under *felina*). Such groups have either been considered valid species (Roberts 1951, Cabral 1966, Schlawe 1981, Honacki *et al.* 1982) or subspecies (Wenzel & Haltenorth 1972, Rosevear 1974, Coetzee 1977, Crawford-Cabral 1980–81, Meester *et al.* 1986, Wozencraft 1993). In addition, the forms *dongolana* and *neumanni* have sometimes been designated distinct populations from East Africa (Crawford-Cabral 1980–81, Wozencraft 1984, Kingdon 1997). Crawford-Cabral (1980–81) recognized two groups (East + South Africa, and West Africa + Maghreb + Europe) and six subspecies in Africa, but suggested that the Common Genet may

be just one polytypic species. However, Wozencraft (1984) distinguished four separated populations from West Africa, East Africa, southern Africa and around the Mediterranean.

A recent molecular phylogeny suggests that the species is paraphyletic, with a southern African clade attributed to the species *felina* (note that *Genetta felina* is not treated here as distinct, but see Gaubert *et al.* 2004b, 2005c). *Genetta genetta* appears to be the sister taxon of the large-spotted genet clade (Gaubert *et al.* 2004b). In addition, three groups were identified within the restricted *G. genetta* clade: (1) West Africa–southern Africa; (2) Arabian Peninsula; and (3) Europe–Maghreb (populations from East Africa were not sampled) (Gaubert *et al.* 2009b). The species is estimated to have diverged during the middle to late Pliocene (Gaubert & Begg 2007).

Major synonyms: *afra*, *bella*, *dongolana*, *felina*, *grantii*, *hararensis*, *neumanni*, *pulchra*, *senegalensis*, *vulgaris* (see Wozencraft 2005 and Gaubert *et al.* 2005c for complete list). Chromosome number: 2n = 54 (nFa = 92) (Matthey 1964, Gaubert *et al.* 2004a) for specimens from France. A karyotyped specimen published by Wurster & Benirschke (1968) under the name *G. genetta neumanni* with a diploid chromosome number 2n = 52 (nFa = 96) is likely to belong to the Large-spotted Genet *G. maculata* (Gaubert *et al.* 2004a).

Description A medium-sized genet, with long hairs and elongated and coalesced thin dorsal spots merging in longitudinal lines. Facial mask relatively marked, with a thin dark vertical line on the muzzle. Sub- and supra-ocular white spots contrast with the dark muzzle. Pelage relatively long and soft. Ground colouration from whitish-grey to pale yellow-rufous. Throat, chest and ventral pelage whitish or pale yellowish-grey to grey. Nuchal stripes well defined. Mid-dorsal line thin and dark with long erectile crest hairs (up to 75 mm) beginning after the shoulder. Hairs of the scapula with a globular medulla containing no air spaces. Hindlimbs and forelimbs same colour as the ground colouration and spotted. Hindlimbs with

outer side and back covered in dark hairs, this colouration extending onto the underpart of the hindfeet and bordering the toes. Upper part of forefoot and hindfoot lightly spotted. Underpart of forefoot dark. Tail relatively long (ca. 95–97% of HB) with long hairs (up to 60 mm) and annulated with 8–10 pale rings. Margins of the rings often not clearly distinguishable due to the overlapping long guard hairs of the preceding ring. Tip of the tail whitish. In two-month-old individuals, pattern of spots similar to adult but coalesced spots of the back tending to form several longitudinal lines. Two pairs of nipples. Skull is of medium size, with a large sagittal crest and weakly marked interorbital constriction (oligostenomic skull; Crawford-Cabral 1980–81). The caudal entotympanic bone is not ventrally inflated.

Geographic Variation It is sometimes difficult to find discriminative and fixed morphological characters between populations and the following is a tentative list of regional variants that have been judged to be subspecies by a variety of authors.

- G. g. genetta*: SW Europe, Morocco, Algeria, Tunisia and Cyrenaica (Lybia). Hair long; ground colouration ash-grey to pale yellowish-grey; spots of the back thin and black, same colour as mid-dorsal line.
- G. g. grantii*: SW Arabian Peninsula (Saudi Arabia and Yemen), Oman. Hair short; ground colouration pale whitish-grey; spots of the back thin and pale orange-brown, contrasting with the black mid-dorsal line.
- G. g. senegalensis*: West Africa. Hair short; ground colouration off-white (Senegal) to pale whitish-grey and light beige; spots of the back large and spaced-out, a rufous-brown contrasting with the black mid-dorsal line. The extreme pelage pattern and colour variability of specimens from Dahomey Gap to Cameroon make a range restriction to W of Volta R. more sensible.
- G. g. dongolana*: populations from East, north-east and central Africa are tentatively placed under the same subspecies. Hair short; ground colouration pale yellowish-grey; spots of the back large and close-set, a rufous-brown contrasting with the black mid-dorsal line. Similar to the form *neumanni* (Tanzania) on the basis of spot patterns (but see Crawford-Cabral 1980–81).
- G. g. pulchra* (here taken to include *bella*; Crawford-Cabral 1980–81, J. Crawford-Cabral in litt.): southern Africa, north of Orange R. to SW Angola, W Zambia and NE Botswana.
- G. g. felina*: probably a distinct species (Gaubert *et al.* 2004b, 2005b). Southern African coast to Namibia, S Angola and W Zambia. Apparently sympatric with *pulchra* in Namibia, S Angola, W Zambia and NE South Africa (Gauteng) (see Gaubert *et al.* 2005b). Hair long, ground colouration bright ash-grey-white; hindfeet covered by a dark 'sock' and posterior part of forefeet completely dark.

All genets inhabiting regions with Mediterranean climate (Europe, Maghreb and southern coastal zone of South Africa) show a similar pelage pattern and colouration, i.e. long hairs, ash-grey to pale yellowish-grey background pelage and black spots, with a mid-dorsal line of the same colour. Other individuals, distributed throughout sub-Saharan Africa and the Arabian Peninsula (hot and dry climates), exhibit a distinct pelage pattern and colouration: short hairs, pale whitish-grey to light beige background pelage and spots rufous-brown

contrasting with the black mid-dorsal line. This colouration appears to reflect climatic conditions. Melanistic specimens occur throughout the Iberian Peninsula, but seem absent from the native range of the species (Gaubert & Mézan-Muxart 2010).

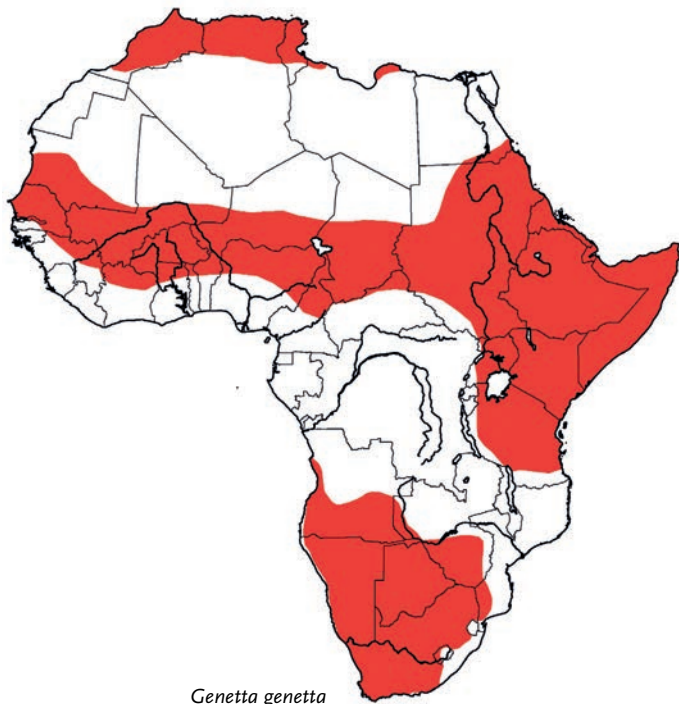
Similar Species

- Genetta thierryi*. Sympatric. Smaller; pelage short; no erectile sagittal crest; dorsal spots and dark rings of the tail rufous-brown; mid-dorsal line split longitudinally by a line of pale hairs.
- G. abyssinica*. Sympatric. Smaller; pelage short; no erectile sagittal crest; mid-dorsal line split longitudinally by a line of pale hairs.
- G. pardina*. Sympatric. Larger; pelage short; no erectile sagittal crest; dorsal spots squared or ovoid, large and not coalesced; tip of the tail black.
- G. maculata*. Sympatric. Pelage short; no erectile sagittal crest; dorsal spots squared or ovoid, larger and not coalesced; tip of the tail black.
- G. angolensis*. Sympatric. Ground colouration usually darker, especially on the legs; spots of the back squared and partially coalesced; tip of the tail black.
- G. tigrina*. Sympatric. Spots of the back squared, large and partially coalesced; tip of the tail black.

Distribution Widespread species, occurring on the northern Saharan fringe (Morocco, Algeria, Tunisia and Lybia), and then in open and dry savanna zones throughout sub-Saharan Africa (extending into parts of Guinea savanna), and drier habitats such as rocky areas, near-desert scrub (reaches Tentane at 19° 49' N, 12° 57' E, Mauritania), and coastal Sahara (Brito *et al.* 2010). Usually absent from rainforests, dense woodlands and woodland–moist savanna mosaics (e.g. miombo woodland in Angola).

In sub-Saharan Africa, the current distribution seems to consist of three large blocks, corresponding roughly to West Africa, East Africa and southern Africa. According to museum collections (Schlawe 1980, P. Gaubert pers. obs.), individuals were regularly collected between the western and eastern ranges (i.e. N Cameroon, S Chad and Sudan), suggesting a continuum between the two populations. The northern limit for both West and East populations ranges between 18 and 22° N. The eastern block has its southern limit reaching approximately 10° S (Schlawe 1980). Both field surveys and museum collections suggest a clear separation between the southern and eastern blocks, with no specimens known from Malawi, N Mozambique and much of Zambia. Populations from the southernmost region are recorded from S Angola and extreme W Zambia, and then southwards throughout Namibia, Botswana and Zimbabwe (except the northernmost and easternmost areas) to the South African coastline. To the east they are replaced by populations of the Large-spotted Genet *G. maculata*, reaching as far as W Lesotho (Lynch 1994), the western parts of the Eastern Cape and NW KwaZulu–Natal in South Africa (Rowe-Rowe 1992a), and SW Mozambique (Smithers & Lobão Tello 1976); they have not been recorded from Swaziland (Monadjem 1998).

Extraliminally, the Common Genet is present in forests and scrublands around the Mediterranean region of SW Europe (Spain, including the Balearic Islands of Mallorca, Ibiza and Cabrera, Portugal, and France, where it is now established in the south-eastern part of the country; Gaubert *et al.* 2008b), and patchily recorded



in the east and north-east European regions (the Alps of France, Switzerland and Italy, NE France, Belgium, the Netherlands and SW Germany; see Léger 1998; Delibes 1999b). Also occurs in hilly and mountainous coastal regions of Arabia, Yemen and Oman (Harrison & Bates 1991). Records of individuals reportedly from Palestine (Tristram 1866) proved to be false (Schlawe 1981, Kock 1983). It has been suggested that this species was introduced as a tamed animal into Spain from the Maghreb and then into S Europe, either through early commercial exchanges (Crawford-Cabral 1980–81, Amigues 1999) or later, at the time of the Moorish invasions. Recent studies have identified North Africa as the geographic source of the European populations, possibly restricted to N Algeria (Gaubert *et al.* 2009b, 2011); Andalusia (S Spain), Catalonia (NE Spain), and the Balearic Is. (Ibiza and Mallorca) were identified as the main ‘hotspots’ of introduction of the species into Europe. Remains found in the South Galala Plateau cave, Egypt, and illustrations on papyrus and in stone relief from the Nile Valley confirm a northern African range before and at the beginning of historical times (Osborn & Osbornova 1998). Known as sub-fossils in the early Pleistocene of Ethiopia and in the late Pleistocene of Barbary (Savage 1978).

Habitat Like other genet species, the Common Genet is usually associated with trees and bushes, but it can also be found in bushy and rocky treeless areas, usually where there is a definite dry season (Kingdon 1977). Its only habitat requirements seem to be available prey and the presence of woody or rocky shelters, and it does not appear to depend on a water supply (Kingdon 1977). The range of the species in Africa suggests that it avoids the most arid zones as well as tropical rainforests.

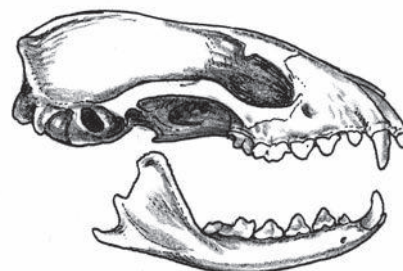
North of the Sahara, in Morocco, the Common Genet is found in *Quercus* spp. and other kinds of forests and in bushy areas, mainly in the mountains (Cabrera 1932; and up to 2700 m in the western High Atlas Mts, Cuzin 2003), but also in rocky ravines, preferably vegetated and in close proximity to water (Panouse 1957) into the

Sahara fringe, where it is common in oases and other productive areas (F. Cuzin pers. comm.). In Algeria it occurs from sea level, where it is found in riparian forests (Delibes *et al.* 1989), up to 2000 m in the Djurjura Mts, where the average annual rainfall reaches 1400 mm; here the species occupies all types of habitats, being most abundant in the old forests of *Quercus ilex* and *Cedrus atlantica* (De Smet & Hamdine 1988).

South of the Sahara, the species occurs in the wooded savannas of the Sahel, Sudan and, locally, the Guinea zones (Happold 1987) where it seems to prefer wooded areas, but also occupies rocks, broken termite mounds and disused dens of jackals and other species (Bigourdan & Prunier 1937). In East Africa it shows a clear preference for areas of high woody cover; in the Ethiopian Highlands, around 3000 m, a female genet showed a distinct preference for woodland (spending 84% of her time there), followed by bush, farmland and grassland (Admasu *et al.* 2004c). In the Serengeti N. P. in Tanzania, the number of genet sightings is significantly correlated with the number of trees and thickets (Waser 1980) and the species is commonly seen on escarpments, rocky outcrops and other hills (Kingdon 1977).

In Botswana, the species has been found in all major vegetation associations and in areas with mean rainfall from less than 200 mm to more than 700 mm; it occurs in the riverine forests of Okavango, the rocky kopjes of E Botswana and the open dry scrub savannas of C and SW Botswana (Smithers 1971). Habitat data were recorded for 100 individuals: 47 were captured in *Acacia* woodland or scrub, including riverine *Acacia*, 16 in Mopane *Colophospermum mopane* woodland or scrub, 12 in *Terminalia*–*Bauhinia* scrub, nine in unspecified riverine forests, nine in open grassland with scattered bushes and trees, and lower numbers in other habitats. In open habitats the species did not occur unless there was some adjacent cover of scrub or isolated patches of trees with underbush; this suggests that scrub cover or woodland is an essential habitat requirement (Smithers 1983). However, the Common Genet penetrates true desert along seasonal water-courses (e.g. Kuiseb and Swakop Rivers in the Namib Desert; C. Stuart & T. Stuart pers. comm.).

Taking a broad west–east transect across the southern African sub-region, the Common Genet is the only genet species occurring in the arid zones of Namibia, is widely distributed in Botswana and W Zimbabwe, but becomes less common eastwards, being replaced by some species of the large-spotted genet group in E Zimbabwe, most of Mozambique as well as KwaZulu–Natal and Swaziland. The Miombo Genet *G. angolensis* broadly replaces the Common Genet throughout the miombo country (J. Crawford-Cabral pers. comm.). This kind of partial replacement also occurs in other parts of Africa (Coetzee 1977, Kingdon 1977, Happold 1987).



Lateral view of skull of Common Genet *Genetta genetta*.

In Europe, the Common Genet is especially abundant in *Quercus* spp. forests, but it is also common in olive groves, *Olea europaea*, riparian copses, ash groves, *Fraxinus* spp. and scrublands, being rare or absent in open areas, marsh and cereal crops (review in Larivière & Calzada 2001). Cold temperatures could restrict the distribution of the Common Genet in C Spain (Virgós *et al.* 2001). In SW Arabia it is said to inhabit dry ravines in hills and mountains (Harrison 1968). The Common Genet is often found in proximity to people and human buildings (e.g. Admasu *et al.* 2004c).

Abundance One of the most common small carnivores, though detailed data on density are scarce. Genets seem to be very abundant in the Djurjura Mts of Algeria, where in 10 days De Smet & Hamdine (1988) captured eight different individuals (seven ♂♂, one ♀) in a few hectares. In Senegal, Sillero-Zubiri & Marino (1997) recorded a night-time frequency of 1.76 per 100 km. In the Kirawira area of Serengeti N. P. a density of 1.5 ± 0.37 individuals per km² was estimated (Waser 1980); previously, Hendrichs (1972) reported densities of about 0.5 individuals per km² in Serengeti N. P. In Europe, density in Doñana N. P., SW Spain, was 0.33 adults per km² and 0.67 animals per km², the latter figure including young individuals (Palomares & Delibes 1994).

Adaptations Long hairs of the black dorsal line and tail, reaching 70 mm or more, can be erected giving the animal an intimidating look; in this situation the enlarged black and white tail is displaced transverse to the antagonist (Gangloff & Ropartz 1972). Three pairs of contrasting white facial spots were thought to help young to orient themselves in relation to their mother (Roeder 1984b).

Sharp and curved semi-retractable claws and some characteristics of the limbs make genets capable of climbing but unable to dig (Taylor 1974, 1976). However, although Common Genets actively climb trees to forage on fruit and roosting birds and to escape predators (Taylor 1970a, Gangloff & Ropartz 1972), most of their activity is on the ground. The usual locomotion is walking and trotting, with the body held very close to the ground surface and the vertebral axis, including the tail, kept horizontal; the shoulders are kept lower than the base of the tail and the centre of gravity for the whole body is very low (Taylor 1970a). They often utilize roads, tracks and dry stream beds when travelling.

Resting places include hollow logs, holes in trees, underbush cover, piles of boulders etc.; in parts of their range, such as Namibia and Botswana, where there are no trees, they use holes in the ground or disused Aardvark *Orycteropus afer* and Southern African Springhare *Pedetes capensis* burrows. They make no attempt to modify holes in the ground to their requirements, nor do they carry in bedding material. Also, in Botswana, they use holes in calcareous cliffs (Smithers 1971), a habit also reported by Delibes (1974) in Spain.

Experimental tests reveal a high level of activity in total darkness, suggesting dependency on senses other than vision (Kavanau & Ramos 1975). However, in Serengeti N. P. they were seen foraging more often in bright moonlight (Waser 1980). One radio-marked lactating ♀ in Omo N. P., Ethiopia, was strictly nocturnal and active throughout the night, its average daily activity reaching 55% of the day (Ikeda *et al.* 1983) and in Botswana the earliest sightings were just after dark, at 19:00h, with records through until 02:00h (Smithers 1971). In Serengeti N. P., Common Genets were observed between

20:00h and 06:00h (n = 11; Hendrichs 1972). In Spain, the highest levels of activity occur after sunset and just before sunrise, the genets being active on average 26% of the 24-hour period (Palomares & Delibes 1994); dial activity coincides with that of the Long-tailed Field Mouse *Apodemus sylvaticus*, the main prey (Palomares & Delibes 2000).

Secretions of sebaceous glands from several regions of the body have a communication role (Roeder 1978a, 1980b, Roeder *et al.* 1989). Especially important are the perineal glands, opening in both sexes in a longitudinally oriented Y-shaped slit between the anus and the genitalia; their blackish secretion has a very persistent musky smell (Skinner & Chimimba 2005). The urine has a pungent smell and is used for marking and under stress.

Foraging and Food The Common Genet feeds mostly on small mammals, but is a generalist feeder that will also eat birds and eggs, reptiles, amphibians, fish, insects, other arthropods, fruits, mushrooms and garbage. It is known to raid poultry. In captivity, its daily energetic requirements were estimated between 150 and 280 Kcal/kg of body weight (Livet & Roeder 1987). The relative length of the intestine might be correlated with a more strictly carnivorous diet than in canids, but less than in felids (M. Delibes pers. obs.).

The main prey in northern parts of North Africa is the Long-tailed Field Mouse, a Palearctic rodent that, as already noted, is also the most common prey in SW Europe (Delibes 1974, Livet & Roeder 1987). However, arthropods reach frequencies of occurrence similar, or even higher, to those of small mammals in faeces collected in Morocco and Algeria, although the ingested biomass of arthropods is low. Birds are consumed as a complementary winter food in Morocco (Delibes *et al.* 1989) and Algeria (Hamdine *et al.* 1993). Reptiles and amphibians were generally scarce in North African genet diet, except during spring in some riverine places of Algeria (Delibes *et al.* 1989). Fruits, including figs, are consumed in the Djurjura region of Algeria (Hamdine *et al.* 1993) and in Moroccan Tafilalet's oasis (F. Cuzin pers. comm.). In Saharan fringes, where the Long-tailed Field Mouse is absent, remains of gerbils *Gerbillus* spp. are found in faeces (F. Cuzin pers. comm.). In East Africa, Waser (1980) observed Common Genets capturing skinks and large locusts and stalking frogs around temporary ponds in Serengeti N. P.; Hendrichs (1972) reported small mammals, reptiles, amphibians, fishes and insects as foods in the same area; in the Ethiopian Highlands genets were occasionally seen foraging in rubbish dumps (Admasu *et al.* 2004c).

In Botswana, Smithers (1971) examined 78 stomachs and found that murids were present in 54%, insects (72%; mainly grasshoppers, beetles, and termites), arachnids (36%; mainly scorpions and hunting spiders), reptiles (18%; snakes, skinks and geckos), birds (6%) and other food items with less frequency. Murid prey in this area included at least ten different species, of which Natal Multimammate Mouse *Mastomys natalensis*, *Mus* spp., Southern African Pouched Mouse *Saccostomus campestris*, Paeba Hairy-footed Gerbil *Gerbillurus paeba*, Common African Fat Mouse *Steatomys pratensis* and *Tatera* spp. had more or less similar importance. In Zimbabwe, an analysis of 29 stomachs (Smithers & Wilson 1979) gave somewhat similar results, although in this case the Natal Multimammate Mouse was the rodent species most frequently consumed. The remains of shrews, normally not palatable to small carnivores, were recovered from stomachs, and in the Botswana sample there was a record of the

Cape Pipistrelle *Pipistrellus capensis*. Wild fruits were represented in both samples, especially raisin bush berries, *Grewia* sp. In the Namib Desert, Stuart (1977) found small mammals in more than 90% of faeces analysed, and insects in about 60% ($n = 125$). Other dietary studies conducted in South Africa (Stuart 1981, Rautenbach 1982) report similar dietary preferences, and Stuart (1981) mentions that a batch of scats collected at De Hoop N. R. in the Western Cape contained the remains of crabs.

Most foraging takes place at night. When locating potential prey, Common Genets move slowly and stalk it in a cat-like fashion, finishing with a sudden pounce or rush (Waser 1980). The rate of prey capture by Common Genets in the East Africa savannas seems to be lower than other more insectivorous small carnivores (Waser 1980). Prey are grabbed with the claws of the forelimbs and bitten at any part of the body, but if they are not killed in a short time, the genet will throw itself on its side and grab the prey with the claws of all four limbs, trying to crush the head and neck with a few bites, in a felid-like fashion (Skinner & Chimimba 2005). Typically, small rodents and other vertebrates are bitten in two or three sections to be swallowed (Delibes 1974).

Social and Reproductive Behaviour Only four of 145 observations in Serengeti N. P. were of pairs separated by less than 100 m; the rest were of solitary individuals (Waser 1980). In SW Ethiopia two ♀♀ (an adult and an immature) foraged solitarily even though their home-ranges did overlap (Ikeda *et al.* 1983); another ♀ radio-tracked in the Ethiopian Highlands was exclusively solitary (Admasu *et al.* 2004c). However, genets in captivity accept the close presence of other individuals.

Communication between different individuals takes place mainly through olfactory and visual marks, but calls are important in the mother–offspring relationships (Livet & Roeder 1987). Olfactory marking by captive genets has been extensively studied (Roeder 1978a, b, 1980a, b, 1983a, b, Roeder *et al.* 1989, Roeder & Thierry 1994). Common Genets use secretions from their perineal glands (mainly ♀♀) and urine (mainly ♂♂), as well as flank and leg rubbing. Anogenital marking behaviour by ♂♂ is higher during the breeding season, while ♀♀ mark more often during the rest of the year. Flank rubbing has been associated with aggressive encounters. Scent-marks allow recognition of individuals and their social and reproductive status. Intimidatory aggressive–defensive behaviour (against conspecifics and potential predators) includes the erection of the long hairs of the tail and the black central dorsal crest, an arch-back stance (like a cat), and explosive hissing accompanied by a head-darting movement towards the antagonist, with the open mouth showing the teeth (Gangloff & Ropartz 1972, Livet & Roeder 1987).

Common Genets defecate in latrines placed on elevated points, mainly on rocks, but also on trees, bird nests, or even on the top of buildings (Roeder 1980b). A large number of faeces (more than 100) can be found in one latrine. Large-sized faeces (on average 15 cm long and 1.4 cm wide; Livet & Roeder 1987) make latrines conspicuous. They have a communicatory function, as faeces are impregnated with the secretion of anal glands. Several individuals use the same latrines, which seem to be more frequent at the border of the home-ranges (Palomares 1993c). Isolated, scattered faeces are also deposited.

Home-ranges are relatively small. In SW Ethiopia, a lactating ♀ radio-tracked during ten weeks used 0.62 km² and an immature ♀ radio-tracked during seven weeks used 0.34 km² (Ikeda *et al.* 1983).

In the Bale Mts, a radio-tracked ♀ used an area of 1.7 km² during 17 months, but its core area (50% of locations) was only 0.2 km² (Admasu *et al.* 2004c). In Serengeti N. P., Waser (1980) estimated through direct observations of marked individuals that ranges were smaller than 0.75 km². In the same area, a well-known individual ranged in about 0.50 km² (Hendrichs 1972). Home-range size seems to be larger in Europe. In S Spain the average size was 7.8 km² (Palomares & Delibes 1994) while in N Spain the home-range of three ♂♂ varied from 2.1 to 10.2 km² (Zuberogoitia *et al.* 2002) and in France an adult ♀ occupied 2 km² (Lodé *et al.* 1991). Some evidence suggests that significant overlaps in home-range occur (e.g. Waser 1980, De Smet & Hamdine 1988). A detailed study on a low-density population in SW Spain indicates that there is large intersexual, but low intrasexual, overlap (Palomares & Delibes 1994). Common Genets in SW Spain moved on average 2.8 km daily and changed their diurnal resting sites, which were placed in dense thickets and hollow trees. The average distance between consecutive diurnal resting sites was 0.73 km (Palomares & Delibes 1994).

Courtship and mating behaviour has been studied on captive animals (Roeder 1979). Between seven and ten days before mating the ♂ increases and the ♀ decreases their ano-urogenital marking activity. At the same time, the ♂ repeatedly sniffs the anogenital region and the flanks of the ♀, emitting a contact call as a repeated coughing. Copulations last two or three minutes and are repeated four or five times during the same night.

Roeder (1984b) and Roeder & Pallaud (1980) studied the ontogenetic development of communicatory and predatory behaviour in captive genets. Young suckle during almost four months, although they begin to consume solid food at the age of 45 days. When 12 weeks old they pursue and try to capture prey and at the age of 18 weeks they have developed all their hunting skills. During the four months of lactation the communication between the mother and the cubs is visual, acoustic and by direct olfactory contact. The use of perineal glands for marking begins very late and seems to mature only when the animals are 19 months old, probably at the time of sexual maturity.

Reproduction and Population Structure In West, East and southern Africa breeding seems to be associated with wet seasons, while it occurs in spring and autumn in the Mediterranean of North Africa and SW Europe (Haltenorth & Diller 1980). One adult ♀ Common Genet was lactating in SW Ethiopia by the end of Nov (Ikeda *et al.* 1983) and Ansell (1960a) recorded a pregnant ♀ in Zambia in Feb. Most gravid ♀♀ were detected in Botswana from Oct to Feb, although the breeding season could be extended through subsequent months (Smithers 1971). Elsewhere in southern Africa, pregnant ♀♀ have been taken in Sep, Oct and Jan (Stuart 1981, Rautenbach 1982).

In Europe, captive and free-living genets can breed almost at any season, but mainly from Apr to Jun and secondarily from Sep to Nov (Delibes 1974, Roeder 1979, Aymerich 1982). Male genets have no clear seasonal testicular activity (Souloumiac & Audy 1979) and ♀♀ can become receptive again if they lose kittens, having two or even three litters in a year (Rosevear 1974, Livet & Roeder 1987). However, there are no reports of free-living ♀♀ successfully breeding twice a year.

Females reach sexual maturity when two years old (Krapp & Delibes 1993). Gestation period is 10–11 weeks (Roeder 1979).

Litters have been found in hollow trees, and the burrows of other animals, in Africa (e.g. Stevenson-Hamilton 1947, Shortridge 1934, Smithers 1971) as well as in Europe (Delibes 1974). Litter-size is 1–4, with a mode of 2 (Livet & Roeder 1987, Krapp & Delibes 1993). Average litter-size in southern Africa was 2.6 ($n = 11$) and two out of the 11 gravid ♀♀ carried four fetuses with implantation 2R : 2L (Smithers 1983). Young at birth are covered with hair, have closed ears and eyes, and weigh 60–85 g (Roeder 1979). They grow slowly: about 300 g when one month old, 450 g at two months, 900 g at four months and 1500 g at eight months (hand-reared young by M. Delibes). Captives have lived to more than 20 years (Jones 1982, Weigl 2005).

There is a paucity of data on population structure and dynamics. In Europe, sex ratio at birth is about 1 : 1 (26 ♂♂ and 24 ♀♀ in 22 litters), but more adult ♂♂ than ♀♀ (1.35 : 1, $n = 648$) were captured (Krapp & Delibes 1993). A sample of individuals measured in Botswana suggested that ♂♂ were captured three times as frequently as ♀♀ (Smithers 1971).

Predators, Parasites and Diseases Servals *Leptailurus serval*, Caracals *Caracal caracal*, Leopards *Panthera pardus*, Ratels *Mellivora capensis* and large owls have been quoted as predators of the Common Genet in Africa (Haltenorth & Diller 1980). Caro & Stoner (2003) have suggested that genets should be vulnerable to inter-specific killing by a large number of other African carnivores.

Common Genets have been recorded as parasitized by the ticks *Haemaphysalis (Rhiphystoma) moreli*, *H. silacea*, *H. spinulosa*, *H. zumpti*, *Amblyomma hebraeum* and *Ixodes pilosus* in sub-Saharan Africa (Camicas *et al.* 1972, Horak *et al.* 1987, 2000) and a flea *Ctenocephalides felis damarensis* in S Angola (Ribeiro 1974). At least three species of hookworms (nematodes, helminths), *Ancylostoma tubaeforme*, *A. genettae* and *A. braziliense*, have been recorded in Somalia (Macchioni 1995, Iori & Lanfranchi 1996), as has *A. caninum* in South Africa and Senegal (quoted in Macchioni 1995). In Africa and Europe, a substantial number of other parasitic helminths and various ticks, fleas and lice have been found on Common Genets (reviewed in Larivière & Calzada 2001). Admasu *et al.* (2004c) emphasize that the ability of genets to live close to humans and their domestic animals could have implications for the transmissions of disease at the domestic–wildlife interface.

Conservation IUCN Category: Least Concern. CITES: Not listed.

Common Genets have a wide distribution on the African continent and extraliminally, have a very broad habitat tolerance, and are present in numerous protected areas. They are occasionally eaten by people in some localities, and the skin and body parts are used for medicinal and decorative purposes while skins may be used for the manufacture of karosses in southern Africa. In Djibouti, Künzel *et al.* (2000) reported genets being for sale in Djibouti city and Ali Sabieh.

Measurements

Genetta genetta

TL (♂♂): 953 (860–1050) mm, $n = 42$
 TL (♀♀): 936 (890–1024) mm, $n = 12$
 T (♂♂): 464 (430–516) mm, $n = 42$
 T (♀♀): 459 (417–516) mm, $n = 12$
 HF s.u. (♂♂): 90 (82–97) mm, $n = 37$
 HF s.u. (♀♀): 88 (83–92) mm, $n = 11$
 E (♂♂): 54 (50–60) mm, $n = 35$
 E (♀♀): 55 (51–65) mm, $n = 12$
 WT (♂♂): 2.0 (1.8–2.3) kg, $n = 20$
 WT (♀♀): 1.8 (1.5–2.2) kg, $n = 10$
 Botswana (Smithers 1971)

HB (♂♂): 490 (465–520) mm, $n = 5$
 HB (♀♀): 480 (465–490) mm, $n = 4$
 T (♂♂): 458 (420–490) mm, $n = 5$
 T (♀♀): 462 (400–485) mm, $n = 4$
 HF c.u. (♂♂): 89 (85–93) mm, $n = 5$
 HF c.u. (♀♀): 86 (84–88) mm, $n = 4$
 E (♂♂): 48 (44–50) mm, $n = 5$
 E (♀♀): 45 (42–50) mm, $n = 4$
 WT (♂♂): 1.9 (1.6–2.3) kg, $n = 5$
 WT (♀♀): 1.6 (1.4–1.7) kg, $n = 4$
 GLS (♂♂): 90.0 (87.0–92.0) mm, $n = 4$
 GLS (♀♀): 84.0, 87.0 mm, $n = 2$
 GWS (♂♂): 45.3 (44.0–46.0) mm, $n = 4$
 GWS (♀♀): 43.0, 44.0 mm, $n = 2$
 Ethiopia (museum specimens: MNHN)

Note: In Zimbabwe, Smithers & Wilson (1979) recorded average weight of ♂♂ as 1.8 kg (range 1.6–2.6, $n = 16$) and ♀♀ 1.9 kg (range 1.5–2.3, $n = 13$); Stuart (1981) recorded average weights of 1.9 kg for ♂♂ (range 1.5–2.5, $n = 19$) and 1.8 kg for ♀♀ (range 1.4–2.0, $n = 11$) in the former Cape Province, South Africa

Key References Crawford-Cabral 1980–81; Gangloff & Ropartz 1972; Larivière & Calzada 2001; Livet & Roeder 1987; Palomares & Delibes 1994; Smithers 1971; Waser 1980.

Miguel Delibes & Philippe Gaubert



G. g. felina (right) is considered a distinct species by Gaubert *et al.* (2004b, 2005b).

Genetta johnstoni JOHNSTON'S GENET

Fr. Genette de Johnston; Ger. Liberiagenette.

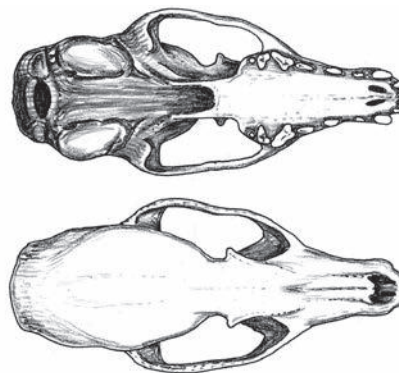
Genetta johnstoni Pocock, 1908. Proc. Zool. Soc. Lond. 1907: 1041 [1908].

'in a district from 15–20 miles west of the Putu Mountains, which lie west of the Duobe and Cavally Rivers', Liberia.

Johnston's Genet *Genetta johnstoni*.

Taxonomy Monotypic. Named by Pocock in honour of Sir Harry Johnston, the artist, explorer and collector who did much work in Liberia. Original description from a headless skin purchased from local Liberian hunters. Though originally described as a new species, both Pocock (1908) and Allen & Coolidge (1930) suggested it only represented a subspecies of the Pardine Genet *G. pardina*. The subgenus *Paragenetta* was erected by Kuhn (1960), and an early phylogenetic analysis by Gaubert *et al.* (2002b) suggested exclusion of this species from the *Genetta* clade. More recent molecular evidence (mitochondrial and nuclear DNA) supports the inclusion of this species with the other genets (Gaubert & Veron 2003, Gaubert *et al.* 2004b, c). The species is estimated to have diverged from other basal rainforest genets during the middle Pliocene (Gaubert & Begg 2007). Synonyms: *lehmanni* (described on the basis of a skull without skin). Chromosome number: $2n = 50$ (Gaubert *et al.* 2004a).

Description A slender genet with a thick, soft coat and elongated face. Sexes similar in colour and size. Face characteristic of the genus, with a dark mask from muzzle to lips, contrasted by a pair of supra- and subocular white spots. Muzzle and forehead generally darker than other genets. Upper labial spots reduced. Large eyes contrasting with thin muzzle. Pupil vertical. Relatively elongated ears. Ground colouration from ochre-yellow to yellowish-grey. Chest and ventral pelage varies from yellowish-grey to buff. Nuchal stripes often fused. Full dark continuous mid-dorsal line strongly contrasting with the surrounding blackish to rufous-brown spots. Dorsal crest with longer hairs sometimes apparent. Large dorsal spots generally aligned in three rows. The first two rows of spots often coalesce into complete or partial lines, especially at the rump. Spots of the flank, thigh and shoulder smaller and dark. Hairs of the scapula with a very large cortex and a globular medulla containing many air spaces. Hindlimbs and forelimbs dark-brownish. Tail densely furred, and

Palatal and dorsal views of skull of Johnston's Genet *Genetta johnstoni*.

annulated with 8–9 pale rings to the tip. Dark rings broaden from the proximal part of the tail. In subadults coat densely spotted and pattern very irregular, but mid-dorsal line clearly marked. Perineal glands developed in both sexes (length: 30–40 mm; width: 15–20 mm), with tripartite structure like other genets. One pair of nipples.

Skull elongated and narrow, with flattening of the mandible and dentition weak.

Geographic Variation None recorded.

Similar Species

Genetta pardina. Sympatric. Larger and more heavily built; broader muzzle; first rows of spots not coalesced; tip of the tail with a large dark ring.

G. poensis. Sympatric. Dorsal spots greatly fused in various parts of body; nuchal stripes not clearly delimited.

G. bournoni. Sympatric. Dorsal spots partly coalesced at the rump; nuchal stripes clearly delimited.

Poiana leightoni. Sympatric. Smaller; ears large and rounded; spots smaller and dark, no mid-dorsal line.

Distribution Endemic to Africa. The range of this species is poorly known due to cryptic and nocturnal habits and a paucity of field studies (23 specimens in collection), but it is largely restricted to the forests of the Upper Guinea rainforest block in West Africa, having been sighted and collected in Liberia (Harbel, Putu Mts, Cavally R., Kpeaple, Bo, Tappita, forest south of Freemantown, Sapo N. P.), Guinea (Kolenté Plates, Macenta, Ziama Forest, Mt Nimba), Côte d'Ivoire (Yalé, Mt Nimba, Tai N. P.) and Ghana (Tarkwa) (see Gaubert *et al.* 2002a). There are no confirmed records from Sierra Leone, but they probably do occur.

Habitat Inhabits dense rainforest. In Tai N. P., frequently observed in wetland areas including swamp forest (poor drainage areas dominated by prop-root trees and raffia palms) and riverine habitat (A. E. Dunham pers. obs.). A specimen collected in a region of moist woodlands and



Genetta johnstoni

savanna (Kolenté Plates, Guinea) makes its restriction to rainforest questionable (Gaubert *et al.* 2002a), and indeed an ecological niche modelling study by Papes & Gaubert (2007) found that Johnston's Genet has a larger potential geographical range than other rainforest genets from West Africa.

Abundance Little is known about the abundance of this species. However, frequent sightings in Taï N. P. near the Centre de Recherche en Ecologie Tropicale (CRET) Station suggest it may be locally abundant, at least in protected areas of suitable habitat (also suggested by museum collections for Ziamia F. R. and Mount Nimba Biosphere Reserve; P. Gaubert pers. obs.).

Adaptations The densely spotted and dark general colouration (especially on the limbs) is characteristic of forest genets, providing camouflage against the uneven patterning of light in a forest environment. The constriction of the zygomatic arch, flattening of the mandible, reduction of the jugal teeth and inflection of the angles of upper and lower incisors suggest adaptation to an insectivorous diet (Kuhn 1960; and see Rosevear 1974, Crawford-Cabral 1981, and Lamotte & Tranier 1983).

Foraging and Food No information, but probably insectivorous as suggested by dentition.

Social and Reproductive Behaviour Radio-tracking data of two individuals and frequent nocturnal sightings in Taï N. P. suggest that this species is mainly solitary and nocturnal. Pairs are occasionally sighted. During the day, it sleeps in tree holes or on large branches in the canopy. Over a period of one month, a radio-collared ♀ returned before dawn each day to sleep in the canopy of a single tree (approximately 20 m high). A radio-collared ♂ was observed sleeping in different trees each night over a period of several weeks (A. E. Dunham pers. obs.). Males are possibly non-

territorial or have larger ranges. Additional information concerning the social or reproductive behaviour of Johnston's Genet is lacking.

Reproduction and Population Structure An adult ♀ caught in late Jul from Taï N. P. showed signs of having recently finished lactating (healing bite marks and hair loss around teats but no milk produced). Assuming a typical lactation period of six months, her young may have been born in Jan or Feb, corresponding with the end of the dry season. Juvenile genets have been observed in Taï N. P. in early Jun; however, species identity was equivocal. Although it is unknown if breeding is seasonal in this species, the timing of reproduction in similar species (Common Genet *G. genetta* and Cape Genet *G. tigrina*) coincides with the wet season, presumably linked with a peak in insect abundance (Taylor 1969). The number of young has not been recorded, although the presence of only two teats suggests that a litter-size greater than two is unlikely.

Predators, Parasites and Diseases Crowned Eagles *Stephanoaetus coronatus* have been reported to prey upon Johnston's Genet in Taï N. P. (Shultz 2002) and may be an important predator throughout their range. Johnston's Genets sleep in the canopy during the day, which may make them particularly vulnerable to other large aerial predators. Remains of viverrids have also been found in scats of Leopards *Panthera pardus* within the range of this species (Jenny 1996).

Adult ticks (*Haemaphysalis moreli*), common parasites on civets and genets in tropical rainforests, were found on specimens from Taï N. P., together with a less specialized species, *Ixodes cumulatimpunctatus* (J.-L. Camicas pers. comm.). Diseases afflicting Johnston's Genet have not been recorded.

Conservation IUCN Category: Vulnerable A2cd. CITES: Not listed.

Johnston's Genet is considered a rare species with a restricted area of occurrence. Because of the lack of field surveys and the cryptic nature of this animal, it is unclear whether this species is common within its limited range or habitat. Intensive deforestation resulting from agriculture, logging and mining pressures has reduced the once continuous forest stretch of the Upper Guinean forest zone to a few remaining blocks of intact forest. Severe hunting pressures may also be affecting populations of Johnston's Genet. Animals are taken by commercial and local hunters for the sale of both meat and skins. In Man, Côte d'Ivoire, skins are used for making purses (P. Gaubert & C. Crémère pers. obs.). Skins of Johnston's Genet (together with Pardine Genet) can also be used for traditional ceremonies (associated with masked dancers at funeral celebrations in Gouléako Dioula, Côte d'Ivoire; A. E. Dunham pers. obs.). Hunting of genets is intense even within protected areas, including Mt Nimba (Lamotte 1998), Ziamia Forest (Wilson 1992) and Taï N. P. (Hoppe-Dominik 1990, 1997). Ecological data and field surveys are needed to determine which habitats are occupied by this species and whether secondary growth and moist woodland areas provide suitable habitat.

Measurements

Genetta johnstoni

HB (♂): 514 mm, n = 1

HB (♀ ♀): 470, 481 mm, n = 2

T (♂): 492 mm, n = 1

T (♀ ♀): 462, 495 mm, n = 2
 HF c.u. (♂): 85 mm, n = 1
 HF c.u. (♀ ♀): 90, 90 mm, n = 2
 E (♂): 38 mm, n = 1
 E (♀ ♀): 45, 46 mm, n = 2
 WT (♂): 1.9 kg, n = 1
 WT (♀ ♀): 2.2, 2.6 kg, n = 2
 GLS: 95.8 (94.0–100) mm, n = 5*

GWS: 43.1 (41.0–44.2) mm, n = 5*
 Body measurements: Côte d'Ivoire (museum specimens: MNHN)
 Skull measurements: Liberia (Kuhn 1960)

Key References Gaubert *et al.* 2002a, 2004a, b.

Amy E. Dunham & Philippe Gaubert

Genetta maculata LARGE-SPOTTED GENET (BLOTCHED GENET)

Fr. Genette commune à grandes taches (Genette à taches rousses); Ger. Gemeine Grossfleckgenette (Rostfleckgenette)

Genetta maculata (Gray, 1830). Spicil. Zool. 2: 9. 'in Africa Boreali' [changed to '6 km from Hirna (Harrar Road, 2180 m), Ethiopia' by Gaubert *et al.* 2003a] (see Taxonomy for type locality).

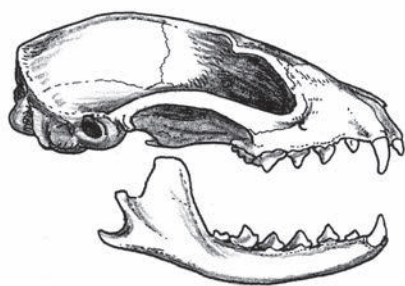


Large-spotted Genet *Genetta maculata*.

Taxonomy First described from a living specimen kept at the Tower of London Menagerie, the type specimen seems absent from any current collection. Schwarz (1930) modified the type locality to 'interior of Senegal', but without argument or justification (Rosevear 1974, Schlawe 1981). Another name used to designate the species over the past 20 years has been *rubiginosa*, but Schlawe (1981) and Crawford-Cabral & Pacheco (1992) have shown that this name is invalid. In order to maintain consistency and introduce stability in the use of species names, Gaubert *et al.* (2003a, b) erected a neotype for *G. maculata*, thus fixing its type locality to a non-ambiguous location. This suggestion is in accordance with Article 75.5 (Replacement of unidentifiable name-bearing type by a neotype) of the International Code of Zoological Nomenclature (1999). The proposed neotype is a female specimen (skull and tanned skin), collected 6 km from Hirna (Harrar road, 2180 m), Ethiopia, on 20 March 1971, during the third 'Mission en Ethiopie' conducted by J. Dorst. It is deposited and catalogued at the Muséum National d'Histoire Naturelle of Paris (MNHN – CG 1972-395). Nevertheless, a recent statement of ICZN (2007) ruled that the specific name *maculata* Gray, 1830 should not be conserved.

There has been considerable debate about the taxonomic delimitations within the large-spotted genet complex (see Gaubert 2003a, Gaubert *et al.* 2003a, b, 2004a, b, 2005b, c, Fernandes & Crawford-Cabral 2004, Grubb 2004b, and Wozencraft 2005 for discussion). Suffice it to say that analyses of discrete morphological characters and skull morphometrics have provided strong evidence for establishing species-level boundaries between *G. maculata* and the Cape and Pardine Genets, *G. tigrina* and *G. pardina*, of South and West Africa respectively (Crawford-Cabral 1980–81, Schlawe 1981, Crawford-Cabral & Pacheco 1992, Gaubert *et al.* 2001). Even so, *G. maculata* appears to constitute a super-species comprising several valid species (Crawford-Cabral 1980–81, Crawford-Cabral & Pacheco 1992, Crawford-Cabral & Fernandes 1999, 2001), including the form *letabae* from south-east Africa (see Gaubert *et al.* 2004a, 2005c), but further studies are required to clarify the structure of *G. maculata* populations before taxonomic conclusions can be drawn. The lineage leading to the clade grouping *G. maculata* and *G. tigrina* is estimated to have diverged in the middle Pleistocene (Gaubert & Begg 2007).

Proposed synonyms: *aequatorialis*, *albiventris*, *deorum*, *erlangeri*, *fieldiana*, *gleimi*, *insularis*, *letabae*, *matschiei*, *mossambica*, *pumila*,



Lateral view of skull of Large-spotted Genet *Genetta maculata*.

schraderi, *soror*, *stuhmanni*, *suahelica*, *zambesiana*, *zuluensis*. Chromosome number: $2n = 52$ ($FN = 96$) (specimen from Ethiopia; Gaubert *et al.* 2004a).

Description A slender genet. Sexes similar in colour and size. Facial mask well marked, with a thin dark vertical line on the muzzle. Sub- and supra-ocular white spots contrasting with the dark muzzle. Pelage relatively short and soft. Ground colouration extremely variable: sandy-grey, pale yellow, rufous-grey and grey-yellow. Throat, chest and ventral pelage whitish-grey to pale yellowish. Nuchal stripes well defined. Mid-dorsal line same colour as spots, and begins after the shoulder. No erectile dorsal crest (hair short). Spots or blotches black to rufous-brown and very variable in shape and size, some specimens having two colourations (mid-dorsal spots rufous-brown and spots of the flanks black). Spots of the first two dorsal rows rounded to squared, and sometimes coalesced at the rump. Hair of the scapula with air spaces interspersed within the globular medulla. Hindlimbs and forelimbs of similar ground colouration and well spotted. Posterior region of hindlimbs densely covered in dark hairs, this colouration extending to the under part of the hindfeet and bordering the toes but much less markedly than in the Common Genet *G. genetta*. Upper parts of forefeet and hindfeet lightly spotted. Under parts of forefeet same as ground colouration. Tail relatively short (ca. 80–90% of HB) with short hair, and distinctly annulated with seven to nine pale rings. Elongated dark tip caused by a suffusion of one or two of the last pale rings with dark hairs. In juveniles, coat densely spotted and general pattern very irregular. Two pairs of nipples.

The skull is of medium size, with a thin sagittal crest and a narrow interorbital constriction. The caudal entotympanic bone is not ventrally inflated. The lingual cusp on P^3 tends to be reduced, but is more marked than in the Cape Genet.

Geographic Variation The extreme variability of size, coat patterns and colouration, within specimens from the same region and sometimes, possibly, from the same litter (e.g. Kingdon 1977), confuses attempts to determine valid subspecies on the basis of morphological considerations. However, the craniometrical work of Crawford-Cabral & Fernandes (2001) proposes at least three distinct taxa in southern Africa:

G. m. letabae: NE Namibia, SW Zambia, South Africa. Differs from *zambesiana* by its larger size and larger dorsal spots (J. Crawford-Cabral pers. comm.). This form was considered a distinct species

following the morphometric and DNA study of Gaubert *et al.* (2005b).

G. m. zambesiana: Mozambique, Malawi, Zimbabwe and Angola. Matschie (1902) described *zambesiana* as being characterized by nine small and narrow spots in the first dorsal row.

G. m. 'mossambica': misuse of subspecies name (see *G. angolensis* profile). Mozambique (Boror). Narrow spots, dark tonalities. Probably relatable to *zambesiana*.

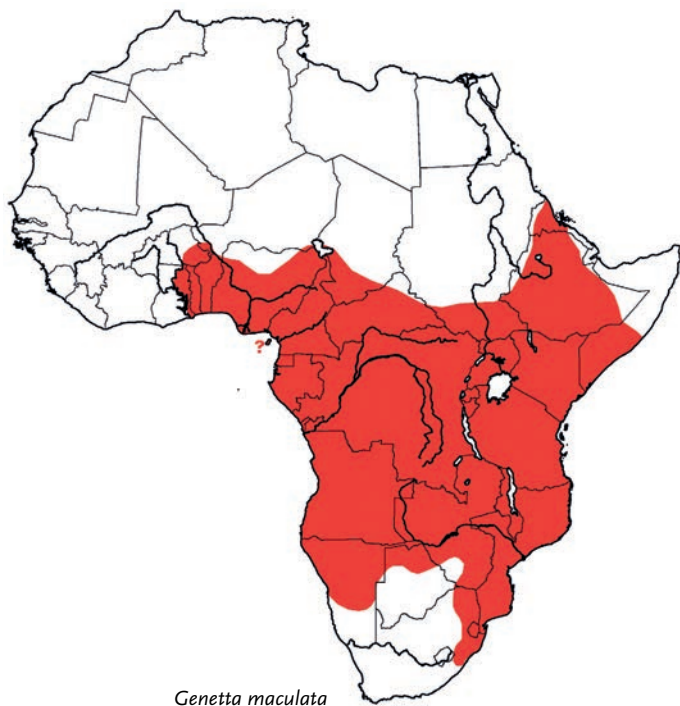
Distinctions amongst East African forms (e.g. *stuhmanni*, *schraderi*, *aequatorialis*, *matschiei*, *pumila*, *deorum*) rely on the colouration of the hindlegs, the number of spots in the first and second rows and the relative breadth of the second caudal ring (J. Crawford-Cabral pers. comm.), thus making the discrimination of clear morphological entities very subjective. Melanistic specimens regularly occur in central and East Africa (e.g. DR Congo, Kenya, Burundi, Tanzania).

Similar Species

- Genetta thierryi*. Sympatric. Smaller; dark rings of the tail rufous-brown, mid-dorsal line split longitudinally by a line of pale hairs.
- G. abyssinica*. Sympatric. Smaller; mid-dorsal line split longitudinally by a line of pale hairs, first rows of mid-dorsal spots fused in stripes.
- G. servalina* and *G. cristata*. Sympatric. Back and flank densely spotted, regular annulation with bright rings to the tip.
- G. victoriae*. Sympatric. Larger; mid-dorsal line only suggested by a median row of spots, back and flank densely spotted.
- G. genetta*. Sympatric. Pelage longer, mid-dorsal line with long erectile hairs; dorsal spots narrow and mainly coalesced; tip of the tail whitish.
- G. pardina*. Occurs west of Volta R., but eastern range limit unknown. Larger. Dorsal spots large and not coalesced.
- G. poensis*. Sympatric. Dorsal spots greatly fused in various parts of body; nuchal stripes not clearly delimited.
- G. angolensis*. Sympatric. Pelage longer, mid-dorsal line with long erectile hairs; feet very dark.
- G. tigrina*. Narrow hybrid zone in KwaZulu–Natal in South Africa (Gaubert *et al.* 2005b). Mid-dorsal line with longer hairs and always dark; mid-dorsal spots large and not coalesced.

Distribution Endemic to Africa. Ranges from north and east of the Volta R. east to the wet regions of Eritrea and Somalia (presence uncertain in Djibouti). The exact northern limits of their range are poorly known, but they reach the Sudanian–Sahelian savannas (Zakouma N. P., Chad; R. Cornette pers. comm.) and L. Chad. Ranges southwards to C Namibia and KwaZulu–Natal (see Gaubert *et al.* 2005c). Possibly present on Bioko I.

Habitat A ubiquitous genet, which can be found in miscellaneous habitats such as rainforest (but usually in open corridors and secondary growth), swamp zones, riverine vegetation, open and closed woodlands, moist forests, savanna–forest mosaics, thickets and even grassy savanna (Smithers 1971, Kingdon 1977, Yalden *et al.* 1996). The Large-spotted Genet avoids extremely dry savanna and truly arid regions, preferring habitats close to water, whereas the Common Genet inhabits drier habitats (Rautenbach & Nel 1978). Opportunistic and commonly occurs in cultivated areas, farmlands and suburban areas (Kingdon 1997, Angelici *et al.* 1999a,



b). Sightings of this species in undisturbed dense rainforest could be due to misidentifications of other genet species, although specimens clearly attributable to this species have been trapped both in primary and secondary rainforests in Nigeria (Angelici *et al.* 1999a, b). According to Nigerian hunters, the best places to capture this species are mixed and mosaic habitats, i.e. the ecotone between rainforest and open fields or between rainforest and cultivated lands (F. M. Angelici pers. comm.). A recent ecological study found that the presence of this species in Nigeria is positively correlated with 'derived savanna', 'oil palm plantations' and other altered habitats, whereas it is negatively correlated with various types of forests (Angelici & Luiselli 2005). The species can often be seen foraging in open habitats, but always near a forested place. Can live at relatively high altitudinal ranges, for example, to 3400 m in the Simien Mts, Ethiopia (Yalden *et al.* 1996), Kilimanjaro, Tanzania (Grimshaw *et al.* 1995), and Mt Kenya (more than 3300 m – BMNH specimen; Young & Evans 1993).

Abundance Relatively common. In Swaziland, this is the most common nocturnal carnivore and occurs at higher densities in protected areas (4.5/km²) than on private ranches (0.3/km²) (Monadjem 1998). May evade observation partly because of its nocturnal and elusive habits. Census techniques greatly influence the frequency of sightings as does habitat and the time of night or year in which observations are attempted. In Bayelsa State, SE Nigeria, where this species is present, sightings are not common (only three contacts for 67 nights of transect survey using spotlights) (F. M. Angelici & L. Luiselli pers. obs.). However, it is rather common in bushmeat markets and frequently trapped by local hunters (Angelici *et al.* 1999b, c).

Adaptations This species is both terrestrial and arboreal. Duckworth (1995) reported that 36 of 41 animals seen in Nechisar N. P. in Ethiopia were on the ground, but they are accomplished

climbers and may regularly be seen climbing amongst clumps of foliage to hide or taking shelter in the forks of branches (Smithers 1971, Kingdon 1977).

This species is predominantly nocturnal, resting up during the day in trees, hollow logs, under tree roots, in disused burrows of Aardvark *Orycteropus afer* or springhares *Pedetes* spp., under piles of boulders, rock overhangs, caves, as well as man-made shelters (e.g. roofs of houses, stacked hay bales). Resting sites are re-used by both sexes. In the Rift Valley, Kenya, and Omo N. P., Ethiopia, genets were recorded to be more active between sunset and midnight than during the day (Ikeda *et al.* 1982, Fuller *et al.* 1990).

A low basal metabolic rate and a high thermal conductance may allow the reduction of heat storage when resting in burrows during the day (Henneman & Konecny 1980). This species shows an unusual occurrence in the urine, namely the presence of sulphocysteine, a sulphur amino-acid derived from the conversion of excessive amounts of sulphite (which is an important intermediary compound in the metabolic pathway from sulphur amino acids to inorganic sulphate), but the adaptive value of this peculiarity is unknown (Crawhall & Segal 1965). Anal sacs contain two complexes of sebaceous glands involved in a steroidogenic function (Kayanja & Schliemann 1981). As with the Pardine Genet, distinctively coloured forest forms might be morphotypes adapted to rainforest.

Foraging and Food The Large-spotted Genet is an active and versatile predator, foraging both in trees and on the ground; they are solitary, foraging mainly by night and occasionally during bright moonlight (Waser 1980). Prey are caught by careful stalking followed by a final pounce and are bitten several times, and sometimes shaken, before being killed (Happold 1987, Skinner & Chimimba 2005). It is mainly carnivorous although vegetable matter is often present in the diet. In some parts of its range, fruits, seeds and berries can be an important source of food. The animal prey spectrum includes terrestrial and aquatic gastropods, bivalves, centipedes and millipedes, spiders, scorpions, insects, crustaceans, fish, amphibians, reptiles (including lizards and snakes), small birds and eggs, and mammals up to the size of a hare. Extrapolating from its low basal



Large-spotted Genet *Genetta maculata*.

metabolic rate, Henneman & Konecny (1980) proposed that it could be less carnivorous than previously suggested.

It seems that the Large-spotted Genet, like the widespread Common Genet, is able to adapt its diet to prey availability, rodents generally constituting the main source of energy. For example, in a sample of 136 stomachs from Zimbabwe, from all seasons, murids had a 68% occurrence (with multimammate mice *Mastomys* spp. the primary prey), followed by insects (40%), birds (15%), arachnids (9%), reptiles (8%), wild fruits (8%), shrews (3%), centipedes (3%), amphibians (2%), lagomorphs (1%) and fish (1%) (Smithers & Wilson 1979). On the other hand, in Botswana, insects predominated (90% occurrence), followed by murids (47%, with the Pouched Mouse *Saccostomus campestris* the most frequent prey), arachnids (27%), wild fruits (17%), centipedes (10%), birds (7%) and reptiles, amphibians and other arthropods (1% each) (Smithers 1971). In both samples, insects were represented mainly by Coleoptera, Orthoptera and Isoptera; Lepidoptera and Hymenoptera (Formicidae) were present in few numbers in Zimbabwe. The prevalence of insects in the Botswana sample could indicate a bias against murids, as a high proportion of the sample was taken at the end of a four-year drought, when murid numbers were low (Skinner & Chimimba 2005).

According to studies in the Shimba Hills in coastal Kenya, the Large-spotted Genet can be rather frugivorous and plays a considerable role in seed dispersal (Engel 1998b, 2000). In 515 defaecations collected from two genet latrines over a period of 31 months, seeds and other fruit remains had a relative occurrence of 74% versus 82% for arthropods and 44% for other food remains (i.e. small mammals, reptiles, birds, snails, leaves). In this area the genets fed on fruits of more than 40 species, many of which were common and shared with the African Civet *Civettictis civetta* and other frugivores; comparative diet analyses indicated niche overlap as well as specific niche separation (Engel 2000).

Males have been reported to kill poultry with greater frequency than ♀♀ and have been supposed to become addicted to this kind of foraging (Carpenter 1970). In Zimbabwe, five of 11 identified birds from stomach contents were domestic fowls (pheasants, young peafowl, pigeons and chickens) (Smithers & Wilson 1979). There is little to suggest that they take carrion, although Rautenbach (1982) recorded the presence of carrion and maggots in stomachs from South Africa. Carpenter (1970) reported two cases in KwaZulu–Natal where genets captured bats (genera *Eptesicus*, *Scotophilus* and *Rhinolophus*) at a fairly high frequency (about six individuals per night). These observations confirmed data of Azzaroli & Simonetta (1966), who found two bats (genus *Tadarida*) in the stomach of a specimen from Somalia, and Rautenbach (1982), who recorded the Cape Pipistrelle *Pipistrellus capensis* in one stomach. Lack (1977) reported a case of unidentified genets feeding on tree nectar in Ghana.

Recently, Angelici & Luiselli (2005) examined 56 stomachs from SE Nigeria. Among small mammals, the following species were recorded: Tullberg's Soft-furred Mouse *Praomys tullbergi*, *Cricetomys* sp. (juv.), West African Pygmy Mouse *Mus musculoides*, Spotted Grass-mouse *Lemniscomys striatus*, Peters's Striped Forest Mouse *Hybomys univittatus*, *Dendromus* sp., Nigerian Shrew *Crocidura nigeriae*, Fraser's Musk Shrew *Crocidura poensis* and *Crocidura* sp. Among insects, Orthoptera were recorded from 11 stomachs and Coleoptera from eight, while other food items included birds and bird eggs, reptiles, fruits and seeds, other insects, centipedes and spiders. Analysis of

biomass contributions indicated that the young giant rats (*Cricetomys* sp.) were the most important prey type, and Tullberg's Soft-furred Mouse was the second most important prey type. In other forest habitats in Nigeria, genets were supposed to be mainly carnivorous, feeding on small vertebrates, and possibly also on eggs, invertebrates and fruits (Happold 1987).

Angelici (2000) calculated food niche overlap values between different species in Nigeria and these indicated that the diet of the Large-spotted Genet was most similar to that of the African Civet, with approximately 70% of the diet in common. A multivariate statistical model on diet composition suggested that the highest potential for inter-specific competition should have concerned this species and the Egyptian Mongoose *Herpestes ichneumon*. Yet, despite obvious niche separation, figures showed that the Large-spotted Genet and the Marsh Mongoose *Atilax paludinosus* had about 61% of their diet in common in Nigerian rainforests. Angelici & Luiselli (2005) indicate that Large-spotted Genets and Crested Genets *Genetta cristata* are grossly similar in terms of dietary preferences, and simulation analyses suggest that competition for food should be relatively high, because about three-quarters of the quantitative diets of the two species were identical. However, the similarity between species is proportionally less evident when biomass is considered. Moreover, it is noteworthy that both species are differently influenced by various environmental factors. This result seems clearly to suggest that, whereas the Large-spotted Genet prefers altered or secondary habitats, the Crested Genet inhabits preferentially primary dry forests, bush-mango plantations and other forest types.

In KwaZulu–Natal this species also has strong spatial niche overlap with both the Marsh Mongoose and Slender Mongoose *Herpestes sanguineus* (Maddock & Perrin 1993). None the less, its nocturnal way of life and use of the vertical dimension probably enables this genet to avoid competition with mongooses.

Social and Reproductive Behaviour It is not clear whether this species is territorial (see Rosevear 1974, Estes 1991), but it seems that ♂♂ defend ranges that overlap those of several ♀♀ (Estes 1991). Carpenter (1970) reported genets using regular latrine sites in KwaZulu–Natal, which was confirmed by Engel (1998a) from Kenya. Furthermore, some ground latrines are shared between genets, civets and some mongoose species (Engel 2000). Females released 35 km away from capture sites returned home within a few days (Carpenter 1970). These data indicate probable territoriality, at least in ♀♀, as in the Common Genet. Males may wander within ranges as large as 500 ha (Carpenter 1970), whereas ♀♀ seem more territorial, with ranges nearing 25 ha. In a radio-tracking study carried out in the Rift Valley, Kenya, five genets were reported to range over areas from 100 to 1000 ha (mean values: ♂♂ 590 ha; ♀♀ 280 ha). Home-ranges overlapped between sexes (Fuller *et al.* 1990). Territories are marked with secretions from the perineal glands, urine and faeces (which include secretions from the anal glands). Tree scratching possibly also plays a role in marking.

Although primarily solitary, pairs are seen during the breeding season. Males, after having sniffed the vulva of the ♀, urinate and/or deposit musk, and exhibit a facial grimace. This facial attitude is provoked by the sensitivity of the vomeronasal organ of the ♂ to the pheromones produced by the ♀. A courting ♂ follows the ♀ closely, and produces grumbling and couching calls. At the beginning, the ♀

keeps turning away from the ♂, tail and hindquarters low, and flees. However, she may eventually answer the male's calls and allow him to come into close contact. Once in contact, both partners sniff their faces and genitalia, and rub their cheeks. The ♀ holds the tail up, and, as a mating signal, crouches with raised hindquarters and tail deflected sideways. The ♂ clasps the ♀ on the groin area with chest and belly resting on her lower back, and intromission occurs with pelvic thrusting as the ♀ curves her spine. The ♂ may sometimes bite the neck of the ♀ during the final seconds of the copulation, which usually lasts five minutes. Coupling pairs often meow. At the end of the copulation, the ♀ may anal-drag and roll on her back, and both partners lick their genitals (Dücker 1965). Births take place in hollow trees, nests of leaves and even under roofs in urbanized habitats (Estes 1991, Skinner & Chimimba 2005).

Reproduction and Population Structure Two breeding peaks have been reported from Kenya, the main peak between Oct and Dec, and a second peak between Mar and May (Taylor 1969). In coastal Kenya, Engel (1998b) trapped a genet and witnessed the birth of one kitten before late Dec at the beginning of the dry season. In South Africa, Pienaar (1964) reported a litter of three young in Feb from Kruger N. P., Rautenbach (1982) recorded two gravid ♀♀ in Nov, both with three fetuses (2L : 1R), and Rowe-Rowe (1971) estimated births to occur between Aug and Mar in KwaZulu-Natal. Elsewhere in southern Africa, there are records of three kittens (two weeks old) found in a hollow tree in N Namibia in Oct (Shortridge 1934), births from Aug to Feb in Zimbabwe and a single ♀ lactating during Feb in Botswana (Smithers 1971); juveniles estimated to be four weeks old were taken in Oct and Nov in Zambia (Ansell 1960a). These data suggest that the breeding season extends from Aug to Mar in southern Africa (Skinner & Chimimba 2005); pregnant ♀♀ from the northern part of the southern African sub-region were caught carrying 2–5 fetuses (average 2.9; n = 10) (Skinner & Chimimba 2005).

The time of gestation is recorded to last 70–77 days (Taylor 1969, Happold 1987, Estes 1991). Neonates are blind but already covered with hair so the coat pattern is readily discernible (Happold 1987). Eyes open at ten days and canines erupt at four weeks. They are shed after the permanent canines have erupted just prior to attainment of asymptotic mass at 11 months (Rowe-Rowe 1971). The mother licks her kittens anogenitally, and consumes their excrements (Estes 1991). Young genets begin to take solid food at about six weeks. Rowe-Rowe (1971) reported that a captive individual started killing prey and eating live vertebrates at about 28 weeks. Longevity is up to ten years (Mitchell 1911, Flower 1931, Anonymous 1960, Depierre & Vivien 1992).

Predators, Parasites and Diseases Predators are likely to include both terrestrial (e.g. large cats, large canids, Spotted Hyenas *Crocuta crocuta*) and aerial (eagles, eagle-owls) species. Miscellaneous parasites may affect the species, including: *Dirofilaria genettæ* (in connective tissue), *Ascaris* sp., *Linguatulidae* sp., *Ctenophalides conversus* and *C. craterus* (external parts of the body) and *Dipylidium gervaisi* (intestines) (Stiles & Baker 1935).

Conservation IUCN Category: Least Concern. CITES: Not listed.

Although it is possible that genets may be undergoing some localized declines in a few areas, they have a wide distribution range,

occur in a variety of habitats and are present in many protected areas on the continent. They are hunted and trapped for bushmeat; in a large study area comprising four regions of SE Nigeria, 22 specimens were found in markets or in the possession of local hunters during a period of 213 days (Angelici 2000). Since genets do have a bad reputation as poultry thieves, farmers sometimes poison or trap this species (e.g. in southern Africa; see Stuart 1990) and they are also occasionally killed by domestic cats and dogs.

Measurements

Genetta maculata

HB (♂♂): 486 (443–521) mm, n = 18
 HB (♀♀): 453 (411–499) mm, n = 16
 T (♂♂): 442 (414–505) mm, n = 15
 T (♀♀): 439 (420–509) mm, n = 14
 HF c.u. (♂♂): 88 (83–92) mm, n = 17
 HF c.u. (♀♀): 87 (81–90) mm, n = 16
 E (♂♂): 46 (42–50) mm, n = 18
 E (♀♀): 47 (42–50) mm, n = 16
 WT (♂♂): 1.9 (1.6–2.3) kg, n = 16
 WT (♀♀): 1.7 (1.3–2.0) kg, n = 13
 Nigeria (F.M. Angelici & B. Egbide pers. obs.)

TL (♂♂): 939 (845–1020) mm, n = 32
 TL (♀♀): 916 (865–1010) mm, n = 28
 T (♂♂): 451 (415–530) mm, n = 32
 T (♀♀): 454 (395–495) mm, n = 28
 HF s.u. (♂♂): 86 (81–90) mm, n = 32
 HF s.u. (♀♀): 84 (80–89) mm, n = 28
 E (♂♂): 45 (41–50) mm, n = 32
 E (♀♀): 44 (41–48) mm, n = 27
 WT (♂♂): 1.8 (1.4–2.3) kg, n = 28
 WT (♀♀): 1.7 (1.5–2.0) kg, n = 28
 Zimbabwe (Smithers & Wilson 1979)

TL (♂♂): 1043 (970–1080) mm, n = 7
 TL (♀♀): 1035 (1005–1060) mm, n = 7
 T (♂♂): 512 (475–535) mm, n = 7
 T (♀♀): 513 (475–540) mm, n = 7
 HF s.u. (♂♂): 92 (87–98) mm, n = 7
 HF s.u. (♀♀): 91 (85–93) mm, n = 7
 E (♂♂): 50 (47–51) mm, n = 7
 E (♀♀): 55 (51–65) mm, n = 7
 WT (♂♂): 2.1 (1.7–3.2) kg, n = 7
 WT (♀♀): 2.0 (1.5–2.5) kg, n = 7
 Botswana (Smithers 1971)

Skull measurements:

GLS: 88.9 (85.5–91.0) mm, n = 3
 GWS: 46.3 (45.2–47.8) mm, n = 3
 Mozambique (Crawford-Cabral 1973)

Key References Angelici 2000; Angelici & Luiselli 2005; Gaubert *et al.* 2003; Rowe-Rowe 1971; Skinner & Chimimba 2005.

Francesco Maria Angelici & Philippe Gaubert

Genetta pardina PARDINE GENET (WEST AFRICAN LARGE-SPOTTED GENET)

Fr. Genette pardine (Genette à grandes taches d'Afrique de l'Ouest); Ger. Westafrikanische (Grossfleckgenette)

Genetta pardina I. Geoffroy Saint-Hilaire, 1832. Mag. de Zool. I. Mammifères 1832–1838: Cl. I, pl. 8. 'intérieur du Sénégal'.Pardine Genet *Genetta pardina*.

Taxonomy Described from a living female specimen at the Ménagerie du Jardin des Plantes, Paris. The species has long been considered synonymous with other large-spotted genets (*G. maculata*, *G. tigrina*) and continues to be so regarded by a number of authors. However, following comprehensive morphological and molecular studies, this species is here recognized as a distinct species (Crawford-Cabral 1980–81, Gaubert 2003a, Gaubert *et al.* 2004a, b). The forest 'forms' *poensis*, *schoutedeni* and the recently described *bourloni* constitute a distinct clade not directly related to *pardina* (see Gaubert 2003a, Gaubert *et al.* 2004b, 2005c, Wozencraft 2005). The form '*schoutedeni*' (provisional name) was considered a distinct species by Gaubert (2003a) and Gaubert *et al.* (2004b) and is characterized by dorsal spots not fused, feet bright, tail distinctly annulated, and skull with caudal entotympanic bone extremely inflated. The taxonomic and geographic status of this form is still in need of further investigation, and is not treated here. The Pardine Genet lineage is estimated to have diverged during the Early to Middle Pleistocene (Gaubert & Begg 2007). The specific epithet is the diminutive of the Latin *pardus* (leopard). Synonyms: *amer*, *dubia*, *pantherina*. The series of specimens representing *genettoides* Temminck, 1853, may represent hybrids between *G. pardina* and Large-spotted Genet *G. maculata* (Gaubert 2003a) and the name is probably best considered *incertae sedis*. Chromosome number: $2n = 52$ (Couturier & Dutrillaux 1986). Specimen karyotyped under the name *G. maculata*, but proved to belong to *G. pardina* after DNA analysis (see Gaubert *et al.* 2004a, b).

Description A heavily built genet. Sexes similar in colour and size. Facial mask well marked, with a thin dark vertical line on the muzzle. Sub- and supra-ocular white spots contrasting with the dark

muzzle. Ear broad-based and slightly rounded. Pelage relatively short and rough. Ground colouration from yellowish-grey (Guinea) to pale or sandy-grey (Senegal, Côte d'Ivoire). Throat, chest and ventral pelage whitish-yellow to grey. Nuchal stripes well defined. Mid-dorsal line wide and dark without long crest hairs, beginning after the shoulder. Dorsal spots elongated and squared, either dark brown or brown-rufous, not coalesced and bordered by a dark ring. First two rows form a line of separated spots. Width of spots equal to the mid-dorsal line. Hindlimbs and forelimbs same colour as the ground colouration and well spotted. Upper parts of the forefeet spotted; upper parts of the hindfeet unspotted. Underparts of feet dark-brown. Tail shorter than the other genets (ca. 70–80% of HB), thickly furred but hair relatively short, and annulated with 6–7 pale rings. Tip of tail with an elongated dark ring caused by the reduction of the last pale ring (7th or 8th). Hairs of the scapula with a globular medulla containing no air spaces. In juveniles of six months, pattern of spots similar to adult but spots of the flank, thigh and shoulder smaller and darker. Two pairs of nipples. The skull is large, with thin sagittal crest and caudal entotympanic bone ventrally inflated.

Geographic Variation None recorded.

Similar Species

- Genetta johnstoni*. Sympatric. Smaller; dorsal spots rufous-red and coalesced; tail annulated with pale rings to the tip.
- G. thierryi*. Sympatric. Smaller and paler; dorsal spots and dark rings of the tail rufous-brown, mid-dorsal line split longitudinally by a line of pale hairs.
- G. genetta*. Sympatric. Longer hair especially on the dorsal crest and tail; dorsal spots thinner and partially merged into lines; tuft of the tail whitish.
- G. poensis*. Sympatric. Dorsal spots greatly fused in various parts of body; tail half part dark; nuchal stripes not clearly delimited.
- G. bourloni*. Sympatric. Dorsal spots partly coalesced at the rump; almost half of the tail completely dark.
- Poiana leightoni*. Sympatric. Smaller; ears large and rounded; spots smaller and dark, no mid-dorsal line.

Distribution Endemic to Africa, with a continuous range in the West African Sudanian and Guinean zones from Senegal to Ghana. The eastern boundary is uncertain. Crawford-Cabral (1980–81) suggested the Volta R. as a possible barrier to the species; however, further studies are needed in the Dahomey Gap region in order to define its eastern range limits and to determine possibilities of overlap or hybridization with the Large-spotted Genet.

Habitat Occurring in a wide range of habitats, but generally restricted to moist, closed habitats such as primary and secondary rainforests, gallery forests and moist woodlands. Also occurs in forest plantations, bush-lands and suburban areas (Coe 1975, Hoppe-



Dominik 1990, Sillero-Zubiri & Marino 1997). Rosevear (1974) suggested that the species could be present in drier open woodlands.

Abundance Thought to be common within its range, but status unknown (Hoppe-Dominik 1990, Grubb *et al.* 1998). Night-time field surveys carried out from a vehicle in Niokolo-Koba N. P. (Senegal) led to an estimated frequency of occurrence of 0.70/100 km (Sillero-Zubiri & Marino 1997). However, the nocturnal and discrete habits of this species might result in artificially low count estimates.

Adaptations Ground colouration seems to depend on habitat (yellow-rufous in forest and moist woodland, and greyer and paler in open woodland and savanna), possibly resulting in crypsis in different environments.

Foraging and Food Diet thought to be similar to that of the Common Genet *G. genetta*, but includes more invertebrate prey and fruit (Sillero-Zubiri & Marino 1997, Grubb *et al.* 1998). Rodents are suspected to be the main staple. A specimen collected in Adopodioumé, Côte d'Ivoire, had its stomach filled with remains of *Lophuromys* sp. (Brush Furred Mice), insects, palm fruits and grass (Rahm 1961). Several individuals were seen regularly lapping the nectar of a savanna tree *Maranthes polyandra* in Mole N. P., Ghana, possibly transferring pollen (Lack 1977) (however, species identity is uncertain because records are from a possible contact zone with the similar Large-spotted Genet; see Gaubert 2003a).

Social and Reproductive Behaviour The Pardine Genet is solitary and nocturnal. As a forest and woodland species, presumed to live mostly in trees (Jones 1966). However, no field

observations or morphological investigations have yet supported this supposition. Rosevear (1974) supposed that it more frequently makes use of rock crevices for shelter and breeding than do the high-forest genets like Johnston's Genet *G. johnstoni* or Servaline Genet *G. servalina*. Additional information is lacking.

Reproduction and Population Structure Poorly known. Two one-month-old juveniles were found in the Lamto region, Côte d'Ivoire, in Apr and one subadult ♂ in Jun (Bourlière *et al.* 1974). Another subadult specimen deposited at the Muséum National d'Histoire Naturelle of Paris (CG 1911-838), originated from Côte d'Ivoire and was collected in Jul (its age was estimated at 5–6 months). Thus, a birth period or peak ranging from about Jan to Mar is possible. Maximum longevity recorded in captivity nears 10 years (Mitchell 1911, Flower 1931, Anonymous 1960).

Predators, Parasites and Diseases Probably susceptible to predation from aerial raptors and larger carnivores. Sambon (1922) recorded *Armillifer armillatus* (Linguatulidae) as a parasite of the species. Ixodid ticks (*Haemaphysalis rugosa*) specializing on Viverridae were found on specimens from moist woodlands of Senegal (Camicas 1978). Adult ticks (*Haemaphysalis moreli*), chiefly hosted by civets and genets, were found in W Côte d'Ivoire and E Senegal (Camicas *et al.* 1972).

Conservation IUCN Category: Least Concern. CITES: Not listed.

Assumed to be common within its limited range, and at least present in several protected areas. Bourlière *et al.* (1974) noted that skins were often seen in the surrounding villages of the Lamto region, Côte d'Ivoire. This statement can be broadened to all the West African bushmeat markets. Coe (1975) reported great pressure on the species by local hunters (Mano tribe, Liberia).

Measurements

Genetta pardina

HB (♂ ♂): 538 (410–553) mm, n = 7

HB (♀ ♀): 557 (410–530) mm, n = 6

T (♂ ♂): 446 (390–490) mm, n = 7

T (♀ ♀): 436 (420–450) mm, n = 6

HF c.u. (♂ ♂): 95 (90–100) mm, n = 7

HF c.u. (♀ ♀): 91 (88–95) mm, n = 4

E (♂ ♂): 43 (39–47) mm, n = 7

E (♀ ♀): 44 (40–45) mm, n = 4

GLS (♂ ♂): 98.3 (95.9–101.4) mm, n = 7

GLS (♀ ♀): 96.1 (91.5–97.4) mm, n = 6

GWS (♂ ♂): 50.3 (48.8–51.6) mm, n = 6

GWS (♀ ♀): 48.5 (45.9–49.8) mm, n = 6

Guinea-Bissau (Crawford-Cabral 1973)

Haltenorth & Diller (1980) give body weight up to 3.1 kg

Key References Crawford-Cabral 1980–81; Rosevear 1974.

Philippe Gaubert & Amy E. Dunham

Genetta piscivora AQUATIC GENET

Fr. Genette aquatique; Ger. Wasserschleichkatze

Genetta piscivora (J. A. Allen, 1919). J. Mammal. 1: 25. 'Niapu, Belgian Congo' [DR Congo, Niapu, 2° 25' N, 26° 28' E)].Aquatic Genet *Genetta piscivora*.

Taxonomy Monotypic species. First named (in the genus *Osbornictis*) for H. F. Osborn, president of the American Museum of Natural History; *piscivora* contains the Latin words *piscis* for fish and *vorare* for 'to devour'. Long included in *Osbornictis* (e.g. Van Rompaey 1988, Wozencraft 1993); Hunt (2001) even included it in a subfamily separate from *Genetta*. Gaubert *et al.* (2004c) suggested that *Osbornictis* and *Genetta* are congeneric, in agreement with Verheyen (1962) and Stains (1983), and this classification was adopted by Wozencraft (2005). Estimated to have diverged in the middle Pliocene from a series of basal, rainforest genets (Gaubert & Begg 2007). Synonyms: none. Chromosome number: not known.

Description Dark rufous, unspotted genet with black, bushy tail. Head pale brown with reddish tinge; two yellowish to white spots on the forehead; front and sides of the muzzle and cheeks white. Eyes large. Rhinarium small, without a median sulcus. Vibrissae white, long, downwardly pointing. Ears exteriorly blackish, naked interiorly. Pelage long and dense. General colour uniform dark chestnut brown; underparts slightly lighter. Greyish underfur dense. Fore- and hindlimbs dull brown; upper surface of feet brownish-black. Feet small; sole of forefoot naked, and sole of hindfoot with distinct metatarsal pads (Gaubert *et al.* 2001, 2002b). Tail black and bushy with long (45–50 mm) black hairs and brownish-grey underfur (25–30 mm). The young are slightly darker.

Compared with the sympatric Giant Genet *Genetta victoriae* the dentition is generally frailer, there is a greater diastema between the premolars (which have high trenchant central cusps) and the molars are more reduced. Also shorter extension of the premaxillae in front of the canines, palatal breadth 10% narrower and abbreviated rostrum. The lingual cusp in the upper third premolar is absent.

Geographic Variation None recorded.

Similar Species

Atilax paludinosus. Larger, overall dark brown to blackish. The Aquatic

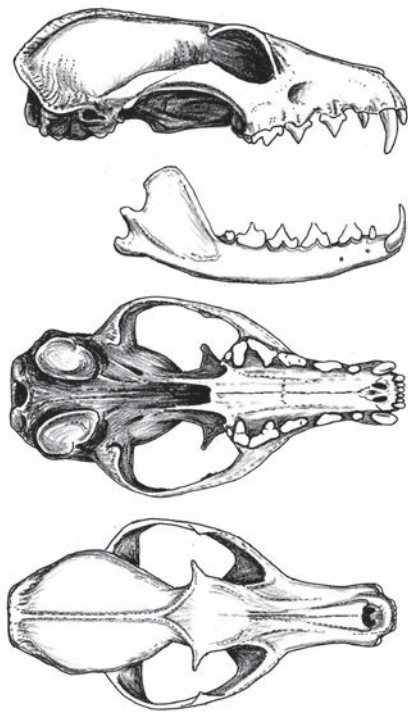
*Genetta piscivora*

Genet's typical colour and facial marking distinguish it clearly from sympatric *Genetta* species (including *G. maculata*, *G. servalina*, *G. victoriae*), which are characterized by having a spotted coat and ringed tail.

Distribution Endemic to DR Congo, from the right bank of the Congo R. eastward to the Rift Valley. Kingdon (1977) speculated that it might occur in W Uganda, and Verschuren (1978) cites an unlikely observation from Burundi (near Kigwena), but thus far no specimens have been collected outside DR Congo.

Habitat Occurs in shallow headwaters of streams, preferably clear and flowing over red clay and sand, as well as small brooks; seasonally limited to pools in rainforests between 460 and 1500 m. The species is discontinuously distributed within its range and most specimens were collected in forests dominated by Limbali (*Gilbertiodendron*) trees (Colyn & Gevaerts 1986). Nearly all specimens were obtained from local hunters who caught them with snares usually put out on trails near small rivers (Van Rompaey 1988).

Abundance Considered among the rarest of African carnivores, and known only from around 30 museum specimens. Both the Bambuti pygmies and neighbouring Bantu agriculturists consider the species to be very rare; in 53 hunts in the Ituri Forest only two individuals (or 1.8% of all carnivores) were captured (Hart & Timm 1978). According to hunters near Katshungu village it is not rare in the region north of Lugulu R. (Verheyen 1962) and also not rare between the Tshopo and Congo Rivers (Colyn & Gevaerts 1986).



Lateral, palatal and dorsal views of skull of Aquatic Genet *Genetta piscivora*.

Adaptations Crepuscular and nocturnal. Sharp narrow carnassial teeth are clearly adapted to deal with slippery vertebrate prey such as fish. Among viverrids olfactory bulbs range in volume from about 3 to 6% of total brain volume with a mean of 4.7%; they form only 3.5% for the Aquatic Genet. Relatively small olfactory bulbs seem to point to a relatively poor sense of smell, expected in a piscivorous species (Radinsky 1975a). Rests in fallen hollow trunks and riverside debris. Can climb sloping trunks up to a couple of metres but without a genet's climbing ability (A. Root pers. comm.). Small, naked feet and bushy tail do not seem adapted for actually swimming in the water but more for prowling around at the margins (W. Duckworth pers. comm.). As such, while able to swim, they do not do so readily and would not be required to do so in the shallow streams they favour (A. Root pers. comm.). The long vibrissae serve to attract insect-eating fish when touching the surface of the water.

Foraging and Food Piscivorous. Small pools or slowly flowing brooks are approached with an extremely slow, gliding stalk. The Aquatic Genet moves slowly along the edge alternately patting the surface (the wrist is bent back almost to the vertical and the surface struck with a downward pivoting action), and testing it with its vibrissae. Possibly the movement of the fish is detected this way, and/or the whiskers and patting action serve to attract the fish. Insect-eating fish such as barbels (*Barbus* spp.), up to 300 mm, catfish (*Clarias* spp.), talking catfish (*Synodontis* spp.) and cyprinids of the genus *Labeo* are caught with a rapid, open-mouthed strike and carried away (A. Root pers. comm.).

According to local hunters the Aquatic Genet also eats cultivated cassava tubercles (*Manihot* sp.) left to soak in small streams (Hart & Timm 1978), and crustaceans (see Schouteden 1950), which is

highly unlikely considering the sectorial teeth. Two adult captives never ate frogs, tadpoles or crabs but a bottle-raised youngster that had never seen the feeding behaviour of an adult tried to eat all three. None of them showed any interest in moths or beetles that flopped into the pools in their enclosure (A. Root pers. comm.).

Social and Reproductive Behaviour The Aquatic Genet seems generally to be solitary in its habits. Two specimens, a pregnant ♀ and an adult ♂, were captured only two-and-a-half weeks apart from the same local area of forest (Hart & Timm 1978). Faeces are deposited in genet-like middens, and urine on several marking spots. Appears to be able to co-exist with the Marsh Mongoose *Atilax paludinosus* (A. Root pers. comm.).

A captive ♂ and ♀ showed no signs of stress at living together in a 8 m × 8 m cage but occasionally would make very aggressive tom-cat-like miaows when the ♂ was pursuing the ♀ and trying to mate. They also had a chuffing call used to each other and their keeper (A. Root pers. comm.).

Reproduction and Population Structure Nothing is known about the reproduction of the Aquatic Genet except that a ♀ collected on 31 Dec contained one embryo 15 cm in length (Hart & Timm 1978).

Predators, Parasites and Diseases There is no information on predation on the Aquatic Genet. Out of 11 skulls examined, one showed frontal sinus damage probably due to a trematode, *Achillurbandia* sp. (Colyn & Van Rompaey 1989).

Conservation IUCN Category: Data Deficient. CITES: Not listed.

Legally fully protected in DR Congo (Ordinance No. 79-244 of 16 Oct 1979). Hunted as bushmeat by the Bambuti pygmies; the meat is taboo to all, except male elders (Hart & Timm 1978, Colyn *et al.* 1987). Present in Okapi N. P. and presumably in several other protected areas in its range. This species is a priority for further survey work to further investigate the limits of its distribution, its population status and precise habitat requirements, and other aspects of its ecology.

Measurements

Genetta piscivora

HB (♂ ♂): 445, 495 mm, n = 2

T (♂ ♂): 340, 415 mm, n = 2

HF c.u. (♂ ♂): 83, 90 mm, n = 2

E (♂ ♂): 40, 40 mm, n = 2

WT (♂): 1.43 kg, n = 1

WT (♀): 1.5 kg, n = 1

GLS: 100.2 (97.0–108.6) mm, n = 11

GWS: 49.0 (46.4–54.3) mm, n = 11

Body measurements: Allen 1924, Hart & Timm 1978

Skull measurements: museum specimens (AMNH, MRAC, SBP)

Key References Kingdon 1997; Van Rompaey 1988.

Harry Van Rompaey & Marc Colyn

Genetta poensis KING GENET

Fr. Genette royale; Ger. Königs-Ginsterkatze

Genetta poensis Waterhouse, 1838. Proc. Zool. Soc. Lond. 1838: 59. 'Fernando Po' [Bioko I., Equatorial Guinea].King Genet *Genetta poensis*.

Taxonomy Described from a skin supposed to come from Bioko I., Equatorial Guinea, but De Pousargues (1896) and Pocock (1908) doubted its geographical origin. The species belongs to the grouping commonly called the large-spotted genet 'forest forms' of West Africa (together with *bourloni*, *pardina* and *schoutedeni*; see Pocock 1908, Rosevear 1974, Crawford-Cabral 1980–81, Schlawe 1981, Gaubert 2003a). *Genetta poensis* has been the focus of much taxonomic debate, being either considered synonymous with, or related to, the Pardine Genet *G. pardina* (see Matschie 1902, Crawford-Cabral 1980–81, Schlawe 1981, Wozencraft 1993, Grubb *et al.* 1998) or listed as a valid species (Rosevear 1974). Its name was erroneously used for designating the Crested Genet *G. cristata* (Jeannin 1936, Happold 1987). Gaubert (2003a) recognized the species on the basis of coat pattern and hair ultrastructure characters, later confirmed by molecular phylogenetic investigation (Gaubert *et al.* 2004b) and accepted by Wozencraft (2005). Estimated to have diverged very recently, during the middle Pleistocene (Gaubert & Begg 2007). Synonyms: none. Chromosome number: not known.

Description Heavily built genet. Similar to Pardine Genet, but spots completely dark and coalesced in various parts of the body, and almost half of the tail is dark. Sexes similar in colour and size. Facial mask well marked, with a thin dark vertical line on the muzzle. Sub- and supra-ocular white spots contrasting with the dark muzzle. Ear broad-based and slightly rounded. Pelage relatively short and rough. Ground colouration from pale yellowish-grey to yellow. Throat, chest and ventral pelage whitish-yellow to grey. Nuchal stripes not clearly delimited. Mid-dorsal line dark without long crest hairs, beginning after the shoulder. Dorsal spots elongated and 'squared', completely dark and greatly coalesced in various parts of the body. Hindlimbs and forelimbs dark and well spotted. Upper parts of the fore- and hindfeet spotted. Underparts of feet dark. Tail thickly furred but hair relatively short, and its proximal part annulated with four to six pale rings; distal half of tail almost completely dark. Skull large, similar to Pardine Genet; temporalis muscles attached to narrow, elevated occipital crest.

*Genetta poensis*

Geographic Variation None recorded.

Similar Species

- Genetta pardina*. Sympatric. Dorsal spots not coalesced; tail annulated almost to the tip, which is covered by a large dark ring.
- G. johnstoni*. Sympatric. Dorsal spots rufous-red and coalesced; tail annulated with pale rings to the tip.
- G. bourloni*. Sympatric. Dorsal spots partly coalesced at the rump; nuchal stripes clearly delimited.
- G. servalina*. Sympatric. Dorsal spots not coalesced; tail annulated with pale rings to the tip; tip bright.
- Poiana leightoni*. Sympatric. Smaller; ears large and rounded; spots smaller and dark, no mid-dorsal line.

Distribution Endemic to Africa, inhabiting rainforest blocks, in Liberia, Côte d'Ivoire, Ghana, Equatorial Guinea (Bioko I.) and Republic of Congo (Gaubert 2003a).

Habitat Collection localities suggest restriction to rainforest (Gaubert 2003a).

Abundance Unknown, but scarcity of records suggests this is a rare and localized species.

Adaptations Coalesced spotted coat patterns suggest long-term adaptation to more humid and closed habitats.

Remarks There is a paucity of information available on the ecology of this species. They are solitary, and probably both carnivorous and frugivorous.

Conservation IUCN Category: Data Deficient. CITES: Not listed.

Hunting pressure is probable, as most of the museum skins were collected from local hunters or bushmeat markets. The species, represented by ten known specimens in collections, has not been collected since 1946 (Gaubert 2003b), and is a priority species for further survey work to establish its status in the wild.

Measurements

Genetta poensis

HB: 602 (427–680) mm, n = 3

T: 415 (350–465) mm, n = 3

Ghana and Côte d'Ivoire (museum specimens: BMNH, MNHN, ZMB)

Skull measurements:

A specimen in the Paris Museum, from Mayombe, which led De Pousargues (1896) to record the species to Congo has GLS = 100.3 mm and GWS = 52.1 mm; a specimen in the British Museum (♂), from Ashanti, Ghana, had GLS = 102.1 mm and GWS = 50.2 mm (J. Crawford-Cabral pers. comm.)

Key References De Pousargues 1896; Gaubert 2003a; Pocock 1908; Rosevear 1974.

Philippe Gaubert

Genetta servalina SERVALINE GENET

Fr. Genette servaline; Ger. Servalgenette (Waldgenette)

Genetta servalina Pucheran 1855. Rev. Mag. Zool. 7 (2): 154. Gabon.

Taxonomy Original description is based on a skin sent to France from Gabon by Audry Leconte. The name presumably refers to the resemblance with the Serval *Leptailurus serval*. Considered to be a 'primitive' genet by Crawford-Cabral (1981), later confirmed by its basal position within the *Genetta* clade (Gaubert *et al.* 2002b, 2004b), with the species diverging in the Late Pliocene (Gaubert & Begg 2007). The Crested Genet *G. cristata*, considered by some authors

to be conspecific (e.g. Coetzee 1977, Wozencraft 1993), is now generally considered to represent a distinct species (Rosevear 1974, Crawford-Cabral 1980–1981, Gaubert *et al.* 2004b, Wozencraft 2005).

Five subspecies are currently recognized (Van Rompaey & Colyn 1998). Of supposed synonyms, the form *aubryana* Pucheran, 1855 is considered to be a lighter colour phase of *G. s. servalina*, while the



Servaline Genet *Genetta servalina*.

form *intensa* Lönnberg, 1917 is recognized by Coetzee (1977) as a subspecies, but considered a colour phase by Crawford-Cabral (1970) and later (1980–81) as a possible ‘subrace’ of *G. s. bettoni*. Synonyms: *archeri*, *aubryana*, *bettoni*, *intense*, *lowei*, *schwarzi*. Chromosome number: not known.

Description Slender, relatively long-legged and long-faced genet. Pelage short, soft and more velvety than other *Genetta*. Ground colour greyish to ochraceous-yellow. Nuchal line poorly developed. Spots may tend to fuse near the spine, suggesting a dark mid-dorsal line. Numerous closely grouped brownish-black spots on the back and flanks, rarely forming longitudinal lines, weaker and more scattered on the ventral side, which is greyish to black. Forelegs may have small spots down to the feet; hindlegs down to the ankle. Feet light to brownish-black. Metatarsal and metacarpal pads not connected to interdigital pads. Tail long, cylindrical with 9–12 dark rings with yellowish-white rings between. Tip of tail white, yellowish, or black. Hairs show a clear banding pattern and a visible, globular medullary configuration with many air spaces. One pair nipples. In the skull, the caudal entotympanic bone is ventrally inflated. In adult animals, the maxillo-palatine suture is aligned with the P³ main cusp (Gaubert *et al.* 2001).

Geographic Variation

G. s. servalina: forests of central Africa west and north of the Congo R. up to the Sanaga R. (although see Gaubert *et al.* 2006 who give records from north of the Sanaga R.). Upperside tawny to greyish. Spots brownish-black. Hindlegs dark brown; feet brownish-black. Populations between the Ubangi and Congo Rivers have lighter tones half-way between the nominate *servalina* and the eastern *bettoni*; both Allen (1924) and Crawford-Cabral (1970) suggested that they might represent distinct subspecies.

G. s. bettoni: montane forests in the Kivu area, E DR Congo, southward to Baraka (on L. Tanganyika, DR Congo), eastward in Uganda to Kenya (Mt Kenya). Similar to *G. s. servalina* but general appearance lighter and size on average one-seventh smaller with corresponding reduction in the size of the teeth. Those from Upper Uele R., Kibali-Ituri, towards Semliki Valley, E DR Congo, are darker, due to the larger and more closely placed black spots and may represent a different subspecies (*G. servalina intensa*) or a dark colour phase of *G. s. bettoni*.

G. s. schwarzi: Congo basin, south of the Congo and Lualaba Rivers. Larger than *G. s. servalina*. Tendency for spots to form rows on the flanks and stripes on the shoulders. Later thought not to merit subspecific rank by Crawford-Cabral (1980–81).

G. s. lowei: geographically isolated in several Eastern Arc Mts blocks, being recorded from the Udzungwa Mts, South Nguru Mts and the Uluguru and Rubeho Mts. Yellow-orange base colour. White facial spots suffused with orange. Legs and feet light coloured.

G. s. archeri: geographically isolated in Jozani Forest, Zanzibar, Tanzania. Upperside ochraceous with rather short velvety pelage and numerous irregular black spots. Throat and ventral part of insides of fore- and hindlegs clear, smoky grey; lower outside parts light-coloured with small spots. Tail of holotype relatively short haired and soft-furred with ten light-coloured rings, these being narrower than the nine darker rings. Dorsally, light-coloured rings have some light-brown hairs mixed intermedially on the dorsal side. Both skull and teeth measurements are considerably larger than in *G. s. bettoni*.

Similar Species

Genetta cristata. South-easternmost limits of distribution not clearly established; possibly sympatric in Gabon and Congo (Gaubert *et al.* 2006). Nuchal or mid-dorsal crest.

G. maculata. Sympatric. Fewer and larger body spots; shorter legs; tapering tail with fewer rings and black tip.

G. victoriae. Sympatric. Much larger; darker coloured, longer legs; prominent suborbital spot, and two black neck stripes starting from behind the ears.

G. poensis. Sympatric. Dorsal spots greatly fused in various parts of body; nuchal stripes not clearly delimited.

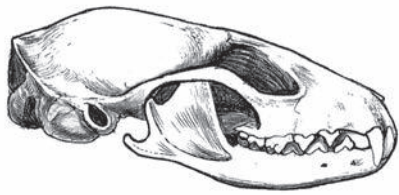
Nandinia binotata. Sympatric. Heavier; more brownish coloured; two light-coloured shoulder spots; soles of fore- and hindfeet naked to wrist or ankle; tail not distinctly ringed.

Poiana richardsonii. Sympatric. Smaller, and more slender; spots smaller; lighter coloured.

Distribution Endemic to Africa. Ranges from S Cameroon, south of the Sanaga R., and Central African Republic and southwards in Equatorial Guinea, Gabon, Congo to S Sudan (Imatong Mts and Didinga Mts; Dieterlen & Nikolaus 1985), Uganda (Muhavura Mt; Gyldenstolpe 1928), Rwanda (Parc National des Volcans and Ruggege Forest; Elbl *et al.* 1966), Kenya (Taylor 1970b, Kingdon 1977), and possibly also in Burundi (Kibira Forest; Wilson 1990). There are discontinuous populations in Tanzania, including from the Udzungwa Mts and Nyumbanitu Mts (Kingdon 1977, De Luca & Mpunga 2002, Brink *et al.* 2002), South Nguru Mts and Uluguru Mts (Rovero *et al.* 2006) and Rubeho Mts (Rovero *et al.* 2008). Gaubert *et al.* (2006) also give museum records from north of the Sanaga R., from several additional localities in Tanzania (Mikindani, Uimba Ebene, Kondoia, and Mandera, the latter a locality lying on the East African coast), as well as from Kitobwe and Lumumbashi in SE DR Congo (but these are not mapped here). Also present on Zanzibar (Van Rompaey & Colyn 1998, Goldman & Winther-Hansen 2003).



Genetta servalina



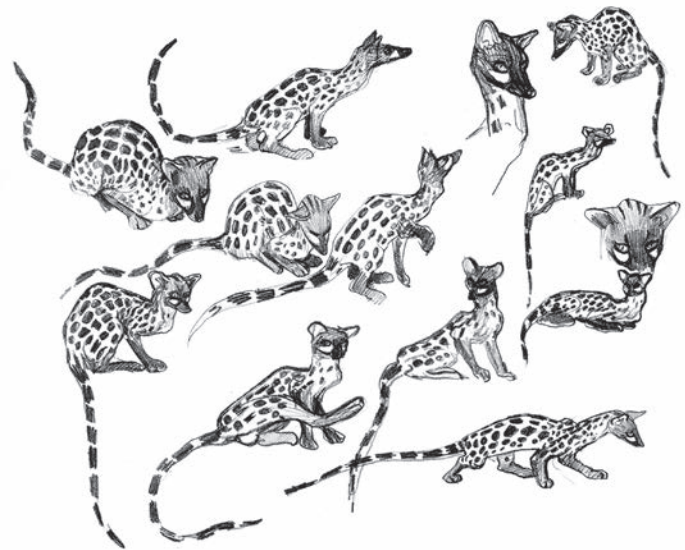
Lateral view of skull of Servaline Genet *Genetta servalina*.

Habitat Primary and secondary lowland, sub-montane and montane forests and gallery forests. Recorded up to 2900 m on Mt Muhavura (Gyldenstolpe 1928) and 3500 m on Mt Elgon, Kenya (Kingdon 1977). Traces of the presence of the Servaline Genet have been found in the sub-alpine and alpine zones up to 4425 m on Mt Wusuwameso, DR Congo (Verschuren 1972). Habitats from which they have been recorded include: wet forests with a rainfall of over 1625 mm a year in Kenya (Taylor 1970b); acacia country on the plains at the south end of the Rwenzori Mts in DR Congo (Thomas & Wroughton 1910); high-altitude bamboo forest in the Udzungwa Mts (De Luca & Mpunga 2002); valley bottom with discontinuous canopy cover but dense understorey (Rovero *et al.* 2006); ground-water forest and coral rag thicket on Zanzibar (Goldman & Winther-Hansen 2003); and open deciduous shrubland in Congo (Gaubert *et al.* 2006).

Abundance Charles-Dominique (1978), walking and canoeing 268 km and checking an area of 6.4 km² primary and secondary forest in Gabon, observed seven individuals and estimated the average density at 1/km². In Equatorial Guinea, density was 0.8/km² (Fa *et al.* 1995). Very common in the Irangi region, DR Congo (Rahm 1966). Kingdon (1977) noted that the species appeared to be particularly common at an altitude between 2100 and 3000 m on Mt Elgon, and it is also common in moist forests of the Udzungwa Mts at altitudes of 300–1800 m (De Luca & Mpunga 2002, F. Rovero pers. comm.).

Adaptations Arboreal and nocturnal. Palmigrade forefoot and semi-digitigrade hindfoot. A high-set scapula allows a great abduction of the forelimb so that walking along a branch the legs are kept in a flexed position and can be swung out in a lateral arc, allowing a faster correcting movement should it slip (Taylor 1970a). Rahm (1966) found it more arboreal than the Large-spotted Genet *G. maculata*; however, they have been both observed and photo-trapped on the ground (Charles-Dominique 1977, Kingdon 1977, Goldman & Winther-Hansen 2003).

Foraging and Food Omnivorous. In Dzanga-Sangha Special Reserve, Central African Republic, 77% of 35 scats contained mammalian prey (mostly shrews and rodents, but also bats, pangolin, monkey, and Blue Duiker *Philantomba monticola* – although the last three prey items were probably scavenged), 71% arthropods (mostly termites, beetles and orthopterans), 14% herpetofauna (snakes, lizards and anurans), 6% birds and 3% fruit (Ray 1996, Hutterer & Ray 1997, Ray & Sunquist 2001). Diet similar to that of the Large-spotted Genet from the same region (Rahm & Christiaensen 1963). A Servaline Genet was observed scavenging a duiker (*Cephalophus* spp.) killed five days before by a Leopard *Panthera pardus* at an altitude of 3400 m (Verschuren 1972). Hunts on the ground and at low level in bushes (Charles-Dominique 1977).



Servaline Genet *Genetta servalina*.

Social and Reproductive Behaviour Either solitary or in pairs (Rahm 1966). Faeces are often deposited under overhanging rocks without forming latrines (Verschuren 1972).

Reproduction and Population Structure Births have been recorded in Uganda from Feb to Aug (Kingdon 1977). Recorded to live more than 14 years in captivity (Weigl 2005).

Predators, Parasites and Diseases A nematode worm *Toxocara vincenti* was recovered from a specimen in Congo (Grabner 1981). Ticks (*Haemaphysalis leachi*) have been recovered from Ugandan animals (Allen & Lawrence 1937). Four of eight fresh heads of Servaline Genets from NE DR Congo contained trematodes, *Achillurbania* sp. in the frontal sinuses and eight out of 36 examined skulls showed frontal sinus damage, probably due to this parasite. *Mammamonogamus* spp., parasitic worms of the respiratory system, were present in the nasal cavities of one specimen and Metastrongylidae in two other specimens from DR Congo (Colyn & Van Rompaey 1989). Trypanosomes responsible for sleeping sickness (*Trypanosoma brucei* non *gambiense* group 1, *T. b. gambiense* group 1, *T. congolense* 'savanna type' and *T. vivax*) have been found in specimens from S Cameroon (Herder *et al.* 2002).

Conservation IUCN Category: Least Concern. CITES: Not listed.

Genets make up nearly 20% of the carnivore bushmeat in NE DR Congo (Colyn *et al.* 1987) and 32/year were sold at a bushmeat market in Equatorial Guinea (Fa *et al.* 1995). Skins used for wrist-bracelets and dancing hats (Carpaneto & Germe 1989) and are a favourite skin for loin-cloths among both Mbuti and Ba'aka pygmies. In Congo, they are hunted for bushmeat and traditional medicine (Wilson & Wilson 1991). Since the recent rediscovery of Lowe's Servaline Genet in the Udzungwa Mountains N. P. (Brink *et al.* 2002, De Luca & Mpunga 2002), after a gap of nearly 70 years, and subsequent records in Uluguru North F. R. and Kanga F. R. (Rovero *et al.* 2006) and Rubeho Mts (Rovero *et al.* 2008), further research is needed to determine whether this species might be more widely distributed in other Eastern Arc Mountain blocks, particularly the Ukaguru Mts that lie between the Udzungwa and South Nguru Mts (Rovero *et al.* 2006).

Measurements

Genetta servalina servalina

HB (♂ ♂): 490, 510 mm, n = 2

HB (♀ ♀): 474 (445–495) mm, n = 5

T (♂ ♂): 450, 465 mm, n = 2

T (♀ ♀): 427 (368–485) mm, n = 5

HF c.u. (♂ ♂): 87, 92 mm, n = 2

HF c.u. (♀ ♀): 88 (80–95) mm, n = 4

E (♂): 46 mm, n = 1

E (♀ ♀): 41 (40–42) mm, n = 3

WT (♀ ♀): 2.27 kg, n = 2*

DR Congo (Allen 1924) and museum specimens (AMNH, BMNH, MCZ, MRAC, PCM and ZMB)

*Range not given

Genetta servalina bettoni

HB: 427 mm, n = 6

T: 381 mm, n = 5

HF c.u.: 77 mm, n = 5

E: 40 mm, n = 5

DR Congo (Allen 1924) and museum specimens (AMNH, BMNH, MCZ, MRAC, PCM and ZMB)

Ranges not given

Skull measurements:

Genetta servalina servalina

GLS: 95.1 (91.2–98.2) mm, n = 15

GWS: 45.1 (41.1–48.9) mm, n = 15

Cameroon

Genetta servalina bettoni

GLS: 82.6 (76.9–86.2) mm, n = 38

GWS: 40.8 (36.1–44.6) mm, n = 38

Mt Elgon, Uganda

Museum specimens (AMNH, BMNH, MCZ, MRAC, PCM and ZMB)

Key References Kingdon 1977; Van Rompaey & Colyn 1998.

Harry Van Rompaey & Marc Colyn

Genetta thierryi HAUSA GENET

Fr. Genette de Villiers; Ger. Haussa-Genette.

Genetta thierryi Matschie, 1902. Verh. V Internat. Zool. Congr. 1901: 1142. 'Hinterland von Togo von 9° N. Br. ab', restricted to 'Borogu = Borgou, (10° 78' N, 0° 65' E)?' by Schlawe (1981).

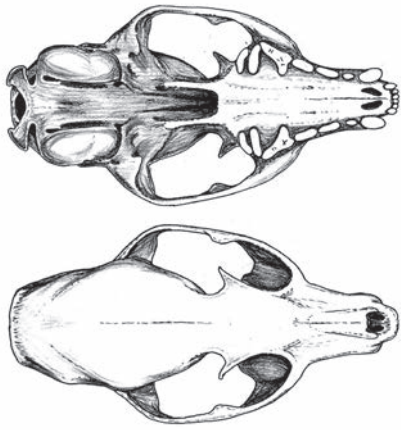


Hausa Genet *Genetta thierryi*.

Taxonomy Monotypic. Named in honour of a Oberleutnant Thierry, supposed by Rosevear (1974) to have been stationed in Togo. Described from a series of skins. Has been included in subgenus *Pseudogenetta* (see Kuhn 1960 and Crawford-Cabral 1980–81) with the Ethiopian Genet *G. abyssinica*. There has been inconsistent use of nomenclature since Schlawe (1981) discovered that the type specimen of *G. rubiginosa* Pucheran, 1855, in fact belonged to the species *G. thierryi*. Following prevailing usage (Articles 23.9.1 and

.2; International Code of Zoological Nomenclature, 1999), *thierryi* should become the *nomen protectum* used for designating the Hausa Genet, and *rubiginosa* should be considered a *nomen oblitum* (Gaubert *et al.* 2003a, b). The species represents the earliest offshoot of the genus *Genetta* (Gaubert *et al.* 2004b), appearing ca. 8 mya (Gaubert & Begg 2007). Synonyms: *villiersi*, *rubiginosa*. Chromosome number: not known.

Description One of the two smallest genet species (second to the Ethiopian Genet). Sexes similar in colour and size. Facial mask lightly marked. Muzzle and forehead pale grey, with a thin dark vertical line on the muzzle. Subocular white spots well marked, but supraocular spots absent. Ears rounded. Hairs short and straight. Pelage pale, blotched with brown-rufous spots following linear patterns down the back. Ground colouration varying from yellow-brown (Mali) and pale grey (Casamance, Senegal) to pale beige (N Senegal). However, variations also exist within the same locality. Throat, chest and ventral pelage greyish-white. Nuchal stripes either irregular or marked by two thin parallel lines. Mid-dorsal line rufous brown, non-contrasting with the rest of the dorsal markings; starts after the shoulder and usually split longitudinally by a line of pale hairs (at least for the upper part). Dorsal spots elongated and aligned in two rows. The row flanking the mid-dorsal line partially coalesces just before the rump. Spots of the flank, thigh and shoulder smaller and darker. Hindlimbs and forelimbs unspotted, same colour as the background colouration. Line bordering the outer side of the forefoot pads and inner side of the hindfoot pads brown. Central depression of the forefoot hairless. Tail narrow but thicker at its base with longer hairs, usually annulated with eight pale rings. Annulation



Palatal and dorsal views of skull of Hausa Genet *Genetta thierrii*.

not distinct because of the brownish to rufous extensions of the dark rings. Tip with a long dark ring caused by the reduction of the last pale ring (9th). In juveniles, general colouration darker, pattern of spots irregular, but mid-dorsal line present and annulation of the tail identical to the adult. Hairs of the scapula with a globular medulla containing no air spaces. Perineal glands present on both ♂ and ♀. Two pairs of nipples. The skull is reduced in size, with an elongated postorbital process. The caudal entotympanic bone is rounded and very inflated in comparison to the ectotympanic bone (bullae).

Geographic Variation None recorded.

Similar Species

Genetta genetta. Sympatric. Taller; black dorsal crest; tuft of tail whitish.

G. pardina. Sympatric. Taller and darker; mid-dorsal line large and dark, spots not fused.

G. johnstoni. Not sympatric, inhabiting only dense rainforest in West Africa. Taller and darker; mid-dorsal line large and dark; tail annulated with pale rings to the tip; tuft of tail whitish.

G. maculata. Sympatric east of the Volta R. Taller; mid-dorsal line large and brownish-dark.

Poiana leightoni. West Africa only, in rainforest habitats. Similar in size, but mid-dorsal line absent, spots small, rounded, and not coalesced, and tail annulated with pale rings present to the tip.

Distribution Endemic to Africa. Sparsely distributed in the West African savanna zone from Gambia and Guinea-Bissau to Cameroon; the easterly limit of distribution requires clarification.

Habitat Usually moist and dry savannas with open woodlands. However, the species seems to adapt to different habitats since specimens have been collected and sighted in moist woodlands (Casamance, Guinea-Bissau), rainforest (Sierra Leone, Ghana, Côte d'Ivoire) and even dry wooded steppes (Senegal).

Abundance Considered rare. Possibly common in some restricted areas like E Senegal and Casamance (from collections of the I.R.D. (former O.R.S.T.O.M.) of Dakar, partially deposited at the Muséum National d'Histoire Naturelle of Paris). Hoppe-Dominik (1990) stated that the species was widespread throughout its range, but provided no evidence.



Genetta thierrii

Adaptations Colouration and length of hair is related to habitat, as with the similar widespread Common Genet *G. genetta*: hair is short and paler in savanna habitat, but longer and yellower in forest habitat. The cross-section shape of the dorsal guard hairs at the base of the spatula is round or slightly ovoid (Gaubert *et al.* 2002b), which is exceptional among the members of the genus (but similar in Ethiopian Genet). This conformation probably makes the hair less flexible, but nothing is known about its actual adaptive value.

Foraging and Food No specific information available, but likely to resemble other genets.

Social and Reproductive Behaviour Little known. It is thought to bear young in holes dug in the ground or amongst rocks (Rosevear 1974). A juvenile specimen was found asleep in a dead tree near the Lamto Station, Côte d'Ivoire (Bourlière *et al.* 1974).

Reproduction and Population Structure Unknown. However, two subadults (estimated age: 8–10 months) from Mali were collected early Nov (L. Granjon pers. comm.), thus suggesting births around Jan to Mar, corresponding with the dry season.

Predators, Parasites and Diseases Probably similar predators as other genets. Ixodid ticks (*Haemaphysalis rugosa* and *H. moreli*) specializing on Viverridae were found on specimens from moist woodlands of Senegal (Camicas *et al.* 1972, Camicas 1978). The mites *Laelaps lavieri* and *L. liberiensis* were also recorded in Côte d'Ivoire (Herrin & Tipton 1976).

Conservation IUCN Category: Least Concern. CITES: Not listed.

Dekeyser (1956) reported that the species is locally hunted and its tail is used for ceremonial and ornamental purposes in Casamance, Senegal (Diola and Bassari tribes). Reported from bushmeat markets throughout its range. In the past, there has also been regional and

international traffic for their skins or as pets, although there was no record of this species (or any other genet for that matter) in commercial trade reported to CITES for the period 1995–2005. During 2001, five kittens were found by customs in transit from Lagos, Nigeria, to Manila, the Philippines (H. Van Rompaey pers. comm.).

Measurements

Genetta thierryi

HB: 448 (443–450) mm, n = 3

T: 415 (400–430) mm, n = 3

HF c.u.: 677 (600–750) mm, n = 3

E: 377 (350–400) mm, n = 3

GLS: 81.5 (78.0–85.0) mm, n = 12

GWS: 43.7 (37.0–45.0) mm, n = 12

Body measurements: Senegal (Dekeyser 1949)

Skull measurements: museum specimens (MNHN)

Haltenorth & Diller (1980) give body weight as 1.3–1.5 kg

Key References Dekeyser 1949; Rosevear 1974.

Philippe Gaubert & Amy E. Dunham

Genetta tigrina CAPE GENET

Fr. Genette à grandes taches d'Afrique du Sud; Ger. Suedliche Grossfleckgenette

Genetta tigrina (Schreber, 1776). Die Säügethiere 3 (17): pl. 115 [1776]; text, 3 (25): 425 [1777].
'von dem Vorgebirge der guten Hofnug', Cape of Good Hope, South Africa.



Cape Genet *Genetta tigrina*.

Taxonomy The specific epithet '*tigrina*' means tiger-like, although coat pattern is in no way reminiscent of tiger stripes. Described from a specimen that died at the Menagerie of Prince William V of Orange-Nassau, near The Hague (iconotype; see Tuijn & Van der Feen 1969). Until recently some authors considered the Cape Genet *G. tigrina* and Large-spotted Genet *G. maculata* conspecific (Coetzee 1977, Meester *et al.* 1986). Others have disagreed with this on the basis of pelage pattern, as well as skull and teeth characteristics (Roberts 1951, Cabral 1966). Both craniometrics (Crawford-Cabral 1980–81, Crawford-Cabral & Pacheco 1992) and discrete morphological characters (Schlawe 1981, Gaubert 2003a) argue for recognition of *G. tigrina* as a valid species. Speciation might be a recent phenomenon or still in progress given the relative uniformity of mtDNA haplotypes distributed between *maculata* and *tigrina* (Gaubert *et al.* 2005b). Hybridization zones with Large-spotted Genet (specifically the form *letabae*) occur in KwaZulu-Natal (Pringle 1977), but are likely to be very localized (Gaubert *et al.* 2005b). The lineage leading to the clade grouping *G. maculata* and *G. tigrina* is estimated

to have diverged in the middle Pleistocene (Gaubert & Begg 2007). There are currently two recognized subspecies. Synonyms: *methi*. Chromosome number: not known.

Description Similar to Large-spotted Genet, but hair slightly longer and dark spots very large and not coalesced. Sexes similar in colour and size. Facial mask well marked, with a thin dark vertical line on the muzzle. Subocular white spots contrasting with the dark muzzle. Supraocular spots less contrasting. Ground colouration whitish-yellow or grey. Throat, chest and ventral pelage grey to whitish-grey. Nuchal stripes well defined. Large mid-dorsal line with crest, intermediate in length between that of the Large-spotted Genet and the Common Genet *G. genetta*, begins behind the shoulder. Hair on the scapula region without air spaces within the globular medulla. Hindlimbs very dark, with a thin row of bright hairs on the anterior surface. Forelimbs with posterior part dark. Upper parts of forefeet and hindfeet lightly spotted. Thigh and shoulder with large spots. Tail relatively short (ca. 81–85% of HB) with hair length intermediate between the Large-spotted Genet and the Common Genet *G. genetta*, and clearly annulated with 7–8 bright rings. The first dark rings are larger than in the Large-spotted Genet, and the last bright ring is more apparent, even though it is covered by a dark dorsal line; tip of the tail is dark. Two pairs of nipples.

The skull is characterized by a thin sagittal crest, caudal entotympanic bone very flattened in comparison with the ectotympanic bone, and lingual cusp of P³ very reduced.

Geographic Variation

G. t. tigrina: southern coastal South Africa from the Western Cape to Eastern Cape. Coat and skull characteristics as in 'Description'.

G. t. methi: known only from the south of Umsigaba R., Pondoland, but may occur slightly further north (Roberts 1951). Colouration and pelage pattern similar to *tigrina*; size considerably larger, especially teeth (P⁴ and M¹), with greatest diameter of P⁴ 11.5 mm (cf. 9.0–9.8 mm in *tigrina*); hair shorter.



Similar Species

Genetta genetta. Sympatric (*felina*; see *G. genetta*). Hair longer, mid-dorsal line with longer erectile hair; dorsal spots narrow and partially coalesced; tip of the tail bright.

G. maculata. Sympatric in S KwaZulu-Natal (*letabae*; see *G. maculata*). Pelage pattern very similar, but mid-dorsal line with short hair; limb and foot brighter; first dark rings of the tail narrower; skull with a more marked postorbital constriction.

Distribution Endemic to South Africa. Well represented in higher rainfall areas from Western Cape through Eastern Cape to S KwaZulu-Natal, south of 32° S, and to the neighbouring S Lesotho border. Sympatric with the Common Genet (*G. g. felina*) throughout its range (see Gaubert *et al.* 2005b). There is a narrow hybrid zone with Large-spotted Genet (*letabae*) in S KwaZulu-Natal (Gaubert *et al.* 2005b).

Habitat Occurs in wooded or dense habitats such as Lowland and Mountain Fynbos (heathland) and forests in the Western and Eastern Cape (Stuart 1981). Mostly present in permanent-watered zones such as riverine associations. Sometimes found in exotic scrub (Western Cape) as well as open grasslands during foraging activities (Stuart 1981).

Abundance There is no information on their abundance, but they are not uncommon. Haagner (1920) reported the species to be common in what was then the Cape Province.

Adaptations Unknown, but clearly bound to the unique climate and vegetation of the Cape.

Foraging and Food Roberts *et al.* (2007) provided the first comprehensive report on the diet of *G. tigrina* as determined from scat analysis ($n = 372$), and found the species to have an opportunistic,

generalist diet. These authors studied seasonal variations in diet in the coastal dune forest of the Dwesa N. R., Eastern Cape Province, South Africa. The food items with the highest relative percentage occurrence were Coleoptera, Orthoptera and Mammalia. However, by volume they ate mostly grass (perhaps to aid digestion, to dislodge hair in the intestines, to induce vomiting, among other purposes), followed by Coleoptera and Orthoptera. Main prey items originated from the litter layer or low-lying bushes, such as arachnids, insects, myriapods and most mammals. The latter included ten rodent species (especially *Dendromus* sp., *Otomys* sp., *Graphiurus* sp. and *Mastomys* sp.), and two golden-mole and two shrew species, from 10 to 100 g mass. Birds appeared under-represented in the diet for a semi-arboreal carnivore, but remains of birds in the diet did peak during winter and spring probably as a result of the main nesting period in spring. Roberts *et al.* (2007) also recorded myrmecophagy (reported as absent in genetids' diet by Wemmer 1977), although this could result from contamination of scats at the latrine sites. The remains of scorpions in scats suggest that *G. tigrina* may have disarmed them by attacking and consuming the pedipalps and stinger un-masticated before consuming the remainder. There was some variation in diet between habitats and seasons.

Elsewhere, rodents (Namaqua Rock Rat *Aethomys namaquensis* and Southern African Vlei Rat *Otomys irroratus*), birds (Egyptian Goose *Alopochen aegyptiaca* and birds of the family Columbidae), insects (Coleoptera and Orthoptera), spiders and pill millipedes, freshwater crabs, earthworms, plants (seeds, leaves and green grass) and even chewed bark and wood have been recorded in the diet (Stuart 1981). They have been seen feeding in rubbish dumps in Cape Point, Goukamma and De Hoop Nature Reserves (Western Cape) (Stuart 1981), and Roberts *et al.* (2007) suspected that fish found in the diet of animals in their study were probably scavenged from the beach or elsewhere.

Social and Reproductive Behaviour Solitary, but pairs occasionally seen during the breeding season. One individual was observed resting during the day in a hollow oak tree, 3 m above the ground, in Jonkershoek Valley, Western Cape (Stuart 1981).

Reproduction and Population Structure A lactating ♀ caught in Jan had recently given birth and a juvenile ♂ of about six weeks was collected in Mar (Stuart 1981). Given these data, it is possible that a birth season extends from Jan to Feb. Longevity reported up to 15 years in captivity (Anonymous 1960).

Predators, Parasites and Diseases Probably same predators as the Common Genet. Two species of ectoparasites (Acaria) were reported in the Cape: *Haemaphysalis leachi* (group) and *Ixodes* sp. (near *oldi*) (Stuart 1981).

Conservation IUCN Category: Least Concern. CITES: Not listed.

Though not particularly subject to hunting pressure, they are sometimes killed by farmers in retaliation for their preying on small domestic stock and poultry. Trapping, poisoning and shooting could have an effect on numbers of the species in certain areas (Stuart 1990). Present in several protected areas throughout its range, such as West Coast N. P. (Avery *et al.* 1990) and Kammanassie Mountain State F. R. (Nel *et al.* 1980).

Measurements

Genetta tigrina tigrina

HB (♂♂): 507 (460–580) mm, n = 11

HB (♀♀): 495 (427–560) mm, n = 5

T (♂♂): 431 (390–459) mm, n = 10

T (♀♀): 403 (385–432) mm, n = 5

HF c.u. (♂♂): 85 (80–90) mm, n = 11

HF c.u. (♀♀): 82 (77–85) mm, n = 5

E (♂♂): 43 (36–55) mm, n = 10

E (♀♀): 42 (39–43) mm, n = 5

WT (♂♂): 1.9 (1.6–2.1) kg, n = 9

WT (♀♀): 1.6 (1.4–1.9) kg, n = 4

GLS: 87.5 (85–90) mm, n = 11*

Northern Cape, Western Cape and Eastern Cape, South Africa (Stuart 1981)

*South Africa (Roberts 1951)

Key References Crawford-Cabral & Pacheco 1992; Stuart 1981; Roberts *et al.* 2007.

Philippe Gaubert

Genetta victoriae GIANT GENET

Fr. Genette géante; Ger. Riesengenette

Genetta victoriae Thomas, 1901. Proc. Zool. Soc. Lond. 1901: 87. Entebbe, Uganda. Corrected to 'Near Lupanzula's, 10 miles west of Beni, Ituri Forest, Congo (Kinshasa)' by Moreau *et al.* (1946).



Giant Genet *Genetta victoriae*.

Taxonomy Monotypic. Has been included with the true servaline genets, Crested Genet *G. cristata* and Servaline Genet *G. servalina*, owing to its densely spotted coat and the absence of a continuous mid-dorsal line (e.g. Crawford-Cabral 1981a, Gaubert *et al.* 2002b); however, the species shows marked morphological differences, particularly in the skull and morphological and molecular studies do not support a monophyletic grouping with servaline genets (Gaubert *et al.* 2004b, Gaubert & Begg 2007). Rather, the species places as a single, second offshoot of the genus *Genetta* (following the lineage leading to *G. thierryi*), diverging in the late Miocene. The name *victoriae* refers to the mistaken locality of the holotype, Entebbe, on L. Victoria. Synonyms: none. Chromosome number: not known.

Description Large, dark-coloured, long-legged genet. Pelage short, close and thick. Top of muzzle and forehead whitish with a black median line starting in front of the eyes. Sides of muzzle and orbital ring black. Prominent suborbital white spot. Nose below nostrils 14 mm wide (cf. 10 mm in other *Genetta* spp.). Vibrissae long; ears rounded. Two black bands on neck, starting behind ear. Dorsal pelage yellowish to ochraceous-white; guard hairs ca. 25 mm long. Ventral pelage paler and also spotted. Conspicuous discontinuous black

mid-dorsal line (with hair relatively long) formed by fusing of spots. Numerous, well-defined, small black spots on body, thighs, shoulder and upper foreleg give the animal its general dark appearance. Legs and feet brown to black; feet relatively small for its size, and soles hairy. Tail relatively short, cylindrical and bushy, tapering near the tip; guard hairs 25–30 mm long. Ca. six white rings between dark rings that are twice as wide; tip of tail dark. One pair of abdominal nipples. In the skull, the caudal entotympanic bone is ventrally inflated.

Geographic Variation None recorded.

Similar Species

Genetta servalina. Sympatric. Smaller; less darkly coloured; larger dorsal spots; shorter legs.

G. maculata. Sympatric. Smaller; less darkly coloured; larger, squared dorsal spots; short legs.

Civettictis civetta. Sympatric. Much heavier; hindlegs longer than frontlegs; relatively shorter, thicker tail.

Distribution Endemic to Africa. Largely confined to an area between the Congo, Lualaba and Oubangui Rivers in DR Congo (approximately 18°E–30°E and 4°N–4°S). Thomas (1901) described the species based on a skin sent to London from Entebbe, but Johnston (1902) stated that he collected the skin from a very dense part of the forest on the Semliki R. in NE DR Congo, and hence not at Entebbe. Moreau *et al.* (1946) restricted the locality to Lupanzula's village and stated that 'although there are no authentic records of this genet from Uganda, we believe it to occur'. Indeed, skins of genet kittens from the Bwamba Forest, Toro District, Uganda, an eastern extension of the Semliki Forest, seemed to be certainly this species, and Bere (1962) mentions its presence from the Semliki Forest in Uganda. Kingdon (1977) observed a specimen along a forest road in W Uganda. Recently, a large genet photographed in Nyungwe N.P. in Rwanda has been positively identified as this species (Dinets 2011).

Depierre & Vivien (1992) mention two specimens from the Sangmelina forest area in Cameroon (ca. 750 km west from its most western expected distribution), possibly mistaken identification for



the Crested Genet. Gaubert *et al.* (2006) provide museum records that expand the range 500 km south, including localities from deciduous forest on the left bank of the Congo R. in S DR Congo (but these are not mapped).

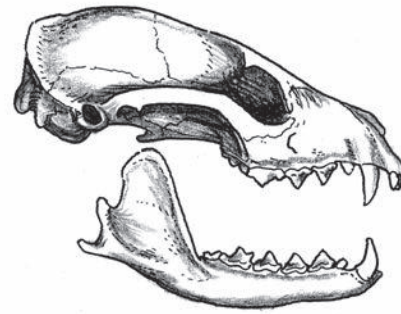
Habitat Occurs in lowland and medium-altitude rainforests up to 1800 m. Two specimens identified as Giant Genets by Gaubert *et al.* (2006) from Kakanga and Mukulu, in S DR Congo, apparently were collected in deciduous forest.

Abundance The Giant Genet is patchily distributed, being quite abundant in some areas and nearly absent in intervening, apparently suitable habitat; for example, they are very rare in the area between the Uma and Enano Rivers, east of Kisangani, and fairly common between Kisangani and Buta, and between the Aruwimi and Lindi Rivers (Schreiber *et al.* 1989).

Adaptations Semi-arboreal; the long legs may be an adaptation to a more terrestrial way of life than shown by other genets. The dark colouration and numerous spots are typical for a forest species.

Foraging and Food Omnivorous, taking carrion, termites, pambaa fruits, bananas (*Musa* sp.) and oil palm fruits (*Elaeis guineensis*). Raids poultry coops (Carpaneto & Germe 1989). In captivity, rice, bananas, milk and rodents are eaten (Rahm 1966).

Social and Reproductive Behaviour Solitary, active either by day and by night or only by night, according to different authors; a



Lateral view of skull of Giant Genet *Genetta victoriae*.

single animal was observed trotting along a forest road at about 22:30h (Kingdon 1977). Sleeps in hollow trunks of dead trees or among vines (Carpaneto & Germe 1989).

Reproduction and Population Structure According to the Mbuti pygmies of NE DR Congo, the Giant Genet has only one young per litter (Carpaneto & Germe 1989).

Predators, Parasites and Diseases Predators probably include aerial raptors and larger forest carnivores. A louse *Felicola* (*Parafelicola*) *lenicornis* was listed by Hopkins (1949). Out of 33 skulls examined, two showed frontal sinus damage probably due to a trematode *Achillurbandia* sp. (Colyn & Van Rompaey 1989).

Conservation IUCN Category: Least Concern. CITES: Not listed.

Hunted as bushmeat (Colyn *et al.* 1987) and for food by Mbuti pygmies; only eaten by elders. Skin used to make hats and other ceremonial objects (Carpaneto & Germe 1989). There are records from the Ituri Forest and Okapi Faunal Reserve in DR Congo and from Nyungwe N. P. in Rwanda, and it probably occurs in several other protected areas in its range, such as Maiko N. P.

Measurements

Genetta victoriae

HB: 568 (550–600) mm, n = 19

T: 441 (413–490) mm, n = 19

HF c.u.: 101 (92–105) mm, n = 19

E: 47 (45–51) mm, n = 18

GLS: 112.7 (106.6–121.4) mm, n = 33

GWS: 55.8 (50.8–59.9) mm, n = 28

Museum specimens (AMNH, BMNH, IRSN, MRAC, PCM, SBP and SMF)

Kingdon (1997) gives body weight as 2.5–3 kg

Key References Kingdon 1977; Carpaneto & Germe 1989.

Harry Van Rompaey & Marc Colyn

GENUS *Poiana* Linsangs (Oyans)

Poiana Gray, 1864. Proc. Zool. Soc. Lond. 1864: 520.

The genus holds two species, the Central African Linsang *Poiana richardsonii* and West African Linsang *P. leightoni*, although the latter has been considered a subspecies by several authors (Wozencraft 1993). The African linsangs, or oyans, are small, slender, genet-like carnivores characterized by a small head, pointed muzzle, long body and short legs. General colour yellowish-brown with numerous small, brownish-black spots and sometimes a narrow mid-dorsal line. Underparts whitish to creamy. Pelage very short, soft and dense with fine underfur. Legs spotted; feet with five toes; sharp, retractable claws. Plantigrade forefeet and digitigrade hindfeet (Taylor 1988), as in *Genetta*. Interdigital depression naked. Metatarsal pads developed as in *Genetta*, forming a naked line nearly up to the heel of the hindfoot. Long, cylindrical tail with 9–14 dark rings. Dental formula: $I^{3/3}, C^{1/1}, P^{4/4}, M^{1/2} = 38$. Dentition differs from *Genetta* in the usual absence of M^2 , which, if present, is very small.

Poiana has often been compared with the Asian Linsang (genus *Prionodon*, formerly genus *Linsang*), both being forest dwellers and having similar morphotypes as well as diet. Pocock (1915)

provisionally classified the African linsangs with the Asian linsangs. However, in addition to skull differences (Gregory & Hellman 1939), *Prionodon* has no scent glands, no metatarsal pads, but an intervening hairy space between the plantar and metacarpal pads. The great distance or 'scattered distribution' between the two species of *Poiana* is generally held to indicate ancient stock (Booth 1954). Crawford-Cabral (1993b) considers *Poiana* a genet that acquired a *Prionodon*-like dental formula and questions the reasons for maintaining *Poiana* as a valid genus distinct from *Genetta*. Molecular phylogenetic analysis has shown that the African and Asian linsangs were distinct lineages having acquired morphological similarity by convergence, with *Poiana* grouping as sister-taxon to *Genetta* whereas *Prionodon* branched as the sister-group of Felidae (Gaubert & Veron 2003). Divergence time between the African linsang lineage and genets was estimated to be middle to late Pliocene (Gaubert & Cordeiro-Estrela 2006).

Harry Van Rompaey & Marc Colyn

Poiana leightoni WEST AFRICAN LINSANG (WEST AFRICAN OYAN)

Fr. Poiane d'Afrique occidentale; Ger. West Afrika Linsang

Poiana leightoni Pocock, 1907. Proc. Zool. Soc. Lond. 1907: 1043 [1908]. 'fifteen to twenty miles [24 to 32 km] west of the Putu Mountains, which lie west of the Duobe and Cavally Rivers. The Cavally R. is the eastern boundary line between Liberia and the Côte d'Ivoire, and the Duobe is one of its tributaries joining the Cavally about seventy miles [113 km], as the crow flies, from its mouth, after running for over one hundred miles [161 km] nearly parallel to the main stream' [Liberia].



West African Linsang *Poiana leightoni*.

valid species (Rosevear 1974) on the basis of pattern differences that are likely to be very ancient (Kingdon 1997) (see also Gaubert *et al.* 2002b, Wozencraft 2005). Synonyms: *liberiensis*. Chromosome number: not known.

Description Small, slender, genet-like carnivore. Ground colour yellowish-fawn but not always different from yellowish to reddish-brown of Central African Linsang. Large, longer than wide, irregular spots on back and flanks; much smaller spots on fore- and hindlimbs and on flanks near belly. Spots are more or less arranged into four to five longitudinal rows and they form longitudinal stripes on neck. Throat, chest and belly white. Underfur of back and flanks greyish-white, of belly white. Dorsal pelage soft and very short. Underfur abundant (hairs ca. 10 mm), guard hairs few (ca. 10 mm). Thin, sometimes interrupted, mid-dorsal stripe from between the shoulders to the root of the tail. Ten to twelve chevron-shaped dark tail-rings, narrower laterally and ventrally; no intermediate dark tail-rings.

Geographic Variation None recorded.

Similar Species

Poiana richardsonii. Allopatric, occurring in central Africa only. Dark tail rings not chevron shaped; spots smaller.
Genetta spp. Various sympatric forms, but all larger in size.

Taxonomy Originally described as *liberiensis*, but a printed amendment slip in *Proceedings of the Zoological Society of London* reads 'Erratum: p. 1043: for Subsp. *liberiensis*, nov. read Subsp. *leightoni*, nov.' Species named after the collector of the type specimen, Leonard Leighton. Although long considered as a subspecies of Central African Linsang *P. richardsonii* (e.g. Wozencraft 1993), it is now treated as a

*Poiana leightoni*

Distribution Endemic to the Upper Guinea forests of West Africa. Present in SW Côte d'Ivoire, where known from two confirmed records: Gagnoa (Beaufort 1965), where a specimen was taken from a bushmeat market, and Nzi-Alakro (Awakro) (Bourlière *et al.* 1974). There is a record from Sangbé N. P. (see Hoppe-Dominik 1990), but this requires confirmation. In E Liberia, there are records from Biple, Bongle, Deaple, Duotown, Igua, Siamonrovia, Tappita, and on the road between Bia and Zwedru (Kuhn 1965) and Mali and Bao Town (Taylor 1989a). The presence of this species in the Kounounkan Massif in SW Guinea (Barnett *et al.* 1996) requires confirmation. Davies (1990) mentioned that the species may occur in the Gola Forest in Sierra Leone, but there is no confirmed record of the species from the country.

Habitat An inhabitant of the rainforest canopy.

Abundance There is no information available on the population status of this species; the most recent confirmed records are from Liberia in the late 1980s. According to Rosevear (1974), the species is rare and very localized.

Adaptations According to H.-J. Kuhn (in Nowak 1999) the West African Linsang builds a round nest of green material at least two metres from the ground, but usually higher, in which several individuals sleep for a few days, and then moves on and builds a new nest. Previously, it was reported that they sleep in abandoned squirrel nests but native hunters claim that squirrels sleep in abandoned nests of the West African Linsang. The former seems more likely as Mudappa (2001) observed in India that Jerdon's or Brown Palm Civet *Paradoxurus jerdoni* prefer resting during the day in nests of the Malabar Giant Squirrel *Ratufa indica*.

Remarks There is little information available on the ecology of the species. Insects, birds, plant material and kola nuts are recorded from the diet (H.-J. Kuhn, in Nowak 1999), and they also prey on small rodents and possibly reptiles.

Conservation IUCN Category: Data Deficient. CITES: Not listed.

Along with the Liberian Mongoose *Liberiictis kuhni*, Johnston's Genet *Genetta johnstoni* and Bourlon's Genet *G. bourloni*, the West African Linsang is one of the few carnivores with a very restricted range in parts of the Upper Guinea rainforest, a region that continues to experience relatively high rates of net forest loss, and highlighting the importance of this region as one of the core areas for viverrid and herpestid conservation in Africa (Schreiber *et al.* 1989). The West African Linsang may occur in Sangbé N. P. in Côte d'Ivoire (Hoppe-Dominik 1990) and the type locality is not far away from the northern boundary of Liberia's Sapo N. P. (Schreiber *et al.* 1989); it probably occurs in other protected areas within its range. There is a clear need for further survey work targeting this species using the appropriate survey techniques, particularly to better determine its current range and population status, and to investigate other basic aspects of its biology.

Measurements

Poiana leightoni

HB: 300–380 mm

T: 350–400 mm

WT: 500–700 g

GLS: 67.1, 70.2 mm, n = 2

GWS: 34.8, 36.4 mm, n = 2

Body measurements: throughout the range (Kingdon 1997)

Skull measurements: Liberia (museum specimens: MRAC, SMNK)

Key References Rosevear 1974.

Harry Van Rompaey & Marc Colyn

Frontal view of West African Linsang *Poiana leightoni*.

Poiana richardsonii CENTRAL AFRICAN LINSANG (CENTRAL AFRICAN OYAN)

Fr. Poiane d'Afrique centrale; Ger. Zentral Afrikanischer Linsang

Poiana richardsonii (Thomson, 1842). Ann. Mag. Nat. Hist., ser. 1, 10: 204. 'Fernando Po' [Bioko I., Equatorial Guinea].Central African Linsang *Poiana richardsonii*.

Taxonomy Two subspecies. Originally described as *Genetta richardsonii*, the generic name *Poiana* given by Gray in 1864, based on the type locality Fernando Po. Species named after Dr John Richardson, Inspector of the Naval Hospital at Haslar. Synonyms: *ochracea*, *poensis*. Chromosome number: not known.

Description Small, slender, short-legged, genet-like carnivore. Muzzle pointed. Ears wide and rounded. Eyes large and yellowish-brown. Rhinarium grey. Ground colour yellowish to reddish-brown. Small, unequal brownish-black spots of various shapes and sizes all over the back and flanks, coalescing into stripes on neck. Spots do not form longitudinal lines and are very small on thighs and forelimbs. Absent or small, sometimes interrupted mid-dorsal line. Throat and underside greyish-pale and unspotted. Underfur greyish to creamy. Pelage short and soft. Underfur abundant (hairs 10–11 mm), guard hairs few (13–15 mm). Feet greyish-fulvous and unmarked. Soles hairy, except for digital pads and a narrow bare line on the plantar surface. Tail cylindrical, slightly shorter or longer than head and body with 9–14 dark rings with often small, distinct to faint dark intermediate rings in the centre of the light rings. Males may be slightly larger than ♀♀.

Geographical Variation

P. r. richardsonii: S Cameroon, Equatorial Guinea (including Bioko I.), Gabon and Congo.

P. r. ochracea: DR Congo from the Rift Valley to Mayumbe. Ground-colour sometimes more rusty-red but not always different; underside and insides of limbs yellowish and darker; spots in general smaller and more widely spaced; dark tail rings smaller than light rings, and no intermediate dark rings.

Similar Species

Poiana leightoni. Allopatric, occurring in West Africa only. Dark tail rings chevron-shaped; spots larger.

Genetta spp. Larger.

*Poiana richardsonii*

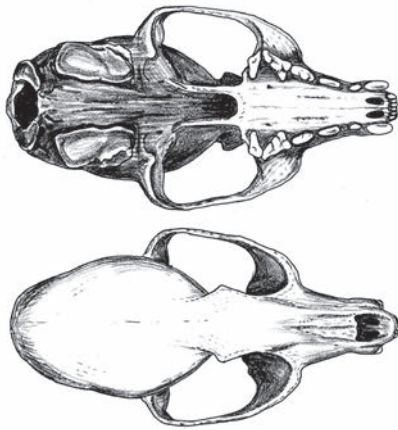
Distribution Endemic to central Africa, ranging from S Cameroon and S Central African Republic, Equatorial Guinea (including Bioko I.), Gabon, Congo and DR Congo up to the Rift Valley.

Habitat The canopy of lowland and montane forests. On Bioko I., at about 17:10h, an individual was observed walking in a dry, rocky stream bed with little vegetation, before it fled to the forest (Harrington *et al.* 2002).

Abundance Not rare on Bioko I. (Eisentraut 1973), and reported as quite common in NE DR Congo (Rahm & Christiaensen 1963). Charles-Dominique (1978) recorded a density of 1/km² in primary forest in Gabon.

Adaptations Probably similar to West African Linsang *P. leightoni*. Nocturnal and arboreal, sleeping on thick tangled vines (Bates 1905) and rarely venturing to the ground. In Gabon trapped with traps set 2 m high on a branch connecting two vegetation blocks. Able to jump by bending the body before jumping (P. Charles-Dominique pers. comm.).

Foraging and Food Both carnivorous and frugivorous according to hunters of NE DR Congo (Rahm & Christiaensen 1963, Nowak 1999), taking rodents, birds, insects and vegetable material. Said to kill chickens (Carpaneto & Germi 1989). P. Charles-Dominique (pers. comm.) did not find the remains of fruit in digestive tracts of two trapped specimens; a captive refused all sorts of fruit.



Palatal and dorsal views of skull of Central African Linsang *Poiana richardsonii*.

Social and Reproductive Behaviour Nothing known.

Reproduction and Population Structure A ♀ had milk in two teats in Oct and there are usually two young (Bates 1905). There may be two litters per year (Nowak 1999). Very few *Poiana* have been kept in captivity, but a captive specimen was still alive after five years and four months (Jones 1982); longevity in the wild is probably much longer.

Predators, Parasites and Diseases Ten out of 11 skulls examined showed frontal sinus damage, probably due to a trematode, *Achillurbandia* sp. This high percentage (91%) of cranial damage could indicate that the animals were caught as a result of abnormal behaviour. The species lives high in the canopy, rarely coming down to the ground; at least eight of the 11 studied specimens were trapped on the ground, possibly as a result of a parasitic infection (Colyn & Van Rompaey 1989).

Conservation IUCN Category: Least Concern. CITES: Not listed.

Although common in its wide range in a region of relatively intact habitat, they are probably experiencing localized declines as a result of forest loss and forest fragmentation due to logging, mining and slash-and-burn farming, as well as due to bushmeat hunting. *Poiana* make up nearly 1% of the carnivore bushmeat in NE DR Congo (Colyn *et al.* 1987). Five *Poiana* were identified out of more than 37,900 animals sold as bushmeat in Malabo market, Bioko I. (Harrington *et al.* 2002). Objects such as tobacco- and medicine-pouches, and ceremonial objects, are made from the skin (Thomas & Wroughton 1910).

Measurements

Poiana richardsonii

HB (♂ ♂): 370 (321–400) mm, n = 9

HB (♀ ♀): 360 (346–395) mm, n = 5

T (♂ ♂): 379 (352–402) mm, n = 9

T (♀ ♀): 357 (340–380) mm, n = 5

HF c.u. (♂ ♂): 61 (57–64) mm, n = 9

HF c.u. (♀ ♀): 59 (57–61) mm, n = 5

E (♂ ♂): 34 (29–37) mm, n = 9

E (♀ ♀): 32 (30–34) mm, n = 5

WT (♂ ♂): 510, 750 g, n = 2

WT (♀): 455 g, n = 1

GLS: 67.0 (63.7–72.5) mm, n = 26

GWS: 33.8 (32.0–38.6) mm, n = 24

Body measurements: museum specimens (BMNH, SMNS)

Skull measurements: museum specimens (AMNH, BMNH, MNHN, MRAC, PCM, SBP, SMNS, ZFMK)

Key References Charles-Dominique 1978; Rosevear 1974.

Harry Van Rompaey & Marc Colyn

Subfamily VIVERRINAE – African Civet

Viverrinae Gray, 1821. London Med. Repos. 15: 301.

The subfamily Viverrinae, as traditionally defined, consists of three African (*Civettictis*, *Genetta*, *Poiana*; see earlier for the taxonomic validity of the genus name *Osbornictis*) and two Asiatic genera (*Viverra*, *Viverricula*), with a total of 22 species in these five genera listed by Wozencraft (2005). More recently, Gaubert & Cordeiro-Estrela (2006), on the basis of both morphological grounds and molecular phylogenetics, proposed differentiating the Viverrinae *sensu stricto* (terrestrial civets) from the Genettinae (genets and oyans), which is the approach followed here. Diagnostic characters of the Viverrinae are: feet digitigrade; thenar and hypothenar pads absent or residual; ratio between head-body and tail > 1.5; black- and white-striped 'collar' on the neck; perineal glands with a deep interglandular poach for musk storage in ♀ ♀; caudal entotympanic bone ventrally inflated, showing a pyramidal shape; paraoccipital process strong, exhibiting a ventral prolongation; and thick dentition, with a well-developed talonid on M1.

The subfamily includes the genera *Viverra* and *Viverricula* (both from Asia), and *Civettictis* (from Africa), which contains a single

species, the African Civet *C. civetta*. African Civets adapt to almost all terrestrial habitats throughout their range, with the exception of extremely arid regions and high-altitude mountain habitats. Size and body mass are the greatest among African viverrids. The genus *Civettictis* has long metapodials and extremely reduced metatarsal pads (Taylor 1988). Limbs are short compared with body length. Digitigrade feet distinguish them from the plantigrade Asiatic subfamilies (Paradoxurinae and Hemigalinae) and the semi-digitigrade Genettinae. The coat is spotted and the tail is clearly annulated with alternating bright and dark rings. The tail is not more than half as long as the body, and there is a characteristic black and white 'collar' on the throat. A well-marked and dark mid-dorsal line is usually present, often extending on the tail. There are no sub-orbital bright spots. The perineal glands are well developed. The caudal entotympanic bone is very inflated, and the paroccipital process is strongly developed and has a triangular shape. Teeth are heavily built, with a large talonid in M₁ and the lingual cusp of P₃ almost unapparent.

General biology and adaptations are as in Viverridae (see Family Viverridae profile). The African Civet has a rather omnivorous diet, and foraging occurs mainly on the ground. Periods of birth may be spread over a wide range, with sometimes poorly marked seasonality; females can have two to three litters a year (Ray 1995b).

Civet-like fossils appear in Eurasia from 20–13 mya, mainly as dental remains. The first records of African taxa occur at the beginning of this period (e.g. *Orangictis*). Plio-Pleistocene records

are rich and show the high diversification of the group into a complex of Eurasian and African taxa, currently still referred to *Viverra*, *Megaviverra*, *Vishnuictis*, *Civettictis* and *Pseudocivetta*. The extant African genus (*Civettictis*) appears in the early Pliocene of Ethiopia (L. Werdelin pers. comm.).

Philippe Gaubert

GENUS *Civettictis*

African Civet

Civettictis Pocock, 1915. Proc. Zool. Soc. Lond. 1915: 134.

The genus contains a single species, the African Civet *Civettictis civetta*, which is distributed throughout much of sub-Saharan Africa wherever there is adequate vegetation cover. African Civets are easily recognized as being the largest members of the Family Viverridae residing in Africa. External characters that separate them from other small carnivores include their disproportionately large hindquarters, low-headed posture, erectile dorsal crest and elongated and robust skull.

Formerly regarded as congeneric with the Asian civets (genus *Viverra*). The species was first included in the genus *Civettictis* by Pocock (1915), and with the exception of Ellerman *et al.* (1953) and Coetzee (1977), who continued to include it in *Viverra*, has been retained in *Civettictis* by most authors (e.g. Gregory & Hellman 1939, Petter 1969, Ewer 1973, Rosevear 1974, Kingdon 1977, 1997, Meester *et al.* 1986, Wozencraft

1993, 2005, Ray 1995b), based on the following differences: auditory bullae of *Viverra* smaller and more rounded than those of *Civettictis*; paroccipital process more rounded in *Civettictis*; molars broader and flatter in *Civettictis*, but sharper and narrower in *Viverra*; the hindfoot in *Viverra* lacks a metatarsal pad (present in *Civettictis*); the soles of *Viverra* are hairy, those in *Civettictis* naked anterior to the central pads; the claws of *Viverra* are short, semi-retractile and protected by skin lobes, whereas those in *Civettictis* are long and non-retractile; and the inner faces of each of the two lobes of the perineal gland of *Civettictis* possess an orifice, which connects with the sac that stores the gland's secretion (absent in *Viverra*).

Justina C. Ray

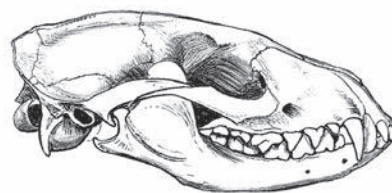
Civettictis civetta AFRICAN CIVET

Fr. Civette d'Afrique; Ger. Afrika Zibetkatze

Civettictis civetta (Schreber, 1776). Die Säugethiere 3 (16): pl. 111 [1776]; Text: 3 (24): 418, 3:index, p. 587[1777]. 'Guinea, Kongo, das Vorgebirge der guten Hoffnung und Aethiopien,' restricted to 'Guinea' (= former French Guinea) by Allen (1924: 117).

Taxonomy As many as six subspecies have been described, but there is so much individual variation in marking patterns and colouration that taxonomic validity of subspecies designations must be viewed with suspicion (Gregory & Hellman 1939, Rosevear 1974, Coetzee 1977, Meester *et al.* 1986, Kock *et al.* 2000). Synonyms: *australis*, *congica*, *matschiei*, *megaspila*, *orientalis*, *pauli*, *poortmanni*, *schwarzi*, *volkmanni*. Chromosome number: 2n = 38; the X chromosome is a large metacentric or submetacentric and the Y is a medium acrocentric or subacrocentric (Todd 1967).

Description Short-legged, blotched and striped, dog-like carnivore with disproportionately large hindquarters, dark facial mask and white neck stripes. Head broad, eyes relatively small. Ears small and rounded, but protrude from head, black on back, and white fronts and rims. Forehead whitish or grey, with black band across face above eyes. Bands of white from behind ears to front of shoulders. Dorsal pelage coarse and wiry in texture. Ground colour varies from whitish to reddish-buff, and underlying spotting pattern distinct. Arrangement of markings is highly variable, with no two individuals having the same pattern; patterning is irregular, with deep brown to black spots arranged in irregular rows. Guard hairs



Lateral view of skull of African Civet *Civettictis civetta*.

longer and thicker than underfur. Erectile crest formed by line of shaggy black hairs (up to 120 mm in length) along the spine from neck to tail. Whitish stripe along contour of back visible when spinal crest erected. Tail (ca. 55% of HB) coarse-haired with long bristles giving bushy appearance, laterally flattened and tip pointed. Dorsal surface of tail black, with five partial white rings. Paws and lower limbs black. Each foot with five digits; first toes set back from others and not visible in tracks. Soles naked anterior and lateral to the central pads. Claws long, curved and essentially non-retractile. Metacarpal pads bi-lobed and connected to palmar pad by one or more thin strips of skin; metatarsal pads on hindfeet present. Two pairs abdominal nipples. Females ca. 10% larger and heavier than



African Civet *Civettictis civetta*.

♂♂, although with broad overlap (Smithers & Wilson 1979, Ray 1995b, F. M. Angelici pers. comm.).

Skull long, narrow, and heavily built, with a long ovoid braincase and flat profile. Well-developed sagittal crest, strong zygomatic arch, prominent bullae and broad but blunt supraorbital processes. Dental formula is $I^{3/3}, C^{1/1}, P^{4/4}, M^{2/2} = 40$. Molar tooththrow is well developed, particularly the first upper molars that are broader and larger than in other viverrids. The canines are short and heavy.

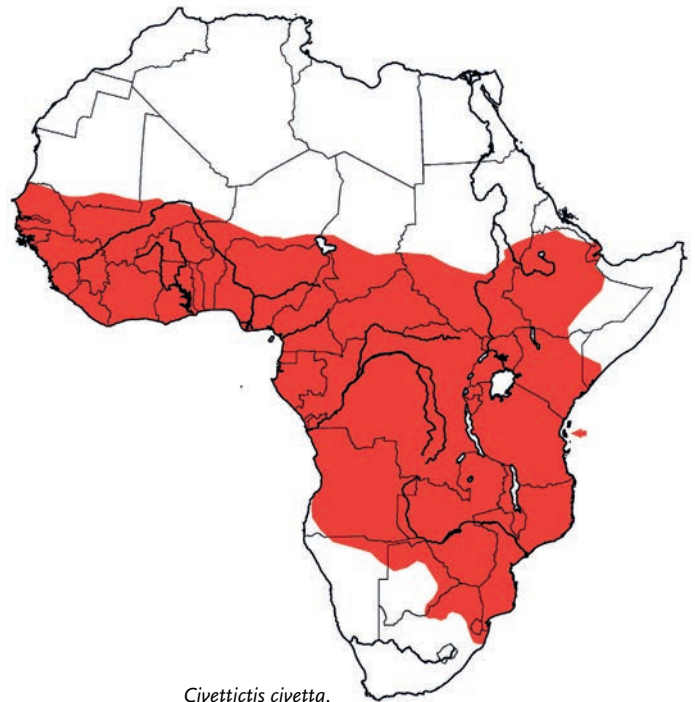
Geographic Variation Although animals taken in Nigeria seem to be slightly heavier than those recorded from southern Africa, there does not appear to be any significant geographic variation in size based on body measurements of specimens from across the range (see Ray 1995b and Measurements). However, there is extensive variation in patterning and colouration across the range. One-third of specimens collected in the north-east of the Congo basin were melanistic (Allen 1924); melanism is less common in West Africa (Rosevear 1974, F. M. Angelici pers. comm.), and not recorded at all in southern Africa (Skinner & Chimimba 2005).

Similar Species

Genetta spp. Smaller body size; dark markings arranged in regular longitudinal lines; longer, less bushy tails (the only genet to approach the African Civet in size is Giant Genet *G. victoriae*).

Proteles cristatus. Disjunct distribution range in southern and East and north-east Africa. Taller, with long ears, and shoulder higher than hindquarters; paler in colour, with thin, widely spaced vertical stripes.

Distribution Endemic to Africa. Distribution has been recorded as extending from 15°N to around 29°S latitude, from Senegal through all West African countries to Cameroon, Central African



Civettictis civetta.

Republic, S Sudan, Ethiopia, the Red Sea coast of Djibouti, and S Somalia (Funaioli & Simonetta 1966, Rosevear 1974, Ray 1995b, Kock *et al.* 2000). Two specimens collected from the dry Sahel savanna of S Mauritania in 2002 extend the range further north than has previously been recorded (Padial & Ibáñez 2005). Southwards they occur widely in all countries, but in southern Africa restricted to extreme NE Namibia (although Berry [1988] recorded a specimen from the Outjo District suggesting that they might be more common than is thought), N and E Botswana, and the north-eastern parts of South Africa south through Swaziland to the coastal region of NE

KwaZulu–Natal (Rowe-Rowe 1992a, Monadjem 1998, Skinner & Chimimba 2005). Present on Zanzibar I. (Pakenham 1984), but absent from Pemba and Tumbatu, and other offshore islands such as Bioko I.

Habitat African Civets are widespread, occupying secondary forest, woodland and bush habitats, as well as aquatic environments. Generally absent from the most arid portions of the continent, with the exception of riverine systems therein (Rosevear 1974, Rautenbach & Nel 1978). African Civets are uncommon in mature interior forest habitats (Sanderson 1940, Grubb *et al.* 1998), but will infiltrate deep forest via logging roads (Ray & Sunquist 2001). In the forest zone of West and central Africa, they thrive under conditions of deforestation and degradation (Grubb *et al.* 1998), and are regularly encountered near villages (Rahm & Christiaensen 1963, Hoppe-Dominik 1990, Angelici *et al.* 1999a). They have been recorded at altitudes as high as 5000 m on Mt Kilimanjaro (Moreau 1944), although they are probably not resident at this altitude (Grimshaw *et al.* 1995).

African Civets sleep in dense vegetation during the day (such as stands of long grass or thickets), in holes made by other animals, under logs, or among tangled roots (Verheyen 1951, Rosevear 1974, Kingdon 1977). One radio-collared male's diurnal resting location was found in the same area of dense juniper 9 of 11 times (Admasu *et al.* 2004c). In Mayombe, DR Congo, terrestrial hollows at the base of uprooted trees used both to hoard whole mature fruits and undigested seeds as well as latrines; such areas were selected according to proximity to fruiting trees and were abandoned once fruiting was over (Pendje 1994). They do not appear to be dependent on the availability of drinking water, but are more common in these areas.

Abundance Generally among the numerically dominant carnivores when present, and common in museum collections. Based on track counts recorded along transects in a lowland forest in SW Gabon, density estimated at 1/km² (Prins & Reitsma 1989). In NE DR Congo, significantly more abundant in post-cultivation regrowth vs. mature forest (Wilkie & Finn 1990). In both study areas, tracks of African Civets were the most commonly encountered of carnivores.

Adaptations Terrestrial, but adept swimmers (Shortridge 1934, Rosevear 1974). Their feet are unsuitable for climbing or digging, the footpad having relatively little overall surface area (Ewer & Wemmer 1974). African Civets climb only rarely (although they are known to clamber along low branches), probably when in pursuit (Rahm & Christiaensen 1963). Both fore- and hindlimbs adapted for sustained trotting, the most common form of locomotion (Taylor 1974, 1976). Heavy lower jaw and accompanying musculature gives the African Civet a powerful bite (Rosevear 1974). The outer upper incisors are enlarged to assist the canines in holding prey. The cheek-teeth are broad and blunt and adapted for grinding and crushing.

The spinal crest is erected when threatened, allowing individuals to assume a large and intimidating posture by increasing lateral body dimensions up to 30% and the size of the light dorsal stripe by as much as six times (Wemmer & Wilson 1983). Scent is not emitted in alarm (Ewer & Wemmer 1974, Kingdon 1977).

Foraging and Food African Civets are omnivorous and opportunistic, with principal food items including fruit, arthropods

and mammals (Bothma 1965, Rosevear 1974, Guy 1977, Randall 1977, Smithers & Wilson 1979, Pendje 1994, Ray 1996, Angelici 2000). Relative importance of these dietary components is variable among localities and seasons. Scats (n = 97) collected from Sengwa valley area, Zimbabwe, were dominated by mammals (84%; mostly rodent and hare), fruits (81%) and arthropods (76%), with birds (22%) and reptiles (10%) also present (Guy 1977). Elsewhere in Zimbabwe, 27 stomachs yielded the highest occurrence for insects (59%), followed by fruit (at least seven species; 52%), murids (41%), reptiles (22%), birds (15%), amphibians (11%) and millipedes (11%) (Smithers & Wilson 1979). Of 30 scats collected from Dzanga-Sangha Special Reserve, Central African Republic, 97% contained arthropods (millipedes, beetles, orthopterans), 73% fruit (at least nine species, dominated by *Staudtia stipitata*) and 30% mammal (rodents and pangolin) (Ray 1996, Ray & Sunquist 2001). In Mayombe district, DR Congo, the fruits of nine species of forest trees are regularly consumed, with *Staudtia stipitata* also favoured (Pendje 1994). In SE Nigeria, 27 stomachs contained mostly rodents, arthropods (millipedes, orthopterans and beetles) and reptiles (snakes and lizards), followed by fruit, birds and shrews (Angelici 2000).

Grass is commonly found in scats, at 60% frequency of occurrence in Dzanga-Sangha Special Reserve, Central African Republic (Ray 1996), and 22% in southern Africa (Smithers & Wilson 1979), but may be consumed more for its mechanical action than nutritional properties. Oil palm nuts are a favoured food source throughout the range, particularly during dry seasons (Pendje 1994, Grubb *et al.* 1998). Aquatic organisms, such as crabs, snails and mudskippers, are also commonly consumed (Rosevear 1974, Kingdon 1977, Grubb *et al.* 1998), and Ewer & Wemmer (1974) noted that captive civets would submerge their faces in water to catch small fish. Domestic poultry houses and gardens are often raided at night (Rosevear 1974, Kingdon 1977). As their teeth are not specially adapted for killing large prey, they have difficulty taking prey as large as Scrub Hare *Lepus saxatilis* and springhares *Pedetes* spp.; however, carrion can be a major food item (Bothma 1965, Guy 1977, Randall 1977). They were recorded preying on prosimian primates in Gabon (Charles-Dominique 1977).

Evidence points towards resource tracking according to availability, with African Civets taking advantage of any food source that happens to be abundant. In Zimbabwe, fruits were increasingly important during the months when fruit was most abundant, with insects taking precedence at other times of the year (Guy 1977). In drier climates, insects generally occur most frequently in African Civet diets during warm and wet summer months when most available (Skinner & Chimimba 2005). In moist forest habitats, where fruits are most abundant, they are often eaten to the exclusion of other foods for long periods of time (Kingdon 1977, Pendje 1994). In tropical forest environments, it is not uncommon for scats to be filled with only one species of fruit for the period of time when it is at its peak (Pendje 1994, J. C. Ray pers. obs.). The highest diversity of fruits is eaten during wet seasons (Pendje 1994). One radio-collared ♂ in the highlands of S Ethiopia utilized a core area that was less than 5% of its home-range, probably in response to enhanced food resources provided by rubbish dumps (Admasu *et al.* 2004c).

Prey is detected predominantly by olfactory and auditory senses, rather than visual (Ewer & Wemmer 1974). Live prey is generally

seized by mouth and secured by teeth. Paws are not used except to hold down the food item while pulling off pieces with incisors (Ewer & Wemmer 1974, Kingdon 1977, Schliemann 1990, Skinner & Chimimba 2005). Able to eat poisonous or distasteful fruits, insects and snakes, and most studies reveal that millipedes are commonly found in their diet (Guy 1977, Randall 1977, Ray 1996, Angelici 2000); they exhibit some degree of tolerance of noxious chemicals, as in the defence secretions of termite soldiers (Richardson & Levitan 1994). Stomach of one specimen killed in Dar es Salaam, Tanzania contained 12 Gutteral Toads *Bufo gutturalis*, the skin of which contains noxious poisons (K. Howell pers. comm.). Prey attack methods detailed in Ewer & Wemmer (1974). African Civets are likely to play an important role in dispersing seeds of forest trees; in Mayombe the average minimum dispersal distance was ca. 40 m from the parent tree (Pendje 1994).

African Civets are predominantly nocturnal, with peak activity beginning just before sunset until midnight (Rosevear 1974, Randall 1977). During a recent camera-trapping survey (55 trap-nights) undertaken in Zanzibar, all photographs of African Civets ($n = 8$) were taken during night hours, between 20:00h and 04:00h (Goldman & Winther-Hansen 2003). Seems to travel and forage habitually along the same routes (Rahm & Christiaensen 1963).

Social and Reproductive Behaviour Solitary, except when breeding (Rahm & Christiaensen 1963, Rosevear 1974, Kingdon 1977, Admasu *et al.* 2004c, Skinner & Chimimba 2005), and probably territorial (Rahm 1966, Randall 1977, Bearder & Randall 1978). One radio-collared subadult ♂ in S Ethiopia ranged over 11.1 km² during a 17-month period (Admasu *et al.* 2004c).

African Civets utilize latrines, depositing faeces in fixed places generally situated alongside roads or trails. Some latrines are used frequently, and then abandoned for several months (Randall 1977). Faeces are never buried, but rather piled on top of one another in shallow hollows (Gaillard 1969, Randall 1977, Bearder & Randall 1978, J.C. Ray pers. obs.). In one study in southern Africa savanna, latrines were communal, composed of scats of multiple individuals, and individuals visited more than one latrine (Randall 1977). However, exclusive use of latrines has been reported in a study in DR Congo (Pendje 1994), and in captive animals (Ewer & Wemmer 1974).

Scent-marking plays a role in communication and marking; both sexes have perineal and anal scent glands for this purpose (Pocock 1915, Ewer & Wemmer 1974, Jacob & Schliemann 1983). Secretions from anal glands added to faeces for long-lasting odour, probably serving a territorial marking purpose (Bearder & Randall 1978). Indeed, Rahm & Christiaensen (1963) followed the tracks of one individual that marked path intersections with anal secretions. Perineal gland secretions are used in marking objects along established routes, the function of which may be to provide olfactory information, such as sexual status, as scents are often overlaid by multiple individuals (Kingdon 1977, Randall 1977). Perineal secretions harden with age, but can retain strong odour for more than three months, even when covered by rain or insects (Randall 1977). Unfamiliar areas marked most extensively (Ewer & Wemmer 1974, Randall 1977, Schliemann 1990).

Adults are generally silent, except for ♀♀ in oestrus. In captive animals, the most frequent vocalization is a contact call, most often heard when cubs communicate with littermates, or when mothers



African Civet *Civettictis civetta*.

summon young (Ewer & Wemmer 1974). Known to hiss or growl in alarm or warning (Rosevear 1974).

All published mating and parturition records are from captive animals. Mating often preceded by courtship chases, which are initiated by the ♀, the dominant member of the pair (Kingdon 1977). Two matings in captive animals lasted 40 and 70 sec (Ewer & Wemmer 1974). Pair bonds not likely to be maintained in the wild following mating; captive ♀♀ are hostile to ♂♂ once cubs are born (Ewer & Wemmer 1974).

Reproduction and Population Structure In southern Africa, breeding occurs during warm, wet summer months with juveniles and gravid ♀♀ have been recorded from Aug to Jan (Skinner & Chimimba 2005). Rosevear (1974) reports no obvious breeding season in West Africa. The majority of births (19/22) at the Jersey Zoo in the Channel Islands occurred during the warmest period of the year (May–Oct) (Mallinson 1969, 1973). Gestation period ranges from 60 to 81 days (Ewer & Wemmer 1974, Kingdon 1977). Litter-size of captive animals 1–4 ($n = 27$; Mallinson 1969, 1973, Ewer & Wemmer 1974), but may be as many as five (Skinner & Chimimba 2005).

Females are polyoestrous, and may have two or three litters in one year. Maximum recorded duration of receptivity during oestrus is six nights; will go into heat 14 days following the loss of a litter (Mallinson 1973, Ewer & Wemmer 1974). Young are born fully furred, weigh about 300 g, with eyes open and in an advanced state relative to most carnivores (Ewer & Wemmer 1974). The coat pattern is poorly defined at birth, becoming clear during early stages of development (Skinner & Chimimba 2005). Weaning takes place from 14 to 16 weeks, with solid food provided by the mother in the second month (Ewer & Wemmer 1974). Captive ♀♀ attain sexual maturity at one year old, and give birth to first litters at 14 months (Ewer & Wemmer 1974). One captive animal lived to 28 years (Jones 1982, Weigl 2005).

Predators, Parasites and Diseases Large carnivores, such as Lions *Panthera leo* and Leopards *P. pardus*, probably prey on African

Civets opportunistically (Kingdon 1977). They were recorded in two of 117 Spotted Hyaena *Crocuta crocuta* scats in Niokolo-Koba N. P. in Senegal (Di Silvestre *et al.* 2000).

The following ticks have been recovered from animals in Kruger N. P., South Africa: *Amblyomma hebraeum*, *A. marmoreum*, *Boophilus decoloratus*, *Haemaphysalis leachi*, *H. zumpti*, *Ixodes* sp., *Rhipicephalus appendiculatus*, *R. evertsi*, *R. kochi* (which has a restricted distribution in NE South Africa, and was recovered from an animal taken near Pafuri), *R. simus*, *R. zambeziensis* and *R. zumpti* (Horak *et al.* 1987, 2000). In Ghana, African Civets appeared to be the major host for *Haemaphysalis leachi* and *Ixodes oldi* (Ntiemoa-Baidu *et al.* 2005). Horak *et al.* (2004) recovered the flea *Ctenocephalides damarensis* from animals in South Africa.

Pozio *et al.* (2005) recorded *Trichinella britovi* from a single animal taken in NW Guinea; trichinellosis is a human disease caused by eating raw or undercooked meat of animals infected with the larvae of *Trichinella* worms, but is typically considered a rare human disease in Africa, because of the practice of eating only well-cooked meats and religious laws that forbid the consumption of pork.

African Civets are also reported to be vectors of rabies (Enurah *et al.* 1988, Bingham *et al.* 1994), and are also susceptible to yellow fever (Dick 1952).

Conservation IUCN Category: Least Concern. CITES: Appendix III (Botswana).

African Civets remain relatively common within their wide distribution range, occur in a variety of habitats and are present in numerous protected areas. However, they may be undergoing some localized declines due to hunting. They are one of the most abundant mammals found in bushmeat markets within SE Nigeria, where they are utilized for both food and skin (Angelici *et al.* 1999c). They are frequently trapped for meat in Sierra Leone (Grubb *et al.* 1998), E DR Congo (Carpaneto & Germi 1989) and the savannas of N Central African Republic (R. Ruggiero pers. comm.). On Zanzibar I., African Civets appear regularly in the summaries of animals taken by National Hunters (subsidized by the Ministry of Agriculture), in spite of their protected status (Goldman & Winther-Hansen 2003). In N Congo, African Civet meat is so highly prized that it is rarely sold, with hunters opting instead to consume it themselves (R. Ruggiero pers. comm.). During one study following 96 hunters over a 1.5-year period in villages surrounding Banyang-Mbo Wildlife Sanctuary, Cameroon, African Civets represented 1% of the total offtake and biomass, and 7% of the carnivore offtake and 18% of the carnivore biomass (Nzouango & Willcox 2000). In Kisangani region, DR Congo, they represented only 2.3% of small carnivores trapped as bushmeat (Colyn *et al.* 1987), although this may have reflected its relative rarity in this forest region. The degree to which this species is killed in retribution for predation on domestic animals (e.g. Weladji & Tchamba 2003) is somewhat confounded by its being hunted for meat in many parts of its range (Ray *et al.* 2005).

African Civets are economically important due to their perineal secretion, a waxy substance which can be refined into the compound civetone, and which was exploited for many centuries as a fixing agent for perfumes (Dannenfeldt 1985). The African Civet musk trade has a long history, with present-day husbandry practices little changed over centuries. Males are preferentially harvested due to their larger perineal glands that are thought to produce a higher quality secretion. Even though there have been synthetic alternatives for this substance since the 1940s, civetone remains an important export commodity for Ethiopia, but also, to a lesser extent, for Niger and Senegal (Ray 1995b, Abebe 2000, Ray *et al.* 2005). Anal secretions (composed of a mixture of lipids, including cholesterol esters, monoester waxes, cholesterol and fatty acids), on the other hand, have no characteristic odour or commercial value (Bearder & Randall 1978, Jacob & Schliemann 1983, Saldern *et al.* 1987).

Measurements

Civettictis civetta

TL (♂ ♂): 1296 (1225–1374) mm, n = 8
 TL (♀ ♀): 1296 (1250–1370) mm, n = 11
 T (♂ ♂): 462 (416–500) mm, n = 8
 T (♀ ♀): 469 (423–492) mm, n = 11
 HF c.u. (♂ ♂): 140 (135–148) mm, n = 8
 HF c.u. (♀ ♀): 139 (130–148) mm, n = 11
 E (♂ ♂): 58 (55–60) mm, n = 8
 E (♀ ♀): 58 (54–63) mm, n = 11
 WT (♂ ♂): 10.9 (9.5–13.2) kg, n = 8
 WT (♀ ♀): 11.6 (9.7–12.7) kg, n = 11
 Zimbabwe (Smithers & Wilson 1979)

HB (♂ ♂): 829 (721–869) mm, n = 21
 HB (♀ ♀): 819 (742–881) mm, n = 15
 T (♂ ♂): 444 (409–502) mm, n = 19
 T (♀ ♀): 451 (413–503) mm, n = 14
 HF c.u. (♂ ♂): 137 (126–144) mm, n = 20
 HF c.u. (♀ ♀): 138 (124–145) mm, n = 15
 E (♂ ♂): 57 (54–62) mm, n = 19
 E (♀ ♀): 56 (54–62) mm, n = 14
 WT (♂ ♂): 12.1 (8.8–14.6) kg, n = 21
 WT (♀ ♀): 13.1 (9.2–16.4) kg, n = 15
 SE Nigeria (F. M. Angelici pers. comm.)

Skull measurements:

GLS: 149.4 (142.8–155.0) mm, n = 9
 GWS: 79.1 (73.5–88.2) mm, n = 9
 DR Congo (Allen 1924)

Key References Ewer & Wemmer 1974; Kingdon 1977; Ray 1995b; Rosevear 1974; Skinner & Chimimba 2005.

Justina C. Ray

Family HYAENIDAE
HYAENAS, AARDWOLF

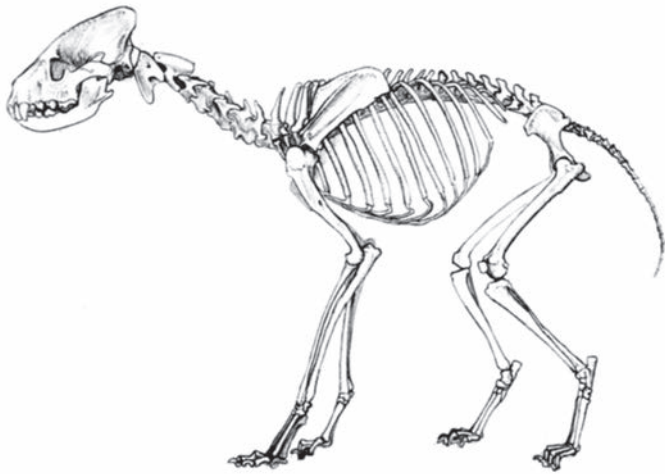
Hyaenidae Gray, 1821. London Med. Repos. 15: 302.

| | | |
|-----------------------------|--------------------------|--------|
| <i>Hyaena</i> (2 species) | Striped and Brown Hyaeas | p. 262 |
| <i>Crocuta</i> (1 species) | Spotted Hyaeana | p. 272 |
| <i>Proteles</i> (1 species) | Aardwolf | p. 282 |

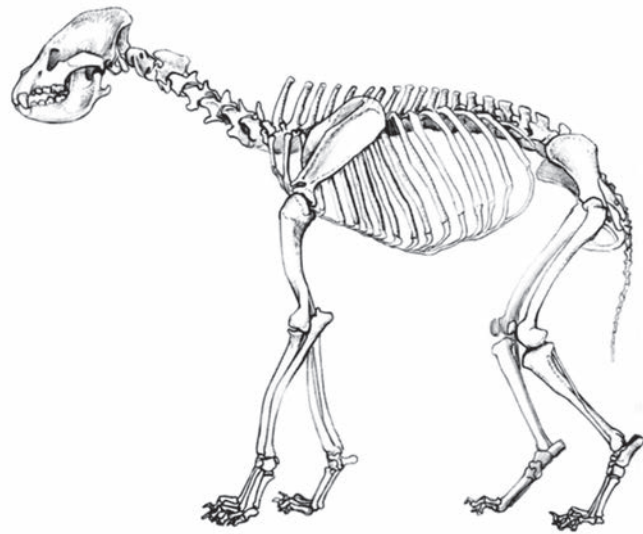
The hyaena family, Hyaenidae, today is the small remnant of a once extensive Eurasian radiation of more or less dog-like, hunting and scavenging carnivores of medium to very large size (Werdelin & Solounias 1991). At the present time, the family includes only four species: Spotted Hyaeana *Crocuta crocuta*, Striped Hyaeana *Hyaena (Hyaena) hyaena*, Brown Hyaeana *Hyaena (Parahyaena) brunnea* and the Aardwolf *Proteles cristatus*. Since the first three species are carnivorous/omnivorous meat-eaters and scavengers (though both species of *Hyaena* include a considerable amount of non-animal protein in their diet; Mills 1990), and the latter is a specialized feeder on social insects, the family retains considerable ecological diversity, despite its limited species richness. However, given that the diets of all four species require adaptations to ingesting food items that would not be healthy or digestible for a majority of carnivores, it is conceivable that the feeding diversity seen in hyaenas today stems from the evolution of such dietary tolerance in a common ancestor of all modern hyaena species living in the Miocene.

There has been controversy regarding the phylogeny and taxonomy of modern hyaenas, but the traditional view, going back to the nineteenth-century discovery of the Brown Hyaeana (Thunberg 1820), was that the Aardwolf was basal to the other three species, with Brown and Striped Hyaeanas closely related, and the Spotted Hyaeana as their closest relative. However, some prominent studies incorporating fossil taxa (Galiano & Frailey 1977, Werdelin & Solounias 1991) concluded on the basis of morphological data that the genus *Hyaena* as traditionally conceived is paraphyletic and that the Brown Hyaeana is the closest relative of the Spotted Hyaeana (though Werdelin & Solounias [1991] acknowledged that the supporting data were meagre). This required raising the subgenus *Parahyaena* Hendey, 1974 to the generic level. The first molecular phylogenetic study of extant hyaenas was that of Jenks & Werdelin (1998). These authors used sequence data from the cytochrome *b* gene of mtDNA to conclude that the traditional view was broadly correct, and that Brown and Striped Hyaeanas were each other's closest relatives. This view has been confirmed by Koepfli *et al.* (2006), who used an extensive data set of seven nuclear gene segments as well as the complete mtDNA cytochrome *b* gene to conclusively show that the Aardwolf is cladistically basal, Brown and Striped Hyaeanas are sister taxa, and Spotted Hyaeanas are a sister to this group. With this study the issue of the phylogeny of extant hyaenas has been laid to rest.

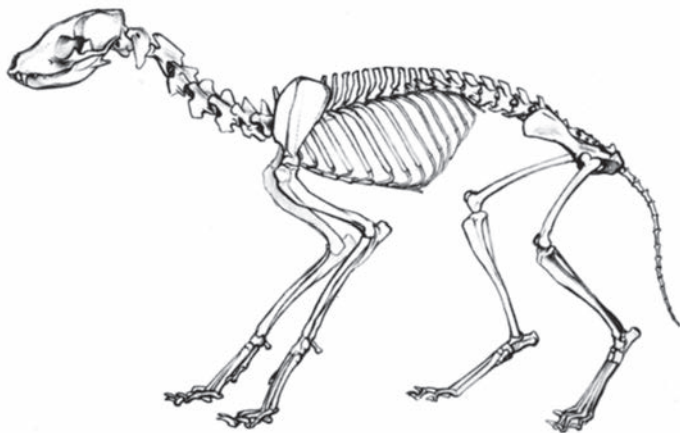
However, that agreement has been reached on hyaena phylogeny does not settle the issue of taxonomy. Brown and Striped Hyaeanas need not be placed in the same genus just because they are each other's closest relatives. This is especially true of a group such as the hyaenas, where the living species form a small, relictual subset of the diversity recorded in the fossil record. Since this is a matter of ranking, there



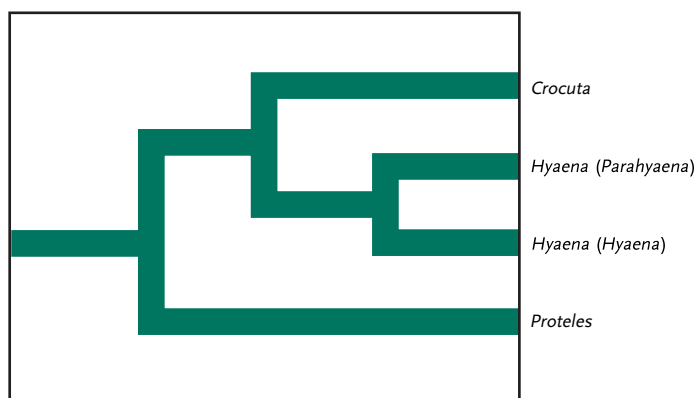
Striped Hyaeana *Hyaena hyaena* skeleton.



Spotted Hyaeana *Crocuta crocuta* skeleton.



Aardwolf *Proteles cristatus* skeleton.

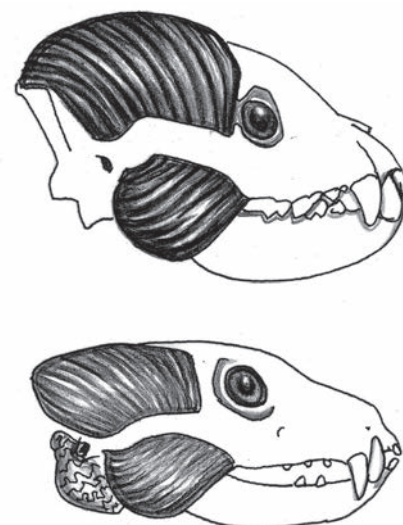


Tentative phylogenetic tree for extant Hyaenidae (after Koepfli *et al.* 2006).

is a strong element of subjectivity, but the rank of different taxa can also be important to public perception, conservation issues and so on, so attempts should be made to find criteria that afford some measure of objectivity and comparability between taxa. One criterion that seems have stood the test of time is that of Hennig (1966), who suggested that the age of a group could be an arbiter of its rank. For Carnivora, a useful cut-off point for the generic level could be the Miocene–Pliocene boundary. In most carnivoran families with a good fossil record and where cladistic precepts of taxonomy have been followed, Miocene taxa tend to have been accorded separate generic status from living taxa, whereas many Plio–Pleistocene taxa have been considered congeners with living ones. There may be exceptions and changes might be due to an end-Miocene turnover in carnivores and carnivore-like mammals (Werdelin & Turner 1996a), but at least this concept can be used as a rule of thumb: if a split between taxa predates the Miocene–Pliocene boundary they should be considered separate genera, if it is younger they should, perhaps, be considered at most subgenera (note that this timetable might not be valid for mammal orders other than carnivores).

When this rule of thumb is applied to hyaenas and combining dates from the fossil record with those from molecular studies (Jenks & Werdelin 1998, Koepfli *et al.* 2006), it is clear that *Proteles* and *Crocuta* derive from lineages that split from the other two taxa in the Miocene. Data for Striped Hyaena and Brown Hyaena are more equivocal. The molecular data of Koepfli *et al.* (2006) suggest a date of 4.2 (6.4–2.6) mya for this split so, if the modal date is accepted, subgeneric status for these taxa is indicated. However, some fossils named *Ikelohyaena abronia*, retrieved from several Miocene and Pliocene sites in Africa, may belong to the Striped Hyaena lineage to the exclusion of Brown Hyaenas. If so, the *Hyaena hyaena* lineage dates back to the Miocene, and *Hyaena* and *Parahyaena* should be raised to the generic level. The data are at present inconclusive and either path is acceptable, both that of Werdelin & Solounias (1991) and Koepfli *et al.* (2006), who use *Parahyaena* as a full genus, and that of Jenks & Werdelin (1998), Wozencraft (2005) and this volume, in which it is treated as a subgenus of *Hyaena*.

Hyaenidae originated in Eurasia in the early Miocene, ca. 20 mya (Werdelin & Solounias 1991), with small forms reminiscent in morphology and presumably ecology of modern-day civets. They went through a major radiation of dog-like forms in the middle and late Miocene, centred on Eurasia, but with extensions into Africa and North America (one genus). The earliest African record of Hyaenidae is from the middle Miocene of Morocco and it is not until the late



Chewing musculature in (above) Spotted Hyaena *Crocuta crocuta* and (below) Aardwolf *Proteles cristatus*.

Miocene (<11 mya) that the family is firmly established in sub-Saharan Africa. Thus, hyaenas came late to Africa and then in the form of well-known Eurasian genera such as *Protictitherium*, *Ictitherium* and *Hyaenictitherium* (Nakaya *et al.* 1984, Werdelin 2003a). Curiously, the only specialist bone-cracking hyaena of the Miocene, *Adcrocuta eximia* (Werdelin & Solounias 1990), although present at some North African sites, never reached sub-Saharan Africa, leaving an apparent ecological vacuum in the carnivore guild there (Werdelin & Turner 1996b). Some endemic African species of Hyaenidae evolved during the Miocene, and towards the end of the Miocene, the first endemic hyaena genera, *Ikelohyaena* and *Werdelinus*, appear (Hendey 1974b, Werdelin & Solounias 1991, De Bonis *et al.* 2010). The former, from the latest Miocene and early Pliocene of South and East Africa, is very similar to, though more primitive than, the modern Striped Hyaena, and could, in fact, be congeneric with it. Shortly after the appearance of this taxon, the first Brown Hyaena evolved, also as an African endemic (Werdelin 2003b), and by 3.5 mya the Spotted Hyaena had also evolved in Africa (Werdelin & Lewis 2008).

The four taxa of Hyaenidae share a number of features of their biology, some of which must have been inherited from the common ancestor, while some have evolved *de novo* in the modern lineages in response to parallel environmental challenges. The hyaenid head is triangular in overall shape, with strongly developed masticatory musculature, a prominent feature in most of the living animals. Unique, caudally elongated frontal sinuses are present in all living hyaenids (as well as several fossil species), except the Aardwolf; the sinuses completely overlie the brain cavity, a condition apparently unique in the history of the Carnivora (Joeckel 1998). The dental formula in living hyaenas is $I^{3/3}, C^{1/1}, P^{4/3}, M^{1/1} = 34$, except for the Aardwolf, which has lost its anterior-most premolars. It is curious that the Aardwolf, in which the cheekteeth have been reduced to pegs, still retains a nearly full complement of teeth, and Koepfli *et al.* (2006) view this as an argument in favour of a relatively late date for the evolution of the Aardwolf.

The pelage is spotted (*Crocuta*) or transversely striped (remaining taxa). In the Brown Hyaena a long mane of dark brown guard hairs covers the forequarters, upper limbs and part of the torso. These

guard hairs, and the hairs of the mane of the Aardwolf, are among the longest of any member of the Carnivora. A 'primitive' coat pattern, at least in the group to which living hyaenas belong, would seem to be transverse stripes to the body and legs. Similarities in the patterns of the Aardwolf and its larger relative, the Striped Hyaena are, therefore, likely due to retention from a common ancestor.

All species are digitigrade and highly cursorially adapted (e.g. Andersson 2004). The differing life-styles of the various taxa suggest that the cursorial features of the skeleton of Hyaenidae (elongated limbs, locked elbow joint, etc.) are more likely to be due to adaptations to long-distance, energy-efficient foraging in open environments than to adaptations to rapid pursuit hunting (Janis & Wilhelm 1993). The sloping-back posture and somewhat rocking-horse running gait of Striped, Brown and Spotted Hyaenas are due to elongation of the forelimb relative to the hindlimb (Kingdon 1977, Spoor 1985, 1986). This is seen to a much lesser degree in the Aardwolf, though in this case it is exaggerated by the erectile mane and robust digging forequarters of the animal.

Hyaenas occur in a wide variety of habitats, from semi-desert, savanna and open woodland to dense dry woodland. The Spotted Hyaena also occupies montane habitats of the Ethiopian and East African domes. Hyaenids differ greatly in social behaviour, though these differences are sometimes exaggerated due to the extreme adaptations of the Spotted Hyaena. Spotted and Brown Hyaenas live in fission–fusion clans of variable size, while Striped Hyaenas often rest in pairs or groups. However, the two species of *Hyaena* forage singly though they may congregate at a food source if it is rich enough, while Spotted Hyaenas often forage in groups of differing sizes. The Aardwolf is monogamous and occupies a perennial territory that is aggressively defended. Greeting ceremonies involving genital sniffing

and anal pouch eversion are similar in the larger species, but more extreme in the Spotted Hyaena.

The fossil record of the Hyaenidae shows living hyaenas to be but a remnant of a once extensive radiation across Africa and Eurasia and into North America. In spite of this, the fossil record for the Aardwolf is currently almost non-existent. Where the fossil record of the extant hyaenas and their lineages has been studied, the trend towards relictual distributions is also evident. The Striped Hyaena spread into western Eurasia and the Indian sub-continent relatively recently, with no fossil record to show for it (Rohland *et al.* 2005). Within Africa, however, its range has contracted in the Pleistocene–Holocene, as it is no longer present in areas of southern Africa where it once occurred, as shown in the fossil record. The Brown Hyaena has apparently always had its distribution centred in southern Africa, but is known to have at least occasionally extended its range into East Africa (Werdelin & Barthelme 1997). A migration corridor for such expansion is hard to perceive in contemporary habitats. The Spotted Hyaena today has a wide distribution in Africa, yet this distribution is only a small remnant of its distribution in the Pleistocene. At the height of its expansion, the Spotted Hyaena (either the modern species or one or more fossil species – the taxonomy is controversial) ranged throughout Eurasia from the Pacific coast of Siberia to the British Isles and throughout those parts of Africa for which a fossil record is known. The Eurasian forms became abruptly extinct towards the end of the Pleistocene and the range of the modern African species appears to have been contracting ever since. Thus, while there is no immediate cause for alarm, it is worth noting that the Spotted Hyaena today occupies only a fraction of its former range, with unknown consequences for its viability as a species.

Lars Werdelin

GENUS *Hyaena*

Striped and Brown Hyaenas

Hyaena Brisson, 1762. Regnum Animale, 2nd ed., p. 168.

A genus of carnivorous/omnivorous Hyaenidae, here subdivided into two subgenera, *Hyaena* (*Hyaena*), Striped Hyaena and *Hyaena* (*Parahyaena*), Brown Hyaena (see discussion in family profile). Both species are solitary foragers but tend to rest in pairs or groups, the Brown Hyaena more so than the Striped. The two species are allopatric today, but were at least potentially sympatric at times in the past, as both species have been recorded from sites in South Africa. However, a more likely scenario may be that their respective geographic ranges have fluctuated somewhat depending on changes in climate and environment during the Plio–Pleistocene and that they have thus replaced each other in the fossil record without being truly sympatric. The *Hyaena* (*Parahyaena*) lineage cannot be followed fully in the fossil record, but given its absence from East Africa after the early Pliocene (although there was a short incursion in the middle Pleistocene; Werdelin & Barthelme 1997), it must be concluded that it has for the most part been a southern African endemic. Fossils from there are known from the early Pleistocene onwards and all appear to represent the modern species (Werdelin & Turner 1996b). The *Hyaena* (*Hyaena*) lineage is more fully documented through the presence of a Pliocene form, *Hyaena makapani*, known from South and East Africa (Toerien 1952, Werdelin & Lewis 2005), which is



Striped Hyaena *Hyaena hyaena*.

smaller and more gracile than the living species (which replaces it in the latest Pliocene–earliest Pleistocene).

Lars Werdelin

***Hyaena brunnea* BROWN HYAENA (STRANDWOLF)**

Fr. Hyène brune; Ger. Braune Hyäne (Schabrackenhyäne)

Hyaena brunnea Thunberg, 1820. K. Svenska Vet.-Acad. Handl. Stockholm, p. 59.
 'Goda Hopps Udden; Södra Afrika' [South Africa, Western Cape Prov., Cape of Good Hope].

Brown Hyaena *Hyaena brunnea*.*Hyaena brunnea*

Taxonomy The taxonomy of the Brown Hyaena is still a matter of some conjecture. Jenks & Werdelin (1998) recommended that in the absence of clear-cut data regarding generic rank among hyaenas, and because genetic data unite Striped Hyaenas *Hyaena hyaena* and Brown Hyaenas as sister taxa relative to *Crocota* and *Proteles*, the former two should be lumped together in the genus *Hyaena*. At the same time, they noted evidence for the timing of the split between the Striped and Brown Hyaena at approximately 6 mya, i.e. in the Miocene. They acknowledged this relatively old date by placing the two in different subgenera, *Hyaena* (for Striped) and *Parahyaena* (for Brown), respectively. Wozencraft (1993), following Werdelin & Solounias (1991), raised *Parahyaena* to genus level (and see Bronner *et al.* 2003), but later Wozencraft (2005), on the basis of the evidence presented by Jenks & Werdelin (1998), returned the species to *Hyaena*.

Substantial individual variation led to early erection of several subspecific names (see synonyms). Pocock (1934a) recognized two subspecies, with *melampus* representing a different form, but most subsequent authors (Ellerman *et al.* 1953, Coetzee 1977, Meester *et al.* 1986) have not adopted this approach, and morphological evidence suggests that they should both be rejected (Jenks & Werdelin 1998). Synonyms: *fusca*, *makapani*, *melampus*, *striata*, *villosa*. Chromosome number: $2n = 40$; there are 70 autosomal arms; the X chromosome is submetacentric and the Y chromosome is acrocentric (Wurster-Hill 1973).

Description Medium-sized, dog-like animal with typical hyaena build, being higher at shoulders than at rump, giving appearance of a sloping back. Head, neck and shoulders massive, hindlegs, in comparison, appear almost wasted. Muzzle black, forehead lighter. Whiskers long and black. Ears long, about 140 mm, and pointed. Pelage shaggy, dark brown to black, except around neck and shoulders, which are off-white to tawny-white, as are underparts and insides of limbs. The long hair along the mid-dorsal line can be raised in a conspicuous display. Close up, body colour is uneven, with darker bands caused by broad black tips of guard hairs lying in juxtaposition. On upper parts of limbs are a series of white bands.

Tail is relatively short, dark and bushy. Forefeet much larger than hindfeet, a feature clearly marked in the spoor and making it possible to distinguish spoor of a Brown Hyaena from a Spotted Hyaena *Crocota crocuta*, where differences in size between forefoot and hindfoot are less marked. There is a clear difference between male and female reproductive organs, with the testes showing clearly just below the anus, unlike with the Spotted Hyaena. Females have two pairs abdominal nipples.

A characteristic feature of the skull is the shape of the braincase, which is narrower than in the Spotted Hyaena and not pear-shaped (Skinner 1976). Skull is highest at about level of intertemporal constriction, sloping off very gradually backwards and abruptly forwards to the nasals. Sagittal crest is well developed, but little evidence of a supra-occipital crest. Zygomatic arches broad (though less robust than in the Spotted Hyaena). Postorbital bars are incomplete (Skinner & Chimimba 2005). Dentition typically hyaenid.

Geographic Variation See Taxonomy.

Similar Species

Hyaena hyaena. Not sympatric, occurring only as far south as N and C Tanzania. Slightly smaller, with a pale grey to beige pelage and darker vertical stripes on the body and legs.

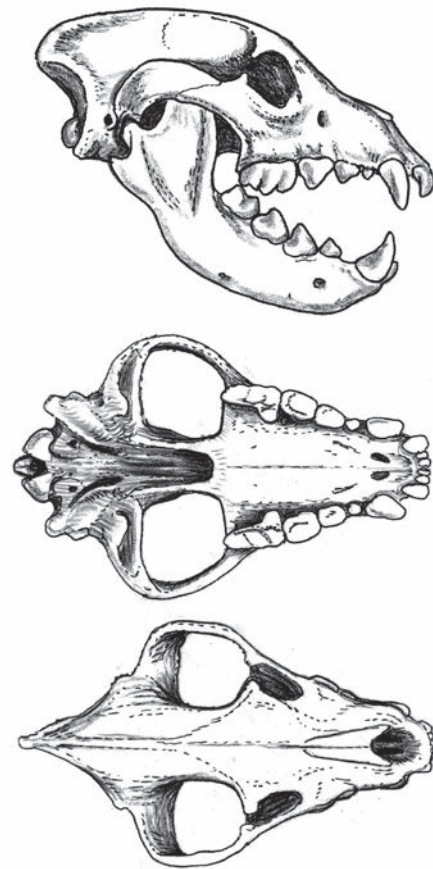
Crocota crocuta. Sympatric. Larger, and with spots on body, with round, not pointed ears and a short coat. Young adults tend to have darker spots and are light around the neck, and in poor light and at a distance may be mistaken for Brown Hyaena.

Distribution Endemic to southern Africa except for a marginal extension into the arid parts of SW Angola. The range of the Brown Hyaena has shrunk significantly since the end of the eighteenth century when it was last recorded from Table Bay in the extreme south-west of the continent. At the end of the nineteenth century it was still regularly found as far south as Malmesbury and Beaufort West in the then Cape Province, South Africa.

Current Distribution Still widespread in southern Africa. In Angola, only recorded from the south-west of the country (Crawford-Cabral & Simoes 1990). In Namibia sporadically encountered over most of the country, mainly along the coast, in Etosha N. P., and in Bushmanland in the north-east (Hofer & Mills 1998a), as well as from the Caprivi strip (Purchase *et al.* 2007). Widespread in Botswana, excluding the extreme north (Smithers 1971). In Zimbabwe mainly in the western parts of the country and also the extreme south (Smithers & Wilson 1979). In Mozambique reported from the Banhine Flats, an arid area in the south-west of the country (Smithers & Lobão Tello 1976). Records from Malawi are erroneous (see discussion in Ansell & Dowsett 1988) and there are no records from Zambia. In South Africa, recorded in recent years from the extreme south in the Western Cape (Gansbaai and Bredasdorp), where it was believed to be extirpated, so may be recolonizing some of these areas (Hofer & Mills 1998a). Occurs sporadically in the northern regions of the Eastern and Western Cape, and in the Northern Cape, particularly north of the Orange R. in the Kgalagadi Transfrontier Park and in the Richtersveld. Historically, they occurred over the entire Free State, but today are very sparsely dispersed over all except the western parts. Still occurs in most of North West Province, and the western parts of Mpumalanga and Limpopo Province; even occurs sporadically in Gauteng near densely populated areas. Found in many of the smaller game reserves, but absent as a breeding species over the eastern lowveld areas encompassing the Kruger N. P. and surrounding private reserves. Never common in KwaZulu-Natal, but recorded irregularly in the drier regions in the north-west; recently introduced into Hluhluwe-iMfolozi Park, the Eastern Shores of the Greater St Lucia Wetland Park, and Itala G. R., although their historical occurrence there is uncertain (Rowe-Rowe 1992a). Occurs only in the west of Lesotho (Lynch 1994). Presence in Swaziland is not confirmed, but they are likely to occur in the north-east and extreme west and north-west of Swaziland (Monadjem 1998).

Habitat Found in desert areas (e.g. the Namib) with annual rainfall less than 100 mm, particularly along the coast, as well as semi-desert, open scrub, and open woodland savanna with a maximum rainfall up to about 650 mm (Mills 1998a). It is independent of drinking water, but needs some type of cover in which to lie up during the day. Mills (1990) found that during the hot summer months in the SW Kalahari in Botswana they favoured the deep shade provided by Shepherd's Bush *Boscia albitrunca* or would use holes in the ground. They also have an ability to survive close to urban areas (see Skinner 1976).

Abundance Studies in Kgalagadi Transfrontier Park concluded that there are about 400 Brown Hyaenas in the park. Because of its secretive nature and nocturnal habits it is easily overlooked; therefore, numbers and distribution records may underestimate population size. Given this proviso, the total population size on the continent has been estimated at a minimum of 5000–8000 individuals, with



Lateral, palatal and dorsal views of skull of Brown Hyaena *Hyaena brunnea*.

Botswana having the largest population (an estimated 3900 animals) (Hofer & Mills 1998b).

Adaptations The powerful teeth and jaws, and associated well-developed head and neck muscles, enable Brown Hyaenas to crack open larger bones than other carnivores, except other hyaenas, and thereby extract highly nutritious marrow locked up in leg bones. The zygomatic arches swing out broadly at the back, providing ample room for the well-developed masseter and temporalis muscles. The teeth, in particular, are large and specialized for crushing bones, especially the premolars where the anterior and posterior cusps are reduced and the central cusp is enlarged, giving the tooth a conical hammer-like structure. The upper outer incisors are larger than the other incisors and canine-like and help the stout lower canines in holding and pulling. The lower canines are more curved than the upper ones and have a cutting ridge on the inside. The first two upper premolars are small, but the third and fourth are larger and more robust, with the fourth also having a shearing function (carnassial). The second lower premolars are small, but the third and fourth premolars are robust and strong and together with the third and fourth upper premolars are the most important bone crushers. The upper molars are elongated, set at right-angles to the toothrow, and occlude against the posterior shelves of the lower molars, performing a grinding function. The first lower molars are mainly for slicing and shearing and form the lower carnassial.

The massive forequarters of the Brown Hyaena enable them to carry large carcasses long distances to their cubs; in one instance an

individual carried 7.5 kg of a domestic cow calf back to a den from a distance of 15 km (Mills 1990). Their senses of hearing and sight appear to be particularly well developed, as is their sense of smell; carrion is mainly detected by smell, and even old and dry carcasses can be detected from 2 km downwind (Mills 1978b, 1990).

An evertable anal pouch is situated between the rectum and the base of the tail. It consists of a central region of enlarged sebaceous glands, a peripheral region of apocrine tissue and a groove running down the middle. The pouch secretes two distinct substances, a white paste rich in lipid (secreted from the sebaceous glands) and a black paste rich in lipo-fuchin (secreted from the apocrine glands). These substances are pasted onto plant stalks in an elaborate scent-marking behaviour, unique to the hyaenas, known as pasting (the black secretion is pasted higher than the white) (Mills *et al.* 1980).

Foraging and Food Brown Hyaenas are primarily scavengers of a wide range of vertebrate remains, supplementing their diet with wild fruits, insects, birds' eggs and the occasional small animal that is killed (Skinner 1976, Mills 1978a, 1982a, 1990, Mills & Mills 1978, Owens & Owens 1978, Skinner & Van Aarde 1981, Siegfried 1984, Stuart & Shaughnessy 1984, Maddock 1993b, Burgener & Gusset 2003, Maude & Mills 2005, Kuhn *et al.* 2008). Hunting is unspecialized and opportunistic, directed at small animals only (including seal pups) and largely unsuccessful. Of 128 hunts observed in the S Kalahari, only six (4.7%) were successful (including kills of Southern African Springhare *Pedetes capensis*, Springbok *Antidorcas marsupialis* lambs and a Bat-eared Fox *Otocyon megalotis*). Their success rate hunting Springbok *Antidorcas marsupialis* lambs was only 6% (far lower than Spotted Hyaenas) (Mills 1990). Carrion forms the primary component of the diet, particularly from ungulate carcasses.

Brown Hyaena exhibit a predilection for Ostrich *Struthio camelus* eggs that are easily carried and opened, something that the larger Spotted Hyaena seems to have greater difficulty in accomplishing. Average daily consumption rate was calculated as 2.8 kg per day (Mills 1990). In the S Kalahari (Kgalagadi Transfrontier Park) the Tsama Melon *Citrullus lanatus* and Gembok Cucumber *Acanthosicyos naudinianus* are important in its diet, providing also much of the animals' moisture requirements.

Along the Namib Desert coast, Brown Hyaenas feed predominantly on Cape Fur Seal *Arctocephalus pusillus* pups, only 2.9% of which were killed by the hyaenas (Goss 1986), and also scavenge other marine organisms washed up on the shore. In faecal analysis studies of hyaenas in the Namib Desert, Cape Fur Seal remains were the predominant prey item present in scats (Skinner & Van Aarde 1981, Siegfried 1984, Stuart & Shaughnessy 1984, Kuhn *et al.* 2008). Skinner *et al.* (1995) observed six occasions of hyaenas actually killing seal pups, when the hyaena would walk among the pups, bite one on or behind the head and carry it out of the seal colony.

Brown Hyaenas are mainly nocturnal with some crepuscular and diurnal activity. In the S Kalahari, they were particularly active from about 18:00 to 08:30h during the summer months and from about 16:30 to 06:00h during the winter months (Mills 1990). They are strictly solitary foragers, covering large distances in search for food. In the S Kalahari it spends on average 80% of the hours of darkness active and covers an average of 31.1 km per night, with the maximum recorded being 54.4 km (Mills 1990). Food items are often taken back to the den to provision the young, and bone assemblages have

been shown to reflect faunal composition of the area at that time (Skinner & Van Aarde 1981, Skinner *et al.* 1998, Skinner 2006, Kuhn *et al.* 2008).

Excess food is often stored. On one occasion a Brown Hyaena came across an Ostrich nest containing 26 eggs. It ate seven eggs in two nights and scatter-hoarded the remainder under bushes or in grass clumps at distances of up to 2 km from the nest. On ten occasions where hyaenas cached food, items were retrieved within 72 hours (Mills 1990).

The impact of the Brown Hyaena on domestic animals is usually small (Mills 1998a), although sheep and goats in particular, but also calves, poultry, domestic dogs and cats have very infrequently been recorded as kills. In agricultural areas of Mpumalanga and Limpopo Province, Skinner (1976) reported two cases of stock killing over several months that ceased once the individual predator was removed, even though there were other Brown Hyaenas in the area; for the most part, carrion and medium-sized and small indigenous animals were commonly eaten.

Social and Reproductive Behaviour Brown Hyaenas live in clans ranging in size from a solitary ♀ and her cubs to groups containing several ♀♀ and their offspring of different ages. Adult ♂♂ either remain with their natal clan, become nomadic, or immigrate into a new clan (Owens & Owens 1979b, Mills 1990). Although members of a clan forage singly, several may come together at a large food source (although when they do they usually feed one at a time) and members of a clan defend a common, fixed territory. In the S Kalahari clan territories were found to vary in size from 235 to 480 km² (n = 6; Mills 1990) and along the Namib Desert coast territory size for eight and 12 animals covered 420 km² and 220 km², respectively (Skinner *et al.* 1995). In agricultural areas of Gauteng, the range of a translocated adult ♂ was only 49 km², suggesting that agricultural development may in some instances be advantageous to the Brown Hyaena (Skinner & Van Aarde 1987). The type of food in the territory determines clan size, while the manner in which the food resources are distributed determines territory size (Mills 1990).

Territorial ownership and probably also information between group members is communicated mainly through pastings as well as by defecating at latrines. Brown Hyaenas distribute pastings throughout the territory, particularly in the core areas; an individual pastes on average 2.6 times per km moved (with no difference between sexes), and increase pasting frequency near territory boundaries. Pastings are placed on grass stalks, bushes or rocks. Pastings are so well distributed over a Brown Hyaena territory that an individual is hardly ever more than 500 m from an active pasting, which lasts for over 30 days (Mills *et al.* 1980, Mills 1990).

Latrines are scattered throughout the territory but tend to be concentrated around the boundary. Boundary latrines are visited more frequently than those within the territory. Latrines have a saucer-shape, are about 1 m in diameter and 150 mm deep. Latrines are used as marking posts, with a small stool placed in each as the hyaena moves from one to the other. Some latrines are used over a short period only, while other latrines are used over a period of years (Skinner & Van Aarde 1981, Mills 1982a).

Meetings between clan members involve mutual sniffing around the head and face, neck and body, and anal pouch. Muzzle wrestling

between subadults, and between subadults and adults (though rarely between adults) and allogrooming between all age classes, was also evident (Mills 1982a, 1990). No dominance hierarchy was found within the clans in the S Kalahari, although this may be different in other areas. In the Central Kalahari, Owens & Owens (1996) found a separate linear dominance hierarchy within each sex, and that the highest-ranking ♀ shared equal rank with the alpha ♂.

Territorial fights are usually ritualized neck-biting bouts between two animals of the same sex from different clans accompanied by loud yelling and growling by the submissive animal. Meetings between individuals of different sexes and from different groups are often amicable.

Both nomadic and immigrant ♂♂ may mate and all adult ♀♀ in a clan may reproduce, although the matriarch appears to produce more cubs than the others (Mills 1990). Mills (1990) described six mating bouts, with mean mating frequency 0.13 mounts/min, the mean interval between mountings 6.6 min, and the mean duration of mounting 42 min.

Cubs are born and raised in dens. The den is usually a single hole in the ground, often a disused Aardvark *Orycteropus afer* burrow, which the ♀ modifies to her requirements, although in some areas caves are used (Skinner 1976, Goss 1986). Dens have a narrow entrance of about 30 cm high and 50 cm wide, and typically have a single entrance (Mills 1990). At most dens a single litter of cubs is raised, but two or even more ♀♀ may share a den in territories where more than one ♀ breeds (Owens & Owens 1979a, Mills 1990). The breeding ♀♀ are usually a mother and her grown-up daughters and although they give priority to their own they may even suckle each other's cubs.

The denning period lasts 15 months, during which time the cubs use several different dens. In the S Kalahari each den is occupied for an average of 3.6 months. Mothers will carry cubs to new dens, but from about six months cubs may even initiate the move themselves (Mills 1990). For the first three months of their lives the cubs are nursed by their mother, typically at sunset and sunrise, after which the milk diet is supplemented to an ever-increasing degree by meat brought to the den. Consequently, Brown Hyaena dens often become littered with bones and other remains. All members of the clan help to feed the cubs by carrying food in the form of meat, skin and bones to the den (see Foraging and Food), although D. Owens & M. Owens (1984) reported differences between the sexes. After weaning, cubs begin to forage for themselves (Mills 1990).

Vocalizations include a loud growl when frightened, a yell or a short deep growl when confronted by Lions *Panthera leo* or in encounters with Spotted Hyaenas, and submissive animals may scream when neck-biting with dominants, or squeal or whine on greeting them. Cubs and subadults utter a soft growl, accompanied by panting, when muzzle-wrestling. Cubs utter a harsh whine prior to suckling, and a soft whine when being groomed. Adult ♂♂ utter a very soft growl when calling cubs in the den. The adults hoot and pilo-erect when approaching others on a kill. The Brown Hyaena has no long distance call analogous to the Spotted Hyaena's whoop, nor do they giggle (Mills 1990).

Reproduction and Population Structure The Brown Hyaena is a polyoestrous, non-seasonal breeder with anoestrous occurring during lactation. In the wild, oestrus in the ♀ lasts 4–6 nights. The gestation period is approximately 97 days and mean litter size is 2.3 (range 1–5; Skinner 1976). Mean inter-litter interval is



Brown Hyaena *Hyaena brunnea* with crest and tail hairs erected.

20.7 ± 4.9 months, although if a litter dies the ♀ will come into oestrus earlier (Mills 1990). Cubs are born with eyes closed, and ear pinnae folded; eyes start to open on Day 8 and are fully open by Day 14, while ears become erect at Day 28 (Schultz 1966). The cubs are weaned at 12–15 months of age. Birth-weight has been calculated as 693 g and full size is reached at about 30 months (Mills 1990). Cub and young adult mortality rates are low, but subadult and old adult mortality appears to be quite high. In the wild, maximum longevity is about 20 years (M. G. L. Mills pers. obs.); a captive individual survived to nearly 32 years (Weigl 2005).

Predators, Parasites and Diseases Over much of its range the Brown Hyaena lives in association with other carnivores and benefits from many of them by scavenging from their kills. Lion kills provide many scavenging opportunities for Brown Hyaenas (e.g. in the Central Kalahari; Owens & Owens 1978), although they are dominated, even sometimes killed, by Lions; Apps (1982) reported an instance in Kgalagadi Transfrontier Park of a Brown Hyaena seemingly shamming death in an attempt to avoid being killed by Lions. The Brown Hyaena is usually dominant over Leopards *Panthera pardus*, Cheetahs *Acinonyx jubatus*, Caracals *Caracal caracal* and often appropriates the kills of these species (Owens & Owens 1978, Mills 1990). Competition for food between the Brown Hyaena and Black-backed Jackal *Canis mesomelas* can at times be severe and vultures too can deprive it of food. The Spotted Hyaena is dominant to the Brown Hyaena and in certain areas deprives it of a significant amount of food. This may have a detrimental effect on Brown Hyaena numbers and may even affect its distribution as where the Spotted Hyaena is common the Brown Hyaena is usually absent or very rare (Mills 1990); this may, for example, partly explain the species' absence in N Botswana.

Wounds inflicted during both inter- and intra-specific fights and starvation, or starvation due to severe wearing down of the teeth and an inability to consume bones, are the main cause of natural mortality in protected areas. Although rabies has been recorded from Brown Hyaena (Swanepoel *et al.* 1993), no evidence for disease being an important form of mortality has been found.

Not a great deal of information is available on parasites. Mills (1982a) mentions fleas often found on cubs, and that the flea

Echinophaga larina was identified from one individual. Hyaenas in the S Kalahari rarely had ticks, although Horak *et al.* (2000) recorded *Haemaphysalis leachi*, *Rhipiceptor nuttali* and *Rhipicephalus simus* on an animal taken in Gauteng. Internal parasites taken from Brown Hyaenas include a tape-worm *Taenia hyaenae* and a nematode *Spirocerca lupi* (Mills 1982a).

Conservation IUCN Category: Near Threatened. CITES: Removed from Appendix II in 1999.

There are a number of large conservation areas with viable populations of the Brown Hyaena, including: Namib-Naukluft, Skeleton Coast, Sperrgebiet and Etosha National Parks (Namibia), Kgalagadi Transfrontier Park (South Africa, Botswana), Pilanesberg N. P. (South Africa) and the Central Kalahari G. R. (Botswana). Outside protected areas the Brown Hyaena may run into conflict with humans, and they are often shot, poisoned, trapped and hunted with dogs in predator eradication or control programmes, or inadvertently killed in non-selective control programmes. In spite of this, they appear to do quite well in many areas. They are also occasionally run over by vehicles in South Africa, though this is unlikely to represent a major threat (Mills 1998a). Although used in traditional medicine and rituals, it is not nearly as sought after in this regard as the Spotted Hyaena (Hofer & Mills 1998b).

Measurements

Hyaena brunnea

TL (♂ ♂): 1445 (1320–1609) mm, n = 16

TL (♀ ♀): 1331 (1105–1516) mm, n = 17

T (♂ ♂): 205 (177–236) mm, n = 14

T (♀ ♀): 223 (170–300) mm, n = 14

HF c.u. (♂ ♂): 211 (191–234) mm, n = 14

HF c.u. (♀ ♀): 212 (200–225) mm, n = 14

E (♂ ♂): 150 (138–161) mm, n = 13

E (♀ ♀): 146 (135–167) mm, n = 14

WT (♂ ♂): 43.6 (35.0–49.5) kg, n = 20

WT (♀ ♀): 40.4 (28.0–47.5) kg, n = 20

Zimbabwe (Smithers & Wilson 1979), S Kalahari (Mills 1982b) and Gauteng and Limpopo Province, South Africa (Skinner & Ilani 1979). Exceptional body weight measurements include those of a ♀ from the Eastern Cape weighing 67.6 kg (P. Swanepoel, in Mills 1998a) and an animal of unrecorded sex weighing 72.6 kg from Mpumalanga (Roberts 1951).

Key References Mills 1982a, 1990, 1998; Owens & Owens 1979a, 1996; Skinner 1976; Skinner & Chimimba 2005.

Gus Mills

Hyaena hyaena STRIPED HYAENA

Fr. Hyène rayée; Ger. Streifenhyäne

Hyaena hyaena (Linnaeus, 1758). Syst. Nat., 10th edn, 1: 40. 'India', restricted by Thomas (1911: 134) to 'Benna Mts, Laristan, S. Persia'.

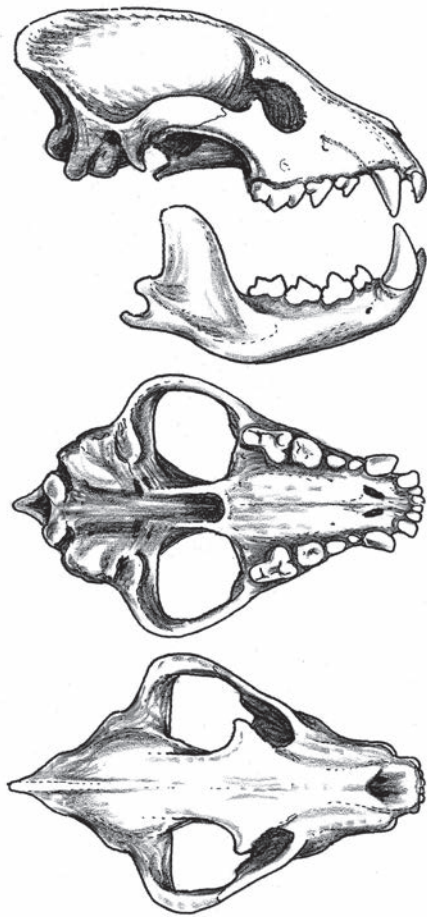


Striped Hyaena *Hyaena hyaena*.

Taxonomy Pocock (1934a, b) condensed the number of subspecies across the entire species' range from the 28 defined by the beginning of the twentieth century to five, based on cranial measurements and pelage characteristics: *H. h. barbara* from north-west Africa, *H. h. dubbah* from north-east Africa, *H. h. syriaca* from Syria, Asia Minor and the Caucasus, *H. h. hyaena* from India and *H. h. sultana* from Arabia (although see Coetzee [1977] who regarded *vulgaris* as a distinct subspecies). Rieger (1979a) suggested integrating these into a smaller, north-east

African-Arabian group composed of *H. h. dubbah* and *H. h. sultana* and a larger, north-west African-Asian group comprising *H. h. barbara*, *H. h. syriaca* and *H. h. hyaena*. However, Jenks & Werdelin (1998) noted the inadequacy of available morphological data on variability to characterize each subspecies and that any classification was provisional. Synonyms: *antiquorum*, *barbara*, *bergeri*, *bilkiewiczzi*, *bokcharensis*, *dubbah*, *dubia*, *fasciata*, *hienomelas*, *hyaenomelas*, *indica*, *orientalis*, *rendilis*, *satunini*, *schillingsi*, *striata*, *suilla*, *sultana*, *syriaca*, *virgata*, *vulgaris*, *zarudnyi*. Chromosome number: 2n = 40, with 32 metacentric-submetacentric and 6 acrocentric autosomes, a metacentric X and an acrocentric Y (Berube-Genest *et al.* 1987).

Description Medium-sized carnivore with overall appearance reminiscent of a dog. Muzzle pointed and head broad with long, pointed ears. Back slopes downward from head to tail. Coat has black vertical stripes on side, horizontal stripes on legs and a distinctive dark patch (or broad, dark 'stripe') on the throat. Underfur colouration pale grey or beige; however, some individuals may appear more white. Pelage colouration varies by region and may vary seasonally in colder parts of its range (Pocock 1934a, Rosevear 1974, Ilani 1975). Ground colour of pelt typically grey to light brown, but may appear strikingly white even within the same population. Cub ground colour appears very white and the contrast between ground colour and black striation patterns is much more apparent (Rosevear 1974, Rieger 1978, A. P. Wagner pers. obs.). Longest hairs are up to 200 mm long (Rosevear 1974) and fall along the mid-dorsal line. The black dorsal mane may be held erect, significantly increasing apparent size of the animal (Schneider 1926,



Lateral, palatal and dorsal views of skull of Striped Hyena *Hyaena hyaena*.

Pocock 1934a, Kruuk 1976, Rieger 1978). Legs appear thin relative to their length and hindlegs are shorter than forelegs. Feet have four toes with short, non-retractable claws (Pocock 1916c). Tail long with long coarse hairs. Well-developed anal pouch, a slit-like glandular orifice over-arching the anus from either side. Anal pouch may be everted and thus be apparent while pasting or presenting during social encounters (Holzapfel 1939, Fox 1971, Kruuk 1976, Rieger 1977, 1978). In juveniles, there is an unusual convergence in genital appearance between sexes (Wagner *et al.* 2007b). Juvenile ♀♀ have well-defined labia-like folds anterior to the vagina. These ridges are hairless and darker than surrounding tissue. Juvenile ♂♂ have smaller, smooth, hairless pre-scrotal skin folds along the middle septum close to, but anterior to, the scrotum. Unlike Spotted Hyena *Crocuta crocuta*, convergence in genital appearance is not complete enough to confuse the sexing of juveniles and adult genitalia appear normal. There is no apparent sexual dimorphism in body measurements and weight (Mendelssohn & Yom-Tov 1987, A. P. Wagner pers. obs.).

Skull differs from that of *Crocuta* in being slightly smaller in size and less massive in overall build (Rosevear 1974) and having a slightly lower profile of the sagittal crest (A. P. Wagner pers. obs.). Permanent dentition distinctly carnassial and dental formula typically hyaenid. Compared with *Crocuta*, the upper molar is much larger, as much as twice or more the size of the first premolar (Rosevear 1974, Coetzee 1977).

Geographic Variation Existing subspecies descriptions are based on limited data except for *H. h. syriaca* in Israel and *H. h. dubbah*

in Kenya (Mendelssohn & Yom-Tov 1987, Wagner 2006). Differences in pelage across the range appear minimal, although the Lebanese population is reported to have a reddish base-coat colour (Lewis *et al.* 1968) and hyaenas on the Arabian peninsula are described as having a yellow mark below the eyes (Gasparetti *et al.* 1985) and the dorsal crest is mixed grey and black rather than predominantly black (Mendelssohn & Yom-Tov 1987). *Hyaena h. dubbah* lacks the pronounced, thickened fold of skin on the throat (somewhat reminiscent in appearance of a goitre), which is apparent in northern populations (A. P. Wagner pers. obs.). Given the comments of Jenks & Werdelin (1998), no subspecies are listed here.

Similar Species

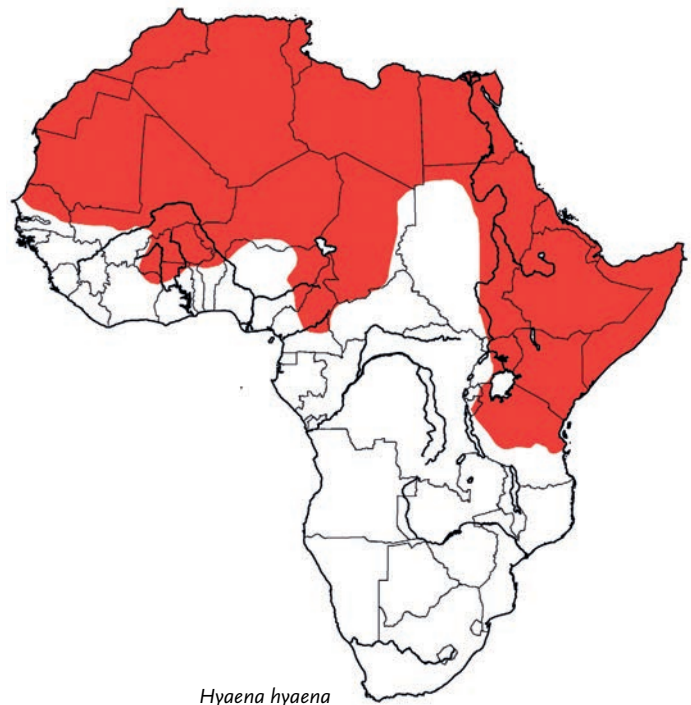
Crocuta crocuta. Sympatric across much of the range. Spotted pelage and back not maned; relatively short tail; short, rounded ears.

Proteles cristatus. Sympatric in East and north-east Africa. Marked difference in body size (about 9 kg) with more gracile build and large pointed ears; finer coat hairs appear glossier than the coarse coat of the Striped Hyena; coat also with black vertical stripes, but more regular; cheekteeth rudimentary.

Hyaena brunnea. Southern Africa only. Stripes on legs only, with characteristic dark, long-haired, shaggy coat, and lacking a distinct mane.

Distribution The Striped Hyena has a very large range extending from Africa, north of and including the Sahel, and including much of East and north-east Africa, through the Middle East and Arabian Peninsula, the Caucasus, Turkey, central Asia, and the Indian sub-continent, though not reaching Bhutan or Burma. Across their wide range, current distribution is patchy and most populations are likely composed of isolated small populations (Hofer & Mills 1998a).

The current distribution of the species was reviewed by Hofer & Mills (1998a). In North Africa, their distribution extends from S Morocco eastward along the extent of the North African coast to



Hyaena hyaena

convergence in male and female external genital appearance from a common ancestral hyaena species (Wagner *et al.* 2007b).

Cubs are raised in dens, which may be holes dug by the mother, holes formed and abandoned by other species (Roberts 1977, A. P. Wagner pers. obs.), deep, natural and sometimes complex, caves (Heptner & Sludskii 1972, Kerbis-Peterhans & Horwitz 1992, Leakey *et al.* 1999), or simple rock depressions less than a metre deep (A. P. Wagner pers. obs.). Where large caves are not available, mothers relocate cubs frequently; starting just a few days after birth, they move cubs to a new (or reuse an old) den every few days or weeks (A. P. Wagner pers. obs.).

Foraging and Food The diet of the Striped Hyaena is still a matter of some debate. However, it has been reported to consume a wide variety of vertebrates, invertebrates, vegetables, fruit and human originated organic wastes (Flower 1932, Harrison 1968, Ilani 1975, Kruuk 1976, Macdonald 1978, Leakey *et al.* 1999, Wagner 2006). It is known to scavenge off Lion *Panthera leo* and Spotted Hyaena kills (Kruuk 1976, Wagner 2006) as well as discarded livestock carcasses (Leakey *et al.* 1999, Wagner 2006). Kruuk (1976), Macdonald (1978), Bouskila (1984), Leakey *et al.* (1999) and Wagner (2006) all found remains of prey items in faecal samples that were likely scavenged. In many areas, Striped Hyaenas have also been described as raiding human graves and carrying away bones (Rosevear 1974, Horwitz & Smith 1988, Leakey *et al.* 1999), and fruit and vegetable crop raiding is considered a serious problem in Israel (Kruuk 1976).

The overall reputation of the species, therefore, is that of an omnivorous scavenger. However, in C Kenya analysis of faecal bone fragments and hairs indicates that hyaenas regularly consume smaller mammals and birds that are unlikely to be scavenged (Wagner 2006). This is in agreement with Kruuk's (1976) observations, but previous interpretations of the limited data available (Rosevear 1974, Skinner & Ilani 1979, Leakey *et al.* 1999) often under-emphasized the evidence for active hunting. In S Kenya, Striped Hyaenas were regularly observed flushing out, chasing and killing juvenile Grant's Gazelle *Nanger granti* (A. P. Wagner pers. obs.). Striped Hyaenas have also been reported chasing hares *Lepus* spp., porcupines *Hystrix* spp., Bat-eared Foxes *Otocyon megalotis*, Cheetah *Acinonyx jubatus* cubs, Dik-dik *Madoqua* spp., and Reedbuck *Redunca* spp. (Kruuk 1976, Skinner & Ilani 1979). Further, there is strong evidence that small livestock (goats and sheep) and dogs are killed (Rosevear 1974, Leakey *et al.* 1999, Kuhn 2005, A. P. Wagner pers. obs.). Thus, the Striped Hyaena foraging strategy includes both active hunting and scavenging.

Several studies have inferred diet by combining data from bone collections with analysis of faecal samples (Kerbis-Peterhans & Horwitz 1992, Leakey *et al.* 1999), while others have inferred diet from den bone collections alone (Skinner & Ilani 1979, Kuhn 2005; and see Skinner 2006). Bone contains organic matter, mostly collagen, at up to 40% in weight (Kruuk 1972). The Spotted Hyaena is able to digest and absorb this organic matter and only the inorganic material is excreted. Striped Hyaenas likely have a similar ability to draw nutrients from digestion of bones. Following a very severe drought in 1962, Kingdon (1977) examined the stomach of one Striped Hyaena that contained nothing but 3 kg of large splintered bones that were so dry that they rattled in the stomach when the hyaena cadaver was shaken! The rest of the digestive tract showed that the animal was subsisting habitually on similar old bones and the digestion was successfully breaking such bones down into congealed white faeces. Bone collections are common at den

sites for the species, but the nutritional role of these bones, the degree to which these collections represent scavenged vs. killed prey and the degree to which bone collections reflect flesh consumed is unclear. In C Kenya, den bone collections represented a much broader range of prey and included far more larger mammals than did scat analysis (Wagner 2006). Significant portions of these bone assemblages were very old bones unlikely to represent scavenging from fresh kills.

Although sometimes found in small groups of up to four individuals while resting, Striped Hyaenas appear to be strictly solitary foragers in Africa (Kruuk 1976, Wagner *et al.* 2008). In Israel, however, groups of hyaenas do converge at feeding sites (Kruuk 1976, Macdonald 1978, Skinner & Ilani 1979, Bouskila 1984), but there is no clear indication of cooperative foraging and relatedness of these observed groups has not been investigated. Foraging activity in Kenya and Tanzania was restricted entirely to night-time except during rain and/or unusually dark and cloudy weather (Kruuk 1976, A. P. Wagner pers. obs.). Under those weather conditions, Striped Hyaenas may return to previously visited kills or carcasses, but do not embark on full foraging forays (A. P. Wagner pers. obs.). Age-specific foraging data are extremely limited, but cubs have been observed accompanying their mothers on foraging forays by 6–12 months of age (Kruuk 1976, A. P. Wagner pers. obs.).

Kruuk (1976) described foraging behaviour in which Striped Hyaenas zig-zagged across the landscape and did not follow set routes, even when returning to the same food source on multiple nights. Striped Hyaenas spent long periods of time sniffing at the base of trees and bushes, but the head was generally held high while travelling. Caching of food under bushes was also observed. Minimum mean distance travelled per night was 19 km at speeds of 2–4 km/h, occasionally trotting at speeds of up to 8 km/h, or running at a maximum of 50 km/h. From observations made at feeding stations in Israel, it was estimated that an adult Striped Hyaena consumes 7–8 kg per night (Skinner & Ilani 1979).

Overall, the evidence indicates Striped Hyaenas in Africa are solitary nocturnal foragers for which fruit and vegetable matter, where available, may play a significant part. Striped Hyaenas also regularly consume insects, invertebrates, small vertebrates and actively hunt small mammals and ground-nesting and/or ground-feeding birds. In addition, they scavenge off carcasses of larger mammals and this activity appears to account for a significant portion of the bones collected at den sites.

Social and Reproductive Behaviour Almost invariably described as solitary in Africa, research in Kenya has shown that Striped Hyaenas routinely rest in pairs and occasionally in groups of up to four individuals (Wagner *et al.* 2008). Adult ♂♂ within a group are typically unrelated or distantly related to other adults in the group (Wagner *et al.* 2007a). However, full-sibling brother–sister and full-sibling brother–brother pairs were observed within groups. Group-living ♂♂ fathered the majority of cubs, but 31% of paternities were extra-group. Multiple paternity was probable in half of the litters examined.

Very little has been recorded regarding direct social interactions outside of captive situations. Kruuk (1976) did note the meeting ceremony between greeting pairs, which involved mutual sniffing of the face, neck and anal regions. The anal pouch was protruded during sniffing and either both hyaenas were standing or one would lie down while exposing the anal region. Observations in captivity (Rieger 1978) match these field observations and Fox (1971) observed anal protrusion displays in cubs at eight weeks of age. The dorsal mane is also erected by Striped Hyaenas in a defensive posture or when threatened and,



Striped Hyaena
Hyaena hyaena.

when aggressive, both the mane and the tail hairs are erected (Schneider 1926, Kruuk 1976, Rieger 1978, A. P. Wagner pers. obs.). Erect or limp dorsal manes have been interpreted as signals that indicate dominant or subordinate status to other hyaenas, respectively (Kingdon 1977).

Home-range sizes in Serengeti N. P. were reported for one ♂ and one ♀ at 44 and 72 km², respectively (Kruuk 1976). In Kenya, mean home-range size for four ♂♂ and six ♀♀ was 68.9 km² (S.E. = 7.8) (Wagner *et al.* 2008), with no significant difference in home-range size between sexes. No two adult ♀♀ were found to have significant home-range overlaps, although groups of up to three ♂♂ and one adult ♀ had almost complete overlap in home-ranges.

Descriptions of mating behaviour come from observations in captivity. Males will follow an oestrous ♀ for several days before being allowed to mate (Bothma & Walker 1999). Mating lasts only one day and consists of up to five mating attempts lasting 15–45 min each, with intervals between mating attempts of about 20 minutes. No pelvic thrusting has been observed (Rieger 1979a).

Cubs are reared in dens (described above) and intense digging behaviour by ♀♀ announces parturition (Rieger 1979a). Mothers carry food back to the den for their cubs (Kruuk 1976, Davidar 1990). When resources are abundant, mothers and their adult daughters may share a range and may use communal dens (A.P. Wagner pers. obs.). Subadult ♀♀ that have not dispersed will frequent their younger siblings' dens and may act as helpers (Wagner *et al.* 2007a). While Bothma & Walker (1999) reported that ♂♂ remain with the ♀ until cubs are raised, given the shared use of space when no cubs are present, it is not clear to what extent ♂♂ participate in cub rearing. In S Kenya, where resident adult ♀♀ (mother-daughter) and a juvenile ♂ routinely provisioned and interacted extensively with cubs at individual and communal dens, visits by the resident adult ♂ were rare, brief and did not include provisioning (A. P. Wagner pers. obs.).

Striped Hyaenas are considerably quieter than Spotted Hyaenas (Rosevear 1974) in terms of both volume and frequency of vocalizations, and are generally silent. However, Kruuk (1976) noted that Striped Hyaenas are more vocal in Israel and their relative silence in East Africa may reflect a behavioural response to avoid dominant carnivores in the region. Vocalizations are similar to those of the Spotted Hyaena and include whining by cubs before suckling, giggling when frightened,

yelling when being chased by conspecifics, howling in a defensive position, growling when play or food-fighting, and a call by the mother to her cub(s) (Kruuk 1976, Rieger 1981, A. P. Wagner pers. obs.).

Reproduction and Population Structure Parturition is aseasonal and gestation lasts 90–91 days (Pocock 1941, Ronnefeldt 1969, Heptner & Sludskii 1972, Skinner & Ilani 1979). Litter-sizes in the wild range from 1–4 cubs and from 1–5 in captivity (Skinner & Ilani 1979, Rieger 1981, Wagner *et al.* 2007a). In captivity, newborn cubs weigh 660–700 g (Skinner & Ilani 1979, Rieger 1981) and reach mean weights of 796 g at one week, 1.5 kg at four weeks, 2.8 kg at eight weeks and 5.6 kg by 28 weeks (Skinner & Ilani 1979). In the wild, cub weights were recorded at 2 kg at 2–3 weeks of age (A. P. Wagner pers. obs.). Cubs are born blind with white to grey fur and clear black stripes. Eyes open at 7–8 days, and teeth erupt at 21 days; cubs start to eat meat after the first month (Rieger 1981). Weaning in captivity takes place after eight weeks, but in the wild cubs have been observed suckling at 4–5 months (Ilani 1975) and 10–12 months (Kruuk 1976). Sexual maturity is reached at 2–3 years (Rieger 1979b), although one ♀ in captivity gave birth at the early age of 18 months (Rieger 1979b). In captivity, postpartum oestrus follows 20–21 days after birth and oestrous cycles last 40–50 days (Rieger 1979a, b).

Little has been reported regarding sex ratios in the wild. However, in Kenya the two complete litters sexed had three ♂♂ in one litter and one male and one female cub in the other (Wagner *et al.* 2007a). The well-sampled adult population had a sex ratio of 0.8 : 1 adult ♀♀ to ♂♂ (Wagner *et al.* 2008). As there are no long-term studies of the species in the wild, longevity has only been reported in captivity at 23–24 years (Rieger 1979a; and see Weigl 2005). From the Laikipia study, non-age-specific probabilities of survival for adult hyaenas (those over two years of age) were estimated for the duration following the time each hyaena was first identified. Survival to six months post-identification was estimated at 0.96 (n = 27), 0.89 for survival to one year post-identification (n = 27), 0.62 for two years (n = 21), and the probability of surviving three years after a hyaena was first identified was 0.47 (n = 17) (Wagner 2006). Of the nine cubs identified before six months of age (three female, four male, two unknown sex), at least four (two female, two male) had survived to at least two years. This is a minimal survival rate as the cubs were not radio-collared and survival could only be confirmed if they were resighted.

Predators, Parasites and Diseases Interactions with other carnivores are best considered in terms of dominance and competition rather than predation. The Striped Hyaena is subordinate to Lions and Spotted Hyaenas, although Kruuk (1976) described a mutual 'attraction' between the two hyaenas. There is also suggestive evidence that competition with Spotted Hyaenas may be important in circumscribing the habitat used by Striped Hyaenas (H. Kruuk pers. comm.). Outcomes of encounters with Cheetahs and Leopards *Panthera pardus* are not as predictable, but adults of those species are likely to dominate Striped Hyaenas. Skinner & Ilani (1979) reported that a Caracal *Caracal caracal* dominated three subadult Striped Hyaenas of about 29 kg each.

The importance of the Striped Hyaena as a reservoir or vector for domestic animal and human disease has not been well evaluated. The spatial overlap with humans and domestic animals in many parts of the Striped Hyaena's range may be significant in this regard.

Conservation IUCN Category: Least Concern. CITES: Not listed.

Humans are consistently indicated as the major source of mortality throughout the evaluated range (Hofer 1998a) and were responsible for 50% of recorded deaths in C Kenya (Wagner 2006). Negative perceptions of the species persist throughout its range and collection of human remains ('grave robbing') and incidents of damage to agriculture and livestock perpetuate negative attitudes. Striped Hyenas are very susceptible to accidental or targeted poisoning as they readily accept strychnine-poisoned bait. For example, along the Mediterranean coast in Israel, the Striped Hyena was exterminated by strychnine poisoning during the rabies eradication campaign administered by the British government between 1918 and 1948. The Striped Hyenas ate poisoned donkey carcasses that were provided to control Golden Jackals *Canis aureus*, then the main carrier of rabies (Hofer 1998a). The population in Niger is apparently declining as a result of officially sanctioned eradication or poisoning and indirectly by habitat destruction through overgrazing and agricultural encroachment (Hofer & Mills 1998b). Habitat destruction is also viewed as a threat in Kenya and effective protection is absent as hyenas are viewed with contempt. In this region, due to the lack of differentiation between the species, Striped Hyenas are often killed when Spotted Hyenas are the intended target (Wagner 2006).

Striped Hyenas are also subject to trade in skins and body parts, mainly for use in traditional medicine. In North Africa, the animal's brain is used as an aphrodisiac and hairs are used as a talisman (Ronnefeld 1969, Rieger 1979a, Osborn & Helmy 1980). In Morocco, where the species is commercially hunted for use in traditional medicine (and may fetch very high prices; F. Cuzin pers. comm.), the population has declined drastically and has withdrawn into the southern mountainous regions. In Egypt, Striped Hyenas are hunted for utilization of the whiskers and eyeballs as protection from the evil eye and the heart for courage (Osborn & Helmy 1980).

Striped Hyenas are present in numerous protected areas, including: Djurdjura N. P. and Mergueb N. R. (Algeria), 'W' N. P. and Arly N. P. (Burkina Faso), Waza N. P. (Cameroon), Awash N. P., Mago N. P., Omo N. P. and Yabello Sanctuary (Ethiopia), Masai Mara National Reserve, Tsavo East & West N. P., Samburu N. R. and

Lake Nakuru N. P. (Kenya), Boucle du Baoulé N. P. (Libya), Reserve integrale de Missou, Tazeka N. P. and Parc National de l'Oriental (Morocco), Boundou, Ferlo Nord, Ferlo Sud and Cayor Faunal Reserves (Senegal), and Serengeti N. P., Tarangire N. P., Ngorongoro Conservation Area and Mkomazi G. R. (Tanzania) (Hofer & Mills 1998a). Recent records also indicate the species occurs outside of protected areas in a number regions, including, for example, in Egypt, in the Nile Valley and near oases in the west, Mediterranean and Red Sea coastal areas, and, in Kenya, in Masailand, L. Natron, the central Highlands including Laikipia and Samburu Districts, L. Turkana region, and parts of Kajiado District (Hofer & Mills 1998a, Wagner 2006). Because they exist outside of formally protected areas in regions where pastoralism is the norm and the potential for human–carnivore conflict is very high, populations in Egypt and Kenya are exceptionally vulnerable to human population growth, habitat destruction and poisoning. Particular attention should be paid to ensuring the survival of the species in pastoral areas by identifying ways to reduce human–carnivore conflict through promotion of methods that ensure adequate numbers of prey persist and/or methods that reduce livestock killing by carnivores.

Measurements

Hyaena hyaena

HB: 1083 (980–1180) mm, n = 55

T: 294 (260–360) mm, n = 55

HF c.u.: 216 (194–245) mm, n = 54

E: 147 (126–160) mm, n = 51

WT: 30.0 (23.0–35.0) kg, n = 35

Laikipia District, Kenya (sexes combined; A. Wagner pers. obs.)

Weights from Serengeti N. P. (Tanzania) and Israel fall within this range (Kruuk 1976)

Key References Hofer 1998a; Kruuk 1976; Leakey *et al.* 1999; Rieger 1978, 1979a, 1981; Wagner 2006; Wagner *et al.* 2007a.

Aaron P. Wagner

GENUS *Crocota*

Spotted Hyena

Crocota Kaup, 1828. Oken's Isis 21. Encyclop. Zeit 21 (11), column 1145.

A monotypic genus, represented by the Spotted Hyena *Crocota crocuta*, and with adaptations to hypercarnivory and scavenging. The fossil history of *Crocota* (within as well as outside Africa) is complex, with at least three species present in Africa during the Plio–Pleistocene, in addition to the living one (Werdelin & Lewis 2005, 2008). These species document morphological changes in the *Crocota* lineage that suggest a transition from probably solitary scavenging in the Pliocene to the socially versatile, sometime group-hunting species of today. These changes imply modifications to ecology and behaviour that this species complex went through as it adapted to changes in climate and environment, as well as competition from an increasingly competent hunter and scavenger, *Homo* spp. (Lewis & Werdelin 1999, 2000).

Lars Werdelin



Spotted Hyena *Crocota crocuta* head in profile.

Crocota crocuta SPOTTED HYAENA

Fr. Hyène tachetée; Ger. Fleckenhyaena (Tüpfelhyaena)

Crocota crocuta (Erxleben, 1777). Syst. Regni Anim. 1: 578. 'Guinea, Aethiopia, ad caput bonae spei in terrae rupiumque caueis', restricted by Cabrera (1911) to 'Senegambia'.



Lateral view of skull of Spotted Hyaena *Crocota crocuta* with dental rooting exposed.

Taxonomy Monotypic. Very variable in morphology, size and pelage; Matthews (1939a) rejected all subspecies (and see Hollister 1918), as have later authors (Werdelin & Solounias 1996, Jenks & Werdelin 1998). However, significant variation in mitochondrial DNA between western, southern and eastern populations suggests that a re-evaluation in terms of at least three subspecies might be appropriate (Albert *et al.* 2000, Rohland *et al.* 2005); if these were to follow established taxonomic conventions, the West African form would be *C. crocuta crocuta*, the southern form *C. crocuta capensis* and an eastern form might be *C. crocuta habessinica*. Synonyms: *capensis*, *colvini*, *crocuta*, *cuvieri*, *encrita*, *felina*, *fisi*, *fortis*, *gariepensis*, *germinans*, *habessinica*, *kibonotensis*, *leontiewi*, *maculata*, *moltei*, *nyasae*, *nzoyae*, *panganensis*, *rufa*, *rufopicta*, *sivalensis*, *spelaea*, *thierryi*, *thomasi*, *togoensis*, *ultima*, *venustula*, *weissmanni*, *wissmanni*. Chromosome number: $2n = 40$ (Wurster-Hill 1973).

Description Largest extant hyaena. Head with a dog-like muzzle covered in short black hair with several rows of vibrissae. Ears rounded. Body strongly built, neck and shoulders muscular, back slightly sloping. Pelage colour light brown, beige, sandy or ginger. Prominent spots of variable size and density on neck, shoulder, back, flanks, rump, legs, base of tail and occasionally belly. Spots, initially black or dark brown, may turn light brown and fade with age. Pelage composed of fine underhair (15–20 mm) and longer, stouter, flat-sectioned bristle hairs (30–40 mm). Hair along back of neck and across shoulders is longer (70–80 mm), giving appearance of a mane. Tail thin and ending in long black hair at tip. Feet four-toed with short, blunt, non-retractable claws and broad and flattened naked pads. Characteristic loping gait when running.

Sexes very similar in appearance. Clitoris elongated and when erected similar in size to erected male penis. No vulva, as the outer labiae are fused (Matthews 1939b, Neaves *et al.* 1980, Cunha *et al.* 2003). No baculum in either sex. Sex can be determined from detailed morphology of the erect 'penis' (Frank *et al.* 1990). Male glans has pronounced incision at base, is asymmetrical and terminates in a tapering tip. In ♀♀ incision at base of clitoris is

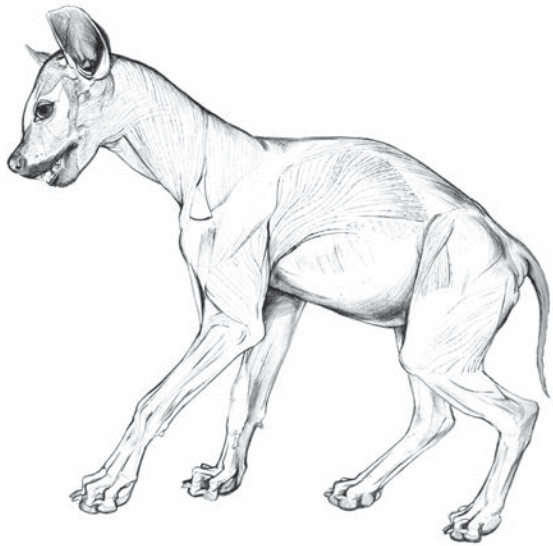


Spotted Hyaena *Crocota crocuta*.

less pronounced and symmetrical, and tip is blunt. Erect clitoris usually straight or points forward; erect male penis usually curves backwards. In older ♂♂ belly line is V-shaped, in reproductively active ♀♀ udder is pronounced and belly line descends towards hindlegs. Four nipples are usually present, but typically only rear pair functional. Sex determination is possible by histological (Wurster-Hill *et al.* 1970, Yost 1977) and molecular methods (Schwerin & Pitra 1994).

Skull massively built and characterized by high sagittal crest extending backwards beyond occipital condyles. In some skulls the supra-occipital crest is represented by a backward sloping narrow flange; in others it is absent or just a low ridge. The rostrum is broad; zygomatic arches are robust and sweep out towards the back to provide ample room for the well-developed masseter and temporalis muscles (Skinner & Chimimba 2005). Dentition typically hyaenid, although upper first molars are often absent, unlike in the Brown Hyaena *Hyaena brunnea* where upper first molars are functional teeth and always present. Lower premolars massive, with rounded central cusps; upper first premolars small, the second and third rounded with high central cusps, while the fourth have distinct protocones on inner edges. Upper canines large, sharp, rounded and slightly recurved; lower canines are stout and recurved. Permanent teeth erupt at about 15 months. Wear of mandibular third premolar and cross-section of dentine lines of upper canines can be used as an index of age (Kruuk 1972, Lindeque & Skinner 1984, Van Jaarsveld *et al.* 1987), as can tooth eruption and replacement (Van Horn *et al.* 2003).

Geographic Variation No subspecies are currently recognized. Individual variation is considerable, and any non-molecular regional characteristics, if they exist, have yet to be identified.

Spotted Hyaena *Crocota crocuta* myology.

Similar Species

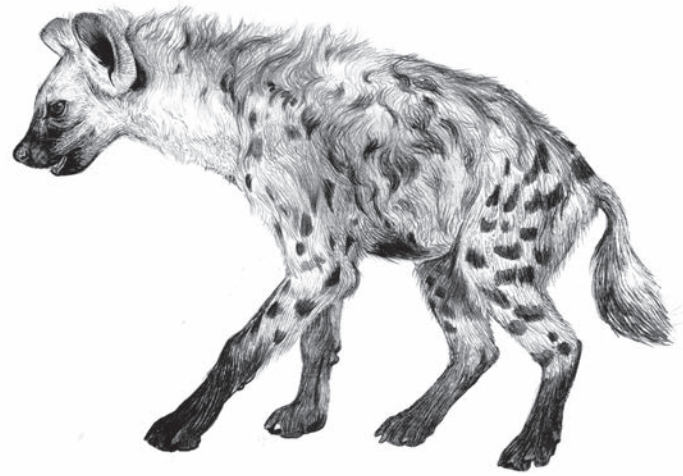
Hyaena brunnea. Sympatric in southern Africa, particularly in the west.

Ears long and pointed; pelage longer and dark brown without spots.

H. hyaena. Sympatric from Tanzania northwards. Long, erectile mane and dorsal crest, and prominent stripes (not spots) on body, legs and neck; ears longer and pointed.

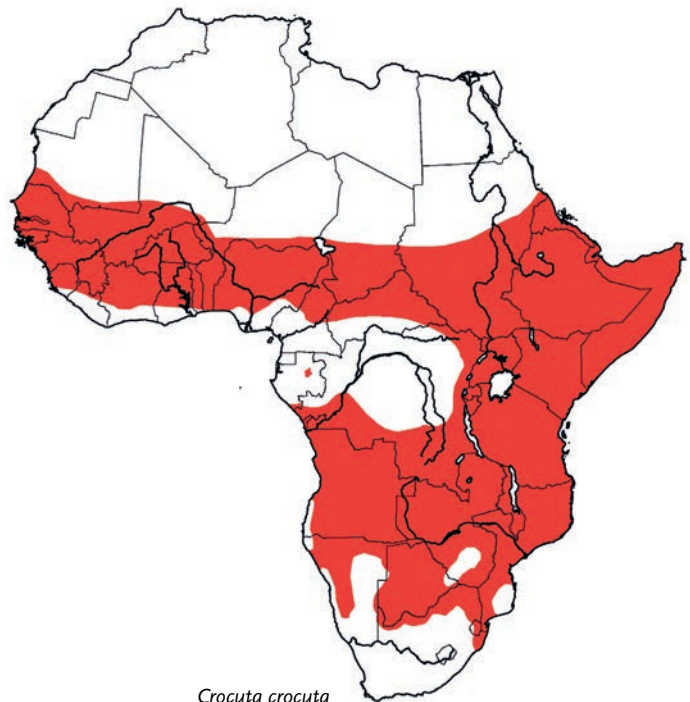
Distribution Endemic to Africa, south of the Sahara, although formerly with a geographic range across almost all of Africa and Eurasia (Werdelin & Solounias 1991). Current distribution is more patchy, especially in West Africa, with populations often concentrated in protected areas. More continuous distributions persist over large areas of Chad, Central African Republic, S Sudan, Ethiopia, Kenya, Tanzania, Botswana, Angola, Namibia and parts of South Africa. Hofer & Mills (1998a) reported the species as extinct in Algeria, where it may have occurred in the Ahaggar and Tassili d'Ajjer, although Kowalski & Rzebik-Kowalska (1991) noted that continued presence in the southernmost regions is not impossible. Hofer & Mills (1998a) also reported no recent records from Djibouti, Eritrea, Gabon, Gambia and Togo. Since then Künzel *et al.* (2000) have confirmed that Spotted Hyaenas are still widespread, albeit in small numbers, in Djibouti, Grubb *et al.* (1998) noted the same for Gambia, images of a single Spotted Hyaena inside Ivindo N. P., a rainforest site in Gabon, were recorded in 2003 (Henschel & Ray 2003) where the species had not been recorded since around 1950 (and see Juste & Castroviejo 1992), and Spotted Hyaenas were reported from Eritrea (P. D. Moehlman pers. comm.). There is no confirmed evidence of their occurrence in Egypt, Liberia or Lesotho.

Habitat Present in all habitats including semi-desert, savanna and open woodland, dense dry woodland and montane habitats, such as the Aberdares, Mt Kenya and the Ethiopian Highlands, up to 4100 m altitude (Young & Evans 1993, C. Sillero-Zubiri pers. comm.). It is absent from, or occurs at very low densities in, extreme desert conditions, the highest altitudes on mountains and tropical rainforests, though they may make deep incursions into forested areas where logging roads provide access (Kingdon 1977, Henschel & Ray 2003). In prime habitat, densities of Spotted Hyaenas are higher than those of other large carnivores (Hofer 1998b). In many parts of their range

Spotted Hyaena *Crocota crocuta* subadult.

they occur in close association with human habitations. Although long periods may elapse between drinking, Spotted Hyaenas are at least somewhat dependent on water, and Tilson & Henschel (1986) recorded an instance where a clan dispersed after the only water source in their range dried up.

Abundance Viable populations still exist in numerous countries and a tentative estimate of the total global population is between 27,000 and 47,000. The largest known populations occur in the Serengeti ecosystem (in the Tanzanian sector, 7200–7700; in the Kenyan sector, 500–1000) and Kruger N. P., South Africa (1300–3900). Significant numbers probably also occur in Selous G. R., Tanzania, and in the Okavango, Botswana. Population densities based on systematic censuses vary substantially, from 0.006 to 1.7 individuals per km² (Hofer & Mills 1998b; and see references therein). Low population

*Crocota crocuta*

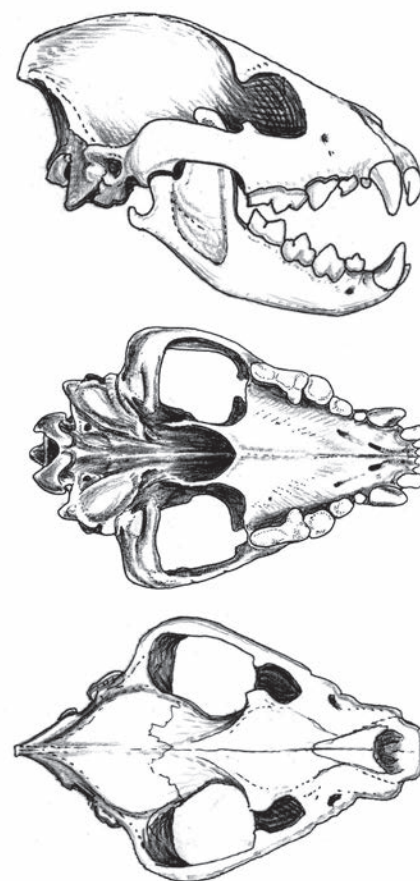
densities occur in semi-desert areas in southern Africa (0.006–0.05 individuals per km²), such as the Namib (Tilson & Henschel 1986) and Etosha Pan (Gasaway *et al.* 1991). High densities occur in savanna and some open woodlands in Tanzania and Kenya, as well as in montane forest (0.32–1.7 individuals per km²), such as Selous G. R. (Creel & Creel 1996), Aberdare N. P. (Sillero-Zubiri & Gottelli 1992a) and Ngorongoro Crater (Kruuk 1972, Höner *et al.* 2005).

Adaptations The sagittal crest of the Spotted Hyaena skull provides the upper attachment for a hugely enlarged temporalis muscle. The bowed zygomatic arch also accommodates this muscle and provides the upper attachment for the masseter muscle. Both muscles are attached to posterior processes on the mandible and, together with an extremely hard, vice-like complex of cheekteeth embedded in dense mandibular bone (the mandibles are buttressed beneath the premolars) represent one of the most extreme forms of bone-shattering dentition known for any living land mammal (Biknevicius & Ruff 1992, Biknevicius & Van Valkenburgh 1996). The feeding behaviour of juvenile Spotted Hyaenas has been studied in terms of the development of a powerful bite and individual independence (Binder & Van Valkenburgh 2000). Adult skull size and full feeding performance is not achieved until sexual maturity at 24 months of age (Watts *et al.* 2009). Acidic digestion permits extraction of nutrients from bone fragments; digested bone results in pale-coloured faeces. Undigested matter (hair, bone and hooves) is regurgitated.

Spotted Hyaenas can pursue prey for long distances at speed with a unique form of galloping gait and can feed immediately once prey is captured. This is possible because the heart is exceptionally large in relation to body size and because of efficient heat loss through the rostrum. Excess heat is also lost through panting, by coating front legs and neck in copious saliva and by lying in water or mud. Young animals reduce energetic costs of thermoregulation and probably water loss by huddling together or resting underground in communal dens. Adults cannot enter the small burrows of the communal den and avoid daytime heat by resting in dense vegetation or large underground burrows of species such as warthogs *Phacochoerus* spp.

The most celebrated peculiarity of this species is its ‘hermaphroditism’. Several hypotheses have sought to explain female mimicry of male external genitalia:

- 1 Mimicry was an incidental by-product of selection for elevated androgen levels to increase aggression, social dominance and body size of adult ♀♀ over ♂♂ (Gould 1981, Frank *et al.* 1991, 1995a). Several facts do not conform to this theory. Large body size is not related to social rank in ♂♂ or ♀♀ (Holekamp *et al.* 1996, East & Hofer 2002, Hofer & East 2003). Androgen (testosterone and androstenedione) concentrations in non-pregnant ♀♀ are not elevated, are similar to those in many other non-pregnant female mammals, including Brown and Striped Hyaenas, and are considerably lower than androgen levels in ♂♂ (Goymann *et al.* 2001, Dloniak *et al.* 2004). Androgen-independent mechanisms contribute to the development of the penile clitoris, as anti-androgen treatment of ♀♀ during foetal development resulted in ♀♀ with an enlarged clitoris (Drea *et al.* 1998). Elevated levels of androgens in neonates of both sexes may be linked to selection for intense sibling rivalry (East *et al.* 1993) leading to facultative siblicide when food resources are low (see below).



Lateral, palatal and dorsal views of skull of Spotted Hyaena *Crocota crocuta*.

- 2 Mimicry occurred as a by-product of selection for androgenized, larger, aggressive ♀♀, and then the clitoris was incorporated into greeting ceremonies, favouring selection for its enlargement (Hamilton *et al.* 1986).
- 3 Mimicry provided the direct selective advantage of a conspicuous structure that facilitated the re-establishment of social bonds among clan members (Wickler 1965, Kruuk 1972).
- 4 After the evolution of female dominance, mimicry and presentation of male-like genitalia facilitated social relations by offering an appeasing, diversionary signal. Such a signal would benefit any animal (regardless of age and sex) seeking to reduce intra-specific aggression (Wickler 1965, Kruuk 1972, Kingdon 1977).
- 5 Mimicry of male external genitalia provided a selective advantage by decreasing infanticide of female cubs belonging to competing adult female clan members (Muller & Wrangham 2002).
- 6 Mimicry was a by-product of genetic translocation (Van Jaarsveld & Skinner 1987).

The reason why ♀♀ have an elongated clitoris remains a matter of debate. Passage of the firstborn cub or litter through the clitoris often results in cases of still-birth (Glickman *et al.* 1992, Frank *et al.* 1995b, Drea *et al.* 2002). This not only implies a reduction in life-time reproductive success of at least 5%, but also positive counter-selection pressure to maintain this costly trait (East *et al.* 1993). One benefit of a penile clitoris might be control over the mechanics of copulation, as this would have favoured selection for active submission by immigrant ♂♂ and therefore provided ♀♀ with a



Spotted Hyaena *Crocuta crocuta*.

high degree of mate-choice and the benefit of maternal investment being dedicated to offspring sired by high-quality or genetically compatible ♂♂ (East *et al.* 1993, 2003, East & Hofer 2002).

Foraging and Food Although often considered scavengers, Spotted Hyaenas are effective and flexible hunters. They prefer prey within a body mass range of 56–182 kg (with a mode of 102 kg) (Höner *et al.* 2005, Hayward 2006), a dietary niche breadth similar, but not identical, to that of the Lion *Panthera leo* (Höner *et al.* 2002). In Kruger N. P., the most important prey items are the Common Wildebeest *Connochaetes taurinus*, African Buffalo *Syncerus caffer*, Plains Zebra *Equus quagga*, Greater Kudu *Tragelaphus strepsiceros* and Impala *Aepyceros melampus*; preferred prey are all resident herbivores, namely the Impala, Greater Kudu, and Common Warthog *Phacochoerus africanus* (Henschel & Skinner 1990a). In the Namib Desert, Gemsboks *Oryx gazella* made up more than 80% of the diet (Tilson *et al.* 1980) and in Etosha N. P. Springboks *Antidorcas marsupialis* were most commonly hunted (Gasaway *et al.* 1991). In the S Kalahari, the principal prey are Gemsboks (the most common resident herbivore), Common Wildebeests and Springboks, followed by Common Eland *Tragelaphus oryx* and Hartbeest *Alcelaphus buselaphus* calves (Mills 1984, 1990). In Chobe they principally hunt migratory Plains Zebras and resident Impalas (Cooper 1990). In the Serengeti ecosystem and the Ngorongoro Crater, Spotted Hyaenas primarily hunt Common Wildebeests, Thomson's Gazelles *Eudorcas thomsonii* and Plains Zebras (Kruuk 1972, Hofer & East 1993a, Höner *et al.* 2002, 2005). In its northern extension in the Masai Mara, they feed mainly on Topis *Damaliscus lunatus* and Thomson's Gazelles when migratory species are absent. Upon arrival of the migratory herds from the Serengeti N. P., they switched to feeding on Common Wildebeests for about three months, until the migratory animals return to the Serengeti N. P. (Cooper *et al.* 1999). In the Aberdare Mts (Kenya) the dominant prey items are Bushbucks *Tragelaphus scriptus*, Sunis *Nesotragus moschatus* and African Buffalo (Sillero-Zubiri & Gottelli 1992b).

The diet of Spotted Hyaenas in West and Central Africa is less well known. In Niokolo-Koba N. P., Senegal, they feed mostly on large and medium-sized ungulates, with African Buffalo the most

frequently consumed prey species; Hartbeests and Common Warthogs were also eaten more often than expected (Di Silvestre *et al.* 2000). In contrast, in Faro N. P., N Cameroon, mainly medium-sized prey were taken, with the main prey being Buffon's Kobs *Kobus kob*, the most abundant prey species in the area (Breuer 2005).

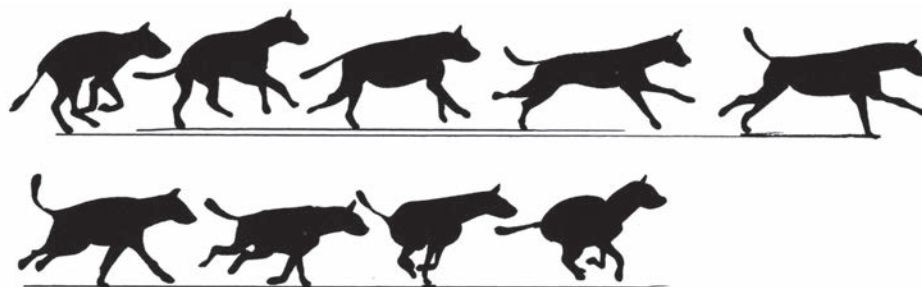
Spotted Hyaenas are opportunistic, occasionally taking larger prey such as Giraffes *Giraffa camelopardalis*, juveniles of Common Hippopotamus *Hippopotamus amphibius*, Savanna Elephants *Loxodonta africana* and White Rhinoceroses *Ceratotherium simum*. They also consume a wide range of small mammal prey, including small carnivores and rodents up to the size of springhares *Pedetes* spp., as well as other vertebrate prey (such as birds, fish, reptiles), insects, crabs, snails, Ostrich *Struthio camelus* eggs, fruits and the faeces of herbivores, carnivores and omnivores (Hirst 1969, Pienaar 1969, Kruuk 1972, Bearder 1977, Cooper 1990, Henschel & Skinner 1990a, Mills 1990, Gasaway *et al.* 1991, Sillero-Zubiri & Gottelli 1992b, Skinner *et al.* 1992, Hofer & East 1993a, Holekamp *et al.* 1997, Cooper *et al.* 1999, Di Silvestre *et al.* 2000, Salnicki *et al.* 2001, Höner *et al.* 2002, Breuer 2005).

Despite being a highly social carnivore that may live in large groups, individuals hunt mostly on their own or in small groups (Kruuk 1972, Gasaway *et al.* 1989, Mills 1990, Skinner *et al.* 1992), although one case of mass killings of Thomson's Gazelles by a group of 19 was recorded in East Africa (Kruuk 1972). Prey is detected by sight, hearing and odour and carrion by smell, the noise of other carnivores feeding, or by watching vultures descending on a carcass. Adult solitary Spotted Hyaenas of around 5–6 years of age can be very efficient hunters, and, in the Masai Mara, are responsible for over 75% of hunting attempts on Common Wildebeest and Topi (Holekamp *et al.* 1997). Spotted Hyaenas are active mostly at night, dawn and dusk, but can forage at any time during the day. During hunts, prey may be chased over several kilometres (the longest recorded chase was 24 km in pursuit of a Common Eland; Mills 1990) at speeds of up to 60 km/h (Hofer 1998b). Spotted Hyaenas have been observed to drown prey, such as Southern Lechwe *Kobus leche* (Child & Robbel 1975), and even to run down Lesser Flamingoes *Phoenicopterus minor* in shallow soda lakes (Brown & Root 1971). Food is cached, mostly in water.

Average adult daily food consumption is estimated at 2.0–4.0 kg/day (Kruuk 1972, Green *et al.* 1984, Henschel & Tilson 1988). An adult Spotted Hyaena can consume approximately 18 kg in one meal (Kruuk 1972, Bearder 1977), equal to up to one-third of adult body mass. They are rapid feeders, an adaptation to strong feeding competition with conspecifics and Lions (Kruuk 1972). At large carcasses, female clan members and their offspring feed before immigrant ♂♂, and high-ranking ♀♀ and their offspring before lower-ranking ♀♀ and their offspring (Frank 1986a). Spotted Hyaena cubs show a remarkable resilience to a lack of regular supply of food or fluids (Hofer & East 1997).

Spotted Hyaenas may travel long distances (30–80 km) in search of prey or water (Eloff 1964, Tilson & Henschel 1986, Mills 1990). In Etosha N. P., migratory movements of main prey species (Springbok, Plains Zebra, Common Wildebeest) to the north-west at the start of the wet season results in a considerable decline in prey density. In response, clans in areas of low prey density follow the migratory herds, thus shifting their activities to the wet season range of the migratory herbivores (Trinkel *et al.* 2004). In contrast, Spotted Hyenas in Serengeti N. P. leave their clan territory (individually or

Serial silhouettes of running/galloping Spotted Hyaena *Crocota crocuta*.



in small groups) on frequent short-term, long-distance (80–140 km return distance) foraging trips (termed commuting trips) to areas containing high densities of migratory herbivores (Hofer & East 1993a,b,c). Low-ranking group members commute more often than socially dominant members. These trips last on average three days for lactating ♀♀ (who frequently return to the clan territory to nurse their young) and 9–10 days for non-lactating ♀♀, and ♂♂. Some 46–62% of the year is spent foraging by commuting between the clan's territory and herds of migratory prey. Lactating ♀♀ may make up to 40–50 trips and commute as much as 3680 km per year (Hofer & East 1993c). As the proportion of each year increases, during which lactating ♀♀ commute, the survival of her offspring decreases (Hofer & East 2003, 2008). Aggression towards commuters by resident clan members is context-specific. Animals in transit through an area are usually ignored, whereas commuters at food resources are attacked if they fail to submit to residents (Hofer & East 1993b).

The Spotted Hyaena is an efficient scavenger of carrion, including the kills of other Spotted Hyaenas and other carnivores like Lions (Kruuk 1972, Henschel & Skinner 1990a, Mills 1990), although in both Masai Mara (Cooper *et al.* 1999) and the Ngorongoro Crater (Kruuk 1972, Höner *et al.* 2002), Spotted Hyaenas obtained most of their annual intake from hunting rather than scavenging. It is also an effective kleptoparasite on other carnivores. The proportion of its diet derived from or lost to other predators varies between ecosystems (Kruuk 1972, Cooper 1991, Mills & Biggs 1993, Höner *et al.* 2002). Lions usually displace Spotted Hyaenas at kills, unless Spotted Hyaena group size is large and male Lions are absent (Cooper 1991, Höner *et al.* 2002). In Etosha N. P., clan sizes of Spotted Hyaenas are small and territories large; consequently, preventing kleptoparasitism by Lions or recruiting sufficient clan members to take over Lion kills is difficult (Trinkel & Kastberger 2005). In some areas, Spotted Hyaenas may kill domestic livestock, domestic cats, domestic dogs and people (Hofer 1998b, East *et al.* 2012). In some areas Spotted Hyaenas are, or used to be, relied upon to dispose of human corpses.

Assemblages of bones are often found at Spotted Hyaena communal dens where all clan offspring are placed, although not to the same degree as in the Brown Hyaena or the Striped Hyaena, because Spotted Hyaenas infrequently carry food back to their young. A variety of items, mostly long bones or skulls of medium- to large-sized ungulates, have been found in dens; bone assemblages tend to reflect the ungulate fauna in an area (Bearder 1977, Mills & Mills 1977, Henschel *et al.* 1979, Skinner *et al.* 1986, Lam 1992; and see Skinner 2006).

Social and Reproductive Behaviour A highly social species that lives in groups (clans) and defends group territories. Clans are a 'fission–fusion' society, and although clan members often operate independently, there is a high degree of cooperation in the defence

of the territory, of food resources and the communal den. Clan social structure consists of a linear dominance hierarchy amongst adult ♀♀, and a separate linear dominance hierarchy amongst immigrant ♂♂, all of which are socially subordinate to clan ♀♀ (Frank 1986a). The mechanisms by which adult ♀♀ and immigrant ♂♂ acquire social status differ (see below).

The average number of adults and subadults in a clan varies from three in desert and semi-desert areas of southern Africa to 90 individuals in the savanna areas of East Africa (Kruuk 1972, Hofer 1998b). Territory size and the density of prey inside a clan's communal territory may limit clan size, unless clan members regularly feed on migratory herds outside their territory (Hofer & East 1993a, b, Höner *et al.* 2005). Clans split if current clan size exceeds a threshold above which the food base of the territory is insufficient (Mills 1990), or if a territory in the neighbourhood has become vacant (Holekamp *et al.* 1993, Höner *et al.* 2005).

Females usually remain in their natal clan; therefore, large clans contain several matriline (Frank 1986b). When ♀♀ attain adulthood, they typically acquire a rank immediately below that of their mother (Smale *et al.* 1993, Hofer & East 2003). Dloniak *et al.* (2006) suggested that rank-related exposure of fetuses to different concentrations of maternal androgens during pregnancy resulted in high-ranking mothers producing more assertive offspring than lower ranking mothers, and that this maternal effect during gestation significantly influenced the rank achieved by offspring at adulthood. However, when individuals were adopted as young cubs and reared by a surrogate mother, they acquired a rank at adulthood close to and below that of their surrogate mother (East *et al.* 2009), similar to the behavioural mechanism termed rank 'inheritance' which explains rank acquisition in many primates and which has previously been described for Spotted Hyaenas (Smale *et al.* 1993). This behavioural mechanism is based on the social support a mother provides to her offspring. During their development, Spotted Hyaena cubs learn that with maternal support they can dominate all clan members socially dominated by their mother, and to submit to all group members that their mother submits to. As a result, they usually acquire a rank at adulthood immediately below that of their mother, but can significantly decline in social status should their mother die (Hofer & East 2003). Adult ♀♀ seek to stabilize their position in the dominance hierarchy by fostering relationships with ♀♀ holding ranks adjacent to their own in the hierarchy, and by supporting such ♀♀ during interactions with other clan member (East *et al.* 1993, Smale *et al.* 1995, Hofer & East 2000, Engh *et al.* 2000).

Males are considered mature at two years of age and typically (but not always) disperse from their natal clan after reaching maturity, immigrating into another clan at approximately 3–4 years of age (Höner *et al.* 2010). At immigration, they join the immigrant male hierarchy at the lowest rank. Because their social status increases as their tenure

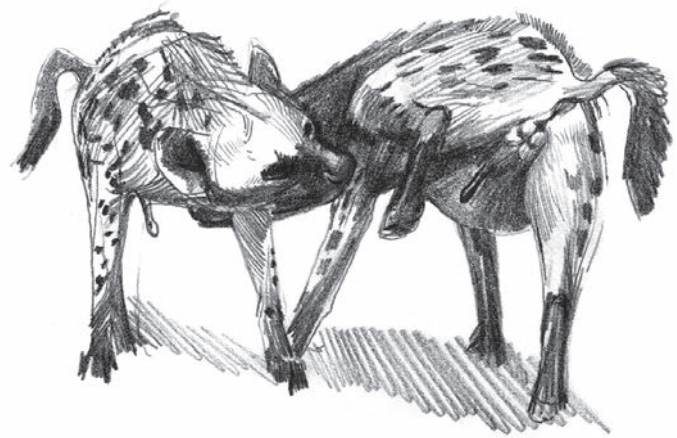
in the clan lengthens and as $\delta\delta$ above them in the hierarchy die or leave the clan, the male hierarchy functions like a social queue (East & Hofer 2001). Queuing $\delta\delta$ observe strict conventions, and so rarely 'jump the queue' or use physical contests to advance in social status. Queuing $\delta\delta$ stabilize their social position in relation to lower ranked $\delta\delta$ by forming long-term alliances with $\delta\delta$ immediately in front and behind them in the queue (East & Hofer 2001). In large clans, such as those in the Serengeti N. P., social queues may contain more than 15 immigrant $\delta\delta$, and queuing $\delta\delta$ require several years to progress from the bottom to the top of the male hierarchy (East & Hofer 2001). Males sometimes undertake multiple dispersals, as observed in the Masai Mara National Reserve where eight of 20 $\delta\delta$ whose fates were known lived in three clans over time (Van Horn *et al.* 2003).

Males with long tenure mostly seek to foster amicable relationships with older adult ♀♀ , whereas recent immigrant $\delta\delta$ more often do so with younger adult ♀♀ . Females aggressively reject unwanted $\delta\delta$. Genetic paternity analyses have revealed that ♀♀ exercise a high degree of mate-choice (East *et al.* 2003, Höner *et al.* 2007). Because younger ♀♀ mostly reject close advances by longer tenured $\delta\delta$, they avoid inbreeding with close relatives, such as their father (East & Hofer 2001, Höner *et al.* 2007). As a result, the offspring of younger ♀♀ are mostly sired by $\delta\delta$ that were not clan members when the ♀♀ was born. Males that start their reproductive careers in a clan containing an above average number of younger adult ♀♀ gain a significant reproductive advantage, indicating that female mate-choice preferences drive male dispersal patterns (Höner *et al.* 2007). In the Ngorongoro Crater, sons of high-ranking ♀♀ reproduce at a younger age (4.8 yrs) than sons of both mid-ranking (5.9 yrs) and low-ranking ♀♀ (6.8 yrs), probably because of their privileged upbringing in their natal clan (Höner *et al.* 2010).

Male reproductive tactics range from extreme harassment to high investment in friendly (affiliative) behaviour with ♀♀ (Kruuk 1972, East & Hofer 2001, Szykman *et al.* 2001, East *et al.* 2003). Females also operate effective counter-tactics against $\delta\delta$ which attempt to harass or monopolize them, including behaviours likely to confuse paternity, such as multiple mating and mating when not in oestrus (East *et al.* 2003). A ♀ may mate with several $\delta\delta$ when in oestrus, with the result that a high proportion (about 35%) of twin litters are sired by two different fathers (Engh *et al.* 2002, East & Hofer 2002).

Territory size in the Spotted Hyaena is variable, ranging from 9 km² in the Ngorongoro Crater (Höner *et al.* 2005) to over 1000 km² in the Kalahari (Mills 1990). Clans defend communal territories against encroachment from neighbouring conspecifics through vocal displays, scent-marking (Gorman & Mills 1984) and boundary patrols (Kruuk 1972). Adult ♀♀ initiate and lead most cooperative territorial behaviours, although border patrols were occasionally conducted by groups composed exclusively of resident $\delta\delta$. Most territory intruders were $\delta\delta$. Resident ♀♀ were more likely to attack intruding ♀♀ than intruding $\delta\delta$, whereas resident $\delta\delta$ were more likely to attack intruding $\delta\delta$ (Boydston *et al.* 2001).

Spotted Hyaenas of both sexes produce a fatty, strongly smelling secretion in anal glands situated on either side of the rectum which discharge at an opening above the anus. During scent-marking ('pasting'), this scent gland is partially protruded and dragged along a grass stalk or herb by bending the hind legs to adopt a semi-crouched position (Kruuk 1972). Scent scattered throughout a clan's territory, termed 'hinterland' scent-marking (Gorman & Mills 1984), may be



Genital inspection ceremony in Spotted Hyaena *Crocuta crocuta*.

a way of optimizing the distribution of scent-marks over a large area with a limited amount of scent and time (Mills 1990). Anal gland scent contains a mixture of fatty acids and other organic compounds (Hofer *et al.* 2001, Burgener *et al.* 2009). Despite previous emphasis on the role of pasting in territory defence, recent studies have demonstrated that it is an important component of communication between clan members (Burgener *et al.* 2009, East *et al.* in press). The anal gland scent of natal animals and immigrant $\delta\delta$ from the same clan have similar chemical signatures, suggesting the presence of an olfactory clan membership badge (Hofer *et al.* 2001, Burgener *et al.* 2009), probably concocted by the remote exchange of scent between clan members when one individual over-pastes a scent mark of another clan member (Burgener *et al.* 2008). Spotted Hyaena anal gland scent also contains olfactory signatures that communicate the identity of the individual that deposited the scent. Female clan members are more likely to respond to scent marks deposited by top-ranking female clan members than ♀♀ of lower social status (Burgener *et al.* 2009). Spotted Hyenas also display behaviour similar to pasting but without protruding the anal gland and thus without depositing scent ('dry pasting'). Dry pasting anoints the body fur with scent deposited on grass stalks (Burgener *et al.* 2008). Juveniles start dry-pasting over scent marks at the communal den when less than two months of age and only start pasting scent when close to adulthood (Theis *et al.* 2008, East *et al.* in press). Spotted Hyaenas also scent-mark by depositing a secretion from their inter-digital glands when they scratch the ground, and by defecating in communal latrines (Kruuk 1972, Mills 1990, East *et al.* in press).

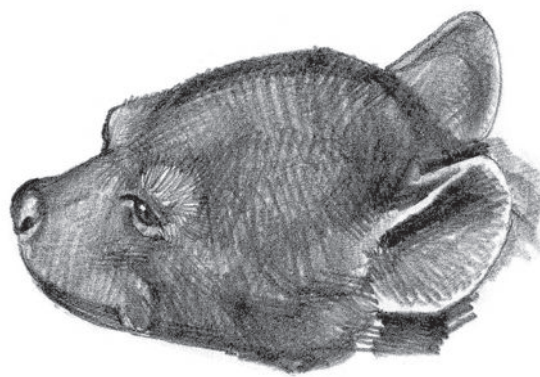
Clan members participate in ritualized greeting ceremonies during which two individuals stand parallel and face in opposite directions, lift their hindleg nearest their partner and sniff or lick the anogenital region of the other. The unique aspect of greetings between individuals is the prominent role of the erect 'penis' in animals of both sexes, and the fact that an erect 'penis' signals submission. Greetings occur between all ages and both sexes, although greetings between adult ♀♀ and immigrant $\delta\delta$ are rare. Cubs can erect their penis or clitoris within several weeks of birth (Frank *et al.* 1990), and engage in greeting ceremonies as early as four weeks of age. Greeting ceremonies are an important element in the maintenance of social status and the formation of alliances with other clan members and thus serve a similar social function to grooming in primates (East *et al.* 1993).

Spotted Hyaenas also have a complex system of acoustic communication (Kruuk 1972, Mills 1990). The loud-call or whoop can

be heard over several kilometres. Animals whoop with their muzzle bent towards the ground. Spotted Hyaenas can recognize the whoops of other members of their clan (East & Hofer 1991a, Holekamp *et al.* 1999) and possibly members of neighbouring clans. Whoops can function as a rallying call to gather scattered clan members together to feeding sites, the communal den and sites of conflict, and as an individual display for ♂♂ and ♀♀. High-ranking animals of both sexes whoop more often than lower-ranking clan members of the same sex and ♂♂ whoop more frequently than ♀♀ (East & Hofer 1991b). Whoops show pronounced non-linear phenomena, predominantly subharmonics, which may enhance individual recognition by adding structural complexity to calls (Peters *et al.* 2004). The laugh or giggle is produced when individuals are nervous, as when challenged by a Lion or when signalling submission to a dominant clan member. Like whoops, giggles contain acoustic signatures which may communicate individual identity (Mathevon *et al.* 2010).

Much of the social life of a clan occurs in the vicinity of the communal den. Communal dens may be used for years, or den sites may be changed several times within a year. A clan may simultaneously have several communal dens separated by up to 7 km (Hofer & East 1993a). Dens are dug by other species, mostly warthog, Aardvark *Orycteropus afer* and Bat-eared Fox *Otocyon megalotis* and then are modified. Cubs excavate underground burrows and adult ♀♀ enlarge the den entrance. The structure of dens does not normally permit the access of adult animals and cubs must emerge at the den entrance to interact with their mother (Golla *et al.* 1999). Small underground burrows may protect cubs from predation by Lions and non-clan members (Kruuk 1972), and may also reduce infanticide by adult ♀♀ and immigrant ♂♂ clan members (Hofer & East 1995, East *et al.* 2003).

Mating in the Spotted Hyaena is facilitated by retractor muscles that allow the ♀ to retract the clitoris on itself, thereby forming an opening into which the ♂ inserts his penis. In order to achieve intromission, the ♂ tucks his rump under the ♀, only assuming an erect posture behind her once engaged (Frank 1996). Females give birth through their penile clitoris that ruptures to permit the passage of the young, creating a large wound of several centimetres. Females may give birth in a private birth den or at the communal den (East *et al.* 1989, Henschel & Skinner 1990b). Communal dens may contain numerous young of different sizes and ages from many litters; Hofer (1998b) reports up to 30. Mothers probably use private birth dens so that they can maintain continuous access to their newborn cubs; at the communal den this is only feasible for top-ranking mothers. Mothers may also use birth dens so that both mother and offspring can learn to identify each other before they move to the communal den (East *et al.* 1989). Young cubs that emerge from a den due to the presence of a ♀ that is not their mother risk infanticide, and mothers that nurse cubs that are not their own risk compromising the growth and survival of their litter. Females usually nurse only their own cubs and reject approaches by other cubs; however, exceptions to this rule do occur (East *et al.* 2009). As there are often several animals present at the communal den, cubs benefit from the vigilance of adults that can alert young to the presence of predators. Social interactions at the communal den between cubs and adult clan members play an important role in the integration of juveniles into the dominance structure of the clan (East *et al.* 1993, Holekamp & Smale 1993). Cubs remain at the communal den for a period of approximately



Spotted Hyaena *Crocuta crocuta* two months old.

12 months and during this period their major source of food is milk provided by their mother (Hofer & East 1993c, Frank *et al.* 1995b).

At birth the eyes are open and deciduous canines and incisors are fully erupted (Pournelle 1965). Litter-mates engage in aggressive interactions immediately after birth, leading to the establishment of a dominance hierarchy between siblings within the first few days of life (Smale *et al.* 1995, Golla *et al.* 1999). When litters are suckling, the dominant cub skews access to maternal teats in its favour by using aggressive behaviours to train its sibling to respond submissively and to stop suckling when challenged (Benhaïem *et al.* in press). If the amount of milk provided by a mother is insufficient for both littermates, dominant littermates increase their monopolization of access to maternal teats. When well fed, subordinate cubs observe social dominance conventions, respond submissively and stop suckling for lengthy periods than when they are hungry and behave more assertively (Benhaïem *et al.* in press). As a result of their reduced submissiveness, the rate of aggression is high in hungry litters (Golla *et al.* 1999). When mothers provide insufficient milk to a twin litter for an extended period, dominant cubs may skew consumption of maternal milk in their favour to such an extent that their subordinate siblings die of enforced starvation (Hofer & East 1997, 2008, Golla *et al.* 1999). Siblicide is therefore facultative and rarely occurs in habitats where mothers have access to sufficient food resources (Smale *et al.* 1999, Wachter *et al.* 2002). A cub that manages to starve its sibling obtains significant benefits, as growth rates of singletons are higher than those of twins, and cubs with a higher growth rate have a better chance of surviving to the age of independence (Hofer & East 1993c, 2003, 2008). It is probable that high maternal investment in litters, a lack of communal suckling and the substantial benefits associated with being the dominant member of a twin litter (or the survivor after the subordinate sibling has been dispatched due to starvation) favoured selection for high neonatal aggression, and elevated levels of androgens in young neonates have been selected to produce cubs primed for sibling rivalry at birth (East *et al.* 1993).

Reproduction and Population Structure Breeding takes place throughout the year, with little evidence for seasonality of births (Kruuk 1972, Mills 1990, Holekamp & Smale 1995, East & Hofer 2002). The gestation period is approximately 110 days, oestrus is thought to last for one day and females cycle every 14 days (Matthews 1939b, Schneider 1952). Females give birth to litters of one, two or rarely three cubs (Holekamp & Smale 1995, Hofer & East 1997, 2008). Triplets typically do not survive, as ♀♀ normally only lactate through two nipples, but

one triplet litter is known to have survived in the Ngorongoro Crater (O. P. Höner pers. comm.). Birth-weight is approximately 1.5 kg (Pournelle 1965). At birth cubs are uniformly black, with ears folded backwards over the head, eyes partially open and deciduous teeth erupted (Pournelle 1965, East *et al.* 1989). Eyes develop white rings at approximately six weeks of age. Lighter hair spreads across the face to the neck and shoulders and eventually the body, and spots emerge. At the age of 6–12 months cubs develop a longer and lighter coloured pelage before assuming the shorter, darker adult coat.

Cubs are nursed for a prolonged period and may not be weaned until 14–18 months of age (Hofer & East 1993c). The milk of Spotted Hyaenas in Serengeti N. P. has the highest protein content (mean 14.9%) recorded for any terrestrial carnivore, a fat content (mean 14.1%) exceeded only by that of Palearctic bears and the Sea Otter *Enhydra lutra*, and a higher gross energy density than the milk of most terrestrial carnivores (Hofer & East 1995). Owing to their milk's high energy content and the long nursing period, the Spotted Hyaena has the highest energetic investment per litter of any carnivore (Oftedal & Gittleman 1989). As high-ranking mothers nurse their offspring more often than subordinate ♀♀, their offspring grow faster (Hofer & East 2003) and survive better than cubs of subordinate mothers (Frank *et al.* 1995b, Hofer & East 1996, 2003). This privileged upbringing provides the important fitness benefit of an early start to reproduction to adult daughters and sons of high-ranking mothers (Hofer & East 2003, Höner *et al.* 2010).

Age at first parturition varies substantially between two and five years (Holekamp *et al.* 1996, Hofer & East 2003). Inter-birth intervals are shorter in dominant ♀♀ than subordinate ♀♀, probably as a result of the dominant female's priority of access to food resources in the clan territory (Holekamp *et al.* 1996, Hofer & East 2003, Höner *et al.* 2005). In the Ngorongoro Crater, the average inter-birth interval of ♀♀ that rear a litter is approximately 18 months (Höner *et al.* 2005). Inter-birth intervals for ♀♀ that lose a litter are likely to be shorter, as Henschel (1986) reported inter-birth intervals of about 135 days in one ♀ in Kruger N. P. that lost five litters in succession.

Sex ratios amongst adults are usually even or slightly female-biased (Mills 1990, Hofer & East 1993a, Frank *et al.* 1995b). Significant deviations in offspring sex ratios in singleton and twin litters have been found in some populations (Frank *et al.* 1991, Holekamp & Smale 1995, Hofer & East 1997, Golla *et al.* 1999), but not in others (Wachter *et al.* 2002). For example, of 114 twin litters recorded by Hofer & East (1997), 16 were female–female, 29 male–male, and 69 male–female. Such deviations in the sex ratio from the expected distribution may either be a consequence of changes in the sex ratio at conception (Holekamp & Smale 1995) or of post-natal sex-specific facultative siblicide (Hofer & East 1997, Golla *et al.* 1999, Wachter *et al.* 2002).

Average annual mortality rates are around 13–15% within protected areas. Approximately 50–60% of Spotted Hyaena cubs survive their first 12 months of life (Hofer 1998b; and references therein). A study conducted over a four-year period in one clan in Kenya found that peaks in cub mortality coincided with life-stage events, including mean age of arrival at a communal den, and age at which cubs began visiting kills (White 2005). Longevity in captivity is in the order of 40 years (Weigl 2005).

Predators, Parasites and Diseases The only major predators of the Spotted Hyaena are Lions (Kruuk 1972, Schaller 1972, Mills

1990, Trinkel & Kastberger 2005), although they do not generally consume the hyaenas they kill. Leopards *Panthera pardus* occasionally kill individual hyaenas (Bailey 2005). Other sources of natural adult mortality include violent encounters between conspecifics (Kruuk 1972, Henschel & Skinner 1991), injuries sustained while hunting, and disease (see below). An estimated 9–18% of ♀♀ may die during their first birth from complications arising during parturition (Frank & Glickman 1994, Frank *et al.* 1995b). Infanticide by adult female clan members, diseases and facultative siblicide are important sources of cub mortality (Mills 1990, Hofer & East 1995, White 2005). White (2005) described selective litter reduction by mothers via partial litter abandonment, a mechanism of filial infanticide not previously described in this species. Cubs may also starve to death when their mothers die. Other sources of cub mortality include predation by Lions and the collapse of communal dens after heavy rain.

Infection with microfilaria, *Dipetalonema dracunculoides*, at least three species of cestodes in the genus *Taenia*, a protozoan parasite in the genus *Hepatozoon* and trypanosomes have been reported (Hofer 1998b; and references therein). An examination of faecal samples from Spotted Hyaenas in the Masai Mara recorded a total of nine parasite genera; most individuals were infected with *Ancylostoma* sp. and *Spirometra* sp., and these had the highest median intensity of infection. Other parasites identified include *Isoospora* sp., Taeniidae, Spirurida, *Toxocara* sp., *Mesocostoides* sp., *Dipylidium* sp. and *Trichuris* sp. (Engl *et al.* 2003). Ectoparasites recorded include ixodid ticks of the genera *Amblyomma*, *Boophilus*, *Haemaphysalis*, *Ixodes* and *Rhipicephalus* from animals taken in the Kruger N. P. and in NE KwaZulu–Natal, South Africa (Horak *et al.* 1987, 2000).

Serological evidence suggests that Spotted Hyaenas survive exposure to many viral diseases. Antibodies against rabies, canine distemper virus, canine herpes, canine brucella, canine adenovirus, canine parvovirus, feline calysi, leptospirosis, feline immunodeficiency virus, coronavirus, calicivirus, feline herpes virus 1, bovine brucella, rinderpest, anaplasmosis and African horse sickness virus have been reported (Hofer & East 1995, Hofer 1998b, East *et al.* 2001, 2004, Harrison *et al.* 2004, Troyer *et al.* 2005). Over 70% of Spotted Hyaenas in the Serengeti N. P. and Masai Mara National Reserve are exposed to coronavirus infection (East *et al.* 2004, Harrison *et al.* 2004).

Between 1993 and 1994 an outbreak of canine distemper virus (CDV) increased mortality among Spotted Hyaena cubs less than 12 months of age in Serengeti N. P. (Haas *et al.* 1996). Mothers that lost cubs produced replacement litters that did not succumb to CDV. The hyaena CDV strain (Haas *et al.* 1996) was similar to that from dead Lions from the same area (Carpenter *et al.* 1998), African Wild Dogs *Lycaon pictus* that died in a captive-breeding facility in Mkomazi N. P. in 2000 (Van de Bildt *et al.* 2002), and from a pack of African Wild Dogs that died close to the Serengeti N. P. in 2007 (Goller *et al.* 2010). The 1993–1994 CDV outbreak spread to Masai Mara National Reserve, but did not affect Spotted Hyaena mortality (Alexander *et al.* 1995). Serological evidence of a subsequent CDV outbreak in Spotted Hyaena in the Masai Mara was not associated with increased mortality (Harrison *et al.* 2004).

Rabies may play an important role in the population dynamics of the Spotted Hyaena in the Kalahari (Mills 1990), and rabies in Spotted Hyaena has been reported in several African countries. A high proportion (37%) of Spotted Hyaena in Serengeti N. P. had significant rabies-specific antibody titre levels, without suffering mortality (East *et al.* 2001).

Many carnivore species have sub-clinical infections with the tick-borne blood parasite *Hepatozoon* sp. Young Spotted Hyaena cubs in Serengeti N. P. can suffer lethal *Hepatozoon* infections, suggesting that this blood parasite may be an important cause of juvenile mortality (East *et al.* 2008).

A *Streptococcus equi ruminatorum* outbreak in Spotted Hyaenas in the Ngorongoro Crater in 2001–2002 caused clinical signs similar to those described for ‘Strangles’ in domestic horses and led to increased mortality (Höner *et al.* 2006). Individuals were observed with clinical signs when prey abundance in their clan territory was low and mortality during the outbreak mostly occurred in animals of low social status and those likely to experience poor nutrition. Infection reduced population growth rate in the Ngorongoro Crater from 13.6% prior to the outbreak to a 4.3% decline during the outbreak. After the outbreak, population growth recovered to 13.9% (Höner *et al.* 2012).

Conservation IUCN Category: Least Concern. CITES: Not listed.

Although the total world population is relatively large and contains sub-populations that exceed 1000 individuals in several countries, it is declining outside protected areas, largely as a result of human persecution through shooting, trapping and poisoning, some of it officially led or sanctioned. Mortality from wire snares set to catch wild herbivores is the most important cause of adult mortality in Serengeti N. P., where snares kill around 400 adult hyaenas each year and are responsible for more than half of all adult mortality (Hofer *et al.* 1993, 1996). Entire clans may be killed by poisoning (Holekamp *et al.* 1993), and many individuals are killed when hit by vehicles.

Most populations in protected areas in southern Africa, such as Kruger N. P. (South Africa), Kgalagadi Transfrontier Park (South Africa and Botswana), Hluhluwe-iMfolozi (South Africa) and Etosha N. P. (Namibia), are considered to be stable, whereas populations in eastern and West Africa, even in protected areas, are considered to be declining because of snaring and poisoning (Hofer & Mills 1998b). The population in the Ngorongoro Crater has significantly increased in recent years (Höner *et al.* 2005, 2012). The Spotted Hyaena may be able to respond rapidly to changing ecological conditions. At the edge of Masai Mara National Reserve, increased human activity during a ten-year period was associated with increased use of daytime resting areas in dense vegetation, and avoidance of areas containing the highest abundance of prey, as these were the areas where intensive livestock grazing by pastoralists was concentrated (Boydston *et al.* 2003).

Official attitudes towards the Spotted Hyaena vary from a legal classification as ‘vermin’ (Ethiopia) to fully protected in conservation areas. There are still countries where farmers may kill hyaenas at their discretion (Hofer & Mills 1998b). The Spotted Hyaena is not an important item in the diet of humans (though it is occasionally harvested as a food source in some countries), or an important species for trophy hunters, although it is killed for body parts for traditional medicines and body parts and live hyaenas are used for witchcraft. Licensed sport hunting is permitted in several countries, but numbers killed for this purpose are probably small. Habitat loss and degradation has reduced the habitat available to species that are suitable prey for the Spotted Hyaena and led to declines in populations (Hofer & Mills 1998b).

Measurements

Crocota crocuta

TL (♂ ♂): 1587 (1465–1735) mm, n = 9
 TL (♀ ♀): 1572 (1440–1794) mm, n = 8
 T (♂ ♂): 249 (227–280) mm, n = 9
 T (♀ ♀): 249 (130–315) mm, n = 8
 HF c.u. (♂ ♂): 230 (220–245) mm, n = 9
 HF c.u. (♀ ♀): 228 (215–250) mm, n = 5
 E (♂ ♂): 112 (100–125) mm, n = 8
 E (♀ ♀): 114 (110–120) mm, n = 7
 Sh. ht (♂ ♂): 802 (775–870) mm, n = 10
 Sh. ht (♀ ♀): 794 (735–845) mm, n = 9
 Ht hq. (♂ ♂): 669 (605–720) mm, n = 9
 Ht hq. (♀ ♀): 648 (575–680) mm, n = 8
 WT (♂ ♂): 62.5 (54.0–70.0) kg, n = 11
 WT (♀ ♀): 68.2 (55.0–81.0) kg, n = 9
 Kruger N. P. (Henschel 1986)

In the Serengeti N.P., average weight for ♂ ♂ is 48.4 kg (range 40.0–58.0, n = 27) and for ♀ ♀ 55.6 kg (range 39.0–74.0, n = 40) (M. L. East & H. Hofer pers. obs.)

Note that published sex differences in weight may be misleading, unless standardized for the amount of food contained in the stomach because ♀ ♀ have priority of access to food and Spotted Hyaenas may consume as much as one-third of their body weight (up to 18 kg) in one meal (Kruuk 1972, Hofer 1998b)

Key References Cooper 1990, 1991; East & Hofer 1991a, b, 2001, 2002; East *et al.* 2003; Frank 1986a, b, Frank *et al.* 1991; Henschel & Skinner 1987, 1990a, b, 1991; Hofer 1998b; Hofer & East 1993a, b, c, 1995, 1997, 2000, 2003, 2008; Holekamp *et al.* 1993, 1996, 1997, 1999; Höner *et al.* 2002, 2005, 2007, 2010; Kruuk 1972; Matthews 1939a; Mills 1990; Smale *et al.* 1993.

Marion L. East & Heribert Hofer



Spotted Hyaena *Crocota crocuta*.

GENUS *Proteles*

Aardwolf

Proteles I. Geoffroy St.-Hilaire, 1824. Bull. Sci. Soc. Philom. Paris 1824: 139.

A monotypic genus represented by the Aardwolf *Proteles cristatus*, a species having specialized adaptations for feeding on social insects, especially the termite genera *Trinervitermes* and *Hodotermes*. The origin and evolution of the Aardwolf are not known. The species is a mixture of very primitive and highly derived anatomical features, making phylogenetic evaluation on this basis very difficult. The recent molecular study by Koepfli *et al.* (2006) dates the split of *Proteles* from other Hyainidae to the earliest late Miocene, which is plausible but leaves no clues as to the geographic origin of the genus. It has been commonly suggested (Thenius 1966, Werdelin & Solounias 1991) that *Proteles* derives from the small, hypocarnivorous genus *Plioiviverrops*. However, this genus is of too ancient an origin to fit with the date proposed by Koepfli *et al.* (2006), who instead resurrect a proposal

by Ewer (Ewer & Cooke 1964, Ewer 1973) that *Proteles* derives from the *Lycyaena* lineage of cursorial hypercarnivorous hyaenas. The fossil record at present gives no support for either hypothesis, as the earliest fossil of the genus is from Swartkrans in South Africa, dated ca. 1.5 mya (though skeletal material of a small hyaenid from ca. 4 mya old deposits at Laetoli, Tanzania, may represent *Proteles*; Werdelin & Dehghani 2011). This South African fossil has been given the name *Proteles amplidentus*, but in all respects is very similar to the modern species and does not represent a transitional form (Hendey 1974c, Werdelin & Solounias 1991). Other fossils are younger and indistinguishable from the living species.

Lars Werdelin

Proteles cristatus AARDWOLF

Fr. Protèle; Ger. Erdwolf

Proteles cristatus (Sparrman, 1783). Resa Goda-Hopps-Udden. I. 1: 581. English translation (Sparrman 1786) of original locality: 'Agter-Bruntjes hoogte ... which takes in the upper part of Kleine Visch-rivier, and is separated from Camdebo by Bruntjes hoogtens ...'; listed in G. M. Allen (1939) as 'Near Little Fish River, Somerset East, Cape Colony' [South Africa].



Aardwolf *Proteles cristatus*.

Taxonomy Two Aardwolf subspecies are recognized (Coetzee 1977, Meester *et al.* 1986). Jenks & Werdelin (1998) provisionally retained the subspecies, while noting that there have been no genetic or morphometric studies done to confirm their validity. Synonyms: *canescens*, *harrisoni*, *hyenoides*, *lalandii*, *pallidior*, *septentrionalis*, *termes*, *transvaalensis*, *typicus*. The diploid number of chromosomes is $2n = 40$, with 72 autosomal arms; the X chromosome is metacentric and the Y chromosome is submetacentric. The chromosomes are similar in number and configuration to the hyaenas, providing further evidence for classifying the Aardwolf in the Hyainidae (Ulbrich & Schmitt 1969). Similarly, haemoglobin of the Aardwolf has the same electrophoretic mobility as that of the hyaenas (Seal 1969).

Description Medium-sized carnivore, larger than a jackal, standing about 0.47 m at the shoulder. Height accentuated by long mane hairs, which are erected when stressed. Face usually greyer than rest of body, while throat is a paler grey-white. Ears long and pointed; brown-black behind, white in front. Hair on the face short (10–15 mm) and grey, muzzle almost hairless and grey-black. Muzzle has minute, delicate light-coloured downy hairs, with a few longer hairs on the upper lip. Seven or eight strong, black vibrissae. Neck long and slender, sometimes with black spots or stripes present (Roberts 1951, Richardson & Bearder 1984, Koehler & Richardson 1990, Skinner & Chimimba 2005).

Background colour of the body varies from yellowish-white or buff to rufous. There are three vertical black stripes on the body and one or two diagonal stripes across the fore- and hindquarters. Body stripes run from mid-back and tail out towards the underparts. Most of the body consists of dense, soft, crinkled underfur interspersed with coarser guard hairs. Hair relatively short, not more than about

10–15 mm; individual hairs are dark at base, then broadly white, with black tips. In South Africa length and density of pelage increases during winter (Anderson 1994, 2004, Anderson *et al.* 1997). Hairs of the mane, which runs from back of head to base of tail, are broadly black-tipped and show as broad black band down mid-back. Mane hairs coarse and long (longest of all carnivores; Wemmer & Wilson 1983), being about 70 mm on back of head, increasing to about 200 mm on shoulders. These hairs have broad white bases, then alternating black and white annulations, terminating in black tips (Koehler & Richardson 1990, Skinner & Chimimba 2005).

Legs long, with regular horizontal stripes, which are darker towards the feet. Stance digitigrade (Sclater 1900). Five digits on the front feet, four on the hind. Presence of the first digit (pollex) on the front feet is one of the characters in which the Aardwolf differs from hyaenas. Claws strongly built and non-retractile (Sclater 1900). Claws on the first digits of the front feet are well developed and distinctly curved, the remaining four only slightly so. Viewed from above the claws are narrow, but in side view they are broad at the bases and strongly built and about 20 mm long over the curve. Claws on the hindfeet are similar, but slightly more curved. The tips of the claws show clearly in the Aardwolf's spoor (Koehler & Richardson 1990, Skinner & Chimimba 2005). Tail bushy and broadly black-tipped. Hair on the tail is long and wiry like that of the crest. Individual hairs are up to 150 mm long, broadly whitish at base and for about two-thirds of their length, remainder black (Skinner & Chimimba 2005). No sexual dimorphism in size (Richardson 1985, Koehler & Richardson 1990), although in overall length (and length of tail) ♀♀ appear slightly larger than ♂♂ (Smithers 1971). The ♀ has two pairs of inguinal nipples (Richardson 1985).

The skull is flat in profile, but falls off abruptly in front of the eye orbits flattening out towards the nasals. The supra-occipital crest is well developed and heavily built, rising 6–7 mm from the braincase; a short sagittal crest joins it at right-angles. The zygomatic arches are broad and heavily built, suggesting well-developed masseter muscles. Orbits are incomplete, although the two postorbital processes approach quite closely. The front chamber of the ear bulla is tiny compared with the hind chamber, which is elongated and swollen, rising high from the braincase when viewed from below. The broad palate accommodates the broad spatulate tongue, while the lower jaw, when viewed from above, is bowed out in front for the same reason. The dental formula is $I^{3/3}, C^{1/1}, P^{3/3}, M^{1/1} = 32$. Although the canines are well developed (the upper canines being long and curved, the lower canines slightly recurved), the cheekteeth are peg-like and much reduced (Koehler & Richardson 1990, Skinner & Chimimba 2005).

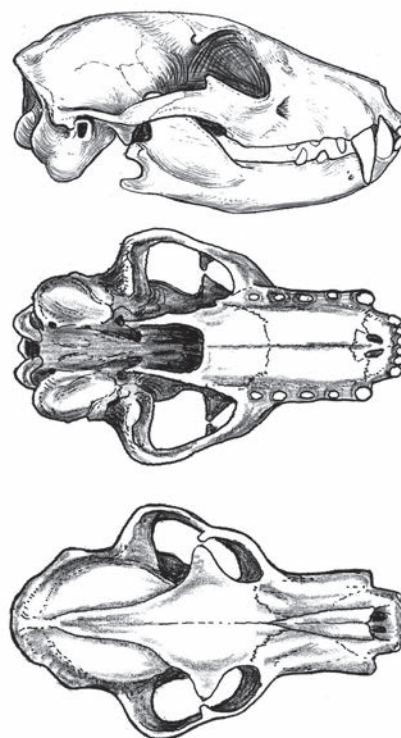
Geographic Variation

P. c. cristatus: southern Africa.

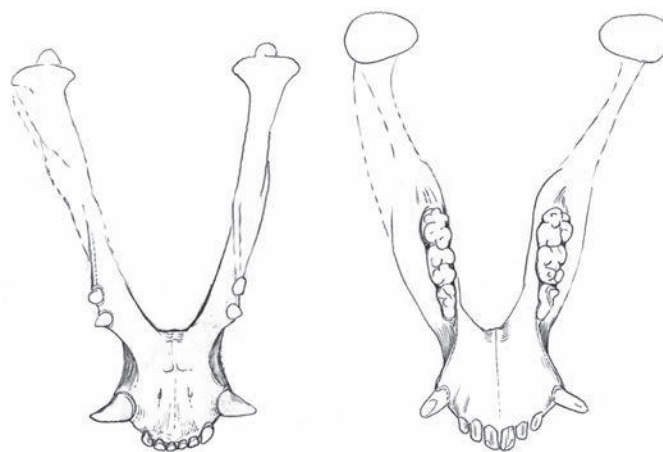
P. c. septentrionalis: eastern and north-eastern Africa.

Similar Species

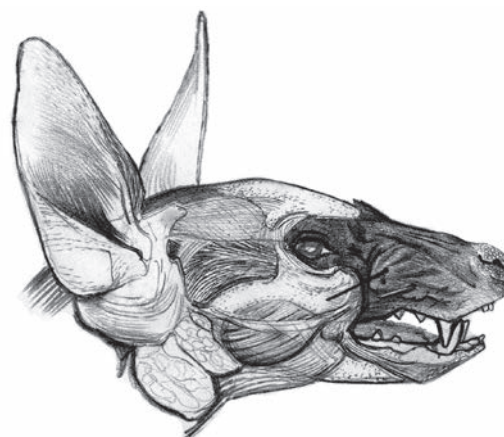
Hyaena hyaena. Sympatric in East and north-east Africa. Also has vertical body stripes, but is >50% larger in size and the stripes are more irregular (Roberts 1951, Richardson & Bearder 1984). Gingerich (1975) suggested that the Aardwolf mimics the Striped Hyaena *Hyaena hyaena* to reduce predation by Leopards *Panthera pardus* and other carnivores. However, as the Aardwolf is half the size of the hyaena and as other animals (including several species of smaller carnivores) seem unperturbed by an Aardwolf, mimicry



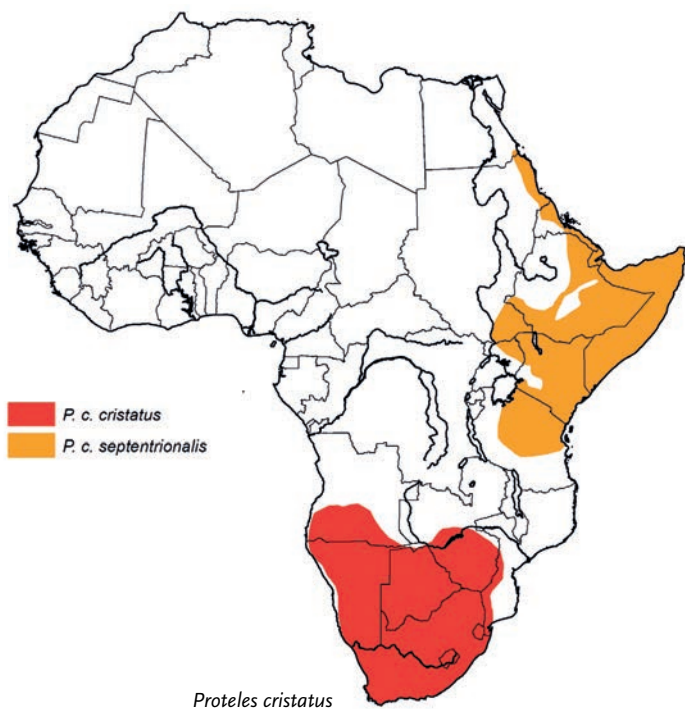
Lateral, palatal and dorsal views of skull of Aardwolf *Proteles cristatus*.



Lower jaw of *Proteles cristatus* compared with juvenile Common Warthog *Phacochoerus africanus*.



Aardwolf *Proteles cristatus* facial myology (note large salivary glands).



seems an unlikely explanation for Aardwolf stripes (Kingdon 1977, Koehler & Richardson 1990).

Distribution Endemic to Africa, with two discrete distributional areas, 1500 km apart, one in East and north-eastern Africa and one in southern Africa. During the Pleistocene epoch, when the climate in central Africa was often drier, the range of the Aardwolf was probably continuous (Coe & Skinner 1993).

The northern population extends from CTanzania to NE Uganda, Ethiopia (including the central Rift Valley; Yalden *et al.* 1996) and Somalia, then narrowly along the coast of Eritrea and Sudan to extreme SE Egypt (in the Sudan Government Administration Area; Hoath 2003) (Hofer & Mills 1998a). Their presence in Djibouti is unclear: no confirmed records are mentioned by Hofer & Mills (1998a) or Künzel *et al.* (2000), although it is mentioned by Simoneau (1974). A road kill from near Mbatwa in the Udzungwa Mts in 2002 may represent the most southerly record for the *P. c. septentrionalis* subspecies (De Luca & Mpunga 2005).

The southern population ranges over most of southern Africa, extending just into SW Angola, S Zambia (apparently south of the Kafue R.) and SW Mozambique (Smithers & Lobão Tello 1976, Ansell 1978, Crawford-Cabral 1989a). It is therefore absent from Malawi, STanzania and most of Zambia (Koehler & Richardson 1990, Hofer & Mills 1998a). The Aardwolf occurs throughout Namibia, except along the Namib Desert coast, Botswana, Zimbabwe (except the north-east), Swaziland, and throughout South Africa, except the forested areas in the south along the coast (Skinner & Chimimba 2005). It is not recorded from Lesotho, but may well occur (Lynch 1994). There are unconfirmed reports of occurrence in NE Central African Republic and Burundi (Koehler & Richardson 1990).

The distribution of the Aardwolf is largely determined by the distribution of *Trinervitermes* termites, which constitute their principal food (von Ketelhodt 1966, Kruuk & Sands 1972, Cooper & Skinner 1979, Richardson 1987a, 1990). The Aardwolf's absence in West

Africa is related to a scarcity of suitable termites (Kruuk & Sands 1972). The surface-foraging *Trinervitermes* termites that occur in West Africa (*T. oeconomus* and *T. occidentalis*) are relatively uncommon and prefer bushy habitats rather than open grassland (Sands 1961, Kruuk & Sands 1972, Ohiagu 1979).

Habitat The Aardwolf's prime habitat is open, grassy plains, although most habitats having a mean annual rainfall of 100–800 mm are occupied (Koehler & Richardson 1990). The Aardwolf is most common in the 100–600 mm range and does not occur in forests or pure desert (Skinner & Chimimba 2005). In southern Africa Aardwolves occupy diverse habitats, ranging from the karroid habitats of the Western Cape and Eastern Cape, the grasslands and scrub of Botswana, the open savanna woodlands of Zimbabwe, and the inland gravel plains of the Namib Desert in Namibia (Skinner & Chimimba 2005). In East Africa the habitat occupied by Aardwolves includes open grassland with virtually no trees (Kruuk & Sands 1972). They are recorded to 2000 m in Ethiopia (Yalden *et al.* 1996).

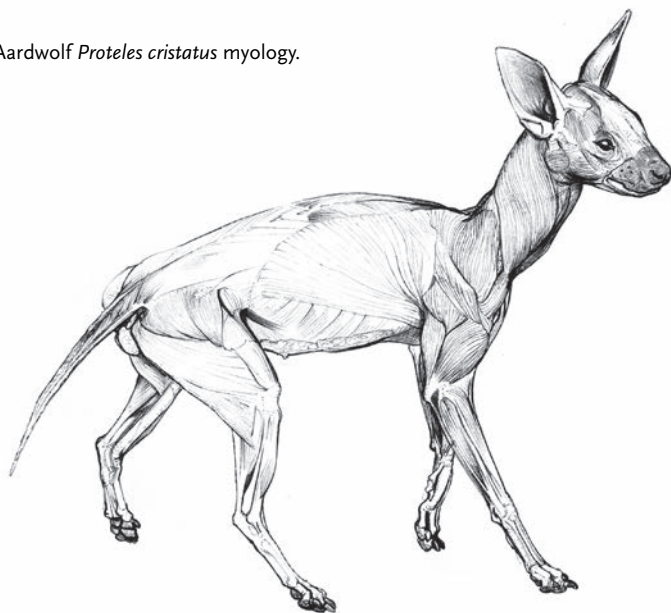
Abundance Although fairly widely distributed in Africa, the Aardwolf is not common within this range. In prime habitat (open grassland and scrub regions), Aardwolf densities may reach 1 adult/km² on farms with good populations of *Trinervitermes* termites and no persecution by farmers (Richardson 1984, 1985, Skinner & Van Aarde 1985, Koehler & Richardson 1990). In Serengeti N. P. the centres of Aardwolf ranges appeared to be 1–2 km apart (Kruuk & Sands 1972).

Adaptations Despite genetic, morphological and behavioural evidence that the Aardwolf is closely related to the hyaenas, its diet and dentition are clearly different from the hyaenas. Hyaenas have strong dentition and are able to crush bones, while the Aardwolf has a slender skull and the cheekteeth are reduced to small, widely spaced, redundant pegs. Unlike the hyaenas, elongated frontal sinuses are conspicuously absent in the extant Aardwolf (Joeckel 1998). Hyaena-like features include: large pointed ears, long erectile mane, sloping back with forelegs longer than hindlegs, and a well-developed anal gland for scent-marking grass stalks (Roberts 1951, Koehler & Richardson 1990, Skinner & Chimimba 2005).

The Aardwolf possesses none of the obvious external physical features of a termite feeding style, characteristics that are typical of other myrmecophagous mammals (Griffiths 1968, Anderson *et al.* 1992). Behaviourally, the Aardwolf differs from the other typical myrmecophages in that it does not dig for its prey, but licks them off the soil surface. Nevertheless, the Aardwolf does have a number of anatomical features that are clear adaptations to this diet (Flower 1869a, Anderson *et al.* 1992, Anderson 2004). The Aardwolf is probably one of the most specialized carnivores and myrmecophagous mammals (Richardson 1987b).

Sight, hearing and smell appear to be well developed in the Aardwolf. Externally the eyes and ears are noticeably large, while internally the auditory bulla and olfactory lobes also are well developed (Flower 1869a, Kruuk & Sands 1972, Richardson 1985, Koehler & Richardson 1990, Skinner & Chimimba 2005). The Aardwolf has a large and hairless muzzle, which prevents the soldier termites' defensive secretions, and hence dirt, from adhering to the same extent as they would if the muzzle was haired (Kruuk & Sands 1972). The most noticeable features of the Aardwolf skull are the widely spaced and small-

Aardwolf *Proteles cristatus* myology.



peg-like teeth, the contrastingly large canines, and the broad and parallel-sided palate (Anderson *et al.* 1992). Therefore, although the Aardwolf probably has the ability to kill vertebrate prey with its large canines, because of a lack of developed molars and premolars it would not be able to process the prey. The canines are used in territorial disputes against other Aardwolves and in defence against predators (Richardson 1985, 1987a, b). The relatively well-developed incisors are almost certainly used for grooming.

An interesting aspect of the Aardwolf's musculature is the relatively large digastric muscle, compared with that of a domestic dog (Turnbull 1970; illustrated in Kingdon 1977). As the digastric muscle is used for opening the jaw, its enlarged size may be explained by the Aardwolf's need to open its mouth rapidly and frequently while feeding (Anderson *et al.* 1992). This is a development that parallels, on a more modest scale, the enlarged digastric of the Bat-eared Fox *Otocyon megalotis* (another myrmecophagous carnivore), where just such a function is unambiguous. Other features of the skull are the well-developed postorbital processes and the extraordinarily large tympanic bulla (Anderson *et al.* 1992).

The Aardwolf has a broad spatulate tongue (117–123 mm long, and 30–32 mm wide) covered with large, hardened papillae (one type, 'incisiform' papillae, may be unique to the Aardwolf) (Flower 1869b, Richardson 1985, Anderson *et al.* 1992). This tongue is used to lick termites from the soil surface and the papillae are adaptations to protect the tongue against abrasion by sand. The broad palate accommodates the rapid licking movements of the broad tongue. It also has posteriorly directed transverse ridges, which presumably act as a catchment area for termites as the tongue is again extruded.

The mandibular salivary glands are very large (about twice the size of the mandibular salivary glands of a similar-sized dog) (Flower 1869b, Richardson 1985) and they are serous and mucous secreting, while the parotid, sublingual and zygomatic glands are serous or mixed. The mucous secretions provide a relatively thick and sticky substrate and facilitate the licking up of termites. In addition, the mucus could provide protection for the oral cavity and oesophagus from the termites' terpene secretions, as has been speculated to be the case in myrmecophagous sengis (Kratzing & Woodall 1988). Like other nasute termites (Nasutitermitinae), *Trinervitermes* possess a highly

effective means of chemical defence: the soldiers have well-developed frontal glands from which they can squirt threads of very sticky and noxious, terpene-based secretions (Prestwich 1983, Braekman *et al.* 1984). It is not known whether the saliva may play a role in the detoxification of the terpene secretions, i.e. similar to the tannin-binding proteins found in the saliva of browsing ruminants (Austin *et al.* 1989). The ability of the Aardwolf to tolerate these terpenes secretions must be its most significant adaptation, as this has made these termites readily available and virtually without competition from any other mammal (Kruuk & Sands 1972, Melton 1976, Kingdon 1977, Richardson 1987b, Richardson & Levitan 1994). It has been suggested that, as the Aardwolf evolved from civet-like viverrids, such as the African Civet *Civettictis civetta*, which has the ability to feed on noxious food items, it was pre-adapted to tolerate the terpenes secretions of *Trinervitermes* (Richardson 1987b, Richardson & Levitan 1994).

The gastrointestinal tract of the Aardwolf follows the typical carnivore pattern and consists of a stomach, small intestine, caecum and colon (Anderson *et al.* 1992). The smooth-walled pyloric region of the stomach has a few irregular folds and the walls are thick and muscular. As *Trinervitermes* termites are small and soft-bodied, chewing is unnecessary and the termites are probably pulverized by the muscular region of the stomach. A similar structure is found in the stomach of anteaters (Myrmecophagidae) and pangolins (Manidae) (Chivers & Hladik 1980). Chewing would not only limit the amount of termites that could be ingested, but also rupture the soldier termites' heads and thus release the terpene contents into the Aardwolf's buccal cavity. The pulverization of termites in the stomach is probably aided by sand and other debris that is incidentally ingested with the termites (up to 50% of the faeces contain sand; Cooper & Skinner 1979). The small intestine is short, a characteristic of animals that feed on soft, easily digestible material. Aardwolf digestion may be more geared to processing large volumes of material and the rapid digestion of the workers' abdomens, as opposed to the more efficient digestion of the whole termites. The small caecum may play a role in the absorption of water and electrolytes. The descending (distal) colon is characterized by thick walls with distinct longitudinal bands. This enables the distal colon to distend, allowing the accumulation of a large volume of faeces (over periods as long as 18 hours). Soon after emergence from their den in the late-afternoon/early-evening, Aardwolves walk to a nearby midden and defecate, with the first defecation of the evening weighing up to 1 kg (Kruuk & Sands 1972, Richardson 1987a). As Aardwolves obtain most of their water from termites and thus very rarely drink (Richardson 1985), the distal colon may also play an important role in the absorption of water (Anderson *et al.* 1992).

There are diel and seasonal variations in the body temperatures (T_b) of Aardwolves in South Africa (Anderson 1994). During winter active Aardwolves maintain an average T_b of approximately 37.3 °C but after returning to their dens their T_b decreases through the rest of the night and early morning until the middle of their inactive period (08:00–10:00h) (Anderson 1994). At 09:00h their average T_b is 34.1 ± 1.6 °C. The lowest T_b recorded during winter was 31.2 °C in one ♀ at 09:00h (Anderson 1994). Hypothermia in the Aardwolf during winter translates to a ca. 18% energy saving (Anderson 1994). The Aardwolf does not fully exploit the energetic advantages of hypothermia, but perhaps the T_b at which Aardwolves rest during the day facilitates the lowest rate of energy expenditure needed to

maintain physical agility for predator avoidance. The Aardwolf's size and the cost of rewarming may preclude it from lowering its T_b below 31–33 °C. A lowered T_b also has adaptive potential for water conservation by a reduction of evaporative water loss (Anderson 1994, 2004). The evaporative water loss rates and rates of water flux are lower than predicted for similar-sized eutherian mammals (Chew 1965, Anderson *et al.* 1997, Williams *et al.* 1997).

Aardwolves have reduced basal and field metabolic rates, further reduced during winter, thus reducing energy requirements during the stressful winter months when termites are generally not available (McNab 1984, Anderson 1994, Anderson *et al.* 1997, Williams *et al.* 1997). The main advantage of a low metabolic rate is that it reduces energy expenditure and thus reduces the minimum energy requirements per feed and/or increases the maximum intervals between feeds (McNab 1983). McNab (1984) suggested that ant- and termite-eating mammals have evolved a low BMR in order to survive on a diet of termites, which are not only nutritionally poor (Phelps *et al.* 1975, Redford & Dorea 1984, Anderson 1994), but also have a patchy distribution in both space and time (cf. Richardson 1985, Anderson 1994).

Aardwolves spend the majority of their inactive period in their dens (Richardson 1985, Anderson 1994). Richardson (1985) found that an average of 5.8 dens (range 2–9) were used by a pair of Aardwolves in a territory each year, with each den being used for about 6–8 weeks at a time before a different den was used. A den may be re-occupied 6–18 months later (Richardson 1985).

The time of departure from, and time of retirement to, dens is highly variable throughout the year but fairly consistent within a specific season (Richardson 1987a, Anderson 1994, Williams *et al.* 1997), with Aardwolves spending a greater proportion of time in their dens during winter. During a study in South Africa, denning times were 19.1 ± 1.2 hours and 15.8 ± 1.72 hours during winter and summer, respectively (Anderson 1994, 2004). The extended period spent in the den during winter, coupled with a reduced metabolic rate, results in Aardwolves conserving at least 639 kJ/day while in their winter dens (Anderson *et al.* 1997). Aardwolf activity patterns and hence den usage are largely determined by the availability of termites. The den also has an important anti-predatory function, especially as it provides a safe refuge for the cubs from predators, such as Black-backed Jackals *Canis mesomelas* (Richardson 1985).

Dens usually have only one entrance, with the entrances being randomly orientated (Anderson 1994). Most den entrances are oval-shaped, being about 320 mm high and 420 mm wide at the entrance, but rapidly narrowing down to about 200×300 mm inside the tunnel (Richardson 1985). Two excavated Aardwolf dens were narrow and well defined with no side tunnels and no obvious enlargements at the end. In contrast, a den excavated by Richardson (1985) had a slight chamber enlargement. The two excavated burrows narrowed into smaller burrows of the Southern African Springhare *Pedetes capensis*, with a tunnel height and width of approximately 100 mm and 155 mm, respectively (Anderson 1994). As Aardwolves do not possess well-developed and powerful limbs to excavate a subterranean den (Anderson *et al.* 1992), they apparently rather enlarge those dug by springhares (Smithers 1971, Anderson 1994, Anderson & Richardson 2005). The Aardwolf may also use old Aardvark *Orycteropus afer* and Cape Porcupine *Hystrix africae australis* burrows (Smithers 1971, Richardson 1985, Anderson 1994). Although it has been stated that Aardwolves may excavate their own

burrows (Smithers 1971, Skinner & Chimimba 2005), there is no conclusive evidence to support this.

In South Africa, the temperature of Aardwolf burrows (T_d) is relatively constant during summer, averaging 27.2 ± 0.2 °C, despite large daily fluctuations at the soil surface where temperatures range from a maximum of 39.5 °C at 11:00h to a minimum of 15.0 °C at 05:00h (Anderson 1994, Anderson & Richardson 2005). The T_d s during summer are high but still within the thermoneutral zone of the Aardwolf (McNab 1984, Anderson *et al.* 1997). During winter, mean burrow temperatures are also constant, averaging 12.2 ± 1.2 °C, substantially lower than that recorded during summer (Anderson 1994, Anderson & Richardson 2005). Although the T_d during winter is below the thermoneutral zone of the Aardwolf, it is still considerably warmer than the T_a s outside the den. It is likely that the relatively low T_d , together with a CO₂ build-up in the den during winter (exacerbated by the extended period spent underground, and den sharing) (Anderson 1994), may stimulate temporal heterothermy in the Aardwolf (see Kuhn 1986).

It has been found that during winter young Aardwolves frequently shared their dens with siblings or one of their parents (Richardson 1985, Anderson 1994). Huddling reduces the Aardwolves' effective surface area, resulting in a reduction in heat loss (Anderson 1994, Anderson *et al.* 1997). Owing to the small size of the den chamber, heat produced by the occupant(s) will also raise the T_d to some extent, so the T_d of the Aardwolf chamber may therefore rise above the lower critical temperature of the thermoneutral zone. The dens are not lined with insulative materials (such as grass, litter or fur) (Richardson 1985, Anderson 1994).

The histopathology of the Aardwolf penile pad, anal pouch and forefoot scent-marking glands have been described by Stoeckelhuber *et al.* (2000). The anal gland is situated immediately above the anus, sharing a common external aperture, and consists of a T-shaped reversible pouch of sebaceous tissue (Flower 1869b, Pocock 1916c, Stoeckelhuber *et al.* 2000). The anal pouch can be everted and retracted again (Stoeckelhuber *et al.* 2000) and is characteristic of all Hyaenidae (Macdonald 1985). A yellowish-orange sebaceous and apocrine secretion is produced, which turns black when it oxidizes (Richardson 1985, Stoeckelhuber *et al.* 2000). The gland structure is very similar to that in the Striped Hyaena and Spotted Hyaena *Crocuta crocuta* (Pocock 1916c) and scent-marking behaviour is similar to Spotted Hyaenas (Kruuk & Sands 1972). Glandular tissue in the forefoot (Stoeckelhuber *et al.* 2000) may have scent-marking functions. At the base of the penis is a pair of oblong clusters of pale sebaceous glands separated by non-glandular tissue (Flower 1869b), the penile pad (Stoeckelhuber *et al.* 2000), present only in the ♂, which is not present in hyaenas. The function of this gland is not very clear (Flower 1869b, Richardson 1985), although it may be used to mark the genitals of the ♀ during copulation to inform other competing ♂♂ that she has already copulated (Sliwa 1996, Stoeckelhuber *et al.* 2000).

Foraging and Food The Aardwolf's diet is the best documented aspect of its biology, with this specialization initially being noted by Sclater (1900), Roosevelt & Heller (1914), Shortridge (1934), Wells (1968) and Smithers (1971). Throughout its distribution, it has been found to feed primarily on nasute harvester termites (genus *Trinervitermes*) and, in any particular region, mainly on one species (Skinner & Chimimba 2005). These include *T. bettonianus* in East Africa

(Kruuk & Sands 1972), *T. rhodesiensis* in Zimbabwe (Smithers & Wilson 1979) and Botswana (Smithers 1971) and *T. trinervoides* in South Africa (Cooper & Skinner 1979, Richardson 1987a). These termites are ecological equivalents: they forage in dense aggregations completely exposed on the soil surface while browsing or collecting dry grass (Richardson 1987a). Most other African termites forage underground, under the protection of mud galleries, or are very irregular in their surface foraging and therefore present a much less reliable food source (Kruuk & Sands 1972). Unlike the Aardwolf, other myrmecophagous generalists (such as the Aardvark and the Ground Pangolin *Manis temminckii*) typically have powerful claws with which they can dig into ant and termite nests, and long, thin tongues for licking up the termites in their tunnels. In contrast, the Aardwolf has a large, broad tongue ideal for licking termites off the flat soil surface (Richardson 1987a, b). Richardson (1987a) estimated that an Aardwolf in the Northern Cape, South Africa, consumes as many as 300,000 termites (1.2 kg) per night, amounting to about 105 million termites per year. Of these, *Trinervitermes* constitute the vast majority, with *Hodotermes mossambicus* being of limited importance during the winter months.

Aardwolves are almost exclusively solitary foragers, except when accompanying their young cubs (Kruuk & Sands 1972, Bothma & Nel 1980, Richardson 1995, 1987a). When foraging, Aardwolves move slowly (speeds of 1–3 km/h) and quietly, head bent slightly forward and ears cocked forward, constantly moving (Kruuk & Sands 1972, Bothma & Nel 1980, Richardson 1987a). An irregular route is followed, but upwind movements predominate (Kruuk & Sands 1972, Bothma & Nel 1980, Richardson 1985). Aardwolves cover 8–12 km/night during summer and 3–8 km/night during winter (Richardson 1985, 1987a). There is one record of an Aardwolf walking 25 km in 10 hours and remaining active until the temperature had dropped to zero, 4 hours after it had last fed on termites (Richardson 1987a).

Patches of termites are found either fortuitously or, more commonly, after the Aardwolf has turned sharply upwind from whatever direction it happened to be walking in (Kruuk & Sands 1972). The upwind turn indicates that food location takes place primarily by scent, or by hearing, or both (Kruuk & Sands 1972, Bothma & Nel 1980, Richardson 1985, Koehler & Richardson 1990), but hearing is probably the most important sense used (Kruuk & Sands 1972). The large bulbus oticus in the Aardwolf skull is indicative of a comparatively well-developed sense of hearing, although sight may be important at close range (Kruuk & Sands 1972, Richardson 1985, Koehler & Richardson 1990, Skinner & Chimimba 2005). The *Trinervitermes* concentrations generate a noise that can be heard by humans at 15–30 cm distance (Kruuk & Sands 1972). Olfaction also plays a role, since the soldiers' defensive secretion has a strong resinous smell, first observed by Kemp (1955) (and see Kruuk & Sands 1972). It is likely that sporadic attacks by small predators (such as ants) on the foraging termites would also cause scattered discharges of terpenoids (Kruuk & Sands 1972).

Having located termites, the Aardwolf licks them off the soil surface with its very broad tongue, pushing the front part of the snout into the vegetation and close to the ground (Kruuk & Sands 1972, Richardson 1987a). Feeding is rapid, with many quick licks and somewhat jerky pushing and rotating head movements. The ears, which are cocked forward until feeding begins, are now laid back. One of the front paws is occasionally used to push aside the vegetation, but during foraging and feeding the feet are never used for digging (Kruuk & Sands 1972).

A female Aardwolf in East Africa fed 44 times in 65 min, on average once every 98 sec (Kruuk & Sands 1972). The mean feeding time per termite patch is between 20 and 28 sec (Kruuk & Sands 1972, Richardson 1985, 1987a). On a second occasion she fed 35 times in 51 min, on average every 87 sec, with the mean feeding time per termite patch being 22 sec. The longest feed was 70 sec, the shortest 3 sec (Kruuk & Sands 1972). Foraging times per termite patch in the Namib Desert are significantly longer (Bothma & Nel 1980). Examination of termite foraging patches after Aardwolf feeding reveals that large numbers of termites are still milling around in a dense concentration (Kruuk & Sands 1972). Aardwolves stop feeding on a termite patch after a critical change in the soldier/worker ratio. The disturbance of the termite patches increases the percentage of unpalatable soldiers as the worker termites go underground and soldier termites emerge to defend the foraging termites (Bothma & Nel 1980).

Aardwolves are primarily nocturnal, although they may be active during the late afternoon, especially during the winter months (Kruuk & Sands 1972, Bothma & Nel 1980, Richardson 1987a). During summer in the Northern Cape, they generally become active 30–60 min after sunset and retire to the dens 1–2 hours before dawn (Richardson 1987a). The winter pattern is more flexible, with Aardwolves on some nights retiring to the den earlier than they had left on others, with these variations being explained by ambient temperature and the activity of termites (Kruuk & Sands 1972, Bothma & Nel 1980, Richardson 1985, 1987a).

A feature of *T. trinervoides* (and probably most nasute termites) is that they are very poorly pigmented and consequently cannot tolerate direct sunlight (Hewitt *et al.* 1972). They are almost entirely nocturnal (Richardson 1987a, b). By contrast, the larger harvester termites, *Hodotermes mossambicus*, are pigmented and are mainly active by day and during winter (Nel & Hewitt 1969, Hewitt *et al.* 1972). This is serendipitous for the Aardwolf, because during winter in southern Africa (May–Aug) it is frequently too cold for *T. trinervoides* to forage at night (they become inactive when air temperature drops to about 9 °C; Richardson 1987a, b), so the Aardwolf becomes more diurnal and frequently feeds on *Hodotermes* during the afternoon (Richardson 1987a). In spite of the utilization of this alternative food source, the Aardwolf consumes only one-fifth the amount of termites per month that it does outside the winter months (Richardson 1987a). This places great stress on the animals, which lose up to 20% of their body weight during winter (Richardson 1987a, b, Anderson 1994, 2004). Through winter, Aardwolves deplete their deposits of subcutaneous fat. This suggests that Aardwolves are very dependent on *Trinervitermes* and unable to feed successfully on alternative sources of food (Richardson 1987a, b). In East Africa, *T. bettonianus* is less active during the wet season (Mar–May), and the diet of the Aardwolf is more varied during this period (Kruuk & Sands 1972).

During the summer months Aardwolves foraged for significantly longer periods than in winter, but the percentage activity over the total foraging period was significantly lower (Richardson 1987a). This is because during winter, with the termites being active for a very limited period each night, Aardwolves made maximum use of the opportunity to feed and therefore did not rest during the night (Richardson 1987a). They did sometimes rest during the afternoon if they had become active earlier, but found no *Hodotermes* foraging (Richardson 1987a). More time is spent foraging on termite patches earlier in the night (Bothma & Nel 1980). Bothma & Nel (1980)

suggested that den emergence in the Namib Desert reflected the success of the previous night's foraging activities.

Aardwolves rest during the night for various lengths of time, from brief grooming bouts (30–60 sec) to 2 h 17 min (Bothma & Nel 1980). They usually cease foraging when it rains (Kruuk & Sands 1972). The sound of raindrops striking the grass may blanket termite activity and this may affect the use of sound in the location of food, or it is possible that during rain termites simply disappear underground (Kruuk & Sands 1972). At the end of the night's foraging session, Aardwolves retreat to their dens, which provide a more equable climate and protect them against the cold nights of winter and the daytime heat of summer (Anderson 1994).

As noted, Isoptera form the main portion of the Aardwolves diet: *Trinervitermes* spp. in the Namib (Bothma & Nel 1980), *Fulleritermes contractus* in SAngola (Dean 1978), *T. trinervoides* in South Africa (Bothma 1965, Cooper & Skinner 1979, Richardson 1997a), *T. rhodesiensis* in Botswana (Smithers 1971) and *T. bettonianus* in Serengeti N. P. (Kruuk & Sands 1972). Across Africa, the dominant food species is replaced by a closely related and ecologically similar member of the same termite species (Kruuk & Sands 1972). Other prey items that have been recorded in very small amounts in the Aardwolf's diet include: Coleoptera, Hymenoptera, Lepidoptera, Diptera, Dictyoptera, Odonata and Orthoptera, Arachnida and Acarina (Smithers 1971, Kruuk & Sands 1972, Kingdon 1977, Dean 1978, Cooper & Skinner 1979, Bothma & Nel 1980, Kok 1996, Matsebula *et al.* 2009, de Vries *et al.* 2011). The beetles in the scats may occupy the faeces after deposition, possibly in search of Diptera larvae (Bothma & Nel 1980). The Diptera pupae are not indicative of carrion consumption and are probably the result of post-deposition fly breeding (Cooper & Skinner 1979). Aardwolf hairs identified in the stomachs of several individuals are probably ingested during grooming (Cooper & Skinner 1979, Kok 1996).

Trinervitermes termites are small, so the Aardwolf's method of feeding results in the simultaneous ingestion of large amounts of debris, indigestible soil and vegetable matter (Kruuk & Sands 1972, Dean 1978, Kok 1996). The sand content of faeces may vary from negligible amounts to 40% in very sandy areas (Cooper & Skinner 1979, Bothma & Nel 1980), or when termites are unavailable (Richardson 1985). Smithers (1971) noted that the stomach contents of three Aardwolves contained 15%, 30% and 31% of indigestible matter including sand. In a study on Aardwolves in the Namib Desert it was found that sand formed 42.4–65.5% of the total dry faecal mass, while plant material formed 3.1% of the total dry organic mass (Bothma & Nel 1980).

Unconfirmed reports of Aardwolves eating lambs, carrion, eggs (even Ostrich *Struthio camelus* eggs), small rodents and reptiles (Sclater 1900, Shortridge 1934, Maberly 1960) are not substantiated by studies of gut or faecal contents and probably result from mistaken identity (cf. Cooper & Skinner 1979, Richardson 1987a, b), with the statements probably referring to hyaenas and/or jackals (Kruuk & Sands 1972). Although Bothma (1965) found that 80% of the contents of one Aardwolf stomach was carrion, in addition to the remains of a rodent and some small pieces of tortoise shell, it is possible that this specimen was a misidentified Black-backed Jackal. The reports of Aardwolves scavenging on carrion (Sclater 1900) are probably the result of Aardwolves feeding on maggots and carrion insects on the carcass, which the Aardwolf will eat when food is scarce (Cooper & Skinner 1979).

Aardwolves occasionally feed on termitaria opened by Aardvarks, especially during the winter months when food is scarce (Kingdon 1977, Bothma & Nel 1980, Taylor & Skinner 2000, M. D. Anderson pers. obs.).

Aardwolves are generally independent of surface water as they get all their water requirements from termites (Skinner & Chimimba 2005). However, during prolonged cold spells during winter, when termites are not active, Aardwolves may walk long distances in search of water. This is the only time of year when they have been observed to drink (Richardson 1985).

Social and Reproductive Behaviour Aardwolves are socially monogamous, with a mated pair occupying a perennial territory with their most recent offspring. Although usually seen singly, pairs and small aggregations of Aardwolves have been reported foraging together (Roberts 1951, Smithers 1971, Kingdon 1977). There are observations during winter of Aardwolves from the same territory coming together in a loose 'colony', spread over 100 m or more, to feed on the harvester termite, *H. mossambicus* (Skinner & Chimimba 2005); however, the reported aggregations of larger numbers (up to 14 individuals; Roberts 1951) is disputed. Usually one Aardwolf occupies a den at a time, although on occasions, especially during winter, cubs will share the den with one of their parents (Bothma & Nel 1980, Richardson 1985).

Aardwolves occupy territories that vary between 1 and 4 km², depending on the density of termite mounds (Kruuk & Sands 1972, Bothma & Nel 1980, Richardson 1985, Skinner & Van Aarde 1985). Territory maintenance is by means of overt aggression and scent-marking (Kruuk & Sands 1972, Richardson 1985, 1987b, c, Sliwa & Richardson 1998). Territory maintenance is energetically expensive (36.6% of daily energy expenditure during summer) (Williams *et al.* 1997). Territory sizes vary according to the density of *Trinervitermes* mounds, with each territory having approximately 3000 termitaria, each containing an average of 55,000 termites (Richardson 1985). The standing crop of these mounds provides approximately half the annual consumption of a family of Aardwolves, so it is presumed that these termites must have a high production/biomass ratio in order to accommodate their high predation rate (Richardson 1985, 1986, 1987a). Aardwolves avoid each other on the boundary of the range, with little overlapping of ranges (Kruuk & Sands 1972, Richardson 1990, 1991).

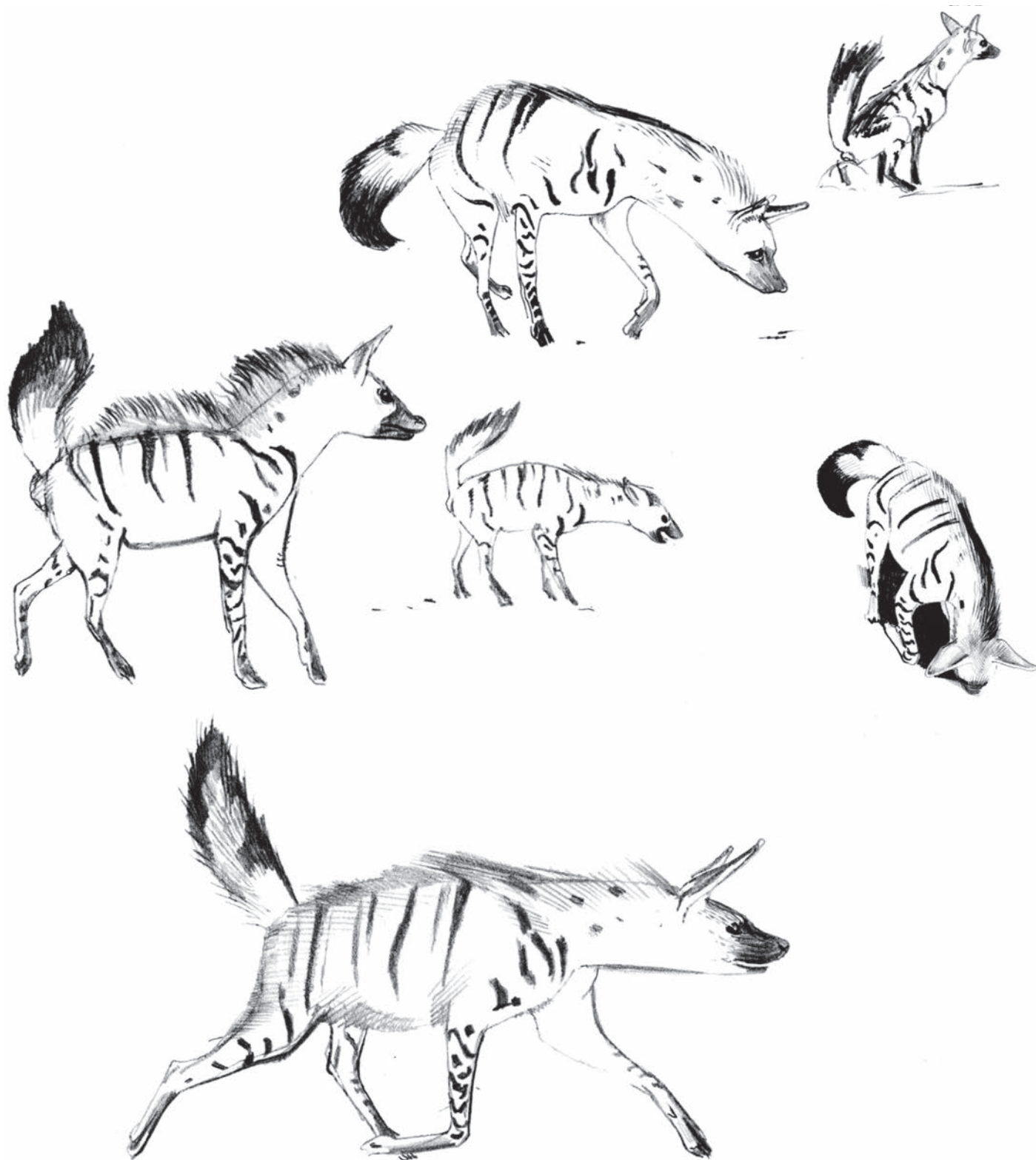
Paste-marking is the predominant form of communication in Aardwolves, functioning as territorial advertisements, mainly to intimidate intruders and to synchronize mating (Richardson 1985, 1990, 1991, 1993, Sliwa & Richardson 1998). Scent-marks help to maintain territorial integrity in the temporary absence of the resident Aardwolf (Richardson 1991, 1993), being used as an unambiguous cue advertising territory ownership, thereby establishing an asymmetry of contest between residents and intruders (Gosling 1982, Richardson 1990). There is a higher density of scent-marks in smaller Aardwolf territories, possibly because the smaller territories have a higher density of resources and, as such, attract the highest intruder pressure (Richardson 1991).

When scent-marking, Aardwolves straddle a single grass stalk, then rapidly crouch while everting the anal pouch and wiping a smear of secretion, ca. 6 mm in length, onto the grass (Kruuk & Sands 1972, Nel & Bothma 1983, Richardson 1985, 1990). The secretion colour varies and this is related to age, sex and mating season (Stoeckelhuber

et al. 2000). The colour of the male secretion is dark brown to bluish-black while the female secretion is orange, greenish to light, or dark brown (Sliwa 1996). The different scent-mark colours may have a communicatory function (Stoeckelhuber *et al.* 2000), but as Aardwolves are primarily nocturnal and the scent marks soon oxidize to a black colour (Apps *et al.* 1989b), a visual stimulus is unlikely (Stoeckelhuber

et al. 2000). The chemical properties of the Aardwolf scent-mark have been described by Apps *et al.* (1989b).

Scent-marking is observed from an early age, with the young animals having a yellowish-translucent (2 months) to light brown (4–5 months) secretion colour (Sliwa 1996). Both sexes scent-mark, although ♂♂ tend to paste more frequently than ♀♀, at mean



Aardwolf *Proteles cristatus*.

intervals between scent-marks of ca. 1 min (Kruuk & Sands 1972). Scent-marking rates do not differ significantly between the sexes (Sliwa 1996). Territorial marking by male Aardwolves plays an important role in the defence of access to their ♀♀ and food resources, while ♀♀ defend feeding territories only (Stoesselhuber *et al.* 2000). Scent-marking plays an important role in the mating season in both sexes (Sliwa 1996, Sliwa & Richardson 1998); however, during the three-month mating season territorial borders are frequently trespassed by both sexes, especially before and during female oestrus (Sliwa & Richardson 1998). Aardwolves scent-mark in neighbouring territories in order to advertise their presence to the resident pair to initiate extra-pair copulations (Richardson 1987c, Sliwa 1996). Pastings are concentrated along the territory boundary and at dens and middens (Kruuk & Sands 1972, Richardson 1987c). Richardson (1985, 1987b) believed this behaviour to be related to territoriality and mate acquisition. Male and female Aardwolves overmark more frequently, change their dens more often and increase their scent-marking rate more when they encounter scent marks of same-sex individuals than opposite-sex individuals, except during the mating season (Sliwa & Richardson 1998). Along territorial borders and at middens, marks are sniffed at for shorter periods and overmarked, with overmarking seeming to assert territorial ownership (Sliwa & Richardson 1998). Aardwolves seldom overmark scent-marks at dens and sniff at them longer, often showing flehmen (Sliwa & Richardson 1998). After locating a neighbour's scent-mark, the resident Aardwolf usually increases its rate of marking and often moves directly to the respective border, demonstrating individual scent-mark recognition (Sliwa & Richardson 1998). This has been confirmed by the different chemical properties of different individual's scent-marks (Apps *et al.* 1989b). Nel & Bothma (1983) reported that in the Namib Desert the Aardwolf makes a second type of pasting in which a very small spot of secretion is deposited; apparently this is related to advertising areas that have been traversed while feeding. This form of pasting has not been recorded elsewhere (Kruuk & Sands 1972, Richardson 1987c, Sliwa 1996).

Upon emergence from a den, Aardwolves either start feeding immediately, scent-mark, or run rapidly to a midden and defecate, and then start feeding or marking (Bothma & Nel 1980). Aardwolves defecate mainly at middens, although they sometimes defecate at random (Kruuk & Sands 1972, Nel & Bothma 1983, Richardson 1985, Koehler & Richardson 1990). Middens are usually 1–2 m in diameter and often are made up of soft, bare sand from frequent digging by the Aardwolves. There may be as many as 20 middens located throughout the territory, but those near the territory boundary seem to be used more frequently (Kruuk & Sands 1972, Richardson 1985, 1990). Up to four middens are used in a territory at one time (Kruuk & Sands 1972). To defecate, a narrow trench is dug with alternating strokes of the forepaws, after which the animal turns around and squats over the trench. The expulsion of the faeces during feeding involves considerable straining (Kruuk & Sands 1972). After defecating the equivalent of one-tenth of its body weight (Kruuk & Sands 1972, Richardson 1990), it scratches the hole closed with its forepaws and moves off (Richardson 1990). Subsequent defecations through the night are smaller. After defecating the Aardwolf usually deposits a few scent-marks before leaving (Richardson 1985, Koehler & Richardson 1990). Aardwolves always urinate in the same hole used for defecating. However, when termites are abundant they

may urinate 5–6 times per night, and simply stop foraging, squat, urinate and then continue foraging (Richardson 1985).

Fresh Aardwolf faeces carry a smell reminiscent of the smell of termites, possibly undigested defence secretions of the soldier termites, and so it is an advantage to concentrate the faeces in middens (Kruuk & Sands 1972, Richardson 1985, 1987a, b, 1990). If scent plays a role in food location, it would be confusing during foraging for the animal to encounter its own faeces (Kruuk & Sands 1972). The middens may also facilitate the decomposition of the dung, as, in East Africa, they contain large numbers of the termite *Macrotermes virescens* (Kruuk & Sands 1972). The middens may also have a territorial function (Richardson 1990, 1991).

Aardwolves will fiercely defend their territories and interactions can result in aggressive altercations. When territorial intruders are detected the resident immediately raises its mane of hair and chases the intruder, usually right to the territory border (Richardson 1985). If an intruder is caught, both animals fall to the ground and bite each other's necks while resting on their carpals (Richardson 1985, Koehler & Richardson 1990). Although the cheekteeth are small and redundant, the canines are well developed and the Aardwolf is capable of inflicting a severe bite (Ewer 1973, Skinner & Chimimba 2005). These anatomical features have almost certainly been retained for fighting (Ewer 1973), as Aardwolves have very aggressive territorial disputes and frequently chase jackals from their breeding dens (Richardson 1985). The use of canines in fighting is reflected clearly in their wear, as in old animals they are broken down to rounded stumps (Richardson 1985, Koehler & Richardson 1990). Generally, however, if another Aardwolf from the same territory is encountered during a foraging bout, both individuals raise the mane of hair along the back as they slowly approach each other (Skinner & Chimimba 2005). Once the other individual is recognized the hair is lowered and they pass by each other without any further greeting (Skinner & Chimimba 2005). Occasionally, particularly in a greeting between a mother and her cubs, the two individuals may sniff each other's noses briefly before separating (Koehler & Richardson 1990, Richardson 1995). Although it is quite widely reported that the Aardwolf ejects the contents of its anal gland as a form of defence when attacked or when it is stressed (Roberts 1951, Smithers 1971), the secretions are not noxious (Kingdon 1977), and such behaviour has not been confirmed.

Although the mated pair occupies the same territory throughout the year, copulations are not necessarily exclusive within the pair (Richardson 1987c, Richardson & Coetsee 1988, Koehler & Richardson 1990, Sliwa 1996). Extra-pair copulations regularly occur between the most aggressive ♂♂ and ♀♀ of less aggressive neighbours (Richardson 1987c). Access is gained to ♀♀ in neighbouring territories by rigorous scent-marking of the adjacent territory during the prooestrous period of the ♀ and then by defeating the resident ♂ in a fight (Richardson 1987c, Sliwa & Richardson 1998). Cuckoldry has evolutionary implications, especially as paternal care, guarding of the cubs from jackals, is energetically expensive and ♂♂ may not have a genetic investment in this generation. Females may accept extra-pair copulations after mating with the resident ♂ (Richardson 1987c, Richardson & Coetsee 1988), possibly resulting in mixed paternity (P. R. K. Richardson pers. comm.). The cuckolded ♂ may then guard the cubs, unless he has the rare opportunity of a ♀ with whom he can breed exclusively. He may desert his promiscuous ♀ to mate with an alternative ♀ (Richardson & Coetsee 1988).

Cubs are born and raised in dens, from which they emerge after about one month. From 4–6 weeks of age they play around the den for short periods when adults are present. From 6–9 weeks they venture further afield to play, but usually remain within 30 m of the den. From 9–12 weeks they may go foraging with an adult and start feeding on termites, but usually remain within 100 m of the den. From 12 weeks to four months, they may forage throughout the territory, but are usually accompanied by a parent. Cubs are weaned at the end of this period. Males help in rearing the young by guarding the den against Black-backed Jackals. Paternal care varies, but during the first two months some fathers may spend up to 6 h/night guarding the cubs while the ♀ is away foraging (Richardson 1985, 1987b, Richardson & Coetzee 1988). The cubs may still be accompanied by a parent for a short period of the night up to seven months of age, but thereafter forage alone. At about one year old the cubs make excursions into neighbouring territories and generally have left the territory by the time the next year's cubs have emerged from the den. Once they have finally left their natal territory, cubs seldom return, becoming transients in a search of vacant territories elsewhere in the region. There is one record of an Aardwolf moving 35.4 km three weeks after it was marked (Bothma 1971b). If a parent dies, a cub of the same sex usually remains in its natal territory (Richardson 1985, 1987c).

Although generally silent, the Aardwolf utters a number of different sounds (Kingdon 1977, Koehler & Richardson 1990, Estes 1991). Although it relies mainly on olfactory communication, it uses diverse acoustic signals (nine sound types) when interacting with conspecifics at close and medium range (Peters & Sliwa 1997). The acoustic signal repertoire is very different to that of the closely related hyaenas. The Aardwolf lacks long-range vocalizations (Peters & Sliwa 1997). Vocalizations during agonistic interactions are most diverse (Peters & Sliwa 1997). Peters & Sliwa (1997) have described the Aardwolf's various vocalizations as: Purring, Whine, Jaw Click, Lip Smack, Growl, Snarl, Bark, Squeal and Whizzing Sound. The Aardwolf is particularly vociferous when under stress, varying from a soft, clucking sound, to a deep-throated growl. During fights or when suddenly surprised Aardwolves may give a surprisingly loud and explosive roar (Smithers 1971, Richardson 1985, Koehler & Richardson 1990, Estes 1991). The cubs are said to make a clicking sound very much like the warning clicks of termites (Bartlett & Bartlett 1967).

As noted earlier, the Aardwolf has been observed to chase Black-backed Jackals from their breeding dens (Richardson 1985, 1987c, Richardson & Coetzee 1988), possibly using their well-developed canines during aggressive encounters. No aggression was observed between Aardwolves and Bat-eared Foxes that foraged 10 m apart (Bothma & Nel 1980). An Aardwolf and two Cape Foxes *Vulpes chama* were once observed chasing each other, but this was thought to be in the context of play, as immediately afterwards the foxes continued chasing one another (Bothma & Nel 1980). Associative feeding has been observed between Aardwolves and Southern Anteater-chats *Myrmecocichla formicivora* (Anderson 1992) and between Aardwolves and Aardvarks (Taylor & Skinner 2000). On one occasion, an Aardvark and an Aardwolf fed simultaneously from the same excavated termitarium, with no antagonistic interactions between the two individuals (Taylor & Skinner 2000).

Reproduction and Population Structure In the Northern Cape, ♀♀ come into proestrus during the last weeks of Jun

(Koehler & Richardson 1990). Mating usually takes place during the last days of Jun and the first two weeks of Jul (Koehler & Richardson 1990, Sliwa 1996). Copulation may last from 1 to 4 hours, with ejaculation, indicated by pelvic thrusting and tail bobbing, occurring after 1 hour and again at approximately hourly intervals (Koehler & Richardson 1990). There is no bulbus glandis (Wells 1968) and thus no copulatory tie (Koehler & Richardson 1990). Females remain receptive for 1–3 days, but normally are not receptive after a copulation lasting >3 hours (Koehler & Richardson 1990), although A. Sliwa (pers. comm.) saw ♀♀ copulate repeatedly after previous 3-hour copulations. A ♀ will recycle if she is not fertilized (Richardson 1985, 1987c). The gestation period is approximately 90 days (Koehler & Richardson 1990), not 60 days as suggested by Richardson (1985). In South Africa the young are born from Oct to Dec (Shortridge 1934, Stuart 1981, Richardson 1985), although with warmer winters further north in Botswana and Zimbabwe, the breeding season seems to be less restricted, as gravid ♀♀ have been found in May, with others lactating in Apr (Smithers 1971, Skinner & Chimimba 2005).

Most litters have 2–4 young, usually three (Roberts 1951), but litters of five have apparently been recorded in zoos (Koehler & Richardson 1990, Skinner & Chimimba 2005). The birth-weight and size of the cubs are not known, although an emaciated 25-day-old cub weighed 350 g (Spinelli 1970). The cubs are born with their eyes open (Meltzer 1993). Asymptotic growth rate is approached by 1.8 years, but may be reached as early as 3–6 months in some individuals (Van Jaarsveld *et al.* 1995). Maximum growth rate is achieved at three months of age (Van Jaarsveld *et al.* 1995). The daily food intake of captive Aardwolf cubs is about 18–20% of their body mass (Meltzer 1993). Litters are born annually.

The Aardwolf has an above average weight and a below average age of maturity (Van Jaarsveld *et al.* 1995). They reach final weight before sexual maturity, an uncharacteristic feature for mammalian species (Van Jaarsveld *et al.* 1995). Aardwolves tend towards an iteroparous life-style, which serves to reduce juvenile mortality. However, species-specific constraints do not allow it to pursue this strategy by maximizing growth rate. Instead, growth is sustained using an extended lactation period and intensive parental care to enable final body size to be reached as soon as possible (Van Jaarsveld *et al.* 1995).

Richardson (1985, 1987b) found that between 1981 and 1984 the survival rates of cubs up to the age of 12 months in the Northern Cape was 68%. However, most of this recorded mortality was during the height of the drought in 1984 when 55% of the cubs died during winter. Record longevity in captivity is about 20 years (Weigl 2005).

Predators, Parasites and Diseases The Aardwolf is probably prone to predation by most large carnivores. However, in the small-stock farming areas of South Africa, where Lions *Panthera leo* and other large carnivores no longer occur, the Black-backed Jackal is probably the only important predator of Aardwolf cubs (Richardson 1985). Although the Aardwolf shares its habitat with many other termite-eating animals, the variety of their feeding habits and specializations reduces competition between them (Kruuk & Sands 1972).

Little information is known on the parasites carried by Aardwolves (Koehler & Richardson 1990). Although intra-erythrocytic piroplasms have been identified from the blood of free-ranging Aardwolves, the collected material was not adequate to identify the parasites to species

(or even genus) level, although they were suspected to be a new species of *Babesia* (Peirce *et al.* 2001). The vectors for the above haematozoa have not been identified; however, three species of ticks that have been collected from Aardwolves are possibilities: *Haemaphysalis spinulosa* (Peirce *et al.* 2001) and *H. zumpti* and *H. leachi/zumpti* (Horak *et al.* 2000). *Felicola intermedius intermedius* and *F. i. hyaenae* (Mallophaga) have been only found on the Aardwolf and Brown Hyaena *Hyaena brunnea*, respectively (Hopkins 1960, Ledger 1968). Although most species of *Babesia* are host-specific, it is not known whether babesiosis could be transmitted from Aardwolves to other carnivores, such as domestic dogs. Blood from a pet Aardwolf with babesiosis was inoculated into a splenectomized dog and cat, but no parasitaemia developed (B. L. Penzhorn pers. comm., Peirce *et al.* 2001). There is no evidence from free-ranging Aardwolves that the haematozoan causes any morbidity; however, under certain conditions (such as with the pet Aardwolf), clinical piroplasmiasis may occur (Peirce *et al.* 2001). Macchioni (1995) recorded *Ancylostoma braziliense* from an Aardwolf in Somalia, and also recorded a new species, *A. protelesis*.

Rabies and rabies-related viruses have been confirmed in specimens sampled from southern Africa (Swanepoel *et al.* 1993). The Aardwolf is reported to be susceptible to canine distemper and canine parvovirus (Meltzer 1993).

Conservation IUCN Category: Least Concern. CITES: Appendix III (Botswana).

In South Africa the Aardwolf was previously persecuted by some farmers for the mistaken belief that it was a predator of livestock, chickens and Ostrich eggs (Sclater 1900, Roberts 1951, Smithers 1966, Richardson 1984, Anderson 1988). This was based on (a) its aggressive behaviour when cornered; (b) its fierce appearance when its mane is raised and when it growls; (c) its well-developed canines; (d) the collection of livestock bones outside their burrows (generally, the remnants of those collected by Cape Porcupines); and (e) the occasional observations of Aardwolves feeding on blowfly maggots at livestock carcasses (Roberts 1951, Smithers 1971, Anderson 1988). This perception has now changed and most farmers actively conserve Aardwolves. They are, however, also the occasional inadvertent victims of problem animal control operations, especially those using gin traps (M. D. Anderson pers. obs.). Aardwolves are probably killed indiscriminately by packs of dogs used to hunt jackals and foxes (Koehler & Richardson 1990).

Loss of habitat, through urbanization and the transformation of natural habitats to agricultural lands, may be having an important negative impact. Some farmers in South Africa destroy termitaria, using a plough or poisons, and these areas then become unsuitable for Aardwolves (M. D. Anderson pers. obs.). Poisons used for termite control reduces food availability and may have an effect on Aardwolves. Aardwolves may be sensitive to some locust-control poisons, especially organochlorines and organophosphates (M. D. Anderson pers. obs., P. R. K. Richardson pers. comm.). Other mortality factors include predation by carnivores and accidental road casualties, which are not uncommon, as Aardwolves fail to move out of the way of oncoming vehicles at night (Smithers 1971, Richardson 1984, M. D. Anderson pers. obs.). Aardwolves were previously hunted with dogs for sport (Sclater 1900).

Some indigenous tribes in Africa feed on Aardwolves and also use parts of the body for medicinal purposes (Richardson 1984, Koehler

& Richardson 1990, M. D. Anderson pers. obs.), but the extent of this usage as a cause of mortality is unknown (Von Ketelhodt 1966, Richardson 1984, Anderson 1988).

Aardwolves are present in numerous well-managed protected areas across their range, and as their nocturnal and shy and retiring nature make them difficult to observe they are probably more common than usually believed (Koehler & Richardson 1990). Grassland burning and overgrazing by ungulates results in a gross increase in the population of *Trinervitermes* (Coaton 1948, Hartwig 1955), so the population of Aardwolves would thus benefit in areas where such management took place (Kruuk & Sands 1972).

Measurements

Proteles cristatus

TL (♂ ♂): 909 (840–990) mm, n = 10

TL (♀ ♀): 924 (900–970) mm, n = 5

T (♂ ♂): 240 (190–260) mm, n = 10

T (♀ ♀): 245 (223–280) mm, n = 5

HF c.u. (♂ ♂): 156 (149–162) mm, n = 10

HF c.u. (♀ ♀): 151 (149–156) mm, n = 5

E (♂ ♂): 97 (90–101) mm, n = 10

E (♀ ♀): 98 (91–102) mm, n = 5

WT (♂ ♂): 8.9 (7.8–10.0) kg, n = 10

WT (♀ ♀): 8.7 (7.7–10.0) kg, n = 5

Zimbabwe (Smithers & Wilson 1979)

Anderson (1994) gave mean body mass for ♂ ♂ as 8.6 ± 1.2 kg (n = 72) and ♀ ♀ as 9.0 ± 1.2 kg (n = 64). Adult body mass varies seasonally with the availability of termites, but maintains an average of 8–12 kg (Richardson & Bearder 1984, Koehler & Richardson 1990, Van Jaarsveld *et al.* 1995). The body mass of individuals during late summer (9.6 ± 1.2 kg, n = 33; Feb, Mar and Apr) differs significantly from the body masses of individuals during mid-winter (8.4 ± 1.1 kg, n = 55; Jun–Aug) (Anderson 1994). Kingdon (1977) gave body masses of up to 14 kg in East Africa

Key References Anderson 1988, 1994, 2004; Anderson *et al.* 1992, 1997; Bothma & Nel 1980; Cooper & Skinner 1979; Koehler & Richardson 1990; Kruuk & Sands 1972; Nel & Bothma 1983; Richardson 1985, 1986, 1997a, b, c, 1991, 1993; Skinner & Chimimba 2005; Van Jaarsveld *et al.* 1995.

Mark D. Anderson



Aardwolf *Proteles cristatus* showing details of muzzle and whiskers.

Family HERPESTIDAE
MONGOOSES

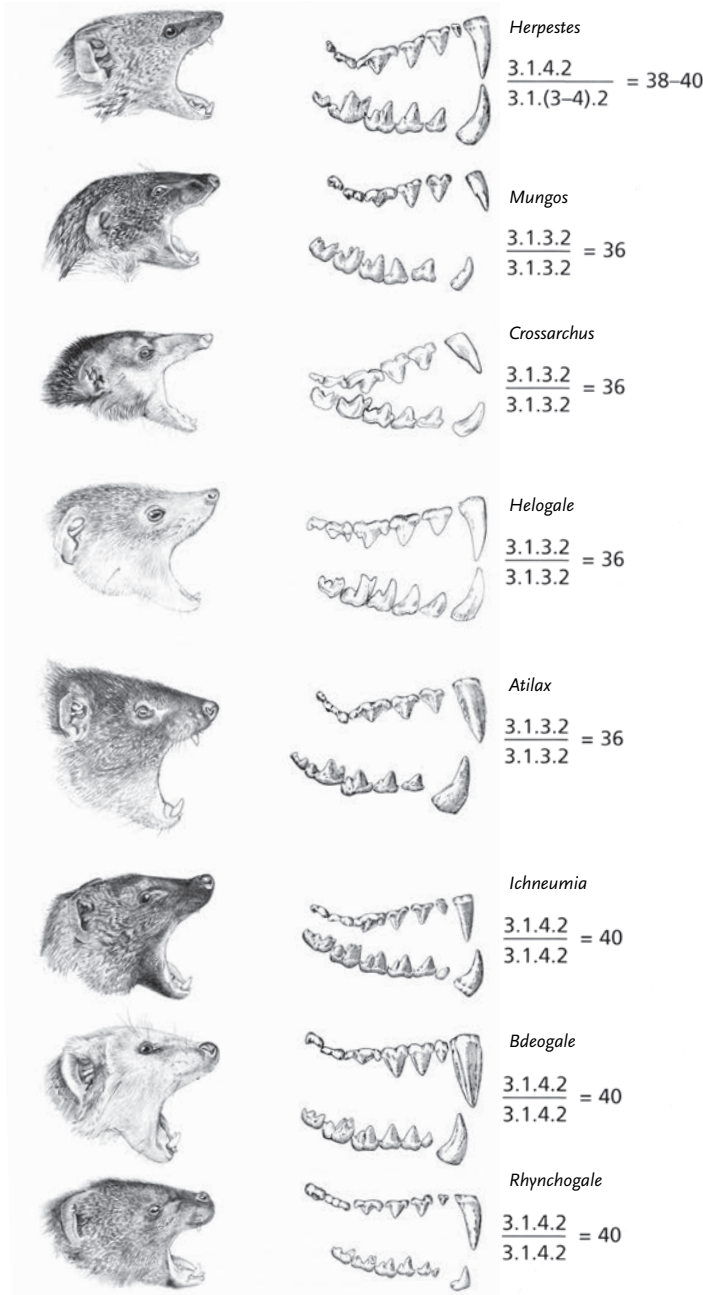
Herpestidae Bonaparte, 1845. Cat. Meth. Mamm. Europe, p. 3.

Table with 3 columns: Subfamily, Species, and Page. Rows include Herpestinae (Xenogale, Atilax, Herpestes, Bdeogale, Rhynchogale, Cynictis, Paracynictis, Ichneumia) and Mungotinae (Suricata, Mungos, Liberiictis, Dologale, Helogale, Crossarchus).

Herpestidae represent a homogeneous family of small to medium-sized carnivores. They are found almost exclusively in Africa, with only the genus Herpestes ranging into southern Europe and throughout Asia. The taxonomy of the family has long been disputed. Traditionally, the family has been held to comprise two subfamilies (Wozencraft 1993): Herpestinae (ca. 14 genera, 32 species) and the exclusively Malagasy Galidiinae (ca. four genera, five species) (see, for example, Wozencraft 1993), with herpestines occasionally being further subdivided into two groups, Herpestinae and Mungotinae, each being accorded subfamilial status together with Galidiinae (e.g. Wozencraft 1989a). However, molecular findings seriously challenge the inclusion of Galidiinae in the family (see below).

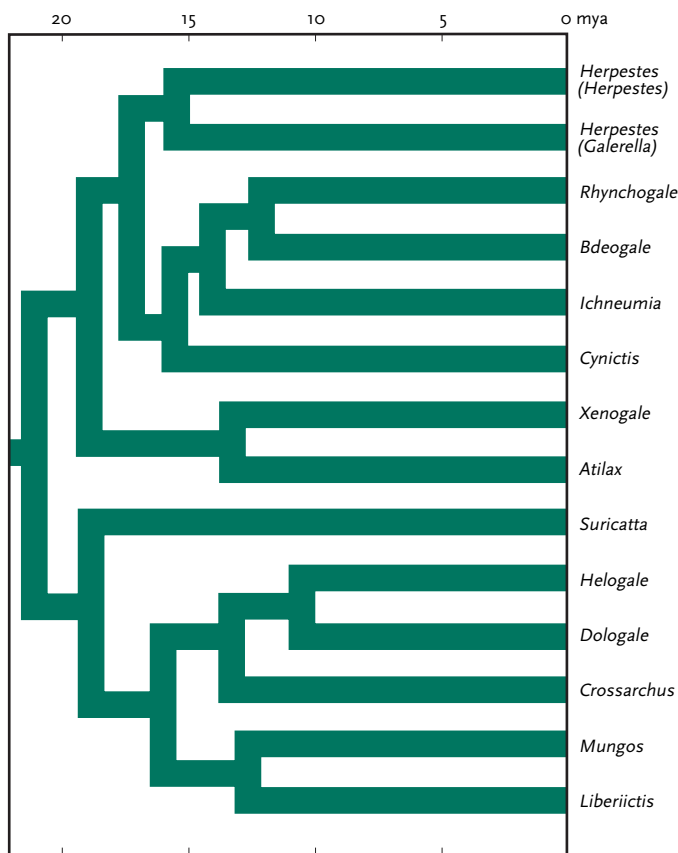
Together with the family Viverridae, Herpestidae strongly resemble the putative ancestor of the Carnivora as represented by Miacoidea. Both families tend to have long, slender body plans with relatively short legs, and skulls that are somewhat elongate in the facial region. Herpestids are distinguished from viverrids by the more complex morphology of their anal scent glands, a relatively shorter tail (only one-half to three-quarters of body length), more uniform coat colouration, non-retractile claws, rounded pinnae that protrude only slightly from the head, slightly less elongate and more robust skull, and largely terrestrial habitat.

Herpestids range in size from the Dwarf Mongoose Helogale parvula (average values: head and body length 250 mm, tail length 190 mm, weight 0.25 kg) to the White-tailed Mongoose Ichneumia albicauda (average values: head and body length 680 mm, tail length 442 mm, weight to 5.52 kg). Extralimital specimens can exceed these values. Sexual dimorphism, when apparent, is minimal, with males being slightly larger than females. Males possess a baculum; females have two or three pairs of abdominal nipples. Pelage colour tends to be uniform and generally grizzled, with banding (e.g. Banded Mongoose Mungos mungo and Meerkat Suricata suricatta) being present in very few species (Ortolani 1999). Differential tail colouration, tail tip patterning and eye contouring and patches are similarly limited (Ortolani 1999). The dental formula for the family is I 3/3, C 1/1,



A key to dental formulae for some major mongoose genera.

PM 3-4/3-4, M 2/2 = 36-40, with the carnassial teeth developed, but the canine teeth relatively small. The general form of the teeth varies according to the diet (e.g. omnivory, insectivory). In particular, the carnassial teeth are better developed in the more carnivorous species. Karyological investigations of the family date back to the pioneering work of Karl Fredga (Fredga 1972). Diploid numbers in the family range from 2n = 36 (the most common) to 2n = 40, 42 or 44, with the changes in number being easily accounted for through centric fission or fusion events. Of more note is that Marsh

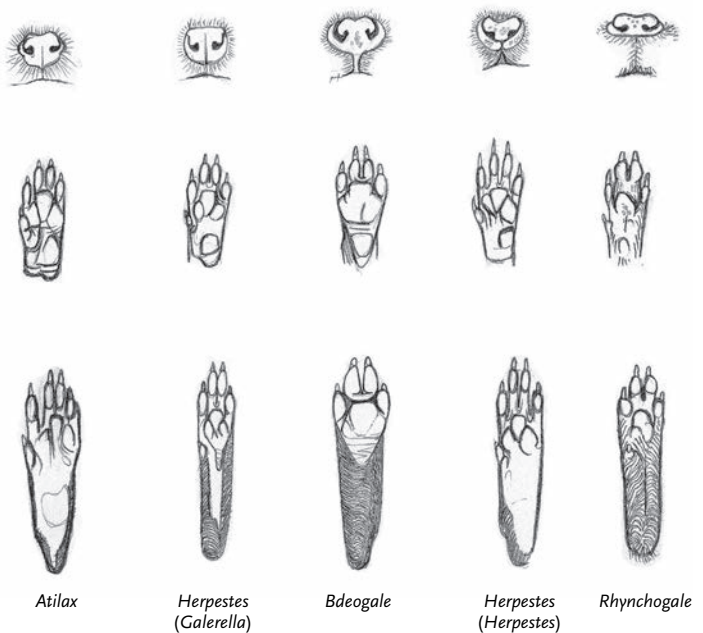


Tentative phylogenetic tree for African Herpestidae (after Patou *et al.* 2009).

Mongoose *Atilax paludinosus* and various species of *Herpestes* possess a 'pseudo-XO-XX' sex-chromosome mechanism, whereby the functional Y-chromosome has been translocated to an autosome (as such, diploid numbers in these species are better represented as $2n = 35/36$, for example.) This feature is unique among carnivores and Fredga (1972) gave two evolutionary scenarios as to its possible origin: 1) a shared derived feature uniting the species in question, or 2) the trait being ancestral for the family, with the typical condition of a separate Y-chromosome being regained by the remaining species. Interestingly, current estimates of the phylogeny of the family (e.g. Perez *et al.* 2006, Patou *et al.* 2009) tend to support the latter, more complex scenario, indicating either multiple independent gains of the trait or its acquisition and subsequent loss. Fredga (1972) concluded that the chromosomal data supported recognition of herpestids, commonly subsumed within Viverridae at the time, as a distinct family.

Herpestids are small opportunistic omnivores, with small vertebrates, insects and other invertebrates constituting the bulk of the diet. They occur in all major habitat types on the African continent, from forests to open woodland, savanna, semi-desert and desert. Unlike many other small carnivores, about half of all species live in pairs or small social groups (notably Dwarf Mongooses, Banded Mongooses and Meerkats). *Herpestes* spp. tend to be uniformly solitary. Social species tend to be diurnal. More species are diurnal than not, in contrast to viverrids, which are almost exclusively nocturnal or crepuscular.

The fossil history of herpestids is cogently summarized by Hunt (1996). Fossil evidence is sparse, with the best records being from Plio-Pleistocene deposits of Africa, mostly the East African Rift



Herpestid noses and fore- and hindfeet.

Valley and South Africa. The first 'modern' herpestid morphotype in Africa (referred to *Galerella sanguinea* = *Herpestes sanguineus*) dates to the late Miocene (7 mya; Peigné *et al.* 2005). The earliest putative herpestid is from the early Miocene deposits at Rusinga and Songhor in Kenya and Uganda (20–18 mya), with many authorities recognizing *Leptoplesictis* from the Rusinga site as being the first definite herpestid. *Leptoplesictis* also comprises the first European herpestid, dating from the middle Miocene. However, the known material for *Leptoplesictis* is admittedly fragmentary (some tooth and mandible fragments) and it cannot be ruled out that the observed similarities with true herpestids comprise primitive (plesiomorphic) features only. In any case, the diversity of the fauna at this time argues for an arrival before the earliest record at ca. 20 mya. It is thought that Herpestidae originated in and emigrated from southern Asia, although fossil herpestid remains are unknown in Asia before the late Miocene. This was followed by an early Miocene migration into Africa from Europe (Hunt 1996). Today, most Herpestidae are located in Africa proper, with *Herpestes* extending significantly back into Asia and Europe.

The phylogenetic relationships of Herpestidae have long been contentious. Most importantly, molecular evidence strongly suggests that Herpestidae as traditionally delineated (see Wozencraft 1993) is paraphyletic, with all the Malagasy carnivores (i.e. the traditional herpestid subfamily Galidiinae and those genera traditionally assigned to Viverridae: *Cryptoprocta*, *Eupleres* and *Fossa*) forming a monophyletic clade within the group (Yoder *et al.* 2003, Flynn *et al.* 2005). This supports earlier suggestions that the enigmatic Malagasy Fossa *Cryptoprocta ferox* is closely related to herpestids, possibly forming a monotypic subfamily (Veron & Catzeflis 1993, Veron 1995). The recent tendency has been to place all the Malagasy carnivores in their own family (Eupleridae; see Wozencraft 2005), which forms the sister group to the redefined Herpestidae (= the traditional Herpestinae). As noted earlier, the family is sometimes (e.g. Wozencraft 1989a) broken down further into two subfamilies: the larger, mainly solitary Herpestinae (*Atilax*,

Xenogale, *Herpestes*, *Bdeogale*, *Cynictis*, *Paracynictis*, *Rhynchogale*, and *Ichneumia*) and Mungotinae for the social species (*Crossarchus*, *Helogale*, *Dologale*, *Liberiictis*, *Mungos* and *Suricata*). Recent molecular work (Veron *et al.* 2004, Perez *et al.* 2006, Patou *et al.* 2009), in particular, appears to support this split. Molecular studies also reveal that *Herpestes* is likely polyphyletic and might need to be restricted taxonomically to only the Egyptian Mongoose *Herpestes ichneumon* (Patou *et al.* 2009).

Within the clade of feliform ('cat-like') carnivores, herpestids have been linked traditionally with viverrids, often as a subfamily of the latter. However, such a placement was typically assumed rather than tested directly, and few primary studies provide strong evidence for such a pairing (see Wozencraft 1989b, although see Radinsky 1975a, Wayne *et al.* 1989a). Instead, both morphological and molecular evidence advocates a sister group relationship with

the Malagasy euplerids and then with hyaenids (Hunt 1987, Veron & Catzeflis 1993, Werdelin 1996a, Flynn & Nedbal 1998, Yoder *et al.* 2003, Flynn *et al.* 2005, Eizirik *et al.* 2010).

Together with Galidiinae, Herpestidae is typified by phenotypic characters such as the absence of a marker chromosome, the structure of the anal glands and presence of a storage pouch located outside the anus proper, and numerous features associated with the auditory bulla and surrounding area (Wozencraft 1989b, Hunt 1996). However, in light of recent phylogenetic evidence, these characters must be regarded as being primitive. Instead, features distinguishing Herpestidae from their close relatives include their more uniform coat colouration, the lack of ear bursae on the lateral margins of the ear flap, and the lack of perineal glands.

Olaf R. P. Bininda-Emonds

Subfamily HERPESTINAE – Solitary Mongooses

Herpestinae Bonaparte, 1845. Cat. Meth. Mamm. Europe, p. 3.

Subfamily Herpestinae includes the larger, mainly solitary, mongooses of the genera *Atilax*, *Xenogale*, *Herpestes*, *Bdeogale*, *Cynictis*, *Paracynictis*, *Rhynchogale* and *Ichneumia*.

GENUS *Xenogale*

Long-nosed Mongoose

Xenogale J. A. Allen, 1919. J. Mammal. 1: 26, 28.

The genus contains only one species, the Long-nosed Mongoose (3–4 kg), which is restricted to equatorial rainforests from Gabon through the Congo basin to DR Congo. On the basis of cranial and external differences, Gregory & Hellman (1939), Simpson (1945) and Orts (1970) retained the genus *Xenogale*, used by Allen (1924), for this species, followed by Rosevear (1974) and Colyn & Van Rompaey (1994a). However, because these differences are no greater than those between the geno-typical Egyptian Mongoose *Herpestes*

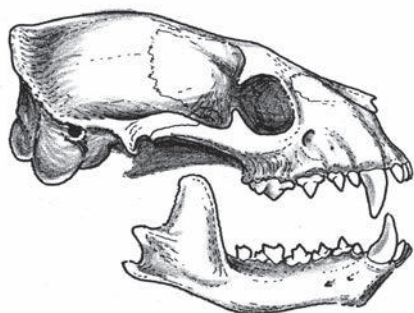
ichneumon and several Asiatic *Herpestes* species, Wozencraft (1993, 2005) included *naso* under *Herpestes* in order to avoid paraphyly. The results of genetic studies (Veron *et al.* 2004, Perez *et al.* 2006, Patou *et al.* 2009) reveal an association between *X. naso* and *Atilax*, suggesting that its placement in *Herpestes* has to be reconsidered. Consequently, the species is here returned to the genus *Xenogale*.

Harry Van Rompaey & Marc Colyn

Xenogale naso LONG-NOSED MONGOOSE (LONG-SNOUTED MONGOOSE)

Fr. Mangouste à long museau; Ger. Langnasenichneumon

Herpestes naso De Winton, 1901. Bull. Liverpool Mus. 3: 35. Cameroon River, West Africa [Cameroon].



Lateral view of skull of Long-nosed Mongoose *Xenogale naso*.

Taxonomy Monotypic. Taxonomic status confused, due in large part to ongoing revision of the genus *Herpestes*, but here retained in genus *Xenogale* following Colyn & Van Rompaey (1994a). The species has occasionally been treated as a subspecies of *Atilax* and *Ichneumia*. Synonyms: *almodovari*, *nigerianus*, *microdon*. Chromosome number: not known.

Description A large, long-muzzled, dark-coloured mongoose. Muzzle long with very short, dark brown hairs up to the eyes; rhinarium black. Iris very dark brown. Ears round, broad, low-set and finely haired. Cheeks, forehead and neck greyish and more grizzled than body. Chin with very short, speckled hairs. Throat with longer,

Long-nosed Mongoose *Xenogale naso*.

forwardly directed hairs. Dorsal pelage long, rough, glossy brownish-black, speckled with yellow to orange. Dorsal hairs 50–60 mm long, irregularly ringed with pale and dark zones. Underfur greyish-brown to orange-brown; the fine hairs are 10–15 mm long with a pale tip. Ventral pelage sparser and paler. Fore- and hindlimbs deep brown to black. Digits webbed. Underparts of fore- and hindfeet fully haired up to the pads. Tail long-haired and tapered, coloured as back. Sexes similar in colour. Males slightly larger than ♀♀. Nipple numbers not recorded.

The rear part of the braincase is less horizontal than in the Egyptian Mongoose and the nasal bones are slightly concave, whereas in the Egyptian Mongoose they form a straight line or are slightly convex. The rostrum of the Long-nosed Mongoose is relatively longer (ratio CBL/ROL in *H. ichneumon*: 3.8 [3.6–4.2], $n = 50$; *X. naso*: 2.9 [2.7–3.2], $n = 42$) and broader (ratio CBL/ROB in *H. ichneumon*: 5.2 [4.8–5.6], $n = 47$; *X. naso*: 4.0 [3.8–4.3], $n = 40$) than that of the Egyptian Mongoose. In addition, the interorbital breadth in the Long-nosed Mongoose is relatively wider (ratio CBL/IOB in *H. ichneumon*: 6.1 [5.4–6.7], $n = 45$; *X. naso*: 5.1 [4.5–5.8], $n = 38$) than in the Egyptian Mongoose (H. Van Rompaey pers. obs.).

The dental formula is $I^{3/3}, C^{1/1}, P^{4/4}, M^{2/2} = 40$. The Long-nosed Mongoose is distinguished from *Herpestes* species by teeth characters: an extra posterior-lingual cusp on P_4 , a longer M_1 talonid, and large M^2 and M_2 (Barry 1983). Orts (1970) and Rosevear (1974) remarked on the significant differences of proportion in comparison with the Egyptian Mongoose.

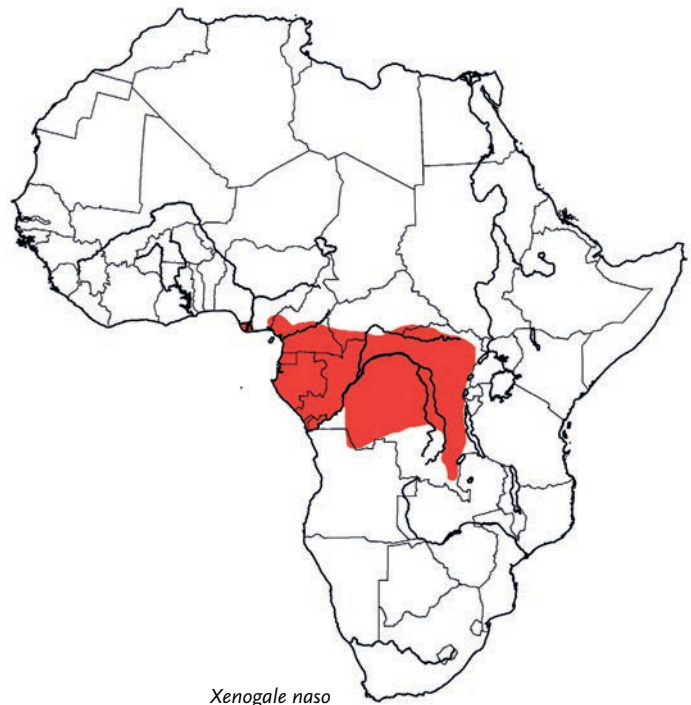
Geographic Variation Examination of a large number of specimens ($n = 103$) shows that the species is geographically more evenly distributed than previously thought and that none of the three described subspecies, *X. n. naso*, *X. n. almodovari* and *X. n. microdon*, can be characterized by any specific cranial character (Colyn & Van Rompaey 1994a).

Similar Species

Atilax paludinosus. Sympatric in western and central Africa. Hindfoot plantar surface naked; feet unwebbed; snout shorter; tail shorter; and dentition more massive.

Crossarchus spp. Smaller with legs much shorter; tail shorter; pelage shaggy; more grizzled and speckled; social, and group-living.

Distribution Endemic to Africa, ranging from the Cross R. in SE Nigeria through the central African forest block eastward to

*Xenogale naso*

Cameroon and Central African Republic and southward to Gabon, Equatorial Guinea, Congo and DR Congo to ca. $10^{\circ} 30' S$. In 1994, what is probably a relic population was discovered in the Niger Delta, Nigeria, approximately 200 km west of the Cross R. (Colyn & Van Rompaey 1994a, Angelici *et al.* 1999b) and a specimen was recovered being sold as bushmeat in Ibeno, just west of the Cross R. (Angelici *et al.* 1999c). Wozencraft (1993, 2005) gives the species as occurring in Kenya, Niger and Tanzania, but there are no museum records or literature to corroborate this statement; Niger may be a lapsus for Nigeria.

Habitat Occurs in forest near swampy places or near streams and stream-beds (Bates 1905, Ray 1995a, 1997). Found in bare parts of the forest floor in recesses of the high deciduous forest in Cameroon (Sanderson 1940). In Dzanga-Sangha Reserve, Central African Republic, they prefer the dense and tangled understorey in forest, avoiding the very open understoreys of the stands of mono-dominant *Gilbertiodendron dewevrei* forest (Ray 1995a, 1997). At least sometimes forages (on dark nights) more than 50 m from the forest edge on open, recently burnt, grassland (T. M. Butynski pers. comm.). Collected from sea level to 600 m (Eisentraut 1963), and observed at 640 m altitude in N DR Congo (T. M. Butynski pers. comm.).

Abundance In SW Central African Republic, the Long-nosed Mongoose is the numerically dominant small carnivore, possibly by virtue of its sole occupancy of the diurnal, terrestrial, predominantly insectivorous niche (Ray 2001). Bates (1905) noted that this species was the small animal most frequently killed by hunters in S Cameroon. In other areas, they are not as abundant relative to other forest carnivores (especially *Crossarchus* spp.), and they are rare in the Niger Delta.

Adaptations Although terrestrial, a semi-captive, subadult female specimen climbed onto chairs and shelves, and tried to climb up

table legs by wrapping limbs around them and 'shimmying up' (Van Rompaey & Powell 1999). When nervous or afraid, the tail fur is erected, showing the pale colour of the underfur.

Although several authors (Rosevear 1974, Depierre & Vivien 1992) state that the Long-nosed Mongoose is nocturnal, data on captive and radio-collared individuals seem to indicate that it is diurnal. In SW Central African Republic, they are strictly diurnal with peak movements at midday (12:00h) but otherwise with little variation, except for smaller peaks at 08:00h and 15:00h (Ray 1995a, 1997). A semi-captive, subadult female specimen was mainly diurnal with sleeping spells during the day (Van Rompaey & Powell 1999). One foraging adult was observed two hours after dark on a moonless night in N DR Congo (T. M. Butynski pers. comm.).

Foraging and Food Omnivorous. In the Niger Delta, Nigeria, stomachs ($n = 2$) contained a centipede, a snail and some remains of fruits and berries (F. M. Angelici pers. comm.). In Dzanga-Sangha, 91% of 346 scats contained arthropods (mostly beetles and orthopterans, followed by termites, ants and millipedes), 52% held mammalian prey (mostly shrews and rodents, occasionally bats [Hutterer & Ray 1997]), 8% anurans, 8% snakes, 4% lizards and skinks, 8% fruit (at least 18 species), 7% birds and 0.3% fish (Ray 1996, 1997, Ray & Sunquist 2001). A high incidence of shrews was notable in the diet (which were almost as frequently consumed as small rodents). Several rodent species were selectively preyed upon in closed and structurally complex micro-habitats (Ray 1998). Mammal prey of more than 5 kg is rarely taken; Blue Duiker *Philantomba monticola* were the most common large prey found in scats (Ray 1996, 1997). They are said to eat crabs (Bates 1905).

As for several other species of mongooses (Banded Mongoose *Mungos mungo*, Gambian Mongoose *M. gambianus*, White-tailed Mongoose *Ichneumia albicauda*, Marsh Mongoose *Atilax paludinosus*), the Long-nosed Mongoose carries hard prey (such as snails) to a favourite spot where it breaks them against a tree or rock by throwing them backwards through the hindlegs with the forefeet. Vernacular names in the Niger Delta ('Norgbene' and 'Lalabene') translate as 'snail breaker' (Van Rompaey & Powell 1999).

Social and Reproductive Behaviour Usually solitary, sometimes in pairs. Home-ranges of 48 ha and 8 ha were estimated for two adult ♂♂, and 41 ha for a subadult ♂ (Ray 1995a, 1997). Mean distance travelled per 30 min during daylight hours by these three ♂♂ was 92 m ($n = 309$). During two 24-hour follows, one individual covered 2324 m (71% of its home-range) and another covered 4605 m (29% of its home-range) (Ray 1997). Night-time resting places are never in the same spot, and there is no evidence for latrine-use (Ray 1997).

A captive specimen was at all times perfectly silent (De Winton 1901). In the wild, loud, repetitive snarling chatter vocalizations are given during aggressive interactions between ♂♂ (J. C. Ray pers. comm.).

Reproduction and Population Structure A juvenile of ca. 2–3 months of age was obtained mid-Mar in Nigeria (Van Rompaey & Powell 1999). Allen (1924) recorded three young in one litter. The

young are full-grown at ca. seven months and permanent dentition is attained at around one year. A captive lived to a little over 11 years (Weigl 2005).

Predators, Parasites and Diseases Remains were found in one Black-legged Mongoose *Bdeogale nigripes* scat (probably scavenged) and one Leopard *Panthera pardus* scat in Dzanga-Sangha (Ray & Sunquist 2001). Larvae of a tongue worm *Porocephalus moniliformis* were found in a specimen from Cameroon (Schäfer 1912). A captive specimen died from myeloid leukaemia (Hamerton 1945).

Conservation IUCN Category: Least Concern. CITES: Not listed.

Although not currently threatened, numbers probably are declining as a result of forest fragmentation and forest loss by logging, mining, slash and burn farming, and from bushmeat hunting. In a study in NE DR Congo, the Long-nosed Mongoose made up 5% of the carnivore bushmeat (Colyn *et al.* 1987).

Measurements

Xenogale naso

HB (♂♂): 544 (430–609) mm, $n = 12$

HB (♀♀): 511 (400–580) mm, $n = 19$

T (♂♂): 380 (320–425) mm, $n = 12$

T (♀♀): 377 (320–425) mm, $n = 19$

HF c.u. (♂♂): 105 (96–112) mm, $n = 10$

HF c.u. (♀♀): 101 (85–113) mm, $n = 18$

E (♂♂): 35 (25–40) mm, $n = 10$

E (♀♀): 35 (30–38) mm, $n = 17$

WT (♂♂): 3.1 (1.9–4.5) kg, $n = 7$

WT (♀♀): 2.7 (2.0–3.4) kg, $n = 10$

GLS (♂♂): 111.0 (100.2–122.4) mm, $n = 36$

GLS (♀♀): 108.2 (100.5–116.0) mm, $n = 17$

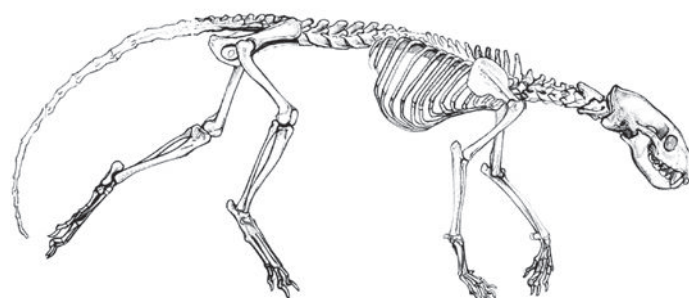
GWS (♂♂): 57.1 (48.5–66.4) mm, $n = 34$

GWS (♀♀): 54.0 (49.3–60.2) mm, $n = 18$

DR Congo (Allen 1924), Central African Republic (Ray 1997), and museum specimens (AMNH, BMNH, FMNH, MCZ, MHNC, MRAC, NMNH, PCM, SBP, ZFMK and ZMB)

Key References Colyn & Van Rompaey 1994; Ray 1997; Rosevear 1974.

Harry Van Rompaey & Marc Colyn



Skeleton of Marsh Mongoose *Atilax paludinosus*.

GENUS *Atilax*

Marsh Mongoose

Atilax F. G. Cuvier, 1826. In: E. Geoffroy Saint-Hilaire and F. G. Cuvier, Hist. Nat. Mammifères, pt. 3, 5 (54), 'Vansire,' 2 pp.

The genus contains only one species, the Marsh Mongoose *Atilax paludinosus*, which is distributed throughout much of sub-Saharan Africa in well-watered habitats with adequate vegetation cover. The unique character among the family Herpestidae of possessing unwebbed toes makes the Marsh Mongoose indisputably generically independent (Allen 1924, Rosevear 1974). Other distinguishing characters include its short and broad muzzle, entirely naked soles of the hindfeet, relatively wide zygomatic breadth and narrow braincase with a well-developed surpaoccipital crest. Unlike other mongooses, *Atilax* has a marked preference for aquatic habitats. Molecular studies have shown *Atilax* to be closer to the Long-nosed Mongoose *Xenogale naso* (Veron *et al.* 2004, Perez *et al.* 2006, Patou *et al.* 2009) than to any species in the genus *Herpestes*.

Fossil remains found both at Kromdraai (Ewer 1956) and Olduvai (Petter 1973) indicate that this genus derives from the Pliocene, but no details are available about whether the number of species within it has increased or declined.



Marsh Mongoose *Atilax paludinosus* in 'basking' posture. (See previous page for an illustration of the skeleton of Marsh Mongoose.)

Carolyn M. Baker & Justina C. Ray

Atilax paludinosus MARSH MONGOOSE

Fr. Mangouste des marais; Ger. Sumpfichneumon (Wasser Manguste)

Atilax paludinosus (G. Cuvier, 1829). Le Règne Animal 1: 158. 'une grand des marais du Cap'
[South Africa, Western Cape Prov., Cape of Good Hope].

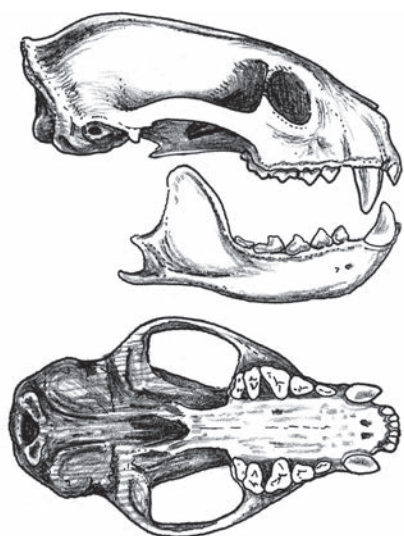
Taxonomy Ten subspecies have been recognized (Coetzee 1977), but their validity is doubtful (Rosevear 1974). Synonyms: *atilax*, *galera*, *macrodon*, *mitis*, *mordax*, *nigerianus*, *paludosus*, *pluto*, *robustus*, *rubellus*, *rubescens*, *spadiceus*, *transvaalensis*, *urinatrix*, *vansire*, *voangshire*. Chromosome number varies with sex, with the diploid number for ♂♂ being $2n = 35$, and that of ♀♀ $2n = 36$; the fundamental number is 66. Fourteen pairs of autosomes are metacentric or submetacentric

and three pairs are acrocentric or subacrocentric; the X chromosome is a medium metacentric (Wurster & Benirschke 1968).

Description A large, dark, shaggy mongoose with an overall grizzled appearance conferred by the white or fawn annulated guard hairs. Muzzle short and pointed, terminating in a pink and black, or wholly black, naked, slightly upturned rhinarium. External nares



Marsh Mongoose *Atilax paludinosus*.



Lateral and palatal views of skull of Marsh Mongoose *Atilax paludinosus*.

dorsolaterally situated. Short, rounded ears partially concealed by hair and carried low on the head. Hair around mouth fawn-coloured. There is no step where the frontals and the nasals meet, thus indicating a smooth transition from the braincase to the nasal region, and the small eyes are positioned somewhat laterally, increasing the lateral field of vision. Overall colour varies from a deep russet to black. Dorsal pelage shorter in the anterior region and longer across the hindquarters; undercoat slightly paler in colour and usually thick and woolly. Ventral surface entirely covered in fur. Limbs and feet short in relation to head-body length and covered with very short, sleek, dark brown or black hair. Fore- and hindfeet bear five, well-defined, flexible digits that lack webbing (present in all other herpestids); each toe bears a stout, curved claw. Plantar surfaces entirely naked and very soft; soles of hindfeet naked to the heel. Tail shorter than head-body length (ca. 65%), with longer hairs (up to 56 mm) at the base, tapering towards the tip. Anal glands open on either side of the anus into an anal pouch. Cheek glands situated at base of genal vibrissae. Two pairs of abdominal nipples in specimens from KwaZulu-Natal (South Africa), although Skinner & Chimimba (2005) report on the presence of three pairs in Zimbabwe.

Skull broad with marked postorbital constriction, and with zygomatic breadth averaging approximately 58% of condylobasal length (Rosevear 1974), and condyloincisive length more than 100 mm in adults (Coetzee 1977). Dental formula usually $I^{3/3}$, $C^{1/1}$, $P^{3/3}$, $M^{2/2} = 36$; marked variation is found with respect to the presence of the first premolar in both upper and lower jaws and, if present in both jaws, the total number of teeth is 40 (Rosevear 1974). Upper and lower outer incisors larger than the others and the canines are robust. Upper canines bear narrow blade-like processes on front and back, these being less evident on lower canines. In older animals, canines usually wear to blunted points, and the fourth upper premolar wears flat (Skinner & Chimimba 2005).

Geographic Variation According to Coetzee (1977), West African specimens ('*pluto*') are virtually black, East African specimens ('*robustus*') more grizzled, and animals from southern Africa ('*paludinosus*') more brownish-black, but colour is not thought to be a reliable indication of subspecies.

Similar Species

Xenogale naso. Sympatric in western and central Africa. Webbed feet, soles of fore- and hindfeet fully haired to pads, longer brush-tail (less tapered) and more slender snout.

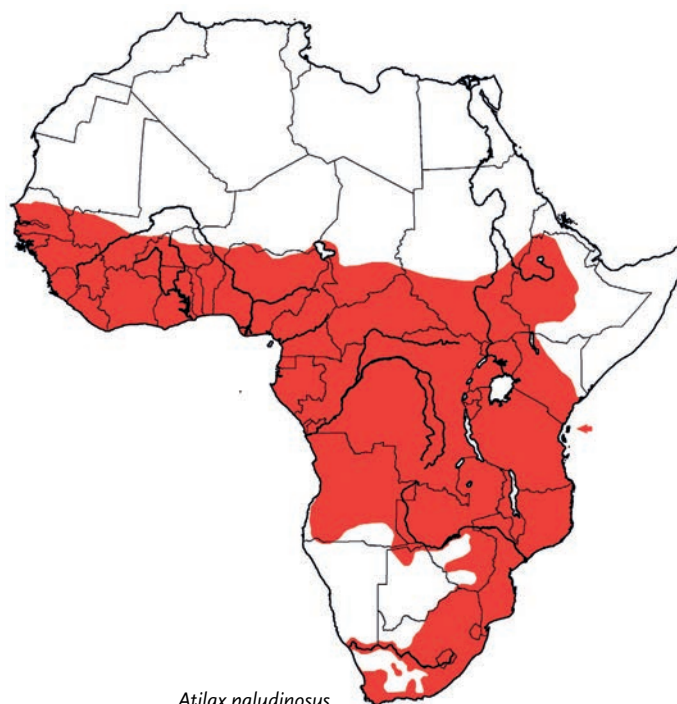
Herpestes ichneumon. Sympatric in most countries south of the Sahara. Paler overall pelage colour; longer tapered tail with black-tufted tip; more slender body-build.

Liberiictis kuhni. Sympatric only in NE Liberia and W Côte d'Ivoire. Medium-sized, with long snout, and distinctive dark neck-stripe; a whitish stripe extends from back of mouth to below the ear; very long curved claws.

Ichneumia albicauda. Woodland and savanna habitats from Senegal to north-east Africa southwards to SE South Africa. Large and distinctive, usually grey, with distal third of tail white (but sometimes black).

Rhynchogale melleri. Woodland habitat from N Tanzania south to NE South Africa. Smaller (less than 3 kg); individuals may have partially white tails, but pelage overall more brown; distinct crest-like parting on either side of neck.

Distribution Endemic to Africa, south of the Sahara, where it is widely distributed from Senegal, Guinea-Bissau, Sierra Leone and Liberia eastward through most West African countries to Cameroon, Equatorial Guinea, Gabon, Congo, Central African Republic, Sudan, DR Congo, Uganda, Rwanda, Burundi, Kenya, Ethiopia and Tanzania. In southern Africa, occurs mostly in the east in Zambia, Zimbabwe, Mozambique, South Africa, Swaziland and E Lesotho. Present in W Angola, but absent from most of Namibia, Botswana and large parts of C South Africa, wherever adequate water and cover are unavailable (Rosevear 1974, Baker 1992a, Skinner & Chimimba 2005). Present on Pemba I., but absent from Zanzibar (Pakenham 1984). Wozencraft (2005) lists this species as occurring in Algeria, presumably an error as there are no confirmed records from this country.



Atilax paludinosus

Habitat Usually restricted to riparian habitats, such as rivers, streams, swamps, marshes and dams, wherever the availability of vegetation cover and proximity of water are guaranteed. They may also be found along estuaries and in coastal areas. On occasion may be found away from water-courses, but for limited periods (Rosevear 1974, Baker 1987, Maddock & Perrin 1993). The degree of restriction to aquatic habitats varies from one locale to the next, and may depend on the relative abundance of other sympatric mongoose species (Ray 2001). Fast-flowing rivers may represent sub-optimal habitat (Louw & Nel 1986), although highest densities in Bwindi Impenetrable N. P., Uganda, were attained in large swamps with the largest river inflows (Andama 2000). Mostly recorded at altitudes from sea level to about 2700 m (e.g. Rowe-Rowe 1992a, Andama 2000), although they have been sighted at 3500 m on Mt Kenya (Young & Evans 1993) and up to 3950 m in Bale Mts N. P., Ethiopia (Yalden *et al.* 1996).

Abundance Marsh Mongooses are generally common in suitable habitat, although in some areas sightings may be uncommon due to their crepuscular habits. Their presence is evidenced near all water sources by means of their very distinctive spoor. One of the most common mongoose species represented in West African museum collections (Rosevear 1974) and the second most photographed species in a camera-trapping study in the Udzungwa Mts, Tanzania (De Luca & Mpunga 2005). In KwaZulu-Natal, density was recorded as 1.8/km² (Maddock 1988).

Adaptations Old individuals have a well-developed sagittal crest joining the supraoccipital crest at the rear of the braincase. It continues forwards to divide into two ridges, ending in the supraoccipital processes. Together with the rough surfaces of the sides of the braincase, these support a powerful set of temporalis muscles that facilitate the crushing action of the jaws. The carnassial teeth show a distinct adaptation to crushing rather than slicing (Petter 1969, Kingdon 1977, Skinner & Chimimba 2005).

Strictly terrestrial, and easily able to leap distances of 60–70 cm (Frese 1981). Forepaws of Marsh Mongooses are highly sensitive and adapted for feeling about under water, rocks and mud for terrestrial

and aquatic prey (Lombard 1958), and for holding and handling food and other items (Gläss & Sedlag 1980). Long, unwebbed digits increase the ability to feel into small crevices for food items as they move along stream edges (Baker 1989). They have been observed to waddle out of the water bipedally, while carrying a large snail in their forepaws (J. Kingdon pers. comm.). Dense underfur, particularly in the shoulder and flank regions, assists in keeping the skin surface dry should the mongooses venture into deeper water during foraging. Marsh Mongooses are excellent swimmers, and swim using lateral movements; they can remain submerged in the water after diving for up to 15 sec (Taylor 1970a). Advanced motor control and tactile sensitivity of the digits is supported by studies on neuroanatomy (Radinsky 1975a). Horizontal pupils increase the lateral range of vision, thus enhancing prey detection.

Glandular secretions from well-developed anal glands serve to inform conspecifics of the identity and sexual status of neighbouring mongooses, thereby enhancing communication in this solitary species. Scent deposition is via an anal drag or in cases of extreme agitation may be expelled more forcefully (Kingdon 1977, Baker 1988).

In KwaZulu-Natal, radio-collared mongooses became active ca. 30 min after sunset and remained active until 01:00–02:00h (Maddock & Perrin 1993). The latter authors found no evidence of diurnal activity, although Rowe-Rowe (1978a) did record them being active in the early morning and late afternoon. Similarly, activity peaks in one ♂ in Dzanga-Sangha, Central African Republic, were recorded in the early morning (04:00–06:00h) and in the evening (17:00–20:00h) (Ray 1997). In general, peaks of activity are linked to several factors such as food availability, reproductive condition, climate and season.

Different day-beds or burrows are used for resting each day; in Central African Republic they are located in dry areas on relatively high ground surrounded by water or deep mud, with dense cover provided by high grass or vine entanglements (n = 24; Ray 1997). Studies in central and southern Africa suggest that each home-range has a number of sites that are easily accessible from anywhere in the range (Maddock 1988, Ray 1997).

Foraging and Food Aquatic prey forms the bulk of the diet, and crustaceans (mainly crabs) usually dominate, which is unusual among herpestids. However, Marsh Mongooses are able to vary their diet quite considerably by including amphibians, fish, molluscs as well as terrestrial arthropods and rodents; birds, birds' eggs, reptiles and fruits are generally less important food items (Rowe-Rowe 1977a, Smithers & Wilson 1979; Du Toit 1980, Whitfield & Blaber 1980, Louw & Nel 1986, Maddock 1988, Baker 1989, Purves *et al.* 1994, Somers & Purves 1996, Avenant & Nel 1997, Ray 1997, Andama 2000, Angelici 2000, Stuart & Stuart 2003a, b).

The diet of this species has been very well studied in South Africa, where two major studies using scat analysis from the highlands (n = 210 scats; Rowe-Rowe 1977a) and lowlands (n = 349; Maddock 1988) of KwaZulu-Natal revealed the following relative percentage occurrence of prey: highlands – 43% crustaceans, 14% mammals, 14% amphibians, 14% birds, 2% fish and 2% insect; lowlands – 21% crustaceans, 15% mammals, 17% amphibians, 2% birds, 0% fish and 19% insects. Elsewhere in southern Africa, the percentage occurrence of items in 29 stomachs from Zimbabwe was 29% amphibians, 24% mammals, 24% crustaceans, 19% insects and 5% fish (Smithers & Wilson 1979).



Marsh Mongoose *Atilax paludinosus*.

Diets of inland-dwelling Marsh Mongooses tend to be more catholic in nature than those in coastal habitats (Louw & Nel 1986). In the Olifants R., most crabs (*Potamonautes perlatus*) consumed had a mean carapace width of 29 mm (range 9–48 mm), with an average weight of 9 g ($n = 85$; Purves *et al.* 1994), while in the Bushman's R., mean crab size was 24 mm (range 10–41 mm; $n = 65$; Somers & Purves 1996). Mean weight of fish (species not identified) consumed by Marsh Mongooses in Dzanga-Sangha was 28 g (3.5–72 g; $n = 39$; Ray 1996), and mean length of fish (*Tilapia sparrmanii*; $n = 8$) consumed in the Bushman's R. was 25 mm (21–39 mm; Somers & Purves 1996). Seasonal variations in dietary components may be associated with variations in local abundance of preferred food items (Avenant & Nel 1997). Some evidence of their scavenging on Water Chevrotain *Hyemoschus aquaticus* (Ray 1997) and domestic stock (e.g. Stuart & Stuart 1998b) has been recorded, and the latter authors recorded the presence of two small carnivores, Yellow Mongooses *Cynictis penicillata* and Cape Grey Mongooses *Herpestes pulverulentus*, in scats from S Namaqualand in the Northern Cape, South Africa; the same authors also recorded the presence of Cape Grey Mongooses in one scat from the central Great Karoo (Stuart & Stuart 2003a).

Marsh Mongooses forage principally in the littoral zones of water bodies, although they are known to dive for food on occasion (Baker 1989). They spend a great deal of their time walking along the water shore or wading in water searching for food (Rowe-Rowe 1978a). In Central African Republic, the average distance covered while travelling over 30-min periods was 320 m (Ray 1997). Both sound and touch have been reported as being the most important senses for locating food (Baker 1989), with vision facilitating prey capture. Prey are forked out with the forefeet from under stones, or from within holes and crevices, and crabs, rodents and other similar-sized prey are seized in the mouth and flicked sideways, presumably in order to stun the prey before killing (Rowe-Rowe 1978a, Rowe-Rowe & Somers 1998).

Prey items taken in water typically are carried out of the water before being eaten. Smaller crabs are eaten whole, while larger crabs are pinned to the ground and the nippers removed with the teeth (Baker 1989). The crab is then turned onto its back and the meat from inside the carapace is consumed first. The carapace usually is discarded (although see Angelici 2000), and the presence of these on river-banks often is an indication of the presence of this species (African Clawless Otters *Aonyx capensis* normally crunch up the carapace; Rowe-Rowe 1977a). Toads *Bufo* sp. are killed by a head bite and then palpated on the ground (perhaps to remove noxious substances; Baker 1989). Rodents are killed by means of a bite to the anterodorsal part of the cranium, parts of which are sometimes found in scats. Insects are captured in mid-flight by grasping them in the mouth or with the forefeet (Rowe-Rowe 1978a, Baker 1989, Rowe-Rowe & Somers 1998). Although small eggs are crushed in the jaws, large eggs are broken by rearing up on the hindlegs and smashing them on a hard substrate (Kingdon 1977, Gläss & Sedlag 1980); the same method may be used to break open mussels and snails.

Social and Reproductive Behaviour Marsh Mongooses are predominantly solitary, but may be seen in small family groups of two or three during the breeding season. Groups consist of mother and offspring, and it is seldom that an adult ♂ and ♀ remain together for any length of time beyond that required for mating. The offspring remain with their mother beyond weaning age until they

are able to fend for themselves at about 20 weeks of age. With the onset of sexual behaviour at about six months, the levels of agonistic behaviour between mother and offspring increase, thus promoting dispersion (Baker 1987).

Marsh Mongooses communicate with both scent and sound. Five different vocalizations are made, of which three are agonistic, accentuating the solitary nature of this species. Compared with some of the more sociable mongooses, the vocal repertoire is limited (Baker 1988). While communication at close quarters is effected by vocalizations and behavioural displays, distance communication is achieved through the deposition of scent, by both cheek and anal glands. Cheek marking is pronounced when mongooses are excited or threatened. Anal marking occurs more frequently and conveys information regarding the identity and sex of the owner, and is used particularly by the ♀ during the breeding season. Anal secretions are also deposited during defecation. Urination takes place in the squatting position in the ♀ ♀, while ♂ ♂ lift a leg. Marsh Mongooses use middens for scat deposition, which serve not only as a reservoir for scent communication, but also as a visual display for other mongooses. These communal defecation sites are particularly significant in this solitary species as conspecifics are able to identify the sex and status of other animals in the vicinity, thus facilitating long distance communication (Baker 1998). In central African forest habitats, middens are usually located on rocks or sandy beaches near streams and in marshy clearings (Ray & Sunquist 2001); in inland areas of southern Africa, they are usually found in areas covered by vegetation, often <10 m from the water edge, or above the high water mark in coastal areas, often on rocks (Louw & Nel 1986, MacDonald & Nel 1986, Purves *et al.* 1994).

On account of their dense pelage and undercoat and also their mode of life that necessitates spending some time in water, Marsh Mongooses groom themselves (and occasionally partners) by licking their fur and combing the fur with the incisors. This behaviour is neither systematic nor prolonged. Rowe-Rowe (1978a) suggested that this behaviour accounted for the presence of its own hair in 67% of the scats he examined.

Home-range sizes vary widely but are generally linear in shape, owing to fidelity to water-courses. One radio-collared adult ♂ in Dzanga-Sangha travelled up and down a stream ca. 5 km in length; its home-range was estimated at 54 ha (Ray 1997). In KwaZulu-Natal, the home-range of one ♂ was smaller (131 ha) than that of one ♀ (204 ha) (Maddock 1988). Ranges may overlap (Maddock 1988), although Kingdon (1977) has suggested that Marsh Mongooses are territorial. It is likely that the ♀ ♀ hold territories with the ♂ being more mobile.



Marsh Mongoose *Atilax paludinosus* myology.

Females tend to avoid ♂♂ until they are ready to be mated. Oestrus lasts for nine days. Mating sequences may last up to 29 min if successful, with copulation lasting for up to 6 min (Baker 1987).

Reproduction and Population Structure In southern Africa, breeding is seasonal occurring in the summer, with mating from as early as Aug through to Feb (Rowe-Rowe 1978a, Stuart 1981). There is no evidence of a breeding season in West Africa (Rosevear 1974). Mean gestation is 10.5 weeks (Baker 1987) and births in captive animals occurred mainly at night. Mean litter-size in the wild in South Africa is 2.5 (range 2–3, $n = 6$; Baker & Meester 1986), and 1.1 in captive individuals (range 1–2; $n = 15$; National Zoological Park, Washington, DC; Frese 1981). Mean birth-weight is 108.5 g (range 78–123, $n = 7$; Baker & Meester 1986). Newborn mongooses are fully furred with eyes and the auditory meatus closed; incisors one and two are present at birth and may function to ensure adequate nipple attachment during suckling (Baker & Meester 1986). Eyes open at around Day 11 (range 9–14, $n = 7$; Baker & Meester 1986) and hearing develops around Day 21 (Baker 1987). The earliest weaning commences is one month, but young continue sucking until eight weeks (Baker 1992a). Deciduous dentition is complete at about Day 44, after which replacement by the permanent set occurs; the permanent canines are only complete by about Day 243 (Baker & Meester 1986). The earliest that young mongooses can successfully capture and kill rodent prey varies around Day 121 (range 102–135; $n = 5$; Baker 1992b). Males have abdominal testis at birth, with descent ranging from Day 204 to Day 307 ($n = 2$; Baker & Meester 1986). Weight of young doubles by Week 4 and is more than eight times by Week 7 (Frese 1981); adult mass is attained at Week 27 (Baker & Meester 1986). A captive animal lived for more than 19 years (Nowak 1999).

Predators, Parasites and Diseases While young Marsh Mongooses are vulnerable to predation by a range of other small carnivores, there are few reports of predation on either juvenile or adult animals; they were recorded in the scats of Leopards *Panthera pardus* in several study sites in Gabon (Henschel *et al.* 2011). A range of parasites has been found on mongooses, including fleas (*Ctenocephalides felis* and *Echidnophaga gallinacea*), ticks (*Rhipicephalus simus*, *R. sulculatus*, *Haemaphysalis subterra*) and lice (*Trichodectes* sp.) (Loveridge 1923, De Meillon *et al.* 1961, Hoogstraal *et al.* 1992, Ntiamoa-Baidu *et al.* 2005). Alimentary parasites include nematodes and ascarids (Loveridge 1923, Stuart 1981). Some bone diseases in the hindfoot have been recorded in mongooses in East Africa (Taylor 1971b).

Conservation IUCN Category: Least Concern. CITES: Not listed.

Dependence on riverine vegetation for shelter that is prone to destruction (Rosevear 1974, Andama 2000, Ray 2001) may have long-term implications. Drainage of swamplands to expand arable land has also been identified as a threat to Marsh Mongooses in eastern Africa (Andama 2000). The Marsh Mongoose is the most common carnivore appearing in bushmeat markets in SE Nigeria (Angelici *et al.* 1999c) and the species made up 5.6% of the carnivore bushmeat in NE DR Congo in one study, the fifth most common carnivore species to appear in markets (Colyn *et al.* 1987). It was also commonly recorded in bushmeat surveys in the Classified Forest of Diécké, Guinea (Colyn *et al.* 2004). They are otherwise present in numerous protected areas across their range.



Marsh Mongoose *Atilax paludinosus*.

Measurements

Atilax paludinosus

HB (♂♂): 554 (471–640) mm, $n = 20$
 HB (♀♀): 515 (465–570) mm, $n = 10$
 T (♂♂): 355 (319–405) mm, $n = 21$
 T (♀♀): 338 (310–385) mm, $n = 10$
 HF c.u. (♂♂): 105 (95–115) mm, $n = 22$
 HF c.u. (♀♀): 102 (95–107) mm, $n = 10$
 E (♂♂): 33 (25–39) mm, $n = 21$
 E (♀♀): 30 (25–37) mm, $n = 10$
 WT (♂♂): 3.0 (2.0–3.8) kg, $n = 18$
 WT (♀♀): 2.6 (2.0–3.2) kg, $n = 19$
 GLS (♂♂): 109 (103–117) mm, $n = 18$
 GLS (♀♀): 106 (102–108) mm, $n = 8$
 Northern Cape, Western Cape and Eastern Cape provinces, South Africa (Stuart 1981)

TL (♂♂): 878 (818–970) mm, $n = 12$
 TL (♀♀): 848 (792–895) mm, $n = 12$
 T (♂♂): 357 (310–410) mm, $n = 12$
 T (♀♀): 348 (330–400) mm, $n = 12$
 WT (♂♂): 3.4 (2.9–4.0) kg, $n = 12$
 WT (♀♀): 3.4 (2.4–4.1) kg, $n = 12$
 Zimbabwe (Smithers & Wilson 1979)

HB (sexes combined): 501 (442–553) mm, $n = 20$
 T (sexes combined): 322 (250–355) mm, $n = 20$
 HF c.u. (sexes combined): 96 (84–102) mm, $n = 20$
 E (sexes combined): 33 (28–40) mm, $n = 20$
 West Africa (Rosevear 1974)

Both Rowe-Rowe (1978a) and Smithers (1971) mention individual ♂♂ with masses exceeding 5 kg

Key References Baker 1987, 1989, 1992a, b; Baker & Meester 1986; Kingdon 1977; Ray 1997; Rosevear 1974; Skinner & Chimimba 2005.

Carolyn M. Baker & Justina C. Ray

GENUS *Herpestes*

Common Mongooses

Herpestes Illiger, 1811. Prodr. Syst. Mamm. Avium., p. 135.

The genus includes 14 species worldwide, five of which occur in Africa: Egyptian Mongoose *Herpestes ichneumon*, Cape Grey Mongoose *H. pulverulentus*, Slender Mongoose *H. sanguineus*, Kaokoveld Slender Mongoose *H. flavescens* and Somali Slender Mongoose *H. ochraceus*. The Long-nosed Mongoose *Xenogale naso*, sometimes included in *Herpestes* (Wozencraft 2005), is here included in the monotypic *Xenogale*. The Small Asian Mongoose *Herpestes auropunctatus*, from South and South-East Asia, has been reported as introduced on Mafia I., off the coast of Tanzania (Moreau & Pakenham 1941, Nellis 1989, Kock & Stanley 2009).

The Egyptian Mongoose (2–4 kg) is found widely through many habitats in much of sub-Saharan Africa. It has been associated with human habitation for millennia and mummified specimens have been found in Egyptian tombs. In much of non-coastal South Africa and S Namibia, it is replaced by the Cape Grey Mongoose (0.6 kg). Both species are relatively uniformly grizzled grey with a tapered tail, with that of the Egyptian Mongoose having a black tuft at the tip. The commonest of the *Herpestes* mongooses is the Slender Mongoose (0.6 kg), which usually has a grizzled pelage, although the colour appears to be associated with the habitats in which it occurs, with the darker colours occurring in the moister habitats. The Somali Slender Mongoose (0.6 kg) is found only in Somalia, and is distinguished by its relatively short broad skull and markedly inflated auditory bullae. The Kaokoveld Slender Mongoose (0.6 kg) is restricted to a semi-arid region of Namibia and S Angola near the coast, and is distinguished by its blackish to reddish pelage.

Mongooses in the genus *Herpestes* are distinguished from other African mongooses by the presence of five digits on fore- and hindfeet, and species in the subgenus *Herpestes* (*H. ichneumon*) have a generalized dentition of $I^{3/3}$, $C^{1/1}$, $P^{4/4}$, $M^{2/2} = 40$, while those in the subgenus *Galerella* (*H. pulverulentus*, *H. sanguineus*, *H. ochraceus* and *H. flavescens*) have $I^{3/3}$, $C^{1/1}$, $P^{4/3}$, $M^{2/2} = 38$. In all species, P^4 has the posterior lobe (metacone) elongated such that the tooth is a distinctive carnassial. The species have maintained a generalist body plan and display no obvious specializations for diet or locomotion (Petter 1969); all are omnivorous, eating more insects during wet times of the year and more vertebrates during dry seasons. This is in contrast to some of the other mongooses in Africa, many of which have evolved into specialist ecological niches such as the earthworm-eating Liberian Mongoose *Liberiictis kuhni* with a very elongated rostrum and short pointed teeth, and the Marsh Mongoose *Atilax paludinosus*, which specializes on aquatic vertebrates and invertebrates.

The basis for assigning species into subgenera is based on the absence of the first lower premolar in the adult of most species and the greater inflation of the auditory bulla (Wozencraft 1993). However, the presence of the lower first premolar is a variable feature and the Small Asiatic Mongoose *H. javanicus* has comparable auditory



Egyptian Mongoose *Herpestes ichneumon* myology.

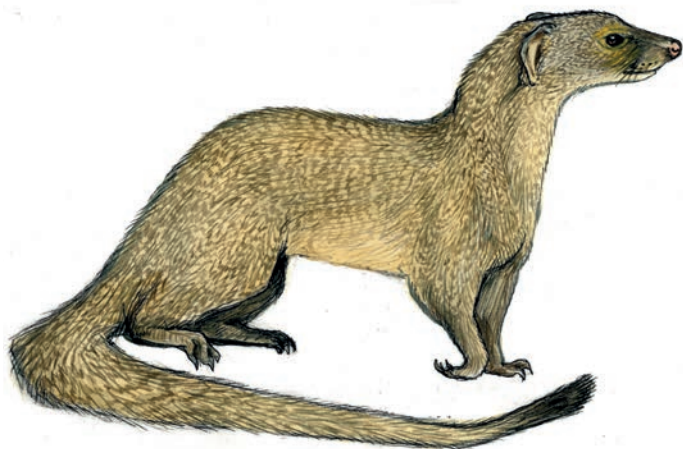
bullae to the small African *Herpestes* (Taylor & Matheson 1999). There are allozyme differences between the Slender Mongoose, Cape Grey Mongoose and Egyptian Mongoose in southern Africa (Taylor *et al.* 1991), though the allozyme variation between all the other *Herpestes* has not been determined. In all *Herpestes*, diploid chromosome number ranges from $2n = 35$ in ♂♂ and $2n = 36$ in ♀♀ (Indian Grey Mongoose *H. edwardsi*) to $2n = 43$ for ♂♂ and $2n = 44$ for ♀♀ (Egyptian Mongoose). The Y chromosome has been translocated to an autosome, thus the chromosomal sexual mechanism (as in other *Herpestes*) affects two pairs of chromosomes (Fredga 1970, 1972, 1977).

The taxonomic position of *Galerella* relative to *Herpestes* has been the matter of some debate, and has been elaborated upon and discussed in detail elsewhere (e.g. Meester *et al.* 1986, Wozencraft 1993, 2005, Bronner *et al.* 2003, Skinner & Chimimba 2005). Chromosomal studies, including forms of *Herpestes* from Africa and Asia, indicate that recognition of *Galerella* would render *Herpestes* paraphyletic (Fredga 1972), while a craniometric study (again, including both Asiatic and African *Herpestes*; Taylor & Mattheson 1999) supported inclusion of *Galerella* in *Herpestes*. McKenna & Bell (1997) included *Galerella* in *Herpestes*, while Wozencraft (2005) continued to recognize *Galerella*. Recent molecular studies (Veron *et al.* 2004, Perez *et al.* 2006, Patou *et al.* 2009) have shown that *Herpestes* is polyphyletic, with the Long-snouted Mongoose grouping with *Atilax*, the Egyptian Mongoose *H. ichneumon* grouping with the species traditionally assigned to *Galerella*, and the Asian *Herpestes* forming a monophyletic clade. Clearly, further investigations are needed, but it certainly seems possible that *Herpestes* could be restricted to *H. ichneumon*, and *Galerella* may need to be raised to genus level and the Asian *Herpestes* assigned to other genera (Patou *et al.* 2009).

Mark E. Taylor

Herpestes flavescens KAOKOVELD SLENDER MONGOOSE (ANGOLAN SLENDER MONGOOSE)

Fr. Kaokoveld Mangouste Rouge; Ger. Kaokoveld Rotichneumon

Herpestes flavescens Bocage, 1889. J. Sci. Math. Phys. Nat. Lisboa, ser. 12, 1: 179. 'Benguella' [Angola].Kaokoveld Slender Mongoose *Herpestes flavescens*.

Taxonomy Included in subgenus *Galerella*. The Kaokoveld Slender Mongoose has a confusing taxonomic history. The species was first described as a subspecies of the Slender Mongoose *Herpestes gracilis* var. *flavescens* (Bocage 1889) from Benguela, SW Angola, although the type specimen was subsequently lost in a fire in the Museu Bocage (Crawford-Cabral 1996). Later, Thomas (1928a) identified specimens from the Kaokoveld in Namibia as a distinct species (*Myonax nigratus*), the holotype of which is in the British Museum of Natural History. Shortridge (1934) also considered *nigratus* a distinct species, including the form *shortridgei* (described by Austin Roberts in 1932 from NW Ovamboland), which he considered an erythristic form. Subsequently, *nigratus* was assigned to subspecific rank in the Cape Grey Mongoose *H. pulverulentus* by Ellerman *et al.* (1953), who suggested that *nigratus* represented a melanistic form of this species, with *shortridgei* an erythristic form of it; this classification was in turn followed by others (e.g. Coetzee 1977, Meester *et al.* 1986, Cavallini 1992; but see Lynch 1981 who referred *nigratus* to *sanguineus*). Meanwhile, Coetzee (1977) assigned the form *flavescens* to *sanguineus*, a form not even mentioned by Meester *et al.* (1986) or Watson & Dippenaar (1987).

Three separate studies using different cranial data sets have confirmed the distinctiveness of *nigratus* as a separate species using multivariate analyses (Watson & Dippenaar 1987, Watson 1990, Taylor & Goldman 1993, Crawford-Cabral 1996). Crawford-Cabral (1989b) noted that *nigratus* should be considered conspecific with the earlier *flavescens* (Bocage 1889) from Angola. However, Taylor & Goldman (1993) considered that available evidence suggested that most Angolan specimens belong to *H. sanguineus*, and proposed that in the absence of cranial material from Angola demonstrating that *H. flavescens* is synonymous with *H. nigratus*, a change in name was not warranted. Wozencraft (1993), without the benefit of the study of Taylor & Goldman (1993) published the same year, accepted the conclusions of Crawford-Cabral (1989b). A subsequent analysis

(Crawford-Cabral 1996) of cranial measurements of specimens from SW Angola found that these agree with *H. nigratus*, reinforcing the proposed synonymy (and this classification was adopted by Bronner *et al.* 2003 and Wozencraft 2005). That the issue is far from resolved is highlighted by Rathbun & Cowley (2008), who consider that animals in N Namibia (referred to these authors as *nigratus*) are a different species than those in SW Angola. The latter authors comment on the occurrence of black (*nigrata*) and chestnut-coloured (*flavescens*) forms in the Kunene R. area that are apparently spatially segregated with no intermediate colour forms, the apparent absence of *flavescens* forms in Namibia, and remark on possible ecological differences. Clearly, a careful reassessment of the taxonomic status of these mongooses is in order, but in the interim we provisionally follow the classification of Wozencraft (2005).

Besides *nigratus* and *shortridgei*, the species also includes the form *annulata* Lundholm 1955a (Watson & Dippenaar 1987, Crawford-Cabral 1989b, Watson 1990, Taylor & Goldman 1993), also previously regarded as an uncertain subspecies of *H. pulverulentus* (Meester *et al.* 1986). However, the status of *annulata* remains uncertain because the holotype and only known specimen is an immature specimen. Synonyms: *annulata*, *nigratus*, *shortridgei*. Chromosome number: not known.

Description A small diurnal mongoose of variable colouration, usually either black or dark brown (*nigrata*) or else a reddish-brown. As name suggests, species is slender in body shape, with long tapered tail about 85% of head and body length. Hair in dark or black individuals not grizzled, although grizzled in erythristic form *shortridgei*. The latter has upper parts chestnut-red to yellowish-orange and yellowish-orange tail has black tip with underparts buffy to yellowish-buff (Crawford-Cabral 1996). Ears small and rounded. Skull intermediate in size between that of Slender Mongoose and Cape Grey Mongoose. Nipple numbers not recorded; probably two or three pairs.

Geographic Variation See Taxonomy.

Similar Species

Herpestus sanguineus. Sympatric in N Namibia. Smaller; dorsal colour greyish-yellow to bright reddish-brown.

H. pulverulentus. Allopatric, occurring only in S Namibia. Larger.

Helogale parvula. Largely allopatric, although both are present in the Erongo Mts of Namibia where this species is also black and is often confused with the Kaokoveld Slender Mongoose (G. Rathbun & M. Griffin pers. comm.). Smaller, with rounder head, relatively shorter tail and less shaggy pelage; social species, diurnal, largely insectivorous and sleeping in old termite mounds (whereas Kaokoveld Slender Mongoose is solitary, diurnal and consumes more vertebrate prey).

Distribution Endemic to Africa. Confined to SW Angola and NW and NC Namibia (Feller 1990, Crawford-Cabral 1996, Skinner & Chimimba 2005). The type locality is Benguela (12° 35' S) in the



Herpestes flavescens

north (Crawford-Cabral 1996) and it ranges from there to the Erongo Mts (Coetzee 1969) and Spitzkoppe (M. Griffin pers. comm.) in NC Namibia, with an eastward extension into the Otavi Highlands in Namibia (M. Griffin pers. comm.). It does not extend inland much beyond the Chela Escarpment in Angola (Crawford-Cabral 1996).

Habitat Inhabits arid hills and kopjes away from water (Shortridge 1934) and appears to be confined between the coastal strip and the interior plateau. In Namibia the species has a restricted distribution to the interior plateau not extending into the pro-Namib Desert. The black form of this mongoose (*nigratus*) seems to be restricted to habitats dominated by large granitic boulders (petrophily), and the drainages and woodlands connecting these, which results in a highly fragmented distribution (Shortridge 1934, Rathbun & Cowley 2008). Animals radio-tracked in the Erongo Mts virtually never ventured into surrounding bushveld, and if they did it was to visit isolated boulders near the main rock area (G. Rathbun pers. comm.).

Sympatric with the Slender Mongoose and Dwarf Mongoose in parts of its range, as in the Erongo Mts. It appears to occur in the more arid habitats, when it is sympatric with the Slender Mongoose, which prefers the more vegetated parts.

Abundance Little information is available, but it is assumed that the species is locally common in arid regions of south-western Africa.

Adaptations The erythristic colour of some forms is assumed to be a camouflage feature in the reddish rocky area of some of its habitats. The black form (*nigrata*) is strictly diurnal and unquestionably camouflaged to hunting in the deep shadows of the rocky habitat that it occupies (Rathbun 2004, Rathbun & Cowley 2008). Kaokoveld Slender Mongooses have been recorded using crevices and small caves among boulders as nocturnal den sites, with no evidence of nesting material in those examined; animals denned alone, using multiple sites haphazardly from night to night (Rathbun & Cowley 2008).

Foraging and Food In Namibia, the species has been recorded feeding on small diurnal rodents (especially Noki *Petromus typicus*; see Rathbun & Rathbun 2006), birds, lizards and insects, and may also feed on freshwater crabs and other aquatic animals (Shortridge 1934, Rathbun & Cowley 2008). In an analysis of 126 scats, insects made up the greatest proportion of scat content (Warren *et al.* 2009).

Cowley & Cunningham (2003) recorded the Namibian Rock Agama *Agama planiceps* as a prey item. Both Nokis and Namibian Rock Agamas are common, diurnal, boulder-dwelling animals typical of the habitat in which the species lives (Rathbun & Cowley 2008). The latter authors also recorded a mongoose unsuccessfully stalk a group of Rock Hyraxes *Procavia capensis*, an attempted capture of a Red-billed Francolin *Francolinus adspersus*, and the successful capture of Helmeted Guineafowl *Numida meleagris*. Remains of reptilian eggs were identified in one scat examined by Warren *et al.* (2009) and the species is also suspected to forage on the eggs and nestlings of the Chatsrike *Lanioturdus torquatus* (Rathbun & Cowley 2008). Adult flies (Sarcophagidae) attracted to rotting carcasses (see below) may be an important (ephemeral) source of food (Rathbun *et al.* 2005).

Social and Reproductive Behaviour There is limited information available, with the most detailed study to date being that of Rathbun & Cowley (2008), who radio-collared six animals in the foothills of the Erongo Mts. Although largely solitary, they were sometimes found in pairs or threes. Mongooses did not maintain exclusive home-ranges or defend these areas as territories, and the home-range of some animals overlapped nearly 100%.

Rathbun *et al.* (2005) reported on a Greater Kudu *Tragelaphus strepsiceros* that died within the home-range of a radio-collared mongoose. Up to seven mongooses fed on adult, larval and pupal sarcophagid flies attracted to the rotting antelope. While one animal fed, others in the vicinity usually waited 5–25 m away and only moved in to feed when no others were present. On a few occasions mongooses arrived as well-coordinated pairs or triads, and if these animals fed on the carcass at the same time they remained at different locations or one animal waited nearby while the other fed. However, five intra-specific fights, lasting about 10–15 seconds, were observed within about 30 m of the kudu. These encounters included initial growling followed by face-to-face biting, rapid rolling about on the ground, and loud screeching or squealing. Intra-specific aggression near the carcass probably produced a dominance hierarchy that determined when individuals fed at the Greater Kudu carcass and reduced further aggression between individuals. Rathbun *et al.* (2005) also recorded the home-range size of the mongoose during the entire observation period (May to Jul 2003), which measured some 145 ha (based on 95% minimum convex polygon method). However, the pre- and post-kudu home-range areas were quite different, roughly 158 ha pre-kudu and 60 ha post-kudu.

Rathbun & Cowley (2008) observed potential scent marking behaviour in the form of urination, defecation, and throat-chest rubbing, but did not observe marking with cheeks or anal glands. These authors also recorded single animals basking in the early morning sun on several near-freezing mornings. Basking was associated with auto-grooming, including licking the abdominal, peri-anal and tail region; allogrooming was not observed (Rathbun & Cowley 2008).

Reproduction and Population Structure No information available.

Predators, Parasites and Diseases Diurnal raptors, such as African Hawk-eagle *Hieraaetus spilogaster*, are potential predators (Rathbun 2004, Rathbun & Cowley 2008).

Conservation IUCN Category: Least Concern. CITES: Not listed.

In Namibia, the species is found in both the Skeleton Coast and Etosha National Parks (M. Griffin pers. comm.), as well as on a number of conservancies, such as the Erongo Mountains Conservancy. Reports of black mongooses from the Waterberg Plateau Park refer to a black form of Dwarf Mongoose (M. Griffin pers. comm.). In Angola, they may occur in Iona N. P., though none of the specimens examined by J. Crawford-Cabral (pers. comm.) from the Namibe Province was collected from inside the Park.

Measurements

Herpestes flavescens

HB (♂ ♂): 343 (335–355) mm, n = 3

HB (♀ ♀): 310, 330 mm, n = 2

T (♂ ♂): 344 (325–362) mm, n = 3

T (♀ ♀): 340, 345 mm, n = 2

HF c.u. (♂ ♂): 70 (69–72) mm, n = 3

HF c.u. (♀ ♀): 64, 66 mm, n = 2

E (♂ ♂): 27.5 (27–28) mm, n = 3

E (♀ ♀): 24, 25 mm, n = 2

GLS (♂ ♂): 67.4 (66.7–67.9) mm, n = 3

GLS (♀ ♀): 64.6 (62.9–65.7) mm, n = 5

GWS (♂ ♂): 36.8 (35.6–38.0) mm, n = 3

GWS (♀ ♀): 32.6 (32.3–33.0) mm, n = 5

Throughout the range (Watson & Dippenaar 1987) and museum specimens (BMNH)

Skull measurements: N Namibia (Taylor & Goldman 1993)

The type specimen of *H. gracilis flavescens* (♀) had HB = 330 mm and T = 335 mm. Five ♂ ♂ radio-collared by Rathbun & Cowley (2008) ranged in weight from 550 to 907 g; a single ♀ weighed 850 g.

Key References Crawford-Cabral 1996; Rathbun *et al.* 2005; Rathbun & Cowley 2008; Taylor & Goldman 1993.

Mark E. Taylor

Herpestes ichneumon EGYPTIAN MONGOOSE (ICHNEUMON)

Fr. Mangouste d' Egypte; Ger. Ichneumon

Herpestes ichneumon (Linnaeus, 1758). Syst. Nat., 10th edn, 1: 43. 'In AEliggypto ad ripas Nili, ... in India primario; mansuescit', restricted by Thomas (1911) to 'Egypt'.

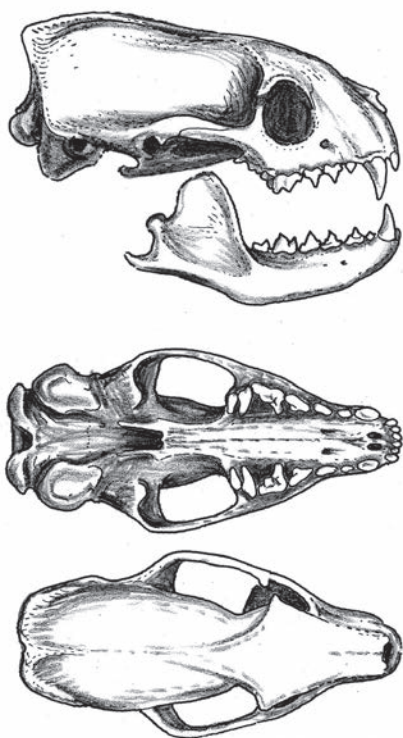
The name 'ichneumon' is derived from the Greek word meaning 'tracker', possibly in reference to their ability to dig out and eat the eggs of crocodiles.

Taxonomy Ten subspecies were listed by Coetzee (1977), but most subspecies descriptions are based on limited specimens, and

examination of specimens reveals an extremely high degree of variation between individuals. No subspecies are listed here, pending taxonomic revision. Synonyms: *aegyptiae*, *aegypti*, *angolensis*, *bennettii*, *cafra*, *centralis*, *dorsalis*, *egypti*, *ferruginea*, *funestus*, *grandis*, *grisea*, *lademanni*, *mababiensis*, *madagascarensis*, *major*, *nems*, *numidianus*, *numidicus*, *occidentalis*, *parvidens*, *pharaon*, *sabiensis*, *sangronizi*,



Egyptian Mongoose *Herpestes ichneumon*.



Lateral, palatal and dorsal views of skull of Egyptian Mongoose *Herpestes ichneumon*.

widdringtonii. Chromosome number: $2n = 43$ in ♂♂, $2n = 44$ in ♀♀; nine pairs are metacentric, three submetacentric, three subtelocentric and eight acrocentric (Fredga 1970, 1972).

Description A relatively short-legged mongoose characterized by elongated body with tail slightly shorter than body length, terminating in a black tassel. Head broad and long with muzzle pointed and black rhinarium. Eyes small with pupils horizontally elongated. Ears short and relatively square, set far back in the head. Guard hairs long (up to 80 mm), with alternate light and black bands producing a generally grizzled appearance. Underfur soft and fine, varying in colour, but typically greyish on the forequarters and flanks. Variations in pelage colour are found (Rosevear 1974). Hair on underparts shorter and sparser than on upperparts, particularly on belly. Hair towards base of tail much longer than towards the tip, although the hair on the tassel may be up to 130 mm in length. Five digits on each foot, with all digits long, except the first. Non-retractile, curved claws well developed and of similar length in both fore- and hindfeet (Skinner & Chimimba 2005). Perianal glands present. Sexual dimorphism in weight and body measurements is apparent (♂♂ generally larger than ♀♀), but there is considerable overlap. Normally, ♀♀ have three pairs of nipples although two pairs have been reported (Harrison 1968).

Skull long and narrow, with supraoccipital crest well developed; sagittal crest not well developed. Postorbital bars complete in older animals. Zygomatic arches broad and strongly built. Posterior chambers of the ear bullae are large, compared with the anterior, rising to a high, rounded apex from the skull. The dental formula is $I^{3/3} C^{1/1} P^{4/4} M^{2/2} = 40$. Outer, upper incisors large, those in the lower jaw less so but broad towards their tips. Upper canines

moderate in size, while those in the lower jaw are recurved (Rosevear 1974, Skinner & Chimimba 2005).

Geographic Variation See Taxonomy.

Similar Species

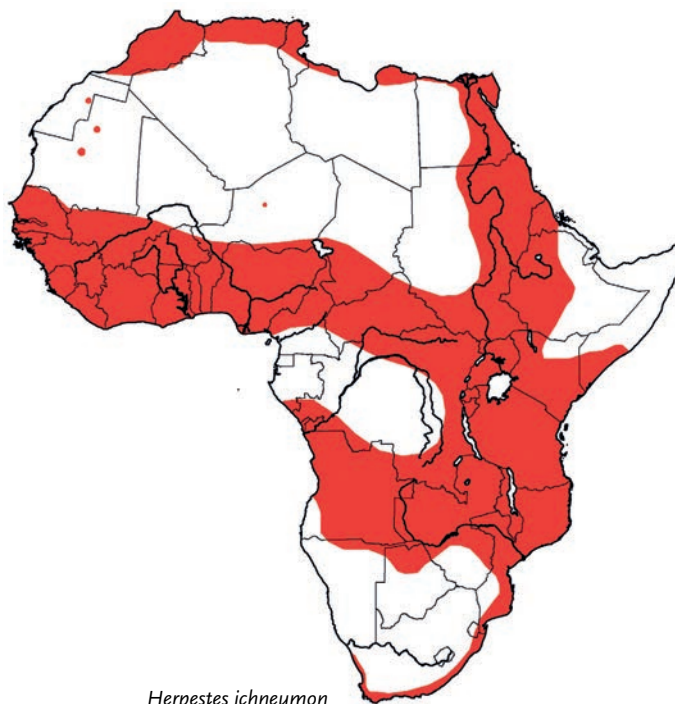
Ichneumia albicauda. Sympatric in much of sub-Saharan Africa, though White-tailed Mongoose is more widely distributed in southern Africa. Longer-legged and the terminal two-thirds of tail usually white (and often black in West Africa).

Atilax paludinosus. Sympatric, except in northern Africa where the Marsh Mongoose is not found and central Africa where the Egyptian Mongoose is absent. Normally darker in colour with shorter tail and longer toes.

Rhynchogale melleri. Sympatric in western part of Africa below the Equator until South Africa (although overlap might be higher). Distinctive crest-like parting on either side of the neck.

Distribution Widely distributed in Africa, with the exception of desert areas and high rainfall forests. Occurs from Senegal and Gambia through most of West Africa, south of the Sahara, to East Africa, then southwards in Angola, Zambia, Malawi and Mozambique. Absent from much of southern Africa, but present in NE Namibia, N Botswana, N and E Zimbabwe and all along the South African coastline (west to about Kleinsee in the Northern Cape; C.T. Stuart pers. comm.). In North Africa they occur in a narrow coastal strip from Morocco to Tunisia, and also from N and E Egypt southwards to Ethiopia (it is unknown whether they still occur in E Libya). Apparently formerly introduced to Madagascar (Haltenorth & Diller 1980), but not recorded recently (F. Hawkins pers. comm.).

Extraliminally, they are present in the Iberian Peninsula (Spain and Portugal), where they were introduced during historical times (Riquelme-Cantal *et al.* 2008), and the Middle East in countries bordering the eastern Mediterranean Sea (Turkey, Lebanon, Jordan)



Herpestes ichneumon

(Delibes 1999a). A century ago the species suffered a retraction of its range in Spain and at present appears to be expanding its range in some areas in Portugal (Borrallho *et al.* 1996).

Habitat Mainly associated with habitats having understorey vegetation in coastal, lacustrine and riparian (streams, rivers, marsh, swamps) locations (Delibes 1982, Ben-Yaacov & Yom-Tov 1983, Palomares & Delibes 1993a, Angelici *et al.* 1999b). In East Africa, this species is commonest in heavily grassed and cultivated areas (Kingdon 1977). In Egypt it is recorded inhabiting desert areas relatively far from the coast (Kasperek 1993), and also from mountainous forest areas up to 1950 m in the Moroccan High Atlas (F. Cuzin pers. comm.); recorded up to 3000 m in the Ethiopian Highlands (Yalden *et al.* 1996). In Morocco, it occurs in forests in higher rainfall areas, and in irrigated and cultivated areas, especially the northern fringe of the Sahara (F. Cuzin pers. comm.). In tropical Africa, the Egyptian Mongoose occurs where there are termitaries, and Kingdon (1977) suggested these could satisfy a need for secure shelter. The presence of other predators may limit the use of optimal habitats, as is the case in Spain where the species is very rare in areas where the Iberian lynx *Lynx pardinus* is abundant (Palomares *et al.* 1996).

Abundance On the African mainland, this species is widespread and locally common. At Vernon Crookes N. R. in KwaZulu-Natal, South Africa, Maddock (1988) estimated a density of 1.2 individuals/km², while Hendrichs (1972) estimated a density of 0.1/km² in East Africa. In Egypt, two family groups of 5–7 individuals each lived in only 900 m² of levees of a fish pond area (Ben-Yaacov & Yom-Tov 1983). In optimal habitats of Spain, where the Egyptian Mongoose has been well studied, this species reaches 2.0 individuals/km² (Palomares & Delibes 1992a).

Adaptations Egyptian Mongooses are entirely terrestrial, but are also good swimmers (Harrison 1968, J. Kingdon pers. comm.). They are well adapted to digging for prey with their strong forelimbs and long, curved claws. Although they have good vision, and apparently have limited colour vision with both cones and rods present in the retina (Dücker 1960), it appears that sense of smell is well developed (Dücker 1965). The dentition is adapted for crushing, with upper and lower second molars occluding closely, and the carnassials having high cusps.

One of the most striking adaptations of this species is its capacity to be largely unaffected by the venom of at least some snakes. It has been proved that the binding site of the nicotinic acetylcholine receptor is resistant to α -neurotoxins (Barchan *et al.* 1992). The secretions of the peri-anal gland contain a mixture of long-chain carboxylic acids and the secretions are specific to each sex (Hefetz *et al.* 1984).

In places where it has been well studied, foraging occurs during the day for 1–2 hours on average after sunrise and an hour or two before sunset (Palomares & Delibes 1992b, Maddock & Perrin 1993, F. Cuzin pers. comm., Skinner & Chimimba 2005). Nocturnal activity is probable in areas where they are subject to disturbance. In Israel they are reported to be crepuscular (Ben-Yaacov & Yom-Tov 1983).

In tropical Africa, Kingdon (1977) reported that this species is commonly mobbed by birds attracted to its antics (which include 'tail-chasing'), a behaviour that seems to derive from the juveniles' 'tracking' or 'following response', which is dependent upon close contact with the mother's (or sibling's) anal glands.

Foraging and Food The Egyptian Mongoose is an opportunistic, omnivorous species that has been reported to consume a great variety of food, including small mammals, birds, amphibians, reptiles, fish, crabs, gastropods, insects, arachnids, carrion, fungi, fruit and other plant material (Rowe-Rowe 1978a, Smithers & Wilson 1979, Stuart 1983). Small mammals have been reported as the main prey in various localities, such as the Western Cape of South Africa (Stuart 1983), where Southern African Vlei Rats *Otomys irroratus* and Four-striped Grass Rats *Rhabdomys pumilio* were particularly favoured; Zimbabwe (Smithers & Wilson 1979), where Angoni Vlei Rats *Otomys angoniensis* and *Mastomys* spp. were common, and the rainforests of SE Nigeria (Angelici 2000). In Israel they are recorded as feeding mainly on poultry and rats (Ben-Yaacov & Yom-Tov 1983), while in some parts of Spain, young European rabbits constitute the main prey (Delibes 1976, Palomares & Delibes 1991).

In spite of the preference for small mammals, the diet can vary between localities and even family groups inhabiting the same area. For instance, in three localities of Doñana (SW Spain) separated by between 3 and 15 km from each other, Egyptian Mongoose mainly consumed lagomorphs in one area, insects, reptiles and small mammals in the second, and birds and small mammals in the third (Palomares 1993a).

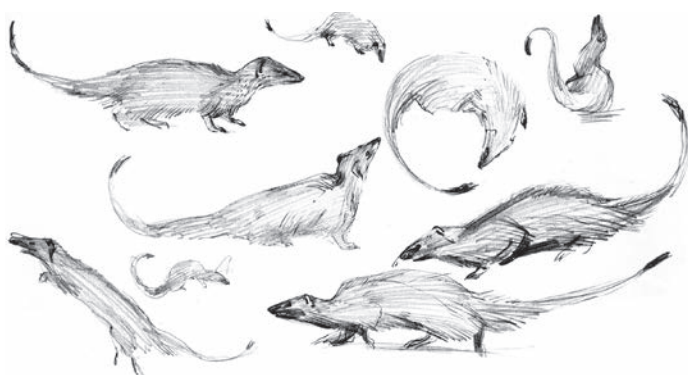
Diet varies seasonally according to the availability of prey. In SW Spain, lagomorphs, small mammals and amphibians were consumed more frequently in the wet season, whereas reptiles were more frequent in the diet in the dry season (Palomares 1993a). Limited sample sizes from Zimbabwe revealed little seasonal variation in diet (Skinner & Chimimba 2005).

Foraging is characterized by intense prey searching, walking with the nose close to the ground, inspecting every small hole in the ground, excavating frequently, sniffing around bushes and shrubs, and investigating larger burrows. Individuals may simultaneously enter underground dens to catch rabbits when a family group travels together. When prey items are large enough, these are shared but certain individuals eat before others. Most of their active time is spent foraging (six hours on average; Palomares & Delibes 1992b), with travelling and social interaction occupying minimal time each day (Palomares & Delibes 1993b).

Large prey are caught and killed by a neck bite, but small prey are typically killed by biting the head (Estes 1991). Snakes are attacked from the rear before the victim can retaliate (Kingdon 1977). The Egyptian Mongoose is reported to deal with eggs in the same manner as Slender *Herpestes sanguineus* and Banded *Mungos mungo* Mongooses (Ewer 1973).

Social and Reproductive Behaviour The Egyptian Mongoose is generally solitary, although pairs and family parties of 4–6 are not uncommon. Solitary individuals were seen most frequently (96% of occasions) in one study in South Africa, the remainder comprising groups of two or three individuals (Maddock & Perrin 1993). Packs of up to 14 have been recorded in Namibia (Shortridge 1934), but this is unusual. In Israel, they live in family groups composed of 2–3 ♀♀ with their young and an adult ♂, though ♂♂ spent most of their time alone (Ben-Yaacov & Yom-Tov 1983).

Although no detailed investigations of social behaviour have been undertaken on this species in Africa, the species has been relatively well studied in SW Spain, where mean group size is 1.7 individuals (range 1–5; Palomares & Delibes 1993c), and solitary individuals



Egyptian Mongoose *Herpestes ichneumon*.

are seen on 62% of occasions. Pairs and groups of three individuals, or more, are frequently observed (18% and 21%). Groups of three, or more, individuals are seen all year around except in spring. Pairs were mainly composed of female–young parties (47%), and adults of different sex (41%). The only observation of two adult ♂♂ together was an agonistic encounter, one ♂ chasing the other out his territory. Groups of three or more individuals mainly comprised an adult ♀, adult ♂ and young (58%), although sightings of a ♀ plus young were also frequent (39%). Grouping patterns in Spain seem to be determined by food characteristics (Palomares & Delibes 1993c), although Kingdon (1977) has suggested that the social proclivities of these mongooses in Spain might be encouraged by the fact that they are the only mongoose species occurring.

Members of the same family group share resting sites, which may be located in underground dens or thickets (Palomares & Delibes 1993d). On several occasions, group members met in frequently used dens after spending the day alone.

Average home-range sizes in SW Spain, for each sex–age class, range between 2.8 and 3.5 km² for young and adult ♂♂, respectively (Palomares 1994). Females are territorial in their core areas, whereas ♂♂ are territorial over their entire home-range. Females defend food resources, so heavier ♀♀ (i.e. the socially dominant ones) have smaller home-ranges than smaller ones because they can stay on patches richer in food. However, the main resource for ♂♂ is ♀♀; therefore, heavier ♂♂ can acquire and successfully defend larger territories than smaller ones, including more ♀♀ within their territories. Males have on average four core areas within their home-ranges whereas ♀♀ only have 1.2. Territorial behaviour and relationships with ♀♀ are not the same for all ♂♂ (Palomares 1993b). It has been observed that ♂♂ larger than ♀♀ will adopt a polygamous life-style, sharing a territory with several ♀♀ (up to four), but spending little time with them (4%). When ♂♂ are similar in size to ♀♀, they consort with only one ♀, with whom he spends most of his time (29%).

In SW Spain, temporary latrines are frequently found in open places in the edge of thickets, inside the thickets, or outside underground dens used as resting places and within core areas. This suggests that the latrines are being used as a communication tool. Scattered faeces were also found in the centre of paths within the most used areas and on those leading to resting sites (Palomares 1993c). In Israel latrines are in permanent locations in order to mark home-ranges (Ben-Yaacov & Yom-Tov 1983). Temporary latrines seem to be the rule in Morocco (F. Cuzin pers. comm.). In addition to marking with faeces, scent-marking with the perianal gland on large stones, rock corners

and so forth has been observed in Israel. In Doñana (Spain) scent-marking has been observed on the ground (F. Palomares pers. obs.).

Prior to mating, the ♂ closely follows the ♀ sniffing and licking her vulva, and the pair engages in prolonged social grooming. Mounting attempts at decreasing intervals usually precede mating. Complete copulation may take 6–7 min, but short copulations without ejaculation lasting 0.5–2 min are frequent. During copulation the ♂ embraces the mid-section of the ♀ and thrusts with his hindlegs pressed against her. Postcopulatory behaviour is marked by unrest and defensive threats from the ♀ (Estes 1991).

In Israel, Ben-Yaacov & Yom-Tov (1983) observed cubs suckling from any breeding ♀ of the group, and they would stay with subadults or adults other than the mother. Adults usually bring food to the pups. Cubs first appear outside dens when about six weeks old. Young stay in the family unit until the following breeding season. Several different types of play have been observed: running, fighting, fleeing, hiding, prey stalking and catching, sexual play and experimenting (Rensch & Dürcker 1959).

Five different calls have been recorded in free-ranging individuals in SW Spain, related to alarm, contact, aggression, intimidation and pain (Palomares 1991). The most frequently repeated is the contact call, which is a short duration call emitted repeatedly by every member of the group to maintain contact during foraging; the alarm call is a deep, sharp growl; aggression calls consist of soft and strong growls of barking or spitting, usually during mating and fighting; the intimidating call is a soft, continuous growl, also usually at mating; and the pain call is a sharp sound.

Reproduction and Population Structure Little information is available from Africa, but three captures of young individuals in Zimbabwe and one of a pregnant ♀ in Sierra Leone suggest that births can occur between Oct and Dec (Rosevear 1974, Skinner & Chimimba 2005); births have been recorded in Sep and Feb in Uganda (Kingdon 1977), and between Feb and Oct in Egypt (Harrison 1968). In SW Spain, births mainly occur (78% of cases) in May, Jun and Jul, so, assuming a gestation period of 9–10 weeks, most matings (64%) take place in Mar and Apr. The mean number of cubs was 2.7 for seven litters (Palomares & Delibes 1992a). In Israel, mating occurred in early spring and the average litter-size for captive animals was 3.3 (range 1–4, $n = 10$) (Ben-Yaacov & Yom-Tov 1983). A single litter is the norm, although captive animals breed again if a ♀ loses her cubs (Ben-Yaacov & Yom-Tov 1983). A second litter has only rarely been observed in the wild.

In captivity, Ben-Yaacov & Yom-Tov (1983) found that cubs have closed eyes and ears when born. At 21 days the cubs react to movements and at 25 days begin to call. Cubs appeared to have a sense of smell at 39 days, and their vision seemed to be well developed at 45 days. Cubs try to stand and walk when 21 days old, but only in their fourth week can they walk properly. Jumping has been first observed at 37 days. At 72 days, cubs show complete hunting behaviour, and, at four months, they can hunt by themselves. At 2.5 months young have all deciduous teeth except the molars, which are present three months later; at nine months old the first premolars are replaced (Ben-Yaacov & Yom-Tov 1983). Sexual maturity appears to be achieved in their second year (Dürcker 1960, 1965).

Females are more frequently trapped than ♂♂, with ratios of 1.8 : 1 for both South Africa and Spain (Palomares & Delibes 1992a,

Maddock 1993a). For the same areas, adult individuals have also been more frequently trapped than young, with ratios of 1 : 0.1 and 1.8 : 1, respectively. A similar situation has been found in Israel (Ben-Yaacov & Yom-Tov 1983). In the same area, life expectancy did not exceed 3% after two years. The majority of deaths (69%) were due to human activities, both direct (illegal hunting) and indirect (road kills). A captive ♀ lived to nearly 13 years (Kingdon 1977; and see Weigl 2005).

Predators, Parasites and Diseases In Spain, Egyptian Mongooses are frequently killed by Iberian Lynxes and large eagles in areas where these predators are abundant (Delibes & Palomares 1993, Palomares *et al.* 1996) and, with the exception of Iberian Lynxes, this likely holds true for Africa. One unsuccessful attack by a Golden Eagle *Aquila chrysaetos* has been observed in Morocco (G. Trochard pers. comm.), while bones of this species have been found under the nest of Martial Eagles *Polemaetus bellicosus* (J. Kingdon pers. comm.). It is likely that they are preyed on by various large African predators.

The louse *Felicola (Felicola) inaequalis* frequently has been recorded in specimens trapped in SW Spain (Pérez-Jiménez *et al.* 1990). Cestodes of the genus *Mesocestoides* and *Dipylidium caninum*, and the coccidia *Eimera vulpis* have been reported in samples of dead animals and faeces (Loos-Frank 1990, Rodríguez & Carbonell 1998).

Conservation IUCN Category: Least Concern. CITES: Not listed.

The Egyptian Mongoose is widely distributed on the African continent, occurring in numerous protected areas across their range, and does not appear to be under any significant threat.

Measurements

Herpestes ichneumon

TL (♂ ♂): 1084 (1005–1168) mm, n = 10
 TL (♀ ♀): 1092 (1050–1125) mm, n = 8
 T (♂ ♂): 517 (452–576) mm, n = 10
 T (♀ ♀): 528 (485–563) mm, n = 8
 HF c.u. (♂ ♂): 111 (105–115) mm, n = 10
 HF c.u. (♀ ♀): 111 (108–114) mm, n = 8
 E (♂ ♂): 36 (30–38) mm, n = 10
 E (♀ ♀): 38 (30–42) mm, n = 8
 WT (♂ ♂): 3.4 (2.6–4.1) kg, n = 10
 WT (♀ ♀): 3.1 (2.4–4.1) kg, n = 8
 GLS: 103.0–105.5 mm, n = 5
 GWS: 51.0–54.0 mm, n = 5
 Zimbabwe (Smithers & Wilson 1979)
 Skull measurements: South Africa (Roberts 1951)
 Measurements fall within these ranges in South Africa (Stuart 1981, Maddock 1993a), and are slightly smaller in Israel (Osborn & Helmy 1980, Ben-Yaacov & Yom-Tov 1983) and Spain (Delibes & Palomares 1993)

Key References Ben-Yaacov & Yom-Tov 1983; Delibes & Palomares 1993; Kingdon 1977; Palomares 1994; Palomares & Delibes 1991, 1992a, b, 1993a, b, c; Skinner & Chimimba 2005.

Francisco Palomares

Herpestes ochraceus SOMALI SLENDER MONGOOSE

Fr. Mangouste de Somalie; Ger. Somali Manguste

Herpestes ochraceus Gray, 1849. Proc. Zool. Soc. Lond. (for 1848): 138–139. ‘Abyssinia’.



Somali Slender Mongoose *Herpestes ochraceus*.

Taxonomy Monotypic. The Somali Slender Mongoose has been considered a subspecies of the pan-African Slender Mongoose *H. sanguineus* (e.g. Coetsee 1977, Yalden *et al.* 1980, Wozencraft 1993), although it was recognized as distinct by Taylor & Goldman (1993). Authors have assigned specimens to *Calogale*, *Galerella*, *Herpestes*, or *Mungos* (Gray 1849, 1864 [1865], Azzaroli & Simonetta 1966,

Coetsee 1977, Taylor & Goldman 1993). Synonyms: *bocagei*, *fulvidior*, *ochracea*, *perfulvidus*. Chromosome number: not known.

Description A small mongoose of variable colouration, ranging from a pale grizzled grey to a dark brown with some specimens having a distinct reddish colour. As the name suggests, body shape is slender, with long tapered tail about 85% of head and body length. Ears small, rounded. Number of nipples not known.

Geographic Variation None recorded.

Similar Species

Herpestes sanguineus. Sympatric, though probably occurs in moister, higher elevations. Similar in coat colour, though Slender Mongoose has a black tip to a longer tail; skull narrower, longer and not as elevated (and with less inflated auditory bullae and smaller molars; Azzaroli & Simonetta 1966, Yalden *et al.* 1980, Taylor & Goldman 1993).

Helogale spp. Sympatric, but smaller, lacks a black tip to the tail, and social.

Distribution Confined to the north-eastern part of Africa, in Somalia and adjacent parts of Ethiopia and marginally into NE Kenya.



The type locality is Abyssinia (Gray 1849 [1850]) and type specimens in the British Museum (Natural History) are from Wandair (Wardair) (06° 59' N, 45° 20' E) and Mandeira (10° N, 45° 10' E) (Azzaroli & Simonetta 1966, Taylor & Goldman 1993). Sympatric with the Slender mongoose in the more vegetated parts of its range in a manner comparable to that of the overlap of the Kaokoveld Slender mongoose *Herpestes flavescens* and Slender mongoose in south-western Africa.

Habitat Probably found throughout N Somalia, especially in the hilly areas (Drake-Brockman 1910), and through much of S Somalia, extending into adjacent areas of Kenya and Ethiopia (Azzaroli & Simonetta 1966), where it may be sympatric with the Slender mongoose. Occurs to around 600 m altitude (Yalden *et al.* 1996).

Abundance Little information available on this species as few specimens are available in museums. There are 14 specimens in the British Museum and five in the Natural History Museum of the

University of Florence (P. Agnelli pers. comm.). It is assumed that it is relatively common in arid regions.

Adaptations The large auditory bullae are believed to be associated with improved hearing in desert environments where the dry air conducts sound waves poorly (Yalden *et al.* 1980). The colour of the pelage is variable and is probably associated with a humidity gradient, darker forms occurring at higher altitudes, while the grizzled grey forms are from lower elevations. The erythristic colour of some forms is assumed to be a camouflage feature in the reddish rocky area of some of its habitats. It is predominantly diurnal.

Remarks There is a paucity of information on the behaviour and ecology of this species. Solitary, or in pairs or small family groups. Other aspects of its behaviour likely to be similar to the Slender mongoose.

Conservation IUCN Category: Least Concern. CITES: Not listed.

It is not known whether this species occurs in any protected areas; it may, for example, occur in Geedkabeleh G. R. in the north. This is a very poorly known species, and although it is not likely to be threatened it remains in need of further study.

Measurements

Herpestes ochraceus

HB (♂ ♂): 274 (254–290) mm, n = 5

T (♂ ♂): 240 (220–273) mm, n = 5

HF c.u. (♂ ♂): 53 (50–56) mm, n = 5

E (♂ ♂): 26 (25–28) mm, n = 5

GLS (♂ ♂): 57.6 (54.7–61.2) mm, n = 9

GLS (♀ ♀): 55.1 (53.3–56.9) mm, n = 2

GWS (♂ ♂): 33.0 (28.7–36.6) mm, n = 9

GWS (♀ ♀): 30.9 (30.7–31.1) mm, n = 2

Museum specimens (BMNH, MZUF)

Skull measurements: Somalia (Taylor & Goldman 1993)

Key References Azzaroli & Simonetta 1966; Taylor & Goldman 1993; Yalden *et al.* 1980, 1996.

Mark E. Taylor

Herpestes pulverulentus CAPE GREY MONGOOSE (SMALL GREY MONGOOSE)

Fr. Mangouste grise du Cap; Ger. Kleinichneumon

Herpestes pulverulentus Wagner, 1839. Gelehrte. Anz. I. K. Bayer. Akad. Wiss. München 9: 426.

'Kap' [Cape of Good Hope, South Africa; exact locality unknown].

Taxonomy The Cape Grey mongoose has been placed in the genus or subgenus *Galerella* (Gray 1864 [1865], Wozencraft 1993, 2005), distinct from *Herpestes* because of smaller size, six upper and five lower cheekteeth (one less premolar on the lower jaw), and two chambers of ear bullae of similar size. Traditionally, six subspecies have been recognized: *ruddi*, *nigratus*, *shortridgei*, *basuticus*, *annulata* and the nominate form (Coetzee 1977, Meester *et al.* 1986, Cavallini 1992), although skull morphological analyses failed to reveal any quantitative differences (Taylor & Goldman

1993). Lundholm (1955a) regarded *nigratus* as a separate species, and described *annulata* as a subspecies of it. Watson & Dippenaar (1987) considered *nigratus* (= *H. flavescens*) as a distinct species with *shortridgei* and *annulata* subspecies of it (and see Crawford-Cabral 1989b, Watson 1990, Taylor & Goldman 1993, Wozencraft 1993, 2005; see also *H. flavescens*). Consequently, three subspecies are recognized here following Cavallini (1992) and Wozencraft (2005). Synonyms: *apiculatus*, *basuticus*, *caffra*, *lasti*, *maritimus*, *ratlamuchi*, *ruddi*, *rufescens*. Chromosome number: 2n = 40 in ♀ ♀ and 2n = 39

Cape Grey Mongoose *Herpestes pulverulentus*.

in ♂♂, less than the Slender Mongoose *H. sanguineus* ($2n = 42$ and 41 , respectively), *H. ichneumon* ($2n = 44$ and 43) and other species of the genus *Herpestes* ($2n = 36$ and 35) (Fredga 1970, 1972, 1977).

Description A small mongoose, typically herpestid in appearance, with short legs and long, bushy tail (ca. 90% of HB). Body and tail grizzled grey (from light grey to dark brown-grey). Ventral surface less grizzled. Muzzle and legs darker, head pointed with ears slightly darker, small, close to the head and partly covered by a band of longer hairs. The rhinarium is small, with a central depression that continues downwards and divides the haired section of the upper lip. Tip of tail sometimes inconspicuously shaded brown (length less than 20 mm). Individual guard hairs black or grey with four to six white to yellowish bands. Five digits on each foot, with the first one reduced. Heel pad not haired and claws not very long. Sexes similar in colour. Males larger than ♀♀ (1.2 times larger in weight). There are three pairs of nipples.

Skull length usually >67 mm (♂♂) and >63 mm (♀♀), with ovoid braincase and short rostrum. The outer incisors are slightly larger than the inner ones. The lower canines are distinctly curved. In the upper jaw, the first molar is small, and the second molar is very small.

Geographic Variation

Herpestes p. pulverulentus: central part of the range, in Western Cape, part of Eastern and Northern Cape and Free State (from the southern and western coast to 32°S in the west and 28°S in the east). Grizzled grey with a similar coloured tail.

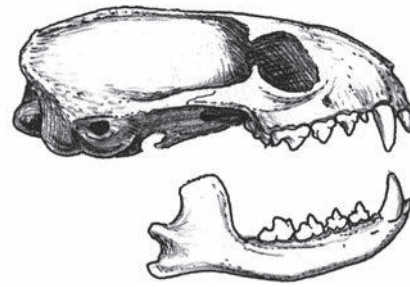
H. p. basuticus: higher altitudes, from E Lesotho to W KwaZulu–Natal in South Africa (approx. 27°E to 30°E and 28.5°S to 31°S). More woolly underfur, and a paler appearance.

H. p. ruddi: extreme north-western section of species range (approx. 16.5°E to 22°E and 25.5°S to 32.5°S). More brownish, with darker underfur and yellowish light bands on guard hair.

In all subspecies, character gradients are present in animals from contiguous areas (Lynch 1981).

Similar Species

Herpestes sanguineus. Marginal range overlap in the western part of the Cape Grey Mongoose's range (north of the Orange R., approx. 16.5°E to 18°E and 25.5°S to 28.5°S ; Lynch 1981). Smaller (skull length usually <64 mm in ♂♂, <63 mm in ♀♀), with black (not brown) tail tip (length 60–95; usually more than 75 mm) contrasting with the rest of the tail.

Lateral view of skull of Cape Grey Mongoose *Herpestes pulverulentus*.

H. flavescens. Allopatric, in SW Angola and NW and NC Namibia only.

Intermediate in size between the Slender and the Cape Grey Mongooses, and may have a conspicuous tail tip (Watson 1990, Taylor & Goldman 1993).

Distribution Endemic to southern Africa, ranging throughout the Northern Cape (with one record from near the Botswana border at Hotazel; C. Anderson pers. comm.), Western Cape and Eastern Cape, west to Lesotho and extreme W KwaZulu–Natal (eastern slopes of the Drakensberg). Two specimens were collected in 1937 and 1974 in S Namibia. One ♀ was trapped in 1990 in Wakkerstroom, Mpumalanga, 200 km north of known records in KwaZulu–Natal and Lesotho; this might indicate a range contraction or a very low density in Namibia and an expansion in NE South Africa, as the area has been extensively trapped before (Bronner 1990) and this species is easy to trap.

Habitat This species has a wide habitat tolerance, and is found in forested areas as well as open country. Cape Grey Mongooses are more common in dry than in wet areas (Crawford *et al.* 1983), especially with a warm temperate climate (Lynch 1981), but absent in the driest parts of the region (Kalahari thornveld; rainfall below 200 mm; Lynch 1983). Present from sea level around the Western Cape to 1900 m in

*Herpestes pulverulentus*

KwaZulu–Natal. They occur mainly in Karoo and karroid bushveld, and sclerophyllous bush (as defined in Acocks 1975), but are often associated with refuge areas, such as dense bushes and rocky outcrops, and avoid open fields with short vegetation where they are easily seen because of their dark colour (Cavallini & Nel 1990b). Adapt easily to human settlements, where they search for food scraps.

Abundance Common throughout the range. Densities of up to 10 individuals/km² have been recorded in suitable habitat; also abundant close to human settlements (Cavallini & Nel 1990b, Stuart 1991).

Adaptations Although mainly terrestrial, Cape Grey Mongooses will climb trees, either when hunting or when under stress. They do not use dens, at least not in summer. In areas with little cover, they rest in holes in the ground, in termitaria or under rocks. The claws of the front feet are not well developed, and they are poor diggers and do not dig their own burrows, rather relying on holes dug by other species (which they adjust to their own requirements) or on natural shelters. Cape Grey Mongooses do not leave scats in faecal piles like other mongooses, but scatter them singly or in clusters in well-used areas, especially around sleeping sites (which are changed from day to day; Cavallini & Nel 1990b). Captive animals exhibit anal gland marking (Stuart 1981).

The species is predominantly diurnal and activity is related to sunset and sunrise; activity is reduced in bad weather and at high temperatures (Cavallini & Nel 1990b). As with other small carnivores, it tends to move along existing tracks and paths and is often observed crossing roads. Unlike the Slender Mongoose, which raises its tail while running, the Cape Grey Mongoose keeps it close to the ground. It shows a certain resistance to the venom of the Forest Cobra *Naja melanoleuca* (over 21 mg venom per kg body weight; Hinton & Dunn 1967).

P⁴ is adapted to cutting in occlusion with the M₁ and P₄. A large protocone on the front inner edge of P⁴ and the back of M₁ are adapted to crushing.

Foraging and Food An eclectic predator, preying on anything from termites and grasshoppers to snakes and rodents. Nevertheless, its staple food is generally small mammals or insects (Stuart 1981, 1991, Cavallini & Nel 1990a, Avenant & Nel 1997, Stuart & Stuart 1998b). Cavallini & Nel (1990a) analysed 234 scats from West Coast N. P. in the Western Cape and found that murids (90.4%) predominated. In another study from the same area, Avenant & Nel (1997) found the same predominance, with insects (4.9%) forming a secondary food resource. *Otomys* spp. and Four-striped Grass Rat *Rhabdomys pumilio* appear to be favoured murid prey (Stuart 1981, 1991, Cavallini & Nel 1990a, Avenant & Nel 1992, 1997). Other studies from elsewhere in South Africa (Du Toit 1980, Lynch 1983, MacDonald & Nel 1986, Stuart & Stuart 1998b) echo these insectivorous and carnivorous dietary tendencies. It has been recorded feeding on larger mammal prey such as Scrub Hare *Lepus saxatilis* and Cape Porcupine *Hystrix africaeaustralis* (Cavallini 1992, Stuart & Stuart 1998b), and has even been known to attack Cape Grysbok *Raphicerus melanotis* lambs by tearing at the nose and mouth, eventually killing them (Langley 1986). However, because it will scavenge (Stuart 1981, Stuart & Stuart 1998b) and take urban refuse (Cavallini & Nel 1990a), it is uncertain to what extent this

occurrence of large prey in their diet is the result of active predation or scavenging.

Usually it moves from bush to bush, inspecting potential foraging sites like holes and rodent nests. It seems to rely mainly on sight and smell for locating prey. It scratches the soil in search of invertebrates, but is not an avid digger as other mongooses. Insects caught on the ground are held down with the front feet and then taken directly in the mouth. Larger prey are stalked, the killing bite delivered to the head. Small mammals are chewed in the side of the mouth, and insects are thoroughly masticated. Larger and tougher prey is held with the front feet firmly on the ground and then torn apart. Like other mongooses, it can break eggs by throwing them against a vertical surface (Ewer 1973). While foraging, individuals usually move 50–100 m every 15 min, with much individual variation (Cavallini & Nel 1990b), moving more than 4 km during the course of a day's foraging (Cavallini & Nel 1995). It has been observed to associate with small raptors (e.g. African Marsh Harrier *Circus ranivorus*) during foraging (Lombard 1989).

Social and Reproductive Behaviour Normally seen singly, sometimes in pairs and rarely in trios (more often in summer and early autumn, after parturition; e.g. Crawford *et al.* 1983). Of 163 sightings made by Stuart (1991), 151 were of single animals, seven were of pairs and five were of groups of three; Stuart (1981) recorded groups of up to five. Groups typically consist of one or two adults and juveniles. The lack of observations of ♀♀ moving with young may be due to the fact that the young are weaned in the breeding holes and eventually leave these only at a stage when they are capable of looking after themselves (Skinner & Chimimba 2005).

Males may show some sociality, with stable dyads comprising a large and a small individual. This behaviour has been observed also in the closely related Slender Mongoose. Males do not seem to maintain exclusive territories. In West Coast N. P., Cavallini & Nel (1990b) gave the home-range size of three ♂♂ as 55–92 ha; a ♀ had the smallest range (30.6 ha) while another ♀, a juvenile, ranged more widely (359 ha), possibly dispersing. Home-ranges overlapped widely, both within and between sexes. Similarly, Stuart (1991) gave the mean home-range size of four animals as between 5 and 36 ha in extent and stated that there appeared to be considerable overlap in home-ranges.

Reproduction and Population Structure Cape Grey Mongooses are seasonal breeders. Lactating ♀♀ have been found in Aug and in Nov–Feb, and the breeding season is probably at the end of winter (Aug–Dec; Stuart 1981, Lynch 1983). Reproductive output is low (1–3 young per litter). Rock crevices, farm outbuildings, fodder stores and woodpiles are used for rearing young (C. Stuart & T. Stuart pers. comm.). A captive mongoose lived for more than 11 years (Weigl 2005).

Predators, Parasites and Diseases Because of their small size, Cape Grey Mongooses have a number of potential predators, including large raptors and various carnivores. Martial Eagles *Polemaetus bellicosus* prey on them frequently (7.4% of items collected at nests; Boshoff & Palmer 1980), and Leopards *Panthera pardus* and Caracals *Caracal caracal* kill and eat them; they have even been recorded in the scats of Marsh Mongooses *Atilax paludinosus* (Stuart & Stuart 1998b, 2003a). Several parasites have been found on individuals of this species, including *Echidnophaga gallinacea*, *Ctenocephalides connatus*,

C. felis, *Procaviopsylla angolensis* and *Ixodes pilosus* (Cavallini 1992), while Horak *et al.* (2000) recorded the ixodid tick *Haemaphysalis zumpti* from an animal in the NW Northern Cape, as well as *Amblyomma marmoreum*, *H. zumpti* and an unidentified *Ixodes* sp. from two animals in the Eastern Cape. Cape Grey Mongooses are vectors of rabies, although they are not considered major carriers (Meredith 1982).

Conservation IUCN Category: Least Concern. CITES: Not listed.

No major threats are known, since the species is relatively adaptable, with a very catholic diet, and occurs in a number of protected areas in its range, including West Coast, Tsitsikamma and Mountain Zebra National Parks.

Measurements

Herpestes pulverulentus

HB (♂ ♂): 350 (340–420) mm, n = 101

HB (♀ ♀): 333 (330–355) mm, n = 81

T (sexes combined): 298 (205–340) mm, n = 182

HF c.u. (♂ ♂): 69 (59–75) mm, n = 101

HF c.u. (♀ ♀): 64 (52–75) mm, n = 81

E (sexes combined): 26 (15–36) mm, n = 182

WT (♂ ♂): 911 (680–1250) g, n = 39

WT (♀ ♀): 683 (491–900) g, n = 28

GLS (♂ ♂): 71.0 (67.5–78.0) mm, n = 30

GLS (♀ ♀): 67.5 (65.2–70.9) mm, n = 14

GWS (♂ ♂): 38.5 (34.6–41.6) mm, n = 30

GWS (♀ ♀): 36.2 (33.6–37.9) mm, n = 14

Free State, South Africa (Lynch 1981)

Skull measurements: S South Africa (Taylor & Goldman 1993)

Key References Avenant & Nel 1992, 1997; Cavallini 1992; Cavallini & Nel 1990a, b; Lynch 1981, 1983; Watson & Dippenaar 1987.

Paolo Cavallini

Herpestes sanguineus SLENDER MONGOOSE

Fr. Mangouste rouge; Ger. Rotichneumon

Herpestes sanguineus (Rüppell, 1835). Neue Wirbelt. Fauna Abyssin. Gehörig. Säugeth. 1: 27. 'Kordofan' [Sudan].



Slender Mongoose *Herpestes sanguineus*.

Taxonomy Included in subgenus *Galerella*. The taxonomy of the Slender Mongoose has been complicated by the description of numerous forms, many of which represent little more than colour morphs. Coetsee (1977) assigned the described taxa to two different sections: the *sanguineus* section, drab brown to yellowish-grey in general colour usually with a black tail tip (31 subspecies), and the *ratlamuchi* section, being reddish in colour and usually with a dark, but not black, tail tip (11 subspecies). Within these sections, Meester *et al.* (1986) listed 18 subspecies for southern Africa alone: 14 in *sanguineus* and four in *ratlamuchi*. In their revision, Watson & Dippenaar (1987) argued for the separation of the forms *nigratus* (here placed in *flavescens*; see species profile) and *swalius*, and considered the form *swinnyi* as *incertae sedis*. In a subsequent study, Watson (1990) could find no evidence to justify the recognition of any subspecies in *H. sanguineus* from southern Africa, and proposed that all subspecies be regarded as synonyms of *H.*

s. cauii, except for *swalius*, which he considered a monotypic species, occurring sympatrically with *H. sanguineus* in C and S Namibia. However, Taylor & Goldman (1993) presented evidence to regard *G. swalius* as conspecific with *sanguineus*, noting that the characters used by Watson (1990) to separate *swalius* (postorbital bar incomplete, coat colour and head and tail measurements) are poor diagnostic features. Azzaroli & Simonetta (1966) also considered *ochraceus* a distinct species, as did Taylor & Goldman (1993) and Wozencraft (2005), and this is followed here. Given the apparent large degree of individual variation within the species, and the unreliability of the features generally used to diagnose subspecies, none are recognized here pending a complete revision of subspecific boundaries. The situation is best summed up by Hinton & Dunn (1967: 112) who remark: 'From a brief examination of the material in the British Museum (Natural History), it would appear that most of the subspecies now recognized are simply seasonal



Lateral view of skull of Slender Mongoose *Herpestes sanguineus*.

or other types of colour variations: the large number of subspecies that have been described testifies to the industry but not to the discretion of taxonomists'.

Synonyms: *auratus*, *badius*, *bradfieldi*, *caldatus*, *canus*, *cauui*, *dasilvai*, *dentifer*, *elegans*, *erongensis*, *fuscus*, *galbus*, *galinieri*, *gracilis*, *grantii*, *ibaeae*, *ignites*, *ignitoides*, *iodoprymnus*, *kalaharicus*, *kaokoensis*, *khanensis*, *lancasteri*, *lefebvreii*, *marae*, *melanura*, *mossambica*, *mustela*, *mutgigella*, *mutscheltschela*, *ngamiensis*, *nigricaudatus*, *ochromelas*, *okavangensis*, *orestes*, *ornatus*, *parvipes*, *phoenicurus*, *proteus*, *punctulatus*, *rendilis*, *ruficauda*, *saharae*, *swalius*, *swinnii*, *ugandae*, *upingtoni*, *venatica*, *zombie*. Chromosome number: $2n = 42$ in ♀♀, $2n = 41$ in ♂♂ (Fredga 1970, 1972, 1977).

Description A small, slender mongoose with elongated sinuous body, short limbs and long tail. Face pointed, and rhinarium small and usually pinkish-brown to light brown in colour; a slit divides the hair on the upper lip. Eyes oval in shape surrounded by bright orange iris. Ears typically herpestid in shape, closely adpressed to side of head. Considerable variation in pelage colour is evident across the range of the species, with some individuals nearly black (melanistic) and others quite red (erythristic); pelage colour seems to correlate with substrate colour and dryness of the environment. Most common colour is grizzled brown or brownish-grey. Length and texture of coat varies. Upperparts of body generally grizzled caused by annulations of buffish-white rings alternating with dark brown to blackish rings. Dark rings are broader than pale rings. Individual hairs have six rings alternating light and dark, the base being pale and the tip dark. Hairs on head more finely grizzled than those on tail. Individual hairs vary greatly in length, those on upper parts reaching as much as 40 mm in length, but shorter on head. Ventral coat more variable, either grizzled or uniform buff, and fur thinner, shorter and softer than dorsal fur due to higher proportion of underfur. Both hind- and forefeet have five toes. First digits are much reduced and situated proximal to plantar pads and generally do not appear in the spoor; sole of hindfoot is nearly naked. A narrow web connects the digits of each foot. Claws sharp and curved, with those on forefeet up to 7 mm in length (measured across the curve). Tail long and slender, approximately equal to HB length; invariably terminates in dark to black tuft (70–130 mm in length). Anal sac beneath tail houses the anus and a pair of anal glands, one on each side of the anus. Anal sac is 20–30 mm in diameter. Males are approximately 9% larger than ♀♀ (Taylor 1971a). Females have two pairs of abdominal nipples, although specimens with three pairs have been reported (Roberts 1951).

Braincase oval, broadest at about level of ear openings and narrowing in front to the postorbital constriction. In adult specimens postorbital bars are complete, enclosing back of eye sockets. Rostrum short and broad. Flange-like supraoccipital crest well developed in adult skulls, but sagittal crest barely noticeable. Coronoid process of lower jaw high, providing ample leverage for temporalis muscles. Canines are sharp, with the upper nearly straight, the lower recurved. Lower incisors smaller than upper

incisors. First upper premolars are small and peg-like and sometimes absent (in a sample of 131 skulls, they were absent in 8%) (Rosevear 1974, Skinner & Chimimba 2005; and see Martinoli *et al.* 2006).

Geographic Variation As noted under Taxonomy, this is a highly variable species with regards to coat colouration, and while there may be some general differences in size (e.g. in West African specimens, southern specimens were generally slightly larger than the northern; Taylor & Goldman 1993), polychromatism is common, even within groups, and the characters generally used to distinguish subspecies appear unreliable.

Similar Species

Herpestes ochraceus. Somalia and Ethiopia. Distinguished by a light sandy coat colour (with black tail tip absent) and a shortened and wider cranium with distinctive inflated auditory bullae.

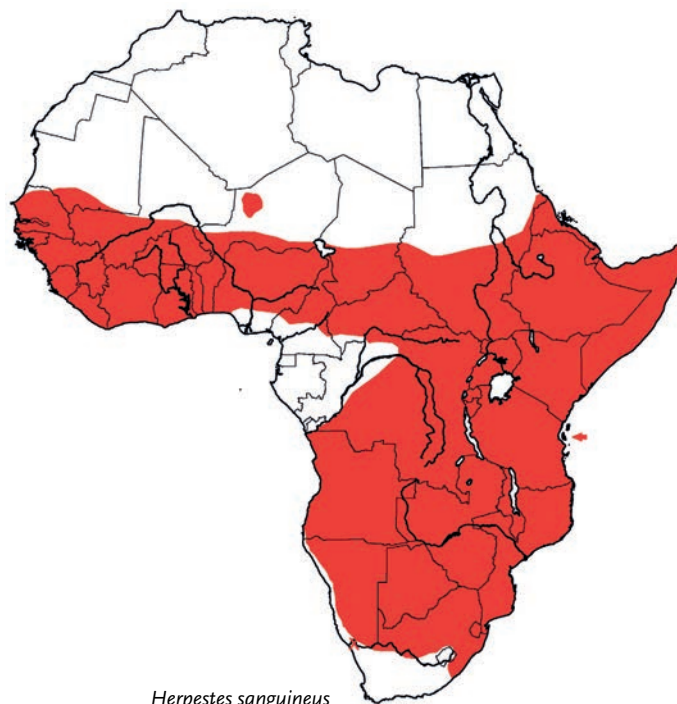
H. flavescens. Apparently sympatric in N Namibia. Generally larger, and usually melanistic or erythristic.

H. pulverulentus. Confined to southern Africa. Slightly larger, generally grey or blackish and lacking a black tail tip (though sometimes with tail tip brown).

H. ichneumon. Sympatric across much of range, but also found across North Africa. Larger, with longer coat and shaggy appearance; generally greyer and with characteristic black-tipped tail.

Helogale parvula. Smaller, has a short tapered tail without a black tip. A colonial diurnal species (while all the *Herpestes* species are primarily solitary and diurnal).

Distribution Endemic to Africa. One of the most widely distributed of the African mongoose species, ranging south of the Sahara from Senegal in the west to the Red Sea coast in Sudan in the east and south to the Northern Cape, north of the Orange R., in South Africa (Taylor 1975, Skinner & Chimimba 2005). Their most southerly distribution limit is probably the far eastern part of the Eastern



Herpestes sanguineus

Cape in South Africa, and they are common throughout most of E KwaZulu–Natal (Rowe-Rowe 1992a). Stuart (1981) mentions a museum record of this species from Mountain Zebra N. P., but this specimen is not mentioned in the studies of Watson & Dippenaar (1987) and Watson (1990). Also occurs on Zanzibar (Pakenham 1984, Stuart & Stuart 1998c, Goldman & Winther-Hansen 2003).

Habitat Occurs in a wide variety of habitats, ranging to altitudes of 2700 m in the Ethiopian Highlands (Yalden *et al.* 1996), but is absent from true deserts (such as the Namib Desert), although Slender Mongooses do occur in the pro-Namib (Coetzee 1969) and in sub-desertic parts of the Sahara such as Aïr, Niger (J. Newby, in Busby *et al.* 2006). They occur on forest fringes, and may penetrate into forests along roads and are sometimes found around villages. Their absence from much of South Africa, south of the Orange R., may well be due to competitive exclusion with the Cape Grey Mongooses *H. pulverulentus*.

Abundance Slender Mongooses are diurnal and are among the most common mongooses in Africa. In the Serengeti N. P., Tanzania, population densities between 1975 and 1990 ranged from three to six individuals/km² (Waser *et al.* 1995).

Adaptations A generalist carnivore, the dentition of the Slender Mongoose is adapted for crushing, but also for slicing. The carnassial shear is well developed. The fourth upper premolar, the carnassial, is large, its length more than 30% that of the total length of the toothrow; the three premolars in the lower jaw are also sharp and high-cusped. All upper premolars have high sharp cusps. The first lower molar is large, and the outer hind cusp enlarged with a sharp cutting edge; the upper first molar is elongated (Rosevear 1974, Skinner & Chimimba 2005).

Although largely terrestrial, Slender Mongooses are more arboreal than most other mongoose species (facilitated by their short, curved claws), and, while not accomplished climbers, they have been recorded running up and down wire netting, stone-walls, trees and branches (Taylor 1970a, T. Struhsaker pers. comm.). Taylor (1970a) investigated the mobility of the limb bones in three animals, and found that the species exhibited a greater degree of flexibility than in Egyptian Mongoose *H. ichneumon*, which was correlated with the high agility of the Slender Mongoose.

Dens are used for shelter and for births. Although capable of digging their own burrows, Slender Mongooses usually make use of pre-existing burrows for their dens. Dens may be either holes in the ground, usually modified Aardvark *Orycteropus afer* burrows, termitaria, rock piles or crevices, under tree roots or at the base of trees, or in hollow logs. Bronner (1992) described four burrows characterized by single entrances connected to single large chambers (398 ± 212 mm long × 327 ± 172 mm wide × 135 ± 54 mm high) via short passages; there was no nesting material present.

Slender Mongooses are predominantly diurnal. Maddock & Perrin (1993) found animals to be active between 08:00h and 18:00h, moving from their resting-sites late in the morning; there was a slight peak in activity about one hour before sunset and activity ceased shortly after sunset. Likewise, camera-trapping studies on Zanzibar found them to be active during the day (Goldman & Winther-Hansen 2003). The Slender Mongoose has a moderate metabolic rate of 0.76 cm³/g/h, comparable with the Small Indian Mongoose *Herpestes javanicus* (Kamau *et al.* 1979).

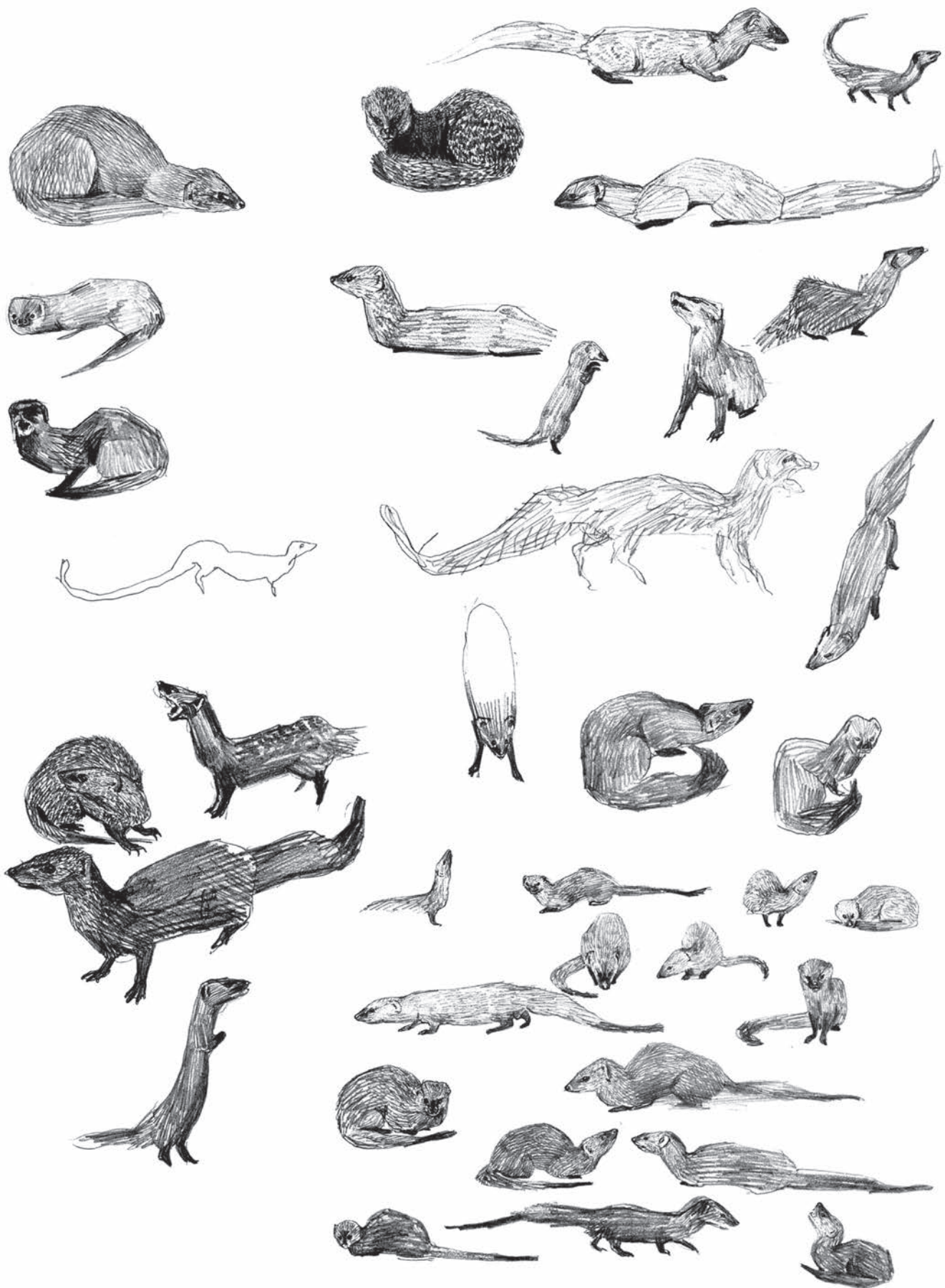
Foraging and Food Slender Mongooses are generalist carnivores, their diet predominated by small vertebrates and invertebrates. In a sample of 60 stomachs from Botswana and Zimbabwe, insects had the highest percentage occurrence (73%), represented mainly by grasshoppers, followed by termites, beetles and ants. Lizards had the next highest percentage occurrence (27%), with a wide range of species recorded, including, for example, the Southern Tree Agama *Acanthocercus atricollis* and the Variable Skink *Trachylepis varia*; murids, next highest in percentage occurrence (25%), included species of the genera *Mastomys*, *Rhabdomys* and the Large Creek Rat *Pelomys fallax* (Smithers 1971, Smithers & Wilson 1979). Ansell (1965) recorded the remains of a squirrel from one stomach. Other prey items recorded in stomachs include snakes (they are reported to take even large, poisonous snakes such as cobras and mambas; Rood & Waser 1978, Skinner & Chimimba 2005) and wild fruits, such as berries of the raisin bush (*Grewia* spp.) and wild figs (*Ficus* spp.). Feathers are occasionally found in both the stomachs and faeces of Slender Mongooses. These are among the few mongooses known to readily climb trees, and have been suggested to actively hunt birds (Bates 1905, Hinton & Dunn 1967).

Seasonal changes in diet appear evident, with insects having a higher percentage occurrence (68%) in stomachs sampled in the warm, wet months from Oct to Apr compared with the dry cold months from May to Sep (30%), corresponding to the increased abundance of insects at the onset of the rains. On the other hand, murids and reptiles had a higher percentage occurrence during the drier months, when insects were less abundant (Taylor 1969, Skinner & Chimimba 2005).

Slender Mongooses will pounce on or chase after small vertebrates, or flush insects, such as grasshoppers, from hiding and catch them in mid-air. They have been observed to move swiftly and silently when hunting, sniffing and searching visually without pausing to scrape and scratch at crevices (Ewer 1973). A captive animal would toy with its prey before delivering a single killing bite to the head/neck region (Jacobsen 1982). Small rodents appear to be consumed in their entirety, including the skin, as evidenced by the presence of heads, tails, feet and intestines in stomach contents and solid masses of hair in faeces (Rautenbach 1982), although Jacobsen (1982) noted that a captive animal would leave the skin, tail and feet. Captive Slender Mongooses show a predilection for eggs, which they handle in the same manner as Banded Mongooses *Mungos mungo*, hurling them between their back legs against a wall or other hard object in order to break them open (Jacobsen 1982, Skinner & Chimimba 2005).

A Slender Mongoose was seen feeding on the carcass of a Cape Porcupine *Hystrix africaeaustralis*; the mongoose stuck its head deep into the exposed flesh of the porcupine's neck and, after biting off a chunk of flesh, backed out and stood erect, chewing the flesh while surveying the surrounds (Bates 1990). Other authors have also recorded utilization of carrion, as in the case of Rautenbach (1982), who recorded *Cyclorrhapha* maggots in stomachs. Vaughan (1976) observed two ♂♂ and a ♀ visiting a Giraffe *Giraffa camelopardalis* kill in order to feed on fly larvae that they dug up from beneath the carcass. Slender Mongooses are known to be poultry thieves (Roberts 1951).

Social and Reproductive Behaviour Slender Mongooses are primarily solitary. In Serengeti N. P. ♂♂ hold single-male territories of approximately 50 ha in size, which usually encompass the territories of several ♀♀; female territories are approximately



Slender Mongoose *Herpestes sanguineus*.

25 ha (Rood & Waser 1978). Female territories do not overlap, and it is likely that the same applies to ♂♂, although two adult ♂♂ have been seen foraging in the same area (though this may have been a transitory association). In such cases, one animal typically proves to be heavier than the other, perhaps suggesting that dominant ♂♂ tolerate subordinates in their territory. Males also sometimes form loose, non-aggressive associations with as many as four individuals using the same home-range, which may overlap the ranges of up to six ♀♀. These coalitions exclude other ♂♂ from access to ♀♀ within a common territory, although no single individual monopolizes matings with ♀♀ within the territory. Such associations are stable in composition, with ♂♂ often closely related, and may persist for up to seven years (Waser *et al.* 1994b; see also Rood 1989). Territories may be larger in other areas; Maddock (1988) and Taylor (1970a) recorded territories up to 100 ha in size.

Slender Mongooses are often seen travelling along roads or pathways, tail low with only the dark tip raised, nose to the ground, and back arched. When pursued, the tail flips up into a vertical position. When disturbed, they may stand motionless. Both ♂♂ and ♀♀ make use of latrines for urination and defecation. Males mark with the anal gland during the mating season. Baker (1981) studied the agonistic behaviour of Slender Mongooses in captivity. Threat displays between a dominant and subordinate individual included snapping and spitting, with subordinates usually responding to the postures of dominants by turning their lowered head away and retracting their lips to show the pink gums, or by approaching in a submissive posture.

Jacobsen (1982) observed sexual behaviour in a captive pair. The ♂ followed the ♀ closely while she was in oestrus (which may last more than a week), and attempted to mount her whenever she stood still. Initial copulations were brief (30 sec), but later copulations lasted longer (150 sec). In one mating instance, the ♂ grabbed the ♀ by her ear and attempted to pull her along, before proceeding to mate with her while clasping her midriff with his forelegs. Young are born in dens, which are not used for more than 3–4 days at a time, the pups being moved from den to den. Mothers are very protective of their young, and, in captivity, ♂♂ also displayed protective tendencies, often carrying their young (Jacobsen 1982).

Five different vocalizations have been recorded in captive Slender Mongooses, including a loud, sharp 'spit', a growl, a snarl and a 'buzz', which are used in agonistic encounters; growling and spitting are produced when threatening a conspecific or warding off attackers, and snarling when two animals approach each other in attack. The fifth vocalization, a 'huh-nwe' call, is used as a distress call (Baker 1982).

Inter-specific interactions include playful interactions with hyraxes, antelopes and monkeys (Estes 1991), and foraging associations between Slender Mongooses and Pale Chanting-goshawks *Melierax canorus* have been documented (Paxton 1988, Lombard 1989, Borello & Borello 1990; and see Macdonald 1990). Social mongooses, such as Dwarf Mongooses *Helogale parvula* and Banded Mongooses *Mungos mungo*, will go on the offensive if a Slender Mongoose approaches too closely (Rood & Waser 1978).

Reproduction and Population Structure Slender Mongooses are seasonal breeders, and births appear to correspond with the wet season. In southern Africa, this corresponds to the warmer

months from Oct to Mar (Ansell 1963, Smithers 1971, Rowe-Rowe 1978a, Stuart 1981, Rautenbach 1982), while in East Africa this corresponds to either the short rains (Oct and Nov) or long rains (Feb–Apr) (Taylor 1969). Rood & Waser (1978) recorded a ♀ in Serengeti N. P. giving birth in Mar and again in Jul. In Liberia, in West Africa, Coe (1975) recorded a lactating ♀ in early Sep.

Gestation is probably in the order of 60–70 days and litter-size has been recorded as 2–4 (Taylor 1969, 1975). In Serengeti N. P. 35 young were observed in 39 female years, suggesting a mean of 0.9 young per ♀ per year (Waser *et al.* 1995). Pups grow rapidly, attaining two-thirds of their adult body weight in about 50 days. Eyes open fully at three weeks, pups begin eating solid food at four weeks and are weaned at 7–9 weeks (Jacobsen 1982). At the age of one year, Slender Mongooses are close to adult weight. Females routinely reproduce as yearlings (Waser *et al.* 1995).

In Serengeti, juveniles dispersed within their first six months, and ♂♂ appeared to disperse earlier and further; ♂♂ were only 25% as likely as ♀♀ to be captured with their mothers, suggesting earlier emigration (Waser *et al.* 1995).

Waser *et al.* (1995) suggested a juvenile survival rate of 0.63. Once established as adults, ♂♂ and ♀♀ had high survival rates: 0.82 for ♂♂ and 0.79 for ♀♀. Maximum observed longevity in the wild was eight years for both sexes (Waser *et al.* 1995). A captive animal lived to 12.6 years (Weigl 2005).

Predators, Parasites and Diseases The main predators include raptors, such as the African Hawk-eagle *Hieraaetus spilogaster*, Tawny Eagle *Aquila rapax* and Martial Eagle *Polemaetus bellicosus* (see, for example, Robinson & Stuart 1975, Steyn 1980) and mongooses are exceptionally alert to aerial predators. Larger carnivores, such as Lions *Panthera leo*, Leopards *P. pardus* and African Wild Dogs *Lycaon pictus* may also take individuals.

Relative to other herpestids, there is a wide body of information available on ecto- and endo-parasites. Taylor (1975; and see references therein), in reviewing the literature available at the time, recorded the helminth *Rictularis myonacis*, nematodes of the genera *Riticularia*, *Filaroides* and *Travassospirura*, and the cestodes *Mathevotaenia herpestis* and *M. ichneumonitis*. Pierce (1972) recorded the protozoan parasite *Babesia* sp., and Iori & Lanfranchi (1996) documented the Slender Mongoose as a new host for *Oxinema* sp. Haeselbarth *et al.* (1966) mention the following arthropod parasites: *Echinophaga bradyta*, *E. gallinacea*, *Pulex irritans*, *Ctenocephalides felis*, *Synosternus burtoni* and *Listropsylla agrippinae*. Horak *et al.* (2000) recovered five species of ixodid ticks from an animal in Kruger N. P. and another animal from Mpumalanga in South Africa: *Haemaphysalis spinulosa*, *H. zumpti*, *Ixodes* sp., *Rhipicephalus appendiculatus* and *R. zambeziensis*; *H. leachi* has been recorded from a specimen from Congo (Bequaert 1930). Hoogstraal *et al.* (1992) recorded a new species, *H. subterra*. Herrin & Tipton (1976) mention the tick *Laelaps liberiensis* from a specimen from Liberia.

In East Africa, the Slender Mongoose is said to be very prone to rabies (Maberly 1960). They may also have antibodies for various rickettsias, including *Dermacentroxenus akari*, which causes a tick-borne disease known as rickettsialpox (Heisch *et al.* 1962).

Conservation IUCN Category: Least Concern. CITES: Not listed.

Cunningham & Zondi (1991) listed this species among those used in traditional medicine in KwaZulu–Natal. Slender Mongooses have also been recorded in bushmeat markets, as in villages in the Classified Forest of Diecké (Colyn *et al.* 2004), although Cansdale (1946) noted that because of its strong odour it was the only carnivorous mammal not eaten. Otherwise, Slender Mongooses are common and widespread, and present in numerous protected areas across their range.

Measurements

Herpestes sanguineus

TL (♂♂): 595 (560–652) mm, n = 25
 TL (♀♀): 555 (506–600) mm, n = 19
 T (♂♂): 278 (240–299) mm, n = 25
 T (♀♀): 261 (233–272) mm, n = 19
 HF c.u. (♂♂): 65 (60–69) mm, n = 25
 HF c.u. (♀♀): 58 (52–60) mm, n = 18
 E (♂♂): 25 (21–28) mm, n = 25
 E (♀♀): 24 (22–25) mm, n = 18
 WT (♂♂): 637 (523–789) g, n = 24
 WT (♀♀): 459 (373–565) g, n = 15
 Zimbabwe (Smithers & Wilson 1979)

TL (♂♂): 555 (410–630) mm, n = 37
 TL (♀♀): 524 (425–590) mm, n = 37
 T (♂♂): 268 (194–310) mm, n = 35
 T (♀♀): 263 (212–290) mm, n = 38
 HF c.u. (♂♂): 59 (45–70) mm, n = 34
 HF c.u. (♀♀): 54 (44–60) mm, n = 37
 E (♂♂): 23 (14–28) mm, n = 35
 E (♀♀): 22 (15–26) mm, n = 35
 WT (♂♂): 531 (363–650) g, n = 14
 WT (♀♀): 402 (277–498) g, n = 11
 South Africa (Rautenbach 1982)

Skull measurements:

GLS (♂♂): 65.0 (60.0–70.4) mm, n = 52
 GLS (♀♀): 63.0 (58.5–68.0) mm, n = 30
 GWS (♂♂): 33.3 (30.0–37.6) mm, n = 52
 GWS (♀♀): 31.1 (28.3–34.4) mm, n = 30
 Kenya (Taylor & Goldman 1993)

Key References Skinner & Chimimba 2005; Taylor 1969, 1975; Waser *et al.* 1994b, 1995.

Michael Hoffmann & Mark E. Taylor

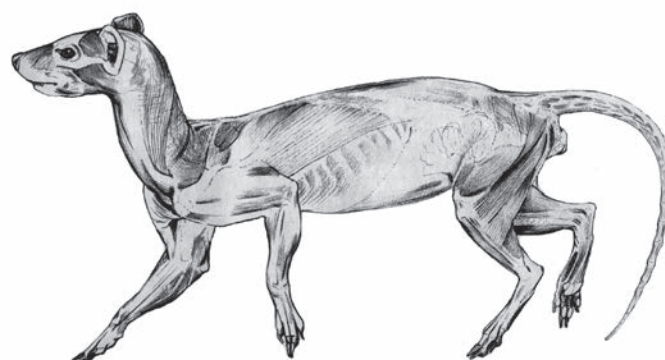
GENUS *Bdeogale*

Bushy-tailed Mongooses (Dog Mongooses)

Bdeogale Peters, 1850 Spenerische Z., 25 June 1850 (unpaginated).



Jackson's Mongoose *Bdeogale jacksoni*.



Jackson's Mongoose *Bdeogale jacksoni* myology.

The genus contains four species: the Bushy-tailed Mongoose *Bdeogale crassicauda*, the Sokoke Bushy-tailed Mongoose *B. omnivora*, Jackson's Mongoose *B. jacksoni* and the Black-legged Mongoose *B. nigripes*.

Mongooses in the genus *Bdeogale* occur in eastern and central Africa. The Bushy-tailed Mongoose occurs in eastern Africa, from E Zimbabwe to Kenya (and including Zanzibar). The Sokoke Bushy-tailed Mongoose, found in the coastal forests of Kenya and NTanzania,

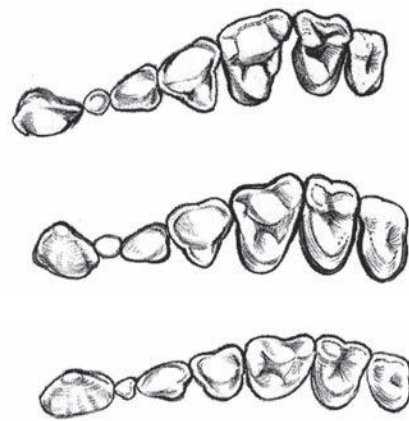
is considered by some authors (e.g. Wozencraft 1993, 2005) to be a subspecies of the Bushy-tailed Mongoose with a distinctively yellowish-orange underfur. Jackson's Mongoose occurs in upland forests in C Kenya, ETanzania and E Uganda and has been included by some authors (e.g. Kingdon 1977) as a subspecies of the Black-legged Mongoose *Bdeogale nigripes*, which is found primarily in the forested regions of N Angola, parts of DR Congo and north-west to Nigeria.

Representatives of this genus are characterized by having a generally dark brown to blackish pelage with distinctly dark legs and feet and four toes on both fore- and hindfeet. The tail is bushy rather than tapered and relatively uniform in colour without any distinctive coloured tip. Head is generally short and rounded and ears rounded. In the skull, the orbits are not closed posteriorly, and the anterior portion

of the bulla is not inflated. Molariform teeth are broad and adapted for crushing rather than shearing; hypocone present. Dental formula is $I^{3/3}, C^{1/1}, P^{4/4}, M^{2/2} = 40$. Species are primarily insectivorous, but will eat fruits, small vertebrates and carrion. Members are solitary, and primarily nocturnal (though may forage during the day). They are adapted for a walking-trotting form of locomotion.

The genera *Bdeogale* and *Galeriscus* have been considered as separate genera by some earlier authors, the latter genus having been created by Thomas (1894b) to include *jacksoni*; several authors included also *nigripes* (e.g. see Rosevear 1974). Coetzee (1977) used *Galeriscus* as a subgenus for *nigripes* and *jacksoni*. *Bdeogale* shares many dental features with *Ichneumia* (Pocock 1919), and molecular data suggest a close relationship with *Ichneumia*, *Rhynchogale* and *Cynictis* (Perez *et al.* 2006, Patou *et al.* 2009).

Mark E. Taylor



Upper right teethrows of (top to bottom) Bushy-tailed Mongoose *Bdeogale crassicauda*, Sokoke Bushy-tailed Mongoose *Bdeogale omnivora* and Jackson's Mongoose *Bdeogale jacksoni*.

Bdeogale crassicauda BUSHY-TAILED MONGOOSE

Fr. Mangouste à queue touffue; Ger Buschschwanzichneumon

Bdeogale crassicauda Peters, 1852. Monatsber. K. Preuss. Akad. Wiss. Berlin 1852: 81.

Africa orient., Tette, Boror, 17–18 Lat. Austr. (pg. 82). Restricted by Moreau *et al.* (1946: 410) to 'Tette' [Mozambique].



Bushy-tailed Mongoose *Bdeogale crassicauda*.

Taxonomy As many as five subspecies of the Bushy-tailed Mongoose have been described (Coetzee 1977, Taylor 1987), but they are poorly defined and are based more on distribution than major structural differences (Taylor 1987; and see Geographic Variation). The closely related Sokoke Bushy-tailed Mongoose *B. omnivora* is treated as a subspecies of the Bushy-tailed Mongoose by some authors (Taylor 1987, Wozencraft 1993, 2005, Engel & Van Rompaey 1995). The four subspecies listed here are provisional, and require critical revision.

Synonyms: *nigrescens*, *puisa*, *tenuis*. Chromosome number: not known, but likely $2n = 36$ as in other *Bdeogale* (Wurster & Benirschke 1968).

Description A medium-sized mongoose with uniform brownish coat, darker limbs and feet and bushy tail about 60% of head and body length. Head rather rounded for a mongoose, giving the appearance of a short muzzle, and the rhinarium divides the hairy portions of the upper lip. Ears rounded. The eye has a horizontal pupil with greyish-brown iris. Underfur dense and greyish-buff in southern forms, grading to yellowish-brown in northern races. Guard hairs about 5 mm long on the forehead, increasing in length towards the rump where they reach about 45 mm; banded with two or three whitish

annulations although the degree and extent of banding is variable (Sale & Taylor 1970, Skinner & Chimimba 2005). Limbs are covered in uniform short black hair. Tail length is less than 300 mm, bushy towards the distal third (Peters 1852) with guard hairs up to 55 mm long. Four digits on both fore- and hindfeet. The relatively short claws are robust. The forefoot has a single symmetrical ovoid pad while the hindfoot pad has two, a larger ovoid distal pad and a distinct smaller proximal lobe. Longest claw length 11 mm (Peters 1852). There is no appreciable difference in size between ♂♂ and ♀♀. The vulva is only a short distance below or in front of the anal sac. The baculum is about 15 mm long. Two pairs of abdominal nipples.

Skull broadest at level of the glenoid articulation, postorbital bars never complete and supraoccipital crest well developed. Sagittal crest high at back of braincase, tapering anteriorly and disappearing at level of the postorbital constriction. Zygomatic arches robust, suggesting well-developed masseters, and the high coronoid process of the mandible indicates a large area for insertion of temporalis muscle (and strong jaw action).

Upper incisors long, well separated, and forming a curved row; lower incisors lie tightly together. Upper canines nearly straight with sharp cutting edges in front and behind though in some specimens they are markedly worn. First premolars small and peg-like, second premolars like members of the genus *Herpestes*, while posterior premolars and molars are broadly rectangular in shape.

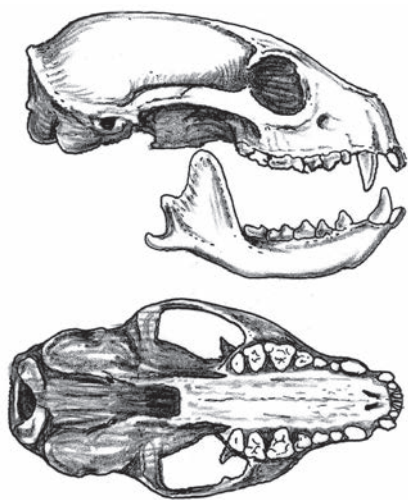
Geographic Variation

B. c. crassicauda: Mozambique, E Zimbabwe, and north through Malawi.

B. c. puisa: NE Mozambique and E Tanzania.

B. c. tenuis: Zanzibar.

B. c. nigrescens: inland at Lukenya near Nairobi in Kenya. This subspecies appears darker than the other subspecies partly due to the darker underfur; tail with dense covering of dark hairs giving a 'bottle-brush' appearance (Sale & Taylor 1970).



Lateral and palatal views of skull of Bushy-tailed Mongoose *Bdeogale crassicauda*.

Populations from the south, *B. c. crassicauda* and *B. c. puisa*, may be slightly larger, though the range in body and cranial measurements for other mongooses in East Africa suggest that this is possibly due to the small sample of published measurements (Peters 1852, Sale & Taylor 1970, Skinner & Chimimba 2005). Sale & Talyor (1970) detail the coat characteristics of the four subspecies.

Similar Species

Bdeogale omnivora. Coastal forests from N Tanzania to coastal S Kenya. Slightly smaller, and generally more yellowish due to the distinct orange underfur and brown rather than black portions of guard hairs (Sale & Taylor 1970).

B. jacksoni. Highland regions of Kenya, SE Uganda, and the Udzungwa Mtns in Tanzania. Head and body length greater than 500 mm (Kingdon 1977).

Paracynictis selousi. Sympatric in Zimbabwe and Mozambique. Larger; greyish, with white end to the tail; P4, M1 and M2 are noticeably thicker and rounded.

Rhynchogale melleri. Woodland habitat from N Tanzania south to NE South Africa. Individuals may have partially white tails, but pelage overall more brown; distinct crest-like parting on either side of neck; no central vertical slit on front of rhinarium.

Distribution Endemic to Africa, the Bushy-tailed Mongoose ranges from the Lukenya foothills of SE Kenya southwards through Tanzania, Malawi and SE Zambia to N and E Zimbabwe (extending about as far west as L. Kariba; see Ansell 1978) and C Mozambique, their most southerly limit of distribution at around 20° 10' S (Taylor 1986, 1987). Also present on Zanzibar (Pakenham 1984, Stuart & Stuart 1998c, Goldman & Winther-Hansen 2003). Camera-trapping surveys have resulted in many new distribution records, particularly in Tanzania including records from Ngorongoro Conservation Area, and from Biharamulo-Burigi-Kimisi G. R. and Mahale Mountain N. P. in the west (Pettorelli *et al.* 2010) and from Udzungwa N. P. (F. Rovero pers. comm.). These records provide evidence that the species is more widely distributed and more common than previously thought, and complement what has been considered an outlying record from Mweru Wantipa in the north of Zambia (Ansell



Bdeogale crassicauda

1978). The species has also apparently been recorded from DR Congo, where Ansell (1974) reported on two specimens (originally identified as Meller's Mongoose *Rhynchogale melleri*) in the Musée Royal de l'Afrique Centrale, Tervuren, from Kansenia (10° 19' S, 26° 02' E) and from Katentania (10° 19' S, 25° 55' E).

The Bushy-tailed Mongoose has been reported from coastal sites in Yemen (Nader & Al-Safadi 1991) where it may have been introduced from traders carrying animals from eastern Africa or Zanzibar; however, Simmons (1995) states that this record requires confirmation using cranial features, inferring that the juvenile female specimen in question could represent the White-tailed Mongoose *Ichneumia albicauda*.

Habitat The Bushy-tailed Mongoose is found in a variety of habitats through its range. It is found in *Acacia* woodlands in Mozambique, on rocky outcrops in NE Zimbabwe and Kenya, in *Brachystegia* woodland in parts of Zimbabwe and Malawi and in riverine woodlands. This species was photographed in most habitats within Udzungwa Mountains N. P., including montane and bamboo forest up to 1850 m (De Luca & Mpunga 2005) and in coral-rag thicket and ground-water forest in Zanzibar (Goldman & Winther-Hansen 2003). There do not appear to be obvious explanations as to its habitat preferences and consequent distribution as it appears to occur in disjunct populations in a variety of habitats.

Abundance In spite of extensive collections of mongooses through eastern Africa during the past 150 years, there are relatively few specimens of this species in museum collections, and it has generally been reported as uncommon (Ansell 1978, Smithers & Wilson 1979, Ansell & Dowsett 1988). Bushy-tailed Mongooses are very rarely observed in the wild: K. Howell (pers. comm.) has not seen this species in ten years of fieldwork, and D. Moyer (pers. comm.) has only seen it twice. John Sale collected two animals in Feb 1965, and Sale & Taylor (1970) collected seven animals in Nov and Dec 1967 at Lukenya, 37 km south-east of Nairobi (from

whence they described the subspecies *nigrescens*), suggesting that the species is relatively easy to catch when present. Indeed, the advent of camera-trapping has shown this species to be more common than supposed. Pettorelli *et al.* (2010) photographed the species in 31 different locations and five different study areas in Tanzania during 11 surveys. A photo-trapping exercise in the Udzungwa Mts took 79 photographs of this species in 674 trap-nights; at 8.5 trap-nights per photo this was by far the most frequently recorded carnivore (by contrast, 126 trap-nights per photo for Leopard *Panthera pardus*; De Luca & Mpunga 2005). This species was also the most common animal camera-trapped in other parts of the Eastern Arc Mts, including the Ulugurus and Ngurus (F. Rovero pers. comm.), and among the most frequently captured during a live-trapping survey in Arusha N. P. (Martinoli *et al.* 2006). J. Kingdon (pers. comm.) also reports the species was relatively common in densely wooded areas along Tanzanian river courses, in many pockets throughout the coastal littoral and around hilly and lower montane areas immediately inland from the coast.

Adaptations The Bushy-tailed Mongoose appears to be modified towards a cursorial form of locomotion. The proportions of the limb bones are indicative of an animal's normal gait, and longer distal elements (metapodials and epipodials) are indicative of cursorial habitats. It lacks first digits, and metacarpals II, III and IV are almost equal in length indicating a digitigrade foot (Taylor 1971a, 1974, 1976, 1988). Teeth are adapted for an insectivorous to omnivorous diet, the molariform teeth being broad and rounded.

Foraging and Food Bushy-tailed Mongooses are omnivorous, and insects, reptiles, amphibians, mice, millipedes, spiders, scorpions, snails and herbage have been found in their stomachs (Smithers & Wilson 1979). It is probable that they are largely opportunistic and eat insects when they are abundant during the wet seasons and eat vertebrate prey during the dry seasons together with any carrion or other food that may be available (Taylor 1986). Information from an examination of microwear of their teeth indicates a 'puncture-crushing' type of mastication (Taylor & Hannam 1987), which is supported by the generally robust nature of the molariform teeth. Teeth of several individuals collected and examined in museum collections were very worn, indicating that a reasonable amount of sand and dirt particles are ingested with the food, causing significant wear. Captive animals were offered a wide selection of fruit, live mice and snakes but were generally inept at catching vertebrates, though eventually they used a neck bite and shaking to kill prey items. These were then held between the forefeet while the mongoose tore pieces off to ingest (Sale & Taylor 1970). Bushy-tailed Mongooses are considered to be nocturnal (as evidenced by camera-trapping surveys), but they may be active during the day (and this is partly borne out by their occurrence in the caches of bones beneath two Crowned Eagle *Stephanoaetus coronatus* nests; J. Kingdon pers. comm.).

Social and Reproductive Behaviour Bushy-tailed Mongooses are primarily solitary, although one would expect to encounter ♀♀ with young for a few weeks or months after birth. Ansell & Dowsett (1988, 1991) mention four seen together at around 16:00h on the Nyika Plateau in Malawi, probably a ♀ and her three young. One of

the most distinctive features of this species is its apparent docility (Sale & Taylor 1970, Kingdon 1977). When animals were live-trapped, they did not behave aggressively, neither barking nor trying to bite. In large cages, where one was observed and filmed for several days, the animal was curious, investigated the author and did not try to hide.

Reproduction and Population Structure Little is known but ♀♀ caught in Zimbabwe in Aug, Sep, Oct and Dec showed no signs of breeding (Skinner & Chimimba 2005). It is probable that the breeding season coincides with the wet season, which varies from two seasons in Kenya to one in Zimbabwe. This presumably affects the reproductive capabilities of the species across its range.

Predators, Parasites and Diseases A Spotted Hyaena *Crocuta crocuta* has been photographed carrying this species in its jaws. Caches of bones collected in 1989 from beneath two Crowned Eagle nests in Matumbi revealed that this mongoose was their third most frequent prey (after monkeys and Natal Red Duikers *Cephalophus natalensis*) (J. Kingdon pers. comm.).

Guinea-worms of the genus *Dracunculus* have been recovered from a captive animal, which had been caught near the confluence of the Lupande and Luangwa rivers, 13°0'S, 31°49'E, in Zambia. The female worm measured 97 cm and was found loosely coiled against the muscles of the inside right hindleg (C. Ogden in litt.).

Conservation IUCN Category: Least Concern. CITES: Not listed.

The Bushy-tailed Mongoose has a relatively wide distribution in a variety of habitats, and although it is not commonly seen, recent camera- and live-trapping work in the Udzungwa Mts and elsewhere in Tanzania suggests that they are not rare. They are present in several protected areas across their range, including Selous N. P., Arusha N. P., Mahale Mountain N. P. and Udzungwa Mountains N. P. (Tanzania), and there is no reason to believe that they are currently threatened.

Measurements

Bdeogale crassicauda

TL (♂♂): 693 (655–740) mm, n = 3
 TL (♀♀): 695 (672–720) mm, n = 4
 T (♂♂): 259 (229–285) mm, n = 3
 T (♀♀): 249 (230–265) mm, n = 4
 HF c.u. (♂♂): 89 (87–94) mm, n = 3
 HF c.u. (♀♀): 89 (87–90) mm, n = 4
 E (♂♂): 37 (34–39) mm, n = 3
 E (♀♀): 37 (33–40) mm, n = 4
 WT (♂♂): 1.93 (1.82–2.10) kg, n = 3
 WT (♀♀): 1.57 (1.34–1.77) kg, n = 4
 Zimbabwe (Smithers 1983)

HB (♂♂): 407 (390–420) mm, n = 3
 HB (♀♀): 380, 385 mm, n = 2
 T (♂♂): 230 (220–240) mm, n = 3
 T (♀♀): 220, 240 mm, n = 2
 HF c.u. (♂♂): 78 (77–79) mm, n = 3
 HF c.u. (♀♀): 75, 75 mm, n = 2
 WT (♂♂): 1.3 (1.1–1.6) kg, n = 3
 WT (♀♀): 1.1, 1.5 kg, n = 2
 Arusha N. P., Tanzania (Martinoli *et al.* 2006)

Skull measurements:

GLS: 84.5 (80.8–87.9) mm, n = 6

GWS: 46.6 (44.1–48.5) mm, n = 6

Throughout range (Sale & Taylor 1970)

Key References De Luca & Mpunga 2005; Skinner & Chimimba 2005; Taylor 1986, 1987.**Mark E. Taylor*****Bdeogale jacksoni* JACKSON'S MONGOOSE**

Fr. Mangouste de Jackson; Ger. Jackson Ichneumon

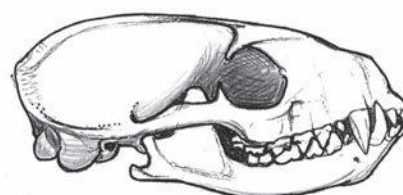
Bdeogale jacksoni (Thomas, 1894). Ann. Mag. Nat. Hist., ser. 6, 13: 522. Mianzini, Masailand, 8000 feet.Restricted by Moreau *et al.* (1946) to 'a few miles E.S.E. of Naivasha, 9000 feet', Kenya.Jackson's Mongoose *Bdeogale jacksoni*.

Taxonomy Monotypic. Originally described as *Galeriscus Jacksoni* (with a capital J) by Thomas (1894b), who created a new genus because of a supposed similarity with the South American Grison (*Galictis* sp.), a mustelid. Named after the collector of the type specimen F. J. Jackson. Although Matschie (1895) and Pocock (1916b) made *Galeriscus* synonymous with *Bdeogale*, Thomas (1928b) recognized his mistake but retained the genus *Galeriscus* for *G. jacksoni* as did Allen (1939), Sanderson (1940), Schouteden (1945), and Rosevear (1974) for *G. nigripes*. Perret & Aellen (1956) and Coetzee (1977) used *Galeriscus* as a subgeneric name for the species *nigripes* and *jacksoni* on the strength of the larger body size and larger last lower molar. Jackson's Mongoose was often regarded as a montane isolate of the Black-legged Mongoose *Bdeogale nigripes* and considered a subspecies of Black-legged Mongoose by Hayman (in Sanderson 1940) and Kingdon (1977), and a subspecies of the Bushy-tailed Mongoose *Bdeogale crassicauda* by J. A. Allen (1914). Recognized as a valid species by Hollister (1918), G. M. Allen (1939), Coetzee (1977), Wozencraft (1993, 2005) and Kingdon (1997). Synonyms none. Chromosome number: not known, but likely $2n = 36$ as in other *Bdeogale* (Wurster & Benirschke 1968).

Description A large, silvery-grey, rather long-legged mongoose with bushy tail. Muzzle blunt. Rhinarium with median groove running down the upper lip. Muzzle and chin brownish-white. Eyes surrounded by a few brown hairs. Ears round, broad and well haired, but less prominent than in other species of *Bdeogale*. Hairs of ears

outside grizzled grey, inside yellowish-white. Cheeks, throat and sides of neck yellowish. Crown grizzled grey. Dorsal pelage long, dense, glossy, grizzled black and white. Dorsal hairs more than 20 mm with basal part white, middle third dark, terminal third white. Underfur dense and woolly. Ventral pelage light grey. Legs distal to elbow and knee blackish-brown. Hind- and forefeet with four digits, hallux and pollex missing. Metacarpal and metatarsal pads naked. Claws thick and strong. Tail ca. 57% (range 53–60; n = 7) of head and body length, bushy with hairs longer than on back. Young but breeding animals may be well below average adult size, probably due to a slow and prolonged adult growth (Kingdon 1997).

Jackson's Mongoose is smaller than the Black-legged Mongoose, but has relatively large teeth (length M_2 : *B. nigripes*: 7.3 mm [range 6.6–8.1, n = 19]; *B. jacksoni*: 7.0 mm [range 6.2–7.5, n = 9]; *B. crassicauda*: 5.35 mm [range 4.8–6.0, n = 29]). The length of both upper and lower last molars of the Black-legged Mongoose and Jackson's

Lateral view of skull of Jackson's Mongoose *Bdeogale jacksoni*.



Mongoose is smaller than that of the Bushy-tailed Mongoose. Whereas there is some overlapping in the case of M^2 , there is none with M_2 .

Geographic Variation None recorded.

Similar Species

Bdeogale crassicauda. Sympatric in Tanzania. Smaller; lacks the yellowish colouring on the cheeks, throat and sides of neck.

B. nigripes. Allopatric, occurring in the central African rainforests. Larger, shorter haired, and silvery-grey in colour.

B. omnivora. Restricted to the coastal forests of Kenya and Tanzania; it is not clear whether or not the two species may be sympatric. Smaller, with distinctive yellow to orange underfur and limbs dark brown to black.

Ichneumia albicauda. Woodland and savanna habitats in sub-Saharan Africa from Senegal eastwards to the Horn of Africa, and southwards to SE South Africa. Larger (up to 6 kg); five digits on each foot.

Distribution Endemic to Africa, and known only from C and S Kenya, including Mt Elgon, SE Uganda (Kingdon 1997) and Matundu Forest in the Udzungwa Mts (900 km to the south) in SC Tanzania (De Luca & Mpunga 2005, De Luca & Rovero 2006). A mongoose corresponding to the description of Jackson's Mongoose was reported at the edge of bamboo forest at 1700 m in Kihulula, Mwanihana forest, which is at an altitude significantly higher than Matundu. If this record is confirmed, it would be in habitat more similar to the montane forest and bamboo reported for the Kenyan records of the Aberdares and Mt Kenya (De Luca & Rovero 2006). It is possible that this species occurs in and around other massifs within the Eastern Arc Mts, including the Uluguru, Nguru and Usambara mountains. Museum specimens are few and originate from Kijabe Station and Murang'a, Aberdare Range; Elgeyo Forest; Mt Kenya; between Murang'a and Nyeri; Naivasha region; and Yala (Lukosa) R.

Habitat Montane forests and bamboo zones up to 3300 m in Kenya, lowland forest mosaics immediately south of Mt Elgon, in Kenya and Uganda (Kingdon 1997), and lowland semi-deciduous forest (about 300–400 m) at the base of the Udzungwa Mts (De Luca & Mpunga 2005, De Luca & Rovero 2006). The presence of remains of rodents of the genera *Dasymys* and *Otomys* in stomachs suggests that they hunt frequently in the thick herbaceous growth around swamps (Kingdon 1977).

Abundance Rare, with a limited distribution range. The Tanzanian population seems to be highly localized: camera-trapping studies conducted over three years in 76 sites throughout the Udzungwa Mts recorded Jackson's Mongoose in only five sites, all within Matundu Forest (De Luca & Rovero 2006).

Adaptations Mainly nocturnal and crepuscular. The animal was photographed 25 times in the Udzungwa Mountains N. P. between 19:00h and 06:00h; 73% of the photographs were taken between 19:00h and 00:00h (De Luca & Rovero 2006). The small amount of ants in subadults' diet (see Foraging and Food) could suggest that coping with well-defended columns of army ants (*Anona* sp.) depends on maturity and learning, which implies that adaptation to this diet could be relatively recent. However, the shorter, hairier ears contrast with larger, barer ears in the Bushy-tailed Mongoose, and the dense, woolly coat suggests improved protection against the bites of army ants. These features could imply species-specific adaptation against the defensive attacks of one of their preferred foods. The very light colouring and white tail of this species make it unusually conspicuous. Vulnerability to attack by Verreaux's Eagle-owl *Bubo lacteus* could be mitigated by this species' preference for very dense vegetation. The adaptive value of such conspicuousness is not known. When the animal is surprised or harassed, scent is released from the anal glands and the tail is fluffed out. A captive ♀ made no noises other than a soft growl and a snort (Kingdon 1977).

Foraging and Food Omnivorous. In the Aberdare Mts, Kenya, analysis of some 40 scats revealed that 40% of the adult diet consisted of insects, principally workers of army ants but also beetles, caterpillars, weevils, millipedes, snails, lizards, birds' eggs and carrion. More than 50% of the diet comprised rodents (genera *Otomys*, *Dasymys* and *Praomys*), and about 80% of the juveniles' diet is rodents (*Otomys*, *Lophuromys*, *Mus*, *Praomys*) complemented with beetles, lizards, birds and a few ants (Kingdon 1977). A captive specimen ignored a live bird but took a dead one, crushing bone and tissue slowly with its molars while sometimes steadying the carcass with a paw. Feeding was nearly always conducted while standing (Kingdon 1977).

Social and Reproductive Behaviour Not infrequently seen in pairs, occasionally in groups of four. Latrines possibly used by both adult and younger animals (Kingdon 1977).

Reproduction and Population Structure No information available.

Predators, Parasites and Diseases No information available.



Jackson's Mongoose *Bdeogale jacksoni*.

Conservation IUCN Category: Near Threatened. CITES: Not listed.

Given its apparent dependence on forest habitat, the main threat to this species is likely to be ongoing forest loss. In Kenya, Jackson's Mongoose is confirmed in Aberdare N. P. and Mt Kenya N. P., and is also likely to occur in Mt Elgon N. P. on the border with Uganda. In Tanzania, all confirmed localities lie within protected areas, including the Udzungwa Mountains N. P. and Matunda F. R., although it may well occur in other smaller forest reserves in other parts of the Eastern Arc Mts. De Luca & Rovero (2006) recommend full protection of adjacent forests (Matundu F. R. outside Udzungwa Mountains N. P.; and Iyondo and Udzungwa Scarp Forest Reserves), and that other East African ground-water-dependent forests (including those near Matundu and Nambiga Forest Reserves) be surveyed for the presence of Jackson's Mongoose. Similarly, surveys of other mountain forests in the Kenyan highlands should also be undertaken.

Measurements

Bdeogale jacksoni

HB: 536 (508–571) mm, n = 8

T: 299 (283–324) mm, n = 7

HF c.u.: 102 (86–108) mm, n = 8

E: 29 (23–35) mm, n = 3

GLS: 109.6 (105.1–113.9) mm, n = 12

GWS: 56.3 (52.5–59.8) mm, n = 10

Museum specimens (AMNH, BMNH, FMNH, NMNH)

Kingdon (1997) gives WT as 2.0–3.0 kg

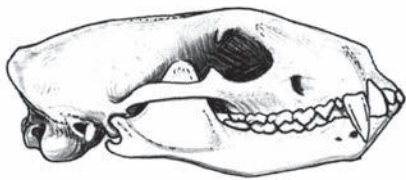
Key References De Luca & Mpunga 2005; De Luca & Rovero 2006; Kingdon 1977, 1997.

Harry Van Rompaey & Jonathan Kingdon

Bdeogale nigripes BLACK-LEGGED MONGOOSE

Fr. Mangouste à pattes noires; Ger. Schwarzfussichneumon

Bdeogale nigripes Pucheran, 1855. Rev. Mag. Zool. 7 (2): 111. 'Gubon' [= Gabon].



Lateral view of skull of Black-legged Mongoose *Bdeogale nigripes*.

Taxonomy Monotypic. Thomas (1894b) created the genus *Galeriscus* to describe a newly discovered mongoose from East Africa *G. jacksoni*, which he mistook for a mustelid. Although subsequently recognized as a mongoose, several authors (Allen 1939, Sanderson 1940, Schouteden 1945, Rosevear 1974) retained genus *Galeriscus* for both *nigripes* and *jacksoni*; the genus *Bdeogale* was accepted by J. A. Allen (1924), Kingdon (1977) and Wozencraft (1993, 2005). There is some question as to the position of *jacksoni*, which has been considered by Hayman (in Sanderson [1940]) and Kingdon (1977) to be a subspecies of *B. nigripes* (see also *Bdeogale jacksoni* species profile).

Examination of endocranial casts shows that the Black-legged Mongoose is unusual among herpestids in lacking a well-developed posterior ectosylvian sulcus and in having a better developed posterior suprasylvian sulcus and less expanded temporal lobe. One out of three examined museum specimens has what appears to be an expanded coronal gyrus with a dimple in it, but its functional significance is somewhat of an enigma. Radinsky (1975a) thought that perhaps more than one species might be included in *B. nigripes*. Synonyms none. Chromosome number: $2n = 36$ (Wurster & Benirschke 1968).

Description A large, short-haired, silvery-grey, rather long-legged mongoose. Muzzle blunt with large rhinarium and a median groove continuing in a narrow, naked strip parting the upper lip. Forehead and muzzle short-haired and lighter coloured than body. Ears short, wide, shallow and hairy on both sides. Pelage greyish-



Black-legged Mongoose *Bdeogale nigripes*.

white but sometimes brownish-red. Dorsal pelage and hair on flanks short and close-lying, with guard hairs 20 mm or less in length. Underfur dense, fine and short with yellow to brown hairs 10–12 mm long. Hairs annulated with white and brown rings and white tip. Colour of throat and belly varies from greyish-white to dark brown. Legs and feet distinctly darker in colour, from light brown to mostly brownish-black. Hind- and forefeet with four slightly webbed digits; hallux and pollex missing. Soles hairy up to the pads. Tail (ca. 63% of HB) white to yellowish, moderately bushy and slightly tapering. Young appear white and long-haired, becoming gradually darker and shorter-haired with age. There are two pairs inguinal nipples (F.A. Ulmer pers. comm.).

Geographic Variation Hayman (in Sanderson 1940) found no appreciable differences between specimens from Nigeria, Cameroon and DR Congo, but Rosevear (1974) felt that on the basis of size, some aspects of colouration and pelage length, the population of E DR Congo merits differentiation. Skull measurements show that specimens from DR Congo are slightly smaller.



Similar Species

Bdeogale jacksoni. Allopatric, occurring in C and S Kenya, SE Uganda and SC Tanzania. Smaller; dorsal pelage longer.

Ichneumia albicauda. Woodland and savanna habitats in sub-Saharan Africa from Senegal eastwards to the Horn of Africa, and southwards to SE South Africa. Larger (up to 6 kg); five digits on each foot.

Distribution Found only in the central African rainforests from the Cross R. in SE Nigeria westward to Cameroon and Central African Republic and southward to Equatorial Guinea, Gabon, Congo and DR Congo, north of the Congo R. eastwards to the western Rift Valley in DR Congo. The species has been reported from Angola (e.g. Hill & Carter 1941). Bocage (1865, 1882, 1889) cites specimens from the district of Duque de Bragança, Caconda and Humbe, Seabra (1908) from an unknown locality, and Themido (1928) from Cassôco-Benguela. Unfortunately, the specimens could not be examined (all were destroyed in a fire), and because skins of Black-legged Mongooses can be confused with those of Selous's Mongoose *Paracynictis selousi*, the species is rejected from Angola by Crawford-Cabral (1989a).

Habitat Dense ground-scrub in deep, tall, deciduous forest (Sanderson 1940) to more than 1000 m. Not usually found in disturbed forest.

Abundance Most authors consider Black-legged Mongooses to be rare or very rare (Bates 1905, Jeannin 1936, Eisentraut 1973). Widespread and more common in the east and south of its range, in Congo and Gabon (Malbrant & MacLachy 1949). In the Ituri Forest, DR Congo, Bambuti pygmies hunting with dogs captured 28 individuals in 53 hunts, representing ca. 25% of all carnivores (Hart & Timm 1978).

Adaptations Largely terrestrial, but a specimen was seen moving around with great agility in a tree 15 m above ground, stalking a

young Potto *Perodicticus potto* at night (Charles-Dominique 1977). A hunted specimen took refuge in a hollow tree trunk on the ground (Durrell 1953). Nocturnal according to pygmies of NE DR Congo, although according to some it is also active by day. Ba'aka pygmies report that this species sleeps in holes between the roots of big trees and in dens of Brush-tailed Porcupines *Atherurus africanus* after killing them (Carpaneto & Germi 1989).

The large molar teeth may be related to the insectivorous diet (Kingdon 1977) but the large, straight, dagger-like upper canines point to the ability to tackle larger prey. Bequaert (1922) thought it likely that the Black-legged Mongoose forages on dead ants since it has no adaptations to devour them without being bitten or stung, but according to Kingdon (1977) it is likely that the peculiar fur, the short woolly ears and the well-plushed muzzle and feet protect all parts of the animal against soldier ants and termites. The light, conspicuous colouring may be related to an offensive smell. When surprised or threatened, scent is released from the anal glands and the tail is fluffed out.

Foraging and Food Omnivorous. In Dzanga-Sangha, Central African Republic, 86% of 21 scats contained arthropods (mostly ants, termites, beetles and orthopterans), 48% held mammalian prey (mostly shrews, but also small rodents, squirrels, porcupines and a Long-nosed Mongoose *Xenogale naso*), 14% herpetofauna (snakes, lizards and anurans) and 5% fruit (Ray & Sunquist 2001). According to the pygmies of NE DR Congo, rodents (primarily Brush-tailed Porcupines), insects, ants, termites, snakes, mushrooms, fruits (bananas, oil palm fruit) and carrion are favoured prey items (Carpaneto & Germi 1989). Termites are an important food item (Verschuren 1972), and termites and driver ants (*Dorylus* and *Myrmecaria* sp.) were found in the stomachs of three of nine specimens examined by Bequaert (1922). Sanderson (1972) mentions a wild specimen stalking a caged squirrel. Kingdon (1997) also cites frogs, snails and crabs as dietary items.

Captive specimens seized a guinea-pig by various parts along its back and by the leg using their forepaws in an attempt to hold it. They bit it almost everywhere while directing their biting to the head several times, then seized it by the throat, and delivered the killing bite while holding it down with the forelegs (Eisenberg & Leyhausen 1972). A cornered wild specimen growled, bared its teeth, barked and defended its prey like a dog (Sanderson 1972).

Social and Reproductive Behaviour Solitary, but often seen in pairs. Latrines may be used (Kingdon 1977, but in reference to Jackson's Mongoose *B. jacksoni*). Nothing else is known of their social behaviour.

Reproduction and Population Structure According to Mbuti pygmies there are usually 1–2 young (Carpaneto & Germi 1989). The capture of three juveniles, born between the beginning of Nov and the beginning of Jan, suggests that the mating time in West Africa is the early dry season, with births from Nov to Jan (Rosevear 1974). A suckling ♀ and one young were collected early Dec in Ituri Forest in DR Congo (F. A. Ulmer pers. comm.). The longevity record for a captive specimen is 15 years and 5 months (Jones 1982).

Predators, Parasites and Diseases Nothing is known about predators. According to the Mbuti pygmies, the species is not eaten because of the bad smell of its skin (Carpaneto & Germi 1989);

nevertheless, Black-legged Mongooses make up 1% of the carnivore bushmeat in NE DR Congo (Colyn *et al.* 1987). Nematode parasites (e.g. *Toxocara* sp.) have been recorded (Warren 1972).

Conservation IUCN Category: Least Concern. CITES: Not listed.

Numbers probably declining as a result of forest fragmentation and forest loss from logging, mining and slash-and-burn farming, and to a lesser degree from bushmeat hunting, but the species currently is not thought to be threatened.

Measurements

Bdeogale nigripes

HB (♂ ♂): 544 (460–630) mm, n = 12

HB (♀ ♀): 568 (450–650) mm, n = 10

T (♂ ♂): 335 (300–385) mm, n = 12

T (♀ ♀): 355 (290–400) mm, n = 10

HF c.u. (♂ ♂): 102 (94–115) mm, n = 12

HF c.u. (♀ ♀): 104 (94–113) mm, n = 10

E (♂ ♂): 36 (30–39) mm, n = 12

E (♀ ♀): 35 (33–37) mm, n = 9

WT: 2.0–4.8 kg*

Museum specimens (AMNH, BMNH, IRSN, MNHN, PCM, MRAC, SBP, SMF and ZMA)

*Kingdon 1997 and a single museum specimen

Skull measurements:

GLS: 116.2 (101.8–127.9) mm, n = 26

GWS: 56.6 (50.6–63.1) mm, n = 24

DR Congo (museum specimens; see below)

GLS: 120.6 (114.7–129.0) mm, n = 23

GWS: 59.4 (55.6–64.2) mm, n = 20

Central African Republic, Cameroon, Gabon and Nigeria (museum specimens: AMNH, BMNH, IRSN, MNHN, PCM, MRAC, SBP, SMF and ZMA)

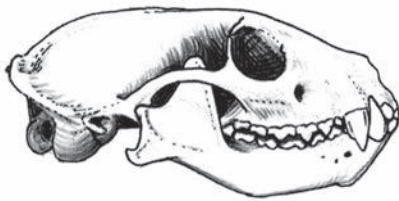
Key References Kingdon 1977, 1997; Rosevear 1974.

Harry Van Rompaey & Marc Colyn

Bdeogale omnivora SOKOKE BUSHY-TAILED MONGOOSE

Fr. Mangouste de Sokoke; Ger. Sokokeichneumon (Swahili Kitu ya Sokoke)

Bdeogale omnivora Heller, 1913. Smithsonian Misc. Coll. 61: 12–13. Mazeras, Kenya 03° 58' S, 39° 33' E.



Lateral view of skull of Sokoke Bushy-tailed Mongoose *Bdeogale omnivora*.

Taxonomy The Sokoke Bushy-tailed Mongoose was described as a new subspecies of the Bushy-tailed Mongoose *Bdeogale crassicauda* (Heller 1913), being different from *B. c. crassicauda* primarily in coat colour and being slightly smaller. Subspecies status has been maintained by most authors (Sale & Taylor 1970, Wozencraft 1993, 2005, Engel & Van Rompaey 1995), but regarded as a distinct species by Kingdon (1997). Synonyms: none. Chromosome number: not known, but likely $2n = 36$ as in other *Bdeogale* (Wurster & Benirschke 1968).

Description A medium-sized mongoose with distinctive yellow to orange underfur and grizzled dark brown guard hairs with lighter annulations. Limbs dark chocolate brown to black. Head shortish with rounded ears. Tail bushy and short. Four digits on both fore- and hindfeet, claws short and stout.

Geographic Variation None recorded.

Similar Species

Bdeogale crassicauda. Unlike Sokoke Bushy-tailed Mongoose, not restricted to the coastal forests of Kenya and N Tanzania, although the precise boundary between the two species requires further investigation. Similar size, but overall darker brown.

B. jacksoni. Currently known only from C and S Kenya, SE Uganda and from the Udzungwa Mts in SC Tanzania; it is not clear whether the two species may be sympatric. Larger (2–3 kg), with blackish legs and light grey to almost whitish body and tail; teeth less rounded.

Distribution Endemic to Africa, and restricted to the coastal forests of Kenya and Tanzania (Engel & Van Rompaey 1995, Engel 1996). In Kenya, the majority of confirmed records are from Gedi, south of Malindi in Kenya, where Taylor (1986) mentions trapping several specimens. Other specimens have been collected in Diani Beach, Shimba Hills N. R., Tiwi, Kwale, Mazeras (the type locality, from which three specimens were recorded in 1911), and Arabuko-Sokoke Forest (Engel & Van Rompaey 1995, Engel 1996); reports of this species from coastal parts of N Kenya have been reported, including museum specimens from the Kipini area and from Milmani in the Boni Forest, close to the Somali border (Engel & Van Rompaey 1995). In Tanzania, they are recorded from Magorota (05° 02' S, 39° 06' E) in the East Usambaras, about 10–15 km from Sigi (Allen & Loveridge 1942) and from Magamba in the West Usambaras (Allen & Loveridge 1927). The latter authors also wrote that the same species had been observed in the Uluguru Mts, though this remains unsubstantiated. There is a recent possible record of this species from the Amani N. R. in the East Usambara Mts (Göller 2005), but this requires confirmation. Indeed, these records from the West and East Usambara Mts are within a few kilometres of the range of the Bushy-tailed Mongoose and it could well have been mistaken for the latter species.

Habitat Confined to forested habitats in a narrow belt on the coast and in mountainous or hilly areas close to the coast (the record from Magamba was taken at 1700 m). An animal was observed in the



Sokoke Bushy-tailed Mongoose *Bdeogale omnivora*.

Shimba Hills along a rough road between a large, open grassland area (with bush and very small islands of forest) and a plantation of pine (*Pinus caribaea*) (Engel & Van Rompaey 1995).

Abundance This mongoose is only locally common and occasionally seen by villagers. Nowhere are members of this genus common, and Taylor (1986) compared this mongoose with other small carnivores and was not able to suggest extrinsic causes of its rarity. The suggestion that habitat destruction is a causal factor cannot be assumed as this species has appeared rare to collectors since it was first described a century ago, and habitat destruction in much of its habitat is a relatively recent phenomenon.

Adaptations The molariform teeth are rounded without a distinct carnassial shear and are adapted for crushing, which results in microscopic pitting of the teeth (Taylor & Hannam 1987). Several specimens examined had very worn teeth, which could be explained by ingesting dirt with insect food.

Foraging and Food The Sokoke Bushy-tailed Mongoose has been observed foraging on insects (either queen termites or male driver ants, *Dorylus* sp.) on a road after rainfall after sunset (Engel & Van Rompaey 1995). The individual would rush a few metres to catch crawling, wingless insects on the road surface and did this for at least 20 min. Beetles and a mouse were recovered from the stomach of the type specimen (Heller 1913), and beetles from specimens caught by Allen & Loveridge (1927).

Social and Reproductive Behaviour Nocturnal and solitary. No other information is available, but likely similar to the Bushy-tailed Mongoose.

Reproduction and Population Structure A female Sokoke Bushy-tailed Mongoose nursing a quarter-grown young was caught in mid-Dec on the Kenya coast. The type specimen,



collected around the same time, had a large foetus (Hollister 1918, Kingdon 1977) that would suggest that breeding occurred during the monsoon periods of Nov/Dec and Apr/May when insect food is usually abundant.

Predators, Parasites and Diseases No information is available. This species is reportedly the type host for the chewing lice *Felicola bedfordi* (Hopkins 1949). Individuals may sometimes be injured or killed by vehicles while foraging after insects on roads at night. A ♂ caught at Gedi had a broken ulna, and showed signs of a broken radius that had since mended (Taylor 1971b).

Conservation IUCN Category: Endangered B1ab(iii). CITES: Not listed.

The population in the Arabuko-Sokoke Forest is under threat from illegal logging and the Shimba Hills population is potentially under threat from afforestation with non-native pine species together with management for the Sable Antelope *Hippotragus niger* (Schreiber *et al.* 1989, Engel & Van Rompaey 1995). There is a need to improve the protection and management of these protected areas. In addition, further survey work is required to confirm the records of this species from the Usambara Mts in Tanzania.

Measurements

Bdeogale omnivora

HB (♀ ♀): 420 mm

T (♀ ♀): 245 mm

HF c.u. (♀ ♀): 81 mm

E (♀ ♀): 34 mm

GLS (♀ ♀): 84.6 mm

GWS (♀ ♀): 45.4 mm

Type specimen (Heller 1913)

The topotype (adult ♀), as provided by Hollister (1918/1924), had measurements: HB = 400 mm; T = 250 mm; HF = 80 mm; E = 37 mm; GLS = 84.5 mm; GWS = 44.6 mm.

Key References Engel & Van Rompaey 1995.

Mark E. Taylor

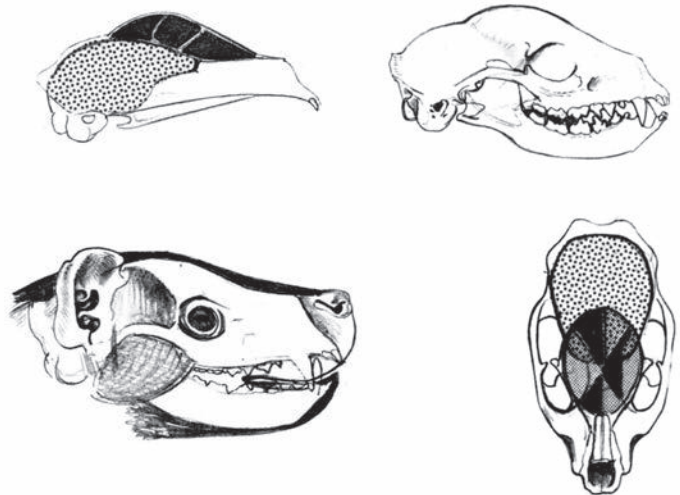
GENUS *Rhynchogale*

Meller's Mongoose

Rhynchogale Thomas, 1894. Proc. Zool. Soc. Lond. 139.

A monotypic genus with an apparently patchy distribution in suitable woodland habitats. The single species, *Rhynchogale melleri*, was originally placed in the genus *Rhinogale* by Gray (Proc. Zool. Soc. Lond. 1865: 573). Pocock (1919) believed this genus to be closely allied with *Ichneumia* and *Bdeogale* on the basis of dental features, and this relationship (together with *Cynictis*) has been borne out by molecular studies (Perez *et al.* 2006, Patou *et al.* 2009).

Chris Stuart & Tilde Stuart



Skull of Meller's Mongoose *Rhynchogale melleri* showing positions of brain, frontal sinuses and rhinarium.

Rhynchogale melleri MELLER'S MONGOOSE

Fr. Mangouste de Meller; Ger. Meller-Manguste

Rhynchogale melleri (Gray, 1865). Proc. Zool. Soc. Lond. 1864: 575 [1865]. 'from a ravine on the outskirts of the Otto Estate, near Mbweni, about 2½ miles [4 km] west of Kilosa, Tanganyika Territory'. The exact locality is unknown; Zomba, Malawi has been suggested – and contested (see Roberts 1951, Ansell 1978).

Taxonomy Coetsee (1977) listed three subspecies, *R. m. caniceps*, *R. m. langi* and *R. m. melleri*, cautioning that *caniceps* and *langi* might not be valid. Ansell (1965, 1978) also expressed doubt as to the validity of *caniceps*. Meester *et al.* (1986) considered *caniceps* synonymous with the nominate form, retaining only *melleri* and *langi*. Differentiation is based on minor aspects of pelage colour, especially on that of the tail, which may be black, brown, white, or variables of these within any one population. Synonyms: *caniceps*, *langi*. Chromosome number: not known.

Description A medium-sized mongoose with tail slightly less than 50% of total length. Head quite short, but muzzle appears somewhat swollen. No central vertical slit on the front of the rhinarium. This mongoose has a distinctive crest-like parting on either side of the neck that is diagnostic, but difficult to see from a distance. Has an overall brownish appearance from a distance, but when close at hand it is coarsely grizzled. Hairs of the coarse guard coat have broad buffy, brown to dark brown annulations that are white to off-white at their bases. Fine underfur greyish at base, browning towards tip.



Meller's Mongoose *Rhynchogale melleri*.

Length of guard hairs on forehead may reach 10 mm, 45 mm on rump, with longest hairs towards tail tip. Lower limbs are darker than upper parts of the body. Pelage of the underparts somewhat paler than upper body. Confusingly, Meller's Mongoose may have predominantly white, brown or black tail hairs, within any one population. In the case of those with black tails the individual hairs are white to brownish-white at the base but black towards the tip. Those with predominantly white tails have hairs with white bases, then broad black annulations, with white tips. In this form the hairs at the tail tip are completely white. Ansell (1960a) recorded that many Zambian specimens have variable tail colouration. Five digits on each foot. Claws on the front feet are short (about 8 mm), curved and sharp, whereas those of the hindfeet are heavier, less curved but similar in length. Anal glands open into a circular pouch. There are two pairs of abdominal nipples.

Skull lightly built, elongated and highest at the level of the mid-point of the zygomatic arches, which are thick and weak; skull slopes gradually back to supraoccipital crest and sharply forward to nasals. The eye sockets are positioned such that the eyes point more forward than in other members of the family. Front chamber of ear bullae much smaller than hind. Rostrum short and broad (Skinner & Chimimba 2005). Dental formula $I^{3/3}, C^{1/1}, P^{4/4}, M^{2/2} = 40$; although Haltenorth & Diller (1980) give a range of 4–5 upper premolars for a total of 40–42 teeth, Skinner & Chimimba (2005) give the total as 40 and this has been confirmed from museum specimens (H. Van Rompaey pers. comm.). The first upper premolars are tiny, the fourth upper premolars broad and molariform, and the fourth lower premolars broad with high cusps. The first and second molars are broad-faced and flat; both first and second molars have three cusps on the front, although those on the first are high (Skinner & Chimimba 2005).

Geographic Variation

R. m. melleri: C Mozambique, C Zimbabwe and extending into Malawi, Zambia, SE Congo and C Tanzania.

R. m. langi: NE South Africa, Swaziland and S Mozambique.



Rhynchogale melleri

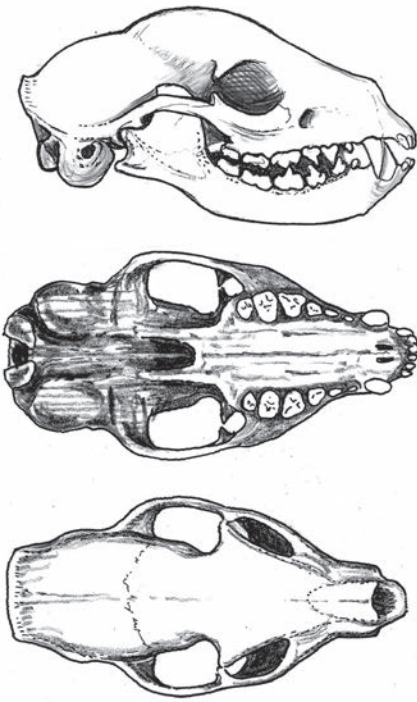
Similar Species

Ichneumia albicauda. Broadly sympatric. Larger, and usually a predominantly white tail and overall grizzled grey appearance (however, black-tailed specimens are known throughout the range); upper lip is divided by internarial groove from nose to mouth.

Bdeogale crassicauda. E Zimbabwe and C Mozambique to Tanzania. Similar in size, but has a relatively shorter tail, appears black at a distance but at close-quarters usually more grizzled; tail and legs very dark to black, with four digits on each foot.

Atilax paludinosus. Riparian habitats from Senegal east to north-east Africa and south to South Africa. Larger (up to 5 kg); overall dark brown to blackish, shaggy pelage.

Paracynictis selousi. Savanna grassland and woodland from Angola to Malawi south to NE KwaZulu–Natal. Smaller; generally pale speckled grey to tawny-grey; feet and legs dark brown to black,



Lateral, palatal and dorsal views of skull of Meller's Mongoose *Rhynchogale melleri*.

contrasting with rest of pelage; partially white tail; fine philtrum between nostrils, dividing haired portion of upper lip.

Herpestes ichneumon. Sympatric in western part of Africa below the equator until South Africa (although overlap might be greater). Lacks distinctive crest-like parting on either side of the neck.

Distribution Endemic to Africa. Meller's Mongoose is often described and depicted as having a disjunct distribution (e.g. Skinner & Chimimba 2005), although several recent distribution records of this species provide some evidence that their range is indeed more continuous than has been supposed. For example, Stuart & Stuart (1998a) photographed a road casualty close to the eastern sector of L. Kariba in N Zimbabwe, which lies between the nearest known locality records for this mongoose in Zambia and the Zimbabwean Midlands. Ansell (1978) remarked that although there were no records from NE Zambia, it probably ranges throughout this part into Tanzania. Other recent records include those from Udzungwa Mountains N. P. in the Mwanihana montane bamboo forest (De Luca & Mpunga 2005), a record from Niassa G. R. in Mozambique (C. Begg & K. Begg pers. comm.) and a possible record from Chobe N. P. in Botswana (Purchase *et al.* 2007), which if substantiated would be the first record for this country. The range of this species, therefore, would appear to be relatively continuous in suitable woodland habitat from C Tanzania south through Malawi, Zambia (probably as far west as the Zambezi R.), Zimbabwe and Mozambique (where they almost certainly occur more widely despite the paucity of records). The species reaches its southernmost limit in the extreme south of Mozambique, extending into NE Swaziland (from which there is only a single confirmed record in 1937; see Monadjem 1998) and parts of NE South Africa (Mpumalanga and Limpopo Province; Skinner & Chimimba 2005). They have not yet been

recorded from N KwaZulu–Natal (Rowe-Rowe 1992a), but may well occur.

Habitat A savanna mongoose that is mainly associated with open woodland and grassland with termitaria. In Zimbabwe and Malawi they are associated with *Brachystegia* woodland (Skinner & Chimimba 2005), where they show a preference for more open grassland and seasonally wet areas. This is similar to the situation over parts of their Zambian range where they occur in open, short-grassed dambos fringed by miombo woodland (C. Stuart & T. Stuart pers. obs.). It is within these areas that their main termite food is located; indeed, in Niassa G. R., two animals were seen in mature miombo woodland with numerous small termitaria (C. Begg & K. Begg pers. comm.). In a recent camera-trapping survey, the species was recorded in montane bamboo forest at 1850 m (De Luca & Mpunga 2005).

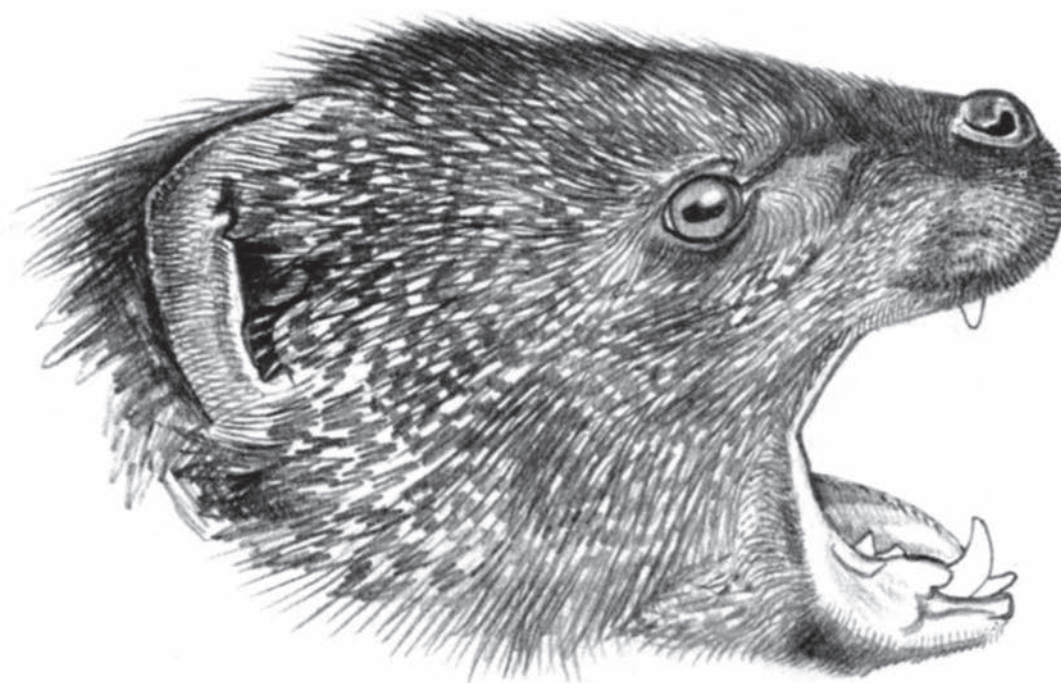
Abundance Apparently uncommon to rare across its range but it may be easily overlooked. During some 800 km of spotlight counts through miombo woodland in Niassa G. R., N Mozambique, their density was 0.3 ind/100 km travelled (C. Begg & K. Begg pers. comm.).

Adaptations The skull has a swelling (of variable size) above the orbit caused by enlarged empty sinuses. Kingdon (1977) has speculated that this could allow this mongoose to give vent to a loud nasal bark. Unfortunately, the call of Meller's Mongoose *Ichneumia albicauda* is unknown, but as the White-tailed Mongoose has a similar skull modification and is known to give a loud barking call it is probable that this is the case. Loud, harsh calls could serve to intimidate potential predators, as well as facilitate contact between widely spaced individuals.

The coronoid of the lower jaw is only of medium height, which suggests that the masseter and temporalis muscles are not well developed and that the jaw action is not very powerful. The molars are broad, somewhat flattened, and highly suited to grinding their mainly termite prey. The densely furred and swollen upper lip and set-back nostrils are possible adaptations to feeding on termites.

Foraging and Food Nothing is known of the foraging behaviour of this terrestrial mongoose, but the nature of their front claws and of their principal prey indicates that they are scratchers rather than active diggers. According to Skinner & Chimimba (2005), termites, and particularly *Macrotermes* spp. and *Hodotermes* spp., are by far the most important prey. Of the 23 stomach contents collected in Zimbabwe, ten contained only termites and one 80% termites and in the remainder termites made up varying percentages. Other invertebrates (grasshoppers, beetles) had only a limited presence and small vertebrates, including a Peters' Thread Snake *Leptotyphlops scutifrons* and a frog, only single occurrences. A single stomach from Zambia (Ansell 1965) was made up only of termites and two centipedes. The same author trapped a specimen using only pumpkin seeds as bait, and Thomas (1894a), quoting a collector, stated that wild fruits are always found in their stomachs.

Social and Reproductive Behaviour A nocturnal mongoose that apparently only starts foraging well after sunset. Most sightings are of single animals, suggesting that they are primarily solitary



Meller's Mongoose *Rhynchogale melleri*.

(Skinner & Chimimba 2005). Ansell (1965) reported finding two old ♂♂ dead together, which suggests a possible territorial conflict had taken place; both specimens were old, with heavily worn teeth and had lost their molars in both jaws. Apart from this meagre information, nothing further is known about these aspects of their biology.

Reproduction and Population Structure The only information available comes from Zimbabwe and Zambia. In the former, a ♀ was collected with three foetuses in Nov, and a ♀ with two young taken from an Aardvark *Orycteropus afer* burrow in Jan (Skinner & Chimimba 2005). A litter of two newborn young was collected in a small cave in hills in Zambia in December (Ansell 1960a) and Wilson (1968) recorded another litter of two from the same general area. In both litters from Zambia, each comprised a male and female youngster. This limited information suggests that young are born during the summer wet season.

Predators, Parasites and Diseases There is no information available on these aspects of their biology, but they may be susceptible to predation by some larger carnivores.

Conservation IUCN Category: Least Concern. CITES: Not listed.

Probably not under any particular threat over much of its range as its favoured habitat is extensive, and in some parts with very low human populations. However, in the Tanzanian and Zambian part of the range there has been considerable expansion of the human

population and their dogs. The latter could represent a significant local threat.

Measurements

Rhynchogale melleri

TL (♂♂): 835 (725–975) mm, n = 6

TL (♀♀): 773 (677–852) mm, n = 6

T (♂♂): 358 (300–412) mm, n = 6

T (♀♀): 339 (312–394) mm, n = 6

HF c.u. (♂♂): 102 (97–106) mm, n = 15*

HF c.u. (♀♀): 98 (95–103) mm, n = 8*

E (♂♂): 38 (31–43) mm, n = 15*

E (♀♀): 37 (35–40) mm, n = 8*

WT (♂♂): 2.31 (1.75–2.67) kg, n = 15*

WT (♀♀): 3.07 (2.41–2.84) kg, n = 8*

GLS (♂♂): 90.5–94.0 mm, n = 6

GLS (♀♀): 88.0–88.5 mm, n = 3

GWS (♂♂): 47.0–49.2 mm, n = 6

GWS (♀♀): 44.0–46.0 mm, n = 3

NE South Africa (Rautenbach 1982)

*Zimbabwe (Smithers 1983)

Skull measurements: South Africa and Swaziland (Roberts 1951); mean value not given

Key References Kingdon 1977; Skinner & Chimimba 2005.

Chris Stuart & Tilde Stuart

GENUS *Cynictis*

Yellow Mongoose

Cynictis Ogilby, 1833. Proc. Zool. Soc. Lond. 1833: 48.

Monotypic genus with a single species, the Yellow Mongoose *Cynictis penicillata*, endemic to southern Africa, where it has successfully colonized semi-arid and largely open habitats (Karoo, fynbos, grassland and arid Kalahari savannas) in the western parts of the sub-continent.

An allozyme phylogeny of some African mongoose species placed *Cynictis* basal to a 'social' lineage (with *Suricata* and *Helogale*), derived from a *Galerella*-like ancestor (Taylor *et al.* 1991). This is consistent with the social organization of *Cynictis*, which has been described as somewhat intermediate between the solitary and social species. On the other hand, a close relationship with *Ichneumia* was previously suggested on morphological grounds, including ear and plantar pad characteristics (Pocock 1919) and has been suggested by recent evidence from cytochrome *b* DNA sequences (Veron *et al.* 2004).

Using molecular data from six nuclear genes, Flynn *et al.* (2005) recovered a strong relationship between *Cynictis* and *Paracynictis* (the latter has been included in *Cynictis*; e.g. McKenna & Bell 1997), but *Ichneumia* was not included in this analysis. Recent molecular studies (Perez *et al.* 2006, Patou *et al.* 2009) group *Cynictis* along with *Bdeogale*, *Rhynchogale* and *Ichneumia*, based on molecular, chromosomal and morphological evidence (*Paracynictis* was not included in these analyses).

Fossil *Cynictis* is known from the late Pliocene of South Africa. Petter (1987) records the possible presence of this genus in the early Pliocene of Tanzania, but this record is in error (L. Werdelin pers. comm.).

Peter J. Taylor

Cynictis penicillata YELLOW MONGOOSE

Fr. Mangouste fauve; Ger. Fuchsmanguste

Cynictis penicillata (G. Cuvier, 1829). Le Règne animal, 2nd edn, 158. 'du Cap', designated as Uitenhage, Eastern Cape [South Africa] (Roberts 1951).



Yellow Mongoose *Cynictis penicillata*.

Taxonomy As many as 12 subspecies have been recognized in the past (Roberts 1951, Ellerman *et al.* 1953), distinguished mainly on the basis of colour, size and length of the tail, all features that are highly variable geographically (see below). Lundholm (1955b) considered all to be part of a cline, and did not recognize subspecies. Three subspecies were defined on morphometric and colorimetric grounds (Taylor *et al.* 1990b, Taylor & Meester 1993b), although data from allozymes (Taylor *et al.* 1990a) and mitochondrial DNA (mtDNA restriction fragment, and mtDNA control region sequences; Jansen van Vuuren & Robinson 1997) revealed little or no geographic partitioning, and no correlation with recognized subspecies, suggesting very recent range expansion, subspeciation and morphometric differentiation (Taylor 1990, Jansen van Vuuren & Robinson 1997). Synonyms: *bechuanae*, *brachyura*, *bradfieldi*, *cinderella*, *coombsii*, *intensa*, *kalaharica*, *karasensis*, *lepturus*, *levaillantii*, *natalensis*, *ogilbyii*, *pallidior*, *steadmanni*, *typicus*. The karyotype is constant throughout the geographic range ($2n = 36$; $NF = 72$) although supernumerary micro-chromosomes have been found in certain populations (Fredga 1972, Taylor 1990, 1993).

Description Tawny to greyish-yellow-coloured mongoose, with relatively large ears (seldom less than 9% of head and body length), projecting above the line of the head (unlike in other mongooses), and long, bushy tail, giving a somewhat fox-like appearance. Upper lip lacks a philtrum (Pocock 1916a). Size similar to Meerkat *Suricata suricatta*, but smaller than most other African mongoose species. Body size and pelage colour highly variable geographically. Southern specimens are larger-sized, with dorsal pelage dark tawny (reddish-brown) to paler yellowish-brown, slightly paler on flanks, paler buffy-cream ventrally and on the legs, chin and throat. Anterior

margin of the ears pallid, with tuft of pale hairs anterior to, and partially covering, the ear opening. Tail colour similar to dorsal pelage basally, becoming heavily pencilled with black over most of its length, but ending in a pure- to dirty-white tail-tip (of variable length, <20 mm to >60 mm). Longer body (>20 mm, mid-dorsal) and tail (>30 mm, mid-tail) hairs. Individual hairs blackish-brown basally, with alternating orange to yellow phaeomelanin and black eumelanin bands, usually two of each, although the terminal band may be dark brown rather than black. The more basal of the two phaeomelanin bands, which is typically longer, may be a richer orange than the shorter, more terminal, yellower band, giving a slightly grizzled, greyish-yellow wash to the deeper orange background colour in some specimens. Subterminal black bands are wide on the tail hairs, but otherwise subequal or narrower than the brown bands. Pelage colour varies seasonally in southern (but not conspicuously so in northern) specimens, resulting in a summer pelage with shorter hairs and a brighter, redder colouration than in winter. A transitional colour, appearing in Nov and Dec, is paler yellow in colour and patchy in appearance due to uneven moult of the winter pelage (Taylor *et al.* 1990b).

Northern specimens are distinctly smaller, with dorsal pelage grizzled, greyish-yellow colour (due to numerous black-tipped guard hairs), becoming paler on flanks, and pure creamy-white ventrally and on the legs, chin and throat. Tail similar in colour to dorsal pelage basally, becoming pencilled with brown over the distal two-thirds of the tail, without a white tip. Shorter body (<15 mm) and tail (<25 mm) hairs, compared with southern specimens. Individual hairs brown basally, with alternating pale buffy and black bands, ending in a terminal black band. Black bands tend to be wider than pale buffy bands, giving grizzled appearance (Taylor *et al.* 1990b). Five digits on forefeet, four on hindfeet; all digits on forefoot, except the first, armed with claws up to 10 mm on Digits 2, 3 and 4. Sole of hindfoot more hairy, forefoot palm naked to wrist. Anal glands open on either side of the anus. Cheek glands are present and used for marking of objects (Earlé 1981, Wenhold & Rasa 1994). There is no sexual dimorphism in size or pelage colour. Three pairs of nipples.

Skull pear-shaped with postorbital bar complete in adults. Rostrum short and broad, zygomatic arches weak, and the supraoccipital crest little more than a slight ridge. Anterior ectotympanic chamber of bulla subequal in size to posterior entotympanic (anterior typically reduced in other mongooses); septum between the chambers angled (vertical in other mongoose genera). Dental formula is $I^{3/3}, C^{1/1}, P^{4/4}, M^{2/2} = 40$; upper and lower P1 sometimes absent, especially the latter.

Geographic Variation

C. p. penicillata: Western Cape, Eastern Cape, Northern Cape (south of Orange R.), Free State, KwaZulu–Natal, North West and Limpopo Provinces, north to the Soutpansberg Mts. Largest of subspecies, head and body length >300 mm, condylobasal skull length >64 mm; dorsal pelage richer and redder overall, from tawny to yellowish-red, with conspicuous white tail tip.

C. p. bradfieldi: Northern Cape (north of Orange R.), S Botswana and S, C and NW Namibia. Intermediate-sized, head and body length 267–370 mm, condylobasal skull length 59–66 mm; colour intermediate, orange to yellowish in hue, pallid and moderately faded, with white tail tip present but not conspicuous.

C. p. coombsii: Limpopo Province, north of Soutpansberg Mts, C and N Botswana, intergrading with *C. p. bradfieldi* in NE and E Namibia and S Botswana. Smallest in size, head and body length <300 mm, condylobasal skull length <61 mm; pelage colour grizzled greyish-yellow and faded, without white tail tip.

A fourth subspecies, *C. p. natalensis*, was proposed by Taylor (1990), but later withdrawn by Taylor & Meester (1993b).

Similar Species

Suricata suricatta. Sympatric across much of the range and often co-exist. Tail not bushy, with a dark tip; ears smaller; dark circles around eyes; mottled upperparts, sometimes forming transverse bars; individuals often adopt a characteristic upright observation stance.

Paracynictis selousi. Only sympatric in parts of N Namibia and Botswana. Larger (as much as twice the body weight of Yellow Mongoose), with general appearance pale speckled grey to tawny-grey and tail white towards the tip. Nocturnal and solitary.

Distribution Virtually endemic to southern Africa, with limited records from extreme SW Angola close to the Namibia border (Crawford-Cabral 1989a). Within this range, Yellow Mongooses occupy the drier western parts, being widespread in Namibia, Botswana and much of C and W South Africa. They are absent from the Namib Desert and Caprivi Strip in Namibia, the Okavango Swamps in Botswana, Zimbabwe (except for an extreme western record) and the easterly regions of southern Africa (including much of KwaZulu–Natal, Swaziland, Kruger N. P., W Lesotho and Mozambique) (Rowe-Rowe 1992a, Monadjem 1998, Skinner & Chimimba 2005).

Habitat Predominantly open grassland, scrub and arid savannas (e.g. *Combretum*/*Terminalia* in the Kalahari) in the drier, semi-arid, western parts of southern Africa, largely corresponding to the South-West Arid Biotic Zone. Absent from deserts and from forested, mountainous and mesic savanna areas in the southern and eastern parts of southern Africa. Owing to their use of burrows, rocky and hard soils are avoided. The availability of water is not an essential habitat requirement.

Abundance Population densities vary geographically, with the highest densities reported for the central plateau grassland region of South Africa (particularly the Free State, North West Province and Gauteng). Since the Yellow Mongoose is the primary vector of viverrid-type rabies in South Africa, high population densities of this species are strongly correlated with areas of high incidence of viverrid-type rabies cases (Snyman 1940, Zumpt 1976). A population density of 6.0–7.1 individuals/100 ha was estimated in West Coast N. P. of South Africa (Cavallini 1993b, Cavallini & Nel 1995) and 4–14 individuals/km² in the Kalahari (Le Roux *et al.* 2008a), whereas a much higher density of 133–200 individuals/100 ha was reported by Earlé (1981) for a study population at the Vaal Dam on the central plateau, which was centred on a large garbage dump that served as a good feeding source. In the Kalahari, numbers of Yellow Mongoose have been found to increase with increasing shrub cover (especially where shrub cover varies between 10 and 15%), but then decrease at higher shrub densities (>17.5%). The amount of

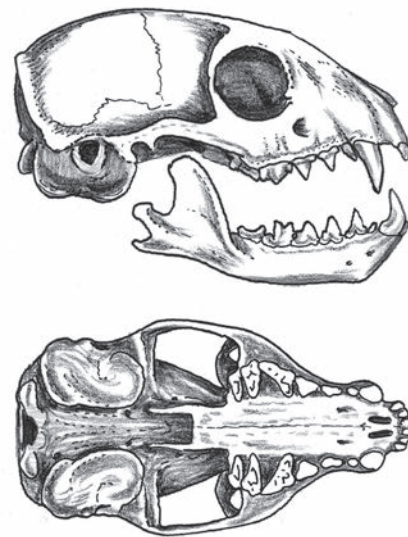


shrub cover presents a trade-off between the abundance of suitable shrubs for reproductive burrows (protection) at small scales and the proportion of shrub cover at large spatial scales (which reduces prey availability and perhaps detection of terrestrial predators) (Blaum *et al.* 2007a, b).

Adaptations The absence of a sagittal crest, and the poor development of the zygomatic arch, both suggest relatively weak masseter and temporalis muscles, indicating a diet of softer food. The dentition is not well adapted for slicing (only the fourth premolar has a sharp outer edge), but molars are suitable for the crushing of insects and similar food (Skinner & Chimimba 2005).

Yellow Mongooses occupy open country where their predominantly insect prey may be more abundant (Cavallini & Nel 1995). Being mostly diurnal (some nocturnal activity has been recorded), their tawny to greyish yellow-coloured dorsal pelage offers an effective camouflage against diurnal predators in open habitats. Their use of burrows also offers protection against predators; in the southern Kalahari, Yellow Mongooses build their burrows preferably under the cover of large and solitary *Acacia* shrubs (shrub diameter 6–9 m) to reduce predation by raptors (Blaum *et al.* 2007a). Burrows also offer a significant thermoregulatory advantage by buffering extremes in ambient temperature. For example, in the Free State, at maximum summer ground temperatures of 39°C, burrow temperature was 14°C cooler, while at a winter minimum of –3.6°C, the burrow temperature was 14°C warmer (Lynch 1980).

Burrows may be simple, with one or two entrances, or much more complex, having up to 60 entrances and comprising linked underground tunnels at two or three levels up to 1.5 m in depth. Nest chambers are excavated at intervals along the tunnels. Yellow Mongooses may construct their own burrows, or even modify existing burrows, and sometimes they share those excavated by Meerkats and Ground Squirrels *Xerus inaurus* with which they may cohabit. Lynch (1980) proposed that the close association between



Lateral and palatal views of skull of Yellow Mongoose *Cynictis penicillata*.

Yellow Mongooses and Meerkats may benefit the former species via improved predator detection. Do Linh San & Somers (2006) described an apparent case of cooperative vigilance between a Yellow Mongoose and three Meerkats while the animals were travelling in open terrain from one termite mound to another. The authors proposed that this interaction was probably favoured by a high degree of inter-specific tolerance emerging through the shared use of burrows and the higher predation risks associated with living in small groups. After leaving their dens in the morning, Yellow Mongooses may sunbathe for periods exceeding an hour, which also has a thermoregulatory function. They have not been observed climbing trees, and may be considered exclusively terrestrial.

The anal glands secrete a milky fluid with a sour, cheesy smell, comprising some 22 volatile compounds (Apps *et al.* 1989a).

Foraging and Food Yellow Mongooses are predominantly insectivorous, preferring Isoptera (termites: *Hodotermes*, *Trinervitermes*, *Microhodotermes*), Coleoptera (beetle larvae and adults) and Orthoptera (locusts and grasshoppers); however, they are highly opportunistic feeders and, depending on availability, will readily hunt rodents, birds, reptiles, amphibians and arachnids (scorpions, spiders) (Zumt 1968, Smithers 1971, Herzig-Straschil 1977, Du Toit 1980, Lynch 1980, Earlé 1981, Stuart 1981, Avenant & Nel 1992, 1997, Cavallini & Nel 1995, Kok & Louw 2000). Detailed reviews of dietary variation in the species, based on many of the dietary studies cited above, are provided by Taylor & Meester (1993b) and Nel & Kok (1999). The latter study analysed diet from populations in the Free State and Northern Cape from 1984 to 1997, and compared these findings with all previous dietary studies. They suggested that termites (Isoptera) were predominant in wetter than average rainfall years (e.g. Lynch 1980) while Coleoptera (beetles) predominated in drier than average years (Nel & Kok 1999).

Diet varies both geographically and seasonally. Contrary to all other studies, in which insects predominate in the diet, in a study of the prey remains in 95 stomachs collected from the central parts of South Africa, Zumt (1968) found rodents to have a higher occurrence than insects. In Botswana, insects occurred more

frequently (92%) than murids (15%), scorpions (13%) and reptiles (11%) ($n = 54$ stomachs; Smithers 1971). In a study in South Africa, invertebrates (mostly termites and locusts) occurred slightly more frequently (87%) than vertebrates (including mammals, birds and amphibians; 28%) ($n = 76$ stomachs; Herzig-Strachil 1977). Rodents were present in 40% of 332 scats analysed at a coastal site in the Western Cape, compared with insects (mostly Isoptera), which occurred in 90% of scats. Five species of rodents were recorded, in order of importance: Four-striped Grass Mouse *Rhabdomys pumilio*, Bush Karoo Rat *Otomys unisulcatus*, Tiny Pygmy Mouse *Mus minutoides*, Pygmy Hairy-footed Gerbil *Gerbillurus paeba* and Cape Gerbil *Gerbilliscus afra* (Avenant & Nel 1992). The occurrence of rodents in the diet of Yellow Mongooses at this site varied considerably during the year, corresponding with fluctuating population densities of rodents. At a site in the Karoo (South Africa), rodents were present in only 3% of a sample of 86 scats, compared with insects (mostly Coleoptera and Orthoptera), which were present in 100% of scats (Avenant & Nel 1992). Isoptera were present in 74% of stomachs ($n = 156$) in a study in the Free State, where other important prey items, in order of importance, were Orthoptera, Coleoptera and Lepidoptera, with vertebrates and other invertebrate groups occurring at much lower percentages (Lynch 1980).

Yellow Mongooses are also known to feed occasionally on fruits, for example, in winter when other food items may be unavailable (Du Toit 1980), and on carrion. Stuart (1981) recorded them feeding on a decomposing Common Duiker *Sylvicapra grimmia*, and they have been recorded feeding on the remains of a Southern African Springhare *Pedetes capensis* (Wenhold 1990). They have been observed feeding on the aloe-type plant *Chlortolirium angolense*, but this may have been for the water content (Zumpt 1968). They have been known to feed on hen's eggs and free-ranging hens, but anecdotal reports by farmers of them preying on newborn lambs are almost certainly false. Snyman (1940) maintained that Yellow Mongooses play an important role in controlling insect numbers, and reported discernible local increases in insect populations following mass eradications of Yellow Mongooses during rabies vector control programmes.

Yellow Mongooses usually forage individually, but also sometimes in pairs or small groups, typically during the early morning and late afternoon. On the west coast of South Africa, a radio-tracking study indicated that 37% of their time was spent foraging (Cavallini 1993a). Timing of activity was correlated with sunset and sunrise times, minimum and maximum temperature, windspeed and meteorological conditions (mist, rain, cloudiness), all variables that in turn are correlated with activity of their main diet of termites (Isoptera). In the Western Cape they have been observed feeding throughout the day, except during the hottest days of the summer (Z. Balmforth pers. comm.).

Social and Reproductive Behaviour Yellow Mongooses have been described as facultatively social. They spend nights in communal dens and even cooperate in raising their young. Based on five studies reviewed by Taylor (1993), mean group size varies from 2 to 13 individuals living together. Since they are mainly solitary away from the burrow, and social at the burrow, their social system appears to be intermediate between that of solitary and social species of mongooses, leading Wenhold (1990) to suggest that this species has a social system representative of a 'missing link' in the evolution of sociality in the

herpestids. Larger group sizes appear to be a feature of areas of high population density, forcing family groups to live together, and young to remain in their natal colony and help raise young.

Although Yellow Mongooses mainly forage alone (unlike social mongooses such as the Meerkat where cooperative foraging is obligatory), they also commonly forage in pairs and small groups, and have been observed following one another whilst foraging (Cavallini 1993b, J. A. J. Nel pers. comm., Z. Balmforth pers. comm.). In contrast to Meerkats, the presence of conspecifics during foraging increases individual vigilance and reduces their foraging time and success. Instead, Yellow Mongooses avoid predator detection by remaining close to safe refuges and making use of inconspicuous vigilance behaviours (avoiding the sentinel behaviour of Meerkats), which do not interfere with foraging (Le Roux *et al.* 2009b). This reinforces the suggestions of Nel & Kok (1999) – who compared low foraging group size of Yellow Mongoose with the high foraging group sizes of Bat-eared Fox *Otocyon megalotis* and Meerkat – that competition may not be a major constraint of group size in foraging Yellow Mongooses.

Groups typically comprise a dominant ♂, with separate hierarchies for the subordinate ♀♀ and ♂♂. Juveniles are the lowest ranking. To assess dominance status, two individuals approach one another and sniff each other's facial glands. The dominant individual rises higher on its feet while biting the subordinate's neck. The subordinate lies on its side and may emit a high-pitched scream. A dominant individual marks a subordinate by straddling it from above and using the anal glands in a standing position. In a colony studied by Earlé (1981), the dominant ♂ marked colony members daily; however, in the study of Wenhold (1990), the dominant ♂ was not involved in dominance interactions, but high-ranking subordinates deferred to the dominant ♂♂, and in turn dominated lower ranking members.

In a radio-tracking study in a coastal area of the Western Cape, ♂♂ moved an average of just over 3 km per day, with ♂♂ and ♀♀ moving, on average, similar distances per hour (292 m/h and 228 m/h, respectively). Home-ranges of ♂♂ (minimum convex polygon method: 102 ha) are larger than for ♀♀ (10–49 ha) (Cavallini 1993b). Overlap among ♂♂ was substantial and individual home-ranges overlapped those of several ♀♀, while the ranges of female groups in different burrows showed almost no overlap (Cavallini 1993b, Cavallini & Nel 1995). There was no evidence for group territories. However, it appears that social structure may vary geographically, again possibly in response to population density, since, in other studies, both ♂♂ and ♀♀ were shown to patrol, mark (with middens) and defend group territories (Earlé 1981, Le Roux *et al.* 2008a, Z. Balmforth pers. comm.). Le Roux *et al.* (2008a) recorded a mean territory size of 76 ha for dominant ♂♂ ($n = 6$) and a home-range size of 20 ha for a dominant ♀. Yellow Mongooses are partly nomadic, and they may rotate the use of several burrow systems on different nights, within a much larger territory (Wenhold 1990).

Defecation takes place on middens close to burrows (or along a group territory in the case of Earlé's study), and the faeces have a distinct odour possibly due to anal gland secretions. The anal glands function in scent-marking of home-ranges and allo-marking between colony members. The dominant pair and juvenile ♀♀ concentrate their markings mainly around the burrow. Objects may also be marked by means of the cheek gland, often preceded by wiping the entire side of the body on the ground or side-swiping (Earlé 1981, Wenhold & Rasa

1994). All members of the group help mark, although Wenhold & Rasa (1994) noted that most marking was done by younger, subordinate individuals, which they suggested was a means of advertising for potential mates. In other studies, dominant ♂♂ were the main territory defenders and demarcators (Earlé 1981). Comparing a low-density population in the Kalahari with that of Wenhold & Rasa (1994), a high-density population on farmland displaying natal philopatry, Le Roux *et al.* (2008a) recorded marked differences in terms of individual contributions to territorial marking: subordinate group members in the low-density population performed almost no territorial marking or defence, but were the primary scent-markers and territory defenders in the high-density population (presumably because larger groups in high-density populations interact with neighbours more frequently, causing more conflict but also opportunities for mating and sexual advertisement between neighbours).

Fights between dominant ♂♂ of adjacent colonies occur frequently and may be violent (Wenhold & Rasa 1994), with dominant ♂♂ often bearing scars on their faces. However, in a low-density population in the Kalahari, aggression between neighbours appeared to be low with encounters of brief duration and seldom drawing blood; territory expansion into neighbouring territories was never observed (Le Roux *et al.* 2008a).

When ♀♀ are in oestrus, ♂♂ purr, 'caw' and scream while following the ♀♀ around and attempting to mount. Oestrous ♀♀ will allow copulation over a two-day period, after which ♂♂ are vocally rebuffed accompanied by bites to the head and neck. Earlé (1981) recorded young-adult ♀♀ mating with dominant and other ♂♂. Two observed copulations lasted 37 and 45 min. During copulation, the ♂ kept up his purring, while the ♀ bit or licked the male's ears and neck. Young are born in nesting chambers in the burrows. The Yellow Mongoose adopts a unique system of infant care, whereby adult 'helpers' (some of the previous year's young that do not disperse but remain in the natal group) provision young at their dens for the first four weeks, carrying back large prey items (rodents, bats, reptiles and large arachnids) (Rasa *et al.* 1992). However, in a low-density population in the Kalahari, Yellow Mongooses lived in small family groups and showed no cooperative breeding; young dispersed by nine months of age (establishing territories 2.5 km from their natal territories; Le Roux *et al.* 2008a) and became parents immediately if they found a mate (Vidya *et al.* 2009). The young first accompany adults on foraging expeditions at about eight weeks of age. By contrast, the young of other social mongooses (*Helogale* and *Mungos*) must accompany the adults to forage and hence suffer greater predation from avian predators (Rasa *et al.* 1992).

Yellow mongooses have a repertoire of at least nine distinct vocalizations that are used in multiple contexts (Le Roux *et al.* 2009a). A tenth reported vocalization, a purring sound that accompanies mating (Earlé 1981, Wenhold 1990), adds to the repertoire. Compared with solitary mongooses, the Yellow Mongoose has a large proportion of 'friendly' vocalizations (five) that enhance group cohesion, but its vocal repertoire is smaller and less context-specific than those of obligate social species, such as the Dwarf Mongoose *Helogale parvula* and Meerkat (Le Roux *et al.* 2009a). Social context has been shown to affect both communicative and flight behaviour of Yellow Mongooses: alarm vocalizations were used almost exclusively when individuals were in a group rather than solitary, while the visual alarm signal, a raised tail, was predominantly used by solitary

individuals when predators were outside attack range (Le Roux *et al.* 2008b).

Reproduction and Population Structure Between one and five young, most commonly two, are born during up to two distinct birth seasons (Wenhold 1990, Rasa *et al.* 1992, Taylor & Meester 1993a, Z. Balmforth pers. comm.). In contrast to earlier reports of monoestry and an extended breeding season, based on anatomical observations of pregnant ♀♀ (Zumpt 1969, 1976, Lynch 1980), later studies based on long-term behavioural observations of breeding ♀♀ have demonstrated the existence of dioestry (Wenhold 1991, Rasa *et al.* 1992). Based on observations of four colonies from geographically widespread localities, ♀♀ first came into oestrus in early Aug, followed by a gestation period lasting 60–62 days, with births occurring in early to mid-Oct. In South Africa, a second oestrus occurs rapidly postpartum in mid-Oct (while ♀♀ were still suckling their young), with births occurring in mid- to late Dec (Rasa *et al.* 1992). In contrast, unpublished observations from the Western Cape (Z. Balmforth pers. comm.) suggest that most second breeding attempts fail, with one birth reported in late Jan, suggesting a two-month postpartum oestrus. In Namibia (Etosha N. P.) and Botswana (Kgalagadi Transfrontier Park) a second oestrus occurred up to two months after birth, in mid-Dec, and births followed in mid-Feb (Rasa *et al.* 1992).

The production of up to two small, but closely spaced, litters annually, and the provisioning of young at their dens by helpers, may be part of an evolutionary strategy to maximize reproductive output whilst ensuring greater survival of young through guarding of dens by helpers (group size is relatively small, so only a few helpers are available per litter). Unlike the situation in the Dwarf Mongoose, there is no reproductive suppression in a colony so that more than one ♀ can breed simultaneously, another factor that may explain small litter-size. Lactation lasts 6–8 weeks, and young are nutritionally independent at 16–18 weeks of age (Rasa *et al.* 1992).

In one study, 41 litters were found to comprise a single sex only. At birth, the male : female sex ratio was 1.6 : 1 whereas in adults this changed to 1.2 : 1 (Zumpt 1976). Yellow Mongooses live up to 15 years in captivity (Jones 1982, Weigl 2005).

Predators, Parasites and Diseases Large snakes (such as Cape Cobra *Naja nivea*) and water monitor lizards *Varanus* spp. prey on young or immature Yellow Mongooses and Black-backed Jackals *Canis mesomelas* may take adults and young. Large raptors such as Tawny Eagles *Aquila rapax*, Martial Eagles *Polemaetus bellicosus* and Wahlberg's Eagles *Aquila wahlbergi* are important avian predators.

Many species of parasites have been recorded, including at least eight species of fleas (among them the plague vector, *Xenopsylla perei*), ten species of ticks (most commonly *Haemaphysalis zumpti*), seven species of mites, two species of lice, nine species of helminths and a nematode parasite, *Tenuostrongylus cynictis* (Hinton & Dunn 1967, Lynch 1980, Horak *et al.* 1999, 2000). After examining 80 Yellow Mongooses, Horak *et al.* (1999) found one species of biting louse *Felicola cynictis* to be the most prevalent ectoparasite. Penzhorn & Chaparro (1994) found a very high prevalence (77%) of infection by the haemo-protozoan *Babesia cynictis* in 97 animals from the Pretoria, Ermelo and Potchefstroom areas of South Africa.

The Yellow Mongoose is the primary maintenance host for the viverrid strain of rabies endemic to the interior plateau of South

Africa, where Yellow Mongoose population densities are highest. The role of the Yellow Mongoose as a maintenance host is promoted by its diurnal and colonial, burrow-living habits. Viverrid rabies was first confirmed in 1928, and, by 1940, the Yellow Mongoose was implicated in 21 human deaths, the deaths of five head of cattle and 80 outbreaks of rabies. By 1992, some 2119 confirmed cases of rabies infections in Yellow Mongooses had been documented (Snyman 1940, Swanepoel *et al.* 1993). The incidence of viverrid rabies increased each decade, peaking in the 1970s. Between the 1930s and 1970s, wholesale eradication of Yellow Mongooses was applied to control the disease, but this is now applied selectively in areas with a high risk of possible infection by humans. A seasonal peak in the incidence of rabies coincides with the peak birth period of Yellow Mongooses (Zumpt 1969, 1976). Chaparro & Esterhuysen (1993) demonstrated that viral maintenance in the Yellow Mongoose was not due to a carrier state, as experimentally infected animals showed high mortality, and serum antibodies to the rabies virus were present only in the terminal stages of the disease. Apart from specific outbreaks, the level of rabies infection in nature may be very low. In one sample of 97 animals from a rabies-endemic area, no rabies virus or antibody was detected in any specimens (Chaparro & Esterhuysen 1993).

Conservation IUCN Category: Least Concern. CITES: Not listed.

The Yellow Mongoose occurs in numerous protected areas across its range in southern Africa, including Etosha N. P. (Namibia) and Kgalagadi Transfrontier Park (Botswana/South Africa), and does not appear to be under any significant threat at present.

Measurements

Cynictis penicillata penicillata

HB: 341 (265–460) mm, n = 169

T: 230 (165–290) mm, n = 169

HF s.u.: 71 (66–76) mm, n = 20*

E: 35 (32–39) mm, n = 20*

WT: 830 (715–900) g, n = 20*

GLS: 67.0 (62.2–73.7) mm, n = 203

GWS: 40.1 (36.3–44.2) mm, n = 200

South Africa (Taylor & Meester 1993b, *Lynch 1980)

Cynictis penicillata coombsii

HB: 304 (275–390) mm, n = 30

T: 210 (150–292) mm, n = 29

HF c.u.: 67 (61–78) mm, n = 67*

E: 30 (24–38) mm, n = 60*

WT: 571 (440–797) g, n = 38*

GLS: 59.7 (56.2–62.9) mm, n = 37

GWS: 35.2 (33.2–39.2) mm, n = 35

Botswana (Taylor & Meester 1993b, *Smithers 1971)

Key References Avenant & Nel 1992, 1997; Earlé 1981; Lynch 1980; Rasa *et al.* 1992; Taylor & Meester 1993a, b; Taylor, *et al.* 1990a, b, 1991; Zumpt 1968, 1969, 1976.

Peter J. Taylor

GENUS *Paracynictis*

Selous's Mongoose

Paracynictis Pocock, 1916. Ann. Mag. Nat. Hist., ser. 8, 17: 177.

Paracynictis is a monotypic genus of south-central Africa, occupying a range of savanna habitats. *Paracynictis* was originally assigned to the genus *Cynictis*, because of its similarities to the Yellow Mongoose *Cynictis penicillata*, a species with which it is probably closely related (and was included in *Cynictis* by McKenna & Bell 1997) (see Flynn

et al. 2005). Molecular data (Patou *et al.* 2009) cluster Yellow Mongoose and Selous's Mongoose as sister species.

Chris Stuart & Tilde Stuart

Paracynictis selousi SELOUS'S MONGOOSE

Fr. Mangouste de Selous; Ger. Trugmanguste

Paracynictis selousi (De Winton, 1896). Ann. Mag. Nat. Hist., ser. 6, 18: 469. 'found on a grassy heap under a tree, EssexVale, Matabeleland ... near Bulawayo' [Zimbabwe].

Taxonomy Coetsee (1977) listed four subspecies: *P. s. bechuanae* from E Botswana; *P. s. ngamiensis* from N Botswana, N Namibia, Angola, Zambia and Malawi; *P. s. selousi* from Zimbabwe, western border of the Vila Pery District, Mozambique, and NE South Africa; and *P. s. sengaani* from N KwaZulu–Natal and S Mozambique. Coetsee (1977) cautioned that this listing was provisional, noting that subspecies were separated on the basis of slight differences in pelage and that they were likely no more than stages in clinal colour variation. Rautenbach (1982) suggested that *P. s. sengaani* is a geographical isolate, and Meester *et al.* (1986) considered *bechuanae* and *ngamiensis* as synonyms of the

nominate race, retaining only *P. s. selousi* and *P. s. sengaani*. Ansell & Dowsett (1988) similarly regarded Malawian specimens as *P. s. selousi*. Synonyms: *bechuanae*, *ngamiensis*, *sengaani*.

Chromosome number: not known.

Description A medium-sized mongoose, with a partially white tail. General appearance pale speckled grey to tawny-grey. At close quarters coat distinctly grizzled, with white annulations on guard hairs. Guard hairs on head about 15 mm long, to 40 mm on rump and up to 100 mm towards tail tip. Underparts slightly paler than



Selous's Mongoose *Paracynictis selousi*.

upperparts but similar in colour. Underfur is thick, woolly and hairs are dark at bases, with buff or buff-grey tips. Rhinarium small for size of head, fine philtrum between nostrils, dividing haired portion of upper lip. Ears rounded and partially covered in front by longer hair. Feet and legs dark brown to black, contrasting with rest of pelage. Four digits on each foot, with stout claws. Light coloured, well-haired tail white towards tip and constitutes about 40% of the total body length. A specimen taken by Hill (1941) in Angola had two pairs abdominal nipples, although the author pointed out that three pairs, one pair pectoral, has been reported as the norm. There is no sexual dimorphism.

Skull elongated, braincase ovoid, narrowing slightly to the interorbital constriction. The rostrum is short and broad, the supraoccipital crest well developed. The width of the zygomatic arches is about half the total length of the skull. Ear bullae large relative to size of skull. Dental formula is $I^{3/3}, C^{1/1}, P^{4/4}, M^{2/2} = 40$. Upper canines short, rounded and slightly recurved, the lower distinctly recurved. Both upper and lower outer incisors are slightly larger than the remainder; the first upper and lower premolars are not always present. The fourth upper premolar teeth have two well-developed cusps on their outer edges and a low cusp on their inner sides. The first molar in the lower jaw has three high cusps towards the front of the teeth (Skinner & Chimimba 2005).

Geographic Variation

P. s. selousi: C and S Angola, S Zambia, much of C and S Malawi, almost throughout Zimbabwe except the north-east, with a marginal occurrence in NE Namibia and in Botswana, north from L. Ngami and in a narrow belt in the extreme east and south-east. Also present in extreme NE and E South Africa.

P. s. sengaani: NE KwaZulu–Natal (South Africa) and S Mozambique.

Similar Species

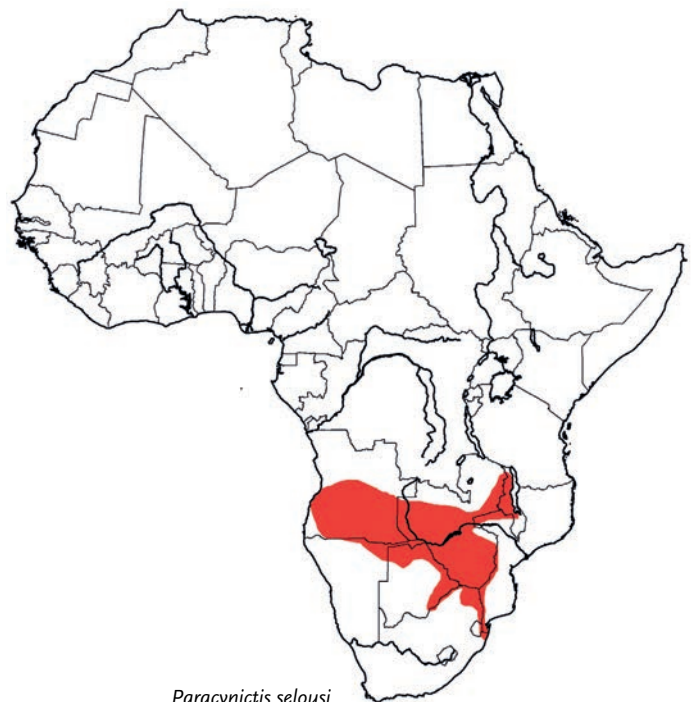
Ichneumia albicauda. Woodland and savanna habitats in sub-Saharan Africa from Senegal eastwards to the Horn of Africa, and southwards to SE South Africa. Much larger (up to 6 kg); limbs longer and more extensively dark to black in colour; rump higher than shoulders and head held low when walking.

Rhynchogale melleri. Woodland habitat from N Tanzania south to NE South Africa. Individuals may have partially white tails, but pelage overall more brown; distinct crest-like parting on either side of neck.

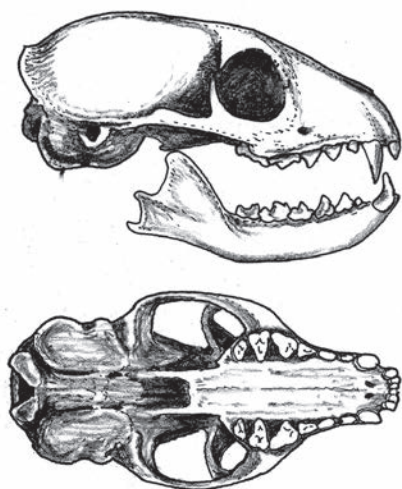
Cynictis penicillata. Only sympatric in parts of N Namibia and Botswana. Pelage reddish-yellow to greyish-yellow, usually but not always with white hairs at extreme tip of the tail; smaller (to 900 g); strictly diurnal.

Bdeogale crassicauda. Sympatric in Zimbabwe and Mozambique. Slightly smaller; uniform brownish coat, limbs and feet not contrasting strongly with the coat.

Distribution Endemic to Africa, ranging from Angola in the west to Malawi in the east, with its most southward extension in NE KwaZulu–Natal. In Angola the species occurs in the central and southern parts, but is absent from the arid coastal part (Crawford-Cabral 1989a). It has a marginal occurrence in Namibia, being limited to the extreme north-east centred on the Caprivi Strip (Skinner & Chimimba 2005). In Zambia, it occurs throughout the south-western parts, including the middle Zambezi Valley, with a possible record from the Mwinilunga District in the north-east (not mapped); its range extends through the Central and Eastern Provinces to Malawi (Ansell 1978). Ansell (1978) cautioned that it was not clear whether there was a break in distribution between the central and eastern provinces of Zambia. In Malawi, Ansell & Dowsett (1988) give the northernmost records as 'eight miles east of Mzimba and the Perekezi Forest' and point out that the species is unlikely to occur east of the Shire R. There are as yet no records from the Tete district of Mozambique (Smithers & Lobão Tello 1976), but they probably do occur. In Zimbabwe, they occur throughout much of the country, except the north-east (Smithers & Wilson 1979); they have been recorded from the western border of the Manica province in Mozambique (Smithers & Lobão Tello 1976). In Botswana they occur mainly in the north-west, apparently as far south as L. Ngami, east to the Zimbabwe border. In South Africa, they are present in the



Paracynictis selousi



Lateral and palatal views of skull of Selous's Mongoose *Paracynictis selousi*.

north-eastern parts (Limpopo Province and Mpumalanga) south to NE KwaZulu–Natal (Skinner & Chimimba 2005). They are not yet recorded from Swaziland (Monadjem 1998), but may well occur.

Habitat A mongoose of savanna grassland and woodland that is absent from forest and arid areas. Known distribution range falls within the 400–1000 mm rainfall zone. Most authors (Shortridge 1934, Ansell 1960a) found them to be associated with areas dominated by sandy substrates. In areas of harder substrates they may occupy more open grassed areas, such as flood-plains and cultivated land (Smithers 1971). Not dependent on the availability of water.

Abundance Appears to be uncommon throughout its range. However, many areas within its known range are zoologically poorly explored and in parts it may be more abundant than currently recorded.

Adaptations The large ear bullae indicate that sense of hearing is well developed and an aid to locating its largely subterranean prey. The carnassial shear has little slicing ability and appears better adapted to a diet of insects and other soft food. Selous's Mongooses carry heavy and stout claws on the front feet, which enable them to excavate their own burrows, as well as dig for prey.

Foraging and Food Selous's Mongoose may be predominantly insectivorous, eating a wide range of species, although in a sample of 51 stomachs from Zimbabwe and Botswana insects from the orders Orthoptera, Isoptera and Coleoptera were the dominant prey items (Smithers 1971, Smithers & Wilson 1979). Other invertebrate groups, especially solifugids and scorpions, were also of importance. A wide range of small vertebrates has also been recorded, including murids, lizards, snakes, amphibians and birds. Earlier authors, such as Shortridge (1934), listed small vertebrates as being more important than insects in this mongoose's diet. In no case is much detail presented but this may indicate regional and seasonal differences in their food. Smithers (1971) found that during a drought period in Botswana stomach contents were dominated by invertebrate remains, but when the rains came and rodent populations increased these became the favoured food.

Selous's Mongoose is a nocturnal, solitary forager that appears to move about only well after sunset. When foraging animals, frequently

stop to investigate possible food sources, and readily dig and scratch for subterranean prey. They move at a rapid walk with nose close to the ground and they are believed to have an acute sense of smell.

Social and Reproductive Behaviour Mainly solitary, but pairs have been recorded and it is presumed that larger young accompany their mothers during foraging (Smithers 1971). In sandy substrates Selous's Mongooses excavate their own burrows, which may be extensive with two, or more, entrances (Skinner & Chimimba 2005, C. T. Stuart pers. obs.). In areas of harder substrate they make use of burrows excavated by other species. Nothing is known of reproductive behaviour.

Reproduction and Population Structure The few records of reproduction, mainly from Botswana and Zimbabwe, indicate that litters of from two to four young are born during the warm, wet summer months, from Aug to Mar. Smithers (1971) recorded two gravid ♀♀ from Botswana, one (Feb) with three and the other (Sep) with four foetuses. A ♀ with three foetuses was collected in W Zimbabwe in Aug (Smithers & Wilson 1979). Shortridge (1934) took a pregnant ♀ in Namibia in Oct, and Hill (1941) recorded that the nipples in an adult ♀, taken in early Dec in Angola, were active. Young animals have been recorded in Dec, Jan and Feb.

Predators, Parasites and Diseases The only record of predation on this species is by Martial Eagles *Polemaetus bellicosus* in Zimbabwe (Steyn 1980). There is limited information available on diseases and parasites, although a preliminary survey found that this species does not play a role in the epidemiology of rabies in Zambia (Sawchuk & Rottcher 1978). Fuhrmann (1943) recorded the cestode *Pseudandrya monardi* from Angola.

Conservation IUCN Category: Least Concern. CITES: Not listed.

Although it occurs at low to fairly low densities right across its range, it remains widespread and the nature of its habitat is such that it faces no known threats.

Measurements

Paracynictis selousi

HB (♂♂): 397 (445–455) mm, n = 22

HB (♀♀): 419 (328–443) mm, n = 25

T (♂♂): 377 (288–435) mm, n = 21

T (♀♀): 325 (307–367) mm, n = 23

HF c.u. (♂♂): 116 (106–124) mm, n = 20

HF c.u. (♀♀): 112 (103–120) mm, n = 25

E (♂♂): 43 (39–48) mm, n = 20

E (♀♀): 45 (41–50) mm, n = 20

WT (♂♂): 1.75 (1.39–2.16) kg, n = 18

WT (♀♀): 1.75 (1.26–1.87) kg, n = 21

GLS: 84.0–87.0 mm, n = 4

GWS: 43.2–44.9 mm, n = 4

Body measurements: Botswana (Smithers 1971)

Skull measurements: southern Africa (Roberts 1951)

Key References Smithers 1971; Smithers & Wilson 1979.

Chris Stuart & Tilde Stuart

GENUS *Ichneumia*

White-tailed Mongoose

Ichneumia I. Geoffroy Saint-Hilaire, 1837. Ann. Sci. Nat. Zool. (Paris), 8 (2): 251.

The genus is monotypic, including only one species, the White-tailed Mongoose *Ichneumia albicauda*, which ranges throughout most suitable habitats in sub-Saharan Africa, and also in Yemen and other coastal regions of Arabia. Molecular data reveal a close relationship

between *Ichneumia*, *Cynictis*, *Rhynchochale* and *Bdeogale* (Patou *et al.* 2009).

Mark E. Taylor

Ichneumia albicauda WHITE-TAILED MONGOOSE

Fr. Mangouste à queue blanche; Ger. Weißschwanzichneumon

Ichneumia albicauda (G. Cuvier, 1829). Le Règne animal, 2nd edn, 1: 158. 'l'Afrique australe et le Senegal' [southern Africa and Senegal].



White-tailed Mongoose *Ichneumia albicauda*.



White-tailed Mongoose *Ichneumia albicauda* melanistic form.

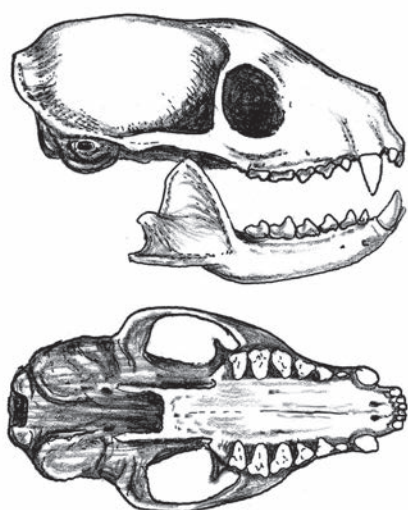


White-tailed Mongoose *Ichneumia albicauda* myology.

Taxonomy Taylor (1972) and Coetzee (1977) recognized six subspecies in Africa. Subspecies have been distinguished on the basis of variations in pelage colour, and since variations in colour and size are probably determined by environmental determinants such as moisture and elevation, there have been doubts as to their validity. Phylogenetic analysis based on partial sequences of the mitochondrial control region lends some support to several of these subspecies (*I. a. grandis*, *I. a. dialeucos* and the nominate subspecies), but has indicated the need for much broader sampling before proposing a new subspecific classification of the species based on molecular data (Dehghani *et al.* 2008). Synonyms: *abuwudan*, *albescens*, *almodovari*, *dialeucos*, *ferox*, *grandis*, *haagneri*, *ibeana*, *leucurus*, *loandae*, *loempo*, *nigricauda*. Chromosome number: $2n = 36$. The autosomes are composed of 14 pairs of meta- or submetacentric and three pairs of acrocentric elements. The X chromosome is a medium-sized metacentric and the Y is a very small submetacentric (Wurster & Benirschke 1968).

Description A large distinctive mongoose, usually grey, with black limbs and grey tail with distal third of tail usually white. Ears rounded and lightly furred, barely protruding above head profile. Upper lip divided by internarial groove from nose to mouth. Head

and body grizzled grey due to banding of guard hairs, with guard hairs longer (up to 90 mm) on nape and back with longer black tips. Undercoat thick, and underfur buffy. Individuals from high rainfall parts of the range often very dark to melanistic, while in arid areas the general colour is light grey. Tail tapers, is usually grey in proximal half and becomes progressively whiter distally. Black-tailed specimens are known throughout the range of the species (e.g. Botswana, Smithers 1971; N Mozambique, C. Begg & K. Begg pers. comm.; East Africa, Kingdon 1977; Ethiopia, Duckworth 1995), and are even more common than the white-tailed variant in West Africa (Rosevear 1974, Grubb *et al.* 1998). Legs are long, with hindquarters higher than their forequarters, and limbs dark brown to black from mid-leg to feet. Feet pentadactyl, the first digit small and set well back from the plantar pads, and palms naked to wrist (but soles hairy from behind first toe to wrist); hindfeet heavier and broader than front feet. Interdigital pads well developed. Claws robust and curved, reaching up to 13 mm over the curve. Anal glands appear to be used for marking territory. No noticeable sexual dimorphism, although



Lateral and palatal views of skull of White-tailed Mongoose
Ichneumia albicauda.

♂♂ slightly heavier than ♀♀ (Smithers & Wilson 1979, Waser & Waser 1985). Three pairs abdominal nipples (Skinner & Chimimba 2005); however, some authors report two pairs (Roberts 1951).

Skull heavy with somewhat inflated nasal region and inflated posterior chamber of tympanic bullae, well-developed supraoccipital crest, robust zygomatic arches and postorbital bar complete in adults. The White-tailed Mongoose retains a more primitive generalized carnivore dentition, with a dental formula of $I^{3/3}, C^{1/1}, P^{4/4}, M^{2/2} = 40$. Upper canines slightly curved and pointed. Taylor (1992) provides additional details on the skull and dentition.

Geographic Variation

- I. a. albicauda*: relatively dry woodlands from Somalia through Uganda and C Sudan to Senegal.
- I. a. loempo*: West African forest fringes.
- I. a. grandis*: southern Africa south of the Cunene–Zambezi, large parts of Zambia, Malawi and N Mozambique.
- I. a. loandae*: Angola and adjacent NW Zambia and S DR Congo.
- I. a. ibeana*: C and S Kenya, Tanzania, Uganda and NE DR Congo.
- I. a. dialeucos*: N Kenya and S Ethiopia and Somalia.

Similar Species

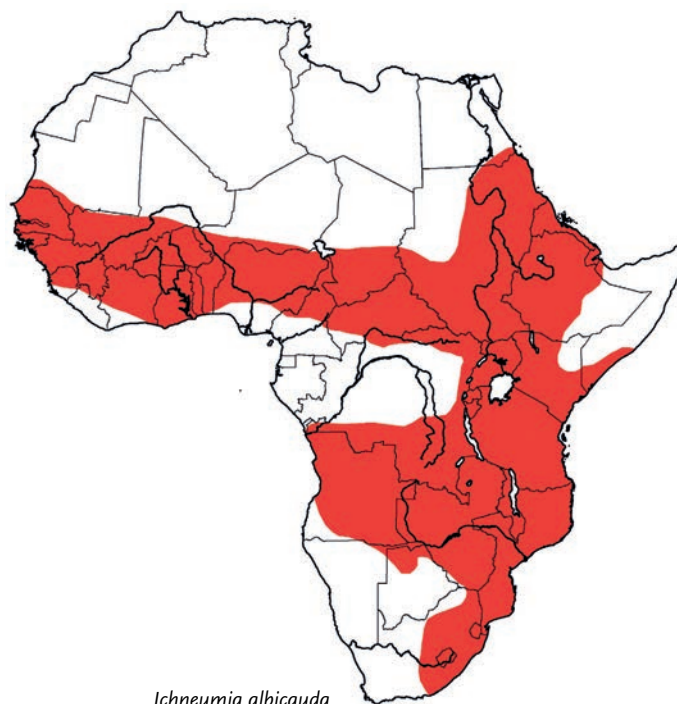
- Herpestes ichneumon*. Widely distributed from Senegal to East Africa, southwards to NE Namibia and E South Africa. Slender tapering tail and a tufted darker tip; more uniformly grizzled grey.
- Atilax paludinosus*. Riparian habitats from Senegal east to north-east Africa and south to South Africa. Uniform brown with a rather shaggy and rich brown coat; relatively short tail; distinctive feet in which the interdigital web is much reduced allowing the digits to be splayed out when walking on soft substrates.
- Rhynchogale melleri*. Woodland habitat from N Tanzania south to NE South Africa. Smaller, and with shorter, whitish tail; dark muddy-grey or buffy-brown; distinctive crest-like parting on either side of the neck; no split in the rhinarium.
- Bdeogale jacksoni* and *B. nigripes*. Larger, generally light-coloured with dark tetradactyl (four digits) limbs; occurring in forested areas rather than savannas.

Paracynictis selousi. Savanna grassland and woodland from Angola to Malawi south to NE KwaZulu–Natal. Smaller; generally pale speckled grey to tawny-grey; feet and legs dark brown to black, contrasting with rest of pelage; partially white tail.

Distribution Occurs in woodland and savanna habitats in sub-Saharan Africa from Senegal and Gambia in the west, eastwards to S Somalia, Ethiopia, Eritrea and Djibouti, and then southwards to SE South Africa. While it occurs throughout the Sahelian region it is absent in the more arid regions. There are as yet no confirmed records from Egypt (Osborn & Helmy 1980, Hoath 2003), though they may well occur in the south-east. They also are absent from the moist equatorial forest regions, but extend through Malawi, Zambia, Zimbabwe and N Botswana to NE Namibia and Angola. They penetrate forested regions along roads and agricultural areas and also penetrate the eastern extension of the low scrub (karroid) vegetation between the Free State and the Northern Cape of South Africa (C. Stuart pers. comm.).

Extralimital to the continent, this species is present in suitable habitats along much of the coast of Saudi Arabia to Oman in the east (Harrison & Bates 1991, Gallagher 1992, Stuart & Stuart 1998d). This population is estimated to have colonized the Arabian Peninsula ~32,500 years ago, making it a relatively long-term resident of Arabia (Fernandes 2011). They are also recorded from Farasan Kabir I. in the Red Sea, where they may have been introduced (Simmons 1995, Masseti 2010).

Habitat Occurs in grasslands, savanna and woodland areas. Absent from moist forested areas, high altitudes above the treeline, desert and semi-desert. Common in farmland and other human-modified habitats in Ethiopia (to about 3500 m) and likely elsewhere in East Africa (Admasu *et al.* 2004b). White-tailed Mongooses are highly flexible in their habits and thus adaptable to human land use, with individuals often found around towns and villages where they feed opportunistically on garbage. In Oman they have been found associated with gardens and



Ichneumia albicauda

plantations (Harrison & Bates 1991). The species requires suitable denning locations to rest in during the day, so the absence of suitable cover may restrict its distribution in short to long grasslands.

Abundance The species is common in parts of its range and densities as high as 4.3 ind/km² were reported from Serengeti N. P., Tanzania (Waser 1980). In some areas density may be limited by the availability of dens for resting up during the day. The most detailed studies have been conducted in Serengeti N. P. where population densities were found to be higher in the west and lower in the east, in parallel with the higher rainfall in the west and associated greater amounts of insect food. High densities have been reported in protected urban areas such as ravines and parks and around livestock operations, where the presence of dung and associated insects provides an ample supply of food.

Adaptations The teeth are broad and heavy, particularly the last premolars and first two molars. They are well adapted to crushing insect prey (though they still have a carnassial shear, unlike *Bdeogale* that has crushing molars), and their diet of insects and small vertebrates results in pitting and grooving of the surface enamel (Taylor & Hannam 1987).

White-tailed Mongooses are the most cursorial of the mongooses, with long metapodials and digitigrade fore- and hindfeet (Taylor 1988). Although accomplished diggers, with stout, curved claws, they are not as long as those of the Banded Mongoose *Mungos mungo* and they do not appear to dig their own burrows, using disused Aardvark *Orycteropus afer* or springhare *Pedetes* spp. holes to rest in during the day. They also use holes in termitaria, which previously have been opened up by Aardvark or other species. In Serengeti N. P., Waser & Waser (1985) found that most occupied dens were inactive termite *Odontotermes* mounds; they appeared to enlarge the ventilation shafts to gain entry to underground chambers. No dens were dug from scratch and several dens were so shallow that the mongoose was visible from outside. Other dens are located in hollows at the bases of trees such as *Acacia* and *Balanites* spp. In farmland adjacent to Bale Mountains N. P. in Ethiopia, diurnal resting sites were found amongst rocks and in disused buildings (Admasu *et al.* 2004b). It is unknown whether they use bedding material.

White-tailed Mongooses are predominantly nocturnal and generally emerge from dens shortly after dusk and may be active through into the early hours of the morning; some diurnal activity is reported in a few areas (Waser 1980, Stuart 1981, Sillero-Zubiri & Marino 1997).

Foraging and Food White-tailed Mongooses are primarily insectivorous, eating medium to large insects (especially termites, beetles, grasshoppers, crickets and beetle larvae) that emerge or are active at night. In a sample of 65 stomachs from Zimbabwe, insects had the largest percentage occurrence at 86%, followed by amphibians (31%), murids (18%) and reptiles (15%) (Smithers 1971). In Kenya, S. Takata (pers. comm.) found their diet to be approximately 55% arthropod, 25% mammal and 20% birds. Insects seem to be a major part of their diet during the wet seasons with a shift to more vertebrate prey during the dry seasons (M. Taylor pers. obs.). They rarely eat fruits and vegetable matter, although these are eaten where available; Pitman (1954) reported them feeding on avocado pears in Uganda.

White-tailed Mongooses usually forage singly (but see Social and Reproductive Behaviour), quartering an area and grabbing insects,

usually larger than 5 mm (Waser 1980). Prey is located mainly by scent. They may forage in a zig-zag fashion, thereby quartering an area more effectively for emerging insects. They may catch several insects a minute and forage for 6–8 hours a night, travelling approximately 4–5 km and usually traversing their entire home-range (Waser 1981, Waser & Waser 1985). They continue foraging during light rain and brief thunderstorms. They occasionally dig for beetles, alates and other insects and will jump or pounce on small vertebrate prey (amphibians, reptiles, mice and other small mammals), although they rarely catch prey on the wing. They are opportunistic and may be attracted to insects below street lights, to dung insects associated with cattle enclosures, and to garbage and refuse associated with human habitations. White-tailed Mongooses often hunt insects on roads at night and this sometimes results in them being hit by vehicles and numerous animals sustain fractures to their pelvis or hindquarters as a result of this hunting activity (Taylor 1972).

The species has been recorded eating carrion: Rowe-Rowe (1978a) states that 17 animals were accidentally killed by coyote-getters, baited with carrion, in KwaZulu-Natal (South Africa). Numerous authors have reported White-tailed Mongooses killing and preying on poisonous snakes. As with other mongooses, they also eat eggs, breaking them by hurling them between their back legs against rocks. Kingdon (1977) reported an account by Pitman (1954) of White-tailed Mongooses using their tail as a lure to attract chickens at night, but while this may occur in some circumstances, their major diet of insects would suggest that this is an unusual use of the white-tipped tail. They may coexist with Bat-eared Foxes *Otocyon megalotis* and Aardwolves *Proteles cristatus*, two other insectivorous nocturnal carnivores, but there is no indication that they actually compete for food resources (Waser 1980).

Social and Reproductive Behaviour White-tailed Mongooses are predominantly solitary. In Serengeti N. P., 87% of about 390 sightings were of solitary animals (Waser 1980), and 79% of 110 sightings in Bale Mountains N. P. were of solitary animals (Admasu *et al.* 2004b), similar to observations obtained in the Ethiopian Rift Valley (88%; Duckworth 1995). Groups usually comprise ♀♀ with large young, but all group sightings in Bale comprised an adult ♀ with an adult ♂ (Admasu *et al.* 2004b). Individuals may be seen foraging together in areas where insects are emerging or there is a concentrated food source (Kingdon [1977] reports up to nine seen foraging together), but the animals are not social in the way in which Dwarf Mongooses *Helogale parvula* or Banded Mongooses are. There may be no advantages conferred on sociality for a mongoose of this size, as well as the fact that most habitats do not provide suitable denning places for groups of individuals and probably the dispersed nature of the food source it exploits.

The species appears to be territorial, though territories of ♂♂ may overlap and ♀♀ often overlap; the ranges of three adjacent radio-tagged adult ♂♂ in Bale were mutually exclusive, and overlapped to a maximum of 3% (Admasu *et al.* 2004b). Once animals have been removed from an area, it usually takes some weeks before new individuals arrive and establish territories. The home-ranges of ♂♂ overlap those of ♀♀, and may include parts of 2–3 females' ranges while the home-range of a ♀ sometimes lay within the ranges of two or more ♂♂. In Bale, ranges of adult ♀♀ overlapped 81% with one ♂ and 25% with a second ♂ (Admasu *et al.* 2004b).

Agonistic encounters between ♂♂ have not been described and it appears that scent-marking of territories and display behaviour may be sufficient to space individuals through suitable habitat, the size of each home-range being dependent upon available food resources and den availability. However, at high densities, home-ranges of ♀♀ may be shared, perhaps by grown daughters (P. Waser pers. comm.). If the food available is largely emerging insects, there are few advantages to be gained by any individual excluding other individuals from the area (Waser 1981); therefore, there is no need for territoriality. The advantages that small social mongooses gain from being social is probably more to do with warning, protection from potential predators, and increased reproductive success, than being able to forage more efficiently, as these species are all considerably smaller than White-tailed Mongooses and are diurnal rather than nocturnal.

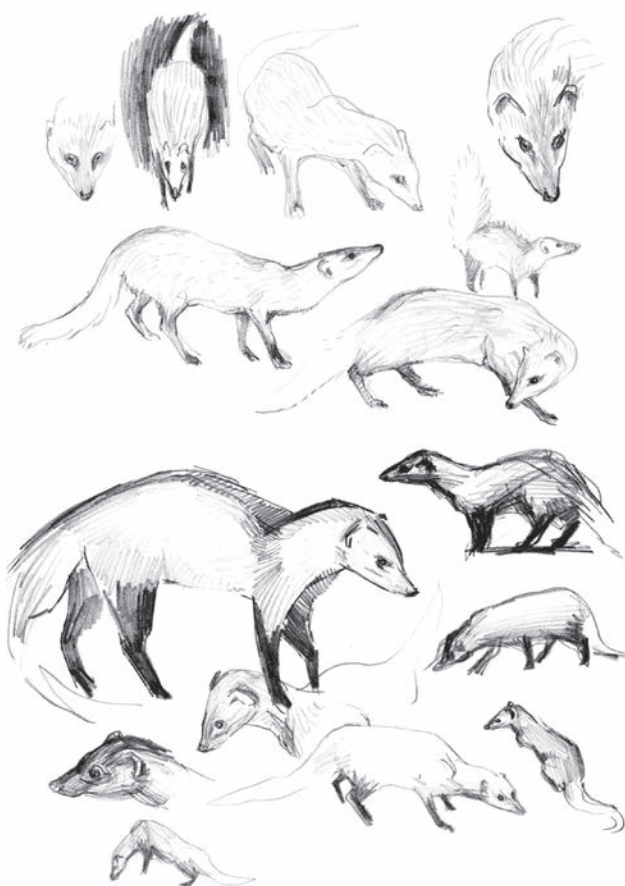
Range sizes appear to vary in different habitats: in Serengeti N. P., Waser & Waser (1985) gave the mean home-range size for ♂♂ as 0.97 km² (range 0.8–1.23; n = 4) and for ♀♀ as 0.64 km² (range 0.39–1.18; n = 9), while in Omo N. P., Ethiopia, a single individual tracked over a few weeks at an artificial food source occupied a home-range of approximately 0.03 km² (Ikeda *et al.* 1982). Range size in Bale over a 14-month period averaged 3.17 km² for three adult ♂♂ and 2.63 km² for one ♀; the large range size was probably due to less abundant food in Bale than in Serengeti, where dung beetles are very common due to the availability of faeces produced by large herds of grazing ungulates (Admasu *et al.* 2004b). Taylor (1972) reports a home-range of 8 km² for a Kenyan animal. The

home-ranges of seven ♀♀ included an average of three den sites, though not all were necessarily in use. Mongooses used the same den for 5–15 days before moving to a new den (Waser 1980), but may return after a period when food supplies have built up again.

Social grooming has rarely been observed, though individuals that come into contact may sniff each other's noses or genitals before proceeding on their way. Aggressive interactions were only observed with outsiders (Waser & Waser 1985). Defecation occurs in the vicinity of the den but often also at a large latrine site. Urination by both sexes involves a characteristic tail-arch that makes the behaviour readily recognizable. White-tailed Mongooses have conspicuous anal scent pouches and mark with a squat or anal drag. All adults as well as independent juveniles engage in this behaviour (Waser & Waser 1985). White-tailed Mongooses are largely silent, though they may make chattering noises and when cornered and defensive they utter a very loud and startling bark screech (M. Taylor, pers. obs.).

During oestrus, a ♂ and ♀ pair up for several hours. Waser & Waser (1985) reported that copulation occurred in bouts of 15–20 mounts, spread over half an hour, with individual mounts lasting 5–40 sec, and being terminated by the ♀ breaking away. In four of six observed copulations, the ♂ and ♀ remained together following copulation, but in one instance the ♀ mated with another ♂ within one hour.

Weaned juveniles forage alone for several hours each night from about nine months of age, although they continue to forage within the maternal home-range for at least four months after weaning. Where mongoose density is high, and food abundant, some female offspring do not disperse (Estes 1991).



White-tailed Mongoose *Ichneumia albicauda*.

Reproduction and Population Structure Pregnant or lactating ♀♀ have been taken from Oct to Feb in Zimbabwe (Smithers 1971), and in Nov in Namibia (Shortridge 1934) and KwaZulu–Natal (Rowe-Rowe 1978a). In East Africa, young are born during the long (Mar–Apr) or short rains (Oct–Dec) (Taylor 1972). Rosevear (1974) suggests the dry season as the favoured breeding period in West Africa, with juveniles having been taken in Jan and Feb. Young are probably born in dens, and litter-size is 1–4; four gravid ♀♀ taken in Zimbabwe had three foetuses each (implantation was 2R : 1L), one ♀ had one foetus only (1R). In Serengeti N. P., the mean size of litters sighted at independence (at about 1.5 kg) was 1.4 (Waser & Waser 1985). A single young mongoose born in a trap weighed 81 g and had body measurements (mm): HB = 152, T = 94, HF = 30 and E = 12 (S. Takata pers. comm.). In captivity they are able to live for 10–14 years (Jones 1982, Weigl 2005).

Predators, Parasites and Diseases Occasionally, White-tailed Mongooses may be preyed upon by larger carnivores, but this is unlikely to occur often. In one observation, a Lion *Panthera leo* flushed a White-tailed Mongoose from a shallow den, and the mongoose barked and stood its ground and the Lion backed down (P. Waser pers. comm.). In another incident, a Leopard *Panthera pardus* killed and ate a White-tailed Mongoose in Zambia (C. Stuart pers. comm.), and Waser (1980) mentions that African Wild Dogs *Lycaon pictus* flushed an animal from a thicket, ran it down and killed it. Kingdon (1977) mentions 45 White-tailed Mongooses being killed by a pack of dogs during the course of a year in an Entebbe township, though this is probably a function of unnaturally high levels of mongooses moving into an urban area for food and being caught by dogs.

The cestode *Pseudandrya mkuzii* was collected from the stomach of a White-tailed Mongoose in KwaZulu–Natal (Ortlepp 1963), and the nematode *Arthrocephalus gambiense* from an animal in Somalia (Macchioni 1995). The brown ear tick *Rhipicephalus appendiculatus* and ticks of the *Haemaphysalis leachi* group, as well as immature individuals of *R. hurti* and *R. jeanneli* group and *Ixodes thomasea* were found on the White-tailed Mongoose in Kenya (Punyua & Newson 1985), *H. paraleachi* was recorded from an animal in Sudan (El Kammah *et al.* 1992), *H. parmata* from an animal in Ghana (Ntiama-Baidu *et al.* 2005), and *Amblyomma hebraeum*, *A. marmoreum*, *Haemaphysalis zumpti*, *Hyalomma truncatum*, *Rhipicephalus appendiculatus* and *R. zambeziensis* from animals in Kruger N. P., South Africa (Horak *et al.* 2000). The flea *Ctenocephalides damarensis* was recorded from two animals in South Africa (Horak *et al.* 2004). Ectoparasite loads are heavy, with fleas, mites and lice being common. The sera of *Ichneumia* tested positive for *Rickettsia* antibodies (Heisch *et al.* 1962).

Admasu *et al.* (2004b) note that there is potential for disease transmission between the species and domestic dogs, although none of their animals had antibodies to canine parvovirus, canine distemper or canine adenovirus.

Conservation IUCN Category: Least Concern. CITES: Not listed.

White-tailed Mongooses are common through much of their range, occur around many towns and villages, and feed opportunistically, so there is little reason to believe they are currently threatened. They may be caught incidentally in control programmes principally aimed

at Black-backed Jackal *Canis mesomelas* and Caracal *Caracal caracal* (Rowe-Rowe 1978a, C. Stuart pers. comm.).

Measurements

Ichneumia albicauda

HB (♂ ♂): 680 (574–1040) mm, n = 18

HB (♀ ♀): 574 (519–591) mm, n = 25

T (♂ ♂): 421 (346–470) mm, n = 19

T (♀ ♀): 442 (392–485) mm, n = 25

HF c.u. (♂ ♂): 139 (130–147) mm, n = 19

HF c.u. (♀ ♀): 138 (130–148) mm, n = 25

E (♂ ♂): 46 (42–50) mm, n = 19

E (♀ ♀): 45 (37–50) mm, n = 25

WT (♂ ♂): 4.49 (3.63–5.22) kg, n = 14

WT (♀ ♀): 4.14 (3.62–4.99) kg, n = 25

GLS (♂ ♂): 116.0–118.0 mm, n = 3

GLS (♀ ♀): 108.0–114.0 mm, n = 5

GWS (♂ ♂): 56.0–59.5 mm, n = 3

GWS (♀ ♀): 51.8–55.8 mm, n = 5

Zimbabwe (Smithers & Wilson 1979)

Skull measurements: South Africa (Roberts 1951)

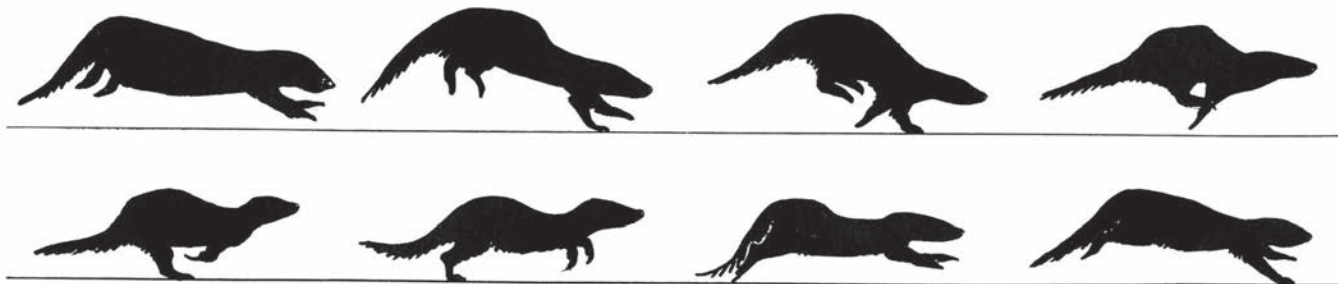
Key References Admasu *et al.* 2004b; Kingdon 1977; Smithers 1971; Taylor 1972; Waser 1980; Waser & Waser 1985.

Mark E. Taylor

Subfamily MUNGOTINAE – Social Mongooses

Mungotinae Gray, 1864. Proc. Zool. Soc. Lond. 1864: 509.

Subfamily Mungotinae includes the mainly smaller social mongooses of the genera *Crossarchus*, *Helogale*, *Dologale*, *Liberiictis*, *Mungos* and *Suricata*.



Serial silhouettes of running Banded Mongoose *Mungos mungo*.

GENUS *Suricata*

Meerkat

Suricata Desmarest, 1804. Tabl. Méth. Hist. Nat. In: Nouv. Dict. Hist. Nat., 24: 15.

The genus is monotypic, and includes only a single species, the Meerkat or Suricate *Suricata suricatta*, which is endemic to the western half of southern Africa, with a marginal intrusion into extreme SW Angola.

David W. Macdonald

Suricata suricatta MEERKAT (SURICATE)

Fr. Suricate; Ger. Scharrtier.

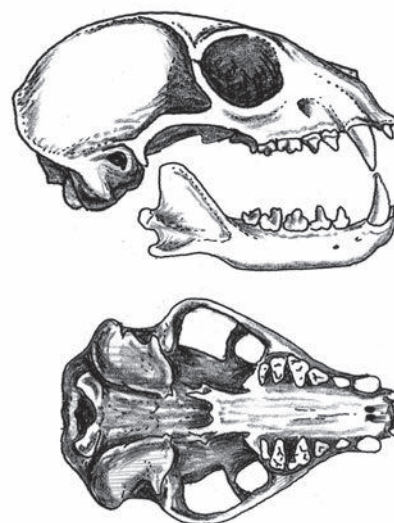
Suricata suricatta (Schreber, 1776). Die Säugethiere, p. 117. Listed as 'Cape of Good Hope' by Meester *et al.* (1986), restricted by Thomas and Schwann (1905: 133) to 'Deelfontein' [South Africa].



Meerkat *Suricata suricatta*.

Taxonomy Polytypic. Three subspecies have been recognized (Coetzee 1977, Meester *et al.* 1986, Van Staaden 1994). Synonyms: *capensis*, *hahni*, *hamiltoni*, *iona*, *lophurus*, *marjoriae*, *namaquensis*, *surakatta*, *tetradactyla*, *typicus*, *viverrina*, *zenik*. Chromosome number: $2n = 36$; there are 34 metacentric, submetacentric and subtelocentric autosomes, a submetacentric X and a telocentric Y (Todd 1966).

Description A long and slender mongoose, with large black eyes, long thin legs and tapering thin tail. Head broad and muzzle short and sharp-pointed. Head pelage greyish-white, with black eye-rings, round black ears and large black nose; a fine dark line extends from above the small eyes towards the tops of the ears. Brows and cheeks white. Dorsal pelage varies considerably across the range, from tan to grey, with brown banding on back, rump and sides. Hair of the guard coat is about 15 mm long, but may reach 30–40 mm on flanks. Individual hairs on upperparts are light-coloured at the base with two dark annulations separated by a light-coloured one, and a silvery-white tip (sometimes dark). Ventral hairs sparse and white (the dark-coloured skin showing through), with greyish-white throat and chin. Tail (ca. 80% of HB) similar in colour to dorsal parts of the body for more than half its length, tapering towards a dark tip with black hairs. Tail thinly haired, with hair at base of the tail long (20 mm), but those on the dark tuft only 12 mm long. Four digits on each foot, each with a swollen digital pad. Claws long and curved, those on the front feet about 15 mm across the curve, those on the hindfeet shorter (about 8 mm). Paired



Lateral and palatal views of skull of Meerkat *Suricata suricatta*.

anal glands, the secretion of which does not differ between ♂♂ and ♀♀ (Decker *et al.* 1992). Females have three pairs abdominal nipples. Sexes are similar in colour and size (Lynch 1980), but dominant animals are heavier than other group members (Clutton-Brock *et al.* 1999a).

Skull lightly built, high and rounded. Eye sockets large, rostrum narrow, supraoccipital crest barely perceptible in some specimens; there is no sagittal crest. Posterior chambers of the ear bullae are ovoid, large and inflated; the anterior chambers are about half the size. Zygomatic arches thin, the coronoid processes of the lower jaw only medium height, which suggests that the temporalis and masseter muscles are less developed than in more carnivorous species. Dental formula $I^{3/3}, C^{1/1}, P^{3/3}, M^{2/2} = 36$. Third upper premolar has a distinct protocone, the fourth premolar and first molar with distinct cusps on their inner extensions; the second premolar is small (Skinner & Chimimba 2005).

Geographic Variation

S. s. suricatta: S Namibia, S Botswana and South Africa.

S. s. iona: SW Angola.

S. s. marjoriae: Namib Desert, including central and NW Namibia.

Similar Species

Cynictis penicillata. Sympatric. Pelage lighter with yellow underfur; tail bushy with white tip; claws shorter; lacks brown banding on back; eyes red.

Mungos mungo. Sympatric. Body larger; tail longer; pelage brownish-grey with alternating dark brown and whitish banding on back; fur is coarser and longer; eyes smaller relative to head.

Distribution Endemic to southern Africa, south of the Cunene and Zambezi Rivers, with a very marginal intrusion into extreme SW

*Suricata suricatta*

Angola in Iona N. P. (see Crawford-Cabral 1971, 1989a). Widespread in arid and semi-arid lands in the western parts of southern Africa, including W and S Namibia, SW Botswana (north to about 21° N and east to about Makgadikgadi Pan) and N and W South Africa, being particularly widespread in the Northern Cape, North West Province and Free State (Skinner & Chimimba 2005). They may occur in the lowlands of Lesotho (Lynch 1994).

Habitat Prefers arid, open country, characterized by short grasses and sparse woody growth. Found in Kalahari *Acacia* bushland, Karoo scrub, Highveld rangelands and fynbos associations, where average annual rainfall is less than about 600 mm, and also in rocky areas associated with dry river beds. Absent from true desert and forested areas, and also from mountainous terrain. Meerkats are usually associated with a hard, often stony or calcareous substrate (Van Staaden 1994, Skinner & Chimimba 2005).

Abundance Densities across the species' distribution are heavily influenced by rainfall and predation pressure, and can fluctuate greatly. In Kgalagadi Transfrontier Park, South Africa (river bed habitat and associated grasslands and *Acacia* bush habitat), densities ranged from 0.95 animals/km² (Apr 1994) to 0.32 animals/km² (May 1995) (Clutton-Brock *et al.* 1999a). This density reduction followed a reduction in rainfall, ca. 10% of long-term average, and virtual cessation of breeding (Clutton-Brock *et al.* 1999a). Total number of Meerkats in study area fell from 100 to 35, six of ten original groups became extinct and mean group size fell from ten to four animals, although mortality was no higher than in any other year (Clutton-Brock *et al.* 1999b). With the resumption of normal rainfall, group size and population size recovered. In Kgalagadi Transfrontier Park, where predators are more abundant and Meerkats more subject to predation, population density was lower compared with those on similar ranchland where predators are reduced (Clutton-Brock *et al.* 1999a).

Adaptations Dentition appears adapted towards an insectivorous diet. Cheekteeth have high cusps, and the carnassial sheer appears poorly developed. The hind part of the first lower molar is relatively flat and together with the second lower molar occludes with the first and second upper molars, to provide a platform for grinding.

Meerkats are well adapted both behaviourally and physiologically to survive the harsh desert environment. They are physiologically adapted to cope with periods of low food supply (necessary during dry winter months and also because feeding may be restricted either by cold winter mornings or hot summer midday) and with the extreme heat of the desert. Meerkat metabolic rate is only 58% of that found in other mammals of a similar size (Müller & Lojewski 1986). A low metabolic rate lowers internal heat production, reduces energy demands during resting (and thus reduces the amount of time required for foraging) and limits evaporative water loss. They also have a high thermal conductance, enabling them to lose heat without concomitant loss of water and a remarkable capacity for heat dissipation through evaporation (Müller & Lojewski 1986). At air temperatures as high as 40° C, Meerkats can resist heating for up to five hours by panting like a dog. Behaviourally, Meerkats avoid both extreme high and low temperatures (Doolan & Macdonald 1996a). As temperatures decrease and day length shortens, Meerkats emerge from the den later, start foraging later and finish activities before sunset. They avoid the problem of rapid heat loss at night (due to their high thermal conductance and extremely high lower critical temperature, 30° C; Müller & Lojewski 1986) by sheltering in burrows (where temperature fluctuations are far less than above ground; Lynch 1980) and huddling in groups for extra warmth. Huddling is particularly important for kits that are vulnerable to cold and as a means of increasing the amount of energy that can be allocated to development (Doolan & Macdonald 1997b). Extreme high midday temperatures in Jan, Feb and Mar are avoided by taking 'siestas', which cease in Apr. Meerkats often sprawl on damp ground or warm rocks to assist with changing body temperature.

Meerkats are accomplished diggers, excavating their own burrows, which usually have many entrances, and forming large warren sites. Entrance holes are about 150 mm in diameter, narrowing to tunnels 75 mm high or more that descend 1.0–1.5 m, end at two or three levels, and are interconnected by chambers 300 mm high and up to 450 mm long (Lynch 1980). They also expel Cape Ground Squirrels *Xerus inauris* and Yellow Mongooses *Cynictis penicillata* from burrows, although they will also share burrows with these two species apparently without competition or agonistic behaviour. They have also been recorded sharing burrows with Southern African Springhares *Pedetes capensis*, *Rhabdomys* sp., African White-tailed Mice *Mystromys albicaudatus*, Highveld Gerbils *Gerbilliscus brantsii*, Rock Hyraxes *Procavia capensis*, Cape Grey Mongooses *Herpestes pulverulentus* and Slender Mongooses *H. sanguineus* (Lynch 1980). Deserted warrens are sometimes found. Digging to maintain bolt-holes and dens is carried out as a group. When burrowing, the ear pinnae fold over the ear opening to prevent the entry of dust and debris into the external auditory meatus.

Meerkats are opportunistic, generalist insectivores, never entirely dependent on a single food category, which allows flexibility to cope with variable abundance of food resources according to habitat and weather. They are highly social, with unique sentinel behaviour when group foraging, thereby increasing predator avoidance in open and exposed habitats. They have a remarkable ability to withstand

snakebites (can tolerate six times the venom that would kill a rabbit), and are immune to scorpion venom, allowing them to use these venomous species as food resources.

Foraging and Food Carnivorous. Meerkats feed mostly on invertebrates, particularly Coleoptera but also Hymenoptera, insect pupae, Orthoptera and scorpions; reptiles (including lizards, geckos, snakes and amphisbaenids) are an important supplement in all months (Meerkats are more reliant on reptiles than are other mongooses) (Zumpt 1968, Smithers 1971, Lynch 1980, Stuart 1981, Doolan & Macdonald 1996a). Termites may also be important (Lynch 1980). Unlike Yellow and Banded Mongooses *Mungos mungo*, Meerkats do not take large active rodents, although during rodent population explosions small murids may be taken. Meerkats will opportunistically feed on birds' eggs.

Doolan & Macdonald (1996a) recorded diet in SW Kalahari, where insects constituted 78.1% of the diet (by frequency of occurrence), of which larvae (33.4%) and adult Coleoptera (27.5%) were most important throughout the year. Snakes and amphisbaenids were a minor prey component, but geckos were more important, especially *Ptenopus garrulus* (53.7%) and *Chondrodactylus angulifer* (13.3%). Two scorpion species were eaten (*Opisthophthalmus* and *Parabuthus* spp.), both of which are tackled according to anatomical differences (although Meerkats are apparently relatively immune to scorpion venom): the large pincers of *Opisthophthalmus* are avoided by eating the rear end first, while the large abdominal sting of *Parabuthus* is avoided by consuming the head first.

Overall, diet varies depending on availability, which is affected by habitat and weather. In the Kalahari, telebrionid beetle larvae are particularly numerous in red sand dunes, Barking Geckos *Nephruroides miltii* and large scarabid beetles in the tangled roots of rhyzozum bushes and Cockchafer Beetles *Melolontha melolontha* in river beds. Beetle larvae are abundant in hot, wet conditions, thus during the dry winter (when general prey abundance is reduced) food is limited to ants and smaller insects. During Jul (winter), much effort is expended in digging deep foraging holes to capture large geckos (Doolan & Macdonald 1996a). On the Makgadikgadi Pans, where Barking Geckos are absent, bullfrogs are an important dietary component (Wilson & O'Riain 2004). Meerkats rarely drink, obtaining their water from succulent prey. However, Tsama Melons *Citrullus lanatus*, succulents, tubers or fruit may be chewed during dry weather (Kingdon 1997).

Meerkats forage by day in tightly cohesive groups; individuals generally within 5 m of one another (often within 1 m), the whole group covering a 20–50 m long axis (up to 100 m in the dry season) (Doolan & Macdonald 1996a). They forage for 5–8 hours per day, meticulously searching through sand (digging up to 20 cm below ground) for prey (Clutton-Brock *et al.* 1999a). Generally, a different area is searched each day – it may be a week or more before a particular route is repeated. Two or three Meerkats may dig together to unearth large geckos. Foraging interference is rare but may occur during the dry season. Food intake decreases in winter. Breeding ♀♀ increase food intake rates when reproductively active (Jan–Apr).

Social and Reproductive Behaviour Meerkats have a sophisticated social organization involving much group cooperation. Groups typically contain ten individuals, although as many as 30 is not

unusual. Groups consist of one to three breeding ♀♀, up to four adult ♂♂, several yearlings and up to a dozen young. In SW Kalahari, groups typically comprised 4.2 adults and 1.9 yearlings (Doolan & Macdonald 1997b). Group size remains relatively constant from year to year although there can be considerable change in individual membership and many individuals may be non-kin (Doolan & Macdonald 1997a).

There is a dominance hierarchy amongst both sexes. Social status increases with age, but ♀♀ can attain dominance (breeding status) by inheritance, by the outcome of aggressive competition (fighting, although challenges by subordinate ♀♀ are rare; Sharp & Clutton-Brock 2011), by immigration into a group without a breeding ♀, or by forming a new group with ♂♂ emigrated from another group (Doolan & Macdonald 1996b, Clutton-Brock *et al.* 1998a). The dominant ♀ is usually the largest and heaviest ♀ in the group (Clutton-Brock *et al.* 1999b, 2001b).

Females are more likely to breed in their natal group than ♂♂ (Clutton-Brock *et al.* 2002). Some individuals of both sexes may remain in the group for all, or much, of their lives although both yearlings and adults of both sexes regularly disperse and join other groups; ♂♂ are more likely to disperse than ♀♀. Both sexes are known to disperse *en masse* (often in groups of kin), although ♂♂ are more likely to disperse as a group (Doolan & Macdonald 1996b). Conversely, dispersing ♀♀ usually travel further than dispersing ♂♂. Old ♂♂ also can be ousted by a gang of ♂♂ taking over the group. Dispersal amongst adults is highest early in the breeding season when within-group hostility is greatest (Doolan & Macdonald 1996b). Subordinate ♀♀ rarely leave the group of their own volition, whereas ♂♂ usually do (Clutton-Brock *et al.* 1998a). However, subordinate ♀♀ can be forcibly expelled from the group by dominant ♀♀ during the latter weeks of the dominant female's own pregnancy, but often return soon after the birth of the pups (Clutton-Brock *et al.* 1998a). Few emigrants successfully establish new groups (Clutton-Brock *et al.* 1999a). Immigrants sometimes have to persist for days to gain acceptance to a group; successful immigrants to established groups are almost exclusively male (Clutton-Brock *et al.* 1999b).

Groups are territorial, inhabiting expansive territories of between 200 and 1000 ha in the S Kalahari. Bolt-holes and dens are important territorial features, with Meerkats seldom being more than 50 m from the nearest safe burrow. Scent-marking is frequent near territory borders, and also used in response to the scent of a neighbouring group; some latrines are found in territorial core regions where they may play a role in mate defence (Jordan *et al.* 2007). Scent-marking is undertaken mainly by the dominant pair in the group, with burrow entrances frequently marked using the anal gland. Territories are actively defended from neighbouring groups, and during skirmishes between troops some individuals may be severely wounded or even killed.

Group members act as sentinels while others forage, using prominent features (e.g. tops of large termite mounds) as look-out posts (see Clutton-Brock *et al.* 1999c for a discussion of the selfishness of this behaviour; it is possible that Meerkats guard when satiated, so, rather than putting themselves at risk are actually safer when guarding as they see the predator first and are often near a bolt-hole). These duties are shared by all group-members but vary with status (e.g. older subordinate ♂♂ spend more time guarding and often from the highest vantage points than other group members).

The entire group is in constant vocal communication during foraging. Complex vocalizations are used to communicate to the group during guarding – they signal that the guard is alert and also when danger is present (calls differ depending on type and severity of threat). A sharp bark from the sentinel sends the colony scattering to their burrows. They can distinguish a Martial Eagle *Polemaetus bellicosus* (that will attack) from a very similar looking Black-breasted Snake-Eagle *Circaetus pectoralis* (not considered a threat). Manser (1999) and Townsend *et al.* (2011) suggest that coordination of vigilance is strongly influenced by vocal communication although does not appear to mediate a strict rotation of guarding duty. Manser & Bell (2004) demonstrated by means of manipulation experiments that Meerkats know in which direction to run when an alarm call is given and must have detailed knowledge of the direction and the distance of specific burrow locations. However, the authors did not conclude that they have a spatial map of their territory, but using place recognition or reorientation of specific landmark features Meerkats were able to escape to the nearest bolt-hole.

Subordinate ♀♀ are reproductively suppressed (Doolan & Macdonald 1997a), the mechanism for which is not fully understood, although hormone excretory patterns during oestrus intervals are possible (Moss *et al.* 2001). This reproductive suppression is aggressively enforced by the dominant ♀ by means of forced emigration and infanticide. Pregnant, dominant ♀♀ frequently kill pups born to subordinate ♀♀, most often those of closely related ♀♀ (Clutton-Brock *et al.* 1998a). However, although dominants monopolize reproduction, subordinates may become pregnant. Pregnant subordinates also kill pups, including those of other subordinates and of the dominant ♀. Litters born to ♀♀ of any rank are less likely to survive their first four days if a subordinate is pregnant. However, dominant ♀♀ are more likely than subordinates to give birth when no other ♀♀ are pregnant, and so lose fewer litters to infanticide than subordinates (Young & Clutton-Brock 2006).

Baseline levels of reproductive hormones are low in subordinate ♀♀. O’Riain *et al.* (2000) suggest that this has more to do with avoidance of incest and lack of unrelated mates than with presence of the dominant ♀, but Young *et al.* (2008) also raise the possibility of subordinate restraint in response to potential dominant interference. Hormone levels are also correlated with age in both sexes, with female levels also affected by body weight and access to unrelated breeding partners. Carlson *et al.* (2004) observed that when these factors are controlled for there are no rank-related differences in the plasma levels of luteinizing hormone among ♀♀ or testosterone among ♂♂. Physiological suppression apparently rapidly reversed as subordinates of both sexes were observed to mate with unrelated roving individuals (O’Riain *et al.* 2000). Griffin *et al.* (2003) identified a strong reproductive skew in favour of dominants, but the extent of skew was variable across sexes and sites suggesting that the skew arises from incest avoidance and reproductive suppression of the subordinates by the dominants. Reproductive suppression in ♂♂ probably operates through behavioural mechanisms (Moss *et al.* 2001), and does not always work. Reproduction suppression amongst ♀♀ may have a more physiological basis and also is not always complete. For example, in SW Kalahari up to three ♀♀ have been recorded as reproductively active simultaneously and each made several breeding attempts within a breeding season. Plural breeding

was common, occurring in 40% of all band years, particularly in larger Meerkat groups and among older individuals (Doolan & Macdonald 1997a), and reproductive suppression likely varies with the relative costs of subordinate breeding to dominants (Clutton-Brock *et al.* 2010). In four groups observed by O’Riain *et al.* (2000), all ♀♀ within each group fell pregnant following immigration of an unrelated ♂, and Young *et al.* (2007), using paternity analyses, estimate that prospecting subordinate ♂♂ sire 20–25% young in the population through extra-group matings.

Social factors tend to determine reproductive success; this contrasts with non-cooperatively breeding social vertebrates in which this is governed by maternal factors (Russell *et al.* 2002). All group members provide food to young and participate in ‘babysitting’ at the den (chasing away predators and huddling with kits to provide warmth) while the mother feeds, and guards the ‘crèche’ when the young are old enough to accompany the group foraging (Doolan & Macdonald 1999, Clutton-Brock *et al.* 2002). Helpers benefit lactating mothers in that increasing the number of helpers reduces a mother’s daily energy expenditure, while every ten helpers (even in the absence of allolactators) allow mothers to decrease their daily energy expenditure during peak lactation by an amount equivalent to the energy cost of one pup (Scantlebury *et al.* 2002). Reduction in the ratio of helpers to pups depresses daily weight gain and growth of pups and daily weight gain of helpers. The effect of helpers on fitness of pups extends beyond weaning: helpers reduce the age at which offspring begin to reproduce as subordinates and increase the probability that they will compete successfully for alpha rank (Russell *et al.* 2007). In turn, helpers may gain direct as well as indirect benefits by feeding pups (Clutton-Brock *et al.* 2001c). The number of helpers within a group is also correlated with the number of litters that ♀♀ deliver each year, probably due to ♀♀ in large groups giving birth earlier with shorter inter-birth intervals (Russell *et al.* 2003). However, Russell *et al.* (2003) found no evidence to suggest that helpers have a direct effect on either litter-sizes at birth or pup weights at weaning, suggesting that the influence of helper numbers up to weaning is indirect through an influence on maternal weight at conception. Female Meerkat helpers contribute more to rearing young than do ♂♂, and also feed female pups more frequently. These sex differences in cooperative behaviour are probably generated by sex differences in philopatry because ♀♀ derive greater direct benefit from raising recruits to their natal group (Brotherton *et al.* 2001).

Doolan & Macdonald (1999) observed allonursing in six of 25 litters that included three incidents of spontaneous lactation when subordinates nursed the young of higher-ranking ♀♀. Clutton-Brock *et al.* (1999b) report allosuckling in around half (8/17) of all breeding attempts in which more than one mature ♀ was present in the group; in this case all allosucklers were subordinate ♀♀ and, in one case, three subordinate ♀♀ suckled one litter. Clutton-Brock *et al.* (2003) observed that dominant breeders contributed less than adult helpers to babysitting and pup feeding, but raised their individual contributions to pup care to a greater extent when helper : pup ratios were low. In contrast to subordinates, dominant breeders did not increase their contributions when they foraged successfully; while subordinates of both sexes assisted in rearing the young when dominants bred, dominant ♀♀ contributed little when subordinates attempted to breed, and male helpers (but not females) reduced their contributions to the care of pups.

Pups are initially incapable of finding their own prey, and use vocalizations in soliciting food from potential feeders. One call type is emitted continuously when following foragers (a repeat call that may be heard up to 20 m away, although pups usually within 2 m of the feeder), another distinct and higher pitched call (heard up to 30 m or more away) emitted when a forager finds prey, possibly to attract attention to them rather than a littermate (Manser & Avey 2000). The two calls differ in length, rate, frequency and amplitude. Using observations and playback experiments, Manser & Avey (2000) demonstrated that pups that called longer and more intensely obtained more prey from feeders, and comparisons of food-deprived and experimentally fed Meerkat pups revealed that hungry pups increased the rate of repeat calls, which adults responded to by increasing their food allocation (Manser *et al.* 2008). Recently, Thornton & McAuliffe (2006) have shown that Meerkats teach pups prey-handling skills by providing them with opportunities to interact with live prey. In response to changing pup begging calls, helpers alter their prey-provisioning methods as the pups grow older, thus accelerating learning without the use of complex cognition. Cessation of begging, and adult provisioning, occurs when juveniles (aged 100–120 days) are no longer able to produce stimulating begging calls (Madden *et al.* 2009).

Individual helpers vary widely in their provisioning, with food items given to pups ranging from 3 to 49% of the total found (average 26%) (Clutton-Brock *et al.* 2001a) and is reduced as pups approach three months (Manser & Avey 2000). The proportion of food given to pups by helpers is higher when more food is acquired by the helper, and is also higher in smaller groups and larger litters. The probability of prey being fed to a pup shows a positive relationship with prey size and a negative relationship with pup distance (Brotherton *et al.* 2001). Females and older individuals contribute more food than either ♂♂ or young individuals, respectively (Clutton-Brock *et al.* 2001a). The authors suggest that kinship is not related to food provisioning. Females are also observed to feed female pups significantly more than male pups, while ♂♂ feed pups of both sexes equally. These sex biases in feeding contributions may result from female group members benefiting more than ♂♂ from higher pup survival, and in particular higher female pup survival, because ♀♀ are the philopatric sex (Brotherton *et al.* 2001). ‘False feeding’ (when helpers carry food to pups and then eat it themselves) may also occur when helpers decide not to deliver food items to pups after assessing the needs of pups relative to their own (Clutton-Brock *et al.* 2005).

Individual contributions to guarding pups at the burrow are also unrelated to kinship, although the amount of time helpers are present at the den ranges from 8 to 42% of the daytime (Clutton-Brock *et al.* 2000). Pups are only rarely left alone at the den and the absence of a babysitter is not affected by group size; a lack of babysitters is compensated for by other helpers contributing more time to babysitting (Clutton-Brock *et al.* 1998b). Females contribute more to babysitting than do ♂♂, with adult ♀♀ contributing the most (amongst ♂♂, yearlings and subadults contribute more than both juveniles and adults), and heavier individuals and those that gained more weight during foraging babysit more than lighter individuals or those that gained less weight (Clutton-Brock *et al.* 2000). Parents rarely contribute to babysitting, yet it seems to incur a substantial energetic cost (Clutton-Brock *et al.* 1998b). Babysitters usually stay at

the burrow for the whole day, feeding little or not at all; consequently, they may suffer substantial weight loss. Over a 24-hour period, an individual babysitter may lose 1–2% of its body weight, while foraging individuals gain about 2%, and frequent babysitters may lose up to 11% of body weight over the entire babysitting period (Clutton-Brock *et al.* 1998b). In ♀♀, at least, weight losses of this magnitude are likely to incur a fitness cost, as breeding is dependent upon weight (Clutton-Brock *et al.* 1998b). Individual differences in foraging success appear to be the principal factor affecting contributions to cooperative behaviour. Contributions to different cooperative activities are positively correlated across individuals, with some helpers consistently contributing more than others to all cooperative activities (English *et al.* 2010).

Reproduction and Population Structure Breeding season in the S Kalahari is from Oct to Jun, generally after heavy rains, but may be extended in wetter years (Doolan & Macdonald 1997b). Most young are born between Jan and Mar, but litters may be born throughout the year (Clutton-Brock *et al.* 1999b). Breeding might not occur when rainfall is low (Clutton-Brock *et al.* 1999b). Generally only the dominant ♂ and ♀ breed, but in particularly productive years subordinates may also breed though at a lower rate than dominants. Females rarely breed before three years old (Doolan & Macdonald 1997b), although animals as young as 14 months old have been recorded breeding (P. Brotherton pers. comm.). Dominant ♀♀ usually produce one to three litters (depending on the amount of rainfall) (average = 1.9) (Doolan & Macdonald 1997b) of 3–7 young per litter at emergence. When subordinates breed they usually produce fewer litters than dominants, and litter-size is in the range 1–8. Mean litter-size at emergence is about four (Doolan & Macdonald 1997b, Clutton-Brock *et al.* 1999b). Daily energy expenditure of lactating mothers increases with litter-size (Scantlebury *et al.* 2002).

Up to four litters per year is possible in dominant ♀♀, but rare when pups from earlier litters survive (Clutton-Brock *et al.* 1999b). About 1.8–1.9 emerging litters are produced per group per year (Doolan & Macdonald 1997b, Clutton-Brock *et al.* 1999b). Gestation is ca. 60–70 days, inter-birth interval (for the same ♀) 82–90 days, with a minimum of 71 days (Doolan & Macdonald 1997b, Clutton-Brock *et al.* 1999b). Young emerge from the den at ca. 19 days, and begin foraging with the group at ca. 26 days (Clutton-Brock *et al.* 1999b). Clutton-Brock *et al.* (1999b) found that pups grow rapidly during their first month: within five days of emergence they averaged 100 g (n = 70), at six weeks 179 g, at three months 394 g (n = 40), and at six months 529 g (n = 28). Pups had a daily growth rate of 4.5 g/day over the first three months. At 12 months, pups had attained roughly 90% of adult body weight.

Population adult sex ratio is ca. 1 : 1, whereas adult/young ratio is ca. 1 : 0.4 (Clutton-Brock *et al.* 1998b). Pup survival between emergence and independence is related to maternal status, pup sex and overnight weight loss as well as group size, daytime temperature and monthly rainfall (Russell *et al.* 2002). Litters may be abandoned during a drought and flooding is a potential risk for litters confined to the den. Between three and five weeks of age the young are particularly vulnerable to hypothermia, and between five and 12 weeks, to predation. Annual mortality rate of adults (>1 year) ranges from 0.32 to 0.68 depending on predator density (Clutton-Brock

et al. 1999a) and from 0.76 to 0.80 for pups (Doolan & Macdonald 1997b, Clutton-Brock *et al.* 1999b). Pup survival continuously decreases from 0.90 at two weeks to 0.19 at one year (Clutton-Brock *et al.* 1999b). These figures are low in comparison with both Dwarf Mongooses *Helogale parvula* and Slender Mongooses in the Serengeti (Clutton-Brock *et al.* 1999b and references therein). However, data are from Kgalagadi Transfrontier Park, which lies towards the edge of the Meerkat's range, thus survival is possibly higher in more vegetated areas (Clutton-Brock *et al.* 1999b). Potential longevity in the wild is ca. 5–15 years (Van Staaden 1994), while in captivity one specimen was 20.6 years of age when it died (Nowak 1999).

Predators, Parasites and Diseases Pups are particularly vulnerable to predators both during the denning period and on foraging sorties (from ca. four weeks), less vulnerable after about three months (Doolan & Macdonald 1997b). Juveniles and pups are preyed by snakes and raptors, including Cape Cobras *Naja nivea*, Martial Eagles, Tawny Eagles *Aquila rapax*, Bateleurs *Terathopius ecaudatus*, Lanner Falcons *Falco biarmicus* and Pale Chanting-goshawks *Melierax canorus* (Doolan & Macdonald 1997b, 1999, Dennis & Macdonald 1999, Clutton-Brock *et al.* 1999a). These predators accounted for ca. 25% of mortalities in young Meerkats (Doolan & Macdonald 1997b). Other larger carnivores (e.g. Lions *Panthera leo*, Spotted Hyenas *Crocuta crocuta* and Black-backed Jackals *Canis mesomelas*) also are a potential threat, as are Ratels *Mellivora capensis*. Jackals, Martial Eagles and Tawny Eagles are the most dangerous predators to Meerkats. Meerkats mob many predators (e.g. Cape Cobras) as a group. Goshawks and other smaller raptors, and small Cape Foxes *Vulpes chama*, are attacked on sight. Black-backed Jackals and Ratels are generally avoided unless Meerkats are cornered. Tendency to mob predators depends on group size: more than five Meerkats will mob a jackal, whereas smaller groups and individuals are more likely to flee to a refuge. Meerkats will attempt to rescue group members and care for injured members.

Lynch (1980) listed a number of parasites taken from animals in the Free State, including fleas and ticks, such as *Amblyomma hebraeum*, *Haemaphysalis zumpti*, *H. leachi*, *Ixodes pilosus*, *Rhipicephalus appendiculatus* and *R. evertsi*; a single *H. zumpti* was taken from an animal in the Northern Cape (Horak *et al.* 2000).

Recently, Alexander *et al.* (2002) described an outbreak of *Mycobacterium tuberculosis*, a human pathogen, in free-ranging Meerkats in South Africa. Animals most at risk of TB infection are groomers (but not groomees), those that receive (but not initiate) aggression, and ♂♂ that rove between groups (Drewe 2010). Meerkats might be highly susceptible to toxoplasmosis (JuanSalles *et al.* 1997).

Conservation IUCN Category: Least Concern. CITES: Not listed.

Relatively widespread within southern Africa, present in several large protected areas, such as Kgalagadi Transfrontier Park (South Africa/Botswana) and Makgadikgadi N. P. (Botswana), and not currently believed to be threatened. Although groups can go extinct during dry years (Clutton-Brock *et al.* 1999a), populations are believed to be stable.

Measurements

Suricata suricatta

TL: 503 (472–545) mm, n = 20

T: 211 (182–235) mm, n = 20

HF s.u.: 65 (60–68) mm, n = 20

E: 19 (17–21) mm, n = 20

WT: 709 (560–915) g, n = 20

GWS: 42.7 (25.8–49.0) mm, n = 57

Free State (sexes combined) (Lynch 1980)

WT (dominant ♂♂): 808 g, n = 8

WT (subordinate ♂♂): 659 g, n = 12

WT (dominant ♀♀): 721 g, n = 6

WT (subordinate ♀♀): 640 g, n = 9

Kalahari (Clutton-Brock *et al.* 1999a)

Key References Clutton-Brock *et al.* 1998a, b, 1999a, b, c, 2000, 2001a, b, c, 2002, 2003, 2004, 2010; Dennis & Macdonald 1999; Doolan & Macdonald 1996a, b, 1997a, b, 1999; Lynch 1980; Russell *et al.* 2007; Townsend *et al.* 2011; Van Staaden 1994.

David W. Macdonald

GENUS *Mungos* Banded Mongooses

Mungos E. Geoffroy & G. Cuvier, 1795. Magasin Encyclop. 2: 184, 187.

The genus contains two species: Banded Mongoose *Mungos mungo* and Gambian Mongoose *M. gambianus*, both endemic to sub-Saharan Africa. The Gambian Mongoose occurs only in West Africa, where it overlaps with the Banded Mongoose, which has a much more widespread distribution from Senegal to Somalia and southwards to South Africa. Both species live in open grass-woodlands and avoid closed forest (but may occur in forest belts).

Members of the genus are small, stout, greyish-brown mongooses with short legs and a short, long-haired tapering tail. Their bristle-haired, yellow-speckled coat lacks any underfur. Head and distal parts of fore- and hindlimb shorter-haired and darker than body and tail. Feet five-toed, with toes slightly webbed; soles of hindfoot

naked to the heel. The Banded Mongoose has about a dozen black transverse bands from mid-back to the base of the tail, while the Gambian Mongoose has a 5 mm wide brownish-black stripe on the side of the neck from ear to foreleg. Dental formula is $I^{3/3}, C^{1/1}, P^{3/3}, M^{2/2} = 36$. Upper and lower first premolars are absent.

Ellerman *et al.* (1953) included the genus *Crossarchus* in *Mungos*. Phylogenetic studies of Herpestidae indicate that *Liberiictis* is closer to *Mungos* than *Crossarchus* (Veron *et al.* 2004, Perez *et al.* 2006, Patou *et al.* 2009).

Harry Van Rompaey

***Mungos gambianus* GAMBIAN MONGOOSE**

Fr. Mangué de Gambie; Ger. Gambiamanguste

Mungos gambianus (Ogilby, 1835). Proc. Zool. Soc. Lond. 1835: 102. Gambia.Gambian Mongoose *Mungos gambianus*.

Taxonomy Monotypic. Originally included in *Herpestes*, but placed in the genus *Mungos* by Gray in 1843. Allen (1939) considered it a species of *Crossarchus* due to an external resemblance to the Common Cusimanse *Crossarchus obscurus*. Synonym: *gambiense*. Chromosome number: not known.

Description A small, compact, harsh-haired mongoose. Ears small and round. Muzzle and ring around eyes black. White or yellowish throat and chest separated from grey nape by a bold, 5 mm wide brownish-black stripe on the side of the neck stretching from ear to foreleg. Dorsal pelage brownish-grey, brightly speckled with yellow. Pelage coarse, with no underfur. Ventral pelage scanty and golden to rust-coloured. Upper surfaces of fore- and hindfeet black. Sole of hindfoot naked to the heel. Toes slightly webbed. Strong claws on forefeet. Tail tapering, ending in a black tip. Anal scent glands probably similar to those of Banded Mongoose *Mungos mungo*. Males slightly larger than ♀. Nipple numbers not recorded.

The skull is very similar to that of the Banded Mongoose. Rosevear (1974) remarked on several differences, including the carotid foramen being almost obscured from view by a peculiar, irregularly formed, angular projection (see Hayman 1935) and the much smaller teeth, with $P^4 \sim 15\%$ longer in Banded Mongoose (average length = 4.27 mm in *M. gambianus* cf. 4.93 mm in *M. mungo*) (Rosevear 1974; and see Colyn *et al.* 2000).

Geographic Variation None recorded.

Similar Species

Mungos mungo. There is nearly a complete range overlap with the Banded Mongoose. Back with prominent transversal bands, and no stripe on the side of the neck.

Crossarchus obscurus. There is nearly a complete range overlap with the Common Cusimanse. Shaggy, with dark pelage; muzzle elongated, distance from rhinarium to mouth opening longer.

Distribution Endemic to West Africa, ranging from Senegal and Gambia east and south through Guinea-Bissau, Guinea, Sierra Leone,

*Mungos gambianus*

Côte d'Ivoire, Ghana, Togo, Bénin (probably) and Nigeria (Rosevear 1974, Van Rompaey 1991). There are no confirmed records from Liberia. Jeannin (1936) states that they were distributed in the centre and even common in the north of Cameroon; either they have disappeared or, more likely, these observations are based on confusion with the Banded Mongoose. There is also a record from Yankari G. R. (Afolayan & Ajayi 1980) from far north above the Cross R.; however, its confirmed presence so far east of the Niger R. awaits additional material. Until then, it is assumed that the Niger R. forms the eastern limit.

Habitat Almost exclusively Guinea woodland, but may penetrate into the rather similar Doka belt, with less abundant grasses and dominated by *Isoberlinia* trees (Rosevear 1974). In Gambia associated with denser coastal woodland (Grubb *et al.* 1998) and dry parts of dense, partly swampy riverine forest (T. Wachter pers. comm.). It also occurs on Bonthe I., off the coast of Sierra Leone in areas with sand ridges and sparse grass (Rosevear 1974), and in coastal scrub areas on the Accra Plains of Ghana (Cansdale 1946).

Abundance Considered to be rare in the nineteenth century in Gambia and Senegal by Rochebrune (1883). Cansdale (1946) found them fairly common on the Accra Plains of Ghana and Booth (1960) considered them easily the most abundant carnivore in the Guinea savanna. In Senegal, they are occasionally seen in woodland; daytime frequency of observations along roads was 0.08/100 km (Sillero-Zubiri & Marino 1997). The high frequency of carcasses seen at local markets suggests that National Park of Upper Niger, Guinea, supports a good population (Ziegler *et al.* 2002). Despite these

statements few specimens have been collected and relatively few localities are cited in the literature (Van Rompaey 1991).

Adaptations Diurnal and terrestrial; in Senegal, they were mainly seen in the mornings (08:00–10:00h; $n = 14$) and sometimes in the evening (18:00–19:00h; $n = 4$) (Sillero-Zubiri & Bassignani 2001). The practice of smashing snails, eggs and other hard objects by throwing them against something hard, either horizontally backwards through the hindlegs or vertically down to the ground, has been observed from the age of about three months, without the animal ever having seen such action before (Darchen 1988). Shelter is sought in termite mounds and probably in other abandoned burrows (Sillero-Zubiri & Bassignani 2001).

Foraging and Food Insectivorous. Rosevear (1974) assumes from the small size of teeth that the food is weak and soft, probably almost entirely insects, and according to Grubb *et al.* (1998) food resembles that of the Common Cusimanse. Booth (1960) adds lizards and mice, and Darchen (1988) snakes, to the diet. Forages in packs (Sillero-Zubiri & Bassignani 2001).

Social and Reproductive Behaviour Packs of up to 40 animals may be encountered, communicating while moving through thick cover by frequent twittering, which clearly helps pack cohesion (Booth 1960). In Nigeria they are rarely observed and packs normally contain only 10–15 individuals (Happold 1987); packs of 5–6 individuals are normal in Ghana (Cansdale 1946), while in Côte d'Ivoire and Gambia up to 31 individuals have been seen together (Bourlière *et al.* 1974, T. Wachter pers. comm.). In Senegal, packs consisted usually of 3–10 animals although on one occasion 40 animals were seen together spread over an area of 1000 m² with distances between individuals ranging up to 5 m (Sillero-Zubiri & Bassignani 2001).

Reproduction and Population Structure Unknown. Young animals have been collected at the end of Jun in Sierra Leone, at the end of Sep, and during Jan and Feb in Ghana (Rosevear 1974). Two pairs, kept in captivity, did not reproduce (Darchen 1988).

Predators, Parasites and Diseases There is no information on predation on the Gambian Mongoose. As with Banded Mongooses, raptors must pose the greatest threat. A hookworm, *Arthrocephalus gambiensis*, was found in the intestine of a captive specimen (Ortlepp 1925); another captive specimen died from rachitis (Scott 1928).

Conservation IUCN Category: Least Concern. CITES: Not listed.

Poorly known species, but apparently locally common and present in protected areas such as Niokolo-Koba N.P. in Senegal (Sillero-Zubiri & Marino 1997), National Park of Upper Niger (Ziegler *et al.* 2002) and Comoé N. P., Côte d'Ivoire (Fischer *et al.* 2002). There are no known major threats, although they are sometimes found being sold as bushmeat, as in Guinea (Ziegler *et al.* 2002).

Measurements

Mungos gambianus

HB (♂ ♂): 345, 355 mm, $n = 2$

T (♂ ♂): 200, 220 mm, $n = 2$

HF c.u. (♂ ♂): 67, 71 mm, $n = 2$

E (♂ ♂): 21, 24 mm, $n = 2$

GLS: 69.9 (66.5–72.8) mm, $n = 9$

GWS: 37.3 (34.8–39.7) mm, $n = 10$

Ghana (museum specimens: BMNH, MNHN and SBP)

Kingdon (1997) gives WT = 1.0–2.0 kg

Key References Rosevear 1974; Sillero-Zubiri & Bassignani 2001; Van Rompaey 1991.

Harry Van Rompaey & Claudio Sillero-Zubiri

Mungos mungo BANDED MONGOOSE

Fr. Mangué rayée; Ger. Zebramanguste

Mungos mungo (Gmelin, 1788). Syst. Nat., 13th edn, 1: 84. 'Bengala, Persia, aliisque asiae', later restricted by Ogilby (1835: 101) to 'Gambia'.

Thomas (1882: 91) thought it likely that the specimens were obtained from the Cape [i.e. the Cape of Good Hope, South Africa], as did Roberts (1929) and Allen (1939); this was not accepted by Ellerman *et al.* (1953) or Meester *et al.* (1986).

Taxonomy Coetzee (1977) recognized 13 subspecies from the continent, but noted that many of them are morphologically and geographically not well defined. Kingdon (1997) provisionally recognized four distinctive regional populations: *M. m. mungo*, in western Africa; *M. m. zebra*, in the Horn of Africa; *M. m. colonus*, in eastern Africa; and *M. m. taenionotus*, in southern Africa. However, both the physical characteristics and boundaries of regional types await systematic definition, and no subspecies are recognized here. *Mungos mungo* has also been used for the Indian Grey Mongoose, *Herpestes edwardsii* (see Allen 1919 and 1924). Synonyms: *adailensis*, *bororensis*, *caurinus*, *colonus*, *fasciatus*, *gothneeh*, *grisonax*, *marcrurus*, *macrosus*, *mandjarum*, *mungo*, *taenionotus*, *ngamiensis*, *pallidipes*, *rossi*, *senescens*, *somalicus*, *talboti*, *zebra*, *zebroides*. Chromosome number: $2n = 36$ (Wurster & Benirshke 1968, Fredga 1972).

Description A medium-sized, squat mongoose, whitish-grey to dark brown in colour, and easily recognized by a pattern of 10–15 dark transverse bands running across the body from shoulders to rump. Head small and broad with short, pointed muzzle. Rhinarium small and lacking a central slit on the front; upper lip intact. Ears small and rounded. Body covered with coarse hair, short at the head, lengthening toward the rump (reaching a length of 45 mm in eastern specimens). Individual hairs of dorsal pelage light in colour at base, with two broad black bands and a narrow dark tip. Dorsal stripes formed by a matched-up alignment of these banded hairs. Guard coat thick. Ventral pelage very sparse. Limbs generally similar in colour to dorsal pelage. Tail covered in hair, darker toward tip. Five digits on forefeet, four on hind. First digit of forefoot is small, but with an unusually long claw (about 8 mm), used for digging. Other digits on

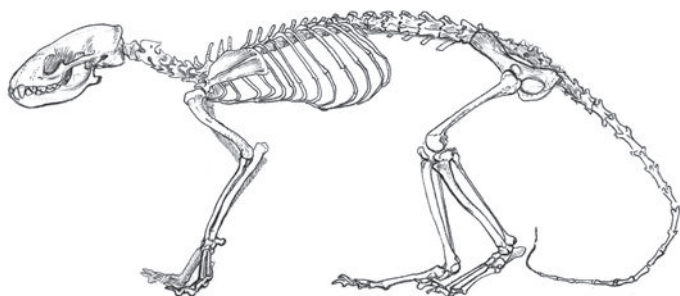


Banded Mongoose *Mungos mungo*.

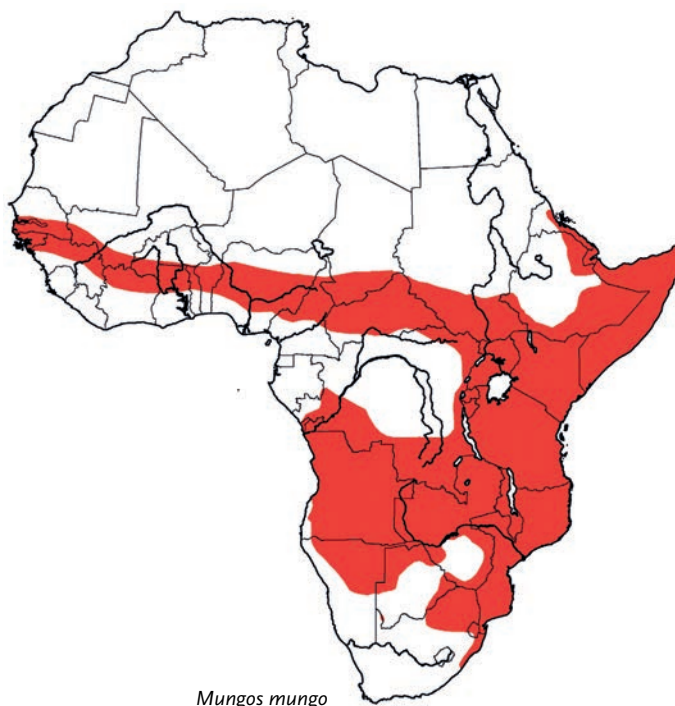
the forefeet are armed with long, curved claws up to 20 mm long. The anal glands open into a subcircular pouch. Females have three pairs of abdominal nipples. There is no sexual dimorphism.

Braincase pear-shaped, broadest at level of ear openings and narrows towards postorbital constriction, which lies well back of the upper portion of the postorbital bars; latter are incomplete, represented by small processes on the zygomatic arch and frontals. Rostrum short and broad. Supraoccipital crest poorly developed; sagittal crest absent. Outer upper incisors considerably larger than the remainder; upper canines slightly curved, short, rounded and sharp, with the lower distinctly recurved. Upper and lower first premolars absent and all cheekteeth have low, rounded cusps (Petter 1969, Skinner & Chimimba 2005).

Geographic Variation There is a wide degree of variation in colouration. For example, in S KwaZulu–Natal (South Africa) specimens that have been attributed to the form *taenionotus* have



Banded Mongoose *Mungos mungo* skeleton.



Mungos mungo

dark reddish-brown upperparts, particularly noticeable between the black bands on the lower back. On the other hand, in specimens attributed to the form *grisonax* of Botswana and Namibia, the upper parts are light grey, with only a faint tinge of reddish-brown between the black bands. Specimens from drier savanna regions tend to be somewhat lighter in colour than those from more lush habitat.

Similar Species

Mungos gambianus. Inhabits moist savannas of West Africa, from Gambia to Nigeria. Brownish-grey mongoose, with dark streaks of fur each side of a lighter coloured neck; no banding pattern. See species profile for discussion on differences in the skull.

Suricata suricatta. Sympatric. Smaller, with shorter tail; dorsal pelage tan to grey with brown banding on back, rump and sides; muzzle short and sharp-pointed.

Distribution Endemic to Africa. Distributed widely across sub-Saharan Africa in a band stretching from Senegal and Gambia to Ethiopia and Somalia, and south to about 31°S in KwaZulu–Natal, South Africa. There is a record of a pack of five Banded Mongooses from the Nossob camp in the Kgalagadi Transfrontier Park (G. Mills pers. comm.). Although fairly widespread in southern Africa, the species appears to be rare in West Africa: it is not recorded from Ghana or Liberia, has never been confirmed in Sierra Leone and Niger, and seems to be known only from the Keneba-Jifarong area in Gambia (Grubb *et al.* 1998). Besides Gambia, Grubb *et al.* (1998) state that there are well-known records from Guinea-Bissau and Nigeria, to which may be added Senegal (e.g. Niokolo-Koba N. P.; Sillero-Zubiri & Marino 1997) and Côte d'Ivoire (e.g. Comoé N. P.; Fischer *et al.* 2002). Grubb *et al.* (1998) conclude that the species may have a disjunct distribution in West Africa. In north-east Africa, their presence has not been confirmed in Djibouti.

Banded Mongooses apparently were introduced to Zanzibar (Pakenham 1984), although neither Stuart & Stuart (1998c) nor Goldman & Winther-Hansen (2003) recorded them during camera-

trapping surveys (despite obtaining images of other elusive species), suggesting they are either now rare or absent.

Habitat Wide range of habitats but primarily found in savanna and woodland, usually close to water. Although commonly found in riverine conditions, it is believed that it is the physiognomy of the vegetation rather than the presence of water that determines their occurrence (Skinner & Chimimba 2005). Often found in habitats containing termitaria, which are used as den sites. Absent from desert, semi-desert and montane regions. Recorded to 1600 m in Ethiopia (Yalden *et al.* 1996).

Abundance Density varies widely between habitats and locations. On the Serengeti plains, Banded Mongooses live at a density of around 3 ind/km² (Waser *et al.* 1995); this is similar to the estimated density of Banded Mongooses in S KwaZulu–Natal (2.4/km²; Maddock 1988). By contrast, a peninsula population in Queen Elizabeth N. P., Uganda, lives at higher densities, averaging 18 ind/km² (Cant 1998, Gilchrist & Otali 2002). Generally less abundant in western regions compared with eastern and south-eastern areas of the distribution. Regional differences in abundance could be related to the specific spectrum of other mongooses present. The greatest overlaps in diet and habitat needs are likely to come from the cusimanses *Crossarchus* spp., the Gambian Mongoose *Mungos gambianus* and the Yellow Mongoose *Cynictis penicillata*.

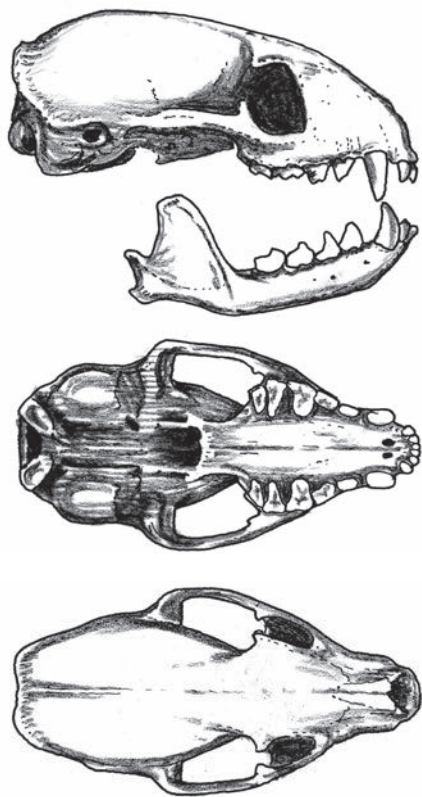
Adaptations The carnassials are better adapted to crushing than slicing, which, together with the weak zygoma and lack of a sagittal crest, suggests an adaptation to a diet of relatively soft or insectivorous

food (Skinner & Chimimba 2005). They have excellent senses of smell, vision and hearing. Terrestrial predators and humans may be sighted at a distance of 100 m or more, and the animals can distinguish avian predators from other, non-predatory birds (e.g. herons) at great distance. Group members respond to distant predators by vocalizing and by standing upright to gain a better view. When danger threatens at closer range, the animals adopt one of two anti-predator strategies, depending on the type of predator. Individuals respond to avian and large terrestrial predators such as Leopards *Panthera pardus* by giving a high-pitched alarm call that sends the entire group running for cover. By contrast, Banded Mongooses group together to drive off smaller terrestrial predators such as jackals *Canis* spp. or Servals *Leptailurus serval*. Group members bunch tightly together and advance slowly, vocalizing aggressively (Kingdon 1977). Banded Mongooses have been known to rescue group members seized by Martial Eagles *Polemaetus bellicosus* (Rood 1983b) and to rescue a pup from a Nile Monitor *Varanus niloticus* (J. S. Gilchrist pers. obs.).

Dens are typically located in abandoned termitaria, but may also be found in the hollows of tree roots, in sheltered spaces in gullies or underneath rock falls. Largely terrestrial, Banded Mongooses do climb to the tops of termitaria, which they use as vantage points, and are also able to climb trees when under stress. Simpson (1964) recorded a pack being chased by African Wild Dogs *Lycaon pictus* that took to the high branches of a fallen tree.

The likely adaptive significance of the banded pattern on the animals' back and rump has been discussed in some detail by Kingdon (1977), who suggested that the primary adaptive purpose of the striped rump was as an advertisement or target for anal scent-marking, thus reinforcing pack cohesion (especially during interactions with other packs or with some predators). In evidence of this, members of a pack were observed to rub their anal glands on a block of ochre and thereafter transfer the pigment to the banded area: in this way all pack members were shown to share a communal odour. The back-marking response is routine, but strongest during periods of intense excitement, such as arrivals, departures and during interactions or exposure to danger (Kingdon 1977).

Scent plays an important role in maintaining group identity and cohesion, with likely a lesser role in the advertisement of territorial boundaries (Jordan *et al.* 2010). Group members regularly mark each other with a sticky, pungent secretion from the anal glands. Individuals that become lost during foraging trips locate the group by scent, and upon reintroduction to the group the returning individuals are vigorously marked by the other group members. Objects such as large rocks or branches are used as marking posts at which group members anal mark, cheek mark, defecate and urinate. Anal marks have been shown to be sexually dimorphic (Jordan *et al.* 2011a) and to differ between individuals with individuals able to discriminate between scents from different individuals (Jordan *et al.* 2011b). Individuals will overmark areas previously anal marked by other individuals, and intra-sexual overmarking rates are higher than inter-sexual rates within groups (Müller & Manser 2008c, Jordan *et al.* 2011a). Males with higher overmarking rates had higher mating success (Jordan *et al.* 2011b). However, there is no evidence that overmarking is correlated with mating success or dominance in ♀♀ (Jordan *et al.* 2011c). Some observations suggest that ♂♂ can determine the reproductive status of ♀♀ in a neighbouring group by monitoring the scent marks at shared marking posts. After



Lateral, palatal and dorsal views of skull of Banded Mongoose *Mungos mungo*.

smelling the scent of groups containing oestrous ♀♀, ♂♂ will sometimes make forays deep into the home-range of a neighbouring group in search of extra-group copulations (M. A. Cant pers. obs.).

Foraging and Food Diet mainly consists of insects, myriapods, snails, small reptiles, the eggs and young of ground-nesting birds, and wild fruits (Smithers 1971, Rood 1975, Smithers & Wilson 1979, Rautenbach 1982, Hiscocks & Perrin 1990). The analysis of a sample of 14 stomachs from Zimbabwe and Botswana revealed that insects occurred in every stomach, mainly Coleoptera and their larvae, followed by grasshoppers, mole crickets, formicid ants, their eggs and larvae, and caterpillars (Smithers 1971, Smithers & Wilson 1979). Groups also take advantage of human waste food at garbage dumps (Gilchrist & Otali 2002, Otali & Gilchrist 2004).

Banded Mongooses are diurnal, typically emerging from refuges in the early morning and retiring before sunset; no nocturnal activity has been recorded for the species. Each morning, the group embarks on a foraging trip lasting several hours before retiring to rest in the shade. There is usually a second foraging session in late afternoon. Foraging distances average 2–3 km in Uganda (Neal 1970) but may be more extensive, up to 10 km, in the more open savanna of Serengeti N. P. (Rood 1975, 1986). Foraging members of the group fan out and search for food independently, sniffing the ground, turning over leaf litter, and digging in the earth with their front paws. Individuals rarely dig more than a few centimetres below the surface for prey. Dung of large herbivores, especially elephants, is enthusiastically tackled due to the high density of beetle prey within. Group members maintain contact with each other by emitting low grunts every few seconds. Individuals generally do not share food but defend potential food items (foraging holes, scrapes or dung) and food items from other individuals.

Millipedes, frogs and other prey that produce noxious secretions are rolled around in the earth before being eaten. Baxter (1993) recorded a Banded Mongoose feeding on a Greater Red Musk Shrew *Crocidura flavescens* in captivity. The mongoose bit off the shrew's head and then proceeded to bite into the thoracic cavity while pulling downwards, with its forepaws and claws, on the skin, progressively removing the skin with its large, unpalatable subcutaneous glands. Eggs and hard-shelled organisms (e.g. dung beetles and pill millipedes) are cracked open by clasping them between the front paws and throwing them back between the hindlegs onto a rock or other hard surface (Simpson 1964, Eisner & Davis 1967, Eisner 1968, Müller 2010), in much the same way as does the Dwarf Mongoose *Helogale parvula*.

Social and Reproductive Behaviour Banded Mongooses are cooperatively breeding mammals that typically live in groups of 15–20 individuals. Around campsites or other artificial food sources groups may number up to 70 (Pienaar 1964). In Queen Elizabeth N. P., nine groups of Banded Mongooses averaged 16 individuals (>6 months old) and occupied home-ranges ranging in size from 0.3 km² to 2.0 km² (Rood 1975, 1986, Cant 1998, 2000, Cant *et al.* 2001, De Luca & Ginsberg 2001, Gilchrist & Otali 2002). In other, drier regions (e.g. southern Africa) home-ranges are apparently larger (>2 km²; Hiscocks & Perrin 1991a). Groups may utilize up to 40 dens within their home-range, changing between dens every 2–3 days (less often when breeding). All members of a group sleep in the same den overnight and pups remain in the den whilst the group forages during their first 3–4 weeks of life. Favourite den sites include abandoned termitaria,

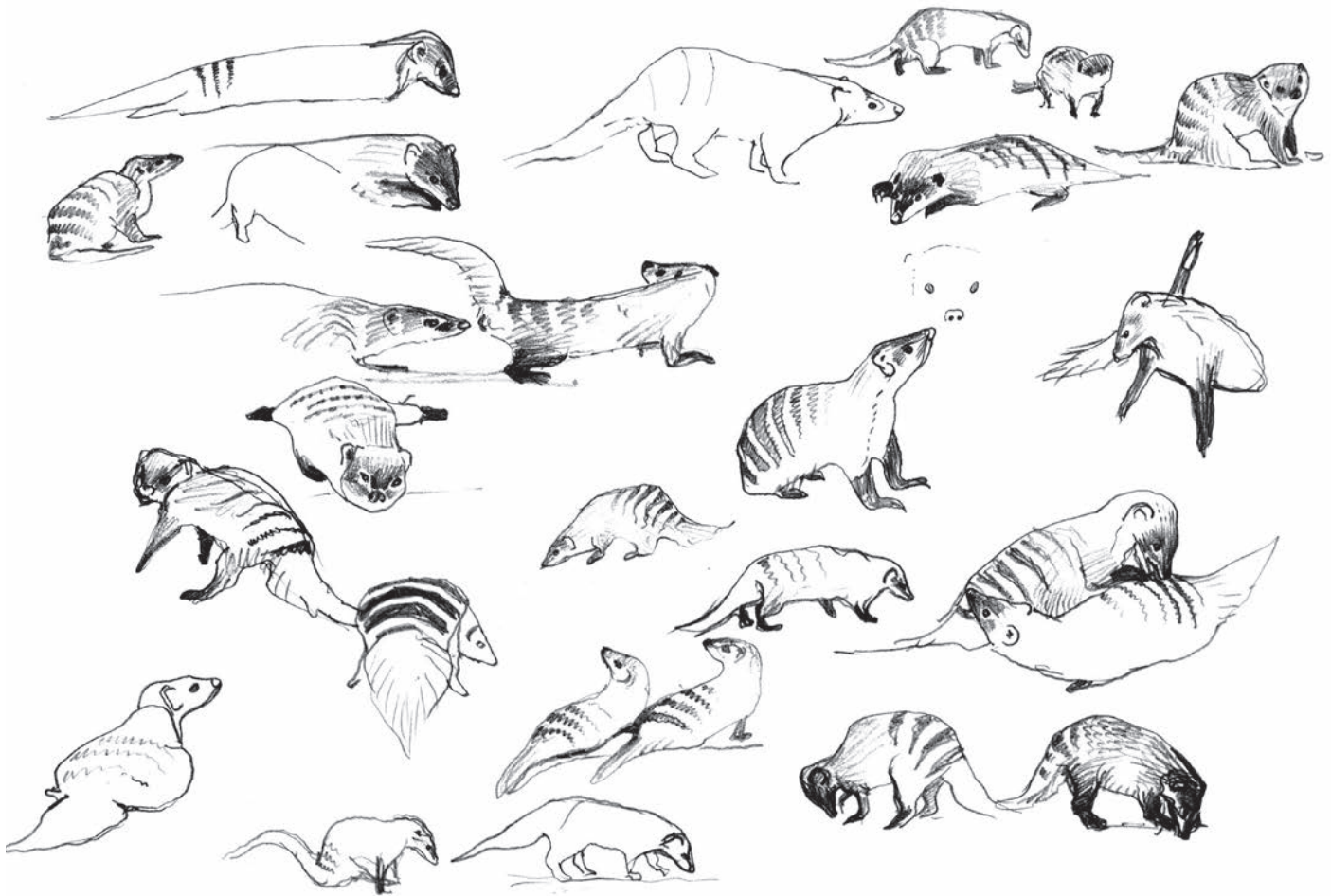
crevices, gullies and thickets, and even the burrows of springhares *Pedetes* spp. and Aardvark *Oryzomys afer*, but the animals will also den in outhouses and other artificial shelters (Neal 1970, Rood 1975, Hiscocks & Perrin 1991a).

Home-ranges are vigorously defended against neighbouring groups of conspecifics. Encounters between groups usually lead to physical conflict, during which animals may be severely wounded and even killed (Rood 1975, Cant *et al.* 2001). Upon sighting each other, members of rival groups respond by standing erect and giving a distinctive, screeching call, which alerts the rest of their group to the presence of a rival group. The response of individuals to the 'screech' call is determined by the location, with greater response within the exclusive area of home-range than peripheral (overlapping) areas, and by group size, with larger groups more likely to respond and bunch than smaller groups (Furrer *et al.* 2011). Groups also respond to scent marks from other groups, and differentiate between strangers and (familiar) neighbours, with a more intensive response to neighbour scent marks (Müller & Manser 2007).

The sight of a large rival group is sometimes sufficient to cause a small group of mongooses to flee, with members of the larger group chasing behind (Rood 1975, Cant *et al.* 2001). Groups more closely matched in size bunch together and approach each other with caution, stopping frequently to stand upright and stare at their opponents. Typically, members of the two groups approach to within 20 or 30 m of each other before rushing forward, with members of both groups fanning out and engaging in one-to-one fights or chases with their opponents. Face-to-face confrontations between individuals are brief (<5 seconds) and violent, involving repeated bites and scratches with the front paws until one of the combatants bolts. Groups that have become scattered sometimes retreat, bunch together and advance again. In this way, fights between large, evenly matched groups sometimes last for over an hour. On rare occasions, infanticide and kidnapping of pups have been observed between groups. Where inter-group infanticide occurred it was the larger group that was responsible on all but one occasion (Müller & Bell 2009).

There is usually no conspicuous dominance hierarchy in the daily lives of a group, except among ♂♂ when ♀♀ are in oestrus. Levels of aggression are usually low because individuals forage independently on small, scattered invertebrate prey (Rood 1975). When aggression over a food item occurs, the finder or owner is usually the winner (De Luca & Ginsberg 2001). During oestrus, which starts around ten days after parturition, ♂♂ exhibit an obvious dominance hierarchy when competing for access to ♀♀. Females, by contrast, do not interfere with each other or directly compete for matings. Despite a lack of overt aggression among ♀♀ during mating, ♀♀ often form an age-based hierarchy in which older ♀♀ enter oestrus a few days before their younger group-mates, and have larger litter-sizes (Cant 2000, Gilchrist *et al.* 2004). Kingdon (1977) reported a previously healthy adult ♀ in a free-ranging pack being consistently deprived of food items by other pack members after temporarily losing some hindlimb coordination in an accident. Thereafter, this individual ♀ remained subordinate to all other ♀♀ in the group in spite of regaining her health.

Oestrous ♀♀ are closely guarded for 2–3 days by dominant ♂♂. The staggered pattern in which ♀♀ enter oestrus allows the same one or two dominant ♂♂ to guard and mate with all the adult ♀♀ in the group (Cant 2000). Dominant ♂♂ follow oestrous ♀♀ closely, and are aggressive to any ♂♂ that attempt to mate. These dominant



Banded Mongoose *Mungos mungo*.

(or mate-guarding) ♂♂ are generally bigger than the subordinate ♂♂, and obtain the great majority of observed matings, but ♀♀ go to considerable lengths to escape their mate-guard in order to mate with other ♂♂ in the group. For example, if a mate-guarding ♂ stops to eat a prey item such as a beetle, the guarded ♀ will often run off to mate with a non-guarding ♂. Despite synchronous female oestrus preventing total monopolization of mating opportunities by dominant ♂♂, 85% of paternities are assigned to the oldest three ♂♂ in each group (Nichols *et al.* 2010).

Both ♂♂ and ♀♀ actively seek copulations with individuals in neighbouring groups. The rate at which neighbouring groups encounter each other increases during oestrus, and both ♂♂ and ♀♀ have been seen to lead the group deep into a neighbouring group's home-range in pursuit of copulations. Females may accept or pursue these matings with extra-group ♂♂ as a way of avoiding inbreeding depression (Rood 1975, Cant *et al.* 2002). Inbreeding depression may be a particular problem for Banded Mongooses because both ♂♂ and ♀♀ often remain in their natal group beyond the age of reproductive maturity.

Banded Mongooses are unusual amongst the social mongooses/social carnivores because most ♀♀ in each group reproduce. Up to ten ♀♀ may give birth within a group (Gilchrist 2006b). Most ♀♀ (80%) conceived in each breeding event, and most pregnant ♀♀ (93%) carried their litter to term (Gilchrist *et al.* 2004). This low reproductive skew occurs despite evidence that subordinate female reproduction is costly to dominant female reproductive success

(Gilchrist 2006b, Cant *et al.* 2010). Female group-mates exhibit an exceptional degree of birth synchrony. In Uganda, multiple breeding ♀♀ gave birth on exactly the same night in 64% of breeding attempts (Hodge *et al.* 2011). Where ♀♀ gave birth on different days, there was rarely more than a few days between births. The failure rate of asynchronous litters was particularly high (Gilchrist 2006a, b, Hodge *et al.* 2011). There is apparently strong selective pressure for synchrony of parturition because ♀♀ have been known to miscarry or abort in order to synchronize with other ♀♀ giving birth (Gilchrist 2006a). Birth synchrony may have evolved as a way of escaping the threat of infanticide by dominant breeders, since it is likely to reduce the ability of infanticidal ♂♂ and ♀♀ to discriminate between offspring, and birth synchrony also likely reduces competitive asymmetry between pups (Gilchrist 2006a, Hodge *et al.* 2011). Additionally, birth synchrony may help to swamp potential predators and minimize the total period that the communal litter must remain in the natal den.

Offspring are kept underground in the den for the first 3–4 weeks of life. Pups may be transferred between dens two or three times during this period. Each day one or more (average two; Cant 2003) 'babysitters' remain behind at the den to guard the pups while the rest of the group goes off to forage. Babysitters guard pups against predators such as snakes and monitor lizards, and, importantly, against rival groups of Banded Mongooses, which sometimes attack a natal den and, if successful, kill the pups inside (Müller & Bell 2009). Adult ♂♂ babysit most and adult ♀♀ least, with subadults

generally contributing less babysitting than adults (Rood 1974, Gilchrist 2001, Cant 2003). Dominant ♂♂ (with higher likelihood of paternity in the litter) babysit more than subordinate ♂♂, but reduce their contribution during oestrous periods, when they compete for paternity in the next litter (Cant 2003).

At around four weeks old pups start to accompany adults on short afternoon foraging trips, and by five weeks the pups leave the den in the morning with the rest of the group. Typically, each pup closely follows an 'escort' (usually an adult), begging frequently. These associations between pups and adults are usually stable over time, with the same pup following the same adult each day, from emergence until independence (at around 90 days) (Cant 1998, Gilchrist 2004). Current breeders tend to contribute more to escorting than non-breeders, and heavier individuals make greater contributions to pup escorting than lighter individuals, with patterns complicated by sex and age (Gilchrist & Russell 2007). Females are more sensitive to personal condition, reducing pup provisioning in response to personal weight loss more than ♂♂, with older individuals also reducing provisioning more acutely than younger individuals in response to weight loss (Bell 2010). The pup is responsible for maintaining the association by following and defending its escort against approaches from other pups (Gilchrist 2004, 2008).

Adults actively care for pups by contacting, carrying, grooming, playing with and provisioning pups, with escorts providing more food and showing individual recognition and concern for their paired pup (Bell 2008a, Gilchrist *et al.* 2008). Pup begging rate corresponds to hunger, and escorts in good condition are more responsive to change in begging intensity (Bell 2008b). Adults provision pups by dropping or leaving whole or partial prey items. Adults also defend pups against potential predators and pups often shelter under the belly of their escort when frightened or threatened. The closer a pup associates with an escort, the more it is fed, the faster it grows and the higher its probability of survival to independence (Gilchrist 2004, Hodge 2005). Each pup learns to forage via imitation during the period of dependence on their escort (Müller & Cant 2010).

Dispersal occurs via two distinct modes (Cant *et al.* 2001). First, groups of ♂♂, ♀♀ or both are sometimes driven out of their natal groups as the result of intense aggression from other group members. The primary agents of this aggression are dominant ♂♂ and breeding ♀♀ but subordinates of either sex may also contribute to driving individuals out of the group. Evictions occur in especially large groups and the timing (during oestrus or early gestation) suggests that reproductive competition may motivate eviction. Notably, ♀ evictions occur in groups with relatively large numbers of reproductive ♀♀, and it is young reproductive ♀♀ that are evicted, again supporting reproductive competition as the primary driver of eviction (Gilchrist 2006a, Cant *et al.* 2010). Evicting subordinate ♀♀ is costly to the remaining ♀♀. Females give birth to lighter pups when other ♀♀ are evicted during their gestation, pups whose dependent period is disrupted by an eviction are lighter at independence, and the proportion of pups in a litter that survive to independence is reduced by eviction during their dependent period (Bell *et al.* 2012). When ♂♂ and ♀♀ are evicted simultaneously they subsequently split into two same-sex subgroups and disperse separately, presumably to avoid inbreeding. Evicted subgroups have been known to disperse over 25 km from their natal group (Cant *et al.* 2001).

The second mode of dispersal occurs when groups of same-sex individuals leave their natal group voluntarily to join members of the opposite sex. Animals of intermediate age (between one and three years old) are most likely to disperse, whether this is forced or voluntary. In the Serengeti N. P. dispersing ♂♂ have been observed to invade an established group and drive out the resident ♂♂ (Waser *et al.* 1995). In Uganda, two group takeovers by groups of ♀♀ have been observed, both of which involved the eviction of the only ♀ previously in the group. Immigration by single individuals is extremely rare. Dispersing animals attempting to establish a new home-range are frequently involved in fights with resident groups. These fights can lead to severe injuries and an elevated mortality rate among adult ♂♂ (Cant *et al.* 2001).

Vocal communication is conspicuous and diverse. Foraging group members emit a more or less continuous stream of low grunts that serve as contact calls. Responses of other pack members to warning and alarm calls vary depending on pitch and amplitude. The response to conspecific recruitment calls is dependent upon the risk associated with the stimulus, with a more intense recruitment in response to calls elicited by a rival group or snake in comparison to calls elicited by predator faeces (Furrer & Manser 2009). Other distinct calls include a screeching contact call, when individuals become separated from the pack, a rally call, used upon seeing members of a neighbouring group, and threat and aggression calls, used in competition over food. A study of one captive group found that there were nine sonographically distinct calls (Messeri *et al.* 1987), but there are probably a number of other additional specialized calls that are used more rarely in a natural setting. Vocalizations are individualized, enabling discrimination between individuals, and both pups and escorts are more responsive to the calls of their partner than to other group members (Müller & Manser 2008b). Banded Mongooses have been observed to respond to plover (*Vanellus*) alarm calls, but do not differentiate between levels of urgency coded within the calls (Müller & Manser 2008a).

Hamerkop *Scopus umbretta* apparently form feeding associations with Banded Mongooses (Steyn 1991). The birds have been observed to chase and eat any small lizards and frogs that escape from the foraging mongooses. Warthogs *Phacochoerus* spp. sometimes lie down or stand still to allow Banded Mongooses to groom them for ticks and other ectoparasites.

Reproduction and Population Structure In Uganda, groups produced an average of four litters per year (Rood 1975, Cant 2000, Gilchrist *et al.* 2004). In drier areas, breeding is less frequent, with groups producing one or two litters per year (Waser *et al.* 1995). Breeding is not tightly synchronized between groups (Rood 1975). However, breeding is to some extent timed to coincide with the wettest months: in Uganda, the probability that groups gave birth in a particular month increased with that month's rainfall (Cant 1998) and groups will stop breeding altogether during periods of drought. In southern Africa, young appear to be born during the warm, wet summer months from Oct to end Feb, as evidenced by Shortridge's (1934) record of a pregnant ♀ taken in Nov in Namibia, and Rowe-Rowe (1978a) finding litters of 2–8 young during the months of Oct, Dec and Feb. Heavier ♀♀ are more likely to conceive (Gilchrist *et al.* 2004).

Gestation period is around nine weeks. Mean foetal litter-size of pregnant ♀♀ 3–4 weeks before parturition was 3.2 (range 1–6) (pooled data of Cant 2000 and Gilchrist *et al.* 2004). Younger, smaller

♀ ♀ carried fewer, relatively smaller foetuses than their older group-mates (Cant 2000, Gilchrist *et al.* 2004). Abortion or miscarriage is generally rare, but more common in young ♀ ♀ conceiving their first litter (Gilchrist *et al.* 2004) and is commonly induced by eviction, with ♀ ♀ that abort frequently being readmitted to the group (Gilchrist 2006a, Cant *et al.* 2010).

In the Serengeti, reproduction in ♀ ♀ was first observed at two years of age (Waser *et al.* 1995). In Uganda, the average age of first conception was 321 days (Gilchrist *et al.* 2004). An average of 81% of adult ♀ ♀ conceived in each breeding attempt, with 92% of pregnant ♀ ♀ carrying to term (pooled data of Cant 2000 and Gilchrist *et al.* 2004). There was no effect of age on the probability of breeding for adult ♀ ♀ (Cant 2000, Gilchrist *et al.* 2004).

In the Ugandan population, the birth-weight of pups ranged from 20 to 50 g. Eleven pups from one litter captured between 33 and 38 days old averaged 275 g. At 65 days old the pups from this litter weighed 423 g. Ten weeks after emergence (100 days) they averaged 541 g ($n = 7$). At one year, 16 individuals from three different litters weighed 1311 g. High growth rates during development reduce the age at which ♀ ♀ breed for the first time, suggesting that helpers can improve the future fecundity of the offspring for which they care (Hodge 2005). Maternal condition may also have serious implications for the success of their offspring. Females in good condition at conception give birth to heavier pups, and heavy pups receive more care and are more likely to win competitive interactions with other pups (Hodge *et al.* 2009).

In the Serengeti, average annual survivorship was 0.67 (Waser *et al.* 1995). In Uganda, annual survivorship of adults averaged 0.78–0.86 (Cant 1998, Otali & Gilchrist 2004). In both populations, adult ♂ ♂ and ♀ ♀ survived at similar rates. Mortality of pups was high. Twenty-one per cent of communal litters failed to produce a single emergent pup, and only 51% of emergent pups survived to three months of age (Gilchrist 2001, 2006b). Few pups were visibly ill prior to disappearance, and the main cause of pup mortality is apparently predation (Otali & Gilchrist 2004). In the wild, maximum life-span is 13 years for ♂ ♂ and 11 for ♀ ♀. Average expected life-span for individuals reaching adulthood (1 year) is 3.6 years for ♂ ♂ and 3.3 for ♀ ♀. In captivity, Banded Mongooses may live to more than 17 years (Weigl 2005).

In Uganda, the sex ratio was male-biased, from emergence of pups to adulthood (Cant 1998, Gilchrist 2001). The underlying cause of these biased sex ratios is unknown: there is no information on the sex ratio at birth, and there are no detectable differences in survival between ♂ ♂ and ♀ ♀ after they emerge from the den.

Predators, Parasites and Diseases Known predators include Lions *Panthera leo*, Leopards *P. pardus* and African Rock Pythons *Python sebae*. Marabou Storks *Leptoptilus crumeniferus* and Nile Monitor *Varanus niloticus* and even Common Warthog *Phacochoerus africanus* have been observed to kill pups (Otali & Gilchrist 2004). Ticks and fleas are common on adults. The following ixodid tick species were recovered from two animals taken in Kruger N. P., South Africa: *Amblyomma hebraeum*, *A. marmoreum*, *Haemaphysalis leachi*, *H. zumpti*, *Rhipicephalus appendiculatus*, *R. simus* and *R. zambeziensis* (Horak *et al.* 2000). Little is known about diseases, but they are a possible vector of rabies and susceptible to human tuberculosis *Mycobacterium tuberculosis* (Alexander *et al.* 2002).

Conservation IUCN Category: Least Concern. CITES: Not listed.

Banded Mongooses are present in numerous protected areas across their wide range on the African continent, and there is no reason to believe the species is threatened.

Measurements

Mungos mungo

HB (♂ ♂): 366 (300–400) mm, $n = 85$

HB (♀ ♀): 361 (330–385) mm, $n = 76$

T (♂ ♂): 220 (193–310) mm, $n = 101$

T (♀ ♀): 219 (194–240) mm, $n = 86$

HF c.u. (♂ ♂): 70 (53–75) mm, $n = 101$

HF c.u. (♀ ♀): 69 (53–74) mm, $n = 86$

E (♂ ♂): 27 (23–26) mm, $n = 12$

E (♀ ♀): 25 (22–26) mm, $n = 5$

WT (♂ ♂): 1450 (890–1880) g, $n = 111$

WT (♀ ♀): 1370 (990–1740) g, $n = 48^*$

GLS: 72.5 (66.1–77.7) mm, $n = 24$

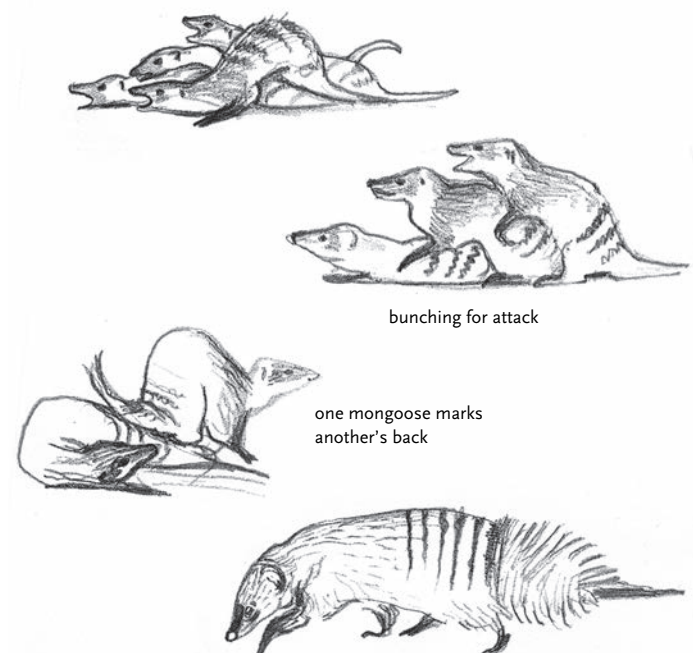
GWS: 39.6 (37.1–44.2) mm, $n = 24$

Queen Elizabeth N. P., Uganda (J. S. Gilchrist pers. obs.); ear measurements: former Transvaal, South Africa (Rautenbach 1982); skull measurements: Rwanda and Burundi (museum specimens: MRAC) and Botswana, Tanzania and Chad (IRSN, MNHN, NMNH, ZSM)

*Non-pregnant ♀ ♀ only

Key References Bell 2008a, b, 2010; Cant 2000, 2003; Cant *et al.* 2001, 2002, 2010; Gilchrist 2004, 2006a, b, 2008; Gilchrist *et al.* 2004; Hodge 2005; Hodge *et al.* 2009, 2011; Jordan *et al.* 2011a; Müller & Cant 2010; Otali & Gilchrist 2004; Rood 1975, 1986; Waser *et al.* 1995.

Michael A. Cant & Jason S. Gilchrist



Banded Mongoose *Mungos mungo*.

GENUS *Liberiictis*

Liberian Mongoose

Liberiictis Hayman, 1958. Ann. Mag. Nat. Hist., ser. 13, 1: 449.

The genus includes only one species, the Liberian Mongoose *Liberiictis kuhni*, recorded only from Liberia and Côte d'Ivoire (Goldman & Taylor 1990). Phylogenetic studies of Herpestidae indicate that *Liberiictis* is closer to other social mongooses, and that it is closer to the banded

mongooses (genus *Mungos*) than to the cusimanse (genus *Crossarchus*) (Veron *et al.* 2004, Perez *et al.* 2006, Patou *et al.* 2009).

Mark E. Taylor

Liberiictis kuhni LIBERIAN MONGOOSE

Fr. Mangouste de Liberia; Ger. Liberia-kusimanse

Liberiictis kuhni Hayman, 1958. Ann. Mag. Nat. Hist., ser. 13, 1: 448. 'Kpeaplay, north-east Liberia, about 6° 36' N, 8° 30' W'.



Liberian Mongoose *Liberiictis kuhni*.



Liberian Mongoose *Liberiictis kuhni* head, frontal view.

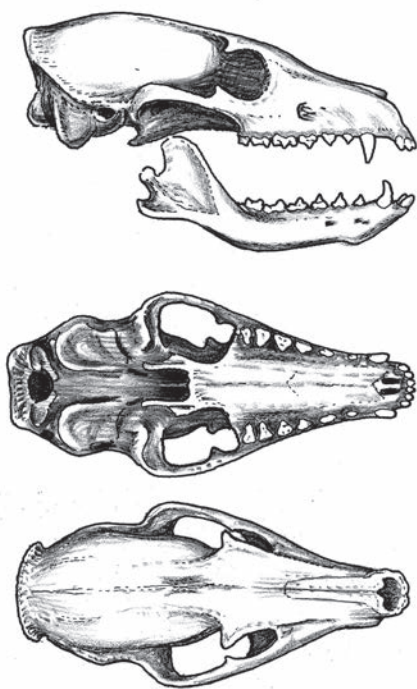
Taxonomy Eight skulls of *Liberiictis kuhni* were obtained in 1957 and 1958 from Gio hunters in NE Liberia at Kpeaple and Gapple by German ethnologist Hans Himmelheber. The type specimen was presented to R. W. Hayman by H.-J. Kuhn of Heidelberg University. Hayman described the genus and species based on these eight skulls, and suggested that *Liberiictis* was related to *Crossarchus*. Its external morphology was only described in 1974 following the collection of two specimens near Tar, Liberia (Rosevear 1974, Schlitter 1974). Another animal was shot by native hunters in the Gbi National Forest in 1988 and the first live specimen was caught in 1989 (Taylor 1992). Synonyms: none. Chromosome number: not known.

Description A medium-sized brown mongoose with long snout, distinctive dark neck-stripe, grizzled stiff guard hairs and buffy-orange underfur. General appearance is a brown mongoose with pale brown and white grizzled chin and chest. Snout is nearly hairless, pink to brown in colour, and long and mobile, extending beyond lower lip. Ears, small and rounded. Hairs of head short (to ca. 8 mm), dark brown and with pale intermediate bands; guard hairs of cheeks and above eyes paler. Whitish stripe extends from back of mouth to below ear and a very dark brown stripe extends from below ear along side

of neck bordered by paler stripes of fur. Guard hairs of throat (ca. 10 mm) pale with dark brown intermediate bands. Guard hairs of body long (ca. 40 mm) with blackish-brown terminal and proximal sections and pale subterminal bands. Underfur ranges from apricot-buff to dark brown. Feet and lower legs uniformly brownish-black. Tail relatively bushy and short (about 45% of HB), tapering evenly from base to tip. Five digits on feet with pollex and hallux reduced. Digits 2–5 on forefeet end in long, curved claws (<18 mm); claw length of hindfeet shorter (<13 mm).

Skull long and narrow with an elongated tapering rostrum; length of rostrum and nasal bones average 38% and 25%, respectively, of the greatest length of skull (Hayman 1958). About 60% of length of skull is anterior to the anterior rim of orbit, while in other mongooses this is about 50%. Dental formula is $I \frac{3}{3}, C \frac{1}{1}, P \frac{4}{4}, M \frac{2}{2} = 40$. Cheekteeth are small in comparison with size of skull and compared with the Common Cusimanse *Crossarchus obscurus*. No carnassial shear; the cusps of the teeth are adapted for puncture crushing, and upper molars are about equal in size (Hayman 1958, Rosevear 1974, Goldman & Taylor 1990).

Geographic Variation None recorded.



Lateral, palatal and dorsal views of skull of Liberian Mongoose *Liberiictis kuhni*.

Similar Species

Crossarchus obscurus. Sympatric. Smaller in size, with shaggy coat but no distinctive neck stripe; condylobasal length about 86.5 mm (cf. *Liberiictis kuhni* >94.7 mm); upper and lower first premolar absent (total dentition of 36 teeth).

Atilax paludinosus. Sympatric, also occurring in forested habitats and usually associated with rivers and water-bodies. Uniform brown fur with no distinctive stripes, and digits that can be widely spread with rugose claws, unlike the Liberian Mongoose that has very long claws well adapted for digging.

Distribution Endemic to West Africa. Currently recorded from NE Liberia and W Côte d'Ivoire. First specimens were based on eight skulls collected from two villages in NE Liberia (Kpeape 6° 36' N, 8° 30' W and Gapele 7° 08' N, 8° 28' W) (Hayman 1958). The mongooses' external characters were described by Schlitter (1974) on the basis of two specimens collected near Tar (6° 13' N, 8° 08' W). Taylor (1989a) collected a specimen, which had been shot by a villager, from a small settlement in the Gbi National Forest (6° 25' N, 8° 45' W) approximately 20 km south-east of Tapeta. A live animal was collected in 1989 from Nimbo When (6° 12' N, 8° 47' W) (Goldman & Taylor 1990). Subsequently, a group of Liberian Mongooses was observed foraging in Tāi N. P., the first record from Côte d'Ivoire (5° 51' N, 7° 23' W) (Taylor 1992, Gartshore *et al.* 1995), later confirmed by the discovery of a dead specimen (Colyn *et al.* 1998). One animal was trapped and radio-collared in Tāi N. P. in 1999, facilitating regular observations of three known groups between 1999 and 2002. In 2011, their presence in Sapo N. P. in Liberia was confirmed by photographic evidence (FDA/FFI/ZSL pers. comm.). The Liberian Mongoose was also sighted in the Nimba Mts in N Liberia (Coe 1975, Schreiber *et al.* 1989). They are likely to occur in suitable habitat in S Guinea.



Liberiictis kuhni

Habitat Occurs in primary and secondary evergreen forests in Liberia and Côte d'Ivoire. Found primarily in swamp forest and stream beds with deep sandy soils where earthworms are abundant. May also be found foraging in forested areas with moist soils or areas that have been cut over. Individuals use higher ground only for travel between foraging areas.

Abundance Declining in many areas due to hunting pressure and loss of quality habitat. Populations in Tāi N. P. estimated at approximately 1.5/km², based on radio tracking and field observations (A. E. Dunham pers. obs.).

Adaptations Reduced cheekteeth, poorly developed masseter muscles and loss of shearing function of premolars and molars are adaptations for eating soft-bodied invertebrates (Pape 1980). Small sharp teeth are adaptations for extracting soil invertebrates and puncture-crushing rather than shearing (Pagel 1985). Elongated mobile snout and large curved claws of the forefeet are used for excavating such prey. Sense of smell is well developed.

Foraging and Food Behavioural observations and scat analyses suggest that the Liberian Mongoose is an earthworm specialist, eating primarily large burrowing species of the family Megascolecidae (some of which may be a metre or more in length, M. E. Taylor pers. obs.). Of 32 scat samples collected in Tāi N. P. all contained worm remains (A. E. Dunham pers. obs.). Remains of caecilians (legless subterranean amphibians) were found in four scats, suggesting that small vertebrates may also be taken if encountered while digging for worms. Insect larvae and fallen fruits are also consumed. Foraging is restricted to riverine wetland areas and swamp forest.

While searching for prey, the Liberian Mongoose digs for earthworms and other soil invertebrates. It has been observed digging like a dog, alternately using its front feet, to excavate soil and then sticking its muzzle into the soil. Sand is often ingested with food.

items (Pagel 1985). Transects in swamp forest suggest mongooses may create an average of 16,700 foraging scrapes per km per day. Groups may plough up large areas of ground in search for worms, creating disturbance of 20–30% of the ground. The result of its foraging activities in a stream bed or swamp forest may result in considerable disturbance of the soil. This physical disturbance may accelerate decomposition and may have important impacts on seedling recruitment and mortality. Groups return to the same area to forage approximately once every three to four weeks. Reported to climb palm trees to forage for worms or beetle larvae occurring in the crowns after the trees have been cut for removing sap for the production of palm wine. A captive ♂ readily consumed ground meat, commercial dry dog food, two-day-old chicks, fresh fish and live insects (Taylor 1992, J. S. Carnio pers. comm., A. E. Dunham pers. obs.).

Social and Reproductive Behaviour Terrestrial and diurnal. Individuals travel and forage alone or in groups of 4–6 animals, though larger groups have been observed (Taylor 1989a, Veron *et al.* 2004). Groups are very quiet, communicating with soft grunting sounds. Adult ♂♂ are frequently observed alone; a radio-collared ♂ frequently travelled between three stable groups of conspecifics, joining them for 1–3 days at a time. Groups are often found in association with Sooty Mangabeys *Cercocebus atys*. This association may be initiated by the mongooses as an anti-predator strategy as no foraging benefit is obtained. The Crowned Eagle *Stephanoaetus coronatus* preys upon both species (Shultz 2002) and the mongooses respond to the monkeys' warning calls by quickly dispersing and running into thick vegetation or under fallen trees. Group members sleep together at night in hollow logs, under fallen trees, or occasionally in termite mounds when flooding is unlikely. Each home-range has numerous den sites that are rarely used on consecutive nights (A. E. Dunham pers. obs.).

An aggressive encounter was observed in Côte d'Ivoire with a group of Common Cusimanses. A group of four Liberian Mongooses initiated the encounter and displaced the larger group of ten cusimanses by advancing and giving threatening growls.

Reproduction and Population Structure In Liberia, three juveniles were collected in Jul and a ♀ was observed lactating in Aug, suggesting that breeding occurs during the wet season (May–Sep) when invertebrates are abundant and near the soil surface.

Predators, Parasites and Diseases Skulls of *Liberiictis* have been found in and under the nests of Crowned Eagles (Shultz 2002). These

eagles exist at high densities in the closed canopy forests of West Africa and are likely the major predator of this species. Leopards *Panthera pardus* occasionally take small carnivores and may also be a threat (Jenny 1996).

The louse *Felicola liberiae* (Mallophaga: Trichodectidae) has been described from the Liberian Mongoose (Emerson & Price 1972); ectoparasites also include ticks (Acarina; *Ixodes* sp.) and fleas (Siphonaptera).

Conservation IUCN Category: Vulnerable A2cd. CITES: Not listed.

Threats include hunting and deforestation from agriculture, logging and mining. They are hunted for food throughout their range with dogs, shotguns and snares. May also be vulnerable to the use of pesticides in forest plantations, as worms are known to accumulate toxins at levels dangerous to mammalian predators. Although present in secondary forests (Taylor 1992), the lack of den sites may restrict distribution. They are known to be present in Taï N. P. in Côte d'Ivoire and Sapo N. P. in Liberia. Further research is required to more accurately determine the limits of their distribution and to better understand the threats facing this species (Schreiber *et al.* 1989).

Measurements

Liberiictis kuhni

HB (♂♂): 423, 555 mm, n = 2

HB (♀): 478 mm, n = 1

T (♂♂): 182, 197 mm, n = 2

T (♀): 205 mm, n = 1

HF c.u.: 88 mm, n = 1

E (♂): 30 mm, n = 1

E (♀): 29 mm, n = 1

WT (♂♂): 2.3, 2.4 kg, n = 2

GLS: 96.9 (94.7–100.4) mm, n = 12

GWS: 44.8 (42.2–47.0) mm, n = 15

Body measurements: throughout the range (Schlitter 1974, A. E. Dunham pers. obs., and H-J. Kuhn pers. comm.)

Skull measurements: Goldman & Taylor (1990)

Key References Goldman & Taylor 1990; Hayman 1958; Taylor 1989a, 1992.

Mark E. Taylor & Amy E. Dunham

GENUS *Dologale*

Pousargues's Mongoose

Dologale Thomas, 1926. Ann. Mag. Nat. Hist., ser. 9, 17: 183.

Dologale is a monotypic genus, represented by Pousargues's Mongoose *Dologale dybowskii*. The species is limited, as far as is known, to a narrow belt of savanna–forest mosaic from Uganda westwards across

N DR Congo. The genus was included in *Helogale* by McKenna & Bell (1997), but without comment.

Chris Stuart & Tilde Stuart

Dologale dybowskii POUSARGUES'S MONGOOSE (SAVANNA MONGOOSE)

Fr. Mangouste de Dybowsky; Ger. Listige Manguste

Dologale dybowskii (Pousargues, 1893). Bull. Soc. Zool. De France 18: 51. Nouv. Arch. Mus. d' Hist. Nat., Paris (3) 6:121. 1894. 'Ubangi, Congo Belge', restricted by Moreau *et al.* (1945) to 'on the Upper Kemo, a tributary to the north of the Ubangui, about 6° 17' N, 19° 12' E [Central African Republic].

Pousargues's Mongoose *Dologale dybowskii*.*Dologale dybowskii*

Taxonomy Monotypic (Coetzee 1977). Originally described as *Crossarchus dybowskii* based on specimens collected in Ubangi, Central African Republic. Kershaw (1924) placed specimens from the Sudan in the genus *Herpestes*, whereas specimens from Faradje in NE DR Congo were mistakenly described as a new subspecies of *Helogale hirtula* (Allen 1924). Synonyms: *nigripes*, *robusta*. Chromosome number: not known.

Description One of the smallest mongooses, and bearing a close resemblance to the Dwarf Mongoose *Helogale parvula*. Head is short-snouted and lacks a groove in the upper lip. Pelage overall dark brown but grizzled yellow to light brown. Head colouration is darker and greyer than body pelage. Underparts less grizzled and more uniform in colour. Hair on the legs darker and feet almost black. Overall pelage is short and fine, although longer on the tail. Claws on forefeet are stout, long and curved, indicative of a digging forager. Didier (1948) provides an extensive description of the os penis. Dental formula is $I^{3/3}, C^{1/1}, P^{3/3}, M^{2/2} = 36$; however, one of the specimens from Faradje examined by Allen (1924) had a supernumerary premolar, with P^1 being fully developed on both sides. Haltenorth & Diller (1980) noted that the dental formula is variable (total of 38) with P^1 either present or absent. Nipple numbers not recorded.

Geographic Variation None recorded.

Similar Species

Helogale parvula. Widely distributed in partially wooded habitats from S Somalia and Ethiopia to NE KwaZulu–Natal. The smallest African mongoose, with distinct groove in upper lip; lives in packs and is never solitary.

Distribution Endemic to Africa. Exact range unknown and based on just 31 specimens. Occurs in NE DR Congo (Schouteden 1945), including the Garamba N. P. (Verschuren 1958), Central African Republic, extreme S Sudan and Uganda. It has been pointed out by Schreiber *et al.* (1989) that old specimens in the Paris Natural History

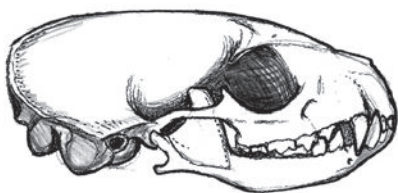
Museum were collected at Sanghe, but it is not clear whether this is the district in Congo, or that in the Central African Republic. Kingdon (1977) published known records, but unconfirmed sightings indicate that it may occur considerably further to the west than present records indicate. Hayman (1936) discusses known distribution.

Habitat Apparently has a fairly wide habitat tolerance in a narrow belt to the north of the Equator. It occupies the thicketed shores of L. Albert, savanna–forest mosaics as well as montane forest grasslands. Kingdon (1977) has suggested that this is a relict mongoose living in the ecotone between high forest and the lower rainfall wooded savanna.

Abundance This species is known from just 31 museum specimens and a handful of possible sightings. The paucity of records can probably be ascribed to confusion with the Dwarf Mongoose and the fact that its known range has seen few scientists or collectors in recent years. There have been no confirmed records for more than two decades.

Adaptations The claws on the front feet are stout and long and are probably an adaptation for digging.

Foraging and Food Given that its claws are suitable for digging it probably has a mainly invertebrate diet. The museum label on one specimen mentions small seeds, small termites and fragments of millipedes in the stomach (H. Van Rompaey pers. comm.).



Lateral view of skull of Pousargues's Mongoose *Dologale dybowskii*.

Social and Reproductive Behaviour Nothing is known about these aspects of its biology. It has been suggested that it may be at least partially diurnal and rest up in holes in trees and termite mounds (Dorst & Dandelot 1970). Kingdon (1977) sighted a mongoose that he felt sure was this species at 09:00h, and which took refuge in a termite mound. This sighting was of a solitary animal and it would seem from the meagre records that there is no indication of its living in groups, like the similar Dwarf Mongoose (in itself of interest, since the species has many features otherwise characteristic of the Mungotinae).

Reproduction and Population Structure No information is available.

Predators, Parasites and Diseases Nothing known, but as with other small mongooses they are probably vulnerable to larger raptors and certain predators. Colyn & Van Rompaey (1989) reviewed frontal nasal parasites in this and other species of viverrid.

Conservation IUCN Category: Least Concern. CITES: Not listed.

The only protected area from which this species has been recorded is Garamba N. P. in NE DR Congo. Lack of knowledge of this species' biology and habitat requirements make this a priority species for study.

Measurements

Dologale dybowskii

HB: 268 (240–296) mm, n = 9

T: 197 (160–220) mm, n = 9

HF c.u.: 56 (52–61) mm, n = 8

E: 23 (22–25) mm, n = 7

WT: 350 g, n = 1

GLS: 56.4 mm, n = 1

GWS: 28.4 (28.0–28.7) mm, n = 4

Body measurements: museum specimens (AMNH, BMNH, MRAC, MNHN)

Skull measurements: Faradje, NE DR Congo (Allen 1924)

Key References Hayman 1936; Kingdon 1977; Schreiber *et al.* 1989.

Chris Stuart & Tilde Stuart

GENUS *Helogale* Dwarf Mongooses

Helogale Gray, 1862. Proc. Zool. Soc. Lond. 1861: 308 [1862].

Allen (1939) recognized 11 species in the genus *Helogale*; Ellerman *et al.* (1953) listed seven. Most recent authors recognize only two: Somali Dwarf Mongoose *Helogale hirtula* and Dwarf Mongoose *H. parvula* (Coetzee 1977, Wozencraft 1993, 2005), both endemic to sub-Saharan Africa where, in the north, the range of the former overlaps that of the more widespread Dwarf Mongoose. Both live in semi-desert and dry open woodland and grassland with termitaries and avoid closed forest.

Helogale are very small (weight up to 350 g) mongooses of variable colour. Dorsal pelage greyish, yellowish, reddish to light or dark brown speckled with pale tips. Dense buffy to dark buffy underfur. Somali Dwarf Mongoose is overall grizzled grey, has a longer, shaggier pelage, coarser speckling and brown to black digits. The dental formula is $I^{3/3}, C^{1/1}, P^{3/3}, M^{2/2} = 36$. Upper and lower first premolars absent.

McKenna & Bell (1997) included the genus *Dologale* in *Helogale*.

Harry Van Rompaey



Dwarf Mongoose *Helogale parvula*.

Helogale hirtula SOMALI DWARF MONGOOSE

Fr. Mangouste velue; Ger. Somali Zwergichneumon

Helogale hirtula Thomas, 1904. Ann. Mag. Nat. Hist., ser. 7, 14: 97. 'Gabridehari, 60 mi [96 km] West of Gerlogobi', restricted by Moreau *et al.* (1946: 410) to 'south-east Ethiopia (Ogaden) at about 7° 0' N, 45° 20' E'. Further restricted by Yalden *et al.* (1980) to 'Gabridehari (= Gabredarre, Kebridar) 6° 45' N, 44° 17' E'.

Somali Dwarf Mongoose *Helogale hirtula*.

Taxonomy Currently, the Somali Dwarf Mongoose is thought to be the only congener of the Dwarf Mongoose *Helogale parvula*, being sympatric in the northern parts of the latter's range. Coetzee (1977) subdivided this species into two parts that he called the *hirtula* and *percivali* sections. The former embraced *H. h. hirtula* from SE Ethiopia towards Somalia; *H. h. annulata* from the Mogadishu area and extreme S Somalia; *H. h. lutescens* from SW Ethiopia and northern L. Rudolf area of Kenya; and *H. h. powelli*, from the central part of the ex-Italian section of Somalia around Obbia. The *percivali* section embraced *H. h. percivali* from N Kenya and *H. h. tenebrosa* from the Kenya side of Mt Elgon, west of the Rift Valley. The credibility of any of these taxa must be tempered by the very incomplete knowledge of this species and the insufficiency of specimens to demonstrate the limits of individual variation. Synonyms: *ahlselli*, *annulata*, *lutescens*, *percivali*, *powelli*, *tenebrosa*. Chromosome number: not known, but probably $2n = 36$ as in Dwarf Mongoose.

Description A very small mongoose with longer, shaggier hair than the Dwarf Mongoose. Colouring varies, but typically overall grizzled grey with warmer coloured underparts and face. Head has small pointed muzzle with few fine vibrissae. Ears relatively inconspicuous. Body slender and elongated, fur of the tail tapered to a point. Feet dark brown. Walks with soles and claws of all feet on the ground. Forefeet have long, sharp nails that leave a characteristic spoor, though indistinguishable from the Dwarf Mongoose. Sexes similar in size and appearance, but ♂ exhibit external genitalia. Unlike the Dwarf Mongoose, the cheekteeth are more heavily built, and not typically sectorial; space between P^4 and M^1 much less than width of their protoconal lobes (Coetzee 1977). Nipple numbers not recorded.

Geographic Variation The very limited number of specimens and observations must qualify recognition of regional difference, which may well fall within ranges of individual variation that are of unknown extent or significance. Following Coetzee (1977), there appear to be two recognizable populations, one of *H. h. hirtula* type in Somalia, Ethiopia and extreme N Kenya, the other, *H. h. percivali* type, in Kenya.

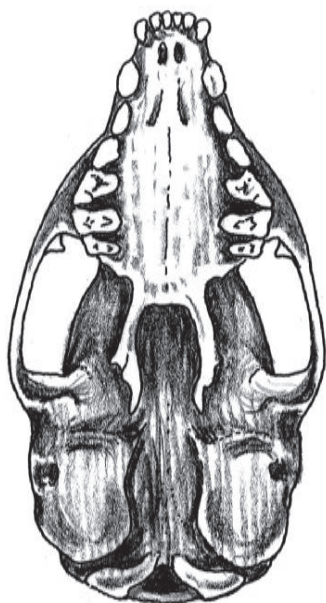
*Helogale hirtula***Similar Species**

Helogale parvula. Sympatric throughout its range, but with sleeker, redder pelage and with feet that share overall body colour; cheekteeth more lightly built, sectorial and the space between P^4 and M^1 on buccal side usually subequal to or exceeding width of protoconal lobes of these two teeth (Coetzee 1977).

Herpestes sanguineus. Widely distributed in sub-Saharan Africa. Substantially larger, with long body and tail, the latter with a conspicuous black tuft; usually solitary or in twos or threes.

Herpestes ochraceus. Sympatric, but larger, and solitary or in pairs.

Distribution Restricted to the Horn of Africa in S and SE Ethiopia, S Somalia and N Kenya. Laurent & Laurent (2002) state that this species has also been sighted at Dittilou in Djibouti (though not noted by Künzel *et al.* 2000), and Anderson (1949) mentions this species from north of L. Turkana. A single, uncertain sighting in Mkomazi, Tanzania, might extend the species' range into the extreme north-eastern borderlands of Tanzania (J. Kingdon pers. obs.). Within a relatively large overall range this species has a patchy distribution that must be constrained by the presence of its very successful and broadly sympatric congener, the Dwarf Mongoose. Nothing is currently known about what form of partitioning must occur between the two *Helogale* species, but the Somali Dwarf Mongoose is clearly more specifically arid-adapted.



Palatal view of skull of Somali Dwarf Mongoose *Helogale hirtula*.

Habitat Limited to a zone of bush, thicket and shrubby deciduous woodlands dominated by *Acacia* (notably *A. bussei* and *A. reficiens*), *Commiphora*, *Grewia*, *Cordia*, *Euphorbia* and *Sterculia* species, *Balanites orbicularis*, *Boscia coriacea* and *Salvadora persica*, up to around 600 m in Ethiopia (Yalden *et al.* 1980, 1996). Like the Dwarf Mongoose, they use termitaria and stony outcrops as dens. The most likely advantage that they have over Dwarf Mongooses is greater ability to go without water during the long dry season.

Abundance Although Somali Dwarf Mongooses may exist at quite elevated densities, they are only abundant in restricted localities; however, estimates of their abundance, overall or local, are not available.

Adaptations As they must forage for food while avoiding predators there are obvious advantages to group living. The colouring of this species is more decisively cryptic than in the Dwarf Mongoose and implies greater vulnerability to predation. It would be interesting to know whether this species has similar partial immunity to bites from snakes as some other mongooses.

Foraging and Food Invertebrates and vertebrates of a similar range to that taken by the Dwarf Mongoose, but presumably more consistently arid-adapted. Such prey would include beetles, termites and larvae from soil or litter. Presumably social groups spread out, like the Dwarf Mongoose, and forage independently with some individuals serving as sentinels. Very young pups are probably fed by adults, but learn by following other pack members. Seasonal patterns of invertebrate availability and ranging patterns are not known.

Social and Reproductive Behaviour Although known to be a social species that forms packs no details have been observed. Their social structure may be not too far different from the Dwarf Mongoose, with social groups forming dominance hierarchies with single breeding pairs. It would be interesting to know whether this species is as highly territorial as the Dwarf Mongoose and how extensive their territories might be.

Reproduction and Population Structure Nothing is currently known, but probably some similarities to the Dwarf Mongoose. Gestation can be extrapolated as being in the region of 50 days. It is also not known how many litters can be produced during a year, nor the timing of reproduction, nor the annual survivorship of individuals. Considering the importance of understanding the ecological determinants of social structures and their evolution, this species should have some priority for further study.

Predators, Parasites and Diseases Although the major predators of this species must resemble those of the Dwarf Mongoose, notably raptors, reptiles and other carnivores, any differences in its habitat could be significant. If this species occupies relatively denser, less exposed habitat it could be predicted that the pressure to be social could be diminished, with further implications for social behaviour. Nothing is known about disease in this species nor about diseases for which they might serve as a reservoir; further reason for study in an area of great significance for pastoralism.

Conservation IUCN Category: Least Concern. CITES: Not listed.

Although poorly known, the species is believed to have a relatively wide distribution and presumably occurs in several protected areas across its range.

Measurements

Helogale hirtula

TL: 400–440 mm

HB: 200–270 mm

T: 150–180 mm

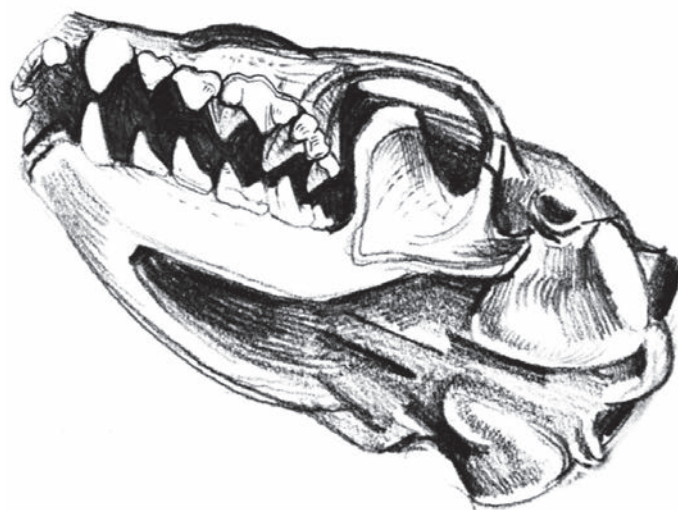
WT: 220–354 g

Kingdon (1997)

Key References Kingdon 1997; Yalden *et al.* 1980.

Jonathan Kingdon & Harry Van Rompaey

Bite in dwarf mongooses employs more sharp points and cusps. Note molars in Dwarf Mongoose *Helogale parvula* (below) more lightly built than in Somali Dwarf Mongoose *H. hirtula* (above left).



Helogale parvula DWARF MONGOOSE

Fr. Mangouste nain; Ger. Zwergichneumon

Helogale parvula (Sundevall, 1847). Ofv. K. Svenska Vet.-Akad. Forhandl. Stockholm 1847, 3 (4): 121 (1847).
 'Caffraria superiore, juxta tropicum', restricted by Roberts (1951) to 'Zoutpansberg' [South Africa].



Dwarf Mongoose *Helogale parvula*.

Taxonomy Polytypic. Coetzee (1977) presented a provisional breakdown of subspecies, grouping them into three sections; the subspecific taxonomy is confused and badly in need of revision, and Coetzee's (1977) framework is only tentatively followed here. It is likely that the current subspecific classification of *Helogale* is due to idiosyncrasies of collection sites and collected individuals. Synonyms: *atkinsoni*, *bradfieldi*, *brunetta*, *brunnula*, *ivori*, *macmillani*, *mimetra*, *nero*, *ochracea*, *ruficeps*, *rufula*, *undulata*, *varia*, *vetula*, *victorina*. Chromosome number: $2n = 36$ (Fredga 1972).

Description Smallest of the mongooses, with long, slender body and furry tail roughly equal to body in length. Head large with small ears that lie close to the head, and a pointed muzzle. The rhinarium, which encloses the nostrils, has a shallow depression on the front between the nostrils, and divides the hair on the upper lip. Smooth, short, finely grizzled pelage on forehead, back, upper limbs and tail, due to agouti banding of multiple shades on single hairs; grizzling less apparent on underparts. Most individuals reddish-brown overall, though shades of tan or darker brown are also common. Hair on upperparts more sparse than on underparts; body hairs longest toward the hindquarters, up to 15 mm in length (these hairs having broad dark tips), although tail hairs may be longer (to 18 mm). Underfur dense. Tail not tufted, but occasionally has slightly darker pelage at tip. No pronounced black tuft as in the Slender Mongoose *Herpestes sanguineus*, which is also substantially larger than *Helogale*. Plantigrade gait, with soles of feet touching the ground. Five digits on both fore- and hindfeet. The front feet are equipped with long curved claws, up to 10 mm across the curve, and well adapted for digging; those on the hindfeet are shorter (8 mm) (Skinner & Chimimba 2005). Both sexes have cheek and anal glands: the anus and openings of the anal glands are enclosed in a subcircular pouch, the lips of which close to a transverse line. Sexes are alike in size and general appearance, but ♂♂ are

relatively easy to identify by the external genitalia; ♀♀ have two pairs of nipples. Young of the year can be distinguished by size because adult body mass is reached only in the second or third year (Creel & Creel 1991). For the first six months, juveniles can be distinguished by relatively large heads with blunt muzzles. For the first few weeks eyes are blue, but later change to brown.

The braincase is pear-shaped, narrowing in the front to the postorbital constriction; the postorbital bars are incomplete even in adults. The supraoccipital crest is well developed, while the sagittal crest is little more than a low ridge on the top of the braincase. The front chambers of the ear bullae are slightly larger than the hind. The rostrum is very short, relative to total skull length. The upper canines are long and sharp, reaching below the level of the base of the lower (Skinner & Chimimba 2005).

Geographic Variation Coetzee (1977) recognized three sections:

parvula section (southern Africa)

- H. p. mimetra*: N Namibia, NW Botswana, S and W Angola, south of the Cuanza R.
- H. p. nero*: Namibia, from Erongo Mts to SE Kaokoveld.
- H. p. parvula*: South Africa, S Mozambique, Zimbabwe and NE Botswana.
- H. p. ruficeps*: Southern Province and Kafue area of Zambia; possibly into SE Angola.

undulata section (East and north-east Africa)

- H. p. atkinsoni*: N Somalia and adjoining Ethiopia.
- H. p. ivori*: coastal N Mozambique and Tanzania.
- H. p. macmillani*: Ethiopia.
- H. p. rufula*: C Kenya, ranging to Arusha in Tanzania (the form in the Serengeti N. P., Tanzania).
- H. p. undulata*: Tete district and lower Zambezi Valley of Mozambique, adjoining parts of E Zambia, Malawi, inland N Mozambique, and southern highlands and C Tanzania.
- H. p. vetula*: coastal Kenya, Kenya east of the Tana R. and S Somalia.

varia section (central Africa)

- H. p. ochracea*: Uganda.
- H. p. varia*: NE Zambia, through Katanga to NE Angola.
- H. p. victorina*: NW Tanzania; possibly in adjacent Kenya and Uganda.

Similar Species

Helogale hirtula. Sympatric in the Horn of Africa region. Shaggier, paler, greyish pelage and noticeably darker feet; cheekteeth more heavily built, and not typically sectorial; the space between P4 and M1 much less than width of their protoconal lobes (Coetzee 1977).

Dologale dybowskii. Central African Republic, NE DR Congo, S Sudan and W Uganda. A dark, brownish grizzled, dwarf mongoose with shaggier and thicker, less tapered tail.

Herpestes sanguineus. Larger, with pelage and body form very similar to the Dwarf Mongoose, but distinguished on the basis of size, long body and long tail with pronounced black tuft. Often sympatric in areas with Dwarf Mongooses, but is likely to be seen alone or in groups no larger than two or three.

Herpestes flavescens. Largely allopatric, although both are present in the Erongo Mts of Namibia where this species is also black and is often confused with the Dwarf Mongoose (G. Rathbun & M. Griffin pers. comm.). Larger, with relatively longer tail; solitary, diurnal and consumes more vertebrate prey.

Herpestes ochraceus. Sympatric in north-east Africa, but larger, and solitary or in pairs.

Distribution Endemic to Africa, widely distributed in partially woody habitats of intermediate thickness from S Somalia and Ethiopia to NE KwaZulu–Natal in South Africa (around 28°S) and westwards to N Namibia and SW and C Angola and SE DR Congo. Mention of the species as being present in Gambia (e.g. Wozencraft 2005) is in error.

Habitat Most common in open woodlands (e.g. *Acacia–Commiphora* woodland), thickets and wooded savannas, particularly where there are termitaria, rock outcroppings or crevices, or hollow logs for use as dens. Indeed, Waser *et al.* (1995) postulated that the most important determinant of Dwarf Mongoose habitat preference is the density of suitable dens. In many areas, large *Macrotermes* mounds are preferred den sites, and Dwarf Mongooses can be seen warming themselves atop these mounds upon emergence around sunrise, and just before re-entering the den at sunset. They avoid montane regions (usually found to altitudes of 2000 m) and thick forests. Dwarf Mongooses are supplanted by Banded Mongooses *Mungos mungo* in open short-grass

habitats (particularly where termitaries or other den sites are scarce), where they are probably more vulnerable to predation. Although they can persist on home-ranges without water during the dry season, and are found in semi-desert regions, Dwarf Mongooses are not found in highly arid areas.

Abundance Dwarf Mongooses are often the most abundant small carnivores in areas of open woodland or wooded savanna, with densities as high as 8 ind/km² (though more typically around 5 ind/km²; Waser *et al.* 1995). Serengeti N. P. was estimated to hold 94,000 individuals, a number that is orders of magnitude higher than larger Serengeti carnivores (Waser *et al.* 1995).

Adaptations In the skull, the zygomatic arches are relatively heavy to support well-developed masseter muscles used to crunch the exoskeletons of robust invertebrates such as millipedes. The coronoid of the lower jaw is high and wide to accommodate the temporalis muscles, which activate the lower jaw. The carnassials of Dwarf Mongooses are lightly built compared with their congener the Somali Dwarf Mongoose *H. hirtula*, and are not particularly adapted to slicing (consistent with their primarily insectivorous diet). The lower first molar has three high cusps on the front and a broad grinding surface on the back half of the tooth; the remaining molars also have high cusps, also suggesting adaptation to a generally insectivorous diet (Skinner & Chimimba 2005).

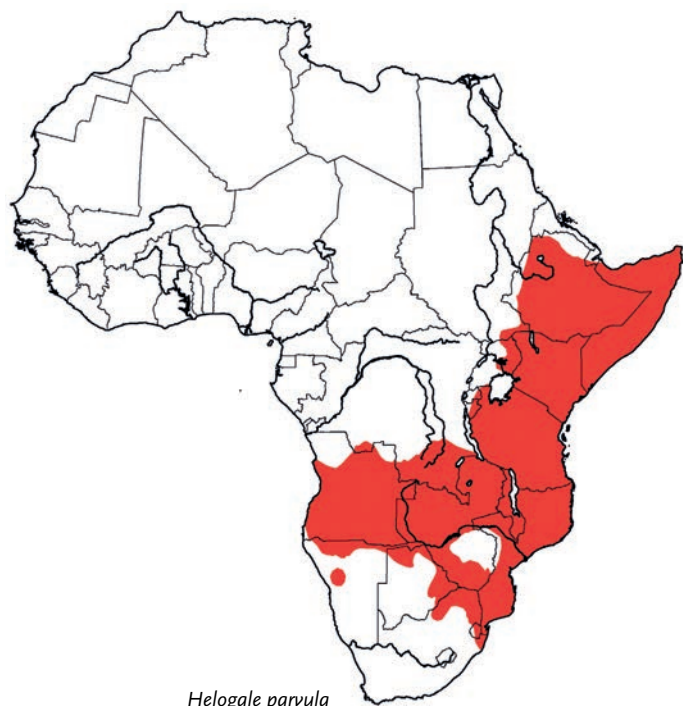
As the smallest of the mongoose family, and given their diurnal activity, Dwarf Mongooses often fall prey to raptors, snakes, small felids and other mongooses. Much of their behaviour and social organization has been shaped by the simultaneous pressures to forage for invertebrates in or on the soil while avoiding predation. Consequently, they live invariably in groups of 2–21 adults (mean of 9), with some individuals serving as guards while others forage (Rasa 1989, Rood 1990).

Dwarf Mongooses commonly are associated with active termite mounds, particularly those of *Macrotermes falciger*. These mounds have a characteristic cone structure, sometimes more than 2 m above ground; the termites cultivate fungus gardens within these mounds, and because the fungus requires a particular temperature to flourish, ventilation shafts are constructed. The latter are not directly occupied by the termites, but the mongooses use these ventilation shafts as night-time dens or daytime cover from predators (Rasa 1985). Dwarf Mongooses will also den in rock crevices and occasionally in hollow logs, but have a strong association with termite mounds, if available.

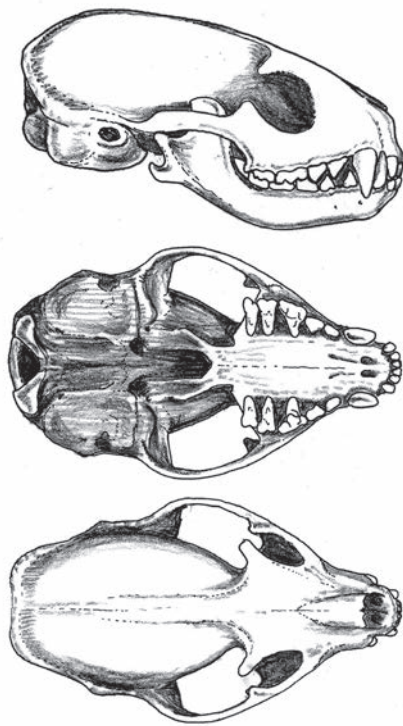
Like other mongooses, Dwarf Mongooses have adaptations of the neurotransmitter system that makes them relatively immune to bites from snakes with neurotoxic venom (see, for example, Barchan *et al.* 1992), such as spitting cobras, and they often mob and attack such snakes to drive them away. While not immune to their venom, Dwarf Mongooses also vigorously mob snakes with haemotoxic venom, such as Puff Adders *Bitis arietans*.

Decker *et al.* (1992) studied the secretions of the anal glands, and found that ♂♂ had vitamin E present in the anal sac, whereas this compound was absent in the ♀♀. This suggests a possible sex-specific function of vitamin E in the Dwarf Mongoose.

Foraging and Food While they occasionally prey upon small vertebrates such as murids, snakes and lizards, Dwarf Mongooses are almost entirely insectivorous (Shortridge 1934, Skinner & Chimimba



Hologale parvula



Lateral, palatal and dorsal views of skull of Dwarf Mongoose *Helogale parvula*.

2005). In a sample of 27 stomachs from southern Africa, Coleoptera, Orthoptera and Isoptera remains had the highest percentage occurrence. Prey identification in scats or stomach contents is hampered by the fact that Dwarf Mongooses masticate their food thoroughly.

Dwarf Mongooses forage for surface-active insects such as beetles, termites and grasshoppers, but very commonly dig up insects and larvae from the soil or litter, alternating bouts of digging, sniffing and listening intently. Packs spread out over an area of roughly 10–200 m² and forage independently within the area, moving slowly as a loose unit, with some individuals pausing to watch for predators. Flying insects are caught in the air with the forepaws, or, if on the ground, with a pounce with both forefeet pinning the insects to the ground. Large insects, such as locusts, are pinned down with a foot, bitten on the head and usually eaten headfirst. Some authors note that the lips are pulled back when Dwarf Mongooses eat stinging insects (Rasa 1973a), but they are often quite nonchalant about eating stinging prey such as scorpions, despite apparently being stung.

Murids, such as multimammate mice (*Mastomys* spp.), when these are taken, are pinned down with the forefeet and killed with a bite to the head. The head is eaten first and then the trunk, but only after skinning, by means of hooking the neck skin with the foreclaws and pulling it down, simultaneously pulling on the neck with the mouth. The entrails are extracted with the teeth. Small snakes are bitten a short distance behind the head then dropped, and repeatedly bitten, then shaken violently until they are quiescent, when they are pinned down with the forepaws and eaten head first. Whereas single animals will prey upon small snakes, larger snakes are usually attacked by the whole group (Rasa 1985). Larger prey, such as large snakes, may be shared by the group, but Dwarf Mongooses rarely share prey with other adults (Rasa 1985). They commonly share food with juveniles, allowing youngsters to learn the job of finding and obtaining prey in gradual steps.

Dwarf Mongooses have been observed standing up on their hind-legs on a rock, beneath a Red Ivory tree *Berchemia zeyheri*, grasping the thin, terminal branches with their forepaws, and pulling these towards them in order to remove the berries with their mouths (Hiscocks & Perrin 1991b). Rasa (1985) also observed them eating eggs; those from small birds are bitten open at the end and the contents licked out, while larger eggs such as those from francolins (*Francolinus* spp.) are clasped in front of them on the ground and thrown backwards under the body and upwards so that the egg is propelled against a hard object to break it open. They then either lick up the contents or use their paws to scoop the contents and then lick these. Dwarf Mongooses do not use this method often, in comparison with Banded Mongooses, which sometimes smash invertebrates in the same manner.

Social and Reproductive Behaviour Dwarf Mongooses are a highly social and cooperative species, found exclusively in groups, except for individuals in the process of dispersing. Packs comprise both related individuals and unrelated immigrants; in the Serengeti N. P., where the species has been the focus of a long-term study, packs average nine adults (range 2–21), with slightly more adult ♀♀ than ♂♂, plus young of the year from one to four sequential litters (Waser *et al.* 1995). Packs are structured by a rigid dominance hierarchy, comprising a single dominant breeding pair with a life-long bond (usually the oldest individual of each sex), and with subordinates reproductively suppressed and helping to raise the young of the dominants (Rood 1978, 1980, 1983a, 1990, Creel *et al.* 1992, Creel & Waser 1994, Keane *et al.* 1994).

Dwarf Mongooses are, like other social mongooses such as the Banded Mongoose and Meerkat *Suricata suricatta*, remarkably cooperative, with pack members collectively defending a shared territory, and most members engaging in behaviour such as watching for predators while others forage, babysit, jointly mark the home-range and allogroom. Relations within packs are amicable and strong, as evidenced, for example, by reports of alpha ♂♂ rescuing pack members from danger (Rood 1983a), and the provision of food and care for incapacitated animals (Rasa 1976b). More routinely, most adults of a pack groom, feed and carry the pack's young, and frequently engage in social grooming with other adults.

Groups are territorial, and will usually attack non-resident mongooses on their territory (though see Rasa 1985). Home-ranges in Serengeti N. P. averaged 27.4 ± 3.3 ha (Rood 1978), and there is some fidelity to these: of seven packs that ranged over a 2.2 km² study area in Serengeti N. P., two were still using the same core areas and dens after five years. Dwarf Mongooses jointly mark their territories, particularly objects near the termite mounds that they use as sleeping quarters. Scent-marking is achieved using both anal and cheek glands, which they rub on objects (and also on partners and offspring); marking with the everted anal gland is achieved in the typical anal drag fashion, or by means of a handstand. It is not unusual to see several packmembers simultaneously leaping onto their forefeet and grabbing a branch with their hindfeet to deposit anal marks. Faeces and urine are deposited in communal latrines. There is little overlap between territories (Rasa 1987), although ranges of adjacent packs may overlap slightly. These may serve as sites of confrontation between neighbouring groups, sometimes leading to injuries. In the short term, larger packs usually displace smaller packs in these conflicts, but this does not necessarily cause long-term changes in territory boundaries.

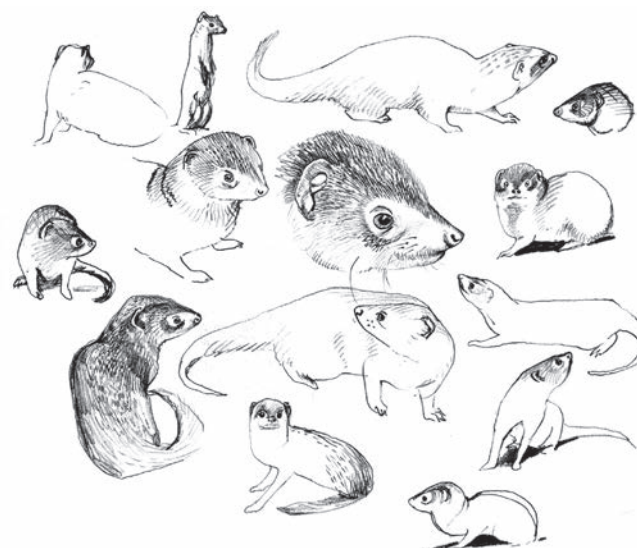
The alpha ♀ usually initiates pack movements each morning. If other pack members try to initiate movements, they are often ignored. Before moving out, guards, or babysitters, are posted to look after the pups that are too young to accompany the group on their foraging trips. Litters may occasionally be left unguarded for a few hours, but usually at least one pack member stands guard until the young are old enough to leave the den around 5–6 weeks; as many as three or more pack members may remain with the pups while the group forages (Rasa 1977a, 1986, Rood 1978). Babysitters remain at the den for several hours, foregoing foraging, until relieved by another set of babysitters (Rood 1978). The breeding ♀ is actually the least likely adult to be found guarding the young during a foraging bout.

Foraging groups remain in close vocal contact while foraging and moving, and also post guards, which watch for predators while others forage. Sentinels will move to a vantage point, such as a termite mound, from which to scan the area (Rasa 1986). If the sentinel sounds an alarm call, usually in response to a bird of prey, the group will freeze, or head straight for the nearest cover if the danger proves immediate (Rasa 1985). In the absence of any danger, the sentinel will return to foraging after a few minutes. Pack members share sentinel duty, with certain male members contributing more time than others. Different alarm calls are used for different predators: the notes are particularly distinct for terrestrial ('tchrr!') versus aerial ('tchee!') predators. Dwarf Mongooses respond to the alarm calls of other species such as hyraxes and hornbills (Rasa 1985), which also respond to mongoose alarm calls.

Dwarf Mongooses are commonly found sunning themselves in the early morning or afternoon near the entrances of the residence-mounds, during which they commonly indulge in allogrooming and autogrooming. Mongooses normally groom themselves and others by nibbling with their incisors. They appear to enjoy grooming in much the same way that some domestic cats enjoy being petted. Trapped mongooses are often relatively free of ectoparasites, suggesting that allogrooming may function in social behaviour in addition to its more typical function. Allogrooming pairs are usually of the same sex, and typically similar in social rank within the pack. Most adults also groom youngsters of both sexes.

As noted earlier, only the dominant pair generally breeds; mongooses that achieve alpha status usually have a tenure of several years. If one of the alpha pair dies, then the individual is replaced from within the pack by the oldest adult of the same sex. During the peak of oestrus, the alpha pair consorts all day, the dominant ♂ seldom being found more than a few centimetres from the ♀ (Rasa 1973b, 1987, Rood 1980), and the ♂ shows a marked increase in aggression towards other ♂♂ (Rood 1980, Rasa 1987). At this time, the pair may engage in as many as 50 mounts per hour (Creel *et al.* 1992, 1993), and may copulate as many as 2386 times, apparently ejaculating in 10% of these (Rasa 1985). Copulation takes a mean of 21 sec ($n = 67$; Rood 1990), the longest recorded being 11 min. The alpha ♀ will occasionally mate with subordinate ♂♂, even during the peak of oestrus (Rood 1980, Creel *et al.* 1992); subordinate ♀♀ mate with ♂♂ of all ranks.

Despite mating, most female subordinates fail to establish pregnancy, their oestrogen levels returning to baseline. In ♀♀, reproductive suppression operates either by blocking ovulation (most probable), fertilization or implantation, though not by abortion of established pregnancies (Creel 1996). Adult subordinate ♀♀ quickly obtain full



Dwarf Mongoose *Helogale parvula*.

reproductive activity after becoming dominant ♀♀, either by dispersing or by inheriting a pack following the death of the prior alpha ♀ (Rood 1980). In ♂♂ reproduction is suppressed mainly by aggressive interference with the mating attempts of subordinates, and reproductive hormone levels in subordinates are not depressed, although their testes are significantly smaller. Subordinates are more likely to mate with other subordinates (Creel *et al.* 1992).

Although subordinate ♀♀ are reproductively suppressed, 12% (usually older subordinates) still become pregnant every year, accounting for about 27% of pregnancies (Creel & Waser 1991). Most of these pups are killed by the alpha ♀ (Rasa 1973b, Rood 1983a); however, their offspring are sometimes raised if they avoid infanticide by the dominant ♀, and particularly if raised in joint litters. Genetic data reveal that 15% of all offspring are produced by subordinate ♀♀, and that subordinate ♂♂ sire approximately 25% of the pups (Keane *et al.* 1994). Occasionally, the pregnancies of subordinates are synchronized with those of the dominants, and then pups may be raised in a joint litter (Creel & Waser 1991, Keane *et al.* 1994). The mean size of joint litters (3.2 offspring at emergence) is significantly larger than that of alpha-male-only litters (2.4 offspring). In such cases, despite the presence of an additional lactating ♀, the dominant's production of mature offspring is reduced by 22% in joint litters; thus the dominant's young do not survive better as a result of communal nursing (Creel 1996). Another form of communal nursing occurs: for every four subordinates that lactate following pregnancy, one ♀ lactates without pregnancy (Rood 1980). This extreme form of alloparental care is known to occur in the wild only in female Dwarf Mongooses and male Dayak Fruit Bats *Dyacopterus spadiceus* (Francis *et al.* 1994).

Young usually are born in termitaria. Adults of both sexes contribute to raising offspring in many ways, by feeding, grooming, guarding and 'babysitting' them (Rasa 1973, 1977, 1989, Rood 1978, 1983a); subordinate pregnant ♀♀ will even suckle young of the alpha pair (Rood 1980, Creel *et al.* 1991). If the group moves to another mound, the subordinates carry the pups until they can walk themselves, from about 3.5 weeks of age. Cooperative breeding is, therefore, highly evolved in Dwarf Mongooses, to the point that unaided breeding pairs very rarely raise any offspring to independence (Creel 1990). The

energetic investment in reproduction is unusually high, both in terms of the number of offspring produced, and the growth rate of individual offspring. Without non-breeding helpers, these costs cannot be sustained. Of 237 breeding attempts in a Serengeti population, only 12 (5%) were made by unaided pairs, and only one (<0.5%) of these pairs raised any offspring to independence (Creel & Creel 1991). On this basis, it is fair to call the species an obligately cooperative breeder.

Both sexes disperse, usually as young adults and often as a group of littermates of the same sex, or a same-sexed group of similar ages. Males are more likely than ♀♀ to disperse (and to disperse farther), and the risks associated with dispersal account for the better survival of ♀♀, which yields a female-biased sex ratio among adults, even though slightly more ♂♂ are born (see Reproduction and Population Structure) (Waser *et al.* 1994a). Dispersal is important because immigrants are more likely to become dominants and reproduce earlier than are individuals who remain within their natal packs. For example, out of a sample of 31 individually known mongooses that achieved alpha status, 25 (13 ♀♀ and 12 ♂♂) were immigrants, compared with six that did not disperse and remained within their natal packs; similarly, seven ♀♀ that emigrated to other packs and attained alpha status bred at two years of age, compared with three ♀♀ that failed to disperse and only bred at four years of age (Creel & Waser 1994, Waser *et al.* 1994a).

Young of the year are initially fed by adult packmates (not only the parents), and learn to forage by following an adult and observing, at first being fed directly, but later being allowed to do the final digging or capture. Food availability varies seasonally and drives seasonal patterns of reproduction, with breeding during the wet season, when invertebrate availability is higher.

As mentioned elsewhere, Dwarf Mongooses use different alarm calls in response to different predators, probably because the best response differs for attacks by raptors and terrestrial predators. While moving and foraging, each mongoose frequently makes a quiet call ('boop') that allows the group to stay in contact even if they cannot see one another. When playing, young mongooses make a wide range of twittering, bird-like noises.

Dwarf Mongooses associate with many other species to reduce predation risk. Although they are frequently present in the same area, they do not share burrows with Banded Mongooses in the same manner as Yellow Mongooses *Cynictis penicillata* and Meerkats. Dwarf Mongooses are sometimes found in association with insectivorous birds such as drongos (*Dicrurus* spp.) and Lilac-breasted Rollers *Coracias caudatus*, but the strongest associations are between mongooses and two bush hornbills (*Tockus* spp.), with the birds awaiting the emergence of the mongooses in the morning before foraging together (and sometimes, if the mongooses are later than usual, the hornbills call down their holes to wake them up!). Hornbills benefit by catching flying insects disturbed by the mongooses, while the mongooses benefit from alarm calls given by the hornbills from their higher vantage point (Rasa 1983, 1985). Rasa (1985) also mentions their association with rough-scaled plated lizards inhabiting the termite mounds and which feed on faecal pellets of the mongooses.

Reproduction and Population Structure In Serengeti N. P. litters are born almost exclusively between the months of Nov and May, with occasional litters in Oct and Jun (Rood 1980); this annual peak is timed so that most litters are born during periods

of substantial rainfall and with at least one month of good rainfall to come, and such that lactation coincides with months of highest insect abundance (Waser *et al.* 1995). In southern Africa, all evidence points to their breeding during the summer wet season when insects are plentiful (Skinner & Chimimba 2005).

Oestrus lasts 1–7 days, and ♀♀ come into oestrus in tight synchrony, with subordinates entering oestrus a day later than the alpha ♀, suggesting that subordinates begin follicular activity in response to dioestrus in the dominant ♀ (Rood 1980, Creel *et al.* 1992, 1993). Gestation lasts 49–53 days (Rasa 1973b, 1987, Rood 1980), with a mean litter-size of 3.3 offspring at emergence from the den (approximately 2–3 weeks after birth) (Creel *et al.* 1992); in captivity, up to seven young may be born. Rood (1990) found that large groups had significantly larger litter-sizes than small groups. Neonates weigh 21.3 g on average, so that an average litter weighs 20% of the mother's mass (Creel & Creel 1991). Alpha ♀♀ may conceive during the postpartum oestrus, and, typically, 2–4 litters (mean = 2.4) are produced during a period of 5–6 months in the wet season, which translates into a ♀ producing pups equivalent to roughly 10% of her own mass each month, for several months in a row (Rood 1980, Creel & Creel 1991, Creel & Waser 1994). Lactation lasts 56 days on average, with pups growing 2.6 g/day (growth being positively affected by the number of adult and yearling helpers in the pack, and by rainfall; Creel & Creel 1991), while the ♀ is often pregnant with her next litter. As noted above, this heavy energetic investment in reproduction cannot be sustained without dominant ♀♀ spending significantly more time foraging than other pack members during the breeding season and without assistance from non-breeding helpers, who assist by feeding pups and guarding them while the breeding ♀ forages (Creel 1990, Creel & Creel 1991, Creel *et al.* 1991, 1995a).

In Serengeti N. P., the sex ratio at birth was slightly biased (52.5%) in favour of ♂♂ in a sample of 846 pups. By the age of two years, the sex ratio is female-biased, due to higher mortality in ♂♂, who are more likely to disperse and suffer increased mortality when not associated with a pack (Creel & Waser 1994, Waser *et al.* 1994a). Mean annual survival in Serengeti N. P. was 0.68 for 182 ♂♂ and 0.74 for 165 ♀♀ beyond the age of one (Waser *et al.* 1995). For juveniles, annual survival from emergence to their first birthday was 0.41 and did not differ by sex. Dwarf Mongooses are sexually mature as yearlings, but very few young adults reproduce, owing to social suppression of reproduction; only 1% of yearling ♂♂ attained dominant breeding positions compared with more than 70% for six-year-olds (Creel *et al.* 1992). Maximum longevity observed in the wild is ten years for ♂♂, 14 for ♀♀ (Waser *et al.* 1995); a captive specimen lived for 18 years (Weigl 2005).

Predators, Parasites and Diseases Major predators include raptors, particularly Pale Chanting-goshawks *Melierax canorus*, Martial Eagles *Polemaetus bellicosus*, Tawny Eagles *Aquila rapax* and Bateleurs *Terathopius ecaudatus*; monitor lizards; snakes, particularly Puff Adders *Bitis arietans* and spitting cobras (*Naja* spp.); and other small carnivores such as White-tailed Mongooses *Ichneumia albicauda*, Egyptian Mongooses *Herpestes ichneumon*, Banded Mongooses (particularly on young), Servals *Leptailurus serval*, Black-backed Jackals *Canis mesomelas* and Ratels *Mellivora capensis* (Rasa 1983, Rood 1990).

As described above, the selection pressure of predation has been an important force in the evolution of sociality in mongooses. Dwarf

Mongoose are small, diurnal, forage in the soil for invertebrates and occupy relatively open habitats. These factors combine to leave a solitary animal very vulnerable to predation when foraging, and sociality allows for a system in which a sentinel keeps watch while others feed, and then feeds in its turn. Other social mongoose species, like the Banded Mongoose, tend to be small, diurnal, prey on invertebrates and occupy open habitats with substantial predation risk (Rood 1986). Solitary mongooses tend to be larger, more nocturnal, occupy thicker habitats and prey on vertebrates.

Little is known about diseases, but they may be affected by some of the viral pathogens known to affect other carnivores, such as canine distemper, rabies and parvovirus. There is also little information available on parasites, but leishmanial parasites have been isolated from this species (Mutinga *et al.* 1982) and Levine *et al.* (1975) recorded at least two species of coccidian parasites, *Isospora garnhami* and *I. hoarei*.

Conservation IUCN Category: Least Concern. CITES: Not listed.

Dwarf Mongooses have a wide distribution, attain high densities and have small territories such that even small protected areas can harbour large populations. They are often the most common carnivore in the habitats they occupy, and because of their abundance and wide distribution, may have greater than appreciated effects on ecosystems, despite their diminutive size.

Measurements

Helogale parvula

TL (♂ ♂): 375 (340–410) mm, n = 34
 TL (♀ ♀): 387 (340–410) mm, n = 19
 T (♂ ♂): 166 (152–183) mm, n = 24
 T (♀ ♀): 165 (142–188) mm, n = 19
 HF c.u. (♂ ♂): 46 (41–51) mm, n = 23
 HF c.u. (♀ ♀): 46 (41–49) mm, n = 19
 E (♂ ♂): 17 (15–21) mm, n = 21
 E (♀ ♀): 18 (14–21) mm, n = 19
 WT (♂ ♂): 269 (223–341) g, n = 13
 WT (♀ ♀): 265 (213–341) g, n = 11
 GLS: 46.0–50.0 mm, n = 35
 GWS: 27.0–30.0 mm, n = 35
 Botswana (Smithers 1983)
 Skull measurements: Southern Africa (Roberts 1951)

Key References Creel 1990, 1996; Creel *et al.* 1991, 1992, 1993, 1995; Creel & Waser 1991, 1994; Rasa 1973a, b, 1976a, b, 1977a, b, 1985, 1987, 1989; Rood 1978, 1980, 1983a, 1986, 1990; Waser *et al.* 1994a, 1995.

Scott Creel

GENUS *Crossarchus*

Cusimanse

Crossarchus F. Cuvier, 1825. In: E. Geoffroy Saint-Hilaire & F. Cuvier, Hist. Nat. Mammifères 3 (47): 1–3.

The genus contains four species: Alexander's Cusimanse *Crossarchus alexandri*, Ansonge's Cusimanse *C. ansongei*, Common Cusimanse *C. obscurus* and Cameroon Cusimanse *C. platycephalus*. *Crossarchus platycephalus* has been considered a subspecies of *C. obscurus* (Wozencraft 1989a, 1993), but Goldman (1984) and Colyn & Van Rompaey (1994b) considered them distinct species (and see Wozencraft 2005).

The genus is restricted to areas of lowland forest between SW Guinea and E DR Congo and W Uganda with isolated populations on Mt Elgon, E Uganda and NE Angola. Common Cusimanse inhabits the West faunal region and Cameroon Cusimanse the West Central region; these two allopatric species are separated by the Volta R. (western Dahomey Gap). Further east, Ansonge's Cusimanse and Alexander's Cusimanse mainly inhabit the lowland forests of the Congo basin.

Members of the genus are small, darkish-brown with a coarse, shaggy pelage ticked with yellowish-white to reddish-brown; hairs on head and face lighter than on body. Ears short and round. All members have a long snout (less pronounced in Ansonge's Cusimanse). No longitudinal groove on upper lip. Head and distal parts of fore-

and hindlimb shorter-haired than body and tail; brownish underfur long but shorter than guard hairs. Tail shorter than head and body length and tapers from base to tip. Legs short; five-toed feet, slightly webbed, with long claws. Plantigrade gait. Area between digital pads and plantar pads naked in fore- and hindfeet; posterior 30% of hindfoot naked. Paired anal scent glands. The genus name, *Crossarchus*, comes from the Greek *crossotos* fringed, and *archos* anus, and refers to the wrinkled folds of the circumanal glandular sac. Ectotympanic portion of bulla larger than entotympanic. Dental formula is $I^{3/3}, C^{1/1}, P^{3/3}, M^{2/2} = 36$. Upper and lower first premolars are absent.

Crossarchus was considered synonymous with *Mungos* by Hill & Carter (1941) and a subgenus of *Mungos* by Ellerman *et al.* (1953). Molecular data place *Crossarchus* as sister taxon to *Helogale* (Perez *et al.* 2006, Patou *et al.* 2009).

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Facial features of three *Crossarchus* species.

Crossarchus alexandri ALEXANDER'S CUSIMANSE

Fr. Mangué d'Alexandre; Ger. Kongokusimanse

Crossarchus alexandri Thomas & Wroughton, 1907. Ann. Mag. Nat. Hist., ser. 7, 19: 373. 'from Banzyville, Ubanghi' [= Mobayi, Zaire (= DR Congo), 4° N, 21° 11' E (Goldman 1984)].

Alexander's Cusimanse *Crossarchus alexandri*.

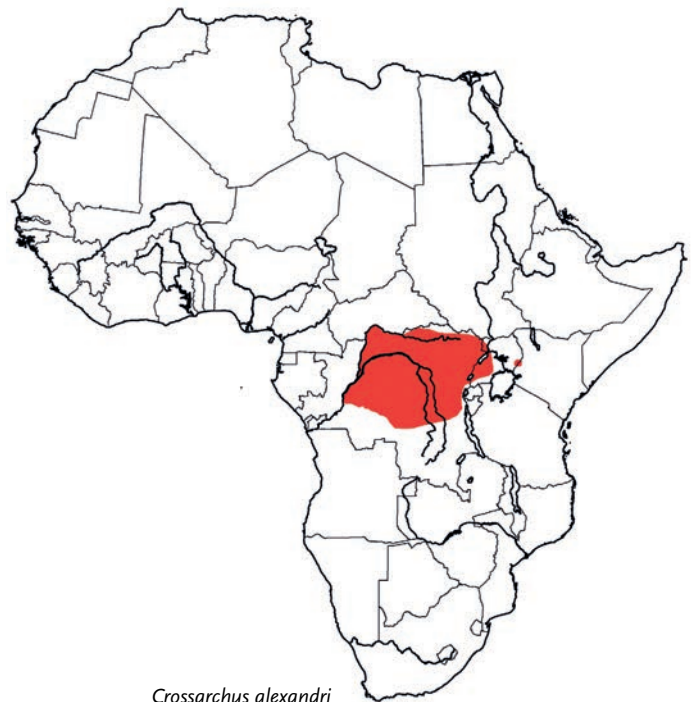
Taxonomy Monotypic. A specimen collected by Emin Pasha in NE DR Congo was mistaken for and described as *C. obscurus* by Thomas (1888). The species has also been confounded with the genus *Mungos* (e.g. *Mungos obscurus alexandri*; Mertens 1925). Species named after the collector of the type specimen, Boyd Alexander. Goldman (1984) described *C. alexandri minor* from extreme E DR Congo and Uganda, including an isolated montane population on Mt Elgon. Recognition of this subspecies, described solely on the basis of smaller cranial measurements, was not supported in the study of Colyn & Van Rompaey (1994b). Synonyms: *minor*. Chromosome number: not known.

Description A small, shaggy-haired, short-legged, long-nosed mongoose. General colour brownish-black, grizzled with grey. Hair on head short; muzzle greyish-buff; lips and cheeks pale buff. Crown blackish-brown; ears pale brown. Snout elongated. Back and flanks covered with long guard hairs (50–60 mm long). Guard hairs grey at the base with upper half black and a whitish tip. Underfur more brownish with hairs brown at base and lighter at tip. Ventral pelage more brownish than back and flanks. Nuchal crest (hairs ca. 60–80 mm long) starting from the crown to the shoulders, continuing in a mid-dorsal crest to the base of the tail. Pair of whorls on back of neck. Fore- and hindlegs short-haired and black; long, sharp claws, especially on forefeet. Tail (ca. 70% of HB) tapering and long-haired at the base, similarly coloured as body. Three pairs of nipples.

Geographic Variation None recorded.

Similar Species

Crossarchus ansorgei. Sympatric. Smaller; pelage less shaggy; snout shorter (length of rostrum ca. 31.5% of condylobasal length; Van Rompaey & Colyn 1992); posterior portion of bulla more inflated.

*Crossarchus alexandri*

Xenogale naso. Sympatric. Larger size and smoother, short-haired pelage; does not live in groups.

Distribution Endemic to central Africa. Confined to the rainforest in DR Congo on both sides of the Congo R., in the north limited by the Ubangi R. and in the south by the Kasai R.; also present in W Uganda. A disjunct population lives on the slopes (between 1500 and 2900 m) of Mt Elgon, E Uganda. Alexander's Cusimanse is present in two faunal regions (East-central and South-central) showing no



Alexander's Cusimanse *Crossarchus alexandri*.

subspeciation, implying that the species survived the last interpluvial in a single faunal region. We hypothesize that Alexander's Cusimanse was formerly isolated in a refugium on the right bank of the Congo R., and that colonization of the South-central region occurred comparatively recently (Holocene) and during a limited time span (Colyn & Van Rompaey 1994b).

In SW Central African Republic, natives use a distinct name to refer to an uncommon mongoose, living in groups, in the area. The presence of a species of *Crossarchus* is suspected (Ray 2001).

Habitat Lowland and montane rainforest. Not known to occur in the forests of the Central Rift. Lives in thick undergrowth and prefers swampy areas (Kingdon 1977). Commonly found near villages in Ituri Forest (J. C. Ray pers. comm.).

Abundance There is no direct information on abundance. The fact that Alexander's Cusimanses make up nearly half of the carnivore bushmeat in NE DR Congo (Colyn *et al.* 1987) suggests that they are widespread and abundant in this region. In the Ituri Forest, Bambuti pygmies hunting with dogs captured Alexander's Cusimanses with greater frequency than other carnivores (76 individuals in 53 hunts, or 67% of all carnivores) (Hart & Timm 1978).

Adaptations Nocturnal according to Rahm (1966) but generally considered as diurnal by the Mbuti pygmies (Carpaneto & Germi 1989, J. C. Ray pers. comm.). It is possible that in the forest undergrowth



Lateral view of skull of Alexander's Cusimanse *Crossarchus alexandri*.

the distinction between day and night is less important than it is in the open (Kingdon 1977). Terrestrial, but they may climb sloping trees and are more adept climbers than the Banded Mongoose *Mungos mungo* (Kingdon 1977); one specimen while fleeing ran up a tree and tried to hide among creepers about 10 m high (R. W. Hayman pers. comm.). Long nose and long, strong claws on the forefeet are adaptations for foraging on the forest floor and opening rotting tree trunks. They are also able to dig their own holes (Kingdon 1977). Communication in dense vegetation is facilitated by an elaborate vocal repertoire and scent-marking, as in the Common Cusimanse *C. obscurus*.

Foraging and Food Frugivorous and carnivorous (Rahm 1966). Stomachs contained frogs, slugs and insects, chiefly crickets, grasshoppers and caterpillars. They are also recorded taking worms and fruit (Kingdon 1977) and butterflies, millipedes, earthworms, termites, snakes, carrion, bananas and oil palm fruits (Carpaneto & Germi 1989). While foraging, individuals push their noses into crevices and scrape and scratch continually.

Social and Reproductive Behaviour A social species, Alexander's Cusimanses have been observed foraging in packs of as many as ten (Carpaneto & Germi 1989) to 20 individuals (Kingdon 1977), grunting and twittering continually. Any alarm excites a loud chatter, after which they run off in silence. Hand-stands are executed in order to mark tree trunks and branches some 25 cm off the ground with the secretion of the anal gland. Captives tend to drop their faeces and urinate in one place and respond to the faeces and urine of other animal species by scratching and then superimposing their own urine or anal deposit (Kingdon 1977). Up to ten individuals sleep together in holes in trunks of dead trees (Carpaneto & Germi 1989). There is no information on their home-range.

Reproduction and Population Structure One ♀ collected mid-Apr contained six embryos (Verschuren 1972). According to the Mbuti pygmies there are 3–4 young per litter (Carpaneto & Germi 1989).

Predators, Parasites and Diseases There is no information on predators or diseases. Nematodes *Subulura schebini* and *Spirura congolense* (Vuylsteke 1956), the nymph of a pentastome *Armillifer armillatus* (Fain 1961), and a louse *Suricatoecus* sp. (Emerson & Price 1967), have been found on specimens from DR Congo.

Conservation IUCN Category: Least Concern. CITES: Not listed.

Overall not considered threatened, but numbers probably declining due to forest loss and bushmeat hunting. Alexander's Cusimanses comprised nearly half (42.3%) of the carnivore bushmeat in a study in NE DR Congo (Colyn *et al.* 1987). It is sometimes caught in traps but mostly hunted with dogs (Carpaneto & Germi 1989). The Mt Elgon population may be threatened by hunting and habitat degradation (Kingdon 1997).

Measurements

Crossarchus alexandri

HB: 406 (375–437) mm, n = 29



Alexander's Cusimanse *Crossarchus alexandri* marking a post.

T: 282 (243–318) mm, n = 29

HF c.u.: 86 (80–91) mm, n = 29

E: 26 (24–30) mm, n = 29

WT (♂♂): 1.19, 1.75 kg, n = 2

WT (♀): 1.45 kg, n = 1

GSL: 80.0 (73.2–90.0) mm, n = 232

GWS: 37.7 (31.2–44.2) mm, n = 226

DR Congo (Allen 1924 and museum specimens: JFBM, LACM, NMNH)

Skull measurements: museum specimens (BMNH, IRSN, MRAC, SMF)

Key References Carpaneto & Germi 1989; Colyn & Van Rompaey 1994b; Kingdon 1977.

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Crossarchus ansorgei ANSORGE'S CUSIMANSE (ANGOLAN CUSIMANSE)

Fr. Mangué d'Ansorge; Ger. Ansorge's Kusimanse

Crossarchus ansorgei Thomas, 1910. Ann. Mag. Nat. Hist., ser. 8, 5: 195. Dalla Tando (Ndala Tando, 09° 18' N, 14° 54' E, Angola).

Taxonomy Species named after the collector of the type specimen, W. J. Ansorge. Two subspecies are recognized (see Colyn & Van Rompaey 1990). Synonyms: *nigricolor*. Chromosome number: not known.

Description A small, dark brown, light-speckled mongoose with a relatively short muzzle. Hairs on muzzle, chin and a mask-like zone around the eyes very short. Whorl present on the back of the neck. Ears short and rounded. Body, limbs and tail a relatively uniform dark brown. Area between digital pads and plantar pad naked in fore- and hindfeet. Claws long (forefeet 8–12 mm; hindfeet 6.5–9 mm) and curved, especially on forefeet. Tail shortish (ca. 66% of HB). Presumably three pairs of nipples.

Geographic Variation

C. a. ansorgei: Angola, escarpment zone north of the Cuanza R. General colour reddish-brown, with crown and ears blackish, and chin and cheeks pale brown; light rings on guard hairs; underfur dense, hairs tipped with tawny or tawny-ochraceous; forelimbs black and hindlimbs tawny; feet black; tail mixed reddish and black basally, more blackish distally.

C. a. nigricolor: DR Congo, probably limited to the forest blocks between the Congo/Lualaba and Kasai rivers. General colouration sepia black, with chin and muzzle short-haired and dirty white continuing in a small stripe above the eyes; white to yellowish-ochreous stripe, 1 cm in width, extends from corner of mouth under external ear to side of neck; ears with a whitish tuft at internal base; back, flanks, neck and head covered with black hairs

(up to 35 mm long) annulated with white to yellowish-ochre band near the top; underparts, tail and limbs completely blackish; tail bushy with hairs up to 4.5 cm long, tapering from base to tip.

Similar Species

Crossarchus alexandri. Sympatric. Larger; shaggier pelage; longer snout (length of rostrum 34–36% of condylobasal length; Van Rompaey & Colyn 1992); anterior portion of bulla more developed.

Xenogale naso. Sympatric. Larger size and smoother, short-haired pelage; does not live in groups.



Ansorge's Cusimanse *Crossarchus ansorgei*.

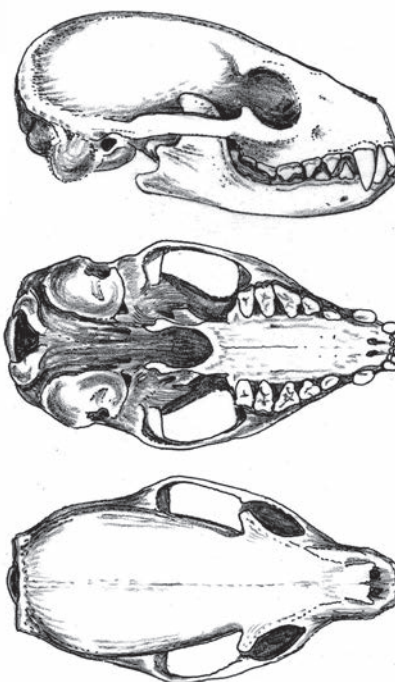
Distribution Endemic to central Africa. Found only in Angola and DR Congo. In Angola, known only from a single specimen (the type) collected in 1908 in the northern part of the escarpment zone in the southernmost portion of the Dembos forest, north of the Cuanza R. (Crawford-Cabral 1989a). In DR Congo, present in the rainforest south-east of the Congo/Lualaba R., where collected from five localities: Amadjabe (00° 04' S, 25° 17' E), Baringa (00° 45' N, 20° 52' N), Ikela (01° 11' S, 23° 16' E), Kodoro (01° 16' N, 20° 06' E) and Yaenaro Plantation (00° 12' N, 24° 47' E) (Coetzee 1977, Colyn & Van Rompaey 1990). Expected to occur down to the Kasai R., but unlikely to range as far as central Kivu, as suggested by Coetzee (1977). Ansorge's Cusimanse, present in the South-central region, has not been able to colonize higher altitude forests in the East-central region (Colyn & Van Rompaey 1994).

Habitat All specimens have been collected from deciduous rainforest. Unlike Alexander's Cusimanse *C. alexandri*, it is not known to visit cultivated or inhabited land (Colyn 1984).

Abundance Up until 1984, this species was known only from two specimens, the type and the specimen from Baringa. However, they have since been found to be quite common in the Tshopo Sub-region (part of Orientale Province, south of Kisangani, DR Congo). During bushmeat surveys conducted in the 1980s in the eastern Congo basin, this species accounted for only 10% of carnivores. By contrast, Alexander's Cusimanse accounted for 42%. Their relative rarity as prey



Crossarchus ansorgei



Lateral, palatal and dorsal views of skull of Ansorge's Cusimanse *Crossarchus ansorgei*.

implied that although Ansorge's Cusimanse formed social groups of similar size to those of Alexander's Cusimanse, Ansorge's Cusimanse groups must have been more difficult to hunt, travelled over much larger home-ranges or, more likely, were specialized in some unknown way for survival in a sub-region or vegetation sub-type (Colyn *et al.* 1987).

Adaptations Diurnal and terrestrial. Strong claws on the forefeet are adapted for foraging on the forest floor and opening rotting tree trunks. The respects in which this species differs from the commoner and sympatric Alexander's Cusimanse are not known, but its shorter, thicker snout implies a less specialized diet and, possibly, a more conservative position in the *Crossarchus* radiation.

Remarks There is a paucity of information available on the ecology of this species. Food includes small vertebrates, insects, larvae and eggs. Two captive individuals refused fruits, mushrooms and berries (Colyn 1984). They are social, living in groups of up to 20 animals (Colyn 1984). According to native hunters in NE DR Congo, their behaviour is similar to that of Alexander's Cusimanse.

Conservation IUCN Category: Data Deficient. CITES: Not listed.

There is a paucity of information available for this species, which makes it a clear priority for research, particularly to determine its current population status and to determine the extent of its geographic range. In particular, a survey for the disjunct population in Angola is urgently needed since the nominate subspecies is known only from the holotype collected in 1908. Threats to this species are not clear, but probably include habitat loss and bushmeat hunting (as mentioned, Ansorge's Cusimanse accounted for 10% of the

carnivores hunted as bushmeat in DR Congo; Colyn *et al.* 1987). Recorded from Salonga N. P. in DR Congo (Schreiber *et al.* 1989).

Measurements

Crossarchus ansorgei

HB (♂): 342 mm

HB (♀): 320 mm

T (♂): 208 mm

T (♀): 212 mm

HF c.u. (♂): 70 mm

HF c.u. (♀): 60 mm

E (♀): 24 mm

WT (♂): 700 g

GLS: 64.1 (60.3–66.9) mm, n = 50

GWS: 33.4 (31.2–35.2) mm, n = 50

Body measurements: Angola (Thomas 1910) and DR Congo (Colyn 1984)

Skull measurements: DR Congo (museum specimens: MRAC)

Key References Colyn 1984; Colyn & Van Rompaey 1990; Colyn *et al.* 1987; Van Rompaey & Colyn 1992.

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Crossarchus obscurus COMMON CUSIMANSE

Fr. Mangouste brune; Ger. Dunkelkusimanse.

Crossarchus obscurus (F. Cuvier, 1825). In: E. Geoffroy-St. Hilaire & F. Cuvier, Hist. Nat. Mammifères 3 (47): 1. 'côtes occidentales de l'Afrique, et vraisemblablement des parties qui sont au midi de la Gambie'; restricted by G. Cuvier (1829: 158 in Wozencraft 1993) to 'Sierra Leone'.

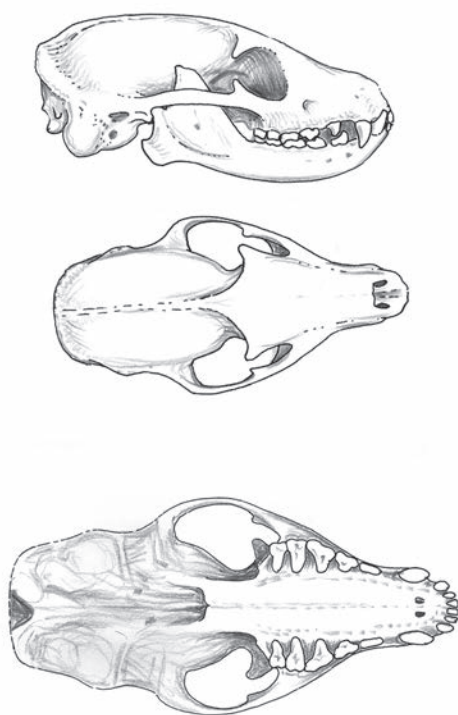


Common Cusimanse *Crossarchus obscurus*.

Taxonomy Monotypic. Thomas (1895) described *Crossarchus somalicus* as 'a new banded mongoose from Somaliland', a form that Wozencraft (1993) included as a synonym of *C. obscurus*; *somalicus* is actually a synonym of *Mungos mungo* and not related to this species or genus. Synonyms: *punctatissimus*. Chromosome number: $2n = 36$ (Fredga 1972).

Description A small-sized mongoose with long nose, strong claws, short legs and dark brown pelage (the specific name, *obscurus*, is Latin for dark or dusky, referring to pelage colour). Nose extends considerably beyond lower lip; longitudinal groove on upper lip is absent. Paired cheek glands between ears and mouth in both sexes. Ears pale brown, short and round; capable of closing by movement of posterior ridges

(Ewer 1973). In some museum specimens there are whorls posterior of the ears and crown, where the hairs spread out around a circular patch with no hair, and a crest between ears along nape. Hairs that form the crest stand erect and are ca. 5–12 mm in length, shorter anteriorly and longer posteriorly. Both whorls and crest, which are present in both sexes and appear not to be seasonal, are more pronounced and frequent in museum specimens of Cameroon Cusimanse *Crossarchus platycephalus*. In 13 adult museum specimens from Sierra Leone, Liberia, Côte d'Ivoire and Ghana, whorls were clearly present in eight specimens (six with one whorl and two with two whorls); the crest was clearly visible in seven specimens. Rosevear (1974: 285), examining specimens of *Crossarchus* spp. from West Africa, noted that 'one of the most characteristic features of the *Crossarchus* pelage is the presence of a pair of large whorls on the back of the neck ... but though these are for the most part very conspicuous they are not always so and may, exceptionally, apparently be wholly lacking'. Whorls and crest have not been observed in live specimens in Tai N. P., Côte d'Ivoire, based on field observations of 54 individuals (A. E. Dunham pers. obs.), or in Tiwai Island Wildlife Sanctuary, Sierra Leone, based on observations of 12 captured individuals (A. L. Olson pers. obs.). The hairs of the head are short (to ca. 3 mm), medium to dark brown, with pale tips; hairs of cheeks and around eyes paler. Dorsal guard hairs ca. 15–20 mm in length posterior of ears, 25–30 mm at mid-body, and 30–35 mm at rump. Guard hairs of body and tail coarse and dark brown with pale tips, giving an overall speckled appearance. Guard hairs along anterior half of back with tips (ca. 4–5 mm) ranging from pale buff



Lateral, dorsal, and palatal views of skull of Common Cusimanse *Crossarchus obscurus*.

to yellowish-buff, with some specimens being considerably more speckled than others. Guard hairs of rump mostly with reddish-brown tips, thus rump appears darker than anterior half of back; rump more blackish-brown in some specimens, where pale tips are few or absent. Hairs of underfur finer than guard hairs and ca. 15–20 mm in length, basal band dark brown, subterminal band (ca. 4–5 mm) pale buff, most often with a reddish-brown terminal band (ca. 4–5 mm). Ventral pelage finer, less dense, shorter and paler than dorsal pelage. Legs dark brown to blackish-brown. Tail (ca. 52% of HB) densely haired tapering evenly from base to tip, with guard hairs ca. 30–35 mm in length at base of tail and ca. 25–30 mm at tip. Guard hairs of tail dark brown with reddish-brown tips or blackish-brown. Forelimbs plantigrade; hindlimbs appear to be semi-digitigrade. Digital, interdigital, thenar and hypothenar pads of forefoot and hindfoot well developed. Claws on forefeet long (9–12 mm, $n = 8$), shorter on hindfeet (4–7 mm, $n = 8$). Paired anal scent glands in both sexes, with external orifices on either side of anus; between the orifices lie fine longitudinal ridges that pass into the central depression of the anal sac. Three pairs of nipples. Sexes similar in colour and size.

Geographic Variation None recorded.

Similar Species

Crossarchus platycephalus. Allopatric in Benin, Nigeria, Cameroon, Equatorial Guinea, N Congo and SW Central African Republic. Similar size; skull broader with shorter palate and tympanic bullae and longer maxillary and mandibular toothrows in Cameroon Cusimanse; posterior margin of palatine with posteromedial spinous projection in most adult specimens (evenly emarginated in most specimens of Common Cusimanse); guard hairs along anterior half of back with reddish-brown tips (pale buff to yellowish-buff

in Common Cusimanse); guard hairs longer along mid-back and rump; underfur with pale yellowish-buff subterminal band, most often with a reddish-brown terminal band (terminal half of underfur is pale buff in Common Cusimanse).

Liberiictis kuhni. Liberia and adjacent Côte d'Ivoire only (and possibly S Guinea). Similar in body form, but larger in size; neck stripe present; upper and lower first premolar present.

Xenogale naso. Allopatric, occurring only in rainforests from SW Guinea to Ghana. Larger, and not group living.

Mungos gambianus. Sympatric over most of the range, albeit generally confined to woodland habitat. Dorsal pelage brownish-grey, brightly speckled with yellow; distinctive dark brown neck-stripe; tapered tail with black tip.

Distribution Endemic to West Africa. Occurs in rainforests of SW and SE Guinea (including the Kounounkan massif; Barnett *et al.* 1996), Sierra Leone, Liberia, Côte d'Ivoire and Ghana, and extending just east of R. Volta (recorded at Breniasi; see Grubb *et al.* 1998). Kingdon (1997) incorrectly gives the distribution of Common Cusimanse as occurring in Nigeria, west of the Cross R., but only the Cameroon Cusimanse is found in Nigeria.

Habitat Found primarily in dense undergrowth of rainforest from sea level to ca. 1480 m (Mt Nimba, Guinea). Also found in farm bush, logged forest and plantations. In Sierra Leone, found mainly in southern forested parts, but has been recorded from Western Area F. R. and Loma Mountains F. R., which are rainforest but beyond the southern forest zone (Grubb *et al.* 1998). In Côte d'Ivoire, also found in humid savanna zone, including Mt Sangbé, Mt Péko and Maraouhé National Parks (A. E. Dunham pers. obs.), and Siensou, and in gallery forests of savanna in Comoé N. P. (Hoppe-Dominik 1990). In Ghana, also found on the Accra Plain (observed foraging in a dry open area of grassland and thicket), including Monkey I. (Grubb *et al.* 1998).



Crossarchus obscurus

Abundance Presumed common within its range. Widespread in Côte d'Ivoire, occurring in all national parks: recorded as common in Comoé N. P. and Mt Sangbé N. P. (Hoppe-Dominik 1990), and population density in riparian forest of Taï N. P. was estimated at 13.2 ind/km² (A. E. Dunham pers. obs.). In old secondary rainforest on Tiwai I. (a 12-km² island in Moa R., Sierra Leone), estimated density was 17 adults/km² (A. L. Olson pers. obs.).

Adaptations Long nose and long forefeet claws are adaptations for foraging within soil and leaf litter. Ability to close ears is an adaptation for frequent digging. Dark brown fur blends well with forest floor. Long coarse hairs of neck and shoulders stand erect during aggressive encounters, making animals appear larger in size. Sight, hearing and smell are well developed. Communication in dense vegetation is facilitated by an elaborate vocal repertoire and scent-marking.

There is no permanent den site, and groups often choose a new shelter every night; one group used 21 different shelters during the 38 nights in which shelters were located, another group 12 shelters over 18 nights (Olson 2001). Animals enter shelters at dusk, during rain and for mid-day resting periods. They take refuge in hollow trees and logs, under fallen trees, in thick vegetation, in burrows made by other animals (often with several entrances), or occasionally in termite mounds in the dry season. In Tiwai Island Wildlife Sanctuary groups take refuge at night in trees, approximately 13 m from the ground (5–25 m, $n = 18$) (Olson 2001). Individuals climb trees using vines to reach sections with many lianas and suspected of having a hollow; trees averaged 32 m in height (22–50 m, $n = 17$) and 85 cm in diameter (20–140 cm, $n = 20$), and the most commonly used tree was deciduous *Piptadeniastrum africanum*. Cusimanses are not adept at descending; on occasion individuals descending trees fell 5 m or more. In Taï N. P., all den sites observed during 16 months of study were located within 2 m of the ground (A. E. Dunham pers. obs.).

Foraging and Food The most common food items include large millipedes, ants, earthworms and termites. Diet also includes other forest-floor invertebrates (including beetles, spiders, snails, woodlice, centipedes, grasshoppers, crickets and insect larvae), crabs, small vertebrates (frogs, snakes, lizards, birds, lizard and bird eggs, and small mammals up to the size of Forest Giant Pouched Rats *Cricetomys emini*), and fallen fruits (*Parinari* sp. and *Sacoglottis* sp.).

Forages largely during the day (but also after dark) individually or in groups of up to 24 individuals. In Taï N. P., groups often forage in association with Diana Monkeys *Cercopithecus diana* or Sooty Mangabeys *Cercocebus atys*; these mixed-species groups may travel as a unit for up to 6 h per day. When foraging, individuals turn over small stones and pieces of wood and scrape and root through leaf litter, and also tear up rotting logs. They often dig with forefeet and long nose when foraging for soil invertebrates. Small invertebrates dug out of the ground usually are given a quick shake as they are picked up (Ewer 1968). Small vertebrate prey are killed with a single bite orientated at the back of the neck and are not shaken. Group hunting for larger vertebrate prey is common. Booth (1960: 66) reports 'the Giant Rat (easily as big as the Cusimanse) is driven from its hole by one member of the party, who goes down after it; then the others pounce as it emerges'. This hunting method has been observed in the cusimanse in W Côte d'Ivoire for several rodent species. In Taï N. P., a group of 14 individuals was observed,

on four occasions, to surround and kill a cobra (one cobra measured 2.5 m in length).

Cusimanses commonly eat millipedes that, in defence, emit a noxious substance (containing benzoquinines) that can irritate sinuses and eyes. When millipedes are found, cusimanses stomp on them with their front feet and rub them in soil until the irritating substance has dissipated. Sooty Mangabeys and Diana Monkeys usually avoid eating millipedes but, in Taï N. P., they have been observed to steal them from cusimanses after the millipedes have been sufficiently processed by the cusimanses.

In some species of mongooses eggs are opened by being hurled with the forefeet back between the hindfeet and against a hard surface, while bouncing the hindfeet off of the ground. A captive Common Cusimanse ♀ observed by Naundorff (1936) exhibited this behaviour using a hard ball and other rolling objects. This behaviour has also been reported with eggs in some captive cusimanses (A. L. Olson pers. comm.), but has not been observed in wild animals in Côte d'Ivoire (A. E. Dunham pers. obs.) and was not reported by Ewer (1973) or Goldman (1987) in their captive specimens.

Social and Reproductive Behaviour Gregarious, highly social and territorial. Groups consist of adults of both sexes and juveniles, possibly representing one or more family units, each with a mated pair and surviving young of one or more litters. Groups are relatively stable, but temporary fission of groups is common during Jun–Aug. Groups rarely stay in the same place for more than two or three days. Animals cover 25–33% of their forested home-range within a day, often revisiting areas in the same day (Olson 2001, A. E. Dunham pers. obs.). Home-ranges appear to vary with habitat and group size: home-ranges observed in Côte d'Ivoire were about 140 ha in size with slight overlap (A. E. Dunham pers. obs.), whereas populations on Tiwai I. have overlapping home-ranges averaging 28 ha (Olson 2001).

Common Cusimanses do not have permanent latrines but groups often deposit faeces and anal gland secretions at the same time in the same area, near frequently used den sites or near territory borders. Secretions of anal glands are also deposited on vertical objects by a hand-stand or leg-lift and on horizontal surfaces by an anal drag; hand-stand secretions are usually preceded with secretions from cheek glands. Marking group members with anal gland secretions is also common, primarily using the leg-lift posture. Cheek gland secretions are occasionally used to mark other individuals (Olson 2001). Both anal and cheek scent-marking are performed by both sexes. In a captive pair both sexes used anal marking most often, with the ♀ showing a lower marking frequency than the ♂ (Dücker *et al.* 1990). The frequency of marking increased in a captive ♂ before mating (Ewer 1973). Individuals mark urine and faeces of other species with anal gland secretions and urine (Ewer 1973, Olson 2001). Olson (2001) suggests a recognition/advertisement function for both cheek and anal gland secretions. Ten compounds were found in the anal gland secretions of two ♀♀ that were not found in a ♂ (Decker *et al.* 1992).

Aggressive encounters among conspecifics are occasionally observed, often over preferred food items or between bordering groups, with the aggressor growling and baring teeth. Fighting is ritualized and biting appears to be directed towards pale cheek patches. An aggressive encounter was observed in Côte d'Ivoire with a group of four Liberian Mongooses *Liberiictis kuhni*, which initiated the encounter and displaced the larger group of ten Common Cusimanses.

Common Cusimanses are easily tamed and frequently kept as pets. The following behaviours have been reported from captive individuals: upon hearing loud rustling or crackling sounds animals retreat to cover. Observed comfort movements include yawning and stretching. Individuals kept as pets have been known to attack dogs much larger than themselves without hesitation (Rosevear 1974). A threat display consists of the hair being fully erected, back arched and limbs extended; the individual moves forward at a walk, moving from side to side, and may alternate moving forwards and backwards; tail is held sloping downwards (with maximal piloerection) and with each step is swung from side to side (Ewer 1973). Tail wagging has been observed during play, when animals are disturbed, and before aggressive encounters (A. L. Olson pers. comm.).

Play behaviour has been observed in both captive and wild individuals. Play is frequently seen among juvenile conspecifics and is occasionally initiated by juvenile Sooty Mangabeys (A. E. Dunham pers. obs.). Aeschlimann (1965: 40) observed six individuals in Côte d'Ivoire 'playing tag in an open space' with a group of Campbell's monkeys *Cercopithecus (Mona) campbellii*.

Copulatory behaviour has been observed in a captive pair on ten separate occasions (C. A. Goldman pers. obs.). The ♂ clasps the female's back just forward of the pelvic region with the forefeet and grasps the ♀ at the back of the neck with his mouth; true neck biting does not occur. The male's pelvic thrusts are frequently accompanied by growls of 2–3 sec duration. Mounting occurs in bouts lasting up to 1 min, with the longest series of bouts observed being 45 min. Copulation was initiated and terminated by the ♂.

When newborn pups are in a den, subgroups leave for short foraging trips while others stay and guard the young. Breeding ♂♂ and ♀♀ provide most offspring care. Non-breeding adults of both sexes assist in guarding pups, carrying them between foraging sites, and respond to begging of pups by offering worms and millipedes (processed and with carapace opened).

Vocal repertoire includes a contact call, lost call, predator alarm, juvenile begging cry, snake alarm, greeting call and a threat growl. The most commonly heard is a whistling call used to maintain contact while in thick vegetation, increasing in volume and frequency when an individual is separated from the group. A contact call is often heard when the group begins to move after a long foraging bout or resting period and is initiated by the leading individual. When a snake is found, a loud whistling call is made and cooperative hunting begins. Grunting and tail wagging are observed during friendly greetings between individuals. A bark alarm has been heard in the presence of Crowned Eagles *Stephanoaetus coronatus*.

Common Cusimanses commonly initiate associations with groups of Sooty Mangabeys or Diana Monkeys, using the monkeys as sentinels. In response to eagle alarm calls by the monkeys, the cusimanses retreat for cover in hollow logs or dense vegetation.

Reproduction and Population Structure Females are polyoestrus; one captive ♀ came into oestrus on nine occasions in 13 months (Ewer 1972). Births in captivity have been recorded for all months of the year, but breeding appears to be seasonal in the wild. Births are most commonly observed in Côte d'Ivoire during Jan–Feb and May–Jun (A. E. Dunham pers. obs.). In Tai N. P., a ♀ in each of three neighbouring groups gave birth to young within the same week in Jun. Gestation is approximately eight weeks (53–60 days) (A. E.

Dunham pers. obs.). Litter-size 2–5 (usually four). At birth, young measure ca. 90–100 mm in head and body length and ca. 30 mm in tail length: eyes are closed, body fully haired with underfur, nose is short and forelimbs are large. Eyes open by Day 12 and guard hairs appear noticeable by Week 5 (Goldman 1987). Young leave the birthing den at Week 2 and are frequently carried from den to den as the group moves throughout the territory to forage; adults provision young with solid food from Week 4 to Week 7 (A. E. Dunham pers. obs.). Young are sexually mature at about nine months (Haltenorth & Diller 1980). Mortality of young in their first year appears to be quite high; in a wild population in W Côte d'Ivoire, five of 11 young (of three litters) died during their first six months (A. E. Dunham pers. obs.). Longevity in captivity is 12–13 years (Goldman 1987, Weigl 2005).

Ewer (1972) observed moulting in a captive ♀ obtained and reared in Ghana: shedding occurred throughout the year with distinct peaks May–Jun and Oct–Nov, corresponding with the beginning and end of the cooler wet season (May–Oct).

Predators, Parasites and Diseases Skulls of the Common Cusimanse have been found in and under the nests of Crowned Eagles; they are estimated to comprise 5% of the diet of Crowned Eagles in Tai N. P. (Shultz 2002). Crowned Eagles exist at high densities in the closed-canopy forests of West Africa and are likely the major predator of the Common Cusimanse. Leopards *Panthera pardus* occasionally take small carnivores and may also be a threat (Jenny 1996); one cusimanse was found among 215 Leopard scats in Tai N.P. (Hoppe-Dominik 1984). Ectoparasites of *Crossarchus* spp. from West Africa include ticks, chewing lice and fleas; endoparasites include protozoa, flukes and pentastomes (Goldman 1987 and references therein).

Conservation IUCN Category: Least Concern. CITES: Not listed.

Common Cusimanses are vulnerable to hunting with dogs and snares, which may pose a threat in some areas; in the Classified Forest of Diécké, Guinea, they were also one of the most commonly trapped small carnivores in three villages sampled (Colyn *et al.* 2004). In some parts of the range, clearance of land for agriculture may be resulting in some localized declines. None the less, they are relatively widely distributed, fairly common, present in several protected areas (such as Western Area F. R., Comoé N. P., Maraouhé N. P. and Tai N. P.), and not believed to be threatened.

Measurements

Crossarchus obscurus

HB: 336 (292–367) mm, n = 21

T: 177 (148–210) mm, n = 20

HF c.u.: 67 (60–74) mm, n = 19

E: 24 (20–26) mm, n = 21

WT: 925 (800–1160) g, n = 19

GLS: 72.2 (65.4–76.7) mm, n = 46

GWS: 35.9 (32.2–37.9) mm, n = 42

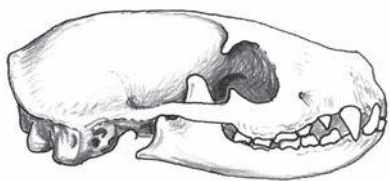
Côte d'Ivoire (A. E. Dunham pers. obs.) and museum specimens (AMNH, BMNH, FMNH, MCZ, MNHN, MRAC, MSUM, NMNH, RMNH, SMNK, SMNS, ZFMK, ZMB, ZSM)

Key References Goldman 1984, 1987; Olson 2001.

Corey A. Goldman & Amy E. Dunham

Crossarchus platycephalus CAMEROON CUSIMANSE

Fr. Mangué de Cameroun; Ger. Kamerunkusimanse

Crossarchus platycephalus Goldman, 1984. Can. J. Zool. 62: 1618. Eséka, Cameroon.Lateral view of skull of Cameroon Cusimanse *Crossarchus platycephalus*.

Taxonomy Monotypic. Considered conspecific with Common Cusimanse *Crossarchus obscurus* by Wozencraft (1989, 1993), but recognized as a distinct species by most other authors (Schreiber *et al.* 1989, Van Rompaey & Colyn 1992, Colyn & Van Rompaey 1994b, Colyn *et al.* 1995, Kingdon 1997; and subsequently Wozencraft 2005). Happold (1987) made no mention of *Crossarchus platycephalus* and listed *Crossarchus obscurus* as the only species of *Crossarchus* recorded from Nigeria. The common name Flat-head Cusimanse (Kingdon 1997, Stuart & Stuart 1997a, Wozencraft 2005), which derives from the specific name (Greek *platys* for broad and *kephale* for head, referring to broad shape of skull) does not accurately reflect the shape of the skull of *Crossarchus platycephalus* (which is wide when compared with *Crossarchus obscurus*, and not flat), and is not deemed an appropriate common name. Chromosome number: not known, but likely the same as Common Cusimanse *Crossarchus obscurus* ($2n = 36$).

Description Small-sized mongoose with long nose, strong claws, short legs and dark brown pelage. Nose extends considerably beyond lower lip. Ears pale brown, short and round. Museum specimens have whorls posterior of ears and crown, where hairs spread out around a circular patch with no hair, and a crest between ears along nape. Hairs that form the crest stand erect and are ca. 5–15 mm in length, shorter anteriorly and longer posteriorly. Both whorls and crest, which are present in both sexes and appear not to be seasonal, are more pronounced and frequent in museum specimens of Cameroon Cusimanse than in Common Cusimanse. In 22 adult museum specimens from Nigeria, and Cameroon, whorls were clearly present in 19 (12 with one whorl, six with two whorls, and one with three whorls); the crest was present in 17 specimens. Rosevear (1974: 285) examined specimens of *Crossarchus* spp. from West Africa and noted that ‘one of the most characteristic features of the *Crossarchus* pelage is the presence of a pair of large whorls on the back of the neck ... but though these are for the most part very conspicuous they are not always so and may, exceptionally, apparently be wholly lacking’. Hairs of head short (to ca. 3 mm), medium to dark brown, with pale tips; hairs of cheeks and around eyes paler. Dorsal guard hairs ca. 15–20 mm in length posterior of ears, 25–35 mm at mid-body and 35–45 mm near rump. Guard hairs of body and tail coarse and brown with pale tips, giving an overall speckled appearance. Tips of dorsal guard hairs (ca. 3–4 mm) reddish-brown, darker reddish-brown

towards rump and tail. Hairs of underfur finer than guard hairs and ca. 15–20 mm in length, basal half dark brown, terminal half pale yellowish-buff. Ventral pelage finer, less dense, shorter and paler than dorsal guard hairs. Legs dark brown to blackish-brown. Tail (ca. 53% of HB) tapers evenly from base to tip and appears less densely haired than in Common Cusimanse, with guard hairs ca. 30–35 mm in length at base of tail and ca. 20–25 mm at tip. Guard hairs of tail dark brown with dark reddish-brown tips. Claws on forefeet long (8.5–11 mm, $n = 18$), shorter on hindfeet (5–8 mm, $n = 18$). Paired anal scent glands in both sexes, with external orifices on either side of anus; between the orifices lie fine longitudinal ridges that pass into the central depression of the anal sac. Sexes similar in colour and size.

Geographic Variation None recorded.

Similar Species

Crossarchus obscurus. Allopatric in Guinea, Sierra Leone, Liberia, Côte d’Ivoire and Ghana. Similar in size; skull narrower with longer palate and tympanic bullae and shorter maxillary and mandibular toothrows in Common Cusimanse; posterior margin of palatine evenly emarginated in most adult specimens (posteromedial spinous projection present in most specimens of Cameroon Cusimanse); guard hairs along anterior half of back with pale buff to yellowish-buff tips (reddish-brown in Cameroon Cusimanse); guard hairs shorter along mid-back and rump; terminal half of underfur pale buff (in Cameroon Cusimanse, underfur with pale yellowish-buff subterminal band, most often with a reddish-brown terminal band).

Xenogale naso. Sympatric in west of range, particularly Nigeria and Cameroon. Larger, with longer limbs and longer tail; coat more uniform in colour; solitary.

Distribution Endemic to Africa. Occurs in rainforests of Benin, Nigeria, Cameroon, Equatorial Guinea, N Congo and SW Central African Republic (Colyn & Van Rompaey 1994b, Colyn *et al.* 1995, Djagoun *et al.* 2009). Not known from the rainforests of Gabon.

Habitat Found in undergrowth of rainforest from sea level to ca. 1600 m (near Buea, Cameroon), often near water. In Nigeria, also found in relic forest in derived savanna (Happold 1987) and areas of fragmented forest mixed with farmland (Angelici *et al.* 1999a); widespread in the Niger Delta, including the largely deforested lowland zone east of Orashi R., but absent from marsh forest and coastal zones (Powell 1995, 1997). In Benin, besides forested areas, found in agricultural fields, fallows and plantations, which may be exploited more in the dry season (Djagoun *et al.* 2009). Two skulls of Cameroon Cusimanse from Ekom, Cameroon, indicate that it is not limited to the Atlantic coastal basin, but also occurs in the Congo basin (Colyn *et al.* 1995).



Crossarchus platycephalus

Abundance There is no direct information on abundance, although they were the most frequently observed of three mongoose species in Lama Classified Forest in S Benin (Djagoun *et al.* 2009).

Adaptations Long nose and long forelimb claws are adaptations for foraging within soil and leaf litter. Sight, hearing and smell are well developed. Communication is facilitated by an elaborate vocal repertoire and scent-marking.

Foraging and Food Diet includes forest floor invertebrates (e.g., locusts, earthworms, ants, maybug larvae, millipedes), and land and river crabs, small vertebrates, fruits (including palm nut *Elaeis guineense*) and berries. Individuals kill prey with a single well-directed bite, crunch the prey up rapidly, and then resume foraging (Happold 1987). An individual was observed wading in shallow water turning over rocks with the aid of its long nose in search of a river crab, which when caught was grabbed with mouth and tossed to the river bank and eaten (Durrell 1958). Stomachs of nine specimens from Mamfe Division, Cameroon, contained only remains of crabs and insects (Sanderson 1940).

Forages largely during the day individually or in groups. Group members apparently travel one behind the other (Bates 1905). At night, individuals may visit cleared land and farms in search of food (Sanderson 1940). Foraging individuals scratch and dig in soil and litter with their elongated noses (Happold 1987), and will climb sloping trees. Two individuals attacked a 2.0–2.5 m long Black Cobra *Naja melanoleuca* some 3 m above ground in a tree (Struhsaker & McKey 1975).

Social and Reproductive Behaviour Gregarious and highly social. In Cameroon, groups usually comprised five to eight individuals, with one captured specimen travelling in a group of nearly 25 individuals, which is reported to be much larger than usual (A. I. Good in litt.). Refuge is taken under fallen logs, in hollow trees



Frontal view of skull of Cameroon Cusimanse *Crossarchus platycephalus*.

with openings near the ground, in thick vegetation, or in burrows. Easily tamed and frequently kept as pets.

Reproduction and Population Structure Births occur throughout the year in Nigeria (Happold 1987). One female specimen from Cameroon had three embryos (Perret & Aellen 1956), another had five embryos (Eisentraut 1963).

Predators, Parasites and Diseases Predators may include larger carnivores and birds of prey. Ectoparasites of *Crossarchus* spp. from West Africa include ticks, chewing lice and fleas; endoparasites include protozoa, flukes and pentastomes (Goldman 1987 and references therein).

Conservation IUCN Category: Least Concern. CITES: Not listed.

Cameroon Cusimanse is reported to occur in Monte Alén N. P., Equatorial Guinea (C. Lasso, in Colyn *et al.* 1995), Nouabelé-Ndoki N. P., Congo (Ososky 1998), and in Dzanga-Sangha Special Reserve, SW Central African Republic (Ray 2001). This species, like other species of cusimanses, is hunted for bushmeat by local villagers; cusimanses accounted for 3.6% of total animals harvested during an 18-month period (1999–2000) in SW Cameroon (Nzouanga & Willcox 2000). They were also recorded widely in bushmeat markets in Equatorial Guinea (Juste *et al.* 1995, Kümpel 2006) and S Benin (Djagoun & Gaubert 2009).

Measurements

Crossarchus platycephalus

HB: 346 (299–407) mm, n = 25

T: 181 (156–210) mm, n = 25

HF c.u.: 68 (61–76) mm, n = 23

E: 24 (20–26) mm, n = 18

WT: 1108 (505–1500) g, n = 6

GLS: 72.5 (68.1–76.9) mm, n = 37

GWS: 38.3 (34.8–41.7) mm, n = 35

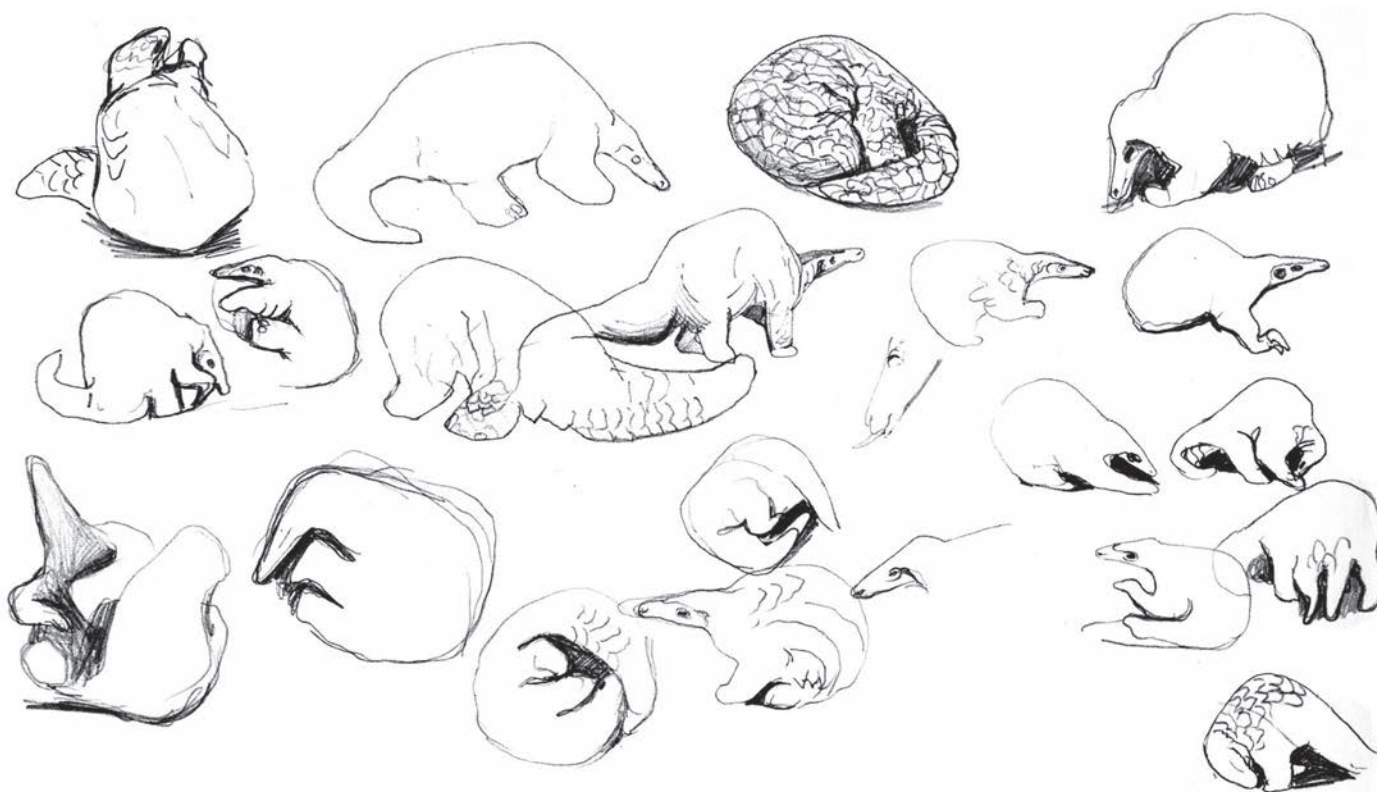
Museum specimens (AMNH, CMNH, FMNH, MCZ, MNHN, NMNH, SMNS, ZFMK, ZMB)

Key References Colyn *et al.* 1995; Goldman 1984.

Corey A. Goldman

ORDER PHOLIDOTA – Pangolins

Pholidota Weber, 1904. Die Säugetiere. Einführung in die Anatomie und Systematik der recenten und fossilen Mammalia. G. Fischer, Jena.



Giant Pangolin *Smutsia gigantea*.

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|--------------------------------------|-----------|--------|
| Manidae (2 genera, 4 species) | Pangolins | p. 387 |
|--------------------------------------|-----------|--------|

Pholidota contains one extant Family, Manidae, comprising eight species in Asia and Africa (given recognition of the Philippine Pangolin *Manis culionensis* as a distinct species; Gaubert & Antunes 2005, Schlitter 2005). Many classifications recognize only a single genus, *Manis*; however, morphological evidence suggests that such an arrangement under-represents morphological diversity, with resulting subdivision of this genus into perhaps as many as six different genera (see Pocock 1924, Allen 1939, Emry 1970, Meester 1972, Patterson 1978, McKenna & Bell 1997, Gaudin & Wible 1999). A comprehensive phylogenetic analysis of the Order, involving seven of the extant forms and nearly all well-known fossil taxa, supports three monophyletic, extant genera (Gaudin *et al.* 2009).

The name Pholidota is from the Greek words *pholis* or *pholidos*, meaning horny scale. The names Manidae and *Manis* are from the Latin word *manes*, meaning spirit of the dead or ghost, referring to the pangolin's quiet nocturnal habits (Gotch 1979). The most obvious characteristic is the protective covering of large overlapping scales on dorsal and lateral aspects of the head and body, and dorsal and ventral aspects of the broad, often prehensile tail. According to earlier authors like Weber (1892), scales are composed of keratinized epidermis on a flattened and caudally directed corium papilla. Tong *et al.* (1995) describe scales as agglutinated hairs made up largely of

alpha- and beta-keratin that gives each scale elasticity and plasticity. Inter-specific variations exist for the extent of scale distribution on the limbs and head, in scale size, topography and colour, from dark brown to yellow-brown. Soft skin with sparse hair covers the ventral aspect of the head, body and inside of the legs. A subcutaneous fat layer is present (Heath 1992a). Scales and skin can comprise as much as 1/5 to 1/3 of the total body mass (Kingdon 1971). Hindlimbs are stout, forelimbs have long robust claws reminiscent of South American anteaters. Five clawed digits are present on each foot. As a defence mechanism, pangolins roll into a sphere with only scaled surfaces exposed to predators. Some species have scent glands near the anus that produce secretions with an obnoxious odour (Grassé 1955, Kingdon 1971).

The skull is pear- or cone-shaped, widest behind the ear openings, tapering off evenly forward to the nasals and abruptly behind to the occiput. Interparietal bones are absent in adults, but present in the juvenile Sunda Pangolin *Manis javanica* (Jollie 1968) as well as in the extinct *Patriomanis americanus* (Emry 1970). With the exception of the Chinese Pangolin *M. pentadactyla* (Emry 2004), the jugal bones are absent, and the zygomatic arches are represented by short processes at either end that never join (see Emry 1970, 2004, Kingdon 1971, Gaubert & Antunes 2005, M. Heath pers. obs.). There are no postorbital processes. The lacrimal is absent in all species except the Tree Pangolin *Phataginus tricupis* and Long-tailed



Ground Pangolin *Smutsia temminckii* foetus.

Pangolin *P. tetradactyla* (Emry 1970). The nasals and supra-occipitals (= fused interparietals, Jollie 1968) are large and the pterygoids are separate and external to the bullae. Bullae are rounded in African, but not Asian, species (Gaudin & Wible 1999). The lambdoid crest is rudimentary or absent in all extant pangolins, and there is a small median vertical crest descending from the centre of the lambdoid crest (Emry 1970). Pangolins have no teeth, but in the position of the tooththrows there are narrow raised ridges of bone on the upper jaw. The mandible consists of a simple thin bony structure, joined in front, with two small bony processes one on either side extending outwards near the junction. The palate is long and narrow. The condyles are simple flattened sections that hinge on the internal faces of the hind process of the zygoma, to which they are attached by cartilage. The total number of vertebrae in the Ground Pangolin *Smutsia temminckii* is 48 whereas the Long-tailed Pangolin has 47 caudal vertebrae alone, and a total of over 70 (Jentink 1882).

Many characteristics are associated with procuring and eating their specialized diet of termites and ants (Grassé 1955, Heath 1992a). Acute olfactory sense is used to find prey and differentiate prey from non-prey ant and termite species. Forelegs have long robust nails used for digging and prying apart ant and termite nests. The eyes are small, black and protected by thick eyelids. Ear openings are present, but the ear pinnae are small or absent. The mouth opening is small, jawbones thin and teeth absent. A long, slender tongue coated with sticky saliva is used for lapping up ant and termite prey. Tongue total length ranges from 30 cm in Tree Pangolins to 25–40 cm in Ground Pangolins and 70 cm in Giant Pangolins (Doran & Allbrook 1973, Heath 1992a), and extends past the mouth 10–15 cm in Ground Pangolins (M. Heath pers. obs.) and 30 cm in Giant Pangolins (Doran & Allbrook 1973). Diameter of the tongue is 0.5–0.7 cm in Ground Pangolins (M. Heath pers. obs.) to 2 cm in Giant Pangolins (Nene 1978).

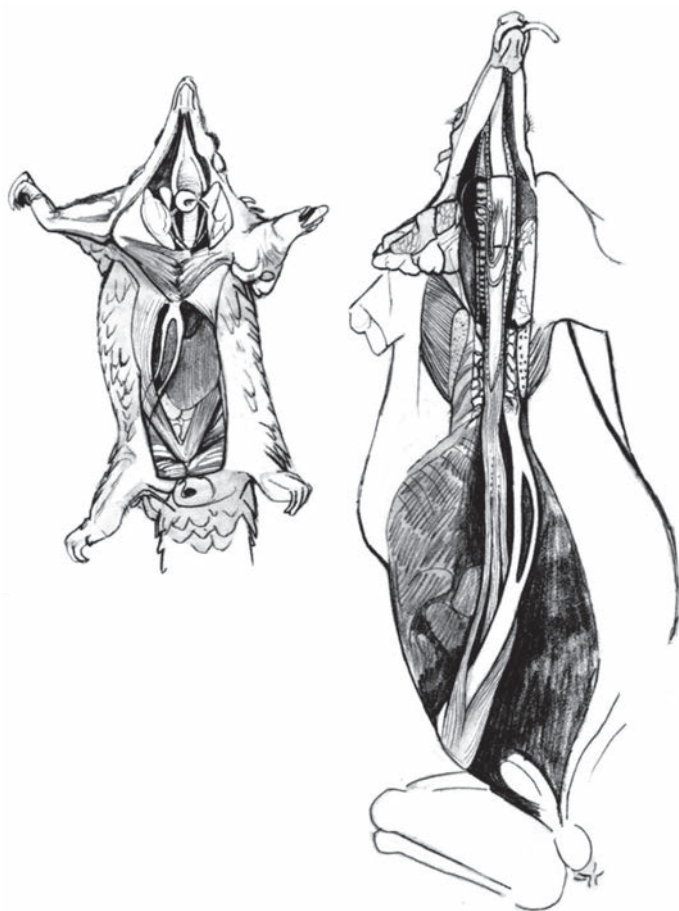
The pangolin's exceptionally long tongue passes from the oral cavity, through the neck and thorax, to the abdomen. The usual attachment to the hyoid in the neck is substituted with an attachment to the caudal end of the xiphoid process in the abdomen (Doran &



Giant Pangolin *Smutsia gigantea* dorsal myology.

Allbrook 1973, Chan 1995). There is some inter-specific variation in the shape and attachment of the tongue and the xiphisternum (Patterson 1978). In the Tree Pangolin this proximal region of the tongue, which is solid muscle and fascia, is 'U-shaped', extending caudally to the right iliac fossa and then turning cranially to terminate under the right side of the diaphragm (Chan 1995). According to Kingdon (1971), muscle attachment is provided by a xiphisternum that is formed from the last pair of cartilaginous ribs and extends from the sternum along the ventral abdominal wall to the pelvic region. From its abdominal attachment, the tongue extends rostrally to the thorax, where the tissues form a glossal tube and a freely moving tongue, which together extend through the neck and oral cavity. When retracted the free tongue resides in the glossal tube (Doran & Allbrook 1973, Chan 1995) and folds into a pocket in the throat (Kingdon 1971, Doran & Allbrook 1973). Chan (1995) hypothesizes that the tongue is extended by hydrostatic pressure. In addition to guiding the tongue, the glossal tube likely provides additional mucous membrane to cover the extra surface area gained during elongation and protrusion. When elongated the surface area of the tongue is twice its resting value and the mucous membrane of the glossal tube is turned inside out, collapsing the glossal tube (Chan 1995).

There are large salivary glands in the pharyngeal and cervical regions that extend almost to the shoulder (Doran & Allbrook 1973, Kuehn



Tree Pangolin *Phataginus tricuspis* and Giant Pangolin *Smutsia gigantea* dissections showing tongue muscles and spatulae extending into abdomen.

1986). These glands secrete a tenacious mucus (pH 9–10, Fang 1981) onto the surface and into the sheath of the tongue (Heath 1992a). The unchewed food is macerated in the stomach, which is undivided in the Sunda Pangolin (Grassé 1955), but has two chambers in the Chinese Pangolin (Fang 1981). Stomachs examined from 100 adult Chinese Pangolins contained as much as 0.5 kg of termites (Fang 1981). The first, thin-walled, larger chamber (~4/5th the total size) is for storage (Fang 1981). The second chamber has thick muscular walls, and a special rough hard semi-spherical tissue near the pylorus (Fang 1981), which is covered in cornified denticles (Grassé 1955). During muscle contractions the structure grinds food before it passes into the intestine (Grassé 1955, Fang 1981).

Females have two small pectoral nipples located in the axillary region of the forelegs. The penis is well developed. At sexual maturity the testes descend through the inguinal canal and enlarge in a fold of skin in the groin (rather than a scrotum). One young per year, rarely two, are produced. Individuals remain solitary in well-defined home-ranges, except for short periods during mating or when ♀♀ are caring for offspring (Pagès 1975, Heath & Coulson 1997a).

Adult body mass ranges from 1.5 kg in arboreal species to 33 kg in the largest ground species (Giant Pangolin), with head and body length ranging from 300 to 950 mm and tail length from 350 to 880 mm. All species tested have a low body temperature (26–35 °C) and a metabolic rate only one-quarter to one-third that of more typical eutherian mammals (see Heath & Hammel 1986). Three notable

cardiovascular adaptations are: (a) greater oxygen affinity of blood and haemoglobin than in more typical eutherian mammals of similar size (Weber *et al.* 1986), (b) retia mirabilia in the vasculature at the axis of the limbs, and (c) several blood vessels that run parallel to the spinal chord the full length of the body (Kingdon 1971).

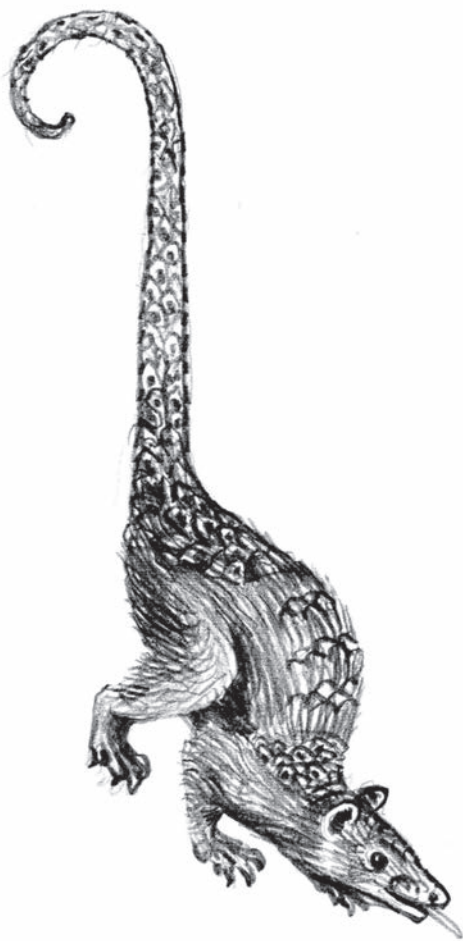
Pholidotes may have diverged from other eutherian mammals as early as the Cretaceous (Springer *et al.* 2005; but see Rose *et al.* 2005). At one time pangolins were included in the order Edentata, along with armadillos, sloths and South American and African anteaters. It is now believed that the resemblance of pangolins to other ant-eating mammals (e.g. Xenarthra, Tubulidentata) is likely due to convergent evolution (Griffiths 1968, Eisenberg 1981, Rose *et al.* 2005; but see Nováček & Wyss 1986). In contrast, some researchers (Matthew 1918, Patterson 1978, Patterson *et al.* 1992, Gaudin 1995) have suggested that Pholidota and Xenarthra share a common ancestor in the extinct North American Palaeonodonta. However, Emry (1970) argued that Palaeonodonta are ancestral to Pholidota and not Xenarthra (see also Glass 1985, Rose & Emry 1993, Rose *et al.* 2005), and the analysis of Gaudin *et al.* (2009) provides support for the monophyly of Palaeonodonta and Pholidota in a clade they termed the Pholidotomorpha. Studies involving comparisons of amino acid sequences of α -crystalline A protein from the eye lens (De Jong *et al.* 1985) and cephalic arterial patterns (Bugge 1979) further indicate that Xenarthra and Pholidota are not closely related. Instead, uniting the Pholidota with the order Carnivora in the Superorder Ferae is now supported by abundant genetic (Liu *et al.* 2001, Murphy *et al.* 2001, Waddell *et al.* 2001, Springer *et al.* 2005, Meredith *et al.* 2011) and some morphological evidence (Szalay & Schrenk 1998, Liu *et al.* 2001).

Fossil records are few. There are three fossil species recorded from middle Eocene Europe: *Eomanis waldi* (Storch 1978, Koenigswald *et al.* 1981), *Euromanis krebsi* (Storch & Martin 1994, Horovitz *et al.* 2005), and *Eurotamandua joresi* (Storch 1981). *Cryptomanis gobiensis* is a newly described genus and species from the late Eocene of the Inner Mongolia region of N China (Gaudin *et al.* 2006). There is also one record from the early Oligocene of Egypt (unnamed, Gebo & Rasmussen 1985). From the latest Eocene, there is one fossil record from North America: *Patriomanis americana* (Emry 1970, 2004, Patterson 1978), which closely resembles fossil pangolins in the genus *Necromanis* from the Oligocene–Miocene of Europe (Koenigswald & Martin 1990, Koenigswald 1999). There are more recent Plio-Pleistocene pangolin records from Europe, Africa and southern Asia, including three referable to *Manis*: *M. palaeojavanica* (Dubois 1907) from Java, which is larger than any extant *Manis* species, and two species of questionable validity, such as *M. lydekkeri* from India (Dubois 1908) and *M. hungarica* from Hungary (Kormos 1934). The oldest pangolins from Africa are Pliocene in age (Botha & Gaudin 2007), not including the aforementioned record from Egypt.

Based on external characteristics of extant species, Pocock (1924) suggested that Asian species are more primitive than African species, and Patterson (1978) suggested that pangolins emigrated in the late Oligocene from Eurasia to Africa. A European origin for Pholidota was strongly indicated in the cladistic analysis by Gaudin *et al.* (2009). These authors noted that the fossil record would seem to support a European origin for the modern forms, with subsequent dispersal first into sub-Saharan African and then to southern Asia.

Family MANIDAE
PANGOLINS

Manidae Gray, 1821. London Med. Repos. 15: 305.

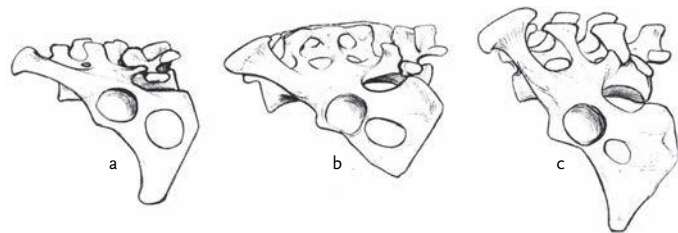


Hypothetical pangolin ancestor with scales spreading from tail to body.

| | | |
|-------------------------------|------------------|--------|
| <i>Phataginus</i> (2 species) | Tree Pangolins | p. 388 |
| <i>Smutsia</i> (2 species) | Ground Pangolins | p. 395 |

The family comprises eight extant species distributed in Asia (four species) and Africa (four species) in a variety of habitats, from rainforests to savannas and semi-desert regions. The Philippine Pangolin *Manis culionensis*, from Palawan and adjacent islands in the Philippines, has traditionally been considered a subspecies of the Malayan Pangolin *Manis javanica*, but is now considered to represent a separate species (Feiler 1998, Esselstyn *et al.* 2004, Gaubert & Antunes 2005; and see Schlitter 2005).

The simplest classification of the family maintains a single genus, *Manis*, often subdivided at the subgeneric level (Jentink 1882, Simpson 1945, Ellerman & Morrison-Scott 1951, Mohr 1961, Meester 1972, Meester *et al.* 1986, Schlitter 1993, 2005). In contrast, Pocock (1924) and Allen (1939) presented a classification including three subfamilies and six genera. Other authors have suggested classifications between these extremes. Patterson (1978) suggested a subdivision at the subfamily or generic level for the Asian and African groups, and further



From left, pelvis of a) Tree Pangolin *Phataginus tricuspis*, b) Giant Pangolin *Smutsia gigantea*, c) Ground Pangolin *Smutsia temminckii*.

subdivision at either the generic or subgeneric level for the African arboreal and ground pangolin groups. McKenna & Bell (1997) proposed subdivision at the subfamily level for the Asian and African groups, maintaining the genus *Manis* for the Asian species, and recognizing three genera to separate the African ground pangolins (*Smutsia*), the Tree Pangolin (*Phataginus*) and the Long-tailed Pangolin (*Uromanis*); this classification was also adopted by Kingdon (1997). The comprehensive morphology-based analysis by Gaudin *et al.* (2009) divided the extant species into three well-supported, monophyletic genera, and is the approach followed here: *Manis* for the Asian pangolins, *Smutsia* for the African ground pangolins and *Phataginus* for the African tree pangolins (a treatment also proposed by Koenigswald [1999] and supported by Gaudin & Wible [1999]). The latter two genera form a monophyletic African assemblage in the subfamily Smutsiinae.

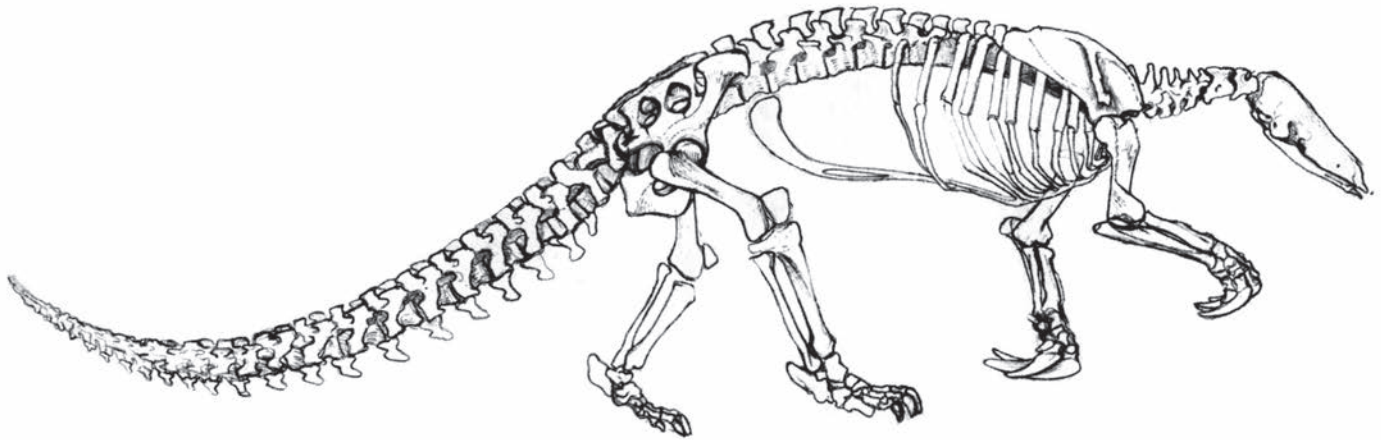
The four Asian pangolin species inhabiting South-East Asia, the Indian Pangolin *Manis crassicaudata*, Chinese Pangolin *M. pentadactyla*, Malayan Pangolin and the Philippine Pangolin, are characterized by the following features: ear pinna present, hair bristles between scales, dorsal medial row of scales extending to tip of tail; outside of fore- and hindlimbs covered with scales; fifth digit of hindfoot as large as first digit; and xiphisternum relatively short and expands into a spade-shaped plate (Jentink 1882, Pocock 1924). In the four African species, the ear pinna are reduced or absent; there is no hair between scales; a dorsal medial row of scales splits in the tail region into two rows of alternating asymmetrical scales; and the xiphisternum is elongated and divided into two branches that extend to the level of the caudal ribs and pelvis (Jentink 1882, Pocock 1924, Kingdon 1971, Patterson 1978).

In the two arboreal species, the Tree Pangolin *Phataginus tricuspis* and Long-tailed Pangolin *P. tetradactyla*, in contrast to the two species of African ground pangolin, the body is slight, with tail longer than head and body, scales are thin and light-weight, there is hair instead of scales on outer surface of foreleg, and the ventral terminus of tail has skin pad rather than scales (Jentink 1882, Kingdon 1971). A lacrimal bone is present (Emry 1970), the epitympanic recess is inflated posteriorly and laterally in the squamosal bone (Patterson 1978), and the eyes are large (Pocock 1924, Patterson 1978). When walking quadrupedally, weight is taken on palms of forefeet, not on the outer margins as in *Smutsia*, and the tail functions as a fifth limb (Kingdon 1971). The claws of the hindfeet are nearly as long as claws of the forefeet (Jentink 1882).

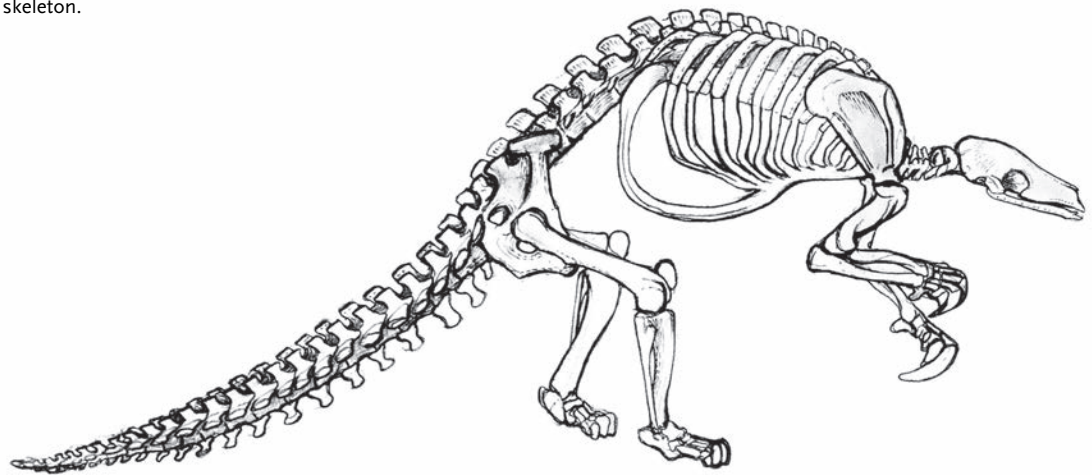
Martha E. Heath

Subfamily SMUTSIINAE – African Pangolins

Smutsiinae Gray, 1873. Brit. Mus. (Nat. Hist.), Lond. 1873: 11.



Giant Pangolin *Smutsia gigantea* skeleton.



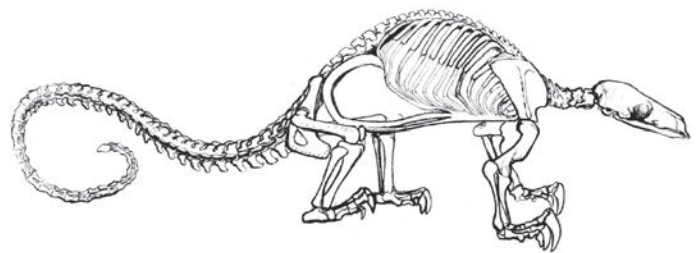
Ground Pangolin
Smutsia temminckii skeleton.

GENUS *Phataginus* Tree Pangolins

Phataginus (Rafinesque, 1821). Ann. Gén. Sci. phys., Bruxelles 7: 214.

Often treated as a subgenus of *Manis* (e.g. Meester 1972, Schlitter 1993, 2005), or raised to genus level and including all African species (Patterson 1978, Grubb *et al.* 1998). Following the revised classification of Gaudin *et al.* (2009), *Phataginus* is here considered to include two arboreal species, the Tree Pangolin *Phataginus tricuspis* and the Long-tailed Pangolin *P. tetradactyla*, both ranging mainly in the forested regions of West and central Africa. An inter-specific comparison of 67 cranial morphological characteristics in Pholidota (Gaudin & Wible 1999) earlier found that the two African arboreal pangolins share more derived similarities than do the African ground pangolins.

The Long-tailed Pangolin is unique in possessing more than 47 tail vertebrae (and a total of more than 70; Jentink 1882), more numerous than any other mammal (hence the common name). It resembles the Tree Pangolin in size and in elongation of the tail, but is distinguished by its longer tail length (twice that of head and body cf.



Tree Pangolin *Phataginus tricuspis* skeleton.

with 1.5 times length of head and body in the Tree Pangolin) and the very numerous scales (19–22 rows) on the body in the Tree Pangolin.

Martha Heath & Jonathan Kingdon

Phataginus tetradactyla LONG-TAILED PANGOLIN

Fr. Pangolin à longue queue; Ger. Langschwanzschuppentier

Phataginus tetradactyla (Linnaeus, 1766). Syst. Nat., 12th edn, 1: 53. 'America Australia' [West Africa].Long-tailed Pangolin *Phataginus tetradactyla*.*Phataginus tetradactyla*

Taxonomy Monotypic. Included in *Manis* by some authors (e.g. Schlitter 2005) and in the genus *Uromanis* by others (Pocock 1924, Kingdon 1997, McKenna & Bell 1997), but here included in the genus *Phataginus* following the classification of Gaudin *et al.* (2009). The specific name *longicaudatus* (Brisson, 1756), which is sometimes used for this species, is unavailable (see Mohr 1961 and Meester 1972 for discussion). Synonyms: *africana*, *ceonyx*, *guineensis*, *hessi*, *longicaudatus*, *macroura*, *senegalensis*. Chromosome number: not known.

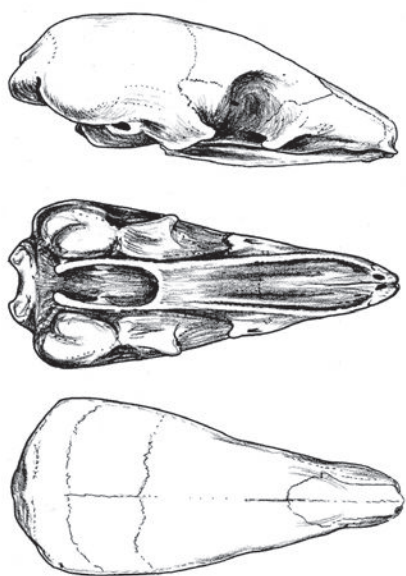
Description Small, arboreal scaly anteater with very long tail, and black face and underparts. Head long and slender with a blunt, mostly bare and somewhat bird-like snout. Nostrils in moist, slightly down-turned nose have elongated form, unlike the Tree Pangolin *Phataginus tricuspis*. Eyes prominent and surrounded by thick, swollen eyelids. Ear openings bordered by raised fleshy ridges. Cheeks, throat, underside and limbs well covered in coarse black hair. Scales cover forehead, back, limbs and tail; on forelimbs the scales approach the wrist but are absent from the upper surface of forefoot. Body scales larger, less numerous (10–13 rows on body) and more heavily built than in the Tree Pangolin, and also darker and less striated (but have conspicuous pale margins). Both fore- and hindlimbs are well clawed. The elongated tail, which is as much as twice the head and body length, has sharply pointed scales, especially along the margins of its flattened underside (there are 44 marginal scales on tail, and 34–35 scales on the uninterrupted portion of the dorsal medial row of the tail, followed by two rows of 9–10 scales each; Jentink 1882), and terminates in a sensitive pad (Kingdon 1971).

Geographic Variation None recorded (see Hatt 1934).

Similar Species

Phataginus tricuspis. Broadly sympatric. Pale- or white-bellied arboreal pangolin, distinguished by very numerous (19–22 rows on body, but 34–37 marginal scales on tail), smaller, light-weight, serrated ('three-cusped') scales; tail length about 1.5 times head and body length. Hatt (1934) discusses diagnostic differences in the skull.

Distribution Endemic to Africa, occurring in forested regions of West and central Africa. Grubb *et al.* (1998) note that there seems to be no confirmed record from west of Sierra Leone, where it is thought to be very rare, although Senegal is often cited as the western limit (e.g. Meester 1972). From Sierra Leone the species ranges eastwards through SE Guinea (Ziama and Diécké; see Barnett & Prangley 1997 for discussion), Liberia, Côte d'Ivoire and SW Ghana, there being an apparent gap in distribution until W Nigeria. Their presence in Nigeria is probably underestimated because of possible confusion with the Tree Pangolin, but the species is certainly present in S Nigeria, both west and east of the Niger R. (see Angelici *et al.* 1999a, 2001). They then occur eastwards through S Cameroon throughout much of the Congo basin forest block to the Semliki valley (and thus, just possibly, but marginally, into Uganda) (Malbrant & MacLachy 1949, Rahm 1955, 1966). Several authors (Mohr 1961, Meester 1972) give the range as far south as Namibe in Angola, but this is in error and the species has to date not been confirmed from this country (though its presence in Cabinda is plausible; J. Crawford-Cabral pers. comm.).



Lateral, palatal and dorsal views of skull of Long-tailed Pangolin *Phataginus tetradactyla*.

Habitat The most arboreal of the forest pangolins, found in riverine and swamp forests, typically dominated by palms, including rattans, and specialized swamp trees such as *Uapaca*, *Pseudospondias* and *Mitragyna*. Their distribution is very localized, and they are never far from permanent water and water-courses. In SE Nigeria, besides being recorded both in primary and secondary rainforests, altered forests (bush) and swamp forests, they have also been found in farmlands (agricultural areas of former lowland rainforests) (Angelici *et al.* 1999a, 2001). Sleeps in tree hollows or hollowed-out insect nests.

Abundance No quantitative data, and the least frequently recorded of all African pangolins, though it may be less rare than available records suggest. The species is extremely shy, almost strictly arboreal, and mainly restricted to little-known and little-penetrated habitats. It is possible that densities are highest in the most extensively flooded areas, with numbers dropping off in areas of range overlap with the Tree Pangolin.

Adaptations A long, prehensile tail is likely to have been one of the primary adaptations of early proto-pangolins and in this respect this might be one of the more conservative species. Even so, an increase in the number of tail vertebrae to 47, the greatest number in any mammal, represents a clear adaptation to a super-arboreal existence and the tail demonstrably serves as a very effective fifth limb, easily able to sustain the entire animal's weight for sustained periods. The species' near-restriction to seasonally flooded and permanently flooded swamp forests implies a still more derived condition, as does the small, finely modelled, probe-like snout. It is likely that the Long-tailed Pangolin's primary advantage is its ability to subsist on the very abundant ants and termites that escape floodwaters by nesting or hiding in treetops above the flood-line. In this respect it may parallel the arboreal *Tamandua* anteaters of the Amazon flood-plain.

These specializations are relevant to the task of interpreting where and in what ways the Long-tailed Pangolin and Tree Pangolin can

have overlapping ranges yet minimal competition for both physical and dietary resources. One dimension of this separation concerns preferred foraging periods, with the Long-tailed Pangolin supposedly more diurnal and the Tree Pangolin emphatically nocturnal. Another, very basic difference centres on preferred foraging substrates: treetops for the former species, the forest floor for the latter. This, in turn, has a strong bearing on what species of ants and termites are to be found and consumed. Insects living in seasonally flooded forests are always adapted to survive the flood period of their life-cycle. Greater exposure to much higher risks of predation, plus frequent, and drastic, alternations in temperature and humidity have armed these insects with formidable chemical defences and exceptional physiological adaptability. In an already highly specialized anteater, the Long-tailed Pangolin must have made still further biochemical, physiological and behavioural adaptation to survive on a super-abundant, but formidably well-protected prey. This barrage of specializations in both predator and prey invites further biological/chemical study.

Foraging and Food Tree ants (*Crematogaster* and *Cataglyphis*) that occur in swampy areas have been reported as preferred food but further study of diet and digestive adaptations would be very interesting because it seems likely that these are among the most highly specialized of pangolins, theoretically subsisting on particularly well-protected ant species. The ants are eaten on branches or broken out of their tree nests and hollows. Some termites are also likely to be taken.

Reports differ widely as to foraging periodicity, with some baldly stating nocturnal, others diurnal. However, Mbuti pygmies in Ituri and the Semliki valley are very familiar with both species as common prey animals (mostly climbing up trees to catch them by hand, dislodging them with sticks or smoking them out of hollows). With this intimate familiarity, they recognize the Tree Pangolin as exclusively nocturnal and the Long-tailed Pangolin as both diurnal and nocturnal (Carpaneto & Germi 1989). On the opposite side of the Congo basin, Pagès (1970) came to a similar conclusion, considering the Long-tailed Pangolin more diurnal than the other species.

Social and Reproductive Behaviour Little known, but this species uses habitual routes and sleeping holes within a well-known home-range (Pagès 1970). Animals follow urine and glandular scent trails. In this way predominantly solitary ♂♂ presumably monitor the condition of ♀♀. So far as is known, ♀♀ spend much of their time with or close to their current offspring but seem to have few other sustained social relationships.

Reproduction and Population Structure Breeding is aseasonal and almost continuous as the ♀ conceives again within 9–16 days of giving birth. Gestation has been estimated at about 140 days (Pagès 1970, 1972a). A single young is born, which is well developed, weighing 100–150 g and measuring 30–35 cm in total length. The young is born in a hole where it may be left during its first week while the mother forages. Thereafter it clings to the mother's rump or tail and begins to glean ants at about two weeks; the young departs at the birth of a new infant. Full adult size is attained at around 15 months (Pagès 1970, 1972a).

Predators, Parasites and Diseases Leopards *Panthera pardus* are known predators, with remains of pangolins having been found in

scats at several sites in Gabon (Henschel *et al.* 2005, 2011). Being partly diurnal and with greater exposure in treetops, this species might be more vulnerable to large eagles and pythons than the Tree Pangolin. It is also possible that they are occasionally killed by Chimpanzees *Pan troglodytes*. In Ituri, Mbuti pygmy hunters rely on mobbing birds (probably honeyguides or barbets) to alert them to the presence of these pangolins (Carpaneto & Germe 1989.) Such mobbing presumably derives from competition for holes and can be predicted to increase the pangolin's vulnerability to other predators as well.

Conservation IUCN: Least Concern. CITES: Appendix II.

As with other pangolins, exploited to some degree both for meat and for medicinal purposes, although they are far less commonly recorded in bushmeat markets than the other species. In 2004, Long-tailed Pangolins formed only 335 kg in terms of harvested biomass (including either whole animals and/or animal parts) from five markets monitored in Gabon, cf. 2053 kg for Tree Pangolins (Projet Gibier Gabon pers. comm.). It should be noted, however, that away from the coast, extensive areas of swamp forest are relatively scarce in Gabon. Long-tailed Pangolins have also been recorded in international trade (Bräutigam *et al.* 1994); according to CITES trade reports for the period 1996–2011, trade in live animals, specimens or skins is reported

in nearly every year, with 40 specimens exported from the Central African Republic in 2000 (www.cites.org). None the less, being small, shy and inhabiting types of forest that are largely inaccessible, this relatively widely distributed species is thought to be secure.

Measurements

Phataginus tetradactyla

HB (♂ ♂): 314 (286–342) mm, n = 4

HB (♀ ♀): 302 (292–311) mm, n = 3

T (♂ ♂): 641 (594–707) mm, n = 4

T (♀ ♀): 633 (606–670) mm, n = 3

HF (♂ ♂): 43 (40–47) mm, n = 3

HF (♀ ♀): 45 (40–48) mm, n = 3

E (♂ ♂): 14 (11–16) mm, n = 5

E (♀ ♀): 12 (10–14) mm, n = 3

WT (♂ ♂): 2.83 (2.2–3.6) kg, n = 4

WT (♀ ♀): 2.74 (2.6–3.1) kg, n = 3

SE Nigeria (F. M. Angelici pers. comm.)

Key References Hatt 1934; Pagès 1970, 1972a.

Jonathan Kingdon & Michael Hoffmann

Phataginus tricuspis TREE PANGOLIN (AFRICAN WHITE-BELLIED PANGOLIN)

Fr. Petit Pangolin; Ger. Weißbauchschuppentier

Phataginus tricuspis (Rafinesque, 1821). Ann. Gén. Sci. phys., Bruxelles 7: 215. 'Guinée', West Africa.



Tree Pangolin *Phataginus tricuspis*.

Taxonomy Included in *Manis* by many authors (with *Phataginus* sometimes considered a subgenus), but here treated along with the Long-tailed Pangolin *P. tetradactyla* in the genus *Phataginus*, to the exclusion of the two ground pangolins (contra Patterson [1978] and Grubb *et al.* [1998], who included all African pangolins in this genus). Meester (1972) recognized two subspecies, with the form *mabirae* from Uganda considered distinct. No subspecies are considered

valid here. Synonyms: *mabirae*, *multiscutata*, *tridentata*. Chromosome number: not known.

Description An arboreal scaly anteater typified by very numerous striated scales and a long tail. Forehead scaled, anterior muzzle bare-skinned with moist, carnivore-like nostrils; face lightly furred with black patches below the eyes. Eyes retractable and surrounded by

thick lids. Ear pinnae absent but the ear opening can be partially closed by a small flange and is surrounded by a fringe of light-coloured fur. Lower jaw very slender, tongue measures some 30 cm in length (Doran & Allbrook 1973). Neck, back limbs and tail covered in very numerous, light-weight, tight-fitting scales, which end at the elbows on the forelimbs but extend to the toes on the hindlimbs; there are 19–22 rows of scales on the body, 34–37 marginal scales on tail, and the uninterrupted part of the dorsal medial row of the tail has 30–33 scales, followed by two rows of 3–6 scales (Jentink 1882). Sparse white hairs on belly, thicker black hair on limbs and face. Prominent anal glands with powerful and unpleasant scent. All four feet are placed palm downwards. Hindfeet relatively long-toed and well provided with claws. Tail has flat lower surface covered in fine, pale, reticulate scales; upper surface with rounded profile and sharply pointed scales along lateral margins. Tip furnished with a finger-like pad on the underside. Body proportions change with growth: young have a short, blunt face, a long strong tail and particularly well-developed forelimbs. One pair pectoral mammae.

Geographic Variation None recorded (see Hatt 1934).

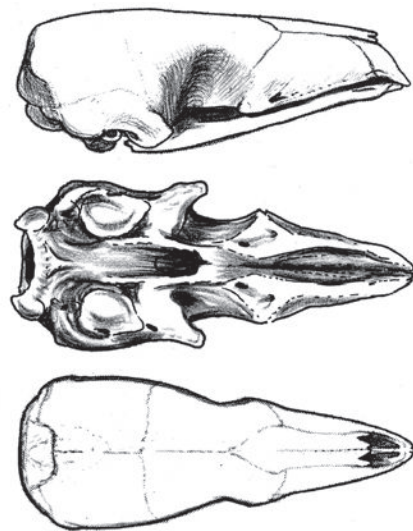
Similar Species

Phataginus tetradactyla. Broadly sympatric. Very long-tailed species (tail twice head and body length) with larger, fewer (10–13 rows) and darker scales, but with 44 marginal scales on tail; intensely black underside; reportedly less nocturnal than the Tree Pangolin. Hatt (1934) describes differences in the skull.

Distribution Endemic to Africa, ranging from Guinea in West Africa through Sierra Leone and much of West Africa to central Africa as far east as SW Kenya and NW Tanzania and as far south (west of L. Tanganyika) as NW Zambia (Mwinilunga District) and N Angola (Hill & Carter 1941, Schouteden 1948, Rahm 1966, Kingdon 1971, Ansell 1978, Grubb *et al.* 1998). Suggestions of the species' occurrence in N Mozambique, Malawi and NE Zambia can be rejected (Smithers & Lobão Tello 1976, Ansell 1982). Senegal often given as

the westerly limit but Grubb *et al.* (1998) found no confirmed records from Senegal, Gambia or Guinea-Bissau. Continues to survive on Bioko I. (Cabrera 1929, Fa *et al.* 2000).

Habitat In West Africa, found in patches of primary forest in both the savanna/forest mosaic and in the Guinea savanna, and in central Africa throughout the lowland forest block. Also favours secondary growth and can survive in cultivation, fallows and forest mosaics (Kingdon 1971). In S Nigeria the species seems widespread in both primary and secondary rainforests, altered forests (bush) and in farmlands (agricultural areas of former lowland rainforests) (Angelici *et al.* 1999a). Sodeinde & Adedipe (1994) also noted that Tree Pangolins were often reported caught on abandoned or little-used oil palm trees in secondary growth. This suggests that the species can adapt to at least some degree of habitat modification. Akpona *et al.* (2008) suggested that the distribution of pangolins in the Lama F. R. in Benin may be more sensitive to forest age than to its composition.



Lateral, palatal and dorsal views of skull of Tree Pangolin *Phataginus tricuspis*.



Tree Pangolin *Phataginus tricuspis* myology.

*Phataginus tricuspis*

The species is broadly sympatric with the Long-tailed Pangolin and there is some habitat overlap but the latter shows a marked preference for swamp forest (Kingdon 1997, Angelici *et al.* 2001).

In Gabon, sleeping sites or refuges were usually hollows in trees, generally 10–15 m above the ground. Occasionally individuals sheltered in shallow burrows in the ground, often in termite mounds (Pagès 1975). In Benin, pangolins were mostly found in hollows in trees of the species *Dialium guineense* and *Ceiba pentandra* in closed natural forests (Akpona *et al.* 2008).

Abundance Commonest and most extensively distributed of forest pangolins. Data are scarce but forest secondary growth being cleared for plantations in Uganda supported ‘substantial’ numbers of Tree Pangolins, suggesting relatively high densities in suitable habitat. A study in Lama F. R. recorded 38 pangolins at a density of 0.84/km² during the dry season, and noted that the number of observations did not differ significantly between plantations and natural forest (Akpona *et al.* 2008). In Gabon, Pagès (1975) regarded this as the commonest of the three pangolin species found in the country (the other two being Long-tailed Pangolin and Giant Pangolin *Smutsia gigantea*). Likewise, in Nigeria, this is the most common of the pangolin species (Angelici *et al.* 1999a, b).

Adaptations Predominantly nocturnal, and equally at home in trees and on the ground; indeed, by means of radio-tracking Pagès (1975) found most feeding took place on the ground. Like other pangolins, they curl up into a ball when threatened, although the relatively flimsy scales are unlikely to be of much of a deterrent against most large predators and their main line of defence, if discovered, probably resides in the repulsive secretions of their anal glands combined with snake-like wheezings, defecation, and the squirting of urine (Kingdon 1971). However, their preference for very dense vegetation and thickets must diminish the likelihood of predation by larger carnivorous animals.

Tree Pangolin *Phataginus tricuspis* poised to strike with claws.

Tree Pangolins have poor vision, except at very close quarters, but they are very sensitive to sound and vibrations and will roll up into a ball at any sudden noise. Their primary sense is olfactory and the search for both food and social contacts is clearly mediated through scent. The prehensile tail with its sensitive, finger-like tip provides a versatile climbing organ, clinging to branches, probing for an attachment, twining around branches or extending out as an apparent balancer. On broad trunks the long, flat lower surface of the tail and the sharp points along its margins press against the surface and take the animal's weight. While climbing, the fore- and hindlimbs move as pairs, with the clawed forelegs probing the surface for a purchase. Once these and the tail are hooked, the hindlimbs come forward together and animals can hump their way up a vertical trunk quite rapidly, a movement that resembles that of a caterpillar. When descending a large tree, the pangolin spirals down the trunk at an angle, gaining much support from the grip of its long, spiny-sided tail (Kingdon 1971). There are interesting reports (see Grubb *et al.* 1998) of them rolling into a ball while still in a tree and dropping to the ground, perhaps a novel method of descending trees during emergencies (such as a branch breaking). When walking on the ground, the back legs take most of the weight, but when walking quadrupedally the weight is taken on palms of forefeet, not on the outer margins as in *Smutsia* (Kingdon 1971).

Foraging and Food Diet comprises forest species of ants and termites, particularly army ants (*Dorylus* and *Mirmicaria*) and adults and nymphs of the termite genera *Nasutitermes* and *Microcerotermes* (Kingdon 1971). Both arboreal and terrestrial termitaries and ants nests are attacked but the much greater availability of the latter makes it likely that foraging on the ground and on fallen tree trunks provides the bulk of their diet (Pagès 1975). Colonies are broken open with the sharp foreclaws, whereupon the pangolin feeds with great rapidity, darting the sticky tongue in and out while the insects swarm over the animal. Continuous movement and shivering of the scales serves to shed attacking soldiers and sweeps of the tail over the ground appear to concentrate insects and assist their consumption. After feeding, animals scratch themselves with their hindlegs, at which time localized



Tree Pangolin *Phataginus tricuspis*.

tracts of scales are erected or depressed to allow claws or the tongue access to any insects that may be concealed close to the skin (Kingdon 1971).

Social and Reproductive Behaviour Commonly solitary, especially ♂♂, but Pagès (1965) often found pairs curled up together in the hollows left by torn-off branches, at some 15 m height or more. On one occasion she found a pair together with a weaned juvenile. In captivity, up to six captives will sleep together and walk in single file with a follower occasionally clambering onto another's tail. Captive adult ♂♂ confined together have been observed to fight one another with synchronized slashes of the foreclaws and in two instances one contestant was killed (Pagès 1965).

Movement may follow regular routines, particularly arboreal routes, as suggested by claw scratch marks on regularly used trunks and branches and the observation of individuals using the same diurnal resting places (such as a tree fork) for weeks at a time (Pagès 1965, Kingdon 1971). Indications are that ♂♂ are territorial, with large mutually exclusive home-ranges (20–30 ha in Gabon), and the home-range of each ♂ overlaps with that of several ♀♀. Female

home-ranges appeared to be considerably smaller, with some overlap between them (Pagès 1975).

It has been noted that Tree Pangolins are scent-oriented animals and highly sensitive to sound and vibrations. All social contacts depend on scent. A young captive that had formed an attachment to its keeper was observed, after separation, to follow a very irregular path in its search for renewed contact. When separated again the animal repeated every detail of its former path but with much greater speed and assurance (Pagès 1965). This and the regular return of a released captive to visit its captors, over a period of some six months, suggests that these pangolins tend to make stronger social attachments than are normal for a strictly solitary species. They make a wheezing snort when touched or surprised (Kingdon 1971).

Reproduction and Population Structure Tree Pangolins breed continuously, and in Gabon adult ♀♀ were seldom found that were not pregnant (Pagès 1965, 1972b), which suggested that the period of inactivity between pregnancies was virtually non-existent or very short. Gestation is thought to be in the region of 150 days. At birth young are pink and hairless, except for a ring of hair around the

eyelids (elsewhere hair only appearing after three weeks), and total length is about 290 mm and weight 100 g. Young are born well developed and active (Kingdon 1971). During the day mothers sleep curled up around their sucking offspring but one captive would leave her young in a corner while she went away to take food in the evening (Kingdon 1971). Like other pangolins, the young will travel attached to the mother's tail, usually close to its root and facing either direction. Young probably become independent of mothers within three or four months of birth but young captives eagerly seek contact with any other pangolins or even with human captors (Kingdon 1971).

Predators, Parasites and Diseases Leopards *Panthera pardus* (see Henschel *et al.* 2005, 2011), African Golden Cats *Profelis aurata*, African Rock Pythons *Python sebae*, jackals *Canis* spp., Ratels *Mellivora capensis*, Chimpanzees *Pan troglodytes* and large owls, even eagles, are likely predators. A subadult killed by a carnivore in Uganda had been carefully skinned out and the viscera, glandular area and cape of scales rejected; it is possible that young animals may be less cautious and have a less developed arsenal of scents to defend themselves (Kingdon 1971). In Ghana, Ntiemoa-Baidu *et al.* (2005) found that one species of ixodid tick, *Amblyomma compressum*, was particularly associated with this species, and, with the exception of one specimen of *Haemaphysalis parvata*, was the only tick species recorded on each of 26 pangolins investigated. The species is reported to host a variety of internal parasites.

Conservation IUCN: Near Threatened. CITES: Appendix II.

While known to occur in a number of protected areas throughout its range, Tree Pangolins are subject to widespread and often intensive exploitation for bushmeat and traditional medicine (e.g. Anadu *et al.* 1988, Fa *et al.* 2000). Indeed, it is by far the most abundant pangolin found for sale in bushmeat markets (Bräutigam *et al.* 1994); for example, during the course of six months' fieldwork in Cameroon in 2002–2003, this species was the fourth most harvested species across 47 sites sampled, after the Brush-tailed Porcupine *Atherurus africanus*, Blue Duiker *Philantomba monticola* and Giant Pouched Rat *Cricetomys emini* (Fa *et al.* 2006). Likewise, in a study in Equatorial Guinea around the village of Sendje (including within Monte Alén N. P.), the Tree Pangolin was the fifth most common mammal species in terms of offtake (carcasses), after the Blue Duiker, Brush-tailed

Porcupine, Black Colobus *Colobus satanas* and Giant Pouched Rat (Kümpel 2006).

As elsewhere, Tree Pangolins are widely used in traditional medicine. Akpona *et al.* (2008) recorded that some organs, such as the skin, heart, intestine and head, are used for treating asthma and cardiovascular and dermatological diseases. A study investigating the utilization of pangolins in traditional Yorubic medicine in SW Nigeria recorded that Tree Pangolins were used to treat a range of medical conditions, including infertility, gastrointestinal disorders, rheumatism, venereal diseases and back pain, but also for conferring invisibility, as love potions, and for appeasing/warding off witches or evil spirits. Some of these uses specifically required juvenile or even pregnant animals (Soewu & Ayodele 2009). Angelici *et al.* (1999b) have reported that the dried tail of the Tree Pangolin is sometimes used to mark and tattoo human skin during the initiation of young unmarried women in some bush-hamlets in SE Nigeria.

Tree Pangolins are recorded in international trade (Bräutigam *et al.* 1994); for example, according to CITES trade reports, during the period 1996 to 2011, Togo exported 30 live specimens in 1996, 16 in 2002, 16 in 2007, and 25 in 2008 (www.cites.org). The scale of illegal international trade, including to Asian markets, is certainly much greater.

Measurements

Phataginus tricuspidis

HB (♂ ♂): 319 (254–375) mm, n = 17

HB (♀ ♀): 310 (265–351) mm, n = 14

T (♂ ♂): 397 (344–479) mm, n = 17

T (♀ ♀): 424 (364–468) mm, n = 14

HF (♂ ♂): 50 (44–53) mm, n = 15

HF (♀ ♀): 49 (42–55) mm, n = 13

E (♂ ♂): 17 (13–21) mm, n = 11

E (♀ ♀): 18 (13–19) mm, n = 8

WT (♂ ♂): 2.36 (1.74–2.86) kg, n = 16

WT (♀ ♀): 2.6 (1.94–2.88) kg, n = 11

SE Nigeria (F. M. Angelici pers. comm.)

Key References Akpona *et al.* 2008; Hatt 1934; Kingdon, 1971; Pagès 1965, 1972b, 1975.

Jonathan Kingdon & Michael Hoffmann

GENUS *Smutsia* Ground Pangolins

Smutsia Gray, 1865. Proc. Zool. Soc. Lond. 1860: 360, 369.

Often considered a subgenus of the genus *Manis* (e.g. Meester 1972, Schlitter 1993, 2005), but here considered a distinct genus (following Pocock 1924, Rahm 1966, Kingdon 1997, McKenna & Bell 1997, Gaudin *et al.* 2009) represented by two species of African ground pangolin, the Giant Pangolin *Smutsia gigantea* and the Ground Pangolin *S. temminckii*. In contrast to the two species of arboreal African pangolins, both are characterized by a stout body, short and stumpy hindlegs, a tail shorter than head and body length, the outside of fore- and hindlimbs covered with scales, and scales covering the

ventral aspect of tail terminus rather than having a terminal pad (Jentink 1882, Pocock 1924, Meester 1972). A lacrimal bone is absent (Emry 1970) and the eyes are small (Pocock 1924, Patterson 1978). When walking quadrupedally, the weight is taken on the outside edge of the wrist (Kingdon 1971). Claws of the hindfeet are smaller than those of the forefeet (Jentink 1882).

Martha E. Heath & Jonathan Kingdon

Smutsia gigantea GIANT PANGOLIN

Fr. Pangolin géant; Ger. Riesenschuppentier

Smutsia gigantea (Illiger, 1815). Abh. Phys. Klasse K. Preuss Konigl. Acad. Wiss. pp. 84. Type locality not indicated.Giant Pangolin *Smutsia gigantea*.

Taxonomy Monotypic. Included in *Manis* by several authors (with *Smutsia* sometimes considered a subgenus), and referred to *Phataginus* by Grubb *et al.* (1998), but here included in the genus *Smutsia*, along with the Ground Pangolin, *S. temminckii*. It is possible that, with further information on the dating of their divergence, observed anatomical and molecular differences between bipedal *S. temminckii* and graviportal *S. gigantea* might justify subdivision of this genus. Synonyms: *africanus*, *wagneri*. Chromosome number: not known.

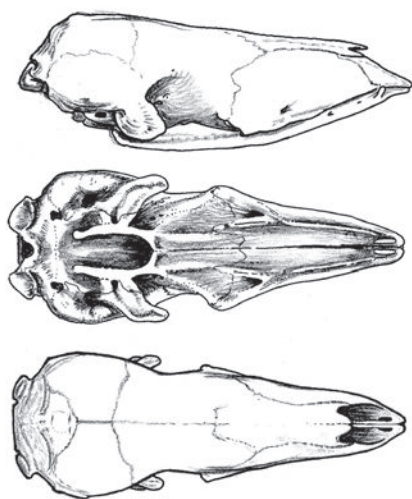
Description Largest and heaviest of all living pangolin species. Also distinctive for its elongated muzzle and powerful, well-clawed forelegs. Pale, pinkish-grey head is naked except for plate of closely fitted scales covering forehead and upper muzzle and fringes of hair around the eyes and auditory meatus. Vestigial and immobile ear cartilages beneath the skin but no external ears. External auditory canals remain widely open unless compressed by lateroventral folds of skin (that usually come into play when the animal curls up). The relatively small black eyes are surrounded by well-muscled, swollen eyelids. When animals become active, eye-bulbs swivel outwards, allowing each eye to look straight down the barrel of the muzzle (apparently permitting a good measure of bifocal vision). When folded up in defence or to sleep, the eyes appear to retract back into their shallow orbital sockets.

External surfaces of the body are covered in keratinous, overlapping scales (17+ rows) that grow from the skin in conformity with an obliquely angled, linear grid, with the largest scales along the middle

of the back, flanks, shoulders and thighs. Sizes and shapes of scales on limbs are graduated and modified to allow maximal flexibility to the limbs without loss of protective armament (especially when the animal is curled up). The soft skin of the underside and inner surfaces of limbs is naked, pinkish or very pale grey. Forefeet have five claws but outer two are vestigial and effectively non-functional. Of the three central claws, the central is the longest and most robust: the two that flank it are flatter and slightly shorter. Claws can be extended forwards and splay when digging but fold backwards and inwards when the animal is walking. Hindlimbs have five toes also but these are short and blunt and aligned along the front of graviportal, elephant-like feet. Giant Pangolins are normally quadrupedal and effectively take their weight on the outer margins of their curled up wrists. Large anal glands produce a white waxy secretion with a powerful odour (Kingdon 1971). There are two pectoral nipples.

When an animal is fully curled up, the muscular tail is broad enough at its base to cover all the space between infolded legs and sufficiently long to reach up, over the tucked-in head, to the shoulders. Outer margins of the tail are bordered by 15–19 sharply angled, pointed scales that interdigitate with the large, thick scales of the convex dorsal surface and the smaller, thinner scales of the slightly concave lower surface. Tip of the tail is slightly pointed and protected by thick, closely interlocking scales.

Geographic Variation None recorded.



Lateral, palatal and dorsal views of skull of Giant Pangolin *Smutsia gigantea*.

Similar Species

Smutsia temminckii. No overlaps in ranges of the two *Smutsia* species have been confirmed; frequently restricted to drier, more open woodlands and savannas. Smaller, with shorter, more rounded tail (HB typically less than 700 mm); fewer rows (11–13 rows) of body scales and 11–13 scales on margin of tail (Jentink 1882, Meester 1972, Heath 1992b). Ground Pangolins are mostly bipedal, and do little digging, so forelimbs are much reduced compared with Giant Pangolins (Kingdon 1971, Heath 1992b).

Distribution Endemic to Africa. Recorded from Senegal (Dupuy 1968) – though there is no evidence of its presence in Gambia – thence eastwards through Guinea, Sierra Leone, Liberia (including the vicinity of Mt Nimba; Coe 1975), Côte d'Ivoire (Rahm 1956) and Ghana, where they have also been reported in the north in Mole N. P. (Grubb *et al.* 1998). No information from Togo, although Grubb *et al.* (1998) map older records from Ghana near Fazao-Malfakassa N. P. on the border with Togo. Sayer & Green (1984) recorded the species from Batia on the border of Pendjari N. P. in the north of Benin in the 1970s, and referred to sightings in neighbouring Burkina Faso and Niger; however, the species was not included by Lamarque (2004) in his work on the large mammals of the WAP complex of protected areas. Presence in Nigeria is unclear, and is not mentioned by Happold (1987), but it may occur in the south. Indications are that Giant Pangolins were more continuously distributed in West Africa up until fairly recently. From the eastern bank of the Sanaga R. in Cameroon the species is fairly continuously distributed throughout the Congo basin to Uganda (Hatt 1934, Schouteden 1948, Malbrant & MacLachy 1949, Rahm 1966, Pagès 1970, Kingdon 1971). Reported as extinct in Rwanda (Bräutigam *et al.* 1994).

In Kenya, L. S. B. Leakey (pers. comm.; referred to in Kingdon 1971) observed it on the lakeshore in W Kenya, close to the Uganda border. Among a number of verbal descriptions and reports from W Tanzania, notably in the Bukoba and Kigoma regions, Kingdon (1971) published an authenticated record from the Mahale Mts, where their presence has been confirmed by camera-traps (C. A. H. Foley pers. comm.). A. R. Archer (pers. comm.) reported a possible sighting from near the base of the Udzungwa Mts in the late 1960s



Smutsia gigantea

(marked with a '?' in Kingdon's 1971 distribution map), but there have been no confirmed records despite much survey work.

No records from Sudan or Burundi, but the animal is known to the Azande people on both sides of the DR Congo–Sudan border. Northern limits of the distribution are not well known but can be expected to broadly coincide with those of the tropical lowland rainforest. The northern banks of the rivers Kasai and Tshuapa apparently define its southern limits within the central forest block. Also present on Bioko I.

Habitat Primarily a forest species, the Giant Pangolin is also found in forest mosaics and in high rainfall secondary grasslands where it can shelter in thicket-covered termitaries. Its tracks are commonly found along the margins of papyrus and other swampy areas and it is totally water-dependent. In S Buganda, animals were known to range from the exposed, ironstone plateaus that cap most low hills down through cultivated and forested hillsides to the swamp forests and papyrus beds that filled valley bottoms. While all these habitats were foraged over, hillside food resources were probably the most intensively used (Kingdon 1971).

It commonly rests under piles of plant debris, in thicket, under fallen tree roots or in partially opened termitaries. It also uses the holes of other animals, notably the Aardvark *Orycteropus afer*, but can also dig long, deep burrows, up to 40 m long and up to 5 m below the surface. More usually, burrows are short, sometimes with side-galleries. An enlarged sleeping chamber may be within a burrow or within an excavated termitary. Entrances are usually plugged from within (Kingdon 1971).

Abundance No data available. The quantity and availability of termites and ants, proximity to water, levels of predation from humans and large carnivores, and frequency of fires are likely influences on relative abundance. An activity cycle from midnight to very early morning has inhibited any easy assessment of relative abundance and a detailed study of this species is overdue.



Giant Pangolin *Smutsia gigantea*.

Adaptations The spread-eagled agility, strongly prehensile tail and strong clinging reflexes of very young Giant Pangolins are clear indications of arboreal origins for this heavily terrestrial pangolin. Powerfully functional, clawed forelimbs are a further indication of an arboreal inheritance, and Giant Pangolins use them to open up hard termitaries and fallen tree trunks, one respect in which it is unlike the Ground Pangolin, which, as a biped and ground surface feeder (in habitats where other ant/termite eaters are common), is indicative of the Ground Pangolin being one step further removed from its arboreal ancestry. The need for large muscular shoulders and powerful claws alters the weight distribution in a Giant Pangolin. Thus a preponderance of bone and muscle at the front end is the primary reason why the Giant Pangolin is predominantly quadrupedal while the Ground Pangolin is frequently bipedal (Kingdon 1971). This difference is particularly evident in the structure of the pelvis, which is massive, elongated and horizontal in the Giant Pangolin. By contrast, the Ground Pangolin's pelvis is more lightly built, shorter and more vertical, better suited to providing a central fulcrum that can support the cantilevered weights of tail and forequarters (Kingdon 1971).

Large, parallel blood vessels run down the length of the vertebral column in pangolin species. Giant Pangolin tails are sufficiently long and robust to serve as a body prop while all four limbs are engaged in digging (Kingdon 1971). Tails are used as clubs when harassed, and the 'tail complex' can make rapid side movements that splay and 'scissor' the long, very sharp scales near the tail's base. These movements and the blades and points on the lateral scales of the tail catch or cut any

animal attempting to probe into a curled-up pangolin. Booth (1960) reported a hunter's encounter with a Giant Pangolin with the head of a dead Leopard held fast in the curl of its tail, and, in Liberia, hunters also warn of the danger it poses, reporting that it 'will wrap you in its tail and drag you to Monrovia!' (R. Hoyt pers. comm.).

The skull is composed of exceptionally dense, thickened bone, a thickening that is clearly protective in function. In common with other pangolins, several cranial bones are absent, notably the zygoma, a reduction that is associated with effective elimination of the chewing muscles (temporalis and masseter), and the jaws lack any teeth. Food passes down directly to the pyloric region where a structure resembling the gizzard of a bird grinds up the chitinous bodies of ants and termites with small stones and sand; this structure is particularly large and well developed in this species (Mohr 1961, Doran & Albrook 1973).

The tongue is exceptionally slender and long (70 cm) and can extend out of the mouth for some 30 cm (Doran & Allbrook 1973). As with other pangolins, the tongue is retracted into a pouch in the throat. This results in a visible lump in the throat, and the profile of a feeding animal's throat can be seen to flex prominently with every ingestion of insects. Likewise, rapid extension and retraction of the tongue is further assisted by the tongue's base extending back into the chest cavity where muscular extensions of the tongue base attach to a spatulate, cartilaginous extension of the sternum. This cartilage and its muscular attachment are free to slide and swing about along the walls of the abdominal cavity with every extension and retraction of tongue and muscle.

Foraging and Food Feeds predominantly on colonial species of termites, notably *Macrotermes*, *Cubitermes*, *Apicitermes*, *Protermes* and ants, such as *Palthothyreus* and *Anomma*, many of which are exposed by speedy excavation of nests and galleries (Vincent 1964, Pagès 1970). Termites and ants are harvested by very rapid extrusions and retractions of the tongue, which is coated with an exceptionally viscous salivary slime (the pangolins' dependence on frequent drinking may well be influenced by their copious production of specialized saliva). Although ants and termites are the main food, other insects may also be taken. L. S. B. Leakey (pers. comm.) reported watching a Giant Pangolin, semi-submerged in lakeside water, whipping its tongue over the surface of the water to corral and ingest water beetles (Dytiscidae) that were swimming there.

Judging from captives in Uganda, animals are most active between midnight and 05:00h (Kingdon 1971) but there are likely to be seasonal and, perhaps local, environmental differences in foraging patterns. Hunters in Liberia report activity patterns from 20:00h to early morning (R. Hoyt pers. obs.). Frequent periods of inactivity have been reported, sometimes very prolonged (Y. Ssenkebuge pers. comm.). This suggests that extensive fat in the abdomen and on the body and limbs of some specimens may signify an ability to wait out periods of food scarcity, possibly in some form of aestivation.

Social and Reproductive Behaviour Normally solitary, but ♀♀ are frequently accompanied by their latest, single young, which does not usually become independent until the next infant is born. Social relations are primarily mediated by scent, and both sexes have anal glands, with those of the ♂ being proportionately large. Presumably all faeces are scented but it is possible that a continuous trail of scent is also laid in spite of marking gestures being inconspicuous. Enlarged anal glands in ♂♂ and marking behaviour imply they may be territorial. In Buganda a distinctively marked individual ♂ was observed to traverse a very limited locality (and regularly used a semi-exposed resting-place in a termitary) for about two years (Kingdon 1971). These limited observations suggest that home-ranges are likely to be small.

Resting pangolins sleep with their muzzles pressed up close to their anal glands. Although Giant Pangolins hiss loudly when harassed, they appear to be largely mute (Kingdon 1971).

Reproduction and Population Structure Breeds throughout the year but may have a peak in some regions. Two birth records of single young from Uganda are from Sep and Oct (Kingdon 1971). Hatt (1934) reported fetuses in specimens from DR Congo in Nov and Dec. Total length and weight of newborns is up to 450 mm and just over 500 g, respectively. Young is born with soft scales and eyes open; it is very active, but unable to take its weight on its legs, scrambling around spread-eagled (Kingdon 1971). A one-day-old pangolin put near its mother immediately worked its way onto the base of her tail; the tail of a newborn is strongly prehensile and the animal has a very strong clinging reflex (Kingdon 1971). Longevity in the wild or captivity is not known.

Predators, Parasites and Diseases Leopards *Panthera pardus* (see, for example, Henschel *et al.* 2005), African Rock Pythons *Python sebae* and crocodiles are all natural predators of Giant Pangolins.

Conservation IUCN: Near Threatened. CITES: Appendix II.

Giant Pangolins are present in a number of protected areas across their range, including National Park of Upper Niger (Guinea), Sapo N. P. (Liberia), Taï N. P. (Côte d'Ivoire), Mbam Djerem N. P. (Cameroon) and Salonga N. P. (DR Congo). As with other pangolins, they are subject to widespread exploitation for bushmeat and traditional medicine and are regularly recorded in bushmeat markets (Bräutigam *et al.* 1994). Colyn *et al.* (1987) found that this species comprised one-tenth of the total number of pangolins (~100) on sale as bushmeat in rural areas around Kisangani. Fa *et al.* (1995) noted that survey records of Giant Pangolin meat in the markets of Bioko were misleading, as only 10% made it to market. In Liberia, only 25% of the harvest is sold, as local hunters preferred it to other species (R. Hoyt pers. obs.). Yet, this species alone accounted for nearly 2% of the total harvested biomass in communities where it had not yet been extirpated. Harvest rates in six communities adjacent to Sapo N. P. were found to be unsustainable (R. Hoyt pers. comm.). In 2004, Giant Pangolins formed 5019 kg in terms of harvested biomass (including either whole animals and/or animal parts) from five markets monitored in Gabon, cf. 2053 kg for Tree Pangolins *Phataginus tricuspis* and 335 kg for Long-tailed Pangolins *P. tetradactyla* (Projet Gibier Gabon pers. comm.).

Formerly protected in some areas as a totemic animal (e.g. for the Olugave clan in Buganda), the breakdown of such taboos now sanctions interference. Local protection afforded by totems in W Côte d'Ivoire have also broken down due to refugee movements throughout the region as a result of conflicts in Liberia and Côte d'Ivoire (L. Bonnehin pers. comm.).

The species is occasionally recorded in international trade, including one instance of four live specimens reported as exported from Togo in 1984 (Bräutigam *et al.* 1994). There are no reports of trade in live specimens in the CITES trade reports between 1996 and 2011, but the true scale of the illegal international trade is unknown. As this species appears to be heavily exploited throughout its range, it is likely threatened with extirpation wherever human populations are high or marketing networks along forest roads and rivers are in operation. Its large size, low reproductive rate and terrestrial habits make it particularly vulnerable to overexploitation. Additional research is certainly required to inform and enhance the currently inadequate conservation situation for this species.

Measurements

Smutsia gigantea

TL (♂♂): 1438 (1370–1530) mm, n = 5

TL (♀♀): 1298 (1185–1365) mm, n = 7

T (♂♂): 674 (650–700) mm, n = 5

T (♀♀): 596 (545–675) mm, n = 7

HF: n. d.

E: n. d.

WT: 30.0–35.0 kg*

Hatt 1934

*Haltenorth & Diller 1980; mean and sample number not given

Key References Kingdon 1971.

Jonathan Kingdon, Michael Hoffmann & Reginald Hoyt

***Smutsia temminckii* GROUND PANGOLIN (TEMMINCK'S GROUND PANGOLIN, CAPE PANGOLIN)**

Fr. Pangolin terrestre du Cap; Ger. Steppenschuppentier

Smutsia temminckii (Smuts, 1832). Enumerationem Mammalium Capensium, Dessertatio Zoologica Inauguralis.

J. C. Cyfveer, Leidae, 105 pp. In the vicinity of Kuruman, Northern Cape, South Africa.

Ground Pangolin *Smutsia temminckii*.

Taxonomy Monotypic. Included in *Manis* by most authors (with *Smutsia* usually considered a subgenus), and referred to *Phataginus* by Grubb *et al.* (1998), but here included in the genus *Smutsia*, along with the Giant Pangolin *S. gigantea*. Synonyms: *hedenborgii*. Chromosome number: not known.

Description Medium-sized, corpulent, streamlined mammal covered with thick pantile-like overlapping yellowish-brown scales giving them a reptilian appearance. In some individuals the scales on the head, shoulders and forelegs are tinged reddish-brown on the tips. Head and shoulders blend into each other so that there is no visible neck. Head small, muzzle pointed and forehead covered with small scales extending beyond the eyes about two-thirds to the nose tip. Lateral and ventral surface of the face is dark grey with sparse short hairs and without scales. Mouth small and toothless with a very delicate lower jaw. The large oval nostrils can be tightly sealed. Eyes small and bulbous surrounded by thick protective eyelids with few fringing hairs. Ear openings large, without pinnae and vertically elongated with soft fluffy hairs inside.

Scales cover the entire body (11–13 rows, and 11–13 scales on margin of tail) except the throat, belly and insides of the limbs, which are sparsely covered with short hairs. Scales on the back point to the posterior in parallel rows, which continue towards the distal end of the tail. Scales on forelimbs also point to the posterior and are arranged in vertical rows, whereas on the hindlimbs the scales point down. Scales of juveniles and subadults terminate with a small point. Tail heavy, very muscular, dorsally convex, ventrally slightly concave and entirely covered with scales. Base of tail is as broad as the hindquarters, which is the widest part of the body, distal end broadly rounded.

Scales on the lateral region of the tail are sharply pointed and folded in half so that one half is positioned dorsally and the other half ventrally. All scales, particularly the larger ones on the back and tail, are honed to a very sharp edge from continually rubbing against underlying scales.

Forelimbs short and strong with five small compact digits on each forefoot, the first with a short claw, the central three with long curved robust claws (the centre claw measuring up to ca. 6 cm) and the fifth with a claw up to ca. 3 cm. Hindlimbs shorter and stockier than the forelimbs with five digits on each hindfoot, each digit with a small nail-like claw. The soles of the hindfeet are cushioned pads that are rounded in front and taper off slightly to the rear resembling miniaturized elephant's hindfeet. Ground Pangolins spend much of the time walking bipedally on the hindlimbs, forelimbs tucked close to the chest, occasionally touching the ground with the knuckles and the tip of the tail to maintain balance. The pelvis is more vertical than in other pangolin species, emphasizing the greater use of the hindlimbs for bearing weight (Kingdon 1971).

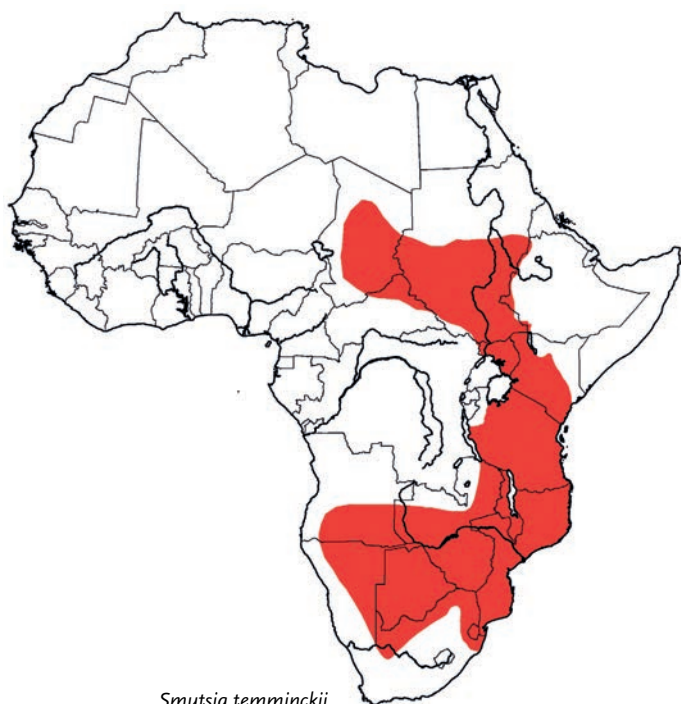
There is no obvious sexual dimorphism, although ♂♂ are slightly heavier (Heath & Coulson 1998). Prominent anal glands are present, which exude a waxy secretion with an unpleasant smell. Testes in ♂♂ are large, situated in a fold of skin in the groin area, anterior to a well-developed penis, and not descending into a scrotum. Females have one pair pectoral nipples.

Geographic Variation No subspecies have been described. There may be some variation in size of animals recorded from across the range.

Similar Species

Smutsia gigantea. No overlap in distribution has been recorded. Larger, with longer, more pointed tail (head and body length more than 700 mm); there are 17 rows of body scales and 15–19 scales on margin of tail (Jentink 1882, Meester 1972, Heath 1992b). The Giant Pangolin is largely quadrupedal, and uses forelegs extensively for digging, thus forelegs are similar in size and power to hindlegs (Kingdon 1971).

Distribution Endemic to Africa. The most widespread African species recorded from E Chad (Malbrant 1952), through S Sudan (Sweeney 1974, Stuart 1980), much of East Africa and southern Africa as far south as the Northern Cape and North West Province of South Africa and NE KwaZulu–Natal (they appear to have vanished from the Free State over the last 15 years; Friedmann & Daly 2004). The northern limits of distribution are not well defined. Malbrant (1952) cited a record from Ouanda Djallé in extreme NE Central African Republic, noting it was likely to be fairly widely distributed in the northern part of the country. Malbrant (1952) also mentions a record for Ennedi in NE Chad, while Yalden *et al.* (1996) remark on a definite collection of this species from the Sennaar region of Sudan, close to the north-western border of Ethiopia. They are also confirmed from the Omo R. basin region of SW Ethiopia (Schloeder & Jacobs 1996).

*Smutsia temminckii*

and so probably do occur, marginally, in the western border regions of Ethiopia (Yalden *et al.* 1996). Their presence in Somalia is doubtful (Funaioli & Simonetta 1966). Records from West Africa undoubtedly refer to the Giant Pangolin (see Grubb *et al.* 1998).

Habitat Inhabits mainly savanna woodland in low-lying regions with moderate to dense scrub (e.g. *Brachystegia–Julbernardia* and *Colpospermum mopane* woodlands) where average annual rainfall is between 250 mm and 1400 mm. Also occurs in flood-plain grassland, rocky slopes and sandveld up to 1700 m altitude (Coulson 1989), but does not inhabit forest or desert. Most important habitat requirements are a sufficient population of the various ant and termite prey species, and available dens or above-ground debris to shelter in. Prefers regions with a mosaic of soil types including loam or clay soils with a firm consistency to support the nest galleries of prey species and sandy soils or rocky outcrops, which are more suitable for den sites.

Abundance Ground Pangolins are rarely encountered since they are mostly nocturnal and usually frequent habitats with relatively thick undergrowth. Individuals seen during the day are usually juveniles or subadults. Their inconspicuous nature has resulted in their abundance being underestimated throughout their range. For example, in South Africa, there were only 73 sightings of Ground Pangolins in Kruger N. P. over a period of 20 years (Anon. 1978). Their estimated density in Kruger N. P. region is 0.24/km² (J. M. Swart pers. obs.) and although their density is expected to be higher in Zimbabwe, since 159 sightings were reported there in one year (Coulson 1989), estimated density in the Gokwe district of Zimbabwe is only 0.15/km² (Heath & Coulson 1997a). Abundance in other regions of Africa is not known.

Adaptations The most prominent characteristic of Ground Pangolins is their armour of hard, sharp, pantile-like overlapping scales, which primarily provides protection against predators; also, though

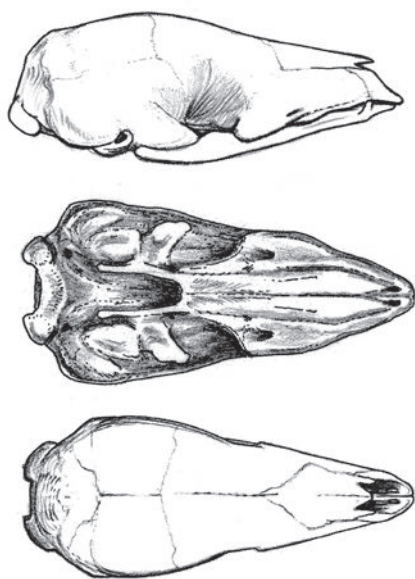
providing little insulation, they protect the skin against abrasions and injuries from sharp objects such as rocks, branches and thorns. Scales constitute a high investment since they could make up one-third of the animal's body weight (Kingdon 1971).

Ground Pangolins stand motionless at any sign of danger and since their brown colour blends with the undergrowth they are easily overlooked. When stressed they curl into a tight sphere concealing their vulnerable head and abdomen, often lashing the tail in a scything action over the body. The scales also assist in removing parasites such as ticks and mites from between the scales, by the abrasive action of the scales assisted by mud, coarse sand or fresh herbivore dung. Ground Pangolins wallow in mud or fresh dung when available; occasionally, they seek out a patch of coarse sand, which they loosen with their sharp claws and impregnate with urine, thereby creating their own wallow. When wallowing they wriggle about on their back while contorting the body and flicking the tail back and forth over the head ensuring that the mud, dung or coarse sand is packed between the scales (J. M. Swart pers. obs.).

The tail is by far the strongest appendage and once clamped in position around the body it is impossible for a predator to prise open an adult without sustaining injury. Since Ground Pangolins walk bipedally, the weight of the tail counterbalances the weight of the head and body so that they maintain a horizontal body posture. The tail is also used as a lever or support when climbing over and down obstacles or steep embankments. Ground Pangolins are predominantly terrestrial, but they will clamber over fallen logs and are also capable swimmers.

Ground Pangolins are anatomically adapted for a myrmecophagous diet. Strong forelimbs with long claws are used for digging to expose ant or termite nest galleries. A small head, slender muzzle and small mouth with thin mandibles afford them greater flexibility when positioning the head while feeding from excavated ant and termite nests. Although they have no teeth, a gizzard-like pyloric region in the stomach uses muscular action to grind the ants and termites with the aid of small stones and sand that are passively ingested (Weber 1892). A long, rod-shaped tongue, slightly flattened towards the tip, can be extended 20–30 cm beyond the lips into ant and termite underground galleries. The tongue is repeatedly inserted with a quick darting action driven by a complicated network of muscles. Muscle attachment is provided by a xiphisternum, which is formed from the last pair of cartilaginous ribs and extends from the sternum along the ventral abdominal wall to the pelvic region (Kingdon 1971). The xiphisternum then curves to the dorsal abdominal wall forming a free-floating spatulate attachment near the kidneys (Kingdon 1971). The length of the tongue, including the muscular apparatus, is longer than the head and body (Kingdon 1971). Large salivary glands secrete copious sticky saliva into the tongue sheath and onto the tongue so that their prey adheres to the tongue. When not used, the tongue is retracted into a throat pouch.

Ground Pangolins have an acute olfactory sense enabling them to locate their ant and termite prey through the soil surface. Their hearing is fairly good but is probably restricted to the lower frequency range since they have no external pinnae. Their eyesight is poor since they are often seen bumping into obstacles (J. M. Swart pers. obs.) and they usually forage in dense undergrowth with the head very low to the ground where the visibility is generally very poor and where good eyesight would be of little benefit. Large pedal glands are situated under the soles of the hindfeet, which are usually



Lateral, palatal and dorsal views of skull of Ground Pangolin *Smutsia temminckii*.

damp from the secretion. The secretion has a fairly pungent odour and appears to be used mainly for orientation in the short term.

Ground Pangolins have adapted to survive on a diet of relatively poor nutritional value by being active for shorter periods and limiting their activity to periods when their food intake can be maximized. They save energy by being active for ca. four hours a day (Swart 1996) and spend the rest of their time resting or sleeping in an underground burrow or occasionally in dense undergrowth. Furthermore, they usually forage at night when the temperature is cooler (11–25 °C) and their ant prey is less active above ground and more concentrated in their underground galleries. To augment these behavioural adaptations they also have a lower resting metabolic rate: the mean resting metabolic rate of four free-ranging pangolins studied in South Africa was 2.34 ml O₂/kg/min (J. M. Swart pers. obs.), ca. half that of other eutherian mammals of the same size according to the Kleiber equation for determining the metabolic rate of eutherian mammals of different sizes (Kleiber 1961). Pangolins also often occur in areas where standing water is available seasonally and are able to survive long periods without sources of free water (Stuart 1980).

Foraging and Food Highly selective myrmecophages, feeding almost exclusively on underground aggregations of ants and termites close to the soil surface. Occasionally, they lick up ants or termites from a dead log, from the soil surface, from under leaf litter or even from a dung pile. A tame individual followed by Sweeney (1956) in Sudan often seized cowpats or pieces of termite-ridden wood, rolled onto its back and broke them up while licking the termites from its chest. However, this unusual behaviour was not observed in other studies.

Ground Pangolins usually walk following a haphazard zig-zag path with the nose held close to the ground while sniffing continuously to locate their underground prey. Sniffing intensity increases when prey is located and following a short dig with the front claws to expose the nest galleries the long, rod-shaped tongue is rapidly inserted to

extract the prey. Feeding bouts are generally short, averaging only 40 sec with the majority less than one minute (Swart *et al.* 1999), probably attributed to the swarming and aggressive nature of their prey. The majority of feedings (ca. 99%) are from ant or termite aggregations below the soil surface, ca. 72% are from a shallow dig ca. 4 cm deep, and ca. 27% directly from an active porthole (J. M. Swart pers. obs.). The location of feeding sites appears to vary from one geographical region to another. For example, in Zimbabwe 45% of feedings are from tree bases and shrub bases and 29% on bare ground (Richer *et al.* 1997). In the Kruger N. P. region of South Africa only 3.7% of feedings are from tree and shrub bases and only 3.8% from bare ground and even though they forage mostly in densely wooded areas 93% of feedings are between grass tufts (J. M. Swart pers. obs.). The mean distance between feedings in this region is ca. 15 m (n = 7670 feedings).

Although most of their activity is devoted to foraging for ants and termites, only 16% of this time is spent actually feeding (Swart *et al.* 1999). However, this value could vary considerably according to the habitat occupied at the time. For example, in the Kruger N. P. region of South Africa 20% of their time was spent feeding whilst foraging in calc brack thicket and only 7% whilst foraging in riverine thicket (Swart 1996). Richer *et al.* (1997) observed an individual that spent 20% of the time feeding in non-mopane and 12% feeding in mopane habitat. The distance they cover each evening while searching for prey varies considerably depending on the habitat and prey availability. In general the distance covered by ♂♂ varies from 202 to 3791 m per night (mean = 1482 m, n = 50 nights) and ♀♀ from 40 to 2176 m per night (mean = 942 m, n = 126 nights) (J. M. Swart pers. obs.).

There is distinct geographical variation in diet. Coulson (1989) recorded nine species in Zimbabwe, Jacobsen *et al.* (1991) 16 species in the North West Province of South Africa, Richer *et al.* (1997) seven species in NW Zimbabwe, and Swart *et al.* (1999) 20 species in the Kruger N. P. region. Only one ant species, *Anoplolepis custodiens*, was recorded in all these studies and only three species were common to two of the above studies. Although a number of species are preyed on, Ground Pangolins predominantly seek out species larger than 5 mm (Swart *et al.* 1999). For example, in South Africa 50 species of ants and termites were recorded as potential prey; however, only 20 of these species were preyed on and only six species ranging from 5.6 to 11.6 mm contributed to 98% of their diet (Swart *et al.* 1999). These six species in order of relative importance were: *A. custodiens*, *Myrmecaria natalensis*, *Camponotus cinctellus*, *Polyrhachis schistacea*, *Hodotermes mossambicus* and *Camponotus* sp. – *maculatus*-group.

Anoplolepis custodiens contributed to 77% of their overall diet and is probably the key species in their diet within southern Africa. Although the relative importance of *A. custodiens* as a prey species decreased from 83% during winter to 72% during summer, *A. custodiens* was still the most important prey species throughout the year. Thus, the distribution of *A. custodiens* is possibly important in determining the distribution of Ground Pangolins in southern Africa. Richer *et al.* (1997) suggest that *A. custodiens* is important only to juveniles and diurnal foragers and not to nocturnal foragers; however, the importance of *A. custodiens* in their diet is clearly exemplified by the above studies. However, *A. custodiens* is never mentioned in the diet of pangolins from Sudan, where main prey selected were *Crematogaster*, *Odontotermes*, *Microcerotermes*, *Microtermes*, *Amitermes* and *Ancistotermes*

(avoiding 30 other ant and termite species present in the habitat, including *Macrotermes* and *Trinervitermes*; Sweeney 1956).

One would expect juveniles to learn the same prey preferences and foraging locations from their mothers while accompanying them as they feed and forage. However, since juveniles never appear to forage with their mothers this knowledge is probably acquired through instinct and by trial and error. The only time they accompany their mother is when being carried on her back while being moved from one den to another. The mother walks directly to the new den without stopping to feed and then leaves the juvenile in the den and comes out to forage alone (J. M. Swart pers. obs.). Juveniles then venture out of the den alone, primarily during daylight hours, and forage within close proximity to the den entrance. As they grow older they venture further away from the den and also start coming out later in the day until eventually as adults they switch from being predominantly diurnal to predominantly nocturnal.

Although essentially nocturnal foragers, adult Ground Pangolins are occasionally crepuscular, particularly during winter. Juveniles on the other hand are predominantly diurnal and subadults are often diurnal or crepuscular foragers (Swart 1996). Although crepuscular and diurnal activity is also documented in other studies there is no reference to the age group of individuals (Coulson 1989, Jacobsen *et al.* 1991, Heath & Coulson 1997a, Richer *et al.* 1997). However, judging by the weights of animals referred to in these studies it appears that the majority are juveniles or sub-adults lighter than 8 kg. Since juveniles and subadults forage within their natal ranges they do not appear to forage earlier to avoid competition with adults for foraging sites and thus probably forage diurnally to avoid predation by nocturnal predators such as Lions *Panthera leo* or Spotted Hyaenas *Crocuta crocuta*. Subadults are considerably smaller and their scales weaker than adults, making them more vulnerable to predation.

The onset of foraging activity for adults ranges from 14:34h to 02:15h (mean = 20:25h) and for subadults from 14:30h to 20:15h (mean = 18:02h) and the duration of foraging activity for adults and subadults ranges from 35 min to 8 h 20 min (mean = 3 h 51 min and 3 h 42 min, respectively) (Swart 1996). The time they remain active each evening appears to be directly related to their feeding intensity (feeding time per hour) such that on evenings when their feeding intensity is higher they are active for shorter periods.

Social and Reproductive Behaviour Besides ♂♂ and ♀♀ coming together to mate and ♀♀ nursing their young, individuals lead an entirely solitary existence. Males do not appear to be territorial since they do not actively defend a territory. However, they are intolerant of one another since they will attack aggressively by wrestling with the tail and scratching with the front claws and may remain engaged in battle for several hours until one relents and leaves the area (J. M. Swart pers. obs.).

In NW Zimbabwe the home-ranges of three adult ♂♂ (measuring 10.35, 10.68 and 11.07 km²) calculated from plots of their respective den locations were larger than the home-ranges of three adult females (5.65, 5.91 and 7.49 km²) (Heath & Coulson 1997a). These home-ranges are probably underestimated since the area utilized around the dens was not included. Home-ranges based on den locations of 14 Ground Pangolins in the Kruger N. P. region increased by 50.3% when the coordinates of foraging excursions were included (J. M. Swart pers. obs.). Home-ranges of adult ♂♂

in this region overlap the home-ranges of up to five adult ♀♀ and vary in size from 9.28 to 22.98 km² (mean = 16.33 km², n = 4). Home-ranges of adult ♀♀ in this region are overlapped by the home-ranges of up to three adult ♂♂ and vary in size from 0.65 to 6.66 km² (mean = 3.66 km², n = 8), ca. four times smaller than home-ranges of adult ♂♂. Adult male and female home-ranges are ca. 4% larger during the wet season.

Home-ranges of adult ♀♀ overlap each other by 0.3–24.9% (mean = 8.8%, n = 6) and the overall proportion of an adult female's home-range that is overlapped by other adult ♀♀ is 0.3–34.1% (mean = 14.6%, n = 6). In contrast, home-ranges of adult ♂♂ overlap each other by 19.5–51.1% (mean = 28.5%, n = 3) and the overall proportion of an adult male's home-range that is overlapped by other adult ♂♂ is 22.9–51.1% (mean = 38.0%, n = 3). The proportion of an adult female's home-range that is overlapped by the home-range of at least one adult ♂♂ varies from 31% to 100% (mean = 72.3%, n = 8) (J. M. Swart pers. obs.).

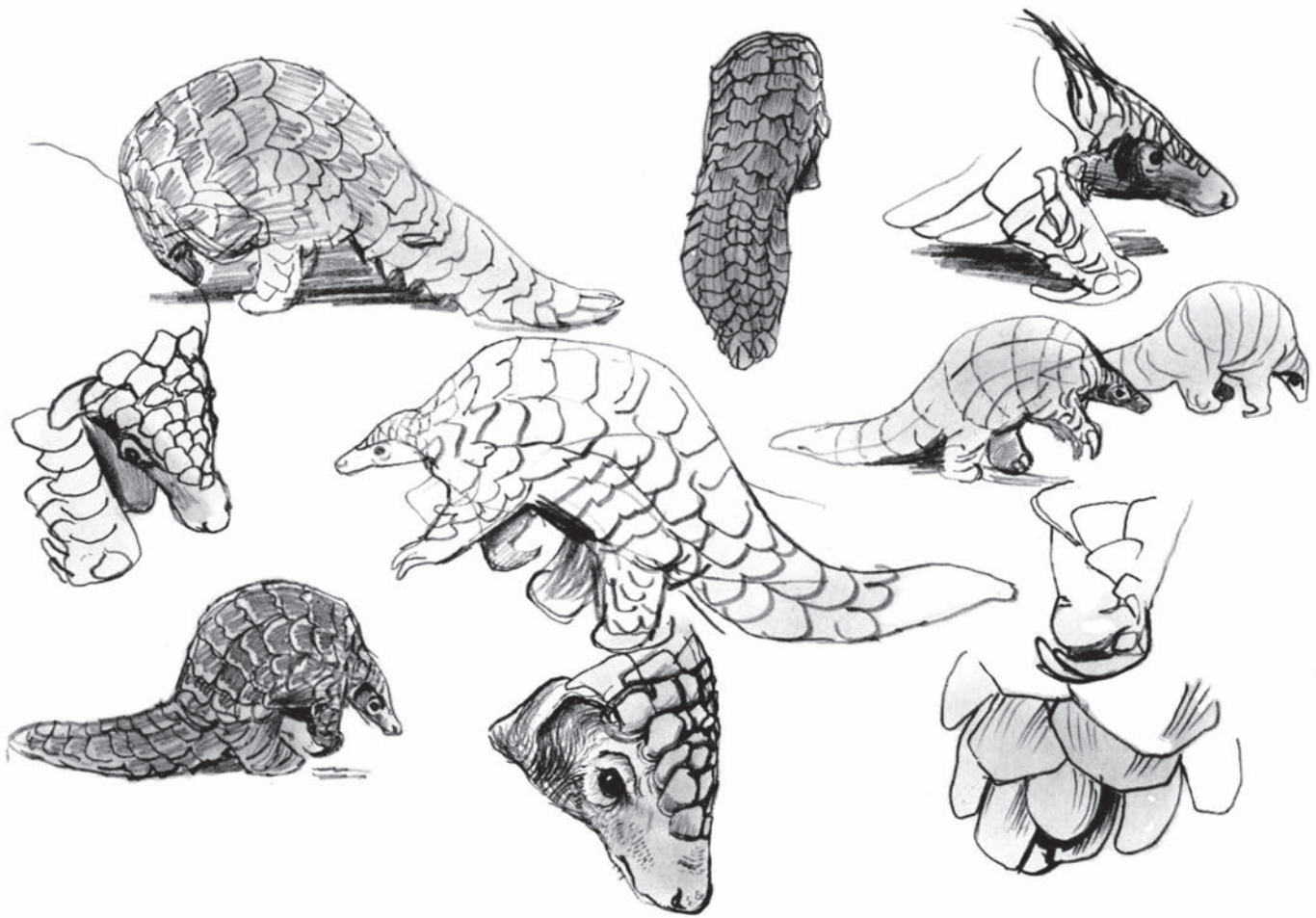
Males and ♀♀ scent-mark with urine. The soil is loosened with the sharp front claws before the animals urinate and roll in the urine-impregnated soil to spread it over the body. As they move off, their scent is transferred onto the vegetation so that their presence is announced to other conspecifics. Males also scent-mark by lifting a hindleg to squirt a small deposit of urine on an object such as a tree or rock.

Dens (mostly abandoned Aardvark *Orycteropus afer*, warthog *Phacochoerus* spp., or springhare *Pedetes* spp. burrows) are predominantly used for resting in during the day and since they are distributed throughout the home-range they are convenient sites for scent-marking. Males and ♀♀ often visit several abandoned burrows during their nightly excursions, which they use as marking posts. These burrows are not necessarily utilized as dens but are frequently used only as scent-marking posts (J. M. Swart pers. obs.).

In the Kruger N. P. area, ♂♂ utilized from 1.5 to 4.1 dens/km² (mean = 3.0, n = 4) and ♀♀ from 3.4 to 22.6 dens/km² (mean = 9.6, n = 8) within their home-range (J. M. Swart pers. obs.). Males spent 1–16 consecutive days (mean = 2.3 days, n = 4) in the same den whereas ♀♀ spent 1–75 consecutive days (mean = 5.0 days, n = 8) in the same den. Once dens were vacated after a period of occupation, ♂♂ returned to only ca. 18% and females to ca. 23% of dens previously utilized. A den described by Sweeney (1974) had an entrance 200–250 mm in diameter and a tunnel 3–5 m long that sloped steeply downward with the end of the tunnel about 1 m below the entrance level.

In the Kruger N. P. region, courtship and mating behaviour was only observed twice in the wild, where on both occasions the ♂ and ♀ only paired off for one day. On each occasion the ♂ approached the ♀ very cautiously hissing at her and sniffing all the time while circling and clambering over her. Coitus was achieved when the ♂ forced his tail beneath the ♀ and they remained in this position for ca. 30 min (J. M. Swart pers. obs.). A pair of captive Ground Pangolins was also observed copulating in the Bloemfontein Zoo, South Africa; the ♂ mounted the ♀ from the side and forced his hindquarters underneath the ♀ (Van Ee 1978).

Females conceal their young in a den for about one month and leave the den to forage alone. After this period the young are moved several times, each time to a new den. The mother and young often share the same den for over a year. A large adult ♀ of 14.1 kg was observed carrying a juvenile weighing 4.7 kg (ca. one year old) on her back (J.

Ground Pangolin *Smutsia temminckii*.

M. Swart pers. obs.). This juvenile was being moved to a new den but also frequently foraged independently and returned to the same den as her mother. If threatened, very young juveniles will take refuge underneath the ♀, who curls up around the juvenile as protection. As the juvenile grows too large to be completely enclosed, the head and shoulders are enveloped thus affording protection to the heads of both the ♀ and juvenile (Skinner & Chimimba 2005).

There are no vocalizations used to communicate between individuals; however, they do emit a soft purr-like growl that causes their body to vibrate when alarmed (J. M. Swart pers. obs.).

Reproduction and Population Structure Mating and birthing seasons have not been documented. However, the two incidences of mating recorded in the wild in Sabi Sand G. R. bordering Kruger N. P. in South Africa were during different seasons. One mating was observed at the end of the wet season in Mar and the other during the dry season in Aug (J. M. Swart pers. obs.). No births were recorded in the wild, but a ♀ killed in May (dry season) in Zimbabwe had a foetus of 8.1 g and a ♀ killed in Jul (dry season) had a ♂ foetus of 113.8 g. No foetuses were recorded in ♀♀ killed during the wet season (Coulson 1989). Other records include gravid ♀♀ taken in Jul (Smithers 1971), a captive birth recorded in Aug (Ansell 1960), and an injured ♀ that gave birth to a possibly premature neonate in Aug and which had a mass of 120 g (Jacobsen *et al.* 1991). A radio-tagged ♂ was found cohabiting with a ♀ in

mid-February after walking 12 km from its original home-range in less than one week. They were documented cohabiting for three days prior to the radio-tag falling off the ♂ (Heath & Coulson 1997a).

A single young of approximately 15 cm long and 340 g in weight is born after gestation of about 140 days (Van Ee 1966); ♀♀ give birth to one young per year (Van Ee 1966). Eyes are open at birth and the scales are soft. At four weeks old the young rode on the mother's back and was seen eating termites for the first time; by 35 days it began eating the artificial diet eaten by the captive adults (Van Ee 1978). Juveniles grow quickly initially, reaching up to 5 kg in the first year and are usually weaned at about five months old. A juvenile born in Bloemfontein Zoo weighed just over a kilogram after three months and 3.5 kg after one year (Van Ee 1978). Sweeney (1974) reported a ♀ still lactating a half-grown juvenile while carrying a well-developed foetus, indicating that ♀♀ mate and become pregnant while still nursing young from the previous year. Young may accompany the mother for a considerable period of time.

The longevity of Ground Pangolins is unknown but is estimated to be in excess of 19 years based on the recorded captive longevity of the Indian or Thick-tailed Pangolin *Manis crassicaudata* (Weigl 2005), which is approximately the same size.

Predators, Parasites and Diseases Lions *Panthera leo* and Spotted Hyaenas *Crocuta crocuta* are probably the major predators, although on most occasions the protection afforded by their scales

allows them to escape unharmed. A Ratel *Mellivora capensis* was observed attacking and killing a large ♀♀ by persistently clawing and biting at the smaller lateral scales close to the back legs until she eventually weakened, enabling the Ratel to penetrate the flesh (J. M. Swart pers. obs.). There is also one record of a Nile Crocodile *Crocodylus niloticus* killing a Ground Pangolin (Coulson 1989).

There is little information on parasites and disease in Ground Pangolins. An adult ♂ found covered with mites *Manitherionyssus heterotarsus* and tampans *Ornithodoros moubata* died two days later and the probable cause of death was diagnosed as progressive paralysis induced by the tampans (Jacobsen *et al.* 1991). Parasites such as these and ticks are removed by occasionally wallowing in mud or fresh herbivore dung.

Conservation IUCN: Least Concern. CITES: Appendix II.

Although present in a number of protected areas across their range, and protected by law in many range countries, numbers of Ground Pangolins may be declining due to the demand for their body parts and scales for medicinal purposes and superstitious value (Coulson 1985, Bräutigam *et al.* 1994, Swart 1996). In Tanzania they are sometimes referred to as the doctor, *Bwana mganga*, because every body part is believed to have some medicinal value (Wright 1954). Many East African people believe that burning pangolin scales keeps away Lions (Kingdon 1971). Other widely believed magical and medicinal properties are: their ability to converse with tribal chiefs; that smoke from burning scales improves the health of cattle and cures persistent nose bleeding; and scales are used as a medicine for good luck and to bring rain. In Zimbabwe it is traditionally a good omen to catch and present pangolins to a superior such as a local chief, and several were even captured and presented to the Prime Minister (Coulson 1985). Cunningham & Zondi (1991) found that overexploitation of Ground Pangolins for medicinal use is occurring in South Africa and is increasingly focused on core conservation areas. They are used as bushmeat in some parts of their range (South Africa, Zimbabwe, Namibia), but are generally unpopular since the meat is fatty; the skins are sometimes used to make leather goods. The species was formerly listed in Appendix I of CITES from 1975 to 1995, but then transferred to Appendix II. There have been reports of organized commercial poaching and export to Asia or other African countries (Bräutigam *et al.* 1994), but there is no or very limited international trade in this species included in CITES annual reports for the period 1996–2011 (www.cites.org).

Other threats to pangolins include pesticide usage, in particular those containing gamma-BHC (benzenehexachloride); death from very small quantities has been documented within 24 hours (Swart 1996). This substance has been used in the past to control locusts in South Africa and it is likely that Ground Pangolin populations are reduced in areas where this has occurred (Swart 1996). Pangolins have also been recorded killed on the lower strands of electric fences in South Africa (Swart 1996, Beck 2010), though this should not necessarily pose a major threat.

Confiscated pangolins are often released in areas far from their original home-ranges, apparently with grave consequences. Jacobsen *et al.* (1991) in South Africa reported that two pangolins released far from their home-ranges were found dead within 10 days after release; however, they also released a third pangolin, this time back in its original home-range, which survived only 14 days. Although the condition of these pangolins on the day of release is not known it can be assumed that they were probably under severe stress during the period of capture, which may have contributed to their deaths. Three other pangolin relocations into the Sengwa G. R. in Zimbabwe (Heath & Coulson 1997b) were met with limited success. One adult ♀ was released 5 km from her original home-range but returned back again after 10 days, a second adult ♀ was released 18 km from her home-range, but unfortunately the transmitter failed after 30 days and could not be followed further, and finally a third pangolin, a juvenile retrieved from a poacher, was released and followed for 85 days before the transmitter fell off. This relocation was apparently successful; however, being a juvenile, this pangolin would not have established a home-range before being relocated and would thus probably naturally settle wherever placed. Clearly, this is a field where more research is needed particularly since pangolins cannot be raised successfully in captivity because of specialized ant and termite dietary requirements (Van Ee 1966, 1978).

Measurements

Smutsia temminckii

HB (♂♂): 431 (297–565) mm, n = 18

HB (♀♀): 458 (350–677) mm, n = 15

T (♂♂): 405 (290–585) mm, n = 18

T (♀♀): 370 (223–440) mm, n = 15

HF c.u.: 60 (52–70) mm, n = 11*

E: n. d.

WT (♂♂): 9.4 (2.5–17.1) kg, n = 42**

WT (♀♀): 9.0 (4.6–15.8) kg, n = 40**

Zimbabwe (Coulson 1989)

*Zimbabwe (Smithers & Wilson 1979)

**South Africa and Zimbabwe (Coulson 1989, Jacobsen *et al.* 1991, Heath & Coulson 1997a, Swart *et al.* 1999, J. M. Swart pers. obs.)

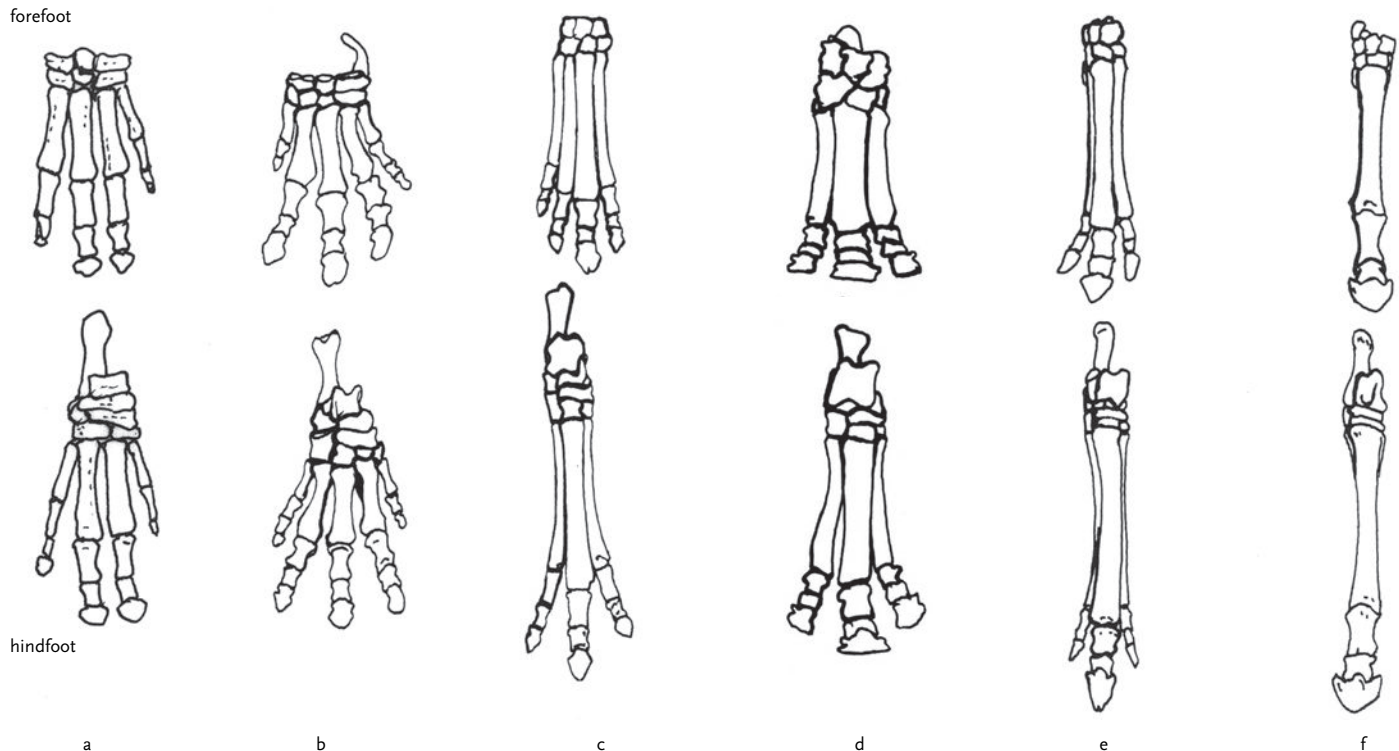
Sweeney (1956) recorded a body mass of 27 kg in Sudan, but this may well refer to a record of the Giant Pangolin; Ansell (1964) reported a mass of 16.8 kg for a specimen from Kafue N. P. in S Zambia. The longest animal recorded in a series from Zimbabwe, including tail, was 1403 mm and had a weight of 15.5 kg (Heath & Coulson 1998)

Key References Coulson 1985, 1989; Heath & Coulson 1997; Jacobsen *et al.* 1991; Kingdon 1971; Richer *et al.* 1997; Stuart 1980; Swart 1996; Swart *et al.* 1999; Sweeney 1956, 1974; Van Ee 1966, 1978.

Jonathan Swart

SUPERORDER EUUNGULATA

Euungulata Waddell, Kishino & Ota, 2001. *Genome Informatics* 12: 148.



Cetartiodactyl and perissodactyl lower limbs, forefoot above, hindfoot below: (a) Common Hippopotamus *Hippopotamus amphibius* (cetartiodactyl); (b) *Phenocodus* (condylarth); (c) *Hyracotherium* (primitive perissodactyl); (d) *Diceratherium* (Miocene rhinoceros); (e) *Miohippus* (Miocene horse); (f) *Equus* (living equid).

For more than a hundred years zoologists have laboured to emphasize the differences between odd-toed and even-toed ungulates. Over much of this time palaeontologists have also charted separate histories for perissodactyls and artiodactyls, which both first appeared around 55 mya. Both morphological and molecular studies show that both lineages share a common origin within the Laurasiatheria (Zhou *et al.* 2012). In the light of contemporary knowledge a new taxon is called for to register a common ancestry that is exclusive of the other, extremely diverse, laurasiatheres. Superorder 'Euungulata' has been proposed (Waddell *et al.* 2001) and we follow Asher & Helgen (2010) in adopting this name.

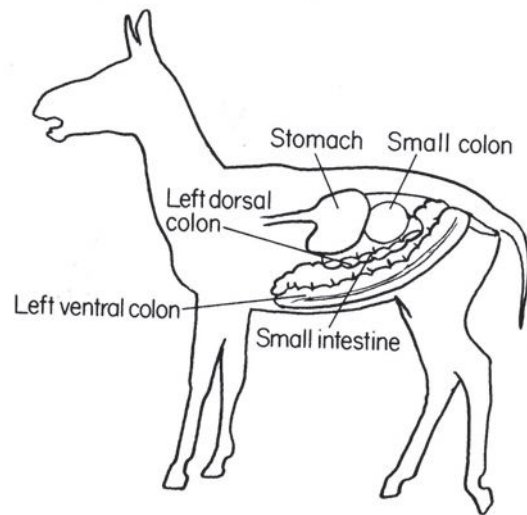
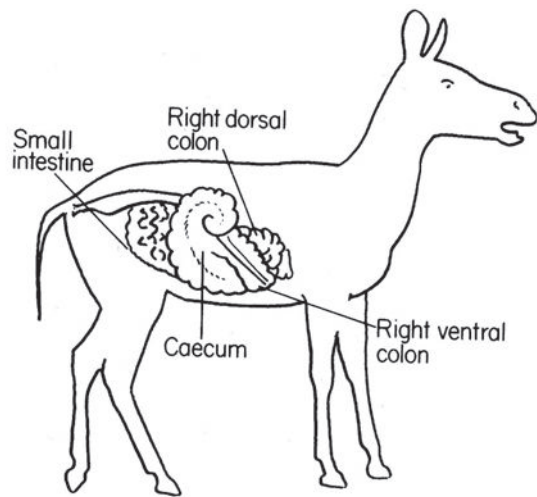
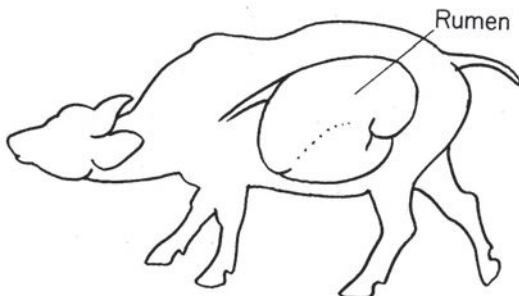
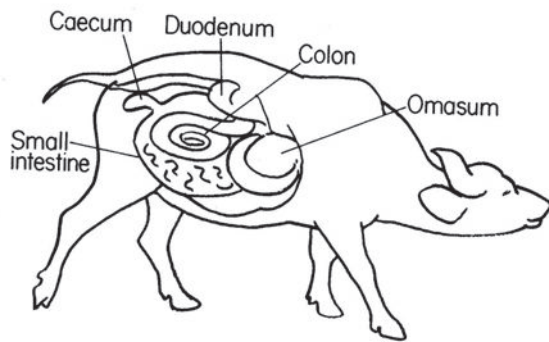
The orders Perissodactyla and Artiodactyla were once distinguished at the superordinal level as Mesaxonia and Paraxonia: mesaxonian means that the axis of the foot passes through the middle toe, i.e. through digit 3; paraxonian means passing outside the middle, i.e. between digits 3 and 4. With the identification, by molecular scientists, of the Afrotheria and the exclusion of afrotherian paenungulates from any close association with perissodactyls, the former category of 'Mesaxonia' (which at one time embraced both paenungulates and perissodactyls) needs to be scrapped as a mere synonym for Perissodactyla. Further, with the discovery that whales

cluster *within* the former artiodactyls, the term Paraxonia, were it to be retained, would now have to include pelagic mammals with non-paraxonid flippers.

A convenient ancestral grouping might plausibly include some 'condylarths' (Palaeogene archaic ungulates) but this systematic issue has not yet been resolved. Both artiodactyls and perissodactyls were originally known from across the northern latitudes (North America and Eurasia). Artiodactyls were mainly small, somewhat omnivorous forms, rather like present-day chevrotains in both size and ecology. Perissodactyls, on the other hand, in general were larger (dog- to pony-sized), and were, from the start, more specialized browsers. A less obvious, but fundamental difference is that many artiodactyls digest their food by foregut fermentation, while perissodactyls employ the less derived mode of hindgut fermentation.

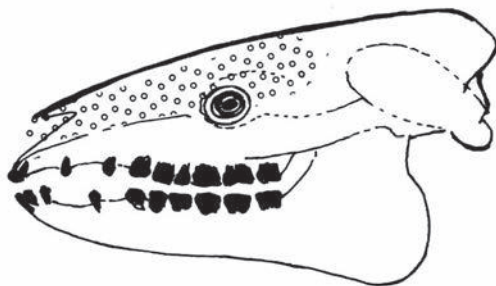
Contemporary perissodactyls, rhinos, horses and tapirs, are but vestiges of a very diverse array that flourished from the Eocene until the late Miocene. By contrast, their even-toed equivalents, cetartiodactyls (discussed in the next volume) have been hugely successful.

Christine Janis, Michael Hoffmann & Jonathan Kingdon



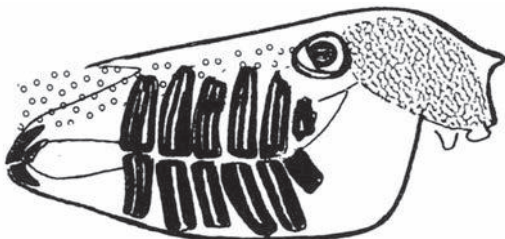
ABOVE: Foregut (bovid, on left) and hindgut (equid, on right) digestive system.

BELOW: Features influencing morphology in perissodactyla.



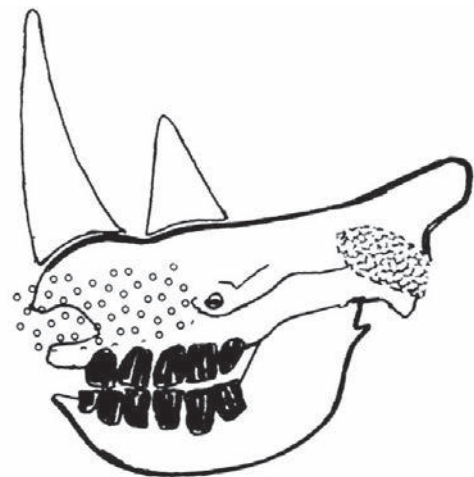
Archaic perissodactyl features

Vegetarian diet; relatively high-crowned molars, deep jaws. Increasing size trend. Well-developed olfaction in extended cylindrical skull.



Equid features

Medium to large size. Elongation of neck, legs and skull. Vision well developed; high head carriage. Diastema, molars with very high crowns with deep rooting. Incisors cut and pull grass. *Defence*: speed. *Weapons*: teeth and hooves.

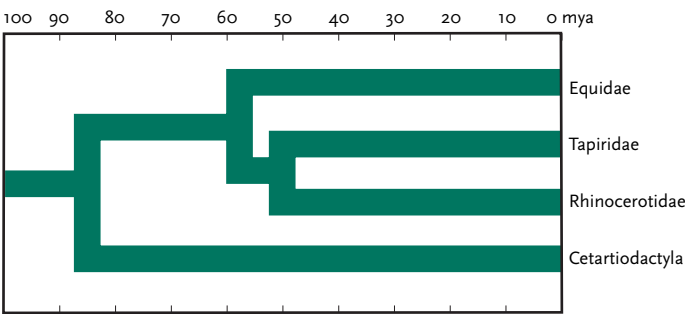


Rhinocerotid features

Great size and weight. Heavy head, low carriage. Short plantigrade limbs. Vision poor; olfaction good. Incisors and diastema lost, lips gather food. *Defence*: size and horns. *Weapons*: nasal horns.

Order PERISSODACTYLA – Equids, Rhinoceroses, Tapirs

Perissodactyla Owen, 1848. Quarterly Journal of the Geological Society of London 4: 103–141.



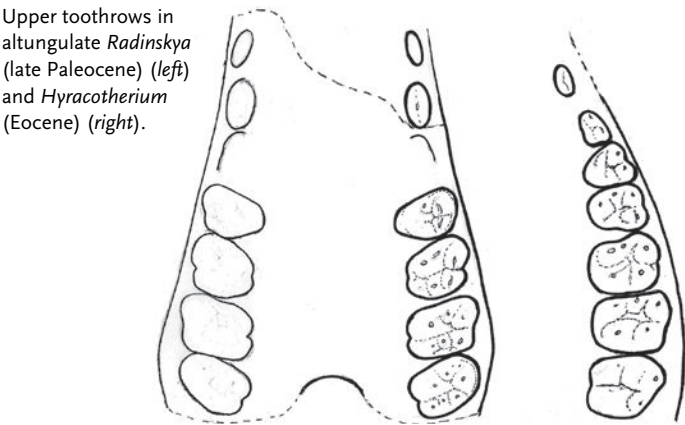
Tentative phylogenetic tree of Perissodactyla (after Bininda-Emonds *et al.* 2007, Meredith *et al.* 2011)

| | | |
|--------------------------------------|---------------|--------|
| Equidae (1 genus, 4 species) | Asses, Zebras | p. 410 |
| Rhinocerotidae (2 genera, 2 species) | Rhinoceroses | p. 444 |

The perissodactyls are the order of herbivorous ‘odd-toed’ hoofed mammals that includes the living horses, zebras, asses, tapirs, rhinoceroses and their extinct relatives. They were originally named by Richard Owen (1848) as a group including horses, rhinos, tapirs and hyraxes, although no recent authors have accepted the inclusion of hyraxes in Perissodactyla. Perissodactyls are recognized by a number of unique specializations (Hooker 2005), but their single most diagnostic feature is the structure of their feet. Most perissodactyls have either one or three toes on each foot, and the axis of symmetry of the foot runs through the middle digit.

The perissodactyls are divided into three subordinal groups (Prothero & Schoch 1989): the Hippomorpha (horses and their extinct relatives); the Titanotheriomorpha (the extinct brontotheres, found in Asia and North America during the Eocene); and the Moropomorpha (tapirs, rhinoceroses, and their extinct relatives). The latter suborder includes, as an infraorder, the Ceratomorpha, uniting the extant tapirs and rhinoceroses.

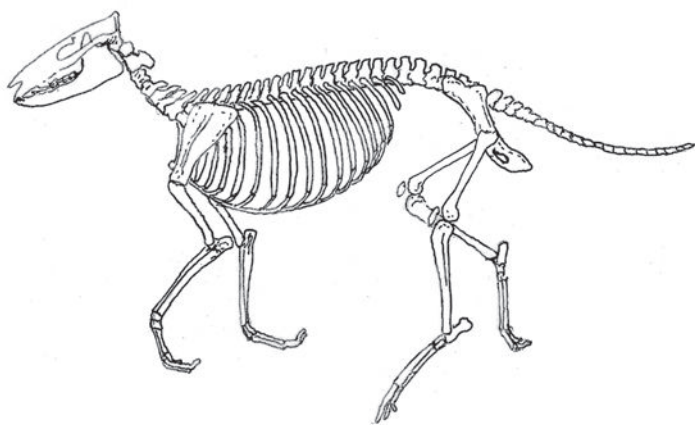
Perissodactyls were once thought to have evolved in Central America from the phenacodonts, an extinct group of archaic hoofed mammals placed in the invalid taxon ‘Condylarthra’. However, in 1989, a specimen recovered from deposits in China dated to about 57 mya was described and named *Radinskya*. This specimen shows that perissodactyls originated in Asia at around this time and were unrelated to North American phenacodonts. By 55 mya the major groups of perissodactyls had differentiated, and migrated from Asia to Europe and North America. Before 34 mya the brontotheres and the archaic tapirs were the largest and most abundant hoofed mammals in Eurasia and North America. After these groups became extinct, horses and rhinoceroses became the most common perissodactyls, with a great diversity of species and body forms. Both groups were decimated during another mass extinction about 5 mya, and today only five species of rhinoceros, four species of tapir, and a few species of horses, zebras and asses cling to survival in the wild. The niches of large hoofed herbivores have, to a large extent, been taken over by the ruminant artiodactyls, such as cattle, antelopes, deer and their relatives.



From their Asian origin, the hippomorphs spread all over the northern continents. In Europe, the horse-like palaeotheres substituted for true horses. North America became the centre of evolution of true horses, which occasionally migrated to other continents. The descendants of *Protorohippus* (once called *Hyracotherium*; Froehlich 2002) evolved into many different lineages living side by side. The collie-sized three-toed horses *Mesohippus* and *Miohippus* (from beds dated about 37–30 mya) were once believed to be sequential segments on the unbranched trunk of the horse evolutionary tree. However, they coexisted for millions of years, with five different species of two genera living at the same time and place. From *Miohippus*-like ancestors, horses diversified into many different ecological niches. One major lineage, the anchitherines, retained low-crowned teeth, presumably for browsing soft leaves in the forests. Some anchitherines, such as *Megahippus*, were almost as large as the living horse. *Anchitherium* migrated from North America to Europe about 20 mya and was the first true horse to reach Europe.

About 15 mya there were at least 12 different lineages of three-toed horses in North America, each with slightly different ecological specializations, a situation analogous to the diversity of modern antelopes in East Africa. The ancestors of this great radiation of horses are a group of three-toed, pony-sized beasts that have long been lumped into the ‘wastebasket’ genus ‘*Merychippus*’. However, recent analyses have shown that the species of ‘*Merychippus*’ are ancestral to many different lineages of horses. True *Merychippus* was a member of the hipparion lineage, a group of three-toed horses that developed highly specialized teeth, and had a distinctive concavity in the bone on the front of the face. Hipparions were a highly diverse and successful group of horses, with seven or eight different genera spread not only across North America, but also migrating to Eurasia. *Merychippines* were also ancestral to lineages such as *Calippus* (a tiny dwarf horse), *Protohippus* and *Astrohippus*.

On two different occasions (*Pliohippus* and *Dinohippus*), three-toed horses evolved into lineages with a single toe on each foot. About 5 mya most of these three-toed and one-toed horse lineages became extinct, leaving only *Dinohippus* to evolve into the modern horse *Equus*. The main lineage of horses that survived the extinctions 5 mya were known as



Hyracotherium skeleton.

the equines. The living genus *Equus* first appeared about 3 mya and was widespread throughout the northern hemisphere. When the Isthmus of Panama rose about 2.5 mya, horses also spread to South America. There they evolved into distinctive horses with a short proboscis known as the hippidions. At the end of the last Ice Age (about 10,000 years ago), horses became extinct in the New World. They were reintroduced to their ancestral homeland by Columbus in 1493. Feral horses that have escaped from domesticated stock are known as mustangs.

The earliest moropomorphs, such as *Homogalax*, occur in strata about 55 mya. They are virtually indistinguishable from the earliest horses, such as *Protorohippus*. From this unspecialized ancestry, a variety of archaic tapir-like animals diverged. Most retained the simple leaf-cutting teeth characteristic of tapirs, and like brontotheres they died out about 34 mya when their forest habitats shrank. Only the modern tapirs, with their distinctive long proboscis, still survive in the jungles of Central and South America (three species) and South-East Asia (one species). All are stocky, pig-like beasts with short stout legs and oval hooves, and a short tail. They have no natural defences against large predators, so they are expert at fleeing through dense brush and swimming to make their escape.

The horse-like clawed chalicotheres are closely related to some of these archaic tapirs. When chalicotheres were first discovered, there was general disbelief that the claws belonged to a hoofed mammal related to horses and rhinos. However, many specimens have clearly shown that chalicotheres are an example of a hoofed mammal that has secondarily developed claws. To begin with, claws were considered useful for digging up roots and tubers, but the fossilized claws show no sign of the characteristic scratches due to digging. Instead, chalicotheres are now thought to have used their claws to haul down limbs and branches to eat leaves (much as ground sloths did). *Chalicotherium* had such long forelimbs and short hindlimbs that it apparently knuckle-walked with its claws curled inward. Chalicotheres were always rare throughout their history in North America and Eurasia, but nevertheless survived until the late Pleistocene in Africa.

Rhinoceroses have been highly diverse and successful throughout the past 50 million years. They have occupied nearly every niche available to a large herbivore, from dog-sized running animals, to several hippo-like forms, to the largest land mammal that ever lived, *Paraceratherium*. Most rhinoceroses were hornless. Unlike the horns of cattle, sheep and goats, rhino horns are made of cemented hair fibres, and have no bony core, so they rarely fossilize. Therefore, the presence and size of the horn must be inferred from the roughened area on the top of the

skull where it once attached. Even without horns, rhino fossils are easy to recognize by a number of anatomical features in the skeleton, skull and braincase. One of the easiest to spot is the crests on the crowns of the upper molars, which look like the Greek letter 'pi'.

The earliest rhinos, known as *Hyrachyus*, were widespread over Eurasia and North America about 53 mya. They apparently crossed back and forth between Europe and North America using a land bridge. From *Hyrachyus*, three different families of rhino diverged. Long before hippos evolved, one family of Rhinocerotidae, the amynodonts, evolved into hippo-like amphibious forms, with stumpy legs and a barrel chest for living in ponds and rivers. The last of the amynodonts, which had a short trunk like an elephant, died out in Asia about 15 mya.

The second family was known as the hyracodonts, or 'running rhinos,' because they had unusually long slender legs compared with other rhinos. They were particularly common in Asia and North America between 42 and 34 mya. The biggest of all was *Paraceratherium* (once called *Baluchitherium* or *Indricotherium*), which was 6 metres tall at the shoulder and weighed 20,000 kg. It must have browsed leaves from the tops of trees, as giraffes do today. Indricotheres were also the last of the hyracodonts, vanishing from Asia about 15 mya.

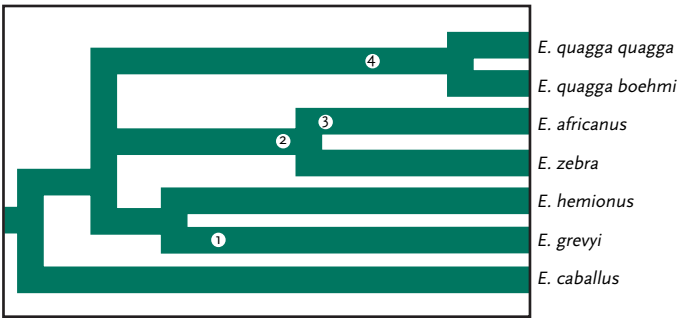
The third family is the true rhinoceroses, or family Rhinocerotidae. They first appeared in Asia and North America about 40 mya, and lived side by side with the hyracodonts and amynodonts on both continents. Rhinocerotids can be distinguished from hyracodonts and amynodonts by their distinctive molars, and by the development of a tusk-like lower incisor that occluded against a chisel-like upper incisor. In the late Eocene and early Oligocene (about 37–28 mya), there were several different genera of rhinocerotids. When the brontotheres died out about 34 mya, rhinocerotids were the largest land mammals in North America, and remained so until mastodonts arrived about 16 mya.

Up until this point, all the rhinoceroses we have mentioned were hornless. Rhinos with horns first appeared about 28 mya; two different lineages independently evolved paired horns on the tip of the nose. Both of these groups went extinct about 18 mya, when two new subfamilies immigrated to North America from Asia: the browsing (leaf-eating) aceratherines, and hippo-like grazing teleoceratines. Between 18 and 5 mya, browser-grazer pairs of rhinos were found all over the grasslands of Eurasia, Africa and North America. The teleoceratine *Teleoceras* was remarkably similar to hippos in its short limbs, massive barrel-shaped body and high-crowned teeth for eating gritty grasses. We know these animals were aquatic because they are usually found in ancient lake or river sediments, and some extraordinary specimens buried in volcanic ash preserve the grass seeds of their last meal.

A mass extinction event that occurred about 5 mya wiped out North American rhinos, and decimated most of the archaic rhino lineages (especially the teleoceratines and aceratherines) in the Old World. The surviving lineages diversified in Eurasia and Africa, and even thrived during the Ice Ages. Woolly rhinos are known from numerous mummified specimens that give us detailed information about their hair, tissues and even stomach contents. The only surviving descendant of the woolly rhino lineage is the Sumatran Rhinoceros *Dicerorhinus sumatrensis*, of which only a few hundred individuals survive in the mountainous regions of Sumatra. Four other species of rhino survive in Asia and Africa, of which the Javan Rhinoceros *Rhinoceros sondaicus* is the most threatened, numbering fewer than 50 individuals in the wild.

Family EQUIDAE
ASSES, ZEBRAS

Equidae Gray, 1821. London Med. Repos. 15: 307.



Tentative phylogenetic tree of extant equids (after Orlando *et al.* 2009). Numbers indicate likely sequence of arrivals in Africa.

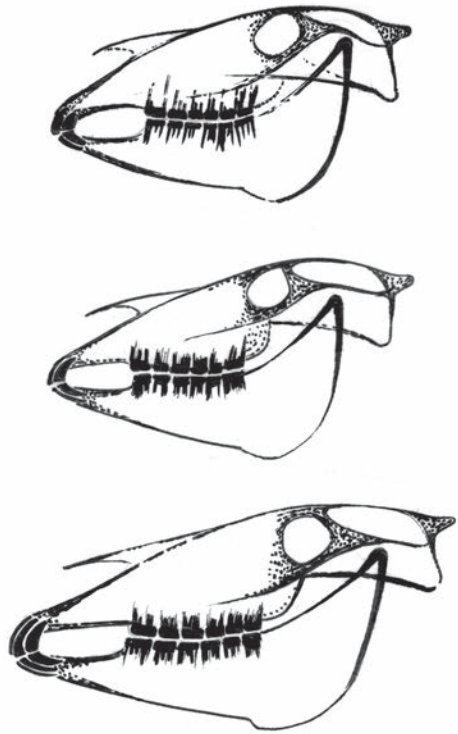
| <i>Equus</i> | | |
|--------------------------------|------------------|--------|
| <i>Asinus</i> (1 species) | African Wild Ass | p. 414 |
| <i>Hippotigris</i> (3 species) | Zebras | p. 417 |

The family Equidae contains the horses, asses and zebras, as well as numerous and diverse extinct forms. Like the rhinoceroses and tapirs, they belong to the order Perissodactyla, or Odd-toed Hoofed Mammals, which rest their weight on a single central toe on each foot. In fact, the Equidae have taken this to its logical conclusion, losing all side toes and retaining just the central, third one. All that remains of the side toes are a pair of sliver-like bones, called splint bones, at the ‘knee’ (really, the wrist) and hock (the ankle). On the forelegs, the ulna is greatly reduced and has fused with the very robust radius, such that all the weight is effectively borne by the radius. In the hindlegs, the reduced fibula is fused to the tibia and it is the latter that bears the weight of the animal.

A single genus, *Equus*, is commonly recognized, with seven species (four African) currently divided into three (but sometimes more) subgenera (Groves & Ryder 2000). The number of species recognized in the family depends on whether the Quagga is considered conspecific with the Plains Zebra *Equus quagga* (the approach followed here, but not, for example, by Grubb 2005), whether Cape and Hartmann’s Mountain Zebras are considered separate species (as proposed by Groves & Bell 2004), whether Przewalski’s Horse is considered distinct from *Equus ferus* (see extensive discussion in Grubb 2005), and species relationships of the taxa *onager*, *kiang* and *khur* relative to *E. hemionus*.

Modern equids are fast-running diurnal grazers of open plains country in north-east, East and southern Africa, as well as arid and semi-arid country in Asia. They do not extend into the West African grasslands or Sahel. Species living in more mesic environments live in harem herds, while in the more arid-adapted species small groups of females and young live apart from the males, which are territorial.

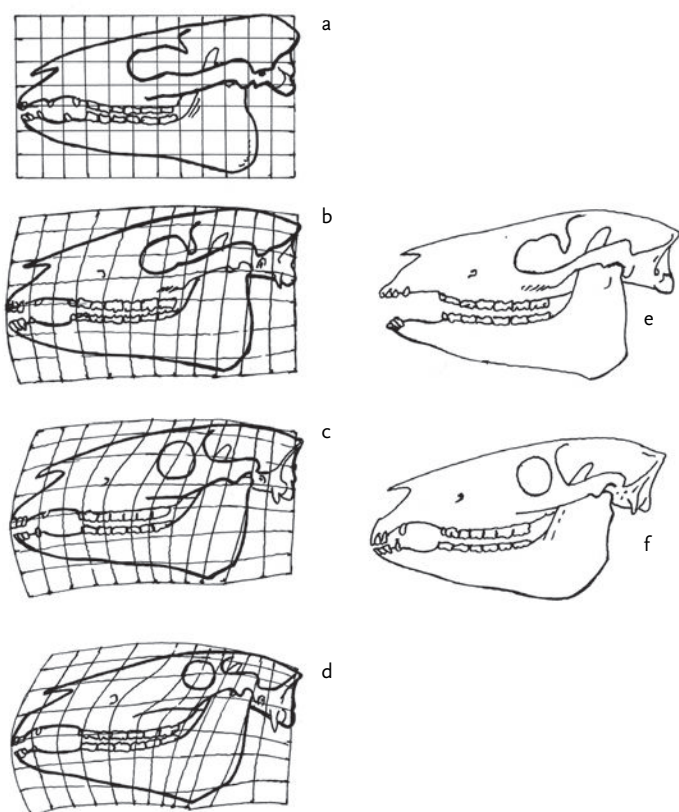
Equids have a long skull, and the jaws are powerfully developed, with a broad angle at the back where the masseter muscle is attached to the mandible. The braincase, although much shorter than the face, is large. The orbits (eye-sockets) are large and face to the side, and are entirely ringed by bone; the visual fields do not overlap, instead equids have all-round vision, and their pupils are even oblong, increasing the width of the visual field. There is a battery of high-crowned premolar and molar teeth with complex folds of enamel,



Functional zones in skulls of equids. From top: Plains Zebra *Equus quagga*, African Wild Ass *Equus africanus*, Grévy’s Zebra *Equus grevyi*.

increasing their wearing life, and chisel-like incisor and canine teeth separated from the cheekteeth by a long gap, the diastema. The typical dental formula is $I^{3/3} C^{0-1/0-1} P^{3-4/3} M^{3/3} = 36-42$. Equids, unlike most other medium-sized ungulates, have virtually no sexual dimorphism, except that the canines, well developed in adult males, are reduced or absent in ♀♀. The deciduous first premolars are rudimentary and soon shed, although the first upper premolar sometimes persists as a reduced tooth. The incisor teeth have an enamel-lined hollow or depression (the infundibulum) that runs down the centre for a variable length; as teeth wear down, the shape of the infundibulum can be used in age determination (e.g. Smuts 1974a, Penzhorn & Grimbeek 1987). The infundibulum is, however, absent in some Plains Zebras, especially many from north of the Zambezi R. Equids have a simple stomach in which the passage of food is not as delayed as it is in bovids (Alexander 1952). Glover & Duthie (1958) determined that horses consume approximately twice the amount that a similar-sized cow does and suggested that this might compensate for inferior levels of protein-assimilation.

The genetics of the Equidae have been investigated and discussed by various authors (e.g. Ryder *et al.* 1978, George & Ryder 1986, Oakenfull *et al.* 2000, Groves & Ryder 2000, Moodley & Harley 2005, Lorenzen *et al.* 2008, Orlando *et al.* 2009). Chromosome number in the equids varies from $2n = 32$ (*E. zebra*) to $2n = 46$ (*E. grevyi*) in the subgenus *Hippotigris*, and $2n = 54$ to $2n = 66$ in other species. The first extinct form to have its DNA cloned was, in fact, the Quagga *Equus quagga quagga*, when traces of DNA from a

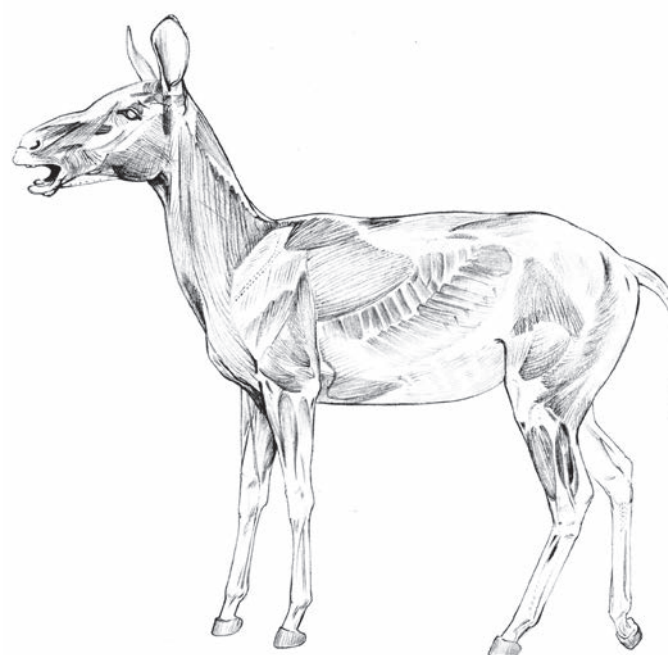
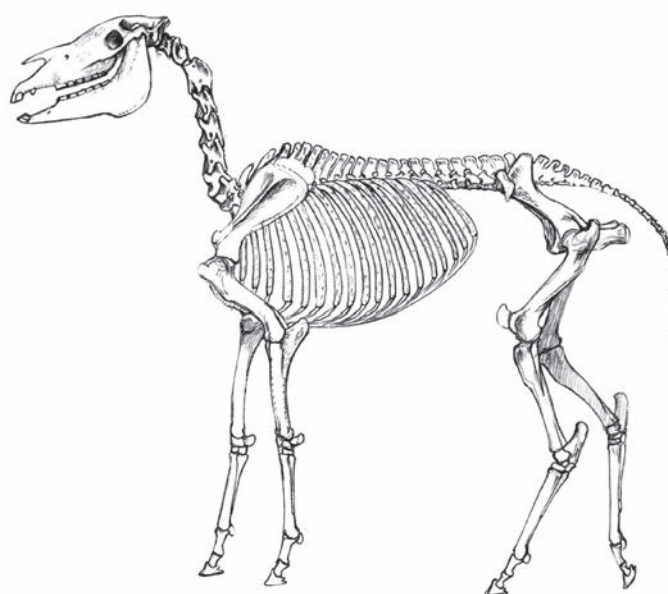


Hyracotherium (a), *Equus* (d), and two intermediate skulls (b and c) constructed on coordinate transformations (from Thompson 1917). (e) *Mesohippus* for comparison with hypothetical skull (b) and (f) *Merychippus* for comparison with (c).

museum specimen were extracted and sequenced, an event achieved even before the development of techniques such as PCR (polymerase chain reaction) (Higuchi *et al.* 1984).

The evolutionary history of the Equidae is very well known and has been discussed in detail by several authors (e.g. Mathew 1926, Simpson 1951, Groves 1974, MacFadden 1988, 1992, 2005; and see Prothero & Schoch 1989). The family has been successful throughout its existence, and has left abundant fossils. The earliest members lived in the early Eocene, about 54 mya, at which time they are difficult to distinguish from the earliest rhinos and tapirs and members of other, now extinct, perissodactyl groups. Previously known as 'eohippus' or *Hyracotherium*, recent work reveals that these Eocene 'hyracothere' horses include an early diversification of a half-dozen genera (Froehlich 2002). These very early, primitive perissodactyls were small animals, less than 30 cm high, with four toes on the forefoot and three on the hindfoot, short skulls, simple low-crowned cheekteeth and small brains with small frontal lobes. The equid fossil record documents in great detail the successive loss of side toes, the lengthening of the legs and feet, lifting the wrist and ankle high off the ground, the increasing complexity of the cheekteeth, the development of the diastema, the enlargement of the brain, and all the many changes that have led to the modern horse, one of the glories of the world of modern mammals.

Hyracothere horses date from the earliest Eocene of America and Eurasia. They lived in forest and probably had a mixed but mainly herbivorous diet (Radinsky 1969). During the later Eocene and Oligocene, equids were apparently restricted to North America where *Orohippus* (approximately 50 mya), *Epihippus* (47 mya),



Grévy's Zebra *Equus grevyi*, skeleton and myology.

Mesohippus (40 mya) and *Miohippus* (36 mya) became more herbivorous, with concomitant changes in dentition. For example, in *Orohippus*, the last premolar became more molar-like, giving *Orohippus* one more grinding tooth, and in *Epihippus* the last two premolars were like molars, giving *Epihippus* five grinding cheekteeth. *Mesohippus*, and all subsequent horses, had six grinding cheekteeth, and, like *Epihippus*, had well-formed crests on the cheekteeth. In addition, *Mesohippus* was very slightly larger in size at the shoulder, and had three toes on both hind- and on forefeet, the fourth front toe vestigial. *Miohippus* split off from early *Mesohippus* and again was slightly larger, with longer skull.

The early Miocene saw a massive radiation of equids, which ranged from small, duiker-sized browsers, such as *Archaeohippus*, to rhino-sized 'anchitheres' such as *Megahippus* (Simpson 1951). A particularly

successful form, *Anchitherium*, lived in Asia and has been recorded through the Miocene. Lineages that survived into the Pliocene include *Neohipparion* and *Nannippus*, but it was the Miocene *Merychippus* (which arose about 17 mya) or *Protohippus* lineage that seems to have given rise to the extant equids. In *Merychippus*, the brain was notably larger, and overall recognizable as a horse. *Merychippus* also displayed some of the modifications of the lower limbs indicative of progressive adaptation to a more cursorial type of locomotion. It was still three-toed, and the side toes were still complete, though of varying sizes; some species had full-sized side toes, while in others they were smaller and only touched the ground during running. The legs became longer, the radius and ulna fused (eliminating leg rotation), and the fibula was greatly reduced. *Merychippus* had an elongated muzzle and high-crowned cheekteeth, and the teeth were bulked out with cement that surrounded less complex precursors of the crenellated lamellae so typical of living horse and zebra teeth (Simpson 1951).

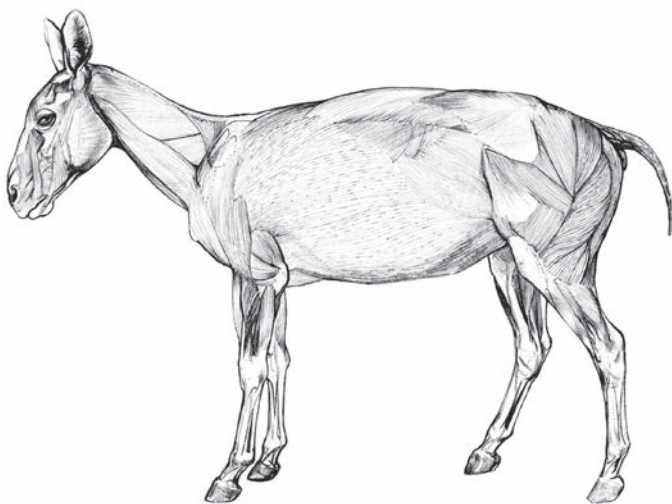
Merychippus gave rise to a line of large equines with small side toes, which in turn gave rise to *Pliohippus*, *Astrohippus* and *Dinohippus*, all of which had lost their side toes. *Dinohippus*, which arose around 12 mya, eventually graded into the modern day genus *Equus*. Members of this radiation only reached Africa in the mid-Pliocene. Within *Equus* there was a radiation that various authors (Hopwood 1936, MacGrew 1944, Groves 1974) have suggested branched into a zebrine lineage living under relatively warm, humid climates (and the living forms of which can be placed under the subgenus *Hippotigris*), *Equus*, a Eurasian subgenus that, after adapting to the onslaught of cold conditions, entered North America (where it displaced the zebrine *E. (H.) simplicidens*), and the subgenus *Asinus*, which evolved in near desert conditions.

Colin Groves

GENUS *Equus*

Asses, Zebras

Equus Linnaeus, 1758. Syst. Nat., 10th edn, 1: 73.



Plains Zebra *Equus quagga* myology.



Equid incisors exposed
(Plains Zebra *Equus quagga*).

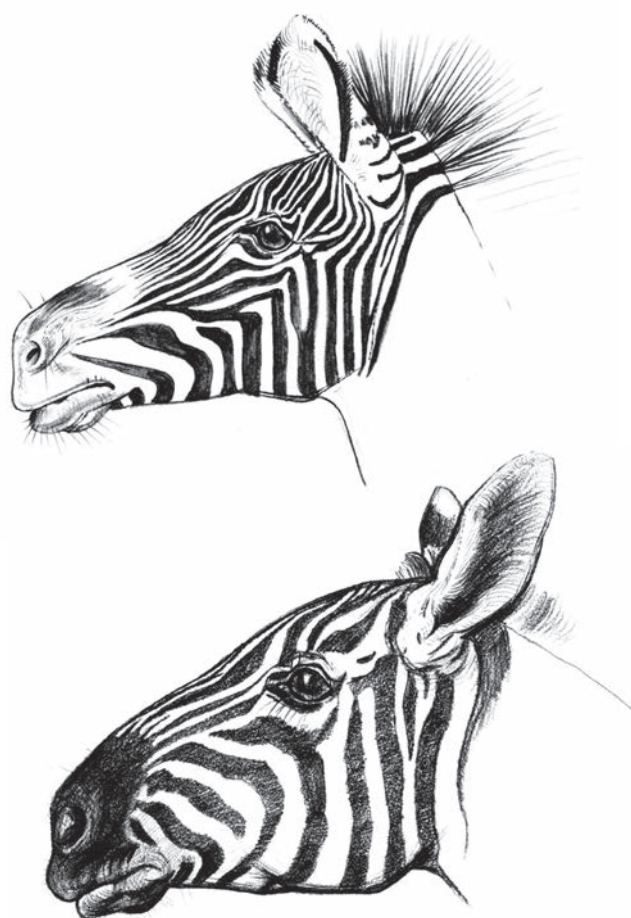
During the Miocene, grasses became a dominant plant form (see illustration in MacFadden 2005) such that in North America by the beginning of the Pliocene (5 mya) savannas and grasslands were more extensive than woodlands. Grazing equids and ruminants expanded into these habitats: the genus *Equus* appeared in North America during the Pliocene, about 4.5 mya, and evolved into 25–30 species, of which seven survive today. A ‘zebrine’ form (*E. stenonis*) colonized the old world by crossing the Bering Strait in the early Pleistocene, 2–3 mya. These animals were replaced in Eurasia by ‘caballine’ and ‘asinine’ species by the late Pleistocene, but descendent forms are thought to have survived in sub-Saharan Africa.

The living members of the genus are divided into three subgenera (Groves & Ryder 2000, Groves & Bell 2004): *Equus*, *Asinus* and *Hippotigris*. Grévy’s Zebra *Equus grevyi* has been included in the subgenus *Dolichohippus* (e.g. Lydekker 1916, Groves 2002), but molecular and morphological evidence reveal its close affiliation with other zebras

(Groves & Ryder 2000). The inclusion here of discussion on the subgenera permits us to explore contentions surrounding the topic of how and why striping evolved in some equids while being lost in others.

The subgenus *Equus* contains the horses, which do not occur naturally in Africa. The only wild horse is the Asian Przewalski’s Horse, *E. ferus przewalskii*, which survived in zoos and has been reintroduced into Mongolia; Przewalski’s Horse is sometimes considered a distinct species (see discussion in Grubb 2005). Subgenus *Asinus* contains the hemionies or onagers, which are strictly Asian, as well as the true asses or donkeys, which includes the African Wild Ass *E. africanus* that was formerly indigenous to an extensive area of northern Africa, but now only survives in sandy and stony deserts in Ethiopia, Eritrea and Somalia. In *Asinus*, the metacarpus is short compared with the metatarsus, and the biischial breadth is high compared with the biacetabular. The coat is striped only on the limbs, or on the shoulder and then only in some populations.

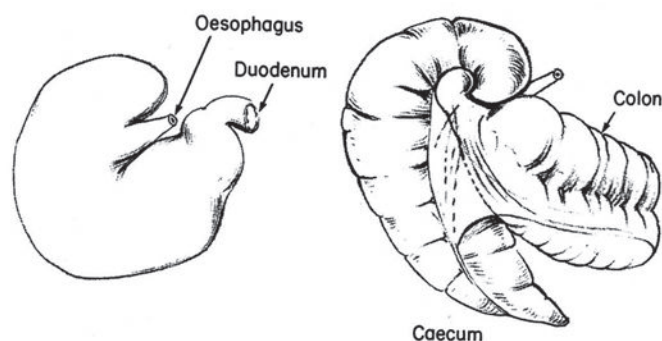
The three species in the subgenus *Hippotigris* (Zebras) are now exclusively African: the *E. quagga* group (Plains Zebra) has the widest range, occurring in mesic savannas and grasslands from the South-West Arid Biotic Zone in southern Africa to the Somalia–Masai bushland Biotic Zone in the Horn. The *E. grevyi* group (Grévy’s Zebra) is confined to the arid and semi-arid savannas of the Horn of Africa (now mainly Ethiopia and Kenya). The *E. zebra* group (Mountain Zebra) contains two subspecies, *E. z. zebra* (Cape Mountain Zebra) and *E. z. hartmannae*



Head of Grévy's Zebra *Equus grevyi* (above); Plains Zebra *Equus quagga* (below).

(Hartmann's Mountain Zebra), which Groves & Bell (2004) regard as distinct species. Members of *Hippotigris* have the metacarpus long compared with the metatarsus, and biischial breadth low compared with biacetabular. Externally, members are distinctly striped at least on head and neck, usually on the whole body. Some authorities regard each of the species groups as forming a separate subgenus (Groves 2002), and the subgenus *Asinus* is occasionally given full generic status.

The living equids are well adapted to eating grasses, have high crowned, very durable teeth, and have survived competition with the highly evolved grazing bovids, such as wildebeest *Connochaetes* spp. and African Buffalo *Syncerus caffer*. In a few systems, like the Makgadikgadi Pans (Botswana), the Plains Zebra is the most abundant medium-sized ungulate. The digestive system of horses (and probably zebras) is more effective at extracting nutrients from grasses than cattle since they eat half again as much grass per day (Ménard *et al.* 2002). Ruminants, however, eat a wider range of plants, and appear to be better adapted for dealing with plant chemical defences, such as terpenes. Zebra populations can be limited by resources (Georgiadis *et al.* 2003); however, at least in ecosystems with high predation pressure, they may suffer heavier predation than do comparable ruminants, wildebeest and buffalo, from the large cursorial predators, such as Lions *Panthera leo* and Spotted Hyenas *Crocuta crocuta*. Equid populations 'turn-over' more slowly than comparable ruminants, which breed earlier in their lives and have shorter gestation lengths (Grange *et al.* 2004).



Stomach and secum of *Equus*.

Equids have contrasting mating systems: in species like Grévy's Zebra, ♂♂ show area-restricted dominance, which resembles the territoriality shown by many ungulates. Plains Zebras and Mountain Zebras have an unusual mating system, which is also found in a few primates like gorillas: dominant ♂♂ acquire and defend harems whose members may stay together for many years. In such harem-forming species, young zebras of both sexes disperse from their natal harem. Feral domestic and Przewalski's Horses show the same social structure and dynamics, and the young ♀♀ leave to avoid incestuous matings. The function of this unusual harem-based mating system is debated: it may allow the ♀♀ to enlist the help of the father of their offspring to combat group hunting predators (like Lions) and/or other breeding ♂♂, which are a potential source of serious harassment. However, functional explanations of variations in equid social and spatial organization and behaviour are today under debate (e.g. Linklater 2000). Equid ♀♀ are polyoestrus, gestation is around 12 months, and parturition tends to be aseasonal, with young being born throughout the year. Maximum longevity in captivity for the various species has been given at between 30 and 60 years, but is typically on the order of 20–25 years for zebras in the wild.

All equid species can interbreed in captivity, including hybrids among zebra species as well as with other Equidae, and produce offspring that, depending on chromosome number, are generally sterile (Roberts 1929, Benirschke *et al.* 1964, Gray 1972, Ryder *et al.* 1978). In the wild, several F1 hybrids and one suspected F2 hybrid between Grévy's Zebra and Plains Zebra are known from ranches in Laikipia, N Kenya. The stripe pattern as well as the behaviour of these specimens exhibits elements of both parent species (Cordingley *et al.* 2009, J. Cordingley pers. comm., H. Klingel pers. obs., and see Grubb 1981). In some areas, such as parts of Zimbabwe, Zebdonks, i.e. hybrids between zebras and donkeys, are not uncommon.

There has, in recent years, been much debate surrounding efforts to bring the extinct Quagga back from extinction, the last individual of which died in Amsterdam Zoo in 1883. Genetic evidence reveals that the Quagga is little more than a subspecies of the extant Plains Zebra *Equus quagga* (Higuchi *et al.* 1984, Leonard *et al.* 2005). Twenty-three preserved skins remain of the extinct Quagga, which reveal that the population displayed much individual variation. Extant Plains Zebra populations also display individual variation, with some individuals displaying characteristics of Quaggas. The project attempts to breed by selection individuals of Plains Zebra, which in external appearance, and possibly genetically as well, will be closer to the Quagga.

Patrick Duncan & Colin Groves

Subgenus *Asinus*

African Wild Ass

Asinus Gray, 1824. Zool. Journ. 1: 244.

The subgenus *Asinus* embraces both the true ass, which is exclusively African (although also claimed from archaeological deposits in the south-western Arabian peninsula) and the Asiatic hemiones, kiangs and onagers. All species inhabit sandy and stony deserts and show some specialization of the hooves, apparently for the particularly tough wear that lower limbs must endure from consistently hard, unyielding substrates. The metacarpus is short compared with the metatarsus, and the biischial breadth is high compared with the

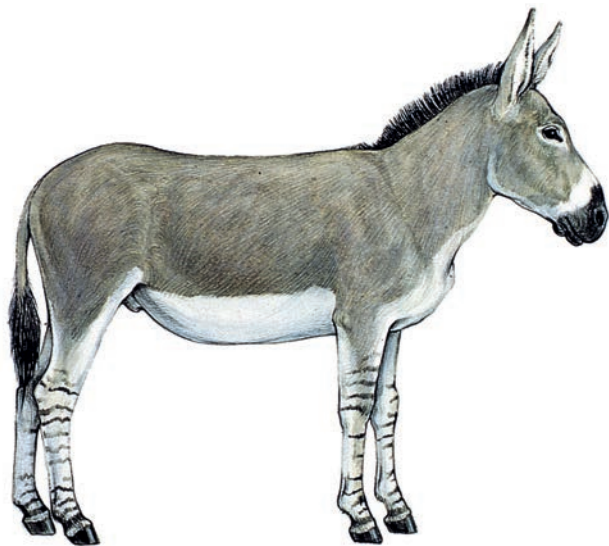
biacetabular. The hoof itself is vertical-sided and leaves a distinctive track. The Asiatic asses (sometimes included in the subgenus *Hemionus*; Groves 2002) have somewhat redder coats than the African ass, which is mainly grey and white and is striped on the lower legs and shoulder (but only in some populations). Such striping could be seen as incipient or vestigial (but see Subgenus *Hippotigris* profile).

Colin Groves

Equus africanus AFRICAN WILD ASS (SOMALI WILD ASS)

Fr. Âne sauvage; Ger. Wildesel

Equus africanus von Heuglin & Fitzinger, 1866. Systematische Übersicht der Säugethiere Nordost-Afrika's mit Einschluss der arabischen Küste, des rothen Meeres, der Somali- und der Nilquellen-Länder, südwärts bis zum vierten Grade nördlicher Breite. Sitzungsberichte der kaiserlichen Akademie der Wissenschaften. Mathematisch-Naturwissenschaftliche Classe, 54: 537–611. Ain Saba, Eritrea (as fixed by Schlawe 1980).



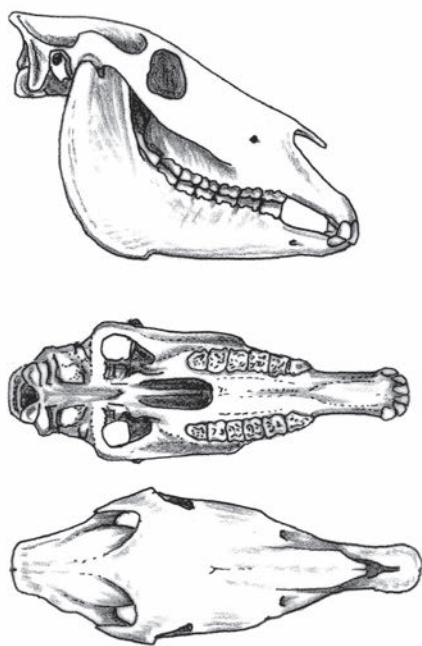
African Wild Ass *Equus africanus*.

Taxonomy The African Wild Ass is the ancestor of the domestic donkey *Equus asinus*. Analyses of ancient DNA (Kimura *et al.* 2011) demonstrate that there are two distinct mitochondrial haplogroups (clades) of domestic donkeys. The Nubian Wild Ass is the ancestor to one of these mtDNA haplogroups; however, the Somali Wild Ass exhibits significant mitochondrial divergence from the Nubian Wild Ass, and both domestic donkey haplogroups, leaving the second ancestor of the domestic donkey undetermined. The earliest archaeological evidence for the donkey, in the Sudan, is dated to 5000 years ago, and only slightly later in Syria and Iran. Phylogenetic analyses suggest that north-east Africa is the most likely location of domestication, and that the donkey might be the only ungulate domesticated solely in Africa (Beja-Pereira *et al.* 2004, Vilà *et al.* 2006). From 4000 years ago, domestic donkeys were brought to Europe by the Greeks in their colonies along the north-east coast of the Mediterranean, and later the Romans distributed them to all parts of their empire.

The International Commission on Zoological Nomenclature ruled (Opinion 2027, March 2003) *Equus africanus*, as the first available name based on a wild population, to be valid for the wild North African ass, and Gentry *et al.* (2004) recommended that *E. asinus* be used for the domestic donkey. Gentry (2006) criticized the incorrect use of the name *E. asinus* for the wild ass by Grubb (2005).

There are two recognized extant subspecies, although there is disagreement as to whether the African Wild Ass is one continuously distributed species exhibiting clinal variation, or if these represent valid subspecies (Ansell 1974, Groves & Willoughby 1981, Groves 1986, Yalden *et al.* 1986). Groves (1986) showed that there is some clinal change from the Atbara population (colour more buffy and shoulder cross thick) via the Red Sea coastal populations (colour greyer, and shoulder cross nearly always thin) to Somalia, and a marked change between N and S Eritrea. A subspecies from North Africa, the Atlas Wild Ass, is depicted in rock paintings and Roman mosaics (such as those from Hippone near Annaba, where one depicts an ass being captured with a lasso by mounted hunters) as having distinct leg stripes and shoulder stripe (often doubled) (Hufnagl 1972, Kowalski & Rzebik-Kowalska 1991, Groves 2002). The name *atlanticus*, often assigned to this form, is unavailable. Groves (2002) lists a third unnamed subspecies, *Equus africanus* ssp. (Saharan Wild Ass), authenticated for Ahaggar, Tibesti and Fezzan, and which is similar to *E. a. africanus*, but smaller and greyer, and with long, thin shoulder cross, but these may actually represent domesticated feral animals (see Kowalski & Rzebik-Kowalska 1991). The nomenclature of African Wild Ass is reviewed in detail by Groves & Smeenk (2007).

Synonyms: *aethiopicus*, *africanus*, *atlanticus* (unavailable), *dianae*, *hippagrus* (unavailable), *nubianus*, *sahariensis* (unavailable), *somalicus*, *somaliensis*, *taeniopus*. Chromosome number: 2n = 62–64, with the most frequently occurring diploid number being 63 (Benirschke & Malouf 1977, Ryder *et al.* 1978, Houck *et al.* 1998). This chromosomal variation is the result of a centric fission accompanied by a heterochromatic deletion. Karyotypes consisted of 34–36 metacentric/telocentric autosomes; the X chromosome is a large



Lateral, palatal and dorsal views of skull of African Wild Ass *Equus africanus*.



Equus africanus

submetacentric, and the Y chromosome a small acrocentric (Houck *et al.* 1998). Hybrids between the two subspecies are fertile.

Description Lean and muscular, grey to reddish-buff in colour with a contrasting white underside and white muzzle with dark grey shading on the nostrils and upper and lower lips. Ears are long and possibly play an important role in heat dissipation. Coat of hair is short and slick and reflects the sun. Both subspecies have an erect, thin mane that is usually pale in colour with a dark terminal border. Thin black dorsal stripe (sometimes absent in *E. a. somaliensis*); the Somali subspecies has distinct leg stripes (less marked, and sometimes absent in Nubian subspecies). Tail tufted. Hooves small and narrow. One pair of nipples.

Groves (2002) describes the skull as being characterized by a very long cranium, short palate, long diastema, squared upturned occipital crest, and wide external auditory meatus. Orbit is high and rounded (not anteroposteriorly elongated as in other species – with the exception of Mountain Zebra *Equus zebra*).

Geographic Variation

E. a. somaliensis (Somali Wild Ass): E Eritrea, NE and E Ethiopia, Somalia. Dorsal stripe sometimes absent (and when present sometimes incomplete); occasionally short, thin shoulder stripes (sometimes absent); and individually distinct leg stripes; ears short; apparently longer legged and shorter bodied than Nubian.

E. a. africanus (Nubian Wild Ass): N Eritrea and NE Sudan. Dorsal stripe present (and nearly always complete from mane to tail-tuft); shoulder stripe only thick in some populations (e.g. Atbara), and sometimes absent; leg stripes sometimes present (and then only restricted to a few bands at the fetlocks); ears longer and thinner.

Similar Species Domestic and feral donkeys often are found in the same habitat as the African Wild Ass. However, domestic donkeys are about two-thirds the size of the African Wild Ass, their coat colour varies from grey to brown to black and they tend to have a longer coat

of hair giving them a 'rough' rather than 'slick' appearance. Domestic donkeys have proportionally shorter legs and cranial length.

Distribution

Historical Distribution During the Pleistocene, the African Wild Ass may have existed in Israel and Syria. Historically, the Atlas Wild Ass was found in the Atlas region of NW Algeria, and adjacent parts of Morocco and Tunisia. It survived in this area until about 300 AD (Antonius 1938). In recent times, there have been reports of wild asses in N Chad and the Hoggar Massif of the C Sahara (e.g. Dupuy 1966; and see Kowalski & RzebiK-Kowalska 1991), but it is doubtful whether these are true wild asses.

The Nubian Wild Ass *E. a. africanus* lived in the Nubian desert of NE Sudan, from east of the Nile R. to the shores of the Red Sea, and south to the Atbara R. and into N Eritrea. During aerial flights in the 1970s, wild asses were seen in the Barka Valley of Eritrea and in the border area between Eritrea and the Sudan.

The Somali Wild Ass *E. a. somaliensis* was found in the Denkelia region of Eritrea, the Danakil Desert and the Awash River Valley in the Afar region of NE Ethiopia, W Djibouti, and into the Ogaden region of E Ethiopia. In Somalia, they ranged from Meit and Erigavo in the north to the Nugaal Valley, and as far south as the Shebele R. A comprehensive review of the historical literature concerning African Wild Ass distribution can be found in Yalden *et al.* (1986) and Bauer *et al.* (1994).

Current Distribution The African Wild Ass is found in Eritrea, Ethiopia and possibly in Somalia. Some animals may persist in Djibouti, but recent surveys have not recorded their presence (Künzel *et al.* 2000). African Wild Asses may still be found in Sudan and Egypt, but their presence has not been documented. In Ethiopia and Somalia the population has been severely reduced, both in population size and range.

Habitat In Ethiopia and Eritrea, African Wild Asses live in arid grass and bushlands of the Great Rift Valley. They are found in a volcanic

landscape and range from rocky mountains (as high as 1500 m) to below sea level in the Dalool Depression.

Abundance In Ethiopia, during the 1970s, African Wild Asses could be found from Yangudi-Rassa N. P. to Mille-Serdo Wild Ass Reserve. At that time there were between 15 and 30 individuals per 100 km². Currently, there are few African Wild Asses left in Yangudi-Rassa and less than 1/100 km² are left in Mille-Serdo Wild Ass Reserve. Even if as many as one individual per 100 km² exists throughout the species' former range (16,000 km²), the population in Ethiopia probably numbers fewer than 160 individuals (Moehlman 2002).

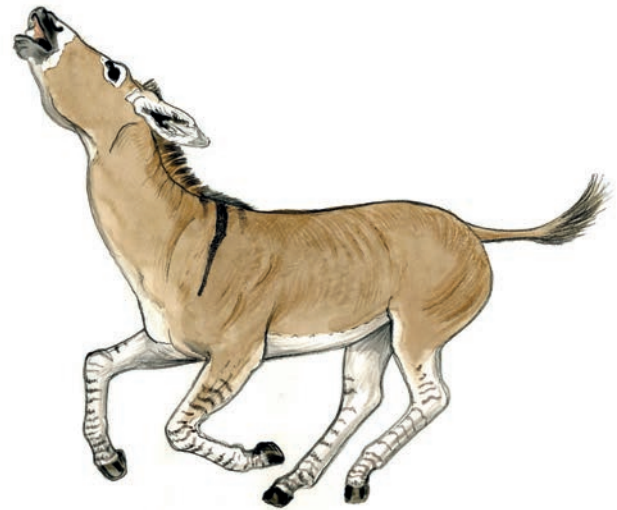
Due to Eritrea's 30-year war for independence, there are no long-term data on African Wild Ass populations for this country. However, recent surveys indicate that viable populations exist in the Northern Red Sea Zone. In this area, the population density is estimated at roughly 47 individuals per 100 km². This is the highest population density found anywhere in the present range of the species and is similar to population densities recorded in Ethiopia in the early 1970s. Given the absence of guns among rural people and the conservation ethic among local Afar pastoralists, the African Wild Ass has good potential for recovery in Eritrea (Moehlman 2002).

In Somalia, in 1997, local pastoralists said that there were fewer than ten African Wild Asses left in the Nugaal Valley; an earlier ground survey in 1989 in the Nugaal Valley yielded population estimates of roughly 135–205 animals or approximately 2.7–4.1/km² (Moehlman 1998). Some animals may remain near Meit and Erigavo, but this area has not been surveyed since the 1970s.

Adaptations Research on domestic donkeys (descendants of the African Wild Ass) has shown that they are physiologically well adapted to life in arid habitats. They can sustain a water loss of up to 30% of their body weight and can drink enough water in two to five minutes to restore fluid loss (Maloij 1970). Tomkiewicz (1979), using temperature-sensitive implants, determined that feral asses varied their body temperature from 35.0 to 41.5°C, depending on air temperature. In hot summer months, ♂♂ had lower mean body temperatures (36.5°C) than ♀♀ (38.2°C). Females maintained higher body temperatures and presumably lost less water due to sweating. A 2°C increase in body temperature could provide a 2% daily water saving in a hydrated 150 kg feral ass. Tomkiewicz (1979) also found that the biological half-life of water for ♀♀ was one day longer than for ♂♂, indicating that their water use was more efficient. Such information indicates that the ancestral species, the African Wild Ass, is probably even more physiologically adapted to life in the deserts of Eritrea, Ethiopia and Somalia. However, the African Wild Ass still needs access to surface water and the movements of lactating ♀♀ are constrained by water availability. During aerial surveys in the Danakil Desert of Ethiopia, most African Wild Asses were observed within 30 km of known water sources.

In a gradient of mesic to arid habitat, the Plains Zebra *Equus quagga* is in the most mesic habitat, Grévy's Zebra *Equus grevyi* is in the drier habitat, and the African Wild Ass survives in the hottest, driest habitat, which also has the lowest plant biomass (Bauer *et al.* 1994). The physiological adaptations of this species allow this equid to live in one of the most extreme habitats in Africa.

Foraging and Food In Eritrea and Ethiopia, limited observations indicate that the African Wild Ass is primarily a grazer, but will also



Male African Wild Ass *Equus africanus* performing 'flehmen' while galloping.

utilize browse (Moehlman *et al.* 1998, Kebede 1999). In Mille-Serdo Wild Ass Reserve the preferred forage is *Aristida* spp., *Chrysopogon plumulosus*, *Dactyloctenium schindicum*, *Digitaria* sp., *Lasiurus scindicus* and *Sporobolus iocladius*.

Social and Reproductive Behaviour In the deserts of Eritrea and Ethiopia, African Wild Asses live in temporary groups that are small and typically comprise fewer than five individuals. The only stable groups are composed of a ♀ and her offspring. Female foals often stay with their mother and are residents in their natal area. Females do associate with other ♀♀ or with ♂♂, but even temporary groups are small. In temporary groups, the sex and age-group structure varies from single-sex adult groups to mixed groups of ♂♂ and ♀♀ of all ages. Adult ♂♂ are frequently solitary, but also associate with other ♂♂. Some adult ♂♂ are territorial, marking (by means of dung piles) and defending large areas for several weeks, and are dominant over conspecifics; only territorial ♂♂ have been observed copulating with oestrous ♀♀. Thus, African Wild Ass exhibit a social organization typical of equids living in arid habitats (Klingel 1977a, Moehlman 1998).

Individuals will form groups when benefits exceed costs in terms of feeding, predation, disease and reproduction. The density, continuity of distribution, and biomass of forage are key factors in the stability of association and the spacing of equids. When forage and water availability allows ♀♀ to be gregarious and form stable groups, then a ♂ can attempt to control access to these ♀♀. Large stable groups are more likely to form when one individual's foraging does not adversely affect a conspecific's foraging. Consequently, closer spacing and larger aggregations are possible when food is abundant. Conversely, low vegetation biomass and food shortages tend to limit group size and stability. This is the case with the African Wild Ass, which lives in an arid, low primary productivity habitat.

In more arid environments, limited food availability (both spatially and temporally) usually does not permit ♀♀ to forage in close proximity and/or to be associated consistently. In dry habitats, equids exhibit the same nutritional and reproductive characteristics (e.g. ♀♀ provide nutrition and ♀♀ tend to come into oestrus asynchronously), which allow ♂♂ to attempt multiple matings, but 'indirectly' control access to the ♀♀. In most cases, they actually control access to a critical resource, i.e. water. In these territorial mating systems, the only stable social group is a ♀ and her offspring.

Thus, the African Wild Ass has a resource-defence polygynous mating system (Klingel 1977a, Moehlman 1998).

Reproduction and Population Structure The African Wild Ass is polyoestrus and foals are usually born from Oct to Apr after a gestation period of 12–13 months. Natality and foal survivorship correlate positively and significantly with rainfall. A known-age African Wild Ass had her first live foal at six years, although ♀♀ are sexually mature much earlier. Females typically have a surviving foal every other year and natality correlates with rainfall during the period of gestation. In captivity the African Wild Ass can live up to 28.5 years (Weigl 2005).

Predators, Parasites and Diseases Spotted Hyenas *Crocuta crocuta* and Lions *Panthera leo* are potential predators, particularly of foals and yearlings. There are no known data on parasites and disease, although *Strongyle* spp. have been recorded in faecal samples collected in the Danakil Desert.

Conservation IUCN Category: Critically Endangered C2a(i). CITES: Appendix I.

The major threat to the African Wild Ass is hunting for food and medicinal purposes, particularly in Ethiopia and Somalia. According to local pastoralists in these areas, body parts and soup made from bones are used for treating tuberculosis, constipation, rheumatism, backache and boneache. The soup is also fed to their livestock to alleviate mineral deficiencies (Moehlman *et al.* 1998). In Eritrea, the Afar pastoralists do not shoot wildlife and guns are strictly controlled. If African Wild Asses were to be adequately protected, then the major remaining threat would be access to water and sufficient forage. Reproductive ♀♀ and their less than three-month old foals are most at risk. Hence, it will continue to be important to determine critical water supplies and basic forage requirements, thus allowing management authorities

to determine (in consultation with local pastoralists) how to conserve the African Wild Ass. In Eritrea, Ethiopia and Somalia, all elders that have been consulted have expressed concern that the African Wild Ass be protected and conserved. A third major threat to the survival of the African Wild Ass is possible interbreeding with the domestic donkey.

In Ethiopia, Yangudi-Rassa N. P. (4731 km²) and Mille-Serdo Wild Ass Reserve (8766 km²) were established in 1969. However, the former has never been formally gazetted, and both areas are utilized by large numbers of pastoralists and their livestock. These areas are remote and extremely arid, and the Ethiopian Wildlife Conservation Organization (EWCO) has not had sufficient funds or personnel for appropriate management (Kebede 1999). In Eritrea, the government designated the African Wild Ass area between the Buri Peninsula and the Dalool Depression as a high-priority area for conservation protection as a nature reserve. There are no protected areas in the range of the species in Somalia.

Populations of Somali Wild Ass are maintained in captivity.

Measurements

Equus africanus

HB: 1950–2050 mm

T: 400–450 mm

HF: n. d.

E: n. d.

Sh. ht: 1150–1250 mm

WT: 270.0–280.0 kg

Kingdon 1997; sample number not given

Key References Kebede 1999; Klingel 1977a; Moehlman 1998, 2002; Moehlman *et al.* 1998.

Patricia D. Moehlman, Fanuel Kebede & Hagos Yohannes

Subgenus *Hippotigris* Zebras

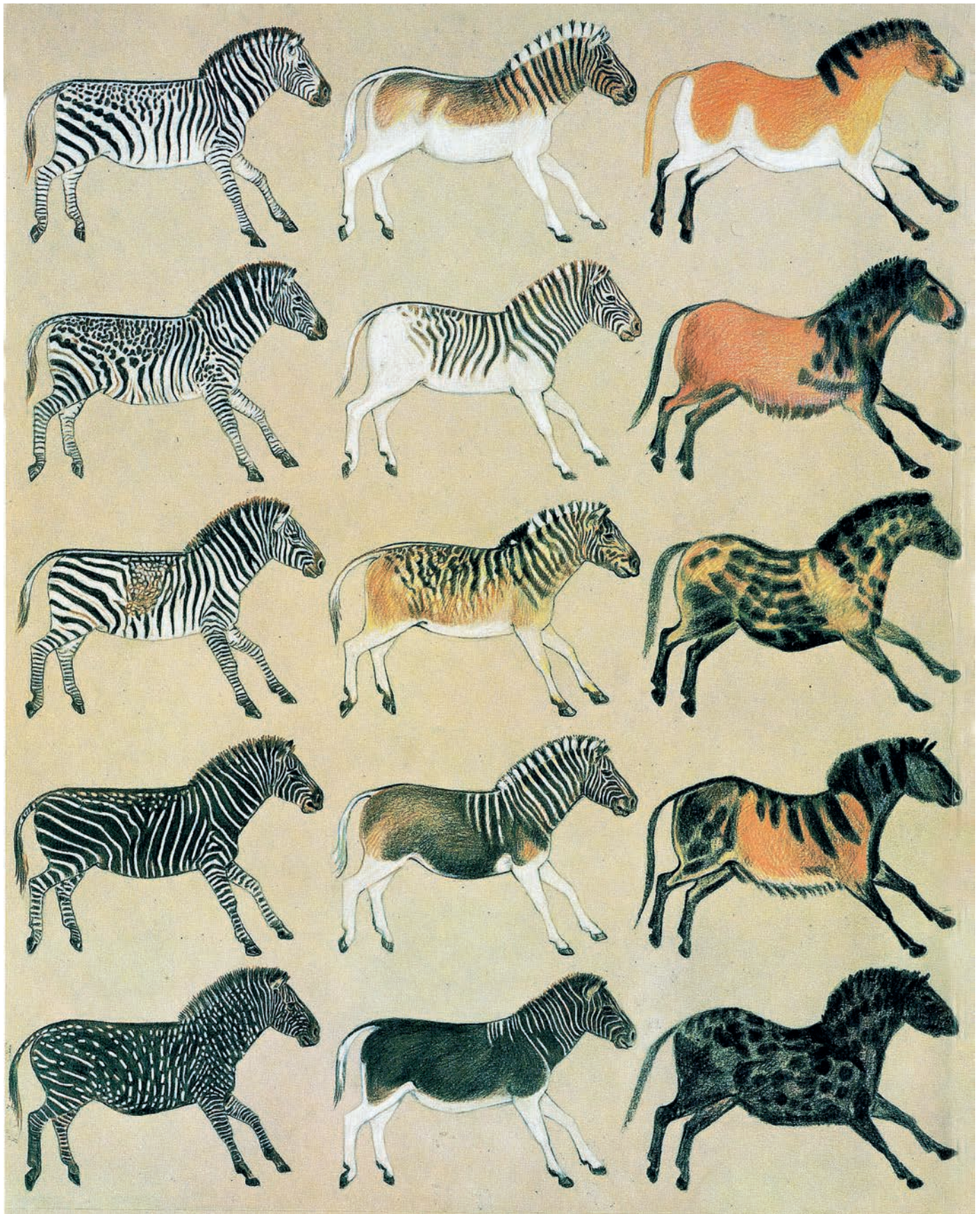
Hippotigris Hamilton Smith, 1841. Jardine's Naturalist's Library, Mamm. 12: 321, pl. 21–25.

The subgenus *Hippotigris* is currently taken to embrace all zebras, the main distinction of which is being wholly or partially striped. The taxonomic name implies a common striped ancestor and an assumption that the various zebra species represent variations derived from that inheritance (whether inclusive of *Equus* and *Asinus* or not; Bard 1977). If all equines had striped ancestors, all the subgenera become redundant (Darwin 1859, Orlando *et al.* 2009).

Striping, whether complete or partial, poses questions of great biological importance so this profile is primarily a discussion as to the possible origins of a visual pattern that is uniquely extreme among mammals, yet is shared to some degree by zebra duikers, zebra finches, zebra fishes and even zebroid insects. The fact that areas of strongly contrasting black and white patterning are found across such a wide range of organisms and presumed functions, reveals that this common, highly conspicuous, visual phenomenon can serve many needs at many different scales. Any universal function for black and white stripes must lie in the peculiar behavioural history of each striped organism and how that behaviour has enlisted optical neurophysiology

in the service of that behaviour. The unstriped relatives of striped animals provide clues to the meaning of striping, and in relation to zebras and horses there are two crucial questions. The first is whether striping is an eccentric embellishment, possibly a convergent one, in a few outlying, even marginal species. The second asks whether striping represents a primary and biologically significant adaptation among an entire lineage of animals, in this case living equids.

Historically, horses and asses were the animal models with which scientifically minded cultures were first familiar; zebras only became an exotic curiosity much later. Even today, zebras remain aberrant animals in minds and vocabularies, engendering a popular folklore that has inhibited serious scientific investigation of an important phenomenon. This legacy is evident in numerous attempts (most of them casual, some even cavalier) to link striping with supposed or real environmental oddities of Africa (Ruxton 2002). Striping, across many taxa of vertebrates and invertebrates, has evolved to be registered in the eyes of whatever animal is most likely to be a beholder; furthermore, for most striped fauna, 'beholders' (or visual signal receptors) are much



Polymorphism in three equine populations. First column, *Equus quagga boehmi*; second column *Equus quagga quagga* (from skins, photos and contemporary paintings); third column *Equus ferus*, from palaeolithic rock paintings in Dordogne (courtesy of Natural History Museum library, London).

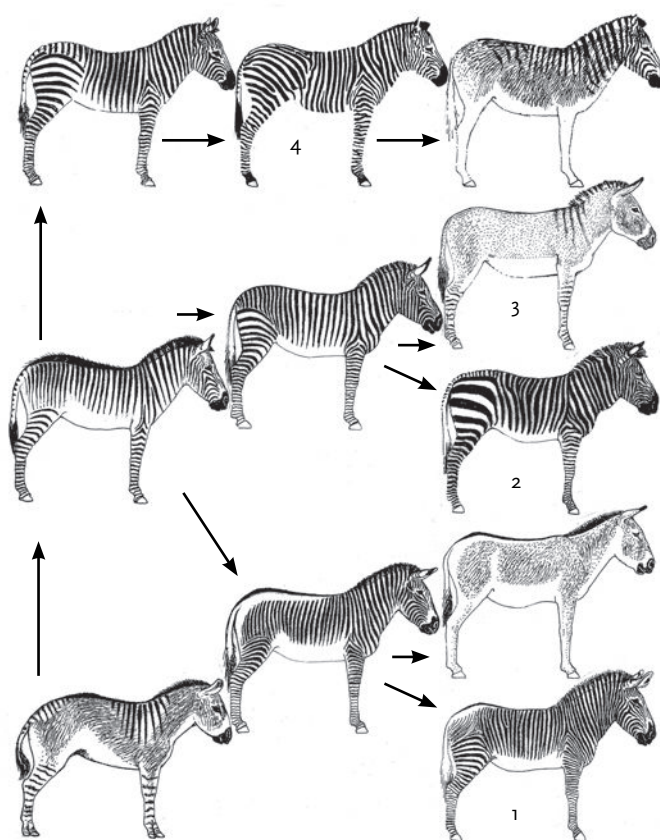
less likely to be predators, competitors or parasites (e.g. Waage 1981) than conspecifics. Thus intra-specific behaviour and the susceptibilities of eyes are the most promising starting points for any enquiry into the primary role of stripes in animals (Gibson 1966).

Several horse, ass and zebra studies have tended to seek out and emphasize differences between species, especially in relationships between ♂♂ and ♀♀ (e.g. Klingel 1967, 1972, Joubert 1972a, Tyler 1972). In spite of such differences within their social systems, zebras actually share some significant behavioural, ecological and biogeographic characteristics that differentiate them from horses and asses. In their wild form, horses were polymorphic animals living at variable densities, and adapted to very cold seasonal temperate climates in the northern continents, while monomorphic asses were mainly desert and near-desert animals living at low densities. Zebras, by contrast, often live at very high densities and originally occupied a very broad spectrum of less extreme, tropical and sub-tropical grassy environments, most of them subject to much seasonal or periodic fluctuation in climate and resources. In terms of ecological zoning, horses and asses occupied the least benign zones, while zebras formerly dominated the prime habitats. In this respect a striking peculiarity of all zebras, and one that is clearly adaptive for fluctuating resources and unpredictable densities, is the ease with which they move, congregate or disperse, often within the space of a single day.

Zebras are famously 'social' in that they can join up with hundreds of other zebras or jostle with herd antelopes at a water source or pasture and then break up into much smaller units. In contrast with other herbivores, notably antelopes (which expend much energy and time in elaborate socio-sexual behaviour), social ties between individual adult zebras are generally remarkably loose and fluid. Time spent on social interaction is more expensive for non-ruminant zebras, which have to cover much more ground and spend about twice as much time grazing as their ruminant equivalents because they have to pass more grass, at a faster rate, through their digestive tract. Adult zebras seem able to bypass elaborate social behaviour and abbreviate their interactions with other zebras and this exceptionally easy coming and going is facilitated by the adults of both sexes lacking any lasting attachments, particularly to members of their own sex. Yet male zebras fight fiercely over oestrous ♀♀ (Klingel 1968a, Joubert 1972a) and latent intolerance is also implicit in diminished or rudimentary attachments among adult ♀♀. By contrast, female zebras and their most recent offspring (and young zebras of similar age) have intense attachments that are most obviously expressed in much mutual nibbling.

A young zebra, growing up beside its mother, and with other neighbouring zebras, is no different from horses, asses, or any other social young animal in associating its mother with milk and its fellows with the security of living within a group, but it differs very strongly in its visual environment. From birth onwards, it is, like any other mammal, 'learning to see', but what it sees within a zebra herd is fundamentally different. In the early stages of visual learning, orientation-selecting neurons are particularly important, and black and white stripes (particularly vertical ones, which are efficient signallers of horizontal movement) are known to activate a set of early-stage, direction and orientation-selective neurons and few other visual stimuli are able to trigger such strong responses (A. Hurlbert pers. comm.).

The presence of stripes introduces an exceptionally assertive type of visual stimulation into the young animal's world and this difference from other, un-striped animals is emphatically not trivial (Kingdon



Stripe patterns on five extant equids and hypothetical ancestral patterns (numbers indicate the likely sequence of ancestral arrival/evolution in Africa): *bottom left*, beginnings of common ancestral pattern; *middle left*, common ancestor of all surviving *Equus* species; *top left*, ancestral pattern for Plains Zebra *Equus quagga*; *top middle and top right*, *Equus quagga* ssp.; *middle centre* common ancestor of African Wild Ass *Equus africanus* and Mountain Zebra *Equus zebra* (to right); *middle bottom*, common ancestor of Kiang *Equus kiang* and Grévy's Zebra *Equus grevyi* (to right).

1984). Anyone who has watched zebras attentively will have become aware that eyes have to work overtime to accommodate to their every movement. Each time an animal changes the angle of its body the eye registers the vertical stripes *actually* getting wider or narrower (depending on how close to broadside it is) while horizontal stripes, instead, keep a similar width. Research has shown that individual visual nerve cells in mammals are programmed to respond to certain primary properties of the seen environment and different cells register different properties (Blakemore 1971). Thus, the process of seeing is essentially modular and is mediated by large batteries of specialized visual receptors (Gibson 1966, Mollon 1974, Zeki 1993). Research has also shown that black and white stripes can trigger an identifiable selection of these specialized visual neurones, notably those that register: (a) brightness contrast; (b) colour contrast; (c) edge contrast; (d) edge orientation; (e) spatial frequency; (f) direction of motion; and (g) temporal flicker (Zeki 1993). In real life it is likely that this battery of receptors play their narrow roles as part of the machinery of seeing, helping eyes and brains to extrapolate such useful information as directional movements and distance and thus contribute to making sense of the total environment. Because zebra stripes are unambiguously a visual phenomenon it becomes important to recognize that the complicated processes of seeing, and responding to what is seen, enlist just such a range of separate,

specialized receptors. Somehow, zebras have evolved a pattern that isolates such visual responses from their normal environmental contexts. Black and white stripes represent a sort of abstraction of what eyes are hungry to see!

Strong physiological responses can be stimulated in mammalian eyes by patterns that successfully isolate the particulate, component-specific properties of cells within the visual cortex. Stripes, particularly vertical stripes, trigger responses in early-stage, motion-selective neurons, which are functionally tuned to register the direction of motion (A. Hurlbert pers. comm.). It is this specialization of visual neurons that is central to the proposal that the overall striping of zebras has evolved in *direct* response to the *separate* sensibilities of these neurons. Also central to this concept is the detachment of striping from individuality, manifest in the observable conditioning, of young zebras, to respond indiscriminately, and with every sign of being 'attracted' to stripes, regardless of their 'owner'. As it matures, the young zebra seems to find almost any fellow zebra attractive and they can even be drawn towards zebras of another species (behaviour that is particularly frequent among Plains Zebras *Equus quagga* and Grévy's Zebras *E. grevyi* in Laikipia in Kenya). More important, especially for its general application to the evolution of visual signals of all sorts, the suggestion here is that visual signals are effectively 'designed' in the eyes of their beholders – in this case, the eyes of other zebras.

Central to understanding the evolution of stripes is relating their beginnings to their function in the behavioural repertoire. There may have been some shifts over time but some continuity must be expected. Stripes could, of course, have derived from the alteration of some pre-existent pattern with stripes aligning themselves out of, say, a scatter of cryptic spots and squiggles, such as are common on many juvenile mammals and birds that need to hide from predators. Additionally, or alternatively, striping in zebras could have begun with exaggeration of some detail of surface morphology that was significant in the behavioural repertoire of the zebras' common ancestor. A scan of the behaviour of contemporary zebras offers hints as to what that detail might have been and suggests an explicitly social function for stripes. The clue comes from one of the few easily observed signs of 'friendliness' among zebras (Kingdon 1979, Cloudsley-Thompson 1984).

Skin-nibbling is integrated into the single most important affiliation in zebra society, namely the mother–young bond. Directly and indirectly, that bond is likely to provide the social glue that holds zebra societies together. Furthermore, zebras do not nibble at random; they approach, nose to nose and prefer the point where the neck meets the shoulder above all other sites, although the root of the tail and lower rump are also popular. Of course, mothers, partly because they are so much taller, have little choice but to nibble the base of their offsprings' manes and backs (which in itself might have established a very early taste for being nibbled on the shoulder and explain its universality among equids). Young foals, instead, cannot reach their mothers' shoulders and must be content with her legs, flanks and face, but the preference for nibbling shoulders is evident in the interactions of similar-aged foals.

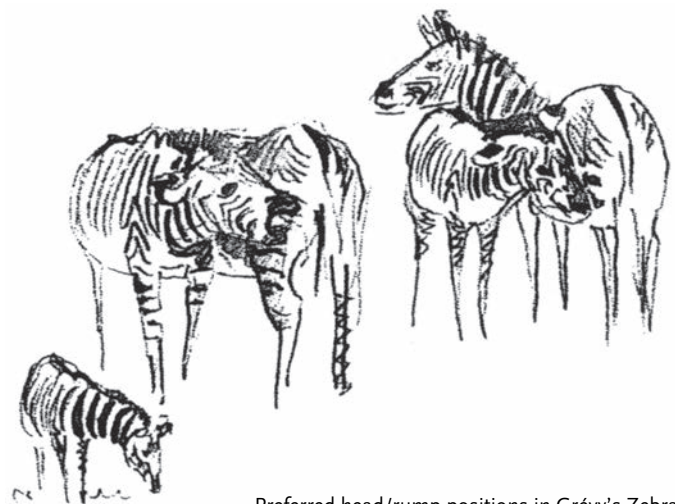
In adopting mutual skin-nibbling as a bonding device zebras resemble some primates and many other social mammals that have appropriately shaped incisors in both jaws. The fact that tactile grooming is such a basic feature of social relations, especially for ♀♀ and their young, yet declines as the animal matures is an anomaly

that has evolutionary implications that, in turn, raise larger questions about the underlying mechanisms that have shaped zebra society. Because body-grooming with the incisor teeth is such a widespread bonding behaviour among many different orders of mammals, assuming similar habits in early equid ancestors is not unreasonable.

The most striking feature of the neck–shoulder junction is that the skin has to be fairly loose there to accommodate to a lot of neck movement. This looseness gives rise to vertical folds or skin wrinkles, which would be unremarkable were it not for the fact that many organisms respond to, or need, just such visual markers to help direct their species-specific behaviour. When such attention-attracting foci become 'target areas' it is not uncommon for them to be visually advertised. Therefore, ancestral equids would have been conforming with a very widespread phenomenon had they evolved light and dark vertical streaks to exaggerate and advertise the vertical skin folds on their shoulders. Knowing that all equids still target the shoulder for grooming and that the majority of species (always or sometimes) have striped shoulders makes it plausible that this preferred 'target area' was the starting point for stripes. Projecting that connection back into evolutionary time to suggest that stripes spread out and away from the shoulders, making the entire animal one huge, three dimensional 'target area' (which living zebras, indeed, *are*), is completely consistent with the functional behaviour of living zebras.

Early equids were relatively small and probably lived permanently on small, exclusive territories as vulnerable browsers, but there was a general trend toward larger body sizes. While some conservative types probably continued in closed habitats the lineage that led to modern equines became mobile grass eaters living in much more open grasslands and savannas, a change evidenced by a progressive elongation and deepening of fossil skulls, ever more hypsodont teeth and progressive elongation and simplification of the limbs (Simpson 1951, Radinsky 1969). A major correlate of this shift into more open habitats would have been greater sociality, a behavioural change that must have been inhibited and complicated by many millions of years of largely solitary existence.

The evolutionary conversion of previously solitary or territorial species into ones that are able to live in large, aggregated groups is generally recognized as being problematic and some of this literature is summarized in the profiles of social carnivores and rodents such as



Preferred head/rump positions in Grévy's Zebra *Equus grevyi* ('empty chewing' by partner on left).

mole-rats. In zebras the fact that young animals are more tactile than adults and some suggestive changes in their behaviour as they mature hint at an extraordinary transformation in social behaviour. The one-on-one tactile bonding of mother and foal, or colt with filly, changes into a more superficial but socially very effective type of visual bonding in which *any* zebra becomes attractive. The sequences of this transformation can be observed in the behaviour of free-living zebras as well as extrapolated from other sources. These have been detailed in Kingdon (1979) but can be summarized as follows.

The browsing ancestors of zebras were unlikely to have had any more than discrete, striped 'target areas' on their shoulders, but the proposed, unique optico-neurological effects of stripes, as described earlier, might, even then, have had a unique 'conditioning' effect on the physiology of nibbling partners. This effect was to associate neuro-physiological sensation (induced by stripes that dominated the visual field of the nibbler) with social interactions that can look quite 'trance-like' to a human observer. The transition from actual nibble-grooming to non-tactile partner-seeking can be observed in the behaviour of maturing Plains Zebras. Nibbling involves small nodding movements of the head (remember that movement, in viewer or viewed, intensifies the physiological impact of stripes) and young zebras can be seen nodding and champing, sometimes centimetres away from their partner, sometimes a metre or more. 'Empty chewing' and head nodding are the clearest indications that a switch in sensory channels is taking place: from tactile to visual. It is at this stage that the young zebra begins to find any other zebra attractive.

A small panel of stripes may have first induced a close-up visual reward, but the social benefits of finding another equine 'attractive' would have exerted real selective pressure for the striped area to expand, thus enlarging the distance at which their physiological sensations could take effect. The progressive evolution of stripes and their refinement would have been based on a preference for heightened contrast and well-defined edges and spacing, in the eye or visual cortex of the viewing zebra. This preference can be predicated on the fact that stripes are powerful visual signals and that any movement is automatically stimulating for the eye. Even when no more than a single stripe is visible in close-up, a single sharp edge should still be sufficient to trigger a strong response in the (nibbling) viewer; a panel of multiple stripes amplifies the effect.

Optimal distances between zebras are a topic in their own right and it is sufficient here to note that there is some evidence that zebra species differ in their preferred inter-zebra spacing: Grévy's Zebras prefer to stand closer than 2 m, while Plains Zebras tend to stand more than 2 m apart (Kingdon 1979, Cloudsley-Thompson 1984). If the spacing of stripe patterns correlates with species-specific behaviour and species prefer particular frequencies or conformations then optimal spacing of individuals may well have a visual component.

The ontogenetic sequences that can be observed in living zebras parallel and approximate to a sequence of evolutionary changes. These effectively allow zebras to convert a one-on-one tactile bond into a multiple-partner visual bonding system. This interpretation helps explain how zebra stripes have evolved to promote the very peculiar social flexibility that is characteristic of zebra societies. Striping may have been a key adaptation for many more ancestral equines than those currently treated as 'tiger-horses' *Hippotragus*.

Jonathan Kingdon



Grévy's Zebra *Equus grevyi* 'empty chewing'.



Accommodations for horizontal leg stripes to vertical body stripes in: (a) Grévy's Zebra *Equus grevyi*; (b) Mountain Zebra *Equus zebra*; (c) hypothetical common ancestor; (d) hybrid *E. grevyi* × *E. zebra*.

Equus grevyi GRÉVY'S ZEBRA

Fr. Zèbre de grévy; Ger. Grevy-zebra

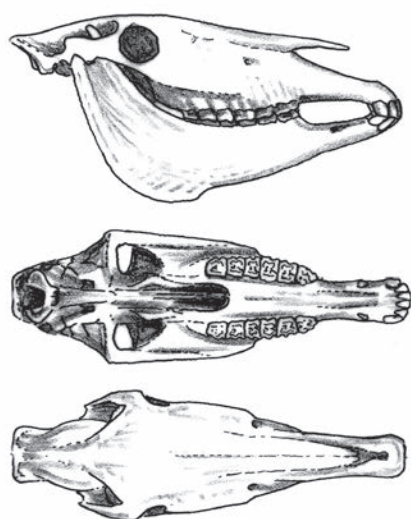
Equus grevyi Oustalet, 1882. La Nature, Paris 10 (2): 12. Described as 'region de l'Afrique orientale qu'on appelle le pays des Gallas', restricted to Awash Valley by Yalden *et al.* (1986).



Grévy's Zebra *Equus grevyi*.

Taxonomy Sometimes included in the subgenus *Dolichohippus* (see Groves 2002). Pocock (1902) described a subspecies of Grévy's Zebra (*berberensis*) that has sometimes been regarded as distinct, although the feature on which it was described (brown rather than black stripes) is an age-related feature (Groves & Bell 2004). Groves (2002) provisionally listed two subspecies of Grévy's Zebra: *Equus grevyi grevyi*, from the northern part of the range, and an unnamed subspecies in the south (with localities in Meru, Ewaso Ng'iro and Lngayo Water). However, Groves & Bell (2004), analysing a small sample of Grévy's Zebra skulls, concluded that the species is indeed monotypic. Synonyms: *berberensis*, *faurei*. Chromosome number: $2n = 46$, with 32 metacentric and 12 acrocentric; both X and Y are metacentric or submetacentric (Benirschke & Malouf 1977, Ryder *et al.* 1978). Cordingley *et al.* (2009) report evidence of natural hybridization between Grévy's Zebra and Plains Zebra *Equus quagga* in Laikipia in C Kenya. All first-generation hybrids were the offspring of Plains Zebra ♀♀ and Grévy's Zebra ♂♂. Two hybrids successfully raised foals to over 3 months of age, including one that reached adulthood, indicating the fertility of female hybrids and viability of their offspring.

Description The largest extant wild equid. Long-legged and long-faced, with characteristic large, ovoid ears. Muzzle brown with white margin before fine black and white stripes. Neck broad with thickest stripes on body. Mane thick and upright, black and white although tips appear black. Body uniformly striped with a chevron at shoulder and haunch. Flank stripes fine and vertical, tapering out at a level above elbow, leaving belly white. Dorsal and ventral black stripes present. Dorsal stripe broad and prominent, particularly over rump where a white margin increases in breadth. Leg stripes dense and merge at fetlock. Stripes on hindquarters curl down from dorsal stripe around hindquarters and taper out leaving buttocks white. Dorsal stripe continues on tail. Sexual dimorphism slight, with ♂♂ weighing 10% more than ♀♀ (King 1965). Males and ♀♀ easily distinguished (notably more so than Plains Zebra) by conspicuous black labia of ♀♀. Foals' stripes brown and less defined than those of adults. Foals' stripes turn black and become more defined as they age, starting with neck and ears, followed by head and limbs, and finally ending with flanks. Dorsal stripe remains brown-black and fluffy for up to two years. One pair of nipples.



Lateral, palatal and dorsal views of skull of Grévy's Zebra *Equus grevyi*.

Groves (2002) mentions a number of characteristic cranial features, including: a very elongated skull, exceeding the cervical spine in length (unlike other subgenera); occiput high and raised; postorbital constriction deep; muzzle and vomer long; and nasal end of the premaxilla rounded and wedged into the nasal. Males have large upper and lower canines, absent in ♀♀.

Geographic Variation See Taxonomy.

Similar Species

Equus quagga. Only species that may be confused because of range overlap in N Kenya. Relatively smaller; head shorter; ears small and pointed; muzzle black; stripes broad, particularly over flanks and hindquarters; hindquarter stripes curl up from ventral stripe back across hindquarters towards buttocks.

Distribution Confined to arid and semi-arid areas of the Horn of Africa, specifically Ethiopia and Kenya.

Historical Distribution Historically, Grévy's Zebra ranged east of the Rift Valley in Kenya (Stigand 1913, Stewart & Stewart 1963) to W Somalia, and from Alledeghi Plain, through the Awash Valley, the Ogaden, and north-east of L. Turkana in Ethiopia to north of Mt Kenya and south-east down the Tana R. in Kenya. There are no confirmed records from Eritrea (Yalden *et al.* 1986, Bauer *et al.* 1994), nor from Djibouti (though mentioned by Simoneau 1974) or adjacent Somaliland.

Current Distribution Today, Grévy's Zebra has a highly discontinuous range, being found from the eastern side of the Rift Valley in Kenya to the Tana R. There is a small, isolated population east of the Alledeghi Plains north-east of Awash N. P. in Ethiopia. From L. Ch'ew Bahir in S Ethiopia, the population is not contiguous, but extends to just north of Mt Kenya although a few animals are found further south-east along the Tana R. There is a small population in and around Tsavo East N. P. in Kenya that was introduced in the 1970s. They are considered to be extirpated from Somalia (where the last confirmed sightings date to 1973); sightings from S Sudan require confirmation (Williams 2002). Over the past four decades, Grévy's Zebras have



Equus grevyi



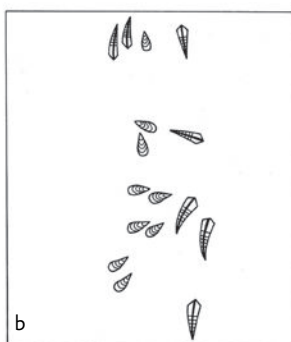
Variations in the width of stripes in Grévy's Zebra *Equus grevyi*.

expanded their range onto the Laikipia Plateau, primarily for anthropogenic reasons.

Habitat Grévy's Zebras live in arid and semi-arid (annual rainfall range 100–650 mm) grass/shrubland where there is permanent water (Klingel 1974, Rubenstein 1986, Rowen & Ginsberg 1992, Williams 2002). The lack of free-standing water ultimately limits their incursion into more arid areas to the east and north, while competition with other grazers, including Plains Zebras, may limit their distribution into more mesic areas (Bauer *et al.* 1994). Yalden *et al.* (1996) recorded them to 1600 m in Ethiopia. Human presence, including corrals and small hamlets, also limit the area available for Grévy's Zebras, affecting both their use of water and rangelands (Williams 1998, Sundaresan *et al.* 2008).



Two examples of bispecific association among zebras: (a) having clumped after a scare, a grazing 'fan' forms in Grévy's Zebra *Equus grevyi*; (b) grazing association, note tendency to form parallel pairs in both spp.



Abundance Grévy's Zebras have undergone significant declines in numbers. In Kenya, a 70% decline in the population took place between 1977 and 1988 (13,700 to 4276 animals, respectively; Rowen & Ginsberg 1992, and references therein). A subsequent survey of N Kenya in 2000 indicated that the number of animals declined to between 2500 and 3000 (Williams 2000); this estimate was later revised to between 1600 and 2000 animals surviving in Kenya (Williams & Low 2004). The largest subpopulation, estimated to harbour over 90% of the global population, is found at the southern end of their range in Kenya; this subpopulation ranges from Lewa to Samburu N. R. from south to north, and from Garba Tula to the Laikipia plateau from east to west. A recent aerial survey of this Laikipia–Samburu subpopulation resulted in an estimate of 2400 animals (Litoroh *et al.* 2010).

A population decline of a similar order of magnitude was also recorded in Ethiopia: the population was estimated at approximately 1500 in 1980 (Klingel 1980, Rowen & Ginsberg 1992), while aerial surveys in 1995 suggested a total of only 500–600 animals (Thouless 1995a, b). Recent counts put the population at perhaps no more than 120 individuals, indicative of a 93% decline in numbers in Ethiopia since 1980 (Williams *et al.* 2003).

In total, then, it is estimated that there are no more than 2700 Grévy's Zebras remaining in the wild.

The density of animals fluctuates seasonally as animals move in their search for resources. During the wet season, the zebras are widely dispersed. During the dry season, when they are dependent on permanent water, they are more concentrated. However, given that they can move up to 35 km from water even during the dry season, their densities are never high. They are most abundant and most easily observed in the southern end of their range in Kenya, where they reach 2.4 animals/km² (S. D. Williams pers. obs.).

Adaptations The physiological adaptations to living in hot arid and semi-arid areas are largely unknown, partly due to lack of detailed research. However, it has been recorded that mares without foals only need to drink every five days (Becker & Ginsberg 1990). In addition, they display behavioural characteristics that may facilitate their survival in such an environment. They will rest – in the shade if it is available – during hot, midday periods. During the dry season, as water availability declines, they have been observed to dig in dry river beds to access water (Klingel 1974, S. D. Williams pers. obs.). Finally, the facultative ability of ♀♀ and bachelor ♂♂ to be highly mobile has been interpreted as an adaptation to the unpredictability of their environment (Williams 1998).

It is thought that foals are energetically constrained (see Reproduction and Population Structure; Rubenstein 1989, Williams 1998) and foals



Characteristic ovoid ears and broad neck stripes (left) and rump 'target' design (right) of Grévy's Zebra *Equus grevyi*.

will not travel to water with their mothers but remain in 'kindergartens' up to 8 km from water (Klingel 1974, Rubenstein 1989, Becker & Ginsberg 1990, Rowen 1992, Williams 1998). While in a kindergarten, foals are vulnerable to predation. Foals display no specific anti-predator behaviour (Klingel 1974), although an adult may sometimes remain with them.

Foraging and Food Grévy's Zebras are predominantly grazers, with preferred grass species including *Cynodon dactylon*, *Pennisetum mezianum*, *Aristida adscensionis*, *Chloris virgata* and *Chrysopogon plumulosus*. In stressed conditions, such as during times of drought, browse (e.g. *Sericocomopsis* spp., *Salsola* spp., *Disperma* spp.) can comprise as much as 30% of their diet (Rowen & Ginsberg 1992). Like other equids, Grévy's Zebras make decisions about where to feed and the time spent feeding (43–62% of the time depending on reproductive condition; Ginsberg 1988) to maximize their intake rates. During the dry season or in overgrazed areas, they feed in swards with the highest biomass (Ginsberg 1988, Williams 1998). These swards are often patches with high fibre grasses (e.g. *Pennisetum* spp.) that are not tolerated by domestic livestock. The level of fibre may become intolerable to the zebras, at which point they disperse, often over large distances, in search of other pastures (Ginsberg 1988, Williams 1998). Consequently, with food availability becoming less predictable with overgrazing of areas by domestic livestock in recent times, Grévy's Zebras were recorded in recent studies to be moving during the dry seasons as they were recorded to do only in droughts in earlier studies (Ginsberg 1988, Williams 1998).

In more mesic areas into which Grévy's Zebras have recently expanded their range, different reproductive classes were recorded to make different habitat selections with bachelor ♂♂ and lactating ♀♀ choosing shorter, greener swards than other reproductive classes (Sundaresan *et al.* 2008).

Free-standing water is a requirement of their diet. In much of their range, this is in the form of springs. In the absence of pastoral people (thus, in protected areas), Grévy's Zebras drink in a four-hour time window at the middle of the day, probably to reduce the risk of predation at water sources. In areas used by pastoral people, they are excluded from the use of water during the day and drinking shifts to night-time (Williams 1998).

Social and Reproductive Behaviour Grévy's Zebras are social animals. They form two types of association, depending on reproductive condition and resource availability. Females with young foals are typically predictable in their patterns of association, forming relatively stable groups with other ♀♀ with whom they are in reproductive synchrony (Ginsberg 1989, Becker & Ginsberg 1990, Rowen 1992, Sundaresan *et al.* 2007b). They also may associate more strongly with one ♂ to reduce male harassment (Sundaresan *et al.* 2007a). Females without young foals (and ♀♀ with foals in overgrazed areas) are relatively less predictable (although more so than some other species of equid – e.g. Onagers *Equus hemionus onager*; Sundaresan *et al.* 2007b). Their associations are fluid since their movements are determined by the availability of resources. Group composition can, therefore, be unstable and can change on a daily basis (Klingel 1974, Ginsberg 1989), implying that decisions of habitat use and association are being made at the level of the individual. Group size is variable (range 1–>150 animals). Territorial ♂♂ are often solitary although they will associate with conspecifics and other animals (including those of other ungulate species such as Beisa Oryx *Oryx beisa*, Giraffe *Giraffa camelopardalis* and Plains Zebra).

Recorded home-range size of non-territorial individuals is up to 10,000 km² (Ginsberg 1988, Rowen & Ginsberg 1992, Williams 1998). They are extremely mobile and individuals have been recorded to move distances of greater than 80 km, sometimes returning to the original area within weeks (Williams 1998). Their movements are determined by resource availability. During the wet season, when not constrained by available water, they disperse. As the dry season progresses, their ranges contract around water sources. During droughts they can disperse huge distances in search of food and water (Ginsberg 1989, Williams 1998). During dispersal episodes resulting from depleted food, different reproductive classes have different thresholds. Females without young foals disperse first as they are not constrained to remain in the vicinity of water. If food resources continue to decline, mares with young foals also disperse often leaving only territorial ♂♂ (Williams 1998). Territorial ♂♂ will disperse only in extreme conditions when resources dictate and will be the first individuals back into an area following the onset of the wet season (Klingel 1974, Ginsberg 1988, Williams 1998).

Breeding ♂♂ defend resource territories (water and food being the key resources) of 2–12 km² distributed in a mosaic across the landscape. The formation of territories may have evolved in response to the distribution of ♀♀, although the possession of a territory is not a guarantee for reproductive success, and thus ♀♀ do not visit all areas of the territory mosaic (Klingel 1974, Ginsberg 1989). They have a high degree of territorial fidelity and may hold territories for up to seven years (Ginsberg 1988). Territorial ♂♂ are generally larger than other ♂♂ (Ginsberg 1989). They mark their territories with dung piles that are not necessarily placed on the periphery of territories but are often found on paths that are frequently used by

other zebra (for example, those to and from water sources; Ginsberg 1988). Territorial ♂♂ also advertise their tenure of a territory using a characteristic vocalization that could be described as a very loud bray followed by a strangled squeak. They also advertise using a distinctive upright posture. The territorial ♂♂ tolerate the presence of bachelor ♂♂ but will chase them in a ritualized manner when an oestrous ♀ is present (Klingel 1974, Ginsberg 1988). Fighting between ♂♂ is uncommon although bachelor and territorial ♂♂ will often spar to establish a dominance hierarchy (Ginsberg 1988).

In contrast to the ♂♂, the reproductive condition of the ♀ determines her resource requirements and thus distribution relative to resources. Thus, when the distribution of grazing allows it, lactating ♀♀ are found predictably closer to water than other classes of ♀♀ and they typically associate with and mate with one ♂ whose territory has access to water (Ginsberg 1989, Rowen 1992, Williams 1998). However, in large parts of their range, where forage is sparse (or where the first 6–7 km from water has been altered by overgrazing by domestic livestock), lactating ♀♀ must move large distances (up to 13 km; S. D. Williams pers. obs.) to and from water to reach adequate grazing (Williams 1998). This means that they move through a number of territories, which, in turn, means that they may mate with many ♂♂. Non-lactating, cycling ♀♀ are similarly typically promiscuous, moving through numerous territories in search of adequate resources and, therefore, mating with many ♂♂.

Male behaviour is dependent on female behaviour (and, therefore, reproductive condition) and they will display mate-guarding with promiscuous ♀♀. During courting, a territorial ♂ will repeatedly mount the ♀ in oestrus, with neither an erect penis nor intromission, while braying and squealing loudly. When intromission does occur, copulation is always silent. Following copulation, ♀♀ will eject up to 300 ml of the ejaculate. Sperm competition and female promiscuity within the species is thought to lead to the large volume of seminal fluid (Klingel 1974, Ginsberg 1989, Ginsberg & Rubenstein 1990).

Foaling has rarely been observed and is assumed to occur primarily at night and away from the herd. Lactating mares and newborn foals rapidly join a nursery herd that remains as close to water as possible. These nursery herds can be stable for up to three months, but in areas where water and grazing are separated by large distances (e.g. in areas where the areas close to water are heavily overgrazed), they tend to be less stable.



Grévy's Zebra *Equus grevyi* braying; note whiskers.



Grévy's Zebra *Equus grevyi*.

Play in foals occurs only when they are in good condition (Rowen 1992). Thus, in the late dry season or droughts, or in overgrazed habitats, play is rarely seen. Unlike other equid species, allogrooming is very rare among individuals of this species.

Vocalizations in reproductive classes other than territorial ♂♂ are uncommon. Bachelor ♂♂ rarely vocalize (J. R. Ginsberg pers. comm.). Mares that become separated from their foals will call with a soft bray, similar to that of the territorial ♂♂, but quieter and without the strangulated squeak (S. D. Williams pers. obs.). When returning from water, mares will also call and their foals will answer (Klingel 1974, S. D. Williams pers. obs.).

Reproduction and Population Structure Breeding is highly dependent on stochastic patterns of climatic variation (Ginsberg 1988, Williams 1998). Females in poor body condition enter anoestrus during times of low resource availability (Ginsberg 1989). A peak in oestrus among ♀♀ follows the onset of high resource availability (usually the wet season), which results in a peak in births 13 months later (Williams 1998).

Over 90% of recorded copulations are by territorial ♂♂ (Ginsberg 1988). Levels of urinary androgens are higher in territorial ♂♂ than for either non-breeding ♂♂ or breeding ♂♂ that abandon their territories. Urinary androgen concentration for a territorial ♂ is, in



Grévy's Zebra *Equus grevyi*.

turn, negatively correlated with the time since ♀♀ last visited his territory (Chaudhuri & Ginsberg 1990).

Gestation period is 58 (range 55–61) weeks (King 1965). Mares give birth to a single foal (probably more often at night) and come into oestrus between 6 and 15 days post-parturition. Oestrus lasts 4–7 days (Asa *et al.* 2001). If they are not impregnated, they will continue to cycle every 27 days ($26.8 \pm \text{S.E. } 0.28$, $n = 9$; Bennett 1980, Ginsberg 1989), but longer in captive animals (28–35 days, Asa *et al.* 2001). Because breeding is dependent on climatic conditions, inter-birth intervals are highly variable. Mean inter-birth intervals for Grévy's Zebras have been recorded as 16.2 months (Williams 1998).

Lactation can continue for up to a year, but most foals are weaned by an average of 11.4 months (Becker & Ginsberg 1990, Rowen 1992). Foals stay with their mothers for up to two years. Wild zebras mature and breed later than captive animals. The youngest first foaling in captivity was recorded at three years and four months (Asa *et al.* 2001). In the wild, ♀♀ may breed only slightly later than captive animals. In contrast, ♂♂ that take over territories are thought to do so only when they are approximately seven years old (Ginsberg 1988).

It is thought that there is an equal sex ratio at birth. However, because of the increasing foal mortality, the mean mare : foal ratio is high (2.74 mares for every foal over a three-year study; S. D. Williams pers. obs.).

Sources of mortality have not been fully determined. However, recent studies have shown that juvenile mortality is critical (Williams 1998). Foal survival has been directly related to the extent to which their mothers move: there is low foal survival when mares make large or frequent small-scale movements (Rowen 1992, Williams 1998). This supports the suggestion that foals are energetically constrained.

One wild-born specimen was about 31 years old when it died in captivity (Weigl 2005).

Predators, Parasites and Diseases In areas where densities of Lions *Panthera leo* are high, such as on the Laikipia Plateau and on the Lewa Wildlife Conservancy, their impact on Grévy's Zebra populations is profound (D. I. Rubenstein pers. comm.). Outside of these areas, the impact of predation is largely unknown, although it is probably low as predator densities – including Lions – are reduced due to poisoning campaigns (using acaricide) by pastoral people (S. D. Williams pers. obs.). None the less, in these areas, Cheetahs *Acinonyx jubatus* and

Spotted Hyenas *Crocuta crocuta* are known to take foals, and Nile Crocodiles *Crocodylus niloticus* take adults (Rowen & Ginsberg 1992, S. D. Williams pers. obs.). In addition, in areas with pastoral people, water sources are generally monopolized during daylight hours. This excludes zebras, which are, therefore, forced to drink at night. This exposes unprotected foals in kindergartens to nocturnal predators.

Little is known about diseases that affect Grévy's Zebras, but Muoria *et al.* (2007) recorded an outbreak of anthrax in the Wamba area of southern Samburu, Kenya, between December 2005 and March 2006, during which 53 Grévy's Zebra succumbed to anthrax. Babesiosis has been recorded in a free-ranging animal due to transmission from the tick *Rhipicephalus evertsi* (Pipano & Tadmor 1978). Muoria *et al.* (2005) examined faecal samples of Grévy's Zebra for gastrointestinal parasites, and found *Trichostrongylus* sp. present in 78% of the samples; other parasites occurring in high frequencies were *Oesophagostomum*, *Haemonchus contortus* (which is highly pathogenic to small ruminants), *Entamoeba coli* cysts and *Balantidium coli* cysts. Data on the impact of these species on Grévy's Zebra are lacking. Endoparasite loads are particularly great when animals are in poor condition (S. D. Williams pers. obs.).

Conservation IUCN Category: Endangered A2ac. CITES: Appendix I. CMS: Appendix I.

Legally protected in Ethiopia. Protected by hunting ban since 1977 in Kenya. The range of Grévy's Zebra has shrunk dramatically as a result of hunting (Ethiopia, Somalia and E Kenya), exclusion from water sources by pastoral people and habitat loss through vegetation change and erosion that result from overgrazing (throughout their range). It has been suggested that hunting for skins in the late 1970s may have contributed to the decline in Kenya (R. Elliott pers. comm.). However, since the CITES listing in 1979, the killing of Grévy's Zebras for their skins seems to have ceased. Recent data suggest that the decline in Kenya is continuing although at a slower rate because recruitment is very low due to low juvenile survival. This is a result of competition for resources – both food and access to water – with pastoral people and domestic livestock (Williams 1998). However, there remains a low level of hunting of Grévy's Zebras for food and, in some areas, medicinal uses (S. D. Williams pers. obs.). In Ethiopia, by contrast, killing of Grévy's Zebras using abundant semi-automatic weapons is the primary cause of the decline.

Besides exclusion of Grévy's Zebras from water sources by pastoral people, the water supply in critical perennial rivers has also declined, most notably in the Ewaso Ng'iro R. in Kenya, where over-abstraction of water for irrigation schemes has reduced dry season river flow by 90% over the past three decades (Williams 2002). This leads to dramatic reduction in the dry season range of Grévy's Zebra (Williams 1998). In contrast, Grévy's Zebras are increasing in numbers on the Laikipia Plateau in Kenya, which, historically, may have been a marginal area for them (Williams 2002). In these areas (and particularly the Lewa Wildlife Conservancy), they are protected and competition with domestic livestock is reduced as cattle are managed to favour wildlife. They have, therefore, been successfully increasing since they first expanded into this area in the early 1970s.

The conservation of Grévy's Zebra and its fragile arid ecosystem are inseparable. For the continued survival of Grévy's Zebra, it is imperative that critical resources on which the zebras depend remain accessible and sufficient to meet their nutritional requirements.

This is predominately dependent on activities of agriculturalists in highland areas and pastoral people in lowlands. These people determine levels of water abstraction for irrigation and domestic livestock management and stocking rates, and thus, by extension, the range and growth, respectively, of Grévy's Zebra populations.

Hybridization with Plains Zebra has been discussed as a potential threat to Grévy's Zebra in Laikipia, although Cordingley *et al.* (2009) argue that, based on behavioural observations, this is unlikely to dilute the Grévy's Zebra gene pool in the short term.

It is also essential that the small, isolated populations of N Kenya and S Ethiopia are protected. Community conservation approaches are probably the best means of achieving some level of protection. At present, protected areas form less than 0.5% of the range of Grévy's Zebra. In Ethiopia, the protected areas are only nominal (Alledeghi Wildlife Reserve, Yabello Sanctuary, Borana Controlled Hunting Area and Chalbi Sanctuary). In Kenya, the Buffalo Springs, Samburu, Shaba N. R. complex and the private land wildlife conservancies on the Laikipia Plateau provide a core and crucial protection of Kenya's southern population of Grévy's Zebras. These areas will be increasingly important to their persistence (Williams 2002). Other protected areas in Kenya appear to be ineffective. These include Sibilo N. P., where

they are now rare, and the nominal Losai N. R. The Grévy's Zebras that were translocated to Tsavo (Tsavo East in 1964 and Tsavo West in 1977) have not been seen in either protected area for some years and only a small number (<20) have been seen in ranches to the east of the National Parks.

Measurements

Equus grevyi

HB: 2.50–2.75 m

T: 0.50–0.75 m

HF: n. d.

E: n. d.

Sh. ht: 1.25–1.50 m

WT (♂♂): 385.8 (352.9–430.9) kg, n = 9

El Barta Plains, Kenya (Ledger 1963)

Key References Churcher 1993; Ginsberg 1988, 1989; Klingel 1974, 1980; Rowen 1992; Rowen & Ginsberg 1992; Rubenstein 1989; Sundaresan *et al.* 2008; Williams 1998, 2002.

Stuart D. Williams

Equus quagga PLAINS ZEBRA (COMMON ZEBRA)

Fr. Zèbre des Plaines; Ger. Steppenzebra

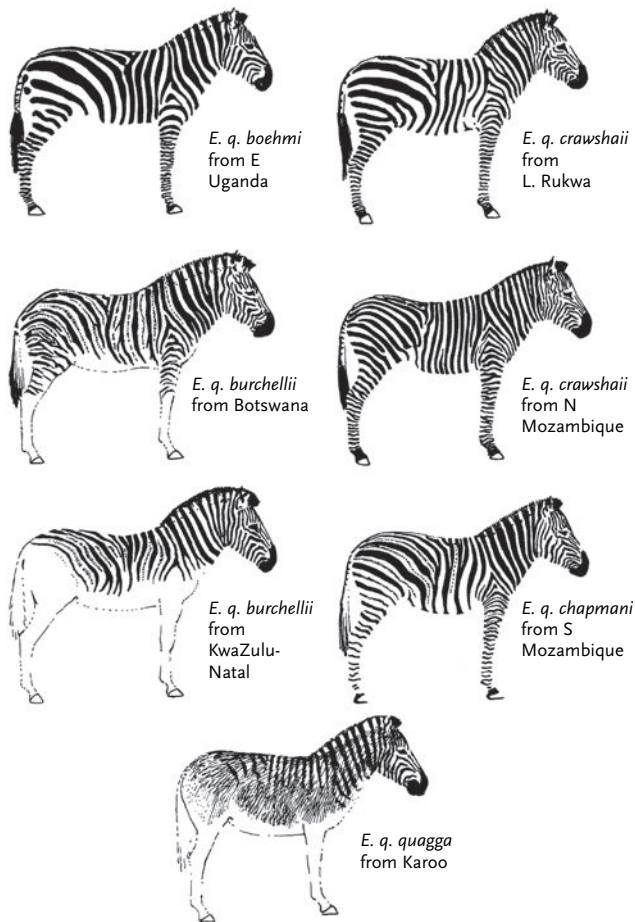
Equus quagga Boddaert, 1785. Elenchus Animalium 1: 160. 'Caffrorum regione'; locality paralectotype now identified as Seekoei R., Colesburg District, Northern Cape Province, South Africa (Grubb 1999).



Plains Zebra *Equus quagga* *crawshaii*.

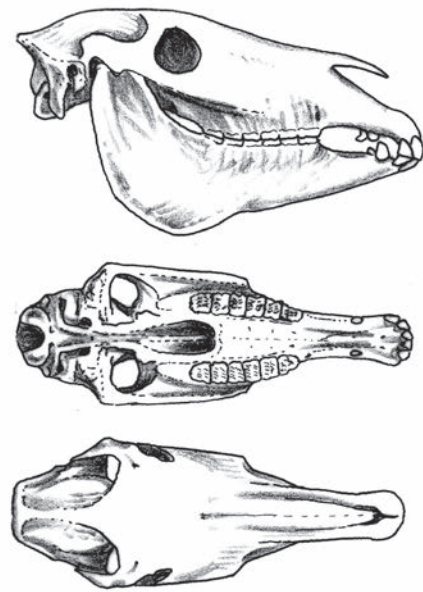
Taxonomy The close genetic relationship of the true Quagga with other Plains Zebras (for which the name *E. burchellii* is commonly used) has been established, indicating the desirability of extending the species *E. quagga* to include all Plains Zebras (Rau 1978, 1986, 1997, Higuchi *et al.* 1984, George & Ryder 1986, Harley 1988, Leonard *et al.* 2005;

but see Bennett 1980, Klein & Cruz-Urbe 1999). Type localities, anatomical details and general characters are given by several authors, including Pocock (1902), Antonius (1951), Grubb (1981, 1999), Groves & Ryder (2000), Groves (2002) and Groves & Bell (2004).

Plains Zebra *Equus quagga*.

A revised subspecies classification, long under discussion (e.g. Ansell 1974, Grubb 1981, Groves & Ryder 2000, Groves 2002), was presented by Groves & Bell (2004), who recognized six subspecies, based on coat patterns, skull metrics (see Measurements) and the presence or absence of a mane and of the infundibulum on the lower incisors. Intergrades are observed. However, molecular studies involving mtDNA and microsatellites failed to distinguish between the six described subspecies and no structuring was found that might be indicative of localized evolutionary units (Lorenzen *et al.* 2008). The latter authors remarked that Plains Zebra showed the lowest overall differentiation recorded in any African ungulate studied so far. The only other species showing a similar absence of genetic structuring is the African Buffalo *Syncerus caffer*, but which lacks the high levels of morphological variation present in the Plains Zebra.

Synonyms: *annectans*, *annectens*, *antiquorum*, *boehmi*, *borensis*, *burchellii*, *burschellii*, *campestris*, *chapmani*, *chapmanni*, *couagga*, *crawshaii*, *crawshayi*, *cunninghamei*, *danielli*, *elongatus*, *festivus*, *foai*, *goldfinchi*, *granti*, *greyi*, *isabella*, *isabellinus*, *jallae*, *kaokensis*, *kaufmanni*, *lorenzi*, *lylei*, *mariae*, *markhami*, *mauretanicus*, *muansae*, *paucistriatus*, *platyconus*, *pococki*, *qouagga*, *quaccha*, *selousi*, *simplex*, *simplicissimus*, *tabeti*, *tigrinus*, *transvaalensis*, *trouessarti*, *typicus*, *wahlbergi*, *zambeziensis*, *zebroides*. Chromosome number: $2n = 44$; there are 17 pairs metacentric and four pairs acrocentric autosomes, and the X chromosome is submetacentric while the Y is a small acrocentric chromosome (Benirschke *et al.* 1963, Heinichen 1969a, 1970, Hsu & Benirschke 1971). Compared with Grévy's Zebra *Equus grevyi*, the Plains Zebra

Lateral, palatal and dorsal views of skull of Plains Zebra *Equus quagga*.

has an extra pair of metacentric chromosomes, but lacks two acrocentric pairs.

Description Muscular equid with relatively short neck, sturdy legs and characteristic striping. Ears are pointed, muzzle is comparatively blunt and tapered. Mane varies from thick and long to short and thin, and sometimes is absent altogether. Stripe patterns are prominent in the northern subspecies, but less so in the south; shadow stripes, brownish stripes between the dark stripes, are thin or absent in the north and wide and prominent in the south. Ground colour is white in the north and cream or buffy in the south. Forelock and mane are thin to absent in the northernmost populations, e.g. Kidepo N. P. in NE Uganda and SE Sudan, and well developed in the southern populations. Body stripes are broader than in Grévy's Zebra and the Mountain Zebra *E. zebra*, although less so in the Cape Mountain Zebra *E. z. zebra*, which has particularly wide stripes on the rump; rump stripes do not meet the dorsal mid-line, while in the northern populations, and many individuals in the southern populations, the stripes extend to the ventral mid-line. Very light individuals with pale stripes only (but not albinos), as well as melanistic individuals with reduced stripe patterns, occur. The basic character of the stripe patterns, width, simplicity versus complexity, i.e. forks, spots, short stripes, is inherited (H. Klingel pers. obs.). Patterns from various subspecies and populations are published in Cabrera (1936), Antonius (1951), Rau (1974, 1978), Kingdon (1979, 1997) and Schürer (1999). Stripe patterns are individually unique and photographic file card systems have been used successfully for identification in the field (Klingel 1965a, 1967). Legs are striped to the hooves in northern populations, but not, or not clearly, in southern ones. Anterior part of tail without tail hair (as in all equids except the horse). There is little sexual dimorphism, although stallions average slightly larger than mares and with thicker necks. One pair of nipples.

Braincase large, forehead markedly convex, with relatively thick and broad zygomatic arches. Ear bullae small relative to the size of the skull; paroccipital process thick and well developed. Postorbital constriction relatively narrow. Mandible massive, deep and wide. The premaxilla curves downward below the level of the alveolar line of the

cheekteeth (Grubb 1981, Groves 2002). Males have larger spade-shaped canines, whereas in mares the canines are lacking or vestigial. Upper incisors have infundibular patterns that change shape with wear and eventually disappear; in the lower incisors, these patterns are absent or reduced to a simple cup in most northern populations, but more usually present in southern ones. Molars deeply hypsodont. Tooth eruption and wear patterns are similar to those of the Horse *Equus ferus* – the first molar is the first tooth to develop, the third incisor the last – and have been used for ageing (Erz 1964, Klingel 1965b, Klingel & Klingel 1966b, Smuts 1972, 1974a).

Geographic Variation

E. q. crawshayi (including *annectens*, *foai*) (Crawshay's Zebra): Zambia, east of the Luangwa R., Malawi, SE Tanzania from L. Rukwa east to Mahungoi, and Mozambique as far south as the Gorongosa district. Large size; stripes numerous and narrow, with five or more stripes meeting the belly stripe; shadow stripes absent, and leg stripes complete and unbroken to hooves; body tone white to off-white; infundibula on lower incisors absent or reduced to a cup.

E. q. borensis (Half-maned Zebra): NW Kenya, from Guas ngishu and L. Baringo to the Karamoja district of Uganda and SE Sudan, east of the Nile R. to the northern limit of the species at 32° N. Similar to *E. q. boehmi*, but larger, more sexually dimorphic, and mane absent or reduced in adult ♂♂; short diastema, and infundibula, on limited evidence, seem to be absent.

E. q. boehmi (including *cunninghami*, *goldfinchi*, *granti*, *isabella*, *jallae*, *mariae*, *muansae*, *zambeziensis*) (Grant's Zebra or Boehm's Zebra): Zambia, west of the Luangwa R., west to Kariba, Shaba Province of DR Congo north to Kibanza Plateau; Tanzania north from Nyangau and Kibwezi into SW Uganda, SW Kenya as far as Sotik, and E Kenya, east of the Rift Valley, into S Ethiopia and perhaps to the Juba R., Somalia. Smallest subspecies; striping pattern broad, with stripes down to hooves; shadow stripes poorly expressed or absent; infundibula on lower incisors often absent. The small, entirely maneless zebras of the Juba region, Somalia, may prove to be a separate subspecies.

E. q. chapmani (including *kaufmanni*, *markhami*, *pococki*, *selousii*, *transvaalensis*) (Chapman's Zebra): NE South Africa, from about 24° S, 31° E, north to Zimbabwe, west into Botswana at about 19° S, 24° E, the Caprivi Strip in Namibia, and S Angola. Largest subspecies; ground colour not pure white; legs striped thinly to the hooves; shadow stripes prominent on haunches, and usually on neck; snout short and narrow; infundibulum usually cup-like but may be complete.

E. q. burchellii (including *antiquorum*, *campestris*, *festivus*, *isabellinus*, *kaokensis*, *paucistriatus*, *typicus*, *zebroides*) (Burchell's Zebra): formerly north of the Vaal and Orange Rivers, extending north-west via S Botswana to Etosha N. P. and the Kaokoveld in Namibia, south-east to KwaZulu–Natal and Swaziland. Now extinct in middle of range. Stripes reach haunches, sometimes upper parts of limbs; one or two shadow stripes on haunches; small, narrow skull with broad, long marston. Size increases from south-east (KwaZulu–Natal) to north-west (Etosha N. P.); Etosha zebra are nearly as large as *E. q. chapmani*.

E. q. quagga (including *couagga*, *danielli*, *greyi*, *lorenzi*, *quagga*, *quaccha*, *trouessarti*) (Quagga): former Cape Province, south of the Orange and Vaal Rivers and west of the Drakensberg; extinct since



Quagga *Equus quagga quagga*.

the end of the nineteenth century (ca. 1883). Stripes only on neck and back, legs unstriped and white; ground colour dark cream to brown (Pocock 1902, Cabrera 1936, Antonius 1951, Ansell 1974, Groves 2002, Groves & Bell 2004; for colour plate see Kingdon 1979 and Smithers 1983).

Plains Zebras have in the recent past been re-introduced in many farms and protected areas in southern Africa. The stock was often taken from different populations disregarding the subspecific identities and producing an undesirable and unnatural mix. Breeding groups of these mixed types have also been exported to zoological gardens.

Similar Species

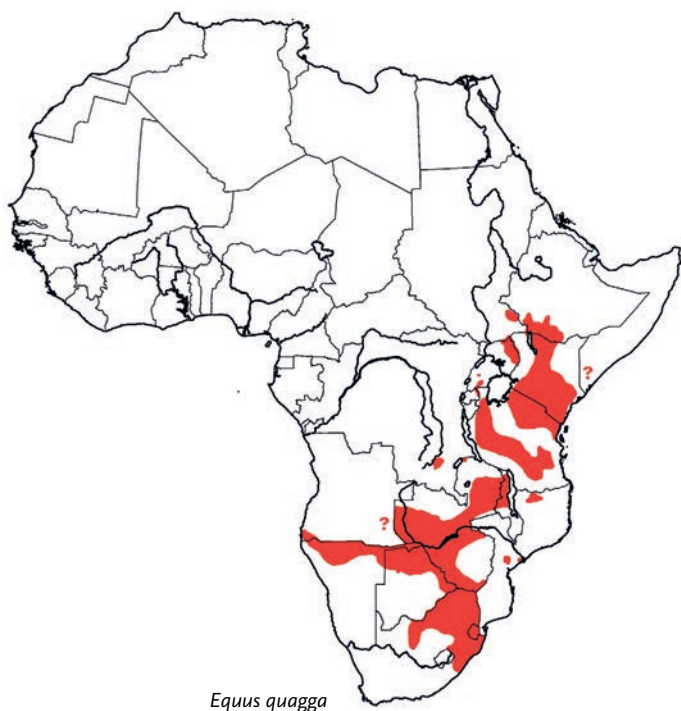
Equus zebra hartmannae. Slightly bigger; dewlap present; narrow black stripes on white background, with grid-iron pattern across rump; belly white; ears pointed. Namibia, esp. Naukluft, Namib, Kaokoveld.

E. z. zebra. Smaller than *E. z. hartmannae*, ♂ smaller than ♀ (the size of a KwaZulu–Natal *E. q. burchellii*); broader muzzle, longer diastema and nasal bones, very broad black stripes and narrow white interspaces. Western Cape and Eastern Cape of South Africa.

E. grevyi. Much larger; fine stripe pattern; adults with black, young with brownish stripes on off-white background; prominent dark dorsal stripe with longer hair; big round ears. N Kenya to S Ethiopia.

Smuts & Penzhorn (1988) describe a number of structural differences between the skulls of the Plains and Mountain Zebras in detail; most important is the uniquely rectangular shape of the foramen magnum. Differences between Plains and Hartmann's Zebras are described by Eisenmann & de Giuli (1974).

Distribution The Plains Zebra is one of the more successful African ungulates, ranging from S Sudan and S Ethiopia to N Namibia and N South Africa (and formerly south of the Orange and Vaal Rivers to the Cape). The species is now extinct in two countries in which it formerly occurred, namely Lesotho and Burundi; there is no current information on their status in Angola where they may also be extinct (Hack *et al.* 2002). In the recent past, Plains Zebras have not occurred west of the Nile R. However, from the early Pliocene



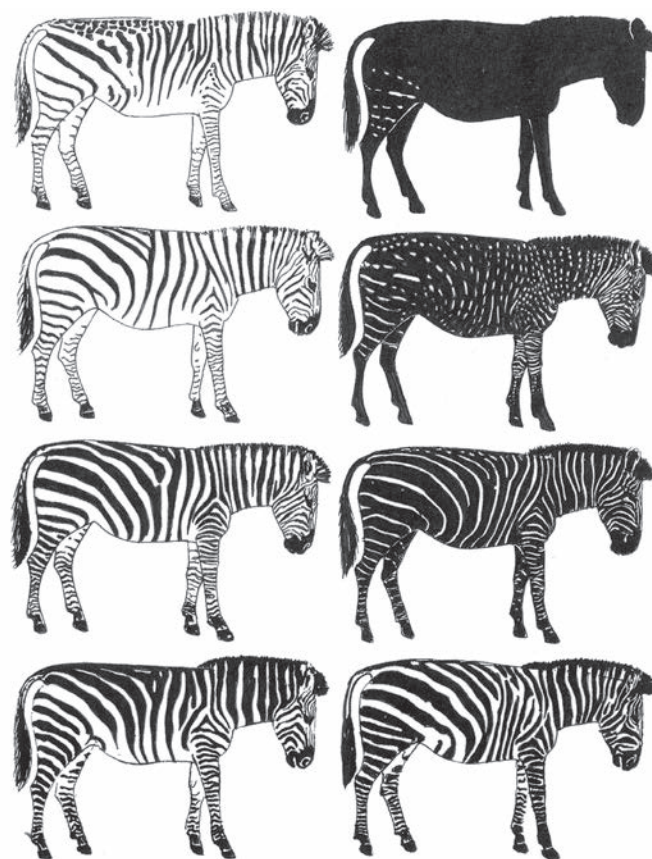
Equus quagga

to the Holocene the species extended over almost the whole African continent. Fossil remains are known from North Africa (Morocco, Algeria, Tunisia, Mali, Libya) to the Cape (Churcher & Richardson 1978).

Habitat Suitable habitats include grasslands and grassland–bushland mosaics (from humid to mesic environments); also present in miombo woodland. On Mt Kenya, Plains Zebras occur up to 4300 m, and individual home-ranges can cover up to 1000 m in altitude (Coe 1972; see also Young & Evans 1993). Absent from the Congo basin rainforest, and from dune desert. Water is an essential habitat requirement, and they seldom move more than 12 km from water sources.

Abundance Locally common throughout its range in protected areas, but also outside protected areas, especially in Kenya and Tanzania. Total numbers may be in the region of 660,000, possibly up to 1 million, with some 200,000 Plains Zebras in the greater Serengeti/Mara ecosystem in N Tanzania and adjacent Kenya (East 1997, Hack *et al.* 2002). The Serengeti migratory subpopulation of >150,000 individuals concentrates during the rains from Nov to May in the Serengeti plains. At the beginning of the dry season in Jun it migrates to the western and northern parts of Serengeti N. P. and adjacent areas, and into Masai Mara National Reserve in Kenya. During the migration it overlaps to some extent with resident populations (1) of the western Serengeti N. P., (2) of the Masai Mara National Reserve in Kenya, and (3) of the Loliondo area north-east of the Serengeti N. P. During the rains, in the Ol Balbal depression south-east of the Serengeti plains, it overlaps with parts of the Ngorongoro population that have moved in from the Crater (Klingel 1969a, pers. obs.). Besides the Serengeti/Mara ecosystem, other current major populations are those in: Kajado/Amboseli (Kenya) – 50,000; Manyara/Tarangire (Tanzania) – 40,000; Laikipia (N Kenya) – 33,000; and Kruger N. P. (South Africa) – 31,000.

Densities range from 0.9/km² in Kruger N. P. (Smuts 1976a) to 22/km² (ground count) (Klingel 1967) and 19.2/km² (aerial

Grant's Zebra *Equus quagga boehmi* illustrating variations in width of stripes.

count) in Ngorongoro (Turner & Watson 1965). Density figures for the Serengeti are 5.8–8/km² (Kingdon 1979, H. Klingel pers. obs.).

For two East African populations, the limiting factors of population size have been identified. In the Serengeti, zebras appear to be limited by high foal mortality; the high predator/prey ratio suggests that predation may be the decisive limiting factor (Grange *et al.* 2004; and see Gasaway *et al.* 1996). In Laikipia, in N Kenya, with a low predator/prey ratio, population size is correlated with rainfall (Georgiadis *et al.* 2003).

Adaptations Disruptive coat pattern is thought to serve as camouflage in bushland and in dim light. In open terrain the air vibration during the heat of the day makes Plains Zebras over some distance less conspicuous to the human eye than uni-coloured antelopes of similar size, such as Common Wildebeest *Connochaetes taurinus*. However, it is not known whether the stripes give Plains Zebras an advantage over other species. In Kruger N. P., Lion *Panthera leo* predation affected Common Wildebeest more severely than Plains Zebras (Mills & Shenk 1992). It has been speculated that striping may confuse attacking predators, although this is not based on observation. At close range the stripe pattern might allow for individual recognition among group members. This is especially obvious when foals that have been left behind are searching for their mothers. They walk from one family to the next, often performing naso-nasal contact, but when near their own family they just head straight for the mother and start sucking – without prior sniffing (Klingel 1967). Recognition by olfaction alone can probably be ruled out. The stripes may protect to some extent against *Glossina* sp. and other biting flies, which prefer uniform white or black

models over striped ones. Protection is only relative as olfactory attractants for the flies are crucial (Waage 1981) and the zebras are nevertheless infected with *Trypanosoma* spp. (Baker *et al.* 1967).

Skin and surface temperatures of the black stripes are much higher than of the white ones, but the stripe pattern has no function for thermoregulation; in terms of temperature regulation, the zebra is a 'grey' coated animal (V. Finch pers. comm.). Using infra-red photography, Cena & Clark (1973) recorded surface temperatures of 39°C for the black and 30°C for the white stripes, whereas recent studies using the same method (Benesch & Hilsberg 2003, Benesch & Hilsberg-Merz 2006) measured 62.5°C and even 71.9°C for the black and 41.6°C for the white stripes of a zebra exposed to direct sunshine. In the dark the black and white surface temperatures were almost identical; however, the black stripes were slightly (0.5–0.7°C) below the white stripes.

From a selection of hypotheses on the function of stripe patterns, Ruxton (2002) analysed and dismissed some while suggesting further experimental approaches. With the exception of individual recognition, all these suggestions assume selection by forces external to the animals themselves. However, Kingdon (1979, 1997) has suggested stripes evolved as a consequence of intra-specific social selection. He suggested that basic susceptibilities of the neurovisual system have been enlisted to receive and transmit socializing stimuli (see genus *Hippotigris*).

Fuller *et al.* (2000) measured brain and arterial blood temperatures in three free-ranging Plains Zebras in their natural habitat, and found that brain temperature consistently exceeded blood temperature, on average by 0.2–0.4°C, and that changes in brain temperature closely tracked changes in blood temperature. There was no evidence of selective brain cooling, even during hyperthermia associated with intense, short-duration exercise. This relationship between brain and arterial blood temperatures in free-ranging zebras was unlike that reported for horses.

As family groups are fully reproductive non-territorial units, they are unrestricted in their movements and thus capable of colonizing new ranges. Plains Zebras are maladapted to drought situations: during a prolonged drought in the early 1970s populations in N Kenya were completely wiped out and others severely reduced whereas Grévy's Zebras in the overlap zone hardly declined at all. Although the two species have basically different types of social organization, physiological differences like the tolerance of saline water are likely to be the cause of different levels of mortality (Klingel 1974).

Foraging and Food Plains Zebras are primarily grazers: over 90% of its diet consists of grass the rest being herbs, which may be taken by accident. In Kruger N. P., Smuts (1972) recorded a list of some 50 species of grass and eight herbs. The choice of grass species broadly reflects the species available, but zebras do show some selectivity: of seven major grass species, one, *Panicum maximum*, contributed 40% of the intake and the same preferences were shown all through the year (Ben-Shahar 1991). Other favoured grass species in studies include *Themeda triandra*, *Cynodon dactylon* and *Eragrostis superba* (Grubb 1981). In extreme dry periods they resort to browse and even to corms and rhizomes (Pienaar 1963, Tinley 1966, Gwynne & Bell 1968). Plains Zebras appear to favour areas of short grass, particularly recently burnt areas with a new flush of growth. However, in the Serengeti, Plains Zebras are the first in a grazing succession. They move into the long grass, grazing it down by feeding mostly from the top stratum

(using their incisors, rather than plucking) and thereby making it attractive to the Common Wildebeest and other more selectively feeding species (Vesey-Fitzgerald 1960, Gwynne & Bell 1968, Bell 1971, Maddock 1979). Considerable overlap in the use of grass species by Common Wildebeest and Plains Zebras was recorded in the Sabi-Sand G. R. in South Africa (Ben-Shahar 1991). In the dry seasons zebras feed mostly on fibrous grass stems (>50% of the diets), which are avoided by other grazers. The diet is fibrous and low quality, but this is compensated for by their ability to eat larger quantities than ruminants; data on horses suggest that this is a result of a faster passage time in the gut (Duncan *et al.* 1990).

In several areas, Plains Zebra movements are directly correlated with the availability of water. They move to grazing areas during the rains and concentrate near permanent rivers or pools during the dry season. Examples are the Rukwa flood-plains, which are suitable only after they have fallen dry (Vesey-Fitzgerald 1965), the Tarangire N. P./Simanjiro Plains system in N Tanzania (Kahurananga & Silkiluwasha 1997) and Makgadigadi Pans G. R. in Botswana (Kgathi & Kalikawe 1993). A similar situation prevails in the Sudd in S Sudan. During the rains the zebras stay on high, dry ground. During the dry season and after the big fires they move close to the river and feed on the fresh growth of *Vossia*, which is an extremely coarse swamp grass and can only be grazed by a hard-hoofed animal during the period when deep, soft soils are no longer waterlogged (J. Kingdon pers. comm.).

Social and Reproductive Behaviour Plains Zebras live in social groups: (1) family (or harem) groups consisting of one stallion, one to several mares and their young, and (2) stallion groups. Some adult ♂♂ are solitary. This type of social organization is exceptional among the ungulates, the only African parallel being the closely related Mountain Zebra (Klingel 1968a, 1969c, Joubert 1972a, Penzhorn 1984a). Family group sizes in the various populations studied ranged from two, i.e. a stallion and a mare, to 16, and averages were from 4.2 and 4.5 in Kruger N. P. (Klingel 1967, Smuts 1976a, b) to 4.7 in Etosha N. P. (Klingel 1969a; and see Gasaway *et al.* 1996) to 7.7 in the Ngorongoro Crater (Klingel 1967, 1969a). The maximum numbers of mares per family ranged from four to six, and population averages were from 2.2 and 2.3 in Serengeti N. P. and Etosha N. P., respectively (Klingel 1969a), to 2.8 in Ngorongoro (Klingel 1969a). Thus, family size differences are largely caused by different portions of subadults and foals in the families (Klingel 1965a, 1967, Smuts 1976a, Monfort & Monfort 1978).

In an investigation of social organization and behaviour in Ngorongoro, more than 600 individually known Plains Zebras were monitored for up to 28 months, using a photographic file-card system. In addition, 122 key individuals were marked with brands and ear tags for quick recognition in the population of 5500 (Klingel 1965a, 1967, 1969a). The family groups were found to be stable social units with respect to the adult members. Apart from rare exceptions, the mares stay on until they die. Stallions are equally attached to their groups, but are replaced by stronger ones when old, weak, wounded, or after death, in this study at the rate of 9% per year. Sick, weak and injured group members are looked after, and the group waits for them, or group members walk back to lead the way. A stallion even grasped with his teeth a sedated mare (after immobilization) by the skin of her neck and led her back to the group (Klingel 1967). The family stallion has the mating rights over his mares. Extra-group matings were not observed.

Group fidelity of the mares, who are unrelated, is independent of a stallion's presence, and the group stays intact even when the stallion has been killed and a new stallion has not yet taken-over.

Adolescents leave their parental groups in a set pattern. Fillies leave at age 1 to 2½ years during oestrus. Departure is not voluntary: they are abducted by other stallions. The family stallion tries to prevent abductions, and often violent fighting ensues. Depending on the number of suitors – 18 in one observed case – the family stallion can succeed for some time to keep his daughter in the group but will eventually be exhausted and defeated. The filly usually does not stay with her first suitor and the same process repeats itself with the next oestrus. The attractive signal is the oestrous stance of the adolescent mare, hindlegs apart and tail lifted. Under the influence of an immobilizing drug (etorphine hydrochloride, M99) young and adult Plains Zebras displayed a similar stance and thereby attracted stallions from the vicinity who fought each other, tried to herd the semi-immobilized individual away and even mounted it – irrespective of its sex. After the drug had worn off the stallions lost interest.

Suitors of adolescent mares are family stallions who thereby enlarge their families, or bachelors who start a family. New family members are initially rejected by the established mares, but they are protected and herded by the stallion and eventually they are integrated. Adult mares display the oestrous stance only just before copulation, thus other stallions are not attracted and she stays with her stallion.

Young stallions leave their parental group at 1–4 years of age, and join other stallions. Departure is voluntary, and there is no antagonism by the family stallion or any other member of the group. On the contrary, the family stallion and the young stallion's mother search for the son and try to bring him back when he has separated. Stallion groups are variable in numbers and composition, but small core groups of two or three are stable over many months. Some groups consist of fully grown adults who in turn are joined preferentially by other adults; in other groups adults and subadults join up. Displaced family stallions were joined by sons and long-term stable associations formed (Klingel 1967).

Families and stallion groups maintain their integrity even when mingling freely with other groups in the grazing areas, on migrations, at waterholes and in the large herds of thousands and tens of thousands of conspecifics as in the Serengeti. Individuals that lose contact, search for their group and are in turn sought by other members of their group. In the family, stallions are sought by mares, foals and subadults; subadult stallions by the family stallion; and foals by their mothers, their father and the rest of the family. During the day searches are mostly by sight; there is strong evidence that zebras recognize group members from the stripe pattern, and, at close range, also by smell. At night, and in more confusing situations or at long range, zebras make contacts by calling. Calls are individually different and recognizable to the human observer and presumably to conspecifics.

Group members perform social grooming, especially of neck and shoulders, which cannot be reached with their own mouths. In families, preferred grooming partners are mares and their own foals, stallions and selected mares, but not mares with other mares. Grooming preferences are also obvious in stallion groups. Plains Zebras like to rub themselves on termite hills, rocks, logs and trees and also like to roll on the ground while taking dust baths.

A dominance order exists in the family groups with the stallion being the alpha individual. He defends the members of his group

against competitors and predators and can direct the group's movements, although he normally brings up the rear. Leadership is vested in the highest-ranking mare. When migrating the mares follow her in the order of their rank, the lowest ranking one being last. The foals walk behind their respective mothers, youngest first. Family stallions are of equally high rank, and higher than bachelors, and as long as they are healthy their position is not challenged.

Like all equids, fighting in Plains Zebras is relatively unritualized, employing hooves and teeth. Because of the bluntness of their weapons they can inflict only minor injuries like torn or bitten-off ears. In intra-specific fights the stallions employ several techniques: (1) neck-wrestling, each trying to get his neck above the other's and push him down; (2) biting match, with bites aimed at head, neck, ears, legs of partner; (3) circling, when each protects his legs from being bitten and they both come to a sitting position; (4) rearing on hindlegs, flailing with the forelegs and trying to get the other off balance, combined with biting; (5) chasing the loser, combined with biting; and (6) kicking as a defence when fleeing. Mares fight mostly by kicking with their hindlegs, but also snap at conspecifics (e.g. when trying to get to water).

Plains Zebras are non-territorial. They live in overlapping home-ranges with seasonal shifts depending on the availability of food and water. In the Serengeti, seasonal home-ranges of the migratory population are in the order of 400–600 km², and annual ranges can be estimated at more than 2000 km² (Klingel 1969b, pers. obs.). In Ngorongoro Crater total annual home-ranges were from 80 to 250 km², the latter being the total crater floor surface. Although sedentary, during the rains, up to one-third of the population moves out of the Crater to the adjacent Ol Balbal depression where they mingle with the migratory Serengeti zebras. However, at the end of the rains the two populations separate and the animals move back to where they have come from. Some exchange, in particular of adolescent mares, is thought to take place, but has so far not been documented (Klingel 1967, 1969a). Home-ranges in Kruger N. P. are from as little as 49 to as much as 566 km² (Smuts 1975a); within the home-range, there are foci of activity around water supplies, while other areas are used less frequently.

Feeding takes ca. 50% of the time, the rest being expended resting and moving. In the evenings the Plains Zebras in Ngorongoro Crater congregate in areas of short grass growth where they spend the night. Three resting periods are observed during which at least one member of a family group stands upright as a sentinel whereas the others lie semi-recumbent or flat on their sides. In the mornings the zebras move to other grazing areas and/or to water, following a regular pattern for weeks; they shift when the ecological conditions change. Daily movements were up to 26 km per day (Klingel 1967, 1969a). Annual movement of the Serengeti population is on the order of several 100 km (Maddock 1979).

Zebra herds in the Serengeti and in the Ngorongoro Crater are anonymous aggregations with the family and stallion groups as units, and no higher level of social organization is evident. Although the herd as a whole grazes in a particular area or moves and migrates in a given direction, the groups move independently of each other. They may leave the herd and later join the same or another one, without regard to previous neighbours and there was no indication of individualized relationships beyond the families and stallion groups (Klingel 1967, Rubenstein & Hack 2004). However, in a

Grant's Zebra *Equus quagga boehmi*.

low-density situation in the Samburu–Buffalo Springs Reserve in N Kenya, Rubenstein (1986) discovered a multi-level individualized relationship as some family groups associated preferentially.

In the Crater, family groups and stallion groups segregate to a certain extent, the stallions keeping more to the slopes, the families more to the floor (Klingel 1967). This feature can distort sex ratio assessments. Sexual segregation has also been observed in the Serengeti population (R. D. Estes pers. comm.).

Plains Zebras establish naso-nasal contacts with conspecifics. In the families, contacts are between all members. During the day, family stallions leave their families several times to contact peers in the vicinity and to perform a greeting ceremony. After the naso-nasal contacts they sniff each other's genitalia, then resume naso-nasal contacts and eventually make a final jump or a jerk with the head, after which they separate and each walks back to his mares. There is no overt aggression in these encounters.

Both bachelor and family stallions perform elaborate defecation ceremonies. When one of them defecates, they all gather around the fresh dung pile, sniff, perform flehmen (lip-curl) and defecate. All present usually do the same, producing a communal dung pile. Often they all start sniffing and flehmen simultaneously, perform naso-nasal contacts and continue playfully with the greeting ceremony, repeating the various sequences again and again.

During oestrus, and rarely at other times, the family stallion monitors the mare's excretions. He walks up to the place, or he waits behind the mare until she has performed. He then sniffs the defecations and urinations, displays flehmen and marks defecations with dung and/or urine, and urinations with urine. The significance of this behaviour remains obscure, especially as it is inconstant and as other stallions ignore the excretions, marked or unmarked, and ignore the stallion's behaviour.

During oestrus mares display an oestrous face (see later) and posture with hindlegs apart and tails slightly raised. This posture is most conspicuously displayed by adolescent mares (see above) and attracts suitors. Oestrus lasts for about a week during which the stallion is in close attendance. Copulations occur during the 1–2 days of high oestrus, before and after the mare kicks the stallion with her hindlegs and prevents mounting by moving forward in a trot or canter. During high oestrus the mare stands, pushes backwards against the stallion, and permits mounting and intromission. Mountings are at intervals of 20–70 min, and several copulations occur during the day (Klingel 1968b).

Birth takes place with the mare lying flat on her side. The foal is expelled head first, and initially fully enclosed by the embryonic membranes. It extricates itself from these without help. A foal can stand after 11 min, make first steps after 19, walk after 34 (and canter



Grant's Zebra *Equus quagga boehmi* showing proportions of a young foal.

after 44), and suck after 67; it drops the meconium after 97 min. The afterbirth is dropped within 1½ h after parturition. The mare licks the foal; she chews the afterbirth and embryonic membranes but does not eat any of it. The stallion stays nearby and watches closely. The rest of the group continues grazing and seems to be indifferent. However, they stay in the vicinity and wait for mare and foal to join them (Klingel & Klingel 1966a).

During the first few days after giving birth, the mare threatens and chases all other members of the group, including her own older offspring and the family stallion, as well as any other zebras. This behaviour is also known from other equids and other ungulates and is considered to be correlated with the critical period of imprinting. It ceases after about ten days and then all members of the group contact the foal, which by then obviously recognizes its mother.

Infanticide has been observed in captive Plains Zebras in the form of induced abortion (feticide) and physical attack of the neonate by a new stallion (Pluháček & Bartoš 2000, Pluháček *et al.* 2006). In the Crater population a number of takeovers were recorded of groups with highly pregnant mares and very young foals, but no instance of successful or attempted infanticide was observed (Klingel 1967). Only one case of infanticide has been reported from the wild, by a tourist in Etosha N. P. in Namibia (Heinrich 1996); status of the infanticidal stallion as well as circumstances are unknown.

Plains Zebras (like the other equids) command a rich repertoire of visual and acoustic signals and expressions (Klingel 1972, 1977b). The contact call consists of one- to three-syllable barking sounds that are produced during exhalation and which can be transcribed with 'quaha, quaha quaha, quaha quaha quaha' (which is spelled 'quagga' in Afrikaans and, in turn, is said to derive from a Khoisan or Chochoqua name that is the origin of the specific name). The frequency is 10–18 sounds in 5 sec. During inhalation a short 'ee' sound is produced. These calls are individually different and are assumed to serve for individual recognition. A short snort of ca. 1 second in duration is obviously a warning sound, emitted when the animals are disturbed and alerted, such as when discovering a predator or before crossing a river. The long snort of >2 seconds is an expression of well-being (e.g. when feeding).

Although the contact calls of the various equine species sound so different to the human ear, they seem to have some genus-specific properties and are recognized and responded to by congenics. Vocalizations of doubtful communicative significance are: (1) a disyllabic 'ee-ha' (warning?); (2) a high-pitched squeal (pain, distress); and (3) a long squeaking (pain, distress in foals) (Klingel 1967).

Six facial expressions can be distinguished. A greeting expression with a friendly connotation is displayed when two adults establish naso-nasal contacts: necks stretched, ears directed forward, corners of the mouth drawn up in jerking movements and chewing with bared teeth; Kingdon (1979) calls this an 'empty grooming gesture'. The oestrous face is displayed by the oestrous mare when approached and contacted by a stallion: exaggerated chewing movements with open mouth, teeth only partly bared, corners of the mouth pulled up, ears folded back. A submissive gesture, similar to the oestrous face, is displayed by subordinate group members: jaw movements faster than in the oestrous face, teeth meeting each time. The threat expression is displayed in confrontations, and different levels are observed. Low intensity threat: ears slightly directed backwards; high intensity threat: ears straight back, head lowered and stretched forward, swaying sideways, teeth bared. The flehmen expression is a reaction to interesting odours, especially in the sexual context: head lifted up, upper lip curled back to expose the incisors, lower lip lowered but jaws remain closed. When inhaling, odorants are drawn into the nasovomer (Jacobson's) organ, a pocket off the nasal cavity lined with highly sensitive sensory cells. The communicative significance of these expressions is still obscure except for the threat expression, which demonstrates readiness to fight, especially to bite, and conspecifics accordingly move out of the way, flee, or get ready to meet the attack. Other facial expressions with doubtful or no communicative significance are lip clapping (when the zebra see something interesting, like a predator or a human observer) and yawning.

Plains Zebras associate with other herbivores, and particularly with Common Wildebeest. Migrating wildebeest tend to lead the zebra, but because of their slightly faster pace the Plains Zebras eventually get to the front of the mixed herd and tend to lead the way (Klingel 1967). This behaviour, which can be interpreted as an anti-predator strategy, is based on inter-specific social attraction and inter-specific facilitation.

In N Kenya, Plains Zebras and Grévy's Zebras join up and stay together for hours or even days, grazing, resting and fleeing together, but eventually they separate again. When there is only one Grévy's Zebra in the area, a lone territorial stallion, he will stay with the Plains Zebras, and a solitary Plains Zebra stallion will seek company with any Grévy's Zebra, in preference to antelope, but closer contacts are not observed (Klingel 1974, see also Keast 1965). In Namibia where Plains Zebras and Hartmann's Mountain Zebras *E. zebra hartmannae* overlap, members of the two species often meet at waterholes but do not seem to recognize their close relative any more than other visiting ungulates (Klingel 1967, 1968a).

Associations of Plains Zebras and Giraffes *Giraffa camelopardalis* are more accidental, and although frequently cited in the popular literature, there is no hard evidence that zebras benefit from the Giraffes' higher outlook: when Giraffes flee, zebras often stay behind, or vice versa (Klingel 1967, Leuthold 1977). Harmless creatures are sometimes attacked, as was the case when a young Thomson's Gazelle *Eudorcas thomsonii* was killed by a mare who attacked by hitting it with the hooves and biting it (Klingel 1967).

Reproduction and Population Structure According to Smuts (1976c), ♂♂ attain sexual maturity at four years, with adult testis mass reached at five years. In the wild, the youngest family stallions whose ages could be determined when they were immobilized were 5–6 years old, the oldest were over 20. In Ngorongoro, mares have their first oestrus at just over one year of age (13 months; Klingel 1965a), but do not conceive until about 2½ years old. As gestation is 12 months, first foals are born at age 3.5 years (Klingel 1965a, 1969a, 1975). In Kruger N. P., ♀♀ have their first ovulation at about 1.5 years, and by 3.25–5.3 years all have ovulated (Smuts 1976b). Oestrus lasts about six days (Smuts 1976b), whereas Wackernagel (1965) gave a range of 2–9 days for animals in captivity. There is a postpartum oestrus, usually 8–10 days after birth.

Foals are born throughout the year, but not evenly. Distribution is linked to the rainfall pattern. In the Ngorongoro population, 28% (of $n = 151$) were born in the peak month (Jan), and 61% during the main foaling season from Jan to Mar and 85.5% during the six months from Oct to Mar, leaving 14.5% for the remaining six months (Klingel 1969b). Similar patterns of seasonality were recorded in the Plains Zebra populations of Serengeti, Etosha and Hwange National Parks (Klingel 1967, 1969a, 1975, Smuts 1976b). Young weigh about 30–35 kg at birth and there are no records of twins. Weaning takes place at 11 months (sometimes earlier), but lactation can continue up to 16 months; if the mare becomes pregnant, lactation ceases one or two months prior to parturition (Smuts 1976b).

Plains Zebra are prolific breeders. Klingel (1965a) recorded foaling intervals of 378 and 385 days. In the Crater population 15% of the adult mares ($n = 120$) had, in three foaling seasons (1963–65), three foals, i.e. the maximum possible, 33% had two, 41% had one and 10% had none at all; these 120 mares produced 184 foals over three years. These figures are of surviving foals only as neonatal mortality could not be assessed; actual natality was, therefore, even higher (Klingel 1969a). Conception rates of culled zebra in Kruger N. P. were 79% ($n = 236$) and 89% ($n = 31$) (Smuts 1976b); in Loliondo (a subpopulation of the Serengeti), 88% of adult ♀♀ in a shot sample were found to be pregnant (R. O. Skoog pers. comm.). In Ngorongoro, survival rate of the newborn foals was high: only 5% of those recorded disappeared in their first year of life. In the Serengeti population juvenile mortality in the first year was 30% (plus the unknown neonatal mortality) (Klingel 1969a). The different performance of Crater versus Serengeti zebra may have been caused by different predation intensity as the Crater Lion population had been decimated by an outbreak of biting flies *Stomoxys* sp.

Sex ratio at birth is close to 1 : 1 (Klingel 1965a, Klingel & Klingel 1966b, Smuts 1976a). Published adult sex ratios, expressed as ♂♂ : ♀♀, include 0.75 (Smuts 1976a) and 0.69–0.88 (Hack & Rubenstein, in Hack *et al.* 2002), indicating selective predation of stallions (see Grubb 1981). However, published adult sex ratios are likely to be inaccurate as family groups and stallion groups segregate to a certain extent (predation also distorts the sex ratio; see Grubb 1981).

In the wild, longevity is on the order of 21 (Smuts 1976a) to 25 years (Klingel 1966, H. Klingel pers. obs.). One wild-born specimen was about 38 years old when it died in captivity (Weigl 2005; and see Jones 1993).

Predators, Parasites and Diseases Major predators of adult Plains Zebras include Lions and Spotted Hyenas *Crocuta crocuta*, while predators of foals include Spotted Hyenas, African Wild Dogs

Lycaon pictus, Cheetahs *Acinonyx jubatus* and Leopards *Panthera pardus*. The impact of predation and the importance of zebras for predators varies among populations (Kingdon 1979, Grubb 1981). In defence against predators stallions use their teeth and hooves, and they can be quite successful against Lions and Spotted Hyenas. When attacked, the family groups close up and flee, except for the stallion, which attacks the predator and then runs after the group. Mares also attack when their foal has been captured.

Resting predators (Lions, Spotted Hyenas, African Wild Dogs, Cheetahs) are carefully observed, with the zebras arranging themselves in a circle or semi-circle around the predator who has then no chance to hide and/or attack as all the zebra in the vicinity are alerted. Predators on the move are equally well observed. When a predator comes close, but is not heading toward the zebra, they will cross the predator's route at high speed only to stop on the other side, roughly at the same distance from the predator as before. Should the predator change direction and head toward the zebras, they will flee. This feature is observed in other plains ungulate species as well (Klingel 1967, H. Klingel pers. obs.).

Plains Zebra are generally considered to be always fat and healthy and 'you never see a thin zebra'. In fact, they come off condition very fast and can die and/or fall prey within a few days. Healthy Plains Zebras have an impressive parasitic burden: Grubb (1981) summarized what was known of parasites at the time, including up to 11 species of nematodes (including *Setaria* spp., *Strongylus* spp. and *Dictyocaula* spp.), three species of cestodes and several trematodes (including amphistomes and *Schistosoma*). The stomach mucosa is covered with the larvae of botflies (*Gastrophilus* spp.), and another species (*G. haemorrhoidalis*) was recorded from the rectum. The adult fly deposits eggs on the hair, the ensuing larvae are ingested and reach the stomach/rectum where they attach themselves with their mouthparts. None of these parasites seem to cause any ill effects in healthy zebras, but when animals are off condition or when wounded or under nutritional stress, the parasite load gets heavy and especially the increase in numbers of *Strongylus* are likely to contribute to rapid deterioration. Nostril fly larvae *Rhinoestrus* spp. have been recorded from the nasal cavity. External parasites include lice (*Haematopinus*) and ticks (Grubb 1981; and see Horak *et al.* 1984b).

Major diseases of Plains Zebras are anthrax caused by *Bacillus anthracis*, African Horse Sickness caused by a virus and transmitted by biting midges, babesiosis caused by the protozoon *Babesia* (*Piroplasma*) spp., brucellosis caused by the bacterium *Brucella* spp., and trypanosomiasis caused by *Trypanosoma* spp. and transmitted by tsetse flies *Glossina* spp. (see Grubb 1981 and Radcliffe & Osofsky 2002 for references). Plains Zebras in the Serengeti have also tested positive for equine herpesvirus (EHV-9), although there is currently no evidence that it induced mortality. Because of the reported virulence of this virus for more susceptible species such as Thomson's Gazelles, viral transmission from infected zebra to other ungulates may result in mortality (Borchers *et al.* 2005).

Conservation IUCN Category: Least Concern (*E. q. quagga* – Extinct). CITES: Not listed.

As a species, Plains Zebras, numbering close to 700,000, possibly even 1 million, are presently one of the most widespread and abundant of African ungulates. They are present in a number of protected areas across their range, including Serengeti N. P. and Masai Mara N. R. (Kenya/Tanzania), Tsavo N. P. (Kenya), Etosha



Variations in interactions between horizontal limb stripe and vertical body-stripe systems.

N. P. (Namibia) and Kruger N. P. (South Africa). However, some populations are at risk, including the Gorongosa–Marromeu population, which by 1995 had been reduced to a mere 65 individuals from ca. 4000 in 1968 (East 1997, Hack *et al.* 2002). The KwaZulu–Natal populations are vulnerable because of their relatively small numbers (Bowland *et al.* 2001). None the less, the Plains Zebra is a relatively resilient species that has demonstrated a remarkable ability to recover from population declines when provided with suitable habitat and protection from overhunting (Hack *et al.* 2002). Restocking, if necessary, should only be with individuals of the same type and origin, irrespective of the nomenclature, which may be misleading. Also, interbreeding of individuals from different origins as has been practised in South Africa must be strongly discouraged.

Measurements

Equus quagga boehmi

TL (♂♂): 2521 (2365–2675) mm, n = 13
 TL (♀♀): 2513 (2250–2600) mm, n = 8
 T (♂♂): 475 (430–515) mm, n = 13
 T (♀♀): 460 (430–490) mm, n = 8

HF c.u. (♂♂): 508 (480–540) mm, n = 13
 HF c.u. (♀♀): 492 (475–515) mm, n = 8
 E (♂♂): 168 (155–178) mm, n = 13
 E (♀♀): 169 (160–177) mm, n = 8
 Sh. ht (♂♂): 1164 (1120–1215) mm, n = 13
 Sh. ht (♀♀): 1134 (1065–1205) mm, n = 8
 WT (♂♂): 247.8 (220.4–284.0) kg, n = 13
 WT (♀♀): 219.1 (175.5–241.5) kg, n = 8
 Serengeti (Sachs 1967)

Equus quagga chapmani

HF c.u. (♂♂): 514 (482–531) mm, n = 3
 HF c.u. (♀♀): 516 (509–524) mm, n = 4
 E (♂♂): 163 (155–169) mm, n = 3
 E (♀♀): 172 (165–176) mm, n = 4
 Sh. ht (♂♂): 1360 (1270–1470) mm, n = 32
 Sh. ht (♀♀): 1340 (1290–1410) mm, n = 32
 WT (♂♂): 318.0 (267.0–373.0) kg, n = 57
 WT (♀♀): 322.0 (273.0–387.0) kg, n = 51
 Kruger (Smuts 1974b, 1975b)

Equus quagga crawshaii

WT (♂♂): 323.0 (277.0–357.0) kg, n = 10
 WT (♀♀): 323.0 (282.0–341.0) kg, n = 7
 E Zambia (Wilson 1968)

Skull measurements:

E. q. quagga

GLS (♂♂): 470, 493 mm, n = 2
 GLS (♀♀): 493, 507 mm, n = 2

E. q. burchellii

GLS (♂♂): 523.5 (500–552) mm, n = 14
 GLS (♀♀): 514.9 (476–545) mm, n = 15

E. q. chapmani

GLS (♂♂): 532.9 (509–555) mm, n = 20
 GLS (♀♀): 531.9 (510–559) mm, n = 14

E. q. crawshaii

GLS (♂♂): 518.1 (489–530) mm, n = 12
 GLS (♀♀): 519.3 (506–532) mm, n = 4

E. q. boehmi

GLS (♂♂): 503.5 (475–548) mm, n = 76
 GLS (♀♀): 498.4 (466–547) mm, n = 66

E. q. borensis

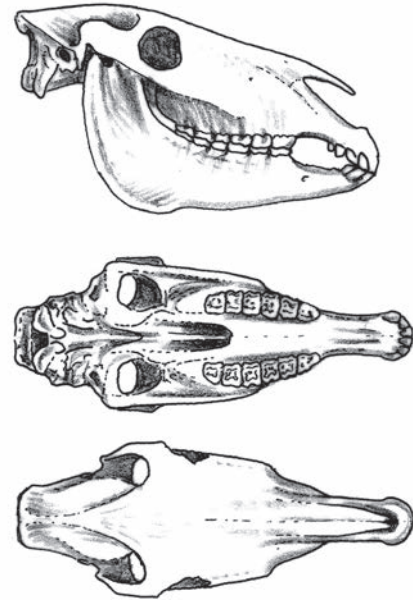
GLS (♂♂): 524.5 (499–550) mm, n = 13
 GLS (♀♀): 517.4 (511–534) mm, n = 5
 C. Groves & C. Bell pers. comm.

Key References Grubb 1981; Hack *et al.* 2002; Kingdon 1979, 1997; Klingel 1965a, 1967, 1969a, b; Smuts 1972, 1974b, 1976a, b, c.

Equus zebra MOUNTAIN ZEBRA

Fr. Zebre de montagne; Ger. Bergzebra

Equus zebra Linnaeus, 1758. Syst. Nat., 10th edn, 1: 74. Original type locality given as 'Habitat in India, Africa', since restricted to Perdekop, Ceres Dist., Western Cape Province, South Africa.

Mountain Zebra *Equus zebra*.Lateral, palatal and dorsal views of skull of Mountain Zebra *Equus zebra*.

Taxonomy Two allopatric subspecies of Mountain Zebra have traditionally been recognized, the nominate race *E. z. zebra* (Cape Mountain Zebra) and *E. z. hartmannae* (Hartmann's Mountain Zebra; type locality between Hoanib and Uniab rivers, 19° S, 13° E, Kunene Province, N Namibia). Groves & Ryder (2000) proposed that the two could be treated as distinct species as they are instantly recognizable externally, and Groves & Bell (2004) presented morphological evidence to support separation of the two subspecies as distinct species based on the diagnosability criterion of the phylogenetic species concept. More recently, Moodley & Harley (2005) found no genetic evidence to regard the two Mountain Zebra forms as anything more than different populations; however, the presence of private alleles at nuclear loci rendered the two subspecies genetically distinct evolutionary significant units.

Synonyms: *campestris*, *frederici*, *greatheadi*, *hartmannae*, *indica*, *matschiei*, *montanus*, *penricei*. Chromosome number: $2n = 32$ (Heinichen 1967, 1969a, 1970). There are 13 pairs of meta-submetacentric, one pair of subtelocentric and one pair of acrocentric autosomes; the X and Y chromosomes are both submetacentric. There is little evidence of hybridization between the two subspecies, but this remains a potentially major genetic threat; however, in Damaraland, Namibia, there are reports of hybridization in the wild between Hartmann's Mountain Zebra and donkeys (Brown & Jenkins 1987). Orlando *et al.* (2009) place *E. zebra* closer to *E. africanus* than to any other striped equine.

Description Stocky equid with long, rather thick upright mane, tufted tail and black to deep chocolate brown stripes on a white to light-buffy background. Tip of muzzle is black. Stripes on lower part of face are suffused chestnut to orange coloured.

Mountain Zebras have a distinct dewlap, the function of which is unknown. Rounded ears are white-tipped with black margins and 210–230 mm long (Penzhorn 1988). Stripes on the head are narrowest, followed by those on the neck and body. Horizontal to oblique stripes on the hindquarters are clearly much broader. Narrow dark markings form a 'grid-iron' pattern on the rump. Underparts are white, although the first few stripes behind the forelegs may extend to the ventral mid-line. The legs are distinctly striped to the hooves. One pair of nipples.

Characteristic features of the skull include: occiput high and raised; postorbital constriction deep; orbit somewhat behind the posterior border of the third molar; dorsoventral diameter of orbit greater than in the Plains Zebra *E. quagga*, giving a more rounded orbit; maxillary tuberosity does not extend as far back as in the Plains Zebra, so pterygopalatine fossa is visible from below; external auditory meatus large (3% of the basal length of the skull) and directed horizontally (instead of upward or backward); nasofrontal suture almost straight, and temporal lines diverge more rapidly rostrally than in the Plains Zebra, and at a wider angle (Smuts & Penzhorn 1988, Groves 2002). Canine teeth are prominent in adult ♂♂, while those of the ♀♀ are rudimentary and normally do not cut through the gums (Joubert 1971). In studies of cranial morphology, sexual dimorphism is evident in *E. z. zebra*, where ♂♂ are smaller than ♀♀, while sexes are the same size in *E. z. hartmannae* (Groves & Bell 2004); however, no sexual dimorphism was found in *E. z. zebra* skulls by Smuts & Penzhorn (1988). Age determination, primarily based on incisor wear, has been discussed by Joubert (1972c), Penzhorn (1982d, 1987) and Penzhorn & Grimbeek (1987).

Geographic Variation

- E. z. zebra* (Cape Mountain Zebra): Western Cape and Eastern Cape of South Africa. Smaller in size; dark stripes broader than the light ones.
- E. z. hartmannae* (Hartmann's Mountain Zebra): SW Angola, Namibia and NW South Africa. Larger, with adult ♂ standing about 1.5 m at the shoulder, and tails 0.5 m and ears 280 mm long; dark and light stripes about equal in width, but in some individuals the light stripes are wider than the dark ones; the mane comes further forward between the ears than in the Cape Mountain Zebra; also has relatively narrower muzzle and shorter nasals and diastema (Penzhorn 1988, Groves 2002, Groves & Bell 2004).

Similar Species

Equus quagga. Larger body size; black stripes on heads and bodies wider and fewer; in most extant populations of Plains Zebras in southern Africa the black body stripes continue around the underparts (whereas Mountain Zebras have white underparts, with a central narrow black stripe running from the chest to the belly); no 'grid-iron' pattern on rump, and legs generally not striped to the hooves; presence of shadow stripes in some subspecies (*burchellii*, *crawshaii*); distinct dewlap absent; ears shorter (160–180 mm). S Sudan and S Ethiopia to N Namibia and N South Africa (and historically south of the Orange and Vaal Rivers to the Cape).

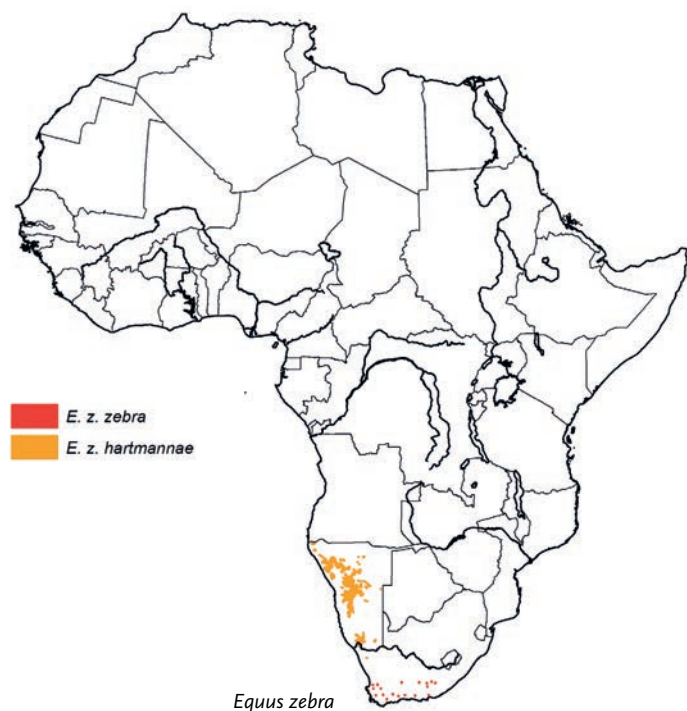
Distribution

Historical Distribution Historically, Mountain Zebras occurred from the southern parts of South Africa through Namibia and into extreme SW Angola. Cape Mountain Zebras were widely, if sparsely, distributed along mountain ranges forming the southern and western edge of the of the central plateau of the Eastern Cape and Western Cape of South Africa, from the Amatola Mts in the Cathcart District westward and northward to the Kamiesberg in Namaqualand in the Northern Cape. Hartmann's Mountain Zebras occur in the mountainous transition

zone between the Namib Desert and the central plateau in Namibia, with a marginal extension into SW Angola. Novellie *et al.* (2002) postulate that the ranges of the two subspecies were separated by an area devoid of mountainous habitat, which occurs between the northernmost point of the Cedarberg and Bokkeveldberg ranges, and the southernmost point of the Kamiesberg range. This large plain, 70 km wide at its narrowest point, which they referred to as the Kamiesberg Gap, may have retarded the flow of genes between the two subspecies.

Current Distribution Today, natural populations of Cape Mountain Zebras occur on the Bankberg (Mountain Zebra N. P.), Gamka Mountain Reserve and the Kamanassie Mts. Populations, mainly from Mountain Zebra N. P., have been re-established in various parts of their historic range, notably Karoo N. P. (Beaufort West), De Hoop N. R., Karoo N. R., now the Camdeboo N. P. (Graaff-Reinet), Commando Drift N. R., Baviaanskloof Wilderness Area, Tsolwana N. R. and Gariep Dam N. R. (Lloyd 2002, Novellie *et al.* 2002).

The present distribution of Hartmann's Mountain Zebras differs from that in historical times, due to the establishment of artificial waterpoints that have allowed it to occupy previously unsuitable habitat. In Angola, a population survived in Iona N. P. (Huntley 1972), though the current status of this population is unknown (Crawford-Cabral & Veríssimo 2005). In Namibia, the subspecies is discontinuously distributed in four populations: from Kunene Province southwards to the Ugab R. and eastwards to the Outjo District; the Erongo Mts; on the escarpment from the Swakop R. southwards to the Naukluft Mts and eastward along the Kuiseb and Gaub drainages into the Khomas Hochland; and the Fish River Canyon and Huns Mts near the Orange R. in the south (Joubert 1973). Hartmann's Mountain Zebras are established in three conservation areas in the Northern Cape, South Africa (Richtersveld and Augrabies National Parks and Goegap Provincial N. R.), and have also been introduced outside of their range in the Western Cape and Eastern Cape (Novellie *et al.* 2002).



Habitat Rugged, broken mountainous and escarpment areas up to around 2000 m with a rich diversity of grass species and perennial water sources. Cape Mountain Zebras in Mountain Zebra N. P. show a regular seasonal movement, from an open grassy plateau in the summer where there are stands of *Themeda triandra* to more wooded hill slopes and ravines in the winter. When the temperature drops sharply, the zebras leave the plateau to seek shelter in the wooded ravines. However, seasonal variations in zebra numbers on the plateau are more closely associated with variations in rainfall than with temperature. The numbers on the plateau are lowest during the driest time of the year (Aug and Sep), rather than the coldest (Jun and Jul) (Penzhorn 1982a, Winkler & Owen-Smith 1995). The movement is associated with a relative change in diet quality (as indicated by crude protein contents of preferred food plants and of the faeces) between the summer and winter habitats. In the summer, faecal and grass protein contents were higher in samples collected on the plateau than in those collected on the hill slopes. In the winter the reverse was the case. On the plateau the cover of grasses in the height range favoured by zebras changed only slightly from summer to winter (Novellie *et al.* 1988).

Mountain Zebras drink daily during the hot, summer months and often do so twice a day, and water is considered an important limiting factor in their distribution (Joubert 1971, Penzhorn 1984a). In spite

of this apparent water dependence, in the Iona N. P. in SW Angola, Hartmann's Mountain Zebras occur on the open sandy plains where they must endure extended periods away from water (Huntley 1972). Where surface water is not available, they will dig for it with a scraping movement of the front hooves, at times excavating to depths of a metre or more.

Abundance By 1998, Cape Mountain Zebras had increased from <100 animals in the 1950s to about 1200 individuals (Lloyd 2002, Novellie *et al.* 2002); the population in 2006 numbered in excess of 1500 individuals (P. Novellie pers. comm.). Hartmann's Mountain Zebras are estimated to number about 25,000 (Novellie *et al.* 2002; and see Conservation).

Adaptations Mountain Zebras are compact, stocky equids and rather resemble donkeys in post-cranial morphology: the scapula and metapodials are short, the ungual phalanges are short on both fore- and hindlimbs, and the metatarsus is shorter than the metacarpus (Groves & Willoughby 1981, Groves 2002). The hooves of Mountain Zebras are compact, with hard ventral surfaces, presumably an adaptation to the type of terrain inhabited (Skinner & Chimimba 2005). Like all equids, the strong, opposing incisors of Mountain Zebras allow them to be coarse grazers. The premolars resemble the high-crowned molars. During cold weather, Mountain Zebras seek shelter in wooded ravines and shallow caves (Penzhorn 1984a). They often graze in the lee of a hill or ridge, protected from the wind. On cold mornings they frequent east-facing slopes to sun themselves (Joubert 1972a).

Foraging and Food Predominantly selective, coarse grazers, only accepting woody plants if forced to do so (Penzhorn 1982, Novellie *et al.* 1988). Mountain Zebras select greener grasses with a high leaf : stalk ratio and little or no moribund material, but use both stem and leaf components. They feed at 40–80 mm above the ground, except when eating seed heads of certain grasses such as *Eragrostis curvula* (and feeding heights range from 310 to 480 mm above the ground). Protein levels of grasses selected generally exceed 5% (Novellie *et al.* 1988). *Themeda triandra* is the favoured grass species in Mountain Zebra N. P., while *Cymbopogon plurinodis*, *Heteropogon contortus*, *Setaria neglecta* and *Enneapogon scoparius* are also eaten. *Digitaria eriantha* is eaten occasionally and *Eragrostis curvula* is used significantly only in winter, when seed heads are eaten (Penzhorn 1982a, Grobler 1983). Certain grasses are uprooted and eaten entirely. There are generally three main grazing periods during the day: a few hours after dawn, late morning, and from mid-afternoon to dusk (Penzhorn 1984a).

Foals will nibble grass when only a few days old (Joubert 1971, Penzhorn 1975). Up to the age of about 14 weeks the foals of both subspecies eat the faeces of adults, particularly that of their own mothers. They paw the faeces and eat parts of two or three pellets, possibly to obtain a supply of the intestinal micro-organisms required to break down cellulose in their food. Mountain Zebras are partial to mineralized soil licks (Penzhorn 1982b).

Social and Reproductive Behaviour Populations consist of small harems of an adult stallion and one to three (maximally five) mares and their dependent foals, and non-breeding groups consisting primarily of bachelors, but sometimes including young fillies (Klingel 1968a, Penzhorn 1984a). The largest breeding herd encountered by



Mountain Zebra *Equus zebra* showing dewlap.

Penzhorn (1975) consisted of 13 individuals, comprising a stallion, five mares and seven foals. The mean number in 21 herds was 4.7 individuals (range 2–13), similar to that given for Hartmann's Mountain Zebras in Namibia (Joubert 1971).

Social hierarchies exist in harems, with the stallion being dominant and a linear hierarchy among the mares. There is no clear-cut association between dominance and leadership, but certain mares tend to initiate most activities in some herds. The stallion usually brings up the rear, except when the group approaches a drinking site in which case the stallion takes the lead. Stallion herd tenure averages seven years (Lloyd & Rasa 1989); one stallion remained with the same harem for >10 years, until he was 17 years old (Penzhorn 1984a). Adult mares typically remain in the same harem for life or until the death or displacement of the stallion. Displacement by younger stallions can lead to serious fighting involving biting and kicking, and stallions can incur severe wounds.

Mountain Zebras are not territorial, but harems inhabit home-ranges, with extensive overlap. Cape Mountain Zebras in Mountain Zebra N. P. had a mean home-range size of 9.4 km² (range 3.1–16.0 km², n = 16). When two breeding herds split up, the home-ranges of the new herds included those of the original herds, but were noticeably larger. Home-range size and shape are probably largely dependent on grazing, permanent water, topography, shelter and lick sites (Penzhorn 1982c). In Hartmann's Mountain Zebra, home-range size varies seasonally: harems have winter home-ranges of 6–10 km² in Daan Viljoen G. R. and 10–20 km² in the Otjovasandu area, Etosha N. P., Namibia; summer home-ranges are considerably smaller at both localities (Joubert 1972a). At Otjovasandu, winter and summer home-ranges are separated by ca. 120 km.

When two harems come into close proximity, the herd stallions approach each other with head erect, and make naso-nasal contact, rub their bodies against each other, sniff at the other's genital area, abruptly resume grazing and move back to their respective herds. Contact between a herd stallion and a bachelor usually consists of brief naso-nasal contact only. The bachelor approaches the herd stallion in a submissive posture (head lowered, grimace, squeal) while



Hartmann's Mountain Zebra *Equus zebra hartmannae* foal.

making chewing motions, possibly grooming-intention movements or a displacement activity derived from nursing behaviour. Fighting, which is rare among Mountain Zebras, consists of biting the opponent's mane, ears, neck or legs, and lashing out with the front or hind legs (Penzhorn 1984a). Playfighting contains all the elements of serious fighting, but the movements are exaggerated.

During its first few weeks of life, the foal remains close to the dam; the dam actively prevents contact between the foal and other members of the group, irrespective of their rank. Suckling intention is signalled to the dam by the foal pressing its body against her chest as it moves around her and attempts suckling on the other side. Weaning seems to depend mainly on the imminent birth of a sibling.

Both colts and fillies leave their maternal harems at about two years of age, slightly younger for the fillies (Penzhorn 1984a, Lloyd & Rasa 1989). Hartmann's Mountain Zebra mares are reported vigorously trying to expel their 14- to 16-month-old foals from the harem before the birth of a sibling. Cape Mountain Zebra foals leave the harem by their own accord; the stallion actively tries herding them back. Birth of a sibling does not appear to be most influential in these foals leaving the harems, as many leave even when no sibling is born. A 37-month-old colt was still with his maternal harem 20 months after the birth of a sibling (Penzhorn 1984a).

Dispersing youngsters tend to join a non-breeding group, colts joining groups with familiar ♂♂ and fillies joining groups with stranger ♂♂. This appears to be a unique incest-avoiding strategy among equids. Fillies joining breeding groups become subordinates in established harems (Rasa & Lloyd 1994). The nuclei of new harems are formed by long-term attachment between colts and fillies within non-breeding groups, the first filly forming such an attachment becoming the dominant mare in the new harem. Generally, colts do not succeed in becoming harem stallions before they are five years old (Penzhorn 1984a).

Vocalizations include a high-pitched alarm call from the stallion when danger threatens and a drawn-out squeal uttered by a bachelor when confronted by a herd stallion. The alarm snort by the herd stallion is actuated by an audible intake of air through the nose, a



Species-specific (signal?) pattern 'gridiron' on rump.

sharp expelling of air, followed by an audible intake. Lipping, a soft sound, audible over short distances near grazing animals, is regarded as a sign of contentment (Joubert 1972, Penzhorn 1984a). It is achieved by forcing air through closed lips, causing them to slap against each other.

Grooming patterns are essentially similar in all equids. Mutual grooming has a utilitarian function as areas that the animal cannot groom itself are groomed by another (especially the neck, mane and shoulders), but it has also attained a secondary function in maintenance of group cohesion. The most frequent mutual grooming in breeding herds is between mares and their foals. This is usually elicited by the foal. Mountain Zebras usually dust-bathe at least once daily, with individual rolling in the sand, first on the one side, then standing up and rolling on the other side.

Mountain Zebras react to flight or alarm signals of large antelope, such as Black Wildebeest *Connochaetes gnou*, but seldom to those of smaller antelope species, with which they seldom associate. Pale-winged Starlings *Onychognathus nabouroup* and rarely Red-winged Starlings *O. morio* and Fork-tailed Drongos *Dicrurus adsimilis* associate with Mountain Zebras, presumably to remove external parasites (and see Predators, Parasites and Diseases).

Reproduction and Population Structure Parturition is aseasonal, although there is a peak in summer. As the gestation period is around 12 months, this also reflects the time of conception (Westlin-Van Aarde *et al.* 1988). In a winter-rainfall area, most foals are born in spring and early summer (Penzhorn & Lloyd 1987); in a semi-arid summer rainfall area, conception occurs later in the season when the spring is dry (Penzhorn 1985). In Mountain Zebra N. P., first conception was recorded at 26 months of age, and mean age at first foaling 66 months (range 38–105 months; $n = 29$); mean foaling interval is about two years (Penzhorn 1985). Gestation is about one year (Joubert 1974b, Penzhorn 1975), and a single foal is born. Hartmann's foals have a mass of about 25 kg ($n = 5$) (Joubert 1974b). Foals have shorter muzzles than the adults, their stripes are less distinct, and they have long woolly hair covering their bodies.

Reproductive success of dominant and subordinate mares is equal and independent of age and social and reproductive variables. However, fitness of dominant mares was significantly higher than that of subordinates, with the latter having higher mortality among foals, part of which could be attributable to dominants' aggression. Dominant mares produce significantly more female than male offspring. This trend is not found for subordinates. A mare's status is positively correlated with dominant status in her female offspring but not related to subsequent status of her male offspring (Lloyd & Rasa 1989).

Sex ratios at birth of Cape Mountain Zebra is usually 1:1 (Lloyd & Rasa 1989). Mortality rates for Cape Mountain Zebra foals at De Hoop was high, with 26% of 42 foals dying. Mortality appears to be related to behavioural factors, as subordinate mares defend their foals vigorously; foals sometimes suffer broken legs probably inflicted by dominant mares (Lloyd & Rasa 1989). Survival rate of Hartmann's Mountain Zebra foals appears higher.

Mares may continue to produce foals up to an age of 21 years and possibly longer, and stallions may remain fertile up to the age of 25 years in the wild (Penzhorn 1985). Jones (1993) gave longevity records for *E. z. hartmannae* in captivity as 26 years and 6 months, and for *E. z. zebra* as 26 years and 3 months, not dissimilar to figures from the wild (Penzhorn 1985, R. Smith pers. comm.). One captive specimen lived for 33.2 years (Weigl 2005).

Predators, Parasites and Diseases In Namibia, Hartmann's Mountain Zebras are subject to predation by Lions *Panthera leo*, Leopards *Panthera pardus*, Cheetahs *Acinonyx jubatus*, Spotted Hyenas *Crocuta crocuta* and African Wild Dogs *Lycaon pictus* (Joubert 1974a). In one instance, it appeared from the spoor and other signs that a stallion had not only kicked an adult Spotted Hyena to death, but had continued to press home its attack over a distance of 100 m, repeatedly kicking the dead hyena (Viljoen, in Skinner & Chimimba 2005). Along the Kuiseb Canyon in the central Namib Desert, significantly more Hartmann's Mountain Zebra mares than stallions are taken by Spotted Hyenas, the only large predators in the area (Tilson *et al.* 1980).

In late winter, Cape Mountain Zebras in Mountain Zebra N. P. carry large tick burdens, especially *Margaropus winthemi* (Penzhorn 1984c, Horak *et al.* 1986). Numerous ixodid tick species have been recorded (Young *et al.* 1973, Horak *et al.* 1984a, 1986, 1992), and between Apr and Nov, Pale-winged Starlings associate with the zebras, and particularly during Jul and Aug. It is thought that the birds exploit a marginal food source during the cold, dry winter months when other food is limited (Penzhorn 1981, Penzhorn & Horak 1989). Various species of bot-flies (*Gasterophilus* spp.) have also been recovered from animals in Mountain Zebra N. P. and Namibia.

Penzhorn (1988) summarizes a lengthy list of nematodes (round worms) recovered from animals across the range (and see Kreczek *et al.* 1994, 1997), as well as at least two tapeworms (*Anaplocephala magna* and *A. perfoliata*), a *Sarcocystis* sp., and the haemoprotozoa *Babesia caballi* and *Theileria equi* that have been reported from Mountain Zebras (Young *et al.* 1973, Markus *et al.* 1983, Penzhorn 1984c, Zweygarth *et al.* 2002).

Epizootics of bovine papillomavirus-induced sarcoid tumours have been reported in several populations in South Africa, including Gariep Dam N. R. (with an incidence of 22% in a population numbering 83 animals) and Bontebok N. P. (53% in 19 animals) and isolated cases in Commando Drif, De Hoop and Gamka Mountain N.

R. (Sasidharan 2006). Available evidence suggests that this predisposition may be a consequence of impaired immune function due to inbreeding (Sasidharan 2006).

Dental abnormalities were found in 7 of 37 skulls collected in Mountain Zebra N. P. (Penzhorn 1984b). Intraventricular thrombosis was found in two Mountain Zebras, while the bacterium *Actinobacillus equuli* was cultured from a three-month-old filly and from various organs of a 20-year-old mare (Bath 1975, 1979).

Conservation IUCN Category: Vulnerable C1 (*E. z. zebra* – Vulnerable D1; *E. z. hartmannae* – Vulnerable C1). CITES: Appendix I (*E. z. zebra*) and Appendix II (*E. z. hartmannae*).

Cape Mountain Zebras were extensively hunted for their skins, because they competed with livestock for grazing, and allegedly because they broke fences (Penzhorn 1988). By the early 1930s it was evident that Cape Mountain Zebras would become extinct if not specially protected, with the subspecies being confined to five localities: mountains west of Cradock, Kouga-Baviaanskloof Mts, Outeniqua Mts, Gamka Mts and the Kammanassie Mts. The Kammanassie, Baviaanskloof and Outeniqua populations occurred on government-owned land at the time and became provincial nature reserves in 1923 (Kammanassie and Baviaanskloof) and 1936 (Outeniqua). In 1937 Mountain Zebra N. P. (1712 ha) was proclaimed in the Cradock District of the Eastern Cape. The zebra population consisted of one mare and five stallions (Pringle 1982). In 1950, when the population had dwindled to two elderly stallions, a neighbouring farmer donated his 11 animals to the park (Bigalke 1952). By 1964 the population had reached 25. In that year a number of adjoining farms were incorporated into Mountain Zebra N. P., increasing the area to 6536 ha and the population to 55 (Penzhorn 1988). Gamka Mountain N. R. was established in 1971; growth of the *E. z. zebra* population in this reserve has been slower than expected, and more intensive management is advocated (Watson *et al.* 2005). Unfortunately, both the Outeniqua and Baviaanskloof populations went extinct, in the early 1970s and 1980s, respectively, perhaps because too many animals were captured to be translocated elsewhere. The remaining three natural populations exist today, while Baviaanskloof has since been restocked.

Today, over 90% of the current total population of 1389 Cape Mountain Zebras in National Parks and Provincial Nature reserves (Lloyd 2002, P. Novellie pers. comm.) are derived from Mountain Zebra N. P. stock. The population in Gamkaberg, which is genetically distinct from the park population, totals around 30–35 animals (Watson *et al.* 2005), while the Kamanassie population totals about 64 (P. Chadwick pers. comm.). All three populations are genetically depauperate. The only population with a relatively high degree of heterozygosity is the one at De Hoop N. R., which derived from Mountain Zebra N. P. and Kamanassie stock (Moodley 2002, Moodley & Harley 2005). The management of the Cape Mountain Zebra metapopulation requires the mixing of at least some animals from the three relict populations, but this has been hampered by the relatively slow growth of the Kamanassie population. Management options to facilitate the growth of this population include changing the fire management in the habitat preferred by zebras, acquiring adjacent land and the translocation of Mountain Zebras onto adjacent land (Chadwick & Watson 2007). Maintaining genetic diversity by establishing new populations is a challenge for the future.

Although vital for the long-term stability of the metapopulation, the De Hoop population received limited monitoring post-1999. Based on a population monitoring programme implemented in 2005, 99 individuals were identified indicating a decline in annual population growth from 6.6% (1995–99) to 4.5% (1999–2005). Furthermore, although population size had increased since 1999, the number of breeding herds had not ($n = 8–10$) and the proportion of adult ♂♂ holding herds of breeding ♀♀ was less than half that in 1999 (17% compared with 38%). The population was male biased (possibly due to the higher mortality rates experienced in ♀♀) and the deficit of ♀♀ is likely to have prevented additional breeding herd formation resulting in excess non-breeding ♂♂. These animals are currently of limited reproductive value to the metapopulation and may be contributing to the decline in reproductive potential at De Hoop by competing for limited resources (Smith *et al.* 2008).

Although most surviving Cape Mountain Zebras are in national parks (793 animals in 2006) or provincial nature reserves (596 in 2006), the numbers on private land have also increased considerably (165; Novellie *et al.* 2002). Some reintroduced populations have performed poorly, such as those in Addo Elephant N. P. and Bontebok N. P. (the latter established in 1985); in total, only 13 of 28 Cape Mountain Zebras reintroductions between 1985 and 1998 were successful (Novellie *et al.* 2002). In those cases where the population increased, the mean number originally introduced was ca. 15. A suitable founder population would be four stallions and ten mares. The average annual rate of increase of the entire Cape Mountain Zebra population from 1985 to 1995 was 8.6% (Novellie *et al.* 1996), and from 1995 to 1998, 9.6% (Novellie *et al.* 2002).

Hartmann's Mountain Zebras occur in four protected areas larger than 1000 km² in Namibia: Skeleton Coast Park, Etosha N. P., Namib-Naukluft Park and Ai-Ais-Hunsberg Park complex. Namib-Naukluft Park, originally established in 1968 as Naukluft Mountain Zebra Park as a refuge for Hartmann's Mountain Zebras, is particularly important, with a population of around 2300 animals (1998 estimate). Around 25% of the national population in Namibia occurs on conservancies

in communal lands with the remainder on commercial livestock and game farms (Novellie *et al.* 2002). In South Africa, an estimated 280 animals occur on private properties and in the Goegap Provincial N. R. in the Northern Cape (numbers in the Richtersveld vary because animals move between South African and Namibia); Hartmann's Mountain Zebras in South Africa's Eastern Cape and Western Cape comprise nearly one-quarter of the population of the subspecies in South Africa, and their removal and replacement with the Cape subspecies is a conservation priority in order to avoid any potential risk of hybridization (Novellie *et al.* 2002).

Measurements

Equus zebra zebra

TL (♂): 2690 mm, $n = 1$

TL (♀♀): 2610 (2550–2690) mm, $n = 5$

T (♂): 420 mm, $n = 1$

T (♀♀): 430 (400–470) mm, $n = 5$

HF c.u. (♂): 510 mm, $n = 1$

HF c.u. (♀♀): 480 (470–490) mm, $n = 5$

E (♂): 220 mm, $n = 1$

E (♀♀): 220 (210–230) mm, $n = 5$

Sh. ht (♂): 1270 mm, $n = 1$

Sh. ht (♀♀): 1240 (1160–1285) mm, $n = 5$

WT (♂): 250–260 kg (est.)

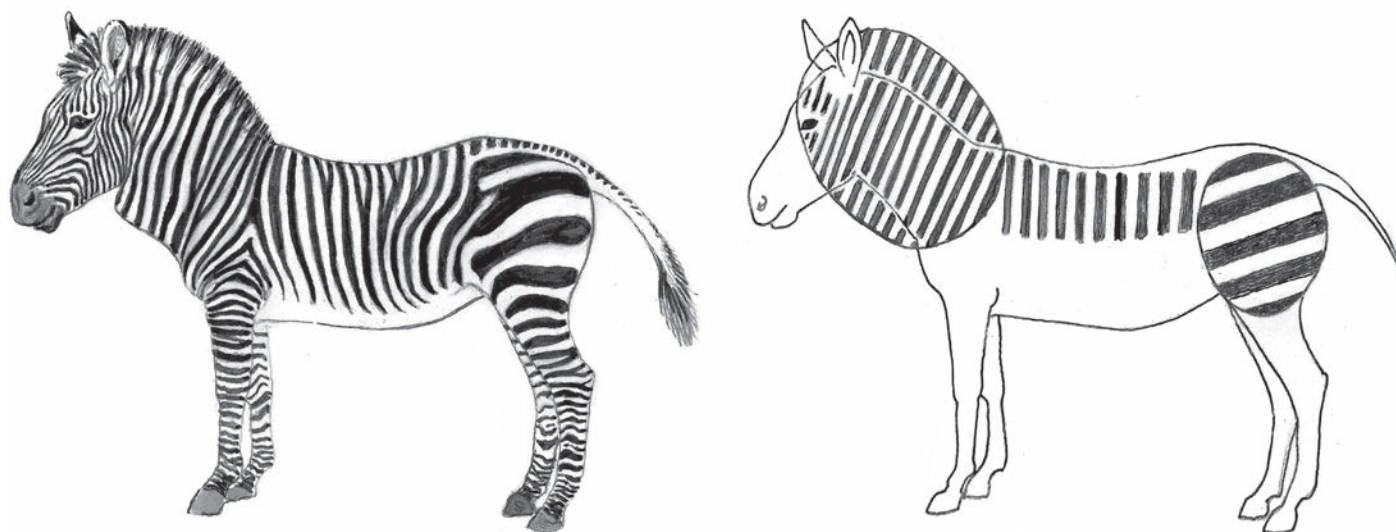
WT (♀♀): 234 (204–257) kg, $n = 5$

South Africa (A. J. Hall-Martin, in Skinner & Chimimba 2005)

Joubert (1971, 1974b) noted that in Hartmann's Mountain Zebra, ♂♂ (mean = 298 kg, $n = 22$) are heavier than ♀♀ (mean = 276 kg, $n = 23$); stallions older than seven years average 343 kg

Key References Joubert 1971, 1972a, b, 1973, 1974a, b; Lloyd 2002; Lloyd & Rasa 1989; Novellie *et al.* 1996, 2002; Penzhorn 1975, 1984a, 1985, 1988; Penzhorn & Lloyd 1987; Rasa & Lloyd 1994.

Banie Penzhorn



Mountain Zebra *Equus zebra* shows two types of visual enlargement: (left) dewlap and mane increases area of vertical neck stripes; (right) horizontal rump stripes enhance visibility over distance.

Family RHINOCEROTIDAE

RHINOCEROSES

Rhinocerotidae Owen, 1845. Odontography: 587. [Previously spelled Rhynocerotidae by J.E. Gray, 1821. London Medical Repository 15: 306.]

| | | |
|----------------------------------|------------------|--------|
| <i>Ceratotherium</i> (1 species) | White Rhinoceros | p. 445 |
| <i>Diceros</i> (1 species) | Black Rhinoceros | p. 455 |

Rhinoceroses were, until recently, among the largest land mammals inhabiting African landscapes. True rhinoceroses, of the family Rhinocerotidae, together with the extinct Amarynodontidae and Hyracodontidae, constitute the superfamily Rhinocerotidae, the largest and ecologically most diverse group of Perissodactyla (Prothero *et al.* 1989). The rhinocerotoids were distributed widely across Eurasia, North America and Africa, and by far outnumber all other perissodactyl groups in terms of valid fossil genera (>50) and species (several hundreds). While the amynodonts and hyracodonts were reduced to a few genera by the early Oligocene, the Rhinocerotidae began to diversify and to dominate the fauna of the northern hemisphere and Africa during the Miocene. The rhinos of North America were extinct by the end of the Miocene, while those of Europe and the northern parts of Asia survived to the end of the Pleistocene. As remnants of this diverse group, the genera *Rhinoceros* (represented by two species) and *Dicerorhinus* (one species) are precariously still extant in Asia, and the monotypic genera *Ceratotherium* and *Diceros* currently survive in Africa.

All recent species have been allocated to the subfamily Rhinocerotinae, and the African species form the tribe Dicerotini and the Asian species the tribe Rhinocerotini. However, there are a number of different views on the phylogenetic relationships of the extant rhinos; for instance, in a classification proposed by Antoine (2002) all five extant species have been combined in tribe Rhinocerotini and subtribe Rhinocerotina, while Prothero *et al.* (1986) and Cerdano (1995) separated the two recent African genera into the subtribe Dicerotina.

According to Tougaard *et al.* (2001), the origin and evolution of African rhinos occurred in the middle Eocene, with the *Diceros*/*Ceratotherium* split dated to 17.1 ± 2.5 mya (middle Miocene). It has been suggested by Geraads (2005) that the Pliocene *Ceratotherium neumayri* was a likely ancestor for both living African species, because it was morphologically and ecologically intermediate between them. The two lineages leading to the recent species split soon after the Miocene–Pliocene boundary leading from an ancestral mixed feeder (*C. neumayri*) to a lineage of grazers (*Ceratotherium* species) and one of browsers (*Diceros*). *Ceratotherium* adapted to open grasslands and savannas, while the *Diceros* ecological niche consisted of more closed habitats (Geraads 2005).

The genera *Diceros* and *Ceratotherium* are morphologically defined by synapomorphies that include the loss of both upper and lower incisors, an astragalus facet that is more or less flattened, an occipital crest angle above 100°, an inclined orbital floor, strong supraorbital processes, and short rounded nasals (Groves 1983, Cerdano 1995, Tougaard *et al.* 2001, D. Geraads pers. comm.). *Diceros* has three molars and 3–4 premolars (total 24–28 teeth), while *Ceratotherium* always has three molars and three premolars (total 24).

Rhinoceroses are large-bodied, pachydermatous animals, endowed with one or two nasal horns consisting of aggregations of keratin fibres (Cave 1969). The skin consists of a heavily keratinized and pigmented

epidermis (about 1 mm thick) and a dense dermis (about 18–20 mm thick) composed of pure collagen fibres (Cave & Allbrook 1959). A covering of very sparse hairs is found in some individuals, especially when young (Neuville 1927). The White Rhinoceros *Ceratotherium simum* exceeds all other extant rhino species in size, with a body length reaching 4.2 m, a shoulder-height up to 1.9 m and weight of 3600 kg in adult ♂♂, compared with 3.75 m, 1.8 m and 1500 kg, respectively, in the Black Rhinoceros *Diceros bicornis* (Zecchini 1998). African rhinos do not show conspicuous folds in the skin characteristic of *Rhinoceros* species.

The cytogenetics of the family have been investigated by several authors. The modal diploid chromosome number for all species is 2n = 82 (the ancestral condition), with the exception of *Diceros* (2n = 84) and the Javan Rhino *Rhinoceros sondaicus*, where the karyotype is unknown; the X chromosome in *Ceratotherium* and *Diceros* is identical (Houck *et al.* 1995).

Rhinoceroses always have one young, after a gestation period of about 480 days in all species (Rookmaaker 1998a). Placentas are large and consist of a thin membrane of allantochorion with rather diffusely scattered villi (Benirschke & Lowenstine 1995). In the wild, rhinos were originally found in a large variety of habitats, probably only avoiding very dense forests. They are generally solitary, but *Ceratotherium* sometimes congregated in groups, aggregations that were much rarer in *Diceros*. They are sedentary and territorial, and consume a wide variety of available plant species shifting preferences according to circumstances. They have few natural enemies, and there are few instances in which predators attack young rhinos.

Rhinoceroses were shown a dozen times in the arenas and menageries of the Roman empire, and some of these must have been caught in Africa (Störk 1977). In Renaissance Europe, most descriptions of the animal in the bestiaries of the period were based on the image of a single-horned animal, probably from India, seen in Lisbon in 1515 (and notably copied in a woodcut by Albrecht Dürer) (Clarke 1986). African rhinoceroses were first observed by European adventurers from about 1650 when the interior of the Cape of Good Hope began to be explored. For at least a century, however, reports were equivocal about the number of horns, and Linnaeus (1758) still called it an obscure species (Rookmaaker 1998b). Rookmaaker (2005a) has pointed out that the distinctions between rhinos from Asia and those of Africa only became formalized at the end of the eighteenth century.

In the course of the nineteenth century adventurers and hunters travelling inland from the South African coast described a proliferating number of rhinoceros species, mainly because they thought that the sizes and shapes of horns were significant characteristics. Two kinds of Black Rhino and two kinds of White Rhino came to be recognized in the southern part of Africa, but when still more types were added the picture became so confused that a prolonged nomenclatural silence followed while a revision was awaited (Rookmaaker 2005b). The first captive Black Rhino arrived in Europe in 1868, while the White Rhino was first seen in a zoological garden as late as 1946 (Rookmaaker 1998a). The studbooks of African rhinos in captivity are kept by the

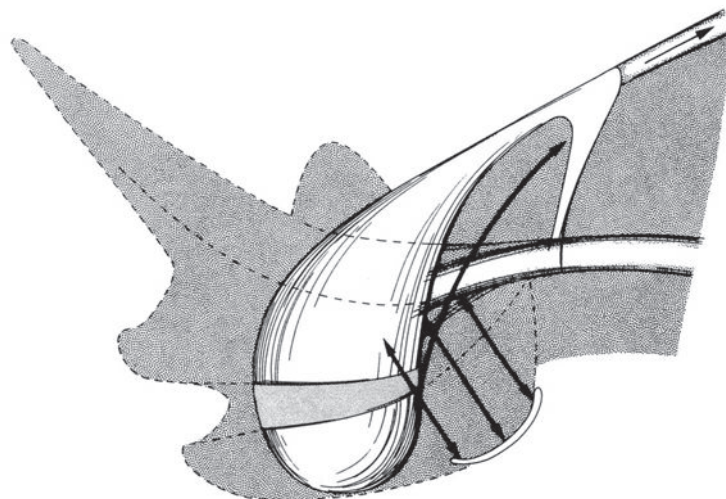
Zoological Gardens in Berlin and contain data on all specimens around the world (Ochs & Mercado 2005a, b, Rookmaaker 2005c).

The rhinoceros has limited value in traditional African societies. In a few cases, the hide was used to prepare shields or the meat was eaten (Lagercrantz 1960). The major threat to rhinos in recent years stems from the immense value of the horns to the Chinese as an essential ingredient in traditional fever-reducing medicine (Martin & Martin 1982, Chapman 1999, Ellis 2005) and to Yemeni to produce handles of the

daggers worn by the men (Leader-Williams 1992, Martin & Vigne 1993). The conservation of the species is discussed in further detail elsewhere.

References to an extensive literature about all aspects of rhinoceros biology and conservation have been listed and discussed by Rookmaaker (1983), Wildi (1989), Miller (1992), Du Toit *et al.* (1994) and Van der Westhuizen (1994).

Kees Rookmaaker



Ceratotherium, principal mass of skull in relation to mastication, horns, vertebral column and suspension.

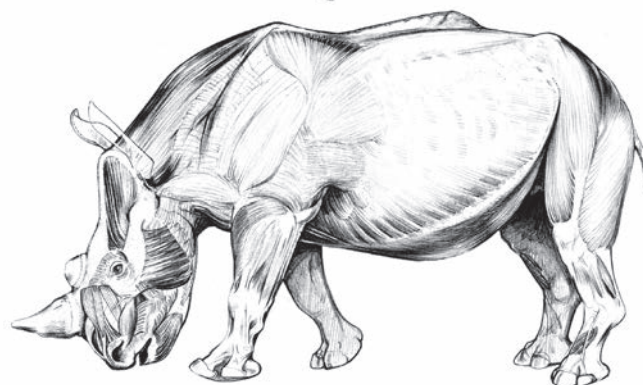
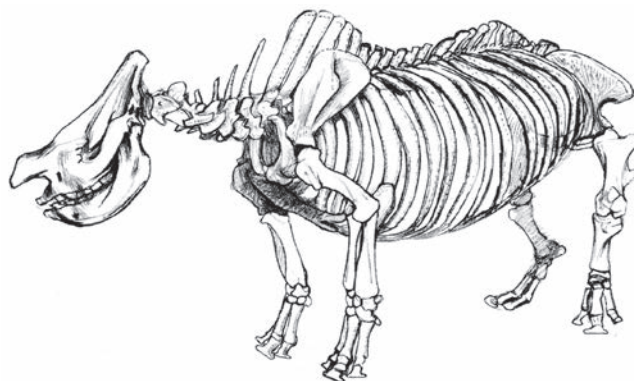


GENUS *Ceratotherium* White Rhinoceros

Ceratotherium J. E. Gray, 1868. Proc. Zool. Soc. Lond. 1867: 1006, 1027.

Ceratotherium is a monotypic genus (but see Groves *et al.* 2010), represented by a single extant species, the White Rhinoceros *Ceratotherium simum*. This species once was found in Africa south of the Zambezi R. and further north in central Africa in parts of Uganda, DR Congo, Sudan, Central African Republic and Chad (Heller 1913, Groves 1972, 1975). The unbridged gap between the two populations merits further investigation. The White Rhino was exterminated in Zimbabwe in 1893, at which time only a small population of a minimum of 20, but most likely about 200, individuals remained in the south-eastern part of South Africa (Player 1972, Rookmaaker 2002, 2003b).

The earliest African representative of *Ceratotherium* in the Pliocene is known from Langebaanweg in South Africa and has recently been identified as *Ceratotherium mauritanicum* (Geraads 2005). In North Africa, *C. mauritanicum* survived into the late Pleistocene; *Ceratotherium simum* was first found in the early Pleistocene. Specimens found in East Africa have been described as *Ceratotherium simum germanoaffricanum* (see Groves 1975). Evidence of skeletal material suggests that the transition from *C. mauritanicum* to *C. simum* took place in East Africa (Geraads 2005). Fossil and extant members of the genus are typical grazers, which shows in the elongation of the occiput and the development of the nuchal hump to accommodate the muscles needed to lift the head from the grazing posture (Alexander & Player 1965).



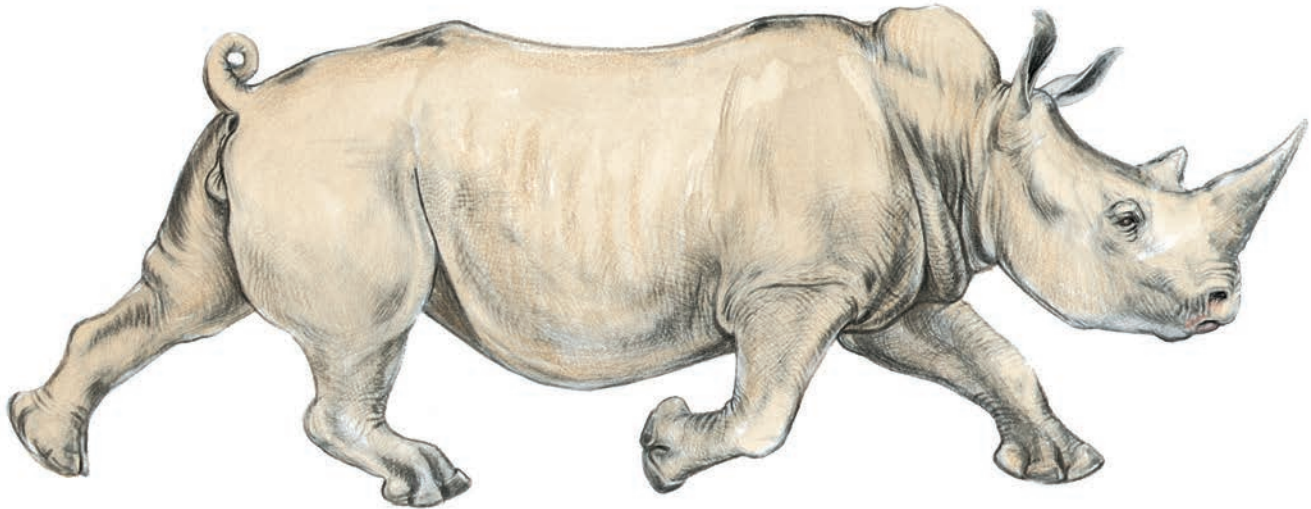
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White Rhinoceros *Ceratotherium simum*: skeleton (top) and myology (bottom).

***Ceratotherium simum* WHITE RHINOCEROS (GRASS RHINOCEROS, SQUARE-LIPPED RHINOCEROS)**

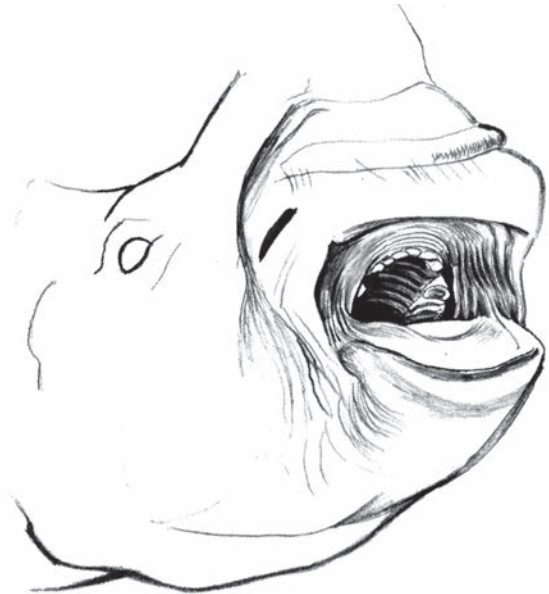
Fr. Rhinoceros blanc; Ger. Breitmaul-Nashorn

Ceratotherium simum (Burchell, 1817). Bull. Sci. Soc. Philom. Paris: 96–97, pl., figs. 1, 2. 'L'interior de L'Afrique Méridionale vers le vingt-sixième degré de latitude'; since fixed as South Africa, North-West Prov., Chue Spring (= Heuningveli), about 26° 15' S, 23° 10' E; see Grubb 1999).

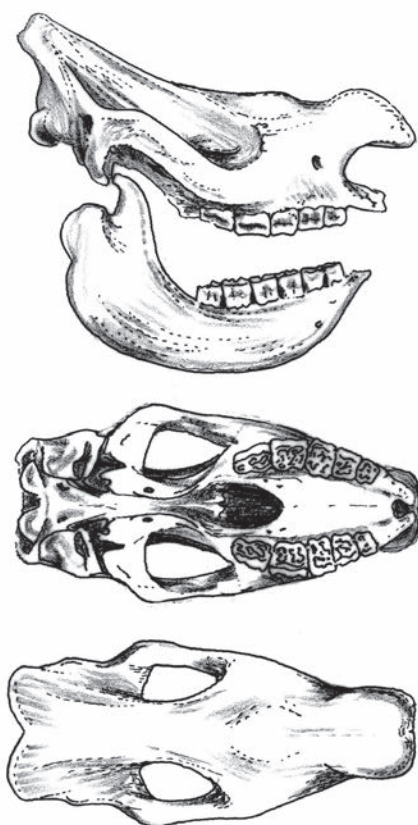
White Rhinoceros *Ceratotherium simum*.

Taxonomy First described by Burchell from a specimen collected 150 km north of Kuruman in what is now the North West Province in 1812 (Burchell gave the type locality as 'Interior of South Africa near 26° S'). He applied the name *Rhinoceros simus*, the genus *Ceratotherium* being proposed by Gray in 1867. Two subspecies are recognized: *C. s. simum* in southern Africa, and *C. s. cottoni* in north-east Africa. The nucleotide sequence divergence between them is only 1.4% (George *et al.* 1993). Groves *et al.* (2010) recognized *C. s. cottoni* as a distinct species. Synonyms: *burchellii*, *camperis*, *camptoceros*, *camus*, *cottoni*, *crossii*, *kiaboaba*, *kulamane*, *kulamanae*, *oswellii*, *prostheceros*. Chromosome number: $2n = 82$, and there is no diagnostic karyotypic difference between the two subspecies (Heinichen 1967, 1969b, Houck *et al.* 1994, 1995); the X chromosome is a large submetacentric, the Y is a small submetacentric, and the autosomes are telocentric and acrocentric (Houck *et al.* 1995). Chromosomal polymorphism, resulting in three individuals with a diploid number of $2n = 81$, has been noted in the Northern White Rhinoceros (Houck *et al.* 1994). Robinson *et al.* (2005) recently confirmed a case of inter-specific hybridization in rhinoceroses, wherein a calf was born to a young White Rhino cow and a Black Rhino bull held in captivity; the hybrid showed a mixture of phenotypic traits characteristic of the two species.

Description Largest extant rhinoceros species, but closely rivalled by the Indian Rhinoceros *Rhinoceros unicornis*. Skull is lengthened and lips broadly squared, with a hump on the neck containing the ligament and associated muscles supporting the massive head. Pointed ears fringed with hair, but otherwise body hairs are sparse and detectable only on close examination. Body is barrel-shaped due to the extended rib cage, with a prominent vertebral crest in the dorsal region and, particularly in the southern subspecies, rib-like markings on the trunk

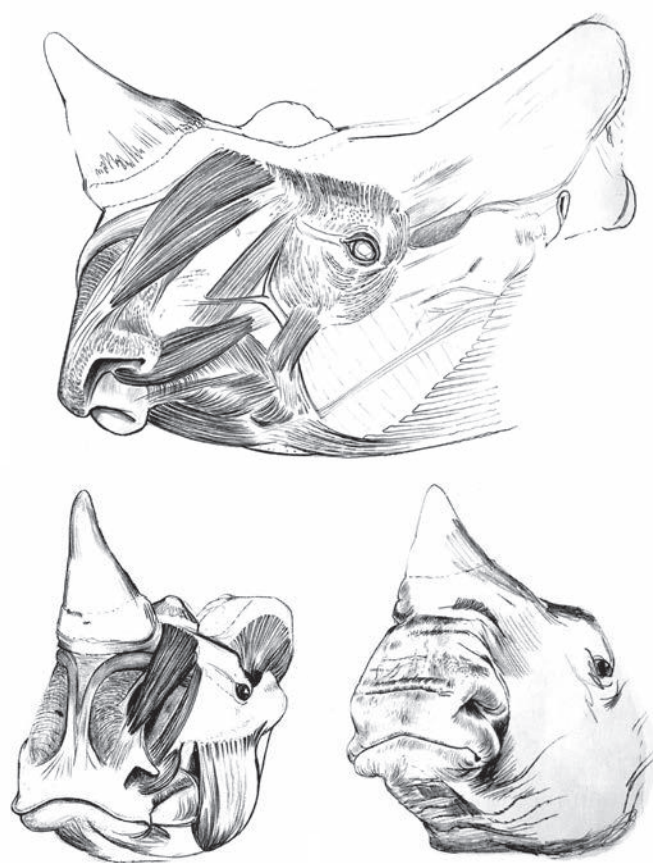
White Rhinoceros *Ceratotherium simum* detail of open mouth.

There are several theories to explain the origin of the name 'white rhino', the most popular explanation being that 'white' is derived from the Afrikaans 'wyd' or Dutch 'wijd' (meaning wide). However, there is no basis for this conjecture, since earliest reports consistently refer to the 'white rhinoceros' or 'witte renoster' (see Rookmaaker 2003a, Feely 2007). The name 'white rhino' may derive from the pale colour of the first specimens encountered where calcareous soils predominate. The more accurately descriptive names 'Square-lipped Rhinoceros' and 'Grass Rhinoceros' have been coined quite recently.



ABOVE LEFT: Lateral, palatal and dorsal views of skull of White Rhinoceros *Ceratotherium simum*.

ABOVE RIGHT: White Rhinoceros *Ceratotherium simum* lips and musculature adapted to grazing.



of the body. There are prominent folds of skin near the top of the forelimbs, and in the flank where the upper part of each hindlimb joins the body. Skin colour is battleship grey, but is modified by the colour of the soil used for wallowing. Limbs are thick-set, with three toes bearing broad, stout nails on each foot. Tail short with a sparse fringe of bristly hairs. Females bear a pair of inguinal nipples. Males lack a scrotum, and the muscular penis points backwards when enclosed in its sheath. Preputial glands are present. Apart from genitalia there is little sexual dimorphism, except that ♂♂ attain a body mass about one-third larger than ♀♀ and have noticeably more heavily set heads, chests and necks.

Two keratinous horns lacking a bony core grow in tandem on the snout, the anterior longer than the posterior. The horns are made up of a mass of tubular filaments similar in substance to hair, and are actually outgrowths of the skin not attached to the bone of the skull. Front horn has a straighter transverse edge in front when compared with that of the Black Rhino. Male horns have a greater mean anterior basal circumference than female horns, while ♀♀ generally bear more slender, and sometimes longer, anterior horns than ♂♂. Adult ♂♂ have heavier horns than ♀♀. Mean mass of horns of adult White Rhinos was 5.2 kg ($n = 163$) for anterior horn and 1.9 kg ($n = 153$) for posterior horn (Pienaar *et al.* 1991, Pienaar 1993). No difference between adult sexes in intrinsic anterior horn growth (mean rate of 50 mm per year; range 25–66); intrinsic horn growth rate is rapid in young animals, about 150 mm in the first year of life, but growth rate of anterior horns decreases with age (Pienaar *et al.* 1991, Pienaar 1993; see Horn Measurements).

Skull elongated, occipital crest rising high at the rear of the skull, with a broad rugose area on top of the skull providing a broad area for attachment of the neck muscles. Zygomatic arches heavily built and provide firm attachment for masseter muscles that operate the lower jaw. Lower jaw massive, condyles very broad and fitting into deep sockets. Adult dental formula is $I^{0/0}, C^{0/0}, P^{3/3}, M^{3/3} = 24$. Four premolars in deciduous dentition; no incisors or canines in deciduous dentition, which are sometimes present in Black Rhinos. Upper and lower second molars are the largest of the cheekteeth (Skinner & Chimimba 2005). Patterns of tooth eruption are discussed by Hillman Smith *et al.* (1986).

Geographic Variation

- C. s. simum*: Southern White Rhinoceros; southern Africa only, though introduced to Kenya, Uganda (where the species, but not subspecies, formerly occurred) and Zambia.
- C. s. cottoni*: Northern White Rhinoceros; formerly in Central African Republic, Chad, Sudan, Uganda and NE DR Congo; now probably extinct in the wild. Dorsal outline of the skull less concave than in the southern subspecies, a shorter tooththrow length, slightly longer legs relative to body length (Heller 1913), slightly smaller size overall (see Measurements), and generally higher head carriage.

Similar Species

Diceros bicornis. Sympatric, over various parts of the range of the southern subspecies. Considerably smaller, with hooked upper lips; skull shorter and broader, with occipital part not produced backwards behind condyles; head generally held high; more rounded ears with ear tips pointing upwards; and concavely saddled outline to the back.

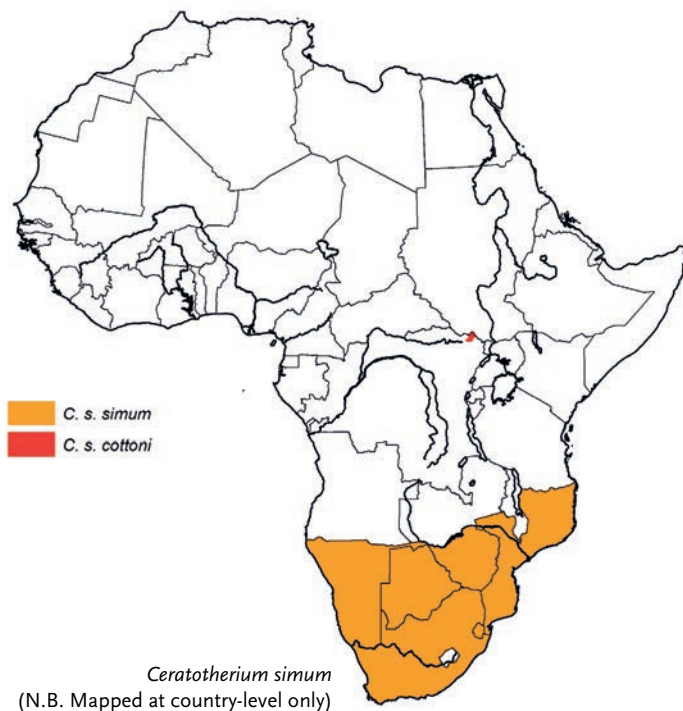
Distribution

Historical Distribution The southern subspecies formerly occurred from the Zambezi R. southwards into South Africa, in the east as far as NE KwaZulu–Natal, and in the west through the Northern Cape north of the Orange R. into NE Namibia. That they ever occurred naturally in Zambia is not definitely known; Ansell (1978) notes they may have occurred between the Zambezi and Mashi Rivers in the south-west of the Western Province, but considers the Zambezi R. as the northern boundary of the southern subspecies. White Rhinos were particularly abundant in the North West Province of South Africa, E Botswana and SW Zimbabwe. The species was absent from the highveld region of interior South Africa. Through hunting the species was almost exterminated, except for a remnant of a few score animals that persisted near the Umfolozi R. in the extreme south-east of the range. This core population has recovered such that White Rhinos have been re-introduced into many parts of their former distribution in southern Africa, and even to parks in East Africa outside the historic distribution range (see also Conservation).

The northern subspecies was found historically to the west of the upper Nile R., from NW Uganda and NE DR Congo northwards into S Sudan and into adjoining parts of the Central African Republic and southern edge of Chad. A feature of the historic distribution of the species as a whole is the limitation by major rivers, presumably because of a limited swimming capability.

White Rhinos formerly occurred through much of East Africa, as is attested by abundant fossil remains in early to mid-Pleistocene deposits in places like Olduvai Gorge. Teeth found on the soil surface in Kenya, and rock paintings in Tanzania, suggest that the species persisted in East Africa until a few thousand years ago (Hooijer & Patterson 1972). Rock engravings in Algeria indicate that the distribution range extended into North Africa in the early Holocene.

Current Distribution South Africa remains the stronghold for this subspecies, with sizeable populations in Kruger N. P. and Hluhluwe–



Umfolozi, but also occurring in numerous protected areas and private reserves throughout the country. There are also smaller re-introduced populations within the historical range of the species in Namibia, Botswana, Zimbabwe, Swaziland and Mozambique (Emslie *et al.* 2007). Populations have also been introduced outside of the former range of the subspecies to Kenya, Uganda and to Zambia. A population introduced to Côte d'Ivoire is considered semi-captive (Emslie & Brooks 1999, 2002a).

The northern subspecies is now extinct in Uganda, Chad, Central African Republic and at least up until 2006 survived in the wild only as a tiny remnant in Garamba N. P. in DR Congo (Emslie & Brooks 1999, Hillman Smith 2001, Emslie *et al.* 2007). The subspecies is now probably extinct in the wild (Milliken *et al.* 2009, Emslie 2011). Reports of rhinos surviving in S Sudan are unconfirmed; none were reported during the survey by Fay *et al.* (2007).

Habitat In southern Africa White Rhinos are typically associated with drier forms of savanna woodland, with mean annual rainfall under 750 mm. In Hluhluwe–iMfolozi Park they favour thornveld dominated by *Acacia* spp., but in Kruger N. P. they have settled abundantly in broadleaf savanna on granitic soils where *Combretum* spp. predominate (Pienaar *et al.* 1993a). Selous (1899) reports that they were partial to broad grassy valleys within savanna woodland regions of Zimbabwe. They were not recorded historically in treeless grasslands of the Highveld and interior KwaZulu–Natal. Being water-dependent, White Rhinos are seldom found further than about 5 km from surface water.

Heller (1913) described the habitat of the northern subspecies in Sudan as an open savanna containing scattered *Combretum* trees, and tall grass over 2 m in height during the wet season. The recent range in Garamba N. P. is likewise mostly tall *Loudetia/Hyparrhenia* grassland on lateritic and granite-derived sandy soils with widely scattered trees of *Vitex doniana* and *Terminalia mollis*. Falling within the Sudano-Guinean Savanna belt, the natural state of this area is tree/bush savanna or *Combretum/Terminalia* woodland, but the southern part of Garamba, where the rhinos are protected, is maintained as more open grassland by frequent intense fires and high elephant density. The area is regularly dissected by flowing rivers with patches of gallery forest. Rainfall from 1980 to 1988 averaged 1265 mm per year, though from 1957 to 1963 the average had been 1627 mm (Hillman Smith 1989). A crucial feature of this habitat is the presence of regularly spaced termitaria clearings. They cover 10–12% of the surface area of the grassland, but an average of 42% of all rhino observations over a ten-year period were in termitaria clearings. The *Loudetia* grass is unavailable to the rhinos as a food source above 0.5 m in height, but in the long grass seasons the termitaria clearings are the site of smaller, more palatable species. The long grass areas are used by the rhinos for cover, both for resting during the day and when disturbed, but it is the termitaria within the long grass that provide the combination of protection and airflow (K. Hillman Smith pers. comm.).

Abundance The Southern White Rhino is the most numerous of all rhino taxa, and its recovery from just a few score individuals has been recognized as among the world's greatest conservation success stories. As of 31 December 2010, there were an estimated 20,160 animals surviving in the wild, the majority of which (18,796) were in South Africa. Namibia (469), Kenya (365) and Zimbabwe (290) are the only other countries with over 250 wild Southern White Rhino, and together they conserve 82% of the subspecies outside of

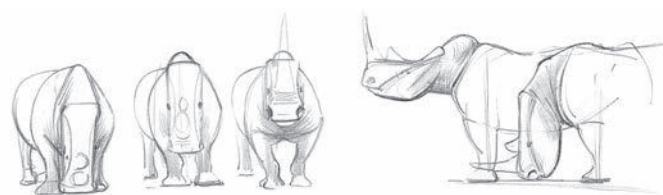
South Africa. Smaller populations exist in Botswana (135), Swaziland (88), Uganda (9), Zambia (7) and Mozambique (6) (Emslie 2011).

In iMfolozi, Southern White Rhinos had attained local densities exceeding 5/km², and a regional density of 3/km², at the time of Owen-Smith's study in 1970 (Owen-Smith 1973). The species constituted about half of the total biomass of large mammalian herbivores. Numbers have subsequently been held below this level through regular live removals. The former high abundance of the species in favourable habitat is attested by reports from early explorers of up to 80 animals being seen during a day's journey with wagons through the Magaliesberg region of South Africa's North West Province (Harris 1838). In Kruger N. P., the growing White Rhino population has attained local densities of 0.5–1.4 animals/km² (Pienaar *et al.* 1993b).

The northern subspecies was locally, rather than generally, abundant (Roosevelt 1910), but several thousand must have occurred in five countries at the start of the twentieth century. In 1960, the population was estimated to have stood at about 2230 individuals (Emslie & Brooks 1999). Four animals were last seen in Garamba N. P. in the Democratic Republic of Congo in 2006 and only spoor found in 2007. Since then there have been no signs of rhino despite intensive ground-based searches, except for a 2–3-year-old poached carcass found in 2008, and it is now believed this population is extinct (Milliken *et al.* 2009, Emslie 2011).

Adaptations The most notable adaptations are those facilitating a grass diet, in particular the lengthened head, widened lips, absence of incisor and canine teeth in both jaws, and high-crowned premolars and molars, possessing convoluted enamel layers on their biting surfaces adapted to grinding up coarse food. The skin is extraordinarily dense, tough and inelastic, varying in thickness from 18 to 24 mm, although the epidermal layer is only 1 mm deep. Large apocrine sweat glands, with myoepithelial cells arranged round the ducts, are distributed over the body. Following extreme exertion, White Rhinos may suddenly become covered in sweat over the whole head and trunk region. Wallowing in pools of water or in mud aids in thermoregulation, although wallowing is not restricted to the mid-day period. The ears may play an additional role in heat loss, being moved around restlessly even when animals are apparently sleeping. The body temperature is fairly low (34–37°C), and may vary over a 3–5°C range during the course of the day (Allbrook *et al.* 1958, Wallach 1969). During mid-day, they congregate in shady rest-places usually situated on ridge-crests. Here they may slumber for up to 8 h during mid-summer, but the rest period is reduced during the cooler winter period. During cold, windy weather animals seek shelter in dense woodland patches. A subcutaneous layer of fat up to 50 mm in thickness may build up on the abdomen, providing a buffer against malnutrition during the dry season.

The nasal sinuses take up almost as much space in the skull as the brain, indicating strong dependency on olfaction. White Rhinos may respond to human scent at ranges as great as 800 m, and can follow the tracks of other rhinos over an hour later. Animals of the southern subspecies walk with head held low and nostrils close to the ground, such that in sandy soil the mouth may make a sinuous track, but the northern subspecies holds the head higher, probably because of the longer grass habitat. Hearing is sharp, but vision poor. Animals react to a person walking past in clear view at ranges of 80 m, but with some uncertainty. However, they appear unable to identify a motionless human observer at ranges greater than 15–20 m.



White Rhinoceros *Ceratotherium simum* grazing and head lift diagram.

The White Rhino is a hindgut fermenter with a capacious large intestine where digestion of plant fibre occurs. The mean retention time of dye-marked food particles in the digestive tract was around 60 h (Foose 1982). As a result of the prolonged retention about 50% of cell wall components of a standard grass hay may be degraded, a digestive efficiency lower than that of grazing ruminants but better than equids. Grass is cropped by grasping material between the upper lip and a pad on the lower lip, then breaking it off by inward movement of the lips or slight jerk of the head. The width of the bite is around 20 cm, the biting rate as much as 80/min, and height of cropping down to as low as 10 mm above ground level (Owen-Smith 1973, Shrader 2003). This enables these large animals to obtain an adequate rate of intake even from short grass swards. Defecation takes place 4–6 times per 24 h, and the boluses contain much coarse grass material.

White Rhinos drink daily during the wet season when water is abundant. During the late dry season when animals must travel perhaps several kilometres to water, they may drink only every 3–4 days. Drinking generally takes place during the late afternoon or early evening through to midnight, so that travelling to and from water occurs during the cooler hours. After wallowing in mud, animals rub various parts of the body against convenient trees, rocks or termite mounds, which become quite highly polished. This action may serve to remove ticks along with the mud. The mud coat may also serve some protection against biting flies.

Despite their large size, White Rhinos move quite gracefully with marked flexure of the carpal joints. The walking speed is 3.0–3.8 km/h. Animals generally trot with a high-stepping action while hastening from a human intruder, and can maintain this gait for several kilometres at a speed of 29 km/h. Galloping takes place only over short distances except by small calves, and the top speed is reported to be 40 km/h. In a study of locomotion and bone strength in the White Rhino, Alexander & Pond (1992) found that the stresses developed in the long bones in running are rather low, in comparison with other large mammals, suggesting that rhinoceros skeletons may be built to unusually high factors of safety.

Foraging and Food Strictly a grazer, with forbs normally constituting no more than about 1% of the diet. Occasional instances reported of White Rhinos chewing on woody stems, otherwise no browsing observed. In Hluhluwe–iMfolozi Park, they favour short grass areas where species of *Panicum*, *Urochloa*, *Digitaria*, *Sporobolus* and *Cynodon* predominate. Such species can constitute over 50% of the diet during the wet season. Since some of these grass species grow in a tufted form elsewhere, a prostrate growth form appears to be cultivated by the grazing pressure of White Rhinos. Much foraging occurs around termite mounds, sites of former human habitation and other areas where nutritious short grasses prevail. During the dry season White Rhino transfer their grazing more towards taller tuft-forming grass species, especially *Panicum maximum* growing

under tree canopies and *Themeda triandra* in more open areas. The latter species can constitute up to half of the diet at this time of the year. Under extreme conditions they may extend their foraging up hillsides where tall grass reserves remain. Apart from lawn-forming species like *Cynodon dactylon* and *Dactyloctenium australe* growing under shade canopies, fibrous grasses growing in sandy soil areas are eaten little. Aromatic grasses like *Cymbopogon* spp. are rejected, although *Bothriochloa* is eaten when short. The grazing impact of White Rhinos promotes the formation of a mosaic interspersed of short and tall grasslands (Owen-Smith 1988, Waldram *et al.* 2007).

White Rhinos of the northern subspecies have been observed feeding on medium-tall grasses of the genera *Hyparrhenia*, *Panicum*, *Chloris*, *Heteropogon* and *Brachiaria* (Foster 1967, Van Gysegheem 1984). In Garamba N. P., *Loudetia arundinacea* was only grazed by White Rhinos when the grass was below 0.5 m in height. Recent park management promoted mosaics of short grass for feeding and long grass for cover, but the remaining rhinos were not at sufficiently high density to maintain lawns themselves. In the later wet season, their feeding was largely restricted to medium-tall grasses of the genera *Brachiaria*, *Pennisetum*, *Sporobolus*, *Cynodon*, bordering termitaria or occurring sparsely elsewhere, certain forbs growing on termitaria, and *Eleusine* along rivers.

White Rhinos are typically active for about 50% of the 24-h cycle, distributed equally between day and night, with most of this time spent foraging. Peak grazing activity occurs during the early morning and late afternoon, extending into the night. However, when food is plentiful daytime foraging activity is reduced. Foraging time tends to decline during the dry season, perhaps to conserve energy when only poor-quality grass is available. Greatest daytime activity occurs during the period of new grass growth at the start of the early wet season, and frequent wallowing indicates that animals are under much thermal stress at this time of the year when their feeding time extends towards the hot mid-day period.

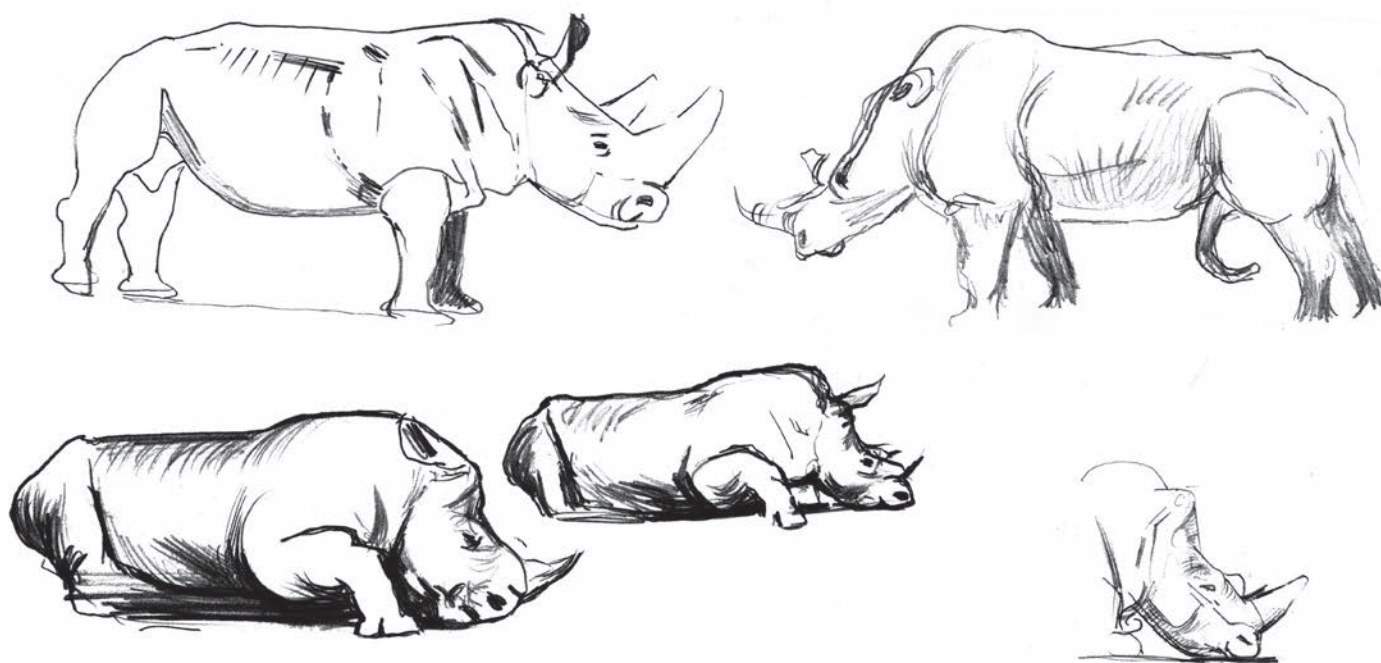
Social and Reproductive Behaviour Social organization is structured around the territorial system of adult ♂♂. Territories are occupied year-round by a dominant adult ♂, and perhaps shared with one or more subordinate adult ♂♂. They encompass 0.8–2.6 km² in high-density regions of Hluhluwe–iMfolozi Park (Owen-Smith 1975) and 2.6–9.0 km² elsewhere in this park (White *et al.* 2007), and are also larger in less favourable habitat: 2.5–13.9 km² in Ndumo G. R. in KwaZulu–Natal (Conway & Goodman 1989), 1.7–3.7 km² in Kruger N. P. (Pienaar *et al.* 1993b), 1.4–5.0 km² at Matobos in SW Zimbabwe (Rachlow *et al.* 1999), and 5–11 km² in SE Zimbabwe (Condy 1973). However, territories as large as 50–100 km² to more than 100 km² have been documented for low-density populations elsewhere (Roche 2000, P. Kretschmar pers. comm.).

Female home-ranges extend over 10–20 km² in Hluhluwe–iMfolozi Park, including a favoured core encompassing 5–10 km² where each ♀ spent most of her time while food and water remained abundant, but some individuals may move over much larger ranges (Owen-Smith 1975, White *et al.* 2007). Home-ranges of 40–50 km² are reported from elsewhere in southern Africa (Pienaar *et al.* 1993b, Rachlow *et al.* 1999). White Rhinos of the northern subspecies introduced into the E Nile region of N Uganda moved over annual ranges approaching 100 km² (Van Gysegheem 1984). In Garamba N. P., where the population is at very low density, adult ♂♂ ranged over areas of 125–

230 km², while ♀ home-ranges covered 200–500 km² (K. Hillman Smith pers. comm.). Both total home-ranges as well as the core areas of ♀♀ generally overlap extensively. Female home-ranges also encompass several female territories (Owen-Smith 1975, Pienaar *et al.* 1993b, White *et al.* 2007). Adult ♀♀ may temporarily abandon their home-ranges during adverse conditions, but return to them thereafter, although some individuals may shift home-ranges over their life-span (Owen-Smith 1973). In Garamba N. P., shifts in the home-range of a ♀ were sometimes associated with the birth of a new calf. Animals peripheral to a ♀ and her current calf tend mainly to be the older offspring of that individual (K. Hillman Smith pers. comm.).

Adult ♂♂ older than 10–12 years are basically solitary, but territory holders were temporarily associated with a ♀ and her companions on about 40% of occasions seen (more in the wet season, less in the dry season). Subordinate adult ♂♂ are likewise usually found alone, and associate only briefly with ♀♀. Adult ♀♀ are most commonly found in dyads consisting of a mother and her offspring, or a ♀ accompanied by a subadult that is generally not her progeny (Owen-Smith 1975). However, in Garamba N. P., 50% of female calves remained with or re-joined the mother and her next offspring (K. Hillman Smith pers. comm.). Occasionally, two adult ♀♀, both lacking an offspring, may join together for a period, and sometimes a young subadult attaches itself to a cow–calf pair to form a triad. Larger social groups may be formed where several subadults join up with a ♀ lacking a small calf, the largest such unit including eight individuals. Subadults most commonly form same- or mixed-sex pairs, triads or larger groups. Temporary associations numbering up to 16 individuals can be observed, usually with an adult ♀ as the core, especially where animals congregate around resting areas or waterpoints. Bonds between individual subadults can endure for several years. Subadult ♂♂ persistently form attachments until about ten years of age. Young ♀♀ separate from subadult companions following the birth of their first calf around seven years of age (Owen-Smith 1988).

Territory holders confine their movements year-round to within their own territories, except for excursions to seek water for drinking during the dry season. Territories are marked through spray-urination concentrated along boundaries, and dung scattering performed at large hollowed-out dung heaps at borders. Territory holders also add their contributions to the middens formed where other rhinos have defecated. Subordinate ♂♂ restrict their movements mostly to a single territory, but do not scatter their dung or spray-urinate. Two dominant ♂♂ meeting at a mutual territory border engage in silent, repetitive horn-against-horn contacts interrupted by wiping the anterior horn on the ground. After periods varying from a few minutes to an hour or longer, the ♂♂ disengage back into their own territories. Fights may develop where a territory holder crossing a neighbouring territory on his return from water is accosted by a rival ♂, and unable to back away to his own territory. Otherwise territorial ♂♂ behave subordinately while off their home territory. Subordinate ♂♂ stand their ground with loud roars and shrieks when confronted by a territory holder, and hold their ground until the territory holder wanders off, having reinforced the dominance relationship. A ♂ displaced as territory holder may remain on as a subordinate, or seek to claim dominance in another territory. Fights can be quite severe, with ♂♂ battering one another around the head, belly and groin with their horns, and not uncommonly result in the death of the loser (Owen-Smith 1975).



White Rhinoceros *Ceratotherium simum*.

If a territory holder detects that a ♀ is about to enter oestrus, he attempts to hold her within his territory until receptivity develops. This entails blocking any movements by the ♀ and her companions to cross over a territory border region, accompanied by loud squeals by the ♂ and threatening roars in response by the ♀. This pro-oestrous consort period lasts a few days to two weeks or longer. Periodically the ♂ sniffs urine deposits, exhibiting the lip-curl (flehmen) posture, as well as dung from the ♀. Courtship begins with approaches by the ♂ accompanied by a hic-throbbing sound. Initially, the ♀ wards off such advances with aggressive roars. After several hours of repeated advances her aggression becomes muted, and the ♂ is able to rest his head on her rump. Eventually mounting, and ultimately intromission, takes place. Copulations last 15–30 min, with repeated ejaculations. A single mating is the rule, with the ♂ continuing to accompany the ♀ for a few more days thereafter without further advances. Subordinate ♂♂ may sometimes attempt courtship when a ♀ is not accompanied by a territory holder, but opportunities are rare and ♀♀ ward off advances from subordinate ♂♂ quite vigorously (Owen-Smith 1975).

The ♀ seeks the seclusion of dense bush, long grass or other remote areas prior to giving birth. Calves follow after the mother when just a few days old. They are very inquisitive, and young animals display great curiosity upon meeting other groups. Calves and subadults, and sometimes even adults of both sexes, may approach each other to engage in playful horn wrestling, and sometimes counter-chasing, for a period. Calves continue to accompany their mothers until around the time of birth of the next offspring (i.e. until about 2–3 years of age). The older calf may be driven off shortly before the birth of the new infant, but in low-density populations ♀♀ may rejoin the mother.

Subadults tend to settle in home-ranges similar in extent to those of adult ♀♀, but these are usually somewhat transient. Subadults form temporary associations with adult ♀♀ or other subadults, and these companionships enable them to explore a wider area than that covered by their own home-ranges, through what has been termed a 'buddy system' (Shrader & Owen-Smith

2002). By reducing the risk of being attacked by territory holders, and uncertainty of finding food in the novel area, such shifting companionships facilitate later dispersal by subadults beyond the region where they were born. Females establish fixed home-ranges around the time of birth of their first calf, ♂♂ when they settle within a territory either as a subordinate or eventually as a territory holder. During their adult period, ♂♂ alternate between territory holder and subordinate status. Testosterone levels are higher in territorial than in non-territorial ♂♂ (Rachlow *et al.* 1998). The average duration of territory tenure within a particular territory exceeds five years. Ageing ♂♂ may eventually settle in retirement within a territory as a subordinate and forego further aspirations to reproduction.

White Rhinos make a variety of sounds, the most frequently heard being the snorts and roars associated with maintaining spacing among individuals. The squeals made by ♂♂ blocking ♀♀ at territory boundaries resemble squeals made by calves seeking to nurse from their mothers. Soft pants serve as a contact sound between companions, and are also made by a mother calling a lost calf. Calves may also make high-pitched mewling sounds when moving. White Rhinos have no alarm call, animals communicate alarm to companions solely by their agitated movements, and in Garamba N. P. have been recorded stamping on the ground and kicking their bellies to make a drum-like sound.

White Rhinos are often found in association with Fork-tailed Drongos *Dicrurus adsimilis*, which hawk insects by flying along the sides of resting rhinoceros, and with Red-billed Oxpeckers *Buphagus erythrorhynchus*, which feed on ticks and skin secretions. The birds also give a harsh alarm call to which the rhinos react immediately by looking around agitatedly to detect the source of the birds' reaction. Any sound or movement causes the animals to run off. Rhinos may remain alert and sensitive to the slightest sound for half-an-hour or longer. Why the birds should give this alarm is not obvious, but the call may serve as a rallying signal in anticipation of their host running off due to some impending danger.

Reproduction and Population Structure In the wild ♀♀ undergo their first oestrous cycles around 4–5 years of age (youngest 3.8 years), and produce their first offspring around 6.5–7 years of age (Owen-Smith 1988, Hillman Smith 2006). In captivity, ♀♀ as young as 4.3 years have given birth (Rieches 1998), but perhaps only because they had reached near adult size by this age due to a high plane of nutrition. In the wild, ♂♂ show reproductive interest around eight years of age, but are not able to contest for territorial dominance until they reach full size around 10–12 years of age (Owen-Smith 1975). In captivity, ♂♂ as young as 4–5 years of age have sired offspring (Rieches 1998).

Births in the wild occur throughout the year, but there is a peak during the early dry season months (Mar–Jul in southern Africa and Dec–Mar in the northern subspecies) (Owen-Smith 1988, K. Hillman Smith pers. comm.). This seems to be an outcome of the stimulating influence of fresh grass growth induced by rainfall on oestrous cycling 16 months earlier, indicated by a marked rise in the number of ♀♀ being accompanied by ♂♂ from Oct–Nov when the wet season commences. During the dry season few ♀♀ show signs of oestrus, and dry spells during the wet season also suppress behavioural indications of oestrus. Hormone profiles obtained from faecal samples indicate that cycling continues, although at a lower amplitude, during these periods of ‘quiet oestrus’ (R. Swaisgood pers. comm.). Under captive conditions some ♀♀ show irregular oestrous cycles, while others go for long periods without overt reproductive activity, and some even switch off completely.

Reproductive activity almost never develops when White Rhinos are housed as male–female pairs in zoos, but the species is not difficult to breed when kept in groups in large enclosures. The presence of more than one ♂, or introduction of a new ♂, seems to be a requirement for ♀♀ to solicit matings (Lindemann 1982, Patton *et al.* 1999). This phenomenon, which enables ♀♀ to exert some control over their choice of a mate, probably operates in the wild as well.

Gestation lasts 16 months with a single offspring born. Calves weigh about 65 kg at birth (range 45–75 kg), or around 3.5% of maternal weight. At birth, the skin is pale grey with a pink tinge. The outer horny layer of the skin is moulted at about 1.5–4.0 months, revealing a new paler skin, and a further moult takes place at about 10 months (Bigalke *et al.* 1950). The calf is born hornless, but in one study animal the anterior horn pierced the skin at five weeks, grew to 39 mm at three months and 100 mm at seven months. Infants less than two months old nurse hourly, while among older calves nursing takes place about every 2.5 h. Calves start nibbling grass at around two months of age, while weaning off mother’s milk takes place from 12–18 months, although occasionally extends to 24 months. The milk is low in fat and protein and high in carbohydrates.

Cows come on heat again when the calf is about 6–12 months old, so that the modal inter-birth interval is 2–2.5 years (minimum 22 months in the wild when the previous calf survived) (Owen-Smith 1988); results from Garamba N. P. were similar, where inter-calf intervals averaged 30 months over a 20-year period, with a range of 21–57 months (Hillman Smith 2006). However, some ♀♀ appear less fertile and may undergo several oestrous cycles of about 30 days duration (range 27–34 days; R. Swaisgood pers. comm.) before conceiving. Hence, at a population level, the mean inter-calving interval is about 2.5 years (and see Rachlow & Berger 1998), or even longer under unfavourable conditions. However, under zoo conditions one ♀ produced six calves

in nine years at an average interval of 18.5 months (Lindemann 1982).

Cementum line counts from tooth sections indicate a maximum longevity of 40 years (Hillman Smith *et al.* 1986), which approximates maximum longevity of 45 years recorded in captivity (Weigl 2005). Elderly ♀♀ exhibit lengthened calving intervals, but one obviously very old ♀ gave birth after a long period with no offspring.

The overall sex ratio of the Hluhluwe–iMfolozi population was close to parity (98 ♂♂ to 100 ♀♀) based on the 1969 census, i.e. prior to distortion by removals. However, the sex ratio of calves born around this time showed a strong male bias (167 ♂♂ to 100 ♀♀, $n = 232$), which had moved up into older age classes by 1974. Early zoo records also show a bias towards male offspring (147 ♂♂ to 100 ♀♀, $n = 121$; Lindemann 1982), but this has not persisted (e.g. 43 ♂♂ to 42 ♀♀ born in San Diego Wild Animal Park; Rieches 1998). In Garamba N. P. there was a strong male bias in calves born during the disturbances of the war period, but overall the birth sex ratio was close to parity (K. Hillman Smith pers. comm.). At Hluhluwe–iMfolozi, primiparous ♀♀ produced mainly sons, and old ♀♀ mostly daughters. Hence the male-biased sex ratio of offspring may have been a temporary phenomenon related to the high proportion of young ♀♀ in the expanding population (Owen-Smith 1988).

Because ♂♂ reach maturity around 10–12 years of age and ♀♀ around 7–8 years, the functional sex ratio in Hluhluwe–iMfolozi in 1969 showed a female bias overall (80 adult ♂♂ to 100 adult ♀♀, $n = 684$). The predominance of ♀♀ and calves was greater in regions where high rhino densities occurred in favourable habitat, while in outlying areas of less suitable habitat there was an even sex ratio among adults. Subadults constituted 32%, and calves <3 years 22% (10% <1 year). Because the population was expanding at this time, it exhibited a higher proportion of young animals than would a stable population (Owen-Smith 1988). The structure of the expanding population in Garamba N. P. was similarly about 40 : 30 : 30% adults to subadults to calves (K. Hillman Smith pers. comm.).

Annual mortality in Hluhluwe–iMfolozi was 1% for adult ♀♀, 3.5% for adult ♂♂ and 3.5% for calves. Mortality appeared somewhat higher among subadults. However, these rates are for a growing population, at a time when few animals would be dying of old age. Much mortality among adult ♂♂ is as a result of fighting injuries, and some subadults are also attacked fatally by territory holders. Neonatal mortality was under 8%. Based on these mortality rates, and an effective natality rate of around 0.4 per adult ♀ per year, the maximum sustained rate of population growth is about 9% per year. The actual rate of increase of the Hluhluwe–iMfolozi population over 1960–72, adjusted for removals, was 9.5% per year, perhaps because the growing population had not yet attained a stable age distribution (Owen-Smith 1981, 1988). The Kruger N. P. population has also been growing at around 9% annually (SANParks pers. comm.). Similarly, between 1983 and 2005, 50 births were recorded in Garamba N. P., and mean annual rate of population growth was about 9% (Hillman Smith 2006). From comparison with other megaherbivores, population regulation is expected to occur largely through lengthened birth intervals coupled with retarded age at first reproduction. However, dispersal movements by subadults of both sexes make an important contribution to dampening local population increases. In Hluhluwe–iMfolozi population growth was slower in the high-density population core than in outlying areas. This indicated a dispersal rate outwards from the core of about 3% per year overall, and about 7.5% per year specifically for subadults (Owen-Smith 1988).

Predators, Parasites and Diseases Adult White Rhinos are effectively invulnerable to predation by carnivores. However, young animals are susceptible to being killed by Lions *Panthera leo* and perhaps Spotted Hyaenas *Crocuta crocuta*. They gain security by associating in groups, and when disturbed adopt a rump-against-rump formation facing outwards in different directions. When threatened by the close approach of a human, ♀ ♀ with young calves stand guard over the calf and do not charge. The long anterior horn could aid in warding off a predator attack. When fleeing, young calves gallop ahead of their mothers, enabling the mother to maintain close contact with the whereabouts of her offspring.

A new threat has developed following the introduction of orphaned young elephants into wildlife parks where White Rhinos occur. Young male elephants nearing adulthood have directed their sexual and aggressive behaviour towards White Rhinos of both sexes, with substantial numbers of rhinos being killed (e.g. Slotow & Van Dyk 2001, Slotow *et al.* 2001). Such incidents are seldom recorded in places like Kruger N. P. where a well-established population of elephants exists.

White Rhinos in southern Africa generally have large swarms of a large blood-sucking fly *Rhinomusca dutoiti* resting on their sides. These flies lay their eggs in rhino dung middens where their larvae develop. Much smaller flies of the genus *Lyperosia* are also commonly associated with rhinos and their middens. Large numbers of gyrostigmatid fly larvae, up to 40 mm long, may be found attached to the stomach walls of rhinos. Small piroplasms (*Babesia* and possibly also *Theilaria*) have been found in blood samples (Keep 1970). Circumstantial evidence indicates that the deaths of three rhinos translocated into Matusadona N. P. in N Zimbabwe were due to trypanosomiasis infection (Taylor 1986), and mortality among animals translocated to East Africa could have been due to the same cause.

Theiler (1962) provided a detailed checklist of ixodid ticks recorded from White Rhinos, and Baker & Keep (1970) a checklist from KwaZulu–Natal. More recently, Knapp *et al.* (1997) updated the lists with their own studies and recorded eight ixodid tick species known to infect White Rhinos in South Africa and seven in Zimbabwe, including *Amblyomma hebraeum*, *A. sparsum*, *Hyalomma marginatum*, *H. truncatum*, *Rhipicephalus maculatus* and *R. simus*. Walker (1991) mentioned that the adults of two species, *Amblyomma rhinocerotis* and *Dermacentor rhinocerotinus*, feed primarily on African rhinos. Penzhorn *et al.* (1994) provide a checklist of the helminths of White Rhinos. Ciliated intestinal protozoa are reported on by Van Hoven *et al.* (1988) and Obanda *et al.* (2008).

Conservation IUCN Category: Near Threatened (*Ceratotherium simum cottoni* – Critically Endangered A2abcd; B2ab(i,ii,iii,v); C1+2a(i,ii)b; D; E). CITES: Appendix I (excluding populations from South Africa and Swaziland, which are on Appendix II).

White Rhinos lived in abundance alongside indigenous peoples in southern Africa. The Zulus did not regard their flesh as edible and so did not hunt them. Only when white adventurers arrived with guns, and rhino hide and horns became a trade commodity, did the situation change. Animals were easily found by waiting at waterholes in the dry season, so that some hunters killed nearly 100 within a single year. Within about 50 years the southern subspecies was reduced to the verge of extinction. The last animals were shot in Botswana during the late 1870s and in Zimbabwe in 1893 (see Rookmaaker 2003b). A remnant pocket of White Rhinos surviving near the Umfolozi R. in South Africa was given legal protection when the Umfolozi G. R. was

proclaimed in 1897. A few individuals persisted in a remote region of Mozambique until the 1930s, when the last individuals were shot.

The first conservator claimed that only 20 White Rhinos remained in the then Umfolozi G. R. when he arrived in 1911. This was almost certainly an underestimate, because the first counts made around 1930 indicated a total population of over 200. Rookmaaker (2002) suggests that there were never less than 200 White Rhinos in Zululand before 1929. However, a founding remnant of 20–50 animals at the beginning of the twentieth century would be consistent with the subsequent population increase (Emslie & Brooks 2002b).

All surviving White Rhinos of the southern subspecies are derived from this remnant. Under protection the White Rhino population grew to reach about 550 in 1948, and about 1800 by 1968 (Emslie & Brooks 1999). Concerned by the risks associated with this single population, the then Natal Parks Board began trials on live capture using drugged darts in 1961. By 1970 a total of 730 White Rhino had been translocated to other parks, but 2000 animals still remained within the enlarged Hluhluwe–iMfolozi complex. The new concern was overpopulation within the now fenced confines of the protected area, which led to the study by Owen-Smith (1973). The immediate management response was an accelerated capture and removal programme, aimed at reducing the population below this high level, restocking the species through its former range, and supplying animals to various zoos (and see Player 1972).

The ecological recommendation from this research was to restrict White Rhino removals to designated dispersal sinks, or vacuum zones (Owen-Smith 1973, 1974, 1981). The aim was to allow the core population to adjust naturally to changing food resources while providing a safety outlet within the fenced area. This policy was eventually put into effect in 1985, but following several adjustments to the sink locations only became properly effective in 1998. Animals of suitable age classes and reproductive status settling within the sink areas are captured and offered for sale annually.

By December 2010, Southern White Rhino numbers stood at an estimated 20,160 (Emslie 2011), up from 6784 in 1993, 7532 in 1995, 8441 in 1997, 10,377 in 1999, 11,640 in 2001, 11,320 in 2003, 14,550 in 2005 and 17,475 in 2007 (Emslie & Brooks 1999, Emslie 2004a, Emslie *et al.* 2007, Milliken *et al.* 2009). The small drop between 2001 and 2003 does not reflect an actual decline in numbers as the difference is due to a lower population estimate for the biggest population (Kruger N. P.). There is no evidence of any actual decline in this park, and the difference is almost certainly an artefact of the sampling variability inherent in the method used to estimate numbers for this large population. Kruger's rhinos are descendants of just 336 founder animals (D. Pienaar pers. comm.). As of December 2010, South Africa held 93% (18,796) of the wild White Rhino population, predominantly in Kruger N. P. (10,500 animals) and Hluhluwe–iMfolozi Park (2312). While the state-run conservation agencies continue to manage most of the White Rhinos in Africa (72%), the private sector also manages a significant proportion (5504, 27%) with likely in excess of 5000 White Rhinos on private land in South Africa (AfRSG data unpubl.).

Around 1960–62, Garamba N. P. and surrounding reserves in NE DR Congo contained more than 1200 Northern White Rhinos, before armed rebels and others reduced the population to 100–200 during the rebellion following independence (Bourliere 1965, Curry-Lindahl 1972, K. Hillman Smith pers. comm.). White Rhinos increased again to about 500 in 1976 (Savidge *et al.* 1976), but between then and

1984 poaching for rhino horn reduced the population by 97% to just 15 animals (five adult ♀♀, six adult and one subadult ♂, and three juveniles) in the southern third of the park (Hillman Smith 2006). The Garamba Project was started in 1984, supported by a coalition of donors, and under protection the remnant population doubled to 30 by 1992 (0.015/km²), but following an upsurge in poaching from mid-2003 (11 carcasses were found in a three-month period between Mar and May 2004 alone), surveys counted only four individuals in the park and up to another four in an adjoining hunting area (Hillman Smith *et al.* 2003, Hillman Smith & Ndey 2005). Given the critical situation and unsustainable levels of poaching, an emergency plan to temporarily translocate five animals to a Kenyan sanctuary was developed, but this was not implemented due to internal political reasons. A survey in 2006 (Emslie *et al.* 2006) only counted two rhinos with another two different animals being seen subsequently. In recent years, there have been no signs or sightings of animals (one carcass was found in 2008), and it is feared this population is now extinct. Until the 1970s, White Rhinos were reportedly seen by hunters in E Central African Republic and S Chad, but their continued existence there seems unlikely. Fewer than 300 were estimated to occur in S Sudan in 1981, but this population also seems now extirpated (Hillman Smith 1981). The species became extinct in Uganda by 1982 (Edroma 1982).

CITES has downlisted South Africa's, and more recently Swaziland's, White Rhinos from Appendix I to Appendix II, allowing limited trade in live animals although not in products like horns. Hunting is permitted under strictly controlled conditions. Whether international trade in rhino horns should be allowed in order to generate funds to conserve this and other rhinoceros species effectively remains highly contentious, especially in the context of the hugely escalated illegal trade through 2009–12, due to rising demand particularly in Vietnam. In 2011 alone, around 450 individuals were killed by poachers, about half in Kruger N. P. Unless effective counteraction is implemented, further escalation of the killings could lead to a down-turn in the population trend of the species and reverse the conservation gains of the past.

Although captive breeding of Southern White Rhinos has been successful (but see Swaisgood *et al.* 2006), especially where a number of animals were held in large enclosures, captive reproduction of Northern White Rhinos has been less so. Emslie & Brooks (1999) noted the last birth among nine individuals held in two zoos had taken place in 1989 (Dvur Kralova in the Czech Republic, and at San Diego Zoo in the USA). At the time of going to press, the last four potential breeding animals from Dvur Kralove Zoo in Czech Republic had been introduced to a private reserve in Kenya. The animals are all related and the ♂♂ are very old, and the best that probably can be hoped for is to conserve some adaptive Northern White Rhino genes by inter-crossing with the southern subspecies. As of December 2005, there were more than 750 of the southern subspecies in zoos worldwide (Emslie *et al.* 2007).

Measurements

Ceratotherium simum simum

HB (♂♂): 3710 (3620–3800) mm, n = 3

HB (♀♀): 3480 (3370–3630) mm, n = 5

T (♂♂): 870 (700–1200) mm, n = 3

HF: n. d.

E: 250 mm*

Sh. ht (♂): 1740–1850 mm*

Sh. ht (♀): 1710–1770 mm*

WT (♂): max. 2300 kg*

WT (♀): max. 1700 kg*

KwaZulu–Natal, South Africa (Owen-Smith 1973)

*Sample number and range not given

Ceratotherium simum cottoni

HB (♂♂): 3660 (3590–3750) mm, n = 4

HB (♀♀): 3120 (2990–3220) mm, n = 4

T: 670 (610–740) mm, n = 5**

E (♂♂): 320 (280–340) mm, n = 3

E (♀♀): 300 (270–340) mm, n = 7

HF: n. d.

Sh. ht (♂♂): 1730 (1630–1820) mm, n = 3

Sh. ht (♀♀): 1530–1770 mm, n = 3

WT: n. d.

Garamba N. P., DR Congo (K. Hillman Smith pers. comm.)

**Sexes combined

Body length increases with age and approaches an asymptote at around 14 years, but chest girth only attains an asymptote at around 20 years (Rachlow 1997)

Skull and horn measurements:

Ceratotherium simum simum

Anterior basal circumference (♂♂): 730.4 ± 65.0 mm, n = 65

Anterior basal circumference (♀♀): 610.0 ± 34.4 mm, n = 39

Anterior horn length (♂♂): 583.4 ± 141.9 mm, n = 72

Anterior horn length (♀♀): 589.4 ± 98.0 mm, n = 107

Anterior horn WT (♂♂): 6.1 ± 1.8 kg, n = 91

Anterior horn WT (♀♀): 4.0 ± 1.5 kg, n = 33

Posterior horn WT (♂♂): 2.2 ± 1.1 kg (n = 69)

Posterior horn WT (♀♀): 1.2 ± 0.7 kg (n = 19)

Kruger N. P., South Africa (Pienaar *et al.* 1991, Pienaar 1993)

Anterior horn length (♂♂): 640 (620–660) mm, n = 4

Anterior horn length (♀♀): 720 (620–820) mm, n = 5

Posterior horn length (♂♂): 310 (270–390) mm, n = 3

Posterior horn length (♀♀): 200 (160–260) mm, n = 5

KwaZulu–Natal, South Africa (Owen-Smith 1973)

Ceratotherium simum cottoni

Anterior horn length (♂♂): 650 (560–740) mm, n = 4

Anterior horn length (♀♀): 540 (480–590) mm, n = 4

Posterior horn length (♂♂): 195 (143–235) mm, n = 4

Posterior horn length (♀♀): 194 (180–210) mm, n = 4

Garamba N. P., DR Congo (K. Hillman Smith pers. comm.)

The record length for the Southern White Rhino is an animal from South Africa which had a front horn measuring 1581 mm; its accompanying rear horn was 566 mm. For the Northern White Rhino, the record front horn length is 1273 mm and 559 mm for the rear, for an animal from East Africa (Selous 1899).

Key References Emslie & Brooks 1999, 2002a, b; Meister & Owen-Smith 1998; Owen-Smith 1973, 1975, 1988; Pienaar *et al.* 1991, 1993a, b; Rachlow *et al.* 1999; Shrader & Owen-Smith 2002; White *et al.* 2007.

Norman Owen-Smith

GENUS *Diceros* Black Rhinoceros

Diceros J. E. Gray, 1821. London Med. Repos. 15: 306.

Diceros is a polytypic genus, represented by a single extant species, the Black Rhinoceros *Diceros bicornis*. This species once was widespread in sub-Saharan Africa, from the Niger R. in the west to Somalia in the north-east, and southwards to South Africa. It was never found in the Congolese rainforests. The animal exists in a large variety of habitats, including savanna, bushveld and dry thornbush, from sea-level to high mountain forests.

The members of *Diceros*, like the other extant African rhinoceros genus *Ceratotherium*, bear two nasal horns. *Diceros* is distinguished from *Ceratotherium* by the shorter skull, pointed upper lip, swayed back, and generally smaller size (Guggisberg 1966, Hillman Smith & Groves 1994, Joubert 1996). The extinct rhino from the regions around the Cape of Good Hope was larger than other populations (Rookmaaker & Groves 1978). Inter-specific hybridization has occurred between a female *Ceratotherium simum simum* and a male *Diceros bicornis* kept in an 800 ha enclosure of South Africa's National Zoological Gardens Game Breeding Centre (Robinson *et al.* 2005).

Fossil remains of species referable to *Diceros* have been found in many parts of Africa. *Diceros douariensis* was found in the Mio-Pliocene of Tunisia (Guérin 1966) and *Diceros australis* in deposits of the middle Miocene of Namibia (Guérin 2000). In East Africa, the genus was represented by *Diceros praecox* in the early to late Pliocene



Black Rhinoceros *Diceros bicornis*.

(Geraads 2005), although previously some of the remains had been classified under *Ceratotherium* (Hooijer & Patterson 1972). *Diceros bicornis* first appears at the 4 mya level in Pliocene deposits in Kenya and Ethiopia, and at 2.5 mya the molar crowns became as high as in the recent specimens (Hooijer 1978, Prothero *et al.* 1986).

Kees Rookmaaker

Diceros bicornis BLACK RHINOCEROS (BROWSE RHINOCEROS, HOOK-LIPPED RHINOCEROS)

Fr. Rhinoceros noir; Ger. Spitzmaul-Nashorn

Diceros bicornis (Linnaeus, 1758). Syst. Nat., 10th edn, 1: 56. 'Habitat in India', but Cape of Good Hope, fide Thomas (1911).

Taxonomy Groves (1967) reviewed earlier classifications and reduced the number of subspecies recognized based on cranial dimensions and other characters to seven in different regions of Africa. This classification has since been questioned, as it was based on small sample sizes (du Toit 1986), and was not supported by a preliminary analysis of data from more skulls (du Toit 1987). A proposal from a 1986 African Rhino Workshop in Cincinnati was adopted by the first IUCN African Elephant and Rhino Action Plan (Cumming *et al.* 1990) resulting in the recognition of four Black Rhino ecotypes or 'subspecies' conservation units (Cumming *et al.* 1990). The IUCN Species Survival Commission's African Rhino Specialist Group recognized these four subspecies conservation units in different areas (Emslie & Brooks 1999) although only three survive: Southern-central (*Diceros bicornis minor*); South-western (*D. b. bicornis*); and Eastern (*D. b. michaeli*); the Western (*D. b. longipes*) was recently declared extinct.

Historically, the boundaries between these subspecies were not 'hard-edged', in contrast to the markedly discontinuous range of the two White Rhinoceros *Ceratotherium simum* subspecies. However, there are major differences in the habitat and climates in the core areas of the three remaining subspecies, and it is likely that each has specific genetic or behavioural adaptations to the environment. While some conservationists have preferred to refer to the Black Rhino subspecies as ecotypes due to their contiguous distribution and perceived

limited genetic differences between them, genetic analyses indicate that the Southern-central, South-western and Eastern Black Rhino are sufficiently distinct to support the current subspecies distinction (Harley *et al.* 2005). The more discontinuous distribution of the recently extinct Western Black Rhino, and the single genetic sample analysed to date, support its classification as a separate subspecies (Harley *et al.* 2005). Genetic variation in mitochondrial DNA of *D. b. minor* (from Zimbabwe animals) and *D. b. michaeli* (from East Africa) revealed that these two subspecies represent separate ancestral lineages, which diverged between 0.93 and 1.3 million years (Brown & Houlden 2000). These genetic studies support recognition of four subspecies, although K. Rookmaaker (pers. comm.) notes they too were also based on small sample sizes and ignored many populations.

Controversy surrounds the formal subspecies nomenclature. *Diceros b. bicornis* has been described as being restricted to the Western Cape and further north, at least to middle Namibia, and is believed to have gone extinct (Ansell 1974, Rookmaaker & Groves 1978) leading to a questioning of the use of the subspecies name *D. b. bicornis* to refer to the animals derived from the surviving arid-adapted animals from N Namibia (Hopwood 1939, Groves 1967, Rookmaaker 2005b, P. Lloyd pers. comm.). However, this view has been challenged. It has been argued that the animals from N Namibia can be amalgamated with those in the Western Cape and

S Namibia that died out (Hall-Martin 1985, Du Toit 1987), on the basis that (1) the largest skulls Du Toit (1987) measured were from N Namibian animals, which was in keeping with Rookmaaker & Groves' (1978) description of *D. b. bicornis* in the Western Cape and S Namibia as a very large rhino; and (2) on the ecological similarities between the earlier postulated range of *D. b. bicornis* and that of extant Namibian rhino (Hall-Martin 1985). Further evidence supporting this amalgamation (which may be correct; Rookmaaker 1996) comes from an old map of Greater Kudu *Tragelaphus strepsiceros* distribution in Namibia (Shortridge 1934), which shows this species had a contiguous distribution along the Molopo, Nossob, Oliphant, Auob, Great Fish and Orange Rivers (i.e. all the way to the south of the country and well into the supposed range of *D. b. bicornis*). Dietary overlap (for both species and size classes) between Greater Kudu and Black Rhino can be quite considerable (Macfarlane 1997), and it has been noted that where Greater Kudu generally do well, the Black Rhino normally also thrives. For these reasons, it is quite possible that at one time there may have been a continuous distribution of Black Rhinos from N Namibia all the way to the Western Cape supporting the current use of the *D. b. bicornis* subspecies name (although much of the clinal genetic variation in the southern part of the range will have been lost). This is the view currently adopted by the SADC Rhino Management Group (SADC RMG).

The current boundary between the South-western and Southern-central subspecies in southern Africa is somewhat arbitrary, imperfectly known and is primarily a practical construct given that all populations of these two subspecies in South Africa outside of Hluhluwe–iMfolozi and uMkhuze in KwaZulu–Natal have been reintroduced. Following from earlier Conservation Plans, the South-western Black Rhino is today considered as the most arid-adapted subspecies. In earlier versions of the South African Black Rhino management plan, the SADC RMG, which manages the plan, used the 400 mm isohyet from Dent *et al.*'s (1989) mean annual precipitation map in Schulze (1997) as the primary basis for setting a putative east/west subspecies boundary in the Eastern Cape. However, since 2007, the subspecies boundary in the Eastern Cape has been revised to take into account the probable impact of a 'Transkei Gap' on rhino movement. This area, in the north-east of the province north of the Kei R., has now been classified as extralimital, and no new populations of Black Rhino will be allowed to be established in this area. The remainder of the province is now designated as *D. b. bicornis* range together with the Western Cape and Northern Cape provinces. Although no new populations will be countenanced, any existing Eastern Cape *D. b. minor* populations are being allowed to remain. Other provinces are demarcated as *D. b. minor* range. Rhinos in the miombo woodlands of the Selous G. R. in S Tanzania are classified as being Southern-central Black Rhinos, while the populations in N Tanzanian areas with more nutrient-rich soils and a dual wet season are classified as being Eastern Black Rhinos. While these classifications of Tanzanian Black Rhinos on habitat and climatic grounds, as well as surviving populations' proximity to rhino populations in neighbouring countries seems reasonable, there have been no genetic analyses to test their validity. Rookmaaker (2005b, pers comm.) argues that due to changes in the perceived geographical ranges for the four groups, and the Principle of Priority, Code of Zoological Nomenclature (4th edition para 23), *D. b. minor* and *D. b. michaeli*

should automatically be renamed *D. b. keitloa* and *D. b. brucii*, respectively (given the current AfRSG subspecies classification and distribution). On account of such concerns about the current classification and subspecies distributions, a continent-wide revision of Black Rhino taxonomy is needed.

Synonyms: *africanus*, *angolensis*, *atbarensis*, *brucii*, *camperi*, *capensis*, *chobiensis*, *gordoni*, *holmwoodi*, *keitloa*, *ketloa*, *ladoensis*, *longipes*, *major*, *michaeli*, *minor*, *niger*, *nyasae*, *occidentalis*, *palustris*, *platyceros*, *pleioceros*, *porrhoceros*, *punyana*, *rendilis*, *somaliensis*. Chromosome number: $2n = 84$; the X chromosome is a large submetacentric (Hungerford *et al.* 1967, Heinichen 1969b, Houck *et al.* 1995). Robinson *et al.* (2005) have recently confirmed a case of inter-specific hybridization in rhinoceroses, wherein a calf was born to a young White Rhino cow and a Black Rhino bull held together in a small enclosure (without an adult White Rhino bull being present); the hybrid showed a mixture of phenotypic traits characteristic of the two species, including ear shape resembling that of the Black Rhino, an upper-lip more in keeping with the shape of the White Rhino (but also exhibiting a small upper-lip protrusion, not unlike the prehensile lip in the Black Rhino), and head length was intermediate between the two. It is not known if the hybrid was reproductively impaired.

Description Second smallest of the rhino species, with the Sumatran Rhino *Dicerorhinus sumatrensis* being smaller. Stands about 1.6 m at the shoulder and has a mass of around 800–1350 kg. Sometimes known as the Hook-lipped Rhino on account of its hooked prehensile upper lip, which it can use like an elephant's trunk to grab hold of branches and pull them into the mouth (unlike the grazing White Rhino, the Black Rhino is a browser eating primarily trees, bushes, herbs and succulents). In silhouette the neck hump is not as pronounced as that of the White Rhino. The much smaller head is generally held higher than the White Rhino, unless feeding at ground level. Back has a much more concave saddle-like appearance in profile compared with the White Rhino whose prominent vertebral crest two-thirds of the way along the back is much more pronounced. Ears rounded and trumpet-shaped, tips pointing upwards from the middle of the ear. Ears fringed with hair (as in the White Rhino), and the amount of hair on the ears varies between individuals. Body hairs otherwise sparse. Body barrel-shaped due to an extended ribcage. Overall body colour a marginally darker battleship grey than that of the White Rhino. However both species of rhino can take on the colour of the soil and mud in which they have been wallowing. Eastern subspecies has marked rib-like skin folds on its flanks. There are also prominent folds of skin near the top of the forelimbs, and where the upper part of each hindlimb joins the body. Limbs thickset with three toes on each foot, each with large nails that mark clearly in the spoor. Toes and feet smaller than those of the White Rhino and so spoor of the Black Rhino is smaller, more rounded and with smaller toe prints compared with the White Rhino, whose spoor is more elongated in appearance with a more pronounced groove in the middle of the back of the print. Cushioned pads on the soles of the feet have a hard surface with a mosaic of irregular cracks; the patterns can be used to identify individual animals for short periods of time, as they can change. Tail is short with a sparse fringe of bristly hairs. Some animals may miss part of their tails, and it is thought this is caused by unsuccessful hunting attempts by Spotted Hyenas *Crocuta crocuta*.



Black Rhinoceros *Diceros bicornis*.

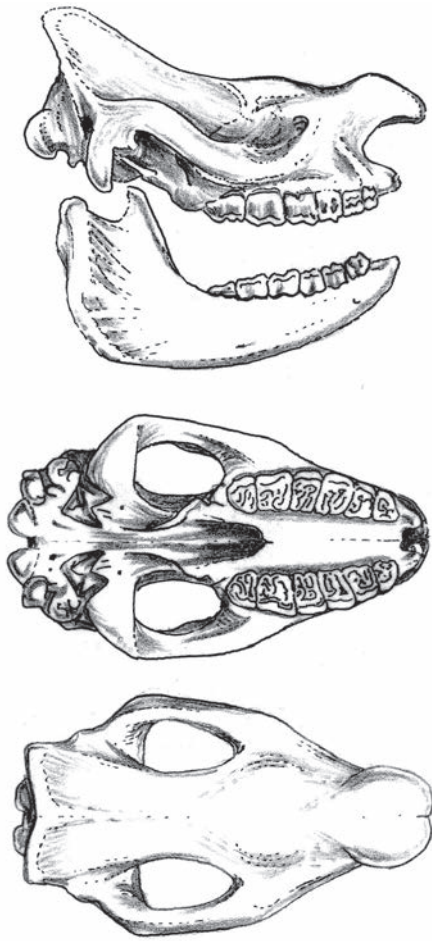
Two horns present on snout; these are made up of compressed keratinous fibres and do not have a bony core. In general, the anterior horn is invariably longer than the posterior horn. For example, in Hluhluwe–iMfolozi in 1973 only 2.5% of ♂♂ had anterior horns equal in length to the posterior, and none shorter ($n = 120$); in 1985, no ♂♂ had anterior horns equal in length or shorter than the posterior. Incidence is slightly higher for ♀♀: 5.7% shorter in 1973 ($n = 106$) and 4.3% in 1985 ($n = 69$) (Hitchins 1989). Horn length and basal circumference greater in adult ♂♂ than in adult ♀♀. In a sample of horns from KwaZulu–Natal and Kruger N. P., the mass of anterior and posterior horns amounted to some 2.65 kg of horn per animal (Pienaar *et al.* 1991, Pienaar 1993; see Horn Measurements). Base of the anterior horn is circular in shape in contrast to the White Rhino, whose anterior horn has a squarish base. In general Black Rhino horns are thinner and less chunky than White Rhino horns. Intrinsic anterior horn growth is similar to the White Rhino (Pienaar *et al.* 1991, Rachlow & Berger 1997). Berger *et al.* (1993) determined regrowth rates for dehorned Black Rhino at 60 mm and 27 mm per year for anterior and posterior horns, respectively; regrowth was more rapid in juveniles, at 89 mm and 44 mm per year, respectively. Horns from both African species are much larger than those of the three Asian species. Chemistry (carbon and nitrogen isotope ratios) of rhino horn differs between the two species reflecting their different diets (Lee-Thorp *et al.* 1992, Emslie *et al.* 2001, Amin *et al.* 2003).

Females bear two inguinal nipples. Males lack a scrotum, and the muscular penis points backwards when enclosed in its sheath. Apart from genitalia, there is little sexual dimorphism, except that ♂♂ attain a bigger body mass than ♀♀, and have noticeably more heavily set chests and necks. In the Southern-central Black Rhino, ♀♀ invariably have thinner longer horns compared with adult ♂♂, which tend to have shorter chunkier horns. However, Eastern Black Rhino horns do not clearly exhibit this trend.



Rhinoceros forelimbs.

Skull is shorter than that of the White Rhino, the supraoccipital crest not extending upwards and backwards to the extent seen in the White Rhino. Occipital crest lacks broad rugose area on top characteristic of the White Rhino, while zygomatic arches are heavily built to give a firm attachment for the masseter muscles that activate the massive lower jaw. The adult dental formula is $I^{0/0}, C^{0/0}, P^{4/3-4}, M^{3/3} = 26-28$. One to two lower incisors in the deciduous dentition. In the adult dentition, sometimes only three premolars are present in the upper and lower jaws. Upper and lower second molars are the largest of the cheekteeth (Skinner & Chimimba 2005). Goddard (1970b) and Hitchins (1978) describe patterns of tooth eruption and toothwear patterns. A slightly modified version of Hitchins' (1978) visual scale together with using horn configuration information (Module 6 of Adcock & Emslie 2004) has become the standardized method used for visually ageing animals across the continent using a six category A–F scale.



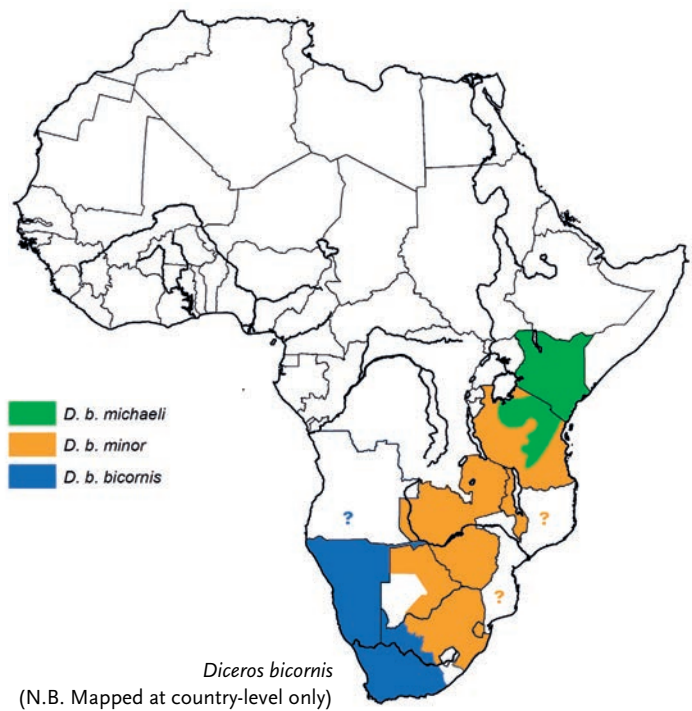
Lateral, palatal and dorsal views of skull of Black Rhinoceros *Diceros bicornis*.

Geographic Variation

D. b. longipes (Western Black Rhino). Formerly occurred in the savanna of central–West Africa, and latterly confined to N Cameroon; recently declared extinct by the IUCN following the failure of surveys to find any surviving individuals. Slightly longer legs relative to body length (hence the subspecies name *D. b. longipes*). The high degree of homozygosity across the nine loci studied in the single Western Black Rhino sample showed the least genetic diversity of all the individuals examined, and was consistent with a major loss of genetic diversity in this population (Harley *et al.* 2005).

D. b. michaeli (Eastern Black Rhino): historically, in S Sudan, Ethiopia, Somalia to Kenya, NC Tanzania and Rwanda; currently only confirmed surviving in Kenya, N Tanzania and Rwanda, with an extralimital population established in South Africa in Limpopo Province. Longer, more slender and more curved horns than the two southern subspecies; noticeable skin folds, which resemble ribs on its flanks (these folds are not obvious in the other subspecies).

D. b. minor (Southern-central Black Rhino): KwaZulu–Natal in South Africa through Swaziland, Mozambique (where now possibly extinct), Zimbabwe, N Botswana (reintroduced), and Malawi into W and S Tanzania. Formerly in N Angola and S DR Congo. Smallest of the subspecies and in some parts of its range is vulnerable to developing large red sores on its chest (see Predators, Parasites and Diseases).



D. b. bicornis (South-western Black Rhino): formerly in Namibia, S Angola, W Botswana and Western Cape and Eastern Cape, south of Kei R. (South Africa), though now extinct in Botswana with perhaps a few individuals surviving in S Angola. Largest of the subspecies; in some parts of the range, and most noticeably in the very arid west Kunene region in NE Namibia, often possesses very thick straight horns (the anterior horns of other Black Rhino subspecies are invariably slim and curved when the animal is adult).

Similar Species

Ceratotherium simum. Sympatric over various parts of the range of the Southern White Rhino (although historically had a more restricted distribution than the Black Rhino). Considerably larger, with lips broadly squared rather than hooked upper lip (indicative of its preference for graze not browse); pronounced nuchal hump visible when the head is raised; skull longer and narrower, with occipital part produced backwards beyond the condyles; high crowned molars and premolars adapted for grazing; more-pointed ears, with tips pointing sideways from the outside edge of the ear.

Distribution

Historical Distribution The probable distribution of the Black Rhinoceros ca. 1700 encompassed pretty much the whole of southern and eastern Africa, including S Angola, and all but the arid south-west strip of Namibia and the north-western parts of Zambia. The far east of DR Congo served as the probable western edge of the distribution with a northernmost distributional band (500–1000 km wide) stretching westwards from S Somalia through Ethiopia, S Sudan, S Chad, N Central African Republic, N Cameroon and N Nigeria (see Cumming *et al.* 1990, Emslie & Brooks 1999).

The former westerly limit of the species, and its distribution in West Africa as a whole, has been investigated by Rookmaaker (2004), who could find no evidence of the existence of the species in Senegal, Gambia, Mali, Guinea Bissau, Guinea, Sierra Leone, or from Ghana,

Togo and Benin. In addition, evidence from Liberia and Burkina Faso mainly rested upon the existence of indigenous names for the species in these countries. Furthermore, records from N Côte d'Ivoire could not be substantiated, the sighting of tracks in 1853 by Heinrich Barth in Niger on the western bank of the river seemingly the only reliable evidence from that region. Based on this, Rookmaaker (2004) proposed two options for the historical distribution of the Black Rhino in 1700 (perhaps coinciding with that in 1900): first, on the basis of the footprints seen by Barth, the species may have occurred westward up to longitude 1°E near the Niger R.; or, second, the western boundary of the range could be placed some 700 km further eastward in the north-central part of Nigeria.

Early in the nineteenth century, the Black Rhino was still the most numerous of the world's rhino species, with several hundred thousand rhinos roaming the African continent from central–West Africa to the slopes of Table Mountain in the far south (Emslie & Brooks 1999). Early European travellers reported Black Rhino to be both widespread and common throughout much of the continent.

Current Distribution Whereas in 1980, Tanzania, Zambia and the Central African Republic were the major range states for the Black Rhino (probably holding around two-thirds of the continent's animals), currently, 98% of the continent's wild Black Rhinos occur in four range states: South Africa, Namibia, Zimbabwe and Kenya (Milliken *et al.* 2009). The same four states also conserve 96% of Africa's wild White Rhinos (Milliken *et al.* 2009). Today, the Black Rhino is extinct in the Central African Republic, and, with the failure of recent surveys to locate any surviving individuals in N Cameroon, has been declared extinct. Smaller numbers of Black Rhinos occur in Tanzania, while small numbers have also been reintroduced into Malawi, N Botswana, Swaziland and Zambia. A very few Black Rhino have been reported to survive in S Angola, while a single animal has been seen in Mozambique (Emslie 2011). A lone individual in Akagera N.P., Rwanda (Milliken *et al.* 2009) has now died; presence in Ethiopia has not been confirmed.

Habitat The Black Rhino can occur wherever herb and woody browse occurs in sufficient amounts to support a population. As a result, Black Rhinos can survive in a wide range of habitats, including deserts, semi-deserts, wooded savannas, woodlands, forests and even sub-alpine heathlands (up to 3700 m on Mt Kenya; Young & Evans 1993). They occur in areas with average annual rainfalls from 100 mm to 1300 mm. The density at which they can exist in these habitats varies over 100-fold, from less than 1 rhino per 100 km² in the desert plains of Western Kunene (Hearn 1999) to more than 1 rhino per 1 km² in the best thicket vegetation. Historically, the highest densities have been found in *Commiphora/Bauhinia* thickets in Tsavo West, Kenya (Goddard 1970a), *Acacia* thickets in Hluhluwe, South Africa in the 1960s (Hitchins 1969), and deciduous thickets in the middle Zambezi Valley in the 1960s (Jarman 1971). These latter areas have annual rainfalls of 600–900 mm. In East Africa, patches of ground-water forest marked by an overstorey of *Acacia xanthophloea* and a dense year-round understorey herb and shrub layer also support very high rhino densities, such as Lake Nakuru N. P., Kenya (Kenyan Rhino Programme data) and Lerai forests of Ngorongoro Crater (Goddard 1967), although currently the forest in the crater is rarely used by rhinos, for which the most plausible explanation is that there is less cover since the 1960s, and greater competition for browse and

disturbance from Savanna Elephants *Loxodonta africana* (Mills *et al.* 2006). Succulent valley bushveld also currently provides high quality habitat. In contrast, rhinos occur at low densities in the open East African savanna grassland habitats within the Serengeti–Mara ecosystem, where browse availability is very sparse (Frame 1980, Walpole *et al.* 2001, Adcock *et al.* 2005).

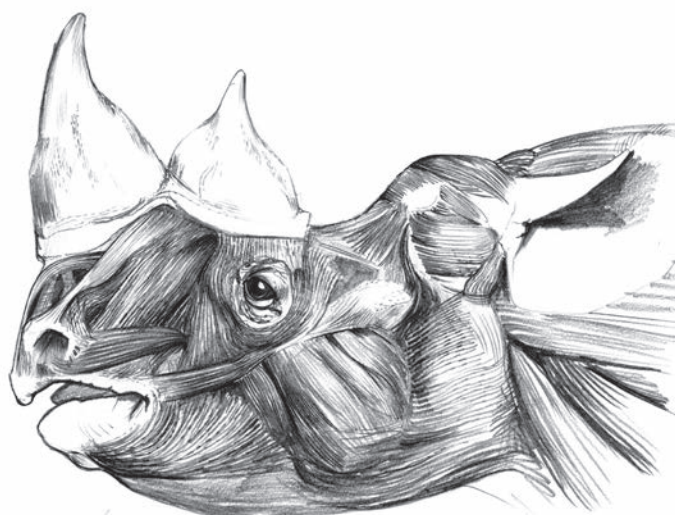
Intermediate rhino carrying capacities of 0.25–0.5 Black Rhino per km² occur in some Kenyan areas, woodland areas in the northern and western Serengeti, succulent valley bushveld in the Eastern Cape and Zululand thornveld (Adcock 2001, Adcock *et al.* 2005). Nutrient-poor habitats including broadleaved miombo woodlands have low carrying capacities. In some parts of southern Africa, frost also reduces Black Rhino carrying capacity. Black Rhino carrying capacities over much of southern Africa are only in the region of 0.1 rhino/km².

The availability of good and intermediate quality browse is the main factor determining Black Rhino density in a habitat (Adcock 2001). How fast the browse grows also influences carrying capacity, and this is determined by amounts of annual rainfall, rainfall seasonality, minimum temperatures, the fertility of the soil and the resulting plant species composition (Adcock 2001). The proportional plant species composition of the available browse and its palatability to the Black Rhino are also important (Adcock 2001, Buk 2004).

Black Rhinos are water-dependent in the majority of habitats, and rhino home-ranges are arranged relative to permanent water sources in an area. Rhinos can, however, move a fair distance from water within their range. In Etosha N. P., only 1.1% of aerial Black Rhino sightings were greater than 14 km from water (R. H. Emslie *et al.* pers. obs.). In other areas, rhinos prefer to stay within 4–8 km of water (Buk 2004, K. Adcock pers. obs.). However, where sufficient water-containing succulent vegetation occurs, Black Rhinos can survive for several months in the total absence of surface water (Olduvai Gorge, Tanzania, Goddard 1968; Liwonde N. P., Malawi, R. Bhima pers. comm.).

Abundance It has been estimated that there may have been as many as 850,000 Black Rhinos in Africa around 1700 (Adcock & Emslie 2004), and throughout most of the twentieth century the Black Rhino was still the most numerous of the world's rhino species. However, relentless hunting of the species and clearance of land for settlement and agriculture resulted in the population being reduced from a probable several hundred thousand at the start of the century. There may still have been as many as 100,000 animals in Africa in 1960, but by 1970 it was estimated that there were only 65,000 left, at which time Kenya still had some 16,000–20,000 animals (Martin & Martin 1982).

Between 1970 and 1992 large-scale poaching caused a dramatic 96% collapse in numbers. The most important cause of this decline was a dramatic increase in the price of rhino horn (Leader-Williams 1988). From 1992 to 1995 total numbers remained relatively stable with increases in some countries (those with the best protected and managed populations) being negated by declines in others. The minimum population estimate in 1995 was approximately 2410 (Emslie & Brooks 1999). Since 1995, Black Rhino numbers at a continental level have steadily increased, reaching 3610 by the end of 2003 (Emslie 2004a), 3725 by December 2005 (Emslie *et al.* 2007), 4230 by December 2007 (Milliken *et al.* 2009) and 4880 by 2010 (Emslie 2011). Two countries have shown net increases in numbers of Black Rhinos over the period 1980–2010: South Africa and Namibia, from estimated 630+300 in 1980 (Emslie & Brooks 1999) to 1915+1750,

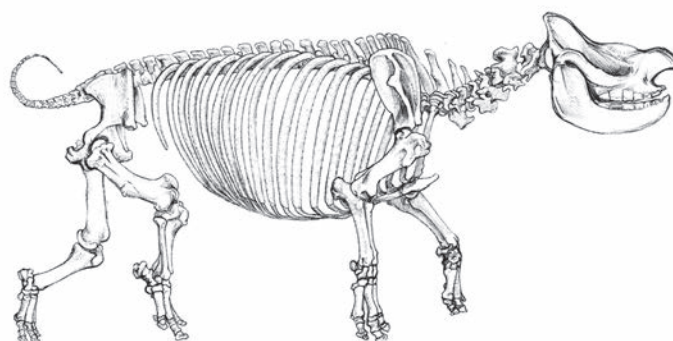


Black Rhinoceros *Diceros bicornis* detail of head myology.

respectively, in 2010 (Emslie 2011). In both countries, investments in conservation programmes, including monitoring and law enforcement, have been high. As of December 2005, an additional 240 Black Rhino (171 *D. b. michaeli* and 69 *D. b. minor*) occurred in captivity worldwide (Emslie *et al.* 2007).

Table 8 gives the December 2010 population estimates (excluding speculative guesstimates) by subspecies by country compiled by IUCN/SSC's African Rhino Specialist Group as of December 31, 2010 (Emslie 2011).

Adaptations Black Rhinos have very good hearing and sense of smell, but their eyesight is poor. Animals can react to a person walking past in clear view at ranges of 60 m, yet if the wind direction is favourable they appear unable to identify a motionless human observer (especially if the person's shape does not contrast with the surroundings) at ranges greater than around 30 m (Schenkel & Schenkel-Hullinger 1969). Black Rhinos downwind of man have been known to react at a distance of 800 m, and in most instances sound or smell will alert rhinos to the presence of humans rather than sight (Schenkel & Schenkel-Hullinger 1969). Sometimes, the screeching of oxpeckers



Black Rhinoceros *Diceros bicornis* skeleton.

Buphagus spp. can alert rhinos to the nearby presence of a human.

The prehensile upper lip is an adaptation that facilitates browsing. The lip is used in much the same way as an elephant uses its trunk to grab and pull browse into the mouth. As in the White Rhino, the big heavy skull, absence of incisor and canine teeth in both jaws, and high-crowned premolars and molars, possessing convoluted enamel layers on their biting surfaces, are adaptations for grinding up coarse food. The Black Rhino is a hindgut fermenter with a capacious large caecum where digestion of plant fibre occurs (and see Clemens & Maloiy 1982).

The skin is thick, and being large animals rhinos have an unfavourable surface area to body-weight ratio making thermoregulation difficult and important. In the heat of the day, they often lie up in wallows, under shady trees, or in areas of closed thicket/woodland. They also like to lie up on ridge tops where they can take advantage of any breezes. A subcutaneous layer of fat and muscle builds up as the condition of the animal improves, providing a buffer against malnutrition during the dry season. Wallowing in mud may condition the skin and give some protection against biting flies whilst also trapping many ticks in mud, which can then get rubbed off against favoured trees/tree stumps or rubbing rocks. Trees and rocks are also used to relieve itches, particularly inside the legs, the chest, around the base of the horns and along the flanks.

In the dry season, when surface water is limited, Black Rhinos may only drink on average every 2–3 days (P. Erb pers. comm).

Table 8. Population estimates by subspecies and by country of Black Rhinoceros (December 2010).

| Country | <i>D. b. bicornis</i>
(South-western) | <i>D. b. michaeli</i>
(Eastern) | <i>D. b. minor</i>
(Southern-central) | Total |
|--------------|--|------------------------------------|--|-------------|
| Angola | 1 | | 1 | 1 |
| Botswana | | | 7 | 7 |
| Kenya | | 594 | | 594 |
| Malawi | | | 24 | 24 |
| Mozambique | | | 1 | 1 |
| Namibia | 1750 | | | 1750 |
| South Africa | 171 | 60* | 1684 | 1915 |
| Swaziland | | | 17 | 17 |
| Tanzania | | 88 | 25 | 113 |
| Zambia | | | 27 | 27 |
| Zimbabwe | | | 431 | 431 |
| Total | 1920 | 740 | 2220 | 4880 |

*The *D. b. michaeli* population in South Africa is out of range.

Drinking generally takes place during the early evening through to early morning, so that travelling to and from water occurs during the cooler hours; in Namibia, 64–100% of drinking occurs between sunset and midnight (P. Erb pers. comm.). Black Rhinos also appear to do much of their feeding when it is dark, and this may aid thermoregulation as well as allow animals to feed more easily in more exposed areas.

Despite their large size, Black Rhinos can gallop at an estimated 55 km/h when charging or fleeing from danger. They are more prone to charge intruders than White Rhinos; however, Black Rhinos will often turn and run away from danger, especially if this is downhill and they can run into cover. When disturbed they are also likely to run further than White Rhinos before stopping. Individual Black Rhinos are idiosyncratic, and while some individuals can be aggressive and may frequently charge people or even vehicles, others are placid and tolerate human activity in their vicinity.

Foraging and Food Black Rhinos are browsers, consuming primarily woody plants and herbs. Grass is generally only eaten incidentally while foraging for low-growing herbs, but new soft grass leaf growth is voluntarily taken on occasion, and can form over 10% of the wet-season diet (Goddard 1968). A wide range of browse species eaten in any given habitat, but while over 100 species may be ingested during a year's foraging, 90% of the diet commonly comprises fewer than 20 species (Hall-Martin *et al.* 1982, Loutit *et al.* 1987, Kotze & Zacharias 1993, Oloo *et al.* 1994, Emslie 1999, Breebart 2000, Brown 2004, Buk 2004).

Species from the families Euphorbiaceae and Tiliaceae, and the Mimosoideae and Papilionoideae subfamilies of the legumes, are important in the diet in most ecosystems. Plant species of the genera *Euphorbia*, *Grewia* and *Acacia* are particularly important and preferred, and *Spirostachys* and *Acalypha* feature prominently among the genera of Euphorbiaceae eaten. Among the more herbaceous plant forms favoured by Black Rhinos, species from the Acanthaceae, Amaranthaceae and Malvaceae family feature strongly, including species from *Barlaria*, *Blepharis*, *Acaranthus*, *Amaranthus*, *Cyathula*, *Hibiscus*, *Pavonia*, *Sida* and *Abutilon*.

A wide diversity of secondary plant chemicals occur in Black Rhino browse species, many of which are potentially harmful. The ability to cope with these chemicals is an interesting feature of their feeding ecology that is not well understood. Black Rhinos produce tannin-binding saliva in response to food types rich in tannins (Napier 1998). The large liver also plays an important role in metabolizing a wide range of chemicals, but they still need to balance their exposure to any one chemical, which they seem to do by limiting intake of some plant species types (even if favoured) and diluting such intake with browse containing different chemicals (e.g. *Spirostachys africana*, Emslie 1999). However, coping with high levels of tannin-type secondary plant chemicals carries a cost, increasing mineral usage (e.g. nitrogen; Illius & Jessop 1995), and negatively affecting food digestibility and mineral and energy uptake (Jansman 1993, Shung-MacCoubrey *et al.* 1997). In habitats on nutrient-poor geologies, where the bulk of available browse biomass contains significant levels of secondary chemicals (polyphenols and tannins), Black Rhino densities are lower than expected from their rainfall and apparent browse availability characteristics alone (Adcock 2001). In Nairobi N. P. Black Rhinos were found to select for plants with low phenol and alkaloid contents (Muya & Ogue 2000).

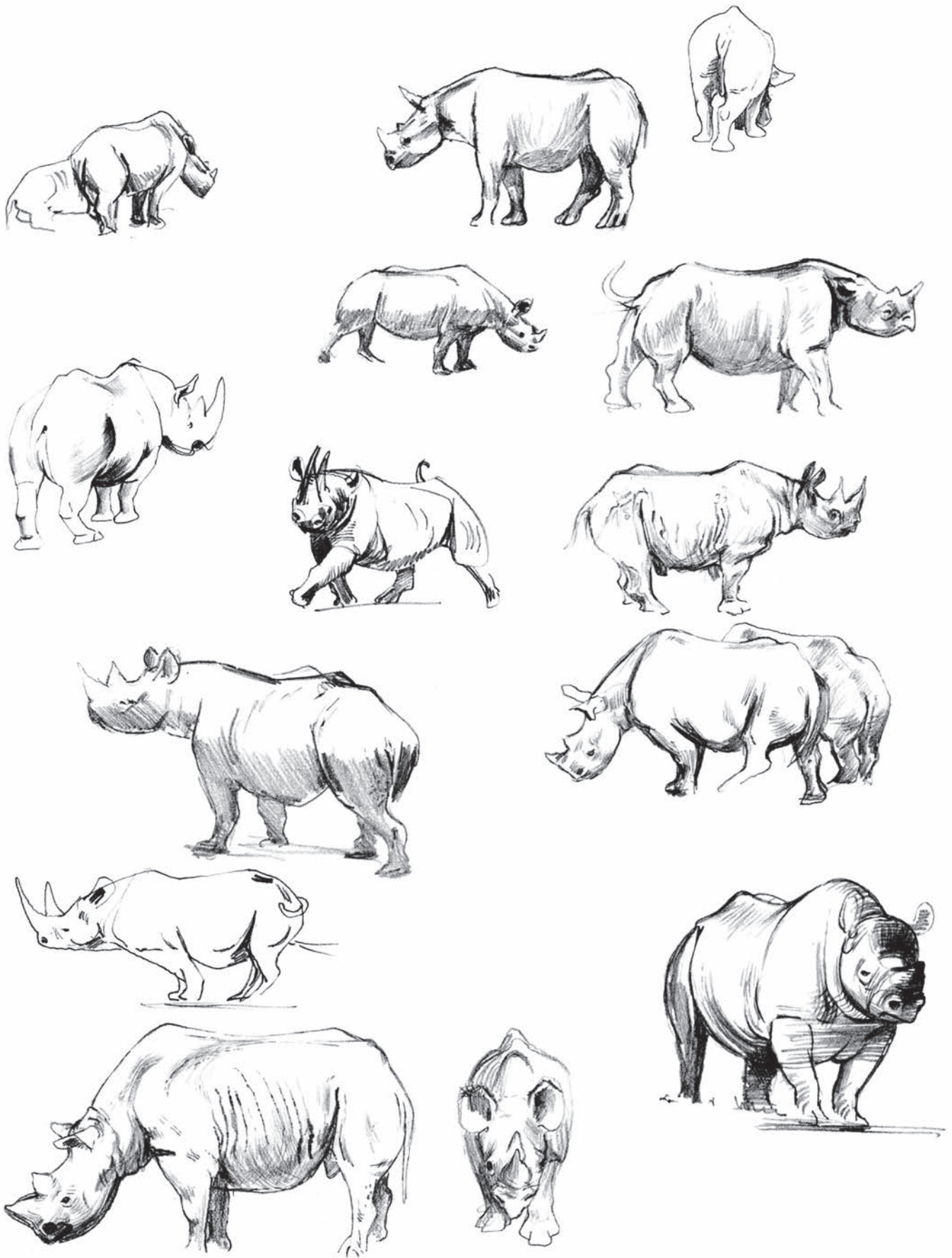
Black Rhinos feed within a specific height range. About 98% of their intake is from browse located within 2 m of the ground, and the 0.5–1.5 m height range is most preferred (Kotze & Zacharias 1993, Macfarlane 1997, Emslie 1999, Breebart 2000, Brown 2004, Buk 2004). They do, however, push over trees, especially those with a spindly growth form, to access browse above 2 m. High branches can also be pulled or broken down to feed on. Because smaller size classes of most woody species are preferred, tall, rank grass growth (common in higher-rainfall ecosystems) can substantially interfere with feeding. This can lead to rhinos avoiding areas of long grass altogether, or to feed on less-preferred, taller plants instead (Emslie 1999). In captivity, they have been recorded feeding on an average of 37.8 ± 9.0 kg (wet mass) of thorny, woody plants per day (Maddock *et al.* 1995). The dung boluses contain much coarse woody material, which exhibits the characteristic neat pruning of twigs at a 30–45° angle. By way of contrast, elephants tend to shred the edges of branches when they browse.

Black Rhinos often feed on burnt plants and recoppicing browse in burnt areas (Mukinya 1977, Emslie 1999, P. du Preez pers. comm.), preferring areas with intermediate intensity burns (Emslie 1999). Increasing attention is being paid to the negative impact that other potentially competing browsers may have or have had on Black Rhino habitats and carrying capacities (Kuria 1995, Birkett 2002, Walpole *et al.* 2004).

Social and Reproductive Behaviour Black Rhinos tend to be solitary animals, although ♀♀ are less solitary than ♂♂, as they are usually associated with one or more of their immature or subadult offspring. Adults spend most of their time and do most of their feeding within defined home-ranges. Mature adult home-ranges tend to be stable in location for several years (Adcock *et al.* 1998). However, in establishing Black Rhino populations, ranges may shift over time (Lent & Fike 2003). The ranges of subadult and young adult animals are not stable and tend to be larger than those of most mature adults (Adcock *et al.* 1998). The log of average adult male Black Rhino home-range size in an area is inversely proportional to the log of Black Rhino carrying capacity of an area, as predicted by regression modelling (Adcock 2001), even though individual rhino home-range sizes vary greatly (Adcock 2001; and see, for example, Hitchins 1969, Mukinya 1973, Frame 1980, Conway & Goodman 1989). Thus, in very arid areas of low rhino carrying capacity, such as 0.01 rhino/km², ranges average around 380 km² (Hearn 1999). Areas that can carry ten times more rhinos (0.1 rhino/km²) tend to have ranges averaging 43–44 km²; while areas that can carry 1 rhino/km² tend to have ranges averaging around 5 km².

Male territoriality has been shown in all areas where the actual ages and range layouts of the ♂♂ have been monitored (Klingel & Klingel 1966c, Frame 1980, Adcock 1998, Tatman *et al.* 2000, Lent & Fike 2003). Mature adult ♂♂ usually show territorial behaviour in that a single 'dominant' bull resides in a specific range, which overlaps little with the ranges of other bulls of a similar status. Such a bull is usually a mature adult well over ten years old. Other 'subordinate' bulls, which are usually subadults or younger adults, are tolerated within a dominant bull's range until they start to display challenging or territorial behaviour. Social dominance seems to be achieved between the ages of 9 and 17, some years after sexual maturity is reached at 7–8 years of age.

A dominant bull will aggressively chase a non-tolerated ♂ from his territory. Young bulls are often killed or injured in these interactions.



Black Rhinoceros *Diceros bicornis*.

Dispelled bulls must lead a fringe existence in unoccupied areas, or must wander continuously to avoid dominant bulls, until they can find or claim their own territory. Old ♂♂ that can no longer defend their territories also die in fights, or can become confined to a small area of marginal habitat until they die. Dominant bulls are predominantly solitary, but younger, subordinate ♂♂ may associate with each other or with adult ♀♀ on occasion. Male territoriality limits the number of mature ♂♂ that can co-exist in fenced rhino sanctuaries (Adcock 1994, 1998).

There is some evidence that overt territorial behaviour can be suspended around specific important, but limited, resources, where rhinos can gather in groups of five or more. Examples include around waterholes in arid ecosystems (e.g. aggregations of up to 16 individuals in Etosha N. P. in Namibia; Cunningham & Berger 1997, B. Loutit pers. comm.), or around prized resources such as succulent euphorbias (e.g. Dwarf Succulent Valley Bushveld habitat in South Africa; Lent & Fike 2003), and, formerly, in patches of deciduous thicket (made up of *Combretum*, *Grewia*, *Baphia*, *Burttia*, *Pseudoprosopis* and *Albizia* spp.) in Uzigua and Manyoni districts of Tanzania (J. Kingdon pers. comm.). They also aggregate over such resources when artificially confined, as in Ngulia Sanctuary in Tsavo West, Kenya (R. Ketch pers. comm.) and in *Euphorbia* forests in Lake Nakuru N. P. (P. Okuku pers. comm.). Females occupy home-ranges that can overlap those of other ♀♀ and ♂♂. Meetings between different adult ♀♀ (and associated calves) are peaceful. Encounters are sometimes deliberately sought if rhinos detect each other when moving through a common area, but these invariably are of a temporary nature.

Black Rhinos use olfactory communication, including scent-marking by dung scattering and urine spraying. Dung middens are scattered seemingly at random along paths and used by all passers-by. Black Rhinos often defecate on White Rhino territorial dung middens where the two species coexist. The depositor of dung may sniff it and may sweep and root it with the forehorn (especially ♂♂) before shuffling through it with stiff legs (Estes 1991). Black Rhinos scatter their dung by kicking backwards in slow motion, leaving characteristic parallel scrapes. Females in oestrus dump whitish urine, which advertises their status to ♂♂ who test this with flehmen behaviour. Bulls also spray-urinate on small bushes (Estes 1991).

When an oestrous ♀ moves into a ♂'s territory, the resident ♂ rhino will court her and mating may ensue. Courting can be a lengthy affair. This involves the ♂ engaging in stiff-legged walking, some jousting of horns with the ♀, and restrained jabbing of his horn under her groin, front legs or belly. Females may attack courting ♂♂ on occasion. Actual copulation may last 12–43 min (Goddard 1966, Hitchins & Anderson 1983).

Related rhinos tend to maintain long-term bonds and often join up with each for short periods over their lifetime. In East Africa, such groups (clans) of related rhinos have been found to occur in particular 'distribution areas', which show little or no overlap with the distribution areas of other such groups (Mukinya 1973, Morgan-Davies 1996, Tatman *et al.* 2000).

Young ♀♀ can wander widely before they produce their first calf. They then settle into a more established home-range that may or may not coincide with that of their mother. Pregnant ♀♀ have been known to return temporarily to their own birth area when they are due to give birth (H. Hansen pers. comm.). As the time for parturition

approaches, the ♀ will chase her previous calf away, and will find a secluded bushy area to give birth in. Females sometimes hide their infant calves when they go to waterholes (P. Erb pers. comm.) or when feeding in exposed areas. Newborn calves walk and suckle within hours of birth. The older, rejected calves (aged 2–3½ years) at this stage become more vulnerable to predation, aggression by ♂ rhinos, and other mishaps. They appear to be insecure on their own, and usually attempt to join another ♀ or occasionally young ♂, or even a White Rhino ♀ who will tolerate their presence. After 3–8 months, the mother may allow her former calves to return to her company. Calves start to break ties with their mother from 2–3½ years on, but ♂ calves in particular may not truly leave their mothers permanently until they are six or seven years.

The explosive puffing snort of an alarmed Black Rhino can precede a dangerous charge, but more often Black Rhinos run away from perceived threats. A calf emits a high-pitched whine or squeal to attract its mother's attention. A ♂ may also squeal when courting a ♀, and all Black Rhinos can make this sound when in pain or distress.

Black Rhinos are often found in association with Fork-tailed Drongos *Dicrurus adsimilis*, which hawk insects by flying along the sides of resting rhinos, and with oxpeckers, which feed on ticks and skin secretions. The birds also give a harsh alarm call, which has led to oxpeckers being called *askari ya faru*, or the 'rhino's policemen' in Swahili.

Reproduction and Population Structure Fertility depends to some extent on body condition and weight. Animals can become sexually mature in their fourth or fifth year if they can achieve 80% of their adult body weight by this stage. Most ♀♀ achieve sexual maturity during their sixth year, resulting in average ages at first calving of 7–8 years (though some breed earlier). Males seem to commonly achieve sexual maturity (spermatogenesis) at an older age of 7–8 years (Hitchins & Anderson 1983, Bertschinger 1994). Fertility can be delayed in both sexes due to nutritional stress, or social pressures in the case of young ♂♂.

Oestrous cycles have a mean of 35 days, but true oestrus only occurs for one or two days during each cycle (Hindle *et al.* 1992, Bertschinger 1994). Cycling can occur year-round, but is influenced by ♀ nutritional status. Several populations have shown conception peaks at times of the year that correspond to improved rainfall conditions, and thus nutritional status of the ♀ in the months preceding conception (Adcock 2000, 2003). The timing of these peaks varies across Africa with the seasonality (winter versus summer) of the annual rainfall pattern.

Gestation period is 15.4 months and calves weigh 25–40 kg at birth (Penny 1987, Bertschinger 1994). The calving interval varies widely, depending on the age of the ♀ and the nutritional conditions in the habitat. Under good habitat conditions and at densities below carrying capacity most ♀♀ can produce several consecutive calves at 2–2.5 year intervals. Where conditions are less favourable, the average inter-calving interval exceeds three years. In many such cases, a calf may be conceived but is lost as the pregnancy nears full term, or shortly after birth. Old ♀♀ (28 years plus) have difficulty regaining body condition after weaning each calf, and tend to have longer intervals between calves.

Mortality rates within the first year of life range from 8–14% on average in South Africa and Namibia. Mortality in subadults averages

2–4%, less than 2% in young and prime age adults (Adcock 2003), and probably 4% or more in older rhinos. Male rhinos have a higher mortality rate than ♀♀, and fighting is the most common cause of their death. Most ♀♀ die of old age. Longevity for *D. b. michaeli* in captivity has been given as 45 years and 10 months (Jones 1993).

More male calves are born than female calves (Adcock *et al.* 2010), but male mortality rate is higher leading to adult sex ratios biased towards ♀♀. Because of male territoriality limiting male numbers in all but the largest fenced areas, adult sex ratios tend to average 1.3–1.5 ♀♀ per ♂ in many populations. Larger populations have average sex ratios of 1.1–1.2 ♀♀ per ♂.

The intrinsic rate of increase in Black Rhinos is around 8–9% annually (Owen-Smith 1988, 2001, Emslie 1999), similar to White Rhinos (although in practice breeding rates of the browsing Black Rhino lag behind those of the grazing White Rhino). In areas that have been stocked with rhinos at below their habitat carrying capacity, and having ♀-biased sex ratios and low mortality rates, they can commonly achieve average population growth rates of 10–15% per year. In populations approaching carrying capacity, overall mortality can exceed 4% annually (involving mainly infants and subadults), and inter-calving intervals lengthen. This results in average growth rates of zero or a few per cent (Adcock 2003). Black Rhino populations that have been allowed to approach or exceed estimated long-term ecological carrying capacity have consistently exhibited declines in population. Vegetation changes and increases in the density of competing browsers, as well as fluctuating rainfall, also will affect performance.

Predators, Parasites and Diseases Calves and subadults are vulnerable to predation by Lions *Panthera leo*, Leopards *Panthera pardus* and Spotted Hyaenas *Crocuta crocuta* (e.g. Goddard 1966, Joubert & Eloff 1970, Elliot 1987, Scott & Scott 2003). Brain *et al.* (1999) reported on the killing of three subadult Black Rhinos by a coalition of three male Lions in Etosha N. P. within the space of a few months; the three rhinos killed were of very similar size (1.27–1.31 m at the shoulder) and age (3–4 years) and the authors suggested that subadult rhinos that have just left their mothers may be particularly susceptible to Lion predation. In N Tanzania, Goddard (1966) estimated that there was a 16% loss of calves less than two years old to Lion and Spotted Hyaena predation.

In contrast to White Rhinos, a Black Rhino calf tends to follow rather than precede its mother when running away from danger. This behaviour is thought to make this species more vulnerable to predation. However, upon hearing alarm squeals of her calf, a Black Rhino mother will turn to defend her calf. Calves less than three months old appear to be at greatest risk from predation.

Black Rhino numbers have increased rapidly in many populations with a full complement of predators, and it appears that, while some young and subadult animals are undoubtedly lost to predation, rhinos stocked at sustainable carrying capacities can withstand predation. Thus, predators are not generally a major influence on population performance in most populations. An exception to this is in the Ngorongoro Crater, where Spotted Hyaena densities have been very high while Black Rhino densities have become very low through poaching, and the terrain has become open with limited bushy areas for cows to hide calves. Mortality of Black Rhinos in their first year of life here is more than 30% (Adcock *et al.* 2004, Emslie 2004b). If

one assumes inter-calving intervals in excess of four years represent undetected neonatal mortalities, neonatal mortality of Black Rhinos in the Crater may have been as high as 41–47% (Adcock *et al.* 2004, Emslie 2004b, Mills *et al.* 2006).

Southern African Development Community Rhino Management Group data since 1989 indicate that the proportion of detected mortalities in populations in areas with large predators that were ascribed to predation was 6.9%, with suspected Lion predation accounting for 13 of 16 predator-linked mortalities out of a total sample size of 233 mortalities (SADC RMG data – K. Adcock unpubl.). Lion predation may be overestimated, as in some cases, lions may have simply discovered a Black Rhino carcass and scavenged from it rather than killing it. Similarly, Spotted Hyaena predation levels are likely to be underestimated from recorded mortality data as little evidence may remain if a very young calf is killed and eaten in the bush.

Aggressive encounters with Savanna Elephants *Loxodonta africana* and African Buffalo *Syncerus caffer* have also been recorded. In 159 encounters between elephants and Black Rhinos in Etosha, ♀ elephants dominated both sexes of Black Rhino, while Black Rhino ♂♂, though not ♀♀, were capable of displacing elephant bulls (Berger & Cunningham 1998). Some Black Rhinos have been killed by young bull elephants in some populations where elephants were re-introduced using young orphaned animals from culls rather than family groups with big mature adult elephant bulls (Slotow *et al.* 2001). To date, many more White Rhinos have been killed by these juvenile, bull delinquents than Black Rhinos. Only 2.1% (5/233) recorded Black Rhino deaths in the SADC RMG region since 1989 have been ascribed to elephants (SADC RMG data – K. Adcock unpubl.). It is still too early to conclude with certainty, but the introduction of large adult bulls into populations such as Pilanesberg and Hluhluwe–iMfolozi appears to have reduced mortality.

Black Rhinos are susceptible to trypanosomiasis, and *Trypanosoma brucei*, *T. congolense* and *T. vivax* have been reported from Black Rhinos (Penzhorn *et al.* 1994). Black Rhinos translocated from non-trypanosomiasis areas to trypanosomiasis areas are at risk until they build up immunity. Translocation mortality risks can be reduced with good boma care and setting up Tsetse Fly traps in the area surrounding holding bomas to reduce fly densities and give the animals time to build up immunity (Wambwa 2004).

Anthrax has killed the occasional animal, but at a continental scale its impact has been limited. Since 1989 only two Black Rhinos have been recorded as dying from anthrax in the SADC RMG region (0.9% of all recorded deaths since 1989). In total, including cancer and anthrax, disease accounted for 3.4% (eight) of all recorded mortalities in parks with large predators (n = 233; SADC RMG data – K. Adcock unpubl.).

A total of 35–38 tick species have been recovered from Black Rhinos (see Penzhorn *et al.* 1994 for checklist), of which three tick species are primarily rhino parasites: *Amblyomma rhinocerotis*, *Dermacentor rhinocrinus* and *Amblyomma personatum* (Penzhorn *et al.* 1994; and see Knapp *et al.* 1997). Common sites of tick attachment are skin folds in the perineal region, in and around the ears and around the eyes (Penzhorn *et al.* 1994). Oxpeckers and terrapins in wallows assist rhinos by eating ticks. Rhinos also wallow in mud and then rub themselves on special rubbing posts, trees and rocks in an attempt to remove ticks on their skin. *Babesia* and *Theileria*

like organisms have been found in healthy White Rhinos (Bigalke *et al.* 1970); however, deaths of a small number of Black Rhinos in Ngorongoro and Addo Elephant N. P. have been linked to tick-borne diseases caused by protozoan parasites identified as *Babesia bicornis* and *Theileiria bicornis*. In these cases it is believed that general stress associated with translocation and drought-induced malnutrition, and a build up of ticks following a lack of burning were key factors predisposing these animals to succumb to babesiosis (Hilsberg *et al.* 2003, Adcock *et al.* 2004, Mills *et al.* 2006). Aspergillosis is another example of a latent infection/disease that can be exacerbated by translocation stress (Kock & Miller 2004).

Large swarms of the large blood-sucking fly *Rhinomusca dutoiti* and *R. brucei* are often seen along the sides of Black Rhinos. Birds such as oxpeckers and drongos *Dicrurus* spp. often hawk these flies. These flies lay their eggs in rhino dung middens where their larvae develop. Much smaller flies of the genus *Lyperosia* are also commonly associated with rhinos and their middens. Large numbers of gyrostigmatid (bot) fly larvae (*Gyrostigma pavesii* and *G. conjungens*), up to 40 mm long, may be found attached to the stomach walls of rhinos. At least 30 species of helminths (see Penzhorn *et al.* 1994 for a checklist) are known to parasitize the Black Rhino. Ciliated intestinal protozoa are reported on by Van Hoven *et al.* (1988) and Obanda *et al.* (2008).

In some areas, such as in KwaZulu–Natal (Schulz & Kluge 1960, Hitchins & Keep 1970) and parts of Kenya (Round 1964, Tremlett 1964) and Zimbabwe (Kock & Kock 1990), Black Rhinos can develop characteristic large skin lesions on their chests and shoulders due to a filarial parasitic worm. Where this parasite is absent, these lesions do not develop. As the positions and size of the lesions change with a rhino's age, over time and with season (Hitchins & Keep 1970), they are not useful features for identifying individual animals (Adcock & Emslie 2004).

Black Rhinos have unusual blood chemistry as their red blood cells are sensitive to oxidative stress. This has predisposed this species to high mortality rates in captivity. Captive Black Rhinos have suffered from a wide range of conditions (Wambwa 2004), including acute episodic haemolytic anaemia, chronic haemolytic anaemia, superficial necrolytic dermatopathy, haemosiderosis, idiopathic and toxic hepatopathies, a susceptibility to fungal pneumonias and other infectious agents, and other incompletely understood disorders (Miller 1992, 1994, Munson *et al.* 1998). These conditions are seldom if ever seen in the wild (Wambwa 2004). Attempts are being made to improve captive diets in an attempt to prevent a build up of iron in captive animals and reduce mortality levels in captivity.

Conservation IUCN Category: Critically Endangered A2abdc (*D. b. minor* – Critically Endangered A2abdc; *D. b. bicornis* – Vulnerable D1; *D. b. michaeli* – Critically Endangered A2abdc; *D. b. longipes* – Extinct). CITES: Appendix I.

The population of Black Rhinos has declined by over 90% over the last sixty-odd years, reaching a low of 2410 in 1995 (Emslie & Brooks 1999). However, since then, numbers have been increasing steadily at a continental level, doubling to 4880 by the end of 2010 (Emslie 2011). For the most part, the large free-ranging populations of rhinos that used to roam over huge areas, and which could not be adequately protected, have been eliminated or reduced to very low

numbers. The bulk of remaining Black Rhinos occur in areas with more concentrated security. However, following surveys over most of its possible range in 2006, the Western Black Rhino in Cameroon has been declared extinct as no signs of any individuals were found by survey teams in 2006 or in the following five years, while evidence of general wildlife poaching was widespread (Emslie *et al.* 2007).

Black Rhinos are found under a range of management and ownership models. In 2010, 71.2% of Africa's Black Rhinos were conserved in state-run protected areas. The bulk of privately managed Black Rhinos in 2010 were under custodianship on behalf of the state (19.9% of all Black Rhinos) with 6.8% being privately owned (AfRSG data unpubl.). This differs from White Rhinos, where, in 2010, 27.3% were privately owned. Approximately 3.2% of Africa's Black Rhinos are conserved on communally owned and managed land. In summary, as of December 2010, there were 17 strongholds of the species with over 50 animals (up from 11 in 1995), including Etosha N. P., Kunene, Hluhluwe–iMfolozi N. P., Kruger N. P., Great Fish Reserve, Nairobi N. P., Lake Nakuru N. P., Pilanesberg N. P., uMkhuze G. R., an intensive protection zone in Hwange N. P., and three Zimbabwean conservancies, three privately managed Kenyan areas and two privately owned South African populations (Emslie 2011).

For practical conservation management, current Continental, Regional and National Black Rhino Conservation Plans all stipulate that the different subspecies of Black Rhino should not be mixed (unless major declines in numbers and loss of genetic variability in future dictates otherwise). See also Taxonomy.

As with White Rhinos, the primary threat remains the high price of rhino horn (Leader-Williams 1988) and the resultant poaching for the illegal international rhino horn trade. Rhino horn has two main uses: traditional use in Chinese medicine, and for making ornately carved handles for ceremonial daggers (Jambiyas) worn in some Middle East countries (Martin & Martin 1982). Since the 1960s wars, the free flow of weapons into Africa, civil unrest, poverty, economic problems and declining conservation budgets have had a significant impact on rhino numbers in many countries (Emslie & Brooks 1999). Habitat changes and increasing densities of competing species can also cause rhino populations to decline, while poor (conservative) biological management also threatens rhino growth rates. Maintaining sufficient capacity and resources to do effective field rhino conservation is a challenge. In Zimbabwe, for example, where Black Rhino numbers (but not White Rhinos) declined slightly (–1.7 %) between December 2003 and December 2005, significant field conservation effort (i.e. protection and translocations to maintain productivity of established populations and create additional populations), coupled with political will, have been the primary reasons for continued successes (Emslie *et al.* 2007).

The Black Rhino has been listed on CITES Appendix I since 1977, with all international commercial trade in Black Rhino and their products prohibited. To help reduce illegal trade, and complement CITES international trade bans, domestic anti-trade measures and legislation were implemented in the 1990s by a number of consumer states. However, live breeding groups of Black Rhino have been translocated between countries to help re-establish populations in a number of range states. At the 13th CITES Conference of the Parties in 2004, proposals for hunting quotas for five surplus male Black

Rhino were also approved for both Namibia and South Africa (for more details on the rationale behind these hunting proposals and the debate at CITES CoP 13, see Emslie 2004c).

Strategies that have been central to increasing numbers include monitoring and managing rhinos on a metapopulation basis for rapid growth (Emslie 2001), and concentrating law enforcement effort at levels where it can be effective (Leader-Williams *et al.* 1990, Emslie & Brooks 1999). Work is currently ongoing to study the social impacts of translocations with a view to developing improved biological management and translocation guidelines (W. Linklater pers. comm.).

Measurements

Diceros bicornis

HB: 2900–3750 mm

T: 600–700 mm

HF: n. d.

E: n. d.

Sh, ht: 1370–1800 mm

WT: 700–1400 kg

Kingdon 1997; sample number not given

Notes: The mean mass of a small sample of Black Rhinos from Hluhluwe G.R., KwaZulu–Natal was 852 kg for ♂♂ (n = 8) and 884 kg for ♀♀ (n = 6) (Hitchins 1968). Du Toit (2005) also gives a slightly lower average mass at maturity for ♂♂ of 852 kg (700–1020 kg) compared with ♀♀ 880 kg (720–1130 kg). Estes (1991), on the other hand, describes ♀♀ as large as ♂♂, but ± 100 kg lighter. Mature adult ♂♂ develop visibly bigger neck muscles, and some ♂♂ are obviously big animals and are likely to be the heaviest animals (J. Flamand pers. comm.); however, a pregnant ♀ normally weighs as much as the average ♂ (Q. Rochat pers. comm.). The heavier mean for ♀♀ in some references may be due to the inclusion of a number of

animals in late pregnancy. Four ♀♀ and four ♂♂ (*D. b. minor*) over 6/7 years of age had average weights of 1020 kg (range 972–1149 kg) and 1164 kg (range 1044–1228 kg), respectively. Q. Rochat (pers. comm.) concurs with statements there is not too much difference in weight between sexes and that some ♀♀ are bigger than some ♂♂. None the less, the largest animals are very big bulls. These latter figures, taken from rhinos weighed in crates using a crane with an electronic scale (accurate to 5 kg), are also higher than previously reported, possibly due to more accurate weighing or because other weights were derived from younger animals being translocated.

Average mass per individual (subspecies not specified) in an entire population is 818 kg (Bothma & Van Rooyen 1990). Du Toit (2005) gives a mean mass for *D. b. minor* of 852 kg but notes that *D. b. bicornis* is larger with adult bulls weighing up to 1300 kg.

Horn measurements:

Diceros bicornis

Anterior basal circumference (♂♂): 492.7 ± 69.5 mm, n = 58

Anterior basal circumference (♀♀): 453.5 ± 44.2 mm, n = 38

Anterior horn length (♂♂): 446.1 ± 101.2 mm, n = 63

Anterior horn length (♀♀): 417.6 ± 107.9 mm, n = 49

Anterior horn WT (unsexed): 1.7 ± 0.7 (0.2–3.8) kg, n = 75

Posterior horn WT (unsexed): 0.9 ± 0.5 (0.02–2.4) kg, n = 74

Kruger N.P. and KwaZulu–Natal, South Africa (Pienaar *et al.* 1991, Pienaar 1993)

Note: The maximum front horn length is 1359 mm from Kenya (Selous 1899)

Key References Emslie 2001; Emslie & Brooks 1999; Frame 1980; Hitchins 1969, 1978, 1989; Mukinya 1973, 1977.

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Glossary

abbrev. = abbreviation

adj. = adjective

cf. = *confer*, compare with; as opposed to

Lat. = Latin

n. = noun

pl. = plural

q.v. = *quod vide*, 'which see'

v. = verb

acetabulum: the concave socket (fossa) in the pelvic bone in which the head of the femur articulates.

acrocentric: describes a chromosome that has the centromere (*q.v.*) very near one end and that therefore appears to have only one arm (= telocentric (*q.v.*) for practical purposes).

ad libitum: (*Lat.*) as much as one likes; having unrestricted access to a resource (e.g. water or food).

aestivate: state of torpor (*q.v.*) induced by cold or drought; usually associated with a reduced metabolic rate and inactivity.

aFN: the total number of chromosomal arms in the autosomal chromosome complement of a species (*cf.* fundamental number [FN], which includes the chromosomal arms of the sex chromosomes as well as those of the autosomal (*q.v.*) chromosomes). Each metacentric (*q.v.*), submetacentric (*q.v.*) or subtelocentric (*q.v.*) chromosome is given a value of 2; each acrocentric (*q.v.*) chromosome is given a value of 1. *See also* fundamental number.

afroalpine: describes habitats and/or vegetation occurring above the treeline on African mountains. Includes montane grassland and heathlands.

afromontane: refers to mountainous regions in Africa, e.g. afromontane forests and afromontane grasslands.

agouti: having an even mixture of pale- and dark-tipped hairs on the pelage creating a grizzled, speckled or 'pepper and salt' appearance.

Albertine Rift Valley: *see* Rift Valley (*q.v.*).

alisphenoid: bone in the skull.

Allee effect: a scenario in which populations at low numbers are affected by a positive relationship between population growth rate and density, which increases their likelihood of extinction.

allele: an alternative form of a gene. A diploid organism carries two alleles (which may be same or different) for each gene locus. At any one locus, there may be several possible alleles (although only two are present in a single organism).

Allelomimetic behaviour: behaviour in social animals in which each animal does the same thing as those nearby.

Allen's Rule: A rule that states that structures in endotherms such as limbs (which are more prone to heat loss) are reduced in size by means of natural selection over time in cooler climates (to reduce heat loss).

allogrooming: grooming behaviour directed at another individual. *cf.* autogroom (*q.v.*).

allomothering: non-parental mothering; caring for young by individuals (male or female) that are not the parents of the young.

allopatry (*adj.* **allopatric**): the situation where populations of the same or different species have non-overlapping geographic ranges; refers also to populations of the same, or different, species that are geographically separated. *cf.* sympatry (*q.v.*); syntopy (*q.v.*).

allozyme: one of a number of forms of the same enzyme having different electrophoretic properties and that are encoded by alternate alleles at the same genetic locus.

altimontane: collective term for the belts of ericaceous and afroalpine vegetation on the high mountains of tropical East Africa (White 1983).

altricial: describes young born in an undeveloped state. *cf.* precocious (*q.v.*).

altruism: behaviour that enhances the reproductive and genetic fitness of another individual at the expense of its own.

alveolus (*pl.* **alveoli**, *adj.* **alveolar**): small cavity; socket that houses the root of a tooth.

angular process: process at the posterior lower corner of the mandible; situated ventral to the coronoid process (*q.v.*).

ante-orbital (= **anteorbital**): in front of the orbit (*q.v.*).

antebrachial: anterior to the arm (forelimb).

anterior palatal foramina: the two foramina (*q.v.*) on the ventral part of the skull.

apomorphy (*adj.* **apomorphic**): situation in which a novel character evolves from a pre-existing character. In cladistics (*q.v.*), an apomorphic character shared among two or more species (synapomorphy [*q.v.*]) indicates shared descent from a common ancestor and hence monophyly (*q.v.*). *cf.* plesiomorphy (*q.v.*).

arboreal: living above the ground (in trees and shrubs). *cf.* scansorial (*q.v.*); terrestrial (*q.v.*).

auditory bulla: *see* tympanic bulla.

auditory meatus (*pl.* **auditory meati**): the external opening of the ear; the passage leading from the tympanic membrane (ear drum) to the external ear.

autapomorphy: derived trait uniquely characteristic of a taxon.

autogroom: grooming behaviour in which an individual grooms itself. *cf.* allogroom (*q.v.*).

autosomal: pertaining to any chromosome other than the sex chromosomes.

bachelor herd: a herd comprised entirely of males, usually mature, but of mixed age.

baculum (*pl.* **bacula**, *adj.* **bacular**): the os penis, or penis bone, which supports the penis in some mammals.

bai (*pl.* **bais**): an opening or clearing.

basal metabolic rate: metabolic rate required for survival in the thermal neutral zone (*q.v.*); a state that requires the lowest expenditure of energy when at rest.

basicranium: the base of the skull.

- basisphenoid**: cranial bone in middle of base of skull; the median posterior part of the sphenoid bone, forming part of the floor of the braincase.
- Bergmann's Rule**: The theory that the size of a warm-blooded animal in a single, closely related, evolutionary line, increases along a gradient from warm to cold temperatures.
- bicuspid**: having two points or cusps (particularly of teeth).
- bifid**: divided by a shallow notch.
- bilophodont**: describes cheekteeth having two transverse ridges.
- bipedal**: body supported by the two hindlimbs; movement not using the forelimbs.
- blastula**: a hollow ball of undifferentiated cells (derived from a fertilized ovum by cell division), which represents one of the earliest stages of embryonic development.
- BP**: (*abbrev.*) before the present.
- brachydont**: describes a premolar or molar tooth with low crowns. *cf.* hypsodont (*q.v.*).
- braincase (= cranium)**: that part of the skull housing the brain; the part of the skull posterior to the front line of the orbits. *cf.* rostrum (*q.v.*).
- buccal**: On the cheek side of the mouth or teeth or penetrating to the cheek or sometimes used broadly as pertaining to the cavity of the mouth.
- bullae**: *see* tympanic bulla.
- bunodont**: describes molar teeth, entirely covered by enamel, that have low, rounded, hill-like cusps (as opposed to sharp, pointed cusps). (*cf.* hypsodont, lophodont).
- bushmeat**: meat for human consumption derived from non-domesticated mammals, birds and reptiles taken from their natural habitats and domiciles.
- bushveld**: savanna vegetation type characterized by a grassy ground layer and a moderately dense upper layer of shrubs and scattered trees.
- BZ**: (*abbrev.*) Biotic Zone.
- C or c**: (*abbrev.*) canine tooth; upper case denotes adult dentition, lower case denotes deciduous dentition (milk teeth). *See also* canine.
- c.u.**: (*abbrev.*) (*Lat. cum unguis* = with nail) measurement of the hindfoot when length of the nail on the claw is included in the measurement. Usually hindfoot is measured without the claw because claws may be broken or worn. When length of claw is included, it is conventional to record as 'HF c.u.'. *cf.* s.u. (*q.v.*)
- caecum (pl. caeca)**: a blind-ending pouch in the alimentary canal (often enlarged as a fermentation chamber) located at the junction of the small and large intestines.
- canine**: the most anterior tooth on the maxilla bone and in a similar position on the mandible; situated immediately posterior to the incisors; if incisors are absent, the most anterior tooth in the jaw. Unicuspid; tall and pointed in most mammals. Never more than one canine on each side of each upper and lower jaw; absent in some taxa.
- caniniform**: having shape and appearance of a canine tooth.
- carnassial shear**: Found in some carnivores and formed by the blade-like cusps of the fourth upper premolar teeth and first lower molar teeth, which, occluding together like the blades of a pair of scissors, provide a shearing action for cutting through tough skin or bone. Sometimes referred to as the carnassials.
- carotid**: pertaining to the carotid artery located in the front of the neck through which blood from the heart flows to the brain.
- cauda epididymides**: the ducts of the epididymides at the posterior end of the testes that carry sperm from the testes to the vas deferens, which, in turn, carries sperm to the penis. Sometimes used to store sperm prior to copulation.
- caudal**: pertaining to the tail; in the direction of the tail.
- Cenozoic (= Cenozoic Era)**: geological era, ca. 65 mya to today, comprising the Quaternary and Tertiary Periods: the Age of Mammals.
- central Africa**: Cameroon (south of the Sanaga R.), Central African Republic (but only south of ca. 7° N), Equatorial Guinea, Gabon, DR Congo (except SE). Mainly rainforest habitats and rainforest-savanna mosaics.
- centromere**: the part of a chromosome where sister chromatids are linked together during mitosis.
- cerebellum**: the part of the hindbrain that controls and coordinates motor movements, posture, balance and muscle tone.
- cerebrum (= cerebral hemispheres)**: the anterior part of the brain that is involved in voluntary movements, processing sensory information, olfaction, learning, memory, communication and other functions.
- cervical**: pertaining to the neck.
- cf.** (in general usage): compare or compare with. In the context of descriptions, implies a difference or contrast: e.g. 'In *Elephantulus edwardii*, first lower premolar single-rooted (*cf.* *E. myurus* in which the first lower premolar is double-rooted).'
- cf.** (in taxonomy): precedes the specific name if there is uncertainty in the assignment.
- cheekteeth**: the premolar (*q.v.*) and molar (*q.v.*) teeth combined.
- choana (pl. choanae)**: the openings of the internal nostrils on the skull, situated immediately posterior to the bony palate.
- chromosome**: one of the thread-like bodies within the nucleus of a cell, which carry the genes (genetic material) in linear order; each chromosome is composed of one long molecule of DNA (and two long molecules at cell division). Chromosomes occur in pairs (one from each parent) and are visible as rod-like bodies in cells that are dividing. The total number of chromosomes in a cell is expressed as the diploid number (2n).
- CI**: condyloincisive length; the length of the skull from the anterior end of the longest incisor tooth to the posterior end of the occipital condyles. *cf.* GLS.
- cingulum (pl. cingula)**: ridge around the base of the crown of a tooth.
- CITES (abbrev.)**: Convention on International Trade of Endangered Species of Wild Fauna and Flora; an international treaty set up to ensure that international trade in wild animals and plants does not threaten the survival of species in the wild. It accords varying degrees of protection to more than 33,000 species of animals and plants. Appendix I lists species that are the most endangered among CITES-listed animals and plants. Appendix II lists species that are not necessarily now threatened with extinction but that may become so unless trade is closely controlled. Appendix III is a list of species included at the request of a Party that already regulates trade in the species and that needs the cooperation of other countries to prevent unsustainable or illegal exploitation.

- clade:** branch of a phylogenetic tree containing the set of all organisms descended from a common ancestor.
- cladistic (analysis):** a methodology that provides a classification in which organisms are grouped in terms of the time when they had a common ancestor.
- cline** (*adj.* **clinal**): in context of geographic variation, a gradual and sequential change of a character(s) without a significant break such as would justify division into separate subspecies or species.
- CMS:** Convention on Migratory Species of Wild Animals (also known as the Bonn Convention). An intergovernmental treaty, concluded under the aegis of the United Nations Environment Programme, concerned with the conservation of migratory terrestrial, aquatic and avian migratory species throughout their range. Migratory species threatened with extinction are listed on Appendix I; Migratory species that need or would significantly benefit from international co-operation are listed in Appendix II.
- CNL:** condylo-nasal length; measurement from the most anterior part of the nasal bone to the most posterior part of the occipital condyle (exoccipital) on the same side of the skull; a similar measurement to 'greatest length of skull'.
- cochlea** (*pl.* **cochleae**, *adj.* **cochlear**): a hollow structure, spirally coiled like a snail's shell, situated in the skull and containing the internal organ of hearing.
- competitive exclusion:** the principle that two different species cannot indefinitely occupy the same ecological niche.
- concatenation:** a chain of linked elements.
- concave:** having a curvature that curves inwards; having an outline or a surface curved like the interior of a circle or sphere. *cf.* convex (*q.v.*).
- concavity:** a concave depression in an outline or surface.
- conceptus:** embryo prior to implantation.
- conductance:** in thermal biology, the rate at which heat passes across a temperature gradient, e.g. the density and thickness of the pelage affects the rate at which body heat passes from the body to the outside. Thick pelage, which traps and holds air, results in low thermal conductance.
- condylar process:** process at the posterior upper corner of the mandible, which forms the lower hinge of the jaw articulation; fits into the glenoid fossa (*q.v.*) of the skull.
- condylarth** (*adj.*): as in the Condylarthra, an extinct order of mammals.
- condyle:** a rounded process on a bone that articulates with a socket-like concavity in another bone.
- condylobasal length:** the length of a skull, measured from the anterior points of the premaxilla (*q.v.*) to the posterior surfaces of the occipital condyles (*q.v.*).
- congeneric:** belonging to the same genus.
- conspecific:** belonging the same species. *cf.* heterospecific (*q.v.*).
- contiguous:** touching; sharing a boundary (as in geographic ranges).
- convex:** having a curvature that bulges outwards; having an outline or a surface curved like the exterior of a circle or sphere. *cf.* concave (*q.v.*).
- coprophagy:** the eating of faeces. Includes the eating of an individual's own faeces as they are voided from the anus.
- copulatory plug:** plug formed in the vagina of the female after copulation; formed from seminal fluids of the male. Prevents or reduces the chance of sperm from another male(s) entering the female reproductive tract if the female copulates again soon after copulation with the first male.
- coronoid canal:** a foramen (canal) in the coronoid process (*q.v.*) of the mandible.
- coronoid process:** angular pointed process on the upper margin of the mandible, situated anteriorly to the condylar process (*q.v.*); does not participate in the jaw articulation.
- corpus luteum** (*pl.* **corpora lutea**): a glandular mass of tissue on the surface of an ovary, that develops after the extrusion of an ovum from a Graafian follicle (*q.v.*); secretes the hormone progesterone.
- cotype:** originally synonymous with syntype but now used as synonym of paratype (*q.v.*).
- CR:** (*abbrev.*) *see* crown–rump length.
- cranial profile:** the shape of the cranium (the part of the skull that surrounds the brain) when viewed from the side.
- craniodental:** pertaining to the skull and teeth.
- cranium:** that part of the skull housing the brain. Also called braincase.
- crepuscular:** at, active in, twilight, when light intensity is higher than at night but lower than during the day. *cf.* diurnal (*q.v.*); nocturnal (*q.v.*).
- Cretaceous Period:** period (within the Mesozoic Era); 146–65 mya.
- crown:** (1) top of head; (2) exposed part of a tooth (visible above gum), especially the grinding surface.
- crown–rump length (CR):** distance from the crown of head to the rump of a foetus (i.e. maximum length of a foetus in its natural form).
- cuckolding:** when an intruding male mates with an oestrous female without her mate being aware of the event.
- cursorial:** pertaining to running.
- cuspidate** (*adj.* **cuspidate**): a prominence or sharp point, such as on the occlusal surface of some teeth. *See also* t.
- cutaneous:** (*adj.*) pertaining to the skin.
- Cyrenaica:** a region of North-East Libya. Includes the Cyrenaican Plateau and that part of the Mediterranean Coastal Biotic Zone between the plateau and the sea, as well as drier terrain south of the plateau.
- cytochrome b:** a protein involved in electron exchange in the mitochondria. It is the product of a gene in the mitochondrial genome. The sequence of this gene is often compared between species in phylogenetic studies to infer relatedness.
- cytogenetics** (*adj.* **cytogenetic**): the study of the microscopic structure of chromosomes, especially the mapping of genes.
- cytonuclear:** (*adj.*) pertaining to the nucleus and the cytoplasm of a cell.
- Dahomey Gap:** the geographic region where savanna habitat extends southwards to the West African coast in E Ghana, Togo, Benin (formerly Dahomey) and extreme SW Nigeria. The presence of savanna forms a break (or gap) in the extensive Rainforest Biotic Zone, which extends along the West Africa coast from Sierra Leone to Cameroon. The Dahomey Gap is an important biogeographical barrier separating the faunas to the east and west of the Gap.
- deciduous teeth:** *see* milk teeth (*q.v.*).

- Dega:** Ethiopian word for the temperate agricultural/economic altitudinal zone, about 2300–3000 m, warm enough for cereal-based agriculture.
- delayed implantation:** a means of lengthening the interval between copulation and parturition by delaying the implantation of the blastula (*q.v.*), so that both copulation and parturition can occur in the most optimal seasons. Development to blastula stage is followed by a period of halted development lasting several weeks or months; then the blastula implants and embryonic development proceeds normally, usually without any further interruption, until the young is born.
- deme:** a unit of population that is interbreeding and is separate from any other such population.
- dental formula:** a simple numerical method of denoting the number of incisor (I), canine (C), premolar (P) and molar (M) teeth on one side of the upper jaw and lower jaw, and the total number of teeth. For example, the dental formula of a primitive mammal is $I^{3/3}, C^{1/1}, P^{4/4}, M^{3/3} = 44$, which means there are three incisors, one canine, four premolars and three molars on each side of the upper jaw and also the lower jaw, making a total of 44 teeth. The formula may also be expressed in the form $^{3143}/_{3143} = 44$. Each incisor, premolar and molar is numbered according to its position in the tooth row; superscript numbers indicate upper jaw, subscript numbers indicate lower jaw (mandible) e.g. P^4 (upper fourth premolar), M_2 (lower second molar).
- dentine:** the substance, also known as ivory, comprising tusks (*q.v.*) and the interior hard part of vertebrate teeth. Lies under the enamel of teeth (but may be exposed if the enamel wears) and surrounds the pulp chamber and root canals.
- diastema:** space in the mouth between the incisor teeth and cheekteeth in those mammals that feed on grasses, herbs etc. (e.g. rodents, hares, rabbits, ruminants, etc.).
- dichromatism:** condition in which members of a species show one of only two distinct colours or colour-patterns.
- dilambdodont:** molar tooth with W-shaped ridges. *cf.* zalambdodont (*q.v.*).
- dimorphism:** *see* sexual dimorphism.
- diphyly:** the derivation of a taxon from two separate lines of descent. *cf.* monophyly (*q.v.*).
- diploid number (2n):** total number of chromosomes (including sex chromosomes) in a somatic cell of an organism.
- distal:** the end of any structure furthest away from the mid-line of the body or furthest from the point of its attachment. *cf.* proximal (*q.v.*).
- diurnal:** at, active in, daytime; when light intensity is high. *cf.* crepuscular (*q.v.*); nocturnal (*q.v.*).
- DNA hybridization:** technique of comparing the similarity between two DNA molecules by reassociating single strands from each molecule and determining the extent of double-helix formation. In phylogenetics, this technique is used to determine the relatedness of two or more taxa.
- DNA:** (*abbrev.*) deoxyribonucleic acid; the very large self-replicating molecule that carries the genetic information of a chromosome; each molecule is composed of two complementary chains of DNA.
- dorsoventral (dorsoventrally):** from dorsal to ventral surface; from back to belly of an animal.
- E:** (*abbrev.*) length of external (outer) ear (= pinna), measured from tip of ear to the posterior point of the ear conch). Length and shape usually affected by preservation.
- East Africa:** Kenya, Uganda, Rwanda, Burundi and Tanzania.
- eastern Africa:** SE Sudan, Ethiopia, Eritrea, Djibouti, Somalia, Kenya, Uganda, Tanzania, Malawi (but only south of L. Malawi and east of the Shire R. Valley) and Mozambique (but only east of Malawi and north of the Zambezi R.).
- echolocation:** the use of reflected ultrasonic pulses of sound to perceive the surroundings (including obstacles, prey and other animals).
- ecotype:** a genetically distinct geographic variety or population within a species, which is adapted to specific environmental conditions.
- ectoparasite:** a parasite that lives on the exterior of an organism (e.g. ticks, fleas, lice). *cf.* endoparasite (*q.v.*).
- ectotympanic:** a bony element within the middle ear that supports the tympanic membrane or eardrum.
- edaphic:** influenced by conditions of soil or substratum.
- emargination:** a distinct notch or indentation.
- embryo number:** number of foetuses within the uterus or uteri of the female (as assessed by autopsy). Expressed as mean number (with range from minimum to maximum, and sample size). *cf.* litter-size (*q.v.*).
- enamel:** hard material that forms a cap over the dentine component of a tooth; usually the most visible part of a tooth.
- encephalization quotient (EQ):** a measure of comparative brain size or weight defined as the ratio of the actual brain weight to the expected brain weight predicted for an animal of a given body weight.
- endemic:** restricted to, peculiar to, or prevailing in, a specified country or region.
- endoparasite:** a parasite that lives in the interior of an organism (e.g. nematodes, cestodes, blood parasites). *cf.* ectoparasite (*q.v.*).
- entoconid cusp:** the posterior cusp on the lingual (inner) side of a lower molar tooth.
- entotympanic:** an independent ossification found in the floor of the tympanic cavity in various extant and extinct eutherian groups, including, for example, Scandentia, Chiroptera, Dermoptera, Hyracoidea, Pholidota, Xenarthra, Carnivora, and Macroscelidea.
- Eocene:** geological Epoch (within the Tertiary Period); 55–38 mya.
- epiphysis (pl. epiphyses):** any part of a long bone that is formed from a different centre of ossification and that later fuses with the bone to form its terminal part.
- epitympanic recess:** a hollow located on the roof of the middle ear.
- erg:** a large, relatively flat area of desert covered with wind-swept sand with little or no vegetation cover (sometimes referred to as a dune sea).
- evaporative water loss:** the loss of water from the body through the skin and/or the lungs. A mechanism used by mammals to reduce T_b (*q.v.*) when T_a (*q.v.*) is high. Excessive evaporative water loss may lead to dehydration if free (drinking) water is unavailable.
- exfoliating:** shedding flakes (e.g. of bark), or breaking into relatively thin slabs (e.g. of granitic rock).
- exoccipital condyles:** a pair of projections from the occipital bone on either side of the foramen magnum (*q.v.*), which articulate with the first of the spinal vertebrae.

extant: living at the present time. *cf.* extinct.

F. R.: (*abbrev.*) Forest Reserve.

facultative: having the capacity to switch from one mode of life or action to another depending on conditions or circumstances. *cf.* obligate (*q.v.*).

female-defence polygyny: a mating system in which males control access to females directly, usually by virtue of female gregariousness (Emlen & Oring 1977).

fenestra (*pl.* **fenestrae**): opening in a bone, or between two bones.

flank: the side of the body of a mammal.

flehmen: an act performed by many species of mammals whereby an adult male sniffs the vulva and urine of a female to test for oestrus. The head of the male is raised, the nose pointed upwards, the lips retracted and the nose wrinkled. This muscular contraction opens the *ductus incisivus* ensuring that scent molecules reach the Jacobsen's organ for olfactory analysis.

FN: (*abbrev.*) *see* fundamental number.

foliaceous: (*adj.*) resembling the leaf of a plant.

folivore (*adj.* **folivorous**): an animal that eats leaves.

foramen (*pl.* **foramina**): an aperture (which is usually small, round or elliptical) in a bone, or between bones, for the passage of a nerve, blood vessel or muscle.

foramen magnum: the large opening at the posterior end of the skull through which the spinal cord passes.

form: a neutral term for a single individual or taxonomic unit that may be employed without reference to the formal taxonomic hierarchy of categories; one of the varieties found in a polymorphic species.

forest island: *see* relict forest.

fossa (*pl.* **fossae**): a depression or hollow usually in a bone (e.g. glenoid fossa, preorbital fossa)

fossorial: adapted for digging; burrowing. *cf.* subterranean (*q.v.*).

founder effect: the loss of genetic diversity that occurs when a new isolated population is derived from a very small number of individuals.

fovea: small pit or depression.

frontal bone: one of a pair of bones forming the anterior part of the braincase.

frugivorous: fruit-eating.

fundamental number (FN): an ambiguous term sometimes defined as (1) the total number of chromosomal arms in the full chromosomal complement of an organism (i.e. including the sex chromosomes), or (2) the total number of chromosomal arms found in the autosomal chromosomes only (i.e. excluding the sex chromosomes). When only the autosomal chromosomes are included, some authors (but not all) use aFN instead of FN to avoid ambiguity. For further details, *see* aFN.

fusiform: elongated and tapering at both ends.

fynbos: the heath shrublands characteristic of the Cape Floristic Kingdom (within the South-West Cape Biotic Zone) of South Africa. Dominant plants are sclerophyllous, evergreen, low (<3 m), bushy and fine-leaved, but there are also scattered taller bushes and, less often, very widely spaced trees. Contains an exceptionally high number of endemic species of plants. The three main components on nutrient-poor sandy soils are species of Ericaceae, Restionaceae and Proteaceae. Also includes 'renosterveld' (*q.v.*) (dominated by species of Asteraceae) on nutrient-rich silt or clay soils.

G. R.: (*abbrev.*) Game Reserve.

gallery forest: type of forest outlier (in a savanna region) found in narrow sheltered valleys and ravines on hillsides, where soils are moist enough, and conditions humid enough, to support rainforest trees (Rosevear 1953).

garrigue: a type of short, Mediterranean shrubland (White 1983).

genetic drift: in population genetics, refers to changes in the frequencies of genes in small, isolated populations that occur with time, as a result of random sampling events as opposed to natural selection.

genotype: genetical term to describe the genetic constitution of an individual inherited from its parents. *cf.* phenotype (*q.v.*).

genus (*pl.* **genera**): taxonomic division superior to species and subordinate to family.

geocarpic: having fruit that mature underground.

geophagy (= **geophagia**): the eating of saline or calcareous soil.

gestation: the development of embryo/foetus, which takes place in the uterus; the period during which this development takes place. The gestation period is defined as the interval between conception and parturition (birth). Strictly speaking, the gestation period is not the interval between copulation (mating) and parturition (birth), although many authors take it to be this interval. The gestation period (*sensu stricto*) may be lengthened by reproductive delays, such as delayed implantation (*q.v.*).

glans penis: the bulbous tip of the penis.

glenoid (= **glenoid fossa**): the cavity (fossa) in the squamosal bone of the skull for the articulation of the condyle of the mandible (lower jaw) in mammals; visible on lateral and/or ventral views of skull depending on the taxon.

GLS: (*abbrev.*) greatest length of skull, measured from anterior end of incisor teeth or nasal bone (whichever is most anterior) to the posterior end of the skull (occiput, occipital condyles or auditory bullae, whichever is most posterior).

Gondwana (= **Gondwanaland**): the southernmost of the two Mesozoic (*q.v.*) supercontinents that later fragmented (as a result of continental drift) into the landmasses of Africa, Madagascar, Antarctica, Australia, South America, the Indian subcontinent and the Arabian peninsula.

Graafian follicle: the structure in the mammalian ovary that contains the developing ovum and from which the ovum is released at the time of ovulation.

gracile: lightly built. *cf.* robust.

graminivore (*adj.* **graminivorous**): feeding on grasses.

granivore (*adj.* **granivorous**): an animal that eats grains and seeds.

graviportal: having limbs adapted to bearing great weights (as in elephants).

gregarious: living together in groups, flocks, herds.

Gregorian Rift Valley: *see* Rift Valley.

guard hair: long thin bristle-like hairs, mainly on the back and flanks that project beyond the soft hairs of the pelage; when present, conspicuous but never as numerous as soft hairs; probably tactile in function.

gular: pertaining to the upper part of the throat (the gula) as in gular gland, gular pouch, gular region.

GWS: (*abbrev.*) greatest width of skull, usually measured across the widest point of the zygomatic arches (*q.v.*).

- haematopoietic** (*n.* **haematopoensis**): pertaining to the formation of blood cells from stem cells.
- hallux**: the first digit of the hindlimb.
- hammada**: flat plain covered with pebbles of various sizes on a hard substrate in an arid environment. Much of the Sahara Desert is formed of hammada.
- haplotype**: the set of alleles borne on one of a pair of homologous chromosomes; a group of genes that is inherited together from a single parent.
- HB**: (*abbrev.*) length of head and body (measured from the tip of the nose to the most posterior point of the pelvis (anterior to the first tail vertebra)).
- hemidiaphragm**: half of the diaphragm, the muscle that separates the chest cavity from the abdomen and that serves as the main muscle of respiration.
- hermaphrodite** (*adj.* **hermaphroditic**): an individual having both male and female reproductive organs.
- heterospecific**: (*adj.*) belonging to different species. *cf.* conspecific (*q.v.*)
- heterothermic**: condition when the body temperature fluctuates in relation to the ambient temperature T_a (*q.v.*). *cf.* homeothermic (*q.v.*).
- heterozygosity**: a measure of the genetic variation in a population, expressed through the presence of different alleles (*q.v.*) at one or more loci on homologous chromosomes.
- HF**: (*abbrev.*) length of hindfoot (measured from the 'ankle bone' to the tip of the longest digit usually without including the claw). *See also* c.u.; s.u.
- hibernaculum** (*pl.* **hibernacula**): a place, domicile or roost where an animal hibernates.
- hibernation**: a state of inactivity accompanied by a reduction in metabolic rate (below basal metabolic rate [*q.v.*]), lower T_b , and slow breathing. Occurs when T_a is low and food is scarce; usually lasts for weeks or months; not common in African mammals (*cf.* torpor).
- high forest**: rainforest that has matured, stabilized and reached the climax stage of succession.
- highveld**: high plateaux characteristic of inland southern Africa, dominated by grasses.
- Holocene**: geological Epoch (within the Quaternary Period) (*q.v.*) following the Pleistocene Epoch (*q.v.*); ca.11,000 mya to today. Sometimes referred to as the 'Recent' Epoch.
- holotype** (= **type**): the single specimen designated or indicated by the original author of the original description of a new species or subspecies, to be the standard reference to the essential characters of the new taxon. *see also* cotype (*q.v.*), lectotype (*q.v.*), neoparatype (*q.v.*), neotype (*q.v.*), paratype (*q.v.*), syntype (*q.v.*), topotype (*q.v.*) and type locality (*q.v.*).
- home-range**: the area (expressed in square metres, or square kilometres) routinely used by an animal for its day-to-day activities and requirements, and that contains the resources required for survival and reproduction. Within the home-range there may be a 'core area' or 'centre of activity' that is utilized more frequently than other parts (e.g. 80% or 90% of known time-based observations). *cf.* territory (*q.v.*).
- homeothermic**: describes an organism having a body temperature that is maintained at a constant level (within limits), independently of the ambient temperature T_a (*q.v.*). For the limits, *see* upper and lower critical temperatures [*q.v.*]. *cf.* heterothermic (*q.v.*).
- homoplasy**: similarity between different organisms or taxa resulting from evolution along similar lines (e.g. convergent evolution) rather than descent from a common ancestor.
- homozygous** (*n.* homozygosity): describes a diploid organism that has inherited the same allele of any particular gene from each of its parents. *cf.* heterozygous.
- hyoid**: a small bone or bones in the throat located at the base of the tongue and supporting the muscles of the tongue.
- hyperthermia**: elevation of body temperature above normal limits due to increase in T_a (*q.v.*) or increase in metabolic rate. *cf.* hypothermia (*q.v.*).
- hypoconulid**: the most posterior cusp on the lingual (inner) side of a lower molar tooth.
- hypogeal**: living or growing underground.
- hypothermia**: drop in body temperature below normal limits; occurs in some small mammals when T_a (*q.v.*) falls, and is a means of conserving energy in cold weather. *cf.* hyperthermia (*q.v.*).
- hypodont**: describes a premolar or molar tooth with high crowns; has short roots. *cf.* bunodont, lophodont.
- I or i**: (*abbrev.*) incisor (*q.v.*) tooth or teeth; upper case denotes adult dentition, lower case denotes deciduous dentition (milk teeth). *See also* incisor.
- I.** (*pl.* **Is.**): (*abbrev.*) Island.
- I¹-M³**: (*abbrev.*) the length of the upper tooththrow from the anterior end of the first upper incisor to the posterior end of the last molar. In taxa where the last molar is M¹ or M² (instead of M³), the measurement is I¹-M¹ or I¹-M².
- implantation**: the embedding of a blastula (*q.v.*) in the lining of the uterus.
- incertae sedis**: (*Lat.*) refers to a taxon of uncertain status and that is perhaps taxonomically invalid.
- incisive foramen** (*pl.* **foramina**): paired foramina located at the anterior end of the bony palate, just posterior to the incisor teeth.
- incisor**: tooth rooted in the premaxillary bone (most anterior bone of upper jaw) and in an equivalent position in the mandibular bone (lower jaw); always anterior to the canine teeth, if present. The number and form of the incisor teeth varies in different species. *See also* dental formula (*q.v.*).
- infraorbital foramen** (*pl.* **foramina**): foramen that connects the orbit (eye-socket) with the rostrum (premaxilla and maxilla bones); this foramen contains the masseter medialis muscle in some taxa. Also referred to as anteorbital foramen and antorbital foramen.
- infrasonic**: describes sounds with frequencies below the range that can be heard by humans.
- infundibulum**: a funnel-shaped cavity or depression.
- inguinal**: situated in the groin, that is the area between the lower lateral part of the abdomen and the thigh.
- inner**: nearest to mid-line of body, e.g. inner incisor, inner margin of ear.
- insectivore** (*adj.* **insectivorous**): an animal that eats insects.
- inselberg**: isolated rocky hill; term used mainly in western Africa. *See also* jebel (*q.v.*); kopje (*q.v.*), krantz (*q.v.*).
- inter-aural**: between the ears.
- inter-digital**: between the digits (e.g. interdigital gland).

- inter-orbit (= inter-orbital constriction):** narrowest part of the skull between the orbits when viewed dorsally at the level of the frontal bones.
- inter-parietal:** bone (not paired) on dorsal surface of the skull, lying between and partly posterior to the parietal bones.
- inter-pterygoid region:** the region between the two plate-like pterygoid bones (*q.v.*) that form part of the roof of the mouth.
- inter-specific:** between different species.
- intra-specific:** within one species; between members of the same species.
- intromission:** insertion of the penis into the vagina during copulation.
- invagination:** the formation of a cavity by the in-sinking of the outside wall or surface of a tissue or structure, thereby drawing an exterior layer into the interior of the structure to form the lining of the cavity; a cavity formed by the process of invagination.
- Isoptera:** taxonomic order containing the termites (within the phylum Insecta).
- isozyme:** any one of several different forms of an enzyme encoded by the same or different genes and that each differ in properties such as optimum pH or isoelectric point.
- iteroparous:** repeated reproduction throughout a season or a lifetime (*cf.* semelparous – reproduces once and then dies).
- ivory:** *see* dentine.
- jebel (= gebel):** isolated rocky hill in savanna and arid habitats; term used mainly in northern Africa. *See also* inselberg (*q.v.*); kopje (*q.v.*).
- jugal:** bone of the skull that forms the middle part of the zygomatic arch (*q.v.*); anteriorly joins the maxillary process (*q.v.*) of the maxilla bone and posteriorly joins the squamosal process of the squamosal bone.
- K-selection:** selection for characteristics suitable in stable environments (slow development of young, small litter size, relatively long time to maturity, relatively long life span) *cf.* r-selection (*q.v.*).
- Kaokoveld:** area of sandstone and lava hills of the Namib Desert (Biotic Zone 11b) in NW Namibia, inland from the Skeleton Coast.
- Karoo:** southern African term for grassy dwarf shrubland on the semi-arid central plateau of the western half of South Africa at altitudes of 500–2000 m.
- karyogram:** a photographic representation of a karyotype (*q.v.*) as it appears at mitosis. Individual chromosomes are arranged in pairs from largest to smallest.
- karyological:** pertaining to the nucleus and chromosomes.
- karyotype:** the chromosomes in the cell of an animal. *See also* karyogram.
- kloof:** a deep, narrow valley or gorge.
- kopje:** rocky hill with boulders, rock crevices and sparse vegetation; term used mainly in southern Africa. *See also* inselberg (*q.v.*); jebel (*q.v.*); kranz (*q.v.*).
- krantz (pl. krantzes):** a wall of rock encircling a mountain or summit; hence any precipitous or overhanging wall of rocks.
- L.:** (*abbrev.*) Lake.
- labial:** pertaining to the lips; situated near the lips; on the outer side of the teeth within the mouth. *cf.* lingual (*q.v.*).
- labially:** in the direction of the lips. *cf.* lingually (*q.v.*).
- lachrymal bone:** small bone in skull situated at the upper anterior margin of the orbit, near the lachrymal (tear) gland.
- lambdoid crest:** *see* supraoccipital crest.
- lamina (pl. laminae):** in the context of premolar and molar teeth, a transverse row of cusps (e.g. t1, t2 and t3, or t4, t5 and t6, etc.) that, when worn, form a transverse ridge of bone and dentine across the tooth.
- larynx (= voice box):** the structure in the throat of mammals that produces sound.
- lauschlag:** a courtship behaviour in antelopes in which the male touches the female's underside with a stiff foreleg, placing it either under her flank from the side or between her hind legs from behind. Also termed the mating kick or foreleg kick.
- Laurasia:** the northernmost of the two Mesozoic (*q.v.*) supercontinents that later fragmented (as a result of continental drift) into the landmasses of Europe, Asia (excluding the Indian subcontinent) and North America.
- lectotype:** a specimen chosen from syntypes (*q.v.*) to stand as 'the type' of a species or subspecies when no holotype (*q.v.*) was designated by the author who described the new species or subspecies.
- lek:** a traditional site where males gather for the sole purpose of attracting and courting females, and to which females come for the sole purpose of mating with the male of their choice.
- limiting factor:** the principle that the growth or functioning of an organism is limited when any essential factor (or resource) is lacking or in short supply, regardless of the quantity available of any other factor (or resource). The principle may also be applied to the proliferation and/or distribution of a population or species.
- lingual:** pertaining to the tongue; situated near the tongue; on the inner (tongue) side of the mouth. *cf.* labial (*q.v.*).
- lingually:** in the direction of the tongue. *cf.* labially (*q.v.*).
- litter-size:** number of young born to a female. Expressed as mean number (with range from minimum to maximum, and sample size). *cf.* embryo number (*q.v.*).
- localized movements:** movements of an animal within part or all of its home-range within a single day or within a limited period of time. *cf.* migration (*q.v.*); nomadic movements (*q.v.*).
- longitudinal:** lengthwise; running in a head to tail direction. *cf.* transverse (*q.v.*).
- lophodont:** molar teeth having the crowns formed in transverse crests or ridges (*cf.* bunodont).
- lordosis:** dorsi-flexion of the spine, often performed by females prior to copulation.
- lower critical temperature:** the lowest ambient temperatures at which the animal must increase its metabolic rate to maintain a constant body temperature. If ambient temperature decreases further, and the animal is unable to increase its metabolic rate sufficiently to maintain a constant body temperature, it will enter hypothermia and may eventually die. *cf.* upper critical temperature.
- lowveld:** savanna at lower altitudes below the Great Escarpment of South Africa, with vegetation consisting of a grassy lower layer and a woody upper layer of shrubs and/or trees, at either high density (woodland) or intermediate density (bushveld, *q.v.*).
- lumbar:** describes vertebrae between the thoracic vertebrae and the sacrum; vertebrae of the lower back in humans.

lyrate: having curvature suggestive of a lyre.

M: (*abbrev.*) molar tooth or teeth. *See also* molar (*q.v.*).

Maghreb: *see* North-West Africa (*q.v.*).

malleus: the most external bone of the three ossicles of the middle ear, the handle of which is joined to the ear drum.

mandible: lower jaw.

mandibular ramus: one of the two branches (sides) of the mandible (*q.v.*); the two rami are joined at the mandibular symphysis (*q.v.*).

mandibular symphysis: the junction, marked by a small vertical ridge, where the left and right sides of the mandible are fused.

masseter muscle: one of the muscles that raises the lower jaw, e.g. during chewing. Particularly well developed and powerful in herbivores.

mastoid: one of a pair of bones, often with a prominent process, situated near the posterior end of the skull behind the auditory meatus (*q.v.*).

matriarchal; describes social groups dominated and/or led by a female (often one of the oldest females in the group).

maxilla (*pl. maxillae*): one of the pair of bones in the skull that forms that part of each upper jaw in which the canine (*q.v.*) (if present) and cheekteeth (premolars and molars) (*q.v.*) are rooted.

maxillary process: projection of bone from the maxilla that forms the anterior portion of the zygomatic arch (*q.v.*); usually orientated vertically to the anterior–posterior line of the skull.

maxillary: pertaining to the maxilla (*q.v.*).

meatus: a passage or channel; the opening of a passage.

medial: situated in the middle.

melanistic: having an abnormally large amount of black or dark pigment in pelage and skin.

mesa: Ethiopian word for the microhabitat (usually on slopes) within afroalpine moorlands and grasslands, where it is higher and drier than surrounding areas, so dominated by (usually) *Alchemilla*.

Mesozoic (= Mesozoic Era): geological era; ca. 250–ca. 65 mya, comprising the Triassic, Jurassic and Cretaceous Periods; the Age of Reptiles.

metabolic rate: *see* basal metabolic rate (*q.v.*).

metabolic water: water produced by oxidative processes within the body; an important source of water for arid-adapted mammals when free (drinking) water and water within the food is in short supply or unavailable.

metacarpals: the long bones of the hand, situated between the carpal bones of the wrist and the proximal phalanges of the fingers.

metacentric: describes a chromosome with the centromere (*q.v.*) at or very near the middle of its length, so there are two arms of equal or almost equal length (ratio not greater than 1 : 1.1). *cf.* submetacentric (*q.v.*).

metacone: the posterior labial (external) cusp of an upper molar tooth.

metacromion: a process projecting backward and downward from the acromion (the lateral triangular projection of the spine of the scapula that forms the point of the shoulder and articulates with the clavicle of the scapula) of some mammals.

metapopulation: in population dynamics and ecology, a group of spatially separated populations of the same species that interact at some level.

metatarsal gland: scent glands on the outside lower hind leg. In the Bovidae, only the Impala *Aepyceros melampus* possesses metatarsal glands.

metatarsals: the long bones of the foot, situated between the tarsal bones of the ankle and the most proximal phalanges of the toes.

microcomplement fixation: in molecular evolutionary studies, species can be compared by the extent to which antibodies to the proteins of one species cross-react to the proteins of another species. The extent of cross-reaction is indicative of the similarity of the proteins and, by inference, the evolutionary affinity of the two species. Albumin is a protein commonly used for these studies.

microsatellite locus (*pl. microsatellite loci*): a region within a DNA sequence where short sequences of one, two, three or four of the nucleotides (A [adenine], T [thiamine], G [guanine] and C [cytosine]) are repeated consecutively; e.g. ACACAC, CAACAA. The number of times a sequence is repeated varies between individuals, within populations of a species, or between species, which makes microsatellite loci useful tools in systematics (*q.v.*).

migration: movements of species that travel, predictably and more-or-less directly, from one habitat to another (and back again), along predetermined routes, in response to seasonal changes in climate, food supply or any other resource. *cf.* localized movements (*q.v.*); nomadic movements (*q.v.*).

milk teeth: teeth occurring in newborn mammals, or appearing soon after birth, and preceding the permanent teeth of the adult animal. Also called deciduous teeth.

Miocene: geological Epoch (within the Tertiary Period); ca. 23–5 mya.

miombo: a vernacular name applied to trees in the genus *Brachystegia*; a type of savanna woodland in the Zambezi region where *Brachystegia* spp. are the commonest trees or one of the commonest trees.

Mistbelt: foothills along the eastern Great Escarpment that experience regular fogs, with vegetation comprising mainly grasslands and patches of afroalpine forest in protected valleys and ravines.

mitochondrial DNA: the small amount of DNA contained within the mitochondria of a cell.

molar: grinding or cutting tooth rooted in the maxilla bone and the mandible; there are usually one, two or three molar teeth in each ramus of the jaw. Together with the premolars, if present, they form the 'cheekteeth'. The number and form of the molar teeth varies in different species. Not preceded by deciduous (milk) teeth.

molariform: similar in form to a molar tooth; used to describe the form of the premolar teeth in some taxa.

monoestrous: Generally, having one oestrus cycle (*q.v.*) during a single reproductive season. In some taxa, having one litter per year. *cf.* polyoestrous (*q.v.*).

monogamy (*adj. monogamous*): a mating system in which one male mates with one female. Neither sex has the opportunity of monopolizing additional members of the opposite sex. Fitness often maximized through shared parental care (Emlen & Oring 1977). *cf.* polygyny (*q.v.*).

monophyletic: describes a taxonomic group descended from a common ancestor that was itself a member of that taxonomic

- group, and including *all* the descendants of that ancestor (Groves 2001). *cf.* paraphyletic (*q.v.*); polyphyletic (*q.v.*).
- monophyly**: derivation of taxa from a common ancestor. *cf.* diphyly (*q.v.*), polyphyly (*q.v.*).
- monospecific**: describes a genus containing only one known species. *See also* monotypic (*q.v.*).
- monotocous**: normally having only one young per litter (twinning, if it occurs, is very rare and abnormal). *cf.* polytocous (*q.v.*).
- monotypy** (*adj.* **monotypic**): describes a taxon containing only one immediately subordinate taxonomic unit, e.g. a monotypic family contains only one genus; a monotypic genus contains only one species. *cf.* polytypy (*q.v.*).
- mopane**: a vernacular name applied to the tree *Colophospermum mopane*; a type of savanna woodland in the Zambezi region in which *C. mopane* is the commonest species of tree.
- Mt.** (*abbrev.*) Mount.
- mtDNA**: (*abbrev.*) mitochondrial DNA (*q.v.*).
- Mts.** (*abbrev.*) Mountains.
- multiparous**: describes either the birth of more than one offspring at once, or a female that has given birth two or more times.
- muzzle**: the snout; the nose and jaws of a mammal.
- MW**: (*abbrev.*) *see* mastoid width.
- mya**: (*abbrev.*) millions of years ago.
- myrmecophagy** (*adj.* **myrmecophagous**): the eating of ants and/or termites.
- mystacine vibrissae**: vibrissae (*q.v.*) resembling a moustache.
- n. d.**: (*abbrev.*) no data.
- N. P.**: (*abbrev.*) National Park.
- N. R.**: (*abbrev.*) Nature Reserve (not National Reserve).
- nares** (*pl.* **nares**): a nostril.
- Neogene Period**: geological period and system; 23.03 ± 0.05 to 2.5 mya, comprising the second part of the Cenozoic Era.
- neonate**: a newly born animal.
- neoparatype**: any specimen described at the same time as the neotype (*q.v.*).
- neotype**: a specimen selected as the type in cases where the primary types are definitely known to be lost or destroyed.
- nipple**: external opening of mammary gland. Nipple number and position vary according to the taxon, but are consistent within a species. Nipples arranged in pairs, one of the pair on each side of body.
- nocturnal**: at, active in, the night; when light intensity is at its lowest; between sunset and sunrise. *cf.* crepuscular (*q.v.*); diurnal (*q.v.*).
- nomadic movements**: irregular and unpredictable movements, from one locality to another, made by species living in unpredictable habitats. *cf.* localized movements (*q.v.*); migration (*q.v.*).
- nomen dubium**: when the available evidence is not sufficient to permit the identification of a species, its name is considered to be a *nomen dubium* and therefore not available for taxonomic purposes.
- nomen nudum**: a name that is not valid because, when it was originally published, the organism to which it referred was not adequately described, defined or sketched. The name is therefore invalid because it is impossible to associate it indisputably with any specific organism.
- nominate subspecies**: the subspecies that bears the name of the species to which it belongs (e.g. *Otocyon megalotis megalotis*), only brought into existence by the creation of one or more other subspecies in the same species (e.g. *Otocyon megalotis virgatus*).
- North Africa**: those parts of Mauritania, Morocco, Algeria, Tunisia, Libya and Egypt that are north of the Sahara Desert.
- North-Central Africa**: Southern Chad and southern Sudan, west of the Nile R. and south of the Sahara. Mainly savanna habitats.
- North-West Africa (= Mahgreb)**: those parts of Mauritania, Morocco, Algeria, Tunisia and NW Libya that are north of the Sahara Desert.
- nuchal**: pertaining to the nape of the neck.
- nulliparous**: not having given birth.
- obligate**: obligatory; limited to one mode of life or action irrespective of conditions or circumstances. *cf.* facultative (*q.v.*).
- occipital condyles**: the pair of smooth, rounded processes of the occipital bone at the posterior end of the skull on either side of the occipital foramen that acts as a hinge between the head and the neck.
- occiput**: the posterior part of the skull, above the foramen magnum (*q.v.*).
- occlusal**: pertaining to the biting surface of a tooth.
- oestrous cycle**: the reproductive cycle in most non-pregnant female mammals, comprising recurring physiological changes induced by reproductive hormones.
- oestrus** (*adj.* **oestrous**): The period when a female is sexually receptive.
- Oligocene**: geological Epoch (within the Tertiary period), ca. 38–23 mya.
- omnivore** (*adj.* **omnivorous**): an animal that eats a wide range of foods.
- orbit**: bony cavity (eye-socket) in which the eye is situated.
- oscillogram**: a visual representation (graph) of sound waves in which amplitude (sound wave pressure) is plotted on the vertical axis, and time on the horizontal axis (*cf.* sonogram *q.v.*).
- osmetrichia**: hairs structurally specialized for the dispersal of scent.
- osteophagia**: the chewing on bones engaged in by herbivorous animals suffering from a deficiency of phosphorus and calcium in their diet.
- outer**: furthest from the mid-line of the body.
- ovulation**: the release of female gametes (ova, eggs) from the ovary.
- ovum**: the female gamete or egg cell.
- owl pellets**: waste material, normally in an egg-like shape, regurgitated by owls, which contains undigested fragments of bone, hair, feathers and scales etc. from the prey; for mammalogists, useful in determining indirectly the species of small mammals in a habitat.
- P or p**: (*abbrev.*) premolar tooth or teeth; upper case denotes adult dentition, lower case denotes deciduous dentition (milk teeth). *See also* premolar.
- pachyosteosclerosis**: a thickening of the bones of the ribs and vertebrae, resulting in unusually solid bone structure with little to no marrow.
- Palaeartic**: a zoogeographic region comprising Europe, North Africa and Asia (except for southern portion of the Arabian Peninsula and tropical and sub-tropical parts of the Oriental Region).
- Palaeocene**: geological Epoch (within the Tertiary Period); 65–55 mya.

- palatal foramen** (*pl.* foramina): a foramen (*q.v.*) in the palatine bone.
- palate**: the roof of the mouth. The anterior part (hard palate) comprises the bony palate (formed by the premaxillae, maxillae and palatine bones), and a covering mucous membrane. The posterior part (soft palate) is composed only of muscular tissue covered by a mucous membrane.
- Paleogene**: geological period and system; 65.5 ± 0.3 to 23.03 ± 0.05 mya, comprising the first part of the Cenozoic Era.
- papilla** (*pl.* papillae, *adj.* papillate): a small projection or protuberance.
- paraoccipital process**: narrow strut-like bone that projects ventrally from the paraoccipital bone on the posterior part of the skull.
- parapatry** (*adj.* parapatric): the situation where two or more species have geographic ranges that are contiguous (*q.v.*) but do not overlap. This abutting may be along a line of habitat discontinuity, ecotone, or altitudinal/climatic contour, but may also arise from competitive exclusion of one (or both) by the other.
- paraphyletic**: describes a taxon containing units that have evolved from a single ancestral taxon but that do not contain all of the descendents of the most recent common ancestor.
- paratype**: a specimen collected at the same time and place as the holotype (*q.v.*) and designated by the original authority as such. There may be one or more paratypes.
- parietal**: one of the pair of bones forming the vault of the braincase, situated between the frontal and the occipital bones.
- parous**: having given birth.
- partim**: in taxonomy, used in context of taxon names and synonyms to indicate that not all material that has been referred to the name is currently considered to belong to that name. e.g. *auritus* (partim) is listed as a synonym of *Plecotus christii* because only some of the specimens, which were earlier identified as *Plecotus auritus*, are now considered to represent *P. christii*.
- parturition**: the act of giving birth.
- pectoral**: pertaining to or situated on the chest.
- pedal glands**: glands that are situated in the feet opening between the hooves.
- pelage**: the hairy, woolly or furry covering of the body in mammals. The pelage variously consists of hairs, guard hairs and underfur according to the species.
- petrophily** (*adj.* petrophilic): occupying habitats dominated by large boulders.
- phalanx** (*pl.* phalanges): one of the bones in a finger.
- pharynx** (*adj.* pharyngeal): the passage leading from the oral and nasal cavities in the head to the oesophagus and larynx (*q.v.*).
- phenotype**: the visible characters of an individual resulting from the interaction between the genotype (*q.v.*) and the environment.
- philopatry**: the tendency to remain in or consistently return to the place where one was born.
- philtrum**: a medial vertical cleft or groove in the rhinarium (*q.v.*) extending from between the nostrils to the upperlip.
- phylogenetics**: pertaining to the line of descent of a taxon; a method of classification that attempts to show the evolutionary relatedness of organisms.
- phylogeny** (*adj.* phylogenetic): the evolutionary history and line of descent of a species or higher taxonomic unit.
- piloerection**: the erection of hairs that occurs as a means of conserving heat (*see* temperature regulation) and, in some mammals, as a threat display.
- pinna** (*pl.* pinnae): the external (outer) ear.
- placental scars**: scars on the inner surface of the uterus of a mammal; the site where a placenta was attached during pregnancy. The number of placental scars can give an indication of the number of litters that a female has had (when the average number of young/litter is known).
- placentation**: the formation, type and structure of the placenta; the arrangement of placentae.
- plantar**: of the sole of the foot.
- plantigrade**: describes locomotion during which the entire sole of each foot touches the ground.
- Pleistocene**: geological Epoch (within the Quaternary Period); ca. 1.7 mya to 10,000 year ago.
- plesiomorphy** (*adj.* plesiomorphic): in cladistics (*q.v.*), describes a pre-existing character state across a wide taxonomic grouping. Sharing of that state (symplesiomorphy [*q.v.*]) amongst a subset of taxa within the wider grouping is not indicative of monophyly (*q.v.*). *cf.* apomorphy (*q.v.*).
- pleural cavity**: the body cavity occupied by the lungs.
- Pliocene**: geological Epoch (within the Tertiary period), ca. 2–5 mya.
- poikilothermic**: the condition when the body temperature varies with the surrounding ambient temperature.
- pollex**: digit 1 ('thumb') of forefoot ('hand').
- polygyny** (*adj.* polygynous): a mating system in which one male mates with several females. *See* resource-defence polygyny; female-defence polygyny. *cf.* monogamy (*q.v.*).
- polymorphism** (*adj.* polymorphic): the existence, within a species or population, of individuals having different forms (colour, size, shape etc.).
- polyoestrous**: Generally, having two or more oestrous cycles (*q.v.*) during a single reproductive season. In some taxa, having more than one litter/year. *cf.* monoestrous (*q.v.*).
- polyovulation**: production of many ova (and hence many corpora lutea) during a single oestrus; sometimes called 'superovulation'; recorded in some species of sengis.
- polyphyletic**: describes a taxon derived from two or more ancestral sources; not of a single, immediate line of descent (Mayr *et al.* 1953). *cf.* monophyletic (*q.v.*).
- polyphyly**: derivation of a taxon from two or more ancestral sources. *cf.* monophyly (*q.v.*).
- polytocous**: normally or often having more than one young per litter. *cf.* monotocous (*q.v.*).
- polytypy** (*adj.* polytypic): a taxon that has several taxa in the next lower taxonomic category, e.g. a polytypic family contains two or more genera, a polytypic genus has two or more species. *cf.* monotypy (*q.v.*).
- postauricular**: behind the external ear (pinna).
- postorbital process**: the bony projection arising from upper rim of orbit and projecting outwards and downwards around the posterior of the orbit.
- postorbital**: behind (posterior to) the orbit.
- postpartum oestrus**: an oestrus cycle immediately after (or very soon after) parturition and while lactating.

- precocious** (= **precocial**): describes young born in a well developed state enabling them to move around and forage soon after birth. *cf.* altricial (*q.v.*).
- premaxilla** (*pl.* **premaxillae**): one of a pair of bones at the anterior end of the skull that bears the incisor teeth.
- premolar**: tooth on the maxilla bone situated immediately anterior to the molar teeth; usually preceded in time by deciduous (milk) tooth; multi-cusped. Structure and function of premolar teeth vary according to species.
- preorbital fossa**: a bilateral depression in the skull, located anterior to the eye.
- preorbital**: anterior to the eye.
- prepuce** (*adj.* **preputial**): the skin surrounding and protecting the head of the penis; foreskin.
- preputial gland**: a gland situated adjacent to the penis or vaginal opening.
- primiparous**: a female that has given birth only once. *cf.* multiparous (*q.v.*).
- promiscuity**: a mating system in which each male mates with several females and each female mates with several males.
- pronking**: *see* stotting.
- protocone**: The main inner (lingual) cusp of an upper molar tooth.
- protuberant**: projecting forward (bulging) beyond the surrounding surface.
- proximal**: nearest to the body or to the mid-line of the body; nearest to the point of attachment. *cf.* distal (*q.v.*).
- proximate cause**: a cause that produces an effect directly without any intervening agency.
- pterygoid process**: one of a pair of narrow, ventrally projecting processes of the pterygoid bones situated immediately posterior to the bony palate and forming the walls of the mesopterygoid fossa (*q.v.*).
- pterygoid**: one of a pair of cranial bones forming part of the roof of the mouth.
- pubic bone**: anterior inferior part of the pelvis, articulating with its opposite number in the anterior midline at the pubic symphysis.
- Quaternary Period**: period within the Cenozoic Era; 2 mya to today, comprising two epochs: the Pleistocene and Holocene (Recent) (*q.v.*).
- r-selection**: selection for characteristics suitable in unstable fluctuating environments (rapid development of young, large litter size, relatively short time to maturity, relatively short life span) *cf.* K-selection (*q.v.*).
- R.**: (*abbrev.*) River.
- radius**: one of the two bones of the lower forelimb between the humerus (upper arm) and the wrist.
- ramus**: one half (left or right) of the lower jaw or mandible.
- range length**: distance between the most distant captures (by live-trapping) of an individual; a rough method of assessing home-range (*q.v.*).
- Recent**: *see* Holocene (*q.v.*).
- relict forest**: a forest that persists where local conditions are favourable after the disappearance of forest from the surrounding area as a result of climate change or human activity. Relict forests include those at the base of inselbergs that are watered by rainwater running off the inselberg, and forests growing in graveyards and sacred sites that are protected. Sometimes known as forest islands.
- relict population**: one that persists where local conditions are favourable after the extinction of the species from at least part of its former range.
- Renosterveld**: a dominant vegetation type in the Cape Floristic Region (*q.v.*), and characterized by the dominance of members of the Daisy Family (Asteraceae), specifically one species - Renosterbos *Elytropappus rhinocerotis*, from which the vegetation type gets its name.
- reproductive capacity**: number of young produced by a female during the breeding season.
- reproductive chronology**: the timing and duration of events, such as spermatogenesis, copulation, ovulation, gestation, parturition, lactation and reproductive inactivity, throughout the year.
- reproductive strategy**: the strategy adopted to maximise reproductive success, determined primarily by litter-size and reproductive chronology (*q.v.*).
- resource-defence polygyny**: a mating system in which a male controls access to several females indirectly, by monopolizing critical resources (Emlen & Oring 1977).
- retarded embryonic development**: a means of lengthening the interval between copulation and parturition so that both events can occur in the most optimal seasons. The implanted embryo enters a period of retarded (slowed) growth that may last 4–8 months, after which development proceeds normally.
- reticulation** (*adj.* **reticulated**): having a net-like pattern.
- rhinarium**: area of naked moist skin surrounding the nostrils.
- ridge** (= **commissure**): in teeth, a ridge connecting two cusps.
- Rift Valley**: deep valley extending from the Red Sea through Ethiopia and East Africa to Malawi; formed ca. 12 mya by subsidence of the valley floor and uplifting of the edges to form mountains and highlands. Four parts: (1) Ethiopian Rift Valley dividing the Ethiopian plateau into two parts; (2) Albertine Rift Valley (Western Rift Valley) in Uganda, E DR Congo and W Tanzania; (3) Gregorian Rift Valley (Eastern Rift Valley) in N Kenya, C Kenya and N Tanzania; (4) Malawian Rift Valley – the extension of the Albertine Rift Valley in Malawi. The Rift Valleys are noted for their many deep and beautiful lakes.
- riparian**: growing on or living on the banks of streams or rivers.
- riverine forest**: forest growing along the banks of a river or stream where conditions are moister than in the surrounding area. Sometimes referred to as ‘fringing forest’.
- Robertsonian fusion**: a chromosomal event involving the apparent fusion of non-homologous single armed (telocentric *q.v.*) chromosomes to form a bi-armed (metacentric *q.v.* or submetacentric *q.v.*) chromosome. Modern studies have revealed that all chromosomes have two arms, even if the smaller one is not detectable by light microscopy. Consequently, the term Robertsonian translocation is becoming more commonly used than Robertsonian fusion.
- rostral**: pertaining to the rostrum.
- rostrum**: that portion of the skull anterior to the front line of the orbits and supporting the upper part of the muzzle, comprised of the nasals, premaxillae and maxillae bones.
- rupicolous**: rock-living.
- s.u.**: (*abbrev.*) (*Lat. sans unguis* = without claw) sometimes added as a suffix to the hindfoot measurement to emphasize that HF has been

- measured without the claw. However, since this is the standard method of measurement, most authors write 'HF', not 'HF s.u.'. *cf.* c.u. (*q.v.*).
- sacrum** (*adj.* **sacral**): the fused vertebrae to which the pelvic girdle is attached.
- sagittal crest**: longitudinal crest of raised bone on the mid-dorsal line of the cranium.
- scansorial**: climbs or scrambles over logs and in low vegetation close to the ground. *cf.* terrestrial (*q.v.*); arboreal (*q.v.*).
- scapholunar bone**: a bone formed by the coalescence of the scaphoid and lunar in the carpus of Carnivora.
- sclerophyllous**: describes vegetation having hard leaves that are resistant to drought.
- scrotal**: pertaining to, or within, the scrotum (*q.v.*).
- scrotum**: an external sac containing the testes and epididymides in male mammals.
- sebkha**: A geological feature, in North Africa, that is a smooth, flat, plain usually high in salt (also sabkha).
- sectorial**: adapted for cutting.
- selenodont**: molar teeth having longitudinal crescent-shaped ridges.
- Senegambia**: Senegal and Gambia.
- sensu lato**: (*Lat.*) in a broad sense.
- sensu stricto**: (*Lat.*) in a strict sense.
- sensu**: (*Lat.*) in the sense of.
- septum**: a dividing wall separating two cavities.
- sex ratio**: the number of males to the number of females, usually expressed as a proportion to one male, e.g. 1 : 1 (equal numbers of males and females), 1 : 0.5 (= twice as many males as females), 1 : 2 (= twice as many females as males).
- sexual dimorphism**: observable (phenotypic) difference(s) (e.g. in colour, size or form) between the males and females of a species or higher taxon.
- Sh. Ht.**: (*abbrev.*) shoulder height (in ungulates, usually taken to be between the pegs, but sometimes measured over the curve).
- sibling species**: pairs or groups of true species that are reproductively isolated, but genetically closely related and so similar in appearance that they are difficult to separate solely on the basis of morphological characters.
- side-stripe**: longitudinal stripe(s) of contrasting colour on each flank, usually from shoulder to rump or upper part of hindlimbs. May be bordered by additional side-stripe above and below.
- singleton**: a neonate that is born singly as opposed to being one of a larger litter.
- sister species**: species that are thought to have arisen from a single dichotomous splitting event.
- sonogram**: a visual representation (graph) of sound in which frequency is plotted on the vertical axis, and time on the horizontal axis; can be analysed manually or with computer programs (*cf.* oscillogram *q.v.*).
- sounder**: a group of pigs.
- South-Central Africa**: Angola, SE DR Congo, Zambia and Malawi (but only west of L. Malawi and the Shire R. Valley).
- southern Africa**: south of the Cunene and Zambezi Rivers, i.e. Namibia, Botswana, Zimbabwe, southern Mozambique and South Africa (after Smithers 1983).
- spatulate**: like a spatula, i.e. narrow at the base but wider, flat and parallel-sided distally.
- species**: population(s) of closely related and similar organisms, which are capable of interbreeding freely with one another and cannot or typically do not interbreed with members of other species.
- sperm storage**: storage of sperm in the cauda epididymides (*q.v.*) of males for some time before copulation, or in the reproductive tract of females for an extended period before ovulation takes place. A type of reproductive delay that, in females, lengthens the length of gestation (*q.v.*).
- sperm**: any male gamete; the male cell that fuses with a female gamete (ovum, egg cell) to produce a fertilized egg or zygote from which an embryo will develop.
- spermatogenesis**: the formation of sperm in the testes.
- stotting**: bouncing up and down with legs held stiffly. Also referred to as pronking.
- sub, sub-**: prefix meaning under, signifying beneath or ventral to (as in anatomical features) or south of (as in sub-Saharan); less than (as in subsonic); not quite, nearly, almost, somewhat (as in subequal, subtriangular). In taxonomy, indicates a group just below the status of the taxa immediately following it (e.g. a genus may contain two or more subgenera).
- subauricular**: below the ear.
- subcaudal**: below the tail.
- subdermal**: just below the skin.
- submetacentric**: describes a chromosome with the centromere (*q.v.*) somewhat nearer one end than the other, so there are two arms of somewhat unequal length (ratio 1 : 1.2–1.9). *cf.* metacentric (*q.v.*); subtelocentric (*q.v.*).
- subspecies**: a geographically localized and isolated subdivision of a species, which differs genetically, morphologically and taxonomically from other subdivisions of the species.
- subtelocentric**: describes a chromosome with the centromere (*q.v.*) much nearer one end than the other, so there are two arms of very unequal length (ratio 1 : >2).
- subterminal**: just below the end or tip.
- subterranean**: living permanently below the ground; *cf.* fossorial (*q.v.*).
- suckling**: the act of a mother giving milk directly from her breast (mammary glands) to her young. Mothers suckle; their young suck.
- sulcus** (*pl.* **sulci**): a groove, fissure or furrow.
- superovulation**: *see* **polyovulation** (*q.v.*).
- supinate**: to turn or rotate the hand or forearm, or the hindlimb and foot.
- supracaudal**: above the tail.
- supraoccipital crest**: ridge of bone, orientated transversely across the back of the skull, at the junction of the parietal and/or supraoccipital bones and the occipital bone. Sometimes referred to as the lambdoid crest.
- supraorbital ridge**: ridge of bone along upper rim of orbit (eye-socket).
- supraorbital**: above (dorsal to) the orbit.
- supraordinal**: describes a taxon above the level of the order.
- sympatry** (*adj.* **sympatric**): the situation where populations of two or more different species have overlapping geographic ranges; refers also to populations of two or more species whose geographic ranges are partly or wholly overlapping. They may or may not interact. *cf.* allopatry (*q.v.*); syntopy (*q.v.*).

- symplesiomorphy**: a primitive or ancestral character shared by two or more groups, which is inherited from ancestors older than the last common ancestor.
- synanthropic**: associated with humans and/or their houses and other buildings.
- synapomorphy** (*adj.* **synapomorphic**): situation in which a homologous character is present in two or more taxa and is thought to have originated in their most recent common ancestor. *See also* apomorphy.
- syndactyly**: of digits; whole of part fusion of two or more digits (e.g. Digits 2 and 3 of the hindfoot in otter-shrews).
- synonym**: one or more of different names for the same taxonomic unit. A synonym may be a 'senior synonym' (the oldest name), or a 'junior synonym' (a more recent name) that is no longer considered as valid. May be used to refer to all names that have been associated, at some time in the past, with the taxonomic unit as currently understood.
- syntopy** (*adj.* **syntopic**): describes the situation where two or more species use the same or similar habitats and activity times. They may or may not interact. *cf.* allopatry (*q.v.*); sympatry (*q.v.*).
- syntype**: any specimen, or one of a series of specimens, used to designate a species when a holotype (*q.v.*) and paratype(s) (*q.v.*) have either not been selected, or have been lost or destroyed.
- systematics**: the science of arranging organisms in a way that reflects their evolutionary relationships; such relationships may be expressed as a phylogeny (*q.v.*). Often defined (somewhat incorrectly) as a synonym of taxonomy (*q.v.*).
- T**: (*abbrev.*) length of tail, measured from anterior of the first caudal vertebra to the posterior end of the last caudal vertebra (excluding any tufts, bristles etc. at tip of tail).
- T_a**: (*abbrev.*) ambient temperature; the temperature in which an animal is living. *cf.* T_b (*q.v.*).
- Ta**: ambient temperature; the temperature in which an animal is living. *cf.* T_b (*q.v.*).
- talonid**: heel at the posterior end of a lower molar tooth.
- tapetum lucidum**: light-reflecting layer behind or in the retina of the eyes of some vertebrates that reflects light back through the retina thereby increasing the sensitivity of the eye to dim light.
- taxon** (*pl.* **taxa**): any defined unit (e.g. family, genus, species, subspecies) in the classification of organisms.
- taxonomy**: the science of biological nomenclature; the study of the rules, principles and practice of naming and classifying species and other taxa. Sometimes considered as an integral part (and near synonym) of systematics (*q.v.*).
- T_b**: (*abbrev.*) body temperature; the temperature of the core (central) part of an animal. *cf.* T_a (*q.v.*).
- telocentric**: describes a chromosome that appears to have a terminal centromere (*q.v.*) and therefore only one arm. Modern studies have revealed that all chromosomes have two arms but the smaller arm of telocentric chromosomes is not visible under a light microscope.
- temporalis**: a broad radiating muscle arising from the coronoid process (*q.v.*) of the lower jaw and attaching to the upper part of the skull.
- termitarium** (*pl.* **termitaria**): a place where termites (Insecta: Isopoda) live. Often a large mound of modified hard soil. The shape and size of a termitarium is unique to each species of termite.
- terrestrial**: living on the ground. *cf.* arboreal (*q.v.*); scansorial (*q.v.*).
- territory**: an area defended by an individual against certain other members of the species, usually by overt aggression or advertisement; territory is marked by the urine, faeces or glandular secretions of the territory's owner. *cf.* home-range (*q.v.*).
- Tertiary Period**: geological period, 65–2 mya, comprising five epochs: Palaeocene, Eocene, Oligocene, Miocene and Pliocene (*q.v.*); followed by the Quaternary Period (*q.v.*).
- testes**: the male gonads, or testicles, in which spermatozoa are formed and in which the male hormone is produced.
- Tethys Sea**: the sea separating the two supercontinents, Gondwana (*q.v.*) and Laurasia (*q.v.*) during much of the Mesozoic Era before the opening of the Indian and Atlantic oceans during the Cretaceous Period (*q.v.*).
- thermal conductance**: a measure of the ability of substances (including pelage) to transfer heat.
- thermolability** (*adj.* **thermolabile**): the ability of a homeotherm (e.g. camel) to allow its body temperature to vary over a 24-hour period, without either hibernating or aestivating.
- thermoneutral zone**: the range of body temperatures within which an animal does not have to increase its metabolic rate to increase T_b (*q.v.*) (when T_a (*q.v.*) is low) and reduce T_b (when T_a is high).
- thermoregulation**: regulation of body temperature, either by metabolic or behavioural means (or both simultaneously) so that T_b (*q.v.*) is kept more or less constant.
- thoracic**: pertaining to, or situated upon, the chest.
- through-put time**: time taken for food to pass through the digestive tract.
- tibia** (*pl.* **tibiae**): one of the two bones forming the lower leg (the shin bone); part of hindlimb between knee and ankle.
- TL**: (*abbrev.*) total length from tip of snout to posterior end of tail. Equivalent to the head and body length and tail length added together. *See also* HB (*q.v.*) and T (*q.v.*).
- toothrow**: Generally, the row of teeth from the most anterior incisor tooth to the most posterior molar. In golden moles, the row of teeth from the canine to the most posterior molar. Sometimes used in contexts of specific types of teeth, e.g. premolar toothrow, molar toothrow.
- topotype**: any specimen from the type locality (*q.v.*), i.e. the same locality as that from which the holotype (*q.v.*) was taken.
- topotypical**: pertaining to the type locality (e.g. a topotypical population is one found at the type locality).
- torpor** (*adj.* **torpid**): a state in which there is a (usually short-term) reduction of metabolic rate and a lowering of T_b (*q.v.*) when T_a (*q.v.*) declines; arousal from torpor occurs when T_a increases and without high energy costs to the individual. Torpor is associated with a state of inactivity and reduced responsiveness to stimuli. Torpor lasts for only short periods of time (hours or days). *cf.* hibernation.
- tragus**: a cartilaginous structure, usually small, projecting from the inner side of the external ear just anterior to the auditory meatus (*q.v.*).
- transverse**: in a direction across the body from side to side. *cf.* longitudinal (*q.v.*).
- Triassic Period**: period (within the Mesozoic Era); 248–208 mya. The first mammals appeared in this period.

- triconid:** describes a molariform tooth having three cusps.
- tricuspid:** having three points or cusps (particularly of teeth).
- trifid:** divided into three by two emarginations (*q.v.*).
- tubercle:** a small rounded protuberance.
- tusks:** long, continuously growing incisor or canine teeth that protrude (usually in pairs) beyond the mouth in some mammals including elephants (in which the tusks are incisors), and warthogs and other pigs (in which the tusks are canines); comprised of dentine (ivory). Some mammals, e.g. hyraxes, have 'tusk-like' incisors.
- tympanic bulla** (*pl. tympanic bullae*): one of a pair of usually rounded bony capsules, on underside of skull (one on each side), housing structures of the middle and inner ear in many mammals. Also called auditory bulla (*q.v.*).
- type description:** the original description of a species; the original description of the holotype (and paratype[s] if included).
- type locality:** the locality from which a holotype (*q.v.*), lectotype (*q.v.*) or neotype (*q.v.*) was collected. Also called topotypical locality.
- type population:** the population from which the holotype was selected.
- type series:** the holotype and all specimens collected at the same place and time and used, together with the holotype, to describe a new species.
- type species:** usually the species that was the first to be described under the name of a new genus. Not all genera had a designated type species when they were first created; in such cases, other rules determine which species will be the type species.
- type specimen:** *see* holotype.
- underfur:** dense and often woolly layer of the pelage, situated close to the skin and below the soft hairs and guard hairs; usually short and present in those species that experience lower T_a .
- unicuspid:** having one cusp or point (particularly of teeth).
- upper critical temperature:** the highest ambient temperatures at which the animal must increase its metabolic rate to maintain a constant body temperature. If the ambient temperature increases above the upper critical temperature and the animal is unable to cool itself, it will enter hyperthermia and may eventually die. *cf.* lower critical temperature.
- uvula:** the conical projection from the posterior edge of the soft palate that plays a role in the articulation of sounds and the closing the nasopharynx during swallowing.
- vagility:** the ability to move about, disperse or migrate.
- vagrant:** an individual that has been found well outside the normal geographic range of its species, e.g. a bat or bird that has been wind-borne, or an animal that has been transported as a stowaway on a ship, to a distant locality.
- vascularized:** infiltrated with capillaries.
- vasoconstriction:** constriction of the capillaries of the blood system near the surface of the skin in order to reduce the rate of heat loss through the skin; a mechanism used by many mammals to conserve heat when T_a (*q.v.*) is low. *cf.* vasodilation (*q.v.*).
- vasodilation:** the dilation (or opening) of the capillaries of the blood system near the surface of the skin in order to increase the rate of heat loss through the skin; a mechanism used by many mammals to cool themselves when T_a (*q.v.*) is high. *cf.* vasoconstriction (*q.v.*).
- veld:** Afrikaans word, used mainly by southern African biologists, to refer to a wide variety of grassland vegetation types typically used for grazing. *See also* bushveld, highveld, lowveld.
- vertebra** (*pl. vertebrae*): any of the bones that make up the backbone.
- vertebral formula:** the number of vertebrae in each part of the spine, from anterior to posterior: the parts are cervical (C), thoracic (T), lumbar (L), sacral (S), caudal (Ca).
- vestigial:** small and imperfectly developed; a structure having a smaller and more simple form than the corresponding structure in an ancestral species.
- vibrissa** (*pl. vibrissae*): long stiff hairs on the face, especially around nostrils and lips; often associated with the perception of tactile sensation; 'whiskers'.
- vlei:** southern African term for a marsh or swamp, either permanent or seasonal.
- wadi:** a desert valley, usually dry at the surface except after heavy rainfall.
- water turnover:** the rate at which water (fluids) is utilized and replaced in the body per unit time (normally expressed as ml/kg body weight/day); the amount of water an animal processes through its body each day. Water turnover is related to water availability, the urine concentrating ability of the kidney, amount of protein in the diet and T_a (*q.v.*). Water turnover rates are characteristically low in arid-adapted mammals when compared with non arid-adapted mammals.
- West Africa:** ca. south of 18° N from Senegal to the Sanaga R. in Cameroon, and Bioko I. (Equatorial Guinea) (Rosevear 1965).
- WT:** (*abbrev.*) weight (mass) of an individual, usually expressed in grams (g) or kilograms (kg).
- xiphisternum:** The posterior segment, or extremity, of the sternum (sometimes called the xiphoid process).
- zalambdodont:** cheekteeth with three main cusps connected by crests (ectolophs) forming a V-shape; largest cusp is at the apex of the V (on the lingual or tongue side of the tooth); assumed to be derived from the primitive tribosphenic teeth found in some extinct early mammals. *cf.* dilambdodont (*q.v.*).
- ZW:** (*abbrev.*) *see* zygomatic width.
- zygomatic arch:** one of a pair of cheekbones, formed of the maxillary process anteriorly, jugal bone medially and squamosal bone posteriorly. Ranges from massive, broad, widely flared and bony, to frail, slender and cartilaginous. When present, provides protection to the eyes and orbits. Also called zygoma.
- zygomatic width (ZW):** greatest width between the outer aspect of one zygomatic arch to the equivalent position on the opposite zygomatic arch. *See also* GWS.

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photograph by Jan Kalina

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ABOVE: from left to right: Jonathan Kingdon, Thomas Butynski, Meredith Happold, David Happold and Andrew Richford.

LEFT: Jonathan Kingdon (left) and Michael Hoffmann.

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Leus, Barbara Leuthold, Walter Leuthold, Rebecca Lewison, Eline Lorenzen, Gideon Louw, Callie Lynch, Alastair Macdonald, Chris Magin, Florence Magliocca, James Malcolm, David Mallon, Athol Marchant, John Mason, Erik Meijaard, Graham Mitchell, Patricia Moehلمان, Renata Molcanova, Steve Monfort, Yoshan Moodley, Michael Mooring, Dominic Moss, David Moyer, Wim Mullié, Souleye Ndiaye, John Newby, Helen Newing, Catherine Ngarachu, Bernhard Nievergelt, David Noble, Peter Novellie, William Oliver, Norman Owen-Smith, Ian Parker, Alexander Peal, Mike Perrin, Norbert Pfannenschmidt, Pierre Pfeffer, Djalle Pierre, Andy Plumptre, Gilfred Powys, Herbert Prins, Melvyn Quan, Wilhelm Räder, Befekadu Refera, Randy Reiches, Paul Reillo, Craig Roberts, Karen Ross, Francesco Rovero, Dave Rowe-Rowe, Ian Rushworth, Mostafa Saleh, Julia Salnicki, Dietrich Schaaf, Cathy Schloeder, Paul Scholte, Susanne Schultz, Erik Seiffert, Russell Seymour, David Shackleton, Steve Shurter, Kirstin Sixx, Claudio Sillero-Zubiri, Alberto Simonetta, Anthony R. E. Sinclair, the late John Skinner, Chris Smeenk, Jan Smielowski, Tommy Smith, Michael Somers, Clive Spinage, Mark Stanley Price, Emma Stokes, Tom Struhsaker, Chris Stuart, Tilde Stuart, Andrew Taylor, Ricky Taylor, the late Simon Thirgood, Kaci Thompson, Chris Thowless, Tom Thurow, Andrea Turkalo, Carlo Utzeri, Herman van Oeveren, Katja Vichl, Petri Viljoen, Fritz Volrath, Wolfgang von Richter, Tim Wachter, Alan Walker, Friedrich Wilhelmi, Stuart Williams, Doug Williamson, the late Vivian Wilson, Achim Winkler, Torsten Wronski, Piet Wit, Johannes Yagos, Derek Yalden, Alberto Zilli and Samuel Zschokke. A special word of thanks to Grant Hopcraft for permission to reproduce the map illustrating the Serengeti Wildebeest migration.

Through the first few formative years of the project, Mike Hoffmann was based in the University of Oxford's Wildlife Conservation Research Unit. This stay was made possible thanks to the efforts of the Commissioning Editor at Academic Press at the time, Dr Andy Richford, and the Director of WildCRU, Dr David Macdonald. Andy and David made it both financially and academically possible for me to move to the UK to join Jonathan on the *Mammals of Africa*. WildCRU further afforded access to the wonderful Bodleian library and that of the Edward Grey Institute, as well as to many like-minded African mammal researchers, several of them *Mammals of Africa* authors (including Andrew Loveridge, Stuart Williams and Claudio Sillero). Claudio became a particularly close and trusted friend, although it is only now that I realize what a novel influence he was. Subsequent to leaving WildCRU, and facilitated by a connection made by Tom

Butynski, I took up a position with Conservation International in Washington, DC., before transitioning into IUCN in 2006. I am particularly grateful to Tom Brooks, Russ Mittermeier and Simon Stuart, key supporters throughout my years at CI and IUCN, who made allowances for some of my time to be spent on *MoA* matters, and who cannot possibly know the profound inspiration that they have had on me personally as a conservationist. That I ever got involved in *Mammals of Africa* owes a great deal to the late John Skinner, my first mentor (with whom I jointly revised the 3rd edition of the *Mammals*

of the Southern African Subregion), for putting in a good word; Dick Estes, for suggesting I get in touch with Jonathan in the first place, and, of course, Jonathan himself, for putting his trust in such a novice as I was then. I look back now on the day Jonathan and I first met on 4 August 2000, and realize how far indeed we both have come. How proud I am to have had the privilege to work so closely with this giant of a man – this legend – and to call him my friend. And, finally, to my parents, for giving me the room to spread my wings, and giving me the courage to do so. To them, I owe everything.

Mammals of Africa: *An Introduction and Guide*

David Happold, Michael Hoffmann, Thomas Butynski and Jonathan Kingdon

Mammals of Africa is a series of six volumes that describes, in detail, every extant species of African land mammal that was recognized at the time the profiles were written (Table 1). This is the first time that such an extensive coverage has been attempted; all previous books and field guides have either been regional in coverage, or have described a selection of mammal species – usually the larger species. These volumes demonstrate the diversity of Africa's mammals, summarize what is known about the distribution, ecology, behaviour and conservation status of each species, and serve as a guide to identification.

Africa has changed greatly in recent decades because of increases in human populations, exploitation of natural resources, agricultural development and urban expansion. Throughout the continent, extensive areas of forest have been destroyed and much of the forest that remains is degraded and fragmented. Savanna habitats have been altered by felling of trees and development for agriculture. Many of the drier areas are threatened with desertification. As a result, the abundance and geographic ranges of many species of mammals have declined – some marginally, some catastrophically, some to extinction. Hence, it seems appropriate that our knowledge of each

species is recorded now, on a pan-African basis, because the next few decades will see even more human-induced changes. How such changes will affect each mammalian species is uncertain, but this series of volumes will act as a baseline for assessing future change.

The study of African mammals has taken several stages. During the era of European exploration and colonization, the scientific study of African mammals was largely descriptive. Specimens that were sent to museums were described and named. As more specimens became available, and from different parts of the Continent, there was increasing interest in distribution and abundance, and in the ecological and behavioural attributes of species and communities. At first, it was the largest and most easily observed species that were the focus of most studies, but as new methodologies and equipment became available, the smaller and more cryptic and secretive species became better known. Many species were studied because of their suspected role in diseases of humans and livestock, and because they were proven or potential 'pests' in agricultural systems. During the past decade or so, there has been greater emphasis on the genetic and molecular characteristics of species. All these studies have produced a wealth of information, especially during the past 40 years or so. These volumes are not only a distillation of the huge literature that now exists on African mammals, but also of much unpublished information.

Readers will notice that there is a huge discrepancy among species in the amount of information available. Some species have been studied extensively for many years, especially the so-called 'game species', some species of primates and a few species that are widespread and/or easily observed. In contrast, other species are known only by one or a few specimens, and almost nothing is known about them. Likewise, some areas and countries have been well studied, while other areas and countries have been neglected. During the preparation of these volumes, the editors have often been surprised by the wealth of information about some species when little was anticipated, and by the paucity of information about others, some of which were assumed to be 'well known'. In addition to presenting information that is based on sound scientific evidence, the aims of these volumes are to point out where there are gaps in knowledge and to correct inaccurate information that has become embedded in the literature. For most taxa, the detail provided in the species profiles allows accurate identification.

Mammals of Africa comprises six volumes (Table 2). The volumes consist mainly of species profiles – each profile being a detailed

Table 1. The mammals of Africa.

| Order | Number of families | Number of genera | Number of species |
|-----------------|--------------------|------------------|-------------------------|
| Hyracoidea | 1 | 3 | 5 |
| Proboscidea | 1 | 1 | 2 |
| Sirenia | 2 | 2 | 2 |
| Afrosoricida | 2 | 11 | 24 |
| Macroscelidea | 1 | 4 | 15 |
| Tubulidentata | 1 | 1 | 1 |
| Primates | 4 | 25 | 93 |
| Rodentia | 15 | 98 | 395 ^a |
| Lagomorpha | 1 | 5 | 13 |
| Erinaceomorpha | 1 | 3 | 6 |
| Soricomorpha | 1 | 9 | 150 |
| Chiroptera | 9 | 49 | 224 |
| Carnivora | 9 | 38 | 83 |
| Pholidota | 1 | 3 | 4 |
| Perissodactyla | 2 | 3 | 6 |
| Cetartiodactyla | 6 | 41 | 93 |
| 16 | 57 | 296 | 1116^b |

^a Including five introduced species. ^b Species profiles in *Mammals of Africa*.

Table 2. The six volumes of *Mammals of Africa*.

| Volume | Contents | Number of species | Editors |
|--------|--|-------------------|--|
| I | Introductory chapters. Afrotheria (Hyraxes, Elephants, Dugong, Manatee, Otter-shrews, Golden-moles, Sengis and Aardvark) | 49 | Jonathan Kingdon, David C. D. Happold, Michael Hoffmann, Thomas M. Butynski, Meredith Happold and Jan Kalina |
| II | Primates | 93 | Thomas M. Butynski, Jonathan Kingdon and Jan Kalina |
| III | Rodents, Hares and Rabbits | 408 | David C. D. Happold |
| IV | Hedgehogs, Shrews and Bats | 380 | Meredith Happold and David C. D. Happold |
| V | Carnivores, Pangolins, Equids and Rhinoceroses | 93 | Jonathan Kingdon and Michael Hoffmann |
| VI | Pigs, Hippopotamuses, Chevrotain, Giraffes, Deer and Bovids | 93 | Jonathan Kingdon and Michael Hoffmann |

account of the species. They have been edited by six editors who distributed their work according to the orders with which they were most familiar. Each editor chose authors who had extensive knowledge of the species (or higher taxon) and, preferably, had experience with the species in the field. Each volume follows the same general format with respect to arrangement, subheadings and contents. Because *Mammals of Africa* has contributions from 356 authors (each with a different background and speciality), and each volume was edited by one or more editors (each with a different perspective), it has not been possible or even desirable to ensure exact consistency throughout. Species profiles are not intended to be exhaustive literature reviews, partly for reasons of space. None the less, they are written and edited to be as comprehensive as possible, and to lead the reader to the most important literature for each species. Inevitably, not all information available could be accommodated for the better-known species, and so such profiles are a précis of available knowledge. Extensive references in the text alert the reader to more detailed information.

In addition to the species profiles, there are profiles for the higher taxa (genera, families, orders, and above). At the very least, there is a profile for each order, for each family within the order, for each genus within the family, and for each species within the genus. For some orders there are additional taxonomic levels, for example, subfamilies and tribes (Bovinae and Bovini, respectively). Species are presented according to phylogeny. The taxonomy used in these volumes mostly follows that presented in the third edition of *Mammal Species of the World: A Geographic and Taxonomic Reference* (Wilson & Reeder 2005), although authors have employed alternative taxonomies when there were good reasons for doing so. Volume I differs from the other volumes in that it contains a number of introductory chapters about Africa and its environment, and about African mammals in general.

The continent of Africa

For the purposes of this work, 'Africa' is defined as the continent of Africa (bounded by the Mediterranean Sea, the Atlantic Ocean, the Indian Ocean, the Red Sea and the Suez Canal) and the islands on the continental shelf that, at some time in their history, have been joined to the African continent. The largest of the 'continental islands' are Zanzibar (Unguja), Mafia and Bioko (Fernando Po). All 'oceanic islands', e.g. São Tomé, Príncipe, Annobón (Pagulu), Madagascar, Comoros, Seychelles, Mauritius, Socotra, Canaries, Madeira and Cape Verde are excluded, with the exception of Pemba, which is included because of its close proximity (ca. 50 km) to the mainland.

The names of the countries of Africa are taken from the *Times Atlas* (2005). The Republic of Congo is referred to as 'Congo' and the Democratic Republic of Congo (former Zaire) as 'DR Congo'. Smaller geographical or administrative areas within countries are rarely referred to except for Provinces in South Africa, which are used extensively in the literature. A political map of Africa, and of the Provinces of South Africa, is given (Figure 1), as well as a list of the 47 countries together with their previous names that are used in the older literature on African mammals (Table 3).

Africa is the second largest continent in the world (after Asia), but it differs from other continents (except Australia and Antarctica) in being essentially an island. At various times in the past, Africa has been joined to other continents – a situation that has had a strong influence on the fauna and flora of the continent. Africa is a vast continent (29,000,000 km², 11,200,000 mi²) that straddles the Equator, with about two-thirds of its area in the northern hemisphere and one-third in the southern hemisphere. As a result, Africa has many varied climates (with seasons in each hemisphere being 6 months out of phase), many habitats (including deserts, savannas, woodlands, swamps, rivers, lakes, moist forests, monsoon forests, mountains and glaciers), and altitudes ranging from 155 m (509 ft) below sea level at L. Assal, Djibouti, in the Danakil (Afar) Depression, to 5895 m (19,341 ft) on Mt Kilimanjaro, Tanzania. Africa is comprised of 47 countries, some of which are very large (e.g. Sudan [2,506,000 km²; 967,000 mi²], Algeria [2,382,000 km², 920,000 mi²] and Democratic Republic of Congo [2,345,000 km², 905,000 mi²]), and others that are relatively small (e.g. Djibouti [23,200 km², 9000 mi²], Swaziland [17,400 km², 6,700 mi²] and The Gambia [11,300 km², 4400 mi²]). The human population of each country also varies greatly, from about 346/km² in Rwanda to only about 2.5/km² in Namibia. With its great size and varied habitats, Africa supports a high biodiversity, including a large number of species of mammals. Likewise, most countries have a high diversity of mammals (especially when compared with temperate countries).

Africa may also be categorized into Biotic Zones (Figure 2). A biotic zone is defined as an area within which there is a similar environment (primarily rainfall and temperature) and vegetation, and which differs in these respects from other Biotic Zones. Africa can be divided into 13 Biotic Zones, two of which may be divided into smaller categories. The Biotic Zones concept provides a general assessment of the environmental conditions in which a species lives, as well as providing an assessment of the geographic distribution of the species. The Rainforest Biotic Zone and the South-West Arid Biotic Zone may be divided into regions and sub-regions that reflect the different biogeographical distributions of species, each region/



Figure 1. (a) Political map of Africa; (b) provinces of South Africa; (c) altitudes and major rivers of Africa. South Sudan and Somaliland are not identified as separate countries in the text.

Table 3. The countries of Africa: names, areas and human population density.

| Country name | Area
(km ²) '000 | Area
(miles ²) '000 | Human population
'000 (2006) | People per km ² |
|--|---------------------------------|------------------------------------|---------------------------------|----------------------------|
| Algeria | 2,382 | 920.0 | 33,500 | 14.1 |
| Angola (includes Cabinda) | 1,247 | 481.0 | 15,800 | 12.7 |
| Benin * [Dahomey] | 113 | 43.0 | 8,700 | 77.0 |
| Botswana [Bechuanaland] | 582 | 225.0 | 1,800 | 3.1 |
| Burkina Faso * [Upper Volta; Burkina] | 274 | 106.0 | 13,600 | 49.6 |
| Burundi [part of Ruanda-Urundi (= part of Belgian Congo)] | 27.8 | 10.7 | 7,800 | 280.5 |
| Cameroon [includes former French Cameroon, German Cameroon and part of Eastern Nigeria] | 475 | 184.0 | 17,300 | 36.2 |
| Central African Republic # | 623 | 241.0 | 4,300 | 6.9 |
| Chad [Tchad] | 1,284 | 496.0 | 10,000 | 5.8 |
| Congo [Republic of Congo] | 342 | 132.0 | 3,700 | 10.8 |
| Côte d'Ivoire * [Ivory Coast] | 322 | 125.0 | 19,700 | 61.2 |
| Democratic Republic of Congo [Belgian Congo; Congo (Kinshasha); Zaire] | 2,345 | 905.0 | 62,700 | 26.7 |
| Djibouti [French Somaliland] | 23.2 | 9.0 | 800 | 34.5 |
| Egypt | 1,001 | 387.0 | 75,400 | 75.3 |
| Equatorial Guinea # (includes Rio Muni [Spanish Guinea] and Bioko I. [Fernando Po]) | 28.1 | 10.8 | 500 | 17.8 |
| Eritrea (formerly part of Ethiopia) | 94 | 36.0 | 4,600 | 48.9 |
| Ethiopia [Abyssinia] | 1,128 | 436.0 | 74,800 | 66.3 |
| Gabon # | 268 | 103.0 | 1,400 | 5.2 |
| The Gambia | 11.3 | 4.4 | 1,500 | 132.7 |
| Ghana [Gold Coast] | 239 | 92.0 | 22,600 | 94.6 |
| Guinea * | 246 | 95.0 | 9,800 | 39.8 |
| Guinea-Bissau [Portuguese Guinea] | 36 | 13.9 | 1,400 | 38.9 |
| Kenya | 580 | 224.0 | 34,700 | 59.8 |
| Lesotho [Basutoland] | 30.4 | 11.7 | 1,800 | 59.2 |
| Liberia | 111 | 43.0 | 3,400 | 30.6 |
| Libya | 1,760 | 679.0 | 5,900 | 3.6 |
| Malawi [Nyasaland] | 118 | 46.0 | 12,800 | 108.5 |
| Mali * | 1,240 | 479.0 | 13,900 | 11.2 |
| Mauritania * | 1,030 | 412.0 | 3,200 | 3.1 |
| Morocco [includes former Spanish Morocco and French Morocco; (now also includes Western Sahara = former Spanish Sahara)] | 447 | 172.0 | 32,100 | 71.8 |
| Mozambique [Portuguese East Africa] | 802 | 309.0 | 19,900 | 24.8 |
| Namibia [South-west Africa] | 825 | 318.0 | 2,100 | 2.5 |
| Niger * | 1,267 | 489.0 | 14,400 | 11.3 |
| Nigeria | 924 | 357.0 | 134,500 | 145.6 |
| Rwanda [part of Ruanda-Urundi (= part of Belgian Congo)] | 26.3 | 10.2 | 9,100 | 346.0 |
| Senegal * | 197 | 76.0 | 11,900 | 60.4 |
| Sierra Leone | 71.7 | 27.7 | 5,700 | 79.5 |
| Somalia* [British Somaliland and Italian Somaliland; Somali Republic] | 638 | 246.0 | 8,900 | 13.9 |
| South Africa | 1,220 | 471.0 | 47,300 | 38.7 |
| Sudan § [Anglo-Egyptian Sudan] | 2,506 | 967.0 | 41,200 | 16.4 |
| Swaziland | 17.4 | 6.7 | 1,100 | 63.2 |
| Tanzania [German East Africa; Tanganyika] (now includes Zanzibar I., Mafia I. and Pemba I.) | 945 | 365.0 | 37,900 | 40.1 |
| Togo [Togoland] | 56.8 | 21.9 | 6,300 | 110.9 |
| Tunisia | 164 | 63.0 | 10,100 | 61.6 |
| Uganda | 236 | 91.0 | 27,700 | 117.4 |
| Zambia [Northern Rhodesia] | 753 | 291.0 | 11,900 | 15.8 |
| Zimbabwe [Southern Rhodesia] | 391 | 151.0 | 13,100 | 33.5 |
| Totals/mean density | 29,448 | 11,383 | 902,600 | 56.8 |

Former names are listed in chronological order in square brackets, with the oldest name listed first. Obsolete names are listed because much of the older literature refers to past colonial entities. * = formerly part of French West Africa. # = formerly part of French Equatorial Africa. § At the time of going to press, the country of Sudan had been divided into two: the Republic of Sudan in the north, and the Republic of South Sudan in the south. *The former British Somaliland is now a self-declared state under the name of the Republic of Somaliland, but remains internationally unrecognized.

The pigs, hippopotamuses, chevrotain, giraffes, deer and bovids of Africa

This volume, Volume VI, is devoted to the order Cetartiodactyla, a large order that unites the traditional 'artiodactyls' (even-toed ungulates) with the whales and dolphins. The order includes three main subdivisions: Suiformes (pigs); Whippomorpha (hippopotamuses, whales and dolphins); and Ruminantia (including the chevrotain, giraffe and okapi, deer and the bovids). In total, the order includes 98 species (treated in 93 species profiles), although the majority comprise the antelopes, which have radiated into a remarkable 76 species in 12 different tribes. A single species of African cetartiodactyl, the Bluebuck *Hippotragus leucophaeus*, is documented as having become extinct since 1500 (though many are teetering on the brink) and is discussed briefly under the genus account, but is otherwise not treated separately. Introduced species are mentioned in the higher-level profiles (where relevant), but are not otherwise profiled.

At the time of going to press, a new species of duiker in the genus *Philantomba* had been described, *Philantomba walteri* (Colyn *et al.* 2010). Unfortunately, it was not possible to include an individual species profile, but we provide general characteristics that distinguish this new species under the genus profile. Details on the type locality description follow (see also the *Philantomba* genus profile).

Walter's Duiker *Philantomba walteri* Colyn, Hulselmans, Sonet, Oudé, de Winter, Natta, Nagy & Verheyen, 2010. Igberé (08° 59' N 01° 57' E), Forêt Protégée de Wari-Marou (328 m altitude), near the Ecological Center of Manigri, Benin.

As *Mammals of Africa* was being finalized, a new work by Colin Groves and the late Peter Grubb, *Ungulate Taxonomy*, was published but it has not been possible to fully consider and evaluate the conclusions and classification presented in that work.



Figure 2. The biotic zones of Africa. The numbers refer to the biotic zones as described in the text.

sub-region having a community of mammals and other animals which is different to any other. Details of the Biotic Zones of Africa, and the regions and sub-regions of the Rainforest Biotic Zone and South-West Arid Biotic Zone, are given in Volume I of *Mammals of Africa*.

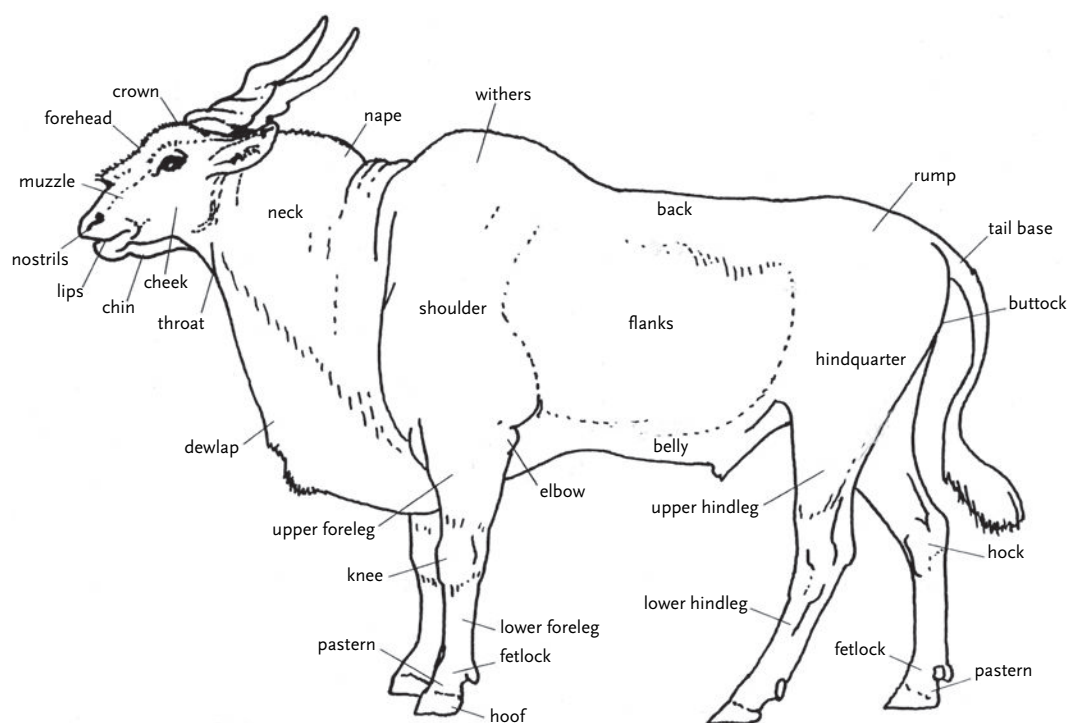
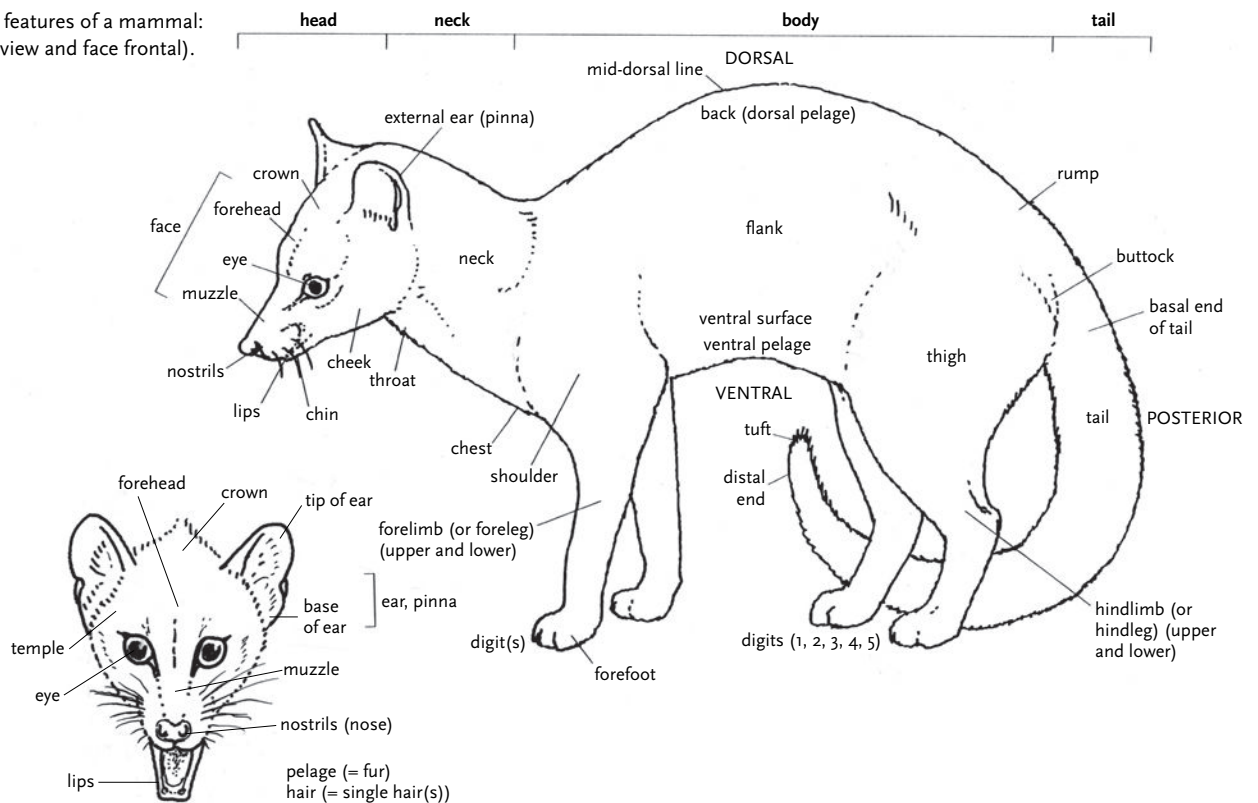


Figure 3. External features of a mammal: Common Eland *Tragelaphus oryx*.

Figure 4. External features of a mammal: *Genetta* sp. (side-view and face frontal).



Species profiles

Information about each species is given under a series of subheadings. The amount of information under each of these subheadings varies greatly between species; where no information is available, this is recorded as 'No information available' or words to this effect. The sequence of subheadings is as follows:

Scientific name (genus and species) The currently accepted name of the species.

Vernacular names English, French and German names are given, as available. The first given English name is the preferred vernacular name for the species; alternative names are given in parentheses for some species. Wilson & Cole (2000) list proposed vernacular names for all the world's mammals; most of these names were also given in the third edition of *Mammal Species of the World* (Wilson & Reeder 2005). Although these works have been consulted, the names used have not always been adopted in *Mammals of Africa*. French and German names were usually provided by authors.

Scientific Citation This provides the full scientific name of the species, i.e. genus name, species name, authority name, and date of authority. Parentheses around the authority's name and date indicate that the species was originally named in a different genus to its present generic allocation. The scientific name is followed by the publication where the species was described, and the location where the type specimen (or type series) was obtained. Most of this information is taken from Wilson & Reeder (2005).

Taxonomy This section contains information on taxonomic problems, if any, associated with the species, and its relationship with other species in the genus. For some species, there is considerable information about these topics; for others, there may be nothing. A list of synonyms (without the taxonomic authority for each) and the number of subspecies (if any) is presented, mostly taken from Wilson & Reeder (2005). The chromosome number is given if available, and in some cases this is followed by other information relevant to the chromosomes.

Description This section, together with the illustrations, provides the reader with adequate information to identify the species. The section begins with a brief overall description of the species, including an indication of size. This is followed by a detailed description of the external features of the species' head (and parts of the head), dorsal pelage, legs, feet, ventral pelage, and tail (in this order), as well as any special characteristics unique to the species. For some species, diagnostic characteristics of the skull and dentition are given, and for bovids the horns. This section may also present information on ageing criteria, where this has been investigated with some degree of rigour. The characters described in this section are common to all subspecies of this species (unless otherwise noted). The mammary formula, i.e. the number and arrangement of nipples in adult females, is noted wherever this feature varies between the taxa being discussed.

Geographic Variation Variation within the species may be of two sorts: (a) clinal variation without subspecies, or (b) subspecific variation. If (a), there is a description of the character(s) that alter clinally across the geographic range of the species. If (b), each of the subspecies is listed with its geographic range and, where available,

the characters that distinguish it from other subspecies of the species. For some species, subspecies have been described that are no longer considered to be valid; in some cases, such names may be listed but without further comment.

Similar Species Species that are sympatric or parapatric with the species under consideration, and with which it may be confused, are listed along with diagnostic characteristics (additionally, readers may refer to profiles of the similar species in question). In some instances, species that are allopatric in distribution are also included.

Distribution The first sentence ‘Endemic to Africa’ informs the reader that this is an African species and does not occur on any other continent; if a species also occurs outside Africa, this is noted at the end of this section with a very brief synopsis of the extralimital range. The distributions of the cetartiodactyls are among the best studied and well documented of African mammals, and the monumental work of Rod East (1999), complemented by subsequent updates from the IUCN SSC Antelope Specialist Group, provides an unrivalled platform for detailing the ranges of most species. For widespread species that generally remain so today (e.g. *Sylvicapra grimmia*), the text provides a general idea of the range, highlighting only places or countries where the species may have been extirpated, recently newly recorded, or providing clarity on previously incorrectly attributed country records and range limits. In the case of widespread species that have undergone significant range contractions and declines (e.g. *Addax nasomaculatus*), the text generally differentiates between former and current ranges in an attempt to elucidate a clearer picture of where species do, or no longer, occur. Finally, for more range-restricted species (e.g. *Beatragus hunteri*), the information provided may be quite precise, detailing even localized distribution within the confines of its small range. For species with recognized and well-differentiated subspecies, we have attempted to present the details of the distributions accordingly, and within the framework presented above. Although great effort has been expended in ensuring this section is current and provides a true picture of the current range of the species, many data gaps remain, especially for parts of North and West Africa, Sudan, Somalia, parts of DR Congo, Angola and Mozambique. A distribution map (see below) augments the information given here.

Habitat This section provides a description of the range of habitats where the species lives. Details of plant communities, plant species, vegetation structure, soil type and/or structure, and water availability, etc. (if available) are also recorded. Other information may include average annual rainfall, altitudinal limits, and seasonal variation in habitat characteristics.

Abundance A general indication of abundance in the habitat. This may be unquantified, such as abundant, common, uncommon, rare, or phrases such as ‘rarely seen but frequently heard’, etc. For better-known species, abundance may be expressed as estimates of density (e.g. number/ha or number/km²) as well as in terms of actual numbers of individuals for the species. Other information may include seasonal changes in density, frequency of observations, or the relative abundance of specimens in collections.

Adaptations This section describes morphological, physiological and behavioural characteristics, which show how the species uniquely interacts with its environment, conspecifics and other animals. This section may also describe species-specific adaptations for feeding, locomotion, burrowing, mechanisms for orientation, production of sound, sensory mechanisms and activity patterns. In some instances comparison with related or convergent species allows the unique adaptations of the species under discussion to be detailed or highlighted.

Foraging and Food This section provides information on the diet and foraging habits of the species. The diet is described either by a list of the taxa of animals or plants consumed, or as a quantitative measure of the contents of the stomach or the faeces. This section can also include any of the following: location of food, foraging behaviour, times when foraging occurs and daily distance moved; hoarding; seasonal changes in diet and food availability; individual or cooperative behaviour used in foraging and hunting; sex and age differences in foraging and diet; and nomadic or migratory movements in relation to food availability.

Social and Reproductive Behaviour Topics in this section may include group structure (whether solitary, social, or colonial), group size and composition; agonistic and amicable behaviour, comfort behaviour, etc.; home-range (including quantitative data), territorial behaviour, courtship and mating behaviour, behaviour of young, parental–young interactions; presence of helpers, vocalizations, and interactions with other species (mammals, birds, etc.).

Reproduction and Population Structure This section begins with an assessment of reproductive strategy (if known) and the times/seasons of the year when individuals are reproductively active (pregnancy and lactation in females, active spermatogenesis in males). Other information may include length of gestation, times/seasons of births, including peaks of births, litter-size, birth-weight and size, spacing of litters, growth and time to weaning, maturity, longevity, and mortality rates. Reproductive strategies, if known, are described with respect to locality, food availability and population density. Population structure (sex ratio, adult/young ratio, abundance of different cohorts in the population at different times of the year) may be described, and related to seasonal variations in reproduction and environmental variables.

Predators, Parasites and Diseases The known predators, parasites and diseases are listed. Information on parasites and diseases is not intended to be exhaustive, but simply to provide an entry point into the literature on the topic. In some cases, information on diseases from captive animals is presented. Additional information is given if the species is a host to diseases that affect humans and domestic stock.

Conservation The conservation status of the species is stated, as given by the *IUCN Red List of Threatened Species* (version 2011.2). The IUCN Red List categories follow the definitions and criteria given in the *IUCN Red List Categories and Criteria Version 3.1* (Table 4). For those species classified as threatened (i.e. ‘Vulnerable’,

Table 4. IUCN Red List Categories (from IUCN – International Union for Conservation of Nature).

| Category | Description |
|-----------------------------------|--|
| Extinct (EX) | A taxon is Extinct when there is no reasonable doubt that the last individual has died. A taxon is presumed Extinct when exhaustive surveys in known and/or expected habitat, at appropriate times (diurnal, seasonal, annual), throughout its historic range have failed to record an individual. Surveys should be over a time frame appropriate to the taxon's life-cycles and life-form. |
| Extinct in the Wild (EW) | A taxon is Extinct in the Wild when it is known only to survive in cultivation, in captivity or as a naturalized population (or populations) well outside the past range. A taxon is presumed Extinct in the Wild when exhaustive surveys in known and/or expected habitat, at appropriate times (diurnal, seasonal, annual), throughout its historic range have failed to record an individual. Surveys should be over a time frame appropriate to the taxon's life-cycle and life-form. |
| Critically Endangered (CR) | A taxon is Critically Endangered when the best available evidence indicates that it meets any of the criteria A to E for Critically Endangered, and it is therefore considered to be facing an extremely high risk of extinction in the wild. |
| Endangered (EN) | A taxon is Endangered when the best available evidence indicates that it meets any of the criteria A to E for Endangered, and it is therefore considered to be facing a very high risk of extinction in the wild. |
| Vulnerable (VU) | A taxon is Vulnerable when the best available evidence indicates that it meets any of the criteria A to E for Vulnerable, and it is therefore considered to be facing a high risk of extinction in the wild. |
| Near Threatened (NT) | A taxon is Near Threatened when it has been evaluated against the criteria but does not qualify for Critically Endangered, Endangered or Vulnerable now, but is close to qualifying for (or is likely to qualify for) a threatened category in the near future. |
| Least Concern (LC) | A taxon is Least Concern when it has been evaluated against the criteria and does not qualify for the Critically Endangered, Endangered, Vulnerable or Near Threatened categories. Widespread and abundant taxa are included in this category. |
| Data Deficient (DD) | A taxon is Data Deficient when there is inadequate information to make a direct, or indirect, assessment of its risk of extinction based on its distribution and/or population status. Data Deficient is not a category of threat. Listing of taxa in this category indicates that more information is required and acknowledges the possibility that future research will show that a threatened classification is appropriate. |
| Not Evaluated (NE) | A taxon is Not Evaluated when it has not yet been evaluated against the criteria. |

'Endangered', 'Critically Endangered'), the criteria met are also indicated. Some species have changed status due to improved knowledge, taxonomic revision, or the impact of threatening processes or conservation actions. Readers can obtain detailed reasons for the past and present status of a species by going to the IUCN Red List website (www.iucnredlist.org). If a species was listed on Appendix I, II or III under CITES (Convention on International Trade in Endangered Species – www.cites.org – as of 22 December 2011) or Appendix I or II of CMS (Convention on Migratory Species – www.cms.int – as of 5 March 2009) this is also indicated. For some species, additional information is provided, such as presence in protected areas, major threats, and current or recommended conservation measures.

Measurements A series of morphological measurements is provided. For each species there is a standard set of measurements. The abbreviations for each measurement are given in the Glossary. A measurement is cited as the mean value (with minimum value to maximum value in parentheses), and sample size. For some, the standard deviation (mean \pm 1 S.D.) is given instead of the range. Where possible, data for males and females are presented separately. In some cases, more than a single set of measurements is given; this is particularly the case for widespread species where geographic variation in size may be evident, and also for species with several well differentiated subspecies (in which case, we have endeavoured to present a set of measurements for each). Some species have additional stand-alone measurements presented beneath the primary series. Skull measurements generally are not provided; however, in the case of the antelopes, maximum recorded horn length (and the location of this record) based on the Rowland Ward (27th edition) measuring system is indicated. The majority of measurements also contain the location(s) where the specimens were obtained, and the source of the

data. Sources are either cited publications, or specimens in museums, or unpublished information from authors or others. The acronyms for museums where specimens were examined and measured are given in Table 5.

Key References A select list of references, which provides more general information on the species, or is generally considered as a key reference work on the species. Each reference is given in full in the Bibliography. Citations given in the text (but not cited in 'Key References') are also given in full in the Bibliography. In general, profiles account for all literature published up until the end of 2007. Authors and editors have endeavoured to keep the species profiles up-to-date throughout the long production schedule, and references published from 2008 onwards have been incorporated wherever possible. None the less, certain key recent papers will have been missed or omitted.

Author The name of the author, or authors, is given at the end of each profile. All profiles should be cited using the author name(s).

Tables With one or two exceptions, the use of tables to present data has been avoided in this volume of *Mammals of Africa*.

Table 5. Museum acronyms.

| Acronym | Museum name |
|---------|--|
| AMNH | American Museum of Natural History, New York, USA |
| BMNH | Natural History Museum, London, UK [formerly British Museum (Natural History)] |
| MRAC | Musée Royal de l'Afrique Centrale, Tervuren, Belgium |
| NMK | National Museums of Kenya, Nairobi, Kenya |
| PCM | Powell-Cotton Museum, Birchington, UK |

Higher taxon profiles

The profiles for orders, families and genera are internationally much less structured than for the species profiles. Each profile usually begins with a listing of the taxa in the next lower taxon; for example, each family profile lists the genera in that family. An exception to this arrangement is where a taxon has only one lower taxon. Higher taxa profiles provide the characteristics common to all members of that taxon. Some of these characteristics (for example, number of nipples or dental formula) may not be repeated in lower taxon profiles (unless essential for identification), so readers are encouraged to consult also the higher-taxa profiles, e.g. the species profile for *Raphicerus campestris* should be consulted in association with the genus *Raphicerus* and the tribe *Raphicerini* profile.

Distribution maps

Each species profile contains a pan-African map showing the geographic range of the species. In the case of the antelopes, the maps draw heavily on the publications of East (1988–1990, 1999), subsequent ASG updates and recent survey reports (e.g. Fay *et al.* 2007 for southern Sudan). The purpose of the maps is to show current known limits of distribution of the species within historical range, recognizing that within this mapped range a particular species' distribution will not be homogeneous. In general, reintroductions within the former range of a species are included and mapped (unless otherwise indicated), but introductions outside of the former known range are not. Even applying these rules, mapping current distributions in some parts of the continent, and especially in southern Africa where the game ranching industry has resulted in major faunistic shufflings, has proved very complicated. After much consideration, it was decided not to map historical ranges for species, given the difficulty in mapping these with any level of accuracy for a number of species, differing concepts on what 'historical' means, and the availability of such maps in other sources (e.g. Sidney 1965, Du Plessis 1969). However, in the absence of more recent and reliable information for some countries (especially Angola, Mozambique, Somalia and so forth), the range maps may actually reflect historical distributions far better than they do current range. Subspecies are

only indicated in cases where the boundaries can be reasonably delineated.

Each map shows the boundaries of the 47 countries of Africa, some of the major rivers (Nile, Niger–Benue, Congo [with the tributaries Ubangi, Lualaba and Lomani], Zambezi and Orange), and Lakes Chad, Tana, Turkana (formerly Rudolf), Albert, Edward, Victoria, Kyoga, Kivu, Tanganyika, Malawi, Mweru, Bangwuela and Kariba. The map projection is Transverse Mercator, with the following parameters: False Easting: 0; False Northing: 0; Central Meridian: 20; Linear Unit: metre; Datum: Clarke 1866.

The geographic distribution of a species is indicated as:

- red shading = current range. Different colour shading denotes subspecies, where appropriate.
- × = isolated locations considered to be separate from the main geographic range(s); some locations indicated by × may include two or more closely spaced locations.
- ? = uncertain, but possible, presence.
- red arrow = recorded from the island indicated by the arrow.

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Order CETARTIODACTYLA – Pigs, Hippopotamuses, Chevrotain, Giraffes, Deer, Bovids

Cetartiodactyla Montgelard, Catzeflis & Douzery, 1997. Mol. Biol. Evol. 14: 550.

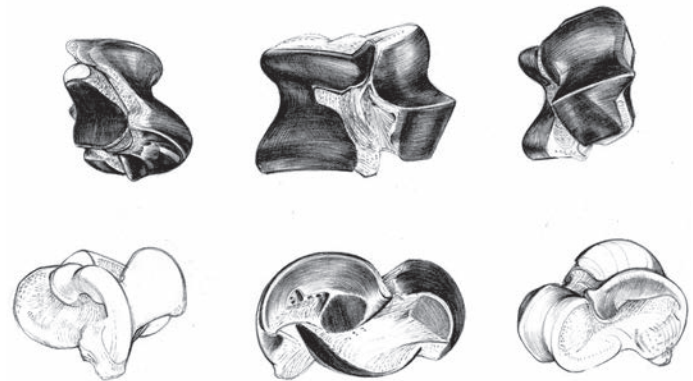
| | | |
|---|----------------|--------|
| Suidae (4 genera, 6 species) | Pigs, Hogs | p. 25 |
| Hippopotamidae (2 genera, 2 species) | Hippopotamuses | p. 63 |
| Tragulidae (1 genus, 1 species) | Chevrotains | p. 87 |
| Giraffidae (2 genera, 2 species) | Giraffe, Okapi | p. 95 |
| Cervidae (1 genus, 1 species) | Deer | p. 116 |
| Bovidae | | |
| Bovinae (2 genera, 10 species) | Bovines | p. 122 |
| Antilopinae (29 genera, 76 species*) | Antilopines | p. 199 |

*including species in the *Nanger (granti)* and *Madoqua (kirkii)* species groups.

Cetartiodactyla, of which 98 terrestrial species occur in Africa, are commonly referred to as the ‘even-toed ungulates’ or Artiodactyla. This placental order contains pigs (suborder Suiformes), camelids (suborder Tylopoda; extralimital to Africa), ruminants (suborder Ruminantia) and the hippopotamuses (hereafter hippos), the latter of which now comprise the suborder Whippomorpha together with the whales and dolphins. The distinctness as well as the relatedness of each of these taxa is now well supported by molecular and genomic data. The etymology of this new taxon therefore combines the two traditional orders ‘Artiodactyla’ and ‘Cetacea’ into an enlarged order ‘Cetartiodactyla’.

Traditional taxonomy, based on morphology, placed whales in their own order, Cetacea, but over the course of the last decade a steady accumulation of nucleotide sequence data and other genomic information has made it clear that whales are actually deeply nested within the ‘artiodactyl’ radiation as the sister-group of Hippopotamidae (e.g. Gatesy *et al.* 1996, Nikaido *et al.* 1999, Murphy *et al.* 2001, Amrine-Madsen *et al.* 2003, Arnason *et al.* 2004, Meredith *et al.* 2011, Hassanin *et al.* 2012). This hypothesis has since come to be supported by phylogenetic analyses of morphological data from living and extinct cetartiodactyls (Geisler & Uhen 2003, 2005), as well as combined molecular-morphological analyses of the order (Spaulding *et al.* 2009). It has been argued that the taxon Artiodactyla should be retained for this assemblage (Archibald 2003, Asher & Helgen 2010), but this practice threatens to engender considerable confusion among specialists, because some workers have used the taxa Cetartiodactyla and Artiodactyla in order to express their recognition of a sister-taxon relationship between a monophyletic Cetacea and a monophyletic Artiodactyla (e.g. Thewissen *et al.* 2001). Relationships among the major cetartiodactyl clades are a matter of ongoing debate, and estimates of cetartiodactyl phylogeny have generated an extensive literature (Gatesy *et al.* 1999, 2002, Nikaido *et al.* 1999, Matthee *et al.* 2001, Murphy *et al.* 2001, Arnason *et al.* 2004, Geisler & Uhen 2005, Spaulding *et al.* 2009, Meredith *et al.* 2011, Hassanin *et al.* 2012).

One of the first responses to the molecular evidence supporting the placement of whales within Artiodactyla was to re-examine artiodactyls and cetaceans, both extant and fossil, to seek morphological evidence for or against this unexpected affinity (Luckett & Hong 1998). In spite of continued scepticism, living and extinct cetartiodactyls can now be recognized on the basis of at least three distinctive postcranial



Astragalus of extinct hippopotamus (from Kingdon 1982).

and dental features: (1) the head of the astragalus is trochlear, leading to the characteristic ‘double-pulley’ shape; (2) manus and pes are paraxonic, which means that the weight-bearing axis passes through digits III and IV (metapodials III and IV have become elongate and thickened, whereas metapodials II and V have been reduced in length and diameter, and digit I has been greatly reduced or lost entirely); and (3) the deciduous fourth premolar (p4) is distinctly trilobed, and the anterior lobe occludes between the outer (paracone and metacone) cusps of the upper deciduous third premolar (p³). The molariform p4 is later replaced by a premolariform p4. Until recently, the astragalar and pedal morphology of primitive cetaceans was not known; however, it is now clear that the archaeocetes *Pakicetus*, *Ichthyolestes*, *Rodhocetus* and *Artioclavus* all had double-pulley astragali (Gingerich *et al.* 2001, Thewissen *et al.* 2001), and *Rodhocetus* had a paraxonic arrangement of the pedal digits (Gingerich *et al.* 2001).

Molecular estimates for the origin of crown Cetartiodactyla extend back to near the K–T (Cretaceous–Tertiary) boundary (Springer *et al.* 2003, Meredith *et al.* 2011), but the group is not known in the fossil record before the earliest Eocene, around 55 mya. The most generalized cetartiodactyl is arguably *Diacodexis* (sometimes called ‘*Gujaratia*’) *pakistanensis*, from the early Eocene of Pakistan (Thewissen & Hussain 1990, Geisler & Uhen 2005). *Diacodexis* appears to have migrated out of Asia into Europe and North America during a brief period of intense global warming at the Palaeocene–Eocene boundary, and thereafter primitive cetartiodactyls (many of which are now of unclear phylogenetic position) are known from all three northern continents, and with time become common members of Laurasian mammal faunas. Recognizable stem or crown members of the Ruminantia, Tylopoda and Suiformes do not appear until much later in the Palaeogene, but all are ultimately of Laurasian origin. The presumably semi-aquatic anthracotheriid artiodactyls first appear in Africa in the late Eocene (Holroyd *et al.* 1996); otherwise, fully terrestrial cetartiodactyls are not known in Africa before the early Miocene.

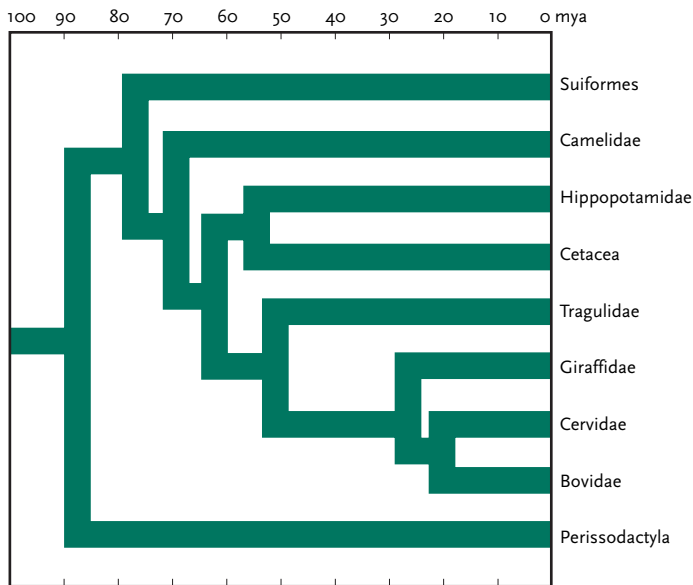
Details of taxonomy and biology among the very diverse cetartiodactyls are discussed under appropriate taxonomic profiles,

but it is difficult to overstate the revolution in biological thinking that has accompanied these molecular discoveries. While earlier scenarios had, for example, suggested that whale ancestors were terrestrial carnivores, more recent discoveries make larger, more omnivorous,

and perhaps superficially pig-like ancestors more likely (Thewissen *et al.* 2007). Reconstructing the earliest history of whale evolution now presents new challenges and an added impetus for scientists to find still earlier proto-whale fossils. Among the challenges will be the plausible reconstruction of sequences and successions of feeding styles between ancient terrestrial artiodactyls and today's fish, squid and krill-eating whales.

Interpolation of purely herbivorous hippopotami into the whales' ancestral tree has brought many new dimensions to study of the Cetartiodactyla, but in spite of the challenges and new uncertainties, one thing remains unchanged, and Dawkins (1996) put it this way: 'there is no doubt that whales and dugongs come with their dry-land history written all over them. If they had been deliberately created for the sea, they'd be very different, and a lot more like fish than they are. Animals that have their history written all over them are among the most graphic pieces of evidence we have that living things were not created for their present ways of life but evolved from very different ancestors' (p. 133).

Modern genetics has forced us to examine hippos with more open minds and eyes. When we get to re-examine other Cetartiodactyla with similar intensity we will find that antelopes, giraffes and others will also have their history written all over them, even if in subtler phrases.

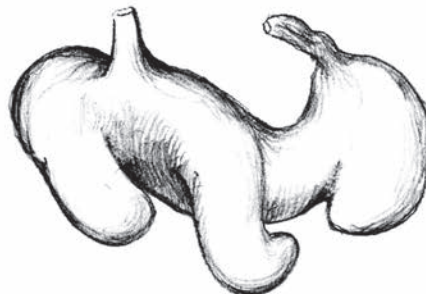


Tentative phylogenetic tree for Cetartiodactyla (after Bininda-Emonds *et al.* 2007 and Hassanin *et al.* 2012).

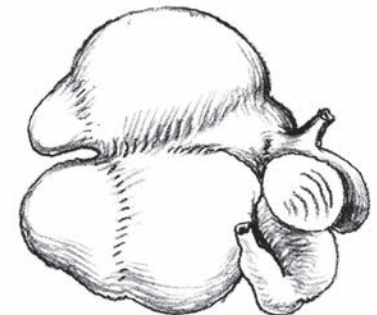
Erik R. Seiffert & Jonathan Kingdon



Suidae



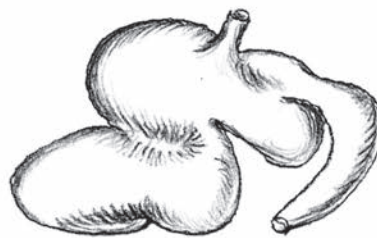
Hippopotamidae



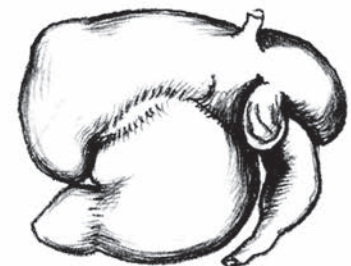
Giraffidae



Camelidae



Tragulidae



Bovidae

Sacculations in cetartiodactyl stomachs (from Kingdon 1982).

Suborder SUIFORMES – Pigs

Suiformes Jaekel, 1911. Die wirbeltiere: eine übersicht über die fossilen und lebenden formen, Berlin. pp. 233.

Traditionally, the Suiformes have been viewed as a clade that included not only the African pigs and hippos, and their extant and extinct Eurasian relatives, but also forms with no known living counterparts, such as the Anoplotheriidae from Europe, the Raoellidae from Asia, the Choeropotamidae from Eurasia and the Oreodontoidea from North America, plus the Dichobunoidea, Anthracotheroidea and Entelodontoidea that are known from both Eurasia and North America (McKenna & Bell 1997). Recent advances in our understanding at the molecular level of artiodactyl evolution, together with new and complete Palaeogene whale fossils and reinterpretation of previously documented fossil evidence, have led to the recognition of the order Cetartiodactyla in which ancodonts (anthracotheres and hippos) are now grouped with cetaceans (whales and dolphins) in the suborder Whippomorpha, whereas pigs and peccaries are retained in the suborder Suiformes.

The Suiformes are today represented in Africa by four genera of the family Suidae, which is in turn grouped with the extralimital peccaries (Tayassuidae) and extinct sanitheres (Sanitheriidae) into the superfamily Suoidea. The Suoidea are united by the uniquely derived features (autapomorphies) of: lack of a lingual cingulum on the upper molars; the similarity of the lower first and second incisors; a rootless lower male canine; paraconid fused to metaconid in the lower cheekteeth; tympanic process of squamosal dorsoventrally elongate and external auditory meatus opening dorsally; and by the presence of ossified tympanic bullae (Liu 2003).

The sister relationship between Suidae and Tayassuidae is well documented on both morphological (Gentry & Hooker 1988) and molecular grounds (Irwin & Arnason 1994, Randi *et al.* 1996). Pigs and peccaries occupy similar adaptive zones (*sensu* Simpson 1944) in the Old and New World, respectively. Both are primarily omnivorous and of the living artiodactyls display the most primitive traits – retaining four distinct digits, separated foot bones, absence of frontal appendages, a simple, non-ruminating stomach, and the less progressive forms having low-crowned cheekteeth with simple bunodont cusps. Sanitheres cheekteeth are bunoselenodont, with a tendency to further complicate the premolars by polycuspy and polycristy accompanied by heavy wrinkling of occlusal enamel. In some dental and cranial features the sanitheres are convergent on selenodont artiodactyls, but the astragalus is characteristically suoid (Pickford 1984).

The oldest suoid fossils now known are from the late Eocene of China (Tong & Zhao 1986, Liu 2001) and Thailand (Ducrocq 1994, Ducrocq *et al.* 1998). Although the evidence is still sparse and incomplete, it would appear that suoids originated in eastern Asia during the Eocene, subsequently dispersing into the New World (Tayassuidae) and elsewhere in the Old World (Suidae) during the Oligocene (Ducrocq 1994, Ducrocq *et al.* 1998, Liu 2001).

John M. Harris

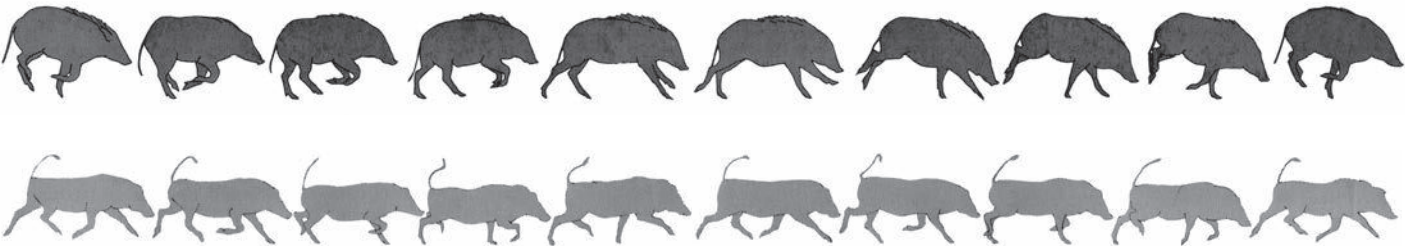
Superfamily SUOIDEA

PIGS

Suoidea Gray, 1821. London Med. Repos. 15: 306.

The superfamily Suoidea describes a taxon that subsequently bifurcates into the New World peccaries (family Tayassuidae) and the Old World pigs of the family Suidae.

John M. Harris



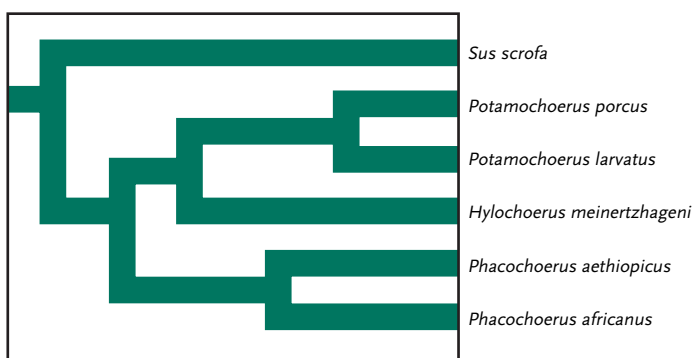
Diversity of morphology and gait in contemporary suids. Comparison of gaits in two suid species: *upper row*: Bushpig *Potamochoerus larvatus* 'gallop'. *Lower row*: Common Warthog *Phacochoerus africanus* 'fast trot' (from film, courtesy of D. Cumming).

Family SUIDAE

PIGS, HOGS

Suidae Gray, 1821. London Med. Repos. 15: 306.

| | | |
|----------------------------------|------------------------|-------|
| <i>Sus</i> (1 species) | Wild Boar | p. 28 |
| <i>Potamochoerus</i> (2 species) | Bushpig, Red River Hog | p. 31 |
| <i>Hylochoerus</i> (1 species) | Forest Hog | p. 40 |
| <i>Phacochoerus</i> (2 species) | Warthogs | p. 50 |



Phylogenetic tree of extant African suidae (modified after White & Harris 1977 and Hassanin *et al.* 2012).

The family Suidae contains the pigs and their relatives. Suids are robust animals with relatively short legs and large heads. The modern forms have a short braincase and an exceedingly elongated facial skeleton forming a tubular snout. Peculiarly characteristic of suids among African ungulates is the terminal position of the nostrils, surrounded by a partly cartilaginous, mobile disc attached to a central prenasal bone; they have leathery, sometimes sparsely haired skin. All pigs have simple stomachs, lacking the fermentation chambers of ruminants.

Suidae are separated from other suoids by the absence of the angular process of the mandible (Liu 2003). Suid molars are also characterized by the presence of three furrows or 'furchen' on each of the four main cusps (Hünemann 1968, Pickford 1986), a feature that is lacking in the bunodont peccaries and bunoselenodont sanitheres. This furrowed enamel is thrown into subsidiary cusps surrounding the main cusps. Suids have developed a diastema between the canine 'tusks' and the masticatory tooththrow with progressive reduction of the premolars in grass-eating species. This trend can be

correlated with improved milling of tough vegetation and finds its most extreme expression in the warthogs *Phacochoerus* spp. where mature individuals only retain M3. The mesial premolars are small and unicuspid, but the premolar and molar series gets progressively more complex distally, with the third molars capable of elongation with three or more pairs of cusps. The upper incisors are small and spaced, the lowers somewhat procumbent. The upper canines are small and pointed in the ♀, large and curved outward and upward in the ♂, and form potent weapons.

The Suidae have been divided into several subfamilies. The Listriodontinae are characteristic of the early to middle Miocene (21–14 mya) in Eurasia and Africa; early forms had low-crowned bunodont teeth but more advanced representatives developed tapir-like lophodont molars. The Kubanochoerinae had a similar temporal and geographic range to the listriodontines; they retained low-crowned bunodont teeth, but some species developed horns on the frontal and above the orbits. Tetraconodontines were most abundant in the late Miocene and Pliocene (9–4 mya) of Africa and Asia and developed very large third and fourth premolars. The Namachoerinae were precociously lophodont, short-snouted suids from the early to mid-Miocene of Africa. Cainochoerines were pygmy forms from the late Miocene of eastern and southern Africa. The bunodont *Palaeochoerus* of Europe (Oligocene to early Miocene, 34–22 mya) was at one time interpreted as an 'Old World peccary', but Liu (2003) reinterpreted it as part of an unresolved stem group of the Suoidea. The lophodont Schizotheriinae of the African and Eurasian Miocene were also interpreted as 'Old World peccaries', but Liu (2003) included them in the Suidae.

The extant suids are sometimes interpreted as representing three subfamilies: Suinae (widely distributed in the Old World), Phacochoerinae (sub-Saharan Africa) and Babyrousinae (eastern Asia), but their similarities to each other, and differences from extinct suid subfamilies, probably only warrants separation at the tribal level (which is the approach followed herein).

Colin Groves & John M. Harris

Subfamily SUINAE – Pigs, Hogs

Suinae Gray, 1821. London Med. Repos. 15: 306.

The first representatives of the Suinae appeared towards the end of the middle Miocene in Europe and Asia. Suinae crania are distinguished by an elongated flange – the prezygomatic shelf – that projects anteriorly from the zygomatic root. This flange separates the chewing musculature from the muscles that operate the snout. It was not present in the hyotheriines, kubanochoeres, listriodonts and tetraconodonts, where the anterior tendinal guides for the snout musculature in the vicinity of the canines were generally poorly developed. This suggested to Pickford (1993) that the characteristic

rooting habit of extant pigs is restricted to the Suinae. Another progressive feature of suines is the development of sagittal cusplets between the labial and lingual cusps of the upper fourth premolar.

The Suinae radiated rapidly and are represented by some 15 genera during and after the late Miocene. The heterogeneous nature of suine molars could permit these pigs to be treated as a subfamily, which could be further subdivided into several component tribes, but there is currently little consensus of opinion as to tribal compositions. However, there is general recognition that the hypsodont African

suines (*Phacochoerus* and the extinct *Metridiochoerus*) form a natural grouping.

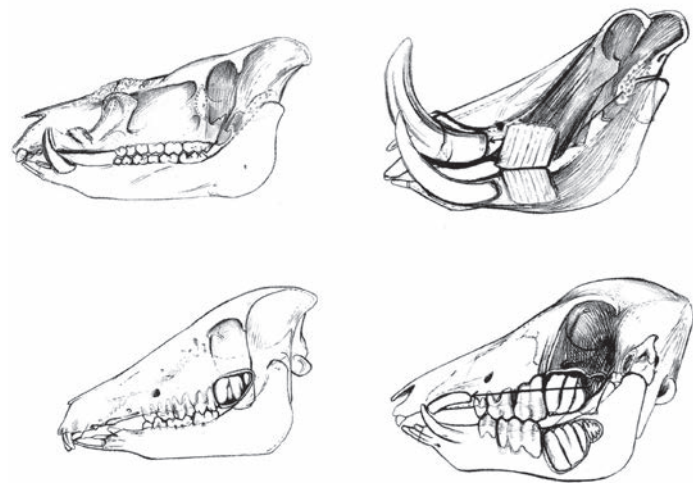
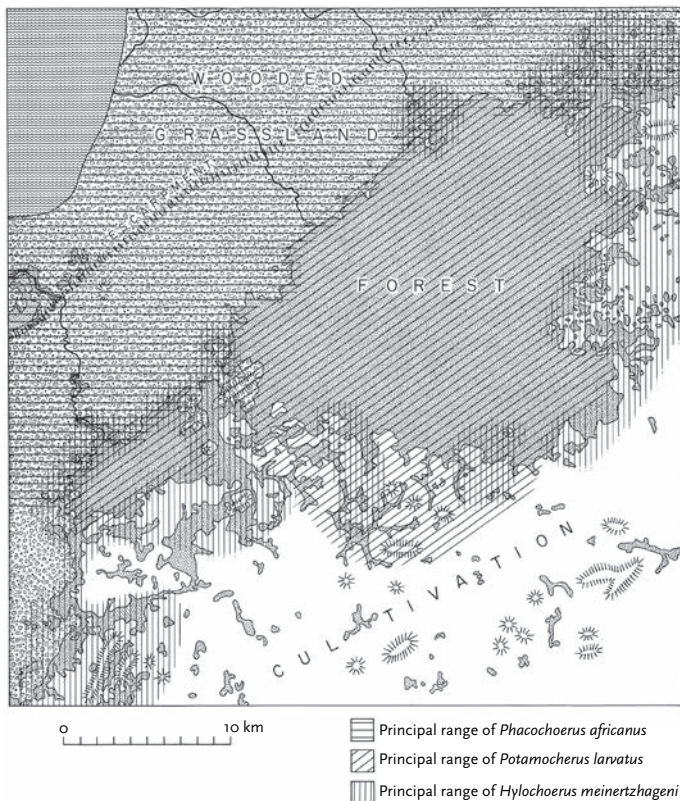
A major faunal turnover occurred toward the end of the Miocene (7–5.3 mya) in sub-Saharan Africa, reflecting the opening up of forested habitats and the spread of C4 grasses (Leakey *et al.* 1996, Cerling *et al.* 1997b). The listriodonts, kubanochoeres and sanitheres characteristic of the African early and middle Miocene were replaced by tetraconodonts in the late Miocene and these were in turn replaced by suines that arrived during the late Pliocene (3–1.8 mya). The contrast in size between the relatively small early and middle Miocene African suids and their larger late Miocene and Pliocene counterparts reflects the more open habitats available to the later forms.

The Suinae are first documented in Africa at about 3.4 mya. *Kolpochoerus*, *Potamochoerus* and *Metridiochoerus* represent the ancestral stocks of the extant forest hogs (*Hylochoerus*), bushpigs (*Potamochoerus*) and warthogs (*Phacochoerus*), respectively (Cooke 1978a, Harris & White 1979). *Potamochoerus* remained virtually unchanged during the ensuing 3-plus million years, but some of the *Kolpochoerus* and *Metridiochoerus* species underwent increase in size and in complexity of the cheekteeth. Later members of both the *Kolpochoerus* and

Metridiochoerus lineages achieved gigantic size but *Hylochoerus* was probably derived from the moderately sized *K. heseloni*, whereas *Phacochoerus* probably originated from the diminutive *M. modestus* (Harris & White 1979).

Today, the African suids live in wooded or thicket country, from rainforest and montane forest to savannas and semi-arid scrub, which provides requisite shelter. In some rare localities the ranges of all three genera overlap, but their ecological preferences and spatial partitioning are clear, with bushpigs preferring forest and thicket formations, warthogs in wooded savannas and the Forest Hog in forest/grassland mosaics. All species are capable of expanding their ecological range in the absence of the other species. They typically live in groups of one or more ♀♀ (sows) with young; adult ♂♂ (boars) are predominantly solitary. Females in most species make nests, to which they constantly return with their young; warthogs occupy burrows. Litters typically number 2–8 and single births are rare. The very large size achieved by some extinct Pliocene and Pleistocene African suids was probably a predator-selected adaptation for living in more open habitats.

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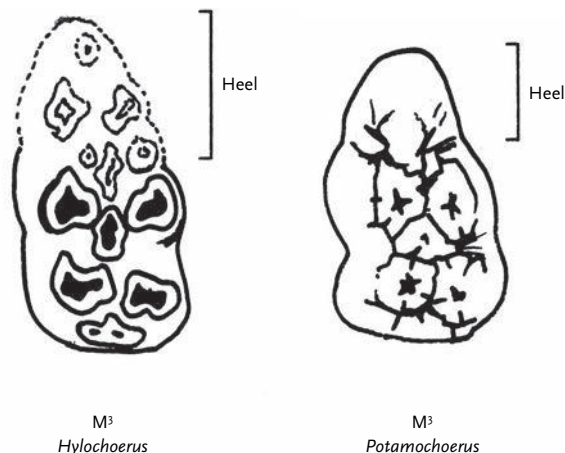
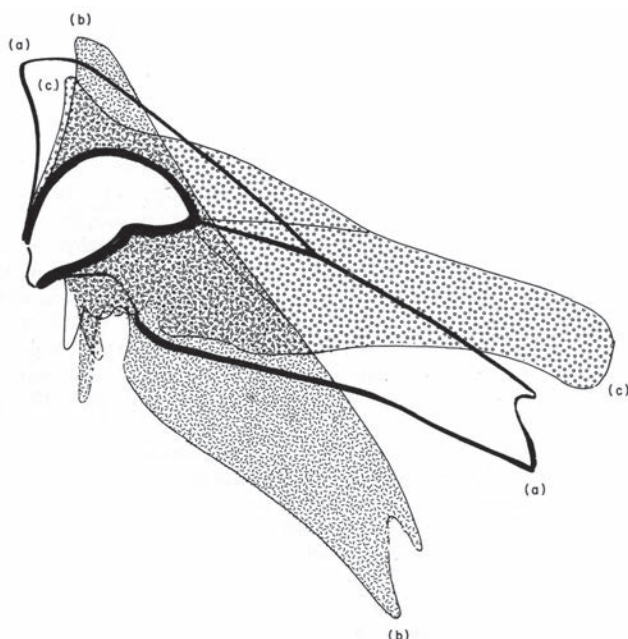
ABOVE: Old adult skulls of (above left) Bushpig *Potamochoerus larvatus* and (above right) Common Warthog *Phacochoerus africanus* compared with juveniles showing succession and differential migration of teeth during life (from Kingdon 1979).

LEFT: Map of habitat use by three suid species in and around Budongo Forest, Uganda: Common Warthog *Phacochoerus africanus*; Bushpig *Potamochoerus larvatus*; Forest Hog *Hylochoerus meinertzhageni*.

Tribe SUINI

Old World Pigs

Suini Gray, 1821. London Med. Repos. 15: 306.



ABOVE: Diagrams of upper third molar in (left) Forest Hog *Hylochoerus meinertzhageni* and (right) Bushpig *Potamochoerus larvatus*.

LEFT: Three suid skulls showing flexion of snout in relation to cranial capsule: a) Bushpig *Potamochoerus larvatus*; b) Common Warthog *Phacochoerus africanus* (down); c) Forest Hog *Hylochoerus meinertzhageni* (upward).

Africa is home to three extant suin genera. The Wild Boar *Sus scrofa* was at one time restricted to North Africa, but feral stock is now also known from western and southern parts of the continent. The Forest Hog *Hylochoerus meinertzhageni* is essentially limited to the equatorial forest belt, but the bushpigs (*Potamochoerus* spp.) are more widely distributed in the less arid parts of Africa. Bushpigs are water-dependent opportunistic feeders that will take advantage of any available food source; Warthogs, in contrast, feed exclusively on C3 plants and are less water-dependent (Harris & Cerling 2002). All three genera were originally bunodont browsers or omnivores, but derived Pleistocene species of the extinct African suin *Kolpochoerus* had high-crowned teeth and a grazing diet (Harris & Cerling 2002).

In common with some other pigs, the braincases of Suini are enclosed in bony capsules that are separate from the skull's outer casing. One benefit of this separation between the cranium, with its associated basicranial axis, and the skull's outer shell is that the latter can be damaged (and often is during violent male fights) without compromising brain function. Another attribute is very ready modification of the outer shape of pig skulls during evolution.

The Suini evidently originated in western Asia (Pickford 1993), from whence they migrated to eastern Asia, Europe and Africa. *Kolpochoerus deheinzeli*, known by teeth from the latest Miocene of Chad (Brunet & White 2001), is the oldest suin yet documented in the African record. The cranium of the Pliocene *K. afarensis* was rather similar to that of bushpigs but with downwardly drooping zygomatic arches and less prominent canine flanges (Cooke 1978b); in ♂♂ of later species, the zygomatic arches were pneumatized. Harris & White (1979) postulated that *Hylochoerus* was derived from *Kolpochoerus* during the early Pleistocene and that the scarcity of fossil *Hylochoerus* specimens is an artefact of their preferred habitat. Although a few teeth attributable to *Potamochoerus* have been recovered from late Pliocene localities in East Africa (Harris & White 1979), fossil bushpigs are similarly elusive and for the same reason. *Sus* appears to have been a post-Pleistocene immigrant to North Africa.

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(Left) 'Snout-boxing' in Bushpig *Potamochoerus larvatus*; (middle) 'forehead-clashing' in Forest Hog *Hylochoerus meinertzhageni*; (right) 'tusk-clashing' in Common Warthog *Phacochoerus africanus*.

GENUS *Sus* Wild Boar

Sus Linnaeus, 1758. Syst. Nat., 10th edn, 1: 49.

The genus *Sus* includes ten extant species (Grubb 2005), of which only one, the Wild Boar *Sus scrofa*, occurs in North Africa. However, this species has been introduced elsewhere on the continent.

Of the extant African suins, the ecologically equivalent Wild Boar and Bushpig *Potamochoerus larvatus* are of similar size and share many characteristics, including small upper tusks, three pairs of upper incisors, and relatively unspecialized, low-crowned bunodont cheekteeth, but *Sus* has a full complement of premolars and its enamel is thinner. The skulls of both *Sus* and *Potamochoerus* are elongate and pointed (or wedge-shaped) with an almost straight profile from the tips of the nasals to the parietals. The braincase is gently domed behind the orbits with a narrow parietal constriction. The snout of *Sus* is long and narrow with parallel-sided nasals, whereas in *Potamochoerus* the nasals widen above the canine flanges and in ♂♂ there is an expanded rugose area on the nasals and the adjoining parts of the maxillae. *Sus* has only small maxillary flanges around the roots of the upper canines, even in ♂♂, whereas in *Potamochoerus* the canine flanges are strongly developed and rugose in their upper portions. The zygomatic arches of *Sus* are narrow and not expanded laterally whereas in *Potamochoerus* the maxillary root of the zygoma juts out sharply and may be quite inflated in ♂♂. *Sus* lacks the distinct small shelf on the back of the mandibular symphysis for

the attachment of the genioglossus and geniohyoideus muscles that are present in bushpigs.

The earliest (mid-Miocene) representatives of the genus *Sus* conceivably derive from Asian *Propotamochoerus* stock. By the end of the Miocene the genus was widespread throughout Eurasia. In Europe, *Sus* was the dominant suid genus from the Pliocene onwards; the small *S. arvensis* characterized the early Pliocene, but overlapped with the very large *S. strozzi* in the later Pliocene. The extant species *S. scrofa* appeared in the late early Pleistocene. In Asia, *Sus* competed with other suine genera during the Pliocene and later diversified into a number of different species whose extant representatives are collectively known as the warty pigs (Groves & Grubb 1993). Curiously, *Sus* was not part of the suine radiation that brought *Potamochoerus*, *Kolpochoerus* and *Metridiochoerus* to sub-Saharan Africa during the early Pliocene and the Wild Boar was a relatively late immigrant to the continent. Cooke & Wilkinson (1978) indicated that remains of *S. scrofa* were present at many later Pleistocene sites in North Africa and the species is also documented at the mid-Pleistocene localities of Ternifine (Pomel 1896) and Mansoura (Joleaud 1933) in Algeria. The genus was not found south of the Sahara until introduced there through human agency.

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Sus scrofa WILD BOAR (EURASIAN WILD PIG)

Fr. Sanglier; Ger. Wildschwein

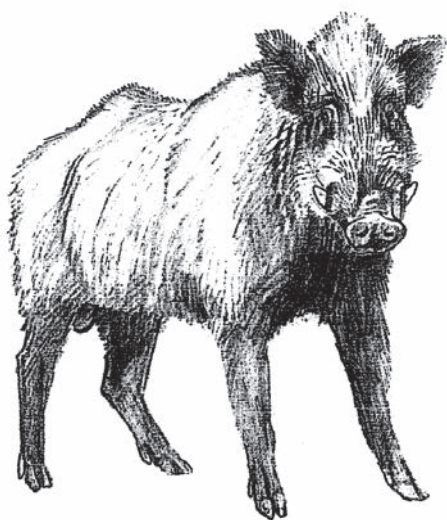
Sus scrofa Linnaeus, 1758. Syst. Nat., 10th edn, 1: 49. 'Habitat in Europa australiore'; shown to be Germany, from where wild boar had been introduced to Sweden, Oeland (Thomas 1911: 140).

Taxonomy Wild Boar populations show considerable variation in body size, cranial morphology and coat colour. Groves (1981a) recognized 16 subspecies, which can be assembled into four regional

groups (Groves & Grubb 1993): the Western subspecies (*S. s. scrofa* and *S. s. meridionalis*, distributed in Europe; *S. s. algira*, in North Africa; *S. s. lybicus*, in south-west Asia, and extinct in the Nile Delta,



Wild Boar *Sus scrofa*.



Wild Boar *Sus scrofa*.



Sus scrofa

though the origin of this population is obscure; and *S. s. attila* and *S. s. nigripes* in Central Asia); the Indian subspecies (*S. s. davidi*, in the sub-Himalayan region; *S. s. cristatus*, in NC India, Myanmar and W Thailand; *S. s. affinis* and a new, undescribed subspecies, in S India and Sri Lanka); the Eastern subspecies (*S. s. sibiricus*, in Mongolia; *S. s. ussuricus*, in eastern Asia; *S. s. leucomystax* and *riukiuanus*, in Japan; *S. s. taivanus*, in Taiwan; *S. s. moupinensis*, in S China and Vietnam); and the Indonesian subspecies *S. s. vittatus*, which is distributed in the Malay Peninsula, Sumatra, Java, Bali). All extant North African Wild Boars belong to *S. s. algira*; *barbarus*, the name sometimes used for this subspecies, is a *nomen nudum*. In Tunisia, molecular data reveal a clear break between northern and southern populations, possibly due to an Algerian origin of the southern animals (Hajji & Zachos 2011).

Synonyms: Grubb (2005) lists numerous synonyms, but only *algira*, *barbarus* and *sahariensis* pertain to Africa. Three variations of chromosome number have been recorded in wild populations, with $2n = 36, 37$ and 38 , due to Robertsonian translocations (Bosma 1976, Mauget *et al.* 1977, Popescu *et al.* 1980, Jotterand-Bellomo & Baetting 1981, Mayr *et al.* 1984, McFee *et al.* 1986, Arroyo-Nombela *et al.* 1990). The chromosome number of Wild Boars in North Africa is $2n = 38$ (El Mastour *et al.* 1983), but this requires confirmation as the origin of the two animals analysed (from Tunis Zoo) is uncertain.

Description A grey, brownish pig of intermediate body size, with relatively short muzzle and no facial warts. The head profile is triangular. Ears rather large, not tufted. Snout elongated, the tip of which is flat and forms a cartilaginous rhinarium, which is used in digging. Limbs relatively long. Hair colouration agouti, in general greyish, blackish or brown; there may be whitish hairs on the face, cheeks and throat. Hairs are often dense, and the bristles on the dorsal line are long, sometimes forming a crest or a mane. Piglets longitudinally striped brownish-red during the first five to six months. Tail has tufts. Females are smaller and about 28% lighter than ♂♂ (El Mastour *et al.* 1983, Abáigar 1990). Females have four to six pairs of nipples.

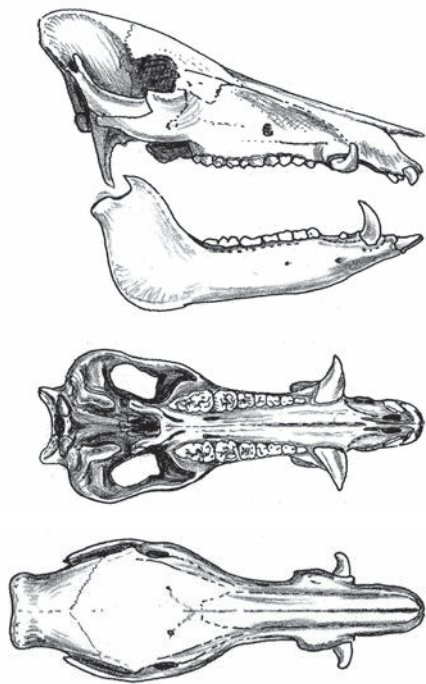
The dental formula is $I^{3/3}, C^{1/1}, P^{4/4}, M^{3/3} = 44$. Large upper canines are present, the length of which depend on the age, with their alveoli directed outward, curved outwards, backwards and upwards.

Geographic Variation As noted under Taxonomy above, there is considerable geographical variation in colour and morphology, and many subspecies have been recognized, which Corbet (1978) states have never been shown to have discrete boundaries.

Similar Species The Wild Boar cannot be confused with any other suid species within its range in Africa.

Distribution The Wild Boar is widely distributed in the Palearctic region and shows the largest range among all the suiforms. On the African continent, the species occurs naturally only in North Africa, then extraliminally formerly in Europe (including the British Isles), through S Russia, the Middle East and South Asia to the Malay Peninsula and the Greater Sundas. They are also present on Japan and Taiwan. The Wild Boar was eradicated in the British Isles and also in southern Scandinavia and N Japan in the seventeenth century. Isolated populations still exist on Honshu, and on Sardinia and Corsica (the only Mediterranean islands to which they are native), but their range also has been significantly expanded through reintroductions and introductions. Local populations in western and central Europe have been intensively restocked with allothonous or hybrid animals for hunting purposes. The species has been introduced in the USA, Australia, New Zealand, the Lesser Sundas, West Indies, and numerous oceanic islands, including the Galapagos and Hawaii (Ellerman & Morrison-Scott 1951, Corbet 1978, Oliver *et al.* 1993, Grubb 2005).

On the African continent, domestic pigs were released into plantations in the Western Cape of South Africa in an attempt to control the Pine Tree Emperor Moth *Nudaurelia cytherea* (Thomas & Kolbe 1942), but their invasive potential has been minimal when



Lateral, palatal and dorsal views of skull of Wild Boar *Sus scrofa*.

compared with other parts of the world (Botha 1989); they also have been introduced to several other African countries (e.g. Gabon, Sudan, Burkina Faso; Vercammen *et al.* 1993).

Historical Distribution Formerly in North Africa (north of 26° N) from Morocco's lower Segua El Hamra (Morales Agacino 1950) through N Algeria, Tunisia and N Libya to the Nile R. in N Egypt (Osborn & Helmy 1980). The origin of Egyptian animals is questionable, as they probably represent indefinite crossings between wild and domesticated animals (Manlius & Gautier 1999). Animals from Sudan are also probably of domesticated origin (Ansell 1972, Manlius & Gautier 1999), as are animals from the offshore islands of Mafia and Pemba (Haltenorth & Diller 1980). Fossil remains of the Wild Boar are common in Pleistocene and Holocene layers in north-west Africa, and the animal is also depicted on Roman mosaics in ancient Libya (Kowalski & Rzebik-Kowalska 1991).

Current Distribution In North Africa, confined to Maghreb (north of 27° N) from Morocco (south-western limit south of the lower Draa R.) to Tunisia. Probably no longer occurs in Libya (where the last observation dates from 1883), and extinct in Egypt since about 1902 (Hufnagl 1972, Osborn & Helmy 1980).

Habitat Inhabits a variety of well-vegetated environments, from forests to dense steppes, including marshes and riparian vegetation, in areas with over 150 mm annual rainfall. Wild Boars are able to inhabit very steep slopes, and usually are more abundant on northern rainy slopes and in gullies (Cuzin 2003). Under drier climate (between 50 and 150 mm annual rainfall), in northern Sahara, confined to humid environments (oases, marshes and riparian habitats, especially in *Tamarix* thickets). In Morocco, they occur from sea level up to 2750 m in the High Atlas, though more common between 1500 and 2250 m

(Cuzin 2003). In Algeria, they range up to 2300 m in Djurdjura (K. De Smet pers. comm.). Usually needs water for drinking, but may live without any water in summer, for example, in Djebel Guettar (Algerian hauts plateaux) (Heim de Balsac 1936).

Abundance In Morocco, Wild Boars seem to attain their highest densities in dense forest, as they do in south-eastern Andalusia, Spain (Abáigar *et al.* 1994). In Algeria and Tunisia, numbers are rising everywhere and the species is recolonizing parts of its former range, as in the Bou Hedma (K. De Smet pers. comm.).

Adaptations Mainly crepuscular and nocturnal, but active also during the day in undisturbed areas (Benhamza 1995). In C Morocco, there are two peaks of activity at night, between 21:00 and 01:00h and between 03:00 and 07:00h (El Mastour *et al.* 1983). Animals tend to stay in the densest available vegetation during the day. Adults wallow in mud, where available.

Foraging and Food Much of what is known about diet in Africa originates from studies in C and N Morocco (El Mastour *et al.* 1983) and N Algeria (Klaa 1992). Wild Boars are mainly herbivorous, the major part of the diet consisting of aerial and subterranean parts of plants. Leaves, stalks and fruits (*Quercus* spp., *Chamaerops humilis*, *Ceratonia siliqua*, *Rhus pentaphylla*) are consumed. In SE Andalusia, during autumn, acorns of oaks *Quercus ilex* may constitute the main part of the diet (Abáigar 1993). Wild Boars intensively dig for roots and bulbs, especially those of *Arisarum vulgare*, when the soil is not too hard, mainly after the rains and under forest cover with well-developed or humid soils; this activity is very limited in dry areas, where soil is usually too hard (Cuzin 2003). A minor, but common, part of the diet consists of insects, annelids, myriapods, snails and other invertebrates, and, occasionally, some meat, eggs, small mammals (Panouse 1957) and larger animals, probably as carrion. Strong canines allow them to open carcasses very efficiently, thereby allowing other small scavengers to feed (K. De Smet pers. comm.). In SE Andalusia, young animals consume more animal matter (Abáigar 1993).

There is some evidence of seasonal variation in diet, with leaves and stalks mainly consumed after rains, usually in winter and spring; fruits are consumed from autumn to spring, and digging activity is more frequent when the soil is not too hard. In Algeria, consumption of animal food seems more frequent in autumn. In the driest habitats, in the absence of rain, animals may move to more productive habitats, e.g. oases (F. Cuzin pers. obs.), where they eat a lot of dates (K. De Smet pers. comm.). After periods of high rainfall in the N Moroccan Sahara, animals moved up to 110 km from their native area, returning there when the habitat dried out (F. Cuzin pers. obs.). Wild Boars are attracted to agricultural fields, especially cereals, maize, wheat and barley.

Social and Reproductive Behaviour Wild Boars are gregarious, occurring in groups of up to 17 animals (Benhamza 1995). In Europe, groups of generally related ♀♀ with piglets, and subadult ♀♀ are the most common social unit, while ♂♂ stay isolated or in small groups, joining female groups only during the rutting season; territorial behaviour is evident only for resting places (Gerard *et al.* 1991).

There are no details of home-range size in North Africa. In S France, home-ranges are very variable according to the season:

Maillard & Fournier (1994) recorded an average of 263 ha for groups and 1063 ha for lone ♂♂ during summer, and 497–15,440 ha for ♀♀ and 1292–3698 ha for ♂♂ during autumn. Dispersal is more common among ♂♂ than ♀♀.

Wild Boars have a wide range of vocalizations, from rhythmic grunting of ♀♀ when leading groups to teeth-chattering when angry.

Reproduction and Population Structure Mating usually occurs from Oct until Jul (thereby avoiding the driest season), with parturition from Feb until Oct, with a peak in Mar (El Mastour *et al.* 1983). Gestation is 112–126 days in Europe (Gerard *et al.* 1991). Mean litter-size is 5.7 (range 2–11; $n = 13$), according to foetal counts, and 5.1 (range 3–8) based on direct observations (El Mastour *et al.* 1983). Time to weaning is not recorded for North Africa, but in Europe, ♀♀ stay alone from the end of gestation until 1–5 weeks after birth (Gerard *et al.* 1991). Young are mature at 7–12 months of age. Longevity and population structure is unknown in North Africa.

Predators, Parasites and Diseases Leopards *Panthera pardus* have been observed feeding on Wild Boar (P. C. Beaubrun & J. Godart pers. comm.), although this species is on the verge of extinction in North Africa (Cuzin 1996). There are also reports of Golden Jackals *Canis aureus* preying on young (Khidias 1986). There is no information available on their susceptibility to disease or parasites in North Africa.

Conservation IUCN Category: Least Concern. CITES: Not listed.

The primary threat to the Wild Boar in North Africa is forest loss and habitat degradation, coupled by a drying of humid habitats, especially on the northern fringes of the Sahara (Cuzin 2003). Nonetheless, Wild Boars are expanding their range in some parts (Cuzin 1996), and in Tunisia and Algeria they are gradually expanding southwards, especially in the wake of the Islamic uproar in the Tell Atlas, and a ban on hunting (Kowalski & Rezebik-Kowalska 1991, K. De Smet pers. comm.). Though considered as impure by Islamic

belief, Wild Boars are a pest in agricultural fields and are sometimes hunted by local people (Monteil 1951, F. Cuzin pers. obs.).

Measurements

Sus scrofa

HB (♂♂): 1471 (1300–1600) mm, $n = 8$

HB (♀♀): 1310 (1200–1430) mm, $n = 8$

WT (♂♂): 94.5 (64.0–110.0) kg, $n = 8$

WT (♀♀): 63.8 (42.0–94.0) kg, $n = 8$

N and C Morocco (El Mastour *et al.* 1983); animals older than three years

HB (♂): 1200 mm, $n = 1$

HB (♀♀): 1160, 1200 mm, $n = 2$

T (♂): 210 mm, $n = 1$

T (♀♀): 165, 190 mm, $n = 2$

E (♂): 110 mm, $n = 1$

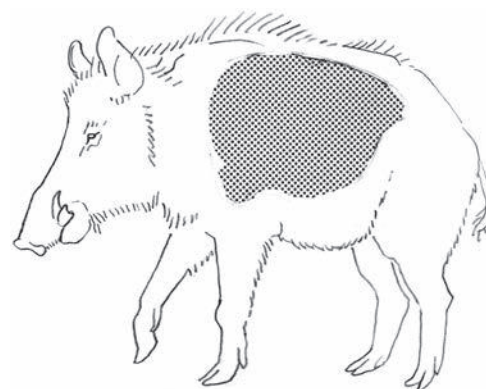
E (♀♀): 105, 110 mm, $n = 2$

HF c.u. (♀♀): 240, 250 mm, $n = 2$

N Morocco (Cabrera 1932)

Key References Cuzin 2003; El Mastour *et al.* 1983.

Fabrice Cuzin & Ettore Randi



Wild Boar *Sus scrofa* male with area of dermal shield indicated.

GENUS *Potamochoerus*

Bushpig, Red River Hog

Potamochoerus Gray, 1854. Proc. Zool. Soc. Lond. 1852: 129 [1854].

This genus is represented by two very distinct species (Grubb 1993b): the monotypic Red River Hog *P. porcus*, characteristic of the rainforest belt but extending north of it into savanna country; and the geographically varying Bushpig *P. larvatus*, of heavy cover in the East and southern African savanna zone. The Bushpig was introduced in precolonial times to Madagascar (also the type locality for the species), where it flourishes; the reasons for its introduction seem obscure, but presumably relate to meat supply.

Potamochoerus is the most plesiomorphic of the three endemic Afrotropical genera of Suidae, and is presumed, on morphological grounds, to be the sister genus of *Sus*, with which it shares the following character states: the rostrum is extremely elongated; there is a deep preorbital fossa; and the temporal ridges are strongly

developed. The canines of the ♂, which are comparatively small, flare sideways and curve upward; those of the ♀ are much smaller, but likewise protrude sideways. The root of the maxillary canine sits in a large bony flange, the canine apophysis, which protrudes from the anterior maxilla lateral to the rostral end of the preorbital fossa. Also in common with *Sus* is the presence of three upper incisors. The premolars, contrary to the two other endemic Afrotropical genera, are not only well developed, but are enlarged and somewhat molarized. The adult dental formula is: $I^{3/3}, C^{1/1}, P^{3-4/3-4}, M^{3/3} = 40-44$.

In contrast to *Sus*, however, pigs of this genus are characterized by several important differences: the braincase bulges outward below the temporal ridges; the occiput is lower; the auditory canal, instead of ascending at 45 degrees or more, is relatively horizontal; and the

nasals are dorsally flattened, and laterally expanded, so that they overhang the lateral walls of the rostrum. The canine apophysis of the ♂ is greatly enlarged and roughened, and rises up toward the shelf-like lateral nasal edge. The anterior premolar is always absent in the mandible, commonly so in the maxilla (see dental formula above). The other premolars are strongly molarized, with flattened, cuspidate occlusal surfaces (in *Sus*, they have narrow blades). The mandibular ascending ramus slopes more posteriorly than in *Sus*, and the condyle is relatively lower. Ewer (1958) described the functional anatomy of

the facial musculature, relating it to the mobility of the snout, especially its terminal disc.

Externally, this genus of mainly nocturnal omnivorous pigs is characterized by the long, pointed ears; and, among the Afrotropical genera, by the longitudinal ridges along the top of the snout and forehead; by the retention of a long, bristly pelage; and by the lack of prominent facial warts, but the presence of a flat wart on either side of the snout supported by the enlarged canine apophyses.

Colin Groves

Potamochoerus larvatus BUSHPIG

Fr. Potamochère; Ger. Buschschwein

Potamochoerus larvatus (F. Cuvier, 1822). Mem. Mus. Hist. Nat. Paris 8: 447. Madagascar.

Taxonomy The Bushpig was originally considered conspecific with the Red River Hog *Potamochoerus porcus*, which is now regarded as a separate allopatric species of West and central Africa (Grubb 1993b, 2005; and see De Beaux 1924). Grubb (1993b) noted that too many subspecies have been recognized in the past, and commented that the primary systematic division within the species is between the white-faced animals of East Africa and populations in southern Africa. He tentatively recognized three subspecies on the African mainland (*Potamochoerus larvatus hassama*, *P. l. somaliensis* and *P. l. koiropotamus*) and an additional two on Madagascar and Comoros Is. (*P. l. larvatus* and *P. l. hova*). However, Vercammen *et al.* (1993) proposed that insufficient evidence exists for the recognition of *P. l. somaliensis* as a distinct subspecies (indeed, Grubb 1993b was not convinced of the validity of *somaliensis* either), and recognized only two from the continent: the White-faced Bushpig *P. l. hassama* (including *P. l. somaliensis*; East Africa) and the Southern Bushpig *P. l. koiropotamus* (from Angola and southern Africa). The Madagascan and Comoron subspecies of the Bushpig were almost certainly introduced during historic times. Synonyms: *africanus*, *arrhenii*, *choeropotamus*, *congius*, *cottoni*, *daemonis*, *edwardsi*, *hassama*, *hova*, *intermedius*, *johnstoni*, *keniae*, *koiropotamus*, *madagascariensis*, *mashona*, *nyasae*, *somaliensis*. Chromosome number: not known, but presumably as for *P. porcus*. Hybrids with introduced feral pigs *Sus scrofa* have been recorded (Milstein 1971, Smithers 1983).

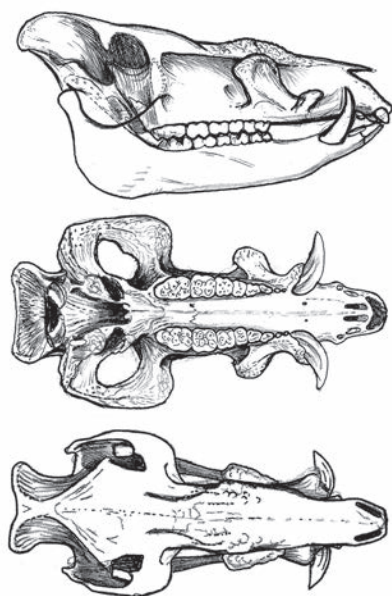
Description Medium-sized, thickset suid. The head is characterized by an elongated muzzle, with naked disc-like snout, cheek beards and terminal ear tassels. The morphology of the head differs between the sexes and the slightly heavier male body mass is related to these differences. Males develop three pairs of wart-like facial structures: over the canine root flanges on the snout (preorbital); on the malar eminences (infraorbital); and on the jaw angles (gonial). Ears pointed with tufts of long hair at tips. Pelage bristly, extending from the head over the whole body, with a striking dorsal crest extending from the head to the base of the tail; hairs long (60 mm), but relatively sparse. Undercoat absent. General colour variable within and between subspecies and individuals, and changes with age. Neonatal pelage of pale, yellowish-buff stripes on a brown ground colour is replaced by a rufous-brown at about three months of age, gradually changing to the colouration of maturity. Adult



Bushpig *Potamochoerus larvatus*.

body colour is predominantly black to dark grey, but, particularly in north-eastern parts of the range, may be light red to brown. Males often have a distinct white facial mask. Tail with sagittally aligned (feathered) black terminal hairs. Males have tusk, orbital (Harderian), digital and preputial glands; orbital and digital glands are found in ♀♀. Females have three pairs of nipples.

The highest point of the skull lies near the back and then slopes forward to the nostrils. Rostrum narrow and elongated, hollowed out on either side to accommodate the powerful muscles and tendons that open and close the rhinarium during rooting and digging. Mandible long and massive, its actuation relying on the powerful masseters provided with firm attachment between the thick zygomatic arches and the angle of the lower jaw. Supraoccipital ridges pronounced. The back of the skull arches high from the occipital condyles and provides a firm base for the attachment of the neck muscles, which actuate the movement of the heavy head. Adult dentition is developed at about two years, M³ being the last to erupt. The incisors are heavily built and persist throughout the life of the individual. The upper canines project outside the mouth cavity but are never as long as in warthogs *Phacochoerus* spp.; the lower canines are sharp-pointed and sharp-edged, lying at an angle sloping outwards from the mandible, which



Lateral, palatal and dorsal views of skull of Bushpig *Potamochoerus larvatus*.

makes them formidable weapons. The molars are brachyodont and bunodont, and in old individuals still retain some ridging indicating a chopping action rather than grinding during mastication (Seydack 1983, Skinner & Chimimba 2005).

Geographic Variation

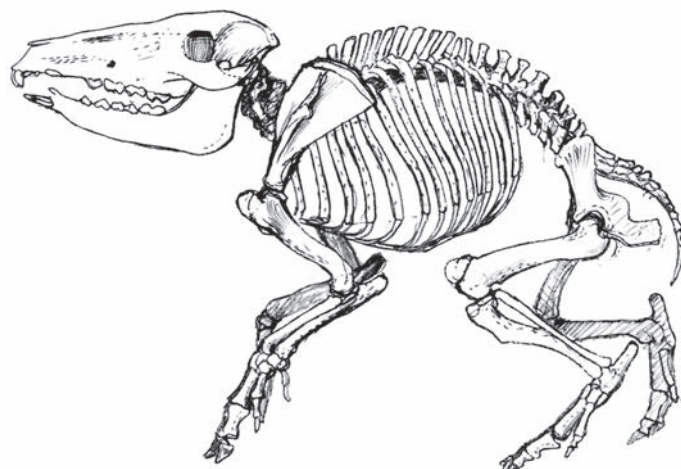
P. l. hassama (including *P. l. somaliensis*) (White-faced Bushpig): East Africa, including Ethiopia, Eritrea, S Sudan (both west and east of the Nile R.), E DR Congo, Rwanda, Burundi, Uganda, Kenya and NTanzania. Characterized by the white colour of the head, usually black body in adult ♂♂ and smaller average size, as indicated by skull length (32.7–35.3 cm in ♀♀ and 34.1–37.7 cm in ♂♂; Grubb 1993b).

P. l. koiropotamus (Southern Bushpig). SE DR Congo, S Tanzania, Malawi, Mozambique, Zambia, W and C Angola, Zimbabwe, Botswana, South Africa and Swaziland. Largest member of the genus (skull length 36.7–41.5 cm in ♂♂ and 34.5–39.5 cm in ♀♀), typically never with contrasting black-and-white colour pattern of *P. l. hassama*, but ♂♂ from an isolated population in the Western Cape and Eastern Cape also generally have white faces contrasting with darker bodies. It is also possible that darker-bodied Bushpig ♂♂ have whitish facial patterns, whilst lighter-bodied ones have darker facial markings for contrast.

Similar Species

Potamochoerus porcus. Allopatric, though ranges are contiguous in places. Predominant coat colour bright russet-orange with a white dorsal line; pelage over much of body short and dense; terminal ear tassels particularly elongated; forehead black or dark brown, with prominent white 'spectacles' around eyes.

Hylochoerus meinertzhageni. Sympatric in some parts of eastern Africa. Larger, more heavily built suid, with long black hair, and a dorsal crest of thick, erectile hair; ♂ has enormous bare cheeks and a broad, flat muzzle.



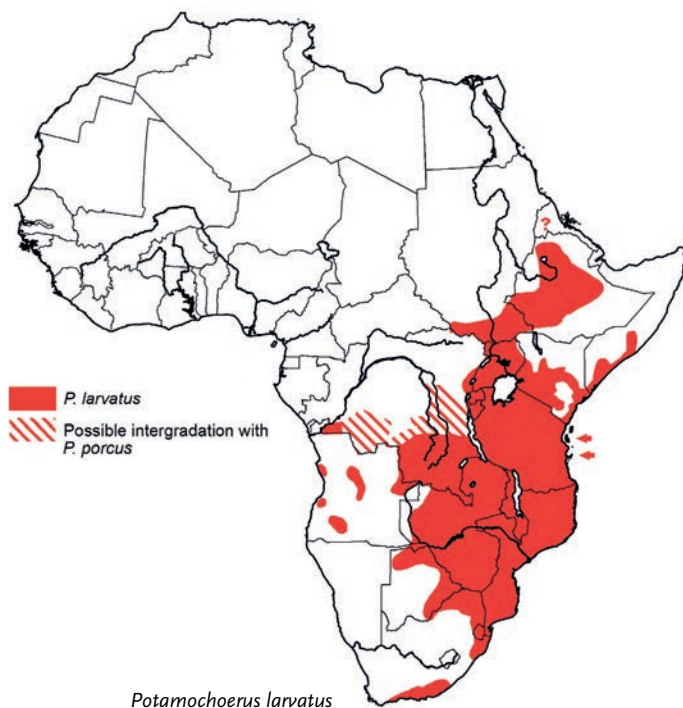
Bushpig *Potamochoerus larvatus* juvenile skeleton.



Bushpig *Potamochoerus larvatus* myology of juvenile.



Bushpig *Potamochoerus larvatus* juvenile.



Distribution Endemic to Africa, extending from S Sudan, Ethiopia and possibly Eritrea in the north-east of the continent, southwards through East Africa and E and S DR Congo to Zambia, Malawi and Mozambique. There are isolated populations in W and C Angola. In DR Congo, the vicinity of the upper reaches of northward-flowing tributaries of the Congo R. are occupied by this species, whereas the continuous lowland forest that surrounds more northerly reaches of the same rivers is inhabited by Red River Hogs. In southern Africa, they are absent from Namibia, though they may occur in the Caprivi Strip. In Botswana they occur only in the northern and north-eastern parts, while in Zimbabwe they occur nearly throughout. In South Africa they are found in the northern and eastern parts of the country (and neighbouring Swaziland) to S KwaZulu–Natal. There is a break in their distribution between S KwaZulu–Natal and an isolated population in the Eastern Cape and Western Cape Provinces (which is also the origin of the holotype). Recorded from Zanzibar (Pakenham 1984) and Mafia I. (Kingdon 1979, Kock & Stanley 2009), and introduced on Madagascar and the Comoro Is. (Mayotte) off the east coast of Africa (Vercammen *et al.* 1993).

Habitat Bushpigs are associated with relatively dense vegetation types with available food, cover and water, occurring in forests and riverine or xeric scrub forests and thicket formations. In East Africa they commonly are found in high-lying areas, such as the Ethiopian Highlands to elevations of 3000 m, and perhaps 3400 m (they are common in the Haremma Forest; Yalden *et al.* 1996), the highlands of the Albertine Rift (where Red River Hogs have never been recorded), and on Mt Kilimanjaro (to 4000 m; Vercammen *et al.* 1993). They also maintain their occurrence in areas now given over to subsistence farming or to agricultural crops such as sugarcane, maize, peanuts and beans, and have long been a serious problem in such areas.

Abundance Mentis (1970) reported 0.22 individuals/km² in Hluhluwe–iMfolozi G. R., KwaZulu–Natal, South Africa. Population density estimates during a study in southern Cape forests, South Africa, range between 0.3 and 0.5/km² (Seydack 1990, 1991).

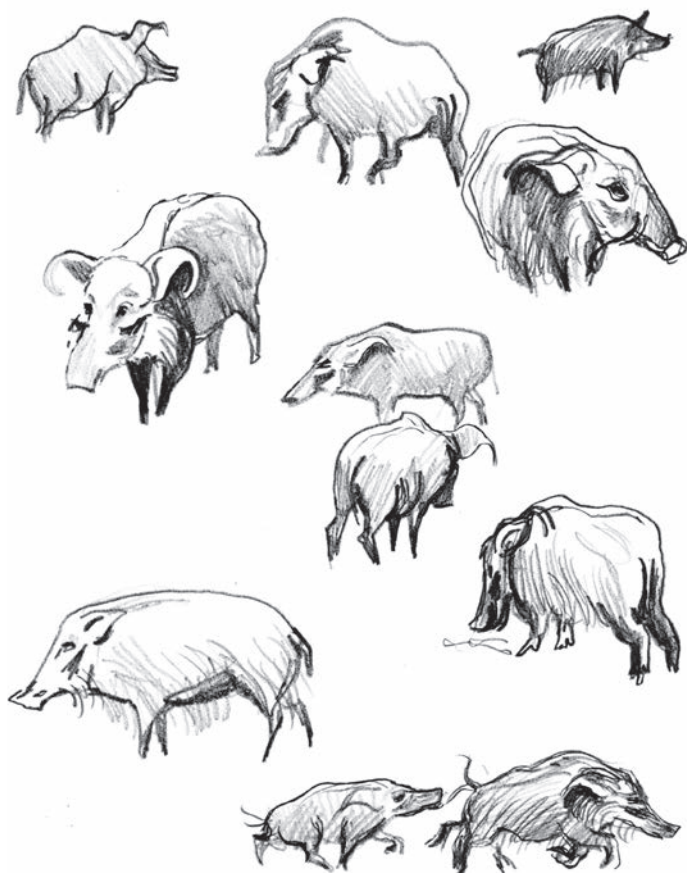
Adaptations Bushpigs obtain the largest proportion of their food from the litter layer through superficial rooting. The compact body and thick short neck allow for the necessary digging forces to be applied. The build of the skull with its long snout, forwardly sloping lower incisors, short canines and bony support for the rhinarium (discussed above) are all adaptations for searching for food by rooting and digging, while their bunodont dentition and monogastric digestive system make the Bushpig well suited to an omnivorous diet. Olfaction plays a prominent role in locating food items.

The thermoneutral zone is between 13 and 30°C for juveniles and between 8 and 25°C for adults (Seydack 1990). Accordingly, Bushpigs avoid temperature extremes, being active preferentially between 18:00 and 22:00h in both summer and winter. In summer, Bushpigs rested mainly between 10:00 and 18:00h and in winter between 10:00 and 14:00h and 2:00 and 6:00h (Seydack 1990). Thus, although primarily nocturnal, more diurnal activity may occur during winter. Behavioural thermoregulation includes wallowing, lying in extended posture and exposure to air movement at high temperatures and resting after midnight in winter, sheltering, huddling and nest-building during cold and wet spells.

Foraging and Food Bushpigs are omnivorous generalists, feeding opportunistically, but primarily on subterranean and above-ground herbaceous plant material. The diet of Bushpigs in the Knysna Forest of the Western Cape and the valley bushveld regions of the Eastern Cape (South Africa) comprised 40% subterranean plant structures (of which 54.3% consisted of rhizomes, 38.9% tubers, 5.7% roots and 1.1% corms), 30% above-ground herbage (of which 46% consisted of monocotyledons, 38.7% fern fronds and 12.3% dicotyledons), 13% fruit, 9% animal matter and 8% fungi (Seydack 1990). The most important dietary items in the Cape were underground fungal bodies of *Rhizopogon*, bracken (*Pteridium aquilinum*) rhizomes and *Blechnum punctulatum* fronds. In the Eastern Cape, tubers of Vitaceae (*Rhoicissus* and *Cyphostemma*), vertebrate animal matter and foliage of *Aloe ciliaris* predominated (Seydack 1990).

In Matobo N. P. in Zimbabwe, Jones (1984) recorded 29 different food items, including invertebrates (earthworms). During the wet season, 37% of identifiable food remains in faeces were fruit, 26% finely digested food and 19% herbaceous plant roots; during the cool dry season 49% was finely digested food and 41% fruit; and in the hot dry season 83% were woody plant roots. Both wild and cultivated fruits are eaten and Bushpigs may be particularly troublesome in maize fields, sugarcane and other planted crops (Skinner *et al.* 1976, Melton *et al.* 1989). Carrion is taken opportunistically (Skinner *et al.* 1976 and references therein, Jones 1984).

Dietary items are procured from a feeding stratum of ± 0.5 m above and below ground surface through superficial rooting, deep rooting and grazing. During superficial rooting, which is the most commonly employed foraging technique, subterranean food items are exposed by lifting the snout forward and upward through the earth or litter layer. In moist or loose earth, the snout may be worked well into the soil in pursuit of deeper subterranean food items.



Bushpig *Potamochoerus larvatus*.

Suitable dietary items for an omnivore are typically widely dispersed in space and time. This requires much searching and Bushpigs move continuously while foraging, stopping only when a clump of food is discovered. When foraging in a group they tend to be spaced out in a variably extended formation. Bushpigs are predominantly nocturnal (Breytenbach & Skinner 1982, Seydack 1990). The main phase of intensive foraging generally occurs from before dusk to midnight, with a secondary activity phase in the morning. Animals are active for an average of 13.7 hours per day (Seydack 1990). This represents a comparatively extended activity period and is presumably related to the search time required where food is dispersed. They visit habitat with poor vegetation cover only during the hours of darkness.

Social and Reproductive Behaviour Bushpig sociality is characterized by the family group, usually consisting of a boar and a sow with one or two generations of offspring. There is typically only one adult sow per family group (sounder). Populations may be subdivided into four socio-spatial classes: territorial male–female pairs with or without progeny; solitary individuals, in the case of ♂♂ occupying non-exclusive home-ranges; and dispersing individuals that are mainly yearlings or subadults and nomadic adults. The average group size for the study populations in the Knysna Forest was 2.4 individuals, ranging between one and ten (Seydack 1990).

Resource territoriality is maintained by spatially related high levels of aggression, notably between ♀♀, and patrolling and marking behaviour. The area of the average home-range or territory

in the Knysna Forest was 7.2 km² (3.8–10.1 km²; n = 8) (Seydack 1990). Home-ranges are traversed every one to four days, with an average daily ranging distance of about 3 km (0.48–5.84 km).

The monogamous mating system is characterized by extended male–female pair bonds, lasting beyond mating and rearing periods, and by breeding of only the alpha-female within each territory. Breeding deferment of sexually mature, pre-dispersal daughter sows may be associated with alloparental care, consisting of grooming and remaining in close proximity to neonates. During rearing of the young, which remain with the parents long past weaning, substantial male parental care is involved. The offspring usually disperse from the family home-range when between 1.5 and 2.0 years old.

Farrowing may take place in shallow ground hollows. During cold or wet conditions, farrowing nests may be prepared during parturition. Nests then consist of a shallow depression lined with grass upon which additional twig material and shrubbery is piled to form an insulating heap. Neonates follow the mother away from the birth nest or hollow within the first one to three days, initially for short distances only. Within the first three weeks postpartum the daily ranging of juveniles hardly exceeds 200 m. When compared with the average daily ranging distance, it is apparent that during these initial weeks the ranging of adults is constrained. One or both parents remain at the resting sites and close to the neonates, lying in body contact to protect the young against both cold and predators. Paternal care involves guarding of, and concern for the young, especially during the temporary absence of the mother on foraging bouts. Maternal behaviour conforms to the general passive suid pattern; in addition to suckling the young, there is some limited vocal communication, naso-nasal contact and defensive responses to neonate distress calls (Seydack 1990).

Sounds made by the Bushpig include grunts, squeals, snarls and snorts as in other suids (Frädrich 1974). Primarily the dominant boar in a sounder may give alarm by uttering a long, drawn-out, resonant grunt. When foraging, individuals in sounders emit monosyllabic soft grunts, presumably to maintain contact.

Male tusk pouch glands and digital glands in both sexes apparently play an important role in olfactory communication (Jones 1978). Marking primarily involves tusk gland marking by the ♂ and ground scratch marking by both sexes. Male Bushpigs mark objects by wiping them with the opening of the pouch gland, usually up and down stems of small trees. Both sexes scratch the ground forcefully with the front feet, leaving clearly visible slashes. It is the dominant boar in the group that marks with his tusk gland, presumably conveying information about social status, whereas ground scratch marking appears to convey information regarding territorial tenure.

Agonistic interactions include threat gestures, snout thrusting, pushing aside, squabbling, snap biting and chasing off. Display contests are apparently confined to ♂♂ and contribute to mutual assessment of dominance ranking. Actual fighting, as described by Skinner *et al.* (1976), is accordingly rare in male Bushpigs. In contrast, territorial ♀♀ are very aggressive in expelling intruders from the territory. When two adult sows fight they rapidly thrust and push with their snouts, striking blows sideways or slashing whenever the opportunity arises ('nose fencing'). Forehead contact forms a crucial part of the contest and the snouts are held in the form of crossed swords against each other. The contestants push-butt each other with vigorous forward movements of the head, continually striving

to regain close head contact. They may sustain severe wounds and wound sepsis is a significant cause of female mortality.

Latrines consist of scattered accumulations of faeces that appear to be used intermittently over long periods of time. Faeces accumulations are sited predominantly where the ground surface is clear of vegetation, such as bare stretches of paths and roads or in canopy openings. They tend to be visually conspicuous, indicating a possible role in communication.

Reproduction and Population Structure Males reach sexual maturity between 16 and 20 months of age, while ♀♀ may first conceive at 17–22 months. Depending on social position and nutritional status, successful breeding usually occurs much later. Only pair-bonded territorial sows rear young successfully. In southern Africa, the farrowing season lasts from spring to early autumn, with a pronounced spring peak (Sowls & Phelps 1968, Seydack 1990). The most favourable nutritional conditions for the lactating sow apparently occur during this period due to the abundance of new plant growth. Mean litter-size in the wild is 2.1 ($n = 32$; Seydack 1990), but often three to four piglets are born, the maximum recorded being eight (Phillips 1926, Milstein 1971). Gestation lasts 17 weeks, and neonates weigh between 600 and 1000 g (Sowls & Phelps 1968, Seydack 1990). Lactation lasts up to 5.5 months (Seydack 1990).

Within all age classes, mortality is often due to starvation. In the Knysna Forests, significant mortality factors are inclement weather and predation for immature Bushpigs, and intra-specific strife for adults, especially in ♀♀. Mortality estimates for one- and two-year-old Bushpigs varied between 40 and 45% and were similar in both age classes. Adult mortality rates varied between 19 and 27% per annum. Sex ratio is usually 1 : 1. The oldest free-ranging Bushpig was estimated to be 18 years old, but only very few individuals reach this age (Seydack 1990).

In a study involving both Western and Eastern Cape Bushpig populations, differences in life history traits were revealed. Generation length and life expectancy at birth were 6.6 and 2.8 years in the Western Cape (nutrient-poor environment) and 5.4 and 1.8 years in the Eastern Cape (nutrient-rich), respectively. Breeding ♀♀ in the Western Cape were fatter, while Eastern Cape ♀♀ were smaller and leaner but exhibited higher fecundity. These regional differences were interpreted as resulting from a higher dietary nutrient to carbon ratio and associated higher population turnover in the Eastern Cape in comparison with Western Cape populations (Seydack 1990, Seydack & Bigalke 1992).

Predators, Parasites and Diseases Verified cases of Leopard *Panthera pardus* predation on subadult Bushpigs are recorded. Bushpigs were also commonly hunted by Robust Chimpanzees *Pan troglodytes* in Gombe N. P., Tanzania (Wrangham & Bergmann Riss 1990). Bushpig mandibles belonging to individuals 2–3 months of age have been

collected below Crowned Eagle *Stephanoaetus coronatus* nests (Seydack 1990). Bushpigs in NE KwaZulu–Natal have been recorded infested with eight ixodid tick species, of which *Rhipicephalus maculatus* was the most abundant, and one louse species *Haematopinus latus* (Horak *et al.* 1991a). Little is known about diseases in Bushpigs. Whether *Potamochoerus* spp. act as vectors of tick-borne diseases, such as trichinosis, African swine fever and trypanosomes, has yet to be verified (Vercammen *et al.* 1993).

Conservation IUCN Category: Least Concern. CITES: Not listed.

Bushpigs still occur widely in suitable habitat, albeit at naturally low population densities, and are present in several well-managed protected areas across their range. There is little indication that the distribution of the species has been, or is at present, substantially altered by human activities. They may be subject to localized declines and range contractions in some areas due to large-scale habitat destruction or as a result of hunting for crop protection and local consumption (Vercammen *et al.* 1993). In southern Africa, they are also sporadically subject to official population control measures when they feed on crops. However, their preferred habitat, nocturnal habits and relatively high reproductive potential are such that it has proved generally difficult to eliminate Bushpigs from larger tracts of relatively densely vegetated habitat.

Measurements

Potamochoerus larvatus

HB (♂♂): 1256 (1100–1540) mm, $n = 80$

HB (♀♀): 1207 (1090–1410) mm, $n = 74$

T (♂♂): 402 (335–432) mm, $n = 6^*$

T (♀♀): 361 (305–432) mm, $n = 4^*$

HF c.u. (♂♂): 247 (225–290) mm, $n = 59$

HF c.u. (♀♀): 241 (217–270) mm, $n = 53$

E (♂♂): 175 (151–203) mm, $n = 6^*$

E (♀♀): 178 (161–190) mm, $n = 4^*$

WT (♂♂): 72.3 (55.0–93.0) kg, $n = 84$

WT (♀♀): 68.9 (54.0–85.0) kg, $n = 104$

Western and Eastern Cape, South Africa (Seydack 1983); *Zimbabwe, Smithers & Wilson 1979)

Mean body weights of 52 ♂♂ and 61 ♀♀ from E Zambia are slightly heavier at 77.5 kg and 72.0 kg, respectively; the upper weight range recorded for a ♀ was 96.0 kg (Wilson 1968)

Record tusk length is 30.17 cm for an animal from the Save R., Mozambique (Rowland Ward)

Key References Seydack 1990, 1991; Seydack & Bigalke 1992; Skinner *et al.* 1976; Sowls & Phelps 1968; Vercammen *et al.* 1993.

Armin H.W. Seydack

Potamochoerus porcus RED RIVER HOG

Fr. Potamochère; Ger. Pinselohrschwein (Flusschschwein)

Potamochoerus porcus (Linnaeus, 1758). Syst. Nat., 10th edn, 1: 50. 'Habitat in Africa' (West Africa); based on animals exported to Brazil (Simoons 1953).



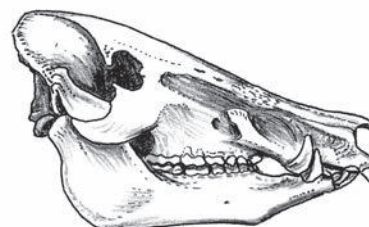
Red River Hog *Potamochoerus porcus*.

Taxonomy The most recent review of the taxonomy of the Afrotropical suids by Grubb (1993b) concluded that the Red River Hog and Bushpig *P. larvatus* should be treated as two separate species based on their clearly distinct morphology, at least until further field studies take place to further investigate possible intergradation or hybridization (and see Lönnberg 1910, De Beaux 1924, Allen 1939). As geographical variation cannot be differentiated from individual variation, no subspecies are recognized (Grubb 1993b). Synonyms: *albifrons*, *albinuchalis*, *mawambicus*, *penicillatus*, *pictus*, *ubangensis*. Chromosome number: $2n = 34$ (Melander & Hansen-Melander 1980). The chromosome complement consists of 12 pairs of (sub)metacentric autosomes and 4 pairs of acrocentric autosomes (Musilova *et al.* 2010). In Wonga-Wongue Presidential Hunting Reserve in Gabon, these animals are reported to have interbred with introduced Wild Boars *Sus scrofa* and to have produced wild offspring (East 1990).

Description Smallest of the Afrotropical suids (Grubb 1993b), characterized by bright, russet-orange dorsal colouration, a narrow, pure white dorsal line starting behind the head, a striking facial mask and narrow, pointed, tufted ears. In boars there is an exostosis on each side of the snout extending laterally toward a hypertrophied apophysis on the canine sheath – each supports a single large external cutaneous wart. No infraorbital warts. Facial mask black with a whitish muzzle, white 'spectacles' around the eyes and white cheek whiskers. Ears black with a whitish upper rim and elongated tip, carrying a tuft of long white hairs. Hair on forehead and body relatively short and dense, flanks and belly carry some longer bristles.

Ventral pelage light orange with long white and orange bristles. Pelage of young piglets brown with beige-yellow longitudinal stripes and some spots. Legs blackish in colour. Sparse tuft of hair at distal end of tail. It is likely that Red River Hogs have the same scent glands as Bushpigs (Seydack 1990): maxillary tusk glands and preputial glands in ♂♂, milky secretions from the Hardarian glands located in the eye sockets, and digital glands in both sexes. De Boer (1980) also describes a chin gland. Females have three pairs of nipples. Males are larger than ♀♀. Skull similar in build to the Bushpig, with upper canines projecting outside the mouth cavity.

Geographic Variation Vercammen *et al.* (1993) note that geographical variation is slight, though there is an east (largest) to west (smallest) cline in body size in specimens from eastern DR Congo and Cameroon, respectively. Grubb (1993b) was unable to differentiate any geographical variation from individual variation.



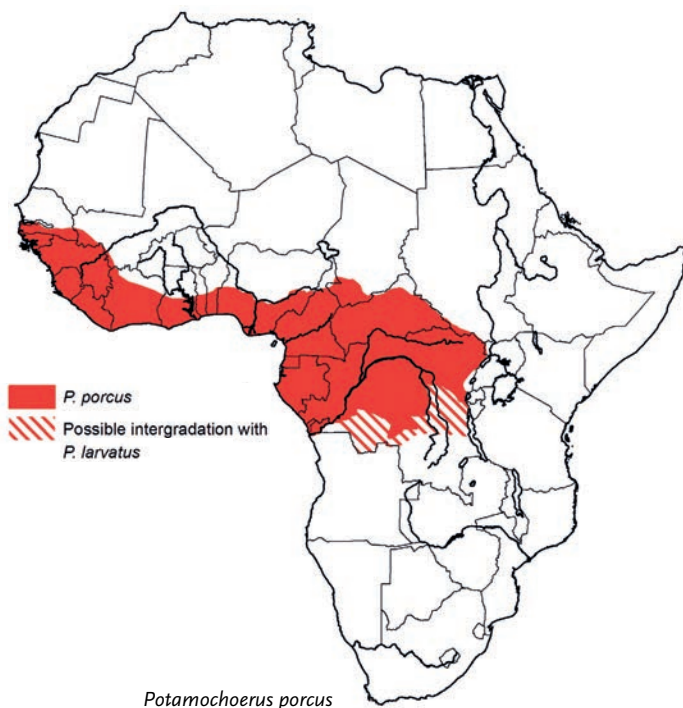
Lateral view of skull of Red River Hog *Potamochoerus porcus*.

Similar Species

Potamochoerus larvatus. As far as is known, the two species are allopatric, although their ranges are contiguous in some places (Grubb 1993b). Larger; pelage dominated by longer, coarse bristles, rather than thinner, shorter hair; much more variable and darker shaded body colouration (reddish-brown, grey and black) and more variable facial pattern (head never masked); ear tufts not so long.

Phacochoerus africanus. Sympatric over the south-west and south-central area of its range (Sahel until S Chad and possibly S Sudan in the east). Occurs on treeless open plains and lightly wooded savannas, but avoids densely wooded vegetation. Grey-brown skin, sparsely haired except for distinct black, brown or reddish mane of long thick hairs on neck and shoulders. Especially young animals often have a fringe of white hairs on cheeks. Ascending process of the mandible elongated; maxilla deepened, zygomatic arch much deepened and orbits displaced posterodorsally so that they rise above the shortened braincase. Tusks very long and curved. Prominent genal and rostral warts.

Distribution Endemic to Africa. Widely, but now patchily, distributed through the West and central African rainforest belt, from Senegal in the west, throughout the Guinea–Congo forest to at least west of the Albertine Rift. Further east and south-east replaced by the Bushpig, although the precise borders between the ranges of the two species remain unclear; for example, along the lower Congo R., below Kinshasa in DR Congo, the two species are separated only by this river – the smaller *P. porcus* occurring on the right bank and the large *P. l. koiripotamus* on the left (Angolan) side (Lönnberg 1910, Schouteden 1947, Grubb 1993b, Vercammen *et al.* 1993). Ghiglieri *et al.* (1982) observed pigs that they considered as intermediates between *P. l. hassama* and *P. porcus*, but Grubb (1993b), while noting that it was possible that the latter species may have made a narrow penetration of Uganda and hybridized with *P. larvatus* in the Kibale Forest, found there was insufficient evidence to support this. There are no confirmed records



from Sudan or Chad, though Red River Hogs may occur in extreme SW Sudan. There are also as yet no reliable records from Gambia, which is just outside their natural range (Grubb *et al.* 1998). Grubb (1993b) mentions a record from Bioko I. based on teeth picked up in the field (now in the Tervuren Museum), but notes this has yet to be evaluated.

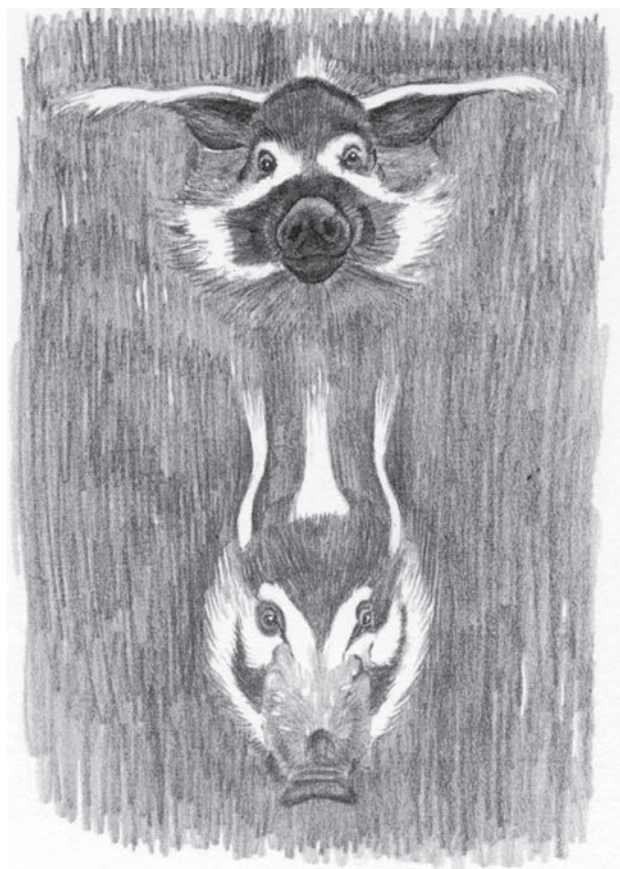
Habitat Typically associated with rainforest and gallery forest, but also found in dry forest, savanna woodland and cultivated areas, although usually in close proximity to the rainforest and in regions with limited seasonality in terms of availability of water, food and cover (Odoro 1989, Vercammen *et al.* 1993). Also frequents hydromorphic forest clearings (Magliocca 2000) and mountains with steep slopes (Malbrant & Maclatchy 1949). Like the Bushpig, Red River Hogs are highly adaptable and may even benefit by the opening up of former forested areas by the creation of secondary habitats, the provision of cultivated foods and reductions in the numbers of their natural predators.

Abundance Densities (individuals/km²) reported for Red River Hogs vary greatly and include: 3.1 (Fa & Purvis 1997); 1.3–5.6 (White 1994: forested part of Lopé N. P., Gabon); 18.4 (Tutin *et al.* 1997: galleries and bosquets in savanna ecotone of Lopé N. P., Gabon); 3.1 (Fa *et al.* 1995: Equatorial Guinea); and 2.0 (Hart, J. A. *et al.* 1996: Ituri Forest, DR Congo). Periodic aggregations on ephemeral resources might explain the higher estimates (see Adaptations).

Adaptations The bright, highly structured colouration and strong pattern of the Red River Hog imply a high premium on intra-specific visual communication; likewise, body stance and positioning of the head and ears are also likely to play roles in visual and social communication. The facial warts of pigs are believed to have evolved in association with tusk length and shape, skull shape and combat patterns between ♂♂. Species with no, or relatively small, warts and short tusks tend to engage in lateral combat postures, whereas species with large warts, large tusks, broad heads and thick skulls tend to use frontal combat postures. Both anatomically and behaviourally, the Red River Hog occupies a somewhat intermediate position between the two types (Frädrich 1974).

Red River Hogs sometimes aggregate into large groups and it is suspected that they migrate long distances (Malbrant & Maclatchy 1949, Abernethy & White 1999). It is at present not certain if such aggregations and migrations are a response to mast fruit crops in the rainforest, as is the case for White-lipped Peccaries *Tayassu pecari* and Bearded Pigs *Sus barbatus*. Observations in the Ituri Forest suggest this may be so: densities in a monodominant *Gilbertiodendron dewevrei* forest near Epulu varied with a factor of 80 (0.1–8.0 animals/km²), with the highest densities occurring during periods when there was a mast crop of *G. dewevrei* seeds. During years with no mast crop, fallen fruit was scarce and during the dry season even almost absent. Densities in a mixed forest type, where variations in fruit abundance were smaller, only varied by a factor of 5 (1.0–5.8 animals/km²) (Hart 2001).

Foraging and Food Omnivores, eating fruits, nuts, seeds, roots and tubers, leaves, fungi, insects, earthworms, small vertebrates and carrion (Carpaneto & Germe 1989, Hart 2001); they also uproot seedlings and saplings. Food items are gathered by walking along and continuously probing the leaf litter and soil with the nose. When visiting a forest clearing at Odzala N. P. in Congo, they spent 53% of



Red River Hog *Potamochoerus porcus* frontal head signals: aggressive (above); submissive (below).

their time feeding, 17% resting and 20% moving about; consumption of roots and herbaceous vegetation (mainly Cyperaceae) occupied 67% of feeding time (Magliocca 2000).

Seeds are a major component of the diet in the Ituri Forest (Hart 2001). They are able to crack open very hard nuts and hard-coated drupes such as *Irvingia* spp. and some Sapotaceae (J. A. Hart pers. comm.). The first sign of their presence is often the sound of nuts and seeds 'exploding' as they are cracked in their jaws, a sound that can be heard up to 200 m away (Abernethy & White 1999, J. A. Hart pers. comm.). Red River Hogs like to root in elephant dung for undigested seeds (Abernethy & White 1999), an activity that occupied 33% of feeding time at a forest clearing in Odzala N. P. (Magliocca 2000). However, the dung is also attractive later in the decay process, when young seedlings come up (J. A. Hart pers. comm.). In Odzala N. P., Red River Hogs mainly foraged for nuts of *Panda oleosa* (Pandaceae) and *Strombosia* sp. (Olacaceae) and for seeds of *Strychnos* sp. (Loganiaceae) (Magliocca *et al.* 2002). Red River Hogs are, therefore, mainly seed and sapling predators rather than seed dispersers; however, seeds of *Uapaca* trees pass through whole and are often found germinating in the dung (Abernethy & White 1999).

In agricultural regions, Red River Hogs will raid crops such as manioc, peanuts and potatoes. Crop raiding becomes more frequent during the main dry season when forest fruit is scarce (Malbrant & Maclatchy 1949).

Social and Reproductive Behaviour Red River Hogs live in family groups, containing ♂♂, ♀♀ and youngsters. Malbrant &

Maclatchy (1949) reported that bands of about 20 were common in Gabon and that large troops could reach 40 individuals; solitary animals are very rare. Elsewhere, Oduro (1989) recorded a mean group size of 10.6 (range 1–15) in Nigeria, while White (1994) mentions a mean group size of 33 in the forests of the Lopé Reserve, and Tutin *et al.* (1997) a mean of 29 in the gallery forests and savanna bosquets of the same park. In Odzala N. P., where both hunting and logging are absent, three groups that visited a clearing during the day were composed of two, seven and three (later joined by a fourth) individuals. During the night a troop of about 40 individuals was observed twice (Magliocca 2000). In Lopé N. P., they sometimes aggregate into groups of more than 100 individuals (Abernethy & White 1999). Groups of 30–60 have been reported from Guinea and the eastern DR Congo (L. Macky & J.A. Hart pers. comm.). In areas with high logging and hunting pressure, Red River Hogs tend to occur in smaller, silent groups active only at night (Abernethy & White 1999). In non-disturbed areas they are also active during the day.

The degree of territoriality, mating system, family relationships and duration of association of adult ♂♂ with ♀♀ are not known. Observations in captivity show that ♂♂ regularly inspect the urine and the anogenital region of the ♀♀ to detect oestrus. The ♂ will follow an oestrous ♀ as she walks around and will regularly nuzzle her vulva, flanks and belly. The ♀ licks the anal and inguinal region of the boar. De Boer (1980) also describes a playful head to head pushing as an element of courtship behaviour. A ♀ that is ready for mating shows the typical immobilization reflex prior to and during mounting. Females leave the group to give birth and lie-up in an elaborate nest, 50–60 cm high and constructed of leaves and twigs (in the forest) and grasses (in savanna regions) (Malbrant & Maclatchy 1949, Abernethy & White 1999). They later re-join the group with their piglets. Red River Hogs are in almost continuous acoustic contact with one another. However, their rich vocal repertoire has never been studied.

Reproduction and Population Structure Analysis of faecal steroid metabolites in captive animals has revealed that reproductive cycles in the Red River Hog start by the end of Dec and last into the summer (Berger *et al.* 2006). In the wild, reproduction indeed appears to be seasonal with most piglets being born at the end of the dry season/onset of the wet season. In Gabon, Malbrant & Maclatchy (1949) found one ♀ with three fetuses in Mar and one with four in Dec. Oestrous cycle length is 34–37 days (Berger *et al.* 2006). An average of 3.4 piglets (range 1–6) is born after a gestation length of 120 days (Macdonald 2000). Piglets weigh 650–900 g at birth and are brown with beige-yellow longitudinal stripes and some spots. The piglets remain tightly huddled in the nest to limit heat loss for the first few days after birth. They soon start to follow the mother while she forages and start to nibble on food items she unearths or that fall from her mouth (Abernethy & White 1999).

Population structure, birth and mortality rates have not been published for wild populations, although Oduro (1989) recorded an immature to adult age ratio of 2 : 1 in groups in Nigeria. In captivity, the oldest zoo-born individual reached an age of 18 years. One wild-caught animal lived at Frankfurt Zoo for 22 years before it died (Winkler 2000, Weigl 2005). However, most individuals probably do not live longer than 15 years (Winkler 2000).

Predators, Parasites and Diseases In rainforest habitat, Leopards *Panthera pardus* prey on adult individuals (Hart, J. A. *et al.* 1996, Abernethy & White 1999), and Red River Hogs made up 20% of the biomass consumed by Leopards in Lopé N. P. (Henschel *et al.* 2005) and up to 50% in Ivindo N. P., Gabon (Henschel *et al.* 2011). Other potential predators include Lions and Spotted Hyenas (Abernethy & White 1999, Breuer 2005), while Robust Chimpanzees *Pan troglodytes* (Alp 1993, Abernethy & White 1999), large pythons and large raptors prey on piglets. Male Red River Hogs fiercely protect themselves and their group members from carnivores and can win a fight with a Leopard (A. Gautier-Hion pers. comm.). Like Bushpigs (Anderson *et al.* 1998), Red River Hogs are most likely vectors for African swine fever and allegedly also trypanosomiasis, and are an intermediate host for trichinosis (Vercammen *et al.* 1993). Ntiemo-Baidu *et al.* (2005) recorded the ixodid ticks *Ixodes cumulatimpunctatus*, *Rhipicephalus cuspidatus*, *R. lunulatus*, *R. simpsoni* and *R. ziemannii* on animals in Ghana.

Conservation IUCN Category: Least Concern. CITES: Not listed.

Although generally widespread and abundant, increased hunting pressure (for subsistence purposes, as an agricultural pest or because it is a vector of livestock diseases, and also for the commercial bushmeat trade) has made the species rare outside protected areas in a number of countries, particularly in the west and north of its range (Vercammen *et al.* 1993, Abernethy & White 1999). At the bushmeat market of Basankusu, DR Congo, 38% of the 13,831 carcasses recorded in 276 counting days were artiodactyls and of these 21% were Red River Hogs (J. Dupain pers. comm.). Seventy-eight per cent of hunters interviewed in Gabon by Lahm (1991) cited the sale of Red River Hog meat as among their most important sources of revenue; only about one-third of their gained bushmeat

was retained for domestic consumption. Consequently, hunting has led to direct declines in abundance in, for example, the forests of S Gabon (Laurance *et al.* 2006); however, Red River Hogs seem to stand up to hunting pressure relatively well in other regions (e.g. DR Congo; J.A. Hart pers. comm.), although this requires further study.

Measurements

Potamochoerus porcus

HB (♂ ♂): 1113 (1030–1190) mm, n = 6

HB (♀ ♀): 1070 (940–1170) mm, n = 11

T (♂ ♂): 433 (405–455) mm, n = 6

T (♀ ♀): 418 (395–435) mm, n = 8

HF c.u. (♂ ♂): 242, 260 mm, n = 2*

HF c.u. (♀ ♀): 235 mm, n = 1*

E (♂ ♂): 190, 205 mm, n = 2*

E (♀ ♀): 180 mm, n = 1**

WT (♂ ♂): 63.0 (51.0–80.0) kg, n = 6

WT (♀ ♀): 43.5 (33.0–56.0) kg, n = 11

Gabon (Malbrant & Maclatchy 1949)

*AMNH (D. Lunde pers. comm.)

**MRAC (W. Van Neer pers. comm.)

Record tusk length is 279 mm for an animal from Gabon (Rowland Ward)

Key References Abernethy & White 1999; Grubb 1993b; Hart 2001; Magliocca 2000; Malbrant & Maclatchy 1949; Oduro 1989; Vercammen *et al.* 1993.

Kristin Leus & Paul Vercammen

GENUS *Hylochoerus*

Forest Hog

Hylochoerus Thomas, 1904. Nature 70: 577.

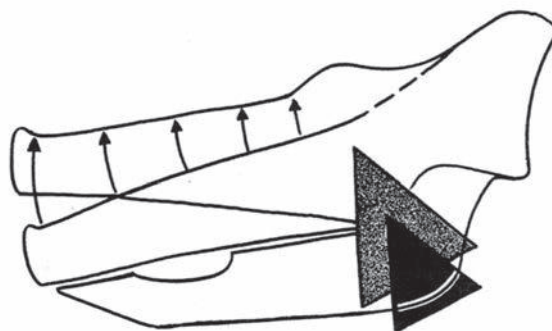
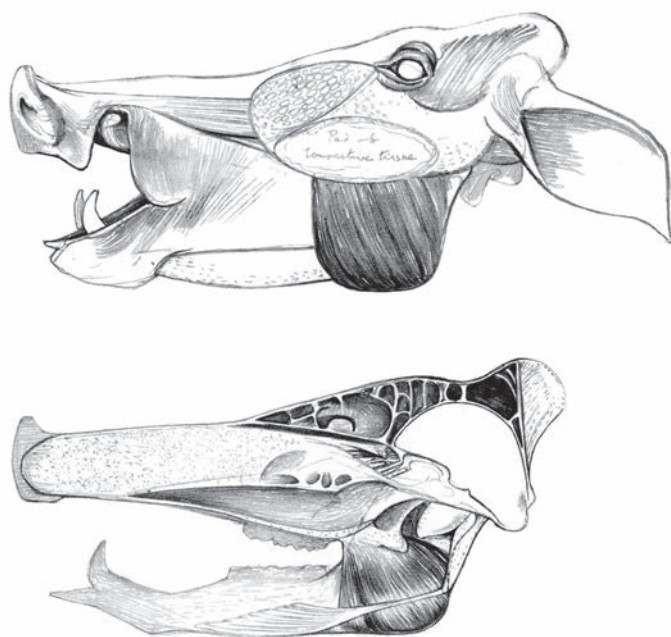
Hylochoerus is a monospecific genus, represented only by the Forest Hog *H. meinertzhageni* that has been, from the first, recognized as generically different from any other type of pig. The teeth and skull, in particular, differ in many ways from those of other, rootling suini

such as Wild Boars *Sus scrofa*, or bushpigs of the genus *Potamochoerus* (Ewer 1958, Harris & Cerling 2002). None the less, the functional significance of these peculiarities was not well understood at first (Thomas 1904).

In the century since the Forest Hog was first described, many suid fossils have been discovered and some of these, notably fossil skulls of the polymorphic *Kolpochoerus heseloni*, have helped illustrate the evolutionary divergence, within Africa, of this genus from a more



Forest Hog *Hylochoerus meinertzhageni* head of female (left) and male (right).



LEFT: Forest Hog *Hylochoerus meinertzhageni* head: above, superficial myology; below, cross-section showing digastric muscle.

ABOVE: Diagram of upward flexion in Forest Hog *Hylochoerus meinertzhageni* skull from less elevated ancestral condition (from Kingdon 1979).

typically suid ancestry. White & Harris (1977) have suggested that *Hylochoerus* derived during the Pleistocene from the Plio-Pleistocene fossil pig lineage *Kolpochoerus*. When correlated with known behaviour, ontogenetic growth patterns and with evolutionary changes manifest in the skulls of fossil pigs, almost all the unique features of *Hylochoerus* cranial anatomy can be attributed to a relatively recent change in diet (Ewer 1970, Kingdon 1979).

Unlike their closest, rootling relatives, *Hylochoerus* are surface-cropping animals, harvesting herbs and grasses with their capacious mouths and broad, sharp-edged lips. The teeth have also been modified for such cropping but all these changes are likely to have been relatively late, Pleistocene, developments (Harris & White 1979) and manifest quite clumsy improvisations in the service of a relatively new mode of mastication superimposed upon an older suine pattern. It can be shown that alterations in the balance of masticatory muscle forces and muscle attachments have led to expansions, contractions, tilts and bucklings in the skulls of *Hylochoerus*.

Typically, suine molar teeth have thick enamel cusps that are well suited to crushing large fibrous material, such as roots, and cement is virtually absent in such hard, compact teeth. Rootling pigs have six teeth aligned down a long, relatively narrow tooththrow that champs up and down in a predominantly vertical action. This exerts little or no lateral pressure on the teeth. By contrast, *Hylochoerus* have higher crowns with thin dentine and enamel spaced out within a thick matrix of cement (Ewer 1970). Wear on such teeth produces sharp ridges and this creates the sort of milling surfaces typical of leaf-eating teeth. However, instead of retaining a complete tooththrow of six chewing teeth, *Hylochoerus* juveniles begin with a row of five teeth, the anterior ones of which are soon shed. This attrition of the premolars (and eventually of the first molar, too) is due to *Hylochoerus* masticating its food with a significant sideways action. This lateral action exerts more movement at the front end of the tooththrow, less at the back. It is clear that the small premolars are ill-suited to withstand the pressure and lateral chewing effectively wears away and gouges out the premolars at a relatively early age.

The main power for this novel type of jaw movement comes from the pterygoid muscles that attach the lower mandible to the roof of the mouth (see Kingdon 1979). To operate effectively these muscles (which are exceptionally well developed in *Hylochoerus*) have several requirements: (1) an increase in the amplitude of their partly lateral action; (2) enlarged muscle size; and (3) an increase in their areas of attachment to the mandible and pterygoid. In addition to these changes, the abandonment of rootling in favour of cropping has greatly diminished the need for powerful leverage at the occiput, which is broad, but very short in *Hylochoerus*. The most obvious results of these alterations have been to broaden the back of the skull and bulk out the region immediately behind the tooththrows. These changes, in turn, have had the phylogenetic effect of lifting the entire tube of the muzzle in relation to the basicranial axis, making the Forest Hog skull, relative to that of a rootling pig, more of a horizontal tube than a diagonal wedge. These functional changes in core regions of the skull's interior have remoulded the plastic, malleable surfaces of the skull's outer shell. Thus, the area between and immediately anterior to the eyes has been forced to 'buckle' outwards as the muzzle lifts. Shrinkage of the occiput has caused the forehead region to cave in and create a deep concavity above the cranium.

The skull of *Hylochoerus* is, therefore, an outstanding example of how changes in a single parameter, in this case diet, have far-reaching effects on cranial structure. The likelihood that these innovations are quite recent suggests that some characteristics, such as early loss of premolar teeth, merely represent incomplete accommodation, by an earlier format, to entirely new challenges. Those challenges would seem to have included an increase in the extent and predictability of formerly closed forests as they became more fragmented, perforated or degraded by a variety of forces, notably drier, colder climates, the actions of elephants, humans and falling trees, and the spread of low-level herbage and grasses in lacunae within these moist habitats. *Hylochoerus* is not, therefore, perfectly adapted to its niche but can, in some respects, be described as the cobbled-together descendant of a lineage that abandoned successful earlier adaptations in response to changing circumstances.

Jonathan Kingdon

Hylochoerus meinertzhageni FOREST HOG (GIANT FOREST HOG)

Fr. Hylochère; Ger. Riesenwaldschwein

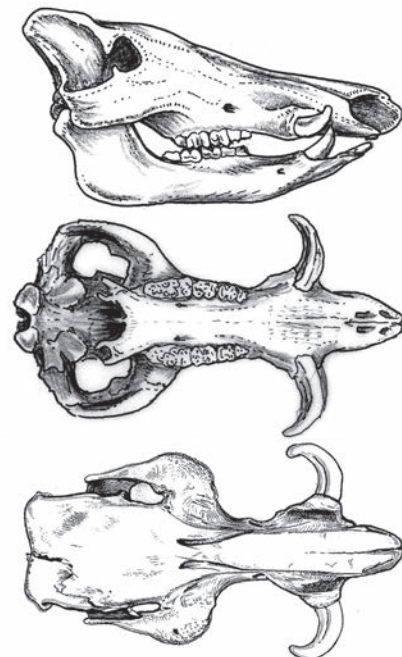
Hylochoerus meinertzhageni Thomas, 1904. Nature 70: 577. Kenya, 'Nandi Forest, near the Victoria Nyanza, at an altitude of 7000 feet'; near Kaimosi [2134 m].



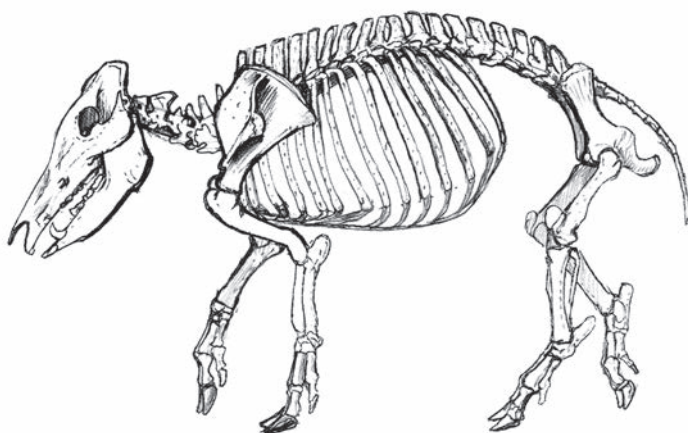
Forest Hog *Hylochoerus meinertzhageni*.

Taxonomy Despite its large size, the Forest Hog was the last wild pig – and one of the last large mammals – to be discovered in Africa. Between 1904 and 1930 seven subspecies were described, but recent taxonomic reviews (Ansell 1972, Grubb 1993b, 2005) only recognize three subspecies. The validity of one subspecies, *H. m. schulzi*, has been refuted by Mohr (1942), and shown to be a synonym of *Potamochoerus larvatus hassama* (Grimshaw 1998, Kock & Howell 1999). Pigs of this genus therefore belong to a single extant, polytypic species. Originally named Forest Pig, *Hylochoerus* was later qualified as 'Giant' Forest Hog, in reference to its great size in comparison with other wild pigs. However, it has been shown that only the nominate subspecies, *H. m. meinertzhageni*, truly deserves this epithet. All living *Hylochoerus* populations are substantially smaller than their prehistoric ancestral stock. Synonyms: *gigliolii*, *ituricus*, *ituriensis*, *ivorienensis*, *rimator*. Chromosome number: $2n = 32$ (Melander & Hansen-Melander 1980).

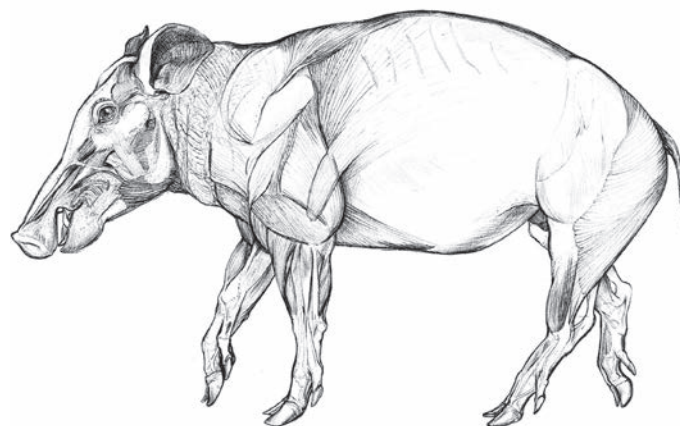
Description A large, heavily built pig covered in long black hair. Hair thickness, length and colour vary with age and location: the dorsal and lateral pelage is thick and dark brownish-grey to coal-black; 'whiskers' on jaw-line callosity white to yellowish; ventral pelage sparse and greyish to black. There is a dorsal crest of long, thick erectile hair. Hairs thick, oval in cross-section, and often split.



Lateral, palatal and dorsal views of skull of Forest Hog *Hylochoerus meinertzhageni*



Forest Hog *Hylochoerus meinertzhageni* (female) skeleton.



Forest Hog *Hylochoerus meinertzhageni* (female) myology.

Broad, pointed ears fringed with black hair. Small orange-brown eyes, but very pale irises also occur, possibly reflecting nutritional or social stress (J. Kingdon pers. obs.). Adult boars significantly larger than ♀♀, with a more bulky body and massive head; a dish-like depression over the forehead is surrounded by a circle of bony crests covered with bare skin. Zygoma are thickened and pneumatized, supporting inflated and naked infraorbital swellings. In boars these swellings commonly become stained with exudates from the preorbital glands which drain from a deep tear duct. The broad, flat snout ends in a very wide (10–15 cm), oval and swollen rhinarium with nostrils set wide apart. Legs robust (but can look spindly by comparison with the body mass); hooves large and rounded. Tail slender, flattened at its end, with long sparse bristles implanted laterally. Piglets are plain coloured, although dark-brown individuals with light-brown stripes have been reported (Grubb 1993b). Females have two pairs of nipples.

The skull is broad when compared with that of *Potamochoerus*. Structure of the skull and facial musculature adapted to a folivorous rather than an omnivorous diet (Ewer 1970; for dissections and diagrams see Kingdon 1979). The dental formula is $I^{1/3}, C^{1/1}, P^{2/1}, M^{3/3} = 30$; the single pair of upper incisors is often shed in adults. Tusks flare out horizontally and curve backwards in the same plane as the face. Dentition is hypsodont and much more specialized than in *Potamochoerus*, with molar cusps of the crown spaced out within a thick matrix of cement and sharp transverse ridges between enamel pillars. The anterior cheekteeth tend to be lost with age.

Geographic Variation Three subspecies are provisionally retained, but most specimens appear to represent variants in a polymorphic species. Smaller specimens predominate in the western and central lowland forests, heavier ones in highland forests, east of the Rift Valley.

H. m. ivoriensis: isolated populations from Guinea to S Ghana. Does not differ significantly from *H. m. rimator* in dimensions or features (length of skull in ♂♂ is 35.5–39.7 cm, and 33.3–37.2 cm in ♀♀; Grubb 1993b), but the shape of the skull is distinctive and unlike that of other subspecies.

H. m. rimator (includes *ituriensis*): SE Nigeria to E DR Congo. Specimens from the western part of the range are on average smaller (length of skull 34.1–38.8 cm in ♂♂, and 33.0–37.7 cm in ♀♀; Grubb 1993b) than those from further east (length of skull 36.6–49.5 cm in ♂♂, and 31.4–43.9 cm in ♀♀; J.P. d'Huart, pers. obs.). Distinctly smaller and lighter than *H. m. meinertzhageni*, with more brown and yellowish hair in pelage.

H. m. meinertzhageni: scattered populations from Albertine Rift Highlands of E DR Congo to Kenyan Rift Valley. Resembles *rimator* in shape of skull, but nominate race differs in its jet black pelage, larger size (length of skull 41.0–46.1 cm in ♂♂ and 38.1–42.7 cm in ♀♀; Grubb 1993b) and size of the tusks. The cheekteeth are also different in that the cementum is developed at the expense of the enamel pillars, which are more widely separated (Grubb 1993b). Intergradation between the lowland forest *rimator* and this large highland race presumably occurs along the foothills of the Albertine Rift (Grubb 1993b).

It is probable that Ethiopian Forest Hogs are derived from a common stock with *meinertzhageni*; however, given a wide separation of these two populations by a well-established eco-climatic boundary, d'Huart (1978) and Yalden *et al.* (1984) have suggested that it is possible that the Ethiopian population comprises a different, as yet undescribed, subspecies.

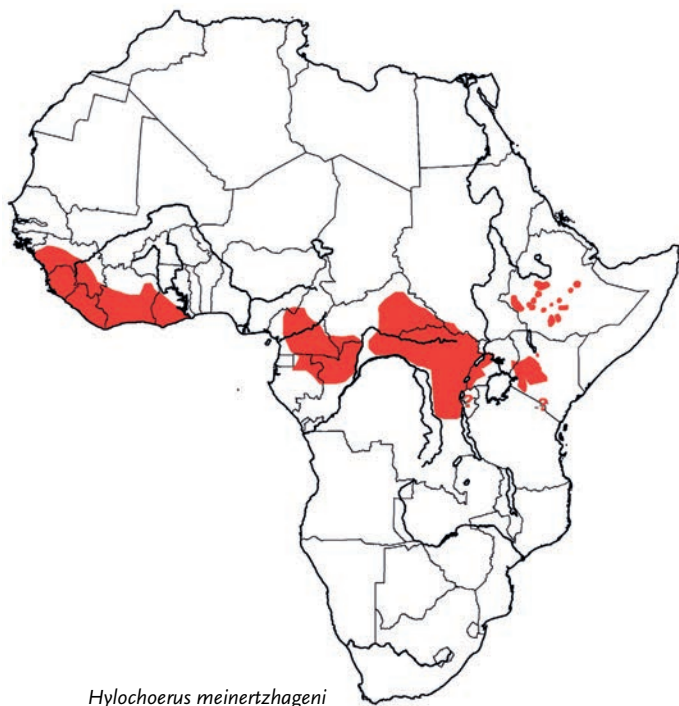
Similar Species

Potamochoerus larvatus. Sympatric in some localities in eastern Africa.

Smaller and more compact, with pale pelage on face and nuchal/dorsal crest; snout less swollen.

Distribution Endemic to Africa. Unevenly distributed in scattered populations throughout undisturbed tracts of lowland rainforest in West Africa and on the right bank of the Congo R. Also present in transition gallery forests in the Guinean savanna zone, in highland mixed forests of Albertine Rift, and in isolated montane forests in Kenya and Ethiopia. Their range resembles that of the Bongo *Tragelaphus eurycerus*, which also exploits unstable forest-edge mosaics.

In West Africa (S Guinea, Liberia, S Côte d'Ivoire, S Ghana), the range of *H. m. ivoriensis* now roughly corresponds with the least

*Hylochoerus meinertzhageni*

disturbed remnants of the lowland humid forest. The species may occur in other parts of Guinea, Sierra Leone and Côte d'Ivoire in montane forests (e.g. Mamou Mts, Foutah Djallon, Loma Mts) and in gallery forests (Outamba N. P., Comoé N. P.), but many records remain unsubstantiated (e.g. see Grubb *et al.* 1998). Forest Hogs have been extirpated from many intervening sites that connected primary forest and Guinean savanna. Their present distribution has become increasingly fragmented, though the full extent and pace of this process is difficult to document because this species is a premium target for the rapidly expanding bushmeat trade. Reports from Senegambia, Guinea-Bissau and Togo are unsubstantiated (Grubb 1993b, Grubb *et al.* 1998).

Western populations of *H. m. rimator* (those between the Rivers Niger/Bénoué and Congo/Oubangui) still occur in five countries from the Nigeria/Cameroon border to N Gabon, N Congo and SW Central African Republic. The species is absent from Bioko I. and is believed to be extinct in the vicinity of Rio Muni in Equatorial Guinea. Forest Hogs have also disappeared from many areas in W Gabon and S Congo. Further east, this subspecies remains almost continuously distributed along the right bank of the Congo R. to the southernmost limits of the equatorial forest in E DR Congo in the south, to extreme N and NE DR Congo, E Central African Republic and SW Sudan in the north. It occurs in all types of primary, secondary and gallery forests. The northern limit of its range is in the vicinity of Massif des Bongo, south of Manovo–Gounda–St Floris N. P. in Central African Republic, where the progressive fragmentation of the forest galleries is likely to isolate this population in the future. This subspecies has disappeared from several sites in N Central African Republic and NW DR Congo.

In the easternmost limits of the Forest Hog's range (along the west branch of the Rift in E DR Congo, W Uganda and Rwanda, and along the east branch in E Uganda, W and C Kenya), the 'giant' form, *H. m. meinertzhageni*, now survives only in isolated montane forests, from 900 to 3800 m. There have been no records of *Hylochoerus* from

Rwanda since the late 1980s (B. Dowsett pers. comm.), but they may possibly survive in Nyungwe Forest. In the absence of reference specimens or photographic records, Forest Hogs are no longer considered to occur in Tanzania (Grimshaw 1998, Kock & Howell 1999). Some connecting corridors still exist within the complex of protected areas from the Rwenzori Mts in the north to the Virunga Mts in the south, but most of the remaining populations in this region are now isolated. A similar situation occurs in SC and WC Ethiopia (d'Huart & Yohannes 1995), where fragmented subpopulations are well isolated from the nearest neighbouring populations of Sudan, Uganda and Kenya.

Habitat In common with the Red River Hog *Potamochoerus porcus*, the Forest Hog is more dependent on forest than other African suids. Throughout its range, it inhabits a wide variety of forest types, ranging from sub-alpine areas and bamboo groves through montane to lowland and swamp forests, galleries, wooded savannas and post-cultivation thickets. Within these habitats, it occurs preferably where there is a convenient and permanent water source, thick understorey cover in some parts of the home-range, and a diversity of vegetation types.

In E DR Congo and W Uganda, the Forest Hog is an ecotone species, preferring intermediate habitat zones where the edge effect is maximized and where resources from different vegetation types can be exploited within a limited area. This was well illustrated in Budongo, Uganda, where Kingdon (1979) mapped a 1600 km² block of mixed wooded grasslands, forest, forest/ woodland mosaics and cultivation where he established the local ecological separation of *Hylochoerus*, *Potamochoerus* and *Phacochoerus*. The former shared habitat with one or other, or both species in areas where uniform forest and grasslands abutted, but *Hylochoerus* became dominant only in areas of extensive forest/grassland mosaic. In the Aberdare Mts in Kenya, the Forest Hog was extremely abundant during the 1970s and, over a period of five years (1970–1974), a total of many hundreds of sightings were recorded visiting Yathabara glade (a major waterhole/salt-lick in the Aberdare Mts of C Kenya). By contrast, there were only two sightings of Bushpigs *P. larvatus* and it is possible that competition for secure shelters (within a montane forest that was freckled with numerous small, grassy glades) might

Forest Hog *Hylochoerus meinertzhageni*.

have been the primary cause of this imbalance between species (Kingdon 1979).

In the central plain of Virunga N. P., Forest Hogs inhabit forest galleries (dominated by species of the genera *Croton*, *Pterygota* and *Rauwolfia*), dry forests (*Euphorbia*, *Olea*) and bush thickets (*Capparis*). These three habitats constitute a sequence in the natural succession from forest to savanna, and the hogs move between them, making full use of their resources. During the 1980s and early 1990s, Forest Hogs from forested areas of the central part of Queen Elizabeth N. P. (Uganda) increased and extended their range into grassland/thicket mosaic areas, including the Mweya peninsula (Viehl 2003, Klingel & Klingel 2004a, b). In dense forest areas, Forest Hogs tend to concentrate in inselberg mosaics of savanna and forest, around clearings, or in mixed forest patches rather than in monodominant forest (Hart 2001).

On a continental scale, the variety of forest habitats occupied implies a high degree of adaptability to local climatic conditions. Forest Hogs live in cold uplands (where night temperatures may fall to 0°C) as well as hot lowlands, but do not tolerate low humidity or prolonged solar radiation. Extreme mean annual rainfalls in *Hylochoerus* habitat vary from 800 mm in Masai Mara National Reserve to 3200 mm in W Liberia.

Abundance A 1990 IUCN questionnaire survey suggested that this species had a restricted distribution at low density over most of its range, but was 'widespread at low density and locally abundant' in Guinea and Côte d'Ivoire, and 'widespread at high density' in Congo. The value of such assessments is obviously limited without further detail and validation, and, in any event, hog abundance has been widely reported to fluctuate over time (due to rinderpest outbreaks, and increases or declines in the number of predators). Until recently, the only explicit population density estimates came from DR Congo and these ranged from 0.4/km² in Garamba N. P. to 2.6/km² in the central plain of Virunga N. P. (d'Huart 1978). Local population densities may be much higher though, since these estimates were based on spot counts over large areas. Between Sep and Oct 1975 Kingdon (1979) estimated about 70 individual forest hogs coming into Yathabara glade from an estimated catchment area of about 70 km² (a density of about 10/km²). Since that time (when the density of this species was thought to have been the highest ever known in the area), Forest Hogs are known to have declined throughout the Aberdare Mts, primarily due to an influx of Lions *Panthera leo* (Klingel & Klingel 2004b); the neighbouring hog population on Lion-free Mt Kenya has seen no such decline.

A 1998 count of known individuals on the very localized Mweya Peninsula, Queen Elizabeth N. P., gave a density of 9–13/km² (H. Klingel pers. comm.). However, Klingel & Klingel (2004a) subsequently recorded a 30% fall in the density of Forest Hogs on the Mweya Peninsula; in two other study areas, the decline was 70–80%. The main cause of decline was predation by Lions, Spotted Hyaenas *Crocuta crocuta* and Leopards *Panthera pardus*, with competition from other herbivores, nutritional stress, diminished reproductive recruitment, emigration and road kills given as further causes. A 1999 sample transect census of Jibat Controlled Hunting Area near Ambo, Ethiopia, suggested a figure of 8.25/km² (F. Kebede pers. comm.). Comparable densities emerged from the frequency of observations and recorded group sizes in areas of suitable Forest Hog

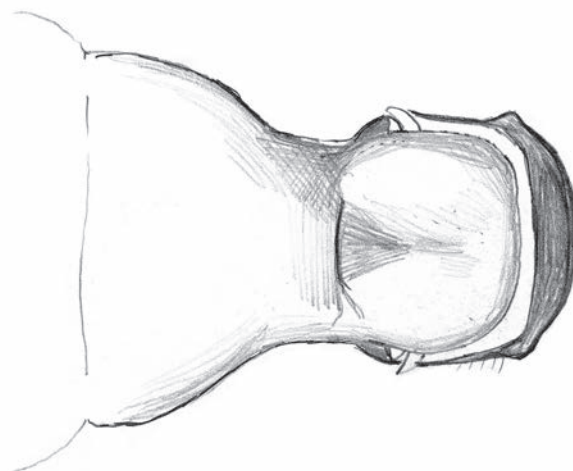


Forest Hog *Hylochoerus meinertzhageni* tooth succession from left: juvenile, adult and aged adult.

habitat in Virunga N. P. and Queen Elizabeth N. P. (K. Viehl pers. comm.).

Seasonal mass movements have been noted in forest clearings in N Congo (R. Ruggiero pers. comm.), and also in the Epulu Forest (Hart 2001). These have been attributed to masting cycles or similar fluctuations in the availability of grasses and other foods. Other explanations have been proffered, but documentation has been poor.

Adaptations Features of fossil ancestors of *Hylochoerus* show that grazing is a relatively late development in this species and that some members of its ancestral lineage may have been substantially larger than the living species. Grass-eating has involved the need for powerful lateral chewing, and shaped the molars in a unique design (Bouet & Neuville 1930). These molar adaptations are very distinct from, and somewhat intermediate between, those of *Phacochoerus* and *Potamochoerus*. In the course of evolution the muscles and bony anchorage needed to support this has caused massive realignments in the skull (Ewer 1970, Kingdon 1979). The most significant of these has been the role of greatly enlarged pterygoid muscles (which serve side to side mastication). This enlargement appears to have acted as an 'evolutionary wedge' opening up the base of the skull, lifting the muzzle and buckling the external bones of the forehead. Thus, the external modelling of the Forest Hog's forehead can be attributed to evolutionary changes in diet and masticatory function (see diagrams in Kingdon 1979).



Forest Hog *Hylochoerus meinertzhageni* underside of lower jaw.

The Forest Hog's huge bulbous rhinarium is rarely used for rooting; unlike *Potamochoerus*, its prenasal bone is progressively losing its mobility by fusing with the intermaxillary septum, making the massive snout quite unsuited for excavating food from hard soil. By discarding use of the rhinarium for digging in all but the softest soils, the Forest Hog's mouth has adapted more fully to grazing, involving a reshaping of

the lips, the tusks and the nasal disc. Skull features are well adapted to competitive and fighting techniques by involving two different, often sequential, forms of frontal combat (Kingdon 1979, Estes 1991a). In the 'snout-ramming/knocking' phase adult and subadult ♂♂ join their broad nasal discs with heads horizontal and then test their weight and strength by pushing; during sparring matches between young ♂♂, both snouts are often pushed upwards, but contestants also deliver sideward blows and try to push the opponent's snout to the side. This form of contest is facilitated by the slightly bulbous, flat-fronted nasal disc and the reinforced median wall of the snout. In the 'forehead butting' phase mature ♂♂ depress their heads and press their massively reinforced foreheads together and push until one withdraws. Sometimes contestants charge each other from a distance, in which case a very loud cracking noise can be produced should their foreheads clap together in exact opposition and thus compress air between their cupped foreheads. Thick protective tissues on the cheeks, heavy hollowed ridges round the forehead and zygomatic arch, a 'double-hulled' cranium (see Kingdon 1979) and the wide curving angle of the tusks can absorb or deflect the impact of these powerful clashes, but skull fractures, and occasionally deaths, can and do occur.

The comparatively thick skin and coarse pelage with sparse hair (intermediate between the dense pelage of *Potamochoerus* and the bare skin of *Phacochoerus*) are adaptations that allow Forest Hogs to live in extreme environmental conditions both in closed and open habitats. Their activity patterns and feeding behaviour are adapted to both open and forested areas. In the grassland/bushland/dry forests mosaic of Virunga N. P., Forest Hogs spend on average 25% of their daily time moving and foraging in savanna, 21% moving, foraging and wallowing in thickets or forested areas, and 54% resting in a sleeping site in the same habitat (d'Huart 1978). In lowland forest (notably in the Maya clearing of Odzala N. P., Congo), Forest Hogs spend 44% of the time feeding, 14% moving and 31% resting (F. Magliocca pers. comm.). In Queen Elizabeth N. P., during the wet season, the hogs feed during the day (as well as wallowing) and sleep at night, whereas they spend much of the day and part of the night feeding during the dry season, particularly if fresh growth is scarce, and may retreat to the lake-side when drought becomes extreme (Klingel & Klingel 1999). In the montane forest of Aberdares N. P., Kenya, the frequency of daylight sightings in Yathabara glade (from 5% to 27% in 1974) is inversely correlated with temperature; daylight foraging was commonest between Apr and Nov and minimal during the hot season, between Dec and Mar (Kingdon 1979). In the salines of Odzala-Kokoua, Nganongo (2000) observed the hogs wallowing in mudpools during the heat of the day, confirming this species' intolerance of prolonged direct exposure to the sun. Social activity in Forest Hogs is strongly influenced by climate and season. Klingel & Klingel (2004b) found all members of family groups joined up in the wet season, stayed close together and synchronized activity when they rested, wallowed or walked, whereas they could split up, sometimes for several days, during the dry season.

Foraging and Food Mainly a grass-eater and folivore. Field observations of feeding habits clearly document that Forest Hogs are by no means pure grazers. Depending on the seasonal content, stage of growth, and quantity of plant resources available in the various portions of their territory, they seem to display a great versatility

in the selection of their food. Both in montane areas and forest/grassland mosaics, many species of grasses, sedges and herbs are cropped. Forest Hogs rootle very much less than other wild pigs and dig only in very soft or muddy soils.

In Queen Elizabeth N. P., on the Mweya Peninsula, Giant Forest Hogs eat 46 of the 115 plant species that have been recorded there (Klingel & Klingel 2004a). In a savanna area of the same park, Forest Hogs were found to select more than 100 food plants and show a high flexibility in choice (Viehl 2003). In central and East Africa, Forest Hogs prefer to browse herbaceous growth or graze on mats of relatively short green grass. Among the monocotyledons, several species of Commelinaceae and Cyperaceae are grazed in addition to a large number of Gramineae. The selected dicotyledons include, among others, numerous species in the families Acanthaceae, Amaranthaceae, Compositae, Convolvulaceae, Euphorbiaceae, Melostomaceae, Portulacaceae, Urticaceae and Salvadoraceae (Rahm & Christiaensen 1963, d'Huart 1978, Kingdon 1979).

Studies on grass preferences in Virunga N. P. show that five major savanna species (*Cynodon dactylon*, *Sporobolus pyramidalis*, *Panicum repens*, *Cenchrus ciliaris* and *Chloris gayana*) were selected on a yearly average during 94% of grazing time (d'Huart 1978). Seasonal preferences by *Hylochoerus* for these grasses is less marked than those shown by *Phacochoerus* in contiguous Queen Elizabeth N. P., but the same grasses are selected by both pigs during the same periods (Field 1970b, d'Huart 1978). However, preferences for the same grasses are not repeated during each of both dry and wet seasons. In Virunga N. P., an order of preference (the same for both dry and wet seasons) was established by correlating the frequency of selection time with the protein and carbohydrate content of the grasses; these data showed that hogs select grasses when their nutrient and energetic content is highest (d'Huart 1978). A study on carbon isotopic composition of *Hylochoerus* hair from the Mweya Peninsula has confirmed this observation, estimating that Forest Hog diet actually comprised more than 95% of C₃ dicotyledons over much of the year, but that the proportion of C₄ grasses rose up to 25% in the wet season (Cerling & Viehl 2004). Young piglets are known to feed on grasses well before weaning.

In dense forest both Forest Hogs and Bongos feed on mast seed in monodominant *Gilbertiodendron* stands in N Congo, but not in E DR Congo (Hart 2001). Of the time hogs spent (mainly in water-logged areas) in a forest clearing in Odzala N. P., 44% was spent feeding on herbaceous plants from hydromorphic areas; these plants, *Enhydra fluctuans*, *Paspalum conjugatum*, *Ludwigia stolonifera* and *Rhynchospora corymbosa*, were significantly richer in calcium and nitrogen than those growing in non-preferred ones and it was concluded that mineral-rich forage was the essential reason for hogs to visit the natural clearings (bais) (actual drinking was never observed; F. Magliocca pers. comm.).

Examination of adult hog dung by various authors has revealed a variety of different materials, including poorly masticated grass stems and leaves, fragments of *Iulus* sp., shields of ticks (*Amblyomma* spp., *Rhipicephalus* spp.), earth, Forest Hog bristles and so forth. The animals seek salty earth, which they excavate with their tusks and their lower incisors; salt-licks may include termite mounds, shallow caves, dry river banks, or even the embankment of a deserted road. Occasionally, they eat meat and bones of carrion, eggs and larvae (Kingdon 1979). Coprophagy is not common, but piglets are fond of fresh elephant dung when available.

Social and Reproductive Behaviour Forest Hogs live in relatively stable, non-territorial family groups (or 'sounders') consisting of one to three (occasionally four) ♀♀ and their young, and a dominant adult ♂. In Queen Elizabeth N. P., group sizes range from 2 to 19 individuals (very occasionally up to 24), with an average of 11.2 (Klingel & Klingel 2003, 2004b, H. Klingel pers. comm.). In contiguous Virunga N. P., average group size was 13.9 (d'Huart 1978). During the early 1970s in the Aberdare Mts, groups numbered 2–18 (average = 6.6); however, it was rare for more than four or five adult ♀♀ to associate for any length of time.

In the Aberdares population some individual boars maintained a stable relationship with a group of ♀♀, but some were effectively ousted during amalgamation episodes that were probably brief and may have been the direct product of convergence on a common resource, namely the artificial mineral lick in Yathabara glade (Kingdon 1979). These short-term displacements might give some support to the theory that dominance hierarchies may exist among ♂♂ observed within the same 'group'. Such 'groups', with up to four adult ♂♂ and at least eight adult ♀♀, have been recorded, but field observers agree that a single dominant boar does not accompany a sounder with more than four sows for any durable span of time. This may be primarily due to a weakening, as group size increases, of the familial bonds that tie sows to one another. Large groups consistently split into smaller groups and into small family units with a single boar predominating.

Generally, only alpha-males have access to the ♀♀, but copulations with peripheral individuals do occur outside the group (d'Huart 1978). In Virunga N. P., male tenures were recorded to last up to four years (d'Huart 1978), but in neighbouring Queen Elizabeth N. P., Klingel & Klingel (2004b) found the longest male tenure reached seven years. These researchers found infanticide was common immediately after a new ♂ joined a group, in spite of all ♀♀ attacking the boar when he pursued any of their offspring (Klingel *et al.* 2001). Paradoxically, such risk to their young must strongly favour females' maintenance of a long-term, stable relationship with one ♂. That this must be so is strongly implied by both sexes taking part in group defence, and by group cohesion being independent even of the alpha-male's physical presence (Klingel & Klingel 1999). Depending on local group dynamics or the overall density of hogs (particularly the relative numbers of adult ♂♂), the durability of male domination over specific groups of ♀♀ might vary or fluctuate from one locality or period of time to another, but the prevalence of infanticide, as revealed by the Klingels' studies, must strongly favour stable family groups (Fimpel 2002). In the Aberdares, between 1970 and 1974, Kingdon (1979) thought that, in general, groups of ♀♀ were not strongly attached to a single boar, but the apparent turnover of ♂♂ attending female groups might have been a local and temporary by-product of a very rapid hog population increase and equally rapid decline over the period of observation.

All studies have concurred that the *core* group of up to four adult ♀♀ is always stable, even in the absence of a dominant ♂; furthermore, with the exception of the alpha-male, all members of the group are directly related to each other. Indeed, younger ♀♀ patiently wait for aged sows and respond to the latter's 'lost' calls (Klingel & Klingel 2004a). While young ♀♀ stay all their life in the group, subadult ♂♂ leave it voluntarily at the age of 2–3 years and form small temporary bachelor groups until they can compete for



Forest Hog *Hylocherus meinertzhageni*.

the possession of ♀♀ and form their own sounder (d'Huart 1978, Klingel & Klingel 2004a). There are considerable fluctuations in the proportion of solitary animals, with a range of between 15% and 48% of all groups (in which singletons scored as a 'group') recorded at Yathabara glade. The number of Yathabara singletons, mostly boars, consistently peaked during periods of high temperature and declined, often very rapidly, when temperatures dropped (Kingdon 1979). A yearly average estimate of singletons among all hog sightings in Virunga N. P. was 17% (d'Huart 1978).

Occasionally, several groups gather and stay together for a few hours forming aggregations of up to 40 or 50 individuals (d'Huart 1978, Kingdon 1979). It is possible that under such circumstances the bonds between certain individuals and their original group break down and new links are formed. These transfers would effectively scramble the individual composition of groups, but Klingel & Klingel (1999, 2004a) have established that female groups are consistently made up of close relatives. Fights between ♂♂ for possession of groups give the impression of being unritualized frontal combats between bachelors or alpha-males from other groups (but see discussion under 'Adaptations'). These fights can result in severe injuries, including skull fractures (see Kingdon 1979) and male–male wounding can lead to significant mortality (d'Huart 1978).

Contacts between groups were rarely observed in Virunga N. P., but when they did occur interactions between individuals from neighbouring groups were usually peaceful and dominated by reciprocal curiosity (d'Huart 1978). In Queen Elizabeth N. P., antagonism between groups is not uncommon in the dry season and takes the form of female-on-female running chases followed by retreat (Klingel & Klingel 2004a). Such fights notwithstanding, neighbouring groups usually actively avoid contact. Young ♂♂, instead, are prone to frequent fights and fights between rival bachelors can go on for weeks; Klingel & Klingel (2004b) recorded as many as 40 head-on collision-fights in just 10 minutes!

Forest Hogs are not territorial as Mohr (1960) once suggested. Home-ranges were estimated to cover an area ranging from 2 to

5 km² in Virunga N. P. (d'Huart 1978). In Queen Elizabeth N. P., Klingel & Klingel (2004a) found that home-ranges covered several square kilometres with very extensive areas of overlap. At Yathabara glade the relative frequency with which particular groups were seen at the waterhole/salt-lick implied a graduated series of multiple, overlapping ranges, with those living nearest the glade being the most frequent visitors and the most distant ones the least frequent (Kingdon 1979). Rahm & Christiaensen (1963) estimated ranges of 7.5 km² in Kahuzi-Biega N. P., DR Congo. Although home-ranges are not marked or defended as territories, and neighbouring groups share at different times the use of the same elements (tracks, wallow, salt-licks, latrines), hogs do defend core areas during periods when food is scarce, as it often is during the dry season; adult ♀♀ are particularly defensive (Klingel & Klingel 2004b).

Dung is seldom dropped at random; favoured dung-sites are generally located at the base of a tree, under a thicket, or around a termite mound. The largest and most frequently used dung deposits are communal 'latrines' situated along access paths around the sleeping sites. The size and number of latrines near sleeping sites depend on the frequency with which the place is used and the size of the contributing group. For the positioning of latrines around typical sleeping sites see sketch-maps in Kingdon (1979).

Courtship is rough and noisy; once the boar has identified an oestrous ♀ he keeps close to her, grunting loudly, urinating frequently and butting her hindquarters and flanks with snout or forehead until she finally stands. Copulation lasts from 1 to 10 min. Females isolate themselves from the group for 2–5 days to give birth, and piglets are born in a dry nest under a dense bush or a stack of branches or hay. They stay close to their mother and suckle standing up (sometimes, and momentarily, while walking) and the piglets respect a teat order (K. Viehl pers. comm.). Lying down and allosuckling are uncommon. Female hogs have been reported to be rather careless mothers, and piglets are frequently kicked, pushed or stepped on (Schneider & Viehl 2000).

Forest Hogs have a wide range of vocalizations, including snorts, grunts and squeals; Fimpel (2002) and Klingel & Klingel (2004a) have recorded 18 different types of call, implying a highly differentiated auditory communication repertoire. Occasionally, Forest Hogs display aggressive and bold behaviour and family groups are known to chase away Leopards, Common Hippos *Hippopotamus amphibius*, Bongos and African Buffalo *Syncerus caffer*. However, they also graze peacefully next to African Buffalo, Savanna Elephants *Loxodonta africana* and various antelopes at Yathabara glade. In central Africa they commonly accompany Forest Elephants *Loxodonta cyclotis*, Western Lowland Gorillas *Gorilla gorilla gorilla* and African Buffalo on marshy bays (J. M. Froment pers. comm.), as well as Sitatungas *Tragelaphus speikii* and Red River Hogs (F. Magliocca pers. comm.).

Reproduction and Population Structure In Virunga N. P. and in neighbouring areas, mating takes place all year round, with a peak in Feb–Mar and Aug–Sep, at the start of the wet seasons. Births occur mainly in Jul–Aug and Jan–Feb when optimal grazing is available for lactating ♀♀ and growing piglets. Weaning occurs after 8–10 weeks. Litters of up to six piglets (average = 2.5 in Virunga N. P.) are born after a gestation period estimated at 18 (Asdell 1946, K. Viehl pers. comm.) to 21.5 weeks (d'Huart 1978). Litters of less

than four piglets account for 96% of field records, but as many as 11 offspring are known (Prickett, in Kingdon 1979).

Body growth is relatively rapid; adult size as well as sexual maturity are reached by both ♂♂ and ♀♀ at 18 months. No variation in female reproductive potential has been detected, and a yearly proportion of 46% of ♀♀ produce young. In the Virunga N. P. population, a reproductive potential of 113.6 young for 100 adult ♀♀ has been calculated. Net reproduction ratio suggests that each ♀ is replaced by 1.3 ♀♀, showing an increasing population in that area during the period of observation (d'Huart 1978).

In Queen Elizabeth N. P., the killing of piglets by newly arrived dominant ♂♂ seems to be sufficiently common to represent a major constraint on group dynamics, with up to 100% mortality in the litters of ♀♀ living with a newly established ♂ (Klingel *et al.* 2001). Although such incidents can be reliably inferred, it is rare for them to be observed directly so that the overall fertility of ♀♀ at parturition has probably been substantially underestimated.

Recorded sex ratios fluctuate between 1 : 1 and 1 : 2. The age ratio of the Virunga N. P. population is 67% adult (>18 months), 15% subadult (6–18 months) and 18% young. Seasonal changes in population structure are detected after the peaks of birth seasons. A mortality rate of 50–60% of piglets is estimated during the first year. It is mainly attributed to predation, but can also be due to weaning stress or to crushing by the mother. Additional mortality factors at adult age include fighting (♂♂), poaching, predation, parasitism and disease. Life tables suggest an average life expectancy of 3.5 years and an average life-span of five years, with a maximum of 18 years (d'Huart 1978).

Predators, Parasites and Diseases Major predators include Spotted Hyenas, Leopards and Lions. Large eagles prey on young piglets in savanna habitats. The high density of Lions in Aberdares N. P. would seem to have been the principal cause of a drastic Forest Hog population decrease since the late 1980s (Klingel & Klingel 2004b, R. Kock pers. comm.). Inversely, the expansion of the Forest Hog population in Queen Elizabeth N. P. is attributed to a temporary collapse of the Lion population combined with several years of high rainfall (H. Klingel pers. comm.).

Forest Hogs are hosts to a large number of ectoparasites, and a list of 11 species of ixodid ticks has been reported (d'Huart 1973). They are reportedly susceptible to rinderpest and populations have been greatly depleted by waves of rinderpest epidemics. Forest Hogs are also known to be a reservoir for African swine fever and trypanosomiasis, but their impact on the species is currently unknown.

Periodic toxicity in food plants (notably *Mimulopsis*) has been invoked for die-offs of Forest Hogs in the Mau forest, Kenya (Simon 1962).

Conservation IUCN Category: Least Concern. CITES: Not Listed.

The status of all West African Forest Hog populations is cause for concern, particularly given the high rates of forest loss and fragmentation in the region. Elsewhere, Forest Hogs are very vulnerable because widespread deforestation and illegal hunting for local consumption and a rapidly expanding bushmeat trade has led to declining numbers, and rapid fragmentation of subpopulations. In some areas of the Congo Basin, Forest Hogs are avoided by shotgun hunters because their flesh is considered to have an unpleasant taste, but this is by no means a widespread aversion nor is the taint widely recognized.

Hogs fall victim to snares and the meat is smoked to conceal its origin and sent to urban markets (R. Ruggiero pers. comm.).

Protected areas known to have important populations of Forest Hogs include: Sapo N. P. (Liberia); National Park of Upper Niger (Guinea); Taï N. P. (Côte d'Ivoire); Bia N. P. (Ghana); Odzala N. P. (Congo); Minkebe N. P. (Gabon); the Sangha Tri-National complex (Central African Republic, Congo, Cameroon), where large groups graze the bais; Maiko N. P., Virunga N. P. and Kahuzi-Biega N. P. (DR Congo); Rwenzori Mountains N. P. and Queen Elizabeth N. P. (Uganda); Aberdares N. P. and Mt Kenya N. P. (Kenya); and Bale Mountains N. P. (Ethiopia). During the 1940s, an exceptionally high concentration of Forest Hogs was reported to have developed in the area of Rutshuru (near Virunga N. P., DR Congo). A special hunting operation around Rutshuru was organized in 1945/1946 to reduce the populations of wild pigs, which were judged responsible for crop damage; some 77 Common Warthogs, 329 Bushpigs and 619 Forest Hogs were destroyed (Hoier 1952).

Both conservation (through captive breeding) and an obvious potential for domestication have been constrained by veterinary regulations designed to protect domestic pigs from any possible source of swine fever. This has led to extensive, but not always wholly rational, international bans on the import and export of wild pig species. The potential contribution of this grazing pig to protein

needs in Africa, under total or partial domestication, continues to be ignored in spite of increasing international calls to alleviate poverty.

Measurements

Hylochoerus meinertzhageni

HB (♂ ♂): 1374 (870–1900) mm, n = 7

HB (♀ ♀): 1172 (588–1780) mm, n = 6

T (♂ ♂): 318 (230–360) mm, n = 6

T (♀ ♀): 282 (105–380) mm, n = 5

HF c.u. (♂ ♂): 905 (790–1100) mm, n = 12

HF c.u. (♀ ♀): 828 (762–1000) mm, n = 10

E: n.d.

WT (♂ ♂): 177.4 (139.0–220.0) kg, n = 9

WT (♀ ♀): 150.6 (130.0–204.0) kg, n = 3

d'Huart (1978)

The longest tusk on record, measured from the base of the extracted tusk along the outer curve to the tip, from Semliki Forest, Uganda, measured 394 mm (Rowland Ward)

Key References d'Huart 1978, 1993; Grubb 1993b; Kingdon 1979; Klingel & Klingel 2004a, b.

Jean-Pierre d'Huart & Jonathan Kingdon

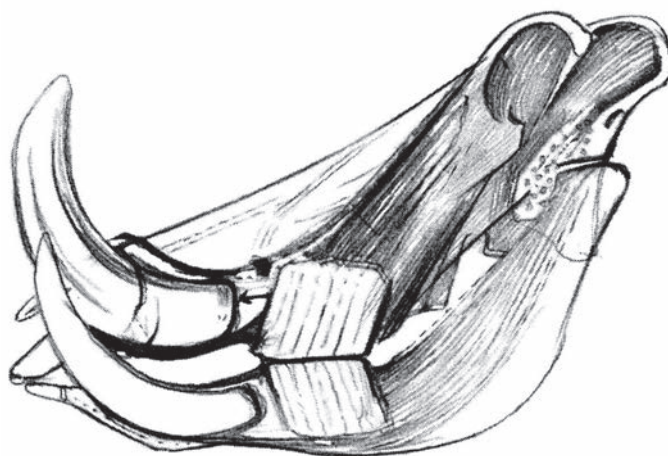
Tribe PHACOCHOERINI

Warthogs

Phacochoerini Gray, 1868. Proc. Zool. Soc. Lond. 1868: 47.

The warthogs may be readily separated from the rest of the extant suids on the basis of their complex, elongated and very high-crowned third molars – often the only cheektooth retained in mature and elderly individuals. Hypsodonty has been selected as an adaptive response to the consumption of more fibrous or abrasive plants in progressively more open and arid-adapted types of vegetation. Hypsodont grazing suoids were thought to be absent in western Eurasia, but Pickford (1988) recognized a suine tribe Hippohyini to accommodate the hypsodont Miocene genera *Hippohyus* and *Sivahyus* from the Siwalik Hills of the Indian sub-continent.

In Africa, three lineages of suids – the tetraconodont *Sivachoerus*–*Notochoerus* lineage plus species of the suines *Metridiochoerus* and *Kolpochoerus* – all displayed increase in size, height and complexity of the third molars through time, making them useful for biostratigraphic correlation (Cooke & Maglio 1972, White & Harris 1977, Cooke 1978a, Harris & White 1979). Kullmer (1999) compared the molar morphology of Plio-Pleistocene African suids with that of their extant counterparts and correlated increases in hypsodonty, length and complexity with adaptation to more open habitat and acquisition of a grazing diet. Harris & Cerling (2002) found, on the basis of stable carbon isotopes, that such a transition occurred during the Pliocene in the *Sivachoerus*–*Notochoerus* lineage, but that the earliest African representatives of the suines *Kolpochoerus* and *Metridiochoerus* were already well-established grazers. The diminutive *Metridiochoerus modestus* had a cranium that was very similar to that of *Phacochoerus*, but its teeth still retained the Y-shaped pillars that distinguish *Metridiochoerus* teeth from those of *Phacochoerus*.



Sectioned Common Warthog *Phacochoerus africanus* skull (old male) illustrating final position of third molars in maturity.

Contemporary warthogs are relatively small animals that probably derive from a still smaller immediate ancestor. However, some fossil Phacochoerini from the Plio-Plietocene were as large as small rhinoceroses, an enlargement possibly selected for as these pigs moved out into more exposed habitats.

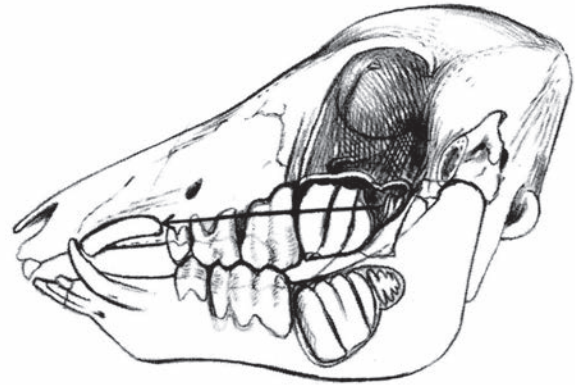
John M. Harris

GENUS *Phacochoerus*

Warthogs

Phacochoerus F. Cuvier, 1826. Dict. Sci. Nat. 39: 383.

Frontal views of: left, Common Warthog *Phacochoerus africanus* and right, Desert Warthog *Phacochoerus aethiopicus*.



Juvenile Common Warthog *Phacochoerus africanus* showing succession and migration of teeth indicated by arrows (from Kingdon 1979).

Phacochoerus includes two extant species, the Common Warthog *Phacochoerus africanus* and Desert Warthog, *P. aethiopicus*. Two species of warthog have long been recognized by palaeontologists (Van Hoepen & Van Hoepen 1932, Ewer 1956, 1957, 1958, Cooke & Wilkinson 1978); Cuvier (1817) also considered them different species, as did Cumming (1970). However, Lydekker (1915) placed all warthogs in one species and, subsequently, during most of the twentieth century, the Common Warthog has been incorrectly referred to as *P. aethiopicus*. The confusion has only recently been clarified with the discovery of an extant subspecies of the extinct Cape Warthog in Somalia, namely, the Desert Warthog (*P. aethiopicus somaliensis*) (Grubb 1993b, d'Huart & Grubb 2001). Divergence in mitochondrial and single-copy nuclear DNA sequences suggests differentiation as far back as the late Pliocene (Randi *et al.* 2002). The two species are distributed throughout wooded or open country of sub-Saharan Africa, and were present in North Africa during the upper Pleistocene. They are now absent from much of southern Africa, where their former extent of range is not well known. A comprehensive review of warthog systematics is provided by Grubb & d'Huart (2010).

Both species are diurnal graminivorous pigs, relatively hairless, with a sparse pelage of coarse bristles not concealing the body outline. 'Whiskers' of long white hair are present along the lower jaw, white hairs in the ears, and there is a long, thick dorsal mane starting between the ears and ending at the base of the tail. The legs are densely haired except for the carpal callus, and there is a terminal tail tuft. The characteristic physiognomy includes a broad snout, enormous canine tusks curving upward as well as laterally, facial warts, and orbits elevated and placed far back; hence, the eyes are at the top of the head providing a clearer and more extensive field of view especially when feeding. There are distinctive warts on the cheeks and just below the eyes, which are better developed in ♂♂, and contribute to absorbing blows and cushioning the skull during combat. Legs are slender, relatively longer than in other genera; hooves relatively narrow.

The skull in warthogs is transformed by adaptations for graminivory, and so differs strongly from that of members of the genera *Sus* or *Potamochoerus*. The lateral outline is wedge-shaped, slanted backward due to the downward flexure of the facial part in relation to the neurocranium. Zygomatic arches are very broad. The snout is much shortened in front of the tusks, not elongated and vertical-sided as in *Potamochoerus* because digging is of reduced importance. The condyle (on the long ascending ramus of the dentary) and glenoid lie well above the level of the toothrow, facilitating crushing or shearing of forage. The ascending ramus of the dentary slopes backward. The superficial masseter closes the jaw and pulls it laterally, producing a shearing action. Raising of the jaw joint is accompanied by a deepening of the maxilla, accommodating the hypsodont cheekteeth. The extreme anteroposterior compression of the postorbital region reflects the reduction of the temporalis muscle, a rapid masticatory action not being required for plucking grass. Paraoccipital processes are lengthened allowing the digastric muscle to act as a jaw opener, even though the neurocranium is raised above the dental arcade.

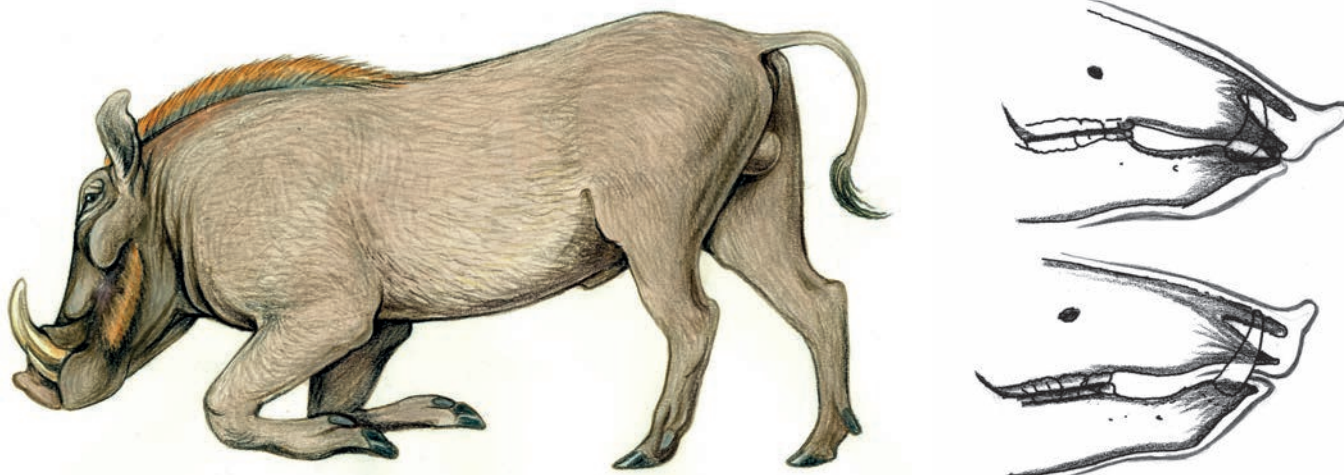
The adult dental formula is $I^{0-1/0-3}, C^{1/1}, P^{3/2}, M^{3/3} = 26-34$. Only the first upper incisors alone are (variably) retained. Lower incisors lie in a shelf-like projection of the dentary, or are impacted, not erupting above the gum. The tubular upper tusk sockets are directed forward and outward; the upper tusks are large, curling outward and backward above the level of the snout, and are not abraded at the tips by wear with the lower tusks, which are compressed, wearing against the anterior face of the uppers. The tusks of ♀♀ are relatively large compared with other genera. Premolars are reduced and together with the anterior molars, commonly shed in adulthood. Molars are hypsodont, and formed of well-cemented, closely packed, little-folded, oval to sub-triangular enamel columns; the third molar is considerably elongated by a large talon (heel).

Peter Grubb

Phacochoerus aethiopicus DESERT WARTHOG

Fr. Phacochère du désert; Ger. Wüstenwarzenschwein

Phacochoerus aethiopicus (Pallas, 1766). Misc. Zool. p. 16. 'Promontoria Bona Spei advectus'; between Kaffraria and Great Namaqualand (South Africa, Eastern Cape Prov.), two hundred leagues from the Cape of Good Hope according to Vosmaer (1766).



ABOVE: Desert Warthog *Phacochoerus aethiopicus*.

RIGHT: *Phacochoerus* spp. Outlines of rhinarium (snout) and underlying nasals and mandibular occlusion in: above, Common Warthog *P. africanus*; below, Desert Warthog *P. aethiopicus*.

Taxonomy The Desert Warthog was the first species in the genus to be scientifically described and illustrated. Knowledge of this species was eventually eclipsed by the volume of information gleaned from the related Common Warthog *Phacochoerus africanus* in terms of numbers of museum specimens collected, extent of field studies, and published photographs, so diagnostic characters have been neglected (Grubb & d'Huart 2010).

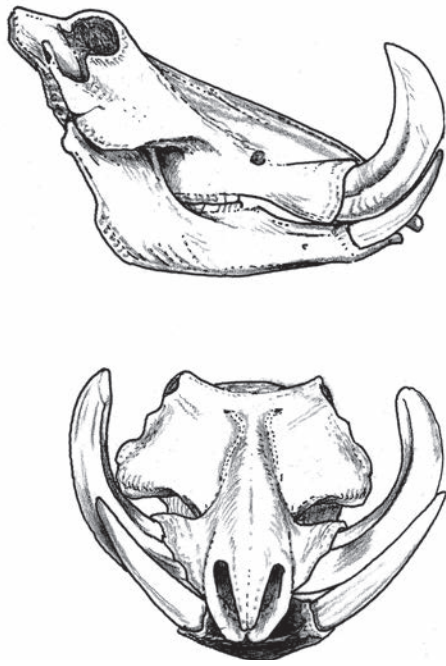
Polytypic, with two nominal subspecies, one extinct since about 1871. An East African population (*delamerei*) was named by Lönnberg (1909), who recognized its resemblance to the South African animal. Lydekker (1915) placed all warthogs in one species and has been followed by most authors in the twentieth century, though palaeontologists were aware that there were two species (Van Hoepen & Van Hoepen 1932, Ewer 1957, Cooke & Wilkinson 1978). Reappraisal of the status of *P. aethiopicus* (Grubb 1993b) has been followed by a study of its distribution in relation to *P. africanus* in the Horn of Africa (d'Huart & Grubb 2001), discovery of considerable genetic divergence from the latter species (Randi *et al.* 2002), and morphological differences between both species (d'Huart & Grubb 2005). See Grubb & d'Huart (2010) for a detailed review of the 'rediscovery' of the species. Synonyms: *angalla*, *delamerei*, *edentatus*, *pallasii*, *typicus*. Chromosome number: not known, but probably $2n = 34$ as in *P. africanus*.

Description Very poorly known species in spite of being relatively abundant in East Africa. South African animals are known from two illustrations indicating a small-eared animal with dark face and snout over a light cheek and lower jaw, and a swelling round the eye, below which is a drooping blunt wart. Skull similar in proportions to that of the Common Warthog, but diagnostically distinguished by other cranial and dental characters. The upper incisors are always absent (d'Huart &

Grubb 2001). Lower incisors are absent or reduced to four or less, very small, hardly protruding from alveoli and probably always concealed by gums. Lower and upper canines are less curved than in *P. africanus*, the wear facet on the lower canine is differently placed, and the lower canines are less compressed (Ewer 1957). The third molars are also different: when all the enamel columns have come into wear, no roots have yet formed, unlike the condition in *P. africanus*. At this stage, all the columns are of about the same length and are able to continue growing, extending the life of the tooth (Van Hoepen & Van Hoepen 1932, Ewer 1957, Cooke & Wilkinson 1978). Sphenoidal pits in the neurocranium floor on each side of the vomer are enormously enlarged and opened out, occupying the whole area between internal nares and basioccipital and basisphenoid, deepening the vomerine ridge; they are separated from the auditory bullae only by a thin wall of bone. Zygomatic arches are robust with large sinuses forming a spherical inflation of the jugal (malar) just in front of its articulation with the squamosal (temporal) (De Beaux 1922, Ewer 1957). A fine ridge runs down the front of the skull from the orbital rim across the lachrymal and maxilla, and while not necessarily diagnostic, characterizes many skulls of this species (d'Huart & Grubb 2001). In the few available samples, skull lengths for the two sexes do not overlap, suggesting perhaps greater sexual dimorphism than in the Common Warthog.

Geographic Variation

P. a. aethiopicus (Cape Warthog): formerly southern part of the species' distribution. Known from two illustrations (eighteenth and nineteenth century). Aart Schouman's painting of the lectotype (Tuijn & Van der Feen 1969) shows a stout animal with relatively small ears, dependent, blunt suborbital warts, and contrasting colouration between a dark face and snout and light cheek and



Lateral and frontal views of skull of Desert Warthog *Phacochoerus aethiopicus*.



Phacochoerus aethiopicus

lower jaw. External differences between a boar in the menagerie of the Zoological Society of London and a Common Warthog from Eritrea were described as ‘very obvious’ (Sclater 1869): flanks less naked, hairs on the back and nape of the head less thick and shorter; ears shorter, less pointed and less naked, densely coated with hair; and whiskers less developed. The illustration of the head shows a swelling round the eye and a broad, drooping suborbital wart with a blunt end.

P. a. delamerei (Lord Delamere’s or Somali Warthog): northern part of the species’ distribution. Suborbital warts in adult ♂♂ of a characteristic shape – curled or bent down at the tip. Skulls from N Somalia are smaller than those from S Somalia and Kenya, but sample sizes are very small. Recorded as having a blond dorsal mane in Somalia. Characters of canines and third molars recorded in *P. a. aethiopicus* not yet studied in this subspecies. Other dental and cranial characters identical with those of the nominate subspecies. Genal warts in adult ♂♂ unlike those known from *P. a. aethiopicus*, characteristically shaped, curled or bent down at the tip though with much variation in volume, form and orientation. Tips of ears bent backwards, appearing to have rounded or blunt tips and an angular contour. Suborbital region swollen, forming pouches that often extend to the base of the genal warts, resembling those known from *P. a. aethiopicus*. The comparatively broader skull and its shorter basioccipital region give the impression that the head is more egg-shaped than diabolo-shaped (d’Huart & Grubb 2005).

Similar Species

Phacochoerus africanus. Largely allopatric, but recorded in sympatry in Tsavo West and Tsavo East N. P. (Culverwell *et al.* 2008). There is also a population occupying an enclave within the range of *P. aethiopicus* in N Somalia (d’Huart & Grubb 2001). Attain larger size, at least in some populations, with skull length up to 466 mm in ♂♂ and up to 409 mm in ♀♀; they possess functional incisors and very small sphenoidal pits; lack thickening of zygoma; canines

reported to be more curved and third molars less specialized; genal warts cone-shaped and usually not with bent or curled tips; ears leaf-shaped, with pointed tips and a sinuous contour; suborbital areas without a pronounced swelling; head looks more diabolo-shaped (differences illustrated in d’Huart & Grubb 2005). Occupy a much wider range of habitats.

Distribution Endemic to Africa. A polytypic species occurring in the Somali–Masai Bushland BZ and formerly in part of the South–West Arid BZ, but not in intervening areas.

Historical Distribution Formerly South Africa, in the south-eastern parts of former Cape Province and apparently adjacent parts of KwaZulu–Natal. Early records of wild pigs do not usually discriminate between Bushpig *Potamochoerus larvatus* and warthogs and the two species of warthogs were not distinguished in the field. There are no records of warthogs from most of the Western Cape and Northern Cape. The Desert Warthog is known by reliably identified specimens from only the following localities: the type locality; between the Sondags and Boesmans Rivers in Eastern Cape; the upper Orange R., Northern Cape; and KwaZulu–Natal (Grubb & d’Huart 2010). It is not known whether the distributions of the two species overlapped or whether they were strictly allopatric, although the Desert Warthog ranged north into the former Transvaal in the late Pleistocene (Ewer 1957).

Current Distribution Distribution in East Africa does not seem to have changed significantly even in recent times, and they remain known only from E Ethiopia and Somalia, and in Kenya mostly north of the Ewaso Ngiro R. The range has been found to extend southwards to Tsavo West and East National Parks (west of Athi River and south of the Galana R.; Culverwell *et al.* 2008, de Jong *et al.* 2009).

Habitat The Desert Warthog is a species of open arid regions. The South African population occurred in the Karoo but there is no

information on habitat preferences and habitat use. Its distribution may have been limited by winter temperatures. The range of the northern population lies within the Somalia–Masai Bushland BZ, with vegetation of ‘Somalia–Masai *Acacia–Commiphora* deciduous bushland and thicket’ and ‘Somalia–Masai semi-desert grassland and shrubland’. These vegetation types range from xerophyllous bush and open woodland to sub-desert steppe. Dominant grasses are *Chrysopogon* species in more arid areas and *Chloris* species in semi-arid habitats. Desert Warthogs prefer plains on predominantly sandy soils, and avoid hilly terrain. Most records are from lowland areas below 200 m, a few are at higher altitudes, but none is above 1400 m. Desert Warthogs are dependent on occurrence of water and shade and occupy regions with rainfall of 100–600 mm per annum. Areas with higher rainfall, which correspond to the zone above the 1000 m contour, are avoided, as are the driest, hottest and most desertic regions with rainfall less than 100 mm per annum, corresponding with the hot coastal zone of Somalia between 12 and 9° N, and extending to the eastern tip of Ogaden.

Abundance The Desert Warthog was one of the most widespread and common game animals in Somalia, at least in the 1960s. Ground and aerial surveys in the Nugaal valley, Somalia, as well as an aerial survey between Garowe and Ras Hafun in 1989, confirmed that warthogs are locally abundant (P. Moehlman pers. comm.). Similarly, field observers reported that warthogs were very abundant in 1996 in Mahadday and Jowhar Districts of Middle Shebelle (A. Massarelli pers. comm.). In Ethiopia, they are common in the whole Ogaden region and can be observed both in family sounders in bushy areas and in larger aggregations of up to 30 individuals around permanent wells and close to towns (Wilhelmi *et al.* 2004). In Kenya, they were reported to be abundant near water-points in Garissa District, Kenya, in 1999 and 2004 (T. Butynski & A. Caron pers. comm.), common on the Laikipia Plateau and in the Samburu/Buffalo Springs/Shaba National Reserves area, but rarer towards Maralal and Marsabit in 2000 (S. Williams pers. comm.).

Adaptations Morphologically, the Desert Warthog is the most specialized living suid, but nothing is known of its habits and physiology. As incisors are functionally absent, lips and gums are used to detach or pick up food items. Rootless third molars suggest adaptation to a more abrasive diet. The specialized condition of the zygoma and differences in wart shape suggest the style of combat between ♂♂ is different from that of the Common Warthog.

Foraging and Food The potentially longer-lived and rootless third molar and absence of functional incisors imply significant differences in diet and feeding techniques from the Common Warthog. These await investigation.

Social and Reproductive Behaviour Physiological adaptation to drier, and perhaps, colder environments than the Common Warthog probably influence, say, their use of shelters and adaptation to watering regime. These, in turn, are likely to be correlated with currently unknown differences in social structure.

Reproduction and Population Structure There is currently no information available for the species.

Predators, Parasites and Diseases Likely predators include Lions *Panthera leo*, Leopards *P. pardus* and hyaenas. Extinction of the South African population may have been hastened by rinderpest.

Conservation IUCN Category: Least Concern. CITES: Not listed.

The Desert Warthog is known to exist in Samburu, Buffalo Springs, Shaba and Doodor National Reserves, and in Tsavo West and East National Parks, Kenya. From the distribution of reliably identified specimens, it will probably be found in Malkamari N. P. and Losai, Marsabit, Arawale and Boni National Reserves of Kenya, and Lag Badana/Bushbush N. P. in Somalia. In Ethiopia, Desert Warthogs are likely to occur in Babile and Yabelo Wildlife Sanctuaries and associated Controlled Hunting Areas (the Lower Wabe Shebelle and Borana, respectively) in Ethiopia (d’Huart & Grubb 2001, Culverwell *et al.* 2008). Although the species is widespread in the Ogaden, there is a concern that hunting for bushmeat trade may become a threat (Wilhelmi *et al.* 2004).

Measurements

Phacochoerus aethiopicus

Skull measurements:

P. a. aethiopicus

GLS (♂♂): 378.0 (366–393) mm, n = 4

GLS (♀♀): 330, 352 mm, n = 2

GWS (♂♂): 224.2 (220–230) mm, n = 3

GWS (♀♀): 179 mm, n = 1

South Africa

P. a. delamerei

GLS (♂♂): 393.0 (369–407) mm, n = 6

GLS (♀♀): 328.7 (325–331) mm, n = 3

GWS (♂♂): 228.3 (209–245) mm, n = 6

GWS (♀♀): 182.0 (169–197) mm, n = 3

Kenya and S Somalia (Jubaland)

GLS (♂♂): 357.0 (348–364) mm, n = 5

GLS (♀♀): 301 mm, n = 1

GWS (♂♂): 202.0 (192–227) mm, n = 5

GWS (♀♀): 167 mm, n = 1

N Somalia

Museum specimens (BMNH, NMK, PCM) and from literature; a single specimen in the AMNH from Galma Galla, Garissa District, Kenya, had the following measurements: TL: 1755 mm; T: 440 mm; HF c.u.: 275 mm; E: 142 mm (T. Butynski pers. comm.)

The record tusk length (measured along the outer curve from the base to the tip) is unclear due to lack of distinction between the two warthog species in most record books (see Butynski & de Jong 2010)

Key References Cooke & Wilkinson 1978; d’Huart & Grubb 2001, 2005; Ewer 1957; Grubb & d’Huart 2010; Tuijn & Van der Feen 1969; Van Hoepen & Van Hoepen 1932.

Peter Grubb & Jean-Pierre d’Huart

Phacochoerus africanus COMMON WARTHOG

Fr. Phacochère; Ger. Warzenschwein

Phacochoerus africanus (Gmelin, 1788). Syst. Nat., 13th edn, 1: 220. 'Habitat in Africa a capite viridi ad caput bonae spei'; restricted to Senegal, 'Cape Verd [Verdel]' (Lydekker 1915: 373).



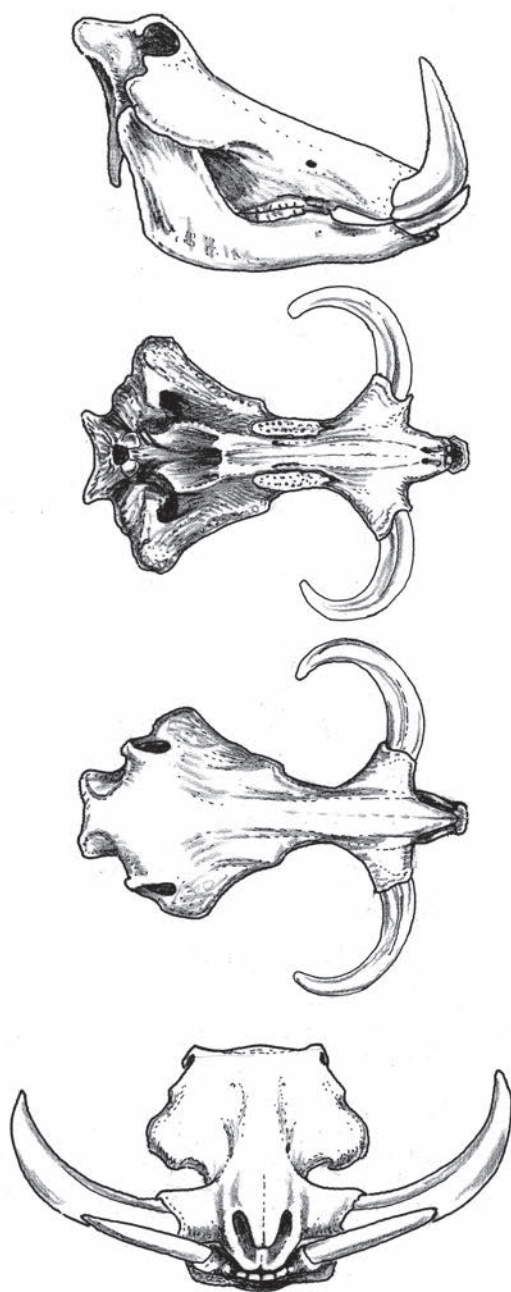
Common Warthog *Phacochoerus africanus*.

Taxonomy The Common Warthog is here treated as a species distinct from the Desert Warthog *P. aethiopicus* (Ewer 1957, Cooke & Wilkinson 1978, Grubb 1993b, 2005). Four geographical variants of *P. africanus* were provisionally recognized by Grubb (1993b) largely on the basis of skull size and proportions indicating a clinal species. Muwanika *et al.* (2003) investigated patterns of genetic variation in 181 specimens from 24 localities in Africa. They identified 70 mitochondrial haplotypes that clustered into three well-defined clades representing individuals from western, eastern and southern Africa. They concluded that differentiation at both mitochondrial and nuclear loci supported the existence of three lineages that resulted from Pleistocene climatic fluctuations. Synonyms: *aeliani*, *barbatus*, *barkeri*, *bufo*, *centralis*, *fossor*, *haroia*, *incisivus*, *massaicus*, *sclateri*, *shortridgei*, *sundevallii*. Chromosome number: $2n = 34$ (Bosma 1978); the chromosome complement consists of 14 pairs of (sub)metacentric autosomes and two pairs of acrocentric autosomes (Musilova *et al.* 2010).

Description At first glance an adult Common Warthog jauntily trotting across an open savanna with its tail and mane erect and large head held high resembles a miniature rhinoceros rather than a typical pig. The head is unusually large, the forehead, muzzle and snout broad and flattened, with the eyes placed high and wide. Ears are prominent and broad rather than pointed, and can protrude well above the level of the head. Warts, from which the animal derives its name, are formed of tough fibrous tissue and comprise the

infraorbital warts attached to the zygoma, mandibular warts along the angle of the lower jaw, and, in ♂♂, supraoral warts situated on the snout behind the tusks. A dense, side-burn-like cover of long white bristles generally obscures the elongated mandibular wart. The neck is short and the nape, withers and back carry a mane of long black and brown bristles. The mane can be erected in displays associated with fight/flight situations. The Common Warthog's dark grey, almost black colour is determined by its skin colour rather than by its sparse coat. The skin is sparsely covered with white bristles and can take on differing hues of grey or brown depending on the colour of the soil in its holes or wallows. The tail is long and slender with a flattened end carrying bristles. The legs are proportionately longer than in other suids and knees bear characteristic callosities that are present even in the foetus. The hooves are narrower than those of the Bushpig *Potamochoerus larvatus*. Both the preorbital area and the lip carry dermal secretory glands (Estes *et al.* 1982). Tusks and warts are markedly larger in ♂♂ and ♀♀ have one pair inguinal and one pair abdominal nipples.

The skull slopes sharply forward from the braincase to the nostrils, and the rostrum is considerably elongated. The orbits are small, and there are distinct supraorbital ridges on the inner sides. The supraoccipital crest is well developed, lying at an angle backwards of the braincase, thereby leaving a wide area at the back for the attachment of the massive neck muscles. The paraoccipital processes are long, extending nearly to the level of the bottom of the angle of the mandible (Skinner & Chimimba 2005). The blunt upper



Lateral, palatal, dorsal and frontal views of skull of Common Warthog *Phacochoerus africanus*.

canines, or tusks, flare upwards from the snout and in older animals, particularly ♀♀, curve inwards. The lower canine is triangular in profile, scimitar-like and is sharpened against the lower edge of the upper canine. Unlike the upper canine, its dentine core is covered by enamel. The key dental features distinguishing this species from the Desert Warthog are the presence of one pair of upper incisors and two to three pairs of lower incisors. Upper incisors are absent in Desert Warthogs and lower incisors, if present at all, are rudimentary (Grubb 1993b). The adult upper and lower incisors of the Common Warthog also have deep roots and prominent crowns, which converge and make contact. The structure of the third molar also differs between the species. In *P. africanus* roots are formed in the anterior molar columns before all the cusps have come into

wear while in the extinct Cape Warthog *P. aethiopicus aethiopicus* and presumably also in *P. a. delamerei* roots are formed only once all of the columns have erupted and are in wear (Shaw 1939, Cooke 1949, Grubb 1993b). Unlike any other African suids, the roof of the skull of *P. africanus* shows two deep sphenoidal pits behind the internal nares region (Grubb 1993b).

Geographic Variation

P. africanus africanus: Mauritania eastwards to S Ethiopia.

P. a. aeliani: confined to Eritrea, N Djibouti and Somalia.

P. a. massaicus: eastern and central Africa, in Zambia, Malawi, N Mozambique, Tanzania and S Kenya.

P. a. sundevallii: SW Angola, N Namibia, Botswana, Zimbabwe, S Mozambique and parts of South Africa.

Similar Species

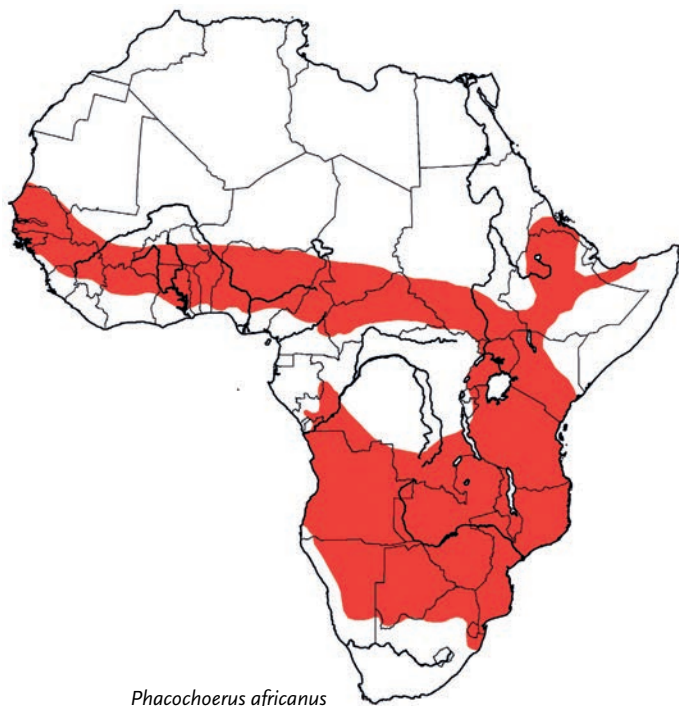
Phacochoerus aethiopicus. Only recently distinguished as a living separate species based on cranial features and molecular evidence (Grubb 1993b, Randi *et al.* 2002; and see Grubb & d'Huart 2010). A supposedly consistent distinguishing feature in the field is the shape of the infraorbital warts in ♂♂: in the Desert Warthog they have a distinct anterior bend, whereas in the Common Warthog these generally point directly outwards (see also species profile for *Phacochoerus aethiopicus*). The differences between the two species are illustrated by d'Huart & Grubb (2005). Largely allopatric, but recently recorded in sympatry in Tsavo West N. P. (Culverwell *et al.* 2008).

Potamochoerus larvatus. Also occurs in moister savanna habitats, but readily distinguished from warthogs in the field by its distinctly shaggy, reddish-brown coat, rounded back, pointed pixie ears, low slung head, more pointed snout without upturned prominent tusks or warts, and its loping gait. Unlike warthogs, the tail is never held erect while running.

The more brightly coloured Red River Hog *Potamochoerus porcus* and the much larger Forest Hog *Hylochoerus meinertzhageni*, which has a well-developed black shaggy coat, occur in forests and their ranges have only marginal overlaps with the Common Warthog.

Distribution Endemic to Africa. Their former distribution extended across the West African Guinea Savannah and Sahelian zone from Senegal, Gambia and extreme S Mauritania eastwards to Sudan, Ethiopia and Djibouti and from there southwards through East Africa to the savannas of southern Africa. The Tugela R. marks their former southerly limit of distribution in KwaZulu–Natal (Rowe-Rowe 1994). Historically, the Common Warthog did not occur in the arid Karoo of South Africa, where it was replaced by the extinct Cape Warthog *P. aethiopicus aethiopicus*.

Today, the Common Warthog remains widespread in sub-Saharan Africa, being found in scattered populations in West Africa eastwards to Ethiopia and then southwards in protected areas and unsettled, or very lightly settled, areas in East and south-central and southern Africa. The continuous expansion of the Sahel-zone has resulted in a marked contraction in the species' former range in the north since the early 1980s, and accounts for its probable extinction in Niger (J. Newby, in Vercammen and Mason 1993) although it is possible they may still persist in the south-central Air Mts (J. Newby pers. comm.).



Common Warthogs are still recorded in the savanna woodlands of SW Mali (Chardonnet 2001a). They have been reintroduced to some parts of their former range in southern Africa (e.g. in Swaziland, where the indigenous population went extinct), and introduced elsewhere (e.g. in NE Algeria, as a result of an escaped captive population, and to the Eastern Cape Province of South Africa).

Habitat Confined to moist and dry African savanna grasslands, open bushlands and woodlands and usually within range of perennial surface water (although water is not considered to be an essential habitat requirement; Skinner & Chimimba 2005). Usually absent from forests, extensive thickets, cool montane grasslands and deserts and succulent steppes. However, the population in the Goda Mts in Djibouti mainly occupies forested areas (Künzel *et al.* 2000). Although typically associated with lowland savannas, they reach elevations of 3500 m in the Ethiopian Highlands (and large numbers survive in Bale Mountains N. P.; Yalden *et al.* 1996).

The need to sleep in holes in the ground at night links the distribution of this species to the formerly more widely distributed Aardvark *Orycteropus afer*, although in some parts of West Africa Bigourdan (1948) reported that Common Warthogs generally did not sleep in holes at night and only used Aardvark burrows as a last resort. They are capable of excavating their own holes and often modify existing holes extensively. Subterranean erosion gullies are also used and holes and gullies may be shared with porcupines that use them by day (Cumming 1975).

In a quantitative study of habitat selection, Cumming (1975) found the highest densities of Common Warthogs in drainage line grasslands on nutrient-rich soils and in *Acacia* savannas on alluvial terraces. These habitats supported highly palatable grasses, such as *Urochloa mossambicensis*, which were grazed during the wet season and other species, such as *Digitaria milanjiana*, which provided an abundant store of rhizomes that were rooted during the dry months. Lowest densities occurred in miombo woodland habitats and in *Combretum* and *Baikiaea* thickets and woodlands on deep sandy soils. Seasonal

shifts in habitat densities occurred as these animals changed from wet season to dry season feeding grounds within their home-ranges in the Sengwa area. Common Warthogs will congregate on the flush of green grass following dry season burns.

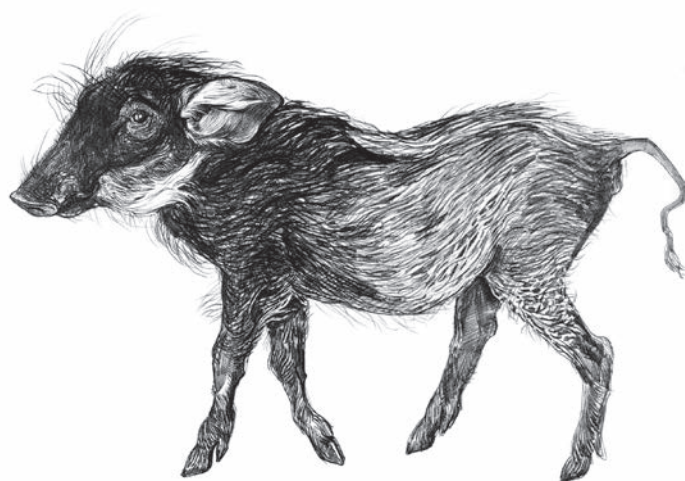
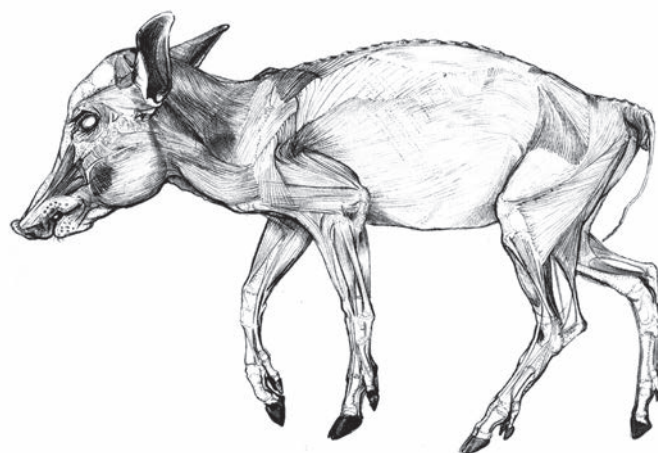
Abundance Seldom a dominant component, either numerically or in terms of biomass, within African large herbivore communities, although in some protected areas local densities may exceed 15–20 ind/km². More typically, densities range between 1 and 10/km² in protected areas, although local densities of 77/km² were found on short grass in Nakuru N. P. (Radke 1985, 1991a).

The overall number of Common Warthogs in southern Africa (Angola, Zambia, Tanzania and southwards) has been estimated at about 250,000 (Cumming 1999). Estimates for the numbers of Common Warthogs in West and north-central Africa are not available although they occur in most protected areas in the savannas. Populations in Benin, Central African Republic and N DR Congo were greatly reduced by rinderpest during the 1980s (Vercammen & Mason 1993). Populations are susceptible to droughts and resulting population crashes have been reported in several parts of Africa (e.g. Mason 1990a). However, the potentially high reproductive rate of Common Warthogs does allow for rapid recovery when conditions improve.

Adaptations Differs from other suids in several important respects and these differences emphasize that Common Warthogs are suids beautifully adapted to dry savannas and steppes. The unusually large head, with eyes set high and wide, provides a wider field of vision than other suids. The snout and teeth are adapted to grazing and to rooting hard ground while the warts and tusks reflect displays and fighting style. Their gait, with head held high, is more akin to that of an antelope than the pigs.

Common Warthogs are the smallest of the diurnal bare-skinned large mammals and, unlike any other ungulate, sleep in holes at night. The subcutaneous fat layer is very thin, if present at all, and, in contrast to other suids, they are markedly thermolabile and their daily range in body temperature can vary by as much as 7 °C (Cumming 1975). Piglets are unable to maintain their body temperature without huddling and access to shelter (Sowls & Phelps 1966) and even at one year old they will die if exposed to early morning temperatures of around 1 °C if denied access to holes (Cumming 1975). In winter, overnight and early morning temperatures approaching zero are common in arid savannas while the temperatures in occupied holes at that time of year are considerably higher (Cumming 1975). Daily temperature was close to 20 °C within Common Warthog holes in the Masai Mara National Reserve and Nakuru N. P. and temperature fluctuations within holes were markedly lower than fluctuations in temperatures outside the hole (Radke 1991b). Geigy (1955) found a temperature of 30 °C and relative humidity of 90% in a burrow close to Mofu in Tanzania. It thus seems probable that the cluster of features involving bare skin, absence of a subcutaneous fat layer, thermolability and sleeping in holes may reflect adaptations to conserving energy and water in arid habitats. Clearly, these adaptations may not be crucial in hotter, more humid areas. Physiological studies to test such a hypothesis have yet to be undertaken.

Ewer (1957) characterized Common Warthogs as highly specialized 'grass pluckers' on the basis of the structure and wear on the incisors and her observations of them grazing short grass 'lawns' in

Common Warthog *Phacochoerus africanus* juvenile.Common Warthog *Phacochoerus africanus* juvenile myology.

KwaZulu–Natal. Their specialized bunodont molars are unlike those of other suids and with their flattened, grinding surfaces are adapted to a graminivorous diet (Ewer 1958). The variable number of incisors (Child *et al.* 1965) suggests that they may be dispensable and that Common Warthogs may use their lips, as do hippos, to graze. Watching the animals graze on short grass from a distance of a few centimetres has not clarified the question (D. Cumming pers. obs.). Common Warthogs change their diet seasonally and this is evident in the structure of the snout and the rhinarium. The dorsal edge of the rhinarium is relatively sharp, tough and firmly anchored to the nasals to allow them to scoop shallow depressions in hard, dry earth to unearth rhizomes – a feat that the Bushpig, with its more bulbous and flexible rhinarium, is incapable of performing (Cumming 1975). Common Warthogs are also capable of grazing efficiently on taller swards during the rains and of using their tusks to shred grass seeds when these ripen towards the end of the rains. The grinding surface of the molars is unlike that of other suids and is adapted to a highly lignified diet of grass leaves and rhizomes. The oft-repeated tale that Common Warthogs use their tusks to dig holes and root for rhizomes and tubers is untrue. The development of callosities on the fore-carpals on which they ‘kneel’ is clearly linked to grazing short grass and rooting for rhizomes. The callosities, absent in other suids, are evident in the embryo. A tame Bushpig that grew up with two Common Warthogs was occasionally seen trying to kneel in the same manner as the Common Warthogs, but once in this position it was clearly perplexed about what to do next and neither rooted nor grazed and soon stood up.

Marked sexual dimorphism in the size of upper canines, or tusks, signifies their role in displays and inter-male rivalry. Linked to this is the sexual dimorphism of the supraoral and particularly the infraorbital warts. While the tusks may serve a similar function to horns in antelope, the three sets of warts (infraorbital, supraoral and mandibular) are situated so as to protect the eyes and underlying bones, tendons and muscles that are intimately associated with feeding.

Warthogs are diurnal and generally emerge from burrows in the morning at about sunrise and retire at dusk. Feeding generally takes place during the cooler periods of the day in the morning and late afternoon with the mid-day period spent resting in the shade or basking out in the open if it is cool. In general, about six hours a day

are spent feeding, two hours walking and 2–3 hours resting with less than an hour spent on other activities such as drinking, wallowing and social activities (Clough & Hassam 1970, Cumming 1975). The remaining time of roughly 12 hours is spent in holes. However, times spent on different activities vary seasonally and with the reproductive cycle. Pregnant ♀♀ will spend a greater proportion of time resting up in late pregnancy and mothers suckling young in burrows during the postnatal period may spend as little as two hours a day feeding (Cumming 1975). The frequency of drinking and wallowing is strongly temperature-dependent.

Foraging and Food Common Warthogs are almost entirely graminivorous, plucking green grass when this is available but also shredding grass seeds towards the end of the rains and rooting for grass rhizomes during the dry season (Cumming 1975). Reports from East Africa (e.g. Field 1970b, 1972) suggest that in some areas they may be predominantly grazers – a feature possibly linked to a dual wet season and availability of green grass through much of the year. In a recent study of the carbon and oxygen isotopes in the tissue of extant and fossil Suidae, Harris & Cerling (2002) characterize *Phacochoerus* as a hyper-grazer.

In southern Africa a single wet season and long dry season spanning 7–8 months leads to clear seasonal shifts in diet and mode of feeding. In the first and so far only quantitative year-round study of Common Warthog diet and feeding behaviour, Cumming (1975) found that Common Warthogs grazed on at least 34 species of grass during the rains. As seed ripened towards the end of the rains they spent more time stripping seeds from the inflorescences of species such as *Urochloa*. During the dry season they rooted for the rhizomes of *Digitaria milaniana* or *Tristachya superba* and occasionally *Oryza barthii* and *Phragmites* or the swollen leaf bases of *Setaria* species. Cumming (1975) reported 3–5 tons of rhizome (*D. milaniana* and *T. superba*) per hectare in favourable dry season habitat in the Sengwa area – enough to support ten Common Warthogs per ha for the six-month dry season. Observed density was 0.28 ind/ha in such habitat. The only other larger mammal found using this major food resource was the Cape Porcupine *Hystrix africaeaustralis*.

Common Warthogs are widely reported in the literature to eat fallen fruits, sedges, tubers and bulbs with the suggestion that the latter may



Common Warthog *Phacochoerus africanus*.

allow them to survive through droughts. At Sengwa fallen fruits formed only a very occasional dietary item and Common Warthogs were never recorded eating tubers and bulbs (i.e. underground storage organs of non-graminaceous plants) although Bushpigs, Chacma Baboons *Papio ursinus* and Cape Porcupines ate these. When offered ripe fallen *Acacia* pods, a favourite food item for many ungulates, tame Common Warthogs rejected them but a tame Bushpig readily ate them. Common Warthogs were regularly seen feeding on stomach and intestinal contents at predator kills in the Masai Mara National Reserve by Radke (1985) and have been recorded eating carrion elsewhere (Wilson 1975). They will, as many ungulates do, chew on old bones (osteophagia) and also exhibit geophagia and coprophagia (Cumming 1975, Mason 1982). The remains of a rodent were found in one of 600 faecal samples examined at Sengwa (Cumming 1975). Although not as large a problem as Bushpigs, Common Warthogs are sometimes a problem in agricultural lands, such as rice fields in Guinea-Bissau and peanut crops in E DR Congo (Vercammen & Mason 1993).

Social and Reproductive Behaviour Common Warthogs are social animals, with the matriarchal sounder (family group), usually comprising an adult ♀ with her immediate litter and sometimes one or two female offspring of previous litters, forming the core social unit. Young ♂♂ leave, or are evicted from, matriarchal sounders at the end of their first year and form bachelor groups with other yearlings or older animals. Adult ♂♂ are usually solitary or in fluid bachelor groups of 2–4 animals. Breeding ♀♀ leave their sounder to farrow alone in holes but they may be joined after a week or two by yearling or subadult female offspring of previous litters. Durable social bonds between sows and their offspring were recorded in the Sengwa area. Where two or more related sows have bred they may join to form larger sounders of 12–18 animals, but sounder size is ultimately limited by the size of the burrows in which they sleep at night (Cumming 1975). More recently both solitary and cooperative breeding strategies within the same Warthog population have been described and analysed in terms of evolutionary pressures acting on sociality in the species (White 2008, 2010, White *et al.* 2010, White & Cameron 2011a, b). As in the Sengwa population (Cumming 1975), Common Warthogs in the Hluhluwe-iMfolozi Park in KwaZulu-Natal, South Africa, were dispersed in clans (White & Cameron 2009).

Home-range areas vary with locality. Average home-range areas of 24 ha in the Eastern Cape, South Africa, 171 ha in Zimbabwe and up to 600 ha in East Africa have been recorded (Somers *et al.* 1994, Cumming 1975, Radke 1991a, respectively). Home-ranges overlap and there is no evidence of boundaries, core areas or sleeping holes within the home-range being defended. The focus of activity within the home-range may shift seasonally, or boundaries may be extended temporally, in response to changing availability of food and water. Occasional exploratory forays beyond home-range boundaries may occur and young animals may disperse several kilometres from their initial home-range. There is no evidence of large-scale seasonal movements of Common Warthogs despite their occurrence in arid zones. Reports of daily distance travelled vary from 6 km in Uganda (Clough & Hassam 1970), to 3.4 km for matriarchal sounders in Sengwa in Zimbabwe (D. Cumming pers. obs.) and 1.6 km in a nature reserve in the Eastern Cape (Somers *et al.* 1994). They change sleeping holes frequently and there are usually many more holes available than there are Common Warthogs (Radke 1991b).

In most parts of their range, and particularly in areas that experience a marked drop in temperature at night, Common Warthogs regularly enter holes at dusk and emerge at about sunrise with actual times of entry and emergence following the seasonal changes in day length (Cumming 1975). Holes may also be used as refuges from the rain. In the Sengwa area, few holes were used more than 70% of the time and animals frequently changed holes with the result that holes were used by more than one sounder. On occasion as many as 15 animals from related sounders, or members of larger filial groups, shared larger holes or burrows in erosion gulleys on the same night (Cumming 1975). On entering smaller and shorter Aardvark burrows, or holes that are being explored for the first time, Common Warthogs will generally approach the entrance, about turn and reverse into the hole (Geigy 1955, Frädrieh 1965).

Scent-marking begins in both sexes at 6–7 months of age (Cumming 1975) and is achieved by rubbing the damp patch in front of the eye (preorbital gland) or flange of the upper lip beside the tusks, on tree trunks, stumps and other solid objects. Adult boars will spray urine, and presumably secretions from the preputial gland, over the urine of ♀♀. Marking with preorbital and lip glands is carried out more frequently by ♂♂ and particularly during fighting and during the mating season, while ♀♀ mark the edges of their home-ranges more



Silhouette of Common Warthog *Phacochoerus africanus* in 'proud posture'.

frequently (Radke & Niemitz 1989). Allo-marking is uncommon (Somers *et al.* 1995). There is no evidence to suggest that Common Warthogs use dung piles in marking.

Intra-specific threat displays include standing tall, raising the mane and pressing the tail against the flank facing the opponent. Fighting between ♂♂ consists of highly ritualized head-on-head duels engaging the snout and tusks with sharp blows to sides of the head that are mostly taken on the warts. The mouth is closed and the sharp lower canines are seldom engaged in these encounters. However, they can be used, with typical suid sideways slashing movements, to good effect against predators.

Greeting behaviour takes the form of naso-nasal or naso-oral contact and sniffing or touching areas of glandular secretion such as the upper lip and the preorbital area (Cumming 1975) and naso-anal contact between warthogs was reported by Frädriich (1975). Subsequent amicable behaviour may take the form of gentle frontal pushing, one animal placing its chin on the other's back, and sometimes play fighting in young animals (Cumming 1975).

Allogrooming, by drawing hairs through closed lips, occurs between family members and may serve to remove nits. Common Warthogs readily huddle together in cool weather and otherwise rest or lean on or against each other. Bouts of vigorous, playful sparring between littermates are frequent, particularly after wallowing. Warthogs are remarkably vocal and emit a wide range of grunts, squeaks and squeals that communicate, *inter alia*, alarm, threat-attack, greeting and submission. Courting ♂♂ emit a loud, rhythmic, almost explosive 'chant de coeur' that resembles the 'phut-phut' of a two-stroke engine. Estes (1991a) considers that clacking the canines together is a major component of the chant, but after watching and listening to a tame boar at close quarters (<1m) the present author believes the noise to be vocally generated (D. Cumming pers. obs.).

The mating system is promiscuous with a dominance hierarchy between roaming ♂♂ (Cumming 1975, Somers *et al.* 1995). During the mating season dominant boars will seek out oestrous ♀♀ by visiting and sniffing around holes during the morning and very occasionally sleeping in the same hole at night (Cumming 1975). Courtship follows a typical suid pattern with a chanting boar following an oestrous ♀ and showing a typical courtship gait followed by resting his chin on her rump until she responds by standing still and allowing him to mount. A vaginal plug is formed after coitus, which may serve to lower risk of insemination from other ♂♂ (Mason 1982); mounting time is about 3 min (Somers *et al.* 1995).

Sows farrow on their own in burrows where their young remain, except when moving to another burrow or playing at the entrance, for the first one to two weeks. Thereafter they increasingly accompany the mother away from the hole for longer periods until they are about seven weeks old when they accompany the mother throughout the day. Although they begin grazing within a few weeks of birth, nursing continues until 3–4 months of age. A strict teat order, as in domestic pigs, has been observed in litters of tame Common Warthogs, with teats drying up on the loss of a member of the litter. Similarly, the number of developed and secreting mammary glands in captured wild animals corresponded to the number of young in the litter (D. Cumming pers. obs.). However, allo-mothering and allosuckling has been reported and studied in wild warthogs (Radke 1991a, Somers *et al.* 1995, Plesner-Jensen *et al.* 1999).

Reproduction and Population Structure Over much of their range breeding is seasonal, with mating at the end of the wet season and births near the start of the following rains. In southern Africa this equates to roughly Oct to early Dec (Cumming 1975, Boshe 1981, Mason 1982, Somers *et al.* 1995). However, close to the Equator breeding may occur throughout the year (Clough 1969). Oestrous lasts up to 72 hours (Clough 1969); oestrous cycle in captives in European zoos lasts about 35 days (Berger *et al.* 2006). The gestation period is about 170 days (Brown 1936, Child *et al.* 1968, Mason 1982). Litter-size is usually 1–4, most often three, but up to eight is recorded (Child *et al.* 1968, Mason 1982, Somers & Penzhorn 1992). Prenatal mortality may be marked, with reports of 9% mortality by Mason (1982) in KwaZulu–Natal and 17% by Child *et al.* (1968) in Zimbabwe. Sex ratio at birth is parity (Child *et al.* 1968) with the proportion of ♂♂ declining in older age classes (Cumming 1975). Birth-weight varies inversely with litter-size: Bigourdan (1948) recorded birth-weights of 480–620 g in larger litters (3–4) and 800–850 g in small litters (twins).

Both ♂♂ and ♀♀ reach sexual maturity at 18 months, with sows producing their first litter at two years old (Boshe 1981, Mason 1986). Males have been recorded mating at the age of 18 months but older boars usually dominate courtship and are presumed to carry out most mating. Growth in body mass is influenced by season, with a high growth rate during the wet season and markedly reduced growth rate in yearlings and subadults during the dry season (D. Cumming pers. obs.). Adult body size and weight is reached at between 36 and 48 months. Adult weight may fluctuate seasonally, with adult ♂♂ losing as much as 20% of their weight through the rut and the following dry season.

Tooth eruption patterns in seasonally breeding populations allow Common Warthogs to be aged to the nearest two months up to the age of 48 months (Child *et al.* 1965). Ageing of older animals is problematic and criteria developed by Spinage & Jolly (1974), based on the ratio of length to height of the third molar, were found to greatly underestimate the age of known-age material from the Sengwa area (D. Cumming pers. obs.) and in KwaZulu–Natal (Mason 1984). An alternative measure using the exposed height of the anterior edge of the third molar in relation to molar length promises to provide a more consistent and useful means of estimating the age of animals older than 48 months (D. Cumming pers. obs.). Mason (1984) found reasonably clear annual cementum lines in the incisors of known-age individuals from the Sengwa area. Common Warthogs may live 18–20 years in captivity (Jones 1993, Weigl 2005), but seldom reach 12 years in the wild. Boshe (1984), using age criteria developed by Spinage & Jolly (1974), calculated life tables for Common Warthogs in the eastern Selous G. R. that were derived from found skulls and a randomly selected sample of shot animals. He found a typical mammalian pattern of high early mortality, reduced mortality in the middle age classes, followed by increasing mortality rates as animals aged.

A population growth rate of 19% per annum was recorded in the Sengwa wildlife research area over a period of five years after which predation by Lions *Panthera leo* reduced the population by 50% per annum in two successive years. Somers & Penzhorn (1992) recorded a population growth rate of 39% per annum in an introduced population subject to minimal predation in the Eastern Cape of South Africa.

Predators, Parasites and Diseases Lions, where they occur, are undoubtedly the major predators of Common Warthogs and this conclusion is supported by several sets of records of natural mortality in Common Warthog populations. In five data sets summarized by Cumming (1975), Lions accounted for between 73 and 100% of predator kills. Other mammalian predators, in order of importance, included Leopards *Panthera pardus*, African Wild Dogs *Lycaon pictus*, hyaenas and Cheetahs *Acinonyx jubatus*. Martial Eagles *Polemaetus bellicosus* have been recorded taking piglets. Schaller (1972), in his study of the Serengeti Lion, concluded that Common Warthogs were highly susceptible to predation because of their lack of height, speed and caution. Lion prides are also capable of becoming 'warthog specialists' and in the Sengwa area Common Warthogs formed some 50% of Lion diet (i.e. in terms of carcass weight) during the late 1960s and early 1970s and about one-third of the animals killed were dug out of their holes.

Common Warthogs are reportedly very susceptible to rinderpest. During the great rinderpest epidemic of 1895–96 populations in southern Africa were greatly depleted and similar impacts were experienced in several West and central African countries during the 1980s (including Benin, Central African Republic and DR Congo). They are unaffected by diseases such as trypanosomiasis and swine fever. Tuberculosis has been recorded in Common Warthogs in Queen Elizabeth N. P., Uganda, and in Kruger N. P., South Africa (Wildlife Tuberculosis Study Group 2002).

Common Warthogs are hosts to a large number of endo- and ectoparasites. Oxpeckers *Buphagus* spp. will remove ticks from warthogs and hand-reared Southern Ground-hornbills *Bucorvus leadbeateri* were observed grooming members of a sounder on ten occasions during which some of the warthogs solicited grooming (Coetzee 2010). Some 65 species of tick have been collected from Common Warthogs across Africa (Cumming 1998). The soft tick *Ornithodoros moubata* feeds on Common Warthogs in their burrows and is responsible for the transmission of relapsing fever in humans and swine fever in pigs. At least three species of flea and one host-specific louse *Haematopinus phacochoeri* feed on Common Warthogs and very high populations of fleas can build up in their burrows. Standing at the entrance to a warthog hole that has not been used for a while can result in a 'mini-sandstorm' of fleas colliding against one's legs. Common Warthogs are also a preferred host of the tsetse fly *Glossina morsitans* (and see Conservation).

In southern Africa, at least 23 species of nematode, six species of cestodes and two species of trematodes have been found in Common Warthogs (Ortlepp 1964, Horak *et al.* 1983a, 1988a, Palmieri *et al.* 1985, Boomker 1990, Boomker *et al.* 1991a). Hydatid cysts of *Echinococcus* spp. have been found in the abdominal cavity of animals in Selous G. R. (Rodgers 1984a), in Kruger N. P. (Horak *et al.* 1988a) and in the Sengwa Wildlife Research Area (D. Cumming pers. obs.).

Conservation IUCN: Least Concern. CITES: Not listed.

The Common Warthog is present in numerous protected areas across its extensive range. However, because of their susceptibility to drought and predation, local populations may, as the work of Somers & Penzhorn (1992) and Somers (1997) suggests, be more prone to extinction than is generally appreciated. Hunting is a particular threat in some parts of their range. In Djibouti, the range of the threatened *P. a. aeliani*, Common Warthogs were the target of heavy hunting pressure before the implementation of a hunting ban in 1977; the maintenance of their habitat in the Goda Mts is essential for the survival of this population (Künzel *et al.* 2000). There is small-scale trade of Common Warthog tusks in some African countries, but no significant international trade in ivory has been documented (Vercammen & Mason 1993).

Common Warthog eradication was vigorously promoted in East Africa to control African swine fever (De Tray 1957), although their role in the transmission of the disease to domestic pigs had not been conclusively demonstrated. Selective game elimination as a means of controlling tsetse fly, the vector of ngana or trypanosomiasis in livestock, also eradicated or depleted Common Warthogs over large areas in East and southern Africa from the 1930s to the 1970s; for example, a total of nearly 68,000 Common Warthogs were shot in Zimbabwe between 1933 and 1957/1958 (Child & Riney 1987).

Measurements

Phacochoerus africanus

HB (♂ ♂): 1323 (1165–1440) mm, n = 56

HB (♀ ♀): 1182 (1090–1268) mm, n = 74

HF c.u. (♂ ♂): 264 (242–280) mm, n = 56

HF c.u. (♀ ♀): 247 (225–262) mm, n = 74

Sh. ht (♂ ♂): 682 (612–720) mm, n = 56

Sh. ht (♀ ♀): 598 (543–657) mm, n = 74

WT (♂ ♂): 79.6 (59.3–103.9) kg, n = 56

WT (♀ ♀): 56.5 (44.6–69.1) kg, n = 74

Hluhluwe G. R., KwaZulu–Natal (Mason 1985)

Body mass, and head and body length of 16 adult ♂ ♂ and 89 adult ♀ ♀ from the Sengwa Wildlife Research Area, Zimbabwe (Cumming 1975), and the body mass of 19 adult ♂ ♂ and 24 adult ♀ ♀ from Selous G. R. (Rodgers 1984a) and 68 ♂ ♂ and 74 ♀ ♀ from E Zambia (Wilson 1968), did not differ significantly from these measurements. The record length for a tusk, measured along the outer curve from the base to the tip, is 609.6 mm (the date and locality of the tusk are not recorded). For 5- to 8-year-old ♂ ♂, more typical lengths of the canine protruding from the gum line would be 120–200 mm

Key References Bigourdan 1948; Cumming 1970, 1975; Frädriich 1965; Kingdon 1979; Mason 1982; Radke 1985, 1991a, b; Somers *et al.* 1995, 1997; White 2008, 2010.

David H. M. Cumming

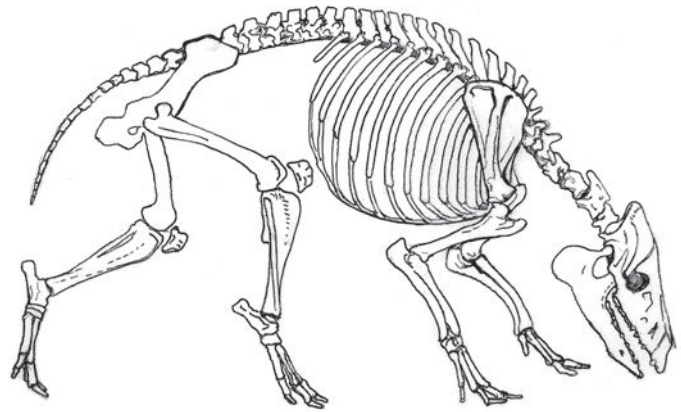
Suborder WHIPPOMORPHA – Hippopotamuses, Cetaceans

Whippomorpha Waddell, Okada & Hasegawa, 1999. Syst. Biol. 48: 2.

The discovery, by geneticists, that whales have derived from an early form of artiodactyl has created upheavals in several fields of biology, but most intensively in nomenclature, where most biologists had become accustomed to a long-established consensus on what to call such well-known animals as cloven-hoofed artiodactyls and the Cetacea (whales and dolphins). Revisions of subspecies and species have been more readily accommodated than the renaming of entire orders. Thus, many biologists are reluctant to change names and ranks that have a hundred years or more of precedent behind them. One compromise has been to avoid the use of ranks and use 'clade' rather than a specific ranked taxon for one of the new groupings revealed by molecular research.

Because the majority of taxa in *Mammals of Africa* follow established practice we have retained ranked taxa, following whatever recent authorities seem in possession of the most facts, parameters and most willing to allocate each newly recognized clade a position within its lineage's evolutionary tree. Thus, we treat Whippomorpha as the cetartiodactyl clade that contains the Hippopotamidae and Cetacea, and we treat it as a suborder within the Cetartiodactyla to give taxonomic recognition to some of the many new discoveries in molecular, palaeontological and other studies. The monophyly of this group is now well supported by concatenated mitochondrial and nuclear gene sequences (e.g. Amrine-Madsen *et al.* 2003, Meredith *et al.* 2011), complete mitochondrial genomes (Arnason *et al.* 2004, Hassanin *et al.* 2012) and retroposons (Nikaido *et al.* 1999), and has also been recovered in morphological phylogenetic analyses of living and extinct cetartiodactyls (Geisler & Uhen 2003, 2005) as well as supertree analyses (Beck *et al.* 2006) and combined molecular-morphological analyses (Spaulding *et al.* 2009). Aside from a few uniquely shared dental and skeletal structures (Geisler & Uhen 2003), hippos and whales also lack sebaceous glands and have very little (if any) hair, and these features may have been present in a common semi-aquatic ancestor (Gatesy *et al.* 1996, Geisler & Uhen 2003). Gatesy *et al.* (1996) have also called attention to the fact that hippos and whales both vocalize, and nurse their young, while underwater. Geisler & Uhen's (2003) character optimizations suggested that the last common ancestor of Whippomorpha was both herbivorous and at least partially aquatic, implying that a shift to a piscivorous diet in archaeocete whales occurred after, and not before, their shift from terrestrial to semi-aquatic habitus.

The most primitive fossil cetaceans are from southern Asia, as is the most generalized cetartiodactyl (*Diacodexis* = '*Gujaratia*' *pakistanensis*) and various other basal members of cetartiodactyl clades – together probably Asian. Whippomorph origins otherwise remain mysterious; the oldest cetacean is the ~53.5-million-year-old (early Eocene) *Himalayacetus* from India (Bajpai & Gingerich 1998), while the oldest definitive hippopotamid is *Morotochoerus*, which first appears around 21.0 mya, in the Early Miocene of East Africa (Orliac *et al.* 2010). Boissérie *et al.* (2004, 2005) have argued that this extensive hippopotamid ghost lineage can be filled in by members of the extinct anthracotheriid



Skeleton of *Elomeryx* (from Scott 1894).

radiation, members of which have been found in Asia, North America, Europe and Africa. In particular, they place the late Miocene bothriodontine anthracotheriid genera *Merycopotamus*, from Asia, and *Libycosaurus*, from Africa, as successive sister taxa of Hippopotamidae. However, the much larger sample of taxa (73 as opposed to 32) and morphological characters (208 as opposed to 80) compiled by Geisler & Uhen (2005) placed the bothriodontine *Elomeryx* as a stem member of Suina, and not of Hippopotamidae (although their study sampled only this one anthracotheriid genus, and not *Merycopotamus* or *Libycosaurus*). Furthermore, Geisler & Uhen (2005) found support for a placement of European Palaeogene *Cebochoerus* and Eocene Asian raoellids as basal whippomorphs, whereas Boissérie *et al.*'s (2005) analysis placed *Cebochoerus* outside of a suoid–cetartiodactyl clade, and did not sample raoellids. The more recent analyses of Thewissen *et al.* (2007) and Spaulding *et al.* (2009) place the raoellid *Indohyus* as the most basal stem cetacean, but situate anthracotheriids far from whales in other positions among non-cetacean artiodactyls. Anthracotheriids, cebochoerids and raoellids clearly all deserve consideration as possible stem or crown members of Whippomorpha, but their relationships can only be resolved through more fossil discoveries and more detailed phylogenetic analyses of the cetartiodactyl radiation.

The oldest fossil whales from Africa have been found in Egypt, Nigeria and Togo, and date to about 45–43 mya (middle Eocene). Anthracotheriids are the only other possible whippomorphs that were present in Africa during the Palaeogene, and probably dispersed there from Asia in the late Eocene, about 36 mya.

The name Whippomorpha, an amalgam of whale and hippo, has not had universal acceptance and Arnason *et al.* (2000) have proposed 'Cetancodonta' for the same entity. However, Whippomorpha has priority (see Asher & Helgen 2010) and is accepted here.

Erik R. Seiffert & Jonathan Kingdon

Infraorder ANCODONTA – Hippopotamuses

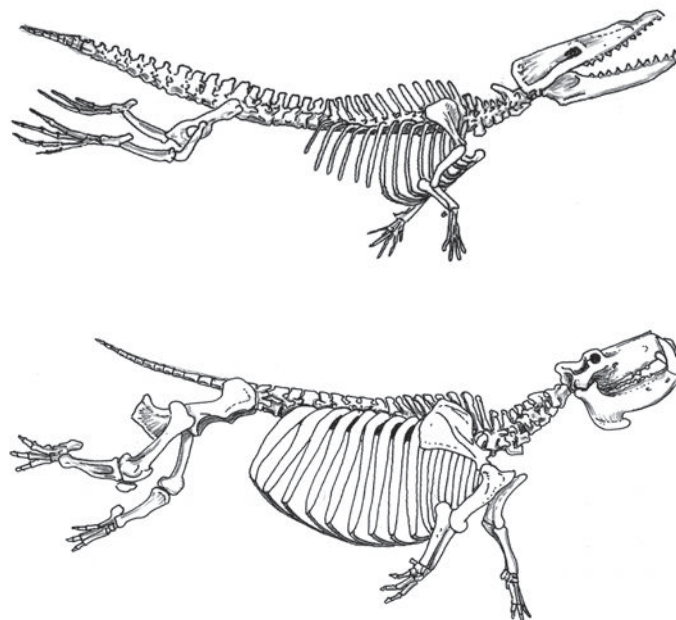
Ancodonta Matthew, 1929. Geol. Soc. Am. Bull. 40: 406.

Ancodonta was established by Matthew (1929) for primitive, tetradactyl, selenodont artiodactyls such as the caenotheres, anthracotheres and oreodonts, but has often been regarded as a subdivision of the Suiformes (McKenna & Bell 1997). Ancodonta is here provisionally interpreted as an infraorder of the Whippomorpha and includes hippos (Hippopotamidae) and anthracotheres (Anthracotheriidae), both of which have significant fossil records in Africa.

The origins of the Hippopotamidae have been hotly debated over the years, with Colbert (1935) championing derivation from the anthracotheres, and Pickford (1983, 1989, 1993) from the peccaries and other suoids. During the past decade, genetic evidence has linked hippos closely with the whales (Gatesy 1998, Ursing & Arnason 1998, Nikaido *et al.* 1999), much to the consternation of some palaeontologists because of the 40-million-year gap between the tetrapod cetaceans of the early Eocene and earliest hippos from the Early Miocene. Nevertheless, recent fossil evidence and morphological studies show close similarities between the limbs of early whales and those of early artiodactyls (Gingerich *et al.* 2001, Naylor & Adams 2001, Thewissen *et al.* 2001). Morphologically based cladistic analysis by Boissérie *et al.* (2005) has now confirmed close relationship between early cetaceans and basal anthracotheres on one hand and between advanced bothriodontine anthracotheres and hippos on the other, thereby validating Ancodonta as a coherent entity within the Whippomorpha.

The anthracotheres were a primitive group of medium- to large-sized browsing artiodactyls that were widely distributed across Eurasia and parts of Africa during much of the Cenozoic, but with a more restricted distribution (middle Eocene to middle Miocene) in North America (Kron & Manning 1998). Anthracothere skulls were often slender with elongated muzzles, robust zygomatic arches, prominent supraoccipital tubercles and elevated sagittal crests (Boissérie *et al.* 2005). Most anthracothere species retained a full complement of teeth although some displayed a reduction in number of incisors and one of the last African anthracotheres (*Libycosaurus pettochii*) evolved a fifth premolar (Lihoreau *et al.* 2006). The canines were often large and sometimes sexually dimorphic. The upper molars are wide and frequently pentacuspitate though sometimes quadricuspitate. They vary from bunoselenodont to fully selenodont and the taxon is generally divided into two clades – Anthracotheriinae and Bothriodontinae – with the latter having a more derived selenodont dentition. The limbs are short and robust and the forelimbs vary from pentadactyl to tetradactyl.

The oldest anthracotheres derive from the middle Eocene of South-East Asia, but are subsequently found elsewhere in Asia and in Europe, Africa and North America (Ducrocq *et al.* 2000). In Africa they are known from the late Eocene or early Oligocene of the Fayum in Egypt (Ducrocq 1997) and persist until the late Miocene (Vignaud



ABOVE: Skeleton of *Rhodocetus*, an early fossil whale (after Gingerich *et al.* 2001).

BELOW: Skeleton of Common Hippopotamus *Hippopotamus amphibius*.

et al. 2002). They were significant elements of the early Miocene assemblages of eastern and southern Africa, but have not been recovered south of the Sahara from sites younger than the middle Miocene. Anthracotheres have been interpreted as water-dependent or semi-aquatic based on their abundance in lignites and fluvio-lacustrine deposits (Pickford 1991). Lihoreau *et al.* (2006) have drawn attention to features such as elevated orbits and nostrils, long auditory tube and dense tympanic bullae, that suggest *Libycosaurus* species behaved similarly to the hippopotamids. That anthracotheres disappear from the fossil record at about the same time that hippos make their first appearance may suggest some kind of functional/behavioural replacement, but, as indicated above, Boissérie *et al.* (2005) have argued that anthracothere-like animals were indeed closely related precursors to hippopotami. Nevertheless, it would appear unwise to include anthracotheres within the direct lineage of living hippos as Bronner *et al.* (2003) implied by treating anthracotheres as a superfamily, the Anthracotheroidea, and interposing this taxon between the Ancodonta and Hippopotamidae.

John M. Harris

Family HIPPOPOTAMIDAE
HIPPOPOTAMUSES

Hippopotamidae Gray, 1821. London Med. Repos. 15: 306.

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|---------------------------------|---------------------|-------|
| <i>Hippopotamus</i> (1 species) | Common Hippopotamus | p. 64 |
| <i>Choeropsis</i> (1 species) | Pygmy Hippopotamus | p. 78 |

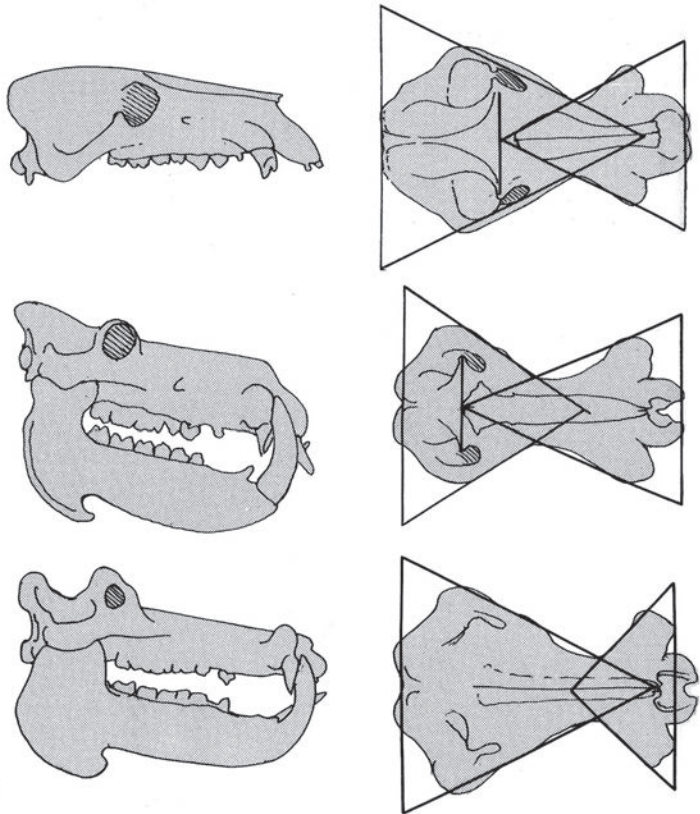
The Common Hippopotamus *Hippopotamus amphibius* is well known as a large, bulky, naked-skinned, herbivorous mammal with a wide mouth and dangerous lower tusks, which spends much of its life in water. Today, it is an exclusively sub-Saharan African species, although several centuries ago it was to be found down the Nile R. to its delta. A second living species is the Pygmy Hippopotamus *Choeropsis liberiensis* (sometimes included in the genus *Hexaprotodon*) from West Africa. This species differs by its smaller size, only two instead of four incisors in the lower jaw, a shorter face, and other characters elaborated upon in the species profile. Both species have four toes on each foot supporting the body weight, with all digits more or less equally well developed.



Common Hippopotamus *Hippopotamus amphibius* sole of hindfoot.

In the scientific history of the hippopotamuses (hereafter hippos), the Pliocene *Hexaprotodon* was long thought to be a pivotal fossil. Its type species *Hexaprotodon sivalensis*, found in India, had been described as early as 1836, and was smaller and more primitive than the Common Hippopotamus. The then new subgenus, as was implicit in its name, had a total of six upper and six lower incisors (hexaprotodonty) in contrast to only four of each (tetraprotodonty) in *Hippopotamus amphibius*. Subsequently, many fossil species of *Hexaprotodon* were collected, especially in Africa. They were predated by the earliest-known hippopotamus, represented by some small and low-crowned teeth from several sites in East Africa: *Morotochoerus*, dated to around 21.0 mya (Orliac *et al.* 2010) and *Kenyapotamus*, from 16.0–8.5 mya (Pickford 1989).

As an attempt to improve hippopotamus classification, Boisserie (2005) confined use of *Hexaprotodon* largely to Indian and South-East Asian species, and founded two more genera, *Saotherium* and *Archaeopotamus*. The first was a newly discovered fossil relative of *Choeropsis* from about 5.0–4.0 mya in Chad, which demonstrated the long separation of this stock from all other hippos. *Archaeopotamus* embraced early hippos with narrow muzzles and shorter faces, unlike the living *Hippopotamus amphibius*. Many subsequent changes centred on the front of the mandible, where the canine roots are thrust forward and outward, increasing the size of the canines and decreasing the



Profile and dorsal views of Pygmy Hippopotamus *Choeropsis liberiensis*, Common Hippopotamus *Hippopotamus amphibius* and *Hippopotamus gorgops* (from Kingdon 1982).

number of incisors. More than one evolution of tetraprotodonty took place and specialized diprotodont (two-incisored) hippos also appeared. Various Pliocene and Pleistocene species extended into western and southern Europe and, at intervals, as far north as N England and as far east as Georgia. Other branches of the evolutionary tree led to various dwarfed forms on some Mediterranean islands and on Madagascar, and to specialized large species like the East African *Hippopotamus gorgops* with periscopically raised orbits. This last species, or a parallel to it, has also been found among the European Pleistocene species in Europe. It seems to have been a feature of hippopotamus evolution that African species have often been endemic to particular drainage basins, in contrast to the present-day post-Pleistocene situation.

Hippos appear rather late in the fossil record (Theodor *et al.* 2005) and their relationship to other artiodactyl families is still being clarified. A slow-moving discussion over many decades (Colbert 1935, Kron & Manning 1998) has debated whether hippos share an immediate common ancestry with suoids (pigs and peccaries, appearing at around 35 mya), or with a different and extinct artiodactyl group, the anthracotheres, which go back to about 45 mya. Then, in the last decade of the twentieth century, came a startling development. Researchers into molecular phylogeny began to find resemblances of hippos to

whales and of the combined hippopotamus–whale group to ruminants (Gatesy *et al.* 1999, Ursing *et al.* 2000). Previously it had been accepted that archaic ungulate mammals called Mesonychidae were the sister-group or closest relatives of whales and that mesonychids and whales together were related to the artiodactyls. However, if whales and presumably mesonychids are to be closely related to hippos and then to ruminants, then the ancestor of whales would already have been an artiodactyl. Otherwise, pigs, peccaries and camels would have to constitute a separate order from other artiodactyls.

The assertion of a relationship between whales and hippos implies a primary importance for adaptations to aquatic life. Perhaps both groups evolved aquatic adaptations that were then carried much further in whales. Alternatively, the genes that hippos shared with the earliest more terrestrial whales might have allowed them readily to take up the opportunity of a life in and near water, even if the pig-related or anthracothere-related intermediates were more or less terrestrial. The intricacies of molecular data are perplexing and much will depend on understanding the sequences of bases (nucleotides)

along genes, the frequency with which they might mutate and back-mutate over thousands and millions of years, whether or not they are affected by natural selection, and the conditions governing movements or transfers of pieces of genetic material.

Within this flux, the old question continues of whether anthracotheres or pigs provide the continuity back from the earliest hippos to other artiodactyls. Boissérie *et al.* (2005) nested hippos within selenodont (= having crescentic-crested teeth) anthracotheres, then linked them to whales, then to pigs and peccaries, and only then to ruminants. The debate will certainly continue. It would be interesting to know how hippos, with or without whales in tow, connect with the family Tragulidae (chevrotains). The latter are small and primitive ruminants and still extant. Like anthracotheres they are poised between bunodonta (teeth with low rounded cusps) and selenodonta, and like hippos they had been supposed until recently to make another unusually late appearance in the fossil record.

Alan Gentry

GENUS *Hippopotamus* Common Hippopotamus

Hippopotamus Linnaeus, 1758. Syst. Nat., 10th edn, 1: 74.



Common Hippopotamus *Hippopotamus amphibius* myology of head.

There is only one living species of *Hippopotamus*, namely *H. amphibius*, which is now confined to sub-Saharan Africa (though it formerly occurred also in the Nile Delta). Dominant features of *Hippopotamus* include a barrel-shaped body, disproportionately short limbs and a large head with the eyes, ears and nostrils high up on the skull so that the animal can see, hear and breathe when almost completely submerged in the water, a condition correlated with life at the interface between water and air. All species of this genus are characterized by four incisors on both upper and lower jaws with strong development of the first lower incisors and of the canines; the enamel on the lower canines exhibits strong, convergent ridges (these ridges are diagnostic for *Hippopotamus*). It is literally amphibious, spending much of the day in lakes or rivers, which it leaves at night to graze away from the

water. Its physiology ties it to water as the skin dries and cracks if exposed to prolonged sunlight and desiccation.

The earliest hippopotamids, from outside Africa, date from the Early Miocene, but by the Pleistocene the genus *Hippopotamus*, with at least six species, was widespread throughout Eurasia although it never reached the Americas or Australia (Coryndon 1967). As with other hippopotamid lineages, there has been a great reduction in both the geographical range and in the number of *Hippopotamus* species (more than ten fossil species have been recognized). During the Pleistocene, the genus extended to Mediterranean islands and Europe north as far as England and Germany and east as far as the Caucasus. It apparently never spread far into Asia, where the genus *Hexaprotodon* dominated from the late Miocene until the late Pleistocene.

Many fossil *Hippopotamus* species have been recovered from East Africa, partly because of intense palaeontological activity in this region and an abundance of lakes and riverine flats in a volcanic region. Securely identified oldest remains of *Hippopotamus* are from late Pliocene deposits in the Western Rift Valley, and were attributed to *H. kaisensis*. This was similar, if not identical, to the living species (Pavakis 1990). Harris *et al.* (1988) and Faure (1994) also refer some early Pliocene remains from Turkana (Kenya) and Nkondo (Uganda), respectively, to *H. kaisensis*. A *Hippopotamus* sp. tentatively identified as *H. kaisensis* has also been reported in early Pleistocene deposits in Malawi (Bromage *et al.* 1995). The earlier, fragmentary African fossils are not clearly identifiable as to genera, a situation obscuring for now the origin of *Hippopotamus* (Pavakis 1990, Gentry 1999). Among other hippopotamids, Plio-Pleistocene species from Turkana and Afar Basins are anatomically the most similar to *Hippopotamus* (Boissérie 2005). Some shared characters, such as elevated orbits or development of particularly extended canine bony sockets, clearly evolved in parallel in different lineages.

Hippopotamid remains have been found over much of East Africa (Coryndon 1973, Coryndon & Coppens 1973). The only fossil



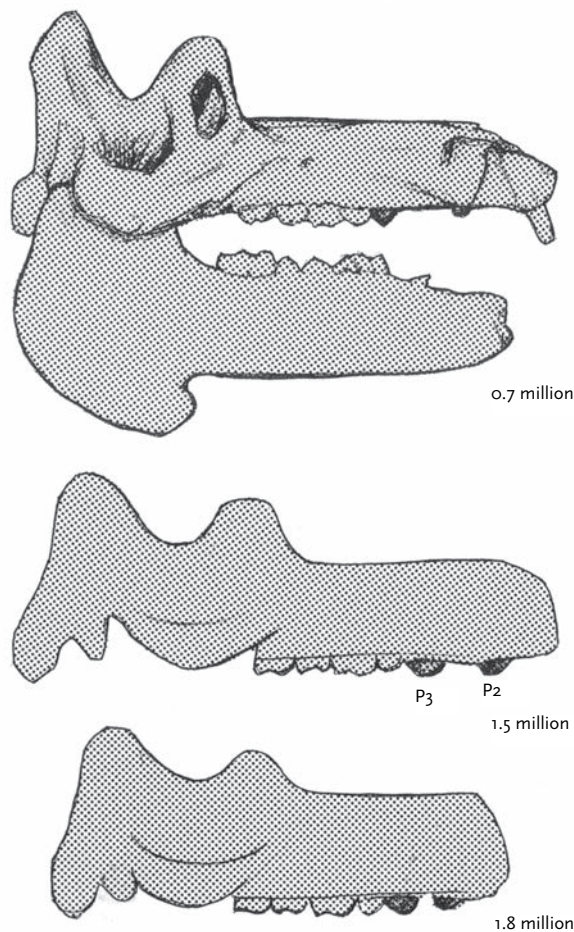
Common Hippopotamus *Hippopotamus amphibius*, yawning displays and jaw-clashing. Note the main contact on the mandible.

Hippopotamus known from southern Africa are *H. amphibius* and *H. gorgops* from the middle to late Pleistocene (Cooke 1949, Hooijer 1958). It is likely that other fossil remains that are widespread in Africa represent undescribed species.

There are several recently extinct hippopotamids that showed island dwarfing including those on Malta and Cyprus. These Mediterranean dwarfs are close to *H. amphibius*, but have been assigned to separate species (Boekschoten & Sondaar 1972, Capasso Barbato & Petronio 1983). Two dwarfed forms on Madagascar described from sub-fossil remains, *H. madagascariensis* and *H. lemerlei*, have also been given specific status (Stuenkel 1989), although Fovet *et al.* (2011) suggest that *H. madagascariensis* is a synonym of *H. lemerlei* (and concomitantly propose a new species, *Hippopotamus guldbergi*, based on a skeleton formerly

attributed to *H. madagascariensis*). *Hippopotamus lemerlei* survived until about 1000 years ago (Dewar 1984, Burney *et al.* 2004). There was also a large species, *H. laloumena*, of Holocene age on Madagascar (Faure & Guérin 1990), but it may reflect an invasion of *H. amphibius* from mainland Africa (Burney *et al.* 2004). This colonization and the discovery of hippos well out to sea confirm its ability to swim and disperse.

It is interesting that during the middle Pleistocene a cranially more archaic species, the extant *H. amphibius*, should have replaced more highly specialized species, among them *Hippopotamus gorgops*. A prime advantage would seem to have been the living species' possession of dentally more derived (higher-crowned) cheekteeth, implying that a greater ability to survive on coarser forage has been decisive. Another implication is that hippos seem to have evolved



Evolution of *Hippopotamus gorgops* at Olduvai (after Coryndon 1970).

to occupy more constrained and constricted niches than those they occupy today. Modern-day *H. amphibius* presumably now occupies a broader niche than it once did.

Hippopotamus gorgops, named for its protuberant, periscope-like eyes, exemplifies several of the most extreme features of its genus (Coryndon 1971). The trend towards ever-heavier, longer lower jaws, but lighter, shallower skulls is well illustrated by a series of fossils of *Hippopotamus gorgops* from 1.8, 1.5 and 0.7 mya, all from Olduvai. Correlated with the heavy lower jaw and its multiple functions, there have been extraordinary reorganizations of articulation between lower and upper jaws (and between skull and backbone) as well as wide expansion at the front of both jaws. The adaptive function of these uniquely hippopotamid peculiarities can all be related to an intensely social life, especially intra-specific competition among ♂♂ fighting for mating rights in confined, relatively shallow waters. With bodies immersed in water or mud, but eyes and muzzle above the surface, dominant individuals snap at one another or threaten with open jaws on or above the water's surface and each tries to catch or engage its opponent's jaws. The outcome of fights, for both contestants, depends on testing strength, weight and the ability to ram, bite or engage with the teeth in a manner analogous to antler-clashing. Since the lower jaw must simultaneously serve as a weapon of offence as well as defence, the incisors and canine teeth (and their bony sleeves) have made a phylogenetic increase in size and breadth to withstand the impact of up to 3000 kg of biomass behind

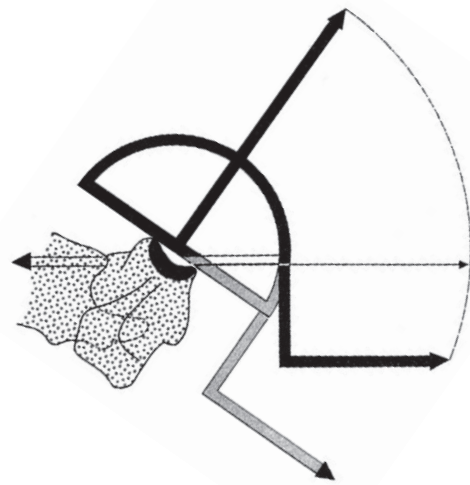
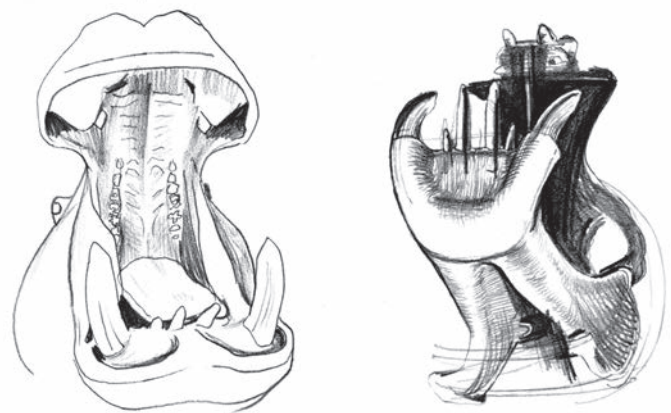


Diagram of the skull and lower jaw rotation on the first cervical vertebra.

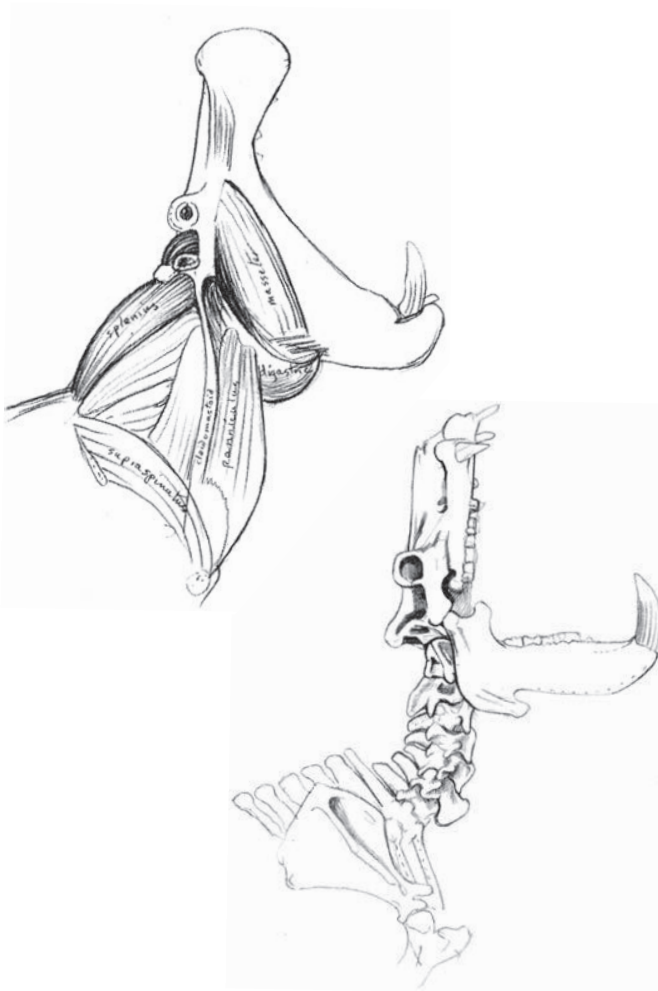
an assault (Kingdon 1979). The celebrated hippo 'yawn' probably serves several social purposes, but among them must encode telling information about the yawner's status.

Hippopotamus is almost unique in evolving a mandible that is heavier than the skull above it and this peculiarity has clearly evolved to both deliver and absorb the main force of such jaw clashes. While the entire body, especially the neck and champing muscles, provide the weight and power behind contests, the neck-skull and skull-jaw articulations would be vulnerable to dislocation were it not for the mandibular condyle migrating to the very back of a heavily reinforced cranium. Here, the condyles are close to the occipital junction with a large and cup-like atlas (first of the cervical vertebrae, all of which are exceptionally dense and compact). This arrangement allows the entire body to deliver and absorb jaw clashes and it also permits the cranial part of the skull to jack-knife vertically upwards while the mandible remains horizontal, a uniquely hippopotamid capacity.

Hippo species have varied in the number, size and orientation of their incisors, sometimes within a species, most notably in *H. amphibius* (Coryndon 1970). Hexaprotodont hippos keep the full complement of six incisors, tetraprotodonts have four, while diprotodonts have reduced their incisors to two. Perhaps the most extreme example of expansion at its front end is the mandible of a highly aquatic



Common Hippopotamus *Hippopotamus amphibius* gaping skull (left) and reinforced front of mandible (right).



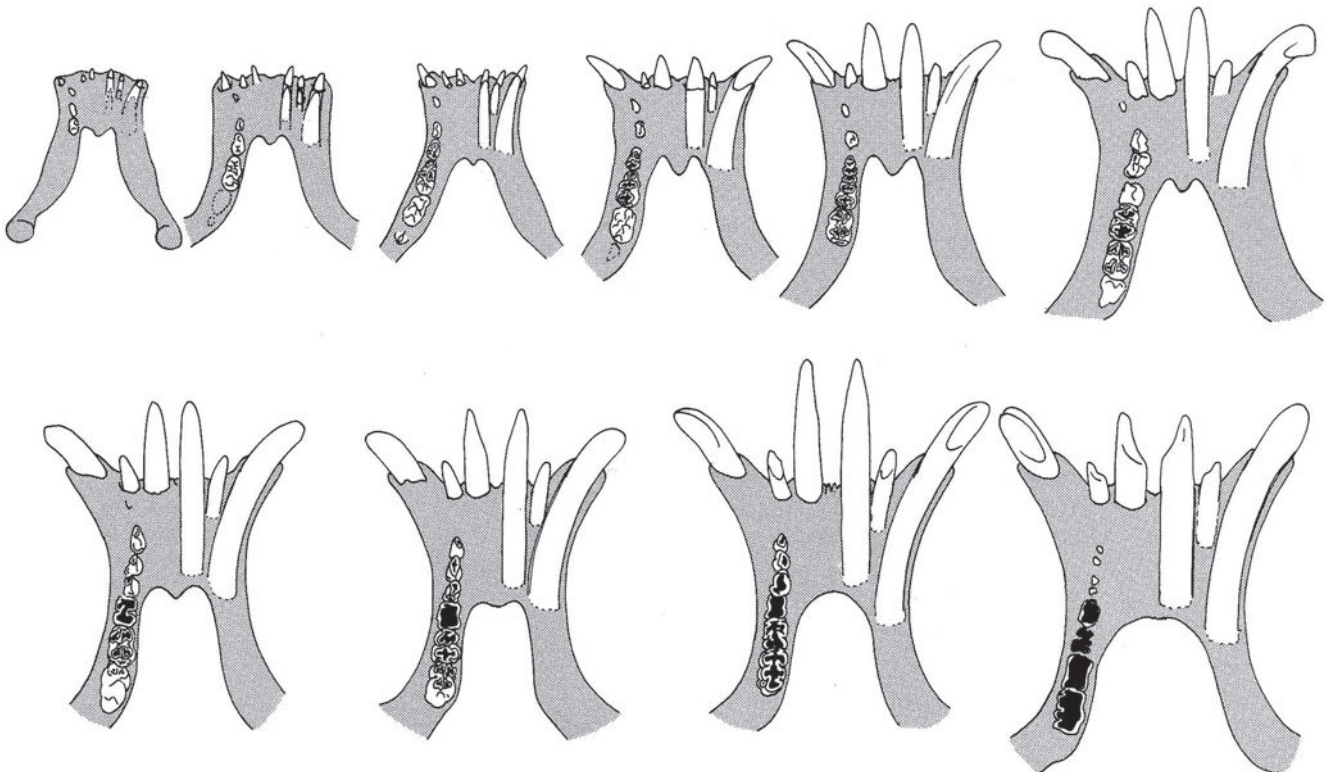
Pleistocene diprotodont hippo, aff. *Hippopotamus karumensis*, where relatively small canines are encased in disproportionately heavy, projecting, antler-like bony sheaths. The single pair of remaining incisors instead are long, massive and also resemble the tines of an antler. Thus, the front end of the mandible (and upper jaw) has widened in every hippo species and genus, with many permutations of tooth proportions, presenting a flattened (but toothy) frontal plane that in some respects resembles the bull-bars attached to heavy cross-country vehicles.

As with any other mammal, a hippo skull accommodates visual, auditory and other sensory equipment, a brain and a battery of masticatory teeth together with all the musculature and anchorage to serve or encase all these functions. In terms of the hippos' external forms, all such functions have become subordinate to weight and aggression-testing behaviour in very large amphibious animals. Front teeth that once took bites of food have been elaborated in various ways to serve these agonistic purposes, leaving the lips to take over the function of cropping. The swollen, flat-fronted mouths that characterize all species in this genus therefore reconcile both cropping and hydrodynamic properties as well as providing a covering for one of the most extraordinary elaborations of incisor and canine teeth to be found in any mammal.

**S. Keith Eltringham, Jonathan Kingdon &
Jean-Renaud Boissarie**

LEFT: Myology and osteology of Common Hippopotamus *Hippopotamus amphibius* gape.

BELOW: Common Hippopotamus *Hippopotamus amphibius* successive age states of mandible (after Laws 1968).



Hippopotamus amphibius COMMON HIPPOPOTAMUS

Fr. Hippopotame; Ger. Flusspferd

Hippopotamus amphibius Linnaeus, 1758. Syst. Nat., 10th edn, 1: 74. 'Habitat in Nilo & Bambolo Africae et ad ostia fluviorum Asiae'; restricted to River Nile (Thomas 1911: 155) in Egypt (G.M. Allen 1939: 457).



Common Hippopotamus *Hippopotamus amphibius*.

Origin of name: Greek *hippos* = horse; *potamos* = river.

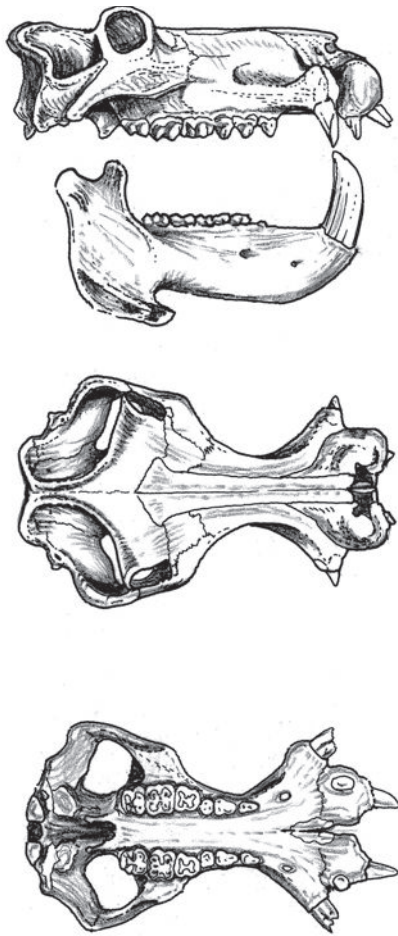
Taxonomy Five subspecies of Common Hippopotamus (hereafter Common Hippo) have been proposed (Lydekker 1915), based primarily on skull shape and proportions, but their validity is uncertain (Ansell 1972, Grubb 1993a, Eltringham 1993a, 1999); subspecies are never distinguished in published studies of Common Hippo ecology or behaviour. Grubb (1993a) noted that there has been no serious attempt to determine the geographic distribution of the species and that additional specimens need to be examined from a wider area in order to determine whether the diagnostic skull characters currently used to differentiate subspecies are more than just abnormalities of certain specimens. Likewise, Eltringham (1993a) remarks that subspecies cannot be distinguished in the field and that given ranges are indistinct. However, a study using mitochondrial DNA from skin biopsies (Okello *et al.* 2005) found low, but significant, genetic differentiation among *H. a. amphibius*, *capensis* and *kiboko*, thus confirming the subspecific division and nomenclature; *H. a. amphibius* is considered the ancestral group. Also, there is evidence that Common Hippos experienced a marked population expansion during or after the Pleistocene, due to an increase in water bodies at the end of this era. Provisional recognition of five subspecies here follows Grubb (1993a). Synonyms: *abyssinicus*, *australis*, *constrictor*, *senegalensis*, *typus*. Chromosome number: $2n = 36$ (Hsu & Benirschke 1977).

Description Unmistakable species, characterized by great barrel-shaped body, naked skin, and short, but stout, legs. Head broad and heavy, the eyes raised on bony sockets on top of the head, and raised

nostrils on top of the rhinarium. Ears are small relative to the size of the head. Body dark reddish-brown, ventral surface pink, with individual variations in extent of pink. Skin with fine short hair, 20–30 per 100 cm², especially on the back, with thick bristles on snout and tail, and sparse covering of hairs on sides of the head and neck, lips and tips of ears. The tail is short and flattened. There are four toes on each foot, with each toe ending in a broad, heavy nail. Adult bulls are recognized by their strong muscular neck, proportionally larger head and, on the muzzle, prominent bulges accommodating the lower canines; ♂♂ are about 10% heavier than ♀♀ (Eltringham 1999). Females have one pair inguinal nipples.

The skull is characterized by a small braincase, high supraorbital ridges (associated with the position of the eyes on top of the head), and high supraoccipital and sagittal crests. The postorbital bar is complete in old specimens, usually with a distinct bony knob at the junction of the two bones. The zygomatic arches are thick and swing outwards at the back, giving room for the temporalis muscles. The massive zygoma give firm anchorage for the masseter muscles, while the high supraoccipital and sagittal crests extend the surface of the sides of the small braincase for the attachment of the large temporalis muscles that pass through the massive zygomatic arch. The temporalis and masseter muscles need to be particularly powerful to lever the massive lower jaw with its accompanying huge, heavy teeth (which may have a mass of up to 16 kg) (Eltringham 1999, Skinner & Chimimba 2005).

The dental formula is $I^{2/2}, C^{1/1}, P^{3-4/3-4}, M^{3/3} = 36-40$, reduced from the ancestral 44. Common Hippos carry four formidable, tusk-like canines, and eight shorter and more rounded incisors. Both canines and incisors have open roots and continue to grow throughout life. The canines in the lower jaw are the largest and



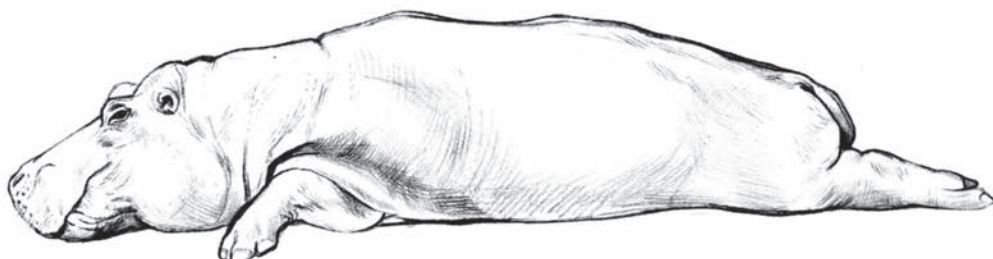
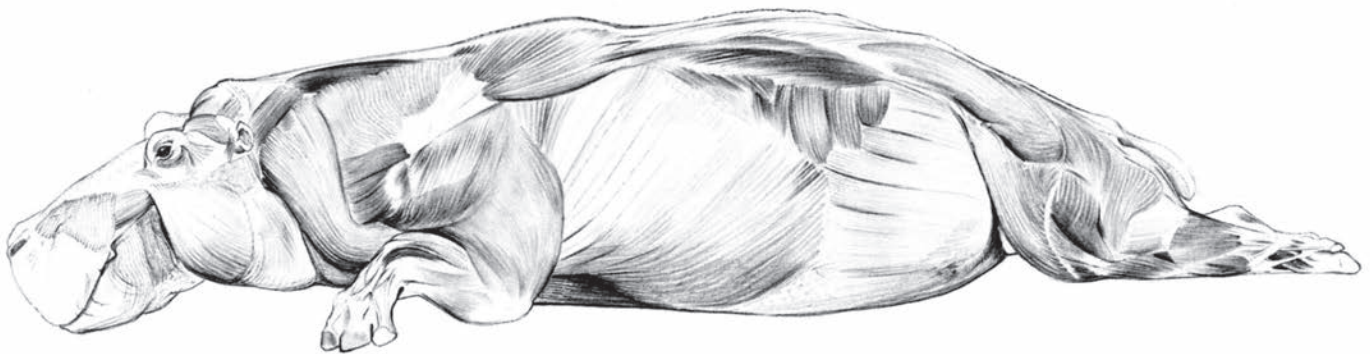
Lateral, dorsal and palatal views of skull of Common Hippopotamus *Hippopotamus amphibius*.

heaviest of the teeth. They are triangular in section, with the flat face on the inner side, and are distinctly ridged along their length. The canines in the upper jaw, through wear, remain short but very sharp-edged. The inner face of the canines, through occlusion with its short counterpart in the upper jaw, is continually honed to a flat surface, keeping the point and sides of the tooth sharp. Canines project for about 300 mm from the gum, although the root may be some 400 mm in length, bringing the total to 700 mm. The incisors, like the canines, wear by occlusion on their inner faces, and remain round and blunt-pointed. The outer incisors are larger than the inner pair. The upper incisors are rounded, while those in the lower jaw are triangular in cross-section. The canines in ♂♂ are markedly larger than those of ♀♀. Neither the incisors nor the canines are used in feeding, this job falling to the cheekteeth. The molars are roughly squarish, with a cusp in each quarter (Eltringham 1999, Skinner & Chimimba 2005).

At birth Common Hippos appear to have only the central incisors and canines protruding through the gums. These are shed within the first few months of their life. Four deciduous premolars may be present below bone level. The second, third and fourth are replaced by permanent teeth; the first is present only in the milk set and not subsequently replaced, although it often persists quite late in life; when retained, the tooth is small and vestigial, and separated from the other premolars by a diastema (Eltringham 1999, Skinner & Chimimba 2005).

Geographic Variation

H. a. amphibius: Gambia east to Sudan, Ethiopia, N DR Congo, Tanzania and Mozambique; extinct in Egypt, where they occurred in the Nile Delta and on the lower Nile R. (and may have represented a distinct subspecies; see Manlius 2000a). Skull with moderate preorbital



Common Hippopotamus *Hippopotamus amphibius* myology.

constriction, convex upper surface, long mandibular symphysis and relatively large cheekteeth (Grubb 1993a).

H. a. tschadensis: Chad and Nigeria. Similar to nominate form, but with prominent orbits. Compared with *capensis*, has shorter and wider facial region and more forward direction of orbits (Grubb 1993a).

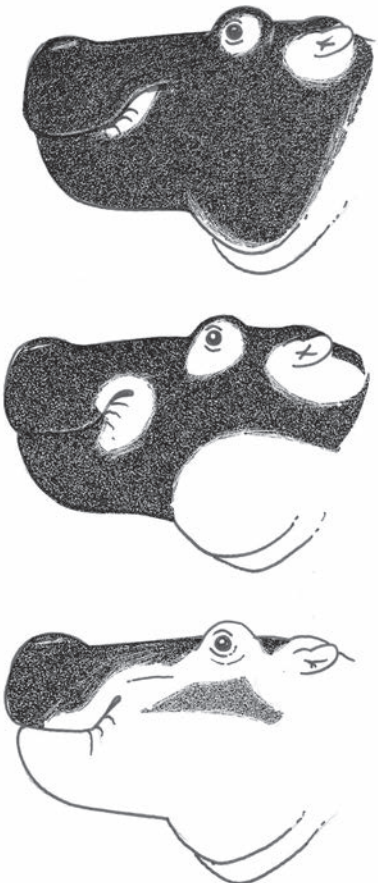
H. a. kiboko: Kenya and Somalia. Skull with broad nasals, relatively small rostral constriction, and elevation of orbits and occipital crest above the hollowed interorbital region. Orbits more circular than *capensis*, and more prominent than in *constrictus* (Grubb 1993a).

H. a. constrictus: Angola, S DR Congo and Namibia. Skull lighter than in typical race with preorbital constriction deeper, upper surface more flattened, muzzle less expanded, mandibular symphysis shorter and cheekteeth smaller (Grubb 1993a).

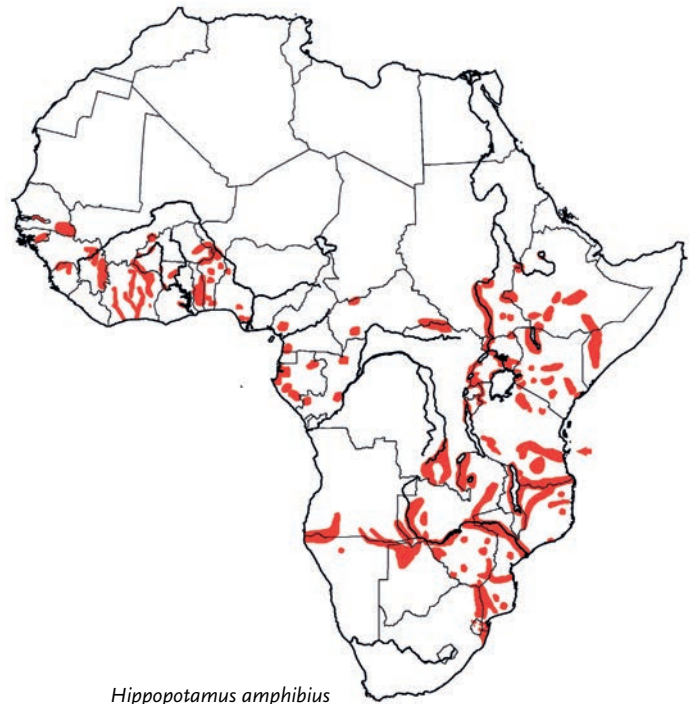
H. a. capensis: Zambia south to South Africa. Skull more flattened than in *tschadensis*, such that width of orbit is greater than height (Grubb 1993a).

Similar Species

Choeropsis liberiensis. Largely allopatric, although range overlaps with *H. amphibius* in the upper stretches of some rivers in Côte d'Ivoire (see Roth *et al.* 1996, 2004) and in NW Sierra Leone (Grubb *et al.* 1998). Smaller overall size, but with relatively longer limbs; one pair of lower incisors only; in the skull, the orbits are positioned on the side of the head and are situated in a more mid-way position along the length of the skull. For a comparative review of *Choeropsis* and *Hippopotamus* see Eltringham (1999).



Common Hippopotamus *Hippopotamus amphibius* variations in skin pigment (from Kingdon 1982).



Hippopotamus amphibius

Distribution Common Hippos are endemic to Africa, ranging widely over most of sub-Saharan Africa, from Senegal and Gambia in the west to Sudan, Ethiopia and Somalia in the east, and south to KwaZulu–Natal in NE South Africa, the Okavango Delta in Botswana and the Kunene R. in Namibia. They are restricted to suitable areas, i.e. grassland with river/lake/swamp; absent from rainforest except for rivers with adjacent grass patches.

In the past Common Hippos occurred in the Nile R. all the way to the Nile Delta, and up until 1700 were still present in two disjunct zones in the Nile Delta and in the upper Nile; the last definite records from Egypt come from the early 1800s, their disappearance principally caused by hunting (see Manlius 2000a). Common Hippos also occurred in the Sahara, and in South Africa right to the Cape where they have been wiped out in historic times (Kingdon 1979). In the recent past they have been locally eradicated or severely reduced (for example, the populations of the crater lakes around Dongobesh, Basodesh and Hanang in Tanganyika have completely vanished over the last 50 years; J. Kingdon pers. comm.), although the general range has not changed much (Eltringham 1999). Apparently, previously present on Mafia I., and possible that they still occasionally occur (see Kock & Stanley 2009 for discussion); excluded from the fauna of Zanzibar and Pemba by Pakenham (1984).

Habitat Common Hippos require water for thermoregulation and skin protection and are therefore never far from a water source, be it river, lake, swamp or wallow. Common Hippos feed predominantly on grasses, so their range is limited to grasslands and grassland–bushland mosaics within reach of water (even where they occur in saline water, grazing and freshwater are essential). They may use established pools over a period of many years, so long as there is sufficient food available and they remain undisturbed; seasonal flooding may cause them to move temporarily from their established resting pools. Jacobsen & Kleynhans (1993) demonstrated the importance of weirs as refuges for Common Hippos in South Africa's

Limpopo R., with 50% of all sightings of Hippos occurring along stretches of the river where weirs, which provide permanent water, are prevalent.

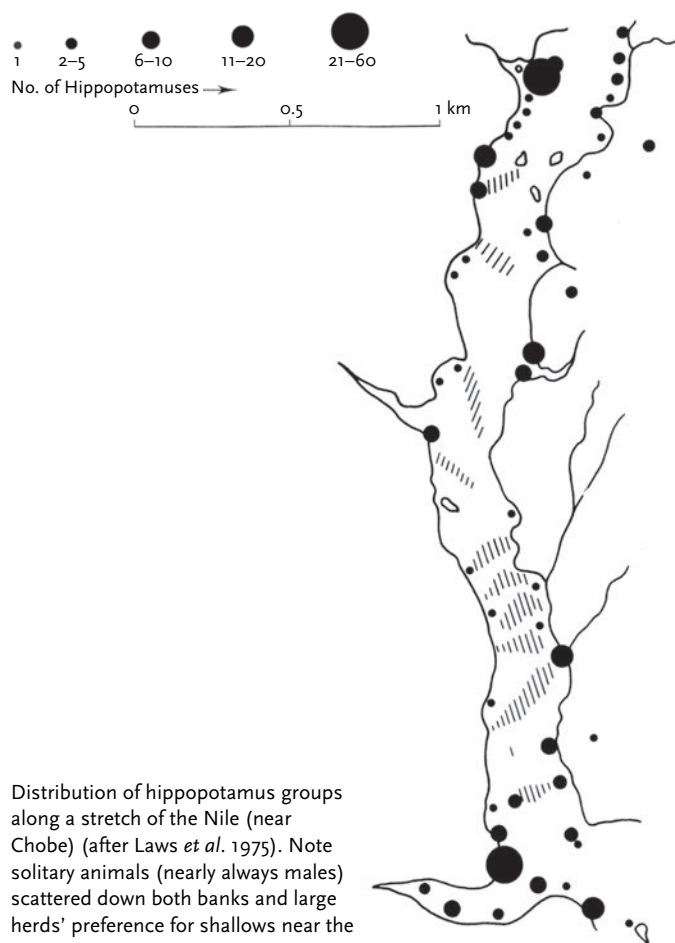
Abundance Common Hippo counts are bound to be inaccurate, as the subjects are usually submerged and do not synchronize their surfacing. Accurate figures can be obtained of individuals and groups when they are in shallow and/or clear water, and when they come on land during the day.

In 1988/1989 Keith Eltringham conducted an Africa-wide survey and estimated a total of 173,690 Common Hippos: West Africa (up to, and including, Chad, Central African Republic, Congo), 7750; East Africa (Ethiopia, Somalia, Kenya, Uganda, Sudan, DR Congo, Rwanda, Burundi, Tanzania), 79,550; and southern Africa (up to, and including, Mozambique, Malawi, Zambia and Angola), 86,400. Only some of the eastern and southern African populations in conservation areas were considered largely stable and reasonably secure. He reports that in 18 of the 34 countries in which surveys were conducted, populations were thought to be declining (Eltringham 1993a, 1999). Lewison (2004) conducted a similar survey and found that, continent-wide, Common Hippo populations have declined between 7 and 20% over the past ten years. This new estimate suggests that total populations are 125,000–148,000, with reported declines in 18 countries. Stable populations were reported in Chad, Ethiopia, Kenya, Malawi, South Africa, Tanzania and Zimbabwe, and increasing numbers only in Zambia. Largest numbers were found in Zambia (40,000), Tanzania (20,000–30,000), Mozambique (18,000) and Malawi (10,000).

Historically, the highest densities have been recorded in the Queen Elizabeth N. P., Uganda, with 28 individuals per km² of suitable grassland. The corresponding biomass amounts to 28 tonnes/km² (Field & Laws 1970). Even larger Common Hippo populations were found in Virunga N. P., DR Congo, in the 1970s (Delvingt 1978). However, civil unrest has resulted in a severe depletion (>90%) of the population in this park (Hillman Smith *et al.* 2003, Lewison 2006).

Adaptations Common Hippos are highly adapted to their amphibious life-style. The epidermis is thin (up to 1 mm thick on the back), and as it is very well supplied with nerve endings, is very sensitive and delicate. Common Hippos reacted strongly when hit with drops of paint ejected from a medical syringe (for marking) (H. Klingel pers. obs). Slight scratches from bushes often result in bleeding wounds that heal quickly. The epidermis dries and cracks easily, so must be kept moist. The dermis is up to 60 mm thick on the back and flanks, thinner on head, neck and belly, and is composed of fibrous collagen. The skin accounts for about 18% of total body weight. Hippos have no true sweat glands. However, a viscous alkaline secretion (pH 8.5–10.5), ranging from colourless to reddish-brown, is produced by large, subdermal glands (distributed at a density of about 1/cm²). This secretion imparts a pinkish tinge to the body and has antiseptic properties, preventing infections and sunburn and helping in thermoregulation (like sweat) (Luck & Wright 1964, Wright 1964, 1987, Eltringham 1999, Saikawa *et al.* 2004).

The skin serves to control body temperature primarily through regulation of evaporation, which is very high compared with other mammals, and is particularly high when the skin is wet with the secretion from the subdermal glands (Wright 1987). This led Eltringham (1999) to suggest that temperature control is not achieved through

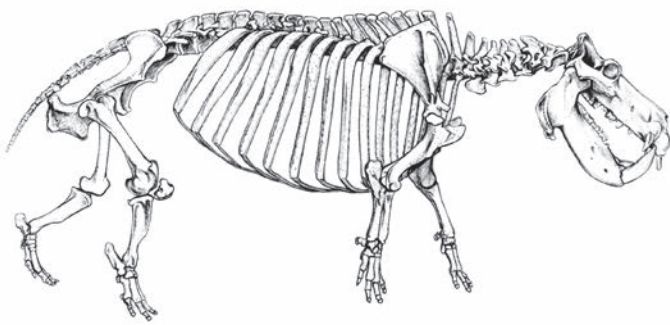


Distribution of hippopotamus groups along a stretch of the Nile (near Chobe) (after Laws *et al.* 1975). Note solitary animals (nearly always males) scattered down both banks and large herds' preference for shallows near the mouths of tributaries.

any mechanism akin to sweating unless the secretion functions like sweat, and that they may not be able to control the rate of water loss from the body. Whether or not the secretion serves the same function as sweat, Common Hippos maintain a constant core body temperature of around 36°C even while on land (though body temperature is certainly also controlled by using its aquatic environment as a means of cooling off) (Eltringham 1999). When dry it gives a shiny varnish-like appearance.

When in the water, Common Hippos lift their slit-like nostrils up to the surface to breathe, at intervals of up to 6 min. A reflex response ensures that the nostrils and ears are closed as soon as they come into contact with water. By lifting the head above the water level, the ears, eyes and nostrils are allowing for visual, acoustic and olfactory perception. Because of the insulating properties of their thick skin, heat loss in the water is greatly reduced, the skin functioning as a 'diving suit'. This, however, is an obvious disadvantage when moving on land as it reduces metabolic heat dissipation. Therefore, Common Hippos undertake the long excursions to their grazing grounds during the cooler night hours.

Although Common Hippos spend much time in the water, they can neither float nor swim – at least there is no convincing evidence that they do in freshwater. They can even sink to the bottom fully inhaled, and they exhale under water or when they come up for the next breath. This can easily be observed in the wild. In Mzima Springs in Tsavo West N. P., Kenya, the Okavango in Botswana, and in some zoos, Common Hippos can be observed walking on the



Common Hippopotamus *Hippopotamus amphibius* skeleton.

bottom. Depending on the depth of the water, the animals lie in sternal recumbency on the bottom, either fully under or with just the tops of their backs showing; in deeper water they stand on all fours, and in even deeper water they stand on their hindlegs. To reach the surface, they either just lift the head or they push themselves off the bottom. Shallow water for the adults is deep water for the infants who have the option of standing on their hindlegs, pushing themselves up for breathing, or of sitting on their mothers' backs, apparently floating like a cork when the mother is submerged. It is quite possible that Common Hippos are able to swim in seawater, and that would explain their former appearance on Madagascar, Cyprus and Malta as well as on islands off the African coast. As the sea levels were lower during the Pleistocene than at present, the distances to be covered would have been considerably shorter. It is still a remarkable achievement for Common Hippos not only to have reached Madagascar, but also to have established viable populations there for tens of thousands of years. This achievement is even more impressive when one realizes that none of the many other ungulate species of Africa that are good to excellent swimmers ever managed to make it across to Madagascar.

The colonizing effort and success of Common Hippos on dry land is also quite remarkable. Examples are the population of the Basodesh–Dongobesh–Hanang craters in the driest part of Tanganyika and of the Ngorongoro population. The founders must have negotiated their way over long and unknown stretches of waterless terrain, and for Ngorongoro they climbed the outer crater slope and down the inner one. A journey of ca. 1800 km over a period of three years over unknown country was well documented in the South African press when, in the late 1920s, Huberta the Hippo travelled from L. St Lucia in KwaZulu–Natal to near Port Elizabeth (Chilvers 1931).

Common Hippos have a graviportal skeleton, being designed specifically to support their great weight. The bones of the skeleton are massive, particularly the spinal vertebrae, although the limb bones are not as heavy as may be expected in such a large animal (presumably because much of the weight of the Common Hippo is supported by water) (Eltringham 1999). When at ease, locomotion on dry land is a slow walk, each step being accompanied with a nod. When fleeing or attacking, Common Hippos perform a speedy trot and can exceed 30 km/h. Indeed, despite their heavy build, they are swift and agile and are able to climb steep slopes. Under water they move as on land except for the head nod, but, in addition, they can perform a series of forward jumps, pushing themselves up from the bottom, breaking the surface and diving in again, all in a seemingly dolphin-like manner and attaining impressive speeds that have not yet been timed.

Common Hippos spend most of the daylight hours resting and most of the night feeding. Activity pattern is influenced by weather. In dry, hot weather most animals come on land in the late morning to rest for several hours in the sun on the foreshore. In cool weather, and when it rains, they either stay in the water or come out to feed near the shore. At St Lucia in South Africa, Common Hippos, especially the subadults, bask mostly during the winter months when the water is coldest (R. Taylor pers. comm.). Where they are disturbed, generally outside protected areas, they stay in the water throughout the day. At dusk they leave the water and walk inland to their grazing areas, which can be up to 10 km from the shore (Kingdon 1979, H. Klingel pers. obs.).

During the dry season when the grass is dry, coarse and scarce, Common Hippos often feed throughout the night and even stay on for some hours in the morning before returning to the water. When during the rains food is abundant, the Common Hippos often take a rest of up to several hours in the grazing area, lying down under bushes, or they even return to the water to rest there, and then walk back to the grazing area for another helping. During the wet seasons, in the Queen Elizabeth N. P., a portion of the population emigrated from the lake-shore and settled down in wallows within the grazing areas. When the wallows dried up the animals returned to the resting places from where they had departed.

The shape of the muzzle is adapted to feeding unselectively, in a lawn-mower-like fashion. The grass is plucked with the horny lips, not with the front teeth, and torn off. The head is swung from side to side during the process. This is a rare feature, the only parallel being the White Rhino *Ceratotherium simum*. The stomach consists of four major compartments. The two anterior ones are diverticula and are fermentation chambers as is the next (third) chamber, the fourth serving for gastric digestion (Crisp 1867, Arman & Field 1973, Clemens & Malojy 1982). The first three chambers are lined with papillae, the fourth is glandular. The anatomical and functional similarities with the stomach of ruminants are obvious, and Common Hippos are often referred to as pseudo-ruminants (Arman & Field 1973, Van Hoven 1978, Eltringham 1999). Ciliate protozoa have been identified as symbionts (Van Hoven 1974). A gall bladder is present (Ganzberger & Forstenpointner 1995).

Foraging and Food Common Hippos are predominantly grazers, although isotope studies show that many Common Hippos have a significant (more than ca. 15%) browse component in their diet (Cerling *et al.* 2008). Lists of species of food plants, seasonal differences in availability and preferences are given by Field (1970a, 1972); in this study, grasses consistently taken included *Bothriochloa* sp., *Bracharia decumbens*, *Chloris gayana*, *Cynodon dactylon*, *Heteropogon contortus*, *Hyparrhenia flipendula*, *Sporobolus pyramidalis* and *Themeda triandra*. Dicotyledons are eaten accidentally where they are interspersed in the grass. In extreme situations Common Hippos feed substantially on woody plant browse (in Queen Elizabeth N. P. especially from *Cassia* sp.) and the fruit of some trees, such as the Sausage Tree *Kigelia pinnata*, are taken as well (Ansell 1965, H. Klingel pers. obs.). Aquatic vegetation is usually rare in Common Hippo waters and thus rarely taken, except locally for the Nile Cabbage *Pistia stratioides*, which, in the Queen Elizabeth N. P., is taken in small quantities during the dry seasons (Field 1970a, H. Klingel pers. obs.). In St Lucia, KwaZulu–Natal, Common Hippos eat fairly large quantities of Water Lilies

Nymphaea cerulean and the submerged macrophytes *Ruppia cirrhosa* and *Potamogeton pectinatus* (R. Taylor pers. comm.). On the plains of L. Rutanzige in Virunga N. P., DR Congo, Mugangu & Hunter (1992) found that when dry season grasses failed to yield sufficient crude protein, Common Hippos were observed to feed on aquatic vegetation.

According to a spatially explicit individual-based foraging model (Lewison & Carter 2004), Common Hippos appear to employ foraging strategies that respond to vegetation characteristics, such as vegetation quality, as well as spatial reference information, namely distance to a water source. Because of their wide, square muzzle, they feed unselectively with respect to individual plant species, but they do select the swards to a certain extent. Grazing grounds are used in an irregular pattern, and they also change with the quality and quantity of available food.

The weights of stomach contents are remarkably low and have been determined at ca. 1% (dry weight) of body weight, which is only 50% of that of other large herbivores. The stomach contains two nights' intake, and daily intake is in the order of 20 kg dry weight (Field 1970a, Arman & Field 1973, Eltringham 1999).

Where they occur in high densities, Common Hippos shape the environment. Olivier & Laurie (1974) recognize a cyclical ecosystem in which Common Hippos play the key role. The heavy grazing pressure reduces the amount of combustible material, thereby suppressing grass fires and enhancing the spreading of bushes. This in turn will lead to a reduction of grazing area and eventually to a reduction in Common Hippo numbers and density. Reduced grazing will result in higher grass growth, fires will spread, bushes and trees will be burnt and destroyed, grassland expand and Common Hippo numbers increase again. In swamps, the paths of the Common Hippos can alter the pattern of water flow, like on the banks of L. St Lucia, and thereby have an important ecological influence (R. Taylor pers. comm.). In extensive swampy areas, like the Okavango, the movements of Common Hippos create and maintain deep, clear channels through the reed-beds and permit freer movement of the water. In backswamp areas, pathways lead to the development of new channel systems during channel avulsion (McCarthy *et al.* 1998) (see also Deocampo 2002).

Exceptionally, Common Hippos have been observed to kill antelope such as Impala *Aepyceros melampus* and Common Wildebeest *Connochaetus taurinus* and livestock (e.g. La Hausse de Lalouvière & Wood 1989, Dudley 1996, 1998, Estes, in Eltringham 1999), and also to scavenge from them and even from the cadavers of conspecifics. The likely explanation is mineral deficiency in the 'normal' diet (Eltringham 1999). Licking the skin of conspecifics (R. Taylor, pers. comm.) may have the same cause. Young animals have the habit of eating dung of conspecifics; this also occurs in other ungulates and is considered to be the mechanism for transmitting intestinal symbionts. Adults are also known to feed on elephant dung, suggesting that partially digested plant material constitutes an important forage resource for Common Hippos during dry periods (Dudley 1996).

By defecating in the water Common Hippos fertilize rivers and lakes. They are thus causal for the vast harvests of fish, for example, of Lakes George and Edward in Uganda and DR Congo.

Social and Reproductive Behaviour Except where noted, the following account is based on the author's investigations from 1974 to 1979 in the Queen Elizabeth N. P., with some follow-up in the same area and in other parts of Africa, namely Mara R., Kenya;

Okavango Delta, Botswana; and Luangwa and Kafue Rivers, Zambia (Klingel 1979, 1989, 1991, H. Klingel pers. obs.). In two study areas in Queen Elizabeth N. P., more than 200 Common Hippos, the majority of the adult and subadult residents and including all key individuals, could be identified from various natural marks like scars, cuts in the ear pinna, missing ear pinnae, damaged or missing tails, colour and colour pattern. Seven Hippos were immobilized and marked with ear tags, streamers and paint, and 20 more were sprayed with paint for recognition at night.

The social organization of the Common Hippo is based on mating territoriality. Although true dominance relationships do not seem to exist in Common Hippo groups, some of the adult bulls, of the order of 10%, occupy territories in which they are dominant over all conspecifics and where they have exclusive, but not unchallenged, mating rights. Among the other group members, vague and anonymous dominance relationships roughly correlated with size can be observed, but there was no evidence for individualized dominance.

Territories extend along the shorelines of lakes and rivers in the water and include a narrow stretch of the bank. The sizes of territories vary considerably: in the Mweya Peninsula study area they measured from 250 to 500 m along the shore of L. Edward, while in the Ishasha R. study area only 50–100 m. In Ishasha, they included both banks of the river; in Mweya the outer, lake-ward boundary was not defined as there were no neighbours. In swamps, the territories were arranged in a mosaic pattern.

Bulls keep their territories for long periods of time, and they never give them up voluntarily. But occupancy is always intermittent as the bulls, like the rest of the population, emerge at night to feed. Actual tenure is considered to depend on the number of competitors, chance and physical strength. In Mweya, four of six territories were occupied by the same bulls for the whole period of observation, i.e. 4.5 years. Two of the bulls were still territorial in their original territories in September 1982, almost eight years after they were first recorded, and one of them even after 12 years. In the Ishasha study area, recorded tenure was from a few months to over two years, i.e. throughout the investigation, changes in territory boundaries, takeovers and the establishment of new territories in previously unoccupied places could be documented. From the available data, the maximum tenure can be estimated to span the whole adult life of a bull, i.e. in the order of 20–30 years.

Size of the territories, frequency of takeovers, boundary changes and length of occupancy seem to be inversely correlated with density. In Mweya, density was only 7 animals/100 m shoreline, whereas in Ishasha it was 33 animals/100 m. However, other factors are important as well. In Ishasha, some of the territorial changes were caused by changes of the course of the river, the water level and current. During the study one branch of the river fell dry and, consequently, the whole territorial set-up changed, as two out of seven bulls gave up and moved out of the area, and the others rearranged their territories. Later, during a flood, all the Common Hippos left the area. Some settled in a dead meander of the same river, others invaded a newly formed swamp, where they immediately started to establish new territories.

Territories are advertised by the bulls through their presence, their dominant behaviour and their ritualized defecation combined with urination. By rapidly wagging their tails, faeces and urine are scattered in the vicinity. This type of defecation is repeated in the



Common Hippopotamus *Hippopotamus amphibius*.

same places and results in impressive dung heaps, measuring several square metres in area. The dung heaps certainly do not function as boundary markers and they do not prevent other bulls from entering the territory, but they are thought to serve as orientation marks for the territorial individual as well as for other Common Hippos. Dung heaps are not produced by the territorial animal alone, but by virtually all passing ♂♂, and they are also found outside the territories in the grazing areas and along the inland tracks. They are rarely found in the open grassland but are regularly produced and maintained at the edges of bushes, at narrow passages between bushes, sometimes at corners of houses.

Territorial neighbours often display ritualized simultaneous defecation at their common boundary in the water. They then stand side by side a few metres apart facing in the same or opposite direction, both demonstrating strength and dominance by holding their heads high and ears forward. In this situation it is quite clear that the behaviour serves as a visual signal, as dung heaps are not produced. Smell is likely to be of importance as well.

When a territorial bull moves across the boundary of his territory, he loses his status and behaves subordinates to the territorial neighbour. Fights between territorial neighbours are generally ritualized frontal combats combined with splashing of water, which serve to demarcate boundaries. Often, the combatants hardly touch each other, advancing and retreating in response to the opponent's actions. However, serious fights occur for the possession of a territory or part of it. Then the bulls fight standing parallel facing in opposite directions and slashing with their lower canines at each other's flanks. Though the hide is several centimetres thick, these attacks can result in serious injury and even death. In these fights the combatants are

usually a territorial defender and a non-territorial challenger, but occasionally two territorial neighbours are involved if one tries to extend his territory into the other's area.

Territorial owners are extremely tolerant of all conspecifics, including adult bulls as long as these behave subordinates. Tolerance goes to the extent of the territorial bull hosting groups of 100 and more fully mature, prime bachelor bulls in the territory. In this situation the function of mating territoriality becomes absolutely clear – only the territorial individual has access to any cow in the territory.

The relations between a territorial bull and subadult bulls in his territory are of an extremely friendly nature. The subadults demonstrate their subordination in an elaborate display: on land they approach from 100 m or more away, head down, the last few paces virtually crawling on the ground, then sniffing the bull's genital region from the side or from behind without him seeming to take notice. A modified version of this behaviour is displayed in the water. Naso-nasal contacts are common. The subadult bulls often stay for hours in the immediate vicinity of the territorial bull, and there is not the slightest indication of antagonism. Rarely, during the submissive display, the territorial bull defecates on the head and back of a subadult. It is not yet clear if this is incidental or if it has a functional significance. During the day, Common Hippos live in social groups of variable size and composition (Olivier & Laurie 1974, Delvingt 1978, Klingel 1979, 1989, 1991, Karstad & Hudson 1986, Viljoen 1995). Solitary animals are generally older ♂♂ or ♀♀ about to give birth. Group size is not a sociological parameter, but rather depends on density and the environmental situation. For example, Common Hippos avoid fast currents and prefer shallow waters with sandy, open foreshores. R. Taylor (pers. comm.) measured 1.3–1.5 m as the preferred water depth for lying up during the day. In such situations the larger groups counted were over 200 animals strong, as in the Ishasha R. (Klingel 1991).

Two types of social groups can be distinguished: nursery schools consisting mainly of ♀♀ and their young, and bachelor groups consisting mainly of bulls. However, the distinction is not clear-cut, and there are often odd members of the other sex in a group. Neither of the groups is a stable social unit but both are loose associations in suitable resting places and the animals are socially but anonymously attracted to each other. Indeed, the existence of individual recognition among adults cannot be proved and it certainly does not play an important role in Common Hippo social life. However, mother and offspring do recognize each other individually, and mother–calf bonds are the only stable associations, usually lasting until the young are almost fully grown at 6–8 years of age.

In the evenings the groups break up and the animals walk singly or in mother–offspring units to their grazing areas. The latter are not monopolized or defended by an individual or group of individuals (i.e. they are not subdivided into territories). Members of a school use an exit near their resting site, or they move along the shore in the water to a place closer to the grazing grounds. They stick to a network of tracks that form through repeated use over the years. At exits the tracks can cut a metre or more into the bank, and on steep inclines tracks erode to become steep gorges that, in the Queen Elizabeth N. P., are characterized by their special plant, bird and small mammal communities. Common Hippo trails can often be recognized from a grassy, belly-smoothed strip in the middle. Regular paths are also used in shallow lakes.

After their nocturnal feeding trips the animals return preferentially to the sites from which they have departed the previous evening, resulting in a certain constancy of group composition. But each individual has, independently of the group, its own home-range and several resting places. In one study area, Mweya Peninsula, the majority of the known animals were located for years in the same day home-ranges of 100–200 m in length. Home-ranges do not coincide with the territories, nor are they restricted to a particular territory. Depending on territory size, a ♀ can be at home in one or in several territories. Changes in group composition also occur during the day. Frequency depends on the spacing of the groups but also on other factors. Some individuals were particularly mobile and, possibly out of curiosity about the observer, their movements were correlated with his, and they moved parallel to the shore in the water, crossing territories and passing groups of conspecifics without any sign of antagonism and without any attempts by the bulls to prevent their departure.

Generally, Common Hippos are quite philopatric and stay within their regular home-ranges. In Queen Elizabeth N. P., a portion of the residents, especially non-territorial ♂♂, used to settle in wet-season pools, utilizing the grazing area nearby. At the beginning of the dry season they would return to where they had come from. When their rivers and wallows dry up, they are eventually forced to move, occasionally over large distances, to find suitable water bodies.

Matings take place exclusively in the aquatic part of territories. Accordingly, for the ♂, the possession of a territory is an absolute prerequisite for reproduction, although it is by no means a guarantee. Some bulls maintained territories in areas that were unattractive to ♀♀ and they probably had no access to cows. However, in the Ishasha R. several 'bad' territories changed to 'good' ones when the course of the river and the water level changed and consequently some ♀♀ moved in. Other territories changed for the worse. It is therefore a better strategy for a bull to occupy a bad territory than to be a non-territorial bachelor.

Oestrus lasts for 2–3 days and up to six copulations occur per day. Although the ♀♀ tend to return in the morning to the place and thus to the territory from which they had departed the previous night, they are promiscuous and likely to visit two or more territories in succession and mate with the respective owners.

A few days before giving birth to a single young, the cows separate from the group. When the cow is undisturbed, birth is in shallow water at the waterline; when she is disturbed, birth can take place in deeper water. The young are precocious and within a few minutes after birth able to suck even under water and to follow their mothers into deeper water. Eltringham (1999) suggested that milk is injected into the calf's mouth by muscular action on the part of the mother, as occurs in some cetaceans. However, young use their tongue and mouth roof around their mothers' nipple while actively sucking, but not the lips, which are inflexible (Kingdon 1979).

Mother and infant stay away from conspecifics and prefer to rest in close proximity at the edge of the water, the mother obviously without eating for several days. For about ten days she is intolerant of all conspecifics and attacks even the territorial bull and her own elder offspring should they approach. This behaviour, which is also observed in other ungulates, is considered to prevent false imprinting. It also serves to protect the infant from attacks by conspecifics. After this period, the mother will graze on the bank during the day with

the infant resting nearby. After several weeks mother and calf will walk, at night, to the grazing grounds where the infant will be parked under a bush whilst the mother feeds. She eventually returns, collects the calf and they return to the water together. Occasionally, calves aged 6–12 months stay behind in a crèche near the water whilst their mothers depart on their nocturnal foraging excursions. The birth of a sibling does not disrupt existing bonds, and ♀♀ with several young, up to three, of different ages, can be observed. The marching order is by age, the youngest first, directly behind the mother.

Numerous cases of infanticide have been reported, some directly observed, others based on circumstantial evidence, and are attributed to ♂♂. However, in a recently filmed episode the infanticidal individual was clearly a subadult, of undetermined sex (M. Deeble & V. Stone pers. comm.). Verheyen (1954) considered adult ♂♂ to be the major enemies of infants. Lewison (1998) analysed the evidence and concluded that infanticide in Common Hippos, as has been demonstrated for Lions, may be a reproductive strategy by which a new territorial ♂ kills his predecessor's offspring to shorten the inter-birth intervals of the ♀ and thus enhance the male's reproductive success. However, the evidence is only circumstantial. In none of the cases was a change of territorial ownership and/or the status of the infanticidal individual observed. As all or most incidents occurred in the dry season, high densities and nutritional stress may have triggered the behaviour.

Common Hippos command a rich repertoire of signals and means of communication, the actual significance of which is only partly understood. The impressive gape signals strength and presence; it is, however, very similar to the yawn, which is of shorter duration, and conspecifics do not seem to be impressed by either. Also, the yawn/gape is displayed by all members of a group including infants, and it occurs with highest frequency just before they go on land in the evenings – suggesting that the yawn/gape may be an expression of excitement, and not a threat (Kingdon 1979, H. Klingel pers. obs.). When attacking, Common Hippos have their mouth only partly open, and this is clearly a threat that is understood by conspecifics. Head up signals dominance, head low, lip smacking and tail wagging with or without defecation are signals of submission, occurring in minor confrontations and by the ♀ during pre-mating activities (Karstad & Hudson 1986, H. Klingel pers. obs.). Behaviour analogous to 'flehmen' has only recently been observed to occur in Common Hippos and probably has no communicative value (Zapico 1999).

Several vocalizations can be distinguished, but interpretations of their significance are still largely speculative. The most common consists of a series of guttural honks preceded and followed by a high-pitched squeal. It is contagious, being started by one individual, repeated by others, and within seconds all members of a group, and soon the neighbours as well join in a cacophony that carries over several kilometres. Calls are individually different and may serve for individual recognition. Sometimes mother and young call and answer after having lost contact while on their walk to the grazing grounds. Other individuals occasionally utter this call at any time of day or night, and they sometimes get answers from far away, but often not (H. Klingel pers. obs.). When fighting and in distress, Common Hippos produce long high-pitched squeals. Barklow (1997) recorded and analysed three types of underwater sounds that are rarely audible on the surface: a whine signalling submission; a croak used by young; and clicks for communication (and see Barklow 2004). When facing

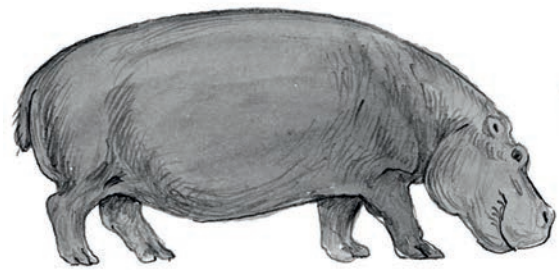
each other they often make a low-pitched loud rumbling noise (R. Taylor pers. comm.).

Many bird species, especially waders, use Common Hippos for perching; some run up and down the animals' backs hunting insects and ticks (e.g. African Jacanas *Actophilornis africanus*), others catch insects that the Common Hippo has disturbed in the water vegetation (see Eltringham 1999 for summary). Hediger (1951) described a case of mutualism between Common Hippos and the Cleaner Fish *Labeo velifer*. M. Deeble & V. Stone (pers. comm.) have observed and recorded on film that Common Hippos actually invite the fish to clean any area of the body, including the mouth cavity, and that they visit cleaning stations where the fish are waiting. Erwee (1996) observed a Common Hippo saving an Impala *Aepyceros melampus* from drowning, by pushing it 'carefully' onto dry land, and there are other instances of Common Hippos displaying similar behaviour, including intervening in attacks on Impalas and other antelopes by crocodiles or large predators.

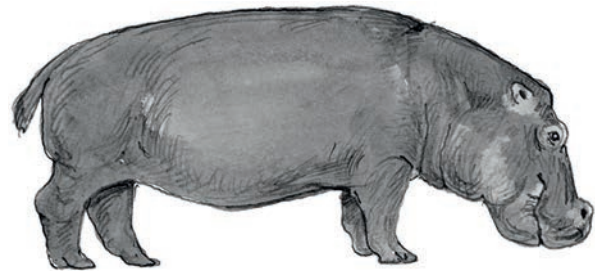
Common Hippos are said to be responsible for more human deaths than any or even all other dangerous wildlife species combined. The truth is difficult to assess as there are no reliable statistics. Common Hippos are certainly dangerous, especially when cornered and wounded or provoked. Most of the casualties are of fishermen who fatalistically drive their boats right through the Common Hippo schools, oblivious to the danger. If the boats are attacked the fishermen will jump out, or may fall into the water, and drown because they generally cannot swim; they may also get bitten by the Hippos and may lose a limb or a life. On land, dangerous situations for humans arise when bumping into a Common Hippo, especially at night, and when inadvertently getting between a mother and her young. Normally, the relations between Common Hippos and people are quite relaxed, with animals idling in the water within as near as 20 m of people bathing or washing their clothes (H. Klingel pers. obs.).

In much of their range crop-raiding by Common Hippos is a big problem. Chain-link fencing is typically ineffective at excluding crop-raiders, especially where it cuts across well-used tracks, because the animals simply trample the fences. Likewise, single strands of electrical wire are only partly effective, as some of the animals, upon contact, rush forward and break the wire. One solution involves constructing a simple barrier like a wooden rail or a shallow ditch about 50 cm in front of and parallel to the electric wire. Both obstacles help slow the animal's pace, thereby serving as a warning before the animal touches the high voltage wire. In KwaZulu-Natal, fields are successfully protected by 1.2–1.5 m deep trenches (R. Taylor pers. comm.).

Reproduction and Population Structure Detailed information on breeding and population structure is available from culling schemes, in particular from Queen Elizabeth N. P. (Laws & Clough 1966), the Luangwa R. in E Zambia (Sayer & Rakha 1974, Marshall & Sayer 1976) and South Africa's Kruger N. P. (Smuts & Whyte 1981). Average age of sexual maturity in ♂♂ (based on testes weights) is 7–8 years (Laws & Clough 1966, Sayer & Rakha 1974, Smuts & Whyte 1981), although spermatogenesis may begin much earlier (as early as two years of age in animals from Kruger; Smuts & Whyte 1981). Based on follicular size, ♀♀ reach sexual maturity at about seven years, although some ♀♀ examined have been found to be sexually mature at much younger ages, including one at three years in Uganda (Laws & Clough 1966, Sayer & Rakha 1974). The age



female



male

Common Hippopotamus *Hippopotamus amphibius*.

at which all ♀♀ are pregnant varies between the three regions in which major studies on reproduction have been conducted: 11 years in Kruger, but 20 years in Uganda and Zambia, indicating different degrees of crowding and nutritional stress (Eltringham 1999). Captive animals may breed at an earlier age, and Dittrich (1976) recorded one ♀ conceiving at only 2 years and 3.5 months. Males are sexually active throughout life, their body weight continuing to increase and testis continuing to grow.

Births are recorded any time of the year; however, there is pronounced seasonality, and most births in Uganda (close to the equator) occur during the rains (Laws & Clough 1966). In Zambia, conceptions occurred throughout the year, but births only during the wet season (Marshall & Sayer 1976). Gestation lasts for about 240 days, and usually a single calf, weighing a mere 50 kg, is born (Laws & Clough 1966, Smuts & Whyte 1981, Eltringham 1999). Twins occur infrequently; in the sample of 276 culled specimens examined by Laws & Clough (1966), twins were recorded twice.

Calving intervals are 2–3 years (see Smuts & Whyte 1981), and oestrous cycle is given as around 50 days (Laws & Clough 1966, Smuts & Whyte 1981, Eltringham 1999). There is some evidence of a postpartum oestrus, as 25% of ♀♀ examined by Laws & Clough (1966) were both pregnant and lactating. Conception rates were close to 40% in Kruger N. P. (Smuts & Whyte 1981) and 27% in Queen Elizabeth N. P. (Laws & Clough 1966). Percentage of lactating ♀♀ in Uganda was almost 60% (Laws & Clough 1966), and 78% in South Africa (Smuts & Whyte 1981). Weaning probably takes place between six and eight months, with most calves weaned by 12 (Eltringham 1999); however, calves as young as six to eight weeks often have considerable quantities of grass in the stomach (Laws & Clough 1966).

Sex ratio is 1 : 1 in foetuses (Bere 1959, Laws & Clough 1966, Smuts & Whyte 1981), infants and young (H. Klingel pers. obs.). Reported adult sex ratios are likely to be inaccurate due to the segregation of sexes. Smuts & Whyte (1981) reported a ratio of 1 : 1.93 in Kruger N. P. (n = 463), while Marshall & Sayer (1976) recorded 1 : 0.98 in 1970

($n = 375$) and 1 : 1.56 in 1971 in Zambia ($n = 210$), the difference in the proportion of ♂♂ due to a greater effort during 1970 to take a more random sample. Laws & Clough (1966) found a nearly exact sex ratio in Uganda, and confirmed that there was a skewed distribution of sexes according to habitat: in small wallows, 313 ♂♂ and 110 ♀♀, and on lake shores, 600 ♀♀ and 821 ♂♂. Population structures of Common Hippos from culling operations exist (e.g. Marshall & Sayer 1976), although samples are biased given the tendency for younger animals not to be culled (and see Eltringham 1999).

Longevity is recorded at 61 years in captivity (Wiesner & von den Driesch 1996).



Common Hippopotamus *Hippopotamus amphibius* juvenile mouth showing adaptation of tongue and upper lip to suck maternal nipple.

Predators, Parasites and Diseases Lions *Panthera leo* succeed occasionally in bringing down an adult Hippo, but they have no impact on the population. Also, young animals are preyed upon by Spotted Hyaenas *Crocuta crocuta* and Lions (Kingdon 1979). In one attack by five hyaenas on an infant, at night, the cow's defence was quite inadequate: she repeatedly chased individual hyaenas that came close, but in the process she again and again left the calf unprotected. The hyaenas took turns in attacking the calf and fleeing from the mother and they eventually managed to bring the calf down. The mother stood for several hours over the body and protected it from being eaten, with the hyaenas sitting nearby. Eventually, after dawn, the mother walked the short distance to the water and the hyaenas had their meal (H. Klingel pers. obs.). Nile Crocodiles *Crocodilus niloticus* are potential predators of Common Hippos, especially young ones, but no records are known. Most observers report Common Hippos to be dominant to crocodiles (see Kofron 1993).

In the wild, Common Hippos are susceptible to rinderpest, a viral disease that was introduced to Africa towards the end of the nineteenth century and which decimated large numbers of domestic and wild ungulates. It is not known if Common Hippos actually succumbed to the disease in any numbers, but they developed antibodies (Plowright *et al.* 1964). Laws (1968) correlated the presence of rinderpest antibodies in culled Common Hippos with

dated outbreaks of the disease and could thereby construct an ageing scale based on tooth eruption and wear, which is one of the most accurate for any wild animal species.

A major and often deadly disease of Common Hippos is anthrax, caused by *Bacillus anthracis*. Outbreaks have been reported repeatedly from Uganda and Congo/DR Congo during the past 40 years, though they were not necessarily diagnosed correctly. One identified outbreak, in 1978, resulted in high mortality in some areas of Queen Elizabeth N. P., but had little impact on the population as a whole (H. Klingel pers. obs.). An outbreak in Zambia in 1987 resulted in the death of >4000 Common Hippos out of a population of 20,000 (Turnbull *et al.* 1991). In 2004, anthrax outbreaks were reported from Zambia and Uganda, the latter claiming about 300 Common Hippos (C. Tumwesigye pers. comm.). Other disease organisms afflicting Common Hippos are *Brucella abortus* (which causes brucellosis) and several species of *Salmonella* and *Trypanosoma*.

Major parasites include flatworms (liver flukes *Fasciola nyansae* are found in the livers of most Common Hippos, while one species of blood fluke, *Schistosoma hippopotami*, is host-specific), nematodes, and ectoparasites, including ticks and a fluke *Oculotrema hippopotami* that lives on the outer surface of the eye (see Du Preez & Moeng 2004). See Eltringham (1999) for an overview.

Conservation IUCN Category: Vulnerable A4cd. CITES: Appendix II.

Today Common Hippos are present in numerous protected areas across the continent, with important populations in Niokolo-Koba N. P. (Senegal), National Park of Upper Niger (Guinea), Comoé N. P. (Côte d'Ivoire), W. N. P./Arly/Pendjari (Benin, Niger, Burkina Faso), Zakouma N. P. (Chad), Queen Elizabeth and Murchison Falls National Parks (Uganda), Salonga, Upemba and Virunga National Parks (DR Congo), Serengeti, Ruaha, Mikumi and Tarangire National Parks, Ngorongoro Crater Conservation Area and Selous G. R. (Tanzania), Amboseli, Lake Nakuru and Tsavo National Parks and Masai Mara and Samburu National Reserves (Kenya), Kasanka, Kafue, North and South Luangwa and Lower Zambezi National Parks (Zambia), Kasungu and Lake Malawi National Parks (Malawi), Hwange and Mana Pools National Parks (Zimbabwe), Chobe N. P. (Botswana), Gorongosa N. P. and Niassa G. R. (Mozambique) and Kruger N. P. (South Africa).

However, across their range, and in particular in West Africa, many populations of Common Hippos are decreasing due to droughts, poaching and to habitat loss and habitat fragmentation from changing land use and damming of rivers (Eltringham 1993a, 1999, Lewison 2007, Zisadza *et al.* 2010). Two very large Common Hippo populations suffered particularly heavy losses through intense commercial poaching by military and civilian poachers. In Uganda, Common Hippos of Queen Elizabeth N. P. declined during the war and unrest of the late 1970s to 1980s from about 20,000 to 2000 (Eltringham 1999). Since then, an increase to only 2600 in 2004 has been recorded (C. Tumwesigye pers. comm.). More recently, in DR Congo, an even more dramatic decline has been reported from the Virunga N. P. population, which, during the recent civil war and turmoil, declined by about 97%, from close to 30,000 in the 1970s (Delvingt 1978) to 1300 in 2003 (A. Plumtre pers. comm.) and to perhaps less than 400 in 2006 (Lewison 2006). Hunting pressure is presently mostly for meat; however, there is increasing demand for tusks, the ivory of which is said to be softer and easier to carve than elephant ivory.



Common Hippopotamus *Hippopotamus amphibius* seated.

An important conservation measure is the translocation of Common Hippos, although immobilization of animals, for research and/or for translocation, poses problems. It has to be done at night in the grazing grounds, to make certain that the drugged animal does not reach deep water and drown. Also, no safe drug combination has been

developed, and the responses of the animals are highly variable (H. Klingel pers. obs.). M. Woodford (pers. comm.) has suggested that the parasite load of the animal might be responsible for the inconsistent effects. In South Africa, Common Hippos are captured by pushing them into a funnel leading directly onto a lorry (R. Taylor pers. comm.). Kingdon (1997) sees much potential in Common Hippos being domesticated as a meat source. The dung also could be made use of in fish farms, thereby producing additional protein.

Measurements

Hippopotamus amphibius

HB (♂ ♂): 3120 (2600–3500) mm, n = 54

HB (♀ ♀): 2990 (2590–3370) mm, n = 156

Sh. ht (♂ ♂): 1500 (1290–1720) mm, n = 32

Sh. ht (♀ ♀): 1440 (1100–1580) mm, n = 36

WT (♂ ♂): 1546 (955–1999) kg, n = 86

WT (♀ ♀): 1385 (995–1850) kg, n = 192

Kruger N. P. (Pienaar *et al.* 1966, I. Whyte, pers. comm.)

Laws (1963, in Eltringham 1999), in Uganda, found the average weight to be 1536 kg for ♂ ♂, with a maximum of 2065 kg, and 1386 kg for ♀ ♀, with a maximum of 1716 kg. Ledger (1968) reported an average of 1490 kg (range 1179–1714 kg, n = 4) for ♂ ♂, and 1277 kg (range 1185–1401 kg, n = 4) for ♀ ♀. Based on the samples of 189 ♂ ♂ and 186 ♀ ♀ in the Luangwa Valley, ♀ ♀ appear to approach an asymptotic weight at around 24 years of age, while ♂ ♂ continue to grow throughout life (Marshall & Sayer 1976). The record tusk length is 1638 mm for animal from Congo (Rowland Ward).

Key References Eltringham 1993a, 1999; Kingdon 1979, 1997; Klingel 1979, 1989, 1991; Laws & Clough 1966; Marshall & Sayer 1976; Smuts & Whyte 1981.

Hans Klingel

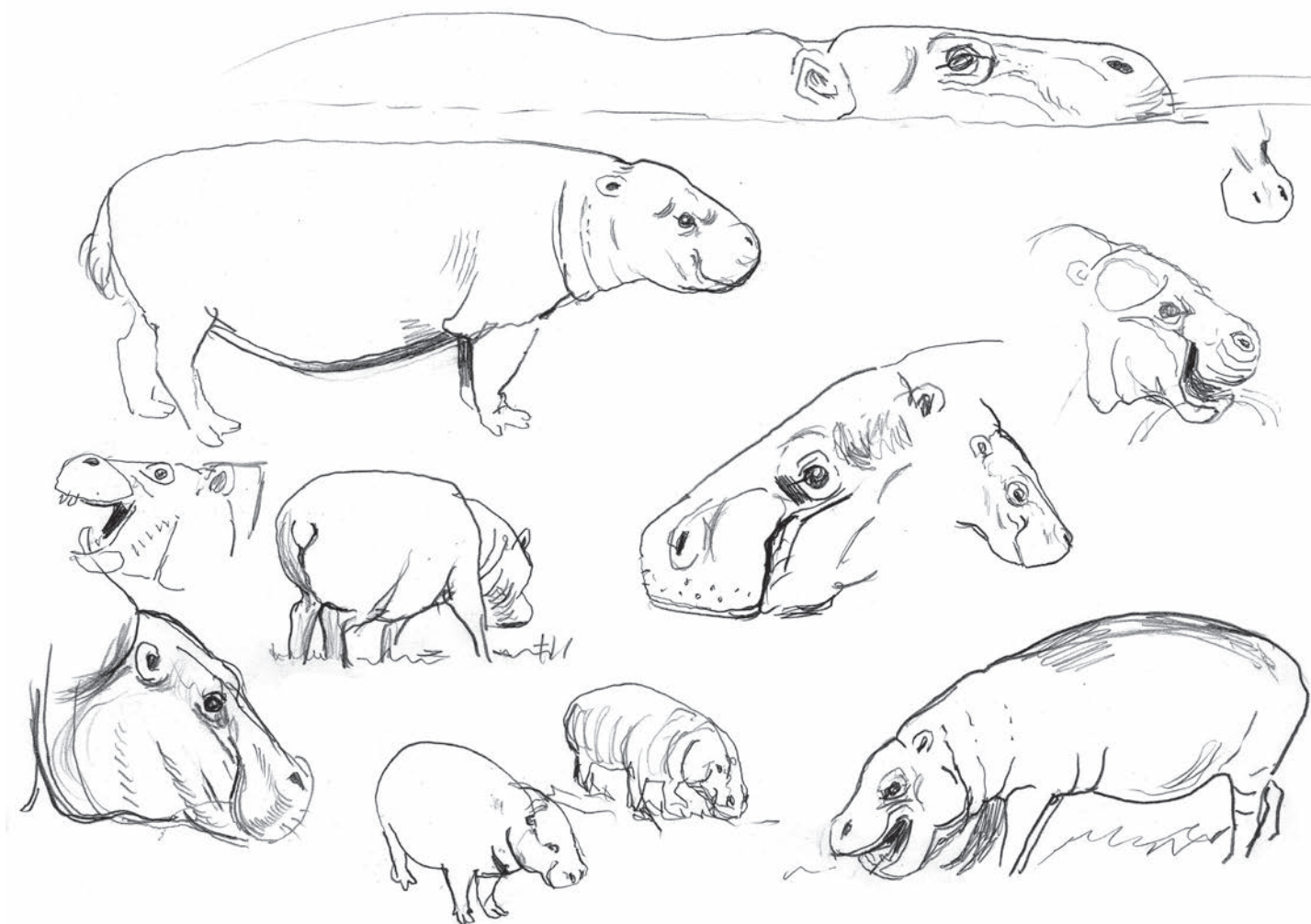
GENUS *Choeropsis* Pygmy Hippopotamus

Choeropsis Leidy, 1852. J. Acad. Nat. Sci., Philadelphia 2 (1): 207.

There is only one living species of *Choeropsis*, the 'Pygmy' or Liberian Hippopotamus, *C. liberiensis*. It is now restricted to lowland forests of Côte d'Ivoire, Sierra Leone, Liberia and Guinea, but in the recent past, it probably also populated coastal regions east of these countries as far as the Niger Delta. The Pygmy Hippopotamus (hereafter Pygmy Hippo) is similar in appearance to the well-known Common Hippopotamus *Hippopotamus amphibius*, but it is much smaller than the latter, its back slopes forward, and its eyes, ears and nostrils are situated lower down on the cranium. Its general proportions are also different, with relatively longer limbs and a proportionately smaller, narrower head. Osteologically, it differs by its sagittal crest sloping backward, its lachrymal separated from the nasal by an anterior extension of the frontal, its low-crowned cheekteeth and the presence of only two incisors on the mandible.

Fossils of actual pygmy hippopotamids are known from several islands, including Cyprus, Malta, Crete and Madagascar. Continental

small hippos were discovered in the Neogene of eastern Africa: *Hexaprotodon ? imagunculus* in the western branch of the Great Rift Valley; aff. *Hippopotamus aethiopicus* and *Archaeopotamus lothagamensis* in the eastern branch. For those continental species, small size probably permitted the use of ecological niches unsuitable for the abundant and much larger species found in the same deposits. In the case of *Choeropsis*, small size could, in fact, be a primitive condition (the oldest known hippos being about the same size or somewhat smaller) and/or could be an adaptation to its habitat, unusual for a hippopotamid. Indeed, very large size is not particularly beneficial for moving through dense forest vegetation and must be sustained by an abundant, nutritious and reliable food supply. Many peculiar traits of *Choeropsis* can in fact be interpreted similarly: its forward sloping back perhaps facilitates passage through dense vegetation, whereas in these conditions low orbits could offer better protection for the eyes. Furthermore, much of this vegetation is woody and



Pygmy Hippopotamus *Choeropsis liberiensis*.

not especially nutritious. *Choeropsis* shows the same sun-sensitive skin histology as *Hippopotamus*, but can venture outside water more frequently in its shady and humid environment, and is less aquatic than its larger extant relative.

The Pygmy Hippo was initially classified in the genus *Hippopotamus* by Morton (1844), then in its own genus (Leidy 1852). In 1977, on the basis of separation between the lachrymal and nasal bones, Coryndon (1977) merged *Choeropsis* into the genus *Hexaprotodon* including most fossil species. However, this morphology was shown to be primitive in the family (Harris 1991a), whereas Harrison (1997) favoured generic distinction of the Pygmy Hippo because of its peculiar overall anatomy. Accordingly, a recent review of the taxonomy and phylogeny of the hippopotamids has restricted the definition of *Hexaprotodon* and thus revalidated *Choeropsis* for the extant Pygmy Hippo (Boissarie 2005).

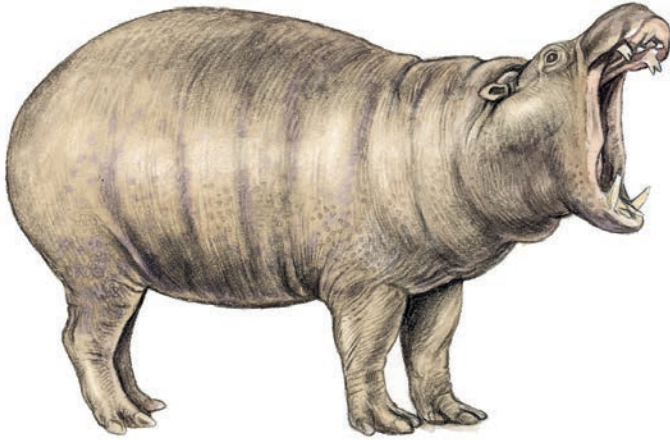
Choeropsis has no known fossil record; its mosaic of primitive (e.g. low sagittal crest), derived (i.e. number of incisors) and unique (i.e. strong nasal spine of the palatine bone) characters among Hippopotamidae suggests that its ancestors separated from other lineages in the late Miocene (Harrison 1997, Boissarie 2005). At this time, hippopotamids underwent a limited radiation, becoming for the first time abundant and diversified in African ecosystems.

At least four main lineages emerged, including *Choeropsis* (Boissarie 2005). Among the three others, the first is recognized in eastern Africa and the Arabian Peninsula as genus *Archaeopotamus*. Its species exhibited an elongated, shallow and narrow mandibular symphysis (Coryndon 1977, Gentry 1999, Weston 2000). The second lineage, the extinct genus *Hexaprotodon*, was seemingly rare in Africa, but flourished in southern Asia, from India to Indonesia, and maybe in southern Europe. Its species were characterized by a robust, high and moderately wide mandibular symphysis. The third lineage, represented by the monospecific *Saotherium* from basal Pliocene in central Africa, has some affinities with *Choeropsis*. Both genera share an elongated braincase rounded in transverse section and relatively large orbits. These characters could be primitive, so may not express actual close phylogenetic relationships. In fact, the relationships between all these lineages – thus, the origin of *Choeropsis* – are still unclear. In any case, *Choeropsis* and *Saotherium* suggest a long and diverse hippopotamid evolutionary history in central and western Africa, despite a fossil record far more sparse than in the eastern part of the continent.

Jean-Renaud Boissarie & S. Keith Eltringham

Choeropsis liberiensis PYGMY HIPPOPOTAMUS

Fr. Hippopotame nain, Hippopotame pygmée; Ger. Zwergflusspferd

Choeropsis liberiensis (Morton, 1849). J. Acad. Nat. Sci., Philadelphia 2 (1): 232. St Paul's River, Liberia.Pygmy Hippopotamus *Choeropsis liberiensis*.*Choeropsis liberiensis*

Taxonomy Two subspecies are recognized. The form *C. l. heslopi*, from the Niger Delta, is originally known from three skulls, one specimen shot by Heslop himself and two skulls obtained from hunters (Heslop 1945); a further two skulls were collected by J. B. I. Mackay in 1928 (Ritchie 1930). It was considered a distinct subspecies by Corbet (1969) and Coryndon (1977), based on variations in cranial anatomy. Synonyms: *heslopi*, *minor*. Chromosome number: $2n = 36$ (K. Benirschke pers. comm.).

Description A secretive, nocturnal, highly solitary, pig-like quadruped resembling, but significantly differing in size, anatomy, behaviour and ecology from, the Common Hippopotamus *Hippopotamus amphibius* (see Similar Species). Overall colouration ranges from grey-brown to purplish-black with creamy-brown underparts. The body profile is raked; the legs less massive than the Common Hippo and the digits are more free and mobile. Nostrils and diminutive ears can be closed by muscular valves, as in *Hippopotamus*.

The dental formula is $I^2/_1, C^1/_1, P^3/_3, M^3/_3 = 34$, which is reduced from the ancestral condition of 44. The incisors are peg-like and the canine teeth, which are used for defence and aggression rather than for feeding, are sharpened by occlusal wear and are open-rooted and continuously growing. The molariform teeth are low-crowned with a grinding function.

Geographic Variation

C. l. liberiensis: Upper Guinean lowland forests, in Guinea, Sierra Leone, Liberia and Côte d'Ivoire.

C. l. heslopi (Heslop's Pygmy Hippo): Niger Delta. Probably extinct. The Nigerian subspecies has been described as having a more horizontal dorsal profile, as contrasted with the more sloped profile characteristic of the nominate subspecies (I. R. P. Heslop pers. comm.); also differs in cranial features (discussed by Corbet 1969).

Similar Species

Hippopotamus amphibius. Largely allopatric, although their ranges overlap in the upper stretches of some rivers in Côte d'Ivoire (see Roth *et al.* 1996, 2004) and perhaps in NW Sierra Leone (Grubb *et al.* 1998). Larger overall size, but with proportionally shorter limbs; nostrils and bony orbits more prominent; toes close-knit; two pairs of lower incisors. Typically solitary or in small groups, and confined to forested regions close to rivers. For a comparative review of *Choeropsis* and *Hippopotamus* see Eltringham (1999).

Distribution Endemic to Africa, where currently confined to the Upper Guinean lowland forests of Liberia, Côte d'Ivoire, Guinea and Sierra Leone. An isolated subspecies, *C. l. heslopi*, formerly occurred some 1800 km to the east, from the Niger Delta east to the Cross R. in Nigeria (Heslop 1945; and see Corbet 1969, Ansell 1972). Reports of this subspecies in the 1930s and 1940s were from the swamps of the Cross R. region of Calabar Province, and from swamps of the Niger R. and its tributaries in the British colonial administrative divisions of Kwale, Asaba, Onitsha and Aboada. The subspecies has not been reliably recorded in more than half a century, and its continued presence seems unlikely. Powell (1995) suggested that the only remaining possibility was in the Upper Orashi Forest Reserve.

Their current distribution is more fragmented than in the past, largely due to the extensive forest loss that has taken place in the lowland rainforests of Upper Guinea. The core of the species' range is centred on Liberia, which has the most extensive tracts of intact lowland forest in the region (Christie *et al.* 2007). Pygmy Hippos are also present in neighbouring E Sierra Leone (in the Gola Forest

region), SE Guinea (including Ziama and Diécké) and SW Côte d'Ivoire (Eltringham 1993b, 1999, Grubb *et al.* 1998, Roth *et al.* 2004, Mallon *et al.* 2011).

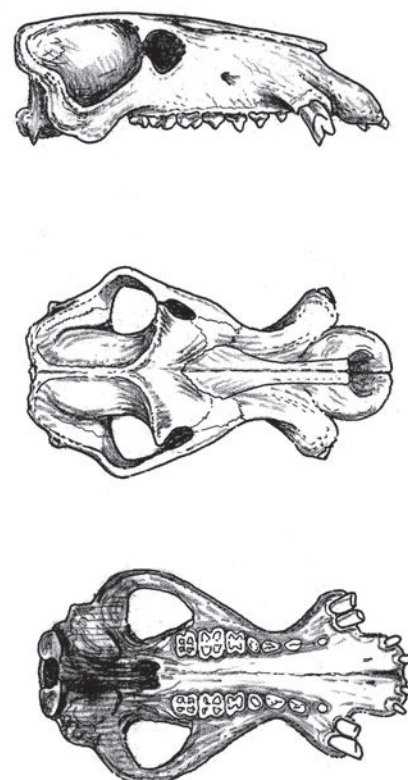
In Côte d'Ivoire, the most northerly occurrence of the Pygmy Hippo is between 7° 20'N and 7° 30'N in the Upper Cavally R. valley, just south of the Guinean border, and along the Upper Boan R., south of the Mt Nimba massif (Roth *et al.* 1996, 2004). They have been recorded from Azagny N. P. and along the Bandama R. in SE Côte d'Ivoire, just west of Abidjan (Roth *et al.* 1996, 2004), which is about the farthest east the nominate form has been recorded (4° 18'W). In Liberia, their distribution seems to be divided between the large remaining forest blocks in the south-east (centred on Sapo N. P.) and north-west of the country (Mallon *et al.* 2011). The farthest west the species appears to have been authentically recorded in the past is near Forécariah, in Kindia, Guinea (Dekeyser 1955; see Grubb *et al.* 1998), but there are no present-day records from further west than NW Sierra Leone (Grubb *et al.* 1998) where it is possible they may survive in Outamba-Kilimi N. P. in sympatry with the Common Hippo. Pygmy Hippos are also still recorded from the Loma Mts in the north of the country.

Except for the reports from NW Sierra Leone (Grubb *et al.* 1998) and Côte d'Ivoire by Roth *et al.* (1996, 2004) and Hentschel (1990), such as on the Bandama R. as far north as the confluence of the Nzi R., no other locations have been verified where the ranges of Pygmy and Common Hippos currently overlap. Historically, however, it is likely that these two species did have small range overlaps; for example, in SW Liberia in the 1930s (Van Ness Allen 1939) and 100 years ago in the Junk River region in Liberia (Schomburgk 1912, 1913, 1922). Heslop (1945) reported seeing Pygmy Hippopotamus tracks within 20 feet of those of a Common Hippopotamus in the Niger Delta region.

Records of the species from Gambia and Ghana were rejected by Grubb *et al.* (1998), while another isolated record from Guinea-Bissau (Cristino & Melo 1958) almost certainly refers to the Common Hippo.

Habitat Lowland primary and secondary evergreen forests, sometimes penetrating savanna regions along gallery forests. Prefers isolated areas with low human disturbance; riverine and swamp areas are frequented much more than upland forest sites. The habitat must offer suitable cover for resting, calving and nursing of calves. Pygmy Hippos often follow water-courses and dry-season forest gullies in their travels and do not hesitate to cross rivers and streams, usually fleeing water to seek refuge in the forest when encountered. Under-cut and eroded banks of forest streams and rivers are not uncommonly used as opportunistic retreats, a habit that is exploited by hunters (Schomburgk 1913, Robinson 1981); the latter author provides a detailed description of one such denning structure in Liberia. Seasonal climate within the species' range is characterized by a major dry season occurring variably between Nov and Mar, with significant rainfall during the balance of the year.

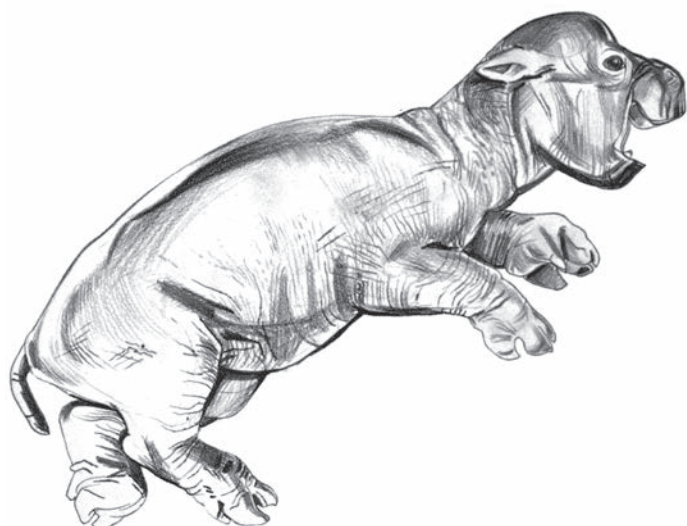
Abundance The total size of the wild population is unknown, but was estimated in the thousands in the early 1990s with the bulk of the population in Liberia, and perhaps less than 100 animals in Sierra Leone (Eltringham 1993b, 1999). However, Roth *et al.* (1996, 2004) present evidence (see below) contradicting the traditional view that Liberia remains the only stronghold for this species. Using faecal



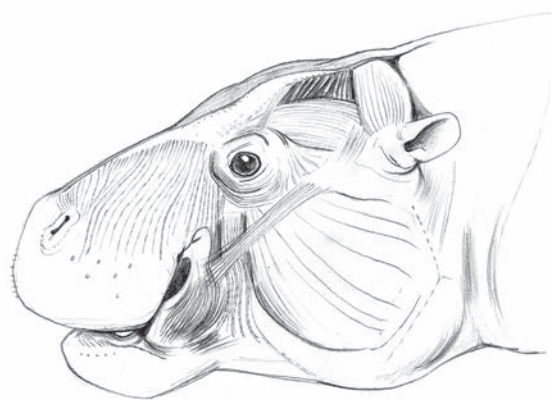
Lateral, dorsal and palatal views of skull of Pygmy Hippopotamus *Choeropsis liberiensis*.

droppings and a decay rate method, Hentschel (1990) estimated mean population densities in Tai N. P., Côte d'Ivoire at 3.6 ind/km² in primary forest and 2.9 ind/km² in secondary forest. Based on these density estimates, Hentschel (1990) estimated a total population of about 14,200 Pygmy Hippos in Tai N. P. and its surrounding areas, although Roth *et al.* (2004) caution that this was probably an overestimate. Subsequently, recent studies in the eastern part of Tai N. P. have revealed that densities decreased to 0.3 ind/km² in 1998 and to 0.2 ind/km² in 2001. Densities in the interior and in the western part of the park ranged from 0.8 ind/km² in 1995 to 1.4 ind/km² in 1998. In the northern adjacent N'zo G. R., densities of up to 2.5 ind/km² existed in 1998. From 1999 to 2001 the Hippo population there increased to 4.1 ind/km² (Roth *et al.* 2004). The latter authors concluded that the total number of Pygmy Hippos in Tai N. P. and its adjacent forest areas was certainly less than 10,000 animals, and estimated the total number in Côte d'Ivoire as probably no more than 15,000 in total. Notwithstanding errors associated with extrapolating population density estimates from dung pellet counts, these figures suggest that the total population of Pygmy Hippos is probably larger than that indicated by Eltringham (1993b, 1999).

Adaptations Compared with the Common Hippo, the Pygmy Hippo is more adapted to terrestrial locomotion. The toes of the feet are less webbed than the Common Hippo, and better suited to frequent movement in and out of rivers and streams and forest travel (Robinson 1970). Ocular orbits are less prominent, consistent with a less aquatic existence. The body profile slopes from the rear to fore facilitating movement through riparian vegetation. As in the Common Hippo, the skin is well lubricated with mucus-like droplets



LEFT: Sketch of neonate.

ABOVE: Pygmy Hippopotamus *Chroeropsis liberiensis* myology of head.

exuding from pores that cover the body. The secretions may take on the appearance of a foamy film over the body surface when rubbed against vegetation.

The digestive system is characterized by a four-chambered stomach (microbial fermentation probably taking place in the first three chambers), lacks a caecum and, like the Common Hippo, has simple small and large intestines (Macdonald & Hartman 1983). They are classified as pseudo-ruminants, as they do not regurgitate and chew their food. Newborn individuals have a lactational groove that diverts milk directly into the glandular portion of the stomach, resembling the same functional morphology found in ruminants (A.A. Macdonald & W. Hartman pers. comm.).

Pygmy Hippos are primarily, albeit not exclusively, nocturnal and crepuscular, spending the daylight hours resting (Robinson 1970, Bülow 1988); evidence from camera traps shows that they may be active throughout the night and also during the day (Mallon *et al.* 2011).

Foraging and Food Pygmy Hippos consume a wide variety of herbaceous materials (forbs, sedges, ferns and fallen fruit), as reported by Hentschel (1990) and Robinson (1970, 1971, 2003). Hentschel (1990) concluded that the feeding spectrum is wide and consists mainly of herbs and fruits. His feeding experiments, direct observations and examinations of damage at feeding sites showed the use, as food, of 17 ferns, 26 dicotyledonous plants, 16 monocotyledons and the fruits of 24 tree species. Feeding preferences varied per individual and some ferns and monocots were readily eaten by all captured animals. The most preferred food plants had high sodium content. Captive diets frequently consist of green leafy vegetables, lucerne, grass hays, carrots, apples, oats, bread and supplements of trace minerals and alpha tocopherol. Robinson (2003) consistently found that a small, recumbent, vine-like forb, widely known as 'Deewinkon' (*Geophila* sp.), is a preferred food throughout Liberia. They do not appear to eat aquatic vegetation or animal matter in the wild. Heaped dung and tail-splattered excrement are commonly found along trailside vegetation. They very occasionally consume crops during wet seasons in remote agricultural areas, but are not regarded as a crop pest. They have been observed standing on their hindlegs (with their front legs against the stem) to reach ferns growing within *Raphia* palms (Bülow 1988).

Social and Reproductive Behaviour Pygmy Hippos are extremely difficult to observe, and even in primary forest areas of low human population density, they are rarely seen. It has been rarely photographed, even with the recent advent of camera-trap technology (e.g. see Collen *et al.* 2011). Consequently, the behaviour of this species in the wild is poorly known, and detailed information is lacking on home-range, territoriality, sexual behaviour and maternal–young interactions. They are known to be highly solitary, and maximum group size reported is three, when a ♀, ♂ and a juvenile offspring may keep transient company while breeding (Robinson 1970). When frightened, they seek forest or rivers for escape from intruders, and are formidable at close quarters if injured or trapped. Considerable time is spent travelling/foraging along meandering, tunnel-like paths that they create in streamside vegetation and through forests and swamps (Robinson 1970).

Hentschel (1990) recorded a home-range size of 50 ha for a radio-collared ♀, and a daily range of 1.8 ha; Bülow (1988) recorded a home range of 180 ha for a ♂. Home-ranges of several female Pygmy Hippos may overlap, and they appear to be very residential. Home-ranges seem to depend on the presence of small streams with submerged trees, root hollows, swampy depressions, and size and density of ground vegetation, rather than nutritional factors or proximity of rivers (Roth *et al.* 2004).

In captivity, copulation has been observed on land and in water. However, parturition, contrary to the Common Hippo, is confined to land. Unlike the Common Hippo, young calves in captivity are not in the constant company of their mothers, but remain in seclusion and suckle intermittently (Galat-Luong 1981). This explains why tracks of young animals are hardly ever found (Hentschel 1990), because young start following their mothers at around 3–5 months of age when they are already quite large.

Reproduction and Population Structure No distinct parturition season has been observed in captivity or in the wild, although some hunters report that newborn animals are observed more commonly in the early dry season between Nov and Jan (Robinson 1970). Oestrous cycle is about 35 days, with oestrus lasting one to two days (Tobler 1988). Gestation period is reported to be 6–7 months in captivity (Zschokke & Steck 2001). They have an

epitheliochorial placenta (K. Benirschke, pers. comm.). A single young is born out of the water with a birth-weight of 4.5–6.2 kg; twinning does occur, but is rare (less than 1% of pregnancies in captivity result in the birth of twins; Hlavacek *et al.* 2005). Weaning occurs at 6–8 months. Reproductive maturity is reported to be 3–5 years (Lang 1975); in captivity, the youngest ♀ to give birth was 2 years 10 months, and the youngest ♂ to mate, 3 years 4 months (Hlavacek *et al.* 2005). Captive adult body size is achieved by three years. Maximum age in captivity is in the order of 35–40 years; one wild-caught captive ♀ lived to nearly 44 years of age (A. Conway pers. comm.). While no data exist for wild animals, it is expected to be substantially less. Bülow (1988) recorded an instance in which a young Pygmy Hippo died as a result of drowning in the Azagny N. P., indicative that swampy areas such as the *Raphia* swamps in Azagny are not optimal for reproduction because young are not accomplished swimmers.

Zschokke (2002) noted that the total captive population of the Pygmy Hippo at the time had a highly female-biased sex ratio at birth (41% ♂♂), exceeding most other known distorted sex ratios in captive mammals. This deviation was not compensated for by a higher juvenile mortality in ♀♀, but seemed to be related to high feeding intensity and ‘hands-on’ husbandry that favoured production of daughters.

Predators, Parasites and Diseases The main predators, particularly for young, are Leopards *Panthera pardus*, Nile Crocodiles *Crocodylus niloticus* and African Rock Pythons *Python sebae*. Hentschel (1990) obtained a photograph of a juvenile Pygmy Hippo killed by a Leopard. Disease in wild animals is undocumented. In captivity, they are relatively hardy with competent husbandry, and most health problems relate to husbandry shortfalls. The author is aware of several cases of dental malocclusion (and see Johnston 2002) and solar dermatitis resulting from exposure to excessive solar radiation (e.g. Olivier 1975).

Conservation IUCN Category: Endangered C1. CITES: Appendix II (as *Hexaprotodon liberiensis*).

The range of this species has diminished dramatically in the past 100 years (Robinson 1970, 1971, 2003), but most acutely in the past 50 years. Forests within the historical range have been steadily logged, farmed, converted to plantations (rubber, coffee and oil palm) and settled, resulting in a fragmented distribution. Unchecked forest destruction and other damaging human disturbances, such as mining activities, pose serious threats to all remaining Pygmy Hippos and their forest habitats. Sierra Leone has important remnant populations in the Gola Forest region (Gola Rainforest N. P.) bordering Liberia (and also in the vicinity of Tiwai I. and in the Loma Mts), while Guinea contains isolated populations along the Liberian frontier (including in the Ziama Biosphere Reserve, and Diécké and Mont Béro Reserves) that are declining rapidly due to the impact of displaced Liberian war refugees. Côte d'Ivoire has lost most of its original forest cover, and, aside from remnant populations bordering Liberia, most hippos reside within Taï N. P. and N'Zo Faunal Reserve and surrounding areas and in Azagny N. P.

Liberia contains the most significant remaining forests suitable for Pygmy Hippos, with the greatest numbers in the central and south-eastern regions, where Sapo N. P. is the only protected area for this

species. However, this refuge has experienced significant encroachments from illegal mining and other human activities between 2002 and 2010, and the effects on Pygmy Hippo numbers remain undetermined. Extensive road-building, logging and settlement activities, accelerating in the 1990s, are destroying and isolating the remaining forest areas of SE Liberia, particularly in the Cestos and Senkwehn riversheds (Robinson & Suter 1999). Due to the exodus of rural Liberian refugees to urban settlements and neighbouring countries starting in 1989, wildlife populations in general rebounded during the Liberian civil war, but that trend is now reversing (P.T. Robinson & J. Suter pers. obs.).

The presence of the Pygmy Hippo may be a highly sensitive indicator of the degree of environmental disturbance; logging, hunting and settlement activities readily cause its disappearance, and seldom will it maintain a sustained presence within 5–10 km of such activities. However, Hentschel (1990) reports they will reoccupy secondary forests derived from logged areas. Primary methods of hunting this species are at night with headlamps and 12 gauge shotguns using solid metal projectiles, and with wire snares and pit traps. Captive animals are ordinarily pit-trapped or taken as young after killing the mother. Some wild-caught individuals have been said to become remarkably tame after very short periods in captivity (Schomburgk 1913).

The Basle Zoo in Switzerland records the most captive births and maintains the captive breeding studbook. Animals are readily maintained in zoos and breeding has been generally successful, with Basle, Washington and Pretoria zoos the most successful breeders (Hlavacek *et al.* 2005). The number held in captivity in 1988 was 340 animals, although the number of zoos exhibiting this species had decreased (Tobler 1988). As of Dec 2009, there were 332 (133 ♂♂, 196 ♀♀ and 3 individuals of unknown sex) known Pygmy Hippos in 134 public zoos and private collections. The captive population is descended from 61 wild-caught founder animals, unequally represented in collections. The last wild-caught individual was imported on 22 September 1982. The current captive population shows a skewed, female-biased, sex ratio and a relative lack of young animals (Mallon *et al.* 2011; and see Hlavacek *et al.* 2005).

In Nov 2010, a workshop was convened in Monrovia, Liberia, attended by representatives from all range states, government agencies, and local and international NGOs working on Pygmy Hippo conservation to develop a conservation strategy for the Pygmy Hippo with the goal to ensure the effective protection of, and connectivity between, known populations (Mallon *et al.* 2011).

Measurements

Chroeropsis liberiensis

TL: 1420–1570 mm, n = 4

WT: 179–273 kg, n = 7

Measurements from across the range (Lang 1975)

Height at the hindquarters for a ♂ and ♀, measured by Lang (1975), was 810 mm and 830 mm, respectively

The longest tusk on record measured 304 mm (Rowland Ward)

Key References Bülow 1988; Eltringham 1993b, 1999; Hlavacek *et al.* 2005; Hentschel 1990; Mallon *et al.* 2011; Robinson 1970, 1971, 1981.

Philip T. Robinson

Suborder RUMINANTIA – Ruminants

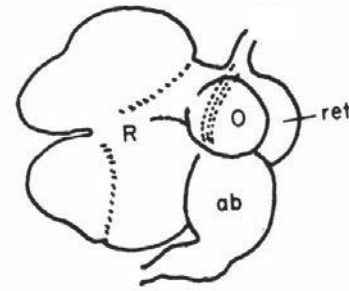
Ruminantia Scopoli, 1777. *Introductio ad historiam naturalem*, Prague, pp. 493-496.

In the taxonomic upheaval that has accompanied the application of genetic analysis to traditional nomenclature, Ruminantia has emerged as the primary category for most, but not all of the two-toed, predominantly herbivorous mammals. The ruminants are subdivided into what might, in functional terms, be called 'proto-ruminants', the chevrotains or Tragulina, and the 'true ruminants' or Pecora, embracing the superfamilies Giraffoidea (giraffes), Cervoidea (deer) and Bovoidea (bovids). This division is well supported by molecular studies (e. g. Hassanin & Douzery 2003, Hassanin *et al.* 2012). The presence of the third forestomach compartment, the omasum, is a primary distinction between chevrotains, which lack this organ, and the Pecora or true ruminants. Extant tragulid species have become restricted in body mass and, although they were abundant and covered a wider body size range before the bovids evolved, they only survive today as relatively small forest dwellers in warm and humid climates.

For more than 100 years, scientists have known that only specific microbes can produce the enzymes necessary for breaking down the complex carbohydrates in plant material, and convert them into the coals of the fire of life, the sugars. The capacity to digest plant material is shared by many mammal groups, such as rodents, horses, rhinos and elephants, in which bacterial fermentation takes place in the hindgut ('hindgut fermenters'), and hippos, kangaroos or colobus monkeys, in which the microbes are housed in a forestomach ('foregut fermenters'). In foregut fermenters, the bacteria flowing out of the fermentation chamber are not lost in the faeces, but enter the glandular stomach (called the abomasum in ruminants), where they are killed by the hydrochloric acid produced in this compartment. The dead bacteria, consisting of highly digestible protein, thus contribute significantly to nutrition in foregut fermenters.

The products of bacterial fermentation of structural carbohydrates such as starch, cellulose, hemicellulose and pectin are always sugars, which are immediately used by the bacteria themselves; the metabolic products of their activity, namely three volatile fatty acids (VFAs), acetic, propionic and butyric acids, are absorbed by the mucosa of the fermentation chamber, be it the hindgut or the foregut. In ruminants, the rumen papillae increase the total mucosal surface, thus vastly enhancing the rumen's absorptive capacity. The rumen papillae are efficiently served by an intricate vascular system, which immediately transports these VFAs to the liver via the portal vein. The liver is vital not only for detoxification, but primarily, as in all herbivores, for re-synthesizing sugars, especially glucose, from these VFAs, a process known as gluconeogenesis.

The problem of toxins, or substances such as polyphenols that suppress digestibility (and are present in many plants, except grasses), may represent a particular advantage for a foregut fermentation system. In the foregut, the gut bacteria can metabolize toxic substances before they reach the sites of absorption in the small intestine. In ruminants, additional support comes from the salivary glands, which produce particular proteins that bind, for example, to the polyphenolic compounds in browse forage. Therefore, many non-grazing ruminants have a more viscous, protein-rich saliva produced in large salivary glands, whereas grazing species, which do not need this kind of defence,



Ruminant stomach. Rumen (R) derives from cardiac region of stomach. Reticulum (ret) is a muscular sac derived from a loop in the body of the stomach. Omasum (o) is a lesser curvature of gastric primordium. Abomasum (ab) represents pyloric atrium (after Young 1962).

have smaller salivary glands that, nevertheless, produce a copious, but more watery saliva.

The ruminant digestive system represents a unique evolutionary step forward by combining both the advantages of conventional microbial forestomach fermentation with a selective retention (and subsequent reprocessing) of large ingesta particles. This intensive use of ingested plant parts means that ruminants gain a comparable amount of daily energy from a distinctly lower amount of forage than non-ruminant herbivores. Ruminants 'chew the cud', but while we are so used to this well-known fact, we should not forget that this revolutionary adaptation necessitates a series of complicated morphophysiological adaptations. The sphincter cardiae (the barrier that prevents vomiting in horses and other animals) had to be removed. The smooth (i.e. involuntary) oesophageal musculature had to change into striated (voluntary) tissue. And in order for the rumination process to make sense, a sorting mechanism in the forestomach had to evolve to separate those particles that needed to be re-chewed from those that had already been digested and could pass on into the lower digestive tract.

Just how this sorting mechanism works is still a matter of debate. It is assumed that it is associated with the 'honeycomb' cells of the second forestomach, the reticulum, and the third forestomach, the omasum; both structures are much more pronounced in grazing ruminants. While the omasum provides a mucosal surface of about 2000 cm² in large browsers such as the Moose *Alces alces* or Greater Kudu *Tragelaphus strepsiceros*, this surface is enlarged up to more than 35,000 cm² in some grazing bovines! And it is in these species that evidence for a particularly effective and selective mode of particle retention has been generated. The fact that grazers excrete very fine particles in their faeces (in contrast to browsing species such as Moose or Greater Kudu) supports the notion that the mechanisms of particle retention and rumination are more effective in the more recently evolved grazing ruminants.

Thus, the forestomach anatomy of the tragulids (chevrotains or 'proto-ruminants') represents an evolutionarily older state, with no omasum at all. In true ruminants, the omasum was small to begin with, with few laminae, a sieve-like structure between the particle-sorting reticulum and the glandular abomasum. The evolutionary

success of the omasum structure can only be guessed at or inferred, partly by noting the displacement of tragulids from nearly all their previous ecological niches by true ruminants.

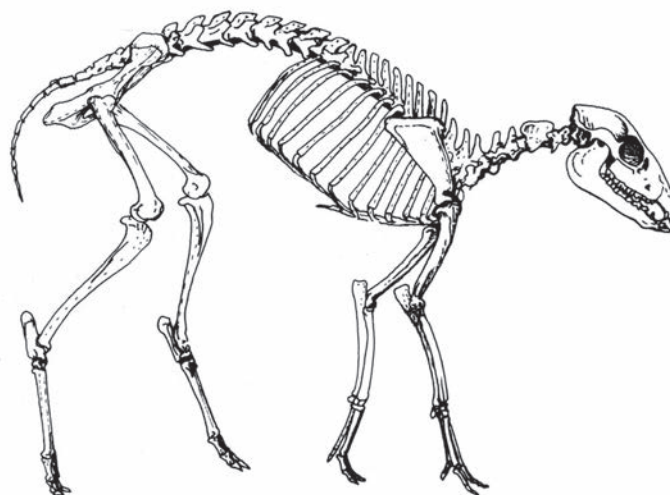
A time scale for ruminant evolution has been inferred by Hassanin *et al.* (2012), who used a Bayesian molecular clock approach as well as evidence from the fossil record. According to their calculations, the primary split between chevrotains and Pecora took place about 51.6 mya, which was well before grasses began to spread widely during the Miocene. So, rumination did not evolve directly in order to digest grass, as has sometimes been assumed. Thus, a high proportion of extant species (approximately 40% of all ruminants) have retained what could be called the early 'ruminant blueprint', both in the anatomy and the physiology of their digestive tract. These, often conservative, species are highly selective and avoid forage rich in cellulose, especially mature grass, which they are incapable of breaking down into a digestible form. They select fruit, litter and foliage with a low cellulose content, but rich in soluble nutrients, and with indigestible, lignified fibre. They chew with more vertical bites (puncture crushing), rather than grinding their teeth sideways. There is little stratification of ingesta in their rumen, in contrast to what occurs in grazers. This category of ruminants has been characterized as 'concentrate selectors' (Hofmann 1973); of the antilopine tribes recognized in this work, the Neotragini, Madoquini, Oreotragini, Raphicerini and Cephalophini are all 'concentrate selectors'.

Only some 25% of about 180 extant ruminant species are true 'grass and roughage feeders' (Hofmann 1973, 1989). These species have refined their ruminal physiology and anatomy to the point where they derive most of their energy from slow ruminal fermentation. This type of rumination mainly processes the cellulose that is provided by the grasses and composites that are now ubiquitous in the extensive grasslands of Africa and other continents. The more these larger ruminants adapted to cellulose digestion, the less important detoxification became, and this has resulted in diminished salivary glands and a relatively smaller liver.

There is also a large and significant category of opportunistic species that are intermediate between the two extremes mentioned above (Hofmann 1989). These 'intermediate strategists' comprise about 35% of all ruminants, and they are able to make use of both strategic avenues. They are especially well adapted to strong seasonality in African and other continental habitats because they can switch from grasses to browse material and vice versa (e.g. most cervids, Antilopini and Caprini). A recent literature review has synthesized dietary information for 78 species of African Bovidae (Gagnon & Chew 2000).

The evolution of ruminant diversity is far from being a linear process; rather, it is more like a bush (or even a baobab tree!) since completely different permutations and variations occur, some of them retaining 'older/conservative' features, while others incorporate innovative morphophysiological adaptations, especially when grass is their main resource.

There are evolutionary changes in the behaviour and morphology of those ruminants that ingest an increasing proportion of grass in their diet. Consuming more slow-fermenting cellulose fibre is accompanied by an increase in the size and capacity of both the rumen and the omasum (as well as changes in the molar teeth). In grazing species, rumination occupies a major portion of the daily activity budget. The exigencies of rumination and grinding cellulose fibre have caused changes in the shapes of mandibles, the fibre arrangement



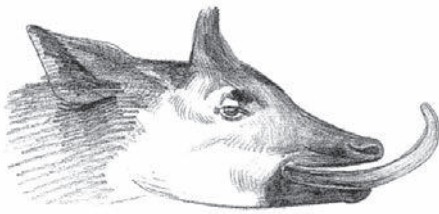
Leptomeryx skeleton (primitive Oligocene chevrotain-like ruminant) (after Scott 1940).

of the masticatory muscles and the basic foraging apparatus. For example, pointed, delicate muzzles with manipulative lips transform into wide and rigid rostra, supported by the powerful gathering tongues that typify grazing bovines.

Some ruminants select forage with a high content of rapidly digestible (and maybe even soluble) nutrients and a rather indigestible (lignified) fibre component. These species, even when large in body size, have retained a relatively small rumen, permitting only a short retention of their ingesta. This results in short (intermittent) rumination periods and frequent foraging bouts. There are striking convergences between bovids and deer in the more conservative species; thus duikers resemble muntjacs in being small 'concentrate selectors', while the Greater Kudu and the Moose are both large browsers with poor cellulose digestion. In contrast to grazers, many non-grazing ruminants show solitary and cryptic behaviour.

There have been attempts to impose conceptual generalizations and categories on the overall trend from small, solitary, territorial browsers to large, social and hierarchical grazers. For example, Jarman (1974) concluded that both body mass and group size is negatively correlated to feeding selectivity, and group size is correlated with 'antipredator behaviour'. However, the diversity of specific adaptations ensures that there are many exceptions. For example, the largest extant ruminant does not fit into the scale of body mass interpretation: the Giraffe *Giraffa camelopardalis* is a browser with a short retention time and has a poor capacity for cellulose digestion. It is true that grazing ruminants are frequently on the large side – but rarely above 1000 kg (compared with a maximum of about 1500 kg for the Giraffe!). Likewise, the Oribi *Ourebia ourebia* is a grazing ruminant that only weighs 15–20 kg, another 'exception' that illustrates that ruminants have evolved unique forms for almost every exigency.

As the most widely distributed forage resource across all the continents, grass has become progressively more widely used by ruminants. Following long periods of adaptation across a wide span of the globe, the morphophysiological diversity of ruminants and the detailed structure of the rumination process in ruminants has changed and accommodated to many local permutations of climate, vegetation and ecology. Thus, the antecedents of grass-eating bovids had, almost



The Okapi *Okapia johnstoni* is one of several ruminants that have conspicuous chins. Such patterns effectively advertise the activity of chewing cud.

certainly, begun to differentiate on the basis of other biotic parameters well before the major expansions of grasslands (Kingdon 1982). The spectrum of surviving ruminant types offers many insights into evolution, especially among bovids, and has implications for classification and nomenclature that are still very largely unexplored. The briefest of surveys of living ruminants reveals that the digestion of grass was a specialization adopted independently by later members of several lineages (notably some Reduncini and Caprini and virtually all Hippotragini, Alcelaphini and Bovini) with concomitant development

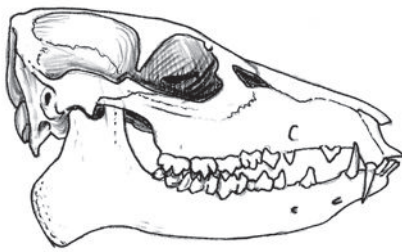
of broad, deep molars. These ‘hypsodont’ species do not represent a single closely related entity, as was supposed until recently (Schlosser 1904, Eisenberg 1981).

In spite of substantial research on domestic stock, the livestock industry has failed to invest in research on the full adaptive range of ruminants and rumination, leaving the field to a handful of dedicated researchers in wildlife biology (e.g. Hofmann 1989, Jiang & Takatsuki 1999, Cerling *et al.* 2003, Sponheimer *et al.* 2003b, Hummel *et al.* 2005, Clauss *et al.* 2006). In the meantime, the politics of livestock promotion are destroying both ruminant diversity as well as the ecological diversity of African ecosystems. Because ruminant adaptive plasticity is an intensely interesting and useful process in its own right, and ruminant evolution appears to be still going on, a change of heart is long overdue. The livestock industry must modify its blinkered attitudes if conservation efforts are to succeed in retaining Africa’s ruminant diversity within their many native habitats; and change is overdue, not only in Africa.

Reino R. Hofmann & Jonathan Kingdon

Infraorder TRAGULINA – Chevrotains

Tragulina Flower, 1883. Proc. Zool. Soc. Lond. 1883: 184.



Lateral view of skull of late Eocene *Hypertragulus* (from Scott 1940).

Recent, molecular-led reformations in mammalian taxonomy support the majority of classifications that divide the order Ruminantia into two infraorders: the true ruminants, or Pecora (generally including those members possessing horns, antlers or ossicones), and the proto-ruminant chevrotain lineage, Tragulina (Hassanin & Douzery 2003, Hassanin *et al.* 2012; and see Hernández

Fernández & Vrba 2005). Since their divergence, some 51 mya (Hassanin *et al.* 2012), the pecoran lineage has diverged into more than 20 major lineages, which have continued to diversify right up to the present. Meanwhile, the chevrotains, after first registering in the fossil record in the late Eocene (in the form of *Archaeotragulus* from Thailand; Métais *et al.* 2001, and see Métais *et al.* 2007), remained a diverse and widely distributed group through the Miocene. They subsequently declined until only one representative remained in Africa, the Water Chevrotain *Hyemoschus aquaticus*. This decline was clearly strongly influenced by a less efficient digestive system than that of pecorans. Their likely ~50-million-year survival as a single lineage calls for the chevrotains’ continued existence to be registered at both infraordinal and superfamily level. In this work, as in most traditional treatments, tragulid peculiarities are described under the Family Tragulidae.

Jonathan Kingdon

Superfamily TRAGULOIDEA

CHEVROTAINS

Traguloidea Gill, 1872. Smithsonian Misc. Coll. 11 (230): 9.

The superfamily Traguloidea accommodates the ancient and once diverse chevrotains and mouse-deer. Chevrotains probably occupied a spectrum of early ruminant niches from at least the late Eocene

to the middle Miocene, but have been in decline ever since. The characteristics of chevrotains are summarized under their family profile, Tragulidae.

Family TRAGULIDAE

CHEVROTAINS

Tragulidae Milne-Edwards, 1864. Ann. Sci. Nat. Zool. Paris, ser. 5, 2: 157.

| | | |
|-------------------------------|------------------|-------|
| <i>Hyemoschus</i> (1 species) | Water Chevrotain | p. 88 |
|-------------------------------|------------------|-------|

The family Tragulidae occupies a threshold taxonomic position as ruminants. Most members of the suborder Ruminantia are also members of the infraorder Pecora comprising the extant families Moschidae (musk deer), Cervidae (deer), Antilocapridae (North American Pronghorn), Giraffidae (Giraffe and Okapi) and Bovidae (cattle, sheep, goats, antelopes). However, the more primitive tragulids are in their own infraorder, Tragulina. Nine tragulids occur in South-East Asia: six species in the genus *Tragulus* (Meijaard & Groves 2004, Grubb 2005) and three in the Indian genus *Moschiola* (Groves & Meijaard 2005). Only a single larger-sized species occurs in Africa, the Water Chevrotain *Hyemoschus aquaticus*, living in parts of the west and centre of the continent.

Tragulids are secretive little forest-dwelling animals with an unusual association with water. They have a cannon bone (lengthened and fused metapodials III and IV) in their back legs, but not always in the front legs. Their legs, especially in front, are not very long and the animals have a low crouched appearance when standing. Each foot has four digits, although in *Hyemoschus* the side digits do not touch the ground when standing. Tragulids lack the horns or antlers found in nearly all pecorans. The dental formula is $I^{0/3}, C^{1/1}, P^{3/3}, M^{3/3} = 34$. Males have curved upper canine tusks as in one or two pecorans such as musk deer, but of different cross-sectional shape; the lower canines look like incisors. Their molar teeth are less fully selenodont (with crescentic cusps) than in pecorans and the few cusps on the lower premolar teeth lie in an anteroposterior line and without additional or 'new' cusps on the lingual side (inside) of the original line. They have a compound stomach like that of pecorans, but without the omasum chamber, and rumination takes place in their digestion of food. Flower (1875) provided an exemplary account of the differences between the musk deer (a pecoran without horns or antlers) and tragulids.

The first fossil tragulid to be named was *Dorcatherium nauai* from early in the late Miocene (about 10 mya) of Germany (Kaup & Scholl 1834). Fortunately, the material included a complete skull. This skull differs from the living *Hyemoschus aquaticus*, which in 1834 had yet to be scientifically described and named, by being bigger (about one-fifth longer), having longer nasals, a preorbital fossa and a first lower premolar which had largely disappeared in ruminants even before 10 mya. Miocene Tragulidae are known from European countries other

than Germany, and also in East Africa, Arabia, India, South-East Asia and China. The largest African fossil species and some of the European species from about 18–10 mya differ from later tragulids by their less selenodont molars with more signs of their former bunodont (with low rounded cusps) condition. It seems likely that the family evolved in southern Eurasia or, just possibly, in Africa. They are known from early in the African Miocene and *Dorcatherium* is generally thought to have migrated into Europe at about 18 mya.

For about 170 years *Dorcatherium* was accepted as the earliest tragulid but, interestingly and anomalously, it is not known as far back in geological time as are pecorans. It occurs no earlier than about 22–20 mya, almost back to the start of the Miocene and a long time after the earliest pecorans, at around 34 mya. The pre-Miocene ruminants, going back to around 45 mya, constitute a varied array of animals with many primitive attributes, the earliest of them even possessing upper incisors and a long tail. They were evolving selenodont teeth with every sign of convergences and parallels between the lineages. Moreover some non-ruminants were also evolving various patterns of selenodonty. The earlier Oligocene *Lophiomyx* and its allies at around 30 mya lagged somewhat in the advance to selenodonty and were sometimes considered to be near tragulids. This could be true if it turns out that Tragulidae did not develop their apparently primitive characteristics as secondary reversals.

Métais *et al.* (2001; and see Métais *et al.* 2007) made a new and substantial contribution to this ongoing discussion by describing late Eocene (ca. 40 mya) fossil dentitions from Thailand, named by them *Archaeotragulus krabiensis*, as a member of the Tragulidae. However, ideas about the concepts and contents of early ruminant and near-ruminant families remain far from stable.

Tragulidae have been contracting their range since the middle of the Miocene epoch. By the late Miocene they were less common in Europe and by the end of that epoch they were extinct there. In East Africa, the latest cited occurrence is Miocene. In China, at the present day tragulids range only into a small southern area. This contraction is like that seen in the anthracotheres, of which the last survivor was the Indian *Merycopotamus* at around 3 mya. These declines must be linked with long-term climatic change leading to diminution of suitable wet-forest habitat and perhaps to the post-Miocene success of pecorans.

Alan Gentry

GENUS *Hyemoschus*

Water Chevrotain

Hyemoschus Gray, 1845. Ann. Mag. Nat. Hist. ser. 1, 16: 350.

Hyemoschus includes only the Water Chevrotain *H. aquaticus* of the West and central African rainforest. Water Chevrotains are small animals with short legs, large lateral hooves, a moderately long bushy tail and naked rhinarium. The limb bones are less reduced and co-ossified than in typical ruminants, with the ulna complete and separate from the radius, and metapodials II and V slender, but complete. Fusion

of the median metapodials is less advanced than in the related Indo-Malayan *Moschiola* and *Tragulus*, with metatarsals III and IV fused to form a cannon bone, but the suture is not complete and still visible, and metacarpals III and IV are unfused; all metapodials are very short.

Peter Grubb

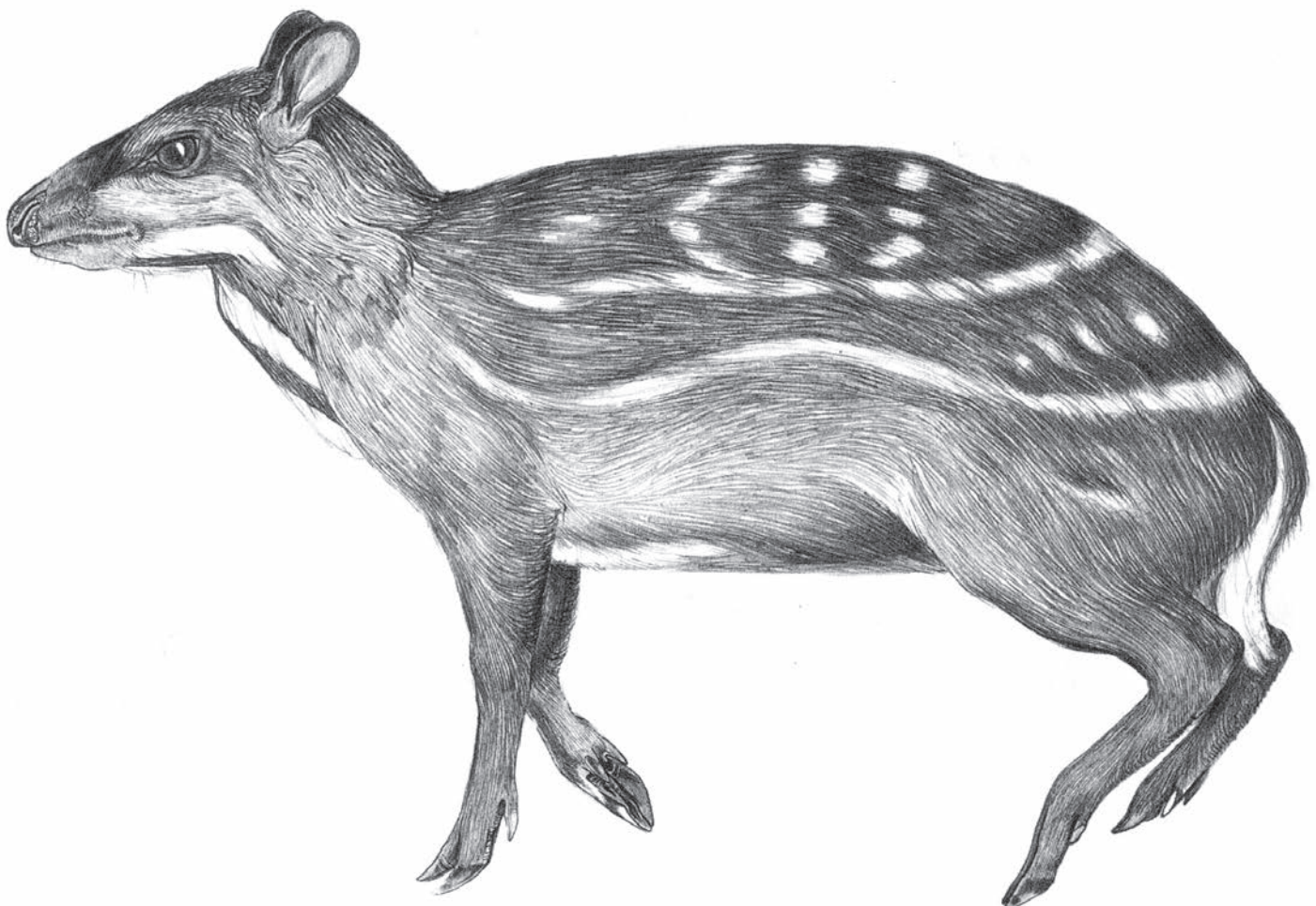
Hyemoschus aquaticus WATER CHEVROTAIN

Fr. Chevrotain aquatique; Ger. Hirschferkel

Hyemoschus aquaticus (Ogilby, 1841). Proc. Zool. Soc. Lond. 1840: 35 [1841], Sierra Leone, Bulham Creek.

Taxonomy No subspecies have been recognized. The species is apparently monotypic across a large range, which is separated by the Dahomey Gap between the Upper Guinea and Congo Basin forest blocks. Synonyms: *batesi*, *cottoni*, *typicus*. Chromosome number: not known.

Description A squat, short-limbed, small-headed ungulate, with a compact body form, largest at the hindquarters, which are often held higher than the shoulders, and strongly tapered toward the head. Body covered with long-haired pelage overall umber brown to reddish-brown, grizzled with paler hairs, and marked with variably

Water Chevrotain *Hyemoschus aquaticus*.



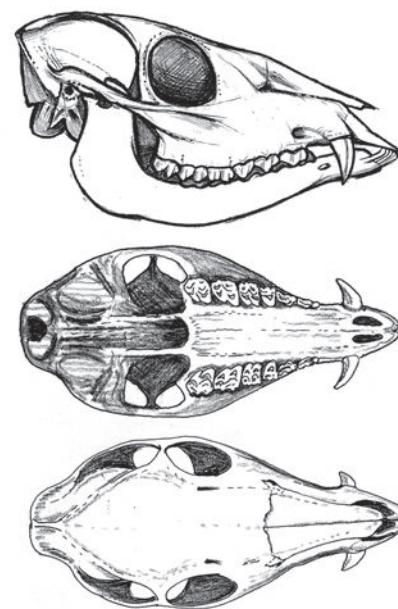
Water Chevrotain *Hyemoschus aquaticus*.

distinct pale to white stripes and spots. The most distinctive white markings include longitudinally oriented white malar and neck patches offset by a darker line of pelage along the side of the neck, extending from below the chin and behind the gape area onto the neck. One to two variable longitudinal white stripes extend roughly in parallel along the sides of the body, gradually disappearing on the rump, and a series of pale dorsal spots, 1–3 cm in diameter are arranged as 6–7 irregular broken bands across the shoulder through the middle back. The small but somewhat elongated head narrows on the crown above large eye orbits and between relatively small ears that are dark on the outside with lighter hairs lining their inner surfaces. The hair on the crown is dark intermixed with variably lighter pelage around the eyes and on the muzzle. The eyes are dark brown and produce a whitish reflection when seen at night under torchlight. The chin and underparts of the neck are white, variably set off by dark brown line of pelage extending posteriorly from the upper chest. The lower chest and abdomen are grizzled brown. Tail dark brown above, white below, extending into a white fringe. The udder with four teats is covered with white hairs and located between the hindlegs. Hooves similar to other small to medium-sized ungulates, though slightly more rounded than those of the similarly sized forest duikers. Prominent hoofed metacarpals are present on all four limbs, though seldom visible in tracks.

Skull not unlike that of Indo-Malayan tragulid genera but more than one-and-a-half times longer, highest at the back and sloping down to the snout. The first incisors are broad. Other incisiform teeth have very narrow crowns; the cheekteeth are bunoselenodont, with relatively large sectorial premolars. Distinctive thin and strongly curved upper canine teeth (tusks) occur in both sexes, but are larger and externally visible in ♂♂.

Geographic Variation None recorded.

Similar Species The only tragulid representative in Africa, the Water Chevrotain is unmistakable. It shares its forest habitat with up to six species of duikers, which are similar in overall body size and share its primarily frugivorous diet. Water Chevrotain tracks might be confused with mid-sized duikers, especially as the print of the ‘dew hooves’ in their tracks is usually not evident. The Water Chevrotain is the only artiodactyl that can recline on its hind metatarsals and frequently does so as it settles to rest (Dubost 1968a, and see illustration in Kingdon 1979). The Neotropical caviomorph rodent, the Paca



Lateral, palatal and dorsal views of skull of Water Chevrotain *Hyemoschus aquaticus*.

Cuniculus paca, which is only slightly smaller than the Water Chevrotain, has a similar pelage and body form, a remarkable case of convergence in two unrelated species with comparable ecology and cursorial mode of existence (Dubost 1968a, Eisenberg & McKay 1974).

Distribution Endemic to West and central Africa; the distribution ranges across the forest belt from Sierra Leone and SE Guinea, through Liberia, S Côte d’Ivoire into SW Ghana. Grubb *et al.* (1998) discuss the validity of supposed records from west of Sierra Leone, concluding that, unless a record from the Kounounkan Forest in Guinea is substantiated (see Barnett *et al.* 1996), the furthest west the species has been reliably recorded is Sierra Leone. However,



Hyemoschus aquaticus

there are recent photographic records of the species from SE Guinea-Bissau in the Boé (P. Wit pers. comm.). The species is apparently absent from the Dahomey Gap, from E Ghana through Togo and Benin. Although formerly widely distributed in S Nigeria, East (1999) mapped it only east of the Niger R., from whence it ranges east through the central forest block, across S Cameroon, Gabon, Cabinda (Angola), Congo and DR Congo to extreme W Uganda, where it is now believed extirpated (East 1999). Crawford-Cabral & Veríssimo (2005) report a record from Angola from the Lunda Norte Province, near the Cassai R., which is the southernmost record of the species from the continent. The Water Chevrotain's occupancy of this range is highly discontinuous, being limited to the vicinity of streams and rivers. Forest loss and continuing forest degradation have further reduced suitable range in many areas, in particular in the remnant Upper Guinea forest block. Pickford *et al.* (2004) recently recovered remains of the Water Chevrotain from the early Pliocene in the Kenya Rift Valley.

Habitat Water Chevrotains are confined to closed-canopy, moist, tropical lowland forest, and within this habitat, they only occupy areas in the vicinity of streams and rivers. When disturbed, they frequently move to water, often using well-established trails and paths. If pursued, they may conceal themselves in the water by remaining still and almost entirely submerged beneath debris or under overhanging stream banks. The Water Chevrotain is not a swamp specialist, nor strictly limited to riverine forest, and often ranges, forages and even rests, in mature upland forest areas. But these areas are almost always within several hundred metres of streams and rivers large enough to provide cover (Dubost 1978). Water Chevrotains do not range out into gallery forests, or into forest savanna mosaic, even along river courses. This underlines the primary importance of large areas of mature evergreen forest for the survival of this species.

Abundance Overall distribution and abundance are limited by the proximity of suitably sized water-courses. In the Ituri Forest, densities have ranged from 1.5 to 5.0/km² (Hart 1985, 2000). Hoppe-Dominik *et al.* (2011) reported a density of 0.5/km² in Tâi N. P. based on transect counts. Much higher densities have been reported in Gabon, where up to 28/km² were recorded on an island in the Ivindo R. (Dubost 1978). East (1999) estimated the total population size at around 278,000 animals. However, given the differences in reported densities, and with current uncontrolled bushmeat hunting over much of its range, any attempt to compute overall current numbers is unrealistic.

Adaptations The Water Chevrotain, along with the Asian tragulids, is considered among the most primitive and conservative of ruminants. Tragulids are thought to have separated from the pecoran ruminants in the early Eocene (Hassanin & Douzery 2003). The Water Chevrotain retains many traits thought to characterize the earliest of the ruminants, including small body size, forest habitat and a selective 'concentrate' diet (Kingdon 1979). Many of the skeletal traits of the species are identical to those of the upper Miocene tragulid, *Dorcatherium*, which was discovered as a fossil before the living *Hyemoschus* was discovered in Africa (Turner & Anton 2004). Water Chevrotains exhibit some behavioural traits of the Suidae, including similar roles for olfactory signals and use of canines in intra-specific combat (Dubost 1975, Kingdon 1979). The



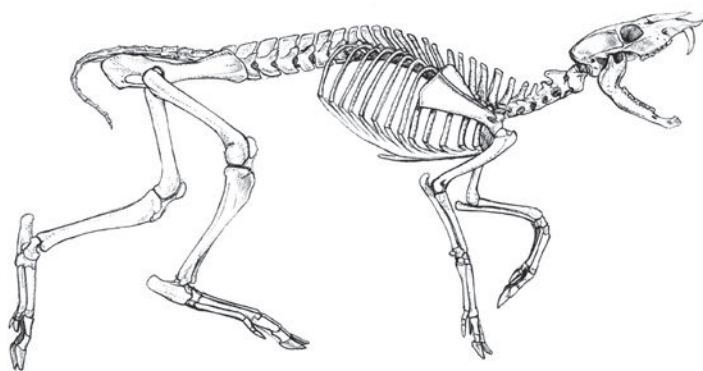
Water Chevrotain *Hyemoschus aquaticus* open-mouthed head myology.

overall adaptations of the Water Chevrotain suggest a species that is specialized for a stable but low energy trophic niche, coupled with a unique strategy for predator avoidance.

Water Chevrotains are nocturnal and spend the daylight hours resting, most often in concealed locations such as between tree buttresses, or in thick cover in tree falls, but surprisingly often in more open settings (Dubost 1978). This species relies on a complex pattern of light and dark colouration combined with immobility to provide camouflage and avoid detection. Resting animals remain immobile and may be approached to within just a couple of metres before they flush.

Water Chevrotains differ from sympatric duikers in their use of water as an avenue of escape. Black-fronted Duikers *Cephalophus nigrifrons* have specialized on swamp forests (an adaptation that is probably influenced by lower predator pressure), but Water Chevrotains, unlike Black-fronted Duikers, do not have elongated hooves and are the only small forest ungulates to actively conceal themselves by submersion in water. Water Chevrotains swim freely, although they are not sustained swimmers. Cinematography of the species under water has revealed that submerged animals move along the surface of the stream-bed using a walking gait reminiscent of submerged hippos (A. Root pers. comm.). The slit nostrils, which bear some resemblance to the valved nostrils of hippos, appear to be adapted to this aquatic escape mode.

Water Chevrotain dentition differs from that of similar sized frugivorous forest duikers in having thinner, finer-edged selenodont teeth that are weakly bedded in the skull, adapted to soft foods and ill-adapted to handle hard or coarse forage. The method of chewing resembles the shearing and cutting movements of some carnivores, and does not resemble the grinding and crushing mastication of other ungulates and suids (Dubost 1964). Water Chevrotains have a well-developed rumen and reticulum as in other foregut fermenting, pecoran ruminants but the omasum, at the posterior end of the fermentation chamber, is minimally developed. Thus the capacity to



Water Chevrotain *Hyemoschus aquaticus* skeleton.



Water Chevrotain *Hyemoschus aquaticus* myology.

retain food in fermentation chambers is limited (Hofmann 1973). The ratio of rumen volume to body weight is lower in the Water Chevrotain than it is in similar-sized sympatric frugivorous duikers, providing further evidence that the rumen is designed for rapid food turnover. This suggests that foregut fermentation in this species has evolved less for efficient breakdown of complex plant carbohydrates than to provide important detoxification functions for a diet that contains a wide range of digestion inhibitors and toxins. Chevrotains produce abundant saliva; this may capture and immobilize tannins, and other digestion deterrents and plant defensive toxins.

While the ability to handle plant toxins allows the Water Chevrotain to exploit a wide range of food sources, detoxification nevertheless incurs energetic and other costs. Water Chevrotains differ from many other ruminant ungulates in the strikingly pale colour of its flesh, in particular the musculature of the limbs. This is indicative of lower levels of myoglobin and lower metabolic capacity in the muscles. Unless they can reach water and find refuge quickly, Water Chevrotains that are flushed from hiding can be readily run down and captured, a characteristic exploited by the Mbuti hunters of the Ituri Forest, who sometimes capture animals by hand after flushing them from hiding and blocking their access to water.

Foraging and Food Fruits, seeds and fallen flowers, eaten from the forest floor, dominate the Water Chevrotain's diet. A wide variety of plant species have been reported in the diet from across its range (Gautier-Hion *et al.* 1980, Dubost 1984). A study of rumen contents taken from ungulate frugivores in the Ituri Forest (Water Chevrotain and six species of duikers) revealed that the Water Chevrotain had the most diverse diet on an annual basis ($n = 22$ stomachs) (Hart 1985). Important plant families in the diet include: Irvingiaceae, Sapotaceae, Euphorbiaceae, Apocynaceae, Sterculiaceae, Annonaceae, Ulmaceae, Sapindaceae and Meliaceae. Soft unripe fruits and unripe seeds were especially prominent in stomachs and included a number of species such as the Irvingiaceae, that were not recorded in diets when ripe. These food sources are all likely to contain protective chemical defences. Mast seed-fall of caesalpinaceous dominant canopy species, *Julbernardia seretii* and *Cynometra alexandri*, were also important seasonally. Animals captured by hunters during periods of mast seed-fall had layers of fat around their kidneys that were absent at other times of year. In Gabon, dicotyledonous families also dominate the

diet. In West Africa, the fruits of the abundant Marantaceae have been listed in the diet (Malbrant & Maclatchy 1949).

Dubost (1964) has suggested that meat may be a significant dietary item. In the Ituri Forest, Water Chevrotains as well as larger duikers, and Red River Hogs *Potamochoerus porcus* are known to feed on carcasses. Consumption of rotting carrion may even be advantageous for the ruminants, as the ammonia produced by the decaying protein is the most immediately available source of nitrogen for anaerobic microbial flora of the rumen. There are also reports that Water Chevrotain eat fish, insects and even aquatic plants (Dekeyser 1955). Rahm (1966) reports that Water Chevrotain are sometimes baited into traps with dead crabs or rats. His captive chevrotains readily ate live freshwater crabs offered to them. No evidence of these food sources was found in the rumens that were studied in the Ituri Forest (Hart 1985).

Social and Reproductive Behaviour Water Chevrotains are primarily solitary. Dubost (1978), describing a population on an island in the Ivindo R. in Gabon, reported stable and mostly exclusive female home-ranges of 13–14 ha, while ♂♂ had larger home-ranges of 20–30 ha that overlapped those of ♀♀, although they spent little time with them. In the Ituri Forest, in an area of small rivers and creeks, two radio-collared ♀♀ utilized home-ranges of 22 ha and 28 ha over the course of a year (J.A. Hart pers. obs.). They are irregularly active during the night, with periods of frequent movement alternating with periods when the animals are quiescent (Dubost 1978). In the Ituri Forest, radio-collared ♀♀ spent on average over 40% of each night resting.

Water Chevrotains have remarkably dense and thickened skins. This may protect the animals from injury in their encumbered environment; however, it also appears to protect against injuries in confrontations between conspecifics (Kingdon 1979). The canines are sharp and exposed. One ♂ caught in the Ituri Forest had a deep gash on its lower neck that might have been caused by a canine slash from a conspecific. Water Chevrotains have numerous epidermal glands, notably in the area under the chin. These are likely used in intra-specific marking, possibly in association with mating, but may also leave chemical signals at bedding sites. As yet there is no evidence for ritualized marking of home-ranges (faecal piles, rubbing posts, etc.). Dubost (1965) described a courting ♂ making brief cries as it approached and followed a receptive ♀. Local Mbuti

hunters attributed 'chuffing' barks heard at night in the Ituri Forest to this species.

Reproduction and Population Structure A single young is born after a gestation variably estimated at between four and nine months, and most likely in the region of 220 days (see Dubost & Feer 1992). In NE Gabon, births were recorded throughout the year, but with higher numbers in Dec, Jan, Apr, Aug and Sep (Dubost 1968b; and see Dubost & Feer 1992). In the Ituri Forest, births were also widely dispersed over the year. Of seven adult ♀♀, three (May, Jun and Sep) either carried full-term foetuses, or had recently given birth. Two young animals, both caught in Jan had been born in Dec. Four ♀♀ were not pregnant (Apr, Aug, Oct and Sep); another had been recently impregnated in Sep. The largest full-term foetus weighed 630 g (about 5% maternal weight). In the forests of Kivu (Utu area), Rahm (1966) reported that a ♀ pregnant at the time of her capture and kept in captivity with a ♂ gave birth in early Mar. Sixteen months later, in late Jul, the same ♀ died and was found to be bearing a full-term foetus. Water Chevrotains appear to grow quickly. In the Ituri Forest, ♀♀ with three molars and deciduous premolars had begun to breed, but no

animals with only two erupted molars were in breeding condition. Based on tooth eruption estimates by Dubost (1978), the estimated age of female maturation would fall between 20 and 24 months.

Predators, Parasites and Diseases Documented predators include Leopards *Panthera pardus* and possibly African Golden Cats *Profelis aurata*. In one study of Leopard diets in the Ituri Forest, Water Chevrotain remains were not as frequent in scats as those of nocturnal duikers (Hart, J. A. *et al.* 1996). It is possible that small ranges and limited movement by Water Chevrotains, even at night, in conjunction with their use of water as a refuge, may reduce vulnerability to predation. There is no information on parasites or diseases.

Conservation IUCN Category: Least Concern. CITES: Appendix III (Ghana).

Water Chevrotains appear to be rare, and may have disappeared from much of their historic range in West Africa. However, the species is still frequently encountered in many areas of central Africa, and is one of the preferred bushmeat species in the Kisangani region where its 'white' flesh is compared, somewhat exaggeratedly, to fish. In the central Ituri Forest, Water Chevrotains are regularly caught by the Mbuti net hunters (Hart 1979, 2000), consistently representing about 5% of total catch, even in areas that have been hunted for years. This low capture rate is probably due to the hunters' avoidance of riverine areas where chevrotains are most likely to occur. Water Chevrotains are particularly vulnerable to snares. One ♀, caught by Pygmy net hunters in the southern Ituri Forest, had a gangrenous snare wound on its front leg. Despite this, the animal had normal body weight and a full-term foetus. Water Chevrotains occur in a number of protected areas, including: Sapo N. P. and Grebo National Forest (Liberia), Tai N. P. (Côte d'Ivoire), Lobeke N. P. (Cameroon), Lope N. P. and Minkebe N. P. (Gabon), Maiko N. P., Kahuzi-Biega N. P. and Okapi Faunal Reserve (DR Congo) and Odzala N. P. and Nouabalé-Ndoki N. P. (Congo) (East 1999). Ultimately, Water Chevrotains will only be conserved by the protection of large areas of mature, undisturbed forest.

Measurements

Hyemoschus aquaticus

HB (sexes combined): 620–1020 mm*

T (sexes combined): 75–150 mm

E: 60 mm

Central Africa (Rahm 1966, Dubost 1975)

*Mean 725 mm (♂♂), 768 mm (♀♀)

Dubost (1975) cited a range of 7–15 kg with a mean 9.7 kg for ♂♂ and 12.0 kg for ♀♀. A sample of 13 adult body weights from the Ituri Forest (J. A. Hart pers. obs.) ranged from 9 to 13.5 kg with a mean of 10.3 kg for ♂♂ (n = 6), and 12.1 kg for ♀♀ (n = 7)

The longest tusk on record, from Cavallo R., Liberia, measured 57 mm (Rowland Ward)

Key References Dubost 1964, 1965, 1968a, b, 1975, 1984; Hart 1985, 2000; Rahm 1966.

John A. Hart



Water Chevrotain *Hyemoschus aquaticus*.

Infraorder PECORA – Horned Ruminants

Pecora Linnaeus, 1758. Syst. Nat., 10th edn, 1: 65.

The Pecora embraces all the extant families of horned ruminants: Cervidae (deer), Giraffidae (Giraffe and Okapi), Bovidae (bovines and antelopes), Antilocapridae (pronghorns) and the hornless Moschidae (musk deer). The last are Asian, while Antilocapridae are exclusively North American. The Giraffidae are now entirely African, although they were also known in Eurasia until the late Pliocene. Inter-relationships between and within these families have been explored in some detail by several investigators using molecular and other techniques (e.g. Hassanin & Douzery 2003, Hernández Fernández & Vrba 2005, Hassanin *et al.* 2012; and see Prothero & Foss 2007).

The Pecora probably arose in the Eurasian land mass during the Eocene: the earliest pecorans were small and hornless (with narrow bladed upper canines in the ♂♂) and resembled modern tragulids (chevrotains) in size and general form, although both tragulids and pecorans are derived in their own different ways from the ancestral traguloid ruminant stock. According to Hassanin *et al.* (2012), the chevrotains branched away from the lineage leading to the Pecora in the Early Eocene, about 51 mya. There are substantial discrepancies between this molecular clock date and the first appearance of modern pecoran families in the fossil record at the start of the Miocene, around 23 mya (Cote 2010). However, there is a record during the Late Eocene of Thailand of a modern tragulid (Métais *et al.* 2001, 2007) and fossils are known from the Late Eocene and Oligocene of traguloids more derived than tragulids (e.g. leptomerycids), and primitive small, hornless pecorans (e.g. gelocids) (Prothero & Foss 2007). The latter would have resembled chevrotains in appearance, but shared a parallel-sided astragalus with other pecorans (Webb & Taylor 1980), indicative of greater cursorial specializations.

Modern pecorans are usually of larger body size, and are typified by the possession of horns, ossicones or antlers in ♂♂ (and even in the ♀♀ of some species and populations). The evolution of horns can sometimes be correlated with living at high densities, sometimes with territorialism, or with larger body masses. Remarkable as it may seem, it is likely that horns (or horn-like organs such as antlers and ossicones) evolved convergently several times, perhaps independently in each horned pecoran family. The living moschids are primitively without cranial appendages (Davis *et al.* 2011).

The mid-Eocene saw several climatic changes in the higher latitudes, but major changes in climate and vegetation only took place in the late Eocene (Hooker 2000, Janis 2007). The issue of timing is important because pecoran ruminants have some physiological advantages and anatomical features that can be correlated with at least two significant changes that are known to have taken place in the late Eocene. One was the development of more seasonal climates; another was an increase in leguminous plants (see Volume 1). Janis (2007) has suggested that the rise of the ruminants corresponded with an innovation in the way plants responded to changes in climate. Before the onset of marked seasons most plants grew thick and durable perennial leaves or leaflets. Up to this time herbivores were therefore adapted to bulk feeding on foliage that had cell walls rich in cellulose. These animals were fast throughput, hindgut digesters,

typified by the perissodactyls that were dominant during the Eocene, so what seems to be at issue in the late Eocene is the beginnings of a decline in bulk processing versus the initiation of selective feeding, possibly with a reduction in the quantity of available vegetation (Janis 2007). While late Eocene climatic changes seem to correlate with the diversification of ruminants in general, this cannot be tied specifically to the type of pecorans that we know today (the rise of the contemporary pecoran fauna is better correlated with changes in the early Miocene; Solounias & Dawson-Saunders 1988). It is only during the Pliocene that the species richness and composition of fossil bovid species starts to resemble the present (Bobe & Eck 2001).

Following the Eocene a great increase in deciduous leafing offered advantages to herbivores that could select out smaller quantities of higher quality foliage and extract more nutrients out of less material, even if the processing of food took longer to pass through the system. The ancestral Pecora may not have been as efficient at extracting and processing nutrients from deciduous foliage as some of the living, highly derived Bovidae or Cervidae, but the primary innovation in Pecora was development of a more advanced digestive capacity which is expressed today in the possession of a fourth forestomach compartment, the omasum. The omasum, situated between the fermentation chamber of the rumen-reticulum and the true stomach (abomasum), increases the digestive capacity of the foregut by enlarging its absorptive surface with extra papillae and laminae (the details of ruminant physiology are outlined in a later section). A primary innovation of the pecoran omasum is probably its conformation into a 'sieve' that helps sort and separate incompletely crushed particles from those digesta that are already sufficiently processed to proceed on their journey through the gut. This innovation helps make rumination much more efficient, but the exact course of its evolution must remain speculative.

While we cannot date the omasum back further than the common ancestor of extant pecorans (which certainly would not be as early as the late Eocene), it is, perhaps, by around the mid-Oligocene when animals such as *Amphitragulus* (an identifiable cervoid) appear as fossils and such a supposition becomes more secure. Rumination has the additional advantage of nitrogen cycling: dietary protein is fermented to form ammonia, which is converted to urea in the liver, and then fed back to the rumen bacteria. The protein actually digested by the animal is from the rumen microbes, which frees ruminants from needing to find all the essential amino acids in their diet. This cycle also ties in with waste urea, which allows for the conservation of urinary water, allowing ruminants to survive in drier habitats.

The craniodental morphology of early pecorans supports the notion of a relatively soft browsing diet and they would likely have had a rudimentary omasum and probably preferred highly nutritious vegetation, such as new shoots and fruit (a preference that is still evident in some bovids, cervids and giraffes). The selection of grasses as food only took place much later and this major shift into graminivory (mainly seen in the bovids, less so in the cervids) led to massive increases in the size of the omasum and the storage capacity of the foregut, together with appropriate modifications of salivary

glands, livers, teeth and chewing apparatus. The development of selenodont cheekteeth seems likely to be coincident with the development of foregut fermentation, the former first appearing in the late Eocene. It has been pointed out that browsing ruminants can be as much as 400 kg heavier than the largest grazing ruminant (giraffe ♀♀ may average about 1200 kg): this is because, with enlargement, ‘packing constraints’ and the production of methane within the abdomen eventually constrain roughage grazers (Clauss *et al.* 2003). Thus, the African Buffalo *Syncerus caffer*, with an enormous rumen, is probably not very far short of that threshold.

Deer are only peripheral to Africa, being particularly successful in temperate latitudes of Eurasia, but with extensions into lower latitudes

in the Americas and Eurasia. Bovids have the broadest geographic range, although unlike cervids they never extended their range into South America. The early Miocene African fossil record is sparse, and at the moment we cannot be certain when bovids entered the continent. Some primitive pecorans of unknown taxonomic affinity are known from around 20 mya (Cote 2010), but definitive bovids are not present until around 17 mya, and it was not until around 15 mya that they (along with giraffids) became a significant part of the fauna (Gentry 2010). The radiation of antelopes, the most successful of pecorans in Africa, is discussed elsewhere in this volume.

Christine Janis & Jonathan Kingdon

Superfamily GIRAFFOIDEA

GIRAFFE, OKAPI

Giraffoidea Gray, 1821. London Med. Repos. 15: 307.

The giraffes are one of four extant groups of ruminating herbivores in Africa: chevrotains (Tragulidae), deer (Cervidae) and bovids (Bovidae) being the others; the Pronghorn *Antilocapra americana* (Antilocapridae) and musk deer (Moschidae) are exclusively American and Asiatic. Today differences are obvious, but from comparing their anatomy (especially teeth), and from their fossil history, it is clear that giraffoids share a common origin with deer (more distantly with the bovids and more distant still, the chevrotains). Molecular clocks estimate the divergence between protogiraffes and protocervid/bovids as occurring about 23.4 mya, while the tragulid/pecoran divergence was closer to 51 mya (Hassanin *et al.* 2012). It is possible that a combined examination of differences in geography, climatic adaptation, body-size, limb proportions, fossils, phylogeny and genes may eventually help explain the origins of differentiation between cervoids and the earliest giraffoids.

The region of origin for cervoids is undoubtedly Eurasia, probably temperate Eurasia. Because the first known fossil giraffe had been found in the 1840s from the Siwalik Hills (*G. sivalensis*), there has long been a presumption that giraffes might have originated in the sub-tropical Indian sub-continent. Given that fossil giraffoids are diverse and well represented in India, this remains a possibility, but the genus *Giraffa* is far too late (evolving only 7–8 mya) to indicate the origins of the superfamily. None the less, the genus *Giraffa* may well have originated in India, and Harris (1991b) considered *G. punjabiensis* the oldest member of the genus (7.3–7.1 mya) and the one most like *Bohlinia*, a widely distributed proto-*Giraffa*.

Giraffoidea had branched into two different families long before the 8-million-year-old *G. sivalensis* and *G. punjabiensis*. The Climacoceratidae are long extinct while modern Giraffes and Okapis exemplify the Giraffidae. Some resemblance between the earliest cervoids and giraffoids are exemplified by the deer-sized, deer-shaped *Climacoceras africanus* (a social herbivore that is common in East African deposits of about 17–15 mya), which had very long, spike-like male ‘antlers’ with short ‘tines’ sprouting along their length; however, it should be noted that Harris *et al.* (2010) recognize Climacoceratidae and Giraffidae as separate families.

In spite of superficial similarities, the physiological origins of giraffoid bony ossicones and non-bony deer antlers differ, although both structures probably derive from damage-minimizing or healing processes on the crania of ancestral stocks. Selection for what began as wound-generated lumps and bumps (that incidentally served *defensive* purposes) eventually became selection for species-specific cones, of dermal origin, with growth patterns that, in the giraffes, transformed cranial structures into genetically programmed, explicitly *offensive* weapons. If correct, this evolutionary progression illustrates the primacy of defensive behaviour and structures, while weapons tend to be secondary structures that become integrated into earlier defensive structures. Most giraffoid genera have ossicones in both sexes. The sivathere *Helladotherium* had ♀♀ without ossicones but that seemed to be the exception rather than the rule.

The earliest known fossil form of giraffine is *Canthumeryx sirtensis*. This fossil was discovered in deposits near Gebel Zelten some 200 miles south of Tunis, which is now desert but at the time of *Canthumeryx* was a flourishing alluvial/flood-plain/savanna/river basin habitat. *Canthumeryx* was a medium-sized antelope, about the same size as a Fallow Deer *Dama dama*, and with the characteristic bilobed giraffoid lower canines (Hamilton 1973, 1978).

Body-size differences clearly separate modern giraffes and deer; even greater contrasts existed between the well-named *Sivatherium giganteum* and any fossil cervid. So, at some quite early stage of the divergence between the giraffe and deer lineages, size may well have become a decisive factor. Large size would have included the advantage of higher feeding zones: thereafter, the elongation of both limbs and necks would have been selectively favoured, because it offered still greater access to high-quality food resources that were out of reach for other herbivores. There are interesting comparisons here to be made with the Gerenuk *Litocranius walleri*, which stands on its hindlegs to augment an already exceptional reach.

A summary of the characteristics of living Giraffoidea can be found in the family and generic profiles and warrants no repetition here.

Jonathan Kingdon & John M. Harris

Family GIRAFFIDAE

GIRAFFE, OKAPI

Giraffidae Gray, 1821. London Med. Repos. 15: 307.

| | | |
|----------------------------|---------|--------|
| <i>Giraffa</i> (1 species) | Giraffe | p. 96 |
| <i>Okapia</i> (1 species) | Okapi | p. 110 |

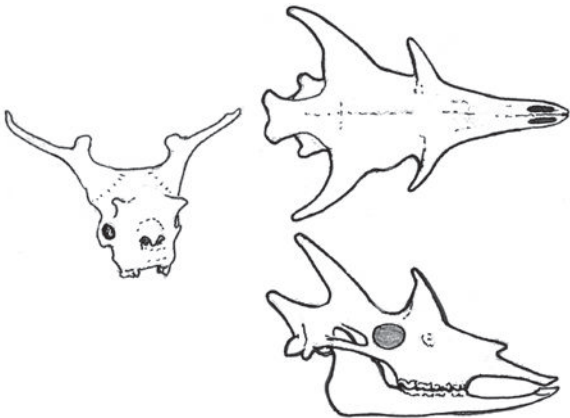
European peoples of the past were familiar with deer (family Cervidae) in the wild places of their own continent. They would also have known of Bovidae as sheep, goats and cattle in their farmed countryside and as ibexes and chamois in the mountains. Some had heard of gazelles in the great desert belt south of the temperate lands, and when Africa was explored it was found to be full of antelopes (Bovidae again). So Cervidae were found in Eurasia, while Bovidae concentrated in Africa. In addition, a single, spectacular large African pecoran ruminant, the Giraffe *Giraffa camelopardalis*, belonged to a different family, the Giraffidae, and in 1901 a second giraffid, the Okapi *Okapia johnstoni*, was discovered in Africa.

The Giraffe and Okapi are large ruminants with long legs and long necks. Both species have somewhat toughened skin over their bony horns, present in both sexes in the Giraffe, but only in ♂♂ in the Okapi. Both have a dental formula of $I^{0/3}, C^{0/1}, P^{3/3}, M^{3/3} = 32$ (Singer & Boné 1960), with small and low-crowned cheekteeth, bilobed lower canines and prehensile tongues. They browse off shrubs and trees well above ground level, yet the Giraffe is an open-country or bushland inhabitant, sometimes in quite dry areas, whereas the Okapi is a true forest inhabitant. It is interesting and instructive that such similar cheekteeth can be found in species of such contrasted habitats.

The earlier relatives of Giraffes go back to early in the Miocene epoch, before 20 mya, in Africa (Morales *et al.* 1999) and perhaps elsewhere. Conclusions about their ultimate continent of origin are much influenced by molecular phylogenies that still do not agree on which pecoran family is most closely related to Giraffidae. Price *et al.* (2005) and others (see Meredith *et al.* 2011, Hassanin *et al.* 2012) have even suggested the North American Antilocapridae, which, it has to be remembered, descend from immigrants from the Old World.

According to Harris *et al.* (2010), the family Giraffidae contains the subfamilies Canthumerycinae, Bohlininae, Giraffokerycinae, Sivatheriinae, Palaeotraginae and the living Okapiinae and Giraffinae. The first unequivocal giraffids, animals like *Canthumeryx* and *Injanatherium*, have been found as fossils from Africa to Pakistan, also in south-eastern Europe and their descendants to other parts of Asia. These early giraffids were large ruminants for their period (17–10 mya) and had widely divergent horns with spreading bases broadened in an anteroposterior direction and flattened mediolaterally. Sometimes they had a small anterior pair of horns in front of the orbits in addition to the main pair, but the nature of the skin covering of the horns is unknown. Their cannon bones or metapodials were longer than in the various deer and antelopes living alongside them.

Coincidental with the arrival of three-toed hipparionine horses from North America between 11 and 10 mya, Old World ruminant faunas changed. Two subfamilies of more advanced giraffids appeared: Giraffinae and Sivatheriinae. Sivatheres started grazing with the spread of C₄ grasses (J. Harris pers. comm.) and became very large and



Sivatherium giganteum skull in anterior view (left); skull of Miocene giraffid *Giraffokeryx punjabiensis* in dorsal view (top right) and lateral view (bottom right).

bulky, heavy-headed animals with branched or bulbously-tined horns, retaining an anterior pair of horns, and re-evolving somewhat shorter cannon bones. They persisted into the Pleistocene in India and Africa, in the latter until 500,000 years ago or possibly later. They became extinct presumably for the same reason that caused the demise of the large grazing bovids (*Pelorovis*, *Megalotragus*) and giant grazing pigs.

The common Eurasian late Miocene giraffines are a separate development from whatever stock gave rise to modern *Giraffa*. Some of them approach hypsodonty in their teeth, and microwear studies have shown that they must have grazed. In this they are very unlike *Giraffa*, as also in that their legs were not invariably lengthened to the same great extent. After flourishing for several million years they declined and later became extinct in the Pliocene.

The precise phylogenetic position of *Okapia* is unclear, the key question being whether it split recently from *Giraffa* or whether it has a long-separate ancestry. Its most obvious difference from Eurasian Miocene giraffes is the closeness of the two horn insertions. This might be considered adaptive for forest dwelling, except that the same character is found in *Giraffa*. There are wide disparities between fossil, molecular and other estimates for the divergence between *Giraffa* and *Okapia*. Molecular clocks suggest a divergence at 15 mya (Hassanin *et al.* 2012), while other reviewers have posited 8 mya (Mitchell & Skinner 2003).

It can be surmised that giraffid ruminants survived by becoming larger than other ruminants, but their Eurasian radiation was curtailed after the end of the Miocene. In Africa both *Okapia* and *Giraffa* specialized in a capability for high-level browsing, one in forests and one in savannas, but sivatheres failed to survive to the present day. *Giraffa* was also found for a long time in India but the date of its extinction there is not known. It can almost be thought of as an unfortunate historical or evolutionary accident that Giraffidae have become confined to the continent of their probable origin.

Alan Gentry

Subfamily GIRAFFINAE – Giraffe

Giraffinae Gray, 1821. London Med. Repos. 15: 307.

Subfamily Giraffinae is a monotypic subfamily, represented by a single surviving species, the Giraffe *Giraffa camelopardalis*.

GENUS *Giraffa*

Giraffe

Giraffa Brisson, 1762. Regn Anim., 2nd edn, pp. 12, 37.

The Giraffe, *Giraffa camelopardalis*, is the only extant representative of the genus *Giraffa*. Together with the only other living giraffid, the Okapi *Okapia johnstoni*, they represent the extant members of a previously more diverse group.

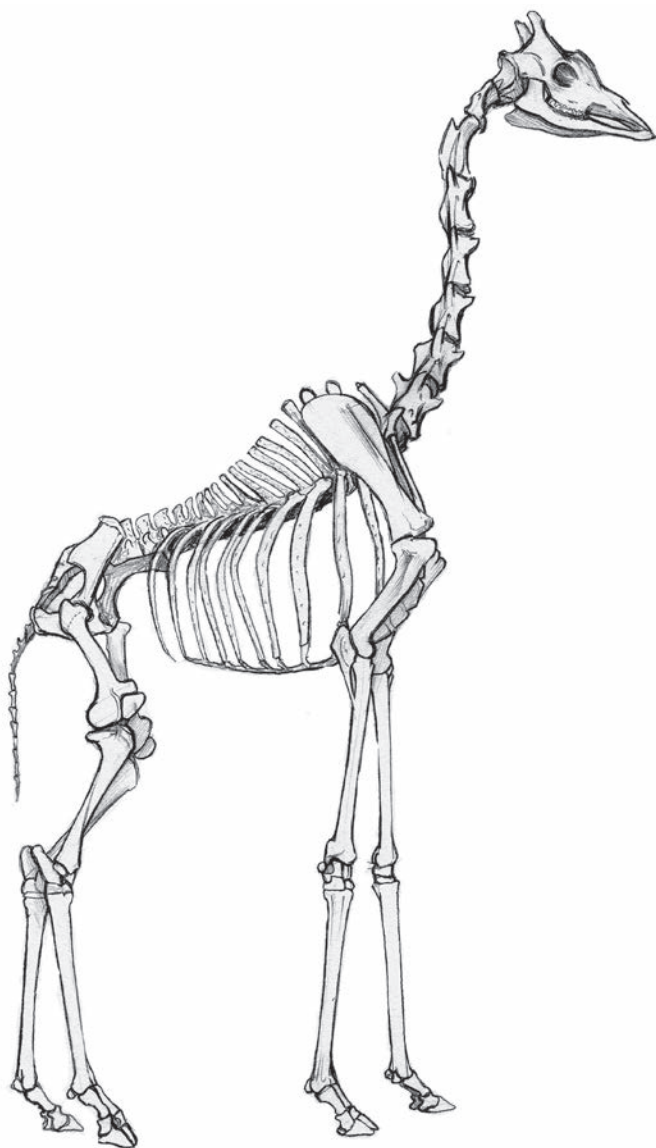
Not long after the description of the species, Levaillant in 1790 described the southern giraffe as a separate species (Dagg & Foster 1982). This separation between northern and southern species

continued through the 1800s (Owen 1841, Lesson 1842; although see Ogilby 1836). Thomas (1901) separated the reticulated giraffe *Giraffa reticulata* as a separate species from all other forms of Giraffe, and this was maintained by Lydekker (1904). Subsequent authors followed either classification scheme: Dollman (1929) and Allen (1939) separated the reticulated giraffe as a separate species, while Stott (1959) maintained the northern versus southern species split. However, for much of the latter half of the twentieth century, only a single living species of Giraffe has been recognized. More recently, Brown *et al.* (2007) identified six genetically distinct lineages, with little evidence of interbreeding between them, and proposed that some may represent distinct species.

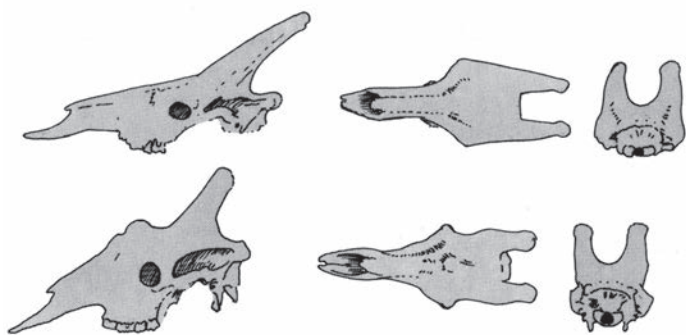
The most obvious features of *Giraffa* are the long limbs and neck. Where paired cranial appendages occur in ruminants they are on the frontal bones in a lateral supraorbital position. In *Giraffa* the paired ossicones are dermal in origin and attach to the skull more posteriorly over the frontoparietal suture. These ossicones are straight with rounded ends and vary individually in form (Singer & Boné 1960). In extant Giraffes the parietal ossicones show strong sexual dimorphism (Dagg 1965, Seymour 2001). The lower incisors and canines are robust and arranged in a semi-circular arcade. The lower canine is typically bifid and occasionally trifid. The cheekteeth are variable in size between species, with premolars relatively complex. Basicranial and basifacial planes typically are not parallel and skull flexion varies individually in the species (Seymour 2001).

The genus has an Asian origin, with the earliest known African specimens of *Giraffa* originating from fossil beds dating to the late Miocene and early Pliocene of Kenya and the early Pliocene of South Africa (Churcher 1978). Churcher (1978) described four extinct members of the genus *Giraffa* in Africa besides the extant species: *G. jumae*, *G. stillei*, *G. gracilis* and *G. pygmaea*. More recently, Gentry (1997) – following Harris (1987, 1991b) – accepted three extinct species, with *G. gracilis* included in *G. stillei*.

Giraffa jumae is known from localities in East Africa and South Africa (though Harris [1976] gives *Giraffa* cf. *G. jumae* at Langebaanweg) dated from the early Pliocene to middle Pleistocene. The South African specimens are isolated teeth and ossicones, while the East African material is more substantial. The species is founded on a nearly complete skull and mandible with a significant proportion of the postcranial skeleton. *Giraffa jumae* specimens are typically larger than contemporary *G. camelopardalis*. While the dimensions of the skull are greater, the teeth are similar in absolute size in comparison between the two species. The ossicones of *G. jumae* originate directly behind the orbital rim, further forward than in *G. camelopardalis*, and extend back parallel to the plane of the skull. The parietal horns end



Giraffe *Giraffa camelopardalis* skeleton.



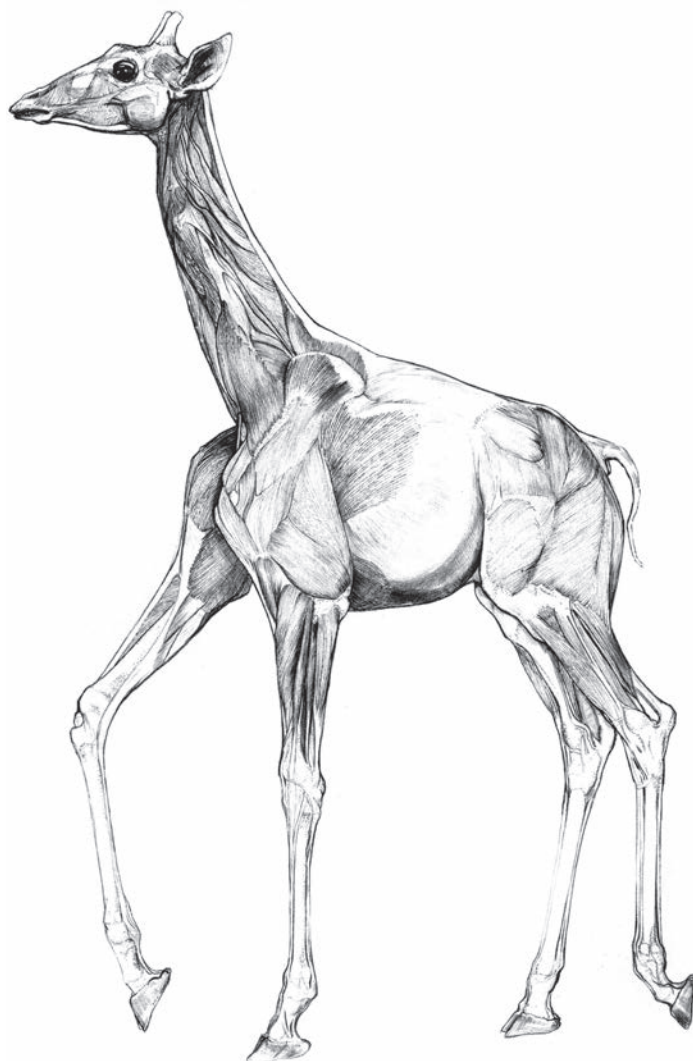
Giraffe *Giraffa camelopardalis* skull outlines (bottom) compared with Plio-Pleistocene *Giraffa jumae* (top).

in knobs. No median horn has been identified in specimens assigned to *G. jumae*. No secondary bone deposition is apparent and the occipital ridge is not enlarged. In accord with the larger cranium, the mandible is more substantial than in *G. camelopardalis*, curving upwards through the diastema and downwards in the incisor region.

Giraffa stillei, from the early Pliocene to early middle Pleistocene of East Africa, was first described as an Okapi based on dental characters and forelimb anatomy. Harris (1976) rediagnosed these specimens to *Giraffa*, according to the premolar morphology. Churcher (1978) suggested that the dental characters used to diagnose this taxon were highly individually variable and showed greater affinity to another giraffid genus, *Palaeotragus*. Churcher (1978) suggested that, without additional material, the affinities of the specimens currently assigned to *G. stillei* remained controversial. However, Harris (1987, 1991b) and Gentry (1997) accepted *G. stillei* and subsumed *G. gracilis* into it.

Specimens of *Giraffa gracilis* have been found in East Africa and possibly in South Africa from beds dating from the late Pliocene to late Pleistocene. The limb bones and neck are of similar absolute length to *G. camelopardalis* but are more lightly constructed and show finer proportions in all parts of the skeleton. Dental characters also differ. The bases of the ossicones are oval in cross-section, smaller than in *G. camelopardalis* or *G. jumae* and oriented at the same angle as in the modern giraffe. Secondary bone deposition occurs over the ossicones. The area between the orbits is convex (Harris 1976) and may or may not have a median horn present. Churcher (1978) suggested that, despite generalizations about the relative size of *G. jumae*, *G. camelopardalis* and *G. gracilis*, the skeletal elements overlapped in size between these purported species making size alone an unreliable character for species identification.

A *Giraffa* species with ossicones smaller and more delicate than those of *G. gracilis* and flattened on the posterolateral surfaces occurs in the early Pleistocene of East Africa. *Giraffa pygmaea* shows (presumed) sexual dimorphism with secondary bone deposition occurring in the (presumed) ♂♂, increasing the proportions of the ossicones relative to the (presumed) ♀♀. Dental characters are typically giraffine, but differ from other species by their small size. Churcher (1978) considered this species to be inadequately defined for certain recognition as a separate species.



Giraffe *Giraffa camelopardalis* myology.

Many of the African *Giraffa* species are based on relatively little material and the status of some species may be equivocal. Many fossil specimens were originally attributed to *G. camelopardalis* and have subsequently been reassigned to the extinct species, bringing forward the earliest recorded fossils of the modern giraffe. Contemporary giraffes vary individually, sexually and geographically in size while skull morphology is also highly variable within the extant taxon. As many of the described differences (particularly in size) may represent extremes of continuous variation further fossil material is necessary to substantiate the status of the species within *Giraffa*. Mitchell & Skinner (2003) reviewed the origin and evolution of Giraffes, while Mitchell (2009) provides a review of the scientific study and classification of Giraffes.

Russell Seymour

Giraffa camelopardalis GIRAFFE

Fr. Girafe; Ger. Giraffe

Giraffa camelopardalis (Linnaeus, 1758). Syst. Nat., 10th edn, 1: 66. 'Habitat in Æthiopia et Sennar'; identified as Egypt, in captivity at Cairo (Thomas 1911: 150); restricted to Sudan, Sennar, by Harper (1940: 322).



Masai Giraffe *Giraffa camelopardalis tippelskirchi*.

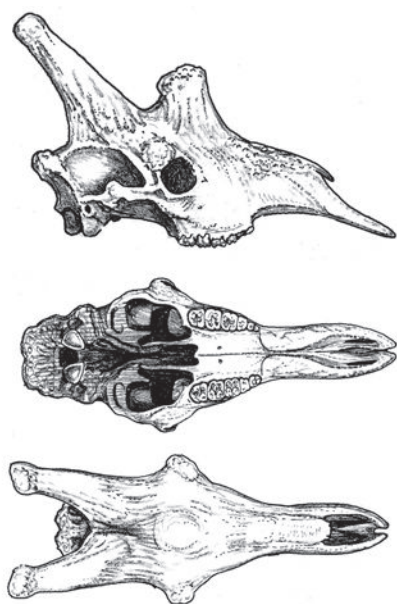
Taxonomy The Giraffe is here considered a polytypic species comprising eight subspecies (and see genus profile). Numerous subspecies have been recognized (e. g. Lydekker 1904), although most recent treatments have acknowledged nine (Ansell 1972, Dagg 1971, Dagg & Foster 1982), eight (Kingdon 1997), or six (East 1999, Grubb 2005). Based on pelage patterns, skull morphology and mitochondrial DNA analysis, Seymour (2001) described six or seven subspecies, and the existence of a distinct northern and southern clade. Considerable uncertainty surrounds the geographic and taxonomic limits of all described subspecies, as well as intergrades or hybrids between supposed subspecies (especially between *reticulata* and *tippelskirchi* in E Kenya; Kingdon 1979, Stott & Selsor 1981). Pelage patterning within subspecies highlights this uncertainty. As a definable characteristic, it is unreliable due to the high degree of individuality and variability within a population, ranging from albino and pure white through pale brown and unspotted to black (Mitchell & Skinner 2003, Fennessy 2004). Many of these variations exist within regionally definable patterns, although these boundaries are often far from clear.

Brown *et al.* (2007) analysed mitochondrial DNA sequences and nuclear microsatellite loci from six of the nine subspecies defined by

Dagg & Foster (1982). They identified six genetically distinct lineages (*peralta*, *rothschildi*, *reticulata*, *tippelskirchi*, *giraffa* and *angolensis*), with little evidence of interbreeding between them, and 11 genetically distinct populations. According to these authors, neighbouring subspecies as well as those that are geographically separated are essentially reproductively isolated, suggesting that some may represent distinct species rather than a single polytypic form. Synonyms: *aethiopica*, *angolensis*, *antiquorum*, *australis*, *biturigum*, *capensis*, *congoensis*, *cottoni*, *giraffa*, *hagenbecki*, *infumata*, *maculata*, *nigrescens*, *peralta*, *renatae*, *reticulata*, *rothschildi*, *schillingsi*, *senaariensis*, *thornicrofti*, *tippelskirchi*, *wardi*. Chromosome number: $2n = 30$ ($FN = 54$). The 28 paired autosomes are mainly metacentric and submetacentric with one pair of acrocentric chromosomes, which are small; the large X chromosomes are submetacentric and the small Y chromosomes metacentric (Wallace & Fairall 1965, Gallagher *et al.* 1994).

Description The tallest of all animals, the Giraffe is characterized by its greatly elongated neck and long limbs. Males, which are taller than ♀♀, range between about 4 and 5 m in height, with records of individuals up to 5.9 m (Shortridge 1934). Shoulders appear higher than the croup, a characteristic enhanced by the long spines of the thoracic vertebrae (see Adaptations). Neck fringed with a short, thick mane. Ears narrow and pointed, eyes large. Pelage short, with a highly characteristic pattern of large, irregularly shaped, dark patches separated by a network of light-coloured bands. This patterning, which extends from about the chin to the limbs, varies predominantly from chestnut-brown to nearly black. Kingdon (1979) considered that all Giraffe network patterns were products of interaction between two different, and genetically controlled, spot formation systems whereby light spots never occur in isolation, whereas dark spots are always isolated unless clustered within a single 'island' of ground colour. Leucistic Giraffes have been recorded (e.g. Tarangire N. P. and Rukwa in Tanzania, and Masai Mara in Kenya; C. Foley pers. comm.). The individuals (both ♂♂) in Tarangire N. P. were predominantly white, though they had regular brown colouration on the lower legs and some black markings on the upper body (C. Foley pers. comm.). Colour and pattern also varies individually, being unique to each Giraffe (although local lineage characteristics can sometimes be recognized). Overall patterns, especially the dark patches, generally tend to darken with age. Towards the hooves the limbs are generally lighter in tone, but there are regional distinctions in the extent of patterned or unpatterned 'socks'. The skin pigmentation is uniformly dark grey. Tail with black terminal tuft. There are no compound odoriferous glands. Two pairs inguinal nipples.

The skull is long, sometimes more than 700 mm, and is characterized by extensive pneumatic sinuses. A characteristic feature of adults is the two or three short, blunt 'horns', more correctly termed ossicones, which rise from the top of the skull. These comprise a parietal pair, and a single median ossicone. Ossicones are covered with skin and hair, and are present in both sexes, but are thinner and with more prominent



Lateral, palatal and dorsal views of skull of adult male Reticulated Giraffe *Giraffa camelopardalis reticulata*.

tufts of hair in ♀♀ and young. The median ossicone, which originates primarily on the frontal bone and the posterior portion of the nasal bone, is less prominent in ♀♀ (sometimes just represented by a bulge) and represents a secondary sexual male character (Spinage 1993). The Giraffe is the only ruminant with paired parietal horns present in the foetus. These ossicones begin as fibro-cartilaginous discs and are not attached to the skull (Owen 1849); they lie against the skull and present no obstruction at birth (Naaktgeboren 1969). They progressively ossify and enlarge, fusing to the skull later in life (about 4–4.5 years in ♂♂ and 7 years in ♀♀) by way of secondary bone deposits (Spinage 1968). The median horn develops in the same manner as the parietal horns (Spinage 1993). Secondary bone deposits may accumulate on male skulls, producing further bony growths. Male skulls often develop rugosities that can resemble supernumerary horns, especially on the nuchal crest (see Adaptations).

The permanent teeth erupt at about three years of age, except for the canines that erupt at around six years (Hall-Martin 1976). No dental abnormalities have been recorded (Colyer 1936, Miles & Grigson 1990).

Geographic Variation The treatment of subspecies presented here is provisional, and largely follows East (1999) except for separation of *giraffa* and *angolensis* (Seymour 2001, Fennessy 2004) and *peralta* and *antiquorum* (following Hassanin *et al.* 2007).

G. c. peralta (Niger or West African Giraffe): Niger. Wider pale bands; the edges of the spots, though somewhat crenulate, are strongly delineated from the paler ground colour. Males have the strongly formed median horn (as in all northern giraffes), but it tends to be more cylindrical (as opposed to conical). Recognized as a distinct subspecies by Hassanin *et al.* (2007).

G. c. antiquorum (including *congoensis*) (Kordofan Giraffe): N Cameroon, S Chad, Central African Republic, W Sudan and presumably NE DR Congo. The blotches, which often appear coarsely divided or constricted, extend below the hocks.

G. c. camelopardalis (including *rothschildi*) and *cottoni* (Nubian, Rothschild's, or Baringo Giraffe): Ethiopia, Kenya, Sudan, Uganda. The blotches are more widely separated than in *reticulata*. The inner sides of the legs are unspotted, with the legs pure white below the hocks. Generally very large body size, especially ♂♂. Although provisionally included in *G. c. camelopardalis* here, the form *rothschildi* may represent, and is often treated as, a distinct subspecies (e.g. see Brown *et al.* 2007).

G. c. reticulata (Reticulated Giraffe): Ethiopia, Somalia, Kenya. The large, almost polyhedral patches are placed closely together with only a fine network of light colour dividing them. Patterning may be very dark in old animals. Generally smaller body size. Integrates with *G. c. reticulata* and *G. c. tippelskirchi* have been recorded (Stott 1959, Stott & Selsor 1981).

G. c. tippelskirchi (Masai Giraffe): Kenya and Tanzania. The blotches are typically deeply dissected, forming all shapes of sharply differentiated leaf or stellate designs. The patterning always continues down to the hooves.

G. c. thornicrofti (Thornicroft's Giraffe): Luangwa Valley, Zambia. Slightly stellate spots, which become oblong on the neck. The neck is usually lighter in colour than the body and the legs are fully patterned.

G. c. angolensis (including *infumata*) (Angolan Giraffe): Namibia, SW Zambia, N Botswana, extreme W Zimbabwe; formerly in Angola, but now probably extinct. Considered as a distinct subspecies based on recent molecular evidence (Seymour 2001, Fennessy 2004, Hassanin *et al.* 2007).

G. c. giraffa (including *capensis* and *wardi*) (Southern or Cape Giraffe): South Africa, S and SE Zimbabwe and SW Mozambique. The blotches, which extend down to the hooves, are more or less round. The colouring may be very dark. Generally large body size.

Similar Species Given its distinctive features, the Giraffe is unlikely to be confused with any other animal.

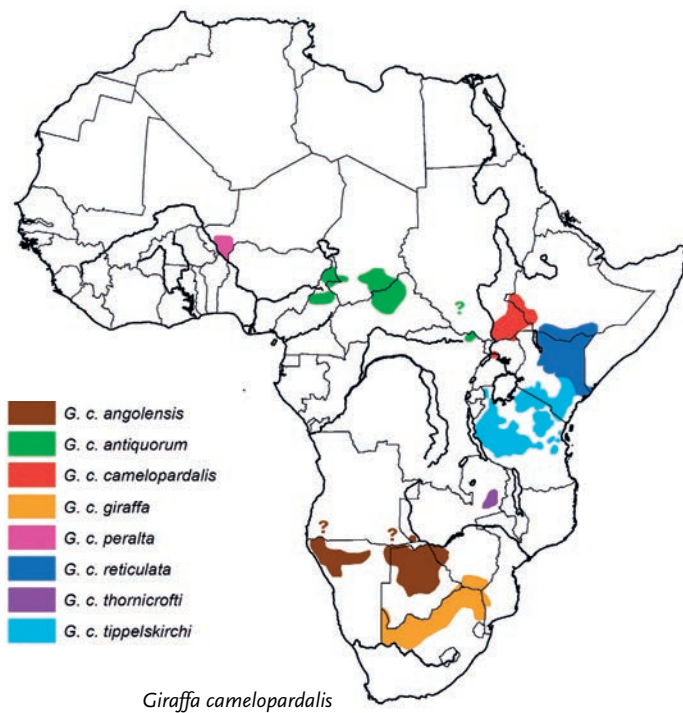
Distribution Endemic to Africa.

Historical Distribution Widespread in N and W Africa, including the Sahara, until the Neolithic. Rock drawings, petroglyphs and skeletons confirm their presence on the banks of the Nile and the plateau of Messak until 4000 BC and later in the Western Sahara and Mauritania (Le Quellec 1999).

Giraffes were historically distributed widely throughout the Sahelian regions of West Africa from C and E Senegal, N Guinea and SE Mauritania through C Mali to C/S Chad, N Central African Republic, Sudan (west of the Nile) and NE DR Congo.

Nubian/Rothschild's Giraffes occurred in SW Eritrea and W and SW Ethiopia, south through Sudan, east of the Nile R., Uganda and W Kenya. Reticulated Giraffes ranged from S Ethiopia south through Kenya, east of the Rift, adjacent S Somalia to north of the Tana R. Masai Giraffes occupied S and E Kenya and much of Tanzania north of the Rufiji R. Thornicroft's Giraffes occurred only in the Luangwa Valley in Zambia (Ansell 1978). There is one exceptional occurrence of a Giraffe being recorded in Malawi (a single individual killed in Sep 1976), presumably a vagrant animal from the Luangwa Valley (see Ansell & Dowsett 1988).

The historical ranges of the two southern subspecies (*giraffa* and *angolensis*) covered Namibia (including the semi-desert areas of Kaokoland in the north-west) and adjacent parts of S Angola (in two

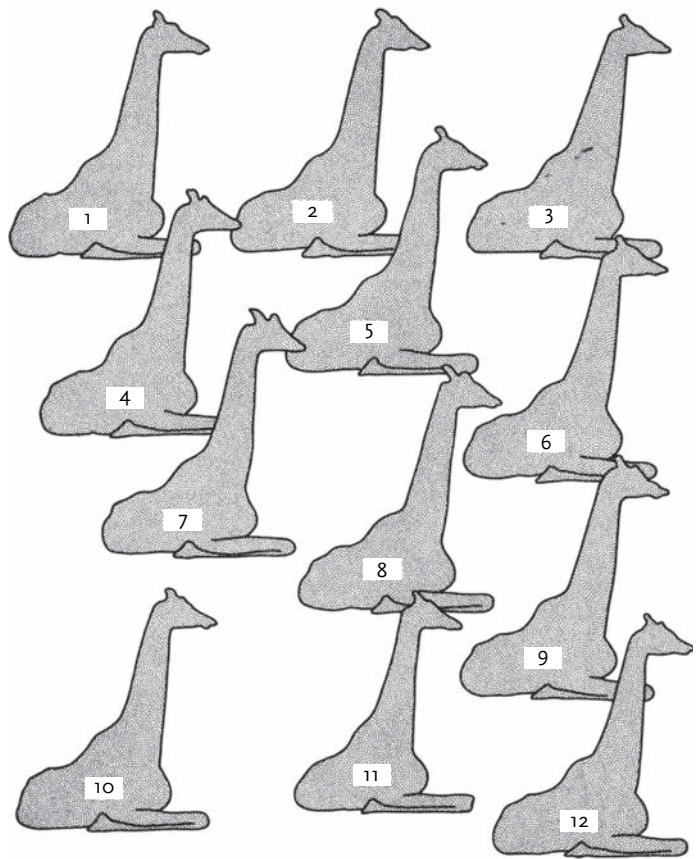


well-separated populations in the SW and SE), N and C Botswana, SW Zambia, W and S Zimbabwe, S Mozambique, and N and NE South Africa (East 1999). Although some have proposed that Giraffe never occurred south of the Komati R. in Swaziland or KwaZulu-Natal (Goodman & Tomkinson 1987), Giraffe were probably present 1000 BP in KwaZulu-Natal, but had died out or been extirpated by ca. 220 BP (Cramer & Mazel 2007). Indigenous San drawings suggest that Giraffe once occurred throughout parts of S South Africa: near Queenstown, in the Tarka area, near Graaff Reinet and on the Tsomo R. around 1650. However, over a period of 300 years, the limit of their range was reduced by nearly 900 km (Dagg & Foster 1982).

Current Distribution Today no Giraffes survive in North Africa, though some may have remained in Morocco as late as 600 AD (Schomber & Kock 1961). The beginning of the twentieth century marks the sharp decline of Giraffes in the West African region. The only surviving population in West Africa is in SW Niger, an area of approximately 15,000 km² delineated as the 'giraffe zone' in a broader Biosphere Reserve. This population co-habits with subsistence agricultural communities and seasonally migrates throughout its range in search of available forage. During the wet season (Jun–Sep), the animals are located on the Koure and Fandou Plateau, but during the dry season they move to the Dallol Bosso North (a sandy agricultural region with permanent water in numerous pools) and the regions of Loga and Dogondoutchi (Ciofolo 1995, 2002, Boulet *et al.* 2004). In 1996, five Giraffes were observed in the Ansongo-Menaka Partial Faunal Reserve in Mali, on the border of Niger (Le Pendu & Ciofolo 1999, East 1999); however, this population is assumed to be extinct.

The Kordofan Giraffe is still present in N Cameroon, S Chad and Central African Republic (mainly Manovo–Gounda–St Floris N.P.). East

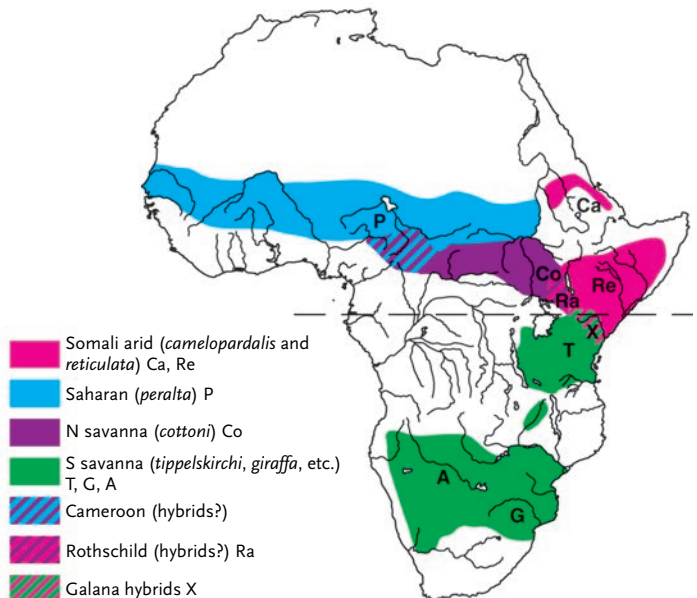
RIGHT: Giraffe *Giraffa camelopardalis* distribution interpreted as four major types with mixed or intermediate populations in between (reproduced from Kingdon 1997).



Key to Giraffe patterns:

1. Nubian Giraffe *G. c. camelopardalis* Ca
2. Reticulated Giraffe *G. c. reticulata* (dark morph) Re
3. Reticulated Giraffe *G. c. reticulata* (light morph) Re
4. Kordofan Giraffe *G. c. antiquorum* P
5. Hybrid Reticulated Giraffe *G. c. reticulata* × Masai Giraffe *G. c. tippelskirchi* (between Tana & Galana Rivers) X
6. Masai Giraffe *G. c. tippelskirchi* T
7. Nubian Giraffe *G. c. camelopardalis* (dark morph) Co
8. Nubian Giraffe *G. c. camelopardalis* (Rothschild's Giraffe) Ra
9. Masai Giraffe *G. c. tippelskirchi* (dark morph) T
10. Angolan Giraffe *G. c. angolensis* A
11. Southern Giraffe *G. c. giraffa* G
12. Masai Giraffe *G. c. tippelskirchi* T

ABOVE: Giraffe patterns display both regional characteristics as well as individual variation. Patterns shown on the page opposite come from localities indicated in the map (below) and correspond to the key (above).





Giraffe *Giraffa camelopardalis* (see key opposite).

of this, there is a paucity of information, with no information available from Sudan, west of the Nile; they were eliminated from Radom N. P. and were not recorded at all from Southern N. P. or Shambe G. R. during recent surveys (Fay *et al.* 2007). Their main remaining nucleus is said to be Garamba N. P. in NE DR Congo (East 1999).

The Nubian/Rothschild's Giraffe survives in SE Sudan (in Boma N. P. and Bandingilo Reserve, but extinct in Dinder N. P. since 1985), SW Ethiopia, Uganda (Murchison Falls N. P. and Kidepo Valley N. P.) and Kenya, predominantly in protected areas; it is now extinct to the north and in Eritrea. The Reticulated Giraffe still occurs in S Somalia and Ethiopia, and occupies some of its historical range in N Kenya, mainly outside protected areas. Likewise, the Masai Giraffe also occupies parts of its historical range, although populations in Tsavo East N. P. in Kenya and Serengeti N. P. in Tanzania, as well as other protected and unprotected areas, have suffered declines; Masai Giraffe have been introduced to Rwanda (East 1999). Thornicroft's Giraffe is still found in large numbers in the Luangwa Valley of Zambia (East 1999).

Having been reintroduced to many parts of the range from which they were eliminated, Angolan and Southern Giraffes are currently common both inside and outside a number of protected areas in Namibia, Botswana, Zimbabwe and South Africa. In Angola, the Giraffes that historically occurred in the south-west of the country had disappeared completely by the 1940s, while the population in the south-east is now assumed to be extinct (Crawford-Cabral & Veríssimo 2005). East (1999) reported that the Angolan Giraffe still survived in small numbers in Sioma Ngwezi N. P. in SW Zambia. In Mozambique, a few individuals of the Southern Giraffe still occur in Coutada 16, adjacent to Kruger N. P. (J. Anderson pers. comm.).

Giraffe have been introduced to Swaziland with stock from South Africa and Namibia (although Namibian animals have done poorly; see Monadjem *et al.* 2003), and have also been introduced to a number of reserves in South Africa, including in KwaZulu-Natal and the Eastern Cape.

Habitat Giraffes are typically associated with *Acacia*, *Commiphora* and *Combretum* savannas. They occur marginally in the miombo *Brachystegia* woodland, while an isolated population (*G. c. thornicrofti*) occurs in the Luangwa Valley (where mopane, *Acacia* and *Combretum* are widespread), and in the *Isoberlina* woodland in Cameroon. Giraffes are today absent from true deserts and from rainforests; they also are absent from coastal savannas and large savanna mosaics (such as Lopé, in Gabon). Nevertheless, in NW Namibia they reside throughout the northern Namib Desert, where annual rainfall is less than 100 mm; here, they are amongst the best adapted ungulates in this desert environment (Scheepers 1992, Fennessy 2004). Giraffes in the northern Namib Desert rely on the riparian forests along the banks of ephemeral rivers, which include *Acacia*, *Faidherbia*, *Combretum* and *Commiphora* species, and surrounded by open gravel plains and sand dunes (Fennessy 2004).

East of the Nile, in S Sudan, Giraffes are never found in the permanently flooded areas of the Sudd, but aerial surveys (Mefit-Babtie 1983) showed that they were widely distributed over the entire floodplain throughout the year. During the height of the flood season, Giraffes were relatively few in the better drained woodlands yet, paradoxically, showed a perceptible seasonal preference for quite deeply flooded areas close to the permanent swamps. Observation revealed that the attraction for Giraffes at this time was vegetation growing on large termite

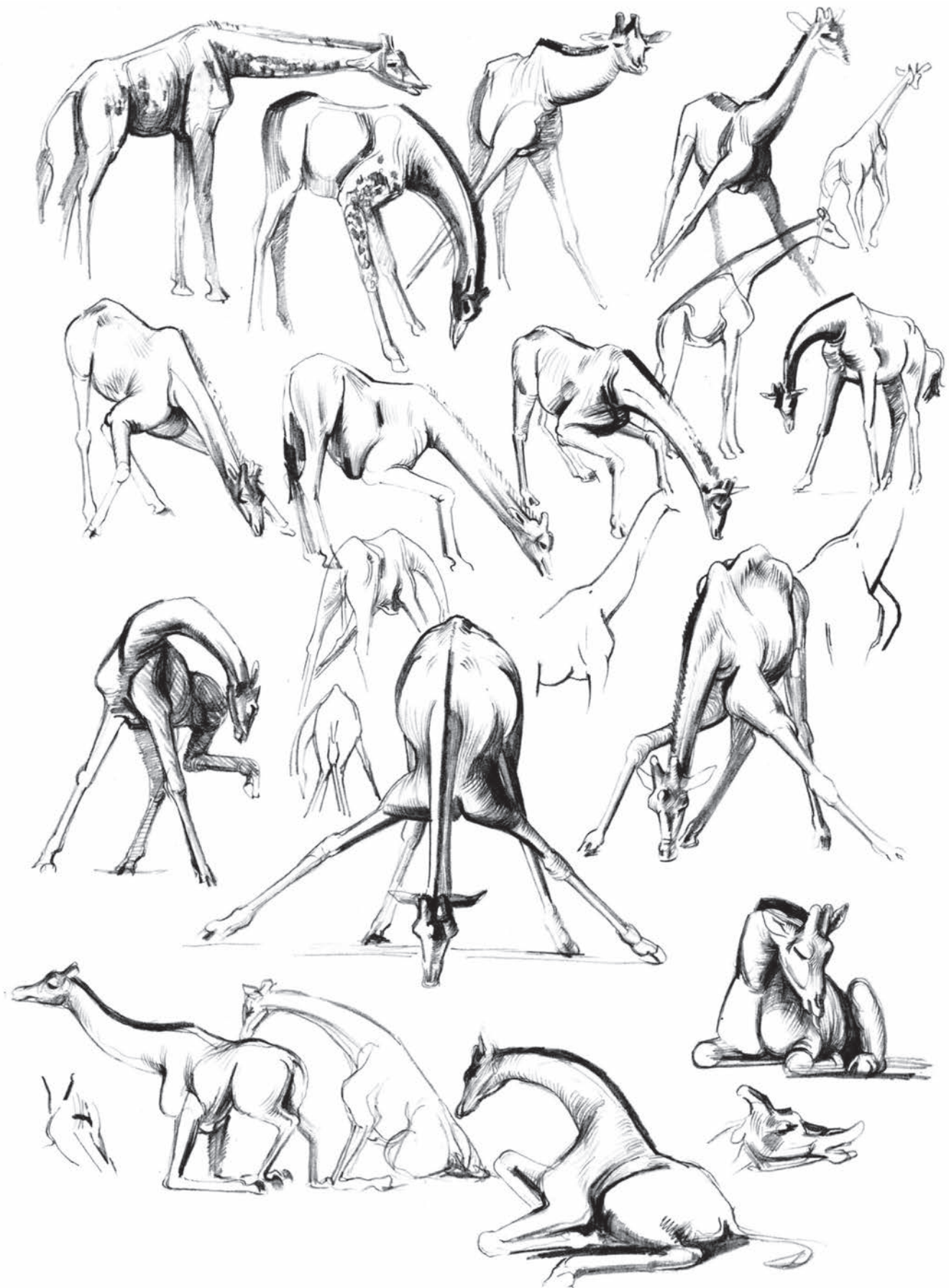
mounds, which are exceptionally abundant in the seasonally flooded grasslands (or 'Toic') and provide islands of soil raised above the surrounding floodwaters (J. Kingdon pers. comm.). In addition to climbers, such as *Ipomea*, the foliage of *Balanites*, *Acacia*, *Cassia*, *Grewia* and *Ziziphus* trees are all in an actively growing state at this time.

Freezing temperatures coupled with wind and rain can kill Giraffes (Dagg & Foster 1982); however, they can tolerate temperatures in excess of 40 °C (e.g. in Namibia and Niger). Spatial and temporal environmental factors, e.g. rainfall, affect their distribution as well as influence their seasonal movements. In Niger, Giraffes aggregate during the wet season where forage resources are limited (Le Pendu & Ciofolo 1999), while in East Africa, they commonly disperse during the wet season, aggregating near rivers in the dry season (e.g. Leuthold & Leuthold 1978a, Estes 1991a).

Abundance East (1999) estimated the total population at about 140,000 animals, predominantly in areas dominated by *Acacia* woodlands and shrublands, including 3500 Niger and Kordofan Giraffes (*peralta* and *antiquorum* combined), approximately 500 Nubian/Rothschild's Giraffes, 36,000 Reticulated Giraffes, 60,000 Masai Giraffes, 1200 Thornicroft's Giraffes (more numerous than at any time during the last 50 years) and more than 40,000 Angolan and Southern Giraffes (*angolensis* and *giraffa* combined). The most recent estimates put the total population at less than 100,000 animals (International Giraffe Working Group pers. comm.); efforts are underway to census the continent's populations more accurately (Fennessy 2007). The population in Niger (estimated to number 79 animals in 1999; Ciofolo *et al.* 2000) has since increased (Boulet *et al.* 2004, Suraud & Dovi 2006), with 193 animals photographed and identified in 2008 (Suraud 2009).

Giraffe density appears correlated with the distribution and density of high-quality forage: where appropriate food plants are abundant, Giraffes can live at densities of up to 2.6/km² (Pellew 1983a, b, 1984b), although Pratt & Anderson (1982) reported extraordinarily high densities in the small Arusha N. P. (3.96 ind/km²). Across its range Giraffe densities can vary between populations with 0.7/km² observed in Kruger N. P. (Hirst 1975) and 0.85/km² in Lake Manyara N. P. (Van der Jeugd & Prins 2000). On the other hand, where the abundance of high-quality forage is scarce, densities are markedly lower: for example, in Southern N. P. in Sudan, where Giraffes probably no longer occur, the population density was estimated at 0.05/km² (0.03–0.1/km²) (Boitani 1981) and in Tsavo East N. P. at 0.2/km² (Leuthold & Leuthold 1978a). The lowest densities have been recorded in the desert-dwelling populations of Niger and Namibia (0.01/km²; Fennessy *et al.* 2003, Fennessy 2004).

Adaptations The Giraffe displays a range of remarkable physiological and morphological adaptations, many linked directly to its standing as the world's tallest animal, perhaps foremost of which is its long neck. The osteology of the neck has been studied by anatomists since Owen (1841). Brownlee (1963) summarized theories concerning its evolution, and more recent contributors include Solounias (1999), Mitchell & Skinner (2003) and Simmons & Altwegg (2010). As is the case in all mammals (except manatees *Trichechus* spp. and sloths *Bradypus* spp. and *Choloepus* spp.), there are seven cervical vertebrae. Solounias (1999) suggested that neck length could be attributed to the presence of an 8th cervical vertebra, but as this vertebra supports a rib it must



Giraffe *Giraffa camelopardalis*.

by definition be a T1 (Mitchell & Skinner 2003, Badlangana *et al.* 2009). In addition, it would seem that the role of articulation between the thoracic and cervical sections of the vertebral column normally performed by C7 is at least partially taken over by T1 (Mitchell & Skinner 2003). Elongation of the neck is the result of uniform lengthening of the entire cervical series, including C7 (Badlangana *et al.* 2009), which is not a foetal process but occurs after birth (van Sittert *et al.* 2010). The neck vertebrae have characteristically pronounced opisthocoelous (or ball-and-socket) joints. Backward retraction of the base of the cervical column (so that it emerges well behind the sternum) and upward bowing of the thoracic vertebrae permits the forelegs to carry a high proportion of the head and neck weight, creating the 'chesty' profile so typical of Giraffes.

The Giraffe has 14 thoracic vertebrae (as noted above, the first thoracic somewhat resembling a cervical vertebra), five lumbar vertebrae and four sacral, although a vertebra may be lost to the tail, which is variable, ranging from 12 to 20. The pelvis is shorter than in most other Pecora and the sacral region is shorter compared with some bovids. Other large species like African Buffalo *Syncerus caffer* and ox have shorter thoracic regions, with 13 vertebrae, a longer lumbar region and similar length sacral. Camels have 12 : 7 : 4, thus their lumbar region is longer than the Giraffe's and the thoracic shorter. The Okapi *Okapia johnstoni* has 24 in the ratio 14 : 5 : 5, thus the sacral region is longest. In terms of length of the cervical vertebrae relative to overall vertebral column length, the neck vertebrae of the Okapi comprise 35% of the total vertebral column, while those of the Giraffe comprise 54% (Badlangana *et al.* 2009). The Okapi is approximately 55% shorter in height at the shoulder than the Giraffe, about 1.65 m compared with 3 m (C. Spinage pers. comm.).

The spines of the thoracic vertebrae are markedly elongated, forming points of origin for some of the neck muscles and for the *ligamentum nuchae* (Mitchell & Skinner 2003). These spines also enlarge the purchase (and therefore the swing of the entire forelimb) for muscles attached to the shoulder blade, notably the trapezius and rhomboid. Hall-Martin *et al.* (1977b) estimated weight for the head and neck combined at about 250 kg, and leverage of such an extended mass is facilitated by several adaptations, including the thoracic spinous processes, the presence of a large and extensive frontal cranial sinus (adding volume, but not mass to the skull; see Badlangana *et al.* 2011) and a reduction in the size of ossicones, compared with some extinct shorter-necked giraffe species. Van Schalkwyk *et al.* (2004) noted that cervical vertebrae mass decreases towards the head (largely a result of the size of each vertebra as the density actually increases), indicating that the bulk of the head and neck weight is supported at the base and that the distal end of the neck and head is comparatively light and more manoeuvrable than would otherwise be the case.

Adaptations that reduce the mass and weight of the head and neck apply much less to adult ♂♂. Their principal intra-specific weapon is the head and its offensive/protective protuberances, which is swung by the neck like a pendulum (Owen 1841, Kingdon 1979). The sometimes violent 'necking' (see Social and Reproductive Behaviour) has a correlation with accumulations of secondary bone growth and heavier skull weight for ♂♂ (up to ~15 kg; Dagg 1965, Seymour 2001), which suggests that male rivalry has resulted in selection for greater head weights (Simmons & Scheepers 1996). Osteoblasts build up and reinforce ossicones, presumably under the influence of male hormones, but osteoblasts also become active in

direct response to trauma. In the latter case they plaster over cracked bones and, in response to bruising, form encrustations on the outermost margins of the frontal bones (which overhang and thus help protect the orbits) along the exposed bridge of the nose (forming lumps on the nasal bones) and, most prominently, on the topmost ridge of the occipital bone. Understandably, occipital or 'nuchal' knobs are often mistaken for 'ossicones' and such giraffes are often described as 'five horned'.

An interesting detail in male Giraffe skulls is the occasional occurrence of bony encrustations on only one side of the head, probably resulting from repeatedly striking with that side of the head (J. Kingdon pers. comm.); indeed, Lydekker (1904) described a subspecies (*cottoni*) from a single specimen citing an 'orbital horn' over the right eye. Males normally appear to be 'ambidextrous', but they also have a choice as to the direction in which they will deliver or absorb blows. When they first engage, the contestants can either stand side by side or face in opposite directions. In the side-by-side position, one fighter swings to the right, one to the left. In the second choice, the same side is involved in both animals. In a small sample of 13 contests, J. Kingdon (pers. comm.) observed six pairs facing in opposite directions, four with their right shoulders engaged, two with the left. It would be interesting to learn whether advantages or disadvantages could accrue for ♂♂ with a particular preference and if there are regional patterns of preference.

Mitchell & Skinner (2003) discussed the possible advantages conferred by height, including protection from predation, increased vigilance, an enlarged surface area for thermoregulatory heat loss, and, in ♂♂, sexual dominance and access to food. These authors considered that the hypothesis that Giraffe height evolved as a response to the advantages conferred by feeding height stratification holds true only for adult ♂♂. For example, Du Toit (1990a) compared preferred heights of Giraffes with Greater Kudu *Tragelaphus strepsiceros*, and found that Giraffes tended to feed at heights of 1.7–3.7 m (♂♂ feeding higher than ♀♀) and Greater Kudu at heights of about 1 m, and occasionally up to 2 m. Greater Kudu were, therefore, competitive with female (and young) Giraffes. Other dietary studies have noted that Giraffes frequently feed well below their maximum foraging height (Leuthold & Leuthold 1972, Pellew 1984a, Young & Isbell 1991). None the less, analysis of the feeding competition hypothesis suggests that a long neck confers at least some advantage when lower leaves of trees have been eaten by these shorter browsers (Cameron & du Toit 2007).

An alternative theory suggested by some authors (Churcher 1978, Simmons & Scheepers 1996) is that the long neck may have evolved in response to the sexual advantage it confers, with ♂♂ using their necks and heads to achieve sexual dominance. However, this 'necks for sex' theory was not supported by empirical data that showed that morphological differences between the sexes are minimal and that any differences that do exist can be accounted for by the larger realized mass of ♂♂ (Mitchell *et al.* 2009a, van Sittert *et al.* 2010; but see Simmons & Altwegg 2010). In reviewing these two primary competing hypotheses, Simmons & Altwegg (2010) noted that the main challenge for the competing browser hypothesis is to explain why Giraffes have remained about 2 m taller than competing browsers for over one million years given the costs involved, while the sexual selection hypothesis fails to account for the long neck of female Giraffe (even though they are shorter than ♂♂).



Giraffe *Giraffa camelopardalis rothschildi* head of subadult female.

Some (Wright 1871, Brownlee 1963) have suggested that the Giraffe's long neck evolved because it assists the detection of predators: Giraffes have excellent sight, and their auditory and olfactory senses are acute. They can detect danger and conspecifics from a greater distance than other savanna species and seem to stay in contact by sight at a distance of over one kilometre (especially in open environments) thanks to their height advantage (Dagg & Foster 1982). Predator avoidance may also explain the coat markings in Giraffe, which could serve as camouflage for calves during the hiding stage, as calves are vulnerable to high rates of predation during the first few months of life (Langman 1977) (see Reproduction and Population Structure). Social factors are a significant modifier of vigilance in Giraffes: in Kruger N. P., bulls scan the most when they are in groups with larger bulls and least when they are with smaller bulls. Conversely, predation risk does not appear to be a significant modifier of vigilance: cows do not change their vigilance behaviour when alone or accompanied by calves (Cameron & du Toit 2005).

In addition to the extension of the neck, there is also elongation of the limbs. However, the elongation of the limb bones is independent of a corresponding increase in their diameter. The more distal limb bones, particularly the metapodials, but not the humerus or femur, are extraordinarily elongated and slender for an animal of such size, suggesting that the increase in length must be compensated for by an increase in strength (Mitchell & Skinner 2003). The latter authors posited that this increase in strength was facilitated by the high density of the lower limb bones, such that about 80% of all skeletal calcium is in the leg bones, with the radius/ulna and metacarpal bone having the highest relative density of any bone at 150% and 178%, respectively. That the weight-bearing bones are denser than others is supported by the study of Van Schalkwyk *et al.* (2004), who also propose that, in addition to increased density, Giraffe limb bone strength is achieved by the bones being much straighter and having much thicker walls than in other artiodactyls. However, Van Schalkwyk *et al.* (2004) also presented evidence that the skeleton of the Giraffe is not unique with respect to bone density. Mitchell *et al.* (2005) have since shown that the Giraffe skeleton contains three times more absolute amounts of calcium and phosphorous than is found in the African Buffalo skeleton. This translates into a 1.5- to 2-fold higher calcium requirement for Giraffes, with which they seem to cope effectively by selecting for calcium-rich, dicotyledonous, browse. However, sources to meet phosphorous requirements are less obvious and a

seasonal deficiency of phosphorous is a probable cause of instances of observed osteophagia (see Foraging and Food).

Both neck and limb elongation requires an unusual cardiovascular and respiratory system. Physiological adaptations of the circulatory system have been investigated in detail by numerous authors (e.g. Amoroso *et al.* 1947, Lawrence & Rewell 1948, Goetz 1955, Goetz & Keen 1957, van Citters *et al.* 1966, Kimani 1983, Badeer 1986, 1997, Hargens *et al.* 1987, Kimani *et al.* 1991a, b, Pedley *et al.* 1996, Mitchell *et al.* 2006, 2008, 2009b). The hydrostatic pressure exerted by gravity on the column of blood in the neck (the heart is ~2 m away from the head; Mitchell & Skinner 1993) necessitates an average systemic blood pressure of ~200 mm Hg compared with the norm of 100 mm Hg in other terrestrial mammals (see Mitchell & Skinner 2009 and references therein). Although widely reported as having a very large heart relative to overall mass, heart mass in Giraffe is only 0.5% of body mass – the same as that in other mammals (Mitchell & Skinner 2009). Instead of cardiac enlargement or an increase in cardiac output, cardiac hypertrophy of the left ventricular and interventricular heart wall muscles (their thickness is linearly related to neck length) is the key to maintaining cerebral blood flow. Further, hypertrophy of the arteries and arterioles at or below the level of the heart helps control blood flow to the organs and, during drinking, the thick-walled arteries help prevent blood from rushing to the head (Mitchell & Skinner 2009). Valves in the jugular vein direct the large amounts of blood returning to the heart via the inferior vena cava into the right atrium, and prevent it regurgitating into the jugular (Mitchell *et al.* 2009b; contra Hargens *et al.* 1987). When a Giraffe raises its head, a momentary pause during head lifting and intense extracranial vasoconstriction helps to prevent fainting (Mitchell *et al.* 2008). Microcirculation haemodynamics, the thick skin and thickened arteries, an autonomic nervous system and innervation of the limbs help prevent oedema (Hargens *et al.* 1987, Pedley 1987).

Other physiological adaptations include an efficient nasal cooling system that regulates brain temperature (up to 3 °C lower than body temperature) and reduces respiratory water loss, while respiratory dead space volume is minimized by a variable diameter of the trachea (Mitchell & Skinner 1993). Whole body thermoregulation might be passively maintained by skin patches acting as heat dissipating windows facilitated by vasodilation of the blood vessels beneath the dark skin surface (Mitchell & Skinner 1993, 2004). In Etosha N. P., Namibia, Giraffes have been observed to face the sun when the temperature is high, probably in order to diminish the surface exposed (Kuntzsch & Nel 1990).

Many of the extant Giraffe's adaptations are essentially those of a very large animal not just a very tall one. While their height has facilitated several detailed physiological adaptations, their size also increases nutritional demands. For example, ♂♂ require some 20 g of calcium per day; by comparison, a human weighing one-tenth the weight of a giraffe has a daily calcium requirement of one-fortieth (Mitchell & Skinner 2003). In order to fulfil their daily nutrient requirements, Giraffes must consume a large amount of browse in the form of legumes. Their molars are heavy, brachydont and selenodont. The lower incisors combine with the bi- or tri-lobed canines to form an arc to comb the leaves and bend/break the thorns off shoots. Horny papillae help protect the lips and tongue from thorns, and thick saliva protects the tongue and buccal cavity.



Giraffe *Giraffa camelopardalis* myology of head.

The tongue is long and mobile, up to 45 cm, allowing the Giraffe to precisely select food items. Although Giraffes drink when water is available, they can survive for a long time without water. In the north of the Namib Desert, Scheepers (1992) observed Giraffes drinking twice during the course of six years of observation, and J. Fennessy (pers. comm.) only ten times during a five-year study period. Giraffes seem to demonstrate a total lack of dependence on available bodies of water and get their water from preformed water in food and dew on the plants (Scheepers 1992, Fennessy *et al.* 2003, Fennessy 2004). A gall bladder may or may not be present.

Giraffes present a biphasic activity budget: energy consumptive activities like feeding and walking occur more post-dawn and pre-dusk, while energy conserving activities such as resting and ruminating occur more during the hottest period of the day (Leuthold & Leuthold 1978b, Pellew 1984a, Fennessy 2004, 2009).

Contrary to most other quadrupeds, Giraffes swing both legs on the same side at almost the same time during their 'pacing' walk (this pattern of limb movement is abandoned when the Giraffe breaks into a gallop). A galloping Giraffe can reach 56 km/h, young running faster than adults. Their long legs enable them to clear fences 1.5 m in height (Dagg & Foster 1982).

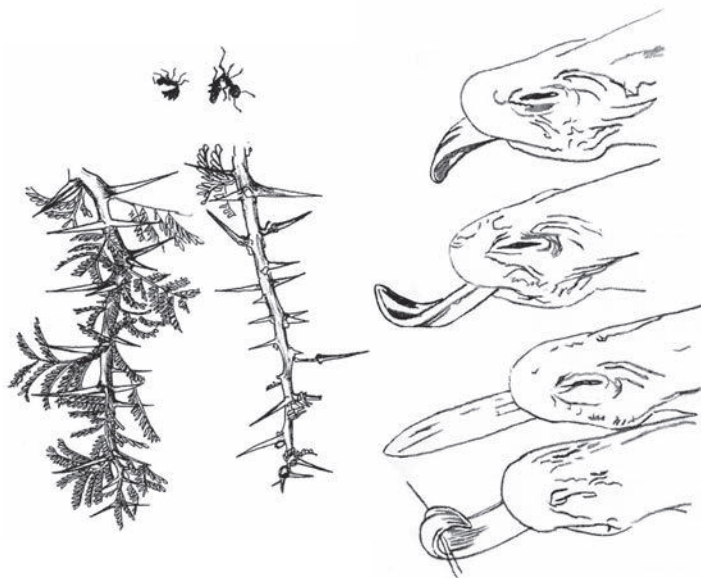
Giraffes emit a scent that can be detected by keen-nosed humans over considerable distances. Wood & Weldon (2002) analysed extracts of hair samples from adult Reticulated Giraffe ♂♂ and ♀♀ and found two highly odoriferous compounds (as well as a number of other major compounds) that appeared to be primarily responsible for the Giraffe's strong scent. They suggested that these compounds may deter microorganisms or ectoparasitic arthropods, as most of these compounds are known to possess antibacterial or fungistatic properties against mammalian skin pathogens or other microorganisms. The levels of p-cresol, one of the compounds detected, in Giraffe hair are sufficient to repel some ticks.

Foraging and Food Giraffes are selective browsers, feeding predominantly on leaves and buds on trees and shrubs. *Acacia* species form the bulk of their diet throughout their range, as well as species of the genera *Balanites*, *Commiphora*, *Detarium*, *Boscia*, *Combretum*, *Ziziphus* and *Grewia*. However, many other species are eaten: at least 25 in Willem Pretorius G. R., South Africa (Kok & Opperman 1980), 29 in the Hoanib R. region, N Namibia (Fennessy 2004), 45 in Serengeti N. P. (Pellew 1984a) and in Niger (Ciofolo & Le Pendu 1998), 69 in Tsavo East N. P. (Leuthold & Leuthold 1972) and 77 in the Middleveld of Zimbabwe (Lightfoot 1978). Seasonally, they feed

on a range of species and plant parts, including herbs (e.g. *Hibiscus asper*) and climbers and vines (species of the genera *Ipomea*, *Cissus*). The proportion of grass species in the diet is very low.

Giraffes are highly selective with regards to the plant's growth stage and phenology. The diet varies according to the season, influenced by the availability of plant species and their growth stage (Hall-Martin 1974, Ciofolo & Le Pendu 2002, Fennessy 2004). Across their range this involves small-scale seasonal movements: in southern and East Africa, Giraffes often feed on deciduous trees, shrubs and vines during the wet season, and on evergreen species, near streams and rivers, during the dry season (Leuthold & Leuthold 1972, Kok & Opperman 1980). In N Tanzania, the ♂♂ move to key resource areas during the dry season (Van der Jeugd & Prins 2000). In West Africa they feed on the shrubby acacias in the tiger bush during the wet season, and on the woody species of a sandy agricultural region in the dry season (Ciofolo & Le Pendu 2002). Pellew (1984a) found that the diet of adult ♀♀ was nutritionally richer than that of bulls that consumed significantly higher proportions of fibres and lignin; furthermore, species-selection and the nutritional quality of diet were not obviously related and energy budgets suggest that Giraffes can maintain a positive energy balance during most stages of the female reproductive cycle (Pellew 1984c). In Niger, nursing ♀♀ seem to avoid high levels of tannins even though it means giving up the high-quality forage preferred by the ♂♂ (Caister *et al.* 2003), while in N Namibia ♀♀ avoided areas of human populations and thus forego richer nutrient food sources in preference for safety (Fennessy 2004).

Pellew (1983a) demonstrated that, when Giraffes are not too numerous, their impact can actually stimulate shoot production in *Acacia* species, which soon declined when the browsing stimulus was withdrawn. Young & Okello (1998) experimentally excluded Giraffes and Savanna Elephants *Loxodonta africana* from access to *Acacia*, thereby reducing consumption of new shoots of the higher branches by 63%, which also induced the growth of longer spines. Pellew (1983a) suggested that *Acacia* species have evolved a high resilience to browsing.



LEFT: Twigs of *Acacia drepanolobium* before and after Giraffe *Giraffa camelopardalis* browsing (plus gall ants).

RIGHT: Giraffe *Giraffa camelopardalis* tongue pulling twig into mouth (from film).

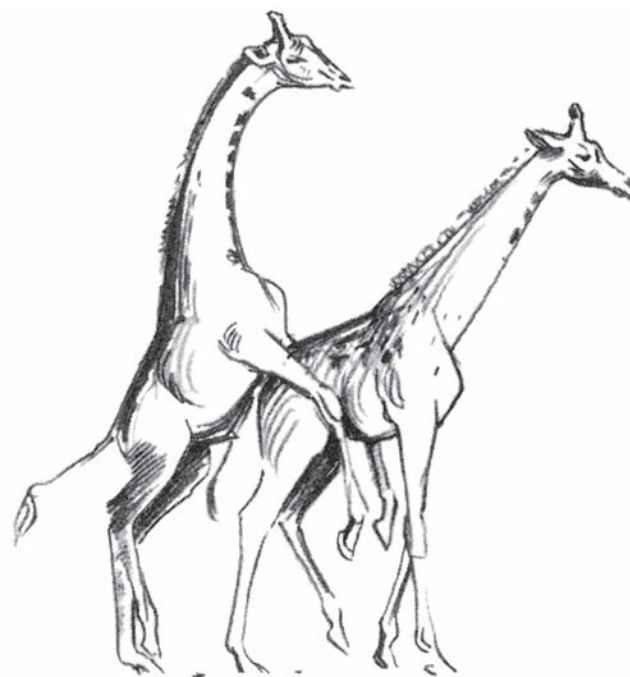
Coe (1998) found that the pods of *A. eriobola* were significantly larger above the browse-line for those trees that had been exposed to Giraffe feeding. In Ithala G. R. (South Africa), some *Acacia* species such as *A. caffra* and *A. karoo* showed high mortality attributable to Giraffe browsing while others including *A. tortilis* did not seem to be affected (Bond & Loffell 2001). In Kruger N. P., Giraffes were highly destructive and detrimental to the overall fecundity of *A. nigrescens* during the season examined (Sep), resulting in a significantly reduced fruit set at heights accessible to Giraffes (Fleming *et al.* 2006).

Carnivorous ants that are symbiotic with some *Acacia* species reduce the amount of time that young Giraffes can spend browsing on any one plant (Madden & Young 1992). On the other hand, *Acacia* seed consumption by Giraffes favours seed dispersal into non-shaded habitats and enhances the potential for seed germination because digestion processes decrease seed infestation by bruchids (Miller 1994, 1996). It has also been suggested that Giraffes play a role in pollination; for example, Du Toit, J. T. (1990b, 1992) posited that Giraffes in Kruger N. P. may be providing a pollination service for *Acacia nigrescens*, although empirical evidence suggests that Giraffes are only flower predators (Fleming *et al.* 2006).

Giraffes sometimes lick soil near termite mounds and chew bones (osteophagia) (Western 1971, Wyatt 1971, Leuthold & Leuthold 1972, Hall-Martin 1975, Ciofolo & Le Pendu 1998). Although Western (1971) maintained that this behaviour was unlikely to appreciably offset any mineral deficiency, Langman (1978) suggested that osteophagia might mitigate seasonal deficiencies or imbalances in calcium, phosphorus and/or magnesium, and Mitchell *et al.* (2005) predict that bone chewing may be a response to phosphorous deficiencies. Nesbit Evans (1970) also observed a Giraffe eating the stomach contents of a Common Eland *Tragelaphus oryx* carcass, and Western (1971) reported them scavenging on the carcass of a Grant's Gazelle *Nanger granti*.

Feeding is the dominant diurnal activity of Giraffes and differs significantly between sexes, season and populations. Females spend more time feeding than ♂♂ in Serengeti N. P. (72% cf. 55%; Pellew 1984a) and in Tsavo East N. P. (Leuthold & Leuthold 1978b), while bulls spend more time feeding in N Namibia: 59% cf. 51% (Fennessy 2004). In Lake Manyara N. P., solitary ♂♂ spent more time feeding than ♂♂ in groups; Giraffes on average spent only 35% of their time on browsing (Van der Jeugd & Prins 2000). In Niger, time spent browsing doubles during the dry season compared with the wet season: 46% cf. 23%, respectively, probably due to variation in forage quality and its spatial distribution (Ciofolo & Le Pendu 2002). The other principal diurnal activities are walking, resting, ruminating and, to a lesser extent, vigilance. According to Ginnett & Demment (1997), there is no sex difference in rumination time but ♂♂ spend more time in activities other than foraging and rumination, such as walking. Giraffes are also active at night, but feed significantly more during moonlit nights (34% cf. 22%, ♂♂ versus ♀♀, respectively) and ruminate more during dark nights (49% cf. 40%, ♂♂ versus ♀♀, respectively) (Pellew 1984a).

Social and Reproductive Behaviour Giraffes are sociable, but herd composition is fluid, unstable and highly variable, comprising any combination of sex and age classes at any given time and rarely consisting of the same individuals for any length of time (e.g. Pellew 1984b, Le Pendu *et al.* 2000, Van der Jeugd & Prins 2000, Fennessy 2004). Mean herd sizes are varied, often ranging between 2.6 and 8



Giraffe *Giraffa camelopardalis* mating behaviour.

(Dagg & Foster 1982), depending on population density and food availability: Katavi N. P. (Tanzania), 3.6 (Caro 1999a), Luangwa Valley, 3.6 (Bercovitch & Berry 2010; and see Berry 1973), NW Namibia, 3.8 (Fennessy 2004), Tsavo East N. P., 4.1 (Leuthold, B. M. 1979), Lake Manyara N. P. (Tanzania), 4.8 (Van der Jeugd & Prins 2000), and Niger, 6.9 (Y. Le Pendu & I. Ciofolo unpubl.). Maximum herd size also varies between populations (for example, from 13 to 47), although as many as 240 individuals have been observed in a herd (Pellew 1983b). Males tend to be solitary or associate in bachelor herds, becoming increasingly solitary as they mature, and often wandering between herds monitoring the reproductive status of ♀♀.

Giraffes are not territorial, but occupy home-ranges that vary in size according to sex/age classes, competition, forage and resource availability (Leuthold & Leuthold 1978a, Le Pendu & Ciofolo 1999, Van der Jeugd & Prins 2000). In Tsavo East N. P., male and female mean home-range sizes were very similar (164 km² and 162 km², respectively), but smaller during the dry season than during the wet season (Leuthold & Leuthold 1978a). Seasonal home-ranges were exclusive in Niger where their mean size during the dry season (90.7 km²) was twice as large as that during the wet season (46.6 km²). Other mean annual home-range sizes recorded for adult ♀♀ (using minimum convex polygon method) were 41 km² in Timbavati Private N. R., South Africa (Langman 1973), 68 km² in the Luangwa Valley (Berry 1978), 200 km² in N Namibia (Fennessy 2009), 285 km² in Kruger N. P., South Africa (du Toit 1988) and 367 km² in Niger (Ciofolo & Le Pendu 1998). Home-ranges recorded for ♂♂ are: 37 km² in Timbavati Private N. R. (Langman 1973), 82 km² in Luangwa Valley (Berry 1978) and 842 km² in Niger (Ciofolo & Le Pendu 1998). The largest home-ranges recorded for ♂♂ are for animals living in desert-dwelling populations: 1950 km² and 1627 km² for two bulls in N Namibia (Fennessy 2009) and 1564 km² in Niger (Le Pendu & Ciofolo 1999); the largest cow home-range reported was also in Niger (1379 km²; Le Pendu & Ciofolo 1999). Giraffes in Niger have been observed to exhibit the longest range of movement,

up to 300 km (Le Pendu & Ciofolo 1999). The longest linear range of movement measured in other populations was 86 km in the Luangwa Valley (Berry 1978), 70 km in N Namibia (Fennessy 2009) and 50 km in Tsavo East N. P. (Leuthold & Leuthold 1978a). The mean daily linear movements of two adult bulls (equipped with a GPS satellite collar) in N Namibia varied between 4.3 and 7.5 km (Fennessy 2009).

Males exhibit flehmen when testing the reproductive status of ♀♀. If the ♀♀ are receptive, dominant ♂♂ actively pursue and fend off competitors. Often such behaviour results in 'necking' bouts, which are assumed to be dominance-driven (Coe 1967). Males with thicker, longer necks appear dominant during violent necking encounters with other ♂♂, and subsequently are more successful in courting ♀♀ (Pratt & Anderson 1982, 1985, Simmons & Scheepers 1996). Serious fights are rare, but when observed they have been brief and violent; Downey (in Kingdon 1979) saw one bull concussed during one such fight, whereupon the fallen animal was hammered with both head and hooves while lying prostrate. Dagg & Foster (1982) also reported an instance where a bull was knocked unconscious and took 20 minutes to recover. Association between adult ♂♂ was random in Lake Manyara N. P., but ♀♀ showed clear non-random association (Van der Jeugd & Prins 2000).

The ♂ follows the oestrous ♀ closely, sometimes resting his head on her rump and/or butting her gently with his horns. Males exhibit lauschlag (the ♂ tapping between or alongside the hindlegs of the ♀ with his forelegs), causing the ♀ to move slightly forward. During copulation the bull stands with head held high, mounting by sliding his forelegs loosely onto her flanks, and then standing bolt upright while at the same time delivering an ejaculatory thrust that also moves the cow forward (Estes 1991a).

Females usually leave the herd to calve. Young are born while the cow is still standing, her back legs slightly bent so as to lessen the fall, which, at two metres in height results in the breakage of the umbilical cord. Calves may stand within half an hour. Lightfoot (in Van Aarde 1976) observed that a Giraffe made no attempt to eat the placenta after giving birth, although Dagg & Foster (1982) and Kristal & Noonan (1979) noted otherwise. Kok (1982) described a free-living Southern Giraffe ♀ scavenging on her dead recently born calf. The mother showed intense interest in the carcass over a period of weeks, no doubt indicative of the mother–calf bond.

Neonates are hidden for a few weeks and thereafter form nursery groups only in populations where feeding and drinking resources are distant from place of birth (Langman 1977, Pratt & Anderson 1979). Mothers and young remain strongly associated for 14–22 months, until around the time of the next parturition (Pratt & Anderson 1982). Young calves are playful and peaceful, but frequent 'necking' occurs between subadult ♂♂.

Vocal folds and laryngeal ventricles are entirely absent, supporting the view that Giraffes are mute (Owen 1841, Hahn & Mayhew 1999). Nevertheless, they infrequently emit various loud sounds, notably under stressful conditions. They can grunt, snort, cough and whistle, and the calves bleat, though what such vocalizations communicate remains undetermined (Dagg & Foster 1982). Captive Giraffes emit infrasonic vocalizations around or below 20 Hz (von Muggenthaler *et al.* 1999). Bashaw (2003) undertook efforts to demonstrate the communicative function of these vocalizations in captive Rothschild's Giraffes by submitting playbacks of infrasonic vocalization; however, this initial work showed no evidence of Giraffes modifying their behaviour.

Reproduction and Population Structure Giraffes breed throughout the year, although birthing peaks have been observed in numerous populations, including: Nairobi N. P. in Kenya (Aug and Sep; Foster & Dagg 1972), Waza N. P. in Cameroon (Nov–Jan, when *Acacia seyal* is flowering; Ngog Nje 1983), Serengeti N. P. (Sep; Sinclair *et al.* 2000) and in N Namibia (Dec; Fennessy 2004), and at different times of the year in the same area (such as Kruger N. P.; see Dagg 1971). Birthing peaks often correlate with rainfall (Hall-Martin *et al.* 1975) and seem to coincide with the production of new *Acacia* shoots that have a high protein content (Sinclair *et al.* 2000, Fennessy 2004). Van der Jeugd & Prins (2000) suggest that differences in ecological circumstances create variability in mating strategies. Giraffes in captivity also breed aseasonally (Backhaus 1961, Bercovitch *et al.* 2004).

A single calf is born, although twins have been recorded (Dagg & Foster 1982, R. Brenneman pers. comm.). Mean gestation period is approximately 457 days or 15 months (Backhaus 1961, Skinner & Hall-Martin 1975, Dagg & Foster 1982); one individual in captivity gave birth to consecutive infants only 420 days apart (Bercovitch *et al.* 2004).

Neonates are heavier in the wild (101 kg) compared with those in captivity (55 kg, Skinner & Hall-Martin 1975). The mean height at birth is 1.8 m and 1.9 m for ♀♀ and ♂♂, respectively (Pellew 1983b). Calves nearly double their height within the first year (Pratt & Anderson 1982), which probably serves as an anti-predator strategy because calves are extremely vulnerable to predation (Estes 1991a; see later). Giraffe milk is rich in fat (13–17%), protein (6%) and ash content, although lactose concentration is lower than in bovine milk (Aschaffenburg *et al.* 1962, Hall-Martin *et al.* 1977a, Dagg & Foster 1982). In the wild, Pratt & Anderson (1979) found that male and female calves suckle at the same rate. Timing of weaning varies: exceptionally as long as two years, but typically around 9–12 months, although calves are able to eat solid food after the third or fourth week and begin ruminating at between three and four months (Langman 1977, Dagg & Foster 1982).

Calving intervals are 19–20 months (Hall-Martin & Skinner 1978, Dagg & Foster 1982, Pellew 1983b, Ciofolo *et al.* 2000, Bercovitch & Berry 2009). Intervals are similar in captivity ($n = 61$), with a range of 14–38 months (Bercovitch *et al.* 2004). The interval between parturition and conception is usually 4–9 months. First conception has been recorded at 50 months in Serengeti N. P. (Pellew 1983b) and 56 months in southern Africa (Hall-Martin & Skinner 1978). In captivity, average age at first parturition was 57 months ($n = 12$; Bercovitch *et al.* 2004). Males are sexually mature at 3.5 years of age (and even earlier in captivity), but in the wild are probably excluded from reproduction by older bulls (Hall-Martin *et al.* 1978).

Adult sex ratios have been recorded as being female-biased in Serengeti N. P. (Pellew 1983b), Nairobi N. P. (Dagg & Foster 1982), Katavi N. P. (Caro 1999a), Luangwa N. P. (Berry 1973) and in Niger (Ciofolo *et al.* 2000), while the opposite was true in Tsavo East N. P. (Leuthold & Leuthold 1978a). In N Namibia, sex ratios differed between subpopulations, although was unbiased across the overall population (Fennessy *et al.* 2003, Fennessy 2004). Sex ratio at birth is 1 : 1 (Dagg & Foster 1982, Bercovitch *et al.* 2004, Bercovitch & Berry 2009). Limited research restricts any real assessment of such variation.

Between 54% and 62% of a given population is more than four years old. Mortality rates are strongly shaped by Lion *Panthera leo* predation, especially on neonates. In Serengeti N. P., 58% of young Giraffes died during their first year of life while only 2% died at the



Neck-sparring and fighting in male Giraffes.

age of four (Pellew 1983b); this is slightly lower than the figure of 75% given by Foster & Dagg (1972) for the same general area. In Kruger N. P., first-year mortality was also high at 48% (Hall-Martin 1975). A breeding ♀ in Luangwa gave birth at 24 years of age (Bercovitch & Berry 2009), and these authors suggest that lifetime reproductive success (which ranged as high as 11 in Luangwa) is more dependent on longevity and calf survivorship than on reproductive rate. The maximum lifespan of male Giraffes, based on individuals in Luangwa Valley, is shorter (22 years) compared with ♀♀ (28 years) (Berry & Bercovitch 2012); maximum longevity in captivity is recorded at 39 years (Weigl 2005).

Given the uniform sex ratio at birth, comparable mortality rates, suckling rates and inter-birth intervals among juveniles, and the similar growth rate of calves while nursing, Bercovitch *et al.* (2004) suggest that adult ♀♀ invest equally in their offspring, regardless of sex, and that ♂♂ surpass ♀♀ in size only after the period of dependency.

Predators, Parasites and Diseases Lions are the main predator (Pienaar 1969a, Pellew 1983b, Hayward & Kerley 2005), although Giraffes are formidable opponents with their long strong legs and hooves; reports of Lions killed or injured by Giraffes are not uncommon. Spotted Hyaenas *Crocuta crocuta*, African Wild Dogs *Lycaon pictus* and Leopards *Panthera pardus* (Scheepers & Gilchrist 1991) have been reported preying on calves occasionally, while observations of Nile Crocodile *Crocodylus niloticus* and Cheetah *Acinonyx jubatus* kills have also been recorded.

Ectoparasites are particularly numerous around the anus and the genitalia. Common tick species recorded from animals in southern Africa include *Amblyomma hebraeum*, *Boophilus decoloratus*, *Hyalomma aegyptium*, *H. marginatum*, *H. truncatum*, *Rhipicephalus appendiculatus*, *R. camelopardalis*, *R. evertsi* and *R. longiceps* (Horak *et al.* 1983c, 1992a, 2007). Helminth parasites include: *Cooperia pectinata*, *C. punctata*, *Fasciola gigantica*, *Haemonchus contortus*, *H. mitchelli*, *Moniezia expansa*, *M. nullois*, *Monodontella giraffae*, *Parabronema skrjabini*, *Pseudofilaria giraffae*, *Setaria labiatopapillosa*, *Skrjabinema* sp., *Trichocephalus gracilis*, *Trichuris globulosa*, *T. giraffae*, *Trichostrongylus* sp. and *Echinococcus* sp.

(Dagg 1971, Boomker *et al.* 1986, Krecek *et al.* 1990; and references therein). Bengis *et al.* (1998) recorded three species of *Sarcocystis* from muscle fibres of a Giraffe in South Africa (*Sarcocystis giraffae*, *S. klaseriensis* and *S. camelopardalis*). Larvae of the oestrid fly *Rhinoestrus giraffae* have been collected from Giraffes (Laurence 1961).

Giraffes are vulnerable to anthrax, gastroenteritis and rinderpest, the latter killing 40% of the Giraffes in N Kenya in 1960 (Dagg 1971 and references therein). Other recorded parasite-induced diseases include listeriosis (Cranfield *et al.* 1985) and brucellosis (Jensen 1999). Polyarthritis and polyosteomyelitis were recorded in a juvenile (Jacobson *et al.* 1986), while a case of Mycoplasma-associated polyarthritis was recorded in a captive Reticulated Giraffe (Hammond *et al.* 2003). Various skin diseases and lesions have been observed.

Conservation IUCN Category: Least Concern (*G. c. peralta* – Endangered D; *G. c. rothschildi* – Endangered C2a(i)). CITES: Not Listed.

East (1999) estimated the total number of Giraffes in Africa to exceed 140,000 (of which 40% were in or around protected areas and private lands); such numbers were thought capable of being maintained were they adequately protected (East 1999). Current estimates put the population at less than 100,000, evidencing declines in some populations. For example, poaching and armed conflict across the range of the Reticulated Giraffe in Somalia, Ethiopia and Kenya has reduced numbers to perhaps fewer than 3000 individuals (Georgiadis, in Fennessy 2007). Smaller, managed populations have also declined: a decline in Lake Nakuru N. P. in Kenya has been attributed to dietary complications from highly concentrated tannin levels because of forced overconsumption of the park's declining acacia trees, which may have compromised young Nubian/Rothschild's Giraffe, making them easy and opportunistic prey for the park's Lion population (Brenneman *et al.* 2009).

Important safety havens include Waza N. P. and the hunting zones of North Province in Cameroon, Zakouma N. P. (Chad), Murchison Falls N. P. (Uganda), Boma N. P. (Sudan), Omo N. P. (Ethiopia), South Luangwa N. P. (Zambia) and, in southern Africa, Etosha N. P. (Namibia), Hwange N. P. (Zimbabwe) and Kruger N. P. (South Africa). Masai Giraffes occur widely both within and outside protected areas in Kenya and Tanzania, but represent a vestige of their former numbers and range. Small numbers of Nubian Giraffes have been introduced to smaller parks and game reserves in Kenya, including Lake Nakuru and Ruma National Parks, while both Angolan and Southern Giraffes have been widely reintroduced and introduced in southern Africa. Giraffes were also introduced to Akagera N. P. in Rwanda in 1986 (East 1999).

In Niger, conservation development projects have facilitated the Niger Giraffe's population increase in an area outside any formal protected park or reserve. None the less, poaching and habitat loss, fragmentation and degradation as a result of increased aridity, and expansion of human activities continue to impact on the Giraffe's distribution. This small population survives only in the wild, since the Giraffes held in captivity in the Vincennes Zoo, France, which were long referred to as *peralta*, in fact belong to the subspecies *antiquorum* (Hassanin *et al.* 2007).

The recently uncovered genetically distinct populations clearly represent evolutionarily significant units that are highly threatened and lack appropriate recognition in current management plans (Brown *et al.* 2007).

Measurements*Giraffa camelopardalis*

TL (♂♂): 5.05 (4.86–5.27) m, n = 15

TL (♀♀): 4.44 (4.16–4.75) m, n = 16

Sh. ht (♂♂): 3.31 (3.13–3.47) m, n = 15

Sh. ht (♀♀): 2.80 (2.72–2.92) m, n = 16

WT (♂♂): 1191.8 (973–1395) kg, n = 18

WT (♀♀): 828.4 (703–950) kg, n = 18

South Africa (from individuals older than eight; Hall-Martin 1975)

Mitchell *et al.* (2009a) reported an upper weight for ♀♀ of 1049.2 kg and 1511.6 kg for ♂♂**Key References** Ciofolo & Pendu 1998; Dagg 1971; Dagg & Foster 1982; Fennessy 2004; Hall-Martin 1974, 1975; Hall-Martin *et al.* 1975, 1978; Leuthold & Leuthold 1972, 1978a, b; Mitchell & Skinner 1993, 2003, 2009; Pellew 1983a, b, 1984a, b; Pratt & Anderson 1979, 1982.**Isabelle Ciofolo & Yvonnick Le Pendu****Subfamily OKAPINAE – Okapi**Okapinae Bohlin, 1926. *Palaeontologia Sinica*, ser. C, 4: 1–179.Subfamily Okapinae is a monotypic subfamily, represented by a single species, the Okapi *Okapia johnstoni*.**GENUS *Okapia*****Okapi***Okapia* Lankester, 1901. *Nature* 64: 24.

The genus *Okapia* includes only the Okapi *Okapia johnstoni*, which is confined to lowland rainforest in DR Congo. The only confirmed fossil record for the species is an early Pliocene ossicone (Cooke & Coryndon 1970). The Okapi exhibits a number of primitive and conservative morphological and behavioural traits. It has been referred to as a living fossil by some authors (Joleaud 1937, Colbert 1938) and some have aligned it with the extinct Palaeotraginae (McKenna & Bell 1997).

Okapia differs from *Giraffa* in being much smaller, as little as one-third the mass, with proportions more like those of other ruminants of similar size; its cervical vertebrae are not elongated, there are five sacral vertebrae (cf. usually four in *Giraffa*) and neck and limbs are only moderate in length. Its 'horns' (ossicones) are hair-covered, situated above the eyes, in ♂♂ only and there is no median ossicone. The skull is elongated, the long braincase in line with the facial part of skull and not flexed.

Peter Grubb***Okapia johnstoni* OKAPI**

Fr. Okapi; Ger. Okapi

Okapia johnstoni (Sclater, P. L., 1901). *Proc. Zool. Soc. Lond.* 1901 (1): 50. DR Congo, 'in sylvis fluvio Semliki adjacentibus' (= Semliki Forest, Mundala).

Taxonomy Monotypic. The discovery and naming of this species is one of the great epics of natural history as well as a vivid illustration of the power of preconceived ideas. While the explorer H. M. Stanley was in the Ituri Forest in 1876 he saw pieces of striped skin, which his interpreters told him came from a type of 'forest donkey'. This unknown animal caught the interest of his friend and admirer, the naturalist, Sir Harry Johnston, who, around the turn of the century, was Governor of Uganda. When the opportunity arose, Johnston visited Ituri and, for a time, thought he was on the trail of the extinct three-toed *Hipparion*. Disbelief in the Okapi's two-toed tracks, together with an attack of malaria made Johnston abandon his quest, but he carried away two hide bandoliers cut from the haunches of Okapis. These were sent to the anti-Darwinian, P. L. Sclater, who provisionally assigned them to the genus *Equus*, naming the new species *Equus johnstoni*. In early 1901 Johnston was sent an entire skin and two skulls

of Okapis by a Swedish agent of the Congo Free State, Lieutenant Karl Eriksson, and immediately realized that the animal was an ally of the Giraffe *Giraffa camelopardalis*. He sent the skin, skulls and his own brilliant pictorial reconstructions of the living animals to Sir Edwin Ray Lankester, Director of the British Museum of Natural History. Latinizing the Mbuti pygmy name into *Okapia*, he described *Okapia johnstoni* in the journal *Nature* in the same year that Sclater's *Equus johnstoni* came out in the slow-to-be-published *Proceedings of the Zoological Society of London*.

Synonyms: *erikssoni*, *kibalensis*, *liebrechtsi*, *tigrinum*. In contrast to Giraffes, which have only 30 chromosomes, the chromosome number of the Okapi recorded from animals in captivity is either 2n = 46, 2n = 45 or 2n = 44 (Ulbrich & Schmitt 1969, Hösli & Lang 1970, Koulischer 1978, Petit *et al.* 1994, Vermeesch *et al.* 1996, Petric 2004a); the 2n = 45 karyotype has been recorded from at least one wild-caught



Okapi *Okapia johnstoni*.

♂ (Petit & de Meurichy 1986), and has occurred in 53 of 116 captive animals examined (K. Leus pers. comm.). This aneuploidy was likely established through a Robertson fusion. These animals appear normal and produced viable offspring (Lindsey *et al.* 1999).

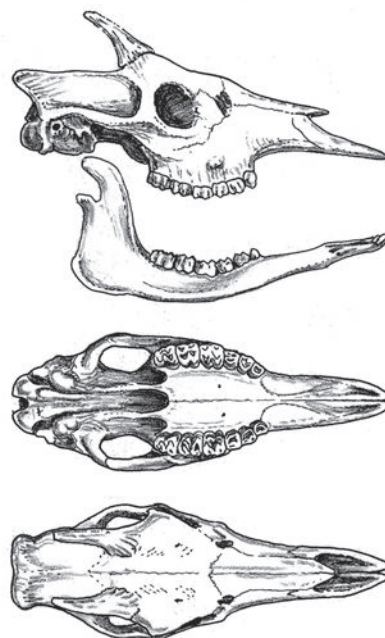
Description A small forest giraffid that may, in some postures, appear strikingly deer-like, with a narrow, long-muzzled head, short, muscular, tapered neck and posteriorly sloping back. The Okapi's bilobed lower canines and hair-covered horn formations originating from epidermal cartilaginous ossicones are features it shares uniquely with all other living and fossil giraffids. The Okapi shares with the Giraffe a distinctive lateral pacing gait in which the weight is momentarily shared by legs on the same side of the body as the animal progresses. The Okapi also differs in having cervical vertebrae that are not elongated; there are usually five sacral vertebrae in the Okapi (cf. four in the Giraffe), and only ♂♂, generally, have ossicones.

The Okapi is a distinctively coloured and patterned animal. Face pale grey, variably grizzled with dark hairs. Crown chestnut brown with fur-covered, posteriorly oriented, bone-tipped 'horns' (see below), although the hair on the tips is sometimes rubbed to the bone. Eyes dark brown, set off by long lashes. Ears large, chestnut brown, with a black fringe of hairs. Neck and body overall dark chestnut brown with maroon overtones. Chest and upper abdomen chestnut brown, lightening and becoming nearly white in the perineal region. Hindquarters dark brown to black with 18–25 or more irregular white horizontal stripes, extending over the buttock and gaskin (tibia) in a pattern that is unique to each animal. Rear cannon or metatarsus white with a black band on the fetlock and white pastern. Similar, though reduced pattern, occurs on the upper forelegs. Fore cannon, or metacarpus, white, with a brown to blackish line running up the front, black hair on the knee and fetlock, white pastern. Tail chestnut brown with black tuft, reaching to the level of the hocks. Young Okapis have patterning similar to adults, but with overall more shaggy pelage, and a distinct blackish mane from the base of the head along the upper back, which gradually diminishes as the animal grows older and all but disappears by 12–14 months. Hooves

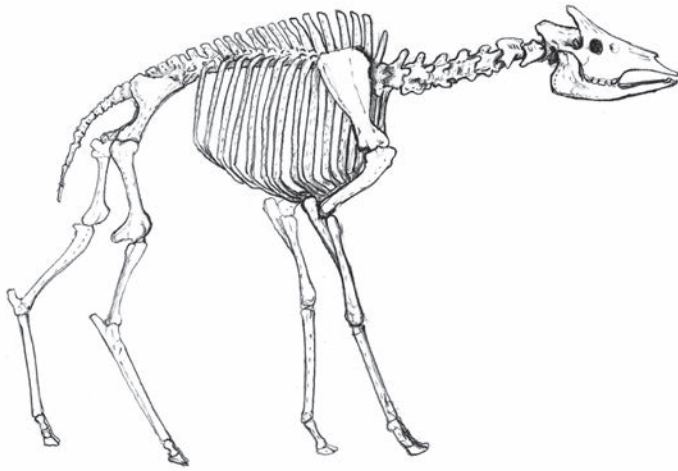
rounded and relatively small for the size of the animal. The pelage is short and lightly oiled from a reddish-brown secretion from the skin that accumulates abundantly in the ears, and renders the pelage somewhat water-resistant. Unlike Giraffes, both sexes have large pedal glands above all four hooves (larger in the fore hooves; Pocock 1936). These drain around the top of the hoof in a channel that leads down between the two toes. Adult ♀♀ are distinctly larger than ♂♂, averaging about 7 cm higher at the withers, and on average 8% larger body mass. Females have four inguinal nipples. Bodmer & Rabb (1992) and Lindsey *et al.* (1999) have provided a detailed description of the Okapi, including variability in coat patterns found in a sample of animals from the central Ituri that were brought into captivity at Epulu.

The skull is elongated, the long braincase in line with the facial part of the skull, and not flexed. There is a large parietal region, and short diastema. The lacrimal fossae are large. The large auditory bullae, and the large frontal and palatine sinuses are unique to the Okapi and separates it from the Giraffe (Colbert 1938, Bodmer & Rabb 1992). The horns measure 6–15 cm in length in ♂♂, but are absent (or rarely present in very reduced form) in ♀♀. These horns ossify and fuse with the frontal bones supraorbitally as the animal matures (Churcher 1990); horn development in ♂♂ begins around one year of age (Bodmer & Rabb 1992). There is no median ossicone. The cheekteeth are low crowned; the deciduous and permanent canines are incisor-like, while the incisors form a semi-circle at the end of the jaw. Skull development and tooth eruption are discussed by Jaspers & de Vree (1978).

Geographic Variation There are no currently recognized subspecies. Okapi populations occurring west and south of the Congo R. are reported to be overall darker than those to the east and north (I. Liengola pers. comm.). While the Congo R. must be a major biogeographical barrier for a species not known to swim, the genetic relationships between populations on either side of this river await investigation.



Lateral, palatal and dorsal views of skull of Okapi *Okapia johnstoni*.



Okapi *Okapia johnstoni* skeleton.

Similar Species In local parlance, might be mistaken for Bongo *Tragelaphus eurycerus* (due to striping), and sometimes even referred to as a zebra (this harkening back to the original misconception of the identity of the species). In the forest, the dung and tracks are distinct from other ungulates, with Okapi tracks being more rounded than Bongo, and smaller than African Buffalo *Syncerus caffer*.

Distribution Endemic to Africa. The Okapi is confined to the forests of DR Congo, occurring between about 500 m and 1500 m elevation over a fairly large range, on both sides of the Congo R. The Okapi ranged occasionally into the adjoining Semliki forest of extreme W Uganda in the recent past (Kingdon 1979). In the forests east and north of the Congo R., the Okapi is known from about latitude 1°S, in a broad arc north through the Maiko and Ituri Forests, then west through the Rubi, Tele and Ebola river basins (irregularly, to the Ubangui R.). The Okapi is also present in central DR Congo, west and south of the Congo R. in the forests of the upper Tshuapa and Sankuru Districts, from the west bank of the Lomami between 1 and 2°S latitude, west to the upper Lomela and Tshuapa basins (confirmed by I. Liengola pers. comm.). The forest–savanna transition defines the eastern and northern limits of the Okapi's range. In contrast, the southern limits east of the Congo R., and the western and southern limits of the species in C DR Congo, are poorly defined. In the west, the species does not appear to occur very far to the west of 24°E. The southern and western limits are not associated with any apparent biogeographical barriers, such as changes in vegetation type and elevation or occurrence of major river barriers (neither do overall forest composition and forest structure change over most of the apparent range boundaries).

The Okapi appears to be absent from large areas of closed-canopy forest in E and C DR Congo. Incidental reports of Okapi occurrence (mapped in Kingdon 1979) and rumours of Okapi presence persist in areas well beyond their currently known range. Okapis are secretive and shy, and their occurrence, especially at low densities, can easily go undetected.

The primary strongholds of the Okapi today are the Ituri/Aruwimi and adjacent Nepoko basin forests, and the forests of the upper Lindi, Maiko and Tshopo basins. The species is also well known in the Rubi-Tele region in Bas Uele. Up until the last two decades of the twentieth century, the Okapi's occurrence remained essentially the same as when it was discovered in the first decades of the century. However, since 1980, major expansions of human settlement



Okapia johnstoni

accompanied by deforestation and forest degradation, have eliminated important portions of their range, in particular in the southern and eastern Ituri Forest, where the species was at one time abundant. The type locality of the Okapi at Mundala has been overtaken by expanding settlement from the growing urban centre of Beni.

Habitat The Okapi is limited to closed-, high-canopy forests, occurring in a wide range of primary and older secondary forest types. It does not range out into gallery forests or into the forest islands on the savanna ecotone and it does not persist in the disturbed habitats surrounding larger forest settlements. Okapis will also forage in regenerating clearings abandoned by shifting cultivators when these are small (generally <1 ha), and when they occur within a habitat complex dominated by forest. Okapis use seasonally inundated areas when the substrate is still wet; however, they do not occur in truly inundated sites or extensive swamp forest. Okapis also do not frequent large areas of dense herbaceous Marantaceae and Zingiberaceae thicket. In the hilly areas of the northern Ituri Forest, where the species is common, Okapis seasonally move into rocky inselbergs during the wet seasons where selected forage plants, uncommon elsewhere, are in full leaf. Okapis, along with most of the other forest ungulates, visit mineral and clay excavations created and maintained by elephants, but they avoid the muddy wallows that also occur in these sites.

Radio-collared Okapis on the Egoro Study Area, in the Réserve de Faune à Okapi (RFO), north-west of Epulu, favoured areas of upland closed-canopy forest with a variably dense and diverse understorey of treelets and shrubs. These areas often had an overstorey canopy dominated by the fine-leaved *Cynometra alexandri*, and a relatively high proportion of deciduous trees (Hart & Hart 1989). This closed, but not heavy, canopy permits filtered light to reach the understorey, favouring the growth of the shade-dependent sub-canopy trees and shrubs that constitute the bulk of Okapi diet.

Tree fall gaps are selected foraging sites for Okapis during the early stages of regeneration (Hart & Hart 1989). Gaps are most heavily

exploited shortly after they are formed, following the emergence of seedlings and the flush of regenerating foliage on plants surviving the tree fall. By the time the gaps are 12–18 months old, most are filled in with vegetation that is either out of reach for Okapis, or not palatable to them, and they no longer use these areas preferentially.

The overall habitat preferences of Okapis suggest a species that evolved in relatively dry, though not strongly seasonal evergreen forest environments. Such a forest type is not widely represented in Africa today, though may have been more widespread during the later Miocene, and through periods of glaciation in the northern hemisphere, as the continent became drier. This suggests that across much of their range today, Okapis could be occupying sub-optimal environments. The remaining strongholds of the species in NE DR Congo may, in fact, be relictual remnants of habitats that by and large have disappeared as the continent returned to warmer and wetter climates in the later Quaternary through to the present.

Abundance Okapi density in the mixed *Cynometera* forests of the Edozo Study Area averaged 0.53 animals/km² (Hart, J. A. & Hart, T. B. 1988). Over a five-year period, 20–35 animals, of which about one-third had radio collars, were estimated to use the 50 km² Edozo Study area on an annual basis. Line-transect counts of Okapi droppings in this area of known Okapi density were used to calibrate counts conducted more widely over the RFO. Okapi density in the RFO varied from 0.1 to 1.2 animals/km², with an average density of 0.45 animals/km² and a total estimated population of about 6500 Okapis in the 13,700 km² reserve (Hart & Hall 1996). Somewhat lower densities were recorded in the northern and central Maiko N. P., where some 4000 Okapis were estimated to occur (Hart & Hall 1996). Okapis decreased south of the Maiko–Oso divide, and have not been found south of the Oso R. Okapis were found at lower densities and more patchy occurrence in the Rubi Tele and (Ebola R.) forests. Extrapolating Okapi density estimates from surveyed areas, in conjunction with available information on hunting, human settlement and habitat suitability within the Okapi's range, yields a global estimate of 35,000–50,000 animals over an estimated range of about 200,000 km².

Adaptations The Okapi is the only living large African ungulate that depends primarily on foliage from the forest sub-canopy for its diet (Hart 2001, Cerling *et al.* 2004). While this provides the Okapi with

a unique niche, their trophic specialization is nevertheless constrained by the overall low productivity of the forest understorey relative to more open environments. Palatable foliage is uncommon and dispersed in the forest understorey. Leaf flush is infrequent and most understorey foliage consists of mature, chemically protected leaves. The limited availability of suitable forage is all the more significant for the Okapi given the animal's large body size and large daily intake needs, averaging from 3.6 to 5.6 kg dry matter/day in captives (Bodmer & Rabb 1992, Hummel *et al.* 2006). These constraints have affected their diet and foraging ecology, as well as their social system and use of space. Yet, in spite of these constraints, young Okapis have one of the fastest growth rates known among artiodactyls, suggesting that heavy predation of young might have selected for rapid growth, presumably fuelled by exceptionally nutritious milk.

Okapis exhibit a number of morphological features that are associated with its specialization as a highly selective folivore. These include fine cusped, low-crowned teeth, adapted for shearing and cutting soft foliage; an elongated, tubular muzzle; and a long, muscular and mobile tongue (which can extend some 25 cm beyond the snout) with which the Okapi can dexterously select and strip foliage from even the finest twigs. Okapis produce copious saliva (and have large salivary glands, resembling those of the Giraffe; Burne 1917), which likely helps them control the protein and carbohydrate binding effects of tannins and other toxins in their foods. Okapis also have a large caecum and colon that assist in microbial digestion (Derscheid & Neuville 1924). They also have a very fast rate of food passage, which allows for lower cell wall digestion than for other ruminants (Prins & Domhof 1984). Characteristics of the morphology of the digestive tract are described elsewhere (e.g. Clauss *et al.* 2002) as are other aspects of digestion and food retention time (e.g. Hummel & Kolter 2003).

The heart of the Okapi is similar to other ruminants (with a weight of approximately 1.85 kg in an adult), and while the jugular vein resembles that of the Giraffe, the axillary and brachial veins are much less complex in the Okapi (see Bodmer & Rabb 1992, and references therein).

Foraging and Food Although Okapis feed preferentially in tree-fall gaps, these represent relatively small and ephemeral food patches. Their staple forage is the mature (though not senescent) foliage of understorey treelets, shrubs and lianas. Diets are dominated by foliage of woody, dicotyledonous species, with monocotyledonous species and herbaceous forbs (including ferns) infrequently eaten. Okapi diets are highly diverse. Foraging animals frequently move between different plant species as they feed, and feed selectively even within an individual plant, smelling and touching foliage with their muzzle and lips before wrapping their tongue around the twig or small branches and stripping the leaves. Dominant plant families in Okapi diets in the Ituri Forest include Acanthaceae, Ebenaceae, Euphorbiaceae, Flacourtiaceae, Loganiaceae, Rubiaceae and Violaceae. Subdominant families include Apocynaceae, Cecropiaceae, Moraceae, Meliaceae, Myrtaceae, Pandaceae, Sapindaceae, Ulmaceae and Vitaceae. Light-dependent saplings of a number of species that regenerate only in treefall gaps are among preferred forage, including *Alstonia boonei*, *Ricinodendron heudelotii*, *Musanga cecropioides*, *Macaranga* spp., *Tremma guineensis* and *Staudtia* spp. (Gijzen 1959, Hart & Hart 1989).

Okapis have a particular preference for foliage of canopy trees that have been broken, but not killed, and subsequently coppice, usually in treefall gaps. These include species that the Okapi will not use at



Okapi *Okapia johnstoni*.

all when they occur as saplings in the understorey. This suggests that many plants may be investing in ungulate-specific feeding deterrents while they occur in the understorey, but that these defences are relaxed as the plant grows into the canopy.

Social and Reproductive Behaviour Okapis are generally solitary, and spend a high proportion of their time standing still, concealed in the forest understorey. Adult ♂♂ on the Edozo Study Area have annual home-ranges of 10 to nearly 17 km² that overlap with those of other ♂♂. Adult ♀♀, in contrast, occupy exclusive home-ranges that vary from 4 to 7 km² (Hart & Hart 1989). Males have highly irregular movements, sometimes occupying relatively small areas of their home-range for days to one week or more, and then abruptly moving long distances to another area. Adult ♀♀ move steadily around their home-ranges, which they only infrequently leave. Home-ranges of breeding ♀♀ have a higher representation of favoured understorey food plants than occurs overall in the forest understorey on average. These plants show signs of heavy browsing during periods when ♀♀ are lactating or are accompanied by their young.

Okapis mark tree trunks by rubbing their neck, leaving on occasion a brownish exudate. Male Okapis mark understorey vegetation by urinating on low shrubs and then walking over or through the foliage. Okapi urine has a strong and distinctive odour and some marking sites are detectable even to the human nose. Both sexes stomp, usually with their front feet, and often after arriving in a new location following directed movement. While this may have infrasound properties, it is also likely that stamping is accompanied by the expulsion of secretion from the highly developed pedal glands and may therefore combine an auditory and olfactory signal. Captive animals may use common defecation sites as marking behaviour (Bodmer & Rabb 1992).

Combat in Okapis has not been observed directly; however, one ♂ caught in the wild had gashes on its side that may have come from the horns of another ♂. Two collared ♂♂, found dead in the same open pit, appeared from the trampled vegetation on the site to have physically confronted each other and pushed each other into the hole.

Play has been observed in all ages and both sexes, though most frequently in young animals. In a play behaviour unique to Okapis termed the 'pooky', the animal stands or spins, with head low and extended, accompanied by vigorous tail wagging (Bodmer & Rabb 1985). In the wild, young Okapis have been seen to greet their mother by gambolling and capering around them (J. A. Hart & T. Hart pers. obs.).

Breeding in free-ranging Okapis takes place on female home-ranges. More than one ♂ may visit receptive ♀♀ over successive days. Both sexes exhibit flehmen behaviour. In free-ranging Okapis, ♂♂ approach the larger receptive ♀♀ cautiously with lowered head, uttering low chuffing calls. Females respond by assuming submissive postures. Mating is rapid, and ♂♂ use a front leg forward kick. In captivity, where ♂♂ and ♀♀ have more continuous contact, ♂♂ can become aggressive with ♀♀. In the wild, male Okapis may spend several hours in the vicinity of receptive ♀♀ over a period of several days.

Females usually stand throughout labour, and eat the afterbirth. From observations in captivity, there is extensive grooming and close contact between mother and calf immediately following birth (Rabb 1978). Infants are precocial and initiate first nursing bouts on average within an hour of birth (Rabb 1978). Infants are then left in a concealed nest, and are only occasionally visited by the mother during the first weeks after birth. Mothers announce their arrival near the young with

a low chuffing sound and young may move quickly to the approaching mother while she is some distance off. Infrasonic calls have been recorded in captive Okapis and these may be used to communicate between mother and young (Lindsey *et al.* 1999). As they grow, young gradually increase their movements, but will still be visited by the mother. Subadult Okapis shifted their home-ranges gradually over time, but some radio-collared subadults, including both ♂♂ and ♀♀, also dispersed from stable, and presumably natal, home-ranges with long movements to new areas (J. A. Hart & T. Hart pers. obs.).

Okapis have only rudimentary vocal chords, with the result that their vocal repertoire is limited. The three best-documented sounds are the chuff, moan and bleat. Chuffs are contact calls used by both sexes and all ages; bleats are uttered by young infants, usually under stress; moaning is elicited by ♂♂ during courtship (Bodmer & Rabb 1985, 1992).

Reproduction and Population Structure Okapis reach adult size at three years, but may breed earlier in captivity (Bodmer & Rabb 1992). Oestrous cycles of captive females are not seasonal and average 14–15 days (Schwarzenberger *et al.* 1993). Breeding is aseasonal. Gestation periods ranging from 414 to 493 days have been recorded, with an average of 440 days in captives (Bodmer & Rabb 1992, and references therein); Schwarzenberger *et al.* (1993) used faecal pregnanediol measurements to determine gestation length in three animals at 423, 424 and 431 days. There is a rapid postpartum oestrus, and captive ♀♀ have recycled and become pregnant within a month or two of birth (Gijzen & De Smet 1974). Twinning is rare (Pearson *et al.* 1978). New-born Okapis range in body weight from 14.6 to 32 kg, and have among the most rapid growth rates of any ungulate species of their body size, tripling birth-weights in the first 50 days (Bodmer & Rabb 1985); male calves have higher percentage increases to begin, but by week 8 their increases are equal to ♀♀ and thereafter their increases are lower than female calves (Boylan *et al.* 2004). The milk of the mother has a very high concentration of protein (one-third higher than cows' milk) and a low fat content (Gregory *et al.* 1965; and see Petric 2004b). Infants in captivity take solid food by the third week, and begin ruminating at around six weeks. Weaning takes place at about six months, although young may continue to suckle for longer. Lindsey *et al.* (1999) summarize extensive observations on reproduction and breeding in captive Okapis. The longevity record for a captive Okapi is 33 years 6 months and 10 days (Galbusera & Leus 2004), and one ♀ reproduced successfully at 26 years of age (Gijzen & De Smet 1974).

Predators, Parasites and Diseases Leopards *Panthera pardus* are the major predator of Okapis: nearly 18% of radio-collared Okapis were killed by Leopards over the five-year Edozo study, with younger animals and adult ♂♂ the most frequent prey. One young Okapi was killed by snake-bite. Over 30 species of parasitic roundworms, nematodes and helminths have been recorded in Okapis. Infestations of the nematode *Monodontella giraffea*, affecting the bile ducts and liver, have been associated with morbidity and mortality of animals brought into captivity in the Ituri Forest. These parasites have been implicated in the death of a number of captives; however, their effect on health, reproduction and predator avoidance in free-ranging animals is not known. Captive animals have shown susceptibility to various bacterial infections, and bacterial and fungal diseases (Bodmer & Rabb 1992, and references therein).

Conservation IUCN Category: Near Threatened. CITES: Not Listed.

The Okapi is a totally protected species under Congolese law and the species is a national symbol, appearing on the insignia of the Congolese National Parks Institute, ICCN. There are two protected areas within the Okapi's principal range, namely Maiko N. P. and the Réserve de Faune à Okapi, one of DR Congo's five UNESCO World Heritage sites. An additional protected area, the Rubi-Tele Hunting Reserve, also occurs in the Okapi's range, although the level of protection is lower. A small population of Okapis still occurs in the northern sector of Virunga N. P., in the Congolese portion of the Semliki Forest (M. Languy pers. comm.).

Okapis are vulnerable to hunting, and decline rapidly in areas where there is persistent use of cable snares. ICCN staff have occasionally found skins among contraband confiscated from poachers. Okapi skins were reportedly readily available on the illegal market during the civil war of 1998–2003. The Mbuti hunter-gatherers in the Ituri Forest hold Okapis in high esteem. While this has not prevented them from killing Okapis, it has elevated this to a special event that requires post-hunt purification. In at least one directly observed case, these taboos actually led a hunter to allow an Okapi to escape unharmed (J. A. Hart pers. obs.)

The greatest risk to the survival of Okapis is the opening of the forest to settlement and logging. Approximately one-third of the Okapi's known area of occupancy is likely to be at risk by major incursions during the first quarter of this century. Areas at high risk include the south-eastern Ituri Forest, the Kisangani area, Rubi-Tele and the western limits of the species' range in the Ebola R. basin. Strengthening protection of the Réserve de Faune à Okapi and Maiko N. P., both of which contain significant Okapi populations, is the single most important means to ensure long-term survival of Okapi. Okapis can coexist with small-scale, low level human occupation of the

forest, but they disappear in areas of active settlement or disturbance.

Okapis have been captured and brought into captivity at Epulu, headquarters for the RFO, since the early 1950s, where a captive population has been maintained in large enclosures for nearly fifty years. These animals have been the source of exports to the world's zoos and also offer a unique opportunity to view Okapis under conditions that approach their natural setting. In June 2012, armed militia opened fire on the RFO headquarters, killing six people and 14 Okapis.

Measurements

Okapia johnstoni

HB (♂): 2.10 m, n = 1

T (♂): 550 mm, n = 1

T (♀): 480 (440–560) mm, n = 4

Sh. ht (♂♂): 1.47 (1.40–1.55) m, n = 5

Sh. ht (♀♀): 1.51 (1.42–1.59) m, n = 8

WT (♂♂): 241 (210–260) kg, n = 20

WT (♀♀): 270 (240–356) kg, n = 22

Captive adults (P. Galbusera pers. comm.)

HB (♂): 2.10 m, n = 1

T (♂): 420 mm, n = 1

Sh. ht (♂): 1.51 m, n = 1

WT (♂♂): 230 (180–260) kg, n = 5

WT (♀♀): 270 (240–290) kg, n = 7

Captive adults, Epulu (ICCN pers. comm.)

Key References Bodmer & Rabb 1985, 1992; Gijzen 1959; Hart, J. A. & Hart, T. B. 1988, 1989; Lindsey *et al.* 1999.

John A. Hart

Superfamily CERVOIDEA

DEER

Cervoidea Goldfuss, 1820. Handb. Zool. 2: xx, 374.

Cervoidea represent one of just three 'true ruminant' superfamilies in the infraorder Pecora, the others being Giraffoidea and Bovoidea. According to the molecular clocks devised by Hassanin *et al.* (2012), their common ancestor diverged from traguloids (ancestral chevrotains) in the early Eocene (about 51 mya), a date that is substantially at odds with the fossil record in which the earliest pecorans (the extinct gelocids) only appear in the Asian Oligocene. This ancestral pecoran stock evolved in Eurasia and the Cervoidea only began to differentiate from giraffes in the Oligocene. Molecular data put the date of that divergence at about 23.4 mya and suggests that they then diverged from a common bovoid stock at about 22.4 mya (Hassanin *et al.* 2012; fossils suggest that the earliest modern type of pecoran emerged about 23 mya (Cote 2010).

Both cervoids and bovovoids are, therefore, the most recently evolved of ungulate superfamilies. The former is widely distributed over Eurasia and the Americas but most diverse in South-East Asia and South America, whereas bovovoids, while abundant and diverse in

Eurasia, much less so in North America, are most highly differentiated in Africa.

While the basic features of rumination were clearly evolved in their common ancestor, further refinements, particularly those concerned with digesting coarse grasses, are essentially late adaptations that run parallel to those of bovovoids, both having continued to diverge and adapt to different diets (Hofmann 1989).

Although climatic boundaries between the two superfamilies are blurred in both contemporary species and in the fossil record, the overall pattern suggests that they originally aligned themselves along the extremities of a geographic and temperature gradient. Eurasian cervoids made an early accommodation to the seasonality and cold of upper latitudes, while various degrees of resistance to heat may have been a major advance for early bovovoids. This may well have inhibited cervoids from invading Africa, particularly if there was any sort of drought belt separating the two continental masses (Thomas 1979b). It is interesting that cervids have been very successful in tropical and

sub-tropical South America within the last 2 mya, but it is surely relevant that this radiation took place in the total absence of bovid competition (C. Janis pers. comm.).

Considering their long common ancestry, it is not surprising that deer and bovids have much in common and are frequently confused with one another in common parlance. Deer have no significant history in Africa, yet, for historical reasons, some African antelopes owe their earliest European names to cervid prototypes, such as ‘eland’ and various ‘bucks’ and ‘boks’. Although deer resemble antelopes very closely in body proportions and ecological niches, their regional origins, and sometimes their continental ones, differ. Likewise, although deer have preorbital, metatarsal, caudal and interdigital scent glands, it is unlikely that these are exactly homologous with similar glands in bovids. The most primitive species have sharp blade-like sabres, like the chevrotains’ upper canines. More advanced forms have tusks and antlers, which serve as defensive

weapons against wounding by canine teeth. In other species, antlers have acquired elaborate branched structures and secondary uses in head-to-head clashes and ‘wrestling’. Unlike the fixed horns of bovids, antlers are shed each year (their fast annual growth has physiological resemblances to forms of wound-healing processes, which suggests that antlers may have evolved from a type of scar-tissue). Antlers first appear in the fossil record in the early Miocene of Eurasia (Gentry *et al.* 1999).

Cervoidea currently includes two families: Moschidae (musk deer), which are entirely extralimital, and the Cervidae (true deer), of which only a single species occurs in Africa. Inclusion of Moschidae in Cervoidea is equivocal, and the family may be more closely related to Bovidae (see Hassanin & Douzery 2003).

Jonathan Kingdon

Family CERVIDAE
DEER

Cervidae Goldfuss, 1820. Handb. Zool. 2: xx, 374.

| | | |
|--------------------|----------|--------|
| Cervus (1 species) | Red Deer | p. 117 |
|--------------------|----------|--------|

The family Cervidae contains the deer. The most recent classification of the family (Grubb 2005) recognizes 51 species, divided among three subfamilies: Capreolinae, Cervinae and Hydropotinae (although the status of the latter is uncertain). The family is widespread throughout the New World and the Palaearctic, although they have also been widely introduced in places as far flung as islands in the Caribbean and Australia and New Zealand (Whitehead 1993, Geist 1999).

Characteristic of adult male cervids are the antlers: only in one (boreal Holarctic) genus, *Rangifer*, are antlers constantly developed in ♀♀. Antlers are absent only in the Hydropotinae, a monotypic subfamily represented by the Chinese Water Deer *Hydropotes inermis*, from China and Korea. Antlers grow in spring as cranial apophyses, covered by highly vascularized skin called velvet; they grow rapidly, usually with a branched structure. In early autumn they reach full growth and the velvet dries up and is shed in patches. The antlers, now solid bone, are used for male–male combat and male–female display, and after the rut are shed. The antlers regrow each year.

Cervids have a battery of premolar and molar teeth (the dental formula is $I^{0/3} C^{0-1/1} P^{3/3} M^{3/3} = 32-34$) with enamel selenes; incisors and canines form a continuous cutting series in the lower jaw, but in the upper jaw the incisors are replaced by a toothless pad, and the canines, usually confined to ♂♂, are short and pointed (though well

developed in some genera, such as *Muntiacus*). The jaws are powerfully developed, with a broad angle at the back where the chewing muscles are attached. The braincase is wide, the orbits (eye-sockets) are tubular and face to the side, and are entirely ringed by bone; the visual fields do not overlap, instead cervids have all-round vision.

In Africa there is only a single indigenous species of deer, the Red (Barbary) Deer *Cervus elaphus*. Fallow Deer *Dama dama* were introduced to Groote Schuur farm in South Africa in 1897, although they had been kept in the grounds at Newlands House in Cape Town as early as 1869. Subsequently, they were widely introduced throughout the country and still are widespread; introduced Red Deer have done less well. Other species released on ranches include Chital *Axis axis*, Hog Deer *Axis porcinus* and Sambar *Rusa unicolor*. Records of Fallow Deer from NE Algeria are likely due to confusion with Red Deer (Kowalski & Rzebik-Kowalska 1991). On the other hand, Brentjes (1969) found archaeological evidence to suggest that Fallow Deer in Ancient Egypt and Ethiopia were not imported, but may have survived in Ethiopia until relatively recently. By and large, the introductions of non-native deer to Africa have not fared well. During the Pleistocene the shores of the Mediterranean and its islands were home to several species of megacerines, the lineage of giant deer. Of these only the Fallow Deer survived into the present.

Colin Groves

Subfamily CERVINAE – Old World Deer

Cervinae Goldfuss, 1820. Handb. Zool. 2: xx, 374.

Subfamily Cervinae (the Old World deer) includes two tribes: Cervini, comprising the genera *Axis*, *Cervus*, *Elaphurus*, *Przewalskium*, *Rucervus*, and *Rusa*; and Muntiacini (*Elaphodus* and *Muntiacus*) (Grubb

2005). Only the former is represented in Africa, and then by a single species, the Red Deer *Cervus elaphus*.

GENUS *Cervus*

Red Deer

Cervus Linneus, 1758. Syst. Nat., 10th edn, 1: 66.

In Africa the genus *Cervus* is represented by a single species, the Red (or Barbary Red) Deer *Cervus elaphus*, which is known to have occurred since the Pleistocene (Geraards 1982, Kowalski & Rzebik-Kowalska 1991, Aulagnier 1992, Laquay 1992), but is now represented by vestigial populations in Algeria and Tunisia. In spite of Red Deer being known from North Africa since the Pleistocene, it is possible that extant Red Deer in North Africa are the product of, or have been genetically influenced by, very early reintroductions from Europe (Davis 1984, Corbet 1978, Dolan 1988, Geist 1999). Whatever the genetic status of North African deer, it is clear that *Cervus* has always been a very marginal genus in Africa. Species belonging to this genus are widespread throughout Eurasia and North America and their ancestral stock probably evolved in Central Asia (Brooke 1878, Groves & Grubb 1987, Janis & Scott 1987, Ludt *et al.* 2004).

There is reason to suspect that Red Deer were repeatedly transplanted by human hand around the Mediterranean basin beginning as early as 8000 BP (Davis 1984). This habit continues into the present as exemplified by the 1952 introduction of Red Deer from Spain along

the coast of N Morocco (Ksar-es-Seghir), where Red Deer were probably found in early historic time. Sika Deer *Cervus nippon* were also introduced there between 1951 and 1953. The Spanish Red Deer *Cervus elaphus hispanicus* released in 1952 have since become established in two small populations (south of Tétouan); the introduced Sika Deer apparently failed to establish themselves.

There are reports of Red Deer having been introduced in 1954 to the island of Bioko (formerly Fernando Poo) off the coast of Cameroon in the Gulf of Guinea (Haltenorth & Diller 1980, Whitehead 1993), but there is no mention at all of this in the works of Basilio (1962) or Eisentraut (1973) and, since several authorities who have spent many years working on the island have been unable to confirm these reports (J. Oates, T. Butynski, J. Juste and J. Perez pers. comm.), it must be regarded as doubtful that Red Deer were ever introduced on Bioko. The origin of the records could stem from confusion from the use of the term 'red deer' for red duikers *Cephalophus* spp. in various dialects (and even in Spanish 'vernados') in that part of Africa.

Valerius Geist

Cervus elaphus RED DEER (BARBARY RED DEER)

Fr. Cerfe de Berberie; Ger. Berberhirsch

Cervus elaphus Linnaeus, 1758. Syst. Nat., 10th edn, 1: 67. S Sweden.Barbary Red Deer *Cervus elaphus barbarus*.

Taxonomy The subspecies of Red Deer that occurs in North Africa is *C. e. barbarus*, which has its type locality in Tunis, near the Algerian/Tunisian border. The information presented in this profile relates specifically to this Red Deer subspecies, which, irrespective of its aboriginal origin, looks like a West-European Red Deer and as such may have been reintroduced into North Africa. Therefore, its taxonomy cannot be judged independently of that of Red Deer from other locations around the shores of the Mediterranean. Great faunal shuffles began here in early Neolithic times, when indigenous faunas of dwarfed island deer, elephants and hippos were abruptly replaced by sheep, goats, Fallow Deer, Red Deer and pigs (Davis 1984), indicating considerable skills at navigation and seamanship in early Neolithic cultures. This is supported by the external appearance of Red Deer from Italy, Corsica, Sardinia and North Africa, which are all West European in their coat characteristics as well as in the rutting roars of the stags. The Red Deer of S Spain (*C. e. hispanicus*) are distinctly different in coat characters from West-European Red Deer and differ somewhat in their rutting calls (Geist 1999).

On islands such as Corsica and Sardinia, Red Deer evolved island dwarf characteristics, such as small body size and short legs, while those exposed to mainland conditions remained normal Red Deer. Numerous scholars have remarked on the similarity of Red Deer from north-west Africa to animals from the islands of Sardinia and Corsica, and Flerov (1952) considered all Mediterranean Red Deer one subspecies (*C. e. corsicanus*); Corbet (1978) also included *C. e.*

barbarus as a synonym of *C. e. corsicanus* (and see Pitra *et al.* 2004), and an affinity with Sardinian Red Deer is borne out by molecular studies (Ludt *et al.* 2004). The current Red Deer of North Africa may be as much an artefact of human culture as are other European Red Deer, but one with minor genetic adaptations and phenotypic adjustments to Mediterranean climatic and biotic conditions (Geist 1999). Synonyms: there are numerous synonyms (see Grubb 2005 for review), but only *barbarus* pertains to African forms. Chromosome number: $2n = 68$.

Description Small-bodied form of Red Deer with a yellowish rump and a coat very similar to the West-European Red Deer *C. e. elaphus*. A character often mentioned is the light spots running in longitudinal lines along the dark mid-dorsal line. The spots are fainter in the dark brown winter coat than in the reddish-yellow summer coat. The conspicuousness of the light spots thus appears to be a function of the length and density of the winter coat, the spots being more conspicuous in struggling populations in warm climates, growing a thin winter coat for reasons of climate and resource shortages. The coat is in all other respects the same as that of the West-European Red Deer, except for hair density. The neck mane in ♂♂ is sparse in the winter coat, and is absent during the mating season as the stags rut essentially in their summer coat. There is much individual variation in coat characteristics. In captivity, these Red Deer reach sizes and appearance typical of northern West-European Red Deer (Meyer 1972, Kacem 1986, Dolan 1988, Whitehead 1993). As with European Red Deer, they have preorbital, metatarsal, caudal and interdigital (hindlegs only) scent glands. Females have two pairs of nipples.

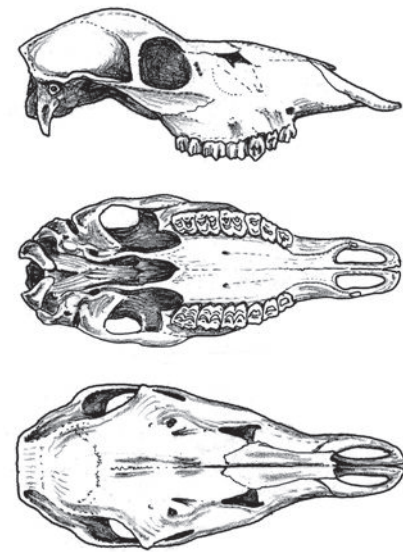
The antlers are small and simple in structure as expected of a small-bodied deer. The bez tine is usually absent; the brow tines and beams tend to be short; occasionally antlers terminate in cup-shaped crowns. Antlers are shed at the beginning of winter, and start growing in Mar.

Geographic Variation None recorded in the species' North African range (and see Taxonomy).

Similar Species In its North African range this species is unlikely to be confused with any other species.

Distribution Red Deer were very popular in North Africa in early historic times as revealed by mosaics and abundant archaeological remains in ancient Carthage and other localities in Algiers and Tunisia. A Pleistocene fossil find in Algiers appears to be that of a Red Deer (Kacem 1986) and the species has been recorded from the late Pleistocene and early Holocene of Morocco (Geraards 1982, Aulagnier 1992, Laquay 1992). They were much more widespread and abundant in Neolithic and early historic times than they are today (Dolan 1988), occurring throughout north-western Africa from Tunisia west to Morocco, although they may have disappeared from Morocco already in Roman times.

In recent times Red Deer have been increasingly confined with remnant populations occurring in NE Algeria and NW Tunisia (Kacem 1986, Dolan 1988, De Smet 1989, Kowalski & Rzebik-Kowalska 1991, Whitehead 1993).



Lateral, palatal and dorsal views of skull of Red Deer *Cervus elaphus*.



Cervus elaphus

Habitat The Red Deer in North Africa currently occupies dense sub-humid, evergreen, montane scrub forests of oak and pine up to 1200 m in altitude.

Abundance There is very little information available on the status and abundance of this species. Salez (1959a, b) discussed their status and distribution in 1953, proposing a total population of some 300–400 individuals. Subsequently, Kock & Schomber (1961) estimated a population size of 200 animals in 1959. In Algeria, the total population in the mid-1970s was reported to be 400–600 (Halis 1975), and by the late 1980s reached an estimated 2000 animals (Dolan 1988, De Smet 1989). However, this population is known to have since declined (K. De Smet pers. comm.), although there are no recent population estimates. The population on the

Tunisian side apparently suffered a dramatic bottleneck with only seven specimens reported to remain in 1962 (Dolan 1988). Genetic data reflect this bottleneck event, but also show that genetic variability of Tunisian Red Deer has not been severely reduced, likely due to augmentation from animals immigrating from Algeria (Hajji *et al.* 2007). The population subsequently increased following conservation interventions, and was estimated at about 800 animals in 2006 (Oumani, in Hajji *et al.* 2007), much lower than the figure of 2000 mentioned by Dolan (1988).

Adaptations The short antlers and antler tines suggest significant food restrictions in summer, particularly during early antler growth, as well as difficult overwintering conditions. The small body size suggests disruptions during the periods of intense postnatal body growth, perhaps indicative of shortages of high-quality food during much of the year, punctuated by brief periods only of forage abundance. The sparse winter hair coat suggests adaptation to a warm climate, as well as resource shortages. Captive and expanding, low-density populations appear to be exempt from food shortages, and respond with body and antler growth comparable to individuals in European populations.

Foraging and Food Much of the food comes year-round from the forest's undergrowth of herbs and shrubs, such as browse and foliage as well as seasonal fruit and acorn crops. The acorn mast and fruit season are especially important as during this season the deer assume their best condition. However, this deer's close dependence on dense forest may be a consequence of the long prosecution suffered by this deer. It chooses cover for security and, consequently, lives off the forage available in cover. Its current food habits, focusing on foliage and browse, may also reflect competition with livestock in overgrazed landscapes. These deer may raid field crops at night (Haltenorth & Diller 1980).

Social and Reproductive Behaviour The few observations available suggest that the social and reproductive behaviour of the Barbary Red Deer is much the same as in European Red Deer, but more subdued and carried out in greater secrecy (Haltenorth & Diller 1980). It is likely that severe persecution in modern times has led to significant deviations in the ecology of this deer from that of earlier times, including changes in hiding behaviour, reduced vocalizations, and nocturnal activity patterns in order to evade detection by humans. Where this deer chooses to stay, what it feeds on and what it does appears to be severely affected by humans, an example of distress biology.

The rut in Aug and Sep is early, suggesting an adaptation to birthing early in spring (Apr to end Jun) to catch the spring growth of vegetation and minimize the effects of summer droughts. Whereas the rut is noisy and conspicuous in many parts of the range, it tends to be more silent in North Africa. An extended calving season is typical of deer from warm climates, a means of reducing predation risk for neonates by dispersing them in time. Calves remain hidden for 2–3 weeks before joining the mother.

Reproduction and Population Structure Sexually mature at 18 months. Gestation lasts 235 days, and a single young is born, which suckles for about seven months. Longevity is usually 12–15 years, but may be up to 20 (Haltenorth & Diller 1980).

Predators, Parasites and Diseases No specific information is currently available. However, since this deer retained the typical body proportions of continental Red Deer, and shows no signs of evolving shorter legs as do Red Deer on Corsica and Sardinia, it may be safely assumed that it evolved under significant predation from large predators. In the past, Barbary Red Deer overlapped in distribution with Lions *Panthera leo*, Leopards *P. pardus*, Cheetahs *Acinonyx jubatus* and Golden Jackals *Canis aureus*. Today stray feral dogs are a more likely danger (Haltenorth & Diller 1980). Where Red Deer overlap with livestock they may become infected with livestock diseases and parasites.

Conservation IUCN Category: Least Concern. CITES: Appendix III (Tunisia).

Protected under national legislation in Morocco, Algeria and Tunisia. Barbary Red Deer were near extinction in the 1960s, mainly as a result of overhunting and habitat degradation from forest fires. Following the Algerian war for independence, conservation measures were put in place. In Tunisia, hunting was banned in 1963, and a forest reserve of 16,000 ha was established to conserve these deer. In 1966, a 417 ha breeding enclosure was established with 17 individuals near El Feidja, from whence animals were reintroduced to other reserves, including at Ain-Baccouch in 1975 (100 ha) and Mehebes in 1978 (300 ha). Deer subsequently increased in numbers, both in Tunisia and in Algeria (Kacem 1986, Dolan 1988, Trense 1989). In Algeria, the species occurs in El Kala N. P. and Beni Salah Nature Reserve; there is currently a joint project between the Forests General Directorate (DGF) and Zeralda Game Centre (Centre Cynégétique de Zeralda) aiming to reintroduce Barbary Red Deer in Akfadou forested areas (Kabylie region) (F. Belbachir pers. comm.). There are two enclosures in Morocco with captive animals, but there have as yet not been any reintroductions (F. Cuzin pers. comm.).

Measurements

Cervus elaphus

HB: 160–250 cm*

T: 12–15 cm

Sh. ht (♂♂): 130–140 cm

Sh. ht (♀♀): 90–100 cm

WT (♂♂): 150–225 kg

WT (♀♀): 100–150 kg

North Africa (Haltenorth & Diller 1980); *Kingdon (1997)

Key References Dolan 1988; Haltenorth & Diller 1980; Kacem 1986.

Valerius Geist

Superfamily BOVOIDEA

BOVOIDS

Bovoidea Gray, 1821. London Med. Repos. 15: 308.

The Pecora comprise three superfamilies of ruminating herbivores: Cervioidea (deer), Giraffoidea (Giraffe and Okapi) and Bovoidea (bovoids) and, in each case, the living forms of each of these superfamilies

do not differ between family and superfamily. Consequently, a summary of the characteristics of bovoids can be found in the family profile and needs no repetition here.

Family BOVIDAE

BOVINES, ANTILOPINES

Bovidae Gray, 1821. London Med. Repos. 15: 308.

| | | |
|-------------------------------------|-------------|--------|
| Bovinae (2 genera, 10 species) | Bovines | p. 122 |
| Antilopinae (29 genera, 76 species) | Antilopines | p. 199 |

The family Bovidae contains the cattle, buffalo, sheep, goats and antelopes, and includes more species than any other extant family of large mammals. According to the most recent classifications, informed by recent molecular discoveries, they belong to the order Cetartiodactyla, which combines the artiodactyls, or even-toed hoofed mammals, with the whales, dolphins and porpoises. As ruminating animals they belong to the suborder Ruminantia and to the infraorder Pecora, which also embraces Cervidae, Giraffidae, the (now non-African) Antilocapridae (North American Pronghorn *Antilocapra americana*) and extralimital Moschidae (musk deer).

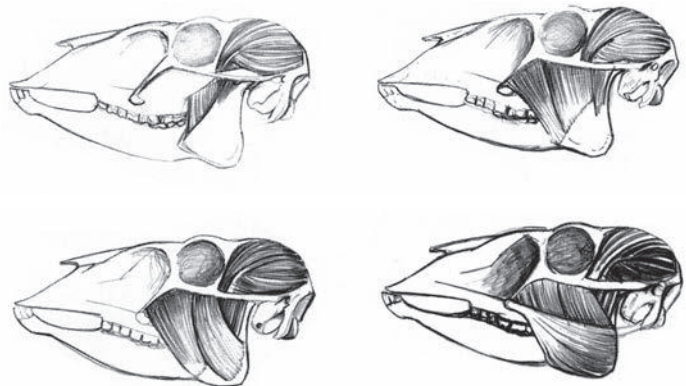
Bovids, like the closely related cervids, have a battery of premolar and molar teeth with enamel selenes; incisors and canines form a continuous cutting series in the lower jaw, but in the upper jaw the incisors are replaced by a toothless pad. The typical dental formula is $I^{0/3}, C^{0/1}, P^{3/3}, M^{3/3} = 32$, although some species, such as the Springbok *Antidorcas marsupialis* and some members of the Alcelaphini (*Connochaetes* spp. and *Hirola Beatragus hunteri*), have lost the second lower premolar; instances of supernumary teeth are reported in other species (e.g. Bushbuck *Tragelaphus scriptus*). The jaws are powerfully developed, with a broad angle at the back where the chewing muscles are attached. The braincase is wide, the orbits (eye-sockets) are tubular and face to the side, and are entirely ringed by bone; the visual fields do not overlap, instead bovids have all-round vision.

The one major difference between bovids and cervids is in the nature of the horns. Bovid horns are epiphyseal: the horn consists of a bony core covered by a keratinous sheath, and is unbranched and permanent (never shed). Horns are intrinsically conical, but are often either keeled longitudinally, ringed transversely or pulled into a spiral by differential growth rates in the horn sheath. Horns may be present in both sexes, or restricted to ♂♂. Minor differences are that the lacrimal duct almost always opens in one circular orifice inside the orbital rim (exception: some *Tragelaphus*, *Bos* and *Bubalus*, in which the orifice may be on the rim, and there may be two orifices), whereas in cervids there are always two, and they are on the rim itself; and that the gully along the mid-line of the fused metatarsi is open for its whole length, whereas in cervids it closes above the distal end of the shaft.

Bovids include both browsers and grazers, and live in all African environments from rainforest to desert. Outside Africa, they live in



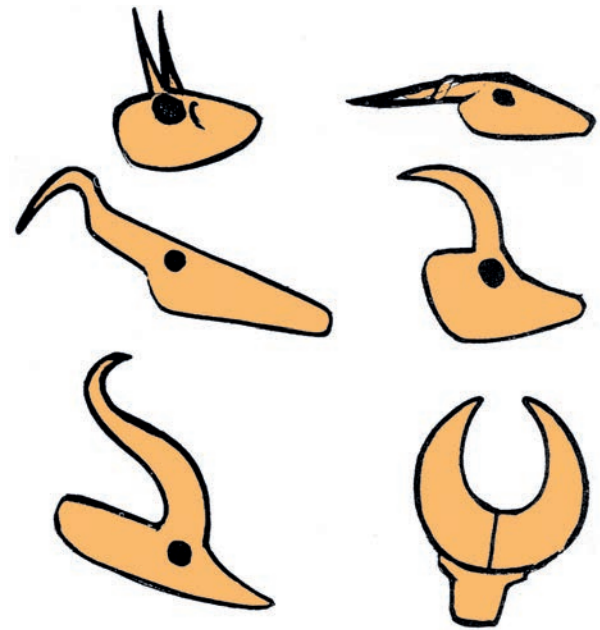
Lesser Kudu *Tragelaphus imberbis* head.



Head of Oribi *Ourebia ourebi* exposing series of deeper components of masseter and temporal muscles and general features of bovid head (from Kingdon 1982).

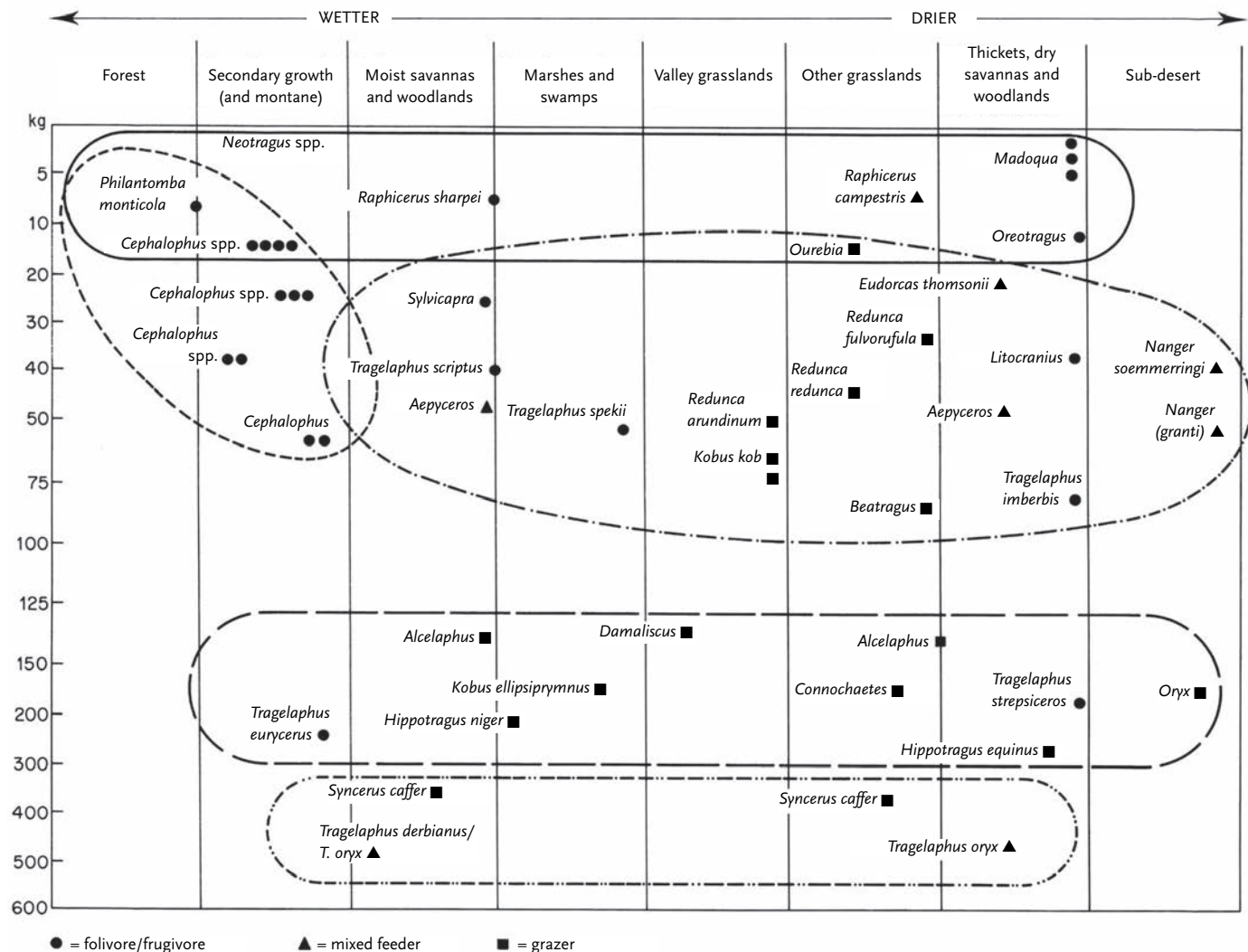
Europe, Asia and North America; however, it is in sub-Saharan Africa that their diversity is greatest, with 70 or more described species (and many more fossil forms), according to whether taxa in some allopatric species-groups are regarded as species or subspecies.

The phylogenetic relationships and taxonomy of this family have been the topic of much controversy (see, for example, Hernández Fernández & Vrba 2005 for review). The study of Gatesy *et al.* (1997), which combined morphological and molecular data, concluded that Bovidae is monophyletic, and this has been supported by subsequent molecular studies (Matthee *et al.* 2001, Hassanin & Douzery 2003, Hassanin *et al.* 2012). However, the classification of the family remains problematic, particularly with regards to recognition of tribes and subfamilies. In the current work, the primary subdivision is between subfamilies Bovinae and Antilopinae (contra Grubb 2005 who recognized eight subfamilies), the former mainly Eurasian, the latter predominantly African. Tribal relationships within the two subfamilies are far from settled as the molecular studies cited above attest. Other defining differences are discussed under the subfamilial and tribal profiles.



Colin Groves Bovid heads are transformed by the shape and orientation of their horns.

Table 6. Diversification of Bovidae.



Subfamily BOVINAE – African Buffalo, Spiral-horned Antelopes

Bovinae Gray, 1821. London Med. Repos. 15: 308.

| | | |
|--------------------------------|-------------------------|--------|
| Tribe Bovini | | |
| <i>Syncerus</i> (1 species) | African Buffalo | p. 124 |
| Tribe Tragelaphini | | |
| <i>Tragelaphus</i> (9 species) | Spiral-horned Antelopes | p. 138 |

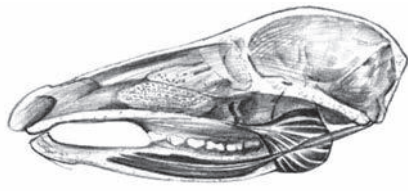
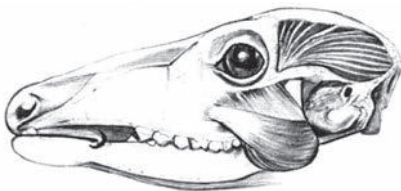
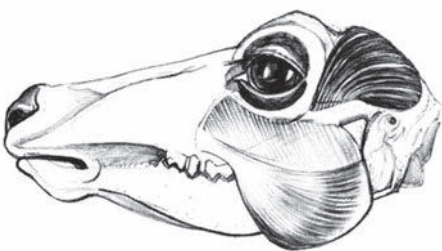
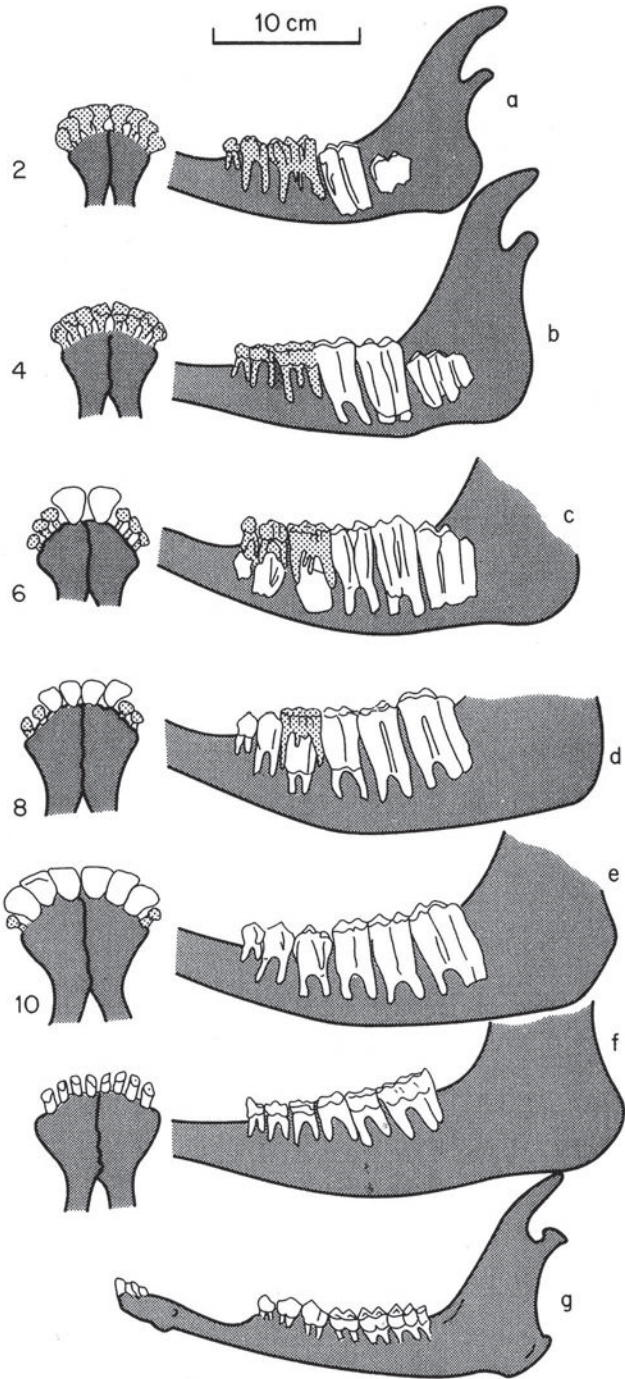
Bovinae are distinguished from the antelopes (Antilopinae) by their generally larger sizes, an absence of facial or pedal glands, and smooth or keeled, rather than annulated horns.



African Buffalo *Syncerus caffer* head.

Until the advent of molecular science and its application to the phylogeny of bovids, there was great confusion as to the relationship between bovid groups that can now be separated into Bovinae and Antilopinae. The main source of this confusion was excessive reliance on the structure of teeth. Increasing graminivory in the more advanced Bovinae has wrought many dental convergences with equivalent large, grass-eating Antilopinae and these convergent resemblances in the breadth, depth and complex folding of enamel ridges (and in-fill with dentine cement) created great confusion in the past, leading to completely erroneous affiliations across the two groups of Bovidae, which were broken down into the so-called ‘Boodonts’, with a long, relatively narrow tooththrow, and ‘Aegodonts’, with hypsodont molars and a shortened premolar row (Schlosser 1904).

RIGHT: Mandibles of African Buffalo *Syncerus caffer* showing patterns of tooth eruption (after Grimsdell 1969): (a) 9 months; (b) 18 months; (c) 2.5 years; (d) 3.5 years; (e) over 4.5 years; (f) very old buffalo; and (g) Bushbuck *Tragelaphus scriptus* for comparison. Note hypsodonty in African Buffalo and low crowns in Bushbuck.



Mouth shape and masticatory muscles in Mountain Reedbuck *Redunca fulvorufula* (left) and Bushbuck *Tragelaphus scriptus* (middle). Bushbuck (right) sectioned to illustrate digastrics and pterygoid muscles.

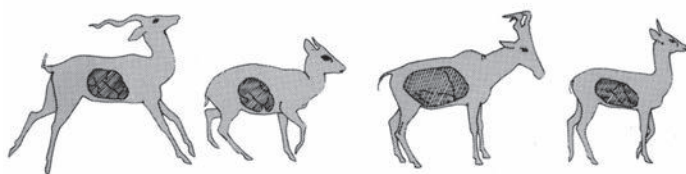


Diagram of relative size of stomach in, left, large and small concentrated selectors (Lesser Kudu *Tragelaphus imberbis* and Suni *Nesotragus moschatus*). Right, in large and small grazers (Hartbeest *Alcelaphus buselaphus* and Oribi *Ourebia ourebi*) (after Hofmann 1973).

The primary divergence between Bovinae and Antilopinae probably had both an ecological and an intercontinental basis. Where food is locally unreliable animals must make periodic movements or become nomadic and selection for territorial behaviour and its associated anatomical structures is reduced or absent. However, animals can only use an unstable habitat if their off-season food is predictable and within reach and if they are adapted to the demands of an unstable existence. A bovid that has to move in search of food can acquire the advantages of more economic, efficient locomotion and a reduction of vulnerability to predators if it increases body size. This must be sustained by the certainty of adequate food and this, in turn, may involve fluctuating densities.

The combination of abundant but fluctuating food supplies might help explain the absence of facial and pedal glands, the rarity of

territorialism, and the trend towards hierarchy and large size. Most Bovinae are mobile and tend to form hierarchies in which ♂♂ generally avoid each other. Hierarchy encourages sexual selection in favour of larger ♂♂. Females are commonly hornless (or less heavily horned than ♂♂), but the development or suppression of horns in ♀♀ is neither primitive nor advanced. Rather, both conditions involve different mechanisms or strategies for getting at resources. Horned ♀♀ tend to resemble ♂♂ in establishing same-sex hierarchies and they are more active in defending their young.

There are three main groups within the Bovinae. In the species-level super-tree of Hernández Fernández & Vrba (2005), the most primitive of these is the Boselaphini (named after the Indian Nilghai *Boselaphus*), which separated around 20.5 mya. The tragelaphine or spiral horned antelopes, Tragelaphini, evolved in Africa from an Asian stock that resembled boselaphines (Gentry 1978). Their divergence took place about 18.3 mya (Hassanin *et al.* 2012), at which time there was a known connection between Eurasia and Africa (commonly called the Proboscidean event). Grubb (2001a) additionally proposed Pseudorygini as a new tribe within the subfamily Bovinae for the recently discovered Saola *Pseudoryx nghetinhensis*, but later (Grubb 2005) included Saola in Bovini.

Jonathan Kingdon

Table 7. Ecological niches of bovines and antilopines.

| weight ranges (in kilograms) of specified lineage | | | | | | | | | | Lineage and feeding strategy |
|--|---|--|----------------------|-----|--|-----|---------------------------|------|--------|---|
| very diverse group | 25 | 80 | 150 | 225 | 300 | 500 | 750 | 1000 | | Former Neotragini Conservative, size-limited radiation |
| Duiker radiation. Reliable scattered food supply
Sedentary in known home-ranges. Hiders | | | | | | | | | | Cephalophini Forest concentrate selectors |
| | Reedbucks
very abundant unstable food supply. Hiders in cover, water or in dense herds | Kob
Locally mobile – without stamina | | | Waterbuck | | | | | Reduncini Valley grazers |
| Antilopini
scattered food, mobile fast runners | Impala | Topi
very abundant unstable food supply, highly mobile, fast, great stamina | | | Hartebeest | | Wilbebeests | | | Antilopini Arid land gleaners / Alcelaphini High density/ecotone catenary grazers |
| | extensive radiation in Eurasia | Oryxes
unstable food supplies, mobile, moderately fast, great stamina | | | Sable | | Roan | | | Caprini Asiatic specialists / Hippotragini Low density and adapted grazers |
| | Bushbuck | Sitatunga | Lesser Kudu | | Greater Kudu | | Bongo | | Elands | Tragelaphini Foliage gleaners |
| | | scattered food, slow hiders but with increasing size faster runners
high density/smaller groups | | | | | low density/larger groups | | | |
| | | | smaller spp. in Asia | | African Buffalo | | | | | Bovini Fresh grass bulk grazers |
| | | | | | abundant food in rel. unstable habitats
large mobile herds, slow gait | | | | | |

Tribe BOVINI

African Buffalo

Bovini Gray, 1821. London Med. Repos. 15: 308.

The tribe Bovini includes at least four extant genera, with only a single living representative in Africa, the African Buffalo *Syncerus caffer*. Extraliminally, the tribe includes: *Bison* (two species), *Bos* (five species), *Pseudoryx* (one species), and *Bubalus* (four species) (Grubb 2005).

Recent molecular studies have broadly agreed with much older classifications in associating Bovini with the tribes Boselaphini (which includes the Nilgai *Boselaphus tragocamelus* and Four-horned Antelope *Tetracerus quadricornis*), which are also Asian, and Tragelaphini, the spiral-horned bovines, which are African, but derive from an Asian immigrant stock (Matthee & Robinson 1999a, Hassanin & Douzery 2003, Hassanin *et al.* 2012). The African Buffalo has been estimated to have separated from its closest relatives, the Asian Buffalo, *Bubalus* spp. between about 7.3 and 5.1 mya (Van Hooft *et al.* 2002), a period in which other exchanges between Eurasia and Africa took place.

Members of the tribe are large and heavy in build, and typified by low, wide skulls with a short face and smooth horns, present in both sexes, which tend to splay out sideways from the skull. Internal sinuses have developed at the base of the horn cores. Species tend to be plainly coloured, and there are no compound odoriferous glands. Females have two pairs of nipples.

Despite the still relatively widespread occurrence of the African Buffalo on the African continent, it is being replaced at a steady pace by the commonest bovin in Africa, the domestic cow *Bos taurus*, which is the descendant of the Aurochs *Bos primigenius*, once widespread in Europe, western Asia and North Africa. Water Buffalo *Bubalus bubalis* also have been introduced in North Africa in Egypt,



African Buffalo *Syncerus caffer*.

Libya and Tunisia, where African Buffalo are now absent, and a few are found in coastal agricultural lands of East Africa.

Jonathan Kingdon

GENUS *Syncerus*

African Buffalo

Syncerus Hodgson, 1847. J. Asiat. Soc. Bengal, ser. 2, 16: 709.

Syncerus is a monotypic genus represented by the African Buffalo *Syncerus caffer*, which is distributed throughout sub-Saharan Africa in habitats ranging from savanna to rainforest, in fact wherever permanent water is found. The most closely related living genus is *Bubalus* (Asian buffalo species), which also belongs to the tribe Bovini, and of which *Syncerus* has been considered a subgenus (Haltenorth 1963). According to genetic studies, the ancestors of these two genera diverged during the late Miocene between 7.3 and 5.1 mya (Van Hooft *et al.* 2002). This is a period with several speciation and migration pulses, initiated by widespread climatic changes (Hassanin & Douzery 1999). Other members of the tribe Bovini – the cattle (genus *Bos*) and bison (genus *Bison*) – appear to have diverged from African Buffalo between 14 and 10 mya (Pitra *et al.* 1997, Hassanin & Douzery 1999) at a time when such ancestral forms would certainly have been morphologically assignable to Boselaphini. The corollary is that Bovini are polyphyletic.

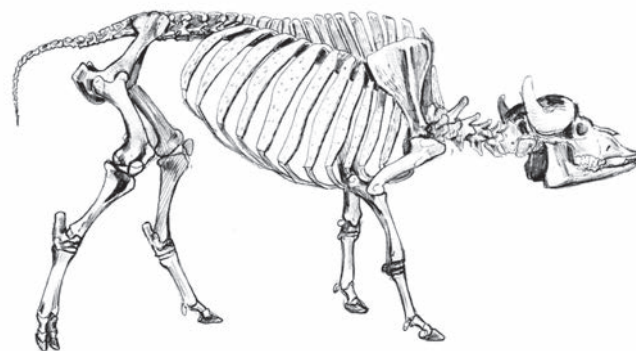
In recent history there was another African species of buffalo, the Giant Long-horned Buffalo *Pelorovis antiquus*, which disappeared from southern and East Africa about 12,000 years ago and from northern Africa about 4000 years ago (Klein 1994). The genus *Pelorovis* diverged from *Syncerus* around the same time as *Bubalus* (Gentry 1990). Fossil remains show that the horns were less dorsoventrally compressed and lacked the heavy bosses of the horns characteristic of the extant buffalo. Peters *et al.* (1994) argued that the postcranial anatomy of *antiquus* indicated that it was simply a long-horned morph of the extant *S. caffer*, and that therefore it should be called *S. c. antiquus*, but Klein (1994) demonstrated that *antiquus* is indeed distinct at species level as evidenced by its singular horns, some dental differences, and its geographic overlap with the latter species through most of the middle Quaternary. Klein envisaged the extinct buffalo as having been in drier and grassier habitats than *S. caffer*.

Pim van Hooft & Herbert H.T. Prins

Syncerus caffer AFRICAN BUFFALO

Fr. Buffle noir (Buffle d'Afrique); Ger. Kaffernbüffel

Syncerus caffer (Sparrman, 1779). K. Svenska Vet.-Akad. Handl. Stockholm 40: 79. 'Seecov Rivier' and 'Akter Brunties hoogte', now restricted to South Africa, Eastern Cape Prov., Uitenhage district, Sunday R., Algoa Bay.

Southern Savanna Buffalo *Syncerus caffer caffer* adult male.African Buffalo *Syncerus caffer* skeleton of adult female.

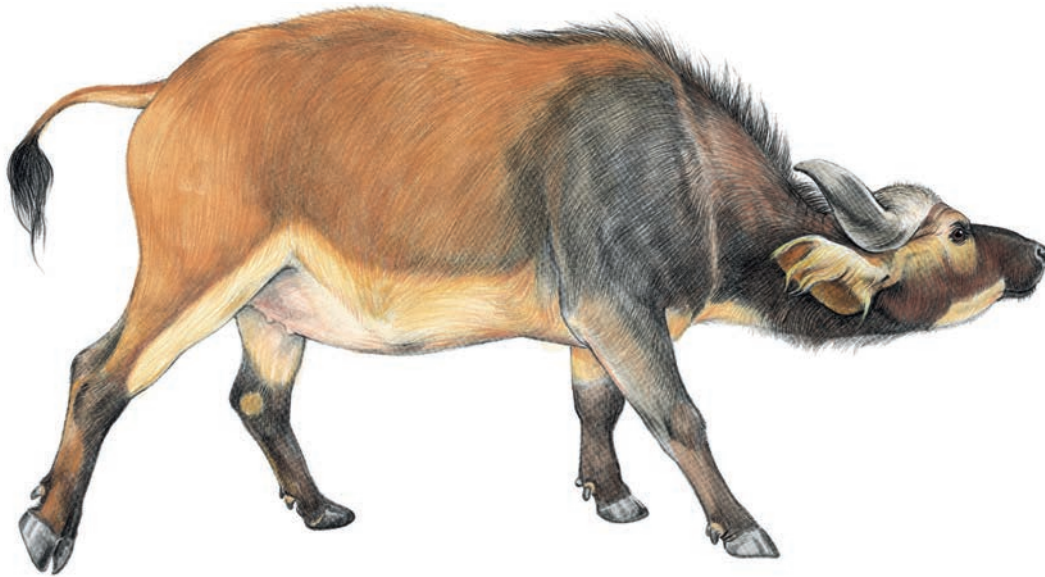
Taxonomy The classification of the African Buffalo has had a somewhat confusing past, detailed discussion of which is beyond the scope of the current work. There is much variation in pelage colour, body size, and shape and size of the horns, often but not always in a geographical context, and apparent intermediates between types are common. Ansell (1972) and Grubb (1972) summarized the earlier subspecific classifications of Lydekker (1913–1916), Christy (1929), Schouteden (1947), Blancou (1935, 1954), Malbrant (1935), Dalimier (1955) and Haltenorth (1963), and concluded that there seemed little doubt that all forms should be regarded as conspecific, including *nanus*, considered by many earlier authors as a distinct species (e.g. Christy 1929, Malbrant 1935, Schouteden 1947). More recently, three or four subspecies within *S. caffer* have been recognized, although the subspecies status of *S. c. aequinoctialis* has been unclear; an East African mountain form (*mathewsi*) has also been treated as distinct (e.g. Kingdon 1982, Grubb 2005).

The subspecies classification presented here is provisional, and is based on East (1999) and Grubb (2005). However, according to mitochondrial DNA data, African Buffalo from East and South Africa comprise a single clade, while populations from Cameroon, Gabon, Angola and, apparently, Namibia form another (Van Hooft *et al.* 2002). The latter study found that African Buffalo have high within-population mtDNA diversity, with little differentiation between populations. One possible explanation for these observations is the recurrent fragmentation of moist habitats during glacial periods, which are characterized by relatively dry climatic conditions in most of Africa, leading to transient increases of genetic differences between populations followed by secondary contact. At the time of going to press, evidence based on an analysis of mitochondrial D-loop sequences across the entire geographical range of the species, further supported the existence of two distinct clades within the species, corresponding broadly to two subspecies: a clade grouping the populations in East and southern Africa (the nominate subspecies), and a clade for populations in the remainder of the range (*S. c. nanus*, i.e. including *brachyceros* and *aequinoctialis*), with a mean estimated divergence time of 180,000 years (N. Smits *et al.* pers. comm.).

The limited genetic differentiation of Southern Savanna Buffalo *Syncerus caffer caffer* between eastern and southern Africa (Van Hooft *et al.* 2000, 2002) can be explained by a Pleistocene population expansion that started between 270,000 and 37,000 years ago, as indicated by phylogenetic analyses. Furthermore, the genetic distance on the basis of mitochondrial DNA from older lineages in central Africa (Cameroon and Gabon) is indicative of a more precise divergence time of 180,000 to 130,000 years (Van Hooft *et al.* 2002). Taken together, these two observations suggest a recent origin of the Southern Savanna Buffalo. The genetic findings are in agreement with fossil data. These data show that the extinct Reck's Elephant *Elephas recki* and Giant Long-horned Buffalo *Pelorovis antiquus*, rather than the Southern Savanna Buffalo, dominated the African savannas until the late Pleistocene (Kingdon 1982, Klein 1988). The recent origin of Southern Savanna Buffalo is supported by the observation that even African Buffalo fossils from the late Pleistocene represent less advanced forms (Kingdon 1982).

Synonyms: as noted by Ansell (1972), numerous names have been published; Grubb (2005) lists some 55 synonyms. *Syncerus caffer*, from savannas, and *S. c. nanus*, from the rainforest, have different chromosome numbers, namely $2n = 52$ and $2n = 54$ (both with $FN = 60$), respectively (X and Y chromosomes are acrocentric) (Wurster & Benirschke 1968, Gallagher *et al.* 1999), the difference being due to a Robertsonian fusion element. It has been postulated that $2n = 52$ evolved from $2n = 54$. A male hybrid had $2n = 53$ (Cribiu & Propescu 1980), and forest buffalo with karyotypes of $2n = 55$ and $2n = 56$ have been reported. Apparently, a rapid morphological evolution took place (with little molecular differentiation) between the forest and savanna buffalo (Modi *et al.* 1996).

Description A large, dark animal varying in colour from reddish-brown to nearly black with large to very large horns in both sexes. Stocky build, with a short powerful neck. Males have a hump above the withers covering the spines, muscles and ligaments that support the heavy head and horns. Muzzle wide with wet, shining, hairless nose, large eyes and big ears that often droop. Ears fringed with long hairs, and frequently scarred. Pelage generally short-haired and infrequently



Forest Buffalo *Syncerus caffer nanus* adult female.

largely absent. However, juveniles are well haired. Calves are born blackish, or reddish-brown in colour and darkening with age. Adult ♂♂ frequently have skin-folds under the chin, often with hair on it, resembling a beard; also often with a small dewlap. Tail long, with a long tuft of dark hair. They have large, rounded hooves and dew-claws. The dew-claws show-up in the spoor in wet terrain. Buffalo have sweat glands and a characteristic scent, though no specialized olfactory skin-glands (preorbital, pedal and inguinal glands are all absent). Female has a small, rounded udder with two pairs of inguinal nipples. Males, when adult, commonly with a penis-tuft.

In the skull, there are no preorbital fossae and there is no ethmoid fissure. Horns are present in both sexes, and are not ridged. Savanna Buffalo ♂♂ have laterally extending curved horns, inflated bosses and, when adult, little or no hair between the horns; ♀♀ have more slender horns, also laterally extending, with hair on the skin between the horns. Forest Buffalo ♂♂ have shorter horns that do not extend sideways. The tips of the horns often show signs of breakage. Bosses do not form until the ♂ is 3–5 years old. There is no relation between the age of an adult buffalo bull (older than five years) and the gap between the bosses (H. Prins pers. obs.). In the dentition, the fourth lower incisor is the last tooth to erupt at about five years of age. Crown height (see Adaptations) and enamel ridge pattern, together with stages of tooth eruption, can be used for ageing buffalo and results are identical for West, East and southern Africa (Spinage & Brown 1988, Grimsdell 1969, 1973a, Taylor 1988, respectively).

Geographic Variation

S. c. caffer (Southern Savanna Buffalo or Cape Buffalo): *Acacia* savanna, miombo woodland, montane woodlands, highveld and lowveld of eastern and southern Africa, from SW Ethiopia and N Kenya southwards to South Africa and including Uganda, Rwanda, SE DR Congo and parts of Angola. This is the largest subspecies, with the biggest horns and a body weight of 500–800 kg. Strong development of bosses in the horns of the ♂♂.

S. c. brachyceros (West African Savanna Buffalo): Guinea savanna, gallery forests, Sudan savanna and the wettest parts of the Sahel (till approximately the 350 mm isohyet) from Senegal to Cameroon.

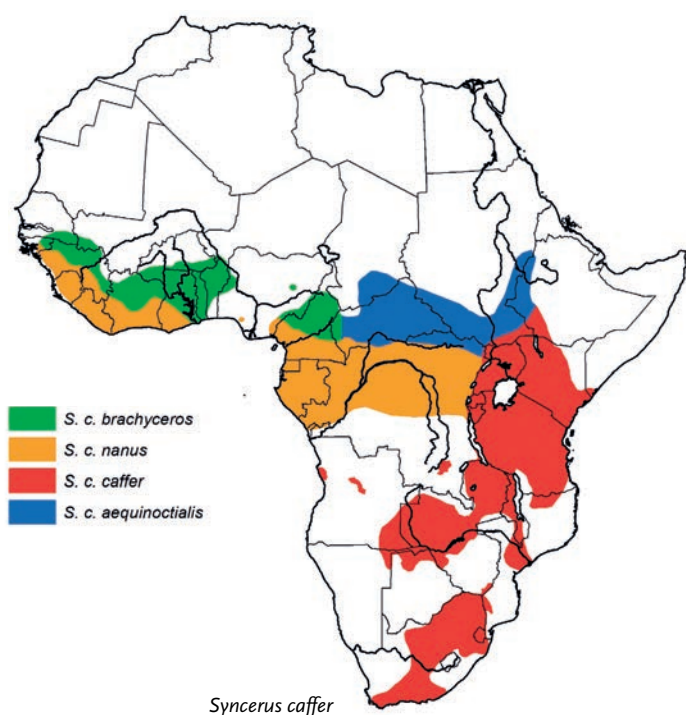
Exact limits with *brachyceros* unclear, but the Chari R. is usually given as the boundary between the two in Chad (Ansell 1972). Horns of this subspecies are more ‘cow-like’ with less well-developed bosses and shorter span in the bulls than in the previous subspecies. Body weight 400–700 kg.

S. c. aequinoctialis (Central African Savanna Buffalo). Following East (1999), this is the form in N Central African Republic, Chad, N DR Congo, S Sudan and W Ethiopia. Little is known about the buffalo occurring in the SE Sudan but they were studied in Dinder N.P. (Hashim 1987). Body weight 400–700 kg, and horns intermediate between the two previous subspecies. This subspecies may include the form *mathewsi* tentatively recognized by Kingdon (1982) from the mountains and uplands to the north of L. Tanganyika, but this form may possibly align with *nanus*.

S. c. nanus (Forest, Dwarf or Red Buffalo): rainforest areas of West and central Africa with an annual rainfall of more than 1500 mm. This is the smallest of the forms, with a body weight of about 250–320 kg. The horns are nearly straight and point backward, with no boss development. Intermediate forms with *S. c. caffer* are known from the area between Queen Elizabeth N. P. (Uganda) and the Ituri Forest (E DR Congo). Buffalo from N Cameroon appear to represent intermediate forms between *S. c. nanus* and *S. c. brachyceros*. Also parts of N Angola appear to contain intermediate forms between *S. c. nanus* and *S. c. caffer* (see Distribution).

Similar Species Water Buffalo *Bubalus bubalis* have been introduced in North Africa (Egypt, Libya, Tunisia) where African Buffalo are absent, and small numbers are used in coastal agricultural lands of East Africa. Similarity in size with Boran bulls (cattle, *Bos taurus*) may cause confusion but generally not with other cattle breeds. The similar, but larger, Giant Long-horned Buffalo went extinct some 4000 years ago (Klein 1994; well-preserved and clear rock engravings known from the Sahara – see McBurney 1960).

Distribution Endemic to Africa. Widely distributed south of the Sahara, though today mainly confined to protected areas. The species has suffered severely from rinderpest (e.g. Van Hooft *et al.* 2002),



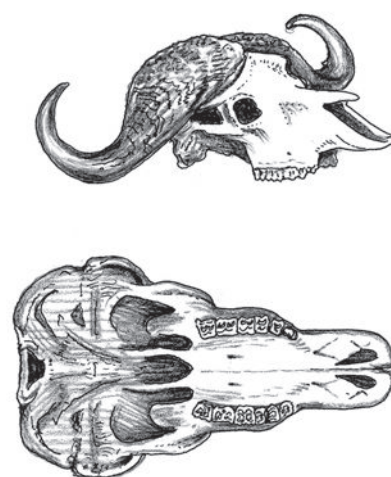
and became locally extinct, even in protected areas of Chad, Central African Republic, Cameroon and possibly Congo in the 1990s.

Historical Distribution Formerly the whole savanna zone between Senegal, Gambia and Guinea and Ethiopia and Eritrea, south to the Cape of Good Hope; also the rainforests of central Africa. There is no palaeontological evidence of the species ever occurring in North Africa or in the Nile Valley to the north of Khartoum. There, aurochs (*Bos primigenius*; wild ancestor of common cattle) occupied a similar niche (Gautier 1988), perhaps preventing the buffalo's spread to the north. African Buffalo expanded their range during the last Glacial (see genus profile) and may have increased in numbers with the extinction of possible competitors, such as *Pelorovis antiquus* and *Elephas recki* (Klein 1988, 1994, Prins 1996). Drawings of buffalo are rare in cave paintings, although representations can be seen in Kondoa in N Tanzania (Leakey 1983: pp. 23, 58, 66). In the 1600s, buffalo occurred close to the Cape, as evidenced by local place names (e.g. 'Buffelsbaai').

Current Distribution Despite having suffered drastic declines in numbers across their range, African Buffalo remain widespread, although they now are mainly restricted to protected areas.

West African Savanna Buffalo are now extinct in Gambia, probably occur only as vagrants in Guinea, and the population in Mali's Bafing Faunal Reserve is probably the country's last. In Niger they have disappeared from much of their former range in the south-west and along Nigeria's border, and survive only in W N. P.; their status in Togo is uncertain. Otherwise, their remaining range includes SE Senegal, N Côte d'Ivoire, S Burkina Faso, Ghana, N Benin, parts of Nigeria and N Cameroon.

Central African Savanna Buffalo are now extinct in Eritrea, but still range from SE Chad through N Central African Republic, S Sudan, W Ethiopia (along the Sudan border, where their recent status is unclear) and NE DR Congo (mainly around Garamba N. P.).



Lateral and palatal views of skull of African Buffalo *Syncerus caffer*.

Southern Savanna Buffalo occur in S Ethiopia (particularly Omo-Mago National Parks) and S Somalia southwards and patchily through much of East Africa to Zambia, Malawi, some parts of Mozambique (particularly in the north), NE Namibia, parts of Angola, N Botswana (north of 20° S), and N, NW and S Zimbabwe. In South Africa they have been reintroduced to some of the territories from which they were formerly extirpated; many of these reintroduced animals originate from Addo Elephant N. P. – a naturally occurring relict population in the Eastern Cape that survived the twentieth century (Winterbach 1998). The indigenous population in Swaziland was extirpated, but they have been reintroduced (Monadjem 1998).

The range of the Forest Buffalo in West Africa extends from Guinea-Bissau to SW Ghana, but their status is generally poorly known. In the central African rainforest block, their distribution is from S Nigeria and S Cameroon through SW Central African Republic, Equatorial Guinea, Gabon and Congo (particularly in the north), east to E DR Congo, and south to Angola (East 1999). Historically, there were two large zones of contact between the forest and the savanna buffalo forms in Angola: the plateau south of the high Cuanza R. (areas of Haco and Mussende, Cuanza Sul Province), where Forest Buffalo occurred in the river valley, and Southern Savanna Buffalo in the *Brachystegia* woodland; and Lunda Norte Province, where Forest Buffalo were found in gallery forests, and Southern Savanna Buffalo in the interfluvies. With the exception of Haco, where Newton da Silva (1970) mentioned the presence of hybrids, there is no evidence of hybridization taking place at these contact zones (Crawford-Cabral & Veríssimo 2005).

African Buffalo had colonized Bioko I. (Equatorial Guinea) (Nosti 1950), but they were probably extirpated sometime between 1860 and 1910 due to overhunting (Butynski *et al.* 1997b). They have not colonized islands such as Zanzibar or Mafia.

Habitat African Buffalo inhabit a wide range of habitats, including semi-arid bushland, *Acacia* woodland, miombo *Brachystegia* woodland, montane grasslands and forest, coastal savannas, and moist lowland rainforests. They are absent only from deserts and sub-deserts, such as the Namib and the Saharan/Sahelian transition zone. Although they are not adapted to arid conditions, they can live in semi-arid environments provided they have access to drinking water. Indeed, they are absent from areas without permanent drinking water within about 20 km, and also from areas where there is no permanent grass.

African Buffalo may ascend and descend steep slopes, up to about 50 degrees (H. Prins pers. obs.) and are not uncommon at high altitudes. They are known to be regular visitors on alpine Mt Kenya, where the carcass of a frozen adult bull was found in a glacier at 4700 m (McGregor Ross 1911); they are apparently common visitors to L. Hoehnel (4200 m) and droppings have been seen far up the Teleki Valley at 4150 m (Young & Evans 1993). On Mt Kilimanjaro they are present throughout the forest on the northern and western slopes, and have been observed in the alpine zone up to 4200 m (with tracks at 4500 m) (Grimshaw *et al.* 1995). Interestingly, in the Lent Valley on Kilimanjaro there are shallow caves in which sodium bicarbonate crystallizes, and buffalo enter these caves to chew off the soda deposits; such behaviour has also been observed on Mt Kenya (Grimshaw *et al.* 1995). On this latter mountain the presence of clay and soil-bound iron may explain geophagy (Mahaney 1987).

Forest Buffalo may spend much of their lives in closed forest, and have been found making use of dry caves in the rainforest of Cameroon for resting (C. A. van der Hoeven, P. Beckhuis & H. Prins unpubl.). Yet, most of their foraging takes place in open glades or clearings (Lopé N. P., Gabon, White 1992; Dzanga-Ndoki N. P., Central African Republic, Melletti *et al.* 2007), in open coastal savannas (near Setté Gama, Gabon, Prins & Reitsma 1989) or along man-made tracks (Campo Ma'an N. P., Cameroon, Beckhuis *et al.* 2008), and not in closed-canopy areas. The reason is that *S. c. nanus* is primarily a grazer, too (see Foraging and Food). Kingdon's (1982) suggestion that buffalo evolved in a 'swampy forest' is not supported by these findings. Swamp forests in the equatorial rainforests are typically devoid of grasses or herbs and shrubs such as *Palisota* spp. palatable to buffalo (Reitsma 1988, Blake 2002, Tchouto 2004). Van Hooft *et al.* (2002) on the basis of DNA-analyses suggest an evolutionary radiation of eastern and southern African buffalo out of the Cameroon–Congo–Gabon area. We suggest that the ancestral niche was in open marshy areas in rainforests with grasses and sedges, but especially in the interface between savanna and rainforest and not in a primeval type of rainforest.

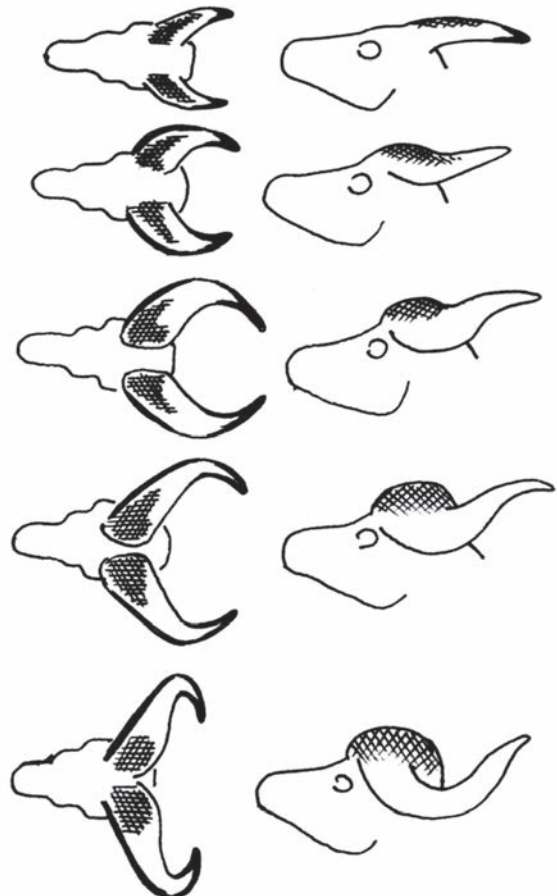
Abundance In the most recent continent-wide assessment of the status of African Buffalo populations, East (1999) estimated the total population of Savanna Buffalo at about 830,000 (correcting for undercounting biases in aerial surveys and extrapolating population

densities for areas where no surveys were available). This figure comprises 27,000 West African Savanna Buffalo, 133,000 Central African Savanna Buffalo and 670,000 Southern Savanna Buffalo (although see note under Geographic Variation re distribution limits between *S. c. brachyceros* and *S. c. aequinoctialis*). Winterbach (1998) estimated numbers in southern Africa (excluding Mozambique) at around $111,900 \pm 10,000$ individuals, including 29,300 (± 9000) in Botswana, 48,200 ($\pm 21,000$) in Zimbabwe, 2800 (± 1000) in Namibia and 31,500 ($\pm 10,000$) in South Africa. Numbers of Forest Buffalo are estimated at around 60,000 (East 1999).

In prime habitat *S. c. caffer* can reach superabundance (20 ind/km² in Lake Manyara N. P. in N Tanzania; Prins & Douglas-Hamilton 1990); in other areas, less extreme densities (e.g. Serengeti N. P. woodlands, 8/km²). In prime habitat permanent freshwater occurs every few kilometres and green grass of sufficient quality (i.e. higher than about 7% crude protein) is available throughout the year, but predation risk by Lions *Panthera leo* is very high (Prins 1996). In drier areas *S. c. caffer* attains lower densities: in Tsavo N. P., Kenya, its ecological density (that is, the density within the home-range) was 4/km² (Leuthold 1972) but the crude density (that is, the average density over the whole ecosystem) was only 0.7/km² (Cobb 1976); in the lowveld of South Africa the density is only 2/km² (Funston *et al.* 1994). Numbers were very high in the northern part of Akagera N. P. in Rwanda until the 1990s (H. Prins pers. obs.), but this area has been degazetted and numbers in the park have declined



Facial details of female Southern Savanna Buffalo *Syncerus caffer caffer* (left) and female Forest Buffalo *S. c. nanus* (right).



Horn proportions and shape in different populations of African Buffalo *Syncerus caffer*.

precipitously (Williams & Ntayombya 1999, Apio & Wronski 2011). Most likely the subspecies suffered heavily from civil unrest and war in Somalia, Burundi, Angola and Mozambique.

In West Africa, *S. c. brachyceros* typically occurs in very low densities, but with good protection they can reach higher densities: De Bie (1991) showed that for the 8000 km² Boucle de Baoulé N. P., Sudan savanna of Mali, in normal rainfall years the area could sustain 12,800 individuals and in dry years 2,700, but the present actual number is very small. The number for the whole country is now some 120 individuals only; similar extremely small populations occur in Niger (500) or Nigeria (200) (East 1999). Relative strongholds occur in Senegal (4000), Côte d'Ivoire (8000) and Cameroon (3000) (East 1999). *Syncerus c. brachyceros* is at present absent from Gambia, Guinea-Bissau, Guinea, Ghana and likely Togo (East 1999).

The Central African Savanna buffalo *S. c. brachyceros* occurs in northern DR Congo (39,000) and southern Central African Republic (19,000) with small numbers in Chad (East 1999). Populations in Sudan must have been large in the past: Southern N. P. and immediate surrounds was estimated to contain at least 75,000 buffalo (Boitani 1981). However, not a single animal was observed during recent survey work in this park, although an estimated 10,000 animals were recorded in the Jonglei, predominantly in the northern part of the Sudd (Fay *et al.* 2007), similar to the estimates of Mefit-Babtie (1983). In Eritrea it is extinct, while it is unknown whether the subspecies survives in Ethiopia (East 1999).

In Campo-Ma'an N. P., the total number of Forest Buffalo *S. c. nanus* is less than 0.01/km² because most of this forest has a closed canopy without grass in the understorey (Bekhuis *et al.* 2008). The same holds for Nouabalé-Ndoki N. P. in adjacent Congo (Blake 2002) or in the coastal rainforests of Gabon (Prins & Reitsma 1989). In Lopé N. P., an area characterized by open grasslands within a closed forest (Tutin & White 1998), densities are higher (0.4/km², White 1992). Even in patches of forest within the forest-savanna mosaic of Lopé N. P., their density is quite high (4/km² [Molloy 1997] to 7/km² [Tutin *et al.* 1997], assuming an average body mass of 250 kg); their density is very low in the surrounding closed-canopy forest (L. Korte née Molloy pers. comm.). Forest Buffalo still occur in small numbers in Guinea-Bissau, Guinea, Liberia, Côte d'Ivoire and Ghana; it went extinct in Sierra Leone (East 1999) although buffalo have been reported from Outamba-Kilimi N. P. (L. Korte née Molloy pers. comm.). The subspecies did not occur in the dry 'Dahomey Gap' (Togo and Benin). It is possibly extinct in Nigeria, but occurs in substantial numbers in the forests of Cameroon, S Central African Republic and Gabon; in Equatorial Guinea, Congo and DR Congo numbers have declined substantially due to poaching and uncontrolled hunting (East 1999).

African Buffalo often comprise a major proportion of the biomass of large herbivores if present in a local assemblage. Major competitors are cattle *Bos taurus*, Savanna Elephant *Loxodonta africana*, Plains Zebra *Equus quagga* and Common Wildebeest *Connochaetes taurinus* (Sinclair 1977a, De Boer & Prins 1990, Plumptre 1995, Prins 1996).

Adaptations The cheekteeth of African Buffalo are truly hypsodont ('high-crowned') and the ridges of enamel are sharp, convoluted and well developed to grind siliceous food. Southern Savanna Buffalo individuals about four years old may have crowns that are higher than 5 cm, but constant use wears them down so that

buffalo older than about 18 years have crowns with less than 2 mm enamel without ridges (Grimsdell 1969). Their stomach structure is described by Hofmann (1973) and is well adapted to a grass diet.

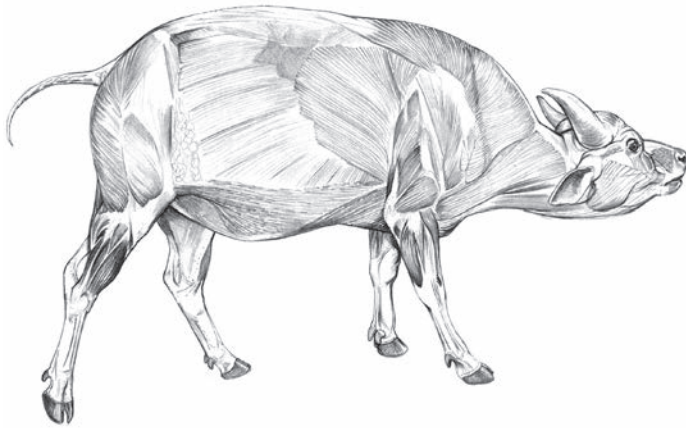
African Buffalo can sweat profusely (Taylor 1970b) and the water content of their faeces is high (about 80%, Prins 1996). Their body-water turnover rate is high (King 1979). These features make them rather water-dependent. They have to drink at least every two days, taking about 45 litres daily, and they are not able to survive on the moisture content of their food (Prins 1996). They raise their body temperature only slightly if the ambient temperature rises, in contrast to small dry- and heat-adapted gazelles, and maintain high body temperature during the night, in contrast to eland antelope (Taylor 1970a, b): in other words, they have not evolved water-saving mechanisms. Physiological adaptations include a very thick skin and a trypanocidal protein (a xanthine oxidase) in their blood that kills trypanosomes (Grootenhuys 2000).



Diversity of horn shapes in African Buffalo *Syncerus caffer*. Elevated, heavily bossed and drooping.

In Savanna Buffalo the horn sheaths often extend medially over the intervening frontals. In the ♂♂ the surface becomes conspicuously roughened after some 4–5 years. Particularly in Southern Savanna Buffalo ♂♂, the basal horn sheaths expand medially and anteroposteriorly across heavily roughened frontals that are up-arched to form prominent bosses (Klein 1994). These bosses are not formed in ♀♀, and the intervening skin is covered with hair. When bulls are sparring, they place their bosses against each other, and push. Extensive bossing is a recently derived feature that developed only in the late Quaternary (Gentry 1978, 1990), but not in the *nanus* forms that are thought to be more similar to the ancestral form (Van Hooft *et al.* 2002). Since extensive bossing only occurs in adult ♂♂, it probably evolved through sexual selection, and because it occurs especially in the Southern Savanna Buffalo forms that are characterized by large group sizes, it seems that bossing has evolved in the context of a complicated male hierarchy (see Social and Reproductive Behaviour). The frontal bones under the bosses have a honeycomb structure. The height of the bony walls of the cells is about 15–20 mm, while cell diameter is about 7 mm. Supposedly, this is an adaptation to absorb strong frontal forces while making the head not even heavier than it is, thus maintaining a maximal ability to move the head fast in any direction to confront attack. While the average weight of a dry skull plus horns was 8 kg in Lake Manyara N. P., the heaviest skulls were 16 kg (H. Prins pers. obs.).

African Buffalo have very good eyesight, and they can spot Lions at more than 1.5 km (H. Prins pers. obs.). Their hearing and sense of smell are equally good. They often graze at night, even without moonlight, and where hunting pressure by humans is severe they may become fully nocturnal, and are rarely seen during daylight hours. They can defend themselves very well against predators, and both sexes use their horns as weapons of defence and offence.



African Buffalo *Syncerus caffer* myology.

African Buffalo defend themselves against Lions by taking refuge in dense thickets, standing with their backs to trees and bushes so that the predators cannot reach their vulnerable hindquarters and are presented with a phalanx of dangerous horns. Similarly, in open habitats they will stand and confront predators in a form of group defence (Sinclair 1977a). African Buffalo can run well for short distances, with a top speed equalling that of a Lion, between 55 and 60 km/h, and they can jump about 1.5 m in height. Their skin, in places thicker than 2–3 cm, is so strong that Lion claws often do not penetrate. Because of its sturdiness, buffalo skin was used for making *riempies*, leather thongs, for harnesses of the big *voortrekker* ox wagons of the Boers. Masai used buffalo skin for their large shields.

African Buffalo often attack Lions, and may even attack or chase them when they have spotted Lions at several hundred metres. In particular, African Buffalo will respond to calf distress calls by approaching the location of the call and chasing off the predators (Sinclair 1977a). In such an attack, subadult bulls are most conspicuous but cows and adult bulls frequently join in. Adult Lions may be gored and tossed into the air, and cubs may be completely trampled. Occasionally, African Buffalo show high degrees of curiosity, and may frolic around monitor lizards or large pythons (H. Prins pers. obs.).

They may ruminate lying down in deep water with only their heads above the water, and are partial to mud-wallowing. Both behaviours are likely adaptations to avoid biting insects. Other behavioural adaptations are lying down on bare open places (Prins & Iason 1989) or spending time at high altitudes (Mugangu *et al.* 1995). This may serve as an adaptation to keeping cool by catching a breeze, because African Buffalo do not appear to be well adapted to heat. Buffalo are good climbers, facilitated by their relatively short legs (cf. Klein 1994), and also good swimmers, and can forage under water in flood-plains (Chobe R., Okavango; Botswana; H. Prins pers. obs.).

African Buffalo show clear patterns of activity, alternating between grazing and ruminating. This pattern is subject to seasonal changes in food quality and weather conditions (Lewis 1977, Sinclair 1977a, Underwood 1983, Beekman & Prins 1989, Prins & Beekman 1989, Taylor 1989, Molloy 1997, Winterbach & Bothma 1998). Grazing often takes place in the early morning or late afternoon, but in some areas more than half the grazing can take place at night (Sinclair 1977a, Taylor 1985, Prins & Iason 1989). They may walk long distances between grazing locations, and often walk single file.

Buffalo herds have been recorded covering distances of as much as 8 km in a 24-hour period (Sinclair 1977a, Stark 1986a), although they may be more sedentary in other regions (see Taylor 1985). Adult bulls are often in the front and at the rear of such a file but adult bulls do not take the decision about where to forage (see next section). Their normal walking speed is about 6 km/h (H. Prins pers. obs.).

Foraging and Food African Buffalo are grazers of grasses and sedges, tolerating grass with a high fibre content but preferring grass with moderate protein levels (of about 12% crude protein) and moderate digestibility. They favour sward-forming grasses, such as *Cynodon dactylon*, but also eat broad-leaved grasses, such as *Panicum maximum*. For example, in Serengeti N. P. their selective preference for the soft, nutritious grass *Digitaria macroblephora* was so pronounced that it eventually survived only under thorny *Acacia* bushes. On the shores of L. Kariba, the availability of *Panicum repens* grassland resulted in large herds of buffalo congregating along the shorelines (Taylor 1985). In general, there seems to be broad agreement between researchers as to the plant species recorded in feeding studies made in East and southern Africa (Sinclair 1977a). Various species are avoided or hardly eaten because of low nutritious quality or presence of aromatic oils. African Buffalo only take tussock grasses when the tussocks do not contain too many old stalks, as occurs during the growing season or after burning (see Drescher 2003). The dry season offers much less potential for grazing and then flood-plain species (*Leersia hexandra*) and riverine forest species (*Setaria sphacelata*) become important, while *Cyperus laevigatus* in areas with upwelling ground-water may form a mainstay at that time. African Buffalo sometimes augment their diet by turning to browse.

In most areas little browse is taken (Lamprey 1963, Field 1972, Leuthold 1972, Sinclair 1977a, Hashim 1987, Beekman & Prins 1989, Prins 1996, Halley & Minagawa 2005). Even in the montane forests of Rwanda (Plumptre 1995) and the rainforests of S Cameroon, their diet mainly comprises grass (43%) and Commelinaceae (18%) (Bekhuis *et al.* 2008), but in southern Africa they consume more herbs (Jarman 1971, Mloszewski 1983) as in Gabon (MacLachly 1932). Browse takes the form of green tree leaves (22% of diet in the Zambezi valley; Jarman 1971), or shrubs such as *Grewia*, *Heeria*, *Combretum* and *Euclea* (Kruger N. P., South Africa; Pienaar 1969b), prickly shrubs such as *Capparis tomentosa* (Uganda; Field 1968), and succulent thorn shrubs (Addo N. P.; De Graaff *et al.* 1973). In the rainforest of Campo-Ma'an N. P., African Buffalo consume *Palisota* spp. (pioneer shrubs endemic to the Guinea-Congolian area). These grow as a rule along the edges of logging tracks and roads (Bekhuis *et al.* 2008). Generally, browse is probably eaten to increase the nitrogen content in the rumen and to facilitate fermentation of fibrous grass and especially sedge, which African Buffalo eat in high quantities during the dry season. They produce large amounts of saliva (about 100 l per day, R. R. Hofmann pers. comm.) that is needed to recycle nitrogen from the blood to the rumen.

Optimal conditions for African Buffalo exist when the grass forms swards and leaf height is above 10 cm, as in flood-plains or in forest glades (Prins 1996). In some areas they maintain or create 'grazing lawns' (Vesey-FitzGerald 1969, 1974) and can do this unaided, if the regrowth interval is short enough (Prins 1996). They can create favourable lawns in conjunction with other large herbivores such as Savanna Elephants at L. Rukwa, Tanzania (Vesey-FitzGerald 1960)

or Common Hippopotamus *Hippopotamus amphibius* in Uganda (Eltringham 1999) and Bénoué N. P. in C Cameroon (H. Prins pers. obs.). Grazing lawns have also been reported from Dzanga-Sangha Reserve in S Central African Republic (A. Blom pers. comm.) and some parts of Lopé N. P. (L. White pers. comm.) but seem to be absent from some rainforests because herd sizes are small and densities low. In East Africa, optimal dietary conditions occur during the wet season, while the end of the long dry season coincides with insufficient quantities of food that can be too low in quality to maintain body condition. Where details of diet have been studied in East Africa, African Buffalo appear to be resource-limited (Sinclair 1977a, Prins 1996). During the period with best diet composition there is a peak in calving so that lactating cows can best meet the demands of their calves. The diet of juveniles, subadults, adult cows or adult bulls does not appear to be different. As with many other ruminants, daily dry matter food intake varies between 1.2% and 3.5% of body mass, but this depends on the quality of the food (Sinclair 1977a, Prins & Beekman 1989).

Social and Reproductive Behaviour Populations of African Buffalo consist of discrete herds with a life-span of many decades, and ♀♀ stay in the herd in which they are born (Sinclair 1977a, Prins 1989b, 1996). Most genetic exchange between herds takes place through male dispersal. Yet, gene-spreading cannot be ascribed solely to bulls because mother–daughter inherited mitochondrial DNA spreads as well. This either implies that philopatry in ♀♀ is not absolute or that on a time horizon of centuries female herds may merge (Wenink *et al.* 1998, Van Hooft *et al.* 2000, 2002). Genetic studies clearly suggest that African Buffalo once formed a vast metapopulation with few barriers to gene flow (Van Hooft *et al.* 2002).

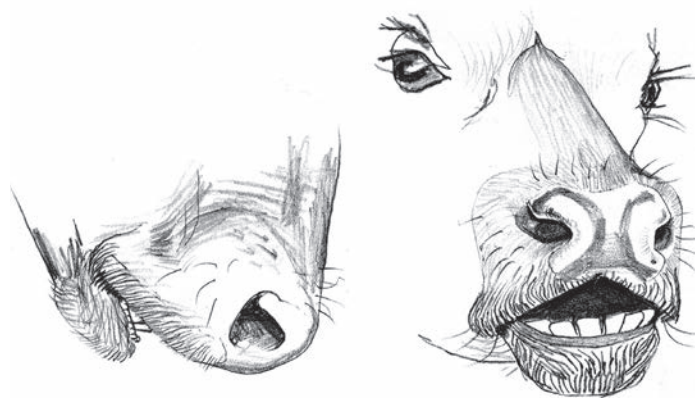
Adult cows and their offspring live in stable herds that vary between about 20 individuals in the forest-living *S. c. nanus* (Happold 1973a) to as many as 1000 in *S. c. caffer* in the open savanna of the Serengeti N. P. (Sinclair 1977a, Prins 1989b). Herds of over 2000–4000 individuals have been reported in the past in Lake Manyara N. P. (Park Warden's Report April 1960). It is possible that these very large groupings are temporary associations of two or more herds, because herd home-ranges overlap, and herds can mingle for a while. Savanna Buffalo can also occur in small herds of less than 20

individuals that can be stable entities (Prins 1989b, 1996). In Savanna Buffalo, ♀♀ and their offspring have a rather fixed location in a herd, which means that some individuals are nearly always observed at the rear end of a herd while others frequently occupy a location at the front end of a herd. Such a location may be inherited, because female offspring stay with their mothers well into adulthood. Aggressive (agonistic) behaviour may also play a role in determining position within the herd. Agonistic behaviour consists of hooking and butting with the horns; among ♀♀ this is typically aimed at the flanks or the rump of other adult ♀♀.

In small herds there may be linear hierarchies, but in larger ones hierarchies are much more complicated. Large herds of Savanna Buffalo reveal a fusion–fission society, wherein herds may split for short periods then come together again. This splitting and merging takes place at a time-scale of days and is independent of season (Leuthold 1972, Prins 1989b; see also Cross *et al.* 2005). Possibly, new herds may ultimately arise in this fashion. The herd as a social entity has a much longer life-span than any single individual, and recognizable herds are known to have existed for over 50 years (Prins 1996). Yet, long distance movements by cows have been reported in Botswana, and cows have shown up in different herds. These cows are possibly individuals of low status (Halley *et al.* 2002). Genetic studies show that the migration between herds is only 5–20% for ♀♀ and close to 100% for ♂♂ (Van Hooft *et al.* 2003).

Three types of social organization have been reported for adult Savanna Buffalo bulls, namely (a) permanent herd-bull, (b) non-synchronized alternation between herd state and bachelor-bull state and (c) synchronized alternation between these two states. Forest Buffalo may live in herds with a permanent herd-bull (Dalimier 1955, Blake 2002; the males' tenure duration is unknown). This may be the best reproductive strategy if ♀♀ occur in small herds that are widely scattered in grassy patches within a rainforest that is otherwise inimical to buffalo.

At very high densities with large herds within walking distance from one another, adult bulls of *S. c. caffer* do not show fidelity to the same herd. This occurs in Lake Manyara N. P., Tarangire N. P. and Ngorongoro Crater (Tanzania). There, social organization is one where mature bulls attach themselves to a herd for about two months during which period there is intense competition between many adult bulls for mating opportunities with receptive cows (termed a re-entrant consecutive polygyny). As an individual bull's condition deteriorates, there comes a point (determined by the condition and prowess of the other bulls in the herd) where the previously successful bull moves to the rear of the herd and a few days later he may leave the herd to become a 'bachelor-bull'. He then wanders around alone, or with other adult bulls outside any female herd for days, during which period he recoups his condition. This takes about one month during which period he can wander some 100 km. When he re-enters a herd, this may be the same herd or a different one. Linear hierarchies between bulls do not occur in this system (Prins 1989a). This wandering and re-entering in different herds explains the strongly male-biased gene flow in Savanna Buffalo (Van Hooft, W. F. *et al.* 2003). These two 'reproductive states' may also explain the big differences in testosterone levels between individual bulls during a season (Brown *et al.* 1991). Such a re-entrant consecutive polygyny was also described for Hluhluwe-iMfolozi (South Africa), but with a much shorter cycle (Turner *et al.* 2005).



Profile (left) and frontal (right) views of grazing mouth of African Buffalo *Syncerus caffer*.



African Buffalo *Syncerus caffer*.

A third type of social organization of adult bulls has been described, also for *S. c. caffer*, where buffalo occur at intermediate densities and where herds may be segregated by expanses without surface water, as in the Serengeti N. P. with its pattern of woodlands interspersed with waterless grasslands. Here bulls also alternate between life as herd-bull and bachelor-bull, but these two states are more synchronized between bulls. Most bulls live as herd-bulls during the wet season (about eight months) and in bachelor herds during the dry season (approximately four months). Bachelor herds in this system have a more stable membership than in the previous system and there is evidence of linear dominance hierarchies in both bachelor and herd ♂♂ (Sinclair 1977a). In the re-entrant consecutive polygyny system the average 'bachelor' bull group numbers only about 3.5, which can be explained by a short duration of stay in a group, weighed against the advantages of group formation against the risk of predation. However, the largest groups can still be close to 50 individuals (Prins 1996). In the Serengeti system bachelor-bull groups comprise on average 5–10 individuals, the largest ones about 50 (Sinclair 1977a).

Before the 1960s some buffalo populations may have made more nomadic or migratory movements in response to locally heavy rainfall or droughts so that wet season ranges were in woodlands and dry season ranges in swamps. At present, African Buffalo are increasingly confined to protected areas, and their home-ranges appear to be more fixed. Home-range size varies depending on availability of water and graze. In the Serengeti N. P., Sinclair (1977a) gave home-range sizes as about 220 km², not dissimilar to those estimated in Sengwa Wildlife Research Area, Zimbabwe, of 250 km² (Conybeare 1980). On the other hand, the mean home-range sizes of four herds on the Botswana/Zimbabwe border were 920 km², 1012 km², 1138 km² and 1455 km² (Hunter 1996).

Cows, juveniles and calves stay together in large to very large herds, and even subadults of both sexes stay within their maternal herd. Leaving a herd, even only temporarily, incurs a high predation risk in areas with Lions. When herds move between foraging areas one or more adult bulls may precede them. However, adult cows are quite often in the lead as well. Lead-animals may stop a whole herd simply by not moving on or by giving a stopping signal, which involves standing and blocking the direction of movement. These lead-animals are not to be viewed as 'leaders', that is, as animals that have taken the decisions about where to forage. It gives the appearance of being a communal decision taken by the adult cows in a procedure that has been named 'voting' (Prins 1996). Communal decision-making appears to take place in a number of species, e.g. Sacred Baboons *Papio hamadryas* or Red Deer *Cervus*

elaphus, and may be linked to information exchange as known from several bird studies. In African Buffalo, 'voting' takes place after a long resting bout, typically at the end of the afternoon when nearly all individuals lie down and even have stopped ruminating. Individual cows rise and elevate their head as if staring in a particular direction. The head position is half-way between a resting position (angle of the neck about 30 degrees from the horizontal) and full alert, when the animal has the head elevated so high as if gazing over its nostrils. The voting stance is maintained for a few minutes, after which the cow beds down again, or after which she may start grazing. The vector of all voting directions of individual cows points to the direction of a grazing ground for the night. A short vector implies little consensus within the group of voting cows, while a long vector means a high degree of consensus (that is, all heads were pointing in the same direction). Little consensus is often followed by a temporal splitting of the herd; the resulting subherds then fuse again after a few days.

African Buffalo calves seldom play, and frolicking around is rarely seen. Social interactions between subadult cows are equally rare and restrained. Subadult bulls show intense sparring behaviour, which is also engaged in by adult bulls. During sparring, horns, and especially the bosses, are placed against each other after which the animals start pushing. The 'winner' often is able to hook the 'loser', but the 'winner' seldom pushes his advantage. He stays put so that the 'loser' can try again. Sparring may function as testing dominance between individuals although it looks as if both contestants enjoy the game. Most such interactions between adult bulls appear to be limited to 'sizing each other up' – both bulls look at each other, often observed by other bulls. A more intense form is the parallel walk. Actual fights occur primarily when both contestants are equally strong and big; they are extremely rare and can result in fatal injuries to both bulls.

African Buffalo are generally silent. They occasionally grunt, especially when a cow is hooked by another animal. They snort and cough when alarmed and when they start running. There is a distinct ritualized threat and submissive behaviour amongst ♂♂. Dominant ♂♂ threaten by standing with head up but muzzle pointing down, thus emphasizing the shoulders, a stance characteristic of most bovine species, including the Gaur *Bos gaurus*, Banteng *Bos banteng* and American and European Bison (*Bison bison*, *B. bonasus*). A submissive ♂, when threatened, approaches the dominant ♂ with head held low and parallel to the ground and will often place the muzzle between the hindlegs of the dominant one. At the same time the subordinate animal utters a loud and long bellow, sometimes continuing for the entire duration of the submissive display. The behaviour is similar to that of small calves when suckling or searching for their mother.

This ritualized submission seems unique to African Buffalo; it is not shown by Water Buffalo.

Bulls can make very loud bellows but they usually do this only when badly injured. Other bulls may or may not react to the sound. Whatever the exact mechanism, in about one-third of the instances that a bull is wounded by Lions or hunters another adult bull will come to his aid. Severely wounded animals may also start searching for other buffalo, finding shelter with them. They do not have an alarm call but have a very efficient warning system, especially at night, by becoming dead silent. Then a 'wave of silence' spreads through the bush making it very difficult to pinpoint individual animals in the dark; this may be a safer way of 'sounding' the alarm than focusing attention on oneself.

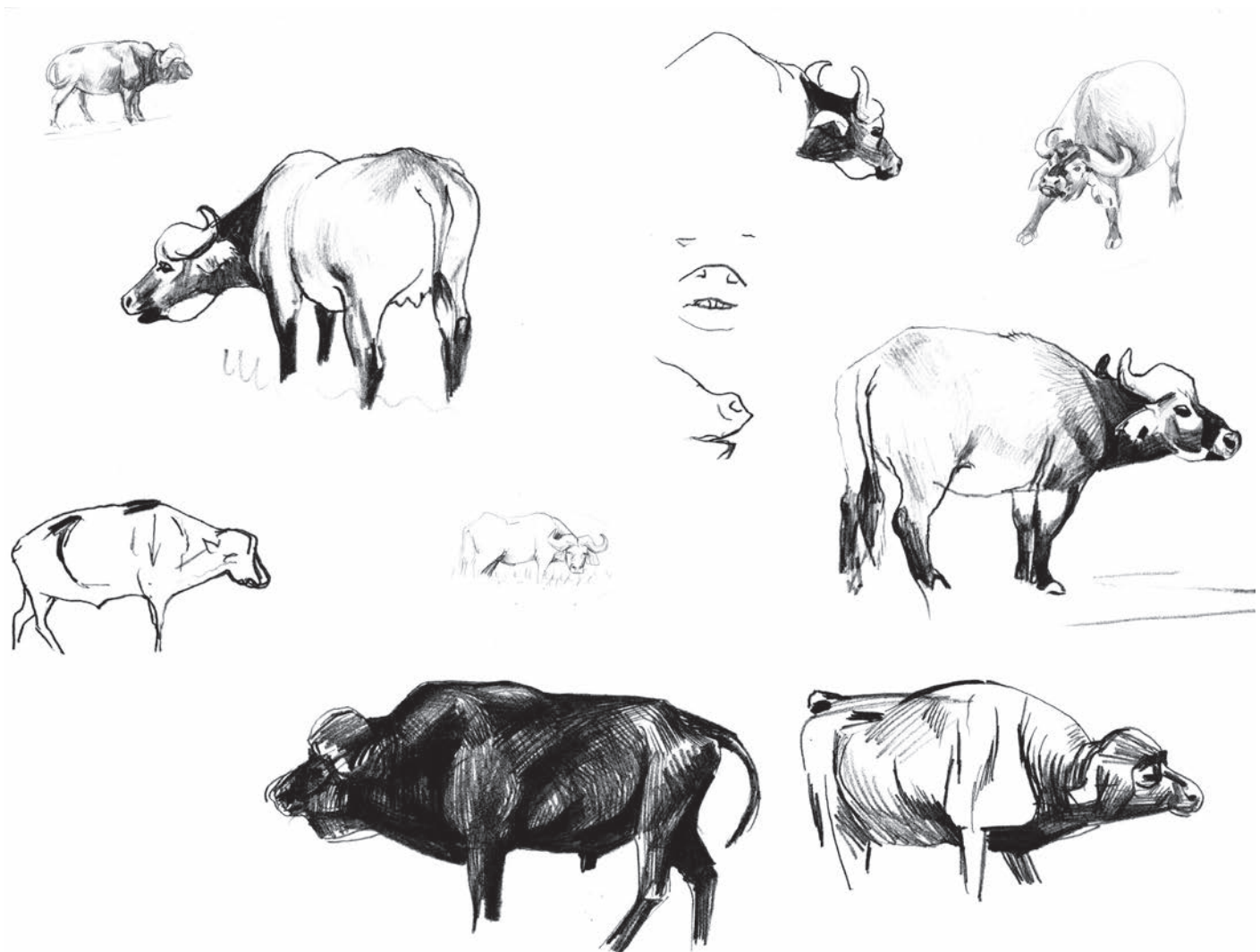
Mating depends on the willingness of a cow to be mounted. In the hours before an adult bull can attempt this, he shows extensive tending behaviour ('consorting'). When receptiveness increases the bull tries to lay his chin on her tail base. In general, she then walks away, after which the bull tries again. Bulls show flehmen when testing urine of receptive ♀♀. When the cow is willing to stay put, the tending bull is often supplanted by a more dominant bull who then mates with the cow. Prior to that, ♂♂ may mount, and even attempt intromission, but ♀♀ then start running making this impossible. If the cow stays put, then mounting, intromission and ejaculation take a few seconds only. Whether ♀♀ mate with more than one ♂ is unknown, but given the tending behaviour described above, this is unlikely. A recent genetic study provides new insights into male mating behaviour. Y-chromosomal gene diversity decreases significantly between subsequent generations in both Kruger N. P. and Hluhluwe-iMfolozi N. P. (South Africa). This implies either a strong selection effect, possibly related to drought or bovine tuberculosis, or a very small number of reproducing bulls (Van Hooft *et al.* 2010, W. F. van Hooft pers. comm.). The cow remains with the herd to calve, although if the herd moves on the mother and calf may be left behind temporarily while the calf is still weak. Calves may associate with age mates. These associations are especially noticeable in ♀♀ and may last for many years (Prins 1996), as in zebu cattle (Reinhardt 1983). Sometimes these coalitions result in coincident death at a much older age when both 'friends' perish in so-called 'multiple kills' by Lions. Multiple kills in Lake Manyara N. P. comprised about 6% of the kills (H. Prins pers obs.).

Reproduction and Population Structure Across the range, there appears to be a birthing peak during the wet season. In Matusadona N. P., Zimbabwe, conceptions occurred between Dec and May, with births between Nov and Apr, nearly two-thirds of them in Jan and Feb (Taylor 1985). This corresponds to observations in N Botswana (Carmichael *et al.* 1977) and Kruger N. P. (Fairall 1968, Pienaar 1969b). In the more arid Serengeti area there is a clear calving peak, with about 50% of all calves born within seven weeks, but in the more mesic conditions of Lake Manyara N. P. such a peak does not show (Prins 1996). This may also be linked to differences in social organization among bulls (see above). Experiments on captive buffalo bulls in South Africa show a seasonal cycle in testosterone levels, endocrine function and seminal quality; but this cycle is not sufficient to explain a breeding or calving season (Brown *et al.* 1991).

In captive Southern Savanna Buffalo, pro-oestrus lasts two or three days, oestrus one day, and the oestrous cycle from 18 to 22 days (Knechtel 1993). Gestation period is about 340 days (Vidler *et al.* 1963) (similar in captivity; Knechtel 1993). A single calf is born with a mass of about 30 kg; twins are extremely rare. Calves have long suckling bouts of about 10 min when they are some four weeks old, reducing to 5 min when they are six months old (Prins 1996). Calves suckle from the rear; when the dam starts walking with the herd the calf can continue receiving milk but the mother does not lose the protection of the herd. Age of weaning depends on density and intra-specific competition. In Lake Manyara N. P., where the density was high and the population stationary, many calves were still not weaned at 18 months of age, while in Serengeti N. P., where the density was much lower and the population increasing fast, weaning took place at the age of 10 months. Calving interval in Manyara was therefore about 36 months (Prins 1996) and in Serengeti N. P. only 15 months (Sinclair 1977a). Birth rates are thus density-dependent. Calving intervals are not known for the other subspecies.

Individuals are called 'calves' when they do not reach the inguinal fold at its highest point on the flank of the cow. Juveniles are normally weaned and younger than three years (if penis or testicles are not observable it is difficult to establish the sex of a juvenile in the field). Subadults begin to show secondary sexual characteristics and horn shape begins to diverge in ♂♂ and ♀♀: those of cows start extending laterally whereas those of ♂♂ curve strongly upwards, and bosses start to develop. Subadult Southern Savanna Buffalo bulls still have skin covered with hairs between the bosses while adult bulls normally do not. Southern Savanna Buffalo cows begin ovulating after about three years of age, and have their first calf at 4–5 years of age (Grimsdell 1973b, Sinclair 1977a, Taylor 1985). Southern Savanna Buffalo bulls reach sexual maturity at 5–6 years of age, but are unlikely to breed until seven years or older. At that age horns become the typical tools of assault (see Prins 1996 Fig. 4.1). The relation between age and development is not known in the other subspecies.

Foetal sex ratio does not deviate from parity in Kruger N. P., and is independent of rainfall, maternal lactation status, or density (Visscher *et al.* 2004). During dry years, calves are sired by bulls with haplotypes that are different from bulls that sire calves during wet years (Van Hooft *et al.* 2007, 2010). Sex ratio at birth does not deviate from parity either in Lake Manyara N. P., but with increasing age the ratio in herds becomes increasingly slanted in favour of ♀♀ (Prins 1996). Males spend considerable amounts of time outside herds as so-called bachelor-bulls, which may explain this. Indeed, life tables show that mortality patterns across ages in ♂♂ and ♀♀ are similar (Grimsdell 1969, Sinclair 1977a). However, new information reveals that the proportion of bulls in the total population of at least Kruger N. P. shows cyclicity associated with wet and dry clusters of years, and may be as low as 3% during part of the wet cycle and 11% during the dry. This is caused by the birth of proportionally more female calves during a dry period and proportionally more bull calves during a wet period (Whyte 2006). The average age of death (ignoring calf mortality because remains of calves are too rare in the wild) is about 12 years. Maximum longevity in the field is approximately 20 years and in captivity 29 years (Jones 1993, Weigl 2005). Life history parameters for the other subspecies are not known.

African Buffalo *Syncerus caffer*.

Predators, Parasites and Diseases The main predators of Southern Savanna Buffalo are Lions, but predation by Spotted Hyaena *Crocuta crocuta* and Leopard *Panthera pardus* has been recorded, the victims usually being young animals (Kruuk 1972, Schaller 1972, Prins & Iason 1989, Ruggiero 1991, Funston *et al.* 2003). In forest areas such as Mt Meru, Tanzania, predation is insignificant. In Serengeti N. P., predators (Lions) account for only 25% of mortality (Sinclair 1977a). In Lake Manyara N. P., Lion-caused mortality figures are very high, up to 85%, in the absence of major diseases. Thus, the effect of predation depends strongly on location. Little to nothing is known of the relation between predators and the other subspecies.

Lions may take African Buffalo from the midst of a herd, sometimes without other buffalo paying attention while in other instances buffalo go out of their way to kill Lions. There appears to be safety in numbers, even for adult bulls, which are invulnerable when in prime condition. However, Lions often kill old ♂♂ in bachelor groups (Schaller 1972). Usually two or more Lions attack from the rear, and they have to pin the buffalo down otherwise it can shake them off. Sometimes buffalo will try to impale the Lions on *Acacia* thorns. Lions unable to take down a standing buffalo have been seen perched on top of the standing buffalo (H. Prins pers. obs.). If the

buffalo is lying down, they have to suffocate it by holding the muzzle (the 'kiss of death') because they cannot break the neck of even a subadult buffalo. Lions use terrain features as cover to stalk herds (Prins & Iason 1989, Mugangu *et al.* 1995). Other infrequent (less than 5%) causes of mortality include getting stuck in mud, falling down cliffs, or fights with conspecifics. Mass mortality of buffalo after being stampeded by Lions over cliffs has been reported from Zambia (63 and 42 buffalo, respectively) and also mass entanglement in floating grass while trying to cross a lagoon (Anonymous 1965).

Diseases may play havoc with populations of all subspecies. The exotic rinderpest virus first spread through Africa in the 1890s and may have caused mortality in the order of 90% of African Buffalo. Subsequent epizootics have caused major die-offs throughout the twentieth century and the disease is still present in parts of Africa. In the Sudd, S Sudan, aerial surveys have revealed that there is virtually no overlap in local distribution between buffalo and cattle in spite of the habitat being broadly suitable to both species. One explanation is that the buffalo, surviving in inner swamp enclaves, have escaped contact with rinderpest-infected cattle (T. Fison pers. comm.). Indigenous diseases such as anthrax may cause mass mortality at the end of a drought (Prins & Weyerhaeuser 1987). Mortality of calves and juveniles may be caused by infestation with cestodes

and trematodes, and many other diseases, such as tuberculosis, are known to occur in African Buffalo (see Sinclair 1977a, Hoppe-Dominik & Harbers 1988, Prins 1996, Penzhorn 2000). African Buffalo are much more threatened by diseases harboured by livestock than vice versa (Bigalke 2000, Grootenhuis 2000). Once infected, populations maintain reservoirs for bovine tuberculosis (Rodwell *et al.* 2001a, b) or foot and mouth disease (Thomson *et al.* 1992, Ayebazibwe *et al.* 2010): these diseases do not affect them badly. If in contact with disease-free domestic stock, African Buffalo can infect domestic stock, which has major repercussions for the food industry (Bruckner *et al.* 2002) even though foot and mouth disease does not seriously affect cattle (Vosloo *et al.* 2002). A particular type of foot and mouth virus (South African Territories serotype C) may have an ancient association with African Buffalo (Vosloo *et al.* 2002). Buffalo are also known reservoirs of theileria parasites, specifically *Theileria parva lawrencei* (e.g. Young *et al.* 1978), which plays an important role in the epidemiology of cattle theileriosis.

Various investigators have reported on external parasites. African Buffalo from three areas in Ngamiland, Botswana, were found to be infested with *Hyalomma truncatum*, *H. rufipes*, *Rhipicephalus evertsi*, *R. tricuspidis*, *R. simus* and *Boophilus decoloratus* (Carmichael 1976). Horak *et al.* (1983c) recorded several of these species (*B. decoloratus*, *R. simus* and *R. evertsi*) on African Buffalo in Hluhluwe G. R. in KwaZulu-Natal, as well as *Amblyomma hebraeum*, *Haemaphysalis silacea*, *Rhipicephalus appendiculatus*, *R. maculatus* and *R. muelhensii* (and see Horak *et al.* 2007).

Conservation IUCN Category: Least Concern. CITES: Not listed.

In the past, African Buffalo formed a metapopulation at sub-continental scale. They are genetically exceptionally diverse and have not suffered any obvious major population bottleneck over the last several thousand years (Van Hooft *et al.* 2000, 2002). In South Africa its distribution was severely diminished with the advance of white 'trekboers' who, in the late 1800s, roamed the veldt with their cattle in search of ivory. However, numbers suffered their most severe collapse during the great rinderpest epidemic of the 1890s, which, coupled with pleuro-pneumonia, caused mortalities as high as 95% among livestock and wild ungulates (Winterbach 1998). They have repeatedly been hammered by new outbreaks of rinderpest that have spread from cattle to wildlife during the whole of the twentieth century resulting in local extinctions (Branagan & Hammond 1965 – Tanzania and Kenya; Sinclair 1977a – Serengeti N. P.; Prins & Weyerhaeuser 1987 – Lake Manyara N. P.; general overviews Plowright 1982, Prins 1996, Grootenhuis 2000). Mistakenly, officials and farmers blame African Buffalo, rather than livestock, for spreading rinderpest or other diseases such as tuberculosis or bovine pleurosis (Bigalke 2000, Grootenhuis 2000). They still insist on local eradication or 'total control' (KwaZulu-Natal in 2001) of wild animals and especially of buffalo without attacking the root cause, namely the disease reservoirs in livestock of local people. Local eradication programmes, corridor barriers and fencing of protected areas have resulted in a break-up of the initial metapopulation. Roads have a negative influence on large mammal populations nearly everywhere because they facilitate hunting and poaching (Blom *et al.* 2004a) and cause further fragmentation of populations. Increasing agricultural activities and high livestock numbers degrade the areas

between protected areas. There, overgrazing makes the habitat a virtual desert for the buffalo. In Tanzania, for example, the devastating impact of charcoal-burning on local woodlands removes both trees and nutrients, and makes the habitat unsuitable for buffalo (Ludwig 2001). Ever more embattled protected areas thus increasingly become isolated from each other, and in each fragment the buffalo population runs an increased risk of being wiped out by the next major outbreak of disease, especially of rinderpest. In most of rural Africa, programmes for the vaccination of livestock have come to a complete standstill. New strains of rinderpest sweep thousands of square kilometres every decade or so (see Rossiter *et al.* 1987) and in many regions a combination of disease and lawlessness is likely to present a major threat to the future survival of buffalo populations.

Savanna Buffalo populations may suffer from drought. In Masai Mara National Reserve, Kenya, for instance, they declined in numbers by some 60% between 1977 and 2007 (Oguto *et al.* 2011). The drought of 1993 had a devastating impact (Dublin 1994) and was the most severe since 1938 (Mduma *et al.* 1998), yet land use changes, displacement by cattle, and encroaching wheat farming may have been important additional influences (Ottichilo *et al.* 2001, Ogutu *et al.* 2011). Data are insufficient to conclude whether buffalo were affected by the drought of 1970/71 (Van Wijngaarden 1985).

Another threat comes from so-called co-management programmes in protected areas whereby local people and their livestock obtain access to once well-protected parks. Demands by people usually result in overgrazing and pre-emption of grass and water for wild animals, and this affects buffalo in particular. The unfounded beliefs and ideologies of development aid organizations that co-management results in better protection has led to bushmeat poaching and this has had a devastating impact on buffalo numbers. Poaching is not only conducted on a local scale by people living in small villages (FitzGibbon *et al.* 1995), but is often carried out by well-organized companies for meat delivery to towns (Dublin *et al.* 1990, cf. Mduma *et al.* 1998). Policies in which armies and government personnel are allowed to exploit bushmeat together with civil wars are all playing a part in severely decimating local buffalo populations (see, e.g. Plumptre *et al.* 1997). Meat-utilization schemes, as in the Zambezi Delta, were devastating when about 40,000 buffalo were killed in the 1970s (F. de Boer pers. comm.).

African Buffalo can have a high commercial value as trophies, a value enhanced by their having a reputation as one of the most dangerous animals of the African bush. Many private and some communal 'game conservancies' and ranches in southern Africa have restocked with disease-free buffalo and turn a good profit (e.g. Hearne & McKenzie 2000, du Toit 2005). In South Africa, for example, restocking of game reserves and private farms can only be done with disease-free buffalo because of fear of disease transfer from this wildlife to livestock (Condy & Hedger 1978, Grobler & Van der Bank 1996). In fact, disease transfer normally takes place from livestock to wildlife (Bigalke 2000, Grootenhuis 2000). A small remnant population in Addo Elephant N. P. in South Africa provides most of the stock for restocking (Grobler & Van der Bank 1996). African Buffalo have an unrealized potential value due to their resistance (both apparent and inherent) against many tropical diseases that are crippling the African livestock industry. It is likely that their resistance against trypanosomiasis, which is spread by tsetse flies, has a genetic basis (Grootenhuis 1991) and the same may be true for their resistance

against East Coast Fever (theileriasis), which may open avenues for genetic engineering of cattle. The transfer of this genetic asset could speed up the extinction of the donor.

Today around 70% of Savanna Buffalo individuals occur in and around protected areas, with those in East and southern Africa occurring in numerous conservation areas, such as Murchison Falls and Queen Elizabeth National Parks (Uganda), Tarangire and Selous National Parks (Tanzania), Lake Nakuru N. P. (Kenya), Kafue and North and South Luangwa National Parks (Zambia), Mamili N. P. (Namibia), the Okavango Delta and Chobe N. P. (Botswana), and Kruger N. P. and Hluhluwe-iMfolozi G. R. in South Africa. In the rest of the range, numbers of the Western and Central African subspecies are restricted to fewer protected areas, such as Mole N. P. (Ghana), the W-Arly-Pendjari protected areas complex (Burkina Faso, Benin, Niger), the protected area and hunting zone complexes of North Province in Cameroon, Zakouma N. P. (Chad) and Sangha (Central African Republic). About three-quarters of Forest Buffalo occur in protected areas, especially Dzanga-Sangha Reserve (Central African Republic), Nouabalé-Ndoki and Odzala National Parks (Congo), Kahuzi-Biega N. P. (DR Congo) and Lopé and various other protected areas in Gabon (East 1999).

The conservation prospects of the four subspecies of African Buffalo are quite different. The outlook appears good for the Southern Savanna Buffalo *S. c. caffer*, which currently numbers about 670,000 individuals. The Forest Buffalo *S. c. nanus* with some 60,000 individuals is threatened by meat poaching but may benefit from forest clearing. The future of the West African Savanna Buffalo *S. c. brachyceros* with only 27,000 individuals remaining can improve only if the ambitious conservation plans are put into effect (e.g. De Bie 1991). Perhaps most worrisome is the future of the Central African Savanna Buffalo *S. c. aequinoctialis*. Their numbers are thought to be some 133,000 individuals, but the protected areas in their range are to a large extent 'paper parks' only, offering little or no protection (Blom *et al.* 2004b).

Measurements

Syncerus caffer

S. c. caffer

TL (♂ ♂): 3387 (3200–3600) mm, n = 8
 TL (♀ ♀): 2895 (2860–2930) mm, n = 2
 T (♂ ♂): 789 (670–900) mm, n = 8
 T (♀ ♀): 767 (755–780) mm, n = 2
 HF c.u. (♂ ♂): 578 (560–610) mm, n = 8
 HF c.u. (♀ ♀): 577 (560–595) mm, n = 2
 E (♂ ♂): 244 (230–265) mm, n = 8
 E (♀ ♀): 252 (235–270) mm, n = 2
 Sh. ht (♂ ♂): 1448 (1360–1530) mm, n = 8
 Sh. ht (♀ ♀): 1383 (1350–1415) mm, n = 2
 WT (♂ ♂): 750.8 (660.7–849.2) kg, n = 8
 WT (♀ ♀): 446.6 (425.7–467.5) kg, n = 2
 Serengeti N. P., Tanzania (Sachs 1967)

HB (♂ ♂): 2510 ± 230 mm, n = 4

HB (♂ ♂): 2360 ± 110 mm, n = 9

Sh. ht (♂ ♂): 1450 ± 80 mm, n = 4

Sh. ht (♀ ♀): 1440 ± 60 mm, n = 9

WT (♂ ♂): 574 ± 76 kg, n = 4

WT (♀ ♀): 433 ± 40 kg, n = 11

Matusadona N. P., Zimbabwe (Taylor 1985)

In E Zambia, Wilson (1968) gave the mean weight of 42 ♂ ♂ as 589.4 kg (range = 472.0–723.4) and of 31 ♀ ♀ as 430.8 kg (range = 385.5–535.5)

The world record horns from Lake Manyara N. P., Tanzania, measured 163.0 cm (Rowland Ward). Bulls with a very extreme span may be hormonally affected (from visual observations in Manyara testes appear to be either absent or shrivelled; H. Prins pers. obs.)

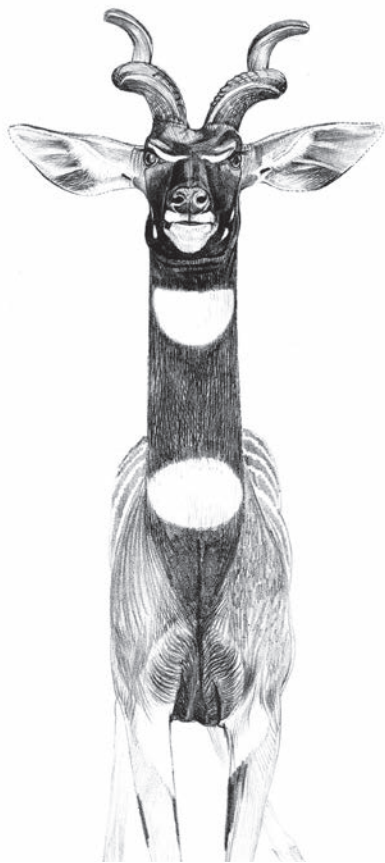
Key References Grimsdell 1969; Mloszewski 1983; Prins 1989a, b, 1996; Sinclair 1977a; Taylor 1985, 1988, 1989.

Herbert H. T. Prins & Anthony R. E. Sinclair

Tribe TRAGELAPHINI

Spiral-horned Antelopes

Tragelaphini Blyth, 1863. Cat. Mamm. Mus. Asiat. Soc., p. 164.



Lesser Kudu *Tragelaphus imberbis* frontal view.

Tragelaphines are medium- to large-sized bovines with deep, slab-sided bodies and narrow heads with large ears and twisted horns (hence the name ‘spiral-horned antelopes’). In most species, the ♀♀ are hornless (all except the elands and the Bongo *Tragelaphus eurycerus*), and ♀♀ tend to retain a generic resemblance that is totally absent in the distinctly larger, heavier ♂♂, which have distinctive (but quite variable) horn shapes and darker, more contrasting coat patterns.

Tragelaphini are of undoubtedly Asiatic origin, but have evolved in Africa since diverging from a common root with Asiatic boselaphines some 18 mya when the ‘Proboscidean Event’ marked a solid connection between continents (Hassanin *et al.* 2012). The entire tribe of nine species derives from a single ancestral type, and many, possibly all, species are capable of interbreeding in captivity, most with reproductively viable offspring.

Tragelaphines have slow, tentative gaits, adapted to reduce their conspicuousness, and their elegant, relatively un-muscular limbs are poorly suited to much more than a short rush for cover. Only the more powerfully built elands are endowed with any stamina; the other tragelaphine species prefer to freeze, rush, or slip away or crouch, prostrate, when disturbed.

The colouring of tragelaphines is appropriate not only to a ‘lying-out’ phase in calves, but to crypsis in adult life as a major strategy for escaping predators. It is therefore interesting that tragelaphines are

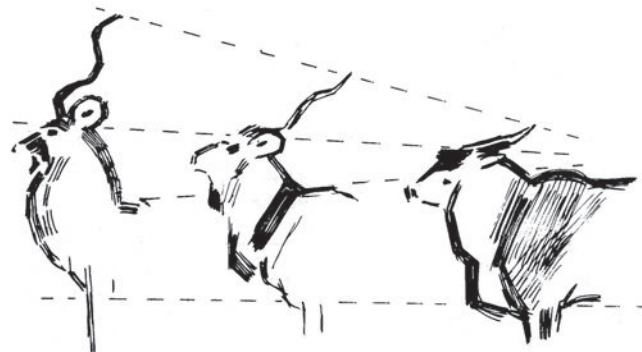
highly visual animals, relying more on vision and hearing than most other bovines. The transformation of camouflage blotches into vertical lines, which are visually arresting only at close quarters, may be of some intra-specific social significance. Rangy, flat-sided figures and the evolution of crests and manes that effectively extend the visual impact of such patterns serve to enhance this mode of display. Tragelaphines are not territorial and most encounters between male tragelaphines are slow, measured, circling rituals that usually end in one ♂ leaving the scene and fights are relatively rare compared with contests between other antelope ♂♂.

Spiral horns are the product of tensions exerted by the horny sheath upon the traverse of an otherwise straightforward symmetrical bony core inside. Extra keratinous material is laid down along a ‘keel’ and this particular zone of keratin grows at a slower rate than that of the main shaft. This ridge of slower-growing horn drags back growth in the rest of the horn because of its greater mass and the impediment it imposes forces the thinner but faster growing sheath to slew round the main shaft. The details of this differential growth system and its capacity to generate several very distinctive types of spiral horns are discussed further in the genus profile (and see Kingdon 1982).

The differences among tragelaphines manifest an important evolutionary array and they provide particularly apt illustrations of the roles of climate, habitat, food distribution, body size, limb, proportions and social system in determining the peculiarity of species. One of the most interesting of these evolutionary progressions has been the transformation of a tall, Greater Kudu-like ancestral tragelaphine into the massive elands. Kingdon (1982) has discussed and illustrated a selection of these comparisons and evolutionary transformations in some detail.

The skull of tragelaphines is characterized by the absence of preorbital fossae, and the presence of an ethmoid fissure. The teeth are low crowned and, like the digestion, adapted to a ‘gleaning’ diet of young, nutritious vegetation. Glandular secretions are mostly diffuse rather than from highly specialized facial or pedal glands (although inguinal glands are present in some species, for example, Lesser Kudu *Tragelaphus imberbis*). Females have two pairs of nipples.

Jonathan Kingdon



Display of head and shoulders in *Tragelaphus* spp. Left, Greater Kudu *T. strepsiceros*; centre, Giant Eland *T. derbianus*; right, Common Eland *T. oryx*.

GENUS *Tragelaphus*

Spiral-horned Antelopes

Tragelaphus de Blainville, 1816. Bull. Sci. Soc. Philom. Paris 1816: 75.

Tragelaphus is a genus that has been split up into several genera or subgenera in the past, based on obvious differences in body size, habitat, tail-type and male–female differences such as possession or absence of horns. Thus, for example, the enormous elands have been included in the genus *Taurotragus*, the forest-dwelling Bongo in the genus *Boocercus* (and also *Taurotragus*), the long-legged, spiral-horned Greater Kudu in *Strepsicerus* and the swamp-dwelling Sitatunga in *Limnocercus*. Several, possibly all species are capable of hybridizing (Boulineau 1933, Jorge *et al.* 1976, Van Gelder 1977a) and producing viable offspring, and molecular studies support keeping all living tragelaphines in the single genus *Tragelaphus* (e.g. Georgiadis *et al.* 1990, Essop *et al.* 1997, Gatesy *et al.* 1997, Hassanin & Douzery 1999, Matthee & Robinson 1999a; and see Hassanin *et al.* 2012), the course that is adopted here.

Thanks to the molecular studies of Willows-Munro *et al.* (2005), the extant members of the genus *Tragelaphus* can now be placed within a single tree with unusually clear lines of descent and plausible dates for divergences between all species. Furthermore, some fossil tragelaphines can also be located, very approximately, within this tree, in spite of known extinctions of prehistoric species.

The entire genus derives from a single ancestor that arrived in Africa between 18 and 14.5 mya. *Tragelaphus* is unknown outside Afro-Arabia and there is abundant evidence to suggest that the modern genus emerged in Africa from an incoming Asiatic boselaphine ancestor (Gentry 1978). That boselaphines gave rise to a parallel lineage in India is supported by the discovery of a Pliocene Indian species, *Selenoportax vexillarius*, which has mixed boselaphine and tragelaphine-like features (Gentry & Gentry 1978).

In the middle Miocene (14 mya) at Fort Ternan, in W Kenya, there are fossils of a medium-sized boselaphine, *Protragoceras labidotus*, which Gentry (1978) has identified as close to the root stock of all tragelaphines. The date of this fossil puts it very close to the first arrival of the putative ancestor of all *Tragelaphus* species. It had a horn structure that provides vital clues to the growth mechanisms that control the diverse spirals typical of all *Tragelaphus* species (Kingdon 1982). Not only does *P. labidotus* serve as a very close approximation to the immediate precursor to the genus *Tragelaphus* in its size and proportions, its ecological context is also of direct relevance in interpreting the tragelaphine radiation.

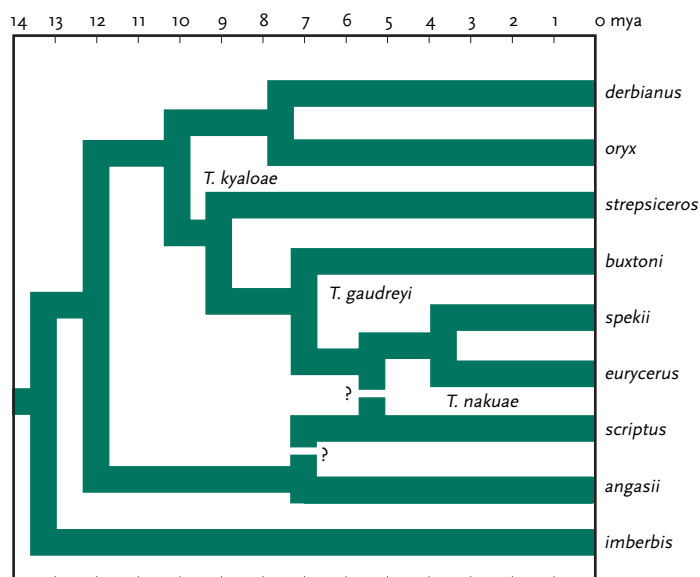
The mosaic of environments represented at Fort Ternan is thought to have included dry, dense woodland types and semi-deciduous thickets (Bromage & Schrenk 1999). These closed, but relatively dry habitats have a very restricted distribution today but were much more extensive in the past, particularly on the eastern side of Africa (C. Jackson & F. White pers. comm.). It is significant, therefore, that the two *Tragelaphus* species with the oldest pedigrees both inhabit thicket country in north-east and south-east Africa. According to the molecular analysis of Willows-Munro *et al.* (2005), the Lesser Kudu *T. imberbis* is the most conservative species in the genus. Its earliest branching as an identifiable lineage has been calculated, by Bayesian molecular clock, as being in excess of 12 mya. When the skull of this species is compared with that of *P. labidotus* there are striking similarities, both in the long face, tooth structure and cranium. A



Sitatunga *Tragelaphus speki* male head frontal view.

detailed reconstruction of *P. labidotus* (Turner & Anton 2004) suggests a long, slender neck, like the Lesser Kudu, but shorter, more stocky legs. The one respect in which they are emphatically different is in the structure of their horns, the details of which will be discussed shortly.

The limb and neck proportions of the Lesser Kudu differ from those of its closest affine, the Nyala *T. angasii*. The latter is stockier, and has a shorter neck and shorter legs, but is otherwise of similar size and habits. The colouring and body markings of immature Nyala ♂♂ are almost identical to those of Lesser Kudu ♂♂, but the horns are loose, open lyres compared with the tighter spirals of the Lesser Kudu. The two species show a mosaic of similarities and differences and this is typical of *Tragelaphus*. While most species exhibit distinct ecological preferences, the *imberbis*–*angasii* pair have a broad ecological equivalence in spite of living in different hemispheres. It is possible that the north/south divide could reflect an attachment, by the more conservative of the two, to the region of earliest adaptation, whereas the Nyala, further from the tragelaphines' north-east African 'homeland', represents a later isolate of the same basal stock. In the light of their genetic pedigrees, both species can be regarded as

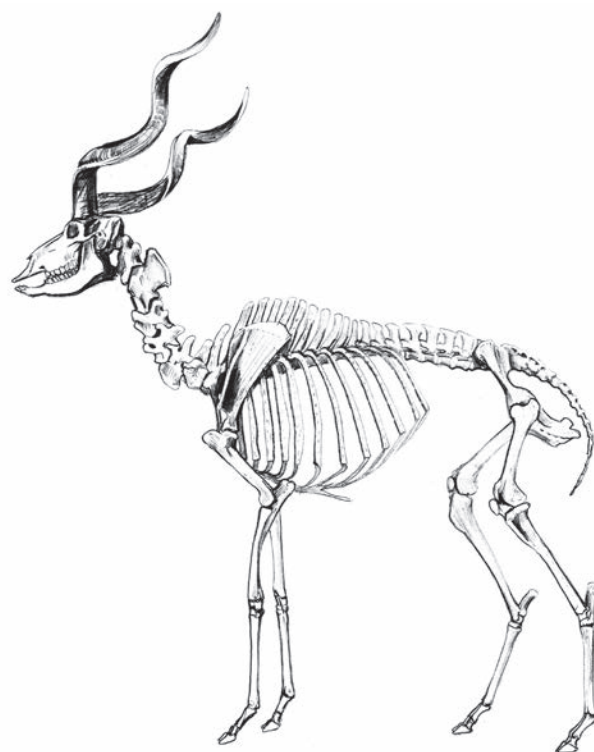


Tentative phylogenetic tree of tragelaphine radiation (in part after Willows-Munro *et al.* 2005 and Hassanin *et al.* 2012). Note that SE and centre-west *Tragelaphus scriptus* might have separate or genetically mixed origins.

little-changed representatives of basal *Tragelaphus*: marginally altered 'living fossils'.

In the discussion that follows, the phylogenetic tree and estimated dates of Willows-Munro *et al.* (2005) are used as the format for an ecological and biogeographic interpretation of the subsequent radiation of *Tragelaphus*. Unlike some students of antelope evolution, I do not look only to global climate changes to explain branchings within trees or morphological innovations, but rather seek intra-continental geographic separations between established populations that, at the grossest level of generalization, might have isolated populations at high or low latitudes, high or low altitudes, north/south, east/west, or some such equivalent. For example, ever since the Oligocene, habitats surrounding the Sahara have been consistently drier and more open whereas more equatorial and south-easterly habitats have tended to be warmer, wetter and less open. Over long periods of time, each wing of an originally common *Tragelaphus* population would have adapted to some dominant features of their habitat. If climate changes subsequently favoured one or other population, it may well have expanded its range, while the other retreated. Yet another climate change and the trend could be reversed. Notwithstanding such expansions and contractions each population was likely to have continued to flourish best and be most numerous at the heart of its earlier 'homeland'. This may help explain why archaeo-tragelaphines such as the Lesser Kudu and Nyala have survived so long with apparent minimal change. Thus, the tragelaphine preference for rather dry woodlands has persisted from their earliest beginnings right up to the present while their expansion into wetter types of closed forest or swamp, or to very open habitats, was more recent. The pattern of moving from drier to wetter and more equatorial regions is an evolutionary trend that is discussed in more general terms elsewhere (Volume I, pp. 51 & 84).

The first major split in *Tragelaphus* began, about 10 mya, between a lineage that maintained a preference for more closed habitats and one that shifted into more open woodlands. Animals in more exposed environments have to become more mobile and increased exposure



Greater Kudu *Tragelaphus strepsiceros* skeleton.

to predation favours an increase in both body size and group size as well as horns on ♀♀. The open woodland lineage has culminated in the two eland species and it is significant that the more conservative eland species, the Giant Eland *T. derbianus*, still occupies the dry woodlands immediately south of the Sahara. Of this 10-million-year-old bifurcation the more conservative branch is today exemplified by the Greater Kudu *T. strepsiceros*, which has an emphatically southern, closed-habitat distribution. It is therefore plausible that the primary divide between ancestral elands and ancestral Greater Kudu was a north-south one. Like the elands, Greater Kudu have reached gigantic proportions in the past but it is likely that the size of the Greater Kudu (as with other tragelaphines) may well be relatively labile, with gigantism being a response to periods of unusually favourable conditions when dietary, competitive or other constraints were temporarily lifted. None the less, Greater Kudu live up to their name and have remained among the largest bovines and have probably always depended on dense cover and prodigious jumps to make effective getaways from large predators.

A wide north-south divide, possibly linked with initial differences in temperature-tolerance, body size and behaviour, may have a bearing on the next phylogenetic divergence, which took place at about 9 mya within a very early population of the *T. strepsiceros* lineage. This offshoot might have begun as the northern wing of a predominantly southern stock, but its primary innovation was to become the first *Tragelaphus* species that was a true ecological 'generalist', not the thicket specialist that so many of its precursors had been. Judging from their living descendants, previous *Tragelaphus* lineages had retained an attachment to dense, dry woodlands (or, in the case of elands, evolved a 'giant' strategy to move into more open habitats). This new lineage retained its dependence on dense vegetation for refuge, but could survive in a very broad spectrum of habitats including open/



Sitatunga *Tragelaphus spekii*.

closed mosaics at a variety of altitudes and latitudes. Its success was based on a broad climatic tolerance, together with early maturity, exceptional fecundity, and cohesive social groups (which we can extrapolate were based on small numbers of closely related ♀♀). This was the lineage that ultimately gave rise to all the remaining *Tragelaphus* species and its relictual survivor is the Mountain Nyala or Gedemsa *T. buxtoni* (which is threatened by the near-indifference of current authorities to the conservation of Ethiopia's unique fauna and flora). This species shows many resemblances with a Pliocene fossil from North Africa, *T. gaudreyi*, which may represent a 'chronospecies' belonging to the same lineage. There are more dispersed fossils that are consistent with a very wide distribution of this lineage during the Mio-Pliocene. In the late Miocene, when the *buxtoni*–*gaudreyi* lineage first emerged, most antelope lineages were still at an early stage of their radiation and ancestral buffalo had yet to arrive. Some of the most lethal predators were also absent, so a combination of less predation and less competition could have facilitated a wide spread of the *buxtoni*–*gaudreyi* lineage through many habitats. Contemporary restriction of the sole survivor of this lineage to cold uplands in S Ethiopia is less the mark of a super-specialist than a measure of the breadth of its one-time adaptive range. This history must qualify the justifiable description of the living species as a 'montane specialist'. Like the Lesser Kudu and Nyala, it is a living fossil, a magnificent has-been, left over from a long career as one of the more splendid and widespread of Africa's Mio-Pliocene bovids.

However, as competition and predation increased, decline of the Mountain Nyala lineage must have been linked with such disadvantages as large body size, the need for a rich diet, very limited stamina and a rather rudimentary form of social coherence. Under these circumstances there probably has been selection for smaller, more agile animals that were better able to escape or conceal themselves. Possible descendants of this type of selection are the many, fragmented, but hugely successful populations of the Bushbuck *T. scriptus*. Bushbucks could be descended from the *T. buxtoni* lineage or, much earlier, from *T. angasii*.

Among the many habitats that the Mountain Nyala lineage moved into was the equatorial rainforest and it was here that pressure from predators and a scarcity of low-level palatable herbage selected for two very different types of 'forest tragelaphine'. Rivers and swamps lace all African forests and, for any large herbivore, represent a very effective refuge from predators because they are heavily obstructed

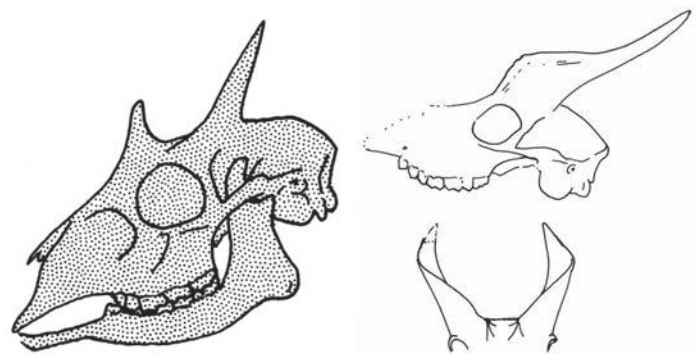
and full of impediments for a carnivore: notably water and mud. For a variety of reasons, swampy areas also tend to offer more browse than is available under a closed forest canopy. It is very likely that the ancestors of Sitatungas *T. spekii* were animals that initially used swamp-forest as a refuge, then adopted it as a habitat and finally became swamp specialists both within and outside the forest belt.

Swamp forest can be characterized as the bottom end of the forest catena: the 'top' or outer end can be taken as the forest edge and because African forests are in a constant state of flux and fragmentation, edges are very numerous, particularly along the outer, northern margins, but also within the forest wherever clearings or tree-fall chablis have formed. Along these forest margins the main resource, for a large browser, is low-level herbaceous, vine, young tree and shrub growth, all of which need sun. Because every gap is soon filled and the forest edge is forever advancing or retreating, large browsers need to be very mobile and cover a lot of territory, some of which is poorly known. Under these circumstances largish group sizes and horned ♀♀ provide some deterrence to predators. In these respects, a large forest browser faces similar challenges to those facing proto-elands in drier, more open woodlands.

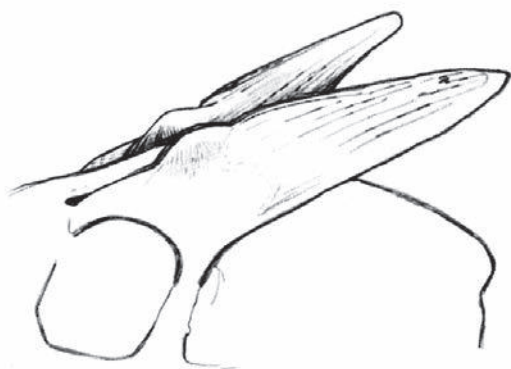
In adapting to the specifics of this habitat the ancestors of Bongos *T. eurycerus* have paralleled the elands in some respects, such as ♀♀ developing horns, but they have modified the proportions of their legs and horns in ways that are typical of other forest-dwelling herbivores. Like forest Bushbucks, Nyalas and Sitatungas, the female Bongos are bright red with stripes and even ♂♂ have predominantly red colouring.

Differences in *Tragelaphus* horn shape have long confounded taxonomists who wanted to use this as a diagnostic feature. In fact, horn shapes vary enormously within species and many throw up aberrant twists and splays whose ontogeny helps reveal why the spirals of these 'spiral-horned bovids' can respond so readily to selection.

To return to *Protragocerus labidotus*, the putative boselaphine ancestor of all *Tragelaphus* species. This species had short 'bladed' horn cores that twisted into the beginnings of an incomplete spiral. Paired blades or keels arose on the top of the horn cores, near the crown, swept up and back before turning in again. A second, less distinct keel began at the back of the horn, just behind the eye socket and its traverse, upwards and inwards, was much less marked. Another African boselaphine, probably a descendant of *Protragoceros*, *Mesembriportax acrae*, had such prominent anterior 'keels' that Gentry



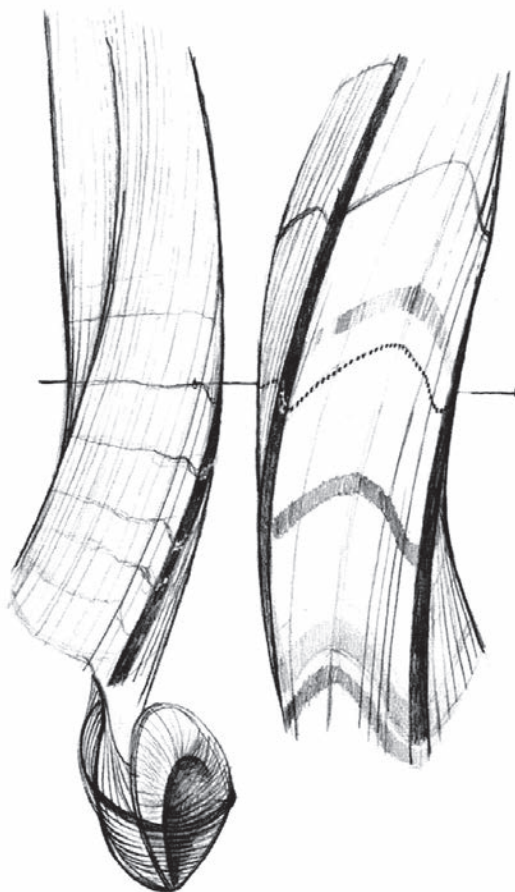
Outline of *Tetracerus* skull indicating positions of four horns (left), compared with outlines of skull of Early tragelaphine, *Protragocerus labidotus* with bladed horns (right).



Bongo *Tragelaphus eurycerus* horn cores in subadult male showing eminence on horn core (vestigial trace of 'branched' horn).

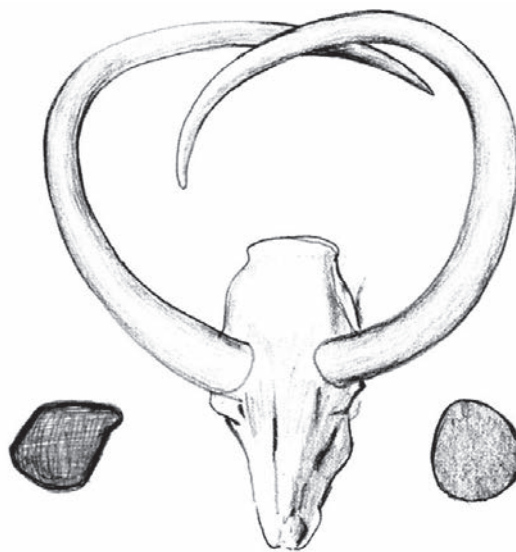
(1978) suggested that the horn sheaths might even have bifurcated at their tips, like the American Pronghorn *Antilocapra americana*.

Young male *Tragelaphus* show the rudiments of these boselaphine 'keels' or anterior horn 'blades'. One takes the form of a small, elongated bony excrescence or bud on the newly grown horn shaft and it is situated on the crown, just above the eye. The other, as in *Protragocerus*, is little more than an angled edge under the horn shaft and behind the eye. But for their vestigial excrescences, the sheaths of newly sprouting *Tragelaphus* horns would approximate to a symmetrical cone of bone sheathed in keratinous 'horn'. The bony core would grow like a straight, pointed wand, were it not for its straitjacket of keratinous horn. Were the keratin laid down as evenly and consistently



Bongo *Tragelaphus eurycerus* growth rings on spiralling horns.

around the bony core, as is the case in *Oryx* and *Pelea*, tragelaphine horns would be just as straight. Instead, young, fast-growing tragelaphine horns almost immediately begin to be deflected from any such trajectory and the main cause of that deflection is a slower rate of horn growth at the two keels (where thicker layers of horny keratin are laid down). The traverse and shape of *Tragelaphus* horns is therefore mainly the product of an interaction between an approximately 'would-be straight' bony shaft and its enclosing horny sheath. It is the latter that pulls the malleable core into a spiral because the rate of sheath-growth around the shaft is as consistently uneven as calcium deposition around a soft-bodied mollusc or spiral-shelled snail (Wentworth Thomson 1942). However, the horn cores of most tragelaphines do not have perfectly symmetrical, circular cross-sections, and this is probably because such primitive symmetry was already compromised in ancestral, boselaphine cores, with their flat-edged keels. Thus, some species tend to combine a rounded section with a slower growing section that is flatter. There seem to be no obvious phylogenetic implications here, thus the conservative Nyala and more derived Bushbuck, Sitatunga and Bongo all have bladed spirals. In other species, the flat section between the two keels disappears because the lower keel is suppressed to a greater or lesser degree. When this happens the horn acquires a more rounded section and it is the single upper keratinous ridge that pulls the horn into a corkscrewing spiral. This type of horn is shared by Lesser and Greater Kudus, both eland species and the Mountain Nyala.



Aberrant Greater Kudu *Tragelaphus strepsiceros* with cylindrical cross-section to non-spiral horns (right). Normal cross-section shown on left.

That the very few determinants of horn shape (more or less material accreting at upper or lower keel, or around the core, thicker or thinner shaft, rounder or less symmetrical cross-section) are each subject to continuous variation is evident in the existence of much individual variation. Natural selection for a particular conformation therefore operates with a rather small number of genetic permutations and much natural variation. This may help explain why change can be rapid and relatively close relatives need not have very similar horns. For further discussion of this topic see Kingdom (1982).

Tragelaphus imberbis LESSER KUDU

Fr. Petit Koudou; Ger. Kleiner Kudu (Kleinkudu)

Tragelaphus imberbis (Blyth, 1869). Proc. Zool. Soc. Lond. 1869: 55. 'Abyssinia'; now known to be Ethiopia, Shoa Prov.



Lesser Kudu *Tragelaphus imberbis*.

Taxonomy Two subspecies have been named, but distinctive characteristics and geographical separation between the two forms are unclear (Ansell 1972). Synonyms: *tendal*. Chromosome number: $2n = 38$; the karyotype is unusual in that X and Y chromosomes are each fused with one of two identical autosomes (similar to situations in other *Tragelaphus* spp.; Benirschke *et al.* 1980).

Description Medium-sized antelope with 10–14 vertical white stripes on the sides. Neck with two white patches, one just below throat, one at the base; there are several small white spots, mainly on the hindquarters. Face fairly dark, with two oblong white spots in front of the eyes and two small white spots on each cheek. Muzzle is blackish with white sides; chin white. Ears are large and rounded.

There are contrasting dark patches on the inside of the legs above the 'knees'. Tail is bushy, white underneath, with black tip. Stripe pattern and throat patches vary individually to some extent. Back horizontal, in contrast to some relatives (e.g. Bushbuck *Tragelaphus scriptus*). There is one pair of inguinal glands; there are diffuse scent glands around the false hooves on the hindfeet (Pocock 1918). There is pronounced sexual dimorphism: the ♂ is considerably larger, with a much thicker neck, darker in colour, and more purplish-grey; the ♀ is a rich rufous-brown, more greyish on the neck. There is a dorsal crest of hair along the neck and entire back of ♂♂, most pronounced over the shoulders; in ♀♀, this crest is much less developed. In contrast to the Greater Kudu *T. strepsiceros*, there is no mane of hair on the underside of the neck (cf. 'imberbis' = beardless). Females have two pairs of inguinal nipples.



Lesser Kudu *Tragelaphus imberbis* myology.

Horns present in ♂♂ only, dark brown with whitish tips, spiralled, but more narrowly and with smaller spread than in the Greater Kudu.

Geographic Variation

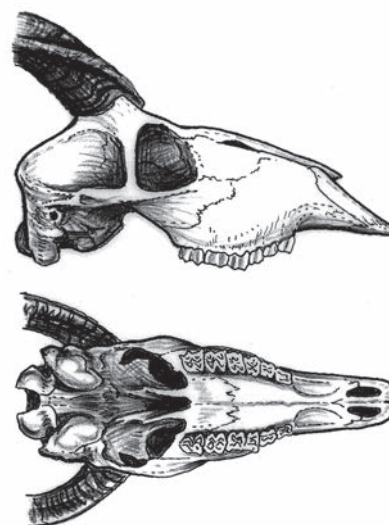
T. i. imberbis (including *tendal*): Ethiopia and Somalia (and probably also Sudan and Uganda).

T. i. australis: Kenya and Tanzania.

Similar Species

Tragelaphus strepsiceros. Geographic range much larger, with 'centre of gravity' in southern Africa, rather fragmented in East and central Africa. Sympatric with the Lesser Kudu in large parts of the latter species' range. Adult ♂ considerably larger, with longer and more widely spread horns and dense fringe of hair along underside of neck; young ♂ and ♀ larger, general colour more greyish, vertical stripes less distinct, more widely spaced, fewer in number. Legs slightly longer in relation to body. Female with more pronounced shoulder hump and dorsal hair fringe. No white patch at base of neck, only on throat, but less distinct.

Distribution The Lesser Kudu is largely confined to the Somalia–Masai Bushland BZ or the 'Horn of Africa'. Historically, this species ranged from ca. 12°N in the Awash area of Ethiopia southward through S and E Ethiopia, much of Somalia except the north and north-east (i.e. east of 46°E and north of 08°N), most of Kenya except the south-west, extreme SE Sudan, NE and E Uganda, to NE and C Tanzania (Leuthold, W. 1979, East 1999). The southern limit lies in or near Ruaha N. P. in Tanzania (Leuthold 1979a), at ca. 08° 30'S, and they are also recorded from the woodland zone of the Udzungwa Mts (Rovero & De Luca 2007). Its former occurrence in N Eritrea has also been reported, but is not confirmed. The exact limits of distribution are not well known, partly perhaps because of occasional confusion with the Greater Kudu, with which it shares much of its range.



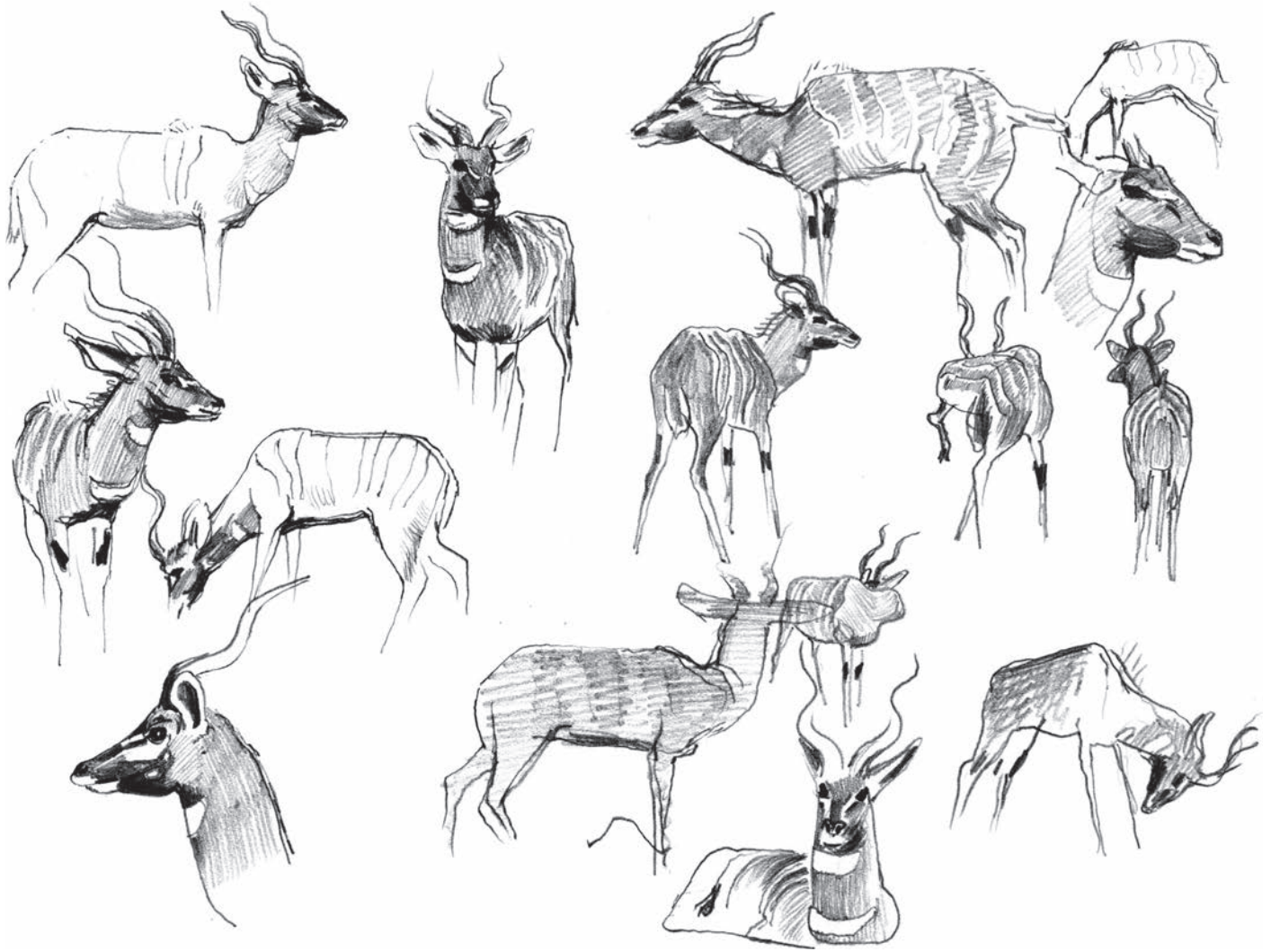
Lateral, and palatal views of skull of Lesser Kudu *Tragelaphus imberbis*.



Tragelaphus imberbis

Within recent history the range has probably not changed much, except locally. In Djibouti, where the Lesser Kudu may have occurred formerly in the south-west, its presence has not been confirmed recently (Künzel *et al.* 2000, Laurent & Laurent 2002, Heckel & Rayaleh 2008). In Somalia, numbers have probably decreased since the 1980s, and there is no information that it survives in the central or north-western parts, though it apparently still occurs widely in the south (East 1999). In Sudan, Fay *et al.* (2007) confirmed its continued presence in the southern section of Boma N. P. In Uganda, it probably now only survives in the eastern part of South Karamoja Controlled Hunting Areas (East 1999).

The purported former occurrence of this species in the Arabian Peninsula is based on a single set of horns obtained in 1967 from an animal reputedly shot in Jabal Halmayn, south-east of Dhala, in S Yemen, and another specimen shot at Nuqrah in Saudi Arabia around



Lesser Kudu *Tragelaphus imberbis*.

1968 (Büttiker 1982, Harrison & Bates 1991). No live animals have ever been reported from the area, and the true origin of those specimens remains in doubt though they probably originated from animals that escaped from private collections.

Habitat The Lesser Kudu inhabits semi-arid areas with medium to dense woody cover, including riverine forest and thickets; it generally avoids open spaces and long grass (cf. Fig. 9 in Lamprey 1963). In its geographic range, this means mainly *Acacia-Commiphora* woodlands and vegetation derived from these, in areas characterized by low and erratic rainfall and long dry seasons. Largely confined to lowland areas up to ca. 1200 m (Stewart & Stewart 1963), the animals do occasionally climb hills, for example, in search of specific food sources. Recorded up to 1600 m in Ethiopia (Yalden *et al.* 1996), and observed on farmland near Ol Molog at about 1740 m near Mt Kilimanjaro (Grimshaw *et al.* 1995). Small-scale seasonal movements related to changes in vegetation condition and availability may result in some concentration of the animals near rivers in the dry season, probably more on account of the vegetation there than the water (Leuthold, W. 1979). Availability of free water does not appear to be essential.

Abundance Because of its habitat preferences, its cryptic behaviour and a somewhat clumped distribution the Lesser Kudu is very difficult

to census, both from the ground and from the air. Available estimates of density and/or total numbers are therefore difficult to evaluate.

Ground counts in Tarangire N. P., Tanzania (Lamprey 1964), and Tsavo East N. P., Kenya, produced density estimates of 0.2–0.3 animals/km², with maximum values of ca. 1/km² in the most favourable habitat (Leuthold & Leuthold 1976). Figures from other areas generally fall within the same range, but East (1999) mentions local densities of 0.5–3 animals/km². Extrapolating from these values, and using a correction factor for undercounting, East (1999) derived a total population estimate of ca. 118,000 animals for the entire range of the Lesser Kudu.

Adaptations The Lesser Kudu shows few specific adaptations to its habitat and way of life. Being rather slender, the animals move easily through dense bush. In situations of possible danger the animals 'freeze', sometimes keeping a foreleg lifted in mid-air, while fixing the source of alarm. This behaviour enhances the cryptic effect of the vertical stripes in dense bush. The camouflage is most effective in the dry season, when the entire vegetation has a drab greyish-brown aspect. Upon being seriously alarmed, they often utter a loud bark, which may be important as a signal to conspecifics, as may be the curling of the tail while running. This exposes the white 'brush' on the underside that serves as a visual signal. Like Greater Kudus, they are accomplished jumpers.

Because of its closed habitat, activity patterns of the Lesser Kudu are difficult to study: data are limited to some incidental observations by Leuthold, W. (1979) and a very brief study by Mitchell (1977) in Tsavo East N.P., during daylight hours only. Overall, foraging takes up about 35% of the animals' time, being concentrated somewhat in early morning and late afternoon. Resting, with or without ruminating, is most pronounced during the middle of the day, when the animals often move into the shade. Activity patterns on single days vary considerably, but tend to show an alternation between feeding and ruminating bouts, as in other ruminants (Leuthold 1977).

The choice of food, including leaves of succulent plants and some fruits, also constitutes an adaptation to the dry environment in that it renders the animals largely independent of free water. Size and structure of the stomach also reflect the strong preponderance of browse in the food (Hofmann & Stewart 1972). In particular, the relatively small rumen, the large reticulum and small omasum characterize the Lesser Kudu as a 'tree and shrub foliage eater' consuming food with a high fermentation rate and quick passage through the digestive system (Hofmann 1973).

Foraging and Food The Lesser Kudu is primarily a browser (Hofmann & Stewart 1972, Cerling *et al.* 2003), consuming mainly leaves of trees, shrubs and herbs. Flowers and fruits may also be taken when available. Grasses are eaten only in small quantities and in early growth stages, i.e. mainly in the wet season. The range of food plants is very broad: 118 species were identified in Tsavo N. P. (Leuthold, W. 1979). A few additional species were found in the stomach contents of animals from other parts of Kenya (Hofmann 1973).

There are considerable seasonal and local variations in the composition of diet. Local variations reflect the composition of the vegetation and thus differential availability of plant species. Seasonal variations reflect vegetation condition, which depends mainly on rainfall. Leaves of trees and shrubs make up 60–80% of the food at all times. The leaves of creepers and vines (e.g. *Thunbergia guerkeana*, some species of Cucurbitaceae and Convolvulaceae) and herbs constitute 15–25% during the wet season, but become insignificant as they dry up. Fruits of various trees and shrubs are eaten mainly in the dry season, which may reflect their availability, but may also be related to their water content.

Within the category of trees and shrubs the species composition also changes considerably between seasons. The most important wet-season food plants include mainly deciduous species, whereas in the dry season some evergreen shrubs predominate (Table 5 in Leuthold, W. 1979). The latter do not seem to be preferred, if there is more choice, but some of them are important as dry-season staples (e.g. *Salvadora persica*, *Thylachium thomasii* and *Boscia coriacea*). As these evergreen species are also eaten by other browsers, particularly Gerenuk *Litocranius walleri* and Giraffe *Giraffa camelopardalis*, there is considerable potential for competition in the dry season (Leuthold, B. 1978b). Selectivity with respect to plant parts can be inferred from the animals' searching behaviour: they 'sniff over' a potential food plant extensively before taking a bite.

Olfactory searching is also employed to find fallen fruits under trees (e.g. *Melia volkensii*). These resemble unripe walnuts in size and shape and are chewed at some length, the large seeds generally being dropped. Fruits of *Acacia tortilis* and some other species are also picked up from the ground; the searching behaviour could easily be mistaken



Lesser Kudu *Tragelaphus imberbis* exposing white brush on underside of tail.

for grazing (Fig. 11 in Leuthold, W. 1979). Much smaller fruits (e.g. *Commiphora* spp.) are often plucked directly from the trees.

Root tubers of *Thunbergia guerkeana*, when found by chance, appear to be highly attractive, presumably on account of their water content. Animals jockey for positions providing access to a root tuber and sometimes are overtly aggressive toward conspecifics. Also, animals may drop onto their carpal joints for better access, a behaviour not seen otherwise in the Lesser Kudu.

Very few species of trees and shrubs appear to be rejected entirely as food by the Lesser Kudu. Among these is *Platycephalum voense*, a widespread and prominent tree in Tsavo N. P. In addition, some species of *Acacia* with very small leaves are not eaten, possibly because of their thorns, the Lesser Kudu being less well equipped to cope with these than, for example, the Gerenuk or Giraffe.

By stretching head and neck upward an adult ♂ can reach up to ca. 2 m, a ♀ ca. 1.8 m. Occasionally, an animal tries to reach even higher by lifting one foreleg and/or by 'angling' with the tongue. Rising up on both hindlegs, as the Gerenuk commonly does, was never observed in the field.

Lesser Kudus do drink from open water, but rarely. In parts of their range there may be no free water for extended periods of time. Water requirements can largely be fulfilled from the water content of the food plants, particularly from succulents like *Sansevieria* spp., *Euphorbia* spp., fruits, or the root tubers referred to above.

Social and Reproductive Behaviour In Tsavo East N. P., Lesser Kudus live singly or in small groups numbering 2–6 animals, and occasionally up to ten. Larger groupings are usually temporary associations of two or more groups. Mean group size varies locally and

seasonally between 2.0 and 3.6, but the largest 'group' seen included 24 animals. Single animals are most often ♂♂, adult or subadult. The latter may also join up in small groups, whereas fully adult ♂♂ apparently do not. Single ♂♂ or male groups often associate with groups of ♀♀ and young (Leuthold & Leuthold 1975a).

Variations in the stripe pattern permit observers to recognize individual animals and thus facilitate the study of group composition and stability. 'Nuclear groups' of one to three ♀♀ and their young remain stable over fairly long periods of time (three known ♀♀ stayed together for at least four years). They may join up with other such groups and/or with ♂♂ temporarily, which accounts for the great variation in group size and composition (Leuthold, W. 1979).

Individuals or stable groups inhabit home-ranges measuring 1–6 km² and overlapping considerably between individuals, even adult ♂♂. The latter are apparently not territorial; there seems to be a hierarchy among adult ♂♂ living in the same area, which tend to avoid close contact. This explains the lack of field observations of serious agonistic encounters.

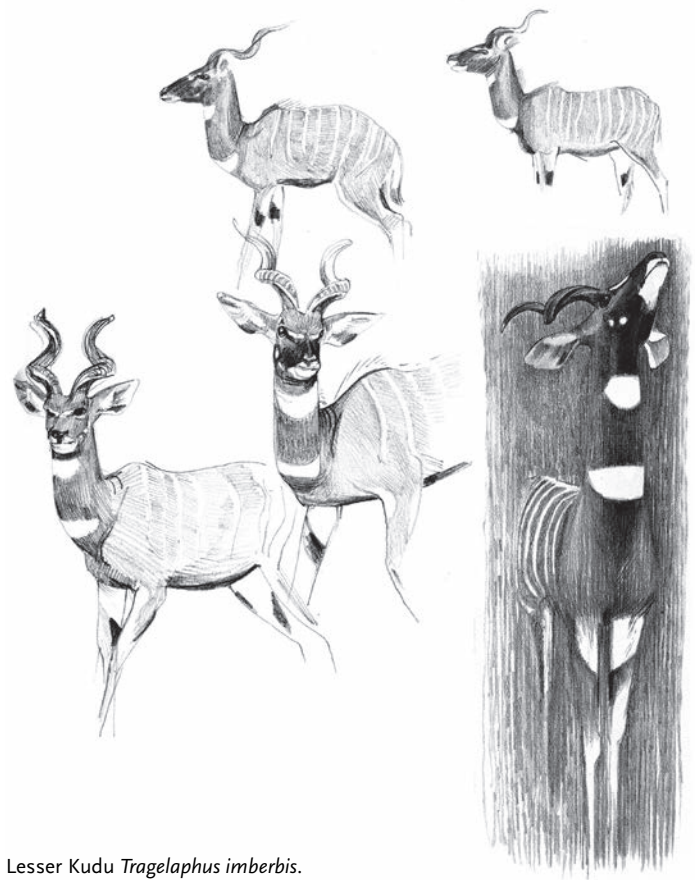
Behavioural elements seen in 'tense' situations include erecting the dorsal hair crest, stiff-legged 'determined' walking, brief rushes and actual chases of opponents. Also prominent is shrub-horning during and/or after such encounters. Actual fighting techniques, observed only among subadult ♂♂ at a toned-down level ('playfighting') are similar to those of many other bovids (for observations in captivity see Walther 1964a). The shape and structure of kudu horns entail a certain risk of their becoming inextricably interlocked, which is likely to result in the death of one or both contestants (cf. Fig. 23 in Leuthold 1977). Agonistic behaviour of ♀♀, relatively rare, involves a short rush and/or butting with the forehead against the head or side of another animal.



Lesser Kudu *Tragelaphus imberbis* courtship behaviour.

The few observations on courtship behaviour made in the field agree largely with those on captive animals (Walther 1964a). The ♂ approaches the ♀ from behind in a pronounced low-stretch posture. If the ♀ urinates, the ♂ almost invariably shows flehmen. He may then move forward alongside the female's flanks, still in low-stretch, perform gasping movements with his lips and rub his head on her sides and neck (cf. Figs 36 & 37 in Walther 1964a). This may be accompanied by low vocalizations barely audible in the field. When mounting, the ♂ rests his head and neck on the female's back, as other tragelaphines do.

A ♀ about to give birth usually separates from her group. The mother–young relationship follows the pattern typical of young bovids of the 'hiding' type (cf. Leuthold 1977). While the young animal remains behind, lying quietly, the ♀ moves off to feed. She returns periodically, mainly in the evening, to suckle the young. In this context, mother and young apparently communicate with low



Lesser Kudu *Tragelaphus imberbis*.

bleating vocalizations also heard in a young captive animal (Leuthold & Leuthold 1973). During or after suckling, the ♀ licks the young, particularly its perineal region, and may consume its urine and/or faeces. At 3–4 weeks of age the young starts to follow its mother more and more, and may then join her original group with her.

Behaviour with social and/or communicative functions, such as mutual grooming, is rarely seen in free-ranging Lesser Kudus, in contrast to captive animals (Walther 1964a). A visual signal, curling the tail upwards and spreading the white hair on its underside, is shown whenever an animal runs, regardless of context. In situations of alarm a loud bark is uttered, but barks may also serve to signal an individual's position to conspecifics (Kingdon 1982). Young animals bleat loudly when in distress. Olfactory signals do not appear to play a prominent part in communication of the Lesser Kudu.

Associations and interactions with other ungulate species are relatively rare, in some contrast to the situation in more open habitats. The Lesser Kudu is seen occasionally with Gerenuk or Impala *Aepyceros melampus*, which may both utilize the same habitat type. In two instances a Lesser Kudu and several other ungulates were aggregated under a fig tree *Ficus sycomorus* in which baboons (*Papio* sp.) were feeding and dropping fruits that were then collected by the ungulates (Leuthold, W. 1979).

Reproduction and Population Structure Lesser Kudu young may be born throughout the year, both in the wild and in captivity (Lang 1976, Leuthold, W. 1979, Váhala 1992). Individually known ♀♀ in Tsavo N. P. gave birth at intervals of 9–10 (Leuthold 1979b) months; inter-birth intervals in captivity clustered around 250–270 days (Váhala 1992). The gestation period is ca. 32–34 weeks (e.g.

Dittrich 1972), but is not well documented. Females reach sexual maturity at 1–1.5 years, ♂♂ at 1.5–2 years of age; in wild ♂♂ reproduction probably does not begin before the age of 4–5 years when they reach social maturity. Birth-weights are ca. 5–7 kg in ♂♂, slightly less in ♀♀. One young is born at a time; as an exception, twin births occurred in an American zoo in 2001 (E. W. Houston pers. comm.). The horns start growing at ca. 9 months, reach ear length and about one complete twist at 1.5 years and are fully developed at 4–5 years (cf. Fig. 27 in Leuthold, W. 1979). Little is known on life-span; some wild animals in Tsavo N. P. attained at least 8–10 years (Leuthold 1979b), captive animals 14–19 years (Váhala 1992, Weigl 2005).

Because of the problems in counting the animals accurately, data on population structure are difficult to evaluate. In Tsavo N. P., adult ♂♂ comprised ca. 10–15% of the sample, and the sex ratio among animals over one year old varied between 1 : 1 and 1 : 2. There were ca. 0.3 juveniles (<1 year) per adult ♀. Other data suggested a rather high mortality of juveniles, with ca. 50% of newborn animals dying within their first six months. It thus appears that natality may be near its potential maximum and that the population is regulated mainly through mortality.

Predators, Parasites and Diseases Adult animals probably fall prey only to the largest predators, i.e. Lions *Panthera leo*, Leopards *P. pardus*, Spotted Hyenas *Crocuta crocuta* and African Wild Dogs *Lycaon pictus*, but there are no data on quantitative aspects of predation. Young animals may also be killed by smaller predators, including large birds of prey (e.g. Martial Eagle *Polemaetus bellicosus*), and possibly baboons *Papio* spp. (Leuthold, W. 1979).

Not much is known on parasites or diseases, except that the Lesser Kudu is highly susceptible to rinderpest (e.g. Stewart & Stewart 1963). Considerable mortality has occurred repeatedly during periodic outbreaks of this disease, most recently in and near Tsavo N. P. in 1994/95 (Kock 1997, East 1999, S. Kasiki pers. comm.). Cleaveland *et al.* (2005) reported infection of bovine tuberculosis, caused by *Mycobacterium bovis* from one Lesser Kudu killed by sport hunters adjacent to Tarangire N. P.

Conservation IUCN Category: Near Threatened. CITES: not listed.

The semi-arid nature of the Lesser Kudu's habitat precludes intensive utilization of the land by man for agricultural purposes. However, pastoralism and other forms of land use, for example collection of firewood, have increased in recent years and this trend is likely to continue with expanding human populations. Political unrest and wars have been prevalent in much of the species' range, which has a three-fold effect. (1) The number of firearms available and thus illegal hunting pressure (meat hunting and/or trophy hunting for skins or horns) may increase; Funaioli & Simonetta (1966) mention up to 20,000 skins having been sold in a single year in Somalia, with an average of 11,000 per year between 1952 and 1963, almost all as a result of poaching. (2) Supervision of the areas concerned, even protected ones, and law enforcement become more difficult and may cease entirely for certain periods of time. (3) All this also makes it more difficult to conduct surveys and to obtain reliable information on the status of wildlife.

The Lesser Kudu is reported to be fairly common outside protected areas in Ethiopia and Somalia, even though its numbers have probably decreased markedly in recent years (M. J. Jacobs & C. A. Schloeder

pers. comm., T. L. Thurow pers. comm., F. Wilhelmi pers. comm.). On the other hand, considerable areas within the species' range are under some kind of legal protection, such as Ruaha N. P. and surrounding game reserves, Tarangire N. P. and Mkomazi G. R. (Tanzania), Tsavo and Meru National Parks (Kenya), Awash, Omo and Mago National Parks (Ethiopia) and Bushbush N. P. (Somalia), in addition to a number of Game Reserves. East (1999) estimates that roughly one-third of the Lesser Kudu populations occur in protected areas.

Overall, the Lesser Kudu is not immediately threatened, but its numbers are likely to decrease further, while its range will become more and more fragmented. Measures to be taken include ensuring the integrity of protected areas, adequate law enforcement elsewhere, and possibly efforts to contain rinderpest.

Measurements

Tragelaphus imberbis

HB (♂♂): 1600–1750 mm*

HB (♀♀): 1100–1300 mm

T (♂♂): 300–400 mm

T (♀♀): 250–300 mm

Sh. ht (♂♂): 1000–1100 mm*

Sh. ht (♀♀): 900–1000 mm*

WT (♂♂): 95–105 kg

WT (♀♀): 80–95 kg

Throughout geographic range (Haltenorth & Diller 1980, *Kingdon 1997)

Ledger (1964) recorded average weight for 10 ♂♂ from Tsavo N. P. at 92.1 kg (range 56–108), though this probably included some subadult ♂♂

Record horn length is 83.5 cm for a pair of horns from the Omo Valley, Ethiopia (Rowland Ward)

Key References Lamprey 1963, 1964; Leuthold, W. 1977, 1979; Walther 1964a.

Walter Leuthold

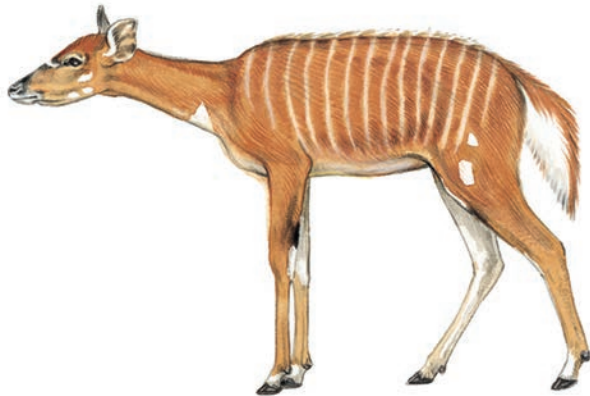


Lesser Kudu *Tragelaphus imberbis*.

Tragelaphus angasii NYALA

Fr. Nyala; Ger. Tiefland-Nyala

Tragelaphus angasii Angas, 1849. Proc. Zool. Soc. Lond. 1848: 89 [1849]. South Africa, KwaZulu–Natal, ‘Hills that border upon the northern shores of St. Lucia Bay, in the Zulu country, lat. 28° south’. [Attribution to Angas, 1849, and not Gray, follows Grubb 2004, 2005].



TOP: Adult male Nyala *Tragelaphus angasii*; MIDDLE: Adult female Nyala *Tragelaphus angasii*; BOTTOM: Subadult Nyala *Tragelaphus angasii*.

Taxonomy There are no recognized subspecies. Genetic variation, on the basis of microsatellite, mitochondrial control region and allozyme markers, occurs between the Malawi, Mozambique and KwaZulu–Natal populations and it is postulated that this geographic variation is a function of a distribution pattern stemming from habitat specificity (Grobler *et al.* 2005). Synonyms: none. Chromosome number: $2n = 55$ for ♂ and $2n = 56$ for ♀ (Wurster & Benirschke 1968, Wallace 1980).

Description No other antelope shows such extreme sexual dimorphism as the Nyala, with adult ♂♂ almost twice the size of ♀♀ (Anderson 1976). Females, and young of both sexes, are russet brown, with up to 18 vertical white stripes running from shoulders to hindquarters. At one year of age general coat colour of ♂♂ is still same as ♀♀, but hair on neck has darkened while that on throat, sides of belly and dorsal ridge has grown noticeably longer than in ♀♀. Change in coat colour and length occurs rapidly between 14 and 16 months of age, the age at which spermatogenesis begins. This is accompanied by rapid increases in testis weight and seminiferous tubule diameter. Adult ♂♂ are predominantly charcoal grey; lower legs remain russet brown, stripes and spots are retained and animals develop a white chevron on top of the muzzle. Up to three white spots on the cheeks and white spots on the upper hindleg. Bases of backs of ears white. Dorsal crest of long hair (dark on neck), and a heavy fringe of long hair (slightly darker than hair on body) on underparts of the neck to the belly. Long hair on tail dark, but underside white; this is very obvious in the male dominance ritual. In older individuals the stripes are reduced to three or four, or are absent entirely. Very rarely adult ♂♂ occur that have retained their juvenile pelage (those that have been examined exhibited either cryptorchidism or had undeveloped testes). Adult ♀♀ may or may not have a white chevron present between the eyes, also have a dorsal crest (though they lack the fringe of hairs on the throat and belly) and the lower parts of the legs do not contrast with the overall body colouration as is the case in ♂♂. Both sexes have glands at the base of the false hooves, but inguinal and preorbital glands are absent. Females have two pairs of inguinal nipples.

Aberrant-coloured Nyalas have been recorded. Dixon (1964) reported a ♂ from Mkuzi G. R., KwaZulu–Natal, which was pale beige in colour, and Lobão Tello & Van Gelder (1975) recorded a pale yellowish-coloured ♀ and a palomino-coloured ♂ from Zinave N. P. in Mozambique.

Only ♂♂ have horns, which are keeled and grow in a shallow spiral. Horns first develop between five and six months (Anderson 1986). In adult ♂♂ the tips of the horns are whitish partly as a result of the frequent ‘horning’ of moist earth when animals visit a waterhole. Age determination is discussed by Anderson (1986): adult dentition is attained at two years by which time the horns are half-grown (reaching mature size at 4.5 years).



Tragelaphus angasii

Geographic Variation None recorded, but see Taxonomy.

Similar Species

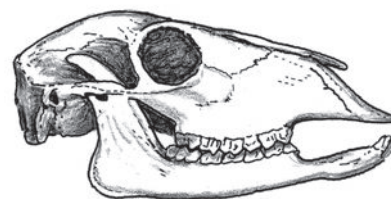
Tragelaphus spekii. Not sympatric. Similar in body size, but less strikingly marked and has typically elongated hooves as an adaptation to its swamp habitat. The male's horns are very similar in size and shape to those of the Nyala.

T. scriptus. Sympatric throughout the range of the Nyala. Smaller, and without long hair on the underside of adult ♂♂; comparatively straighter and shorter horns and more dependent on closed habitats and a dicotyledonous diet. A similar though less pronounced sexually dimorphic colour change is shown, particularly in the southern subspecies *T. s. sylvaticus*.

Distribution Endemic to Africa. Inhabits dense thickets and open thicket woodland mosaics in Malawi, Mozambique, Zimbabwe, South Africa and Swaziland.

Historical Distribution Originally confined to the hot, low-altitude areas of south-eastern Africa, below the 18° isotherm. North of the Zambezi R., found only in the Lower Shire valley in Malawi (Sidney 1965, Ansell 1981). South of the Zambezi R., Nyalas were widespread in Mozambique and occurred as far south as the Hluhluwe R. (about 28° 20'S) in KwaZulu–Natal, South Africa. In Zimbabwe, NE South Africa (KwaZulu–Natal) and NE Swaziland they were found in scattered pockets in suitable habitats, mainly along the major river valleys. In South Africa, Rautenbach (1982) remarks that Nyala occurred naturally as far west as Ellisras in what is now Limpopo Province. Nyalas suffered severe mortality during the 1895/96 rinderpest epizootic and this may account for the discontinuous distribution and low numbers encountered at the end of the nineteenth century (Selous 1909).

Current Distribution Currently more widespread, because since the early 1960s animals have been translocated from game reserves in



Lateral view of skull of Nyala *Tragelaphus angasii*.

KwaZulu–Natal to other protected areas and private ranches in areas both within and outside of their former distribution range (including even the farming districts in N Namibia). Where habitats are suitable and the areas selected do not experience cold wet winters, the species has adapted well to artificial dispersion. Animals from NW South Africa have spread into neighbouring parts of Botswana, such as the Tuli Block.

Habitat Thicket and forest are essential habitat requirements for Nyalas. They use these when resting during the heat of the day and seek shelter in them during cold and inclement weather. When alarmed, Nyalas always escape to the nearest cover. At least 10% of the home-ranges of animals studied in Hluhluwe G. R. consisted of forest (Anderson 1976) and, in Mozambique, Lobão Tello & Van Gelder (1975) showed that in one year 90% of Nyalas observed were in association with thickets. They frequent both flat and hilly landscapes, naturally occurring up to an altitude of about 400 m, and, although it is not essential, prefer to be in the vicinity of permanent water. At night, Nyalas use open habitats more readily than in daylight, but they are seldom far from cover. In the dry season they regularly use the river flood-plains in Ndumo G. R. in KwaZulu–Natal.

Abundance The demand for Nyalas on private ranches has increased their distribution and numbers in South Africa, Swaziland and Zimbabwe, and also in Namibia, where the species has never occurred naturally. East (1999) estimated the total population of Nyalas to exceed around 32,000 individuals. However, more recent estimates suggest South Africa has at least 30,000 (a slight increase from the estimate of East [1999]), with the largest populations (25,000) in KwaZulu–Natal (P. Thomson pers. comm.). The major populations are in the Game Reserves of Ndumo (4000), Mkhuze (7000) and Hluhluwe–iMfolozi (7000) (Rowe-Rowe 1994). Kruger N. P. and adjoining game reserves have in excess of 3000 animals.

In Swaziland, the species was extinct by the 1950s, but they have been successfully reintroduced (and introduced to other parts of the country) and there are now more than 1000 on protected areas and ranches (Monadjem 1998). Nyalas are still widespread in Mozambique but, because of uncontrolled hunting, at very low densities and numbers probably do not exceed 3000 (J. Anderson, pers. obs.). Zimbabwe has more than 1000, the majority in Gonarezhou N. P. and on game ranches in the south-east. Numbers in Malawi have declined from 3000 (East 1999) to about 1500, most notably in the population in Lengwe N. P. (which was originally created especially for this species) and in Mwabvi G. R. where a relict population is thought still to occur (S. Munthali pers. comm.). There are about 350 in two populations on private property. Extralimital to the species' natural range, Namibia has about 250, all on private ranches.

Adaptations The conspicuousness of the dominance display (see below) between Nyala ♂♂ is accentuated by the long fringe of hair on each side of the belly and hindlegs and the erectile ridge of white hair running along the spine. These increase the visual surface area presented in the lateral display by up to 40%. Furthermore, the body appears to be laterally compressed, in cross-section being more elliptical than oval. The torso of a Nyala ♂ is 67% of its lateral silhouette, whereas that of an Impala *Aepyceros melampus* ♂, which does not have a lateral display, is only 58% (Anderson 1976).

Although adult ♂♂ are twice the weight of ♀♀, their molariform toothrows are the same length. The need to eat more than ♀♀ may influence a greater rate of tooth wear in ♂♂. At the end of the dry season, this has implications for physical condition and related mortality (Anderson 1976). The morphology of the stomach is similar to that of intermediate feeders (Hofmann 1973). The rumen papillae are not as 'leaf-like' as those tragelaphines that are concentrate selectors, but more closely resemble those of 'browsing' Impala (Hofmann 1973).

Foraging and Food Nyalas are intermediate feeders or generalists that feed selectively on both the leaves and fruits of woody plants as well as grasses (Hofmann 1973, Gagnon & Chew 2000), and this is borne out also by studies involving stable carbon isotopes (in which their diet was estimated to contain approximately 33% grass; Sponheimer *et al.* 2003b). The proportions of these components change in relation to their seasonal availability (Anderson 1976, Van Rooyen 1992). In Ndumo G. R., grasses formed the bulk of the diet during the rainy summer months and, as these dried out in winter, the proportion of browse eaten increased. Munthali (1991) found that in Lengwe N. P. in Malawi, Nyalas were primarily browsers but increased their intake of grasses over the wet season.

The most important grasses were those that grew under shade such as *Panicum maximum* and *Dactyloctenium australe*. The most commonly recorded woody plants eaten in Ndumo G. R. were *Trichelia emetica*, *Spirostachys africana*, *Sclerocarya birrea*, *Maytenus heterophylla*, *Gardenia cornuta* and *Ziziphus mucronata* (Anderson & Pooley 1977). In Lengwe N. P., the most important browse plant was *Salvadora persica* (Munthali 1991). Lobão Tello & Van Gelder (1975) recorded 108 species of browse plants utilized by Nyalas in Mozambique, with the Mustard Tree *Salvadora persica* particularly heavily utilized. The incidence of fruits and flowers in the diet is seasonal. In some areas animals venture onto open grasslands or flood-plains at night to feed on green grasses and forbs.

Although Nyalas drink daily where water is available, in parts of their range in Mozambique and Zimbabwe they are found where no surface water is present for several months of the year (Davison 1971, Lobão Tello & Van Gelder 1975).

Social and Reproductive Behaviour The social organization is based on the female unit, consisting of an adult ♀ and her offspring of varying ages (Anderson 1980). The typical female herd size (5.6) is formed by the association of two or more ♀♀ and their young. This association is not entirely random and there is a positive association between related female units. Loose temporary aggregations of up to 30 animals occur at water points.

Males leave the female unit of their own accord at between 14 and 24 months and begin to associate with other ♂♂, particularly those of similar age. The typical male group size is 2.7, but these are

not cohesive and seldom last for more than a day. With increasing age and body size, ♂♂ become more dominant and progressively more solitary, probably because of avoidance by younger ♂♂.

Nyalas are not territorial, and both sexes have overlapping home-ranges of approximately equal size; these appear to be inversely correlated with food availability. In Zinave N. P., the average home-range of adult ♂♂ was 5.5 km² (Lobão Tello & Van Gelder 1975) whereas in the more mesic Hluhluwe G. R. both ♂♂ and ♀♀ had home-ranges of about 1 km² (Anderson 1980). Home-range size may increase during the dry season in relation to the distribution of surface water. There is no marking, but adult ♂♂ frequently horn moist ground at water points and occasionally 'weave' and thrash bushes. These offensive threats often take place in isolation and are not directed towards other ♂♂.

Sire selection is achieved by temporary dominance asserted in the presence of an oestrous ♀. Dominance is achieved by a striking ritual where the main feature is a slow and deliberate lateral display with lowered head, raised dorsal ridge, and tail arched over the hindquarters with the long white hairs fanned out. Body size, and those physical features that serve to accentuate this, usually decide the outcome of the display. Young ♂♂ spar with one another, but this becomes less frequent with age. Occasionally, there is a clash of horns in the presence of an oestrous ♀. Fighting is very rare, but when it does occur is fierce and can often result in severe injuries or deaths (Anderson 1980).

When a ♂ encounters a ♀, he will test her for oestrus by smelling at the base of her tail. Males tested ♀♀ and performed flehmen in 127 of 130 male–female encounters recorded (Anderson 1976). Males only show strong flehmen in response to oestrous ♀♀. Overt oestrus lasts for about two days, during which more dominant animals may progressively replace each consorting ♂. The ♀ permits copulation for a period of about six hours, towards the end of overt oestrus when mating takes place repeatedly. The female unit is disrupted during this period and this generally accounts for sightings of lone juvenile animals.

Birth usually occurs in cover, rarely in the open (Lobão Tello & Van Gelder 1975). It is assumed that the ♀ leaves the group at this time. After giving birth, the ♀ cleans the newborn calf and eats the placenta and placental membranes. The calf lies up for about 18 days (Anderson 1980) until strong enough to accompany its mother. Female calves remain with their mothers until they in turn have their own first calf.

Nyalas are usually silent, but they do emit an alarm call, akin to a dog-like bark (and somewhat similar to that of Bushbucks *Tragelaphus scriptus* and Greater Kudus *T. strepsiceros*), which results in other animals nearby taking flight. Animals bleat when in distress and ♀♀ make a soft throaty clicking when in oestrus or tending a young calf.

In suitable habitats, Nyalas may be found feeding in association with Bushbucks, Impalas and Chacma Baboons *Papio ursinus*. Nyalas show no concern for baboons in these circumstances, and this is when adult male baboons occasionally prey on young Nyalas. Dean & MacDonald (1981) recorded an instance of a Chorister Robin-chat *Cossypha dichroa* gleaning a Nyala.

Reproduction and Population Structure Spermatogenesis starts at about 12 months and by 14 months of age all ♂♂ show active spermatogenesis. However, in a wild population, ♂♂ may only

breed when they are around five years old (Anderson 1984). There is no seasonal sexual cycle in ♂♂ (Anderson 1984). Ovulation first occurs between 14 and 18 months of age. By 20 months, 50% of the ♀♀ sampled from Ndumo G. R. were sexually mature. In captivity, ♀♀ as young as 11 months have conceived, presumably because of a high plane of nutrition. Between sexual maturity and senescence, at about 14 years of age, ♀♀ are either pregnant or at some stage of the oestrous cycle (i.e. anoestrus does not occur).

Implantation is homolateral and the gestation period is about 220 days. A single calf is the norm; twin foetuses were recorded only once in 217 conceptions examined in KwaZulu–Natal (Anderson 1984). The average weight of two newborn young was 5.6 kg. The shortest parturition interval recorded was 231 days, though the average parturition interval in Ndumo G. R. was 297 days. The interval between overt oestrous cycles ranges between 10 and 34 days. There is a postpartum oestrus that occurs between two and seven days after parturition. The ♀ will continue to come into oestrus until she conceives again. Lactation lasts about seven months (Anderson 1984).

Conceptions occur throughout the year in the wild (and in captivity, see Skinner *et al.* 2002), but there are two peaks, one in autumn and the other in spring. It is possible that these peaks are initiated by two, as yet undetermined, light or photoperiod cues. The absence of strong environmental feedback does not reinforce these cues enough to make the peaks very obvious or allow one to become dominant. They are further obscured by the seven-month gestation period and individual differences in the age of sexual maturity, oestrous cycles and duration of the parturition intervals (Anderson 1979).

There is an even sex ratio at birth and up to the age of a year (Anderson 1976). Males made up 45% of the adult population in an undisturbed population in Hluhluwe. Over a period of six years, the proportion of ♂♂ ranged from 32% to 64% of the adult segment of the population in Ndumo G. R. The percentage of immature animals recorded in various populations was 31% (Zinave N. P.), 32% (Hluhluwe) and 43% (False Bay Park). The different sex ratios between populations, and within the same population over time, can be ascribed to differences in habitat, predation pressure and management regime.

Seasonal changes in condition of Nyalas in Ndumo G. R. were measured and correlated with the rainfall of the previous month. Following periods of less than 50 mm rainfall per month (Anderson 1985), adult ♂♂ were in significantly lower condition than other sex/age classes. This was attributed to the fact that adult ♂♂ required 62% more kcal/day than adult ♀♀, yet had the same size jaw and tooththrow as ♀♀.

There is an increase in mortality towards the end of the dry season. Sporadic die-offs in protected areas in KwaZulu–Natal occur when unseasonable rain falls in the winter or early spring and is accompanied by a cold wind (Keep 1973, Anderson 1985). In 'die-offs' due to nutritional stress, significantly more young adults survived and significantly more adult ♂♂ died than would be expected to occur at random. Also, significantly more ♂♂ died than ♀♀ (Anderson 1985). Munthali (1993) recorded similar 'die-offs' in Lengwe N. P., and also noted that adult ♂♂ regained body condition slower than ♀♀.

Life tables from Ndumo G. R. showed that ♂♂ very rarely lived beyond 12 years of age and ♀♀ seldom beyond 14. There was also

a 34% mortality of calves within the first six months (Anderson 1976). Jones (1993) gives a longevity record in captivity of 15 years and 10 months.

Predators, Parasites and Diseases Nyalas are preyed upon by all the larger African carnivores that share their range and also by Nile Crocodiles *Crocodylus niloticus* and African Rock Pythons *Python sebae*. In Hluhluwe-iMfolozi Park, Lions *Panthera leo* account for the majority of kills. Young animals frequently fall prey to adult male baboons and occasionally to larger eagles.

No diseases have been found responsible for Nyala deaths in southern Africa in recent years. However, many Nyalas died as a result of the rinderpest epizootic that swept through Africa in 1895 and 1896.

Keep (1971) collected ten species of ticks and 13 species of helminth parasites from Nyalas in KwaZulu–Natal game reserves. He also recorded *Theileria*-like piroplasms and *Trypanosoma ingens*-like parasites in the blood (and see Bigalke *et al.* 1972). He found a high incidence of endarteritis caused by the filarial parasite *Cordophilus sagittus* in the lungs of Nyalas in Ndumo G. R. and *Cordophilus* cysts in 22% of a sample from the coronary vessels of outwardly healthy animals. In Mkhuzi G. R., Boomker *et al.* (1996) recorded helminths from a sample of 64 Nyalas, and amended the list of helminth parasites recorded from Nyalas to 30 species (see Boomker *et al.* 1991a), including five trematodes, three cestodes and 22 nematodes; *Camelostrongylus harrisi* and *Camelostrongylus* sp. were the most numerous and prevalent of the nematode burden. They concluded that the faecal egg counts could not be used to determine the nematode populations in antelope in the reserve, and also found that the magnitude of the total burdens was insignificant and in no way detrimental to Nyalas.

In iMfolozi, Mkhuzi and Ndumo Reserves, Horak *et al.* (1995a) recorded ten ixodid tick species, two louse species (*Damalinea* sp. and *Linognathus angasi*) and a louse fly (*Lipoptena paradoxa*); the most abundant tick species on Nyalas were *Rhipicephalus muelhensi* (and see also Horak *et al.* 1983c), *Rhipicephalus appendiculatus* and *Boophilus decoloratus*, the former two species preferring the ears, heads and upper necks of male Nyalas as attachment sites. The Nyala is the host to the wingless hippoboscid fly *Echestyphus pardoxus*, which is not known to cause any skin damage or carry any infectious disease (Keep 1971).

Conservation IUCN Category: Least Concern. CITES: Not listed.

Although Nyalas have disappeared from some parts of their former range, and have undergone some declines even in protected areas (such as Lengwe N. P.), they continue to survive in good numbers in a number of effectively managed protected areas (in particular the reserves of Ndumo, Mkhuzi and Hluhluwe-iMfolozi in KwaZulu–Natal, and in Kruger N. P.) and on private land, both within and outside their natural range. Currently, more than 80% of the Nyala population in South Africa occurs in protected areas (East 1999). The dispersion of Nyalas and their increase in numbers in South Africa is due primarily to the high demand for adult ♂♂ by trophy hunters. Efforts to rehabilitate the protected areas network of Mozambique (in particular Gorongosa, Banhine and Zinave National Parks) will be beneficial for the species.

In the absence of natural predation or population management, there have been several instances where Nyalas have increased to the detriment of Bushbuck and Suni *Nesotragus moschatus* populations. This is probably because, where the three species occupy the same habitat, Bushbucks and Sunis are almost exclusively browsers, but Nyalas being mixed feeders with a greater browse height have a competitive advantage in the late dry season when available browse is limited. Seymour (2002) found that where Nyalas, Bushbucks and Greater Kudus occurred together, there was little overlap with Bushbucks during the wet season as Nyalas selected slightly more open habitats and fed primarily on grass. During the dry season there was a high degree of overlap between Nyalas and Bushbucks in both diet and habitat use.

Measurements

Tragelaphus angasi

HB (♂ ♂): 1676 (1590–1980) mm, n = 20

HB (♀ ♀): 1432 (1323–1463) mm, n = 19

T (♂ ♂): 427 (370–470) mm, n = 22

T (♀ ♀): 360 (342–399) mm, n = 10

HF c.u. (♂ ♂): 474 (425–557) mm, n = 21

HF c.u. (♀ ♀): 422 (402–443) mm, n = 11

Sh. ht (♂ ♂): 1121 (1040–1210) mm, n = 17

Sh. ht (♀ ♀): 966 (825–1060) mm, n = 8

WT (♂ ♂): 107.5 (92.5–126.5) kg, n = 13

WT (♀ ♀): 61.8 (54.9–68.1) kg, n = 8

Zinave N. P., Mozambique (Lobão Tello & Van Gelder 1975)

Maximum recorded horn length is 83.5 cm for a pair of horns from KwaZulu–Natal, South Africa (Rowland Ward)

Key References Anderson 1976, 1979, 1980, 1984, 1985; Davison 1971; Lobão Tello & Van Gelder 1975; Munthali 1991, 1993.

Jeremy Anderson

Tragelaphus strepsiceros GREATER KUDU

Fr. Grand Koudou; Ger. Grosskudu

Tragelaphus strepsiceros (Pallas, 1766). Misc. Zool. p. 9. 'Prom. B. Spei' (Cape of Good Hope); restricted to South Africa, south-eastern Cape Prov. (= eastern part of Western Cape Prov.) by Grubb (1999: 36).

Taxonomy Originally classified simply as an 'antelope', the Greater Kudu was assigned by Blainville to the genus *Tragelaphus* in 1816. Ansell (1972) distinguished four subspecies on the basis of stripe patterns: *T. s. bea*, from Tanzania, N Mozambique and Kenya; *T. s. chora*, from Somalia, Ethiopia and E Sudan; *T. s. burlacei*, from Chad and Central African Republic, and possibly W Sudan; and the nominate form, from Zambia, Malawi southwards. Kingdon (1997) recognized three subspecies: *T. s. strepsiceros* (East Africa and South Africa), *T. s. chora* (north-east Africa) and *T. s. cottoni* (Chad, W Sudan), although the latter name is not available. Both Ansell (1972) and Haltenorth (1963) cautioned that since the stripes are so variable, the basis for subspecific recognition is dubious. An isolated naturally occurring population in South Africa's Eastern Cape Province has been regarded as a separate subspecies. Mitochondrial DNA markers suggest a substantial differentiation of the south-west African lineage from those elsewhere in Africa, although morphological differences are not apparent (Nersting & Arctander 2001). A single sample from N Kenya suggests that this population is genetically distinct, supporting the subspecies differentiation as *T. s. chora*, but confirmation from a larger sample is needed. The combined analysis of individual lineages, relationships and population genetics suggests a colonization process from southern Africa towards East African regions. Synonyms: *abyssinicus*, *bea*, *burlacei*, *capensis*, *chora*, *cottoni*, *excelsus*, *frommi*, *hamiltoni*, *koodoo*, *torticornis*, *typicus*, *zambesiensis*. Chromosome number: 2n = 31 for ♂ and 2n = 32 for ♀ (Gallagher & Womack 1992). There are two well-documented records of hybrid male offspring between a Greater Kudu and Common Eland *Tragelaphus oryx*, one known to be sterile, the other unknown (Jorge *et al.* 1976, Van Gelder 1977a).

Description Large majestic antelope characterized by striped body, humped shoulder region, long neck and huge spiral horns carried by ♂ ♂, which are also much larger in body size than ♀ ♀. Head markings include a V-shaped white bar on the forehead between the eyes, white



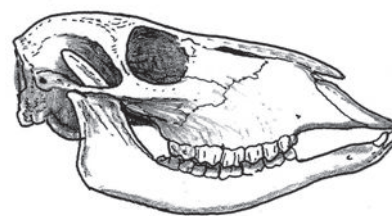
Greater Kudu *Tragelaphus strepsiceros*.



Greater Kudu *Tragelaphus strepsiceros* in strutting posture.

lips and chin, and one to four spots on the cheek. Ears are large and rounded, pinky-brown on the interior with tufts of white hairs near the base and white margins. Body colour varies from fawn or cinnamon to grey-brown, lower legs more tawny than the body with dark mark on inner knee and black band above hooves. White stripes on the body are variable in number, spacing and boldness, with 3–9 in the flank region and 2–5 on the hindquarters. Some stripes may be forked, and some animals show spots or bars between the stripes. Stripes tend to fade with age. Both sexes have a dorsal fringe of hairs extending from the neck along the back to the tail base, commonly white-tipped, with a prominent crest of hairs on the shoulders. Males also bear a long mane from the throat along the underside of the neck almost to the chest, commonly showing a dark middle band, plus a fringe of short dark hairs on the belly. Tail broadly fluffy with long hairs, white on the underside with a dark brown tip. Interdigital glands are present. Testes are quite small compared with most other antelopes, their combined weight only 0.04% of body mass even during the peak mating period (Skinner & Huntley 1971). The Nyala *Tragelaphus angasii* is similar in this respect (Anderson 1984), while in the Bushbuck *T. scriptus* the testes are relatively about twice as large (Allen-Rowlandson 1986). Necks of mature ♂♂ bulge markedly during mating season. Females have two pairs of inguinal nipples.

Horns of fully adult ♂♂ complete two full spirals with the tips extending forwards or even outwards and back, with a prominent ridge following the curvature. Females are hornless, although horned ♀♀ are occasionally recorded. Males can be placed into age categories by the direction of the spiralling horn tips. Three-year-olds have the horn tips pointing back and out, four-year-olds have the horn tips directed back and inwards, and five-year-olds have the tips curving forwards. By six years, both tips point forwards.



Lateral view of skull of Greater Kudu *Tragelaphus strepsiceros* female.

However, there is individual variation related to how narrow or wide the span is between the horn tips (N. Owen-Smith pers. obs.; see also Simpson 1971, 1972b). Patterns of tooth eruption are described by Simpson (1966), who demonstrated that ♂♂ could be aged up to about eight years by counting the cementum layers in the teeth, and relating these to the 'cheeks' or transverse ridging on the horns caused by seasonal fluctuations in growth.

Geographic Variation Individuals vary quite widely in their stripe patterns, but without any clear geographical variation. Ansell (1972) suggested a pattern of clinal variation from darker colour, more stripes and longer horns, in the south, to paler colour, fewer stripes and shorter horns in the north.

Similar Species

Tragelaphus imberbis. Sympatric in northern parts of the range. Similar in basic appearance and spiral horns (though not having the same spread), but attains less than half the body mass. Adult ♂♂ lack the dense fringe of hair along underside of neck. White patch at base of neck.

T. buxtoni. Ethiopian Highlands only, potentially sympatric in some mountain slopes. Similar in size and body colour, but has less distinct stripes and shorter horns with fewer spirals.

T. eurycerus. Allopatric. Somewhat heavier with numerous bright stripes against a dark chestnut-brown background.

Distribution Endemic to Africa.

Historical Distribution In South Africa, formerly occurred in the Northern Cape, NE KwaZulu–Natal and the North West, Limpopo, Mpumalanga and Gauteng Provinces, with an isolated population in the Eastern Cape, and scattered populations in the Free State. From South Africa the species ranged widely through Namibia (excluding the drier coastal parts), Botswana, Zimbabwe, S and C Angola, Zambia (absent from the wetter savanna woodlands of the northern plateaux), Mozambique, Malawi, SE DR Congo, to Tanzania and Kenya (East 1999). Somewhat rare and localized in occurrence (often in hilly areas) north of the equator, from Kenya and east Karamoja in E Uganda through the Rift Valley and western, eastern and southern lowlands of Ethiopia, W Eritrea, S Djibouti, Somalia, W and SE Sudan (and along the Ethiopia/Eritrea borders), S and SE Chad and N Central African Republic (north of the Ouandja and Koumbal Rivers) (East 1999). Naturally absent from the Serengeti region of N Tanzania and adjoining plateau region of S Kenya.

Current Distribution Greater Kudus have remained common through most of their southern range, even on ranching land and close to settlements, and have extended their distribution westwards in



parts of southern Africa, such as the Karoo and Kalahari. Only in SE DR Congo is their status unclear, although they survive at least in Kundelungu N. P. (East 1999). To the north, the species may now be extinct in Djibouti, where a few were reported to survive in the south on the Ethiopia border in the mid- to late-1980s (East 1999, Heckel & Rayaleh 2008). In Somalia, Simonetta (1988) suggested they may survive on the northern slopes of the Gaan Libah in the north-west, while East (1999) considered them extinct; recently discovered museum records of specimens collected in the 1960s from S and C Somalia that expand the known historical range suggest this may be premature (Gippoliti & Fagotto in press). There is no recent information on their status in Sudan (they were not recorded during recent surveys in the south; Fay *et al.* 2007) or Uganda (East 1999).

Habitat Greater Kudus occupy a wide range of savanna vegetation types, from dry thornbush with rainfall as low as 200 mm through to mixed broad-leaf woodlands with rainfall approaching 1000 mm. Most widely abundant in drier savanna regions where they are commonly associated with rocky hillslopes, and especially common in succulent thickets or 'valley bushveld' where there is a high evergreen component including the leaf-succulent Spekboom *Portulacaria afra*. Absent from closed forests and treeless grassland, but may forage into quite open parkland where denser woody vegetation adjoining hillslopes or water-courses occurs nearby. They occur in arid shrubland and semi-desert along riparian corridors. Absent from extensive areas of Umbrella Thorn *Acacia tortilis* savanna where a dry season reserve of evergreen or semi-evergreen browse is lacking. Males concentrate more in riparian woodland and thicket along drainage-lines than female herds (du Toit 1995), although ♀♀ shift their feeding towards river-lines during the dry season (Simpson & Cowie 1967). Greater Kudus have been recorded to elevations of 2400 m in Ethiopia (Yalden *et al.* 1996).

Abundance Densities in savanna woodland reach 2–3/km² locally (Owen-Smith 1990), but can exceed 10/km² in succulent

thickets of the Eastern Cape (Allen-Rowlandson 1980). Population densities obtained from aerial counts are generally less than 0.5/km² even in areas where the species is reasonably common (see East 1999), but may underestimate the true population by a factor of two. East (1999) estimated a total population of around 482,000 Greater Kudus, with the largest populations found in Namibia (more than 200,000), where the species remains widely abundant on private farmland, and South Africa (more than 60,000).

Adaptations The trophic morphology and anatomy of the Greater Kudu is fairly typical of a browser, but with physiology deviating from that of small concentrate selectors like duikers. The muzzle and incisor toothrow are relatively narrow, and the premolars and molars have prominent cusps adapted for puncture-crushing of dicotyledonous foliage. The reticulum has a heavily keratinized lining apparently protective against thorns and woody stems ingested. The capacity of the rumen plus reticulum is moderate, about 27 litres in adult ♀♀ and 58–71 litres in adult ♂♂ (Hofmann 1973). The rumen is generally filled to no more than 60% of capacity with solid material, presumably to accommodate gases released from rapidly fermenting forage. The wet mass of rumen contents averages 11% of body mass, or 1.8% as dry mass ranging from 1.55% in the wet season to 2.1% in the dry season (Giesecke & Van Gylswyk 1975, Boomker 1987). This is somewhat smaller than in grazing ruminants. Fermentation rate of rumen contents is substantially lower than in small browsers, and a fairly high proportion of acetic to propionic acid is produced, indicative of substantial fibre digestion. The absorptive surface of the rumen mucosa is greatly enlarged by dense papillae. The omasum is well developed with laminae increasing the absorptive surface for water and electrolytes. Parotid salivary gland quite small, about 0.06% of body mass (Robbins *et al.* 1995), in contrast to Giraffe *Giraffa camelopardalis* and most other browsers. This suggests that detoxification via the liver is more important than salivary deactivation of tannins.

Greater Kudus have a fairly sparse pelage, enabling them to be active despite temperatures as high as 36°C during summer, but develop a more shaggy coat during the South African winter (Owen-Smith 1998). They can exist for long periods without drinking, obtaining sufficient moisture from their food (du Toit 1995), but become water dependent at times when the vegetation is very dry. In semi-desert areas of Namibia and the Kalahari they satisfy their moisture requirements by consuming Tsama Melons *Citrullus lanatus*. Drinking usually takes place during the late morning.

Greater Kudus are renowned jumpers, with adult ♂♂ able to clear fences 2 m in height from a standing position. While running through thick vegetation ♂♂ hold their noses forwards so that the long horns are extended over the back. Vision, hearing and sense of smell are all good, and they are difficult to approach closely in the dense vegetation they usually inhabit. While moving through open habitats they are cautious and tend to follow corridors of denser vegetation.

Greater Kudus are active nocturnally as well as during daylight, and the species is a common cause of road accidents along highways at night. The main foraging periods are during the morning, and from the late afternoon into the night, plus commonly a brief foraging spell around midday during the hottest time of the day. On average about 63% of daylight and 48% of the night is devoted to foraging. Activity levels are highest during the dry–wet season transition when

high-quality food becomes available in small amounts, and lowest over the late wet season when food is most abundant (Owen-Smith 1998). A sleeping spell occurs in the pre-dawn period, when animals lie curled with the head laid on the flank.

Foraging and Food Greater Kudus are browsers, as evidenced both by direct observations and dietary studies involving stable carbon isotope analysis (Cerling *et al.* 2003, Sponheimer *et al.* 2003b). They have an exceptionally broad diet, both in terms of plant species eaten as well as food types. Almost 150 species of plants were recorded as eaten in Kruger N. P., South Africa (Brynard & Pienaar 1960), while in Nylsvley N. R. in the Limpopo Province of South Africa they consumed on average 40 species per day (maximum 59), subdivided equally between forbs and woody plants (Owen-Smith 1994). Deciduous woody plants form the staple dietary component for most of the year, especially various mimosa thorn-trees (*Acacia* spp.), bush-willows (*Combretum* spp.) and raisin-bush (*Grewia* spp.) (Owen-Smith 1979, 1994, Novellie 1983, Owen-Smith & Cooper 1989). In Zambia, other woody species commonly browsed include *Diplorhynchus condylocarpon*, *Pseudolachnostylis maprouneifolia*, *Trichilia roka*, *Bauhinia petersiana* and *Albizia harveyi* (Wilson 1965). However, forbs are especially favoured, particularly soft-stemmed creepers, annuals and perennials like *Justicia* and *Commelina* spp., and form 40–60% of the wet-season diet in Kruger N. P. and Nylsvley N. R. Certain fruits are sought out when available, notably the pods of certain *Acacia* spp., *Dichrostachys cinerea* and *Piliostigma thonningii*, succulent drupes of marula *Sclerocarya birrea* and *Ximenia caffra*, large hard-shelled monkey-oranges (*Strychnos* spp.), kudu-berries (*P. maprouneifolia*), goat apples (*Solanum* spp.) and wild cucumbers (*Cucumis* spp.).

During the dry season the diet is widened to include the foliage of less palatable woody species, notably certain evergreens, including Monkey-orange (*Strychnos pungens*) and Mountain Karee *Rhus leptodictya*, as well as robust forbs and shrublets. *Combretum* spp. retaining leaves quite late into the dry season may also be important during this period. By the late dry season when little green foliage remains, Greater Kudus consume even the foliage of unpalatable evergreens like gwarrie (*Euclea* spp.) that are high in condensed tannins, although in limited amounts. The leaf succulent Spekboom *Portulacaria afra* forms the year-round staple in Eastern Cape thickets (Zeeman 1991). Greater Kudus are renowned for eating certain plant species reputed to be poisonous, including the large succulent leaves of *Euphorbia* and *Aloe* spp. Grasses are consumed in limited amounts when green, with animals selecting the most nutritious species (e.g. *Panicum maximum*) or green flush on burns. Occasional stomach samples may contain 30% or more grass (Conybeare 1975). Flowers are also eaten, especially those produced abundantly ahead of leaves (e.g. Wild Pear *Dombeya rotundifolia*), or exceptionally large (Sausage Tree *Kigelia pinnata*).

Chemical analyses suggest that the prime factor distinguishing unpalatable woody browse is a high content of condensed tannins relative to protein in leaves (Cooper *et al.* 1988). Some high-tannin species are readily consumed in the new leaf phase when protein levels are elevated relative to tannin contents. Hydrolysable tannins prevalent among the Combretaceae do not seem to be a deterrent (Owen-Smith 1993d). Unpalatable species commonly show low fibre digestibility *in vitro*, presumably because condensed tannins or other secondary chemicals interfere with bacterial fermentation

(Boomker 1987). Greater Kudus rarely browse woody stems lacking leaves, but eat many forbs whole. Males use their horns to pull down branches, thereby bringing leaves within feeding reach. Dietary protein levels vary from 12 to 14% during the late wet season to 9% by the late dry season (Owen-Smith & Cooper 1989). Dietary fibre content varies from 40 to 55%, total phenolic content 3.3–6.6% and condensed tannins 1.8–3.5%. Kudus sometimes chew on bones, suggesting a deficiency of phosphorus or calcium, and also lick white sodic encrustations near pans (Conybeare 1975).

Food availability becomes considerably depleted during the dry season when deciduous trees shed their leaves (Owen-Smith 1994), and kudus can lose considerable body reserves over this period (Wilson 1970, Huntley 1971).

Social and Reproductive Behaviour Greater Kudu ♀♀ and young live in cohesive social groups or clans sharing a common home-range. In Kruger N. P., the modal social clan size is 7–10 (range 3–21), comprising 4–6 adult ♀♀ (range 2–11) plus juveniles, yearlings and young ♂♂ up to two years of age (Owen-Smith 1984, see also Underwood 1978). Clans larger than ten animals are frequently split into sub-units, so that the observed group size is typically 6–7 (range 1–21) in Kruger N. P. Larger aggregations may occasionally be seen when social units mingle temporarily. Group size tends to be largest during the early dry and early wet seasons, and smallest during the calving period in the late wet season. In Hwange N. P., Zimbabwe, a modal group size of 5–6 (maximum 19) was recorded (Conybeare 1972; see also Simpson 1968). In the Eastern Cape, the typical female group size was about five (range 2–11; Perrin 1999). In areas where the species is hunted, the modal group size is about four (Wilson 1965, Du Plessis 1986).

Female home-ranges cover 3–25 km² in Kruger N. P. (Owen-Smith 1984, du Toit 1988), but can be as small as 1 km² in succulent thicket (Perrin & Allen-Rowlandson 1993) and exceed 25 km² in parts of Zimbabwe (D. H. M. Cumming pers. comm.). Home-ranges of neighbouring social units overlap extensively, but with an exclusive core area that is not defended in any overt way. The extent of the home-range utilized expands in the wet season, when some habitats become temporarily favourable, and contracts during the dry season to sections containing more persistent browse, such as water-courses and hillslopes. Young ♀♀ generally remain within their mother's clan, forming extended matriline. Dispersal between clans occurs at a low rate of about 0.5% per ♀ per year. Large clans may eventually subdivide and partition the former home-range.

Some social units have an obvious leader, generally an older ♀ that tends to move independently and is followed by other group members. Aggressive gestures, like butting, generally take place between an adult and a young animal that is not her offspring, and there is little evidence of any dominance ranking among mature ♀♀. Allogrooming occurs commonly. Group members maintain contact through hearing as well as visually, and can track down companions by following their scent trail over some distance. Tail flagging displaying the white underside is a signal given when starting to move on, and also when fleeing from a predator. When different social units meet, their members largely ignore one another, and may mingle temporarily without losing their group affiliation.

Adult plus subadult ♂♂ form loose groups typically numbering 3–4 animals, both in Kruger N. P. (Owen-Smith 1993c) and in



Greater Kudu *Tragelaphus strepsiceros*.

Eastern Cape (Perrin 1999). The largest male group recorded in Kruger N. P. study areas numbered 12 animals, but as many as 16–25 ♂♂ have been seen together elsewhere (N. Owen-Smith pers. obs.). Older ♂♂ tend to become increasingly solitary. In Kruger N. P., ♂♂ move over large home-ranges covering perhaps 50 km², while in the succulent thickets of Eastern Cape male home-ranges averaged 1.6 km² (max. 2.7 km²; Perrin & Allen-Rowlandson 1993). There is no territorial exclusion, and ♂♂ may roam beyond the area they normally inhabit to seek out ♀♀ during the mating season.

The onset of mating activity is evident merely through the attachment of mature ♂♂ to the female herds. Males do not advertise their presence vocally. In contrast to the active rut shown by Red Deer *Cervus elaphus* and other northern ungulates, Greater Kudu bulls show little reduction in their feeding time during this period (Owen-Smith 1984). Males remain associated with a particular group of ♀♀ for a week or two, presumably after detecting that some members are about to come into oestrus. Attachments are temporary as bulls shift between different female groups as well as spending periods alone during the conception period. More than one bull may be associated with a female herd, but invariably only one of these is a fully mature ♂, the others being younger hangers on. The latter are tolerated through an age-graded ranking in dominance. Upon meeting, one or both ♂♂ may adopt a hunched broadside posture with elevated manes, designed to emphasize size. The incoming ♂ may merely walk past seeming not to notice, seem distracted by various itches, or circle slowly round the displaying ♂. Thereafter both animals relax, but sometimes fights develop when equal-sized rivals meet. The spiral horns lock the bodies of the combatants as they push and twist in a test of power and strength. The loser departs from the scene, followed a short way by the victor. Occasionally, the horns get so inextricably tangled that both animals die.

While associated with a female group, the ♂ periodically solicits urine samples, approaching with soft bleats to press his nose into the perineal region of the ♀. Frequently, this results in the ♀ ejecting a small amount of urine, and the bull mouths the liquid followed by the flehmen or lip-curl action. Oestrus is indicated by the formation of a tending bond between the bull and a particular ♀, with the pair occasionally separating from the herd. Courtship actions by ♂♂ include standing head held high, sometimes with the nose pointing skywards, behind or beside the ♀, and stretching the neck over her back (see Walther 1964a). Mating is not attempted until the ♀ is ready. Copulations are brief, lasting 5–14 seconds, including pelvic thrusts. Tending bonds usually last a day or less, but occasionally extend over two days (Owen-Smith 1993c).

Young animals lie out after birth, not moving with the herd until 8–10 weeks old. The mother leaves the herd each day to seek out the offspring where she last left it. Once in the vicinity she gives soft moos, and the baby bounds from its hiding place to join her. While the calf is suckled the mother licks the perineum, and consumes urine and faeces that may give away the offspring's presence. After nursing the baby moves away to hide itself again. As calves get older they move for a period with the mother (and later with the herd) before they hide, so that the location of the hiding place changes daily. The mother seems not to notice when her offspring hides, yet encounters no difficulty in relocating it from day to day. Within the herd, calves tend to move as a sub-unit rather than following closely after their individual mothers.

A loud bark is used as an alarm call, given when a human or a predator is detected. When a predator is in clear view Greater Kudu may move off without any call. When suddenly disturbed the herd may scatter and reassemble later. In contradiction of some reports, barks seem not to play any role in spacing herds.

Reproduction and Population Structure In Kruger N. P., the peak mating season extends through Apr into May, with calves born mostly during Jan and Feb, but some out-of-season conceptions and births occur in other months (Owen-Smith 1984, 1993c). In the Eastern Cape, most births occurred between Dec and Feb, while adult ♂♂ were seen associated with ♀♀ between Apr and Jul (Perrin 1999). In Zimbabwe and Zambia, the peak calving months are Feb and Mar, with some calves born as late as May (Wilson 1965, Simpson 1968). In captivity, they also exhibit seasonal breeding, with a peak in Mar, but some calves born as late as Jul (Skinner *et al.* 2002). Young are thus conceived when ♀♀ are in prime condition at the end of the wet season, and born during the time when forbs and other high-quality browse are most abundant.

A gestation period between 259 and 271 days is indicated by records for captive animals (Dittrich 1972) as well as by the months of observed matings and births (Owen-Smith 1993c, Perrin & Allen-Rowlandson 1995). A single young is the rule, with the birth mass of 16 kg representing 9% of maternal mass (Allen-Rowlandson 1980). Occasionally, two calves may nurse from the same ♀, but whether these represent twins or allofostering is unclear. Calves commence browsing when 6–8 weeks old, and are weaned around 6–7 months of age.

Females generally first conceive at 2.3 years of age and bear their first offspring at three years, but in some populations up to half reproduce a year earlier (Perrin & Allen-Rowlandson 1995). Females are capable of breeding annually, but with apparent variation in fertility among individuals within clans. Conception rate approaches 100% among prime-aged ♀♀. On average only about 50% of calves survive to the end of their first dry season, with most losses occurring perinatally before young emerge from the lying out period. Calf survival is strongly dependent on the annual rainfall total over the preceding year, which probably controls foetal growth during late gestation as well as the mother's milk supply after parturition via the amount of high quality forage available (Owen-Smith 1990). Maternal mortality averages about 8% per year during the prime stage from two to six years of age, mostly due to additive predation. Thereafter, the mortality rate rises as senescence takes effect (Owen-Smith 1993a). Potential longevity in the wild is 15 years for ♀♀.

Males commence spermatogenesis around 18 months of age (Perrin & Allen-Rowlandson 1995). They generally break away from their maternal unit around two years of age, although some individuals may remain associated with their mother's herd for up to a year longer. Thereafter ♂♂ move initially in pairs or larger associations of similar aged animals, temporarily joining up with older ♂♂. Individual affiliations become less persistent as ♂♂ grow towards maturity. Apparently playful sparring between ♂♂ in these shifting groups may facilitate the assessment of relative size and hence dominance. Males do not attain full horn growth and weight, and hence prime dominance status, until six years of age (Owen-Smith 1993b).

Annual mortality rates climb as ♂♂ grow larger than ♀♀ after two years. By six years of age, a ♂ has only a 50% chance of surviving

another year (a mortality rate comparable to that of a 12-year-old ♀), and no ♂ older than nine years was recorded in Kruger N. P. (Owen-Smith 1993a). Hence, few bulls retain prime breeding status for longer than two years. In captive conditions, Greater Kudus may live to be much older: Jones (1993) gives a longevity record for *T. s. strepsiceros* of just over 22 years.

As a consequence of the male-biased mortality the population sex ratio is strongly skewed towards ♀♀. For all adults plus subadults older than two years, the sex ratio varies between 2.1 and 2.5 ♀♀ per ♂ among different populations (Owen-Smith 1993a). However, the operational breeding ratio of prime-aged (>6 years) ♂♂ to receptive (>2 years) ♀♀ is 1 : 12. Since there are barely enough bulls to go around among female groups (effectively one mature bull for every 2–3 female units), ♂♂ rarely need to contest dominance through overt aggression or territorial exclusion. Five-year-old bulls even get mating opportunities when no older ♂ is present. This system was called ‘mating enhancement by attrition of rivals’ (Owen-Smith 1993b). The prime cause of the differential male mortality is not clear. It seems basically a consequence of larger-than-optimal body size, with larger size benefiting reproduction at the cost of survival. Costs probably arise through malnutrition as well as lessened agility in evading predators. Unlike many other ungulate species, Greater Kudu ♂♂ show relatively little reduction in foraging time during the breeding period (Owen-Smith 1984).

Greater Kudus are susceptible to mortality when cold wet spells occur at the end of the winter dry season in southern Africa (Wilson 1970, Simpson 1972a). In Kruger N. P., a maximum daily temperature of 14 °C associated with overcast conditions, rain and wind resulted in a doubling of adult mortality from 10% to 20%, especially among old ♀♀, and reduction in calf survival from 60% to 25%, despite prior good rainfall (Owen-Smith 2000).

Predators, Parasites and Diseases Greater Kudus, or at least ♀♀ and young, are subject to predation by all the larger carnivores, including Lions *Panthera leo*, Spotted Hyenas *Crocuta crocuta*, Leopards *Panthera pardus* and African Wild Dogs *Lycaon pictus*. They usually are not the major prey species for any of these predators, except in areas where abundant (e.g. see Pole *et al.* 2004). Even though predation is the direct cause of death of almost all animals, except during severe droughts, it is generally interactive with nutrition because of the strong correlation between the mortality rates of all except the prime age class and rainfall relative to population density (Owen-Smith 1990).

Greater Kudus are among the main hosts of tsetse flies, although they do not seem to suffer ill effects from the trypanosome microparasites transmitted by these flies. They seem especially susceptible to several wildlife diseases causing severe mortality during outbreaks. Greater Kudu were among the ungulate species decimated during the rinderpest panzootic that spread through Africa during the 1890s (Mack 1970, Rossiter 1994). Animals in E Kenya were adversely affected by a rinderpest epidemic in 1993–97 (Kock *et al.* 1999). The species seems to be centrally involved in spreading anthrax during outbreaks of this disease in Kruger N. P., as well as suffering severe mortality, resulting in a population decline by as much as 40% in infected areas (De Vos & Bryden 1996, Bengis *et al.* 2003). Greater Kudus pick up spores through feeding on leaves where blowflies have defecated after feeding on infected carcasses. However, in Etosha N. P. in Namibia,

where anthrax is endemic, Greater Kudus make up a very small proportion of the animal deaths (Lindeque & Turnbull 1994). Rabies caused severe mortality among Greater Kudus in Namibia in 1981, amounting to 16–20% of the estimated population per farm, and up to 50% losses in some areas (Hassel 1982). Transmission seems to occur via salivary contamination of browse, and the outbreak was associated with an abnormally high density of Greater Kudus at that time. Greater Kudus also suffer from bovine tuberculosis, and may play a role in maintaining the disease in the system (Bengis *et al.* 2003). They also appear to be very susceptible to Bovine Spongiform Encephalitis (Cunningham *et al.* 2004).

Greater Kudus carry high tick loads, especially of *Boophilus decoloratus*, *Amblyomma hebraeum* and *Rhipicephalus* spp. (Horak *et al.* 1992b, Gallivan & Surgeoner 1995, Zieger *et al.* 1998b). The Red-billed Oxpeckers *Buphagus erythorynchus* that commonly clamber over them probably play an important role in controlling the tick burdens, along with the reciprocal grooming that Greater Kudus show. They are also subject to bites from swarms of tabanid flies as well as tsetse flies (Boomker *et al.* 1989b, N. Owen-Smith pers. obs.), probably on account of their comparatively sparse hair coat.

The nematode roundworm burdens carried by Greater Kudus are somewhat lower than those found in grazing ungulates. Species commonly found include *Haemonchus veglii* and *Cooperia neitzi*, *Cooperia acutispiculatum*, *Cordophilus saggitus* and *Trichostrongylus deflexus* (Boomker *et al.* 1988, 1989b). Lactating ♀♀ may show substantially elevated worm loads, but no increase in nematode numbers was evident in a drought year.

Conservation IUCN Category: Least Concern. CITES: Not listed.

Greater Kudus are much sought after by hunters, both for the magnificent horns of bulls and more generally for their high-quality meat. Populations seem to be quite resilient to hunting pressure, aided by their alert and reclusive habits and their apparent ability to persist in settled areas that have suitable cover. They are also a favoured game-ranching species, because as browsers they do not compete with domestic livestock. In southern Africa, Greater Kudus are common on private farms and conservancies; East (1999) estimated that some 60% of the global population occurs on private land, and they seem to be expanding their distribution outside protected areas.

In the southern and south-central parts of their range, Greater Kudus are generally well represented in protected areas, with important populations in Ruaha N. P. and Rungwa and Selous Game Reserves (Tanzania), Luangwa Valley and Kafue National Parks (Zambia), Etosha N. P. (Namibia), Chobe G. R. (Botswana), Hwange and Mana Pools National Parks (Zimbabwe), Niassa G. R. (Mozambique) and Kruger N. P. (South Africa). However, in the northern parts of the species' range, the Greater Kudu seems to be in decline, with its status threatened further by the species' fragmented distribution and susceptibility to diseases transmitted by cattle. Key populations in this part of the range include those in Zakouma N. P. (Chad), Nechisar, Omo, Mago and Awash National Parks (Ethiopia), Laikipia and Tsavo N. P. (Kenya) and Tarangire N. P. (N Tanzania) (East 1999).

Measurements

Tragelaphus strepsiceros

HB (♂♂): 2170 (2060–2490) mm, n = 33

HB (♀ ♀): 1970 (1520–2160) mm, n = 68
 T (♂ ♂): 450 (400–520) mm, n = 33
 T (♀ ♀): 410 (350–470) mm, n = 68
 E (♂ ♂): 260 (245–290) mm, n = 33
 E (♀ ♀): 240 (210–255) mm, n = 68
 Sh. ht (♂ ♂): 1340 (1220–1430) mm, n = 17
 Sh. ht (♀ ♀): 1240 (990–1390) mm, n = 48
 WT (♂ ♂): 249.0 (174.0–344.0) kg, n = 94
 WT (♀ ♀): 160.0 (112.0–210.0) kg, n = 97
 Southern Africa (combined from Wilson 1965, 1970, Skinner &

Chimimba 2005, V. De Vos pers. comm. and J. D. Skinner pers. comm.)
 Record horn length is 187.6 cm for a pair of horns picked up near the Save R., Mozambique (Rowland Ward), the longest of any antelope recorded.

Key References Owen-Smith 1979, 1990, 1993a, b, c, 1994; Owen-Smith & Cooper 1989; Simpson 1968, 1972a.

Norman Owen-Smith

Tragelaphus buxtoni MOUNTAIN NYALA (GEDEMSA)

Fr. Nyale des montagnes; Ger. Bergnyala

Tragelaphus buxtoni (Lydekker, 1910). Nature 84: 397. Ethiopia, Bak Prov., 'Arusi plateau of Gallaland, in the Sahatu Mountains, and south-east of Lake Zwei [Zwai], at an estimated height of 9000 feet [2700 m] above sea level'.



Mountain Nyala *Tragelaphus buxtoni* male.

flank and spiral horns with a strong posterior keel, but of stockier build, thicker neck and heavier horns. Adult ♂ ♂ have a dun brown coat, which gets progressively darker with age, with white markings on face, throat, legs and poorly defined stripes on back and upper flanks. Coat texture varies, possibly by season, from sleek to shaggy; hair in back of thighs longer and stiffer. An erectile white crest or mane, 100 mm high, runs from neck to tail; the bushy tail reaches the heel. Females smaller and lighter in colour, resembling a Red Deer hind in size and proportions; dark greyish-brown coat, with paler undersides, white markings on legs and face and faint spots and stripes; erectile crest absent. Young cows bright rufous, with older cows as grey as a young bull. Ears large, lined with tracts of white hairs and a narrow black smear-like mark on the lower margin. Only ♂ ♂ have horns, which are lyre shaped, and grow outwardly in a spiral with 1–2 turns, a distinctive back ridge, and sometimes having ivory tips. Females have two pairs of inguinal nipples.

Geographic Variation None recorded.

Similar Species

Tragelaphus strepsiceros. Drier wooded areas of Ethiopia, potentially sympatric on some mountain slopes. Taller, colour paler and more graceful; horns longer, with 2–3 spirals and tips more separated.
T. angasii. Southern Africa only, in Malawi, Mozambique, Zimbabwe and South Africa. Smaller and readily distinguishable by an abundant fringe of long hair on throat and neck; horns similar, although slender and narrower.

Taxonomy Monotypic. Described from a specimen brought to England in 1908 by Major Ivor Buxton, the Mountain Nyala is the last major large mammal to be discovered in Africa. Despite its common name, studies involving nuclear DNA reveal that the species forms a monophyletic clade with the Bongo *T. eurycerus*, Sitatunga *T. spekii* and Bushbuck *T. scriptus*, all species adapted to closed forest (Willows-Munro *et al.* 2005). Synonyms: none. Chromosome number: not known.

Description A large tragelaphine similar in appearance and size to the Greater Kudu *T. strepsiceros*, sharing a row of spots along the

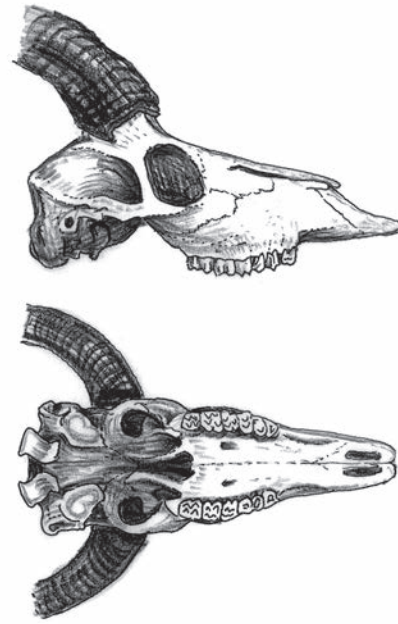
Distribution Endemic to Ethiopia. Restricted to a few scattered populations alongside an arc of mountains south-east of the Rift Valley, between 6°N and 10°N. Formerly occurred from Gara Muleta in the east to Shashamane and north Sidamo in the south, but eliminated from a large proportion of its former range. Presently, up to half of the world population is found in the Bale Mountains and the eastern escarpments of the Bale massif (Shedem, Odo Bulu, Abasheba). Smaller relict populations occur in Chercher (= Amhar) Mts (Kuni-Muktar, Arba Guggu, Din Din), Arsi Mts (Chilalo, Galama, Mt Kaka, Munessa) and West Bale (Somkaro-Korduro ridge) (Hillman 1988a, East 1999, Malcolm & Evangelista 2005).

*Tragelaphus buxtoni*

Habitat Ideal habitat is provided by montane woodlands (3000–3400 m), dominated by *Juniper*, *Podocarpus* and *Olea* in the lower parts and *Hagenia*, *Juniper* and *Hypericum* in the upper reaches. Mountain Nyalas frequent the fringes of montane grasslands (2800–3100 m) dominated by sage brush *Artemisia afra*, red-hot pokers *Kniphofia foliosa* and everlasting *Hypericum* spp. Highest densities (up to 21 ind/km²) have been recorded in the montane grasslands of Gaysay, Bale, where there is a combination of browse and grass with woodland cover to retreat into during the day (Hillman & Hillman 1987).

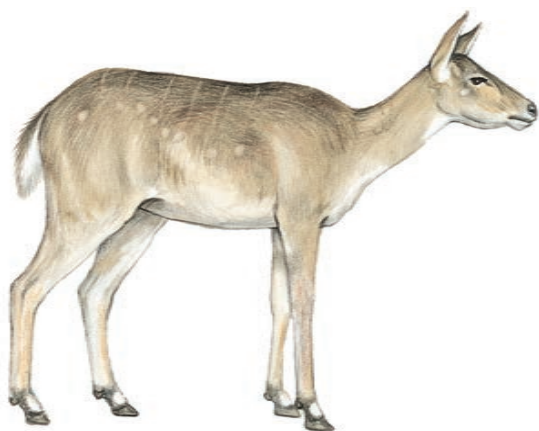
What were formerly large continuous blocks of suitable woodland and afroalpine habitat have now been reduced to a series of habitat islands in a sea of cultivated fields. It appears likely that Mountain Nyalas have been forced into even higher areas due to human increase and livestock grazing, with animals also found above 3400 m on heath forest and ericaceous heath lands (*Erica* and *Phyllippia* spp. with *Hypericum*, *Euphorbia* and *Helichrysum* shrubs) and on afroalpine grasslands (*Alchemilla* spp., *Festuca* spp.) up to 4300 m. In the eastern extreme of its distribution, a relict population was recorded in forests as low as 1800 m (Bolton 1973); the Munessa population occurs at 2400 m (Malcolm & Evangelista 2005).

Abundance The world population of Mountain Nyalas was estimated at 7000–8000 (and perhaps even as high as 12,500) in the 1960s by Leslie Brown (Brown 1969a), and at between 2000 and 4000 individuals in the 1980s (Hillman 1988a). Global numbers have declined since. Habitat suitability projections indicate that there may be as little as 8333 km² (Atickem *et al.* 2011) or up to 40,000 km² (Evangelista *et al.* 2008) of forest habitat available to the species, but the latter estimate includes many areas heavily impacted by human activities. Mountain Nyalas are possibly extinct in the eastern and southern extremes of their distribution, but small numbers may still occur in Asba Tafari and in the border between Bale and Sidamo south of Kofele. The total population was calculated by East (1999) at 2650, but subsequent

Lateral and palatal views of skull of Mountain Nyal *Tragelaphus buxtoni*.

information indicates that this may be an overestimate. The main extant population occurs in and around the Gaysay grasslands in the northern extreme of the Bale Mts, where numbers have been monitored since 1983. In response to the creation of a national park in the 1970s, which provided protection from poaching and the exclusion of cattle grazing, the Mountain Nyal population in Gaysay increased to 1050 by the late 1980s (Hillman 1988a). Woldegebriel (1996) put the population prior to 1990 between 1500 and 1900. Unfortunately, as a result of the political unrest that followed the end of the war in 1991, most Mountain Nyal habitat in northern Bale was encroached by cattle and there was extensive shooting of nyalas. Consequently, the Gaysay population decreased to only a fraction of what it was, and park staff estimated it to be 150–260 by 1994 (Woldegebriel 1996). There have been signs of recovery since, and the population was tentatively estimated in 1997 at 530–1000 using transect counts (Stephens *et al.* 2001), although this result may be biased due to transect design, and a conservative population estimate should be put close to the lower figure. More recently, the Gaysay population was estimated at 550 by Refera & Bekele (2004) and Malcolm & Evangelista (2005).

In addition to the population in Gaysay there may be as many as 80–120 Mountain Nyalas elsewhere in Bale Mountains N. P., less than 100 in adjacent hunting areas to the north of the park and 30–60 in Somkaro in W Bale (C. Sillero-Zubiri pers. obs.). Malcolm & Evangelista (2005) estimated as many as 500 Mountain Nyalas may occur in hunting blocks east of Bale. This would give a total population estimate for the Bale massif of 1000–1400. Small fragmented populations found in Arsi (Galama, Chilalo, Kaka and Munesa) and elsewhere (Kuni Muktar, Din Din, Arba Gugu) would total some 600 animals (Malcolm & Evangelista 2005). Although Atickem *et al.* (2011) estimated a population of over 3000 using faecal pellet counts, it is likely that only 1500–2000 Mountain Nyalas survive throughout the range. There are none currently kept in captivity (East 1999).



Mountain Nyala *Tragelaphus buxtoni* female.

Adaptations Mountain Nyalas are shy, rather elusive antelope, and have adapted to life in the relatively rich highland habitats, resulting in a specialized diet and physiology; they have a limited diet of montane vegetation, and have adapted to extreme temperature variation. As a result, it is likely that they are outcompeted by Greater Kudus in the surrounding arid lowlands. The animal's skeletal proportions, with relatively short distal limb segments, are characteristic of a mountain quadruped, which probably evolved in the relatively richer and varied periglacial habitats.

In a richer environment there is a premium on early reproduction and more open conflict over ♀♀. This ecological role is correlated with a relatively neotenic horn morphology. Males have lyrate horns that provide an effective jabbing weapon for male–male contests, but are ineffective as defensive shields. Mountain Nyalas living in continuous forests at lower elevations have an extra second spiral, suggesting that populations living in more stable lower productivity habitat may be more similar to the Greater Kudu in life history parameters (J. Malcolm pers. comm.).

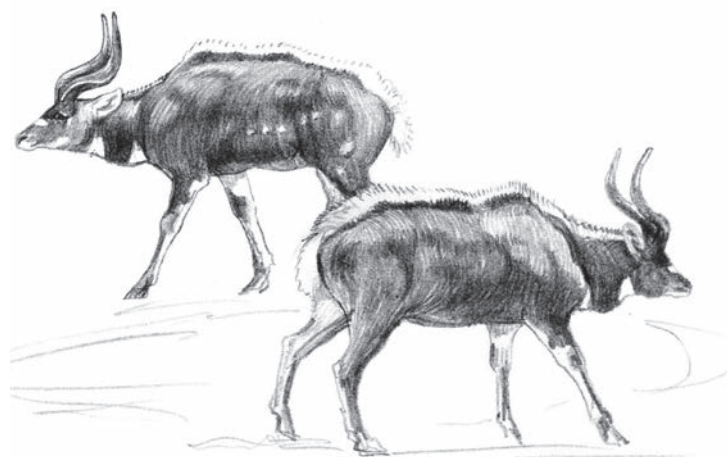
Foraging and Food Mountain Nyalas are mainly browsers, and were classified as such by Gagnon & Chew (2000) in their review of the dietary preferences of African bovids. They are selective feeders, feeding on low-growing herbs and sprigs of shrubs and bushes, and tree foliage, with more grasses eaten during the early wet season. Favoured species include *Artemesia afra*, *Hypericum revolutum*, *Kniphofia foliosa*, *Solanum sessilistellatum* and *Hagenia abyssinica* leaves, which they either pick from the ground or use their horns to bring branches within their reach.

On the afroalpine grassland, Mountain Nyalas frequently eat *Alchemilla rotti*, *Helichrysum splendidum* and the lower leaves of *Lobelia rynchopetalum*. They sometimes feed on the site of a fresh burn or on the lush green of abandoned homesteads, and have been observed eating lichens, ferns and aquatic plants (Hillman 1986a).

Mountain Nyalas spend the night in the forest fringes where they probably feed part of the time, coming out early in the morning and late afternoon to feed in the grassland fringes, using the woodland and heather thickets during the hotter and colder times of the day. However, some animals often feed briefly in the middle of the day, laying down between feeds. This pattern is probably determined by the weather, with animals preferring to stay in cover during frosts and midday heat and coming out when it is overcast or raining. In the dry season (Nov–Mar), when the grassland is in poor condition, many Mountain Nyalas

move up into wooded areas and into the thick ericaceous heath. They move mostly at night to avoid human disturbance by day.

Social and Reproductive Behaviour Mountain Nyalas have a highly cohesive basic social group consisting of an adult ♀, accompanied by her calf of the previous year, and a calf of the current year. Family units aggregate with others for short periods of time to form small herds of 4–5 (mean group size = 9) (Hillman 1986a). Apparently, herds have always been small, even when the species was more common, with herds of 4–12 reported by Maydon (1925). Larger more fluid groups of up to 100 animals are often seen in Bale, with family units moving in and out (Hillman 1988a). Size and longevity of these larger groups varies with season, habitat type and time of day. Female–young groups are often monitored by adult ♂♂, depending on the presence of oestrous ♀♀. Young ♂♂ leave the family herds at around two years of age and join other adult and young bulls to form bachelor groups of up to 13 animals (Hillman & Hillman 1987).



Circling dominance display by male Mountain Nyala *Tragelaphus buxtoni*.

Males are not territorial, and have home-ranges of 15–20 km² in the wet season, with ♀♀ and juveniles using smaller wet season home-ranges of 5 km² (Hillman 1986a). Dry season ranges are significantly larger for both sexes. A dominance hierarchy is apparent in male herds, maintained by pushing and tussling of horns in the young and ritualized displays in the older ♂♂. Old bulls live alone, occasionally approaching a herd to check for receptive ♀♀. More ♂♂ are associated in mixed-sex groups during the period when most mating, pre-mating and follow-up behaviour takes place. Although intense following is occasionally observed throughout the year bulls are more likely to be seen alone during the dry season.

Bulls follow receptive ♀♀ persistently and test their vulvas, followed by flehmen behaviour. Often, 3–4 bulls follow in ritualized parallel walks. When two evenly matched bulls meet, they engage in a wary circling dance. They move very slowly, with strutting gait and head lowered, their spinal crests and fluffed tail raised. Sometimes the strut gives way to a stiff sideways shuffle, until eventually smaller ♂♂ give way and drift away. Less often the ♂♂ take the challenge with a brief heated clash of horns. Rutting ♂♂ engaged in these ritualized walks often carry 'decorations' of soil, branches and grass tussocks hanging off their horns.

Calves lie up for several weeks in cover, later rejoining their mother. Mountain Nyalas are mainly silent, but ♀♀ may utter a low bark when alarmed or 'cough' when the threat is less serious (Brown 1969a).

Reproduction and Population Structure Females first mate at two years of age, giving birth to a single calf about 8–9 months later. In Bale, calving takes place throughout the year, with a peak of births (70%) from Sep to Nov, towards the end of the wet season (Hillman 1988a). There is a high calf to adult ♀ ratio, suggesting a calving rate of at least 50%, and a high survival rate of calves (Hillman 1986a).

Predators, Parasites and Diseases Possible natural predators include Leopards *Panthera pardus*, Spotted Hyenas *Crocuta crocuta*, Servals *Leptailurus serval*, Ethiopian Wolves *Canis simensis* and domestic dogs. The latter two species have been known to kill Mountain Nyala calves in and around the Gaysay grasslands in Bale (Sillero-Zubiri & Gottelli 1995, Woldegebriel 1996), but there are no records available for the other species. None is thought to have a serious effect on adult Mountain Nyalas (Brown 1969a). Lions *Panthera leo* could take adults, but they are not common in Mountain Nyala range. Calves and juveniles may be taken frequently by Leopards and Spotted Hyenas at night but the effect on survival, if any, is unknown.

Almost nothing is known regarding diseases in Mountain Nyalas, although they are susceptible to rinderpest (Fekadu Shiferaw pers. comm.). Females are often found dead during the wet season in Bale, showing symptoms compatible with those of poisoning from eating certain vegetation. Graber *et al.* (1980) recorded a fluke (*Cotylophoron cotylophoron*) and two nematodes (*Oesophagostomum walkeri* and *Haemonchus vegliai*).

Conservation IUCN Category: Endangered C1. CITES: Not listed.

Threatened directly by illegal hunting and indirectly by disturbance and destruction of montane forest and heath lands, encroachment by cattle, harassment and hunting by dogs, high-altitude cultivation, and roads. In the past, Mountain Nyalas were often seen living alongside pastoralists when the latter were present at low densities (Maydon 1925). However, permanent occupation of suitable habitat as a result of increasing human pressure and livestock populations is exerting tremendous pressure on Mountain Nyala habitat throughout the range, with anecdotal evidence suggesting the animals actively avoid livestock (C. Sillero-Zubiri pers. obs.).

This pressure is also apparent within Bale Mountains N. P., home to 60–80% of the world's Mountain Nyala population, and which was created primarily to protect the Mountain Nyala (Brown 1969a). The impact of effective conservation measures in northern Bale during the 1970s and 1980s was phenomenal, and the Mountain Nyala population flourished as a result of the exclusion of domestic stock (Hillman 1986a). Unfortunately, a decline in (and at times collapse of) park management during the 1990s resulted in human encroachment, overgrazing, illegal hunting and Mountain Nyalas

moving out of optimal habitat. Additionally, the constant passage of people through their range disturbs their foraging habits.

Although Mountain Nyalas are fully protected by law there has been a proliferation of hunting licences issued out to hunting concessions around Bale. The absence of enforcement and the general ignorance of protective legislation among the local people, and the failure of police and other officials to make any serious attempt to enforce the law, restrict effective protection to a small area of habitat (20 km²) in Gaysay and around Bale Mountains N. P. headquarters. Elsewhere, Mountain Nyalas are extensively hunted for meat and horns, the latter used for local medicine and to make teats for traditional milk bottles.

Conservation action required in Bale Mountains N. P. and adjacent hunting areas includes the enforcement of patrolling to curb cattle grazing and the protection of the Mountain Nyala population from illegal hunting. The park should ideally be extended northward to include suitable habitat within hunting blocks. There is also a need to extend patrolling to the higher-altitude areas of the park, where uncontrolled livestock grazing needs to be checked. Elsewhere illegal hunting needs to be controlled throughout the Arsi Mts, where the recent establishment of an additional protected area may deliver some conservation benefit for the species. Although it has been argued that high licence fees may finance conservation measures and derive a benefit to local people the current quota of adult bulls made available for trophy hunting may be unsustainable in the long term. Hunting blocks in Arsi have been hunted out and concessions moved to Bale, with continued pressure by the industry for additional hunting blocks and larger quotas. While legal hunting is restricted to adult ♂♂, trophy size needs to be monitored carefully. Absence of old bulls or a sex ratio imbalance may affect reproduction and population dynamics.

Measurements

Tragelaphus buxtoni

HB (♂♂): 2400–2600 mm

HB (♀♀): 1900–2000 mm

T: 200–250 mm

HF c.u.: 550–600 mm

E: 230–250 mm

Sh. ht (♂♂): 1200–1350 mm

Sh. ht (♀♀): 900–1000 mm

WT (♂♂): 180–300 kg

WT (♀♀): 150–200 kg

Chercher and Bale Mts, Ethiopia (Oboussier 1978, park records unpubl.); mean and sample number not given

Record horn length is 100.3 cm for a pair of horns from the Chercher Mts (Rowland Ward)

Key References Atickem *et al.* 2011; Brown 1969a; East 1999; Evangelista *et al.* 2008; Hillman 1986a, 1988a; Hillman & Hillman 1987; Maydon 1925; Refera & Bekele 2004.

Claudio Sillero-Zubiri

Tragelaphus scriptus BUSHBUCK

Fr. Guib Harnaché (Antilope Harnaché); Ger. Schirrantilope

Tragelaphus scriptus (Pallas, 1766). Misc. Zool. p. 8. No locality cited but based on 'Le Guib' of Buffon, from 'Sénégal'.



Senegal Bushbuck *Tragelaphus scriptus* (*scriptus* group).

Taxonomy No fewer than 27 subspecies were recognized by Allen (1939) and this was reduced to 23 by Haltenorth (1963); only nine were accepted by Ansell (1972). Kingdon's (1997) treatment largely echoed that of Ansell (1972), except that he did not recognize *powelli* (which Haltenorth [1963] had included in *decula*), and accepted two subspecies found in the montane regions of E Uganda (*barkeri* and *heterochrous*, which Ansell [1972] included in *bor*) for a total of ten subspecies. Grubb (1985) recognized six subspecies in East Africa, and Meester *et al.* (1986) three from southern Africa. Most of the variation within the species has been analysed based on coat colour, patterns of black/dark brown and white markings on the legs, lower shoulder, belly line and haunches, and patterns of spotting and stripes. It might be that some of the characteristics are controlled by hormones or diet given the large variation that can occur even at a single site (Kingdon 1982).

Recently, continent-wide variation in the Bushbuck has been investigated using mitochondrial markers (control region, cytochrome *b*) revealing that the Bushbuck comprises two genetically divergent lineages: a *scriptus* group from the north-western half of the continent, and a *sylvaticus* group from the south-east (Moodley & Bruford 2007). Further molecular analysis (Moodley *et al.* 2009; and see Hassanin *et al.* 2012) suggests that these may represent two distinct species as suggested by early taxonomists (e.g. Sclater & Thomas 1899/1900). The subspecific taxonomy adopted here is a combination of several taxonomies, principally those suggested by Grubb (1985, 2005) and Meester *et al.* (1986), with modifications from Kingdon (1997) and the study by Moodley & Bruford (2007). Synonyms: *barkeri*, *bor*, *brunneus*, *cottoni*, *dama*, *decula*, *delamerei*, *dianae*, *dodingae*, *eldomae*, *fasciatus*, *fulvochraceus*, *gratus*, *haywoodi*, *heterochrous*, *insularis*, *johannae*, *knutsoni*, *laticeps*, *locorinae*, *makalae*, *massaicus*, *meneliki*, *meridionalis*, *meruensis*, *multicolor*, *nec*, *nigrinotatus*, *obscurus*, *olivaceus*,

ornatus, *phaleratus*, *pictus*, *powelli*, *punctatus*, *reidae*, *roualeyni*, *roualeyni*, *sassae*, *signatus*, *simplex*, *sylvaticus*, *tjaderi*, *typicus*, *uellensis*. Chromosome number: 2n = 33 for ♂, 2n = 34 for ♀ (Wallace 1977).

Description A medium-sized antelope with a great variation in coat colour and patterning across its wide geographical range. Head red or brown with white spots or flashes on the cheeks below the eye. Ears large with white around the rim and black flash inside the ear towards the base contrasting with the pink above it. Females and young are generally red whereas adult ♂♂ become progressively darker with age, sometimes to a dark brown and almost black. All age/sex groups have a white belly extending back to a broad, woolly tail that is red/brown above and white below. A dorsal crest of lighter coloured hair is present down the back of the animal. Legs are long and thin, with white fetlocks above black hooves. Hindquarters are more developed than the forequarters. The back is rounded due to shorter forelimbs (metacarpus is 20% shorter than metatarsus; Hofmann 1973). Western forms have a 'harness' with vertical and horizontal white body stripes whilst the eastern and southern 'sylvan' populations are plainer with fewer light streaks or spots on the flanks or haunches. Some montane forms have longer hair around the neck and face. Young are similar in colour to adult ♀♀ but stripes are more marked. Males are larger in body size than ♀♀, sometimes up to 50% larger (Wilson & Child 1964). Females have two pairs of inguinal nipples.

Only ♂♂ bear horns, which are smooth and have one twist in the spiral and can be straight or slightly kinked. Simpson (1973), who discussed tooth replacement and wear in *T. s. ornatus*, recorded cases where skulls had supernumerary teeth (one specimen had 16 premolars, four of which probably developed from the twinning of tooth buds).

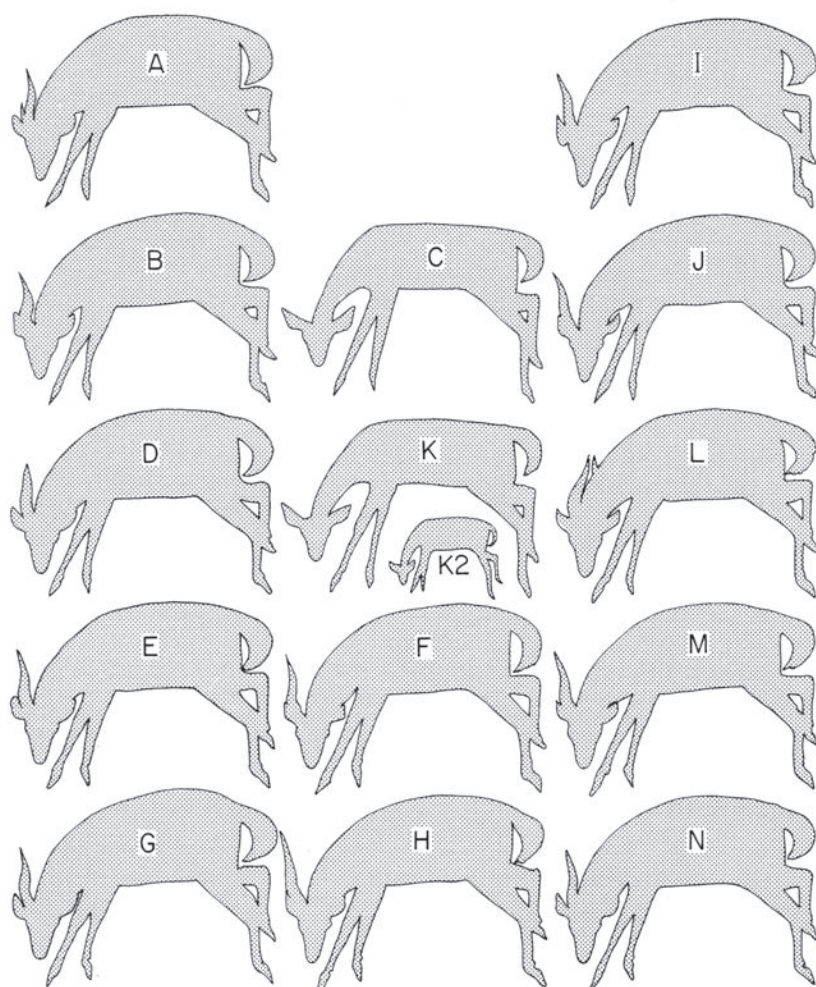
Geographic Variation Based on molecular data, Bushbucks can be grouped into two main groups: a *scriptus* group that includes most of the Bushbucks found in West and central Africa, and which tend to be more clearly striped and spotted, and a *sylvaticus* group that is found in East and southern Africa and is generally plainer in coat patterns. Between these two groups several forms occur that show some intermediate phenotypic characteristics, but which can be clearly assigned, at least on genetic analysis, to one of the two groups (Moodley & Bruford 2007, Moodley *et al.* 2009). Grubb (1985) identified four main groups, including the *scriptus* and *sylvaticus* groups, and then grouped the intermediate subspecies into a further two groups, namely *decula* and *fasciatus* (but later lumped *fasciatus* with *sylvaticus*; see Grubb 2005).

Scriptus group (Harnessed Bushbucks):

T. s. scriptus (incl. *gratus*, *typicus* and *obscurus*) (Senegal Bushbuck): West Africa, from Senegal to Liberia. Males rich dark rufous with black suffusions, with vertical stripes down the back and horizontal



Bushbuck *Tragelaphus scriptus* polymorphism (see key opposite).



- A A dark morph of West African *scriptus* male
- B West African *scriptus* male
- C West African *scriptus* female
- D A light morph of West African *scriptus* male
- E } Three males from a single locality (Kasulu, Tanzania) to show variation in pattern and colour (*dama*)
- F }
- G }
- H Pale male from Ujiji, Tanzania (*dama*)
- I Ethiopian Mts male (*meneliki*)
- J Pale male from Moyale, North Kenya
- K } Four animals from a single high-altitude locality (Mt Elgon) (K + K2: female and her young) (*heterochrous*)
- (K2) }
- L }
- M }
- N Male from Fort Portal, Uganda (*dama*)

stripes with spots on the shoulders, flanks and hindquarters; ♀♀ chestnut with fewer white stripes; this subspecies has the largest number of white markings on the body.

T. s. phaleratus (incl. *knutsoni* and *johannae*) (Kabinda Bushbuck): Cameroon, Gabon, Equatorial Guinea, W Congo R., W DR Congo. A montane form (*knutsoni*) confined to the region above the forest zone on Mt Cameroon is sometimes recognized as a separate subspecies (e.g. Grubb 2005). *Tragelaphus s. phaleratus* lies within the phenotypic range of *T. s. scriptus* (indeed, Grubb [2005] included *phaleratus* as synonymous with the nominate form), but without any blackish suffusions except on the withers and upper legs. A longitudinal band is often absent, particularly in ♀♀.

T. s. bor (incl. *cottoni*, *dodingae*, *meridionalis*, *pictus*, *punctatus*, *signatus* and *uellensis*) (Nile Bushbuck): NE Nigeria, Lake Chad, E Cameroon, Central African Republic, N DR Congo, S Sudan and NW Uganda, Ethiopian lowlands. Males and ♀♀ yellowish-brown in colour with ♀♀ yellower (in ♂♂ this contrasts strongly with black markings on belly); ♂♂ have relatively short and straight horns. Molecular data evidence intergradation with the Niger basin form (see below), with *T. s. phaleratus* in Cameroon and *T. s. dama* in NE DR Congo and NW Uganda.

T. s. decula (Abyssinian Bushbuck): N, S and W Ethiopia and parts of Eritrea. Small in size, with short horns in ♂; ♂ is dull sandy-ochre with grizzled hairs, giving appearance of dark brown or blackish-brown coat; ♀ light sandy-ochre with dark brown dorsal stripe

expanded into broad blackish saddle; few white markings on coat except an upper dorsal white stripe (Grubb 1985). Here attributed to the *scriptus* group following Moodley & Bruford (2007).

Moodley & Bruford (2007) distinguished three further distinct forms geographically intermediate between *T. s. scriptus* and *T. s. phaleratus*: two forms from the Upper Volta and Lower Volta, and a third form ranging from Togo to about the Cross R. in E Nigeria.

Sylvaticus group (Sylvan Bushbucks):

T. s. sylvaticus (Cape Bushbuck): southern and eastern coast of South Africa, from the Western Cape to S KwaZulu–Natal. Male dark brown, with hair at base of neck often lost in old ♂♂; little or no trace of white stripes on body (typical of *T. s. ornatus*), but some spots on sides of belly and hindquarters; ♀ fawn brown with some spotting as in ♂ (darker in colour than *T. s. ornatus*). Intergrades with *T. s. delamerei* and *T. s. roualeyni* in NE South Africa.

T. s. roualeyni (Limpopo Bushbuck): south-east Africa (NE South Africa, S Mozambique, E Swaziland and S Zimbabwe, E Botswana). Phenotypically intermediate between *T. s. ornatus* and *T. s. sylvaticus*. Males dark red and ♀♀ darker than *T. s. sylvaticus*; both sexes lack the vertical white stripes on the coat and are less spotted than *T. s. ornatus*. Treated as distinct by Meester *et al.* (1986), but considered synonymous with *sylvaticus* by Grubb (2005).

T. s. ornatus (Chobe or Zambezi Bushbuck). South-central Africa (N Zimbabwe and N Botswana, NE Namibia, S DR Congo, C and E Zambia, and ranging into Tanzania). Males dark red with distinct vertical stripes (up to eight) on coat and extensive white throat, and ♀♀ chestnut with fewer white stripes; both sexes have extensive white spots on shoulders and particularly the hindquarters. Due to its pronounced harness pattern, initially classified with the *scriptus* group, but more appropriately included in the *sylvaticus* group (Grubb 2005, Moodley & Bruford 2007). Treated as a distinct subspecies by both Grubb (1985) and Meester *et al.* (1986), but considered synonymous with *sylvaticus* by Grubb (2005).

T. s. dama (incl. *barkeri*, *dianae*, *heterochrous*, *locorinae*, *sassae* and *simplex*) (Uganda or Kavirondo Bushbuck): Uganda, including Mt Elgon (*heterochrous*), W Tanzania, the Albertine Rift (*dianae*) and the Imatong Hills in SE Sudan (*barkeri*). Male yellowish-chestnut to chestnut on haunches; belly and upper limbs dark grey to black; ♀ chestnut above and buff below; flank and rump spots occur with some vertical striping; large in size with large horns in ♂♂. The montane forms (*barkeri* and *heterochrous*) are considerably darker, and were considered distinct subspecies by Kingdon (1982, 1997). Intergrades with *T. s. bor* in the north: the montane forms occur in the same area as *T. s. bor*, but are separated altitudinally. Intergrades with *T. s. ornatus* in the south-west and *T. s. delamerei* in the east. This subspecies is considered synonymous with *sylvaticus* by Grubb (2005).

T. s. delamerei (incl. *eldomae*, *haywoodi*, *meruensis*, *olivaceus* and *massaicus*) (Maasai Bushbuck): C and E Tanzania, C and S Kenya, Mozambique, Malawi, E Zambia, E Zimbabwe and E South Africa. Large size, with large horns in ♂♂. Male dark brown, lighter at rump; belly and upper limbs dark brown; ♀ reddish-chestnut with yellowish cheeks contrasting with white throat. The montane form (*haywoodi*) from Mt Kenya, Kilimanjaro, Meru, Hanang and the Gregory Rift is phenotypically distinct, and is given subspecies status by Moodley & Bruford (2007). Intergrades with *T. s. dama*, but with less rump and flank spots. Treated as distinct by Grubb (1985), but later considered synonymous with *sylvaticus* by Grubb (2005).

T. s. fasciatus (Somali Bushbuck): NE Tanzania, E Kenya, E Somalia and presumably along the Juba R. into E Ethiopia. Adult ♂♂ usually greyish-ochre, sometimes brownish-grey; ♀♀ yellow-ochre; both sexes have greyish necks; relatively large in body size with large, widespread horns in the ♂; dorsal neck hairs relatively short in the ♂. Grubb (1985) regarded it as a very distinctive subspecies, though he later included it in *sylvaticus* (Grubb 2005).

T. s. meneliki (incl. *powelli*) (Menelik's Bushbuck): Ethiopian Highlands. Adult ♂ dark chocolate brown (though some are paler), with only white spots on rump as coat markings; ♀ dark russet brown with no dorsal stripe and 1–3 buffy spots on haunches; horns in ♂ relatively narrow and straight. Here attributed to the *sylvaticus* group following Moodley & Bruford (2007).

Moodley & Bruford (2007) distinguished three further forms: two in the Luangwa Valley and the middle Zambezi Valley, and a third from Angola; Angolan animals were referred to the subspecies *T. s. ornatus* by Crawford-Cabral & Veríssimo (2005).

Similar Species

Tragelaphus spekii. Swamp and swamp forest-dwelling species from central Africa and, marginally, from West Africa to Uganda, W

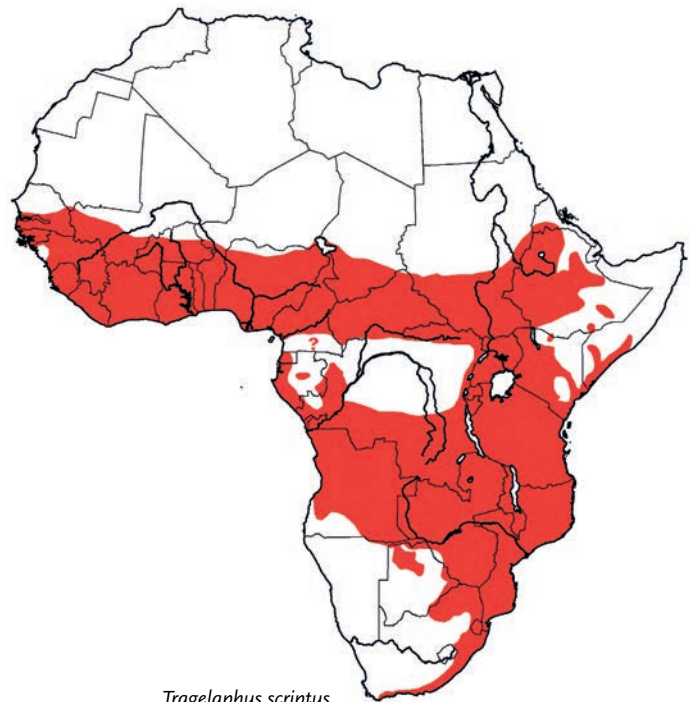
Tanzania and Zambia. Larger with longer hooves; shaggier ♀♀ are most similar but ♂♂ are darker grey/brown with long sharply keeled horns; generally found in waterlogged or swampy habitats.

T. angasii. Thicket and forest habitats of Malawi, Mozambique, Zimbabwe, South Africa and Swaziland. Larger; in ♂♂ horns longer (typically >560 mm), well-developed dorsal crest, plus fringe of long dark hair along throat and ventral surface to between hindlegs, and rufous 'socks' (carpal and tarsal) contrast with dark upper legs; in ♀♀ vertical stripes more well developed than southern forms of Bushbuck, and tail longer.

T. eurycerus. In West Africa, from Sierra Leone to Benin, and from the Sanaga R. in Cameroon along the lowland forest zone to E DR Congo; isolated montane populations exist on Mt Kenya, Mau and Eburu forests, and the Aberdares. Larger and stockier; dark russet red colour, which tends to darken on the forequarters and limbs with age; black legs with patches of white distinguish this species from the Bushbuck, which has more red/brown and white legs.

Distribution Endemic to Africa. The Bushbuck is among the most widespread of African antelopes, occurring in some 40 African countries, more than any other antelope species (East 1999). The species ranges widely from Mauritania, Senegal and Guinea-Bissau across West Africa, south of the Sahara, around the forests of the central Congo Basin to north-east Africa (SW Eritrea, W and C Ethiopia) then southwards throughout East Africa and the more mesic areas of southern Africa to around Bredasdorp in the Western Cape of South Africa (East 1999, Skinner & Chimimba 2005). It also occurs on some small islands off the African mainland including Orango N. P. in the Bijagos Archipelago off the coast of Guinea-Bissau (East 1999). The only sub-Saharan country from which it has not recently been recorded, and where it may formerly have occurred, is Lesotho (Lynch 1994).

Habitat Bushbucks occur in a wide variety of habitat types across Africa, being absent only from arid and semi-arid regions and dense

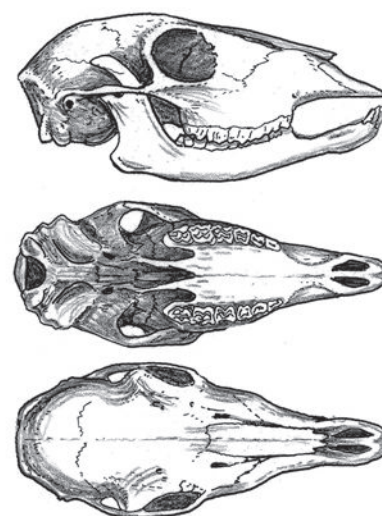


Tragelaphus scriptus

closed-canopy forest (as typical of parts of DR Congo). They range from low altitudes near the coast in southern, East and West Africa (Keep & Broker 1986, Coates & Downs 2006) up to 4000 m on the mountains of East Africa (Plumptre 1991, East 1999). Bushbucks require some cover and are most often associated with woodland, scrub and forest edges. Bushbucks appear reluctant to utilize areas away from surface water, which may be explained by them exhibiting high evaporative heat loss response, mainly due to the production of strongly diluted urine (Schoen 1971). In some areas, Bushbucks exhibit seasonal movements; in the Zambezi Valley, Simpson (1974a, b) recorded them dispersing from the riverine underbush in the warm, wet summer months (Sep–Mar), to the thickets, where water is temporarily available, returning to the riverine associations during the drier periods. In Mole N. P. in Ghana, Bushbucks preferred marshy habitat over riverine and open savanna (Dankwa-Wiredu & Euler 2002). Bushbucks are often able to survive in human-dominated landscapes such as on large farms as well as on coffee and timber (eucalypt and pine) plantations (Odendaal & Bigalke 1979, Odendaal *et al.* 1980, Schmidt 1983) and may cause severe damage to seedlings (de Zwaan 1977, Schutz *et al.* 1978). The species has disappeared from some of its former range, particularly in drier areas where habitat destruction and desertification have occurred, but is expanding where equatorial forest is being opened up by agriculture and logging, creating more forest edge and bush (East 1999).

Abundance Owing to the cryptic nature of this species, abundance is generally underestimated by aerial flights and gives densities of 0.01–0.5/km². Ground surveys (Plumptre 1991, Plumptre & Harris 1995, Mizutani 1999) and individual recognition (Jacobsen 1974, Waser 1975a, Allsopp 1978) provide very much higher, more accurate, estimates. In grassland with thickets on the Mweya Peninsula in Queen Elizabeth N. P., W Uganda, Bushbucks occurred at densities of about 26/km² (Waser 1975a), whilst in mixed-forest, bushland and grass in Nairobi N. P., Kenya, density was estimated to be similar at 30.1/km² (Allsopp 1978). In montane forest of the Virunga Mts, Rwanda, estimated densities (using faecal counts) were 11.1–44.2/km² in different habitats with highest values in or at the edge of woodland (Plumptre & Harris 1995). In riverine forest along the Sengwa R., Zimbabwe, Jacobsen (1974) recorded the highest-known densities of up to 67/km². In ground surveys that counted several species at the same time in central and western Africa, lower estimates from 0.08 to 2.0/km² have been obtained (East 1999, Fischer & Linsenmair 2001a, Brugière *et al.* 2005). For the Ethiopian Highlands (Denkoro Forest), a mean population density of 11.8/km² was reported (Yazew *et al.* 2011). East (1999) estimated total population size in Africa at about 1.34 million individuals, which is probably an underestimate.

Adaptations The widespread distribution of the Bushbuck across several habitat types implies an exceptionally adaptable physiology. The cryptic coat patterning provides camouflage in a wide variety of habitats. They apparently are excellent swimmers, taking to water to feed and also to flee from predators. Their large ears are probably an adaptation to detect predators and are particularly large in calves relative to body size. Bushbucks typically give a warning bark when danger threatens and other species use this as a warning too; baboons (*Papio* spp.) and Vervet Monkeys *Chlorocebus pygerythrus* have been



Lateral, palatal and dorsal views of skull of Bushbuck *Tragelaphus scriptus*.

recorded associating with Bushbucks as possibly a strategy to avoid predation by Leopards *Panthera pardus* (Allsopp 1971, Elder & Elder 1971, Wronski 1996). It is unclear why Bushbucks bark, given that they are principally a solitary species. It is possible that the bark indicates to a predator that it has been spotted, which may reduce the predator's likelihood of attacking. Possibly, other Bushbucks in the vicinity tend to be more related (e.g. matrilineal clan members; Wronski & Apio 2006, Apio *et al.* 2010) so their genes may be passed on more successfully as a result of warning them. Similarly, the white flashes of the underside of the tail when fleeing may also serve as a warning to others. Kingdon (1982, 1997) suggested that barks may function as indicators of rank, status, identity and physical movement within a local community of Bushbucks.

Bushbucks are the smallest of the tragelaphines, and yet have been the most successful in terms of distribution across Africa. Their small size and cryptic colouring and behaviour have probably allowed them to survive in smaller habitat patches and around human settlements better than the larger species. Cover seems to be the most limiting resource for Bushbucks, while food, competition and predation had no effect on female home-range size in Queen Elizabeth N. P. (Wronski *et al.* 2006e). Unlike other tragelaphine antelopes, Bushbuck horns are small and tend to spiral much less. This could be because this species lives in dense habitat and relies on flight into dense habitat to avoid predation (similar to strategies duikers use). It has been suggested that the horns of larger tragelaphines have evolved due to sexual selection rather than for defence (Walther 1964a) and it is possible that the Bushbuck's small size and greater vulnerability to predation has selected for smaller and straighter horns.

Foraging and Food Bushbucks are primarily browsers, tending to prefer herbs selected from between grasses, or young leaves of shrubs and trees; they also select young green leaves of grasses (Wilson & Child 1964, Jacobsen 1974, Simpson 1974c, Odendaal 1983, Allen-Rowlandson 1986, Plumptre 1995, Seymour 2002, Apio & Wronski 2005, Yazew *et al.* 2011; and see Gagnon & Chew 2000, Cerling *et al.* 2003, Sponheimer *et al.* 2003b). In a study of food preferences in South Africa, Bushbuck showed a strong selection for plants with high digestibility and low fibre content (Haschick & Kerley 1997a), but a



Bushbuck *Tragelaphus scriptus* adult female.



Bushbuck *Tragelaphus scriptus* young adult male.

relatively small bite size and bite rate (Haschick & Kerley 1997b). The preferred feeding height was determined as 52.5 ± 3.8 cm from the ground (Haschick & Kerley 1996).

In sites with strong seasonal variation, the diet seems to consist of herbs and young grass leaves in the wet season, replaced by the leaves of shrubs and trees in the dry season (Wilson & Child 1964, Jacobsen 1974, Okiria 1980, Smits 1986, MacLeod *et al.* 1996). Where there is little variation between seasons in a montane environment, herbs and grasses are selected throughout the year, particularly the grasses *Festuca schimperi*/*Agrostis* spp. and herbs, *Impatiens* and *Solenostemon sylvaticum* (Plumptre 1991, 1995). In drier areas such as Mole N. P., Bushbuck primarily consume herbs and rarely take grass unless young and green; *Raindia macaritha*, *R. captiatum* and *Eurene lobata* were the dominant foods in Mole N. P. (Dankwa-Wiredu & Euler 2002). *Dichrostachys cinerea*, *Pavetta albertina* and *Indigofera* spp. were preferred foods in Queen Elizabeth N. P. (Apio & Wronski 2005). In South Africa (Woody Cape N. R.), Bushbuck also fed on dicotyledonous herbs, in particular *Lycium afrum* and *Schotia afra* (MacLeod *et al.* 1996). Staple foods consumed throughout the year in Zimbabwe included leaves of three tree/shrub species, namely *Combretum mosambicense*, *Grewia flavescens* and *Trichilia emetica* (Jacobsen 1974), while in a study in Mpumalanga, South Africa, *Acacia nigrescens*, *Combretum heroense*, *Ficus* spp. and *Ziziphus mucronata* comprised up to 20% of the diet in all seasons (Seymour 2002). Where available, the pods of *Acacia* species and other fallen fruit are consumed, including *Ficus*, *Ricinodendron*, *Cordia*, *Balanites* and *Diospyros* (Wilson & Child 1964, Jacobsen 1974). Seymour (2002) has demonstrated how Bushbucks may be out-competed, during times of nutritional stress, by Nyalas *Tragelaphus angasii*, since the latter species is a mixed feeder with a greater browse height and

therefore has a competitive advantage in the late dry season when available browse is limited.

Mycophagy may be an important mechanism by which Bushbucks are able to exist in areas such as forests and plantations in which trace elements, such as copper, are not readily available (Odendaal 1983). Geophagia also has been recorded (Jacobsen 1974). Bushbucks may enter agricultural fields at night and in the early morning to eat crops and are considered a pest in some places. For example, around Parc National des Volcans in Rwanda they consume the leaves of potatoes, maize, cabbages, beans, peas, pyrethrum, wheat and tomato plants (Plumptre & Bizumuremyi 1996).

Where undisturbed, Bushbucks feed throughout the day and night (Waser 1975b, Wronski *et al.* 2006b) in regular cycles. Where there is a likelihood of detection and predation during the day they will feed mainly at night but may rest in dense cover, occasionally feeding during the day. Their movements are often associated with dawn and dusk. In Queen Elizabeth N. P., Bushbucks moved towards the thickets along the river at dawn, where it is presumably cooler during the heat of the day, and then back to the more open ridge at night (Waser 1975b). In the Virunga Mts, Bushbucks moved towards open meadows at dusk and back into the denser woodland and nettles during the day around the Karisoke Research Station (A. Plumptre pers. obs.) and they fed throughout the period they were in dense nettles (Plumptre 1991).

Social and Reproductive Behaviour Bushbuck are generally solitary or in pairs, with single ♂♂, single ♀♀ and male–female pairings accounting for most observations in the areas where the species has been studied: 91% in N Zimbabwe (Wilson & Child 1964), 79% in N Botswana (Elder & Elder 1971), 74% in W Uganda (Wronski 2004) and 71% in Knysna, South Africa (Odendaal & Bigalke 1979).

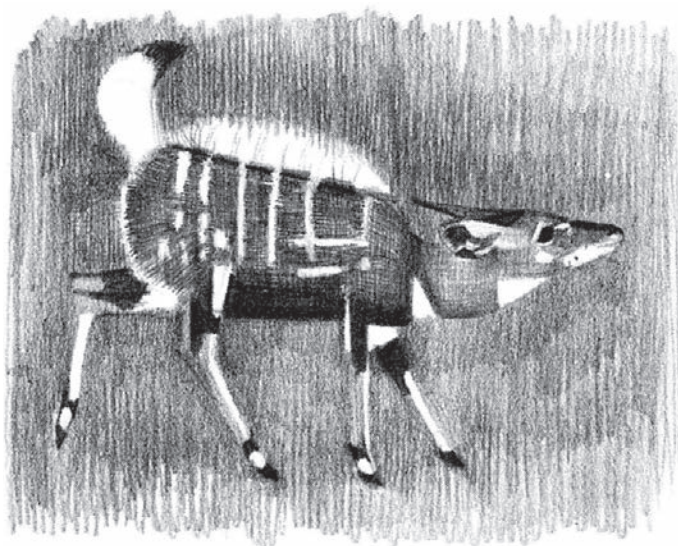
Other small associations usually consist of adult ♀♀, adult ♀♀ with young or subadults, or two or more adult ♂♂ (though such male groupings are both unusual and ephemeral). Larger groups of 9–12 have been recorded (Simpson 1974a, Simbotwe & Sichone 1989, Brugière *et al.* 2005, A. Plumptre pers. obs.). In the Virunga Mts, Bushbucks were generally solitary during the day when in dense vegetation but when they moved to clearings in the forest to feed in the evening it was not uncommon to see several individuals together (A. Plumptre pers. obs.). In this case the animals were not in the strict sense forming a group but were associating with each other only because of a common attraction to the same resources. They did not move and function as a coordinated group. Wronski *et al.* (2009b) compared group sizes among six different populations and found no significant difference in relative frequencies of group size categories.

A study in Uganda showed that ♀♀ are organized in matrilineal clans, sharing a common home-range and jointly defending that area against non-related ♀♀ (Wronski & Apio 2006, Apio *et al.* 2010). Home-range overlap between related ♀♀ was significantly higher than that between non-related individuals. Agonistic interactions between ♀♀ appeared significantly more often between non-related ♀♀ but rarely between kin (Wronski & Apio 2006). Moreover, ♀♀ keep close social bonds (e.g. reciprocal grooming, also between adult related ♀♀; Walther 1964a, Wronski *et al.* 2006d) and individuals communicate through localized defecation sites (mostly females to males and females to females of the same clan; Wronski 2006b). Localized defecations function neither in terms of parasite avoidance nor as a consequence of allelomimetic behaviour (Apio *et al.* 2006a).

Individual home-ranges overlap (Jacobsen 1974, Allsopp 1978, Allen-Rowlandson 1986, Coates & Downs 2005, Wronski 2005, Wronski & Apio 2006); some studies have shown that there is little defence of territories (Waser 1975a, Allsopp 1978), while others have recorded pronounced territoriality (Verheyen 1955, Walther 1964a, Jacobsen 1974). Owen-Smith (1975) discusses territoriality in Bushbuck in light of social patterns that have evolved in tragelaphine antelopes. Recent

studies have revealed further insights into the question of territoriality in Bushbuck. In a study in KwaZulu–Natal, South Africa, Bushbucks utilized a core area within their home-ranges in which 50% of their time was spent in approximately 17.0% and 11.7% of their total home-range for ♂♂ and ♀♀, respectively, and there was substantial overlap in core areas (Coates & Downs 2005). However, in Uganda, a considerable defence of 50–70% of home-range cores (territories) was observed (Wronski 2005, Wronski *et al.* 2006, 2007b, Wronski & Plath 2006). Home-range cores of adult ♂♂ did not overlap and were therefore considered exclusive areas. Moreover, adult territorial ♂♂ perform intense scent-marking (i.e. vegetation horning, front rubbing; Wronski *et al.* 2006d, 2007b) and these marked areas correspond with exclusive core areas (Wronski *et al.* 2006a). A dominance hierarchy as suggested by former studies (e.g. Jacobsen 1974) could explicitly be excluded (Wronski 2004, Wronski *et al.* 2009a). Instead, male Bushbuck exhibited two age-dependent mating tactics: adult territorial ♂♂, and young adult non-territorial ♂♂, which frequently attempt to mate with ♀♀ although they indulge in less pre-mating behaviour, herding and monopolization of ♀♀ (Apio *et al.* 2007). Males and ♀♀ advertise their presence and position by standing on termite mounds or close to vertical structures (Wronski *et al.* 2007a).

Home-range sizes vary between sites. In Nairobi N. P., small ranges of 0.25–2.0 ha were recorded, the larger ranges being occupied by juvenile animals (Allsopp 1978), whereas the home-range of a dominant ♂ in Sengwa Valley, Zimbabwe, was 5 ha (Jacobsen 1974). In an area of valley bushveld in KwaZulu–Natal, total home-range size for ♂♂, using minimum convex polygons, was estimated at 33.9 ha and for ♀♀ at 12.0 ha (Coates & Downs 2005). In Queen Elizabeth N. P., Waser (1975a) recorded home-ranges of adults varying from 6.3 to 26.5 ha for adults with one subadult ♂ having a range of 35.2 ha. In contrast to these recorded home-range sizes, average home-range size in Knysna Forest (South Africa, which is a more temperate climate) was 102 ha (Odendaal & Bigalke 1979), while Allen-Rowlandson (1986) recorded a mean



Bushbuck *Tragelaphus scriptus* display.



home-range size of 120 ha for ♂♂ and 60 ha for ♀♀ in afro-montane forest in KwaZulu-Natal. Home-range size apparently increases with decreasing density across the range of the species, and density appears to increase with an increase in rainfall during the growing season (Odendaal & Bigalke 1979).

In Queen Elizabeth N. P., animals spent 38% of their time feeding, 50% resting, immobile or ruminating and 12% moving (Waser 1975b). In the montane habitats of the Virunga Mts a similar amount of time was devoted to these activities: 50% feeding, 44% resting or ruminating, 6% walking or grooming (Plumptre 1991). Similar patterns were described for Bushbuck from Denkoro Forest in the Ethiopian Highlands (Yazew *et al.* 2011). Wronski *et al.* (2006c) investigated differences in activity patterns in relation to time of day, season, radiation, moonlight, age and sex. Bushbucks were found to show peak activities around sunrise and sunset. No difference in the mean activity rates was found between the dry and wet season. Daytime activity was not predicted by differences in sun radiation, nor was night-time activity predicted by the presence or absence of moonlight. The activity of adult territorial ♂♂ was strongly positively correlated with that of ♀♀, whereas that of non-territorial ♂♂ was not correlated with the activity of ♀♀.

As noted already, Bushbucks often associate with baboons (*Papio* spp.) at various sites across the continent and it is thought that both species benefit from the association with the Bushbuck's sense of smell and the baboon's ability to spot predators from trees (Elder & Elder 1971, Allsopp 1978, Wronski 1996). Bushbucks were accompanied by baboons in about 35% of sightings in Chobe N. P., Botswana and Nairobi N. P. (Elder & Elder 1971).

Males threaten other ♂♂ by a stiff-legged walk and lateral presentation, with the head up (Walther 1964a, Kingdon 1982, Estes 1991a, Wronski *et al.* 2006d). They raise the hairs on the dorsal crest, arch the back and raise the tail to expose the white underside and may circle each other. In Uganda, territorial ♂♂ were observed escorting intruders to the edge of their territories (Wronski *et al.* 2006d). Occasionally, a ♂ will feint attack and lower his horns and horn at the ground. If closely matched, the ♂♂ may raise the intensity of combat with head-on clashes and locking horns, and attempts made to gore the flanks of the opponent (Walther 1964a, Allsopp 1978, Wronski *et al.* 2006d). Defensively, a ♂ keeps the head low, turns away and licks the aggressor. Females also show agonistic interactions, but on a much lower scale (Wronski & Apio 2006, Wronski *et al.* 2006e). When approached by a predator, ♂♂ or ♀♀ freeze, sinking to the ground with the neck and head stretched out along the ground. If the danger is close, they sometimes bark and flee with their tails raised, exposing the white underside in a bright flash. The young have a bleat not unlike a goat's call when lost from the mother, but adults do not vocalize much other than barking.

When courting, ♂♂ nuzzle the female's genitals, lick her, rub cheeks on her rump, press the neck or head on her rump and test urine by licking the stream as it falls to the ground. In the urine test, the ♂♂ approach with neck extended and head low, with no dorsal crest showing and the ♀ responds by crouching, a position typically used in urinating with the hindlegs bent and the tail raised. Males tend the ♀ while she is receptive, chasing off other ♂♂ unless supplanted by another ♂ (Walther 1964a, Estes 1991a).

Calves are born in areas of dense cover and lie still whenever the ♀ is away feeding. They may spend up to four months like this

before venturing into more open habitat (Estes 1991a). At about 6 months of age young ♂♂ leave their mother's home-range and join a bachelor group. From this pool they challenge existing territorial adult ♂♂ until they take over a territory (Wronski 2005). Females will stay with their mothers (and other female kin) throughout life, forming matrilineal groups (Wronski & Apio 2006, Apio *et al.* 2010).

Reproduction and Population Structure Calves are born throughout the year in the wild (and in captivity, see Mentis 1972, Skinner *et al.* 2002), although there are certainly some seasons where more calves are dropped than others (Ansell 1960a, Allsopp 1971, Simpson 1974a, Plumptre 1991, Apio *et al.* 2009). In Kenya, there were peaks in births in Feb and Sep, just prior to the two main wet seasons when more nutritious forage was available (Allsopp 1971). In the Virunga Mts, births were more clumped from Jun–Sep, a drier period of the year in an environment where the cold rain can lead to mortality (Plumptre 1991). In Zambia, calves were recorded throughout the year (Wilson & Child 1964).

Gestation length is around 24–35 weeks with the average being around 25–26 weeks (Allsopp 1971, Dittrich 1972, Mentis 1972) and calves dropped weigh 3–4 kg. Usually one calf is born although occasionally twins occur. Calving intervals measured in captive animals are around 35–36 weeks and a ♀ can produce another calf within 48–54 weeks after the previous birth (Mentis 1972, Dittrich 1974, von Ketelhodt 1976a). Male calves develop horns about seven months after birth (von Ketelhodt 1976a) and ♂♂ develop the secondary sexual characteristics of a dorsal crest and darker pelage about two-and-a-half years after birth (Kingdon 1982). Males become sexually mature from about ten months of age, but do not take part in breeding until they are at least two years old (Mentis 1972). Females become sexually mature at 14–19 months (Dittrich 1972, Mentis 1972, Simpson 1974a, Allen-Rowlandson 1986). In Zimbabwe, the mean age at maturity was about 11 months in both sexes, coinciding (in ♂♂) with a combined testes weight of about 15 g (Morris & Hanks 1974).

Sex ratios at birth are equal, but adult ratios have varied from 45–115 ♂♂ to 100 ♀♀ in different sites (Wilson & Child 1964, Mentis 1972, Waser 1975a). Adult sex ratio obtained from a tsetse fly control area in Zambia was reported to be 80 ♂♂ to 100 ♀♀ (or 1 ♂ : 1.48 ♀; Wilson & Child 1964). Longevity in the wild has been reported at about 12–13 years (Mentis 1972); in captivity, maximum longevity has been recorded as 16 years and nine months for *T. s. sylvaticus* (Jones 1993).

Predators, Parasites and Diseases Leopards (Bushbuck are a significantly preferred prey, Hayward *et al.* 2006a), Lions *Panthera leo*, Spotted Hyenas *Crocuta crocuta*, Cheetahs *Acinonyx jubatus*, African Wild Dogs *Lycaon pictus*, Nile Crocodiles *Crocodylus niloticus* and African Rock Pythons *Python sebae* have all been recorded killing adults, and Robust Chimpanzees *Pan troglodytes*, baboons, Caracals *Caracal caracal* and several eagle species have been reported taking calves. African Golden Cats *Profelis aurata* also are probable predators (Kingdon 1982).

Zieger *et al.* (1998c) recorded a Bushbuck found dead on a ranch in Zambia with multiple superficial abscesses in the neck region, extensive granulomatous lesions in the lung, the bronchial and

mediastinal lymph nodes and several nodular lesions in the spleen. Histologically the lesions resembled those of tuberculosis, but mycobacteria could not be isolated. In Queen Elizabeth N. P., one reported case of rabies, a viral disease (Lyssavirus) that causes acute encephalitis was confirmed for Bushbuck (A. Apio & O. Bwangamoi pers. comm.).

Round (1968) provides a checklist of helminth parasites of the Bushbuck from all over Africa. The internal parasites of the Bushbuck have been relatively well investigated, particularly in southern Africa (e.g. Boomker & Kingsley 1984, Boomker *et al.* 1984, 1986), and Boomker *et al.* (1987) provided an updated list of all helminth parasites recorded from Bushbuck in South Africa at the time, including two species of cestodes (*Cysticercus* spp. and larvae of *Taenia* spp.) and 24 species of nematodes. Zieger *et al.* (1998a) recorded *Stilesia hepatica* from an animal in Zambia. Bwangamoi (1968), Woodford & Sachs (1973), Pullan *et al.* (1971) and Apio *et al.* (2006b) report on helminth parasites from Bushbuck in Uganda. Strongyle eggs recorded in faecal samples from Queen Elizabeth N. P. include *Oesophagostomum* spp., *Haemonchus* spp., *Bunostomum* spp. and the eggs of the cestodes *Moniezia benedini* and *M. expansa* (Apio 2003, Apio *et al.* 2006b). Generally, the prevalence of gastrointestinal tract parasites in Bushbuck from Queen Elizabeth N. P. is low. Apio *et al.* (2006c) tested the risk of infection with gastrointestinal parasites at different foraging height levels, and suggested that high browsing levels are responsible for low parasite infestations in Bushbuck. In the same park, Woodford (1976) reported on muscular and aberrant cysticercosis, which are conditions caused by larval stages of tapeworms infesting the musculature and connective tissues of their host. Sarcosporidiosis and larval pentastomidosis were also regularly found in the tissues of Bushbucks. Amongst the herbivores of Queen Elizabeth N. P., Bushbucks were the most commonly infested species (Woodford 1976). A filarial worm (*Setaria* sp.) was detected in blood samples of Bushbucks in the same study area. Apio & Wronski (2004) reported further on post-parturient changes in faecal helminth egg and coccidian oocyst counts of female Bushbucks in Queen Elizabeth N. P. *Eimeria* spp. was the most common coccidian infection, but did not lead to any clinical or pathological signs in the study population (Apio 2003). Apio *et al.* (2006b) investigated also seasonal, sexual and age-related variation in helminth egg and coccidian oocyst counts in the same population. The prevalence of *Moniezia* spp. and strongyle eggs was significantly higher during the wet season than during the dry season, and peak counts were recorded either during or soon after a peak rainfall. The same was true for *Eimeria* sp. Sexual and age-related differences in the prevalence of either parasite types were not found.

Other parasites recorded infesting Bushbucks include *Babesia* sp. (Bigalke *et al.* 1972) and the trematode *Schistosoma leiperi* (Malek & Ongom 1984). Trypanosomiasis, the nagana pest of cattle, is a condition commonly found in Bushbucks (Ferrante & Allison 1983, Moloo *et al.* 1995); the parasites (e.g. *Trypanosoma brucei*, *T. rhodesiae*) are transmitted by several *Glossina* spp. (tsetse flies).

In some areas, Bushbucks suffer heavy tick loads consisting predominantly of hard ticks (Ixodidae, De Castro & Newson 1984). The ixodid ticks of Bushbucks have been reported on by various authors (e.g. Dinnik *et al.* 1963, Woodford 1976, Terenius *et al.* 2000, Ntiamoa-Baidu *et al.* 2005), and Horak and co-workers (Horak *et al.* 1983c, 1989) determined actual tick and lice burdens of the species

in South Africa. Bushbucks have been infected with some tickborne diseases like bovine petechial fever (Davies 1993a), a rickettsial disease of cattle for which the Bushbuck is the reservoir host, as well as East Coast Fever, caused by a protozoan parasite regularly found in several tragelaphine species (Grootenhuis 1991).

Conservation IUCN Category: Least Concern. CITES: Not listed.

Due to its widespread distribution, presence in numerous protected areas across its range, and its ability to survive around anthropogenically disturbed habitats, this species is not thought to be threatened. The Bushbuck's tendency to hide in dense cover has enabled it to survive in areas where hunting pressure is not too high (e.g. Parc National des Volcans in Rwanda; Plumptre *et al.* 1997). However, after larger-bodied species have been extirpated from an area, this species probably succumbs prior to the smaller-bodied species such as the duikers. Indeed, there are reports of Bushbuck being replaced by species such as Common Duiker *Sylvicapra grimmia* when human impacts (e.g. frequent burning, cattle grazing) are extensive (Kumanenge 1980). In areas where hunting pressure is severe, such as the Ankole Ranching Scheme around Lake Mburo N. P. in Uganda, the reduced competition from species that became less abundant outside the protected area (such as Bushbuck) may actually benefit other species, such as Common Duiker. Indeed, Common Duiker exhibited a significant change in habitat use around L. Mburo encroaching on the vegetation type otherwise normally used by Bushbuck (Averbeck *et al.* 2009a).

Most bushmeat research has been carried out in dense tropical forests where this species either does not occur or is not very common. Data from Rwanda show that Bushbuck meat is significantly lower in price than domestic meat and was the bushmeat most commonly purchased (Plumptre & Bizumuremyi 1996, Plumptre *et al.* 1997). In Sierra Leone (Kenema & Lalehun markets, respectively), Bushbuck meat accounts for about 2.5–6.6% of all traded animals and 3.1–23.5% of total biomass (Davies *et al.* 2007). The price for 1 kg of meat on a Ghanaian bushmeat market was reported as US\$2.63 and the distance travelled until it reached the consumer was 65 km (Cowlshaw *et al.* 2007). More research is needed on the savanna/forest-edge bushmeat trade in East and southern Africa to better understand how this species is affected by the trade.

Measurements

Tragelaphus scriptus

HB (♂ ♂): 1270 (1170–1420) mm, n = 8
 HB (♀ ♀): 1200 (1140–1320) mm, n = 13
 T (♂ ♂): 210 (190–240) mm, n = 8
 T (♀ ♀): 200 (190–220) mm, n = 13
 HF c.u. (♂ ♂): 300 (290–320) mm, n = 8
 HF c.u. (♀ ♀): 280 (270–300) mm, n = 13
 E (♂ ♂): 135 (121–152) mm, n = 8
 E (♀ ♀): 136 (127–152) mm, n = 13
 Sh. ht (♂ ♂): 700 (640–740) mm, n = 8
 Sh. ht (♀ ♀): 640 (610–670) mm, n = 13
 WT (♂ ♂): 42.0 (29.0–54.0) kg, n = 15
 WT (♀ ♀): 28.0 (24.0–34.0) kg, n = 16
 Zambia (Wilson & Child 1964)

*T. s. bor**

HB (♂ ♂): 1220–1310 mm, n = 6

HB (♀ ♀): 1180–1260 mm, n = 3

Sh. ht (♂ ♂): 780, 780 mm, n = 2

Sh. ht (♀ ♀): 700, 720 mm, n = 2

*T. s. decula**

HB (♀ ♀): 1090, 1090 mm, n = 2

Sh. ht (♀ ♀): 650, 670 mm, n = 2

*T. s. fasciatus**

HB (♂ ♂): 1440, 1500 mm, n = 2

HB (♀ ♀): 1080, 1520 mm, n = 2

Sh. ht (♂ ♂): 860, 870 mm, n = 2

Sh. ht (♀ ♀): 550, 710 mm, n = 2

*T. s. delamerei**

HB (♂ ♂): 1250–1540 mm, n = 8

HB (♀ ♀): 1070–1380 mm, n = 3

Sh. ht (♂ ♂): 770–910 mm, n = 8

Sh. ht (♀ ♀): 620–760 mm, n = 3

*Eastern Africa (Grubb 1985)

The longest pair of horns of Bushbuck on record is a pair from Tolwe, North West Province, South Africa, which measured 51.4 cm (Rowland Ward)

Key References Allen-Rowlandson 1986; Allsopp 1970, 1971, 1978; Apio *et al.* 2007, 2009, 2010; Grubb 1985, 2005; Jacobsen 1974; Kingdon 1982; Plumptre 1991, 1995; Simpson 1974a, b, c; Walther 1964a; Waser 1975a, b; Wilson & Child 1964; Wronski 2005; Wronski & Apio 2006; Wronski *et al.* 2006a, b, c, d, e.

Andrew J. Plumptre & Torsten Wronski

Tragelaphus spekii SITATUNGA

Fr. Sitatunga; Ger. Sumpfantilope

Tragelaphus spekii Speke, 1863. Journal of the Discovery of the Source of the Nile, p. 223. Tanzania, Karagwe, E of L. Victoria, at a lake named 'Little Windermere' by Speke; identified as Bukoba district, L. Lwelo, 2° S, 30° 57' E by Moreau *et al.* (1946: 441).



Sitatunga *Tragelaphus spekii* gratus male.



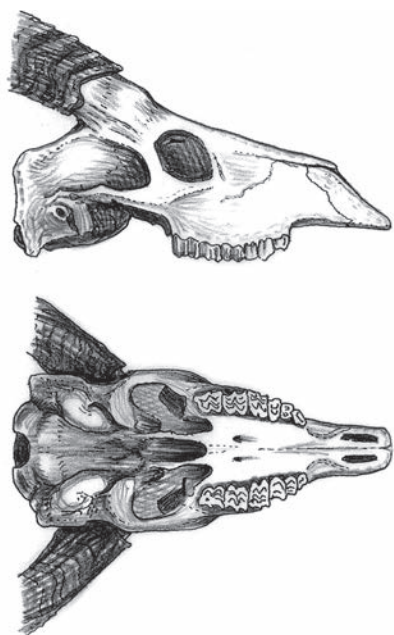
Sitatunga *Tragelaphus spekii* gratus female.

Selous (1881) found the peoples of the lower Chobe and central Zambezi Rivers using the name 'sitatunga' (*sic*), the latter confirmed by Ansell (1978) who remarks that the Lozi and Tonga of Zambia use the name 'sitatunga'.

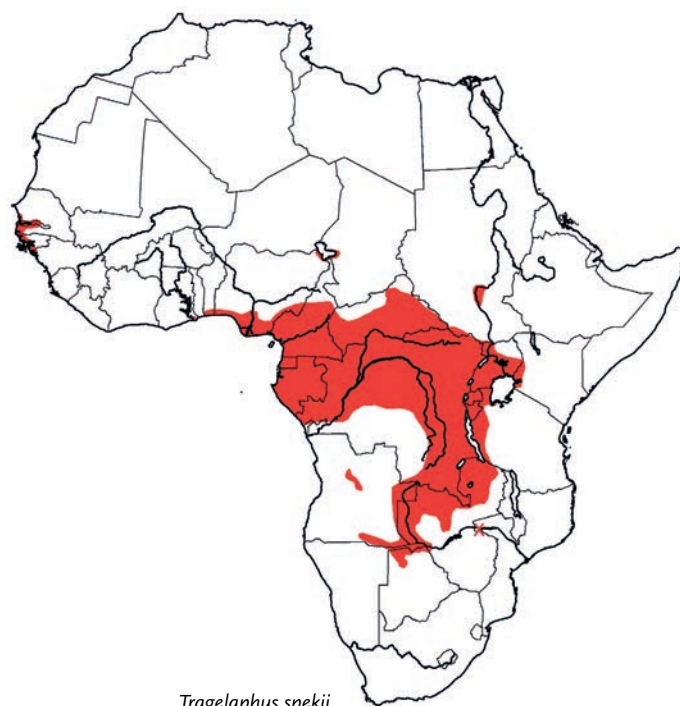
Taxonomy The scientific name has been given variously as *spekei* or *spekii* and the authority as Sclater or Speke. J. H. Speke described a young nzoé (the Kiswahili name for Sitatunga) in his Journal published in 1863 and stated in a footnote that the animal had been named by P. L. Sclater as *Tragelaphus spekii*. A year later Sclater published a description in a scientific journal under the heading *Tragelaphus spekei* sp. nov. Although Sclater's contemporaries clearly regarded him to be the authority, the rules of Zoological Nomenclature acknowledge the person who provided the first

description, and as this is clearly Speke, he is the authority and *spekii* (the genitive of the Latinized Spekius) is then the original and correct spelling (Grubb 2004).

As many as ten subspecies have been described, mainly based on hair texture, pelage colour and absence or presence of body stripes and spots. However, hair texture probably varies with climate, and pelage colour and presence of stripes and spots are highly variable even within the same population (some individuals are born with stripes and spots and others without). Furthermore, pelage colour darkens with age in some individuals, especially in older ♂♂, and stripes and spots fade with age, again especially in ♂♂ (E. Stokes pers. comm.). Sitatunga are probably monotypic, but until verified, at best only three subspecies, centred on different drainage systems, are provisionally retained (Kingdon 1982; and see Ansell [1972] who listed five). However, a



Lateral and palatal views of skull of Sitatunga *Tragelaphus spekii*.



Tragelaphus spekii

comparison of recent field descriptions spanning these basins (E. Stokes pers. comm., C. Thouless pers. obs., J. May & R. Lindholm pers. obs.) reveals that these three subspecies cannot be reliably distinguished on the oft-cited characteristics of pelage colour and pattern (see Geographic Variation). Synonyms: *albonotatus*, *anderessoni*, *baumii*, *gratus*, *inornatus*, *larkenii*, *selousi*, *speckeii*, *spekei*, *sylvestris*, *typicus*, *ugallae*, *wilhelmi*. Chromosome number: $2n = 30$ (Wurster & Benirschke 1968). Sitatungas have unusually large sex chromosomes, the X chromosome comprising 13% and the Y 7.3% of the haploid chromosomal complement in contrast to the mammalian norm of 5% (Wurster *et al.* 1968). Only one other member of the Bovidae, the Blackbuck *Antelope cervicapra*, has this peculiarity.

Description A medium-sized, swamp-dwelling antelope, exhibiting quite marked sexual dimorphism. The widely splayed, very long and narrow hooves (more than half the length of the foot) are unique. Adult ♂♂ have long pelage (4–7 cm), which is coarse to silky, dense or sparse, and uniform dark-chocolate brown, greyish-brown to grey. Top of the head and ears dark grey to dark brown, with a white chevron forward of the eyes; cheeks paler with one or two white spots, front of upper lips, chin and eyebrows white, inner ears with broad white margins. There is a white band across the throat and another across the chest. Body stripes and spots conspicuous, faint or absent. An inconspicuous, narrow, white stripe along the mid-line of the back is occasionally present. Tail dark brown at centre with white tip above, all white below. Legs same colour as body, sometimes darker at knee joint. Underside of feet naked. Adult ♀♀ similar to ♂♂, but smaller and less robust especially about the neck (see Measurements) and shoulders. The pelage is uniform bright to pale reddish-brown (usually), drab brown or rarely brownish-grey. Vertical white stripes across back, lateral stripe along flanks and white spots on thighs either conspicuous, faint or absent. Dark brown stripe usually along mid-line of back. White chevron forward of eyes usually less

distinct than in ♂ and sometimes absent. Calves woolly coated, more vibrant, but otherwise similar to ♀♀ in pelage colour and body stripes and spots. Females have two pairs of inguinal nipples.

Horns, present in ♂♂ only, are long and smooth, with spirals of up to two twists, almost triangular in cross-section, tips ivory-coloured, spread highly variable within populations.

Geographic Variation

T. s. spekii (Eastern or Northern Sitatunga) (includes *larkenii*, *ugallae* and *wilhelmi*): L. Victoria basin. Only faint shadow stripes on body of both sexes.

T. s. gratus (Western Sitatunga) (includes *albonotatus*): Congo Basin, West Africa and Sudan. Bold body stripes and spots in both sexes, but fading in adolescent ♂♂.

T. s. selousi (Southern or Zambezi Sitatunga) (includes *inornatus*): Bangweulu, Zambezi and Okavango basins. Body stripes and spots often present in ♀♀ and young, but absent in ♂♂.

Meinertzhagen (1916) erected the name *sylvestris* for Sitatungas on Nkose I. in the north-west corner of L. Victoria, which had stouter and stronger hooves than a population on a larger island nearby. Nkose I. is <1 km², dry, and densely forested to its edge, and separated from other Sitatunga populations by about 20 km of open water. Meinertzhagen's measurements plus a drawing of a hoof confirm that the Nkose I. Sitatungas clearly have wider feet than usual. However, to give this inbred, restricted population equal status to subspecies that range over thousands of kilometres seems hard to justify (Kingdon 1982).

Similar Species

Tragelaphus scriptus. Broadly sympatric. 'Hunched' appearance; short, wide and not splayed hooves; hairy lower feet. Inner upper forelegs white. Best identified by habitat and their habit of fleeing to dry ground when disturbed.

T. eurycerus. Sympatric through much of West and Central Africa, but in the forest – savanna ecotone. Large size; short, wide and not splayed hooves, and hairy lower feet. Legs banded black and white.

T. angasii. Allopatric, occurring in dense thickets and thicket woodland in south-east Africa from Malawi to South Africa. Short, wide and not splayed hooves, and hairy lower feet. Males with distinct fringe of long hair hanging down from under chin, down neck and along sides of belly to between hindlegs.

Distribution Endemic to Africa. Confined to the wetlands of the central latitudes between 13.5°N and 20°S. Sitatungas have a disjunct distribution, centred on the wet regions of central African forests and savannas.

Historical Distribution Widespread in wetlands throughout the central latitudes of Africa, from SW Senegal to W Guinea, and then from SE Ghana to W Kenya and from L. Chad and S Sudan to the Okavango Delta in Botswana. They probably once occurred throughout the lowland forest zone of Sierra Leone, Liberia and Côte d'Ivoire, but there are no confirmed records between Guinea and the Volta R. (Sidney 1965, Grubb *et al.* 1998).

Current Distribution Probably much the same as historical geographical range although there has been some reduction in area of occupancy. Where there has been loss or modification of the Sitatunga's habitat as a result of human population pressure, extinctions have occurred, such as in Togo (where they may have survived in small numbers on the Mo-Kaitcha Rivers in C Togo into the late 1980s; East 1999), or numbers are greatly reduced. Given the highly cryptic nature of Sitatungas and inaccessibility of their habitat, the extent of the loss is difficult to verify. Their secretive behaviour means that Sitatungas can survive in close proximity to human habitation, as long as some of their habitat remains: they have been observed from the air, feeding 10–20 m from villages, separated only by a narrow strip of dense papyrus (J. May & R. Lindholm pers. obs.).

Sitatungas are widespread and locally common in central African forests (SE Cameroon, Gabon, SW Central African Republic, Congo and DR Congo) and swamps within savannas of south-central (Zambia), East (Rwanda, Burundi, SW Uganda, NW Tanzania) and southern Africa (N Botswana). Sitatungas are also recorded in the Zambezi R. in extreme NW Zimbabwe, and an isolated population may still persist in western Tete Province in Mozambique (East 1999). They are not uncommon throughout coastal wetland areas of West Africa (Senegal, Gambia, SE Ghana and Nigeria), although at much lower population levels compared with those in central Africa (J. Mason pers. comm.). East (1999) reported that Sitatungas are now extinct in Niger, where they once occurred in the south-east around L. Chad. However, Sitatungas are still seen in the eastern and southern parts of L. Chad, during the most recent aerial surveys aiming at counting waterfowl in Lake Chad Basin (January 2008), Trollet *et al.* (2008) observed 13 individuals (10 males and 3 females)

Habitat Tall and dense vegetation of perennial and seasonal swamps, marshy clearings within forests, riverine thickets and both brackish (Galat-Luong & Galat 2002) and freshwater mangrove swamps. Within savanna environments, Sitatungas are typically found in extensive monospecific stands of papyrus *Cyperus papyrus*

and the reeds *Phragmites* spp. and *Echinochloa pyramidalis*, or a mosaic of all three species, often interspersed with bullrush *Typha* spp., sedges *Cyperus* spp., pampas grass *Miscanthus junceus*, hippo grass *Vossia cuspidata* and short grass clearings (e.g. *Acroceras macrum*, *Panicum repens* and *P. parvifolium*). They occur only on soft, moist to wet substrates, where vegetation provides adequate camouflage and density is sufficient to hinder predators. They favour extensive areas of swamps more than 1 km wide, although they do occur in relatively narrow patches of less than 50 m and in tall, dense grass of wet dambos adjacent to deep streams. Sitatungas commonly occur on floating mats of vegetation, particularly papyrus sudd, where underlying water depth may be up to 4 m; also on rooted vegetation in water depths up to ca. 1 m. They visit swamp margins, where sedges and grass growing on moist substrate meet dry flood-plains or gallery forest. Within seasonally flooded forests, Sitatungas occur in marshy clearings ca. 20–30 ha in diameter of mainly short sedges and grasses (Magliocca *et al.* 2002). In areas free of predators they may occur on dry terrain (such as Nkose and Rubondo Is. in L. Victoria).

Sitatungas usually avoid open water devoid of vegetation. They require dry resting areas on floating vegetation, thick vegetation that can be trampled to form a mat above water, or small dry patches of ground within swamp (J. May & R. Lindholm pers. obs.). They readily disperse into sedge and grass flood-plains during the wet season, if depth of water and density of vegetation provide sufficient cover, especially where small 'termitaria islands' ca. 25 m diameter are common (J. May & R. Lindholm pers. obs.).

Abundance Sitatungas are under-reported and are more common than sightings indicate. Their cryptic nature and the relative inaccessibility of their habitat have, until recently, hindered reliable estimates of abundance. For eastern and southern savanna swamps estimates vary widely, but are probably a function of survey technique and timing and frequency of observations rather than a true difference in density. Early estimates, which are crude and conservative, include an average of 44 visible Sitatungas in the tiny 2 km² Saiwa Swamp, Kenya (Owen 1970); at least 10–15/km² or 18,000–27,000 in Bangweulu Swamps, Zambia, total range ca. 2000 km² (Manning 1975); 0.3–1.3/km² or 234 in the Panhandle of the Okavango, Botswana, which has about 1000 km² of permanent swamp (Games 1983a); and 0.5/km² or about 4000 for the whole Okavango Delta, which includes some 8000 km² of permanent swamp (Ross 1992). Recent surveys from low-flying aircraft have produced more realistic densities, of up to 64/km² with 5700–9900 in Akagera N. P., Rwanda (Beudels *et al.* 1992b, Beudels-Jamar *et al.* 1997) and up to 60/km² with about 1000 in the Busanga Swamps (total range ca. 18 km²), Zambia, the latter supported by mark-recapture estimates (J. May & R. Lindholm pers. obs.).

There are only limited estimates of abundance in the forest habitats of West and central Africa. In the Congo rainforests, the Mbeli Bai (0.13 km²) in Nouabale-Ndoki N. P. supports 10–12 animals or 92/km² (E. Stokes pers. comm.). The slightly larger Maya Nord clearing (0.2 km²) in Odzala N. P. supports 30–36 animals or 180/km². Since there are about 100 clearings (Magliocca *et al.* 2002), or about 20 km² of Sitatunga habitat, a rough abundance for Odzala N. P. could be about 3000–4000 Sitatungas.

East (1999) estimated a total population size for Sitatungas of 170,000, but this was based on a general 'area of occupancy' of

1,230,000 km², which includes vast areas of unsuitable habitat rather than occupied range. The occupied range of Sitatungas includes a diversity of habitats from vast papyrus and reed swamps in savanna to small swampy clearings in wet forests and each type of habitat can be expected to support different densities. Even within specific habitats some parts will support significantly more Sitatungas than others (Beudels *et al.* 1992b, J. May & R. Lindholm pers. obs.). Unfortunately, the extent of the occupied range is unknown and given the extreme variation in densities the overall total abundance of Sitatungas cannot be reliably estimated.

Adaptations Sitatungas are adapted to fully exploit the swamp niche. They are the only large mammal that both lives and feeds in deep water and the only one to consume large quantities of papyrus and so utilize the high productivity of tropical swamps. Their unique long and splayed hooves with their rubbery water repellent-like coating provide purchase over slippery, muddy substrates and mats of floating vegetation; a wedge-shaped profile, combined with the lowering of the head, and in ♂♂ the laying of the horns on the back, facilitate movement through dense and tangled vegetation. Slow and deliberate movement makes them difficult to see and, combined with their toe-pointing gait, allows almost silent passage through water (Williamson 1986). To escape detection, they may 'freeze' in action, their colour providing perfect camouflage. When flushed, Sitatungas move towards flooded areas where their plunging run is very efficient through shallow water and clumped vegetation. They are awkward on dry ground and highly vulnerable to predators there. They use pathways to move efficiently between resting and feeding grounds, but rarely when fleeing an intruder, as they can move through the dense vegetation of the swamp swifter than any other large mammal.

Sitatungas are good swimmers and are often in water up to their backs but rarely enter water devoid of profuse vegetation, thereby avoiding crocodiles. In extreme circumstances (for example, when troubled by flies and bees or when pursued) some will submerge themselves fully with only the nose breaking the surface. Sitatungas often sun themselves after a bout of feeding in water. To this end they trample thick vegetation in a turning motion, to make a dry platform above a water-logged environment, or a grassy bed on dry-ground.

Hearing is acute and directional; their swivelling, saucer-shaped ears allow Sitatungas to pinpoint exactly where a sound originates, an important skill in dense vegetation where long sight is of little benefit.

Foraging and Food Sitatungas are selective mixed feeders taking a range of grasses, sedges and browse. Sitatunga select for new grass shoots and newly emerged leaves, new shoot tips and flowering spikes of sedges, the base of young shoots of *Typha*, new shoot tips and new foliage of herbs, shrubs and tree saplings as well as flowers and fallen fruits (Owen 1970, Games 1983b, J. May & R. Lindholm pers. obs.). In studies involving stable carbon isotope analysis of animals in both East and southern Africa, Sitatungas in East Africa (where samples came from the Ituri Forest and Garamba N. P.) had no grass in their diet, while animals in southern Africa had a diet of about 34% grass. However, these differences do not necessarily relate to regional differences in the consumption of grass or browse, since Sitatungas have regular access to both food sources (Cerling *et al.* 2003, Sponheimer *et al.* 2003b).

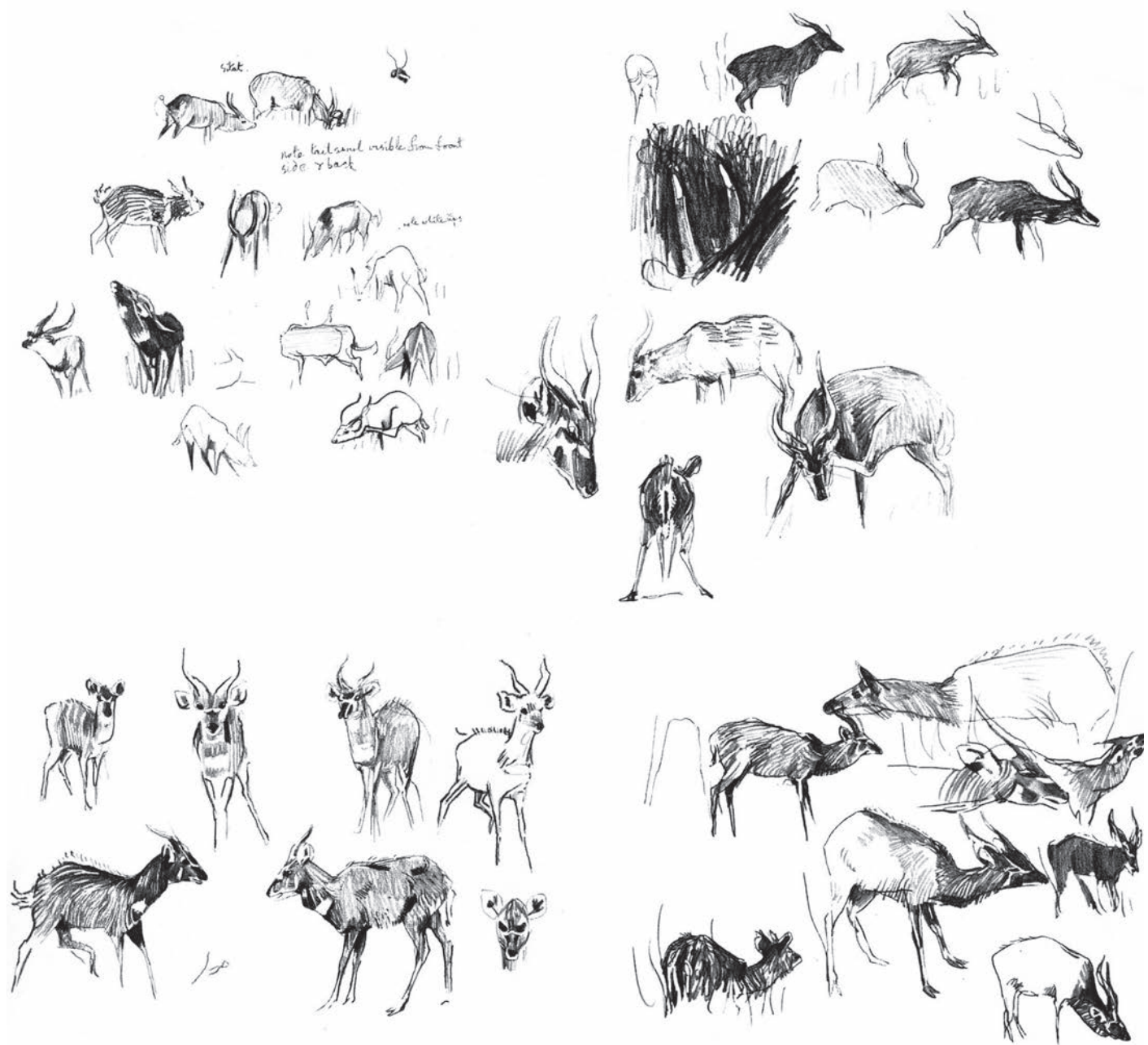
Bullrushes (*Typha* spp.), sedges (*Cyperus* spp.), aquatic grasses such as *Vossia*, *Echinochloa*, *Pennisetum*, *Leersia*, *Acroceras*, *Panicum* and species in the families Umbelliferae and Acanthaceae in Saiwa or Leguminosae in Bangweulu and Busanga, are the most common plants eaten. The first three are usually abundant and form the bulk of the Sitatunga's diet. However, others that are sparsely distributed are often sought after, such as *Hydrocotyle ranunculoides* and *Oenanthe palustris* (Umbelliferae), *Hygrophila spiciformis* (Acanthaceae), *Aeschynomene* spp. (Leguminosae), *Persicaria* spp. (Polygonaceae) and *Amaranthus* spp. (Amaranthaceae) (Owen 1970, J. May & R. Lindholm pers. obs.). *Cyperus papyrus* and *V. cuspidata* form the bulk of food in the Okavango Panhandle (Games 1983b), but neither occurs in Saiwa where *Typha* and *Pycnus* are commonly eaten (Owen 1970). Major food items in Busanga are *Typha*, *Cyperus* spp. and *V. cuspidata*, the latter two also commonly eaten in Bangweulu (J. May & R. Lindholm pers. obs.).

Seasonal changes in diet occur in those swamps that experience a significant rise in water level. Temporarily flooded areas give access to new growth of sedges, aquatic grasses, flood-plain and termitaria herbs and in some cases the forest edge, providing access to trees such as *Acacia nigrescens*, *Diospyros mespiliformis* and dry-ground herbs.

Sitatungas mostly forage in water up to their knees or belly and often browse on floating vegetation in water up to their backs. Within the savanna environment they start feeding at dawn and may move to a clearing, the swamp interface, or during the wet season, the termitaria edge or flood-plain from ca. 07:00h, usually returning to the swamp or termitaria centre after about 1–2 hours in the open. Bouts of feeding continue to alternate with resting and ruminating. They may emerge into the open again at dusk and again feed until satiated around 20:30h. There may be a short period of activity around midnight (J. May & R. Lindholm pers. obs.). Within the seasonally flooded forests most individuals remain permanently in the swampy clearings during the day, spending 27% of their time feeding and some move into the forest at night, especially as more of the clearing floods (Magliocca *et al.* 2002, 2003). On a daily basis Sitatungas are sedentary, an individual usually only traversing a small area up to around 250 m wide while foraging, the average distance travelled being ca. 25 m/h (J. May & R. Lindholm pers. obs.).

To reach favoured plant parts, Sitatungas may stand up on their hindlegs like the Gerenuk *Litocranius walleri*, or flatten or bend the plant with a hoof or horns (J. May & R. Lindholm pers. obs.). In the Maya Nord clearing, where Sitatungas have year-round access to mineral-rich sedges (Cyperaceae) and grasses, ♀♀ also spend ca. 20% and ♂♂ ca. 50% of their feeding time foraging in elephant dung for the seeds of *Strombosia pustulata* and *Strychnos camptoneura* (Magliocca *et al.* 2003). Sitatungas will immerse their heads and necks in deep water to reach these seeds and use their muzzles to break open the dung and select the larger seeds.

Social and Reproductive Behaviour Sitatungas are more sociable than is generally supposed. Of more than 2000 observations of Sitatungas from the air in the Busanga swamps, over half of all animals were within sight (less than ca. 10 m) of one or occasionally two others and sometimes up to seven others. The spacing of these 'groups' can be very close and these most likely form parts of larger associations (J. May & R. Lindholm pers. obs.). In Saiwa, where only parts of groups were visible, over half of the 359 observations were of groups of two or more Sitatungas (Owen 1970), while in the



Sitatunga *Tragelaphus speikii*.

marshy clearings of the Congo group size varied from 16 to 36 over ca. four years in Maya Nord (Magliocca *et al.* 2002) and averaged 10–12 in Mbeli Bai (E. Stokes, pers. comm.).

Females generally associate with ♀♀, and ♂♂ generally with other ♂♂; 75% of ♀♀ and 70% of ♂♂ in Busanga were either alone or with only the same sex (J. May & R. Lindholm pers. obs.). Around 59% of ♀♀ were either alone or only with other ♀♀ in Saiwa, although ♂♂ rarely associated only with ♂♂ probably because of the low number of ♂♂ (Owen 1970); 82% of resting groups in Maya Nord were female-only subgroups consisting of adults and subadults with or without young, and 4% male-only, the latter influenced by the low number of ♂♂ (Magliocca *et al.* 2002). In Maya Nord, the mother–offspring subgroup was the most stable and, while other subgroups fluctuated on a daily basis, many

of the female subgroups often included the same members indicating preferential social affinities (Magliocca *et al.* 2002).

In Busanga, home-ranges both within and between sexes overlap extensively and are seasonal (J. May & R. Lindholm pers. obs.). Individuals use the same centres of activity in consecutive years. Dry season home-ranges are always within permanent swamp and are occupied from about May to Jan (mean = ca. 190 ha, range ca. 9–1180 ha, $n = 31$). Some individuals have only one centre of activity during the dry season, others range widely between two or three areas ca. 5 km apart. The considerable variation between individuals is apparently not related to either sex or age. Dispersal to wet season ranges begins mid- to end Jan, when the plains begin to flood. Most move out of the swamp onto the flooded plains and the distance travelled from their dry season range varies, usually 2–5 km but some less than

1 km and rarely up to 12 km. There is only one centre of activity in the wet season (mean = ca. 60 ha, $n = 32$) that the individual occupies until about May when the flood-plain becomes too dry. In Bangweulu, home-ranges also overlap extensively (mean = 32 ha, $n = 9$) but apparently expand only very slightly during the wet season (Manning 1983). During the wet season, Situngas inhabiting the permanent river swamp in Bangweulu move into the seasonally flooded sedge marsh (Manning 1983), at least some Situngas move onto flood-plains in the Okavango (Games 1983b, Ross 1992) and some ♂♂ are reported to wander away from the swamp in Uganda and Tanzania (Kingdon 1982). In Maya Nord clearing, the core group remain all year round (Magliocca *et al.* 2002) while in Mbeli Bai Situnga visits drop in the dry season indicating that at least some individuals may undergo seasonal movements (E. Stokes pers. comm.).

Situngas are polygamous. A dominant ♂ forms a 'tending bond' with an oestrous ♀ for 1–2 days, testing her urine and keeping other ♂♂ away until she is ready to mate. While ♂♂ are usually not territorial, there is evidence in the Busanga that some establish temporary territories for part of the wet season (J. May & R. Lindholm pers. obs.). Occasionally, serious fights between two prime ♂♂ occur on termitaria, with the winner chasing the other off for at least 100 m, then returning to 'patrol' his area, running around its perimeter and occasionally ploughing the ground with his horns. Combats resulting in fatalities have been reported (Selous 1881, Starin 2000, Breuer & Hockemba 2008). In Maya Nord, the resident group apparently functioned as a harem, with the same adult ♂, the stouter of the two present, monopolizing all ♀♀ for at least 44 months (Magliocca *et al.* 2002). All ♂♂ born within the clearing were driven off by this ♂ and the subordinate adult eventually emigrated (Magliocca *et al.* 2002). In Mbeli, intermittent fighting for 90 min followed by an intensive battle of 30 min between two adult ♂♂ culminated in the death of one and the winner becoming the dominant ♂ visiting the bai over the following three years (Breuer & Hockemba 2008).

Calves hide alone for about the first seven weeks in Abuko N. R., Gambia (Starin 2000) and about two weeks in Maya Nord (Magliocca *et al.* 2002), except for brief bouts of suckling. After this 'lying out' phase the calf closely follows its mother and will remain with her even after the next calf is born (Owen 1970, Starin 2000), the mother and very young calf rarely associating with others (J. May & R. Lindholm pers. obs.).

The behaviour of Situnga has been studied in captivity (Walther 1964a), but rarely recorded in the wild. In Maya Nord, time devoted to social behaviour is surprisingly low, Magliocca *et al.* (2002) recording less than 1% of daytime observations. Various postures, mostly involving the head and neck, communicate 'status'. The following are most likely to be seen in the wild: when Situngas meet they touch noses first and sometimes examine each other's anogenital area; social licking and nibbling often follows. When alert the head is up, the neck curved and ears swivelling; if the animal is alarmed the head is raised as high as possible, and if startled animals may freeze in action, often with one leg raised. The head is lowered and the neck extended when the animal is investigating a suspicious object, such as a crocodile. Threat displays include feinted attacks, where the animal jumps forward raising the forelegs while the hindlegs remain planted, and ♂♂ frequently horn the ground or bushes. Feinted attacks are also seen in running games where individuals run and caper about, usually alone. Fighting in the ♂♂ involves combatants, with horns engaged at bases, trying to push each other backwards (J. May & R. Lindholm pers. obs.).

Situngas occasionally emit one to several coughing-barks, usually at night (Owen 1970). Sometimes the barking of one individual may be taken up serially by others, up and down the swamp (Owen 1970, J. Kingdon pers. comm.). Females bark when chasing off other ♀♀ (Magliocca *et al.* 2002). A low-pitched squeak is uttered amongst feeding Situngas and the calf's call to its mother is a sheep-like bleat (Owen 1970). In captivity, a sheep-like bawl is heard when moving, particularly during running and jumping games (Walther 1964a) and a similar sound is often emitted when Situngas are captured in the wild (Manning 1983, J. May & R. Lindholm pers. obs.). In captivity, ♂♂ emit a suppressed bellow while following a ♀ during the mating ceremony or approaching a herd of ♀♀ (Walther 1964a).

Situngas occasionally feed or lay down close to small groups of Southern Lechwes *Kobus leche* but do not intermingle. Calves playfully chase off Spur-winged Geese *Plectropterus gambensis*, as do ♂♂ occasionally (J. May & R. Lindholm pers. obs.). Situngas tolerate Yellow-billed Oxpeckers *Buphagus africanus* and African Jacanas *Actophilornis africanus* perching on their backs and Great Egrets *Casmerodius albus* grooming their ears and genital-perianal areas for arthropods (Ruggiero & Eves 1998); Maisels (2003) recorded White-tailed Alethes *Alethe diademata* and a bulbul (Pycnonotidae) gleaning ectoparasites from a Situnga. They are wary of crocodiles, but will continue to feed close to them when out of water, keeping them carefully in sight.

Reproduction and Population Structure Situngas give birth throughout the year (Owen 1970, Magliocca *et al.* 2002, J. May & R. Lindholm pers. obs.); however, there are reports of a peak in the dry season for Caprivi, Namibia (Davison 1950) and in wetter months for Saiwa (Owen 1970), although the evidence is weak.

Estimates of gestation vary, from 27–34 weeks in captive ♀♀ (Manning 1983) to as little as 24 weeks in Maya Nord ($n = 1$, Magliocca *et al.* 2002). Single calves, weighing ca. 5 kg (Manning 1983) are born at intervals ranging from 8.5–12 months in Abuko N. R. ($n = 3$, Starin 2000) to 5.5–9.0 months in Maya Nord ($n = 6$, Magliocca *et al.* 2002); the shorter period in the latter possibly related to the extraordinary high quality of food available. Calves are suckled until about four months old (Magliocca *et al.* 2002). They suckle for 2–21 min in captivity ($n = 52$; Walther 1964a). Females are sexually mature at 24–30 months in Maya Nord ($n = 3$, Magliocca *et al.* 2002), 14–23 months in captivity (Manning 1983), and in Busanga one young ♀ of ca. 16 months and only 60% of mean adult body weight was pregnant. Age at first birth in Mbeli is 2.8 years ($n = 2$, E. Stokes & T. Breuer pers. comm.). In captivity, ♂♂ are sexually mature at ca. 18 months although unlikely to mate in the wild until approaching their maximum weight at six years (Manning 1983).

In Maya Nord, all nine adults gave birth to at least one young in one year, and at least 78% did so in another (Magliocca *et al.* 2002). In Mbeli, one ♀ gave birth ten times in ten years (E. Stokes & T. Breuer pers. comm.) and the single ♀ in Abuko N. R. gave birth four times in four years (Starin 2000); and in Busanga 70% of ♀♀ examined were pregnant and 20% were lactating (J. May & R. Lindholm pers. obs.). The birth rate in Mbeli was 0.79 (births/♀/year $n = 31$; E. Stokes & T. Breuer pers. comm.).

More ♀♀ (60–75%) than ♂♂ are seen (Owen 1970, Manning 1983, Magliocca *et al.* 2002, J. May & R. Lindholm pers. obs.). Given the extended 'lying out' phase of calves, their much lower visibility in dense vegetation, and the difficulty of distinguishing young from adult

♀ ♀, the proportions of young to adults observed are crude, ranging from 10 to 36% (Owen 1970, Games 1983a, Manning 1983, J. May & R. Lindholm pers. obs.). In Maya Nord, where the whole group was visible, on average 34% were young ($n = 16\text{--}36$, Magliocca *et al.* 2002).

Mortality rates in good-quality habitat in Busanga were low with only 10% of 20 collared Sitatungas dying, equating to an annual survival rate of 0.94; but in marginal habitat mortality rates were very high, 58% of 12 collared animals dying, the annual survival rate being 0.76, many being killed by Lions *Panthera leo* shortly after fires (J. May & R. Lindholm pers. obs.). In rainforest clearings, the survival rate of calves is very high. In Maya Nord, 80% of young less than five months ($n = 10$, Magliocca *et al.* 2002), and in Mbeli 76% of young less than six months survive ($n = 28$, E. Stokes & T. Breuer pers. comm.). In captivity, Sitatungas live to at least 21–22 years (Jones 1993, Weigl 2005), and in the wild to at least 11 years (Manning 1983).

Predators, Parasites and Diseases Nile Crocodiles *Crocodylus niloticus*, Lions, Leopards *P. pardus*, African Wild Dogs *Lycaon pictus* (Games 1983a) and African Rock Pythons *Python sebae* (E. Stokes & T. Breuer pers. comm.) are known predators, and Spotted Hyenas *Crocuta crocuta* and jackals *Canis* spp. probably also prey on Sitatungas.

Sitatungas host the protozoans *Trypanosoma congolense*, *T. vivax* and *T. brucei*, all three causing ngana (trypanosomosis) in cattle, and two subspecies of the latter, *T. b. rhodesiense* and *T. b. gambiense*, are the agents of sleeping sickness (trypanosomosis) in humans. Although Sitatungas were implicated in the Uganda sleeping sickness epidemic in the early 1900s, recent evidence suggests that the main causative agent was *T. b. rhodesiense*, a zoonosis with a principally domestic cattle reservoir, and that movement of cattle during livestock restocking at the end of the rinderpest pandemic was most likely the cause (Fèvre *et al.* 2004). The riverine tsetse fly *Glossina palpalis*, an important vector of African trypanosomes, feed on Sitatungas in S Cameroon (Njiokou *et al.* 2004a).

Sitatungas are also susceptible to rinderpest caused by the virus *Morbillivirus* (Shanthikumar & Atilola 1990), while captive animals have shown susceptibility to bovine tuberculosis, a chronic disease in domestic ruminants caused by the bacterium *Mycobacterium bovis* (Pavlik *et al.* 2002), heartwater caused by the rickettsial agent *Ehrlichia ruminantium* (Okoh *et al.* 1986), and to malignant catarrhal fever (Barnard *et al.* 1994, Flach *et al.* 2002). Sitatungas would be vulnerable to all four diseases in areas where cattle invade flood-plains such as the Okavango panhandle (Games 1983b).

Two new species of flukes have been described from Sitatungas: the liver fluke *Fasciola tragalaphi* from Chobe Swamps (Pike & Condry 1966) and later found in Ugandan Sitatungas (Pullan *et al.* 1971); and the bilharzia fluke *Schistosoma leiperi*, from Zambia (Le Roux 1955). The latter species is one of the many schistosomes causing bovine schistosomiasis. A *Stomoxys* fly outbreak in Congo caused adult ♂♂ to lose condition over several weeks in the Mbeli clearing and finally disappear, presumed dead (Huchzermeyer *et al.* 2001, Elkan *et al.* 2009).

Sitatungas are known to host the ticks *Rhipicephalus compositus*, *R. aquatilis* and *Haemaphysalis aciculifer* (Manning 1983, Walker *et al.* 1993) and the amphistome *Carmyrius spatiosus* (Pike & Condry 1966).

Conservation IUCN Category: Least Concern. CITES: Appendix III (Ghana).

Loss of habitat is the main threat to the future persistence of the species. In the past it was most likely that Sitatungas were able to

move along drainage lines during wet seasons, facilitating exchange between populations. However, with the ever-increasing loss of wetlands throughout their range, these routes of dispersal are being cut and many populations are becoming isolated. Sitatungas are highly vulnerable to long-term changes in water level because it alters vegetation structure, which in turn largely determines their distribution and abundance (Beudels-Jamar *et al.* 1997); both lower and higher water levels make them more accessible to hunters and predators.

Surprisingly, perhaps, swamps are extremely vulnerable to fire; up to 75% of the Okavango (Games 1983a) and vast areas of Bangweulu and Busanga (J. May & R. Lindholm pers. obs.) are burnt each year. Hunting has probably not had a significant effect in the past because of the inaccessibility of their habitat, but with fragmentation of swamps, increasing human population and modern technology this is changing. Hunting for bushmeat throughout West Africa is now a major threat (J. Mason pers. comm.).

Over the long term, only those populations living in extensive swamps that are relatively isolated can be considered secure. Major populations occur in areas of low human density, for example Dja Wildlife Reserve and Lobeke N. P. (Cameroon), Bangassou F. R. (Central African Republic), Odzala N. P. and Nouabale-Ndoki N. P. (Congo), Salongo N. P. (DR Congo), Bangweulu and Busanga Swamps (Zambia), Okavango Delta (Botswana) and Akagera N. P. (Rwanda) (East 1999). A population also occurs on Rubondo I., which is a National Park (Tanzania) (East 2002). However, very few large populations are to be found within genuinely protected areas and the extensive swamps such as the Okavango and Bangweulu, which can be expected to provide the most secure habitat in the long term, generally have no special protection status. To secure the long-term survival of Sitatungas, a system of stable protected areas is needed, each of a size resilient to burning. These areas must contain permanent swamps together with the adjacent seasonal swamps, flood-plains and associated gallery forest. Fire management is essential.

Measurements

Tragalaphus spekkii

T. s. selousi

HB (♂♂): 1610 (1360–1770) mm, $n = 30$

HB (♀♀): 1320 (1040–1460) mm, $n = 91$

T (♂♂): 300 (140–350) mm, $n = 24$

T (♀♀): 250 (170–370) mm, $n = 92$

E (♂♂): 140 (120–170) mm, $n = 21$

E (♀♀): 120 (110–140) mm, $n = 81$

Sh. ht (♂♂): 1010 (810–1160) mm, $n = 30$

Sh. ht (♀♀): 820 (720–900) mm, $n = 89$

WT (♂♂): 98.0 (76.0–119.0) kg, $n = 28$

WT (♀♀): 45.0 (24.0–57.0) kg, $n = 92$

Bangweulu Swamps, Zambia (I. Manning pers. comm.) and Busanga Swamps, Zambia (J. May & R. Lindholm pers. obs.)

Maximum horn length recorded is 83.8 cm for a pair of horns from Gabon (Rowland Ward)

Key References Games 1983a, b; Magliocca *et al.* 2002; Manning 1975, 1983; Owen 1970.

Janice May & Rolf Lindholm

Tragelaphus eurycerus BONGO

Fr. Bongo; Ger. Bongo

Tragelaphus eurycerus (Ogilby, 1837). Proc. Zool. Soc. Lond. 1836: 120. West Africa [1837]. 'Their origin is unknown, but I have reason to believe they [the syntypes] came from Western Africa.'



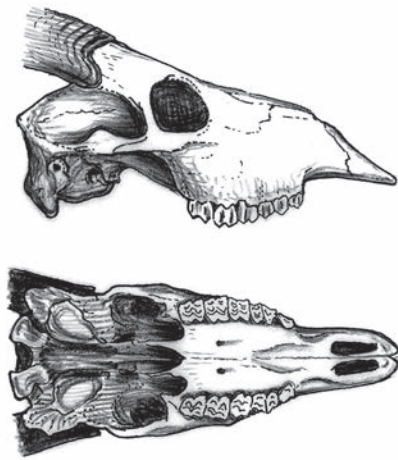
Mountain Bongo *Tragelaphus eurycerus isaaci* male.

Taxonomy Historically, classification of this species has been problematic. Originally described as *Antelope eurycerus*, it was subsequently included in the genus *Tragelaphus* by Lesson (1842). Later it was shifted to a new genus, *Boocercus*, and then to *Taurotragus* (Thomas 1902, Simpson 1945, Haltenorth 1963). Most recent authors include the species in the genus *Tragelaphus*, sometimes in the subgenus *Boocercus* (Ansell 1972, Van Gelder 1977a, Ralls 1978, Grubb 2005). The shifts in nomenclature were due to confusion about key morphological characteristics. The Bongo has two characteristics that are more similar to the elands (sometimes placed in the genus *Taurotragus*) than other members of the genus *Tragelaphus*, namely the presence of horns in both sexes and the ox-like tail. However, the Bongo's open 'one-twist' spiral horns, the lack of a dewlap and non-ox-like feet are similar to other members included in *Tragelaphus* (see Ansell 1972). The name *euryceros* Gray, 1850, sometimes used for the species name, is an incorrect subsequent spelling (see Grubb 2004, 2005).

Up to five subspecies were previously described, but only two are presently recognized: *T. e. eurycerus* and *T. e. isaaci* (Kingdon 1997,

East 1999). Analysis of genetic characters will help elucidate the status of subspecies in *Tragelaphus eurycerus*. Synonyms: *albovirgatus*, *cooperi*, *euryceros*, *isaaci*, *katanganus*. Chromosome number: $2n = 33$ in ♂ (translocated Y) and 34 in ♀ (Wurster 1972, Wallace 1978a, Benirschke *et al.* 1982).

Description Large, reddish-brown, heavy-bodied antelope with white and black markings and long spiral horns. Lower jaw dark, upper crossed by a white chevron. Underside of the chin is white, the throat black with 1–2 variable white markings on rear cheek. Pelage around eyes lighter, ears large spreading outwards with white-and-black-fringed markings. Pelage light brown to dark maroon, with 9–15 thin, vertical, white stripes running from the dorsal ridge to the belly, and extending from the shoulder to the hindquarters. Hair short (1–2 cm) over much of body, longer at throat. Dorsal crest brown and white (3–4 cm) extending from withers, along back, to base of tail. Chest crossed by white marking at base, legs marked with dark and white from elbow to fetlock. There is no dewlap. Tail (ca. 25% of HB) is brown, ending in a black tuft. Facial, pedal



Lateral and palatal views of skull of Bongo *Tragelaphus eurycerus*.

and inguinal glands absent. Colouration similar in ♂♂ and ♀♀, but there is pronounced dimorphism in body size. Females have two pairs of nipples.

With the exception of the elands, this is the only other member of the genus *Tragelaphus* with horns present in both sexes. Horns are long and dark with white-yellowish tips curving up and backward in an open spiral. Horns of ♂♂ are thicker and have a wider spread than ♀♀.

Geographic Variation

T. e. eurycerus (Lowland or Western Bongo): patchily distributed across the lowland forest and savanna-forest transition areas of West and central Africa. Generally smaller than Mountain Bongo, and adult ♂♂ tend not to darken with age.

T. e. isaaci (Mountain or Eastern Bongo): mountain forests of Kenya. Taller, heavier and longer-legged, with head and neck of older ♂♂ a dark chocolate-brown in colour.

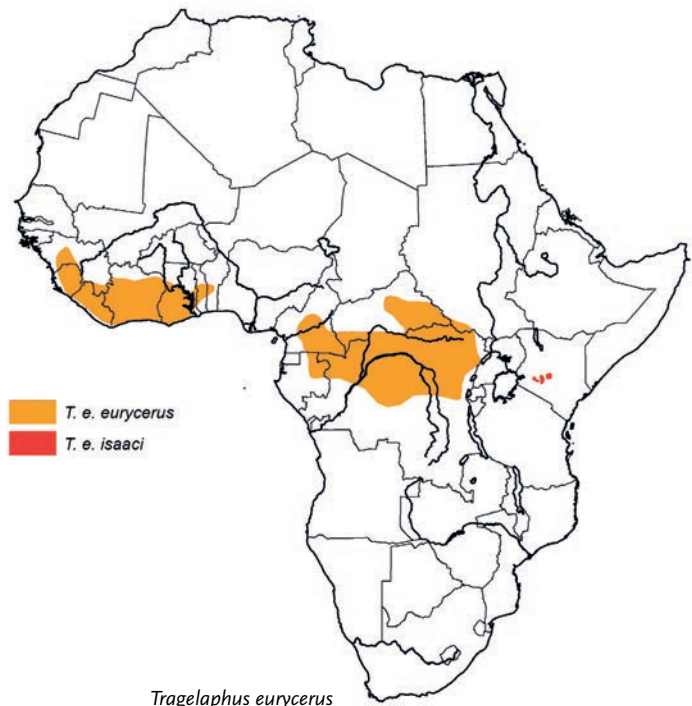
Similar Species

Tragelaphus scriptus. Broadly sympatric. Substantially smaller (24–80 kg). Shorter horns on ♂♂ with tighter spiral.

T. spekii. Smaller, with longer hooves and shaggier pelage. Restricted to swamps and swamp-forest and largely absent from West Africa, west of the Volta R.

Distribution Endemic to Africa, associated with disturbed forest areas and the forest–savanna ecotone in the lowlands of West and central Africa and the Kenya highlands (East 1999).

Historical Distribution In West Africa, the Lowland Bongo occurred from SW Guinea and Sierra Leone to Benin, but was absent east of the Dahomey Gap to Cameroon. The central African populations ranged from S Cameroon along the lowland forest zone to E DR Congo and S Sudan (Ralls 1978). Historically, the Mountain Bongo occurred in and around forested zones of Mt Kenya, the Aberdares, Mau forest, Cherangani hills and Chepalungu hills in Kenya and Mt Elgon in Kenya and Uganda (Kingdon 1982, East 1999). Reports of Bongos from SW Ethiopia and N Tanzania have not been confirmed (Ansell 1972).



Tragelaphus eurycerus

Current Distribution The West Africa populations of Lowland Bongo are declining throughout much of their range in Guinea, Sierra Leone, Liberia, Côte d'Ivoire, Ghana and Togo (where they now probably only occur in Fazao N. P.); a few Bongos may still exist in the Mt Kouffe area of Benin. Most of the central Africa populations of Lowland Bongo still maintain their historical distribution extending from just north of the Sanaga R. in Cameroon and from NE Gabon east to Congo, Central African Republic, DR Congo and SW Sudan (East 1999).

Some sources note that Bongos occur only east of the Sanaga R. (e.g. Ralls 1978), but they are definitely recorded from Mbam Djerem, north of the river (Maisels *et al.* 2000), suggesting that the forest–savanna transition zone, east of the Adamawa highlands, is their northerly limit in Cameroon. Reports of Bongos in Campo-Ma'an N. P., well to the west of their known distribution in Cameroon (see East 1999), have not been verified during intensive field surveys (Matthews & Matthews 2003). Although the Ivindo R. was taken to be the southern limit of distribution in Gabon, there is a camera-trap record of the species from south of this river in Ivindo N. P. (P. Henschel pers. comm.). There is also an unsubstantiated record from Mt Fouari in the Niari region in the south-west of the Congo (Hecketsweiler 1988); however, recent surveys have failed to record the species here, and they certainly no longer occur, if they ever did.

The distribution of the Mountain Bongo has been reduced to four small, completely isolated populations in patches of forest on Mt Kenya, the Mau and Eburu forests, and the Aberdares in Kenya. It was extirpated from Uganda (Mt Elgon) around 1913–14 (Kingdon 1982, East 1999).

Habitat The Bongo is described as an ecotone species, thriving on transition vegetation at the forest edge and in new-growth areas that occur after disturbance (i.e. post-timber exploitation, elephant disturbance, tree-falls, landslides, burned fields) (Kingdon 1982, Elkan 2003). Bongos in the savanna–forest transition zone in SW

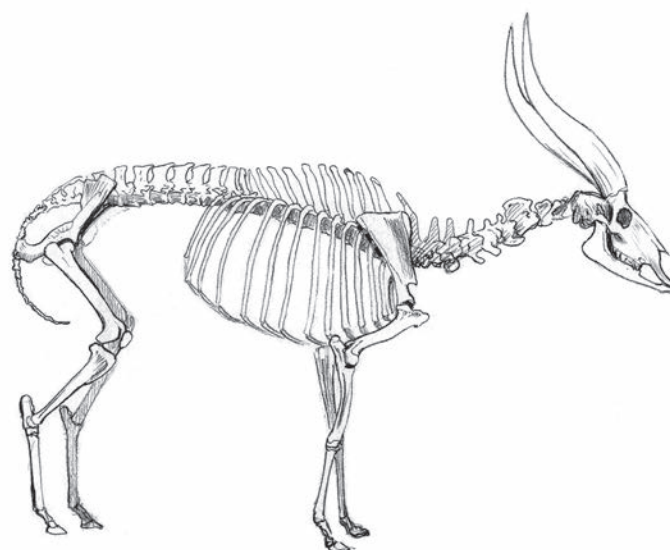
Sudan move during the wet season to rich food patches that are often a considerable distance from forested areas and retreat in the dry season to dense forest in search of food (Hillman 1986b). Similarly, in the Aberdares Bongos have been recorded moving in the wet season (Apr–May and Sep–Dec) to lower altitudes (below 2500 m) where secondary growth has invaded formerly cultivated areas, and in the dry season (Jan–Mar and Jun–Aug) move back up to the upper reaches of montane forest and *Hagenia/Podocarpus* cloud forest and bamboo thickets over 3000 m (Edmond-Blanc 1960, Kingdon 1982); however, recent wet-season observations from the Aberdares indicate that Bongos are not necessarily moving to formerly cultivated areas only, but are now primarily found along valleys where an abundant herbaceous layer (of preferred browse species) underlies tall, semi-open forest (L. Estes pers. comm.). Young & Evans (1993) discuss a possible record from 4300 m on Mt Kenya.

Forest clearings and mineral licks are important for geophagy and socialization (Kingdon 1982, Hillman 1986b, Turkalo & Klaus-Hugi 1999, Klaus-Hugi *et al.* 2000, Elkan 2003; L. Estes pers. comm.). In Congo, Elkan (2003) observed Bongos visit a mineral lick complex from >50 km. They do not usually frequent large expanses of swamp habitat. Bongos generally do not wallow and only cautiously enter deep water. However, during a widespread *Stomoxys* fly outbreak that caused a major die-off in N Congo in 1997, they did wallow in muddy pools along roads and deep water in forest clearings (Elkan *et al.* 2009).

Abundance The Mountain Bongo has been reduced to less than a few hundred individuals (East 1999). Pointing out that the wet season dispersal of Bongos in Aberdares N. P. in Kenya depended on low-level secondary growth on abandoned cultivation sites, Kingdon (1982) thought that the long-term survival of this confined population would be compromised if trees in and around these sites were permitted to reach climax and shade out low-level herbage. The formerly cultivated areas are now dominated by woody shrubs (such as *Toddalia asiatica*) that may be somewhat depauperate in the forbs that Bongos prefer (or may not offer the type of cover that Bongos like) (L. Estes pers. comm.).

The status of the Lowland Bongo in West Africa is uncertain or rare with populations fragmented and declining in many areas (East 1999). In contrast, thousands of Lowland Bongos probably still exist in central Africa. However, they are rare over large areas of closed-canopy forests of N Congo and in the Ituri Forest, DR Congo (Elkan 2003, S. Blake pers. comm., J.A. Hart pers. comm.). The highest recorded density of Bongos occurs in the forest–savanna transition zones in S Sudan (Hillman 1986b). After Sudan, some of the highest concentrations of Lowland Bongos are found discontinuously in Cameroon, Central African Republic and Congo.

Detailed ecological surveys in the Ndoki-Likouala lowland forests of N Congo demonstrated that Bongos occur in highly clumped local distributions, reaching the highest abundance near forest clearings and areas of high herbaceous growth. Although Bongos occur in unlogged primary forest such as Nouabale-Ndoki N. P., they are found in much higher abundance in adjacent logging concessions, which have secondary growth and a high density of forest clearings (Elkan 2003, S. Blake pers. comm.). There are also poorly understood differences in abundance. For example, in both logged and unlogged forests in the Lobeke area of Cameroon there was higher Bongo abundance than for any areas surveyed in N Congo (Elkan 1995, 2003).

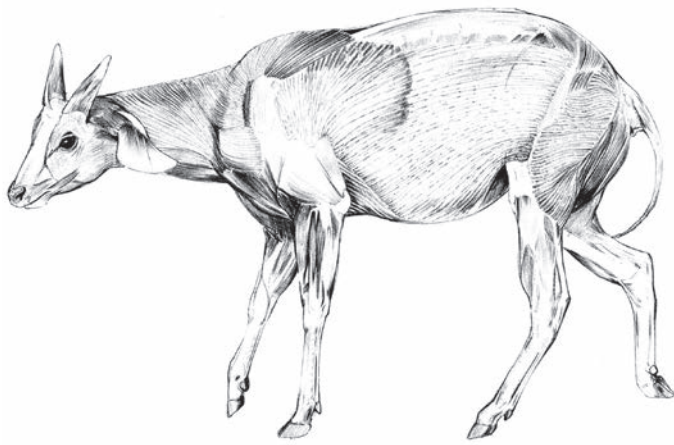


Bongo *Tragelaphus eurycerus* male skeleton.

Dense forest habitat, patchy distributions, wide-ranging patterns, retiring behaviour and crepuscular/nocturnal activity patterns hinder estimation of Bongo densities. Hillman (1986b) estimated 1.2/km² in S Sudan based on group-size observations and mineral-lick distribution. Remote camera trapping identified 65 ♂♂ and 109 ♀♀ visiting the Mombongo forest-clearing complex in the Kabo forest concession in N Congo over a six-year period. Using mark-recapture techniques, Elkan (2003) estimated 139 (± 33) Bongos in the Mombongo area during a one-month period in 1996.

East (1999) estimated 28,000 Bongos remaining, with Mountain Bongo populations in the few hundreds, and populations of Lowland Bongo in the order of a few thousands in the west, and tens of thousands in the central African forest zone. However, these estimates must be considered with caution and a large error margin. Patchy distribution, population declines irrespective of habitat availability, rapid ecological change in unstable habitats, and wide ranging behaviour call for extreme caution in extrapolating local abundance estimates to density calculations for large areas (Elkan 2003).

Adaptations With the high point of the body in the lumbar region and head frequently lowered, short legs compared with other tragelaphines (Ralls 1978), and horns that can be laid against its back, a Bongo can run full speed through dense forest. Although they prefer to go under or through objects, rather than over them, they are (like other tragelaphines) capable jumpers. Horns of both sexes, but particularly in the ♀, assist in defending young against predators (Kingdon 1982), and are sometimes employed to break high branches. They are also able to rear up on their hindlegs to reach leaves and twigs at heights of 2.5 m above ground. Although they lack or have very rudimentary external glands, Bongos secrete strong scents from their skin. This odour is hypothesized to assist in locating other individuals despite the dense habitat in which they live. The Bongo's white stripes and its reddish-maroon colouring blend in to the forest's filtered light making detection difficult. Kingdon (1982) noted that although a full frontal view of a Bongo can be quite conspicuous, animals often offset this by turning their striped cryptic backs on a disturbance. By keeping very still in the



Bongo *Tragelaphus eurycerus* myology.

face of any potential threat, Bongos tend to leave the option of flight to the last moment.

Bongos are most active in the evening, night and early morning when, between bouts of feeding and using mineral licks, they often walk long distances at several kilometres/hour. There is one camera-trap record of an old ♀ (and occasionally her calf) spending several hours at a salt-lick in broad daylight (L. Estes pers. comm.). Bongos typically ruminate and rest in the hotter parts of the day (Hillman 1986b, Elkan 2003); *Gilbertiodendron* forest habitat with relatively open understorey as well as dense vine areas were frequently used for resting in N Congo (Elkan 2003) while bamboo habitat provides refuge to Mountain Bongos (Kingdon 1982).

Foraging and Food Diet varies greatly (107 species of food plants recorded in Sudan, 100 in Central African Republic, >80 in N Congo), but consists primarily of browsing on dicotyledonous plants, with some seasonal grazing on grasses (Hillman & Gwynne 1987, Klaus-Hugi *et al.* 1999, Elkan 2003; and see Gagnon & Chew 2000). These observations are borne out also by studies involving carbon isotope analyses (at least, on Mountain Bongos) (Cerling *et al.* 2003). Bongos prefer young leaves and new growth in recently burned or perturbed areas (i.e. post-timber exploitation, tree falls).

In central Africa, just after early rains, Bongos concentrated feeding on seasonally palatable grasses, the new leaves of the highly aromatic invasive herb *Chromolaena odorata*, and *Ipomoea involucreta*, *Macaranga barteri*, *Triumfetta cordifolia*, *Sida alba*, *Paspalum conjugatum*, *Alchornea cordifolia*, *Adenia cissampeloides*, *Cissus dinklagei*, *Manniophyton fulvum*, *Diodia* sp., *Costus* sp. found along roadsides and forest openings (Klaus-Hugi *et al.* 1999, Elkan 2003). During the dry season, they moved further into forest as forage quality and water decreased in ecotone areas. Important food plants included *Thomandersia laurifolia*, *Palisota ambigua*, *Whitfieldia elongata*, *Rinorea* sp. and *Barteria* sp. in closed-canopy forest. *Gilbertiodendron dewevrei* was also occasionally an important food source during rare, intermittent masting periods when Bongos would feed for days on this super-abundant food source (Elkan 2003). Bongos submerged their heads for tens of seconds to feed on algae (*Spirogyra* sp.) at a pond in N Congo. They also seasonally entered cleared fields near villages for manioc leaves and shoots of corn (Elkan 2003).

Mountain Bongos inhabit a very different and botanically less diverse habitat with fewer food plants available. Edmond-Blanc (1960)

identified *Parochetus communis* and *Senecio bigrae* as important food items on Mount Kenya. *Impatiens* spp., *Sericostachys scandens*, *Rubus*, *Asplenium* and *Mimulopsis* spp. are common in the diet at high altitudes in the Aberdares with *Cassia didymobotrya*, *Vernonia auriculifera* and *Crotalaria agatiflora* readily consumed at lower altitudes (Kingdon 1982, L. Estes pers. comm.). Other species commonly encountered as browse/graze plants include: *Cynodon dactylon*, *Pennisetum clandestinum*, *Hypoestes forskalei*, *Plectranthus* spp., *Achyranthes aspera*, *Cyathula* spp., *Vernonia amygdalina*, *Impatiens fischeri* and *I. hoehnelii* (L. Estes pers. comm.).

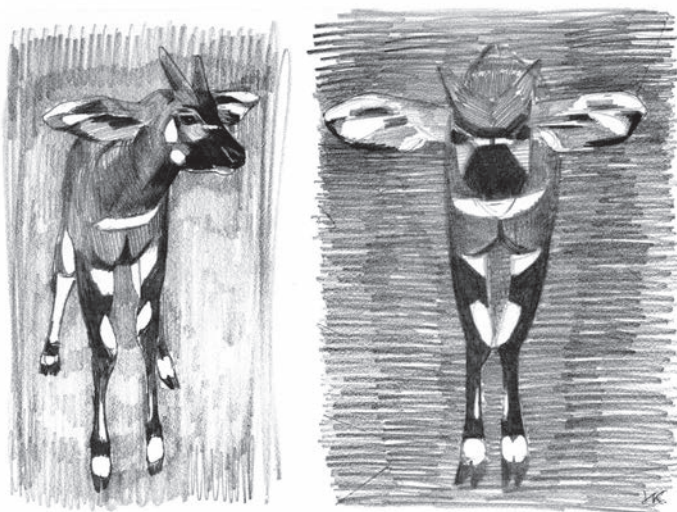
Bongos visit mineral licks where they consume water and soil high in sodium, other mineral salts and trace elements (Hillman 1986b, Elkan 1995, 2003, Klaus-Hugi *et al.* 1999). Their drive for salt was demonstrated by a concentration of activity around artificial salt-licks in Congo (Elkan 2003). Ingestion of soil with high clay content is thought to buffer the rumen and assist in the digestion of high levels of secondary compounds and alkaloids found in much of its browse (Klaus-Hugi *et al.* 1999, Elkan 2003). When licks become baked, hardpan activity decreased.

Social and Reproductive Behaviour The Bongo is a highly social antelope, and, next to the Common Eland *Tragelaphus oryx*, forms the largest herds of any tragelaphine (Estes 1991a). Aggregations of up to 50 animals have been recorded in the forest mosaic of S Sudan (mean = 9.1, $n = 42$) (Hillman 1986b), although, in dense lowland Ituri Forest, group size is often only a few individuals (range 2–8) (Hart 2001). Mean group size in N Congo was 5.7 (range 2–23; $n = 93$) (Elkan 2003) and in SW Central African Republic, 13 (range 2–28; $n = 78$) (Turkalo & Klaus-Hugi 1999). In the Aberdares, group size ranges from 2 to 21 (Kingdon 1982).

Females and young of both sexes including calves accompanied by an adult ♂ were the most common and largest social grouping in N Congo (Elkan 2003). In contrast to ♀♀, adult ♂♂ are often solitary; 75% ($n = 114$) of solitary individuals observed in N Congo (Elkan 2003) and 78% ($n = 41$) in S Central African Republic (Turkalo & Klaus-Hugi 1999) were ♂♂. However, seasonally, adult ♂♂ form temporary associations with female groups. When not associating with ♀♀, single ♂♂ overlap in home-range, and show little or no territoriality. More than 34 adult ♂♂ visited the Mombongo forest-clearing complex over a six-month period in 1996 in N Congo. These activity levels coincided with high levels of female group visitation of the area.

Resighting of individuals in N Congo has shown that Bongos range over distances >50 km and with broad herd movements that suggest seasonal habitat shifts (Elkan 2003). Home-range sizes on Mt Kenya and the Aberdares show a distinct dry/wet season shift with, tentatively, an annual home-range of 100–300 km² (Kingdon 1982).

Fighting is rare and probably dangerous (Estes 1991a). Aggressive male–male interaction has been observed; however, ♂♂ were not aggressive or threatening towards ♀♀ during courtship (Ralls *et al.* 1985). Mutual tolerance in groups, lack of aggressive behaviour, and larger body size in dominant ♂♂ indicate establishment of dominance hierarchies (Elkan 2003). No fighting was observed in N Congo and other agonistic behaviour was rare; however, ♂♂ did displace other ♂♂ for access to licks and young ♂♂ were observed locking horns and strength testing. Bongos exhibit dominance through lateral presentation with head up and a slow stiff-legged walk (Hamaan 1979, Estes 1991a).



Bongo *Tragelaphus eurycerus* frontal view of signal patterns.

Bongos have a keen sense of smell. Males have been observed wandering through clearings following the scent of a group that had passed hours earlier. They also have been observed to horn ground and rub in soil leaving a strong odour (Elkan 2003). There is some evidence that their body secretions are soluble in water and run off the body in raindrops (Kingdon 1982). This would assist the scent-marking of trails and resting places. Adult ♂♂ frequently mark small trees by rubbing their horns to scrape the bark or breaking them over at 1.25–1.5 m. Although marking of presence seems to be common, no evidence of defence of territories has been observed (Elkan 2003).

Males in the wild followed potentially receptive ♀♀ with a low body posture, neck outstretched and lips curled back exposing the upper gums to test for oestrus (flehmen) (Elkan 2003). Males did not herd ♀♀ but tended to follow behind the group when entering and leaving forest clearings. Ralls *et al.* (1985) categorized Bongo male behaviour towards oestrous ♀♀ in captivity as similar to other tragelaphines and most like that of the Sitatunga *Tragelaphus spekii*. Males regularly test ♀♀ by sniffing and licking the vulva and prodding to provoke urination (Ralls *et al.* 1985). Flehmen behaviour followed sniffing urine, faeces, or a place on the ground where a ♀ had recently lain. Males assumed a 'low stretch' posture laying their head against the female's side often with a soft vocal 'clicking' sound. Mounts were preceded by ♂♂ assuming 'frozen' or 'facing away' posture, a behaviour that may be distinctive to this species (Ralls *et al.* 1985). This type of behaviour was also observed in an attempted copulation observed in the wild in N Congo. Oestrous ♀♀ are more restless and urinate and defecate more often than non-oestrous ♀♀ (Ralls *et al.* 1985). Oestrous ♀♀ engaged in mutual licking with ♂♂. Copulation was preceded by circling away and then back to the ♂ with the ♀ then often sniffing or licking the male's genitals. Females assumed a 'mating face', head and neck extended in a concave curve, raised nose, and mouth open.

Females with new calves lie out for a period prior to joining groups (Kingdon 1982, Elkan 2003). Calves stay close to the mother during the early months and then form close associations with other young Bongos. Bongos are relatively quiet animals and make few vocalizations. Males utter a loud bellow when alarmed or when entering a social group.



Bongo *Tragelaphus eurycerus* adult female.

Reproduction and Population Structure Females are thought to begin breeding at 2.5 years old and ♂♂ probably at 3–4 years (Ralls 1978). There appear to be bi-annual calving peaks in both Lowland and Mountain Bongos. Peaks in Lowland Bongo birthing occur from May to Jun and Sep to Nov in the short and long wet seasons, respectively (Turkalo & Klaus-Hugi 1999, Elkan 2003). As the calves are dropping in May and Sep at the beginning of the wet seasons, forage quality would be high (P. Elkan pers. obs.). Mountain Bongos calve in Jan and Sep (Kingdon 1982).

Gestation periods of 282–287 days (Ralls *et al.* 1985) have been observed in captive Bongos. Oestrous cycle is 21–22 days and oestrus lasts three days (Ralls *et al.* 1985). Captive ♀♀ conceived at 2.3 and 2.7 years of age and inter-birth intervals were 466 and 525 days.

A single calf weighing an average of 20 kg is born (Forthman *et al.* 1993), although twins have been recorded in captivity (Schürer 1999, Ibler 2001). Females with new calves lie out for a period prior to joining groups (Kingdon 1982, Elkan 2003). Calves stay close to the mother during the early months and then form close associations with other young Bongos. In captivity, calves were able to eat vegetation during the first week (Forthman *et al.* 1993). Horns are visible after 2–3 months, growing rapidly to 100 mm after six months and 200 mm by about one year. Observations of young in captivity suggest that Bongo calves exhibit less aggressive behaviour and slower horn development than do Common Elands.

The sex ratio estimates from individually recognized Bongos was 0.6 adult ♂♂ to 1 ♀ (Elkan 2003). Mortality and birth rates for Bongos are not known and are likely to be site-specific. Differences in adult to calf/juvenile and adult to subadult ratio suggest higher mortality in young, probably due in part to Leopard *Panthera pardus* predation (Turkalo & Klaus-Hugi 1999, Elkan 2003). Adult ♂♂ had the highest mortality rate of any age/sex class during a 1997 die-off of Bongos in N Congo (Elkan *et al.* 2009). They live to 25 years in captivity, but are unlikely to attain that age in the wild.

Predators, Parasites and Diseases Young Mountain Bongos are vulnerable to African Rock Pythons *Python sebae*, Leopards and Spotted Hyenas *Crocuta crocuta* during the lying up period (Verschuren 1975), as well as to predation from Lions *Panthera leo*

(D. Western pers. comm.). In Central Africa, all ages, but especially young, are subject to predation by Leopards (Elkan 2003).

Percival (1928) reported that rinderpest drastically reduced the populations of the Mountain Bongo in 1890 and 1896 and populations are thought to have suffered greatly in later epidemics in the early 1900s. Unusual cases of widespread mortality have been registered in both Lowland and Mountain Bongos. A case involving the mortality of a large number of Bongos was reported from the Mau Forest, Kenya in 1960 (Simon 1962). Local hunters indicated that foraging on poisonous second-year growth of an irregular *Mimulopsis* sp. cycle (after the extensive flowering and die-off of bamboo *Arundinaria alpina*) caused extensive mortality not only in Bongos, but also in Forest Hogs *Hylochoerus meinertzhageni* and domestic cattle. Although symptoms of death did not resemble those of rinderpest, Davies (1993b) later argued that this artiodactyl disease was a more likely explanation for the deaths. Resolution of this controversy is of practical importance for the conservation of this species in Kenya. *Theileria* may also be an important disease affecting wild Kenyan populations (P. Reillo pers. comm.).

Parasitological investigation of several Bongos in Congo found evidence of *Elaeophora sagitta* and nematode parasites (Huchzermeyer *et al.* 2001). In Apr and May 1997 a *Stomoxys* fly outbreak contributed to the mortality of large numbers of Bongos and other ungulates over a broad area of the tri-national region of Cameroon–Congo–Central African Republic. A prolonged severe dry season followed by exceptionally heavy rains created ideal conditions for several highly abundant generations of *Stomoxys* flies. Clouds of biting flies attacked large mammals in the region leading to mortality of Bongos, Sitatungas and Yellow-backed Duiker *Cephalophus silvicultor*. Mortality rates were highest in adult male Bongos. Elkan *et al.* (2009) hypothesized that the multifactorial mortality resulted largely from disruption of foraging patterns and the extreme fatigue of attempting to fight off and escape the biting flies.

Conservation IUCN Category: Near Threatened (*T. e. isaaci* – Critically Endangered C2a(i); *T. e. eurycerus* – Near Threatened). CITES: Appendix III (Ghana).

Mountain Bongos are now rare on Mt Kenya and have been substantially reduced in Aberdares N. P. and its surrounding forest reserves. There is evidence of a remnant population in the Mau and Eburu forests, which are both subject to high levels of illegal logging and hunting. The Eburu population, located as it is in a small, isolated forest, is under especially intense pressure (L. Estes pers. comm.). The decline of Mountain Bongo populations in the Aberdares in recent years has been attributed to increased hunting by local people and habitat loss and transformation (Hillman 1986b, T. Butynski pers. comm.), and even to the increased numbers of Lions in the area (D. Western pers. comm.). Although these factors have surely played a role in the decline of Mountain Bongo, the impact of disease has probably been underestimated (L. Estes pers. comm.). The continued grazing of cattle in the forest reserves of Mt Kenya and the Aberdares may have greater implications for Bongo conservation than hunting pressure in terms of disease transmission; cattle have been found all the way up in *Hagenia* forest on the Aberdares plateau in the dry season – in an area where they certainly overlap with Bongos (L. Estes pers. comm.). The negative impact of forest succession as a result of total protection needs further investigation (Kingdon 1982)

and ongoing research at the time of going to press might shed some light on this issue (L. Estes pers. comm.).

Two conservation initiatives are currently in progress on Mountain Bongos, including: (1) a multi-phased international programme to reintroduce captive Bongos from North America to Mt Kenya; and (2) the Bongo Surveillance Programme (BSP), which protects and investigates the status of the remaining wild Bongos in Kenya. The first phase of the Bongo reintroduction programme, spearheaded by the Rare Species Conservatory Foundation (RSCF), began in 2004, when 18 animals were flown from North American zoos to a captive-breeding facility at Mt Kenya Game Ranch, on the north-western slopes of the mountain. The second phase began in 2005, with the commencement of a research programme into the Mountain Bongo's ecology. The research project, currently ongoing, is investigating the configuration of Bongo habitat on both the Aberdares and Mt Kenya, using recently collected field and remotely sensed data. Since 2004, the BSP has been surveying potential Bongo habitat, focusing primarily on the Aberdares, but also Mt Kenya and the Mau and Eburu forests; plans to survey the Cherangani Hills are also afoot. The BSP was created, and is run entirely, by Kenyans local to the Aberdares and Mt Kenya, and is largely responsible for the current state of knowledge about the remaining populations (L. Estes pers. comm.).

Direct threats to Lowland Bongo conservation include snare hunting associated with expanding commercial forestry exploitation, high demand for Bongo trophies, and changing land use (Elkan 1995, 2003). Traditionally, due to taboos against eating of the meat, Bongos



Bongo *Tragelaphus eurycerus*.

are not considered a preferred game species by local people in many parts of Africa, such as N Congo, S Sudan, SW Central African Republic and SE Cameroon (Hillman 1986b, Elkan 1995, 2003). However, there is still heavy loss due to snaring that indiscriminately kills young and wounds adults. Eroding traditional beliefs and expanding commercial hunting are creating new pressures on populations and its meat is sometimes smoked and sold as 'buffalo'. Bongos are also the primary target of tourist safari hunting in the forests of central Africa. Demand for Bongo hunting safaris has been increasing greatly over the past decade and the use of dogs and inadequate regulation has resulted in over-hunting in several areas (Elkan 1995, 2003). H. Planton and A. DeGeorges (pers. comm.) reported that hunter success and trophy quality were declining in Cameroon. Hunters have argued that 'trophy' ♂♂ taken are 'solitaires' and are too old and no longer involved in mating. While this may sometimes be the case, age estimation data indicate that many of these ♂♂ observed as solitary are likely to be reproductively active (P. Elkan pers. obs.).

Although the distribution and numbers of Lowland Bongos have declined over large parts of their former range, and particularly in West Africa, they remain patchily distributed, with localized concentrations in areas of favourable habitat (East 1999). Populations of Lowland Bongos in Central Africa receive protection in Dzanga-Ndoki N. P. and Bangassou areas of Central African Republic, Lobeke N. P. (Cameroon) and in Nouabale-Ndoki and Odzala National Parks (Congo) (East 1999). In Gabon, they are reliably recorded from Mwagne, Minkebe and Ivindo National Parks (Maisels *et al.* 2004, P. Henschel pers. comm.). In Congo, the highest known Bongo densities occur in the Kabo and Pokola logging concessions (Elkan 2003). In West Africa, where declines have been more severe, the Lowland Bongo remains common in only a few areas, such as Taï N. P. (Côte d'Ivoire), Sapo N. P. (Liberia) and Kakum N. P. (Ghana) (East 1999). East (1999) estimated that perhaps 60% of Bongo numbers were confined to protected areas.

Because the highest known abundances of Bongos in central Africa occur in logging concessions not protected areas, an approach is needed that incorporates both protected areas and logging concessions. The goal is to devise a strategy that reduces indiscriminate killing of Bongos by snares, strictly regulates and monitors safari hunting outside of reserves, and incorporates a landscape analysis of the effects of different land ownership, land use practices and resource needs of local people. This approach is being pioneered in Congo by establishment of community-supported subsistence hunting regulations in logging concessions that aim to ensure a sustainable supply of wildlife meat without illegal killing of Bongos and other protected species. Forest blocks are zoned as non-hunting or subsistence hunting areas. Separate hunting zones are designated for each village and logging camp. Transport and

commercial sale of meat across these zone boundaries is prohibited and regulations are enforced by a staff of both government officers and ecoguards (Elkan 2003). Rational allocation of hunting rights, promotion of alternative meat sources for logging company employees, and wildlife law enforcement are developed and combined with an intensive education programme that emphasizes both general conservation and the utilitarian practicality of non-hunting areas adjacent to hunting zones.

Current Bongo distribution patterns are patchy and not well understood. It is important to begin developing and testing an ecological model of their distribution and conservation based on data on abundance and distribution in relation to forest cover and condition, critical forest clearing habitat and current and historical logging and hunting. The model can then be used to explore how the Bongo will respond to different logging and other anthropogenic factors.

Measurements

Tragelaphus eurycerus

T. e. eurycerus

HB (♂♂): 2043 (1860–2190) mm, n = 12

HB (♀): 2010 mm, n = 1

T (♂♂): 561 (530–610) mm, n = 13

Sh. ht (♂♂): 1210 (1100–1260) mm, n = 13

Sh. ht (♀): 1220 mm, n = 1

Congo (P. Elkan pers. obs.)

Record horn length is 89.2 cm for a pair of horns from the Kerre R., Central African Republic (Rowland Ward)

T. e. isaaci

HB: 1700–2500 mm

T: 450–650 mm

Sh. ht: 1100–1250 mm

WT (♂♂): 362 (335–400) kg, n = 3

WT (♀♀): 229 (182–276) kg, n = 7

Kenya

Body measurements: Haltenorth 1963 (mean and sample number not given)

Weight: L. F. Bosely (pers. comm.)

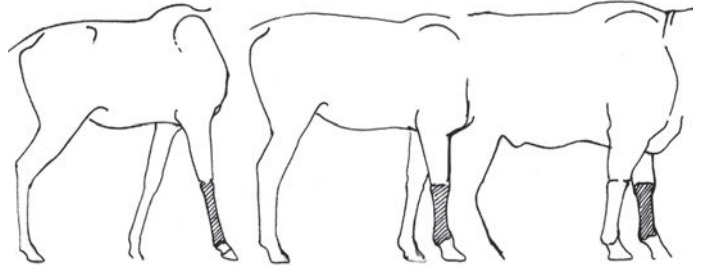
Record horn length is 87.9 cm for a pair of horns from Mt Kenya, Kenya (Rowland Ward)

Key References Elkan 1995, 2003; Hillman 1986b; Kingdon 1982; Klaus-Hugi *et al.* 1999; Ralls 1978; Turkalo & Klaus-Hugi 1999.

Paul W. Elkan & James L. D. Smith

Tragelaphus derbianus GIANT ELAND (LORD DERBY'S ELAND)

Fr. Éland de Derby; Ger. Reisenelenantilope

Tragelaphus derbianus (Gray, 1847). Ann. Mag. Nat. Hist. (1) 20: 286. Gambia, Western Africa.LEFT: Giant Eland *Tragelaphus derbianus* male.ABOVE: Foreleg/metacarpus proportions compared in Greater Kudu *T. strepsiceros* (left), Giant Eland *T. derbianus* (centre) and Common Eland *T. oryx* (right).

Taxonomy First described by Dr J. E. Gray, keeper of the Department of Zoology at the British Museum in London from 1840 to 1874, from horns, then skins, sent from Senegambia (type specimen). The species was originally placed in the genus *Boselaphus*, then *Oreas*, and then *Antilope*. *Taurotragus*, referring to the size and shape of the largest antelope, rather massive and more or less ox-like, has been used since the late 1800s, but is here included in *Tragelaphus* (see genus profile). The species has been treated as conspecific with the Common Eland *Tragelaphus oryx* (Haltenorth 1963), but is considered a distinct species by most authorities.

Four Giant Eland 'races' have been recognized in the past (Clark 1931): *T. derbianus derbianus* from Senegambia; *T. d. cameroonensis* from Cameroon; *T. d. congolanus* from Congo; and *T. d. gigas*, from Sudan. Only two subspecies are now recognized: *T. d. derbianus* is dedicated to the 13th Earl of Derby who employed the collector of the first horns sent to England, while *T. d. gigas* was described by von Heuglin from a pair of horns collected during travels to the White Nile region in 1863 (von Heuglin 1864). Synonyms: *cameroonensis*, *colini*, *congolanus*, *derbii*, *gigas*, *typicus*. Chromosome number: $2n = 31$ in ♂ (translocated Y) and 32 in ♀, the same as the Common Eland *T. oryx* (Nguyen *et al.* 2008).

Description The largest of all antelopes, massive, and often said to show a 'bovine' appearance (though more finely shaped) and sometimes exceeding the size of the African Buffalo *Syncerus caffer*. Long muzzle, but much narrower than that of an ox, with a black mark starting below the eyes and extending down to the nostrils (narrow on ♀ and young, wide on old bulls); there is a white chevron between/below the eyes, except on old dark bulls. Ears broad and expanded, rufous outside, whitish with black patches on the hind margins. There is a mat of dark hair on the forehead of adult ♂♂; a prominent dewlap commences below the chin. Coat hair short,

general colour ruddy fawn, sides (shoulder to rump) of body marked with usually 10–18 long vertical white stripes. A mostly black stripe runs along neck and back, with white hair on top of stripes. There is a short, darkish mane on the bull's neck and withers; neck covered with rufous grey to blackish hairs, bordered at its rear end by a paler (♂♂) or even white (♀♀) collar. Dark marks are present behind the knees of the forelegs, and surrounding all four pasterns and fetlocks, with white spots often marking the front face of pasterns. Internal side of legs paler than body, or whitish. Hooves grey. Tail long, reaching hocks, with terminal black tuft 100–150 mm below the hocks, always moving (the most prominent detail when seen from a distance in dense bush). Females more lightly built and smaller, with no mat of hair on the forehead. Variation in size and shape of dark and white marks as well as horns permit individual identification. Females have two pairs inguinal nipples.

Horns, present in both sexes, are thick-set, very large and massive, especially in ♂♂ (smaller in ♀♀), diverging from the base and almost straight, tightly spiralled, with anterior ridge more pronounced than the posterior.

Geographic Variation

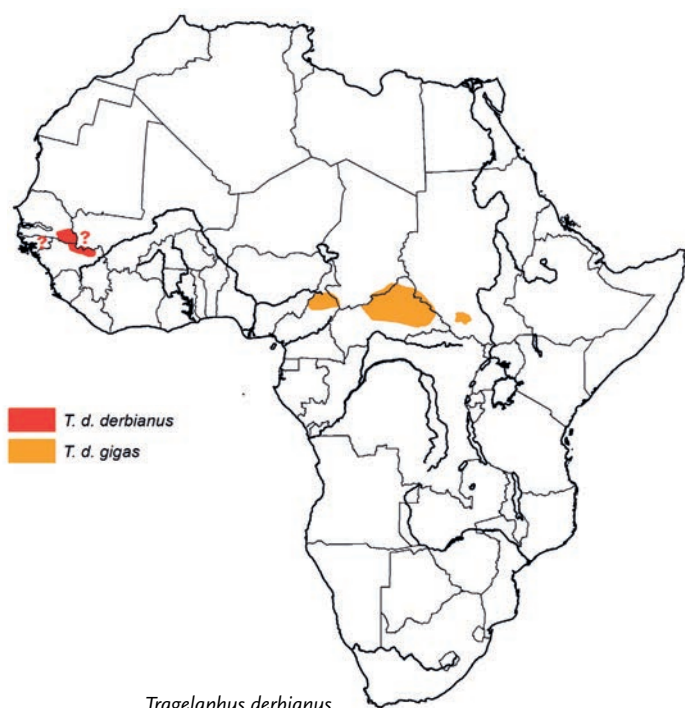
T. d. derbianus (Western Giant Eland): Senegal, Mali, Guinea and possibly E Guinea-Bissau. Bright rufous ground colour.

T. d. gigas (Eastern Giant Eland): Cameroon, Central African Republic, Chad and Sudan. Somewhat larger (the name Giant Eland is most applicable to this form), with a sandy ground colour.

The number of white stripes has often been noted as a distinctive feature between these taxa, with the western subspecies (*derbianus*) said to have more stripes (approximately 15) than the eastern (*gigas*; 12). However, individuals observed in Central Africa may have as many as 10–18 stripes (mean = 14) (H. Planton pers. obs.), and individuals of the western subspecies 12–16 stripes (mean = 14) (M. Antonínová & P. Hejčmanová pers. comm.).

Similar Species

Tragelaphus oryx. Allopatric species from open or lightly wooded savannas of eastern and southern Africa. General appearance



similar, though body slightly smaller, colour fawn or tawny, turning to greyish or bluish-grey with age, except for lower parts of legs; sides almost uniform or lightly striped (4–9 stripes); mane only on back of neck; dewlap commencing on throat; chevron often not visible between eyes; horns shorter, thinner; ears narrower, more pointed, without black marks.

Distribution Endemic to Africa. The historical range of the Giant Eland is not well known, but they probably occurred throughout the relatively narrow belt of savanna woodland extending across West and central Africa from Senegal to the Nile (East 1999).

The distribution of the Western Giant Eland is centred on and around SE Senegal, with the Eastern Giant Eland occurring in the central African region. The Western Giant Eland has been formerly reported from Senegal to Togo (Bigourdan & Prunier 1937, Baudenon 1952, East 1990), though its occurrence in Togo might have been a mistaken confusion with the Bongo *Tragelaphus eurycerus* (Grubb *et al.* 1998). The distribution has been reduced since the 1950s to small, scattered populations (Jeannin 1951). The subspecies still occurs in SE Senegal (Chardonnet 1997, G. Mauvais pers. comm.), the far north of Guinea (Sournia *et al.* 1990, Chardonnet 1997, Darroze 2004), probably SW Mali (Chardonnet 1997, Darroze 2004) and possibly E Guinea-Bissau (Chardonnet & Limoges 1990, East 1999).

The Eastern Giant Eland was formerly distributed from NE Nigeria to NW Uganda; it is now apparently extinct in both of the aforementioned countries, surviving in the former in the northern part of Gashaka-Gumti N. P. until the 1970s (Anadu & Green 1990), and being exterminated in the Uganda part of its range during military operations in 1970 (Kingdon 1982). The species now occurs mainly in NE Central African Republic, and in N Cameroon, with herds crossing the Chad border to the east; occasional vagrants may enter Nigerian territory (East 1999). There has been some recolonization by Giant Elands of hunting blocks of SE Chad since

the late 1990s (P. Chardonnet pers. comm.). They may still occur widely in SW Sudan (and indeed were recently recorded in Southern N. P.; Fay *et al.* 2007), and perhaps still occasionally visit NE DR Congo and NW Uganda (East 1999).

Habitat Giant Elands inhabit woodlands and forested Soudanian to Guinean savannas (1000–1500 mm rainfall in 5–7 months/year), and are never far from hilly/rocky landscapes or from water. They are frequently found in or near *Isoberlinia doka* woodlands (Kingdon 1997), although their range includes *Terminalia–Combretum–Afzelia* woodland, where *Isoberlinia* is not found (Bro-Jørgensen 1997). The western distribution corresponds to *Combretum glutinosum–Annona senegalensis* woodland and a mosaic of grass and woody savanna dominated by Combretaceae (Nežerková *et al.* 2004). Giant Elands move large distances daily (5–20 km/day) and all year round, and usually return to the same places during the same season. Wet season habitat is not clearly known, though it is widely believed that they spend the wettest months on rocky hills.

Abundance Densities in the order of 0.15–0.30/km² have been recorded, with great variations as herds in Cameroon move a lot within home-ranges of some 1000–1500 km² (H. Planton pers. obs.); they can be locally abundant during a few weeks/months and then totally absent for months. Thus, the same herd can be observed in very distant places at different times and densities are easily overestimated. A single study in Central African Republic reports an average home-range of 223 km² (Graziani & d'Alessio 2004).

Although no specific count has been carried out, it is estimated that some 200 or less individuals of the Western Giant Eland survive in Senegal (G. Mauvais pers. comm.). According to East (1999), there are probably more than 15,000 Eastern Giant Elands remaining, with over 12,500 in the Central African Republic. Since the early 1990s, numbers have tended to increase, at least for Cameroon (Planton *et al.* 1995), Chad and the Central African Republic (Blom *et al.* 1995). There is no information on numbers surviving in Sudan, although Fay *et al.* (2007) estimated a population of 165 for Southern N. P.

Adaptations Giant Elands drink daily when water is available, but even youngsters will trot or walk tirelessly all day long if disturbed, without stopping at any water point. They browse day and night, and do not rest except, when undisturbed, during the heat of the day. They use their strong horns to knock down or break branches and gain access to leaves of trees. Giant Elands have an excellent sense of smell and hearing, as well as excellent sight even at long distances.

The visual impact of the black-and-white markings on legs and ears is greater than in the Common Eland. This difference could be related to their less open habitat, to a greater role for ear and foot signals or to carry-overs from an ancestral condition. Ears are substantially larger than in the Common Eland and this, too, could be due to evolutionary inertia, but is more likely to represent selective pressure to maximize acuity of hearing in wooded environments.

Prior to a well-marked breeding season there are colour (and, perhaps, physiological and olfactory) changes that are exclusive to the foreheads and necks of breeding bulls. This overall darkening of the bulls' forequarters might signify a visuo-olfactory advertisement of the males' reproductive condition. A dense brush of hair on the

forehead of adult ♂♂ is often employed in 'marking' behaviour. Supposed territories are marked by adult bulls urinating on a patch of moist soil, and they then rub their forehead and horns to pick up the odour. Bulls anoint themselves on their sides and back and thereby more effectively proclaim their presence. The thick mat of woolly dark hair on the forehead acts as a paintbrush and allows the bull to leave samples of his scent on tree trunks at just the right level to be noticed by other elands (Ruggiero 1990).

Foraging and Food Giant Elands feed mostly on leaves, shoots, herbs and fruits (but occasionally on grasses), and are classified as browsers by Gagnon & Chew (2000) in their review of the dietary preferences of African bovids. Movements are to a certain extent determined by the presence of certain trees or shrubs, the young leaves of which form their favourite diet. Feeding habits have been observed in several places, but systematically studied only in N Cameroon (Bro-Jørgensen 1997, Michaux 1998), where more than 80 plant species were eaten (the ingestion of 16 of these having been directly observed). Shortly after bushfires, a lot of dried leaves and dry fruits, and ashes, are eaten. During the driest season (Jan–Mar), they feed mainly on *Terminalia* spp. and *Combretum* spp. leaves, which remain important until the rains (Jun). Where *Adenodolichos* sp. occurs, herds will actively look for sweet young shoots of this plant after fires and until the rains. *Isobertlinia* spp. leaves are eaten during the dry season, but never exceed 20% of the diet. When rains fall, Giant Elands start looking for *Tephrosia* spp. and *Acacia* spp. leaves and pods. Legumes form by far the major part of their diet during the wet season (40–85%). Grasses can be eaten all year round, but never exceed 4–5% of the diet. Salt-licks are visited every day when possible.

Social and Reproductive Behaviour Herds comprise ♀♀ and young of both sexes, plus young adult ♂♂ and sometimes adult breeding bulls. The latter regularly wander alone or in small male groups outside breeding herds. Herd size varies a lot according to season. Most often herds include about 20–30 individuals; large herds of 150 individuals and more are observed early in the dry season (Dec and Jan: Cameroon), before the mating season, and stay together almost until the rains (Jun). In such herds, an adult ♀ often calls continuously, which has the effect of keeping youngsters together near her (H. Planton pers. obs.). Before and during the wet season, herds tend to split into smaller groups of less than ten, often a few ♀♀ and one ♂ plus young. The same herd can be observed in various places of the home-range over which elands move continuously. They are locally abundant for a few weeks/month and then move to another part of the range.

Relations between individuals within the group consist mainly of smelling or licking or rubbing nose, mouth, forehead, horns, ears, belly, tail and anogenital region (Altmann & Scheel 1976). Close relationship is sometimes observed between two specific individuals for a couple of days, during which they often rest their heads on each other's back. Males, mainly young, seem to establish their status in the group's hierarchy by simulating threats and fights, often kneeling, near muddy places or salt-licks. The dominant action is to charge the other, head down, and/or snort noisily; the weaker usually gives up and walks away. However, serious fights are sometimes observed or evidenced by scars or broken horns. These often occur early in the wet season, but also during the mating season. Fighting ♂♂ engage



Giant Eland *Tragelaphus derbianus* head in profile.

their horns and wrench their heads sideways in an effort to twist each other's neck and unbalance their opponent. Marking behaviour by adult ♂♂ has been mentioned earlier.

Before mating, the bull approaches the ♀ with neck and head stretched out. The ♀ jumps aside then pushes the ♂ away. The ♂ tirelessly tries again to approach, turns around her, smells her, rests his head on her rump, until she is ready to mate. Pregnant ♀♀ tend to stay together with young individuals, while breeding bulls wander in search of other ♀♀ on heat. Young often stay together and playfully chase each other among and around the adults (Ruggiero 1990). Females accompany their offspring for about one year.

Giant Elands have often been said to be silent. Actually, when undisturbed and browsing, they often sniff and growl discreetly; the ♀ keeps contact with her youngster by a high-pitched call, to which the latter answers. Though they can often be close to other species, Giant Elands very seldom mix with them. Like Common Elands, they are easily tamed when captured as young, and can behave then like domestic stock.

Reproduction and Population Structure In Cameroon, mating mainly takes place in the first half of the dry season (Dec–Feb). Prior to this, changes in the breeding bull's forehead and neck have been mentioned and are quite noticeable in the field (H. Planton & I. Michaux pers. obs.). Mean gestation length is 39 weeks. Calving has yet to be observed in the wild, but occurs between Sep and Jan, i.e. before (peak) and shortly after the last rains. Under captive conditions in Senegal, calving takes place between Nov and Feb, in the early dry season (Al-Ogoumrabe 2002, M. Antonínová & P. Hejčmanová, pers. comm.). Usually a ♀ gives birth to a single calf, about 25–35 kg, which stays hidden and out of the herd for one week. The calf starts browsing from one week old, and is weaned after six months. Maturity is reached between 15 and 24 months, and animals are full size by 4–5 years. Bulls do not usually succeed in mating before they are seven



Giant Eland *Tragelaphus derbianus* subadult male.

years old. Sex ratio among calves is 1 : 1, but adult ♀♀ outnumber adult ♂♂ (Altmann & Scheel 1976, H. Planton pers. obs.).

Predators, Parasites and Diseases Little information is available regarding predators, which include Lions *Panthera leo* and African Wild Dogs *Lycaon pictus*, while Leopards *Panthera pardus*, Spotted Hyenas *Crocuta crocuta* and Cheetahs *Acinonyx jubatus* also prey on calves, which ♀♀ try to protect.

Major epizootic diseases cause great variations in numbers. In particular, Giant Elands have suffered heavy mortality from rinderpest, e.g. in the early 1900s (Blancou 1960), to which it is said to be more susceptible than any other antelope. Its demise in Gambia has been attributed primarily to the devastating effects of this disease (Camara 1990). Populations in the central African region crashed by 60–80% during and after the 1983–84 rinderpest outbreak, but have almost recovered now facilitated by the bush encroachment that accompanied the severe reduction in elephant numbers by poachers during the 1980s and the prevalence of uncontrolled fires (East 1999).

Studies on parasites have been carried out in Cameroon through helminthological necropsies and year-round faeces collection/analysis

(Michaux 1998). Cestodes, trematodes and nematodes have been found, but in low numbers compared with neighbouring wild grazers (e.g. Kobs *Kobus kob*) and in very low numbers and species diversity compared with domestic stock. Parasitic load was almost nil in the dry season. The Giant Eland is a new host for five parasite species (*Moniezia monardi*, *Haemonchus vegliai*, *Cooperia yoshidai*, *Cooperia* sp. and *Ostertagia angusdunni*), and two other species found might represent undescribed new species of *Cooperia* (Michaux 1998).

Conservation IUCN Category: Least Concern (*T. d. derbianus* – Critically Endangered C2a(ii); *T. d. gigas* – Least Concern). CITES: Not listed.

Uncontrolled hunting (notably assisted by fire) and loss of habitat have contributed greatly to the reduction of Giant Eland numbers, particularly in West Africa where they have been exterminated throughout most of their former range. Traditionally, the Fulani people did not hunt them, as they are believed to transmit diseases and cast spells. Their current distribution range includes a number of sizeable protected areas, including Niokolo-Koba N. P. and Falémé Hunting Zone in Senegal (*derbianus*); Faro, Bénoué and Bouba Ndjida

National Parks and most of the 27 surrounding hunting concessions in N Cameroon, Bamingui–Bangoran and Manovo–Gounda–St Floris National Parks and most of the hunting blocks in N and NE Central African Republic, and Southern N. P. in Sudan (*gigas*). Further development and maintenance of sustainable trophy hunting and improved protection and management of national parks within its range states will be essential to ensure this antelope's long-term survival (East 1999).

Attempts to capture Giant Elands and establish herds of both subspecies outside the species' natural distribution area have been made on at least ten occasions for purely commercial purposes. The Eastern Giant Eland is held in captivity in two countries outside their distribution range: South Africa and the USA. Historical captures were undertaken in Sudan (1938–46), Cameroon (1958) and Chad (1967–70). Of an unknown number of Giant Elands handled, 31 were delivered to six European or American zoos, none of which has any representation in the current captive populations. More wild animals were caught in 1985 in the Central African Republic. The survivors (3 ♂♂, 5 ♀♀) were the initial founders of the current North American captive population (Romo 2001). Animals in captivity derive from the population established in the USA, initially at Cincinnati and Los Angeles zoos, from nine wild-caught animals imported from the Central African Republic in 1986. As of 23 December 2011, the North American population stood at 49 individuals (20 ♂♂, 29 ♀♀) in five institutions: San Francisco Zoological Gardens, White Oak Conservation Center, San Diego Zoo Safari Park, Miami Metrozoo and Houston Zoo. This suggests a 30% decline compared to the number of 69 reported in March 2004 (ISIS records).

In mid-2000, a private South African capture team caught 23 Giant Elands in Central African Republic, of which two died and 21 were flown to Togo. IUCN's Antelope Specialist Group has no information on the fate of the ten captive Giant Elands that are believed to have remained in Togo (East 2001), but 11 of the 21 were later shipped to John Hume's Mauricedale Game Ranch (Mpumalanga, South Africa), with a three-month temporary import permit. Four more died there, and the seven survivors were moved to Johannesburg Zoo in December of the same year following an outbreak of foot-and-mouth disease (East 2001, Estes 2003), shortly after which another one died. The two remaining ♂♂ died during blood transfusion procedures, and since then there have been additional age-related deaths (D. Moss pers. comm.). The survivors, two ♀♀ only, are held at Johannesburg Zoological Gardens. No births have been reported in RSA since October 2001 (ISIS records).

No Western Giant Elands are known to have been held in captivity until recently. Captures made by San Diego Zoo Safari Park in Falémé Hunting Zone, Senegal, in 1979, resulted in all nine animals dying during or shortly after capture (S. Diouf pers. comm.). The next captures were conducted in Niokolo-Koba N. P., Senegal, in 2000

by a South African team for the Ministère de l'Environnement et de la Protection de la Nature and private Société pour la Protection de l'Environnement et de la Faune au Sénégal. Some 126 animals were removed alive from the park, including nine Giant Elands (eight ♀♀ and one ♂). Some of these animals were shipped to South Africa, but none of the elands. Three of the elands died in quarantine, the six survivors (one ♂, five ♀♀) were kept in a 25 ha enclosure (enlarged to 50 ha in 2004) of unsuitable habitat in Bandia G. R., Senegal, just next to exotic (South African) species including Common Elands, with which they could potentially have hybridized (East 2000). There were four births at Bandia in 2002 (Nežerková *et al.* 2004), and 30 in total between 2000 and 2006 (M. Antonínová & P. Hejčmanová pers. comm.). A second enclosure was built in Fathala Reserve, to which a male-only group (9) and a breeding nucleus (1, 3) were translocated in mid-2006 (Antonínová *et al.* 2006). In 2009, the semi-captive population comprised 54 individuals (26 ♂♂, 28 ♀♀), with an annual population growth of 1.4% (Koláčková *et al.* 2011).

Further translocation of Giant Elands to areas such as private hunting reserves outside the species' natural range could potentially have serious consequences in terms of spreading diseases and destroying trophy hunting activities in West and central Africa, which are currently the main support and reason for wildlife conservation in these regions.

Measurements

Tragelaphus derbianus

T. d. gigas

HB: 2620–2930 mm, n = 30

T: 600–700 mm, n = 30

HF c.u.: 100–110 mm, n = 30

E: 230–280 mm, n = 30

Sh. ht: 1650–1780 mm, n = 30

N Cameroon (H. Planton & I. Michaux pers. obs.)

Depierre & Vivien (1992) recorded a maximum HB of 3200 mm

Average estimated weight is around 450 kg for ♀♀ and 900 kg for ♂♂ (H. Planton pers. obs.); Haltenorth & Diller (1980) recorded a mass of 300 kg for ♀♀ and 1000 kg for ♂♂

Record horn length for *T. d. gigas* is 142.9 cm for a pair of horns from Ouanjia R., Central African Republic, and for *T. d. derbianus* the record is 115.6 cm for a pair of horns picked up from an undefined locality (Rowland Ward)

Key References Akakpo *et al.* 2004; Altmann & Scheel 1976; East 1999; Jeannin 1951; Michaux 1998; Nežerková *et al.* 2004; Ruggiero 1990.

Hubert P. Planton & Isabelle G. Michaux

Tragelaphus oryx COMMON ELAND

Fr. Éland de cap; Ger. Elanantilope

Tragelaphus oryx (Pallas, 1766). Misc. Zool. p. 9. Known to the Dutch 'ad Promontorium B. Spei', restricted to South Africa, Western Cape Prov., near Cape Town by Shortridge (1934: 607).

Common Eland *Tragelaphus oryx* male.Common Eland *Tragelaphus oryx* female.

Taxonomy The Common Eland *Tragelaphus oryx* and Giant Eland *Tragelaphus derbianus* have been considered conspecific by some authors (e.g. Haltenorth 1963), but are usually treated as full species. Three subspecies are generally recognized (Ansell 1972, Kingdon 1997), although their validity requires confirmation. Lorenzen *et al.* (2010) recorded a significant regional divide between mtDNA lineages in Common Eland in East and southern Africa, and posited a more recent origin of the East African population that could result from colonization following extinction from the region. Synonyms: *alces*, *barbatus*, *billingae*, *canna*, *kaufmanni*, *livingstonei*, *livingstonii*, *niediecki*, *oreas*, *pattersonianus*, *selousi*, *triangularis*, *typicus*. Chromosome number: $2n = 31$ in ♂, and $2n = 32$ in ♀, the difference being due to a Y-autosome translocation; the X chromosome is large and acrocentric (Wurster & Benirschke 1968, Wurster 1972, Buckland & Evans 1978, Robinson *et al.* 1997). There are two well-documented records of hybrid male offspring between a Common Eland and Greater Kudu *Tragelaphus strepsiceros*, one known to be sterile, the other unknown (Jorge *et al.* 1976, Van Gelder 1977a).

Description Common Elands are large, cow-like bovines, with straight spiral horns and a dewlap. The pelage is tawny with short hairs, becoming blue-grey with age, especially in ♂♂. There are variable white stripes on the back and flanks, which usually become less distinct with age. The pelage is whitish on the belly, inside the legs and ears and above the hooves. A dark mark is present above the knee on the back of the forelegs. Dark hair on ridge along back and on tufted tail tip. The dewlap is long, thin, pendulous, with a terminal tuft that is lost in older ♂♂. Neck thick and muscular, darker than body; there is no mane, but pale curly hairs on the upper surface. Tufts of hair on the nose and forehead vary in size and colour between individuals and over time within individuals. The mat of hair on the

forehead has a strong smell due to a secretion from a glandular area in the skin (and frequent rubbing in urine). Females are smaller than ♂♂, with the dewlap much smaller and thicker, a terminal tuft of black hair, and no facial hair tufts. Females have two pairs of inguinal nipples.

Horns, present in both sexes, are nearly straight, slightly diverging, with a heavy spiral ridge at the base. Horns of oldest ♂♂ are shorter than those of younger animals. The horns of adult ♀♀ are less heavy and thinner in diameter and more uneven, and without the heavy spiral ridge at the base. Age determination based on horn growth and teeth eruption is discussed by several authors (Kerr & Roth 1970, Attwell & Jeffery 1981, Jeffery & Hanks 1981). Horn buds are present at birth, and the horns grow rapidly until about seven months of age, and thereafter more slowly. At about 18 months of age, the horns of ♂♂ clearly show signs of the developing spiral ridge at the horn base. In the dentition, molars 1, 2 and 3 erupt at 6–8, 14–20 and 24–27 months, respectively, and permanent premolars erupt at 36–37 months; full adult dentition is attained in the fourth year of life.

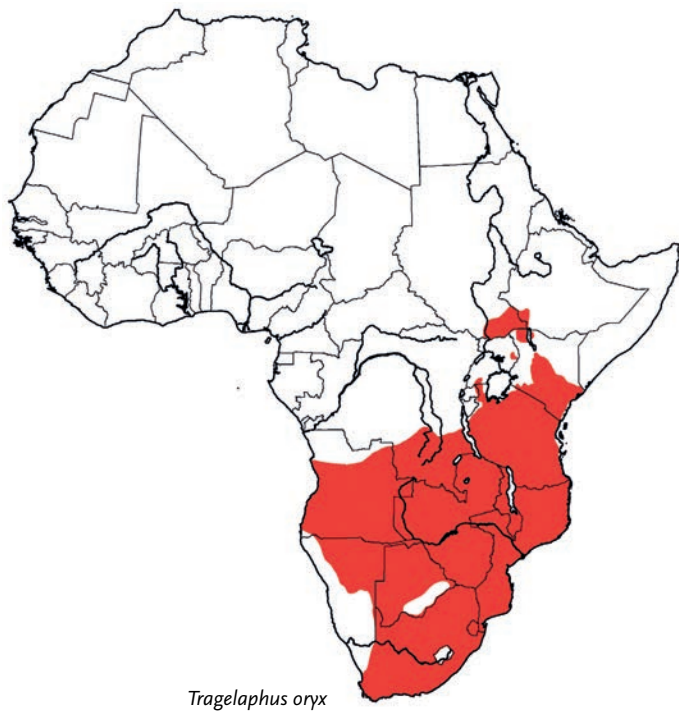
Geographic Variation

T. o. oryx: Southern Africa, with its range extending north to S Botswana and N Namibia.

T. o. livingstonii: East-central African woodland areas.

T. o. pattersonianus: Tanzania northwards.

Common Elands in the southern part of the range (*T. o. oryx*) are dull fawn in colour, the white stripes on the body not particularly distinct, and having a dark brown mark on the back upper region of the forelegs. Common Elands further north have distinct body stripes, but a less distinct dark mark on the back of the forelegs; body colour tends to be richer in Common Elands from northern areas. However, there is a large degree of intergradation and also considerable variation within

*Tragelaphus oryx*

regions. For example, animals in Zimbabwe show traits characteristic of both *T. o. oryx* and *T. o. livingstonii*. Likewise, Common Elands from Angola have been referred to the subspecies *T. o. livingstonii*, although Ansell (1972) noted that Angolan Common Elands occur in an area of intergradation between the nominate form and *livingstonii*. Crawford-Cabral & Veríssimo (2005) note that Angolan animals are more comparable to the nominate form, and thought that at least animals from the west of the country were representative of *T. o. oryx*.

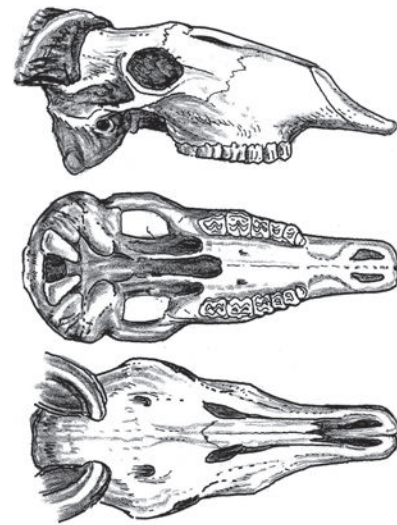
Similar Species

Tragelaphus derbianus. Savanna of West Africa and central Africa in N Cameroon, Central African Republic to SW Sudan (west of the Nile R.). Larger, with longer horns; horns in ♂♂ are longer, more widely splayed, and have a looser spiral; neck of ♂ darker, with dewlap hanging from jaws and neck only, rather than continuing between legs; ears broader, and more conspicuously marked, as are hocks.

Distribution Endemic to Africa, being widespread in savanna and woodland areas in eastern and southern Africa from SE Sudan and SW Ethiopia southwards to South Africa.

Historical Distribution From the Cape Peninsula (South Africa) to forest margins in the Congo Forest basin, the Nile flood-plain and arid N Kenya. Interestingly, a fossil specimen attributed to the Common Eland (and not to the older, now extinct *T. arkelli*) has been found at Ternifine in Algeria (Arambourg 1962).

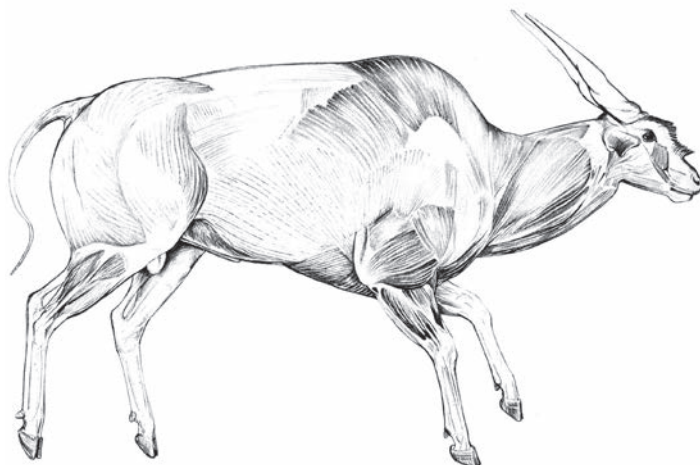
Current Distribution Still present in much of its former range, except in Burundi, where the species is considered extinct, and Uganda and Rwanda, where it is close to extirpation (East 1999). In Sudan, Common Elands are confined to the south-east, where they still occur in Boma N. P. (Fay *et al.* 2007); in Ethiopia they are known only from the Omo region (Hillman 1988a, East 1999). In Angola, where it was formerly widespread, the species is also believed to be

Lateral, palatal and dorsal views of skull of Common Eland *Tragelaphus oryx*.

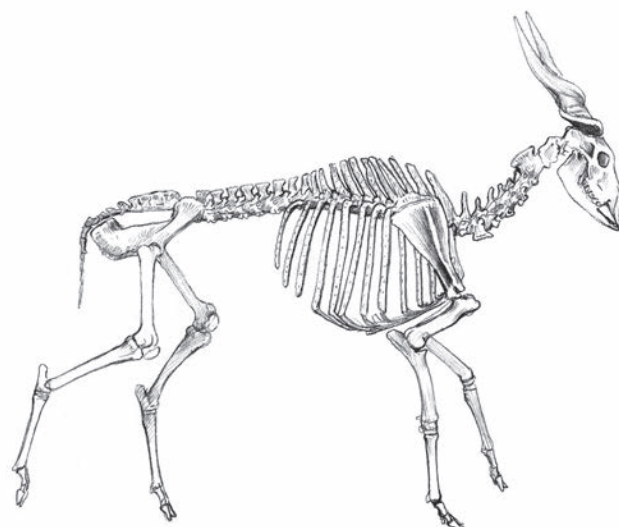
close to extinction, although there is no recent information on its status across much of the country. In South Africa, natural surviving populations are confined to the Northern Cape near Botswana (and where populations move into the area from S Botswana), parts of the North West and Limpopo provinces, and in the KwaZulu–Natal Drakensberg mountains (East 1999). In Lesotho, Common Elands occur only in Sehlabathebe N. P. (Lynch 1994). Within the rest of its range, it has been increasingly restricted to protected areas and regions with low human populations. Common Elands have been widely reintroduced in southern Africa (e.g. to Zimbabwe, many parts of South Africa, and Swaziland).

Habitat Common Elands occupy a wide variety of habitats, from semi-desert scrub in the Kalahari, to open *Brachystegia* woodland, to alpine moorlands on the slopes of Mt Kenya, Mt Kilimanjaro, the Nyika Plateau and the KwaZulu–Natal Drakensberg. In the KwaZulu–Natal Drakensberg, they occur up to 2400–2700 m, favouring slopes of 20° or less (Rowe-Rowe 1983, 1994), while in East Africa they have been recorded to 4750–4890 m on Mt Kilimanjaro (Grimshaw *et al.* 1995; and see Kingdon 1982). They are not found in deep forest, in true deserts, or in completely open grassland, though they do occur in grassland with good herb cover or which is interspersed with browsing habitat along drainage lines. Although they no longer occur in coastal regions, they do still occur at relatively low altitudes throughout their range.

Abundance Estimated to number more than 130,000 in the wild (correcting for undercounting biases in aerial surveys), with local density estimates (based on aerial counts) ranging from 0.05 to 0.4/km² (e.g. Laikipia Ranchlands in Kenya, Selous in Tanzania, Etosha N. P. in Namibia and Kgalagadi Transfrontier Park). Higher density estimates (0.6–1.0/km²) have been obtained in areas such as Omo N. P. in Ethiopia and Nyika N. P. in Malawi; ground surveys reveal similar estimates in areas such as Lake Nakuru N. P. (Kenya) and De Hoop N. R. (South Africa) (East 1999). The largest populations are in Namibia (ca. 32,000, where the majority are on private land), Tanzania (ca. 24,000), Zimbabwe (ca. 14,000), Botswana (ca. 14,000) and Kenya (ca. 13,000).



Common Eland *Tragelaphus oryx* adult male myology.



Common Eland *Tragelaphus oryx* skeleton

Adaptations Common Elands are unusual among browsing bovinines since they move long distances in search of ephemeral food sources. They have other attributes that are more typical of grazers such as an open social system. This life-style allows Common Elands to exploit a resource that is not available to other browsers – bushy vegetation and herbs sparsely scattered in grassland. In the Kalahari, the only other large browsers (Greater Kudu) are confined to patches of thicker vegetation, while Common Elands move freely through the system, and make use of dune areas, where the only bushy vegetation consists of dwarf shrubs.

Adaptations to a mobile life include the ability to go without water for prolonged periods. While they will drink when water is available, they are also able to obtain sufficient moisture from their food. Common Elands followed on a daily basis using satellite technology in the south-western Kalahari in Botswana never went close to a water source throughout the entire dry season (C. Thouless pers. obs.). Common Elands have a number of physiological adaptations that allow them to survive without drinking. Their body temperature can vary substantially. Under experimental conditions, body temperature increased from 33.9 to 41.2 °C while ambient temperature was kept at 40 °C, although body temperature generally remained below ambient temperature once it had exceeded 40 °C. The excess heat accumulated during the day is dissipated at night through conduction and radiation, and in order to reduce water loss at night Common Elands breathe more slowly and deeply (Taylor 1969). Recent studies have shown that selective brain cooling does not occur in Common Elands, and brain temperature remains constant at around 0.4 °C above carotid blood temperature (Fuller *et al.* 1999). Common Elands have a very high metabolic rate considering their size. Compared with Hereford cattle, their metabolism was 30% higher within the thermoneutral zone, and they excreted a far greater amount of urea in their urine (Taylor & Lyman 1967).

Activity patterns in Common Eland tend to vary depending on environmental factors and food availability (see, for example, Lewis 1978). In hot climates, such as Tsavo N. P., they may rest up in the shade all day feeding at night (Hillman 1979). On Loskop Dam N. R. in South Africa, Common Elands exhibited four main periods of activity during the day in winter, while in summer they moved and

fed in the morning, rested around mid-day, and fed again intensively in the late afternoon (Underwood 1975).

Although Common Elands, with their considerable bulk, usually move deliberately, they are capable of moving at great speed. When disturbed, they gallop, and jump high into the air, sometimes leaping over the backs of other animals. The gallop generally develops into a fast trot, which can be sustained for a considerable time. They are remarkably good at jumping, and can easily clear a two-metre-high obstacle.

There are a number of displays carried out by Common Eland ♂♂, involving the horns and the frontal brush of hair. These include vigorously rubbing the face in mud, particularly mud pats created by urine – either their own or from another animal. Adult ♂♂ also thrash vegetation with their horns, and break branches, and also rub their frontal brushes on tree stumps and broken branches. The effect of these behaviours is to change the appearance of the animal, with mud and/or vegetation being attached to the frontal brush and horns, and to accentuate the animal's smell. They appear to prefer 'smelly' substances for rubbing, such as aromatic shrubs and wet ash after grass fires (Hillman 1979).

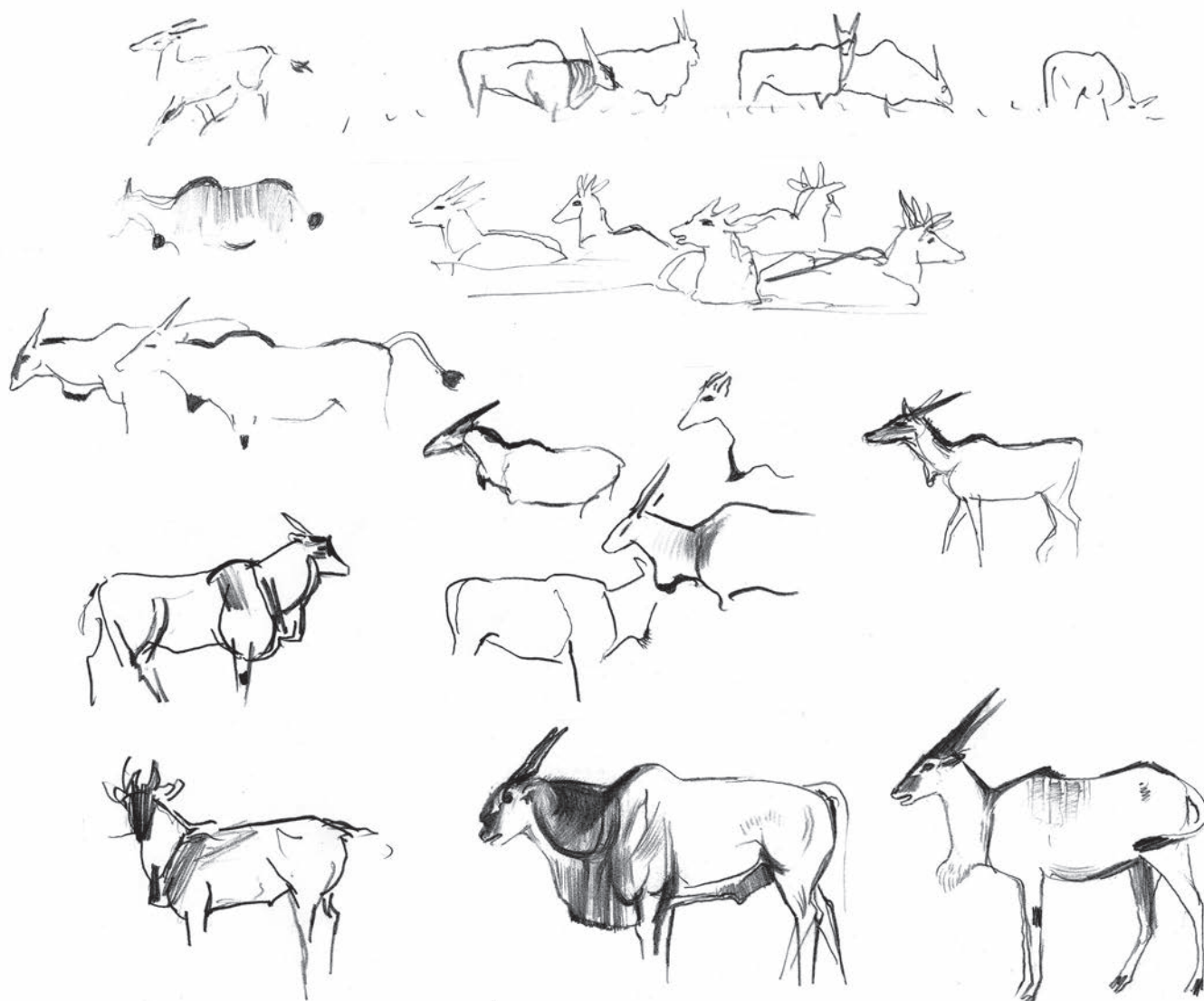
Foraging and Food Common Elands are primarily browsers, though the degree to which grass forms an important component of the diet is debated. They have been classed as intermediate mixed feeders (Hofmann & Stewart 1972, Hofmann 1973), and Gagnon & Chew (2000), in their review of the diets of African bovids, considered them as browser–grazer intermediates taking as much as 50% grass. Analysis of rumen contents of shot animals in Kenya indicated that they were feeding on up to 60% grass in the wet season, but less than 10% during the dry season (Hillman 1979). Other studies (Lamprey 1963, Underwood 1975) have also indicated high proportions of grass in the diet, although Watson & Owen-Smith (2000) have highlighted the unreliability of these studies. Grass appears to be eaten in quantity only during the wet, summer months, and most stomachs examined from other times of the year contained only a small percentage of grass (Wilson 1969, Kerr *et al.* 1970, Scotcher 1982, Buys 1990, Watson & Owen-Smith 2000). In the study by Watson & Owen-Smith (2000), grass formed 45% of the diet in early Dec, but only 6–10% of the diet in other months of the early wet season. Studies involving

stable carbon isotope analyses of animals in both East Africa (including the Athi Plains region) and southern Africa indicate that although Common Elands may consume some grass, they have a significant component of browse in their diet and that few populations consume as much as 50% grass (Cerling *et al.* 2003, Sponheimer *et al.* 2003b; and see Wallington *et al.* 2007).

Diet usage has been associated with habitat use: Common Elands show a preference for bush habitat for the dry part of the year and for grassland in wet periods, although ♂♂ tend to use thicker bush areas than ♀♀ (Buys 1990, Fabricius & Mentis 1990). Common Elands introduced to Mountain Zebra N. P. in the Eastern Cape of South Africa showed similar habitat preferences, but habitat selection was unrelated to the availability of palatable grasses in the habitat (Watson & Owen-Smith 2000). Common Elands in Mountain Zebra N. P. have a diet comprising as much as 94% browse (Watson & Owen-Smith 2000), and have fared very well since their introduction. Watson & Owen-Smith (2002) have suggested this is because Common Elands have been able to select a diet sufficiently low in fibre content by eating young shoots of most woody species encountered and by consuming large proportions of palatable woody species with low fibre content.

In the wet season in Shinyanga, Tanzania, Common Elands were observed to eat herbs, particularly *Ipomaea* spp. and *Commellina africana* (Harrison 1936). During the dry winter months in southern Africa, they also eat dry fallen leaves. They also are known to eat fruits, such as those of *Sclerocarya caffra* and *Ximenia caffra*, and in the dry season have been known to eat the fleshy leaves of aloes (Harrison 1936, Wilson 1969).

Feeding takes place from ground level up to about 2 m. They use their lips, rather than tongue, to grasp food. Common Elands may strip the leaves off twigs by drawing them through their lips. The use of horns to break down high branches has been reported from some populations. Common Elands insert their horns on either side of a branch, and then twist until it breaks off or hangs down, when it can be reached (Skinner & Chimimba 2005). This behaviour was not observed in the Kitengela in Kenya or the Nyika Plateau in Malawi (Hillman 1979), but was seen in Common Elands confined in an enclosure with Camphor Bush *Tarchonanthus camphoratus* and in a wild population in E Zambia (Wilson 1969).



Common Eland *Tragelaphus oryx*.

Social and Reproductive Behaviour Common Elands have a very fluid social structure, and there appear to be no stable long-term relationships between individuals. The strong bonds between calves, and the ecological differences between ♂♂ and ♀♀, have resulted in an unusual social structure. Only one study has been carried out on the social organization of a large, naturally occurring, free-ranging Common Eland population – in the Kitengela Plains of Kenya (Hillman 1979, 1987); some aspects of this study differed from those of smaller enclosed populations such as that studied by Underwood (1973, 1975).

Group sizes are very variable, both between and within populations. In many areas the groups are usually small, but in some places and times groups in excess of 500 individuals may form. These have been reported from Hwange N. P., Zimbabwe (Wilson 1975), and from the south-western Kalahari, Botswana (C. Thouless pers. obs.). Groups show a high degree of flux, and adult Common Elands appear to move freely between groups. Association between individual animals is slight, rarely lasting more than a few days (Hillman 1987).

Common Elands are very seldom seen alone, and solitary animals are almost always the older 'grey' ♂♂. The most frequently observed herds are small groups of adult ♂♂, groups of ♀♀ (typically with less than ten individuals), or slightly larger mixed adult groups (usually of 10–20 individuals). However, groups containing juveniles in addition to adults are much larger, and those with calves larger still. Thus, these groups often include a large proportion of the total population in an area even though they are not the most frequently observed groups (Hillman 1979).

Male Common Elands appear to be more typical tragelaphines than the ♀♀. Males are most often seen in smaller, adult-only groups, particularly in all-male groups. Adult ♀♀ are mainly in calf-containing groups, and to a lesser extent in mixed all-adult groups. As a subadult animal matures it spends more time away from mixed groups, and with the small adult groups. Females then return to the nursery groups as they begin to calve, while ♂♂ continue to gravitate towards the very small all-male groups. These differences between the sexes are affected by their different feeding and ranging behaviour (see later).

Within large groups, young Common Elands are more closely associated with each other than with their mothers, and it is believed that this 'within-age-group' bond is the main reason why these large groups form. Most animals within a group are well spread out, with the exception of calves, which tend to form a tight 'creche'. Nursery groups are larger when environmental conditions are good, increasing to several hundred animals in grassland areas in times of high rainfall and good vegetation condition. This may be an anti-predation measure only possible during times of good food supply.

Common Elands in the KwaZulu-Natal Drakensberg display an unusual social organization, whereby they form large, mixed herds of up to 200 animals during summer (Dec/Jan), during which time breeding ♀♀ are mated by dominant ♂♂. From autumn (Mar) the large herds break up and they disperse widely in small groups of 4–10 animals, which may be of varying combinations of sexes and age classes. Shortly after the calves are born (Sep and Oct), the small groups start to join to form larger herds again (Scotcher 1982, Rowe-Rowe 1994).

There is no evidence of territoriality in Common Elands (Underwood 1973, 1975, Hillman 1979), and no evidence that faeces are used for marking. Urine and secretions from the frontal tuft may be used in some kind of marking. However, there is a dominance hierarchy within

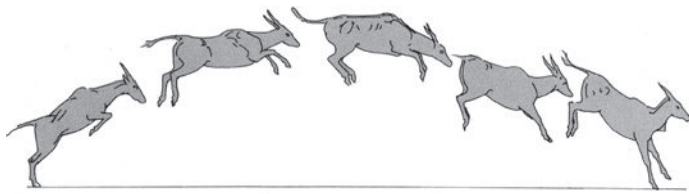


Common Eland *Tragelaphus oryx* development of male colouring.

a population. A range of threats is used between individuals, including a threatening look, wiping the horns across the animal's own back, pointing the horns forward, and lunging with the horns (Hillman 1979). These threats usually result in the other animal moving away, and seldom escalate into more serious conflict. Sparring between the younger classes of ♂♂ is common. It involves the deliberate lowering of the heads, and tangling of the horns, followed by a pushing contest; this is often followed by the subordinate ♂ mounting its sparring partner or another nearby animal (Hillman 1979). Fighting is much less common, and results only when two old 'grey' ♂♂ are competing over ♀♀ in a group. Instead of deliberate tangling of the horns at close quarters, this involves charging together from a distance of 1–2 m, followed by pushing and manoeuvring to throw the other animal off balance. This can result in serious injuries. Apart from displays involving the males' frontal brush (described above under Adaptations), displays are in general not particularly 'ritualized' and are not unique to the Common Eland (Kiley-Worthington 1978).

Self-grooming is carried out regularly and involves scratching their bodies and faces on trees and other objects (or the front part of the body with a hindleg), and grooming with lips, teeth and tongues. Mutual grooming usually occurs between standing animals while chewing the cud, and involves the head and neck – parts of the body that cannot be reached by the animal itself. Mutual grooming only occurs between young or adult ♀♀.

Common Elands have a reputation as great wanderers; in some places this is thought to take the form of regular migrations, while in others there seem to be irregular movements, and some populations are believed to be more or less sedentary (such as those in SE Zimbabwe). The movements of free-ranging animals have only been studied in detail in the Athi-Kapiti area of Kenya, and in the south-west Kalahari of Botswana. Many populations are now confined within fenced areas, restricting what natural tendency there may be to move further. Hillman (1988b) studied the movements of Common Elands by repeated sightings of individually recognized individuals. Adult ♂♂ had home-ranges of approximately 30 km² while adult ♀♀ and juveniles had home-ranges of approximately 200 km². For both sexes most of these areas were used in the wet season; dry season ranges were considerably smaller. Male home-ranges were centred on areas of bush along gorges and drainage lines, or on forest edges. Females



Common Eland *Tragelaphus oryx* serial outlines of leap (from film).

and juveniles were found in similar areas in dry periods, but used areas of open grassland for longer periods in the wet seasons.

Common Eland movements have been studied in the south-western Kalahari, where they are largely confined to Kgalagadi Transfrontier Park, using radio-telemetry and satellite technology over a number of years (R. Brett, M. Knight, S. Makhabu, N. Nagafela & C. Thouless unpubl.). Aerial surveys in the park show that there is a tendency for the main concentrations of Common Elands to be in the bushy north-central part of the park in the wet season, with a surprising shift towards the drier sand dune areas of the south-west during the dry season (Verlinden 1998). In some dry years, such as 1985, this movement is particularly pronounced, and very large numbers of Common Elands may congregate in the south-west, including the fossil valley of the Nossob. Since animals fitted with collars were known never to go close to artificial watering holes, there must be some presently unknown ecological reason (and not a need for water) for this movement down the rainfall gradient in the dry season. Individual Common Elands in this area have very large home-ranges, averaging 8449 km² for ten ♀♀ tracked for at least one year, with a range of 1691–19,761 km² (minimum convex polygon).

Unlike other species, which tend to use a particular area for some time before moving on, Common Elands moved considerable distances on a daily basis. Typically they would be about 20 km distant from where they were 24 hours previously, and straight-line movements of up to 55 km were recorded over a 24-hour period. This pattern of movement was not dramatically affected by the onset of the rains. However, they do seek areas that have 'greened up' in response to the rains (R. Brett pers. comm.). In addition to migratory movements, Common Elands also make vertical movements in relation to food availability. In the KwaZulu–Natal Drakensberg, Common Elands spend most of their time in open grassland areas, particularly during the late spring and summer when the grass is green and nutritious. There is a vertical movement away from the central grassland area at the onset of the dry and cold winter, when green grass becomes unavailable. Animals then move into the montane forests and turn to browsing. The amplitude of movement ranges from between 5 and 40 km (Keep *et al.* 1972, Scotcher 1982, Rowe-Rowe 1983).

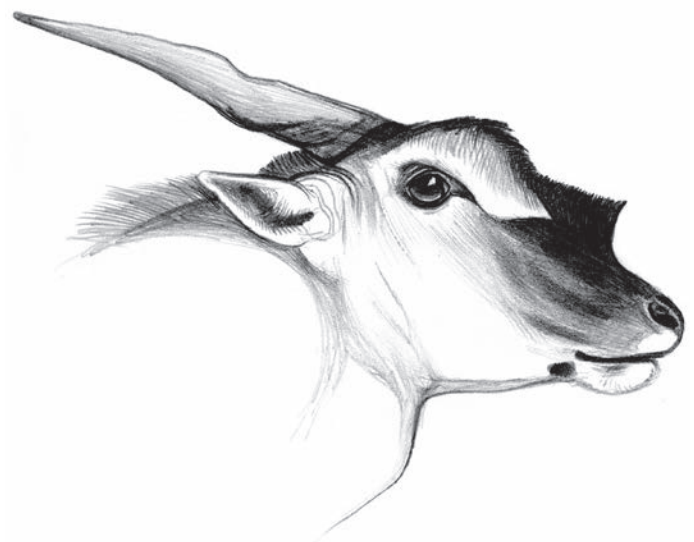
Flehmen plays an important part in courtship and is exhibited by all Common Elands from about three months old. However, it is most prominent in adult bulls, and they actively solicit urine from ♀♀ by pushing at the vulva. Females in oestrus are closely followed by the dominant bull in the herd, who chases and attacks less dominant ♂♂, and often lays his head on the female's rump or close to her side. Eventually she stands still to allow mounting, and intromission is brief.

Most births take place between 04:00h and 08:00h, peaking just at sunrise (Underwood 1979). The ♀ becomes restless then lies down on her side to give birth; calves, when born, are licked carefully before the afterbirth is eaten by the ♀. The calves struggle to a standing

position very soon after birth and can run within three or four hours. Calves lie up away from the herd for a few days. However, they soon join a herd and the great majority of calves are found in large nursery groups with other calves and juveniles. Within these groups the calves keep very close to each other in a calf crèche, and are often in close physical contact. Most of their activities take place in this group, and they leave it only to suck. Females visit the crèche to suckle their calves, calling as they approach. Usually the calf will run a short distance from the others to suck. Females do not suckle the calves of others, and sometimes even drive strange calves off. There is no evidence of a bond with the calf lasting beyond the time of weaning (Hillman 1979).

Common Elands are not very vocal. They make a deep gruff 'alarm' bark similar to that of the Bushbuck *Tragelaphus scriptus*. Females communicate with their calves using a series of repeated clicks; or by mooing and grunting or a combination of these (Underwood 1973, 1975). The calves respond by whimpering or moaning. At closer proximity the ♀ and calf exchange a weak bleat, and a similar noise is heard from adult ♂♂ during courtship (Hillman 1979). Adult bulls bellow in expressing their dominance or emit a belching grunt in repelling others from food. The larger adult 'grey' ♂♂ make a sharp clicking noise while walking as they lift each forefoot, which is audible up to several hundred metres away. Various sources have suggested the sound emanates from the hooves clicking together when the animal walks or from the carpal bones, but Posselt (1963), who worked with domesticated animals for many years, indicated it came from the knees, likely produced when a tendon slips over a carpal bone (Estes 1991a). Hillman (1979) suggested that the sound may act as an indication of the size and dominance of the animal. Subsequently, Bro-Jørgensen & Dabelsteen (2008) have shown that the dominant frequency of the knee-clicks in Common Eland is an honest signal of body size, reflecting both inter-individual variation and intra-individual changes over time.

Reproduction and Population Structure Common Elands are not strongly seasonal breeders, but there is a peak in calving during the early summer months of Aug–Nov in summer rainfall areas (Skinner & Van Zyl 1969, Skinner *et al.* 1974, Jeffery 1979,



Common Eland *Tragelaphus oryx* profile of male frontal 'brush'.



Common Eland *Tragelaphus oryx* frontal view of male 'brush'.

Underwood 1979, Scotcher 1982, Buys & Dott 1991), although in the south-western Kalahari the peak appeared to be in Nov (R. Brett pers. comm.). In Kenya, births occurred throughout the year, with a possible peak in Sep–Dec (Hillman 1979).

Oestrus occurs at 21–26 day intervals and lasts three days (Posselt 1963). Females typically have a postpartum oestrus (usually about two weeks following parturition; Posselt 1963) and this results in a shorter inter-calving interval. Jeffery (1979) reported the annual inter-calving interval for Common Elands in KwaZulu–Natal as ranging between 281 and 532 days ($n = 120$; mean = 373); the gestation period was around 273 days ($n = 53$; also recorded by Stainthorpe 1972). Usually only a single calf is born, with twins produced in about 2% of births in captivity (Zuckerman 1953). Recorded average birth weights of captive *T. o. oryx* calves include: 27 kg for ♂♂ ($n = 6$) and 25 kg for ♀♀ ($n = 9$) (Jeffery & Hanks 1981), and 30 kg ($n = 20$) and 26 kg ($n = 30$), respectively (Skinner & Van Zyl 1969; see also Stainthorpe 1972). Weaning takes place at about 4–5 months of age. The age at first conception is between 18 and 39 months (Hillman 1979), while ♂♂

do not breed under natural conditions at less than three or four years of age.

In the KwaZulu–Natal Drakensberg, sex ratio at birth is 1 : 1 (Stainthorpe 1972, Scotcher 1982); among adults, sex ratio has been given as 1 ♂ to 1.6–2.0 ♀♀ (Rowe-Rowe 1994). The sex ratio among adult Common Elands in the Athi–Kapiti population studied by Hillman (1979) was strongly female-based, with 1.9 ♀♀ to every ♂. Part of the reason for this may have been the tendency for adult ♂♂ to occur in smaller groups and in thicker vegetation, making them more vulnerable to predators. Rudnai (1974) found a male-to-female ratio of 9 : 1 in Lion *Panthera leo* kills in Nairobi N. P., Kenya. Over a five-year period in KwaZulu–Natal, mean sex and age structure comprised 15% adult ♂♂, 47% adult ♀♀, 12% yearlings and 26% calves (Scotcher 1982). Maximum longevity for wild Common Elands is 14–17 years, and captives have lived 25–26 years (Hillman 1979, Weigl 2005).

Annual calving rates in the Athi–Kapiti population were estimated to be 67% in 1972 and 68% in 1973 (Hillman 1979); those in southern Africa are higher at up to 90% (Buys & Dott 1991) to 95% (Scotcher 1982).

Predators, Parasites and Diseases Lions are the main predators of Common Elands throughout their shared range in Africa, but Common Elands seldom exceed 3% of their prey. This is probably because of the relatively low density of Common Elands compared with other prey species. Wright (1960) stated that Common Elands formed about 2% of Lion kills in S Kenya and C Tanzania, and Rudnai (1974) calculated that Lions killed approximately 2% of the Common Eland population annually in Nairobi N. P. Mitchell *et al.* (1965) found that Common Elands comprised 3% of Lion kills and 1% of African Wild Dog *Lycaon pictus* kills in Kafue N. P., Zambia. In a total of 817 African Wild Dog hunts recorded by Creel & Creel (2002) in Selous G. R., Common Elands were hunted on less than ten occasions. Young animals may rarely be taken by Cheetahs *Acinonyx jubatus*.

Starvation caused by drought can be a major cause of death, but Common Elands can sometimes escape its worst effects by moving long distances (Hillman & Hillman 1977). In the 1985 drought in the south-western Kalahari, it was estimated that 35% of the population died (Knight 1995a). In the KwaZulu–Natal Drakensberg, mortality was highest during Aug–Oct following the long, harsh winter, especially among calves and yearlings (Scotcher 1982).

Common Elands are described as bovine antelopes and it is reasonable to assume that the species, in its natural habitat, will contract similar viral, bacterial or parasitic infections as described for the cow in Africa, but the severity, symptoms and pathology will vary. For example, the species is susceptible to rinderpest (Thomas & Reid 1944, Robson *et al.* 1959), and, in an outbreak in Nairobi N. P. in 1996, there was an infection rate of 20% and mortality rate of 10% in Common Elands (Kock *et al.* 1999). Other important viruses such as foot and mouth disease have minimal impact on the species and they appear to be insignificant as carriers. They show no tendency to contract malignant catarrhal fever virus and their status as carriers of Rift Valley Fever and Lumpy Skin Disease is unknown. Bacterial diseases such as anthrax and parasitic diseases such as anaplasmosis have been reported in the species, and under certain conditions ticks and tick-borne diseases (e.g. theileriosis, transmitted by ticks of the

genus *Rhipicephalus*) can be significant; Rowe-Rowe (1994) notes that some introductions of Drakensberg animals to lowveld areas in KwaZulu–Natal failed because the animals succumbed to tick-borne diseases. The bacterium *Theileria taurotragi* is pathogenic and has caused deaths (Grootenhuys *et al.* 1980). Their resistance to trypanosomosis (which is transmitted by tsetse flies) is similar to other antelope. Except for the highly infectious diseases such as rinderpest and foot and mouth disease, the behaviour of the species (living in relatively small herds, timid and highly mobile) would reduce the chance of inter-specific infection. Once an individual in a herd contracts an infection, such as tuberculosis or anthrax, a high incidence is likely, since intra-specific dynamics are similar to cattle and buffalo.

Common Elands host a variety of ticks. Two animals taken in Central Province, Zambia, were host to seven species: *Amblyomma variegatum*, *Boophilus decoloratus*, *Rhipicephalus appendiculatus*, *R. evertsi*, *R. lunulatus*, *R. simus* and *R. supertritus* (Zieger *et al.* 1998b). Common Elands in Kruger N. P. harboured large numbers of *Amblyomma hebraeum*, but were also host to *B. decoloratus*, *Rhipicephalus appendiculatus*, *R. zambeziensis*, *R. evertsi* and *R. simus* (Horak *et al.* 1983c). In the Karoo of South Africa, Common Elands are good hosts for *Ixodes rubicundus* (Horak *et al.* 1987). Another animal examined post mortem was host to seven species of tick (*Amblyomma gemma*, *A. variegatum*, *Boophilus decoloratus*, *Rhipicephalus appendiculatus*, *R. evertsi*, *R. pulchellus* and *R. praeus*; Grootenhuys *et al.* 1980). Helminths recorded from Common Elands include three species of nematodes from Central Province of Zambia, *Cooperia rotundispiculum*, *Haemonchus contortus* and *Oesophagostomum* sp. (*H. contortus* is a blood-sucking parasite that can be pathogenic at even low levels of infection); the tapeworm *Moniezia benedeni* was also recorded (Zieger *et al.* 1998a). In Mountain Zebra N. P. and West Coast N. P., Boomker *et al.* (2000) recorded *Haemonchus mitchelli*, *Nematodirus spathiger*, *C. rotundispiculum* and *Bronchonema magna*.

Conservation IUCN Category: Least Concern. CITES: Not listed.

Common Elands still occur over a large area of southern and eastern Africa, but their numbers and range have declined considerably. Their meat is highly prized and each animal provides a large quantity of meat, so they are particular targets of illegal hunters. In Botswana, their range has contracted over the last 20 years, so that now they are almost entirely confined to protected areas and to private lands. The Common Eland's habit of wandering over large areas may affect its future in ways that cannot be fully predicted. As available habitat declines, animals' ability to range widely is being reduced. It is possible that this will make populations that already tend to occur at low densities more vulnerable to environmental disturbances, such as drought and disease. However, Common Elands have been reintroduced to a number of game ranches and private ranchland in southern Africa (particularly South Africa), and this has done much to bolster numbers. In addition, animals have been introduced widely outside of their natural range, primarily to private ranches. For example, although their natural range in Namibia is restricted to the north-eastern parts, they now occur widely on game ranches in the southern and central parts (East 1999).

Important naturally occurring populations are protected in Omo N. P. (Ethiopia), Boma N. P. (Sudan), Serengeti N. P. (Tanzania), Kafue and North Luangwa National Parks (Zambia), Nyika N. P. (Malawi),

Etosha N. P. (Namibia), Kgalagadi Transfrontier Park (Botswana/South Africa) and Ukhahlamba-Drakensberg Park (South Africa). According to East (1999), approximately half the total population occurs in protected areas and 30% on private land. At present, the Common Eland is not in any immediate threat of extinction, and this situation is likely to continue as long as there are sufficient protected areas and private ranches to sustain viable populations.

Much has been written and published on the topic of domestication of Common Elands, which have been domesticated in Russia, Ukraine, England, Zimbabwe, South Africa and Kenya, for a number of perceived advantages: they provide a high yield of nutritious, 'long life', anti-bacterial milk, which has a high fat content; they can be readily tamed and herded; they can survive in arid regions unsuitable for cattle due to low water requirements; they have a long life expectancy in captivity; and they have a varied diet (Uspenskii & Saglanskii 1952, Posselt 1963, Skinner 1967, Lightfoot 1977, Lightfoot & Posselt 1977a, b). However, although captive animals reproduce successfully, management practices such as high food supplementation costs, confining them at night and herding them during the day are likely to negate their advantages over cattle in many environments (Hillman 1979).

Measurements

Tragelaphus oryx

HB (♂ ♂): 2510 (2390–2630) mm, n = 5

HB (♀ ♀): 2270 (2200–2330) mm, n = 5

T (♂ ♂): 620 (570–720) mm, n = 5

T (♀ ♀): 530 (500–550) mm, n = 5

E (♂ ♂): 220 (210–240) mm, n = 5

E (♀ ♀): 210 (190–230) mm, n = 5

Sh. ht (♂ ♂): 1630 (1580–1790) mm, n = 7 (on the curve)

Sh. ht (♀ ♀): 1423 (1250–1530) mm, n = 7 (on the curve)

Sh. ht (♂ ♂): 1422 (1355–1500) mm, n = 6*

Sh. ht (♀ ♀): 1296 (1245–1330) mm, n = 6*

WT (♂ ♂): 494 (450–540) kg, n = 5

WT (♀ ♀): 344 (317–370) kg, n = 5

Athi-Kapiti Plains, Kenya (Hillman 1979)

*Serengeti, Tanzania (Sachs 1967), taken between the pegs

Common Elands in southern Africa generally are larger than the figures given here. Wilson (1969) gave the mean mass of five mature bulls as 604 kg (range 530–690), and ten ♀ ♀ had a mean weight of 445 kg (range 385–470). Skinner (1967) gave the mean mass of 19 mature bulls from bushveld areas as 650 kg (range 425–840). However, wild Common Elands from the KwaZulu–Natal Drakensberg are lighter, with mean adult masses of 453 kg (n = 17) for ♂ ♂ and 305 kg (n = 61) for ♀ ♀ (Scotcher 1982; and see Keep 1972). While weights of ♂ ♂ in Serengeti N. P. were similar to those of the Athi-Kapiti plains, weights of ♀ ♀ were considerably lower, with a range of 277–321 kg, and horns were shorter in both sexes (Sachs 1967)

Maximum recorded horn length is 118.4 cm for a pair of horns from Grootfontein, Namibia (Rowland Ward)

Key References Hillman 1979, 1987, 1988b; Posselt 1963; Scotcher 1982; Taylor 1969; Underwood 1973, 1975, 1979.

Chris R. Thouless

Subfamily ANTILOPINAE – Antelopes, Sheep, Goats

Antilopinae Gray, 1821. London Med. Repos. 15: 307.

| | | |
|---------------------------------|-------------------------------|--------|
| Tribe Neotragini | | |
| <i>Neotragus</i> (2 species) | Dwarf Antelopes | p. 207 |
| <i>Nesotragus</i> (1 species) | Suni | p. 213 |
| Tribe Cephalophini | | |
| <i>Philantomba</i> (2 species) | Blue Duikers | p. 223 |
| <i>Sylvicapra</i> (1 species) | Common Duiker | p. 235 |
| <i>Cephalophus</i> (16 species) | Forest Duikers | p. 244 |
| Tribe Raphicerini | | |
| <i>Raphicerus</i> (3 species) | Grysboks, Steenbok | p. 303 |
| <i>Dorcatragus</i> (1 species) | Beira | p. 315 |
| Tribe Madoquini | | |
| <i>Madoqua</i> (7 species)* | Dik-diks | p. 320 |
| Tribe Antilopini | | |
| <i>Gazella</i> (4 species) | Slender Gazelles | p. 339 |
| <i>Eudorcas</i> (4 species) | Ring-horned Gazelles | p. 356 |
| <i>Nanger</i> (5 species)* | Greater Gazelles | p. 372 |
| <i>Ammodorcas</i> (1 species) | Dibatag | p. 387 |
| <i>Litocranius</i> (1 species) | Gerenuk | p. 390 |
| <i>Antidorcas</i> (1 species) | Springbok | p. 398 |
| Tribe Ourebiini | | |
| <i>Ourebia</i> (1 species) | Oribi | p. 405 |
| Tribe Reduncini | | |
| <i>Pelea</i> (1 species) | Grey Rhebok | p. 416 |
| <i>Redunca</i> (3 species) | Reedbuck | p. 421 |
| <i>Kobus</i> (5 species) | Kobs | p. 437 |
| Tribe Oreotragini | | |
| <i>Oreotragus</i> (1 species) | Klipspringer | p. 469 |
| Tribe Aepycerotini | | |
| <i>Aepyceros</i> (1 species) | Impala | p. 479 |
| Tribe Alcelaphini | | |
| <i>Beatragus</i> (1 species) | Hirola | p. 490 |
| <i>Damaliscus</i> (2 species) | Damalisks | p. 495 |
| <i>Alcelaphus</i> (1 species) | Hartebeest | p. 510 |
| <i>Connochaetes</i> (2 species) | Wildebeests | p. 527 |
| Tribe Hippotragini | | |
| <i>Hippotragus</i> (2 species) | Roan Antelope, Sable Antelope | p. 547 |
| <i>Addax</i> (1 species) | Addax | p. 566 |
| <i>Oryx</i> (3 species) | Oryxes | p. 571 |
| Tribe Caprini | | |
| <i>Ammotragus</i> (1 species) | Aoudad | p. 594 |
| <i>Capra</i> (2 species) | Ibexes | p. 599 |

*including species-groups

The particular selection of antelope taxa that have been allocated to this subfamily has varied greatly over the years as has the relative ranking of Antilopinae within the family Bovidae: both remain subject to debate. In the treatment presented here, the Antilopinae embraces all the non-Bovinae bovids and these, colloquially referred to as antelopes, sheep and goats are held to share a common ancestry. A basal split between bovine and non-bovine taxa has long been recognized on morphological, physiological, ecological and behavioural criteria. Furthermore, a number of recent molecular studies have confirmed the reality of this most fundamental division of the family Bovidae (Hassanin & Douzery 1999, 2003, Matthee



Thomson's Gazelle *Eudorcas thomsonii* (frontal view).

& Robinson 1999a, Matthee & Davis 2001, Hassanin *et al.* 2012). Antilopinae, being the prior sub-familial name for all non-bovine antelopes, is therefore used in that broader sense, to the exclusion of nomenclatures that would restrict this rank to a smaller subset of gazelle-like species (Eisenberg 1981, Rebholz & Harley 1999, Hernández Fernández & Vrba 2005 and others), which are herein classed as the tribe Antilopini.

In distinguishing Antilopinae from Bovinae there are physiological differences that have a much broader, adaptive and biogeographic significance. Antilopinae regulate their body temperature by the advanced water-saving mechanism of nasal panting (although many of the Reduncini cool their bodies by sweating, this is almost certainly the secondary reversion of antelopes that have become tied to well-watered habitats). The thermoregulatory mechanism employed by all Bovini is the older, typically mammalian system of sweating, which is dependent upon continuous access to water and can be presumed to be the original condition of the main stem or founding bovid stock (for example, Gentry [1978] regarded the Asiatic boselaphines as the closest living descendants of early bovids and these bovines are also 'sweaters'). The development of 'nasal bellows' and nasal panting is possibly linked in some way with nasal 'whistling' calls that are uttered by all but the largest antelopes: the nasal areas of Bovinae are not modified for sound and they never utter any such calls. Antilopinae frequently have pedal glands (although individual species or groups have secondarily suppressed them), whereas all Bovinae lack these glands. Antilopinae also usually have facial glands (or their putative ancestors had typical glandular fossae on their skulls), although they are lacking in some species (e.g. Aepycerotini). Bovinae, on the other hand, lack facial



Bright's Gazelle *Nanger (granti)*
notata black and white design on
female udder.

glands (although some have glandular areas with a different histology). Antilopinae often have a single pair of nipples, although a number of tribes retain the older pattern of two inguinal pairs; all Bovinae have two pairs of nipples. Most Antilopinae have annulated horns (although a few conservative species have short, smooth spikes). Bovinae, by contrast, have smooth horns with a circular section or spiral ones (generated by differential growth rates at the base of the horn sheath).

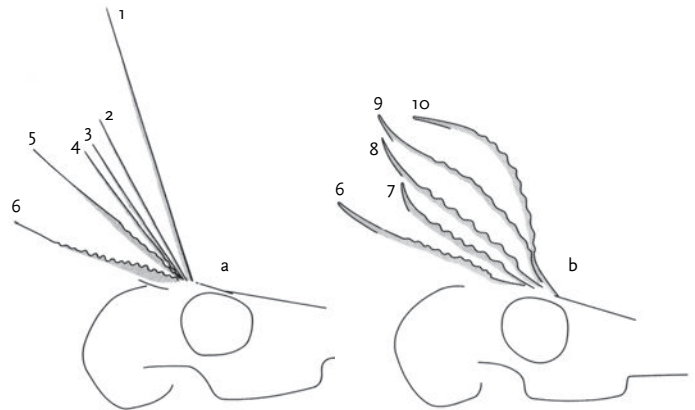
The differences listed above (and more detailed physiological study will undoubtedly uncover more) are merely morphological markers for a fundamental divergence among early ancestral bovids. The more conservative species of Antilopinae are generally small or very small and are limited to small and stable home-ranges: the founding antilopine lineage would appear to have become adapted to hot and relatively dry conditions at an early date. Bovines, instead, generally have large or very large body sizes, often live nomadic lives in unstable habitats, and are adapted to wetter and generally cooler conditions.

The original divergence between Bovinae and Antilopinae probably involved a continental separation between the two ancestral stocks with the majority of some 24 species of Bovinae (sensu Grubb 2005) incontestably of Eurasian origin, whereas two-thirds (and by far the most diverse array) of about 120 Antilopinae are African. This separation broadly corresponds to adaptation by Bovinae to more temperate climates in the northern continents whereas stem Antilopinae adapted to the generally tropical climates of Africa. Recent molecular studies have shown that some small and very conservative species of African antelopes are basal Antilopinae, and their ecological and genetic distinctness implies speciation taking place very early on in the radiation of this group. The existence of small-bodied folivores among Australian macropods and Eurasian deer demonstrates that there are niches for small-bodied folivores in a wide range of habitats in all continents. Once such niches are occupied (and small African Antilopinae evolved more than 20 mya, probably at the beginning of the Miocene), the main selective pressure on them is to become better adapted to the specifics of their particular habitats, such as hot, arid thickets, cooler scrubs, equatorial forest or rocky hillsides. In particular, there is much to suggest that the smaller Antilopinae have made progressive improvements in physiological adaptation to local climates and environments. On the other hand, there has been much less pressure to alter the basic anatomical specifications incumbent on small size because selection has continued to favour a narrow range of body-sizes no less in Africa than other taxa in other continents. Although the common ancestor of all Antilopinae was likely to have

been a small animal, molecular evidence suggests that enlargement took place at a very early stage in antelope evolution (implied, for example, by the demonstration of basal status for the Impala *Aepyceros*; e.g. Georgiadis *et al.* 1990, Hassanin *et al.* 2012). The evolution of bigger bodies involves a chain of other adaptive changes and it seems significant that a majority of the more highly divergent, larger-bodied antelopes appear to derive from the same large-bodied basal lineage as the Impala. The survival of several very conservative basal lineages needs to be understood in this context of very narrow parameters for anatomical change in small antelopes, but much greater potential for elaboration in the larger lineages.

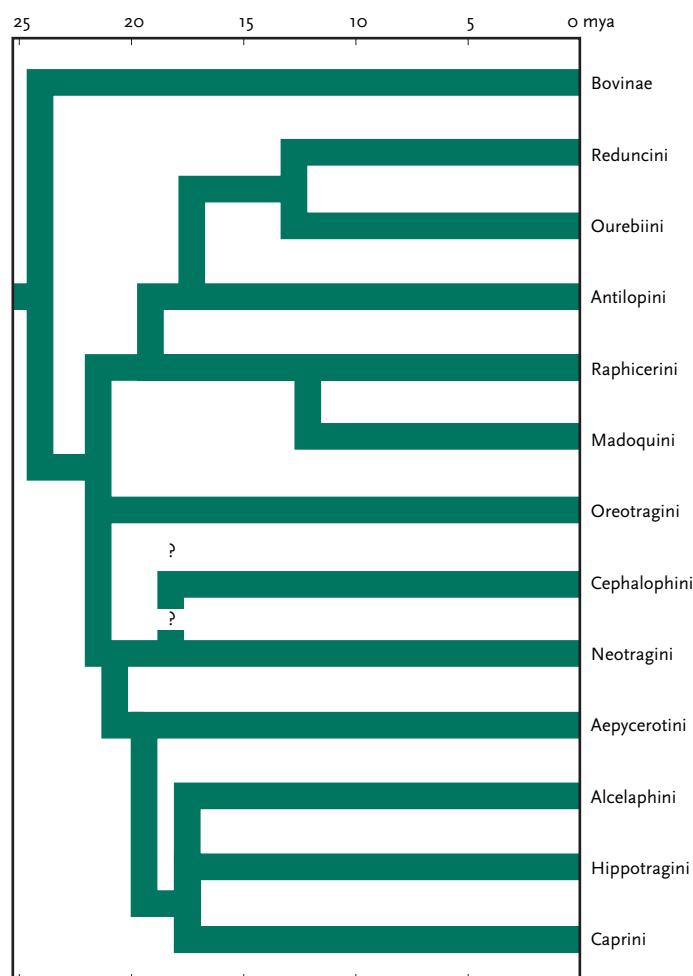
Taking account of dated antilopine fossils and the probable time needed to achieve today's very diverse radiation, Kingdon (1982) estimated a divergence date between Bovinae and Antilopinae of about 23 mya (Early Miocene). Using molecular clock techniques, Hassanin *et al.* (2012) have estimated that the split took place around 19.7 mya. Soon after arrival in Africa, antilopines began to adapt to local extremes of habitat and climate and sometime in the early or middle Miocene an early antilopine found its way back into Eurasia and this lineage gave rise to the predominantly Asiatic Caprini (Hassanin & Douzery 2003, Hernández Fernández & Vrba 2005).

Subdivisions within the Antilopinae remain problematic, but seven major groups have long been recognized: the duikers, Cephalophini; the dwarf antelopes, Neotragini; the kobs or waterbucks, Reduncini; the gazelline antelopes, Antilopini; sheep and goats, Caprini; horse-like antelopes, Hippotragini; and the alcelaphines, Alcelaphini. Each of these groups has radiated (in the case of caprines, into as many as 32 species). However, with the advent of molecular trees and clocks, a much more complex radiation has become apparent. The 'Neotragini', a grouping that formerly embraced some 13 or 14 species, and long suspected to represent contemporary survivors of a



a. Evolution of the brow buffer illustrated by a gradient between upright, smooth stabbing horns and slanted corrugated horns in some Antilopinae.

1. Grey Rhebuck *Pelea capreolus*; 2. Steenbok *Raphicerus campestris*; 3. Klipspringer *Oreotragus oreotragus*; 4. Beira *Dorcatragus megalotis*; 5. Oribi *Ourebia ourebi*; 6. dik-diks *Madoqua* and Suni *Nesotragus moschatus*.
b. Progressive elevation of the corrugated anterior surface in the horns of Antilopinae: 6. primitive condition, as in dik-diks *Madoqua* and dwarf antelope *Neotragus*; 7. initial elevation primarily due to thickening of horn (tip upturns, as in some Reduncini); 8. elevation, lengthening and thickening of horn in primitive Antilopini, as in Dibatag *Ammodorcas clarkei*; 9. elevation of longer, thicker horn with increased convex curvature, as in some gazelles *Gazella* spp. and Gerenuk *Litocranius walleri*; 10. horn arched high above orbit as in some advanced Antilopini, Caprini and Hippotragini.



Tentative phylogenetic tree for Bovidae (modified from Hassanin & Douzery 2003, Hernández Fernández & Vrba 2005 and Hassanin *et al.* 2012).

basal type from which all the Antilopinae evolved (Kingdon 1982), has now been confirmed to be paraphyletic (Georgiadis *et al.* 1990, Gentry 1992, Gatesy *et al.* 1997, Matthee & Robinson 1999a, Rebholz & Harley 1999). Recognition that several living species occupy basal positions, and do not belong to any of the seven traditional subgroups of antilopinae, has suggested a bold biogeographic pattern that accords with much broader patterns of adaptation by Eurasian immigrant biota into Africa. New outlines for the primary and secondary radiations of Antilopinae are beginning to emerge and, in spite of numerous discrepancies between published trees, some convergent data (and opinions) are emerging, and these accord reasonably well with the following reconstruction of the antilopine adaptive radiation, based on a best fit between ecology, behaviour, palaeontology, anatomy and genetics. In spite of having been assembled before the advent of molecular trees or clocks, the first detailed effort to reconstruct this radiation (Kingdon 1982) conformed, to a surprising degree, with contemporary molecular findings.

Some mammalian immigrants entering Africa were able to do so because they were already very widespread, cosmopolitan species, but others, perhaps the majority, would have entered with ready-made ecological preferences compatible with the environments of (the usually rather narrow) corridor that permitted intercontinental exchange. Subject to the particular climatic cycle of their incursion,

whether cool or hot, the majority were probably adapted to dry but seasonally variable habitats. In the 27–23 million years since Africa regained contact with Eurasia there has been no true tropical forest connection and, barring some bat species, even the most adaptable mammals would have taken time to adapt to equatorial habitats. It is, therefore, significant that the three or four basal lineages that have emerged from molecular studies imply a very early adaptation by the first antelopes to three or four major adaptive niches.

The closest living approximation to the primary adaptive niche and to the relatively generalized anatomy of the earliest Antilopinae is the Cape Grysbok *Raphicerus melanotis*. Supposing then that the ancestral immigrant antilopine was a small, thicket-dwelling ruminant living under seasonally hot, but relatively dry, climates, a primary challenge for any such incoming group was to adapt to the more equatorial habitats of Africa, where diseases and all manner of environmental challenges awaited any immigrant. For small herbivores living on the forest floor, wetter climates meant higher, darker canopies and less ground-level foliage. Smaller bodies for an already small-sized antelope were the most likely outcome and the primitive dwarf antelope tribe Neotragini conforms with just such a prediction in terms of primarily equatorial distributions, sizes, habitats and feeding ecology. Genetically, neotragines are basal antelopes close to the primary radiation of all Antilopinae (Gatesy *et al.* 1997, Rebholz & Harley 1999, Hassanin *et al.* 2012), but they must have made their accommodation to tropical forest well after the first Antilopinae differentiated from ancestral Bovinae.

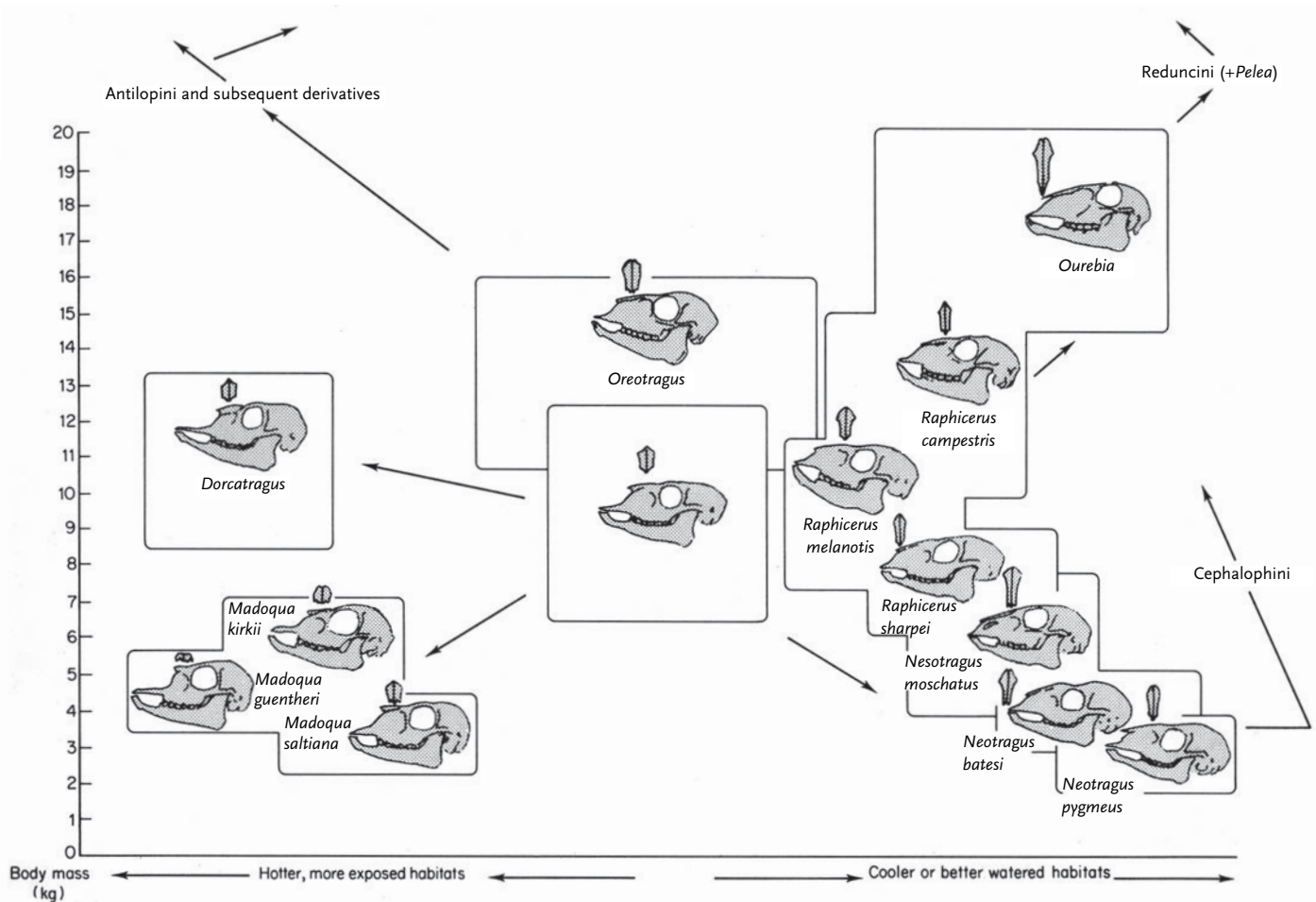
Because a very mountainous region lies immediately south of the main connection between Africa and Eurasia, many mammal immigrant groups can be shown to have made initial adaptations to the mountains of north-eastern Africa. Here, too, molecular trees agree in suggesting a basal position for the Klipspringer *Oreotragus oreotragus*, the only representative of the Oreotragini (and an archotypically Ethiopian species, although now widespread down the south-eastern half of Africa).

Another primary innovation would have been exploitation of more open, thicket-edge habitats. Here larger-bodied, longer-legged populations can be predicted because resources are more dispersed and predators at more of an advantage. Here, too, there is good conformity with molecular trees with a very early split accounting for the Impala as the only representative of a basal lineage, the Aepycerotini.

All molecular trees imply that the major antilopine lineages have each developed lineage-specific and identifiable adaptations to particular habitats, but none is consistent in distinguishing primary from secondary radiations. The primary ones suggested here are:

- 1 Small-bodied, thicket-dwelling lineage under dry climates typified by an early and conservative derivative, *Raphicerus*.
- 2 Dwarfed, forest-dwelling lineage typified by *Neotragus*.
- 3 Smallish, mountain- and rock-dwelling lineage typified by *Oreotragus*.
- 4 Larger, ecotone-dwelling lineage typified by *Aepyceros* (which might share common roots with either one of the two previous lineages or the common ancestor of all three).

It is suggested here that all other major antilopine tribes are likely derivative from one or other of the four primary lineages listed above, a conclusion that is broadly consistent with most recent molecular studies.



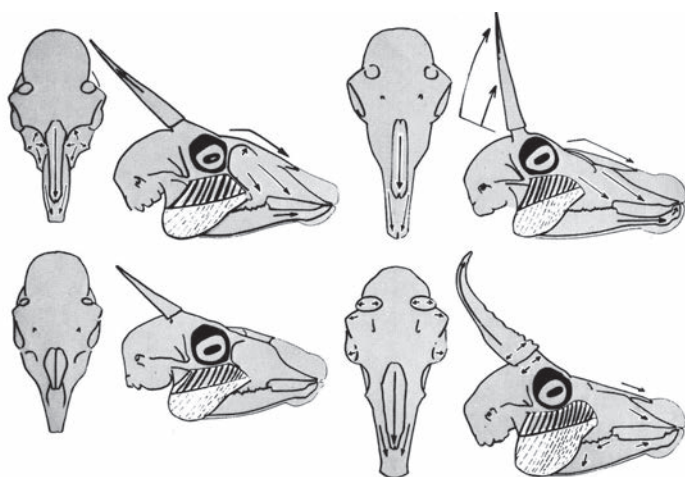
Body size and climate as major parameters in the radiation of antilopines. Some derivative lineages are indicated outside the 20 kg box.

Gazelline antelopes (Antilopini), as well as dik-diks (Madoquini) and kobs (Reduncini), can plausibly be derived from the earliest antilopine ancestral stock. The Beira *Dorcatragus megalotis* shows both morphological and molecular characteristics that suggest genetic links between *Raphicerus* and the gazelles and their kin. The dik-diks also relate to the same lineage on both counts. All these lineages show progressive physiological adaptation to heat-tolerance and water-conservation, but remain conservative in relation to a browsing, or 'concentrate-selector' diet (Hofmann 1973, 1989). The gazelles span a wide range of sizes and degrees of sociality, whereas dik-diks retain residential, territorial habits, small size and a highly selective fresh leaf diet.

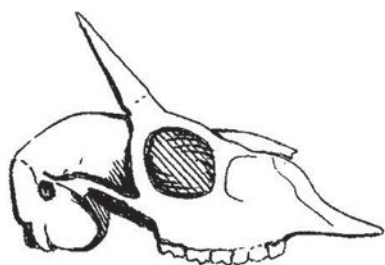
The Reduncini have been proposed as a basal group (Hassanin & Douzery 2003), but they have a still unresolved relationship with two other antelopes. One, the Grey Rhebok *Pelea capreolus*, seems to represent the localized derivative from a very early reduncine. The other, the successful and widely distributed Oribi *Ourebia ourebi*, shares an odd mix of characteristics with the Steenbok *Raphicerus campestris* and members of the Reduncini. The Oribi's basal relationship to *Raphicerus* has been confirmed (Hernández Fernández & Vrba 2005), but its link to the Reduncini has been less widely accepted. However, its resemblances with reduncines are too numerous and too detailed to be easily explained by convergence. In direct opposition to the previous thicket-dwelling or arid-adapted Antilopini, reduncines and Oribi have become open valley grazers, relying, to a greater or lesser degree, on a very abundant but unstable food supply and continuous access to water.

This has involved very substantial physiological changes compared with most other Antilopinae, notably a water-dependent mode of cooling, by sweating, but also remarkable resistance to direct radiation from the sun. A conservative reliance on hiding, whether in dense grass, in swamps and water-logged areas or in large, dense herds, betrays the fact that Reduncini have very poor stamina and are, in that respect, conservative antilopines. They are most likely to be an early but secondary offshoot of *Raphicerus*-like Antilopini.

The duikers (Cephalophini) were once assumed to be among the most primitive of bovids (Estes 1974). In an early genetic analysis, Georgiadis *et al.* (1990) clustered duikers with the non-Bovinae but were unable to associate them with any other antilopine group (an outcome that could have suggested basal status). Duiker origins have proved remarkably opaque to molecular analysis and suggestions as to their closest affinities include Bovinae (Gentry 1992), somewhere in between Bovinae and Antilopinae (Jansen van Vuuren & Robinson 2001), Reduncini (Gatesy & Arcander 2000a, Kuznetsova *et al.* 2002) and Antilopini (Matthee & Davis 2001). They have been grouped in a variety of supposed clades; one permutation linked duikers with reduncines, hippotragines and alcelaphines (Gatesy & Arcander 2000b), another placed them with caprines, alcelaphines and hippotragines (Castresana 2001), and still other studies highlighted a close association with the Klipspringer (Hassanin & Douzery 1999, Matthee & Robinson 1999a, Hassanin *et al.* 2012). Thus, geneticists have invoked virtually every major bovid tribe as sister taxa for the Cephalophini!



Transformation of the head in three related antelopes. Frontal and profile diagrams of Oribi *Ourebia ourebi* (top left), Grey Rhebok *Pelea capreolus* (top right) and Mountain Reedbuck *Redunca fulvorufula* (lower right) compared with reconstruction of hypothetical ancestor (lower left). Note depth of masseter is an indicator of fibre in diet.



Reconstruction of ancestral African antelope skull.

Duikers share forest environments with the dwarf antelopes of the genus *Neotragus*, but differ in many aspects of their anatomy and behaviour (see Kingdon 1982). Instead of relying on scarce vegetation, duikers have enlarged their diet to include some animal matter, but rely to varying degrees on fallen fruits, seeds and other plant debris from the canopy. While their social systems show some adaptive variation, they tend to live spaced out in territories and they have not elaborated horns beyond short spikes. The radiation of duikers appears to originate in a very diminutive ancestor with the larger species being among the most recently evolved (Kingdon 1982, Jansen van Vuuren & Robinson 2001). This implies that duikers might represent a secondary radiation deriving from a diminutive *Neotragus*-like ancestor and the arguments for this origin were detailed in Kingdon (1982) and are summarized on p. 220. As for dating the divergence of duikers, the date of 6.3–5.6 mya (Jansen van Vuuren & Robinson 2001) seems rather late and extrapolated dates of 12.3–8.9 mya (Hassanin *et al.* 2012) might be possible.

The Klipspringer has no close genetic relatives (Gatesy *et al.* 1997, Matthee & Robinson 1999a, Rebholz & Harley 1999), and can be characterized as the single highly specialized survivor of a primary stem lineage. Some molecular resemblances with duikers have been observed and could suggest a phylogenetic connection, but the degree of specialization in the Klipspringer is so great that any very early relationships with later groups, whether duikers or caprines, are now obscured. What is clear is that this species

has paralleled some of the adaptations of goats and chamois and its early capture of the rocky mountain niche in Africa has probably discouraged the expansion of more recently evolved wild caprines into any habitats other than those in the Sahara and the highest reaches of Ethiopia. Whether these similarities are wholly convergent, or not, is debatable but some peculiarities of caprines would seem more likely to have found their roots in something like an early oreotragine or aepycerotine than in any other basal Antilopinae. Molecular analyses have suggested that the caprines might share ancestry with several superficially non-caprine antelopes and their common ancestor must have been very close to being a stem lineage. It is in this context that Aepycerotini is treated here as a true basal lineage that may be as close to Neotragini as it is to Oreotragini.

The Impala is the single surviving species of the Aepycerotini. At least one synthesis of recent studies (Hernández Fernández & Vrba 2005; and see Hassanin *et al.* 2012) has suggested that this apparently basal group has given rise to three major secondary radiations, the Caprini (over 30 spp.), the Hippotragini (7 spp.) and the Alcelaphini (6 spp.). Following Gentry (1978) and Vrba (1984), many authors have treated *Aepyceros* as a primitive alcelaphine, a relationship that has been shown to be only remotely true because it may be as closely related to the hippotragines and caprines. The more advanced members of the Caprini are late, mainly Asiatic and unquestionably belong to a secondary radiation. The Hippotragini are mostly arid-adapted grazers, living at low densities in arid or impoverished zones. The Alcelaphini, by contrast, are high density, ecotone/catenary grazers in open but less arid habitats. All three groups can be regarded as secondary radiations deriving from a single stem lineage. However, the living survivor of that stem lineage, the Impala, bears more resemblance to one of its derivatives, *Beatragus*, an alcelaphine, than it does to any of the horse antelopes or caprines.

The radiation of Antilopinae is summarized on p. 201 as a composite tree in which the dates of splits or branchings (as currently understood) are derived from disparate sources. The prolific radiation of antelopes has attracted several theoretically minded scientists, and the complex diversity of species has been broken down into various simpler categories (e.g. Schlosser 1904, Jarman 1974, Gagnon & Chew 2000). Vrba (1980) sought to explain their evolution and diversity by an 'effect hypothesis' in which less speciose 'generalists' were contrasted with speciose 'specialists'. Every such hypothesis has been hostage to the slender information-base that was available at the time of its inception, but recent field and laboratory studies have significantly improved our knowledge and potential for understanding one of the major radiations of large mammals in the world.

The current spectrum of Antilopinae embraces a diversity of folivorous, graminivorous (and frugivorous) niches and the ability of so many species to inhabit the same landscapes is based upon very precise foraging and digestive techniques. The details of many of these herbivorous strategies are described in the profiles that follow, but the likely development of antilopine niches can be summarized as follows.

The initial traits that distinguished early Antilopinae (in contrast to Bovinae) were small size, stable home-ranges and improved temperature and water regulation that allowed them to inhabit

Table 8. Diversification by habitat of Bovinae and Antilopinae.

| | | |
|-------------------------------------|--|--------------|
| → Asian origin | Large. Grazing, humid/unstable habitats | Bovini |
| → Asian origin. Africa entry 15 mya | Broad spectrum foliage gleaning | Tragelaphini |
| | | |
| | African origin (17 mya?). Solitary gleaning (fruit, etc.), closed habitats | Cephalophini |
| → Early Africa entry (22 mya) | Small, solitary, initially drier habitats | Dwarf bovids |
| | | |
| | Grazing in moist valleys | Reduncini |
| | | |
| African origin | | |
| Mainly African | Gleaning in open arid habitats | Antilopini |
| | | |
| African origin | Enlargement pioneer. Browse closed-to-open | Aepycerotini |
| | | |
| | | |
| African origin | Large. High-density grazing, less arid habitats | Alcelaphini |
| | | |
| | Large. Low-density grazing, impoverished zones | Hippotragini |
| | | |
| | Generalized diets, impoverished habitats | Caprini |

drier habitats than their competitors. Their ruminant digestion ensured that they could maximize the extraction of nutrients and were therefore metabolically superior to the hyraxes, herbivorous macrotelids, rodents, chevrotains and larger non-bovid herbivores that preceded them. That dietary advantage is undoubtedly one reason for the success of antelopes in Africa.

Among Antilopinae, members of the tribe Antilopini have become 'gleaners' for high-quality foliage in arid or semi-arid habitats. Body sizes range from small to moderately large and the more advanced species are relatively social.

Among the most conservative of Antilopinae are the grysboks and Steenbok (*Raphicerini*), while most arid-adapted of all the small conservative tribes are the Madoquini.

The Reduncini have moved furthest from this pattern and have become specialists in exploiting tropical valley grasslands, often at very high densities. Body sizes range from medium to large.

Neotragini (*Neotragus* and *Nesotragus*) are minuscule and solitary gleaners of ground-level foliage in or on the edge of true forest.

The Cephalophini are also gleaners, but mainly of fallen fruit and have developed many interesting sub-strategies, some of which are directly dependent on the wasteful feeding habits of primates, hornbills and bats. They are mostly solitary and territorial and range from 3.5–80 kg.

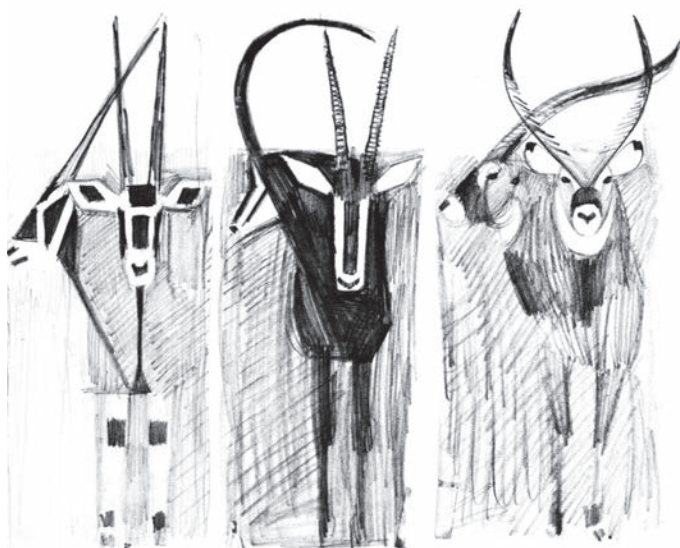
The Alcelaphini have become large-bodied ecotone and catenary grazers, mostly in open habitats and tend to live at relatively high densities.

The Hippotragini are large-bodied antelopes that have adapted to arid habitats or impoverished zones and live, for the most part, at low densities.

Caprini are predominantly a late Asian radiation that evolved in direct competition with Cervidae. Many are adapted to extreme seasonal variations in diet and have colonized or recolonized mountain habitats in between glaciations. In Africa, a unique monospecific genus (*Ammotragus*) inhabits desert hills, mountains and plateaux and the slopes of desert valleys in the Sahara, and a second genus, the ibexes *Capra*, have colonized mountains down the western shores of the Red Sea as far as Ethiopia.

Antilopinae span a wide range of body sizes, weighing as little as 1.5 kg (Royal Antelope *Neotragus pygmaeus*) to 300 kg (several spp.). Many of the larger Antilopinae have interesting coat patterns that show increased contrast along the margins of limbs or those body regions that are typically counter-shaded in small cryptic species. Common origins for all antilopines are evident in similarities of patterning among members of different tribes.

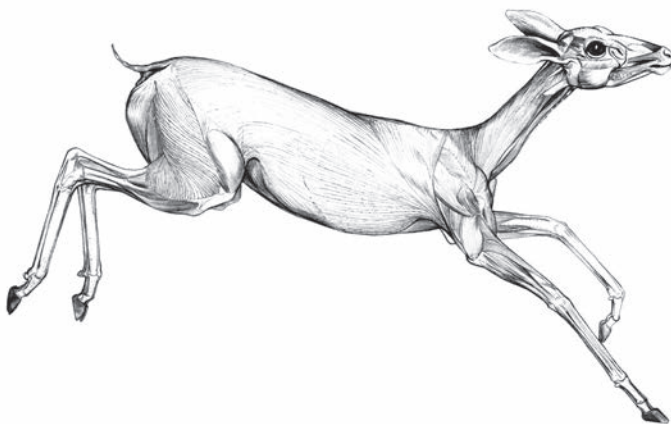
Antelope skulls range from tiny compact structures with short spike horns, large preorbital fossae to enclose large facial glands above



Sketches of 'signal geometry' in three antilopine species; from left Beisa Oryx *Oryx beisa*, Sable Antelope *Hippotragus niger* and Waterbuck *Kobus ellipsiprymnus*. Note eye emphasis or eye suppression.

a short, finely pointed muzzle to heavy, elongated skulls surmounted by heavily reinforced horn cores. In spite of their diversity, horns share a basic structure among all Antilopinae: differential rates in the growth of horn sheaths and in the thickness of keratin deposits are the main determinant of species-specific horn shape and these have been explored in some detail in Kingdon (1982).

The teeth of Antilopinae have been widely misinterpreted, and in one of the first efforts to classify bovids, Schlosser (1904) broke down the wide variety of dental types into 'boodonts' (with a long shallowly rooted tooththrow with molar lobes and basal pillars) and 'aegodonts' (with hypsodont teeth, deeper teeth and roots in a shortened tooththrow). This classification became entrenched in the literature on bovids for nearly 80 years and was misleading because the teeth of different lineages responded to tougher diets and increased body size in very similar ways. Thus, larger-bodied, more hypsodont lineages, such as Hippotragini and Reduncini, became unnaturally clumped on the basis of similarities that are primarily due to larger size and more grass in the diet. A shift from softer diets in smaller antelopes to harder diets in larger



Oribi *Ourebia ourebi* myology.



Occlusal views of upper right tooththrows. (Upper left) Oribi *Ourebia ourebi* (grazer). (Upper right) Mountain Reedbuck *Redunca fulvorufula* (grazer). (Centre left) Cape Grysbok *Raphicerus melanotis* (generalized diet). (Centre right) Aders's Duiker *Cephalophus adersi* (partial frugivore). (Lower left) Suni *Nesotragus moschatus* ('concentrate selector'). (Lower right) Bates's Pygmy Antelope *Neotragus batesi* (strict folivore).

ones takes place *within* Antilopini, Reduncini and Caprini, while the largest antelopes in Reduncini, Hippotragini and Alcelaphini have all become hypsodont independently (Kingdon 1982). The transformation of a typical 'early' antilopine tooththrow can be illustrated by comparing the rows of *Raphicerus melanotis* with those of *Ourebia ourebi* (as an intermediate type) and *Redunca fulvorufula* (as a specialized grazer). The masticatory action of a browser slices rather than mills soft leaves and the tooththrow can be compared with the action of pinking shears or a long saw-edged blade: this functional morphology is most evident in the Neotragini. To turn a long narrow tooththrow over to a macerating action, milling edges across the face of each molar can be increased by simply folding enamel surfaces while the spaces in between the layers of crenellated enamel are bulked out with dentine filler. The combination of extra enamel folds and pillars, more soft dentine and greater depth and rooting both improves the milling action of mastication and lengthens the life of the tooth. The front end of the tooththrow declines in importance among grazers because a side-to-side or lateral mode of mastication, while more efficient for milling hard grasses, needs to be concentrated and needs maximum buttressing for the mechanical advantage to be optimal, hence the decline of premolar teeth in grazers.

All antelopes share longish, slender lower limbs and large-eyed, horned heads above longish necks but proportions differ greatly depending on size, habitat, range and other factors. The smaller, more conservative types have hunched postures and are able to make short, very fast dashes into cover but have no stamina. The larger, grazing species tend to have straight backs, longer legs, necks and faces and many are able to run far and fast, especially those living in open plains where there are numerous predators.

The social behaviour of antelopes has been widely studied, and has been extensively summarized in several works, in particular Estes (1991a). The more conservative species are territorial and residential, with male and female territories generally shared. Many of the larger species are highly mobile and land tenure and behaviour are varied (Jarman 1974). Antelopes occupy all the major habitats of Africa from forests to deserts and from sea level up into the high mountains.

Tribe NEOTRAGINI

Dwarf Antelopes

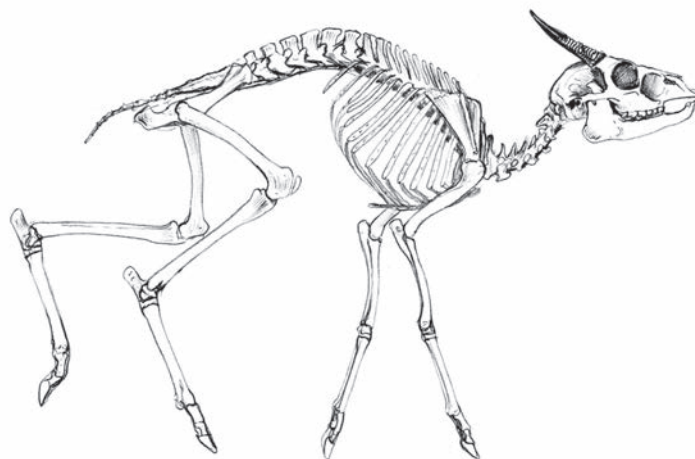
Neotragini Sclater & Thomas, 1894. The Book of Antelopes 1: 2.

Suni *Nesotragus moschatus*.

The tribe Neotragini has long been the acknowledged 'waste-paper basket' receptacle for a diverse collection of small-sized antelopes that resembled each other in their short straight horns, compact skulls, preorbital glands and slender legs. However, several recent studies have shown that the Neotragini, traditionally including *Dorcatragus*, *Madoqua*, *Neotragus*/*Nesotragus*, *Ourebia*, *Oreotragus* and *Raphicerus*, is paraphyletic (Georgiadis *et al.* 1990, Gentry 1992, Gatesy *et al.* 1997, Hassanin & Douzery 1999, Matthee & Robinson 1999a, Rebholz & Harley 1999). Since the differences between these antelope genera have long found acknowledgement, tribal status within Neotragini has herein contracted to only three former members of the Neotragini. All the rest have been allocated to other tribes.

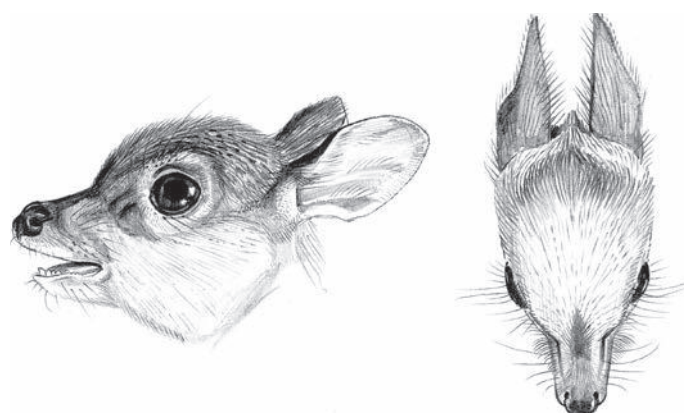
With the advent of molecular science and the prospect of objective measures of genetic affinity, several former neotragines have been

shown to be more distantly related to one another than they are to other, less conservative groups. Furthermore, their resemblances can be interpreted as retentions indicative, in several instances, of their basal position in the radiation of African antelopes. The dwarf antelope genera *Neotragus* and *Nesotragus* constitute one such basal group, but more than one genetic study has associated the little Suni *Nesotragus moschatus* with another basal species, the much larger, rather gazelle-like Impala *Aepyceros melampus* (Georgiadis *et al.* 1990, Hassanin & Douzery 1999, Matthee & Robinson 1999a, Hassanin *et al.* 2012; but see Matthee & Davis 2001). This has served to emphasize the genetic isolation of *Neotragus* and has accelerated abandonment of the former 'waste-paper basket' category. Neotragini is here considered to embrace two species in the genus *Neotragus*, Bates's Pygmy Antelope *N. batesi* and the Royal Antelope *N. pygmaeus*, and the monospecific genus *Nesotragus* for the Suni.



LEFT: Suni *Nesotragus moschatus* adult male myology.
ABOVE: Suni *Nesotragus moschatus* skeleton.

Neotragine species resemble one another in retaining their attachment to a narrow range of forest types and retaining, too, a conservative dentition and feeding habits. It would seem likely that those primitive antelopes that succeeded in abandoning such dietary and ecological attachments became transformed and effectively founded entirely distinct lineages. The earliest precursors of such lineages were probably somewhat Suni-like or grysbok-like and the retention of a way of life typical of the earliest antelopes continues to give the behaviour and ecology of *Nesotragus* and *Raphicerus* a special interest. On a personal note, the decision, in 1964, to embark on a regional inventory of mammals and to entitle it *An Atlas of Evolution in Africa* (Kingdon 1971–1984) was my realization of the significant role that the then ‘Neotragine’ antelopes must have played in bovid evolution. Contemporary molecular studies have borne out the validity of that proposition. Other aspects of the contemporary biology of this tribe are discussed under *Neotragus* and *Nesotragus* and in the species profiles.



Suni *Nesotragus moschatus* juvenile head. Details of sensory hairs around muzzle, eyes and ears.

Jonathan Kingdon

GENUS *Neotragus* Dwarf Antelopes

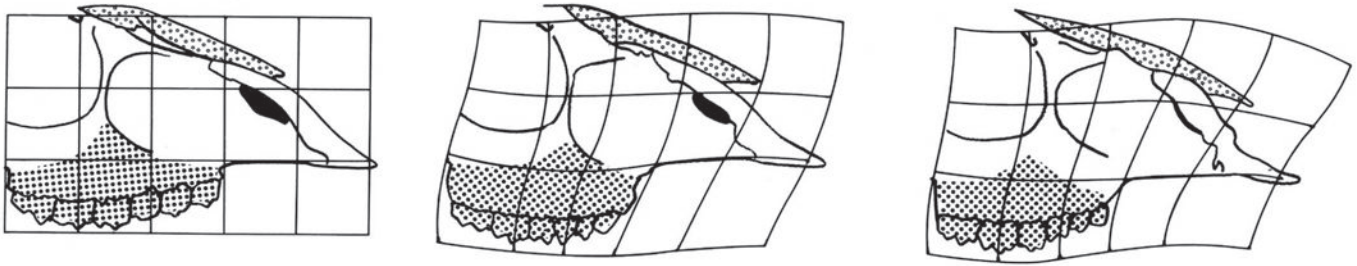
Neotragus C. H. Smith, 1827. In: Griffith et al., Anim. Kingd. 5: 349.

Most recent classifications include the allopatric Royal Antelope *Neotragus pygmaeus*, Bates’s Pygmy Antelope *N. batesi* and the Suni *Nesotragus moschatus* in *Neotragus* (e.g. Grubb 2005). However, the species have been split into three genera in the past: *Neotragus sensu stricto* for the Royal Antelope, *Hylarnus* for Bates’s Pygmy Antelope and *Nesotragus* for the Suni. In this work, only *Neotragus* and *Nesotragus* are retained (see genus *Nesotragus* profile for further discussion). *Neotragus* in this sense only occurs in the rainforests of western and central Africa (including *N. pygmaeus* and *N. batesi*) – the only other small rainforest antelopes apart from duikers. The Suni, here retained in the genus *Nesotragus*, occupies a wider range of more mesic habitats in eastern Africa from Kenya south to KwaZulu–Natal.

Members of *Neotragus* are dwarf antelopes (shoulder height 20–33 cm, mass 1.4–3 kg), with relatively long hindlegs, and pelage

plain coloured or with traces of agouti-speckling or streaked. The rhinarium is naked. Preorbital glands open by a pore; inguinal and pedal glands are both present. There are no lateral hooves. Females have two pairs of nipples. Horns are present in the ♂ only, directed backward more or less in the plane of the forehead. They are short, thin and smooth in both Royal Antelope and Bates’s Pygmy Antelope (cf. the longer and stouter horns, with up to 20 well-marked annuli, in Suni).

In the skull, a premaxillo-maxillary vacuity is no more than a kink in the Royal Antelope, but vestigially present in Bates’s Pygmy Antelope. Apart from the Suni, this character is unknown in other extant bovids except the Impala *Aepyceros melampus* (Ansell 1972). Its possible evolutionary significance was discussed in Kingdon (1982) and elsewhere in this volume. A small ethmoid fissure is present in



Cartesian co-ordinates applied to the nasal maxilla and premaxilla of: Suni *Nesotragus moschatus* (left), Bates's Pygmy Antelope *Neotragus batesi* (centre), Royal Antelope *Neotragus pygmaeus* (right).

the Royal Antelope, but absent in Bates's Pygmy Antelope. In the former, the nasals are posteriorly narrow and pointed, whereas they are broadened and blunt in the latter species. There are large but shallow preorbital fossae accommodating the preorbital glands (larger in ♂♂). The incisiform teeth are small, the first incisors broad and others narrow. Upper milk canines are absent in Bates's Pygmy Antelope (and in the related Suni), but often present in the Royal Antelope. The cheekteeth are low-crowned, much like those of *Raphicerus*, and the premolars well developed.

Neotragus differs from *Raphicerus* in the shape of the muzzle, larger preorbital fossa, less upright horns, longer tail and presence of inguinal glands. Gene analysis suggests *Neotragus* and *Nesotragus* are distantly related to other traditional neotragine antelopes, and are probably better considered the only members of the tribe Neotragini (Hassanin & Douzery 1999, Matthee & Davis 2001), a course that is followed in this work.

Peter Grubb

Neotragus batesi BATES'S PYGMY ANTELOPE (DWARF ANTELOPE, BATES'S DWARF ANTELOPE)

Fr. Antilope de Bates; Ger. Batesbockchen

Neotragus batesi de Winton, 1903. Proc. Zool. Soc. Lond. 1: 192. 'Efulen, Bulu Country, Kamarun [Cameroon], 1500 ft [457 m] above the sea'.



Bates's Pygmy Antelope *Neotragus batesi*.



Upper-right tooththrow of Bates's Pygmy Antelope *Neotragus batesi*.

Taxonomy Polytypic species with two recognized subspecies. Originally designated as a monospecific genus, *Hylarnus* (De Winton 1903), it has also been allocated to the subgenus *Nesotragus* (Haltenorth 1963), but *Nesotragus* is here retained only for the Suni *N. moschatus*. Synonyms: *harrisoni*. Chromosome number: not known.

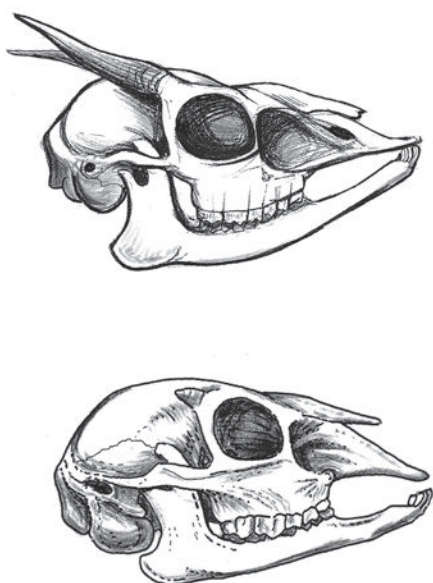
Description Very small antelope, with short muzzle, large eyes and long thin legs. Pelage sleek and fine mahogany-brown, darker on back, crown and forehead. White spots at the base of ears; chin and throat white. Young may have a cream spot above eye. Preorbital glands large, especially in ♂♂, round and not invaginated. Chest, belly, inner parts of upper forelegs and hindlegs, front fetlocks white. Lateral hooves rudimentary. Pedal glands are present. Tail short, inconspicuous brown, lighter below. Females are 6% larger (total length) and 21% heavier than ♂♂. Narrow folivorous teeth.

Horns present in ♂ only, small, smooth, weakly ringed at base, parallel to forehead line, tips slightly converging. In contrast to the Royal Antelope *N. pygmaeus* and the Suni, the ethmoid fissure is absent in Bates's Pygmy Antelope. There is a vestigial hiatus between the maxillary and intermaxillary (the premaxillo-maxillary vacuity, as in the Suni), and there is no anteorbital vacuity.

Geographic Variation

N. b. batesi: SE Nigeria, east of Niger R. to Cross R., and S Cameroon, Equatorial Guinea, Gabon, SW Central African Republic and Congo.

N. b. harrisoni: NE DR Congo and SW Uganda. More contrasted pelage, with more white on the legs (see Thomas 1906).



Bates's Pygmy Antelope *Neotragus batesi* skulls, adult male above, subadult below.

Similar Species

Neotragus pygmaeus. Only occur in forests west of Dahomey Gap. Smaller in size, more reddish pelage, rufous collar thinner than in Bates's Pygmy Antelope; lateral hooves absent.

Nesotragus moschatus. Only occur in forests and thickets east and south of the Eastern Rift Valley. Larger in size, freckled dark brown pelage; horns of ♂ longer, finely annulated and slightly uprising; lateral hooves absent.

Philantomba monticola. Broadly sympatric. Larger in size and of more stocky build, grey or grey-brown.

Distribution Endemic to Africa. Patchily distributed in moist lowland forest in three disjunct regions: SE Nigeria, east of the Niger R. to the Cross R.; S and SE Cameroon (south of the Sanaga R.) to SW Central African Republic (west of the Sangha R.), Gabon, and NW and SW Congo; and NE DR Congo, north and east of the Congo–Lualaba, extending marginally into SW Uganda (East 1999). The gap in distribution may be due to ancient dry corridors during past glacial periods. Today, swamp forests from N Congo and DR Congo may constitute a barrier of unfavourable habitat.

Habitat Bates's Pygmy Antelopes inhabit moist lowland forest. They prefer dense, low undergrowth along rivers, tree falls within mature forests, areas regenerating after logging or cultivation, road sides, village-gardens and plantations where they exploit patches of high-quality forage growing where light reaches soil (Dragesco *et al.* 1979, Feer 1979, Hart 1985). According to Mbuti hunters of NE DR Congo, they avoid damp, swampy habitats (Carpaneto & Germi 1989).

In NE Gabon and S Cameroon, they apparently are excluded by drought during dry seasons (expressed as rainfall minima in the driest season, 25–50 mm per month) (Feer 1979).

Abundance Locally very abundant within optimal habitat such as in cocoa or cocoa plantations mixed with secondary forest in NE Gabon (35–75/km²; Feer 1979); uncommon in the Lopé N. P. in



Gabon (White 1994, P. Henschel pers. comm.). Densities over more extensive areas of forest are 1.5–2.2/km² (Hart, J. A. *et al.* 1996, Fa & Purvis 1997). In forests of S Central African Republic, encounters of Bates's Pygmy Antelopes during net hunts represent only 0.2% of total artiodactyls (Noss 1999). In the Ituri Forest, NE DR Congo, it represented 3.6% of the captures by nets (Carpaneto & Germi 1989). Here, estimated densities in mature forest are similar to those in regrowth (Wilkie & Finn 1990). Despite higher hunting pressure, encounter rates within 14 km from a village in Dja Reserve in Cameroon were higher than at distances further away (Muchaal & Ngandjui 1999). East (1999) estimated a total population size of about 220,000 individuals.

Adaptations Typically slow-moving while foraging, with a high-stepping and hesitant gait in dense vegetation. Ratio of free height under chest to shoulder height is higher than for duikers (tribe Cephalophini). When alarmed may freeze a long time before jumping for cover. Flees quickly at short distances, occasionally with barking. Active both at night and day, with rests around mid-day and in the early and middle evening. In cultivated zones, animals rest in the densest areas by day and relatively more open areas by night. At night they move 51% less in open habitats (generally rich in food) than in other habitats. Lactating ♀♀ and young prefer dense protective habitats (Feer 1979).

Foraging and Food Folivorous; classed as browsers by Gagnon & Chew (2000) in a comprehensive review of dietary preferences in African Bovidae. Bates's Pygmy Antelopes delicately pluck leaves, buds and shoots, choosing small young items, but also consuming very large leaves (e.g. *Dioscorea*, *Calocasia*). They browse selectively on more than 200 species in cultivated areas in Gabon (Feer 1979), with recorded preferences for species in the genera *Brillantaisia*, *Momordica*, *Phaulopsis*, *Cyathula* and cultivars, notably sweet potatoes, peanuts and peppers. Near villages, they adapt their home-ranges

to the seasonal rotation of clearings and growth of small plants; on average, half of their home-range is composed of dense herbaceous strata (Feer 1979). Their diet in deep forest is poorly known. They consume four species of forest fruit and various leaves according to Mbuti Swa from the Ituri Forest (Carpaneto & Germe 1989).

Cerling *et al.* (2003) found that three different teeth taken from a single individual from the Ituri Forest had the most ^{13}C -depleted bioapatite values from the more than 1000 extant mammals they had analysed, indicating that the species effectively has no capacity to survive on coarse grass or leaf diets.

Social and Reproductive Behaviour Most often solitary (61% of observations, Feer 1979); two or more adults are rarely seen within short distance (<50 m) of each other. Adult ♂♂ seem to occupy exclusive home-ranges and mark the tips of browsed plants with black preorbital secretion; ♀♀ do not mark. Middens or ritualized defecation were not observed. Male home-ranges (2–4 ha) include several overlapping female home-ranges. Short nasal moans are a common contact call.

Reproduction and Population Structure Histology suggests sexual maturity is attained at 8–18 months for ♂♂ and ca. 16 months for ♀♀. Reproduction occurs all year round, although births peak twice a year at the end of the wet seasons. Around 80% of subadult (16–26 months old) and adult ♀♀ are pregnant. Newborn weight is ca. 300 g. Weaning takes place during the favourable following wet season (Dubost & Feer 1992). In Gabon, a sample of 103 individuals from a weakly hunted population comprised 47% adults. Males accounted for 42% of adults. Mortality of subadult ♀♀ is higher than in ♂♂ (Feer 1979).

Predators, Parasites and Diseases In the Ituri Forest, Bates's Pygmy Antelopes represent 2.1% of prey items in scats of Leopards *Panthera pardus* and 4.0% of African Golden Cats *Profelis aurata* (total felids 2.7%, Hart, J. A. *et al.* 1996). Mbuti hunters report predation by African Golden Cats and Crowned Eagles *Stephanoaetus coronatus* (Carpaneto & Germe 1989). They are fragile and die from stress after prolonged chases. Very little information is available on diseases and parasites; Durette-Desset (1973) recorded a new species of filarial parasite (*Setaria pujoli*) from this species in Cameroon.

Conservation IUCN Category: Least Concern. CITES: Not listed.

The status of Bates's Pygmy Antelope should remain stable wherever forests remain sparsely settled. However, increasing pressures of hunting, logging and clearing for cultivation in central African forests represent a serious threat. Despite the ability of the species to use disturbed habitat, its future survival may be increasingly dependent on protected areas. At present the protected areas within which it is common, including Dja Reserve (Cameroon), Dzanga-Sangha Special Reserve (Central African Republic), Odzala N. P. (Congo Republic), Monte Alén N. P. (Equatorial Guinea) and Kahuzi-Biega N. P. and



Bates's Pygmy Antelope *Neotragus batesi*.

Okapi Faunal Reserve (DR Congo), receive very unequal levels of protection and management. Consumption in the rural areas around Kisangani (DR Congo) represents 8% of total artiodactyls and 0.9% of total game, but Bates's Pygmy Antelopes are very rare in the urban bushmeat market (Colyn *et al.* 1987). They are totally absent from the market of Makokou (Gabon) (Lahm 1993, F. Feer pers. obs.) at 70 km from the species' distribution limit, and in five markets visited across the country in 2004, Bates's Pygmy Antelopes made up only 285 kg in terms of biomass (Projet Gibier Gabon pers. comm.). Consumption is limited by various food restrictions and taboos in NE Gabon (F. Feer pers. obs.) and DR Congo (Carpaneto & Germe 1989).

Measurements

Neotragus batesi

HB (♂♂): 513 (470–560) mm, n = 25

HB (♀♀): 548 (480–580) mm, n = 33

T (♂♂): 88 (70–100) mm, n = 25

T (♀♀): 88 (70–100) mm, n = 33

HF c.u. (♂♂): 147 (130–160) mm, n = 25

HF c.u. (♀♀): 152 (140–170) mm, n = 39

E (♂♂): 47 (40–50) mm, n = 23

E (♀♀): 48 (40–50) mm, n = 36

Sh. ht (♂♂): 306 (280–310) mm, n = 24

Sh. ht (♀♀): 318 (280–335) mm, n = 33

WT (♂♂): 2.19 (1.8–2.6) kg, n = 26

WT (♀♀): 2.76 (1.9–3.4) kg, n = 30

Gabon (Feer 1979, F. Feer pers. obs.)

Record horn length is 4.4 cm for a pair of horns from Uganda (Rowland Ward)

Key References Dragesco *et al.* 1979; Feer 1979, 1982.

François Feer

***Neotragus pygmaeus* ROYAL ANTELOPE**

Fr. Antilope royale; Ger. Kleinstbockchen

Neotragus pygmaeus (Linnaeus, 1758). Syst. Nat., 10th edn, 1: 69. 'Habitat in Guinea, India'; restricted to 'Guinea' (West Africa) by Thomas (1911: 152).



Royal Antelope *Neotragus pygmaeus*.

The common name derives from Bosman (1704), who reported that people in the Gold Coast (Ghana) called it 'The King of Antelopes'. He failed to note whether the name was symbolic, gastronomic or ironic, but stories about the guile of the Royal Antelope are widespread in West Africa. In Sierra Leone it is known as 'the cunning rabbit' in stories where it sometimes plays an equivalent role to America's 'Brer Rabbit' (where such stories might have been transplanted from West Africa).

Taxonomy Monotypic. See Grubb (2005) for detailed discussion regarding former misidentification of this species as a tragulid. *Neotragus pygmeus* is an incorrect original spelling. Synonyms: *perpusillus*, *pygmeus*, *regius*, *spinigera*. Chromosome number: $2n = 36$ (K. Benirschke *in litt.*).

Description A tiny antelope, with very thin, long legs, large eyes, relatively small, flesh-coloured ears and a diminutive tail with white underside. Pelage is fine and soft, reddish or golden-brown and particularly red on the rump; darker brown on upper back, crown and forehead. Sides of face sandy-red; white spots at the base and upper margins of ears. Lower jaw, throat 'bib' and chest are white; underparts and inside of limbs whitish. Preorbital glands are small, both relatively and absolutely (see Kühn 1976 for further information on these glands). Lateral hooves absent or vestigial. Pedal glands are present. Sexes of similar size, but ♀♀ are marginally larger and heavier than ♂♂.

Tiny conical horns, in ♂♂ only, follow the line of the nose and forehead and may be concealed by crest hair. Unlike other *Neotragus* species, the hiatus between the maxillary and intermaxillary (the premaxillo-maxillary vacuity) is filled by what appears to be a phylogenetic migration of the maxilla, premaxilla and nasal. The anterior, premolar section of the toothrow is reduced and the masseter and its attachments are proportionally smaller than in



Neotragus pygmaeus

Neotragus batesi. Upper milk canines are often present in the dentition (Dekeyser & Derivot 1956).

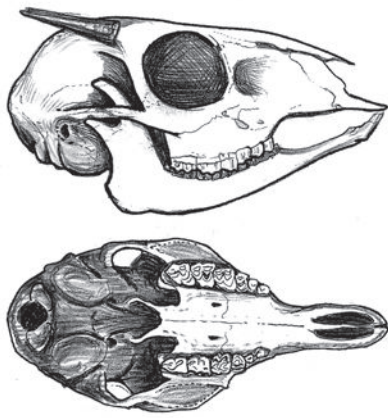
Geographic Variation None.

Similar Species

Neotragus batesi. Only occur in forests east of Niger R. Slightly larger in size, longer legged, less brightly coloured.

Philantomba maxwelli. Sympatric. Larger in size and more strongly built; grey or greyish-brown.

Distribution Endemic to Africa, ranging in lowland rainforest (and marginally in the forest-savanna mosaic to the north) from SW Guinea (the Kounounkan Massif perhaps representing the westerly known limit; see Barnett *et al.* 1996; Barnett & Prangley 1997), Sierra Leone, Liberia, SE Guinea, Côte d'Ivoire, to the Volta R., Ghana (Grubb *et al.* 1998, East 1999). The species has apparently been recorded from the forests east of the Volta R. in NE Ghana, where R. Jamieson observed it on sale in the Binaba market, but this record remains questionable (Grubb *et al.* 1998); it was also thought possible that it may occur in Digya N. P., east of the Volta (Ankudey & Ofori-Frimpong 1990), but this seems doubtful. Fischer *et al.* (2002) reported what they considered to be reliable observations of the tracks of Royal Antelopes in Comoé N. P. in NE Côte d'Ivoire. Records of the species' presence in Cameroon (Jeannin 1936) refer to Bates's Pygmy Antelope *N. batesi*, and records of the species' presence in Togo (Happold 1973b) are also in error.



Lateral and palatal views of skull of Royal Antelope *Neotragus pygmaeus*.

Habitat Royal Antelopes inhabit moist lowland forest and secondary vegetation habitats, and can adapt well to the farm bush regrowth that follows forest clearance. In Sierra Leone, where the species is encountered more commonly in logged forest with some undergrowth than in primary forest, it has been reported mainly caught by hunters by means of duiker snares set in fences round farms and in nets when swamps and bush areas are netted and subjected to game drives during the dry season (Grubb *et al.* 1998). It is commonly reported from cultivation, both small-scale and commercial, and grassy or leafy road verges. It prefers dense undergrowth at ground level along forest edges and clearings, both within the moist forest belt and in forest galleries in drier forest–savanna mosaics. The animals seek out areas where sunlight reaches the soil and generates fresh green growth. Because it is essentially dependent on very fresh green growth at ground level and because it becomes vulnerable to predators when exposed, open areas under the closed canopy of high forests do not support Royal Antelopes. They are able to persist in relatively small forest fragments.

Abundance Said to be locally abundant, notably in Côte d'Ivoire where it is common in bushmeat markets. East (1999) has suggested an extrapolated density range of 0.2–2.0/km² and estimated the total population at a little over 60,000, which he acknowledged was likely to be a substantial underestimate. In the main bushmeat market in Kumasi, Ghana, Wilson (2001) found an annual sale of about 1200 carcasses of Royal Antelopes. He also found that most animals are consumed locally so the carcasses reaching urban markets are less than half of the hunters' actual catch. For such an off-take to be sustainable, which seems likely, East's upper estimate of 2.0/km² is certainly a minimum realistic density.

Adaptations Exceptional alertness to danger is the dominant characteristic of this species and it is typically extremely cautious whenever exposed. As with other small antelopes, it has a high-stepping and hesitant gait, freezing at the slightest alarm. It 'scurries', fast, with head down, when mildly disturbed but can dash through cover very fast when necessary. Its disproportionately large hindquarters power leaps and bounds that assist a quick escape.

Such a very small antelope is prey to a very wide range of predators and its adaptations to such vulnerability could, perhaps,

have helped deter scientists from investigating the world's smallest ruminant. Considering our need to thoroughly understand the central process governing the productivity of our three main domesticates (cattle, sheep and goats) it is obvious that rumination in the smallest bovid should offer special insights into rumen physiology. The little that is known suggests that the Royal Antelope has adapted its behaviour and physiology to the special problems of extracting nutrients from the tiny 200–250 g fermenting vat that is its stomach. In ruminants, the products of fermentation must be absorbed while, at the same time, pH levels remain tolerable for the micro-organisms in the rumen and for the tissues of the rumen itself. Nagy (1970) correlated lowering of pH in the rumen with increases in lactose-fermenting organisms so it would be interesting to know what role these organisms play in the Royal Antelope. Hofmann (1973) has noted that ruminoreticula of small capacity compensate for their reduced volume by enlarging their absorptive surface enormously while at the same time increasing the rapidity of fermentation, thus removing fermentation products before they damage the system. Extrapolating from Hofmann's studies of other small ruminants it could be predicted that the Royal Antelope would select highly digestible foods and that it would keep augmenting its food intake. In spite of grossly inadequate data, both predictions are tentatively borne out.

Although it is often described as nocturnal, casual sightings in Tai N. P. (e.g. see Hoppe-Dominik *et al.* 2011) are consistent with other sightings, hunters' observations and the behaviour of captives that suggest the Royal Antelope is intermittently active both at night and during the day.

Unlike other members of the Neotragini this species has significantly smaller preorbital glands. As these glands are associated with the marking of home-ranges or territories their reduction implies that home-ranges are not marked or defended in the same way or with the same intensity as other small antelopes. On the other hand, the area of the skull devoted to olfaction is relatively greater than it is in Bates's Pygmy Antelope or the Suni *Nesotragus moschatus*, both of which have compressed narrow snouts, especially towards the snout. Effectively, the Royal Antelope has enlarged and elongated its muzzle *vis à vis* its relatives. However, it is unclear whether this is primarily linked to efficient plucking of foliage or part of an improvement in olfactory performance.

Foraging and Food Folivorous, but precise preferences currently unknown. Royal Antelopes have a muzzle that is longer, with relatively broader lips, but smaller mouth and smaller chewing muscles than in Bates's Pygmy Antelope. There are also constraints on the digestibility of their food, so that any growth that is at all lignified must be excluded or rejected. This combination suggests that this species is peculiarly dependent on physically soft, nutritionally digestible leaves, buds and shoots. Because canopies, high or low, are constantly changing in its habitat it is likely that the frequent 'shading out' of its food supply makes fresh growth effectively unpredictable and ephemeral in its distribution. Even for the very small quantities that are eaten, foraging is probably opportunistic and involves movement over areas that are not intimately known. Animals are snared on bush farms where they are attracted to the new foliage of crops such as yams, sweet potatoes, amaranthus and peppers. It is possible that they have adapted to the

particular cultivation cycles of forest edge farms and to the growth of so-called weeds along road verges.

Social and Reproductive Behaviour Commonly seen singly, but their ranging and territorial behaviour is unknown. Unlike other small antelopes they have not been reported to mark plants with preorbital secretions (which is interesting in the light of this species having greatly reduced preorbital glands). Contact behaviour between individuals has not been studied and ritualized defecation has yet to be noted. Owen (1973) described a hand-raised captive making an audible contact call.

Reproduction and Population Structure A remarkably consistent harvest of these antelopes throughout the year suggests that they do not have a marked breeding season. Consistently high catches over many years suggest a high level of fecundity but nothing has been recorded about their population structure. A single young is born, and there are no records of twins in the literature. A young captive observed by Owen (1973) began ruminating at four months of age. Other information on breeding is not available. Longevity in captivity is 6 years and 8 months (Jones 1993).

Predators, Parasites and Diseases Leopards *Panthera pardus*, African Golden Cats *Profelis aurata* and Servals *Leptailurus serval* are now rare over much of their range and snaring, netting, trapping, hunting with dogs and guns represent the main sources of mortality. Crowned Eagles *Stephanoaetus coronatus* probably take them on occasion. Ntiemoa-Baidu *et al.* (2005) examined 58 animals in Ghana and recorded the following ixodid tick species: *Haemaphysalis*

parvata, *I. muniensis*, *I. moreli*, *I. aulacodi*, *Rhipicephalus ziemanni* and *R. simpsoni*. Diseases are unknown.

Conservation IUCN Category: Least Concern. CITES: Not listed.

Still relatively widespread, even within its small range, and somewhat abundant in some parts. Their ability to survive well even in secondary habitats has helped it fare better than other species in the face of habitat loss, and they are present in several protected areas including Gola N. P. and Tiwai Island (Sierra Leone), Tai N. P. (Côte d'Ivoire) and Kakum N. P. (Ghana). However, they are at risk from bushmeat hunting, and high prices are sometimes paid for the meat of this species in urban markets. East (1999) reported that local taboos on hunting or consumption of Royal Antelope still operate in Liberia, where the species is regarded as the epitome of cunning by rural people.

Measurements

Neotragus pygmaeus

HB: 430 mm

T: 50 mm

Sh. ht: 260 mm

WT: 2.4 kg

Captivity (Owen 1973)

Record horn length is 3.4 cm for a pair of horns from Totota, Liberia (Rowland Ward)

Key References East 1999; Owen 1973.

Jonathan Kingdon & Michael Hoffmann

GENUS *Nesotragus*

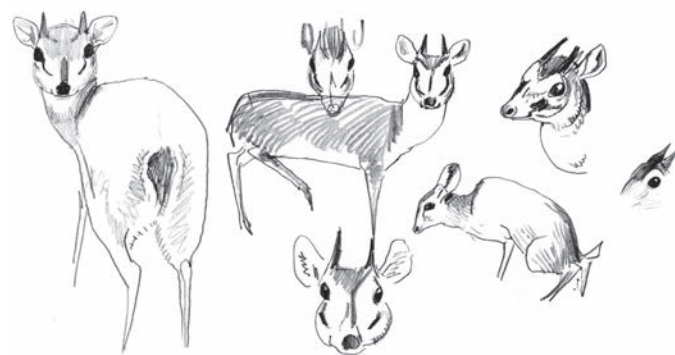
Suni

Nesotragus von Dueben, 1846. In: Sundevall, C. J. Ofvers. Ventensk Akad. Forh. Stockholm III.

In most recent nomenclatures, the Suni *Nesotragus moschatus* is included, together with the Royal Antelope *Neotragus pygmaeus* and Bates' Pygmy Antelope *N. batesi*, in *Neotragus* (see e.g. Ansell 1972, Meester *et al.* 1986, Grubb 2005). In this work we provisionally retain the older practice of treating the Suni as a monospecific genus (see Allen 1939, Roberts 1951, Ellerman *et al.* 1953).

The principal external distinctions include: longish male horns (up to 13 cm) with 13 or more irregular ridges on the basal half or three-quarters of the horns; a longish muzzle in which there is an ethmoid vacuity between the maxilla and premaxilla (only vestigially present in Bates's Pygmy Antelope, and otherwise unknown in any other bovid, except the Impala *Aepyceros melampus*; Ansell 1972); the rear of the bony palate extends beyond the back end of the toothrow; processes on the lower anterior surfaces of the basioccipitals; exceptionally large preorbital glands and fossae; and well-developed premolars.

Further subdivision of *Neotragus*, or a return to older nomenclature, is still conceivable; for example, the retention of *Hylarnus* for *N. batesi* might be justified were molecular studies able to demonstrate a great age for the divergences within the three members of the tribe Neotragini. *Nesotragus moschatus* has been shown to be a basal member



Suni *Nesotragus moschatus*.

of the Antilopinae (Hassanin & Douzery 1999, Rebholz & Harley 1999, Matthee & Robinson 1999a) and while its close relationship with *Neotragus* is not contested there are several anatomical details that suggest that both *Neotragus batesi* and *Neotragus pygmaeus* are derived species from a more *Nesotragus*-like ancestor. Roberts (1951)

thought that the three forms not only deserved generic status, but even thought that they could be considered representative of different subfamilies!

The likelihood that *Nesotragus* is the most conservative of the Neotragini finds support in an examination of the nasal region. Both species of *Neotragus* have diminished premolars, shortened maxilla and elongated nasals. Feeding on tough foods, including roots, in the drier forests and thickets of eastern Africa, the Suni's retention of robust premolar and molar teeth would not only be favoured by selection; it almost certainly resembles more closely the condition of an early, thicket-dwelling ancestral type.

Nesotragus moschatus SUNI

Fr. Antilope musquée; Ger. Moschusboeckchen

Jonathan Kingdon

Nesotragus moschatus (von Dueben, 1846). In: Sundevall, Ofv. K. svenska Vet.-Akad. Forhandl., Stockholm 3 (7): 221. 'in Chapani (Anglis French island) occisa insula prope Zanzibar in Lat. Austr. 6° 9', Long. Orient. 39° 14' a Greenwich sita, fructibus dense tecta et fonte irrigata' (Tanzania, Chapani I., 3 km from Zanzibar).



Suni *Nesotragus moschatus*.

The common name is derived either from the Kikuyu name for the species, *kasuni*, or from the *suni* of the related Wachagga people, or from the *suni* of a related tongue, Kichagga.

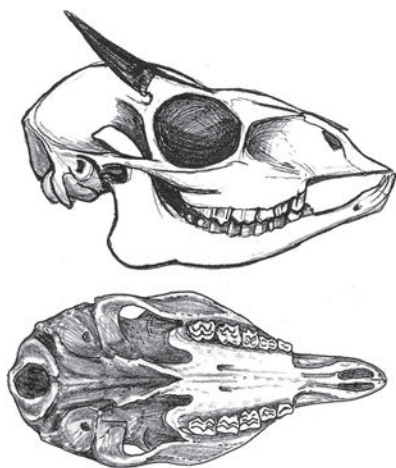
Taxonomy Several earlier authors, including Allen (1939), Roberts (1951) and Ellerman *et al.* (1953), included the Suni in the monotypic genus *Nesotragus*, although the species has traditionally been classified as one of three dwarf antelopes in the genus *Neotragus* (e.g. Ansell 1972, Grubb 2005). As outlined under the genus profile, we retain the species in genus *Nesotragus*. Synonyms: *akeleyi*, *deserticola*, *kirchenpaueri*, *livingstonianus*, *zanzibaricus*, *zuluensis*. The chromosome number of southern African populations is $2n = 56$ (Robinson *et al.* 1997). Kingswood *et al.* (1998a) also reported a diploid number

In invading the equatorial rainforests, *Neotragus batesi* and *N. pygmaeus* have made an evolutionarily significant shift away from an earlier, more arid-adapted condition. We consider that it is worth retaining *Nesotragus*, if only provisionally, because the Suni clearly retains a more conservative way of life and some key dental and cranial features associated with its less derived condition. Because this is a monospecific genus the species profile should be consulted for all descriptive details.

of $2n = 56$ (for the form *zuluensis*), but populations from Kenya (*akeleyi*) had $2n = 52$. They also recorded $2n = 53-55$ cytotypes, which they suggested were probably the result of hybridization in captivity between the two subspecies, and stated that it was possible that these cytotypes could occur in the wild.

Description A small, brown antelope with long, slender legs, a compact stance and a broad head and short neck. Preorbital face glands are disproportionately large, especially in adult ♂♂. The skin surrounding the eyes is almost bare but there is a short row of long vibrissae above the eye and others on the muzzle. Oval-shaped ears bear a brush of white hairs along their upper, inner margin. Inner surfaces of the ear are naked, pinkish and semi-transparent in strong light. The chin and upper throat are whitish, as is the lower chest. Body and neck are relatively uniform dark brown, the pelage being sleek and shiny with a very fine freckle. There are individual and possibly regional variations in tints of rufous or grey to body colour. The underside and inner surfaces of the legs are white or pale grey. Legs are tawny brown on their outer surfaces. The tips of the feet are black or dark brown ending in small, sharp, glossy black hooves; there are no lateral hooves. Deeply evaginated pedal glands are revealed when the toes of the hindfeet are splayed. The area of longer black hairs around and under the hoof coincides with the zone of scent diffusion from the pedal glands. Tail short, well haired and black on its outer surface, vivid white below: it is frequently wagged from side to side. Inguinal glands are present. Females have two pairs of inguinal nipples.

Males have strongly ridged horns that reach a maximum length of around 130 mm, and are heavily annulated with up to 20 well-marked annuli. Females are hornless. The skull is distinctive in that there is a vacuity or fontanelle between the maxilla and premaxilla. This suggests that the latter bone might have made an evolutionary migration upwards from a shorter, lower attachment to the maxilla (Kingdon 1982). Likewise, the nasal bones appear to be secondarily elongated forwards and downwards. The maxilla and lachrymal bones appear to have accommodated massive enlargement of the preorbital glands by becoming deeply convex, thus narrowing the



Lateral and palatal views of skull of Suni *Nesotragus moschatus*.

nasal chamber. This, together with the downwardly bent nasals, give the diminutive snout of the Suni a distinctly 'pinched' appearance. Kingdon (1982) interpreted these peculiarities in terms of a phyletic shift into more humid environments and abandonment of a 'nasal bellows' mechanism in a drought-adapted ancestor. A small ethmoid fissure is present (as in the Royal Antelope *Neotragus pygmaeus*). The teeth, particularly the premolars, are proportionally exceptionally robust for such a small antelope. Upper milk canines are absent.

Geographic Variation Five subspecies have been recognized: *N. m. moschatus* (including *zanzibarcus*), from the Zanzibar Is.; *N. m. akeleyi*, from Mt Kenya, the Aberdares and south to Nairobi; *N. m. kirchenpaueri*, from coastal S Kenya, NE Tanzania and Mafia I.; *N. m. livingstonianus*, from S Tanzania, Malawi and N Mozambique; and *N. m. zuluensis*, from NE South Africa, S Mozambique and Zimbabwe (Haltenorth 1963, Ansell 1972). However, the limits between them are equivocal and the descriptions are based on limited specimens. Consequently, most authors have regarded the validity of these forms as doubtful. Nevertheless, geographical variation is evident in some areas. In East Africa, authors have distinguished between a dark highland form (considered by some as the subspecies *N. m. kirchenpaueri*) and a paler, coastal form (*N. m. moschatus*). Grubb (1989) examined skins of Sunis collected from Malawi and found that the Malawi population exhibits a range of variation comparable to that of Sunis in East Africa (but with more intergradation between extremes and in a smaller area) and allied these to the East African forms. In examining specimens from Mozambique, Grubb (1989) noted that these appear quite different from those in Malawi, being unspeckled and overall bright rufous brown with little contrast between the upperparts and shanks. These Sunis also were larger than East African animals, which Grubb (1989) noted implies an association with the form from KwaZulu–Natal in South Africa (*N. m. zuluensis*). However, because the Malawi and Mozambique specimens were



Upper-right tooththrow of Suni *Nesotragus moschatus*.



Nesotragus moschatus

taken from relatively close localities, Grubb (1989) suggested that the Zambezi R. marks a narrow zone in the geographical variation of this species, and recognized two divisions: the nominate *moschatus* division (including *kirchenpaueri* and *akeleyi*) and the *livingstonianus* division (including *zuluensis*).

Similar Species

Philantomba monticola. Sympatric in Tanzania, Kenya, S Malawi and Mozambique. Larger, greyer, with shorter legs, less conspicuous ears; tail mostly flipped up and down, not from side to side.

Neotragus batesi. Allopatric species from central and West Africa; smaller, more russet.

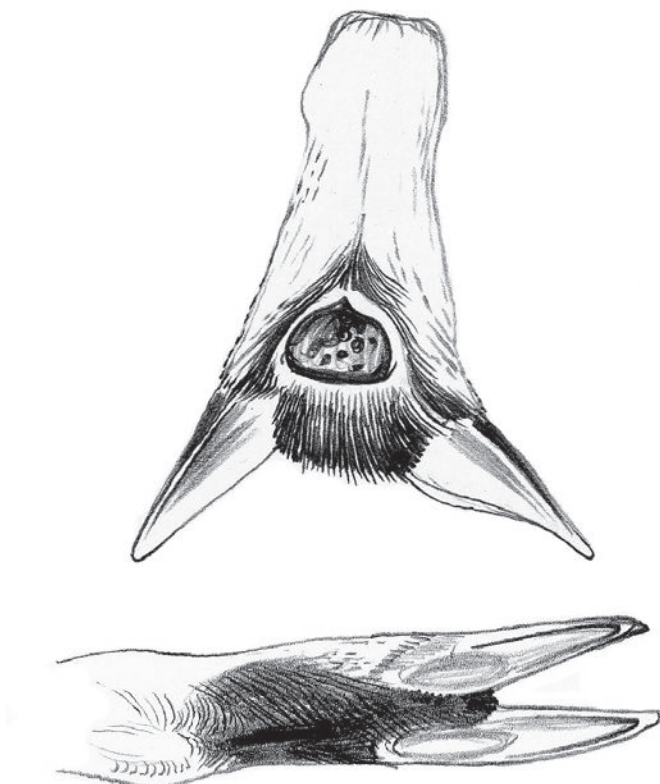
Neotragus pygmaeus. Allopatric species from West African Guinea forests; very small with russet rump.

Distribution Endemic to evergreen and semi-deciduous forests and thickets of eastern Africa from Kenya to KwaZulu–Natal, South Africa, mostly east of the Eastern Rift Valley. In Kenya, it occurs about as far north as Mt Kenya and the Aberdares, and, along the coast, has been recorded as far north as the Boni-Dodori forests (Andanje *et al.* 2011b). The species ranges southwards through the eastern half of Tanzania, including Mt Meru, Mbulu, the Ngorongoro Crater highlands and the Eastern Arc Mountain forests (such as North and South Pare, East Usambara, Nguu Mts and Udzungwa Mts; Cordeiro *et al.* 2005, Rovero *et al.* 2005), the lower Shire valley in S Malawi, NE and SE Zimbabwe, parts of Mozambique, and E South Africa. Their southerly limit of distribution is around L. St Lucia in NE KwaZulu–Natal (ca. 28°S). They probably also occur in extreme E Swaziland, although their occurrence is not confirmed (Monadjem 1998). There are no confirmed records from Zambia, although there are records south of the Zambezi around Kariba. Recorded from Zanzibar and some adjacent islands (Mafia and Chapani, the type locality), but not Pemba; introduced to Rubondo I. in L. Victoria in the 1960s (Rodgers *et al.* 1977).

Suni distribution was probably always discontinuous and fragmented but agricultural expansion into forests and thickets has accentuated this tendency. Whereas the area inhabited by Sunis has probably diminished considerably, the overall extent of their geographical range may not have contracted very much.

Habitat Thickets, forests and dense, evergreen woodlands from sea level to 2700 m. Commonest in forests fringing the foothills of larger mountains, in coastal forests on hills and in thickets and woodland on coastal coral-rag and sand dunes. Less common in montane forests dominated by cedar. Locally most abundant where there is thicker undergrowth along forest margins and water-courses. In some areas it probably benefits from the expansion of secondary thicket habitat that has resulted from human activity (e.g. on Zanzibar), and it readily colonizes degraded forests (East 1999).

Abundance In prime habitat (such as foothills of north Tanzanian mountains) relatively high population densities have been estimated. Ground surveys suggest densities of 13.0–17.0 ind/km² in areas like Zanzibar and Lengwe N. P., Malawi (East 1999). Sunis from fragmented, degraded and suboptimal habitats probably survive at lower densities. Densities of 0.9/km² are recorded from Mkhuzi G. R. in KwaZulu–Natal (Rowe-Rowe 1994). Based on these density estimates, East (1999) estimated a total population size of around 365,000 animals. Populations are probably stable over much of the range, but decreasing where hunting pressure is high. In addition, where they occur in protected areas with high densities of Nyala *Tragelaphus angasii*, and a corresponding decrease in the density of the shrub layer, their numbers decline.



Suni *Nesotragus moschatus* hindfoot splayed to expose pedal gland – note fan of hairs. Black fur coincides with area in which scent diffuses.

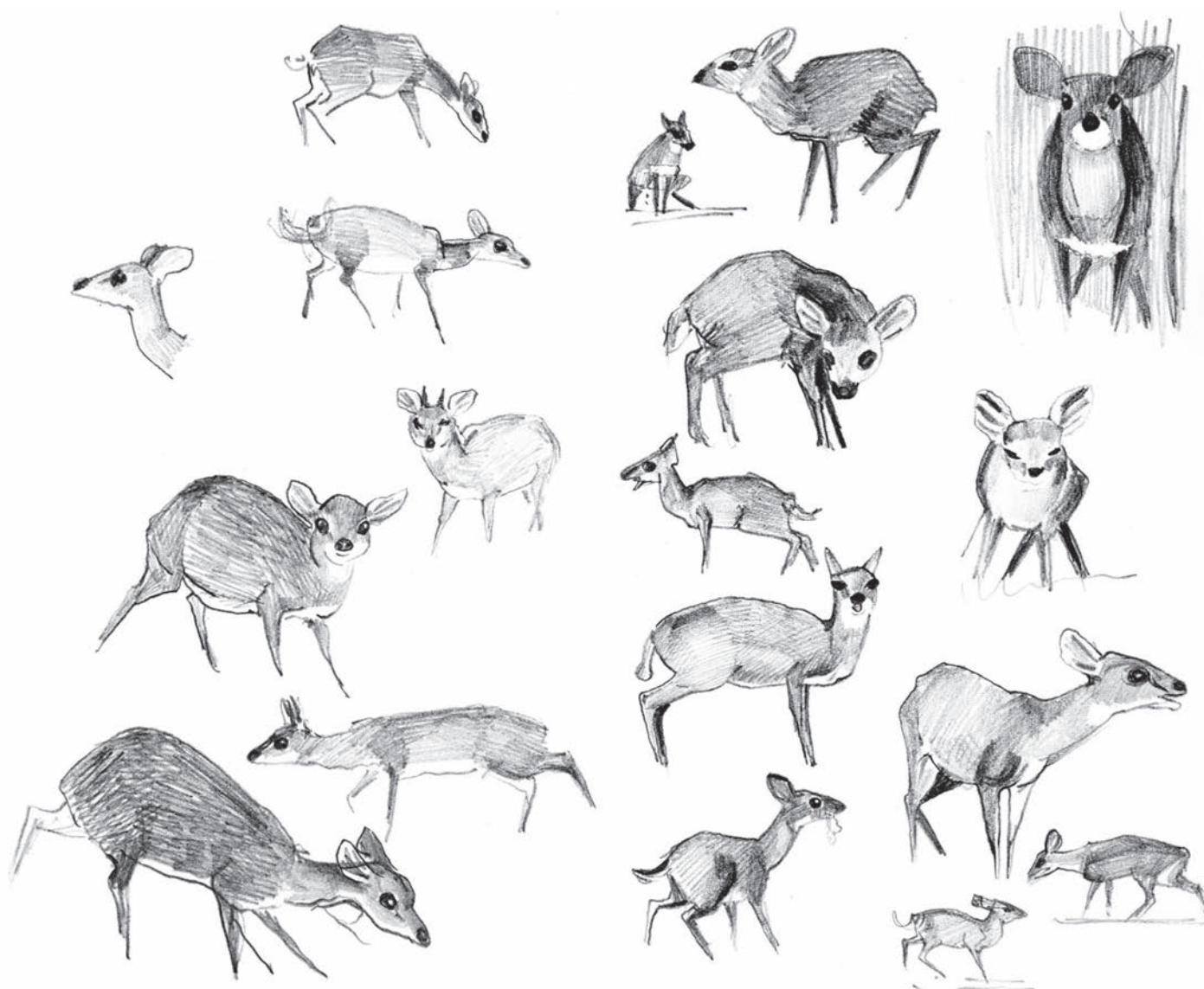
Adaptations The most striking peculiarity of the Suni is its strong, musky body scent and the inflated size of the preorbital face glands, especially in ♂♂. Although face glands may decline in size when animals are very old or sick, there seems to be no visible fluctuations in their size that can be correlated with sexual or seasonal cycles. Face glands on ♂♂ are used for frequent and intensive scent-marking of exceptionally small and compact territories. The tips of twigs and stems are inserted into the deep, central pocket of the gland, emerging with a blob of scented black secretion. Stems are mostly the product of browsing by folivores, but Sunis sometimes bite off leaves or buds before marking the cut stem tip. Somers *et al.* (1990) studied marking behaviour in captive Sunis and found that short, vertical twigs between 15 and 280 mm in height are favoured as marking posts. The secretion dries to a hard, dark, crystalline substance that, due to repeated markings, forms visible bulbous deposits. Such marks last about four days. Stander *et al.* (2002) employed gas chromatographic and gas chromatographic–mass spectrometric techniques to identify 83 compounds in the preorbital secretion of the male Suni. Facial scent-marks are mainly concentrated along regularly used trails that form a network throughout the territory. Trails are also likely to be well scented by interdigital pedal glands on the back feet (the other main source of scent production). Communal dung piles around the boundaries of territories provide further evidence for the supreme importance of scent signals in Suni life history.

Scents clearly serve internal communication among Suni, but there could be other dimensions. Although Sunis are ‘hiders’ when born and mothers swallow their young’s excreta, young acquire a strong scent very soon after birth. Such seeming advertisement of the young implies that ‘olfactory’ predators entering Suni territories might be effectively ‘swamped’ with scent clues. The ability to generate pheromones sufficient to scent all the paths in its habitat would count for very little where the antelope’s environment is less constricted. The Suni’s ability to spread its scent around is therefore dependent on a small home-range that, in turn, is made possible by an eclectic choice of food plants. Another, possibly incidental, effect of the Suni’s scent is that it may deter some species of flying insects: Sunis have been observed without attendant flies while neighbouring antelopes of other species were severely pestered (J. Kingdon pers. obs.).

In their dense habitat, Sunis are cryptic animals. Both sexes display a very conspicuous and species-specific visual signal by wagging their black and white tails from side to side (unlike the Blue Duiker *Philantomba monticola*, which mainly flips its tail up and down). This wagging may also serve as a short-range dispersal mechanism of scent from the anal region. The white scrotum of the ♂♂ is also an obvious visual feature when viewed from behind.

Sunis are most active after rainstorms or spells of dense mist, especially between nightfall and 22:00h and after 04:00h, and rest during the heat of the day. These observations are borne out by camera-trapping work in the Udzungwa Mts where Sunis are primarily crepuscular and nocturnal (Rovero *et al.* 2005). They avoid exposing themselves outside dense cover during the day. They are largely independent of drinking water, obtaining their moisture requirements from their food.

Foraging and Food Sunis are browsers, as classified by a detailed review of dietary preferences in African bovids (Gagnon & Chew 2000) and studies using stable carbon isotopes (Cerling *et al.* 2003).



Suni *Nesotragus moschatus*.

Experiments conducted in captivity have shown that Sunis are highly selective feeders, with a distinct preference for dicotyledonous leaves (Hoppe *et al.* 1983, Lawson 1986, 1989, Maloiy & Clemens 1999). In the wild, Sunis browse from a wide variety of understorey plants that occur in the semi-deciduous and evergreen forests and thickets of eastern Africa. Leaves and shoots of the aptly named 'Suni Hemp' *Crotalaria* spp. are favoured, and other common food plants include species from the genera *Acacia*, *Acalypha*, *Achyranthes*, *Cissus*, *Clematis*, *Commelina*, *Grewia*, *Justicia*, *Leucas*, *Microglossa*, *Sapium*, *Strychnos* and *Toddalia*; *Fleurya* and *Ipomoea* are preferred when wilted and they pick up various dry leaves fallen from the canopy (Heinichen 1972, Kingdon 1982). Prins *et al.* (2006) recorded a total of 70 items eaten in a dietary study in Maputo Elephant Reserve in S Mozambique.

In West Kilimanjaro, Sunis gather under feeding colobus monkeys to pick up dropped leaves and shoots, notably those of a local dominant, *Nuxia congesta*. They have also been recorded eating the fallen fruits of the wild fig *Ficus* sp. in KwaZulu-Natal (Taylor 1978), and *Ficus sycomorus* was an important part of the diet in the early wet season in

a study in S Mozambique (Prins *et al.* 2006). They also eat charcoal and termitary mushrooms, and have been reported to scrape soil away to expose the roots of certain herbs (Heinichen 1972, Kingdon 1982). Although grasses, such as finger grass *Digitaria* spp., have been recorded in the diet, Sunis, like dik-diks, are not equipped to digest cellulose efficiently (Hoppe *et al.* 1983). Hoppe *et al.* (1983) examined the rumens of Sunis in East Africa and found that their contents consisted of 84% dicotyledonous leaves, 4% stems, 6% fruit and 6% monocotyledonous material. On the other hand, Prins *et al.* (2006) recorded between 14% and 27% monocotyledons in the diet of animals in S Mozambique. Captive studies have shown that daily forage consumption rates are in the order of 30.6 g/kg of body weight and fluid intake 106 ml/kg body weight (Maloiy & Clemens 1999).

Sunis prefer to eat in an alert posture, with the head raised, after wrenching parts off their stems: larger leaves and branches are sometimes shaken vigorously. Sunis have a high metabolic rate (Lawson 1986) and feed in short bursts interspersed with rests.

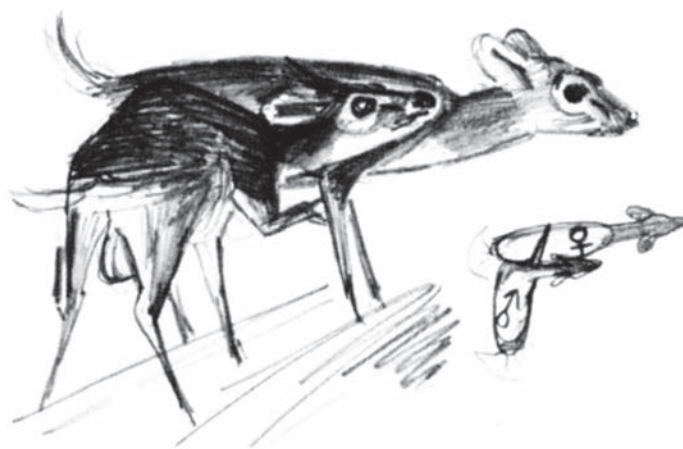
Social and Reproductive Behaviour Sunis occur solitarily or in pairs, and occasionally in groups. Pairs comprised 50% of all encounters in one study (M. Davies, in Kingdon 1982), while in KwaZulu–Natal 77% of sightings were of single adults and 12% of adult pairs (Lawson 1986). Sunis are territorial and defend territories of approximately 3 ha (Kingdon 1982); Lawson (1986) recorded territories of 0.5–1.0 for ♂♂ and 0.9–4 for ♀♀ in KwaZulu–Natal. Male territories have well-defined borders (with little overlap), while territories of ♀♀ often occur almost entirely within the territory of a ♂.

Territories normally appear to be exclusive to a pair or family group. Where more than one ♀ (up to four recorded) shares a territory, the single ♂ associates more closely with just one ♀. Both sexes contribute to dung deposits that tend to be on or close to boundaries. Deposits are visited, checked and augmented on a regular, often daily, basis. Both urine and dung pellets are added on each visit. The ♀ generally precedes the ♂ in urinating and then excreting pellets on established dung deposits; the ♂, when present, then follows, overlaying his contributions to the pile. Sunis approaching one another briefly touch noses and apparently sniff one another's face glands before parting. On meeting, a ♂ sometimes briefly licks the face of its preferred female partner. Mutual grooming is not commonly seen in free-ranging Sunis, but when it does occur takes the form of one individual grooming the head, neck and shoulders of another, which then reciprocates. Animals tend to lie up alone, although a ♂ may rest within sight of his ♀. There is no evidence for seasonal movements or changes in territorial boundaries.

Males actively defend their territories, and ♂♂ entering the territories of others are met with energetic grating of the horns on plants and chases in which the aggressor champs his jaws while trying to strike glancing blows or parry horn jabs. During such confrontations, contestants have been seen to use their long tongues to self-lick their facial glands. In captive groups that ranged free in a confined area of natural habitat, ♀♀ sometimes exhibited aggression towards others, lowering the head with ears drawn back as if ready to butt. In this position, black markings on the top of the ears simulate horns and such threat gestures commonly caused the threatened ♀ to retreat.

When disturbed, animals 'freeze' or else creep away with the head held low, walking carefully on the points of their hooves. Frights (which can be set off by such familiar stimuli as the choruses of colobus monkeys) precipitate a very fast, zig-zag rush, sometimes accompanied by a wheezing double screech, followed by a stop and total immobility. Normally, flight does not seem to take animals out of their known territory but two family groups confined in a one-hectare paddock in natural habitat accommodated to their confinement by maintaining two separate territories. A dense thicket in each of these territories offered all animals a choice of refuge during alarms or frights. However, each ♂ always escorted his favourite ♀ back to his territory after every scare.

When a ♀ comes into oestrus the ♂ follows her closely, at which time her normally limp tail is raised and wagged horizontally. During her postpartum oestrus the ♂ closely and continuously attends the ♀ for about 12 hours. Before mating, the ♂ commonly approaches the ♀ from the side, pressing his chest into her flank. He strokes or strikes her belly or ribcage with one foreleg until she stands still and permits him to mount her, very briefly, from the rear. A captive ♀



Suni *Nesotragus moschatus* male arresting female movement with 'laufschatz' or foreleg-lift.

gave birth lying down on her side and uttered some high-pitched bleats before the young came out. The placenta, which emerged 15 minutes later, was eaten immediately. The newborn young hides in thick vegetation and only emerges in response to the mother's soft bleat. The young makes a call that sounds like two marbles being ground together, so quiet that it is inaudible to the human ear at a distance of one metre; it may have ultrasonic components. The young finds the nipple with strong combing and champing movements and suckles strongly but very briefly. It can only suck through the very front of the narrow mouth. Any alarm sends the young in a fast, skulking run straight for cover with its ears back. As it gets older, the young emerges more frequently to seek or anticipate its mother. After suckling, she stimulates the young to excrete by licking the genital area and swallows its excreta. After weaning, juveniles begin to excrete on dung piles.

Sunis are not only alert to predators but seem to pay attention to the activity of monkeys, notably Angola Colobus *Colobus angolensis* and Guereza *C. guereza*. This attention often rewards the Sunis with a rich supply of fallen leaves and shoots.

Reproduction and Population Structure Breeding is known to occur in most months of the year. However, there is thought to be a birth peak between Nov and Feb in NE Tanzania (during the 'short rains' that follow the long dry season). This effectively ensures that both the mother and her offspring benefit from renewed growth. In captivity, Sunis exhibit no peak birth season (Spence 2003) and Lawson (1986) recorded mean age of ♀♀ at birth of the first young was 589 days and mean parturition interval 221 days; Pretorius *et al.* (1996) give mean age of ♀♀ at first birth as 472 days, and mean parturition interval as 209 days (which is similar to recorded birth intervals of 203 and 214 days for two captive ♀♀; Spence 2003). The oestrous cycle ranges from 20 to 25 days (Loskutoff *et al.* 1990). Gestation periods, recorded from two known instances of conception, were 172 and 192 days (Pretorius *et al.* 1996); Spence (2003) gives an estimated gestation period of 171–180 days based on captive animals.

Normally only one young is born at a time, with a birth weight of approximately 700–800 g. The lactation period is short and the young start nibbling at vegetation within a few days of birth (and

start ruminating at 30–32 days). Females mature at about a year; ♂♂ may be sexually potent before they are one year old but only acquire fully adult characteristics (full body size, enlarged face glands, sharp, annulated horns and a particularly sleek pelage) at about 14 months. The territorial ♂ expels young ♂♂ when they show the first sign of horns (about 6–8 months). Lawson (1986) reported that in captivity ♂♂ eight months of age had to be separated from adult ♂♂ because they started to fight. Young ♂♂ placed in separate enclosures showed no signs of overt fighting, although a definite dominance hierarchy was evident. However, the introduction of a young ♀ to the enclosure caused fighting.

In captivity or confinement, ♀♀ commonly remain with the parents after maturity and it is possible that some 'harem-like' wild groups include the female offspring of resident pairs. While some 50% of recorded encounters in one N Tanzanian study were of pairs, a surplus of ♀♀ in some localities was reflected in other single-male groups with 2–4 ♀♀. A higher ratio of ♀♀ in some populations is probably due to male deaths following fierce territorial contests. Male/female ratios appear to vary locally but were estimated to be in the region of 1 : 2.5 in the foothills of Mt Kilimanjaro (M. Davis pers. comm.). Captive animals have been recorded living to more than 13 years (Jones 1993, Weigl 2005).

Predators, Parasites and Diseases Suni remains are commonly found below the nests of Crowned Eagles *Stephanoaetus coronatus* (e.g. Brown 1966). Other species of large eagle, such as the Martial Eagle *Polemaetus bellicosus*, are also likely to take them. Other likely, but probably less frequent, predators include African Rock Pythons *Python sebae*, Side-striped Jackals *Canis adustus* and Leopards *Panthera pardus*. Sillero-Zubiri & Gottelli (1992) reported them being preyed on in the Aberdares Mts by Spotted Hyenas *Crocuta crocuta*.

Khalil & Gibbons (1976) recovered ten helminth species from Sunis in Kenya, two of which were new species of nematodes, *Trichostrongylus moschatus* and *Megacooperia woodfordi*. Boomker *et al.* (1991a) recorded nine nematode species from KwaZulu–Natal, South Africa, including two *Cooperia* spp., *Haemonchus vegliai*, *Setaria cornuta*, *Strongyloides papillosus* and two *Trichostrongylus* spp. Eight of these were new parasite records for the Suni in Africa, with the exception of *M. woodfordi* (probably a host-specific parasite). Golezardy & Horak (2006) recorded the ticks *Haemaphysalis parvata* and *Rhipicephalus kochi* from three animals in South Africa.

Conservation IUCN Category: Least Concern. CITES: Not listed.

Although very localized in an environment that is subject to much depletion (for wood, charcoal and farmland), Sunis remain widespread through much of their range, presumably aided by their ability to adapt to secondary degraded vegetation. However, domestic dogs do pose a problem for this species. For example, Sunis were common in the natural thickets of the Langata suburban properties of Nairobi in 1968. At that time few properties were fenced. However, in the next decade or so many were fenced with chain-link or wire netting through which Sunis could not pass. As soon as this happened, the Sunis were quickly eliminated by domestic dogs that they had hitherto managed to evade (I. Parker pers. comm.). Several studies that have reported on hunting of Sunis confirm the widespread use of dogs (e.g. Carpaneto & Fusari 2000, Cordeiro *et al.* 2005).

Sunis are well represented in the conservation areas of several eastern African countries, notably: Mt Kenya N. P., Aberdare N. P., Shimba N. P., Sokoke/Arabuko F. R. (Kenya), Udzungwa Mountains N. P. and other forest reserves in the Udzungwas, Ulugurus, Usambaras and Southern Highlands, Selous G. R., Lake Manyara N. P. and Jozani F. R. (Zanzibar) in Tanzania; Lengwe N. P. (Malawi); Gorongosa N. P. and Maputo G. R. (Mozambique); and Tembe N. P., Mkhuzi G. R. and Ndumo G. R. (KwaZulu–Natal, South Africa).

Measurements

Nesotragus moschatus

TL (♂♂): 699 (659–727) mm, n = 6

TL (♀♀): 692 (663–716) mm, n = 3

T (♂♂): 97 (91–110) mm, n = 6

T (♀♀): 96 (93–98) mm, n = 3

HF c.u. (♂♂): 197 (193–204) mm, n = 6

HF c.u. (♀♀): 195 (193–198) mm, n = 3

E (♂♂): 80 (77–84) mm, n = 6

E (♀♀): 75 (72–78) mm, n = 3

WT (♂♂): 5.0 (4.5–5.2) kg, n = 6

WT (♀♀): 5.4 (5.1–5.9) kg, n = 3

Mozambique (Lawson 1986)

Record horn length is 13.3 cm for a pair of horns from Mozambique (Rowland Ward)

Key References Hoppe *et al.* 1983; Kingdon 1982, 1997; Lawson 1986, 1989.

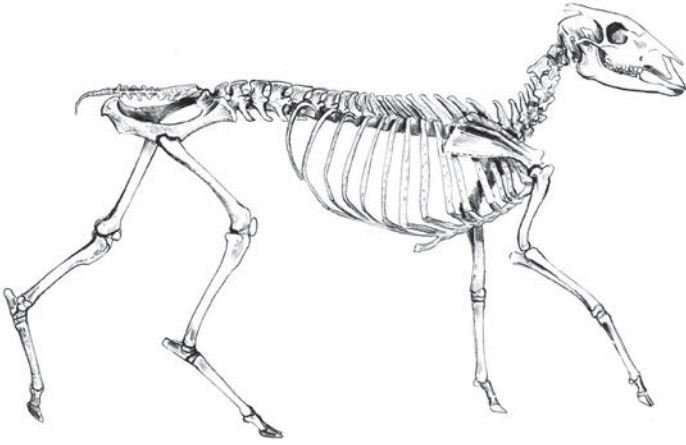
Jonathan Kingdon & Michael Hoffmann

Tribe CEPHALOPHINI

Duikers

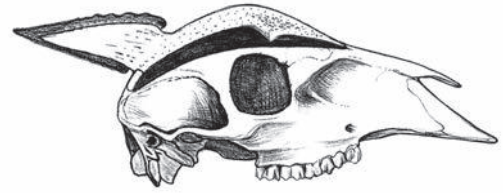
Cephalophini Blyth, 1863*. Cat. Mamm. Mus. Asiat. Soc., p. 167.

*Attribution of Blyth as the author, and not Gray, 1871, follows Grubb (2001a).



Weyns's Duiker *Cephalophus weynsi* skeleton.

The tribe Cephalophini includes the duikers, and, at least in the current work, comprises three genera and 19 species (see Grubb & Groves 2001 and Grubb 2005 for alternative recent classifications). Duikers are, and always have been, uniquely African forest antelopes. They have compact bodies and are small- to medium-sized animals, ranging in size from 3.5 to 80 kg in Jentink's Duiker *Cephalophus jentinki*. Both sexes (though not, normally, *Sylvicapra*) usually have short, simple horns and short wedge-shaped heads. The mouth is large, with a wide maw, which can, in most species, be correlated with eating fruit. Less obvious is their possession of brains that are larger and more complex than in any other bovid (Oboussier 1966, 1979). This is a clear indication that duikers are not simply a primitive group, and large brains also hint at the dependence of duikers on tracking events in the forest canopy, where most of their food derives from the wasteful foraging of arboreal animals, from wind and from gravity. The skull is characterized by massive enlargement and thickening of the frontal bones, which have expanded front and back with concomitant rooting of the horns in a more posterior

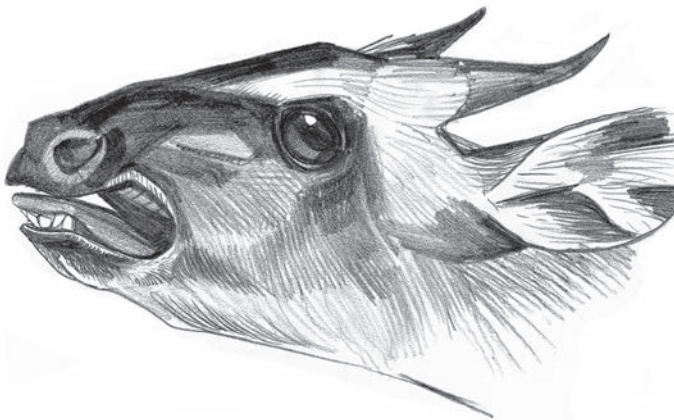


Weyns's Duiker *Cephalophus weynsi* forehead and horn sectioned to show exceptional thickening of frontal bone (from Kingdon 1982).

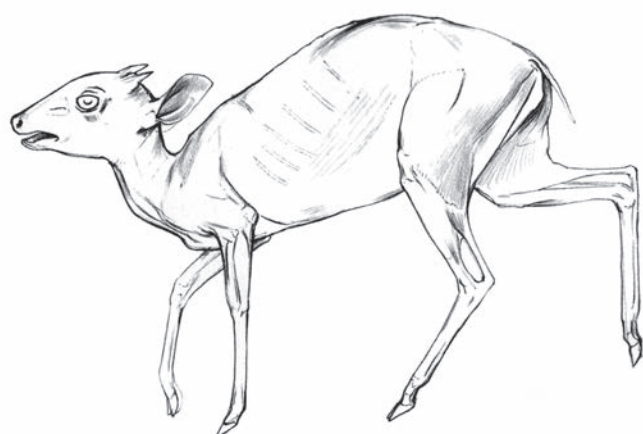
position. In some species there has been such heavy ossification of the frontals that it clearly serves as a shield and battering ram, a feature unique to duikers. Kingdon (1982) ascribed this frontal shield (and other peculiarities) to extensive remodelling following dwarfing in a remote ancestor.

All species have preorbital glands on the sides of their muzzle (with concomitant preorbital fossae), each of which has eight or more secreting pores that are aligned in roughly horizontal rows across the surface of the glands. These are unlike the single invaginated pockets of many other antelope groups (which are adapted to place long-lasting gobs of secretion on twigs or stems). In relation to the evolution of multiple pore-like preorbital glands it may be significant that the smallest of living *Neotragus* species, the Royal Antelope *N. pygmaeus*, has greatly reduced, but still mono-orificed, preorbital glands. This implies that if the earliest proto-duikers had minuscule glands there might have been more potential for restructuring of a semi-vestigial gland, which could help explain such a marked difference from most other Antilopinae. The small, multiple pores are 'smeared' on vertical stems, tree trunks or on other duikers. Some species have inguinal glands, under tufts of hair on the legs or between the hooves. General body proportions vary from species to species, but all follow a 'run and hide' strategy to escape predators and the length of their legs bears no comparison with open-country antelopes that escape danger by running. Females often larger than ♂♂. Females have two pairs of inguinal nipples. Further details specific to individual species are provided below in the individual species profiles. Wilson (2001) has provided a detailed overview of the duikers, of a sort well beyond the scope of the current work.

The affinities and supposed origins of duikers have generated more diverse suggestions than perhaps any other group of antelopes. They were once thought to be among the most primitive of bovids, mainly because they are relatively omnivorous and had 'remained' in the forest habitats that were once assumed to be the ancestral home of bovids. These assumptions pictured duikers forming some sort of phylogenetic bridge between chevrotains and bovids (Estes 1974). Making bovid-wide comparisons between different morphologies, scientists studying bovids have put forward their closest affinities as follows: (1) sister-group of the Bovinae (Gentry 1992); (2) in an intermediate position between Bovinae and Antilopinae (Jansen van Vuuren & Robinson 2001); (3) clustered with the non-Bovinae (Georgiadis *et al.* 1990, authors who did not specifically associate them with any other tribe);



Black-fronted Duiker *Cephalophus nigrifrons* facial features.

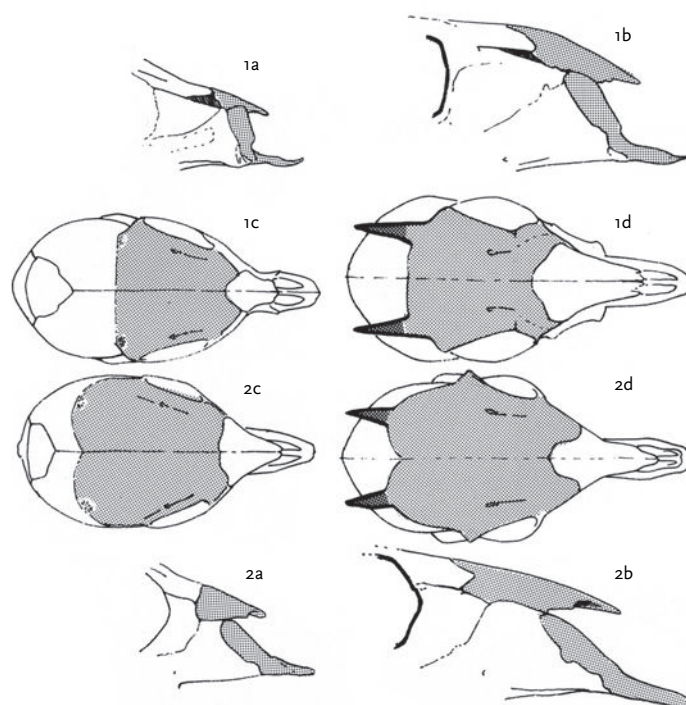


Aders's Duiker *Cephalophus adersi* myology.

(4) allied with the Reduncini (Gatesy & Arctander 2000a, Kuznetsova *et al.* 2002), a suggestion that was reiterated by Hernández Fernández & Vrba (2005); (5) with a clade containing reduncines, hippotragines and alcelaphines (Gatesy & Arctander 2000b); and (6) as sister taxon to the Klipspringer *Oreotragus oreotragus* (Hassanin & Douzery 1999, Matthee & Robinson 1999a, Hassanin *et al.* 2012), although evidence to the contrary was presented by Matthee & Davis (2001). The diversity of these suggestions derives from the mosaic of similarities and dissimilarities that seem as evident in the genes of duikers as in their gross morphology.

A different approach has been to turn to what duikers do that is different from other bovids and place those differences in the biogeographic and ecological contexts that might have led to this uniquely African radiation of at least 19 forest antelope species. Such an approach can then be compared with molecular data, particularly for clues as to which species and characteristics might be primitive and which specialized. For a start, where do duikers stand if they are, as genetic research suggests, not a basal, primitive group? Those antelopes retaining a predominance of primitive states are mostly small and their initial adaptation, on entering Africa, was not to moist forests, but to dry thickets; most significant of all, primitive Antilopinae were/are unambiguously folivorous. There is nothing in their biology to suggest that duikers could have evolved in such habitats and frugivory, their principal characteristic, could only have evolved within the equatorial forests of Africa, where most of them still live today. What kind of incremental progression could convert a dry, low, thicket-dwelling folivore in north-eastern or eastern Africa into moist, high-forest frugivores living mostly along the equatorial axis?

Ignoring any possibility of early changes in the fundamentals of antilopine diet, it becomes much more likely that the earliest lineage of antelopes to adapt to the forests of equatorial Africa remained folivorous. Such antelopes exist today, in the form of three species of dwarf antelope (*Neotragus* and *Nesotragus*), which do, indeed, retain primitive conditions, but it is important to remember that contemporary species can only hint at what happened amongst their ancestors some 17–15 mya. It is more likely than not that duikers share a very ancient ancestry with today's dwarf antelope species (or, according to some authors, from some unknown, extinct offshoot from the Oreotragini). It seems at first peculiarly counter-intuitive to accept that advanced ruminant folivorous diets could be 'primitive' whereas highly nutritive and easily digested fruit and seed diets are



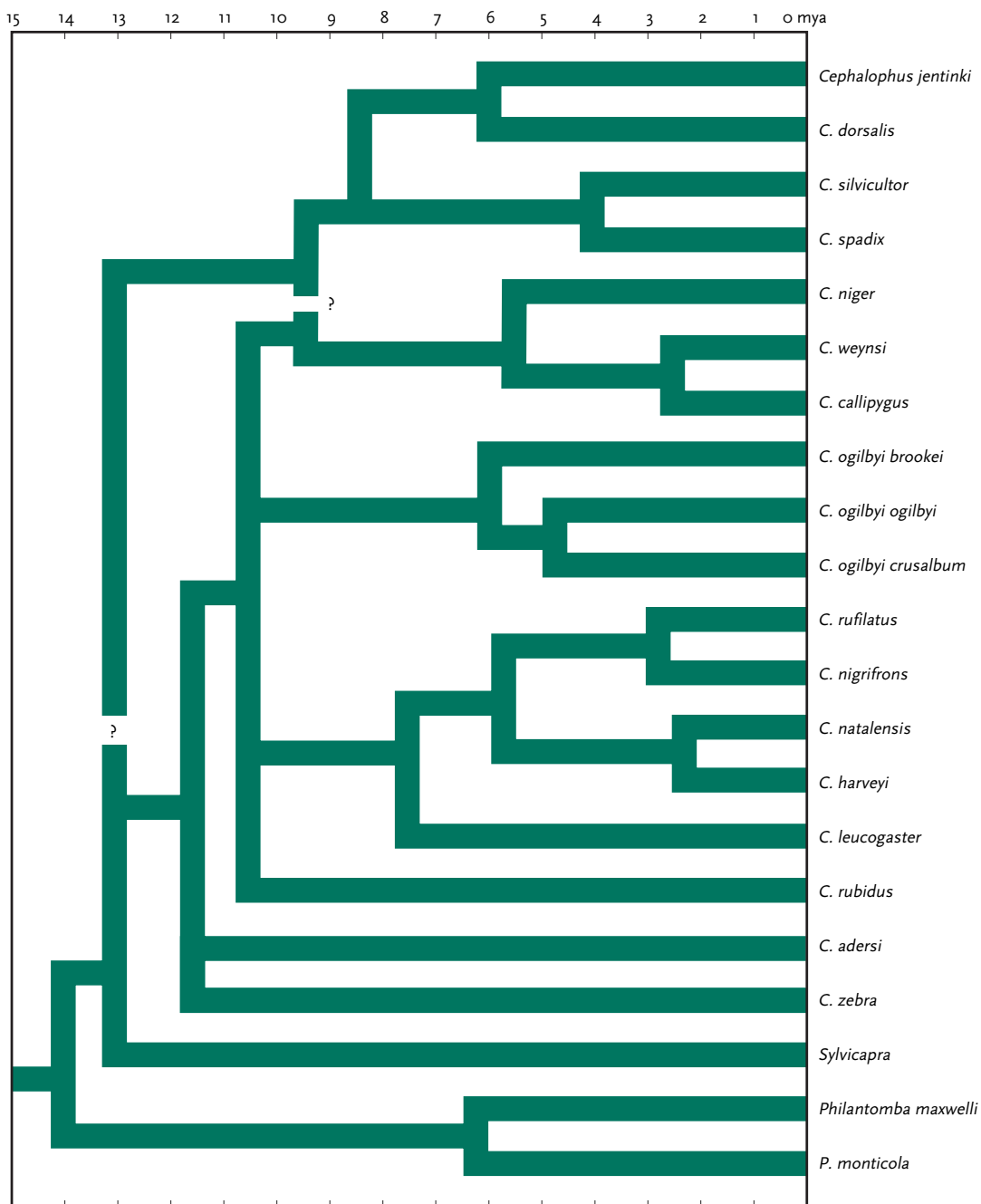
ABOVE: Differences in relationships of frontal, nasal and premaxilla in Neotragini and a duiker (Blue Duiker *Philantomba monticola*): 1a and 1b side view of muzzle in neonate and subadult Royal Antelope *Neotragus pygmaeus*; 1c and 1d, dorsal views of neonate Royal Antelope *N. pygmaeus* and adult Bates's Pygmy Antelope *N. batesi*; 2a and 2b profile views of neonate and adult Blue Duiker *P. monticola*; 2c and 2d dorsal views of neonate and adult Blue Duiker *P. monticola*.

BELOW: Superimposed skull outlines of Bates's Pygmy Antelope *Neotragus batesi* and Blue Duiker *Philantomba monticola*. (a) Three areas in which there are minimal differences in dimensions, i.e. nasals, parietal and tooththrow; (b) Three areas in which there are maximal differences in dimensions, i.e. in frontal, occipital and bullae, premaxilla.



'advanced' when it comes to duikers, yet this dietary staple in itself implies a specialist niche, dependent for its very existence on the presence of a diverse guild of arboreal forest frugivores.

Biogeographic and ecological interpretations of the beginnings of duiker evolution invoke multiple lines of evidence and can be measured against certain environmental constraints on what is or is not possible. What were the primary characteristics of a proto-duiker? At least three groups of antelopes show a rough progression from smaller conservative types to larger derived ones; a natural outcome since most ancestral Antilopinae were relatively small. Among duikers, the very small species are the most conservative (at least two species buffer shortages of fruit with leaves), while all the largest are the most derived and the most recently evolved (and for the most part, strongly frugivorous). Intermediate forms follow an almost linear progression from smaller to larger, and dwarfing is one mechanism whereby a leaf-eating herbivore can survive in high forest



Phylogenetic tree for Cephalophini (adapted from Jansen van Vuuren & Robinson 2001 and Hassanin *et al.* 2012).

where ground-level herbage is scarce. A dwarf ancestor for duikers is therefore wholly consistent with the facts.

The suggestion that duikers originate from diminutive ancestors has found some corroboration in molecular trees that show that the larger species are among the most recently evolved while the smallest are the more ancient, in the sense of being more deeply divergent (Jansen van Vuuren & Robinson 2001). The duikers are therefore likely to be a secondary radiation diverging from early Neotragini or Oreotragini. As for timing, Hernández Fernández & Vrba (2005) suggest duikers emerging at about 14 mya (similar to Hassanin *et al.* 2012), although the earliest fossils are only about 3 mya (Makapansgat, South Africa; Gentry 1978). Extended arguments for the duikers' origins were detailed in Kingdon (1982), and summarized in Kingdon (1997).

Most duikers live only in forest but some have adapted to more open, swampy or montane environments. Duikers are rare in the fossil record and there are no fossils to suggest that they ever crossed the Sahara, let alone left Africa. The species profiles that follow detail some very interesting forms of ecological partitioning among duikers. The proliferation of at least 19 living species (and probably more) involves both isolation, regional specialization and partitioning of the habitat by food type and seed-size, activity (diurnal and nocturnal, localized, dispersed) and, above all, size differences. All duikers are dependent, to a greater or lesser degree, on primates, birds and fruit-bats to dislodge the fruits, flowers and leaves on which they feed. Part of their alertness and 'strategic intelligence' is linked with this sensitivity to what is happening in the canopy.

Some duikers can clamber up sloping trunks or dense tangles. One group have specialized in skilled concealment (mostly during the day), relying on a short, fast dash to escape if found. These, the fibre duikers, the Bay Duiker *C. dorsalis* and Jentink's Duiker *C. jentinki*, have a different body build from other duikers (notably in their powerfully muscled hindquarters). Explosive leaping is less typical of species with more continuous exposure, but all can make prodigious leaps when pursued.

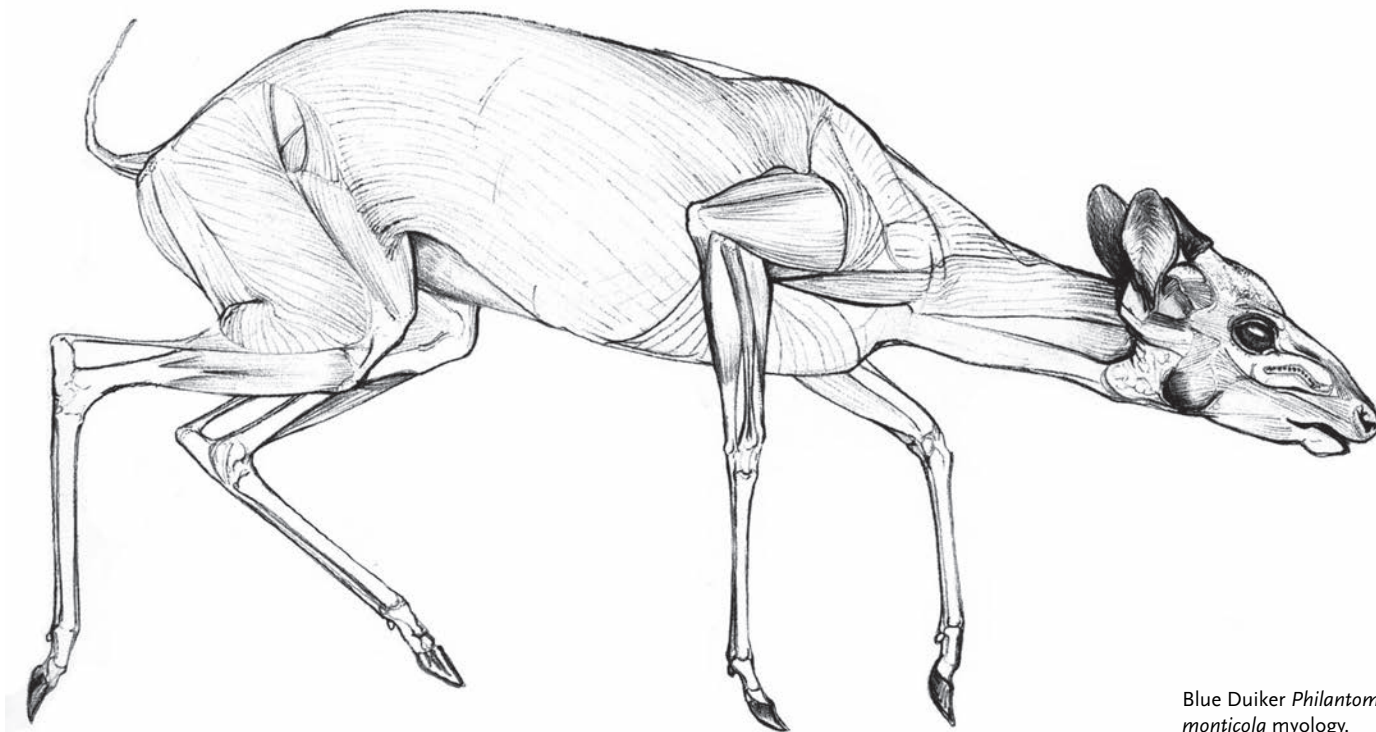
All species are thought to be territorial and most form close associations between the sexes, each excluding others of their own sex. The size of territories and degree of exclusivity, particularly along margins, probably varies a great deal. Well-trodden paths connect habitual feeding, ruminating, sleeping and refuge areas. All species use scents and vocalizations to regulate social contacts. Precocious young are born after a relatively long gestation. All are slow to reach full maturity, suggesting that prolonged learning may be necessary for successful exploitation of a difficult environment.

The thickened and enlarged frontal bones of duikers and their short, sometimes vestigial horns grow from further back on the skull than in other antelopes. This can be correlated with hard head-butting in some species, directed at rivals and (less commonly) predators and hard

fruits. Their reduced horns and other neotenuous features are further indications of dwarfed origins.

As an actively speciating group, some duiker species could be predicted to be actively expanding their range while others might be in competitive decline or subject to 'hybridization' with close relatives. The evidence for such processes taking place is detailed in some species profiles. However, all such possibilities are overshadowed by the massive and totally unregulated onslaught of the highly profitable bushmeat trade on all species. Duikers are easy to snare, net, call up to a lure, dazzle by flash-light and hunt with dogs. The rarer, large-bodied species are already close to extinction and many others are known to be in decline. As one of the most interesting and complex of bovid evolutionary radiations, they deserve much more attention than they have to date. The most likely of all predictions about duikers is the imminent extinction of many of the rarer species. With that extinction science and culture will be deprived of a vast store of information about the evolution of African forests and their inhabitants.

Jonathan Kingdon & Colin Groves



Blue Duiker *Philantomba monticola* myology.

GENUS *Philantomba*

Blue Duikers

Philantomba Blyth, 1840. In: Cuvier's Anim. Kingd., p. 140.

Traditionally, this genus has been regarded as a synonym or, at most, a subgenus of *Cephalophus*. However, Grubb & Groves (2001) regarded it as a valid genus and their cladistic analysis placed it as sister not to *Cephalophus*, but to *Sylvicapra*. Independently, Jansen van Vuuren & Robinson (2001), using two mtDNA sequences, found that *Philantomba* is sister to *Sylvicapra* + *Cephalophus*, with good bootstrap support.

Philantomba are diminutive duikers, the head and body being less than 75 cm in length. Characteristic is the thick mat of hair on the forehead, which is darker and more brown than the face itself. There is usually (but not always) a red or buff-coloured stripe above each eye. The pelage does not change with age; the hairs are uniformly coloured, usually some shade of brown, darker on the dorsum on the flanks, and there

is commonly a sharp transition between the dark and light tones on the haunch. As in *Sylvicapra*, the tail is even-haired, not tufted. The skull is small and delicate, relatively broad across the braincase and frontal region, and suddenly constricted on the rostrum, so that the anterior width of the nasals is only half that at the frontonasal suture. The occipital plane and paraoccipital processes are oblique; the orbits are somewhat tubular, and their dorsal rims protrude somewhat above the plane of the frontals (all these features are as in *Sylvicapra*). The preorbital fossa is very extensive, but shallow. The horns are very small and delicate, and upturned at the tips; in ♀♀ they are much reduced and often absent. In the pelvis the lengths of the ilium and ischium are approximately equal, as in *Sylvicapra*. Apart from these diagnostic features, other characters (sometimes also found in members of the genus *Cephalophus*) include the fully haired, untufted tail, the lack of inguinal glands, the absence of a true crest and the tendency to show reversal of the neck hair (Grubb & Groves 2001).

The genus includes two species with allopatric distribution: Maxwell's Duiker *Philantomba maxwelli*, which occurs west of the

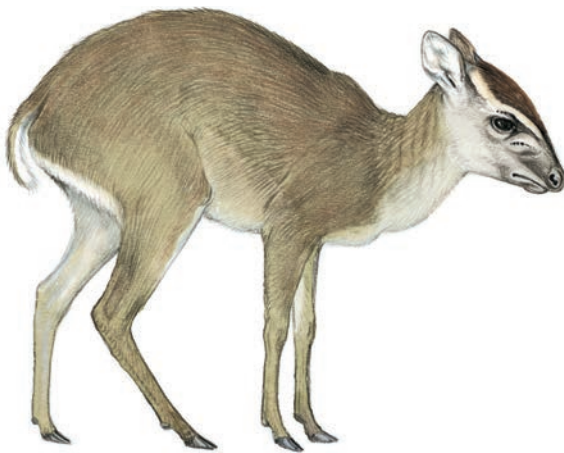
Cross R.; and Blue Duiker *P. monticola*, which ranges from east of the Cross R. to southern Africa. Note that as *Mammals of Africa* was being finalized, a species-level revision of the genus in West Africa, involving both morphology and genetic data, revealed the existence of a third species, Walter's Duiker *Philantomba walteri*, occurring in the Dahomey Gap (Togo, Benin) and the Niger Delta (Colyn *et al.* 2010). Although we have not been able to include a species profile, Walter's Duiker is intermediate in size between the larger *P. maxwelli* to the west and the smaller *P. monticola* to the east. Externally, the new species resembles *P. maxwelli* because of its relatively long tail (>15 cm), large pedal gland, a striking superciliary line, the absence of a strongly marked break on the haunches between the dark croup, light colored flanks and lower haunches. Craniometrically, *P. walteri* can be differentiated from the two other species in the genus by a clearly smaller nasal constriction and cranial height (Colyn *et al.* 2010).

Colin Groves

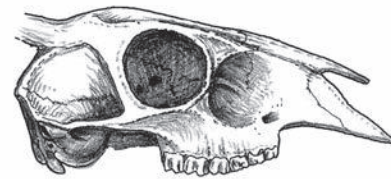
Philantomba maxwelli MAXWELL'S DUICKER

Fr. Céphalophe de Maxwell; Ger. Maxwellducker

Philantomba maxwellii (C. H. Smith, 1827). In: Griffith *et al.*, Anim. Kingd. 4: 267. Sierra Leone.



Maxwell's Duiker *Philantomba maxwelli*.



Lateral view of skull of Maxwell's Duiker *Philantomba maxwelli*.

The species is named for Sir Charles William Maxwell, who was Governor of Senegal in 1809 and then of Sierra Leone (origin of the type) in 1811.

Taxonomy Ansell (1972) and Ralls (1973) recognized three subspecies: the nominate form from Senegal and Gambia to Sierra Leone; *P. m. lowei* (including the form *danei*) from the islands in the Rokelle R. in Sierra Leone and with unknown limits; and *P. m. liberiensis*, from Liberia eastwards. Grubb & Groves (2001) recognize two subspecies: the nominate form, *P. m. maxwelli*, is distributed through the species range except for the Yatward and Sherbro Is., where it is replaced by the subspecies *P. m. danei*, which is smaller (skull length under 136 mm). Synonyms: *danei*, *frederici*, *liberiensis*, *lowei*, *philantomba*, *whitfieldi*. Chromosome number: $2n = 60$; Maxwell's Duiker has only acrocentric X chromosomes (Hard 1969, Robinson *et al.* 1996b).

Description Small-sized antelope varying in colour from light, sandy-brown to greyish-brown or brownish-black. The narrow and angular face tapers off to a small pointed muzzle. The upper jaw clearly surpasses the lower jaw and the mouth droops, which gives the Maxwell's Duiker a grim facial expression. There is no definite crest between the horns. The curved preorbital glands are heavily demarcated, and studded with as many as 25 pores. There is frequently a lighter brow-like line above the large black eyes. The oval ears are frequently fringed with white, and together with the tail, which is white below, are constantly flicked back and forth, making conspicuous fieldmarks. The belly and inside of legs are paler than the rest of the body. The slightly elongated rump and relatively narrow neck give a lighter build to this animal than to other duikers. The legs are very slim and relatively long, and the buttocks are angular. The tail is fully haired and untufted (Grubb & Groves 2001). There are no inguinal glands, and the well-developed pedal glands lie in a subcircular sac at the end of a narrow canal (Pocock 1910). Horns are short (seldom more than 6 cm), heavily ridged, thick at the base, and bent slightly inwards and backwards. Horns are frequently lacking in ♀♀, and when present are usually much shorter and less heavy at the base (Wilson 2001).

Geographic Variation

P. m. maxwelli: distribution as for species, but not present on Yatward and Sherbro Is. There is some evidence of geographical variation in anatomical features, but patterns of variation are complex (Grubb & Groves 2001). The frequency of nuchal hair reversal increases from west to east. Most measurements of skull size increase from east to west between Togo and Liberia, but there are discrepancies from this pattern in Ghana, and the pattern does not hold for the extreme eastern and western parts of the range. The length of horns in ♂♂ decreases from east to west, but again, Ghana does not entirely fit the pattern, and horns are largest in the extreme west. The proportion of ♀♀ with horns decreases westwards from 100% in Nigeria and Togo to only 5 out of 80 in Liberia, but there are few data for the west of the range. Geographical variation in coat colour is masked by a high degree of individual variation (Grubb & Groves 2001).

P. m. danei: Yatward and Sherbro Is. Small size: skull length 128–136 mm (cf. >136 mm in *P. m. maxwelli*); nasals 40–44 mm (cf. >45 mm in *P. m. maxwelli*); preorbital 64–65 mm (cf. >66 mm in *P. m. maxwelli*); and toothrow 36–41 mm (cf. >41 mm in *P. m. maxwelli*).

Similar Species

Philantomba monticola. The two species are separated geographically, with Maxwell's Duiker occurring to the west of the Cross R., and the Blue Duiker to the east. Blue Duikers are significantly smaller; according to Grubb & Groves (2001), the largest skull of a Blue Duiker they recorded was 139 mm, whereas this is closer to the minimum for Maxwell's Duiker; also differs in colour (with strongly marked break on the haunches between the dark croup and the light colour of the flanks and lower haunches; cheeks are darker and superciliary streaks less prominent); length of tail (usually less than 100 mm); a shallower, smaller pedal gland; and cranial characteristics (skull narrower across the zygomata; orbital borders more protuberant; rostrum more

constricted; narrower palate; free ends of nasals narrower on average) (Grubb & Groves 2001).

Distribution Endemic to Africa. Widespread within the Upper Guinean forest zone, in lowland forests and extending into forest–savanna mosaics, from W Gambia and SW Senegal east to the Cross R. in Nigeria (East 1999, Wilson 2001). Distribution is restricted by the drier savanna–sahel zone in the north. Since they do occur in gallery forests within savanna woodlands in parts of West Africa (e.g. N Côte d'Ivoire and SW Burkina Faso), it is reasonable to assume that they may occur in SW Mali, though there are no confirmed records to date (Wilson 2001). Their current distribution is probably not much changed from their historical distribution, although much of their original habitat has been modified or lost.

Habitat Found in mature and secondary forests, gallery forests and forest patches, coastal scrub and farmland (Aeschlimann 1963, Davies 1987, Newing 1994, 2001, Grubb *et al.* 1998). They have a preference for dense undergrowth, but occasionally penetrate into fields close to forest patches. They adapt well to farmland and in Sierra Leone they occur on montane grassland over 1400 m on the Loma Mts. The animals do not require permanent water within their territories, even if nursing, provided enough fresh fruits are available (Nett 1999).

Abundance Abundant throughout the forest zone in both mature forests and secondary vegetation, but decreasing where hunting pressure is high. Davies (1991) estimated population densities of 15–30/km² in mature logged forest in Gola N. P., Sierra Leone, and Wilson (2001) thought this was the most common antelope in the country. This is also the most common duiker in Côte d'Ivoire, where Newing (1994, 2001) recorded a density of 79/km² in a mixed, hunted farmland near Tai N. P. and 63/km² in lightly logged primary forest with minimal hunting, within the Park. Elsewhere in Côte d'Ivoire, Nett (1999) recorded 16–20/km² in heavily hunted and logged semi-deciduous forest patches in the eastern part of the country, and Hoppe-Dominik (1989) found 2.7/km² in the savanna–forest mosaics of Marahoué N. P. In the National Park of Upper Niger, Guinea, Maxwell's Duikers had the highest density (3.7/km²) of a total of ten species of ungulates present (Brugière *et al.* 2005). East (1999) suggested a total population size of 2,137,000 individuals – likely a conservative estimate.

Adaptations Maxwell's Duiker is the smallest and most opportunistic of seven sympatric duiker species in the Upper Guinean forest block. It inhabits even heavily degraded forest patches and hides in the dense cover of the exotic Akyempong weed species *Chromolaena odorata* (Newing 1994, 2001, Nett 1999). Wilson (2001) suggests that numbers may even have increased as a result of forest clearance for farmland and the spread of Akyempong. The success of Maxwell's Duikers in secondary vegetation types is doubtless made possible by a very broad diet including a large variety of small fruits and leaves, and an ability to adapt to a more leafy diet at times of fruit scarcity (Newing 1994). In contrast, the sympatric species are significantly larger than Maxwell's Duiker (Bay Duiker *Cephalophus dorsalis*, Black Duiker *Cephalophus niger*, Yellow-Backed Duiker *Cephalophus silvicultor* and Jentink's Duiker *Cephalophus jentinki*) and/or more restricted to mature forest (Zebra Duiker *Cephalophus zebra*,



Philantomba maxwelli

Jentink's Duiker and Ogilby's Duiker *Cephalophus ogilbyi*) or to secondary forest (Yellow-backed Duiker) (Newing 2001).

Foraging and Food Maxwell's Duikers are primarily frugivorous, but also eat leaves and mushrooms and may depend on leaves at times of fruit shortage. The two most comprehensive studies of feeding ecology to date are those of Hofmann & Roth (2003) and Wilson (2001). Hofmann & Roth (2003) examined 139 stomachs from the bushmeat market of Toumodi in Côte d'Ivoire. These authors recorded 78 different types of fruits eaten, with Maxwell's Duikers showing a particular preference for *Nauclea latifolia*, *Ficus capensis*, *Canthium vulgare*, *Blighia sapida*, *Griffonia simplicifolia*, *Alchornea cordifolia*, *Phoenix reclinata* and *Spondias mombin*. Wilson (2001) examined 250 stomachs from bushmeat markets in Ghana, and listed 33 species of fruit, including *Ficus* spp., *Solanum* spp., *Blighia* spp. and *Uvaria* spp.; all fruits eaten were from cultivated lands, secondary forest or savanna. Both Wilson (2001) and Hofmann & Roth (2003) recorded an average of three fruits per stomach. In the eastern semi-deciduous forests of Côte d'Ivoire, hunters named the fruits of *Ricinodendron heudelotii*, *Strombosia glaucescens*, *Trichilia monadelpha* (= *T. heudelotii*), *Ficus exasperata*, *Celtis adolfi-fridericii* and *Ceiba pentandra* as their primary food sources (D. Nett pers. obs.). Aeschlimann (1963) examined two stomachs of Maxwell's Duikers in the evergreen forest zone and found seeds of *Turraeanthus africanus* and *Pycnanthus angolensis*; fruits of *Musanga cecropioides*; leaves of *Griffonia simplicifolia*, *Ficus barteri*, *Baphia nitida* and *Fagara parvifolia*, and several varieties of mushrooms. Newing (1994, 2001) listed 26 species of fruits found in eight stomach samples and a further two species eaten during direct observations of free-living animals in mature forest. Hofmann & Roth (2003) and Wilson (2001) both recorded animal matter in the form of ants from stomachs.

In suitable habitats Maxwell's Duikers are said to follow groups of colobus monkeys and guenons, in order to profit from fallen fruits. The guenons include the Lesser Spot-nosed Guenon *Cercopithecus (cephus) petaurista*, Mona Monkeys *Cercopithecus mona* and Diana Monkeys *Cercopithecus diana*. In heavily degraded forests Maxwell's Duikers are often found in close association with squirrels, which may take over the primates' ecological role when the latter are no longer abundant (Nett 1999). Maxwell's Duikers have a bimodal diurnal activity pattern with peaks in the early morning and late afternoon.

Social and Reproductive Behaviour Maxwell's Duikers live in monogamous pairs or occasionally polygamous groups (e.g. Tai N. P.; Newing 1994) with or without young, with a common territory. Newing (1994) recorded home-range sizes of about 5 ha in mature forest and 3.6 ha in secondary vegetation, while Nett (1999) recorded 18.4 ha in relict forest. Territory size seems to increase with the age of the animal (e.g. 12.5 ha for one subadult compared with an average of 20 ha each for three adult animals). Territory size also appears to decrease in accordance with increasing available resources (especially fruits) and shows no seasonal changes. Overlap between territories of neighbouring groups is small (0–23%) and temporary. In a shared territory the borders of the female's territory sometimes lie outside the male's, suggesting that both sexes mark and defend against conspecifics (Nett 1999). Newing (1994) observed physical fights between neighbouring ♂♂ and chases of ♂♂ or male–female couples by neighbouring ♂♂. Ralls (1975) observed Maxwell's Duikers in captivity and documented agonistic behaviour in both

sexes, even though fighting was much more aggressive in ♂♂. The author described Maxwell's Duikers as extremely pugnacious with the ability to chase even other antelopes such as the larger Bay Duiker. Territorial boundaries are marked by middens and scent-marking. Mutual scent-marking with the preorbital glands strengthens the bonds of a monogamous pair; it is also carried out by two individuals of the same sex prior to heavy fighting. All marking is carried out by both sexes.

Courtship is initiated by the ♂, who pursues the ♀ and attempts to lick the base of her tail while the ♀ may be lifted off her hindfeet. Ralls (1973) reports that the tail of an oestrous ♀ is often wet and frayed from the male's intensive chewing and biting. Circling nose-to-tail, flehmen (lip curling) and laufschiag (leg tapping) precede mounting attempts; the ♀ only stands still once she is ready to mate, and copulation is very brief. Maternal care is reduced to a minimum in Maxwell's Duikers even though the mother grooms the young by licking its fur. The young does not follow its mother but is laid up in a protected spot until about three months old, when it begins eating significant amounts of fruits and leaves (Wilson 2001, H. Newing pers. obs.).

Two kinds of nasal vocalization accompany fighting, sexual and anti-predator displays: an often repeated short snorting and the louder intense alarm-call. The latter seems to have disappeared in some areas where hunting pressure is heavy, since hunters try to attract the animals by imitating these calls, and even playbacks no longer elicit a response. This might be an adaptation of Maxwell's Duikers to human pressure (Nett 1999).

Reproduction and Population Structure Births occur throughout the year. In Côte d'Ivoire and Nigeria there is a suggestion of two birth peaks – one in the main dry seasons, from Dec to Mar, and one from Jul to Sep (Aeschlimann 1963, Happold 1987, Newing 1994), but Wilson (2001) could not find any evidence of a birth peak in Ghana. Of 131 uteri examined by Wilson (2001), every one had the foetus implanted in the right uterine horn, although ovulation took place from either ovary. A single young is born that resembles the parents in colour, and weighs between 600 and 950 g (Aeschlimann 1963, Wilson 2001).

Basic information on length of gestation period and age at sexual maturity remains contradictory. Numerous authors have cited a gestation period of 120 days (e.g. Aeschlimann 1963, Ralls 1973); however, Kadjo (2000) gave gestation as 188 days and Wilson (2001) gives a mean gestation length of 205 days ($n = 4$; range 198–213). Hofmann *et al.* (1998) recorded first oestrus in ♀♀ of a heavily hunted wild population at six months. Wilson (2001) recorded four captive ♀♀ conceiving at between 8 and 12 months, and earliest successful mating by a ♂ at 10 months. However, Kadjo (2000) recorded first oestrus only at 18 months. Females become receptive 3–5 days after giving birth.

Hofmann *et al.* (1998) found a male to female sex ratio of 1 : 1.04 in the markets of Toumodi, Côte d'Ivoire ($n = 1721$) and 1 : 1.11 in Kumasi, Ghana ($n = 858$). The ratio of adult to young was 1 : 2.86 and 1 : 1.75, respectively. The maximum birth rate was 1.8 young/year/reproductive ♀; 81–93% of the adult ♀♀ were pregnant. These high figures may have been due to hunting pressure. Maxwell's Duikers can live for more than ten years in captivity (Aeschlimann 1963, Ralls 1973).

Predators, Parasites and Diseases Common predators are African Rock Pythons *Python sebae*, Crowned Eagles *Stephanoaetus coronatus*, Leopards *Panthera pardus* and African Golden Cats *Profelis aurata*. Helminths recorded include nematodes (genera *Ostertagia*, *Bunostromum*, *Setaria*, *Skrjabinodera*, *Trichuris*) and cestodes (*Avitinella*) (Round 1968, Kamara 1975). In a study of the ticks associated with wild mammals in Ghana, Ntiemoa-Baidu *et al.* (2005) recorded the following species from duikers in Ghana: *Haemaphysalis parvata*, *H. leachi*, *Ixodes aulacodi*, *I. cumulatimpunctatus*, *I. moreli*, *I. muniensis*, *Rhipicephalus senegalensis*, *R. simpsoni* and *R. ziemanni*. Maxwell's Duiker has not been identified as an important vector for diseases of domestic animals and humans although it is doubtless susceptible to all major ungulate diseases.

Conservation IUCN Category: Least Concern. CITES: Not listed.

Maxwell's Duikers are widespread and seem to support hunting pressure better than other duikers, due to a broad tolerance of habitat disturbance and diet (Newing 2001). Nevertheless, they are among the most hunted ungulates in much of their range, and around 30% of the hunted ungulates in secondary forest zones in Côte d'Ivoire are Maxwell's Duikers, which means an average of nearly 3% of the hunted mammal populations in this region (Nett 2002). Some 30% of the delivered biomass in the bushmeat restaurants in the region of Taï N. P. is made up of Maxwell's Duikers (Caspary *et al.* 2001). Intense poaching in Comoé N. P. in Côte d'Ivoire led to numbers of Maxwell's Duikers declining by more than 90% within 20 years, resulting in a low density estimate of 0.04/km² (Fischer & Linsenmair 2001a). Brugière *et al.* (2005) also recorded significant decreases in this species between 1997 and 2002 (whereas other ungulate species increased or remained stable), and attributed this to changes in hunting patterns in the area. Whereas hunters used to come from the whole of the Haut Niger region and hunted in large groups for several weeks in the Mafou forest prior to its gazettelement as a core area of the Park in 1997, solitary or small groups of hunters now originated

mainly from nearby villages and enter the forest for short periods (less than a day), hunted opportunistically (almost exclusively by night), and hence focused on the most abundant species.

Maxwell's Duikers are still common in several protected areas in their range, particularly Ziama and Diécké Forest Reserves, National Park of Upper Niger and Mt Nimba Strict N. R. (Guinea), Gola N. P. and Tiwai Island Game Sanctuary (Sierra Leone), Sapo N. P. (Liberia), Taï, Azagny, Mont Sangbe and Marahoue National Parks (Côte d'Ivoire) and Kakum, Bia and Mole National Parks (Ghana).

Measurements

Philantomba maxwelli

TL (♂ ♂): 860 (820–940) mm, n = 184

TL (♀ ♀): 890 (830–950) mm, n = 91

T (♂ ♂): 140 (120–160) mm, n = 184

T (♀ ♀): 150 (120–160) mm, n = 91

HF c.u. (♂ ♂): 200 (180–240) mm, n = 184

HF c.u. (♀ ♀): 210 (180–230) mm, n = 91

E (♂ ♂): 62 (58–69) mm, n = 184

E (♀ ♀): 60 (58–69) mm, n = 91

Sh. ht (♂ ♂): 350 (320–420) mm, n = 184

Sh. ht (♀ ♀): 360 (330–420) mm, n = 91

WT (♂ ♂): 7.5 (6.5–11.2) kg, n = 184

WT (♀ ♀): 8.0 (6.5–12.0) kg, n = 91

Ghana (Wilson 2001)

Includes only non-pregnant ♀ ♀. Average body weight for 131 pregnant ♀ ♀ was 9.1 kg (range 7.5–12.6)

Maximum recorded horn length is 6.6 cm for a pair of horns from Sierra Leone (Rowland Ward)

Key References Aeschlimann 1963; East 1999; Nett 1999, 2002; Newing 1994, 2001; Ralls 1973, 1975; Wilson 2001.

Dorothe Nett & Helen Newing



Philantomba spp. frontal views of Maxwell's Duiker *P. maxwelli* (left); Blue Duiker *P. monticola conigicus* (centre); and Blue Duiker *P. m. monticola* (right). Several current subspecies may well prove to be full species.

Philantomba monticola **BLUE DUIKER**

Fr. Céphalophe bleu; Ger. Blauducker

Philantomba monticola (Thunberg, 1789). Resa uti Europa Africa, Asia ..., 2: 66. South Africa, 'Lange Kloof'; since identified as borders of Western and Eastern Cape, Uniondale and Humansdorp Dist., Langkloof, 33° 48' S, 23° to 24° 30' E; see Grubb (1999: 21).



Blue Duiker *Philantomba monticola* adult female.

Taxonomy Ansell (1972) recognized 16 subspecies, noting that the range limits and validity of many require further investigation. Grubb & Groves (2001), in their review of the classification of the duikers, recognized 12 subspecies, divided in two major groups, a grey-legged and a red-legged group (see Geographic Variation). Synonyms: *aequatorialis*, *aequinoctialis*, *anchietae*, *bakeri*, *bicolor*, *caerulea*, *caffer*, *congius*, *defreisi*, *fuscicolor*, *hecki*, *ludlami*, *lugens*, *melanorheus*, *musculoides*, *minuta*, *nyasae*, *pembae*, *perpusilla*, *pygmaea*, *ruddi*, *schultzei*, *schusteri*, *simpsoni*, *sundevalli*. Chromosome number is $2n = 60$, the same as *P. maxwelli* (Hard 1969, Robinson *et al.* 1996b).

Description The smallest duiker in Africa, which varies greatly in colour and has differentiated into a large number of regional and insular forms. Blue Duikers have large eyes, somewhat swollen nostrils, small ears, lined with off-white hair, and a very wide, flexible mouth. The forehead profile is relatively flat. The pelage varies greatly in tonality and colour ranging from near black in some subspecies to slate-grey, bluish-grey and various shades of brown. The length and density of hair-cover varies between populations. The lower legs are generally lighter in tone than the back and the black

hooves are narrow and pointed. There are no inguinal glands, and the pedal gland (which secretes a whitish liquid) has a simple orifice, unlike that of Maxwell's Duiker *P. maxwelli* which has a subcircular sac at the end of a narrow canal between the hooves (Pocock 1910). The preorbital gland exudes secretions through a series of pores that are arranged along an oblique arc across the swollen gland (the pores in most other duikers have an almost straight alignment). The secretion, while fresh, has a pale bluish-grey colour, and the chemical compounds are discussed in detail by Burger & Pretorius (1987). The tail, which is vigorously whisked up and down (not side to side), has very conspicuous white hair lining on its underside and a nearly black dorsal surface.

Compared with Maxwell's Duiker, the skull is notably smaller, shorter (typically <139 mm) and narrower, but with orbits somewhat tubular; the rostrum is sharply constricted so that the palate and snout are narrower, and the nasals narrow strongly towards the tips. The horns, which are very short (usually 4–5 cm), are well ridged around their bases and tend to be partially concealed under a crest of elongated hair. Females in some populations have horns, but they may be absent in others (Grubb & Groves 2001).

Geographic Variation The enormous range of variation within this species was bisected into two super-divisions by Grubb & Groves (2001), who used leg colour as a distinguishing feature. The first grouping, from northern parts of the species' range, was characterized by greyish legs (*aequatorialis*, *congicus*, *lugens*, *melanorheus*, *musculoides* and *sundevalli*). The more southern grouping was identified by its reddish legs (*anchietae*, *bicolor*, *defriesi*, *hecki*, *simpsoni* and *monticola*). Another geographically based arrangement (Kingdon 1997) was broadly consistent with the above, but recognized seven main populations plus three montane and three insular isolates. Here, we selectively combine the two treatments, which also approximate to the 'Northern/Southern Forest Faunas' model suggested in Kingdon (1971). Characteristics of subspecies follow Grubb & Groves (2001).

Southern group:

- P. m. monticola*: Western Cape and Eastern Cape Provinces of South Africa. Lighter than *bicolor*, light grey or fawn; legs reddish-tan; haunches slightly reddened with very little transition from rump.
- P. m. bicolor* (includes *fuscicolor*): Zambezi south to KwaZulu-Natal, South Africa. Intermediate in tone between *hecki* and *lugens*; flanks normally dark rufous-orange.
- P. m. hecki*: Malawi, Zambia (east of the Luangwa Valley), N Mozambique. Back light fawn-grey; flanks light red, and rump medium to dark brown; there is a fairly distinct transition line to the reddish-fawn of haunches; legs reddish-tan; underside white. Intergrades with *lugens*.
- P. m. anchietae*: N Angola. Back pale grey-brown; flanks grey with hint of red; legs pale red-fawn; haunches red grading into grey of flanks anteriorly; there is a well-marked transition on the haunches to the rump; tail black; underside broadly grey-white, extending half-way down the legs. The largest subspecies overall.
- P. m. defriesi*: Zambia, west of the Muchinga escarpment. Paler than *hecki*, with a distinct dark grey zone on the mid-dorsal region; flanks pale red-fawn, and haunch and legs noticeably reddish; rump and tail dark; white below, extending down inner surface of upper half of the legs. Intergrades with *aequatorialis*.
- P. m. simpsoni*: between lower Congo R. and Kasai R. Flanks red-brown, fading to a broadly white belly; haunches redder than flanks; legs brownish, pale on inner surfaces; there is a well-marked face-stripe. Females occasionally lack horns. Intergrades with *anchietae* and *defriesi*.

Northern group:

- P. m. congicus*: from east bank of the Cross R. to the Congo R. across the Oubangui into DR Congo as far east as Lisala; south through Cameroon, Gabon and Congo to the Mayombe district of DR Congo, north of the Congo R. mouth. The dorsum is bright, grey-brown to black in colour, the flanks pale greyish, and the haunches browner; a clear dark-brown stripe marks the transition from the blackish-brown rump to the haunches; underside white; cheeks red-tinged.
- P. m. aequatorialis*: from the contact zone with *congicus* east and south-east across DR Congo into Uganda, at least to Bunyoro and probably to the Nile R.; north-east to Imatong Mts in Sudan and south, in DR Congo, as far as Namoyo. Range in the west bounded by the Congo R. Drabber and browner than *congicus*; underside of rump usually light grey; transition on haunches less sharp than in *congicus*, but still noticeable. Females usually hornless.

P. m. musculoides: E Uganda to Kenya, as far as the Rift Valley. Also on Mt Elgon. Darker than *aequatorialis* on dorsum, but flanks lighter; the haunch stripe is less well marked. Females are apparently always hornless.

Montane isolates:

- P. m. lugens*: Southern Highlands of Tanzania, to the border of Malawi (but the Nyika plateau population is difficult to assign with any certainty to either *lugens* or *hecki*). Very dark, grey-brown, with little contrast between flanks and dorsum; rump black, with no perceptible transition to the dark haunches; legs dark, except for light streak down front; underside greyish; hair generally reversed on mid-line of neck.
- P. m. schusteri*: Eastern Arc Mts of Tanzania. Uniformly coloured, with fawn-tinted medium-grey body colour extending to head and down legs, but slightly paler on throat and cheeks; rump has small, but graduated, near-black patch immediately adjacent to tail; hair is sleek and of medium length and density on both body and neck; upper part of inner hindlegs and belly white; upper lips pale, lower lips dark; pencil-thin pale brow-stripe above orbit.

Insular forms:

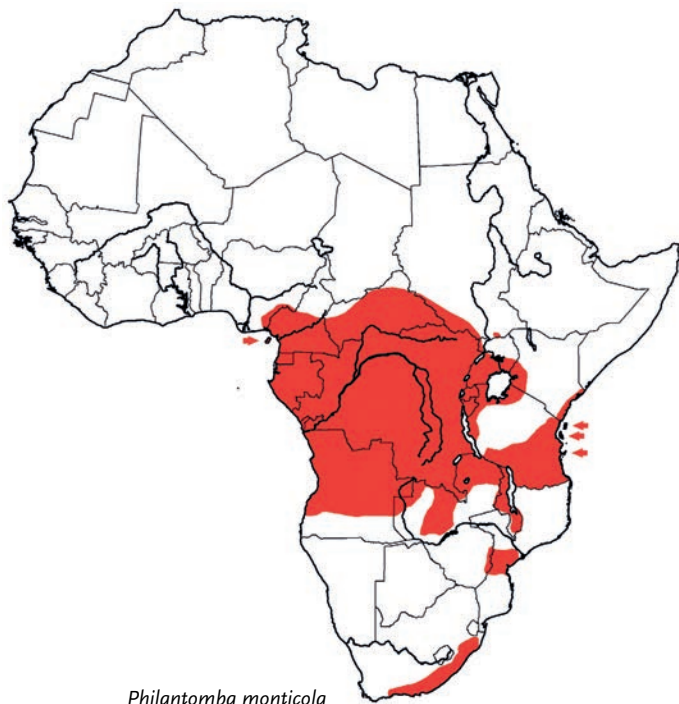
- P. m. sundevalli* (includes *pembae*): islands of Pemba, Mafia and Zanzibar (Unguja); also coastal East Africa (specimens from Shimba Hills and Sokoke). Light brownish colour, with little differentiation between dorsum and flanks; white below.
- P. m. melanorheus*: Bioko, Equatorial Guinea. Related to the form *congicus*, but with black dorsum, pinkish-grey flanks. Fur long and thick. Very small size.

Similar Species

Philantomba maxwelli. Allopatric, occurring only west of the Cross R. Significantly larger (skull length usually >139 mm), and with longer tail, as much as 160 mm in length, whereas in Blue Duiker few specimens have tails longer than 100 mm. Also differs in colour, lacking the strongly marked break on the haunches between the dark croup and the light colour of the flanks and lower haunches; the cheeks are lighter and superciliary streaks more prominent (Grubb & Groves 2001).

Distribution Currently, many populations occur nearly contiguously across all of central Africa, but the two major clusters of subspecies, as described above, represent a significant and potentially long-standing geographic separation. Past climatic fluctuations are likely to have fragmented both northern and southern types, but two principal barriers appear to have maintained the primary north-south divide. These barriers are the Congo R. in the west and the semi-arid corridor that, in East Africa, separates well-established, south-eastern, and mainly coastal, biota from a more recently expansive, predominantly western and equatorial biota (Kingdon 1971, 1982, 1990).

Until recently, the Blue Duiker ranged throughout much of central, eastern and southern Africa. Localized populations occurred wherever suitable forest and thicket existed and this is still one of the few species of duiker that continues to survive over most of its historically known range (East 1999). In the west, the species occurs eastwards from the Cross R.; Happold (1987) mapped the Niger R. as the western



limit, but the Blue Duiker seems to be absent or extinct in the intervening area, although Maxwell's Duiker occurs (see Wilson 2001 for discussion of western limits). This species then ranges east through the forest and ecotone belts of S and C Cameroon, Gabon, Equatorial Guinea (including the island of Bioko), Congo, Cabinda (Angola), most of DR Congo, across S Central African Republic and locally north, with populations in gallery forests and dry relict forest patches in the north of the country. Recorded at 8° 17' N on the Koumbala R., in Manovo-Gounda-St Floris N. P. (Malbrant & Maclatchy 1949), through extreme SW Sudan (Azande lowlands) and SE Sudan (Imatong and Dongotona Mts). Its range in East Africa comprises a number of disjunct populations in forest patches of S and W Uganda, W Kenya and E and S Tanzania and possibly in W Rwanda and Burundi, as well. The species is absent from the dry country east of L. Tanganyika, but occurs again in the coastal forests and scrub of Mozambique, Kenya and in Tanzanian forests. Andanje *et al.* (2011a) have confirmed the presence of the species in low numbers north of the Tana R. in the Boni-Dodori forests in N Kenya, a range extension of some 200 km.

The Blue Duiker occurs on the islands of Pemba, Zanzibar and Mafia (Moreau & Pakenham 1941, Pakenham 1984, Kock & Stanley 2009) and there have been somewhat implausible suggestions that one or more of these isolates could have been the result of human introduction. It is also found in forested areas of the Tanzanian Southern Highlands (including Ufipa) and the Eastern Arc Mts (Usambara, Uluguru and Udzungwa). The species' southern range includes localized populations in N and C Angola, where the current distribution is not well known (but is mapped south to at least 15° S by Crawford-Cabral & Veríssimo 2005), through remnant forests and thickets in Zambia, Malawi, E Zimbabwe and parts of C Mozambique on both sides of the Zambezi (East 1999, Wilson 2001). In South Africa, this species is primarily confined to the evergreen forest and thicket along the coast and adjacent hinterlands from N KwaZulu–Natal to the eastern Western Cape Province; there are no records of the Blue Duiker occurring west of George (Wilson 2001). Some

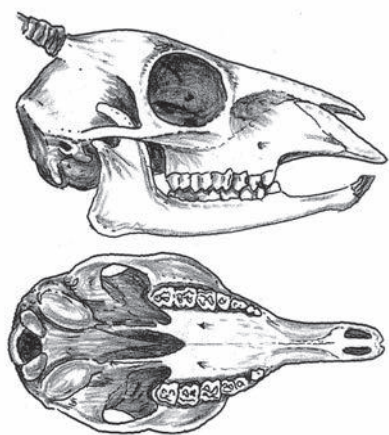
authors (e.g. Bowland 1990) make mention of Blue Duiker in the Magaliesberg Mts in Limpopo Province, but Rautenbach (1982) never recorded them anywhere in the former Transvaal. There are, as yet, no confirmed records from Swaziland (Monadjem 1998) and none from southern Mozambique (Smithers & Lobão Tello 1976), suggesting a break in distribution from N KwaZulu–Natal to E Zimbabwe/C Mozambique.

Habitat Thrives in a wide range of forested and wooded habitats, including mature and secondary forests, gallery forests, dry forest patches, coastal scrub farmland and regenerating forest from sea level up to 3000 m. Bowland (1990) found the species in *Podocarpus* mist forests on the KwaZulu–Natal coast. In eastern Africa and eastern DR Congo, the species has a preference for areas with dense undergrowth, but animals that were living at exceptionally high densities in Gabon were thought to prefer areas with relatively little undergrowth (Dubost 1980). Blue Duikers can persist in small patches of modified or degraded forest and thicket, even on the edge of urban centres. Availability of free-standing water is not an essential habitat requirement (Dubost 1980, Mockrin 2010).

Abundance Usually the most abundant duiker in communities where it occurs, and co-exists with up to seven other small ungulate species (including up to five other duikers) in some central African forests. Dubost (1980) recorded densities of 70/km² in a small area (74 ha) at Ipassa, Makokou, in NW Gabon, though it is unlikely that such high densities can be extrapolated over larger areas. In the Ituri Forest, DR Congo, non-hunted populations surveyed on 5 km² study areas range from 21/km² in mixed evergreen forest, to 10/km² in large stands of mono-dominant *Gilbertiodendron dewevrei* forest, representing about half the total small ungulate population in a community of eight species and 17–18% of small ungulate biomass (Hart 2000). Most population surveys report densities from 5 to 35/km² across the species' range, with the exception of some very small populations in isolated habitats in southern Africa (Payne 1992, Bowland & Perrin 1994, Hart 2001, Newing 2001, Wilson 2001, Lannoy *et al.* 2003). East (1999) estimated total population size at more than 7 million animals.

Adaptations The ecological and demographic success of Blue Duikers is made possible by several factors, not least among which is their extraordinary fecundity, which, in turn, seems to depend upon their ability to maintain a high nutritional plane across a wide range of habitats. Blue Duikers' consistently good metabolic and reproductive condition is assisted by a rumen anatomy (e.g. densely papillated rumen and fungiform papillae) that is typical for antelopes with concentrated nutrient diets (Faurie & Perrin 1995), but the animals are also sustained by an exceptionally broad diet. In addition to small fruits, seeds, gum, fungi and fallen flowers, they eat standing and fallen foliage, including, remarkably, dry fallen foliage especially when fruits are in short supply (Kingdon 1982, Hart 1985, Newing 2001, Wilson 2001).

Possible explanations for such dietary adaptability are more complex than would appear at first sight. For example, their small body size allows them to occupy smaller patches of habitat and exploit dispersed food sources, but the combination of small size and a more leafy diet is counter-intuitive, even contradictory, in the



Lateral and palatal views of skull of Blue Duiker *Philantomba monticola*.

sense that most ruminant bovids become *better* able to cope with difficult foliage diets the *larger* they are: yet this *small* duiker is *better* able to sustain itself on dead leaves than many of the larger duikers.

Philantomba is a basal group that derives from the earliest beginnings of the duiker radiation (Jansen van Vuuren & Robinson 2001). Therefore, the Blue Duiker's ability to shift to a leafy diet may be as much a reflection of its phylogenetic history as a proximate or late specific adaptation. Duikers are thought to derive from small, already folivorous ancestors with the larger species having made ever-more decisive secondary shifts into frugivory and omnivory (Kingdon 1982). In the course of evolution the folivorous habits of early, small duikers would have pre-adapted them to buffer temporary shortages of the more nutritious elements in their diet. This residual flexibility, deriving from their folivorous ancestry, might have combined with their small size to give them advantages over less flexible competitors.

It is possible, therefore, that the ecological success of the Blue Duiker is of very long standing. Furthermore, a long evolutionary history, relative to other duikers, could have special implications for understanding progressive adaptation by some Blue Duiker populations to the localized conditions of their region or phytogeographic zone. This offers scientists unique opportunities to study refinements of physiological adaptation along several parameters or gradients (such as altitude, latitude, relative humidity or vegetation type) as well as the role of genetic drift or selection in isolates.

Here is an economically important forest mammal that spans an enormous geographic range, has adapted to strong seasonal changes on the forest floor while regional populations have further refined their adaptation to quite localized conditions. While this duiker remains reasonably numerous across most of its far-flung range the opportunity should be seized to try to understand the foundations for its extraordinarily wide range and sustained ecological success. Wilson (2001) has pleaded for an intensification of research on digestive physiology and reproduction in duikers (and on this species in particular), before it is too late.

The most eye-catching feature of this species' behaviour is the continuous flagging, up and down, of the tail, the fringe of which is composed of slightly crinkled white hairs that reflect light exceptionally well. In appropriate lighting conditions this flashing resembles a discrete heliographic signalling device. Quite remarkably for a species that characteristically spends much time alone, this flashing (which in the



Blue Duiker *Philantomba monticola*.

dim lighting of the forest understorey may be the only visible feature of an otherwise sombrely coloured animal) would appear to be oriented towards other animals in its dispersed community, including individuals that share a territory.

Of special interest is the development of horns in the ♀♀ of some populations and their absence in others. Extrapolating from the Klipspringer *Oreotragus oreotragus*, it is possible that recently, or at some time in the past, there was a correlation between high population densities and the development of female horns. Given the very substantial differences in density that have already been recorded, this subject offers opportunities for interesting and fundamental research.

Foraging and Food Blue Duikers feed selectively from the forest floor on a wide diversity of ripe and unripe fallen fruits and seeds. They also eat freshly fallen foliage, flowers, pieces of bark, fungi, resin (in particular exudates from *Albizia* spp.) and some animal matter (Wilson 2001). Of 18 stomachs examined by Wilson (2001) in Chirinda Forest, Zimbabwe, the average stomach contained 75% fruits, 15% browse, 5% flowers and 5% fungi. In Gabon, foliage averaged 20% of rumen contents collected throughout the year, while over 67% of contents consisted of small fruits and seeds measuring 0.5–2 cm, the balance being made up of flowers, animal matter and fungi (Dubost 1984). Gautier-Hion *et al.* (1980) recorded that stomach contents contained 79% fruit, 20% leaves and very small quantities of animal matter, flowers and gum. On the other hand, in KwaZulu-Natal, Bowland (1990), also from an analysis of stomach contents ($n = 12$), found that about 70% was made up of dicotyledonous leaves and 23% seeds and fruits, probably because fruit was an unreliable resource whereas freshly fallen leaves were available year-round and abundant. Similarly, Hanekom & Wilson (1991) reported that dicotyledonous leaves constituted 57% of stomach contents from Tsitsikamma N. P., South Africa. None the less, Bowland (1990) recorded a strong correlation between fruit and freshly fallen leaves in the diet, suggesting a much greater preference for the former. Animal matter is not uncommonly recorded in stomachs (Grimm 1970, Gautier-Hion *et al.* 1980, Dubost 1984, Wilson 2001), and Dubost (1984) witnessed Blue Duiker hunting ants by licking them off the ground; ingestion of

Diptera was less common, although duikers were seen snapping at them in flight.

In Chirinda Forest, the fruits of the various *Ficus* species were the most favoured fruits, with duikers eating large numbers of fruits (one stomach contained over 65 *F. chirindensis* fruits); other fruits eaten included *Croton sylvaticus*, *Dovyalis macrocalyx*, *Rauvolfia caffra* and *Diospyros abyssinica* (Wilson 2001). In Uganda, the seeds and fruit of the genera *Maesopsis*, *Ricinodendron*, *Cordia*, *Musanga* and *Pycnanthus* and the leaves of the genera *Mammea* and *Mildbraediodendron* have been recorded as preferred foods (Kingdon 1982). Most of these genera occur in the Ituri Forest and have been recorded in duiker diets (Hart 1985). Other important foods recorded in the Ituri Forest include fruits and seeds from a variety of species in the families Caesalpiniaceae, Sapotaceae, Sapindaceae, Sterculiaceae, Rubiaceae, Ulmaceae and Euphorbiaceae. The seeds of *Pancovia harmsiana*, *Landolphia* spp. and *Cola* spp. are frequent in the diet. Blue Duikers prefer a number of fruits only at an unripe stage, notably *Klainedoxa gabonensis*, *Irvingia grandifolia* and *Blighia welwitschii*, all large trees that regularly abort large portions of developing fruit crops at an early stage. When ripe, these fruits are too large for Blue Duikers to handle, though they are eaten (and in the case of *K. gabonensis* and *I. grandifolia*, the seeds dispersed) by the larger duiker species (Hart 1985). The species also joins many other primary consumers by concentrating on seeds of *Julbernardia seretii*, *Cynometra alexandri* and *Gilbertiodendron dewevrei* during periods of mast fruiting, and body fat levels rise during these periods (J. A. Hart pers. obs.). Blue Duikers, like the larger duikers, though to a lesser extent, forage on several species of fruits with large armoured seeds (*Ricinodendron heudelotii*, *Chrysophyllum pruniformes*, *Celtis adolfi-friderici*, *Canarium schweinfurthii*) that they regurgitate during rumination and disperse (Hart 1985, Feer 1995).

In feeding trials with captive animals, Blue Duikers were consistently selective and had reduced capacity to digest structural carbohydrates compared with several of the larger duiker species (Hart 1985, Faurie & Perrin 1993, Newing 2001, Plowman 2002). Preferences of forest fruits and seeds determined by paired food choices in trials were not correlated with any single nutritional or chemical constituent (Molloy & Hart 2002). Blue Duikers preferred fruits over foliage, but when confronted with less preferred fruit choices, they increased foliage intake to a greater extent than larger species (White-bellied Duiker *Cephalophus leucogaster* and Bay Duiker *C. dorsalis*). Fruits and seeds with high levels of tannins and indigestible fibre were preferred if they also contained readily digested simple carbohydrates and protein. Blue Duikers produce large quantities of saliva, suggesting a capacity to bind and limit the effect of some digestion inhibitors and toxins. High dietary diversity may prevent rumen fermentation from being overwhelmed by any specific plant toxin in the foods.

Blue Duikers forage slowly and methodically over small areas, picking over the forest floor for individual food items; they browse standing vegetation only infrequently. In common with other duikers, they locate and follow groups of colobus monkeys and guenons, as they pass over their home-range. The duikers feed from fruits, leaves and other plant parts that fall beneath the primates. Activity peaks in the early morning and late afternoon with relative inactivity in the middle of the day and at night (Bowland & Perrin 1995, Wilson 2001). Blue Duikers are variably active at night, possibly on a seasonal basis (Bowman & Plowman 2006).

Social and Reproductive Behaviour Pairs or small groups live permanently on small home-ranges (Dubost 1983, Bowland & Perrin 1995). Territories may be grouped in loose aggregations and animals appear to form a dispersed social unit possibly composed of related individuals. Dubost (1980) found that territories on a 74 ha study area in Gabon with a very high density of Blue Duikers were exclusive and averaged 2.5–4 ha. He noted that discontinuities in the terrain, such as large fallen trunks, small streams (wet or dry) and the pathways of larger animals served to demarcate boundaries. At the heart of each territory was a regularly inhabited zone or core area from which brief excursions were made, mainly to feed on temporary food sources.

Core home-ranges of radio-collared Blue Duikers in the Ituri Forest ranged from 2.6 to 11.9 ha and were similar in size for both ♂♂ (mean = 6.2 ha, n = 10) and ♀♀ (mean = 6.0 ha, n = 9), which is not dissimilar from a hunted population in Congo (Mockrin 2010). Males and ♀♀ in adjacent home-ranges spent over one-third of their time together. Subadults of both sexes dispersed away from the maternal home-range. Dispersal distances were <1 km, and mostly less than 500 m for 21 animals monitored in mixed forest (Hart 2000), whereas 2 of 17 collared animals dispersed >1 km in a monitored population in mono-dominant *Gilbertiodendron dewevrei* forest (Mockrin 2010). Neighbouring radio-collared individuals sometimes aggregated into temporary groups of four to five animals, in particular when pursued by hunters.

Of 11 ♂♂ and 12 ♀♀ monitored by Dubost (1980), only one, a subadult ♀, changed her mate, indicating that couples generally tend to be stable and maintain permanent pair-bonds. He found that young ♀♀ left the parental home-range at age 1–1.5 years old whereas ♂♂ tended to stay on until they were nearly two years old and fully mature, at which point they appeared to depart voluntarily. In spite of apparent tolerance within families, Dubost found that resident ♂♂ were intolerant of other fully adult ♂♂ on their territories and captured adults of either sex were extremely aggressive to any adults placed in the same pen. Dubost found that the ♂ of a mated pair greatly reduced the time spent with his mate immediately after parturition and he even observed one or two unknown subadult ♂♂ keeping company with postpartum ♀♀.

Blue Duikers of both sexes mark tree trunks, branches and other objects in their territories with their preorbital glands. Dung may be somewhat aggregated in a home-range, but they do not create dung middens. Adult ♂♂ and ♀♀ and young of both sexes greet, groom and mark each other by touching their facial glands upon contact (Dubost 1980, Bowland 1990, Wilson 2001). Blue Duikers make a highly distinctive 'sneeze-whistle', which is commonly uttered when the animal has been disturbed and is running away. Populations of hunted duikers whistle more than those that are less hunted, the latter often moving away without signalling (Croes *et al.* 2007). The whistle is mimicked by hunters, and actually serves to attract animals, suggesting that this species-specific loud call is a generalized auditory advertisement (Kingdon 1982). A less distinctive and relatively quiet snort signifies a lower level of excitement. Individuals apparently seeking contact with another animal utter a soft groan, especially ♂♂ in pursuit of ♀♀ (Dubost 1983). Animals also stamp their forefeet, which may release secretions from pedal glands between the hooves, and ♂♂ grate their horns on plant stems.

Courtship is initiated by the ♂ who follows the ♀ closely and practises laufsclag (leg tapping) when the ♀ permits it. Females that



Blue Duiker *Philantomba monticola*.

are not in oestrus tend to evade the ♂ and keep their tail down. If pursuit of an unreceptive ♀ is sustained she may even utter a 'sneeze-whistle' (Dubost 1983). Animals bleat in distress and are said to make cat-like yowls. After birth the young does not follow its mother but keeps hidden until it is about three months old. The temporary absenteeism of ♂♂ after the birth of their mate's lamb has been interpreted as a mechanism to reduce risks of predation on the young (Kingdon 1982).

Reproduction and Population Structure The gestation period has been variously estimated at 4–7 months, with estimates based in part on figures for the similar congeneric Maxwell's Duiker. Aeschlimann (1963) gives a gestation period of four months or about 120 days. Mentis (1972) reports a figure of 167 days, a figure similar to the 188 days recorded by Kadjo (2000). Dittrich (1972) reports 205 days, the same figure cited by von Böhner *et al.* (1984) and Wilson (2001). The latter author notes that he determined gestation based on 19 known instances where copulation was observed and the day of birth recorded. An analysis of foetal growth rates of Blue Duiker in the Ituri Forest supports a gestation period of 120–150 days, with a lower likelihood of a gestation period over 200 days (J. A. Hart pers. obs.). Shorter gestation periods would also be consistent with the relatively high fecundity observed in a number of populations. Animal keepers at Epulu Okapi Station who maintained a colony of Blue Duikers over a number years also report (unpublished) that gestation is about four months. New observations, possibly supported by hormone studies, will be required to clarify gestation period for this species.

Von Böhner *et al.* (1984) reported that, in captivity, ♂♂ are sexually mature at nine months, and ♀♀ at 6–17 months; Hofmann *et al.* (1998) recorded first oestrus in ♀♀ of a heavily hunted wild population at six months. Wilson (2001) notes that female Blue Duikers usually become sexually mature before 13 months, and that the earliest a ♀ became sexually mature was eight months. He notes that ♂♂ become sexually mature much later than ♀♀, from 11–14 months.

Births occur throughout the year (Brand 1963, von Ketelhodt 1973, 1977a, Dubost & Feer 1992, Wilson 2001) with lowered birth rates around the dry season. A single young is born. Full-term foetuses in the Ituri had mean weight of 726 g (range 590–950, $n = 13$) or 13.2% of mean maternal body weight. There is a postpartum oestrus of 3–5 days following birth (OIA 1991). Wilson

(2001) reports an inter-birth interval of 202–248 days ($n = 32$ captive births), while von Ketelhodt (1977a) reports a mean inter-birth interval of 266 days in captive animals. In a multi-year project inspecting animals killed by local hunters in the Ituri Forest, 78.6% of 196 adult ♀♀ presumed to be multiparous were pregnant and 28% were both pregnant and lactating, the highest percentage of the six species of duikers occurring at the site (other species ranged from 0 to 25% for adult ♀♀ both pregnant and lactating). Composition of Blue Duiker milk is reported on by Taylor *et al.* (1990) and von Ketelhodt (1976b). Young are reported to be weaned in five months. Captive animals have lived for 16 years (Weigl 2005).

Using mark-and-release in an area of undisturbed rainforest (near Makokou, NE Gabon), Dubost (1980) determined that 62% of the population were reproductively mature animals (of even sex ratio) with 38% immature, i.e. less than one year old. Over one-third of young died in their first year of life, whereas adult annual mortality rates ranged from 7.3 to 10.4% (and see Hart 2000).

In the Ituri Forest, sex ratios in a heavily hunted population were even but were skewed toward ♂♂ (1.28 : 1 and 1.22 : 1) in two unhunted populations. Pre-reproductive individuals represented 33% of an unhunted population in mixed forest, but less than 18% of an unhunted population in mono-dominant *Gilbertiodendron dewevrei* forest. In the latter forest type, duikers also had lower mortality and higher rates of emigration (Hart 2000). In unhunted populations, female Blue Duikers reach maturity at about the same time that their third molar (M3) erupts. Females in hunted populations mature earlier, with 20–45% of subadults with the second molar only erupted with full udder development or pregnancy. Less than 5% of ♀♀ with the second molar erupted were sexually mature in the unhunted populations (Hart 2000).

Predators, Parasites and Diseases Common predators include the African Rock Python *Python sebae*, the Crowned Eagle *Stephanoaetus coronatus* and the Leopard *Panthera pardus* (Wilson 2001). Wilson (2001) reported Crowned Eagles being a major predator in NE Zambia, and several other studies of the diet of Crowned Eagles have recorded Blue Duikers as being important prey items (Jarvis *et al.* 1980, Boshoff *et al.* 1994; and see Vernon 2001); predation by these raptors is also reported in Uganda and Tanzania (J. Kingdon pers. obs.). Blue Duikers represented less than 5% of eagle prey in one survey in the Kibale Forest, in an area with a very high primate biomass, and where primates were the dominant eagle prey (Mitani *et al.* 2001). Leopards and African Golden Cats *Profelis aurata* are primary predators in the Ituri Forest and Blue Duikers were the single most abundant prey species in felid diets. However, they were not killed disproportionately in relation to their abundance, and were not the most selected prey (Hart, J. A. *et al.* 1996). Annual predation rates of 2.3 kills per km² and 1.1 kills per km² were recorded over a four-year study of radio-collared animals monitored in mixed and mono-dominant forest, respectively (Hart 2000). Annual per capita predation rates of Blue Duikers were 14–34% those of the larger duikers, which are selected prey of Leopards. In Tsitsikamma N. P., Hanekom & Wilson (1991) reported Blue Duiker remains found in 27% of Leopard scats and 7% of Caracal *Caracal caracal* scats.

In a health evaluation of 95 individuals of five species of duikers (including 37 Blue Duikers) in the Ituri Forest, all the animals examined were healthy and in physically good condition. Faecal parasite ova

were detected in about one-third of animals examined, comparable with frequencies in most other duiker species. Serologic titres for bluetongue, epizootic haemorrhagic disease, infectious bovine rhinotracheitis and leptospirosis were recorded, indicating widespread exposure to these diseases (Karesh *et al.* 1995).

Round (1968) provided a checklist of helminth parasites recorded from Blue Duiker at the time, including *Haemonchus lawrencei*, *Oesophagostomum eurycephalon*, *Setaria caelum*, *S. dipetalamotoides*, *S. labiotapapillosa*, *Acuaria dartevelli*, *Moniezia expansa* and *Stilesia hepatica*. Jooste (1984) reported additional parasites from three animals taken in E Zimbabwe, including *Cooperia chabardi*, *Trichostrongylus axei*, which Boomker *et al.* (1986) also recorded from a Blue Duiker from Tsitsikamma N. P. Boomker *et al.* (1991b) reported on helminth parasites of three Blue Duikers from KwaZulu–Natal, including: *Taenia hydatigena*, *Gonglynesia* sp. and several *Trichostrongylus* spp. The only record of an arthropod parasite in Blue Duiker is that of a *Rhipicephalus* sp. recorded by Karesh *et al.* (1995).

Conservation IUCN Category: Least Concern. CITES: Appendix II.

Arguably the most important wild ungulate economically and ecologically in Africa, the Blue Duiker is one of the most frequent species reported in bushmeat surveys across the continent (Wilson 2001) and withstands hunting pressure better than most of the larger duikers (Hart 2000, Waltert *et al.* 2006, Van Vliet *et al.* 2007). Unlike many of the other forest duikers, Blue Duikers tolerate and even thrive in a range of human-modified habitats, even in the vicinity of settlement, and often persist well in small habitat patches. However, some South African populations may be vulnerable to isolation and local extinction due to habitat fragmentation (Lawes *et al.* 2000), while the long-term decline since the mid-1970s of at least one Blue Duiker population in the coastal Cape forests is attributed to decreasing habitat quality associated with raising ambient temperatures brought on by climate change (Seydack *et al.* 1998). In East Africa, Blue Duiker are now relatively rare in the Eastern Arc Mts, being apparently absent from Nguru, Ukaguru, Rubeho and Pare. In the Udzungwa Mts, it has a very localized occurrence, but it is generally absent from lowland forests, such as Matundu. In some places this may be due to poaching, but competition with very abundant Sunis might be another factor in localities where trapping pressure is still light (F. Rovero pers. comm.). None the less, Blue Duikers occur in large and stable numbers in many protected areas across the bulk of the species' range (East 1999).

Blue Duikers adapt well to captivity (Bowman & Plowman 2006) and have been considered as potential candidates for domestication and for use as a ruminant model in research (OIA 1991). However, singleton births and high aggression levels between adult ♂♂ limit their potential for husbandry.

Like other duikers, the Blue Duiker is largely dependent on the rain of plant parts falling from the canopy. This derives, in large part, from the activities of arboreal mammals such as primates and fruit-bats, and of birds. How the elimination, or depletion, of arboreal animals might affect duikers is unknown. The difficulties of inferring effects of hunting on duikers are compounded because heavy hunting hits both arboreal and terrestrial fauna and the details of interactions between arboreal and terrestrial communities are seldom taken into account.

Measurements

Philantomba monticola

TL (♂♂): 715 (627–731) mm, n = 10
 TL (♀♀): 700 (645–727) mm, n = 10
 T (♂♂): 75 (64–83) mm, n = 10
 T (♀♀): 78 (61–81) mm, n = 10
 HF c.u. (♂♂): 170 (156–190) mm, n = 10
 HF c.u. (♀♀): 165 (150–185) mm, n = 10
 E (♂♂): 55 (52–60) mm, n = 10
 E (♀♀): 56 (53–61) mm, n = 10
 Sh. ht (♂♂): 340 (330–360) mm, n = 10
 Sh. ht (♀♀): 350 (320–370) mm, n = 10
 WT (♂♂): 4.5 (4.0–5.3) kg, n = 10
 WT (♀♀): 5.4 (3.8–6.1) kg, n = 10
 KwaZulu–Natal, South Africa (Wilson 2001)

TL (♂♂): 675 (630–700) mm, n = 10
 TL (♀♀): 680 (650–710) mm, n = 8
 T (♂♂): 88 (79–91) mm, n = 10
 T (♀♀): 88 (83–95) mm, n = 8
 HF c.u. (♂♂): 175 (165–180) mm, n = 10
 HF c.u. (♀♀): 171 (170–185) mm, n = 8
 E (♂♂): 56 (50–59) mm, n = 10
 E (♀♀): 55 (50–60) mm, n = 8
 Sh. ht (♂♂): 340 (320–350) mm, n = 10
 Sh. ht (♀♀): 340 (330–350) mm, n = 8
 WT (♂♂): 4.8 (3.9–5.4) kg, n = 10
 WT (♀♀): 5.3 (4.0–6.5) kg, n = 8
 Chirinda Forest, Zimbabwe (Wilson 2001)
 Maximum recorded horn length is 7.3 cm for a pair of horns from Irumu in DR Congo (Rowland Ward)

Key References Bowland 1990; Dubost 1980, 1983; Hart 1985, 2000; Kingdon 1982; Mockrin 2010; Wilson 2001.

John A. Hart & Jonathan Kingdon

GENUS *Sylvicapra*

Common Duiker

Sylvicapra Ogilby, 1837. Proc. Zool. Soc. Lond. 1836: 138 [1837].

These are the 'bush duikers', which appear to have reversed many of the deep-forest adaptations of the Cephalophini as a whole, such as the wedge-shaped form and the swept-back horns. They are slenderly built, with long legs (particularly the distal segments) and have a longer neck than other duikers. With *Philantomba*, this genus shares the elongated ischium, the evenly haired (untufted) tail, the somewhat curved horns, the somewhat tubular orbits, and the oblique occipital plane and paraoccipital processes. On the other hand, the hairs of the pelage are agouti-banded, and the hairs on the forehead are restricted to a coronal tuft, as in *Cephalophus*. The horns, which are largely restricted to ♂♂, have more of an upright direction than in other duikers, and the coronal tuft is dominated by forwardly directed hairs. The dorsal profile of the

skull is straight, rather than convex as in most other duikers, and the nasal opening is enlarged.

According to Jansen van Vuuren & Robinson (2001), this genus is not, as has been previously supposed, the most phylogenetically distinct of the duikers (that position belongs to *Philantomba*). Further, recent molecular evidence reveals that *Cephalophus* is paraphyletic with respect to *Sylvicapra* (Hassanin *et al.* 2012). Normally, a single species is recognized in this genus, but two or more could prove to be valid; for example, Grubb & Groves (2001) suggested that the taxon *coronata*, from far West Africa, may be a distinct species.

Colin Groves

Sylvicapra grimmia COMMON DUIKER (GREY DUIKER, BUSH DUIKER, GRIMM'S DUIKER)

Fr. Céphalophe de Grimm (Céphalophe couronne, Céphalophe du Cap); Ger. Kronenducker.

Sylvicapra grimmia (Linnaeus, 1758). Syst. Nat., 10th edn, 1: 70. 'Habitat in Africa'; based on a specimen seen by Grimm in the fort at Cape Town (Thomas 1911: 153) so now known to be South Africa, Western Cape Prov., Cape Town.



Common Duiker *Sylvicapra grimmia*.

that he thought corresponded well with general biogeographic patterns, while allowing for high-altitude isolates of lowland parent populations as well as supposed hybrid swarms from 'overlap zones'. Meester *et al.* (1986) listed six subspecies for the southern African sub-region. Grubb & Groves (2001) recognized 14 subspecies (including one undescribed form from Mt Kilimanjaro). Wilson (2001), who examined thousands of skulls and skins in many museums and dozens of live animals throughout the species' range, concurred with this treatment, which is followed here. As the distribution of *S. grimmia* is continuous in sub-Saharan Africa and some forms show individual variation, there are obviously substantial intergradations between different subspecies or regional populations and it is currently impossible to accurately delineate boundaries between the subspecies listed under Geographic Variation. Synonyms: Grubb (2005) lists 38 synonyms. Chromosome number: $2n = 60$; the X chromosome is a metacentric (Robinson *et al.* 1996b).

Description The Common Duiker is a medium-sized animal with a body colouration that varies from light grey in Botswana through many ranges of grey, yellow-ochre to almost red on the Nyika Plateau in Malawi to specimens in West Africa that are grey on the hindquarters to rufous coloured on the shoulders. In Malawi, Mozambique, E Zambia and even parts of Zimbabwe a distinct white ring occurs around the eyes (hence the name *orbicularis* for the subspecies occurring in that region). The colour of the ears varies, with some animals having a great deal of white inside the ears and others no white at all. The ears are comparatively long and pointed. A long tuft of hair occurs on the head and in many cases it is very long and pointed and in other animals short and 'square-topped'. Colour of the frontal tuft varies from black to grey and even rufous. A dark-coloured frontal blaze is found in almost every animal, but

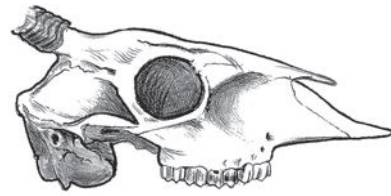
Taxonomy Haltenorth (1963) recognized 19 subspecies of *Sylvicapra grimmia* and these, with some changes, were accepted by Ansell (1972). However, Ansell indicated that the validity and distributional limits of many were doubtful. Kingdon (1982, 1997) broke down more than 30 named forms into eight regional groupings

occasionally no dark band occurs at all (especially in animals from East Africa). This frontal blaze varies in colour from light brown to pitch-black and occurs from the rhinarium to the front of the eyes and occasionally even beyond to the frontal crest. Underparts are snow-white in some populations to greyish-brown in others. Many Zimbabwean and Zambian specimens have snow-white bellies. Body hairs are fairly short in most animals, but several specimens examined in Botswana had hair that were, in places, in excess of 6 cm long; in the central Kalahari of Botswana, both long- and short-haired duikers can be found in the same population (Wilson 2001). Some isolated montane populations have long hair, such as those on Mt Kilimanjaro and Mt Elgon, likely an adaptation to the environment. The legs are generally the same colour as the body and the fetlocks brownish-black to pitch-black, the black colour often extending up the front of the legs to the body. The tail underneath is white and reddish-brown to black above, but again this varies with animals even in a small area. Albinos, characterized by white fur and pink eyes, are also recorded (Wilson 2001).

Preorbital glands are present, and consist externally of a row of pores exuding from a bare streak of skin. The length of this streak varies, being much shorter in specimens from Ghana than those from Botswana (Wilson 2001). The secretion consists of a thick black melanin-containing component and a thin, yellowish clear liquid. The secretion is heterogeneous, comprising water, mucus, a thin yellowish oil and large concentrations of heavy waxy material in varying proportions. Burger *et al.* (1990) isolated 33 constituents of this preorbital gland secretion. Pedal glands are also present in all four feet, those on the forefeet being deeper and larger, and contain a creamy-white secretion. Inguinal glands are also present, as much as 65 mm long, and contain large quantities of a white to creamy secretion with a powerful odour (Wilson 2001). The size of the hooves depends a great deal on the environment and soil on which the animal lives. Those on Kalahari sand have very long hooves while those on the Nyika Plateau are short and rounded. Lateral (false) hooves are present in all animals. Females are generally larger than ♂♂.

Males have a pair of stout pointed horns; occasionally ♀♀ have been recorded with horns (Miller 1912, Shortridge 1934, Ansell 1960b, Wilson & Clarke 1962). Shortridge (1934) considered that 10% of all Common Duiker ♀♀ in Namibia have horns. Horned ♀♀ appear to be more frequent in some localities than others (Wilson 2001). Wilson (2001) found that in E Zambia, in a sample of 980 female skulls examined, 0.6% had horns. In Zimbabwe, of 720 female skulls, 3.8% had horns (Sebungwe area) and in Botswana in a sample of only 55 female skulls, 12.7% had horns. In all cases horns appearing in ♀♀ were short, thin and often stunted.

The skull has a straight profile, enlarged nasal opening, and somewhat tubular orbits. The median palatal notch is very broad, and V-shaped (Grubb & Groves 2001). The dentition of the Common Duiker is diphyodont and similar to most other bovids. Riney & Child (1960) established ageing criteria for the Common Duiker based on a series of skulls with known collection dates supplemented by a few captive 'known-age' animals ranging from a neonate to one individual aged 21.5 years. This was revised by Wilson *et al.* (1984) after working with a very large collection of more than 90 known-age skulls (and see Wilson 2001). As with some other ungulates the Common Duiker has a modified lower canine tooth that has become the last incisiform. The first premolar has also been lost in the process



Lateral view of skull of Common Duiker *Sylvicapra grimmia*.

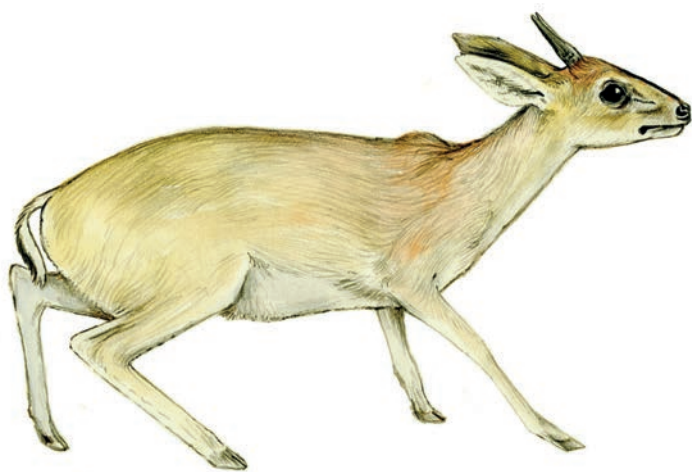
of evolution. At birth the Common Duiker has either partially or fully erupted lower milk canines and incisors with erupting upper and lower premolars; interestingly, P₃ was usually the first premolar to be fully erupted and not P₂ as one would expect. At the age of 26 months both mandibular and maxillary permanent molariform teeth are fully erupted and in wear. There is very little variation in the age of eruption and replacement of all molariform teeth making it a very useful feature for age determination (see Wilson 2001: Table 16). However, there is considerable difficulty in distinguishing deciduous incisiform teeth from permanent ones because of the great variability in eruption. The Common Duiker is one of the few ungulates in which the canines and incisors are replaced last and long after the eruption of the third molar. The final eruption and replacement of the canines and incisors usually takes place at between 30 and 38 months. Dental abnormalities, including, for example, having one or two upper canines present or the lower second premolar absent, are discussed by Riney & Child (1960) and Wilson (2001).

Geographic Variation As already mentioned above, the distribution of the Common Duiker is continuous in sub-Saharan Africa, and therefore it is currently impossible to delineate exactly where one subspecies starts and another takes its place. However, several of the subspecies do have clear distinguishing characteristics and some of these features are discussed below. There is considerable colour and size variation in this species even within very limited areas.

- S. g. grimmia*: in the extreme south of the continent this subspecies is a great deal greyer than any other subspecies (it is known as the Grey Duiker in the Cape). It is not in any way tawny-coloured, and there is no white on the belly, but there are traces of white on the throat and on the upper half of the inner side of the legs. Roberts (1951) described medium development of speckling and an incomplete face-blaze, which does not extend to the frontal tuft on the head.
- S. g. caffra*: occurs north of *S. g. grimmia* and common in KwaZulu-Natal and Limpopo Provinces of South Africa, S Mozambique (Coguno) and E Zimbabwe. It is speckled, fawn-brown to grey-yellow in colour with the mid-dorsal zone being much darker. The face-blaze is nearly black and well marked up to the eyes. Some white occurs on the belly, but the underside is mainly light buff. The tail is nearly all black on the upper surface and white below (Grubb & Groves 2001). Intergrades between *S. g. grimmia* and *S. g. caffra* occur in the 'Caffraria' (Algoa Bay area).
- S. g. steinhardti*: occurs throughout Namibia; south as far as Port Nolloth in the Northern Cape of South Africa; north to Namburi and Cahama in Angola, and east to Kazungula and Chobe district in Botswana. This subspecies is very pale sandy-coloured or even fawn. Very little speckling. In this subspecies the face-blaze fails

to reach even the level of the eyes. The undersides are off-white, chest and throat buff.

- S. g. splendidula*: the subspecies occurring in Angola, from Mupa district north to Kunungu, DR Congo, and across the Congo R. to Odzala (Congo). It also occurs in the south-east of DR Congo to the southern end of L. Tanganyika, north-east to Uvira and in Zambia west to the Luangwa Valley and north as far as Mpika. It is also found in W Zimbabwe (Grubb & Groves 2001). This subspecies is the largest of all the common duikers. It has a light reddish-ochre colour and a short face-stripe. Specimens from Hwange N. P. in Zimbabwe are intergrades between *S. g. steinhardtii* and *S. g. splendidula*. The Latin name (*splendidula*), meaning 'splendid animal', is appropriate, given its bright, contrasting colour, unparalleled in any other form of *Sylvicapra*.



Common Duiker *Sylvicapra grimmia orbicularis* crouching.

- S. g. orbicularis*: occurs north of the Zambezi R. in Mozambique, Malawi and in Zambia east of the Luangwa R. It is also present throughout Tanzania (perhaps absent from the extreme far north-west), along the Kenya coast and inland to Voi and the Juba R. in Somalia. This beautiful subspecies has a distinct white ring around the eyes in specimens from E Zambia and much of Malawi. The general body colour is light fawn with a narrow face-blaze, the tail is black and so are the pasterns. Females are considerably larger than ♂♂. The controversial form *walkerii* is a melanistic example of *S. g. grimmia* (Grubb 1988) and can be assigned to *S. g. orbicularis*.
- S. g. hindei*: Kenya highlands, east of the Great Rift Valley, as far east as Machakos and Sultan Hamud and south as far as Moshi in Tanzania. This subspecies has much speckling along the mid-dorsal region on a generally ochre-coloured body. The face-blaze is bold, broad and dark and extends up to the frontal tuft of hair on the head. The belly is white, throat buff with no white line. This is a small subspecies, but has a broad skull.
- S. g. nyansae*: in Kenya, west of the Rift Valley west to Busoga district in Uganda and to the eastern levee of the Nile in S Sudan north to Reseires in Ethiopia on the Blue Nile. This subspecies is brighter than *S. g. hindei*, but with less mid-dorsal darkening and much whiter underparts. The face-blaze is deep brown rather than blackish.
- S. g. altivallis*: Afroalpine zone of the Aberdares and also probably on Mt Kenya. On Mt Kenya, *S. g. hindei* reaches up to the edge of the forest belt at 1980 m and the two subspecies are isolated from one another by montane forest. It is much greyer than *hindei* with heavier speckling, more marked face-stripe, black pasterns and drabber tone on underparts. It has long, thick fur (Grubb & Groves 2001).
- S. g. lobeliarum*: Afroalpine zone on Mt Elgon. Has a pinkish-grey coat with heavy speckling and a wide face-stripe, which is chocolate-brown. The ears are short and pointed and the pasterns black. In most of its characters this race seems to be the most distinctive of the afroalpine forms.
- S. g. grimmia* subsp. nov.: this is the duiker described by King (1975) from Mt Kilimanjaro. This distinct form has a grey-brown colour, thick black face-blaze, reduced black on tail, and off-white underparts not extending down the inner sides of the limbs. It differs from *altivallis* in having heavier speckling, less black on tail, foreleg stripe usually reaching the knee, 'squared off' ears and a shorter tail (Grubb & Groves 2001).
- S. g. madoqua*: Ethiopian Highlands, both east and west of the Rift Valley, as high as 2990 m in the Sahatu Mts and as low as 610 m at Hawash Station. It is generally grey-buff to brownish-ochre with heavy speckling and the mid-dorsal zone darkened. The face-stripe is complete in the highland form, less so in those from the lowlands. According to Grubb & Groves (2001) this is a very variable race, difficult to define although the various component samples do differ as a whole from the Kenya races and from *campbelliae*.
- S. g. campbelliae*: savanna country from Burundi and Karagwe in the south-east to north of Bahl-el-Ghazal; also occurs in the north-east of DR Congo, southernmost Central African Republic, S Chad, N Cameroon and Nigeria, west to Ghana, Burkina Faso (Fada-N-Gourma) and Sierra Leone. This is a dull ochre to grey-buff duiker, heavily speckled and dark on the mid-dorsal zone. It has a dark face-blaze, which extends to the crest, the tail black above and brown pasterns. The foreleg stripe is well marked. The belly is buff-white to white and no throat patch.
- S. g. pallidior*: distribution of this subspecies is not accurately known, but it does occur in the Sahel Zone from Mani (furthest west locality) as far east as Gallabet on the borders of the Ethiopian Highlands; north as far as Jebel Marra Darfur; south as far as Fort Archambault. *S. g. pallidior* is much paler than the previous race, it is pale buff and weakly speckled but still has a mid-dorsal darkening. The face-blaze extends to the crest.
- S. g. coronata*: this subspecies has only been recorded from a small area on the borders of Guinea, Guinea-Bissau, Senegal and Gambia. It is a beautiful bright orange-yellow colour with no speckling and a mid-dorsal darker shade, which is almost reddish. The face-blaze is red and not extending to the crest. The foreleg stripe is indistinct and not reaching the knee. It has yellowish white underparts and no throat streak. This is the most distinctive of all the subspecies and could possibly be raised to specific rank depending on its relationship with the neighbouring *campbelliae* (Grubb & Groves 2001).

Similar Species

Ourebia ourebi. Occurs on open grassland and could be confused with the Common Duiker in places where both species occur. Much taller, with longer horns, and a much longer neck. Oribi normally

occur in small family groups, whereas the Common Duiker is a solitary animal.

The Common Duiker is the only duiker species found in open savanna woodlands and, therefore, unlikely to be confused with any of the other duikers (although, to a lesser extent, the Red-flanked Duiker *Cephalophus rufilatus* occurs in some open country in West Africa in the Guinea Savanna zone).

Distribution The Common Duiker is one of the most widely distributed antelopes on the African continent, and in spite of dense human populations in many areas its historical distribution has remained largely unchanged, managing to survive where many other species of large mammals have been exterminated. In West Africa, the Common Duiker is widespread and common in savanna woodlands from C and S Senegal, Gambia and Guinea-Bissau east through N Guinea, SW Mali, N Côte d'Ivoire, S and C Burkina Faso, N Ghana, Togo, N and C Benin, N and C Nigeria, SW Niger and N Cameroon. They are naturally absent from the Guinean rainforests, being entirely absent from Liberia; however, there is one old record from NE Sierra Leone (Stanley & Hodgson 1929; and see Grubb *et al.* 1998). From Cameroon, their distribution extends through S Chad, Central African Republic and S Sudan to north-east Africa. Here, while still widespread and common in many areas in W and C Ethiopia, they are now rare and hardly ever seen within their former range in S Somalia and SC Eritrea; they are recorded only from the Forêt du Day in Djibouti, but there have been no confirmed records in several decades (Künzel *et al.* 2000, Heckel & Rayaleh 2008). In East Africa, the Common Duiker occurs throughout Kenya (except semi-arid and arid northern rangelands from which it is naturally absent), Tanzania, Uganda, Rwanda and Burundi, west into N, E and S DR Congo. They then occur southwards widely in all countries, with the exception of the arid coastal deserts of Namibia (East 1999, Wilson 2001). In central Africa, the Common Duiker occurs in the savannas of C and SE Congo, and in neighbouring

E and SE Gabon, where little is known of the species' distribution (East 1999, Wilson 2001).

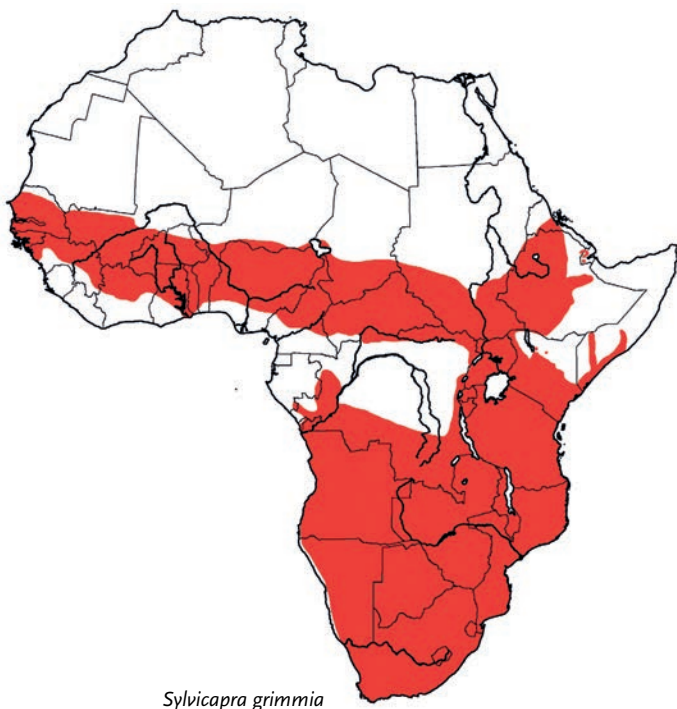
Habitat Although the Common Duiker is typically a savanna woodland species, it is often found in relatively open country and even extends into the alpine zone in some mountainous areas such as on Mt Kenya (to 4900 m; Young & Evans 1993) and Mt Kilimanjaro (to 5600 m; see King 1975, Grimshaw *et al.* 1995), the highland plateau to 3300 m in the mountains of Arssi and Bale in Ethiopia (Yalden *et al.* 1996), and at altitudes above 2200 m in the Drakensberg Mts of South Africa (Vincent 1962, Rowe-Rowe 1994).

Although the species is generally associated with rather open country and woodland it nevertheless still requires at least some small patches of bush in which to hide. This is well demonstrated on the open montane grasslands on the Nyika Plateau in N Malawi and NE Zambia. In this area the species is often seen on the open grasslands but once disturbed it rushes into the edges of the montane forests to hide. Wilson (2001) identified six vegetational types as habitats for the Common Duiker: *Brachystegia*–*Isoberlinia* woodland – one of the preferred habitat types; Mopane *Colophospermum mopane* woodland – while the Common Duiker is not plentiful in this habitat type it nevertheless can still be found in many places where Mopane woodland occurs; Montane Grasslands – the species is common in this habitat and especially on the border of such grasslands where *Uapaca* and stunted *Brachystegia* woodland is found; Kalahari/Acacia veld – the species is common in these dry areas where it can go without drinking water for months at a time; Guinea Savanna – as with the southern African savanna woodlands, the species is plentiful in the northern Guinea savannas; and *Terminalia* woodlands, on Kalahari sand – a much-favoured habitat. In reality, the Common Duiker can be found in almost every habitat type in sub-Saharan Africa, with the exception of dense evergreen rainforests, and in more open areas as long as sufficient cover exists in which it can hide.

Abundance The Common Duiker can be found in very large numbers in many places in Africa. In several places where game elimination as a means of controlling tsetse flies has been carried out, tens of thousands of individuals have been shot and yet today the species is still very common in those places. For example, 83,784 duikers were shot in Zimbabwe between 1924 and 1945 (White 1954), and yet the species is still very common in these areas today. Similar operations were undertaken in the Chipata district of E Zambia (see Wilson & Clarke 1962 and Wilson & Roth 1967 for details), yet they still occur widely in this part of the country.

Wilson (2001) summarizes some recorded densities of Common Duikers from various localities in Africa in different vegetation types using line transects, including: 3.2/km² in the Guinea savanna of Mole N. P. in N Ghana; 2.9/km² in *Brachystegia*–*Isoberlinia* woodland in Lukuzuzi G. R. in E Zambia; 2.0/km² in *Acacia*/*Combretum*/*Grewia* savanna in the south-west lowveld of Zimbabwe; 2.4/km² in the Matopo Hills of Zimbabwe; and 9.0/km² in the *Baikiaea* woodland of Hwange N. P.

East (1999) indicates that aerial surveys generally produce estimates of population densities in the range of 0.01–0.15/km², such as in W N. P. (Burkina Faso) (Belemsobgo & Chardonnet 1996), and Pendjari (Benin) (Chardonnet 1995). However, East (1999) notes that aerial surveys underestimate the numbers of this small, secretive



Sylvicapra grimmia

species by a large but unknown factor. Ground surveys in areas where the species is common often produce density estimates of the order 0.3–1.7/km². As the Common Duiker is a species that is capable of altering its periods of activity depending on disturbances caused by local conditions it becomes extremely difficult to assess the size of populations accurately. Therefore, ground surveys are often inaccurate if undertaken at a time when duikers are not active. The very best times of the day for surveys are very early in the morning soon after sunrise and late in the afternoon just before sunset and early evening. East (1999) estimates the total population for sub-Saharan Africa as 1,660,000, indicating that this is a conservative figure. The present author believes the total population of the Common Duiker is more likely to be in the order of 10 million animals.

Adaptations This duiker is a most adaptable species and capable of occupying a wide range of habitat types. Apart from the Rwenzori Red Duiker *Cephalophus rubidus* on the Rwenzori Mts, the Common Duiker appears to be the only species of African antelope able to adapt to habitats high up on the mountains, often to the snowline. It also occurs in the hot and seasonally dry valleys of the Zambezi and Limpopo valleys and is very common in the waterless and very dry Kalahari Desert in Botswana and Namibia. An experiment carried out on a captive duiker in Zambia indicated that one animal went without water for 40 days (Wilson 1966a). Dietary flexibility, the ability to survive without surface water and fecundity all contribute to this species' success, but the basis of its adaptive flexibility is undoubtedly physiological, an aspect of the Common Duiker's biology that awaits a comparative investigation.

Studies of the preorbital gland secretion of male and female Common Duikers have shown that two compounds, both thiazole derivatives, are present in higher concentrations in ♂♂ than in ♀♀. This is the only consistent difference between the secretions of the sexes, and coupled with the fact that only ♂♂ mark territories, could be seen as evidence that these two compounds play a role as sex recognition cues and in territorial behaviour (Burger *et al.* 1988, 1990). There is a great increase in the size of the preorbital gland of the ♂ while the ♀ is in oestrus and he will mark trees, shrubs and even stones far more vigorously than normal. The secretion, which is squeezed out by rubbing the gland against some hard object, crystallizes and forms a dark stain on the object marked. In E Zambia, and on several occasions in Zimbabwe, the author has observed a ♂ rubbing his preorbital glands on the hindquarters of a ♀ in his enclosure, leaving the secretion on her. Sikes (1958) also observed a ♂ marking a ♀ in Nigeria.

During a detailed study of food and feeding habits in Matobo N. P. (W Zimbabwe), Wilson (2001) watched a duiker feeding under foraging monkeys: every now and then the duiker would look up into the trees to see where the monkeys were, seemingly waiting for them to drop more flowers to the ground. Such behaviour reveals *Sylvicapra* as a typical duiker and can be presumed to have derived from forest-dwelling ancestors.

Foraging and Food The Common Duiker is a browser and frugivore, rarely taking grass, and has been recorded feeding on a very large number of plants. In one study, in E Zambia, the leaves of 44 different plants were identified from the rumens of 191 duikers. In addition, from the same sample 33 different fruits and seeds were recorded as well as 15 species of flowers (Wilson 1966a).

A detailed study of the food and feeding habits of the Common Duiker was carried out in Matobo N. P. (see Wilson 2001). Tame male and female duikers were used for the study in granite hills where the vegetation consisted of *Colophospermum mopane* in addition to *Brachystegia* spp. and *Julbernardia globilifera*, *Parinari curatellifolia*, *Terminalia sericea* and *Peltophorum africanum* were also common. Contrary to what was expected, green leaves of large trees and shrubs were not the most important foods eaten by the duikers studied. Most of the leaves of the larger trees are well out of reach unless the trees occurred in a shrub form or as seedlings. Fallen leaves of some of the large trees were often gleaned from the ground even though they were partly dry, as in the case of *Kirkiana acuminata*, which were eaten in large amounts during the dry season. Instead, leaves, stems, flowers and fruits of many small herbs were eaten in very large quantities, for example, *Commelina welwitschii*, *C. benghalensis*, *Ipomoea omaneyi* and *Sida cordifolia*. In this study 65% of the duikers' total feeding time was spent feeding on these plants. The duikers often climbed among the boulders at the base of rocky outcrops in the study area and both animals fed on herbs growing in the litter between the boulders. The duikers often pulled entire small plants out of the soft soil among the boulders and ate the entire plant, including the roots.

After herbs, fruits and seeds were most important in the diet. The fruits, seeds and flowers of many species of trees and shrubs were eaten, when available, in very large quantities. The fallen dry pods and also green pods of *Acacia robusta* and *A. nilotica* were eaten in fair numbers. The following fruits were eaten whenever they were available and formed a major part of the duikers' diet: *Ximenia caffra*, *Dovaylis caffra*, *Flueggea virosa*, *Flacourtia indica*, *Ziziphus mucronata*, *Grewia flavescens*, *Solanum* sp. and *Pseudolachnostylis maprouneafolia*. Both green and dry pods (in bunches) of *Dichrostachys cinerea* were much sought after as were the ripe bunches of *Lannea discolor*. Various species of *Ficus* fruits were also greatly relished and in some instances eaten in very large quantities. *Flueggea virosa* was an important tree as the tiny white fruits were eaten, when available, in vast amounts. On numerous occasions the ♂ was seen to stand on his hindlegs in order to get to fruits and leaves of shrubs that were just out of reach. This was particularly noticeable when feeding on the ripe fruits of *Ximenia caffra*, *Flacourtia indica*, *Grewia* spp. and *Flueggea virosa*.

The flowers of most species were eaten, some in large numbers, while in other species only a few were eaten. In nearly all cases the flowers had fallen from the larger trees and these were gleaned from the ground. The duikers were like vacuum cleaners as they moved about sucking up the flowers. Flowers eaten included: *Bauhinia petersiana*, *Cassia abbreviata*, *Brachystegia* spp., *Hibiscus* sp., *Loranthus* sp., *Dichrostachys cinerea* and *Acacia* spp. In the case of the small legumes, *Crotalaria podocarpa*, *C. sphaerocarpa*, *C. virgulata* and *Dolichos daltonii* flowers were often plucked from the plants and eaten in bunches together with any green pods and leaves that were present on the plant. In one part of the male duiker's home-range there were four *Cassia abbreviata* trees. Vervet Monkeys *Chlorocebus pygerythrus* were on two occasions seen feeding on the recently flushed yellow flowers and on both occasions the male duiker picked up some of the fallen flowers from the ground and ate them.

In the Matobo Hills study, although the leaves of trees and shrubs were not the most important dietary item, the following were eaten: *Grewia flavescens*, recently flushed *Parinari curatellifolia*, *Dichrostachys cinerea*, *Acacia nilotica*, *A. robusta*, *Combretum hereroense*, *Dombeya*

rotundifolia, *Combretum apiculatum*, *Ximena caffra*, *Pavetta schumanniana*, *Terminalia brachystema*, *Flueggea virosa*, *Lannea edulis*, *Flacourtia indica*, *Ziziphus mucronata*, *Pseudolachnostylis maprouneifolia*, *Pterocarpus angolensis* and newly flushed *Protea angolensis*. *Albizia amara*, *Burkea africana*, *Euclea divinorum*, *Lannea discolor*, *Azara garkeneana*, *Faurea saligna*, *Peltophorum africanum* and *Rhus tunuinervis* were occasionally eaten but only in very small quantities. *Dichrostachys cinerea*, *Flueggea virosa*, *Combretum hereroense*, *Flacourtia indica* and *Combretum apiculatum* were some of the more important trees from which leaves were picked and eaten. The leaves and fruits of the small tree *Securingea virosa* were often eaten in very large quantities. Taking all three years of the study into account, only 25% of the total feeding time was spent feeding on the leaves of large trees.

As soon as the wet season ended in late Mar the trees and other plants started drying out. This normally started with the small herbs and climbers and ended with the leaves of the large trees falling to the ground. By late Jul there were very few large trees with leaves still on them and the country looked extremely dry. It was at that time of the year that fruits were still falling and these became extremely important in the duiker's diet. By Aug temperatures were already increasing and fires had swept through the countryside including the study area. With the increase in temperature after the winter, many trees and shrubs started flushing new leaves. By Sep and Oct, long before the rains fell in the middle of Nov, the vegetation in the entire study area, for each of the three years of the study, was attractively green and provided good supplies of food for browsers. With the commencement of the wet season in late Nov and early Dec, most of the small herbs and climbers flushed, and for the following five months there was an abundance of vegetation again. The onset of the dry season led to the drying out of the vegetation and both the male and female duikers had to cover a larger area in order to find food. A lot of time was spent slowly walking about sniffing at dry plants and looking for food. By Aug both duikers were ranging over an area almost twice the size of the area occupied during the wet period and both duikers appeared to have lost weight.

Soon after the first rains had fallen the duikers fed on a small quantity of freshly sprouted grass yet, even though the grass was luxuriant, it did not represent even 2% of their diet. Interestingly, the rains brought an abundance of harvester termites. On seven occasions (four times with the ♀ and three times with the ♂) the duikers were seen feeding on termites emerging from holes in the ground. On one occasion the ♂ was seen to lick up at least 50 harvester termites *Trinervitermes rhodesiensis* as they emerged. On the other six occasions not more than between 10 and 20 termites were eaten. With the rains, fungi also became evident. Three species were eaten by the duikers, but only one or two plants at a time. After eating the top umbrella part of the fungus the duikers would occasionally also eat the entire stem. Once the ♀ dug a plant out of the ground and tried to dislodge the remaining small parts of the stem that remained in the ground. For over eight minutes she dug with her front hooves into the soft ground, removing the remains of the fungus and picking up and eating all the small pieces.

During the study, it was noticed that resin that exuded from the trunk of *Acacia robusta* and *Acacia karroo* trees were eaten by both the male and female duikers. They pulled soft balls of resin from the trees and these were chewed thoroughly before being swallowed. On one occasion the ♂ removed six balls of resin from one tree and

spent another 10 minutes at the tree licking the bark and removing small pieces of bark. Common Duikers will also feed on cultivated crops, including beans, sweet potatoes, tomatoes and groundnuts. Analysing faeces in Grants Valley, Eastern Cape, South Africa, Kigozi (2003) found that chicory provided more than one-third (35.6%) of the winter diet and a substantial proportion (14.4%) of the spring diet of the Common Duiker.

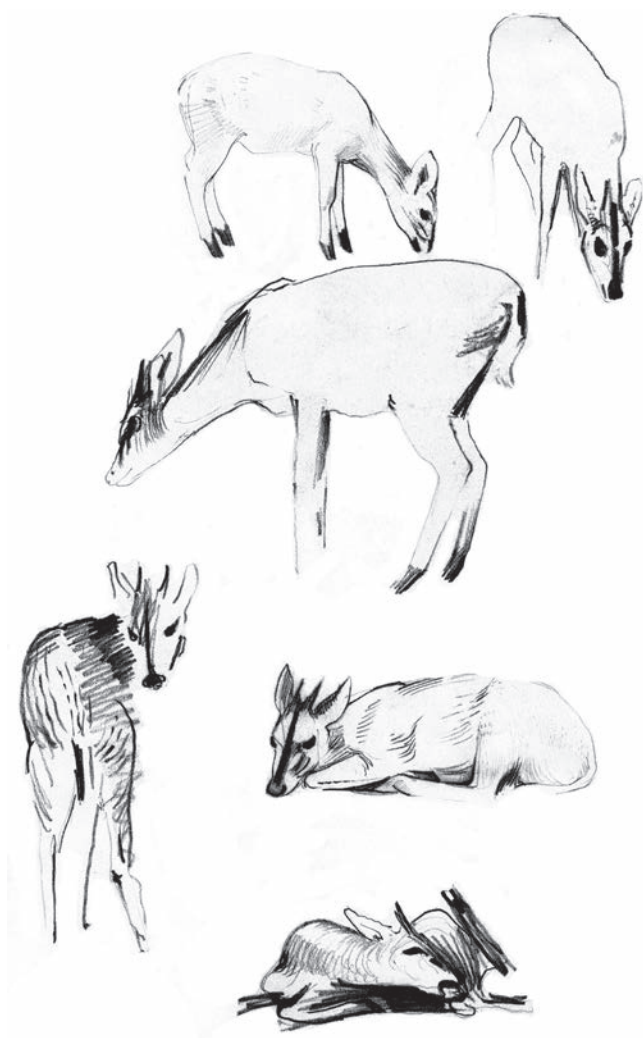
The species is well known for its tendency to eat meat, and there are records of Common Duikers feeding on Helmeted Guineafowl *Numida mitrata* chicks, ducklings, Red-billed Queleas *Quelea quelea*, a Laughing Dove *Stigmatopelia senegalensis*, mopane caterpillars *Conimbrasia belina*, lizards and insects (Smithers 1971, Wilson 2001). Hofmann (1973) once saw a duiker take a striped mouse *Rhabdomys* sp.

The Common Duiker is independent of water and even when water is available the animal rarely drinks (Skinner & Chimimba 2005).

Social and Reproductive Behaviour Common Duikers are generally solitary animals. However, when a ♀ is in oestrus a ♂ and ♀ will come together. They will often stay together for several days at a time and once mating has taken place they will separate again. Pairs will nevertheless still remain in the same general area and will come together from time to time, especially if a tree producing fallen fruit is in their home-range and in that case they will often be seen together. When two duikers are seen together it is usually an adult ♂ with an adult ♀, but a ♀ with her young is another common pairing. When three duikers are seen together it is usually an adult pair and a young animal that has not yet been weaned.

One of the most important factors influencing distribution, territorial behaviour and the home-range in the Common Duiker is food supply. The home-range is determined by the availability of the preferred foods at different times of the year. Therefore, the daily activity and home-range of the duiker is determined by its need to obtain sufficient food and this basic function is complemented by its drive to reproduce. As Allen-Rowlandson (1986) has pointed out, territorial behaviour that limits a species to any given area is likely to affect its performance. A number of authors have briefly mentioned that the Common Duiker does not often move very far and is restricted to a small area (Dixon 1964, Wilson 1966a, Dunbar & Dunbar 1979). In the Ethiopian Highlands, Dunbar & Dunbar (1979) found that known duikers occupied home-ranges that overlapped only to a limited extent. Allen-Rowlandson (1986) found that some adult ♂♂ shared part of their home-ranges with ♀♀. He found that the mean size of the home-range of Common Duikers in KwaZulu-Natal was about 21 ha, which varied between 21.1 and 27.4 ha. In a study in E Zambia, Wilson (2001) found that one adult ♂ had a home-range of 13.2 ha and another a home-range of 15.7 ha. These two ♂♂ had distinct home-ranges that did not overlap, while adult ♀♀ had home-ranges of about 13 ha, which overlapped with each other and also with those of ♂♂. Adult ♂♂ that are sexually mature will defend their territory and drive out any competing adult ♂♂. However, subadult ♂♂ are tolerated and not driven away.

The Common Duiker has a number of behavioural patterns that characterize courtship, including: the ♂ chasing the ♀ when in oestrus; flehmen; constant flicking of the tongue; low-pitched bleats; laufsclag (leg tapping); false mounting attempts; biting of the female's hindquarters and tail; and increased marking of objects with secretion from preorbital glands and final mounting of ♀. Although



Common Duiker *Sylvicapra grimmia*.

these various forms of behaviour are connected with courtship, they do not necessarily follow each other sequentially and some adult ♂♂ do not exhibit all the behavioural patterns. The chasing of the ♀ in oestrus is often very pronounced and ♂♂ in captivity can become most aggressive and will not tolerate other sexually mature ♂♂ in the same enclosure. Very often a ♂ would chase a ♀ in oestrus to near exhaustion and in captivity the ♀ would often lay down in some secluded spot in order to get away from the ♂. If that happened he invariably persisted in attempting to get her to her feet by pawing her with his front feet, or even biting her. If the ♀ rose to her feet the chase would continue. This chasing behaviour was often observed in the wild early in the morning and again late in the afternoon and at sunset.

In the male Common Duiker, flehmen is not as noticeable as it is in other ruminant species, but after close genital olfaction or after testing freshly voided urine from a ♀ in oestrus, the ♂ would raise his head and a slight lip-curl could be seen. After genital olfaction, reproductive activity in the ♂ is increased considerably and this is also noticed if freshly voided urine is tested. It is therefore clear that olfaction is essential in the stimulation of reproductive activity in the ♂. Frequent urination by the ♀ is a common characteristic while she is in oestrus, which suggests maximum output of urine and, therefore, endocrine contents.

During courtship the ♂ follows the ♀ persistently but only seriously begins to court her when she proves to be in oestrus. The flicking of the male's tongue and low-pitched bleats are closely linked and can be clearly observed in ♂♂ following a ♀ in oestrus. The male's tongue will also occasionally come in direct contact with the female's hindquarters, her tail and even her vulva. Low-pitched bleating is a vocal communication between the adult ♂ and ♀ during courtship. The ♀ on the other hand also bleats from time to time but not nearly as much as the ♂ and usually only when running away.

Another form of mating behaviour consists of the ♂ striking out with a stiff, straight forelimb (a behaviour known as laufs Schlag). He nudges the ♀ either between the hindlegs or on her hindquarters. If the ♀ moves slowly away the ♂ will follow and flehmen and laufs Schlag continue. However, once the ♀ stands the ♂ attempts to mount her, and false mounting attempts by the ♂ are extremely common. In this behaviour the ♂ shows no serious attempt to clasp the ♀ with his forelegs as he would do if she is receptive. When he rises onto his hindlegs they are usually too far behind her to complete copulation. As soon as he mounts, the ♀ takes a couple of steps forward and he drops onto all fours again. Often in these false mounting attempts the ♀ would raise one or both of her hindlegs and kicks the ♂. Either of these activities is sufficient to prevent mating, but does not prevent the ♂ from continuing to pursue the ♀. False mounting is carried on repeatedly and long before actual copulation takes place. In the false mounting position the ♂ will never rise to a fully upright stance on his hindlegs as he would when mounting a wholly receptive partner.

It has been recorded in the wild and also with captive duikers that the ♂ will actually bite the female's hindquarters and tail. The continual biting of the ♀ in the same spot will often leave an area of about 4 cm diameter bare of hair and often raw and bleeding. A ♂ has also been recorded actually biting off the tip of a female's tail, leaving a raw stump (Wilson 2001).

Once the ♀ is receptive and no longer runs from the ♂, he rises onto his hindlegs, positioning them as close to those of the ♀ as possible, and, clasping the ♀ with his forelegs, mates with her. Intromission and ejaculation are performed very rapidly. Following ejaculation there is a short refractory period of about half an hour before mounting takes place again. The ♂ will often mate three or four times before moving off. He then loses interest in her but later in the day more mating bouts will take place continuing for as long as the ♀ is receptive.

Females retire to the cover of dense vegetation to give birth. Parturition seems to take place either early morning or late afternoon, or in the hours of darkness (Wilson 2001). The ♀ cleans the lamb immediately following birth, and usually eats the afterbirth; young are precocious and stand up and attempt to suckle shortly after birth. The lamb is hidden near the birthplace, but the ♀ remains in close association with her young for several days following birth, frequently visiting it (four to six times per day) and strengthening the mother–young bond. Lambs will suckle as much as eight times per day, usually early in the morning, late afternoon and during the night (Wilson 2001).

Reproduction and Population Structure The information that follows is summarized from Wilson (2001), unless otherwise indicated. Females become sexually mature when they are between 8.5 and 10.5

months old; a known-age ♀ born in captivity came into oestrus at eight months, and had her first lamb when 15 months old. Males become sexually mature about 3–4 months later. Ovulation takes place in the right horn of the uterus. Of 231 reproductive tracts dissected, Wilson (2001) recorded 110 cases where ovulation was from the left ovary and 121 from the right ovary. In all cases implantation was in the right uterine horn. The gestation period of 29 captive births, in which mating and subsequent births were witnessed, was between 189 and 216 days with an average of 200 days.

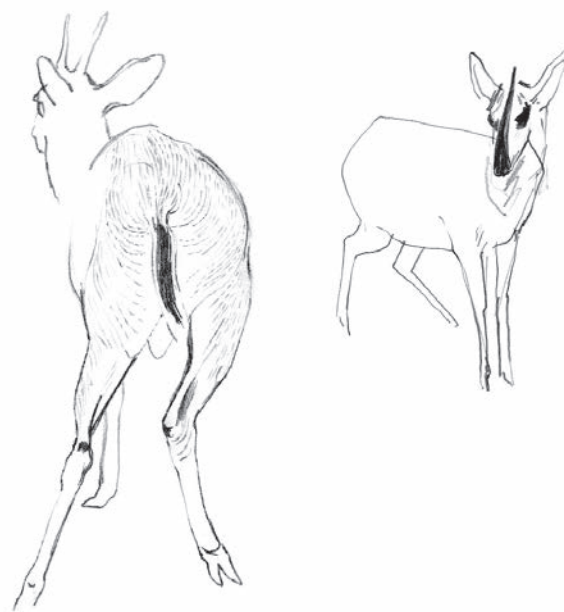
Neonates have a mass of about 1.7 kg, but this can vary considerably depending on the size of the ♀. Newly born Common Duikers in Botswana have a mass almost twice those from Ghana, where adults are half the size of those in Botswana. Young gain as much as 600 g in weight in the first week of life (Wilson *et al.* 1984). Lactation lasts approximately 3–4 months and weaning is gradual, with young starting to nibble on leaves when only two weeks old. Common Duiker milk has a crude protein percentage of about 8.5%, ash 1.2%, moisture 79%, fat content 8.2% and lactose 3.9%.

In view of the fact that the gestation period of the Common Duiker is so long for such a small animal and secondly that the ♀ will often come into oestrus soon after giving birth (see below), there is no clear season of birth. However, Wilson (2001), when studying duikers in E Zambia, recorded young throughout the year, while in a similar study in the south-east lowveld of Zimbabwe where the rainfall is a lot less than E Zambia, young duikers were recorded from Nov to Mar, suggesting a birth peak.

Females often come into oestrus within a week of giving birth and many ♀♀ of breeding age are often pregnant and lactating at the same time. Very little information is available on the inter-birth interval of the Common Duiker and all the data that are available come from animals in captivity. Mentis (1972) mentions 267 days while von Ketelhodt (1977b) gave the average interval as 259 days. However, his records were for only one pair of duikers that produced 11 young over a period of seven years. From data collected by Wilson (2001) over an extended period of time from several localities in southern Africa, the mean interval between births was 237 days with a range of 199 to 271 days ($n = 20$).

Jones (1993) gave a longevity record for *S. g. grimmia* in captivity of 11 years and 10 months, but Wilson (2001) noted that the oldest 'known-age' captive duiker reached an age of 26.5 years, while there were several other captive animals that attained ages of 15, 17, 19 and 21.5 years.

Predators, Parasites and Diseases The Common Duiker has a very large number of predators and there is hardly a mammalian carnivore or bird of prey that does not feed on this species. Two very detailed studies of the predators of the Common Duiker, undertaken in E Zambia and in the Matobo Hills in Zimbabwe, showed that at least 22 species of mammals and birds were recorded feeding on this duiker (Wilson 1966b, 2001). The adults are taken by, among others, Leopards *Panthera pardus*, African Wild Dogs *Lycaon pictus*, jackals *Canis* spp., Cheetahs *Acinonyx jubatus* and hyaenas, while young may be taken by baboons *Papio* spp., many of the larger birds of prey, including Martial Eagles *Polemaetus bellicosus*, Verreaux's Eagles *Aquila verreauxii* and Wahlberg's Eagles *A. wahlbergi*, as well as Giant Eagle-owls *Bubo lacteus* and African Rock Pythons *Python sebae*. While the Secretary Bird *Sagittarius serpentarius* feeds on rodents, snakes and



Common Duiker *Sylvicapra grimmia*.

insects, there is a record of a young duiker being killed by one in Matobo N. P. (V. J. Wilson pers. obs.).

Crotalaria, intoxication due to the legume *Crotalaria*, is the only known cause of extreme overgrowth of horn affecting all four feet in domestic animals and some wild antelopes. In the Common Duiker, crotalaria is the laminitic form of crotalism caused by an acute inflammation in the horn-forming tissue due apparently to some toxic process resulting from the ingestion of one or more species of *Crotalaria*. In the acute form there is great pain that later subsides. This induces abnormality of gait, which, together with the excessive growth, results in an elongated and deformed foot becoming noticeable after a period, often showing a succession of rings. Laminitis has been recorded in a number of Common Duiker in Matabeleland, Zimbabwe. Additional details of this disease can be found in Wilson (2001).

A very large number of both external and internal parasites have been recorded from the Common Duiker, including roundworms (nematodes), flukes (trematodes), tapeworms (cestodes), and arthropod parasites such as flies, lice and ticks. Nematodes include species of the genera *Cooperia*, *Haemonchus*, *Impalpia*, *Longistrongylus*, *Nematodirus*, *Ostertagia*, *Teladorsagia*, *Trichostrongylus*, *Trichuris* and *Setaria*, as well as *Oesophagostomum columbianum*, *Skrjabinodera kuelzii*, *Subulura distans* and the lung-worm *Dukerostrongylus kenya* (Round 1968, Dinnik & Boev 1982, Boomker *et al.* 1983, 1986, 1987, 1989a, Boomker & Reinecke 1989). Trematodes include *Paramphistomum* sp. (Boomker *et al.* 1983), *Cotylophoson cotylophoson* (Round 1968), *Schistosoma bovis* (Sobrer 1975) and *Fasciola hepatica* (Graber *et al.* 1980). Cestodes include *Moniezia expansa*, *Cysticercus* spp., *Echinococcus* spp., *Avitinella centripunctata*, *Stilesia hepatica*, *Taenia* spp. and *Thysaniezia* sp. (Round 1968, Graber *et al.* 1980, Boomker *et al.* 1987, 1989a).

Arthropod parasites are also numerous, including: ixodid ticks, such as *Amblyomma hebraeum*, *Boophilus* spp., *Haemaphysalis* spp., *Ixodes* spp. and *Rhipicephalus* spp.; sucking lice, *Linognathus breviceps* and *L. zumpti*; biting lice, *Damalina*; and the louse fly *Lipoptena paradoxa* (Boomker *et al.* 1983, Horak *et al.* 1989).

Conservation IUCN Category: Least Concern. CITES: Not listed.

The Common Duiker is in the very fortunate position that, at the present time, no special conservation measures are necessary to protect this species. Its wide distribution in sub-Saharan Africa, coupled with its adaptability and the fact that it is capable of eating almost anything, means that it survives in many areas where most other antelopes have been eliminated. It occurs in good numbers in many specially protected areas throughout sub-Saharan Africa.

Measurements

Sylvicapra grimmia

TL (♂♂): 920 (910–932) mm, n = 12
 TL (♀♀): 948 (932–954) mm, n = 14
 T (♂♂): 122 (100–149) mm, n = 12
 T (♀♀): 123 (101–146) mm, n = 14
 HF c.u. (♂♂): 262 (231–286) mm, n = 12
 HF c.u. (♀♀): 269 (234–289) mm, n = 14
 E (♂♂): 93 (90–107) mm, n = 12
 E (♀♀): 103 (92–125) mm, n = 14
 Sh. ht (♂♂): 433 (402–461) mm, n = 12
 Sh. ht (♀♀): 448 (386–478) mm, n = 14
 WT (♂♂): 11.2 (9.7–13.6) kg, n = 12
 WT (♀♀): 12.4 (10.3–14.7) kg, n = 14
 NW Ghana (Wilson 2001)

TL (♂♂): 1000 (950–1060) mm, n = 126
 TL (♀♀): 1050 (980–1120) mm, n = 97
 T (♂♂): 120 (110–140) mm, n = 126
 T (♀♀): 130 (100–150) mm, n = 97
 HF c.u. (♂♂): 290 (270–300) mm, n = 126
 HF c.u. (♀♀): 290 (270–320) mm, n = 97
 E (♂♂): 115 (104–127) mm, n = 126
 E (♀♀): 115 (103–132) mm, n = 97
 Sh. ht (♂♂): 530 (500–560) mm, n = 126
 Sh. ht (♀♀): 530 (499–570) mm, n = 97
 WT (♂♂): 13.9 (12.9–16.6) kg, n = 126
 WT (♀♀): 15.4 (12.7–16.8) kg, n = 97
 E Zambia (Wilson 2001)

TL (♂♂): 1080 (1020–1140) mm, n = 52
 TL (♀♀): 1110 (1060–1150) mm, n = 61
 T (♂♂): 130 (120–140) mm, n = 52
 T (♀♀): 130 (100–140) mm, n = 61
 HF c.u. (♂♂): 300 (290–310) mm, n = 52
 HF c.u. (♀♀): 310 (300–320) mm, n = 61
 E (♂♂): 125 (123–126) mm, n = 52
 E (♀♀): 126 (125–128) mm, n = 61
 Sh. ht (♂♂): 550 (540–560) mm, n = 52
 Sh. ht (♀♀): 560 (530–580) mm, n = 61
 WT (♂♂): 15.9 (14.5–17.3) kg, n = 52
 WT (♀♀): 18.2 (17.2–19.1) kg, n = 61
 SW Zimbabwe (Wilson 2001)

TL (♂♂): 1100 (1010–1260) mm, n = 45
 TL (♀♀): 1165 (1050–1280) mm, n = 48
 T (♂♂): 132 (105–164) mm, n = 45
 T (♀♀): 153 (120–195) mm, n = 48

HF c.u. (♂♂): 330 (280–350) mm, n = 45
 HF c.u. (♀♀): 338 (240–360) mm, n = 48
 E (♂♂): 134 (113–151) mm, n = 45
 E (♀♀): 135 (116–153) mm, n = 48
 Sh. ht (♂♂): 570 (490–630) mm, n = 45
 Sh. ht (♀♀): 600 (490–680) mm, n = 48
 WT (♂♂): 19.3 (14.8–22.4) kg, n = 45
 WT (♀♀): 21.8 (16.1–26.3*) kg, n = 48
 Kalahari Desert, Botswana (Wilson 2001)

*The heaviest mass recorded by Wilson (2001); this ♀ had a total length of 1280 mm and stood 680 mm at the shoulder
 Maximum recorded horn length is 18.1 cm for a pair of horns from South Africa (Rowland Ward)

Key References Allen-Rowlandson 1986; Dunbar & Dunbar 1979; Wilson 1966a, 2001; Wilson & Clarke 1962.

Vivian J. Wilson



Common Duiker *Sylvicapra grimmia*.

GENUS *Cephalophus*

Forest Duikers

Cephalophus C.H. Smith, 1827. In: Griffith et al., Anim. Kingd. 5: 344.

Cephalophus is a genus that currently embraces all duikers except for the two or more species of *Philantomba* and the monospecific *Sylvicapra*. The separation of *Philantomba* based on morphological characters (e.g. Pocock 1910) has had strong support from molecular studies that indicate that these small duikers were the first of the extant species to diverge from the rest of the duikers (Jansen van Vuuren & Robinson 2001). The Common Duiker *Sylvicapra grimmia* occupies a much more ambiguous position, with different molecular trees positioning it wholly outside, marginally outside and wholly within the *Cephalophus* mainstream duikers (Heyden 1968, Robinson *et al.* 1996b, Jansen van Vuuren & Robinson 2001, Hassanin *et al.* 2012).

Molecular studies have confirmed that duikers as a whole, as well as the genus *Cephalophus*, conform with the prediction (Kingdon 1982) that small duikers should be the more conservative while the larger duikers are among the most recently evolved (Robinson *et al.* 1996b, Jansen van Vuuren & Robinson 2001). According to the molecular studies of Jansen van Vuuren & Robinson (2001), the most consistently conservative *Cephalophus* species is the small Aders's Duiker *C. adersi*, with another apparently early branch being the smallish and somewhat specialized Zebra Duiker *C. zebra*. The bulk of the radiation is made up of a large number of medium-sized 'red duikers' with a very densely complex genealogy and a later offshoot of 'giant duikers' and 'fibre duikers'. The complexity of red duiker relationships may well be further complicated by long-term hybridization along the frontiers of expanding and contracting ranges.

The most plausible match between the very tentative trees devised by molecular scientists and the biology and biogeography of living species invites the following sketch of possible evolutionary sequences. The relictual Aders's Duiker, confined to Zanzibar and isolated forest fragments along the east African littoral, is the last 'eastern peripheral' relic of a once widespread, very early red duiker. The Zebra Duiker might be an equivalent 'western peripheral' species that has mitigated its marginal status by becoming more highly specialized. The rest of the 'red duikers' are of substantially larger size and can be divided into the following categories:

1. 'Successful peripheral generalists': relatively conservative species living in forests or galleries that are outliers geographically speaking and ecologically degraded (see map right). The relative poverty of fallen fruit and foliage ensures there are few other duikers with which to compete. This category includes the Natal Red Duiker *C. natalensis* and Harvey's Duiker *C. harveyi*. The Red-flanked Duiker *C. rufilatus* could also come here, but fits better in the next category.
2. 'Successful specialists' (deriving from older lineages): species that have escaped competition by becoming specialized in forest types that are less well endowed with a rich variety of fruits. These forests range from mono-dominant patches such as the *Gilbertiodendron* 'Limba' forests of central Africa to a variety of forest 'margins' such as actual forest edges (notably the broad swathe of forest mosaics and galleries along the northern boundaries of the main forest block), swamp forests at both low and high altitudes and the high, cold reaches of tall mountain massifs. Species in this category include

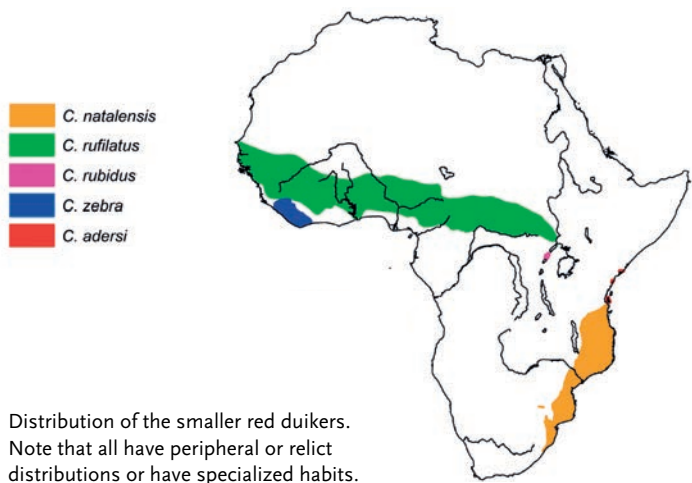
the White-bellied Duiker *C. leucogaster*, Red-flanked Duiker, Black-fronted Duiker *C. nigrifrons* and Rwenzori Red Duiker *C. rubidus*.

3. 'High-forest frugivores': species that only really flourish in highly diverse forests with multi-species fruiting trees and a broad spectrum of primates and birds assisting the wind in dropping high-quality debris from the canopy. Species in this category are highly competitive and suitably rich forests only support one species in this size class (15–25 kg). The situation is complicated by the likelihood that the older members of this class (Ogilby's Duiker *C. ogilbyi* and allies) are being actively displaced by larger and more recently evolved forms (Peters's Duiker *C. callipygus*, Weyns's Duiker *C. weynsi* and the Black Duiker *C. niger*).

Molecular trees are somewhat contradictory in tracing the origins of the remaining *Cephalophus* species. All are large, heavily built animals and they probably derive from an early, large 'high-forest frugivore'. They fall into two groups: the first comprises very large but slender, generalized duikers, including Abbott's Duiker *C. spadix* and the Yellow-backed Duiker *C. silvicultor*, while the second consists of two mainly nocturnal 'fibre duikers' that are primarily nocturnal and seek out widely dispersed, heavy and often fibrous fallen fruit, namely the Bay Duiker *C. dorsalis* and Jentink's Duiker *C. jentinki*. It is possible that nocturnal duikers may be longer-lived than other forms and this might well be an advantage for species that need to get to know a large home-range.

Most duikers are subject to very high levels of predation, particularly by humans. They are easy to snare, net, call up to a lure, dazzle by flash-light and hunt with dogs. The rarer species are already close to extinction and many others are known to be in decline. As one of the most interesting and complex of bovid evolutionary radiations, they deserve much more attention than they have to date. The extinction of once common and widespread providers of high-quality meat will only impoverish further already marginalized forest people. Both research and conservation are urgent.

Jonathan Kingdon



Cephalophus zebra ZEBRA DUIKER (BANDED DUIKER)

Fr. C  palophe z  br   (C  palophe ray  ); Ger. Zebraducker

Cephalophus zebra Gray, 1838. Ann. Mag. Nat. Hist. 1: 27–30. Sierra Leone.Zebra Duiker *Cephalophus zebra*.

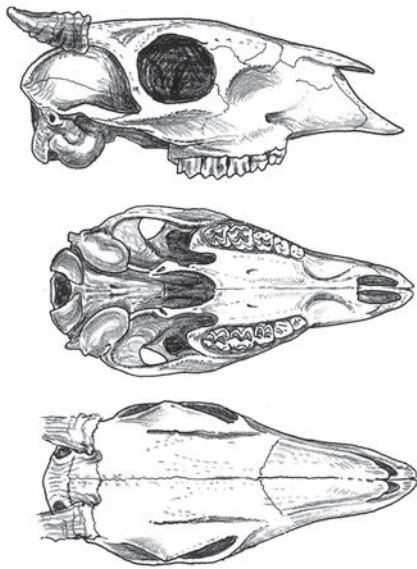
Taxonomy Monotypic. Ogilby's (1837) account of *Antelope doria* is actually a reference to the Mhorr Gazelle *Nanger dama mhor* (see Kuhn 1966). Following a request from Ansell (1980), the ICZN ruled that *zebra* is to be given priority over *doria* whenever the two specific names are considered synonyms (see also Grubb 2004 for a discussion). In a multiple analysis of mtDNA, Jansen van Vuuren & Robinson (2001) found the position of this species within the duiker molecular radiation particularly obscure. Parsimony analysis hinted that *C. zebra* and Aders's Duiker *C. adersi* might be sister taxa, but this was not supported by maximum likelihood analysis, which was consistent with both species having basal positions between the 'red duiker' and 'giant duiker' complexes. Other, apparently anomalous linkages with Ogilby's Duiker *C. ogilbyi* (which gives several indications of being an early, conservative relict species) could also imply that *C. zebra* derives from a relatively early stem duiker. Synonyms: *doria*, *doriae*, *zebrata*. In contrast to all other duiker species studied to date, the diploid number is $2n = 58$, with a pair of submetacentric autosomes; the X chromosome is similar to that of other duikers karyotyped, but the Y is one of the smallest acrocentric chromosomes (Bogart *et al.* 1977, Hsu & Benirschke 1977).

Description Small- to medium-sized duiker, with a panel of vertical, vivid black and cream stripes from behind the shoulder to the tail. There is a frontal rufous-coloured tuft, though it is never

very long, and it usually obscures the short horns (with the result that animals may appear hornless, especially ♀♀). Head, shoulders and lower legs russet red with hocks and leg joints nearly black; muzzle slate-grey and nose black. Hair on the neck and shoulders is distinctly shorter than on the body, while the underparts also have rather short hair. The number of dark brown or black vertical stripes varies between 12 and 16, sometimes with light shadow stripes in between, and the width of individual stripes varies greatly (Wilson 2001). Tail tufted, well haired and relatively long, black hairs intermixed above, but white below. Lateral hooves very small. Preorbital glands present. Tarsal glands prominent and tufted just below the heels of the back legs. Inguinal glands entirely different to those of any other duiker, with tiny round holes in the groin (Zeller & Kuhn 1991, Wilson 2001).

Both sexes have small (about 4 cm) but robust, conical, smooth and very sharply pointed horns above a forehead and nasal area where the bone is massively thick and reinforced. The horn cores of the frontalia rise less above the profile line of the frontalia than in other species. The enlarged nasal cavity is particularly conspicuous in the skull. Preorbital depressions are relatively tiny. The second incisor and canine of the lower jaw are further reduced than, for example, in the Bay Duiker *C. dorsalis* or Black Duiker *C. niger* (Kuhn 1966).

Geographic Variation None recorded.



Lateral, palatal and dorsal views of skull of Zebra Duiker *Cephalophus zebra*.

Similar Species Several species, notably Maxwell's Duiker *Philantomba maxwelli*, Bay Duiker, Black Duiker and Brooke's Duiker (*C. ogilbyi brookei*) are sympatric with Zebra Duikers. However, the striped colour pattern of the Zebra Duiker renders this species quite unmistakable.

Distribution Endemic to West Africa, ranging from E Sierra Leone (Moa R.) to Côte d'Ivoire (Niouniourou R.) within the primary forest zone. Most common in east-central Liberia. Its distribution and numbers have declined markedly because of forest destruction and excessive hunting for bushmeat. Its remaining strongholds are Sapo N. P. and other forests of SE Liberia, and Tai N. P. and adjacent forest reserves in Côte d'Ivoire (East 1999).

Historical Distribution In Sierra Leone, the Zebra Duiker probably occurred quite widely in the southern and central moist lowland forests. It appears to be dependent on undisturbed primary forest and has retreated as forest has been cut down and converted to farmland (Teleki *et al.* 1990, East 1999). By the 1980s, it was very rare and localized and known to occur in only a few localities, such as Gola N. P. (Davies 1987), the eastern part of Gaura Chiefdom and, possibly, Western Area F. R. (Grubb *et al.* 1998).

In Liberia, it appears to have been relatively common in some regions. In 1974–75, Jeffrey (1977) recorded that this was the third most frequent duiker species encountered in a survey of bushmeat in east-central Liberia. It was also the third most frequently encountered duiker species in the surveys reported by Kranz & Glumac (1983). It was thinly distributed along the Sehkwén R., but common in the Buto Oil Palm Plantation, and reported by local observers to be abundant along the Sinoe R. (Peal & Kranz 1990).

In Côte d'Ivoire, its distribution never extended further east than the Niouniourou R. (which lies between the Sassandra and Bandama Rivers), such that Zebra Duikers have historically always been restricted to the lowland forests in the south-west. Sightings of Zebra Duikers further to the east, for example in Comoé N. P. (see discussion in Fischer *et al.* 2002), are unsubstantiated.



Cephalophus zebra

Current Distribution Continued presence in Liberia was confirmed in 1997 in Sapo N. P. and from the forests bordering Côte d'Ivoire (East 1999). In Côte d'Ivoire the species is now confined to remaining areas of primary forest within its former range, namely Tai N. P. and the adjoining Haute Dodo–Rapide–Grah–Hana Forest Reserves, and the Cavally–Goin, Scio and Niegé Forest Reserves. Its main stronghold is Tai N. P., where it is seen regularly, and its abundance varies from common in the west to uncommon in the centre and rare in the east (Hoppe-Dominik *et al.* 1998). In Sierra Leone they persist in the Gola N. P. in the south-east (Lindsell *et al.* 2011, F. Dowsett-Lemaire & R. J. Dowsett pers. comm.), but their presence in the west is unclear.

The presence of Zebra Duikers in Guinea was not mentioned by Sournia *et al.* (1990) or Grubb *et al.* (1998), but East (1999) remarked that their presence was confirmed by a report from the Ziamá and Diécké Forest Reserves, presumably a reference to Butzler (1994). Wilson (2001) thought it likely that they should occur. The species was not reported by Barrie & Kant (2006) in a rapid survey of Diécké in 2003.

Habitat Found in undisturbed primary forests and along their margins and in clearings, sometimes extending into secondary growth and swidden cultivation (Newing 2001). It favours intact lowland forest (notably the Sinoe and other river valleys in Liberia), but may also live in low montane and hill forests.

Abundance Assuming average population densities of 2.0/km² where it is known to be common and 0.2/km² elsewhere, East (1999) gives an estimated total population of about 28,000. However, Wilson (2001) regarded this as an overestimate, and doubted that there could be more than 15,000 animals across the range at most. Davies (in Grubb *et al.* 1998) estimated peak population density in little-hunted areas in Sierra Leone at 3–10/km². Hoppe-Dominik *et al.* (2011) calculated a population density of 0.4/km² in Tai N. P.

using night counts and a total population of perhaps 2000 animals. The population trend is generally downwards because of bushmeat hunting and continuing destruction of West Africa's few remaining primary forests. The only exceptions are a few localities where hunting pressures are low and/or there is effective protection against logging and poaching, such as the western section of Tāi N. P. (East 1999, Hoppe-Dominik *et al.* 2011).

Adaptations Known to be a strong stimulus to the eye/brain sensory system, stripes may serve as a focus for social attraction (in which case the resemblance of these duikers to zebras may be more than superficial). An advantage of stripes in this species could be to inhibit goring of the soft abdomen during aggressive encounters. Thus, while other animals shield themselves from the worst effects of aggressive rivalry with thickened skin, bony plates and so forth, these duikers may have a subtler strategy for reducing excessive aggression (Kingdon 1997).

Grubb *et al.* (1998) suggested that Zebra Duikers are both diurnal and nocturnal. Captive animals in Monrovia Zoo, Liberia, were active about 70% of the daytime (Newing 2001); animals in Tāi N. P. were mainly active at night (Hoppe-Dominik *et al.* 2011).

Foraging and Food Diet comprises fruits and foliage. Details are unknown, but the Zebra Duiker does not appear to have specialized teeth or diet. The stomach contents of four duikers shot in Liberia indicated that at least 79% of plants eaten were fruits and seeds, and all four stomachs contained large numbers of the fruits of *Diospyros sanza-minika*; two stomachs contained seeds of *Bussea occidentalis* (Wilson 2001). The animal may use its head to break open the shells of larger fruits. In captivity, occasional consumption of meat (self-caught mice) has been observed (Schweers 1981), and indeed one of the stomachs mentioned by Wilson (2001) contained the remains of an unidentified rodent.

Social and Reproductive Behaviour All of 35 field observations from Tāi N. P. were of lone animals, suggesting a primarily solitary

social system (G. Radl pers. comm.). Friendly relations between captive pairs involve mutual rubbing and licking, suggesting that breeding pairs are the normal social unit (as they are in many duikers). Because both sexes have horns and a thickened skull (which do not appear to correlate with a specialization in ecology or diet), it seems likely that bonded pairs share defence of their home-range against intruding duikers and their offspring against predators. Scarred heads suggest that the collisions that are normal in duiker confrontations are particularly vigorous and uninhibited in these exceptionally stocky and muscular antelopes (Kingdon 1997).

Schweers (1984) conducted a detailed study of breeding behaviour and reproduction on captive Zebra Duikers in Frankfurt Zoo. Males will determine the female's reproductive status by smelling her urine and performing flehmen. While a consorting pair mutually mark each other even outside of the female's oestrous period, the frequency of this marking increases in the ♂ as the ♀ approaches oestrus, with the ♂ applying secretions from his preorbital glands to the head, neck and back of the ♀. As the ♀ approaches oestrus, the ♂ follows the ♀ more closely, and licks her neck, hindlegs and anogenital region. The ♂ usually follows directly behind the ♀, sometimes making grunting sounds, his head stretched forward such that his neck is horizontal and the head is held at the height of the female's tarsal gland. Mounting attempts occur when the ♀ stops moving, and is preceded by the ♂ smelling and licking the female's anogenital region; Schweers (1984) also recorded frequent high lifting of the foreleg past the female's hindlegs (in contrast to between the legs as occurs with laufschiag in gazelles). Copulation is brief, lasting only a few seconds, but is repeated frequently. Birth in captivity is normally in the morning hours, and typically takes place while the mother stands, the neonates mainly appearing front first. The mother then eats the afterbirth. The young are precocious, but remain alone lying up until Day 20 (Schweers 1984).

Expressions of sound are rare and, besides during mating, have only been observed in captivity during initiations of contact between mothers and their offspring, and during fighting (Schweers 1984).

Reproduction and Population Structure Detailed information about reproduction is given by Schweers (1984) and Barnes *et al.* (2002) from observation of captive animals. After a postpartum oestrus, ♀♀ are normally successfully mated as little as 10 days after birth (Schweers 1984). Gestation is between 221 and 229 days (although Pfefferkorn 2001 gives a range of 190–245 days) and the birth interval 241 days (Schweers 1984). A single young is born. The birth weight is around 1270–1550 g for ♂♂ and 1300–1750 g for ♀♀ (Barnes *et al.* 2002). Neonates are born with the dark stripes visible, although they appear closer together, giving the young an overall darker appearance (Schweers 1984). The weight development during the first 60 days ranges from 47 to 74 g/day; at 40–45 days weights are around 4450 g for ♂♂ and 3620–4620 g for ♀♀ (Barnes *et al.* 2002). Young are able to nurse shortly after birth, and for the first few weeks will nurse about four times per day for several minutes (Schweers 1984); solid food is consumed from the fifth week. The young animal is weaned after about 95–111 days (Barnes *et al.* 2002). Horns begin to appear at 1–2 months of age, and at the age of 7–9 months juveniles have the adult colouration and have reached adult height (Schweers 1984). Males reach sexual maturity at about two years of age (Barnes *et al.* 2002). A wild-born animal survived to 13 years in captivity (Weigl 2005).



Zebra Duiker *Cephalophus zebra*.

Predators, Parasites and Diseases The main predator in undisturbed habitat is undoubtedly the Leopard *Panthera pardus*. Hoppe-Dominik (1984) showed that the Zebra Duiker and Black Duiker made up a large part of the spectrum of prey (up to 10%) in Tāi N. P. Immature Zebra Duikers are present in the prey of the Crowned Eagle *Stephanoaetus coronatus* in Tāi N. P., but in low frequency (S. Shultz pers. comm.). Further, the African Golden Cat *Profelis aurata* and the African Rock Python *Python sebae* are likely predators. There is no information available on parasites or diseases.

Conservation IUCN Category: Vulnerable A2cd, C1. CITES: Appendix II.

Formerly widespread over much of Liberia and Sierra Leone, Zebra Duikers are declining fast as their habitat is being destroyed and commercial bushmeat hunting becomes more entrenched and comprehensive in its onslaughts. Wilson (2001) considered them the least adaptable to deforestation of all West African duiker species and therefore the least likely to survive hunting pressure and habitat degradation. Actual consumption of bushmeat was measured by Caspary *et al.* (1999) in a one-year study in the region of Tāi N. P. For the year of 1988 they estimated that 73,000 subsistence hunters killed about 1500–3000 tonnes and a group of professional hunters killed 52–650 tonnes of bushmeat in the region (2700 km²). The share of weight of the Zebra Duiker was about 2.1% of meat at market stands in the east of the park (26 Zebra Duikers out of a total of 2171 animals killed) and 1.8% in the west (36 duikers out of a total of 5101 animals killed there). The share of the Zebra Duikers killed in the forests to the west of the R. Cavally in Liberia and smuggled into Côte d'Ivoire was around 5%. Of a total of 11,215 animals, 440 Zebra Duiker cadavers were counted. Data collected from hunters (representing approx. 3% of the total village population) in three villages in Sinoe County in Liberia over 10 months (2001–2002)

demonstrated that Zebra Duikers represented the fourth most commonly killed animal (R. Hoyt pers. comm.).

Due to undiminished demand for game meat and unsustainable hunting, there is a high risk that species with restricted ranges such as the Zebra Duiker (which is dependent upon primary rainforests) will be extirpated. Existing protected areas therefore need to be extended, networked and their protection considerably improved. Important conservation areas for the protection of this species include the Gola complex of reserves in Sierra Leone, Sapo N. P. and Grebo National Forest (Liberia), and Tāi N. P. and surrounding forest reserves in Côte d'Ivoire (East 1999, Wilson 2001).

Measurements

Cephalophus zebra

HB (♂ ♂): 846 (830–870) mm, n = 4

T (♂ ♂): 125 (122–127) mm, n = 4

HF c.u. (♂ ♂): 221 (215–227) mm, n = 4

E (♂ ♂): 79 (77–80) mm, n = 4

WT (♂ ♂): 13.5, 14.2 kg, n = 2

WT (♀): 14.7 kg, n = 1

Liberia (Kuhn 1966)

Wilson (2001) gives an average of 17 kg for five ♂ ♂ (range 15–21 kg), and 18 kg for four ♀ ♀ (range 15–23 kg). Shoulder height of ♀ ♀ averages 460 mm, compared with 440 mm in ♂ ♂

Maximum recorded horn length is 7.9 cm for a pair of horns from Liberia (Rowland Ward)

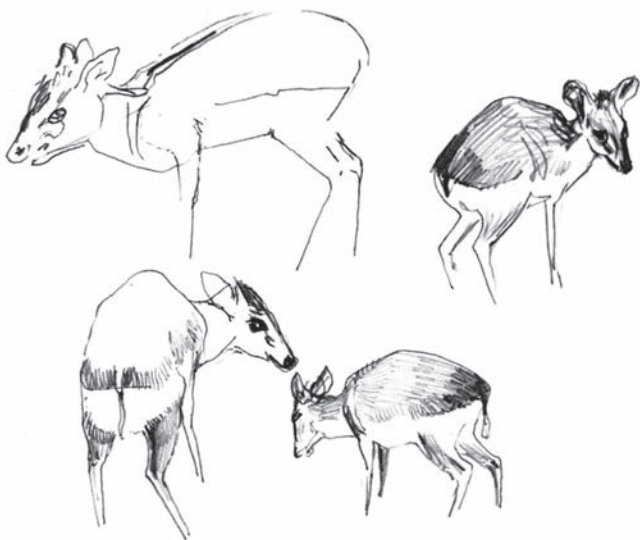
Key References East 1999; Kingdon 1997; Schweers 1984; Wilson 2001.

Bernd Hoppe-Dominik

Cephalophus adersi ADERS'S DUIKER

Fr. Céphalophe de Aders; Ger. Adersducker

Cephalophus adersi (Thomas, 1918). Ann. Mag. Nat. Hist., ser. 9, 2: 151. Tanzania, 'Zanzibar'.

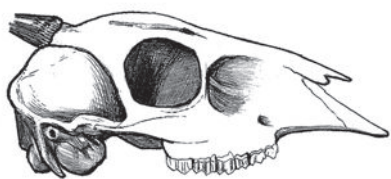


Aders's Duiker *Cephalophus adersi*.

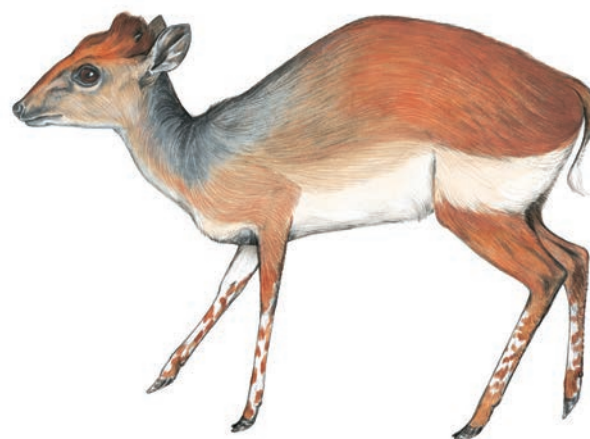
The vernacular name is after William Mansfield-Aders, a zoologist for the government in Zanzibar in the first few decades of the 1900s.

Taxonomy Monotypic. The species has been considered conspecific with both Natal Red Duiker *C. natalensis* and/or Peters's Duiker *C. callipygus* (e.g. Heyden 1968, Dorst & Dandelot 1970, Haltenorth & Diller 1980), but is currently regarded as a separate species (Kingdon 1982, 1997, Grubb & Groves 2001, Wilson 2001, Grubb 2005). On the basis of a molecular study of duikers, Jansen van Vuuren & Robinson (2001) found that this species occupied a consistently basal position in the duiker radiation, confirming Kingdon's (1982) prediction that this might be a relictual species from an early phase in the evolution of 'red duikers'. Synonyms: none. Chromosome number: not known.

Description A small to medium-sized duiker standing about 40–45 cm at the shoulder when fully grown and weighing 8–12 kg (Kingdon 1982, Williams *et al.* 1995, Wilson 2001). The fur is soft and



ABOVE: Lateral view of skull of Aders's Duiker *Cephalophus adersi*.
BELOW: Occlusal view of the upper-right tooththrow in Aders's Duiker *Cephalophus adersi*.



Aders's Duiker *Cephalophus adersi*.

silky, with a marked cow-lick or whorl of hair on the nape of the neck but little change in texture from the neck to the main body (Kingdon 1982, 1997). The muzzle is pointed, with a flat front to the nose. The overall colour is a reddish-ochre but grey on upper shoulder and back of neck and light fawn on the sides of the face, neck, shoulder and flanks. The bridge of the nose and crown are richly red with a prominent darker tuft at the horns. The underbelly is clear white. Aders's Duiker can be distinguished from other red duikers by the white freckling on the lower limbs and a broad white band on the rump, which merges into the underparts (Kingdon 1982, Wilson 1987, Williams *et al.* 1995). Preorbital glands present; pedal glands long, narrow and well developed. Inguinal glands are absent.

Aders's Duiker have simple spiked horns that grow to a little over 5 cm in length (Kingdon 1982, Williams *et al.* 1995, Wilson 2001). In the skull, the preorbital fossae are deep with a sharply defined upper margin; there is no interfrontal groove and no marked frontal convexity. The nasals broaden distally (Grubb & Groves 2001).

Geographic Variation The species is monotypic, although Kingdon (1982) reported hunters' assertions that animals from NE Zanzibar (Kiwengwa) were darker and heavier than animals from Jozani Forest (south-central), which were paler and lighter in weight (see Wilson 2001).

Similar Species

Cephalophus harveyi. Sympatric in coastal Kenya. Larger, redder and lacks white belly and buttock stripe.

Distribution Endemic to Africa. In Kenya, Aders's Duiker has been described as once widespread in the forests, woodland and thickets north of Mombasa up to the Somali border (Kingdon 1982). However, as a result of rapidly shrinking suitable habitat, the population has succumbed to a severe decline in numbers. Until recently, the species was thought to have become confined to a very small population in the Arabuko-Sokoke Forest north-west of Kilifi (East 1999), which covers approximately 416 km². However, in 2004, an Aders's Duiker was sighted in Dodori National F. R. north of the Tana River Delta on the N Kenya coast (Andanje & Wachter 2004), where earlier recorded by Gwynne & Smith (1974). Since then extensive camera-trapping work has found that Aders's Duiker is the most frequently recorded antelope in the Boni-Dodori forests (Andanje *et al.* 2011a, b). One reason for their distribution and habits being poorly known is that Aders's Duikers

inhabit coastal forests and thickets that often grow on very coarse coral rag, an inhospitable, waterless and, in places, impenetrable, habitat. Given such habitats and a presumably recent connection between the Zanzibar and coastal populations it is possible that the species may survive in other pockets of similar habitat elsewhere along the East African coast, especially in coastal habitats between the Pangani/Rufiji and Galana/Tana rivers (Andanje *et al.* 2011b). Because they show no signs of being exceptionally specialized and because of their likely basal position in the duiker radiation, a primary constraint on their distribution may well be the existence of competition from other red duikers, suggesting that their overall distribution is intrinsically relictual (J. Kingdon pers. comm.).

In Tanzania, Aders's Duikers still occur on Unguja (Zanzibar) I., although the population has declined substantially and now faces an increasingly uncertain future. There is a possibility that Aders's Duikers may have once occurred on Fundo I., off the coast of Pemba I. (see Williams 1998), and it is reported to have been introduced to Funzi I., Pemba (Kingdon 1997), but has since become extinct on both these islands. Archer & Mwinyi (1995) mention unconfirmed, but reliable, reports indicating a thriving population on Tumbatu I. – a small island lying off the north-west of Unguja I. While this was once certainly the case, the Aders's Duiker population on Tumbatu has heavily declined and may now no longer exist. In February 2000, five Aders's Duikers were translocated to Chumbe I. (a private marine reserve) lying off Unguja I. to complement a single previously translocated ♀ (see Mwinyi & Wiesner 2003). A few individuals were also translocated to Mnemba I. off the north-east coast of Unguja and are breeding (K. Siex pers. comm.).

Habitat In Zanzibar, Aders's Duikers inhabit tall, undisturbed thicket known locally as 'msitu mkubwa' (Archer 1994) in the waterless coral-rag on the eastern side of the island. Aders's Duiker is very sensitive to habitat disturbance, but occasionally occurs in secondary thicket (Williams *et al.* 1995). In prime habitat south of Jozani Forest, the emergent tree layer is dominated by *Mystroxydon aethiopicum*, *Diospyros consolatae* and sub-dominantly by *Euclea schimperi*. The shrub layer is dominated mainly by *Polysheria multiflora* and *Canthium hibracteatum* (Swai 1983). In Arabuko-Sokoke Forest, Aders's Duikers are most often sighted in the undisturbed *Cynometra* vegetation, mostly on red soil, with fruiting vegetation (Kanga 1995, 2002). In Dodori National F. R., Aders's Duiker has been recorded

from dense coastal thicket with full canopy cover to ca. 4–5 m and a ground layer of leaf litter and tangled stems on sandy substrate (Andanje & Wacher 2004).

Adaptations Wilson (2001) commented that the preorbital gland of Aders's Duiker was different to any other he had studied, being about one-quarter the size of the preorbital gland of even the smallest duikers. He found the gland to be near-vestigial and only a small part was active from which only small quantities of secretion could be squeezed. The gland of a ♂ had short rufous hair on top of the gland and above the opening, while below the slit there was no hair at all, and the slit of the gland was about 8 mm long and 2 mm wide. Wilson (2001) suggested that Aders's Duikers might not mark their territories to the same extent as other duikers and might, therefore, be losing the use of their preorbital glands. On the other hand, J. Kingdon (pers. comm.) thinks it possible that *C. adersi* conserves an earlier or transitional stage in the evolution of the duiker type of preorbital gland.

Aders's Duikers survive in a very demanding and specifically coastal environment where they must periodically derive their water needs from the plant parts that they eat. To this extent they are coastal specialists and probably have appropriate physiological adaptations. Apart from this they do not exhibit very marked specialization in diet or foraging techniques and their distribution accords with the suggestion that their geographically and ecologically marginal existence may reflect a relictual status (J. Kingdon pers. comm.). These duikers are diurnal/crepuscular and very shy (Archer 1994, Kingdon 1997, Andanje *et al.* 2011a).

Abundance To date three surveys have been carried out on Unguja I. The first in 1982 (Swai 1983) estimated the Aders's Duiker population to be in the region of 5000 individuals. A second, more detailed survey undertaken in 1995 (Williams *et al.* 1995) placed the population between 1200 and 2000. The populations were shown to be located in five main sub-populations with varying degrees of interconnectedness: Kiwengwa Forest in the north, localities in the central Jozani-Chwaka Bay area and Mtende in the south. A third survey carried out in 1999 (Kanga & Mwinyi 1999) placed the population at 614 ± 46 within the same study area as Williams *et al.* (1995). Although the surveys all adopted different methodologies, they show a very substantial decline in the population over a 17-year period. In 1995, Aders's Duikers on Zanzibar were found to occur at an overall density of $4.5 \pm 1.2/\text{km}^2$ in high thicket (comparing favourably with that of $4.3/\text{km}^2$ recorded by Swai [1983]), with higher population densities of up to $11.4 \pm 5.2/\text{km}^2$ in limited areas of particularly undisturbed high thicket habitat (Williams *et al.* 1995). The impact of hunting was not controlled so the species must have once occurred naturally at higher densities than those measured.

Until recently Aders's Duiker in Kenya was thought to have become restricted to the Arabuko-Sokoke Forest where it was once common but is now considered very scarce. A very approximate figure of about 500 individuals was estimated in 1999 based on a small drive-count survey in the Arabuko-Sokoke Forest (Kanga 2002). In Arabuko, Aders's Duikers were found to occur at a density of $2.8/\text{km}^2$ (Kanga 2002, 2003a). Overall, recent surveys have only sighted very low numbers (three in 1999, two in 2002 and two in 2003) (Kanga 2002, 2003b).

Camera-trapping surveys have shown that Aders's Duiker is the most frequently recorded antelope in the camera grids in the Boni-



Cephalophus adersi

Dodori forests and surrounds, being present at 51 of 52 camera sites, returning a standardized photo rate of 75 encounters/100 days across three grids dispersed over 1200 km². In contrast, at Arabuko-Sokoke, a comparable sampling effort returned 0.09 encounters/100 days (Andanje *et al.* 2011a).

Foraging and Food Aders's Duikers are browsers selecting for dicotyledonous leaves, seeds and fruit (Swai 1983). They show a particular dependence on the flowers and berries that grow prolifically from common trees, such as *Diospyros consolataei*, *Cassine aethiopica* and *Euclea schimperi*, and bushes such as *Canthium* spp. and *Polyspheria* (Kingdon 1997); Wilson (2001) recorded the fruits of *D. consolataei*, *Ficus sur* and *Tetracella littoralis*. In addition to these foods they will eat sprouts, buds and other fresh growth found at ground level (Kingdon 1997). Individuals may sometimes follow troops of Gentle Monkeys *Cercopithecus mitis* and Zanzibar Red Colobus *Procolobus kirkii* feeding on discarded fruits and dislodged edibles from the canopy above (Swai 1983, S. Imani pers. comm.).

Feeding occurs from dawn to around 11:00h, followed by a period of rest and rumination, before becoming active again from about 15:00h when they continue to forage until nightfall (Kingdon 1997). The species has been reported as being independent of water (Kingdon 1982).

Aders's Duikers are sympatric with Harvey's Duikers *C. harveyi*, Blue Duikers *Philantomba monticola* and Sunis *Nesotragus moschatus* on the mainland, and with Blue duikers and Sunis on Zanzibar. Little is known regarding their feeding and ecological separation, but camera trapping data suggests that Aders's Duikers hold their own in relative numbers at key sites such as Boni-Dodori (75 encounters/100 days compared with 55 Suni encounters and two for Harvey's Duiker), with broadly similar diurnal activities patterns in all three (T. Wacher pers. comm.). It can be predicted that diurnal feeding allows these duikers to benefit from monkey and bird activity in the canopy (Kingdon 1982).



Aders's Duiker *Cephalophus adersi*.

Social and Reproductive Behaviour Aders's Duikers have been reported to live in pairs and to defend territories (Kingdon 1997). However, Aders's Duikers have also been recorded singly (Williams *et al.* 1995); out of 3021 separate camera-trap records at Boni-Dodori, only 8.5% comprised two animals (mostly adult pairs, but also mother and young) with less than 1% involving trios (T. Wachter pers. comm.).

Reproduction and Population Structure Aders's Duikers reportedly breed throughout the year (Rodgers & Swai 1988). During a six-month survey on Zanzibar, Archer & Mwinyi (1995) recorded 40 Aders's Duikers shot by local hunters, 24 of which were pregnant. Pregnant ♀♀ were recorded in all months, with three of eight and three of four pregnant ♀♀ having large fetuses in Aug and Sep, respectively.

Predators, Parasites and Diseases Natural predators, apart from people, have been eliminated on Zanzibar, most notably the Zanzibar Leopard (sometimes afforded the trinomial *Panthera pardus adersi*), but on the mainland Leopards may still take individuals. At Boni-Dodori, predators such as Lion *P. leo*, Leopard, Caracal *Caracal caracal*, African Wild Dog *Lycaon pictus* and Spotted Hyaena *Crocuta crocuta* all co-occur with Aders's Duiker (T. Wachter pers. comm.). A parasite taken from an animal in Zanzibar was described as *Tricholipeurus pakenhami* (Pakenham 1984).

Conservation IUCN Category: Critically Endangered A4cd. CITES: Not listed.

Aders's Duiker has undergone severe long-term population declines in both Kenya and Zanzibar (Tanzania) due to habitat loss and hunting pressure. In Zanzibar there has been a large amount of deforestation and forest degradation, particularly over the last 30 years, as the human population has increased. Much of the habitat loss has been driven by a demand for domestic fuelwood by a rapidly expanding urban population. This has led to extensive loss of habitat for Aders's Duikers but also severe habitat fragmentation. Habitat destruction is probably the most significant threat to the species' survival on Zanzibar, and one that is unlikely to be solvable in the short term. Jozani-Chwaka Bay N. P., which was gazetted in 2004, includes important but only small parts of suitable habitat for Aders's Duikers as does the proposed Kiwengwa-Pongwe F. R.

In Kenya, the Arabuko-Sokoke Forest is one of the last major remnants of lowland forests on the East African coast. Illegal wood-cutting has led to the deterioration of the species' habitat and contributed to the decline of the population. Kanga (2003b) reported that levels of wood-cutting increased between the surveys he carried out in 1998 and 2002. It is likely that habitat destruction will constitute the most difficult threat to address in terms of the species' future security in Arabuko-Sokoke (Kanga 2003b). The discovery, then, of a significant population of Aders's Duiker in the Boni-Dodori forest to the north improves the conservation prospect for the species, and highlights the need for improved management efforts in the Boni-Dodori forest (Andanje *et al.* 2011b).

Aders's Duikers are traditionally hunted in Zanzibar but an increase in hunting pressure likely followed the revolution of 1964 after which enforcement of the wildlife laws became largely non-existent (Finnie 2004). It would appear that, partly as a result of

hunting, the mini-antelope populations of Zanzibar (especially Aders's Duikers) have undergone long-term declines (for example, see Williams *et al.* 1995, Kanga & Mwinyi 1999). The Department of Forests and Non-Renewable Natural Resources began to address the hunting situation in Zanzibar in 1994, through community-based conservation initiatives. Although hunting has now come under an increasing level of control in Zanzibar (both at the village and governmental level) it remains a significant threat up to the present (Finnie 2002).

In the Arabuko-Sokoke Forest, trapping is common. In 1991, more than 2600 households lived within 2 km of the forest and at least 33% carried out hunting and/or trapping (FitzGibbon *et al.* 1995). It is thought that the high level of snare-trapping in the Arabuko-Sokoke Forest represents a significant threat to the continued existence of Aders's Duikers in this forest (Kanga 1995, 2002, Finnie 2004) as the species is a favoured target because of its sweet meat, which fetches a good price at market. Kanga (1995) stated that when hunters found an area where they suspected Aders's Duikers occurred, they would saturate the pathways with a large number of traps. Hunters told Kanga that Aders's Duikers were often caught in the 1970s, but that since the 1980s their hunting success with this species was low. However, Kanga's (1995) observations can be contrasted with FitzGibbon *et al.*'s (1995) assertion, without documentation, that trapping for duiker species in 1991 was well within sustainable limits. The impact of hunting on the Aders's Duiker population that may exist in the vicinity of the Boni-Dodori forests is unknown.

Measurements

Cephalophus adersi

HB (unsexed): 714 (630–780) mm, n = 14

T (unsexed): 111 (60–138) mm, n = 14

E (unsexed): 78 (75–87) mm, n = 14

Sh. ht (unsexed): 404 (375–440) mm, n = 14

WT (♂♂): 9.2 (8.7–10.2) kg, n = 9

WT (♀♀): 9.0 (6.8–10.1) kg, n = 5

Zanzibar (Kanga & Mwinyi 1999)

Wilson (2001) noted that Kanga & Mwinyi (1999) failed to indicate how their measurements were taken, and draws attention to the doubtful reliability of their measurements of the hindfoot (mean = 452 mm). Wilson (2001) gave the measurements of two adult ♂♂ as TL: 823–830 mm; T: 100–122 mm; E: 73–81 mm; HF c.u.: 195–214 mm; Sh. ht: 400–420 mm; and WT: 8.5–10.7 kg. Measurements for three ♀♀ were TL: 790–846 mm; T: 120–131 mm; E: 68–76 mm; HF c.u.: 210–225 mm; Sh. ht: 410–435 mm; and WT: 10.5–12.4 kg.

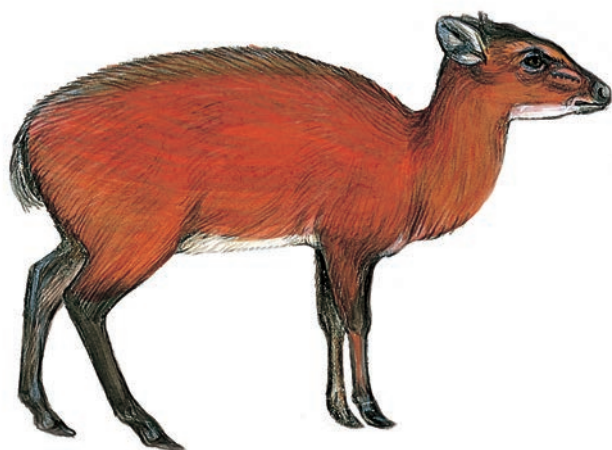
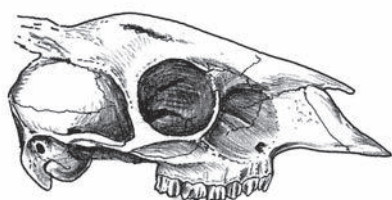
Maximum recorded horn length for this species would appear to be that of a ♂ captured in Jozani Forest in 1999, measuring 5.3 cm and reported by Kanga & Mwinyi (1999). The longest pair recorded by Wilson (2001) was 4.8 cm, on an adult ♂ killed by hunters and measured by the side of a road near Jozani Forest, which exceeds the 3.8 cm pair recorded by Rowland Ward from the Arabuko-Sokoke Forest

Key References Kanga 2002; Kanga & Mwinyi 1999; Williams 1998; Williams *et al.* 1995; Wilson 2001.

Andrew Williams

***Cephalophus rubidus* RWENZORI RED DUIKER**

Fr. Céphalophe de Rwenzori; Ger. Rwenzoriducker

Cephalophus rubidus Thomas, 1901. Proc. Zool. Soc. Lond. 1901 (2): 89. 'Ruwenzori District'.Rwenzori Red Duiker *Cephalophus rubidus*.Lateral view of skull of Rwenzori Red Duiker *Cephalophus rubidus*.

Taxonomy This species has been treated as a subspecies of *C. natalensis* (Schwarz 1914) and as a subspecies of the Black-fronted Duiker *C. nigrifrons* (St Leger 1936, Ansell 1972, Groves & Grubb 1981). Because this species occurs on the same Rwenzori mountain range as another race of the Black-fronted Duiker (*C. n. kivuensis*), yet differs from it in features that suggest other affinities, Kingdon (1982, 1997) regarded this as a distinct high-altitude red duiker, proposing that it might have been pushed up into its present sub-alpine and upper montane forest habitat by the later arrival of the Black-fronted Duiker. Molecular studies have also indicated that *C. rubidus* is a distinct taxon with relatively old and ill-defined affinities with other red duikers, although admittedly the only material available for the analysis was a single tooth from a specimen in the Swedish Museum of Natural History (Jansen van Vuuren & Robinson 2001), which may itself be misidentified. Wilson (2001) was reluctant to consider *rubidus* a distinct species, and Grubb & Groves (2001) and Grubb (2005) both considered it a subspecies of *C. nigrifrons*. Synonyms: none. Chromosome number: not known, but given their conserved karyotype it is likely to be $2n = 60$ (B. Jansen van Vuuren pers. comm.).

Description A medium-sized duiker with a glossy rufous coat with long coarse hair on the neck changing to dense soft hair over the hindquarters. Black or dark brown blaze on the forehead. Zone

*Cephalophus rubidus*

of dark grey underlies uniform red tips of fur down mid-line of the back and neck, while underfur of the flanks is cream. Chin and belly white. Hindlegs almost black, dark brown markings on the joints of the forelegs. Tail bushy. Pedal and preorbital glands present. The horns, present in both sexes, reach 8–9 cm in length (Kingdon 1982).

Geographic Variation Currently believed to be restricted to the upper reaches of the Rwenzori Mts, no significant variation is known or likely. However, sightings of very russet duikers from the bamboo zone of the Bwindi forest in SW Uganda suggest a distinctive duiker in a relictual habitat once similar to that in which *C. rubidus* occurs on the Rwenzori Mts.

Similar Species

Cephalophus nigrifrons. Long-legged and long-hooved species from montane and lowland forest habitats. Kingdon (1982) suggested that *C. rubidus* and *C. n. kivuensis* (which occurs in the lower altitudes of the Rwenzoris Mts) might hybridize where their ranges overlap.

Distribution Endemic to Africa, where confined to the Rwenzori Mts (Kingdon 1982, Grubb & Groves 2001). Although it presumably occurs on the section of the Rwenzori Mts that lies within Virunga N. P. in DR Congo, the presence of this form in this country has not been confirmed (East 1999, Wilson 2001).

Habitat Mostly found in alpine and sub-alpine habitats between the snow/glacier line and bamboo zones, at altitudes of 1300–

4200 m. They occur along the margins of *Carex* tussock bogs, in afroalpine moorland dominated by *Helichrysum*, *Alchemilla*, giant groundsels *Dendrosenecio* and giant lobelias *Lobelia* and in heath 'woodlands' dominated by tree heaths, *Philippia* and *Erica*.

Abundance Data are scarce, but daylight sightings and hunter's middens reported before the mid-1960s suggest that it was once very abundant in its preferred habitats. East (1999) suggested that the population of the Rwenzori Red Duiker may number at least in the thousands.

Adaptations Apparently able to tolerate very low temperatures at night and frequent cold rain or snow, as well as periodic strong insolation during the day. The peculiarly soft, dense texture of the pelage on the body of this species would seem to be adapted to these peculiar conditions, although no attempt has been made to assess the insulating or water-proofing properties of the hairs. Activity periods are likely to be strongly influenced by the very frequent rain on the Rwenzoris.

This species is of some significance for our understanding of mammalian adaptation to an extreme habitat, especially as such situations are rare in Africa. As the only large mammal to inhabit the high, cold and wet afroalpine vegetation zones of the Rwenzori Mts it offers unique opportunities for the study of physiology, dietary habits and behavioural repertoires in a ruminant that has several apparent equivalents in temperate Eurasia, North and South America (notably Goral *Naemorhedus goral*, Chamois *Rupicapra rupicapra*, Pudu *Pudella mephistophiles* and Musk Deer *Moschus moschiferus*). Molecular studies imply that this species is likely to derive from a population of duikers that preceded the evolution of the specialized Black-fronted Duiker (Jansen van Vuuren & Robinson 2001).

While the legs and hooves of this species appear to be less specialized in their proportions than those of the Black-fronted Duiker, it is likely that less obvious physiological adaptations could be significant.

Foraging and Food No direct information is available, but the absence of fruit and abundance of afroalpine herbs (especially *Alchemilla*) and lichens in the sub-alpine zone suggest that these are possible staples. Rock-cress *Arabis alpina*, violets *Viola* spp. and ground orchids *Disa* spp. are also common, but other flowering plants are few

and small in size. Around bogs, the sedge *Carex petitiiana* as well as the nettle *Laportea alatipes* might be eaten; a few high-altitude grasses, the heavy rain-exposed bark and roots of plants both large and small are all likely forage. Along the lower margins of its habitat the fruits of *Rubus* might be important and herbs such as goose-grass *Galium*, sorrels *Rumex* spp., wild parsley *Peucedanum* spp. and borage *Cynoglossum* spp. are very abundant and probable foods.

Social and Reproductive Behaviour Casual observations suggest that these duikers are generally solitary except when juveniles or subadults accompany their mothers or ♂♂ are accompanying an oestrous ♀.

Reproduction and Population Structure Nothing is known about the timing of breeding or any other aspect of reproduction in this species.

Predators, Parasites and Diseases Known predators include African Golden Cats *Profelis aurata* and probably Leopards *Panthera pardus*. Large, migratory eagles sometimes fly over the Rwenzori Mts, but are not likely to be any more than a rare hazard.

Conservation IUCN Category: Endangered B1ab(iii); C2a(ii) (listed as *C. nigrifrons rubidus*). CITES: Not listed.

A very vulnerable species owing to the ease with which it can be snared and the increase in illegal hunting within Rwenzori Mountains N. P., Uganda, the species' only known protected area stronghold. This species has long been a highly desirable quarry for Bakonjo hunters from the inhabited foothills. As noted earlier, the species presumably occurs on the section of the Rwenzori Mts that lies within Virunga N. P., but the presence of this form within DR Congo requires confirmation.

Measurements

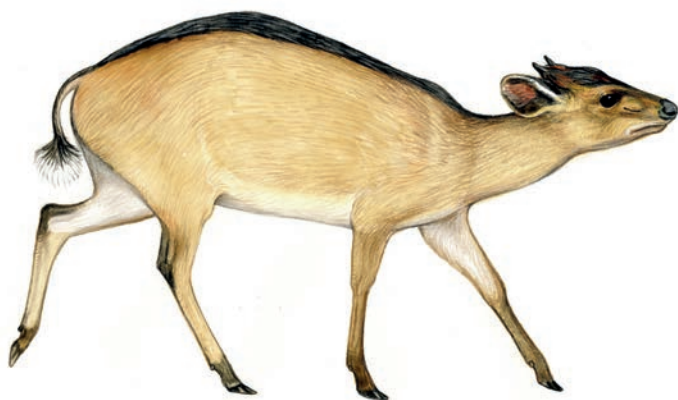
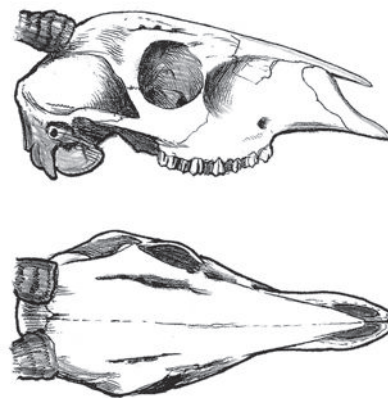
No reliable measurements are available. Grubb & Groves (2001) gave mean GLS as 172 ± 4.2 mm ($n = 3$) for ♂♂ and 180 mm for a single ♀.

Key References Kingdon 1982; St Leger 1936; Wilson 2001.

Jonathan Kingdon

Cephalophus leucogaster WHITE-BELLIED DUIKER

Fr. Céphalophe à ventre blanche (Céphalophe du Gabon); Ger. Weusbauch Ducker

Cephalophus leucogaster Gray, 1873. Ann. Mag. Nat. Hist., ser. 4, 12: 43. 'West Africa, Gaboon' (Gabon).White-bellied Duiker *Cephalophus leucogaster*.Lateral and dorsal views of skull of White-bellied Duiker *Cephalophus leucogaster*.

Taxonomy Type specimen named from an immature animal collected by Du Chaillu in Gabon. Rode (1943) mistakenly lumped *leucogaster* and *ogilbyi* as subspecies of the Bay Duiker *C. dorsalis*. Ansell (1972) included the form *arrhenii* as a subspecies of the Bay Duiker, but this form is actually attributable to *C. leucogaster* (Grubb & Groves 2001). Synonyms: *arrhenii*, *seke*. Chromosome number: not known, but likely $2n = 60$.

Description Pale, sandy-coloured 'red duiker' with a distinctive narrow black dorsal patch, broadest in the middle back. A sleek animal with short dense hair, and gracile build, this species is one of the more delicately built of the forest duikers. Sides of face pale rufous; forehead contains a strong admixture of black hairs, darkening toward the nose producing a distinctive dark frontal blaze. Back of ear pinnae rufous admixed with dark hairs on the outer surface, and variably fringed with light hair on the upper rim and black hairs toward the base of the rim. Inner surface of ear with black patch on lower third of the ear. Both sexes have a coronal tuft of upright, bright rufous hairs between the horns. The dark dorsal patch begins as a narrow dark streak at the base of the neck, intergraded with dark rusty hairs over the shoulders, widening into a nearly pure black, distinctively marked, dorsal patch, widest in the middle of the back, where it sharply contrasts with the pale sandy-coloured sides, narrowing again and ending in a point just above the tail. Neck and sides pale rufous, sprinkled with darker hairs dorsally, and white hairs ventrally. Chest, abdomen and inside of upper legs pale cream, becoming nearly pure white on the lower abdomen. Limbs pale rufous admixed with darker hairs on outer surface on front legs and shoulder. Rear hocks with indistinct black patches. Lower limbs, from metacarpals distally, black. Tail pale rufous-sandy colour at base and along upper surface, with large brush of long black hairs, many with the distal third white-tipped. Preorbital glands, producing a greyish exudate, are present in both sexes, and run from under the eye toward the muzzle. Inguinal glands and pedal glands present in both sexes. Inguinal secretions

are rusty-coloured and are visible on the white ventral surface of some animals. There is little sexual dimorphism: ♂♂ and ♀♀ have similar pelage, but adult ♀♀ average between 8% (Congo) and 11% (Ituri Forest, NE DR Congo) larger body mass than adult ♂♂ (see Measurements). Pelage of newborns differs from adults in being overall pale grey, with less distinctive dorsal patch. This pelage is replaced by adult colouring before weaning.

Cranium with broadened toothrow and palate, though the skull is not as robust or broad as in the Bay Duiker *C. dorsalis*. Horns present in both sexes, stout and strongly annulated at base, and variably over three-quarters of their length, turned inwardly at the tips in older ♂♂.

Geographic Variation

C. leucogaster leucogaster: range of the species, except NE DR Congo.

Colour darker and redder. Dorsal stripe narrow (e.g. between 21 and 84 mm on the Cameroon coast); slightly smaller in size.

C. leucogaster arrhenii (includes *seke*): NE DR Congo. Colour paler, browner. Dorsal stripe broader (in Ituri 80–156 mm wide); size slightly larger.

Similar Species

Cephalophus ogilbyi. The White-legged Duiker (*C. o. crusalbum*) is partially sympatric with White-bellied Duiker in W Gabon. Distinguished by its overall more russet colour and white patches on its legs.

C. dorsalis. Broadly sympatric in Gabon. Larger and overall darker in colour and with the dorsal band widest over the rump, not in the middle of the back.

C. callipygus. Sympatric in western central Africa. More rufous; dorsal patch widest over the rump.

C. weynsi. Sympatric east of the Ubangi R. Deeper rufous in colour and lacks the black dorsal patch.

Distribution Endemic to the central African lowland forest zone, and apparently restricted to forest below 1000 m. The White-



bellied Duiker ranges in the west from S Cameroon (south of the Sanaga R.), through Gabon, Equatorial Guinea, N and SW Congo (where the species is reported in the forest savanna complex along the Atlantic coast), and extreme SW Central African Republic (East 1999, Wilson 2001). The provenance of museum specimens north of the Sanaga R. remains uncertain (P. Grubb, in Lamarque *et al.* 1990, Grubb *et al.* 2003). The species is found again with certainty in NE DR Congo in the Ituri Forest, Maniema and North Kivu. It is uncertain if the species ever occurred north of the Mboumu R. into the forest blocks of SE Central African Republic (for example, East [1999] and Wilson [2001] both map its possible occurrence from Bangassou Forest, from whence there are no confirmed records). There are no records from Cabinda (Angola) (Crawford-Cabral & Veríssimo 2005), but it may occur, perhaps ranging into the Bas-Congo province in DR Congo.

The species' occurrence in DR Congo's central cuvette is also hypothetical (von Richter *et al.* 1990, Wilson 2001). Schouteden (1947) shows four records west of about 24°E along the Congo R., including two from locations on the left bank of the river, but it is uncertain if these specimens originated from these locations. A skin reportedly of this species has been reported from Salonga N. P., but no details are known, and the skin was apparently not examined; more recent surveys of animals taken by local hunters in the park failed to produce any evidence of the species (von Richter *et al.* 1990, Hart *et al.* 2008). There is no further evidence of the species' occurrence south of the Congo R.

The White-bellied Duiker is not known to range east of the lowland forest block bordering the Albertine Rift, although it was thought possible that it may exist in the Kayonza Forest, in W Uganda (Kingdon 1982). It may still occur in the forests west of the Semliki R. in DR Congo. The range of the White-bellied Duiker, with distinct western and eastern block populations, resembles that of another small forest ungulate, Bates's Pygmy Antelope *Neotragus batesi*.

Habitat The White-bellied Duiker is restricted to areas of extensive, intact closed tropical moist forest. It occurs in upland, terra firma, primary forest and older secondary forests. It is absent from areas of recent clearing and disturbance. The species does not occur in swamp forests and does not range into gallery forest or the forest–savanna ecotone north of the main forest block. Its characterization by Malbrant & Maclatchy (1949) as a common species of secondary forest and savanna ecotone and not of deep forest has not been supported by subsequent research. In the central Ituri Forest, radio-collared individuals frequented areas of open understorey, and tended to avoid dense stands of herbaceous thickets. In the Ituri Forest and the Nouabale–Ndoki area of N Congo this is one of the characteristic species in the monodominant *mbau/limbali* forests, a closed-canopy formation dominated by *Gilbertiodendron dewevrei*. Fruit and seed availability in monodominant forests is strongly seasonal with periods of very low availability juxtaposed by brief pulses of abundance during the supra-annual mast flowering and seed production by the dominant *G. dewevrei* (Hart 1985). In the Ituri Forest, where six species of frugivorous duikers, and the Water Chevrotain *Hyemoschus aquaticus* co-occur, population densities of all species except the White-bellied Duiker are lower in large monodominant stands than in the more productive, and seasonally less variable, mixed-canopy formations (Hart 1985, 2001). For White-bellied Duikers, the monodominant forest appears to represent a competitive refuge from the more densely occupied mixed-forest areas, where combined densities of all small ungulates can reach 45–50/km². In large monodominant stands, in contrast, total small ungulate densities are about half this value, and the White-bellied Duiker's nearest competitor, the similarly sized, diurnal Weyns's Duiker *Cephalophus weynsi*, is absent.

Abundance A little known species over much of its range, the White-bellied Duiker is reported as uncommon or rare in most areas where it occurs. Dubost (1984) reported the species comprising less than 11% of all individuals reported in hunter catches in E Gabon (Makokou area). Elsewhere in Gabon, the species is most frequently reported in Lopé N. P., but is uncommon and poorly known elsewhere (Blom *et al.* 1990). White-bellied Duikers were represented by only 2 of 198 skulls collected in SW Central African Republic (Wilson 2001). Colyn *et al.* (1987) report the species as the least common among duikers in surveys of the Kisangani bushmeat markets. The species appears to be more common in the Ituri Forest where densities of unhunted radio-collared populations averaged about 4.5/km² in mature mixed forest and about 6/km² in monodominant *Gilbertiodendron dewevrei* forest, contributing about 15% and 35% of the total small ungulate biomass in mixed and monodominant forest, respectively (Hart 2000, 2001). East (1999), assuming average population densities of 2.0/km² where it is known to be common/abundant and 0.2/km² elsewhere, estimated the total population at 287,000 individuals.

Adaptations The White-bellied Duiker is a diurnal species that occupies large home-ranges. The species has long legs, a gracile build and a broadened, but lightly built dental arch and palate. These adaptations are associated with a trophic niche specifically adapted to widely dispersed high-quality food patches. This specialization provides the White-bellied Duiker with a

relative advantage over more generalist duikers in monodominant forests where food resources can be uncommon and patchy, and are successfully exploited by the duiker that 'gets there first'. In the Ituri Forest, radio-collared adults ranged widely over annual home-ranges that averaged 63 ha in mixed forest and 58 ha in mbau forest. These home-ranges were comparable in area with those of the larger nocturnal Bay Duiker, and nearly twice the area of the similarly sized diurnal Weyns's Duiker. Radio-collared animals regularly patrolled widely dispersed, known fruit sources, and frequently accompanied troops of primates. While other duikers also feed beneath primates, White-bellied Duikers actively seek and follow moving troops to a much greater extent than other more sedentary duiker species. They feed not only on fallen fruit parts, but more remarkably are coprivorous, foraging selectively on primate faeces when these contain concentrations of nutrient-rich seeds, and in particular *Landolphia* spp. The relatively broad mouth and wide maw indicate that the species is capable of ingesting large-sized fruits. However, unlike the Bay Duiker, which has a still broader tooththrow, the dentition of the White-bellied Duiker is less robust, and lacks the developed cranial supports for expanded musculature to deal with coarse foods. It would seem that aggressive intra-specific conflict is sufficiently rare given the light build of the skull and lack of reinforced cranial boss. The wide ranging and wandering movements of the White-bellied Duiker would appear to obviate the need for armoured defences typical of some of its immediate competitors, such as Weyns's Duiker, which occupy smaller more intensively defended territories.

Foraging and Food The diet is dominated by fruits and seeds. Gautier-Hion *et al.* (1980) and Dubost (1984) recorded that fruit comprised almost three-quarters of stomach contents collected in Gabon. In captive feeding trials, White-bellied Duikers invariably selected fruits over foliage, even when these contained relatively higher levels of fibre (Molloy & Hart 2002). Hart (1985) found the White-bellied Duiker to be among the most dedicated frugivore of all the forest duikers in the Ituri Forest, with ripe fruits, unripe fruits and edible seeds comprising from 80% to 100% of rumen contents in all but the most extended periods of fruit and seed dearth. Seasonally dominant dietary items included seeds of *Landolphia* spp., and the unripe and still soft aborted fruits of *Kalinedoxa gabonensis* and *Irvingia grandifolia*. These relatively uncommon and ephemeral, but high-quality, foods were less frequently found in the diets of other duiker species. Like other duikers, White-bellied Duikers feed on caesalpinaceous mast when this is available. Fungi and fallen flowers picked up from the forest floor dominated diets during periods of low fruit availability. In common with other frugivorous duikers, the White-bellied Duiker disperses seeds of a number of species of forest trees (Feer 1995). These tree species have characteristically large, heavily armoured seeds, which duikers spit out undamaged when they ruminate. A number of these trees appear to be specialized for ungulate dispersal and the fruits are not regularly eaten by other frugivores. In the Ituri Forest, two of these species, *Donnella pruniformes* and another unidentified Sapotaceae, were characteristically eaten and seeds dispersed by White-bellied Duikers. Both tree species are uncommon, and produce large, soft, latex-rich fruits in small numbers over extended periods that are

optimally exploited by this species' wide-ranging, patrol-foraging strategy.

Social and Reproductive Behaviour Male and female home-ranges overlap, and pairs are perhaps drawn together by the noise made by the primates that both sexes seek to accompany. Nevertheless, sexes often range separately. Radio-collared juveniles often travelled in company with their mothers; however, both sexes disperse from maternal home-ranges at the onset of sexual maturity.

Reproduction and Population Structure A wide seasonal spread of birth and pregnancy records in the Ituri Forest implies that some breeding goes on throughout the year. Seven of nine estimated birth months occurred during the late rains (Aug–Nov), when fruits are seasonally most abundant, a pattern also found in some other duikers in Gabon (Dubost & Feer 1992). In the Ituri Forest, about 60% of 20 adult ♀♀ examined were pregnant. Gestation period has been estimated at six months (Dubost & Feer 1992). Females produce a single young. The weights of two full-term foetuses were 1300 and 1500 g.

Predators, Parasites and Diseases White-bellied Duikers are killed by Leopards *Panthera pardus* in the Ituri Forest (Hart, J. A. *et al.* 1996); however, the species is not among the most selected prey. Per capita annual predation of radio-collared White-bellied Duikers was lower than for nocturnal duikers, such as Bay Duikers and Yellow-backed Duikers *C. silvicultor* (Hart 2000). Serological surveys of duikers in the Ituri Forest revealed potentially significant exposure to bluetongue, epizootic haemorrhagic disease, infectious bovine rhinotracheitis and leptospirosis (Karesh *et al.* 1995). This study also recorded several ixodid tick species, including *Haemaphysalis parvula*, *Ixodes cumulatimpunctatus* and a *Rhipicephalus* sp.

Conservation IUCN Category: Least Concern. CITES: Not listed.

White-bellied Duikers appear to be rare or declining in many areas of their range. The species is extremely vulnerable to over-hunting and is one of the first species to drop out of the small ungulate fauna in areas subject to heavy snare pressure. Some populations may have become locally extinct in recent time with the advent of uncontrolled hunting and the bushmeat trade. In Ituri Forest, indigenous Mbuti hunters regularly catch White-bellied Duikers on net drives. Since the persistence of hunting is often determined by the frequency of capture of more abundant species such as the Blue Duiker *Philantomba monticola*, White-bellied Duikers could be hunted to local depletion or extirpation, even when already rare (Hart 2000). The species' wide-ranging movements over large home-ranges expose it to higher risk by snare capture than more sedentary species. Important protected areas for this species include Lopé N. P. (Gabon), Monte Alén N. P. (Equatorial Guinea), Dzanga-Ndoki N. P. (Central African Republic), Odzala N. P. and Nouabalé-Ndoki N. P. (Congo) and Kahuzi-Biega N. P., Maiko N. P. and Okapi Faunal Reserve (DR Congo) (East 1999). Management of the bushmeat trade in Okapi Faunal Reserve, a stronghold for White-bellied Duikers, would improve overall prospects for the species' conservation (Wilkie *et al.* 1998).

Measurements*Cephalophus leucogaster*

HB (♂): 1050 mm, n = 1

T (♂): 105 mm, n = 1

Sh. ht (♂): 490 mm, n = 1

WT (♂♂): 16.8 (14.7–18.1) kg, n = 15

WT (♀♀): 18.9 (16.8–21.0) kg, n = 23

Ituri Forest, DR Congo (J.A. Hart pers. obs.)

WT (♂♂): 15.5 (14–17) kg, n = 5

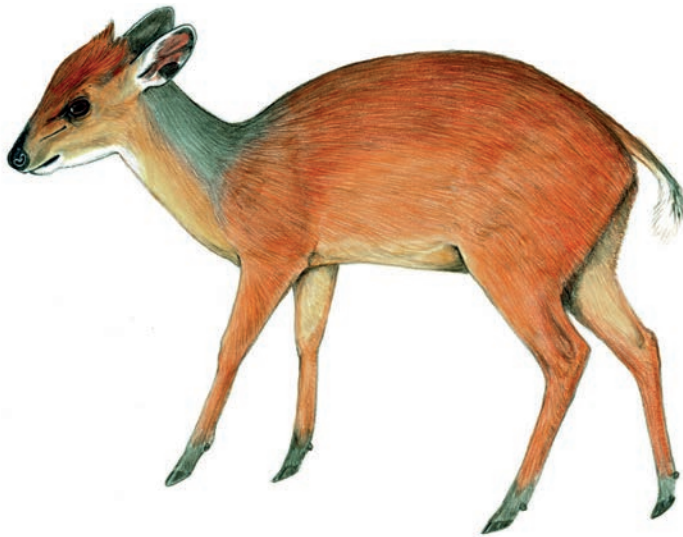
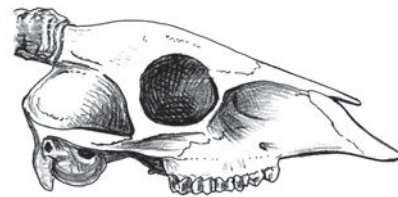
WT (♀♀): 16.8 (15.5–17.5) kg, n = 8

N Congo (Wilson 2001)

The record pair of horns measured 12.7 cm from Sette Cama, Gabon (Rowland Ward)

Key References Hart 1985, 2000, 2001; Wilson 2001.**John A. Hart*****Cephalophus natalensis* NATAL RED DUIKER**

Fr. Céphalophe du Natal; Ger. Natal-Rotducker

Cephalophus natalensis A. Smith, 1834. S. Afr. Quart. J. 2: 217. South Africa, KwaZulu–Natal, ‘Port Natal’ (Durban).Natal Red Duiker *Cephalophus natalensis*.Lateral view of skull of Natal Red Duiker *Cephalophus natalensis*.

Taxonomy In a revision of the duikers, Grubb & Groves (2001) included Harvey's Duiker *C. harveyi* as a single subspecies of the Natal Red Duiker *C. natalensis* (and see Jansen van Vuuren & Robinson 2001 and Hassanin *et al.* 2012). Ansell (1972) considered Harvey's Duiker *C. harveyi* and Weyns's Duiker *C. weynsi* as conspecific with *C. natalensis* and he offered a provisional list of 11 subspecies (including 'walkeri' from Malawi, which was actually a *Sylvicapra*; see Grubb 1988, 2005). Excluding these extralimital or mistaken forms, Ansell still retained four described subspecies of *C. natalensis* (as defined here). Following Swynnerton & Hayman (1951), Kingdon (1982, 1997) and East (1999), we provisionally treat *C. natalensis* and *C. harveyi* as separate species and recognize two subspecies within *C. natalensis* (following Meester *et al.* 1986). Synonyms: *amoenus*, *bradshawi*, *lebombo*, *robertsi*, *vasei*. Chromosome number: 2n = 60 (Robinson *et al.* 1996b).

Description A small duiker, often giving a first impression of being an all-over, uniform red. Although there is substantial regional and individual variation, the upperparts of the body are typically a deep chestnut-red, the lower part of the flanks and underparts pale chestnut, and there is a prominent crest of long, bushy, chestnut-coloured hair on the top of the head, which often conceals the horns. The sides of the muzzle, the sides and underparts of the neck, and the inner upper

surfaces of the limbs range from tawny or pale fawn to a rich red, only marginally lighter than the upperparts. The lower jaw behind the black or brown chin is always white and white or cream sometimes extends onto the upper throat. Ears short and rounded with a fringe of black hair on the outside margins; insides with three alternating black and white, rather 'smudged' markings. The back of the neck varies in colour with animals from the southern part of the range tending to uniform red while those in the north are more variable, sometimes having the entire nape light or dark grey. The pasterns and hind part of the hocks are also variable, sometimes red but more commonly darker in colour, with a tinge of dull violet or grey. The upperparts of the tail are the same colour as the back, darkening towards the whitish tip. Preorbital glands are present as a perceptible swelling below and in front of each eye. The gland exudes secretion along a streak of black skin that is studded with a row of small pores (Mainoya 1978); the secretion is a clear sticky fluid with a faint aromatic odour, the chemical constituents of which have been investigated by Burger *et al.* (1988). Interestingly, the preorbital gland secretions of the Natal Red Duiker and Common Duiker *Sylvicapra grimmia* contain two major constituents absent from the preorbital gland secretion of the Blue Duiker *Philantomba monticola*. Pedal glands are present, and discussed in detail by Mainoya (1978); there are no inguinal glands.

Horns, present in both sexes (those of ♂♂ twice the length of ♀♀), are short, straight, with coarse basal rings and longitudinal striations, but smooth towards the tips.

Geographic Variation

C. n. natalensis (including *amoenus*, *lebombo*): S and NE KwaZulu–Natal, E Mpumalanga and possibly S Mozambique. General description as above with strong erythrismic tendency.

C. n. robertsi (including *bradshawi*, *vasei*): Mozambique, north of the Limpopo R. northwards through S Malawi to SE Tanzania. Specimens

from Mozambique tend to be more orange/rufous in colour on the upperparts of the body than their counterparts from KwaZulu–Natal. In addition, the head is darker and there are slight traces of a dark frontal blaze, not present in animals from KwaZulu–Natal (Wilson 2001). Grey napes are also more common (J. Kingdon pers. comm.). Comparing specimens from lowland STanzania (south of the Rufiji R.) with specimens of *C. natalensis* from many other parts of their range, Swynnerton & Hayman (1951) had no hesitation in allocating them to *C. n. robertsi*.

Similar Species

Cephalophus harveyi. Larger red duiker ranging from N Malawi, NE Zambia, through suitable forested areas of C and NE Tanzania to SE Kenya and S Somalia. Legs dark grey to brownish-black; mid-facial zone blackish; crest with more black in it. Bolder, more strongly contrasting facial and ear patterns. For intermediate-looking animals along the interface between *C. natalensis* and *C. harveyi*, see discussion in next section.

Distribution Endemic to Africa. The Natal Red Duiker formerly occurred widely in coastal and riverine forests and thickets from SE Tanzania to NE KwaZulu–Natal. The species' distribution within this range is patchy and discontinuous and the clearing of forests and thickets to make way for agricultural development has destroyed much suitable habitat. Natal Red Duikers still occur locally in forest patches and coastal scrub in SE Tanzania, while in Mozambique they are still believed to occur widely in the eastern, coastal parts of the country, as well as in a few scattered localities inland; they are reported to occur at high densities in Maputo G. R. Their distribution range extends southwards through Mpumalanga and the Limpopo Province of South Africa (in the Soutpansberg), Swaziland, to KwaZulu–Natal, where they occur mainly in the north-eastern parts (East 1999, Wilson 2001, Skinner & Chimimba 2005). The southernmost limit of distribution has been given as extending as far

south as Pondoland (Bowland 1990) and even to George (Skead 1980); Rowe-Rowe (1994) shows the species occurring in small isolated populations along the coast south to about Oribi Gorge at about 31°S. Today they probably do not occur much further south than Durban. There are no confirmed records of this species from Zimbabwe (Smithers & Wilson 1979, Wilson 2001). East (1999) shows the species occurring in NE Zambia and N Malawi, but these records relate to Harvey's Duiker, the Natal Red Duiker being known only from S Malawi (Ansell 1978, Ansell & Dowsett 1988).

Red duikers from the area between the Ruvu and Rufiji valleys in E Tanzania approach *C. harveyi* in colouring and this area may represent a hybrid zone (Kingdon 1982). A similar hybrid frontier is implied by Wilson's (2001) observations on the Nyika Plateau in N Malawi where animals he observed looked like intermediates between *C. natalensis* and *C. harveyi*. The relationship between these very closely related duikers awaits a scientifically rigorous resolution.

Habitat Throughout their range, Natal Red Duikers are associated with forests and dense thickets, occurring in riverine forest and in thickly wooded ravines and dense coastal bush. In NE KwaZulu–Natal they occur up to about 200 m elevation (Rowe-Rowe 1994). They are independent of water; in KwaZulu–Natal, only one of the home-ranges of the duikers studied by Bowland (1990) had a perennial water supply.

Abundance The only reliable density estimates available for Natal Red Duikers are from KwaZulu–Natal, where Bowland (1990) recorded densities varying from 1 ind/0.5–1.0 ha in favourable habitat (such as at St Lucia) to 1 ind/2.5–5.0 ha in less favourable areas. East (1999) estimated the total population to stand at about 42,000, but noted this could be an underestimate. Rowe-Rowe (1994) gave the population size for KwaZulu–Natal as between 2000 and 3000 animals; the largest population in this province occurs in Greater St Lucia Wetland Park (1000). A substantial part of the range of this species occurs in Mozambique, where an overall recovery in wildlife populations is likely to include this duiker.

Adaptations Natal Red Duikers are diurnal, with peaks in activity at dawn and dusk, and little evidence of nocturnal activity (Bowland 1990, Wilson 2001), a pattern that is confirmed by the frequency of their bones in the debris below nests of the diurnal Crowned Eagle *Stephanoaetus coronatus* in STanzania (J. Kingdon pers. comm.). They are shy and secretive, and if disturbed seldom stand for more than a few seconds before bounding away into thick bush, often emitting a hoarse alarm 'whistle'. They are said to display a remarkable jumping ability; De Vos (1979) reported an instance of two adults clearing a 1.6 m high fence.

Metabolic rates are high, and energy requirements are met by utilizing easily digestible and fermentable plant parts while less digestible parts (lignin, cellulose) are poorly digested due to the fast digesta passage rates (Faurie & Perrin 1995, Perrin *et al.* 2003). The rumen has been described as similar to that of the Blue Duiker, displaying many adaptations typical of concentrate selectors, including a densely, evenly papillated rumen for maximum nutrient absorption (Faurie & Perrin 1995). High rates of food intake, frequent rumination and rapid fermentation ensure efficient supply of energy and nutrients (Perrin *et al.* 2003).



Cephalophus natalensis

Foraging and Food Natal Red Duikers are browsers and frugivores, feeding primarily on leaves (fresh and fallen), wild fruits and flowers, and shoots of low-growing shrubs. An analysis of the contents of 19 stomachs from KwaZulu–Natal found that dicotyledonous leaves had a relative occurrence of 66%, seeds and fruits 25% and flowers 1% (Faurie & Perrin 1993, Bowland & Perrin 1998). Although Gagnon & Chew (2000) reported a very small percentage (1%) of monocotyledons in the diet (and see Sponheimer *et al.* 2003b), Prins *et al.* (2006) recorded between 15% and 20% of monocots in the diet.

Bowland (1990) directly observed Natal Red Duikers eating the freshly fallen leaves of *Cussonia sphaerocephala*, *Strychnos spinosa*, *Celtis africana*, *Ficus stuhlmanii*, *Sapium integerrimum*, *Harpephyllum caffrum*, *Barringtonia racemosa*, *Apodytes dimidiata*, *Acacia robusta* and *Ziziphus mucronata*. Heinichen (1972) recorded them feeding on *Dichrostachys cinerea*, *Strychnos madagascariensis*, *Gardenia cornuta*, *Azima tetracantha*, *Asparagus falcatus* and *Justicia protracta*. Other species recorded from the examination of stomach contents include *Justicia* sp., *Commelina africana* and *Grewia* sp. (Heinichen 1972). Elevated water and protein content of leaves influence the food choice of Natal Red Duikers, but there is no evidence that condensed tannin concentrations influence leaf choice, since some highly preferred species have tannin concentrations exceeding 18% while other rejected leaves have concentrations of less than 2% (Faurie & Perrin 1993, Bowland & Perrin 1998, Perrin *et al.* 2003). Wilson (2001), after Bowland (1990), provides a detailed list of dietary items in the diet of Natal Red Duikers recorded in southern Africa.

Prins *et al.* (2006) investigated niche segregation among three small antelopes – Natal Red Duikers, Common Duikers and Sunis *Nesotragus moschatus* – in a coastal savanna woodland/forest mosaic in S Mozambique to determine whether they exhibited any obvious differences in diet to avoid competition. Some 80 dietary items were recorded being used by Natal Red Duikers. On average, only about 10% of the food items used by all three small bovids were specific to one species only. Diet overlap was considerable in the wet season, but the use of exclusive species was significantly larger in the dry season, and significantly larger for the Natal Red Duikers (Prins *et al.* 2006). Likewise, Blue and Natal Red Duikers are sympatric in many localities, with home-ranges of the two species often overlapping. Both generally have similar diets, and they exhibit no temporal separation since both are diurnal, with only subtle differences in spatial utilization (e.g. Natal Red Duikers sometimes forage beyond the forest margin) (Perrin *et al.* 2003).

Social and Reproductive Behaviour Natal Red Duikers are primarily solitary, although it is not uncommon to encounter a ♀ with her offspring, or pairs or small groups of three to five (♂♂ sometimes form temporary associations in the absence of a ♀). Home-ranges usually cover an area of 2–15 ha in size, and decrease in size with an increase in population density and availability of food resources. Communal dung heaps are used to demarcate the boundaries. The secretion from the preorbital glands is also dabbed onto stems and branches as a means of marking the home-range. However, there is no evidence of territoriality (as in Blue Duikers) and home-ranges may overlap by as much as 80–100%; there was also extensive overlapping of core areas of home-ranges (Bowland 1990, Bowland & Perrin 1995).

Vocalizations include an alarm whistle, and a loud ‘tchie-tchie’ sound, which is louder and more penetrating than that of the Suni (Heinichen 1972). Natal Red Duikers are known to ‘thump’ or ‘alarm stamp’ prior to fleeing.

Natal Red Duikers have been recorded in association with Vervet Monkeys *Chlorocebus pygerythrus*; the monkeys were seen actively grooming a duiker, which itself solicited grooming on several occasions (Borland & Borland 1979).

Reproduction and Population Structure Breeding occurs throughout the year, and three-month-old lambs have been observed in Feb, Jul and Aug (A. E. Bowland pers. obs.); in captivity, young are also born throughout the year, with no discernible peak (Spence 2003). A single young is born; captive animals had an average mass at birth of 979 g ($n = 2$) and an inter-birth interval of 236 days (range 222–273, $n = 5$; Spence 1991). Gestation period is in the order of 7 months. Bowland, in Rowe-Rowe (1994), gives age at first conception at 18–24 months, but a captive ♀ conceived when just under a year old (Spence 1991). Bowland (in Rowe-Rowe 1994) gives a potential life-span of 8–9 years; Weigl (2005) gives a longevity record in captivity of 15 years.

Predators, Parasites and Diseases Natal Red Duikers, in particular infants or juveniles, are likely to fall prey to a number of medium to large carnivore species (e.g. Roche 2003), as well as birds of prey (such as the Crowned Eagle; Wilson 2001) and African Rock Pythons *Python sebae*. Very little was known of the helminth parasites of Natal Red Duikers until the studies of Boomker and co-workers in KwaZulu–Natal (Boomker *et al.* 1984, 1991d). The latter authors summarized what was known at the time, listing 17 species of nematodes, two species of cestodes (*Moniezia benedeni* and *Stilesia hepatica*) and trematodes (paramphistomes). Ectoparasites in Natal Red Duikers have been investigated by various authors, primarily in KwaZulu–Natal; Horak *et al.* (1991a) examined 20 duikers from two reserves in NE KwaZulu–Natal and recorded the following ixodid ticks: *Amblyomma marmoreum*, *Haemaphysalis leachi*, *H. parvata*, *Rhipicephalus appendiculatus*, *R. maculatus*, *R. muehlensi* and *R. evertsi*. In addition, they recovered two species of lice (*Damalina* sp. and *Linognathus* sp.).

Conservation IUCN Category: Least Concern. CITES: Not listed.

Natal Red Duikers have disappeared from large parts of their former range, largely as a result of the loss of suitable habitat in the face of expanding human settlement and agriculture, combined with the impacts of hunting. None the less, despite what is likely to be a gradual population decline across much of their range, they are not likely to be threatened as a species, and remain well represented by healthy populations in a number of protected areas, such as Selous G. R. (Tanzania), South Vipya F. R. (Malawi), Maputo G. R. (Mozambique) and Greater St Lucia Wetland Park, Hluhluwe–iMfolozi and Ndumo G. R. (South Africa) (East 1999).

Measurements

Cephalophus natalensis

TL (♂♂): 864 (809–900) mm, $n = 9$

TL (♀♀): 890 (855–950) mm, $n = 8$

T (♂♂): 96 (70–115) mm, $n = 8$

T (♀ ♀): 103 (85–125) mm, n = 8
 HF c.u. (♂ ♂): 231 (220–245) mm, n = 9
 HF c.u. (♀ ♀): 227 (220–240) mm, n = 8
 E (♂ ♂): 77 (74–81) mm, n = 9
 E (♀ ♀): 77 (72–80) mm, n = 8
 Sh. ht (♂ ♂): 412 (380–480) mm, n = 9
 Sh. ht (♀ ♀): 418 (385–450) mm, n = 8
 WT (♂ ♂): 11.7 (9.8–12.6) kg, n = 9
 WT (♀ ♀): 11.9 (10.3–13.2) kg, n = 9
 KwaZulu–Natal (A.E. Bowland pers. obs.)

TL (♂ ♂): 869 (805–903) mm, n = 5
 TL (♀ ♀): 910 (850–920) mm, n = 7
 T (♂ ♂): 96 (80–106) mm, n = 5
 T (♀ ♀): 100 (84–114) mm, n = 7
 HF c.u. (♂ ♂): 230 (220–240) mm, n = 5
 HF c.u. (♀ ♀): 235 (219–240) mm, n = 7

E (♂ ♂): 78 (74–82) mm, n = 5
 E (♀ ♀): 75 (73–77) mm, n = 7
 Sh. ht (♂ ♂): 419 (390–460) mm, n = 5
 Sh. ht (♀ ♀): 420 (388–460) mm, n = 7
 WT (♂ ♂): 11.9 (9.8–12.7) kg, n = 5
 WT (♀ ♀): 12.0 (9.9–13.6) kg, n = 7
 Mozambique (Wilson 2001)

Maximum recorded horn length is 10.4 cm for a pair of horns from Mufindi, Tanzania (Rowland Ward), but these measurements undoubtedly refer to Harvey's Duiker *C. harveyi*.

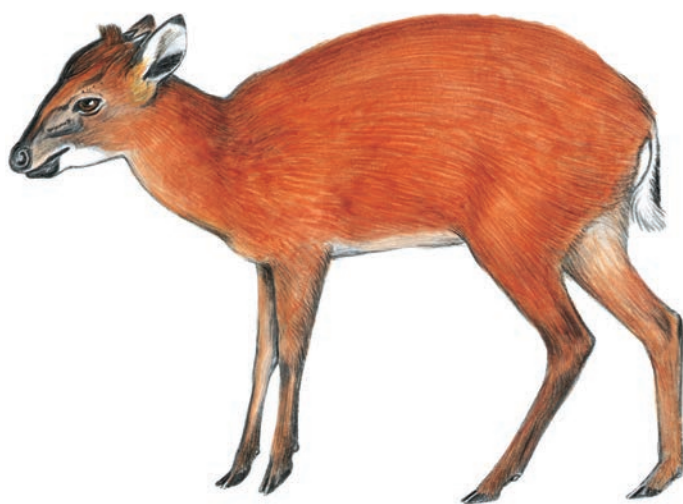
Key References Bowland 1990; Bowland & Perrin 1994, 1995, 1998; East 1999; Heinichen 1972; Skinner & Chimimba 2005; Wilson 2001.

Michael Hoffmann & Anthony E. Bowland

Cephalophus harveyi HARVEY'S DUIKER

Fr. Céphalophe de Harvey; Ger. Harveyducker

Cephalophus harveyi (Thomas, 1893). Ann. Mag. Nat. Hist., ser. 6, 11: 48. Kahe Forest, Moshi District, Tanzania.



Harvey's Duiker *Cephalophus harveyi*.

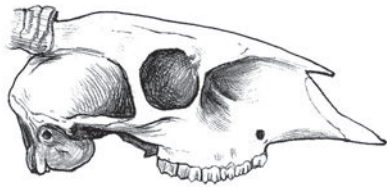
Thomas named the species for Sir Robert G. Harvey, a member of the hunting party which took the type specimen.

Taxonomy Treated as a subspecies of Natal Red Duiker *C. natalensis* by some authors (Heyden 1968, Ansell 1972, Groves & Grubb 1981, Grubb & Groves 2001, Wilson 2001, Grubb 2005; and see Jansen van Vuuren & Robinson 2001 and Hassanin *et al.* 2012), Kingdon (1982) considered that subsuming this very distinctive population in *C. natalensis* risked obscuring the complex evolutionary history of red duikers. None the less, likely hybrids between *C. harveyi* and *C. natalensis* are known from some of the lowland areas where their ranges appear to overlap (Kingdon 1982). Wilson (2001) considers animals from N Malawi on the Nyika Plateau as intermediate between Harvey's Duiker and the

Natal Red Duiker, commenting that the red duikers he saw in Selous G. R. were very similar to these duikers. Synonyms: *bottegoidi*, *keniae*. Chromosome number: not known, but likely to be $2n = 60$ as in *C. natalensis* (B. Jansen van Vuuren pers. comm.).

Description A richly russet-red duiker with the red of the rump and back becoming lighter below. The dorsal portion of the head shows a very distinct black band that covers the bridge of the nose and becomes wider above the eyes. The centre of the crest is also black and this line is continued down the back of the neck where it gives way to a dark freckle. In southern parts of its range this melanistic tendency extends to the dorsal portion of the neck, shoulders and, in the same area, the legs can be entirely dark sepia brown. Hundreds of camera-trapping photographs of Harvey's Duikers from several sites in the Udzungwa Mts show that there is large variation in the extent of these dark portions of the pelage between individuals within the same area (Rovero *et al.* 2005, F. Rovero pers. obs.). By contrast, animals from Mt Kenya tend to be more consistently red. As with the Natal Red Duiker, preorbital glands are embedded in a large swelling below and in front of each eye, the external expression of which comprises a black streak of skin studded with a row of small pores (Mainoya 1978). Pedal glands are present, and discussed in detail by Mainoya (1978); there are no inguinal glands.

Geographic Variation Populations in the northern part of their range (Kenya and N Tanzania) differ from those in SC Tanzania, but the boundaries or clinal areas between them remain to be elucidated. It may eventually be possible to characterize these two populations as subspecies. Three names have been applied to this duiker: *harveyi* from Kilimanjaro, *keniae* from Mt Kenya and *bottegoidi* from lowland coastal forest on the extreme northern edge of its range. These names should be treated as synonyms until their taxonomic status has been assessed.



Lateral view of skull of Harvey's Duiker *Cephalophus harveyi*.

Similar Species

- Cephalophus nigrifrons*. Lowland forest block and montane isolates on Mt Kenya, Mt Elgon and the Aberdares. Long-legged, long-hooved species with dark, finely freckled pelage.
- C. natalensis*. A primarily southern African duiker, reaching its northerly limit in the Rufiji Valley, STanzania. Smaller; legs slightly grey or not at all; facial mid-line in front of eyes darker.
- C. weynsi*. Mainly found in central Africa and Uganda extending as far as the Mau forest in Kenya. A larger species with longer, more arched muzzle and duller orange-red colouring. Kingdon (1982) suggested some red duikers from the Mau massif in Kenya might be hybrids between Weyns's Duiker and Harvey's Duiker.
- C. adersi*. Restricted to Zanzibar and the East African coast (notably the Arabuko-Sokoke Forest and Boni-Dodori forests, but also, perhaps, other East African isolated coastal forest pockets). Smaller, with white underbelly, white freckling on the lower limbs, and a broad white band on the rump.

Distribution Endemic to Africa. Patchily distributed through various forest types in the moister eastern parts of C and SE Kenya and NE and C Tanzania and, marginally, in extreme S Somalia (including, formerly, the lower Shebelle and Juba Rivers where now probably extinct) and N Malawi (Wilson 2001). There is a single record of this species from the Zambian side of the Nyika Plateau (Ansell 1978; mapped by East [1999] as *C. natalensis*).

Red duikers seen in the Hareenna Forest on the Bale massif (Hillman 1988a, Yalden *et al.* 1996) and another population in Omo N. P. in SE Ethiopia (Schloeder & Jacobs 1996) probably represent this species (East 1999), although the Omo duikers could be Weyns's Duiker *C. weynsi*, which occurs in the Imatong Mts of S Sudan, some 400 km to the south-west of Omo (East 1999, Wilson 2001; and see Grubb *et al.* 2003).

Habitat Found in both moist coastal forests and riverine gallery forests in the eastern parts of its range. It ascends into montane forests on Mt Kenya, the Aberdares and the Eastern Arc Mts in Kenya and Tanzania (see below). There it is found in both drier and moister forest types but predominantly in the vicinity of permanent water. In the Udzungwa Mts, Tanzania, it has been recorded in miombo woodland at 400 m; in dry, *Commiphora*-dominated bush at 1400 m; also up to about 2200 m in mixed upper montane forest and bamboo thickets (F. Rovero pers. obs.) and may well range to the highest forested slopes of Mt Luhomero to about 2400 m. It has also been reported as widespread in the highest Forest Reserves of the Uluguru Mts, which range to over 2400 m (Doggart *et al.* 2004).

Abundance Data scarce, but observations suggest that the species may be more abundant on the moister eastern or windward sides of



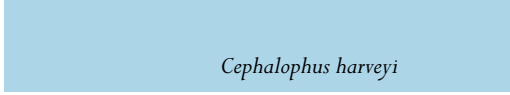
Cephalophus harveyi

massifs and scarcer on the drier western rain-shadow sides. Assuming an average population density of 2.0/km² in favourable areas and 0.2 in other parts of its range, East (1999) estimated a total population of 20,000 individuals, but notes that this could be an underestimate. A sharply downward trend in the overall population is evident in the rapid clearance and human settlement of its preferred riverine habitat.

Extensive camera-trapping and line transect censuses conducted in the Udzungwa Mts indicated high variation in the density of Harvey's Duikers even within relatively close and similar forest sites, presumably related to a combination of past and current hunting pressure and habitat features. Highest densities of about 13.3/km² were recorded in Matundu Forest in ground-water semi-deciduous forest at 300–500 m within Udzungwa Mountains N. P. However, in areas of the same forest where hunting had occurred, the density decreased to 8.2/km², and in the highly disturbed Uzungwa Scarp forest density dropped to about 2.1/km² (Rovero & Marshall 2009). Similarly, in Mwanihana Forest, at an altitude of 300–1000 m, the density resulted in the range of 4.8–9.5 ind/km² for moderately disturbed and undisturbed forests within the National Park (Rovero & Marshall 2009). These results confirm that East's (1999) average density estimations for favourable areas might be underestimates and that more data are required before a sound, overall estimation can be attempted.

Adaptations Contemporary molecular studies suggest that the closest relatives of the *harveyi*/*natalensis* group are the swamp-forest adapted Black-fronted Duiker *C. nigrifrons* and woodland adapted Red-flanked Duiker *C. rufilatus* (Jansen van Vuuren & Robinson 2001). Since both the latter species have moved into habitats that are atypical of other duikers, the very generalized Harvey's Duiker could be a passable model for their common ancestral type.

Until very recently Harvey's Duikers were abundant in the montane forests of East Africa and neighbouring coastal areas. This abundance and the absence of a clearly defined habitat preference confirms that this species fills the niche of medium-sized frugivorous antelope within



Cephalophus harveyi

Cephalophus harveyi

Cephalophus harveyi

Cephalophus harveyi

Cephalophus harveyi

the bushes *Acokanthera frisorum* and *Warburgia ugandensis* are also eaten. *Parinari excelsa* is dominant in some montane areas and *Ficus*, *Cordia* and *Lannea* spp. are widespread; all are known foods. Within its range the following are known sources of fruit and/or leaves: *Annona senegalensis*, *Anthocleista grandiflora*, *Tabernaemontana pachysiphon* and species of the genera *Bridelia*, *Canthium*, *Coccinia*, *Diospyros*, *Euclea*, *Grewia*, *Mammea*, *Parkia*, *Poliscias*, *Rhus*, *Sapium*, *Strychnos*, *Trema* and *Uapaca* (Kingdon 1982, T. Jones & F. Rovero unpubl.).

Digestion in the forestomachs has not yet been investigated. However, the strict preference for dicotyledonous leaves and fruits likely results in a high rate of volatile fatty acid production in the rumen. This is indicated by anatomical features such as a dense papillation of the mucosa to enhance absorption and inconspicuous thin rumen pillars (Hofmann 1973) resulting in a short rumen retention time, and a paucity of rumen protozoa (Hoppe *et al.* 1981). This contrasts with a surprisingly large capacity of the rumen, which is atypical for dicotyledon selectors and more typical of grass-eating antelopes.

Harvey's Duiker is primarily diurnal. In the Udzungwa Mts, activity pattern of this species, as indicated by camera-trapping times, resulted in 98% of more than 350 photographs being taken between 07:00h and 20:00h. Activity peaked between 07:00h and 10:00h and between 15:00h and 18:00h, and decreased significantly between 12:00h and 15:00h (F. Rovero pers. obs.).

Social and Reproductive Behaviour Little is known, but the species resembles other red duikers in being mostly solitary, although Wilson (2001) observed three adult male red duikers (here considered to be Harvey's) together on the Nyika Plateau; in the same region, he recorded an adult Gentle Monkey *Cercopithecus mitis* grooming a female duiker. The solitary habit of this duiker has been confirmed from both direct observations and camera-trapping in the Udzungwa Mts, with only occasional (fewer than 10%) observations and photographs of pairs (T. Jones & F. Rovero unpubl.). Harvey's Duikers have often been seen foraging below trees occupied by colobus monkeys and moving in association with the predominantly ground-foraging Sanje Mangabey *Cercocebus sanjei*; they are also groomed by this mangabey species (T. Jones & F. Rovero unpubl.). Other than facilitating access to food resources (i.e. fruits dropped by the monkeys), this behaviour must also increase anti-predator vigilance.

As with some other red duikers, Harvey's Duiker utters a shrill, fluty whistle when disturbed. If these animals live in a mosaic of territories (whether exclusive or overlapping), as is supposed, the most likely function of such calls is to inform conspecific neighbours as to the whistler's movements as well as alert them to disturbance. It is not known how much information these whistles might contain about the identity of the caller or the nature of the disturbance.

Reproduction and Population Structure Wilson (2001) recorded newborns on the Nyika Plateau in Dec, Mar, Aug and Feb. There is no other published information.

Predators, Parasites and Diseases Known predators include Leopards *Panthera pardus*, notably in the Udzungwa Mts (Rovero *et al.* 2005). Predation by Crowned Eagles *Stephanoaetus coronatus* has been recorded in the Udzungwa Mts (F. Rovero & A. Bowkett unpubl.); other potential predators are Lions *Panthera leo* and Spotted Hyenas *Crocuta crocuta*. Round (1968) documented cestodes from the genera

Moniezia and *Cysticercus* and a nematode (*Setaria* sp.) from Harvey's Duiker. Hoppe *et al.* (1981) recorded a number of species of the protist *Entodinium*.

Conservation IUCN Category: Least Concern. CITES: Not listed.

Harvey's Duikers are declining due to hunting and destruction of habitat. East (1999) notes that this species is heavily hunted throughout its Tanzanian and Kenyan range, where animals are hunted with dogs in several areas; wire snares are probably the largest cause of mortality through most of its range. The species has lost most of its habitat in Somalia along the lower Shebelle and Juba Rivers. Clear evidence of decreased abundance related to habitat degradation and hunting resulted from comparison of line-transect and camera-trapping data across contrasting sites in the Udzungwa Mts (Rovero & Marshall 2004, F. Rovero pers. obs.).

Important protected areas with known populations of Harvey's Duikers include Aberdare N. P., Mt Kenya F. R., Arubuko-Sokoke, Boni, Dodori, Tana River and Shimba Hills National Reserves (Kenya), Bush Bush N. P. (Somalia), Bale Mountain N. P. (Ethiopia) and Mikumi, Udzungwa, Kilimanjaro, Lake Manyara and Arusha National Parks (Tanzania) (East 1999, Wilson 2001).

Measurements

Cephalophus harveyi

TL (♂ ♂): 873 (796–891) mm, n = 3

TL (♀ ♀): 879 (849–910) mm, n = 4

T (♂ ♂): 94 (88–96) mm, n = 3

T (♀ ♀): 98 (90–108) mm, n = 4

HF c.u. (♂ ♂): 230 (222–239) mm, n = 3

HF c.u. (♀ ♀): 229 (219–240) mm, n = 4

E (♂ ♂): 76 (73–80) mm, n = 3

E (♀ ♀): 77 (74–79) mm, n = 4

Sh. Ht (♂ ♂): 413 (390–460) mm, n = 3

Sh. Ht (♀ ♀): 417 (399–449) mm, n = 4

WT (♂ ♂): 11.3 (9.9–12.6) kg, n = 3

WT (♀ ♀): 11.9 (9.7–12.9) kg, n = 4

Selous G. R., Tanzania (Wilson 2001)

TL (♂ ♂): 868 (802–913) mm, n = 6

TL (♀ ♀): 886 (855–917) mm, n = 4

T (♂ ♂): 96 (82–104) mm, n = 6

T (♀ ♀): 101 (90–117) mm, n = 4

HF c.u. (♂ ♂): 227 (220–239) mm, n = 6

HF c.u. (♀ ♀): 229 (218–240) mm, n = 4

E (♂ ♂): 78 (74–80) mm, n = 6

E (♀ ♀): 79 (75–81) mm, n = 4

Sh. Ht (♂ ♂): 416 (386–470) mm, n = 6

Sh. Ht (♀ ♀): 419 (385–449) mm, n = 4

WT (♂ ♂): 11.0 (9.7–13.2) kg, n = 3

WT (♀ ♀): 11.8 (9.9–13.6) kg, n = 4

Arusha, Tanzania (Wilson 2001)

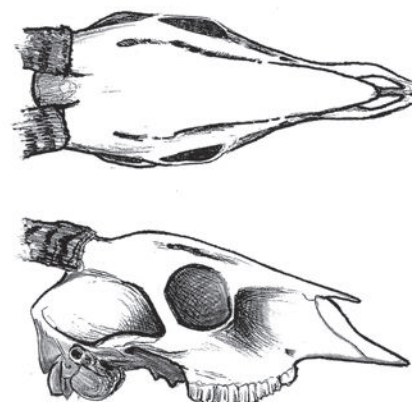
Maximum recorded horn length is 12.7 cm for a pair of horns from Elgeyo Forest, Kenya (Rowland Ward)

Key References Kingdon 1982; Wilson 2001.

Jonathan Kingdon & Francesco Rovero

Cephalophus rufilatus RED-FLANKED DUIKER

Fr. Cephalophe à flancs roux; Ger. Rotflankenducker

Cephalophus rufilatus Gray, 1846. Ann. Mag. Nat. Hist., ser. 1, 18: 166. 'Sierra Leone, Village of Waterloo'.Red-flanked Duiker *Cephalophus rufilatus*.Dorsal and lateral views of skull of Red-flanked Duiker *Cephalophus rufilatus*.

Taxonomy In the nineteenth century, several taxonomists confused this species with *Sylvicapra grimmia coronatus* (Sclater & Thomas 1899). A densely haired neck and coarse coat ally this species with other coarse-haired red duikers. Jansen van Vuuren & Robinson (2001), using mtDNA, found a consistently close relationship with the Black-fronted Duiker *Cephalophus nigrifrons*, in spite of very different proportions, morphology and habitat (and see Hassanin *et al.* 2012). They found a slightly more distant relationship with the Natal Red Duiker *C. natalensis*, which has similar proportions and dimensions, and the larger Harvey's Duiker *C. harveyi*. Two subspecies are usually recognized (St Leger 1936, Ansell 1972, Kingdon 1997), with the Chari R. thought to mark the boundary between them. Grubb & Groves (2001), who did not list subspecies, noted that two types of colouring are found at the extremities of its range: pale ochraceous with dorsal stripe sharply marked in the west, and darker, redder, with dorsal stripe more diffuse towards the eastern end of its range, and that skins from intervening areas show intermediate colouring. Size also varies rather sporadically. Synonyms: *cuvieri*, *rubidior*. Chromosome number: $2n = 60$; the X chromosome is a metacentric (Hard 1969).

Description A prettily coloured, relatively short-legged duiker with bright orange-red on the face, neck and flanks, dark brown or grey limbs and similarly coloured dorsal 'patch'. It belongs to the coarse-haired duiker group and its pelage, notably on the neck and throat, resembles that of the Black-fronted Duiker. The shiny black nose is broad and prominent. A dark line down the mid-line of the face is subject to much individual variation in breadth and colour. Likewise, the length and thickness of hair growing vertically from the crown varies individually, but is mostly black in colour. Underside of chin white, posterior surface of ear black, anterior surface lined with short white hairs except for black band close to lower margin. Underside light reddish. Tail with black tuft and its very frequent movements are always from side to side. Long, narrow pedal glands present on both fore- and hindfeet. Inguinal glands absent. Preorbital glands well developed in both sexes. Rostrum is long and narrow, and the frontals are evenly convex as far forward as the proximal nasals, as far back as bases of horns, which are raised up (Grubb & Groves 2001).

Geographic Variation

C. r. rufilatus: Senegal to Chari and Benue Valleys. Back and legs light grey.

C. r. rubidior: Chari R. to Nile Valley. Back and legs dark grey.

Similar Species

Cephalophus nigrifrons. Niger R. to East Africa. A larger, long-legged, long-hooved swamp-forest and mountain dwelling red duiker.

Philantomba maxwelli. Senegal to Cross R. A smaller, forest-dwelling duiker of overall dull brown colour.

P. monticola. Cross R. to East and south-eastern Africa. A smaller, forest-dwelling duiker of overall grey-brown colour.

Distribution Endemic to Africa, ranging from S Senegal, Gambia and Guinea-Bissau through to the Nile Valley in SW Sudan in forest-savanna mosaics north of the main forest block (East 1999, Wilson 2001). Formerly widespread in NW Uganda, as far east as the Albert Nile (Kingdon 1988, East 1999); a small relic population was discovered on the eastern side of the Nile in Bugungu G. R., immediately south of Murchison Falls N. P. (Allan 1996). The boundaries of its range are poorly defined and the species has been recorded in the southernmost regions of several 'Saharan' States (SW Mali, SW Niger and extreme S Chad). Not recorded from Liberia. Dowsett (1993) rejected all records from Gabon and Congo, though Grubb *et al.* (2003) remark that a supposed record of this species from the coastal lowlands of SE Gabon deserves further investigation.

Habitat A diurnal species finding refuge in forest edge, forest relics and riverine thickets, but also commonly emerging into open savanna and woodland. Heringa (1990) reported a distinct preference for riverine woodlands and thick vegetation close to permanent sources of water such as springs within rocky areas. In Nigeria it prefers places with rocky outcrops and forest outliers, even dry valleys within savanna, riparian or forest areas but never in high forest (Agbelusi 1992). In Mole N. P., Ghana, this duiker was

*Cephalophus rufilatus*

found in open savanna woodland in which tree cover averaged 30% (range 5–65%); the main trees were *Burkea africana* and *Terminalia avicennoides* together with other typical woodland trees such as *Gardenia*, *Lannea*, *Pterocarpus*, *Piliostigma*, *Grewia* and *Isoberlinia* spp. (Schmitt & Adu-Nsiah 1993). Wilson (2001) found them to be abundant in open savanna in Central African Republic in a region where there were tens of thousands of small termite mounds. In some regions the replacement of primary forest with farm bush and other secondary vegetation has enabled this species to expand its range (East 1999).

Abundance Data are scarce, but the species is generally widespread over most of its range. Estimates of density vary: Wilson (2001) recorded densities of 3–4/km² in prime habitat in Mole N. P., while Fischer & Linsenmair (2001a) estimated densities of 0.45/km² in 1995 in Comoé N. P., Côte d'Ivoire (though these declined to 0.14/km² in 1998). Heringa *et al.* (1990) estimated densities of less than 0.1/km² from ground surveys in Burkina Faso. This was the second most commonly observed antelope in the National Park of Upper Niger in Guinea, with a density of 2.6/km², although it had none the less declined by 50% since a previous census in 1997 (Brugière *et al.* 2005). East (1999) estimated total population numbers at 170,000.

Adaptations The Red-flanked Duiker is unusual in being an inhabitant of relatively open woodlands and savannas, degraded forests and riverine wooded environments. In this adaptation to drier, more exposed environments the Red-flanked Duiker has followed a similar evolutionary trajectory to the Common Duiker *Sylvicapra grimmia*. However, this adaptation has involved much less departure from the general red duiker morphotype. Molecular studies confirm that the Red-flanked Duiker (and its genetic sibling, the Black-fronted Duiker *C. nigrifrons*) diverged very much later than the bush duiker, which split away from other species quite early in the duiker radiation (Jansen van Vuuren & Robinson 2001).

The discovery of genetic affinity between the less specialized Red-flanked Duiker and swamp-adapted Black-fronted Duiker offers special opportunities for the study of evolutionary history and adaptive radiation in duikers. One question concerns habitat. The Black-fronted Duiker has long legs and elongated, splayed hooves that parallel those of another swamp-dwelling antelope, the Sitatunga *Tragelaphus spekii*. Distribution patterns for both species suggest that their ancestral populations originally adapted to swamp forests bordering lakes and rivers running immediately north of the Equator (Kingdon 1982). As the Red-flanked Duiker is distributed along the furthestmost northern tributaries of the same system both *rufilatus* and *nigrifrons* can be viewed schematically as 'outliers' that have been displaced onto the northern and southern margins of an ancestral range. In this construction their common ancestor was likely to have inhabited a long east–west forest belt running north of the Equator. This is a zone that currently supports a considerable diversity of duikers, all of which are ecologically partitioned by size, food and habitat type (Gautier-Hion *et al.* 1980, Kingdon 1982). Within this partitioned community, the Black-fronted Duiker has departed furthest from the generalized duiker type, whereas the Red-flanked Duiker has not. Instead, the latter's distribution implies a sort of evolutionary 'displacement' out onto the northern margins of duiker habitats with minimal external change to show for it. None the less, both species are likely to possess inconspicuous but substantial physiological adaptations and among these is an observed difference in scent glands. The Red-flanked Duiker is without glands in the groin, whereas the Black-fronted Duiker has developed large, deep inguinal glands.

Understanding this divergence has the potential of throwing light on the overall functions of scent glands in antelope biology, a topic that is still deeply problematic. Antelopes belonging to several lineages have developed inguinal glands and the emission of their secretions is unequivocally directed at conspecifics where they augment other olfactory signals. Unlike facial, pedal and excretory scents, where animals betray a direct interest in the scent and may deliberately mark places or other animals, inguinal glands are generally cryptic in expression. Exactly what purposes these glands serve is uncertain, but they are known to signify excitement and presumably assist conspecifics to identify sex, age and condition and then track the individual. Although pedal glands are best suited to the last task, constant switching of the tail might help disperse inguinal scent along trails. It is resting places or 'forms' (possibly urine puddles too) that must be the main scent-depositories. When a previously glandless lineage develops such glands there is the distinct implication of a change in social structure or a heightened need for intra-specific contacts. The principal external cost of developing such very odoriferous scents is facilitating predators that track their prey by scent: a selective agency that is greatly reduced in densely obstructed, boggy habitats.

In lacking inguinal glands, the Red-flanked Duiker resembles a majority of duiker species and it is likely that this is the original condition for these predominantly solitary animals. A careful and detailed comparison of Red-flanked Duiker social behaviour with that of Black-fronted Duikers might reveal currently unknown aspects of social behaviour in the latter. In any event, there is much still to be learned about communication and the evolution of social structures in duikers and antelopes in general. The preorbital glands are wiped on a wide variety of sites, vegetable and mineral, including termite mounds (Wilson 2001). The same site is often wiped with both sides of the face.

Foraging and Food Red-flanked Duikers feed on the fruit, flowers and foliage of numerous trees, shrubs and herbs. Some of their foods consist of large cumbersome fruits, others are little more than berries or seeds and every size of fruit in between. In Bangangai, Sudan, on the outermost borders of its range, Hillman (1982) noted fallen fruits, flowers, dry leaves, root tubers and the meat of dead animals. In the Toumodi area, Côte d'Ivoire, stomachs ($n = 15$) of duikers killed in and around forest-cleared farms contained the fruits of 21 different plants that were typical of the forest/savanna mosaic, with preference given to *Phoenix reclinata*, *Nauclea latifolia* and *Ficus capensis*, although other species consumed included *Combretum racemosum*, *Griffonia simplicifolia*, *Alchornea cordifolia*, *Phyllanthus discoideus*, *Anthocleista djalensis*, *Carapa procera*, *Antiaris africana*, *Ficus mucosa*, *Macuna pruriens*, *Canthium vulgare*, *Blighia sapida*, *Malacantha alnifolia* and *Solanum* spp. They also contained cultivated plants such as mangoes, cassava, cocoa and pawpaw as well as raphia and oil palm dates (Hofmann & Roth 2003).

In Mole N. P., these duikers have been recorded feeding on the figs of eight species of *Ficus* as well as fallen fruit of large trees, in particular *Uvaria chamae*, *Xylopia parviflora*, *Elaeis quineensis*, *Nauclea latifolia*, *Pavetta crassipes* and *Anthocleista vogelii* (Wilson 2001). In Nigeria, this duiker was found to mainly browse the leaves of shrubs, such as *Piliostigma thonningii*, *Pterocarpus erinaceus*, *Annoa senegalensis*, *Grewia arborea*, *Landolphia oweriensis*, and *Vitex domiana* (Agbelusi 1992). Such flexibility in diet suggests an ability to survive fruitless periods or areas with few fruits by switching to browse and may help explain why this species thrives outside true forest.

Red-flanked Duikers commonly rise onto their hindlegs to reach plant parts above their heads. They pay close attention to monkeys and exploit dropped waste beneath the primates' food trees (Wilson 2001).

Social and Reproductive Behaviour Red-flanked Duikers are solitary, resident animals living in spaced-out territories at densities of about 3–4/km² (Wilson 2001). Male and female territories overlap, but each sex spends most of its time on its own. Of 386 observations in Mole N. P., 325 were of solitary animals, 47 were male–female pairs and ten were of ♀♀ with their young. In the same area, Wilson (2001) found two animals that had 5–7 different resting places within an area of 2 ha. Middens were prominent landmarks in this habitat and Wilson (2001) found 90% of them deposited on open ground, well away from vegetation. Unlike some other antelope species, faeces were not piled up on top of each other and anything between 15 and 80 single deposits, of varying age, were found scattered over an area of 15–50 m². The sexes have distinctively different urination postures, ♂♂ with their hindlegs stretched out behind while ♀♀ bunch up and lower their hindquarters to the ground.

In captivity, ♂♂ are almost continuously interested in ♀♀ (even attempting to mount ♀♀ not in oestrus), approaching the ♀ from the rear with body stretched out and exhaling with a snort while following the ♀ (Dubost & Feer 1988). The ♀ utters a short moan as she exhales and ♂♂ exhibit flehmen when sampling her vulva or

urine (Wilson 2001). A captive pair copulated four times in 40 min and oestrus lasted for a day and a half (Wilson 2001).

Reproduction and Population Structure There is no information on timing of parturition in the wild. Gestation period has been cited as 223–245 days (Schweers 1984). Based on records from captivity, birth-weights average 1.0 kg (range 0.8–1.2 kg) and weaning takes places at 93–98 days (Wilson 2001), although the latter author also notes a record of 58 days. A captive ♀ gave birth at 26 months (Hayssen *et al.* 1993). Animals in captivity have survived more than 15 years (Weigl 2005).

Predators, Parasites and Diseases Martial Eagles *Polemaetus bellicosus* and Crowned Eagles *Stephanoaetus coronatus*, pythons and various carnivores, notably Lions *Panthera leo*, Leopards *Panthera pardus*, Servals *Leptailurus serval* and jackals *Canis* spp. are all likely predators. Dipeolu & Akinboade (1984) recorded the ixodid ticks *Amblyomma variegatum* and *Boophilus decoloratus* from animals in Nigeria, while Ntiemoa-Baidu *et al.* (2005) recorded the following ixodid tick species from Red-flanked Duikers in Ghana: *Haemaphysalis parvula*, *Ixodes muniensis*, *I. moreli*, *Rhipicephalus simpsoni* and *R. ziemanni*.

Conservation IUCN Category: Least Concern. CITES: Not listed.

This species is declining due to hunting, but, as East (1999) remarked, has shown much resilience to both hunting and the spread of settlement and probably still occurs reasonably widely throughout much of its historical range. The species is common in many protected areas and reserves (about half of the total population occurs in and around protected areas), including Niokolo-Koba N. P. (Senegal), National Park of Upper Niger (Guinea), Comoé N. P., Haut Bandama Fauna and Flora Reserve and Marahoue N. P. (Côte d'Ivoire), Mole, Bui and Digya National Parks (Ghana), W N. P. (Benin), Bouba Ndjida, Bénoué and Faro National Parks (Cameroon), and Manovo–Gounda–St Floris and Bamingui–Bangoran National Parks (Central African Republic) (East 1999).

Measurements

Cephalophus rufilatus

HB: 600–800 mm

T: 70–100 mm

Sh. ht: 300–380 mm

WT: 6.0–14.0 kg

Throughout geographic range (Kingdon 1997; mean and sample number not given)

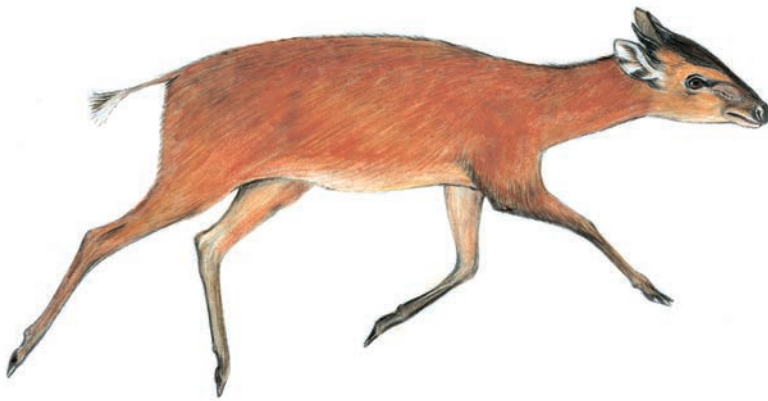
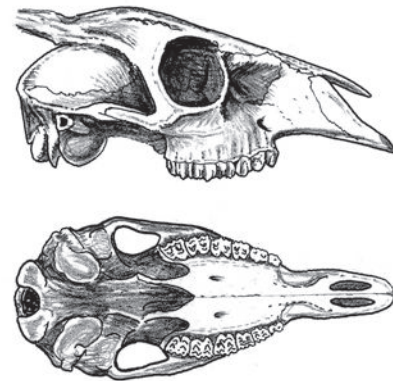
Maximum recorded horn length is 10.4 cm for a pair of horns from Kozo, Central African Republic (Rowland Ward)

Key References East 1999; Kingdon 1982; Wilson 2001.

Jonathan Kingdon & Michael Hoffmann

Cephalophus nigrifrons BLACK-FRONTED DUIKER

Fr. Céphalophe à front noir; Ger. Schwarzstirnducker

Cephalophus nigrifrons Gray, 1871. Proc. Zool. Soc. Lond. 1871: 598. 'Gaboon' (Gabon).Black-fronted Duiker *Cephalophus nigrifrons* adult male.Lateral and palatal views of skull of Black-fronted Duiker *Cephalophus nigrifrons*.

Taxonomy Five subspecies have been recognized (see Ansell 1972), with four confined to montane areas of eastern Africa and the nominate race found in the forests of the Congo Basin. The Rwenzori Red Duiker *Cephalophus rubidus* has been included as a subspecies of *C. nigrifrons* (St Leger 1936, Groves & Grubb 1981), although Kingdon (1982) considered *rubidus* to be a full species (and see Grubb 1993c, Kingdon 1997). Jansen van Vuuren & Robinson (2001) presented molecular evidence supporting the recognition of the species as distinct, although the only material available for the analysis was a tooth from a specimen in the Swedish Museum of Natural History. Wilson (2001) was reluctant to consider *rubidus* a distinct species, and Grubb & Groves (2001) and Grubb (2005) both considered it a subspecies of *C. nigrifrons*. Grubb & Groves (2001) also described a new subspecies from the Itombwe Mts, west of the north end of L. Tanganyika, *C. n. hypoxanthus*. *Cephalophus fosteri* and *C. hooki* were considered evolutionarily distinct species by Cotterill (2003a). Synonyms: *apanbanga*, *aureus*, *claudi*, *emini*, *fosteri*, *hooki*, *hypoxanthus*, *kivuensis*, *lusumbi*, *mixtus*. Chromosome number: not known, but given their conserved karyotype it may be $2n = 60$ (B. Janssen van Vuuren pers. comm.).

Description A medium-sized red duiker, similar to other red duikers, but with relatively long legs. Crown and forehead black with black or very dark red or brown frontal blaze (the blaze that gives this species its name), and a black tuft of hairs between the ears. A well-developed preorbital gland runs from the eye towards the muzzle. Pelage glossy red with coarse body and neck hair, some hairs with black or darker red tips, with a darker back and rump grading to a paler red belly. The pelage is shorter in lowland areas, but long and shaggy in high-lying areas; similarly, montane animals are darker and more grizzled. The legs are darker than the body and tend to almost black at the hocks. Some animals have a large amount of black on the shoulders. Hooves are long and thinner than in any other duiker (Wilson 2001). Tail is the same colour as the rump, red or dark red with a white underside that is constantly flicked as the

animal is moving and feeding. The very young have a darker pelage colour, which is lost within a few weeks of birth (J. A. Hart pers. comm.). The pedal glands are large and there are virtually no hairs blocking the opening to the glands (Wilson 2001). Well-developed inguinal glands occur in most individuals, but are sometimes missing from *C. n. kivuensis*. Sexes similar with the ♂ slightly smaller.

The skull is narrower with the muzzle 'pinched in' so that the nasals obscure the maxillae in dorsal view (Grubb & Groves 2001). Both sexes have horns, which are black, short and straight, pointing backwards at about 45° to the vertical.

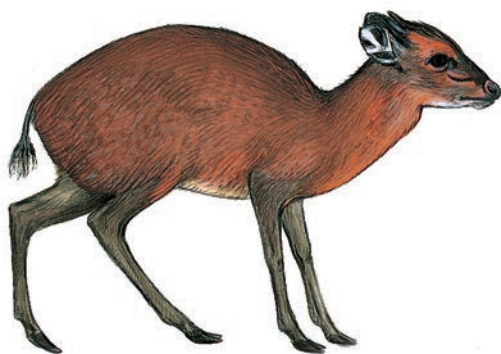
Geographic Variation

C. n. nigrifrons: from the Niger Delta and Mt Cameroon, lowland forest of SE Cameroon, Gabon and Congo through the lowland forests of the Congo Basin and N Angola to the Albertine Rift Valley. In lowland forest, almost solely found in swamp forest along streams and rivers. Shining chestnut-brown, with forelegs black as far up as the elbow, and hindlegs usually up to hock; chest black. Forehead generally black; chin yellow (sometimes white) (Grubb & Groves 2001). Hooves are particularly elongated because swamp forest is the main habitat they occupy.

C. n. kivuensis: mountains along the Albertine Rift from the Kahuzi Biega massif to the Rwenzori Mts. Very contrasting colouration, the limbs being grey-black and the facial blaze very black; hair thick and coarse; chin pale reddish, but more whitish in specimens from higher altitudes (Grubb & Groves 2001).

C. n. fosteri: confined to Mt Elgon at 2600–3700 m. Brownish colour, with face and sides of neck reddish, not grey; chin white; coronal tuft short, entirely black; hair thick and coarse; smaller in size than other subspecies (Grubb & Groves 2001).

C. n. hooki: confined to Mt Kenya at 2800–3300 m, and in the Aberdares. Chestnut or reddish-grey, with face and sides of neck greyer; chin reddish-white; face-blaze bordered by red stripe; coronal tuft short, entirely black; fur thick and coarse, and tail bushy;



Black-fronted Duiker *Cephalophus nigrifrons hooki*.

smallest of the subspecies after *fosteri*. This subspecies is supposedly ecologically separated (by altitude and habitat) from Harvey's Duiker *C. harveyi* on Mt Kenya (with Harvey's Duikers not occurring above the bamboo line), although it is unknown whether they interbreed at all at the interface of their ranges (Grubb & Groves 2001).

C. n. hypoxanthus: confined to the Itombwe massif in E DR Congo. Pale, light yellow-chestnut colour, with greyish legs rather than black; hair fairly long and very soft (more coarse in other highland races); chin white (Grubb & Groves 2001).

The four montane forms generally are found between 2000 and 3800 m on their respective mountains, while *C. n. nigrifrons* occurs at much lower altitudes. The Rwenzori Red Duiker generally occurs above the range of *C. n. kivuensis* on the Rwenzori massif (up to 4200 m).

Similar Species

Cephalophus rubidus. Restricted to the upper reaches of the Rwenzori Mts. Dark grey underlying red tips of the hairs down the mid-line of the back and neck. Underfur of flanks cream; very pale to white belly.

C. harveyi. Sympatric in the Aberdares and Mt Kenya. Black and white chin and whiter ears with black tips; belly pale cream or white; shorter legs.

C. rufilatus. Allopatric. Smaller in size, this species has a grey-brown back and grey-brown legs that contrast with the red-orange on the face, neck and flanks. White on lower jaws contrasts with black nose. This species has no inguinal glands.

C. ogilbyi. Sympatric in western central Africa (*C. o. crusalbum*) and presumably Nigeria/Cameroon (the nominate form). Paler pelage and in *C. o. crusalbum* with white legs; shorter legs.

Distribution Endemic to equatorial Africa. Widespread from SE Nigeria in the Niger Delta (where only recently confirmed; Powell & Grubb 2002), through the forests of S and SE Cameroon, south of the Sanaga R., mainland Equatorial Guinea, Gabon, SW and SE Central African Republic, Congo and N (Cabinda, Uige and Cuanza Norte Provinces) and NE Angola (Lunda Norte and Lunda Sul Provinces) eastwards across the Congo Basin to the Albertine Rift (East 1999, Wilson 2001, Crawford-Cabral & Veríssimo 2005). In Uganda they are known only from Mt Elgon and remnant forest on mountains along the Albertine Rift, including the Rwenzori Mts, Bwindi Impenetrable N. P. and the Virunga Mts, while in Rwanda and Burundi they are now restricted to Volcanoes N. P. and Nyungwe

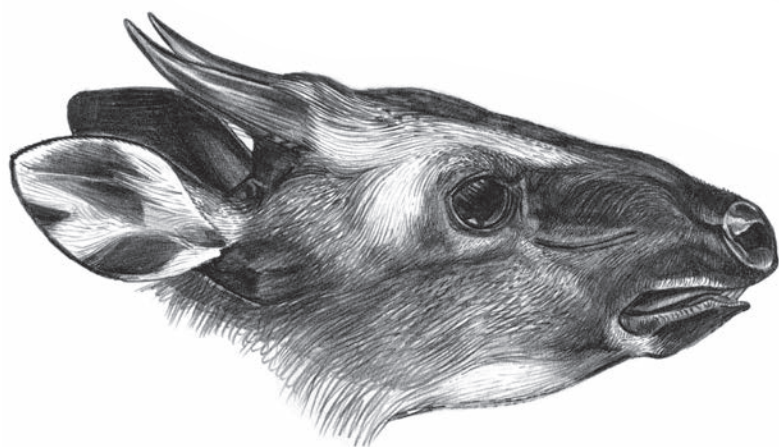


Forest Reserves, and the Nyungwe-Kibira forest on the Rwanda–Burundi border. In Kenya they occur only in three widely separated populations, on Mt Elgon, Mt Kenya and in the Aberdares (East 1999, Wilson 2001).

Isolated populations of this species were recorded on Mounts Cameroon, Kupe and Manengube by Bowden (1986); however, Grubb *et al.* (2003) were not convinced these records relate to Black-fronted Duikers, and thought they may represent an undescribed species.

Habitat Found in lowland tropical forest in the Congo Basin from altitudes near sea level to more than 4000 m in montane forest and moorlands in East Africa. Typically occurs in swampy or waterlogged habitats along streams where its long hooves help it move around more easily. In the Ituri Forest, DR Congo, it was equally abundant in monodominant *Gilbertiodendron* forest as in mixed forest, although in both forest types it is confined to the courses of streams and rivers (Hart 1985, 2000). In the Virunga Mts there was a preference for wooded habitat with an open understorey dominated by dense herbs such as nettles up the sides, and in the saddle between the volcanoes (Plumptre & Harris 1995, Plumptre & Bizumuremyi 1996). On Mt Elgon it occurs in dense bamboo forest where it is probably not abundant (J. Kingdon pers. comm.), but in the Virungas this was not a preferred habitat and densities were low in bamboo (Plumptre 1991). On mountains there is less dependence on waterlogged areas than there is in the lowland forest although the long hooves are still present, implying that the original form may have occurred in lowland forest where its adaptations to waterlogged soils might have favoured its colonization of moist forested areas and spread up the mountains. There is some evidence that this species avoids predation by Leopards *Panthera pardus* by being better adapted to swamp forest in lowland areas where the supply of fruit is lower and animals survive on herbs (Hart 2000, 2001).

Abundance In the Virunga Mts, densities ranged from 5 to 22/km² across a range of different habitats (Plumptre & Harris 1995). In the



ABOVE AND RIGHT: Black-fronted Duiker *Cephalophus nigrifrons kivuensis* adult male facial features and forehead.



Ituri Forest, density was lower, at about 1.3–2.0/km² (Hart, J. A. *et al.* 1996, Hart 2000, 2001). Assuming average densities of 2/km² in high-density areas and 0.2/km² in low-density areas, East (1999) estimated the total population at around 300,000.

Adaptations The long hooves enable this species to inhabit swampy and waterlogged areas. J. A. Hart *et al.* (1996) have suggested that this gives it an advantage in keeping away from Leopards, one of its major predators. The foot-stamping that is typical of other duiker species appears to be absent in this species. It is possible that species-specific vocal signals may compensate. When feeding or moving, animals constantly flick their tails, exposing the white undersides that may be used to advertise their presence to others. The bone of the skull on the foreheads is thickened, probably to minimize the impact of head butting between individuals. Black-fronted Duikers are primarily diurnal, but occasionally are active at night.

Foraging and Food Diets vary where they have been studied. In the Ituri Forest, 29% of the diet determined from rumen contents was leaf material (primarily herbs) and the remainder was fruit and seeds, with some flowers and fungi (Hart 1985). Those fruits consumed tend to be fairly fibrous, such as *Ricinodendron heudelotti*, rather than fleshy. However, it was the most folivorous of all the duikers in the Ituri Forest and the only one to eat herbs. The diet varied seasonally depending on the availability of fallen fruit, and seed content increased dramatically in most years for *Gilbertiodendron dewevrei*. In Makokou, Gabon, rumen analysis indicated 73% of the diet consisted of fruit (mostly 1–3 cm in diameter) with the remainder consisting of leaves, flowers, petioles and fungi (Gautier-Hion *et al.* 1980); the Black-fronted Duiker was again the most folivorous duiker of those studied in Makokou (Dubost 1984). At higher altitudes (2900–3700 m) in the Virunga Mts there was very little fruit available and 80.7% of the diet consisted of leaves of herbs and grasses, with 14.8% lichen and 4.5% bark/roots based on faecal pellet analyses (Plumptre 1995). The low tannin and alkaloid levels in montane herbs probably allow this species to survive on such a drastically different diet and to live at high densities (Plumptre 1995). *Usnea* lichen was highly preferred, with individuals competing over pieces that fell to the

ground and standing on their hindlegs to reach lichen that was within reach. The desire for this lichen may be due to its reasonably high level of soluble carbohydrates (A. Plumptre unpubl.), which may substitute for those found in fruit consumed at lower altitudes. Diet in the Virungas did not vary seasonally as there was little variation in the availability of food.

Social and Reproductive Behaviour Generally solitary with occasional sightings of pairs (either mother–infant or male–female). They are territorial, using preorbital glands to mark territories, and tending to defecate near the boundaries of their territory. Territorial defence may be aided by the use of a thumping sound that appears to be vocal (Kingdon 1982), and a loud whistle-like call that is also used as an alarm call. Very occasionally two individuals will fight, which involves rearing up and butting heads together, pausing to recover and then repeating this, reminiscent of the way goats fight. Individuals have also been seen to snap at each other (Walther 1984). Fighting usually ends with a pursuit through the vegetation.

Anti-predator behaviour involves freezing, often in mid-stride, sinking down to the ground or sneaking away to hide in dense vegetation if they believe they have not been detected. If they know they have been detected they flee, giving a loud whistle, dashing through the vegetation with their head down for a short distance, often in a zig-zag manner to throw off any predator.

Like many ungulates, young when born are left concealed by the mother in dense vegetation and she returns to suckle at regular intervals.

Reproduction and Population Structure Nothing is known about reproduction of this species either in captivity or in the wild. Wilson (2001) mentions two lactating ♀♀ recorded in Feb and Mar

from the Central African Republic, and two pregnant ♀♀ in Dec. Longevity in captivity has been given as nearly 20 years (Jones 1982).

Predators, Parasites and Diseases Leopards are a major predator of all duiker species in the Ituri Forest and have a significant impact on their populations (Hart, J. A. *et al.* 1996). Leopards account for 87% of duiker mortality in areas where humans do not hunt in the Ituri Forest (Hart 2000, J. A. Hart pers. comm.). However, this species only formed about 1.7% of Leopard diet in the Ituri Forest, the lowest of any duiker species, despite being reasonably abundant, and occurred in only half of a calculated expected number of Leopard scats (Hart, J. A. *et al.* 1996). They also had the lowest mortality rate of any duiker species in the Ituri Forest (Hart 2000). Other large cats, such as African Golden Cats *Profelis aurata*, and African Rock Pythons *Python sebae* will also take this species. Large eagles such as the Crowned Eagle *Stephanoaetus coronatus* will take juveniles and very occasionally adults. Robust Chimpanzees *Pan troglodytes* and Nile Crocodiles *Crocodylus niloticus* occasionally take individuals.

Helminths recorded from Black-fronted Duikers include cestodes (genera *Avitinella*, *Stilesia*) and nematodes (*Bunostromum*, *Dipetalonema*, *Ochocera* and *Setaria*) (Round 1968, Bain *et al.* 1978, Chabaud *et al.* 1978). A study of the diseases and parasites found in wild duikers in the Ituri Forest showed that most Black-fronted Duikers in this forest contain gut parasites (Karesh *et al.* 1995). Of the five individuals sampled all had at least evidence of one parasite species in their faeces and for most parasites the percentage of individuals infected was higher for this species than the four other duiker species tested. Evidence of parasites in the blood included: 'bluetongue' virus, which was at a similar level to other species; epizootic haemorrhagic disease and infectious bovine rhinotracheitis, which were generally at a lower level than other species; and leptospirosis, which was at a higher level of infection compared with most of the other species sampled (Karesh *et al.* 1995). Some of these infections, particularly leptospirosis, could be transmitted to humans through the bushmeat trade in this species.

Conservation IUCN Category: Least Concern. CITES: Not listed.

Numbers of Black-fronted Duiker are probably declining across the range, mainly due to hunting, particularly with the opening up of the Congo Basin by timber extraction companies. The three subspecies confined to Mt Elgon, Itombwe Massif and Mt Kenya are probably at greater risk of extinction. This is particularly the case for *C. n. hypoxanthus* on the Itombwe Massif, which is not currently protected.

In central and West Africa this species is hunted heavily wherever it occurs in proximity to man. There is some evidence that red duikers

can accelerate their maturation in ♀♀ under low population densities but not as well as blue duikers can (Hart 2000). They are easily trapped, as there is some indication that they follow regular paths from the swamps to drier parts of the forest (Rahm & Christiaensen 1963, Wilson 2001). Data from Rwanda revealed that Black-fronted Duiker meat is significantly lower in price than domestic meat (Plumptre & Bizumuremyi 1996, Plumptre *et al.* 1997) and they were a favoured species for hunters. There was evidence that poaching of this species had increased in Volcanoes N. P. during and after the insecurity created by the civil war and genocide in Rwanda (Plumptre *et al.* 1997).

Protected areas important for the continued persistence of the species include Apoi Creek F. R. (Nigeria), Dja Faunal Reserve (Cameroon), Monte Allen N. P. (Equatorial Guinea), Lopé N. P. (Gabon), Dzanga-Sangha Forest Reserve and Bangassou Forest (Central African Republic), Nouabalé-Ndoki and Odzala National Parks (Congo), Kahuzi-Biega, Maiko and Virunga National Parks and Okapi Wildlife Reserve (DR Congo), Bwindi Impenetrable and Rwenzori Mountains National Parks (Uganda) and Volcanoes N. P. (Rwanda).

Measurements

Cephalophus nigrifrons

TL (♂♂): 1080 (1020–1120) mm, n = 6

TL (♀♀): 1090 (1040–1140) mm, n = 7

T (♂♂): 155 (130–160) mm, n = 6

T (♀♀): 150 (140–160) mm, n = 7

HF c.u. (♂♂): 295 (281–304) mm, n = 6

HF c.u. (♀♀): 296 (281–310) mm, n = 7

E (♂♂): 90 (87–94) mm, n = 6

E (♀♀): 91 (86–95) mm, n = 7

Sh. ht (♂♂): 560 (540–570) mm, n = 6

Sh. ht (♀♀): 560 (540–580) mm, n = 7

WT (♂♂): 13.8 (12.7–14.9) kg, n = 6

WT (♀♀): 14.0 (13.1–16.3) kg, n = 7

Cameroon, Central African Republic and Congo Republic (Wilson 2001)

Hart, J. A. *et al.* (1996) recorded the mean weight of two ♀♀ as 15.5 kg (range 15–16 kg) and 14.3 kg for two ♂♂ (14.0–14.5 kg). Maximum recorded horn length is 12.0 cm for a pair of horns from Ntem R., Cameroon (Rowland Ward)

Key References Hart 1985, 2000, 2001; Kingdon 1982; Plumptre 1991, 1995; Plumptre & Harris 1995; Wilson 2001.

Andrew J. Plumptre

Cephalophus ogilbyi OGILBY'S DUIKER

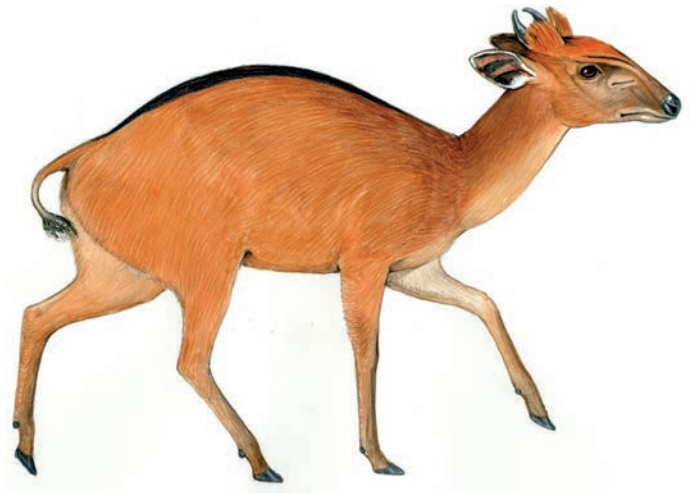
Fr. Céphalophe d'Ogilby; Ger. Ogilbyducker

Cephalophus ogilbyi (Waterhouse, 1838) Proc. Zool. Soc. Lond. 1838: 60. Equatorial Guinea, 'Fernando Po' (= Bioko).

Taxonomy Ogilby's Duiker, as described here, probably represents a species group that embraces three allopatric species. While acknowledging this probability we follow Wilson (2001) in provisionally continuing to treat this complex as a single species. The type of *C. ogilbyi* was described in 1838 from the island of Fernando Poo (Bioko); *C. o. crusalbum* was described in 1978 from Gabon and *C. o. brookei* in 1903 from Ghana. Brooke's Duiker *C. o. brookei* has been recognized as a full species by several recent authors (Grubb *et al.* 1998, Grubb & Groves 2001, Grubb 2005). *Cephalophus o. crusalbum* has been recognized as a full evolutionary species by Cotterill (2003a).

Molecular studies suggest that Ogilby's Duiker is an ancient relict duiker that has ambiguous genetic links with other duiker species, notably with Peters's Duiker *C. callipygus* (Jansen van Vuuren & Robinson 2001; and see Hassanin *et al.* 2012). Payne (1992) considered Ogilby's Duiker and Peters's Duiker to be particularly close, and Grubb (1978a) thought the population he named *C. o. crusalbum* was 'intermediate' between Peters' and Ogilby's Duikers. Wilson (2001) drew attention to the 'intergrading' of some Ogilby-like characteristics in individual Peters's Duikers, at or close to their zones of contact. This raises the possibility of occasional, or even sustained, long-term hybridization, past and present, between individuals or even entire populations. As ancestral duiker populations have been replaced by later ones the nature of that replacement could include various permutations of genetic admixture. As Ogilby's Duiker gives every sign of being a relictual form in the process of decline, the possibility of genetic admixture should be borne in mind. Unscrambling such mixed genetic backgrounds will be an interesting task for future molecular scientists. It is, therefore, appropriate to point out that the *C. ogilbyi* complex represents an enigmatic and puzzling taxonomic entity. Our uncertainties about the status of Ogilby's Duiker populations challenge science, yet their rarity, their relictual nature and their vulnerability to hunting may soon deprive scientists of important clues to the nature of duiker radiation. Synonyms: *brookei*, *crusalbum*. Chromosome number: not known.

Description A trim orange to mahogany-coloured duiker with chunky hindquarters and a bold black dorsal stripe (10–60 mm wide) that tapers to a point just above the tail. Nose and crown are black, but red or orange 'brows' of variable width may meet on the forehead. Horns may be partially obscured by short tufts of red or black fur. Pinnae are sepia behind and have narrow white margins with tracts of short paler hair in their forward aspect. On Bioko I., necks are well furred with soft but longish fur, while mainland populations tend to have short-haired darkish necks; hair on the neck is frequently reversed. Body colour extends down relatively long, slender legs, but *C. o. crusalbum* has off-white legs while *C. o. brookei* has narrow black lines or smears down the front of the limbs. Small lateral hooves are present. Inguinal, preorbital and pedal glands are all present. Tail narrow but ends in a distinct tuft that is sometimes quite large, like a pompom, with hairs up to 75 mm long (as in *C. o. crusalbum*).

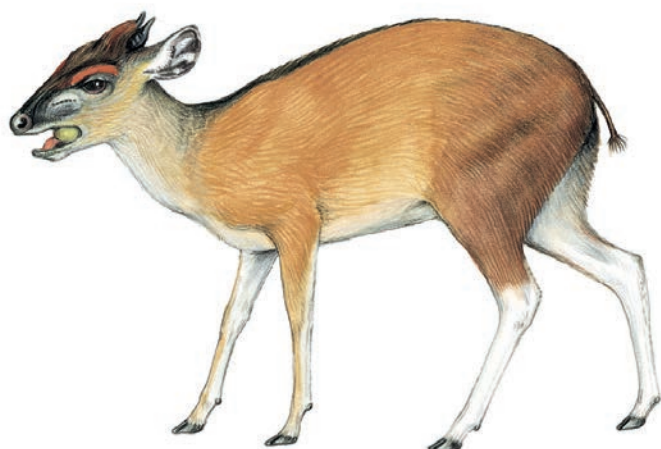
Ogilby's Duiker *Cephalophus ogilbyi ogilbyi*.

The horns are short but peculiarly incurved and heavily corrugated and can occur on both sexes. The skull is characterized by the extreme inflation of the forehead behind the nasofrontal suture, such that the skull has a marked frontal boss, but which is reduced laterally so that the infraorbital foramina are not roofed over; the zygomatic arch is more curved than in the Black Duiker, flaring out in the middle (Grubb & Groves 2001).

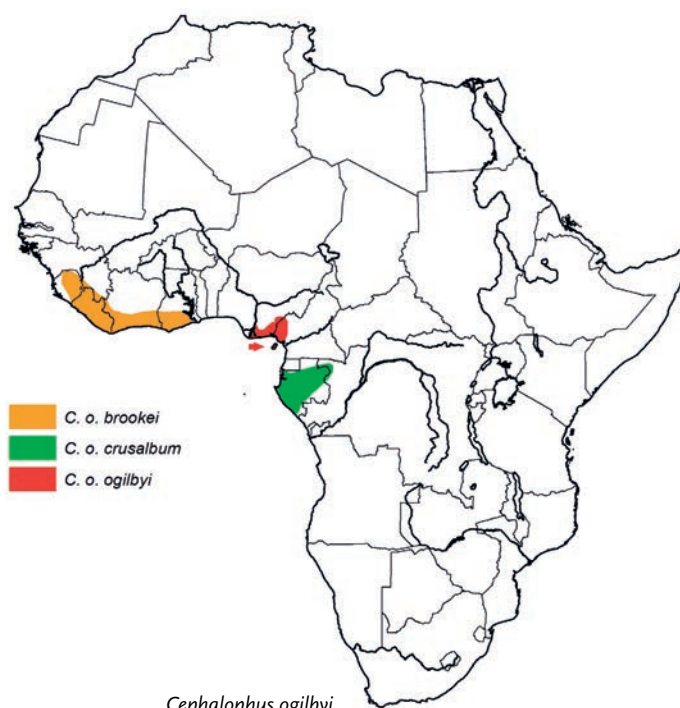
Geographic Variation

C. o. ogilbyi (Ogilby's Duiker): Bioko I., Equatorial Guinea, and Cameroon/Nigeria borderlands. Larger body size. Relatively uniform golden-rufous colouring overall but with whitish underside, throat and chin. Crisp, narrow, black mid-dorsal line. Neck pelage not noticeably shorter than rest of body. Heavily bossed forehead.

Brooke's Duiker *Cephalophus ogilbyi brookei*.



White-legged Duiker *Cephalophus ogilbyi crusalbum*.



Cephalophus ogilbyi

C. o. brookei (Brooke's Duiker): Sierra Leone, possibly SE Guinea, Liberia, S Côte d'Ivoire and Ghana, west of the Volta R.; Kingdon (1997) mistakenly described this population occurring in Cameroon. Pale golden colour with slightly redder rump; broad dorsal stripe narrows to a point above tail; red coronal tuft; neck hair very short; forehead not obviously bossed. Probably a distinct species.

C. o. crusalbum (White-legged Duiker): Gabon, mostly south of Ogooué R., and extreme NW Congo. Smaller body size; golden or orange-ochre torso, redder rump, but lighter on the flanks; somewhat greyer neck and face; neck hair very short; broad dorsal stripe; legs white from knee and hock to hoof, in contrast to all other duikers; tail orange-ochre with median stripe black and pronounced tail tuft; forehead not conspicuously bossed.

Similar Species

Cephalophus nigrifrons. Sympatric in Gabon and Congo (with *C. o. crusalbum*) and Nigeria/Cameroon (*C. o. ogilbyi*). A long-legged, long-hooved, dark red duiker with no dorsal band and a strong preference for swamp forest.

C. callipygus. Sympatric in Gabon (e.g. in Forêt des Abeilles and Lopé N. P.) and Congo. A large species with dark legs and extensive black dorsal stripe on upper rump. Hybridization may occur and *C. o. crusalbum* sometimes appears to be intermediate between *C. ogilbyi* and *C. callipygus* (see Grubb 1978a).

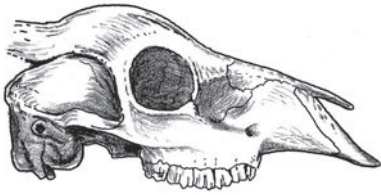
C. dorsalis. Sympatric throughout mainland range of Ogilby's Duiker. A broad-headed, short-faced, slender-horned, heavily built and usually dark red duiker, which is readily confused with Ogilby's Duiker. Nocturnal.

C. niger. A black duiker, restricted to Upper Guinea forests from SW Guinea to the Niger R.

Distribution Endemic to Africa, Ogilby's Duiker is distributed in four distinct populations. In West Africa it occurs in the forests of Upper Guinea, from Sierra Leone (where the only confirmed records are from the Outamba part of Outamba-Kilimi N. P. and Lalehun) through Liberia and S Côte d'Ivoire to Ghana, west of the Volta R. (Grubb *et al.* 1998, East 1999, Wilson 2001). May occur in SE Guinea, where reported from Ziama-Diécké F. R. by East (1999), but not by Butzler (1994). There is no recent information on the presence of this species in SW Ghana, and East (1999) noted that it had disappeared

from the Bomfobiri and Owabi wildlife sanctuaries where it occurred formerly. There is a break in distribution until reappearance (in the form *C. o. ogilbyi*) in the moist lowland forest in SE Nigeria and SW Cameroon. An isolated population occurs on Bioko I., particularly at higher altitudes. The white-legged form of Ogilby's Duiker, *C. o. crusalbum*, occurs in Gabon, mostly south of the Ogooué R., and is reported to occur in NW Congo (East 1999, Grubb *et al.* 2003). There is no record of this species from mainland Equatorial Guinea.

Habitat Found in all forest types, from sea level up to 2260 m and perhaps even higher on Bioko I. (Butynski *et al.* 2001), where it is the only large duiker species, and where it occurs in the *Schefflera* Forest Zone (ordinarily occupied by other species on the mainland). No clear specialization in forest type. Occurs in dense forest patches on the Guinea savanna edge in Sierra Leone (Grubb *et al.* 1998). Reported from a mixture of undisturbed high and also logged forests in Liberia (Wilson 2001). Found in forest patches within forest-savanna mosaic in northern part of Lopé N. P. in Gabon (East 1999). A different permutation of other duiker species is found in every one of the areas where Ogilby's Duiker occurs but there is virtually no overlap in range with 'main line' broad-spectrum red duikers (exclusive of Bay Duikers) (Kingdon 1982). The absence of any clear specialization in habitat or diet suggests that duikers of the *C. ogilbyi* complex represent relictual populations of an early lineage that may be in the process of succumbing to competition and genetic contamination from other forest duikers. The most notable of these is Peters's Duiker, which is almost allopatric and a very similar species. This similarity is most marked along the borderlands between the two species where occasional 'intermediate' specimens suggest that the 'relationship' between the two species may be complicated by long-term hybridization. In any event, the situation calls for further investigation. In Upper Guinea, where Black Duikers and Bay Duikers are the commonest large duikers, *C. o. brookei* was formerly widespread but never common (Grubb *et al.* 1998).



Lateral view of skull of Ogilby's Duiker *Cephalophus ogilbyi ogilbyi*.

Abundance Data are scarce, but during a survey conducted in 1990 in the Gran Caldera on Bioko I., Butynski *et al.* (2001) found evidence for their presence at the rate of 0.24 per linear transect km in suitable habitat. Figures from bushmeat markets and hunter interviews suggest an annual off-take of 4000 Ogilby's Duikers on Bioko I.; about 2/km² of forest habitat. A more localized estimate was 2250 from 160 km² (Fa *et al.* 1995). While it is not known how sustainable such off-takes are, East (1999) assumed an average density of 10/km² on Bioko I., 2/km² in other areas where the species is known to be common, and 0.2/km² elsewhere, and estimated a population of 12,000 animals on Bioko I. and in the Nigeria/Cameroon area. Elsewhere, he estimated 5000 individuals for *C. o. brookei* and 18,000 for *C. o. crusalbum*. It is worth noting that Wilson (2001), who conducted extensive survey work over a period of ten years in various parts of West Africa, only saw *C. o. brookei* in the wild once, in Kakum N. P., Ghana.

Adaptations A very generalized, but variable type of duiker; the possibility of a relictual status has been discussed above. There is also the possibility, raised by several authors (Grubb 1978a, Kingdon 1982, Wilson 2001), that hybridization may complicate our understanding of the duiker radiation, and of this species in particular. This possibility is central to any attempt at defining the adaptive niche of Ogilby's Duiker. There are several reasons to suspect that this duiker is a relict species in active decline and in the process of replacement by other species of the same generalized red duiker lineage. First is the lack of any distinct specializations. Second are peculiarities of its disjunct distribution, which lack any clear correspondence with vegetation or climatic zones. Third is a peculiar interdigitation in its distribution with that of the commoner Peters's Duiker, which implies competition, decline and retreat from the latter. Fourth, Ogilby's Duiker, from the margins of this 'frontier' zone, shows several characteristics that imply previous long-term hybridization. Likewise, some Peters's Duikers show variations in the form of their dorsal stripes that could be taken to imply hybridization between the two species. Fifth, current molecular evidence allies this species with several other species, including Peters's Duiker, and such ambiguities of affinity could imply both/either archaic status and/or a history of hybridization. The sixth reason to suspect an overall decline in the face of competition from other duiker species is the fact that the Bioko form is very common on the island, yet naturally rare in many of its remaining mainland sites. Unlike the long-haired island population, mainland duikers have short-haired necks that could imply genetic admixture because neck pelage is generally a clear distinguishing characteristic between two separate duiker lineages (Kingdon 1982). These and many other unanswered questions about the *C. ogilbyi* complex preclude any easy definition of the adaptive niche of this species.

The apparent restriction of bossed foreheads to Bioko duikers, combined with known recent high densities, suggest that this isolated species/subspecies lives in smallish, frequently defended territories. It is interesting to speculate whether frontal bossing once occurred in the ancestral populations of *C. o. brookei* and *C. o. crusalbum*. The anomalous occurrence of this physiologically expensive characteristic in just one population implies that reduced densities and less frequent conflict among mainland populations might have caused rapid atrophy in what might otherwise have been taken as a relatively immutable diagnostic characteristic (as tends to be the case in descriptions of the skulls of *C. weynsi*, *C. callipygus* and *C. niger*, all species that live at high densities).

Foraging and Food The ability of this duiker to range through all forest zones on Bioko I. implies a catholic diet and ability to adapt to different vegetation and rainfall zones. Like other duikers, it is known to feed on fruit, flowers and, presumably, foliage from the forest floor. Gautier-Hion & Gautier (1994) observed a subadult *C. o. crusalbum* eating the hard fruits of *Klainedoxa gabonensis*. The stomach contents of a specimen of *C. o. brookei* examined by Newing (2001) comprised 92% fruits and seeds, 7% vegetative parts and 1% flowers.

Social and Reproductive Behaviour A single adult ♂ that was radio-collared in Korup N. P., Cameroon, provided valuable information on the movements and activity (as determined from a mercury activity switch) (Payne 1992). The lucky capture of this individual followed a large number of fruitless drives and capture efforts in an area where Ogilby's Duikers were already acknowledged to be rare. The home-range of this ♂ was estimated to be 10.6 ha (as determined by the minimum convex polygon method). Within this home-range there was a small central area that was consistently and almost exclusively used for sleeping by this strictly diurnal duiker. By contrast, diurnal resting areas, mainly used between mid-day and 15:00h, were on the peripheries of the home-range. Peak activity was immediately after dawn (06:30–11:00h) and between 16:00h and 19:00h. Of 50 sightings, only three, thought to be mother-offspring pairs, were not solitary; this is in agreement with the findings of Gautier-Hion & Gautier (1994), all of whose observations were of solitary individuals or pairs.

In contrast to mainland species, which have been consistently described as rare and shy, Bioko duikers, when surveyed between Jan and Mar 1986, were abundant and vocal, implying a more complex social structure. They were frequently heard to make a loud 'wheet' call (Butynski *et al.* 2001) and East's (1999) estimate of 10/km² was probably realistic for the time of Butynski's surveys (and partly also due to the general absence of predators on duikers on Bioko; see Predators, Parasites and Diseases).

Reproduction and Population Structure Currently, there is no published information, but the dynamics of population structure are likely to differ radically between high-density *C. o. ogilbyi* on Bioko and very low density populations on the mainland. There is no indication of a breeding season.

Predators, Parasites and Diseases Leopards *Panthera pardus* may prey on Ogilby's Duikers in some mainland habitats, and African Golden Cats *Profelis aurata* are also likely to take young and possibly

adults, as are African Rock Pythons *Python sebae*. Young animals are probably taken by Crowned Eagles *Stephanoaetus coronatus*. Mandrills *Mandrillus sphinx* probably prey on young and infirm duikers (Lahm 1986, T. Butynski pers. comm.). Butynski *et al.* (2001) suggested that the main predators likely include Drill *Mandrillus leucophaeus* on Bioko, where hunters imitate the cry of an Ogilby's Duiker young to bring in Drill close enough to shoot.

Conservation IUCN Category: Least Concern (*C. o. crusalbum* – Least Concern; *C. o. brookei* – Vulnerable C1; *C. o. ogilbyi* – Vulnerable C1). CITES: Appendix II.

The main threats to Ogilby's Duikers are habitat degradation and overhunting, and on current trends these duikers will become extinct or will survive in a few well-protected areas. The effective protection of the Gran Caldera de Luba Scientific Reserve is crucial to the survival of this species on Bioko I. On the mainland, Upper Guinea populations of *C. o. brookei* have few remaining strongholds. Among them might be Sapo N. P. (Liberia) and Tai N. P. (Côte d'Ivoire), although hunters resident in Tai N. P. have been reported harvesting 1500–3000 tonnes of wild animal meat per year in parts of this park (Caspary *et al.* 1999) and heavy exploitation of bushmeat has been observed around Sapo N. P. (R. Hoyt pers. comm.). This form has also been recorded recently in Gola N. P. in Sierra Leone (Lindsell *et al.* 2011). *Cephalophus o. ogilbyi* occurs in Korup N. P. (Cameroon), where it is very rare (Payne 1992), and in Cross River N. P. (Nigeria); they are also present in several forest reserves in SW Cameroon, such as Mone and Ejagham (Forbeseh *et al.* 2007). The distinctive white-legged form is now known to be relatively widespread and numerous in Gabon, including protected areas such as Lopé N. P. and the Gamba complex of National Parks, as well as Odzala N. P. (Congo).

This species is hunted throughout its range, but with particular intensity in Bioko, where the bushmeat trade has been well studied over a period of years (Colell *et al.* 1994, Fa *et al.* 1995, 2000, Juste *et al.* 1995, Butynski *et al.* 2001). Of 94,616 wild animal carcasses brought to the bushmeat market in Malabo between the last quarter of 1997 and the first 10 months of 2006, 5.3% were Ogilby's Duikers and this species ranged between the fourth and seventh most common in the market over this period (W. Morra & G. Hearn

pers. comm.). This is similar to the 6% recorded between October 1990 and October 1991, when Ogilby's was the fifth most common species in the market at that time (Juste *et al.* 1995; and see Fa *et al.* 2000). These 1991 market harvest levels were clearly unsustainable (Fa *et al.* 1995), yet availability increased to 89% in 1996; in 1996, estimated daily abundance was about 3.4 carcasses per day (Fa *et al.* 2000). Since then, however, the availability of this species at the Malabo market has undergone a steady decline reaching 1.9 carcasses per day in 2006 (W. Morra & G. Hearn pers. comm.).

Colell *et al.* (1994) found that of animals taken by hunters in south-east Bioko, Ogilby's Duiker was the fourth most frequently collected species; 71% of these were shot and 29% were trapped. Less than 10% were consumed locally, the rest being taken to market, where prices as high as US\$14 per carcass were paid in 1986 (Butynski *et al.* 2001). As of 2006, the average price paid had increased to US\$94 (W. Morra & G. Hearn pers. comm.). The top priority for the conservation of Ogilby's Duiker on Bioko is to stop openly illegal hunting of this species in the two nominally 'protected' areas (T. Butynski pers. comm.).

Measurements

Cephalophus ogilbyi

HB: 850–1150 mm

T: 120–150 mm

E: 88 mm*

HF c.u.: 260 mm

Sh. ht: 550–650 mm

WT: 14.0–20.0 kg

Kingdon (1997); *single adult (sex not noted) from Bioko I. (T. Butynski pers. comm.)

Payne (1992) gave the weight of three adult ♂♂ from Korup N. P., Cameroon, as 18.0, 19.0 and 20.0 kg

Maximum recorded horn length is 12.3 cm for a pair of horns from Grebo, Liberia (Rowland Ward)

Key References Payne 1992; Wilson 2001.

Jonathan Kingdon

Cephalophus weynsi WEYNS'S DUIKER

Fr. Céphalophe de Weyns; Ger. Weynsducker

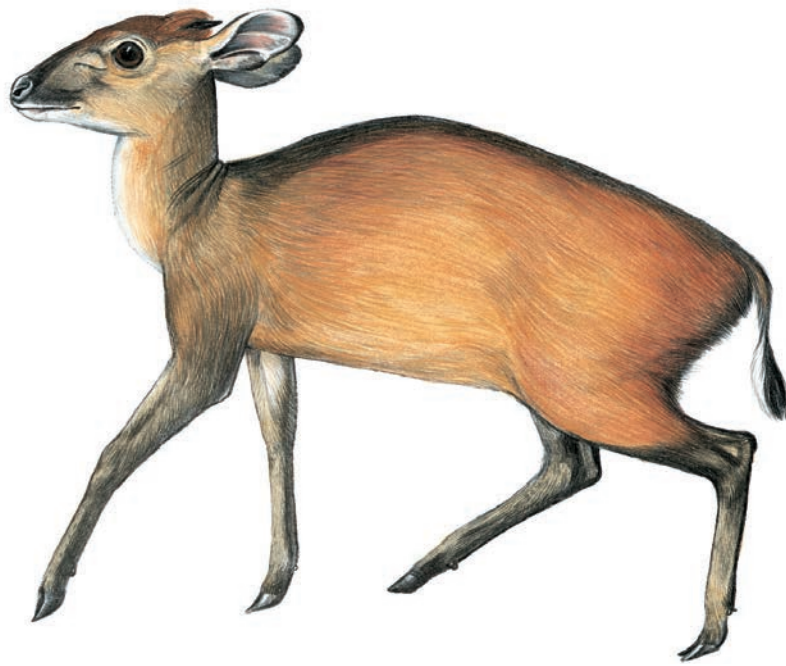
Cephalophus weynsi Thomas, 1901. Ann. Mus. Congo Zool. 2 (1): 15. 'district des Stanley-Falls' (DR Congo, near Stanley Falls).

The duiker is named for Lt. Col. Auguste F. G. Weyns, a Belgian explorer for whom Weyns's Weaver *Ploceus weynsi* is also named.

Taxonomy Previously treated as a subspecies of Peters's Duiker *Cephalophus callipygus* (Kingdon 1982, East 1999, Wilson 2001), or even lumped variably in the past with the Natal Red Duiker *C. natalensis* (Ansell 1972) and Harvey's Duiker *C. harveyi* (Haltenorth & Diller 1980). Considered a distinct species by East *et al.* (1990), Groves & Grubb (1974), Grubb & Groves (2001) and Grubb (2005). Specific designation is supported by genetic analysis (Jansen van Vuuren & Robinson 2001; but see Hassanin *et al.* 2012). Three subspecies were recognized by Grubb & Groves (2001). Synonyms:

barbertoni, *centralis*, *ignifer*, *johnstoni*, *leopoldi*, *lestradei*, *rutshuricus*. Chromosome number: unknown, but likely 2n = 60.

Description A medium-sized, coarse-haired, rufous-coloured duiker, distinguished by its lack of a black dorsal back stripe. The species is variably darker, especially on the limbs, shoulders and underparts, especially in some eastern populations. Crown and forehead red to reddish-brown with a coronal tuft of thick, bright, rufous hairs located between the horns, and covering the horn base in both sexes. The crown is rounded and uplifted in a distinct vaulted boss. Sides of face and ears variably brownish-rufous. The lips are thickened, giving the animal a coarse appearance. Back, sides and abdomen bright rufous with hairs



LEFT: Weyns's Duiker *Cephalophus weynsi* adult female.
ABOVE: Lateral view of skull of Weyns's Duiker *Cephalophus weynsi* adult male.

longest on the rump. Neck and shoulder rufous, mixed with darker hairs, especially on the shoulder. Neck and shoulder hairs shortened and hair on the neck reduced, markedly in some populations, exposing the pale-coloured skin beneath. Pelage on limbs uniformly dark below the hocks, extending variably onto the upper limbs, chest, upper abdomen and shoulders in some populations and individuals. Lower abdomen covered with sparse pale hairs. Tail rufous at base, dark distally, with small dark tuft containing scattered white hairs. Preorbital glands are large, running from the eye towards the muzzle. Inguinal glands are well developed, producing a reddish secretion, which, in populations in the Ituri Forest in NE DR Congo, is sweet-smelling. Pedal glands are present on all four feet (Wilson 2001). Sexes are similar in colouration, and while ♂♂ are smaller than ♀♀, as is true in all forest duikers, sexual dimorphism is reduced; adult ♀♀ average less than 3% larger body weight than adult ♂♂. Pelage of newborns is overall brown, darker above and liberally grizzled with red hairs. The coronal tuft is present, even when horns occur only as buds. This pelage is replaced by adult colouration before the animal is weaned.

The skull has an elongated rostrum and is distinguished by the vaulted forehead and robust horn bases. Both sexes have horns, which are black, short, thickened and strongly annulated at the base and over two-thirds of their length. Horns, distinctly longer in ♂ than ♀, are often curved downward and inward at the tips.

Geographic Variation A variable species, with the taxonomic status of a number of forms, in particular east of the Albertine Rift and south of the Congo R., still uncertain (Wilson 2001). *Cephalophus w. weynsi* (including *leopoldi* and *centralis*), the most rufous form, ranges across DR Congo, on the right bank of the Congo R. east into the sub-montane forests of Kivu, south through Maniema and south Kivu to the forest limit. The forms in the montane forests of the Itombwe Massif, west of L. Tanganyika appear to be this race. Weyns's Duikers from the forest patches of SE Sudan and Uganda (west of L. Victoria) may also be attributable to this form, though some populations of the latter have been lumped as *C. w. johnstoni*. *C.*

w. lestradei, characterized by overall darker pelage, is reported from the sub-montane and montane forests along the eastern Albertine Rift, including Rwanda (Groves & Grubb 1974), and in the forests east of L. Tanganyika; however, the occurrence of this form, as well as the probably now extirpated *C. w. rutshuricus*, named from a now deforested area of eastern Kivu, and their relations to the nominate race on the west side of the Albertine Rift, are not well defined. The taxonomic status of a number of eastern forms, characterized by their smaller size and lumped as *C. w. ignifer* (Grubb & Groves 2001, Grubb 2005), and including duikers from Mt Elgon (*C. w. barbertoni*) through the forest patches of W Kenya, is also poorly known.

Possible hybrids between *C. weynsi* and *C. harveyi* are reported from the Mau escarpment (Kingdon 1982). Duikers south of the Congo R., ranging through the central cuvette to Kasai, and Sankuru have been attributed to this species; however, these forms have a black dorsal patch, and may be better grouped with *C. callipygus*.

Similar Species

Cephalophus callipygus. Allopatric, occurring only west of the Congo and Ubangui Rivers. All forms have a distinctive dark patch on the back and rump, which distinguishes them from Weyns's Duiker.

C. leucogaster. Sympatric east of the Ubangui R. Distinguished by paler colouring, and dark dorsal patch.

C. dorsalis. Sympatric in the east of its range, east of the Ubangui R. Broader-headed, shorter-muzzled, darker rufous, and with a distinct dorsal black patch.

C. harveyi. The species occurs mainly east of the Rift Valley in Kenya, but may hybridize with Weyns's Duiker along the Mau escarpment (Kingdon 1982, Wilson 2001). Black and white chin and whiter ears with black tufts; belly is pale cream or white; shorter legs.

Distribution Endemic to equatorial Africa. Widespread in DR Congo, including large areas of contiguous range north of the Congo R., from the Ubangui R. in the west, through the Ituri Forest to the limits of continuous forest on the western flanks of the Albertine

Rift, then south to the forest limits in Maniema, Kivu and possibly into northern Katanga province. The northern and southern range limits appear to be defined by the forest/savanna boundary on both sides of the Equator. The species' eastern distribution is more fragmented, with populations recorded historically from a number of lowland, sub-montane and montane forest islands in W Uganda, W Rwanda and Burundi, W Tanzania (Mahali Mts and Gombe), S Sudan (Imatong and Dongotona Mts), east to Mt Elgon and the forests of Kakamega and the Mau Escarpment in W Kenya. This species has not been recorded east of the Rift Valley in Kenya. Some eastern populations may now be seriously reduced or extinct.

Habitat In its lowland range in DR Congo the species is restricted to large blocks of closed forest and does not range far out into gallery forests or forest islands in the savanna ecotone. However, in East Africa, Weyns's Duiker occurs in relatively small and isolated forest remnants. Its limited occurrence at the forest edge in the north of its range may be due to the presence of Red-flanked Duiker *C. rufilatus*, which has specialized on the forest/savanna ecotone. In the Ituri Forest, Weyns's Duiker occurs widely in primary and older secondary forests, avoiding recent clearings and deep swamps. The species is common in mixed canopy forests, but is rare or absent from large stands of monodominant *Gilbertiodendron dewevrei* (Hart 2001). The species ranges from altitudes of 400 m to about 2000 m in forests of the Albertine Rift highlands, while east of the Albertine Rift, it occurs locally in sub-montane to montane forests up to 3000 m (reportedly on Mt Elgon; Haltenorth & Diller 1980).

Abundance In the Ituri Forest, Weyns's Duiker is the second most common duiker species after Blue Duiker *Philantomba monticola*. Densities of unhunted populations averaged 15 animals/km² (Hart 2000). East (1999) estimated a total population 188,000.

Adaptations Weyns's Duiker is a robustly built duiker with a strongly developed head and neck. Relatively large male body size, in association with the distinctive bony vaulted crown and reinforced horn bases, present on both sexes, but most developed in the ♂, are indicative of regular intra-specific combat. In the Ituri Forest, preorbital glands of Weyns's Duiker ♂♂ are often strongly swollen with visible exudates, suggesting frequent marking behaviour. Males, and possibly ♀♀, also mark by rubbing the coronal area against the stems of small trees. Animals that are excited or stressed show a red flush on the pale skin of the neck (which is exposed because the hair is so sparse). Weyns's Duiker has an elongated rostrum, and the tooth arch is not markedly widened, but the dentition is robust, and suggests the capacity to handle coarse foods. Relatively high rumen volume to body weight ratios also confirm the species' ability to digest a broad range of food quality (Hart 1985). Weyns's Duiker is diurnal, like the closely related Peters's Duiker (Wilson 2001).

Foraging and Food Ripe and unripe fruits are the most frequent foods in the diet of Weyns's Duiker in the Ituri Forest, comprising between 18% and 100% (mean = 69%) of a sample of rumens across the seasonal fruiting cycle (Hart 1985). In this same sample, foliage, primarily mature leaves fallen from the canopy, comprised the second most frequent food item (annual mean = 23%), with seeds, fallen flowers and fungi comprising the remainder of the diet. Many



Cephalophus weynsi

rumen contents contained small numbers of ants. It is not certain if these were ingested separately from other foods. Kingdon (1982) observed the species feeding on *Spathodea* flowers in W Uganda. In the Ituri Forest, fruits selected tend to be large to intermediate sized. Important plant families include: Irvingiaceae, Sapotaceae, Euphorbiaceae, Apocynaceae, Annonaceae, Ulmaceae, Sapindaceae and, seasonally, the mast seed-fall of dominant caesalpinaceous canopy species, *Julbernardia seretii* and *Cynometra alexandri*. The composition of Weyns's Duiker diets suggests that the species has a generalized foraging strategy, feeding on a range of species and food patch sizes in proportion to their availability (Hart 1985). Animals captured by hunters during periods of mast fruit seed-fall had layers of fat around their kidneys that were absent at other times of year. Several preferred fruit species (notably, *Klainedoxa gabonensis*, *Ricinodendron heudelotii* and *Irvingia grandifolia*) have large armoured seeds that Weyns's Duiker regurgitates intact during rumination. These species are adapted to ungulate and elephant dispersal (Feer 1995).

Social and Reproductive Behaviour Radio-collared Weyns's Duikers in mixed forest in the Epulu area, in the Ituri Forest, occurred in stable, highly cohesive and presumably related parties of 3–4 individuals. Two groups consisted of an adult male–female pair, accompanied by a subadult, and one group of four consisted of a pair accompanied by a subadult and another older animal of undetermined sex. The group of three (adult ♂ and ♀, with a subadult ♀) had individual core home-ranges that overlapped nearly completely over an entire year, and the animals often moved in spatial synchrony. Individual home-ranges in two other social groups also widely overlapped. These synchronized movements suggest strong territorial behaviour, with both sexes taking part in territorial defence. Radio-collared animals had average core home-ranges of 13 ha (adult ♂♂, $n = 4$) and 11 ha (adult ♀♀, $n = 5$), with total annual occupancy of 26–30 ha (adult ♂♂ and ♀♀, respectively) (J. A. Hart pers. obs.). East of the Albertine Rift, populations of Weyns's Duikers are most often observed as solitary



Weyns's Duiker *Cephalophus weynsi*.

animals (Kingdon 1982) or occasionally pairs; however, detailed information on home-range use and social behaviour are not available.

Development of group living in at least some populations of Weyns's Duikers is unusual in forest duikers, and separates this species from the closely related Peters's Duiker (Feer 1989a). In the Ituri Forest, the small individual home-ranges and defence of shared space, in combination with a generalized diet, may permit Weyns's Duikers to control areas of relatively higher overall food availability. However, intensive mate-guarding by adult ♂♂ is also not excluded as a driving factor. Group living may also contribute to anti-predator defence. Both ♂♂ and ♀♀ frequently utter whistled contact calls, in addition to loud bleating calls that they, as well as other duikers, utter when distressed. In the Ituri Forest, where Weyns's Duiker co-occurs with five other duiker species and the frugivorous Water Chevrotain *Hyemoschus aquaticus*, group living may provide this species with an advantage in inter-specific competition. In the Ituri Forest, White-bellied Duikers *C. leucogaster* occur in reduced numbers in areas where Weyns's Duikers are abundant in comparison with areas where they are uncommon or absent. Radio-collared White-bellied Duikers avoid areas controlled by Weyns's Duiker parties.

The commitment to social living has restricted this otherwise highly successful species from occupying some habitats. In the Ituri Forest, Weyns's Duikers are almost entirely absent from large areas of monodominant *Gilbertiodendron dewevrei* forest. Fruit resources in this forest are rare and widely dispersed over most of the year due to the low floristic diversity. This limitation is alleviated only during brief irregular periods of mast flower and seed production by *G. dewevrei*. The small, stable home-ranges of Weyns's Duiker, coupled with their reduced mobility, do not permit the species to take advantage of high-quality ephemeral food sources, unless these occur on the animal's home-range.

Reproduction and Population Structure In the Ituri Forest, 50% (11 of 22) of adult ♀♀ examined were pregnant over the course of a two-year study in a moderately to intensively hunted

area (Hart 1979, 2000, J. A. Hart pers. obs.). Pregnant ♀♀ were recorded in nearly every month. Seven of a total of ten lactating ♀♀ were recorded during the period Sep–Dec. This is the period of late rains, when fruit supplies are generally at their most abundant. One young is born at a time, and gestation period is not known. Two full-term embryos (1500 g and 1510 g) were recorded in Jun. Weigl (2005) reports longevity at 15 years in captivity. In the Ituri Forest, ♂♂ represented 42% of a total of 55 individuals captured. Of the 23 ♂♂, 52% ($n = 12$) were adults; in contrast, adult ♀♀ ($n = 24$), comprised 75% of a total of 32 ♀♀ captured ($n = 32$). The combination of skewed sex ratio, and younger cohort age, suggests higher mortality in ♂♂ in this population.

Predators, Parasites and Diseases Leopards *Panthera pardus* are the most important predator of Weyns's Duikers in the Ituri Forest; however, numbers killed are lower than would be expected given the species' abundance in the community (Hart, J. A. *et al.* 1996, Hart 2000). Diurnal habits and group living may contribute to reducing the extent of predation. African Golden Cats *Profelis aurata* are reported to capture this species occasionally (Y. Sugiyama pers. comm.). One carcass was reported from the nest of Crowned Eagles *Stephanoaetus coronatus* in Uganda (Skorupa 1989).

High frequencies of seropositive titres were recorded for bluetongue, leptospirosis and viral haemorrhagic fevers in a sample of animals tested in the Ituri Forest (Karesh *et al.* 1995). None of these individuals exhibited outward signs of disease; however, stressed animals frequently succumb to a herpes-like condition when brought into captivity, and latent infections may reduce overall fecundity. Helminths were found in the body cavity, often on the rumen surface of almost all freshly killed, butchered animals observed in the Ituri Forest (J. A. Hart pers. obs.).

Conservation IUCN Category: Least Concern. CITES: Not listed.

Weyns's Duiker is among the primary species hunted by the Mbuti net hunters in the Ituri Forest and populations may be severely reduced where hunting pressure is high (Hart 1979, 2000). Overall, however, this species, like the Blue Duiker, is among the more resilient species to human hunting pressure. Populations in some East African locations are at higher risk, especially in the isolated forest islands at the eastern edge of the range; at least one population in Nyungwe Forest, Rwanda, is suspected to be locally extinct. Otherwise, populations of the species occur in a number of protected areas, including Okapi Faunal Reserve and Maiko and Salonga National Parks (DR Congo), Kibale N. P. (Uganda), Mount Elgon N. P. (Kenya) and Mahale Mountains N. P. (Tanzania) (East 1999).

Measurements

Cephalophus weynsi

WT (♂♂): 17.1 (15.5–19.5.5) kg, $n = 12$

WT (♀♀): 17.5 (16.0–20.0) kg, $n = 22$

Ituri Forest, DR Congo (J.A. Hart pers. obs.)

Key References Hart 1985, 2000, 2001; Kingdon 1982; Wilson 2001.

John A. Hart

Cephalophus callipygus PETERS'S DUIKER

Fr. Céphalophe de Peters; Ger. Petersducker

Cephalophus callipygus Peters, 1876. Monatsb. K. Akad. Wiss. Berlin, p. 483. 'Africa occidentalis (Gabun)' (Gabon, Gabon River).

LEFT: Peters's Duiker *Cephalophus callipygus* adult male.
 ABOVE: Lateral view of skull of Peters's Duiker *Cephalophus callipygus* adult male.

Taxonomy Monotypic. Associated with the Natal Red Duiker *C. natalensis*, Aders's Duiker *C. adersi* and Weyns's Duiker *C. weynsi*, as a potential superspecies (Ansell 1972). Considered to be conspecific with the Natal Red Duiker (Wilson 1987) or not related (Groves & Grubb 1974). Weyns's Duiker has been described as a subspecies of Peters's Duiker (Kingdon 1982, 1997) or as a distinct species (Grubb & Groves 2001, Grubb 2005). The latter conclusion has been followed in this work. Molecular data have consistently placed Weyns's Duiker as a sister taxon to Peters's Duiker, within the 'West African red duiker' lineage (Jansen van Vuuren & Robinson 2001; and see Hassanin *et al.* 2012). Synonyms: none. Chromosome number: not known, but likely $2n = 60$.

Description Medium-sized duiker, with overall pale tawny pelage becoming red on the loins. The forehead and frontal crest is rich reddish in colour; the crest hair is forwardly curved. Sides of face greyish-fawn, and lips, chin and throat white. A fine black dorsal line begins in the middle of the back and widens on the base of the tail and croup. Underparts lighter coloured than the flanks. Legs darker than body, and there is a large blackish tail tuft. Females are about 12% heavier than ♂♂. There are large preorbital glands, covered with short rufous hair, present in both sexes, although those in ♂♂ are larger and more active; the slit is about 40 mm long, with 13–16 distinct large pores (Wilson 2001). Inguinal pouches not present. Well-developed pedal glands present. The newborn is darker in colour than adults, and Wilson (2001) notes that a newborn from the Central African Republic had the dark brown almost black dorsal stripe present extending down the back to the tail.

Horns present in both sexes, striated with massive transverse ridges, tips slightly converging and curving upward. Skull with strongly developed frontal boss as in Weyns's Duiker. Preorbital fossae deeper in ♂♂.

Geographic Variation None recorded.

Similar Species

Cephalophus weynsi. Allopatric sibling species, occurring in forests from

E DR Congo, east of the Cogo and Ubangui Rivers, to the western side of the Eastern Rift Valley. Darker pelage with longer dorsal stripe extending in a dark zone on withers; face with blackish tones. *C. ogilbyi*. The White-legged Duiker (*C. o. crusalbum*) is sympatric with *C. callipygus* in Gabon (e.g. Forêt des Abeilles) and NW Congo. Generally brighter colour with black dorsal line, black muzzle and marked dark brows; *C. o. crusalbum* has conspicuous white lower hindleg (Grubb 1978b, Gautier-Hion & Gautier 1994). J. Kingdon (pers. comm.) suggests that some individual specimens of Peters's Duiker with apparent *ogilbyi*-like characteristics might be wild hybrids between the two species. *C. leucogaster*. Broadly sympatric west of the Congo and Ubangui Rivers. Smaller in size, pale body with thick black dorsal stripe, underside sharply white. *C. dorsalis*. Sympatric nocturnal species, occurring in forests from Senegal to L. Tanganyika. Similar in size, but shorter-legged and smaller-headed, rich dark red body with black dorsal stripe and legs. *C. niger*. An entirely allopatric duiker from West Africa that resembles this species in morphology and size, but has glossy black pelage and lacks a black dorsal stripe.

Distribution Endemic to western central Africa in moist lowland forests of S and SE Cameroon, SW Central African Republic, mainland Equatorial Guinea, Gabon and N and SW Congo (East 1999, Wilson 2001). The Sanaga R. appears to be the northerly limit of distribution in Cameroon, although there are apparently museum specimens from north of the river (P. Grubb, in Lamarque *et al.* 1990). It is unlikely that this species occurs in extreme W DR Congo, east of the Ubangui R. and north of the Congo R., since there are large collections from this region in the Tervuren Museum in Belgium, which include other antelopes but not this species (P. Grubb, in von Richter *et al.* 1990).

Habitat Peters's Duikers inhabit moist lowland forest. They prefer primary forest, but are also present in logged forest, probably because they prefer heterogeneous undergrowth (Feer 1989a). In Gabon, Peters's Duikers mostly occupy mature forest, but have also been recorded in remote old secondary forest, riverine forest and seasonally



inundated terrain (Lahm 1993). In S Cameroon, Peters's Duikers occur in secondary forest and farm-bush (Fotso & Ngnegueu 1997).

Abundance Peters's Duiker is the second or the third most abundant duiker in undisturbed forests of NE Gabon, where densities can reach 25/km² (net capture Dubost 1979), 13–15/km² (net capture Feer 1988) and 6.7/km² (line transect Lahm 1993). In forests of S Central African Republic they rank third among duikers and densities are 0.9/km² (line transect) and 0.9–1.2/km² (net count Noss 1999). As a result of hunting, densities decrease near villages in NE Gabon (Lahm 1993), in S Cameroon (Muchaal & Ngandjui 1999) and S Central African Republic (Noss 1999). East (1999) estimated a total population size of about 382,000.

Adaptations When alarmed, Peters's Duikers may freeze before running for cover; they flee quickly at short distances, occasionally with barking. The median and distal segments of the hindleg are relatively longer than in the Bay Duiker *Cephalophus dorsalis* and correspond to the 'semi-runner' type of duiker (Feer 1988).

Living under a canopy with numerous fruit-plucking and fruit-dropping primates, bats and birds, this species is able to sustain a more frugivorous diet than other species of duiker. Dependence on a year-round fruit supply may explain why this species is mainly restricted to the consistently fruit-rich main forest block in west-central Africa while its very closely related sibling, Weyns's Duiker, occupies equivalent areas to the east of its range and the somewhat less closely related, but very similar Black Duiker *C. niger* occupies the main medium-sized duiker frugivore niche to the west of its range (J. Kingdon pers. comm.).

Peters's Duikers are active during the day, resting from around mid-day to late afternoon. As in other diurnal duiker species, the orbits are less dorsally oriented than in the nocturnal Bay Duiker. Females mostly prefer dense undergrowth, both for diurnal rest and for activity (Feer 1989a).

Foraging and Food One of the most frugivorous of duikers (Dubost 1984, Feer 1989b, Gagnon & Chew 2000, Wilson 2001). In two studies in Gabon (Dubost 1984, Feer 1989b), fruit comprised between 82.7% and 89.6% of the diet by dry weight based on examination of stomach contents. Leaves comprised between 7.9% and 10.0% of the diet, with petioles and stems following at 6.2%. Fruit and leaves were found in all stomachs in both studies. Flowers, fungi and animal matter (mostly insects) are found in fewer than 50% of samples and comprise less than 1% of the diet (Dubost 1984). Unweaned animals eat much less fruit than adults (52.7%) and more leaves (37.0%) (Dubost 1984). Fruit consumption is lowest from Mar to May (short wet season) whereas leaves are eaten significantly more throughout the rest of the year (Feer 1989b). Most of the fruit consumed are drupes or berries (77%), 1–5 cm in size (80%). Dubost (1984) identified 55 fruit species ($n = 20$ stomachs) and Feer (1989b) recorded 110 species ($n = 68$). The favoured species of fruits are *Xylopia hypolampra*, *Cylindropsis parvifolia*, *Canarium schweinfurthii*, *Klainedoxa gabonensis* (Dubost 1984) and *Dacryodes büttneri*, *Santiria trimera*, *Polyalthia suaveolens* and *Irvingia gabonensis* (Feer 1989b). During rumination, Peters's Duiker spit out intact protected seeds of ten plant species (Feer 1995). While foraging, the daily mean ranging distance in subadults and adults varies between 2600 m and 4090 m in ♂♂ and between 1870 and 4290 m in ♀♀ and decreases during the long wet season (Feer 1989a). Peters's Duiker increases its daily range when food resources become rare. Wilson (2001) mentions an interesting observation of this duiker deliberately hunting and capturing a Hartlaub's Duckling *Pteronetta hartlaubi*.

Social and Reproductive Behaviour Peters's Duikers are most often solitary (67% of observations, Feer 1988). Adult ♀♀ have stable home-ranges of ca. 40 ha. Male home-ranges are of similar size and include several overlapping ranges of ♀♀ and young. Adult ♂♂ are very intolerant of other ♂♂ in captivity and their home-ranges do not overlap. Female home-ranges are completely separated or overlapping when family bonds exist between them. Both sexes preferentially use locations situated near the perimeter of home-range. Males use a larger portion of their home-ranges on a daily basis than do ♀♀ (Feer 1989a). Males and ♀♀ frequently mark by scraping twig bark with their horns and depositing preorbital secretions (Dubost & Feer 1988). Middens or ritualized defecation were not observed. Social play, reciprocal allogrooming and marking of the partner were observed in captive animals (Dubost & Feer 1988).

Reproduction and Population Structure Histology suggests a sexual maturity at 17 months of age for ♂♂ and ca. 20 months for ♀♀. In Gabon, reproduction occurs all year round, although births peak twice a year at the beginning of the dry seasons when fruit availability or food qualitative richness is most favourable (Dubost & Feer 1992). Around 29% of ♀♀ over 20 months old are pregnant. This figure seems underestimated possibly because of a bias of the sample related to lower mobility, and thus less capture of some pregnant animals (Feer 1988). Two near-term fetuses measured by Wilson (2001) had masses of 2.7 kg and 2.9 kg. Weaning takes place when the maximum amount of fruit resources or leaves is available (Dubost & Feer 1992). In Gabon, a sample of 339 individuals from a moderately hunted population comprised 35% adults; ♂♂

accounted for 43.5% of adults. However, in a sample captured by nets, the proportion of ♂♂ was 27.3%, corresponding more to the observed social life pattern. Mortality of subadult and young adult ♀♀ is higher than in ♂♂ (Feer 1988).

Predators, Parasites and Diseases Peters's Duiker is potentially preyed upon by Leopards *Panthera pardus* (Hart, J. A. *et al.* 1996); hairs of red duikers were observed in a felid scat in Gabon (F. Feer pers. obs.). Diseases and parasites in the wild are unknown.

Conservation IUCN Category: Least Concern. CITES: Not listed.

The primary threats to the survival of the species are habitat loss due to human settlement and hunting (Lahm 1993, East 1999). Because Peters's Duiker prefers undisturbed primary forest, its future survival may be increasingly dependent on protected areas. At present the protected areas within which it is common, for example Dja Wildlife Reserve and Lobéké N. P. (Cameroon), Dzanga-Sangha Special Reserve and Dzanga-Ndoki N. P. (Central African Republic), Odzala and Nouabalé-Ndoki National Parks (Congo), Lopé, Ivindo, Minkébé, Loango and Moukalaba-Doudou National Parks (Gabon) and Monte Alén N. P. (Equatorial Guinea), receive unequal levels of protection and management.

Peters's Duiker is frequently the most abundant medium-sized duiker species in undisturbed areas, but its populations are heavily harvested. Peters's Duiker is especially affected by snare hunting. In the Central African Republic, Peters's Duikers accounted for 29% of all animals captured in snares, a level that appears to be unsustainable (Noss 1998a). In Gabon, the proportion of Peters's Duikers among duikers captured in snares is five times the proportion harvested with guns (Lahm 1993). In N Congo, they comprised 21% of all animals

killed with shotguns (Mockrin *et al.* 2011). In Dja Reserve they are the most frequently captured species and accounted for 48% of duikers hunted (Fotso & Ngnegueu 1997), but at another site in the same area this species accounted for 20% of duikers killed (Muchaal & Ngandjui 1999). In Gabon, Peters's Duikers comprised 9% of duikers caught by village hunters and trappers (Lahm 1993). In Congo, Peters's Duikers represent only 4% of duikers for sale in Brazzaville bushmeat markets (F. Feer pers. obs.) and is rarer in Pointe Noire (Wilson & Wilson 1991). Peters's Duiker ranks between third and fifth among the game species proposed in Libreville (Gabon) markets, with a mean number of animals sold ranging from 2.0 to 6.6 per day (Ntsame Effa 2005).

Measurements

Cephalophus callipygus

HB (♂♂): 977 (940–1060) mm, n = 11

HB (♀♀): 1025 (970–1090) mm, n = 14

T (unsexed): 120–150 mm

HF c.u. (♂♂): 251 (240–270) mm, n = 7

HF c.u. (♀♀): 250 (240–260) mm, n = 7

Sh. ht (♂♂): 532 (490–550) mm, n = 12

Sh. ht (♀♀): 549 (510–570) mm, n = 13

WT (♂♂): 19.6 (17.5–21.5) kg, n = 10

WT (♀♀): 21.9 (18.6–25.2) kg, n = 7

Gabon (Feer 1979, F. Feer pers. obs.)

Maximum recorded horn length is 14.9 cm for a pair of horns from Lomié, Cameroon (Rowland Ward)

Key References Dubost & Feer 1988; Feer 1988, 1989a, b; Wilson 2001.

François Feer & Miranda Mockrin

Cephalophus niger BLACK DUIKER

Fr. Céphalophe noir; Ger. Schwarzducker

Cephalophus niger (Gray, 1846). Ann. Mag. Nat. Hist., ser. 1, 18: 165. 'Guinea', but apparently Ghana, Shama.



Black Duiker *Cephalophus niger*.

Taxonomy Seven years after Gray first named this species, Temminck described it under the name *Antelope pluto*. According to Grubb (2005), the type 'came from the Leiden Museum, one of a series from Chama (= Shama) and Dabocrom, Ghana, including the syntypes of *pluto*. Only the specimens from Dabocrom were retained in Leiden (Jentink, 1892) so presumably the type is from Shama.'

In morphology, size, behaviour and ecology this duiker is the Upper Guinea equivalent of Peters's Duiker *C. callipygus* and Weyns's Duiker *C. weynsi*. In colour and in a smooth neck and swollen nostrils it resembles the larger Abbott's Duiker *C. spadix* and Yellow-backed Duiker *C. silvicultor*. In some formulations of their mtDNA studies, Jansen van Vuuren & Robinson (2001) suggested that the *callipygus/weynsi* and *spadix/silvicultor* lineages were widely divergent whereas in other, more plausible, topologies they associated all these large, smooth-necked duikers in a single but complex cluster of species. Synonyms: *pluto*. Chromosome number: 2n = 60; the X chromosome is a submetacentric (Hard 1969).



Lateral view of skull of Black Duiker *Cephalophus niger*.

Description A heavily built, long-bodied, long-headed, glossy black duiker with swollen nostrils and relatively short stocky legs. Short hair on the face is often very thin or absent, probably abraded by frequent rubbing of the face and preorbital glands. Bridge of the nose black or dark brown graduating to a coronal tuft of dense reddish hair; rest of the face dull grey or, in some individuals, red. Lower jaw and upper throat off-white, dull cream or grey. Backs of ears dark brown, anterior surfaces with short, sparse off-white hairs. Neck black or brown, covered in short hair, and with thickened skin. Back intensely black, long and coarsely haired; legs, flanks and underside black or very dark brown with rufous tinge on upper, inner surfaces and on buttocks. Individual hairs have straw-coloured bases (Grubb & Groves 2001). Wilson (2001) comments that of 186 adults examined across the range of the species, only two exhibited any signs of small patches of white on them: a ♂ from Kumasi had a circle of white hair on the left hindleg near the tail, and another ♂ from Cape Coast in Ghana had three irregular patches of white hair on the left side between the front- and hindlegs. Tail brown and thinly haired except for a terminal tuft, which has a whitish tip. Juveniles similar in colour, but with less red on face and paler below (Grubb & Groves 2001). Sexes of similar size, although ♀♀ are on average larger, especially in mass (Wilson 2001); ♂♂ have longer, more robust horns. Wilson (2001) notes that the average preorbital gland of an adult ♂ was 500 mm long, with a single line of 35–50 pores, from which a white secretion could be squeezed; preorbital glands are smooth and the area surrounding the slit and pores is naked. Pedal glands are present on both fore- and hindfeet. No trace of inguinal glands has been found.

Grubb & Groves (2001) include among distinguishing characteristics of the skull: preorbital pits extending forward to premaxillae, and downward to molar alveoli; a well-defined groove between frontals, which are thickened and slightly convex; zygomatic arch straight; and supraorbital foramina often partly roofed over by lateral extension of frontal thickening.

Geographic Variation No significant variation has been recorded, but individuals vary in intensity of black and in the extent of rufous colour on head.

Similar Species

Cephalophus callipygus. An entirely allopatric duiker from western central Africa that resembles this species in morphology and size, but has rich red colouring and a black dorsal stripe.

C. ogilbyi. Brooke's Duiker (*C. o. brookei*) is sympatric from Sierra Leone to Ghana. A smaller, almost extinct sympatric duiker of reddish colour.

C. spadix. A larger, allopatric duiker from East Africa that closely resembles this species in colour, but is distinctly larger.



Cephalophus niger

C. silvicultor. A much larger sympatric species with prominent yellow back.

Distribution Endemic to Africa, occurring in forested and formerly forested areas from near Kindia in SW Guinea and eastwards through Sierra Leone to the Niger R.; there are no confirmed records from Benin or from Burkina Faso (East 1999, Wilson 2001). There is no indication that the species has ever occurred east of the Niger R., and reference to the species occurring in Cameroon (Jeannin 1936) are in error; similarly, records from Boshi–Okwango forests on the Nigerian border with Cameroon cannot be accepted (Anadu & Green 1990). It is particularly common and successful in the central parts of its range, from Liberia to Ghana, but is rare or declining both east and west of this heartland.

Habitat Primarily found in disturbed and secondary forest, but also inhabits forest galleries, thickets and is especially common in secondary 'farm-bush'. Black Duikers are also found, albeit more rarely, in primary rainforest (Jeffrey 1974). In Liberia, Peal & Kranz (1990) described them favouring secondary bush and riparian habitats. In Côte d'Ivoire, the Black Duiker was one of the two most frequently observed species in mixed farmland mosaics (along with Maxwell's Duiker *Philantomba maxwelli*), and the least frequently observed of the five small- and medium-sized species present in closed-canopy forest (Newing 2001). In a study of 251 carcasses in Ghanaian markets and 41 sightings, Wilson (2001) recorded the majority from various categories of secondary vegetation; less than 10% came from unlogged high forest. Of a smaller sample of 46 records, Anstey (1991) found only 13% in high forest. Wilson (2001) attributes these habitat preferences to a greater variety of food plants and to the denser cover growing under a felled or partial canopy. Of special interest is the role of an American invasive hemp-like species, *Chromolaena odorata*, which forms dense thickets after forests have been cleared. For Black Duikers the attraction of these 'Akyempong

weed' thickets seems to be the cover they provide as the plant did not feature in an exhaustive study of Black Duiker diets (Wilson 2001).

Abundance The Black Duiker's preference for regrowth after forest felling probably led to initial increases in abundance throughout the former forest zones of Upper Guinea, but intensification of agriculture and the spread of vehicles, road networks, markets, firearms, spotlights and snares, all in the service of an increasing human population, eventually offsets initial increase. Once regarded as extremely abundant in Sierra Leone, where eight species of duiker were known, Stanley (1925) reported 'by far the commonest are the black duiker and Maxwell's duiker (the bushgoat and fritambo of the Creoles), which are found everywhere in Sierra Leone where there is plenty of cover, preferably forest regrowth'. By 1990 this species had become restricted to isolated pockets where it continued to decline (Teleki *et al.* 1990). In Liberia, Anstey (1991) considered it the most widely sighted duiker, and the second most frequently recorded in bushmeat markets in Liberia. In Côte d'Ivoire, Newing (2001) recorded the species as being very common in secondary habitats. Wilson (2001) suggested that the Black Duiker was more common in Ghana than anywhere else in West Africa, and the second most common forest duiker in the country after Maxwell's Duiker. This species is still abundant in many other parts of its range and a density of 2/km² in the more favourable localities has been suggested by East (1999), who estimated the total population to be about 100,000.

Adaptations There are interesting questions raised by a switch from predominantly red to black colouring in several lineages of duikers. Within the *callipygus/weynsi/niger* complex, melanistic colouring occurs in the far west and far east of their range. Both Peters's Duiker and Weyns's Duiker are vividly coloured red duikers, but one race of the latter, *C. w. lestradei*, and occasional individual variants from other parts of this species' range are very dark brown or nearly black (a change in colouring that seems to derive from extensions of the very variable black dorsal stripe). It has been reported that the Black Duiker is nocturnal (Sclater & Thomas 1899) or crepuscular (Wilson 2001), and it could be argued that dark colouring might represent a type of crypsis appropriate to this activity, with predation by Leopards *Panthera pardus* providing the principal selective pressure. However, captives in Monrovia Zoo were found to be active at night only 24% of the time and 69% during the day (Newing 2001), and other authors (Dunn 1991, Anstey 1991, and see Hoppe-Dominik *et al.* 2011) have recorded diurnal activity, so the link between dark colouring and nocturnal habits seems unlikely. An alternative explanation could be that visual communication has some intra-specific utility for bright red duikers that live at high densities in relatively open undergrowth, whereas equally large numbers of duikers living in denser vegetation rely more on auditory, olfactory or indirect clues to regulate intra-specific contacts. If this is so, then dark colouring could be characterized as a sort of 'cancelling out' of the visual channel, except at very close quarters, where ear and face markings can enhance expressions and intention movements.

This species shares with both Peters' and Weyns's Duikers a strongly reinforced forehead that is especially thick in ♂♂. This peculiarity implies adaptation to exceptionally severe concussion during intra-specific fighting. The special development of this reinforcement in

♂♂ makes it less plausible that it evolved to break open large, hard fruits or even to butt fruit-bearing trees. These might, of course, be secondary benefits of hard-headedness. To date neither aspect of behaviour has been confirmed, but there are widespread hunter's stories of this species felling banana *Musa paradisiaca* and pawpaw *Carica papaya* trees to get at the fruit (Wilson 2001). Assuming that the selective pressure favouring reinforcement of the forehead was the ability to withstand head-butting, especially among ♂♂, the frequency of confrontations implies either a naturally high density of territorial ♂♂ or a high level of competition for ♀♀. What little is known of all three species supports the former explanation. A significant difference, however, is that Peters' and Weyns's Duikers inhabit well-developed, multi-species mature high forest whereas the Black Duiker prefers thick secondary growth, a preference that places it closer to Abbott's Duiker and the Yellow-backed Duiker. This suggests that the Black Duiker occupies an ecological position in between the two giant duikers and the larger red duikers of the main forest block. This conclusion has some support from the molecular trees of Jansen van Vuuren & Robinson (2001) and there is the implication that with phylogenetic enlargement of duiker body sizes there may have come a point where high-quality diets might have had to give way to less selective, broader-band feeding habits, especially in disturbed or secondary forests. If that is the case, the Black Duiker's biology might illustrate some of the conditions that favoured increase in the size of duikers.

Black Duikers are well known for digging up subterranean plant parts and for employing their sharp hooves to slash and break up edible roots. Among the tubers regularly excavated and eaten by Black Duikers are those of the introduced exotic cassava *Manihot esculenta*. As these tubers are known to harbour strong toxins in their unprocessed state it is clear that the Black Duiker has a natural resistance to certain plant poisons (Wilson 2001).

Foraging and Food Fallen fruits, flowers and leaves from the forest floor, as well as bulbs, rhizomes, fungi, bark and occasional animal matter, make up the diet. In Liberia, Black Duikers have been recorded following Western Pied Colobus *Colobus polykomos* for canopy waste, presumably mostly leaf and stem material. The bulk of their diet is fruit, and every one of 131 stomachs retrieved from Ghanaian markets and examined by Wilson (2001) contained pieces of fruits or whole fruits and seeds. Figs *Ficus* spp. were a major food throughout the year, as were *Nauclea latifolia*, *Canthium vulgare*, *Lecaniodiscus cupanoides*, *Blighia sapida* and *Solanum* spp. Other more seasonal fruits were *Cola gigantea* (May, Jun and Sep–Dec), *Anchomanes difformis* (Nov–Mar), *Griffonia simplicifolia* (Oct–Mar), *Musanga cecropoides* (Feb–Mar), *Alchornea cordifolia* (Feb–Apr), *Phyllanthus discoides* (Jun–Aug), *Antholeista djalensis* (Mar–May) and *Canavalia ensiformis* (Sep–Nov).

This spread of wild fruits was augmented by visits to cultivated crops; in 35 of the stomachs, the bulk of the food was from cultivation. The most important of these were: oil nut palm dates *Elaeis guineensis*, avocados *Persea americana*, cassava, coffee *Coffea canephora*, new cocoyam *Xanthosoma* sp., cocoa *Theobroma cacao*, pawpaws, bananas and cow-itch *Mucuna pruriens*. As a very high proportion of these food plants are exotic to Africa, it is clear that Black Duikers have a naturally catholic diet and, in spite of intensive hunting, have found some benefits from partial forest clearance and low-intensity

agriculture. Wilson (2001) found animal matter in 15% of his sample and he also recorded Black Duikers feeding on an open sea-side beach where he thought minute shells (perhaps salt-retaining types?) were the attraction. In total, Wilson (2001) recorded some 27 species of fruit or cultivated crops eaten. In a similar study, Hofmann & Roth (2003) examined 57 stomachs and recorded a total of 33 different types of fruit eaten. Their study also confirmed that Black Duikers frequent cultivated lands for feeding and are not dependent on primary forest habitat for food; leaves of cassava were found in 53% of stomach samples, and leaves of *Alchornea cordifolia* in 18% of stomachs. Black Duikers are believed to play an important role in the dispersal and germination of small seeds, such as *Solanum verbascifolium* (Alexandre 1982). Newing (2001) found that Black Duiker mouths and teeth could break open food items up to a diameter of 6 cm.

Social and Reproductive Behaviour A territorial and mainly solitary species: of 53 sightings made by Wilson (2001), 39 were of single animals, ten were of male–female pairs (three accompanied by an infant) and four were of ♀♀ with young. Duikers in general are known to respond to bleat-like calls and this susceptibility is widely exploited by hunters. The Black Duiker appears to be particularly responsive to artificial lures blown on whistles that are cut from fern stems in Liberia (Wilson 2001). What attention-getting calls could signify in the social and spatial structures of a solitary species remains to be elucidated.

Reproduction and Population Structure Although pregnant ♀♀ have been recorded in every month of the year, Wilson (2001) recorded a very marked birth peak between Nov and Jan (the wet season) based on reproductive tracts of 106 sexually mature ♀♀ collected mainly in Ghana. Of the ♀♀ examined, 72.6% were either pregnant or lactating and of these nearly 10% were both pregnant and lactating. Females are capable of conceiving at one year of age (Wilson 2001). Such fecundity helps explain how Black Duikers have managed to survive very high mortality rates from the bushmeat trade in West Africa. Although ovulation had taken place in both ovaries, Wilson (2001) found that single foetuses were always implanted in the right horn of the uterus; he found that neonates weighed between 1.65 and 2.31 kg at birth (with no difference between the sexes). Captive Black Duikers weigh 1.4–2.2 kg at birth, doubling in weight after the first month (Barnes *et al.* 2002). Weaning occurs at between 80 and 108 days (Wilson 2001). Captive animals have lived to more than 14 years (Weigl 2005).

Predators, Parasites and Diseases Lions *Panthera leo*, Leopards and African Rock Pythons *Python sebae* are known predators (Wilson 2001, Bodendorfer *et al.* 2006). Young may be predated upon by

Servals *Leptailurus serval*, African Golden Cats *Profelis aurata*, Eagle-owls *Bubo* spp., Martial Eagle *Polemaetus bellicosus* and Crowned Eagle *Stephanoaetus coronatus*. Ntiemoa-Baidu *et al.* (2005) recorded the following ixodid tick species from animals in Ghana: *Haemaphysalis parvata*, *H. leachi*, *Ixodes muniensis*, *I. moreli*, *I. aulacodi*, *Rhipicephalus ziemanni*, *R. simpsoni* and *Amblyomma compressum*.

Conservation IUCN Category: Least Concern. CITES: Not listed.

Their adaptability to degraded and secondary forests has enabled Black Duikers to withstand settlement better than other medium-sized forest duiker species in West Africa, and while they have been eliminated from the more densely settled parts of their range they still occur relatively widely within their historical range. They also show resilience to hunting and remain locally common; they have been recorded as extirpated from several reserves in Ghana (e.g. Digya N. P. and Kalakpa Resource Reserve; Wilson 2001), but in fact do still persist in these areas (R. J. Dowsett pers. comm.). Dunn (1991) noted that long after all primates had been shot out in parts of Liberia, the Black Duiker persisted. None the less, East (1999) has warned 'If current trends continue, including a complete lack of effective protection and management over most of its range, its status will eventually decline to threatened.' Black Duikers are well represented, generally in stable numbers, in protected areas such as Sapo N. P. (Liberia), Western Area F. R. (Sierra Leone), Taï N. P. and Comoé N. P. (Côte d'Ivoire) and Bia, Nini-Suhien and Kakum National Parks (Ghana).

Measurements

Cephalophus niger

TL (♂♂): 1060 (1020–1100) mm, n = 30

TL (♀♀): 1080 (1020–1160) mm, n = 44

T (♂♂): 100 (90–120) mm, n = 30

T (♀♀): 110 (100–140) mm, n = 44

HF c.u. (♂♂): 250 (240–260) mm, n = 30

HF c.u. (♀♀): 250 (240–260) mm, n = 44

E (♂♂): 94 (91–99) mm, n = 30

E (♀♀): 95 (90–100) mm, n = 44

Sh. ht (♂♂): 460 (450–480) mm, n = 30

Sh. ht (♀♀): 470 (440–500) mm, n = 44

WT (♂♂): 21.0 (19.0–23.0) kg, n = 30

WT (♀♀): 24.0 (17.0–26.0) kg, n = 44

Ghana (Wilson 2001)

Maximum recorded horn length is 17.46 cm for a pair of horns from Ghana (Rowland Ward)

Key References Newing 2001; Wilson 2001.

Jonathan Kingdon & Michael Hoffmann

Cephalophus spadix ABBOTT'S DUIKER

Fr. Céphalophe d'Abbott; Ger. Abbottducker

Cephalophus spadix True, 1890. Proc. U.S. Natl Mus. 13: 227. 'High altitudes on Mt. Kilima-njaro, frequenting the highest points' (Tanzania, Mt Kilimanjaro; at 2400 m according to Grimshaw *et al.* 1995).

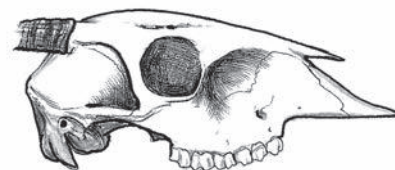


Abbott's Duiker *Cephalophus spadix*.

The common name is after W. L. Abbott, an American naturalist and explorer who spent 1888–89 in the Kilimanjaro district, collecting zoological specimens.

Taxonomy According to Sclater & Thomas (1899), F. True suggested that '*C. spadix* was closely allied to *C. niger* and even possibly identical with it'. Roosevelt & Heller (1915) suggested that it was more closely related to the group of giant duikers of which the Yellow-backed Duiker *C. silvicultor* is typical, and Hattenorth (1963) considered Abbott's Duiker a subspecies of *silvicultor*. Kingdon (1982) indicated that Abbott's Duiker was closely related to the Yellow-backed Duiker and probably represented a relic of an ancestral population. Wilson (2001) interpreted the skull morphology to suggest that Abbott's Duiker is primitive with respect to both the Yellow-backed Duiker and the Bay Duiker and considered it a near-perfect morphological ancestor. A cladistic analysis that considered 41 morphological characters highlighted the monophyly of the *silvicultor* group and, within this, a split between *dorsalis* versus *jentinki* / *silvicultor* / *spadix* (Grubb & Groves 2001). Molecular phylogeny of seven duiker species representative of four supposed adaptive lineages has confirmed the existence of a distinct, giant duiker lineage that includes *silvicultor*, *spadix* and *dorsalis* (Jansen van Vuuren & Robinson 2001). Synonyms: none. Chromosome number: not known.

Description A large, stocky duiker with a glossy, dark brown pelage, especially on the back, flanks and upper legs. Neck and face are paler, greyer brown. A prominent russet hair tuft between the ears is dense, tinged with black and usually lighter basally. Throat, ventrum and inner thighs are sometimes paler brown, with white fur in the genital area. The extent of the paler ventral hair can vary between individuals within the same population (T. Davenport & S. Machaga unpubl., F. Rovero pers. obs.). The wedge-shaped head ends with a broad, flat-



Lateral view of skull of Abbott's Duiker *Cephalophus spadix*.

fronted nostril pad that overhangs the mouth (as with Yellow-backed Duikers). The rhinarium is shiny black. Ears are rounded with naked and grey-pinkish inner surfaces. Lower parts of the legs are slightly darker brown to almost black and end in black hooves, the front ones longer than the hind ones. Tail short, dark grey to black on the outer, dorsal portions and paler grey to white on the inner surfaces and tip. A six-month old juvenile from West Usambara appeared uniformly paler brown than adults, including head and neck, and had a darker brown dorsal stripe. The skin of a juvenile from Mount Rungwe exhibited longer fur than adults (T. Davenport & S. Machaga unpubl.).

Kingdon (1982) mentioned 'a hint of the yellow-back of *silvicultor* is visible in the form of a small grey patch above the root of the tail', and Grubb & Groves (2001) mention a 'vague dark dorsal stripe' and note that two skins in the British Museum show what may be rudiments, or precursors, of the *silvicultor* dorsal markings at the base of the tail. Wilson (2001) found no signs of such markings in two adult ♀♀ examined and no markings were evident on at least four individuals camera-trapped in the Udzungwa Mts (F. Rovero pers. obs.). However, in three of five skins from Mt Rungwe, a very slight, approximately 5 cm-wide, darkening of hair along the spine from the lower neck to the rump is visible, although there is no obvious grey patch above the root of the tail (T. Davenport & S. Machaga unpubl.).

Both sexes possess horns (8–12 cm long), which are mostly hidden in the hair tuft. Horns are without any conspicuous thickening at their base.

Geographic Variation No subspecies have been described and no geographical variation is reported. The coat colour of a captive adult pair from West Usambara appeared remarkably darker brownish, almost black, with less evident, contrasting paler underparts, than several individuals camera-trapped in the Udzungwa Mts (F. Rovero pers. obs.); the same is true of Mt Rungwe animals (T. Davenport & S. Machaga unpubl.). It is likely that variation in coat colour occurs within populations as much as between populations.

Similar Species

Cephalophus niger: Allopatric species from West Africa. Considerably smaller, the body is black with more contrasting paler neck and head, and similar reddish hair tuft.

C. silvicultor: Allopatric species from the Guineo-Congolian forests. Slightly larger, greyish-brown with a vivid cream-coloured patch on the back.



Distribution Endemic to Africa, being confined to a few isolated forested massifs in N, E and SW Tanzania (Kingdon 1982, 1997, East 1999). It is currently reported from Mt Kilimanjaro, W Usambara Mts, Rubeho Mts, Udzungwa Mts and Mt Rungwe (Wilson 2001, Moyer 2003, F. Rovero pers. obs.), as well as the forests of Livingstone (now part of Kitulo N. P.), Irungu, Irenga, Ndukunduku and Madehani in the Southern Highlands (Wilson 2001, Machaga & Davenport 2004, T. Davenport & S. Machaga unpubl.). Surveys in the Udzungwa Mts have extended their known distribution to nine discrete forests (Jones & Bowkett 2012). However, recent work in Madehani failed to record the animal (T. Davenport pers. obs.). In the Uluguru Mts, the most recent published record is from Swynnerton & Hayman (1951), and no signs were obtained during extensive surveys in the last few years (Frontier-Tanzania 2005), including a camera-trap survey in Uluguru North F. R. in 2005 (F. Rovero & A. Bowkett unpubl.). A previously unknown population of Abbott's Duiker, estimated at a maximum of 50 individuals, was discovered in 2006 in a montane forest locally called 'Ilole', in the southern Rubeho Mts (Rovero *et al.* 2008), while no records are reported from other forests of this area (Doggart *et al.* 2006, F. Rovero pers. obs.). Among other highland forests of Tanzania, Abbott's Duiker was not reported to occur from recent surveys in North Pare, South Pare, Nguru, Nguu, Ukaguru and Mahenge Mts (Tanzania Forest Conservation Group unpubl., Frontier-Tanzania unpubl.).

The historical distribution also included forests on the Rift Wall near Babati in C Tanzania, forests above L. Manyara, the Poroto Mts and Mfrika Scarp in the Southern Highlands (Rushby & Swynnerton 1946, Swynnerton & Hayman 1951), as well as Mporoto, Mpara, Sawago and Njombe Forest Reserves and possibly Mbeya Range (T. Davenport & S. Machaga unpubl.). However, it is probable that they have been extirpated from all these sites (Rovero *et al.* 2005). Reports of this species being present in Sierra Leone and Ghana are clearly in error, and likely refer to Black Duiker *C. niger* (see references in Grubb *et al.* 1998).

Habitat Typical habitat is montane and sub-montane moist forest; in Mt Kilimanjaro it is reported as commonest between 1300 and 2700 m (see Grimshaw *et al.* 1995) in forest and high-altitude swamps, scrub and moorland. In the Udzungwa Mts, Abbott's Duiker has been recorded as low as 300 m in Matundu Forest, a large, lowland and semi-deciduous forest (Rovero & Marshall 2009), as well as on the highest peak (Mt Luhombero, 2600 m; Rodgers & Swai 1988). It has been camera-trapped on several occasions in semi-deciduous to evergreen forests with dense understorey in Matundu and Mwanihana forests at 500–800 m in Udzungwa Mountains N. P. (Rovero *et al.* 2005, F. Rovero pers. obs.). On the Uzungwa Scarp it has been sighted on bamboo-dominated ridges at 1700 m (J. Fjeldså pers. comm.). It is known from disturbed and secondary montane forest and bamboo forest to 2500 m and occasionally plateau grassland to 2800 m on Mt Rungwe and in Livingstone–Kitulo in the Southern Highlands (T. Davenport & S. Machaga unpubl.). These records suggest that Abbott's Duiker, if undisturbed, occurs also in lowland, semi-deciduous forest with clearings and large areas of secondary vegetation.

Abundance Abbott's Duiker is one of the rarest duiker species (East 1999). However, there is very little information to infer reliable estimates of population densities. It is sighted too infrequently to be counted using diurnal, line-transect methods (Rovero & Marshall 2004), while camera-trapping is proving a potentially useful technique (Rovero *et al.* 2005). East (1999) used comparative data to derive a conservative estimate of 1 individual per km² in optimal habitat. Camera-trapping data from the Udzungwa Mts fed into a regression equation relating sighting rates to estimated densities obtained for Harvey's Duiker *Cephalophus harveyi* suggest maximum densities of 1.3 Abbott's Duikers per km² (F. Rovero pers. obs.). Albeit preliminary, this figure matches the estimation given by East (1999). From in-forest follows, tracking, habitat suitability analyses and hunting surveys, it is estimated that there are fewer than 40 individuals throughout Mt Rungwe and Livingstone (T. Davenport & S. Machaga unpubl.). East (1999) and Moyer (2003) gave total population size in the range of 1500–2500 individuals based on estimated area of occupancy. However, these did not account for the dramatic decline of Abbott's Duiker due to hunting in potentially suitable habitat, especially over the last decade (e.g. Uzungwa Scarp F. R., Mt Rungwe and Livingstone, West Usambara Mts and West Kilimanjaro). Therefore, although the total population size is unknown, it is probably less than 1500 individuals (Rovero *et al.* 2005).

Adaptations This is an extremely secretive species, occurring at low densities and very rarely seen even where it is considered relatively common. Furthermore, it appears to be mainly nocturnal and crepuscular (F. Rovero pers. obs.), and capture times of 25 photographs from several sites in Udzungwa Mts N. P. show that 52% were taken at night, 16% from 06:00h to 07:00h and from 18:00h to 19:00h, and 32% in the day (F. Rovero pers. obs.).

Foraging and Food Kingdon (1997) indicates that the diet of this species includes fruits, flowers, green shoots and herbage, and that it has been recorded browsing the leaves of a balsam (*Impatiens elegantissima*). In the Udzungwa Mts, it has been seen browsing both on understorey leaves in closed forest and on marshy vegetation in forest clearings (T. Jones & F. Rovero pers. obs.), and one individual was camera-trapped

with a large frog in its mouth (Rovero *et al.* 2005). Wilson (2001) reports Abbott's Duikers on the lower slopes of Mt Kilimanjaro crop-raiding and feeding on sweet potato leaves and tubers, bananas, cassava leaves and cowpeas; he also saw an adult Abbott's Duiker eating pieces of green moss from rocks. In the Southern Highlands on Mt Rungwe, Abbott's Duikers have been reported eating various balsams *Impatiens* spp., the climbing herb *Begonia meyeri-johannis* and beans from local shambas (Machaga & Davenport 2004).

Social and Reproductive Behaviour There is an almost complete lack of behavioural notes on Abbott's Duiker. All sightings and camera-trap records are of single individuals except for one mating pair (see below) and a ♀ with a two-month-old juvenile (Wilson 2001). It is likely that Abbott's Duiker is mainly solitary, as claimed by all hunters of the species in the Southern Highlands (T. Davenport & S. Machaga unpubl.) and as reported for the Yellow-backed Duiker (Kingdon 1997). When disturbed, no alarm vocalization is usually emitted (T. Jones pers. obs.), in contrast to other forest antelope species. In the Udzungwa Mts, an adult Abbott's Duiker was briefly observed following a large group of Sanje Mangabeys *Cercocebus sanjei*, which were foraging on the forest floor (T. Jones pers. obs.).

Reproduction and Population Structure A camera-trap photograph of a mating pair was taken on 27 Jan in Mwanihana Forest, Udzungwa Mts (F. Rovero & T. Jones pers. obs.). Wilson (2001) reports two births that occurred in Aug/early Sep and suggests that as Abbott's Duikers are found mainly in wet and fairly moist habitats they may not have a fixed breeding season, and as claimed by hunters in the Southern Highlands (T. Davenport & S. Machaga unpubl.). A pair kept in captivity was observed mating on 28 May, and a birth occurred on 13 Jun, these observations being recorded in different years (J. Beraducci pers. comm.).

Predators, Parasites and Diseases The main non-human predator of Abbott's Duiker is the Leopard *Panthera pardus* (Wilson 2001, Rovero *et al.* 2005, D. Moyer pers. comm.). In the Udzungwa Mts, Lions *Panthera leo* and Spotted Hyenas *Crocuta crocuta* are also potential predators. Juveniles are probably preyed by Crowned Eagles *Stephanoaetus coronatus* and pythons *Python* spp.

Conservation IUCN Category: Endangered C2a(i). CITES: Not listed.

Wilson (2001) reports Abbott's Duikers as having been quite common until the early 1960s and mentions frequent records of hunted animals from several sites until the late 1980s. There is little doubt that increasing hunting, habitat destruction, alteration and fragmentation have caused a dramatic decline in the last few decades in the abundance of most populations and probably their extirpation from many areas. This is the case of small/marginal forests in the Udzungwa Mts (Kigogo, Mufindi Scarp East and Mufindi Scarp West Forest Reserves; Moyer 2003), many sites in the Southern Highlands, and Chonwe Forest in the Uvidunda (Bismark) Mts. Near-extinction is probably occurring in the Uluguru Mts, Uzungwa Scarp F. R., Kising'a-Lugalo F. R., New Dabaga-Ulang'ambi Forest in the Udzungwa Mts and throughout the Southern Highlands (Bowkett *et al.* in press).

A comprehensive survey of duiker hunting was carried out in Mt Rungwe and the adjacent Livingstone forest in 2003 (Machaga

& Davenport 2004, T. Davenport & S. Machaga unpubl.). All 114 hunters interviewed reported having seen Abbott's Duiker. Some 77% hunt for domestic purposes, whereas 23% hunt for commercial purposes. Abbott's Duiker is not sought after for medicinal properties, but its skin is used in making drums. In 2003, an Abbott's Duiker carcass was valued in the villages at \$US20–30, although only 3% of hunters successfully trapped one that year. The vast majority used snares and the number of snares laid per hunter ranged from 300 to 1000. All hunters had noted a dramatic reduction in the number of Abbott's Duikers caught, especially over the last decade, and only 5% said hunting was still worthwhile.

The heavy hunting pressure in unprotected forests has probably left the Kilimanjaro and Udzungwa populations as the two strongholds of this species, while in other areas it most likely persists at very low densities. The current distribution on Mt Kilimanjaro is not known, but the area is mainly protected as a national park. Udzungwa Mountains N. P. holds a healthy population of Abbott's Duikers, while the species' presence in adjacent, unprotected forests such as Uzungwa Scarp F. R. is severely threatened by recent and alarming increases in levels of poaching (Moyer 2003, Rovero *et al.* 2005, 2010). However, a recent, preliminary study on the genetic structure of the Udzungwa population found that genetic diversity values are low relative to Harvey's Duiker in the Udzungwa Mts or published values for other mammal species (Bowkett *et al.* in press). This may be the result of habitat fragmentation and the resulting isolation of small subpopulations. In the West Usambara Mts, heavy hunting is seriously threatening the survival of this population, and recent interviews of hunters indicate that Abbott's Duikers might be left only in Shume-Magamba F. R. (F. Rovero pers. obs.). The situation in the East Usambara Mts is reported to be even more critical (Moyer 2003), and Abbott's Duiker is very likely to have been extirpated there already. Livingstone Forest, now part of Kitulo N. P., is the only Southern Highland habitat that is currently being effectively managed, although moves to upgrade the protected area status of Mt Rungwe are under way (T. Davenport pers. obs.).

Unless major conservation efforts are urgently applied within the next few years, Abbott's Duiker will probably become restricted to the Udzungwa Mts and Mt Kilimanjaro (Moyer 2003). Thus, coordinated survey work should be carried out throughout its range to assess current status and distribution. Conservation and education initiatives should also be instigated as a matter of priority. Current work in the Southern Highlands employing hunters in environmental education initiatives in exchange for stopping hunting has met with some success. It is too early to say if this will have a significant positive impact on Abbott's Duiker populations, although it may prove a valuable model for conservation at other sites.

Major conservation management measures that would enhance the protection of Abbott's Duiker are increased protection to include important forests in the Udzungwa Mts currently poorly protected, in particular Uzungwa Scarp, Iyondo and Matundu (Sumbi *et al.* 2005). The expansion of Kilimanjaro N. P. to annex lower altitude forests has been recently gazetted. Also necessary is the inclusion of Mt Rungwe within the new Kitulo N. P. and greater law enforcement enacted in those areas that are currently not adequately protected (such as Southern Highland forests, Usambara and Uluguru Mts). Critical forest connections, such as the degraded Bujingijila corridor linking Mt Rungwe to Livingstone Forest in Kitulo, must be adequately

protected. The ca. 25 km² of moist montane forest in the Rubeho Mts, where a new population of Abbott's Duikers was discovered in 2006, does not benefit from any legal protection, and therefore measures to give protected status to this forest should be urgently considered.

Measurements

Cephalophus spadix

HB (♂): 1240 mm, n = 1

T (♂): 110 mm, n = 1

HF (slot) length (♂): 50 mm, n = 1

E (♂): 1190 mm, n = 1

Mt Rungwe, Tanzania (T. Davenport & S. Machaga unpubl.)

HB (♂): 1330 mm, n = 1

T (♂): 135 mm, n = 1

E (♂): 112 mm, n = 1

Sh ht. (♂): 710 mm, n = 1

WT: 58.0 kg, n = 1

Mt Kilimanjaro, Tanzania (Wilson 2001)

Kingdon (1982) gave the following measurements: HB: 970–1400 mm;

T: 80–130 mm; Sh. ht: 660–740 mm; WT: 50.0–60.0 kg

Maximum recorded horn length is 11.1 cm for a pair of horns from the Usambara Mts, Tanzania (Rowland Ward)

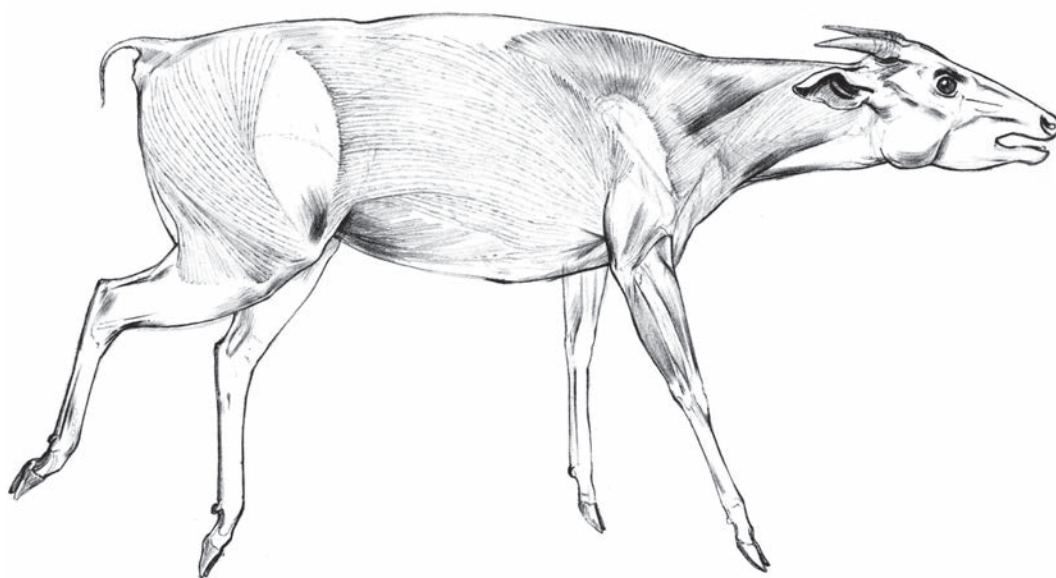
Key References Machaga & Davenport 2004; Moyer 2003; Wilson 2001.

Francesco Rovero, Tim R. B. Davenport & Trevor Jones

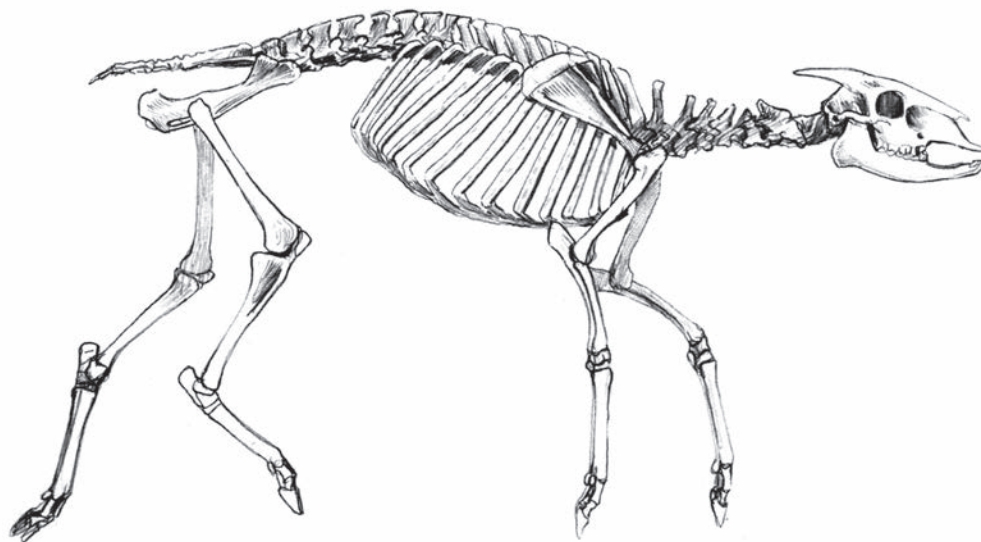
Cephalophus silvicultor YELLOW-BACKED DUIKER

Fr. Céphalophe à dos jaune; Ger. Riesenducker

Cephalophus silvicultor (Afzelius, 1815). Nova Acta Reg. Soc. Sci. Upsala 7: 265, pl. 8, fig. 1. 'Habitat in montibus Sierra Leone & regionibus susuensium fluvios Pongas & Quia adjacentibus frequens'; since restricted to Sierra Leone, vicinity of Freetown (Grubb *et al.* 1998).



Yellow-backed Duiker *Cephalophus silvicultor*
adult female myology and skeleton.





Yellow-backed Duiker *Cephalophus silvicultor*.

Taxonomy The type species of the genus, this species was described at a surprisingly early date for a tropical forest duiker. The reason was that the botanist Adam Afzelius, a pupil of Linnaeus, provided an illustrated account to the Swedish Royal Scientific Society on his return to Sweden after serving in Sierra Leone between 1792 and 1794. Ansell (1972) recognized three subspecies (the nominate form, *C. s. ituriensis* and *C. s. ruficrista*), but noted that their validity was in some doubt. St Leger (1936) had earlier only considered *ituriensis* as distinct, though Hill & Carter (1941) and Ansell (1960b) both recognized *ruficrista* (and which they considered to include the form *coxi*, which St Leger included in the nominate form). Haltenorth (1963) recognized *ruficrista*, but not *ituriensis*, and included *coxi* in the nominate form. More recently, a comprehensive review by Grubb & Groves (2001) recognized four subspecies, including the description of a new subspecies. The correct spelling of the species name is *silvicultor*, not *sylicultor*, which is an incorrect subsequent spelling (Grubb 2004). Synonyms: *coxi*, *curticeps*, *ituriensis*, *longiceps*, *melanoprymnus*, *punctulatus*, *ruficrista*, *sclateri*, *silvicultrix*, *sylicultor*, *thomasi*. Chromosome number: $2n = 60$; the X chromosomes are submetacentric, while the Y chromosome is assumed to be a small acrocentric (Hard 1969, Robinson *et al.* 1996b).

Description The largest of the duikers, dark brown, with a vivid cream-coloured patch on the back. The long wedge-shaped head has a grey muzzle and cheeks ending in a shiny black rhinarium. Pale off-white colouring on the throat and lips is very variable in extent but tends to blend into the darker body colour without sharp demarcation. Eyes and ears are relatively small. Facial vibrissae are not obvious, nor do they grow out of light-coloured patches. Preorbital glands are large and prominent and can measure 44 mm with as many as 15 large pores (Wilson 2001). A coronal tuft of red or maroon hair, of variable length and conspicuousness, sticks up between the horns. Neck covered in short hair, variable in extent of pale throat

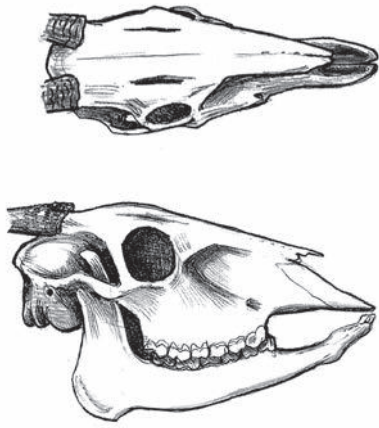
colouring. The skin in this area forms a thickened 'neck shield'. The yellow dorsal triangle is variable in its extent, tonality and colour. Although there are no obvious glands beneath this triangle, the entire coat, which is sleek but softly haired, is slightly oily, presumably due to secretions by sebaceous and apocrine glands. The triangle begins just behind the shoulder blades and widens, ending on the croup. Behind this long-haired triangle is a short-haired light coloured area, which Grubb & Groves (2001) call a 'haunch spot', and which varies, both individually and regionally, in its colour (yellow to pale grey or white) and extent. Body and legs are very dark brown, almost black in some individuals. Tail very short and thinly haired except for a wispy terminal tuft. Sexes of similar size and colour, but ♂♂ tend to have thicker horns and larger preorbital glands. Pedal glands are present on both fore- and hindfeet. Inguinal glands absent.

Horns slightly arched, with no or very small inner ridges, and possessed by both sexes, measuring up to 21 cm. Relative to Jentink's Duiker *C. jentinki* and the Bay Duiker *C. dorsalis*, the skull has a more convex frontal region; the supraorbital foramina are not sunk into channels, and the lateral nasal processes are usually conspicuous. The rostrum is narrower, but shorter than in Jentink's Duiker. Median pillars are commonly developed on the buccal sides of the cheekteeth (Grubb & Groves 2001).

Geographic Variation

C. s. silvicultor (including *silvicultrix*, *punctulatus*, *sclateri*): formerly from Senegal and Gambia to Niger R. Very large; brown with greyish tones, and with broad yellow dorsal triangle; no 'haunch spot'.

C. s. longiceps (including *melanoprymnus*, *thomasi*, *ituriensis*): from Niger R. to Congo R. and eastwards to extreme S Sudan and Western Rift Valley. Somewhat smaller than *C. s. silvicultor*, and darker to blackish-brown, with narrower dorsal triangle; 'haunch spot' absent, rare or weakly developed.



Dorsal and lateral views of skull of Yellow-backed Duiker *Cephalophus silvicultor*.

C. s. curticeps: predominantly montane form between Western and Eastern Rift valleys, including in E DR Congo, Rwanda, Burundi, Uganda and SW Kenya. Smallest of the subspecies, very dark brown coat (similar to *C. s. longiceps*), dark golden-ochre dorsal triangle; 'haunch spot' present, usually well developed.

C. s. ruficrista (including *coxi*): extensive area south of lower Congo R. to N Angola, and Zambia; some intergradation with *C. s. longiceps*. Similar in size to *C. s. longiceps*, but colour lighter (light to dark brown) and dorsal triangle broader; 'haunch spot' always present.

Similar Species

Cephalophus spadix. A large allopatric duiker that resembles this species in colour and conformation but lacks a dorsal triangle.

C. jentinki. Sympatric in Sierra Leone, Liberia and SW Côte d'Ivoire. A large, grey-bodied duiker of similar size but much stockier build, with black head and neck and white shoulder halter.

C. niger. A smaller, partially sympatric black duiker that lacks a dorsal triangle.

C. dorsalis. Broadly sympatric. A squat red duiker with short broad head; smaller than *C. silvicultor*.

Distribution Endemic to Africa, the Yellow-backed Duiker has the widest distribution of the forest duikers (Ansell 1972, Wilson 2001). Originally, the species ranged from SW Senegal through all West African countries to extreme S Chad, the Congo Basin and east to SW Sudan and SW Uganda, from the northernmost extensions of gallery and riverine forests (almost up to the Sahel) to equivalent forest extensions in N Angola (including Cabinda) and Zambia, east of the Zambezi R. and north of the Muchinga Escarpment (East 1999, Wilson 2001). It is rare in primary forest of DR Congo, but is present in 800–1000 m montane forest in the Bélinga mountains, NE Gabon (G. Dubost pers. comm.). Its equivalent habitats east of the Gregorian Rift are occupied by its close relative Abbott's Duiker *C. spadix*. It has also been recorded from montane forest and bamboo in the Mau Forest in SW Kenya (Kingdon 1982, Hillman *et al.* 1988, East 1999), and is reportedly present on Mt Elgon (Kingdon 1982), although no museum specimens are available to corroborate this (Grubb *et al.* 2003).

Within their range Yellow-backed Duikers are still common in some localities, but in other parts they have undergone significant

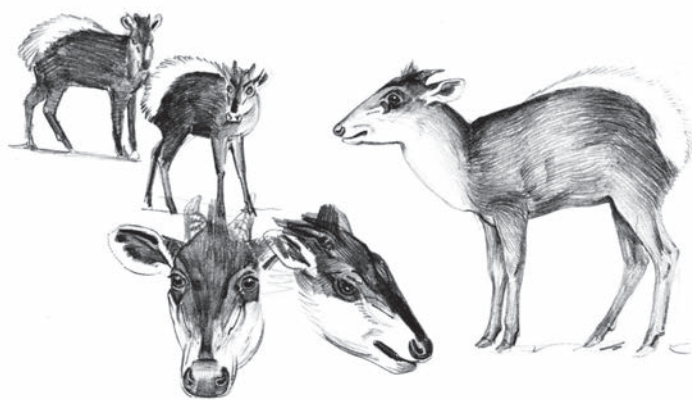


Cephalophus silvicultor

declines or are now absent. They are now considered extinct in Gambia (East 1999), although whether they actually ever formerly occurred is uncertain (Grubb *et al.* 1998, 2003). Malbrant & Quijoux (1958) recorded Yellow-backed Duikers from S Chad, but there is no recent information on their occurrence in this country. They also were thought to have been extirpated from Rwanda (East 1999), but have been confirmed as surviving in Nyungwe N. P. (F. Mulindahabi & A. Vedder pers. comm.). In Uganda, East (1999) recorded them surviving with certainty only in Bwindi Impenetrable Forest N. P.

Habitat An animal of lowland and montane primary and secondary forest, riverine galleries and many permutations of forest–savanna mosaics, including secondary swidden 'farmbush', the borders of plantations and, in montane areas, bamboo groves and steep forested valley slopes. It is typically an ecotonal species and survives well in narrow riverine strips and fragmented woods. Often found close to deep swamps, perhaps seasonally. During very dry periods small aggregations have been reported around salt-licks. Throughout its range it lives only in strips or pockets of suitable habitat, where it can be quite numerous. Yellow-backed Duikers in densely forested NE Gabon exhibited strong associations with riparian habitat, and to a lesser extent with old secondary forest and advanced fallowing fields (Lahm 1993). In Tāi N. P., Côte d'Ivoire, Newing (2001) observed this species only in secondary forest.

Abundance The density of these large duikers varies enormously, partly due to habitat preferences and natural constraints that limit them to quite specific localities and partly to very high levels of predation by human hunters over the greater part of their range. In a particularly choice locality in forest–savanna mosaic in Lopé N. P., Gabon, Tutin *et al.* (1997) estimated a density of 2.1/km². Elsewhere, in the National Park of Upper Niger, Guinea, Brugière *et al.* (2005) recorded individual and group densities of 0.79/km² and 0.69/km², respectively; Prins & Reitsma (1989) estimated 0.26/km² in coastal



Yellow-backed Duiker *Cephalophus silvicultor*.

forest/savanna of SW Gabon, while in the heavily poached Comoé N. P., Côte d'Ivoire, Lauginie (1975) estimated $0.09/\text{km}^2$. Lahm (1993, 1997) had encounter rates of $0.005/\text{km}$ and $0.03/\text{km}$ for this species in hunted and non-hunted areas, respectively, of densely forested NE Gabon, and $0.32/\text{km}$ in an unexploited logging concession now part of Lopé N. P. In the Ituri Forest, DR Congo, where these duikers are naturally rare (but even so opportunistically hunted on a regular basis), densities ranged from $0.1\text{--}0.7/\text{km}^2$ near settlements and $0.5\text{--}1.6/\text{km}^2$ in remote areas (Hart, J. A. *et al.* 1996, Hart 2000). As the largest duiker, it consumes a greater proportion of widely dispersed large-sized fruits than smaller species (Dubost 1984). Comparing the relationship between the body weights and known home-ranges of some duiker species, Feer (1988) suggested that its home-range size may attain 200 ha. East (1999), assuming a density of $1.0/\text{km}^2$ where Yellow-backed Duikers were common and $0.1/\text{km}^2$ elsewhere, arrived at an overall population estimate of 160,000 animals.

Adaptations Among the most striking peculiarities of the Yellow-backed Duiker are its pale dorsal triangle, its considerable size (up to 70 kg), its ability to make an explosive and intimidating thumping noise, and its rather bovine appearance. Dubost (1979) estimated that its body is proportionally heavier than the diurnal duikers, but less than the strictly nocturnal species.

Especially interesting is the fact that it has a black dorsal stripe at birth, as do young and adults of its closest relative, Abbott's Duiker. Nocturnal duikers tend to be dark-coloured and it is possible that the common ancestral population of Abbott's Duiker and Yellow-backed Duiker was predominantly nocturnal. However, both species are essentially crepuscular, being most active both before and after dawn and dusk but intermittently active at other times of the day and night as well. When quietly browsing or resting back hairs lie flat and are not particularly conspicuous (even while fleeing). This is partly due to the freckled forest light and the existence of other light streaks, such as stems and trunks and partly because the surrounding dark pelage 'encroaches' on the dorsum when the coat is sleeked down. However, the dorsal hairs are elongated, erectile and in this condition are able to catch the light and make the back the single most arresting feature of the animal. Evolution of the near-white dorsal triangle is clearly linked to sending a signal to other forest dwellers, the most susceptible being members of the same species. What sort of information could such a vivid pattern have in a mainly solitary species?

Dorsal hair is raised whenever there is a disturbance that has put an animal on the alert. This is often described as 'alarm' behaviour, but the observations of J. Kingdon (pers. obs.) and those of Wilson (2001) suggest that an animal on the alert is generally static and closely monitoring its surroundings. It may even approach to investigate. It is during this phase of active interest that the back is hunched in readiness to run and the hair is at its most erect and conspicuous; S. Lahm (pers. obs.) observed this behaviour during both day and night surveys in Gabon. There are four likely main sources of disturbance: the first, and probably the most frequent, are neutral agents such as falling branches or monkeys' noisy leaps. The second is any animal or event with a potential for harm, such as a hunter or Leopard *Panthera pardus*. The third is another Yellow-backed Duiker. The fourth is any potential competitor, such as duikers of other species, Red River Hogs *Potamochoerus porcus* or Mandrills *Mandrillus sphinx*. Species-specific signals of this sort are only likely to have selective value when received by animals belonging to the last two categories (and a conspicuous back can easily address either). Because an alert animal typically bunches its back, the yellow patch effectively enlarges and advertises the highest part of a big black body mass (thereby emphasizing the signaller's height and bulk). This can simultaneously identify and intimidate, particularly if accompanied by the 'humming' sound peculiar to Yellow-backed Duiker.

Competing duikers and some smaller carnivores can immediately see that they are dwarfed by a Yellow-backed Duiker, while conspecifics have the choice of approaching or fleeing. There is, as yet, no evidence that the dorsal triangle overlies a glandular area but the entire animal is faintly greasy and the hairs may well serve as dispensers for a generalized body odour with all the information that entails. Overall the most likely function of this pattern is to invite retreat from an animal that has been selected to advertise its height and bulk and back this with an alarming 'thump'. Dubost (1980) suggested that this species uses fewer visual signals than strictly diurnal duikers, but more than nocturnal species.

Morphology and genes unite in suggesting that the Yellow-backed Duiker is an end-of-the-line species, one of the most recently evolved of duikers. That conclusion is also consistent with the idea that all duikers have derived from a diminutive ancestor and that the living radiation of duikers represents a protracted adaptation to the very varied opportunities offered by fruit-fall in the diverse forest habitats of Africa (Kingdon 1982).

Where duikers belong within the larger radiation of bovids is a contentious topic that has a bearing on the strikingly 'bovine' appearance of this large duiker. Duikers have been seen as occupying an ambiguous position in the primary divide between bovines and antilopines. Most authors have placed them within the latter (as in this volume), but Gentry (1992), Groves & Schaller (2000) and Grubb & Groves (2001) noted the resemblance between duiker skulls and those of the Asian Four-horned Antelope *Tetracerus quadricornis* and other Asian boselaphines. They suggested that duikers might be as close to the bovines as to any other antilopine group and therefore proposed recognition of a new subfamily Cephalophinae to reflect a supposed intermediate position and relative distinctness from both Bovinae and Antilopinae.

As cattle and buffalo have evolved into ever larger forms they have acquired that complex of characteristics and appearance that we sum up in the vernacular term 'bovine'. It is therefore interesting that the



Yellow-backed Duiker *Cephalophus silvicultor*.

evolutionary enlargement of this duiker species seems to parallel that transformation in the Bovinae and that this has led some scientists to doubt the duikers' affinity with other antelopes.

Foraging and Food Fallen seeds, fruits, berries and the bark of shrubs, fungi, ground moss and many herbs. In montane areas, waterberry *Syzygium*, dog plum *Ekebergia* and yellow-wood *Podocarpus* are favoured fruits (Kingdon 1982). Wilson (2001) emphasized that this species shows a marked preference in lowland forests for dry fruits, pods and seeds, which accounted for 79% of the diet, leaves, shoots and traces of animal matter making up the balance of his central African sample (three stomachs). Wilson (2001) recorded them having ingested large pieces of *Piliostigma thonningii* pods (and leaves), *Gardenia* sp. fruits and *Swartzia madagascariensis*. Gautier-Hion *et al.* (1980) recorded 71.3% fruit, 28.6% leaves and 0.1% animal matter in four stomachs in Gabon. Dubost (1984) found ten fruit species and two *Eremospatha* spp. as preferred foods in four stomachs.

Feer (1995) also found them feeding on mature fruits, noting *Irvingia* spp. and *Detarium macrocarpum*. He recorded 30 species in 23 stomachs with large quantities of pulp, and recorded duikers swallowing fruits of up to 4.7 cm diameter. Small seeds passed through the digestive system unharmed, but several fruits were chewed so thoroughly that their seeds were actually destroyed: these were *Chrysophyllum* spp., *Mammea africana*, *Pseudospondias longifolia* and *Ricinodendron heudelotii*. The most important species by order of decreasing frequency were: *Panda oleosa*, *Polyalthia suaveolens*, *Irvingia* spp. and *Gambeya beguei* (F. Feer pers. obs.). In the south of its range, forest/savanna ecotonal species such as *Pseudolachnostylis dekindtii*, *Oncoba spinosa*, *Swartzia madagascariensis* and *Canthium venosum* are recorded foods (Ansell 1960b); other records are of African Mangosteen *Garcinia* and Duiker-tree *Sapium* fruits. It was mentioned as a crop raider of maize shoots and cassava leaves in five of 218 villages sampled in Gabon (Lahm 1994).

Yellow-backed Duikers may also take carrion (Dekeyser & Villiers 1955), and one captive duiker was observed to capture, kill and eat pigeons (Kranz & Lumpkin 1982). Wilson (2001) recorded the remains of a lizard from one stomach, those of a chameleon from another in Congo, and reported that they would readily eat newly hatched tortoises. This species has also been observed feeding on a Forest Buffalo *Syncerus caffer nanus* carcass (L. White pers. comm.) and fresh Leopard *Panthera pardus* scat (P. Henschel, pers. comm.) in Gabon, and a White-nosed Guenon *Cercopithecus nictitans* carcass in Congo (N. Shah pers. comm.). Mbuti pygmies in DR Congo described its diet as comprising fruits, leaves, insects and dead animals (Carpaneto & Germe 1989).

Of 23 Yellow-backed Duiker stomachs, four contained meat, bones and hair, and two contained the remains of pangolins (F. Feer pers. comm.).

Being both nocturnal and diurnal, there is no clear period of activity (Gautier-Hion *et al.* 1980, Newing 2001, Wilson 2001). It is physically adapted for rapid flight, unlike strictly nocturnal species such as the Bay Duiker and Water Chevrotain *Hyemoschus aquaticus*, which are relatively slow (Dubost 1979). The greater proportion of more diffuse large-sized fruits in its diet (compared with other duikers) may necessitate a 24-hour activity rhythm in a large home-range (Feer 1989b). Hart (2000) inferred that it is mainly nocturnal near human settlements. This may be a behavioural adjustment to avoid contact, as suggested by Lahm (1993) for this species and other large ungulates in hunted areas of Gabon.

Social and Reproductive Behaviour Although this appears to be a mainly solitary species and most records have been of single animals, Wilson (2001) found what he called 'bonded pairs' living in discrete home-ranges centred along a riverine forest strip in Mole N. P. in Ghana. The gallery was about 3.5 km long, but a 600 m dry break separated the two home-ranges. Both sexes mark their home-ranges with large preorbital glands but ♂♂ mark three times more often (Wilson 2001). Lying-up on termittaries or slight elevations on the forest floor suggests that they regularly monitor their surroundings and broken horns on female skulls suggests that ♀♀ may be actively intolerant of other ♀♀. Individuals lie up singly (very occasionally in pairs) between the buttresses of large trees, under fallen trunks or dense tangles, in 'forms', which show signs of regular use and where the duiker may shelter from rain (even entering the remnants of pit-sawyers' or hunters' lean-tos). As many as six such resting places can be found within a square kilometre. Given the absence of marked ridges on the inner side of the horns, this species probably does not scrape the bark of small trees, as do some other duiker species (G. Dubost pers. comm.). Courtship resembles that of other duikers: the ♂ tests the condition of the ♀ with flehmen and, if she is in oestrus, pursues her relentlessly, licking her but also butting and biting, and striking her with a foreleg. Meanwhile the ♀ grunts or bleats (Wilson 2001).

Reproduction and Population Structure Ansell (1960a) thought there was no fixed breeding season in Zambia, but reported a lactating ♀ in Mar and young in Oct and Dec. Ionides (1964) noted young in Kenya during Jan, and J. A. Hart (pers. comm.) recorded very young lambs in Ituri Forest in Jan and May. In Gabon, where births occur year-round in duikers, bats, rodents and other forest antelope, there are two peaks that differ among species (Brosset 1986, Feer 1988). The frugivorous duikers and Water Chevrotain generally had more births during the two annual dry seasons compared with rainy months in NE Gabon (Dubost & Feer 1992). S. Lahm (pers. obs.) saw small lambs in Jan (dry month) and Oct (wet month) in the same region and in Jun (wet-dry transition) in SW Gabon. Wilson (2001) found that even when ovulation originates from the left ovary, the foetus implants in the right horn of the uterus.

There has been much discussion about the length of gestation. Most authenticated captive records are between 210 and 282 days, but extremes of 151–310 days have been published (see Wilson 2001, and references therein). A single young is born. Captive birth-weights range between 2.3 and 6.1 kg (Wilson 2001); the young is born a dark umber colour with strong reddish tint, particularly on



Yellow-backed Duiker *Cephalophus silvicultor*.

the underparts and freckled flanks. The dorsum is jet black but begins to pale at 40 days, visibly whitening at five months and fully developed by seven months (Schürer 2002). It begins to eat plant material at about two months and is weaned by five months (Wilson 2001). In captivity, birth intervals range from 213 days to three years (Kranz & Lumpkin 1982). A captive ♀ at Miami Metro Zoo produced several young, the last of which was born when the ♀ was 18 years old. The ♂ of the pair was still alive in 2005 at age 23, the oldest known Yellow-backed Duiker in captivity (L. Rohr pers. comm.).

Predators, Parasites and Diseases Known to be taken by Leopards and pythons *Python* spp. and young are probably taken by Servals *Leptailurus serval*, African Golden Cats *Profelis aurata* and Crowned Eagles *Stephanoaetus coronatus*.

In N Congo, a considerable number of Yellow-backed Duikers and other bovids succumbed to an epidemic of a pneumonia-like disease possibly transmitted by biting *Stomoxys* flies (Stockenström *et al.* 1997; and see Elkan *et al.* 2009). A health evaluation of 77 duikers representing five species in the Ituri Forest revealed the presence of strongyles, trichurids, coccidia, *Moniezia* sp. and occasionally ticks (*Rhicephalus* spp., *Haemaphysalis parvata*, *Ixodes cumulatimpunctatus*). Many animals had positive antibody titres to leptospirosis serovars, bluetongue virus, infectious bovine rhinotracheitis and epizootic haemorrhagic disease (Karesh *et al.* 1995). The sample did not include any Yellow-backed Duikers, although the species is part of the local duiker community, and thus must be exposed to the same parasites and diseases. Dekeyser (1955) recorded the tick *Ixodes rarus*.

Conservation IUCN Category: Least Concern. CITES: Appendix II.

This species was formerly subject to strict taboos that once protected it in some parts of its range (Kingdon 1982). It is still considered non-preferred game in parts of central Africa, owing to its dark colour, scavenging habits and aggressive temperament when hunted (Carpaneto & Germi 1989, Lahm 1993). In Gabon, where it is also believed to be a 'were-animal', 17% of 144 villagers

sampled declared it to be non-edible (Lahm 2002). However, the Yellow-backed Duiker is now declining over most of its range due to intensive and unregulated hunting and the disappearance of taboos. It has disappeared from Gambia and is rare in Senegal, Guinea, Sierra Leone, Nigeria, Kenya and Uganda and over much of the peripheries of its range (Anadu & Green 1990, Anstey 1991, Wilson 2001).

Important protected areas include Ziama and Diécké Forest Reserves (Guinea), Gola Forests (Sierra Leone), Sapu N. P. (Liberia), Mbam Djerem N. P. and Lobéké N. P. (Cameroon), many of those in Gabon, including Odzala N. P. and Nouabalé-Ndoki N. P. (Congo), Monte Alén N. P. (Equatorial Guinea), Bwindi Impenetrable N. P. and Queen Elizabeth N. P. (Uganda), Kafue N. P. and Kasanka N. P. (Zambia), and Okapi Faunal Reserve (DR Congo). Comoé N. P. was once a stronghold for this species, but with 100–500 poachers operating on a daily basis in this park it had already become rare by the mid-1990s (Fischer 1997). Wilson (2001) regarded Yellow-backed Duikers as extinct in at least seven protected areas in which they formerly occurred, although subsequent surveys have confirmed that they do still occur in Digya N. P., and that they are present in Bui N. P. and Gbele Resource Reserve (R. J. Dowsett pers. comm.).

Although the species was described as easy to breed and hand-rear in captivity (Kranz & Lumpkin 1982), there were only 65 animals in about 23 North American zoological parks and eight known in international institutions in 2005. Within these captive groups a birth rate of 10 per year has been stable, and improved husbandry and population management practices in recent years have increased the Yellow-backed Duiker's survival potential in captivity (L. Rohr pers. comm.).

Measurements

Cephalophus silvicultor

TL (♂ ♂): 1420, 1460 mm, n = 2

TL (♀): 1620 mm, n = 1

T (♂ ♂): 120, 125 mm, n = 2

T (♀): 115 mm, n = 1

HF c.u. (♂ ♂): 295, 330 mm, n = 2

HF c.u. (♀): 350 mm, n = 1

E (♂ ♂): 116, 121 mm, n = 2

E (♀): 115 mm, n = 1

Sh. ht (♂ ♂): 748, 775 mm, n = 2

Sh. ht (♀): 730 mm, n = 1

WT (♂ ♂): 66.5, 68.6 kg, n = 2

WT (♀): 71.0 kg, n = 1

SE Central African Republic (Wilson 2001)

A ♀ from NE Gabon was subadult, yet weighed 74.5 kg (G. Dubost pers. obs.), so maximum weights (and other measures) probably exceed those shown here. It should be remembered that regional populations differ in body size, although the extent of this variation remains to be quantified.

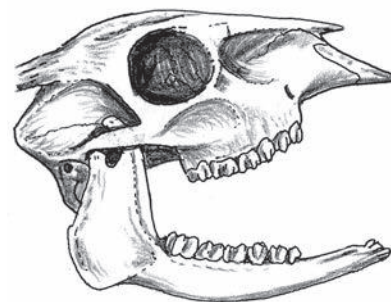
Maximum recorded horn length is 21.2 cm for a pair of horns from Tchibota, DR Congo (Rowland Ward)

Key References Dubost 1979, 1984; Dubost & Feer 1992; Feer 1988, 1989b, 1995; Kingdon 1982; Kranz & Lumpkin 1982; Wilson 2001.

Jonathan Kingdon & Sally A. Lahm

Cephalophus dorsalis BAY DUIKER

Fr. Céphalophe bai; Ger. Schwartzruckenducker.

Cephalophus dorsalis Gray, 1846. Ann. Mag. Nat. Hist., ser. 1, 18: 165. 'Sierra Leone'.

LEFT: Bay Duiker *Cephalophus dorsalis*.
 ABOVE: Lateral view of skull of Bay Duiker
Cephalophus dorsalis.

Taxonomy Named from a menagerie specimen from Sierra Leone; Gray named another specimen *C. badius*, which is now regarded as a synonym. Rode (1943) mistakenly lumped *leucogaster* and *ogilbyi* as subspecies of *C. dorsalis*. St Leger (1936) separated out *dorsalis*, based on horn characters. *Cephalophus dorsalis* is sympatric with both Brooke's Duiker *C. ogilbyi brookei* and the White-bellied Duiker *C. leucogaster*. Ansell (1972) included the form *arrhenii* as a subspecies, but this form is actually attributable to the White-bellied Duiker (Grubb & Groves 2001). Synonyms: *badius*, *breviceps*, *castaneus*, *kuha*, *leucochilus*, *orientalis*, *typicus*. Chromosome number: $2n = 60$; the X chromosome is a metacentric (Hard 1969, Robinson *et al.* 1996b).

Description Heavily built duiker with a red or yellowish-brown glossy coat, black or dark brown legs and a black dorsal mid-line. Also a dark brown mid-line down the chest and belly. Muzzle is reduced and strongly tapered. Eyes are larger, more prominent and higher in the skull and the entire head is broader and flatter than in any other duiker. The black dorsal line, which varies greatly in length and width and darkness, usually extends up the neck, over the crest and down the nose, especially in western populations, where much of the head can be black; however, the extent of black on face and back is very variable. Frontal crest reduced to some long hair at the base of horns. In common with some other duiker species, there are vibrissae on the muzzle and above the eye. These have black bases set in distinctive white flashes on the upper lip and upper eyelid. Chin and throat also white. Backs of the pinnae are black or brown; their fronts have white margins and some very sparse off-white hair inside. Hair on the shoulders is somewhat shorter than on the back and hindquarters. Legs black or brown, but sometimes show rufous streaks. Tail black with a white underside and somewhat tufted towards the tip. Deeply brown or black at birth,

rufous colouring appears between 5 and 6 months of age; the black dorsal stripe is only partly visible on the rump. Preorbital glands are relatively small compared with some other medium-sized duikers (Wilson 2001), although in Gabon the preorbital glands of ♂♂ were twice as large as in Peters' Duiker *C. callipygus*. Preorbital glands have 11–14 pores set in a straight line about 21 mm long (Wilson 2001). The inguinal glands are very distinctive, comprising deep, flask-like sacs in the lower flanks that exit from a narrow tube immediately inside the fold between thigh and abdomen. Their odour is said to be very disagreeable to the human nose. Pedal glands are large and active. Sexes are of similar size, although ♀♀ are slightly heavier. Preorbital glands are larger in ♂♂ than in ♀♀, as are the slender, cylindrical, parallel, spike-like horns.

Geographic Variation

C. d. dorsalis: Guinea, Guinea-Bissau and Sierra Leone to the Niger R. Grubb & Groves (2001) considered the boundary between the two forms to be the Adamawa Highlands in Cameroon. Redder body colour, black facial blaze and crest; dorsal stripe comparatively narrow. Smaller body size.

C. d. castaneus: east of the Niger R. to the Rwenzori Mts and Albertine Rift Valley and south to NE Angola. Darker body colour, redder face and crest. Larger body size. Grubb & Groves (2001) remark that there is considerable geographical variation in this subspecies. Hornless adult ♀♀ have been observed east of the Congo R.

Similar Species

Cephalophus ogilbyi. Sympatric across most of the range. A diurnal red duiker of similar size, and often confused with the Bay Duiker, but of paler red colour with a long narrow face and lighter-coloured legs.

C. leucogaster. Sympatric in central Africa north of the Congo R. A more gracile, pale-cream-coloured duiker with prominent white belly and two-toned legs.

C. callipygus and *C. weynsi*. Red duikers of similar size with long faces, prominently swollen foreheads and thick annulated horns.

C. silvicultor. Broadly sympatric. A larger, dark greyish-brown duiker with cream-coloured patch on lower back.

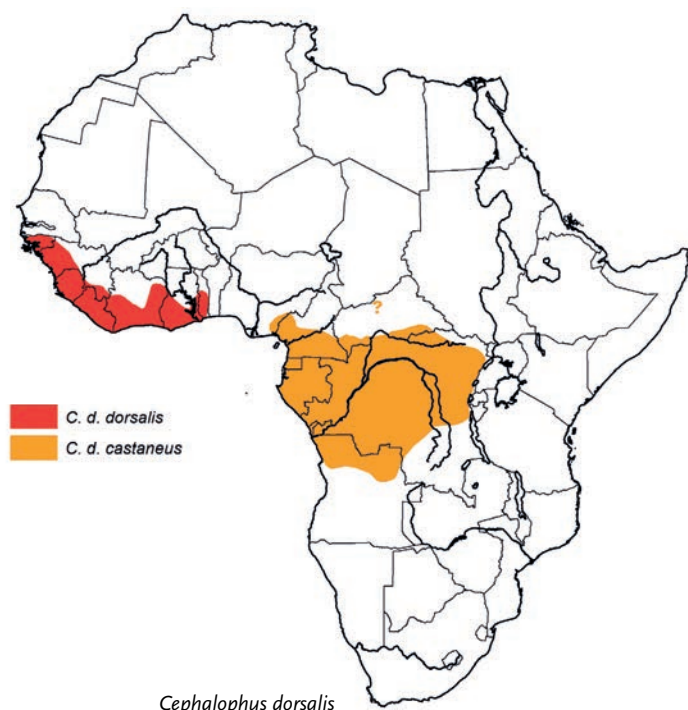
Distribution Endemic to Africa and closed-canopy areas within the rainforest block from Guinea-Bissau to the Rwenzori Mts, Albertine Rift Valley and L. Tanganyika, and south to NE Angola to about 11°S (Grubb *et al.* 1998, East 1999, Wilson 2001, Crawford-Cabral & Veríssimo 2005). The westerly limit is Guinea-Bissau, where East (1999) reported Bay Duikers from forest patches in five restricted areas of the mainland, including Cacheu R. and L. Cufada. In Guinea, they are recorded from the south-west and south-east, including Mount Nimba Biosphere Reserve and Ziamia and Diécké Forest Reserves, and then eastwards to Togo, where they were recorded in the forests of the Fazao and Togo mountains (East 1999). However, there are no confirmed records from Gambia (Grubb *et al.* 1998, 2003) or from Benin. There are also no records from Nigeria, west of the Cross R. (Grubb *et al.* 2003), their distribution continuing again east of the Cross R. in SE Nigeria, and then through S Cameroon, SW and SE Central African Republic, mainland Equatorial Guinea (being absent from Bioko I.), Gabon, Congo, east to the montane forests in E DR Congo. Fay *et al.* (1990) mentioned a doubtful record from Manovo–Gounda–St Floris N. P. in the north of Central African Republic, and another record from east of Bamingui–Bangoran N. P., but considered these as doubtful; however, Grubb *et al.* (2003) subsequently report on a specimen from N Central African Republic from Kabo, just south of the Chad border, and to the west of Gribingui–Bamingui Faunal Reserve. There is a single record from Uganda, below the north-western foothills of the Rwenzori Mts, but this area is now densely populated, and the

Bay Duiker probably no longer occurs in Uganda (Kingdon 1982, East 1999).

Habitat An inhabitant of the entire equatorial lowland rainforest block with a marked preference for high primary rainforest (Wilson 2001); also, if undisturbed, may occupy patches of forest within savanna mosaics. Within the rainforest zone Bay Duikers may visit edges of clearings and well-diversified areas with both dry and seasonally waterlogged areas (Dubost 1979). They generally avoid montane forests, although they are found in moist lowland forests on the slopes of the montane regions in E DR Congo. Very slow to recolonize felled or disturbed forest, but does occur in old farm-bush and old secondary forest (Fotso & Ngnegueu 1997, Wilson 2001). They seek out the most densely vegetated areas, piles of dead branches in forest gaps, the spaces between buttresses and large hollow logs to lie up in during the day, refuges that they freeze in and only leave when discovered (J. Kingdon pers. obs.).



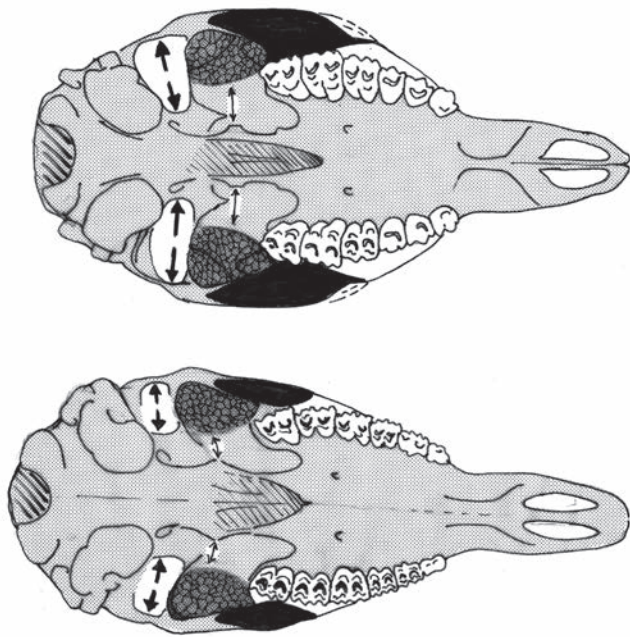
Frontal view of Bay Duiker *Cephalophus dorsalis* (right) compared with Yellow-backed Duiker *C. silvicultor* to show former's larger eyes and shorter muzzle.



Cephalophus dorsalis

Abundance Estimates of home-range data in Makokou, Gabon, suggested densities of 7.5–8.7/km² in prime habitat (Feer 1988). In Makokou, Dubost (1979) calculated a density of about 19/km² (net capture). Lahm (1993) estimated by transect a density of 5.8/km². In S Central African Republic, the species ranks second among duikers, with densities of 0.3–6.6/km² (line transect and net count; Noss 1998b). Densities are 1.5/km² in the Ituri Forest (DR Congo) (Hart 1985) and 1.9/km² in Tāi N. P. based on night transect counts (Hoppe-Dominik *et al.* 2011). Using modest densities of 0.2–2.0/km², East (1999) calculated an overall population of 725,000 animals.

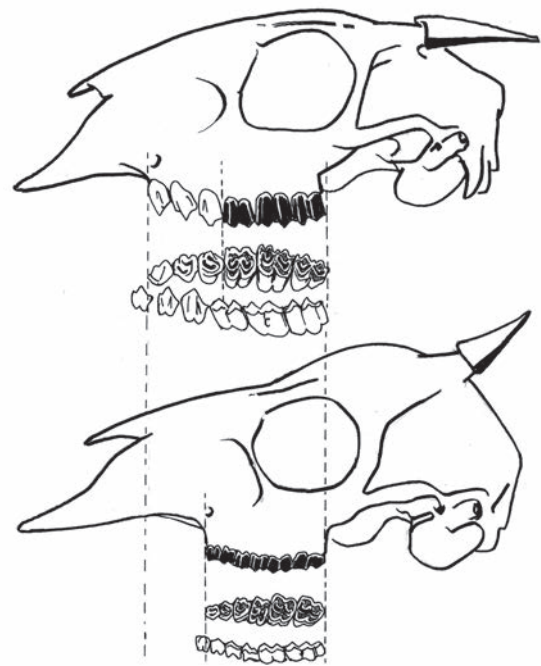
Adaptations Striking features of this species are the enlarged eyes and orbits, adaptations that are clearly related to improved night vision in an animal with very strictly nocturnal habits. Protrusion of the eyes on either side of a rather flat-topped head and dorsally oriented orbits are also likely to improve bifocal vision (Kingdon 1982, Feer 1988). However, the most significant peculiarity lies in the broad, flattened skull. When Bay Duiker skulls are compared with those of other duikers they show inflation of the zygomatic bones, outward bowing of the zygomatic arches, lateral expansion of the molar tooththrow (without equivalent modification of the premolars), widening of the mandibular condyles, and significant narrowing of the choanae so that the pterygoid bones are closer together. Taken all together this combination of



Palatal views of Bay Duiker *C. dorsalis* skull (above) and Black-fronted Duiker *C. nigrifrons* (below) to show broader molar teeth, greater mandibular traverse and enlarged masseter and pterygoid muscles.

characters signifies a significant amplification of the lateral element in chewing by introducing a wide lateral swing at the maxillary condyles (Kingdon 1982). This lateral action means that the duiker can grate or rasp fruits without cutting them open with a sharp vertical bite: a dangerous risk when seeds are protected by poisonous compounds. This risk might have exerted significant selection on anatomy and physiology during this duiker's evolution. The estimated mass of the masseter and zygomatic-mandibular muscle is large compared with duikers of similar size (such as *C. callipygus*). This, combined with broad upper and lower molars (Feer 1988), signifies more powerful jaws able to process hard fruits and seed.

The maxilla has also contracted, and this shortening of the maxilla, combined with a wide, elastic mouth and lips, allows the gape to widen to the point where a 7 cm fruit can easily be taken into the mouth and a 5 cm fruit can be bitten open. Few other duikers can cope with fruits that have large hard seeds and most prefer easily managed ones with abundant soft pulp and small fruits/seeds such as figs. It has been calculated that fruits measuring less than 4 cm make up about 94.5% of the fruit-fall in a representative forest in Gabon (Dubost 1979), so small fruits represent the primary food source for most duikers. However, any animal that can process larger seeded fruits has fewer competitors (although the resource is more dispersed because there are fewer trees bearing such fruit). The Bay Duiker has specialized in stripping away pulps (that are often quite thin) from relatively large, hard (and sometimes poisonous) seeds. The majority of such seeds are high forest, closed-canopy species. Feer (1989b) and Wilson (2001) have documented at least 15 larger forest fruits that are preferred by Bay Duikers. These fruits range from 2 to 20 cm in size, but most are about 2–7 cm, dimensions that the Bay Duiker can easily cope with. The hard seeds within these fruits range from 1.5–5 cm and Bay Duikers swallow and regurgitate seeds that are up to 2.8 cm (Feer 1989b). Seeds over this size are not swallowed but are stripped within the

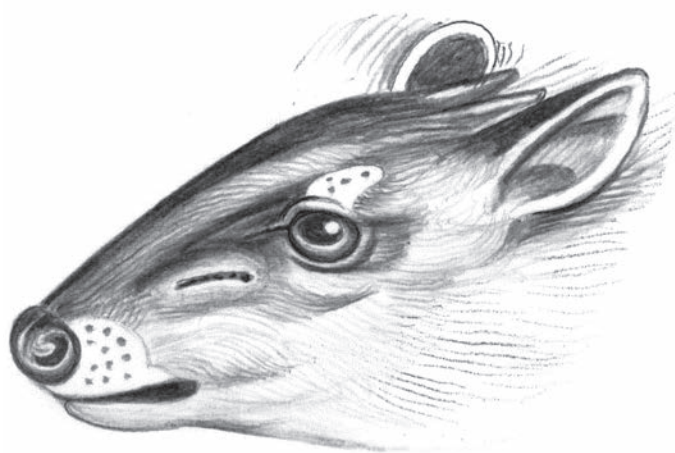


Bay Duiker *Cephalophus dorsalis* skull (above) compared with Blue Duiker *Philantomba monticola* (below) to show proportions in relation to tooththrow (not to same scale).

mouth and spat out. It is this ability to process relatively large seeds that distinguishes the Bay Duiker and explains its cranial anatomy.

These animals can combine mitigating competition and avoiding predators by consuming large numbers of fruits quite rapidly at the fruit-fall and the Bay Duiker has been recorded as being active for as short a period as 5–6 h per night (Wilson 2001). Once a duiker has fed it removes itself to a secure, sheltered place to rest and ruminate; here it regurgitates and spits out undamaged seeds, thus helping disperse them away from the parent tree (Feer 1995). It would be interesting to investigate the possibility of co-evolution between the Bay Duiker and some of its food trees. Many forest tree seedlings need some light during their early growth spurt and the Bay Duiker does sometimes deposit seeds in tree-fall gaps; however, these duikers also spit out large numbers of seeds from closed-canopy, high forest species in very densely shaded (but possibly less predated) sites. Under such circumstances only very shade-tolerant seedlings have any chance of growing to maturity. It is therefore likely that the duikers' regurgitation habits would only favour those seeds best able to survive under deep shade. If so, Bay Duikers might be actively selecting and propagating those food trees that contribute most to the maintenance of a closed canopy. Theoretically, and on an evolutionary time-scale, these habitat-specific duikers could be favouring precisely those tree species that combine food supply with the maintenance of habitat. If these duikers are exterminated it is possible that many major closed-canopy tree species could also decline and even die out.

Another peculiarity of the Bay Duiker skull is an enlarged olfactory region and this can be correlated with observed 'tracking' behaviour, and more generally with a nocturnal mode of life. The more dispersed a food supply the greater the demands on finding it and olfaction has to be a major sense guiding this task. Captives have been seen to sniff out and excavate well-buried fruits (Wilson 2001) by scraping soil with front hooves or incisors (Dubost 1983).



Head of Bay Duiker *Cephalophus dorsalis* female indicating vibrissae embedded in white 'signal' patches above eye and behind rhinarium.

Because the Bay Duiker is nocturnal, has large, prominent eyes and lives most of its life in dense vegetation, its facial vibrissae play an important role in avoiding potential snags. The positioning of such vibrissae above the eyes and around the nostrils is therefore appropriate, but it is interesting that in both instances the vibrissae are advertised by being embedded in small patches of vivid white fur. As with many other exclusively nocturnal mammals it would seem that unique combinations of white flashes on an otherwise dark facial 'mask' serve as intra-specific signal devices.

Foraging and Food The Bay Duiker has very precise preferences for fruit species and the characteristics of these fruits have been extensively studied by Feer (1988, 1989b, 1995) and by Wilson (2001). Of the larger, mango-like species, 'Gaboon chocolate' *Irvingia* spp. and the Tallow tree *Detarium macrocarpum* are favourites; another is the globular, latexy, fibrous fruit (7–10 cm) of Oboto *Mammea africana*. These large seeds are rasped for their pulp or 'flesh' and the seed spat out, not swallowed. The commonest seeds to be found in stomachs and at resting sites are from the yellow fruits of two *Antrocaryon* species, the indented, button-like seeds of which are appropriately known as 'antelope buttons'. Also eaten are the oval yellow fruits of climbers *Hugonia* spp. and the bilobed 6×3 cm fruits of *Ricinodendron heudelotii* (a forest relative of the Manketti tree *Schinziophyton rautanenii* that produces mugongo nuts) and oil-palm dates *Elaeis guineensis*, and the orange plums of milkwood *Chrysophyllum bequei* (4–6 cm), the olive-like, turpentine-scented fruit of *Pseudospondias longifolia* (3.5 cm), the green, strongly fibrous plums of *Panda oleosa* (5–7 cm) and the cocoa-pod-like *Cola rostrata*, which has a shell about 8×20 cm, but contains many small pulp-covered seeds.

Softer seeds without a hard shell or rind tend to be chewed up, and Feer (1989b) never found the seeds of such species at resting places but did record them being eaten. They included the sweet, yellow, apple-like *Drypetes gossweileri* (8–14 cm), the oil-seed *Staudtia gabonensis* (2–6 cm), blue ozigo olives *Dacryoides buettneri* (2–4 cm), Anguek *Ongokea gore* (2–4 cm), ebap, red beans of *Santiria trimera*, the African soursop *Annonidium mannii* (20–50 cm) and owala oil seeds (flat discs from the giant pods of *Pentaclethra macrophylla*).

There are occasional records of Bay Duikers stalking and killing birds (they discard legs and wings) and eating embryos from about-to-hatch eggs (Kurt 1963, Wilson 2001). They eat carrion, and the remains of African Porcupines *Atherurus africanus* (F. Feer pers. obs.) and cuscumanses (*Crossarchus* spp.) (Hart 1985) have been found in stomach contents. Termites, beetles and ants have also been recorded in their diet. Live prey are stalked and struck with a slash of the forefoot.

Social and Reproductive Behaviour Usually solitary, but occasionally observed in pairs. Two ♀♀ and their offspring have been found to occupy the home-range of a single ♂ (Feer 1989a), so as many as six or seven animals may live within a recognizable male territory or home-range of 79 ha. The existence of very pungent inguinal glands and exceptionally large pedal glands suggests that intra-specific contacts are probably regulated by scent. Males mark tree and shrubs with preorbital secretion (Dubost 1983). A lightly built skull and short, slender spike-like horns imply that fights do not involve head-clashing. Stabs into the haunches or sides of contestants are the most likely outcome of male competition. Nocturnal habits and intense wariness has hidden much of this duiker's social behaviour from view.

The ♂ pursues an oestrous ♀ with great persistence, meanwhile humming continuously and occasionally striking out with a foreleg (a rudimentary form of laufschiag) (Wilson 2001). On accepting to be mounted, the ♀ squats and holds her tail to the side.

Reproduction and Population Structure A wide spread of birth and pregnancy records implies that some breeding goes on throughout the year and no birth peak is currently known to occur. In Gabon, birth peaks were observed during and before maximum availability of fruit (Dubost & Feer 1992). About 57% of ♀♀ over 20 months old are pregnant. Oestrus only lasts about 18 hours (Wilson 2001). Females may conceive at about 18 months and always implant in the right horn of the uterus although both ovaries ovulate; gestation is cited as about 238 days (Wilson 2001). At birth the young weighs 1600–1690 g, and begins to take solid food within a few weeks; it is weaned by 3.5 months and is unusual in eating fruit almost exclusively from the beginning (Wilson 2001). In Gabon, a sample of 151 individuals from a moderately hunted population was composed of 20% adults. Males accounted for 58% of adults, a sex ratio most probably biased in favour of ♂♂ (Feer 1988). Longevity in captivity has been given as 17–18 years (Weigl 2005).

Predators, Parasites and Diseases Data from scats have confirmed that Leopards *Panthera pardus* are important predators (Hart, J. A. *et al.* 1996, Wilson 2001). Kudo & Mitani (1985) observed a Mandrill *Mandrillus sphinx* preying on a young Bay Duiker. Young animals are also known to be taken by Crowned Eagle *Stephanoaetus coronatus* (Wilson 2001), and African Golden Cats *Profelis aurata* are also likely to take young or subadults. The failure of an attempt to reintroduce Bay Duikers to Azagny N. P., Côte d'Ivoire, was blamed on large numbers of African Rock Pythons *Python sebae* in the park (Roth & Hoppe-Dominik 1990).

In a study investigating the health status of Bay Duikers, bacterial and viral serology tests returned positive for bluetongue disease, epizootic haemorrhagic disease, infectious bovine rhinotracheitis and *Leptospira* (which causes leptospirosis) (Karesh *et al.* 1995). Helminths recorded

include nematodes (genera *Cooperia*, *Strongylus*, *Cecropithifilaria*, *Filaria*, *Setaria*, *Skrjabinodera*, *Pygarginema*) and cestodes (*Moniezia*, *Avitinella*) (Round 1968). Infection with coccidia (Karesh *et al.* 1995) and trypanosomes (e.g. *Trypanosoma brucei*) (Njiokou *et al.* 2004b) has been recorded. Ntiemoa-Baidu *et al.* (2005) recorded the following ixodid tick species from Bay Duikers in Ghana: *Haemaphysalis parvata*, *H. leachi*, *Ixodes muniensis*, *I. moreli*, *I. cumulatipunctatus* and *Rhipicephalus ziemanni*. Beaucournu & Bain (1982) recorded a new species of flea (*Ctenocephalides chabaudi*) from the Bay Duiker in Gabon.

Conservation IUCN Category: Least Concern. CITES: Appendix II.

The combination of systematic habitat destruction and the commercialization of hunting and trapping likely will ensure the eventual elimination of this species outside protected areas. Even then they are unlikely to survive in smaller protected areas because of habitat degradation and poaching; in Ghana, for example, this species has been extirpated from seven parks and protected areas (Wilson 2001; although it does still occur in Kalakpa Resource Reserve; R. J. Dowsett pers. comm.), and Van Vliet *et al.* (2007) recorded its likely extirpation from Ipassa Natural Reserve in NE Gabon. Important populations survive in areas such as Sapo N. P. (Liberia), Taï N. P. (Côte d'Ivoire), Bia and Kakum National Parks (Ghana), Campo-Ma'an N. P., Lobéké N. P. and Dja Wildlife Reserve (Cameroon), Dzanga-Sangha Special Reserve and Bangassou F. R. (Central African Republic), Monte Alén N. P. (Equatorial Guinea), Lopé, Ivindo, Minkébé, Loango and Moukalaba-Doudou National Parks (Gabon), Odzala N. P., Nouabalé-Ndoki N. P. and Léfini Faunal Reserve (Congo) and Kahuzi-Biega, Maiko and Salonga National Parks (DR Congo).

This is a very popular quarry for hunters because it is compact, muscular and good-eating. It is hunted across its entire range, together with all other forest fauna, year-round and at increasingly intense, unregulated levels. In the Central African Republic, Bay Duikers accounted for 6.8% of all animals captured with nets (Noss 1998b). In Gabon, they accounted for 12% of duikers caught by village hunters and trappers (Lahm 1993). In the Dja area (Cameroon) they represent 17–25% of duikers killed (Fotso & Ngnegueu 1997, Muchaal & Ngandjui 1999). In Congo, Bay Duikers represent 15% of duikers for sale in Brazzaville bushmeat markets (F. Feer pers. obs.) and only 3.7% in Pointe Noire (Wilson & Wilson 1991). They rank between sixth and ninth among the game species on offer in Libreville (Gabon) markets (Ntsame Effa 2005), and were among the top five most hunted species in a bushmeat study in Nigeria (Fa *et al.* 2006). Studies in Equatorial Guinea, W Cameroon and Central African Republic have shown that current harvest rates are entirely unsustainable (Fa *et al.* 1995, Noss 1998b, Muchaal & Ngandjui 1999); in the Monte Mitra region of mainland Equatorial Guinea, Fa &

Garcia Yuste (2001) studied the offtake patterns of 42 hunters over a period of 16 months. The principal hunting method employed was cable snaring, and the Bay Duiker was by far the most heavily exploited species. As mentioned earlier, the extermination of this species could have much wider repercussions in the long-term ecology of those tree species (several of them highly desired commercial timbers) that are dispersed by Bay Duikers.

Measurements

Cephalophus dorsalis

TL (♂ ♂): 1040 (1030–1074) mm, n = 5

TL (♀ ♀): 1031 (1011–1049) mm, n = 4

T (♂ ♂): 97 (89–107) mm, n = 5

T (♀ ♀): 100 (91–110) mm, n = 4

HF c.u. (♂ ♂): 226 (201–232) mm, n = 5

HF c.u. (♀ ♀): 219 (202–231) mm, n = 4

E (♂ ♂): 75 (75–76) mm, n = 5

E (♀ ♀): 76 (74–77) mm, n = 4

Sh. ht (♂ ♂): 472 (448–486) mm, n = 5

Sh. ht (♀ ♀): 479 (454–489) mm, n = 4

WT (♂ ♂): 19.9 (18.1–23.0) kg, n = 5

WT (♀ ♀): 20.6 (19.1–22.6) kg, n = 4

Liberia (Wilson 2001)

TL (♂ ♂): 1041 (1019–1064) mm, n = 8

TL (♀ ♀): 1044 (1021–1073) mm, n = 7

T (♂ ♂): 100 (87–116) mm, n = 8

T (♀ ♀): 99 (84–112) mm, n = 7

Sh. ht (♂ ♂): 480 (460–497) mm, n = 8

Sh. ht (♀ ♀): 478 (453–491) mm, n = 7

WT (♂ ♂): 21.2 (17.9–22.7) kg, n = 8

WT (♀ ♀): 20.9 (18.3–22.6) kg, n = 7

Ghana (Wilson 2001)

HB (♂ ♂): 948 (880–1000) mm, n = 8

HB (♀ ♀): 963 (880–1050) mm, n = 13

WT (♂ ♂): 19.0 (16.2–23.0) kg, n = 6

WT (♀ ♀): 22.2 (20.0–24.5) kg, n = 5

Gabon (Feer 1988, F. Feer pers. obs.)

Maximum recorded horn length is 12.3 cm for a pair of horns from Yakadouma, Cameroon (Rowland Ward)

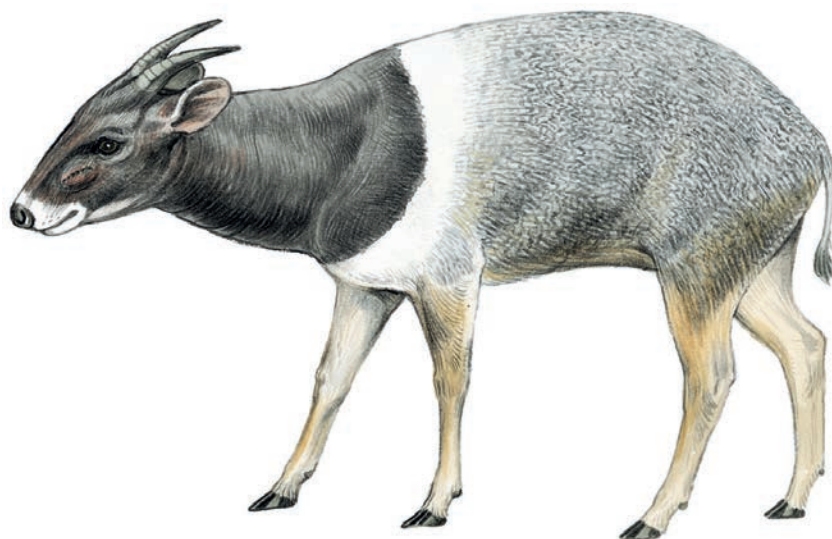
Key References Dubost 1979, 1983; East 1999; Feer 1988, 1989a, b, 1995; Kingdon 1982; Wilson 2001.

Jonathan Kingdon & Francois Feer

Cephalophus jentinki JENTINK'S DUIKER

Fr. Céphalophe de Jentink; Ger. Jentinkducker

Cephalophus jentinki Thomas, 1892. Proc. Zool. Soc. Lond. 1892: 417. 'Liberia'; since identified as Junk R. opposite Schieffelinville, Sharp-Hill (Kühn 1965).



LEFT: Jentink's Duiker *Cephalophus jentinki*.
ABOVE: Lateral view of skull of Jentink's Duiker *Cephalophus jentinki*.

Taxonomy Monotypic. Rode (1943) mistakenly suggested this species was conspecific with the Yellow-backed Duiker *C. silvicultor*. A multiple analysis of mtDNA sequences was consistent in always showing that *C. jentinki* was most closely allied to the Bay Duiker *C. dorsalis* and, more distantly, to Abbott's Duiker *C. spadix* and the Yellow-backed Duiker (Jansen van Vuuren & Robinson 2001). Synonyms: none. Chromosome number: $2n = 60$; the X chromosome is a submetacentric (Hard 1969, Robinson *et al.* 1996b).

Description A very robust, short-legged duiker with a bold pattern of black, white and grey. Very darkly coloured head and neck offset by a vivid white halter over the shoulders and lower chest and a white border surrounding lips, muzzle and nose. This colouring involves both skin and fur, the latter being extremely short and fine. In contrast to the fore-end, the hindquarters are grey agouti. There is an inconspicuous dark crest on the forehead. Young Jentink's Duikers are almost completely brown, similar to young Yellow-backed Duikers, and apparently have long lateral hooves. The tail is short. Preorbital glands are very large. Inguinal glands also are large, and often contain quantities of soft secretion (Wilson 2001). Pedal glands are present. The local inhabitants have many different names for them, and they are known as 'forest goat', 'white woman', 'white antelope' or as the duiker 'onto which the dew has fallen'.

Both sexes bear long (up to 21 cm) black horns, which are straight and smooth, oval in cross-section, extending backwards from the head in the plane of the face and curve very slightly downward towards the tips. The frontal outline of the skull is flat and the facial region above the toothrow and below the anteorbital fossa is markedly swollen out laterally, so that the teeth and their alveoli are quite hidden in an upper view of the skull. Grubb & Groves (2001) list a number of features that differentiate the skull of this species from the similar-sized Yellow-backed Duiker, including: the cranium

is longer and narrower; orbit larger; rostrum relatively longer but bowed anteriorly; forehead almost flat with grooves in which the supraorbital foramina are located; frontonasal suture more pointed; nasal and mandibular profiles more convex; mesopyterygoid fossa much narrower; bullae less angular; zygomatic arches more suddenly contracted in ear region; and no or rudimentary lateral nasal flanges.

Geographic Variation None recorded.

Similar Species

Cephalophus silvicultor. Sympatric and similar in size, but dark greyish-brown with a vivid cream-coloured patch on the back; horns less depressed.

Distribution Endemic to West Africa, being found only in the western part of the Upper Guinean forest block, from Sierra Leone through Liberia to W Côte d'Ivoire. In Sierra Leone, Jentink's Duikers were only positively reported from the country in 1989, from Western Area F. R. (southern part of the Freetown Peninsula). There is photographic evidence of their presence in the Gola F. R. complex (Ganas & Lindsell 2010), and their presence has been reported in areas such as the Mokañji Hills, Loma Mts and Tingi Hills (Davies & Birkenhäger 1990, Wilson & Wilson 1990, Grubb *et al.* 1998).

Kranz & Glumac (1983) indicated that the species occurred widely in E Liberia. It was found to be thinly distributed along the Sehnkwehn R., possibly present along the Sinoe R. and common at the Buto Oil Palm Plantation. Probably occurs locally throughout Liberia in areas of suitable habitat. The 1989/90 WWF/FAD survey confirmed its presence in the south-eastern forests including Grebo N. P. and surrounding forests. Also present in north-western forest blocks as well as in North Lorma National Forests. Presence in Sapo N. P. was confirmed in 1997 (East 1999). During a survey of hunters'



quarry in the area north of Sapo N. P. and along the logging road through the Krahn-Bassa Forest, Jentink's Duikers were readily recognized throughout the survey (R. Hoyt pers. comm.). A bushmeat study from Caspary *et al.* (1999) confirmed the presence of the species in the forests on Liberia's eastern border.

In Côte d'Ivoire, Jentink's Duiker, like the Zebra Duiker *Cephalophus zebra*, has apparently never occurred further east than the Niouniourou R., its historical distribution therefore having been limited to the south-western part of the Guinean forest zone (Roth & Hoppe-Dominik 1990). Widespread forest destruction and expansion of agriculture in this region during the last 25 years have confined the species to the remaining areas of primary forest: Haut Dodo, Rapid Grah, Hana, Cavally-Gouin and Scio Forest Reserves. Its main stronghold is Taï N. P., where it is found in primary forest and rarely in secondary forest. It is observed relatively frequently in the well-protected western part of Taï N. P., including the isolated Mt Nienokoué, and the IET scientific study area near the city of Taï (Hoppe-Dominik *et al.* 1998). It is seen less in the central part of the park and the heavily poached eastern part of the park.

Jentink's Duiker is sometimes reported as occurring in Ziama and Diécké forests in Guinea (e.g. Brugiére & Kormos 2009), based on a report by Butzler (1994). However, Jentink's Duiker is not recorded or mentioned at all by Sournia *et al.* (1990), Grubb *et al.* (1998), East (1999), or Wilson (2001), and was not reported by Barrie & Kanté (2006) in a rapid survey of Diécké in 2003. However, recent records from Mont Nimba Strict N. R. and the nearby Déré Classified Forest in 2009 (N. Granier pers. comm.) would lend support to their presence in SE Guinea.

Habitat Jentink's Duiker is only found in the high primary forest zone between Sierra Leone and the R. Niouniourou, a distribution that broadly coincides with many primate populations and also that of the Zebra Duiker. Within this zone, it does enter secondary growth, scrub, farms and plantations for brief periods (Davies & Birkenhäger 1990,

Wilson 2001), and is even known to visit the sea-shore, presumably for salt. It is a 'hider' choosing hollow trees, fallen trunks and the buttress bays of kapok (*Ceiba*), *Bombax* and mututu trees (*Klainedoxa*) for shelter. It is so secretive that it continued to survive less than 30 km from Free-town, a city of half a million people, hiding on steep, densely forested slopes in the city's water catchment area (Davies & Birkenhäger 1990). Its most basic requirements appear to be a diversity of fruiting trees and very dense shelter rather than a specific forest type (Kingdon 1997).

Abundance Jentink's Duiker appears to be uncommon to rare throughout its range. East (1999), assuming an average population density of 0.1/km², estimated the total population at about 3500, although Wilson (2001) doubted whether there were even more than 2000 animals left throughout the range. Peal & Kranz (1990) give densities of 1.0/km² in Liberia. Results from a survey in Taï N. P. in 2009 and 2010 covering 365 km recorded only a single sighting (N'Goran *et al.* 2009).

In 2000, most hunters described Jentink's Duikers as plentiful, but when pressed for information they reported only killing one or two individuals in their lifetime, even among hunters in their 60s. During a 10-month survey of hunters (representing 3% of the village populations) in three villages along the Juarzon–Pynes Town road near Sapo N. P., Jentink's Duikers were the ninth most commonly killed species ($n = 10$) (R. Hoyt pers. comm.). The population trend of the species is downwards except for a few remote areas where forest destruction and forest hunting pressures are lower, for example Sapo N. P., and the few areas where there is better protection, such as the western section of Taï N. P. (Hoppe-Dominik *et al.* 1998, 2011).

Adaptations As Jentink's Duiker is very shy and secretive, few direct observations exist. In Taï N. P., the species has been observed mostly during the day (Hoppe-Dominik *et al.* 2011), and animals held in captivity in Monrovia Zoo were active day and night (Newing 2001). It has been reported that Jentink's Duikers use their horns to uproot cassava plants so they can feed on the leaves, bark and tubers. Like Bay Duikers, they bolt from these daytime refuges with great speed if discovered, but have no stamina and do not go far. They are very residential and supposedly territorial, but make nocturnal forays out of thick forest, especially during periods when fruit is scarce (Davies & Birkenhäger 1990, Kingdon 1997).

Foraging and Food Fruits and foliage. Known to enter plantations to eat palm nuts, mangoes and cocoa pods. The growing stems of tree seedlings are eaten, including *Chlorophora* and *Hannoa klaineana* (Davies & Birkenhäger 1990). Hunters familiar with the animal's habits have identified many fruits with hard seeds or shells in its diet, notably kola nuts, erimado *Ricinodendron* sp., cherry mahogany *Tieghemella* sp., sand apples *Panaria* sp. and tallow tree *Pentadesma* sp. Jentink's Duiker has also been reported chewing roots after exposing them with its hooves (Kingdon 1997).

Social and Reproductive Behaviour Occasionally observed in pairs (Kranz & Glumac 1983), but most field observations are of lone animals, suggesting a primarily solitary social system.

Reproduction and Population Structure Observations in Liberia from Sapo N. P. (Kranz & Glumac 1983) indicate that young

are usually born between Mar and Jun, but young have been born in captivity in Monrovia between Nov and Jan. In captivity, young weigh 3–6 kg at birth (Pfefferkorn 2001). General recommendations of management and husbandry of captive duikers including the Jentink's Duiker are given by Barnes *et al.* (2002). A captive individual lived to 21 years (Weigl 2005).

Predators, Parasites and Diseases D. Jenny (pers. comm.) only once found hair from Jentink's Duiker amongst 200 examined scats of the Leopard *Panthera pardus* in Tāi N. P. It is possible that young animals are occasionally taken by the Crowned Eagle *Stephanoaetus coronatus*; however, they have not been found in prey remains examined in Tāi N. P. (S. Shultz pers. comm.). The extent to which African Golden Cats *Profelis aurata* and the African Rock Python *Python sebae* are to be regarded as predators is unknown. There is no information on diseases or parasites.

Conservation IUCN Category: Endangered C1. CITES: Appendix I.

Due to the continued demand for bushmeat and unsustainable hunting, the risk that species dependent upon primary rainforests such as Jentink's Duiker will die out is high. According to an examination by Caspary *et al.* (1999) in the region of Tāi N. P., the influence of hunting on these species is considerable. Subsistence hunting provides inhabitants of the park with an estimated 1500–3000 tonnes of wild animal meat per year. In this way the rural population consumes about 28–55 g of meat/inhabitant/day. Jentink's Duiker is poached both in the east and the west of Tāi N. P. For example, a market examination of a stand in the east of the park counted about 3.3% Jentink's Duiker (ten of a total of 2171 animals killed here). The share of Jentink's Duiker killed in the forests to the west of the Cavally R. in Liberia and smuggled into Côte d'Ivoire was 2.5%. Of a total of 11,215 dead animals, 55 Jentink's Duikers were counted. During a survey conducted in Liberia in 2002 by the Philadelphia Zoo, Jentink's Duikers were not common in the Monrovia bushmeat markets and no preference for Jentink's Duiker meat was identified, but carcasses were observed during the survey (R. Hoyt pers. comm.).

Although poaching still has a highly negative influence on the population, the long-term survival of Jentink's Duiker is closely linked to the future of the remaining blocks of primary forest of the Guinean forest zone. At present only the western part of Tāi N. P. receives effective protection. Rehabilitation of Sapo N. P. and development and implementation of protection and management programmes for the forests and wildlife as key areas are important. Better protection of areas such as Cestos–Sehnkwen, Sapo–Putu–Range, Grebo, Upper Krahn–Bassa in Liberia, Haute Dodo and Cavally Goin Forest Reserves in Côte d'Ivoire, and Western Area F. R. and Gola Complex Forest Reserves in Sierra Leone could result in a dramatic improvement of this species' current conservation status (East 1999).

Measurements

Cephalophus jentinki

HB: 1300–1500 mm

T: 120–160 mm

WT: 55–80 kg

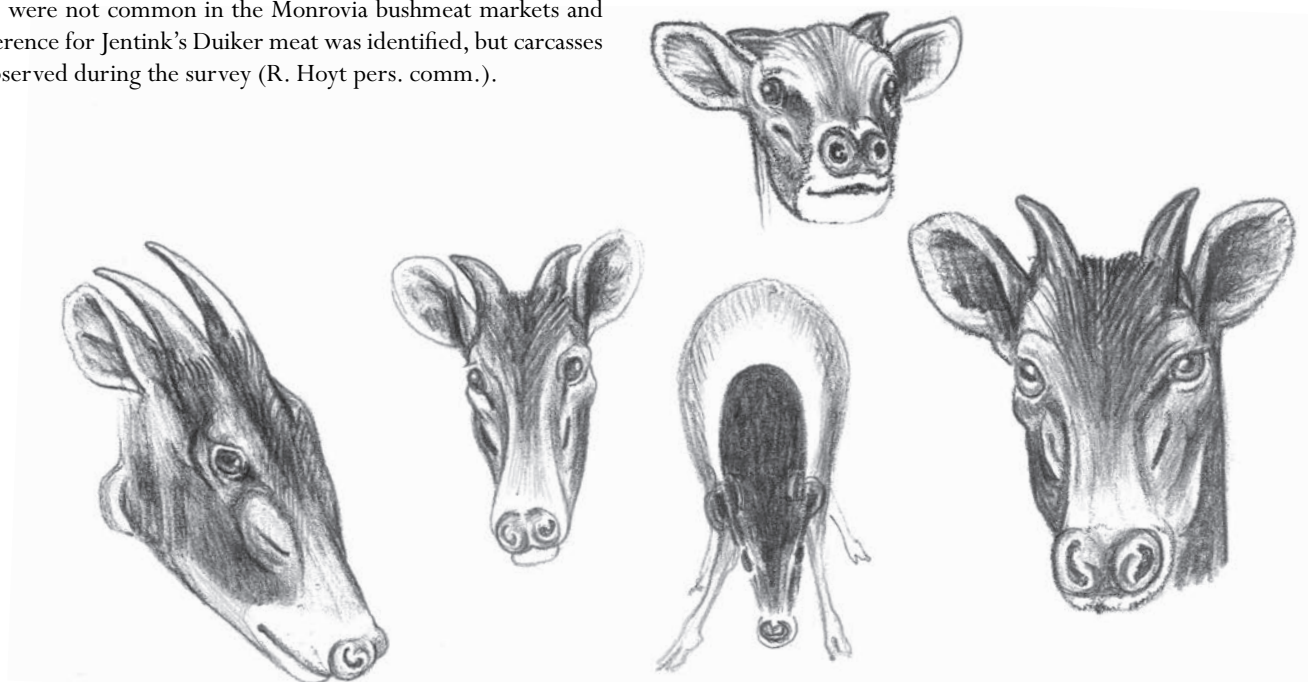
Throughout geographic range (Kingdon 1997)

There are no reliable body measurements available, but weights reported by Wilson (2001) for animals from captivity (♂♂: 56.5–79.4 kg, n = 3 and ♀♀: 60.3–76.7 kg, n = 4) compare favourably with those measures given above. Haltenorth & Diller (1980) give a shoulder height of 750–850 mm

Wilson & Wilson (1990) recorded horn lengths ranging from 14.4 to 21.2 cm, and Davies & Birkenhäger (1990) recorded a pair 21.5 cm in length, which is slightly longer than the maximum horn length recorded by Rowland Ward of 21.3 cm from NE Liberia

Key References East 1999; Kingdon 1997; Kranz & Glumac 1983; Wilson 2001.

Bernd Hoppe-Dominik



Jentink's Duiker *Cephalophus jentinki*.

Tribe RAPHICERINI

Grysboks, Steenbok, Beira

Raphicerini Knottnerus-Meyer, 1907. Arch. Naturgesch. 73: 49.

Many of the small antelopes formerly allocated to the taxon Neotragini have long been thought to be basal to the antelope radiation, but so long as genealogical trees were not attempted the issue scarcely arose that these antelopes might not be monophyletic. Contemporary efforts to construct phylogenetic trees on the basis of relatedness (Hennig 1966) and newly available genetic information have challenged the monophyly of Neotragini as traditionally defined (Georgiadis *et al.* 1990, Gatesy *et al.* 1997, Hassanin & Douzery 1999, Matthee & Robinson 1999a, Rebholz & Harley 1999) and that taxon is now redundant for all of its former members barring *Neotragus* and *Nesotragus*. This dissolution of a convenient 'waste-paper basket' has raised, once again, the position of grysboks *Raphicerus* (and the Beira *Dorcatragus megalotis*) in relation to other antelopes and revived, in an entirely new context, the validity of assigning *Raphicerus* an exclusive tribe (including, very tentatively, *Dorcatragus* as a species that may have more complex affinities than are currently supposed). Haldenorth (1963), who used the tribe Raphicerini to accommodate *Raphicerus* as well as the Oribi *Ourebia ourebi*, included *Dorcatragus* in the tribe Dorcatragini.

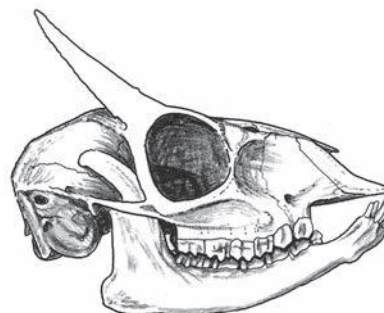
The nomenclatural history of this taxon has been summarized by Grubb (2001a): 'Knottnerus-Meyer (1907) used the form Raphicerotinae; this was based on "*Raphicerus* Hamilton Smith, 1827", a misquotation of *Raphicerus* Hamilton Smith, 1827. The correct form, Raphicerinae, was used by Frechkop (1955) ("justifiable emendation of Raphicerotinae"); Haldenorth (1963) used Raphicerini, which of course is just the tribal form of Raphicerinae and so counts as the same name under the Principal of Coordination. The Code, Art. 35.4.1, says "A family-group name based on an unjustified emendation ... or an incorrect spelling of the name of the type genus must be corrected".'

In a composite tree of ruminant phylogeny, calibrated against a molecular clock, Hernández Fernández & Vrba (2005) estimated a 20 mya divergence for the *Raphicerus* lineage (they included the Beira as a sister species; see also Price *et al.* 2005). The dik-diks *Madoqua* spp. and the Oribi lineages were estimated to be equally old. Although these authors lumped the three lineages within Antilopini, 20 mya is between 5 and 10 millions years earlier, according to the same methods and authors, than the emergence of reduncines, hippotragines, alcelaphines and caprines, all well-defined and long accepted taxa. Aside from the issue of divergence times (according to Goodman *et al.* 1998, a 20–14 mya divergence is the acceptable time-rank for a tribe), there are also many unsolved puzzles about details of the antelopes' earliest radiations.

The excessive lumping or glossing over of differences implicit in the neotragine 'waste-paper basket' has deterred recognition of polyphyly. Uncritical transfer of basal or near-basal taxa from a 'Neotragini' that is now known to have been polyphyletic (and see Gentry 1992) to similarly polyphyletic groupings under an enlarged 'Antilopini' merely perpetuates the problem. We have, therefore, resuscitated Raphicerini, hoping it will help underline the complexity and subtlety of the antelopes' evolutionary radiation and provoke further research into the earliest radiations of antelopes.



Lateral view of skull of Steenbok *Raphicerus campestris* female.



Lateral view of skull of Cape Grysbok *Raphicerus melanotis* male.



Upper-right tooththrow of Cape Grysbok *Raphicerus melanotis*.

The cranial morphologies, ecology and distribution of contemporary *Raphicerus* and *Dorcatragus* manifest two divergent trends in temperature regulation: the former species are adapted to relatively moderate temperatures, whereas the Beira tolerates much higher levels of heat. The ecological and geographic distributions of the two genera help provide a proximate explanation for such differences but any (very ancient) common ancestor was probably closer to living at the hotter end of the spectrum (although it is unlikely that any such primitive ancestor was as highly adapted to heat as the living Beira). The principal indication of divergent heat-tolerances lies in the sizes and proportions of the nasals and premaxilla, well developed in *Raphicerus*, much reduced in *Dorcatragus*. An opened-up nasal area allows for a flexible 'nasal bellows' mechanism to develop a cooling system that is illustrated in its most extreme form in the dik-diks.

Sorting out the precise genetic relationships between the provisional tribes that are presented here (formerly all included in Neotragini), including Raphicerini, Madoquini, Ourebiini (and perhaps other lineages), is a task for the future. Details of behaviour and ecology in the four very different species that have been allocated to Raphicerini appear in the generic and species profiles.

Jonathan Kingdon

GENUS *Raphicerus*

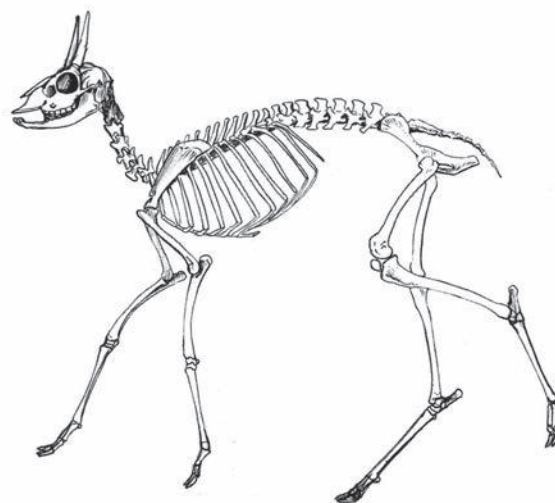
Grysboks, Steenbok

Raphicerus C. H. Smith, 1827. In: Griffith et al., Anim. Kingd. 5: 342.

Living *Raphicerus* species are the Cape Grysbok *R. melanotis* and Sharpe's Grysbok *R. sharpei*, constituting what Ansell considered a superspecies (Ansell 1972), and the Steenbok *R. campestris*. The Cape Grysbok is endemic to South Africa, being restricted almost entirely to the Cape Floristic Region; Sharpe's Grysbok occurs in the savanna woodland from Tanzania to Swaziland, with a particular association with *Brachystegia* woodland; and the Steenbok has a disjunct distribution in East Africa (S Kenya, N and C Tanzania) and southern Africa. Earliest fossil records are of *R. paralius*, from 5.0 to 2.6 mya in South Africa (Gentry 1980, Vrba 1995); Steenboks and Cape Grysboks are known from Pleistocene deposits in South Africa.

The three species are generally small, but absolutely larger than species of the genus *Neotragus* or *Nesotragus*. The pelage is uniform or streaked, with white underparts. The rhinarium is naked. Ears are large or very large; the tail is short and not tufted. Preorbital glands open through single small orifices, and pedal glands are present (the Cape Grysbok ♂ also has a preputial gland); however, there is no subauricular gland, and no inguinal glands. Females have two pairs of inguinal nipples. Horns are present in ♂♂ only, rising nearly vertical, slender, cylindrical and smooth with almost no indication of annuli. The skull is stout with the rostrum much shortened and tapered compared with *Ourebia*. Other characteristics of the skull include: small but deep lachrymal depressions with upper and lower margins not forming sharp ridges; secondary deposition of bone on frontals and parietals; well-marked, widely spaced temporal ridges; ethmoid vacuity present; and the dentary with rounded angle. The first incisors are less broadened than in *Ourebia*; other incisiform teeth are narrow, but the second incisors are broader than the rest. The cheekteeth are small (though the premolars are relatively large) and low-crowned; the occlusal pattern is simple with styles not well marked.

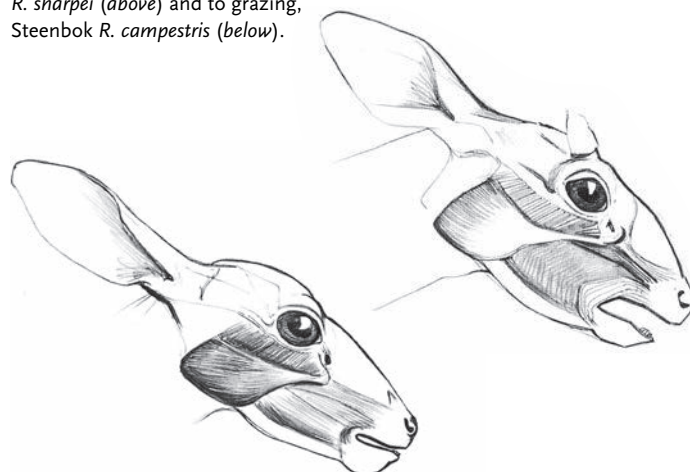
Cape Grysboks were formerly assigned to their own genus *Nototragus* (Thomas & Schwann 1906), based on their retention of small lateral or false hooves and substantial differences in limb proportions and stance. Subsequently, both Shortridge (1934) and Roberts (1951) included both the Cape and the closely related Sharpe's Grysbok in *Nototragus* to distinguish the two shorter-legged, broader-mouthed grysboks from the longer-legged, smaller-mouthed and nominate Steenbok. Kingdon (1982) pointed out the differing lips and mouth structure between *R. melanotis/sharpei* and *R. campestris* and correlated these differences with diet and habitat. Haltenorth (1963) even considered the two grysbok species conspecific. However, Ellerman *et al.* (1953) and Ansell (1972) thought there were no grounds for recognizing *Nototragus*, considering both *R. sharpei* and *R. melanotis* as distinct enough to warrant species status; subsequent authors have followed this treatment (e.g. Meester *et al.* 1986, Grubb 1993c, 2005, Bronner *et al.* 2003). Species are distinguished by colour of pelage, size of ears, length of horns, relative length of limbs, and presence or absence of lateral hooves.



TOP: Steenbok *Raphicerus campestris* myology.

ABOVE: Steenbok *Raphicerus campestris* skeleton.

BELOW: Facial myology of *Raphicerus* spp. compared, showing mouths predominantly adapted to browsing, Sharpe's Grysbok *R. sharpei* (above) and to grazing, Steenbok *R. campestris* (below).

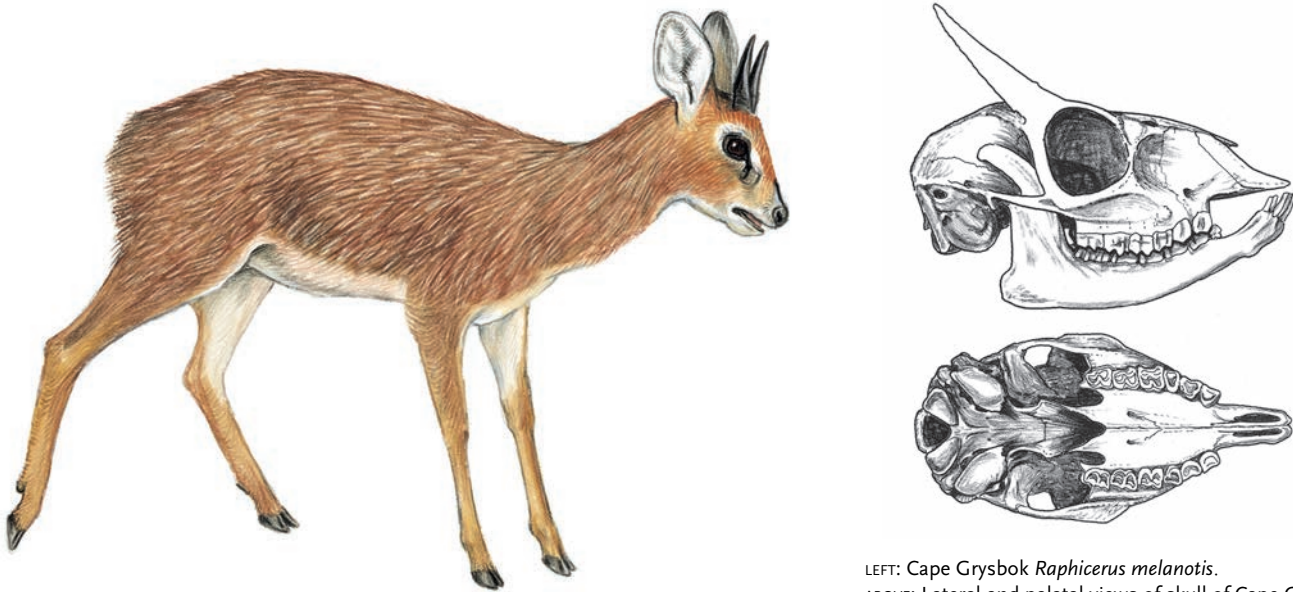


Peter Grubb

Raphicerus melanotis CAPE GRYSBOK

Fr. Grysbok du Cap; Ger. Kaapgreisbock

Raphicerus melanotis (Thunberg, 1811). Mem. Acad. Imp. Sci. St. Petersburg 3: 312. No locality cited, but selected as the Cape Peninsula, Western Cape Province, by Grubb (1999c) based on the records of Levaillant who encountered the species on the peninsula. Rookmaker (1988) noted that the Cape Grysbok was first named by J. R. Forster as both *Antelope melanotis* and *A. grisea*, both considered as *nomina nuda*.



LEFT: Cape Grysbok *Raphicerus melanotis*.
ABOVE: Lateral and palatal views of skull of Cape Grysbok *Raphicerus melanotis*.

Taxonomy Monotypic. Several authors (Haltenorth 1963, Haltenorth & Diller 1980) have considered the Cape Grysbok and Sharpe's Grysbok *Raphicerus sharpei* to be conspecific (separating the species into two subspecies), but Ellerman *et al.* (1953), Ansell (1972) and many other authors have treated them as distinct (and see Genus profile). Synonyms: *grisea*, *rubroalbescens*, *rufescens*. Chromosome number: not known.

Description A small reddish-brown antelope, standing only about 0.5 m at the shoulder, with a hunched or curved back, and short inconspicuous tail. The muzzle is short and with a black bridge to the nose. The common name is derived from the conspicuous white hairs visible in the overall rufous pelage on the sides and the back, which creates a greyish appearance ('grys' is grey in Afrikaans); the undersides are a lighter uniform brown. Ears relatively large with prominent whitish hairs on the inside whereas the outside is greyish. Supplementary or 'false' hooves are present above the fetlocks on all four legs (commonly absent in other *Raphicerus* species). Active preorbital glands are present, and pedal glands are present on all four feet; ♂♂ also have preputial glands (Manson 1974). Horns present in ♂ only, smooth and rising vertically from the head with a slight forward curve.

Geographic Variation None recorded.

Similar Species

Raphicerus sharpei. Allopatric in savanna woodland from Tanzania to Swaziland. Slightly smaller (mass of ± 7.5 kg), and a slightly paler reddish-brown pelage, also interspersed with white hairs, whilst

the underparts are also comparatively lighter having been described as buffy-white; false (lateral) hooves absent, being reduced to areas of thickened skin (Ansell 1972).

R. campestris. Broadly sympatric. Slightly heavier (± 11 kg), with a relatively straight back (as opposed to the hunched or arched appearance of Cape Grysbok), and tends to live in more open areas than the scrub-loving Cape Grysbok; more uniform red-brown without interspersed white hairs, the underparts are white or nearly so; horns longer (up to 190 mm); false (lateral) hooves absent.

Distribution The Cape Grysbok is endemic to South Africa. Boshoff & Kerley (2001) referred to the Cape Grysbok as nearly endemic to the Cape Floristic Region, occurring in montane and lowland habitats (with the exception of dense forest) to the south and west of the Cape Fold Mts. Skinner & Chimimba (2005) stated it occurs 'from the Cedarberg Mts in the Western Cape to the Vredenburg area and southwards and eastwards coastally to the Albany (= Cacadu) and Bathurst (= Cacadu) districts in the Eastern Cape, with records from the Komga (= Amatole) district'. Shortridge (1934) gave the extreme north-eastern limits as Port St Johns although there appears to have been some contention as to the precise limits for the Cape Grysbok along the E South African coastline (Skead 1987). Skead (1980) cited the reports of Barrow (1804) who stated that 'steenbok, oribi and grysbok were still plentiful in 1799 in the "Onder Bokkeveld"' but went on to warn that doubts should be cast on the records of both Cape Grysboks and Oribis (*Ourebia ourebi*) for that region.

Distribution extends into the mountain renosterveld of the Nieuwoudtville region and Cape Grysboks have been observed in

Oorlogskloof N. R. (C. T. Stuart & T. Stuart pers. comm.). The distribution of the species within this vegetation transition zone between the Fynbos and Succulent Karoo biomes of southern Africa is likely to be restricted to valleys and gorges with dense vegetation. Their northern limits would appear to have been the southern parts of the Great Karoo, probably south of the Escarpment. An apparently isolated population in the Eastern Cape has been indicated by two questionnaire surveys (Bigalke & Bateman 1962, Lloyd & Millar 1983) supported by personal interviews (Lynch 1989). Records from landowners have been substantiated by additional observations from the Barkly East district (Stuart 1984) and skins obtained in the vicinity of Maclear (Feely 1992). Archaeological records from this region also point to the presence of Cape Grysbocks in the area dating back some 2000–8000 years ago (Feely 1992). The species has also been recorded in the southern Drakensberg (Vincent 1962, Bourquin 1966, cited in Rowe-Rowe 1994) (for earlier records see Du Plessis 1969). There is a substantial gap between the southern limits of Sharpe's Grysbock and the north-eastern limits of the Cape Grysbock.

Habitat Bigalke (1979) stated that although it occurs in other vegetation types, the Cape Grysbock is 'essentially an animal of the Cape fynbos', in both winter and non-seasonal rainfall areas. Cape Grysbocks prefer dense cover and closed-canopy habitats. The propensity of the species to select dense vegetation is particularly true in the western portion of its distribution, where dense fynbos (scrub) communities dominate. Towards the east of their range Cape Grysbocks also utilize the dense thicket habitats associated with many of the river valleys and coastal regions. Presence in the high-altitude grasslands of the north-eastern Cape is conditional on the proximity of forest fragments and bush clumps, but, in some areas, Cape Grysbocks may also use long grass for cover. Although much of the Cape Floristic Region is now cultivated, the Cape Grysbock is one of the few antelope that can survive in relatively small patches of natural vegetation surrounded by cultivated lands (Manson 1974), and Skinner & Chimimba (2005) suggest that such cultivation may sometimes actually improve habitat for Cape Grysbocks provided that some dense cover is nearby. As commercial rooibos tea plantations have become established in the Cedarberg Region, the Cape Grysbock has been blamed, along with the Common Duiker *Sylvicapra grimmia*, for extensive damage to new shoots (C. T. Stuart & T. Stuart pers. comm.).

Abundance Cape Grysbocks are normally solitary and cryptic in their behaviour and therefore seldom seen. Visibility is further reduced in dense vegetation and this is exacerbated in fire-prone areas such as the fynbos of the Western Cape. Fires, bush clearing, grazing and agriculture all affect the visibility of Cape Grysbocks in the field and can influence counts. Boshoff *et al.* (2002) estimated the spatial habitat requirements of medium- to large-sized mammals in the Cape Floristic Region and compared some of their predictions with empirical data. Predictions from the model, based on intact habitat, suggested that Cape Grysbocks required between 6 and 456 ha per animal depending on the nature of the vegetation type. Based on the available habitats this would suggest that Cape Grysbock numbers could lie between 231,448 (post-habitat transformation) and 322,977 (pre-habitat transformation) in the Cape Floristic Region (Kerley *et al.* 2003). This is almost an order of magnitude higher than earlier estimates of their abundance in an area covering 61,000 km² (East 1999).



Cape Grysbock numbers in the Eastern Cape appear subject to local cyclical fluctuations in population numbers (Skead 1980, 1987), but this may also apply more widely to the Western Cape (P. H. Lloyd pers. obs.). Gamkaberg N. R. in the late 1990s had a notably conspicuous population of Cape Grysbocks on top of the mountain (as illustrated by the fact that Norton [1986] listed Cape Grysbocks, Klipspringers *Oreotragus oreotragus* and Grey Rhebocks *Pelea capreolus* as the most abundant antelopes). In the early 2000s, animals were rarely seen because a large fire had intervened and it is possible that the animals were destroyed, as well as much of their cover being destroyed, necessitating movement to less accessible areas. Skead (1987) also stated that outbreaks of ophthalmia (with increased vulnerability to predation) might have been implicated in some of these declines.

Scott (1991) studied the distribution of small antelopes in De Hoop (Provincial) N. R. between 1985 and 1987 and recorded density indices (number of animals per 100 km travelled) of 0.21 for Cape Grysbocks compared with 2.64 for Steenbocks. This might suggest that Steenbocks are at least ten times more abundant than Cape Grysbocks but, when habitat preferences and relative visibility are taken into account, it is likely that Cape Grysbocks have been substantially underestimated. In some protected areas the abundance of Cape Grysbocks appears to be linked to the density of other herbivores, particularly where such herbivores alter the structure of the vegetation. Grysbock ranges have seen local declines in numbers from areas such as Addo Elephant N. P., where escalating numbers of elephants have opened up or transformed thicket habitats (J. G. Castley pers. obs.).

Adaptations As described elsewhere, the Cape Grysbock is the only member of the genus *Raphicerus* that consistently has false hooves, a peculiarity that implies a more primitive evolutionary state within the Bovidae. Likewise, skull structure conforms with that of early, relatively unspecialized antilopine bovids (Kingdon 1982). In general, therefore,

the Cape Grysbok appears to represent the relatively unmodified descendant of an early line of antelope, rather than a more recently adapted form.

Only the ♂ is horned in this species and Novellie *et al.* (1984) have gone into some detail on the nature of conflict encounters between ♂♂ and suggested that damaging encounters rather than ritualized ones might be the more appropriate evolutionary strategy for the Cape Grysbok. Their arguments were based on the assertion that for small species, occupying small territories, retreats from conflict encounters put the retreating individual at a disadvantage. They argued that losing meant loss of access to forage as well as mating opportunities. Hence the unelaborated horn shape, a lack of observed rituals and retention of short, smooth, stabbing weapons in ♂♂.

The need to hold and demarcate small territories has probably influenced the intensity of other activities such as scent-marking using the preorbital glands. To date a total of 85 chemical compounds have been isolated from the black aqueous secretion of the preorbital gland (Burger *et al.* 1981b, 1996), implying a highly complex olfactory signalling system.

Cape Grysbocks are small antelopes that appear to be dependent on dense, bushy or scrubby vegetation. The archaeological record suggests that their abundance has been directly related to the bushiness of the vegetation (Klein 1983). In the archaeological sites evaluated (which were southern and south-western areas of the Cape Floristic Region, as opposed to grassland areas further east), its abundance was thought to have fluctuated over the last two interglacials according to the availability of bushy vegetation.

Foraging and Food Cape Grysbocks are predominantly browsers, although earlier accounts reported Cape Grysbocks as predominantly grazers (Dorst & Dandelot 1970, Smithers 1983). Manson (1974) recorded Cape Grysbocks grazing, but he only made one such observation out of 30 in total (although he conceded that grass might play a more important dietary role in other areas of their distribution). Kigozi *et al.* (2008), by investigation of faecal samples, also concluded that Cape Grysbocks were selective browsers and had a restricted diet of only nine species in the *Acacia*-dominated coastal dune fynbos of the Port Elizabeth region. Interestingly, these invasive species, notably *Acacia cyclops*, formed a significant part of the diet; no monocotyledonous plants were identified in the grysbok faecal samples. A wider variety of species is eaten in the western portions of their range where Cape Grysbocks have become a problem to farmers as more and more of the habitat has been taken over for vineyards, orchards (Manson 1974) and rooibos tea plantations (C. T. Stuart & T. Stuart pers. comm.). More recent evidence suggests that Cape Grysbocks are able to broaden their diet in response to changing forage availability. Such dietary flexibility also influences the amount of grass in the diet, which at times can be substantial (Kerley *et al.* 2010, Faith 2011).

Because they tend to eat fresh-growing shoots, Cape Grysbocks' water requirements are limited, but they have even been observed to utilize water with a high salt content (Manson 1974). During the period of his study Manson (1974) found that the greater part of the animals' feeding time was at night. He found feeding periods of 2–3 hours interspersed with periods of rest during which they ruminated. Browse is mostly cut by the premolars, but the bite selection process also occasionally involves the lower incisors.

Social and Reproductive Behaviour Cape Grysbocks are primarily solitary animals. Out of approximately 40 sightings in the wild, only two were of pairs: in one case a ♀ with her offspring, and in the other a ♂ with a ♀, during Sep (Manson 1974). Cape Grysbocks are territorial, particularly the ♂♂, but even the more tolerant ♀♀ exhibit strong territorial characteristics (Manson 1974). Novellie *et al.* (1984) noted that Cape Grysbocks, particularly ♂♂, had well-defined home-ranges averaging 2.5 ha (range 1.26–4.84 ha) and suggested that pairs did not share territories.

Males mark their territories by using their preorbital glands to mark twigs and grass stalks, leaving a conspicuous black sticky deposit. Females also have prominent preorbital glands with secretions clearly visible, but they appear to mark infrequently (only two observations being recorded, and those in captive animals) while juveniles of both sexes have never been observed using their preorbital glands (Novellie *et al.* 1984). On several occasions ♂♂ have been noted biting off twigs prior to marking the stems with their preorbital glands. Marking tends to take place at night and dominant animals mark more frequently than subordinates (Novellie *et al.* 1984). The effect of pedal, or interdigital, gland marking is less obvious, but animals were noted scratching the ground whenever establishing a new dung midden. Number of middens used in the wild has yet to be established, but both adults and juveniles use the same midden in captivity (Novellie *et al.* 1984).

In captivity, adult ♂♂ appear, without exception, to exhibit aggression to other adult ♂♂, with the dominant animal deposing subordinates regardless of supposed territorial boundaries (Novellie *et al.* 1984). Unrelated ♀♀ also exhibit relatively little tolerance of other ♀♀. Subordinate animals generally exhibit submissive behaviour by lying down, upon which the dominant animal approaches and makes naso-nasal contact. Occasionally, subordinate animals creep closer on their knees. At no stage can more than one adult ♂ be kept together in an enclosure. All attempts at keeping two rams have ended in major aggression, necessitating separation.

When a ♂ discovers a midden with female excretions, he first smells it, frequently following this with flehmen behaviour (typically lip and tongue movements and outstretched horizontal neck). Once oestrus has been detected and contact is made the ♂ marks the ♀ with preorbital gland secretions, thereby (according to Manson 1974) making her a part of his known environment. Once visual contact has been made the ♂ approaches and rubs against the female's head and neck, sometimes the rest of her body, occasionally licking her face, neck and shoulders. This sequence of behaviour is often repeated during the early courtship phase, but abates later. Manson (1974) also cited Ewen (1956) as having observed 'butting matches' during courtship, but did not observe it himself.

Males pay particular attention to the female's urogenital region during later stages of courtship, continually licking and following as the ♀ moves forward: the intensity increases and following becomes incessant. This appears to stimulate urination by the ♀, notably on established middens, and each time the ♂ again exhibits typical flehmen behaviour. Unsuccessful mating attempts often follow and these are caused by sudden forward movements by the ♀, with the ♂ standing on his hind legs, front legs folded to the chest, and very little, if any, actual body contact. Males often make bleating sounds while licking the ♀, or just prior to mounting. Females also bleat during encounters but less frequently than ♂♂. Novellie *et al.* (1984) also reported a greater frequency of licking and bleating behaviour by the ♂ during

periods of successful mating and he suggested that there are seasonal peaks (Mar–Jun) in this reproductive behaviour. Successful copulation only lasts for a few seconds and laufschiag (foreleg mating kick) was never observed in Cape Grysbooks (Novellie *et al.* 1984).

The young of territorial species are typically concealed, or conceal themselves, until sufficiently mature to emerge. Manson's (1974) sole observation of such an event was of a Cape Grysbook young that hid itself after being suckled. Suckling apparently takes place with the mother either standing or lying down.

Reproduction and Population Structure A single young is born at any time of the year, although a captive group showed a birth peak between Sep and Dec (Novellie *et al.* 1984); Spence (2003) notes birth peaks in captivity in Mar/Apr and Oct/Nov. Skinner & Chimimba (2005) noted that under favourable conditions ♀♀ can have up to two young in one year.

Skinner & Chimimba (2005) indicated that ♀♀ have their first young at 17–26 months while ♂♂ become sexually mature at 17–18 months. Manson (1974) observed a ♀ give birth at the age of approximately 18½ months, suggesting that sexual maturity in ♀♀ can occur at least as early as 12 months (which agrees with Spence [2003]). Based on subsequent observations, the gestation period appears to be approximately 192 days, or six months (Manson 1974). In captive animals at Tygerburg Zoo, Spence (2003) estimated gestation at 171–180 days, and recorded inter-birth intervals of 177–215 days. One captive specimen lived to more than seven years (Weigl 2005).

Predators, Parasites and Diseases Stuart (1981) identified Cape Grysbook remains in the stomach contents of both Caracals *Caracal caracal* and Leopards *Panthera pardus*. Skead (1980) reported that a considerable number of farmers were convinced that Cape Grysbook numbers had declined due to an alleged increase in Caracal numbers, but he noted that, at least in the Eastern Cape, these appeared to be cyclical events for both Caracals and Cape Grysbooks. In West Coast N. P., Cape Grysbooks are likely to have contributed to the diet of Caracals even though they are a low-density species compared with other ungulates. Even so, Avenant & Nel (1997, 1998) found that ungulates only made up about 7% of the Caracal diet (the bulk being rodents). Another probable carnivore predator is the Black-backed Jackal *Canis mesomelas*, whilst Ratels *Mellivora capensis* could potentially prey on young. Langley (1986) reported a number of attacks on Cape Grysbook young by Cape Grey Mongooses *Herpestes pulverulentus*, suggesting that newborns may be under predation risk, even from small carnivores. Other predators known to prey on Cape Grysbooks include some of the larger raptors, such as Crowned Eagles *Stephanoaetus coronatus* (Boshoff *et al.* 1994), Verreaux's Eagles *Aquila verreauxii* (Boshoff *et al.* 1991), and probably Martial Eagles *Polemaetus bellicosus* (Boshoff & Palmer 1980, Boshoff *et al.* 1990).

A number of studies have investigated the parasite loads on Cape Grysbooks and compared them with other susceptible species (Boomker *et al.* 1989a, MacIvor & Horak 2003, Watermeyer *et al.* 2003). Boomker *et al.* (1989a) reported that nematodes of nine species as well as a further two genera and cestodes of one species

and a further genus were recovered. Highest loads were of the nematodes *Skrjabinema* spp., *Trichostrongylus pieterse* and *T. rugatus*. High numbers of the nematode *Skrjabinema* spp. (parasites that are commonly reported to occur in high numbers in grazing antelopes) has lent indirect support for some grazing activity taking place in Cape Grysbook (Boomker *et al.* 1989a). The nematodes *Haemonchus contortus* and *Impalaia tuberculata* were not recorded in this survey and Boomker *et al.* (1989a) felt that earlier records (Mönnig 1931, 1933) should be treated with caution as the hosts may actually have been Steenboks. Watermeyer *et al.* (2003) identified a new parasite record for the Cape Grysbook (*Setaria saegeri*).

One of the most frequent disease issues reported to conservation authorities in the Western Cape (P. H. Lloyd pers. obs.) and Eastern Cape (Skead 1987) is that of infectious ophthalmia in Cape Grysbooks. By contrast, relatively few reports have been received of incidents of this infection in Steenboks. Since the organism causing the disease, *Rickettsia conjunctivae*, is frequently found in, and dispersed by, a variety of flies and other arthropods, it would appear that the Cape Grysbook's selection of dense vegetation could be a contributory factor, since many flies use shaded areas under vegetation.

Conservation IUCN Category: Least Concern. CITES: Not listed.

The Cape Grysbook is officially conserved in the majority of formal conservation areas in the Western Cape, as well as in many others in the Eastern Cape. It is known from seven National Parks, including Table Mountain N. P., West Coast N. P., Agulhas N. P. and Wilderness N. P., and at least 27 Provincial Nature Reserves. The long-term viability of state parks and reserves as well as the increasing number of privately owned reserves will be contributory factors to the future persistence of the species. For many of the private reserves and even some of the state-protected areas the continued presence of undesirable species (extralimital, exotic or domestic) that out-compete or negatively impact on the Cape Grysbook should be a major concern.

Measurements

Raphicerus melanotis

TL (♂♂): 771 (450–810) mm, n = 4

TL (♀♀): 793 (720–815) mm, n = 5

T (♂♂): 58 (40–72) mm, n = 4

T (♀♀): 54 (44–60) mm, n = 5

HF c.u. (♂♂): 245 (240–250) mm, n = 4

HF c.u. (♀♀): 248 (235–265) mm, n = 5

E (♂♂): 113 (105–115) mm, n = 4

E (♀♀): 115 (110–120) mm, n = 5

WT (♂♂): 10.0 (10.0) kg, n = 4

WT (♀♀): 10.5 (8.8–11.4) kg, n = 5

Western Cape (C. T. Stuart, in Skinner & Chimimba 2005)

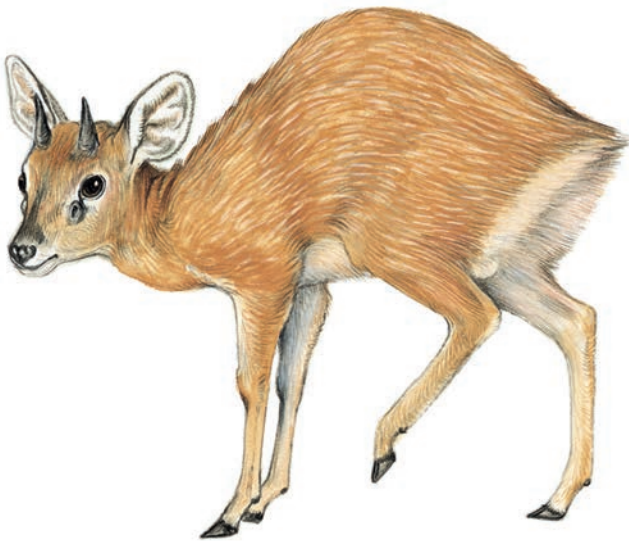
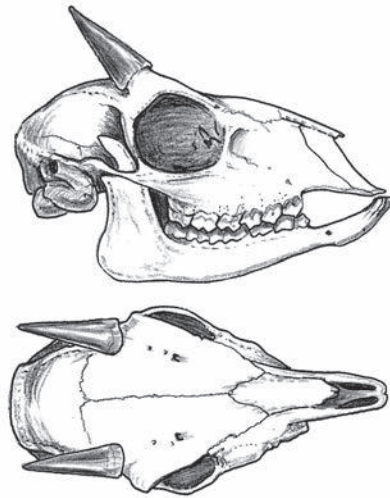
Maximum recorded horn length is 13.3 cm for a pair of horns from the Western Cape, South Africa (Rowland Ward)

Key References Manson 1974; Novellie *et al.* 1984.

Guy Castley & Peter Lloyd

***Raphicerus sharpei* SHARPE'S GRYSBOK**

Fr. Grysbok de Sharpe; Ger. Sharpegreisbock

Raphicerus sharpei (Thomas, 1897). Proc. Zool. Soc. Lond. 1896: 796, pl. 34 [1867]. S Angoniland, Malawi.Sharpe's Grysbok *Raphicerus sharpei*.Lateral and dorsal views of skull of Sharpe's Grysbok *Raphicerus sharpei*.

Taxonomy Sharpe's Grysbok has been considered synonymous with the Cape Grysbok *Raphicerus melanotis* (Haltenorth 1963, Haltenorth & Diller 1980), but Ellerman *et al.* (1953) and Ansell (1972) regarded both as distinct species (and see Genus profile). Ansell (1972) recognized two subspecies: *R. r. sharpei*, a supposedly smaller, paler form from the northern parts of the species' range, and *R. r. colonicus*, a larger, marginally darker form from the southern parts of the range. However, the precise limits of distribution between the two have never been very clear, and the validity of these subspecies is doubtful. Synonyms: *colonicus*. Chromosome number: not known.

Description Small antelope with a rich, reddish-fawn body colouration and a liberal sprinkling of white hairs on the dorsal parts, shoulders and flanks. Eyes surrounded by an ill-defined whitish ring. Ears with buffy-white hair inside; dark on the outside. A short, dark band on top of the muzzle extends from the rhinarium to the front of the eyes. Sides of the face, outer parts of the limbs, forehead and upperparts of the muzzle yellowish-brown, lacking the white grizzling seen on the dorsal parts. Underparts, throat and insides of the legs paler than upperparts, almost white. Body hairs fairly long (30 mm). Lateral (false) hooves are absent (present on hindlegs of Cape Grysbok). Preorbital glands are present as small patches of black naked skin, about 2 mm in diameter and 3 mm deep (Ansell 1964). Preputial gland present, the opening lying anterior to that of the urethral canal. Pedal glands on both fore- and hindfeet, opening into the interdigital cleft that is well covered with hair (in contrast to the Cape Grysbok in which it is very sparsely haired [Ansell 1964]). No obvious sexual dimorphism, although meagre data from animals taken in Zimbabwe and E Zambia suggest that ♀ is slightly larger. Horns present in ♂ only, short and sloping slightly backward, tapering to sharp points.

Geographic Variation See Taxonomy.

Similar Species

Raphicerus campestris. Marginally sympatric in the northern and southern parts of the range of Sharpe's Grysbok, but absent from the miombo *Brachystegia* woodlands of N Mozambique, Malawi and much of Zambia. Slightly larger (± 11 kg), with smoother coat, more uniformly coloured, and lacking white speckling; black-rimmed eyes very conspicuous against pure white margin; horns longer (max. 190 mm); back profile more horizontal and less hunched.

R. melanotis. Allopatric, with distribution nearly confined to the Cape Floristic Region. Slightly larger (mass of ± 10 kg), with conspicuous white hairs visible in an overall rufous pelage; false (lateral) hooves present.

Distribution Endemic to Africa, occurring in savanna woodland from Tanzania to Swaziland. They are recorded from the western and southern parts of Tanzania (close to L. Victoria at their northern limits). Distribution then extends southwards through SE DR Congo, most of Zambia (though not west of the Zambezi R.), Malawi and Mozambique (not including the coastal forested regions), to extreme NE Botswana and the eastern Caprivi Strip in Namibia, much of Zimbabwe (including the dry western parts, such as Hwange) and NE South Africa (Limpopo Province, E Mpumalanga), and E Swaziland (Ansell 1978, Kingdon 1982, Ansell & Dowsett 1988, Monadjem 1998, East 1999, Skinner & Chimimba 2005). Not yet recorded from SE Angola or N KwaZulu-Natal Province.

Habitat Across much of their range (Zimbabwe, Zambia and Tanzania) they appear to be associated with *Brachystegia* woodland where there is good undercover in the form of low-growing scrub or medium-length grass (Smithers & Wilson 1979, Kingdon 1982). In some parts of Zimbabwe and Tanzania they live in rocky terrain with low bush and grass cover, often around kopjes and stony ridges. In



Raphicerus sharpei

Hwange N. P., Zimbabwe, they are common in riverine vegetation, but also occur in broken country where there are thickets at the base of kopjes (Wilson 1975).

Although they appear to be associated with areas of good ground cover, Wilson (1975) recorded that, in Hwange N. P., they were also found in pure stands of mopane *Colophospermum mopane* with very little good cover and in Chobe N. P., Botswana, they were seen on a sandy plateau in open woodland with light grass and scrub cover.

Wilson (1975), referring to his 1969/71 survey of Hwange N. P., indicated that Sharpe's Grysbok was confined to the northern part of the Park, and was replaced in the southern sections by the Steenbok. At that time the species was common along the Lukosi R. where there were considerable riverine thickets. Over a distance of 10 miles, 19 Grysbocks were seen on the evening of 9 October 1969. In 1996, another detailed survey of the Park was undertaken and Wilson (1997) noted: 'the Lukosi River Marked Transect was covered on no less than 18 occasions by several different teams and at different times of the day throughout the year and not one Sharpe's Grysbok was seen'. Wilson (1997) goes on to say: 'I have mentioned previously ... that 25 years ago the riverine vegetation along the Lukosi River was very dense and that was when grysbocks were found there. Today [1996] the vegetation has thinned out considerably as a result of elephant destruction and grysbocks no longer occur along the Lukosi River Drive where 25 years ago they were common. However, their distribution may well have shifted southwards into the broken country south of Lukosi and east to Shumba where they are now found.' The species also still occurs in other areas in the northern parts of Hwange N. P.

Abundance East (1999) summarized recorded population density estimates for this species (0.3–0.7 ind/km²), and estimated a total population size of about 95,000 animals. Sharpe's Grysbocks are predominantly nocturnal, exceptionally shy and secretive, and can be overlooked in areas where in reality they are reasonably common, so they may be more abundant than supposed.



Sharpe's Grysbok *Raphicerus sharpei* detail of head.

Adaptations This species has remarkably robust teeth correspondingly deeply embedded in skull and mandible. The mouth has a substantially wider maw than in the Steenbok. These dental and oral peculiarities correspond to a more demanding diet, probably including more lignified and mature growth than is taken by Steenbocks, which prefer newer younger shoots. The extreme caution and mainly nocturnal activity of this species also contrast strongly with the commonly diurnal and often conspicuous behaviour and appearance of the larger Steenbok. The shorter legs and cryptic colouration of Sharpe's Grysbocks imply greater vulnerability to predators, which probably include both coursers and large raptors. Flight behaviour includes a brief, stamping pronk and a fast dash for dense cover. The longer-legged Steenbok instead may race away in the open, jinking from side to side before hiding. During the game rescue operations that took place during the formation of L. Kariba, Sharpe's Grysbocks were recorded as readily taking to water, and were said to swim well for their size (Child 1968).

Foraging and Food Predominantly a browser, but they also will graze, and as such are classified as browser–grazer intermediates by Gagnon & Chew (2000) in their review of the dietary preferences of African bovids. In SE Zimbabwe, stomach contents consisted of 70% browse and 30% grass, with important browse items including: *Acacia* spp., sand olive *Dodonaea viscosa*, buffalo thorn *Ziziphus mucronata*, false marula *Lannea edulis*, horn-pod tree *Diploerhynchus condylocarpon*, beechwood *Faurea saligna* and bitter albizia *Albizia amara* (Smithers & Wilson 1979). Wilson (1975), in Hwange N. P., recorded *Diospyros lycioides* fruits, *Grewia flavescens* fruits and leaves, the leaves and soft stems of *Commelina* sp., the leaves and fruits of *Cyphostemma burchanani*, and a number of unidentified grasses.

Although they feed mainly at night, Sharpe's Grysbocks may be seen foraging in the early morning or late afternoon, lying up during the heat of the day in dense cover (Smithers 1971).

Social and Reproductive Behaviour Very little is known about the behaviour of this species. They usually occur solitarily, in pairs, or a ♀ with her single offspring. A loosely connected pair may share a territory throughout the year (Kingdon 1982). Droppings are apparently placed in small middens, which are used over long periods (Smithers 1971). The latter suggests that Sharpe's Grysbocks do not undertake extensive seasonal movements.

They are notoriously secretive and reclusive, inclined to lie up very tightly hidden in the undergrowth. When they do run off they often



crouch low to the ground as they run through the thick underbush, in contrast to the Common Duiker *Sylvicapra grimmia*, which bounds through the undergrowth, or the Steenbok (described above). They have been recorded hiding in Aardvark *Orycteropus afer* burrows (Shortridge 1934, V. J. Wilson pers. obs.).

Reproduction and Population Structure Pregnant ♀♀ have been recorded throughout the year (Shortridge 1934, Ansell 1960a, Kerr & Wilson 1967, Smithers 1971, Smithers & Wilson 1979, V. J. Wilson pers. obs.), suggesting that they are aseasonal breeders. A single young is born following a gestation of about seven months. Birth-weight in captivity is around 830 g (range 790–863 g, $n = 5$; V. J. Wilson pers. obs.). There is limited information available on population structure, although during the game rescue operations on L. Kariba, of 222 sexed individuals recorded in reports, there were 113 ♂♂ and 109 ♀♀ (V. J. Wilson pers. obs.).

Predators, Parasites and Diseases Predators include Lions *Panthera leo*, jackals *Canis* spp., Caracals *Caracal caracal*, African Rock Pythons *Python sebae* and large raptors. On one occasion a 10-foot python, captured on the Lukosi R. in Hwange N. P., was being stretched out in order to measure it and it regurgitated a partly digested adult Sharpe's Grysbok ♀ (V. J. Wilson pers. obs.). A single animal examined in the Central Province of Zambia was infected with *Amblyomma variegatum*, *Rhipicephalus appendiculatus*, *R. kochi* and *R. punctatus*; *R. appendiculatus* constituted 94% of all ticks present (Zieger *et al.* 1998b).

Conservation IUCN Category: Least Concern. CITES: not listed.

Although they have been extirpated from parts of their range by expanding human settlement and localized hunting for bushmeat, Sharpe's Grysbok remain relatively widespread with about one-third of the total population occurring in protected areas, including: Selous G. R. (Tanzania), Upemba N. P. (DR Congo), Kafue N. P. and North and South Luangwa National Parks (Zambia), Lengwe N. P. (Malawi),

Banhine N. P. (Mozambique), Hwange N. P. and Gonarezhou N. P. (Zimbabwe) and Kruger N. P. (South Africa) (East 1999).

Measurements

Raphicerus sharpei

TL (♂♂): 751 (710–800) mm, $n = 12$

TL (♀♀): 757 (725–800) mm, $n = 11$

T (♂♂): 58 (50–70) mm, $n = 12$

T (♀♀): 59 (45–70) mm, $n = 11$

E (♂♂): 90 (83–98) mm, $n = 12$

E (♀♀): 91 (85–98) mm, $n = 11$

WT (♂♂): 7.3 (6.8–8.9) kg, $n = 12$

WT (♀♀): 7.7 (6.4–8.9) kg, $n = 11$

SE Zimbabwe (Smithers & Wilson 1979)

TL (♂♂): 760, 880 mm, $n = 2$

TL (♀♀): 763 (550–820) mm, $n = 8$

T (♂♂): 60, 70 mm, $n = 2$

T (♀♀): 78 (50–90) mm, $n = 8$

WT (♂♂): 8.9 (6.3–11.8) kg, $n = 4$

WT (♀♀): 9.0 (7.2–10.8) kg, $n = 19$

E Zambia (V. J. Wilson pers. obs.).

In E Zambia, an additional seven adult ♂♂ had a mean mass of 8.9 kg (range 7.1–10.7 kg), and eight adult ♀♀ 9.9 kg (range 8.5–11.9 kg). The mean masses of animals caught at Kariba during game rescue operations was: ♀♀ 10.1 kg (range 8.6–11.1 kg, $n = 9$); ♂♂ 9.6 kg (range 9.0–10.1 kg, $n = 6$) (V. J. Wilson pers. obs.).

Maximum recorded horn length is 10.4 cm for a pair of horns from Massingir, Mozambique (Rowland Ward)

Key References Smithers 1971; Wilson 1975; Smithers & Wilson 1979.

Michael Hoffmann & Vivian J. Wilson

***Raphicerus campestris* STEENBOK (STEINBUCK, STEINBOK)**

Fr. Steenbok; Ger. Steinbockchen

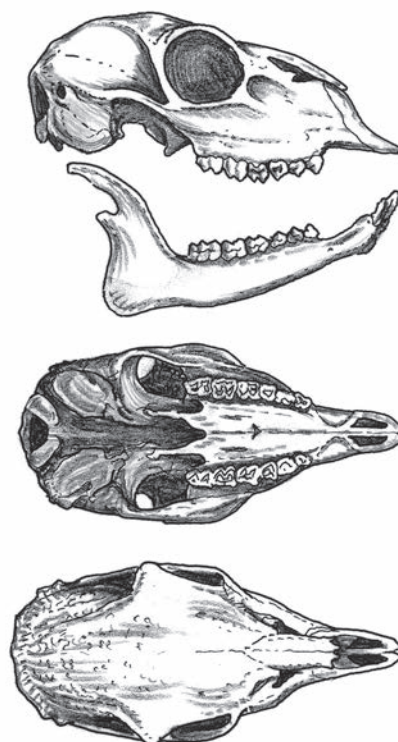
Raphicerus campestris (Thunberg, 1811). Mem. Acad. Imp. Sci. St. Petersburg 3: 313. No locality cited; since selected as Western Cape Prov., Malmesbury Div., Swartland (Grubb 1999: 23).



Steenbok *Raphicerus campestris*.

Taxonomy The colouration of Steenboks varies widely throughout their range, and has partly contributed to the recognition of so many subspecies. Ansell (1972), in his revision of the taxonomy of the species, listed eight subspecies, noting that their acceptance was provisional and that study of a more complete series of specimens would lead to a reduction in the number of recognized subspecies. Of the eight listed by Ansell (1972), only one was listed for East Africa, namely *R. c. neumanni*, one (*R. c. kelleni*) for Angola and Zambia, and the remaining six for southern Africa; Meester *et al.* (1986) reduced this list to five. Pending a much-needed taxonomic revision, the most reasonable approach appears that of Kingdon (1997), who lists only two subspecies: the nominate form from the southern part of the range, and *R. c. neumanni* for East Africa. Synonyms: *acuticornis*, *bourquii*, *capensis*, *capricornis*, *cunenensis*, *fulvorubescens*, *grayi*, *hoamibensis*, *horstockii*, *ibex*, *kelleni*, *natalensis*, *neumanni*, *pallida*, *pediotragus*, *rufescens*, *rupestris*, *steinhardtii*, *stenbock*, *stigmatus*, *subulata*, *tragulus*, *ugabensis*, *zukowskyi*, *zuluensis*. Chromosome number: $2n = 30$ (Wallace & Fairall 1967a). All autosomes are metacentric; the X-chromosome is a large acrocentric and the Y is a small metacentric.

Description A small, gracile antelope (about 0.5 m at the shoulder), with long, slender legs, a glossy light brown to reddish-brown pelage on the flanks and back and white underparts. Ear pinnae large with white inside, light grey on the back and a thin black line around the pinnae rims. Throat and chin white, nose and dorsal ridge of rostrum black, and there is a distinctly pale or white eyebrow line, giving the animal a neatly groomed appearance. The brown eyes are rimmed by black skin that enlarges their visual impact. Hooves narrow and sharp; false



Lateral, palatal and dorsal views of skull of Steenbok *Raphicerus campestris*.

hooves absent. Tail short, brown above and white underneath. Hairs on the tail and the posterior margins of the hindquarters are longer than on the rest of the body. Steenbok have preorbital glands, pedal glands in all feet, but no inguinal glands. Build and colouration similar in ♂ and ♀, except that ♂ has short, sharp, straight, smooth and upward-pointing horns (usually 100–150 mm long) that are relatively widely spaced on the head; as in some other bovids, horned ♀♀ are known. Juveniles are darker than adults, especially on the rump where there is a greyish tinge, and have longer hair all over the body. Juveniles also have two distinctive black spots on the crown of the head where horns would be expected, and these fade with maturity.

Geographic Variation

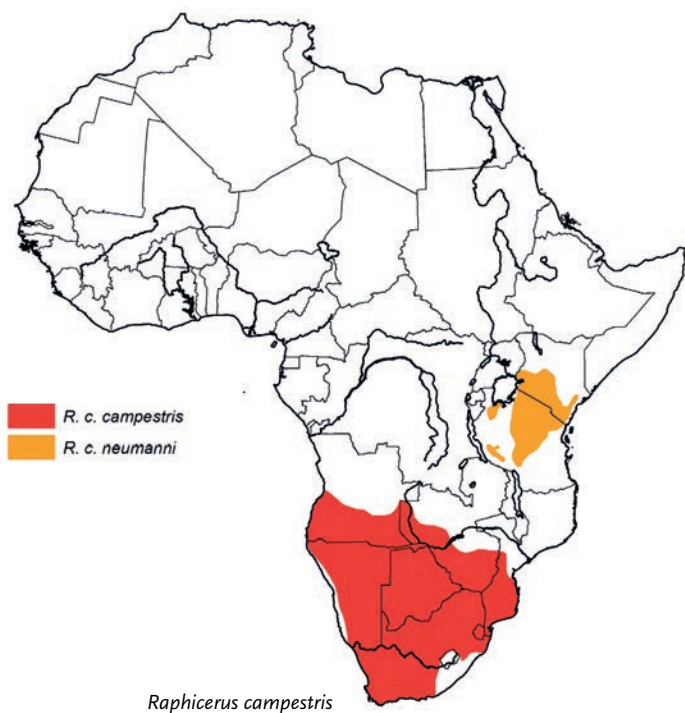
R. c. campestris: southern Africa, including Angola and Zambia.

R. c. neumanni: East Africa.

Similar Species

Raphicerus melanotis. Sympatric in SW Africa. Slightly smaller (ca. 10 kg), with slightly hunched or arched appearance; grizzled hairs on back, sides and neck; lateral hooves present; ♂ has a preputial gland.

R. sharpei. Marginally sympatric especially in Zimbabwe and S Mozambique. Slightly smaller (ca. 10 kg), with shorter legs and more hunched profile; horns shorter (max. 104 mm); pelage grizzled with white flecks.



Sylvicapra grimmia. Broadly sympatric. Larger, with sagittal hair tuft.
Ourebia ourebi. Sympatric in parts of range. Larger, with longer neck, and black patch above the tail; inguinal glands present; bare glandular patch below the ear.

Distribution Endemic to Africa. Steenboks have a disjunct distribution, with one population in East Africa (S Kenya, N and C Tanzania) and a larger one in southern Africa, the isolating barrier being the tall miombo *Brachystegia* woodlands of C Zambia, Malawi (from which there are no records) and N Mozambique.

Historical Distribution In East Africa, their distribution covers most of S Kenya and N and C Tanzania. They formerly occurred in E Uganda but are now believed extinct. Not recorded from Somalia (Funaioli & Simonetta 1966, Simonetta 1988).

In southern Africa, their range extends southwards from S Angola and W and SW Zambia, into most of Namibia (except the arid coastal parts), throughout Botswana and W, C and S Zimbabwe (though naturally absent from the Zambezi Valley below Victoria Falls), S Mozambique (being very common south of the Save R.), to South Africa. In South Africa, they occur almost throughout, being absent from S and SE KwaZulu–Natal and much of the neighbouring Eastern Cape (Ansell 1978, Kingdon 1982, East 1999, Skinner & Chimimba 2005). They are not recorded from Lesotho (Lynch 1994).

Current Distribution Their distribution is largely unchanged in southern Africa, but in East Africa Steenboks no longer occur in Uganda, where most of the suitable habitat is now cultivated (East 1999).

Habitat Steenboks are found in a variety of habitat types, from Kalahari semi-desert to alpine moorland zones up to 3500 m on Mt Kenya (Young & Evans 1993). However, within any particular ecosystem, Steenboks use a relatively narrow range of habitats with a common factor being the presence of pioneer plants and encroaching

thorn bushes in areas where vegetation is disturbed. For example, they are often seen feeding along road verges. In southern Africa, they show a particular preference for heavily grazed areas, where the herb layer has a high forb : grass ratio and the woody layer is dominated by encroaching thorn scrub, typically comprising *Acacia tortilis* and *Dichrostachys cinerea*. Such conditions often occur around watering points although the availability of drinking water is not a habitat requirement for Steenboks. The key habitat requirement is the availability of high-quality food items (green browse, geophytes, berries, flowers or pods) throughout the year. In the lower Kuiseb River Canyon, Namibia, there was a strong relationship between the distribution of Steenboks and the occurrence of *Acacia albida* (staple food) and *Salvadora persica* (shelter) (Cloete & Kok 1986b).

Abundance Steenboks are common throughout their range. Aerial surveys underestimate population numbers, but ground surveys, in areas where the species is common, give density estimates of 0.3–1.0/km² (East 1999). Based on these estimates, East (1999) estimated a total population size in excess of 600,000, but this clearly is an underestimate. In general, there are no reliable estimates of Steenbok population density, as census methods are too unreliable for this cryptic species.

Adaptations The ability to survive without access to drinking water in arid regions might suggest that Steenbok physiology is specifically adapted for advanced water economy, but in fact this is not the case. Steenboks in the Namib Desert were found to have a water turnover rate of 135 ml/day and their rate of faecal water loss was 145 ml/day, while their dietary water intake rate was 343 ml/day (Cloete & Kok 1986a). The surplus of 63 ml/day would be lost in breathing and evaporative cooling. From kidney structure and function there is no evidence that Steenbok renal efficiency is any higher than average for ruminants, indicating that water balance is maintained largely by behavioural means. These include feeding very selectively on food items of high water content, avoiding heat stress by lying in shade in the heat of the day, restricting diurnal activity mostly to morning and late afternoon, and being active nocturnally. Being small-bodied, Steenboks gain and lose body temperature relatively quickly. They have a low metabolic rate and a high overall thermal conductance (Haim & Skinner 1991). When ambient temperatures exceed about 38 °C, typical heat-shedding behaviour is to stand panting in the shade, with legs spread to dissipate heat from thermal ‘windows’ in the armpits, groin and belly.

Their requirement for highly nutritious food items precludes sociality, since such food items are rare and widely dispersed in the environment. If Steenboks foraged in groups there would never be enough food to share at each feeding stop. An implication is that living alone, or sometimes in mixed-sex pairs, precludes the sharing of vigilance costs among herd members. Steenboks do not, in fact, invest more in vigilance, but rely almost entirely on crypsis for predation avoidance (du Toit & Yetman 2005). Steenbok are adapted for vigilance by having relatively large ears and apparently good eyesight. When an approaching predator is detected, the Steenbok will lie motionless in the grass with its ears laid flat and usually the predator will pass by. It is only when a predator approaches within a few metres that the Steenbok will bolt suddenly and at high speed, employing a bouncing hare-like gait and jinking in sharp zig-zags,

then stopping suddenly to stand stock-still or dropping into cover to lie motionless again. Besides Sharpe's Grysbok, Steenboks are the only antelope species known to take refuge in burrows, especially those of Aardvarks *Orycteropus afer*, for predation avoidance and possibly thermoregulation (Smithers 1971, J. T. du Toit pers. obs.).

Foraging and Food Although they are frequently referred to in the scientific literature as mixed feeders, largely because of Hofmann & Stewart's (1972) classification based on stomach structure, Steenboks are predominantly browsers throughout the year. In Kruger N. P., South Africa, both Cohen (1987) and du Toit (1993) found that grass leaves are ingested when they are green and tender after rains but, overall, grass contributes an insignificant amount to the mean monthly diet. These field studies are supported by a review of dietary preferences in African bovids (Gagnon & Chew 2000) and dietary studies involving analysis of stable carbon isotopes that show that Steenboks eat far less grass than is believed (Cerling *et al.* 2003, Sponheimer *et al.* 2003b). However, in Zimbabwe, a sample of 91 stomachs from shot animals comprised 30% grass on average (Smithers 1971), and the same author notes that in a sample of 25 stomachs from Botswana, there was an average of 50% browse and 50% grass. This is surprising but indicates that grazing can be important at times. Indeed, in Kenya, Hofmann (1973) noted from stomachs that grass predominated in the diet after rain had stimulated new growth.

Steenboks in Kruger N. P. allocate most of their feeding time to forbs during the wet season (>80% feeding time) with the balance being made up mainly of leaves of woody plants, of which *Flueggea*, *Acacia* and *Ziziphus* species are staples (du Toit 1993). The monthly proportional allocation of feeding time to forbs varies closely with the three-month running mean of rainfall, which is an indicator of soil moisture content. During the late dry season in Kruger N. P. (Jul–Oct) forbs make up only about 30% of the diet, with the rest being mainly leaves of woody plants, although the fallen pods of *Acacia tortilis* are avidly sought out. It appears that the availability of these highly nutritious pods is a key factor enabling Steenboks to remain resident within their territories during the dry season and not to move down-slope to feed along river lines, as most of the other ungulates do during this 'lean' period. Also, Steenboks benefit from the micro-climate created within the recumbent canopies of trees felled by elephants, where forbs remain green well into the dry season. Bigger browsers are excluded from this resource by the cage of branches, through which Steenboks are able to creep.



Steenbok *Raphicerus campestris*.

The mean height above ground at which Steenboks feed varies from 140 mm in the wet season when forbs are the staple, to 390 mm in the late dry season when woody browse predominates in the diet. At full neck stretch, Steenboks cannot browse any higher than about 1 m above ground (du Toit 1990a) and they do not rise up on their hindlegs to gain additional height.

Being one of the smallest ruminant species, Steenboks have a narrow dietary tolerance range and thus have to be efficient at maximizing net energetic gains from foraging. Steenboks spend about one-third of their day foraging (feeding and walking in search of food items) in both wet and dry seasons, and the same proportion of the night in the wet season, but in the dry season they spend almost 60% of their night foraging. When not foraging, Steenboks generally lie ruminating or resting to conserve energy (and heat, in winter), and throughout the year they spend about half of their time lying down. Rumination is important for processing ingested food as quickly and thoroughly as possible, and in the wet season this accounts for an additional 26 min for every hour spent foraging, rising to 33 min per foraging hour in the dry season. Steenboks seek out flowers and fruits when they are available, although frugivory appears to be regulated by plant toxins. For example, a radio-collared Steenbok in Kruger N. P. would eat only one *Solanum panduraeforme* fruit per day, even when they were abundantly available.

Geophagia is common. When a Steenbok is seen standing head down near the water's edge of a pan it may mistakenly be assumed to be drinking, but on close inspection it will invariably be licking the salt crust off dried mud. Steenboks in Kruger N. P. are sometimes seen digging with their front hooves and apparently consuming bulbs or tubers. The only documented observation of this behaviour is by Smithers (1983) in Botswana.

Social and Reproductive Behaviour Steenboks are solitary, unless a ♂ is consorting with a ♀, or a ♀ has a juvenile with her. Both sexes maintain territories and a defender will drive a conspecific intruder of the same sex out of its territory in an energetic chase, although physical combat is rare. It is unclear what cues are used among ♀♀ to assess dominance and submission, since without horns the options for physical combat seem limited. However, in ♂♂, opponents kneel on their forelegs and present their horns to one another, with the loser breaking away and running after only a few seconds. This behaviour is most frequently seen when a ♂ is consorting with an oestrous ♀ and other ♂♂ attempt to gain access to her.

Scent-marking entails depositing secretions from the preorbital glands on the browsed stumps of forbs and shrubs. Burger *et al.* (1999a) examined the organic constituents of the preorbital secretion of the Steenbok, and identified 109 different compounds. However, these authors noted that although the secretion is similar to that of the Cape Grysbok *Raphicerus melanotis*, it is far more complex, with more than 260 different compounds present in the secretion. Steenboks also scent-mark by means of urinating and defecating in latrines. A shallow scrape is prepared with the front hooves, the animal then squats to deposit urine and/or faeces in the scrape and then fresh soil is kicked over the latrine with the front hooves. This behaviour presumably is to keep the deposit moist and maintain the odour for longer than if it was uncovered. The home-range (and presumably also territory) of adult ♀♀ in Kruger N. P.



Side and frontal views of male Steenbok *Raphicerus campestris* head.

covered about 0.6 km² (du Toit 1993), although it is unknown if ♂♂ use more or less space than this.

When a ♀ is in oestrus the attending ♂ will kick and stroke her hindquarters with his forelegs and lick her genital region until she squats to provide a sample of urine, which he tests in typical flehmen posture. During this interaction the ♀ may be uncooperative and the ♂ may make a loud cat-like growl. Mounting occurs suddenly, with the ♂'s body held almost vertical, forelegs folded back not clasping the ♀, and involving a few quick pelvic thrusts before dismounting. Mounting and penetration may be repeated two or three times in quick succession, after which the ♂ and ♀ typically lie down together resting. The young lies hidden for its first three or four months of life while the mother moves around foraging, but she visits it regularly for suckling (Cohen 1987). When an oestrous ♀ has offspring with her the consorting ♂ sometimes attacks the juvenile with his horns, which suggests that infanticide could occur, presumably when the attacking ♂ has recently attained dominance, at which time the juvenile cannot be his offspring. If infanticide is a real risk, this probably explains the adaptive value of juveniles having black spots on the head where horns would be expected. An approaching adult ♂ could see these 'pseudo-horns' and mistake the juvenile for an attending adult ♂, at least for long enough to allow the juvenile to move away.

Reproduction and Population Structure Females attain reproductive age at about seven months. Steenboks are aseasonal breeders, although examination of 188 female specimens in Zimbabwe suggested a possible birth peak shortly after the onset of the rains (Nov/Dec) (Wilson & Kerr 1969). A single young is born with a birth-weight of <1 kg; twins are rare. Gestation lasts about 170 days (Hofmeyr & Skinner 1969). Steenboks can live for about nine years in captivity (Weigl 2005), although life expectancy in the wild is considerably shorter due to predation.

There has been debate about Steenbok sex ratios, with some small data-sets having given rise to the suggestion that ♂♂ outnumber ♀♀ in all age classes (e.g. Van Bruggen 1964, Wilson & Kerr 1969). In fact, the sex ratio does not differ from parity. Males are more easily sighted and positively sexed than the shyer ♀♀: when horns are seen the sighting is immediately labelled 'male'; when no horns are seen the sighting is unconfirmed and labelled 'sex unknown' if the head cannot be scrutinized to establish that indeed the animal has no horns and is thus female. In Kruger N. P., Cohen (1987) found

a ♂ : ♀ sex ratio of 1 : 1.04 in a sample of 4600 adults, and results from Namibia (Stuart 1975) and KwaZulu–Natal (Mentis 1972) based on large sample sizes yielded an even adult sex ratio.

Predators, Parasites and Diseases The biggest impact of predation on Steenbok populations probably occurs in the juvenile age class (0–3 months) when jackals *Canis* spp. and avian raptors such as Martial Eagle *Polemaetus bellicosus* encounter the undefended young lying in the grass. In the South African lowveld, adult Steenboks are important prey in the dry season for Cheetahs *Acinonyx jubatus* and African Wild Dogs *Lycaon pictus* in particular (Radloff & du Toit 2004); other known predators include Caracals *Caracal caracal* and Cape Foxes *Vulpes chama* (Kok & Nel 2004, Melville *et al.* 2004).

Not much is known about parasites. Boomker *et al.* (1986) recorded that an animal from the Kalahari harboured the helminths *Trichostrongylus* sp. (subsequently identified as *T. auriculatus* by Boomker [1986]), *Paracooperia serrata* and *Skrjabinema* spp.; elsewhere, Steenboks were recorded infested with helminths of the genera *Trichostrongylus*, *Skrjabinema*, *Haemonchus*, *Longistrongylus*, *Impalaia* and *Moniezia* (Boomker *et al.* 1986), and, in a separate study, *Setaria scalprum* and *S. saegeri* (Watermeyer *et al.* 2003). There is no single disease to which Steenboks are known to be particularly susceptible.

Conservation IUCN Category: Least Concern. CITES: Not listed.

The conservation status of the Steenbok is satisfactory and no specific conservation action is required at present. However, Steenboks are locally vulnerable to predation by domestic dogs and subsistence herdsman who frequently capture and kill juveniles in particular (when they are found lying alone in cover). Important protected populations include those in Serengeti–Mara (Tanzania, Kenya), Tsavo N. P. (Kenya), Etosha N. P. (Namibia), Hwange N. P. (Zimbabwe), Kgalagadi Transfrontier Park (Botswana/South Africa) and Kruger N. P. (South Africa).

Measurements

Raphicerus campestris

TL (♂♂): 843 (773–910) mm, n = 38*

TL (♀♀): 856 (790–920) mm, n = 39*

HF c.u. (♂♂): 273 (253–290) mm, n = 39

HF c.u. (♀♀): 271 (250–287) mm, n = 38

E (♂♂): 114 (101–125) mm, n = 37

E (♀♀): 113 (100–126) mm, n = 38

WT (♂♂): 10.9 (8.94–13.2) kg, n = 37

WT (♀♀): 11.3 (9.65–13.2) kg, n = 39

Botswana (Smithers 1971)

*The total length (TL) includes a very short tail, for which measurements are not available

Maximum recorded horn length is 19.0 cm for a pair of horns from the former Cape Province, South Africa (Rowland Ward)

Key References Cohen 1987; du Toit 1990a, 1993; Smithers 1971; Smithers & Wilson 1979.

Johan T. du Toit

GENUS *Dorcatragus*

Beira

Dorcatragus Noack, 1894. Zool. Anz. 17: 202.

Dorcatragus includes only the Beira *D. megalotis*, a small and slender gazelle-like antelope with very large ears, confined to N Somalia and adjacent parts of Ethiopia and Djibouti in rocky upland habitats, but not on steep slopes. The Beira was first described as a kind of Klipspringer (genus *Oreotragus*). Pocock (1918), noting that the footglands of Beiras are similar to those found in the genera *Madoqua* and *Rhynchotragus*, allied them with the dik-diks (as did Allen 1939). While traditional classifications consider them as forming a

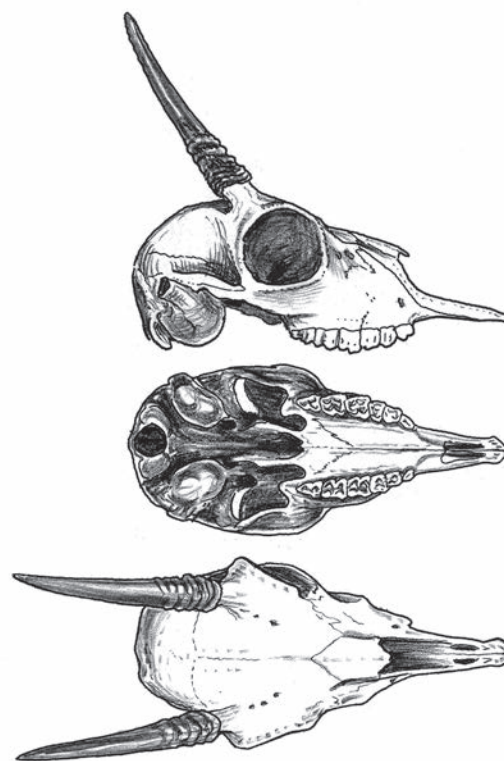
clade with the other dwarf antelopes traditionally included in the paraphyletic Neotragini (including *Madoqua*, *Ourebia*, *Oreotragus*, *Neotragus*/*Nesotragus* and *Raphicerus*), *Dorcatragus* is here tentatively included along with the genus *Raphicerus* in the tribe Raphicerini. It is just possible that Haltenorth (1963), who resurrected the tribe Dorcatragini for the species, might eventually prove correct.

Peter Grubb

Dorcatragus megalotis BEIRA

Fr. Beira; Ger. Beira

Dorcatragus megalotis (Menges, 1894). Zool. Anz. 17: 130. Somalia, 'in den Schluchten des Hekebo' (ravine in the Hekebo region); 35 mi (56 km) south-west of Berbera (Moreau *et al.* 1946: 437).



ABOVE: Beira *Dorcatragus megalotis*.

RIGHT: Lateral, palatal and dorsal views of skull of Beira *Dorcatragus megalotis*.

Taxonomy Monotypic. Synonyms: none. Chromosome number: not known.

Description Small and slender gazelle-like antelope with very big and oval ears and somewhat overbuilt rump, about the same size as a Klipspringer *Oreotragus oreotragus*, but with longer legs and neck. Head is short and broad with a small muzzle. Russet-coloured front and bridge of nose, yellow-brown cheeks, and conspicuous white rings around dark eyes. Ears from front show darkish lines in

dense white hair tracts, and are light brown with blackish margins from behind. Neck, back and rump are dove-grey to bluish-grey. Back separated from cream underparts by a dark grey oblique strip along the flank extending from forelegs to the groin. Inner limbs are cream, like the underparts; outer limbs yellow-brown. Rather long, bushy tail of the same grey colour as the rump. Preorbital glands are absent, but they have pedal glands, and cushion-like pads on the short hooves; small lateral hooves present. There is a single pair of inguinal nipples. Female is larger than ♂. There are no obvious differences in

*Dorcatragus megalotis*

colouration between the sexes, but slight inter-individual variations are noticeable.

Only ♂ has horns, which are thin, cylindrical and relatively short (9–13 cm) and straight, with tips slightly curving forwards. The skull is characterized by short nasals, and elongated premaxillae that taper to a narrow tip. An ethmoid vacuity is present. Lateral incisiform teeth are mostly narrow, but the first incisors are broader than the rest; the premolars are relatively large, as in other small antelopes.

Geographic Variation None recorded.

Similar Species

Oreotragus oreotragus. Sympatric in many parts of the range. More sturdily built than Beira, with shorter legs. Ears smaller and darker, head with the same grey-brown colour as the rest of the body, and visible preorbital glands.

Madoqua saltiana. Co-exists on the lower slopes occupied by Beira. Similar coat colour, but much smaller in size, with very short horns and a short erectile crest; preorbital glands present; ♀♀ with two pairs of inguinal nipples.

Redunca fulvorufula. Allopatric. Larger, with short, heavily ridged, forward-curving horns; black subauricular patches present; upperparts predominantly grey, with underparts pure white; ♀♀ with two pairs of inguinal nipples.

Pelzeln's Gazelle *Gazella dorcas pelzelni*, Dibatag *Ammodorcas clarkei* and Gerenuk *Litocranius walleri* overlap in range, but are not found in mountainous regions. Pelzeln's Gazelle is a bit taller than the Beira, with horns present in both sexes; the female's horns are about the same size as those of the Beira ♂, and male Pelzeln's Gazelles have bigger and longer horns, inclined backward. Two lateral white stripes are visible on the head and the coat is brown with white underparts and a black tail. The Dibatag has a similar colour to the Beira, with a grey body and ochre legs, but the head has white lateral stripes. It is

taller, has a rather long tail, and ♂♂ have horns that are annulated at the base with tips sharply angled forward. The Gerenuk is much taller, with a very long neck, a long tail and ♂♂ have S-shaped and heavily ridged horns.

Distribution Endemic to the Horn of Africa, in S Djibouti, NE Ethiopia and N Somalia.

Historical Distribution In Djibouti, recent investigation shows that Beiras were found in four distinct areas in the mid-1940s: Arta region, Yaguer massif, Mt Garbi and Arrey–Assamo massif (Chédeville, in Laurent *et al.* 2001). In Ethiopia, there is at least one historical record of an individual killed close to Hadjin (Poncins 1899) about 10 km south to Assamo, on the Ethiopian–Djiboutian boundary (Laurent *et al.* 2001). In Somalia, it is doubtful whether they ever occurred south of the Nogal Valley. There is no evidence of their historical occurrence in Eritrea (Laurent *et al.* 2001).

Current Distribution The species' existence in Djibouti was only confirmed in 1993, when Beiras were observed on hillsides at two sites in the south-east, close to the borders with Somalia and Ethiopia (Künzel & Künzel 1998). Subsequent surveys have shown that the area of distribution in Djibouti is about 250 km² and located in the mountainous Ali Sabieh–Ali-Addé–Assamo region (Künzel *et al.* 2000, Laurent *et al.* 2001, Giotto *et al.* 2009).

The exact range in Somalia is unknown but seems to be restricted to the northern part of the country, mainly Somaliland, north of the Nogal (Nugaleed) Valley, from southern hills above Kandala, ca. 11° 20' N, 49° 50' E (Chazée 1987), to Garoowe in the south (reliable location approximately 30 km south of the town; P. Moehlman pers. comm.) and to Guban–Bodaleh region in the east. From historical and recent information (Moustapha Elmi 1992), the remaining core areas of the population are: Asse hills–Lahan Sheik, Garoowe area (Bur Cobohille), Wagar, Buuraha and Golis mountains, Araweina, Ali Haidh and Guban region. Between these locations, occasional sightings have been reported. Mallon (2011) recorded Beira in the stony hills east and west of Hargeisa and on rocky ridges in the coastal hills east of Berbera.

In Ethiopia, the species is known from the Marmar mountains along the border with NW Somalia (Bolton 1973, Hillman 1988a); there is no evidence of their occurrence in the Ogaden region (Wilhelmi 1997).

Habitat Beiras inhabit rocky hills and edges of plateaux at medium altitudes up to 1800 m (Ansell 1972). In Djibouti, the present altitudinal range is between 600 m (Go'ondâle Addé) and about 1300 m (Arrey; Giotto *et al.* 2009) and Mallon & Jama (2012) reported seeing Beira at sites ranging in elevation from 600 m to 1450 m in Somaliland.

Beiras frequent rocky or stony hillsides, rarely steep slopes, where the dominant vegetation is a woody steppe of mixed *Acacia* scrub. In Djibouti, they have been reported in association with ligneous steppes supporting *Acacia etbaica uncinata* (sometimes *A. horrida*, *A. asak*, *A. oerfota*, *A. tortilis* and rarely *A. sarcophylla*), patches of *Commiphora* spp. and *Maerua* spp., low spiny shrub *Rhigozum somalense* on slope bottoms (less than 5% soil cover), and grasses such as *Cenchrus*, *Eragrostis* and *Cymbopogon* (Laurent *et al.* 2001). This vegetation is heavily exploited by domestic livestock resulting in a prevalence of grass species such

as *Zygophyllum simplex*, *Aerva javanica*, *Aizoon canariense*, *Iphionopsis rotundifolia* and *Arnebia hispidissima* (Collenette & Mallet 1993, N. Giotto pers. obs.).

In Somaliland, Mallon & Jama (2012) noted that most sites where Beira were observed consisted of dry, flat-topped hills with steep stony slopes and scattered trees (*Acacia etbaica*, *A. tortilis* and *Commiphora* spp.), a habitat described as typical for the species by Drake-Brockman (1911). Kingdon (1997) reported that dominant plants in some supposed habitats are *Acokanthera*, *Buxus*, *Cadaba*, *Cadia*, *Carissa*, *Dodonea* and various succulents, such as aloes, euphorbias and *Sanseveria*, as well as hemps (*Crotalaria*), and that this might indicate some plasticity in their diet. His list referred to the high plateau's succulent steppes (e.g. Yaguer, Gamaré and Siyyarou plateaux in Djibouti) that show differences in abundance and variety from the vegetation cover in Ali Sabieh–Assamo region.

Abundance In Djibouti, the total population has been estimated at between 50 and 150 individuals (Künzel & Künzel 1998, Laurent *et al.* 2001, Giotto *et al.* 2009). Nevertheless, a recent study in the south of Djibouti revealed a local density of ca. 7 ind/km² (Giotto 2004), suggesting that Beiras could be concentrated in some areas within their range. There is no recent information from Ethiopia, where the population is considered small and localized (Hillman 1988a). In Somalia, information on numbers is meagre, but they are probably rare (Simonetta 1988). Population trends are unknown, although probably stable in areas with few settlements. However, in some parts of their range where settlements are expanding and livestock densities are high, numbers are likely decreasing. East (1999) estimated a total population of perhaps 7000 individuals.

Adaptations The Beira is not adapted to mountainous regions like the Klipspringer, but is essentially an animal of high hills and low-elevation mountains. The rounded, cushion-like pads on the lower face of the hooves maintain balance by ensuring a firm grip on slippery and unsteady ground. Stealth and colouration make direct observations of the species very difficult and chance sightings very unlikely, especially when animals are motionless (Poncins 1899, Bolton 1976).

The areas where the species lives have no permanent water source. This suggests a high level of adaptation to dry and hot conditions, accompanied by morning condensation (dew) during some parts of the year (at least in Djibouti; A. Laurent pers. obs.).

Morning feeding is followed by a period of rest and rumination in the middle of the day (Laurent *et al.* 2001), the duration of which increases with temperature (Giotto 2004, Giotto *et al.* 2008). Resting sites are generally under the shade of trees, mostly *Acacia etbaica*, but when mid-day temperature exceed 38°C, Beira often rest in the shade of rock shelters (N. Giotto pers. obs.). According to Prévot (1993) and Laurent *et al.* (2001), those sites are often located at the top of the slopes close to the summits, above fallen rocky areas with views over the valleys (Prévot 1993, Laurent *et al.* 2001). As with the Klipspringer, the choice of these upper zones is likely linked to vigilance. On the other hand, during the study conducted by Giotto *et al.* (2008), the observed daytime resting sites were very rarely located on the top of slopes, but rather in rocky areas on the middle or even on the bottom of hillsides. Thus, the many resting sites observed on the top of hillsides might be used during night-time when temperatures are cooler (J.-F. Gerard pers. comm.). A

second feeding period takes place in the afternoon, and lasts until sunset (Giotto 2004, Giotto *et al.* 2008). Whether Beiras also feed at night is unknown, but it seems likely in the hot season at least, as the mid-day resting period can last for more than seven consecutive hours, leaving limited time for daytime foraging (Giotto 2004). As a non-negligible part of the incoming water seems to come from the food plants, length of time spent foraging might correlate with the hydration level of food plants (A. Laurent pers. obs.).

Foraging and Food Based on direct observations and enquiries among herders in Djibouti, the plants eaten by Beiras are rather similar to those eaten by goats (Laurent *et al.* 2001, Giotto *et al.* 2008). Indeed, the diets of both species include the leaves of *Acacia etbaica* as a major component (N. Giotto pers. obs.). Nevertheless, analysis of faeces reveals that species like *Aizoon canariense* and *Croton somalense*, which are largely consumed by goats, are not as preferred as other less abundant species such as *Solanum adoens*, *Cordia* spp. and *Hibiscus* spp. (N. Giotto pers. obs.). Accordingly, Beira seem to be strict browsers, eating almost exclusively the leaves of woody plants and forbs.

Social and Reproductive Behaviour The most common grouping includes a single ♂ and one to several adult ♀♀ with or without young (Kingdon 1997, Laurent *et al.* 2001, Giotto *et al.* 2008, Giotto & Gerard 2010). Solitary ♂♂ and ♀♀ are also observed, as well as unisex groups of 2–4 ♀♀ (Giotto 2004). Single-sex groups of ♂♂ have never been recorded. A group of six individuals including two ♂♂ has been observed in one instance, but as one of them was smaller and had shorter horns than the other (about half the size), he was probably the young of one of the adult ♀♀ of the group (N. Giotto pers. obs.). Mixed-sex groups of 12 individuals including two ♂♂ have been reported (Walther 1990), although these are likely to be temporal associations. In a study conducted in S Djibouti, group size never exceeded five individuals, and mean group size was 2.7 (n = 56 sightings). Solitary animals comprised 26.7% of sightings, of which 50% were ♀♀, 43.8% were ♂♂ and 6.2% were young. Among groups observed, 25% were female groups and 72.7% were mixed-sex groups of 2–5 individuals, none including more than one adult ♂ (Giotto 2004, Giotto *et al.* 2008, Giotto & Gerard 2010). A pair with three apparent offspring has been observed, although this interesting social grouping has not been explained (Prévot 1993). This particular group composition could be indicative of some group instability, as on one occasion a ♀ was seen to leave the group for an entire day despite having dependent young (Giotto 2004). Within a group, individuals remain in close proximity, the distance between them rarely exceeding 10 m (N. Giotto pers. obs.).

Beiras are sedentary (Prévot 1993, Laurent *et al.* 2001, Giotto & Gerard 2010, J. Roche pers. comm.), with groups regularly seen in the same areas for several months and at different periods of the year (Prévot 1993, Künzel *et al.* 2000, Giotto 2004, Moustapha Elmi pers. comm.). The presence of domestic cattle has been identified as a primary cause of daily movements (Prévot 1993, A. Laurent pers. obs.), although even when domestic livestock were present in the same areas as Beiras the area of movement covered during a period of about 9 hours (n = 8) never exceeded 15 ha, and mean size was

4.0 ha (Giotto 2004). The small distance covered when fleeing is probably due to the topography of the area, as the animals only have to pass a high point to be out of sight of the source of disturbance.

Dunging ceremonies have been recorded in the Beira (Laurent *et al.* 2001, Giotto 2004, Giotto *et al.* 2008, Mallon & Jama 2012), and comprise scratching the soil and urinating and/or defecating, and displaying in turn by members of a group at the same place. Either ♂♂ or ♀♀ may initiate this activity, which lasts from 5 to 20 min. Laurent *et al.* (2001) observed a group of five animals involved in a dunging ceremony that was initiated and carried out vigorously by the ♂, followed by a ♀, then a mother and her offspring, and finally by the last ♀ of the group. In a study conducted on the same site in spring 2004, N. Giotto (pers. obs.) observed ♀♀ initiating these dunging ceremonies, with ♂♂ then following them and urinating and/or defecating in the same places.

An observation of one ♂ chasing another before rejoining the group of ♀♀ he was attending suggests that adult ♂♂ do not tolerate the presence of other ♂♂ (Giotto *et al.* 2008, Giotto & Gerard 2010). Such behaviour reinforces the proposals of Prévot (1993) and Laurent *et al.* (2001) that ♂♂ are territorial. Indeed, in a 10-month study in Djibouti, Beira were found to live in relatively stable socio-spatial units whose ranges were almost non-overlapping (mean home-range was about 0.7 km²) (Giotto & Gerard 2010). However, there is no evidence that the dunging behaviour described above has a territorial marking function (Giotto & Gerard 2010).

When alarmed, Beiras utter a whistling alarm call and adopt an alert posture, remaining motionless with head up and ears oriented toward the source of potential danger, sometimes maintaining this posture for more than an hour (A. Laurent pers. obs.) until they flee trotting, galloping or jumping, or until the source of disturbance disappears. Laurent *et al.* (2001) suggest that the ♂ occupies a special (dominant?) position in the group, as he guides the group's escape, takes up guard and leads movements. However, Giotto (2004) observed that ♂♂ were not always the leaders of fleeing groups, and that ♀♀ were also (and seemed to be even more often) involved in vigilance activity, and often initiated movements of groups engaged in foraging.

There are limited data on reproductive behaviour. During courtship the ♂ sniffs the vulva of the ♀, performs flehmen and taps the female's hindlegs or the ground with his forelegs (laufschiag). The ♂ may approach bipedally and mounts with head up, without resting upon the ♀, while the ♀ carries head and neck raised when mounted (N. Giotto pers. obs.). For the first few weeks of life young remain motionless in hiding places where they are difficult to see (Laurent *et al.* 2001).

Reproduction and Population Structure Births are known to occur in spring (Mar and Apr). However, spring is also the mating season, as copulations have been recorded at the end of Mar and in May (Giotto *et al.* 2008), suggesting a second birth season in autumn. A single young is born, following a gestation period estimated at about six months (Hammer & Hammer 2005, Hammer 2011). During the study conducted in SDjibouti, the observed sex ratio was biased toward ♀♀ and was found to be 1 : 2.5 (N. Giotto pers. obs.).

Predators, Parasites and Diseases Carnivores known to be present in S Djibouti include the Caracal *Caracal caracal* and the Leopard *Panthera pardus*, both of which are potential predators of Beiras. Spotted Hyaenas *Crocuta crocuta* and Striped Hyaenas *Hyaena hyaena* are also present, but seem less likely predators (Laurent & Laurent 2002, Giotto 2004). Hamadryas Baboons *Papio hamadryas*, as well as Verreaux's Eagle *Aquila verreauxii* and Bonelli's Eagle *Hieraaetus fasciatus* may take young animals (Giotto 2004, Giotto *et al.* 2008). There is no information available about parasites and diseases.

Conservation IUCN Category: Vulnerable C1. CITES: Not listed.

In Djibouti, Beiras are restricted to a limited area and likely decreasing in number due to desertification by overgrazing and disturbance from an incoming population of refugees (Giotto *et al.* 2009). In Somalia, animals underwent a marked decline in number during the 1975 drought (Simonetta 1988), and may have suffered due to uncontrolled hunting and habitat deterioration caused by overpopulation of livestock (Moustapha Elmi 1992, East 1999), but there is limited recent information.

There have been several proposals to help ensure the future prospects for Beira in Djibouti (Laurent 1993, Künzel *et al.* 2000). The classification of a limited area (the Assamo region) as a Community Protection Area has been proposed by local people and a pilot *in situ* conservation project, based on income from tourism and familial socio-economic activities, such as handicraft and agro-alimentary production, is in preparation with local NGOs (Association de Développement Durable Local Aser-Jog and DECouvrire et Aider la Nature). Due to a long-lasting partnership with the international network T2D2 (Tourismes, Territoires et Développement Durable), the patrimonial value of Beiras, a species whose presence was unconfirmed a little more than two decades ago, is now increasingly being recognized and offers much potential for future conservation efforts in the region.

There is a captive self-sustaining population of about 40 Beira at Al Wabra Wildlife Preservation/Sheikh Saoud Mohammed Bin Ali Al-Thani in Qatar (Heckel & Rayaleh 2008, Hammer 2011).

Measurements

Dorcatragus megalotis

HB: 760–870 mm

T: 50–80 mm

WT: 9.0–12.0 kg

Throughout geographic range (Kingdon 1997)

Maximum recorded horn length is 13.9 cm for a pair of horns from Somalia (Rowland Ward)

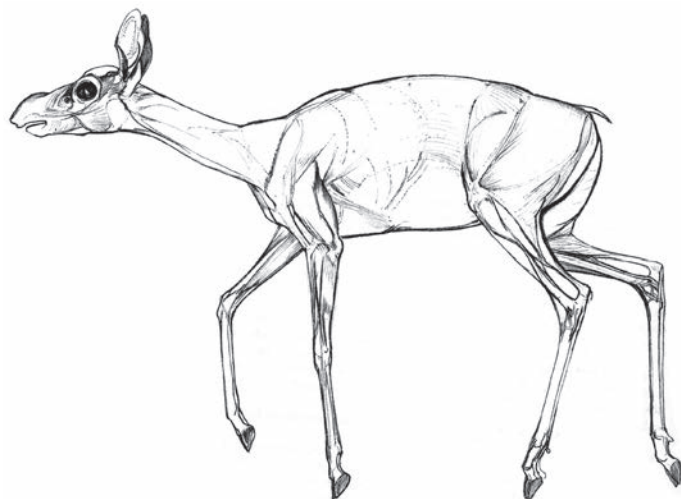
Key References Giotto 2004; Giotto *et al.* 2008, 2009; Giotto & Gerard 2010; Künzel & Künzel 1998; Künzel *et al.* 2000; Laurent 1993; Laurent *et al.* 2001; Prévot 1993.

Nina Giotto, Alain Laurent & Thomas Künzel

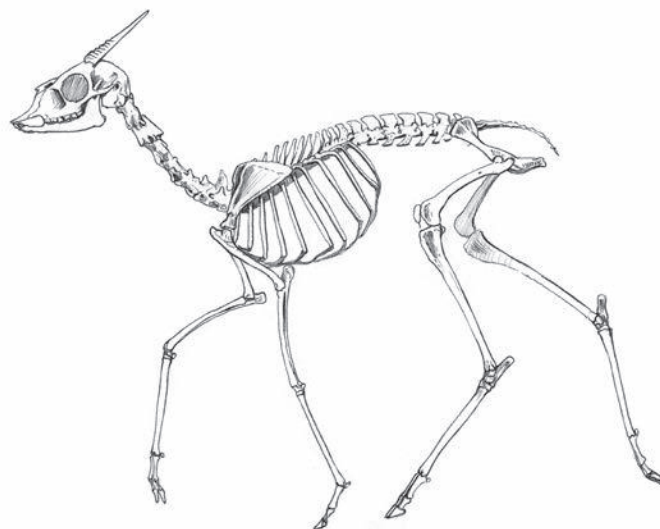
Tribe MADOQUINI

Dik-diks

Madoquini Pocock, 1910. Proc. Zool. Soc. Lond. 1910: 876.



ABOVE: Günther's Dik-dik *Madoqua guentheri* myology.

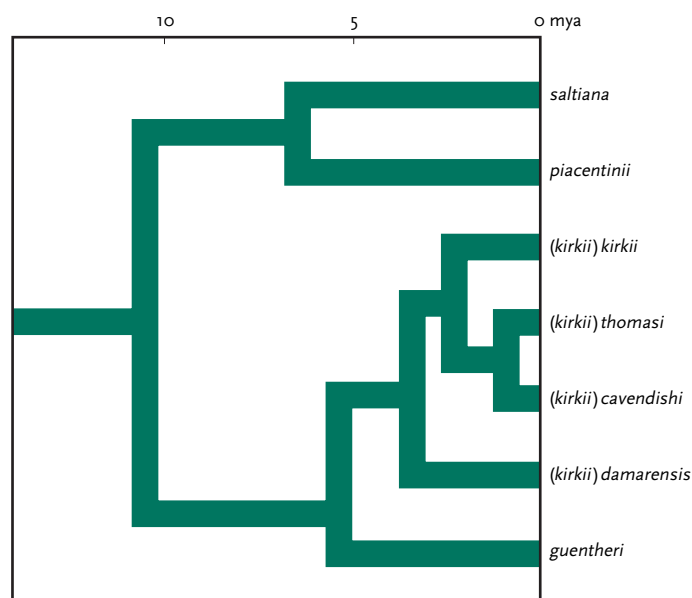


RIGHT: Salt's Dik-dik *Madoqua saltiana* skeleton.

The arid-adapted dik-diks are very small, long-legged antelopes with fine, grizzled (sometimes colourful) pelages. They have relatively large eyes and ears, a prominent crest and a fur-covered nose that is enlarged into a very flexible proboscis that is especially long in Günther's Dik-dik *Madoqua guentheri* and the dik-diks of the *M. (kirkii)* complex. The dik-diks have traditionally been included along with other dwarf antelopes in the tribe Neotragini (e.g. Grubb 2005), but with increasing evidence of paraphyly of this taxon (Georgiadis *et al.* 1990, Gentry 1992, Matthee & Robinson 1999a), it has been necessary to disaggregate its members and to resurrect the tribe Madoquini for the dik-diks.

In most arid habitats there is so little food in the dry season that it is only possible for a very small ruminant to live within a limited area all year round. Permanent residence in sub-desert means having to do without water yet needing to keep cool. This is problematic because the large surface area of a small animal relative to its weight heats up fast. Dik-diks minimize heat production and reduce water-loss by means of inconspicuous adaptations in the water economy of their kidneys and digestive tracts and in subtle adjustments of their activity cycles, but the specialized nose is probably their major cooling device.

Proboscides are visible signs of a technique of temperature control that is more highly developed in dik-diks than in any other African antelope. The proboscis is lined with numerous blood vessels in the mucous membrane where the blood can be cooled by evaporation off the inner lining of the nose, a method of cooling that is very economical with water, a precious commodity in arid areas. These surface blood vessels are cooled by increasing the normal breathing rate from one to nearly eight breaths per second (Schoen 1972, Hoppe 1977a, Frey & Hofmann 1996). The cooled blood returns to the heart via a sinus below the brain, where hot blood going to the brain is cooled in a heat exchanger (rete mirabile) (Baker & Hayward 1968). This very selective cooling allows general body temperatures to rise without risking brain function. The nose of each species shows a different degree of elaboration, implying different levels of efficiency in



Tentative phylogenetic tree for *Madoqua* radiation (adapted from Hernández Fernández & Vrba 2005).

temperature control and, perhaps, in water economy. This adaption seems to be the outcome of prolonged and progressive specialization in a faculty that is of great utility in the arid Horn of Africa.

It is significant that north-east Africa has been home to the greatest variety of heat-tolerant antelopes and that some of them, most notably the dik-diks, belong to basal groups. The concentration of antelopes in this region further implies that it is, or is very close to, the geographic centre of origin for Antilopinae as a whole. In this perspective, Madoquini can be seen as one of the earliest lineages of conservative antelopes to refine and benefit from the heat tolerance and water economy that first defined and separated the Antilopinae from the Bovinae (which have remained predominantly Asian).

Dik-dik fossils are only known from some 7–4 mya, but the lineage has been estimated (by molecular clock techniques) to have emerged some 20–18 mya (Hernández Fernández & Vrba 2005), almost certainly in the Horn of Africa. The distribution and physio-morphology of living forms is some guide to the progress of evolution. Thus, the most conservative, least specialized forms, namely Salt's Dik-dik *M. saltiana* and Silver Dik-dik *M. piacentinii*, remain confined to evergreen thickets that fringe the Ethiopian plateaux and the Somali coast. The most advanced and most heat-tolerant species, Günther's Dik-dik, lives in the driest deserts and sub-deserts of the region while intermediate types, of the *Madoqua* (*kirkii*) complex, occupy a much broader range of habitats. Essentially, these antelopes are endemic to the Horn of Africa, with a single outlying and isolated population in south-west Africa. An arid corridor has clearly connected the two regions many times in the past, as is clear from other species (e.g. *Oryx*) with similar patterns of distribution.

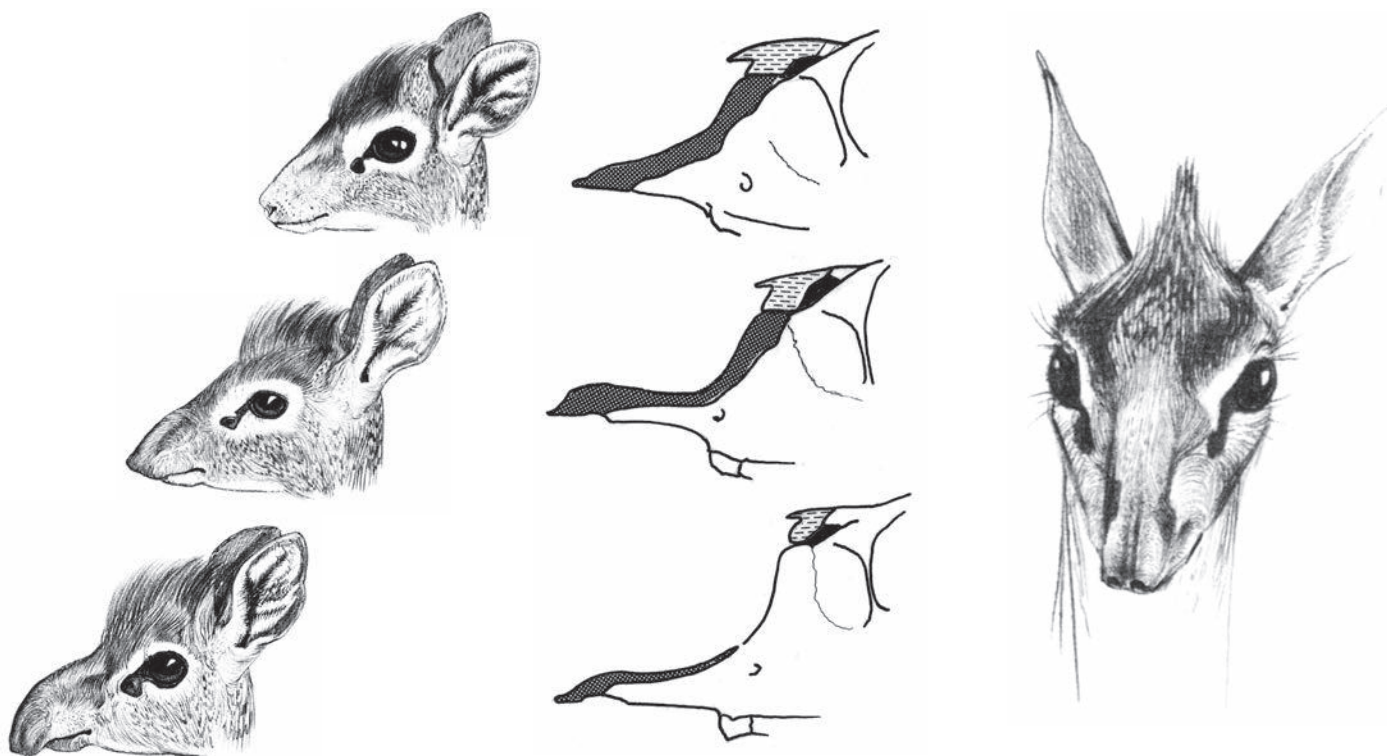
The more primitive species minimize the effects of high temperatures by being largely nocturnal (Simonetta 1966). The long-nosed Günther's Dik-dik, with the greatest tolerance of heat, is more diurnal. All species depend on low-level thickets and succulents growing on well-drained soils where there is little grass growth. Dung, urine and face-gland deposits are the boundaries, landmarks and focal centres of social life: the preorbital glands, especially in males, can be so large that they rival the eyes and lie in comparably sized 'sockets'. Males are the principal markers and defenders of territories but their movements are entirely subordinate to those of the ♀♀ – in a real sense *he* marks *her* territory. Both sexes make breathy shrieks through a specially modified nasal whistle. Whistle-like calls are characteristic of many antelopes and distinguish them from Bovinae. Dik-diks have refined the acoustic properties of their calls, an aspect of social communication that awaits further research. The name dik-dik is an onomatopoeic rendering of one of their calls.

Jonathan Kingdon

GENUS *Madoqua*

Dik-diks

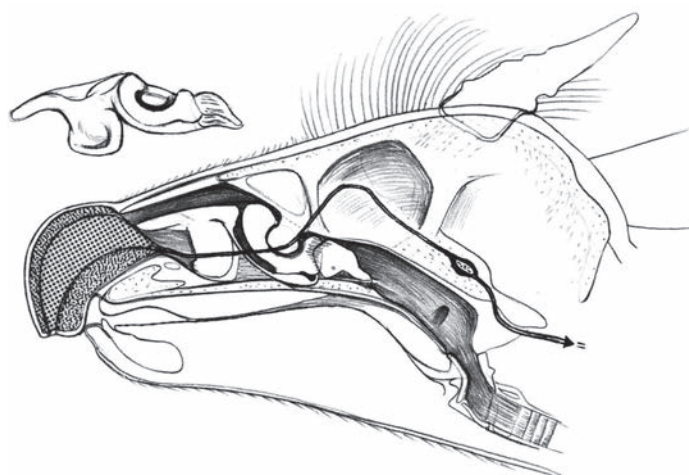
Madoqua Ogilby, 1837. Proc. Zool. Soc. Lond. 1836: 137 [1837].



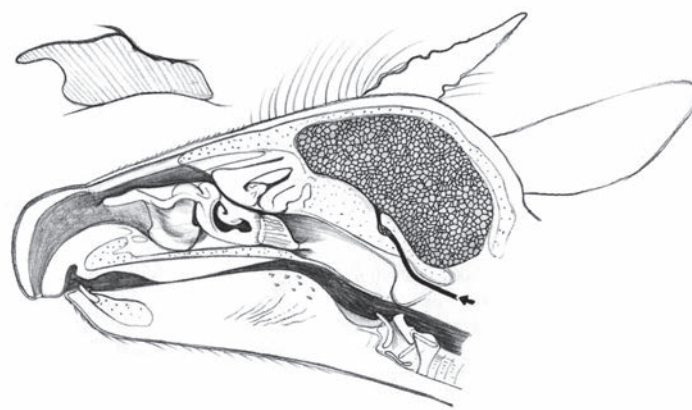
LEFT: Salt's Dik-dik *Madoqua saltiana* (top). Kirk's Dik-dik *M. (kirkii)* complex (centre). Günther's Dik-dik *M. guentheri* (below).
 CENTRE: Diagram of nasals and premaxilla in Salt's Dik-dik *Madoqua saltiana* (top). Kirk's Dik-dik *M. (kirkii)* complex (centre).
 Günther's Dik-dik *M. guentheri* (below).
 RIGHT: Naivasha Dik-dik *M. (kirkii) cavendishi* female.

This genus was formerly subdivided between two genera, *Rhynchotragus* for the 'Long-snouted Dik-diks', namely Günther's Dik-dik *M. guentheri* and the dik-diks of the *M. (kirkii)* complex, and *Madoqua* for the 'Short-snouted Dik-diks', Salt's Dik-dik *M. saltiana* and Silver Dik-

dik *M. piacentinii*. *Madoqua* have longer premaxillae, longer nasal bones and a less prominent nasal notch than *Rhynchotragus*. Given the homogeneity of this group, a single genus comprising two subgenera seems appropriate, but should it be shown that separation between



Cross-section of Günther's Dik-dik *M. guentheri* head. Shows vestibule of nose served by blood vessels in the mucous membranes. Venous blood returns via cavernous sinus below brain. Whistle-like maxilla turbinal shown *in situ* and above, left. Glottal region shown in breathing position.



Cross-section of Günther's Dik-dik *M. guentheri* head. Arterial blood to brain passes through a rete mirabile in cavernous sinus below brain. Inner surface of right maxilloturbinal is shown *in situ*. Oesophagus illustrated with epiglottis closed.

the two groups is of very long standing, the resuscitation of two genera might be justified.

Likewise, regional populations of Salt's Dik-diks have differentiated into ten forms, which were formerly grouped under five species (Allen 1939). The nomenclature of this group was revised and simplified by Yalden (1978) and this work provisionally follows his inclusion of all these forms as subspecies of Salt's Dik-dik (and see Grubb 2005). None the less, further molecular analysis of this complex of dik-diks could justify the resurrection of some species within Salt's Dik-dik as well as the two genera.

The dik-diks represent a distinctive gradient in the adaptation of a very small antelope to heat and desiccation. The most obvious external sign of this adaptation is modification of the nose into a flexible, bellows-like mechanism for cooling the blood. The workings of this adaptation have been summarized in the tribe profile above and in more detail in the profiles of Günther's Dik-dik and the Kirk's Dik-dik complex (and see Frey & Hofmann 1996). Paradoxically, the less specialized Salt's Dik-dik occupies some very arid parts of the dik-diks' overall range. This species avoids excessive overheating by lying up in the shade during the day and restricting most of its activity to the night-time (Simonetta 1966). This escape from diurnal heat is facilitated by preference for evergreen *Salvadora* scrub, which is characteristic of the eastern foothills of the Ethiopian massif. Thus, restriction to the Horn of Africa may have much to do with a long-standing dependence on evergreen growth for food and shelter.

While the Long-snouted Dik-diks have much in common with Salt's Dik-diks and Silver Dik-diks, and clearly derive from a similar shorter-snouted ancestral stock, they live in more exposed situations. The beginnings of their adaptation to such exposure merit speculation. An early dik-dik population living south of the Ethiopian dome (or, perhaps in Somalia) during periods of aridification would have faced the twin challenges of scarcer food and less shelter. This could have forced these animals into longer activity periods and further development of the nasal cooling chamber to enhance their capacity to withstand heat. Once emancipated in this way, a southern population could have responded to every dry phase of every past climatic fluctuation, each of which would have opened up

very extensive areas of suitable habitat to dik-diks in eastern Africa (and sometimes beyond). Parts of the L. Turkana basin and areas to the south-east have probably remained relatively arid since the mid-Miocene and this arid focus, decisively separate from the Ethiopian dome, must have become the most consistent home of the long-snouted lineage.

The most highly specialized of them all is Günther's Dik-dik and, appropriately, this species inhabits the driest and most exposed of all dik-dik habitats. It is obvious that Günther's Dik-dik derives from a form that was more advanced than Salt's Dik-dik, so it has to be significant that the dik-diks belonging to the *M. (kirkii)* complex are, indeed, intermediate between Salt's and Günther's (though much closer to the latter).

The likely sequence of evolutionary events that followed has been outlined in Kingdon (1982). During a period in which arid habitats were very extensive (possibly during the Messinian, 6.5–5.3 mya), 'Long-snouted Dik-diks' spread as far as south-western Africa along the Somali–Namib corridor. The modern survivor of this expansion is the Damara Dik-dik *M. (k.) damarensis*, which has genetic similarities with Günther's Dik-dik. A warmer, moister period (perhaps the mid-Pliocene?) then separated the 'Long-snouted Dik-diks' into two populations: ancestral *guentheri* in the east, ancestral *damarensis* in the south-west. A subsequent re-opening of the Somali–Namib corridor (possibly during the first Glacial, 3–2.5 mya) allowed proto-*damarensis* to expand northwards and colonize a band of less extreme habitats surrounding the arid core around L. Turkana. The arrival, from the far south-west, of a competitor presumably exerted strong selection on Günther's Dik-dik to become even more arid-adapted and probably led to some contraction of range back towards the arid core. Because the invading population tolerated a broader range of habitats it spread widely but soon became subject to the climatic vicissitudes of the late Pliocene and Pleistocene. These oscillations probably led to the genetic isolation that has culminated in the three East African species of the *Madoqua (kirkii)* complex.

While there is insignificant overlap between the dik-diks of the *Madoqua (kirkii)* complex and Salt's Dik-dik, the interaction with Günther's Dik-dik is more complex, interesting and still very poorly

understood. There is a narrow belt over 1000 km long where the margins of the L. Turkana basin and the Somali interior meet the moister habitats fringing the Kenya highlands and the coastal strip. North of the Tana R., *M. (kirkii) kirkii* does not extend beyond the isohyet for 50 cm mean annual rainfall (or the boundary between savanna and dry bushland). Along this interface, the two species meet and in places co-exist side-by-side without any interbreeding (Hollister 1924, Hofmann 1973). However, skins and skulls from localities as far apart as the Shebelle R. (Somalia), south Turkana and the Kenya–Uganda border display intermediate or mixed characteristics, suggesting that hybridization may be persistent and widespread. More problematically, strongly reduced premaxillae in some *M. (k.) kirkii* specimens (notably from Tsavo and Manda I.) imply either convergence or past mixing between the two species. For observers inspecting individual dik-diks in these areas of overlap the possible presence of hybrids (albeit presumably infertile ones) needs to be considered.

In spite of such local ambiguities, the primary effect of the radiation of dik-dik species has been to increase the overall ecological range and diversify the responses of a very small ruminant to exceptionally difficult conditions. The main mechanism in achieving this has been the separation of subpopulations in geographically and ecologically distinct areas, demarcated by moist forested rivers valleys and mountain slopes, and subsequent expansions and contractions under the influence of many oscillations in climate.

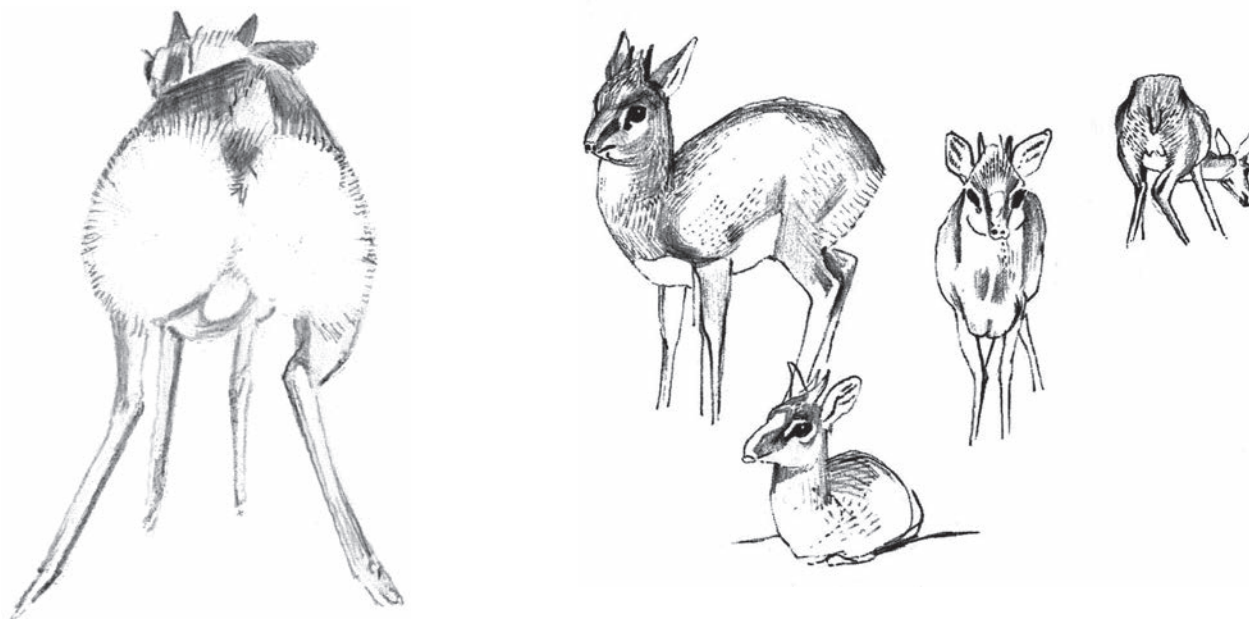
Dik-diks are widespread throughout arid north-eastern Africa and they are particularly common in some localities. Their success is due to a variety of physiological specializations, which are discussed in further detail in the sections on Adaptations in both the *M. guentheri* and *M. (kirkii)* complex species profiles. Among the many

morphological changes that have taken place in the nasal area of dik-diks is a remarkable modification of the ethmoid turbinal, which seems to have been turned over to function as a whistle. Drawings (above, from Kingdon 1982) illustrate the position and shape of this whistle within the nasal area and these cross-sections also illustrate how the aforementioned ‘nasal bellows’ cooling mechanism works.

The colouring of dik-diks is interesting, exemplifying complex interplays between crypsis (directed at predators) and conspicuousness (directed at conspecifics). The eye margins, ears, belly and buttocks have white or very pale fur in all species and the last is an important signalling device. The long hair of the buttocks is capable of being opened out into two circular flares, a display that seems to advertise oestrus but may also signify subordination. In most species the overall colouration is subdued and subservient to the overall cryptic effect. Legs and crest are plainer and warmer in colour while rump and neck tend to have a cooler, greyish, grizzle. This distribution of warmer and cooler tints is common to all dik-diks but finds its most exaggerated contrasts in *M. saltiana lawrancei*. It correlates with crouching or head-down creeping by an appeasing subordinate and a head-up, fluffed-crest, high-stepping strut by dominant individuals, notably territorial ♂♂. The latter shows off warm orange tints while the subordinate postures flatten the orange crest and present predominantly grey areas to view. The pelage therefore represents a sort of intra-specific, status-linked colour-code, half concealed under a coat of camouflage.

The long-term future of dik-dik species will largely depend on what sort of policies emerge from the present era of conflict in the Horn of Africa.

Jonathan Kingdon

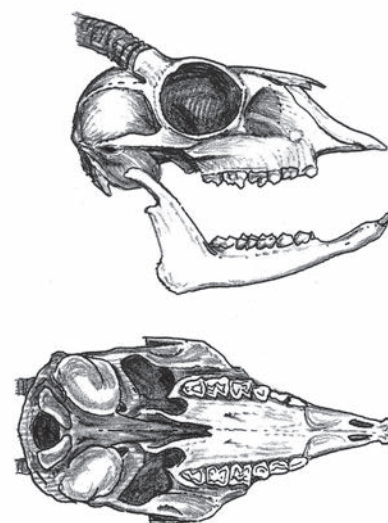


LEFT: Flaring of white rump fur in male Günther's Dik-dik *Madoqua guentheri*.
ABOVE: Naivasha Dik-dik *Madoqua (kirkii) cavendishi*.

Madoqua saltiana SALT'S DIK-DIK

Fr. Dik-dik de Salt; Ger. Eritrea-Dikdik

Madoqua saltiana (de Blainville, 1816). Bull. Sci. Soc. Philom. Paris 1816: 79. 'Abyssinie' (Ethiopia). The author of the name is usually cited as Desmarest, 1816 (Nouv. Dict. Nat., Nouv. ed., 2: 192), who acknowledged de Blainville's paper and cited the page number where *saltiana* was named, confirming that de Blainville is, in fact, the author (Grubb 2005).



LEFT: Salt's Dik-dik *Madoqua saltiana phillipsi*.
ABOVE: Lateral and palatal views of skull of Salt's Dik-dik *Madoqua saltiana*.

The species is named for Sir Henry Salt, who in 1809 was tasked with establishing contact with the King of Abyssinia on behalf of the British Government.

Taxonomy Although Yalden (1978) included the forms *phillipsi* and *swaynei* as subspecies of *saltiana* (the arrangement followed here), the relationships of these two forms to *saltiana* are uncertain, and they have been treated as distinct species (e.g. Ansell 1972). Yalden (1978) argued that there was a series of geographically allopatric subspecies, with some clinal variation in size and colour. Synonyms: *citernii*, *cordeauxi*, *erlangeri*, *gubanensis*, *hararensis*, *hemprichiana*, *hemprichii*, *lawrancei*, *madoka*, *madoqua*, *phillipsi*, *swaynei*. Chromosome number: not known.

Description A small, dainty antelope showing modest sexual dimorphism, with ♀ slightly larger than ♂. The nominate *saltiana* has dorsal pelage grizzled greyish-brown, shading into pale sandy-orange, plain (ungrizzled) legs. Ventral pelage is white, with a sharp demarcation line from the dorsal colour. The top of the head has a short, reddish-brown erectile crest. Snout enlarged into a slight proboscis, though not so much as in, for example, Günther's Dik-dik *M. guentheri*. Face and neck paler and greyer than trunk. Conspicuous, black preorbital gland, set off by a white ring around the eye. Ears large, white internally, but a greyish grizzled colour posteriorly. Tail short and inconspicuous, white, in a white peri-anal region. Females have two pairs of inguinal nipples.

Horns are present in ♂ only; black, essentially straight, short and barely project above the ears or crest (when erected). Like the Silver Dik-dik *M. piacentinii*, the M₃ lacks the third (posterior) lobe, and the upper line of the premaxillae is slanting and not strongly curved.

Geographic Variation

M. s. saltiana: Sudan, Eritrea, Djibouti, Afar triangle. As above, larger than forms further south.

M. s. phillipsi: N Somalia. Dorsal surface paler, greyer (brown tinges absent); pale orange of forelegs extending into flares over shoulders.

M. s. hararensis: N Somalia, south from mountains through Ogaden region of Ethiopia, to the Shebelle R. Both grizzled dorsal colour and flares reddish-brown, giving overall chestnut appearance.

M. s. lawrancei: coastal Somalia. Silver-grey grizzled dorsal colour, contrasting sharply with the deep reddish-brown legs, flanks and shoulders.

M. s. swaynei (includes *citernii*): S Ethiopia, S Somalia, from the Shebelle R. to Juba/Dawa Rivers. Colour as for nominate form.

Similar Species

Madoqua piacentinii. Sympatric with *M. s. lawrancei* in coastal Somalia, and with *M. s. hararensis* in well-vegetated lowland areas of the Shebelle R. in the Ogaden. Smaller, both in body mass and mean length of maxillary tooththrow (P²–M³, 25.7–31.5 mm cf. 28.2–36.8 mm in *saltiana*); uniformly speckled silver-grey dorsally (lacks the red-brown shoulder flares of *lawrancei*).

M. guentheri. Sympatric in Somalia and Ethiopia. Characterized by enlarged and elongated proboscis.

Distribution Endemic to the Horn of Africa. Marginal occurrence in NE Sudan, along the Eritrean border, southwards along the coastal plain of Eritrea into the northern and eastern lowlands of Ethiopia, Djibouti and Somalia, extending southwards round the Ethiopian



mountains possibly just into the border region of Kenya (Mandera district) and southwards to the Juba valley, Somalia (Yalden 1978, Kingdon 1982, Yalden *et al.* 1984, East 1999, Künzel *et al.* 2000).

Habitat Typically found in semi-desert scrub, and usually associated with *Aloe* and *Sanseveria*; probably avoids true desert, and limited in range by the mountains of Ethiopia. Ingersol (1968) remarks that they are usually found in valley bottoms and hillsides, whereas sympatric Günther's Dik-diks are only found on drier, scrub-covered hillsides. Common from sea level to 1500 m, but perhaps as high as 2000 m (Yalden *et al.* 1984, Künzel *et al.* 2000). A. Simonetta (pers. comm.) remarks that in Somalia there are distinct differences in habitat usage, with Günther's Dik-diks confined to thick bush, whereas *M. s. lawrancei* is found in open conditions, even sub-desert, wherever there are scattered thickets.

Abundance A common antelope where it occurs, although there are few detailed studies. Künzel *et al.* (2000) counted only 73 during recent survey work in Djibouti, far fewer than the 600 Pelzel's Gazelles *Gazella dorcas pelzeni* or 190 Soemmerring's Gazelles *Nanger soemmerringi* seen, and estimate a density of only 0.04/km². Laurent & Laurent (2002) confirm that although Salt's Dik-diks are still widespread throughout Djibouti, they have declined over the last 20 years. On the Haud plateau in N Somalia, P. Moehlman (pers. comm.) saw 41 individuals while driving 72 km in April 1997, compared with only three grey dik-diks (presumably Günther's), yielding a density of 11.6/km² in N Somalia, perhaps an overestimate (East 1999). Road counts also gave an estimate of 1.8/km² in the Ogaden of Ethiopia, perhaps an underestimate (Wilhelmi 1997). A three-year study in Awash N. P., Ethiopia, using monthly road surveys, gave a density of 14.1/km² (ranging from 13.3 to 15.3/km² across three different routes) (M. Jacobs & C. Schloeder pers. comm.). Using a modest density of 2/km² across a putative range of 242,800 km², East (1999) estimated the total population as at least 485,600 individuals.

Adaptations Colouration serves as good camouflage, emphasized by the animal lying prostrate in shade when not active. It is probable that variation in colour between subspecies is at least in part matched to soil colour locally. The proboscis/nasal cavity is believed to serve a thermoregulatory function and to assist in water conservation. Salt's Dik-diks are thought not to drink, relying entirely on water in dew and food; indeed, a captive animal deprived of food took only small amounts of water (Simonetta 1966). Their kidneys are extremely efficient in retaining water, and their faeces are very dry and urine highly concentrated. Salt's Dik-diks are mainly nocturnal and crepuscular, lying up in shade during the day, and during the mid-day heat they pant with their mouth partly open and tongue slightly protruding (Simonetta 1966, Kingdon 1997).

Foraging and Food There are no detailed studies on feeding, but Salt's Dik-diks are selective browsers. In Awash N. P., they have been reported browsing on *Acacia* shrubs (leaves), fruits of *Grewia tenax* and *Cordia gharaf*, *Lantana viburnoides*, *Seddera bagshewai* and *S. arabica*, shrubby herbs *Abutilon*, *Hibiscus micranthus*, *Melhanian ovata*, *Sida ovata*, *Plecanthus*, *Vernonia cinerescens* and *Pavonia propinqua*, the herbs *Corchorus*, *Blepharis edulis*, *Achyranthus aspera*, *Justicia* and various Labiatae, and monocots such as *Cyperus*, *Tetropogon* and *Sporobolus* (M. Jacobs & C. Schloeder pers. comm.). It is not known how their diet differs from the sympatric Günther's Dik-dik in the south of their range, or from the Silver Dik-dik *M. piacentinii* in coastal Somalia.

Social and Reproductive Behaviour Salt's Dik-diks are territorial, and usually seen in pairs or family groups of a pair with 1–2 young. Künzel *et al.* (2000) recorded 34 groups, ranging from 1 to 6 (mean = 2). Simonetta (1966) described the formation of territories in captivity, with young ♂♂ displacing their fathers; in the wild, it is assumed that young would be displaced from the parental territory. Territories are marked by means of urine over-marking and dung piles, including over-marking the dung of other species. Females and subordinate ♂♂ place the deposit from their preorbital gland on the tip of the dominant male's horns, presumably as a form of submission. Males erect their crest as a threat display to subordinates. In courtship and threat, ♂♂ may use a high-strutting gait that emphasizes the paler colours of the legs and shoulder flares. The white rump is flared by the ♀ in oestrus, and may also be used as a warning 'flag', but the usual warning is a double 'whistle' that is responsible for the onomatopoeic name dik-dik.

Reproduction and Population Structure The very limited observations available suggest that there is usually only one young per litter, despite the presence of four teats in the ♀. M. Jacobs & C. Schloeder (pers. comm.) report only 0.2% juveniles and 3.5% subadults during surveys in Awash N. P.; the sex ratio of adults was equal.

Predators, Parasites and Diseases Salt's Dik-diks are probably vulnerable to predation from most large predators, including jackals *Canis* spp., Caracals *Caracal caracal*, Servals *Leptailurus serval*, Leopards *Panthera pardus* and larger eagles. Predation by adult male Olive Baboons *Papio anubis* and Olive-Sacred baboon hybrids *P. anubis* × *P. hamadryas* on young was witnessed in Awash N. P. (M. Jacobs & C. Schloeder pers. comm.). There is no information available on parasites or diseases.

Conservation IUCN Category: Least Concern. CITES: Not listed.

Salt's Dik-diks are vulnerable to overhunting and to habitat loss/degradation, especially through overgrazing or irrigation and agriculture. For example, Laurent & Laurent (2002) remark on declines evident in Djibouti due to overgrazing in some areas and overhunting in others (although the latter is now banned). Simonetta (1988) remarks that in Somalia dik-diks are rarely shot, are usually hunted in nets and that they have become scarce near human habitation. Although there are only a few protected areas within their range (such as Awash N. P. and Yangudi Rassa N. P. and several wildlife reserves), they remain widespread throughout, and are considered to be in a satisfactory conservation status (East 1999).

Measurements

Madoqua saltiana hararensis

HB (♂ ♂): 510 (495–517) mm, n = 9

HB (♀ ♀): 509 (479–550) mm, n = 9

T (♂ ♂): 34 (30–38) mm, n = 9

T (♀ ♀): 31 (21–40) mm, n = 9

HF c.u. (♂ ♂): 174 (170–183) mm, n = 9

HF c.u. (♀ ♀): 175 (160–188) mm, n = 9

E (♂ ♂): 65 (61–70) mm, n = 9

E (♀ ♀): 64 (60–70) mm, n = 9

WT: 2.7–4.0 kg

Ethiopia (Ingersol 1968)

Maximum recorded horn length is 11.8 cm for a pair of horns from Sudan (Rowland Ward)

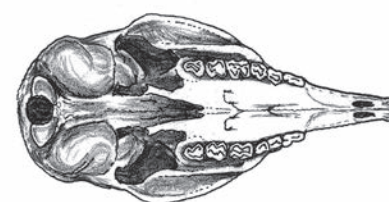
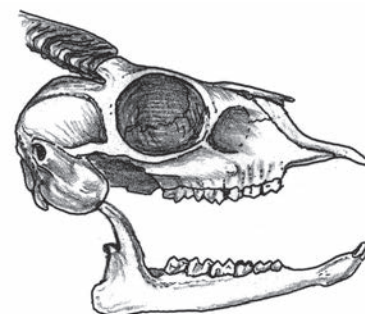
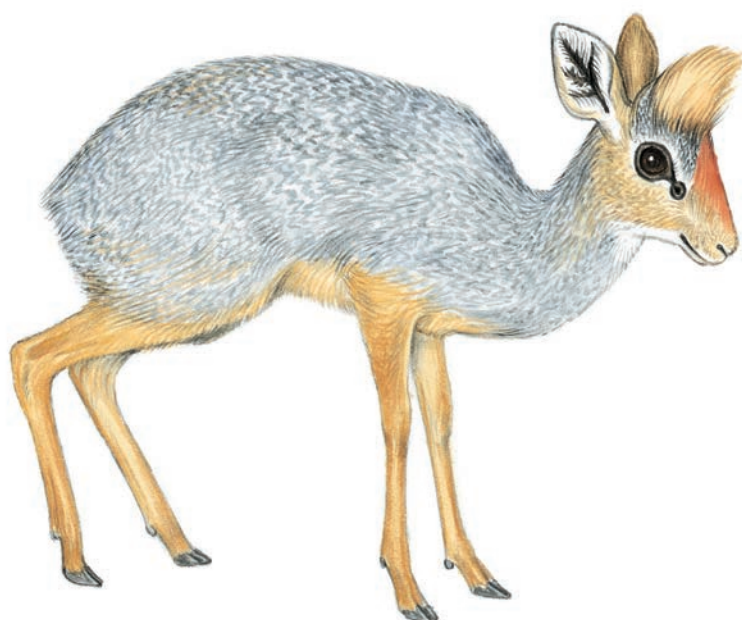
Key References East 1999; Simonetta 1966; Yalden 1978.

Derek W. Yalden

Madoqua piacentinii SILVER DIK-DIK (PIACENTINI'S DIK-DIK)

Fr. Dik-dik argente; Ger. Piacentini Dik-dik

Madoqua piacentinii Drake-Brockman, 1911. Proc. Zool. Soc. Lond. 1911: 981. E Somalia, 'Gharabwein, within a day's march of Obbia [5° 25' N, 48° 25' E], in the Mijertain country, Italian Somaliland'.



LEFT: Silver Dik-dik *Madoqua piacentinii*.

ABOVE: Lateral and palatal views of skull of Silver Dik-dik *Madoqua piacentinii*.

Taxonomy Ansell (1972) considered this species a subspecies of *M. swaynei*. However, Yalden (1978) in his revision of the genus included *swaynei* as a subspecies of Salt's Dik-dik *M. saltiana*, and treated the Silver Dik-dik *M. piacentinii* as a distinct species (and see Funaioli & Simonetta 1966), which is the classification followed by Grubb (2005) and here. Synonyms: none. Chromosome number: not known.

Description A small antelope, statistically the smallest of the genus, although its measurements overlap with those of the other Somali dik-diks (*M. saltiana lawrancei* and *M. s. swaynei*). Uniformly silvery-grey due to fine speckling of the individual hairs, except for a

bright, rust-red, erectile crest and part of the dorsal side of the nose and the equally reddish legs; there is a narrow white ventral stripe. Pelage is fine and soft. Sexual dimorphism is modest, with ♀ slightly larger than ♂. Females have two pairs inguinal nipples. The skull of the Silver Dik-dik is immediately distinguishable from that of the sympatric *M. s. lawrancei* from coastal Somalia in several respects: it is distinctly narrower, especially in the orbital region; the zygomatic arch in the suborbital region is distinctly narrower than in all other dik-diks; and the profile of the suborbital fossa is comparatively narrower and elongated in its antero-posterior axis. Like Salt's Dik-dik, the Silver Dik-dik has the lower M₃ without a third (posterior) lobe.

Geographic Variation None recorded.

Similar Species

Madoqua saltiana. Although possibly ecologically separated, the Silver Dik-dik is sympatric with *M. s. lawrancei* in coastal Somalia, and with *M. s. hararensis* in the Ogaden region of Ethiopia. Larger, both in body size and mean length of maxillary tooththrow (P^2-M^3 , 28.2–36.8 mm cf. 25.7–31.5 mm in *piacentinii*); the reddish colour always extends considerably both on the shoulders and on the sides of the body.

M. guentheri. Sympatric at the limit of the inland distribution of Silver Dik-dik, and also in the lowland areas of the Shebelle R. in the Ogaden where reported in sympatry (Wilhelmi *et al.* 2006). Duller overall colouring, and the proboscis is noticeably enlarged and elongated.

Distribution The Silver Dik-dik is an enigmatic species. It is recorded as occupying the central, coastal plain region of Somalia, where its range apparently does not extend more than 10 km inland (Ansell 1972, Simonetta 1988, East 1999). The species is represented in museums by two series of specimens: one in the British Museum (Natural History Museum) in London, collected by Drake-Brockman at Eil Hur, near Hobyo, and one in the Natural History Museum of Florence (Italy). However, it is not recorded whether the specimens in London were personally collected by Drake-Brockman or whether he obtained them from local hunters. Hobyo itself is a big village in the middle of a low coastal steppe and, at least when visited by the current author in 1982, no dik-diks of any kind were seen, although Speke's Gazelles *Gazella spekei* were quite common in the vicinity. Most of the specimens in Florence were obtained either from local hunters from the vicinity of Mogadishu or from skin dealers in the town. Specimens were obtained from local hunters of Balad, a large village on the Shebelle R. just north of Mogadishu, which reported the animals to be found within a few miles of this locality. Some were

personally collected about 10 miles west of Mahaddei Wein, a village on the Shebelle R. about 90 miles north of Mogadishu. However, having repeatedly visited the area inland and north of Mogadishu between 1969 and 1982, apart from this single occasion the only dik-diks found were Salt's Dik-diks (*M. s. lawrancei*).

Recently, this species has been reliably reported (and photographed) further up the Shebelle R. valley and in the valley bottoms of its seasonal tributaries in the Ogaden of Ethiopia (Wilhelmi *et al.* 2006). It therefore seems likely that this species might occur in other well-vegetated lowland areas of the Shebelle R. valley up to about 500 m above sea level. South of Mogadishu, in the strip between the coast and the Shebelle R., only Kirk's Dik-diks *Madoqua (kirkii) kirkii* have ever been reported. In the more open areas on the right bank of the Shebelle R. only *M. s. swaynei* is to be found, and in areas of denser scrub one finds Günther's Dik-diks, with rare specimens of intermediate characters with Kirk's, which may be either hybrids or representative of the transition between the two taxa.

Habitat Very little is known of the habitat of Silver Dik-diks. The specimens obtained from west of Mahaddei were found in low bush with large open spaces, a habitat commonly used also by Salt's Dik-dik (*M. s. lawrancei*) and, occasionally, by Günther's Dik-dik, both species having been observed within a few miles from the locality where Silver Dik-diks were collected. In the south-eastern part of the Ogaden, *M. piacentinii* have been observed in dense to semi-dense *Acacia-Commiphora* bushland and in one area of less than 2000 m² three species of *Madoqua* (*M. guentheri*, *M. saltiana* and *M. piacentinii*) were found together (Wilhelmi *et al.* 2006). The latter authors listed *Acacia bussei*, *A. mellifera*, *A. ziziphospina*, *Commiphora hoday*, *C. ogadensis* and *Boswellia neglecta* as prominent members of this 'Acacia-resin bush', with sparse *Chrysopogon* and *Dactyloctenium* grasses below a mostly closed canopy.

Abundance In the Ogaden, where this species is probably on the very edge of its range, a density of 1–2 individuals was estimated in an area of less than 2000 m² where the habitat was shared with *M. guentheri* and *M. saltiana* (Wilhelmi *et al.* 2006). East (1999), assuming a population density of 2.0/km², estimated the total population at about 30,000, but remarked that this might be an overestimate.

Adaptations As the morphology of these dik-diks is extremely similar, apart from the colour pattern, to that of the other dik-diks of the subgenus *Madoqua* it may be expected that their adaptations are also very similar. Kingdon (1997) suggested that this was possibly the least arid-adapted of the dik-diks. Although most dik-diks are usually active both during the day and night, since Silver Dik-diks appear to be especially elusive, it may be suspected that it is somewhat more nocturnal than other species. In any event, studies of partitioning of the habitat in those areas where three *Madoqua* species occur would be very interesting and valuable.

Foraging and Food Silver Dik-diks generally are browsers, yet, as with most aspects of this species' ecology, no reliable information is available. The captive specimens observed in Florence used the same food as captive *M. s. lawrancei*: pellet food, with an addition of a variety of fresh green food, and the animals did not appear to be



Madoqua piacentinii

very selective. During their brief period of captivity in Somalia, the animals were fed with the fronds of various *Acacia* species.

Social and Reproductive Behaviour As all other species of dik-diks are strictly territorial, and their territories stretch at most across a few hundred metres, this almost certainly applies to Silver Dik-diks. Some animals kept in captivity in Florence did not show any behavioural differences compared with other dik-diks.

Reproduction and Population Structure No observations have been made in the wild. Observations from captive specimens in Florence revealed behavioural similarities to Salt's Dik-dik. Two hybrids with *M. s. lawrancei* survived to adulthood; however, no hybrids have ever been reported from the wild.

Predators, Parasites and Diseases There are no reliable records, but Silver Dik-diks are probably vulnerable to the same predators and diseases as the other species in the genus.

Conservation IUCN Category: Data Deficient. CITES: Not listed.

Up to about 1965–70, when Somalia was still officially exporting trophies, an average of 200,000 dik-dik skins were exported annually and skins of the Silver Dik-dik were commonly obtainable from the tanning firm in Mogadishu. As a moderate increase in most species of game was observed after the ban of legal hunting in 1971, it is possible that the Silver Dik-dik enjoyed a brief period of recovery. However, the complete turmoil that has especially affected C and S Somalia over the last decades suggests that the species probably is in decline.

Prior to the civil war in Somalia a reserve had been declared covering a considerable stretch of the presumed range of the Silver Dik-dik. This reserve was to be transformed into a National Park bounded to the south by a line joining from the Shebelle R. about 15 km north of Balad to the village of Warsheik on the coast and extending north to Adale. Unfortunately, the National Park has never been formally gazetted and, at present, there is no information available concerning the status of the species or on the condition of its habitat. The only conservation measures available are the establishment of secure protected areas within its range (which seems unlikely in the foreseeable future) or the establishment of secure, self-sustaining populations in captivity (East 1999).

Measurements

Madoqua piacentinii

HB (♂ ♂): 425 mm

HB (♀ ♀): 430 mm

T (♂ ♂): 23 mm

T (♀ ♀): 30 mm

HF c.u. (♂ ♂): 140 mm

HF c.u. (♀ ♀): 155 mm

E (♂ ♂): 45 mm

E (♀ ♀): 45 mm

Somalia (A. M. Simonetta pers. obs.)

Key References Ansell 1972; Funaioli & Simonetta 1966, Wilhelmi *et al.* 2006.

Alberto M. Simonetta

Madoqua (kirkii) KIRK'S DIK-DIK SPECIES GROUP

Sir John Kirk was a Scottish naturalist who served as David Livingstone's chief assistant from 1858 to 1863.

Taxonomy For the purposes of this handbook, *Madoqua kirkii sensu lato* is treated as a species complex or superspecies that provisionally includes four species. Molecular research has confirmed there are at least four cytotypes that are genetically well demarcated (Ryder *et al.* 1989, Kumamoto *et al.* 1994, Zhang & Ryder 1995, Kingswood & Kumamoto 1997).

That *Madoqua kirkii sensu lato* may represent a complex of more than one species first became evident when crosses involving specimens of Kirk's Dik-dik (captured at two different localities in Kenya) resulted in sterile male hybrids (Ryder *et al.* 1989). Subsequent studies of chromosome number and morphology revealed that these were the result of cross-breeding between two distinct cytotypes ($2n = 46$, $FN = 48$ and $2n = 46-47$, $FN = 56-59$), which, given their advanced state of reproductive isolation (male hybrid sterility), had to be considered separate species, respectively *M. (k.) cavendishi* and *M. (k.) kirkii* (Ryder *et al.* 1989). A third cytotype from Tanzania was also identified, *M. (k.) thomasi*, with $2n = 48$ and $FN = 52$ (Kingswood & Kumamoto 1997). Karyotyping of the south-western population, the Damara Dik-dik *M. (k.) damarensis*, also revealed this to have a distinct cytotype within the *M. kirkii* complex ($2n = 48$, $FN = 50$; Kumamoto

et al. 1994). According to Kingswood & Kumamoto (1997) the four cytotypes can be identified by six chromosomal rearrangements: two heterochromatic additions/deletions, two pericentric inversions, one tandem fusion and an autosome-to-X translocation.

A re-assessment of the status of subpopulations within *M. kirkii* has, therefore, been warranted, with the need to distinguish four genetically distinct forms. Molecular evidence strongly suggests that these are effectively full species, but it needs to be recognized that the details of taxonomy as well as the biogeography of the species remains uncertain and the nomenclature proposed here is provisional. For example, while Cotterill (2003a) recognized four evolutionary species (*M. kirkii*, *M. cavendishi*, *M. thomasi* and *M. damarensis*), Grubb (2005) was of the opinion that *thomasi* grades into *cavendishi* and is not a separate taxon. For this reason we place all members of this complex under a single profile. Differentiating the biology of these species and elucidating their evolution will be a task for future scientists. Long before molecular techniques became available, seven geographically and morphologically defined subspecies had been recognized (Ansell 1972). We present a synthesis that provisionally distributes Ansell's seven subspecies within the four molecular cytotypes.

Synonyms: *M. (k.) kirkii*: *minor*, *nyikae*; *M. (k.) cavendishi*: *hindei*, *langi*; *M. (k.) damarensis*: *hemprichianus*, *variani*; *M. (k.) thomasi*: none.

Chromosome number: *M. (k.) cavendishi* is characterized by cytotype A ($2n = 46$, $FN = 48$); *M. (k.) kirkii* is characterized by cytotype B ($2n = 46-47$, $FN = 56-59$); *M. (k.) thomasi* is characterized by cytotype C ($2n = 48$, $FN = 52$); *M. (k.) damarensis* is characterized by cytotype D ($2n = 48$, $FN = 50$). In captivity, dik-diks of the *M. (kirkii)* complex have hybridized with Günther's Dik-dik *M. guentheri* (Kumamoto 1995) and hybridization in the wild is believed to occur at low frequencies across the range (Kingdon 1982).

Description A grouping of very small, elegant antelopes with distinctive elongated and flexible noses. There is an erectile tuft of hair on the crown of the head between the large ears, these hairs reaching 45 mm in length. Large eyes surrounded by white eye-rings and with black preorbital scent glands in front of the eyes, especially prominent in ♂♂; the latter are enclosed by connective tissue and consist of a black core of sebaceous glands surrounded by a white layer of apocrine glands (Skinner & Chimimba 2005). External rhinarium is absent. Colouration is cryptic and paler in more arid regions (Estes 1991a). Dorsal pelage is grizzled with grey to brown hairs and white flecks, face and legs are tan-coloured and chin and belly are whitish. Long hindlegs give a hunched, almost hare-like appearance. Hooves are black and pointed and have pedal glands opening through narrow

cylindrical tubes between the hooves; however, these are absent in the Damara Dik-dik, having in their place invaginated folds of skin, with tufts of hair about 15 mm in length, and underlying sweat and sebaceous glands (Skinner & Chimimba 2005). Very small tail, white underneath. Females are about 10% heavier than ♂♂, and have two pairs of inguinal nipples.

Typical features of the skull include: posterior cranial roof strongly angled downward; anterior sides of the braincase widen anteriorly; temporal ridges very wide; lachrymal pits large and shallow to accommodate preorbital glands; maxillary tuberosities prominent; infraorbital foramina high and more posterior; auditory bullae large; and horn cores keeled and strongly inclined (Gentry 1992). Horns in ♂♂ only, short and spike-like, with strong annular rings towards the base. Molars and premolars are high crowned and the lingual walls of the lower molars are flattened. A small pair of upper canines is sometimes found in juvenile skulls and, rarely, in adults (Poggesi *et al.* 1982).

Geographic Variation As discussed above, the well-established *Madoqua kirkii* taxon is here considered to embrace four genetically distinct species that encompass the seven subspecies recognized by Ansell (1972).

Madoqua (kirkii) kirkii KIRK'S DIK-DIK

Fr. Le Dik-dik de Kirk; Ger. Kirkdikdik

Madoqua kirkii (Günther, 1880). Proc. Zool. Soc. Lond. 1880: 17. Somalia, 'near Brava, in the South Somali country'.



Kirk's Dik-dik *Madoqua (kirkii) kirkii*.

M. (kirkii) kirkii species ($2n = 47$): north-east African coastal and lowland regions south to Pare, Usambara.

M. (k.) k. kirkii: S Somalia and along the Kenyan east coast, south to the Tana R. One of the smallest subspecies; dorsal pelage darker ochre-tawny, flanks pale buff graduating into white underparts.

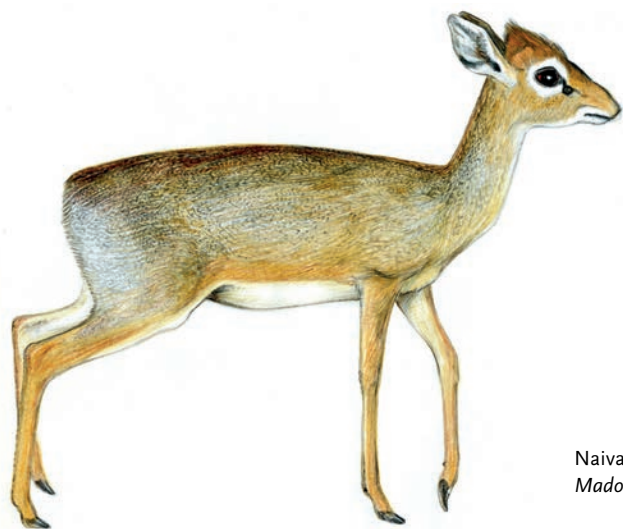
M. (k.) k. minor: Kenya, from just south of N Ewaso Nyiro R., north to Merelle Water and east towards Lorian Swamp. One of the smallest subspecies; pale desert subspecies, dorsal pelage bleached buff, flanks showing little contrast to white underparts.

M. (k.) k. nyikae: SE Kenya from Taveta eastwards, and into NE Tanzania. Dorsal pelage darker ochre-tawny, flanks pale buff showing little contrast to white underparts; sometimes with white spots on legs.

(Dik-dik images not to scale)

***Madoqua (kirkii) cavendishi* NAIVASHA DIK-DIK (CAVENDISH'S DIK-DIK)**

Madoqua cavendishi Thomas, 1898. Proc. Zool. Soc. Lond. 1898: 278. Probably from region of L. Baringo, British East Africa.



The vernacular name Naivasha Dik-dik follows Roosevelt & Heller (1915).

M. (kirkii) cavendishi species ($2n = 46$): uplands from E Uganda to Eastern Rift Valley and into N Tanzania.

M. (k.) c. cavendishi: E Uganda south through Rift Valley and into N Tanzania between Mt Kilimanjaro and L. Victoria; exact southern limits unknown. One of the largest subspecies; darker dorsal pelage, flanks rufous and in strong contrast to white underparts.

M. (k.) c. hindei: C Kenya, from Nairobi area, east to Kitui and south to Mtito-Andei; exact limits unknown. Darker dorsal pelage, flanks rufous and in strong contrast to white underparts.

Naivasha Dik-dik
Madoqua (kirkii) cavendishi.

***Madoqua (kirkii) thomasi* UGOGO DIK-DIK (THOMAS'S DIK-DIK)**

Madoqua thomasi (Neumann, 1905). Sitzber. Ges. Nat. Freunde Berlin 1905: 89. Itiso, Northern Ugogo, central Tanganyika Territory.



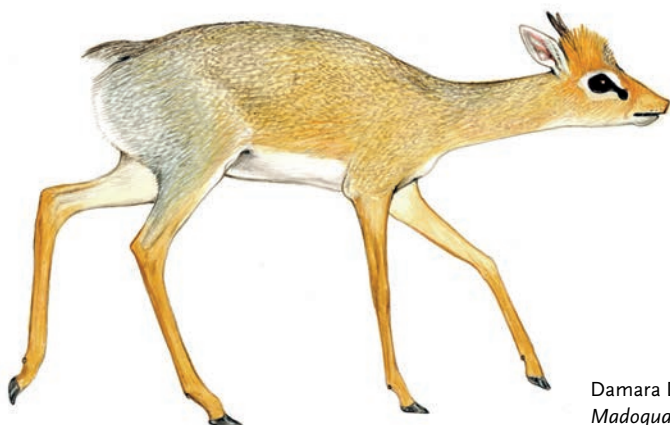
The vernacular name Ugogo Dik-dik (in reference to the type locality) follows Swynnerton & Hayman (1951).

M. (k.) thomasi species ($2n = 48$): Tanzania. Thicket and *Acacia* bushlands from C Tanzania south to L. Rukwa and the Udzungwa Mts, west to south-eastern shores of L. Tanganyika and northwards to the southern and western shores of L. Victoria as far as the Kagera R. More rufous on the flanks, which are in strong contrast to white underparts. This population inhabits a unique vegetation zone within a discrete geographic area.

Ugogo Dik-dik
Madoqua (kirkii) thomasi.

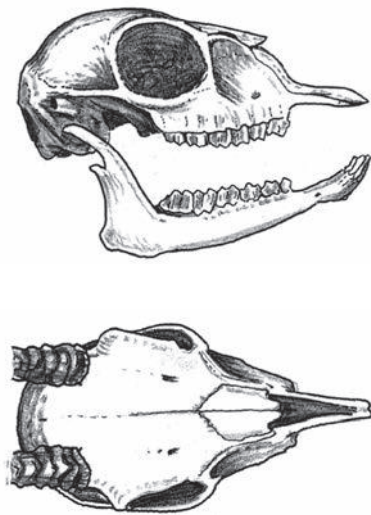
***Madoqua (kirkii) damarensis* DAMARA DIK-DIK**

Madoqua damarensis (Günther, 1880). Description of two new species of dwarf antelope. Proc. Zool. Soc. Lond. 1880: 17–22. Damaraland.



M. (kirkii) damarensis species ($2n = 48$): south-western Africa. C and NW Namibia and SW Angola. One of the largest species in the group; anterior of the back slightly lighter, and hair tuft between the ears darker; hooves have no pedal glands, but have a rubbery pad, which may be an adaptation to rocky ground.

Damara Dik-dik
Madoqua (kirkii) damarensis.



Lateral and dorsal views of skull of Damara Dik-dik *Madoqua (kirkii) damarensis*.

Similar Species

Madoqua guentheri. Sympatric in Kenya and Somalia; very similar but has longer nose, with the length of the nasal chamber exceeding the interorbital width of the skull, unlike that of dik-diks in the Kirk's complex.

M. saltiana and *M. piacentinii*. Sympatric in Somalia, but both are smaller and have shorter noses.

Oreotragus oreotragus. Broadly sympatric. Yellow-grey pelage; larger (12 kg), and with a more upright stance; invariably close to rocky terrain.

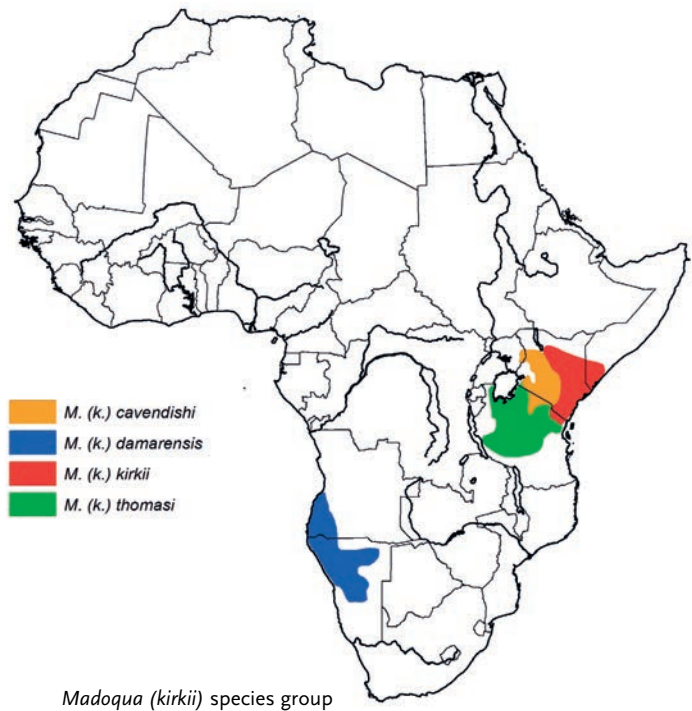
Distribution Endemic to Africa. Over 2000 km separates the East African populations (*cavendishi*, *thomasi* and *kirkii*) from *damarensis* in south-west Africa. Several authors (e.g. Kingdon 1971, Coe & Skinner 1993) have suggested that this division was brought about by climatic changes that took place during the Pleistocene, and that this has resulted in the intervening terrain experiencing wetter climates during interglacials with consequent changes in the vegetation structure.

Kirk's Dik-dik, the nominate species, has a lowland semi-littoral range that extends from S Somalia (formerly as far north as the Shebelle R.), through N and E Kenya and just into N Tanzania.

Naivasha Dik-diks inhabit uplands in the interior of eastern Africa. Mount Elgon, the Karamoja/Acholi border, and the southern tip of L. Turkana mark the western and northern boundaries. To the east, their range ends with the lowland Chalbi, Kaisut and Isiolo deserts. Their southernmost extension is the Mbulu highlands.

Ugogo Dik-diks inhabit the C Tanzanian bushlands. They extend to the southern and western shores of L. Victoria as far north as the Kagera R. and westwards to parts of the eastern shores of L. Tanganyika, south to L. Rukwa and the Udzungwa Mts and eastwards to the coastal lowlands.

In south-western Africa, Damara Dik-diks occur at least as far north as Lobito in SW Angola, and extend into NW and C Namibia, with isolated pockets further south along the Fish R. and around Mt Brukkaros (Crawford-Cabral & Veríssimo 2005, Skinner & Chimimba 2005).



Madoqua (kirkii) species group

Habitat Restricted to arid areas where they inhabit dense thorn scrub or open woodland in which the ground layer is mostly free of grass, but has a well-developed shrub layer (Tinley 1969). This provides good browse and shade, cover from predation, and an open understorey at eye-level. May also be found on isolated rocky hills or outcrops in savanna habitats, such as Serengeti N. P. in Tanzania (Hendrichs 1975a), and in riverine woodland and thickets. In W Kenya and Tanzania, dik-diks occur in areas receiving up to 1000 mm of rainfall per annum (Hendrichs & Hendrichs 1971). Reliably recorded up to about 2000 m (Hendrichs & Hendrichs 1971); records from upper Kilimanjaro (to 4270 m) are the result of a misidentification with a duiker (Grimshaw *et al.* 1995).

In Namibia, Damara Dik-diks are largely restricted to areas of hard, usually stony, ground, and are typically confined to areas with a mean annual rainfall of between 75 and 500 mm (Skinner & Chimimba 2005). In East Africa, Kirk's Dik-diks inhabit hot lowlands dominated by *Acacia* spp., *Boswellia*, *Indigofera* and *Duosperma* spp., Naivasha Dik-diks occupy dry uplands dominated by species of the genera *Acacia*, *Olea*, *Turrea*, *Tinnea*, *Aspileia*, *Psiadia*, *Aloe* and *Sansevieria*, and Ugogo Dik-diks inhabit dry bushlands characterized by very irregular rainfall and *Grewia*, *Baphia*, *Acacia* and *Pseudopropsis* thickets.

Abundance Widespread and locally abundant in areas of high shrub density. Based on average population densities, East (1999) estimated a total population size of 971,000 for the species group. Ground surveys have revealed density estimates for Kirk's Dik-dik of 109 ind/km² in Tsavo East N. P., Kenya (Komers 1996). Coe *et al.* (1999) made a gross overall estimate of about 33/km² for Mkomazi G. R., N Tanzania, but local densities in prime habitat were clearly much higher. Densities have been estimated at 55/km² in Arusha N. P., Tanzania (Amubode & Boshe 1990) and 24/km² in Serengeti N. P. (Hendrichs 1975a). In Etosha N. P., Namibia, Brotherton (1994) estimated the density of the Damara Dik-dik at 90/km².

Adaptations These animals are superbly adapted to life in an arid, hot climate. In these habitats water is at a premium, so dik-diks are faced with the problem of staying cool while conserving water (Schoen 1972, Maloiy 1973, Hoppe 1977a). They overcome this by a combination of physiological and behavioural adaptations. Water economy is high due to slow water turnover, the kidneys' ability to form highly concentrated urine and voiding very dry faecal pellets (Maloiy 1973, Hoppe 1977a, Maloiy *et al.* 1988). Indeed, dik-diks have the lowest daily water use and excrete the driest faeces and most concentrated urine of any ungulate so far studied; this ability is probably due to the kidney's relatively high volume (47%) of renal medullae and its long loops of Henle (Schoen 1969, Maloiy *et al.* 1988). During dehydration, the faecal water content reduces to 68 g/100 g dry faecal material, compared with 76/100 g in camels (Maloiy *et al.* 1988). This enables them to live entirely independently of water, even during long dry seasons (though dik-diks with standing water in their territories have been observed to drink, P. Brotherton pers. obs.). In captivity, voluntary water intake is just 278 ml/day (Hoppe 1977b) while in the field, dry season water intake has been estimated at a mere 134 ml/day (Manser & Brotherton 1995). In captive trials, dik-diks were observed to consume forage at a rate of 40.4 g per kg body weight per day, while daily water intake was about 68 ml per kg body weight (Maloiy & Clemens 1999).

Dik-diks conserve water further by licking condensation droplets that form on the nose, and panting instead of sweating (Hoppe 1977a); a histological examination of dik-dik skin revealed a sweat gland density of 120 glands per cm², far less than that of actively sweating ungulates such as cattle (1500 glands per cm²) (Maloiy *et al.* 1988). One of the most striking features of dik-diks is the elongated nose and this, too, is an adaptation to reduce water loss. The nasal chamber is enlarged to accommodate the proboscis and the roof of the nasal cavity is supported by cartilage for greater flexibility (see Kingdon 1982, Frey & Hofmann 1996). The elongated nose is richly vascularized, allowing cooling of the blood by nasal panting; the wide, flexible trunk functions like a bellows to increase air flow while the hairy muffle and tiny nostrils reduce water loss. This serves to cool the blood going directly to the brain, keeping this most sensitive organ at the correct temperature, while the body core temperature may rise up to 43°C (Maloiy *et al.* 1988). This excess body heat is apparently stored or lost to the environment without using water for evaporation.

Dik-dik activity patterns are also adapted to their hot, arid habitat. They are mainly crepuscular in their activity (and intermittently throughout the night) and rest in the shade of dense bushes during the hottest times of the day. This also means that they feed on plants at the times when the water content of their leaves is highest (Bowker 1978).

Like Günther's Dik-dik, these dik-diks have a relatively small stomach, and a digestive tract designed for rapid passage and absorption of high-quality food (Hofmann 1973, Hoppe 1977b). The rumen is simple, with dense papillation that increases the absorptive mucosal surface as much as 18-fold. Volatile fatty acid production in the rumen is about three-fold the rate found in roughage-eating grazing antelopes. The short residence time of rumen contents precludes fibre digestion and survival of intra-ruminal protozoa except, in a few individuals, *Entodinium* (Hoppe *et al.* 1983) that are tolerant to or degrade tannins (Odenyo *et al.* 1999) (see also Günther's Dik-dik profile).

Being independent of water enables dik-diks to remain in their territories and reduces the risk of predation. Cryptic colouration and

small size also help dik-diks to hide from their numerous predators. Their long hindlegs are powerful and enable dik-diks to make explosive bursts of speed when they encounter predators (see also Günther's Dik-dik profile). The Damara Dik-dik has a rubbery pad behind the hooves, which may be an adaptation to rocky ground (Tinley 1969).

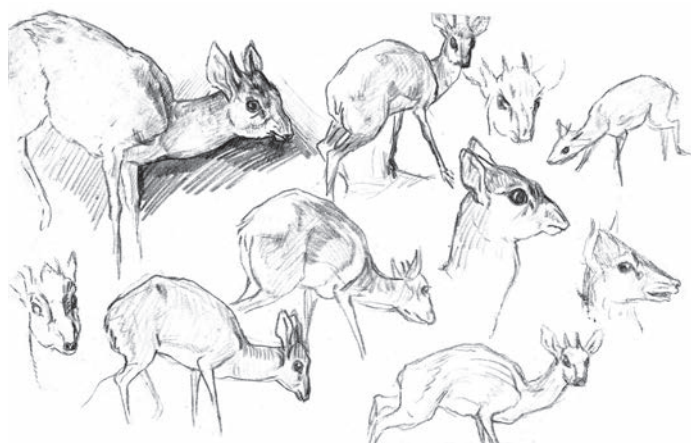
Foraging and Food Like their congeners, dik-diks of the *M. (kirkii)* complex are selective browsers, consuming the leaves, flowers, shoots and fruit of shrubs, bushes and trees, selecting the freshest parts of the plant available and only rarely eating grass (when sprouting). In Kenya, Bowker (1978) found that they browsed almost every available species of tree and bush. In Tarangire G. R., Tanzania, their diet comprised 56% shrubs, 23% trees, 17% grasses, 3% forbs and 1% sedges (Lamprey 1963).

In Namibia, Damara Dik-diks were found to eat from over 85% of the species of woody plants occurring in their territories during the course of the year (Manser & Brotherton 1995), although species with less palatable fibrous leaves were only utilized in the dry season, a time when leaf litter also became an important part of the diet. Availability of the latter is increased by other browsing species, such as Greater Kudu *Tragelaphus strepsiceros*, Giraffe *Giraffa camelopardalis* and Savanna Elephants *Loxodonta africana*, which break down the browse plants. Tinley (1969) recorded 28 species of browse and four grass species eaten during the wet season in Etosha N. P. (including *Securinega virosa*, *Rhus marlothii* and *Ziziphus mucronata*), to which he added a further 22 browse species consumed in the dry season (including *Boscia albitrunca*, *Grewia* spp. and *Terminalia prunioides*). Other species, such as thorn trees and sickle bushes *Dichrostachys cinerea*, were eaten all year round. In CTanzania, Harrison (1936) noted Ugogo Dik-diks switching from *Acacia pennata* and various other woody plants in the dry season to *Acacia senegal* in the wet season, at which time ephemeral herbs such as *Ipomoea* spp. and *Leonotis* spp. were also eaten.

In Namibia, the period of lowest food availability at the end of the long dry season coincides with the flowering of certain tree species, notably *Lonchocarpus nelsii* and *Boscia albitrunca*, and dik-diks may temporarily leave their territories to feed on fallen flowers; up to nine dik-diks at a time have been observed feeding under large flowering trees. Dik-diks make use of their long proboscis-like snout to search for preferred foods. Like the Gerenuk *Litocranius walleri*, dik-diks may feed bipedally, standing on their hindlegs to reach browse otherwise out of reach.

Simonetta (1966) found that regular access to mineral salts was important for maintaining captive dik-diks, and in the wild they are known to eat sand, visit salt-licks and chew on bones to gain minerals (Harrison 1936, Bowker 1978, P. Brotherton pers. obs.).

Social and Reproductive Behaviour The typical social unit is a monogamous pair (Hendrichs 1975a) accompanied by a single juvenile from the most recent breeding event, though sometimes an older offspring is also present. The pair-bond apparently lasts until one member dies, and genetic studies have confirmed fidelity within the pair bond (Brotherton *et al.* 1997). Occasional polygynous groups occur, comprising a ♂ and two unrelated ♀♀ (10% of groups in Etosha N. P.); these groups apparently form in response to a lack of territorial vacancies for ♀♀ (Brotherton & Manser 1997). Temporary aggregations may form during the dry season at sites of food abundance (see Foraging and Food above).



Ugogo Dik-dik *Madoqua (kirkii) thomasi*.

Both sexes defend the pair's territory (female territoriality is rare in antelopes), mainly against same-sexed intruders, and the territory boundaries can be stable for several years (Amubode & Boshe 1990). Depending on local resource availability, territories may vary in size from under 1 ha to over 10 ha. Territories are marked with dung piles and scent from the preorbital gland. Dung piles are most commonly situated on the territory boundaries and can be several metres in diameter. Dung piles are typically located next to animal trails, presumably to increase the likelihood of intruders encountering them. The behaviour of the pair at dung piles follows a distinct pattern: the ♀ enters the dung pile and urinates before defecating (urination and defecation is linked, as in many antelopes). Sometimes, especially as the ♀ approaches oestrus, the ♂ puts his nose in her urine flow and displays flehmen. After the ♀ has defecated, the ♂ smells her deposit and then scrapes dirt over it with his front hooves before urinating and defecating on top (Hendrichs 1975a). In a similar fashion, ♂♂ over-mark the deposits of any other group members. Dik-diks may also defecate on top of the dung of other species and the faeces of unfamiliar dik-diks (Hendrichs & Hendrichs 1971). Preorbital secretions are dabbed onto protruding twigs throughout the territory, and accumulate into black, tar-like deposits. Between 200 and 500 mg of this substance is deposited per day (Hoppe 1977a). In Namibia, ♂♂ were observed to preorbital mark at a rate of about 19 marks/h, compared with a female rate of about 6 marks/h (Brotherton 1994), and ♂♂ over-mark any female scent marks that they encounter. Male over-marking of female dung deposits and preorbital secretions appears to have two functions: concealing the oestrous status of the ♀ from neighbouring and intruding ♂♂; and advertising that the ♀ has a pair-mate who will defend her.

Fights may occur when neighbours, especially ♂♂, encounter each other at territory boundaries, although physical contact during fights is uncommon. When dik-diks fight in captivity, where one cannot escape, the results can be fatal (Kingdon 1982). In the wild, combatants typically engage in highly ritualized 'air-cushion' fights, in which they make frequent short charges at each other, but stop about 50 cm apart (Estes 1991a). During these fights dik-diks erect the tuft of hair between their ears and display by thrashing vegetation with their heads. Males also erect their hair tuft and thrash vegetation during periodic displays of dominance over their ♀♀. It is typically the ♀ that initiates changes of activity for the group, and determines where the group moves within the territory, although if she attempts to leave the territory the ♂ may chase her back (Komers 1996).

Oestrus lasts less than 24 hours (Dittrich & Böer 1980) and copulation behaviour follows a distinctive pattern: the ♀ adopts an upright stance with her back curved downwards and her tail erect, and the ♂ mounts without touching her with his forelegs (Brotherton 1994). Intromission occurs in approximately 10% of mounts and copulation lasts about two seconds. Occasionally, the ♂ licks or nuzzles the female's anogenital region before mating. Dik-dik young are precocious: they can stand 5–15 min after being born and suckle within 1–2 hours. For the first few weeks of life, the young remain hidden in dense vegetation and mothers return to feed them. At 10–14 days of age, young begin browsing and thereafter they increasingly accompany their mothers until they are constantly with their parents from 5–6 weeks of age. Males have no role in parental care (Brotherton & Rhodes 1996). Reciprocal grooming is sometimes observed between mothers and offspring.

Brotherton (1994) recorded six vocalizations in Damara Dik-diks, most notably a high-pitched nasal whistle given as an alarm call. Explosive utterances of this whistle while stotting sound like 'zik-zik' and this may be the source of the dik-dik's name. This loud whistle may also be used to threaten intruders. The five other vocalizations are a trill (a soft whispering call, apparently used to warn other group members of danger and also used during submissive display by ♀♀, juveniles and intruders); bleat (occasionally made by fleeing intruders); chatter (almost horse-like grunt, used by ♂♂ during intra-group dominance displays); 'phee-oo' (a mother–infant contact call), and a scream (when captured by predators).

Reproduction and Population Structure Birth peaks coincide with wet seasons. In East Africa, where two wet seasons occur, ♀♀ typically give birth twice a year, with most young being born in Apr–Jun and Nov–Dec (Hendrichs & Hendrichs 1971, Bowker 1978). In Namibia, where one wet season occurs, most ♀♀ of the Damara Dik-dik give birth only once a year, usually between Dec and Apr (Shortridge 1934, Brotherton 1994).

Females give birth to a single young after a gestation period lasting 166–174 days (Dittrich & Böer 1980). Male young weigh about 650 g (range 585–795 g, $n = 5$) at birth (which, at over 10% of maternal body weight, is relatively large for an ungulate) while female young average 607 g (range 560–680 g, $n = 5$). Captive young reach half adult mass by four months, and adult mass at about a year (Dittrich & Böer 1980). Sexual maturity is reached at about 6–8 months of age (Kellas 1955), and ♀♀ may have their first calf at one year.

Female offspring disperse prior to their first oestrous period at about six months of age. Female dispersal typically is associated with little or no aggression from either parent, and a ♀ whose mother had died still dispersed even though she was the only ♀ left in the territory, suggesting that ♀♀ leave to avoid mating incestuously with their fathers (P. Brotherton pers. obs.). Sons disperse later than daughters, at about one year, and this may be the result of aggression from their father (Hendrichs 1975a). However, if no territorial vacancies are available sons may remain with their parents until they are up to two years old (Brotherton 1994). Males are more philopatric than ♀♀: in one study in Namibia, four out of eight ♂♂ dispersed to territories within 250 m of their parents while all daughters moved further away (Brotherton 1994).

Mortality rates vary according to predation pressure. About 50% of dik-diks die before the age of four months (Bowker 1978,

Brotherton 1994). In a Serengeti N. P. population, adult annual turnover rates were 7% for ♀♀ and 16% for ♂♂ (Hendrichs 1975a); at one site in Kenya, 16% of adults (of both sexes) died in a 10-month period (Bowker 1978); and in Namibia, average adult mortality was about 20% for both sexes (Brotherton 1994). Records from captivity show a slight, but significant, male bias in the sex ratio at birth (of 372 captive births of known sex, 166 were ♀, 206 were ♂; Kingswood & Kumamoto 1997). Since dik-diks are monogamous, adult sex ratio among territorial individuals is necessarily close to 1 : 1. However, following the death of a resident animal, ♂♂ are typically replaced much quicker than ♀♀: in Namibia, ♂♂ were replaced within three days while ♀♀ were replaced on average after 32 days (Brotherton 1994). In Serengeti N. P., a male dik-dik remained unpaired for over five months after his mate died (Hendrichs & Hendrichs 1971). This suggests that there is likely to be a male bias in the non-territorial population. In captivity, ♂♂ and ♀♀ have been known to live for 16–17 years (Kumamoto 1995, Weigl 2005); the oldest dik-dik recorded in a wild population was about ten years (Hendrichs 1975a).

Predators, Parasites and Diseases Dik-diks are taken by a broad spectrum of terrestrial and aerial predators. Known predators of adults include Leopards *Panthera pardus*, Cheetahs *Acinonyx jubatus*, jackals *Canis* spp., African Wild Dogs *Lycaon pictus*, Caracals *Caracal caracal*, Lions *Panthera leo*, Martial Eagles *Polemaetus bellicosus* and Tawny Eagles *Aquila rapax*; while predators known to take juveniles include Olive Baboons *Papio anubis*, African Rock Pythons *Python sebae* and African Hawk-Eagles *Hieraetus fasciatus* (Tinley 1969, Bowker 1978, Kingdon 1982, Spinage 1986).

Virtually nothing is known about diseases suffered by dik-diks in the wild, although they apparently have low susceptibility to rinderpest (Plowright 1982). Bowker (1978) noted two young ♂♂ heavily infected by unidentified external parasites on their necks and heads, but both recovered. In C Namibia, some individuals have been observed with stump-like ears (P. Hoppe pers. comm.), which may have been due to frost-bite damage. Also in Namibia three individuals were observed to suffer from a severe eye infection, which in each case led to the loss of the infected eye, and was usually followed by death (P. Brotherton pers. obs.). Ectoparasites include a range of fleas (*Ctenocephalus* spp.), lice (*Linognathus* spp.), muscid flies (*Stomoxys* sp.) and ticks; numerous endoparasites are recorded, including nematodes, cestodes, pentastomids and protozoans (see Kingswood & Kumamoto 1997, and references therein).

Conservation IUCN Category: Least Concern. CITES: Not listed.

Dik-diks are trapped for food by local people throughout their range, and are also taken by trophy hunters. Their ability to exist in scrub and overgrazed areas has made their populations resilient to the vegetation changes that have accompanied human population growth,

and may have even favoured them in the short term. Populations in protected areas include those in Samburu, Tsavo, Amboseli and Lake Nakuru National Parks (Kenya), Serengeti, Arusha and Mkomazi National Parks (Tanzania) and Etosha N. P. (Namibia) (East 1999).

Measurements

Madoqua (kirkii) species group

TL (♂♂): 676 (570–780) mm, n = 31

TL (♀♀): 690 (640–750) mm, n = 35

T (♂♂): 45 (30–77) mm, n = 22

T (♀♀): 51 (32–70) mm, n = 20

HF c.u. (♂♂): 198 (159–218) mm, n = 41

HF c.u. (♀♀): 203 (191–216) mm, n = 34

E (♂♂): 78 (57–86) mm, n = 39

E (♀♀): 79 (57–85) mm, n = 35

Sh. ht (♂♂): 383 (300–445) mm, n = 189

Sh. ht (♀♀): 397 (240–444) mm, n = 157

WT (♂♂): 4.59 (2.6–6.0) kg, n = 181

WT (♀♀): 5.17 (3.5–6.4) kg, n = 151

Throughout geographic range (Kingswood & Kumamoto 1997). Note that local species or subspecies may differ in dimensions, *M. (kirkii) kirkii* in particular having smaller dimensions than the other species. This can be appreciated by comparing total length of skull measurements:

Madoqua (k.) kirkii (including *minor*)

GLS (♂♂): 105 (101–108) mm, n = 10

GLS (♀♀): 110.5 (105–114) mm, n = 4

Madoqua (k.) cavendishi

GLS (♂♂): 120.8 (116–124) mm, n = 8

GLS (♀♀): 119.5 (116–127) mm, n = 6

Madoqua (k.) thomasi

GLS (♂♂): 115 mm, n = 126

GLS (♀♀): 117 mm, n = 85

Madoqua (k.) damarensis

GLS (♂♂): 109.7 (105–113) mm, n = 3

GLS (♀♀): 118 (116–120) mm, n = 3

Kellas (1955) gave mean head and body length (\pm S.D.) for ♂♂ as 595 (\pm 26) mm (n = 126) and for ♀♀ 615 (\pm 26) mm (n = 83)

Maximum recorded horn length is 11.4 cm for a pair of horns from Selous, Tanzania (Rowland Ward)

Key References Bowker 1978; Brotherton & Manser 1997; Hendrichs 1975a; Hendrichs & Hendrichs 1971; Kingdon 1982; Kingswood & Kumamoto 1997; Tinley 1969.

Peter N. M. Brotherton

Madoqua guentheri GÜNTHER'S DIK-DIK

Fr. Dik-dik de Günther; Ger. Zwerg-rüsselantilope

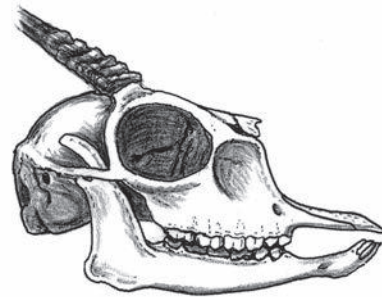
Madoqua guentheri Thomas, 1894. Proc. Zool. Soc. Lond. 1894: 323–329. Ethiopia, 'Central Ogaden, 3000 feet [914 m]'; identified as 'District immediately north of Imi and Karanle on the Webi Shebeli, Ogaden, Ethiopia, about 6° 30' N, 42° 30' E by Moreau *et al.* (1946: 437).



Günther's Dik-dik *Madoqua guentheri*.

Taxonomy Four subspecies were recognized by Ansell (1972), although one of these (*M. g. hodsoni*) is based on a single specimen whose skull is indistinguishable from *M. g. guentheri* (Drake-Brockman 1930), and there is some debate as to the validity of another of the four possible subspecies, *M. g. wroughtoni*, which is probably also allied with *M. g. guentheri* (Yalden *et al.* 1984). If these two subspecies are indeed synonymous with the nominate subspecies, then the total number of subspecies is two. However, for the purpose of this handbook, all four subspecies are provisionally retained (and see Kingswood & Kumamoto 1996).

Synonyms: *gussuleh*, *hodsoni*, *nasoguttatus*, *smithii*, *wroughtoni*. Chromosome number: $2n = 48-50$; there are 8–10 submetacentrics and 36–40 acrocentrics, with acrocentric sex chromosomes (Ryder *et al.* 1989). Variation in diploid number results from putative centric fusion occurring in homozygous ($2n = 48$) and heterozygous ($2n = 49$) forms; $2n = 50$ forms lack the fusion. $2n = 49$ heterozygotes of both sexes are fertile (Kumamoto 1995). In the wild, skins and skulls displaying intermediate characteristics of *M. guentheri* and dik-diks of the *M. (kirkii)* complex have been found from parts of Somalia, Ethiopia, Kenya and the Kenya–Uganda border, suggesting that hybridization may occur over a wide area (Kingdon 1982). Crosses between these species in captivity have produced sterile male hybrids (with $2n = 48$) and backcrossing a F1 hybrid ♀ with a *M. guentheri* ♂ produced stillborn offspring (Kumamoto 1995). This high level of reproductive isolation confirms that the two are indeed distinct (albeit sometimes difficult to distinguish).



Lateral view of skull of Günther's Dik-dik *Madoqua guentheri*.

Description A small, delicately built antelope, with a trunk-like nose, a tuft of hair on the crown and cryptic colouration with inconspicuous markings. Head small, with an elongated, mobile nose resembling that of a tapir (*Tapirus* spp.). Portions of the face and ears sandy, pale rufous, or greyish-red (Lönnberg 1907, Drake-Brockman 1930). Eyes large and black, surrounded by white; ears large with white interiors. Brown crest of long hairs on the crown is longer, coarser and brighter in ♂♂ than ♀♀ (Drake-Brockman 1930). Dorsal pelage grizzled yellowish-grey to greyish-brown, flanks light rust-red or sandy-white, and sandy-white on chin, throat, chest, belly and inside thighs; pelage colour varies geographically, although certain pinkish hues of the underparts are often the result of soil colour (Kingswood & Kumamoto 1996). Lumbosacral height is greater than shoulder height; legs are long and slender. Tail short, hirsute dorsally and naked ventrally. Hooves (more than 15 mm long) are black, with soft foot-pads, and minute lateral hooves (Roosevelt & Heller 1915). Pedal glands are present consisting of a deep invagination (ca. 9×4 mm) opening ventrally between the two digits on each foot. Preorbital glands are black and large in relation to body size compared with other antelopes, and larger in ♂♂ than ♀♀ (Sokolov *et al.* 1994, Spinage 1986). Females have two pairs of inguinal nipples. Males are smaller, weighing 15% less than ♀♀.

Horns are present in ♂♂ only, short and straight or slightly curved, elliptical at base and circular toward the tips, strongly ringed for about two-thirds of their length (Drake-Brockman 1930); small horn cores on the upper surface of the frontals occur on the skulls of some ♀♀ (Poggesi *et al.* 1982). The crest of long hairs on the forehead covers about two-thirds of the length of horns, sometimes making it difficult to distinguish the sexes (Drake-Brockman 1930).

Characteristic features of the skull include large orbits and lachrymal fossae (the latter accommodate preorbital glands), somewhat inflated tympanic bullae, small supraorbital foramina and small nasals that have greater width than length. Premaxillae are short, ending above P¹ and not reaching the nasals as in dik-diks of the *M. (kirkii)* complex (Frey & Hofmann 1996). Length of proboscidean nose amounts to 60–70% of skull length providing much room for respiratory heat exchange and water recovery (Frey & Hofmann 1996). Skull measurements and photographs are given by Kingswood & Kumamoto (1996).

Geographic Variation

M. g. guentheri: eastern form, apparently not reaching the coast, where it is replaced by Kirk's Dik-dik *M. (kirkii) kirkii* (Drake-Brockman 1930); range extends from the Ogaden, south and westerly through Somalia and Ethiopia into NE Kenya. Relatively small, like *M. g. wroughtoni*, though it can be distinguished from this subspecies by its lighter colour and pinkish-buff underparts (Lydekker 1914).

M. g. wroughtoni: distribution extends from the northern bank of the Wabi R. in Ethiopia, south and east between the Shebelle and Juba Rivers (Drake-Brockman 1930). One of the smaller subspecies, although its ears are wider and longer than in other dik-diks, except Naivasha Dik-dik *M. (kirkii) cavendishi*, to which it bears a superficial resemblance.

M. g. hodsoni: known only from a single specimen collected at Mt. Mega, Ethiopia. Skull indistinguishable from *M. g. guentheri*. Palest of the subspecies, hairs lacking the grizzled appearance of other dik-diks; faint reddish-brown line on the flank.

M. g. smithii (including *nasoguttatus*): SE Sudan, NE Uganda, SW Ethiopia and N Kenya. Largest of the subspecies; more grey and less yellow than other subspecies, and the anterior portion of the face and proboscis are spotted with white. Middle of the body is reddish-brown; the sides of the face, back of the ears and lower legs are light buff; the snout is bright tawny.

Similar Species

Madoqua (kirkii) species group. Mainly found south of the Tana R., but sympatric in N Kenya, and perhaps Somalia. Similar to *M. guentheri*, but larger, weighing up to 20% more.

M. saltiana. Sympatric in Somalia and Ethiopia. Short, squared-off, furry nose, not showing the enlargement seen in Günther's Dik-dik.

M. piacentinii. Least arid-adapted species, inhabiting dense, low-level, green thickets along the Obbia coastal littoral of Somalia, and further inland in the upper reaches of the Shebelle R. in the Ogaden where known to be sympatric with Günther's Dik-dik (Wilhelmi *et al.* 2006); smallest dik-dik, with soft, fine, silvery-grey fur and bright red erectile crest; proboscis noticeably less developed.

Distribution Endemic to hot, semi-desert areas of East and north-east Africa centred around L. Turkana where mean annual rainfall is low (less than 500 mm) and highly variable. The distribution includes N and S Somalia, the eastern and southern lowlands of Ethiopia, SE Sudan (east of the Nile R.), NE Uganda, and N and W Kenya. In Somalia, Günther's Dik-dik does not occur near the coast except possibly in one small area at the Gulf of Aden. Occurrence south of the Shebelle R. is controversial, but the ranges of both *M. (kirkii) kirkii* and *M. guentheri* may overlap in the Juba–Shebelle drainage (Kingswood & Kumamoto 1996, Kingdon 1997). The north bank of the Tana R. appears to be the southern border of distribution (Hillman *et al.* 1988, East 1999).

Habitat Of all dik-diks, Günther's live in the driest, hottest and thickest thornbush (Kingdon 1997). They occur mostly on stony ground compared with Salt's and Silver Dik-diks, which prefer sandy soil. In Omo N. P., Ethiopia, the habitat types occupied (means, as percentage of total area) included *Combretum–Selima* bush (56%), *Acacia mellifera* savanna (33%), riverine forest (12%), human



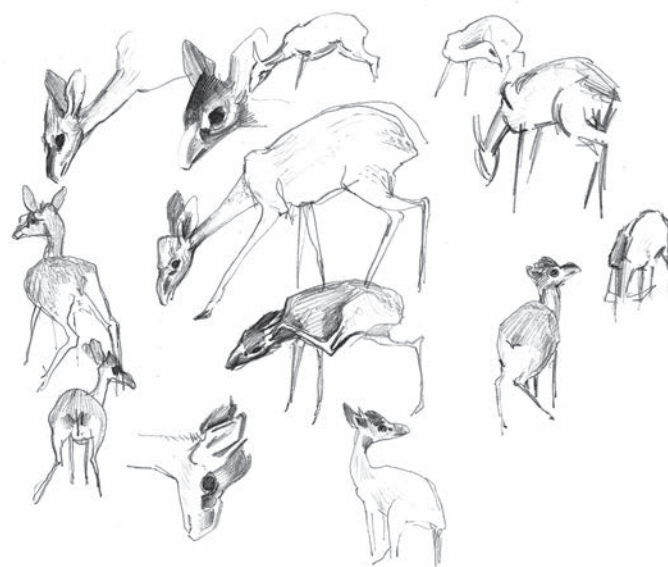
Madoqua guentheri

settlements (10%), old fields (9%), *Ischaenum–Pennisetum* grassland (8%), *Combretum* forest (3%), *Acalypha–Sansevieria* thicket (3%) and *Acacia nilotica* savanna (1%) (Ono *et al.* 1988). Suitable cover seems to be an important habitat requirement as they are seldom seen far from cover. They occur from sea level to about 2100 m elevation (Yalden *et al.* 1996).

Abundance In Sudan, Günther's Dik-dik were common in the 1980s, but there is no recent information. In Ethiopia, they are widespread and common to abundant in the eastern and southern lowlands (East 1999). In Somalia, they are recorded as common in the bushland of the Haud plateau in the north but less abundant than Salt's Dik-diks, occurring at a ratio of about 1 : 10 (East 1999). In Uganda, they are thought to still occur widely in the north-east from Kidepo Valley N. P. to southern Karamoja where the species has benefited from expansion of evergreen scrub resulting from overgrazing (East 1999). In Kenya, they are widespread and common in suitable habitat in the north and east.

Population densities of 0.7–1.1/km² have been recorded in the Haud plateau, Somalia, and the Ogaden region of Ethiopia (East 1999, and references therein). In Omo N. P., a higher density of 23.8/km² was observed in 1988 within a 75 ha study area (Ono *et al.* 1988). In 2003, transect counts in the central Ogaden around Kebri-Dehar found a density of 25/km² (F. Wilhelmi pers. comm.). The total population has been estimated at around 511,000, assuming an average population density of 1/km² (East 1999).

Adaptations Günther's Dik-diks are adapted to heat and aridity. As described for dik-diks of the *M. (kirkii)* complex, water economy is high due to slow water turnover, the kidneys' ability to form highly concentrated urine and voiding very dry faecal pellets (Maloiy 1973, Kamau 1988, Maloiy *et al.* 1988, Hoppe 1997a). They are largely independent of surface water, relying on water within dicotyledonous plant cells, hygroscopic water on plant surfaces and

Günther's Dik-dik *Madoqua guentheri*.

water produced in metabolism (in rare instances when dik-diks drink, they lap water like a cat). Panting is employed for evaporative cooling, aided by the moist mucosal surface of the proboscis (Hoppe 1977a, Frey & Hofmann 1996). The cooled venous blood draining the proboscis selectively cools the carotid rete in the brain while peripheral body temperature is allowed to stay high. Excess heat stored by the body is dissipated during the night without expenditure of water (Kamau 1988). Sweating plays no role in thermoregulation. During the hottest hours of the day they lie or stand in the shade thus avoiding heat production from locomotion and heat uptake from solar radiation. Any movement at this time is in slow motion.

Günther's Dik-diks have a relatively large mouth, allowing the sideways stripping of branches or the gnawing of flowers or fruits (Hofmann 1989). Anatomically, the small rumen resembles a simple folded tube with dense papillation (which increases the absorptive mucosal surface 15–17 times) that lacks the food-retaining muscular pillars typical of grazing ruminants; the muscular omasum has horny papillation, probably for grinding and straining. The gastrointestinal tract is discussed in detail by Hofmann (1973), and is designed for rapid passage and rapid absorption of high quality food (Hofmann 1973, Hoppe 1977b). Food and feeding behaviour involves frequent short feeding periods ranging from 1 to 36 min alternating with equally frequent, short rumination periods of 5–15 min (Hofmann 1973, Hoppe 1984). This results in almost continuous supplementation of intra-ruminal fermentation with new substrate, in the release of intracellular nutrients that are more rapidly fermented to volatile fatty acids than cell-wall constituents like cellulose, and in a copious flow of saliva to buffer intra-ruminal pH (Hofmann 1973).

Behavioural adaptations to survive predators include the ability to dart away quickly (the back is rounded and the knee and tibio-tarsal joints are strongly flexed, possibly as an adaptation to rapid starts; Hofmann 1973), intimate knowledge of the territory, and permanent alertness (Hendrichs & Hendrichs 1971).

Foraging and Food Günther's Dik-diks are classed as browsers in a detailed analysis of dietary preferences in African bovids (Gagnon & Chew 2000), in agreement with studies involving stable carbon

isotopes (Cerling *et al.* 2003). They are highly selective feeders, classified as fruit and dicotyledon foliage selectors (Hofmann & Stewart 1972, Hofmann 1973) or 'concentrate selectors'. Forty-five food plants were identified in Kenya including six *Acacia* species, three *Commelina* species, representatives of the families Euphorbiaceae, Salvadoraceae, Rhamnaceae and Papilionaceae, and two grasses, of which only seeds appear to be eaten (Hofmann 1973). Leaves are selected foremost and are frequently taken up as litter. Flowers, fruits, seeds and pods of shrubs and trees are eaten, but few stems are taken. Plant selection may be based on olfactory cues. They sometimes make use of a foreleg to pull browse within reach or feed standing on their hindlegs like the Gerenuk *Litocranius walleri*. They also dig for roots and tubers with their hooves and horns (Kingswood & Kumamoto 1996). They are most active from dawn to early morning and in late afternoon to dusk, but are sometimes active during a full moon (Kingdon 1982). Kingdon (1982) has suggested that Klipspringers *Oreotragus oreotragus* could be competitors for food in some localities during the dry season.

Social and Reproductive Behaviour Günther's Dik-diks are territorial and monogamous, usually occurring in groups of three or four, typically comprising an adult pair with one or two offspring (Bryden 1899, Estes 1991a). Occasionally, groups of 6–12 are found within sight of one another (Kingdon 1982). The pair usually occupy a fixed territory, although in areas of high density more than one adult ♀ may share a territory. Members of a pair are sometimes seen singly.

During the day they are believed to remain in their territories. At night they may forage far beyond their territorial boundaries, the pair remaining close together (Ono *et al.* 1988). Home-ranges vary from 4 to 13.7 ha, with large ranges during dry seasons (Ono *et al.* 1988); home-ranges of ♂♂ may overlap by 65% so home-range size does not correspond directly to territory size. Distances between pairs range from 200 to 600 m (Kingdon 1982). Pair bonds are independent of territorial bonds, with pairs occasionally shifting their territories to neighbouring regions (Ono *et al.* 1988).

Territories are defended by ♂♂. Scents from preorbital and pedal gland secretions are used for marking territories, as are urine and faeces that are deposited on dung piles along territorial

borders (Kingdon 1982). Preorbital gland secretions are deposited as a black mass on branches at head-height throughout the territory and dung piles tend to demarcate boundaries. Dung piles are used repeatedly and may be up to 5 m² in size. Urination and defecation proceed in a ceremony where the ♀ defecates and urinates first and the ♂ smells and tests her urine, scrapes over her deposit and then urinates and defecates on the same spot (Kingdon 1982). Male territorial behaviour peaks when ♀♀ are in oestrus and constantly attended by their ♂. Aggression between territorial ♂♂ involves dominance or threat displays and fighting behaviour such as chasing, mock fighting, horn contact and horn-stabbing. Serious fighting is unusual, and dik-diks mostly use mock fighting maintaining an 'air-cushion' between them (Kingdon 1982, Ono *et al.* 1988, Estes 1991a).

Females in oestrus exhibit lordosis, and receptive ♀♀ respond to genital licking by raising their tail and squatting slightly. Genital licking may be followed by urine testing, but is less common in dik-diks, which Kingdon (1982) suggests could be related to water economy and might have been augmented by the revelation of circular ruffs of brilliantly white hair on each haunch. Males mount bipedally without claspings or resting on the ♀ (Kingdon 1982, Estes 1991a).

After parturition, the ♀ eats the afterbirth. Female and sire stay near the newborn for the first day of life. Thereafter, the ♀ attends to it four times a day at about sunrise, noon, dusk and midnight for about 15 min each for suckling (about 1–2 min) and grooming (Kingdon 1982). The ♂ remains on the lookout for predators while the ♀ feeds. The young is concealed for 2–3 weeks then follows the parents for a few months.

When excited or frightened Günther's Dik-diks erect the crest, vocalize with a whistling hiss ('zik-zik') with a downward extension of the proboscis, and freeze or race into the nearest vegetation. The dik-diks profit from hyraxes and guinea-fowls that alert them to the presence of large predators. Anti-predator behaviour discriminates between predators: for example, the dik-diks will whistle at Leopards *Panthera pardus*, but not at hyaenas.

Reproduction and Population Structure In the wild, in Ethiopia, births have been recorded during Aug and Sep, but throughout the year in captivity. Sexual maturity is reached before one year of age, although, in captivity, ♀♀ can conceive at less than four months of age. Duration of oestrus and interval between oestrus ranges from 1–7 and 13–21 days, respectively (Fitzgerald & Hnida 1994). Gestation period is 170–180 days (Fitzgerald & Hnida 1994). A single young is born. Offspring are precocious and colouration at birth is identical to adults. Mean birth-weight in captivity was 684 ± 100 g, about 15% of maternal weight; ♀♀ are heavier than ♂♂ although weight gain in captivity is the same in both sexes. Young are nursed for 3–4 months, but begin eating browse after one week; adult mass is attained between 12 and 18 months. A postpartum oestrus occurs about ten days after birth, which means ♀♀ can be pregnant most of the year while still having dependent young. In captivity, inter-birth intervals range from 169 to 289 days ($n = 71$; Kumamoto 1995). Longevity in the wild is believed to average 3–4 years (Kingswood & Kumamoto 1996) or 7–8 years (Hofmann 1973, Haltenorth & Diller 1980); in captivity, longevity is extended, with one wild-born specimen about 17 years old when it died in captivity (Weigl 2005).

A population in Raume Erer, Ethiopia, comprised 52–78% ♀♀ and 22–48% ♂♂ (Kurt, in Kingswood & Kumamoto 1996). The sex ratio in the wild is largely unknown, but of 126 births in captivity, 60 were ♀♀ and 66 ♂♂ (Kumamoto 1995).

Predators, Parasites and Diseases Predators include Black-backed Jackals *Canis mesomelas*, Spotted Hyaenas *Crocuta crocuta*, Caracals *Caracal caracal*, Serval *Leptailurus serval*, Leopards, Cheetahs *Acinonyx jubatus*, Verreaux's Eagles *Aquila verreauxii*, Martial Eagles *Polemaetus bellicosus* and African Rock Pythons *Python sebae* (Kingswood & Kumamoto 1996). Not a great deal is known of parasites and diseases (see Kingswood & Kumamoto 1996 for review). The larval stage of the tapeworm *Taenia madoquae* occurs in the musculature; the adult tapeworm is found in Black-backed Jackals (Jones *et al.* 1988), indicative of the predator–prey relationship between dik-diks and jackals. Acute visceral toxoplasmosis (*Toxoplasma gondii*) was diagnosed in two captive dik-diks (Dubey *et al.* 2002).

Conservation IUCN Category: Least Concern. CITES: Not listed.

Günther's Dik-diks have probably benefited by the ecological changes resulting from overgrazing by domestic stock. Traditionally, no hunting by resident nomadic pastoralists was permitted except by the odd individual, and although these dik-diks are probably subject to some poaching in areas, the current population trend appears to be stable. They are common in several protected areas, including: Omo, Mago, Yabelo and Nechisar National Parks (Ethiopia) and Marsabit, Sibiloi and Meru National Parks and Samburu National Reserve (Kenya) (East 1999). However, the bulk of the total population occurs in unprotected rangelands. If current trends continue, their status is likely to remain secure (East 1999).

Measurements

Madoqua guentheri

TL (♂♂): 588 (500–680) mm, $n = 11$

TL (♀♀): 600, 670 mm, $n = 2$

T (♂♂): 32 (20–50) mm, $n = 7$

T (♀♀): n.d.

HF c.u. (♂♂): 183 (165–205) mm, $n = 6$

HF c.u. (♀♀): 203 mm, $n = 1$

E (♂♂): 72 (60–80) mm, $n = 6$

E (♀♀): n.d.

Sh. ht (♂♂): 324–355 mm, $n = 9$

Sh. ht (♀♀): 355–365 mm, $n = 5$

WT (♂♂): 3.72 (3.5–3.9) kg, $n = 3$

WT (♀♀): 4.5, 4.6 kg, $n = 2$

Throughout geographic range (Kingswood & Kumamoto 1996)

A single adult ♀ found dead on a road (killed by a vehicle) just a few km north of Baragoi, Kenya, had the following measurements: TL: 650 mm; HF: 196 mm; E: 71 mm; Sh. ht: 385 mm; T: 32 mm; WT: 3.2 kg (Y. de Jong & T. Butynski pers. comm.)

Maximum recorded horn length is 10.8 cm for a pair of horns from Kenya (Rowland Ward)

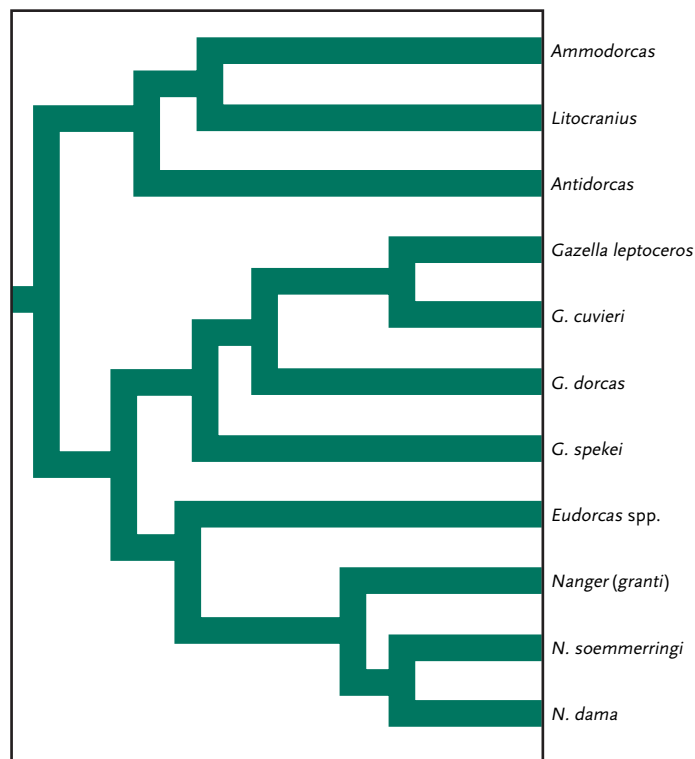
Key References East 1999; Kingswood & Kumamoto 1996; Ono *et al.* 1988; Kamau 1988.

Peter P. Hoppe & Peter N. M. Brotherton

Tribe ANTILOPINI

Gazelline Antelopes

Antilopini Gray, 1821. London Med. Repos. 15: 307.



Tentative phylogenetic tree of Antilopini (modified after Hassanin *et al.* 2012).

The genera of antelopes judged to belong to the tribe Antilopini and distinctions between tribe and subfamily have been the source of considerable confusion right up to the present. In fact, the present picture is probably even more confused than it was in the past. However, a core of ‘gazelline’ species have been consistently recognized as representing the Antilopini. These are the gazelle-like Indian Blackbuck *Antelope cervicapra* and the true gazelles, now subdivided into *Gazella*, *Eudorcas* and *Nanger*, the Dibatag *Ammodorcas clarkei* and the Gerenuk *Litocranius walleri*. It has long been questioned whether the Springbok *Antidorcas marsupialis* belongs to this group (partly because there are very early fossils with antidorcine features). Knottnerus-Meyer (1907) even erected a subfamily, Antidorcatinae, which accommodated the Springbok and some other gazelline antelopes (and see Haltenorth 1963 and Kingdon 1997). Until further research suggests otherwise, we tentatively retain *Antidorcas* as a part of Antilopini. Further, Gentry (1992), Matthee & Robinson (1999a), Groves (2000) and others unequivocally support inclusion of the extralimital Saiga *Saiga tatarica* in the Antilopini; the exact affinities of *Procapra* remain unresolved.

In recent years several authors have substantially enlarged the number of taxa in Antilopini by inserting many of the genera and species formerly clustered under Neotragini (Grubb 1993c, 2005, Hernández Fernández & Vrba 2005). Before molecular science confirmed the long-held suspicion that several of the small antelopes traditionally called ‘neotragines’ were probably living survivors of

root stocks from which more advanced lineages emerged, authors were content to use Neotragini as a convenient ‘waste-paper basket’ to accommodate a diverse collection of conservative and/or specialized small antelopes (Kingdon 1982, 1997). Wholesale allocation of ‘neotragines’ to the Antilopini, *before* their affinities have been convincingly elucidated, effectively transfers a clutch of acknowledged uncertainties from one taxon to another. This course is not followed here.

Instead of emptying problem taxa from one basket to another we have accepted that a proliferation of taxa (even if temporary and tentative) more usefully reflects current efforts to come to grips with the intricacies of antelope evolution, while acknowledging the many uncertainties and current inability of genetics to resolve many important questions. We are confident that molecular techniques will steadily improve to the point where such questions can be convincingly settled. In the meantime, it is important to advertise the challenges that antelope evolution poses and to emphasize the ecological and behavioural bases for their historical radiations.

Because most molecular studies have allocated basal positions to all the taxa formerly classed as Neotragini (Georgiadis *et al.* 1990, Allard *et al.* 1992, Gatesy *et al.* 1997, Hassanin & Douzery 1999, 2003, Matthee & Robinson 1999a) we have therefore excluded them from Antilopini and very provisionally broken up the former Neotragini into five tribes: Neotragini for *Neotragus* and *Nesotragus*, Oreotragini for *Oreotragus*, Raphicerini for *Raphicerus* and *Dorcatragus*, Madoquini for *Madoqua* and Ourebinii for *Ourebia*. Molecular analyses have been consistent in showing that *Pelea*, sometimes included in Neotragini and sometimes the only occupant of its own tribe, is a sister taxon to the Reduncini.

The Antilopini, in the sense proposed here, represents gazelle-like antelopes supposed to have adapted initially to very dry thicket in north-eastern Africa. It has been proposed that at a very early date at least one lineage entered Asia and gave rise to the Saiga. Later emigrations took gazelles and the ancestor of the blackbuck to Asia. As gazelles evolved some became larger and most adapted to open plains and deserts, acquiring exceptional resistance to scarcity of water and to heat stress. Adaptive trends toward dry-and-hot and to dry-and-cold have a strong regional bias, with the former predominantly African and the latter mainly Asian, suggesting that *Gazella* and *Antelope* may have Asian origins while *Nanger* and *Eudorcas* are decisively African.

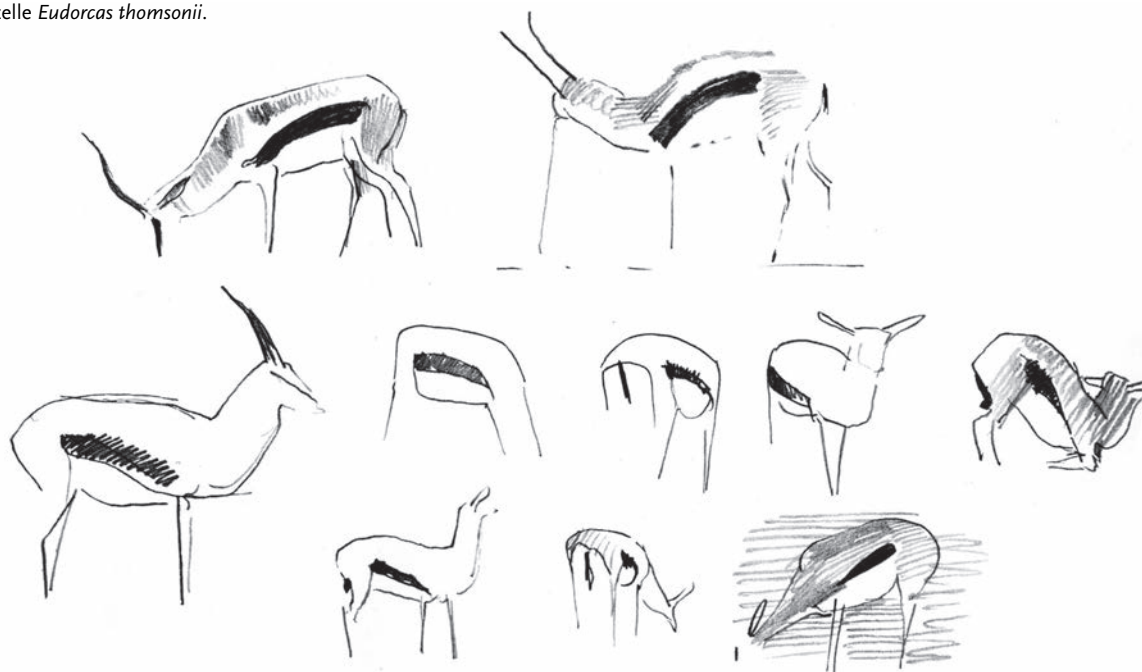
Antilopines are small- to medium-sized, long-legged, long-necked antelopes with a light-coloured pelage, large eyes and ears, and a small mouth. Females are horned (*Gazella*, *Eudorcas*, *Nanger* and *Antidorcas*) or hornless (*Litocranius* and *Ammodorcas*), although where present they are markedly less developed than in ♂♂. Pedal and preorbital glands are generally present (*Ammodorcas* lacks pedal glands). Glandular knee-tufts are present in all members except *Antidorcas* (which, in turn, has dorsal glands). Inguinal glands are present in the true gazelles only (being absent in *Ammodorcas*, *Litocranius* and *Antidorcas*) as well as in the extralimital *Saiga*; females of *Ammodorcas* and *Litocranius* have two pairs of inguinal nipples (as

does *Saiga*), whereas all other members have one (though *Antidorcas* sometimes has two pairs). While advanced in their tolerance of heat and lack of water (most employ nasal cooling techniques), their land tenure systems, brains, dentition, dietary habits and stomachs tend to be conservative. The trend towards longer limbs and necks has been taken to extremes in *Litocranius* and *Ammodorcas*, greatly enlarging their vertical feeding zones.

This is one of the few groups of antelopes (other than caprines) that have been consistently successful outside Africa, notably in Arabia and the more arid regions of Asia. The major factors influencing their success must lie in their tolerance of heat, their ability to extract adequate moisture from their diet, and their speed and wariness. Upper limits on body-size are principally determined by their reliance on protein-rich diets.

Jonathan Kingdon

Thomson's Gazelle *Eudorcas thomsonii*.



GENUS *Gazella* Slender Gazelles

Gazella de Blainville, 1816. Bull. Sci. Soc. Philom. Paris 1816: 75.

This genus formerly embraced all the gazelle-like antelopes, except for the Springbok *Antidorcas marsupialis*, Gerenuk *Litocranius walleri* and Dibatag *Ammodorcas clarkei*, and the Indian Blackbuck *Antelope*. Because the genetic profiles of the last species have been shown to nest within the diverse forms of the genus *Gazella* (in the former, more inclusive concept of that genus) (Effron *et al.* 1976), the more distantly related *rufifrons*- and *granti*-groups were formally removed from *Gazella* by Groves (2000), and placed in separate genera, *Eudorcas* and *Nanger* respectively, thereby leaving *Gazella* as a monophyletic genus. Grubb (2005) recognized ten species, four of which occur in Africa: Slender-horned Gazelle *Gazella leptoceros*, Cuvier's Gazelle *G. cuvieri*, Speke's Gazelle *G. spekei* and Dorcas Gazelle *G. dorcas*.

The horn cores are less compressed than in related genera, and the rings are comparatively less marked. In the teeth, the lingual stylids and anterior folds of the molars are well developed. Unlike the related

genera, the nasofrontal sutures are straight, forming together either a V-shaped wedge into the frontals, or a mild arch. Characteristic of the genus is the noticeably long and narrow basioccipital, with only small anterior and posterior tuberosities with a wide, smooth space between them rather than a narrow channel. The auditory bullae are greatly enlarged, as expected in arid zone animals. The rhinarium extends all along the dorsal rims of the nostrils.

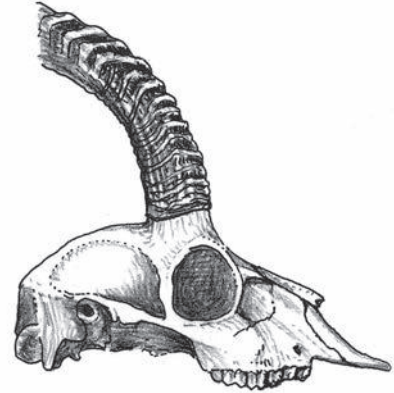
Most members of the genus are unambiguously arid-adapted, and are noticeably pale in colouration, usually pale fawn, with any trace of flank stripe being only somewhat darker than the overall body tone, and rarely black; the facial markings however may be quite well expressed. In Africa, the distribution is centred around the Sahara and in the northern part of the Somali Arid zone or Horn of Africa.

Colin Groves

Gazella dorcas DORCAS GAZELLE

Fr. Gazelle dorcas; Ger. Dorkasgazelle

Gazella dorcas (Linnaeus, 1758). Syst. Nat., 10th edn, 1: 69. 'Habitat in Africa'; restricted to Lower Egypt by Blaine (1913: 292), west of the Nile R. (Osborn & Helmy 1980: 508).

LEFT: Dorcas Gazelle *Gazella dorcas*.ABOVE: Lateral view of skull of Dorcas Gazelle *Gazella dorcas*.

Taxonomy Polytypic. Six subspecies are generally recognized (Groves 1981b, 1985a, Yom-Tov *et al.* 1995, Grubb 2005), with the extinct Saudi Gazelle *G. saudiya* once considered a subspecies, but now regarded as distinct (Groves 1988, Rebholz *et al.* 1991, Grubb 2005; and see Hammond *et al.* 2001). The Indian Gazelle or Chinkara *Gazella bennetti* was also formerly included as a subspecies of *G. dorcas* (Groves 1969, Corbet 1978), but is also now considered distinct (Furley *et al.* 1988, Groves 1988, Grubb 2005), as supported by genetic evidence showing *G. bennetti* grouping in a clade with the Goitered Gazelle *G. subgutturosa*, Slender-horned Gazelle *G. leptoceros* and Cuvier's Gazelle *G. cuvieri* (Hammond *et al.* 2001, R. Hammond pers. comm.). In previous classifications, Lange (1972) and Gentry (1972) retained the forms *littoralis* and *neglecta* as separate subspecies of *G. dorcas*, while Groves (1981b) considered *neglecta* as a synonym of *osiris* and included *littoralis* in *G. d. isabella*; Alados (1986/87) included *osiris* in *G. d. dorcas*. However, one recent phylogeographic analysis, involving only mitochondrial DNA, found no evidence for any clear-cut geographic pattern of genetic structure and sheds doubt on the

validity of any proposed subspecies (Lerp *et al.* 2011). The treatment presented here provisionally follows Grubb (2005), pending the availability of studies involving nuclear markers. *Gazella d. pelzelni* has sometimes been considered a separate species (Haltenorth 1963), a viewpoint that was contested by Gentry (1972) and Groves (1985b); the form remains of uncertain taxonomic status (Lerp *et al.* 2011). Synonyms: *beccarii*, *cabrerae*, *corinna*, *isabella*, *isidis*, *kevella*, *littoralis*, *maculata*, *massaesyra*, *neglecta*, *osiris*, *pelzelni*, *rueppelli*, *sundevalli*. Chromosome number: $2n = 31$ in ♂, $2n = 30$ in ♀; the karyotype has an X-chromosome translocation; all autosomes are metacentric, but the Y is a small acrocentric (Effron *et al.* 1976).

Description A small gazelle, pale sandy-fawn in colour with paler sandy stripes on the flanks bordered underneath by a dark-brown stripe that extends to the hindquarter and there merges with the white belly. The dark brown varies in expression, being sometimes distinct and sometimes faint and grading into the paler zone. The dark stripe is darker in winter and fades in summer (Groves 1981b). The forehead

is darker and bristles surround the mouth. There is a tawny stripe on the cheeks, starting from the preorbital gland and ending above the mouth, separated by a white band from the base of the horn to the upper lip. Eyes large, with white circumocular rings. Tawny colour darker above the base of the tail and there is a black, hairless patch on the buttock just beneath the tail. Anus forms a horizontal bar beneath the tail in ♂♂; perineum includes the vulva and appears as a wide 'T' in ♀♀. Upper buttock white with dark, tawny stripes on periphery. Tuft of hair on hock of hindleg and at the end of tail. Horns in ♂ are medium-sized, lyrate and strongly ringed (20–24 rings); in ♀ horns are thin, and weakly ringed (usually 16–18 rings).

Geographic Variation

- G. d. pelzelni* (Pelzel's Gazelle): N Somalia (northern coastal plain of districts of Awdal, Ouest Galbeed and Ouest Sanaag), below 1000 m in Djibouti and Eritrea, and Ethiopia (Afar, Harar, Tigray and Wollo). Distinct large-bodied, long-necked race. Long horns with tips hardly or not at all turned inwards, widely flared, and sparsely ringed; colour brightly sandy-ochre with well-marked lateral flank band and dark face stripes, dark knee-tuft and a trace of dark nose-spot.
- G. d. isabella* (includes *isidis* and *littoralis*) (Isabelline Gazelle): east of the Nile R., in N Ethiopia and Eritrea, Sudan (including the Red Sea Hills, Mohamed Gol range, Atra Rabai Hills, Khorasot, Berha, Suakin, Khor Hadhad, Jebel Bawati), extending into Egypt and S Israel; perhaps Gaza; probably SW Jordan. A large race, darker and less lively coloured than *pelzelni*; brown-grey with reddish tones and dark markings, including the dark nose-spot; horns shorter, stouter, more widely spread than *pelzelni* with inwardly turned tips.
- G. d. beccarii*: Baraka and Bogos, in the highlands of the upper Anseba R., Eritrea. Richer, more chestnut coloured than *G. d. isabella*; flank-band is red-brown; nose-spot absent; very large skull and nasals are long.
- G. d. osiris* (includes *neglecta*): Sudan (Nakheila, Dongola, Sennaar, Singa, Omdurman, Abu Hamed Bapr, Kassala, Shendy, between Aswan and Khartoum, Kordofan, El Fasher, El Baja), west into Chad, Niger, Burkina Faso, Mali, Mauritania (between Rosso and Nouakchott), Western Sahara (Rio de Oro, Rio de Oro–Mauritania border, loom radius of Villa Cisneros, Peninsula of Dakhla), Morocco (Lower Drâa R.) and Algeria (Hoggar, Tadmeit). Much paler than the previous three subspecies; dark band not well marked, though pygal band more so; face markings paler, with light face stripes pure white; no nose-spot; skull small; horns longer, more narrowly ringed in ♂ and relatively longer in ♀.
- G. d. massaesyla* (includes *cabrerai*): Algeria (between Constantine and Biskra, Biskra, Weinat el Aries, Bled Salawin, Medjedj, Chott el Honda, between Ain Tabia and Messegem) and the Rif Plateau of Morocco. Richer, more ochre-coloured than *osiris*; skull narrow across the horn-base; horns lyrate and more widespread, tips less inwardly turned than in *osiris*. A small distinct population occurs in M'Sabih Talaa (Sidi Chiker) Reserve (middle Atlantic Morocco) (Alados 1986/87, Godinho *et al.* 2012).
- G. d. dorcas*: Egypt (Western Desert including Aswan), Sudan (Wadi Halfa), Libya, Tunisia, Chad (Tibesti). Brighter, less ochre and more rich-fawn than *massaesyla*; flank-band well marked and well expressed; pygal band clearer; lateral face-stripes dark; skull short-snouted and broad; horns long in both sexes, lyrate in ♂ with numerous close rings.

Similar Species

Gazella leptoceros. Sympatric. Slightly larger, with more elongated upright horns; paler-coloured and almost without head marks (Dragesco-Joffé 1993).

Eudorcas tilonura. Sympatric with the Isabelline Gazelle *G. d. isabella*. Larger, with a straight back when standing; forehead and bridge of the nose are rufous; horns very short, inwardly hooked at the tips and prominently ringed in ♂♂; deep reddish band on flanks, extending from the shoulder to the hindquarters; tail relatively long, its base rufous and gradually changing to black.

E. rufifrons. Sympatric with *G. d. osiris*. Larger, with more robust build. Deep reddish in colour with a uniformly tan-coloured upper coat; forehead red; faint red and cream-coloured lines run from the eyes to the nose; horns fairly long, slightly S-shaped over their length and diverging towards the tips; flanks with thin dark-brown stripe, which runs along the side between the legs, demarcating the edge of the white underparts; tail relatively long, ending in a black tuft that contrasts sharply with the white buttock.

Distribution The most widely distributed Sahelo-Saharan antelope, Dorcas Gazelles are also the only African gazelle species to occur outside of the continent, their range extending into the Sinai, S Israel and W Jordan (Mallon & Kingswood 2001a); may also persist in S Syria (Masseti 2004).

Historical Distribution Dorcas Gazelles once ranged widely from Morocco, Western Sahara, Mauritania and Senegal (as vagrants during droughts only; Bourlière *et al.* 1976) in the west, throughout the Sahelo-Saharan region to the Red Sea and the Afar region in Eritrea–Ethiopia west of longitude 50°E (see East 1999, Mallon & Kingswood 2001a, Lafontaine *et al.* 2005).

Current Distribution Populations have been massively reduced north of latitude ca. 31° 14' N and disjunct populations extend southwards to latitude ca. 13° 30' N. In Morocco, only one group remains north-west of the Atlas in the M'Sabih Talaa Reserve (near Chichaoua) (Cuzin 1996), whereas east and south of the Atlas small groups are widely scattered throughout the Moulouya River Valley; along the Moroccan–Algerian border; on the plains between Zagora and Tafilalet, and throughout the Oued Drâa Valley; small groups survive in Western Sahara, particularly in the south in the Adrar Soutouf (Cuzin 1996, 2003, Aulagnier *et al.* 2001).

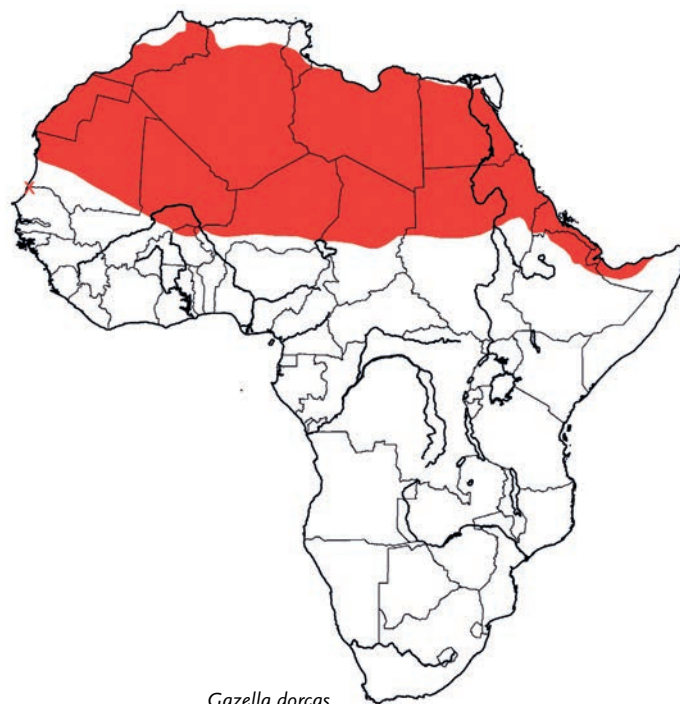
The species' distribution in the other northern range states remains poorly known and scattered. In Algeria, where its current range still includes much of the Algerian Sahara, the northern limit is now generally marked by the Saharan Atlas, although a few Dorcas Gazelles are reported to survive on the Hauts Plateaux near the border with Morocco (Kowalski & Rzebiak-Kowalska 1991, De Smet & Smith 2001). In Tunisia, Dorcas Gazelles had largely disappeared from the northern part of the country by the 1960s, and today are limited to the southern half of the country, south of a line running from Tamerzna, at the Algerian border, eastward to Gafsa and Maknassy, southward to Matmata, and south-eastward to Medenine and Ben Gardane, near the Libyan border (Kacem *et al.* 1994, Smith *et al.* 2001). There is limited information on their current distribution and status in Libya, where Misonne (1977) reported them as quite common in the south-east in 1968–69 (estimating

more than 100 in the Jabal Uweinat region, with a further 30–40 in Wadi Ghazal) and where Essghaier (1980) reported on herds of up to 100 Dorcas Gazelles seen in the 1960s in the Hamada al Hamra in W Libya. They are now extirpated in many areas, but are probably still the most widespread antelope in the country (Khattabi & Mallon 2001). In Egypt, they are still found in highly fragmented populations scattered throughout the Western Desert. In the north they occur in the western Qattara Depression, westwards to the Libyan border (including around the Siwa oasis). Small populations are found in the depressions west of L. Nassir, and in uninhabited oases of the Nubian Desert and in wadis of the Gilf El Kebir Plateau. Dorcas Gazelles are found in small numbers in the wadis east of the Nile R., with the largest population in the southern part of the Eastern Desert towards the Sudan border (Saleh 1987, 2001, Saleh *et al.* 2003, El Alqamy & Baha El Din 2006).

South of the Sahara there is limited information on the status of the species in Mauritania, where it has been largely extirpated and survives only in small numbers in very remote areas (Sournia & Verschuren 1990); a few animals survive in the south-eastern corner of Banc d'Arguin N. P., while a small population of ~40 individuals survives on Tidra, an island situated in the south-west of Banc d'Arguin N. P. (Araújo *et al.* 2005, Lamarque *et al.* 2006). In Senegal, animals were reintroduced from Mauritania to Djoudj N. P. in the north-west (Dupuy 1984), but there is no recent information on this population; they were also reintroduced to enclosures in Guembeul Special Reserve in 2007 (Abáigar *et al.* 2008) and Ferlo-Nord in 2009 (not mapped). In Burkina Faso, where they occurred in the northern Sahel zone, they may survive in the northern part of Sahel Partial Faunal Reserve, while in Nigeria, where they used to occur in the north-east in the vicinity of L. Chad (Anadu & Green 1990), they are now probably extinct. The strongholds for Dorcas Gazelles are North Tamesna in Mali (south-west of the Adrar des Iforas), Termit in E Niger (Newby *et al.* 2004, Wacher *et al.* 2004a, b, 2008), and Manga and the Ouadi Rimé–Ouadi Achim Faunal Reserve in Chad (Monfort *et al.* 2004, Wacher & Newby 2010, Wacher *et al.* 2011). In Sudan, they still occur in the deserts in N Sudan and in the Red Sea Hills. In Djibouti, the Dorcas Gazelle is the most frequently encountered large mammal, occurring throughout the territory (Laurent & Laurent 2002, Heckel & Rayaleh 2008), while in Ethiopia, Eritrea and Somalia they still tend to occur relatively widely within their historical range (East 1999).

Habitat The Dorcas Gazelle occurs in a wide range of habitats. These include steppe-like coastal desert and stony coastal wadi outwash plains, uninhabited oases, (vegetated) wadis, edges of inland sabkhas, small marshes, acacia groves, open acacia woodland and undisturbed margins of rivers with sparse vegetation. Rainfall in the species' range varies from almost nil to 400 mm per annum. Although they occur in coastal plains and desert depressions (Osborn & Helmy 1980), and even the sparsely vegetated areas above 2000 m in Hoggar (Dupuy 1967), they are absent from hyper-arid deserts and upper elevations of the central Saharan massifs (Grettenberger 1987). Dorcas Gazelles are, however, found in vegetated depressions in the hyper-arid interior of the Egyptian Western Desert (Osborn & Helmy 1980, Saleh 1987, 2001).

During the hot season, Dorcas Gazelles concentrate in habitats associated with temporary water resources and river beds where



Gazella dorcas

trees and shrubs provide shade and cover. The gazelles disperse into less woody habitats during the wet and cooler season (Grettenberger & Newby 1990). Seasonal dispersion does not seem to take place in Egypt, where Dorcas Gazelles were frequently observed in areas without surface water throughout the year (M. Saleh pers. comm.). At the southern limit of its range, where the Red-fronted Gazelle *Eudorcas ruffifrons* occurs, the latter is generally found in the more wooded wadi valleys, whereas Dorcas occurs in the more open grasslands. In areas with high hunting pressure Dorcas Gazelles tend to frequent more often those habitats where access is more difficult, such as sand dunes and hills (Cuzin 2003).

Abundance Early reports from the nineteenth and early twentieth centuries generally recorded Dorcas Gazelles as common and locally abundant (e.g. Lavauden 1926a, Joleaud 1929). Despite a massive reduction in numbers and depletion of habitat by humans and their livestock, the Dorcas Gazelle survives, albeit in reduced numbers, in almost all range states, in which it is often the most common gazelle species.

Population numbers in Morocco totalled 200–600 in the mid-1990s, excluding Western Sahara where the population may number in the several hundreds (Cuzin 1996, Aulagnier *et al.* 2001); the current wild population has been estimated at 800–2000 animals (Cuzin *et al.* 2007). There are no recent reliable population estimates for Algeria, Tunisia and Libya, although the population in each country is unlikely to exceed 1000 individuals and only small groups are now encountered. A population of 1000–2000 is in rapid decline in Egypt, mostly outside protected areas (Saleh 2001).

South of the Sahara, numbers of Dorcas Gazelles are more substantial, and East (1999) estimated a total population for sub-Saharan Africa of 35,000–40,000 animals, although actual numbers are almost certainly lower. The strongholds for the species include: Mali, where the population is in the order of 2000–2500 (East 1999); Niger, where Dragesco-Joffé (1993) earlier estimated

the population at 20,000 (though these numbers are pre-1991); and Chad, where they survive in the thousands in the Manga and especially the Ouadi Rimé–Ouadi Achim Faunal Reserve (East 1999, Scholte 2001, Monfort *et al.* 2004, Wacher *et al.* 2004b, Wacher *et al.* 2011). A survey of the Termit Massif estimated the population of Dorcas Gazelles at 3000 gazelles, distributed primarily through the southern parts in association with trees (Wacher *et al.* 2008). Dorcas Gazelles also survive in good numbers in the Horn countries, although reliable population estimates are not available.

In the driest habitats, observed Dorcas Gazelle densities range from 0.1 to 0.6 gazelles/km². Even lower densities were found in habitats in proximity to human settlements: from 0.04 to 0.1/km² (Essghaier 1981, Hashim 2000). In higher-quality habitat, such as is found in large wadis and foothills, observed densities range from 0.31–3.2/km² in Sudan (Essghaier 1981, Hashim 2000), 1.2–7.3/km² in Chad (Monfort *et al.* 2004), and up to 9.6/km² in Morocco (Loggers *et al.* 1992). Encounter rates are reported by various authors, including 0.23/km in the Ahaggar in Algeria (Wacher *et al.* 2005) and 0.83/km in the Termit (Wacher *et al.* 2004b).

Adaptations Unlike camels and antelopes such as Beisa Oryx *Oryx beisa*, the Dorcas Gazelle is not bradymetabolic (i.e. having a low resting metabolism) and its main means of heat dissipation are thermal panting and sweating (Wilson 1989). Some protection is also obtained via the pelage. The coat consists of a short, dense undercoat with a covering of guard hairs up to 35 mm that can be erected to form an insulating barrier (Ghobrial 1970, Wilson 1989).

In Sudan, Dorcas Gazelles with access to free water drank an average of 3.1 and 4.5% per day of their body-weight in winter and summer, respectively (Ghobrial 1970). In winter, 69.1, 4.5 and 26.4% of total water was obtained by free, preformed and metabolic water, respectively. In summer, these percentages were 82.4, 2.4 and 15.2%, respectively (Ghobrial 1974, Wilson 1989). Often, however, there is no surface water available in the Dorcas Gazelles' range, particularly during the dry season. Dorcas Gazelles, as most other desert herbivores, react by reinforcing physiological mechanisms with behavioural ones. They resort to mechanisms of escape (southbound migration into the Sahel) and retreat (shade-seeking at mid-day) to survive (Wilson 1989). Dorcas Gazelles strongly depend on moisture-rich food throughout their range (Grettenberger 1987, Wilson 1989). However, they can survive extreme dehydration: animals maintained under minimal water conditions for 10 days showed a decrease in feed intake by 42%, while body weight was reduced by 29%, water content in faeces by 41% and urine volume by 66%. Serum concentrations of sodium, potassium and chloride increased by 23, 44 and 18%, respectively. The gazelles appeared normal after rehydration (Mohamed *et al.* 1988). Ghobrial (1974) presented lower values in what was probably a less extreme dehydration experiment.

Foraging and Food Under dry conditions Dorcas Gazelles primarily browse because of the high moisture content and availability of browse. Herbaceous plants, including many annual grasses, are the most important components of the diet during the wet season (Grettenberger 1987, Wilson 1989). In Morocco, faecal analysis of an enclosed population north of the High Atlas (M'Sabih Talaâ) indicated the shrub *Ziziphus lotus* as dominant forage in summer, while

forbs dominated forage in autumn. Grasses were only significant in spring when forming 46% of identified items (Loggers 1991). In S Morocco during a dry season, preferred plants were *Maerua crassifolia*, *Acacia raddiana*, *Nitraria retusa*, *Argania spinosa*, *Antirrhinum ramosissimum*, *Salsola sieberi* and *Launea arborescens*, and animals never seemed to drink (Cuzin 1998). Year-round observations (Essghaier 1981, Abdelhamid 1998), showed that ca. 26% of the diet comprised grass, 19% forbs and 55% trees, and especially (dwarf) shrubs. The latter include *Anabasis oropediorum*, *Atriplex mollis*, *Artemisia herba-alba*, *Astragalus armatus*, *Calligonum comosum*, *Helianthemum* spp., *Gymnocarpus decander*, *Leptadenia pyrotechnica*, *Periploca laevigata*, *Rhanterium suaveolens* and *Suaeda* spp. Trees include *Acacia raddiana*, *A. tortilis*, *Balanites aegyptiaca*, *Maerua crassifolia* and *Ziziphus lotus*. In addition to a selection of annual grasses, grasses include: *Aristida uniplumis*, *Cenchrus ciliaris*, *Panicum turgidum*, *Stipagrostis uniplumis* and *Stipa* spp. Forbs represented in the diet include *Chrozophora broechiana*, *Colocynthis vulgaris*, *Erodium* sp., *Lycium arabicum*, *Medicago trunculata*, *Plantago ovata*, *Salvia vermiculata* and *Tribulus* spp. In the Western Desert of Egypt, the diet comprised *Nitraria retusa*, *Calligonum comosum*, *Alhagi maurorum*, *Calligonum comosum*, *Phragmites australis*, *Sporobolus spicatus*, *Acacia raddiana*, *Panicum turgidum* and *Zygophyllum album* (Salem & Saleh 1998).

The Dorcas Gazelle exhibits seasonal movements in response to the availability of forage. In El Baja, Sudan, the movement is southerly during the late dry season and northerly immediately after the beginning of the wet season and lasts often throughout the cold season (Hashim 2000).

Social and Reproductive Behaviour Dorcas Gazelles form groups varying in size, depending on the season and the extent of disturbance. Occasionally, aggregations of several groups can be found, totalling over 100 individuals, most often in areas with sudden ample food resources, as may occur after locally abundant rains (Scholte 2001, Laurent & Laurent 2002, Monfort *et al.* 2004). In heavily poached and disturbed habitats in Sudan, the mean group size was 1.9 ± 0.3 ($n = 21$). The groups were smaller (mean 1.6 ± 0.2 , range 1–3, $n = 14$) during the wet season compared with the dry season (mean 2.4 ± 0.8 , range 1–7, $n = 14$), suggesting pairing up for breeding (Hashim 2000). Pairing for breeding has been reported in hostile conditions, but larger groups are formed in response to disturbance by humans or dogs (Loggers 1992). Mean observed group size of Dorcas Gazelles in Niger was 2.5 ± 81 (range 1–13), varying in four different habitats from 2.2 ± 1.5 ($n = 297$), 2.4 ± 1.3 ($n = 141$), 2.6 ± 1.9 ($n = 133$) and 3.3 ± 2.2 ($n = 46$); these differences in group sizes were attributed to seasonal changes in localized areas as habitat quality changes (Grettenberger 1987). In Feb–Mar 2002, Dorcas group sizes ranged between 2.5 and 3 in three different habitats in Niger (Manga, Termit and Aïr–Ténéré) (Newby *et al.* 2004). In C Chad in September 2001 (the Manga and Ouadi Rimé–Ouadi Achim Faunal Reserve), most frequent group sizes encountered were ones and twos, but mean group size averaged 3.5 (S.D. 4.66, $n = 1145$ groups) with 87% of individuals in groups up to 20 strong and the remainder in scattered assemblages of 50–100 or more (Monfort *et al.* 2004, Wacher *et al.* 2004b). Generally, groups are highly mobile and on many occasions mingle with Red-fronted Gazelles *Eudorcas rufifrons* in the southern parts of the Dorcas Gazelle's distribution.

Females groups consist of adult ♀♀ and their young, juvenile ♀♀ and juvenile ♂♂ less than about 18 months old. These female groups frequent (male) territories and when accompanied by the ♂ their groups average 1.5 young (range 1–5) and 2.5 ♀♀ of reproductive age (range 1–8). Single adult ♀♀ were also often seen (Loggers 1992). Males either live alone, territorially or in bachelor groups of up to ten individuals (Loggers 1992). Temporary associations of ♂♂ and ♀♀ occur when bachelors encounter a female group that is not attended by a territorial ♂; these bachelors attempt to court ♀♀ but are usually unsuccessful.

Adult ♂♂ occupy territories throughout the year, and establish dung heaps throughout territories rather than concentrating them on the peripheries (Essghaier & Johnson 1981, Loggers 1992). Territories are apparently delineated by topographic features such as the tops of ridges and sebkhas (Essghaier & Johnson 1981). A conspicuous display is used in the formation of the faecal heaps: first a ♂ paws at the ground, then stretches the scraped area to urinate and finally crouches with his anus just above the ground to deposit dung heaps. Males periodically scrape old dung from heaps especially during peaks of sexual activities (Essghaier & Johnson 1981).

The ♀ comes into oestrus between the beginning of Nov and the end of Dec (I. Hashim pers. obs.), when she attracts the ♂ by lifting the tail and slightly curving her back. The ♂ sniffs the female's perineum, retracts his lips, lifts the head and stretches his lips. If the ♀ gallops, the ♂ gallops behind her, showing a series of courtship manoeuvres, including licking the face and muzzle of the ♀, nose-forward posture, flehmen, following in a walk, circling with horn clashes, touching the buttocks with the base of the horn, and standing beside the ♀ with the head alongside her neck and belly with an erect penis. Mounting is preceded either by the ♂ tapping the ♀ at the buttock or striking her underside with his foreleg (laufs Schlag). In mounting, the ♂ does not hold the ♀, but rather stands on his hindlegs, holding his forelegs, bending backward from the knee, above the ♀. He then makes a quick pelvic thrust with penetration lasting only a few seconds. After mating, the ♂ almost immediately leaves the ♀ (Essghaier 1981, Sayeid 1999).

Newborn Dorcas Gazelles are well developed, with eyes fully open, and attempt to stand within the first hour of birth. The ♀ eats the afterbirth. Young lie down for three weeks during the day and during the night, with the neck and the head stretched on the ground. They show no tendency to escape when approached by an intruder. Nursing usually takes place away from the delivery place and the neonate suckles only for a very short time, but on several occasions during the day. Mothers induce defecation in nursing young and ingest faeces, probably a means of water conservation and protection (Dragesco-Joffé 1993). The mother produces milk for six months after birth but the neonate starts foraging at 17 days of age (Sayeid 1999).

Reproduction and Population Structure In Niger, births peak in Dec with a ratio of one juvenile to 4.7 adults (Grettenberger 1987). In Morocco, young are born mainly during late Oct and Mar; the ratio of young to adult ♀♀ is 0.91 in Sep and 0.83 in Jan–Feb (Loggers 1992). In Djibouti, births occur in the cold season (Nov–Jan) and the wet season Feb–May (Laurent & Laurent 2002).

Gestation period is about six months (Slaughter 1971, Dittrich 1972). One young is born, rarely two (Furley 1986, Grettenberger

1987, Sayeid 1999). Young weigh about 910 g at birth (Mohamed Nour 1998), and birth-weight is positively correlated with the longevity of the ♀ (Alados & Escos 1991). In captivity, the age of the ♀ at first birth varies from 346 to 929 days (Mentis 1972, Loggers 1992). It has been suggested that sexual maturity and age at first birth follow an allometric pattern among *Gazella* species (Cassinello 2005).

Loggers (1992) reports longevity in the wild at 4.2 years ($n = 12$) for adult ♂♂, 5.4 years ($n = 5$) for adult ♀♀ and nine years for oldest specimens of both sexes; Weigl (2005) gives longevity in captivity as more than 23 years. As a general rule, and as expected in polygynous mammals, ♀♀ live longer than ♂♂, high inbreeding coefficients causing a generalized decrease in female longevity (Cassinello 2005).

Sex ratio in Dorcas Gazelles is skewed (68 ♂♂ : 100 ♀♀), possibly due to the males' vulnerability to predators while holding territories (Grettenberger 1987). Fecundity in captivity ranges from 0 to 2.18 calves per year, being lower in young ♀♀ than middle-aged ♀♀ (Alados & Escos 1991).

It has been suggested that Dorcas Gazelles may experience sperm competition due to their relatively high gonadosomatic index (testes weight/body weight), which might explain its higher sperm quality in comparison with other *Gazella* spp. (Cassinello *et al.* 1998).

Predators, Parasites and Diseases Large predators such as the Cheetah *Acinonyx jubatus* have been mostly exterminated throughout the range of Dorcas Gazelle. Remaining predators are Golden Jackals *Canis aureus*, while young may be taken by smaller predators such as Red Foxes *Vulpes vulpes* and Rüppell's Foxes *Vulpes rueppellii* and large eagles. In populated areas, domestic dogs are important predators.

In Morocco, low levels of nematode ova were reported from six individuals and *Strongyle* ova from one gazelle (Loggers 1992); Hufnagl (1972) reported that gazelles usually harboured stomach and intestinal worms such as *Strongyloides* and *Trichurus*, and the faeces often contained eggs of Anoplocephalidae (cestodes) and *Oxyurus*. Haenichen *et al.* (2002) reported on infection of pregnant gazelles with an unusual form of algae, *Chorella*, which causes the green granulomatous inflammation known as 'Chlorellosis'. In captivity, the presence of nematode eggs in faeces was relatively low in a comparative study with other gazelle species, and not related to individual inbreeding coefficients (Cassinello *et al.* 2001). Diseases such as myocardial infarct and aortic arteriosclerosis are reported by Griner (1983), and Furley & Wardman (1985) recorded necrotic stomatitis in Al Ain Zoo. Dittrich (1970) attributed some deaths in captivity to septicaemia and gastroenteritis. In Egypt, diseases transmitted by domestic herbivores to gazelles are becoming a serious problem (Baha El Din 1998).

Conservation IUCN Category: Vulnerable A2cd. CITES: Appendix III (Tunisia). CMS: Appendix I.

Since the late 1800s, the distribution of Dorcas Gazelles in the northern Sahara has been in decline, and by the mid-1900s Dorcas had largely disappeared from the Atlas Mts and Mediterranean coastal areas (Mallon & Kingswood 2001a, Lafontaine *et al.* 2005). From the 1950s onwards numbers south of the Sahara declined rapidly as well (East 1999). Motorized hunting has had a major impact on populations aggravated by drought, as well as habitat loss and degradation due to expanding agriculture and overgrazing by sheep and goats. In N Niger only 0.3% of Dorcas Gazelle observations

were made in the vicinity of nomads, 0.6% with goats, 1.9% with donkeys and 10.9% with camels (Grettenberger 1987). On the other hand, Dorcas Gazelles survive in El Baja, Sudan, amongst large herds of sheep and camels that intensively utilize the area during the dry season, but they avoid close contact with humans and livestock (Hashim 2000). Competition with livestock and capture of young for the pet trade are said to be the main threats to the survival of Pelzeln's Gazelle in Djibouti (Laurent & Laurent 2002). In addition to persecution by local communities and militia, there have been reports of massive slaughters by visiting Arab hunting 'parties' in parts of Africa, including the Sahel (Cloudsley-Thompson 1992), Egypt (Saleh 1987, 2001) and Morocco (Cuzin 2003).

Dorcas Gazelles still occur, in much reduced numbers, in all range states (Lafontaine *et al.* 2005). Even in areas under severe pressure, such as in the coastal plain of N Somalia, tens of Pelzeln's Gazelles were observed close to the expanding cities of Berbeira and Bosaaso (Laurent & Laurent 2002). Relatively large numbers were observed in central grasslands of Oudi Rimé–Ouadi Achim Faunal Reserve in Chad in 2001, when more than 4000 were counted over 20 days, with groups of 70–100 animals seen in some places (Monfort *et al.* 2004, Wachter *et al.* 2004b; and see Wachter *et al.* 2011). The survival of Dorcas Gazelles, relative to some other congenics, may be explained by their high fecundity rate, and its ability to make seasonal shifts that allow it to exploit localized areas with high-quality and moisture-rich forage (Dragesco-Joffé 1993, East 1999).

When protected, Dorcas Gazelle populations recover rapidly, as shown in Djibouti after the 1971 hunting ban (Künzel *et al.* 2000, Laurent & Laurent 2002). In Israel, an annual population growth of 8% was observed during 1964–85 following the implementation of appropriate conservation measures (Yom-Tov *et al.* 1995). Protected areas known to hold important populations of the species include: M'Sabih Talaa Reserve and El Kheng Reserve, established near Tarda (Morocco); Tassili and Ahaggar National Parks (Algeria); Bou-Hedma, Sidi Toui, Dghoumes, Oued Dekouk and Djebil National Parks (Tunisia); New Hisha N. R., Sabratha, and Surman (enclosed) and El-Kouf N. P. (Libya); Elba N. P. (Egypt); Banc d'Arguin N. P. (Mauritania); Ouadi Rimé–Ouadi Achim Faunal Reserve (Chad); and Mille-Sardo Wildlife Reserve (Ethiopia). Numbers in Aïr–Ténéré National Nature Reserve (Niger), a former stronghold, have declined dramatically (J. Newby pers. comm.).

In managed breeding programmes *G. d. osiris* is the best represented subspecies with around 170 captive individuals (T. Abáigar pers. comm.). The limited information available suggests that other subspecies are poorly represented. However, Dorcas Gazelles are believed to be widely present in privately owned, captive collections in the Middle East. Most of these stocks are imported from Egypt, the horn of Africa and Sudan, although in most situations little attention is paid to managing them according to origin. A notable exception are the stocks at Al Wabra in Qatar where separate groups from Egypt, Sudan and the southern Red Sea coast (*G. d. pelzelni*) have been managed with the objective of keeping them separate.

In Morocco, a stock of captive Dorcas Gazelles has been maintained at 100–200 animals for many years at the Royal Hunting Park at Bouznika, from which many have been exported to the zoo community, though comparatively few have survived. There are no records as to the precise origin of this stock. They are believed to be exclusively Moroccan (P. Rousselon pers. comm.), although it

is suspected that they may represent animals from both north and south of the High Atlas (F. Cuzin pers. comm.), in which case they might represent a mix of putative *massaesyia* and *osiris*. Up to 150 of this stock were placed in a high-altitude enclosure at Enjil, in habitat normally occupied by *G. cuvieri*. They have not flourished and only three ♀♀ and some 20+ ♂♂ were present in 2006.

Two important enclosed populations in Morocco are believed to be based on animals of local wild origin from north and south of the major ecological barrier in the region, the High Atlas mountain chain. These populations offer an opportunity to investigate any biological basis for subspecific differences between *massaesyia* and *osiris*. At M'Sabih Talaa near Marrakesh, Dorcas Gazelles from the plains north of the High Atlas (putative *massaesyia*) have been protected since 1952 and fenced for most of that time, numbering more than 250 in 2006 (HEFLCD, Morocco). A smaller group (ca. 30 in 2006) enclosed south of the High Atlas at El Kheng should represent the southern form and should compare directly with the Dorcas Gazelles of southern origin held at Almeria in Spain (and see Godinho *et al.* 2012).

In summary, the species seems to do well in captivity when properly managed. The future conservation of Dorcas Gazelles would greatly benefit from a comprehensive update of its taxonomy over the entire range, more effective protection of the species' remaining populations and strongholds, and well-managed captive-breeding programmes.

Measurements

Gazella dorcas

G. d. dorcas

HB (♂♂): 902 (871–958) mm, n = 8

HB (♀♀): 869 (830–924) mm, n = 6

T (♂♂): 152 (120–180) mm, n = 8

T (♀♀): 138 (120–179) mm, n = 6

E (♂♂): 125 (120–130) mm, n = 8



Dorcas Gazelle *Gazella dorcas*.

E (♀ ♀): 125 (120–129) mm, n = 6
 WT: 15.4 (14.0–18.0) kg, n = 5
 Egypt (Osborn & Helmy 1980)

G. d. osiris

TL (♂ ♂): 938 (910–1000) mm, n = 8
 TL (♀ ♀): 920, 1030 mm, n = 2
 T (♂ ♂): 173 (150–195) mm, n = 9
 T (♀ ♀): 155, 175 mm, n = 2
 E (♂ ♂): 150 (136–170) mm, n = 9
 E (♀ ♀): 155, 160 mm, n = 2
 Sh. ht (♂ ♂): 668 (650–695) mm, n = 9

Sh. ht (♀ ♀): 640, 695 mm, n = 2
 WT (♂ ♂): 15.8 (14.0–17.5) kg, n = 3
 WT (♀ ♀): 13.3, 16 kg, n = 2
 Air, Niger (Brouin 1950)

Maximum recorded horn length is 39.6 cm for a pair of horns (attributable to *G. d. isabella*) from Ethiopia (Rowland Ward)

Key References Essghaier 1981; Grettenberger 1987; Lafontaine *et al.* 2005; Loggers 1992; Mallon & Kingswood 2001a (and chapters therein); Yom-Tov *et al.* 1995.

Paul Scholte & Ibrahim M. Hashim

Gazella spekei SPEKE'S GAZELLE

Fr. Gazelle de Speke; Ger. Spekegazelle

Gazelle spekei Blyth, 1863. Cat. Mamm. Mus. Asiat. Soc., p. 172. 'Somâli-land' (= Somalia).

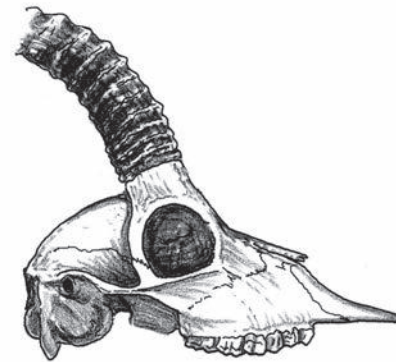


Speke's Gazelle *Gazella spekei*.

The species is named for Captian John Hanning Speke, who explored the region in 1855 and recorded the existence of this species.

Taxonomy Monotypic (see Gentry 1972, Groves 1985a, 1988). Synonyms: none. Speke's Gazelle has a highly derived karyotype and is closely related to *Gazella dorcas*. Like many of its relatives, Speke's Gazelle carries an X-autosome translocation. As a result, the diploid number is $2n = 32$ for ♀ ♀ and $2n = 33$ for ♂ ♂ (♂ has an XY1Y2 configuration) (Effron *et al.* 1976).

Description A relatively small gazelle, differentiated from other gazelles by the presence of a flabby, corrugated patch of pale grey skin on the muzzle that can be inflated to the size of a human fist when alarmed (a sharp snort is produced when the air is expelled). The light tan face contrasts with a dark cheek band that extends from the eye to the corner of the mouth. Dorsal pelage is light tan, flank band dark brown to black, and ventral pelage white. White buttocks



Lateral view of skull of Speke's Gazelle *Gazella spekei*.

are bordered by a vertical dark stripe. The tail is black. Horns slightly divergent, strongly curved backwards, with tips recurved upwards; ♀ is distinguished by shorter horns, which are thinner, straighter and less deeply annulated than in ♂.

Geographic Variation None recorded.

Similar Species

Gazella dorcas. Pelzeln's Gazelle (*G. d. pelzelni*) occurs sympatrically in coastal N Somalia. Horns lyrate.

Nanger soemmerringi. Observed in mixed herds on the coastal grasslands in Ceel Dhere District, Somalia, in the late 1980s; however, there is no recent information to confirm whether the Soemmerring's Gazelle still occurs in this area. Larger, and lacks a dark flank band.

Distribution Endemic to the Horn of Africa. Inhabits the 20–40 km wide grassland plain that extends along the Indian Ocean coastline of Somalia (hunting has eliminated Speke's Gazelle from coastal grasslands south of 2° 30' N latitude). Northern limit delimited by steep hills of the Gulis Range. Kingdon (1997) noted that the Nugal Valley in north-central Somalia was once considered the centre of its range. Scattered groups of Speke's Gazelles were still rarely encountered in the northern Ogaden in E Ethiopia in the mid-1980s (Hillman 1988a), but relentless hunting was on the verge



Gazella spekei

of eliminating the species from the Ogaden at that time and there is no recent information to indicate that they are still present there (Wilhelmi *et al.* 2006).

Habitat Most common on semi-arid grasslands, but found throughout dwarf shrub (e.g. *Indigofera intricata*) and barren rangelands, at altitudes below 2500 m. The presence of a biting tabanid fly (*Haematopota* sp.) during the mid-growing season prompts movements to the coast or large inland sand dunes where the breeze disperses the flies. They also move to these areas in the late dormant season because the sparse vegetation stays green longer on these sites, possibly because the roots access soil moisture stored deeper in the dunes.

Abundance Speke's Gazelle is one of the most widespread and abundant Somali gazelles (Funaioli & Simonetta 1966), and observations in the 1990s indicate this is still the case (Thurrow 1996, East 1999), although numbers have been reduced in portions of the range as a result of hunting, drought and overgrazing of existing habitat by domestic livestock (East 1999). Densities of Speke's Gazelle have been estimated at 2.0 ind/km² in the eastern Nugal Valley, and 0.2/km² in the central Nugal Valley (East 1999). Thurrow (1996) recorded an average density of about 4/km² on good condition coastal plains grasslands of C Somalia (Ceel Dhere region); occurrence is more scattered and much less dense on dwarf shrub and barren rangelands. Based on this evidence, East (1999) suggests that total numbers are in the tens of thousands.

Adaptations The most striking peculiarity of this species is the inflatable nasal sac. The more obvious functions for this sac include: (1) an auditory signal made by expelling air with a loud snort (this may advertise the callers' whereabouts, as in other gazelle species, but its relative loudness may provide a measure of the size and vigour of the caller); (2) at close quarters it may help disperse scent from the facial glands; (3) a visual signal (when inflated) of the status and

mood of the signaller; and (4) all the above may derive from a nasal mechanism for evaporative cooling as air passes over moist skin inside the nasal cavity.

Foraging and Food Classed as an intermediate browser–grazer by Gagnon & Chew (2000) in their review of dietary preferences of African bovids. *Cyperus chordorrhizus* and *Indigofera intricata* are the most common forage species consumed on the coastal grasslands where they respectively comprised 26% and 18% of the growing season diet, and 15% and 16% of dormant season diet. Other commonly consumed species include *Tephrosia* spp. and the grasses *Sporobolus brockmanii*, *Enneapogon schimperanus* and *Leptothrium senegalense* (Thurrow *et al.* 1995).

Social and Reproductive Behaviour Most of what is known of the ecology of wild Speke's Gazelles comes from the work of Thurrow (1996), on which the discussion that follows is based. Adult ♂♂ generally restrict their movements to a home-range, which may vary in size from about 1.5 to 5 km² and are broadly overlapped by home-ranges of neighbouring ♂♂. The home-range is not defended but represents an area in which a ♂ concentrates his activities. The home-range is marked throughout by dung heaps that average 0.7 m in diameter and several centimetres deep, which appear to function as sources of information about which ♂♂ are in an area rather than as territorial markers.

Adult ♂♂ defend a harem of 1–18 ♀♀ by maintaining a 50–100 m territory around the mobile harem. Thus, while the home-range of the ♂ is not defended, the ♂ attempts to possess the ♀♀ present within his home-range. Adult ♀♀ determine the direction in which the harem moves and the ♂ follows. If the direction of movement takes the harem near the edge of the male's home-range, he attempts to turn them back by blocking their progress with a broadside presentation that forces the harem to alter course. Males not occupying a home-range congregate in bachelor herds numbering up to 40 individuals; these herds reside on poor-condition rangeland.

If an intruding ♂ approaches within 100–200 m of a harem, the defending ♂ positions himself between the harem and the intruder. The defending ♂ stands rigid, staring at the intruder while holding his forelimbs straight and hindlimbs normal and occasionally inflating his nasal sac and snorting. If the intruding ♂ is clearly smaller than the harem ♂, the harem ♂ lowers his head slightly, holding horns perpendicular to the ground, and gallops toward the intruder who usually flees. In cases where the two ♂♂ are closely matched in size, a broadside presentation is made with the two gazelles ending up standing about one metre apart facing opposite directions. While in these broadside positions they engage in head-flagging (i.e. incline their necks sideways in a variety of positions). If neither ♂ leaves the site after head-flagging, they both back away, directly face each other at a distance of several metres, then lower their heads so that the horns are perpendicular to the ground. After lowering their heads several times, both charge and lock horns for several seconds, repeating this process until one leaves the area.

When a predator approaches, Speke's Gazelles stand with straight legs and stare intently, occasionally inflating their nasal sac and snorting. Their tails, which are generally flipped back and forth throughout the day, are flipped at a much more rapid speed when a predator is near. This rapid movement of a black tail across a white rump serves as a visual signal to other gazelles. Other visual signals

include stotting, brief erection of body hair producing a contrasting flash of pelage colour, and perhaps the light grey bulge produced by the inflated nasal sac.

A ♂ investigates the reproductive status of a ♀ by following her with nose extended and the horns laid along its back. Females often respond to this attention by urinating, which prompts flehmen behaviour by the ♂ (i.e. standing with head erect, mouth open and ears back). This interaction apparently gives a signal to the ♂ about the female's reproductive status because after flehmen he either breaks off courtship or continues to pursue the ♀. While pursuing her, the ♂ occasionally delivers stiff leg kicks (*laufschlag*) to the female's hindquarters and emits short cough-like grunts. Males frequently combine these actions with a nose-upward posture. Copulation is preceded by the ♀ responding to sexual pursuit by running in a zig-zag pattern, which then slows to trotting and finally to a slow walk. In the later stage the ♀ walks in a defensive/submissive posture of lowered head with her posterior toward the ♂. During copulation, the ♀ continues walking so the ♂ has to accomplish intromission with a single ejaculatory thrust. He accomplishes this by taking several steps while walking erect on his hindlegs. The front legs normally do not touch the ♀. When copulation is completed, the ♂ immediately loses all apparent interest, but after about an hour the cycle of courtship may be renewed.

Reproduction and Population Structure Breeding is aseasonal and copulations and newborn lambs have been recorded in every month of the year. Sexual activity is bimodal with the peaks coinciding in the mid-growing seasons (i.e. late May and mid-Nov). Peak birthing coincides with the onset of the growing season. Based on information from captivity, Read & Frueh (1980) recorded gestation at 169–190 days, and birth-weights of the single young at 1344–1792 g. Females remain apart from a harem for several weeks after the lamb's birth (Thurow 1996).

The adult sex ratio is about 40% ♂♂ and 60% ♀♀. Eight per cent of the population comprises young less than approximately six months old. The sex ratio distribution is not evenly dispersed across the landscape. In barren areas or grass/shrub ecotones, the ♂ : ♀ ratio is 1 : 1.1, and mean harem size is 2.0 ♀♀; grasslands in good condition have a ratio of 1 : 2.2, and the mean harem size is 4.5 (Thurow 1996).

Predators, Parasites and Diseases Large predators (i.e. large cats, hyaenas and large raptors) have been virtually eliminated throughout the range of Speke's Gazelle, but Common Jackals *Canis aureus* and Black-backed Jackals *Canis mesomelas* prey on young. There is limited information on parasites or diseases, although Iori & Lanfranchi (1996) report on the helminths recorded from Speke's Gazelle, including *Teladorsagia hamata*.

Conservation IUCN Category: Endangered A2cd. CITES: Not listed.

The native ungulate community that historically inhabited the grassland and dwarf shrubland were primarily Speke's Gazelle and the Beisa Oryx *Oryx beisa*. The soft, durable hide of the Beisa Oryx is highly prized by pastoralists, and they have been hunted to extinction through most of the range of Speke's Gazelle. In contrast, Speke's Gazelles are not molested by the pastoralists, who take pride in relying on their livestock to meet their food needs; there is a stigma among

coastal plain pastoralists against hunting Speke's Gazelles (referred to as the devil's livestock). However, in areas of civil conflict (e.g. along the Somalia/Ethiopia border and between clans of N and C Somalia) the influx of armed soldiers has eliminated gazelle populations near the few roads in the region. The spread of this sort of activity over the past several decades is the primary reason for their threatened status. Furthermore, there is increasing evidence of the illegal trade and export (to Gulf countries) of Speke's Gazelles (as well as other Somali antelopes), aided by the introduction of new hunting and trapping techniques and improved transportation methods such as wooden boxes (rarely seen in the 1980s and 1990s) (Amir 2006). The absence of any protected areas or measures means that its conservation status is likely to decline further unless some means of effectively protecting existing populations is developed (East 1999).

The small number of breeding stock present in zoos has resulted in Speke's Gazelle being the subject of captive-breeding programmes designed to simultaneously maintain genetic diversity while reducing the severity of inbreeding depression; both goals appear to have been achieved (Templeton & Read 1998, Templeton 2002).

Measurements

Gazella spekei

HB: 950–1100 mm

T: 150–200 mm

Sh. ht: 500–650 mm

WT: 15.0–25.0 kg

Somalia (adapted from Kingdon 1997)

Maximum recorded horn length is 31.7 cm for a pair of horns from Somalia (Rowland Ward)

Key References East 1999; Thurow 1996.

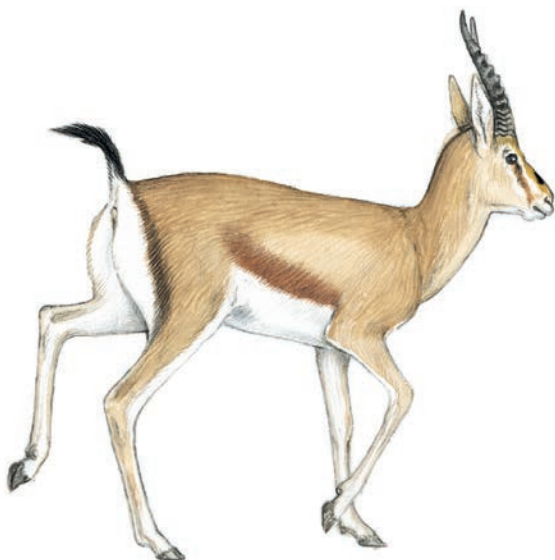
Thomas L. Thurow



Speke's Gazelle *Gazella spekei* male with nasal sac inflated.

Gazella cuvieri CUVIER'S GAZELLE (ATLAS GAZELLE, EDMI GAZELLE)

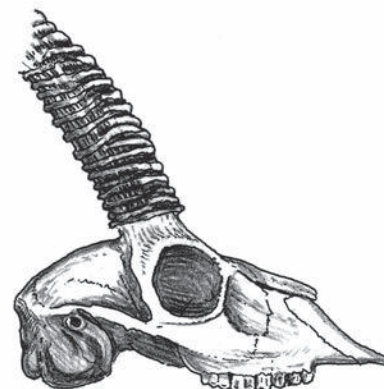
Fr. Gazelle de Cuvier (Gazelle de montagne); Ger. Echtgazelle

Gazella cuvieri (Ogilby, 1841). Proc. Zool. Soc. Lond. 1840, p. 35 [1841]. Morocco, Mogador.Cuvier's Gazelle *Gazella cuvieri*.

Taxonomy *Gazella cuvieri* is generally considered a monotypic species (Gentry 1972, Grubb 1993c, 2005). Groves (1969) treated it as a northern representative of the Red-fronted Gazelle *Eudorcas rufifrons*, but later (Groves 1985a, 1988) confirmed its position as a distinct species, though possibly allied to the Goitered Gazelle *G. subgutturosa* and Slender-horned Gazelle *G. leptoceros*. Genetic analyses have indicated that it forms the westernmost representative of a group of mainly twin-producing gazelle species comprising Slender-horned Gazelles, Goitered Gazelles and the Asian Chinkara *G. bennetti* (Hammond *et al.* 2001, R. Hammond pers. comm.). Synonyms: *corinna*, *cineraceus*, *kevella*, *setifensis*, *subkevella*, *vera*. Chromosome number is $2n = 32$ in ♀, and 33 chromosomes in ♂. This is due to a Robertsonian translocation of the X chromosome to an autosome (Kumamoto & Bogart 1984). Vassart *et al.* (1995) delineated the cytogenetic arrangements of gazelle chromosomes, using the caprine banded karyotypes as the presumed ancestral form. These authors found the karyotypes to be similar to that of the Slender-horned Gazelle.

Description A tallish, dark grey-brown gazelle, with broad, lighter and darker brown bands across the flanks, white belly and buttocks, and black tail. Comparatively bulky body, dark brown and greyish tones and upright horns are all useful for identifying the species at long distances. The top of the nose has a prominent dark spot on a brown face. Typical gazelle face-stripe pattern, with pale patches in front of each eye with light and dark bars running from the eye to the corner of the mouth. Ears are pale, long and narrow. Pelage is long and thick. Dark tufts on metatarsals prominent and very dark pygal bands characteristic.

Horns of ♂ are long (25–37 cm), strongly annulated, rising vertically before diverging out and back, with the smooth tips curving in and

Lateral view of skull of Cuvier's Gazelle *Gazella cuvieri*.

forwards (Dupuy 1964, Groves 1985a, 1988). Female horns are shorter, thinner and less heavily annulated, but still characteristically upright on the top of the head.

Geographic Variation None recorded.

Similar Species

Gazella dorcas. Sympatric mainly in N Morocco, though historically there was greater overlap in distribution. Brighter rufous tawny body colour; smaller size; more visible bands across the flanks; usually lacks prominent black spot on the nose; horns shorter, more backswept and typically lyrate in front view. Usually found at lower altitudes, and in less rugged terrain.

Confusion with the Slender-horned Gazelle, which shares similar horn and body shape, but is generally much paler with less robust horns, and usually in sandier lower altitude habitats, may account for the report of a single *G. l. loderi* ♂ shot near Boumia in Morocco in 1954 (Loggers *et al.* 1992) in an area otherwise inhabited only by Cuvier's Gazelle. Ambiguous preliminary genetic results indicating unexpectedly close similarity between samples of *G. cuvieri* and *G. leptoceros* collected in Tunisia (but not between Moroccan *G. cuvieri* and Tunisian *G. leptoceros*), indicate that additional sampling is required to clarify the relationship between these two species (R. Hammond pers. comm.).

Distribution Cuvier's Gazelle is endemic to the mountains of the Maghreb, and historically occupied the Atlas Mts, and neighbouring ranges, in Morocco, Algeria and Tunisia, to the lowlands in W Morocco.

Historical Distribution Formerly reached the Mediterranean and Atlantic coast in certain localities (e.g. Ben Slimane and the Ajou Mts). In Morocco it occupied all the mountain chains (eastern Rif, High Atlas, Middle Atlas and Anti-Atlas, pre-Saharan mountains, Aydar south of the Drâa) and the associated plateaux with the exception of the western Rif (Cabrera 1932, Panouse 1957). In



Algeria it occupied the slopes of the Tellian mountain chains, those of the more southern massif formed by the Saharan Atlas, and the massifs in the eastern part of the country (Joleaud 1929, Heim de Balsac 1936, De Smet 1991). In Tunisia, in the nineteenth century, Cuvier's Gazelle was present throughout the northern half of the country, occurring in all the Tunisian mountains, especially in the high chains of the Ridge in the region of Kasserine, in the northern chains of the Ridge near Ghardimaou, Tunis and Zaghuan, and in the southern pre-Saharan chains around Gafsa and Tamerza (Sclater & Thomas 1899, Kacem *et al.* 1994, Smith *et al.* 2001).

De Beaux (1928) notes the discovery of a Cuvier's Gazelle horn in Al Jaghbub, in the east of Libya, specifying that its source was unknown. It is the only mention of the species for the country. In 1994, six Cuvier's Gazelles were introduced from Tunisia into Kouf N. P. in the north of Libya (K. De Smet pers. comm.).

Current Distribution In Morocco, Cuvier's Gazelle has undergone a marked decline in its distribution range, and today populations are fragmented along the southern side of the eastern Middle Atlas, the southern High Atlas and the Anti-Atlas, extending to the northern Sahara (Aulagnier *et al.* 2001). The range diminished considerably in the first half of the twentieth century; in the 1960s it disappeared from the region of Rabat and Casablanca. The species disappeared from several localities in the Middle Atlas at the same time. In the mid-1980s, the species vanished from the north-east (eastern Rif), and it also disappeared from numerous localities around Agadir in the 1990s (Cuzin 1996). The species has been nearly extirpated from the Jbel Saghro, where it was abundant in 1981 (Cuzin 1996). Recently, this species was discovered on the southern gradient of the eastern Middle Atlas, towards Outat Oulad El Haj and Missouri, as well as on the High Plateaux, slightly further south, until the area of Figuig (Cuzin 1996, 2003, Caron *et al.* 2004). Some small, transient groups were also seen on the southern gradient of the central and eastern High Atlas, from the region of Ouarzazat to that of Rich, reaching an

altitude of 2600 m south of Imilchil (Cuzin 1996). A small population of 12–17 animals survives north of Ouarzazat (F. Cuzin pers. obs.). In the Sahara, a group of three animals was observed south of Fom Zguid in 1994. A larger population was recorded in 1995 in a region situated from the Drâa Wadi, about a hundred kilometres upstream from its mouth, to the last hills north-east of Smara in the Aydar. This confirmed older data (Morales Agacino 1950, Aulagnier & Thévenot 1986) and pushed the southern limit of known distribution about 60 km further south (Cuzin 1996, 2003).

In Algeria, the distribution of Cuvier's Gazelle is limited to the northern part of the country: it is not found either in the north of the Tell Atlas nor south of the Saharan Atlas. The species has only recently disappeared from a few localities and these are mainly in the north of its range of distribution. It was still noted on the Mediterranean coast until about 1930 (Lavauden 1926b, Joleaud 1929, Seurat 1930). The populations of the western Tell Atlas, Batna-Biskra and the Aurès mountains are no longer contiguous, and some groups of the Saharan Atlas were recently eliminated (De Smet & Smith 2001). In the north-west of the country Cuvier's Gazelle is much more widespread than was previously thought. Almost all the large national forests of Aleppo Pines *Pinus halepensis* shelter small populations and there are contact zones between the majority of these populations. It is also relatively common in the hills between Mascara, Relzane, Tiaret and Frenda, living in open countryside with a mosaic of grain crops, vineyards and pasture lands at the top of the hills. In the Saharan Atlas, most of the summits that are higher and less disturbed still harbour small groups of Cuvier's Gazelles, the most important being near Djelfa (Khirredine 1977). The most recent information indicates that some of these populations are growing. The most eastern populations are found in the Aurès, the Némentcha Mts and the hills near the Tunisian border. Near Tebessa there is a concentration of Cuvier's Gazelles, which move to and from Djebel Chambi N. P. in Tunisia.

In Tunisia, the species was still fairly abundant in the 1930s in the entire Tunisian Ridge from the Algerian border to the Djébel Bou Kornine, 17 km south of Tunis (Kacem *et al.* 1994), but numbers declined steeply due to overhunting and the events of World War II. The species no longer survived in the 1970s except in the vicinity of the Djebel Chambi and Khchem El Kelb between Kasserine and the Algerian border (Kacem *et al.* 1994). However, the population currently seems to be increasing, essentially as a consequence of efficient conservation measures implemented in and around Djebel Chambi N. P. (Kacem *et al.* 1994). Observations made in 1991, in the region of Siliana, indicate that the species is spreading towards the north-east in the Ridge, mainly from the principal population core in the surroundings of Djebel Chambi N. P. Kacem *et al.* (1994) listed the species from 13 hunting reserves and massifs, covering an area of around 720 km².

Habitat Cuvier's Gazelle is associated with the middle and low slopes of the folds in the Maghreb, occupying the relatively dry, and now increasingly open, forests of semi-arid Mediterranean type that are dominated by *Pinus halepensis*, *Juniperus phoenicea*, *Tetraclinis articulata* scrub, *Cedrus atlantica*, *Quercus ilex*, *Q. coccifera*, *Argania spinosa* and *Olea europaea*. These areas are characterized by an undergrowth of maquis or garrigue, which can be relatively thick or relatively open, and that often includes *Rosmarinus* spp., *Phyllirea*

angustifolia and *Globularia alypum* (Sclater & Thomas 1899, De Smet 1989, 1991, Loggers *et al.* 1992, Karem *et al.* 1993, Kacem *et al.* 1994, Cuzin 2003, Beudels-Jamar *et al.* 2005b). The Mediterranean forests were formerly much more widespread, steppes of *Stipa tenacissima* representing the first stage of substitution and which themselves have greatly regressed. Cuvier's Gazelles are frequently found in association with these steppes (De Smet 1991, Karem *et al.* 1993). In such dry areas the availability of complementary and richer pastures (for example, with *Cynodon dactylon*) seems to be important (F. Cuzin pers. obs.). In summer, Cuvier's Gazelle may be found in high-altitude habitats, with low sclerophyllous bushes, such as *Artemisia negrei*, *Alyssum spinosum*, *Bupleurum spinosum* and locally scattered trees such as *Juniperus thurifera* and isolated patches of dense herbaceous vegetation (F. Cuzin pers. obs.). In the south-western part of its distribution, in the northern Sahara, Cuvier's Gazelle occurs in areas where it is associated with *Argania spinosa*, spiny *Euphorbia* and *Acacia* spp. (Aulagnier *et al.* 2001, Cuzin 2003). In Algeria, their habitat also includes desert hamadas near Bechar and open oak forests (a mixture of *Quercus suber* and *Q. ilex*) in the Mascara region (De Smet & Smith 2001, Beudels-Jamar *et al.* 2005b).

Cuvier's Gazelles have been recorded from sea level up to 3300 m altitude (F. Cuzin pers. obs.), and although found mainly in hills and small mountains, animals are able to live on very steep slopes (up to 45 degrees) (Cuzin 2003). They avoid heavy snow-cover areas, where they may be present only in summer (Cuzin 2003).

Abundance Historically, Cuvier's Gazelle was reputed to be common and locally abundant (e.g. Heim de Balsac 1936). Cabrera (1932) mentioned it as particularly numerous in the central part of the Middle Atlas, the territories of Beni Mguild and Ait Aiach, and the length of the contact line between this chain and the High Atlas. Carpentier (1932) notes that it was formerly abundant in the Zaïan district near Sidi Lamine and Khenifra (C Morocco).

The total population of Cuvier's Gazelles currently is estimated in the region of 1750–2950 individuals. In Morocco, the population is estimated at between 900 and 2000 individuals, including a population of several hundred individuals recently rediscovered in the lower Drâa (Cuzin 1996, 2003, Aulagnier *et al.* 2001, Cuzin *et al.* 2007). The main populations are in the western Anti-Atlas (where the population is increasing) and in the Lower Drâa–Aydar area (where the population is decreasing), and in SE Morocco (including the southern slopes of the Middle Atlas, High Plateaux and Saharan Atlas). Small groups are spread on the southern slopes of the High Atlas, in the eastern High Atlas, in the central Anti-Atlas and in the western part of the High Atlas (north and east of Agadir) (Cuzin 1996, 2003).

In Algeria, a study of the distribution and numbers of the species carried out at the end of the 1980s estimated the population at 445 individuals (Sellami *et al.* 1990); based on field observations made in 1987, De Smet (1989) estimated the population to be between 400 and 500 individuals. In 1991, his estimate was revised to 560 individuals, with 235 in the Tell Atlas, 140 in the Saharan Atlas, 135 in the east and 50 in the central group of Mergueb N. R. (De Smet 1991).

In Tunisia, the number of Cuvier's Gazelles is not known with precision, but probably numbers less than 500 (Smith *et al.* 2001). The main population in the region of Djebel Chambi N. P. was estimated at 300 individuals in the early 1990s (Kacem *et al.* 1994),

and the total population is likely a little higher. A few individuals were reintroduced from Almeria (Spain) to Boukornine N. P. in Tunisia in the 1990s (Abáigar *et al.* 2005).

Adaptations Extrapolating from their distribution and biogeographic history, Cuvier's Gazelles are likely to possess physiological adaptations to cold and to rough terrain, but no studies have been made.

Foraging and Food Cuvier's Gazelle is a mixed feeder, taking herbs, shrubs and grasses. In Tunisia, it feeds mainly on grasses, acorns of *Quercus ilex* and young leaves of legumes (Smith *et al.* 2001), while in Morocco preferred plant species during the dry season include: *Chrysopogon aucheri*, *Nitraria retusa*, *Argania spinosa*, *Maerua crassifolia*, *Rhus tripartitum*, *Launea arborescens*, *Asparagus pastorianus*, *Periploca laevigata*, *Caylusea hexagyna*, *Acacia raddiana* and *Lavandula stricta* (Cuzin 1998). In E Morocco, Cuvier's Gazelles have been observed feeding on *Olea silvestris*, *Periploca laevigata*, *Teucrium polium*, *Salsola vermiculata*, *Stipa parviflora*, *Cynodon dactylon*, *Plantago* sp. and young shoots of *Nerium oleander* (a reputedly toxic plant) (F. Cuzin pers. obs.). It can utilize water from plants as well as dew, but, in areas with no dew, it needs to drink frequently. Normally, animals spend the day in the hills, descending to the valleys to feed at night or in the early morning.

Social and Reproductive Behaviour Cuvier's Gazelle generally occurs in small groups of three to five individuals, rarely more than eight, but occasionally as large as 20 (Pease 1896, Lavauden 1920). Joleaud (1929) mentions erratic movements and a somewhat nomadic life. On the southern slopes of the High Atlas, animals moved to higher altitudes (up to 2600 m) in summer, but were absent in winter (Cuzin 2003).

Reproduction and Population Structure Middle-aged ♀♀ can produce two litters in one year when food and water resources are available (Alados & Escos 1991). In captivity, mating occurs in early winter, with births occurring in spring (Apr–May) and secondarily in autumn (Oct–Nov) (Olmedo *et al.* 1985, Abáigar & Cano 2005). Calving also has been observed in the fall in Mergued reserve, Algeria (K. De Smet pers. comm.). The gestation period is between 161 and 180 days (Furley 1986, Olmedo *et al.* 1985, Abáigar & Cano 2005).

There is usually a single offspring, but in captivity twinning is frequent (40%) (Olmedo *et al.* 1985, Abáigar & Cano 2005); twins were of the same sex in 69% of litters and were thus (statistically) considered to be dizygotic. The high frequency of twin births observed in this species is in keeping with its known genetic relationship to other twin-producing species (Slender-horned Gazelles, and all forms of Goitered Gazelles), but is otherwise unusual in view of the rarity of twins in other *Gazella* species (Furley 1986). Longevity in captivity has been recorded at nearly 18 years (Weigl 2005).

Predators, Parasites and Diseases Golden Jackals *Canis aureus*, Caracals *Caracal caracal* and Golden Eagles *Aquila chrysaetos* reportedly prey upon Cuvier's Gazelle, primarily calves (Loggers, in De Smet 1989, Sellami *et al.* 1990). Toxoplasmosis has been reported by Stiglmair-Herb (1987), and a variety of helminths were found in captive animals in Spain (Ortiz *et al.* 2001).

Conservation IUCN Category: Endangered C2a(i). CITES: Appendix I. CMS: Appendix I.

Cuvier's Gazelle has declined over its entire range owing mainly to increases in human pressure, particularly hunting, and the transformation of forested zones into cropland and pastures for livestock (and also for charcoal) (Cuzin 2003, Beudels-Jamar *et al.* 2005b). Predation by dogs, on young gazelles at least, is also a threat, and foiled an attempt to introduce Cuvier's Gazelle into Souss-Massa N. P., south of Agadir in Morocco (Loggers *et al.* 1992).

In Morocco hunting was banned in 1985, but this came too late for some populations and did not, in any case, prevent declines experienced in other populations. For instance, the species seems to have been extinct in the north-east since 1985, and was greatly reduced in the Ida massif or Tanane, north of Agadir, where the species seems to have disappeared in 1993 following a local drought of several years. However, recent discoveries of new populations have been made, and the range of the species has even expanded southwards somewhat.

The state of conservation of the species in Algeria was detailed by De Smet (1989, 1991) and De Smet & Smith (2001). The species was officially legally protected in Algeria in 1975, although poaching continued and it is only through increased protection in reserves that numbers have been able to increase.

The distribution range and population numbers had decreased considerably in Tunisia until the 1970s, before the Forest Office took appropriate conservation measures. In 1975, a 300 ha protected area was established at Mt Keche, and in 1980 Djebel Chambi N. P. was gazetted primarily for this species. Such measures to protect the species, combined with other important measures of habitat management for Cuvier's Gazelle, have enabled the Tunisian Forest Office to greatly improve the state of conservation of this species; the objectives of the Tunisian programme aim to naturally recolonize its historical range.

Important protected areas across the range include Outat el Haj in Morocco (containing remnants of a larger group of 40-plus animals caught from a local wild population that persists in the area; T. Wachter pers. comm.), Saharan Atlas N. P., Belezma N. P. and Mergueb N. R. in Algeria, and Djebel Chambi N. P. in Tunisia. Mallon & Kingswood (2001b) highlighted Djebel Chambi as of extreme importance as it holds the largest population in Tunisia and is important for the recolonization of the historical range. These authors also called for stringent protection from hunting for all

populations in Morocco and Algeria, and the establishment of a number of new protected areas that had been proposed in Morocco (including Western Sahara) and Algeria. A captive population, originating from animals in Western Sahara, is maintained in Almeria, Spain (Abáigar & Cano 2005). Cuvier's Gazelle also has been re-introduced in Djebel BouKornine N. P. in Tunisia, with individuals originating from the Almeria station in Spain (Abáigar *et al.* 2005).

Elucidating the taxonomic and ecological relationship between *G. cuvieri* and *G. leptoceros* is a priority for North African gazelle conservation.

Measurements

Gazella cuvieri

TL: 1050–1160 mm

T: 190–210 mm

E: 170 mm

Sh ht: up to 680 mm

WT (♂♂): 20–35 kg

WT (♀♀): 15–20 kg

Throughout geographic range (Beudels-Jamar, Lafontaine *et al.* 2005)

Maximum recorded horn length is 38.1 cm for a pair of horns from Midelt, Morocco (Rowland Ward)

Key References Abáigar & Cano 2005; Beudels-Jamar *et al.* 2005b; Cuzin 1996, 2003; De Smet 1989, 1991; Mallon & Kingswood 2001a (and chapters therein).

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Cuvier's Gazelle *Gazella cuvieri*.

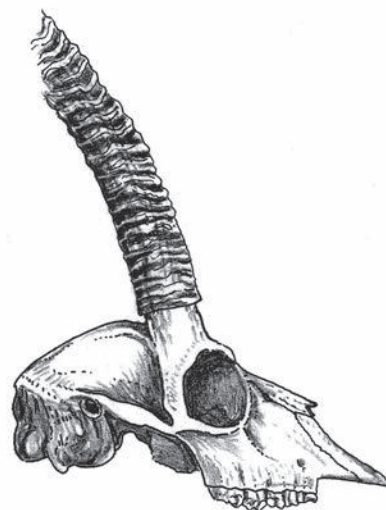
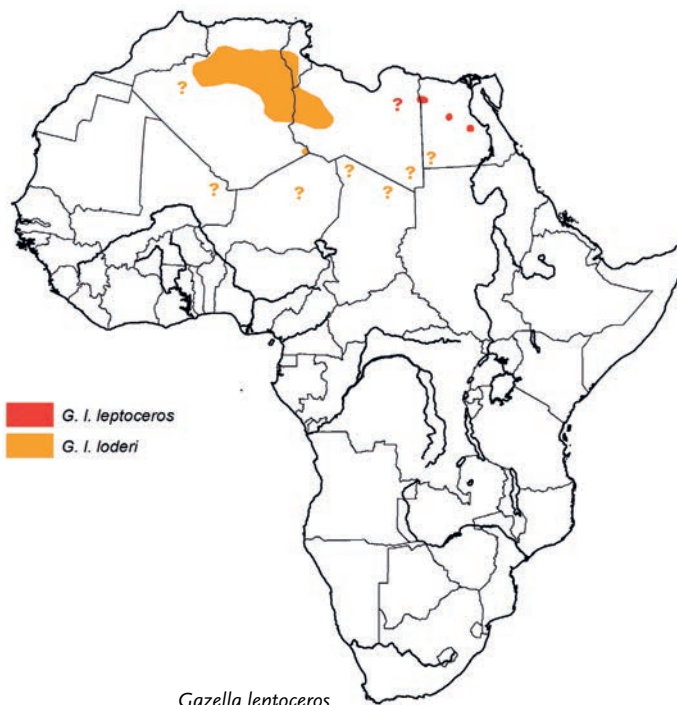
Gazella leptoceros SLENDER-HORNED GAZELLE (RHIM GAZELLE, LODER'S GAZELLE)

Fr. Gazelle leptocère (Gazelle leptocère, Gazelle blanche, Gazelle à longues cornes); Ger. Dünengazelle

Gazella leptoceros (F. Cuvier, 1842). In: E. Geoffroy & F. Cuvier, Hist. Nat. Mammifères, pt. 4, 7 (72): 1–2, pls 473, 474, 'Antilope aux longues cornes'. 'rapportés du Sennaar [=Sudan, Sennar] par M. Burton'; corrected to 'desert between Giza and Wadi Natron, lower Egypt, as the type-specimen was brought to Paris by James Burton, circa 1833' (Flower 1932: 438).

Taxonomy *Gazella leptoceros* has been included along with the Goitered Gazelle *G. subgutturosa* in the subgenus *Trachelocele* (Groves 1988). The species comprises two subspecies, which seem geographically isolated and ecologically distinct, although Gentry (1972) thought they may not warrant subspecies recognition. Subspecific differentiation was made at an early stage in the discovery of the species by western

science and has always rested on very few specimens. It requires verification with modern techniques since knowledge of the species' habitat preference and wide-ranging ecology, combined with results of genetic studies of its close relative, the Arabian Sand Gazelle *G. s. marica*, both suggest that genetic partitioning would be slow to form in this nomadic desert-adapted species (T. Wachter pers. comm.).

LEFT: Slender-horned Gazelle *Gazella leptoceros*.ABOVE: Lateral view of skull of Slender-horned Gazelle *Gazella leptoceros*.*Gazella leptoceros*

Synonyms: *abuharab*, *cuvieri*, *loderi*. Slender-horned Gazelles have a translocation of the X chromosome to an autosome (Effron *et al.* 1976), which results in ♂♂ having $2n = 33$ and ♀♀ only $2n = 32$ (and see Vassart *et al.* 1995).

Description A medium-sized gazelle, of a very pale yellowish-beige to grey-brown body colour separated from the white belly by a faintly marked flank band. Face markings similarly poorly defined. Ears are long and narrow. Outer hooves are broader than inner ones, which facilitates movements on sand. Tail short, terminated by a tuft of blackish-brown hair (Groves 1988). Horns are long and nearly straight (appreciably thicker and longer in ♂), with 20–25 well-defined rings.

Geographic Variation

G. l. leptoceros: Western Desert of lower Egypt and NE Libya. Smaller, longer horned (33.7 ± 2.8 cm, $n = 6$; Groves 1969).

G. l. loderi: W and C Sahara. Reported to be larger, but shorter-horned (29.8 ± 1.6 cm, $n = 6$; Groves 1969).

Similar Species

Gazella dorcas. Sympatric in its entire distribution on the margins of ergs. Reddish colouration; smaller size; horns lyrate and curved.

Distribution Endemic to Africa, where confined to the sand dune regions of the Sahara, west of the Nile R.

Historical Distribution The nominate subspecies *Gazella l. leptoceros* formerly occurred in the northern part of the Western Desert in Egypt, south of the Mediterranean coastal belt, where it seems linked especially to the great oases, characteristic of this desert, and to the interdunal valleys populated with *Acacia* spp. (Flower 1932, Osborn & Helmy 1980, Goodman *et al.* 1986, Le Houérou 1986, Zahran & Willis 1992, Saleh 1987, 2001). It is, or was, noted in Siwa in the north-west, the Quattara Depression, Wadi Natroun and Wadi el Ruwayan near the lower Nile, in the Nile Valley, in dune fields between Faiyum and the Quattara depression (Osborn & Helmy 1980), in Bahariya (Saleh 1987) and in Kharga (Elbadry 1998). It has also been found in the same chain of oases beyond the Libyan border in the surroundings of the Jaghbug oasis (Bundy 1976, Essghaier

1980, Goodman *et al.* 1986), where small groups of 10–20 were observed. The Slender-horned Gazelles noted more to the west in Libya, in particular near Ajdabiyah in western Cyrenaica and near Dahra, north of Zella (NC Libya) (Hufnagl 1972, Essghaier 1980), probably also belong to this form.

The subspecies *G. l. loderi* is believed to have had a wide Saharan distribution, although there are few historical data for this taxon.

Current Distribution The nominate subspecies *G. l. leptoceros* has been eliminated from the greater part of its range in the Egyptian Western Desert. In the 1980s, the species was considered extinct in five of its six known localities in the eastern part of the Western Desert and very rare in the sixth, the complex of the Wadi el Ruwayan and its extension, the Wadi Muweilih; in the western part of the desert, around the Quattara depression and the Siwa oasis, its status was uncertain (Saleh 1987). A small group of about 15 animals that survived in the Wadi el Ruwayan has since been exterminated (Saleh 2001). However, small groups (2–6) of Slender-horned Gazelles were observed and photographed west of the Siwa oasis in 1998 (T. J. Wachter pers. comm.), although the situation has become uncertain since reports of more than 20 being killed by a single hunting party in that region in 2005. Small numbers may persist in other parts of the Quattara Depression, the Jaghbub oasis, the Farafra oasis, and the Kharga (Saleh 2001, Devillers *et al.* 2005a, El Alqamy & Baha el Din 2006). The current status of this subspecies in Libya is unclear.

Gazella l. loderi is a characteristic species of the central Sahara (Dragesco-Joffé 1993). The centre of its distribution is found in the Great Western Erg, the Great Eastern Erg, and the sandy zone that stretches from the Hamada de Tinrhert in Algeria to the Fezzan in Libya. Although formerly present in the smaller ergs in the periphery of the central Saharan massifs of the Hoggar and the Tassili des Ajers, especially the Erg Amder and Erg Tihodaine (Setzer 1957, Dupuy 1967, De Smet 1989, Kowalski & Rzebik-Kowalska 1991, Dragesco-Joffé 1993, Kacem *et al.* 1994, De Smet & Smith 2001, Khattabi & Mallon 2001, Smith *et al.* 2001), they have not been observed in recent years, though they do still exist in the Erg of T'im Merzouga (K. De Smet pers. comm.).

In the ergs of the southern and eastern Sahara, the status of this species is unclear. It has been observed in the Great Ténéré Erg in small numbers in the contact zone between the Aïr and the Ténéré (Jones 1973, Grettenberger & Newby 1990, Poilecot 1996), although there have been no confirmed records for some years. In the Tibesti, the species was noted by Malbrant (1952) near Bardaï and Soborom, in the north of the massif, but there is no recent information on its presence here. The species is also thought to be present between the zone of the Erdi and the Mourdi depression in the Borkou of NE Chad and the Jebel Uweinat at the borders of Libya, Sudan and Egypt. This is a region in which a number of dunal systems stretch more or less from the south-west towards the north-east. At the Chadian extremity of this zone, Edmond-Blanc *et al.* (1962) gathered secondhand information of presence. At the Libyan extremity, Misonne (1977) found three skulls on the border of the Jebel Uweinat massif. Recent data also exist from the Gifl El Kebir in SW Egypt (Elbadry 1998). Although Setzer (1956) doubted their presence in Sudan, there are records from the north-west (Wilson 1980, K. De Smet pers. comm.). The subspecific affinities of these

animals are not known, but what is known of their ecology suggests that they are *G. l. loderi*.

Outside these regions, the species is mentioned as occurring in Mali (Heringa 1990, Duvall *et al.* 1997), where it may occur in the Adrar des Iforhas, although Sayer (1977) and Sidiyène & Tranier (1990) declared it absent from the entire country. The only observation of Slender-horned Gazelles in Morocco is from the region of Boumia south-east of the High Atlas, during the 1950s (Loggers *et al.* 1992), but this is far outside the species' normal habitat and very probably represents a misidentified Cuvier's Gazelle *Gazella cuvieri*.

In summary, the species is believed to have had a very wide Saharan distribution until relatively recently. However, in the last ten years, firm evidence for its presence is limited to the Great Ergs of Algeria, Tunisia, Libya and the extreme Western Desert of Egypt. No reports of occurrences to the south of these locations have been supported by photographs or any other hard evidence during this period.

Habitat In Egypt, the Slender-horned Gazelle occurs in hyper-arid desert areas, in particular sandy depressions with sparse vegetation and isolated *Acacia raddiana* woodlands, to sandy outskirts of oases supporting *Nitraria retusa*, and to interdunal depressions of *Cornulaca monacantha* (Osborn & Helmy 1980). *Gazella l. loderi* is principally linked to ergs (Schnell 1977, Ozenda 1991), which seem to constitute its only habitat, at least in the central Sahara (Sclater & Thomas 1899, Lavauden 1926a, b, Heim de Balsac 1936, Dupuy 1967). It has been suggested that they were once found in a variety of habitats, but that persecution has probably driven them to living in remote, inaccessible regions (Dupuy 1967).

Abundance At the beginning of the 1980s, the population of Slender-horned Gazelles surviving in Egypt was small and widely dispersed, especially near uninhabited oases, and in the Wadi El Rayan (Saleh 1987). The numbers that seem to survive in NW Egypt and perhaps in Kharga are certainly low, although current population size is unknown (Saleh 2001, Devillers *et al.* 2005a). Population numbers in Libya are similarly unknown.

The figures for Slender-horned Gazelles in the western part of its range are very difficult to estimate. However, it seems clear that it was much more abundant in the Algeria–Tunisia Great Ergs at the end of the nineteenth and beginning of the twentieth century than it has been in recent years. Large numbers were found, apparently relatively easily, by several naturalists of this period (Sclater & Thomas 1899, Lavauden 1926a, Heim de Balsac 1936), whereas Le Houérou (1986) notes having seen only one throughout 25 years of prospecting while mapping the vegetation of North Africa. The species was observed in small numbers by Jones (1973) and by Grettenberger & Newby (1990) on the edge of the Aïr–Ténéré, but there are no reliable estimates of abundance.

Surveys in Tunisia (Jan–Feb and Apr–May 2006) confirm that the Slender-horned Gazelle is still present through the Tunisian part of the Great Oriental Erg from Djebil N. P. to Senghar N. P., but that densities are probably very low. Evidence of poaching and disturbance is high. Observations suggest that the Tunisian population may number a few hundred individuals but more data are needed to verify this preliminary assessment (Wachter 2006, T. Wachter pers. comm.).

Adaptations Clearly, the restriction of the Slender-horned Gazelle to sandy ergs where few other large mammals can live must be facilitated by special adaptations. The sandy substrate has demanded some modification of the hoof structure and/or techniques of locomotion. Extreme exposure to insolation and reflected radiation probably involves species-specific physiological adaptations. The degree to which these gazelles escape predation as a result of their preference for ergs might also have been significant in their original adoption of such a difficult environment. None of these topics has received attention.

Foraging and Food In the eastern part of the range the Slender-horned Gazelle consumes a significant amount of foliage, including *Nitraria retusa*, a halophyte plant, *Deverra tortuosus* and *Acacia raddiana*, *Cornulaca monacantha*, *Launaea capitata* and *Calligonum comosum* (Osborn & Helmy 1980). In the western part of the range the species grazes mainly on *Aristida pungens* (Heim de Balsac 1936), but it also uses plants with an elevated water content, such as *Anabasis articulata*, *Arthrophytum schmittianum*, *Helianthemum kahiricum*, and the fruits of *Colocynthis vulgaris*, to meet its water needs (Kacem *et al.* 1994). Following good rainfall early in the year, Slender-horned Gazelles in the Tunisian Grand Erg were recorded selectively browsing on flowering plants of *Helianthemum confertum*, *Lotus pusillus*, *Herniaria* sp., *Echium* sp. and the leguminous shrub *Genista saharae* in Apr and May (T. Wachter pers. comm.).

They are mostly nocturnal and somewhat crepuscular, foraging and moving during these periods of the day, and resting during the hot hours in the shade or in hollowed depressions (Osborn & Helmy 1980). They appear to be highly nomadic, moving frequently between desert depressions in search of food (Kacem *et al.* 1994, Saleh 2001). Larger movements, carrying the species far from its preferred habitat, take place under the effect of long and severe droughts (Heim de Balsac 1928).

Social and Reproductive Behaviour Like other desert gazelles and antelopes, social organization is likely to be flexible and adaptable to variation in conditions. In good conditions, Slender-horned Gazelles may become territorial during the mating season, typically Aug–Sep. In general, they have been observed to form groups of 3–10 individuals, comprising one dominant ♂, several adult ♀♀ and their young. The ♂ remains vigilant, rounding up his group and attempting to herd additional ♀♀ into his territory to gain extra-mating opportunities. But not all ♀♀ will cooperate and younger satellite ♂♂ who may try to intervene in the resulting confusion.

Reproduction and Population Structure Birth season is typically in winter and early spring. The length of gestation is between 156 and 169 days (Furley 1986). One, sometimes two, young are born; twinning, which is not uncommon (Flower 1932, Kacem *et al.* 1994), is a trait shared with its closest relatives, the Goitered Gazelle and Cuvier's Gazelle (Hammond *et al.* 2001). The calves are weaned at three months, but do not mature until 6–9 months in ♀♀ and 18 months in ♂♂. Longevity has been recorded up to 14.6 years in captivity (Weigl 2005).

Predators, Parasites and Diseases Historically, the major predator sharing the habitat of Slender-horned Gazelles has been the Cheetah *Acinonyx jubatus*, but this species is now radically diminished or extirpated from most of the known range and no locations are currently known where the two certainly overlap. Golden Jackals *Canis aureus* are frequent at known gazelle areas such as the margins of the Great Ergs and west of Siwa oasis, and are likely to be opportunistic predators of young calves. At the margins of its range, Slender-horned Gazelles may encounter other large carnivores such as African Wild Dogs *Lycaon pictus*, Leopards *Panthera pardus* and Striped Hyenas *Hyaena hyaena*.

Conservation IUCN Category: Endangered C2a(i). CITES: Appendix I. CMS: Appendix I.

The Slender-horned Gazelle is reported to be nearly extinct in Egypt, and there is limited current information on its population status other than that the population is small and scattered in small groups; in the westerly part of the range, recent observations from the southern extent of their original distribution range are lacking, despite suitable habitat, and they are now presumably largely confined to remote and inaccessible areas.

Across the range, the main threat is undoubtedly modernized hunting/poaching, though disturbance and degradation of natural habitats (especially erg vegetation) through desertification also play a negative role (Devillers *et al.* 2005a). Protected areas known to be important for the species include Djebil and Senghar National Parks in Tunisia, Tassili N'Ajjer N. P. in Algeria (where still present in the Erg of T'im Merzouga; K. de Smet pers. comm.), and possibly Aïr–Ténéré National Nature Reserve in Niger. Enforcement of bans on hunting across the range, additional land and air surveys of regions of suitable habitat to determine population numbers, and the protection of existing populations in protected areas (such as Djebil and Senghar National Parks and those of Siwa and White Desert in Egypt) are immediate conservation priorities (Mallon & Kingswood 2001b, Devillers *et al.* 2005a).

The species is present in captivity in about 20 institutions in North Africa, Europe and North America (Devillers *et al.* 2005a).

Measurements

Gazella leptoceros

HB (♂♂): 937 (885–999) mm, n = 4

HB (♀♀): 955 mm, n = 1

T (♂♂): 162 (155–166) mm, n = 4

T (♀♀): 125 mm, n = 1

E (♂♂): 140 (132–145) mm, n = 4

E (♀♀): 130 mm, n = 1

Egypt (Osborn & Helmy 1980)

Kingdon (1997) gave estimated weight as 14–18 kg

Maximum recorded horn length is 41.2 cm for a pair of horns from Egypt (Rowland Ward)

Key References Devillers *et al.* 2005a; Kacem *et al.* 1994; Kowalski & Rzebik-Kowalska 1991; Mallon & Kingswood 2001a (and chapters therein); Osborn & Helmy 1980.

Roseline C. Beudels & Pierre Devillers

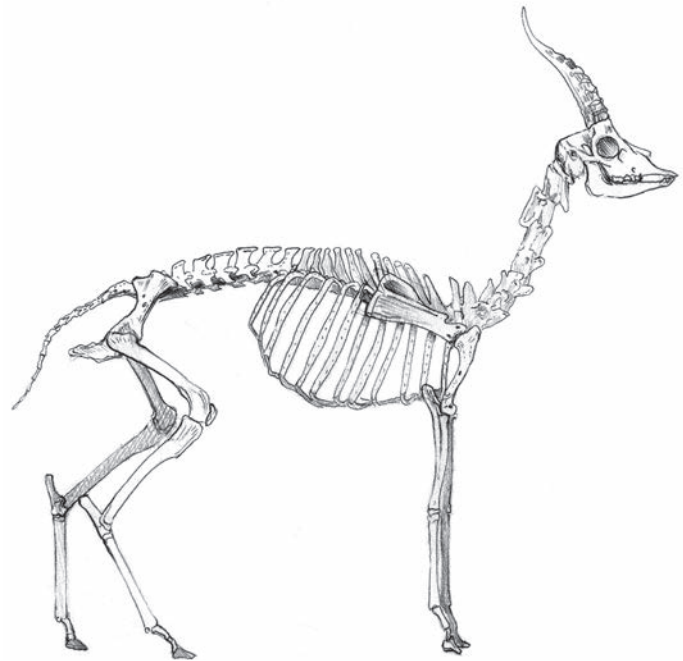
GENUS *Eudorcas*

Ring-horned Gazelles

Eudorcas Fitzinger, 1869. Sitzb. K. K. Akad. Wiss., Wien, math.-nat. Cl., 59 (sect. 1): 159.



Thomson's Gazelle *Eudorcas thomsonii* myology.



Thomson's Gazelle *Eudorcas thomsonii* skeleton.

The gazelles of this genus have traditionally been placed in the genus *Gazella*. It was Vassart *et al.* (1995) who first pointed out that *Eudorcas* and *Nanger* are more closely related to each other, whereas *Gazella* is closer to the Indian *Antelope*. Groves (2000), based on a cladistic analysis mainly of cranial, dental and horn characters, found that at the very least the four can be considered about equally related, and, wishing to preserve the generic distinction between *Gazella* and *Antelope*, raised *Nanger* to generic rank and revived the name *Eudorcas* for the present group.

Eudorcas form a group of comparatively large, relatively short-legged, less arid-adapted gazelles, differentiated from the generally smaller, more slender, longer-legged, more desert-living gazelles of the genus *Gazella* by a number of features of teeth and horns. In the ♂ the horns back at 45 degrees to the plane of the head, whereas they are more upright in other gazelles; the horn cores are more strongly compressed, their transverse diameter being only about 60% of the anteroposterior diameter; the horn rings are also more prominent. The molar teeth are less elongated than in other gazelles, with better-developed styles on the upper molars, less developed lingual stylids and less developed anterior folds. The shape of the posteriorly lower molar is distinctive: its lingual is closed off distally, whereas in other gazelles it is open both distally and mesially. In the skull, the lacrimal bone does not extend so extensively on the face as in *Gazella*; the ethmoid fissure is longer; the nasofrontal sutures are curved forward; and, perhaps most distinctively, the median tips of the nasal bones are very long, the lateral prongs being relatively inconspicuous.

The colour pattern in all species is conspicuous and 'disruptive': the main body tone varies from light brown to quite reddish, the

underside is strikingly white, and there is always a strongly marked black band along the flanks, which may either border the white of the underside directly or be separated from it by a red band. The dark longitudinal stripes on the face, from muzzle to eye, are conspicuous and black, but the white stripes are often largely obliterated, leaving little but a white eye-ring. Characteristically, the rhinarium hardly extends at all along the upper margins of the nostrils.

The karyotype possesses not only the X-autosome translocation characteristic of *Gazella*, *Nanger* and the related genus *Antelope* (Effron *et al.* 1976, Vassart *et al.* 1995), but also, like *Nanger*, a Y-autosome translocation in addition.

Eudorcas contains at least two species, the Red-fronted Gazelle *E. rufifrons* and Thomson's Gazelle *E. thomsonii* (which have been considered conspecific by several authors; see species profiles), and there are grounds for raising *albonotata* and, especially, *tilonura* to specific rank, which is the treatment provisionally followed herein. They are much less arid adapted than species in the genus *Gazella*, being distributed mainly through the Sahel, from Senegal east to the Ethiopian Highlands, whence they extend north into Aïr and south through the grasslands of the southern Sudan into the East African savanna, south to the Wembere flood-plain.

The Red Gazelle *Eudorcas rufina* from N Algeria is an enigmatic form known only from three male specimens (one in the BMNH in London, another in the MNHN in Paris and a third in the collections of the University of Algiers) bought in Algeria and of unknown origin (Kowalski & Rzebik-Kowalska 1991, De Smet & Smith 2001). Although it has been listed as a subspecies of Red-fronted Gazelle (e.g. Ellerman & Morrison-Scott 1951; and see Joleaud 1929), other authors have recognized it as a distinct form (Gentry 1964, Corbet

1978, Grubb 2005). According to Gentry (1972), the form (which he noted shared some similarities to Cuvier's Gazelle *Gazella cuvieri*) was characterized by: fur thick and reddish-brown; dark flank band with brown fur below it; pygal band very slight; reddish-brown face markings; skull with heavily built bones; ♂♂ with large horns; large preorbital fossae; posterior suture of nasals in an almost transverse

plane; and ethmoid fissure small or absent. According to Lavauden (1930), the Red Gazelle inhabited forests and bushes in the region of Saida. The form has sometimes been considered a valid extinct species, but is not considered a valid species here.

Colin Groves

Eudorcas rufifrons RED-FRONTED GAZELLE

Fr. Gazelle à front rouge; Ger. Rotstirngazelle

Eudorcas rufifrons (Gray, 1846). Ann. Mag. Nat. Hist., ser 1, 18: 214. Senegal.



Red-fronted Gazelle *Eudorcas rufifrons*.



Eudorcas rufifrons

Taxonomy The number of subspecies recognized in the past has varied depending on whether *E. rufifrons* was treated as conspecific with related forms, namely Thomson's Gazelle *E. thomsonii*, the Mongalla Gazelle *E. albonotata* and Heuglin's Gazelle *E. tilonura* (Gentry 1972, Groves 1975, 1985a, Kingdon 1997, East 1999). In this account, *E. rufifrons sensu stricto* occurs west of the Nile R. only; *E. tilonura* and *E. albonotata*, which Grubb (2005) considers subspecies of *E. rufifrons*, occur east of the Nile, and are treated as separate species. Schwarz (1914) and Lydekker (1914) divided this species into five subspecies: *rufifrons* from Senegal; *hasleri* from Kano, Nigeria; *kanuri* from lower Chari; *centralis* from upper Chari; and *laevipes* from Sudan. Gentry (1972) followed this treatment, although he included *tilonura* as a subspecies noting that it appeared largely indistinguishable from *rufifrons*. Groves (1975), based on skull examination, considered *centralis* to be synonymous with *kanuri*; although this latter subspecies is sharply bordered, in some respects it is intermediate between *laevipes* and *rufifrons*. The form *hasleri* was considered synonymous with *laevipes*.

The Red Gazelle *E. rufina* is an enigmatic taxon, known only from three specimens obtained from Algeria towards the end of the nineteenth century (De Smet & Smith 2001). The gazelle was listed as a possible subspecies of *E. rufifrons* by Ellerman & Morrison-Scott (1951), but based on skull morphology Gentry (1964) argued that it represented a separate species related to Cuvier's Gazelle *G. cuvieri*. Synonyms: *centralis*, *hasleri*, *kanuri*, *laevipes*, *salmi*, *senegalensis*, *typica*. Chromosome number: $2n = 58$ (Vassart *et al.* 1995); the karyotype is nearly identical to that of Thomson's Gazelle.

Description Medium-sized, deeply reddish-coloured gazelle, with a uniformly tan-coloured upper coat. Forehead red, from which the name of the species is derived. Faint rufous and cream-coloured lines run from the eyes to the nose. Eyes large and black with a faint white ring. Flanks with dark band, 20–40 mm broad, running from the shoulder to the haunches, demarcating the edge of the white underparts. Legs slender, rufous on their outer side and whiter on the inside. Tail relatively long, ending in a black tuft that contrasts sharply with the white buttocks. Horns fairly long, slightly S-shaped over their length and diverging towards the tips; thick and strongly ringed in ♂ compared with ♀.

Geographic Variation

- E. r. ruffrons*: Senegal to Mali. Reddish-chestnut; mid-face bright rufous; light face-stripes light buff, dark ones rufous; no dark spot on the nose, thin red stripe present below the black flank-band.
- E. r. laevipes*: Niger to the Nile R. Larger, less reddish; light face-stripes whitish in colour.
- E. r. kanuri*: south of L. Chad. Intermediate in size; cinnamon-coloured.

Similar Species

- Eudorcas albonotata*. Allopatric, in SE Sudan, east of the Nile R., in the Sudd ecosystem. More brown in colour, with horns in ♂♂ curving backwards and then slightly forwards.
- E. tilonura*. Allopatric, ranging east of the Nile R. and the Blue Nile.
- Gazella dorcas*. Sympatric with *G. d. osiris* (for example, in the Sahelian rangelands of C Chad). Smaller, paler in colour; dark flank-band not well marked, but more clearly bordered above with very pale band; pygal band slightly marked; face markings paler, no nose-spot; face stripes pure white; ears paler; little or no darkening on knee-tufts; skull small; horns longer, narrowly ringed in ♂ and relatively longer in ♀.

Distribution Endemic to Africa. Confined to the Sahelian bushland and grassland from Mauritania and N Senegal to the western side of the Nile R. in Sudan, between the deserts in the north and the moist savanna woodlands in the south (East 1999). From Senegal to Niger only small scattered remnant populations of Red-fronted Gazelles remain, except in and around W N. P. (Niger, Burkina Faso), where it still occurs in good numbers (East 1999, Lamarque 2004). They are probably now extinct in Ghana, where they were always restricted to the Bawku district in the extreme north-east, or otherwise only occur as a rare vagrant from neighbouring countries (Ankudey & Ofori-Frimpong 1990, East 1999). There have never been any reliable confirmed records from Benin (Sayer & Green 1984), but they may occur in the north in Benin's W N. P.; however, they have never been recorded from Pendjari N. P. (Green & Chardonnet 1990, Sinsin *et al.* 2002, Rouamba & Hien 2004). There are also records from just north of Keran N. P. in Togo during the late 1970s and 1980s, which are well to the south of the species' range in Burkina Faso (see Chardonnet *et al.* 1990), but there is no recent information on their occurrence. No recent confirmed reports from Nigeria, but stragglers from Niger and especially Cameroon are expected to occur. The former occurrence of this species in Gambia is unclear, but if they did ever occur it was as a rare vagrant (see Grubb *et al.* 1998 for discussion).

Farther east, Red-fronted Gazelles still persist in many parts of their former range, particularly in Cameroon, Chad and Sudan. In Cameroon, Red-fronted Gazelles seem to have increased since 1960 in Kalamaloué N. P. and Waza N. P., due to the extension of open habitat induced by flood-plain degradation and damage by elephants (Scholte 2003, 2005, Scholte *et al.* 2007), but increased poaching is expected to have greatly reduced numbers more recently (P. Scholte pers. obs.). However, outside protected areas, numbers of Red-fronted Gazelles have declined considerably. In Chad, the gazelle is locally common south and west of L. Fitri, and also occurs locally in small to moderate numbers in largely unexploited rangelands in the Dourbali-Boussou region east of the Chari R. in Chari-Baguirmi, in parts of Mayo Kebi in the south-west, and in Ouaddai and the northern Salamat in SE Chad (Scholte

2001). There is a healthy population in Zakouma N. P. (but see Mackie 2004), and lower population numbers in Siniaka Minia Faunal Reserve (Dejace *et al.* 2000). There is a continuous presence of a very small population in the northern section of Manovo-Gounda-St Floris N. P., Central African Republic, on the southern limit of its distribution area (East 1999). Red-fronted Gazelles occur widely in C Sudan, west of the Nile R., in Jebel Marra, Southern Kordofan and Northern and Southern Darfur States (Wilson 1979, 1980, I. Hashim pers. obs.).

Habitat Inhabits dry grassland and open *Acacia* and *Combretum* shrubland. In the southern parts of the range, where rainfall reaches 1000 mm, Red-fronted Gazelles prefer open habitats and hence may be found in proximity with humans and cultivation. In the northern parts of the range, with an average annual rainfall sometimes as low as 100 mm, these gazelles prefer the wooded wadi areas. Much of the species' habitat is fragmented by agricultural encroachment, and generally grazed by domestic herbivores.

Abundance Numbers of Red-fronted Gazelles are decreasing rapidly due to poaching and habitat loss and degradation resulting from drought and agricultural and pastoral encroachment. This gazelle now occurs in low numbers in mosaic habitats throughout most of its range. The total number of Red-fronted Gazelles has been estimated at about 20,000 (correcting for undercounting biases), with large numbers known to survive in Niger (ca. 4000) and Mali (ca. 3000) (East 1999).

In protected areas density estimates range from 0.1/km² in W N. P., Niger (H. Talatou pers. comm.), 0.2/km² in Zakouma N. P., Chad (Dejace *et al.* 2000), 0.35/km² in Waza N. P. (Scholte 2005) to as high as 4.0–9.0/km² in Kalamaloué N. P. (Scholte 2003), albeit inflated by temporary immigration. In prime gazelle habitat in Waza N. P. (open *Lannea humilis* shrubland) densities ranged from 0.5 to 2.5/km² in a 7 km² plot surveyed by total counts from 1974 to 1998 (Ecole de Faune mission reports).

Adaptations The Red-fronted Gazelle is the least arid-adapted of Sahelo-Saharan gazelles, unable to inhabit the Saharan regions, but successfully exploiting the desert's southern margins.

Foraging and Food The Red-fronted Gazelle is a mixed feeder, preferring grasses during the wet season, and trees and shrubs during the dry season. The principal food plants include *Acacia* spp. (including *A. mellifera*, *A. tortilis*), *Balanites aegyptiaca* and *Boscia senegalensis* (Dorst & Dandelot 1970).

In regions devoid of water Red-fronted Gazelles obtain most of their moisture requirements from their food. However, they are more water-dependent than other gazelle species in the same region (Koster 1983). Some seasonal movements are known (north during the wet season, returning to the south in the dry season), especially from Chad and Sudan, but increasingly limited by human settlement.

Social and Reproductive Behaviour Red-fronted Gazelle social behaviour has not been studied in detail; the only quantitative information available is from wildlife counts in Kalamaloué N. P. (Scholte 2003) and Waza N. P. (Scholte 2005). Group composition (n = 294 individuals) comprised mixed groups (38%), pairs and young (24%), single ♂♂ (14%), harems (14%), single ♀♀ (4%), bachelor groups (3%), and ♀♀ plus young (2%) (P. Scholte pers.

obs.). Single individuals and pairs dominate during the dry season, as well as mixed groups and possible temporary harems that do not normally exceed 5–7 individuals (Koster 1983, Grettenberger & Newby 1990, P. Scholte pers. obs.). Occasionally, mixed groups of up to 19 have been observed during the wet season in Kalamaloué N. P., suggesting the short-term creation of assemblages as known from other gazelle species, related with food availability. Mean herd size was 1.98 ± 0.28 (Waza N. P., Apr), 3.04 ± 0.96 and 3.12 ± 1.16 (Kalamaloué N. P., Feb and Jul, respectively) (P. Scholte pers. obs.).

Breeding ♂♂ defend territories, the boundaries of which are marked with dung piles and secretions from preorbital glands. Frequent and fierce fighting between ♂♂ has been recorded, as also indicated by the occasional presence of ♂♂ with only one horn (see also Malbrant 1952). Like other gazelle species, mounting in Red-fronted Gazelles lasts for a few seconds in which the ♂ stands erect on the hindlimbs and holds the forelimbs bent backwards from the knee, above the female's back.

Reproduction and Population Structure Red-fronted Gazelles reproduce throughout the year, but births are skewed towards the wet season and early dry season (Malbrant 1952) or first part of the dry season (Bourlière *et al.* 1976). Reported gestation periods are 184 and 198 days (Mentis 1972). A single young is born, which remains hidden. Weaning takes place at about three months; ♀♀ reach maturity at about nine months of age, ♂♂ at 18 months. Longevity of captive gazelles is to 14.5 years (Weigl 2005). No systematic studies have been undertaken on population structure. Sex ratio (♂ : ♀) in all observations ($n = 278$ individuals) in counts in Waza and Kalamaloué National Parks was 1 : 1, yet varied from 1.3 : 1 (Kalamaloué, Feb 1994) and 1.2 : 1 (Waza, Apr 1998) to 0.57 : 1 (Kalamaloué, Jul 1994). Juvenile percentage in these observations increased from 3% in Feb to 7% in Apr to 9% in Jul (P. Scholte pers. obs.).

Predators, Parasites and Diseases Main predators in the past would have included Cheetahs *Acinonyx jubatus*, African Wild Dogs *Lycaon pictus*, Lions *Panthera leo*, Leopards *Panthera pardus*, Spotted Hyenas *Crocuta crocuta* and African Rock Pythons *Python sebae*. Most of these species are now locally extinct or extremely rare in the range of the Red-fronted Gazelle, with the exception of some protected areas. Domestic dogs, jackals *Canis* spp. and birds of prey (particularly on calves) are presently the main predators; in Sudan, the Secretary Bird *Sagittarius serpentarius* may take young (I. Hashim pers. obs.). Red-fronted Gazelles strictly avoid regions infested with tsetse flies (see also Malbrant 1952). There is no other information on parasites or diseases.

Conservation IUCN Category: Vulnerable A2cd. CITES: Not listed.

Populations of the Red-fronted Gazelle have decreased due to poaching, especially for skins and as pets. Jeannin (1936) reported on a group of hunters that, with dogs and nets, had collected more than 1600 skins in a three-and-a-half month period in N Cameroon. The hundreds of gazelles kept in cities such as N'Djamena have generally been taken as young from the wild and subsequently raised with goats. Drought, habitat loss, and competition with livestock have further reduced the presence of Red-fronted Gazelles to scattered remnants throughout its former range. Viable populations survive in Burkina Faso, Mali, Niger, Cameroon, Chad and Sudan, but numbers are decreasing except in a few protected areas such as W N. P. (Niger, Burkina Faso), Waza N. P. and Kalamaloué N. P. (Cameroon) and Zakouma N. P. (Chad) (Dejace *et al.* 2000, Scholte 2005, Scholte *et al.* 2007).

Only a very limited number of individuals are maintained in captivity in zoos (<25), in San Diego, Warsaw and Dubai, without formal captive breeding programmes (E. Handrus pers. comm.).

Measurements

Eudorcas rufifrons

E. r. kanuri

Head (♂♂): 339 ± 27 mm, $n = 59$

Head (♀♀): 309 ± 17 mm, $n = 36$

Body (♂♂): 892 ± 68 mm, $n = 59$

Body (♀♀): 923 ± 49 mm, $n = 36$

T (♂♂): 294 ± 33 mm, $n = 59$

T (♀♀): 323 ± 24 mm, $n = 36$

E (♂♂): 150 ± 9 mm, $n = 59$

E (♀♀): 159 ± 16 mm, $n = 36$

Sh. ht (♂♂): 687 ± 62 mm, $n = 59$

Sh. ht (♀♀): 695 ± 43 mm, $n = 36$

WT (♂♂): 30.7 ± 2.4 kg, $n = 59$

WT (♀♀): 28.1 ± 1.5 kg, $n = 36$

Cameroon (Nchanji & Amubode 2002)

Two adult *E. r. laevipes* ♂♂ from Aïr, Niger, had the following measurements: TL (1140–1200 mm); Sh. ht (770–810 mm); T (145–170 mm); and WT (26.0–29.0 kg) (Brouin 1950)

Maximum recorded horn length is 35.2 cm for a pair of horns from the White Nile, Sudan (Rowland Ward)

Key References East 1999; Groves 1975; Scholte 2005

Paul Scholte & Ibrahim M. Hashim

Eudorcas tilonura HEUGLIN'S GAZELLE

Fr. Gazelle d'Eritrée; Ger. Eritreagazelle

Eudorcas tilonura (Heuglin, 1863). Nova Acta Acad. Caes. Leop.-Carol., Jena 30 (2): 6. Plains near Ain-Saba, Bogosland, Abyssinia.

Taxonomy Monotypic. Usually considered a subspecies of the Red-fronted Gazelle *E. rufifrons* (Gentry 1972, Grubb 1993c, 2005), but here considered a distinct species. It has been assumed that this species has hybridized with *E. r. laevipes*, but the distribution of *E. tilonura* lies east of the Nile R. and the Blue Nile (P. Grubb pers. comm.). *Eudorcas tilonura* is redder than *E. r. laevipes*, and smaller, with horns bowed

outwards and hooked inwards at the tips (Groves 1985a). Synonym: *melanura*. Chromosome number: not known.

Description A small gazelle, having a straight back in profile. Forehead and bridge of nose rufous, bordered by white stripes that encircle the eyes and extend down to the mouth; there is no dark

spot on the nose. The space between the horns is white. Preorbital glands are more conspicuous in ♂ than ♀. A deep reddish band along flanks extends from the shoulder to the hindquarters, separating the sandy-fawn colouring above and white below. The intensity of this band changes with season, being fainter in summer and darker in winter; the band is also darker in younger animals. Buttocks white. Tail relatively long, its base rufous and gradually changing to black. Horns very short, inwardly hooked at the tips, and prominently ringed in ♂. Female horns weakly ringed; they grow straight at first, curve outward and then inward.

Geographic Variation None recorded.

Similar Species

Eudorcas rufifrons. Allopatric, confined to the Sahelian bushland and grassland regions from Mauritania and N Senegal to west of the Nile R. in Sudan. See also Taxonomy.

Nanger soemmerringi. Largely allopatric, but ranges overlap in SW Eritrea (and formerly in NE Sudan, although Soemmerring's Gazelle is now probably exterminated from its historical range in this country). Larger, paler gazelle with extensive white on the rump; facial blazes strongly marked; horns heavy, short and swept backward, the in-pointed, hooked tips forming a lyrate shape; legs long with big hooves; tail with many white fringes of short hair.

Gazella dorcas. The Isabelline Gazelle *G. d. isabella* is sympatric. A more gracile gazelle, brown-grey with reddish tones and dark markings, and a dark nose-spot; horns lyrate, short, stout and widely spread with in-turned tips.

Distribution Endemic to Africa (see species profile of Mongalla Gazelle *E. albonotata* for map). Confined to the eastern side of the Nile R. and the Blue Nile between the southern part of the Red Sea hills in Sudan and the southern foothills of the Ethiopian massif in W Eritrea and NW Ethiopia (East 1999). Currently, Heuglin's Gazelle is thought to occur through much of its historical range, but in localized patches as a result of poaching, agricultural encroachment and overgrazing by domestic herbivores.

Habitat Heuglin's Gazelle inhabits dry grassland, open steppe and thorn bushland, ranging up to 1400 m in the savannas of NW Ethiopia (Yalden *et al.* 1996). Rainfall varies between 1000 mm in the southern part and 100 mm in the northern part of its range. Part of the habitat in the southern range is characterized by heavy, cracking clay ('black cotton') soils that swell when they are wet and become sticky. The gazelles avoid the sticky clay by moving to lighter, better-drained soils during the wet season, but return to the clayey sump areas during the dry season. Here they favour a mosaic of habitats, including woodland, which are subject to seasonal burning (Hashim 1998). They avoid thick cover. As Heuglin's Gazelle inhabits arid regions devoid of water, water is consumed when it is available but it is not an essential habitat requirement.

Abundance Heuglin's Gazelles are now found in low numbers in disjunct patches of remaining habitat and in localized areas such as the Dinder N. P. of Sudan where a density of ca 1.0 ind/km² has been recorded (Hashim 1998). East (1999) estimated a total population size of 3500–4000 animals.



Eudorcas tilonura

Adaptations Heuglin's Gazelle has been isolated from other members of its genus by the Nile R. and by mountains, and has adapted primarily to living on the plains on either side of the Atbara R.

Foraging and Food Heuglin's Gazelles both browse and graze, grazing during the wet season when grasses and forbs are readily available. *Ipomoea* spp. are preferentially selected, particularly in secondary successional areas (Hashim 1998). Heuglin's Gazelles forage in small groups of 3–4 and feeding usually takes place early in the morning and in the evening. In arid savanna regions such as Dinder N. P., where the habitat is unfavourable during the wet season, the gazelles move outside the park to habitats with short grasses that are more nutritious compared with the tall grasses inside the park (Hashim 1998).

Social and Reproductive Behaviour Heuglin's Gazelles occur in groups ranging from two to four (mean = 1.8; n = 11; Hashim 1998). During the heat of the day they take shelter under large trees or shrubs, depending on the type of habitat. In arid savanna the preferred tree is *Balanites aegyptiaca* under which the gazelle scrapes shallow bedding sites. Usually a couple of gazelles use the bedding site for a considerable period of time as indicated by the accumulating dung heaps. In habitats dominated by shrubs, *Acacia nubica* is preferred (under which deeper bedding sites are excavated). Apparently, in these habitats, the gazelle uses these bedding sites only for short periods as indicated by the few tracks and the absence of dung heaps (Hashim 1998).

There is no information concerning territorial behaviour in free-ranging animals. However, in captivity, the ♂ shows signs of territorial behaviour by making dung heaps at the peripheries of the fence, sniffing the heaps and scratching the ground surrounding them. This is followed immediately by urination and defecation. Objects close to the fence are frequently marked with well-developed preorbital glands. Mounting lasts for a few seconds, when the ♂ stands erect on his hindlimbs

holding the forelimbs bent back from the knee, above the back of the ♀. At this time, ♂ and ♀ may be moving slowly or standing still.

Reproduction and Population Structure In free-ranging Heuglin's Gazelle, births occur during the wet season (I. M. Hashim pers. obs.). The gestation period is approximately six months. No other information on reproduction and population structure is available.

Predators, Parasites and Diseases Little information is available, but of the predators now found in areas inhabited by the Heuglin's Gazelle the most common are jackals *Canis* spp., which probably prey on young. Hyenas are less common but in a small forest reserve like Wad Kabu in E Sudan, it is possible that they could play a significant role in controlling the population of this gazelle.

Conservation IUCN Category: Vulnerable C1 (listed as subspecies of *E. rufifrons*). CITES: Not listed.

Heuglin's Gazelle have been reduced to small fragmented populations throughout their range because of illegal hunting, competition with domestic livestock and habitat degradation resulting from drought, overgrazing and agricultural encroachment. Viable populations survive in Sudan and Eritrea, but their numbers are decreasing. The gazelle is protected in Dinder N. P., but East (1999) noted that it does not receive effective protection here, as the open sites that it prefers are utilized intensively by camel herders

who trespass into the park in the dry season and destroy the gazelle's favourite shade trees to feed their camels and goats. This species is also subject to heavy poaching, particularly during the wet season, when animals move outside the boundary of the park. The declining trend of this gazelle species can be reversed by improved management of existing protected areas, and the extension of effective protection to additional populations besides those in Dinder N. P. (East 1999).

Measurements

Eudorcas tilonura

HB (♂): 678 mm, n = 1

HB (♀): 550, 590 mm, n = 2

T (♂): 290 mm, n = 1

T (♀): 250 mm, n = 1

HF c.u. (♂): 290 mm, n = 1

HF c.u. (♀): 290 mm, n = 1

E (♂): 140 mm, n = 1

E (♀): 140 mm, n = 1

Sudan (I. M. Hashim pers. obs.)

Maximum recorded horn length is 30.1 cm for a pair of horns from Atbara R., Sudan (Rowland Ward)

Key References East 1999; Hashim 1998.

Ibrahim M. Hashim

Eudorcas thomsonii THOMSON'S GAZELLE

Fr. Gazelle de Thomson; Ger. Thomsongazelle

Eudorcas thomsonii (Günther, 1884). Ann. Mag. Nat. Hist., ser. 5, 14: 427. 'the range of country from Kilimanjaro to Baringo and at various heights above 6000 ft [1830 m]'; restricted to 'Kilimanjaro district' (Lydekker 1914) in Kenya (G. M. Allen 1939).

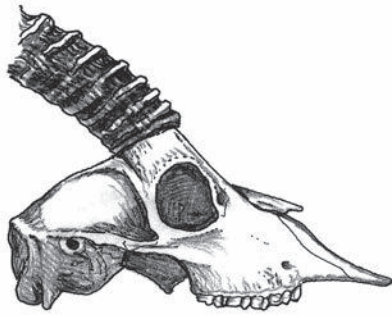


Thomson's Gazelle *Eudorcas thomsonii*.

The species is named for the British explorer, Joseph Thomson, who was the first to discover the gazelle.

Taxonomy It has recently been proposed that Thomson's Gazelle be moved from the genus *Gazella* to the genus *Eudorcas* (Groves 2000), along with the Red-fronted Gazelle *E. rufifrons* and the Mongalla Gazelle *E. albonotata*. This change is the result of genetic analysis that shows that although there is very little genetic difference between these species, they are collectively distinct from the other members of the genus *Gazella* (Groves 2000). *Eudorcas* was originally coined by Fitzinger (1869) in reference to *E. laevipes*, currently considered a subspecies of the Red-fronted Gazelle (Groves 1985a, 2000, Grubb 2005). Groves (1969) included *thomsonii* in Cuvier's Gazelle *Gazella cuvieri*, and many authors (Groves 1985a, 1988, Kingdon 1997, East 1999, Rebholz & Harley 1999) have included *thomsonii* in *E. rufifrons*. However, Gentry (1964, 1972) presented evidence that they are distinct from both (and see Grubb 2005).

The Mongalla Gazelle *E. albonotata* from the S Sudan is sometimes regarded as a subspecies of Thomson's Gazelle (Gentry 1972, Grubb 1993c), but is here treated as a distinct species. Grubb (2005) noted that skull and horn proportions associate *albonotata* with *rufifrons* rather than *thomsonii* (and see Gentry 1972). Synonyms: *arushae*, *baringoensis*, *behni*, *bergeri*, *bergerinae*, *biedermanni*, *dieseneri*, *dongilanensis*, *langheldi*,



Lateral view of skull of Thomson's Gazelle *Eudorcas thomsonii*.

macrocephala, *manyarae*, *marwitzi*, *mundorosica*, *nakuroensis*, *ndjiriensis*, *ruwanae*, *sabakiensis*, *schillingsi*, *seringetica*, *wembaerensis*. Chromosome number: $2n = 58$ (Effron *et al.* 1976, Vassart *et al.* 1995).

Description A small, compact gazelle with a cinnamon-brown back, cream underparts and prominent dark brown or black side-stripe under a buff band. Tail black, contrasting markedly with the cream rump patch, although the cinnamon-brown back colour extends down to base of tail. Face boldly marked with cream and dark brown/black stripes. Ears are of moderate length and narrow. Male slightly larger than ♀ both in weight and body length (Brooks 1961, Robinette & Archer 1971); the two sexes look alike except for the horns and the fact that the neck is thicker in ♂. Horns of ♂ relatively long, mildly undulating and heavily annulated. Females have short, smooth horns or they may be absent completely. The preorbital glands are prominent in adult ♂♂. Carpal, pedal and inguinal glands are also present. The skull follows the typical patterns of the family Bovidae with no incisors in the upper toothrows and unlobed canines in the lower toothrows. When horns are present, there is no suture separating the horn from the frontal bone (Gentry 1972).

Animals can be aged on external characteristics and behaviour (Walther 1973a), as follows:

- 0–2 weeks. Darker in colour than older age classes. At this age the neonate lies out and joins its mother only to suckle and be cleaned.
- 3 weeks to 2 months. When standing beside its mother, the juvenile's

back is below the mother's belly or level with it. Sometimes juveniles have a little white mane on the neck near the chest. Horns are not present, or at least not visible in the field. Increasingly out of 'hiding', accompanying mother for more and more of the time.

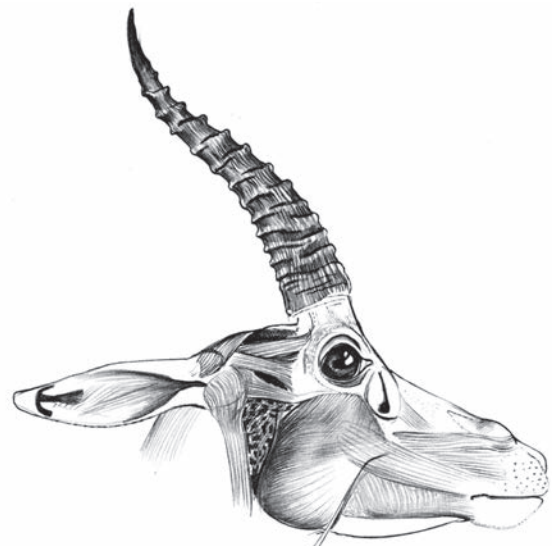
- 3 months to 4–6 months. When standing beside an adult ♀, the dorsal surface of the half-grown juvenile is approximately at the level of half of the adult's body. At the end of the half-grown stage, the tips of the horns are usually visible in the field; however, they do not yet allow a distinction between ♂ and ♀. The lying out period is over.
- 5–8 months (adolescents). Still smaller than adult ♀♀ and have a proportionally shorter snout. The horns of adolescent ♂♂ are shorter than their ears or, at maximum, equal in length. Although the horns of adult gazelle ♀♀ are about the same length or even longer, the horns of adolescent ♂♂ are much sturdier than those of ♀♀. At the beginning of this age class, they are about 3 cm tall and look like little cones. Later, they also show the typical rings of male horns. The horns of adolescent ♀♀ may or may not be visible under field conditions. They are much thinner than in adolescent ♂♂ and reach, at maximum, three-quarters, but in most cases only one-third, of the length of the ears. The little white mane near the chest may still be visible. Thus, in many cases, only the smaller size and different body proportions are the criteria for distinguishing an adolescent ♀ from an adult. Adolescents of both sexes are for the most part weaned.

The above two ages classes overlap and cannot be entirely distinguished.

- 8–12 (possibly up to 15) months (subadults). Subadult ♂♂ are very similar in size to adult ♀♀, but tend to have a slightly thicker neck; but, the neck is clearly thinner than an adult male's. The horns are longer than the ears, with a characteristic 'tilde' or recurved shape, but have not reached full length. Subadult ♀♀ are difficult to distinguish from adult ♀♀, but are a little smaller, with a more slender body and neck. Their horns may be half to full length of the ears.
- 16–24 months (young adults). This age group is impossible to recognize in the case of ♀♀ but in ♂♂ the horns are about 20 cm long and show the beginning of the lower curvature of



Thomson's Gazelle *Eudorcas thomsonii* head.



Thomson's Gazelle *Eudorcas thomsonii* head myology.

mature horns. The body is full size but with a slightly thinner neck than the adult ♂. Widely spaced annulations at the horn base also distinguish young from mature bucks.

- *Full adulthood seems to be reached at the end of the second year of life.* Adult ♂♂ have full-length double-arched horns, ca. 25–43 cm long. The horns of adult ♀♀, when present, are ca. 8–15 cm (Haltenorth 1963), but are often broken or bent. Generally, by about ten years Thomson's Gazelles seem to reach 'very old age' (Walter 1973a), in which the belly hangs deep, the ribs are often visible and sometimes the lower lip appears somewhat protruded. The normally brown forehead may become completely white.

Geographic Variation Geographic variation in Thomson's Gazelle is uncertain and no genetic differentiation within the species has been reported apart from work to identify differences between Thomson's Gazelle and the Red-fronted Gazelle. However, several authors have recognized two subspecies:

E. t. thomsonii: Rift Valley and east, south of a line from the L. Eyasi escarpment to Speke Gulf on L. Victoria.

E. t. nasalis: west of the Rift Valley, and north of the line from the L. Eyasi escarpment to the Speke Gulf.

Brooks (1961) contended that there were four geographically definable variants of Thomson's Gazelles, their distinctness, perhaps, reinforced by social behaviours (Kingdon 1982).

Similar Species

Eudorcas albonotata. Very similar in appearance, but occurs further north, being restricted to the Sudd ecosystem in SE Sudan. Sometimes considered conspecific (see Taxonomy).

Nanger (granti) granti. Sympatric; larger and paler, and also has longer horns. Immatures of the two species can be confused, but the white rump patch extends over the tail onto the croup in Grant's Gazelles.

Distribution Endemic to Africa. Thomson's Gazelles currently inhabit a relatively small range in N Tanzania and S Kenya, largely restricted to the high plains and *Acacia* savannas above 500 m (Estes 1991a, East 1999). Its upland distribution is essentially associated with the highest areas of the Eastern Rift Valley, spilling over to the east and west. This distribution suggests contraction from a wider range during the Ice Age (J. Kingdon pers. comm.).

Habitat Thomson's Gazelle is usually found on short grassland with dry, firm footing although it will move into tall grassland and open wooded habitats during migration (Estes 1991a). Principally a grazer, it tends to concentrate in open areas (plains or grassland patches in woodlands) with short grass, preferring heavily grazed, trampled or burnt grassland with emergent vegetation (Vesey-Fitzgerald 1960, Wilmshurst *et al.* 1999a). It stays on grasslands long deserted by other, larger herbivores as long as some grass remains. In Serengeti N. P. it has been highly successful, along with the Common Wildebeest *Connochaetes taurinus* and Plains Zebra *Equus quagga*, at exploiting the seasonal productivity of semi-arid savanna (Vesey-Fitzgerald 1973), taking advantage of the naturally short grasslands in the south and east of the ecosystem during the rains and migrating to wetter areas to the north-east mostly to the Kirawira, Nyasirori and Ruwana



Eudorcas thomsonii

Plains (rarely further north than the Togoro Plains) in the dry season. Although Thomson's Gazelles pass through the high grass plains during migration, they tend not to remain there for long periods.

Abundance Locally common. East (1999) estimated the population size at around 550,000 animals. The migratory population of this species in the Serengeti–Mara ecosystem on the Tanzania/Kenya border is Africa's largest and most spectacular protected gazelle population. Data from the 2003 wet season in the Serengeti ecosystem estimates the Thomson's Gazelle population at 174,015 ($\pm 37,406$ S.E.) (Mduma 2003). In the early 1970s, numbers stood at 0.66 million animals but had decreased to less than 0.25 million animals in 1985 (Borner *et al.* 1987). East (1999) reported a figure of 342,000 in 1996. However, changes in survey methodologies over the years and large variance in population estimates make determination of true population trends difficult (Borner *et al.* 1987). Nevertheless, this decline is consistent and concurrent with a substantial loss of large wild herbivores in the Masai Mara ecosystem in Kenya (Ottichilo *et al.* 2000, 2001, Ogotu *et al.* 2011).

There are smaller resident populations of this gazelle in the western and northern Serengeti N. P., particularly on the Togoro Plains and in the open woodland towards Bologonja (ca. 10,000; East 1999) and Ngorongoro Conservation Area (estimated to be ca. 1300 in 1992 by Runyoro *et al.* 1995, and an average of ca. 1400 between 1986 and 2005 by Estes *et al.* 2006). There are an estimated 20,000 Thomson's Gazelles in Arusha region, outside the Ngorongoro Conservation Area (East 1999). The species also occurs in Tarangire N. P., Tanzania, where the resident, wet season population of ca. 600 is augmented in the dry season by a migratory population of ca. 3000 that spends the wet season on the Simanjoro Plains (East 1999). A southern population of ca. 1000 animals occurs in the north-east of Tabora region and on the Wembere Plains (East 1999).

In Kenya, Thomson's Gazelles are present in the west of the country, including Masai Mara National Reserve, where the population declined

from about 20,000 in 1977–79 to 8100 in 2007 (Ogutu *et al.* 2011). A further 2500 animals are present in the Laikipia district (Georgiadis *et al.* 2003), and ca. 10,000 in the Ewaso Ngiro basin (including Mt Kenya N. P., Aberdares N. P., the Samburu N. R., Buffalo Springs N. R., Shaba N. R. and Meru N. P.) as of 1997, a decline from ca. 33,000 in 1977 (Muchoki 2000).

Adaptations Thomson's Gazelles are relatively drought-resistant, enabling them to remain out on the dry plains, long after most other ungulates have moved off to find wetter habitats (Vesey-Fitzgerald 1960, Bell 1969). They are less adapted to arid conditions than Grant's Gazelles (Taylor 1970a), relying on evaporative cooling by panting to keep their body heat several degrees below the ambient temperature (Taylor 1972). However, when water supply is restricted, evaporation is reduced and the body temperature of the gazelles increases to a point where they are in thermal balance with their environment without panting (Taylor 1972). Selective cooling of the blood to the brain may enable the gazelles to survive high body temperatures (Taylor 1972, Jessen 1998). Although gazelles will travel long distances (up to 16 km) to water every other day or so (Brooks 1961) in the dry season, some individuals remain out on the short grass plains in Serengeti N. P. at considerable distance from rivers and pools, and appear to be independent of water.

Thomson's Gazelles are ruminants and have been classified as 'intermediate feeders preferring grasses' based on analysis of stomach morphology (Hofmann & Stewart 1972, Hofmann 1989), stable carbon isotope analysis (Cerling *et al.* 2003) and comparative anatomy of dental wear patterns (Fortelius & Solounias 2000). Skull proportions suggest that they are adapted to be selective feeders with the narrowest muzzle of all the gazelles (Janis & Ehrhardt 1988). This would appear to be an adaptation to dry season conditions during which dicotyledonous plant material is being selected from within swards of coarse grasses. During the wet season Thomson's Gazelles graze on more uniform swards of prostrate grasses (Bell 1969, Stewart & Stewart 1971), for which fine selection may not be advantageous. Nevertheless, their relatively small body size constrains the amount of forage that a Thomson's Gazelle can consume and digest daily (Arman & Hopcraft 1975, Meissner & Paulsmeier 1995). Hence, they appear to be adapted to foraging on sparse but high-quality plant material (Wilmschurst *et al.* 1999a).

In Serengeti N. P. a large proportion of the population migrates between the open plains and the woodlands, enabling Thomson's Gazelles to take advantage of ephemeral food resources and maintain higher numbers than would otherwise be possible. Movement patterns vary, but the gazelles tend to leave the open woodland when rains start, around Nov, and migrate towards the open plains in the south-east of the ecosystem. They stay there, moving between L. Ndotu and Lemuta Hill, until the end of the long rains (ca. May). As the plains dry up, they cross the central Serengeti Plains in a north-westerly direction, heading towards the 'corridor' (i.e. the area of the park towards L. Victoria) or the Grumeti and Ikoma areas until the onset of the rains. Not all the Thomson's Gazelles migrate out onto the open plains during the wet season – some remain in the woodland, concentrated in the open woodland and clearings (Schaller 1972, Durant *et al.* 1988). The number of Thomson's Gazelles on the eastern Serengeti Plains is closely associated with rainfall levels (Durant *et al.* 1988). McNaughton (1985) noted that Thomson's Gazelles arrived on the Serengeti Plains within three days of significant rainfall there.

There is no close association between rainfall and gazelle numbers in the north and west of the plains, suggesting that they are unlikely to have moved there in response to growth of new shoots; instead they may be feeding on high protein dicotyledons which maintain higher dry-season levels of protein than grasses (Stelfox & Hudson 1986) and which are made accessible by wildebeest feeding in the same area earlier in the year (Bell 1971, Maddock 1979) or because of their need for water. Thomson's Gazelles do collect in areas previously grazed by wildebeest (McNaughton 1976).

On account of their size, Thomson's Gazelles are preyed upon by a wide range of predator species. Living in open habitats and unable to rely on crypsis to avoid predation (except as juveniles in hiding), they have evolved a number of other strategies to minimize predation. Other than their physical adaptations of high speed (80 km/h; Christiansen 2002) and agility (Walther 1969), they have a range of behavioural anti-predator strategies (Walther 1968, FitzGibbon 1988, FitzGibbon & Lazarus 1995), the main ones being grouping and vigilance (see below). In addition to grouping with conspecifics, Thomson's Gazelles are often found in mixed-species groups with Grant's Gazelles (Estes 1967, Sinclair 1985, FitzGibbon 1990a). However, Grant's Gazelles are less water-dependent and a higher proportion remain on the open Serengeti Plains in the dry season. In the plains during the wet season and in the woodland during the dry season they are also found together with Common Wildebeest, Plains Zebra, Topi *Damaliscus lunatus jimela*, Kongoni *Alcelaphus buselaphus cokii*, Impala *Aepyceros melampus*, Waterbuck *Kobus ellipsiprymnus* and Giraffe *Giraffa camelopardalis* (Walther *et al.* 1983).

In contrast to the adults, the young, unable to outrun predators, rely on crypsis, remaining hidden for the first few weeks of their life. Predators have considerable difficulty in finding hidden juveniles: Cheetahs *Acinonyx jubatus*, Spotted Hyaenas *Crocuta crocuta* and jackals *Canis* spp. have all been observed to walk within 5–10 m of hidden gazelle juveniles without detecting them. The cryptic colouration and lack of scent, resulting from the inactivity of its scent glands (Gosling 1969a, Walther 1969) and the ingestion of urine and faeces by the mother, help to make the young gazelle difficult to find. In addition, antelope young in the prone response have been shown to have lower respiration and heart-beat rates than young in the normal resting position (Jacobsen 1979).

Thomson's Gazelles constantly twitch their tails from side to side. The function of this behaviour is unknown, but it may be a species recognition signal (Estes 1991a).

A study in Serengeti N. P. found that four basic activities – lying, standing, grazing and moving – were recorded regularly through the day (Walther 1973b). Grazing was concentrated in four major periods, in the early morning, at noon, in the evening and around midnight. Generally activity was slightly higher during daylight than at night. Adult gazelles spent about half their time lying down, in bouts of 0.5–5 hours. They slept for ca. 0.5–1 hour/day with eyes closed a few minutes at a time. At the hottest time of day, in the afternoon, the gazelles sought shade, but sometimes sunbathed in the morning, seeking open areas and orienting their hindquarters or flanks towards the sun (Walther 1973b). Young and subadult gazelles sometimes participated in running and jumping games (play), usually with several animals participating at once. The games were concentrated in the morning and evening (Walther 1973b). Aggression also peaked early and late in the day, sexual activities in early morning, mid-day and midnight (Walther 1973b).

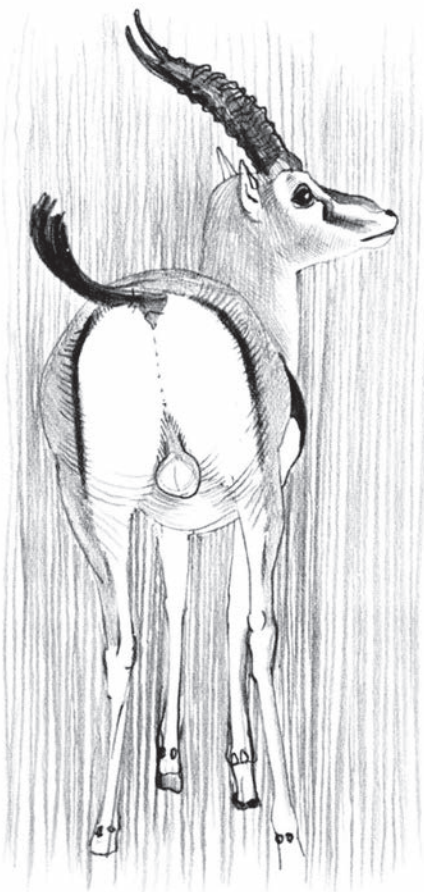
Foraging and Food During the wet season, their diet consists of 80–90% grasses (Talbot 1962, Stewart & Stewart 1970), but during the dry season when only coarse grasses are available, they include considerably more forbs and fruits in their diet (Stewart & Stewart 1971, Hoppe *et al.* 1977), up to approximately 40% (Gwynne & Bell 1968, Bell 1969). Stomach content and tooth enamel analysis using stable carbon isotope analysis has found Thomson's Gazelles' diet to be approximately 64–68% grasses (identified via their C_4 carbon structure) and 32–36% forbs (identified via their C_3 carbon structure) (Cerling *et al.* 2003).

As specialists on sparse, but relatively high-quality, grasses (Arman & Hopcraft 1975, Wilmshurst *et al.* 1999a), they will tend to segregate in space and time from larger grazers (Jarman & Sinclair 1979). This pattern has led some observers to suggest that they form the final stage of a 'grazing succession' based on timing of grazing patches and local topography (Vesey-Fitzgerald 1960, Gwynne & Bell 1968, Maddock 1979). However, it seems unlikely that this pattern is solely the result of the larger species improving the grazing conditions for Thomson's Gazelles (de Boer & Prins 1990, Huisman & Olff 1998). Further research has shown that Thomson's Gazelles concentrate in areas of higher than average food quality (Fryxell *et al.* 2004), including aggregating on patches of grass regrowth following recent fires (Wisley 1996). Details of food plants, including seeds, in the more wooded southern parts of their range have been listed by Burt (1929) and use of the herb layer has been studied in detail, for Serengeti N. P., by Bell (1969, 1970, 1971).

Social and Reproductive Behaviour The social organization of Thomson's Gazelles is characterized by the occurrence of mixed herds ($\sigma\sigma$ and ♀♀), female groups (♀♀ with or without offspring), all-male groups (or 'bachelor' groups containing $\sigma\sigma$ of all age classes) and single territorial $\sigma\sigma$ (Brooks 1961, Walther 1964b, Estes 1967, Hvidberg-Hansen & de Vos 1971). The typical group size is 6–60 animals, but far larger groups of over 1000 animals may occur at some times (Jarman 1974). In Ngorongoro Conservation Area, Tanzania, female herds averaged 23 animals, compared with an average of 13 $\sigma\sigma$ in bachelor herds (Estes 1967). In Serengeti N. P., groups are larger on the short-grass plains than in tall-grass areas (FitzGibbon & Lazarus 1995), probably because of a change in food distribution and the difficulty of maintaining contact when visibility is restricted.

Mixed herds are typical during migration or may occur when a bachelor group intermingles with a group of ♀♀ . Females may be found on their own or in small groups when keeping watch over hidden young, and other gazelles have moved away. Bachelor groups tend to be found in more marginal areas, with the ♀♀ and young on the best habitat contained within the network of male territories (Estes 1991a). Social groupings of Thomson's Gazelles are very loose and open, especially during migrations and at high densities.

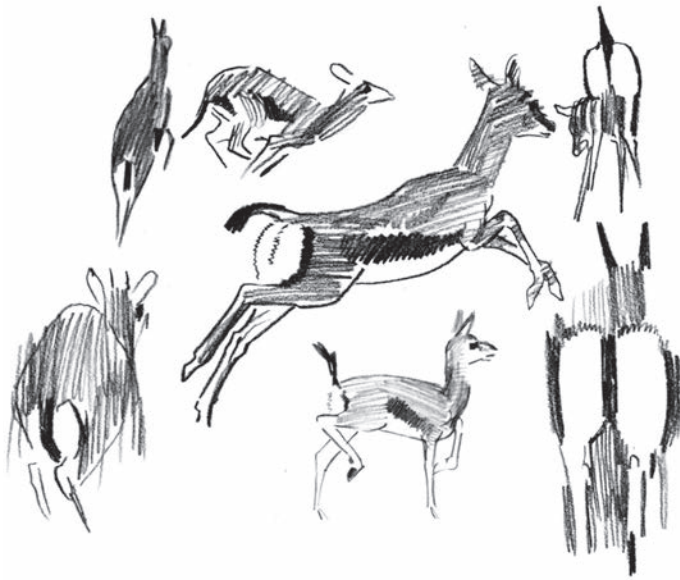
Reproduction is mainly carried out by the territorial $\sigma\sigma$ (Walther 1964b, 1968, Estes 1967). The ♀♀ roam their home-ranges and 'visit' the territorial $\sigma\sigma$, usually only for a few hours per day. The territories of $\sigma\sigma$ are usually between 10 and 30 ha in area and of irregular shape (Walther 1978a). However, they may be as small as 2.5 ha or as large as 200 ha (Walther 1978a). The territories are often close together. Non-territorial $\sigma\sigma$ are driven away when they happen to enter a territory.



Thomson's Gazelle *Eudorcas thomsonii* rear view.

Males mark grass stems and branches with their preorbital glands, depositing a dark sticky secretion at the tip of the object, and they urinate and defecate sequentially and in striking postures (Walther 1964b, Estes 1967). When a σ stays in a territory for some time, he may repeatedly urinate and defecate at the same spots, establishing dung piles. The creation of these dung piles and secretion marks serve to mark a territory, although non-territorial σ in bachelor groups may also perform these activities. It seems that it is the concentration of marks by one individual within a limited space that marks the territory. In one territory mapped (Walther 1978a), one or two dung piles were in the centre of the territory, with ca. 10–20 around the boundary. The secretion marks were also concentrated around the boundary (Walther 1978a), particularly in areas that bordered another male's territory. Territories are rarely defended for a whole year, at least in Serengeti N. P. (Walther 1978a). Once a territorial σ moves into an area, it takes ca. 1–2 weeks to fully mark the territory and territorial activity often declines after 3–5 months (Walther 1972a).

Territoriality is not limited to a particular season. A territorial σ may establish a territory, keep it and abandon it at any time of year. However, there are seasonal peaks in territoriality, linked to levels of reproductive behaviour. Walther *et al.* (1983) noted that, in Serengeti N. P., a peak reproduction period begins with the end of the small rains (usually mid-Dec) and is continued with some fluctuations until the end of the long rains in May. Another peak seems to be in Sep. However, there is considerable variation from year to year and from place to place, depending on local conditions (e.g. the onset and duration of the rains). Reproductive behaviour appears to be at its lowest from the beginning of Jun to mid-Aug.



Thomson's Gazelle *Eudorcas thomsonii*.

Males defend their territories with a range of agonistic behaviours (Walther 1978b). They may present their horns towards an intruder (horn threat), showing their intention to fight. If the other ♂ reciprocates, the interaction usually leads to a fight. Otherwise, the recipient simply walks away, sometimes followed by the challenger in a 'pursuit march'. Fights normally involve the clashing and occasionally locking of horns; body attacks are rare. Fights may be interspersed with and normally end with ritualized grazing, in which opponents graze facing each other, then parallel to each other and then facing in opposite directions (some or all of these positions may be shown).

Among adult territorial ♂♂ fights normally take place between neighbours, serving to establish territory boundaries. Non-territorial ♂♂ who happen to enter a territory normally leave, after the initial horn threat, and are then driven out in a pursuit march or chased away at a full gallop by the territory holder, sometimes with the chaser uttering a typical 'chasing call' through the nose ('pferr-pferr-pferr-'). Fights also take place between bachelor ♂♂, particularly if an oestrous ♀ comes close. The ♀ usually runs away as the ♂♂ begin to fight (Walther 1978b).

Males herd ♀♀ that come within range, attempting to prevent them leaving their territories, trying to head off those threatening to escape, and trying to ensure they remain towards the centre of the territory. A ♂ may be successful in the short term but rarely in the long term, particularly when a group of ♀♀ decides to move off (Estes 1991a).

A courting ♂ usually approaches a ♀ with the head and neck stretched forward (neck-stretch). Typically, this is followed by a nose-up movement; in the most extreme version, the nose, head and neck are pointed straight upwards towards the sky and the ♂ performs a rapid goose-step called the 'drumroll' by Walther. A ♀ driven by a ♂ normally urinates. The ♂ will then sniff the urine and perform flehmen, after which he may either lose interest in her or begin to court her intently, with repeated neck-stretch and nose-up movements. When following the ♀, the ♂ often kicks with his rather stiffly straightened foreleg in the direction of the female's hindquarters and may contact her hindlegs (laufschiag). Mounting and copulation normally takes place while the ♂ and ♀ are walking.

The ♂ normally mounts the ♀ several times before copulation. Occasionally, a ♂ may copulate with the same ♀ a second or even third time, at intervals of up to several hours (Walther 1978b). While non-territorial bachelor ♂♂ may occasionally court ♀♀ and even mount them, copulation was never observed in a three-year long study by Walther (1978b).

Female herds are usually unstable with continual exchange between those in adjacent territories (Estes 1991a). In one study in Serengeti N. P., ♀♀ moved around within home-ranges of 1–3 km diameter in separate herds (Walther 1973b). The home-ranges overlapped and when the herds met, they combined, exchanged members and often fragmented into subgroups. One large herd varied in numbers from 50 to 200 head and ranged over an area of ca. 10 km², encompassing the territories of some 24 ♂♂, sharing this range with three other female herds and one bachelor herd. The large herd met and mingled with the bachelor herd and with another female herd almost daily in late afternoon (Walther 1973b, Estes 1991a).

Although Thomson's Gazelles are gregarious animals, in the wild they rarely groom or interact closely. Even during copulation, the body contact between ♂ and ♀ is kept to a minimum (Walther 1977). Mutual grooming is largely limited to mothers and offspring (Walther 1977). The preferred distances between adjacent individuals is usually greater when grazing than when resting or moving, and greater between ♂♂ than between ♀♀ (Walther 1977). Females typically remain 1–3 m from other group members while moving together and resting, and >3 m apart when grazing (Walther 1977). Bachelor ♂♂ generally remain further apart, often 7–12 m apart when grazing. The spacing of territorial ♂♂ is dependent on territory size, from ca. 300 m down to 100 m at high densities.

Between birth and maturity these gazelles pass through a series of growth stages with behaviour characteristic of each age (Walther 1973a). Neonates (0–2 weeks) lie out, hidden in vegetation (which on the short grass plains may only be a small clump of grass), only joining the mother to suck and be cleaned. Juveniles of 3 weeks to 2 months still spend time lying out and join the mother to suck and be cleaned. However, increasingly they come out of 'hiding' and accompany the mother for more and more of the time. Juveniles begin to take solid food towards the end of this stage. By the time the young animal is half-grown (3 months to 4–6 months) the lying out period is over. The young may still rest more frequently and for longer periods than the adults, but they now participate in adult activities and move around with their mothers. Thus, half-grown young are in female herds or mixed herds. The young of this age have converted to solid food but may still try to suck, with or without success. Adolescents (5–8 months) of both sexes are for the most part weaned. Male subadults, ca. 8–12 (possibly up to 15) months, are not usually found in female herds, but instead are in all-male groups or in mixed herds. By the age of 16–24 months gazelles have become young adults, but full adulthood, particularly for ♂♂, seems to be reached at the end of the second year of life when they acquire full-length, double-arched horns.

Reproduction and Population Structure Females generally give birth to a single offspring (Furley 1986), after a gestation period of approximately 180 days (Bradley 1977). In Serengeti N. P., young are born throughout the year, but there is a birth peak during the wet season (Hvidberg-Hansen & de Vos 1971, Sinclair *et al.* 2000). Caro

(1994) recorded most ♀♀ with attendant neonates or juveniles in Serengeti N. P. between Nov and Mar. Females typically come into oestrus within two weeks of giving birth (Estes 1991a). Some ♀♀ may give birth to two offspring per year, as heavily pregnant ♀♀ have been seen with adolescents (4–8 months of age: Brooks 1961, Hvidberg-Hansen 1970), but it is not known if this is related to animal density. The age at which ♂♂ and ♀♀ can first breed in the wild is uncertain, but, in captivity, ♂♂ can breed at 16 months and ♀♀ have been reported to give birth at 18 months (Furley 1986). The oldest gazelle that has been found in the wild was 11 years old (Robinette & Archer 1971); captive animals have lived to 20 years (Weigl 2005).

The Thomson's Gazelle population in Serengeti N. P. appears to be strongly female-biased. In the early 1970s, only 36.8% of the adult population were ♂♂ (Bradley 1977), although the sex ratios at birth and adolescence (approximately 4–8 months) did not appear to differ from parity (Hvidberg-Hansen 1970, Bradley 1977). Robinette & Archer (1971) found that the west Kilimanjaro population only comprised 19.6% ♂♂. Comparing data from Brooks' (1961) study of free-ranging populations in Tanganyika with age-class distributions on a fenced, predator-free ranch in Kenya, Hvidberg-Hansen & De Vos (1971) demonstrated the effects of heavy predation on wild stocks with vastly increased survival on the ranch. Several other studies have also concluded that the bias results from differential predation, because a preponderance of adult ♂♂ is found in the prey of a number of predator species, in particular African Wild Dogs *Lycaon pictus* (Estes & Goddard 1967, Fanshawe & FitzGibbon 1993) and Spotted Hyenas (Kruuk 1972).

Predators, Parasites and Diseases Many predators prey upon Thomson's Gazelles. In Serengeti N. P., the larger predators, such as Cheetahs, African Wild Dogs, Spotted Hyenas and Lions *Panthera leo* take both adults and immatures (Kruuk & Turner 1967, Kruuk 1972, Schaller 1972, FitzGibbon & Fanshawe 1988, Fanshawe & FitzGibbon 1993), while jackals, baboons *Papio* spp., Martial Eagles *Polemaetus bellicosus* and Lappet-faced Vultures *Torgos tracheliotus* generally concentrate on young (Kruuk 1967, 1972, Wyman 1967, Walther 1969, Bradley 1977, FitzGibbon 1988).

Cheetahs are particularly specialized at hunting gazelles; on the Serengeti Plains gazelles make up ca. 66–89% of their diet (Schaller 1972, Caro 1994, Hunter *et al.* 2007), rather less in the woodlands (S. Durant pers. comm.). Caro (1994) calculated that predators kill between 51% and 82% of the estimated 73,000–86,000 adult gazelles recruited into the Serengeti population each year. In Nairobi N. P., McLaughlin (1970) estimated that Cheetahs killed 64–92% of the gazelles recruited into the adult population annually.

Much of the predation of Thomson's Gazelles is concentrated on immatures, particularly young under 2 months of age, which are not only vulnerable to a greater range of predators as a result of their smaller size, but also have poorly developed flight responses (Walther 1969). Predation on adult gazelles appears to be concentrated on ♂♂ (Estes & Goddard 1967, Walther 1969, Kruuk 1972, Schaller 1972, FitzGibbon 1990b), contributing to the female-biased sex ratio in the adult population (Bradley 1977). The reasons for the increased vulnerability of ♂♂ are unclear, although such male-biased predation rates are observed in a number of ungulate species. Males may be more vulnerable to stalking predators, such as Cheetahs, on

account of their tendency to be found in smaller groups, to remain in exposed positions and to be less vigilant (FitzGibbon 1990b). Male gazelles may also be in worse condition than ♀♀, predisposing them to predation, particularly by coursing predators. African Wild Dogs take more Thomson's Gazelles in poor condition than do Cheetahs (FitzGibbon & Fanshawe 1989).

Thomson's Gazelles rely primarily on flight and vigilance to avoid predation. Crypsis is of limited utility in open habitats (Jarman 1974) and competes with other behavioural adaptations, such as attracting mates (Owen-Smith 2002). Infants remain hidden for the first few weeks of life (see adaptations section), behaviour which minimizes their exposure to predators at a time when their ability to outrun them is minimal (FitzGibbon 1990c, 1994a). FitzGibbon & Lazarus (1995) calculated that hiding results in an increase in survivorship per year of at least 2.6% from decreased predation by Cheetahs alone.

While feeding, Thomson's Gazelles intermittently raise their heads about a metre from the ground to scan for predators, reducing the time available for foraging (Illius & FitzGibbon 1994). The level of individual vigilance behaviour declines with increasing group size, in shorter vegetation and when closer to their nearest neighbours. Females are more vigilant on average than ♂♂ (FitzGibbon 1988). Gazelles that are less vigilant than others in a group may experience higher predation rates, as Cheetahs tended to select less vigilant animals (FitzGibbon 1989). Although grouping enables gazelles to reduce their vigilance level, it does not necessarily result in improved predator detection (FitzGibbon 1988). However, it still reduces an individual's risk of predation, as a result of the dilution effect.

Compared with remaining in a smaller group of conspecifics, joining Grants Gazelles to form larger mixed-species groups has anti-predator advantages; the Thomson's Gazelles can 'share' vigilance to some extent with the Grant's Gazelles, leaving more time available for feeding. In addition, when hunted by Cheetahs, the Thomson's Gazelles are safer as a result of improved predator detection, the lowered success rate of hunts and the tendency for Cheetahs to avoid hunting such mixed-species groups (FitzGibbon 1990b).

If a Thomson's Gazelle sees anything unusual, it adopts the stare or alert posture (illustrated in Walther 1969) and in some cases it may also alarm-snort (only audible from distances of less than 50–100 m). Once a gazelle has detected a predator, it may not immediately flee but may wait until the predator approaches closer. The flight distance depends on the predator species and its speed of approach and appears to be adjusted to the risk posed by the predator. On fleeing from predators, gazelles often twitch their flanks, possibly to alert other gazelles (Brooks 1961, Estes 1967). If the predator does not chase, the flight usually ends after 200–300 m. On some occasions, the group, rather than fleeing, may actually approach the predator, following it from 50–100 m away for periods even exceeding one hour (average 14 minutes) (FitzGibbon 1994b). This so called 'fascination' or predator inspection behaviour is primarily observed in response to ambush predators such as Cheetahs, Lions and Leopards. It seems likely that this behaviour has a number of functions: informing the predators that they have been detected, causing stalking predators to move out of the vicinity, enabling gazelles to monitor the predators' movements and providing an opportunity, particularly for younger animals, to learn about predators (FitzGibbon 1994b).

When fleeing from coursing predators, like Spotted Hyenas and African Wild Dogs, which run down their prey with long, wearing

chases, the gazelles frequently stot, leaping in the air with legs held stiff and straight (Walther 1969, Caro 1986a, FitzGibbon & Fanshawe 1988). Such behaviour may inform the predators of the gazelles' ability to outrun them. Stotting rarely occurs in response to ambush predators, like Cheetahs and Lions, which stalk their prey and then run it down with short, very fast chases. Caro (1986b) suggested that the occasional stotting in response to Cheetahs may serve to inform these predators that they have been detected.

Thomson's Gazelles can outrun many predators, running at up to 80 km/h (Estes 1991a) but with a relatively slow acceleration of 4.5 m/s (Elliott *et al.* 1977). However, they lack the endurance of cursorial predators, beginning to tire after 1–2 km and are exhausted within 4–6 km, partly due to a 5–6° rise in body temperature (Walther 1969, Taylor & Lyman 1972).

When chased by predators, Thomson's Gazelles often change direction very sharply, particularly at the end of chases, when they jink from side to side, frequently causing their pursuers to overrun. If a young animal is chased, the mother may perform a similar behaviour, running backwards and forwards between the predator and her young, apparently trying to distract its attention (Kruuk 1972, Caro 1986b). In certain cases, she may even attack the predator, butting it with her head and horns. Although usually only one ♀ is involved (presumably the mother), up to three other ♀♀ (possibly also with young hidden nearby) may also join in. In the case of jackals, attack behaviour is likely to be more effective when there is only one jackal, compared with when there are two (Wyman 1967). Adult gazelles have never been reported to actively defend themselves.

If hidden juveniles are disturbed from their hiding place they commonly stot. This behaviour may inform mothers that their offspring have been disturbed and are in need of assistance (Caro 1986b). If actually chased by predators, the young animal may drop down, adopting a prone position. Predators have been observed to walk within 5–10 m (Kruuk 1972) of hidden juveniles without apparently noticing them. Adults have only rarely been observed to drop down when chased by predators.

No comprehensive review of the parasites associated with Thomson's Gazelles has ever been conducted; however, partial information from them and other gazelles is available. The susceptibility of gazelles to diseases and parasites varies from wild to captive populations, from dry to wet years, and can vary among wild populations with different conservation status. *Neospora caninum*, a parasite commonly found in domestic dogs, has been reported for Thomson's Gazelles (Ferroglia *et al.* 2003). Faecal egg counts conducted at Mpala Ranch in Kenya showed 525 internal parasite eggs per gramme of Thomson's Gazelle faeces in normal rainfall years and an increase to 1622 eggs per gramme of faeces in dry years (Ezenwa 2004b). Strongylida nematodes and coccidians were detected in faeces in a subsequent study and their prevalence increased with group size (Ezenwa 2004a). However, in studies of several threatened gazelles (Cuvier's Gazelle *G. cuvieri*, Dama Gazelle *N. dama* and Dorcas Gazelle *G. dorcas*), lower group size correlated with inbreeding depression contributed positively to nematode density in faeces (Cassinello *et al.* 2001).

Sarcoptic mange (*Sarcoptes scabiei*) caused by ectoparasitic mites has been reported for Thomson's Gazelles (Sachs & Sachs 1968, Bornstein *et al.* 2001) and ticks are commonly found in wild and captive populations (Olubayo *et al.* 1993). Isolates from Thomson's Gazelles have caused mild infections in cattle due to tick-borne

anaplasmosis (Potgieter & Stoltz 1994). Grooming, although rare in Thomson's Gazelles, is observed in captive ♀♀ (Mooring *et al.* 2004), suggesting the presence of mites and ticks.

The viral and bacterial diseases of Thomson's Gazelles are by and large those shared with other Bovidae, with again great variation between wild and captive populations. Rinderpest has been reported in wild populations (Plowright 1963). Other local diseases such as malignant catarrhal fever (Reid *et al.* 1975, Bedelian 2004) and lumpy skin disease (LSD) (MacOwan 1959) have not been found, although field tests and studies with zoo animals suggest that gazelles may be susceptible (MacOwan 1959, Griner 1983). Infectious bovine rhinotracheitis antibody has been reported for Thomson's Gazelles in Tanzania (Rweyenanu 1974, Rampton & Jessett 1976). In addition, antibodies to the bluetongue virus have been found in wild Thomson's Gazelles in Tanzania (Hamblin *et al.* 1990).

Conservation IUCN Category: Near Threatened. CITES: Not listed.

The species is protected in a number of national parks and protected areas. The core areas of the Serengeti–Mara population are protected by Serengeti N. P. and Masai Mara National Reserve, where wildlife tourism is the only permitted land use. The core areas are surrounded by buffer zones: Maswa G. R., Grumeti G. R. and Ikorongo G. R. to the south-west, Ngorongoro Conservation Area (NCA) and Loliondo Game Controlled Area (LGCA) to the south-east and the Mara Ranches (MR) to the north. The Game Reserves allow tourism and hunting, the NCA and MR allow tourism, settlement, livestock and cultivation but no hunting, and the LGCA allows all of the above and hunting (Thirgood *et al.* 2004). Poaching is a major concern in the west and north of the Serengeti–Mara ecosystem (Arcese *et al.* 1995a) and may, therefore, affect population levels. In Tanzania, Thomson's Gazelles are also protected within Tarangire N. P., although the park protects at most one-half of the annual home-range of local Thomson's Gazelles and excludes their breeding grounds (Voeten 1999). In Kenya, these gazelles are protected within Tsavo West and Hell's Gate National Parks and in Lewa Wildlife Conservancy, a conservation area owned and managed by a charity.

As noted already under Abundance, there is evidence from monitoring studies that some populations are declining. In the Serengeti ecosystem, the population of Thomson's Gazelles in Serengeti N. P., Tanzania declined by almost two-thirds over a 13-year period from 1972 to 1985. The population seems to have recovered to ca. 340,000 in 1996 and then declined sharply until the survey in 2003 at which time a small recovery was recorded. Runyoro and colleagues (1995) recorded a 63% decline in the Thomson's Gazelle population in the Ngorongoro Conservation Area between 1974 and 1992, which they attributed to the removal of pastoralists. A subsequent reanalysis of the most consistent data from that era has confirmed the decline (60% from 1978 to 1995) (Estes *et al.* 2006) and cites many complex reasons for it (water, tourist impacts, habitat modification due to exotic plant invasion, fire management and road development).

Measurements

Eudorcas thomsonii

TL (♂♂): 1219 (1135–1290) mm, n = 40

TL (♀♀): 1163 (1040–1246) mm, n = 18

T (♂♂): 231 (200–270) mm, n = 40
 T (♀♀): 221 (195–260) mm, n = 18
 HF c.u. (♂♂): 309 (290–325) mm, n = 40
 HF c.u. (♀♀): 292 (280–305) mm, n = 18
 E (♂♂): 111 (105–124) mm, n = 40
 E (♀♀): 110 (100–122) mm, n = 18
 Sh. ht (♂♂): 606 (570–655) mm, n = 40
 Sh. ht (♀♀): 578 (550–615) mm, n = 18
 WT (♂♂): 20.4 (17.5–23.4) kg, n = 40
 WT (♀♀): 16.2 (12.1–19.9) kg, n = 18

Serengeti N. P., Tanzania (Sachs 1967)

Kingdon (1982) notes that there is a north-to-south decrease in average measurements

Maximum recorded horn length is 43.8 cm for a pair of horns from Gurumeti, Tanzania (Rowland Ward)

Key References Bradley 1977; Brooks 1961; Estes 1967, 1991a; Walther 1964b, 1969, 1978a, b; Walther *et al.* 1983.

Clare FitzGibbon & John Wilmshurst

Eudorcas albonotata MONGALLA GAZELLE

Fr. Gazelle de Mongalla; Ger. Mongallagazelle

Eudorcas albonotata (Rothschild, 1903). Nov. Zool., vol. 10, p. 480. East side of White Nile, 40 miles north of Kero or Kiri, Mongalla Province (Sudan).



Mongalla Gazelle *Eudorcas albonotata*.



Mongalla Gazelle *Eudorcas albonotata*.

Taxonomy Monotypic. The Mongalla Gazelle is usually regarded as a subspecies of Thomson's Gazelle *Eudorcas thomsonii* (Gentry 1972, Grubb 1993c), which in turn has been widely treated as conspecific with the Red-fronted Gazelle *E. rufifrons* (e.g. Groves 1985a, Kingdon 1997, East 1999; and see Rebholz & Harley 1999). Gentry (1972) and Grubb (2005) noted that skull and horn proportions associate *albonotata* with *rufifrons* rather than *thomsonii*. The species is to some extent intermediate between *E. r. laevipes* and the East African Thomson's Gazelle, and is similar in size to *laevipes*, but with a narrower skull and slightly longer rostrum (Groves 1969). Synonym: *albonota*. Chromosome number: not known.

Description The Mongalla Gazelle is a medium-sized gazelle, brown-coloured with a white belly and buttocks. Forehead entirely white and eyes surrounded with a white ring. Tips of ears pointed. Lateral band broad with a rufous shadow stripe beneath it. Knee tuft large. Tail short with hair all along its length. Horns short and prominently ringed in ♂, curved backwards and then slightly forward, and slightly in-turned at the tips. Female horns thin and straight, their length only 50% of the male's.

Geographic Variation It is possible that a small population of Mongalla Gazelles occurring north of the Sobat R. differs from the main population in the Sudd (Mefit-Babtie 1983). Because the latter appears to make a self-contained annual circuit on the eastern Sudd flood-plain, any possibility of a genetically distinct subpopulation around the Machar marshes merits further investigation.

Similar Species

Eudorcas rufifrons. A Sahelian species, occurring west of the Nile R. and absent in the Sudd ecosystem. Redder with face stripes buffy, if present at all, and black flank band very thin.

E. thomsonii. An East African species, present in S Kenya and N Tanzania. Smaller in size, with longer horns in ♂, forehead entirely red, black line running from the eyes to the nose and a black tuft on the tail contrasting with the buttocks.

Distribution Mongalla Gazelles inhabit the flood-plains and flat savanna grasslands in SE Sudan, east of the Nile R. (Hillman 1982, Hillman & Fryxell 1988, East 1999), but their normal range does not reach the Ugandan and Kenyan borders. The western margin of their

*Eudorcas albonotata*

range is close to Kongor and Ayod (about 31° E, 8° N), the eastern limits lying in the Anuak district of Ilubabor region, Ethiopia (34° E, 8° N). The current range is known to extend from Mongalla and Jebel Lafon in the south to the vicinity of Malakal between about 32° E, 5° N to 32° E, 10° N. There are gazelles north of the Sobat R., but these may belong to a distinct population that possibly ranges as far north as Renk. It is important to determine whether these gazelles belong to this species or not.

Habitat The Mongalla Gazelle lives mainly in open grassland (Hillman 1982, Hillman & Fryxell 1988). The dry-season range in Boma N. P. comprises open to light savanna woodland in which thatch grass *Hyparrhenia* spp. is associated with *Acacia zanzibarica*. The gazelles often aggregate in burnt areas with green flush (Hillman & Fryxell 1988). The wet-season range of the eastern Sudd flood-plains is savanna grassland with medium and tall grasses in low rainfall areas to the south of the National Park (Hillman & Fryxell 1988).

Abundance Using a crude sampling system, Watson *et al.* (1977) estimated the global population of Mongalla Gazelle at 300,000. A more intensive study conducted in the late dry season in Jonglei Canal area in S Sudan estimated 66,000 for about one-quarter of their total range (Mefit-Babtie 1983). Within this area the numbers of gazelles declined to about 1000 in the mid-wet season because of wholesale emigration out of the study area, to the east and south-east. In a still more limited sample, the Boma N. P. region hosted a little over 20,000 gazelles during peak periods (Hillman & Fryxell 1988). East (1999) suggested that the total population could number 100,000, but more recent survey work in S Sudan has shown this to be a significant underestimate, with nearly 300,000 animals estimated to occur, mainly in the southern section of the Jonglei and Boma N. P. (Fay *et al.* 2007).

Adaptations This gazelle is adapted to following a nomadic annual cycle over the eastern Sudd flood-plains, an ecologically peculiar region where extensive floods are followed by extreme aridity. A major reason why Mongalla Gazelles are able to inhabit a flood-plain that dries out during the dry season is that they do not need water for drinking and can withstand intense solar radiation (Hillman 1982). Their tolerance of insolation is tempered at the height of the dry season by most animals resting during the heat of the day, taking advantage of scanty shade under *Acacia drepanolobium* and occasional, scattered *Balanites* or *Piliostigma* trees (Mefit-Babtie 1983). Another major adaptive trait is that this species, like its close relative the Thomson's Gazelle, is a 'gleaner' (Vesey-Fitzgerald 1960, Brooks 1961). This is a strategy that relies on other, larger plains bovids, zebras, fires or cattle to flatten or remove rank (and for the gazelles, almost impassable) long grass and thus expose regrowth that they can eat. Which of these grass-removing agencies is most useful to the gazelles at any one time changes with the seasons (J. Kingdon pers. comm.).

In the eastern Sudd flood-plains there are two separate migration patterns, one being that of the White-eared Kob *Kobus kob leucotis*, the other that of the Tiang *Damaliscus lunatus tiang*. In both instances dense herds of these animals gather during the flood season and make localized movements on higher ground to the south and east of the flood-plains. In both instances the herds move north as the floods recede, only to return southwards as the waters rise again. The Tiang, as a flood-plain specialist, follows a westerly traverse, close behind the retreating waters and the largest herds often graze close to the Nile or to the deep, permanently flooded swamps that define the western and northern boundaries of the eastern Sudd flood-plain. A sizable proportion of the total gazelle population is known to follow the Tiangs for the earlier part of their migration and probably depends upon them even more during the height of the wet/flood season (Mefit-Babtie 1983). The White-eared Kob, on the other hand, favours very open, broad shallow valleys where fires and large numbers of grazers cut back the rankest of the grass. The White-eared Kobs follow a more easterly pattern of migration well away from the Sudd swamps, and Hillman & Fryxell (1988) documented a smaller number of gazelles associating with this eastern migration.

Mongalla Gazelles take advantage of both these larger species to process the sward for them but actively avoid getting caught up in dense herds of larger animals that are on the move. The gazelles are, therefore, 'camp followers', trailing a month or so behind the main herds, gleaned the regrowth that sprouts in their wake. However, as the dry season progresses the frequency and extent of fires increases and the gazelles' dependence on trampling and grazing to clear the long grass therefore declines. At this time, the gazelles, for the most part, cease to follow the Tiangs onto the 'Toic' (flooded grassland) pastures. By about Mar they can begin to spread out and drift north-eastwards (Mefit-Babtie 1983) and are probably at their most widely dispersed during Apr and May (see map opposite).

During the dry seasons of 1981 and 1982, between Dec and Apr, the movements of those Mongalla Gazelles that were following up the main body of migrating Tiang were recorded and mapped by means of aerial surveys, supplemented by observations on the ground. The gazelles were largely absent from the western part of their range between about May and Oct (Mefit-Babtie 1983).

and their occupation of distant eastern plain margins during the intervening months was confirmed by extensive questioning of local travellers. Because the wet, grass-growing season is the most problematic for the gazelles and assuming that they therefore intensify their 'gleaning' 'camp-follower' strategy throughout the wet season, their movements at this time can be tentatively extrapolated from the known wet/flood season ranges of the Tiang and White-eared Kobs (Mefit-Babtie 1983, Hillman & Fryxell 1988). How large a proportion of the entire population travels in the wake of the Tiangs has not been determined, but in 1981–82 it accounted for more than 60,000 animals. A reconstruction of this population's annual cycle of movement around a roughly circular traverse is shown here. It can be surmised that in the course of a year some individuals within these gleaning mobs of gazelle may travel close to the perimeters of virtually their entire flood-plain range. While the vast majority of Mongalla Gazelles follow some such circuit, a scatter of individuals and very small groups seem able to remain resident in proven favourable localities (J. Kingdon pers. obs.).

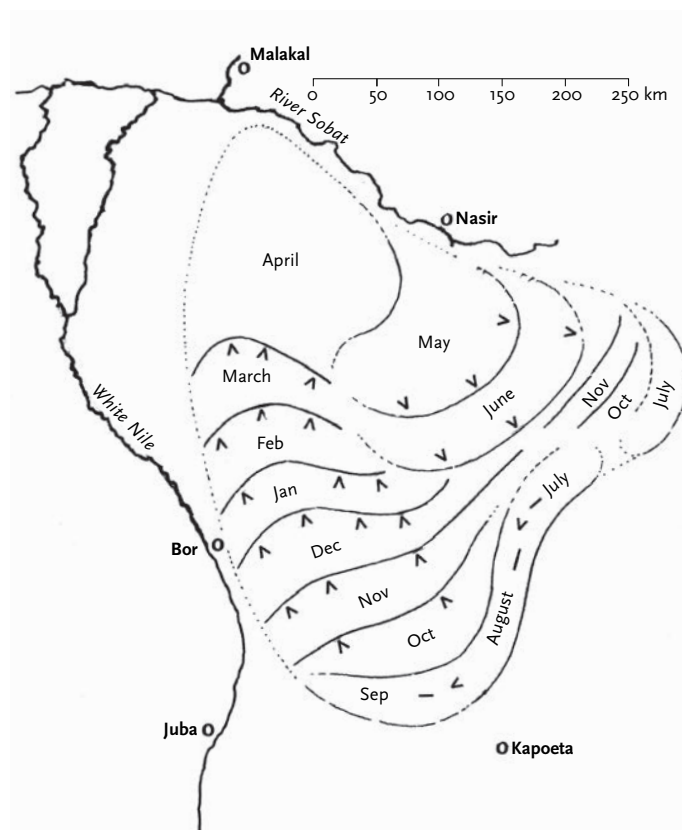
In summary, it would seem that Mongalla Gazelles are only able to survive the wet and flood seasons on the eastern Sudd flood-plain through their dependence on larger grazers. The adaptations to drought, which they share with other gazelles, only come into play during the dry season but, unlike water-dependent species, allow them to inhabit a large part of the flood-plain.

Foraging and Food The Mongalla Gazelle is mainly a grazer but also browses during the dry season when the nutritive value of herbaceous vegetation is very low; browsing comprises leaves and twigs of herbs and bushes (Hillman & Fryxell 1988). Very young *Hyparrhenia* regrowth appears to be an important part of the dry-season diet (Mefit-Babtie 1983).

Social and Reproductive Behaviour The Mongalla Gazelle is a social antelope. Groups of 10 to 50 are common (Hillman 1982) especially in prime feeding areas, i.e. burnt areas, where groups of more than 30 gazelles often occur (Hillman & Fryxell 1988). Females form groups of more than five individuals; young ♂♂ live in bachelor herds and adult ♂♂ are territorial (Hillman & Fryxell 1988). During the wet season, the Mongalla Gazelle aggregates in high population densities (several hundred per km²) with other migratory species such as White-eared Kobs, Tiangs and Plains Zebra *Equus quagga* (Hillman 1982, Hillman & Fryxell 1988).

Reproduction and Population Structure Besides the fact that most young are born in the early wet season from Apr to Jun (Hillman & Fryxell 1988), there is no information available.

Predators, Parasites and Diseases Mongalla Gazelles are taken by Lions *Panthera leo*, Cheetahs *Acinonyx jubatus* and hyaenas, but low numbers of these predators and large numbers of alternative prey buffer mortality to very small numbers. Eagles and the larger vultures may take the young. Diseases and parasites are a more significant factor. Prevalent parasites observed at post-mortem (Mefit-Babtie 1983) include nematodes (*Longistrongylus sabi*, *Trichuris glouloosa*, *Pneumostrongylus calcaratus*, *Skrjabinema tanganyikae*, *Setaria sculprum* and *S. boulengeri*), cestodes (*Cysticercus tenuicollis*, *Avitellina*



Mongalla Gazelle *Eudorcas albonotata* annual circuit over east bank of the Sudd flood-plain. Note dispersal over eastern portion of the flood-plain is less well known and might include a separate minor circuit by possible subpopulation(s) (from data gathered by Mefit-Babtie Srl wildlife studies team 1983).

centripunctata and *Taenia crocuta*) and pentastomid larvae. In the wet season a greater number of worms are found in the abdomen, small intestine and large intestine compared with the dry season. The species likely to be contributing to worm burdens are *Haemonchus contortus*, *Longistrongylus sabi*, *Oesophagostomum* or *Agriostomum* sp.



Mongalla Gazelle *Eudorcas albonotata* neonate.

Conservation IUCN Category: Least Concern. CITES: Not listed.

There are significant numbers in Boma N. P. (more than 20,000 animals; Fay *et al.* 2007) and in Mongalla G. R., but seasonal movements cause very large fluctuations in numbers. The population in the Boma ecosystem is apparently stable and not exposed to serious hunting pressure. The large population surviving in the Jonglei remains entirely unprotected. Part of the Mongalla Gazelle range is devoid of water in the non-flood season, making access to this part of their range by poachers difficult.

Measurements

Eudorcus albonotata

No reliable body measurements are available. Groves (1969, 1975) provides various skull measurements

Maximum recorded horn length is 35.6 cm for a pair of horns from Gemmeiza, Sudan (Rowland Ward)

Key References East 1999; Hillman 1982; Hillman & Fryxell 1988; Mefit-Babtie 1983.

Ibrahim M. Hashim & Jonathan Kingdon

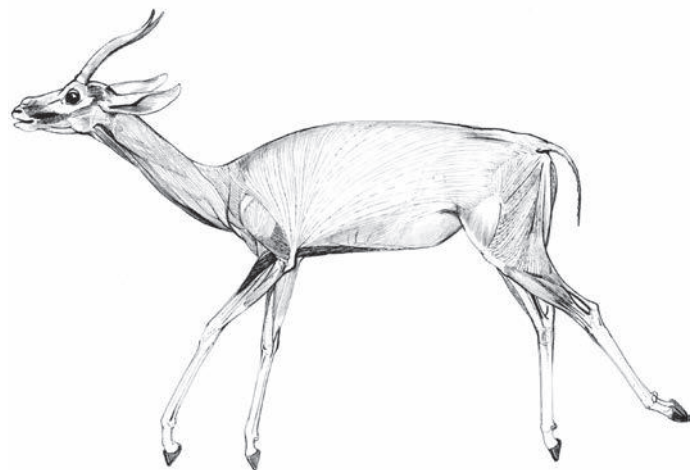
GENUS *Nanger*

Greater Gazelles

Nanger Lataste, 1885. Actes Soc. Linn. Bordeaux 39: 183.



Grant's Gazelle *Nanger (granti) granti* rectilinear signal from rear.



Bright's Gazelle *Nanger (granti) notata* myology.

Externally, apart from the characteristic white haunch-wedge, *Nanger* gazelles are characterized at once by their very large size, and also by the fact that the rhinarium does not extend as far along the dorsal rim of the nostrils as in *Gazella* (although further than in *Eudorcas*). The pattern varies from contrastingly coloured in the gazelles of the Grant's Gazelle *N. (granti)* complex and in Soemmerring's Gazelle *N. soemmerringi* to almost completely white, with just a small pale reddish area on the head and neck, in some populations of the Dama Gazelle *N. dama*.

Like gazelles of the genus *Eudorcas*, the karyotype has both an X-autosome and a Y-autosome translocation (Effron *et al.* 1976, Vassart *et al.* 1995).

Unlike the two genera of small-bodied gazelles, which though they overlap in distribution have distinct ecological contexts, species of *Nanger* are very diverse in their ecological settings. Gazelles of the *Nanger (granti)* complex live in the East African savanna, and extend north-east into the southern part of the Somali Arid zone; in the northern part, they are replaced by Soemmerring's Gazelle, which extends north of the Ethiopian Highlands, including some fairly arid country; while Dama Gazelle is quite different, living in extremely arid environments in the southern Sahara, extending into more



Bright's Gazelle *Nanger (granti) notata* adult female.

mesic environments only in the north-westernmost part of its range, in S Morocco.

Colin Groves

Nanger (granti) GRANT'S GAZELLE SPECIES GROUP

Taxonomy In the current work Grant's Gazelles, traditionally classified as a single species, are treated as a species group comprising three distinct species, based on the level of genetic differentiation among them. This complex belongs, together with Soemmerring's Gazelle *N. soemmerringi* and the Dama Gazelle *N. dama*, in the genus *Nanger* (Haltenorth 1963, Lange 1971, Groves 2000).

Arctander *et al.* (1996) studied the structure of Kenyan populations of Grant's Gazelles. They sequenced 371 nucleotides of the maternally inherited mitochondrial d-loop from 44 individuals and found an extreme genetic divergence among three population groups. A broader study by Lorenzen *et al.* (2008) increased the sample size to 178 individuals from 17 locations in Kenya and Tanzania (constituting the main distribution range of the species). This extended study confirmed the existence of three distinct population groups and, except in one case, the three groups had DNA sequences that were not found in any of the other groups (see Geographic Variation). The genetic distance between *N. (g.) petersii* and each of the other two groups was 12%. This was as large as the distance to their closest relative, the Soemmerring's Gazelle. The genetic distance between *N. (g.) granti* and *N. (g.) notata* was 8%, suggesting a closer relationship. Of the total amount of genetic variability found in the samples, 74% was found between groups. This, together with allopatric or parapatric distributions, and an almost completely disjunct distribution of highly diverged DNA sequences, has confirmed the need to raise the three groups to species level. This had been mooted in some older literature for *N. petersii* (Heller 1913a), the group which shows the highest divergence morphologically as well as genetically. In spite of such acknowledged differences, most recent works, including Kingdon (1997), have treated them as allopatric subspecies.

Genetic variation within the three species also varies. *Nanger (g.) granti* and *N. (g.) notata* have nucleotide diversities of 3.2% and 4.1%,

respectively, which is comparable with the level observed in other bovids (Simonsen *et al.* 1998, Arctander *et al.* 1999, Nersting & Arctander 2001). On the other hand, *N. (g.) petersii* has a lower level of nucleotide diversity, 1.6%, which might reflect smaller long-term population sizes.

Gazelles are characterized by extensive rearrangements of chromosome arms through Robertsonian fusions. Diploid chromosome numbers range from 30 to 58 with a constant number of autosomal arms of 56–58 (Vassart *et al.* 1995). Fifty-eight autosomes and 2 sex chromosomes is considered to be the ancestral state in Bovidae (Gallagher & Womack 1992). As with many other African gazelles, an autosome/X-chromosome translocation has taken place, resulting in different chromosome numbers among the sexes. Effron *et al.* (1976) reported that a *N. (g.) granti* ♀ had a diploid number of 30, i.e. 28 metacentric autosomes and 2 large sub-metacentric X chromosomes. Males had 31 chromosomes, 28 autosomes, 1 X chromosome and 2 small acrocentric Y chromosomes, Y1 and Y2 (Effron *et al.* 1976, Gallagher & Womack 1992).

The different species in the complex are expected to differ in their karyotypes (as has been noted for the other species in the genus *Nanger*). In *N. dama* the subspecies *N. d. ruficollis* and *N. d. mhorri* differ in their diploid chromosome number having $2n = 38$ and $2n = 40$, respectively. *Nanger soemmerringi* is even more variable, with diploid chromosome numbers varying between 34 and 39 (Benirschke *et al.* 1984). In the latter the chromosome variability is accompanied by poor reproductive success, suggesting post-zygotic isolation mechanisms are important in the speciation within this group.

A number of subspecies have been described based on horn shape and colouration, nine of which were recognized by Haltenorth (1963) and Gentry (1972). Due to poorly known ranges, variability

of the traits within populations across species and lacking genetic evidence, we do not go into detail with them here. Synonyms: *N. (g.) granti*; *robertsi*, *roosevelti*; *N. (g.) notata*: *brighti*, *raineyi*, *lacuum*; *N. (g.) petersii*: *gelidjiensis*, *serengetae*

Description Tall, pale gazelles with long, upright horns above relatively small eyes, set in highly characteristic, black, leaf-shaped eye patches. They are characterized by having a substantial white rump patch. The rump patch matches the underside, which is white like the throat and inner sides of legs. The rump patch is accentuated by dark thigh-stripes. Flank-bands are common in young and ♀♀, often disappearing with age. In ♂♂ the flank-bands disappear earlier, except in the Laikipia region of Kenya (Bright's Gazelle) and perhaps other populations that are allopatric with Thomson's Gazelle *Eudorcas thomsonii* (R. Estes pers. comm.). Colouring of the upper side varies from pale, reddish-brown to dark brown. Tip and underside of the tail is dark, with a black tuft.

On the face, a white band extends from the horns, in front of the eye down to the small muzzle. The black mask that surrounds the eye extends tenuously down towards the mouth. The relatively long ears are lancet-shaped. Preorbital glands are vestigial. Glands are present between the hooves and on the knees; ♀♀ have a pair of inguinal nipples with a striking black and white pattern. Males have long horns with 20–30 rings; horns in ♀♀ are shorter, with 15–20 rings.

Geographic Variation Although it has long been regarded as a single species, we consider Grant's Gazelles as a species complex comprising three genetically distinct, broadly allopatric species. Past climatic fluctuations have influenced the isolation, diversification and distributions of the three species. In response to changes in vegetation and habitat, contact zones between the gazelles have shifted geographically over time.

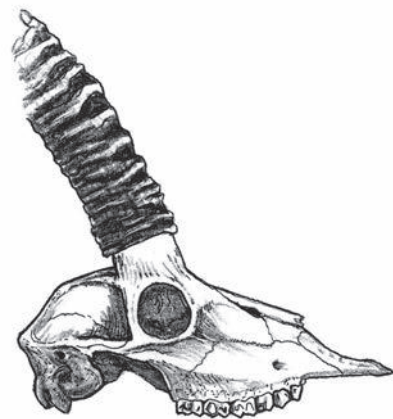
Nanger (granti) granti GRANT'S GAZELLE

Fr. Gazelle de Grant; Ger. Grant-Gazelle

Nanger granti (Brooke, 1872). Proc. Zool. Soc. Lond. 1872: 601-602. Tanzania, 'Western Kinyenye, in Ugogo'.



Grant's Gazelle *Nanger (granti) granti*.



Lateral view of skull of Grant's Gazelle *Nanger (granti) granti*.

The species is named for Colonel James Grant, the Scottish naturalist and explorer.

N. (g.) granti species: distributed from the north bank of the Ruaha R. in C Tanzania to Kenya south of L. Baringo and Mt Kenya, and from L. Victoria in the west to Voi R. in Tsavo in the east. Has a dark, triangular patch on the nose and an undivided white rump patch, leaving the upperside of the tail white. Horn shape is highly variable, and horn spans range from 26 to 66 cm (Grubb 2000).

The genetic profiles of populations from Masai Mara and Serengeti revealed a genetic distance of ~1% between these and populations further east. This could support the validity of two previously described subspecies *N. (g.) g. granti* and *N. (g.) g. robertsi*. However, as the genetic data were inconclusive we do not consider the subspecies well authenticated.

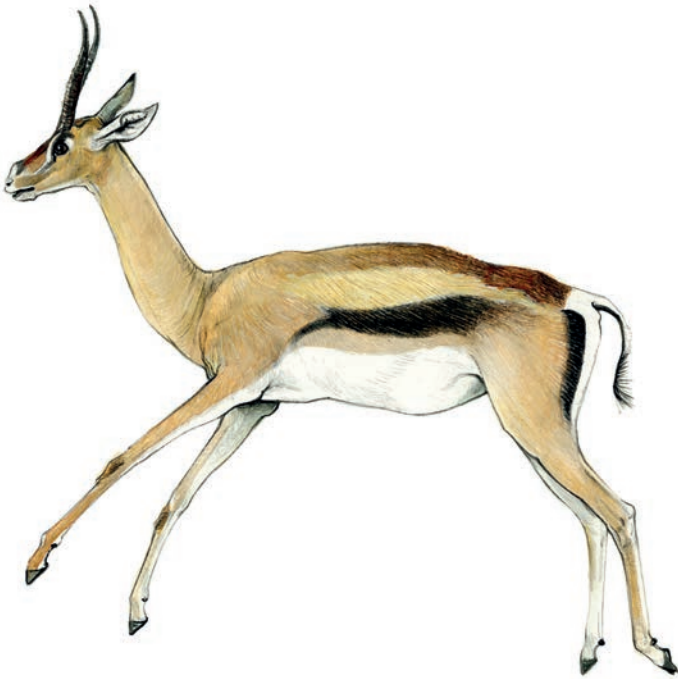
N. (g.) g. granti: distributed from the Ruaha R. through NE Tanzania to Kenya south of Mt Kenya, across the plateau west of Voi in Tsavo and up the Rift Valley as far as L. Baringo. The horns are lyrate, spreading evenly with the tips approaching each other. The horn span is about 36 cm, with a range from 26 to 48 cm (Grubb 2000).

N. (g.) g. robertsi: limited to NW Tanzania and SW Kenya, immediately east of L. Victoria. Horns are very distinct; their spread is wide and they curve outward with the tips turning backwards. The horn span has an average of about 50 cm, with a range from 34 to 66 cm (Grubb 2000).

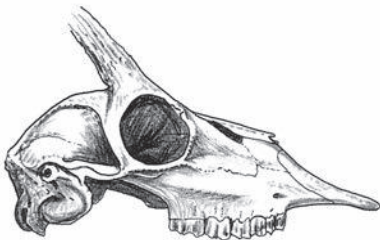
Nanger (granti) notata BRIGHT'S GAZELLE

Fr. Gazelle de Bright; Ger. Bright-Gazelle

Nanger notata (Thomas, 1897). Proc. Zool. Soc. Lond. 1897: 53-54. West slope of Lorogi Mts, Kenya Colony.



Bright's Gazelle *Nanger (granti) notata* female.



Lateral view of skull of female Bright's Gazelle *Nanger (granti) notata*.

Nanger (g.) notata species: distributed from NE Uganda to S Somalia with a range that surrounds L. Turkana and extends across the very arid regions of N Kenya. A belt of uplands and forest is thought to have separated Grant's Gazelle from Bright's Gazelle (Simon 1962, Stewart & Stewart 1963). It differs from Grant's Gazelle in having more parallel horns, but is otherwise similar in rump pattern and nasal spot. Horn span is ~24 cm with a range of 18–32 cm that overlaps with Grant's Gazelle. It is, therefore, not possible to allocate individuals to the correct species based on horn shape alone (Grubb 2000). There is variation in the tonal contrast of flank- and pygal-bands within the species. Individuals from the Lorogi plateau in the southern part of the range (the type locality for this species) are at the darkest end of the colour spectrum. They have longer pelage and both pygal- and flank-stripes are often present in mature animals of both sexes.

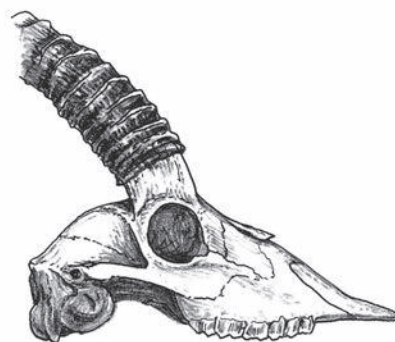
The vernacular name Bright's Gazelle derives from a supposedly smaller subspecies *brighti* (named for Colonel R. G. T. Bright who collected the first specimen), which was thought to be distributed west of L. Turkana as far as NE Uganda and SE Sudan. Another previously recognized subspecies, *raineyi* – locally known as Rainey's Gazelle – was thought to range east of L. Turkana in very arid country. Yet another named subspecies, *lacuum*, was described from Ethiopia and was supposedly distinguished by the absence of side stripes. Populations distributed east of L. Turkana are genetically differentiated from the remaining populations, but due to small sample size, the data are judged as insufficient to warrant their classification into distinct subspecies (Lorenzen *et al.* 2008).

***Nanger (granti) petersii* PETERS'S GAZELLE (TANA GAZELLE)**

Fr. Gazelle de Peters; Ger. Peters-Gazelle

Nanger petersii (Günther, 1884). Ann. Mag. Nat. Hist., ser. 5, 14: 425–429. Gelidja near mouth of Osi and Tana Rivers, Kenya Colony.

Nanger (g.) petersii species: the most distinctive species within the *Nanger (granti)* species complex. Two characteristics distinguish it from the others: the fawn-brown body colouring extends back onto the tail – a feature that links it with non-*Nanger* gazelles and is presumably conservative – and the lack of a triangular nose patch (indeed, the facial colouring is altogether somewhat bleached). The relatively short and straight horns are not easily distinguished from those of Grant's Gazelle, but Grubb (1994) regarded them as less developed than in the other two species. Peters's Gazelle is distributed in E Kenya from the lower Tana Valley to west of the Juba R. in Somalia (Kingdon 1997). This species has recently extended its range to most of Tsavo East N. P. in Kenya.

LEFT: Peters's Gazelle *Nanger (granti) petersii*.ABOVE: Lateral view of skull of Peters's Gazelle *Nanger (granti) petersii*.

The border between Bright's Gazelle and Peters's Gazelle is primarily defined by elevation and also by differences in vegetation, with Bright's Gazelle preferring higher, more wooded country than Peters's Gazelle. Within Tsavo N. P. in Kenya, the former comes into close contact with the latter (Leuthold 1981). This contact is recent and is the result of range expansion, possibly by both species.

The *Acacia–Commiphora* woodlands formerly acted as a barrier between Peters's Gazelle and Grant's Gazelle. A relatively small and scattered Peters's Gazelle population was reported to be virtually surrounded by dense vegetation barriers to the south and west of their range during the nineteenth century (Leuthold 1981, I. Parker pers. comm.). The transformation of the *Acacia–Commiphora* woodland to more suitable open grassland (under the influence of elephants, fire and charcoal burning), expanded the distribution of Grant's Gazelle and increased the relative abundance of Peters's Gazelle; road counts on the Galana Ranch from 1963 and 1981 recorded a fourfold increase in the proportion of Peters's Gazelles prior to and after the destruction of *Acacia–Commiphora* (Parker 1983).

In the extended genetic study that confirmed the existence of three species within Grant's Gazelles, one mitochondrial DNA sequence from an individual Grant's Gazelle from Mkomazi G. R., Tanzania, grouped with the sequences from Peters's Gazelle. This horizontal

transfer of the maternally inherited genome between the two species suggested hybridization had taken place. If the *Acacia–Commiphora* woodland had presented a barrier to gene flow, Peters's Gazelle and Grant's Gazelle had come into contact following the thinning of the woodland.

That the Peters's Gazelle genotype may have extended to the south is further implied by the existence of an additional form *serengetae* (Heller 1913a) (from Taveta, on the eastern foothills of Mt Kilimanjaro, not the Serengeti N. P. area). Characterized by the back colour extending dorsally in a narrow stripe onto the tail, Grubb (1994) noted that this characteristic might have been the result of hybridization between Grant's Gazelle and Peters's Gazelle (in the individual's immediate, or earlier ancestry) as both locality and morphology suggested an intermediate condition between the two species.

Similar Species

Nanger soemmerringi. Allopatric, but ranges are close in Ethiopia.

Smaller, paler and with a characteristic horn form: short, lyrate, back-swept and with tips curling out and then sharply inwards.

Eudorcas thomsonii. Sympatric, with ranges overlapping in Tanzania and C and SW Kenya. Smaller, shorter-legged gazelle with brighter, redder back and bold black flank-stripe. Estes (2000) considers the

colouration of Grant's and Thomson's Gazelles as an example of character displacement, serving to distinguish sympatric populations and discourage interbreeding.

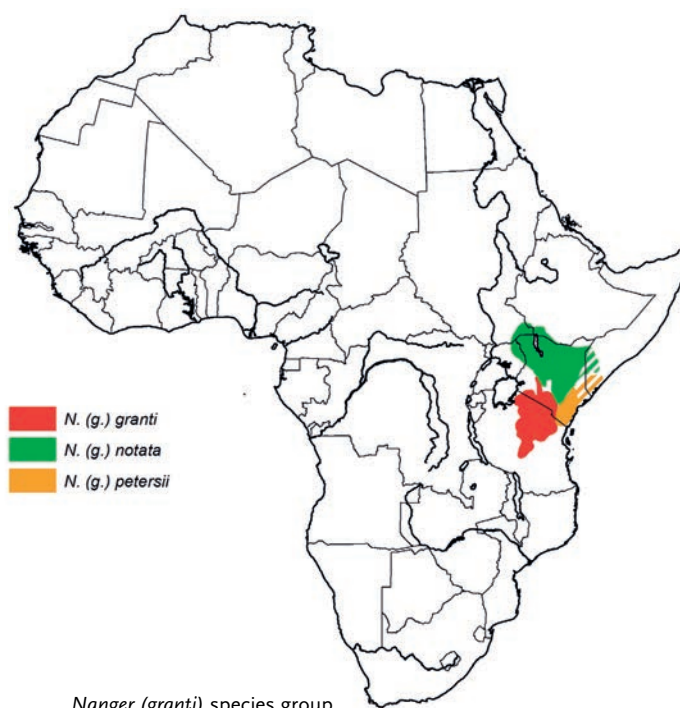
Distribution Endemic to Africa. The Grant's Gazelle species complex ranges from NE Uganda to Somalia and from S Ethiopia and SE Sudan to C Tanzania. The details of each species' distribution are discussed in the previous and following sections.

Habitat The habitat of all species encompasses open savannas and extends into the hot, arid semi-desert regions (Taylor 1970a). In more densely bushy country the gazelles are restricted to glades or open, scrubby valleys. They do not tolerate soft soils but inhabit, if only seasonally, longer grass than most other gazelles. Their distribution coincides with rain shadows and with an arid corridor of unstable climate across the East African plateau that is known to have been much more arid in the past (Kingdon 1997). Grant's Gazelle inhabits open, dry plains and open savannas, including some high, cool uplands. Its habitat is typified by the plains and savannas of Serengeti. N. P. Peters's Gazelle is essentially a lowland species and in the Tana R. delta lives on very flat plains that are periodically flooded. A large part of the range of Bright's Gazelle is very dry, but it periodically inhabits cool upland savannas and semi-deserts. In more south-eastern parts it tolerates more wooded country than the other species.

Adaptations These gazelles are adapted to life in a hot, semi-arid environment and can survive without drinking. Taylor (1968a) followed a herd of Bright's Gazelles for four days during which they apparently did not drink. They eat predominantly at night, and the water available in their food renders them nearly independent of surface water. In the course of nearly four decades of work in the Ngorongoro Conservation Area, R. D. Estes (pers. comm.) has only once seen a Grant's Gazelle drink. The gazelles tolerate very high body temperatures, and let their body temperature increase and exceed air temperature when water is in short supply. If body temperature exceeds that of the air, heat flows from the body to that of the surroundings, thereby avoiding evaporative cooling (such as panting) and dehydration (Taylor 1970a). At 45 °C dehydrated animals had rectal temperatures exceeding the air temperature by 0.5–2 °C. Such high temperatures would be lethal in most mammals, but result in large water-savings in this species (Taylor 1970b).

Abundance Kenya and C and N Tanzania are the core areas of the *Nanger (granti)* species complex. Kenya supports the largest number of individuals, around 100,000, although the country has lost >50% since the 1970s. Although numbers have been diminished due to poaching and competition from livestock and most of the larger populations are in gradual decline, the species complex remains widespread within and outside protected areas. Correcting for undercounting bias in aerial surveys, East (1999) estimated the total population size of the entire species group at about 350,000, of which one-third are found in protected areas.

The largest population of Grant's Gazelles occupies the Serengeti ecosystem and the Tarangire area, with estimates of 26,020 and 8060, respectively (TWCW *et al.* 1997). Smaller populations have been recorded from Mkomazi G. R., unprotected rangelands of Narok and Kajiado, and the Masai Mara region. Although a number of the



populations have experienced declines (e.g. the Mara; Ogotu *et al.* 2011), the population size of this species probably exceeds 75,000.

In Uganda and Sudan, Bright's Gazelle has been reported to have decreased considerably. The latest survey in Uganda, in 1995, found it only in the southern part of Karamoja, with an estimated population of 150 (Von Richter *et al.* 1997). Surveys in S Sudan in the 1970s and 1980s estimated the population at 15,000 (including 3000 in Boma N. P.). Recent surveys in S Sudan estimated the total population in Boma N. P. at ca. 2500 (Fay *et al.* 2007). In Ethiopia, the species is mainly confined to the extreme south-west and the estimate of 6340 was considered stable (Schloeder *et al.* 1997, East 1999). The largest populations of this species are found in Kenya's rangeland districts: Turkana (8750), Marsabit (21,160), Samburu (2490) and Isiolo (9740) (Butynski *et al.* 1997a). Total population size is in the order of about 50,000 animals.

The total population size of Peters's Gazelle in the rangelands of Wajir, Garissa and Tana R. has been estimated at 12,120 (Butynski *et al.* 1997a). In Tsavo, south Kitui, Ngai-Ndeithia and protected areas, some 3300 animals have been recorded. These numbers probably include Bright's Gazelle in the northern part and Grant's Gazelle to the south. The population size of Peters's Gazelle is probably less than 15,000.

Recorded population densities for the species group estimated from aerial surveys range from 0.04 to 3.8/km² in Amboseli N. P., while estimates obtained by ground counts in areas where the species is common range from 1.0 to 3.7/km² (East 1999, and references therein).

Foraging and Food These gazelles are mainly browsers, borne out both by direct observations and analysis of stomach contents, as well as studies involving stable carbon isotope analysis (Cerling *et al.* 2003). Averaged over a year, 69% of the analysed rumen content of ♀♀ (n = 51) from Longido G. R., Tanzania, was categorized as browse and 27% was considered graze (Spinage *et al.* 1980);

male stomachs ($n = 18$) had a higher fraction of browse (86%). The amount of browse was correlated with the amount of rainfall (Spinage *et al.* 1980).

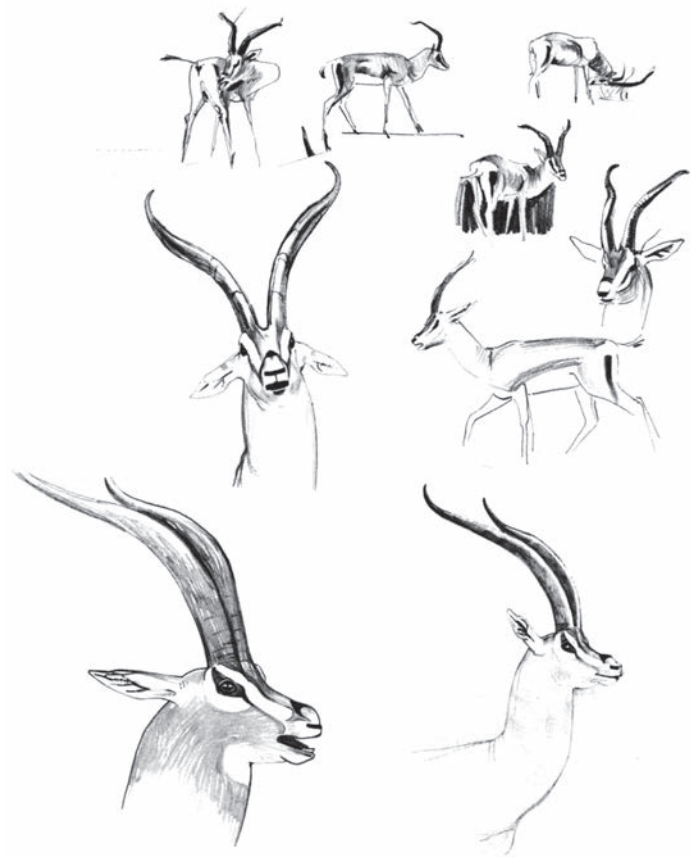
Hofmann (1973) has characterized Grant's Gazelle as a seasonally adapted, intermediate feeder, preferring herbs and shrub foliage. During the dry season, and while grass is tall and rank, *Solanum*, *Indigofera*, *Sida* and *Disperma* have been recorded as common foods. Fruits of *Balanites*, *Solanum* and *Calotropis* have also been recorded. Among grasses, *Cynodon* and *Harpachne schimperi* are taken in the early rains as is the early growth of *Hyparrhenia* and *Themeda*, although these are generally avoided at later stages of their growth (Kingdon 1982).

Talbot (1962) drew attention to some preferred foods that were typical of abused, overgrazed ranges. Sinclair & Norton-Griffiths (1979), noting an increase of these gazelles in Serengeti N.P. from 30,000 in 1967 to 52,000 in 1978, attributed this increase to the expansion of Common Wildebeest *Connochaetes taurinus* that had reduced competition from grasses and therefore benefited herbs, thereby increasing the food supply for Grant's Gazelles.

In Serengeti N. P., some Grant's Gazelles make seasonal movements, while others remain behind (Walther 1972b). Sometimes movements reverse those of other species and the gazelles are found in drier areas; this possibly reduces competition for food (Estes 1991a). A major part of the population probably joins other migrants back onto the open plains during the wet season (Estes 1991a) and move to bushier areas in the dry season. Grant's Gazelles are the last to leave the plains in the dry season (Walther 1972b).

Social and Reproductive Behaviour Studies on social structure have been carried out on Grant's Gazelle in Serengeti N. P. and the Ngorongoro Conservation Area (Walther 1965, 1972b, Estes 1967, 1973) and have been summarized by Estes (1991a). Group sizes and composition varied with habitat and season. In Serengeti N. P., mixed herds of ♂♂ and ♀♀ constituted a large fraction of groups on the open plains (49%), but a much smaller fraction in the woodland (12%). The proportion of solitary ♂♂ was similar in the two habitats (14%) whereas single ♂♂ with female groups comprised 16% in the open plains and 34% in the woodlands. Herds of ♀♀ alone made up 8% on the plains, 7% in the woodland and ♂♂ alone constituted 20% on the plains, 15% in woodland. Herd size differed in the two habitats. The largest herds are found out on the open plains. In bush areas the largest size recorded was 40, whereas 26% of all herds on the plains exceeded that number, with an upper limit of more than 400 individuals. Large associations were not stable; they broke up into smaller units within a couple of hours. The latter author attributed the differences in group size between habitats to the difficulty of maintaining visual contact in the bush area. The size of other social groups averaged 4.6 for bachelor ♂♂, 6.1 for ♀♀ and 9.6 for harem herds (Walther 1972b).

Sexually mature ♂♂ of Grant's Gazelle form territories in Serengeti N. P., on which they stay from Dec/Jan to Jun/Jul. During this time they acquire harems of 10–25 ♀♀, mostly in open areas surrounded by woodland. Below a minimum of 10 ♀♀, they tend to leave and search for larger groups. An upper limit of about 20–25 may be determined by the ability of a ♂ to keep the ♀♀ on his territory. Harems are 'half open' groups in which ♀♀ can move into, but less easily out of, a male's territory (Walther 1972b). Females do not maintain territories, but may be restricted to an area by territorial



Grant's Gazelle *Nanger (granti) granti*.

♂♂. Sizes of territories range from a diameter of 300 m (Walther 1965) to 600 m (Estes 1967) in the Ngorongoro Crater, but a diameter of 1–2 km in Serengeti N. P. (Walther 1972b).

The territorial behaviour of Grant's Gazelles differs from that of Thomson's Gazelles: Grant's Gazelles regularly horn long grass and rely on linked urination–defecation for scent-marking, whereas Thompson's Gazelles mark with their preorbital glands. Grant's Gazelles pursue ♀♀ far less vigorously than Thompson's Gazelles, probably due to their much larger territories. A conspicuous trait of Grant's Gazelles is lying alone where their presence is obvious, visually advertising their territorial status. Grant's Gazelles use head-flagging in their dominance display, whereby the head is abruptly turned from side to side, perhaps to advertise the neck development characteristic of adult ♂♂. This behaviour is not found elsewhere in the Antilopini (Estes 1967, 1991a).

On the open plains of Serengeti N. P., mixed herds are typical of Grant's Gazelle. They have home-ranges of up to 5 km in diameter, in which they move in daily circuits. The home-ranges of different groups may overlap and individuals may switch from one to another. During daily circuits herds may enter male territories in which they may remain for some hours. Male territory holders show dominance displays toward other ♂♂ and monopolize all copulations (Walther 1972b).

Less is known about the social structure in the other species of the species complex. Peters's Gazelle has been studied by Leuthold (1981) in Tsavo East N. P., both north and south of the Voi R. Group sizes scarcely differed between the two areas, but those in the south averaged 4.7, those in the north 3.7. Group sizes did not vary between rainy and dry seasons. For the ♂♂, about one-quarter to

one-third were found in all-male groups, the rest in groups consisting of one ♂ with several ♀♀ or in mixed groups with several individuals of each sex. All-female groups were less than 20% of the individuals and groups with a single ♂ were more common (Leuthold & Leuthold 1975a).

Females indicate receptiveness by straightening the tail horizontally. The ♂ follows or approaches with his tail in a similar position, neck vertical and nose lifted. He walks in a stiff-legged manner and performs low-amplitude goose-stepping, kicking with his forelegs (cf. Thomson's Gazelle). Having been followed for a while, the ♀ also slows to a walk and may then toss her head back and to the side, indicating receptivity. Shortly after this the ♂ mounts, standing and walking on two legs in an almost vertical position (Walther 1972b), because the ♀ keeps walking, a gazelle trait.

Reproduction and Population Structure Females start breeding at 1.5 years of age, whereas ♂♂ mature at three years (Estes 1991a). Gestation in captive ♀♀ has been reported at 198–199 days ($n = 3$) (Furley 1986). Grant's Gazelles give birth to offspring throughout the year with a peak in Dec–Feb and another in Aug and Sep. The first peak is within or after the short rains, the second in the dry season (Estes 1991a). In Karamoja, Bright's Gazelle ♀♀ gave birth in Nov/Dec and in Jun (Kingdon 1982). Twin births have not been recorded. Grant's Gazelles in captivity have been reported to live to 19 years (Weigl 2005).

Predators, Parasites and Diseases In Serengeti N. P., larger predators, such as Lions *Panthera leo*, Leopards *P. pardus*, Cheetahs *Acinonyx jubatus* and African Wild Dogs *Lycaon pictus* regularly prey on these gazelles although the gazelles only make up a minor fraction of the prey species. This is in contrast with Thomson's Gazelles, which are the main prey of Cheetahs and African Wild Dogs (Estes 1991a, Caro 1994). Because they drink infrequently this may help protect them from some of the larger predators, which tend to hunt closer to watering places. Golden Jackals *Canis aureus* and Black-backed Jackals *C. mesomelas* are major predators of gazelle young. These may be defended by the mother, often successfully when a single jackal attacks. Quite often, particularly in maternal groups, a second ♀ may join the defence (Estes 1991a, Walther 1995).

Conservation IUCN Category: Least Concern. CITES: Not listed.

Considering that some populations have decreased substantially over the last 30 years and that this has affected the three species differently, the conservation status for each of the three species requires re-evaluation. Grant's Gazelle seems to be relatively well protected and secure since a substantial fraction of its population is found in protected areas, such as Serengeti N. P., Tarangire N. P., Mkomazi G. R. (Tanzania), and Masai Mara National Reserve, and Lake Nakuru, Amboseli and Nairobi National Parks (Kenya). Bright's Gazelle has a lower fraction of its population in protected areas. Peters's Gazelle has the lowest population size, probably below 15,000, and since Tsavo N. P. (where numbers were declining in the 1990s) and Tana River National Reserve are the only protected areas within its range, this species might be more vulnerable than the other two species.

Measurements

Nanger (granti) species group

N. (g.) granti

TL (♂♂): 1646 (1580–1750) mm, $n = 9$

TL (♀♀): 1575 (1507–1635) mm, $n = 7$

T (♂♂): 310 (280–350) mm, $n = 9$

T (♀♀): 289 (267–305) mm, $n = 7$

HF c.u. (♂♂): 444 (433–455) mm, $n = 9$

HF c.u. (♀♀): 409 (400–425) mm, $n = 7$

E (♂♂): 153 (150–158) mm, $n = 9$

E (♀♀): 154 (150–157) mm, $n = 7$

Sh. ht (♂♂): 888 (865–915) mm, $n = 9$

Sh. ht (♀♀): 803 (745–835) mm, $n = 7$

WT (♂♂): 61.7 (53.2–70.1) kg, $n = 9$

WT (♀♀): 42.5 (40.0–45.9) kg, $n = 7$

Serengeti N. P., Tanzania (Sachs 1967)

Maximum recorded horn length for the three forms are as follows:

N. (g.) granti, 80.6 cm for a pair of horns from Kimali, Tanzania; *N. (g.)*

notata, 74.6 cm for a pair of horns from Kameube, Kenya; and *N. (g.)*

petersii, 69.5 cm for a pair from Voi, Kenya

Key References Estes 1967, 1973, 1991a; Leuthold 1981; Walther 1965, 1972b.

Hans R. Siegismund, Eline D. Lorenzen & Peter Arctander



Peters's Gazelle *Nanger (granti) petersii* (left) marking postures (superimposed) and (right) prominent 'flagging' of horns and white rump and tail.

Nanger soemmerringi SOEMMERRING'S GAZELLE

Fr. Gazelle de Soemmerring; Ger. Sömmerring-Gazelle

Nanger soemmerringi (Cretzschmar, 1828). Rüppell, Atlas Reise Nordl. Afr. Zool., Saugeth., p. 49, pl. 19. 'an dem östlichen Abhange Abyssiniens' (E Ethiopia); since restricted to 'Tal E'Sabb, Abyssinia' (Ethiopia, El Shab Valley).

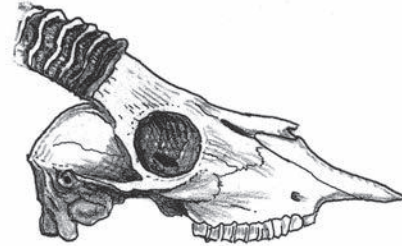


Soemmerring's Gazelle *Nanger soemmerringi*.

The species is named after Samuel Thomas von Soemmerring (1755–1830), a Polish scientist skilled as an electrician and in anatomical work.

Taxonomy Soemmerring's Gazelle is here included in the genus *Nanger*, together with the Grant's Gazelle *N. (granti)* species group and Dama Gazelle *N. dama* (Groves 2000). Gentry (1972) listed six subspecies, noting that two subspecific names would probably suffice, namely *soemmerringi* and *berberana*. Currently, there are three recognized subspecies (Groves 1985a, Kingdon 1997, Grubb 2005). Synonyms: *berberana*, *butteri*, *casanovae*, *erlangeri*, *sibyllae*, *typical*. A study of the chromosomes of seven male and 20 female Soemmerring's Gazelle found 12 different karyotypes with chromosome numbers varying between $2n = 34$ and $2n = 39$. The variability is due to a Robertsonian chromosome system of fusions operating to make three metacentric pairs from six acrocentric pairs. The reason for this karyotypic variability is likely not due to hybridization and it is not yet known whether the poor reproductive success of the species is related to this chromosomal polymorphism (Benirschke *et al.* 1984; and see Vassart *et al.* 1995). There is no evidence as to whether the karyotypic variability might be related to geography or subspecies (C. Groves pers. comm.).

Description One of the larger gazelles, uniformly pale fawn in colour on its upper side, and bright white on the entire underside



Lateral view of skull of Soemmerring's Gazelle *Nanger soemmerringi*.

of the body, inside of legs, back of hindlegs and tail. The transition from fawn to white occurs abruptly along the flanks and upper edges of the rump. The face has several distinctive markings including a dark muzzle, a dark stripe running down the nose to the muzzle, a white stripe parallel to the dark nose-stripe, and a black stripe passing through each eye and ending at the muzzle. The tail is short and tapered, and tipped with black.

Both sexes have backwards-bent lyrate horns with inward-facing tips, and strongly ringed bases. The horns of the ♂♂ are larger, more strongly bent, and more heavily ringed than those of the ♀♀. The skull resembles that of other *Nanger* species, with large basioccipital tuberosities (C. Groves pers. comm.).

Geographic Variation

N. s. butteri: S Ethiopia. Faint dark band along its flank and adjacent to the rump patch; mid-face black; horns longer and more slender.

N. s. berberana: Somalia and NE Ethiopia. Entirely black face and longer horns.

N. s. soemmerringi: Sudan, Eritrea. Smallest subspecies; brown face and shorter horns; no dark flank.

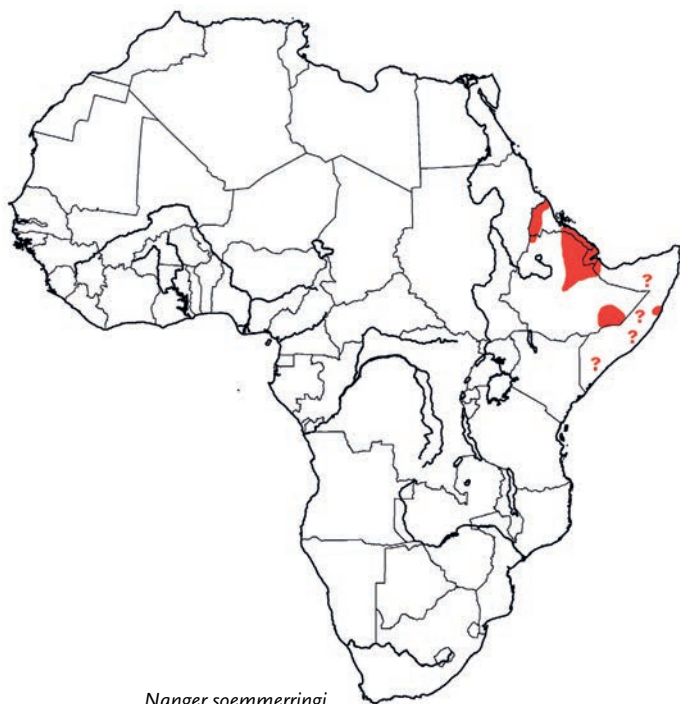
There is an unnamed population of Soemmerring's Gazelle found on Dahlak Kebir I., Eritrea (Yalden *et al.* 1996). This form varies from its mainland counterparts in that it is considerably smaller in size.

Similar Species

Nanger granti. Allopatric, but ranges were formerly very close in Ethiopia/Kenya borderlands. Longer, straighter horns and less extensive white on rump.

Gazella spekei. Observed in mixed herds with Soemmerring's Gazelle on the coastal grasslands in Ceel Dhere District, Somalia, in the late 1980s; however, there is no recent information to confirm whether Soemmerring's Gazelle still occurs in this area (Laurent & Laurent 2002). Smaller, with shorter horns, swollen nose, and black side-stripe.

Gazella dorcas. Pelzeln's Gazelle *G. d. pelzelni* overlaps in range in Djibouti (Künzel *et al.* 2000). Smaller, more gracile, with long pointed ears.



Eudorcas tilonura. Largely allopatric, but ranges overlap in SW Eritrea (and formerly in NE Sudan, although Soemmerring's are now probably eliminated from their historical range in this country). Small gazelle, redder in colouration, with horns bowed outwards and hooked inwards at the tips.

Distribution Endemic to the Horn of Africa region.

Historical Distribution Formerly widely distributed throughout most of Djibouti, N Somalia and the central coastal plain and locally between the Shebelle and Juba Rivers; NE and EC Sudan; the lowland areas of Eritrea and the eastern lowland areas of Ethiopia (East 1999). At one time this gazelle may have occasionally ventured as far south as extreme NE Kenya, though it is unclear whether they still sporadically occur there today (Kingdon 1982, East 1999). A population on Dahlak Kebir I. was probably introduced over 100 years ago (Yalden *et al.* 1996).

Current Distribution Still occupies substantial parts of its historical range, mainly in Djibouti, Eritrea and Ethiopia, but at lower densities and as isolated populations, primarily due to a long history of uncontrolled hunting, habitat destruction and livestock grazing, which have most probably eliminated this species from its historic range in Sudan (East 1999, I. Hashim pers. comm.). Funaioli & Simonetta (1966) mentioned that the species was almost exterminated in the southern region of Dafet in Somalia, and East (1999) states that by the early 1980s it had been eliminated from most of its former range in this country, but was still present in reasonable numbers in parts of the central coastal hinterland and occurred seasonally in mixed herds with Speke's Gazelle *Gazella spekei* on the coastal grasslands in Ceel Dhere District.

In addition to the Dahlak Kebir population, there is a resident herd on Dahlak Norah I. following the introduction of this species in the late 1980s (J. C. Hillman pers. comm.).

Habitat Occupies a wide range of habitats ranging from arid coastal plains and mudflats, to arid and semi-arid *Acacia* savannas, and semi-arid grassland plains. Tends to favour rough hilly country, but may also be found in open short-grass plains (Spinage 1986, Kingdon 1997), open bush savannas, and thinly wooded grass steppes (Haltenorth & Diller 1980), thornbush and open grassland plains in hilly country (Estes 1991a, Künzel *et al.* 2000), and open bushland areas with an abundance of forbs (Jacobs & Schloeder 1993, Laurent & Laurent 2002). Recorded to 1500 m in Ethiopia (Yalden *et al.* 1996).

Abundance There is no detailed information on abundance throughout their current range. However, reports from Eritrea, Somalia and Sudan, and population estimates from Ethiopia and Djibouti, suggest that there are less than 15,000 gazelles remaining today (East 1999). Ethiopia is still considered the stronghold for this species. Several stable populations can be found throughout the middle and lower Awash River Basin and parts of the Ogaden region, with an estimated average density of 0.3 gazelles/km² (Jacobs & Schloeder 1993, Thouless 1995, Wilhelmi 1997, East 1999); Wilhelmi *et al.* (2006) noted that probably at least a few hundred to a few thousand Soemmerring's Gazelles may survive in the Ogaden region.

Adaptations Soemmerring's Gazelle can go for days without drinking, meeting its water requirements by selecting protein-rich forage and foraging when it is coolest. It is also known to seek out tall *Acacia* and evergreen trees and rest in the shade during the hottest times of the day during the dry season (M. Jacobs & C. Schloeder pers. obs.). Other water-conservation adaptations include concentrating its urine, adjusting its body temperature and evaporative cooling (Estes 1991a).

Foraging and Food Both a browser and a grazer (and classified as a browser-grazer intermediate by Gagnon & Chew [2000]), this gazelle is often found at lower elevation plains during the wet season, where it exhibits a preference for grasses and forbs (and, to a lesser extent, shrubs). Once the dry season is under way and the availability of herbaceous forage declines, it tends to move to higher elevations with moderate to rough relief, and switches to a diet that includes a variety of *Acacia* shrubs and woody herbs. The behaviour of the subspecies found on Dahlak Kebir I. differs somewhat from those on the mainland. The island subspecies tends to move from the interior open-shrubland areas at the onset of the dry season, to forage on the mudflats and on algae growing in the shallow coastal waters (J. C. Hillman pers. comm.). Disturbed areas such as abandoned settlements and grazing arenas are considered important foraging sites because a variety of annual forbs and grasses typically colonize these sites following abandonment (Barker *et al.* 1990, Jacobs & Schloeder 1993, Laurent & Laurent 2002). In addition, salt, mineral licks and the soil in abandoned domestic livestock compounds are sought out by this gazelle, particularly when ♀♀ are lactating (Laurent & Laurent 2002, M. Jacobs & C. Schloeder pers. obs.).

Social and Reproductive Behaviour Herd size varies seasonally, with animals tending to congregate during the wet season in large groups (up to 150); the dry season is characterized by smaller group sizes (1–9), as a result of dispersal. Most herds comprise primarily adult ♀♀ and their young (both subadults and calves). The

exception is those rare occasions when ♂♂ form small, male-only groups (1–3 ♂♂), and when ♂♂ join the female groups during the breeding season. Males attempt to keep the female groups within their own territory for breeding (Jacobs & Schloeder 1993). They may occur in mixed herds with other gazelle species. For example, they have been seen in mixed herds with Speke's Gazelles on the coastal grasslands in Ceel Dhere District, Somalia (East 1999), and in mixed herds with Pelzen's Gazelles in most areas in Djibouti (Künzel *et al.* 2000).

Reproduction and Population Structure Breeding generally occurs between Sep and Dec (Djibouti), with birthing tending to coincide with the onset of the wet season (Kingdon 1982, A. Laurent pers. comm.). The appearance of new offspring as late as Sep in Awash N. P., Ethiopia, indicates that this species also breeds as late as Jan (Jacobs & Schloeder 1993).

One young is born after a gestation period of about 198 days (Walther 1990). The young are usually kept hidden until they are at least one month old. Weaning takes place after six months and sexual maturity typically occurs after 1.5 years. The species has been known to live as long as 15 years in captivity (Weigl 2005).

There is little information about the population structure of this species with the exception of one study from Ethiopia. This study indicated that the population in Awash N. P. was comprised of 84% adults, 10% subadults and 5% calves; the estimated proportion of ♀♀ and ♂♂ was 63% and 37%, respectively (Jacobs & Schloeder 1993).

Predators, Parasites and Diseases Predators include most large carnivores, although large predators are now absent from many, if not most, of the regions in which the species now occurs. Yearlings are most vulnerable to predation (Walther 1990). There is little information about this species' susceptibility to parasites and diseases, but it is probably vulnerable to the helminths and ticks common to other gazelles (Graber *et al.* 1980, W. Karesh pers. comm.).

Conservation IUCN Category: Vulnerable A2cd; C1. CITES: Not listed.



Soemmerring's Gazelle *Nanger soemmerringi* head.

In general, this species is in decline throughout its historic range with the exception of certain areas in Eritrea, Ethiopia and Djibouti, and the Dahlak Islands, largely as a result of uncontrolled hunting, in combination with a loss of habitat and livestock grazing (East 1999, Künzel *et al.* 2000). The largest protected population occurs in the Awash N. P. (about 200 animals).

Measurements

Nanger soemmerringi

HB: 1250–1500 mm

Sh. ht: 800–920 mm

T: 180–280 mm

WT: 30.0–55.0 kg

Throughout the geographic range (Kingdon 1982, Laurent & Laurent 2002)

Maximum recorded horn length is 58.4 cm for a pair of horns from Somalia (Rowland Ward)

Key References East 1999; Estes 1991a; Jacobs & Schloeder 1993; Kingdon 1982, 1997; Walther 1990.

Catherine Schloeder & Michael Jacobs

Nanger dama DAMA GAZELLE (ADDRA GAZELLE)

Fr. Gazelle Dama (Biche-Robert); Ger. Damagazelle

Nanger dama (Pallas, 1766). Misc. Zool., p. 5. No locality cited; based on 'Le Nanguer' of Buffon from 'Sénégal'.

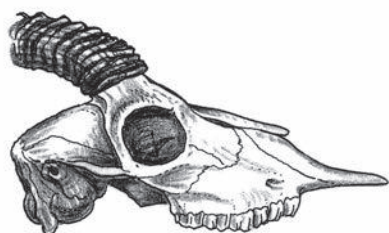
Taxonomy The Dama Gazelle belongs, together with Soemmerring's Gazelle *N. soemmerringi* and the Grant's Gazelle *N. (granti)* complex, in the genus *Nanger* (Groves 2000).

In the type description of Pallas (1766), based on Buffon (1764), no reference to a type specimen is made. Buffon's illustration clearly corresponds to *N. dama*, showing a square-cut transition from dark back to white rump, with no rufous colouring extending onto the hindleg, not unlike the *N. d. dama* colour type (although a transition toward *N. d. mhorh* can be debated). Information on location in Buffon (1764) is limited to the observation that 'this is an animal which according to M. Adanson, is called Nanguer or Nanguer au Sénégal'. Buffon (1764) also reports Adanson's

observation 'qu'il y a trois espèces ou variétés de ces nanguers, qui ne diffèrent entr'eux que par les couleurs du poils, mais qui tous ont les cornes plus ou moins courbées en avant'. Malbrant (1952) and Grubb (1993c) suggest that the Dama Gazelle's type location is L. Chad. However, it is curious that specimens of three different types were already identified in 1764, some 60 years before the first recorded European expedition entered central parts of the range near L. Chad (and shot two Damas) (Denham *et al.* 1826). Cretzschmar (1826) reported the first specimen from Sudan and noted that only one juvenile specimen from elsewhere, 'Senegal', was known. Other reports (Bennett 1833, 1835, Sclater & Thomas 1899) report specimens from Morocco or Western Sahara from



Dama Gazelle *Nanger dama dama*.



Lateral view of skull of Dama Gazelle *Nanger dama*.

where two live specimens and one damaged skin arrived in London (ZSL) in 1833.

There is a wide variation in colour pattern, which has led to the description of numerous subspecies (see Gentry 1972). Cano (1984) distinguished three morphologically defined subspecies (*N. d. mhorr*, *N. d. ruficollis* and *N. d. dama*), each with a light and dark variant. Preliminary biochemical and cladistic analyses support this distinction (E. Handrus pers. comm.), possibly reflecting the limited genetic base of the sampled captive populations. However, Vassart *et al.* (1995) concluded that the morphological cline of these subspecies could not be related to a chromosomal one ($2n = 38, 39$ or 40 being found in the same cline). Further, thousands of animals in Chad, from one area and even in the same herd, could be attributed to either *ruficollis* or *dama*, without expressing any geographic gradient (Malbrant 1952). Sclater & Thomas (1899) earlier questioned the distinction between *N. d. mhorr* and *N. d. dama* (as did Groves 1985a and Kingdon 1997). With the small and isolated wild populations, few specimens collected and the limited genetic stock of captive

populations, it will be difficult to clarify the subspecies status. For pragmatic reasons we provisionally retain the distinction of the three subspecies of Cano (1984) as colour forms; *permista* from Senegal may also represent a distinct form (C. Groves pers. comm.). Synonyms: *addra*, *damergouensis*, *lazoni*, *lozanoi*, *mhoks*, *mhorr*, *mohr*, *nanguer*, *occidentalis*, *orientalis*, *permista*, *reducta*, *ruficollis*, *weidholzi*. Chromosome number: $2n = 38-40$ (Effron *et al.* 1976, Vassart *et al.* 1995). Vassart *et al.* (1993) published a karyotype with $2n = 34$, from a ♀ of unknown origin.

Description The tallest and largest of all gazelles, brightly marked and coloured in the west and centre of the range, with eastern forms often appearing almost white from a distance. The long-necked and long-limbed structure, with a slight shoulder hump, creates a characteristic profile and running action. The upper and front part of the head is white, regularly with a dark stripe through the eye (especially pronounced in *N. d. mhorr*). The neck is rufous with a conspicuous white spot visible half-way up the neck. Body with decreasing red-brown colouration on the upper half, from (north-) west (*N. d. mhorr*), which shows solid rufous back sharply delineated from a large bright white rump area, through forms showing varying and intermediate reduction in the rufous back colouring through the central range (*N. d. dama*), to eastern forms (*N. d. ruficollis*) in which the rufous cape on the back and upperparts fades out rapidly through a grizzled roan area starting anywhere from the base of the neck, shoulder or mid-back. Legs white, with a variably prominent rufous stripe down the front of the lower forelegs. Rufous extension of back colouring onto white outer thigh is broad, well delineated and prominent in *N. d. mhorr*, narrower, or faded or absent in *dama*, and absent in *ruficollis*. Flank- or pygal-bands are absent. Underside of tail darkish, upperside white. Preorbital glands are small.

Young are uniform apricot-tan colour for first month of life, and noticeably more bulky than young of other gazelles, with coarser features. Adult body colouration develops rapidly except for the face, which is initially strongly patterned with a very dark-brown nose-spot, near-black flashes below the horn bases separated from pale bands around the eyes, a narrow dark eye-stripe, pale-brown cheeks and a tawny central muzzle, reminiscent of the face pattern in Soemmerring's Gazelle. Nose-spot and central muzzle to the level of the narrow eye-stripe replaced with pure white by around 18 months, but dark marks above eyes and across forehead may persist (T. Wachter pers. comm.). Many subadults retain variably prominent dark forehead marks, which continue to grizzle and whiten into full adulthood, the white colouring in many eventually spreading around the horn bases to the nape to create the near fully white head of older animals.

Horns are comparatively short relative to other large gazelles, and lyrate and sharply backswept, before curling forward. They are heavily built with pronounced annulations and swollen bases in ♂; much lighter and weaker in ♀.

Geographic Variation

N. d. mhorr (Mhorr or Mohor Gazelle) (including *lozanoi*): North Africa. The range between this colour form and the Sahelian populations of *N. d. dama* in SE Mauritania may have been in contact (Sclater & Thomas 1899), although historical observations gathered by Trotignon (1975) suggest the existence of a gap. In

this colour form the upperparts have the full extent of reddish colouration from the head to the rump and down the hindlegs to at least the hock.

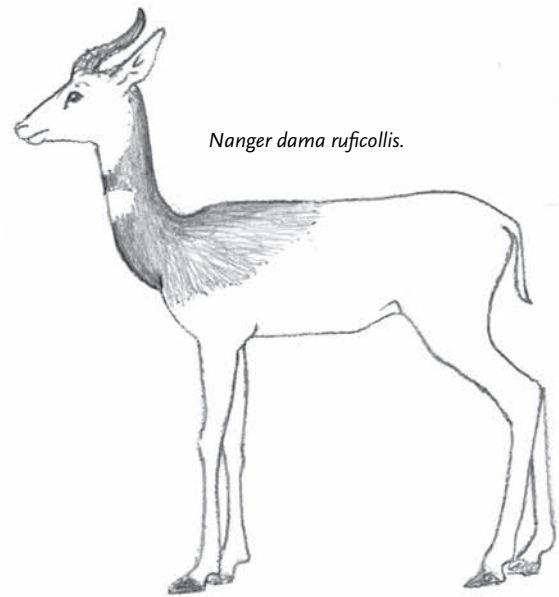
N. d. dama. Senegal to Aïr – L. Chad. Upperparts fawn to reddish in colour, extending along the back to the rump and down the hindleg to the hock; stripes on the face.

N. d. ruficollis (Red-necked Gazelle). Aïr – L. Chad to Sudan. Upperparts red-brown, but restricted to the neck or only part way along the back, the rest of the body being white; legs usually white, at most suffused with reddish; face-stripes obliterated.

Similar Species At close proximity, this species is unlikely to be confused with any other species, although at greater distances especially *N. d. ruficollis* may appear similar to other 'large white' antelopes such as the Scimitar-horned Oryx *Oryx dammah* and possibly the Addax *Addax nasomaculatus*. Although the body shape is distinctive, colour pattern of *N. d. mhor* is reminiscent of related, but allopatric, Soemmerring's Gazelle in the lack of a flank-band, large white rump area and the face pattern of young.

Distribution Endemic to Africa.

Historical Distribution The range of the Dama Gazelle resembles that of the Scimitar-horned Oryx. North of the Sahara, the former Atlantic distribution of the Dama Gazelle encompassed a 200–300 km-wide band of oceanic and sub-oceanic desert from the Oued Noun in S Morocco to NW Mauritania (Valverde 1957, Trotignon 1975, Loggers *et al.* 1992). Dama Gazelles also used to occur in NW Algeria (Heim de Balsac 1936, Kowalski & Rzebik-Kowalska 1991, De Smet & Smith 2001) and extreme S Libya (Hufnagl 1972, Essghaier 1980, Khattabi & Mallon 2001), from where it extended into the central Saharan massifs. In Tunisia they are believed to have occurred in the south and to have disappeared before the twentieth century (Kacem *et al.* 1994, Smith *et al.* 2001). That they formerly



Nanger dama ruficollis.



Nanger dama dama.



Nanger dama mhor.



Nanger dama

ranged into Egypt is evidenced by fossilized remains from the upper Pleistocene in the south-western part of the Western Desert (Osborn & Osbornová 1998).

South of the Sahara, Dama Gazelles formerly occurred in N Senegal during the dry season, or periods of drought, only (Bourlière *et al.* 1976). Also formerly present in SE Mauritania, SE Algeria, Mali, Niger, Chad and NW Sudan (Wilson 1980, East 1999), but not extending east of the Nile R. (East 1999, Devillers *et al.* 2005b). They have also been recorded, albeit rarely, from the Sahel zone of NE Nigeria (in the region of L. Chad and the Jawa) and N Burkina Faso (East 1999). There may still be a potential link between populations north and south of the Sahara across the Hoggar (where they were recorded in the central ranges until 1964; Kowalski & Rzebik-Kowalska 1991), and Air–Tassili N'Ajjer–Plateau du Djado–Tibesti (C. Magin pers. comm.).

Current Distribution Numbers of Dama Gazelles have declined drastically since the 1940s in the Atlantic Sahara and central Saharan massifs, and since the 1960s from the Sahelian part of its range. In North Africa, Dama Gazelles (*N.d.mhorr*) are probably extinct, though they may survive in the Drâa Basin (where the last observations were made by nomads in 1993) (Cuzin 1996, 2003, Aulagnier *et al.* 2001). They may survive in very small numbers along the border between Western Sahara and Mauritania (Cuzin *et al.* 2007), but this is not confirmed. Dama Gazelles are now extinct in the Hoggar in S Algeria (Kowalski & Rzebik-Kowalska 1991; Wachter *et al.* 2005), but they may survive in the Tassili de Tin Rehror in S Algeria (K. De Smet pers. comm.). They have been reintroduced in Bou-Hedma N. P. in Tunisia (mapped).

South of the Sahara, Dama Gazelles are reported to still be present in the Tamesna region in E Mali (Lamarque 2005, Lamarque *et al.* 2007), the Aïr and Termit/Tin Toumma in Niger (Newby *et al.* 2004, Wachter *et al.* 2004a, b), and in the Chadian Manga and Ouadi Rimé–Ouadi Achim Faunal Reserve between 13°N and 18°N in C Chad (Monfort *et al.* 2004, Wachter *et al.* 2004b, Wachter & Newby 2010, Wachter *et al.* 2011) (see Conservation). Aerial and ground surveys conducted in the Termit and a contiguous block of the Tin Toumma dune system in 2007 failed to record any Dama Gazelles (Wachter *et al.* 2008), but surveys in December 2008 recorded the presence of gazelles in both the northern and central parts of the Termit massif (Wachter *et al.* 2009).

Dama Gazelles are now thought to be extinct in Mauritania (F. Lamarque pers. comm.), despite reports that they may still survive in the remote south-east and in the vicinity of Tidjika in the west (East 1999). They also are probably extinct in Nigeria, Burkina Faso (Heringa [1990] reported they could have survived in the Seno-Manga area) and Libya (although a relict population could survive in the Tibesti region near the Chadian border; Essghaier 1980). There are no recent confirmed records from the Sudan, although East (1999) mentioned anecdotal information from local people who suggested that they still occurred at low densities in northern Darfur and northern Kordofan. Dama Gazelles have been (re-)introduced in Senegal where they went extinct (not mapped; see Conservation).

Habitat Contrary to what its present distribution suggests, the Dama Gazelle prefers sparsely wooded savanna rather than open desert and is more Sahelian than Saharan. The early travellers

Denham *et al.* (1826) and Nachtigal (1879–89) reported Dama Gazelles from dense woodlands around L. Chad in the late dry and early wet season, contrasting to its present habitat such as the scarcely vegetated Manga area north of L. Chad (Scholte 2012). Early travellers also observed Dama Gazelles in the wadis between the massifs of the Aïr Mts (Barth 1857–1859) but not from the extensive deserts they crossed. Compared with the Dorcas Gazelle *G. dorcas*, Dama Gazelles used to be less abundant and confined to large dry river beds with (sparse) woodland with short migration into the desert zone in times of abundant (high-quality) forage. In Chad, the area east of the Bahr al Ghazal used to be particularly suitable, with wadi habitat of flood-plains with woody vegetation (Ouadi Rimé, Ouadi Haddad, Ouadi Kharma and others), with Dama Gazelles together with the Red-fronted Gazelle *Eudorcas rufifrons*, whereas the Scimitar-horned Oryx and the Dorcas Gazelle used to be dispersed in the inter-wadi areas (J.E. Newby pers. comm.). Occasionally, Dama Gazelles can be found far out in sandy seas or ergs and they have been observed with Addaxes near Fachi and to the south-east of the Erg du Ténéré (Dragesco-Joffé 1993). Habitat north of the Sahara is said to be treeless (Cuzin 1996), likely the result of human pressure.

Abundance The Dama Gazelle was formerly widespread and abundant, but numbers have declined drastically since the 1950s and 1960s. For example, the population in Ouadi Rimé–Ouadi Achim Faunal Reserve in C Chad, one of the strongholds of the species, was estimated at 10,000–12,000 individuals in the early 1970s or 0.14/km². These figures are from a population that had already been reduced since the 1950s. Surveys undertaken in early 2011 in Ouadi Rimé–Ouadi Achim provided the first formal records of Dama Gazelle persisting in this region for many years (Newby & Wachter 2011, Wachter *et al.* 2011). In the mid-1980s, the other main surviving population, in the Aïr–Ténéré reserve in Niger, was estimated at 150–250 individuals (Grettenberger & Newby 1986); by the late 1980s it was estimated at approximately 170 (Magin 1990). Numbers have dropped dramatically there as well, and observations in March 2002 were limited to a few animals and tracks in the eastern Aïr, especially on the Takoloukouzet plateau (Newby *et al.* 2004). However, there are reports of others further north and to the west; a population was reported to still exist in the Termit Massif (Wachter *et al.* 2004a, b), although more recent surveys recorded no signs of them (Wachter *et al.* 2008).

In summary, in the last decade, only scattered observations of Dama Gazelles have been made (Scholte 2001, Claro 2004, Monfort *et al.* 2004, Newby *et al.* 2004, Wachter *et al.* 2004a, b, Wachter & Newby 2010, Wachter *et al.* 2011), including one survey which confirmed the existence of the species in the south Tamesna region of E Mali (Lamarque *et al.* 2007). In all areas surveyed, numbers were very low and the size of observed gazelle groups very small (range 1–5 individuals), and the number of gazelles observed was less than 0.05/km² (Lamarque *et al.* 2007). The total current wild population is almost certainly less than 500 individuals (J. Newby pers. comm.).

Adaptations The current distribution of this species in more arid areas largely reflects marginalization due to hunting pressure and is not an adaptive preference (Scholte 2012). This, and its

seasonal migrations north into the Sahara during the wet season (retreating again into the Sahel during the dry season), explains why some authors considered the Dama Gazelle as more Saharan than the Dorcas Gazelle. The Dama Gazelle is reputed to be more water-dependent than the Dorcas Gazelle, but compensates for this by browsing. Light pelage is an additional physiological adaptation (Wilson 1989). With their long legs, Dama Gazelles are one of the fastest mammals, although reported speeds of up to 100 km/h (Dragesco-Joffé 1993) seem exaggerated. Dama Gazelles are able to reach tree branches by standing on their hindlegs, but probably only do this in periods of food scarcity.

Foraging and Food During the dry season, Dama Gazelles browse leaves, flowers and pods of *Acacia ehrenbergiana*, *A. tortilis*, *Maerua crassifolia* and *Balanites aegyptiaca*, obtaining a crude protein content above 12% (Le Houérou 1989). Dama Gazelles also browse the abundant coarse shrubs *Capparis decidua*, *Leptadenia pyrotechnica* and *Salvadora persica* (Grettenberger & Newby 1986). Dama Gazelles were recorded browsing on *C. decidua*, *S. persica*, *A. tortilis* and on a mixed sward green flush of short herbs and grasses. Freshly chewed bark of *Maerua crassifolia* was found while inspecting a recently vacated feeding site in E Chad in mid-Sep (Monfort *et al.* 2004). Bark chewing on *Acacia gummifera* and browsing of *A. gummifera* and *Ziziphus lotus* has also been observed in the extralimital enclosed population at R'Mila in Morocco. During the dry season moisture is obtained through browse and, additionally, consumption of the wild melon *Citrullus colocynthis* (Dragesco-Joffé 1993). Abundant grass species such as *Panicum turgidum* (perennial grass) and various annual grasses and sedges are only selectively consumed during the rainy and early dry season, after which their feed value drops dramatically. During the early wet season, temporarily available high-quality forbs such as *Tribulus terrestris* and *Indigofera aspera* may constitute an important part of the diet (Dragesco-Joffé 1993).

Social and Reproductive Behaviour The only reliable studies on social behaviour are from the Aïr area (Niger) in the late 1980s. Dama Gazelles probably used to live mainly in harem herds, comprising a single dominant adult ♂ and many ♀♀, but human pressure has led to the disintegration of this system. Based on a data set collected from 1979 to 1990 (J. Newby pers. comm., incorporating Grettenberger & Newby [1986] and Magin [1990]), Dama Gazelle group composition (n = 229 individuals) consists of pairs with young (11+ 8%), single ♂♂ (17%), harems (17%), mixed groups (13%), single ♀♀ (11%), females with young (11%), ♀♀ (5%), bachelor groups (3%) and single immatures (2%); average herd size was 2.1. Observations in relatively undisturbed populations indicate the presence of groups up to 200 individuals (Lavauden 1926b), uniting in the late dry season (Dragesco-Joffé 1993) or early wet season (J. E. Newby pers. comm.), probably because of the concentration of (nutritious) pastures. There are occasional observations of large assemblages during the dry season, such as 500–600 in the Aïr (Brouin 1950).

Limited field observations suggest that the social behaviour of Dama Gazelles resembles that of members of the Grant's Gazelle complex (Walther 1995). Frequent male fighting has been a major constraint in reintroduced populations, mainly due to confined space (Cassinello & Pieters 2000). Mungall (1980) studied courtship

behaviour in captive *N. d. ruficollis* and concluded that general behaviour follows that observed in other gazelle species (Walther 1995). Striking was the Dama Gazelle's frequent use of foreleg kicking (laufs Schlag), without pronounced nose-up display, whereas foreleg kicking of Grants' and Soemmerring's Gazelles was reduced to special steps with nose-up display (Mungall 1980). It remains speculative whether this can be related to the need by the latter species to minimize horn-threat profile, whereas Dama Gazelle horns are smaller and less conspicuous.

Reproduction and Population Structure Births are highly seasonal, and probably influenced by food availability. In Chad, Newby (1978a) recorded births and young from Jul to Dec, corresponding largely with the onset of rains in Jun; in Niger, Dragesco-Joffé (1993) noted births from Oct to Mar; and in Western Sahara births occur from Feb to Mar (Cuzin 1996). A captive population in Senegal (which had a supplemented diet) showed continuous breeding throughout the year (unpublished birth log, from Guembeul N. P. 1984–2000). Based on observations from captive animals, the mean duration of the oestrous cycle is 18.6 ± 0.3 days (range 16–22; Pickard *et al.* 2001).

Gestation length has been given as about 6.5 months (Drüwa 1985, Furley 1986, D. Noble pers. comm.). Females have a single young weighing 4–6 kg. In captivity, ♀♀ breed when they reach two years of age; fecundity ranged from 0 to 1.86 (mean 0.91) offspring annually (Alados & Escos 1991). One captive lived to 19 years (Weigl 2005). The ♂ : ♀ sex ratio in Aïr was 0.89 : 1 (Poilecot 1996).

Predators, Parasites and Diseases No observations reported, but Cheetahs *Acinonyx jubatus* and especially African Wild Dogs *Lycaon pictus* might have been important predators when they were in greater abundance. In the wooded areas where the early European travellers found Dama Gazelles, Lions *Panthera leo* and Leopards *P. pardus* were mentioned as common. Not necessarily confined to heavily wooded areas, these predators may have been present until the early 1960s. Newborns and young are potentially taken by Striped Hyaenas *Hyaena hyaena* and Golden Jackals *Canis aureus*, as well as eagles *Aquila* spp., Ratels *Mellivora capensis* and Rüppell's Foxes *Vulpes rueppellii*. There is no information on parasites or diseases.

Conservation IUCN: Critically Endangered A2cd; C2a(i). CITES: Appendix I. CMS: Appendix I.

The decline of the Dama Gazelle, as with other Sahelo-Saharan antelopes, can be attributed to the combination of habitat degradation, particularly due to the increase in grazing pressure from domestic livestock, and direct exploitation (exacerbated by the introduction of modern firearms and 4×4 vehicles) (East 1999, Devillers *et al.* 2005b). Apart from hunting by military, hunting of Dama Gazelles by Arab hunting parties has been frequent in Sudan (Cloudsley-Thompson 1992) and in 1998 and again in 2001 in Chad, where it was, temporarily, halted after a local NGO made it public.

Ouadi Rimé—Ouadi Achim Faunal Reserve was designated in 1969, at least on paper, to protect, amongst others, Addaxes, Scimitar-horned Oryxes, Ostriches *Struthio camelus* and Dama Gazelles. Part of the Aïr Mts and Ténéré Desert in Niger also received protected area status in 1988 (Aïr—Ténéré N. P.), stimulated by the activities of a conservation-development project (Newby 1992). Both reserves still

harbour Dama Gazelle populations, but have suffered from military unrest resulting in the collapse of conservation infrastructure. International interest for arid-land species has remained low despite the largely improved security situation (Scholte 2001). In early 2012, Niger established the Termit and Tin Toumma National Nature Reserve, a 97,000 km² tract of desert and sub-desert specifically designed and managed to protect Addax, Dama Gazelle and other species.

Captive Dama Gazelles originate from two locations only: *N. d. mhor* from Rio de Oro, Western Sahara (Cano *et al.* 1993) and *N. d. ruficollis* from Ouadi Haouach, NE Chad (G. van den Brink pers. comm.), although some captive Dama Gazelles (Al Ain Zoo) could be *N. d. dama* (T. Smith pers. comm.), and small numbers of *N. d. dama* were present at Al Wabra (Qatar) in the 1990s (T. Wachter pers. comm.). The number of founders is limited with 2 ♂♂, 10 ♀♀ and 5 ♂♂, 20 ♀♀, respectively (Sausman 1998, Thuesen 1998). Animals from Almeria (Spain) – stock originating from Western Sahara – were introduced to an enclosure (R'mila) near Marrakech (130 present in 2007; Cuzin *et al.* 2007) and gazelles from Munich Zoo (originally bred at Almeria) were released into an enclosure in Souss-Massa N. P. (12 animals in 2006 HCEF Rabat); these semi-captives are intended to form part of a reintroduction programme in Morocco (see also Wiesner & Muller 1998, Cuzin *et al.* 2007).

Elsewhere, Dama Gazelles (*N. d. mhor*) were released into the 2000 ha Bou-Hedma N. P. in Tunisia in the early 1990s (Abáigar *et al.* 1997), where around 17 were present in 2006 (T. Wachter pers. comm.), and gazelles (*N. d. mhor*) were reintroduced to Guembeul Faunal Reserve in Senegal in 1984 (Cano *et al.* 1993), although they have not fared well of late (Moreno *et al.* 2012); a reintroduction programme in Ferlo-Nord Reserve is underway. *Nanger d. ruficollis* has not been reintroduced and priority should be given to the conservation of the remaining wild populations.

Measurements

Nanger dama

N. d. mhor

HB (♀♀): 1118–1168 mm, n = 4*

Sh. ht (♂♂): 864, 914 mm, n = 2

Sh. ht (♀♀): 813–838 mm, n = 4*

WT (♂♂): 49.9, 57.7 kg, n = 2

WT (♀♀): 45.4 (42.7–46.3) kg, n = 4

Oregon Wildlife Center, animals originating from Western Sahara (D. Noble pers. comm.)

*Mean not given.

N. d. dama

HB (♂♂): 1520 (1440–1660) mm, n = 29

HB (♀♀): 1470 (1420–1550) mm, n = 14

T (♂♂): 306 (207–350) mm, n = 29

T (♀♀): 298 (270–315) mm, n = 13

E (♂♂): 190 (180–210) mm, n = 28

E (♀♀): 198 (180–210) mm, n = 14

Sh. ht (♂♂): 1120 (1025–1180) mm, n = 29

Sh. ht (♀♀): 1063 (1000–1100) mm, n = 14

WT (♂♂): 63.0 (46.0–75.5) kg, n = 25

WT (♀♀): 50.8 (42.0–61.5) kg, n = 13

Air Mts, Niger (Brouin 1950)

N. d. ruficollis

HB (♀♀): 1118–1218 mm, n = 7

T (♂♂): 203–254 mm, n = 4

T (♀♀): 203–254 mm, n = 7

E (♀♀): 200–320 mm, n = 7

Sh. ht (♂♂): 914–991 mm, n = 4

Sh. ht (♀♀): 864–914 mm, n = 7

WT (♂♂): 59.0 (55.4–72.6) kg, n = 4

WT (♀♀): 49.9 (44.9–55.4) kg, n = 7

Oregon Wildlife Center, descendants from animals captured in Chad (D. Noble pers. comm.); means not given

Maximum recorded horn length is 43.1 cm for a pair of horns from Oum Chalouba, Chad (Rowland Ward)

Key References Cano 1984; Dragesco-Joffé 1993; East 1999; Grettenberger & Newby 1986; Mallon & Kingswood 2001a (chapters therein); Mungall 1980.

Paul Scholte

GENUS *Ammodorcas*

Dibatag

Ammodorcas Thomas, 1891. Proc. Zool. Soc. Lond. 1891: 207, pl. 21, 22.

Ammodorcas includes only the Dibatag *A. clarkei*, confined to dry wooded habitats in the Somali–Masai Bushland BZ of Somalia and E Ethiopia. The genus was originally thought to be related to *Redunca* only because of the course of the horns, and was placed in the genus *Cervicapra* by Thomas (1891a); based on further samples, it was later amended by the same author to *Ammodorcas clarkei* (Thomas 1891b). Its affinities were later widely regarded as uncertain, and it was even placed in a distinct tribe, Ammodorcadini (see Ansell 1972, East 1999).

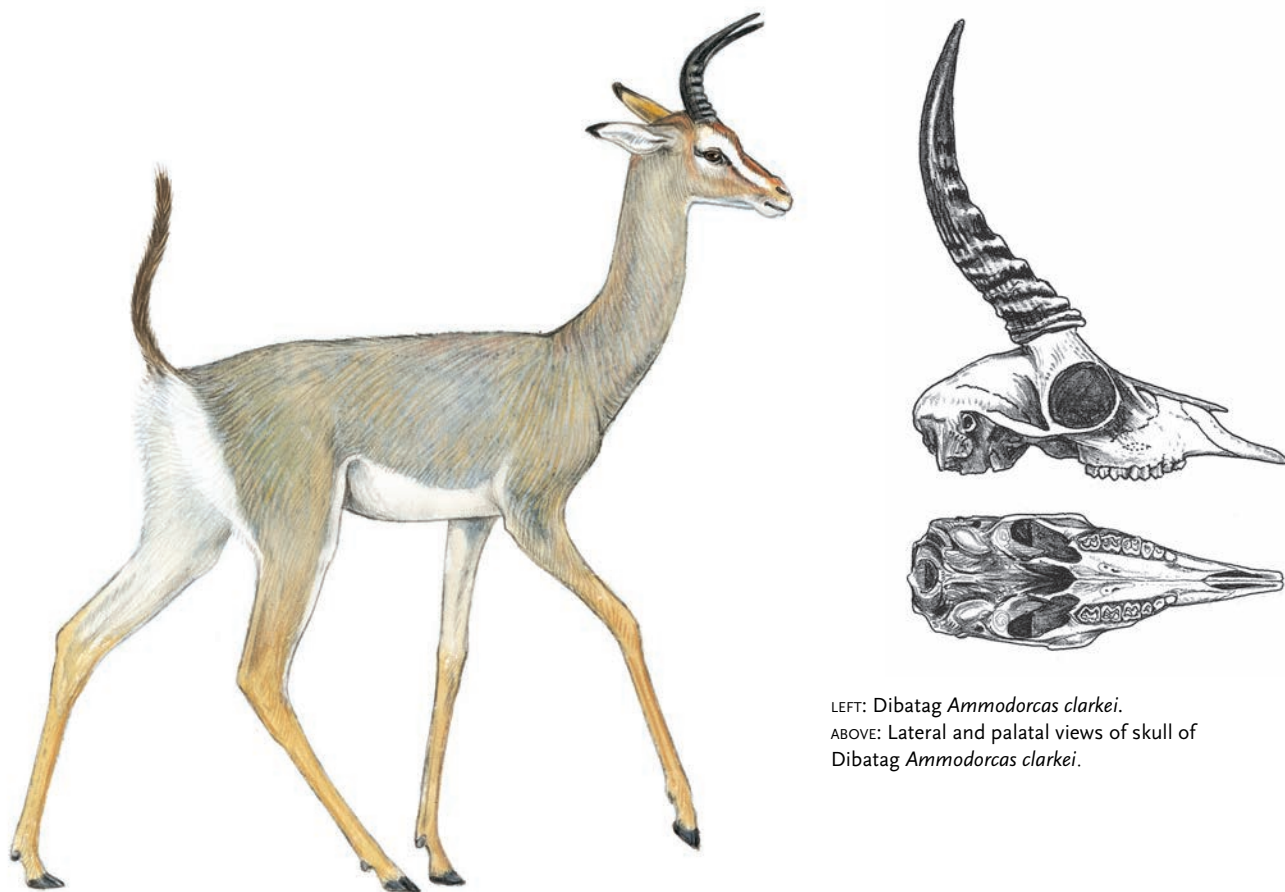
The Dibatag is very similar to the Gerenuk *Litocranius walleri* in facial pattern, proportions, brachyodonty and many cranial features; nevertheless, it differs significantly in the form of the horns, horn cores, tail, postorbital region of skull and basioccipital processes, as well as the absence of a two-tone flank-pattern and in lacking pedal glands (the latter feature unique among members of the Antilopini).

Peter Grubb

Ammodorcas clarkei DIBATAG (CLARKE'S GAZELLE)

Fr. Gazelle du Clarke; Ger. Lamagazelle (Stelzengazelle)

Ammodorcas clarkei (Thomas, 1891a). Ann. Mag. Nat. Hist., ser. 6, 7: 304. 'Northern Somali-land'; according to the collector Clarke (in Sclater and Thomas, 1898: 220), 'about three hours from "Bairwell" or about one day from "Buroa Well, Habbergerhagi's country"' (N Somalia, vicinity of Burao and Ber).



LEFT: Dibatag *Ammodorcas clarkei*.
 ABOVE: Lateral and palatal views of skull of
 Dibatag *Ammodorcas clarkei*.

The now widely used vernacular name 'Dibatag' derives from Somali *dabu* 'tail' and *tag* 'erect'.

Taxonomy Monotypic. Synonyms: none. Chromosome number: not known.

Description Medium-sized, graceful antelope similar in appearance to the Gerenuk *Litocranius walleri*, with slender body and elongated neck and legs. Head small, flat, wedge-shaped and pointed. Eyes large, ears medium-sized, broadly lancet-shaped with dark, rounded tips. Lips very mobile, with the upper lip slightly elongated, and mouth opening very small. Facial markings strongly marked and gazelle-like; there is a chestnut-brown streak from the crown along the bridge of the nose to the nostrils, on both sides paralleled by a distinctive white stripe, circling the eyes and running down to the nostrils (these are bordered by a narrow chestnut band from the preorbital glands to the muzzle). Pelage short, smooth and very soft. Dorsal pelage and flanks uniform cinnamon-brown to rufous, but may appear silver-grey depending on the incidence of sunlight. There is a white spot at the throat. No dark band on the

flanks or buttocks. The underparts and insides of the legs are white. The tail is rounded and long, dark in colour, reaching the hocks, and is well furred but with no distinct tassel. Insides of the ears have a branched black pattern, similar to other gazelles; the lower fringe of the ear, towards the tip, has an inward curved lobe (distinct from the Gerenuk). Lateral (false) hooves are small. Preorbital and carpal glands present, the latter with hair tufts; pedal and inguinal glands absent. Females are slightly smaller than ♂♂, and have two pairs of inguinal nipples.

Horns present in ♂ only, reedbuck-like, basal half with 6–10 large and well-spaced annuli, and angling back from forehead; terminal half smooth, curving around with pointed tips facing forward. Horn cores are grooved, with transverse ridges marking annuli of overlying horn sheath, not supported by pedicular extensions of the frontal bones. The skull is long and shallow; premaxillae long, tapering to very narrow tips, and extending back to reach (or almost reach) the long nasals. An ethmoid fissure is present. Preorbital fossa shallow without marginal ridges. There are prominent basioccipital processes. The median incisiform teeth are broad, the remaining pairs narrow with third incisors narrowest.



Geographic Variation None recorded.

Similar Species

Litocranius walleri. Sympatric in E and C Somalia and SE Ethiopia (Ogaden). Two-tone body colouration; horns in ♂ thick and strong and S-shaped; tail with distinct tassle. Generally flees headlong with tail never upright.

Distribution Endemic to the Ogaden region of SE Ethiopia and adjoining semi-arid to arid lowlands of C Somalia.

Historical Distribution Southern parts of N Somalia throughout SE Ethiopia and C Somalia between coastline of the Indian Ocean and Fafan R. in the west and the Shebelle R. in the south-west (Funaioli 1958, Schomber 1966). Rock drawings of two Dibatags on the west bank of the Nile, north of Aswan, suggest a southwards retreat of this species in the Ite Predynastic period of Egypt (Osborn & Osbornová 1998).

Current Distribution The Dibatag has disappeared from substantial parts of its former range, and is reported in viable numbers only from the Ogaden south of Degeh Buur down to the northern foothills of the Shebelle R. (Wilhelmi 1997). Repeated sightings from Kebri Dehar and Warder District indicate an east- and southward distribution up to the Somali border and into the Hiiran region of S Somalia (H. Kaariye pers. comm.). In 1988, reported by pastoralists as present in Bay Region and west of the Juba R. in S Somalia (T. Thurow pers. comm.), but not verified by the author's own extensive ground and aerial survey in 1987 and 1988. Their possible persistence in the coastal hinterland of C Somalia has been discussed by several authors (Funaioli 1971, East 1999), and was confirmed in 2005 (N. Dougherty pers. comm.).

Habitat Dibatags inhabit semi-arid dense to scattered bush, low- to medium-height thornbush savanna and plains with thicket/grassland mosaics. They prefer sandy to moderately gravelled, ferrous oxide-rich

red soils, characterized by numerous termite mounds. Occasionally, Dibatags visit treeless grasslands (Meester 1960). Their occurrence is assumed to be correlated with the presence of *Commiphora* shrubland (Lawrie 1953) and probably associated with areas very far from any form of present and historical shifting cultivation (T. Thurow pers. comm.). They have an altitudinal range of approximately 200–1200 m (Yalden *et al.* 1984, 1996). No significant seasonal changes in habitat preference are evident.

Abundance Based on the results of Scott's expedition in 1959, the population size was estimated at approximately 12,000 individuals with an average density of 1 animal/km² (Schomber 1966). After three decades of political unrest and armed conflicts, East (1999) cautiously estimated a total population in the low thousands (East 1999). The current author estimates the population in the C Ogaden (about 46,000 km²) to be a maximum of about 4000 individuals. If security in the area improves, standardized counting methods or even aerial surveys may allow for more reliable estimates. Since Dibatags are very secretive, it is likely that actual population numbers are higher than currently believed.

Adaptations Dibatags are well adapted to their semi-arid environment. They probably obtain their water requirements from food alone, and indeed there are no records of them drinking water in the wild. The long neck and the ability to stand like Gerenuks on their hindlegs, with forefeet in the branches of a tree, enable them to reach a considerable height when browsing. The long upper lip facilitates browsing in thorny vegetation. The body shape and colouration of Dibatags render them practically invisible as they hide behind vegetation, remaining motionless while keeping track of potential threats. Once discovered, they bound away in an ambling gait with upright neck and tail erect like an antenna – hence the Somali name; galloping is reserved for true emergencies. Pronking is performed when alarmed, but is more often seen in a playful burst of motion.

Foraging and Food Primarily browsers (Gagnon & Chew 2000), Dibatags feed on foliage and young shoots of trees and shrubs using their flexible lips and front teeth to pluck or bite off leafy material. The diet includes species such as *Commiphora* (myrrh trees), *Acacia*, *Boscia*, *Dichrostachys* and *Maerua* spp. (Meester 1960). Animals most likely congregate seasonally in areas with foliated *Commiphora* stands due to the high water content of leaves and shoots (Maydon 1957). Young, soft grass is taken following the onset of the rains (Swayne 1895). In the dry season various fruits, flowers and buds of trees, shrubs and tall herbs are preferred. More than 60 browse species have been identified in the diet; the lack of any clear dietary specialization does not help explain the species' restricted distribution.

Social and Reproductive Behaviour Very little information is available regarding social and reproductive behaviour in the wild (Meester 1960). Dibatags are vagrants throughout most of the year, foraging within a confined area. They probably maintain temporary defended territories at favourite sites demarcated by secretions from the preorbital glands, urine and faeces (Walther *et al.* 1983). They defecate at regular points forming dung piles (Wilhelmi 1997). Fighting techniques to defend territories have not been described and not yet observed by the author. Dibatags move in family parties

of 3–6 individuals, comprising only one adult ♂, in pairs, or solitarily; groups of more than four individuals are now very rare. N. Dougherty (pers. comm.) observed three sightings of larger mixed groups of 20, 15 and 8 individuals on the Somali coastal plain just north of the town of Jariban; these probably comprised an amalgam of several loosely associated smaller groups. Loose associations with Gerenuks and Soemmerring's Gazelle *Nanger soemmerringi* have been reported (Schomber 1966), although there are other reports of Dibatags actively avoiding Gerenuks (F. Wilhelmi pers. obs.).

Courtship and mating behaviour has only been observed in detail with a captive pair at the Zoo of Naples, and parts of the 'mating march' have been observed in the field by the author. Behaviour appears to be similar to that of the Gerenuk (Walther 1963). The ♂ marches behind the ♀ in erect posture with the nose lifted. Laufsclag (leg tapping) is exceptionally ritualized and pronounced. Standing close behind the ♀, the ♂ slowly raises a straightened foreleg between her hindlegs until contact is made. Prior to any mating attempt, the ♂ marks the ♀ on her chest, back and rump with the preorbital glands. This behaviour is, with the exception of the Gerenuk, otherwise unrecorded in the Antilopini (Walther 1958, Estes 1991a). Flehmen, nosing of female genitalia and mutual urine testing are part of courtship behaviour. Copulation takes place with the ♂ walking upright behind the moving ♀, with his forelegs dangling. Following parturition, young lie out concealed for one to two weeks and the nursing ♀ remains close to it during dependence.

Reproduction and Population Structure Females are thought to give birth from Sep to Nov to a single young after a gestation period of 6–7 months (Dittrich 1972, Walther 1990). Young are also reported in Jun and Jul (Meester 1960), thus rutting seems to be correlated with the onset of rain in different parts of the distribution range. Further details on reproduction, longevity and population structure not known.

Predators, Parasites and Diseases Large cats and Spotted Hyenas *Crocuta crocuta*, still present in the Ogaden, are probably

the most important predators. Black-backed Jackals *Canis mesomelas*, Caracals *Caracal caracal* and large eagles probably prey on young. Ticks (*Rhipicephalus parvus*, *R. pulchellus* and *Hyalomma detritum*) and filarial worms (*Artionema* spp.) have been reported from hunted Dibatags (Meester 1960). Nothing is known concerning other diseases. Captive individuals suffered from pneumonia (Schomber 1966).

Conservation IUCN Category: Vulnerable A2cd. CITES: Not listed.

Numbers of Dibatags have been severely affected by habitat degradation (due to excessive numbers of livestock), drought and overhunting. While their status appears to be precarious, its alertness, flight distance and the difficulty of hunting it in dense bush have enabled it to survive locally in viable numbers. In Ethiopia the species is legally protected from hunting, yet it does not occur in any protected areas, and enforcement of protective measures is needed. Given that this species is not known to occur in any formal protected areas in any part of its range, initiation of action to conserve this species is a very high international priority in antelope conservation. No Dibatags are known to be held in captivity.

Measurements

Ammodorcas clarkei

HB: 1030–1170 mm

Sh. ht: 800–900 mm

T: 300–360 mm

WT (♂♂): 20.0–35.0 kg

WT (♀♀): 22.0–29.0 kg

Somalia (Schomber 1966)

Maximum recorded horn length is 33.0 cm for a pair of horns from Somalia (Rowland Ward)

Key References East 1999; Meester 1960; Schomber 1966; Walther 1963; Wilhelmi 1997.

Friedrich K. Wilhelmi

GENUS *Litocranius*

Gerenuk

Litocranius Kohl, 1886. Ann. K. K. Naturhist. Hofmus. Wien 1: 79.

Litocranius includes only the Gerenuk *Litocranius walleri*, confined to the Somali–Masai Bushland BZ in dry wooded habitats. The species was mistakenly described as 'a new species of Gazelle from Western [sic] Africa'. There is some controversy about the spelling of the generic name: '*Lithocranius*' (= stony skull) is said to relate to the hard braincase. The original (and probably correct) spelling *Lito-* refers to the small size and relative flatness of the skull, compared with that of other Gazelles (cf. discussion in Schomber 1966).

Gerenuks are medium-sized antelopes (with a shoulder height up to about 100 cm, and mass of up to about 50 kg) similar in proportions to the Dibatag *Ammodorcas clarkei*. However, *Litocranius* differs from *Ammodorcas* in the more extreme specialization of skull, shorter

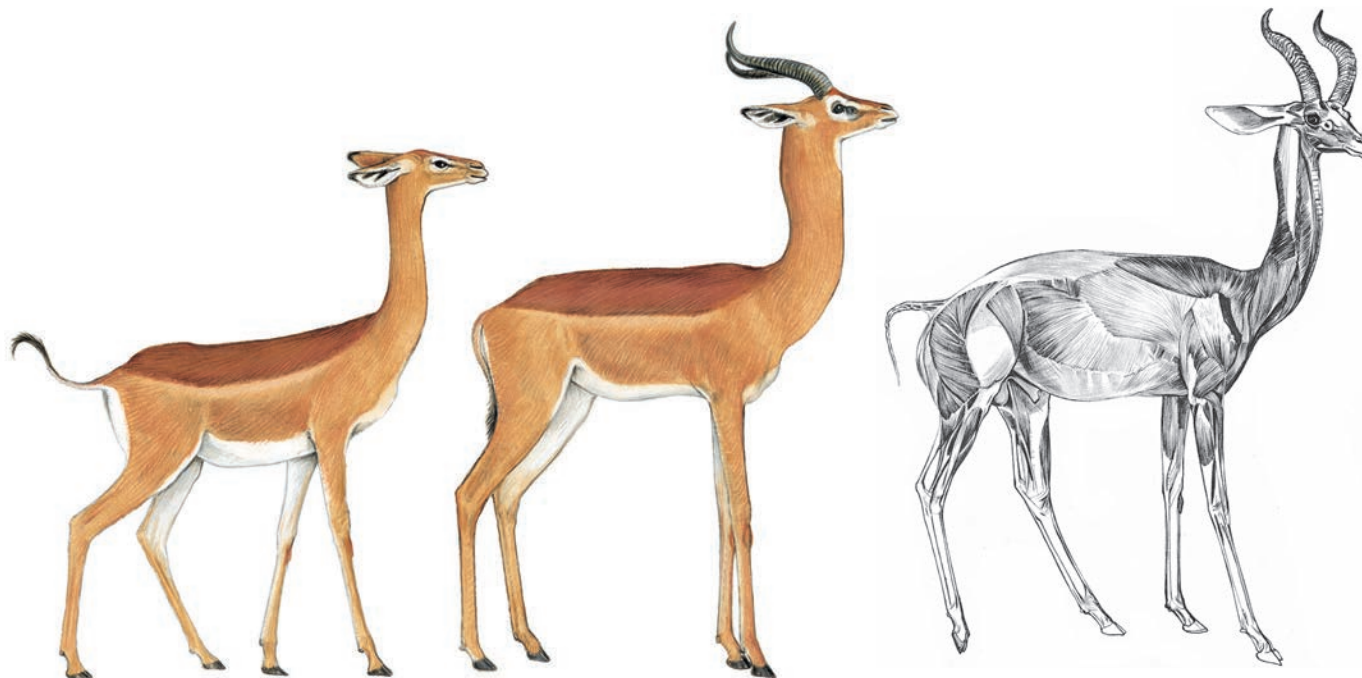
premaxilla, different horns and horn cores, presence of pedal glands, and a tufted tail. The Gerenuk differs from gazelles in its elongated body proportions, great elongation of the skull (gazelles being characterized by the shape of the cranium that does not narrow to form a projection, but is more rounded and the depression in front of the orbit is not fenestrated), low-crowned cheekteeth, close annulation of the horns, lack of inguinal glands, presence of two pairs of inguinal nipples, and colour pattern. Gerenuk regularly adopt a markedly upright bipedal feeding position that, together with their long limbs and neck, allow access to forage otherwise unavailable to a ruminant of its mass.

Peter Grubb

Litocranius walleri GERENUK (WALLER'S GAZELLE)

Fr. Gazelle-Girafe (Gazelle de Waller); Ger. Giraffengazelle (Gerenuk)

Litocranius walleri (Brooke, 1879). Proc. Zool. Soc. Lond. 1879: 929, pl. 56. '... mainland of Africa, north of the island of Zanzibar, about lat. 3° and long. 38°'. This was originally assumed to be in SE Kenya, but first specimens were later shown to have come from S Somalia, 'coast near Juba River' (Sclater & Thomas 1899). Type locality now accepted as 'the vicinity of Chisimaio' in S Somalia (Grubb 2002).



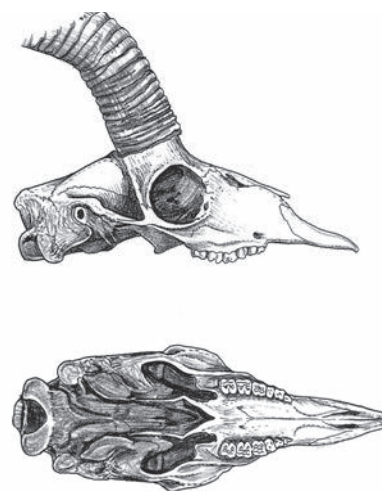
Gerenuk *Litocranius walleri* female (left) and male (right).

Gerenuk *Litocranius walleri* male myology.

The common name is derived from Somali (or other local) language, meaning 'giraffe-necked' (Simon 1962).

Taxonomy The first specimens (three skulls) of this animal were brought to England by one Gerald Waller, who obtained them from his brother (deceased in East Africa), hence the species name. Two subspecies have been named, the southern *L. w. walleri* and the northern *L. w. sclateri*, but their geographic separation has been unclear. Schomber (1966) called the Gerenuk a good example of a species with a discontinuous distribution and hence two clearly separable subspecies, but this was erroneous. The data available to him fortuitously included no records of Gerenuks from the area between the Galana and the Tana Rivers in Kenya, where the species is actually quite common. According to Schomber, the northern subspecies was somewhat larger than the southern one, which is confirmed by Grubb (2002) in his revision of the subspecies of the Gerenuk. Synonyms: *sclateri*. Chromosome number: $2n = 60$ ($FN = 60$) (Wurster & Benirschke 1968).

Description Extremely slender antelope with very long legs and an exceptionally long neck; head small with pointed, hairy muzzle and highly mobile lips. Eyes large, and surrounded by a whitish eye-ring. Ears fairly large with dark tips and black leaf-shaped markings on the inside. Facial pattern is indistinct: two whitish stripes separated by dark stripe from eye to muzzle; adult ♂♂ have a pronounced black spot around the orifice of the anteorbital gland. The centre of the



Lateral and palatal views of skull of Gerenuk *Litocranius walleri*.

face is fairly dark, and crown of ♀♀ blackish. Throat pale, tending to white. General body colour reddish-brown with a cinnamon tinge; back darker and sharply delimited against the flanks. No dark stripe along the sides. Underparts, inside of legs and buttocks white, clearly separated from brown parts. As a curiosity, an all-white adult male Gerenuk was observed in three consecutive years (1964–66) in the then Marsabit National Reserve in N Kenya (Kayser 1970). There are dark hair tufts on the 'knees'. Lateral (false) hoofs are minute. Tail of medium length with tapering terminal tuft of dark hair. Anteorbital

(functional probably in ♂♂ only), pedal and carpal ('knee') glands are present, but there are no inguinal glands. The neck in adult ♂♂ is considerably thicker than in ♀♀ and does not taper toward the head; the back in adult ♂♂ is often somewhat slanting.

Horns are found in ♂ only, and are blackish, rather thickset, lyrate, with tips curved forward; the spread is quite variable. The anterior surface of the horns is heavily ringed. Horn cores are smooth, with no ridges, and grooves only on the posterior surface; horns are not raised on pedicular extensions of the frontal bones. Skull is elongated and shallow with long slender jaws. Basicranium is very broad. Occiput is relatively flat on top, and sharply angled posteriorly compared with the more rounded cranium of other gazelle species; this appears to have been the principal basis for the separate generic name. The angle is even visible in living animals, particularly adult ♂♂, in lateral view (e.g. Fig. 15 in Schomber 1966). The premaxilla does not reach the long nasals. Preorbital fossae are shallow without marginal ridges. Median incisiform teeth are broad, remainder narrower but with both second incisors and canines somewhat broader than the third incisors; cheekteeth are low crowned.

Geographic Variation

L. w. walleri: NE Tanzania, Kenya, S Somalia and S Ethiopia. Smaller, with shorter cranial measurements (see Grubb 2002).

L. w. sclateri: restricted to the northernmost parts of the species' range (Djibouti, N Somalia, adjacent parts of Ethiopia). Larger (see Grubb 2002).

The subspecies have been said to differ in colouration (Neumann 1899), but this was not confirmed in the study by Grubb (2002), although the latter author did draw attention to a band of reversed hairs directed towards the head on the dorsal mid-line of the neck present in seven skins from Tanzania, Kenya and S Somalia (but absent in 12 skins from N Somalia) and that may have potential systematic significance.

Similar Species

Ammodorcas clarkei. Range overlaps entirely with that of the Gerenuk, but found only in E and C Somalia and SE Ethiopia (Ogaden) with a preference for more open habitat. Very similar in general appearance, especially ♀, but smaller, colouration more greyish (and lacking the two-tone body colouration), uniform on flanks, turning to reddish on legs and parts of head; tail blackish, carried upright in flight; horns (in ♂ only) shorter and sharply curved forward, as in reedbuck (*Redunca* spp.).

Aepyceros melampus. Sympatric only in East Africa. Similar colouring, but lacks the elongated legs and neck and has prominent dark thigh stripes; horns in ♂♂ noticeably longer.

Distribution Endemic to Africa. The Gerenuk is confined to the Somali–Masai Bushland BZ, mainly the 'Horn of Africa'. Its range extends from ca. 11° 30' N in S Djibouti (Künzel *et al.* 2000, Laurent & Laurent 2002) through E and S Ethiopia, much of Somalia, most of Kenya (except W and SW) to NE Tanzania. The southern limit lies in or near Tarangire N. P. in Tanzania, at ca. 05° 30' S. In the west the range extends to the east slope of the Great Rift Valley, and locally into it, to ca. 36° E. Information on occurrence of Gerenuk west of L. Turkana is conflicting, with some recent affirmative reports (Grunblatt *et al.* 1996, M. Dioli pers. comm.); in SW Ethiopia it



Litocranius walleri

is not recorded from west of the Omo R. (Yalden *et al.* 1996). In E Kenya, the Gerenuk's range is continuous, as far as habitat conditions are suitable.

Within recent history the Gerenuk's range has probably not changed much, except locally. In Kenya, the Gerenuk apparently disappeared from the vicinity of L. Baringo in the Rift Valley around the end of the nineteenth century (Stewart & Stewart 1963). More recently, local populations have decreased or even been eradicated in various areas through human encroachment (see Conservation).

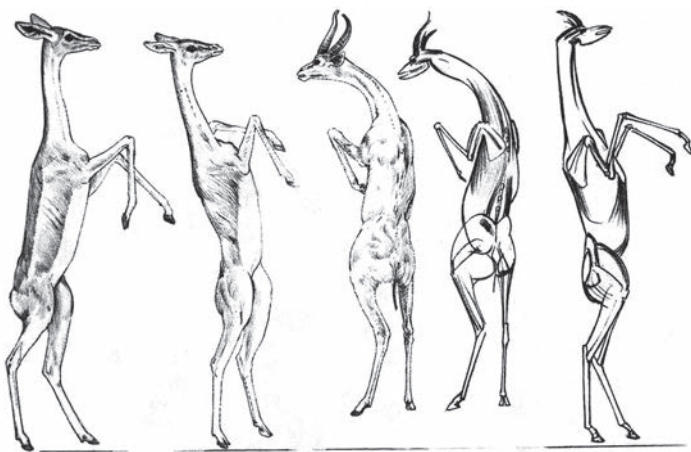
Rock paintings and engravings of animals resembling the Gerenuk, found in Egypt, have been interpreted as indicating a much wider distribution in prehistoric and Predynastic times (e.g. Fig. 2 in Schomber 1966, Kingdon 1982, Osborn & Osbornová 1998; and see Manlius 2002).

Habitat The Gerenuk inhabits a variety of habitats that can all be characterized as semi-arid to arid, with some degree of woody cover. Colloquially called 'thorn bush', these habitats range from almost semi-desert to fairly dense woodlands and patchy thickets, notably of the *Acacia–Commiphora* type widespread in the Gerenuk's range. A certain proportion of shrubs, rather than trees only, are essential, and this is closely tied to the species' feeding habits (see below). Dense woodlands, for example, near rivers, are generally avoided, as are very open grass-dominated habitats, particularly areas with long grass (Leuthold 1978b). Reduction of woody cover through fire, elephants (as in Tsavo N. P., Kenya) or human activities may have led to a decline of Gerenuk populations locally (see Conservation). On the other hand, the species may benefit from encroachment of trees and shrubs due to overgrazing in some areas (Simon 1962).

The Gerenuk is largely confined to relatively flat areas and does not usually enter hilly country. It inhabits lowland areas up to an altitude of 1200–1600 m (Stewart & Stewart 1963, Yalden *et al.* 1996), except for coastal regions with unsuitable habitats. Water is not an essential requirement for the Gerenuk.

Abundance Because of its preferred habitat, small group size and somewhat cryptic colouration, the Gerenuk is difficult to census, both from the ground and – even more so – from the air. Figures on density and abundance thus have to be evaluated with some caution. Aerial surveys have suggested an estimated mean density of ca. 0.05 animals/km² (e.g. East 1999), a substantial underestimate for reasonably favourable habitats. Aerial counts near Amboseli N. P., Kenya, resulted in density figures of 0.2 ind/km² as a maximum (Grunblatt *et al.* 1995). In Tsavo N. P., mean density derived from road counts was 0.5–1 ind/km², with considerable variation between habitat types, but only minor seasonal differences (Leuthold 1978b). Densities may be considerably higher in areas with particularly favourable habitats, for example, up to 8 ind/km² in Samburu G. R., Kenya (Räder 1982, 1989).

Recent population estimates, derived mainly from aerial counts, add up to a total of 24,000 animals (East 1999), which is probably a substantial underestimate of actual numbers. Using correction factors for undercounting in aerial surveys, East (1999) revised the total population estimate to 95,000 animals over the species' entire range. The largest surviving populations occur in SW Ethiopia and the northern and eastern rangelands of Kenya, although East (1999) noted that the estimated total Kenyan Gerenuk population had decreased by about 50% since the 1970s.



Gerenuk *Litocranius walleri* female and male in bipedal posture.

Adaptations The most striking features of the Gerenuk are its very long neck and legs, which are similarly developed only in the Dibatag *Ammodorcas clarkei*. The skeletal basis consists of an elongation of the cervical vertebrae and the metacarpal and metatarsal bones (Richter 1970). In addition, the Gerenuk shows a phenomenal ability to rise up on its hindlegs and feed at up to 2 m above ground level. Basically, all ungulates can rise onto their hindlegs (they do it when mounting), but the Gerenuk is extreme in reaching a very erect bipedal posture that it can maintain for a considerable time. This erect stance is facilitated by some modification of the lumbar vertebral spines (Richter 1970). While feeding bipedally a Gerenuk may, but does not need to, rest its forelegs on the tree/bush being browsed, and it can even do several steps sideways on its hindlegs only. The Gerenuk uses this ability much more frequently than a few other ungulates that possess it, too (e.g. dik-diks of the Kirk's Dik-dik *Madoqua kirkii* complex), and several individuals may feed side by side in a bipedal stance. Occasionally, they may even pull down a branch with a foreleg for better reach (Räder



Gerenuk *Litocranius walleri* head myology.

1982). The ecological advantage of all this is to permit the Gerenuk to gather food at higher levels than animals of similar weight with more 'normal' proportions, an important aspect of ecological separation (Leuthold 1978a). As further adaptations to feeding from trees and shrubs, particularly thorny ones, the Gerenuk's muzzle is rather narrow and pointed, and the lips and tongue are highly mobile, enabling the animals to pluck small leaves from among thorns of, for example, *Acacia* trees. These characters, coupled with the long and pliable neck, make possible the Gerenuk's highly selective feeding style. Sensory hairs on various parts of the head may help avoid injuries to the eyes from thorns or twigs.



Gerenuk *Litocranius walleri* frontal view of head.

As in some other browsers, the stomach of the Gerenuk is characterized by a small rumen, omasum and abomasum, but a large reticulum. These features are related to its food choice (see following section), implying a quick turnover and a high fermentation rate, in contrast to the situation in grazers (Hofmann & Stewart 1972). In structure (and function) the Gerenuk's stomach is very similar to that of the Giraffe *Giraffa camelopardalis*, providing a good example of convergent evolution (Hofmann 1973). Also related to the Gerenuk's feeding habits are the relatively low crowns of the molar teeth, compared with the much higher ones of grass-eating relatives, and the spoon-shaped, sharp-edged incisors.

The Gerenuk appears to be entirely independent of free water. There are no well-documented observations of a Gerenuk drinking, not even in captivity (Schomber 1966). Evidently, the animals can satisfy their water requirements entirely from their food. The 'capacious, heavily papillated ruminoreticulum [forms] ... an ideal substrate for water absorption' (Hofmann 1973).

While undisturbed, a Gerenuk walks slowly, with fairly long steps; when alarmed it uses a somewhat slinking pace, which quickens into a bouncing gallop in full flight. The latter is reminiscent of the 'stotting' of Thomson's Gazelle *Eudorcas thomsonii*, but not as pronounced. Sometimes the hair of the perineal area is spread in flight, forming a white rump patch.

In the relatively hot climate of the Gerenuk's range, regulation of body temperature may be a potential problem. Daytime activity patterns vary widely from day to day and between seasons. In Tsavo N. P., the mean proportions of foraging time are 47% (range 32–64%) in adult ♂♂ and 60% (range 51–68%) in adult ♀♀, the latter probably being higher because of additional requirements for pregnancy and/or lactation. Conversely, ♂♂ spend more time (25%) ruminating than ♀♀ (15%). An alternation between foraging and ruminating bouts is apparent but not very pronounced. Movements and foraging time are reduced in very hot weather, when the animals may remain in the shade of trees or bushes. In cool conditions, and especially during rain, a Gerenuk may lie down. This reduces the surface exposed to heat loss (Leuthold & Leuthold 1978b). Nocturnal activities vary with light conditions, being lower in very dark nights. In Samburu G. R., the

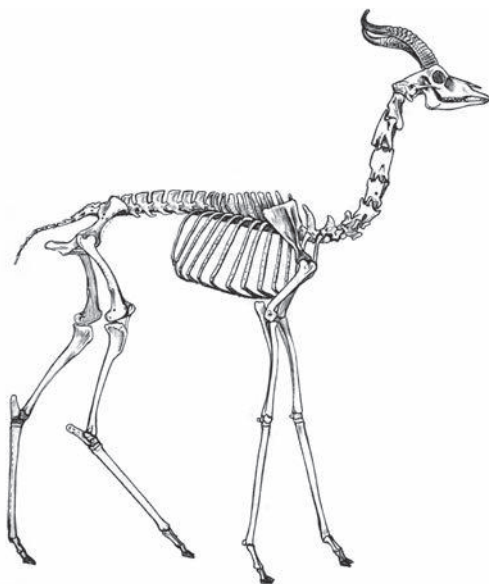
animals usually move to areas of more open vegetation for the night, which presumably facilitates detection of predators (Räder 1982, 1989).

A behavioural adaptation related to the great length of the neck entails a slight modification of fighting technique in the Gerenuk, compared with that of other antelopes (see Social and Reproductive Behaviour). The elongation and relative flatness of the cranium can also be seen in this context (Kingdon 1982).

Foraging and Food The Gerenuk is one of the most exclusive browsers among bovids, i.e. eating leaves, flowers and occasionally fruits of broad-leaved (dicotyledonous) plants only. No grass was recorded among over 5000 food items identified in Tsavo East N. P. (Leuthold 1978b) or in stomach contents examined by Hofmann & Stewart (1972). Indeed, in their review of the dietary preferences of African bovids, Gagnon & Chew (2000) classified Gerenuk as browsers, with a diet comprising as much as 95% dicotyledons and 5% fruit; this is largely mirrored by studies involving stable carbon isotope analysis (Cerling *et al.* 2003).

Gerenuks utilize a wide range of food plants, with over 80 plant species recorded as being eaten in Tsavo East N. P. The great bulk of the food consists of leaves of trees and shrubs, with considerable seasonal variation. Many of the woody plants typical of the Gerenuk's habitat are deciduous, shedding their leaves during the – often very long – dry seasons. In the wet season a considerable number of climbers and vines grow leaves, which in Tsavo East N. P. may constitute up to 25% of the Gerenuk's diet (e.g. *Thunbergia guerkeana* and several species of Cucurbitaceae). Woody plants commonly eaten at that time include *Premna resinosa*, *Bauhinia taitensis* and several species of *Acacia* and *Commiphora*. In the dry season leaves of trees and shrubs make up 95% or more of the diet, including mainly evergreen species, such as *Thylachium thomasi*, *Boscia coriacea* and *Salvadora persica*. The extent of seasonal variations depends on the composition of the available vegetation and the local and temporal distribution of rainfall. In Samburu G. R., where *Acacia* species are much more abundant, these constituted the bulk of the Gerenuk's food, and no climbing plants were recorded as being eaten (Räder 1982).

Particularly in the dry season, the Gerenuk appears to be highly selective with respect to plant parts eaten. The evergreen species mentioned above have rather coriaceous leaves, and a Gerenuk often 'sniffs over' the plants at some length before accepting anything. Conversely, some of the climbers taken in the wet season clearly appeared to be 'sought-after'. Presumably, this behaviour serves to optimize protein – and perhaps water – intake. When available, the fruits of *Solanum incanum* ('Sodom Apple') are also consumed in some quantity, constituting up to 30% of solid stomach contents (Hofmann 1973). As they are round and fairly hard, they have to be chewed at some length, which makes feeding on them very obvious to the observer. This is also a situation in which a Gerenuk may collect food items extensively at or near ground level. Leaves of the trees *Melia volkensii*, *Sterculia* spp. and the slightly succulent shrub *Euphorbia scheffleri* seem to be rejected entirely (although eaten by Lesser Kudu *Tragelaphus imberbis* and Giraffe). The seasonal changes in plant condition and availability are the probable reason for at least small-scale seasonal movements related to vegetation type and stratification (Figs 3 & 4 in Leuthold 1978b; and see Räder 1982).



Gerenuk *Litocranius walleri* skeleton.

Young animals appear to develop their specific feeding habits by closely following their mothers and consuming plant material eaten by those. A young Gerenuk raised in captivity together with a young Lesser Kudu ate several plant species not recorded as being eaten by free-ranging Gerenuk, evidently as a result of imitating its companion (Leuthold 1971a).

Social and Reproductive Behaviour The Gerenuk lives singly or in small groups rarely exceeding 5–6 animals. Groups of 25–30 animals (Schomber 1966) appear to be highly exceptional and may be temporary aggregations caused by favourable feeding conditions. Group size, composition and stability vary between populations of different densities. In Tsavo East N. P. (low density), mean group size was ca. 2.5, with a maximum of 13 and did not vary seasonally (Leuthold 1978c). Animals of different sex/age classes associate in various combinations. Apart from the mother–young bond, there appear to be few stable associations. Subadult ♂♂ tend to join up with ‘peers’ to form loose groupings that may persist for some time. Adult ♂♂ occur singly more often than expected on the basis of their proportion in the population, suggesting territoriality. In Samburu G. R. (high density), groups of both ♀♀ and subadult ♂♂ are somewhat larger, more stable and tend to develop a rank order based mainly on age (Räder 1982, 1989, 1998).

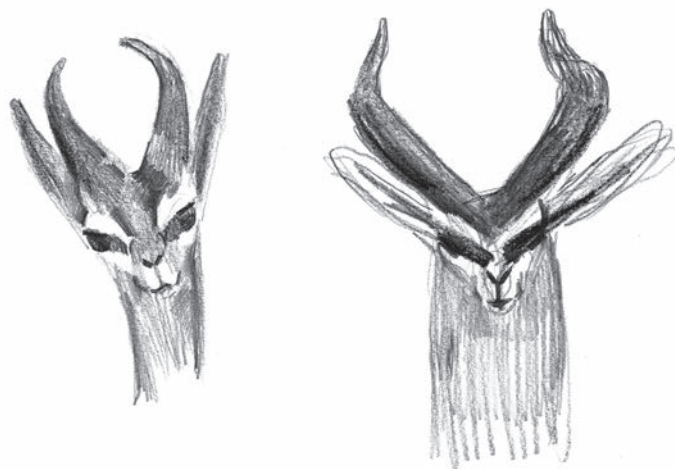
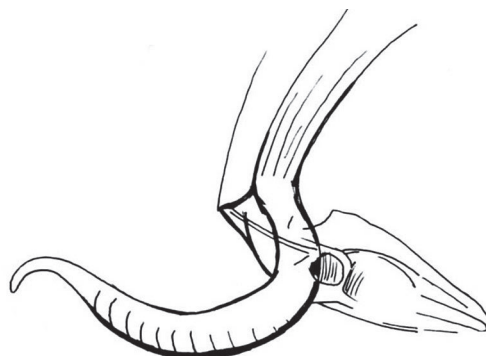
Home-ranges of individually known animals measured 1.5–3.5 km² and were occupied year round. Those of six adult ♂♂ in one area averaged 2.5 km² and showed little or no overlap. Behaviour associated with territoriality includes intolerance of other adult ♂♂, a striking defecation posture and scent-marking with anteorbital glands. Only adult ♂♂ adopt a strongly crouched posture for defecation, which is usually preceded by sniffing the ground and/or scraping it with a forefoot. Often old dung is present at a defecation site, suggesting the formation of dung heaps with a possible olfactory significance (Leuthold 1978c). However, large amounts of dung, as in some other species, do not accumulate.

Adult ♂♂ mark protruding stems and twigs of trees and shrubs with a tar-like secretion of their anteorbital glands (Fig. 21 in Leuthold 1977). The sites are sniffed at before marking and are often used repeatedly, so that small ‘tar balls’ accumulate. The marking sites are concentrated at a height of 105–125 cm above ground and occur

almost exclusively on plant species that are eaten by the Gerenuk. In one case examined in detail, scent-marks were arranged in an oval-shaped polygon, measuring 30 and 12 ha in consecutive years, with additional ones ‘radiating outward’ (Gosling 1981). All these characteristics may ensure a high probability of the markings being detected, irrespective of their function, which remains unclear.

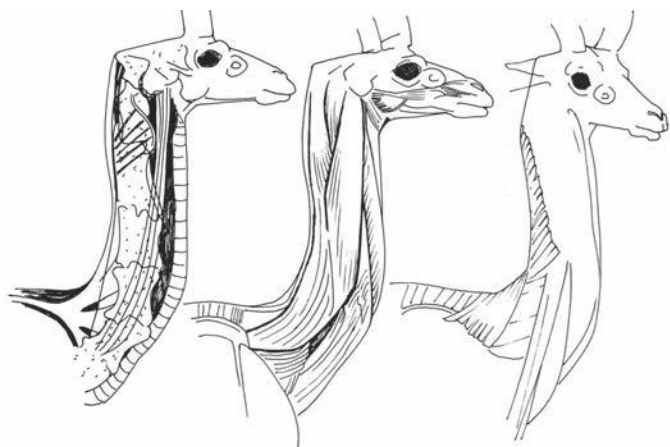
Thus, adult ♂♂ are territorial, whereas ♀♀ have individual home-ranges that may overlap with those of other ♀♀ and the territories of one or several ♂♂. In Samburu G. R., several ♀♀ share the same home-range, which is essentially congruent with the territory of one ♂♂. Subadult ♂♂, individually or in small groups, also occupy home-ranges overlapping those of other individuals. As they grow older, they are increasingly harassed by territorial ♂♂. Overall, the social organization of the Gerenuk resembles that of several other small antelope species (SO-type 4 of Leuthold 1977). Apart from olfactory marking with urine, faeces and the secretion of anteorbital glands, territories may be advertised visually by ♂♂ standing upright on elevated spots such as termite mounds (Fig. 9 in Leuthold 1978c).

In mixed groups adult ♂♂ are clearly the most dominant individuals, from which other animals withdraw in situations of possible conflict. However, they do not usually initiate or lead a group’s movements but

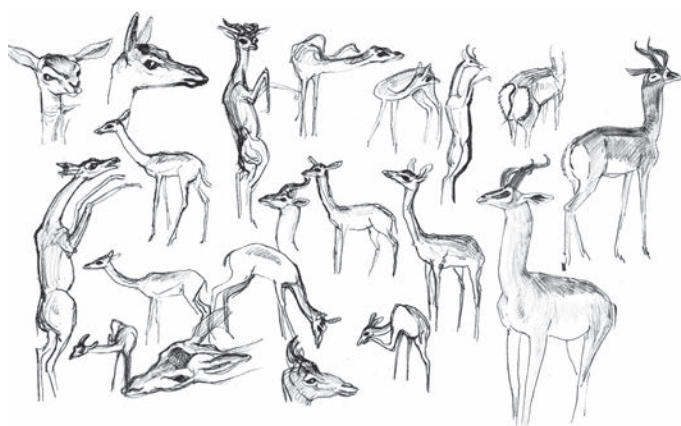


Gerenuk *Litocranius walleri* sketches of subadult and adult male head silhouettes. Clues to rank?

Gerenuk *Litocranius walleri* diagram of leverage and reinforcement in skull and horns.



Gerenuk *Litocranius walleri* diagram of head-neck articulation and neck musculature.



Gerenuk *Litocranius walleri*.

tend to trail behind. Agonistic behaviour includes shrub-horning, i.e. thrashing branches of shrubs or small trees with the horns, and possibly horning the ground, though the latter has been observed only in captivity (Walther 1968). Serious fighting is observed rarely in the wild because of the rarity of encounters between adult ♂♂. Subadult ♂♂ often engage in sparring or play-fighting, and this is accompanied by other playful elements (e.g. cavorting, feinting). These behaviours look particularly 'graceful' in the Gerenuk because of its long limbs and neck. They are accompanied by much head-jerking, head-low threats, and occasional 'facing away' (head upright, turned sideways), as well as vigorous tail-swishing. Actual fighting among adult ♂♂ differs somewhat from that of other bovids in that heavy head-to-head clashes are avoided, the long and slender neck not being suited to withstand them. Instead, male Gerenuks clash horns by vigorous nods or jerks of the head, with necks held low. The power for the nods is developed by the heavy muscles near the top of the neck, while the elongated cranium provides additional leverage (Kingdon 1982). When pressed hard, young ♂♂, and sometimes ♀♀ too, lift the tail and curl it over the back in what appears to be a submissive gesture (Fig. 9 in Leuthold 1971b). Lying down as a submissive behaviour, described from captive animals (Fig. 28 in Walther 1968), was not observed in the field.

Courtship behaviour resembles that of other gazelles, with prolonged attempts of the ♂ to approach the ♀ from behind, but no special posture is adopted in this context as, for example, in Thomson's Gazelle (Walther 1968). Particularly striking on account of the Gerenuk's

long legs is lauschlag, in which an outstretched foreleg is raised slowly into a near-horizontal position, usually from behind the ♀. This may induce the ♀ to urinate; in response, the ♂ commonly shows flehmen, as most bovids do. The mating posture is very upright, as in other gazelles (perhaps even more so), with forelegs dangling and not touching the ♀; copulation may be achieved while the ♂ walks bipedally. A feature characteristic of the Gerenuk – also shown by the Dibatag – is marking of the female's shoulders or rump by the ♂ with his anteorbital glands (Backhaus 1958, Walther 1958; Fig. 10 in Leuthold 1978c). In captivity, the ♂ produced a 'humming' sound during courtship; this may be too low to be audible in the field.

In two cases observed in captivity, the ♀♀ gave birth while standing. The young was able to stand within about an hour and uttered low-pitched calls that were answered by the mother. The latter consumed amniotic fluids and the entire afterbirth, which appeared 2–3 hours postpartum (Kirchshofer 1963). Behavioural interactions between mother and young correspond to those of other gazelles (Walther 1968). Females lick their offspring frequently, particularly in the perineal area, and the young lie out for extended periods of time while their mothers move up to 1 km away. The young animals use hiding places with different characteristics for day and night, respectively (Reif & Klingel 1991). The ♀ returns to the young's hiding place periodically, mainly in the morning and evening (no data for the night). Suckling takes place in a few bouts lasting about 2 min each, timing and duration being determined mainly by the mother. The latter consumes her offspring's urine and faeces. The young animal often runs and cavorts about playfully after being suckled (Leuthold 1978c). When about 4–6 weeks old the young gradually change their activity pattern, start feeding on plants and begin to follow their mothers. They attempt to rise onto the hindlegs from two weeks of age, but become adept at it only at 2–3 months. The mother–young association lasts 8–9 months, i.e. until the following young is born. If the latter dies soon after birth, the previous young may rejoin its mother, particularly if it is a ♀. Otherwise it will leave its mother's group and attempt to join another female group. The fate of a young ♂ depends to a large extent on the tolerance of the territorial ♂. But at one year of age, at most, young ♂♂ leave their original home-range and join a bachelor group.

Captive animals observed by Walther (1958) showed much mutual licking and nibbling but in the wild such behaviour was rather rare; the main contact behaviour observed consisted of mutual head rubbing while standing close together (Fig. 11 in Leuthold 1978c). Also, vocalizations were rarely noticed in the wild, perhaps because they were too low to be audible. Young animals utter a short bleating call before being suckled, which was also noticed in a young ♂ raised in captivity. When alarmed, as by a predator, a Gerenuk may utter a short snorting sound, apparently by forcing air through the nostrils, with abdominal contractions being visible.

Reproduction and Population Structure Reliable data on reproductive parameters are difficult to obtain in the wild. Births are distributed throughout the year, though not quite evenly, and one young is born at a time. Inter-birth intervals are 7.2–9 months (Leuthold 1978b, Räder 1982).

The Gerenuk has been bred successfully in zoos, particularly in North America, where information on over 430 births since 1977 is

available (R. Barnes pers. comm.). Females attain sexual maturity at about one year of age and, with an estimated gestation period of 28–29 weeks, can give birth at less than two years of age (Backhaus 1958). With a postpartum interval of 3–4 weeks (or even less), a ♀ can produce four young within three years (Kirchshofer 1963, Ditttrich 1970, Leuthold 1978b). Mean birth-weight of 90 young born at Los Angeles Zoo was 3.4 kg, ♂♂ being slightly heavier than ♀♀ (R. Barnes pers. comm.). Detailed parameters of reproductive physiology and artificial insemination studies are discussed by Penfold *et al.* (2005).

For ♂♂ the situation differs in that, in the wild, reproduction is usually contingent upon holding a territory. Whereas physical maturity may occur earlier, a ♂ will reach social maturity towards three years of age. Horns begin to grow at 6–8 months and reach the full double curve at ca. 2.5 years. It takes some additional time for the neck to attain the thickness typical of adult ♂♂ (Leuthold 1978b). Little is known on longevity. Animals observed in Tsavo East N. P. were estimated to be 7–8 years old. Weigl (2005) reports a captive specimen living to 17 years.

In view of the low density, data on population structure are difficult to obtain. In Tsavo East N. P., a sex ratio of 65 ♂♂ to 100 ♀♀ over about one year of age suggests that ♂♂ suffer higher mortality during adolescence than ♀♀, a phenomenon well known in other ungulate species.

Predators, Parasites and Diseases There is no quantitative information on predation and its possible influence on Gerenuks. Adult animals may fall prey to any of the larger predators in their range, such as Leopards *Panthera pardus*, Cheetahs *Acinonyx jubatus* and African Wild Dogs *Lycaon pictus*, whereas many smaller predators, including large birds of prey, could be dangerous for young animals. Because of its small size, remains of a Gerenuk killed by predators are unlikely to be found. Neither is there much information on parasites or diseases in the Gerenuk. Like other artiodactyls the species is said to be susceptible to rinderpest, which occurs in periodic outbreaks in Africa, and apparently contributed to the decline of the population in Tsavo N. P. (East 1999). In captivity, a considerable proportion of young died at an early age, but causes of death were usually unknown (in addition, there were several stillbirths at Frankfurt Zoo; Kirchshofer 1963).

Conservation IUCN Category: Near Threatened. CITES: Not listed.

Living in semi-arid to arid areas, in which agriculture and other human activities mostly remain at a low level, the Gerenuk is not immediately threatened. Expanding human populations and concomitant intensification of land use (such as pastoralism, collection of firewood, illegal hunting) have led to a substantial decrease of Gerenuk numbers in some areas and to minor reductions in the species' range locally (East 1999, F. Wilhelmi pers. comm.; see also Distribution). Some of these adverse influences of human activities will doubtless continue and may even increase locally. Serious problems are created by the recurrent political unrest and warlike situations in parts of the Gerenuk's range (particularly Somalia and Ethiopia). These cause law enforcement and supervision of conservation areas to subside, so that illegal hunting may become prevalent. Such conditions also make it difficult to obtain reliable information on the situation in the

areas affected. The exact status and the degree of potential threats thus cannot be assessed accurately, nor can possible conservation measures be devised and implemented.

Fairly large areas within the range of the Gerenuk are under some kind of protection, particularly in its southern parts, e.g. Tsavo East, Sibiloi, Meru and Amboseli National Parks, Samburu and neighbouring Game Reserves in Kenya, and Mkomazi G. R. and Tarangire N. P. in Tanzania. In Ethiopia, the species occurs in Mago and Yangudi-Rassa National Parks and several Wildlife Reserves, and in Somalia in Bush Bush N. P. About 10% of the total population are estimated to live in protected areas (East 1999). Provided that protection of the areas mentioned remains effective, the survival of the Gerenuk is likely to be assured. However, this statement applies only to the southern subspecies *L. w. walleri*; the range of *L. w. sclateri*, as defined by Grubb (2002), includes few well-protected areas at present. Actions are necessary to remedy this situation.

Measurements

Litocranius walleri

HB (♂♂): 1550–1600 mm

HB (♀♀): 1400–1550 mm

T: 250–350 mm

Sh. ht (♂♂): 950–1050 mm

Sh. ht (♀♀): 900–1000 mm

WT (♂♂): 40.0–52.0 kg

WT (♀♀): 35.0–45.0 kg

Schomber (1966), localities and original sources not indicated

Sh. ht (♂♂): 890–960 mm, n = 7

Sh. ht (♀♀): 800–880 mm, n = 4

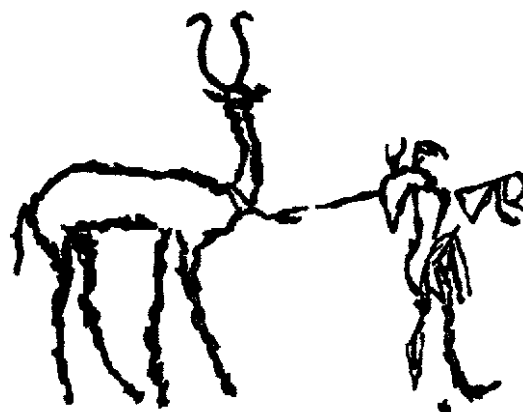
WT (♂♂): 31.3 (28.5–34.3) kg, n = 5*

Kenya (Hofmann 1973); *Tsavo N. P. (Ledger 1964)

Maximum recorded horn length is 44.7 cm for a pair of horns from Isiolo, Kenya (Rowland Ward)

Key References Kingdon 1982; Leuthold 1978b, c; Räder 1982, 1989; Schomber 1966; Walther 1968.

Walter Leuthold



Stone engraving from Wadi Sab' er Rigal, east of the Lower Nile 4000–9000 bc (after Schomber 1966).

GENUS *Antidorcas*

Springbok

Antidorcas Sundevall, 1847. Kongl. Svenska Vet.-Akad. Handl. Stockholm 1845: 271 [1847].

Antidorcas includes only the Springbok *A. marsupialis*, a small- to medium-sized antelope of slender proportions limited to South Africa, Namibia and SE Angola. The genus was assigned to its own tribe by Haltenorth (1963; Antidorcatini) and Kingdon (1997; Antidorcini), though correctly this should be Antidorcadini (see Grubb 2001a). In this work, the genus is included in the tribe Antilopini, which is consistent with current molecular (Hassanin & Douzery 1999, Matthee & Robinson 1999a, Matthee & Davis 2001; Hassanin *et al.* 2012 and see Hernández Fernández & Vrba 2005) and morphological (Groves 2000) studies.

Fossils belonging to the genus *Antidorcas* occur in Pliocene and Pleistocene deposits in East and southern Africa, and more doubtfully in North Africa. This antilopine type often predominates among the Antilopini of Pleistocene faunas (*A. Gentry pers. comm.*). The entirely southern distribution of the single species today contrasts starkly with the abundance of several fossil species in deposits over several million years, and their wide distribution in Africa is indicative of the ecological range and success of this genus in the past. The antilopine niche is one of foragers living in arid to semi-arid biomes with unreliable rainfall and, as a result, dispersed resources.

Few palaeontological studies of *Antidorcas* have been undertaken. However, Vrba (1973) suggested that fossil species *A. recki* and *A. bondi*, and to a lesser extent *A. australis*, are closer to the ancestral antidorcine condition than is the extant *A. marsupialis*. She hypothesized, based on cranial and dental morphology, that *Antidorcas* arose in East Africa from the ancestral *Gazella* more than 3 mya during the Pliocene, giving rise to the three fossil species mentioned. Moreover, there is good evidence that *A. bondi* and *A. recki* occurred in South Africa, and that *A. bondi* was present during the late Pleistocene (Brain 1981).

Brink & Lee-Thorp (1992), examining the feeding niche of the extinct, and extremely hypsodont, *A. bondi*, suggest that a small- to medium-sized grazing antelope had a high fibre diet. *Antidorcas bondi* disappeared quite suddenly 7000 years ago at the end of the last glacial when the environment became significantly drier (Scott 1992). Following this aridification, *A. marsupialis* arose from *A. recki* (Vrba 1973, Brain 1981). *Antidorcas marsupialis* is recorded in Herold's Bay Cave deposits that are at least 80,000 years old (Brink & Deacon 1982), and it is possible that the Florisbad *A. marsupialis* is more than 100,000 years old (Brink 1987, 1988).

The specific name of the species '*marsupialis*' derives from *marsupium*, a pouch (derived from the dorsal fan of long white hairs, which, when not erected, lie flat) hidden by the brown hair on the back, a characteristic unique to this species. Springbok stand ca. 75 cm at the shoulder and body mass varies geographically. Their slim sleek appearance gives the impression of speed and grace. Their distinctive cinnamon-brown colouration contains a reddish-brown band running from the upper region of the foreleg to the hip. This band separates the dark dorsal areas from the pure white ventral surfaces. The skull, which is typical of the family Bovidae, can be distinguished from other mixed dicotyledenous feeders by the exceptionally short premolar row (Spencer 1995). The anatomy of the postcranial skeleton is also typically that of a cursorial bovid, but sufficiently different from that of the extinct *A. bondi* to allow separation of fragmented skeletal remains of the two species (Plug & Peters 1991). A thorough and detailed review of the Springbok is provided by Skinner & Louw (1996).

John D. Skinner

Antidorcas marsupialis SPRINGBOK (SPRINGBUCK)

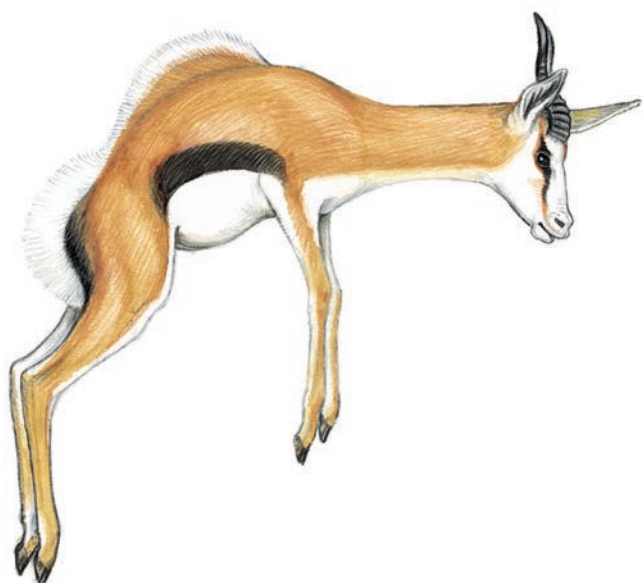
Fr. Springbok; Ger. Springbok

Antidorcas marsupialis (Zimmermann, 1780). Geogr. Gesch. Mensch. Vierf. Thiere 2: 427. South Africa, 'die Lander am Cap der guten Hoffnung', since restricted to 'Cape Colony [Cape Prov.]' (Lydekker 1914: 111).

Taxonomy Three subspecies have been recognized (Ansell 1972, Groves 1981c, Meester *et al.* 1986), although Robinson (1979) concluded that there was little support for their continued recognition and that those advocating subspeciation ignored the interaction between heredity and the environment on certain traits. Subsequently, Peters & Brink (1992), examining skulls from specimens of Kalahari Springboks and from the South African interior, concluded that size differences were indeed apparent between animals north and south of the lower Orange and Vaal Rivers, and that these differences might well result from subspeciation (see also Geographic Variation). Synonyms: *angolensis*, *centralis*, *dorsata*, *euchore*, *hofmeyri*, *pygargus*, *saccata*, *saliens*, *saltans*. The species has a monomorphic karyotype, with chromosomes $2n = 56$; the X chromosome is large and acrocentric, while the Y chromosome is small and metacentric (Robinson & Skinner 1976).



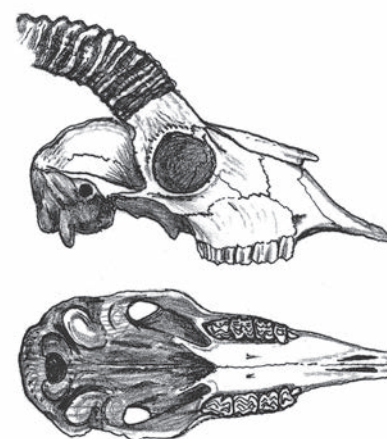
Springbok *Antidorcas marsupialis*.



Springbok *Antidorcas marsupialis*.

Description Medium-sized antelope similar in appearance to Thomson's Gazelle *Eudorcas thomsonii*, and standing about 750 mm at the shoulder. Males reach their asymptotic mass of 34 kg and length of 1400 mm at three years cf. 28 kg and 1340 mm for ♀♀ at 2.5 years in the Eastern Cape (Penzhorn 1974). The back appears to slope forward because the hindquarters appear higher than the forequarters. Face white with reddish-brown line running from anterior margin of eye to corner of mouth. Ears long, narrow and pointed. Back is bright cinnamon-brown with a distinct reddish-brown band running from the upper region of the foreleg to the hip, separating dark dorsal areas from white ventral surfaces that continue onto the flanks and marginally onto the anterior of the thighs. The medial surface of the rump is also white, narrowing into the dorsal crest of long (100–120 mm) white hairs, usually not apparent unless the crest in the pouch is erected (see Adaptations). Unlike hairs on the rest of the body, these are implanted at right-angles on the body (Findlay 1989). 'Black' and 'white' colour variations are rare, but exist, although the latter are not albinos (Kruger *et al.* 1979). Both black and white, and variations thereof, occur in herds with normally coloured individuals (Skinner & Louw 1996). Visual differences in the pelage are due to differing quantities of melanin and the translucency thereof, as well as to pale yellow horny cells in white hairs, and to the medulla, rather than due to colour as such (Findlay 1989). The hairs are concavo-convex in cross-section with gutters and an irregular waved scale pattern, two or three scales across the width (Keogh 1983). Tail white, with a terminal tuft of black hair. Legs long and slender. Preorbital and pedal glands are present, but there are no glandular knee-tufts as in other Antilopini and no inguinal glands. Adult ♀♀ are similar to ♂♂, but smaller. Females typically have a single pair of inguinal nipples, though individuals with two pairs are known.

Males possess heavily ridged horns that slope backwards, then diverge outwards and, in mature ♂♂, curve sharply inwards in a hook at their tips (lyrate). Female horns are more lightly ridged, distinctly smaller and more gracile. The skull is typically bovid, with well-developed mandibles and zygomatic arches. The supraorbital



Lateral and palatal views of skull of Springbok *Antidorcas marsupialis*.

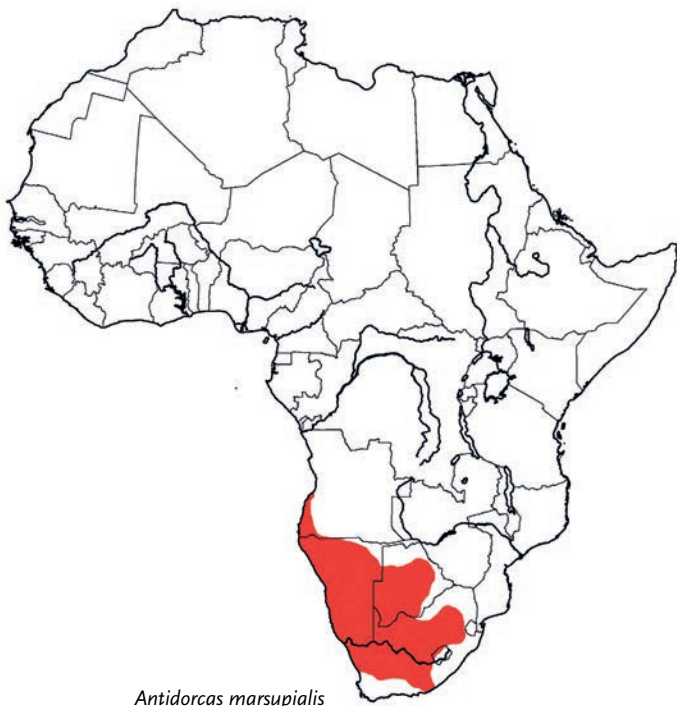
foramina is large, and the auditory bullae are small. Both anteorbital fossae and preorbital fossae are present. The premaxillae are wide aposteriorly, narrowing anteriorly. The dental formula, in contrast to the normal bovid dentition, is $I^{0/3}, C^{0/1}, P^{2/2}, M^{3/3} = 28$. The premolar tooththrow is short, with upper and lower first premolars lost and upper and lower second premolars, if present, small and non-functional. Adult dentition is reached at 22 months of age (Skinner & Louw 1996).

Geographic Variation Springboks vary in size, as mentioned earlier, and colour, which has given rise to former claims of subspeciation, but as these are both traits affected by environmental differences, there has been little consensus on the recognition of subspecies. In the eastern Highveld, where nutritional levels are low, Springbok mass is low, increasing south-west to the Karoo where, although body mass is heavier, this is further confounded by large ♂♂ having been consistently hunted for centuries. In Kgalagadi Transfrontier Park (South Africa/Botswana), Springboks are heavier, giving rise to a demand for rams to be imported, especially into the Karoo. However, there are no results from 'crossing' these rams with Karoo ewes in controlled experiments, to prove any beneficial effects. Kgalagadi Springboks are paler in colour, probably due to evolution through millennia in response to a duneveld environment. The largest Springboks occur in the Namibian Kaokoland where the soils are the most alkaline and herbage more protein-rich, in contrast to the situation in the north-west Highveld. Springbok in the Namib Desert in Angola are smaller with variable horn shape, although the sample taken there was small.

Similar Species Within their current range, Springboks cannot be confused with any other species, being the only 'gazelle' occurring in southern Africa.

Distribution Almost entirely confined to southern Africa, south of the Cunene and Zambezi Rivers, with the exception of a marginal intrusion into SW Angola in the Namib Desert west of the Escarpment.

Historical Distribution Rookmaker (1989) provides evidence of the abundance and widespread distribution of Springbok in the former



Cape Province, throughout the eastern, western and northern regions, where they were especially common on the arid plains. However, after 1870 the commercial demand for skins and the advent of the breech-loading rifle markedly reduced their numbers. Millais (1919) reported that nearly two million Springbok, Blesbok *Damaliscus pygargus* and Black Wildebeest *Connochaetes gnou* skins were exported between 1878 and 1880. One feature of Springbok distribution was migration or treks, which rarely, if ever, now take place. These were invariably triggered by a lack of pasture, with Springboks moving from an arid to a more mesic region (Skinner 1993). The impact of rinderpest, which killed thousands of antelopes, and reached the Cape in 1896, was another important factor affecting the frequency of Springbok treks. The last major treks occurred at the end of the nineteenth century, but, when numbers in the pristine Kgalagadi again increased, Sir Laurens van der Post, then Native Commissioner in Botswana, witnessed mass aggregations and trekking in the south-west (Skinner & Moss 2004). Today, this is an extremely rare occurrence due to a decline in numbers in the Kgalagadi and stock fences in the Karoo.

Current Distribution In Angola, restricted to coastal Namib Desert, from the Cunene R. north to Benguela. They remain widespread in Namibia, apart from the north-east, particularly on private farmland. In Botswana they occur in the south and west, north to 20° S on the Namibian border. In South Africa they have been widely reintroduced throughout their former distribution range, and also introduced to regions outside of their historical range (e.g. southern and central KwaZulu-Natal) (Skinner & Louw 1996, East 1999, Skinner & Chimimba 2005). There is no evidence that Springboks ever occurred in Swaziland (Monadjem 1998), although they ranged into the western lowlands of Lesotho (Lynch 1994).

Habitat Typically a species of arid regions and open grassland, Springboks are partial to the wide, short grass fringes of pans and

to fossil river beds and valley terraces. They occur from sea level to 2000 m on the Highveld. They do not occur in woodland savanna almost certainly due to the presence of heartwater, spread by the tick *Amblyomma hebraeum*, and to which they show no resistance (Neitz 1944). Springboks tend to occur in areas where surface drinking water is unavailable or only available seasonally.

Abundance East (1999) estimated the total population in southern Africa at more than 670,000, noting that it was probably an underestimate. Indeed, recent estimates for Namibia alone put the population at 730,000, itself an underestimate (P. Lindeque pers. comm.). Elsewhere in the range, numbers are probably in the order of 10,000 for Angola, 40,000 in the Botswana side of Kgalagadi Transfrontier Park (and an additional 60,000 at least in the rest of the country), 75,000 in the Free State, 75,000 in Gauteng and North West, 1,000,000 in the Karoo and about 100,000 in the Cape provinces outside of the Karoo. Numbers are extremely hard to estimate, but based on these figures the total population size in southern Africa is estimated at ca. 2,000,000 to 2,500,000 animals and increasing.

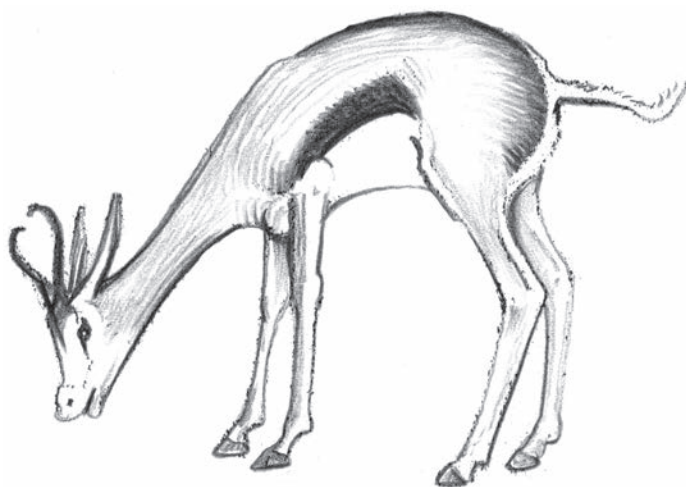
Springboks are a commercially important game species and, while numbers in the Kgalagadi have plunged in the past decade (the reasons for which are unknown), estimates in the Karoo show an opposite trend and are currently some 1,000,000 animals despite an annual cropping rate (for meat and skins) of 200,000 (Skinner & Moss 2004).

Adaptations Springboks have a thinner pelage and higher conductance than would be predicted for their body mass (Hofmeyr & Louw 1987). Advantages include the ability to off-load excessive heat rapidly without resorting to evaporative cooling, if ambient temperature is lower than body temperature, e.g. after sprinting away from predators. The white belly fur and long hairs of the dorsal crest reflect 72% of the sun's radiation, including that reflected from the desert surface. Disadvantages of the pelage are that the animals lose heat rapidly and begin shivering at moderately low temperatures and gain heat rapidly when ambient temperatures high. These are offset by behavioural adaptations, with Springboks seeking cooler areas and shade, orienting the long axis of the body towards the sun, and foraging mainly in the post-dawn and pre-dusk hours (and often at night), so that in free-ranging Springboks, extreme responses were never exhibited (Hofmeyr & Louw 1987).

Hetem *et al.* (2009) measured core body temperature in ♀♀ of three colour morphs of Springbok (normal, black, and white), free-living in the Karoo. During winter, white Springbok displayed lower daily minimum body temperatures ($37.4 \pm 0.5^\circ\text{C}$), than both black ($38.1 \pm 0.3^\circ\text{C}$) and normal ($38.0 \pm 0.6^\circ\text{C}$) Springbok; during spring, black Springbok displayed higher daily maximum body temperatures ($40.7 \pm 0.1^\circ\text{C}$) than both white ($40.2 \pm 0.2^\circ\text{C}$) and normal ($40.2 \pm 0.2^\circ\text{C}$) Springbok. Black Springbok had lower diurnal activity in winter, explained by their having to forage less because their metabolic cost of homeothermy was lower, but were disadvantaged in hot periods. White Springbok, by contrast, were more protected from solar radiation, but potentially less able to meet the energy cost of homeothermy in winter. Consequently, energy considerations may underlie the rarity of the various colour morphs.

Mitchell *et al.* (1997), in their studies on wild Springboks, found no evidence for adaptive heterothermy. Although selective brain

cooling is activated at high body temperatures, this is absent during vigorous exercise even when body temperatures are high. Fuller *et al.* (2005) found that mean monthly body temperatures are strongly positively correlated with photoperiod and that annual and daily variations in body temperature reflect an endogenous rhythm, entrained by the light:dark cycle, but largely independent of fluctuations in the environmental thermal load. Springboks exhibit remarkable homeothermy and Fuller *et al.* (2005) confirm that Springbok do not employ adaptive heterothermy to survive in their natural environment.



Springbok *Antidorcas marsupialis*.

The anatomy of the digestive system is well adapted to a diet of mixed forage, but the ability to digest highly fibrous food is limited (Hofmann *et al.* 1996). During droughts, even when sufficient lignified monocotyledons are available and consumed by, for example, sheep *Ovis aries*, Springboks starve to death (Davies *et al.* 1986).

Springboks have a *marsupium* or pouch extending along two-thirds of the back, which gave rise to its specific name. This fold encloses a dorsal fan of long white hairs, which, when not erected, lie flat as in a pouch and hidden by the brown hair of the back. The sebaceous glands within the pouch secrete an exudate with a strong, sweet odour, which most probably functions as a specific alarm signal when the back is arched, legs stiffened and the fan of white hair fully erected as the Springbok stotts or pronks (Burger *et al.* 1981a, Skinner & Louw 1996). Stotting comes into play when Springboks are alarmed, and particularly in response to sighting coursing predators.

Foraging and Food Primarily a browser, but taking also grass, the Springbok belongs to the intermediate group of feeders (Hofmann *et al.* 1996), a classification supported also by a detailed review of dietary preferences in bovids (Gagnon & Chew 2000) and by stable carbon isotope analysis (Sponheimer *et al.* 2003b). Springboks graze young succulent grass before it begins to lignify, and select succulent browse plant parts with a high ratio of leaf to stem. They have been found to browse a large number of species in the Karoo (Davies *et al.* 1986); in the latter study, the diet of adult ♂♂ and ♀♀ differed, rams preferring more palatable shrubs, especially *Salsola* spp. and *Eriocephalus ericoides*. Ewes preferred *Delosperma* spp.,

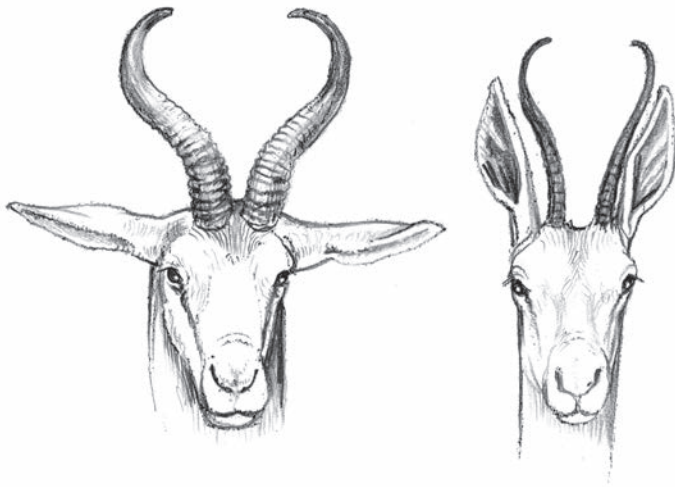
Plinthus karoocicus and significantly more *Eberlanzia spinosa*. The larger body size of Springbok rams and their larger fermentation capacity in their digestive system, enable them to use more fibrous material than ewes and juveniles. Bigalke (1972) found that karroid shrubs *Pentzia incana*, *P. tenuifolia*, *P. globosa*, *P. lantana*, the shrub *Rhus ciliata* and *Acacia tortilis* were important in the Springbok's diet.

In Kgalagadi Transfrontier Park, Leistner (1967) listed 57 species eaten, including grasses, shrubs and ephemerals. Grasses *Stipagrostis obtusa* and *Schmidtia kalahariensis*, shrubs *Monechma australe* and *Rhigozum trichotomum* and the legume *Psoralea obtusifolia* were preferred food plants and another 14 plant species of shrubs and ephemerals were eaten frequently. In the transition zone between the Karoo and Kgalagadi, Liversidge (1970) noted that, of 33 species eaten, monocotyledons predominated in rumen samples in the wet season and dicotyledons in mid-winter. On the other hand, van Zyl (1965) listed 68 species of plants eaten on the north-west grassland Highveld, of which 20 were the main food plants, including nine grasses and 11 shrubs. Important grasses were *Themeda triandra*, *Cynodon* spp., *Panicum* spp., *Eragrostis* spp. and *Sporobolus* spp. Nagy & Knight (1994) estimated that an adult ♂ consumes ca. 504 kg of dry matter a year, cf. 409 kg for an adult ♀.

Possibly as a result of the high mineral content of their diet, Springboks use mineral licks to a much lesser extent than other species (Leistner 1967). Where freshwater is available in Kgalagadi Transfrontier Park, Springboks drink 2.63 ± 0.45 litres per individual every second day (Dreyer 1987). They make use of heavily mineralized water in the Kgalagadi where this is available in the dry season (J. D. Skinner pers. obs.), but otherwise they satisfy their moisture requirements by browsing on succulent vegetation, such as the leaflets of blackthorn *Acacia mellifera* and candle thorn *Acacia hebeclada*. Springboks are able to maintain body water balance feeding on plant food containing 67% water (Nagy & Knight 1994). As such, they supplement their diet by digging for succulent roots such as *Acanthocycios naudinianus*, *Brachystelma* spp., *Cucumela cinerea* and *Talinum tenuissimum*, all of which have a moisture content exceeding 62% (Williamson 1987), or eating fruits such as wild cucumbers *Cucumis africanus* (83% moisture) and Tsama Melons *Citrullus lanatus* (90% moisture) (Cooper 1993) and the fruits of the snake berry *Solanum* spp.

Social and Reproductive Behaviour Springboks are gregarious, congregating and moving in small herds during the dry months of the year (Apr–Sep), although the sporadic occurrence of larger aggregations numbering hundreds of thousands (treks; see Distribution) has been documented (Skinner 1993). Larger summer concentrations usually result when there has been patchy rainfall and Springboks congregate on resultant greenery; however, such aggregations now seldom number more than a few thousand individuals (Bigalke 1972). On the other hand, as only territorial ♂♂ mate, they are sedentary and remain on their territories for as long as there is an adequate nutritional supply, abandoning them only at the end of the dry season when resources are exhausted. Territorial ♂♂ show great fidelity to these territories, returning to them after the first summer rains (Jackson & Skinner 1998).

Territorial ♂♂ take up conspicuous positions in open areas to advertise their presence to other rams; this also serves as an anti-predator mechanism (Jackson 1995). Territory size in Kgalagadi is variable, being roughly 0.2 km² during optimum times but five



Springbok *Antidorcas marsupialis* male (left) and female (right).

times that during periods of drought. There is no evidence to show that ♂♂ use preorbital glands in marking. Instead, territorial ♂♂ have a unique urination–defecation ritual (very occasionally used by bachelors): spreading the hindlegs far back and widely spaced, belly close to the ground, they urinate, then bring the legs forward and squat to defecate on the same place (Jackson 1995). This may be preceded by scratching the ground and concluded by tail wagging (Novellie 1975). Territorial ♂♂ also indulge in horn sweeping, which tends to make them more conspicuous. Non-territorial ♂♂ occur in groups ranging from two to 50 or more individuals. Bachelor herds sometimes associate with female herds but are usually easily distinguishable as they position themselves on the fringes of the latter.

The mating system is one of resource-defence polygyny, whereby ♂♂ defend their territory and endeavour to retain transient ♀♀ by herding them with head stretched forward, the horns laid back and the tail held stiffly horizontal, lifted vertically or curved forward. Defence of the territory is by advertising and fighting. Males rut infrequently, the rut occurring at any time of the year and lasting from five to 23 days (Skinner & Louw 1996, Skinner *et al.* 1996). At these times they vocalize loudly with grunting bellows and are very active chasing off rams intruding onto their territories. Only territorial ♂♂ mate, other ♂♂ being to all intents and purposes emasculated, and the presence of the ♂ has a marked influence on inducing oestrus in anoestrous ewes and synchronizing oestrus in cycling ewes (Skinner *et al.* 2002). This results in clumping of births for predator swamping, an advantage in an arid-adapted aseasonal breeder (Skinner & Louw 1996). Flehmen in the ram, nostril wrinkling following urine or vaginal smelling of the ewe and lauschlag by the ram (tapping of the ewe's hindleg with his stiff foreleg), occur particularly when ♀♀ are in pro-oestrus. Females usually mate once, but occasionally may mate several times, sometimes with more than one ♂ (Jackson & Skinner 1998). There may be up to eight false mounts until the ♀ finally stands, when penetration, followed immediately by ejaculation, takes place with a violent thrust forwards and upwards, the ram only being held upright by the inserted penis. There is no thrusting when penetrated and the ram withdraws the penis immediately, the whole procedure lasting less than a minute. Afterwards, there is no mate guarding.

Following parturition, the ♀ eats the afterbirth and hides her young in tall vegetation or underbrush for a day or two, during which

the neonate is immobile. Juveniles tend to congregate in nursery herds together, while their mothers browse in the vicinity (Skinner & Chimimba 2005). Young are weaned ca. four months, depending on food availability as they grow faster in optimum seasons. They continue to associate with their mothers for much longer; ♀♀ remain with the herd but ♂♂ join up with bachelor herds from 10 to 12 months of age.

Young ♂♂ indulge in playful sparring. Fighting among adult ♂♂ results in horn interlocking and side-to-side wrestling. Stabbing may result in mortality but usually one ♂ submits before either is seriously injured. Fighting is most common during the rut, when territorial ♂♂ no longer tolerate bachelors within the vicinity of female herds.

Springboks are vocal at particular times, the most common being a loud grunting bellow by ♀♀ in response to bleating by their young. When alarmed, Springboks emit a high-pitched whistling snort. Males are very vocal during the rut, emitting low-pitched grunt-like bellows when chasing intruders or rounding up ♀♀ (Novellie 1975, David 1978, Jackson 1995).

Springboks associate with other ungulate species at waterholes but rarely at other times, although they very occasionally migrate with species such as the Common Eland *Tragelaphus oryx* or Hartebeest *Alcelaphus buselaphus*. Individual vigilance decreases as herd size increases and Springboks on the periphery tend to be more vigilant than central animals. Springboks are also more vigilant at night and in woodland compared with walking in the open (Bednekoff & Ritter 1994; and see Burger *et al.* 2000).

Mutual grooming does not occur although self-grooming is important and this is facilitated by a dental grooming comb similar to that described in Impala *Aepyceros melampus* by McKenzie (1990).

Reproduction and Population Structure Springboks are aseasonal breeders and have the ability to multiply rapidly (Skinner & Louw 1996). Although ♂♂ are fertile throughout the year (Skinner & Van Zyl 1970), ♀♀ have been shown to have a clear endocrine anoestrus of between 4 and 5 months, the timing and duration of which is synchronized between some individuals but the time of onset and duration varies from year to year; the prevailing ambient temperature may influence the onset of ovarian activity (Skinner *et al.* 2001). The oestrous cycle is 16 days.

Single young, rarely twins, with a mass of 3.8–5.0 kg, are born after a gestation period of 25 weeks (Skinner & Louw 1996). Under optimum climatic conditions Springboks have a postpartum oestrus when the uterus involutes after about a fortnight, enabling ♀♀ to give birth twice a year (Skinner *et al.* 1971). Young are weaned at about four months of age (Liversidge & de Jager 1984); the composition of the mother's milk is discussed by Van Zyl & Wehmeyer (1970). Females are physiologically capable of conceiving at six months; ♂♂ produce sperm at one year, but probably are not able to breed until about two years (Skinner & Van Zyl 1970, Liversidge & de Jager 1984). Longevity has been given as 19.8 years in captivity (Weigl 2005), but is probably around ten years in the wild.

Foetal sex ratios are normally 1 : 1, but can change in response to climatic conditions (Liversidge 1993). Male-biased fetal sex ratios occur during periods with successive years of high rainfall, and female-biased foetal sex ratios following drought conditions. Liversidge (1993) hypothesized this might be of selective advantage to ensure high

reproductive rates following population declines. Adult male to female sex ratios have been recorded at 43–57 : 100 in Etosha N. P., Namibia, and Kgalagadi Transfrontier Park and up to 130 : 100 in Mountain Zebra N. P., Eastern Cape, South Africa (Bigalke 1970, Penzhorn 1974). Female-biased adult sex ratios may result from misclassification of subadult ♀♀ as adults, or because of higher mortality rates for adult ♂♂.

Predators, Parasites and Diseases Apart from the coursing predators such as Black-backed Jackals *Canis mesomelas*, Spotted Hyenas *Crocuta crocuta* and African Wild Dogs *Lycaon pictus*, Springboks may be preyed upon by Cheetahs *Acinonyx jubatus*, Leopards *Panthera pardus*, Lions *P. leo* and Caracals *Caracal caracal*, while young are predated by Brown Hyenas *Hyaena brunnea*, Wildcats *Felis silvestris*, Ratels *Mellivora capensis* and eagles, particularly Martial Eagles *Polemaetus bellicosus*, Tawny Eagles *Aquila rapax* and Verreaux's Eagles *A. verreauxii* (Skinner & Louw 1996). In Kgalagadi Transfrontier Park, Springboks constituted 87% of Cheetah kills, 65% of Leopard kills, 13% of Lion kills and 12% of hyaena kills (Mills 1984). In Etosha N. P., 97% of Cheetah kills were Springboks (Berry 1981).

Springboks carry very low tick burdens, but large numbers of lice, while numbers of helminth parasites varied in different regions from nine to 18 (Young *et al.* 1973a, Horak *et al.* 1982c, 1991b, 1992a, De Villiers *et al.* 1985); *Sarcoptes scabiei*, an ectoparasite associated with mange, was isolated from a Springbok in the Kalahari (see Young *et al.* 1973a). Fourie & Horak (1987) investigated six Springboks that had died of tick paralysis, a form of tick toxicosis, which is caused by the adult female Karoo paralysis tick, *Ixodes rubicundus*. A neurotoxin causes paralysis and initial signs are lower motor-neurone paralysis with varying degrees of incoordination and ataxia, animals eventually succumbing to respiratory failure (Gothé 1984). Other than these, there are apparently no documented deaths from parasite infestation in Springboks, although heavy infestations of the nematode internal parasite *Bronchonema magana* may in time cause death (Boomker *et al.* 2000). The latter authors counted helminth parasite loads in nine Springboks shot in four different National Parks in the Western Cape and Eastern Cape Provinces of South Africa. The species differed marginally depending on locality. Of 11 species identified, *Trichostrongylus falculatus* was the most numerous nematode, contributing 72% to the mean adult nematode burden, followed by *Cooperioides antidorca* (8%), *Normatodirus spathiger* (8%) and *Paracooperia serrata* (8%), making up 96% of the total internal nematode parasite burden. The larvae of several oestrid or nasal bot flies parasitize the nasal passages and sinuses of Springboks, including *Rhinoestrus antidorcitis*, which is host specific (De Villiers *et al.* 1985, Horak 2005).

Records about susceptibility to disease are scanty. Springboks have long been known to be susceptible to heartwater (Spreull 1922, Neitz 1944) and anthrax (Ebedes 1976), which has limited its introduction to some regions.

Conservation IUCN Category: Least Concern. CITES: Not listed.

Special measures to conserve Springboks are unnecessary. They are amongst the most valued species in the expanding game ranching industry in southern Africa due to the excellent quality of their meat, and therefore are found not only in numerous protected areas (including Etosha N. P. and Kgalagadi Transfrontier Park), but also extensively on private land. Of four popular species examined, Springboks were superior in terms of muscle fibre diameter, flavour intensity and acceptability, their prolific reproductive potential and fast growth rate in arid regions, and the fact that they are ideally suited to multi-species farming systems, especially in combination with domestic livestock such as sheep *Ovis aries* (Von la Chevallerie 1972, Davies & Skinner 1986a, b, Skinner 1989). Springboks are no longer regarded as strictly feral on many ranches, because they can be confined by ordinary stock fences. However, they would be a most difficult species to domesticate due to their highly nervous disposition. Some advances have been made in establishing cues for triggering reproductive cycles, but ♂♂ use resource-defence polygyny as their breeding system and such ♂♂ are intolerant of intruding rams; in an enclosed ranching system this will result in frequent fighting and mortality. Moreover, Springboks are not disposed to herding.

Measurements

Antidorcas marsupialis

TL (♂♂): 1501 (1390–1623) mm, n = 30

TL (♀♀): 1484 (1375–1580) mm, n = 13

T (♂♂): 244 (146–286) mm, n = 30

T (♀♀): 256 (200–305) mm, n = 13

HF c.u. (♂♂): 427 (400–455) mm, n = 30

HF c.u. (♀♀): 416 (395–462) mm, n = 13

E (♂♂): 177 (153–195) mm, n = 30

E (♀♀): 173 (150–187) mm, n = 13

Sh. ht (♂♂): 730 mm (690–770 mm), n = 20*

Sh. ht (♀♀): 692 mm (640–730 mm), n = 20*

WT (♂♂): 41.0 (33.0–47.6) kg, n = 30

WT (♀♀): 37.1 (30.4–43.5) kg, n = 13

Botswana (Smithers 1971)

*Skinner *et al.* (1971)

Kruger *et al.* (1979) reported a mean shoulder height of 857 mm for ♂♂ (n = 21) and 714 mm for ♀♀ (n = 9) from Kgalagadi Transfrontier Park, South Africa, and 843 mm (n = 10) and 816 mm (n = 10) for ♂♂ and ♀♀, respectively, from the Kaokoland, Namibia, and Iona N. P., Angola.

Maximum recorded horn length is 49.2 cm for a pair of horns from Prospect, Namibia (Rowland Ward)

Key References Jackson 1995; Skinner & Chimimba 2005; Skinner & Louw 1996; Skinner *et al.* 1971.

John D. Skinner

Tribe OUREBIINI

Oribi

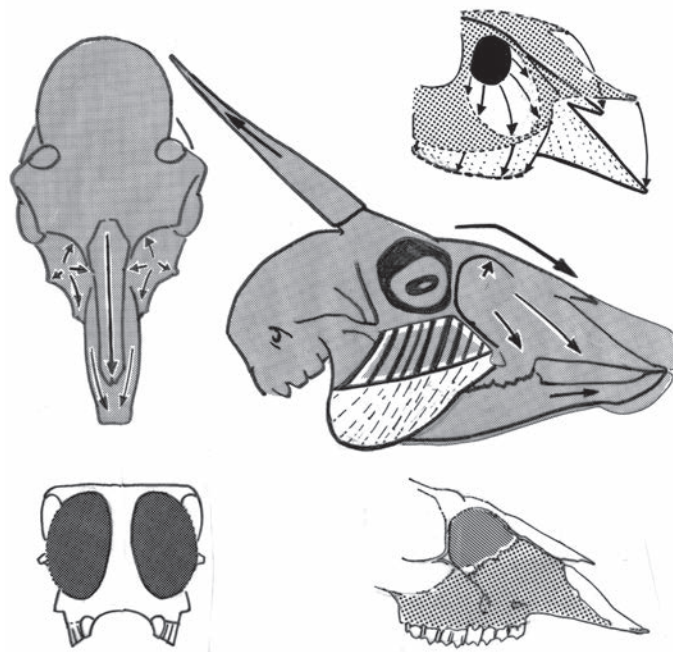
Ourebiini (tribe nov.)

Oribi *Ourebia ourebi* head of adult male showing skin gland patch below ear.

The particular permutation of the Oribi's *Ourebia ourebi* adaptation to its environment is unlike that of any other antelope and its affinities have long been a puzzle. None the less, its possession of subauricular glands and several other anatomical and adaptive features that are very unlikely to be convergent suggest a distant but likely relationship with the very earliest proto-reduncines. None the less, Oribis are too different to merit inclusion in Reduncini. Emptying of the neotragine 'waste-paper basket' (wherein *Ourebia* was formerly placed along with *Oreotragus*, *Raphicerus*, *Neotragus*/*Nesotragus*, *Madoqua* and *Dorcatragus*) has made it impossible to allocate the Oribi to any other major antelope grouping (certainly not to the Antilopini), even though it shares individual features with more than one other acknowledged tribe. Haltenorth (1963), who was the first to dismember the Neotragini into several tribes, included *Ourebia* with *Raphicerus* in the tribe Raphicerini, but we consider Raphicerini to include only members of the genus *Raphicerus*, plus, tentatively, the Beira *Dorcatragus*. In the absence of any new evidence for an unambiguous genetic affiliation, we have therefore seen no alternative other than to erect a new tribe to accommodate this extraordinary antelope.

The Oribi is the smallest open-country grazing antelope; it is small to medium in size, but tall and slender with a sandy-yellowish or reddish tinted body colour, white undersides, upper throat, mouth and ear linings. Unlike the Steenbok *Raphicerus campestris* (with which it is sometimes confused), the eyes are not rimmed by intensely black lids and the ears are of moderate size. In addition to pedal and inguinal glands, the Oribi has scent brushes below the knees and ankles and complex black skin gland patches below the ears.

A dominant peculiarity of the Oribi head is super-development of the preorbital glands, which are exceptionally large and well developed. The sheer size and depth of these glands has caused an extreme



Diagrams of unique features of Oribi *Ourebia ourebi* skull. Top left: elongated nasals, narrow premaxilla, enlarged fossa for pre-orbital gland. Lower left: Voluminous pre-orbital glands on either side of narrowed nasal passage. Top right: outline of muzzle superimposed on hypothetical ancestral form (note deepening toothrow, enlargement of gland and elongation of snout appear to have resulted in progressive downward deflection of entire muzzle). Centre right: skull profile corroborates evolutionary deflection of muzzle. Lower right: deflection of a more vertical maxilla-frontal suture (beneath the pre-orbital gland) to a more horizontal angle conforms with downward deflection of muzzle in evolution of the Oribi.

narrowing of the nasal chamber. Massive enlargement of the preorbital glands has also demanded expansion and deepening of the bony linings of the huge preorbital fossa within which they are contained, forcing both maxilla and lachrymal bones to expand or extend in this part of the face. When the Oribi is compared with smaller, more conservative antelopes, a marked elongation of the muzzle is also evident. Elongation of the face and neck is typical of open-country herbivores that have long legs because it helps them maintain contact with the ground when grazing. It is this combination of muzzle lengthening and expansion of the bones lining the preorbital pit that has resulted in a sharp downwards deflection of the muzzle, effectively bending the skull's basicranial axis in a way that is unique to the Oribi.

The crisp, clear-cut border of the preorbital fossa delimits the forward margin of the masseter. Thus, the gland's spread over the lachrymal and maxilla bones has served to shorten the reach of the masseter in its superficial anterior part. Narrowing the area of bony attachment further reduces the efficiency of this muscle component so the Oribi has compensated for this by greatly increasing the prominence of a bony knob on which all anterior fibres of the superficial masseter converge. It seems significant for the evolution of Reduncini and

their supposed relationship with the Oribi that this knob is also well developed in many reduncine species and that some fossil and living reduncines exhibit vestiges of preorbital glands. In reduncines, atrophy or outright disappearance of this gland has allowed a thickened masseter to extend its purchase on the unhollowed sides of their faces. However, the Oribi, as a grazer, has also had to enlarge the bulk of its masseter and to achieve this the lower margins of the orbits jut out, making the eyes quite prominent. A very similar arrangement occurs in the skulls of Reduncini, further hinting at an ancient common ancestry.

It can be assumed that the ultimate ancestors of the Oribi were smaller, shorter-legged and folivorous and that they marked out their territories with glandular secretions. Furthermore, it can also be assumed that the Oribi lineage, like any other that moved out into open country, acquired its slender proportions as a direct result of selection by predators (with fleeing replacing hiding). They also needed to cover more ground in enlarged ranges. It is therefore reasonable to suppose that many of the multiple expressions of scent-signalling found in the Oribi are grossly exaggerated retentions from a system that was originally only adaptive for small bovids in closed habitats. It also seems likely that the Oribi has reached upper limits, both for body-size and for the utility of scent-labelling in the larger, more open ranges that it occupies. This helps explain some basic limits put on the Oribi lineage and hints at the sort of constraints that an earlier, proto-reduncine would have had to overcome in order to become larger in body-size, less dependent on broadcasting scent over the entire home-range and less tied to the limited land-holdings that such scenting imposed. Even so, all Reduncini are clearly very olfaction-oriented and they uniquely share the Oribi's subauricular scent signals as well as relying on trails and land-marks created by glands or defecation. The ecological and behavioural resemblances

between the Oribi and reduncines are not trivial and serve to differentiate both groups from all other antelopes.

Increased body size and proportional lengthening of a spike-like horn has made male Oribis exceptionally dangerous. The possession of lethal weaponry may help to explain why male Oribis have intensified and ritualized scent-marking behaviour to the degree to which they have: ♂♂ cannot afford to wound or scare the hornless ♀♀. Females are larger than ♂♂ and are independent in their movements, but by becoming the object of continuous attention from a single ♂ each adult ♀ determines the area in which the ♂ is intolerant of other ♂♂. This area becomes the shared territory in which each partner repels members of its own sex. Within a shared territory, both occupants (and their offspring) are bombarded with the males' olfactory signals and both sexes avoid trespassing on neighbouring territories. Oribis therefore seem to have replaced direct attacks with ostentatious scent-marking that deters or minimizes risks of lethal confrontation.

There are also striking contrasts between periodic, semi-social and self-advertising behaviour and their otherwise solitary, cautious and inconspicuous habits. These behavioural differences have some correspondence with seasonal changes in their habitat. For example, when the grass is long and dense during the rains and visibility is cut to a metre or less, Oribis, and many other animals, are primarily reliant on scent and hearing. After fires and heavy use by big herbivores the Oribis become very exposed and sight becomes their primary sense. It is at this time that they are particularly alert and shy and their piercing whistle is frequently uttered as they flee with a characteristic rocking-horse gait.

Jonathan Kingdon

GENUS *Ourebia*

Oribi

Ourebia Laurillard, 1842. In: d'Orbigny, Dict. Univ. d'Hist. Nat. 1: 622.

Ourebia includes only the Oribi, *O. ourebi*, a small antelope larger than *Raphicerus* species (shoulder height 65 cm, mass 15–21 kg). The Oribi differs from members of the genus *Raphicerus* in proportions of the head (notably in the downwards deflection of the muzzle from the basicranial axis), in the form of the dentition, jaws and preorbital fossa, and in the presence of inguinal and subauricular glands, carpal tufts, tail tuft and ringed horns (see species profile).

Ourebia combines characters typical of small antelopes (solitary or in pairs, territoriality, dung piles, marking with preorbital secretion) with features of much larger species (predominantly graminivorous diet and associated hypsodonty and other dental specializations). The

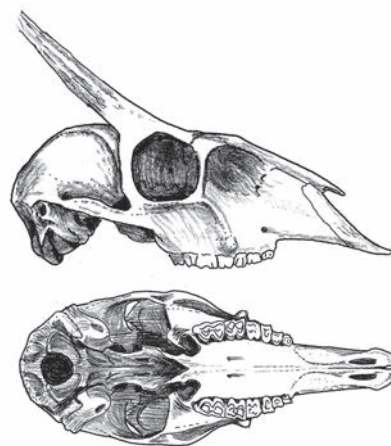
subauricular gland, if it is an apomorphic character shared with reduncine antelopes, could imply membership of the same clade (see Hofmann 1972, Kingdon 1982, Vrba *et al.* 1994). However, this relationship has not found support in some other studies (e.g. Matthee & Robinson 1999a, Vrba & Schaller 2000, Hernández Fernández & Vrba 2005), and the affinities of the genus remain uncertain. In this work, the genus has been provisionally allocated to its own tribe, the Ourebiini.

Peter Grubb

Ourebia ourebi ORIBI

Fr. Ourebie; Ger. Bleibbockchen

Ourebia ourebi (Zimmermann, 1783). Geogr. Gesch. Mensch. Vierf. Thiere 3: 268. 'Bewohnt die Cafferen' (South Africa, Eastern Cape Prov., Kaffraria); since restricted to one of the syntypical localities: South Africa, Eastern Cape Prov., Somerset East Dist., Bruintjieshoogte (Grubb 1999).

Oribi *Ourebia ourebi*.Lateral and palatal views of skull of Oribi *Ourebia ourebi*.Upper-right tooththrow of Oribi *Ourebia ourebi*.

Taxonomy As many as 13 subspecies of Oribi have been proposed to account for considerable variation in body size and colouration across the species' range (see Haltenorth 1963, Ansell 1972). Animals in East Africa appear larger and darker than western, northern and southern conspecifics, but this trend, and the validity of many proposed subspecies/race distinctions, has not been tested using molecular techniques. Variation in body size and colouration among populations is sufficiently large to confound past efforts to identify suites of morphological traits specific to regions, and the listing of subspecies here is provisional (and adapted from Ansell 1972). Synonyms: *aequatoria*, *brevicaudata*, *cottoni*, *dorcas*, *gallarum*, *goslingi*, *grayi*, *haggardi*, *hastata*, *kenyae*, *leucopus*, *masakensis*, *melanura*, *microdon*, *montana*, *nigricaudata*, *pitmani*, *quadriscopa*, *rutila*, *scoparia*, *smithii*, *splendida*, *ugandae*. Chromosome number: not known.

Description Slender, small to medium-sized antelope similar in appearance to Steenbok *Raphicerus campestris*, but taller and larger with markedly smaller and narrower ears, more pronounced preorbital glands, tail longer and darker, and with a naked patch of black skin beneath the ear (the subauricular gland, which is sometimes covered by hairs). Pelage sandy to rufous with white undersides, throat, chin, mouth, eyebrows and ear linings. Dark patch on crown present in both sexes, but more visible in ♀♀, often extending to a narrow peak on the forehead, and sometimes absent in older individuals.

Insides of legs white to sandy; udders, hooves, nostrils and eyes black. Body colour and size and shape of white patches and dark crown patch highly variable between individuals. Tail short but with a prominent tuft; tail colour variable from sandy or rufous with a black tip to mostly black. Carpal brush of long hairs present below knees. Lateral hooves small. Preorbital gland large, opening by a slit; inguinal and pedal glands present. Animals in southern Africa exhibit a marked difference between the summer coat, which is shorter and smoother, and the winter coat, which tends to be thicker and more shaggy (Skinner & Chimimba 2005). However, in East Africa, and probably other areas close to the Equator, the difference in coats between cool and warm seasons is not marked. Adult ♀♀ are similar to ♂♂ but ca. 15% larger (Jongejan *et al.* 1991). Females have two pairs of inguinal nipples.

Horns present in ♂♂ only, short, straight and sharp-tipped, Steenbok-like, but thicker and annulated in adults older than one year of age, and angled more to the anterior (ca. 60° angle from plane of crown); during early growth, horns are enveloped in a deciduous keratinous sheath, which is lost at the time the adult dentition is completed, revealing the annuli. Horns appear at ca. 4.5 months of age and grow rapidly up to ca. 20 months of age. Horn length and number of annulations can be used to estimate age of ♂♂ ≤20 months, but the technique awaits validation for older animals (Jongejan *et al.* 1991).

The rostrum is relatively long, more elongated than in *Raphicerus*, not tapering towards the tip, and unlike *Raphicerus* the ethmoid vacuity is narrow or closed. Deep sharply margined preorbital fossae (to accommodate the preorbital glands) compress the rostrum laterally; the margin forms a sharp ridge between the fossa and origins of the masseter muscle, running diagonally forward from the orbit down to the masseteric knob just above the cheekteeth, a diagnostic feature of the genus most prominent in ♂♂. The dentary is deep and sharply angled. The first incisors are considerably broadened at the tip (more so than in *Raphicerus*); other incisiform teeth are narrow, with the second incisors a little broader than the remainder. Cheekteeth are relatively hypsodont with large enamel islands. The enamel varies in thickness and forms prominent styles.

Geographic Variation

O. o. ourebi: South Africa and S Mozambique.

O. o. hastata: SE Tanzania, E Zambia, Malawi, Zimbabwe and N Mozambique.

O. o. rutila: Angola, N and NE Botswana, and W Zambia; perhaps also SE DR Congo.

O. o. cottoni: SW Kenya to C Tanzania.

O. o. masakensis: S Uganda, Rwanda and NW Tanzania.

O. o. aequatoria: N Uganda and S Sudan. Apparently intergrades with *montana* to the north and *cottoni* to the east.

O. o. kenya (Kenya Oribi): isolated on the lower slopes of Mt Kenya. Extinct (Hillman *et al.* 1988).

O. o. haggardi (Haggard's Oribi): coastal Kenya to S Somalia, entirely isolated from other forms.

O. o. gallarum: C Ethiopia.

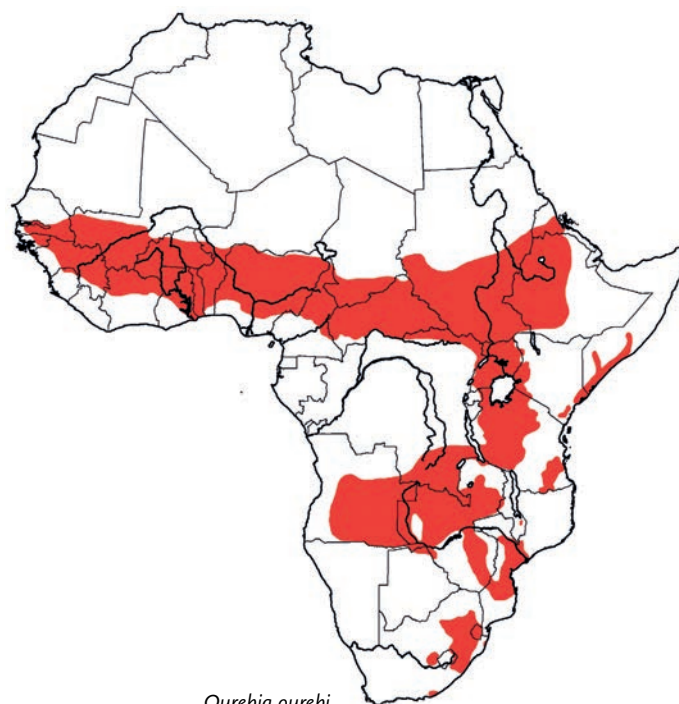
O. o. montana: SE Sudan to W Ethiopia.

O. o. goslingi: N DR Congo.

O. o. quadriscapa: Senegal to Nigeria.

Similar Species Similar sympatric species include the Steenbok *Raphicerus campestris*, Sharpe's Grysbok *Raphicerus sharpei*, Common Duiker *Sylvicapra grimmia* and Mountain Reedbuck *Redunca fulvorufula*. The Steenbok and Sharpe's Grysbok are smaller, stockier and more crouched in appearance than the Oribi; both lack the Oribi's striking black patch of skin beneath the ear and both have wider ears and a much shorter tail than the Oribi. Largest examples of the Common Duiker may come close to the Oribi in body mass, but this species is more crouched, shorter, lacks the black subauricular patch and has a much shorter neck than the Oribi. It is typically, but not always, darker in body colour than the Oribi and possesses a striking crest of hair between the horns. The Mountain Reedbuck is significantly heavier (ca. 30–50%) than the Oribi and typically greyer in body colour. It has a subauricular patch similar in appearance to that of the Oribi, but the horns of the Mountain Reedbuck are much thicker and noticeably curve forward at the ends. The Mountain Reedbuck's tail is much longer than the Oribi's and the tail's underside is white with no black markings.

Distribution Endemic to Africa. The distribution of the Oribi is extensive, but patchy, occurring in Guinea savanna habitat from Senegal, Gambia, Guinea-Bissau and N Guinea east to N Cameroon. In Sierra Leone, they were known to survive only in and around Outamba-Kilimi N. P. in the north, but there is no recent information



Ourebia ourebi

on the status of this population (East 1999). East of Cameroon, they range from S Chad and Central African Republic through S and E Sudan (where recent surveys in the dry season in the south have shown them surviving in much reduced numbers) and extreme NE DR Congo to C Ethiopia (within and to the west of the Rift Valley) and north to SW Eritrea. Their range extends in moist savannas and woodland mosaics from N Uganda and SW Kenya south through eastern and central-southern Africa to montane grasslands in SE South Africa. The only country in which they formerly occurred and are now considered extinct is Burundi, while in Rwanda they survive only in Akagera N. P. (East 1999, Apio & Wronski 2011). Shortridge (1934) recorded Oribis from N Namibia, and Smithers (1971) reported them from the eastern Caprivi, although the species was not reported during a questionnaire survey (Joubert & Mostert 1975); mention of the species in this country is oddly missing in Van der Walt (1989) and East (1999). In Botswana, they occur only in extreme north-east, from the eastern part of Chobe N. P. to the Zimbabwe border (East 1999). Their historical distribution is likely to have been more continuous across much of this range, whereas the current distribution is highly fragmented. An isolated and vulnerable population (*O. o. haggardi*) occurs in a coastal stretch from S Somalia into SE Kenya (East 1999).

Habitat Flat and gently sloping grasslands and mixed woodlands maintained by fire, grazing, or soil characteristics where mean annual rainfall is at least 500 mm. Altitude ranges from ca. 50 m (coastal Kenya) to over 2000 m (KwaZulu-Natal, South Africa and Mt Kenya). Proximity to open water (including dew) is essential in areas where rainfall is light or unevenly distributed through the year, although in many areas Oribis are considered to be water-independent, obtaining most of their moisture requirements from succulent herbage (Monfort & Monfort 1974, Oliver *et al.* 1978, Viljoen 1982). Vegetation varies from dry scrub, to mixed woodland, to treed savanna, to open grassland, to montane grassland, to moist

coastal savanna, to open flood-plain. Within each of these habitat types preferred micro-habitats are well-drained open pastures of short to medium grasses (100–1000 mm) with good visibility and cover for hiding and shade. Highest densities (i.e. 45 animals/km²) occur in moist tropical grasslands where annual rainfall is above 1100 mm and frequent (e.g. *Loudetia simplex* grassland in Rwanda). High densities (i.e. >30/km²) are also common on treeless flood-plain habitat (e.g. Kafue Flats, Zambia; Plewman & Dooley 1995).

Oribis often occur in close association with larger, less selective grazers such as the Plains Zebra *Equus quagga*, wildebeest *Connochaetes* spp., Common Hippopotamus *Hippopotamus amphibius*, African Buffalo *Syncerus caffer*, Topi *Damaliscus lunatus*, Thomson's Gazelle *Eudorcas thomsonii* and Hartbeest *Alcelaphus buselaphus*, which keep pastures short without diminishing greatly the Oribi's food supply (Estes 1991a), and which may enhance predator detection (Mduma & Sinclair 1994). Kingdon (1982) suggested that Oribi numbers decline where larger ungulates are extirpated and, thus, no longer serve to maintain short grasslands.

Abundance Oribis are locally common in suitable habitats at densities of 2–10 animals/km² (Mduma & Sinclair 1994, Arcese *et al.* 1995b, Adamczak 1999, Goldspink *et al.* 2002), but have been recorded at densities up to 45 animals/km² in exceptionally productive tropical grasslands and treeless flood-plains (Monfort & Monfort 1974, Plewman & Dooley 1995). In areas where it is uncommon or populations have been depleted, densities based on ground counts range from 0.1 to 0.4/km² (East 1999). Local densities are linked to abundance and evenness of rainfall and quality and quantity of preferred grasses (Brashares & Arcese 2002). Assuming an average density of 2/km² where common, and 0.2/km² elsewhere, East (1999) estimated a total population size of 750,000 animals. Numbers of Haggard's Oribi are probably in the low thousands.

Adaptations Oribis have several striking morphological and behavioural characteristics, including an enlarged digestive system adapted to processing grasses, an array of scent glands for olfactory communication and a highly variable social and mating system. This unique combination of 'primitive' and advanced traits has led to suggestions that the Oribi represents an evolutionary link between conservative thicket-dwelling antelopes and more recently derived grassland species (Kingdon 1982, Estes 1991a).

The Oribi is the only small bovid (<20 kg) that feeds primarily on grasses (Hofmann 1973, Gagnon & Chew 2000). The Oribi's use of foods that require slow fermentation and long passage times is possible because of a greatly enlarged forestomach (Hofmann 1973). Hofmann (1973) reports that a captive Oribi fed only browse gradually lost condition and died (see also Foraging and Food).

The Oribi possesses an arsenal of at least six sets of scent-glands including preorbital glands, subauricular glands, pedal and inguinal glands, and glands on the front and rear legs (Gosling 1985). Secretions from these glands are used in combination with urine and faeces to demarcate and maintain territory borders (Brashares & Arcese 1999a, b), in pair-bonding and group cohesion (Monfort & Monfort 1974), and most likely have many other functions that remain poorly understood. The most obvious scent gland to human observers is the preorbital gland, a trademark of Oribis, bulging prominently between the eye and mouth of the adult ♂.

As already noted, the architecture of the Oribi skull is modified to accommodate these considerable glands, most notably by the large fossae beneath the eyes in which the glandular tissue sits. Up to 45 times per hour, the ♂ tilts its head and inserts the distal portion of a plant stem into the vertical opening of the preorbital gland and deposits a black tar-like secretion (Brashares & Arcese 1999a). Mo *et al.* (1995) analysed the chemical constituents of the Oribi's preorbital gland secretions and identified 75 distinct chemical compounds that range widely in their volatility. It generally is assumed that the marks of each animal are chemically distinct and thereby serve as individual-specific olfactory signals, but this has yet to be demonstrated.

The Oribi displays flexibility in its mating system exceeding that seen in any other species of smaller antelope (Arcese *et al.* 1995b). Oribis are monogamous, polygynous and polygynandrous depending on habitat conditions (Rowe-Rowe *et al.* 1992). Oribis are dispersed in male–female pairs on overlapping home-ranges in drier and more seasonal habitats (e.g. KwaZulu–Natal, South Africa, Adamczak 1999, and N Ghana, Brashares & Arcese 2002). In wetter and less seasonal habitats, 1–4 ♂♂ assiduously defend a year-round territory and 1–8 adult ♀♀ (Arcese 1999, Brashares & Arcese 1999a). This variation in mating system is evident across and within populations. In Ghana, and likely elsewhere, Oribis display behavioural plasticity within subpopulations (Brashares & Arcese 2002). In micro-habitats characterized by abundant and high-quality green grasses (e.g. riverine habitats), adult ♀♀ form groups of 2–5 animals and ♂♂ defend a small territory encompassing the range of this group. In adjacent dry areas, ♀♀ are solitary and range widely and ♂♂ pair with a single ♀ and adopt a 'following' strategy throughout their large and non-exclusive home-range. 'Follower' ♂♂ quickly become polygynous and territorial after occupying a recently vacated territory in a high-quality habitat (Brashares & Arcese 2002).

Foraging and Food A selective grazer, the Oribi relies on fresh green grasses, but feeds also on forbs, legumes and tree foliage when fresh grass is unavailable. In their review of the feeding preferences of African bovids, Gagnon & Chew (2000) classed Oribis as 'variable grazers', taking as much as 90% grass in their diet; this is broadly supported by studies involving stable carbon isotope analyses of southern and East African bovids, which found that Oribis in these regions had 82% and 84% grass in their diet, respectively (Cerling *et al.* 2003, Sponheimer *et al.* 2003b).

When feeding, Oribis typically remove new leaves and seed heads of grasses and ignore older leaves and stems. Preferred grasses include *Themeda*, *Hyparrhenia*, *Loudetia*, *Eulalia*, *Andropogon* and *Pennisetum* (Kingdon 1982, Viljoen 1982, Awad 1985, Everett *et al.* 1992); the use of grass varies seasonally. In Ghana, Oribis in moist coastal savanna habitat feed year-round on green bunch-grasses (e.g. *Andropogon* sp.), while Oribis in dry Guinea savanna habitat to the north often (ca. 15% of time spent foraging) feed on forbs, tree leaves and nuts of the shea tree (*Butyrospermum parkii*) in the dry season (J. Brashares pers. obs.). Oribis in Serengeti N. P., Tanzania, occasionally eat flowers and large boletus mushrooms when available (J. Brashares & P. Arcese pers. obs.). Reilly *et al.* (1990) reported that Oribis in Golden Gate N. P., South Africa, would dig for corms of *Watsonia* sp.

Oribis regularly visit mineral licks and will travel across territory borders and gather in groups at preferred licks. Groups in Serengeti N. P. were observed on three occasions to break apart termitaria with their hooves and horns and consume the soil found within, presumably for its mineral content (J. Brashares pers. obs.). Oribis avoid planted croplands and plantations, but will use planted hayfields and occasionally may feed on field crops such as wheat, oats and new sprouts of sugarcane (Kingdon 1982, Perrin & Everett 1999, A. Marchant pers. obs.). In many areas, Oribis show a clear preference for sprouting grass in recently burnt areas (Oliver *et al.* 1978, Rowe-Rowe 1982a, Everett *et al.* 1991, Mduma & Sinclair 1994).

Foraging is most common during cool hours of early morning and late afternoon to early evening, often continuing into nightfall. During mid-day Oribis typically rest in tall grass or beneath a tree or shrub to escape the heat. Average time spent foraging varies between populations, ages and sexes. In Serengeti N. P., feeding comprised less than 10% of daytime activity for ♀♀ and juveniles and less than 5% for adult ♂♂ (J. Brashares & P. Arcese pers. obs.). In Red Volta F. R., Ghana, adults and juveniles spent ca. 20% of daytime actively feeding (J. Brashares pers. obs.). Oribis generally do not feed in heavy wind and rain.

Social and Reproductive Behaviour Group size, apparent mating system and territorial behaviour are extremely variable across the species' range and even within Serengeti N. P., where more than 500 individually identified Oribis were studied in detail over a period of seven years. Oribis are observed most often in male–female pairs, often with one (rarely two) young present; but also as single-male, single-female (0–82% of groups) or multimale, multifemale groups (0–39% of groups) (Arcese *et al.* 1995b). Sightings of lone animals in most instances are probably of ♂♂ patrolling the territory perimeter, young or old ♂♂ unable to secure or defend a territory, ♀♀ in the vicinity of young lying out, or other animals temporarily out of sight of a social group (J. Brashares & P. Arcese pers. obs.). Mean size of adult groups is 1.8 (Burkina Faso) to 3.92 (Murchison Falls, Uganda); group size is related positively to rate of apparent polygyny across populations in Africa ($r = 0.90$, $n = 9$) and years in Serengeti N. P. ($r = 0.88$, $n = 5$) (Arcese *et al.* 1995b). Apparent polygyny is also related positively to adult sex ratio and population density across years in Serengeti and populations in Africa (Arcese *et al.* 1995b). Group size including all ages in Serengeti N. P. is 3.1–4.3 (mean = 3.6, $n = 5$ yrs; Arcese *et al.* 1995b). Occasionally, Oribis occur in groups of up to 12 adults and young (Roosevelt & Heller 1915, Ansell 1960b, J. Brashares pers. obs.). Estimates of group size based on re-sightings of identified Oribis averaged 33% larger than estimates based on roadside counts of Oribis encountered at random (Arcese *et al.* 1995b).

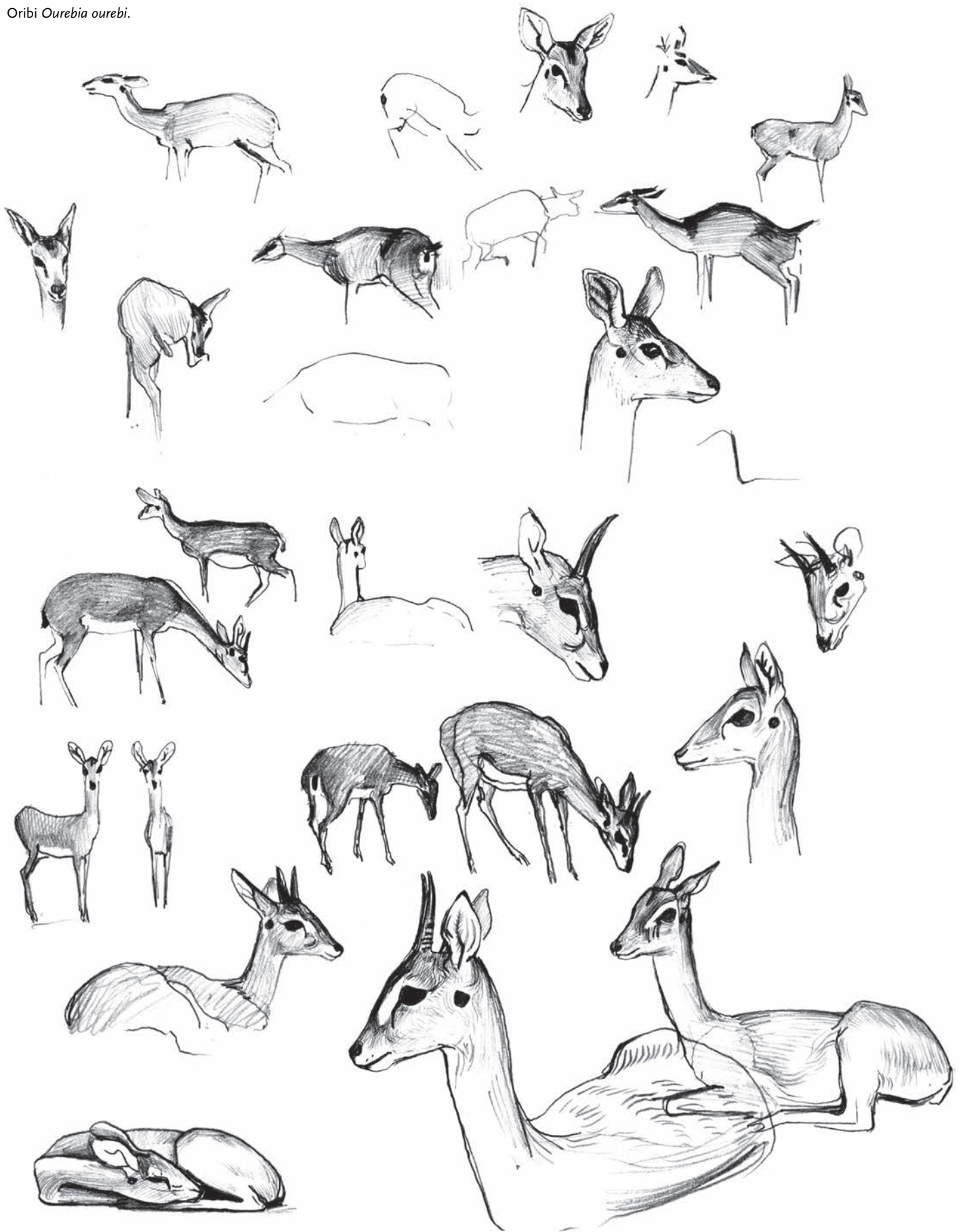
Smaller groups (especially lone animals) are more common in drier, cooler and/or less productive habitats and where concealing cover reduces the detection of group members often resting or feeding at distances of up to ca. 100 m (Rowe-Rowe *et al.* 1992, Arcese *et al.* 1995b, Brashares & Arcese 2002). In Ghana, geographic variation in rainfall is related closely to forage quality and quantity, with each of these variables also related positively to group size (Brashares & Arcese 2002). In Serengeti N. P., experimental reduction of tall grass cover by cool-season patch burning resulted in a marked increase in group size relative to unburned controls (P. Arcese pers. obs.). Median inter-individual distance of identified

group members was 7 m in north-west Serengeti N. P. during the 'dry-season' (ca. Jul–Dec), when migratory grazers and/or intermittent fires reduce grass cover (Arcese *et al.* 1995b); inter-individual distance was greater, but unquantified, during the wet season (P. Arcese pers. obs.). Large groups in less productive habitats are probably aggregations of non-territorial groups at sites of local resource abundance, but groups of up to 11 (5 adult ♂♂, six ♀♀) occupied strongly defended territories in productive habitats of north-west Serengeti N. P. (Brashares & Arcese 1999a). Aggregations also form during border conflicts between territorial groups (Arcese *et al.* 1995b). Studies of group size in Ghana and Zambia suggest that predator abundance does not predict social group size (Brashares & Arcese 2002, Goldspink *et al.* 2002, respectively).

In Serengeti N. P., 25% of 32 adult ♂♂ and 27% of 26 adult ♀♀ were present after four years on the territory where they were first identified, but only 14% of 35 male–female dyads remained intact over this period; this indicates a moderate rate of year-to-year residency within groups, but a low rate of long-term pairing (Arcese *et al.* 1995b). Consistency of group membership requires study where territories are defended seasonally or not at all.

Over most of their range Oribis occupy seasonal to year-round territories 0.1–60 ha in size, with territories generally being larger and defended less assiduously where annual rainfall is less than ca. 800 mm and/or mean minimum temperatures less than 5°C. In north-west Serengeti N. P., territories defended year-round range from 10 to 90 ha in size (mean = 60; Brashares & Arcese 1999a), similar to those in Akagera N. P. (8–61 ha; Monfort & Monfort 1974). Territories are more or less seasonal in South Africa but generally similar in size; in KwaZulu–Natal, recorded territory sizes were 60.2 ha (Everett *et al.* 1991) and 59.4 ha (Adamczak 1999). Oribis may abandon territoriality entirely in driest, coolest and/or least productive parts of their range, for example, at high-altitude sites in South Africa and the driest sites in Ghana (Oliver *et al.* 1978, Rowe-Rowe *et al.* 1992, Adamczak 1999, Brashares & Arcese 2002). On the Kafue Flats, Zambia, Oribis defend territories seasonally in lowland flood-plains (T. H. Clutton-Brock pers. comm.), but important details concerning group membership, site fidelity and social behaviour during the wet season are unstudied.

Defence of territory is primarily by the ♂ via active border patrols, chasing intruders, sparring with neighbours, and regular scent-marking with secretions of the preorbital gland, dung and urine (Gosling 1972, Brashares & Arcese 1999a, b). Rate of scent-marking varies seasonally and with social status of the ♂; rates are higher among dominant versus subordinate ♂♂ and for singleton ♂♂ versus those in multimale groups (Arcese 1999, Brashares & Arcese 1999a, b). Territories defended by male groups are marked more thoroughly than others, and in these groups dominant ♂♂ remained on territories longer than ♂♂ that defended territories without the aid of subordinate 'auxiliary males' (Arcese 1999); about half of auxiliaries in Serengeti N. P. were probably the offspring of dominants, but others immigrated as adults or remained philopatric on the natal territory after the dominant and presumed sire was replaced by a challenger (Arcese 1999). In Serengeti N. P., territory borders are marked by dung middens, often located on flat, open soil of eroded termitaria at distances of 30–150 m (Brashares & Arcese 1999b). Middens typically have 3–12 identifiable pellet groups, depending on rainfall and activity of dung beetles.



Preorbital marks are almost exclusively made by ♂♂, though 2–3 instances of marking by ♀♀ were observed in >3000h of observation (Brashares & Arcese 1999a). Marks are placed on vertical grass stems (ca. 50–70 cm in height; rarely on lateral branches of shrubs where grasses are burnt or otherwise absent). Marks are more common near shared borders, particularly those of multimale groups (Brashares & Arcese 1999a). Males mark at rates up to 70/h while patrolling the territory, more often in Serengeti N. P. during seven months prior to the main birth period.

Agonistic behaviour is observed often among ♂♂, especially at shared territory boundaries, but less often in ♀♀ (Arcese *et al.* 1995b, Arcese 1999, Brashares & Arcese 1999a, b, 2002). Monfort & Monfort (1974) described each sex as territorial towards same-sex intruders. In Serengeti N. P., individually identified adult ♀♀ sometimes moved 1–5 territory-widths without notable aggression in groups involved. One radio-collared ♀ dispersed in late gestation, then left her subadult female offspring several months later to rejoin her former group (P. Arcese pers. obs.; see below). On two occasions, established female group members attempted at first to smell and then to chase from their territory a newly arrived subadult ♀. In one case, two resident ♀♀ avoided a territorial ♂ that used his body and horns to maintain a 2–6 m distance between the residents and the newcomer. Upon avoiding the ♂, each of the residents chased the subadult ♀, who settled subsequently with two bachelors defending an adjacent territory. Other obvious signs of agonistic behaviour in ♀♀ were not observed (P. Arcese & J. Brashares pers. obs.), suggesting that female agonistic interactions may occur mainly when young female dispersers attempt to settle. Allogrooming has not been reported.

Agonistic encounters among ♂♂ have been described in detail (Monfort & Montfort 1974, Estes 1991a, Arcese 1999). Briefly, dominance interactions among group-living ♂♂ are generally subdued, with subtle threats observed most often. In this case a dominant ♂, with a slightly lower head and extended neck, may tip his horns towards a subordinate as they pass within a metre of one another. Subordinates may respond by veering slightly from their current path, jumping sideways or, occasionally, by lowering their head, neck and chest towards the ground (subadults). More obvious agonistic interactions are common among ♂♂ on adjacent territories and between a territorial ♂ and challenger. In rare cases, one can observe short distance chases, interspersed with bouts of ‘air-cushion fighting’, as well as actual contact of one male’s horns with the flank or head of another. The most severe encounters result in severe injury and the loss of territory. More commonly, ♂♂ engage in short bouts of one or more of the behaviours above. Arcese (1999) used maps and time courses to depict the dynamics of territory turnover and use of aggression in Serengeti N. P.

Oribis more than three months old use 1–3 sharp, nasal whistles to note their alarm, usually upon detecting a potential threat (Estes 1991a, P. Arcese & G. Jongejan unpubl.). In Serengeti N. P., Oribis that whistled generally held their neck erect, aimed their head at the object of interest, and then either changed paths, fled or accustomed themselves to the situation (e.g. presence of human observers, passing baboon troop). Whistles were recorded more often from ♀♀ than ♂♂ and more often from adults than younger animals (P. Arcese & G. Jongejan unpubl.). Oribis may also stamp a front foot

when standing alert. Young Oribis, and occasionally oestrous ♀♀, ‘bleat’ when pursued (see also Estes 1991a).

Oribis avoid predators in open areas mainly by maintaining a distance of >60 m from potential threats. Oribis also take advantage of sparse cover in open areas, such as by sitting adjacent to a small shrub, in a small depression, or among scattered rocks. In these conditions, Oribis approached closely will often jump up and then flee in a stiff-legged gait with tail erect. Estes (1991a) notes that this ‘rocking horse’ run may also be employed by territorial ♂♂ to advertise ownership. Fleeing Oribis often travel 100–200 m before stopping to face the perceived threat, and then sometimes whistle. A different pattern of escape is observed in conditions of dense cover and tall grass. In this case, Oribis sometimes tolerate an approach to within 10 m, before scurrying away in a low zig-zag run reminiscent of duikers and the Steenbok.

Genetic evidence of a mating system is absent, but detailed observations of ♂♂ and oestrous behaviour of ♀♀ suggests one ♂ monopolizes matings by following receptive ♀♀ closely and defending against the advances of subordinates in multimale groups (J. Brashares & P. Arcese pers. obs.). However, in multimale, multifemale groups, overlap in oestrous periods of co-habiting ♀♀ may allow successful reproduction by subordinates, who are observed to mount ♀♀ on occasion (Arcese 1999).

In Serengeti N. P., oestrous behaviour was recorded in detail for several individually identified ♀♀ over one or more behavioural oestrus periods, and later verified via assay for steroid hormone products in faeces (P. Arcese pers. obs.). During oestrus ♂♂ maintained a close proximity to ♀♀, often lying or standing within 1 m. Among group-living male Oribis, one dominant ♂ usually isolated the ♀ from other group members, but in a few cases two or more ♂♂ engaged simultaneously in courtship. During courtship, ♂♂ habitually test female urine, and often lick the female’s side or hindquarters as she stands or sits. Males may perform repeated front leg lifts to the side or rear of a standing or sitting ♀, and they often follow closely even those ♀♀ that bleat or run short distances to avoid them. The intensity of courtship varies over the ca. 4–6 day behavioural oestrus, but reaches a plateau 1–2 days in duration. Several times during this plateau ♀♀ will stand to be mounted instead of running ahead and will allow the ♂ to ejaculate. Montfort & Montfort (1974) and Estes (1991a) also provide descriptions and drawings. In two ♀♀ in Serengeti N. P., two successive behavioural oestrous periods were observed via behavioural and hormonal assay to have been separated by about 14 days (P. Arcese pers. obs.). Mounting is rare among Oribis in Serengeti N. P. outside of the oestrous period, but tail marking by ♂♂, leg-lifts and testing of female urine are common outside of behavioural oestrus.

Young lie out for 2–10 weeks before joining the mother and the group during regular movements (J. Brashares & P. Arcese pers. obs.), but are much more precocious in captivity (Le Riche 1970). During this time, young are visited several times daily by the mother, who stands as the young sucks in bouts for up to 30 min. Hiding sites are located in areas with rocks, shrubs or grass that provide concealing cover and are visited occasionally by the entire social group. From the account of a captive birth, there is a suggestion that ♂♂ act as sentinels and engage in other parental behaviour (Le Riche 1970). These observations are supported in the field by observations of ♂♂ alarm-calling when predators are detected in

the vicinity of hiding young (J. Brashares & P. Arcese pers. obs.); more work is required to determine the extent of male parental care. Young 1–3 months old generally remain close to their mother, often lying within 1 m, occasionally straying to 30 m while foraging or frolicking. One-month-old young have been observed with the social group in 12% of 42 observations, compared with 73% of 51 sightings of groups with young ca. 3.5 months old. Oribi juveniles ca. five months old were observed with their social group as often as expected by adult re-sighting rate (81%; Jongejan *et al.* 1991). The proximity of the mother and young is often less than that between other group members less than 7–10 months of age (J. Brashares & P. Arcese unpubl.).

Frolicking is common in Oribis under four months of age, most often as kicking, jumping, dashing and head-butting. One young male twice butted his mother vigorously in the side in play, but was then rebuffed by the female's threatening head-down posture (J. Brashares & P. Arcese pers. obs.).

In Serengeti N. P., pregnant ♀♀ occasionally distanced themselves from the social group, or dispersed to another territory 1–2 weeks prior to giving birth. One radio-collared ♀ dispersed ca. 2 km (ca. four territories) to join a new social group occupying unburned savanna with tall, rank grasses. Her former territory encompassed an area wherein mature grasses had burned and cover was scarce, but where much regrowth was available as forage; this suggests that the motivation for the move was security cover for young. This ♀ returned to her former territory ca. 8 months later without her surviving daughter.

Reproduction and Population Structure Oribis breed year-round where climate allows (e.g. north-west Serengeti N. P.), but with peak breeding and birthing seasons evident (Jongejan *et al.* 1991, Sinclair *et al.* 2000); the former precedes the latter by a gestation of ca. 6.5–7 months. In Serengeti N. P., births are commonest from Mar to May, coinciding with long wet-season rains and resulting grass growth, but births have been observed in all months of the year (Jongejan *et al.* 1991, Sinclair *et al.* 2000). Here, vulnerability of young to depredation may select as strongly for seasonal breeding as forage volume (Jongejan *et al.* 1991). Peak birth period, generally lasting 3–4 months, varies regionally but coincides with or is restricted to the wettest months of the year (Montfort & Montfort 1974, Estes 1991a), especially in more arid, seasonal and cooler climates; in southern Africa, the main birthing season is from Oct to Dec (Oliver *et al.* 1978, Viljoen 1982). A single young is born, but many ♀♀ experience an immediate postpartum oestrus that facilitates a potential reproductive rate of more than 1.5 young per year (Le Riche 1970, Dittrich 1974, Jongejan *et al.* 1991). Data are unavailable to test whether inter-birth interval depends on survival of the young, climate or available forage, but some data suggest it is independent of the sex of the young (Jongejan *et al.* 1991).

Young Oribis grow rapidly, attaining near-adult size in about seven months. In Serengeti N. P., median age of young about one-third shoulder height of adult ♀ = 2.2 months; median age at half size = 3.6 months; at two-thirds size = 4.7 months; and at three-quarters size = 7.0 months (Jongejan *et al.* 1991). Various reports suggest age at maturity is 10–14 months in ♂♂, but ca. three months earlier in ♀♀ (Cade 1966, Kingdon 1982, Jongejan *et al.* 1991, Estes 1991a). The single estimate for ♂♂ is from a hand-reared Oribi

that inseminated captive ♀♀ at 14 months of age (Cade 1966); this precedes slightly the typical age at which ♂♂ first defend a territory (15 months: Estes 1991a; 17 months: Jongejan *et al.* 1991, Arcese 1999). Females in Serengeti N. P. typically elicited courtship interest from ♂♂ at more than seven months of age and occasionally stood to be mounted. One nine-month-old ♀ was mounted repeatedly and appeared via hormone assay of faecal progesterone concentration to have experienced normal oestrus (J. Brashares & P. Arcese pers. obs.).

In Serengeti N. P., about half of social groups contained a juvenile less than seven months old (range 0.3–0.8; Arcese *et al.* 1995b). Sex ratio is highly variable across the species' range, 0.83–3.55 ♀♀ per ♂; sex ratio is related positively to apparent rate of polygyny for populations in Africa and years of study in Serengeti N. P. (Arcese *et al.* 1995b). However, forage quality and quantity are a better predictor of adult sex ratio and apparent polygyny in Ghana (Brashares & Arcese 2002). Longevity in captivity is on the order of 14–16 years (Estes 1991a, Weigl 2005).

Predators, Parasites and Diseases Leopards *Panthera pardus* are the most important predator of adults in Serengeti N. P. (two of three radio-collars recovered), but Cheetahs *Acinonyx jubatus*, Lions *Panthera leo*, Spotted Hyaenas *Crocuta crocuta* and African Rock Pythons *Python sebae* probably kill adults opportunistically. Various anecdotal reports suggest that major predators elsewhere are similar to the Serengeti N. P., and that abundance is increased where these predators are extirpated. A freshly dead adult male Oribi in Serengeti N. P. that was found within 5 m of resting territorial group members showed no obvious signs of cause of death, but necropsy revealed free-flowing blood consistent with haemolytic snake venom; anthrax, common in the region and often associated with absence of coagulation, was ruled out by lack of inflammation in internal organs/lymph glands. Young are susceptible to a wide range of opportunistic predators due to small size, including large predatory birds and snakes and small felids and canids. Adult male baboons *Papio* spp. in Serengeti N. P. killed a young Oribi lying out, and regularly elicit the alarm calls of adult Oribis.

There is very little information on parasites and diseases. A single Oribi sampled in KwaZulu–Natal harboured the following parasites: *Trichostrongylus falculatus*, *T. colubriformis*, *Trichostrongylus* sp. and *Cooperia yoshidia* (Boomker *et al.* 1984). These were somewhat similar to those recorded from Oribis in Kruger N. P. (where Oribis no longer occur), although *Impalaia tuberculata*, *Cooperia fuelleborni* and *Oesophagostomum colombianum* were not present in Oribis from KwaZulu–Natal (Boomker *et al.* 1986). Other parasite records include *Setaria scalprum*, *Haemonchus contortus* and *Onchocerca* spp. (Ortlepp 1961, Round 1968).

Conservation IUCN Category: Least Concern (*O. o. haggardi* – Vulnerable C1; *O. o. kenya* – Extinct). CITES: Not listed.

The Oribi is now rare or absent in much of its former range, with hunting (both legal and illegal) the primary reason for declines of populations outside, and often inside, protected areas. The Oribi's poor stamina makes it vulnerable to hunting with dogs (Kingdon 1982, J. Brashares pers. obs.); in Kenya, a rancher related a case of her poodle running-down and killing an adult Oribi (sex unknown). Its tendency to whistle and approach potential predators also makes

it an easy target for hunters using firearms (J. Brashares pers. obs.). In Ghana, hunters report that the Oribi's reluctance to leave its territory makes it easy to follow and shoot, and that ♀♀ are shot first because a ♂ rarely abandons a fallen mate and, thus, can be taken easily with a second shot (J. Brashares pers. obs.). Oribi meat is much sought after in West Africa, where it is considered to be of high quality (J. Brashares pers. obs.). In Comoé N. P. in Côte d'Ivoire, Oribis experienced a decline of around 92% between 1978 and 1998 primarily due to poaching (Fischer & Linsenmair 2001a). Conversion of open grassland for agriculture and forestry has also resulted in declines and extirpation of Oribi populations throughout Africa (East 1999).

Populations of Oribis appear stable in areas where hunting is minimal or where snares rather than guns or dogs are the main tool used in hunting. When left unmolested Oribis can occur in close proximity to human settlement and often thrive on private ranches, as in South Africa (Van Teylingen & Kerley 1995, J. Brashares & P. Arcese pers. obs.). Large populations occur in a number of protected areas throughout their range, including Niokolo-Koba N. P. (Senegal), Comoé N. P. (Côte d'Ivoire), W N. P. (Niger), Arly-Singhou (Burkina-Faso), Pendjari N. P. (Benin), Bénoué, Bouba Ndjida and Faro National Parks (Cameroon), Omo N. P. (Ethiopia), Serengeti N. P. (Tanzania), Kafue and Liuwa Plains National Parks (Zambia), Liwonde and Kasungu National Parks (Malawi), and Golden Gate Highlands N. P. (South Africa) (East 1999). Recent surveys in the

dry season in S Sudan have shown Oribis to be surviving in much reduced numbers in Boma and Southern National Parks (Fay *et al.* 2007). Haggard's Oribi occurs in Boni-Dodori National Reserve in Kenya and Bush Bush N. P. in Somalia, but there is no information available on its status.

Measurements

Ourebia ourebi

HB (♂♂): 1000 (930–1050) mm, n = 14

HB (♀♀): 1050 (1010–1110) mm, n = 8

Sh. ht (♂♂): 640 (600–660) mm, n = 16

Sh. ht (♀♀): 650 (630–690) mm, n = 8

T (♂♂): 120 (80–150) mm, n = 14

E (♂♂): 120 (100–130) mm, n = 14

WT (♂♂): 17.0 (15.0–20.0) kg, n = 13

WT (♀♀): 19.0 (17.0–21.0) kg, n = 5

Tanzania (Jongejan *et al.* 1991, G. Jongejan & P. Arcese unpubl.)

Maximum recorded horn length is 19.0 cm for a pair of horns from Zomba, Malawi (Rowland Ward)

Key References Arcese *et al.* 1995b; Brashares & Arcese 2002; Goldspink *et al.* 2002; Jongejan *et al.* 1991; Monfort & Monfort 1974; Rowe-Rowe *et al.* 1992.

Justin S. Brashares & Peter Arcese

Tribe REDUNCINI

Reduncines

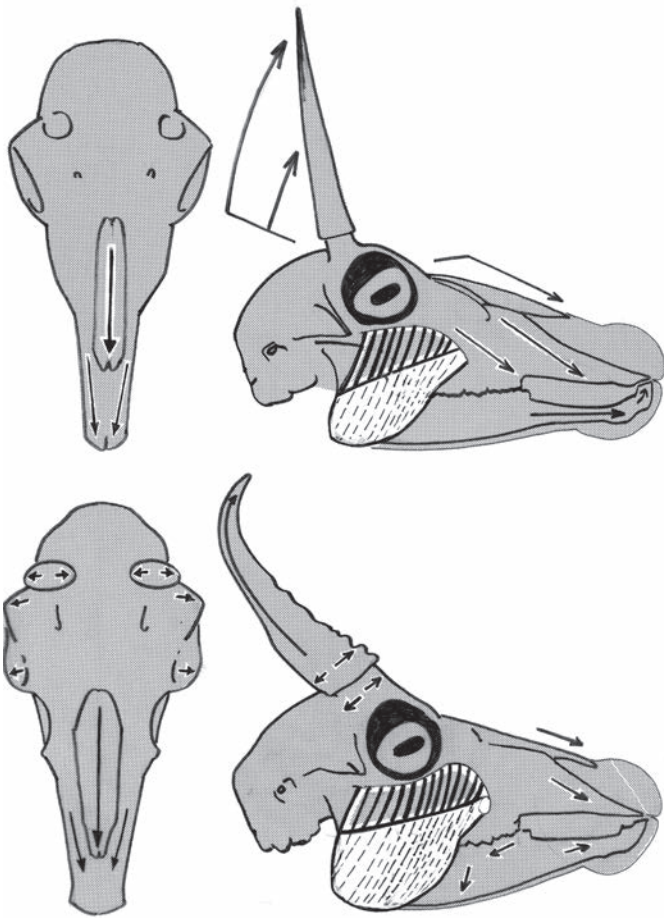
Reduncini Knottnerus-Meyer, 1907. Arch. Naturgesch. 73: 39.

The Reduncini comprises nine species arranged in three genera. *Redunca* is a unified group of three small- to medium-sized species. *Kobus* is a more diverse assemblage of five medium- to larger-sized species and this makes it harder to apportion morphological characters between the tribe and genera in a clear-cut manner. *Pelea*, containing only the Grey Rhebok *Pelea capreolus*, has sometimes been included in a separate tribe or subfamily of its own (e.g. Roberts 1951, Ansell 1972), but has been shown to cluster with the reduncines (Vrba & Schaller 2000, Birungi & Arctander 2001, Hernández Fernández & Vrba 2005) having diverged shortly before the separation between *Kobus* and *Redunca*. We therefore treat *Pelea* as a reduncine in this work. There are cranial similarities between *Pelea* and the Mountain Reedbuck *Redunca fulvorufula*, but the bullae are smaller and the cheekteeth differ. *Pelea* also differs from other Reduncini in lacking inguinal and subauricular glands (but possessing pedal glands and a preputial gland), while the horns are short, straight spikes instead of curved hooks.

Reduncini, even the smaller species, are more heavily built than Antilopini. Reduncines have slender to stocky legs, a long, well-muscled body and a relatively thick neck, especially in ♂♂. Pelages of the larger species are shaggy while smaller ones are sleek or slightly fleecy. Coat colours are usually brown, greyish or tan, sometimes with leg and throat markings. More striking colours and sexual dimorphism of colour and body weight can be seen in kobs and lechwes, particularly the White-eared Kob *Kobus kob leucotis* and



Myology of the neck in male Kob *Kobus kob* showing enlarged *longus capitis* muscle compared with same, slender muscle in Oribi *Ourebia ourebi*.



Skull architecture in (above) Grey Rhebok *Pelea capreolus* and (below) Mountain Reedbuck *Redunca fulvorufula* showing fine, straight horn and narrow, elongated muzzle in former. Deeper mandibles, enlarged masseter and thicker curved horn in latter.

the Nile Lechwe *Kobus megaceros*, both in the Sudan and both coloured dark brown or even black, with pale or white markings.

Female reduncines, with very rare exceptions, do not possess horns. The horns of ♂♂ are annulated and curve forward at the tip to a greater or lesser degree (this is pronounced in reedbuck, but less so in the Kob, Southern Lechwe *Kobus leche* and Waterbuck *Kobus ellipsiprymnus*), and corresponds with forward striking with the head, powered by muscles that help shape the characteristic bulging neck of ♂♂. The ontogenetic growth sequences in antelope horns have phyletic significance and are discussed in Kingdon (1982); thus, an upright, vertical base section is not typical for reduncines, is only seen in the Kob and Puku *Kobus vardonii*, and appears last in their ontogenetic developmental sequence. Horns of the Nile Lechwe have more of a low backward sweep, and those of adults of the Southern Lechwe a slightly sigmoid curve at the very base. Consequently, much of the length in lechwe horns and all of the length in the Waterbuck and reedbucks curves upwards from a nearly horizontal inclination and has a concave profile of the anterior edge.

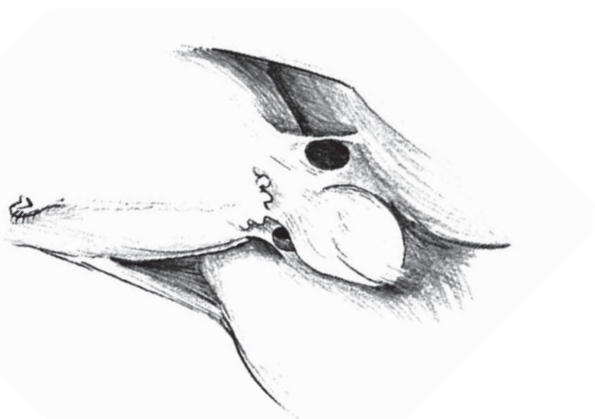
Preorbital glands are absent, except in the Puku (which has active facial glands) and in the Kob (and then only vestigial), and as such there are no preorbital fossae. Pedal glands are also absent or vestigial, although pedal glands are present on all four feet in *Pelea*.



TOP: Superficial myology of Waterbuck *Kobus ellipsiprymnus* adult male.

ABOVE: Waterbuck *Kobus ellipsiprymnus* adult male skeleton.

All members, except *Pelea* and the Waterbuck, have well-developed inguinal glands in the groin. All have a pungent overall odour that emanates from sebaceous glands and films the entire body. This provides a seal against water-loss and possibly some insulation against temperature extremes but is also likely to carry socio-sexual signals (as must their musky urine). Reduncines, again with the exception



Invaginated inguinal glands in groin of Bohor Reedbuck *Redunca redunca*.

of *Pelea*, have black, glandular patches below the ears, which, among other messages, advertise the females' breeding condition. The smaller species whistle and make ritualized 'rocking-horse' displays, which apparently signify subordination. These might be the long-grass equivalent of the stotting or pronking of antelopes from more open habitats. Females of all species have two pairs of inguinal nipples.

In understanding the evolutionary history of Reduncini, we need to take account of their fossil record in the Asian Siwaliks deposits, which has been known since the nineteenth century. Recognizable reduncines of fairly small size are first known from the late Miocene (8.0–6.0 mya) in the Siwaliks (Barry *et al.* 2002) and in Africa. They may have started with horn cores that were gazelle-like but with strong transverse ridges (sometimes separated as an extinct genus *Dorcadoxa*). They quickly diversified before the Miocene ended (Vrba & Haile-Selassie 2006) and even spread briefly into parts of southern Europe. During the Pliocene in Africa there were a number of more or less kob-like lineages, sometimes with more advanced features of certain premolar teeth than in modern reduncines (Gentry 1981). A distinctive genus, *Menelikia*, appeared in East Africa and survived into the early Pleistocene. An interesting study by Spencer (1997) concluded that its food must have been homogeneously distributed like grass, but tender and soft. Could this have been some type of swamp vegetation? The oddest-known reduncine fossil is a unique Pleistocene frontlet from Olduvai Gorge, Tanzania, *Thaleroceros radiciiformis*, with large, disproportionately massive but short horn cores mounted on a united horn pedicel (Reck 1937, pl. 8).

Other Pleistocene fossils in Africa are mostly recognizable as related or ancestral to living species. The Southern Lechwe seems to have separated from the Waterbuck stock around the start of the Pleistocene, but it is worth noting that the skull of the Nile Lechwe has some sinus development within its frontal bones, a character otherwise better seen in the extinct *Menelikia*.

Fossils of *Redunca*, as at present understood, are less common than *Kobus*. In the Indian sub-continent, reduncines survived at least until the early Pleistocene. They were reminiscent of lechwes or kobs, but had stronger temporal ridges on their cranial roofs. It is noteworthy that such a water-associated group of antelopes, apparently poor dispersers and now restricted to well-watered areas of Africa, must, therefore, once have ranged across parts of Arabia, as did hippos. This implies former long periods of moist conditions along the Nile



Upper right occlusal surface of toothrow in Mountain Reedbuck *Redunca fulvorufula* with deciduous milk teeth still in position.

Valley, other Asian rivers and along moist coastal zones, notably in Arabia.

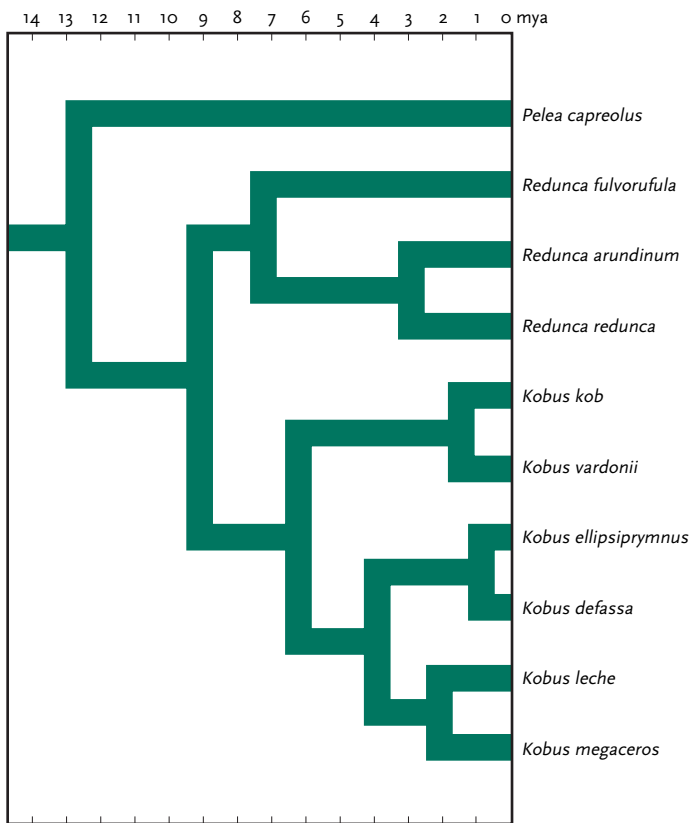
The occlusal complexity of present-day reduncine teeth resembles that of the much larger extant Bovini, and the temporal ridges of the Plio-Pleistocene Siwaliks reduncines prompted Gentry & Gentry (1978) to accept Reduncini as related to Boselaphini, which also have such ridges and from which Bovini evolved. This view was wrong, and the simpler and more antilopine-like characters of fossil reduncine teeth at Langebaanweg (Gentry 1980) suggested that parallel evolution may have occurred.

Kingdon (1982) discussed the ecological, behavioural and anatomical reasons for Reduncini sharing ancestry with the Antilopinae (in the sense used in this volume), and this phylogenetic affiliation has been confirmed by molecular studies (e.g. Gatesy *et al.* 1997, Matthee & Robinson 1999a, Birungi & Arctander 2001, Hassanin & Douzery 2003). Molecular studies agree in suggesting that Reduncini are probably close to the earliest origins of the Antilopinae, but vary in the details: Matthee & Robinson (1999a) placed the reduncine divergence after the caprines, but before the divergence of alcelaphines/hippotragines. A link with Cephalophini was proposed by Gatesy *et al.* (1997), an idea taken up by Hernández Fernández & Vrba (2005). Hassanin & Douzery (2003) treated Reduncini, Cephalophini, Antilopini and Aepycerotini as basal groups of Antilopinae. Kingdon (1982) and Vrba *et al.* (1994) and this volume have posited some form of association between Reduncini and the Oribi *Ourebia*.

Below the tribal level, molecular relationships among species of the genera *Kobus* and *Redunca* have now reached some general agreement with earlier morphology based assessments (Birungi & Arctander 2001) and the phylogenetic tree of relationships presented here reflects the results of these studies.

Reduncines are grazing antelopes with a diet of fresh rather than coarse grasses. Their prime need is for grassland habitats in the vicinity of water, such as lake margins or river flood-plains, and they have not developed any physiological capability for drought endurance. They find cover among tall grasses or in water, and the two lechwes feed in water. Waterbucks can be found in both grassland and adjacent woodland. The Mountain Reedbuck is exceptional in inhabiting montane rather than edaphic grasslands, but still needs regular access to water. Species of *Redunca* are less gregarious than *Kobus*, they lead more concealed lives within the cover afforded by long grass, and they are more active nocturnally.

The preferred habitats of most reduncines consist of valley sumplands, which are rich in food for grazers but are unstable because they dry out or catch fire. Antelopes find it difficult to cope with fluctuating water-levels, sticky soils and rapid growth of nearly impenetrable grasses. Only the lechwes, with swamp-adapted hooves, can reside permanently in wetlands. For the rest, accommodation



Tentative phylogenetic tree for Reduncinae (modified from Hernández Fernández & Vrba 2005).

to radical seasonal changes inhibits extreme specialization, making reduncines unusually homogeneous. The instability of their very productive habitats encourages substantial fluctuations in numbers. This is exacerbated by their inability to disperse. Seasonal changes lead to short-distance movements that also cause crowding, sometimes of spectacular proportions (notably in *Kobus*).

To accommodate both crowding and short-range dispersal, reduncines have very flexible relationships between the sexes. Females are relatively independent and are the object of intense competition between ♂♂. Substantial differences in the size, morphology and behaviour of the sexes correspond to separate male and female strategies. The ♀♀ of different reduncine species have more in common than the ♂♂ (which look and behave very differently from species to species).

Because they are the major bovid lineage adapted to valley grasslands, reduncines have considerable potential for rational exploitation, having the fastest growth rates of any bovid, insignificant disease problems (compared with cattle) and very acceptable meat and hides. Large populations of the more social species are unlikely to survive unless their potential for sustained yield cropping is realized because they occupy habitats with a high priority for agriculture or livestock development.

Jonathan Kingdon & Alan Gentry

GENUS *Pelea* Grey Rhebok

Pelea Gray, 1851. Proc. Zool. Soc. Lond. 1850:126 [1851].

Pelea includes only the Grey Rhebok *P. capreolus*, a small- to medium-sized antelope of slender proportions limited to South Africa, Lesotho and Swaziland, mainly in upland habitats.

The genus has a troubled history. It has been included with the Antilopini (Oboussier 1970a), Caprini (Gentry 1978), Neotragini (Georgiadis *et al.* 1990, Gentry 1992), or even in its own tribe or subfamily (Roberts 1951, Ansell 1972, Vrba 1976). Recent analyses of morphological (Vrba & Schaller 2000) and molecular data (Gatesy *et al.* 1997, Hassanin & Douzery 1999, Matthee & Robinson 1999a, Matthee & Davis 2001; but see Birungi & Arctander 2001) concur with those earlier classifications (e.g. Pocock 1910, Simpson 1945) that suggest that *Pelea* should be included as a primitive taxon within the Reduncini, and Grubb (2005) included it in his subfamily Reduncinae. Grouping of *Pelea* with other reduncines has

been unambiguously established in a composite phylogenetic tree (Hernández Fernández & Vrba 2005).

Pelea is distinguished from *Kobus* and *Redunca* by strong morphological differences. The skull of this species is similar to that of the Mountain Reedbuck *Redunca fulvorufula* in outline, but is characterized by: small auditory bullae; cheekteeth not so nearly specialized, with less prominent styles and much less complicated enamel figures in the wear pattern; long lachrymal and ethmoid fissure; and a low-placed ridge marking the origin of masseter. In addition to some behavioural differences, *Pelea* has no inguinal glands, no subauricular gland and the horns are quite different.

Peter Grubb

***Pelea capreolus* GREY RHEBOK (VAAL RHEBOK, RHEBOK)**

Fr. Rheboux; Ger. Rehantilope

Pelea capreolus (Forster, 1790). In: Levaillant, Erste Reise Afrika, p. 71. 'Ouwe-hoeck', now specified as South Africa, Western Cape, Caledon, Houhoek Pass; see Skead (1973: 79).

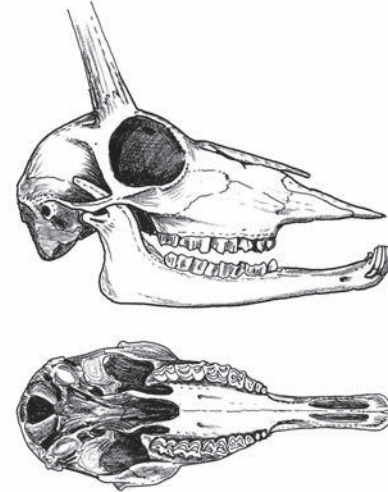


Grey Rhebok *Pelea capreolus*.

The name 'roebuck' appears often in early records of settlers in the Cape (South Africa); this animal probably reminded these settlers very much of the European Roe Deer *Capreolus capreolus*. The pronunciation and spelling over the years have changed through roe, rabock, reebok, raybuck to rhebok in English and 'ribbok' in Afrikaans (Skead 1980).

Taxonomy Monotypic. Synonyms: *lanata*, *villosa*. Chromosome number: not known.

Description A graceful, slender antelope of small to medium size, with neck long and slender, forehead swollen and muzzle elongated. Nose black, large and swollen (slight pressure after death yields droplets of moisture from this glandular structure). Ears long, narrow and pointed, with white hairs inside. Black-lidded eyes very prominent and surrounded by a conspicuous white ring. Some white also present on sides of the muzzle and chin. No subauricular patches. Upperparts of the body and flanks greyish-brown, face and outer parts of the legs tawny; underparts pure white. Pelage is soft, short, dense, thick and woolly. Dorsal 'guard' hairs have a brownish-grey base, a lighter shaft and a darker band near the tip; under 'guard' hairs are white. In cross-section, guard hairs are uniform oval or circular. Scales at the base of these hairs have a regular waved mosaic pattern, while those of the shafts and tips have irregular waved patterns. Scale margins are smooth, but rippled at tip (Keogh 1983). Tail bushy and white below. Hooves short, triangular and compact; lateral ('false') hooves are present. Preorbital and inguinal glands are absent, but



Lateral and palatal views of skull of Grey Rhebok *Pelea capreolus*.

there is a preputial gland (unique amongst the Reduncini), and pedal glands are present on all four feet (the glandular sacs contain a pale-coloured, foul-smelling secretion).

Horns, present in ♂♂ only, are straight, upstanding and ringed (about ten annuli) for about half their length. Skull characterized by a short, rounded braincase, small auditory bullae, and the long rostrum, nasals and lachrymal bones and ethmoid vacuity. Orbits are tubular and there are no preorbital fossae. First incisors are broad; other incisiform teeth are narrow, but second incisors are a little broader.

Geographic Variation None recorded.

Similar Species

Redunca fulvorufula. Co-occurs at higher altitudes in Swaziland and Lesotho, and several provinces in South Africa (Free State, Mpumalanga, KwaZulu-Natal, Eastern Cape, Western Cape and Limpopo), although Mountain Reedbucks tend to prefer tall grass areas. Subauricular patches are present; ears more rounded; belly sharply demarcated from the rest of the body; horns of Mountain Reedbuck ♂♂ curve forward. Females of the two species are difficult to distinguish and neither possesses horns. Mountain Reedbucks seldom lift their tail when running.

Distribution Endemic to a small region within southern Africa, inhabiting montane and plateau grasslands of South Africa, Swaziland and Lesotho (Skead 1980, 1987, Ferreira 1983, Lynch 1983, 1989, 1994, Rowe-Rowe 1994, Monadjem 1998, East 1999). Their distribution is discontinuous and patchy due to the decline in numbers, and they no longer occur north of the Orange R. in the Northern Cape, South Africa, or in parts of the North West Province (see Du Plessis 1969 for historical distribution). They formerly occurred widely



in the highveld of western Swaziland, but have disappeared from parts of their range; they remain fairly common in Malolotja N. R. and still survive locally in unprotected areas (Monadjem 1998). In Lesotho, they probably occurred widely in the past, but have been reduced to a few scattered remnant populations (Lynch 1994).

East (1999) notes that they are believed to have occurred in SE Botswana, in hilly country around Gaborone (presumably based on Shortridge 1934), but Smithers (1971) remarks that evidence of their occurrence in historical times is based on hearsay and there is no conclusive evidence of their former occurrence in Botswana.

The prehistoric distribution of Grey Rhebok is vague (Vrba 1975). Fossil remains from Kromdraai, Swartkrans and Sterkfontein in South Africa apparently date back to the lower Pleistocene.

Habitat Grey Rhebok are associated with rocky hills, mountain slopes and plateaux with good grass cover. They are found on slopes of up to 35 degrees in the Drakensberg, but prefer gentler slopes of less than 20 degrees (Ferreira 1983, Rowe-Rowe 1983). A preference for open, short grassveld (<20 cm) is associated with areas that have few stones or rocks and is related to defensive behaviour (Ferreira 1983). Habitat selection is according to the structure of the vegetation rather than floristic composition (Ferreira 1983). Rowe-Rowe (1982a), Beukes (1987) and Scott (1991) found that Grey Rhebok prefer short, burnt veld for feeding and longer grass for cover. In the Drakensberg there is a significant preference for the warmer north, north-east and east facing aspects throughout the year (Ferreira 1983, Rowe-Rowe 1983).

Abundance Owing to hunting pressure and habitat destruction, Grey Rhebok numbers have declined over the years. In South Africa, total numbers of Grey Rheboks are in excess of 9600, with at least 4600 found in protected areas and around 5000 on private land (East 1999). Grey Rheboks are the only bovid found in reasonable numbers in Lesotho, where the total population is thought to be in excess

of 200 animals (East 1999). Numbers in Swaziland are unknown, but Monadjem *et al.* (2003) report that they do well in Malolotja N. R. and are protected in Mlilwane Wildlife Sanctuary. East (1999) suggested that total population numbers stand at around 18,000.

The largest population in a protected area is in Ukhahlamba–Drakensberg Park (2000–3000 individuals), where ecological densities range from 1.8/km² to 4.3/km² (Rowe-Rowe 1994). Density at Highmoor State Forest in KwaZulu–Natal was 2.4/km² (Oliver *et al.* 1978), and at Sehlabathebe N. P., Lesotho, 1.6/km² (Kopij 2006). At Sterkfontein Dam N. R., Free State, densities were higher at 6.4/km² (Taylor *et al.* 2007), similar to the 6.7/km² in Bontebok N. P. in the Western Cape (Beukes 1984).

Adaptations Grey Rheboks occur in a range of climatic zones and vegetation types, from coastal fynbos to the Drakensberg alpine zone, and their densities vary due to the influence of the prevailing environmental factors. In colder areas, warmer air zones associated with topographic features are selected (for example, in the Drakensberg where the average minimum temperature during winter drops to below 0°C; Ferreira 1983). Although Mountain Reedbucks co-inhabit the hills and mountains in the range of Grey Rhebok, they have a different feeding behaviour and use physiographic features and vegetation types differently. While Grey Rheboks prefer short open veld, Mountain Reedbucks are common on steeper valley sides with taller grass and scattered woodland. In the Drakensberg, Mountain Reedbucks also have a narrower altitudinal range than Grey Rheboks. The latter occur at greater densities than Mountain Reedbucks and may occur at altitudes above the montane belt (above ca. 2800 m) (Vincent 1962, Ferreira 1983, Rowe-Rowe 1983). Grey Rheboks have developed a fleeing behaviour, important when evading natural predators in their ‘open’ environment. When disturbed, Grey Rheboks utter a sharp bark, taking flight towards open, higher areas from where the enemy can be easily seen. Flashing of the white underside of the tail also serves as a warning mechanism to conspecifics.

Foraging and Food Grey Rheboks are predominantly browsers (Beukes 1984, Ferreira & Bigalke 1987, Taylor 2004, Skinner & Chimimba 2005), and were classified as such by Gagnon & Chew (2000) in their review of the dietary preferences of African bovids. However, although they are almost entirely browsers, they feed selectively (Taylor & Skinner 2006a). In the Free State (summer rainfall region) faecal analysis showed that dicotyledons comprise 88% of their diet in areas with basal cover of dicotyledons less than 3% (Ferreira 1983). This changes only slightly during the year and ranges from >90% in winter to 78.5% in summer. In Bontebok N. P. (winter rainfall region), dicotyledonous shrubs and forbs account for 96.9% of the diet (Beukes 1984). Here roots, seeds and flowers contribute to between 1.5% and 14.6% of rumen contents (especially in the months Jun, Aug and Oct when these were more easily available). Shrubs and forbs lower than 250 mm were selected for, with the genera *Disparago*, *Metalsia* and *Aspalathus* the most important food plants (Beukes 1987, 1988). Observations when feeding on *Leucosidea sericea*, *Cliffortia nitidula* and an *Euryops* sp. further suggest that Grey Rheboks select the growing tips that provide the greatest concentration of protein (Ferreira & Bigalke 1987). Low nutrients, especially crude protein, effectively control Grey Rhebok

numbers in the sourveld of the KwaZulu–Natal Drakensberg. Here peak mortality occurs from Aug to Oct, the period immediately following the coldest and driest time of year when herbage quality is lowest (Mentis 1978, Oliver *et al.* 1978, Rowe-Rowe 1983, Rowe-Rowe & Scotcher 1986).

A typical diurnal and nocturnal feeding pattern comprises alternating bouts of 1–2 hours' duration of feeding and lying up/rumination (Taylor *et al.* 2006a). Grey Rhebok spend on average ca. 30% of daylight hours feeding; at night they are active for 57% of the time, though not all this time is spent feeding (Taylor *et al.* 2006a). They are less active during the middle of the day in summer (Oliver *et al.* 1978, Ferreira 1983), and, during winter, cover greater distances for foraging than during summer. Being water-independent, they appear to obtain most of their water requirements from their food; however, at Sterkfontein Dam N. R., Grey Rhebok were regularly seen drinking water from the dam between May and Aug (Taylor *et al.* 2007).

Social and Reproductive Behaviour Grey Rheboks are found in two social groups: harem herds (usually consisting of one adult ♂ plus up to five ♀ with young) and as single territorial adult ♂ (Esser 1973, Oliver *et al.* 1978, Rowe-Rowe 1982b, 1994, Ferreira 1983, Taylor 2004). Although there are no bachelor herds, young ♂ sometimes form temporary associations that may last for up to three weeks (Ferreira 1983). Typical herd size is between three and five animals, but up to 15 and even a group of 28 individuals has been recorded (see Lynch & Watson 1990). Larger herds are presumably ♀ and young from harem herds that have joined temporarily. Herd size differs between regions, with mean group size and typical group size in the E Free State recorded as 3.5 and 4.6 ($n = 184$), respectively (Ferreira 1983), and 2.9 and 4.0 in the KwaZulu–Natal Drakensberg (Oliver *et al.* 1978). In the Free State, herds do not fluctuate significantly in size and composition between summer and winter, and the frequency of occurrence of solitary ♂ is also constant (Ferreira 1983).

The social structure of territorial male Grey Rheboks can be described as a system of female defence polygyny (Taylor & Skinner 2006a). Territories are marked by means of faeces, and territorial ♂ are often seen defecating at visible landmarks, such as at the base of termite mounds or against shrubs, rocks or tall grass tufts (Ferreira 1983, Taylor & Skinner 2006b). Although scent-marking is performed throughout the year, Taylor & Skinner (2006b) recorded that the frequency of scent-marking in three territorial ♂ in the Free State was highest between Oct and Dec, coinciding with the period when they evicted juvenile ♂ (which, in turn, were more submissive at this time of year) from their natal herds and when ♀ were due to start lambing. Although territories are scent-marked, display and acoustical behaviour play a prominent role in territorial advertising. Territorial ♂ will advance with exaggeratedly slow movements towards a trespassing ♂, displaying laterally and frontally, while stamping and snorting. This behaviour usually has the effect of driving an intruder away. Physical encounters take place where this behaviour is unsuccessful.

Home-range sizes of territorial ♂ ranged between 23 and 135 ha, averaging 53 ha in the Free State (Ferreira 1983), 60 ha on Sterkfontein Dam N. R. (Taylor 2004), 77 ha at Highmoor (Drakensberg) (Oliver *et al.* 1978), 42 ha at Royal Natal N. P. (Drakensberg) (Southgate

1979) and 70 ha for Ukhahlamba–Drakensberg Park (Rowe-Rowe 1994). In seven different areas throughout South Africa, home-range size did not correlate with Grey Rhebok density. According to Ferreira (1983), their home-range size is determined by the quality of the habitat, and not by the pressure of density. Ferreira (1983) also found no correlation between group size and various categories of slope, topography, aspect, geology, altitude and vegetation height, and no seasonal differences in the frequencies with which animals were observed in these categories.

Males court ♀ in oestrus by sniffing the vaginal area, resting their heads on the female's buttocks and back, and tapping the inside of the female's hindlegs with their forelegs. Multiple matings may follow (A. Taylor pers. comm.). Pregnant ♀ leave the herd 2–3 days before parturition and return after about one week. Young are concealed for ca. 4–6 weeks during which they are regularly visited and suckled. Young can be found lying with their heads characteristically flat against the ground and at considerable distance from the mother (Oliver *et al.* 1978). Juveniles of up to eight months seek their mothers when danger threatens and follow closely during flight.

Yearling ♂ leave the harem herd or are evicted very aggressively by the harem ♂ between Oct and Dec, just prior to the start of the birth period (Rowe-Rowe 1982b, Taylor *et al.* 2006b). They become physically mature at about 1.5–1.75 years (Esser 1973) and soon try to establish territories. Males that fail to establish their own territories are forced to the peripheries of those of established ♂. Taylor *et al.* (2006b) also recorded four occasions on which harem ♂ evicted young ♀ of ca. 8 months of age from their herds; two of these ♀ were allowed to return after two months, but before being allowed back they remained on the peripheries of their home-ranges and avoided contact with their natal groups.

Four vocalizations are recognized: barking, moaning (or bleating), hissing and snorting (or grunting). When disturbed, they utter a sharp, nasal-sounding bark whistle before taking flight with their characteristic 'rocking-horse' gait. Adult ♂ generally utter this alarm; the flight is then led by an adult ♀ with the ♂ following at the back of the group. Both sexes snort when the source of disturbance is not recognized (and snorting may last for up to 45 min).

Reproduction and Population Structure Reproduction is seasonal (see Oliver *et al.* 1978, Ferreira 1983, Beukes 1984, Rowe-Rowe 1994, Taylor *et al.* 2006b). Mating occurs from Feb to May and a single young is born after a gestation of 37.3 weeks between Nov and Feb (Brand 1963, Taylor *et al.* 2006b), but sometimes from as early as Oct and as late as Jul (Taylor *et al.* 2006b). Beukes (1984) recorded a birth peak in Aug in Bontebok N. P. due to winter rainfalls in this region. Even in captivity, where they have access to good-quality forage, Grey Rheboks remain seasonal (Brand 1963, Skinner *et al.* 2002). During a study in the Free State, two ♀ started breeding at the age of 16 months and gave birth for the first time at two years. The inter-birth interval for adult ♀ was generally one year, although one ♀ had an average interval of nine months (Taylor *et al.* 2006b).

Sex ratios differ between the E Free State and the KwaZulu–Natal Drakensberg, being 1 : 2.2 in the Free State and between 1 : 1.5 and 1 : 1.9 in the Drakensberg (see Ferreira 1983, Scott 1991, Rowe-Rowe 1994). Juveniles (less than one year old) comprise 22% of the population (Southgate 1979, Rowe-Rowe 1982b). Average fecundity

rate in a study in the Free State was 74% and the sex ratio in offspring was 22 : 19 (Taylor *et al.* 2006b).

In Ukhahlamba–Drakensberg Park, mortality is highest between Aug and Oct, following the severe winter when food availability and quality drop to critical levels (Rowe-Rowe & Scotcher 1986). In the Free State, Taylor *et al.* (2006b) lost 27% of their study population due to hypothermia after heavy snow at the end of winter; ♂♂ and ♀♀ were affected to the same degree by the snow, but juveniles suffered more than adults (there was no evidence of mortality due to infectious disease or predation in this study). Potential life-span not known, but longevity in captivity is about 12 years (Jones 1993, Weigl 2005).

Predators, Parasites and Diseases Although Black-backed Jackals *Canis mesomelas* do prey on Grey Rheboks, Rowe-Rowe (1982b) showed that their influence on Grey Rhebok numbers is not significant. Other contemporary predators include Caracals *Caracal caracal* (e.g. Palmer & Fairall 1988) and large raptors.

In surveys of Grey Rheboks from Bontebok N. P., one trematode (*Fasciola hepatica*) and 12 nematode species were recovered (Boomker *et al.* 1981, Horak *et al.* 1982b, Boomker & Horak 1992; and see Lichtenfels *et al.* 2001 and Boomker & Durette-Desset 2003). The nematodes *Paracooperioides peleae* and *Ostertagia triquetra* have been recovered from this host only (Boomker *et al.* 1981, Boomker & Durette-Desset 2003). Taylor *et al.* (2005) identified five nematode species from Grey Rheboks at Sterkfontein Dam N. R., including *Cooperia yoshidai* and *P. peleae*.

In a ten-year-study of tick infestations of Grey Rheboks in Bontebok N. P., Horak *et al.* (1997) collected six tick species of which *Rhipicephalus nitens*, *R. glabroscutatum* and *Ixodes pilosus* were the most abundant on both Grey Rheboks and Bonteboks *Damaliscus pygargus pygargus*. In an earlier study, Horak *et al.* (1986) also recorded two species of lice, and three oestrid fly larvae, including *Gedoelestia* sp. from the eyes of three animals. Horak *et al.* (in Ferreira 1983) reported lesions in Grey Rhebok hides and eyes caused by infestation of the larvae of oestrid flies. Skead (1987) mentions infestation by the larvae of the antelope warble fly, *Strobiloestrus clarkii*. Subcuticular parasitic fly larvae make their meat unattractive (Rautenbach 1978).

Conservation IUCN Category: Least Concern. CITES: Not listed.

Grey Rhebok numbers have declined mainly due to habitat

alteration and hunting pressure. The most marked change in its habitat has been the vegetation; for example, the vegetation of the central plateau region of South Africa, from Graaff-Reinet northwards to the Orange R. and S Free State, has changed from sweet grassveld to degenerate false Karoo veld since the arrival of Europeans (see Ferreira 1983). Because Grey Rheboks flee to open spaces (where they become more vulnerable), and because landowners are antagonistic to this species (it is believed to be aggressive towards the sheep, goats and the more palatable Mountain Reedbucks with which they often co-exist), their numbers and distribution have declined. In KwaZulu–Natal, predation by uncontrolled dogs has been singled out as a major cause of losses (Rowe-Rowe 1994).

Grey Rhebok populations are stable in at least six national parks and 29 provincial reserves in South Africa, and occur in Malolotja N. R. and Mlilwane Wildlife Sanctuary in Swaziland, and Sehlabathebe N. P. in Lesotho (East 1999). The proposed Maluti–Drakensberg Transfrontier Conservation and Development Project should further contribute to the protection of this species.

Measurements

Pelea capreolus

HB (♂♂): 1100 (1040–1150) mm, n = 5

HB (♀♀): 1190 (1150–1360) mm, n = 5

T (♂♂): 140 (100–170) mm, n = 5

T (♀♀): 130 (120–160) mm, n = 5

HF c.u. (♂♂): 350 (340–360) mm, n = 5

HF c.u. (♀♀): 340 (330–350) mm, n = 5

E (♂♂): 171 (147–200) mm, n = 5

E (♀♀): 164 (152–184) mm, n = 5

Sh. ht (♂♂): 720 (690–740) mm, n = 5

Sh. ht (♀♀): 710 (690–730) mm, n = 5

WT (♂♂): 20.0 (16.0–24.0) kg, n = 5

WT (♀♀): 21.0 (20.0–23.0) kg, n = 3

Free State (adults >1 year old) (Ferreira 1983)

Maximum recorded horn length is 30.2 cm for a pair of horns from South Africa (Rowland Ward)

Key References Beukes 1984; Esser 1973; Ferreira 1983; Mentis 1978; Rowe-Rowe 1982b; Taylor 2004; Taylor *et al.* 2006a, b.

Nico L. Avenant

GENUS *Redunca*

Reedbucks

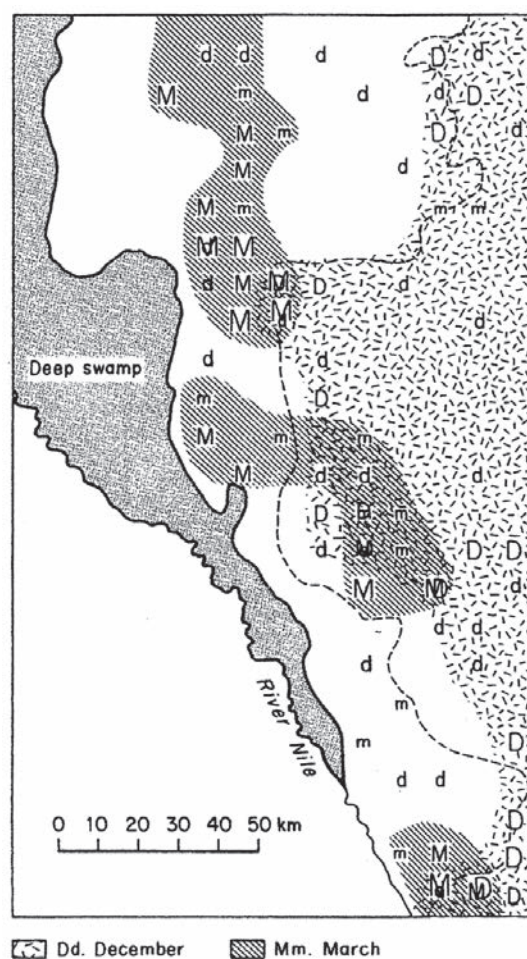
Redunca C. H. Smith, 1827. In: Griffith et al., Anim. Kingd. 5: 337.

The three reedbucks species of the genus *Redunca* represent the least derived members of the Reduncini (excepting *Pelea*) and the size gradient within this genus, as within the Reduncini as a whole, supports the hypothesis that the reduncines have descended from smaller ancestors (Kingdon 1982). The Oribi *Ourebia* may represent a highly specialized offshoot from the same ancestral stock and the two antelope groups share similarities in behaviour and ecology (Kingdon 1982), as well as having a uniquely structured ear-gland, or 'ohrenplaketten', in common (Hofmann 1972, Claasen & Jungius 1973). Vrba *et al.* (1994) even went so far as to include *Ourebia* in Reduncini. That *Redunca* represents the most conservative genus within the true reduncines was confirmed by the molecular study of Birungi & Arctander (2001), with the Mountain Reedbuck *R. fulvorufula* shown to make the earliest divergence.

There are three species of reedbucks, the smallest being the Mountain Reedbuck *Redunca fulvorufula*, with a widely disparate distribution in three mountainous regions of southern, East and West Africa. The other two, the Bohor Reedbuck *R. redunca*, and the Southern Reedbuck *R. arundinum*, are ecologically equivalent species, the first in savannas north of the equatorial forests, while the latter inhabits the south, with a region of overlap between the two species in Tanzania.

The Mountain Reedbuck is the closest in size and overall morphology to a generalized pecoran herbivore. Its restriction to cool uplands was probably the outcome of its immediate ancestor, an early reedbucks stock, having extended its range across a broad spectrum of grasslands. This pioneering reedbucks type then had to relinquish the lowlands to larger-bodied, more advanced populations of *Redunca* and, perhaps, *Kobus*. Today, the Mountain Reedbuck is physiologically distinct in being able to tolerate drier and colder regions and in being able to digest very much drier, coarser material (Hofmann 1973). This development in a single member of the Reduncini implies an ancient restriction to habitats with coarse grass resources and, by implication, a long history for all members of this genus. In fact, the currently earliest fossil of a reduncine similar to *Redunca* is from Lukeino, Kenya, dated to 6 mya (Gentry 1970).

Given their phylogenetic relationship with basal antelopes, the loss of functional pre-orbital and pedal glands in *Redunca* is significant and must have some relation to enlarged body-size. There are no implications here of a decline in sensitivity to scent signals; on the contrary, all reedbucks have, in addition to the ear glands, highly structured inguinal pockets that enclose scent-secreting inguinal glands. Loss of facial, pedal and other glands is consistent with the abandonment of territory-labelling systems because both scenting and physically demarcating a wet and highly obstructed substrate are impractical activities. Furthermore, home-ranges in sumplands that are generally rather homogeneous and prone to annual floods and fires, demand relatively short range, but decidedly seasonal, movements by reedbucks. In compensation, these habitats have exceptionally rich resources, with fast regrowth of palatable grasses



Seasonal distribution of Bohor Reedbuck *Redunca redunca* in an area east of the Nile, South Sudan. The dotted line separates *Hyparrhenia* to the east and *Oryza* communities to the west. Capital letters = 2–100/sq km. Lower case letters = 1/sq km. M = late Dry. D = very early Dry.

after fires, especially where the water table is close to the surface, as is often the case. As smaller, more cryptic and less social animals, *Redunca* species are better able to weather burn-offs without moving very far. Under these circumstances *Redunca* species seldom need to make any more than localized movements between wet-season (or flood-season) and dry-season pastures. This is well illustrated by records of Bohor Reedbuck concentrations on 'Duk Ridge', a levee on the eastern bank of the Nile in S Sudan. This is a locality where the local reedbucks populations have probably been following similar patterns of movements over very great periods of time. If so, proximity to water and their seasonal preferences for levee or flood-plain are likely to represent an enduring pattern of movements among valley-dwelling reedbucks.

Jonathan Kingdon

***Redunca fulvorufula* MOUNTAIN REEDBUCK**

Fr. Redunca de montagne; Ger. Bergriedbock

Redunca fulvorufula (Afzelius, 1815). Nova Acta Reg. Soc. Sci. Upsala 7: 250. No type locality originally identified; restricted to eastern Cape Colony (Lydekker 1914: 221) (South Africa, Eastern Cape).

Mountain Reedbuck *Redunca fulvorufula*.Lateral view of skull of Mountain Reedbuck *Redunca fulvorufula*.**Geographic Variation**

- R. f. fulvorufula* (Southern Mountain Reedbuck): South Africa, Lesotho, Swaziland, Botswana, S Mozambique. Larger, and more intensely rufous; also has larger horns.
- R. f. chanleri* (Chanler's Mountain Reedbuck): SE Sudan, Ethiopia, Uganda, Kenya, N Tanzania. Smaller and greyer, with less rufous tinge; horns shorter than the southern race.
- R. f. adamauae* (Western Mountain Reedbuck): isolated subspecies in Nigeria and Cameroon.

Taxonomy Polytypic species with three recognized subspecies (Ansell 1972). Synonyms: *adamauae*, *chanleri*, *eleotragus*, *lalandia*, *landiana*, *schoana*, *subalbina*. Chromosome number: $2n = 56$; the karyotype comprises 26 acrocentric and two bi-armed chromosome pairs. In some animals, 57 chromosomes have been detected. Both X and Y chromosomes are large and acrocentric (Rubes *et al.* 2007).

Description Mountain Reedbuck are the smallest of the reedbucks, but can be categorized as a medium-sized antelope. Ears are long, narrow and the tips rounded. Snout has distinctively raised, swollen-looking nostrils. Eyes are prominent. Black subauricular patches serve as scent dispensers (Hofmann 1972). Upperparts are predominantly grey, but the head and shoulders are a reddish-brown. Underparts are pure white and sharply demarcated from the rest of the body. Head and neck are reddish-yellow. Pelage soft and woolly. Fluffy tail greyish on top and pure white underneath. A description of guard hair characteristics, such as length, scale pattern and colour, is given by Keogh (1983). Inguinal glands in the groin are well developed. Sebaceous glands film the entire body, resulting in a pungent overall odour. Functional pedal and preorbital glands are absent. Males are slightly larger and heavier than ♀♀ (see Measurements).

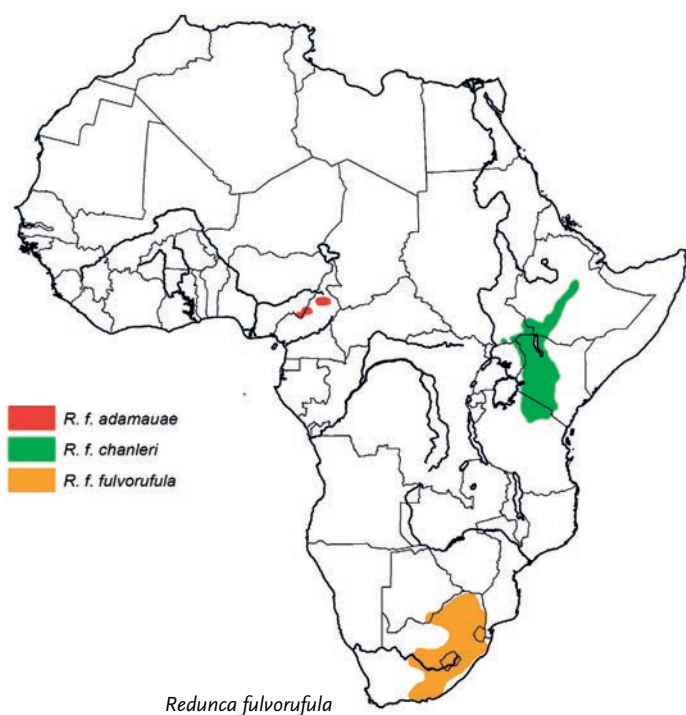
Only ♂♂ have horns; these are short, black, heavily ridged, curve forward and end in smooth, blunt points. They reach full length at around five years (Norton & Fairall 1991).

Similar Species

Redunca arundinum. Some marginal overlap in range in E South Africa. Larger in size, standing higher at the shoulder; typically has a black stripe on foreleg; one pair inguinal pouches.

Pelea capreolus. In southern Africa, both species occur at higher altitudes in the Free State, Mpumalanga, KwaZulu–Natal, Eastern Cape, Western Cape and Northern Cape Provinces in South Africa, and also in Swaziland and Lesotho. The ♀♀ of the two species are difficult to distinguish at a distance, as ♀♀ of both species lack horns. Characteristics of Grey Rhebok include: (1) they always lift their tail the moment they start running, showing the white underparts; (2) they generally avoid areas with tall grass; (3) the horns of ♂♂ are straight; (4) they usually take flight up the slope, but will sometimes run downhill when disturbed from above; (5) they have no subauricular patches; (6) their ears are pointed; (7) their neck is greyish-brown.

Distribution Endemic to Africa, occurring in three widely separated populations (represented by the respective subspecies) in southern Africa, East Africa and West Africa; these three populations are probably vestiges from a glacial period thousands of years ago when climate was different and caused the vegetation to be more suitable for Mountain Reedbucks all the way up the escarpments of the eastern side of Africa (Newmark 1996). Although there are



extensive areas of highland with apparently suitable habitat between Mt Hanang (the southern limit in East Africa) and the southern African population, these areas are occupied by the Common Reedbuck *Redunca arundinum*, which suggests that this species may be a direct competitor while the Bohor Reedbuck *R. redunca* is not (Kingdon 1982).

The Southern Mountain Reedbuck occurs in Mozambique, where it is restricted to the Lubombo Mts on the south-western border with South Africa, while in Botswana these reedbucks are present in the Mannyelanong Hill G. R., but are otherwise confined to other small, rocky hillsides in the south-east (East 1999). In South Africa they are widely distributed in the eastern mountainous areas above ca. 1200 m, ranging southwards into the Eastern Cape up to the Baviaanskloof and Kouga Mts (H. Gerber & H. Niewoudt pers. comm.). In Swaziland, they are present in the highveld and Lubombo regions (Monadjem 1998), and in Lesotho in the high mountains (Lynch 1994).

Chanler's Mountain Reedbuck is known from hilly areas in SE Sudan, and in Ethiopia is confined to broken country and rocky hillsides in scattered localities within the Rift Valley and southern lowlands. In Uganda, these reedbucks occur on rocky hillsides in eastern Karamoja, and in similar habitat in C and S Kenya where the species is protected in areas such as Aberdare, Nairobi and Lake Nakuru National Parks. In N Tanzania, they are present in localized areas of high-altitude grassland and rocky hillsides including protected areas such as Arusha and Tarangire National Parks and the Ngorongoro Conservation Area, but unprotected populations in areas such as the Hanang, Mbulu, Lolkisale and Loliondo Mts are threatened or extinct (East 1999).

The Western Mountain Reedbuck occurs only in Nigeria in Gashaka-Gumti N. P. and the Gotel Mts adjoining the park's southern boundary (East 1999, Nicholas 2004a, b), and in Cameroon in the Adamaoua Mts and the hunting zones below, as well as in the hunting zones between Bénoué and Bouba Ndjida N. P. (Pfeffer 1962, East 1999, T. Breuer pers. comm.).

Habitat Mountain Reedbucks live in cool, mountainous regions mostly above 1500 m and up to 5000 m (Stewart & Stewart 1963, Kingdon 1982, Lynch 1983, 1989, 1994, Rowe-Rowe 1983, Lynch & Watson 1990, Newmark 1996, Nicholas 2004b). They prefer grassy ridges and steep (20–40-degree) mountain slopes in broken rocky country, small outcrops and volcanic lava flows and cinder cones. Mountain Reedbucks favour areas with large bushes or scattered trees (for shade and predator evasion), but will move onto adjacent flats to feed or drink (Mentis 1974, Mason 1977, Irby 1979, Rowe-Rowe 1983, Dunbar & Roberts 1992). In southern Africa, they make use of all mountain slopes, including the moister, 'sour' southern and south-eastern slopes (Rowe-Rowe 1983). In Kenya, Mountain Reedbucks prefer the scrub-grass ecotone between slopes covered in camphor (*Tarchonanthus*) and open grassy valleys (Kingdon 1982). The availability of water is an essential habitat requirement.

Abundance A density of 5–7 individuals per km² is typical of most study populations (Irby 1977a). Estimated densities in protected areas in South Africa vary from 0.1/km² or less in areas such as Karoo, Addo-Zuurberg and Marakele National Parks to 3.0/km² in Golden Gate N. P. and 7.5/km² in Mountain Zebra N. P. (Anderson *et al.* 1996). In the Drakensberg, ecological densities range from 3.1–9.1/km² (Oliver *et al.* 1978, Rowe-Rowe & Scotcher 1986); at Sterkfontein Dam N. R. in the Free State, on the western boundary of the Drakensberg, densities were 11.5/km² (Taylor *et al.* 2007). In East Africa, Blankenship & Qvortrup (1974) estimated an average of 11/km² (Kekopey Ranch, Kenya).

The largest population of Southern Mountain Reedbucks can be found in Ukhahlamba Drakensberg Park with 1700–2000 individuals (Rowe-Rowe 1994); numbers in South Africa total nearly 32,000 (East 1999). In Swaziland, there are less than 200 individuals (Monadjem *et al.* 2003). Numbers of Southern Mountain Reedbucks are unknown for Botswana and Lesotho (East 1999). Both Chanler's and Western Mountain Reedbucks are uncommon to rare in their distribution areas (East 1999). Overall population estimates have been estimated as 33,000 for Southern, 2900 for Chanler's and 450 for Western Mountain Reedbucks (East 1999).

Adaptations Mountain Reedbucks have a specially adapted stomach (large subdivided rumen with keratinized mucosa that permits the maximum delay of coarse, fibrous food, a small reticulum with deep cellulase, and a large omasum with pronounced mucosal surface enlargement) that allows it to feed almost entirely on grass (Hofmann & Stewart 1972), which is particularly coarse and of low quality in the dry season. The smaller body size and aggregations (the smallest of the reduncines) are also adaptations to survive on this lower quality food in the drier uplands; their larger relatives keep in larger groups to valley habitat with its good quality grass.

Mountain Reedbucks are most active during the early mornings, late afternoons and at night. During the middle of the day they lie in the shade, often tightly together and right inside bushes (Irby 1981, 1982, Roberts & Dunbar 1991). Temperature is the most likely proximate factor regulating diurnal activity, movement and rumination patterns (Irby 1982, Roberts & Dunbar 1991). They tolerate a wide range of climatic conditions and ignore light rain. In heavy rainstorms or high wind they will orientate themselves with their hindquarters in its direction or seek sheltered slopes, standing or lying down until

the weather conditions improve. Seasonal activity variations in Chanler's Mountain Reedbucks are strongly related to rainfall, with levels of activity and feeding lower in the wet season when forage quality and availability increase (Roberts & Dunbar 1991).

Foraging and Food Mountain Reedbuck are predominantly grazers (for example, monocotyledonous plants constitute ca. 99.5% of the rumen contents of Chanler's Mountain Reedbuck; Irby 1977b, Mason 1977), and were classified as obligate grazers by Gagnon & Chew (2000). This is also borne out by studies involving stable carbon isotope analyses of animals in both southern and East Africa (Cerling *et al.* 2003, Sponheimer *et al.* 2003b). Mountain Reedbucks are selective feeders (Taylor & Skinner 2006a) and their preference for different grass species varies seasonally (Irby 1984a, Dunbar & Roberts 1992). On Loskop Dam N. R. in Mpumalanga, favourite grass species included *Themeda triandra*, *Hyparrhenia* spp. and *Cymbopogon* spp. (Irby 1977b), and in the Drakensberg of KwaZulu-Natal the distribution of Southern Mountain Reedbucks corresponds closely with the distribution of *Themeda triandra* and *Hyparrhenia* spp. (Rowe-Rowe 1983). Mountain Reedbucks also select for plant parts, preferring young green shoots when these are available. They may therefore benefit from the farming practice of frequent burning to stimulate new growth (Rowe-Rowe 1982a).

Roberts & Dunbar (1991) found unexpectedly high levels (up to 20.6%) of browse in Chanler's Mountain Reedbuck diet at the end of the long, dry period and for the first two months after the first rains. They suggested this to be an adaptive response to low forage quality and availability (although high-quality grass is available from one month after the first rains, gut-fill or induced imbalances in rumen pH may be the reason why Mountain Reedbucks only utilize a limited amount of this food item during this period). The two holotrichs found among 22 protozoan rumen ciliates in Southern Mountain Reedbucks also suggest that this species can digest some browse (Van Hoven 1983). Irby (1976) has shown that Southern Mountain Reedbucks have to eat more during the dry season to compensate for the low food value of the grasses during this period, but did not find any switching from monocotyledons to dicotyledons (Irby 1984a).

Feeding trials have shown Mountain Reedbucks to take ca. 584 g dry matter per animal per day, consisting of 13% crude protein, 54% nitrogen-free extract, 21% fibre, 3% fat and 8% minerals (Špála *et al.* 1987). Of the nutrients, 73% dry matter was consumed, 39% minerals, 76% organic matter, 73% crude protein, 76% nitrogen-free extract, 79% fibre, 66% fat and 75% energy. At the average body weight of 27.4 kg, the daily intake of metabolizable energy, 5947 kJ, exceeded the daily basal energy requirement by a factor of 1.695, which was higher than in domestic ruminants.

The first dry season following birth is a critical time for the young, as they have not accumulated the fat reserves of adults during the preceding wet season (Norton 1989). In the sourveld of the KwaZulu-Natal Drakensberg, food (and in particular food quality) is a major factor limiting numbers. Nutrients, especially crude protein, drop to critical nutritional levels during the coldest, driest time of the year (Aug–Oct), when a peak in deaths occurs (Mentis 1978, Oliver *et al.* 1978, Rowe-Rowe 1983, Rowe-Rowe & Scotcher 1986, Taylor *et al.* 2006b).

Mountain Reedbucks are dependent on drinking water (Norton 1989), but drink more often during dry weather than during cold, cloudy weather. They feed mostly in the early morning, late

afternoon and at night when they may move from the hillsides to feed on adjacent flat ground (Smithers 1971, Irby 1981, 1982, Roberts & Dunbar 1991, Taylor *et al.* 2006a).

Social and Reproductive Behaviour The social organization consists of territorial ♂♂, non-territorial ♂♂, bachelor groups and herds of ♀♀ with young. Non-territorial ♂♂ generally occupy the periphery of male territories or may temporarily form bachelor groups. Female herds typically consist of 1–8 individuals, with group sizes of 1–4 being most common (e.g. Dunbar & Roberts 1992, Taylor 2004). Larger groups (up to 40 individuals) may form temporarily (Irby 1977a). These larger herds are unstable as ♀♀, or ♀♀ with young, move from herd to herd. Seasons have some influence on group sizes in southern Africa with somewhat smaller groups forming in the late dry season and the largest average sizes occurring in the early dry season.

The social structure of territorial male Mountain Reedbucks can be described as a system of resource-defence polygyny (Irby 1979, Taylor & Skinner 2006a). Territorial ♂♂ guard, and sometimes actively defend, their territories throughout the year and only move from them to feed in adjacent areas when their territories are burned or to establish temporary contact with other ♂♂ (Mason 1977, Dunbar & Roberts 1992). They are clearly nervous and alert when outside their territories (Irby 1979). Female herds move from one male territory to another, and territorial ♂♂ have been seen herding ♀♀. In Kenya and in South Africa, ♀♀ preferred territories that contained the highest available slopes, which would provide security from predators (Dunbar & Roberts 1992, Taylor *et al.* 2007). Territorial ♂♂ at Sterkfontein Dam N. R. used smaller areas (8–21 ha; Taylor *et al.* 2007) than ♂♂ at Loskop Dam N. R. in Mpumalanga (28 ha; Irby 1977a, 1979), but used larger areas than ♂♂ in Kenya (3.1–5.5 ha; Dunbar & Roberts 1992). Female home-ranges overlap those of several ♂♂; female territories in South Africa range between 36 and 76 ha (mean = 57 ha) (Irby 1976). These female territories cover a sample of the available habitats, running from hilltop to valley.

A courting ♂ will approach a ♀ with outstretched head and neck. Foreleg striking, or laufsclag, has also been observed. If the ♀ is prepared to accept him, she adopts a submissive posture by lowering her head. Females leave their group to give birth in isolation. Young remain hidden for up to three months before joining the mother's group. This has been identified as a time of high mortality (Irby 1976). A mother will visit her young cautiously once or twice a day to suckle and clean it. The constant changing of hiding places (after every visit by the mother) and the ingestion of the young's faeces and urine reduces the likelihood of the young's detection by predators. When the young is in danger or is attacked it may utter an alarm call that will bring the mother to its aid. Lactation does not appear to inhibit fertilization since Els (1991) found 11% of reproductively active ♀♀ to be both pregnant and lactating. The bond between mother and young is broken when she is about to give birth to her new offspring; should she lose it, the bond may continue.

Territorial ♂♂ tolerate juvenile ♂♂ up to the age of ca. six months, but will drive them from the female herd when they reach the age of ca. 9–15 months (Kingdon 1982, Skinner & Chimimba 2005). It is during this time that juvenile ♂♂ are most exposed to stress, malnutrition, disease and predators, and an even juvenile sex ratio becomes altered to two or even three ♀♀ for every ♂ (Kingdon 1982; and see later).

Stotting or stiff-legged jumping has been observed to be combined with short whistles. Longer whistles are used as an advertisement of territory. The shrill alarm call is given by the herd ♂ when an intruder is seen. The latter sends the herd, now led by an adult ♀, running along the side of the hill or indirectly downhill. After fleeing some 300–400 m they pause and look for the source of disturbance. While it has been suggested that the flashing of the white underside of the tail is a warning mechanism for conspecifics, it may also be possible that it is a 'pursuit deterrent signal' to the predator.

Reproduction and Population Structure Mountain Reedbucks are capable of breeding throughout the year, although, in southern Africa, a peak in breeding activity is reported around Apr and May, and a peak in births in early and mid-summer (Oct–Jan) (Oliver *et al.* 1978, Irby 1979, Skinner 1980, Norton 1989, Els 1991, Rowe-Rowe 1994, Taylor *et al.* 2006b).

Mountain Reedbucks reach adult body weight at two years. Males produce spermatozoa (a description of the spermatozoa is given by Dott & Skinner [1989]) before the age of 12 months, but mate only after they have established their own territory. Els (1991) reported ♂♂ reaching sexual maturity at about 27 months. First oestrus in ♀♀ can be as early as nine months (when nutritional conditions are ideal), but normally they do not become reproductively mature until 12–14 months old (Irby 1979) and most ♀♀ conceive for the first time when 12–16 months of age (Els 1991). Thereafter, they may produce one young every 12–14 months for the rest of their lives. The average gestation period is 34.3 weeks (range 33.7–35.9 weeks; Irby 1979). Neonates weigh about 3 kg at birth (Kingdon 1982).

In the Drakensberg, ♂ : ♀ adult sex ratios ranged from 1 : 1.9 to 1 : 2.6 at three different study areas (Oliver *et al.* 1978, Southgate 1979, Rowe-Rowe 1982b); juveniles comprised 10–16% of the population, with the young to adult ♀ ratio 1 : 3.4. At Loskop Dam ♂ : ♀ ratio was 1 : 2 and young to adult ♀ ratio 1 : 3.3 (Irby 1977a). At Sterkfontein Dam N. R., average fecundity rate was 92% and

young ♂ : ♀ sex ratios were 12 : 8 (Taylor *et al.* 2006b). Potential life-span is 12 years and four months (see Mentis 1972); longevity in captivity has been given as 15 years (Weigl 2005).

Predators, Parasites and Diseases In both South Africa and Kenya, baboons *Papio* spp. are considered as a threat to infants only (Irby 1984b). Both Martial Eagles *Polemaetus bellicosus* and Verreaux's Eagles *Aquila verreauxii* were observed harassing adult ♀♀ on cliff faces in Kenya, apparently with the intention of causing them to fall (Roberts & Dunbar 1991). Other predators include jackals *Canis* spp., Cheetahs *Acinonyx jubatus*, Leopards *Panthera pardus*, Lions *Panthera leo*, Caracals *Caracal caracal*, Servals *Leptailurus serval*, Striped Hyenas *Hyaena hyaena*, African Wild Dogs *Lycaon pictus* and African Rock Pythons *Python sebae*.

Irby (1976) identified 17 helminth parasites, at least four ticks, lice and the parasitic fly *Strobiloestrus*, the larvae of which develop under the skin and are most frequent in immature animals during the wet season (see Kingdon 1982). Boomker *et al.* (2000) discussed what was known about the helminths of Mountain Reedbucks, including adding two new parasite records, *Moniezia benedeni* and *Trichostrongylus falcatus*, for the species. Seventeen species of helminths, including 15 nematodes, one trematode and one cestode were recovered from Southern Mountain Reedbucks at Sterkfontein Dam N. R. and Tussen die Riviere N. R. in the Free State (Taylor *et al.* 2005), one of them the newly described *Cooperia pigachei* (Boomker & Taylor 2004). At Sterkfontein Dam N. R. the most prevalent and abundant species were *Cooperia yoshidai*, *Longistrongylus schrenki* and *Haemonchus contortus*, with the latter two being more abundant during Nov and Dec than at other times of the year; at Tussen die Riviere N. R., helminths were less prevalent and abundant than at Sterkfontein Dam N. R., with the most important species *Nematodirus spathiger*, *Trichostrongylus falcatus* and *Cooperia rotundispiculum*. In Mountain Zebra N. P., Horak *et al.* (1991b) recorded eight species of ixodid ticks, including the Karoo paralysis tick *Ixodes rubicundus*, and Mountain Reedbucks were preferred hosts for *Rhipicephalus glabroscutatum* and *R. lounsburyi*.

In a study of Mountain Reedbucks in the Free State, 43 deaths were recorded over the course of two years, of which 32 resulted from hypothermia following a single snowfall event; this represented 51% of the population at the time. Females were affected by hypothermia more than ♂♂. There was no evidence of disease in the population from the examination of culled animals, and no evidence of predation (Taylor *et al.* 2006b).

Conservation IUCN Category: Least Concern (*R. f. adamaue* – Endangered C2a(i); *R. f. chanleri* – Vulnerable C1; *R. f. fulvorufula* – Least Concern). CITES: Not listed.

The main threats to Mountain Reedbuck include the expansion of human settlement, poaching, widespread disturbance by cattle herders and their livestock, and hunting by dogs (see Rowe-Rowe 1994, East 1999). Range expansion is limited by the specialized habitat requirements of Mountain Reedbucks; their strictly sedentary habits inhibit dispersal, rendering isolated populations vulnerable to extermination during prolonged periods of drought (Kingdon 1982).

Numbers of Southern Mountain Reedbucks appear to be stable, and they occur in sizeable numbers in both protected areas and on



Mountain Reedbuck *Redunca fulvorufula* head (young male).

private land. For example, in South Africa, East (1999) estimated that around 6880 individuals are protected in conservation areas, while the rest of the population resides on private land. Indeed, Mountain Reedbucks recommend themselves in several ways for improving productivity from farmland: their meat is palatable and usually free of parasites; they graze rough terrain frequently marginal for domestic stock; their social structure ensures an even distribution of the population over available habitat; and they have a high reproductive potential (Irby 1975, Skinner 1980). In South Africa, Mountain Reedbucks are protected in at least nine National Parks, and in numerous provincial reserves and conservancies. In Swaziland they are protected in Malolotja and Mlawula Nature Reserves and in Mlilwane Wildlife Sanctuary (Monadjem *et al.* 2003), while in Lesotho, where Lynch (1994) recorded single animals or pairs at a few localities in the central, northern and eastern parts of the country, they are known to occur in Sehlabathebe N. P. In Mozambique, their range will include Limpopo N. P., the latter part of a greater transfrontier park with South Africa. In Botswana, they are protected in the small (1.5 km²) Mannyanong Hill G. R., but there is no recent information on the species' status.

Chanler's Mountain Reedbucks occur in viable populations in Awash, Nechisar, Omo and Mago National Parks (Ethiopia), the Aberdares, Nairobi and Lake Nakuru National Parks (Kenya) and Arusha and Tarangire National Parks and the Ngorongoro Conservation Area (Tanzania) (East 1999). A healthy population of Western Mountain Reedbucks occurs in Gashaka-Gumti N. P. in Nigeria (Nicholas 2004b), and they are present in the Gotel and Hamman Kankadu Mts, adjoining the park's southern and eastern boundaries, while in Cameroon there is some protection from poachers in the hunting zones below the Adamaoua Mts, as well as in the hunting zones between Bénoué and Bouba Ndjida National Parks (T. Breuer pers. comm.). The continued persistence of both the Chanler's and Western subspecies depends

greatly on the protection and management of these populations.

Measurements

Redunca fulvorufula

HB (♂ ♂): 1340 (1190–1450) mm, n = 57

HB (♀ ♀): 1330 (1210–1460) mm, n = 67

T (♂ ♂): 187 (140–250) mm, n = 58

T (♀ ♀): 169 (130–260) mm, n = 8

HF c.u. (♂ ♂): 360 (330–380) mm, n = 58

HF c.u. (♀ ♀): 350 (310–370) mm, n = 67

E (♂ ♂): 144 (120–160) mm, n = 58

E (♀ ♀): 142 (120–170) mm, n = 68

Sh. ht (♂ ♂): 780 (720–840) mm, n = 22

Sh. ht (♀ ♀): 770 (730–820) mm, n = 12

WT (♂ ♂): 30.0 (22.0–37.0) kg, n = 108

WT (♀ ♀): 28.0 (22.0–36.0) kg, n = 129

South Africa (combined measurements from Anderson & Koen 1993, Taylor 2004 and S. Vrahimis pers. comm. data collected at Tussen die Riviere N. R., Free State, South Africa)

Norton & Fairall (1991) report a mean asymptotic adult mass of 31.4 kg for ♂ ♂ (n = 93) and 29.5 kg for ♀ ♀ (n = 229), with a maximum recorded mass of over 38 kg for both sexes.

Maximum recorded horn length for *R. f. fulvorufula* is 25.4 cm for a pair of horns from the former Cape Province, South Africa, and for *R. f. chanleri* 24.5 cm for a pair from Mt Kaka, Ethiopia (Rowland Ward)

Key References East 1999; Irby 1976, 1977a, 1979, 1982; Norton 1989; Roberts & Dunbar 1991; Taylor 2004; Taylor *et al.* 2006a, b.

Nico L. Avenant

Redunca arundinum SOUTHERN REEDBUCK

Fr. *Redunca grande*; Ger. Grossriedbock

Redunca arundinum (Boddaert, 1785). Elench. Anim. 1: 141. 'Habitat ad Cap. Bn. Sp.' (Cape of Good Hope); since selected as South Africa, Free State, Bethulie, based on known collecting localities of syntypes (Grubb 1999: 25).

Taxonomy Polytypic species. Numerous subspecies have been named, but only two are usually recognized (Ansell 1972, Meester *et al.* 1986). The status of the form *thomasinae* (from Malawi), which includes *penricei* as a synonym, is unclear. Ellerman *et al.* (1953) included this as a synonym of *arundinum*, but Ansell (1972) noted that it may instead be the prior name for *occidentalis*. Synonyms: *algoensis*, *arundinacea*, *caffra*, *cinerea*, *coerulescens*, *eleotragus*, *isabellina*, *multiannulata*, *occidentalis*, *oleotragus*, *oreotragus*, *penricei*, *thomasinae*. Chromosome number: not known.

Description The largest reed buck, with a fine, almost woolly coat. Head and body very variable in colour, ranging from yellowish-buff to greyish-brown. Back usually darker in colour than neck and head, and dorsal part of tail. Ears nearly naked on the backs (dark grey skin). White hair on insides of ears grows outwards in three longitudinal strips and the orifice is also ringed with white hair. Anterior surfaces of front legs have conspicuous dark brown vertical lines down the

front. Body colour continues onto upper surface of tail. Underside of body paler, nearly white, as are chin and throat. Long-haired underside of tail pure white, making a prominent visual signal when raised or flashed. Young lighter coloured than adults, appearing more yellowish. Melanistic individuals and albinos have been reported (Skinner & Chimimba 2005). There are also inguinal gland pockets in the groin; ♂ ♂ have one pair, but ♀ ♀ sometimes have two. The glandular pouches have a funnel-shaped opening and secrete a yellow waxy substance. Functional pedal and preorbital glands are absent. Some individuals possess a glandular, black, hairless patch situated near the base of the ear (conspicuous in some populations), but this is absent in other individuals (see Claassen & Jungius [1973] for further discussion of this gland). Males average 30% larger in body mass.

Only ♂ ♂ have horns, which grow up to 45 cm long and are black, annulated for two-thirds of their length, and resemble a diminished version of the horns of the Waterbuck *Kobus ellipsiprymnus*, curving evenly forward; the remaining third of the horns is smooth and tends

Southern Reedbuck *Redunca arundinum*.

to be hooked forward towards the tip. There is a soft bulbous swelling at the base of each horn, which has a conspicuous whitish colour and is most developed in old adults (Skinner & Chimimba 2005). They were long thought to be glandular, but Jungius & Claussen (1975) showed that they are composed of tissue from which the horns grow. The whitish colour is caused by small horn particles that flake off continually. Horns have been recorded in ♀♀, but they are typically abnormally shaped, curving downwards (Venter 1984).

Geographic Variation

R. a. arundinum: south of Zambezi R.

R. a. occidentalis: north of Zambezi R. to L. Victoria.

Similar Species

Redunca redunca. A species of the northern savannas with some overlap (of total range) in S Tanzania. Smaller, shorter-horned, with sandy colouration.

R. fulvorufula. A montane species with only overlap of range in extreme south-eastern Africa. Smaller, greyer reedbuck, with relatively smaller muzzle and swollen nose; horns curving forward level with tips of ears; two pairs of inguinal pouches.

Kobus vardonii. A social species restricted to flood-plains and open savannas around the headwaters of the Zambezi R. and southern tributaries of the Congo R. More robustly built, with lyrate horns on ♂♂; redder.

Distribution Endemic to Africa. A southern species originally ranging widely from the Cape Peninsula to L. Victoria in the east and extreme S Gabon in the west. In Tanzania, its range overlaps with that of the Bohor Reedbuck *Redunca redunca* (which is essentially an equatorial species). Examination of the two species' current and former

Lateral view of skull of Southern Reedbuck *Redunca arundinum* female.*Redunca arundinum*

distributions in Tanzania revealed that the Bohor Reedbuck dominated the lower reaches of major rivers and flood-plains while the Southern Reedbuck was commoner in the higher reaches of the same rivers but along their smaller tributaries and streams (Kingdon 1982).

Southern Reedbucks remain relatively widespread throughout their former range, with the exception of S Congo, where their presence was last confirmed in 1974 in Mount Fouari Faunal Reserve and they may now be extinct (East 1999). In Gabon, they survive in small numbers in the south-western and perhaps coastal savannas (though they seem to have disappeared from within the Gamba protected areas complex; P. Henschel pers. comm.), while in DR Congo they are presumably still locally common in the southern savannas, particularly on the high plateau grasslands of Upemba and Kundelungu National Parks (East 1999). In East Africa, they still range widely in S and W Tanzania, generally at low densities (Kingdon 1982, East 1999). Southwards, they occur widely in protected areas in Malawi and Zambia (East 1999), while in Angola (where they occurred throughout, except Cabinda and the more arid south-west) they survive locally within their former range (East 1999, Crawford-Cabral & Veríssimo 2005). In Mozambique, they survive in Gorongosa N. P. and in smaller numbers in areas such as Maputo Elephant Reserve, Banhine N. P., Zinhave N. P. and Marromeu G. R. (East 1999); they are also recorded from NE Mozambique right at the coast (Messalo R.; T. Wachter pers. comm.).

South of the Cunene and Zambezi Rivers, Southern Reedbucks still occur in their natural range in NE Namibia, but they have been introduced to private land outside of their former range in the northern parts of the country (East 1999). In Botswana, they still survive throughout the Okavango Delta, in Moremi G. R. and in the Linyanti area further north (East 1999). In Zimbabwe, they are reported (East 1999) to occur throughout, except in the Zambezi and Limpopo valleys and the western parts (Smithers & Wilson 1979; East 1999). In South Africa, they occur in Limpopo, Mpumalanga and North West Provinces, widely in KwaZulu–Natal, where they occur in considerable numbers on the eastern and western shores of L. St Lucia and marginally in the Eastern Cape. Although largely eliminated from the Free State, they occur in scattered localities on private land and have been reintroduced to protected areas such as Willem Pretorius G. R. Southern Reedbucks have been reintroduced to several reserves in Swaziland, and are now flourishing in some areas (such as Malolotja N. R.) (Monadjem 1998). Lynch & Watson (1990) sighted one in Sehlabathebe N. P. in Lesotho, but this may have been a vagrant from KwaZulu–Natal.

Habitat The most significant habitats in South Africa are valleys in which the grass cover is tall (or there is suitable herbaceous cover) and permanent water is available (Jungius 1971a). Typically, this species lives on ‘islands’ of grass and they actively avoid the surrounding woody vegetation. Jungius (1971a) noted that when persistent firing and heavy grazing was abandoned in parts of Kruger N. P., South Africa, fire-climax grasses such as *Themeda triandra* were replaced by a tall grass veld made up of *Elyonurus argenteus*, *H. dissoluta*, *Heteropogon* spp. and *Andropogon* spp. This community change favoured the Southern Reedbuck, the key species being *Hyparrhenia dissoluta*, which grows culms of up to 2.5 m that remain upright for most of the year, thus providing essential cover (Jungius 1971a). The other key habitat was reed-beds on wet soils, depressions and river beds. Here reeds *Phragmites communis* dominate, growing up to 4 m high, providing both food and cover for the reedbuck. In the foothills of the Drakensberg in KwaZulu–Natal, Howard (1986a) found that they tended to inhabit vleis (wetlands) and hilly veld (natural grasslands) in summer (since these provided adequate cover by way of boulder outcrops, gullies and ledges), switching to agricultural land and adjacent cover in winter. Areas of flat open veld were avoided at all times. Southern Reedbuck range to 1800–2000 m in the Drakensberg mountains (Rowe-Rowe 1994).

Abundance A common and widespread species in South Africa, Rowe-Rowe (1994) highlighted just how abundant this species could become, under ideal (but essentially temporary) conditions, densities of 1 reedbuck per 3–4 ha having been recorded in Eastern Shores State Forest of KwaZulu–Natal (Venter 1979). On mixed farmland, Howard (1983) estimated 1/13 ha to 1/7 ha on a farm that had a high proportion of fire-resistant winter pastures and cover. Aerial surveys generally result in density estimates in the order of 0.1–0.2/km², or less (East 1999). Aerial surveys in Nyika N. P., Malawi, where Southern Reedbucks are common, produced a density estimate of 1.9/km² (Mkanda 1998), but this was almost certainly an underestimate, given the difficulty of detecting reedbucks from the air. The fact that this species occupies ‘islands’ of suitable habitat makes

generalized density figures very difficult to compute. Furthermore, its responses, both positive and negative, to protection and changes in fire regimes mean that very rapid build-ups or declines in numbers can take place. East (1999) used a contemporary average density of 0.3/km² for areas where it is still ‘common’, and 0.03 elsewhere, to arrive at a total population estimate of 73,000.

Adaptations Southern Reedbucks, like other reduncines, are adapted to a very abundant, but unstable, food supply. This predominantly temperate and sub-tropical species has a lower drought tolerance than the Bohor Reedbuck and is not able to last long without water. It probably has less resistance to solar radiation and desiccation than the Bohor Reedbuck, an important factor in the overlap zone between these species in Tanzania.

Jungius (1971a) identified the inguinal gland pockets as the source of popping sounds that are released by a sudden backwards and sideways jerk at the peak of ritualized high jumps. He only recorded popping during flight behaviour, but cited a game scout’s observation that it was emitted during courtship behaviour. Jungius (1971a) recorded popping being followed by whistling and pronking, both behaviours common to the Bohor Reedbuck.

Nasal whistling is produced by suddenly forcing air through the nasal passages and nostrils and Eibl-Eibesfeldt (1957) proposed that the evolutionary derivation and ‘primary’ function of this signal was an expression of fright or alarm. Jungius (1971a) considered the ‘secondary meanings’ for whistling in the Southern Reedbuck were acoustic advertising, displays between rival ♂♂, or a ♂ making contact with a ♀. Whistling can take place during flight, while jumping or from an alert, standing position, or the whistling may combine with pronking, notably when the animals are in long, thick grass. Jungius (1971a) explained static whistling in terms of the whistler’s great feeling of insecurity and uncertainty as to where to flee! He considered whistling a way of indicating presence to neighbours and, when culminating in a real chorus of whistles, the response-whistles also functioned as territorial advertising that indicated ‘territorial rights’. A common preliminary to whistling, but one that is restricted to ♀♀, consists of a low clicking sound, also nasal in origin.

Social grooming has not been recorded in Southern Reedbucks, but they rub their cheeks on their flanks, nibble and lick themselves and scratch neck and head with the hindfeet. Normally, they rest in the cover of tall grass or reed-beds, but occasionally will lie out in full sun. When resting together, individuals lie several metres apart, and never close together.

Foraging and Food Southern Reedbucks are predominantly fresh grass grazers, but will occasionally take small quantities of herbs, and in some areas may even browse extensively (Jungius 1971a, b). These dietary preferences are borne out by studies involving stable carbon isotope analysis (Sponheimer *et al.* 2003b). Jungius (1971b), working in Kruger N. P., noted that the most important grasses in the reedbucks’ year-round diet were *Hyparrhenia* spp., *Trachypogon* spp., *Panicum* spp., *Cenchrus ciliaris*, *Ischaemum brachytherum*, *Chloris guayana* and *Heteropogon contortus*. During winter, hygrophilous grasses were important, notably *Leersia hexandra*, *Imperata cylindrica*, *Cymbopogon validus*, *Hemarthria altissima*, *Phragmites communis* and *Eragrostis* spp. Herbs, notably *Commelina* spp., *Polygonum* spp. and

Cyperus spp. were also taken. Where there is extensive tree and bush cover, and a dearth of edible fresh grasses, the reedbuck may browse dwarf shrubs and *Acacia* and *Albizia* foliage (mostly during the winter). Seasonal movements are primarily determined by the need for cover, thus hillsides are avoided while the ground is bare, although these are preferred habitat once the grass is tall enough to conceal the reedbuck. With the onset of fires and heavy grazing of the slopes by other herbivores the reedbucks descend into the valley bottoms where they can find extensive brakes of *Phragmites* and green grasses growing in wet soils.



Southern Reedbuck *Redunca arundinum*.

Jungius (1971b) found that most feeding took place at night, but that animals extended their grazing and activity periods during the cooler dry season when bouts of feeding and ruminating took place over much of the day. In the rains, reedbucks only became active an hour or less before dark and for up to 2.5 h after dawn. During the day (the only period the animals could be monitored), grazing occupied about 3 h in 12, and a series of ruminating bouts made up a similar total. The rest of the day was spent resting (between 7 and 8 h in total). Extended grazing and frequent trips to water in the dry season presumably compensated for reduced quality forage and to meeting moisture requirements that were otherwise met from dew and succulent herbage in the wet season (Jungius 1971a, Estes 1991a).

Social and Reproductive Behaviour Southern Reedbucks live in male–female pairs, or mother–young pairs with or without an attendant ♂ and Jungius (1971a) never found Kruger N. P. reedbucks associating in herds. He never saw ♂♂ or ♀♀ associate in bachelor groups, but did occasionally observe temporary aggregations of up to 20 individuals, but only in the colder, winter months from about May to Aug. If aggregations were disturbed the individuals immediately dispersed. In the only other major study on the species to date, Howard (1986b), working in the highland region of KwaZulu–Natal, recorded that of more than 550 different sightings, the most usual were solitary adult ♂♂ or ♀♀ and subadults were also occasionally solitary. Of groups, Howard (1986b) found all-female groups made up about 14%, male bachelor groups 8% and family groups 14% of all sightings. Before, and during, the rut, the proportion of solitary adult ♂♂ was highest. During winter, adult ♀♀ tended to be either solitary, associated with adult ♂♂, or in family groups. Adult ♂♂ became solitary towards the summer when family groups broke down and ♀♀ tended to associate together with subadults in female groups (Howard 1986b).

A ♂ and ♀ occupy a territory or home-range that seems to lack clearly demarcated boundaries, but elicits distinctive behaviour in the holders. For example, ♂♂ commonly mount any small eminence such as a termite mound (uncharacteristically ostentatious behaviour in an otherwise cryptic animal), stand on watch and whistle in response to the sight of any other reedbuck. Whistling may or may not be accompanied by a short series of high bounds or almost static, ritualized bouncing jumps or ‘stots’. Within the area shared by male–female pairs, auditory, visual and, presumably, olfactory signals permit almost continuous indirect mutual awareness although physical contact may be irregular, particularly while the ♀ is nursing. Visits away from the territory, some quite distant, were observed by Jungius (1971a), but he was unable to determine how stable pairs were nor was he able to follow the movements of known individuals affected by drought or fire. He found that male home-ranges or territories fluctuated and differences were influenced by the condition of individual ♂♂, by external ecological cycles and by the relative density of conspecifics. Thus, two territories close to a permanent waterhole were only 35 ha in the dry winter, when there was a lot of reedbuck traffic, but expanded to 48–60 ha in the summer long-grass season.

Jungius (1971a) recorded various threat displays used by the territorial ♂, including defecation and urination in a ‘proud’ attitude in front of a contestant with legs held stiff and head erect. Jungius

(1971a) regarded this as an odd form of threat, resulting in either an immediate attack reaction or causing the contestant to move off. Other threat displays involve horn presentation, which may lead to opponents pushing each other with the horns locked and eventually to fighting when the opponents lunge forward and clash horns. Such displays may continue at intervals throughout the day, the contestants occasionally breaking off to graze or rest, but fighting seldom, if ever, leads to serious injury. At the conclusion of fighting, the victor sometimes adopts the 'proud' attitude and defecates, but seldom chases the defeated opponent. Young ♂♂ or ♀♀ may show submission to aggressive territorial ♂♂ by lowering their heads and holding their horns backwards.

In KwaZulu–Natal, Southern Reedbucks do not appear as strictly territorial as those in Kruger N. P.: at St Lucia a social hierarchy is evident by which dominant ♂♂ compete to serve ♀♀ in oestrus, while in the highland regions, ♂♂ display evidence of territoriality only during the rut with dominant ♂♂ occupying territories closest to the food source (Venter 1979, Howard 1983, 1986b; and see Rowe-Rowe 1994). Howard (1986b) hypothesized that this difference between populations could be explained in terms of environmental differences between the areas of study. In his study population in upland KwaZulu–Natal, there was a close correlation between the amount of cover and the number of reedbucks supported by any given area, and this might have been the result of only a finite number of individuals being able to establish territories in limited habitats where cover was abundant. Howard (1986c) recorded home-range sizes in these highlands as varying from 73 ha for adult ♂♂ (subadult ♂♂ had ranges of 210 ha) to 123 ha for adult ♀♀; on the shores of St Lucia, Venter (1979) found mean home-range sizes of 5 ha for ♂♂ and 6 ha for ♀♀. Both male and female individual ranges showed considerable overlap in Howard's study (1986c).

Females do not easily accept approaches from ♂♂ other than their apparent 'mate' and Jungius (1970) saw ♀♀ thwart strange ♂♂ by avoidance and even kicking. Mounting resembles other antelopes in being extremely rapid, and courtship (which involves a territorial ♂ approaching the ♀ with head laid back and nose forward) may be accompanied or followed by rare examples of physical contact as the ♂ licks or rubs his head on the ♀. Females seclude themselves for about a month before giving birth. The young are classic 'hiders' and mothers presumably have a very well developed spatial memory because they do not betray any perceptible signals when visiting their young. Suckling lasts up to 4 min but there may be up to half an hour of play and movement before the juvenile retreats into cover, changing its hideout with every nursing session. Juveniles only emerge and join their mothers at about three months. Female offspring mature and leave the maternal home-range within their second year, around the time that she is due to give birth again. Male offspring mature more slowly and are tolerated for longer, but make elaborately obsequious gestures to the resident adult ♂.

Reproduction and Population Structure Age at first parturition in ♀♀ has been given as between 20 and 24 months (Howard 1983) and 23 and 35 months (Venter 1979) in KwaZulu–Natal. Males reach puberty at nine months, but do not take part in the rut until they are older (Rowe-Rowe 1994). No strict breeding season has been observed, but there is a birth peak between Dec and May (Fairall 1968, Jungius 1970) in Kruger N. P. and from Dec

to Jan in the KwaZulu–Natal highlands (Howard 1983); no obvious peak has been observed at St Lucia (Venter 1979). In Kyle N. P., Zimbabwe, births run from Sep onwards (Ferrar & Kerr 1971).

Gestation period is about 7.5 months (Mentis 1972). Irregular oestrus, staggered maturation times in young ♀♀ and variation in the gestation period might all serve to temper any trend towards truly seasonal breeding (Jungius 1970, 1971a).

Sex ratio at birth is 1 : 1 (Venter 1979, Howard 1983), but among adults Venter (1979) recorded a sex ratio of 1 ♂ to 1.4 ♀♀, and Howard (1983) a ratio of 1 : 1.1. In KwaZulu–Natal, juveniles (less than one year) comprised 19% of the population. Howard (1983) gave the mean life-span of ♂♂ in the wild as four years and ♀♀ as five years, and very few reedbucks live beyond ten years (Venter 1979, Howard 1983). Jones (1993) gave a longevity record of 16 years and nine months in captivity.

Predators, Parasites and Diseases Records from Kruger N. P. between 1954 and 1966 (Pienaar 1969a) showed that Leopards *Panthera pardus* were by far the greatest threat to Southern Reedbucks, with 124 kills, which represented 78% of the Leopards' total recorded kills. Cheetahs *Acinonyx jubatus* followed with 60 (68% of recorded kills), then African Wild Dogs *Lycaon pictus* 36 (87%) and Lions *P. leo* 35 (20%). Less regular predators included crocodiles (3 observed kills), Spotted Hyenas *Crocuta crocuta* (2), a Chacma Baboon *Papio ursinus* (1) and an African Rock Python *Python sebae* (1). The main response to predators is to freeze, skulk into cover and lie down, pressed close to the ground. So-called 'alarm' whistles and jumping or stotting gaits are almost certainly directed at other reedbucks, not the predator (although the predator often appears to lose interest after such displays).

Southern Reedbucks suffer from a similar range of helminths and parasites as Bohor Reedbucks. In KwaZulu–Natal, animals recovered from Howard's (1983) study area were infested with four ixodid tick species (*Boophilus* sp., *Ixodes* sp., *Rhipicephalus evertsi* and another *Rhipicephalus* sp.), while animals taken from the Eastern Shores had seven species and several animals recovered from Charter's Creek and St Lucia had six species; *Rhipicephalus evertsi* was the only tick common to the four localities (Horak *et al.* 1988b). The lice *Damalinea reduncae* and *Linognathus fahrenheitsi* were present on the reed buck from each locality. A single reed buck examined in Zambia was host to three ixodid tick species, namely *Amblyomma variegatum*, *Rhipicephalus appendiculatus* and *R. evertsi* (Zieger *et al.* 1998a).

Helminth parasites have been investigated in detail by Boomker *et al.* (1989c). These authors recovered ten nematode species, two cestodes (*Moniezia benedeni* and *Taenia hydatigena*) and one trematode (*Paramphistomum* spp.) from 26 animals taken in Howard's (1983) study area. *Cooperia yoshidai* was the most numerous and most prevalent helminth with peak burdens occurring in summer. At St Lucia 31 Southern Reedbucks harboured between four and 11 nematode species, one cestode and one trematode. *Cooperia yoshidai* was again the most abundant and prevalent parasite, with peak burdens during autumn to spring. Boomker *et al.* (1989c) provided an amended list of helminth parasites of Southern Reedbucks in South Africa, including 21 nematode species, three cestodes and a trematode (*Paramphistomum* spp.). In Zambia, Zieger *et al.* (1998a) recovered the nematodes *Cooperia rotundispiculum* (a new record) and *Setaria bicoronata* from one individual.

Conservation IUCN Category: Least Concern. CITES: Not listed.

The Southern Reedbuck has been peculiarly vulnerable to all types of hunting and poaching because it is slow and easily brought to bay by dogs and is of a convenient size to be dismembered and carried off by a single or very few hunters (Jungius 1971a). Its early decline and local extirpation over much of southern Africa has been documented by several authors (Harris 1840, Kirby 1896, Sclater 1900). Like the Bohor Reedbuck, this species has a preference for well-watered habitats that attract agricultural and pastoral settlement. Consequently, over much of its original range the Southern Reedbuck has been extirpated or confined to protected enclaves. Protected areas known to represent strongholds for the species include Selous G. R. (Tanzania), Kafue N. P. (Zambia), Nyika N. P. (Malawi), Gorongosa N. P. (Mozambique), the Okavango Delta region (Botswana), and Kruger N. P. and Greater St Lucia Wetland Park (South Africa) (East 1999). East (1999) warned that some peripheral populations, such as those in S Gabon, faced an uncertain future, but that they should survive so long as protected areas and conservancies remained viable.

Measurements

Redunca arundinum

TL (♂ ♂): 1600 (1560–1790) mm, n = 16

TL (♀ ♀): 1580 (1380–1690) mm, n = 20

T (♂ ♂): 250 (220–300) mm, n = 16

T (♀ ♀): 250 (200–300) mm, n = 20

E (♂ ♂): 160 (150–180) mm, n = 16

E (♀ ♀): 160 (140–170) mm, n = 16

WT (♂ ♂): 51.8 (42.7–68.2) kg, n = 16

WT (♀ ♀): 38.2 (31.8–50.9) kg, n = 20

Zimbabwe (Smithers & Wilson 1979)

In the highlands of KwaZulu–Natal, Howard (1983) recorded the average mass of ♂ ♂ as 67.7 kg (n = 60) and ♀ ♀ at 47.2 kg (n = 70); average total length for ♂ ♂ was 1690 mm (n = 60) and for ♀ ♀, 1550 mm (n = 70). At St Lucia ♂ ♂ had a mean mass of 67.8 kg (n = 12) and ♀ ♀, 49.4 kg (n = 46) (Venter 1979)

Maximum recorded horn length is 48.9 cm for a pair of horns from KwaZulu–Natal, South Africa (Rowland Ward)

Key References Howard 1983, 1986a, b, c; Jungius 1970, 1971a, b; Venter 1979.

Jonathan Kingdon & Michael Hoffmann

Redunca redunca BOHOR REEDBUCK (COMMON REEDBUCK)

Fr. Redunca (Cobe de Roseaux); Ger. Gemeiner Riedbock

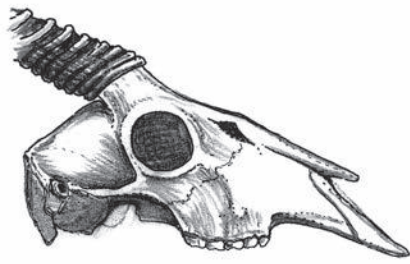
Redunca redunca (Pallas, 1767). Spicil. Zool. 1: 8. No locality cited; based on 'Le Nagor' of Buffon from Senegal, 'dans les terres voisines de l'île de Gorée' (mainland opposite Goree I.).



Bohor Reedbuck *Redunca redunca*.

Taxonomy Polytypic species. Seven subspecies have been recognized (Haltenorth 1963, Ansell 1972), mainly on the basis of small differences in pelage colouration and horn shape, but the limits and intergradation between them are not clear. Kingdon (1997) listed only four, among others including *nigeriensis* in *redunca*; we provisionally retain the two as separate, but a review of subspecies limits is necessary. Synonyms: *bayoni*, *bohor*, *cottoni*, *dianae*, *donaldsoni*, *nagor*, *nigeriensis*, *odrob*, *reversa*, *ridunca*, *rufa*, *tohi*, *typical*, *ugandae*, *wardi*. Chromosome number: not known.

Description Bohor Reedbucks are medium-sized, sandy-coloured antelopes in which the slender proportions of ♀ ♀ contrast strongly with the thick-necked, hook-horned ♂ ♂. Leaf-shaped ears have sandy backs, but fronts are lined with dense white hair. Head and body are a rich sandy colour above with white underparts and white chin and bib covering the upper throat. Black eyelids have white surrounds so that the dark eyes stand out visually. Pelage around the black subauricular patches (which are occasionally absent in some individuals) is also white. A dark vertical line may or may not be present down the front of the foreleg. Coat is sleek and soft and somewhat woolly in young and juveniles. Body colour continues onto outer surface of the tail, but long-haired underside is pure white. There are large inguinal gland pockets in the groin; functional pedal and preorbital glands are absent. Sebaceous secretions film the entire pelage, scenting the entire animal quite pungently. Only ♂ ♂ have horns, which are commonly short, black, heavily ridged and curve forward sharply.



Lateral view of skull of Bohor Reedbuck *Redunca redunca*.

Geographic Variation

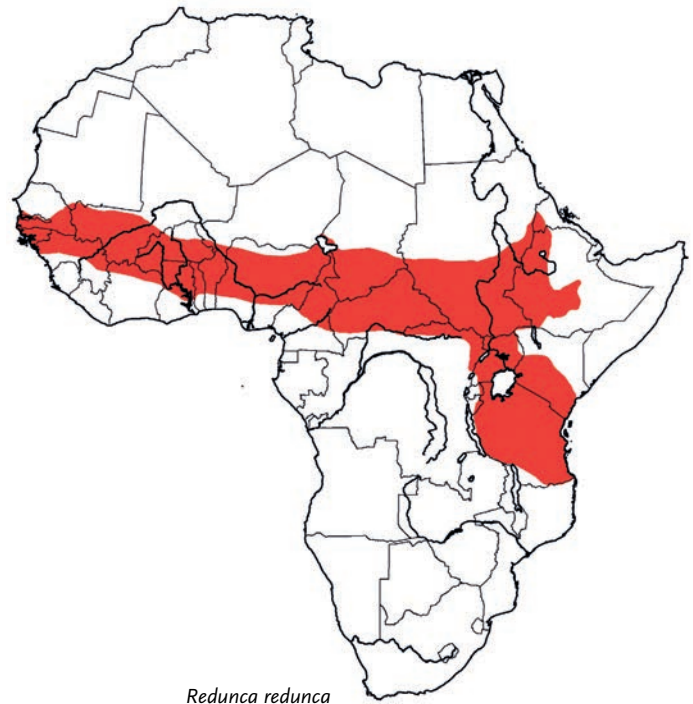
- R. redunca redunca*: Senegal east to Togo. Relationship to *nigeriensis* unclear. Smallest subspecies; lacks dark stripe on the forelegs; short tightly curled horns, with forward-pointing tips.
- R. r. nigeriensis*: Nigeria, N Cameroon, S Chad and Central African Republic. Tips of horns often depressed below the level of the frontal plane. Possible synonym with *R. r. redunca*.
- R. r. cottoni* (including *dianae*): Sudd region in S Sudan, NE DR Congo and possibly N Uganda. The largest subspecies with the longest horns, their tips less hooked and sometimes point inwards.
- R. r. bohor* (Abyssinian Bohor Reedbuck): W, C and SW Ethiopia, and Blue Nile of Sudan. Body colour a grizzled buffish-yellow; horns short and stout, but with the hooks pointing forward.
- R. r. wardi* (including *tohi*): Uganda, E DR Congo and East Africa. Sharply hooked horns, very richly tinted in colour, having black tips to the hairs on the dorsal surface; a dark stripe present on the forelegs, and underparts white.

Similar Species

- Redunca arundinum*. Overlaps in total range in S and W Tanzania. Larger, longer-horned reedbuck, with a more southerly distribution, and dark fronts to forelegs.
- R. fulvorufula*. Strictly montane reedbuck, of very limited distribution in East Africa and Cameroon. Smaller, greyer, and with relatively smaller muzzle and swollen nose.
- Kobus kob*. A broadly sympatric, but social species. Much more robustly built, taller, redder (or, in Sudd, ♂♂ black and white).

Distribution Endemic to Africa, ranging north of the forest zone from Senegal, Gambia, N Guinea and SW Mauritania through the woodlands and flood-plain grasslands of the savanna zone of West Africa through N Cameroon (Adamaoua Plateau northwards), S Chad, the savanna woodlands of the Central African Republic, extreme N and NE DR Congo, C and S Sudan, to W and C Ethiopia and south to L. Tanganyika and the Rovuma R. in Tanzania.

In West Africa, they have undergone fairly large range contractions, particularly in Togo, where formerly widespread in the north, and now possibly extinct; Ghana, where formerly widespread in savanna woodlands, but now of uncertain status; Niger, where they have been eliminated from much of their former range in the south-western savannas and along the border with Nigeria (but survive in W N. P.); and Nigeria, where they have been eliminated from most of their former range in the northern and central parts (East 1999). They are also possibly extinct in Côte d'Ivoire (F. Fischer pers. comm.); the species was not recorded at all in Comoré N. P. by Fischer *et al.*



Redunca redunca

(2002), despite its former presence in the northern parts (Roth & Hoppe-Dominik 1990). There is no evidence that Bohor Reedbuck ever occurred in Sierra Leone (Grubb *et al.* 1998).

Elsewhere, Bohor Reedbucks formerly occurred in the south-western savannas of Eritrea, but there is no recent confirmation of the species' status in that country; likewise, their current status in Burundi, where Verschuren (1988) reported at the time that they may still occur in Ruvubu N. P., is unknown (East 1999).

In some marginal parts of its range, such as the Aberdares in Kenya and the Ethiopian Highlands, it co-exists with the coarse-grass grazing Mountain Reedbuck *Redunca fulvorufula*. Over much more extensive areas, in Tanzania, its range overlaps with that of the Southern Reedbuck *Redunca arundinum* (which is adapted to southern temperate and austral seasonal cycles). However, a more detailed examination of the two species' current and former distributions in Tanzania revealed that the Bohor Reedbuck dominated the lower reaches of major rivers and flood-plains while the Southern Reedbuck was commoner in the higher reaches of the same rivers but along their smaller tributaries and streams (Kingdon 1982).

On the extreme north-eastern margins of its range this species has colonized montane areas, such as the Bale Mts, beyond its usual preferred habitats. Climatic change and the retreat of glacial habitats in Ethiopia after 16,000 BP and subsequent forest clearance by humans might help explain this peripheral but significant extension of range and habitat.

Habitat Associated with woodland and flood-plain grassland across much of their range. For example, in N Cameroon they occur in two discrete habitats: in seasonally flooded grasslands (*Vetiveria nigritana*, *Echinochloa pyramidalis*) in the Sahelo-Sudanian areas (Scholte 2005) and in *Isberlina* woodland in the Sudano-Guinean zones (Van Lavieren & Esser 1979). The most distinctive feature of adaptation to their habitats is how animals accommodate to radical seasonal changes in edaphic and fire-climax grasslands: tall and rank

in the wet or flood season, dry, burnt or trampled flat in the dry season. In the wet-season phase, animals are surrounded by ample cover, food and water, and all contacts with other animals, whether conspecifics or predators, are at very close quarters. In the dry-season phase, individuals may or may not be able to find some cover but the greater part of their environment is open, often waterless, and dangerously exposed. Many features of the Bohor Reedbuck's behaviour only become comprehensible when viewed in the light of this annual contrast.

In common with other reduncines, the Bohor Reedbuck is effectively water-dependent, but it shows a strong preference for extensive areas of flood-plains and open inundated grasslands where access to water may become restricted in the dry season. Seasonal movements out of burnt, overgrazed or waterless areas are usually relatively local, often involving a general shift up or down the catena. Typically, animals congregate closer to water and fresh grass growth during the dry season. There is a strong preference for flat, low-lying land but they also live on slopes, foothills and upland plateaux, especially along the margins of major sump areas. The most significant of these peripheral areas is the Ethiopian Highlands, where they occur to about 3200 m (Abdi 1987, Yalden *et al.* 1996) on montane grasslands, moorlands and secondary woodland grassland mosaics. As much of the Ethiopian upland habitats are anthropogenic, deriving from human clearance of montane forest and woodland, it is likely that Bohor Reedbucks have colonized such areas in relatively recent times. Significantly, almost all such areas lie close to westward-flowing tributaries of the Nile R., where one of the largest blocks of flood-plain habitat in Africa, the Sudd, supports a major population. The most isolated north-eastern subpopulation of Bohor Reedbucks, on the Bale Massif, seems to have crossed the Rift Valley and derives from a western Ethiopian source.

Abundance Originally a very common and widespread species, the Bohor Reedbuck has a preference for flat, well-watered habitats that also have high agricultural and pastoral potential. It is therefore in rapid decline over the greater part of its range. In exceptional and very restricted localities, such as the Gemmeiza levee in S Sudan, temporary densities of up to 110/km² were recorded (Mefit-Babtie 1983). In the Nile/Jonglei section of the Sudd region, aerial surveys of 67,900 km² revealed a total of 33,380 animals in the late dry season (an overall density of 0.5/km²), at which time a high proportion of animals were exposed. By contrast only 2547 were seen during the height of the wet season, when animals were easily concealed in grass. Although some of this discrepancy of over 90% could be attributed to migration off plains to the east of the survey area it was also clear that aerial counts, especially those conducted while the grass is long, can substantially underestimate Bohor Reedbuck numbers (Mefit-Babtie 1983). Fryxell (1980) estimated a dry-season population of nearly 30,000 in Boma N. P. Recent surveys conducted in the dry season in S Sudan, found Bohor Reedbucks to be abundant in the Jonglei, with large concentrations in the central plains together with Mongalla Gazelle *Eudorcas albonotata* and Tiang *Damaliscus lunatus*: as many as 11,000 animals were estimated to occur in the Jonglei area, with a further 2050 in Boma (a notable reduction from Fryxell's earlier estimate) and 257 in Southern N. P. (Fay *et al.* 2007).

In the Sahelo-Sudanian habitat of Waza N. P. (N Cameroon), of which approximately 40% is flood-plain, numbers were estimated,

mostly through terrestrial counts, at 4000 in 1960, dropping to 500 in 1967 and to less than 100 following the 1970s droughts (respectively, 2.4 to 0.3 to 0.06/km²) (Scholte 2005, Scholte *et al.* 2007). In the Sudanian-Guinean area of N Cameroon, Van Laveren & Esser (1979) surveyed Bouba Ndjida N. P. and estimated the total population at 5663 (ground counts) and 3221 (aerial counts), or a density of 2.6 and 1.5/km², respectively.

Butynski *et al.* (1997b) made an overall estimate of 5.6/km² in prime, protected habitat at Ruma, Kenya, a figure that corresponds well with figures deriving from the Ankole-Masaka 'tsetse clearance scheme' where 6630 Bohor Reedbucks were shot in about 1000 km² of suitable habitat (Kingdon 1982). Campbell & Hofer (1995) estimated 1.0/km² in Serengeti N. P., a figure that might approximate to an average for populations in relatively undisturbed areas of patchy habitat. Field (1970b) estimated 0.65/km² for good habitat around L. Edward, Uganda. Elsewhere, aerial surveys in many parts of Africa have produced figures of 0.1–0.3/km² (East 1999). Such very low figures could reflect any of the following constraints: dense vegetation cover, cryptic behaviour (crouching reedbucks are very difficult to see), uneven sampling of extensive plains where animals disperse widely in the wet season, but congregate in the dry, or counts from heavily hunted (and therefore depleted) areas.

East (1999) calculated total population size at around 100,000 individuals, including about 4500 animals for the Sudan, but acknowledged that this was likely to be a substantial underestimate.

Adaptations Bohor Reedbucks, like other reduncines, are valley grazers adapted to a very abundant but unstable food supply. Hofmann (1973) differentiated this species from the Mountain Reedbuck by describing the latter as a montane 'roughage grazer' and the Bohor Reedbuck as a sump-land 'fresh grass grazer'. Some physiological peculiarities can be added to this distinction in diet. Judging from the ability of some individuals to survive for weeks on dry plains (up to 25 km from water) in the S Sudan, this species would seem to have a higher drought tolerance than the Southern Reedbuck. As 'shaders' (Percival 1928) they can dispense with water so long as they can find even vestigial shade and graze off fresh grass regrowth. This ability to last longer without water might be augmented by greater resistance to solar radiation and desiccation than the Southern Reedbuck and permit them to exploit much wider, hotter tropical flood-plains. Schoen (1971) noted that the entire pelage and skin of the Bohor Reedbuck is infused with sebaceous secretions that might act as a seal against water loss as well as providing insulation against radiant heat.

Typically, Bohor Reedbucks are 'hidiers', avoiding detection by predators through freezing or sinking smoothly to the ground, where they lie down, neck extended, their colouring blending in well with the grass. Their social behaviour, by contrast, is noisy and conspicuous. Whistling and bounding are the two most characteristic behaviours. In any interaction within a closed environment there is the primary problem of identifying the sex and status of individuals. The leap and whistle are probably the main mechanism by which the reedbucks recognize each other. There are, therefore, differences in the amplitude, length and style of leaps and in the pitch and number of whistles. This species has to invest these displays with information content appropriate to a normally closed, long grass habitat. In addition to the auditory and visual signals it seems likely that there is

at least one strong olfactory signal. Bohor Reedbucks have 'pockets' in the groin that contain inguinal glands and it would seem that these pocket glands are responsible for loud 'popping' sounds that accompany high leaps. Presumably the pockets evacuate puffs of scent during these leaps and give other Bohor Reedbucks detailed information on the age, sex and condition of the jumper. Whistle/leap displays are most frequent in young ♂♂ and ♀♀ and contrary to most accounts seem to be directed at other reedbucks, especially adult ♂♂, rather than predators. Such displays have been observed in the open, in daylight, amongst mixed sex, mixed-age aggregations (Vesey-FitzGerald 1967), but it would seem likely that the whistles and leaps are specifically designed to take effect in long grass and at night (Kingdon 1982).

This species appears to be exceptionally mobile and flexible in its social behaviour: ♂♂ typically defend well spaced-out mating territories, but readily accommodate to fires and the destruction of cover and food by congregating on temporary pastures. In the dry season they commonly undertake long treks between diurnal hiding places and nocturnal pastures and water-sources.

Food and Foraging That Bohor Reedbucks are fresh grass grazers has been borne out by both observations and stomach analysis (Field 1970b, Hofmann 1973; and see Gagnon & Chew 2000) and studies involving stable carbon isotope analysis (Cerling *et al.* 2003). In Rwenzori Mountains N. P., Uganda, Field (1970b) recorded a very strong and perennial preference for *Sporobolus consimilis*, leading to concentrations of these animals in *S. consimilis* swards. Other preferred grasses are *Hyparrhenia filipendula*, *Heteropogon contortus* and *Themeda triandra*, all dominant species in fire climax

and heavily grazed grasslands. He noted that *Cynodon dactylon* and *Cenchrus ciliaris* were preferred in the rains and *Sporobolus pyramidalis* and *Panicum repens* in the dry season. At the southern margins of their range, Vesey-FitzGerald (1967) recorded them as most numerous on swards of *Echinochloa*, *Cynodon* and *Cyperus* spp. Along water channels it favours *Leersia* and newly sprouted *Vossia* and grazes *Imperata* on regularly burnt pastures. Hofmann (1973) noted that dicotyledons were rare, but these could include *Capparis*, *Sida* and the aromatic leaves of a small forb.

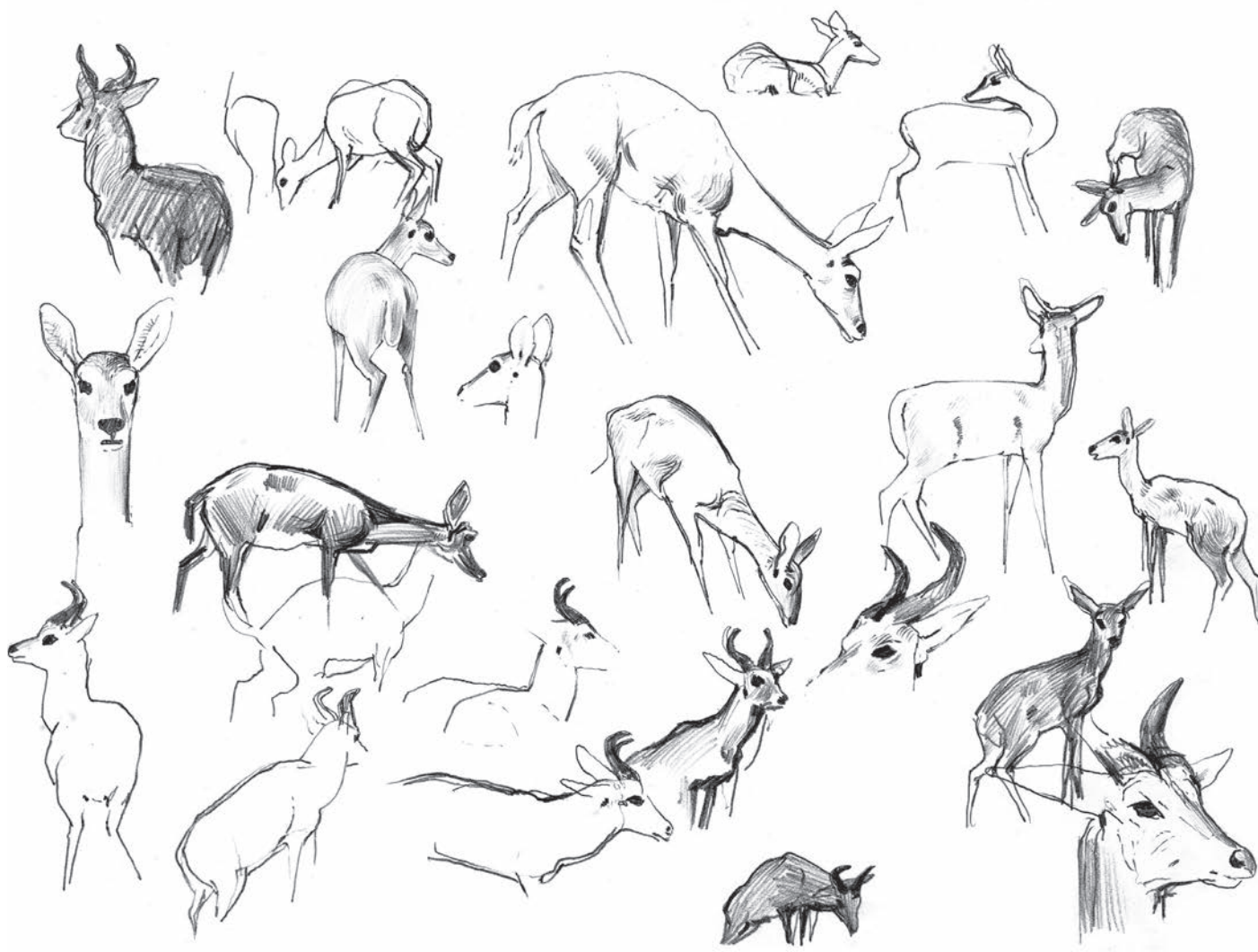
Although active mainly at night, grazing may also take place during the day in some areas. Nocturnal grazing can take place a very long way from daytime refuges. Seasonal differences in the amount of time devoted to grazing seem to be a response to the availability and quality of grasses (D. F. Vesey-FitzGerald pers. comm.).

Social and Reproductive Behaviour Bohor Reedbucks' social structure is highly flexible and adjustable to the annual cycle of change in their grassy environment. Typically, ♀♀ (1–5 adults) with young have home-ranges that overlap those of single, spaced-out adult ♂♂; bachelor male groups numbering up to 19 may spend time within the established mating territory of a dominant ♂ and are tolerated unless there are ♀♀ around. In a very short-term study in Serengeti N. P., ♀♀ were found living within home-ranges of 15–40 ha and their movements overlapped those of other ♀♀. Male mating territories were estimated to be between 25 and 60 ha (Hendrichs 1975b). In many narrow valley environments, Bohor Reedbucks appear to remain well spaced in twos or small groups throughout the year. In less confining valleys, as in Kidepo Valley N. P., Uganda, there are regular dry season congregations of reedbucks numbering up to 23 animals. Likewise, in Bale Mountains N. P., Ethiopia, large aggregations (up to 59 individuals) were observed during the dry season as a result of local immigration to swamp grassland habitat (Afework *et al.* 2010). Subgroups can be recognized within these aggregations, each accompanied by an adult ♂.

In the vast open flood-plains of the Sudd region, Sudan, dry-season fires and intensive grazing by both wild and domestic herds deprive Bohor Reedbucks of cover over immense areas. Across some 200 km of dry, open plains an aerial flight in Mar (at the end of the dry season) revealed occasional solitary ♂♂ that could be seen almost continuously. Often such ♂♂ were sheltering under the flimsiest of shade. When disturbed by the aeroplane these ♂♂ invariably ran in a tight circle, implying some attachment to one spot in spite of an absence of other animals, water and any obvious grazing. In contrast to these solitary ♂♂, the majority (of both sexes) of Bohor Reedbucks on the Sudd flood-plains desert the driest, burnt areas and collect closer to water and fresh grass grazing. These aggregations are commonly relatively dispersed, particularly when the reedbucks are mixed up with numerous other grazers. On both the eastern and western borders of the flood-plain (and sometimes on temporary pastures), Bohor Reedbucks congregate so closely that they almost resemble 'herds'. On the 'Duk Ridge', which lies between the eastern Sudd flood-plains and the Nile R., Bohor Reedbucks concentrate in a relatively narrow north-south belt for the worst part of the dry season and then disperse eastwards with the arrival of the rains. Along the narrowest section of this levee, at Gemmeiza, this pattern of dispersal is modified because large numbers of reedbucks remain in the area for



Bohor Reedbuck *Redunca redunca* calf 'freezing' prone.



Bohor Reedbuck *Redunca redunca*.

more than half the year. The Gemmeiza population has long been known to trophy hunters for exceptionally long-horned reedbucks, suggesting a direct correlation between sustained high densities and larger horns. The Bohor Reedbucks in this locality are also of special interest for the light they might throw on the evolution of sociality in an otherwise semi-solitary species.

When ♀♀ come into oestrus the hormonal clues for ♂♂ may include increased activity in the subauricular patch-glands as copulation and increased male interest have been seen to coincide with sudden visible exudation from these glands (T. Nuti pers. comm.). At Kikagati, Uganda, a ♂ was seen to approach an apparently oestrous ♀ and run around her, jumping and uttering a harsh, toy trumpet-like bleat. In some respects Bohor Reedbucks resemble other reduncines in their courtship, a ♂ approaches a ♀ with head lowered and stretched out and if the ♀ is in oestrus and permits a close approach the ♂ repeatedly strikes up at her belly with his foreleg. Copulation is extremely fast and accurate. When a ♀ visits her offspring, to suckle it, breaking off contact can be difficult; J. Kingdon (pers. obs.) has watched a young chasing its mother round and round a termity until the mother suddenly detached herself,

giving the distinct impression that she used the termite mound as a contact-breaking device.

Reproduction and Population Structure Because the young are kept very well hidden for at least two months, actual birth records are scarce. Very young animals are scarcely ever seen during the peak of the drought in S Sudan, due partly, perhaps, to the fact that grass fires would incinerate or expose most very young animals and partly to subsequent exposure to predators and heat-stress. Such constraints are likely to exert strong selection for birthing during the wet and flood seasons. Breeding activity, therefore, seems to peak in the wet season (Apr–Oct over most of their range) (Kingdon 1982). Gestation has been estimated at about 225 days. In Bale Mountains N. P., Ethiopia, with a very different ecology, almost 60% of ♂♂ exhibited territorial behaviour during the wet season and over 78% of young were observed during the dry and early wet season (May–Oct), although young were recorded in all months of the year (Hillman 1986a). Males reach adult size and sexual maturity at about two years, but ♀♀ are probably capable of conception at a little over one year (P. Fox pers. comm.). In Katavi N. P., Caro (1999b)

recorded a sex ratio of 0.45 males to females, and 0.33 young per female.

There are reports of captives living to 18 years, but maximum longevity recorded in captivity is 10.7 years (Weigl 2005).

Predators, Parasites and Diseases Adults are taken by all the main large predators, including Lions *Panthera leo*, Leopards *P. pardus*, Cheetahs *Acinonyx jubatus*, Spotted Hyenas *Crocuta crocuta*, African Wild Dogs *Lycaon pictus*, Nile Crocodiles *Crocodylus niloticus* and African Rock Pythons *Python sebae*. Young are taken by large raptors, jackals *Canis* spp., Serval *Leptailurus serval* and Caracals *Caracal caracal*.

Bohor Reedbucks have been recorded hosts to a number of helminths, including: *Carmyrius papillatus* in the rumen, *Stilesia globipunctata* in the small intestine, *Trichuris globulosa* in the caecum, *Setaria* spp. in the abdominal cavity, *Dictyocaulus* sp. in the lungs and *Taenia* cysts in the muscles (Mefit-Babtie 1983, Tag Eldin *et al.* 1986). Other recorded parasites are *Schistosoma bovis*, *Amphistoma* sp., *Oesophagostomum* sp., *Stilesia* sp., *Cooperia rotundispiculum*, *Haemonchus contortus* and *Hypoderma* larvae. Van Hoven (1983) recorded 18 protozoan parasites from rumen contents in the Bohor Reedbuck, including seven entoninia and two new *Diplodinium* species. They are also hosts to ticks, such as *Amblyomma* spp. and *Rhipicephalus evertsi* (Mefit-Babtie 1983, Ntiemo-Baidu *et al.* 2004).

Conservation IUCN Category: Least Concern. CITES: Not listed.

The primary threats to the species include habitat destruction, drought and overhunting. In some parts of their range, such as N Cameroon, flood-plain degradation through the construction of upstream dams has been a major reason for the decline of Bohor Reedbucks, while in other parts of their range (Tanzania, Chad), the spread of settlement, cultivation and agriculture have had an impact on their available habitat. None the less, even in N Cameroon, Bohor Reedbucks can still be observed even in flood-plain areas with (relatively) high population pressure (P. Scholte pers. comm.). Over much of their current range Bohor Reedbucks are most likely to be killed by humans with dogs, a mode of hunting to which they are peculiarly susceptible because they are quickly outpaced by dogs and readily brought to bay. They are also easily snared or shot, particularly when dazzled by lamps at night. They are often hit by vehicles at night and have been recorded being drowned.

Becoming uncommon in many parts of its former range, especially in West and central Africa, the Bohor Reedbuck survives in a number of important parks and other conservation areas, including Boucle du Baoule (Mali), Niokolo-Koba N. P. (Senegal), Arly-Singou Faunal Reserve (Burkina Faso), Bouda Ndjida N. P. (Cameroon), Manovo-Gounda-St Floris N. P. (Central African Republic) and Bale Mountains N. P. (Ethiopia) (East 1999). There is no recent information on their presence in Boucle du Baoule N. P. (Mali), which has been severely depleted of edible animals. It may no longer occur in Comoé N. P. in Côte d'Ivoire (Fischer *et al.* 2002), while its presence in Mole and Digya National Parks in Ghana (reported by East 1999) is doubtful.

They are surely on the verge of extinction in Akagera N. P., their last-known stronghold in Rwanda (Apio & Wronski 2011). It occurs in all but the most arid of East African conservation areas (East 1999).

Measurements

Redunca redunca

HB (♂ ♂): 1250–1450 mm

HB (♀ ♀): 1150–1300 mm

T (♂ ♂): 200–250 mm

T (♀ ♀): 150–230 mm

Sh. ht (♂ ♂): 700–800 mm

Sh. ht (♀ ♀): 650–800 mm

WT (♂ ♂): 45.0–65.0 kg

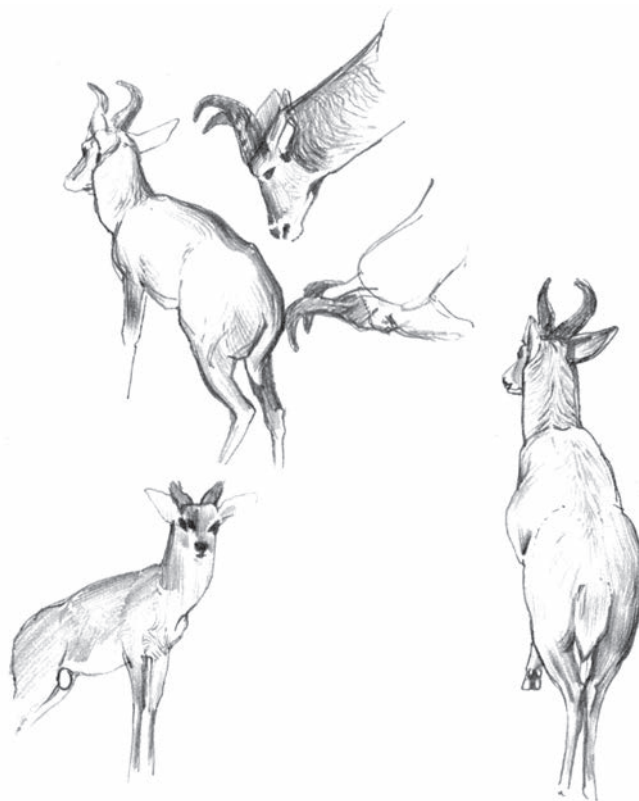
WT (♀ ♀): 35.0–55.0 kg

Throughout the range (Haltenorth & Diller 1980); means and sample size not given.

Maximum recorded horn length is 42.5 cm for a pair of horns from Gemmeiza, Sudan (Rowland Ward)

Key References Hendrichs 1975b; Kingdon 1982; Vesey-FitzGerald 1967.

Jonathan Kingdon & Michael Hoffmann



Bohor Reedbuck *Redunca redunca*.

GENUS *Kobus*

Kobs

Kobus A. Smith, 1840. Illustr. Zool. S. Afr. Mamm. Part 12, pl. 28 plus text.



Kob *Kobus kob* superficial myology.

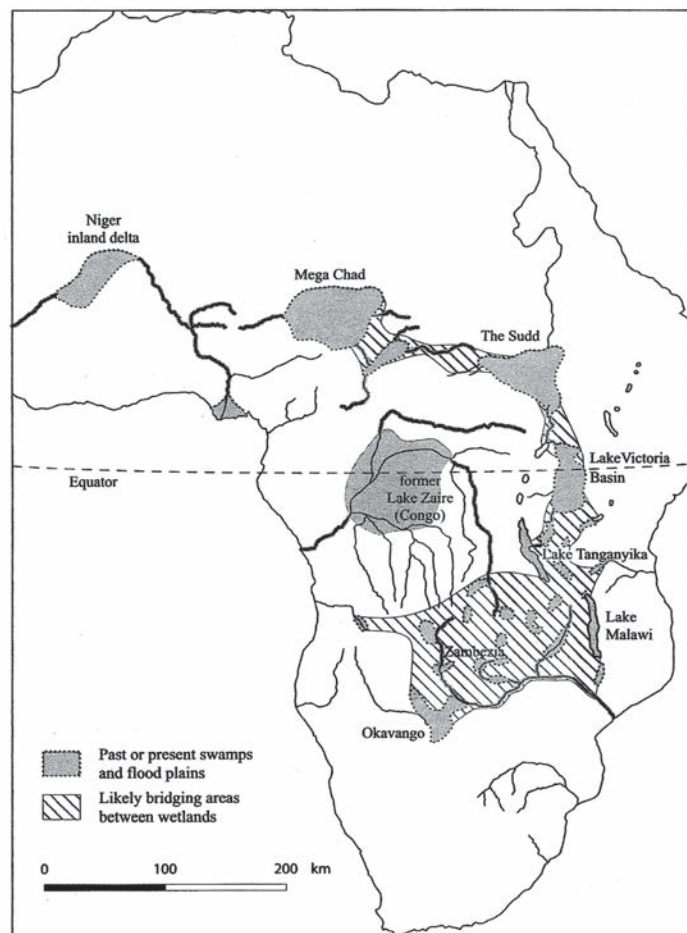
The genus *Kobus* embraces all the larger reduncines, which, in this work, are considered to number five species. Some 15 species of fossil African *Kobus* have been described, dating back some 7 mya, an age several times older than that estimated by molecular clocks. Fossils identified as *Kobus* are known from the Indian subcontinent, so there is an Asian dimension to reduncine evolution, although the surviving species probably represent an exclusively African radiation.

As with other reduncines, the primary habitats of *Kobus* are valley grasslands wherein these antelopes make local movements, of variable amplitude, in pursuit of super-abundant but unstable resources, namely fast-growing, nutritious valley grasses. Members of the genus are strong, sturdy antelopes but are relatively slow and with little stamina. These differences can be best appreciated by contrasting the proportions of Kob *Kobus kob* with those of the Grant's Gazelle *Nanger (granti)* complex, antelopes of comparable shoulder height. A lack of stamina and speed may have played a significant part in the restriction of early reduncines to wet, muddy habitats where many predators are at a disadvantage. In this perspective, all *Kobus* species probably had to evolve special strategies to mitigate predation, such as deeper retreat into swamp, hiding in dense vegetation and 'hiding' in large, dense herds.

The species have a wide range of weights, from about 50–290 kg, and although there has been a broad and unambiguous trend within the Reduncini to evolve from smaller to larger, the contemporary species of *Kobus* are broadly equally successful within their particular niches in spite of their diversity of weights and sizes. This suggests that there are probably optimal body-sizes for each of the particular niches that *Kobus* now occupy. Furthermore, in the evolution of reduncines, it was probably essential for true swamp-dwellers to

reach a minimal size (of about 60 kg) before they had the muscle and weight to cope with heavily obstructed reedbeds, deep muds and floods. Could a combination of taking refuge from predators and exploiting the intrinsic food resources of swampy habitats have driven the trend towards larger size in *Kobus*? The tendency for Waterbuck *K. ellipsiprymnus* to escape predators by wading into water hints that the Waterbuck might represent an early, but essentially secondary, return onto dry (but still very well-vegetated) ground.

The most likely speciation pattern for *Kobus* was adaptation by two *Redunca*-like populations to two (spatially and climatically distant) extremes of valley habitats. One of these would have tended towards seasonal drying out, and the other towards more or less permanently wet swamp. If exclusively intra-African, and on a continental scale, the former was more likely to have been south of the Sahara, but, perhaps, still within its aridifying influence. The second was likely to have been closer to the Equator, with its two wet seasons and greater likelihood of ever-wet conditions. This prediction of a phylogenetic bifurcation has been borne out by two studies of the *Kobus* radiation. According to the molecular results of Birungi & Arctander (2001), *Kobus* emerged from a *Redunca*-like ancestor and diverged into two branches – 'non-swamp'



Web of tropical wetlands linking Zambezia and Okavango with L. Victoria basin, the Sudd and L. Chad.

Kobus and the swamp-dwelling lechwes. More plausibly, another study (Brashares *et al.* 2000, drawing on Gatesy *et al.* 1997) allied lechwes with the still larger Waterbuck, suggesting that the primary bifurcation was between a smaller (50–100 kg) Puku/Kob lineage and a larger (60–130 kg) Lechwe/Waterbuck lineage.

The Kob has exploited the super-abundance of grazing resources on flood plains to reach huge densities and survive in a combination of greater numbers and mobility between dry and wet season pastures. In their much more modest seasonal concentrations, some reedbuck populations illustrate the ecological context in which such a strategy might have evolved. The Kob is a boom-and-bust species that can rapidly recoup its numbers after droughts and until recently occupied a region that extended from Senegal to W Kenya. The Puku, which is sometimes treated as conspecific with Kob (and see Birungi & Arctander 2000), probably represents a later, southern off-shoot of the Kob.

At the time of a primary bifurcation between ancestral Puku/Kob and ancestral Lechwe/Waterbuck, the depression that is now L. Victoria was probably one of the prime areas of shallow, grassy wetlands in Africa. To the north it connected to the Nile R.; to the south, only Lakes Tanganyika and Rukwa separated it from the wide scatter of flat sump-lands at the headwaters of the Zambezi and southern Congo rivers. For these reasons it is likely that the Equatorial L. Victoria region was where a common Lechwe ancestor first emerged.

In the progressive adaptation of lechwes to swamp-dwelling there would have come a time when these antelopes were unable to survive outside swamps. From that point on, populations within specific basins would have tended to become genetically distinct. The northern and southern foci of lechwe dispersion probably became separated from one another quite early on, possibly even before the latest episode of flooding of the L. Victoria basin. Intermittent droughts during the Pleistocene would have reinforced such separation and even the Southern Lechwe shows clear genetic differences between populations that inhabit geographically closely clustered, but separate, basins. These differences can be ascribed to more recent disconnections between populations that were formerly part of a shared gene pool.

The swamp-loving lechwes, so far as is known, never reached West Africa, but the Nile's former connections with the Niger make an extension of proto-lechwe range to L. Chad and the Niger's inland delta plausible. During very wet periods, when their spread was most favoured, the earliest forms probably had opportunities to spread over a more or less continuous network of river systems, swamplands and lake margins from the Okavango delta in the south to at least the Sudd in the north, with extensions further west quite likely. Nonetheless, out in the far west, repeated periods of Saharan expansion and aridification of shallow basins would have inhibited large-bodied *Kobus* from becoming wholly swamp-adapted.

Fossils and some differences between the western population of *K. e. defassa* and the south-eastern *K. e. ellipsiprymnus* give credence to the proposal that Waterbuck differentiated in West Africa from an ancestor that was more like a Lechwe than a Kob. The former are tropical, tolerate high temperatures and more humid conditions; the latter tolerate colder temperatures as well as drier habitats and probably emerged later. Fossil Waterbuck first appear at about 2.3 mya in sites that lie close to or north of the Equator and, in addition to becoming larger, their horn bases show a gradual loss of the Lechwe-like backward curve and distal hook (Gentry 2010). Still earlier, about 4 mya, a fossil lechwe-sized reduncine, *Kobus sigmoidalis* appeared,



Frontal aspect of the Black Lechwe
Kobus leche smithemani.

was particularly common in the mid Pliocene, and fits the profile of a Lechwe/Waterbuck ancestor.

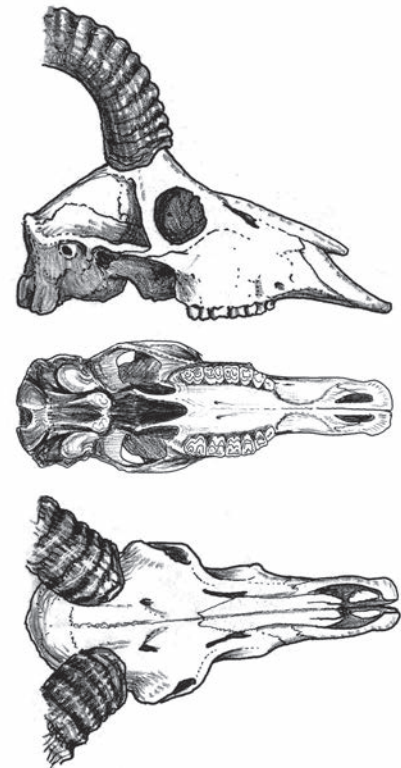
Unlike lechwes, the very much larger Waterbuck seldom congregates in great numbers but they are much more widely, albeit patchily, dispersed along river-courses over a large part of Africa. Their diet consists of valley-bottom grasses, but they resemble other reduncines in seeking out dense thickets, reedbrakes and other dense vegetation to rest up in. They are 'hidiers' that gain some immunity from small and medium-sized predators by virtue of their large size, high fecundity and efficient exploitation of a wide variety of valley habitats.

In addition to its ancestral implications, the emergence of *K. e. ellipsiprymnus* in the south-east and *K. e. defassa* in the centre-west follows a biogeographic pattern that is of general significance in the evolution of African biota. In the exceptionally benign ecological and climatic conditions of the recent past the two populations of Waterbuck interbreed along a very broad and complex overlap zone. During several dry cold Glacial periods the overall ranges of Waterbuck can be confidently predicted to have shrunk into two much more restricted core regions (Kat 1993), a prediction corroborated by molecular studies (Lorenzen *et al.* 2006b). The western *K. e. defassa* has probably enlarged its range from a core of moist watersheds that feed the Congo, Nile, Niger and other great rivers. The eastern *K. e. ellipsiprymnus* is likely to have expanded from a precariously narrow eastern African littoral zone which runs north-south and consists of moist habitats sustained by precipitation off the Indian Ocean. The mechanism that has kept the two populations apart (probably more than once) is the long corridor of arid country that has periodically opened up to connect the Horn of Africa with the Namibian and Kalahari deserts, and which has been identified as the eco-geographic barrier that caused the bifurcation of many related forest and moist woodland-adapted animals and plants into distinct eastern and central African forms (see Kingdon 1990). In the case of Waterbuck populations, the length of their separation has been insufficient to result in total reproductive isolation, but Kingswood *et al.* (1998b) have found fixed chromosomal differences that imply reduced fertility in hybrids or their offspring (see species profile).

Jonathan Kingdon

Kobus kob KOB

Fr. Cobe de Buffon; Ger. Grasantilope.

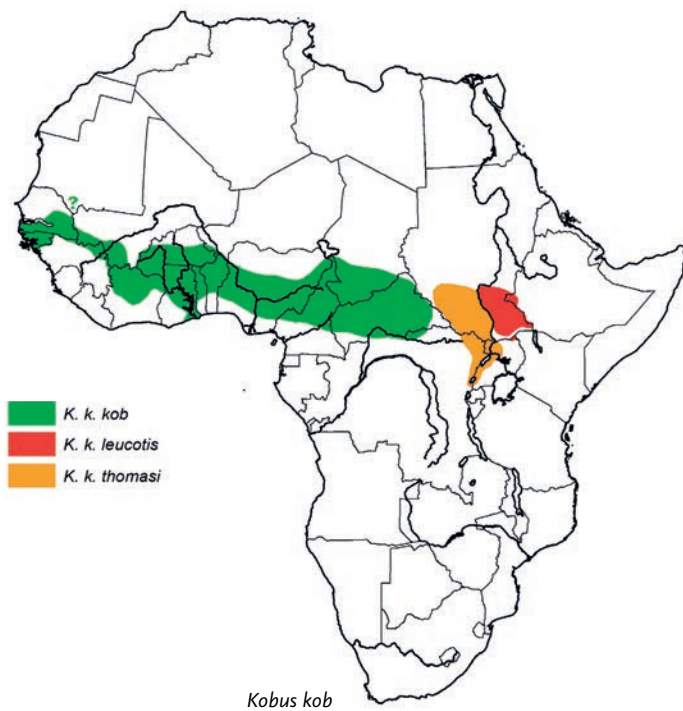
Kobus kob (Erxleben, 1777). Syst. Regni Anim. 1: 293, 1777. 'Senegal'.Kob *Kobus kob* male.Lateral, palatal and dorsal views of skull of Kob *Kobus kob*.

Taxonomy Kobs were at one time regarded as a separate genus (*Adenota*), but were later included in the genus *Kobus* on evidence of hybridization with other members of the genus (Gray 1972). Ansell (1972) listed ten subspecies, but more recent treatments favour recognition of only three (Kingdon 1997, East 1999); some of these show wide intra-specific genetic divergence (Birungi & Arctander 2000). Lorenzen *et al.* (2007) question the taxonomic status of *K. k. kob* and *K. k. thomasi* as two separate subspecies due to the joint evolutionary history of their mtDNA sequences. A study by Birungi (1999) analysing the entire mitochondrial cytochrome *b* gene supported the idea that the Puku *Kobus vardonii* might well be regarded as a subspecies of the Kob rather than a distinct species (see Haltenorth 1963). Synonyms: *adansoni*, *adenota*, *adolphi*, *adolphi-friderichi*, *alurae*, *annulipes*, *bahrkeetae*, *buffonii*, *cob*, *coba*, *forfex*, *fraseri*, *koba*, *kul*, *leucotis*, *loderi*, *neumanni*, *nigricans*, *nigroscapulatus*, *notatus*, *pousarguesi*, *riparia*, *thomasi*, *typicus*, *ubangiensis*, *vaughani*, *wuil*. Chromosome number: $2n = 50$; the X chromosome is a large acrocentric and the Y chromosome is a small metacentric/submetacentric (Taylor *et al.* 1967, Kingswood *et al.* 2000). Gray (1972) documents records of hybridization between Defassa Waterbuck *K. ellipsiprymnus defassa* and Kob, and between Nile Lechwe *K. megaceros* and Kob, and these are expected to exhibit reduced fertility (Kingswood *et al.* 2000).

Description Kobs are medium-sized antelopes. Horned ♂♂ are robust (about 50% heavier than ♀♀) with a muscular neck; hornless

♀♀ are more slender. There are more or less prominent white rings around the eyes and there is a white throat patch. Facial characteristics include black muzzle and nostrils, as well as white lips and chin. Ears are large and laterally placed; white inside and at the outer base, brown on the outer surface with black tips. In White-eared Kob *K. k. leucotis*, ears are white and pelage dark brown. Eyes in all subspecies are large and brown. Pelage is short, ranging from light brown to reddish, and dark brown depending on age, sex and subspecies. Ventral coat and inner parts of legs are white. Upper front of hindlegs is white; otherwise limbs are similar in colour to body. There are large dark vertical stripes on front of forelegs; smaller dark patches on front of hind legs. Tail short, thin, lighter underneath with terminal tuft that is dark on top. Rudimentary preorbital glands are present, and Kobs possess one pair of inguinal glands. Large, diffuse sebaceous glands make the pelage greasy and strong-smelling.

Although only ♂♂ bear horns, horned ♀♀ occur at a rate of 1/1000 animals (Buechner *et al.* 1966). The male's horns are thick, lack spirals and are strongly ridged at the base, extending upwards, backwards and upwards again giving them an S-shaped appearance. The horn tips are either parallel or extend slightly outwards or inwards. Horns are wider at their tips than at the base in most cases. Female horns are thin and twisted without prominent ridges (Fischer 2001). In the dentition, p4 is usually the last deciduous tooth to be replaced, and is easily identified by three distinct cusps, whereas the permanent tooth has only two (Ledger & Smith 1964).



Geographic Variation

- K. k. kob* (Buffon's or Western Kob): Senegal to Central African Republic and DR Congo. Coat colour is golden-brown and sometimes reddish-brown, with white underparts and white areas above the eyes; forelimbs have black front edges; ♀♀ show more variation in colour from rather pale to having black back and/or face; notably smaller than either Uganda or White-eared Kob, with smaller horns.
- K. k. thomasi* (Uganda Kob): NE DR Congo, SW Sudan and Uganda. General appearance like *K. k. kob*, but larger and about 40% heavier (see Measurements); in some northerly areas ♂♂ are variable in colour, having dark patches or even almost black coats.
- K. k. leucotis* (White-eared Kob): SE Sudan, SW Ethiopia and extreme NE Uganda. Pelage in ♂♂ is dark reddish-brown, sometimes almost black (young ♂♂ and ♀♀ have a chestnut hue); ears white, as the name implies; in older ♂♂ the muzzle, chin, throat and inner surfaces of legs also become white.

Similar Species

- Kobus megaceros*. Sympatric with *K. k. leucotis*. Larger, mature ♂♂ are black and white with relatively shaggier coats; ♀♀ larger, with shorter faces, less sleek coats (but similar in colour to Kob).
- K. vardonii*. Allopatric. Similar but longer-haired.
- K. ellipsiprymnus*. Defassa Waterbuck is broadly sympatric, south of the Sahel and west of the Rift Valley. Much larger, with longer, straighter horns on ♂♂. Dark brown.
- Ourebia ourebi*. Sympatric over much of the range. The Oribi is similar to young Kob, but with naked patch of black skin beneath ear, short, straight-tipped horns and pelage mainly sandy to rufous.
- Redunca redunca*. Sympatric over much of the range. Subadult ♂♂ of Uganda and Buffon's Kob resemble adults, but pelage longer, horns hooked and lack black markings on forelegs.

Distribution Kobs are endemic to Africa with a patchy distribution within a geographical belt running from Senegal to Uganda, Sudan and SE Ethiopia. In the past natural barriers such as mountain ranges, forests and deserts would clearly inhibit Kob dispersion (Wanzie 1991), but the nearly continuous distribution of Buffon's Kob across the flat lands well to the south of the Sahara would have been facilitated, rather than hindered, by river and flood-plain systems during humid periods. Late Pleistocene remains of this species are reported from S Egypt (Osborn & Osbornová 1998).

Historical Distribution Buffon's Kob has the widest distribution range of all the subspecies, and was formerly distributed from Senegal, Guinea-Bissau, Gambia, the extreme south of Mali and SW Mauritania, eastwards through all countries, including Sierra Leone, to SW and SE Niger, C and N Nigeria, C and N Cameroon, S Chad, Central African Republic and N and NW DR Congo (East 1999). The White-eared Kob, on the other hand, has the most restricted range of the three subspecies, being confined to the flood-plains east of the Nile R. in SE Sudan (Stevenson-Hamilton 1919, Forbes 1948, MacKenzie 1954, Mefit-Babtie 1983, Hillman & Fryxell 1988). White-eared Kobs also occurred in the Gambella area of SW Ethiopia, at least seasonally when migrants entered from Sudan (Sorell 1952), and NE Uganda (as vagrants from Sudan). The Uganda Kob formerly occurred widely throughout Uganda, and also ranged into SW Sudan, NE DR Congo, SW Kenya and lakeside areas of NW Tanzania (Kingdon 1982, East 1999).

Current Distribution Kobs have undergone extensive declines across much of their range. In West Africa, Buffon's Kob is extinct in Gambia and apparently in Sierra Leone (see Camara 1990, Grubb *et al.* 1998, Jallow *et al.* 2004) and most likely in S Mauritania, and now survives mainly in and around protected areas in much of the remainder of its range.

In Sudan, the flood-plains east of the Nile have, even in recent decades, supported up to a million White-eared Kobs that undertake seasonal migrations on a scale to rival that of the Common Wildebeest *Connochaetes taurinus* in the Serengeti ecosystem (Fryxell 1985, Fryxell & Sinclair 1988, Hillman & Fryxell 1988). Although numbers of White-eared Kobs were thought to have been depleted, recent surveys indicate that they still survive in good numbers particularly in the north and along the western boundary of Boma N. P. (Fay *et al.* 2007). White-eared Kobs still occur as sporadic migrants in Kidepo Valley N. P. in NE Uganda and in Gambella N. P. in Ethiopia.

Uganda Kobs survive mainly in Uganda, particularly in western and north-western parks and reserves (such as Queen Elizabeth N. P. and Murchison Falls N. P.), and in NE DR Congo, in Garamba and Virunga National Parks; a few Uganda Kobs remain in SW Sudan, mostly in Southern N. P. Populations of Uganda Kobs that formerly occurred in SW Kenya and NW Tanzania have been eliminated from these areas by expanding human settlements and unsustainable hunting (East 1999).

Habitat Kobs are confined to regions of open or wooded savanna that have year-round access to water. They are common in riverine and lake-shore grasslands, flood-plains, open grassland, open woodlands, grassy shrublands and on grasslands within the forest/savanna transition zone. Exceptionally, Kobs have been claimed to

have once occurred in or around mangrove swamp forest in Guinea-Bissau (Wanzie 1991). In Nigeria, a combination of cover from woody plants and good visibility was judged important for Kobs (Amubode & Akossim 1989, Sodeinde 1989). In Uganda, Kingdon (1982) emphasized the role of other grazers, of fire, a high water table and even the Kobs' own numbers in maintaining a sward suited to grazing by Kobs; indeed, he posited that this species evolved to exploit the shifting mosaic of heavily grazed conditions that are common in riparian habitats. Kingdon (1982) pointed out that the Kobs' dependence on daily movement routines serves to reinforce the animals' attachment to proven resting or short-term grazing sites and that longer-term fluctuations in population size may cause concentrations to build up or decline at particular sites. Better-drained, raised areas become 'islands of occupation' during the wet season and Kobs sometimes continue to be attracted to such sites out of season and over many years. Kingdon noted that male territorial grounds, which attract both sexes, tend to be located on open ground close to geographic discontinuities, such as rocky gulleys, slopes or other changes in topography. He also noted that during daily movements between pastures and water, such discontinuities induce pauses and that over a period of hours Kobs continue to collect on these grounds until the build-up of numbers seems to offset the risk of possible ambush from predators. Use of the landscape by Kobs was mapped by Bindernagel (1968), showing the year-round movements and territorial grounds of a resident population of Kobs in N Uganda. Deutsch & Weeks (1992) confirmed that ♀♀ preferred high-visibility territories and territorial grounds in Uganda to avoid predators. Recently burnt areas are preferred as are those with short pasture. Mineral licks are visited regularly and hence influence habitat preferences (Sodeinde 1989).

Abundance Overall, numbers of Kobs are declining throughout their range. Whereas East (1990) estimated that the total numbers of Buffon's Kobs could exceed 225,000, a decade later his estimate was in the region of 95,000 (East 1999). The population of the White-eared Kob was estimated at more than 100,000 by East (1999), a significant decline from the nearly 1 million animals that were known to occur in the Boma ecosystem in the early 1980s (Fryxell 1985, Hillman & Fryxell 1988). Recent surveys in the dry season covering some 150,000 km² of S Sudan have shown that this population has survived the period of civil war relatively well, with the population in Boma N. P. alone estimated to number nearly 700,000, with a further 46,000 animals on the contiguous Lotilla plains and nearly 12,000 in the Jonglei area (Fay *et al.* 2007). Numbers of Uganda Kobs within parks and reserves may be reasonably stable, with an estimated total population size of 100,000 for this subspecies (East 1999).

The highest densities of Kobs (1000/km²) have been reported around drinking sites in the dry season (Fryxell 1987; and see Scholte 2005), but even at other times densities might be as high as 140/km² (Balmford *et al.* 1992). Where Kobs are well protected, local densities of 15–40 animals/km² are common (Modha & Eltringham 1976, Wanzie 1988, Amubode & Akossim 1989), but in areas of heavy hunting pressure densities decline to less than 1/km² (Fischer 1998).

Adaptations Kingdon (1982) considered that the major evolutionary innovation of *Kobus kob* has been their ability to move en masse from one resource to another and that this species evolved to



White-eared Kob *Kobus kob leucotis* male head.

take advantage of heavily grazed conditions on fertile pastures in the vicinity of lakes and rivers (created by hippos, African Buffalo *Syncerus caffer* and other large ungulates), and that Kobs have subsequently extended their range further into fire-climax grasslands. Kobs can maintain their own pasture when occurring at high densities.

Kobs do not necessarily seek shade and frequently can be observed lying in the sun during the hottest part of the day. However, Fryxell (1987) has reported that, where possible, White-eared Kob individuals almost always sought shade in SE Sudan. Kobs depend on free water, which they usually drink in the morning or afternoon, making their movements very predictable. Their ability to form large groups that stay together while being chased is an adaptation to mitigate the effectiveness of predator attacks.

While Uganda and Buffon's Kobs perform only small-scale seasonal movements, White-eared Kobs extend such movements, effectively becoming migratory in relation to food, floods and water supply, at which time they form mobile herds of many thousands (MacKenzie 1954, Fryxell & Sinclair 1988). Kobs have the ability to increase rapidly in number when they are protected and conditions are favourable.

Foraging and Food Kobs are almost exclusively grazers, borne out not only by field observations but also by studies involving stable carbon isotope analysis (Cerling *et al.* 2003), and were classified as obligate grazers by Gagnon & Chew (2000) in their review of the dietary preferences of African bovids. Kobs are selective in terms of species as well as parts of plants eaten (Agbelusi 1989). Uganda Kobs showed a preference for short to medium-height pyrophilous perennial grasses such as the Andropogoneae (Field 1972). In Comoré N. P. (Côte d'Ivoire), preferred grass species for Buffon's Kob were *Hyparrhenia rufa*, *Andropogon africanus* and *Schizachyrium sanguineum* (Prauser 1980, Radl 1987). In Sudan, *Echinochloa pyramidalis* was favoured (Fryxell & Sinclair 1988).

Seasonal changes in diet occur (Field 1972) due to better palatability of certain grass species in the wet season (*Bothriochloa*, *Heteropogon*, *Imperata*) or greater abundance (*Brachiaria*, *Cynodon*, *Setaria*). In Uganda, leaves of shrubs such as *Sida* sp. and *Capparis tomentosa* were eaten occasionally (Hofmann & Stewart 1972); non-grass species accounted for 4.8% of plant matter eaten, although fruits were not part of the diet

(Radl 1987). Fat content of graminoids showed a significant correlation with Kob density in Nigeria (Amubode & Akossim 1989). Greenness of grass was an important predictor for female presence throughout the year, but most influential during the dry season (Deutsch 1994).

Social and Reproductive Behaviour Social organization in the Kob is dependent on density and includes two discrete mating systems. Typically, 50–90% of adult ♂♂ (three years or older; Leuthold 1966, Fischer & Linsenmair 1999) defend territories that are either resource-based (Buechner 1961, Mühlenberg & Roth 1985, Amubode & Akossim 1989) or based on territorial grounds (leks) (Buechner & Roth 1974, Floody & Arnold 1975, Fryxell 1987, Wanzie 1988, Balmford 1992). When the overall density of Kobs declines within the same population (as in Comoé N. P. post 1974), the territorial mode can change from a lek system at high densities (>14 animals/km²) to a resource-defence system (Fischer & Linsenmair 1999, and references therein).

In contrast to ♂♂, adult ♀♀ and young do not occupy territories, but form groups that are unstable, changing in both size and composition on a day-to-day basis, and sometimes numbering up to 120 animals (Fischer 1998). Groups are larger when visibility is good (during days or moon-lit nights, or when grass is short), but decline when visibility decreases (Fischer & Linsenmair 2000); even large groups often contain only one adult ♂. Unstable multimale groups occur only outside territories, for example, where animals group together before visiting dangerous drinking sites. Non-territorial ♂♂ live in bachelor groups of 2–200 animals.

Annual female home-ranges in Comoé N. P. averaged 245.8 ± 34.8 ha while those of ♂♂ were 91.7 ± 11.3 ha (Fischer & Linsenmair 2001b). Female home-ranges in Queen Elizabeth N. P. (Uganda) averaged 1560 ha (Balmford 1992); male home-ranges in the same area were 520 ha for non-territorial and 300 ha for territorial ♂♂. The home-ranges of most ♀♀ underwent shifts in location between seasons, but not those of territorial ♂♂ in Comoé N. P. Daily walking distance of ♀♀ in Comoé N. P. was 2300 ± 100 m (Fischer & Linsenmair 2001b) and 2480 m in Queen Elisabeth N. P. (Balmford 1992).

The size of single territories has been estimated at 2–127 ha (Grant *et al.* 1992, Fischer & Linsenmair 1999), but on leks an arena of some 200–400 m in diameter (i.e. no larger than a single conventional territory) may be shared by 30–40 ♂♂ spaced at distances of 15–30 m, such that effective territory size is compressed to a notional 10–60 m in diameter only (Leuthold 1966, Floody & Arnold 1975). The continued presence of the territorial ♂♂, as well as the activity of the transient ♀♀, results in these arenas having little or no grass; however, limited availability of food is more than compensated for by the presence of ♀♀ and opportunities for mating.

Resource territories are defended close to the birthplace (Wanzie 1988, Fischer & Linsenmair 1999). Males patrol their territories (in Comoé N. P. covering on average 2400 ± 200 m during daylight hours) and frequently whistle 4–5 times in a row, possibly advertising their territory tenure or their reproductive status. Object horning (bushes or soil) probably serves similar purposes. Since ♂♂ that enter foreign territories intensively sniff the ground it is likely that olfactory signals are important for Kobs although no explicit scent-marking behaviour is known. Visual communication is important, with territorial neighbours probably knowing each other from



Kob *Kobus kob*.

sight. Agonistic behaviour consists of a parallel walk and lateral body presentation with extensive vertical and lateral head-shaking with penile erection; more static agonistic behaviour consists of an erect posture often looking away from each other. Serious fighting occurs if the intruder does not withdraw. Components of fights are heavy clashes as well as horn-twisting and front-pressing close to the ground. This sometimes results in broken horns and almost inevitably in wounds at the head and neck. The fight is over if one combatant flees, being chased and targeted for stabbing by the winning chaser. Fighting over territory tenure is rare when population density is low and tenure in such populations can be as long as four years (Leuthold 1966, Fischer & Linsenmair 1999). In contrast, territories on leks can usually be defended for a few days only. Males who lose their territory tend to join bachelor herds and may attempt another turn at territoriality after regaining strength.

Where lekking occurs ♀♀ appear to visit territorial grounds where oestrous individuals are invariably mated. Females have access to all territories within their home-range but their choice of mate is likely to be determined by their reproductive physiology, which, in turn, may very well be influenced by external influences such as the scents and activities on territorial grounds. Males on central territories are preferred and the choices of other ♀♀ are copied, using olfactory clues (Balmford *et al.* 1992, Deutsch & Nefdt 1992). Males stay on their territories even when no ♀♀ are around except while visiting drinking sites in the dry season.

Courtship includes the ♂ sniffing and licking the ♀, flehmen, repeated foreleg lifting (laufs Schlag) and rising up bipedally up to 20 times before a vigorous ejaculatory thrust. Females may bleat when harassed by ♂♂. The ♀ can terminate courtship at any stage by lying down or leaving the territory (Balmford *et al.* 1992). Males rarely try to hinder ♀♀ leaving their territory and have not been observed to be successful in their attempts. Females may mate up to 17 times with up to nine different ♂♂ (Balmford *et al.* 1992) during their 24-hour oestrus. If fertilization does not occur, ♀♀ cycle at 20- to 26-day intervals and mate again until conception is achieved (Buechner *et al.* 1966). Females separate from groups shortly before giving birth. After parturition the ♀ visits and suckles the calf twice per day, but never moves very far away. Male calves move about alone or in the female herds as early as three months old. After weaning at 6–7 months, ♂♂ join bachelor herds and are chased away by territory holders when approximately one year old (by which stage their horns are about the length of their ears).

Behaviour depends on group size, with animals in smaller groups and single animals spending less time on behavioural traits that make them prone to predation, such as feeding and ruminating (Fischer & Linsenmair 2007). Anti-predator behaviour includes ♂♂ and ♀♀ approaching predators while whistling and jumping on the spot with stiff legs. Alarm whistles are shorter and emitted in higher temporal frequency compared with the territorial whistle of ♂♂.

Social grooming does not occur in Kobs, but ♀♀ lick their young and ♂♂ sniff, rub and lick ♀♀ during courtship. Females might poke, butt and snap at other ♀♀ when they get too close while feeding. There is no greeting behaviour and Kobs ignore each other when joining groups. However, ♂♂ approach each ♀ entering their territory and determine her reproductive status by sniffing the anal region.

Reproduction and Population Structure Kobs are polygamous. Spermatogenesis starts when ♂♂ are about one year of age. Ovulation begins when ♀♀ are 13–14 months old. Length of cycle is 20–26 days, with oestrus lasting probably less than 24 hours (Buechner *et al.* 1966). Breeding in most populations occurs throughout the year, although breeding peaks are known; for example, there is a birth peak in the dry season between Nov and Feb in Nigeria (Happold 1987), a mating peak in the late wet season (Oct–Nov) in Comoé N. P. (Fischer & Linsenmair 2002), Sep–Dec in S Sudan (Hillman & Fryxell 1988), and in the two wet seasons (Mar–May and Sep–Nov) in Uganda (Balmford 1992). Gestation has been recorded at about 180 days (Happold 1987), and 233–240 days (Buechner *et al.* 1966). A single calf weighing 4–5 kg is born; twins were either born dead or died shortly after birth (Buechner *et al.* 1966). There is a postpartum oestrus, and ♀♀ have the capacity to bear three calves within two years. In Comoé N. P. recruitment is much lower, with one calf every other year (Fischer 1998).

In Comoé N. P., adult ♀♀ accounted for 61.2% and adult ♂♂ 10.2% of the population (Fischer & Linsenmair 2002); the authors of this study attributed the sex ratio (0.34 males/female) to high poaching pressure, since Geerling & Bokdam (1971) had observed a sex ratio of 0.74 at a time when poaching pressure was lower. In 1986, during a severe drought, the overall sex ratio of Kobs around Waza N. P., Cameroon, was 0.53, not dissimilar to that in 1997, after a period with average rainfall; however, in 1986 the percentage of young was

only half of that in 1997 (Scholte 2005). A population of Uganda Kobs contained 16% adult ♂♂ and 54% adult ♀♀ (Balmford 1992). Adult sex ratio in Comoé N. P. population was 0.73 males/female in the 1970s and dropped to 0.34 in the 1990s (Geerling & Bokdam 1971, Mühlenberg & Roth 1985, Fischer 1998). Annual natality in Comoé N. P. ranged from 12.8 to 30.0% and newborn mortality was 48.5%. In captivity, Kobs live for more than 20 years (Weigl 2005). The oldest individually recognizable ♂ in the Comoé N. P. died in his eighth year and the oldest ♀ in her ninth year.

Predators, Parasites and Diseases The most important predators are Lions *Panthera leo*, Leopards *P. pardus*, African Wild Dogs *Lycaon pictus* and Spotted Hyaenas *Crocuta crocuta*. Wanzie (1986) found Lions to be the most important predator of Kobs in Waza N. P., accounting for 68.5% of predation (and see Van Orsdol 1984). Where Lions are rare, as in Comoé N. P., Leopards and Spotted Hyaenas take over the primary predator role. Baboons *Papio* spp. are known to take young calves and Side-striped Jackals *Canis adustus* predate young during their lying-up stage. One case of a Martial Eagle *Polemaetus bellicosus* killing a Kob was observed in Cameroon and a total of 15.3% of all deaths were due to drought in the same area (Wanzie 1986). African Rock Pythons *Python sebae* are also known to take Kobs in Uganda.

Thal (1971) reported the following ecto- and endo-parasites infesting Buffon's Kob: *Amblyomma variegatum*, *Linguatula nuttali*, *Stilesia* sp., *Fasciola gigantica* (and see Bindernagel 1972), *Setaria bicornata*, *S. pillersa* and *Theileria* sp. In Ghana, Ntiemoa-Baidu *et al.* (2005) recorded the following ixodid ticks on seven animals: *Haemaphysalis aciculifer*, *Rhipicephalus lunulatus*, *R. senegalensis*, *R. simpsoni* and *A. variegatum*. Küpper *et al.* (1983) found the following parasites and diseases in Kobs from the Comoé N. P.: *Theileria mutans*, *Babesia* sp., *Anaplasma marginale*, *Trypanosoma brucei*, *Eimeria intricata*, *Ascaris* sp., *Strongyloides* sp., *Trichuris* sp. and *Paramphistomum* sp.; Okaeme (1987) also recorded *Paramphistomum cervi* in Buffon's Kob. Graber *et al.* (1973) reported *Taenia hyaenae* in the muscles.

Conservation IUCN Category: Least Concern (*K. k. kob* – Vulnerable A2cd; *K. k. leucotis* – Least Concern; *K. k. thomasi* – Least Concern). CITES: Not listed.

Although very abundant in the past, Kobs are victims of unsustainable hunting over most of their range. Buffon's Kobs, formerly one of the most abundant antelopes in West and central Africa, are declining in most parts of their range, and are already extinct in Gambia and Sierra Leone (and perhaps Mauritania), and are considered rare in Guinea-Bissau, Guinea, Nigeria and N DR Congo. In many areas where they survive, they are largely confined to protected areas, although poaching has led to large-scale declines in many key populations. For example, Kob numbers declined by more than 80% within 20 years in Comoé N. P. in Côte d'Ivoire (Fischer & Linsenmair 2001a) and in N Central African Republic (Bouché *et al.* 2010), and numbers in Arly-Singou Faunal Reserve and surrounds (Burkina Faso) decreased from 5000 in 1982 to 700 in 1999 (Chardonnet 2001b). Such declines show that populations of Buffon's Kobs are very vulnerable to hunting, notwithstanding the fact that some 85% of the current population is estimated to occur in and around protected areas (East 1999). On the other hand, the population numbers in Waza N. P. decreased from 25,000 in 1962 to 2000 in the mid-1980s, largely due

to a general drying out of the habitat caused by droughts (especially in 1969–74) and disruption of the natural flooding regime from 1979 by the construction of the Maga Dam on the Logone flood-plain, which formed L. Maga. Rinderpest (1982/83) and poaching also probably contributed to declines. Further declines 1982–86 were exacerbated by the 1985/86 drought. Numbers recovered to 5000 in the 1990s (Scholte 2005, Scholte *et al.* 2007).

Protected areas important for the survival of Buffon's Kobs include Niokolo-Koba N. P. (Senegal), Comoé N. P., Arly-Singou Faunal Reserve (Burkina Faso), Mole N. P. and Bui N. P. (Ghana), Pendjari N. P. (Benin), Waza, and Bénoué and Faro National Parks of the North Province (Cameroon), Zakouma N. P. (Chad) and various reserves in Central African Republic (East 1999). Under strict protection Kob numbers can recover quickly, allowing sustainable off-takes of about 7% of the population (Mayaka *et al.* 2004).

White-eared Kobs were believed to have been affected by the ongoing civil war in S Sudan, particularly since this migratory subspecies is believed vulnerable in its wet-season concentration area along the southern margins of the Sudd; East (1999) estimated that less than 1% of the population is resident in nominal protected areas (such as Boma and Badingilo National Parks). However, White-eared Kobs appear to have withstood the pressures well, and the migrations described by Fryxell (1985) and Mefit-Babtie (1983) are continuing in what appear to be general patterns and size similar to those documented in the early 1980s (Fay *et al.* 2007).

Although some 98% of the remaining Uganda Kobs in East Africa occur in protected areas, particularly Queen Elizabeth N. P. and in Murchison Falls N. P. and Toro-Semliki (Uganda), these vestiges represent less than 1% of its original distribution in East Africa (J. Kingdon pers. comm.). The status of park populations likely will not change, although ongoing instability in DR Congo may affect populations in Garamba and Virunga National Parks (East 1999).

In conclusion, even though Kobs still occur in large numbers in some protected sites the species' future should cause grave concern. Due to their preference for open areas and the need to drink daily, these relatively slow animals are easy to hunt and their habitat tends to have prime agricultural or pastoral potential; population densities are therefore likely to decline further. Especially in West Africa and Sudan, formal protection of the species is not effective. West African national parks need to be managed professionally and efficiently. The flood-plain ecosystem that supports a viable population of White-eared Kobs in Sudan should receive protection status. 'They respond very well to protection and build up their numbers rapidly. Their potential as a managed resource is very considerable: ... an exceptionally valuable natural resource is going to waste unless more positive wildlife policies are implemented' (Kingdon 1982). Sustainable use projects of Kobs outside protected areas, especially the higher density areas in central Africa, might help to ensure the future survival of the species and provide practical incentives for their protection.

Measurements

Kobus kob

K. k. kob

HB (♂ ♂): 1410 (1360–1450) mm, n = 6

HB (♀ ♀): 1280 (1190–1310) mm, n = 12

T (♂ ♂): 300 (270–330) mm, n = 6

T (♀ ♀): 250 (240–300) mm, n = 13

HF c.u. (♂ ♂): 390 (380–400) mm, n = 6

HF c.u. (♀ ♀): 370 (350–380) mm, n = 13

E (♂ ♂): 140 (120–140) mm, n = 4

E (♀ ♀): 120 (110–150) mm, n = 13

Sh. ht (♂ ♂): 870 (850–900) mm, n = 5

Sh. ht (♀ ♀): 830 (750–890) mm, n = 11

WT (♂ ♂): 63.0 (58.0–67.0) kg, n = 3

WT (♀ ♀): 46.0 (36.0–52.0) kg, n = 6

Comoé N. P., Côte d'Ivoire (F. Fischer pers. obs.)

Maximum recorded horn length is 65.0 cm for a pair of horns from Mundu, Chad (Rowland Ward)

K. k. thomasi

HB (♂ ♂): 1521 (1420–1623) mm, n = 10

HB (♀ ♀): 1402 (1330–1505) mm, n = 10

T (♂ ♂): 301 (270–335) mm, n = 10

T (♀ ♀): 279 (235–312) mm, n = 10

E (♂ ♂): 153 (147–163) mm, n = 10

E (♀ ♀): 144 (127–158) mm, n = 10

Sh. ht (♂ ♂): 955 (934–972) mm, n = 10

Sh. ht (♀ ♀): 864 (802–908) mm, n = 10

WT (♂ ♂): 96.9 (88.4–107.9) kg, n = 10

WT (♀ ♀): 62.2 (54.5–66.5) kg, n = 10

Semliki Valley, Uganda (Ledger & Smith 1964)

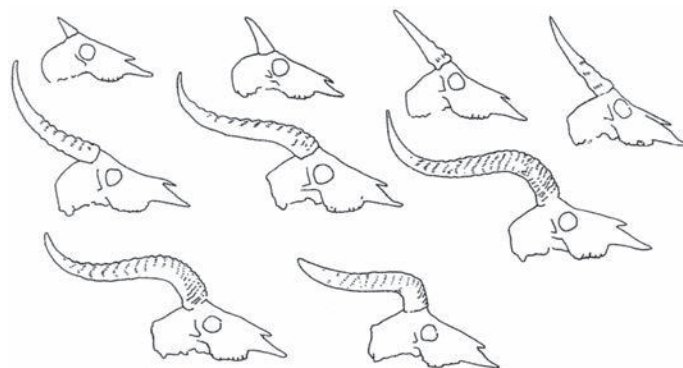
Maximum recorded horn length is 69.2 cm for a pair of horns from Lolim, Uganda (Rowland Ward)

K. k. leucotis

Maximum recorded horn length is 66.0 cm for a pair of horns from Bahr el-Zeraf, Sudan (Rowland Ward)

Key References Buechner & Roth 1994; Buechner *et al.* 1966; Deutsch 1994; East 1999; Fischer & Linsenmair 1999, 2000, 2001a, b, 2002; Fryxell 1987; Leuthold 1966; Sodeinde 1989; Wanzie 1986, 1988, 1991.

Frauke Fischer

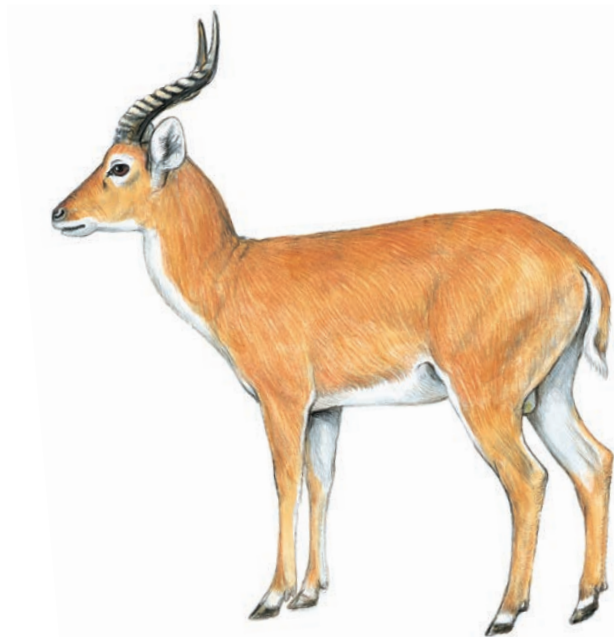


Development and ultimate abrasion of horns in Kob *Kobus kob*.

Kobus vardonii Puku

Fr. Puku; Ger. Puku

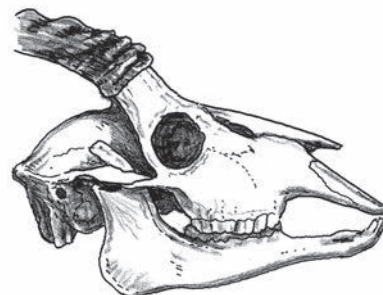
Kobus vardonii (Livingstone, 1857). Missionary Travels and Researches in South Africa, p. 256. Zambia, Barotseland, Chobe Valley, near Libonta (40° 30' S, 23° 15' E).

Puku *Kobus vardonii*.

Taxonomy The Puku was named in honour of a British elephant hunter, Major Frank Vardon, in the 1850s. Some authorities consider the Puku a subspecies of (e.g. Haltenorth 1963), or superspecies with (Ansell 1972), the Kob *Kobus kob*. Although Gentry (1990) included all Kobs and Pukus in *Kobus kob*, they have more recently been considered as two distinct species based on morphological data (Vrba *et al.* 1994). Molecular data (Birungi 1999, Birungi & Arctander 2000) reveal that the Puku lineage is highly distinct from that of other Kobs, but that the Puku is paraphyletic with respect to the Kob. Two subspecies have been recognized (Ansell 1972). Synonyms: *senganus*. Chromosome number: not known.

Description The Puku is a medium-sized, sexually dimorphic bovid. Pukus can be considered as the southern savanna equivalent of the Kob (Rodgers 1984b), although they differ in their smaller size, paler colouration, shaggier coat, absence of black markings, and shorter, thicker horns. Face has white bands extending forward from the top of the eyes to their inner margins. Upper lip is white and there is a white patch just behind the rhinarium on the sides of the muzzle. Forehead generally browner in colour than the rest of the body; upperparts golden-yellow, extending down outsides of the limbs. Throat, underparts of the body and insides of the limbs white. Tail same colour as body, with tuft of long hair towards tip. Pukus have well-developed inguinal pouches (40–80 mm deep), and, in contrast to other reduncines, active face glands (face glands are only poorly developed in Kob).

Horns (rarely recorded in ♀♀; see Ansell 1960b) are strongly ridged for two-thirds of their length, and smooth towards the tips.

Lateral view of skull of Puku *Kobus vardonii*.

Geographic Variation Geographical variation between the scattered and isolated remaining Puku populations has not been investigated, but considerable potential exists and its properties will depend on several, as yet unstudied, features (e.g. the history of population isolation, gene flow between populations, selection pressures). Ansell (1972) referred to the nominate *K. v. vardonii*, from parts of Angola, Zambia and NE Botswana, and also provisionally accepted *K. v. senganus* as a subspecies from the upper Luangwa Valley, Zambia. Swynnerton & Hayman (1951) allocated all Tanzanian populations to this subspecies, which also once occurred in Malawi. Further investigations into geographical variation in the Puku are needed, especially as recent work suggests that Pukus in Tanzania differ considerably from those in Zambia and may represent two evolutionary distinct forms (Cotterill 2003a, b).

Similar Species

K. ellipsiprymnus. Sympatric across much of the range. Larger size, and darker grey colouration with white buttock markings (in *ellipsiprymnus*, but not *defassa*); preference for dry bush and savanna habits.

K. leche. Sympatric in parts of Zambia (e.g. Kafue N. P.) and Botswana (De Vos & Dowsett 1966, Child & Richter 1969). Distinctive, elegant, swept-back horns and black marking on forelegs. Often form large aggregations and regularly move through shallow areas of open water.

K. kob. Allopatric, ranging from Senegal to Uganda, Sudan and SE Ethiopia.

Distribution Endemic to Africa. Historically, Pukus were widely distributed across the south-central African plateau (Schouteden 1947, Ansell 1978). East (1999) recorded Pukus present in eight countries (Angola, Botswana, DR Congo, Malawi, Namibia, Tanzania, Zambia, and marginally in Zimbabwe), distributed across south-central Africa, although some of these populations were reported to be very small and/or transient.

Current Distribution Rodgers (1984b) speculated that the current distribution of Puku was caused by the fragmentation of a once inter-



connected network of populations associated with major river valleys and is an explanation for the Puku's current association with upper basins of large rivers such as the Rufiji, Upper Congo and Zambezi. Many of these populations are small and under intense pressure from illegal hunting, and large populations of Puku can now only be found in Zambia and Tanzania (East 1999).

In Zambia, ca. 85% of Pukus occur within the protected area system, especially in parts of the Luangwa Valley (North and South Luangwa National Parks), the northern region of Kafue N. P., and Nsumbu and Mweru-Wantipa National Parks and Tondwa Game Management Area in the north-east (East 1999). Pukus have been reintroduced into several game ranches in Zambia, where they have proved a successful game ranching species. In contrast to Zambia, most Tanzanian Puku are restricted to the unprotected Kilombero Valley, where this still large population is under increasing pressure from changes in land use (Haule *et al.* 2002, Jenkins *et al.* 2003, Bennington *et al.* 2010). It is estimated that the Kilombero Valley contains at least 50% of all remaining Pukus (East 1999); a smaller population survives around L. Rukwa, but a population that survived along the northern shores of L. Malawi was extirpated before 1960 (Rodgers 1984b). In Malawi, they survive in Kasungu N. P. and Vwasa Marsh G. R., with occasional vagrants seen in Nyika N. P. (East 1999). Populations of Pukus still occur in NE Botswana on the Chobe River flood-plain (Child & von Richter 1969, Stuart 1989, Cotterill 2000, Dipotso & Skarpe 2006), and they occurred occasionally along the Upper Zambezi in NW Zimbabwe until the 1930s (F. P. D. Cotterill pers. comm.); they occur as a very rare vagrant in the middle Zambezi Valley (e.g. Dunham & Tsindi 1984), presumably through dispersal of animals from the Luangwa Valley in Zambia (Wilson & Cumming 1989). In Namibia, Pukus probably occur only as vagrants in the eastern Caprivi Strip.

Pukus were formerly abundant in much of Katanga, DR Congo (notably Upemba N. P.), but were greatly reduced by poaching along

with all large mammal populations (Frechkop 1954, von Richter *et al.* 1990, Hasson & Wolanski 1999); they survive in Kundelungu N. P. and perhaps in the Luama Hunting Zone. In Angola, there is no reliable information on the status of Pukus in the north-east (Lunda Norte and Lunde Sul provinces), where they were formerly widespread; they probably still survive in greatly reduced numbers, with a small population also in Luando Reserve (East 1999, Crawford-Cabral & Veríssimo 2005); Crawford-Cabral & Veríssimo (2005) also remark on their occurrence in the south-east, in the swamps and flood-plains between the Cuando and Luiana Rivers, but there is no information on their status in this area.

Habitat Pukus are closely dependent on perennially moist grasslands, and are a characteristic species of the grassy dambos that dominate the drainage across the south-central African plateau (Cotterill 2000, Moore *et al.* 2007). Favoured habitat types include river flood-plains and nutrient-rich, swamp grasslands, and they are rarely found far from permanent water during the dry season. In Kasanka N. P., Zambia, Goldspink *et al.* (1998) found the highest abundance of Pukus in open areas of river flood-plains and dambos. Although associated with wet areas and swamp vegetation, Pukus avoid deep standing water, and in that sense are ecologically distinct from lechwes. Lake-level rise was invoked as the reason for the decline in the L. Rukwa population in Tanzania (Rodgers 1984b) and an avoidance of water is the driving force behind reported movements out of flood-plains onto higher ground during the wet seasons (e.g. Jenkins *et al.* 2002a).

Descriptions of Puku habitat preference are most commonly reported from the dry season (e.g. Rodgers 1984b, Goldspink *et al.* 1998, TWCM 1999, Waltert *et al.* 2009), when the animals are easy to count from the air or on foot patrols. Many authors have reported that Pukus leave the flood-plains when the water level rises and move into more densely vegetated habitats on raised ground (e.g. Child & von Richter 1969, Goldspink *et al.* 1998). Jenkins *et al.* (2002a) compared Puku habitat use in the land at the edge of the Kilombero Valley flood-plain and found the highest levels of activity (assessed using dung and tracks) in the grassland with lower use of farmland and miombo woodland. They also found highest rates of Puku activity along flood-plain margins at the end of the wet season (Apr–May); however, Pukus did not use these areas in the dry season (when direct observations confirmed concentrations on the central flood-plain). Assessment of Puku use of woodland habitat and raised ground during the wet season has been largely neglected to date, but these habitats probably play an important role in Puku ecology (e.g. in explaining ecological responses to habitat loss or predation pressure). Given that the wet season is the period of calving and when human–wildlife conflict is at its highest, there is priority need to better understand habitat use by Pukus during the period spent away from savanna flood-plains.

Abundance East (1999) estimated the total population size at 130,000, with ca. 66,964 in the Kilombero Valley, Tanzania (TWCM 1999) and a further 21,000+ in Zambia. A recent aerial survey of the Kilombero Valley employed two complementary methods to assess the population size of Puku (TWRU 2003). When surveyed using the same methods as used on previous counts (e.g. TWCM 1994,

1999) the population was estimated at $23,301 \pm 5602$ SE, a notable decrease from the previous estimates of $55,769 \pm 19,428$ SE in 1989, $53,020 \pm 13,577$ SE in 1994 and $66,964 \pm 12,629$ in 1998. However, a more intensive survey was also undertaken (using 2.5 km transect spacing as opposed to 10 km) specifically to count the Puku and this resulted in a population estimate of $42,352 \pm 5927$ SE (TWRU 2003). Based on ground surveys, Bonnington *et al.* (2010) presented evidence of a significant decline in local Puku abundance over a five-year survey period at two sites in the Kilombero Valley from 1999 to 2003. Waltert *et al.* (2009) estimated the population in L. Rukwa at ~ 770 individuals, a decline from estimates made in the 1980s by Rodgers (1984b).

The population of Pukus on the flood-plains along the Chobe R. was believed to be in decline since the last census in 1965–67, following profound habitat changes caused by an increase in elephants and other large herbivores in the area. However, the population has shown a strong increase in numbers compared with the 1960s, although the concentration of the population has shifted eastwards, possibly as a result of direct human disturbance in the western part of the riverfront (Dipotso & Skarpe 2006).

Adaptations A key feature of Pukus and other kobs is their readiness to aggregate and their ability to assimilate poor-quality food, which promotes a rapid growth rate (Kingdon 1997). The high population growth rate of Pukus has been suggested to explain the rapid recovery of some populations following cessation of unsustainable poaching levels (Goldspink *et al.* 1998) and has also been discussed in relation to the commercial harvest of meat from large populations (Kingdon 1982).

The stomach structure of the Puku is typical of a roughage feeder and is similar in form to the Uganda Kob and Waterbuck *Kobus ellipsiprymnus*, which possess features typical of a grazer antelope dependent on water (Stafford & Stafford 1990).

Foraging and Food Pukus are obligate grazers (as classified by Gagnon & Chew [2000] in their review of dietary preferences in African bovids) and feed primarily on short grasses alongside permanent water bodies. Preferred grasses include *Brachiaria* (especially Jan–Mar), *Eragrostis* (Jul–Aug), and *Vossia* shoots in Dec (Child & von Richter 1969). Other grasses eaten include *Sporobolus*, *Panicum*, *Digitaria*, *Cynodon* and *Chloris*. Puku respond quickly to the presence of new food sources following fire and in the Kilombero Valley, Tanzania, they quickly appeared on lawns at the edge of the flood-plain in the wet season following the clearance of miombo woodland to make way for new teak plantations (G. R. Corti pers. comm.). Feeding activity is generally limited to early mornings and late afternoons but can also occur during the night.

Most of the information available on Puku habitat selection originates from Rosser's (1989, 1992) study in South Luangwa N. P., Zambia, with comparisons made between three seasons, wet (Nov–Apr/May), cool and dry (May–Aug) and hot and dry (Sep–Nov/Dec). Female Pukus selected six vegetation communities (swale sedge, swale forb, swale short grass, swale *Echinochloa*, back plain *Echinochloa* and *Oryza*) during the wet season (Rosser 1992). Habitat preferences changed according to the season and there was increased selection for long grass during the late dry season (Rosser 1992). Forage was superabundant during the wet months with

little variation in quality or quantity between the main vegetation communities. However, during the drier months, female selection was correlated with moisture (May), the percentage of green material (Jul) and the proportion of grass material composed of leaf (Sep). Male habitat selection differed between bachelors and territory holders (Rosser 1992). During the wet season, bachelor ♂♂ selected the mopane community and territorial ♂♂ selected the swale sedge community. In the drier months, although all ♂♂ selected the swale short grass community, bachelor ♂♂ also selected longer grass communities.

Social and Reproductive Behaviour Group composition varies and social bonds between the sexes are rare. Males defend territories (mean size 4.4 ha, Rosser 1992) and have not been observed lekking. In areas of suitable habitat and high Puku density, many ♂♂ have no territories and aggregate together in bachelor groups. Surveys in Kasanka N. P., Zambia, found that group size varied from one (lone males) to a maximum of 39, and density ranged from $25.2/\text{km}^2$ to $45.8/\text{km}^2$ (Goldspink *et al.* 1998). Male groups were smaller than female groups and maximum group size was 25 and 39, respectively. Males were mostly confined to bachelor herds, but a few lone individuals were noted stationed on prominent areas of relief. In Rodgers' (1984b) aerial survey of the Kilombero Valley, Puku modal group size was 1, 2 and 6–10, with a small number of larger groups (11–15 individuals). This group structure was also reported from a ground-based count in the Kilombero Valley by Corti *et al.* (2002), who found that modal group size for ♂♂ was 1, but it was larger for females (6–10) and calves (11–15). The results of these studies are largely consistent with earlier studies (De Vos & Dowsett 1966, Child & von Richter 1969), although De Vos & Dowsett (1966) recorded herds of up to 50 individuals.

Territorial ♂♂ differ from bachelor ♂♂ in both physical characteristics and behaviour (Rosser 1990). Territorial ♂♂ have thicker necks, copiously secrete from a seasonal 'neck-patch' and are more vocal (whistling) compared with bachelor ♂♂.

Goldspink *et al.* (1998) reported a scarcity of ♂♂ in Kasanka N. P. and a polygynous mating system probably based on the acquisition of territories. Comparisons of highly dispersed territories held by ♂♂ in sites with low habitat quality with grouped territories in areas of high habitat quality (and Puku density) revealed differences between male morphology and behaviour. Males in grouped territories had a higher incidence of horn damage, higher neck-patch intensity, higher territory loss rate and smaller territories (Rosser 1992). Females in the study area selected the largest territories with the largest area of short grass defended by ♂♂ with the darkest neck-patches and best condition. Female distribution and mate choice is thought to be simultaneously and independently related to both territory properties (e.g. high-quality forage, predation risk) and male phenotype (e.g. quality of the neck-patch). Males defended territories throughout the year, such that there is a trade off of foraging efficiency (unable to disperse to more optimal habitat to forage) against benefits conferred from territory ownership (Rosser 1992).

Males herd only oestrous ♀♀ and approach ♀♀ with head high, which is followed by laufsclag, urine-sniffing and finally flehmen and copulation. Calves lie concealed in thick vegetation for about a

month after birth and are retrieved and suckled each morning and evening (Estes 1991a). Males play no role in parental care.

Reproduction and Population Structure Rosser (1989) found calves in all months of the year, with a peak in births during the four wet-season months; only a few ♀♀ give birth during the dry season when food quality, quantity and cover is reduced. As with other kobs, Pukus' reproductive phenology is related to food availability, which in turn is related to seasonal patterns of rainfall and levels of standing water. Puku reproductive phenology is adapted to ensure calf survival through maximizing maternal nutrition to meet the demands of late pregnancy and early lactation, and possibly also takes advantage of ground vegetation to protect calves.

Oestrous behaviour rarely lasts more than 24 hours and the length of the oestrous cycle varies from 19 to 21 days. Gestation time is eight months (Rosser 1989) and a single calf is born weighing about 5 kg. Calves are weaned at seven months. Inter-birth interval is about 390 days (Rosser 1987). Estes (1991a) reports that ♂♂ are mature at three years and ♀♀ at two years, though Rosser (1987) reported them capable of conceiving as yearlings. Studies have consistently reported a female-biased sex ratio (De Vos & Dowsett 1966, Goldspink *et al.* 1998).

Predators, Parasites and Diseases Pukus are usually associated with open areas of wet grassland but readily move into cover if disturbed (Goldspink *et al.* 1998). The Kilombero Valley Puku population was struck by an eye infection during 1998 that may have increased their susceptibility to people and predators (reported in Jenkins *et al.* 2003). No quantitative data are available on predation pressures on Pukus, but they are likely to be the main prey of Lions *Panthera leo* and Spotted Hyaenas *Crocuta crocuta* when aggregated on flood-plains during the dry season. A single animal examined by Zieger *et al.* (1998b) in Zambia was host to the following ixodid ticks: *Boophilus decoloratus*, *Rhipicephalus appendiculatus* and *R. evertsi*.

Conservation IUCN Category: Near Threatened. CITES: Not listed.

Habitat fragmentation caused by expanding human settlements and cultivation is a major threat to Puku populations. Suitable habitats are either vacated by Pukus when disturbance/poaching is high (Goldspink *et al.* 1998) or are divided into smaller areas with a reduced population size and often with limited connectivity with the founders (e.g. Rodgers 1984b). The social/breeding system is particularly vulnerable to disruption by habitat fragmentation and hunting, with the longer-term impact of a collapse of population recruitment.

Pukus are relatively easy to approach during the dry season, when densely aggregated on flood-plains, and are consequently very vulnerable to illegal hunting. Unsustainable hunting and especially heavy poaching appear to have extirpated the Puku across its range (East 1999). Populations have collapsed since the early twentieth century, with widespread extirpations. The proliferation of firearms and the urban demand for bushmeat in central Africa during early 1900s signalled the first demise in Puku populations. Today, the burgeoning bushmeat problem in addition to the demand for land

by expanding human populations is subjecting the remaining Puku populations to intense pressure. The vulnerability of Pukus to unsustainable hunting underlies their decimation (Hughes 1933, Vesey-Fitzgerald 1961, Cotterill 2000). In Kasanka N. P., areas of suitable habitat remained unoccupied by Pukus due to high levels of poaching and disturbance (Goldspink *et al.* 1998).

In the Kilombero Valley, Jenkins *et al.* (2002) reported that the major threat to Pukus came from the expansion of cattle herds onto the flood-plain boundary and damage to wet season habitat by farmers who cleared miombo woodland. The fertile soils, flat land and good road and rail access to the Kilombero Valley makes it an attractive destination for immigrant farmers and new areas of forest are cleared each year for agricultural expansion (Haule *et al.* 2002). Levels of off-take by local people are difficult to determine, but are likely to be high in areas near to human settlements (Jenkins *et al.* 2002), because the Puku is a highly desired source of meat and also a valuable non-food resource (the skin is used for drums and furniture). Almost 20% of school children in Haule *et al.*'s (2002) household questionnaire survey reported eating Puku in their last meal.

When human settlements and farms expand into the areas traditionally used by antelopes during the wet season there is a greater risk of crop damage. In a questionnaire survey in the Kilombero Valley, 13% of respondents reported damage to crops by the seasonally abundant Puku, but animals like the Bushpig *Potamochoerus larvatus* (58%) and Yellow Baboon *Papio cynocephalus* (25%) that are present in the miombo woodland-evergreen forest-farm mosaic all year round accounted for most damage (Haule *et al.* 2002). During the wet season Pukus disperse out of protected zones into the surrounding mosaic of farms and miombo woodland bringing them into closer contact with humans. This is when poaching levels are probably most severe, but this part of the Puku's life history and ecology is poorly understood.

Comparisons of recent aerial surveys of the Kilombero Valley (TWCN 1994, 1999, TWRU 2003) revealed the small population (previously less than 120 individuals, East 1999) in the Selous G. R. has been extirpated and increased human activity in the south-eastern Kilombero Valley is effectively prohibiting its recolonization. The same surveys also indicated a decline in numbers of the main population (TWRU 2003). It is clear that the Kilombero Pukus have declined recently, and that increasing human activity, especially cattle-rearing, seriously threatens the remaining population (Haule *et al.* 2002, Jenkins *et al.* 2002, TWRU 2003, Bennington *et al.* 2010). Waltert *et al.* (2009) have also suggested that the Puku's current distribution to the south-west and east of Rukwa G. R. may be negatively affected by the seasonal presence of livestock and humans.

Today, besides Kilombero, key areas for the survival of the Puku include: Katavi N. P. in S Tanzania, Kafue N. P., the Luangwa Valley and Nsumbu-Tondwa-Mweru Wantipa in Zambia, and the smaller populations in Kasungu N. P. in Malawi and Chobe N. P. in Botswana (East 1999). Priority action to conserve the Puku across its range should include the following: (a) improving policing levels and management within existing protected areas; (b) habitat management and conservation in areas outside of parks that Pukus use during the wet season; (c) a detailed study of the interaction between seasonality, cattle distribution and Puku habitat selection

in the Kilombero Valley; (d) upgrading the conservation status of the Kilombero Valley in Tanzania, with establishment of a core protected area to include both dry and wet season refuges; (e) national surveys across the species' entire range to fully quantify and monitor abundance and distribution; (f) a thorough taxonomic reassessment of historical (using museum specimens) and extant populations employing morphological and molecular characters; and (g) continued promotion as a game ranch species within its historical range.

Measurements

Kobus vardonii

TL (♂♂): 1467 mm, n = 17

TL (♀♀): 1337 mm, n = 27

Sh. ht (♂♂): 921 mm, n = 17

Sh. ht (♀♀): 837 mm, n = 27

WT (♂♂): 77.3 kg, n = 17

WT (♀♀): 61.3 kg, n = 27

Zambia (Rosser 1987); mean values

Maximum recorded horn length is 56.2 cm for a pair of horns from the Luangwa Valley, Zambia (Rowland Ward)

Key References Child & von Richter 1969; De Vos & Dowsett 1966; Jenkins *et al.* 2002, 2003; Rodgers 1984b; Rosser 1987, 1989, 1990, 1992.

Richard Jenkins

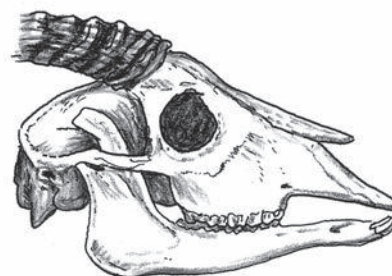
Kobus leche SOUTHERN LECHWE

Fr. Le Cobe lechwe; Ger. Moorantilope (Litschi)

Kobus leche Gray, 1850. Gleanings, Knowsley Menagerie 2: 23. Type locality originally described as 'banks of the river Zoaga, Lat. 21°'; now known to be the Botete R. past its junction with the Thamalakane at 20° 7', Botswana, although the species no longer occurs there (Smithers 1971).



Southern Lechwe *Kobus leche*.

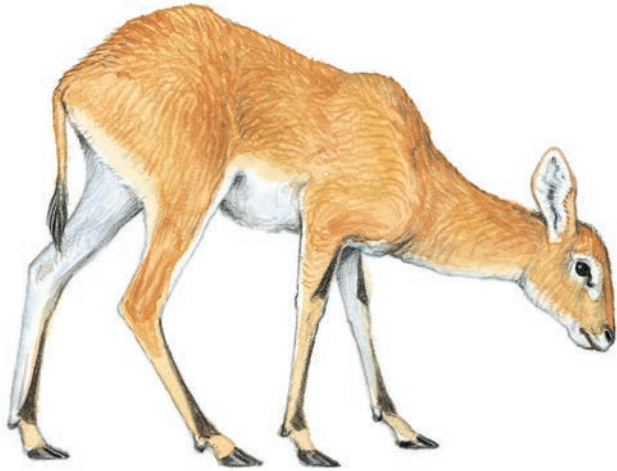


Lateral view of skull of Southern Lechwe *Kobus leche*.

Taxonomy The morphological and phenotypic distinction between the Southern Lechwe *Kobus leche* and the Nile Lechwe *Kobus megaceros*, which occurs in Africa north of the Equator, is supported by karyotypic differences between the species (Kingswood *et al.* 2000). Four distinct lechwe populations (one extinct) are recognized as subspecies, based on a combination of differences in pelage colour, body size and skull measurements (Ansell 1972, Ansell & Banfield 1979), and corroborated by genetic studies (De Meneghi *et al.* 1995, Birungi & Arctander 2001). The latter authors found that genetic variability was lowest in the Red Lechwe *K. l. leche*, possibly due

to a genetic bottleneck that the Zambian population experienced in the past. A fifth population from Katanga in SE DR Congo, conventionally considered a form of the nominate species, may warrant treatment as another subspecies (provisionally the approach adopted here) or a separate species altogether (see Cotterill 2005). Synonyms: *amboellensis*, *anselli*, *grandicornis*, *kafuensis*, *lechee*, *leechi*, *notatus*, *robertsi*, *smithemani*. Chromosome number: 2n = 48; the X chromosome is a large acrocentric and the Y chromosome is a small metacentric/submetacentric (Kingswood *et al.* 2000). Putative subspecies *K. l. leche* and *K. l. kafuensis* exhibit karyotypic similarities (Kingswood *et al.* 2000). Gray (1972) reports a case of hybridization, in captivity, of a Nile Lechwe *Kobus megaceros* with a Southern Lechwe.

Description Stocky, medium-sized antelope, easily recognized by trotting gait with head thrust forward below the shoulders, accentuating the hindquarters, which are higher than the forequarters. Muzzle relatively short, eyes large and widely spaced. Tip of muzzle, gape, orbital surrounds and undersides of ears white. Posterior belly-skin naked and grey, as are udders. Pelage woolly in young, short to medium length in adults, light to dark brown or black (usually darker on the dorsal aspects), with thorax, insides of legs, throat,

Southern Lechwe *Kobus leche* female.

chin and undersides of ears and underside of tail white. Anterior of forelegs and lower hindlegs (excluding knees and pasterns) and tip of tail are dark brown or black. Hooves elongate and splayed when in contact with the substrate. Fetlocks naked or thinly covered with hair. Inguinal glands rudimentary; preorbital and pedal glands are absent.

The horns, present in ♂♂ only, are long, lyrate and annulated, with sharp forwardly curving tips.

Geographic Variation

K. l. leche (Red Lechwe): Botswana, Namibia, Angola and Zambia.

Pelage reddish-brown, usually slightly darker on the dorsal aspects; asymptotic mass of ♂ about 60% greater than ♀ (Williamson 1979).

K. l. kafuensis (Kafue Lechwe): restricted to the Kafue Flats, Zambia.

Distinguished by light brown pelage with dark brown to black patterning on forelegs, extending into patches on the shoulders of ♂♂; similar body size to nominate form, but mass of adult ♂ only about 30% greater than ♀ (Robinette & Child 1964); horns longer than those of Red Lechwe and Black Lechwe.

K. l. smithemani (Black Lechwe): restricted to the Bangweulu Swamps and Chambeshi system, Zambia. Pelage brown to dark brown or black, particularly on the dorsal aspects of older animals and especially in ♂♂; smaller than Red and Kafue Lechwe and mass of adult ♂ only 30% greater than ♀ (Grimsdell & Bell 1975).

K. l. robertsi (Roberts' Lechwe): extinct. Formerly restricted to the Luongo R., Luapula, Zambia. No significant association with other three subspecies (Ansell & Banfield 1979).

The lechwe recorded as occurring in SE DR Congo, previously assumed to be a form of the nominate species, has now been described as the Upemba Lechwe *Kobus leche anselli*, surviving in the Upemba wetlands of the Kamalondo depression (Cotterill 2005). It appears to be more closely related to the Black Lechwe than any of the other subspecies, while, like all the subspecies, its relationship to the extinct Robert's Lechwe remains enigmatic. Cotterill (2005) described this taxon as being smaller than the Red Lechwe, much smaller than the Kafue Lechwe in dimensions of skull and horns,

and most similar in stature and size to the Black Lechwe, but in all respects more gracile. However, the pelage of the Upemba Lechwe is similar in general colouration to the Kafue and Red Lechwes.

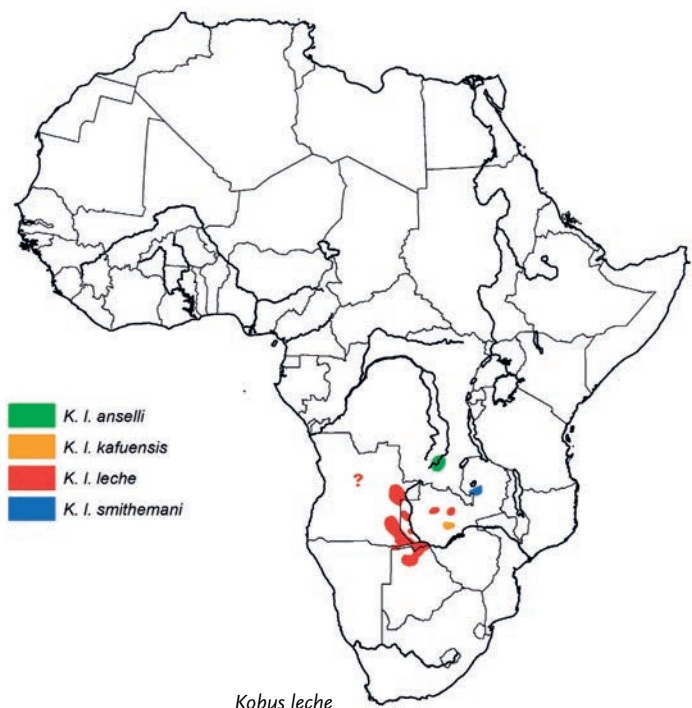
Similar Species

Kobus ellipsiprymnus. Sympatric with Red Lechwe, principally in the Busanga Plains of Zambia and the Okavango Delta of Botswana. Easily distinguished by greater size and grey, woolly pelage.

K. vardonii. Sympatric in parts of Zambia (e.g. on the Basunga Plains of Kafue N. P.) and Botswana (De Vos & Dowsett 1966, Child & von Richter 1969). Similar in appearance, but stockier build and more uniform reddish-brown, thicker pelage.

Distribution Endemic to Africa. The distribution of the Southern Lechwe is discontinuous, with major populations restricted to extensive wetlands in Botswana, Namibia, Angola and Zambia, and SE DR Congo. Present distribution is much the same as its historical distribution, except that range has contracted, particularly over the last century. There are no records of Southern Lechwes ever having occurred in Zimbabwe (Smithers & Wilson 1979).

The Red Lechwe is found in significant numbers in the Okavango Delta, and the Kwando/Linyanti/Chobe system of N Botswana; the Okavango, Kwando/Linyanti/Chobe, Mashi and Zambezi River systems of NE Namibia; and the upper Zambezi and middle Kafue of Zambia. Red Lechwes were also once common in Sioma Ngwezi N. P. of SW Zambia and the Lukanga Swamps of the upper Kafue in Zambia, the Kwando (Cuando) system of SE Angola (contiguous with the Kwando/Linyanti/Chobe system of Namibia and Botswana), the Zambezi flood-plains of E Angola, the Cuanza and Luando Rivers of C Angola, and the Cunene R. of SW Angola. The status of these last-mentioned populations is unknown, although reports indicate that they persist, with the exception of the Cunene population (Crawford-Cabral & Veríssimo 2005).

*Kobus leche*

The Kafue Lechwe is confined to the Kafue Flats, a large wetland area of the middle Kafue R. system of C Zambia.

The Black Lechwe is confined to the southern half of the Bangweulu Swamps of N Zambia. It is unlikely to survive in its former range on the Chambeshi flood-plains along the upper Luapula flood-plain that forms the common frontier between Zambia and SE DR Congo, at the western extremity of the Bangweulu Swamps. A population of Black Lechwes introduced in 1974 from the Bangweulu Swamps to the Bwela Flats on the upper Chambeshi between Kasama and Chinsali is reportedly extinct.

Remnants of a distinct population of lechwes known to occur in the Lualaba R. system of the southern Congo Basin of DR Congo, including the western extension of Upemba N. P., persist in the Kamalondo depression and have been described as the Upemba Lechwe (Cotterill 2005).

The extinct Robert's Lechwe is described as having been restricted within the Luongo and Kalungwishi drainage systems of the lower Luapula locality of NE Zambia, contiguous with the Congo Basin catchments of both the Black and Upemba Lechwe, but apparently a distinct population.

Habitat Lechwes are associated with wetlands of the Zambezan phytochorion of southern Africa, preferring the shallow water margins of flood-plains and swamps (less than a metre deep), although they may occasionally swim across deep-water areas. They typically frequent light woodlands and termitaria grasslands on the periphery of inundated flood-plains, flood-plain grasslands and water-meadows among seasonally inundated flood-plains, shallow water-meadows of permanently inundated swamps and lagoons, and occasionally papyrus and reed-beds of permanent deep-water swamps. Vegetation across these ecotones includes grasses, reeds and sedges such as *Loudetia* spp., *Sporobolus* spp., *Setaria* spp., *Oryza barthii*, *Echinochloa* spp., *Vetiveria nigritana*, *Brachiaria* spp., *Paspalum scrobiculatum*, *Acroceras macrum*, *Panicum repens*, *Leersia* spp., *Vossia cuspidata*, *Cynodon dactylon*, *Eragrostis* spp., *Phragmites* spp., *Typha* spp., *Cyperus* spp., *Eleocharis* spp. and *Pycnus* spp., aquatic herbs such as *Aeschynomene* spp., *Ipomoea* spp., *Polygonum* spp., *Potamogeton* spp., *Pistia stratiotes*, *Nymphoides* spp., *Nymphaea* spp. and *Utricularia* spp., and trees such as *Acacia* spp., *Albizia* spp., *Ficus* spp., *Syzgium* spp., *Phoenix reclinata* and *Hyphaene ventricosa*.

Abundance Estimates of abundance based on sampling techniques are relative, and thus more useful for determining population trends rather than actual numbers. Unless otherwise specified, the following estimates of abundance have been drawn from East (1999).

The most stable and well-documented population of Red Lechwes is in the Okavango Delta, Botswana, where numbers were estimated during the mid-1990s to be 69,520. Numbers of Red Lechwes in Botswana's Kwando/Linyanti/Chobe system appear to have declined from some 10,000–15,000 in the 1970s (Williamson 1979) to 2310 in the mid-1990s. The Red Lechwe population of Namibia's Protected Areas and communal lands of the Caprivi Strip was estimated to be 4470 in the late 1980s, with the majority (4300) occurring in the communal areas. Populations of Red Lechwes elsewhere are not well documented, but significant populations remain in the Liuwa Plains (including the upper Zambezi flood-plains) and Busanga Swamps of Zambia (R. Jeffery & R. Nefdt pers. obs.). The overall numbers of Red Lechwes, then, in central and southern Africa are likely to

be not less than 80,000, with the majority of the population in the Okavango.

The Kafue Lechwe population has been monitored for many years, and probably has the most reliable time-series of population records of all the subspecies. In the 1930s, numbers were reputed to be in the order of 250,000 (Pitman 1934). Although this early estimate was not determined by systematic surveys, it is plausible considering that the maximum carrying capacity of the Kafue Lechwe's range has been estimated to be 360,000 (Bell *et al.* 1973). In the early 1970s, estimates consistently put the population at between 90,000 and 110,000 (Bell *et al.* 1973). By the early 1980s the population had been reduced to between 40,000 and 45,000, but it then slowly increased fluctuating thereafter between 50,000 and 70,000 (Jeffery *et al.* 1993). The most recent estimate (2005) put the population at $38,448 \pm 7392$ (Chansa & Kampamba 2010).

As with the Kafue Lechwe, historical population estimates of Black Lechwes were high, with a figure of 450,000–600,000 being proposed for the Bangweulu Swamps (Pitman 1934). Early records have been extrapolated with ecological criteria to suggest a more realistic estimate of 200,000 Black Lechwes for the early 1900s up to 1936 (Grimsdell & Bell 1975). Dramatic increases in water levels of the Bangweulu Swamps and hunting after 1936 are likely to have had a major impact on Black Lechwe numbers. By 1944, the population had decreased to between 30,000 and 60,000, falling further to about 17,000 in 1969, but increasing slightly by 1973 to 25,000 (Grimsdell & Bell 1975). The population increased further to about 40,000 by 1983, but decreased again to about 32,000 by 1994 (Kamweneshe *et al.* 1994, Thirgood *et al.* 1994). A figure of 150,000 Black Lechwes has been proposed as the carrying capacity for the current range of Black Lechwes in the Bangweulu Swamps (Grimsdell & Bell 1975).

The Upemba Lechwe population of DR Congo has declined from about 20,000 to less than 1000 since the 1980s (Cotterill 2005).

The overall population trend of lechwes in central and southern Africa is negative, probably as a result of excessive hunting, habitat encroachment and both natural and human-induced changes in the flooding regimes of the lechwes' wetland habitats (Grimsdell & Bell 1975, Sayer & Van Lavieren 1975). Negative population trends have been exacerbated in the 1990s by increased human access to wetlands following a period of lower than average rainfall hence reduced water levels. There may have been as many as a million lechwes in southern and central Africa in the early 1900s, taking into account the species' historical distribution and abundance suggested above. By 2000, the total population of the species was probably in the order of 200,000.

Adaptations Although different and not as extreme as the adaptation to aquatic habitats of the Sitatunga *Tragelaphus spekii*, the Southern Lechwe's slightly elongated and splayed hooves facilitate locomotion in muddy swamps while their naked fetlocks minimize the risk of infections of hooves under constantly damp conditions. Southern Lechwes are thus well adapted to wetland habitats, and are often found foraging in water up to shoulder-height. They are proficient swimmers and readily cross inundated flood-plains, lagoons, channels and even rivers to reach habitats preferred for a variety of activities. During periods of extreme flooding, lechwes move to drier (and often more wooded) areas on the margins of their usual range. They also move into drier areas during periods

of heightened reproductive activity, but during calving may take refuge in deeper swamps that are less prone to disturbance. Diurnal movements may occur between flood-plain margins and deeper swamps, probably alternating between foraging, resting and seeking refuge. Lechwes readily take to the water when threatened by predators and other disturbances.

Stomach physiology is similar to other water-dependent grazers, such as reedbucks *Redunca* spp., Waterbucks *Kobus ellipsiprymnus*, Pukus *K. vardonii* and Kobs *K. kob*. Stafford & Stafford (1991) have suggested functional adaptation to grazing on aquatic grasses.

Lechwes provide an example of how a species may adapt its reproductive behaviour to changes in ecology, including those induced by human activities. Peak calving period in most populations has been reported to be between Jun and Oct. However, following the construction of hydro-electric facilities on the Kafue R. in Zambia and change in the flooding regime of the Kafue Flats, calving in the Kafue Lechwe shifted by three months into the wet season between 1989 and 1991 (Nefdt 1996). It is possible that rising water levels stimulate lechwe to mate, resulting in maximum calving after the flood recedes, a period where exposed high-quality forage provides ideal conditions for lactating ♀♀ and their calves. Delaying or prolonging flooding of the Kafue Flats by a few months due to operation of the hydro-electric dams may have caused mating in the Kafue Lechwe population to occur later, thus delaying the period of peak calving (Nefdt 1996).

Foraging and Food Southern Lechwe are grazers, feeding mainly on flood-plain and aquatic grasses, including *Vossia cuspidata*, *Panicum repens*, *Acroceras macrum*, *Paspalum orbiculare*, *Oryza barthii*, *Oryza longistaminata*, *Cynodon dactylon* and a number of *Echinochloa*, *Brachiaria*, *Leersia*, *Sacciolepis*, *Eragrostis* and *Setaria* spp. (Rees 1978a, b, Williamson 1979, 1990, Nefdt 1993). They also feed on sedges, reeds and other aquatic plants, including *Scirpus*, *Pycneus*, *Cyperus*, *Eleocharis* and *Aeschynomene* spp., and may feed in water up to shoulder height. The exposure of large expanses of flood-plain grasslands during flood recession can lead to the concentration of lechwe in large numbers, and densities as high as 1000/km² have been recorded in the Kafue Flats.

Food supply is greatly dependent on the seasonal flooding of wetlands. In southern Africa, peak flooding generally occurs towards the end of the wet season (Mar–Apr) receding gradually through the cool dry season, but considerably later in the Okavango Delta (Jul–Aug) where it is dependent upon distant floodwaters reaching the Okavango R. and its delta system from the Cubango and Cuito Rivers deep in Angola. On the Kafue Flats, seasonal flooding has been artificially regulated by hydro-electric impoundments since 1971.

Changes in the waterline by seasonal inundation of flood-plain habitats result in lechwes moving between areas with a diversity of plant communities (Nefdt 1993). Lechwes are subject to their greatest nutritional stress at the height of flooding when flood-plain grasslands are too deeply inundated for grass to grow or lechwes to forage easily. Under these circumstances, lechwes may be forced out of flood-plain habitats into peripheral woodlands to graze on poor quality grasses and even to browse on shrubs. Lechwes may thus move over several kilometres within a day, often crossing dry areas, after which they usually drink upon arriving at new water sources.

In common with other ungulates, Southern Lechwes spend most of their time (between 54 and 76% depending on age/sex class) feeding and ruminating, with all activities demonstrating the effect of seasonal and environmental conditions on behaviour (Williamson 1993). However, diurnal variation in activity patterns is far less distinct than in dryland antelopes due to their association with wetlands, reducing their exposure to heat-stress and enabling them to indulge in all activities at all times of the day (Williamson 1993).

Social and Reproductive Behaviour Lechwes are among the most gregarious of the ungulates, and may move considerable distances (20 km or more in a matter of days) in large mixed herds of as many as 5000 animals following flooding and flood-recession in their wetland habitats. Group sizes and associations can be broadly divided into several types. The most common are mixed-sex herds that consist typically of over 65% ♀♀ and calves. Males continuously compete for ♀♀ and supremacy, resulting in dominant ♂♂ excluding large numbers of mature and immature ♂♂ from these herds. Excluded ♂♂ assemble in bachelor herds, and where such population densities are high, such as in Black and Kafue Lechwes, male herds can consist of more than 1000 individuals (Williamson 1979, Nefdt 1993).

Mating systems and associated reproductive behaviour are highly variable both within and between subspecies, and appear to be determined by social structures and population densities that in turn are influenced by the variability of habitats and conditions they must adapt to within the wetlands environment. Red and Black Lechwe breed on stable resource-defence territories, or defend harems of ♀♀ that move within relatively small home-ranges (Williamson 1994a, Nefdt & Thirgood 1997), whereas Kafue Lechwes breed predominantly on mating arenas or 'leks' (Schuster 1976, Deutsch & Nefdt 1992, Balmford *et al.* 1993, Clutton-Brock *et al.* 1993, Nefdt 1995).

Reproductive studies of Kafue Lechwes (Balmford *et al.* 1993, Clutton-Brock *et al.* 1993, Nefdt 1995, Nefdt & Thirgood 1997) show that this subspecies exhibits the most variability in mating behaviour, probably owing to the highly variable habitats and ecological conditions they encounter, and probably exaggerated by artificial flood regulation of hydro-electric facilities at either extremity of the Kafue Flats. Mating strategies include: scramble competition in large mixed-sex herds, resource-based territories, harem defence polygyny and lek-breeding. Harassment of oestrous ♀♀ by many ♂♂ in large mixed-sex herds, and the subsequent reduction in successful matings, may play a part in over 90% of all ♀♀ preferring to mate with ♂♂ defending tiny territories or 'leks' (Nefdt 1995).

Leks are traditional sites used as mating grounds, where up to 100 ♂♂ defend tiny territories that ♀♀ visit solely for mating. A sexual frenzy is the norm at these leks during sunrise and sunset, with ♀♀ attempting to mount ♀♀ (over 100 attempts per hour) and ♂♂ copulating with oestrous ♀♀ every 10 min. Deliberate mate choice by oestrous ♀♀ on these leks is quite clear with 10% of lek ♂♂ achieving 80% of all matings (Deutsch & Nefdt 1992, Clutton-Brock *et al.* 1993). It appears that ♀♀ also use olfactory cues in the soil on lek territories to choose mating partners (Deutsch & Nefdt 1992).

Between one and three ♂♂ often mate with more than 30 ♀♀ in a day (Clutton-Brock *et al.* 1993, Nefdt 1993). A few peripheral

territorial ♂♂ are able to intercept oestrous ♀♀ and mate, but this usually represents less than 5% of all matings. Younger ♂♂ often exhibit cleptogyny, by roaming between lek territories and intercepting oestrous ♀♀, and ejaculating within seconds of mounting.

A single ♂ may mate with over 300 ♀♀ on the same 100 m² lek territory over a period of one month, but successful ♂♂ are usually replaced within seven days. With such turnover rates, it is estimated that not more than 1000 ♂♂, out of a total male population of 20,000, are able to mate per year. Therefore, approximately 5% of ♂♂ in the entire Kafue Lechwe population are the fathers of all offspring each year.

Although Black Lechwes have also been reported to breed on leks (Grimsdell & Bell 1975), more recent studies have been unable to record such behaviour and found that ♂♂ defended contiguous 1–2 ha resource-based territories (Thirgood *et al.* 1992). During the wet season, from Nov to Mar, networks of thousands of these territories are spread across the vast flood-plains of the Bangweulu. On some elevated sites, ♀♀ form harems and dominant ♂♂ defend these small areas. These sites superficially resemble leks, but resources on the territories influence females' choice, and, therefore, these areas must still be regarded as resource-based territories. Lekking may not develop in the Bangweulu because vegetation resources and hence female lechwes are evenly distributed. Harassment rates of oestrous ♀♀ on single territories are considerably lower than in the Kafue Flats. Males with territories containing better grazing generally gain more ♀♀ and achieve higher mating rates than ♂♂ defending territories with poorer resources.

Males ascertain the reproductive status of the ♀ by sniffing her vulva or urine flow and performing flehmen. If the ♀ is in oestrus, he moves alongside her, lifting his foreleg from the ground (laufs Schlag), while grunting and flicking his tail. If the ♀ is receptive, copulation may follow, intromission being achieved with a single pelvic thrust, although many mountings sometimes occur (Robinette 1963).

Females about to give birth leave the herd singly or in groups. The calf remains hidden for the first few weeks, the ♀ returning

to suckle at regular times throughout the day. Thereafter, only very young calves accompany their mothers, moving independently when older. Individual crèches of up to 50 calves have been seen on the Kafue Flats.

A variety of vocalizations and behavioural displays have been recorded in Southern Lechwes. Vocalizations consist mostly of bleats, grunts and snorts, these varying in pitch, intensity and duration depending on age and sex, and functional associations with greetings (such as mother–young calls), dominance, courtship, alarm and distress (Williamson 1994a). Typical behavioural displays include erect postures and horn threats in dominant ♂♂, laying back of horns and rapid head-tossing in submissive ♂♂, agonistic horning, agonistic grazing, grooming, head and neck stretched forward with rapid tongue-flicking in ♂♂ approaching ♀♀, courtship displays including laufs Schlag and flehmen, and post-copulatory displays (Williamson 1994a).

Reproduction and Population Structure Breeding occurs throughout the year in Southern Lechwes, but with peaks in calving between Jun and Oct (Robinette & Child 1964, Grimsdell & Bell 1975, Sayer & Van Lavieren 1975, Williamson 1991, Thirgood *et al.* 1992). Variations in both reproduction and population structure occur as a result of natural or artificially induced ecological changes (for example, from the effects of fluctuating seasonal rainfall and hydro-electric impoundments on hydrological regimes) that in turn affect nutrition.

Males are sexually active from about 18 months (all animals weighing more than 55 kg showed active spermatogenesis; Williamson 1992), ♀♀ from about 24 months (Williamson 1991), and later in populations under nutritional stress. However, ♂♂ are unlikely to mate successfully until they acquire territories (from 4–5 years). The gestation period is about 7.5 months (Grimsdell & Bell 1975). Females produce a single calf, weighing about 5 kg; twinning is rare. The parturition interval is about one year. Lactation continues for up to seven months (Robinette 1963), but weaning often extends into a following pregnancy. During the first few months the horns grow straight, but as they grow they gradually curve backwards and outwards. In captivity, they have been known to live for more than 25 years (Weigl 2005).

Mean reproductive rates in ♀♀ are in the order of 73%, with fecundity approaching 100% in healthy female populations between five and ten years old. Southern Lechwes are capable of rapid rates of population increase, and up to 25% per annum has been observed for Red Lechwe in the Busanga Swamps and Black Lechwe in the Bangweulu Swamps. An intrinsic rate of increase was calculated to be 0.265, or a finite rate of increase of 30% per annum (Grimsdell & Bell 1975). Actual rates of increase vary according to population status and condition.

Where population sizes are large, such as in the Kafue and Black Lechwe populations, herds can consist of as many as 5000 individuals of mixed ages and gender. However, adult ♀♀ usually outnumber adult ♂♂, partly because dominant ♂♂ exclude other ♂♂ from these herds, but possibly also because male mortality is higher. Outcast ♂♂ usually congregate in bachelor herds sometimes consisting of more than 1000 individuals. In contrast, population densities of Red Lechwes are much lower, with groups usually containing less than 200 animals.



Colouring in male Southern Lechwe *Kobus leche* (and in other reduncines) emphasizes expression by concentrating white patterns around the mouth, eyes and ears.

Predators, Parasites and Diseases Principal predators include Nile Crocodiles *Crocodylus niloticus*, Lions *Panthera leo*, Leopards *P. pardus*, Spotted Hyenas *Crocuta crocuta*, Cheetahs *Acinonyx jubatus* and African Wild Dogs *Lycaon pictus*, while predation by jackals *Canis* spp. and African Rock Python *Python sebae* has also been recorded.

In their natural environment, Southern Lechwes appear resilient to or tolerant of livestock diseases such as trypanosomiasis. However, bovine tuberculosis (e.g. Gallagher *et al.* 1972, Stafford 1991, Zieger *et al.* 1998c) and heartwater (Pandey *et al.* 1992) have both been recorded from lechwes. Kock *et al.* (2002) examined 22 Kafue Lechwes and diagnosed the following conditions: microscopic granulomatous lesions with prominent giant cells, consistent with tuberculosis, in the lungs of two animals; microscopic hepatic granulomata, presumably caused by schistosomiasis, in eight animals; splenic haemosiderosis in six; splenic extramedullary haematopoiesis in six; acute to subacute perifollicular eosinophilic splenitis and lymphoid hyperplasia in four; periportal hepatitis in seven; myocardial sarcosporidiosis in 11; and pulmonary anthracosis in four. However, other than a case of bronchopneumonia, none of the lesions was considered of clinical importance. Heartwater was not detected, but may be due to the small number of animals sampled.

Parasitic infections include liver flukes, lungworms, nematodes (e.g. *Haemonchus contortus*; Zieger *et al.* 1998a), trematodes (such as *Callicophoron* sp., *Schistosoma* sp. and *Fasciola gigantica*; Gallagher *et al.* 1972, Zieger *et al.* 1998a, Kock *et al.* 2002) and warble flies (particularly *Strobiloestrus vanzyli*; see Stafford 1991, Zieger *et al.* 1998a), particularly where there is regular contact with domestic livestock or under captive conditions when infections may become pathogenic. A survey of helminths in Kafue Lechwe recorded 11 different types of helminths, with amphistomes (100%) and *Oesophagostomum* (60.9%) the most common identified. There was no evidence that infections, in the intensities observed, adversely affected the health of the lechwe, although these animals could serve as a potentially stable source of infection to domestic livestock (Phiri *et al.* 2011). Infections with *Eimeria* spp. were documented in all but one of 22 culled animals examined by Kock *et al.* (2002).

Ixodid ticks collected from Southern Lechwes include *Amblyomma variegatum*, *Boophilus decoloratus*, *Rhipicephalus appendiculatus*, *R. evertsi* and *R. lunulatus* (Stafford 1991, Zieger *et al.* 1998b).

Conservation IUCN Category: Least Concern (*K. l. smithemani* – Vulnerable D2; *K. l. kafuensis* – Vulnerable D2; *K. l. robertsi* – Extinct; *K. l. anelli* – Critically Endangered A2cd; *K. l. leche* – Least Concern). CITES: Appendix II.

The principal populations of Southern Lechwes in southern Africa are distributed amongst wetlands that all enjoy some degree of status as protected areas (excluding captive and game-ranch populations). In spite of this, poaching, encroachment and habitat destruction pose growing threats to the conservation of lechwes. Poaching has been implicated in apparent large-scale changes in the dry season distribution of the Black Lechwe, with a dramatic decrease in the numbers occupying the western end of the main Bangweulu Swamps (East 1999).

In Botswana, Red Lechwes occur in Moremi G. R. and Chobe N. P. but are also widespread outside these protected areas. In Zambia, Red Lechwes occur in Sioma Ngwezi, Liuwa Plains and Kafue

National Parks, and the West Zambezi and Kasonso-Busanga Game Management Areas. In Namibia, small numbers of Red Lechwes occur in Western Caprivi G. R. and Mahango Game Park, but the majority fall outside Namibia's protected areas. In Angola, Red Lechwes occur in Kameia N. P. and Luando, Mavinga and Luiana Game Reserves.

Kafue Lechwes occur only in Lochinvar and Blue Lagoon National Parks, both designated as wetland sites of special importance under the Ramsar Convention, and the Kafue Flats Game Management Area in Zambia. The population appears to be declining due to hunting and the construction of the Iteszi-tezhi dam.

Black Lechwes occur only in Bangweulu Game Management Area, which includes Chikuni Special Conservation Area (also a Ramsar site), and Kalasa-Mukoso Game Management Area in Zambia. The small population reintroduced to the Bwela Flats of the upper Chambeshi has not survived. Black Lechwes no longer occur in any National Parks, and Isangano N. P., established partly to protect this subspecies, is currently encroached and depleted of most wildlife.

In DR Congo, Upemba Lechwes still occur in the western extension of Upemba N. P., where they are highly threatened, mainly by commercial poaching (Cotterill 2005).

Measurements

Kobus leche

K. l. leche

HB (♂ ♂): 1641 mm, n = 89

HB (♀ ♀): 1525 mm, n = 142

E (♂ ♂): 151 mm, n = 89

E (♀ ♀): 143 mm, n = 142

HF c.u. (♂ ♂): 487 mm, n = 89

HF c.u. (♀ ♀): 477 mm, n = 142

Sh. ht (♂ ♂): 1014 mm, n = 89

Sh. ht (♀ ♀): 920 mm, n = 142

WT (♂ ♂): 118.1 kg, n = 89

WT (♀ ♀): 74.1 kg, n = 142

Asymptotic measurements (means and ranges not available) from Kwando/Linyanti/Chobe, Botswana (Williamson 1979)

Maximum recorded horn length is 88.9 cm for a specimen from Ngamiland, Botswana, held in the British Museum (Rowland Ward)

K. l. kafuensis

HB (♂ ♂): 1618 (1613–1689) mm, n = 25

HB (♀ ♀): 1536 (1499–1734) mm, n = 81

T (♂ ♂): 345 (279–368) mm, n = 25

T (♀ ♀): 328 (292–368) mm, n = 81

HF c.u. (♂ ♂): 488 (470–503) mm, n = 24

HF c.u. (♀ ♀): 472 (452–508) mm, n = 81

E (♂ ♂): 147 (140–152) mm, n = 22

E (♀ ♀): 145 (132–155) mm, n = 81

Sh. ht (♂ ♂): 1039 (991–1118) mm, n = 24

Sh. ht (♀ ♀): 968 (902–1061) mm, n = 80

WT (♂ ♂): 102.9 (86.5–127.7) kg, n = 38

WT (♀ ♀): 78.7 (61.6–96.9) kg, n = 83

Kafue Flats, Zambia (Robinette 1963)

Maximum recorded horn length is 93.9 cm for a specimen from Zambia (Rowland Ward)

Kobus l. smithemani

HB (♂♂): 1604 mm, n = 9

HB (♀♀): 1527 mm, n = 29

WT (♂♂): 90.1 kg, n = 9

WT (♀♀): 70.2 kg, n = 29

Asymptotic measurements (means and ranges not available) from Bangweulu Swamps, Zambia (Grimsdell & Bell 1975)

Maximum recorded horn length is 80.0 cm for a specimen from Zambia (Rowland Ward)

Key References Grimsdell & Bell 1975; Nefdt 1993, 1995, 1996; Nefdt & Thirgood 1997; Thirgood *et al.* 1992, 1994; Williamson 1979, 1991, 1992, 1994a.

Richard Jeffery & Rory Nefdt

Kobus megaceros NILE LECHWE (MRS GRAY'S LECHWE)

Fr. Le Cobe de Madame Gray; Ger. Frau Grays Wasserbocke (Weissnacken-Moorantilope)

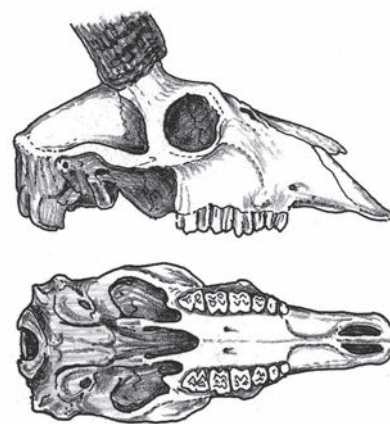
Kobus megaceros (Fitzinger, 1855). Sitzb. K. Akad. Wiss. Wien XVII: 247. Sudan, Upper Nile Prov., 'Bahr el abiad' or according to the collector, von Heuglin (Nov. Act. Acad. Caes. Leop. Carol. Germ. Nat. Curios., Abhand. 30, part 2, p. 14 [1863]), 'am Sobat, Bhar ghasál und untern Kir' (Bahr el Abiad or White Nile, Bahr el Ghazal, Kir River or lower Bahr el-Jebel, and Sobat River); restricted to 'Mouth of the Bahr el Ghazal at its junction with the White Nile' (Roosevelt & Heller, 1915: 519).



Nile Lechwe *Kobus megaceros*.

Taxonomy Monotypic. The Austrian naturalist Theodor von Heuglin discovered this antelope in 1853. In 1854, he brought some skins and skulls of this species to Vienna and a living ♀ was kept at the Imperial Menagerie at Schönbrunn. Leopold Fitzinger described von Heuglin's specimens and the environment in which they were captured, thus taking priority for the species' name. He mentioned von Heuglin's intention to name the new species 'Adenota megaceros Heuglin' (a name that emphasizes the size of the horns: Greek *mega* big and *kera* horn), but von Heuglin did not publish a description until 1863. The name *Kobus maria* (Gray, 1859), was established on the basis of specimens collected on the White Nile and in ignorance of Fitzinger's description. Gray named the species in honour of his wife, Maria, and this gave rise to the popular name 'Mrs Gray's Lechwe'. The Nile Lechwe was once subsumed in the genus *Onotragus* (Patrizi 1937). To date there are no known fossils that can be related to this species (Gentry 1978).

Synonyms: *maria*. Chromosome number: $2n = 52$; the X chromosome is a large acrocentric and the Y chromosome is a



Lateral and palatal views of skull of Nile Lechwe *Kobus megaceros*.

small metacentric/submetacentric (Wurster & Benirschke 1968, Kingswood *et al.* 2000). Gray (1972) documents records of hybridization between Defassa Waterbucks *K. ellipsiprymnus defassa* and Nile Lechwes, which produced a fertile ♀, and between Kobs *Kobus kob* and Nile Lechwes, and between Southern Lechwes *Kobus leche* and Nile Lechwes.

Description Medium to large-sized robust antelope, with short face, elongated and slender limbs and long rough hair; the long hindlegs and well-muscled haunches tend to elevate the rump. There is pronounced sexual dimorphism, both in terms of size and patterning. Male pattern and colouring differs greatly according to age and is, perhaps, also under hormonal control. In subadult ♂♂, starting at the age of two, the pelage changes from yellow-ochre to tawny russet eventually reaching the reddish to blackish-brown colour characteristic of adult ♂♂. Mature ♂♂ have a white patch (with or without interruptions) running from the head, between the ears, down the nape to the upper shoulders. This is variable in width and brightness, but generally, at the age of two, the white patch begins as a light-coloured area, gradually becoming bright white and contrasting very strongly with the dark colour of the rest of the body with maturity. Occasionally, the patch is absent and sometimes it can

darken in relation to individual hormonal and social status. Typical facial pattern has white markings strongly contrasting with the blackish forehead and suborbital areas; white supraorbital markings loop incompletely around the eyes; chin, lips and margins of the nostrils white. Inguinal pelage is white. Hair is longer and thicker, like a beard, from the cheeks to the lower throat to the dewlap. Legs are dark, with a light whitish area above the hooves.

Adult ♀♀ are smaller than ♂♂. Pelage from yellowish-ochre to tawny-chestnut brown, with dark patches appearing in some older ♀♀, mainly on the upper forelegs and hindlegs. Throat, belly, shoulders, hindquarters and legs lighter. Cheeks darker brown; area under the eyes blackish, with incomplete white 'spectacles' around the eyes; upper lips and chin bright white; white-lined, pointed ears also conspicuous, but backs of ears are ochre or tawny-chestnut in ♀♀ (and immature ♂♂). Aged ♀♀ have longer and thicker pelage on the throat. In both sexes, the tail is long, sometimes whitish, with a conspicuous terminal black tuft. Young of both sexes are coloured like ♀♀. Calves, until the fourth month, are pale grey-yellowish. Hooves of the species are spread out and very elongate; inner hoof narrow, and outer hoof wide and stubby; back of the pasterns naked. Inguinal glands present; pedal and preorbital glands absent.

Horns, present in ♂♂ only, annulated (from 20 to more than 30 annulations), lyrate, double-curved; the first section broadly curved backwards and outwards, the second section, shorter, varies in shape and direction of the curve (more or less diverging outwards, but in some individuals the tips converge inwards). Horn cores with little mediolateral compression inserted farther behind the orbits than in other reduncines; wide nasals and very strong longitudinal ridges on the basioccipital (Gentry 1978).

Geographic Variation None recorded.

Similar Species

Kobus kob. White-eared Kob (*K. k. leucotis*) occurs sympatrically.

Similar in colouring, but with sleeker pelage, with shorter legs and less measured gait. Kob ♂♂ distinguished by white underside, chin and upper throat.

Distribution Endemic to Sudan and Ethiopia. Once possibly more widespread along the Nile R. and indeed they probably once occurred as far north as Egypt based on evidence of archaeological remains (Osborn & Osbornová 1998). Today, populations occur in S Sudan, in the 'Sudd' swamps and wetlands, along the Bahr el Gazal, at its confluence with the Sobat, along the Bahr el Zeraf, the Bahr el Jebel (White Nile) and in the Machar marshes at the Ethiopian border. More peripheral herds (most likely overspill from the Machar marshes population) have been recorded from the Pibor, Akobo, Gilo and Baro Rivers, and also from near Gambella, in SW Ethiopia (Yalden *et al.* 1984, Hillman 1988a, Hillman & Fryxell 1988, East 1999). Several herds comprising a hundred individuals were observed near the Lakes Nyuborn and Yirol (Hillman & Fryxell 1988). Recent surveys in S Sudan reveal that the Nile Lechwe remains widespread along the Nile R. (Fay *et al.* 2007).

Habitat The primary habitat is swamps and marshes subject to seasonal inundation. They are almost always in shallow waters on the edge of deeper swamps where the water is between 10 and



Kobus megaceros

40 cm deep (Mefit-Babtie 1983). In all areas occupied by the Nile Lechwe, differences between dry and wet seasons are marked but local patterns of flooding have the most influence on the species. In the Sobat system rains begin in Apr, peak in May and by mid-Jun the whole Sobat area is flooded. Rainfall tails off and ceases completely in Nov when the dry season begins. In Mar and Apr temperature reaches 45 °C.

In the Sudd proper, Nile Lechwes are mainly confined to the river-flooded grasslands that lie between deep swamp (dominated by *Cyperus papyrus* and Sudd grass, *Vossia*) and the drier rain-flooded grasslands (dominated by thatch grass, *Hyparrhenia rufa*). This river-flood zone, or *toic* (an ecotype named from a local Dinka term), is dominated by swamp antelope grass (*Echinochloa stagnina*), rice-grass (*Leersia*) and wild rice (*Oryza*) and has numerous pools edged with bulrushes and water-lilies. Within the *toic* the lechwes follow fluctuating margins between shallow floodwaters and drier ground. This involves continuous seasonal drifting up and down the flood tide lines. As floods deepen (about May), the lechwes move further from the river and/or upstream, travelling as far as 30–40 km between high- and low-flood seasonal pastures. Because movement is today severely constrained by dense settlement and livestock herds all around the swamps, the lechwes tend to converge on levees and termite complexes deep within the *toic* until the floods begin to subside in about Oct. By the time fires are burning the flood-plain (Jan–Mar) the lechwes occupy the patchy margins of the permanent swamp where they avoid papyrus, but are commonly found in Sudd grass. At this time competition for grazing is keen and large herds of cattle tend to force the lechwes deeper into the swamps (Howell *et al.* 1988, Kingdon 1997).

The Nile Lechwes' strong preference for river-flooded *toic* and their progressive forcing, by cattle, into deeper swamps during the late dry season was evident in the results of three aerial surveys made in 1981 and 1982. These surveys covered the eastern flood-plains and swamps of the Sudd (about half of the entire range of this species)



Distribution of Nile Lechwe *Kobus megaceros* in a part of the Sudd flood-plains and swamps. Movements indicate that the lechwes' preference is for flood waters that are 10–40 cm deep (from Mefit-Babtie 1983).

and were made during the middle of the wet season, early dry season and then again in the late dry season. The lechwes were virtually free of competition for pasture during the wet season, but put under progressively more pressure during the dry season, suggesting that competition (and occasional hunting) at this time are currently the major constraint on population size (Mefit-Babtie 1983)

Abundance The aerial surveys of Mefit-Babtie (1983) produced an estimated total of 30,000–40,000 individuals, 95% of which were concentrated in the Sudd and the rest scattered between Sudan and Ethiopia. The Machar population was estimated at 900 individuals (Hillman & Fryxell 1988). In Gambela, Duckworth (1974) reported that the species was rare: 'a few hundred of individuals' and may have decreased further (Hillman 1988a). In 1967, Blower (1968) estimated about 150 individuals in Ghilo R. swamps. In 1973, in the same area and season, Duckworth scored only 52 animals (Bolton 1973). In 2001, the population in Fanyikang G. R. in SE Sudan was estimated at 109 individuals in the early dry season and 209 in the late dry, a possible decline, since illegal hunting has accompanied the ongoing civil war (Ogilo 2001). The dry season surveys of Fay *et al.* (2007) estimated the total population along the Nile R. at nearly 4300 animals, particularly in and around Zeraf G. R.

Nile Lechwes are likely to be very strongly constrained by large numbers of cattle that penetrate deep into the Sudd during the dry season and they are commonly very close to dense herds of cattle during the day, but always in water that is too deep for the latter to graze in. It is likely that numbers of lechwes were very much greater and herds much denser before pastoralists developed techniques for exploiting the Sudd (estimated at about 1000 years ago).

Adaptations Long legs and splayed, elongated hooves facilitate life in the shallows; the shape of the hooves is suited to walking in grassy mud without sinking. The lack of pedal and pre-orbital glands is probably connected with the ineffectiveness of scent-secretions in an aquatic environment; in compensation other forms of marking have developed. The conspicuousness of white chins and lips in ♀♀ suggests that chewing movements may have some signal value and may advertise subordination in a social milieu that is dense, with very frequent and close interactions between individuals. Nile Lechwes are also exceptionally vocal and this must also facilitate communication and help regulate social relationships. They make croaks that resemble those of a full-throated frog.

Male colour pattern assumes great importance in social organization. Marked sexual dimorphism in colouration, uncommon among antelopes, facilitates distant recognition within the herds, both for mating, regulating social encounters and priorities in access to food. The male's white nape patch, contrasting with the black of the body, emphasizes the threat display, which consists of rapid lowering of the head, putting the horns into an attack position. Kingdon (1982) suggested that the white colouring on the neck advertises such head movements and helps to provide an easy assessment of the size of the horns; markings are dorsal because the animal's lower surfaces are normally hidden. Age-graded colour-coding has culminated in an extreme visual contrast, which serves to reduce ambiguity and thus limit competition for access to female herds to a relatively small cadre of adult ♂♂ in prime condition. Intimidation displays probably help define temporary boundaries through repetitive stand-offs. Moreover, colour and brightness of the pelage provides a measure of the status and vigour of individual ♂♂. In captivity, the

acquisition of adult patterning by subadult ♂♂ living with dominant ones is delayed, or some individuals may even resume juvenile colouring. Also, ♂♂ that have lost their hierarchical dominance have been observed to revert to the juvenile pattern or lose brightness and contrast in their colouring (Falchetti *et al.* 1994). It seems that these changes, which are probably under hormonal control (with testosterone presumably playing a prominent role) serve to reduce the likelihood of aggressive encounters between strong dominant ♂♂ and the subordinate or temporarily weak or exhausted ones. Colour-coding by age, sex and rank assists social hierarchies while marked differences between ♂♂ and ♀♀ probably enable each sex to pursue independent life-cycles. In predator-rich environments, highly conspicuous animals invite attention but, under normal conditions, the threat to Nile Lechwe ♂♂ from large visual hunters is negligible so they can afford to be conspicuous. It is significant that the one Southern Lechwe population in which the ♂♂ are black and white (Black Lechwe *K. l. smithemani*) also lives on a very wide, flat flood-plain in the Bangweulu basin, Zambia, with few resident predators.



Nile Lechwe *Kobus megaceros* foetus showing elongated hooves and dark pigment around eyes and mouth.

Foraging and Food Predominantly grazers, with food consisting of swamp grass and shoots (generally in water 10–40 cm deep). They graze on growing wild rice *Oryza longistaminata* during the early flood season, but mainly rice grass *Leersia hexandra*, swamp antelope grass *Echinochloa stagnina* and Sudd grass *Vossia cuspidata* as the floods recede (Kingdon 1997). It is not entirely clear whether *Vossia cuspidata* comprises more than one species, but it exists in two very distinct forms. One is tall with multiple inflorescences and urticaceous leaf sheaths. The second, much shorter form is without irritant hairs, has single or double inflorescences and appears to be more attractive to grazers, including Nile Lechwes. Herds often graze in or very close to areas that are dominated by papyrus *Cyperus papyrus* or rushes *Typha domingensis*, but neither of these species is normally eaten, especially in their mature state. However, small patches of *Leersia hexandra* and, perhaps, *Digitaria debilis* and *Paspalum scrobiculatum*, seem to be the dietary attractions. It is uncertain whether aquatic bladderworts, *Utricularia* spp., are eaten but animals have been seen to pull similar vegetation up out of shallow water (J. Kingdon pers. obs.). Likewise,

it is uncertain to what extent the lechwes take common swamp herbs such as *Ipomoea aquatica*, *Hybiscus cannabinus*, *Vallisneria aethiopica* or *Ludwigia leptocarpa*.

Social and Reproductive Behaviour At the present time, Nile Lechwes form loose, temporary herds of 50–100 individuals, sometimes up to a few hundreds, which include adult ♀♀ with calves, young ♂♂ and ♀♀, some adult ♂♂ and marginal groups of bachelors. These split into breeding and bachelor herds in the late wet/early dry season. The size of herds depends on food abundance and availability of resting-places on dry ground, islets or even on the sides of termite mounds. It seems likely that temporary herds of many hundreds would be less rare, were it not for competition from cattle for pasture.

The behaviour of animals in the wild is poorly known; however, observations in the field and in captivity (Falchetti 1997, 1998, Kingdon 1997) reveal a complex social organization, in which ♂♂ and ♀♀ pursue largely independent existences. In 1980–82, J. Kingdon (pers. obs.) observed adult ♂♂ tolerating the presence of several other well-horned ♂♂, but only ones that could be graded by colour. These clearly represented hierarchically ordered age-classes. In captivity, social relationships appear to be based on a strong hierarchical dominance within male and female groups. Among ♂♂ there is a despotic hierarchical order; at the apex there is only one adult, which does not defend any particular area and tolerates the presence of other ♂♂ only if they are subordinate. Dominant ♂♂ have priority in feeding, in space utilization and exclusiveness in mating. Male dominance is not stable but changes according to the outcome of challenges from other ♂♂. Defeated ♂♂ may lose their bright colour and seclude themselves in small 'arenas' away from the herds and deeper within the swamps; alternatively, and more rarely, they stay within a herd and behave as subordinates. Inter-male encounters are characterized and, perhaps, regulated by, displays of threat and dominance. Postures shown by dominant or challenging ♂♂ serve to emphasize size and physical strength. Subordinate ♂♂ display submission through the lowered position of their head, ears and neck and backward-facing horns. These appeasement gestures reduce the frequency and intensity of fights. In contrast, combats between ♂♂ in prime condition are violent and continuous until one of the challengers submits or retreats. Dominant ♂♂ mark themselves, squirting urine forwards onto their own necks and 'beard', rubbing necks and horns on their own faeces. In this way they reinforce their scent in their own home area, presumably advertising their status within the herd.

The female hierarchical organization is strong, stable and based on age and body size. Rank order is expressed in feeding priority, the capacity to defend individual space, in superior exploitation of hiding places for offspring and in more effective defence of calves. The highest-ranking ♀♀ are the most aggressive; they threaten by suddenly lowering the head and neck, and folding back the ears. Head-butting, kicks and bites are frequent. Females are very vocal and groups on the move emit a chorus of frog-like croaking.

Kingdon (1997) reported that in the early dry season single ♂♂ successfully excluded other piebald ♂♂ from herds that can be in excess of 100 individuals. By Mar these ♂♂ were spaced out in a rather linear scatter along the margins of the swamps and there was much sexual activity that would seem to have attained a peak



Nile Lechwe *Kobus megaceros* adult male performing flehmen. The brow and area behind and below eye is white in adult male and serves to emphasize the typically swollen brow and rolling of eye at close quarters. Likewise mouth expressions are enhanced by white outline; ear movements are also advertised by white colour.

around Apr. Males exhibit flehmen and follow oestrous ♀♀ with great persistence, trying to isolate them from the herd. In courtship the ♂ puts his neck on the back of the ♀ and touches her belly or flanks with an upward strike of one of his forelegs (laufs Schlag). This behaviour induces her to accept mounting.

After parturition, captive mothers are observed eating the placenta, cleaning the calf and ingesting its urine and faeces, typical behaviour of all the 'hider' antelopes. Despite their capacity to walk immediately after birth, newborns remain hidden for nearly 30 days in secluded and shady places, and meet the mothers only for nursing. Their fawn pelage optimizes concealment. Outside their hiding places, calves are vulnerable to aggression from other members of the herd; mothers defend them and nudge them actively with the muzzle toward suitable hiding places. Sometimes they vocalize toward their offspring. During their second month, calves gradually join the herd and pass most of the time with calves of the same age. Kingdon (1997) observed young calves gathering for playful chases, circling and jumping about in the shallows.

Reproduction and Population Structure In the wild, the peak of births is reached in the early dry season (Nov–Dec), and calves are observed emerging from lying-up in the reeds in Feb (Kingdon 1997). In captivity, births are scattered throughout the year (Falchetti & Mostacci 1993, Bercovitch *et al.* 2009).

Studies of captive animals show that one calf is born per reproductive cycle, after a gestation period of approximately 33 weeks, and is suckled for 24–32 weeks (Falchetti & Mostacci 1993). Average interval between two births has been given as 47 weeks (Falchetti & Mostacci 1993) and 52 weeks (Bercovitch *et al.* 2009). Ovulation occurs one month after the previous birth. Sexual maturity and the age of first reproduction are reached at 20 months in ♂♂ and 19 months in ♀♀ (Falchetti & Mostacci 1993), although Bercovitch *et al.* (2009) reported the youngest ♀ to bear progeny was 466 days of age. The maximum number of reproductive events per ♀ is ~14 (Falchetti & Mostacci 1993, Bercovitch *et al.* 2009). In captivity, sex ratio at birth is roughly 1 : 1 (Falchetti & Mostacci 1993, Bercovitch *et al.* 2009). Sex and adult–young ratios in wild



Nile Lechwe *Kobus megaceros* adult male in pursuit. At a distance the white nape draws attention to the length of the horns.

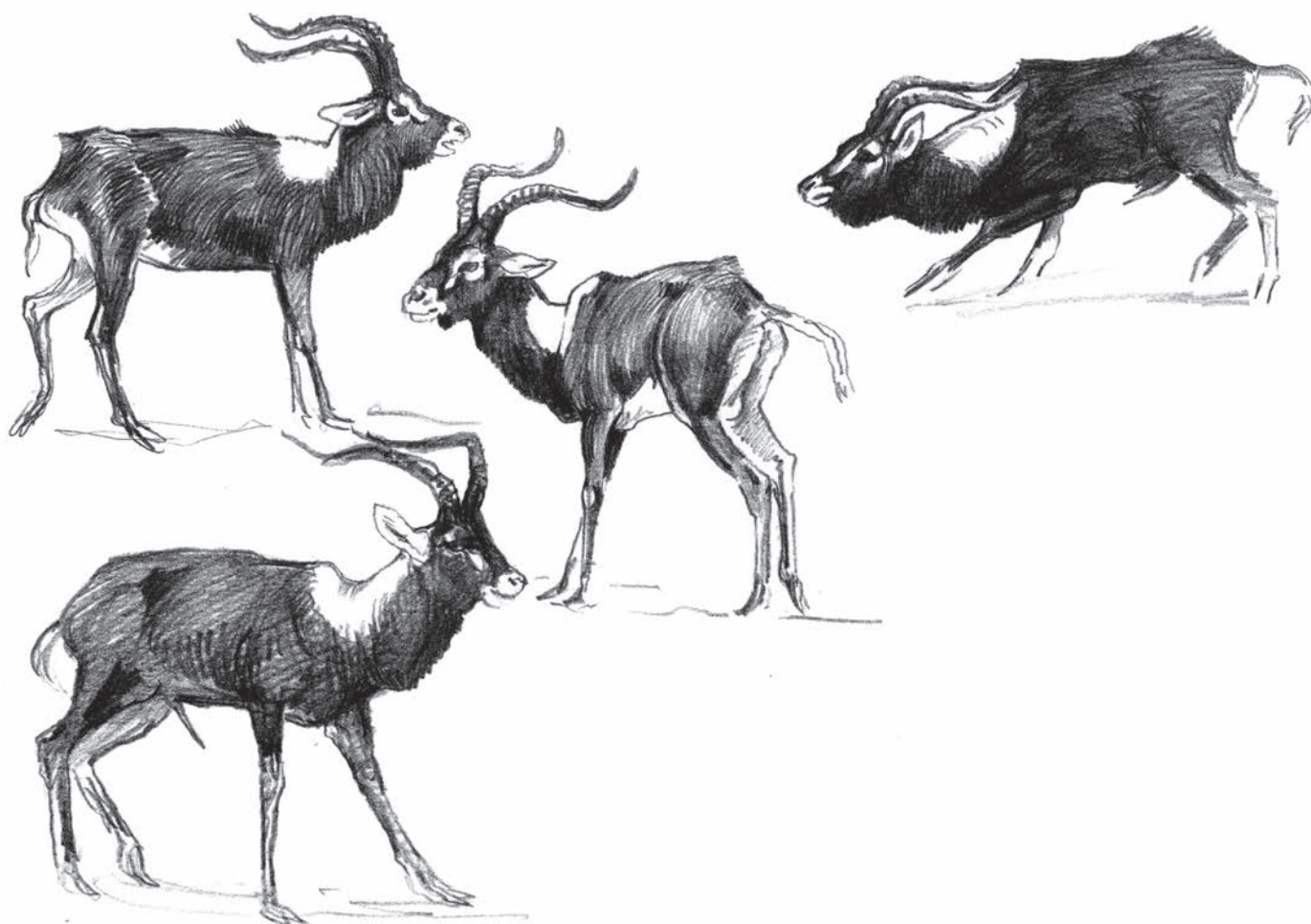
herds are known to be very variable, but have yet to be assessed. Studies in captivity have also shown that older female Nile Lechwe were more likely to bear sons than daughters, male calves weighed more than female calves, neonatal mortality was greater among ♂♂ than ♀♀, and neonatal mass was strongly correlated with maternal age (Bercovitch *et al.* 2009). The maximum longevity recorded in captivity is 21 years (Weigl 2005).

Predators, Parasites and Diseases Although there is an influx of predators such as Lions *Panthera leo* and Leopards *P. pardus* into the Sudd following the large herbivore migrations during the dry season, the Nile Lechwe is protected by the inaccessibility of the swamps; moreover, it is an excellent swimmer and, if disturbed, does not hesitate to enter even the deepest channels. Nile Crocodiles *Crocodylus niloticus* and African Rock Pythons *Python sebae* are known predators.

In captivity, Nile Lechwes have been subject to virus infections such as infective bovine rhinotracheitis, herpes virus 1 and to bacterial bovine tuberculosis (A. Croce & P. Alfonsi pers. comm.). Among the parasites recorded from two animals collected in the Sudd were *Oesophagostomum columbianum*, *Gigantocotyle symmeri*, *Carmynerius exoporus*, *Calicophoron phyllerouxi*, *Stephanopharynx compactus* and *Setaria bicornata*. *Haemonchus contortus* was recorded from the abomasum and intestine. All these parasites were common in other Sudd antelopes (Mefit-Babtie 1983). Of special interest was the presence of a fluke species resembling *Schistosoma leiperi*. Extracted from the mesenteric veins, this parasite was previously well known from Southern Lechwes in central Africa. In that region there has been epidemiological evidence of suppression of other schistosomes that are known to be damaging to humans and livestock. Infection with *S. leiperi* appeared to exclude *S. haematobium* and *S. mansoni* in humans and *S. matthei* in cattle (Pitchford 1976). Although domestic stock and other Sudd antelopes had substantial tick burdens, no tick species were found on Nile Lechwes (Mefit-Babtie 1983).

Conservation IUCN Category: Endangered A2a. CITES: Not listed.

Civil war, and the displacement and resettlement of people, have affected the Sudd region in various ways. Hunting by men armed with automatic weapons takes place without any effective control



Nile Lechwe *Kobus megaceros* adult male.

and the shooting of wild animals has reportedly increased, assisted by easy access to modern firearms. The construction of the long-proposed Jonglei Canal has been interrupted by civil war. If ever completed, it could reduce the extent of marshland and change local patterns of flooding. The impact on the Nile Lechwe and its habitat could be significant and certainly would be detrimental to both (Howell *et al.* 1988). Oil exploration and exploitation in the Sudd is a major and immediate threat to the wildlife of these wetlands and the Zeraf Reserve (Fay *et al.* 2007).

In the Sudan, populations of Nile Lechwes occur in three nominal game reserves: Zeraf G. R., extending over 9700 km² along the Bahr el Zeraf; Fanyikang G. R., north of the Bahr el Gazal, which separates them from Zeraf G. R.; and Shambe N. P. over 620 km², along the Bahr el Jebel. However, Nile Lechwes are known to move in and out of these nominally protected areas and most occur in areas that are shared seasonally with vast herds of cattle. In Ethiopia, they occur in Gambella N. P., which is yet to be officially gazetted.

An effective captive-breeding programme aimed at enhancing and conserving viable and self-sustaining populations could help to ensure the survival of viable populations outside their potentially vulnerable natural home-range, but the gene pool is small (320 individuals as of 2005) and problems with inbreeding have been reported (Falchetti

& Mostacci 1993, 1995).

Measurements

Kobus megaceros

HB (♂ ♂): 1600–1800 mm

HB (♀ ♀): 1300–1700 mm

T (♂ ♂): 500 mm

T (♀ ♀): 450 mm

Sh. ht (♂ ♂): 1000–1050 mm

Sh. ht (♀ ♀): 800–850 mm

WT (♂ ♂): 90.0–120.0 kg

WT (♀ ♀): 60.0–90.0 kg

Sudan (Haltenorth & Diller 1980, Kingdon 1997)

Maximum recorded horn length is 87.0 cm for a pair of horns from Yirol, Sudan (Rowland Ward)

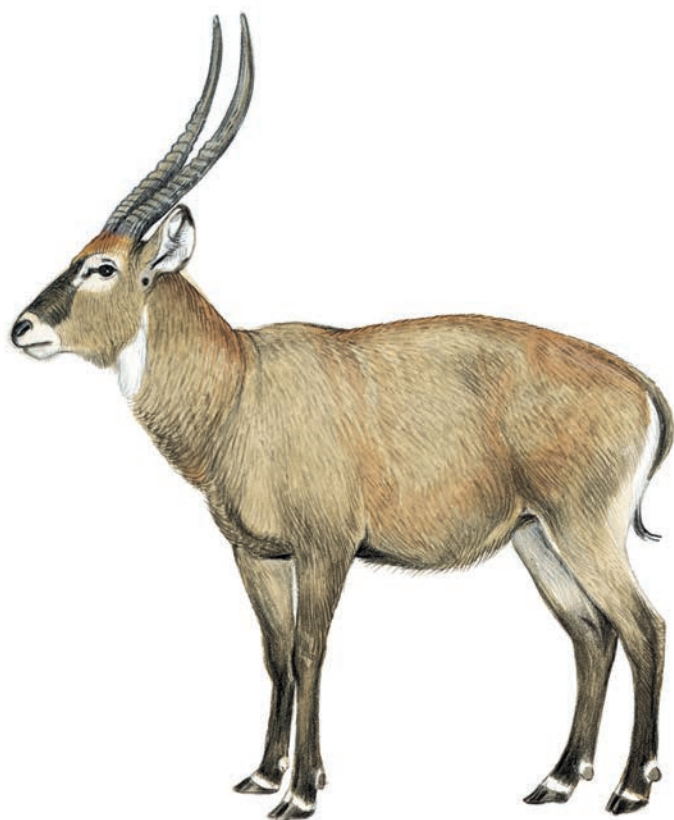
Key References Falchetti 1997, 1998; Falchetti & Mostacci 1993; Falchetti *et al.* 1994; Kingdon 1982, 1997; Mefit-Babtie 1983.

Elisabetta Falchetti & Jonathan Kingdon

Kobus ellipsiprymnus WATERBUCK

Fr. Cobe onctueux; Ger. Wasserbock

Kobus ellipsiprymnus (Ogilby, 1833). Proc. Zool. Soc. Lond. 1833: 47. 'about twenty-five days' journey north of the Orange River between Latakoo and the western coast of Africa'. Since restricted to Gaborone, Botswana, the top reaches of the Ngotwane R.; see Smithers (1971: 233) and Grubb (1999: 25).



Waterbuck *Kobus ellipsiprymnus*.

Taxonomy The Waterbuck is here considered a putative species with two subspecies, Common *K. ellipsiprymnus ellipsiprymnus* and Defassa *K. ellipsiprymnus defassa*. The latter was originally described as a full species by Rüppell (1835), but the two are generally regarded as conspecific (Grubb 1993c, 2005); Ansell (1972) treated these as two distinct superspecies groups, with four subspecies in his *ellipsiprymnus* group and nine in his *defassa* group. Each has a different chromosome number, $2n = 50-52$ ($FN = 61-62$) in *K. e. ellipsiprymnus* and $2n = 53-54$ ($FN = 62$) in *K. e. defassa*, as well as differing Y chromosomes: in Common, the X chromosome is a large metacentric and the Y a small acrocentric, whereas in Defassa the Y is a small submetacentric (Kingswood *et al.* 1998b, 2000). Overlapping is recorded in at least three East African localities, apparently due to allopatric hybridization, zones of intermediate pattern remaining narrow possibly due to reduced fertility of hybrids. DNA analysis revealed that hybrid individuals from Nairobi N. P. (Kenya) have only Common mitochondrial haplotypes, whereas both Defassa and Common haplotypes are found in the Samburu N. P. (Kenya) population, suggesting eastward expansion of Defassa (Lorenzen *et al.* 2006b). Spinage (1982) suggests separation resulting from the last Rift Valley arid phase sometime after 20,000–12,000 BP. The

work of Lorenzen *et al.* (2006b) suggests Defassa and Common were restricted to west and southern African refuges, respectively, and subsequent dispersal northwards of Common from a southern Africa locus could have resulted in contact between previously allopatric groups. Some 80 races described on pelage colour and horn length have been limited to five by morphometric analysis of horn shape by Spinage (1982), as differences in colour and markings can be found within a single population, but genetic variation is insufficient to substantiate races.

The study of Lorenzen *et al.* (2006b), based on variation in 478 nucleotides of the mitochondrial DNA control region and 14 polymorphic microsatellite loci, showed a high degree of genetic differentiation between the subspecies and strongly confirmed hybridization in Kenya's Nairobi N. P. population (which shows an intermediate rump pattern). The data suggest admixture was a recent event, their mitochondrial DNA is not completely separated into two distinct clusters, but chromosomal differences could hinder gene flow between the species providing an emerging reproductive barrier. Isolation by distance was not statistically supported within subspecies, or between all the sampled populations. A population of Common Waterbucks at Matetsi Safari Area in the extreme west of Zimbabwe just south of the Victoria Falls had exclusively private haplotypes and was genetically further apart from East African Common populations than it was from Defassa. Whereas one cannot discount differences in sample size influencing the results, or the Common having been through a population bottleneck, which would decrease its diversity, genetic distances within Defassa were markedly lower than between Defassa and Common, while Common was shown to have a higher level of genetic drift in the period between the original split and the hybridization event, confirming an originally smaller population size of Common. Since hybridization, a population at Samburu N. P. in Kenya and the Nairobi N. P. population have experienced about a 20- to 90-fold increase in drift compared with that of Common and Defassa. The estimated level of genetic input from Common to the Samburu N. P. and Nairobi N. P. populations was 0.58% and 0.32%, respectively, the Nairobi N. P. population being grouped genetically mid-way between Defassa and Common. Although phenotypically Common, the Samburu N. P. population had a high maternal Defassa contribution of 42%. The genetic analysis indicates that hybridization in the Nairobi N. P. and Samburu N. P. populations is very recent, perhaps within the past few centuries, and perhaps is still ongoing. The genetic distance between the Tsavo N. P. and Matetsi Safari Area Common populations is markedly higher than that between the Tsavo N. P. and the hybrid populations. This could suggest introgression into Tsavo N. P., which would have to be historic as there are no Defassa Waterbuck within several hundred kilometres today. The alternative would be that the variable rump patterns identified here (Spinage 1982) were due to natural variability, but such variability has not been identified elsewhere.

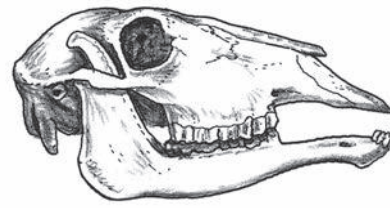
That all *Kobus* species are able to hybridize in captivity (see Gray 1972) suggests a recent radiation of the entire genus. A recent phylogenetic analysis (Birungi & Arctander 2001) based on complete mitochondrial cytochrome *b* sequences places the Waterbuck within the Reduncini as a derived paedomorph reduncine, also confirming the subspecies differentiation between Defassa and Common Waterbucks, but identifies them as a sister clade to the Kob *Kobus kob* and Puku *Kobus vardonii*, while the Southern Lechwe *Kobus leche* forms a separate phyletic branch. The Waterbuck is thus supported as a plesiomorph relative to other *Kobus* species. Little indicates the ancestry of the Waterbuck other than that the species is considered to derive from the lower Pleistocene *K. sigmoidalis* from Olduvai 5 mya (Gentry 1978).

Synonyms: *abyssinica*, *adolffriderici*, *albertensis*, *angusticeps*, *annectens*, *avellanifrons*, *breviceps*, *canescens*, *cottoni*, *crawshayi*, *defassa*, *dianae*, *ellipsiprymnos*, *frommi*, *fulvifrons*, *griseotinctus*, *harnieri*, *hawashensis*, *kondensis*, *kulu*, *kuru*, *ladoensis*, *lipuwa*, *matschiei*, *muenzneri*, *nzoiae*, *pallidus*, *penricei*, *powelli*, *raineyi*, *schubotzi*, *senegalensis*, *singsing*, *thikae*, *tjaederi*, *togoensis*, *tshadensis*, *ugandae*, *unctuosus*, *uwendensis*. Chromosome number: see above.

Description One of the heaviest antelopes, and largest of the genus *Kobus*, the two subspecies are distinguished by the distinctive patterning on the rump. Common Waterbucks have a white ellipse on the rump, whereas Defassa Waterbucks are all white. Intermediates exhibit all degrees. Gorget, muzzle, eye surround and inside ear are white. Large ears are tipped black and forehead area tends to black. Pelage shaggy in appearance, especially on the neck, but not dense, generally russet-coloured in Defassa, and grizzled tending to grizzled light grey in Common. Belly is greyish, lower legs shading to black with short white spats. A pale phase once existed in the region of the Lorian Swamp and parts of the Uaso Nyiro, Kenya; and white forms are occasionally reported, but not true albinos. Philtrum is black and hairless. Waterbucks are much heavier in the forequarters than many other antelopes, and the long neck has skin up to 2.5 cm thick in the ♂. Neck girth relates to weight of the long horns, hence hindleg weight is not a good indicator of body weight as it is in other antelopes studied. False hooves are large and conspicuous. Tail, reaching almost to the hocks, terminates in a black tassel. Females are 20% lighter in weight. There are no compound odoriferous glands. A very dark appearance is due to an oily musky skin secretion. This makes the flesh very distasteful to most palates if contaminated by it.

Males bear sharply pointed, long, inwardly curving horns, ridged on the anterior face, first appearing at about eight months and growing at some 16 cm per year to age five, with growth then slowing abruptly to approach an asymptotic level at six years continuing to old age with wear at the tips equalling growth.

Skull is massive, relatively long with large lachrymal vacuities, large auditory bullae and the premaxillae reaching to the long nasal bones. Skull of ♂ is 6% longer than ♀. Adult ♀ has paired rugosities on the frontal bones that bear the horns in the ♂. Teeth are hypsolenodont, arranged in a similar manner to those in *Redunca*. Replacement of deciduous dentition takes place between 3 and 3.5 years. Dental abnormalities are rare, Colyer (1936) recorded only three cases in 57 specimens: one rotated mandibular P₄ and a left and right rotated maxillary P₄. C. Spinage (pers. obs.) observed one left



Lateral view of skull of female Waterbuck *Kobus ellipsiprymnus*.

maxillary rotated P₄ in 46 animals from Akagera N. P., Rwanda, and no abnormalities in 164 animals from W Uganda. Foley & Atkinson (1984) described a type of uneven and excessive tooth wear affecting 50% of Defassa Waterbucks of all ages in Lake Nakuru N. P., Kenya, predominantly affecting P₄ and the molars. Miles & Grigson (1990) suggested the type of wear could be due to an inherited regular pattern of difference in mineralization between individual teeth in the dentitions, perhaps, as Foley & Atkinson (1984) suggest, caused by overcrowding and inbreeding. Kisia *et al.* (2002) demonstrated abnormal bone mineralization due to soil mineral imbalances, undoubtedly also reflected in the teeth.

Geographic Variation

K. e. defassa (Defassa Waterbuck): West, north-east and central Africa.

Lacks the white crescent that characterizes Common subspecies, having an all-white rump. Five Defassa races are recognized by Spinage (1982) according to width between the horn tips in the ♂, which reflects the 'bow' of the horns: West Africa (*unctuosus*), ranging from Senegal and Gambia eastwards to the Semliki Valley and southwards north of the Congo rainforest and the Congo R. to the west coast; Uganda (*ugandae*), from the foot of the Abyssinian highlands through S Sudan, the Bahr el Ghazal basin and southwards through Uganda to W Tanzania; Rwenzori (*avellanifrons*), from the Western Rift from the southern end of the Rwenzori Mts to south of L. Edward; Rhodesia (*crawshayi*), in Zambia and Zimbabwe north of the Zambesi R.; and Angola (*penricei*), from Congo and S Gabon through Angola to the upper Okavango and the eastern end of the Caprivi Strip. Separation on coat colour and pattern is discounted as this is variable within single populations. Due to overlapping measurements, the width between the tips of the horns of each race following a curve of normal distribution, identification of races depends upon the statistical comparison of samples and their geographical origins.

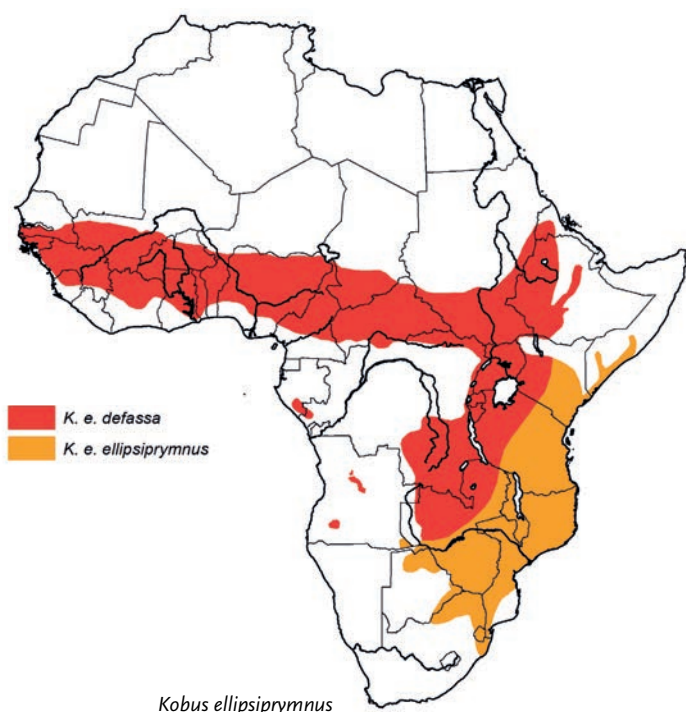
K. e. ellipsiprymnus (Common Waterbuck): south-east Africa, broadly east of the Eastern Rift Valley. Most diagnostic feature is the white ellipse on the rump. No races of the Common subspecies are recognized by Spinage (1982).

Similar Species

Kobus kob. Broadly sympatric south of the Sahel and west of the Rift Valley. Smaller with a bright gold fulvous pelage; male horns short but thick and S-shaped. Inhabits open plains.

K. vardonii. Sympatric across much of the range. Smaller, more similar in size and shape to the Kob. Tends to inhabit the fringes of plains more than open plains.

K. leche. Red Lechwe sympatric, principally in the Busanga Plains of Zambia and the Okavango Delta of Botswana. Smaller, bright



chestnut to blackish pelage with contrasting white underparts; male horns long and lyre-shaped. Very aquatic in habits.

Distribution Endemic to Africa, ranging widely throughout most of sub-Saharan Africa in savanna woodlands and forest–savanna mosaics, although their current distribution is fragmented, having been eliminated from many parts of their former range.

Current Distribution The Waterbuck has been eliminated from many parts within its former range, but still ranges widely. Defassa is found in well-watered savanna west of the Western Rift Valley and south of the Sahel from Eritrea in the east to Guinea-Bissau in the west; its most northerly point of distribution is in S Mali, formerly in Boucle du Baoulé N. P. but not recently confirmed there although still present in Fina Faunal Reserve, 75 km to the south-east (B. Chardonnet pers. comm.). A population still exists in Senegal in Niokolo-Koba N. P. 450 km to the west and 75–125 km south of the most northerly known distribution (A. Galat-Luong & G. Galat pers. comm.). Defassa Waterbucks range eastwards reaching west of the Western Rift Valley and east of the Congo Basin forest, and then spreading west below the basin's southern limit through the western and northern plateaux of Zambia into Angola. Another arm extends north, west of the Congo Basin to the savannas of SW Gabon. East of the Eastern Rift Valley, Defassa is replaced by Common, which extends southwards to just below 28° in Hluhluwe-iMfolozi N. P., KwaZulu–Natal, and west, south of the escarpment in Zambia, and north of the Kalahari, to the Caprivi in Namibia.

Of the 42 African states south of the Sahara, the Defassa Waterbuck occurs in 28 and the Common in 11. Defassa became extinct in Gambia by around 1990 (although they may still occur as vagrants from Niokolo-Koba N. P. in Senegal; see Grubb *et al.* 1998, Jallow *et al.* 2004) and Common is believed extinct in Ethiopia since 1988 (although Defassa remains).

Habitat Waterbucks are a water-dependent species partial to scattered woodland and bush where mean annual rainfall is 400–1600 mm; Defassa generally is limited to areas receiving at least 750 mm annual rainfall, whereas Common persists in drier regimes. Waterbucks are most numerous in fairly humid habitats, with an optimum temperature range of 13–37°C for Defassa. In southern Africa, where mean surface temperature falls to 12°C, Common withstands low winter night temperatures that fall to freezing. Highest densities are in lakeside regions or in well-watered valleys where there is good quality grass. Waterbucks are always limited by distance from permanent water in the dry season; in the wet season female groups are more dispersed and range farther. They have been recorded with certainty to at least 2100 m in Ethiopia, and perhaps to 3000 m (Yalden *et al.* 1996).

Feeding and daily behaviour patterns apparently vary according to latitude and climate. In W Uganda, completely open grassland was not the most favoured habitat, grassland with moderate nearby cover being preferred. In Lake Nakuru N. P., where Lions *Panthera leo* are absent, male preference changed with increasing age from open woodland to dense shrub, open shrub and finally open grassland. Adult ♀♀ were more often in dense shrub than were subadults but all favoured open grassland during rainfall (Wirtz & Kaiser 1988). In other areas the preference is predominantly for riverine woodland, and Hirst (1975) in Mpumalanga, South Africa, found no preference of the Common for open grassland.

Abundance Undisturbed densities range from 0.23/km² (Kruger N. P., South Africa) (Pienaar 1966) to >30 (Lake Nakuru N. P.) (Kutilek 1974), but corrected density estimates from recent aerial surveys, assuming 46% is detected (East 1999), range from 0.1–0.3/km² in many areas where the species is regarded as reasonably common to 0.4–1.8/km² in a few higher density areas. Ground surveys where the species is regarded as common have produced density estimates of the order of 0.4–1.5/km² (East 1999). A conservative corrected continent-wide estimate of numbers based mainly upon aerial surveys is 95,000 Defassa and 105,000 Common (East 1999).

Adaptations Only Defassa physiology has been studied in detail, and in view of the spatial separation between the subspecies and genetic differences, Common possibly exhibits a distinctive physiology, able to withstand lower, but not as high, temperature, and more arid conditions. Defassa is highly water-dependent, lacking almost any ability to conserve water, unable to withstand even short periods of dehydration in a hot environment. Unlike most mammals, Waterbucks do not reduce urine volume when water is restricted, reducing only faecal water, eating less food and digesting it more completely. Maintaining body temperature almost constant at 39.2°C, it does not store heat, and does not drink excess water when available, always forming a nearly maximally concentrated urine. Its high protein intake (see below) results in a high production of urea demanding a high water intake to flush it out. A higher than normal energy intake is required to maintain thermoneutrality at low temperatures, but in southern Africa the cold season is a time of low vegetative quality, which could be the cause of reported high winter mortality.

Measurements indicate the Common Waterbuck from South Africa is possibly larger than the Defassa from W Uganda, which would accord with Bergmann's Rule and the colder seasons experienced in

South Africa or the largest races being found in areas colonized last by the population concerned, but there are insufficient accurate sampling records to confirm an increase in body mass. Also possibly shorter ear and tail lengths conform to Allen's Rule and the colder climate. Although horn length appears greater, the sample is probably biased in favour of the longest horns, compared with the random sampling of adults in W Uganda. Swayne (1895) considered that the Waterbuck in Somalia had shorter horns than Waterbucks further south. Smaller size of northern Waterbucks is tentatively confirmed by considering the greatest length of skull, which in a single Defassa ♂ from Setit (Eritrea) was 7.25% shorter than the mean value of a sample from W Uganda (n = 19). The greatest skull length of Common ♂♂ from Somalia (n = 8) was 9.4–12.7% shorter than two Kenya specimens, and 11.6% shorter than the sample from South Africa (n = 5). Greatest skull length of the ♀ (n = 3) was 12% shorter than one specimen from Kenya and specimens from South Africa (n = 3).

The Waterbuck perhaps owes its success to being a generalist able to exploit the range of habitats to which its congeners are specifically adapted, albeit only to a varying degree, not as aquatic as the Southern Lechwe (although its prominent false hooves allow it to travel over marshy ground), nor as independent of water as the Kob. The ♂ also adapts its behaviour to lessen excessive strife, e.g. to permit other adult ♂♂ access to water where this is in another's territory, and the resource-defence system of the territorial ♂ does not demand a reduction in feeding time. The species does suffer competition in lacustrine or riverine shorelines from Common Hippopotamus *Hippopotamus amphibius*, and in open grassland possibly from herding grazing species where these are numerous. Despite their name, Waterbucks do not spend much time in water, although in southern Africa they sometimes stand belly-deep grazing aquatic emergents, but never bathe, only taking to water to escape predators.

Foraging and Food Waterbucks are classified as grazers according to the classification of Cerling *et al.* (2003), taking 70–95% grass. Studies involving stable carbon isotopes from Waterbuck samples from both East and southern Africa revealed grass dominating in the diet, 92% (Cerling *et al.* 2003), and 97% and 100% (Sponheimer *et al.* 2003b), but these percentages should be viewed as $\pm 15\%$ (M. Sponheimer pers. comm.). In Kruger N. P., isotopic analysis of Waterbuck faeces suggests seasonal differences in diet, but at the same time supports the idea that Waterbucks in that region are, on average, fairly dedicated grazers. With the exception of the late dry and early wet season, where there is evidence for over 20% browsing, the Waterbuck samples were nearly identical to those of Common Wildebeest *Connochaetus taurinus* (M. Sponheimer pers. comm.). Carbon isotope analyses of teeth from eight male and 22 female Defassa Waterbucks collected in Queen Elizabeth N. P. in Uganda 1964–67 (Copeland *et al.* 2008) confirmed that the species consumed on average 98% C₄ grass with some C₃ browse, indistinguishable from most other grazers studied, including the African Buffalo *Syncerus caffer*; however, variation was as much as 28% between individuals.

In taking some browse, Defassa Waterbucks are not opportunistic browsers, browse being essential to boost their protein intake. The empirical studies of Taylor *et al.* (1969) demonstrated that Defassa Waterbucks require a protein diet four times higher than that of other grazing bovids studied (domesticated Hereford steer, African Buffalo *Syncerus caffer* and Beisa Oryx *Oryx beisa*), necessitating

feeding them lucerne in place of hay; however, Cerling *et al.* (2003) show both the African Buffalo and oryx taking much more browse than the Waterbuck. From observations of continuous 12-hour periods, Spinage (1982) found that an adult ♂ in the dry season spent 11.1% of feeding time on browse, and at night 20.7%, giving an estimated total for the 24 hours of 31.8%. In the wet season, no time was spent browsing either during the day or at night. The adult ♀ spent only 10.2% of time in the day browsing, so assuming the same increase in rate of feeding at night, she would spend 19% of time browsing, which added to the day's total would approximate to 29.2%. It is questionable whether a Waterbuck could survive the dry season on 97% or 100% graze, or even on 92% graze, and the similarity to Common Wildebeest feeding found in Kruger N. P. is puzzling. However, where stable carbon isotope sampling is from P4 tooth enamel, the food intake refers only to a period between 10 and 25 months in the animal's life when the enamel is laid down prior to tooth eruption, and the animal is subadult, which may reflect anabolic feeding, the diet changing to one of maintenance when the animal is adult (or the Waterbuck may be a structurally very selective feeder).

Waterbucks eat both medium-height and pyrophilous protein-rich short grasses with a high ratio of leaf to stem (Chloridae, Paniceae and Sporobolidae), taking the greatest range of species in the wet season. Variability in choice of grass species is dependent upon location rather than frequency of occurrence. In W Uganda, where 20 different grass species were taken, *Sporobolus pyramidalis* was favoured in some areas, *Themeda triandra* in others (Field 1972). In one area of South Africa, Common Waterbucks favoured *Heteropogon contortus* (third choice by Defassa in W Uganda), and the creeping, protein-rich *Cynodon dactylon* was also highly favoured, compared with only 50% by Defassa (Wilson & Hirst 1977). Annuals seem to be avoided. In southern Africa, feeding on *Typha* and *Phragmites* aquatic emergents has been observed (Child & von Richter 1969, Herbert 1972, Tomlinson 1980a, 1981), but riparian topography and drought conditions could determine such behaviour, which was not witnessed in W Uganda. Dry season protein deficiency in graze was supplemented in W Uganda by browsing, especially *Capparis tomentosa*, particularly the heavily scented inflorescences, and *Acacia sieberiana*.

Defassa ♀♀ in W Uganda spend some 64% of daylight hours feeding in the dry season, ♂♂ 43.5%, with only slightly more time in the wet. In ♂♂ feeding at night falls to some 38% of time, the difference being spent in ruminating. Only some four minutes are spent in deep sleep. Anything from as little as 3% to as much as 18% of time is spent in resting and light dozing, with the longer times in the wet season. Tomlinson (1980a) in Zimbabwe recorded almost identical percentages of feeding time for ♂♂, but diurnal feeding of ♀♀ in the hot dry season was 35%. Wirtz & Oldekop (1991) in Lake Nakuru N. P. recorded only 27% of time spent by adult ♂♂ in feeding, and 40% for ♀♀. But the results are not comparable as a grazing animal moving forward to the next bite was recorded as 'walking'. If anything, they show that the animal moves about more when feeding, confirmed by three times as much time occupied in 'walking and other activities' in W Uganda (21% compared with 7%). They also show ♀♀ spent more time feeding than ♂♂, 32.5% more compared with 29% in Uganda. Only 1.1% of time was spent in browsing but the seasons of observation were excessively wet, perhaps leading to more abundant food requiring less searching time.

Oxygen isotope ratios from the teeth of subadult ♀♀ in Queen Elizabeth N. P., which reflects the composition of drinking water and water in plant foods, showed greater variability than did those of subadult ♂♂, which may be a reflection of larger home-ranges (Copeland *et al.* 2008).

Social and Reproductive Behaviour Females are sedentary with overlapping home-ranges of 200–600 ha in W Uganda. Within these ranges, sedentary and strongly territorial adult ♂♂ defend territories of from 4 to 146 ha depending upon population density, suitability of habitat regarding food resources and age of holder. As soon as horns begin to appear, subadult ♂♂ are chased from the dam's side by territorial ♂♂. Such ♂♂ associate in bachelor groups within the female home-ranges where they are tolerated by territorial ♂♂. Males indicate submissiveness by holding the head low, neck stretched out, horns directed backwards. Females respond with a similar submissive posture accompanied with jaw champing to signify rejection. Outside the equatorial regime, bachelors may be excluded from territories during part of the year. At extremely high (and probably unnatural) densities of 72–106/km² as in Lake Nakuru N. P., territory holders may tolerate adult satellite ♂♂, which also defend the territory, appearing to 'assist' the dominant territory holder (Wirtz 1981, 1982). Territories are marked by presence and the strong pungent odour. Dung is dropped randomly and it is unlikely it serves as a territorial marker.

Males are territorial for up to five years, the largest territories being occupied between occupier ages six and nine, when ♂♂ are in their prime. Territory seeking begins at the age of about five years and is usually always successful by age seven. Largest territories have the most female visits and ♀♀ stay from a few hours to three months. Although ♂♂ attempt to herd ♀♀ to prevent leaving, this is never successful. Males do not remain throughout life on the first territory obtained, but graduate to bigger ones, not enlarging an existing one, even when a neighbour is killed in combat. After nine years of age a ♂ is in decline and once over ten usually loses out to a younger ♂. Such

♂♂ do not rejoin bachelor groups, but continue a solitary existence in a small, undefended area (Spinage 1982).

When an adult ♂ is approached by another ♂ of subadult or adult age, it adopts a display attitude typical of the Bovidae, standing in lateral view with the neck arched stiffly, variously referred to as the 'lateral-present', 'present-threat' or 'proud-posture', tail held out stiffly in line with the body. When displaying strongly, the penis is extruded and the urethral process extended. If the other ♂ continues the approach, the horns are inclined stiffly towards him. He makes no attempt to look taller by raising his hackles as the ♀ does when alarmed. Horn size is not a mark of rank; those with the longest horns are often the most timid in conflict situations. If the approaching ♂ does not lower the head in submission then he is faced and the horns can be engaged. Tomlinson (1980b) studied the behavioural display of Common Waterbucks in Zimbabwe in detail, noting some differences with Defassa Waterbucks in Uganda, but lack of a behavioural observation in Defassa does not mean it does not occur.

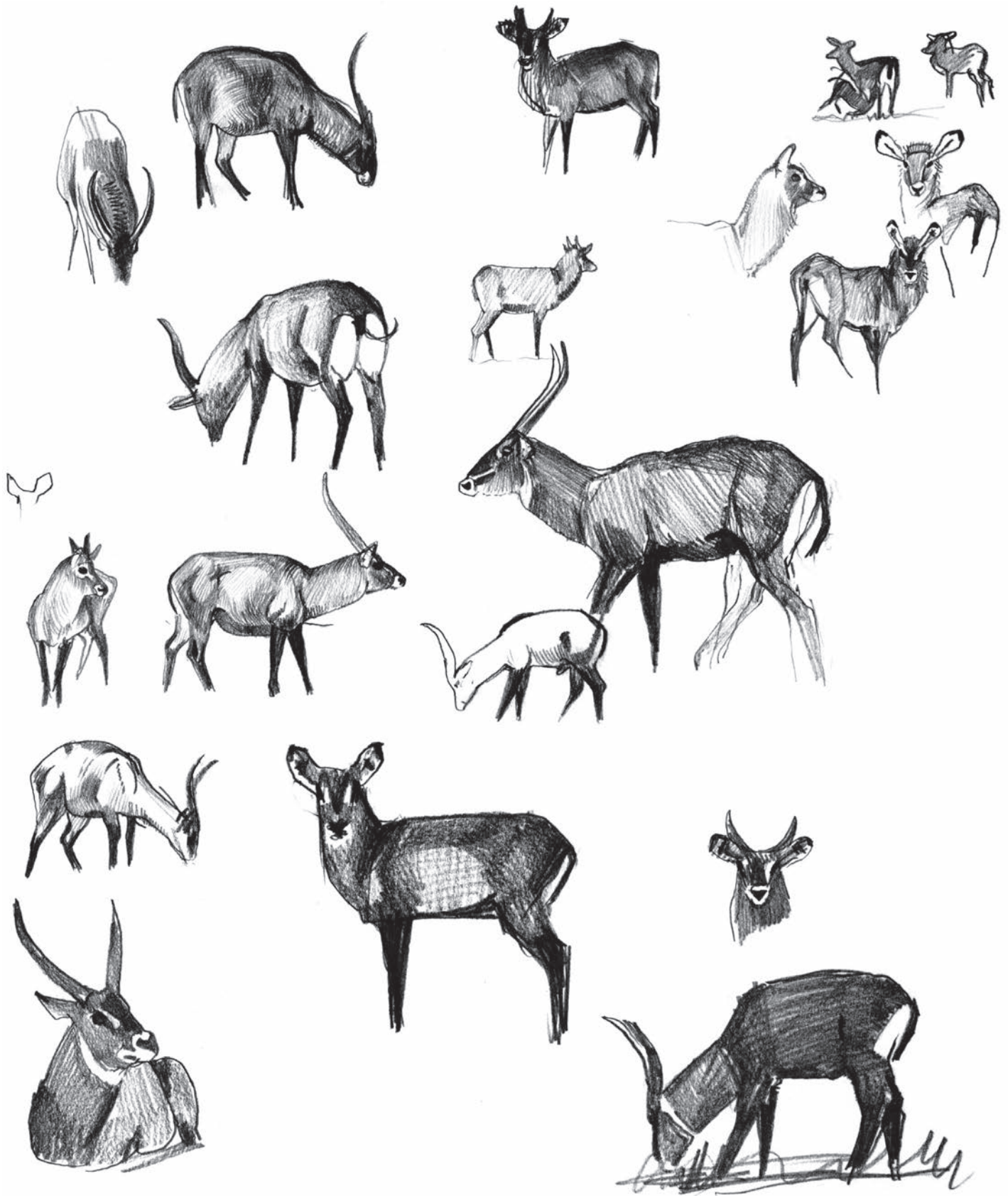
Territorial ♂♂ (and bachelor ♂♂ if they have the chance), examine chosen ♀♀ that enter the territory, nuzzling the hindquarters to induce tail-lifting and urination. Urine is sampled exhibiting typical lip-curling (flehmen). Females leave the group about two days prior to calving, returning to the same spot each time. Birth takes place early in the morning, the dam ingests the placenta and the calf stands and suckles after about 30 minutes. A 'hider', the calf remains concealed for three weeks, the mother remaining in the vicinity. She reacts to alarm bleats of her calf by attempting to chase off intruders using head-butts. After parturition, territory holders follow the ♀ closely until she comes into oestrus again 21 days later, when she is willing to receive the ♂. Males play no part in defence of the calf. Producing a concentrated milk, the dam visits the calf once during the day for suckling, which takes 10 min or more. The calf plays during the visit of an hour or so, scampering around the dam. When she walks off it hides itself. In the early stages the mother licks the calf's perianal region to induce defecation, which she ingests to remove traces of the calf's presence. The calf's scent does not develop until about 14 weeks, but some scent is transferred from the dam at birth and during visits. Once the calf starts to walk about the dam leads it to a new hiding place and prompts the calf to follow her by holding the tail stiffly erect (Spinage 1982).

Some dams drive their female young away from their side. At the age of 18 months these ♀♀ form spinster groups, perhaps remaining in the group until four years of age, while others emigrate up to 30 km. These spinster groups undergo a phase of wandering and emigration, until individuals settle into a home-range when they first come into oestrus and are temporarily attended by a territorial ♂. Female dispersal is unusual among bovines. Female groups run to greet each other, but no mutual sniffing or bodily contact occurs. Groups are dynamic within the home-range, with numbers ranging from one to 70, forming randomly. Mean group size in W Uganda was 5.3, but ♀♀ were most commonly found alone or in twos. Increases in group size are related to population density and were the same in wet and dry seasons in W Uganda's relatively benign habitat, where there was a tendency for larger groups to form in the morning (or during the night) that broke up later in the day. Juveniles making too close contact with adult ♀♀ are rebuffed vigorously (Spinage 1982).

The young ♂, becoming sexually mature at 3–4 years, is unable to obtain a territory and mate until 6–7 years. Before this he is too light



Waterbuck *Kobus ellipsiprymnus* detail of adult male exhibiting 'flehmen'.



Waterbuck *Kobus ellipsiprymnus*.

in weight to defeat a territory-holding adult. In the unnaturally high and restricted densities of Lake Nakuru N. P., Wirtz (1982) suggested dominant bachelor herd ♂♂ could be as successful as territory holders in the number of copulations achieved. Young ♂♂ join a 'home' bachelor group, which does not readily accept young ♂♂ from other areas. Bachelor groups are essentially random associations, their home-ranges of 30–340 ha being roughly co-incident with that of local ♀♀. Frequent sparring or dominance contests occur between bachelors of similar age and emigration, which can extend outside of the local territory mosaic, follows when there are too many of a similar older age group. Emigrants tend to form their own groups, but can sometimes join others. When old enough to quit the group the ♂ must fight a territory holder to obtain a place of his own and adopts different ruses, such as stationing himself where three territories meet, and running into another's territory if approached.

Waterbucks normally appear to be silent animals, but the dam calls her calf with low, penetrating bleats. Calves bleat when alarmed.

Reproduction and Population Structure Females first give birth at just under 2.5 years and can be reproductively active for ten years. Equatorial breeding takes place throughout the year, with most conceptions in May, Jun and Nov, producing births in Apr, May and Aug. There are conflicting reports whether distinct breeding seasons occur in the latitudes, but it appears calving peaks in the wet season (Spinage 1982).

A single calf is born after a gestation of 40 weeks (Heinroth 1908), weighing about 13.6 kg (Spinage 1982). Twins have been recorded, even triplets (Frechkop 1954), but such records are exceptional. Where breeding is continuous there is a calving interval of 325 days (Spinage 1982). Weaning takes place at about 40 weeks, and young ♀♀ are ready to conceive at 20 months. Mortality up to weaning is greater than 50% (Spinage 1982).

Recorded sex ratios range from 1 : 0.5 to 1 : 4.3 (Bourlière & Verschuren 1960, Foster & Kearney 1967, Hanks *et al.* 1969, Mentis 1970, Herbert 1972, Kutilek 1974, Elliott 1976, Wirtz 1978, Spinage 1982). They can live to 18 years in the wild (and 30 years in captivity; Weigl 2005), but mean life expectation at birth is four, with mean length of life in ♂♂ under five. During fights among adult ♂♂ it is not uncommon for deaths to occur from abdominal or chest puncture wounds; battles can last up to 30 min.

Predators, Parasites and Diseases Lions *Panthera leo* are the main natural predators on adults, but Leopards *P. pardus*, Cheetahs *Acinonyx jubatus*, African Wild Dogs *Lycaon pictus* and Nile Crocodiles *Crocodilus niloticus* are also known to take adults. Leopards and Spotted Hyenas *Crocuta crocuta* are important predators on calves.

Waterbucks are known to suffer ulcers (including perforated), pleuritic lungs probably resulting from lungworm infection, and kidney stones (Spinage 1982). Positive responses are reported for foot-and-mouth disease, bluetongue and bovine virus diarrhoea (Fay 1972) as well as for several mosquito-borne arboviruses: Group A (Sindbis), Group B (Yellow Fever, West Nile, Uganda S, Zika, Wesselbron) and ungrouped Zinga (Thal 1972), several of which are fatal to man. Deaths have been reported from anthrax (Pienaar 1967) and one positive brucellosis isolation was made in South Africa (Herbert 1972). They are relatively resistant to rinderpest virus (Carmichael 1938). Fairly heavy trypanosome infections of *Trypanosoma vivax* and

T. congolense–*T. brucei* are recorded (Wenyon 1926), although the vectors, tsetse flies *Glossina* spp., feed on Waterbucks least of all. Reactions to tick-borne protozoa *Theileria parva* (causing East Coast Fever in cattle), *Anaplasma marginale* (gall-sickness in cattle) and *Babesia bigemina* (redwater in cattle) have been identified (Fay 1972).

Internal parasites include tapeworms *Moniezia benedeti* (Spinage 1982) and *Stilesia hepatica* (Baer & Fain 1955), the liver-fluke *Fasciola gigantica* (Stunkard 1929) and stomach-flukes *Paramphistomum phillierouxi*, *P. microbothrium*, *Calicophoron calicophorum* and *Carymerius* sp. (Herbert 1972, Spinage 1982). Other helminths recorded include: *Linguatula nuttali* (Thal 1972), *Dictyocaulus* sp. (Zieger *et al.* 1998a), and *Haemonchus bedfordi*, *Cooperia yoshidai*, *C. hungi*, *C. fuelleborni*, *Impalalia tuberculata*, *Oesophagostomum columbianum* and *Parabronema* sp. (Boomker *et al.* 1986). In the faeces, larvae and eggs of the coccidian *Eimeria aubumensis*, the hookworm *Bunostomum trigonocephalum* and the whipworm *Trichiuris ovis* have been found (Elliott 1976). All appear superficially identical to those found in domestic animals, but could be host-specific. *Haemonchus* sp. in Common Wildebeest, for example, does not infect bovine calves. Boomker *et al.* (1986) noted cross-infection among antelopes of a number of helminths. Perhaps a first stage to determining host specificity would be DNA analyses.

A total of 27 species of ixodid ticks has been found on Waterbucks, and a healthy animal has been estimated to be carrying more than 4000 ticks mainly in their nymph and larval stages (the commonest being *Amblyomma cohaerens* and *Rhipicephalus tricuspis*) (Spinage 1982). Impaired calf survival due to apparently high, but unquantified, levels of *R. appendiculatus* infestation in the iMfolozi G. R., South Africa, has not been proved (Melton 1987). The large numbers of ticks suggest the Waterbuck's prolific oily secretion is not a deterrent and unlike many other ungulates, Waterbucks only rarely tolerate oxpeckers *Buphagus* spp. The Biting Louse *Damalinea (Bovicola) hilli* is not uncommon, while in W Uganda the ear mite *Railletia hopkinsi* causes considerable discomfort, large, scab-covered swellings under the ears frequently resulting from repeated scratching. Bloodsucking flies *Siphona minuta* and *S. latifrons* were often seen around the head in W Uganda. The ectoparasitic hippoboscid fly *Hippobosca hirsuta* also occurs, particularly in the long hair on the neck (Spinage 1982).

Conservation IUCN Category: Least Concern (*K. e. defassa* – Near Threatened; *K. e. ellipsiprymnus* – Least Concern). CITES: Not listed.

Waterbucks are particularly susceptible to poaching because of their sedentary nature and fondness for cultivation. Of the 36 countries in which Waterbucks are known to occur, the population trend is considered to be decreasing in half (with the status in four not known); only in South Africa is the species regarded as 'increasing' (East 1999).

About 60% of Defassa Waterbucks occur in protected areas, with important populations including: Niokolo-Koba N. P. (Senegal), Comoé N. P. (Côte d'Ivoire), the complex of 'W' N. P. (quite rare in Niger), Arly-Singou Faunal Reserve and Pendjari N. P. (Burkina Faso, Benin, Niger), Mole N. P. (Ghana), Gashaka-Gumti N. P. (Nigeria), Zakouma N. P. (Chad), Awash N. P. and Omo-Mago-Murale (Ethiopia), Murchison Falls N. P. and Queen Elizabeth N. P. (Uganda), Serengeti N. P. and Katavi N. P. (Tanzania) and Kafue N. P. (Zambia). Of the 105,000 Common Waterbucks estimated to survive in Africa, more than 50% are in protected areas, with the particular strongholds including: Tsavo N. P. and Lake Nakuru N. P. (Kenya), Tarangire N. P. and Selous G. R.–Mikumi N. P. (Tanzania), North and South Luangwa

N. P. (Zambia) and Kruger N. P. and Hluhluwe-iMfolozi G. R. (South Africa) (East 1999, Chardonnet & Chardonnet 2004).

Although the species is relatively well represented in protected areas, population declines have been reported even within protected areas: 59% between 1977 and 1995 in Queen Elizabeth N. P., and 67% between 1967 and 1995 in Murchison Falls N. P. (von Richter *et al.* 1997); 91% between 1979 and 1993 in Lake Nakuru N. P. (Butynski *et al.* 1997a), the latter largely due to natural mortality; and 75% between 1978 and 1998 in Comoe N. P. (Fischer & Linsenmair 2001a). Discounting Lake Nakuru N. P., this represents an average loss of 3.2% per year. The disappearance of Waterbucks from the flood-plain areas around Waza N. P. in N Cameroon, where they used to occur only in small numbers, can be attributed to the construction of the upstream Maga Dam in 1979 and subsequent low rainfall. Its subsequent return to the area may be associated with the re-flooding that took place from 1994 onwards (Scholte 2005, Scholte *et al.* 2007). In 1997, the 300 km² Mutara reserve, and northern and western sections of Rwanda's Akagera N. P., were degazetted; fortunately, recent surveys suggest that numbers of Waterbuck in the new Park (estimated at 1640) have recovered to a level higher than that reported for the period 1997/98 (Apio & Wronski 2011).

Measurements

Kobus ellipsiprymnus

K. e. ellipsiprymnus

HB (♂): 2080 mm, n = 1

HB (♀): 2050 mm, n = 1

T (♂): 360 mm, n = 1

T (♀): 330 mm, n = 1

HF c.u. (♂): 460 mm, n = 1

HF c.u. (♀): 460 mm, n = 1

E (♂): 190 mm, n = 1

E (♀): 160 mm, n = 1

Sh. ht (♂): 1290 mm, n = 1

Sh. ht (♀): 1220 mm, n = 1

WT (♂♂): 276 (224–309) kg, n = 10

Southern Africa (Roberts 1951). The weights of ♂♂ given in Roberts (1951) are suspiciously high but there are no other records for South Africa. Elsewhere, Wilson (1968) recorded weights of 238 (range 223–253) kg for ♂♂ (n = 9) and 169 (range 163–191) kg for ♀♀ (n = 4) from E Zambia. Other mean ♀ weights recorded are 188 (range 186–193) kg (n = 4) (Hitchins 1968) and 170 (range 159–181) kg (Herbert 1972)

Maximum recorded horn length for *K. e. ellipsiprymnus* is 99.7 cm for a pair of horns from Sand R., South Africa (Rowland Ward)

K. e. defassa

TL (♂♂): 2405 (2260–2630) mm, n = 7

TL (♀♀): 2269 (2245–2290) mm, n = 3

T (♂♂): 468 (445–530) mm, n = 7

T (♀♀): 402 (385–420) mm, n = 3

HF c.u. (♂♂): 525 (485–562) mm, n = 7

HF c.u. (♀♀): 509 (497–520) mm, n = 3

E (♂♂): 208 (200–215) mm, n = 7

E (♀♀): 199 (193–210) mm, n = 3

Sh. ht (♂♂): 1170 (1100–1240) mm, n = 7

Sh. ht (♀♀): 1110 (1060–1130) mm, n = 3

WT (♂♂): 226.6 (192.3–286.8) kg, n = 7

WT (♀♀): 175.4 (160.0–195.0) kg, n = 3

Serengeti N. P., Tanzania (Sachs 1967)

HB (♂♂): 2430 (1970–2690) mm, n = 31

HB (♀♀): 2210 (1870–2480) mm, n = 31

T (♂♂): 450 (350–550) mm, n = 31

T (♀♀): 400 (330–500) mm, n = 31

HF c.u. (♂♂): 530 (500–560) mm, n = 31

HF c.u. (♀♀): 510 (480–540) mm, n = 31

E (♂♂): 220 (200–240) mm, n = 31

E (♀♀): 210 (190–320) mm, n = 31

Sh. ht (♂♂): 1260 (1170–1360) mm, n = 31

Sh. ht (♀♀): 1180 (1070–1450) mm, n = 31

WT (♂♂): 236 (198–262) kg, n = 25

WT (♀♀): 186 (153–214) kg, n = 40

Queen Elizabeth N. P., W Uganda (Spinage 1982, C. A. Spinage pers. obs.)

Meinertzhagen (1938) gave a range of 222–272 kg for 21 ♂♂ from Kenya

Maximum recorded horn length for *K. defassa* is 99.7 cm for a pair of horns from Toru, Uganda (Rowland Ward)

Key References East 1999; Hirst 1975; Melton 1987; Spinage 1982; Tomlinson 1980a, 1980b, 1981; Wirtz 1981, 1982; Wirtz & Kaiser 1988; Wirtz & Oldekop 1991.

Clive A. Spinage



Rear views of female *K. e. ellipsiprymnus* (above right) and male *K. e. defassa* (left).

Tribe OREOTRAGINI

Klipspringer

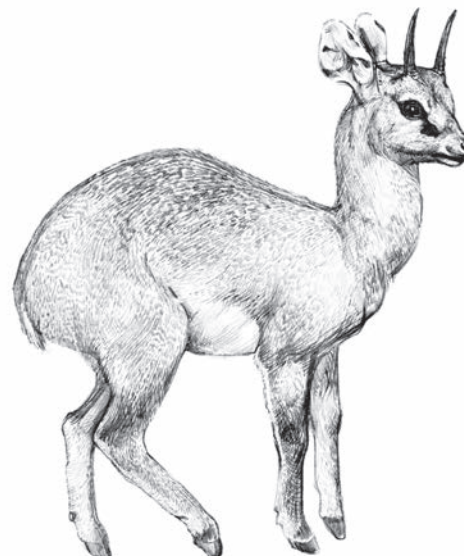
Oreotragini Pocock, 1910. Proc. Zool. Soc. Lond. 1910: 885.

The Klipspringer *Oreotragus oreotragus* has always been recognized as an anomalous and highly specialized species, but with the advent of molecular phylogeny the species has become recognized as the survivor of a unique type of basal antelope, deriving directly from the earliest Antilopinae and deserving recognition as the monospecific representative of a singular lineage, the Oreotragini.

The previous allocation of the Klipspringer to the former Neotragini 'waste-paper basket', grouped *Oreotragus* with other small antelopes such as the dwarf antelopes (genera *Neotragus* and *Nesotragus*) and grysboks, *Raphicerus* spp., which have also been shown to be ancient, but separate, basal lineages. However, *Oreotragus* is clearly distant from other neotragine genera; molecular data (Hassanin & Douzery 1999, Matthee & Robinson 1999a, Hassanin *et al.* 2012) even concluded that the Klipspringer was closest to duikers Cephalophini (but see Matthee & Davis 2001). Grubb (2005), who provisionally retained *Oreotragus* in a traditional Neotragini, remarked that *Oreotragus* was not shown to share any synapomorphies with *Cephalophus*, and that *Oreotragus* should perhaps be restored to tribe Oreotragini (originally erected by Haltenorth 1963), which is the approach followed here (and see Bronner *et al.* 2003).

Characteristics of the tribe include: the presence of horns in ♂♂ only, except in ♀♀ in parts of East Africa; the presence of false hooves; preorbital and preputial gland present, but no interdigital and inguinal glands; and the presence of preorbital fossae (to accommodate the preorbital glands) and an ethmoid fissure. Relative to other antelopes, there are some unique changes to the digital bones that enable the Klipspringer to move quickly over slippery rocky surfaces. A remarkable feature of the Klipspringer, unique amongst African antelopes, is the hollow nature of the hairs, which provides an insulating layer of air to deal with temperature extremes (Norton 1980). Of some fifteen named subspecies some might merit specific status, given the likelihood of ancient and prolonged isolation on widely separate massifs. However, Robinson *et al.* (1996) were unable to find any genetic differences in the regional specimens that they sampled.

Jonathan Kingdon



TOP: Klipspringer *Oreotragus oreotragus schillingsii*.

ABOVE: Klipspringer *Oreotragus oreotragus schillingsii* myology.

GENUS *Oreotragus*

Klipspringer

Oreotragus A. Smith, 1834. S. Afr. Quart. J. 2: 212.

Oreotragus is a monotypic genus including only the Klipspringer *O. oreotragus*, widely distributed in the savanna and arid zones in precipitous rocky habitats. *Oreotragus major*, recorded as late as 0.7 mya in South Africa (Vrba 1995), has recently been regarded as conspecific with the living species (Watson & Plug 1995).

Klipspringers are small antelopes (shoulder height about 60 cm, mass up to about 16 kg) adapted to a life among rocks and distinguished

from all other antelopes by stance on short hooves and short limbs, very short muzzle, and peculiar pelage. Unique aspects of its morphology have led to its placement here in a distinct tribe following Haltenorth (1963).

Peter Grubb

Oreotragus oreotragus KLIPSPRINGER

Fr. L'Oréotrague; Ger. Klippspringer

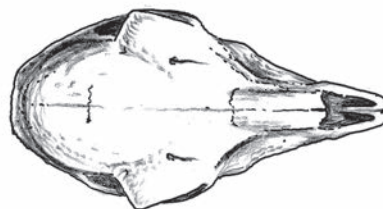
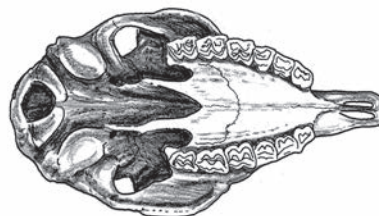
Oreotragus oreotragus (Zimmermann, 1783). Geogr. Gesch. Mensch. Vierf. Thiere 3: 269. 'Die Caffern'; now known to be South Africa, Western Cape Prov., Cape Dist., False Bay (Grubb 1999).



Klipspringer *Oreotragus oreotragus schillingsii*.

Taxonomy Ansell (1972) listed 11 subspecies from different parts of the geographic range, based mainly upon the treatment of Haltenorth (1963), the most notable being the isolated western race, *O. o. porteousi*, from Nigeria, and the East African *O. o. schillingsii*, the only subspecies in which ♀♀ are horned (Roosevelt & Heller 1915, Kingdon 1982). We provisionally list these subspecies here, noting that Kingdon (1997) reduced the list to seven subspecies without comment, though earlier (1982) he implied that *stevensoni*, *transvaalensis* and *tyleri* are synonymous with the nominate form (and *aureus* with *schillingsii*). Robinson *et al.* (1996a) demonstrated the apparent lack of any regional cytotypes within the species. Synonyms: *aceratos*, *aureus*, *centralis*, *cunenensis*, *hyatti*, *klipspringer*, *porteousi*, *saltator*, *saltatrixoides*, *schillingsii*, *somalicus*, *steinhardti*, *stevensoni*, *transvaalensis*, *tyleri*. Chromosome number: $2n = 60$; all chromosomes, including X and Y, are acrocentric (Robinson *et al.* 1996a).

Description A small and stocky antelope, yet supremely agile in its rocky habitat. Pelage is sandy-yellow to grey, with white undersides and, in some populations (e.g. *O. o. centralis* in SW Tanzania), a russetting around the shoulders. Black skin on the insides of the ears partially covered by white hair, giving rise to a black-and-white pattern that can aid individual identification. Pelage coarse and pithy as in some deer. Hooves short and unusually shaped so that the animal appears to walk on tip-toes – this provides good purchase on slippery rocky surfaces. The tips are oval in shape and leave characteristic tracks in moist ground. The false hooves on the forelimbs are much better developed than those on the hind. Tail short and untufted. Distinct,



Lateral, palatal and dorsal views of skull of Klipspringer *Oreotragus oreotragus*.

black preorbital glands are present in both sexes, but are larger in ♂♂. A preputial gland is present; interdigital and inguinal glands are absent. Females have two pairs of inguinal nipples. Females are usually about 10% larger than ♂♂.

Males have straight, sharp, spike-like horns, reaching up to 16 cm but averaging about 9 cm (S. C. Roberts & R. I. M. Dunbar unpubl.); ♀♀ are horned in parts of Kenya, NE Tanzania and E Uganda. Horns have no more than six annulations (sometimes less or none). Norton (1980) recorded that horn growth started at about four months of age, and that horns protruded above the hair at 5.5–6 months. They then grow rapidly up to 12 months attaining adult size at about 17–18 months.

The rostrum is short, even more so than in *Raphicerus*, and an ethmoid vacuity is present. The preorbital fossae are very much larger than in *Raphicerus*, with sharply ridged posterior and dorsal margins; there is no secondary bony growth on the frontal and parietal. Lower incisiform teeth are relatively small, median pair broader; cheekteeth are relatively larger than in *Raphicerus*, with large premolars.

Geographic Variation

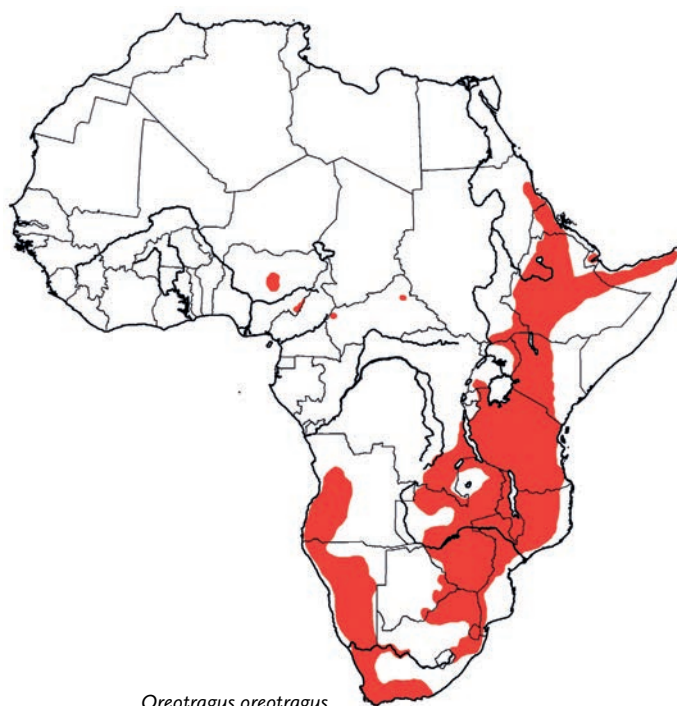
- O. o. oreotragus*: South Africa, in the Cape and E Free State.
O. o. transvaalensis: N and E South Africa, possibly into S Mozambique.
O. o. tyleri: Namibia and SW Angola. Exact limits and degree of intergradation with *oreotragus* unclear.
O. o. stervensoni: Zimbabwe and E Botswana.
O. o. aceratos: south-east Africa between the Rufiji and Zambezi Rivers.
O. o. centralis: Zambia, SE DR Congo, SW Tanzania, N Malawi; also ranges south into Zimbabwe (Ansell 1978).
O. o. schillingsii: Tanzania (except the south-east where replaced by *aceratos* and south-west where replaced by *centralis*), S Kenya, SW Uganda and presumably Rwanda and formerly Burundi. Females often have well-developed horns (averaging 7 cm in length, $n = 5$; S. C. Roberts pers. obs.).
O. o. aureus: N Kenya, NE Uganda and S Ethiopia; distinguished from *schillingsii* only by hornless ♀♀.
O. o. saltatrixoides: Ethiopian Highlands, Eritrea and Sudan.
O. o. somalicus: N Somalia and Djibouti (see Künzel *et al.* 2000).
O. o. porteousi (Western Klipspringer): isolated populations in suitable habitat in Nigeria (particularly around the Jos Plateau) and Central African Republic.

Similar Species

- Raphicerus* spp. More slender build; ears larger; pedal glands present.
Ourebia ourebia. Sympatric in much of East and south-eastern Africa. More slender build, with a distinctive black patch below the ears; inguinal glands present.
Sylvicapra grimmia. Broadly sympatric. Similar in outline, though taller and heavier, and has much smaller, backward-pointing horns.

Distribution Endemic to Africa. Klipspringers have a wide distribution from NE and SE Sudan, Eritrea, N Somalia and the Ethiopian Highlands southwards through East and southern Africa to the Western Cape in South Africa, and along the west coast in Namibia and SW Angola. More isolated populations occur in Central African Republic (two separate areas in the north-eastern and north-western uplands) and Nigeria, where they occur in and around the Jos Plateau (East 1999), and also in the east in Gashaka–Gumti N. P. (Nicholas 2004a); there are no records from Cameroon (Lamarque *et al.* 1990). They are confined to suitable rocky or mountainous areas, including largely contiguous habitat (e.g. the Rift and Zambezi Valleys, and the southern African escarpment) and isolated kopjes in savanna and scrublands. The current distribution is probably very similar to its historical one, as their dependence on mountainous terrain and browsing feeding habits protects them from loss of habitat to agriculture and from competition with cattle. The only country in which they formerly occurred, but are now probably extinct, is Burundi, while in Rwanda they are now confined entirely to Akagera N. P. (East 1999).

Habitat As its name implies (Klipspringer means ‘cliff-jumper’ in Afrikaans), Klipspringers are dependent on rocky and mountainous terrain, occurring up to 4380 m in the Ethiopian Highlands (Yalden *et al.* 1996). With this crucial exception, they are adaptable and have a wide climatic range. In the Kuiseb Canyon in Namibia, for example, mean annual rainfall is only 17 mm and is highly seasonal, and mean monthly temperatures vary from 10 to 33 °C (Tilson



Oreotragus oreotragus

1980). In contrast, the Ethiopian Highlands have an annual rainfall of 1385 mm falling over half of the year, and monthly temperatures of only 2–8 °C (Dunbar 1979). Klipspringers are common in both areas, and in other parts of Africa with intermediate conditions. Since there is wide botanical variation associated with these environmental conditions, there is no specific vegetation type that can be associated with Klipspringer abundance.

Klipspringers often have two main habitat types within their territories: (i) rocky slopes, outcrops or cliffs, and (ii) flat, often sandy, scrubland at the base of the slopes. They typically feed at the base of the cliffs where suitable plants are abundant, and then seek suitable resting sites high up on the slopes to rest and ruminate. There are usually two or three favoured resting sites in each territory, where family groups may spend the entire mid-day period. Such sites are often rocky ledges under overhangs, providing both shade and excellent vantage points over the slopes below.

Abundance Klipspringers are locally abundant in suitable habitat, reaching high densities (e.g. an estimated 10–14/km² in the Simien Mts in Ethiopia; Dunbar 1978). Abundance is closely related to the extent of suitable rocky terrain, and overall population density is more typically in the range of 0.01–0.1/km² in restricted areas of suitable habitat, to 0.15–0.30/km² in areas with more extensive habitat (East 1999). Based on these average population densities, East (1999) estimated a total population of about 42,000 animals, but which is almost certainly an underestimate. The species occurs in substantial numbers on private farmland in Namibia.

The numbers of the Western Klipspringer in Nigeria and Central African Republic are unknown, but are unlikely to exceed a few thousand at most, and are probably declining.

Adaptations Unique changes to the digital bones have occurred, relative to other antelopes, to provide the Klipspringer with the traction necessary to move quickly over slippery rocky surfaces.



Klipspringer *Oreotragus oreotragus* vertical leap (from film). Note bunching of forefeet.

The third phalangeal bone has rotated about 30 degrees posteriorly so that, in effect, the animal actually walks on the anterior tips of the hooves, which wear down as youngsters mature (Norton 1980). The hairs, which range in length from 15 to 28 mm, are springy in texture and hollow, another feature unique amongst African antelopes, providing an insulating layer of air to deal with both upper and lower extremes of temperature (Norton 1980).

Klipspringers are unique in that ♀♀ are horned in some high-density areas in eastern Africa and hornless elsewhere. Involvement of the ♀♀ in territory defence has led to the suggestion that ♀♀ may be the primarily territorial sex, rather than ♂♂ defending territorial food resources for the ♀ (Roberts & Dunbar 2000). Females initiate up to 90% of scent-marking bouts, choosing where and when to carry out this important territorial advertisement. In contrast, ♂♂ follow ♀♀ and over-mark every one of the female's scent marks, perhaps a form of mate-guarding. In between-pair encounters, ♀♀ also engage other ♀♀ in bouts of violent head-butting, even where they are hornless. Further evidence for this suggestion comes from comparisons of the ecology and social behaviour of horned and hornless female populations (Roberts 1996, S. C. Roberts & R. I. M. Dunbar unpubl.). Female horned populations in East Africa have by far the smallest territories, where the highest rates of physical encounters are expected. High aggression rates between ♀♀ may thus have led to horn expression, but because horns make fighting more dangerous, ♀♀ appear to avoid fights. Since ♀♀ initiate group movements, this also reduces the number of male intra-sexual encounters, theoretically driving reduced selection for large male horns in East African populations (S. C. Roberts & R. I. M. Dunbar unpubl.).

Foraging and Food Klipspringers are browsers, preferring food of high energetic and protein content. This includes young leaves, flowers, flower buds, seeds and fruits. Between 4 and 13 (mean = 8) plant species are eaten per day in South Africa (Norton 1984), with up to 90% of feeding records being of fruit and flowers in the wet

season (as low as 19% in the dry season). While browse forms the bulk of their diet, they have also been found to include up to 30% of new, green grass growth in Ethiopia where there is high rainfall. However, this appears to be exceptional, and in drier areas grazing is less common: less than 10% of the diet in Zambia (Wilson & Child 1965), 1.5% in Kenya (Qvortrup & Blankenship 1974) and only one observation in 1000 in the Cape (Norton 1984). Indeed, studies involving stable carbon isotope analysis in East African Klipspringers found that their diet includes only 4% grass (Cerling *et al.* 2003).

Favoured food in Zambia (Wilson & Child 1965) included leaves of *Diplorhynchus mossambicensis*, *Pseudolachnostylis maprouneifolia* and *Lannea edulis*, and fruit of *P. maprouneifolia* and *Dicrostachys cinerea*. Some of the same items were also eaten in a Zimbabwe study (Smithers & Wilson 1979), as well as the fruit and leaves of *Ziziphus mucronata* and flowers of *Aloe chabaudii* and *Diospyros mespiliformis*. In the far south of Zimbabwe, the same items crop up, in addition to fruits of *Hexalobus monopetalus*, fruits and leaves of *Grewia bicolor* and *G. flava*, and leaves of *Croton pseudopulchellus* and the herb *Tephrosia rhodesica*, as well as the succulent *Sansevieria pearsonii* (Roberts 1994). Norton (1984) recorded very selective seasonal feeding of *Aspalathus hirta* flowers and fruits of *Maytenus oleoides*, *Rhus undulata*, *Indigofera spinescens* and *Euphorbia mauritanica*, often stripping shrubs entirely of their fruit.

During the dry season in Zimbabwe, ♀♀ have been observed to rear up on their hindlegs to reach food items out of reach, and measurements taken later show that this confers a maximum range of 106 cm above the ground (S. C. Roberts pers. obs.). This behaviour is different from that commonly observed in Gerenuk *Litocranius walleri*, as they do not rest their forelegs against branches for support while feeding in this way. Under the most extreme conditions in Namibia, Klipspringers have even been known to climb ana trees *Acacia albidia*, up to a height of 5.4 m, in order to reach their favoured food (Kok & Van Wyk 1982) and have been seen to take refuge in trees in Tanzania (Kingdon 1982). Norton (1980) recorded osteophagia and geophagia from termitaria.

Klipspringers have been thought to obtain all their water requirements from their food, a conclusion based on observations of groups living far from water (Wilson & Child 1965). However, in the dry season in Zimbabwe, Klipspringers cross several neighbouring territories to visit permanent springs and they have even been observed drinking from small pools in the sandy bed of the seasonally flooding Limpopo R. (S. C. Roberts pers. obs.). Such excursions are risky, taking them up to several hundred metres away from the safety of the cliffline across difficult, sandy terrain. Notably, all excursions away from the rocks were made during the hottest, middle hours of the day, when predation risk is lowest. They also regularly drink from rock-pools after rainfall. These observations suggest that Klipspringers in some areas are not tolerant of water-deprivation.

Social and Reproductive Behaviour The basic social unit is an adult male–female pair, often accompanied by one or sometimes two offspring (Dunbar & Dunbar 1974a, Tilson 1980, Roberts 1994). Short-term observations can overestimate the proportion of single individuals, while the size of female offspring can lead to the conclusion that some ♂♂ are accompanied by two adult ♀♀. Although up to nine animals have been seen together (Kingdon 1982), these instances appear to be temporary and formed by two



Klipspringer *Oreotragus oreotragus*.

or more groups meeting. Subadult offspring are driven away by the same-sexed adult, young ♂♂ being expelled earlier than ♀♀ (Norton 1980).

Adult pairs occupy territories that adjoin those of 2–4 neighbouring pairs. Territory size varies across Africa and is inversely related to annual rainfall (S. C. Roberts & R. I. M. Dunbar unpubl.). The smallest recorded territories (about 1.4 ha) are in Tsavo N. P. in Kenya (annual rainfall 750 mm), increasing to 5.5 ha in Matobo N. P. in Zimbabwe (558 mm), 8 ha in Ethiopia (1385 mm), 10 ha in the Drakensberg Mts, South Africa (941 mm), 15 ha at Gamka in South Africa (400 mm), 20 ha in the Limpopo Valley, Zimbabwe (332 mm), 49 ha at Springbok in South Africa (160 mm) and 90 ha in the Kuiseb Canyon, Namibia (18 mm).

Territories are defended throughout the year. The most common form of territory delineation is by scent-marking at latrine sites and on vegetation. All family members defecate and urinate in the same visit to dung middens (up to 2 m across), of which there are 5–10 dotted around the territory, often along boundaries (Dunbar & Dunbar 1974a). Scent-marking on vegetation is done by depositing secretion from the preorbital glands onto twigs and leaves. The same twigs are used repeatedly, leading to a visible accumulation of secretion that resembles a black bead. The secretion contains a number of ketones and esters, which are considerably more volatile than those found in the preorbital secretions of other antelopes (Burger *et al.* 1997). Over 50% is protein, which probably acts as a controlled release system for the volatiles. Marking is often preceded by licking the old marks, probably to release volatiles to check who marked there last (Roberts 1998). Very fresh marks are detectable by humans, the smell resembling aniseed (S. C. Roberts pers. obs.). Three territories in the Limpopo Valley, Zimbabwe, which were mapped in detail (Roberts & Lowen 1997), contained 403, 644 and 836 discrete scent-marking sites. Half of all the surveyed sites contained either one or two marked twigs, but up to 22 different twigs could be marked within one site. The number of these sites marked in a 24-hour period varied seasonally between 60 and 140, increasing during the mating season and towards the end of the dry season (Roberts 1994). Most marks were revisited at least every 5–7 days, and some marks every two days. Visit rates to marking sites appear to coincide with the length of time over which scent is detectable: an experiment with captive Klipspringers indicated that marks retain efficacy for seven days but not ten days (Roberts 1998). To increase chances of being detected by territorial intruders, pairs scent-mark in highly predictable spots (even to human observers), above bare rock surfaces in elevated areas, especially in areas with good vantage points. Food plants are also marked more often than unpalatable species (Roberts 1997). Marks are placed throughout the territory, not just at boundaries, although boundaries with neighbours are marked more than boundaries not directly adjoining another territory (Roberts & Lowen 1997; see also Kruger *et al.* 2002).

Physical territory defence between neighbouring pairs occurs at a much lower frequency, which is predicted by both rainfall and territory size. Fights and chases are more common in areas with high rainfall and small territory size (S. C. Roberts & R. I. M. Dunbar unpubl.). The highest rates of physical aggression are about 1 per 12 h at Sankaber in Ethiopia (Dunbar & Dunbar 1980), while in the Kuiseb Canyon in Namibia, in the largest territories recorded, no

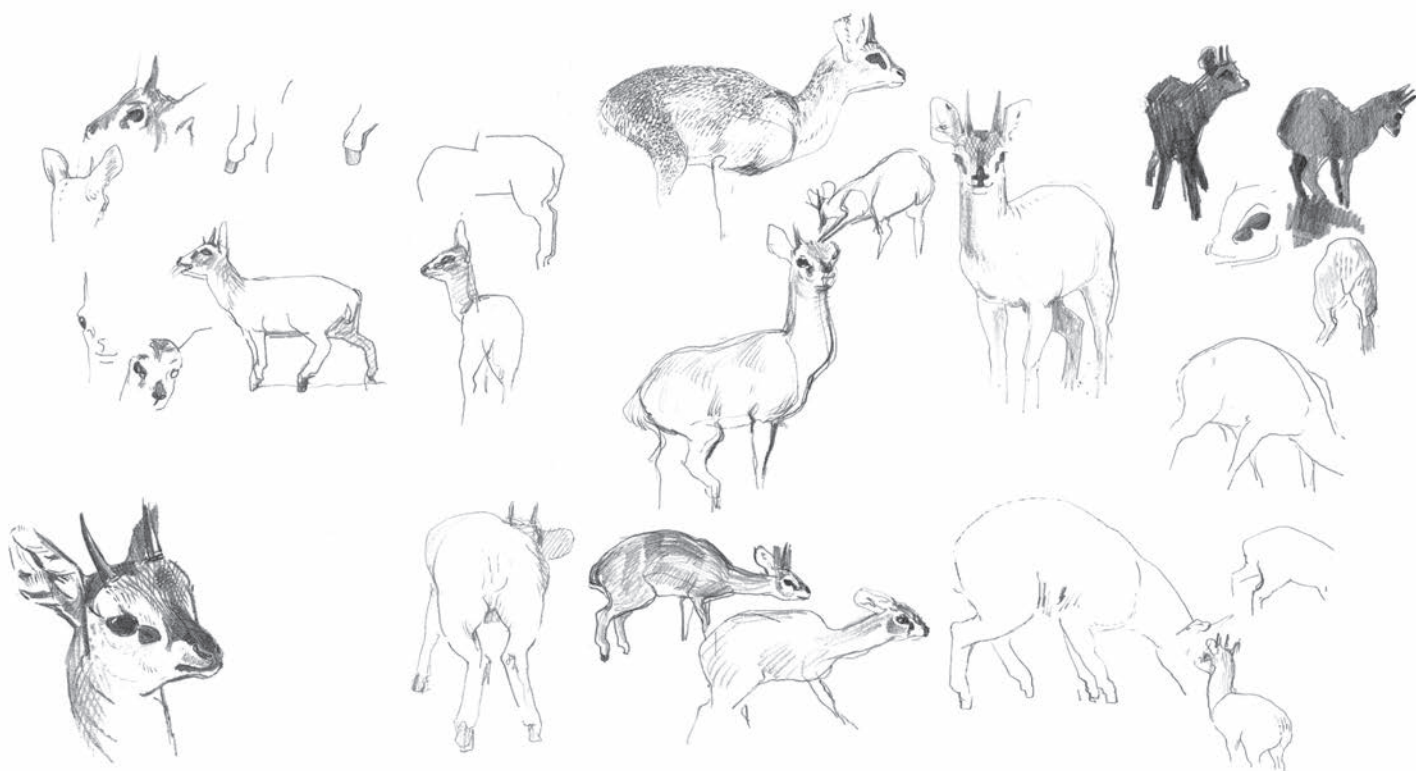
encounters were observed in over 900 hours of observation time (R. L. Tilson pers. comm.). Both sexes are involved. Of 21 encounters observed in various studies, ♂♂ were involved in 18 (86%) and ♀♀ in eight (38%); in three cases both sexes confronted the same-sex members of another pair (Roberts 1994). Klipspringers do not have ritualized 'air-cushion' fights (common in the related dik-dik), in which actual contact is avoided. However, physical contact is rare and was made in seven cases (33%; female–female physical contact in two), the rest were chases without observed contact. Males have been known to die from horn-jab wounds sustained in fights (Norton 1980). Female territorial defence, the possibility that ♀♀ may be the primarily territorial sex, and the correspondence between high densities and the appearance of horns in ♀♀ have been discussed above in the Adaptations section.

Pair bonds between adult ♂♂ and ♀♀ are remarkably strong and stable. Behavioural synchrony is high, with pair members engaged in the same activity for between 50 and 80% of the time (Dunbar & Dunbar 1980, Norton 1980). Distances between pair members are usually 5 m or less, but more when feeding. This cohesiveness is apparently not seasonally variable, even though the ♀ is only receptive for a fraction of the year. Pairs are thought to last until one of the pair dies and the longest recorded pairing is nine years (Norton 1987). Since ♀♀ can (at least partly) defend their own food resources, this raises the question of why Klipspringers maintain such well-maintained pair bonds. These pair bonds persist outside the breeding season and so are unlikely to be solely due to mate-guarding by ♂♂ (Roberts & Dunbar 2000). The reason may be that ♂♂ provide a vigilance service against predators while ♀♀ are feeding: pairs alternately take turns to stand guard from an elevated vantage point while the other feeds in the bushes below. Males spend more time being vigilant and are more likely to detect a threat than ♀♀. By guarding the ♀ and offspring, ♂♂ thus increase their own reproductive success (Dunbar & Dunbar 1980), in addition to benefits gained by mate-guarding.

When a predator is observed, a brief alarm call is given by the first to spot the danger. The group flees 30–50 m to an elevated vantage point, then turns to keep the predator in view. They may then give further alarm calls. About 64% of encounters with predators elicited such calling. In Namibia, the adult ♂ and ♀ may continue to call every 3 sec for up to 20 min (average 5 min) in what has been termed 'alarm duetting' (Tilson 1977a). These calls are audible up to 700 m away and appear to act as a pursuit deterrent signal to the predator (Tilson & Norton 1981).

Courtship is typified by the ♂ sniffing the female's rear, performing flehmen and tapping the female's hindlegs with his forelegs (laufschiag). Observations in captivity suggest that oestrus appears to last about a week and that 4–6 copulations occur during this time. Young are born in the shelter of rocks or in thick vegetation in the rocky habitat and remain hidden for up to three months before joining the pair. At least during the very early part of their lives, the young, if approached, lay their heads flat on the ground, with their ears flat and make no attempt to move off. Their cryptic colouration makes them very difficult to see when lying up in shelter (Skinner & Chimimba 2005).

Reproduction and Population Structure Breeding seasonality varies across the range. In Zimbabwe, mating was observed



Klipspringer *Oreotragus oreotragus*.

in three pairs and courtship behaviour in another; all cases were in Jul and no mating or courtship occurred during the rest of the year. Lambing would then be timed to coincide with the wet season (Roberts 1994). In Ethiopia, the mating season is probably in Aug–Sep (Dunbar & Dunbar 1974a). However, in Zambia, pregnant ♀♀ were recorded in all months except Dec–Jan, and small lambs were found in Apr, Jun and Nov (Wilson & Child 1965). A late foetus was found in an animal taken in Jul in Angola (Hill & Carter 1941). Fecundity varies across populations and is related to temperature: it is lowest in colder areas at high altitude (Dunbar 1990).

Gestation has been estimated at five months (Norton 1980) and weaning at four months (Cuneo 1965, Norton 1980). Birth-weight of a female lamb was 1.13 kg (Wilson & Child 1965). No genetic studies have been carried out to investigate the possibility or extent of extra-pair paternity. However, an observation in Namibia (R. L. Tilson pers. comm.) indicates that extra-pair copulations can occur: a neighbouring or transient ♂ copulated with a mated ♀ while her mate was further down a canyon, busy alarm-calling at a jackal. The other ♂ had disappeared by the time he returned to the ♀, but he spent the next few minutes sniffing the ♀ and scent-marking, so it is possible that he was aware of the other male's visit.

Of 44 completely sexed groups at Sankaber, Ethiopia, 33 were male–female pairs and 11 were trios of one ♂ and two ♀♀ (Dunbar & Dunbar 1974a). The same authors recorded the following group compositions at Geech in Ethiopia: 12 male–female pairs, three two-female trios and one two-male trio at Geech (they reported similar findings at a third site, Bole, but this area was subject to regular hunting, which would reduce male numbers). Dunbar & Dunbar (1974a) conclude that a typical group (roughly three-quarters of all groups) consists of an adult pair, with a quarter consisting of two

♀♀. Other studies agree with this estimate, though group sizes of up to five can occur in exceptional cases (Norton 1980). Based on this information, an adult sex ratio can be estimated at about 1 ♂ to 1.2 ♀♀, although the sex ratio at birth may well be at parity.

Predators, Parasites and Diseases The major predator of adult Klipspringers is probably the Leopard *Panthera pardus*, which favours similar rocky habitat and is present across almost all of its range. In Matobo N. P., Klipspringers appeared in 9–13% of 449 leopard scats and an adult ♂ killed by a Leopard was also found (Smith 1977). Similarly Klipspringers were the most common prey item (with Rock Hyrax *Procavia capensis*) in the Cedarberg Mts of South Africa (Martins *et al.* 2011). Klipspringer remains have also been found in Caracal *Caracal caracal* scats (Stuart & Hickman 1991). Both adult and young Klipspringers may occasionally be killed by African Rock Pythons *Python sebae* and large raptors (Roberts 1994), and baboons *Papio* spp. and Black-backed Jackals *Canis mesomelas* have been observed taking young lambs (Tilson 1980, Davies & Cowlshaw 1996). Attempts to reintroduce Klipspringers in the Free State in South Africa have been unsuccessful mainly due to healthy populations of predators such as Black-backed Jackals and Caracals (S. Vrahimis pers. comm.).

Klipspringers are hosts to an unusual parasite. While all ungulates pick up ticks on the legs and body from vegetation, one tick species aggregates specifically on branches scent-marked by Klipspringers, using this as a means of crawling onto the face of Klipspringers when they return to scent-mark again (Rechav *et al.* 1978, Spickett *et al.* 1981). The ticks appear to locate marks by following the aqueous scent trail formed by rainwater washing scent down the bush. The tick, *Ixodes matopi*, is named after Matobo

N. P. where it was first observed. It would be interesting to learn how widespread this host–parasite relationship is, because it was not present on marks in the Limpopo Valley, only 300 km away, despite careful daily search of 2000 marks, including after rain (Roberts 1995). The tick completes its life-cycle on Jameson's Red Rock Rabbit *Pronolagus randensis*.

Klipspringers are also host to other tick species (e.g. *Rhipicephalus* spp. in the Limpopo Valley), and these are gleaned, with the apparent acceptance of Klipspringers, by at least four passerine birds: Pale-winged Starlings *Onychognathus nabouroup*, Red-winged Starlings *Onychognathus morio*, Yellow-bellied Greenbul *Chlorocichla flaviventris* and Familiar Chats *Cercomela familiaris* (Tilson 1977b, Steyn & Hosking 1988, Roberts 1993, 1995, Anderson 2006). There is some evidence that these birds may also specifically ingest proteinaceous preorbital gland secretion direct from the glands (Roberts 1995). Klipspringers also self-groom, combing pelage through the incisors to tease out ticks (Hart, L.A. *et al.* 1996).

Conservation IUCN Category: Least Concern (*O. o. porteousi* – Endangered C2a(i)). CITES: Not listed.

Klipspringer populations often persist in areas devoid of other ungulates, because their preference for rocky habitat does not conflict with agricultural needs. The population currently is believed to be stable, or slightly declining. However, recent information on the status of populations in several countries is lacking, including Sudan, Somalia and Angola. Roughly one-quarter of the total population is estimated to occur in protected areas, including strongholds such as Simien and Bale Mountains National Parks (Ethiopia), Tsavo N. P. (Kenya), North and South Luangwa N. P. (Zambia), Nyika N. P. (Malawi), Niassa G. R. (Mozambique), Matobo N. P. (Zimbabwe), Hester Malan N. R. and Augrabies Falls N. P. (South Africa) and Namib–Naukluft N. P. (Namibia) (East 1999).

The status of the Western Klipspringer *O. o. porteousi* is an exception to the above, with this subspecies occurring in fragmented populations in Nigeria and the Central African Republic. It is known to occur in Lamé G. R. (East 1999) and in Gashaka–Gumti N. P., which is thought to represent a stronghold for this isolated subspecies (Nicholas 2004a). There is a need for close monitoring of the population status of this subspecies.

Measurements

Oreotragus oreotragus

HB (♂ ♂): 862 (820–920) mm, n = 13

HB (♀ ♀): 905 (883–1000) mm, n = 10

T (♂ ♂): 76 (65–90) mm, n = 13

T (♀ ♀): 84 (65–103) mm, n = 10

HF c.u. (♂ ♂): 223 (215–230) mm, n = 13

HF c.u. (♀ ♀): 224 (215–240) mm, n = 10

E (♂ ♂): 93 (87–100) mm, n = 13

E (♀ ♀): 92 (85–99) mm, n = 10

WT (♂ ♂): 10.6 (9.1–11.6) kg, n = 13

WT (♀ ♀): 13.2 (10.5–15.9) kg, n = 10

Southern Africa (Smithers 1983)

Maximum recorded horn length is 16.2 cm for a pair of horns from Gravelotte, Limpopo Province, South Africa (Rowland Ward)

Key References Dunbar 1978, 1979, 1990; Dunbar & Dunbar 1974a, 1980; Norton 1980, 1984; Roberts 1994, 1997, 1998; Roberts & Dunbar 2000; Roberts & Lowen 1997; Tilson 1980; Wilson & Child 1965.

S. Craig Roberts



Klipspringer *Oreotragus oreotragus* head showing vertical horns above eyes.

Tribe AEPYCEROTINI

Impala

Aepycerotini Gray, 1872. Cat. Ruminant Mamm. Brit. Mus. p. 4, 42.

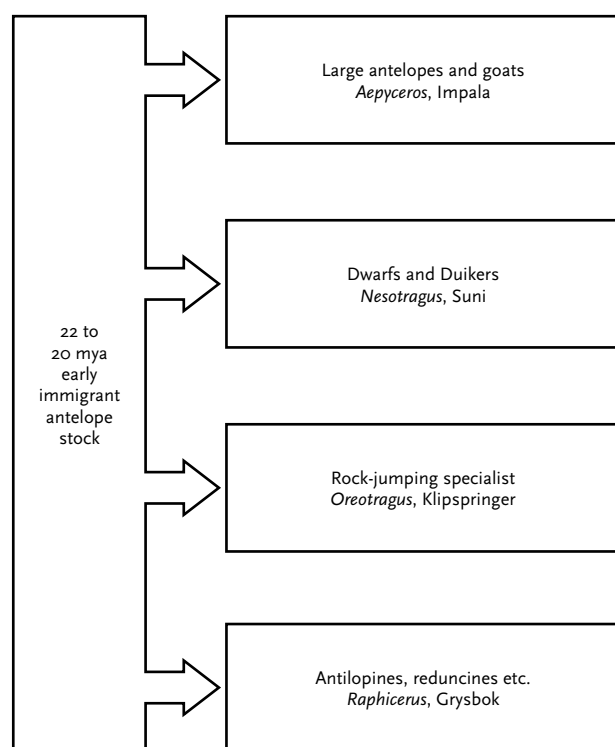
A taxonomic puzzle for many years, the Impala *Aepyceros melampus* has been recognized as a distinct evolutionary lineage by some authors (e.g. Ansell 1972, Vrba 1979, Gentry 1992). It had previously been linked to the gazelline antelopes (Simpson 1945, in his tribe Antilopini), on the basis of its proportions approximating to various gazelles, and to the reduncines (Ellerman *et al.* 1953) based on even closer superficial resemblances with *Kobus* and *Redunca*. A less obvious relationship with the Alcelaphini was first proposed by Gentry (1966, 1978) on the basis of many cranial resemblances between living and fossil forms (both lineages showing elongation of the skull and hollowing at the base of the horns). Gentry's placement of the Impala in Alcelaphini was followed by Kingdon (1982, 1997) and Vrba (1984). A molecular association with Alcelaphini was also proposed by Lowenstein (1986), and Essop *et al.* (1997) found some weak support for sister status between *Aepyceros* and *Alcelaphus* on the basis of restriction sites of mtDNA. Gatesy *et al.* (1997) noted that while the precise phylogenetic affinity of *Aepyceros* was not clear, the Impala placed as the sister group to Hippotragini, Alcelaphini, Caprini and *Pantholops* (the Chiru or Tibetan Antelope).

On the basis of molecular work, the Impala is here included as the sole member of its own tribe (Hassanin & Douzery 1999, 2003, Matthee & Robinson 1999a, Matthee & Davis 2001). These molecular analyses generally agree with Georgiadis *et al.* (1990) that the Impala represents the sole survivor of a basal lineage with a proposed lineage ancestry of about 21.5 million years (Hernández Fernández & Vrba

2005). In agreement with Gatesy *et al.* (1997), the phylogenetic supertree by Hernández Fernández & Vrba (2005) aligned the Impala as sister species of a clade containing caprines, hippotragines and alcelaphines (contra Vrba & Schaller 2000).

However, basal positions have invited further analysis or speculation on the Impala's possible relationship with other basal groups as well as its position in regard to later, secondary radiations. Hernández Fernández & Vrba (2005) envisaged the earliest bovids splitting three-ways into 'Bovinae', 'Aepycerotinae' and 'Antilopinae', with many subsequent derivatives, but omitted behavioural or ecological arguments for the bovid radiation. Exploring molecular relationships among bovids, others (Matthee & Robinson 1999a, Hassanin & Douzery 1999, Hassanin *et al.* 2012) found the Impala clustering with the Suni *Nesotragus moschatus*, another basal antelope (but see Matthee & Davis 2001). This is of special interest as both the Suni and Impala share the peculiarity of a vacuity between the maxilla and premaxilla. The resemblance has been noted by many authors and has generally been assumed to be due to convergence, but demonstration of at least some genetic linkage forces a reappraisal of this common peculiarity.

In both instances the significance of the vacuity seems to lie in a phylogenetic elongation of both nasals and premaxilla to create a solid joint between the side and top of the muzzle. In structural terms this looks like improvised 'casing' that helps elongate the muzzle. This implies that both species had an ancestor with reduced nasals and premaxilla, but was this ancestor common to both? An open 'nasal bellows' mechanism for sophisticated heat-control by nasal panting is found in many gazelline desert antelopes (Antilopini), the Beira *Dorcotragus megalotis* and, most extremely, in the Saiga Antelope *Saiga tatarica* and in the dik-diks (Madoquini) (Kingdon 1982). All these antelopes have ancient pedigrees (for example, the Saiga has been estimated to have diverged from other Antilopini about 20 mya; Hernández Fernández & Vrba 2005). There are important



Four antelope radiations over last 20 million years and most conservative surviving genus.

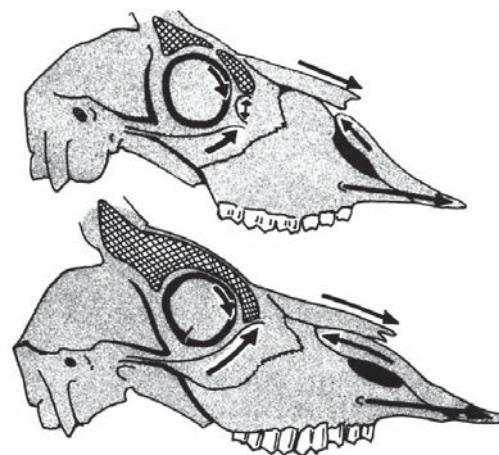
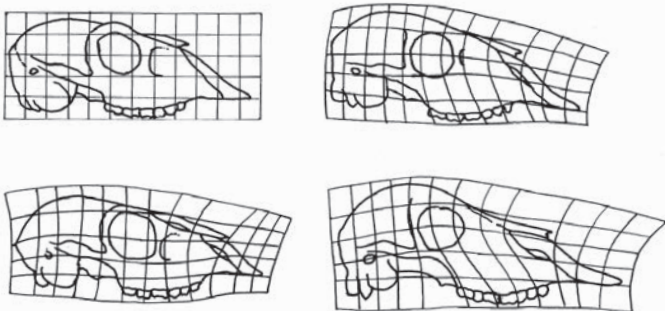


Diagram of Impala *Aepyceros melampus* skull compared with hypothetical and more generalized antelope. Distinctive evolutionary traits/trends/peculiarities in structure suggested by arrows.



Top left: symmetrical grid imposed on skull outline of hypothetical ancestral antelope. Below left: cartesian co-ordinates imposed on Suni *Nesotragus moschatus* skull. Below right: cartesian co-ordinates imposed on Impala *Aepyceros melampus* skull. Top right: cartesian co-ordinates used to construct a skull intermediate between the previous three.

evolutionary implications for a more heat-adapted precursor to both the Suni and Impala. For a start, such a conclusion is consistent with the putative adaptive difference that separated and distinguished ancestral Antilopinae from ancestral Bovinae (Kingdon 1982). It is also consistent with the Bovinae/Antilopinae split first taking place along the hot, dry interface between Eurasia and Africa. It follows from this that the predominantly southern and eastern African ranges of Impalas and Sunis are consistent with a long-established, but essentially secondary, preference for cooler, well-shaded habitats. Because these regions are more distant from the putative centre of origin for Antilopinae it seems likely that both Aepycerotini and Neotragini represent very early branching into founding lineages, the former larger, longer in the legs and emphatically gregarious, the latter remaining small, short-legged, solitary and territorial. Lengthening of the legs can be correlated with lengthening of the skull in the Impala but not, of course, with the Suni.

Although Impalas have no facial, pedal or inguinal glands, the backs of the lower hindlegs have thick oval tufts of black hairs that

cover metatarsal glands, a feature unique among Bovidae, and that presumably plays an important role in scent communication. Other characteristics of the tribe besides those already mentioned include the presence of lyrate, strongly ridged horns in males only, and the absence of preorbital fossae or an ethmoid fissure in the skull.

Survival of the Impala lineage in an unstable ecotone between woody bushlands (mainly in the dry season) and more open grassland and savanna (in the wet season) is probably partly due to a browse/graze dietary adaptation (Harrison 1936) and partly to exceptional versatility in its social relations (Schenkel 1966, Jarman, P. J. & Jarman, M. V. 1973, Monfort *et al.* 1973, Warren 1974). Individuals have no lasting attachments and can disperse or assemble easily. The laying of scent-trails and very loud calls assist this easy coming and going and the morphological adaptations associated with these behaviours are described in the species and generic profiles.

Gregariousness in the earliest Aepycerotini and increases in body size, leg-length and spatial range were probably the key adaptations that ensured survival of the Impala lineage. Perhaps it was their early acquisition of sociality, physical enlargement and an ability to escape predators that ensured that it was this branch of the earliest Antilopinae that subsequently gave rise to the majority of larger-bodied antelopes, goats and sheep. If, as suggested by others (e.g. Gentry 1978, Vrba 1984, Lowenstein 1986, Gatesy *et al.* 1992, 1997), Alcelaphini share a common ancestry with Aepycerotini, their relationship, though distant, is manifest in such shared characteristics as elongation of the legs and face and an ability to live at higher densities. Other supposedly related groups may also share different permutations of characteristics such as hollow foreheads and exceptional agility in caprines, grass-eating and still larger body sizes in the hippotragines. In any event, future molecular techniques can be expected to greatly refine our understanding of the relationship of Aepycerotini to other antelopes in the near future.

Jonathan Kingdon



Impala *Aepyceros melampus* leaps (from photos) showing flared glandular patches on rear hocks.



Impala *Aepyceros melampus* adult male.

GENUS *Aepyceros*

Impala

Aepyceros Sundevall, 1847. Kongl. Svenska Vet.-Akad. Handl. Stockholm 1845: 271 (1847).

The Impala is the only representative of the tribe Aepycerotini and the only species in the genus *Aepyceros*. Impalas superficially resemble many medium-sized antelopes in their general proportions and, in their colouring, have an even closer resemblance to the Gerenuk *Litocranius walleri* (except that Impalas have prominent dark thigh stripes that seem to mimic the black genital cleft and serve to widen the angle at which an attractive, species-specific rump signal can be transmitted). Impalas also resemble some gazelle, kob and reedbuck species, resemblances that formerly led to suggestions of affinity with the gazelles (Simpson 1945) and with reduncines (Ellerman *et al.* 1953), and display some less obvious resemblances with the Hartbeest *Alcelaphus buselaphus* that led Vrba (1984) to consider the Impala as a sister-clade to the alcephalines (Hartbeest, wildebeest), and Gentry (1978) to include *Aepyceros* in Alcelaphini.

A striking conclusion of the study by Vrba (1984) is that Impalas have been unchanged in their basic form for at least 5 million years (the oldest fossil Impala is smaller but otherwise unchanged from the modern representative), whereas in that same time period the alcelaphine common ancestor has diverged at least 18 times in various forms of hartbeest and wildebeest of quite diverse morphology. The greatest change that can be observed in modern Impalas is between the isolated population of Black-faced Impalas *A. m. petersi* in Namibia and the Common Impalas *A. m. melampus* found everywhere else throughout its range, and even here the differences between the subspecies are modest (though several authors have proposed treating *petersi* as distinct; Shortridge 1934, Oboussier 1965, Cotterill 2003a). The implication is that Impalas were and are superbly adapted to their environment, and thus there has not been selection for any major changes in morphology or behaviour. These adaptations include a mixed feeding strategy, the ability to straddle both sides of an ecological frontier between wooded and grassy habitats, high population growth rate, gregarious habit with weak social bonds (see below), flexible territorial system, excellent anti-predator behaviour, and a unique system of tick-defence adaptations that includes an 'antelope toothcomb', reciprocal allogrooming and tolerance of and cooperation with tick-eating oxpeckers (see species account).

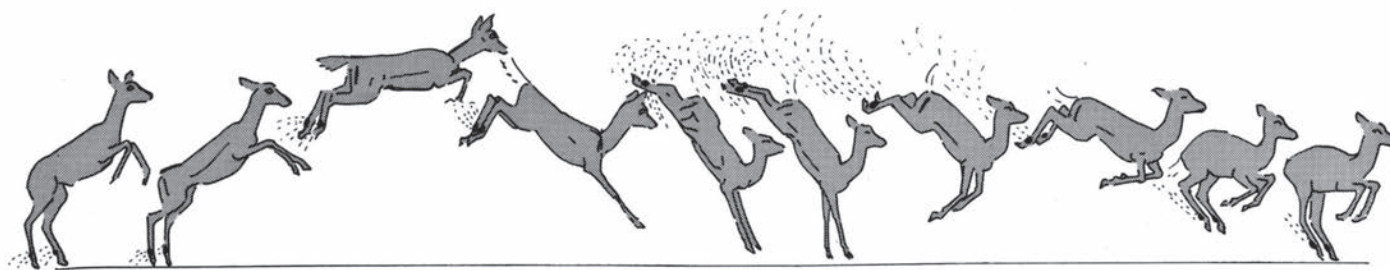
A particularly outstanding peculiarity of Impalas is their ability to form and to break up into loose aggregations of very variable size without any obvious attachment to other individuals or to permanent territories. Linked to their ability to disperse and then assemble in groups is their ability to transmit very effective visual, olfactory and auditory signals; notably 'empty-kicking' and 'tongue-flashing' displays, energetic modes of laying glandular scent trails by means of the metatarsal glands, and extraordinarily loud roars, in all of which they are unlike any other antelope.



Impala *Aepyceros melampus* tongue-flashing while roaring.

The horns of the Impala are unusual in being circular in section and hollow at their bases. For their strength and flexibility they rely as much on the thickness of the horn layer as on their relatively slender bone cores. They consist of two inverted arches so that blows can be delivered, caught or interlocked in a light wrestling technique that seeks to throw the opponent off balance. Their very wide span arcs through an extended catchment volume so that clashing horn surfaces dull the impact of blows and keep potential damage well away from the cranium. This favours the locking of horns rather than the ramming through of bruising blows.

Jonathan Kingdon



Impala *Aepyceros melampus* female leaping and making 'empty kicks'.

Aepyceros melampus IMPALA

Fr. Impala; Ger. Schwarzfersenantilope

Aepyceros melampus (Lichtenstein, 1812). Reisen Sudl. Africa 2, pl. 4 opp. p. 544. Khosis, Kuruman, South Africa.

ABOVE: Lateral, palatal and dorsal views of skull of Impala *Aepyceros melampus*.
LEFT: Impala *Aepyceros melampus*.

Taxonomy Ansell (1972), largely following Haltenorth (1963), provisionally listed six subspecies, noting that the limits and intergradation between the subspecies are not well defined. Recent classifications, supported by molecular data (Nersting & Arctander 2001, Lorenzen *et al.* 2006a), recognize two subspecies: the nominate form, the Common Impala *A. m. melampus*, and the Black-faced Impala *A. m. petersi*. The Black-faced Impala has been considered a distinct species (Shortridge 1934, Oboussier 1965), and the two are highly genetically differentiated (Lorenzen & Siegmund 2004). Lorenzen *et al.* (2006a) also split the Common Impala subspecies into two genetically distinct groups, conforming with regional geographic affiliation to southern or East Africa, and also revealed the genetic distinctiveness of the Samburu population in Kenya, possibly indicative of a population bottleneck. More recently, Bastos-Silveira & Lister (2007) have examined morphometric data in more detail and have proposed four subspecies: *A. m. melampus* in South Africa; *A. m. petersi* in SW Angola and Namibia; *A. m. johnstoni* in Malawi and Zambia; and *A. m. suara* (including *rendilis*) in East Africa. Until these regional forms have been described in more detail and the exact boundaries of their ranges have been drawn we provisionally retain the conservative division into two subspecies. Synonyms: *holubi*, *johnstoni*, *katangae*, *pallah*, *petersi*, *rendilis*, *suara*. Chromosome number: $2n = 58-60$; these differences are due to fusion metacentrics (Wallace & Fairall 1967b).

Description A medium-sized antelope with long, thin legs, slender body and clear sexual dimorphism. Easily identified by its marked two-tone, short-haired coat: back, nape and upper flanks are reddish-brown and have a distinct sheen – although in *A. m. petersi* upperparts

are duller, lacking distinct reddish-brown colour – while limbs and lower flanks are paler. Ventral pelage white. Hair is closely pressed to the body and averages 12 mm in length on the top of the shoulders, being slightly longer on the underparts (about 15 mm). Hairs are off-white at the base and broader and reddish-brown at the tip, though duller at the tip in *A. m. petersi*. Most of head is reddish-brown with white patches above eyes and around mouth. Chin and throat white. Crown, between the ears, is black. Ears large, inside white with tip black. On each buttock and upper thigh there is one vertical and distinct black band (surrounded by patches of pale brown hairs) running from the level of the tail to the upper hindleg. Paler patches occur on insides of legs, while on back of lower hindleg there are thick oval tufts of black hairs that cover metatarsal glands, unique to the Bovidae. Tuft of tail is black and continues in a thin black line that runs up to the rump. Underparts of the tail are white, and the white hairs are long (~100 mm). Preorbital, pedal and inguinal glands are absent. Females have two pairs of inguinal nipples. In adults, the cloven hooves have an average length of 47 mm (40–52 mm); there are no false hooves. Sexual dimorphism is distinct: ♂♂ are taller and heavier than ♀♀ in all age groups.

Only ♂♂ carry horns, which are deeply ridged for most of their length, but smooth towards the tips: in juveniles the horns are straight, vertical and short (<150 mm). They become curved like upright brackets (<250 mm long) when individuals are 12–18 months old. With age, the horns curve backwards in a lyrate shape, with an average length of 500 mm (365–820 mm) for adult ♂♂. The skull is characterized by the absence of preorbital fossae or ethmoid fissure and a premaxillo-maxillary vacuity is present, which is known otherwise only in Bates' Pygmy Antelope *Neotragus batesi* (albeit vestigially) and

the Suni *Nesotragus moschatus* (Ansell 1972). Tooth eruption has been used as a means of estimating age up to 2.5 years, after which age can only be estimated based on tooth wear (Lane *et al.* 1994).

Geographic Variation

A. m. melampus (Common Impala): C Kenya to South Africa and west to SE Angola. Description mainly as above.

A. m. petersi (Black-faced Impala): NW Namibia and SW Angola. Larger and darker than Common Impala; a dark, nearly black band extends from the nostrils to between the eyes, and continues in a thinner band to the top of the head (these black facial markings are variable, and the thinner band is sometimes missing); black ear tip is larger and the tail almost 30% longer and much bushier than in the Common Impala.

There is a black colour variant of the Common Impala, which is recessive to the common red colour of the pelage. Individuals are totally black and farmers in southern Africa have isolated individuals in large paddocks resulting in pure black populations (J. D. Skinner pers. comm.).

Similar Species

Litocranius walleri. Sympatric only in East Africa. Of similar colouring, but with elongated legs and neck. Males with very robust horns that are shorter than in the Impala.

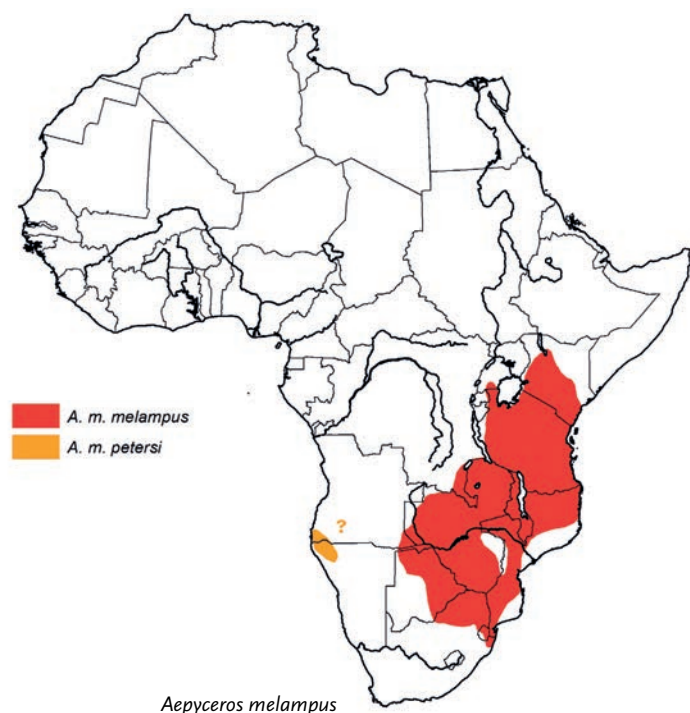
Distribution Endemic to Africa. Widespread in both the eastern and southern parts of the continent from Kenya to South Africa in savanna and woodland habitats close to water. The distribution range of Impalas remains largely unchanged from their historical range, although they have been eliminated from some parts through hunting and human settlement (East 1999). The northern extent of their range is the dry central and southern regions of Kenya, particularly in Kajiado and Laikipia Districts. Their range includes SW Uganda,

mainly in Lake Mburo N. P., although they formerly also occurred in the north-east of the country. They still occur in Rwanda where they are confined to Akagera N. P., but they have been extirpated from Burundi. Their range extends southwards throughout Tanzania, Zambia (except parts of the country west of the Zambezi R.), and Malawi, where they are confined mainly to protected areas. They formerly occurred marginally in extreme SE DR Congo, but there is no recent information on their status (East 1999).

In Mozambique, they occurred throughout much of the country, except apparently much of Nampula and Zambezia Provinces, but the civil war had a detrimental impact on their populations and they survive mainly in protected areas such as Gorongosa and Zinhave National Parks, Niassa G. R. and in W Gaza province; ongoing efforts to rehabilitate wildlife populations in this country will no doubt benefit this species. In Zimbabwe, they occur nearly throughout (although herds have been decimated by poachers since 2000), but are naturally absent from the miombo-*Brachystegia* woodland in the north-east. In Botswana, they are confined to the northern, north-eastern and eastern parts, particularly around the Okavango Delta (occasionally turning up in the eastern parts of the Kalahari), while the western part of their range extends to extreme SE Angola and NE Namibia in the E Caprivi Strip. The southern natural limit of the range of the species includes the Limpopo, North West and Gauteng Provinces of South Africa, E Swaziland and N KwaZulu-Natal as far as the Mhlatuze R. (East 1999, Skinner & Chimimba 2005).

In the last four decades, Impalas have been introduced to numerous privately owned game ranches and small reserves throughout southern Africa, such as Free State Province and much of KwaZulu-Natal in South Africa, Namibia and Zimbabwe and widely in Namibia (East 1999). Today Impalas also occur in Gabon, central Africa, where they have been introduced into two protected areas, though they are now in decline (P. Chardonnet pers. comm.). It has been noted that Impalas easily colonize new areas, such as the south-eastern part of Hwange N. P. in Zimbabwe, providing that a regular supply of surface water is available (Matson 2003).

In NW Namibia, the Black-faced Impala is naturally confined to Kaokoland and neighbouring SW Angola. Kaokoland was set aside as a protected area in 1928, when it formed part of Etosha N. P., Namibia, but lost its protection status in 1970. To guard against extinction, Black-faced Impalas were translocated to SW Etosha N. P. on the edge of the historic Black-faced Impala range (Green & Rothstein 1998). Today, this subspecies occurs between the Otjimborombonga area (ca 12°45'E) and Swartbooisdrift on the Cunene R., southward to the Kaoko Otavi area in the south-western part of Etosha N. P., and Kamanjab District just south of the Park (see also Conservation). There is no information on the current status of this subspecies in Angola, but they survive in Iona N. P. and may still occur in Bikuar and Mupa National Parks (East 1999, Crawford-Cabral & Veríssimo 2005). Historically, the two subspecies were separated in Namibia by Ovamboland, an old geographical barrier stretching over a distance of more than 300 km, with *A. m. petersi* occupying the Cunene R. area and *A. m. melampus* the Okavango R. area (though see Crawford-Cabral & Veríssimo 2005). Migration from the latter area would have been possible to Botswana and South Africa provided there was availability of suitable surface water (and see later) (Skinner & Chimimba 2005).



Habitat Throughout its range, the Impala is water dependent and a typical ecotone species, associated with light woodlands and savannas (see Estes 1991a, Skinner & Chimimba 2005 for reviews), selecting open *Acacia* savannas with nutrient-rich soils providing good-quality grass, and high-quality browse in the dry season (Pettifer & Stumpf 1981, Dunham 1982, Skinner *et al.* 1984, Fritz *et al.* 1996). In southern Africa, Impalas are sometimes found in association with mopane *Colophospermum mopane* woodlands (Jarman & Jarman 1974, Dunham 1982). Interestingly, both bachelor and breeding herds use the same habitat selection criteria, lightly wooded grassland and open woodlands, with ♂♂ tending to be more opportunistic in the dry season (Bourgarel 2004, H. Fritz & W. Crosmayr unpubl.); these ecological criteria appear to be robust as they do not vary with changes in density (Gaidet 2005). Impalas often concentrate on areas of short grass, particularly close to lakes, or on post-fire flushes of grass (Monro 1978). In their semi-arid environment, Black-faced Impalas also select the interface between wooded savanna and open grassy vleis (Joubert 1971, Matson *et al.* 2005).

Impalas require canopy cover for shade and thermoregulation as they are not well adapted to dry heat (Klein & Fairall 1984, 1986; and see Matson *et al.* 2005), but their most important requirement is surface water, perhaps associated with a physiological need to eliminate nitrogenous waste imposed by a high crude protein intake (Fairall & Klein 1984). They were rarely found further than 5 km from water in Tsavo N. P. (Kenya) during the dry season (Ayeni 1975), and less than 8 km from water in Kruger N. P. (Young 1972) or 2 km from the Chobe R. in Botswana (Omphile 1997). Impalas are thus rarely recorded in arid regions, except where they can use artificial man-made supplies such as spillage from wells and boreholes, as in Botswana. In Hwange N. P., the range expansion of the Impala population was probably favoured by the introduction of permanent waterholes, and in Etosha N. P. Impalas are restricted to areas close to waterholes, being found on average within 3.5 km around waterholes (Matson *et al.* 2006). Impalas have been noted to go for 2–3 days without drinking water in Serengeti N. P., Tanzania, provided there is sufficient succulent food available (Jarman, M. V. & Jarman, P. J. 1973), while in the Zambezi valley marked individuals drank at 3–4 day intervals in the dry season (Gaidet 2005). This water-dependency, coupled with fairly strong territorial behaviour, often leads to clumped distributions. Impalas are absent from montane ecosystems, recorded to about 1700 m on the slopes of Mt Kilimanjaro (Grimshaw *et al.* 1995).

Abundance East (1999) details population estimates for most of the Impala's current range states, giving a total population of around 1,600,000 Common Impalas, with more than half in South Africa, and 2200 Black-faced Impalas. However, East (1999) cautions that the former does not account for undercounting in aerial surveys or areas for which population estimates are lacking. The latter estimate for Black-faced Impalas is slightly lower than that estimated by Green & Rothstein (1998), who estimated the population in Etosha N. P. at around 1500 individuals, with an additional 1200 on private land; the total population in Kaokoland was estimated at around 500. The number of Black-faced Impalas is currently estimated at more than 3200 individuals in Etosha, with a further 50–100 on communal conservancies and perhaps 1000 individuals in the north-west (J. Jackson pers. comm.). Correcting for undercounting biases, East

(1999) provides a crude estimate of nearly 2,000,000 Impalas, of which about half are on private land and one-quarter in protected areas.

The recorded densities of Impalas vary greatly, from less than 1/km² (Mkomazi N. P., Tanzania) to as many as 135/km² on the shores of L. Kariba, Zimbabwe (Bourgarel 1998) and 214/km² in the wooded savanna of the old (i.e. including areas later degazetted) Akagera N. P. in Rwanda (Monfort 1972). The average density in Kruger N. P., where they are a dominant ungulate, is around 7/km² (calculated from Owen-Smith & Ogutu 2003). In Lake Mburo N. P. and adjacent ranches in SW Uganda, highest population densities of 53.1/km² were found inside the park, while outside the protected area densities varied between 20.7 and 24.6/km² (Averbeck 2002). Such variation also exists within sites and between seasons, reflecting the heterogeneity of habitats and the availability of surface water (Dunham 1994, Jarman 1972b). These differences may also reflect difference in census techniques (and see East 1999).

Adaptations The 'metatarsal glands' on the hindlegs are covered by tufts of black hair. Kingdon (1982) noted that these glands give the appearance of expanding at precisely the moment in which jumping Impalas make their characteristic 'empty kicks'. In behaviour that is unique to Impalas, they kick their hindlegs almost vertically while landing on their forelegs, rebound, and bring their hindlegs down before landing again. This action probably emits trails of scent that Kingdon supposes assist animals to regroup after frequent dispersals. The chemical constituents of the metatarsal glands have been analysed by Wood (1997a).

The Impala appears to be the only ungulate to perform, in addition to self-grooming, 'allogrooming', i.e. reciprocal grooming to get rid of ticks and other ectoparasites on the head or neck (Hart *et al.* 1988, McKenzie 1990, Hart & Hart 1992, Mooring & Hart 1992, 1993). Like many small- and medium-sized antelopes, the Impala has a set of lateral incisor teeth that have been morphologically modified to form grooming tools. The second and third incisors, and the incisiform canine, are thin and needle-like, and arranged in the form of a comb on both sides of the lower jaw. These teeth are loose to facilitate see-saw action and are spaced to assist in the removal of parasites (McKenzie & Weber 1993) (see also Social and Reproductive Behaviour).

Foraging and Food Impalas are mixed feeders, consuming both grass and woody plants. The proportion of these food types in their diet varies greatly with season and location. A recent synthesis and attempt to classify the diet of African bovids has classified the Impala as a 'mixed-feeder, browser-grazer intermediate', with an average diet composition of 45% dicotyledon, 45% monocotyledon and 10% fruit (Gagnon & Chew 2000). This classification is in agreement with dietary classifications based on stomach morphology (Hofmann 1973), dental mesowear (Franz-Odenaal & Kaiser 2003) and stable carbon isotopes (Cerling *et al.* 2003, Sponheimer *et al.* 2003b). Even their digestive physiology, such as the rate of fermentation, seems to be adapted to their principal food (Giesecke & van Gylswyk 1975, Hoppe *et al.* 1977, Gordon & Illius 1994).

When succulent palatable green grass is available, Impalas graze: just after the first major rains, the proportion of grass in the diet peaked around Jan at 75% in Sengwa, Zimbabwe, while it decreased to less than 10% in the dry season (Jun/Jul) (Dunham 1980). Similarly, in Serengeti N. P. the proportion of browse in the diet increased as the

dry season progressed (Jarman & Sinclair 1979), and these patterns are mirrored in other studies (e.g. Van Rooyen 1992, Meissner *et al.* 1996). In the Midlands of Zimbabwe, dominated by miombo and mopane dry woodlands where primary productivity of grasses was poor, Impalas mostly browsed, even during the wet season (Fritz *et al.* 1996). The peak of browsing is often in the middle of the dry season, as some grass may be available at the end of the dry season, due to early sprouting of species like *Cynodon dactylon*, or post-burn re-growth (Moe *et al.* 1990, Wisley 1996). In the open areas of Hwange N. P., around waterholes, the re-growth of grass (particularly *Cynodon dactylon*) in the middle of the dry season induces Impalas to graze. Similar observations were made in Lake Mburo N. P. where regular fires changed the foraging behaviour of Impalas from predominantly browsing to pronounced grazing in the dry season (Wronski 2003). The timing of fires and the possibility of early showers may occasionally allow Impalas to graze throughout the year (Underwood 1982). Impalas can also vary their habitat use to ensure the availability of green grass, as in Serengeti N. P. where they move up and down the catena, switching from the upper slopes in the wet season to drainage-line greenbelts during the dry season (Jarman 1979). A wide variety of grass species is eaten by Impalas, 13 in Hwange N. P. (Wilson 1975) and 23 in Nylsvley, South Africa (Monro 1979). Preferred species include *Cynodon dactylon*, *Themeda triandra*, *Digitaria eriantha*, *Sporobolus* spp., *Panicum maximum*, *Eragrostis* spp. and *Urochloa* spp. Impalas exhibit a strong selectivity for green parts, across all heights (from 0 to >21 cm; Arsenault & Owen-Smith 2008). Short grasses are often used, but taller swards are also well utilized.

A wide variety of browse species is eaten, with *Acacia* leaves and twigs commonly found in the diet, along with *Combretum* spp., *Dichrostachys cinerea*, *Grewia* spp., *Boscia* spp., *Maytenus* spp. and *Commiphora* spp. Wilson (1975) listed 28 browse species eaten in Hwange N. P., and Monro (1979) 46 species eaten in Nylsvley. Fallen leaves of mopane may contribute the bulk of their diet during the dry season in the woodlands of southern Africa. Impalas also eat fruit, particularly pods, with those of *Acacia tortilis* and *Acacia nilotica* being actively sought for their high protein content. These feeding observations explain why most feeding is at ground level (Dunham 1982, du Toit 1990a). The high browsing pressure on *Acacia* spp. by Impalas is thought to be responsible for the low regeneration rate of these trees in some ecosystems (Prins & Van der Jeugd 1993, Moe *et al.* 2009). Joubert (1971) listed 21 browse plants and 12 grasses utilized by Black-faced Impalas in N Namibia.

The ratio of dicotyledons to monocotyledons in the diet may also vary with sex and social status (Van Rooyen & Skinner 1989). Territorial ♂♂ eat less dicotyledons (31% of diet) than ♀♀ (48%) or bachelor ♂♂ (49%). This difference between the sexes was also noted at L. Mburo, Uganda (Wronski 1999, 2002) and in a study in Kruger N. P. using stable carbon isotopes (Sponheimer *et al.* 2003a). It may reflect the fact that dominant ♂♂ monopolize habitat where the grass layer is of prime quality, but probably reflects the fact that the time devoted to holding a territory prevents a ♂ seeking the dispersed, high-quality dicotyledons, as suggested by the greater proportion of dicotyledons in the diet of ♀♀ that share the home-ranges of dominant ♂♂.

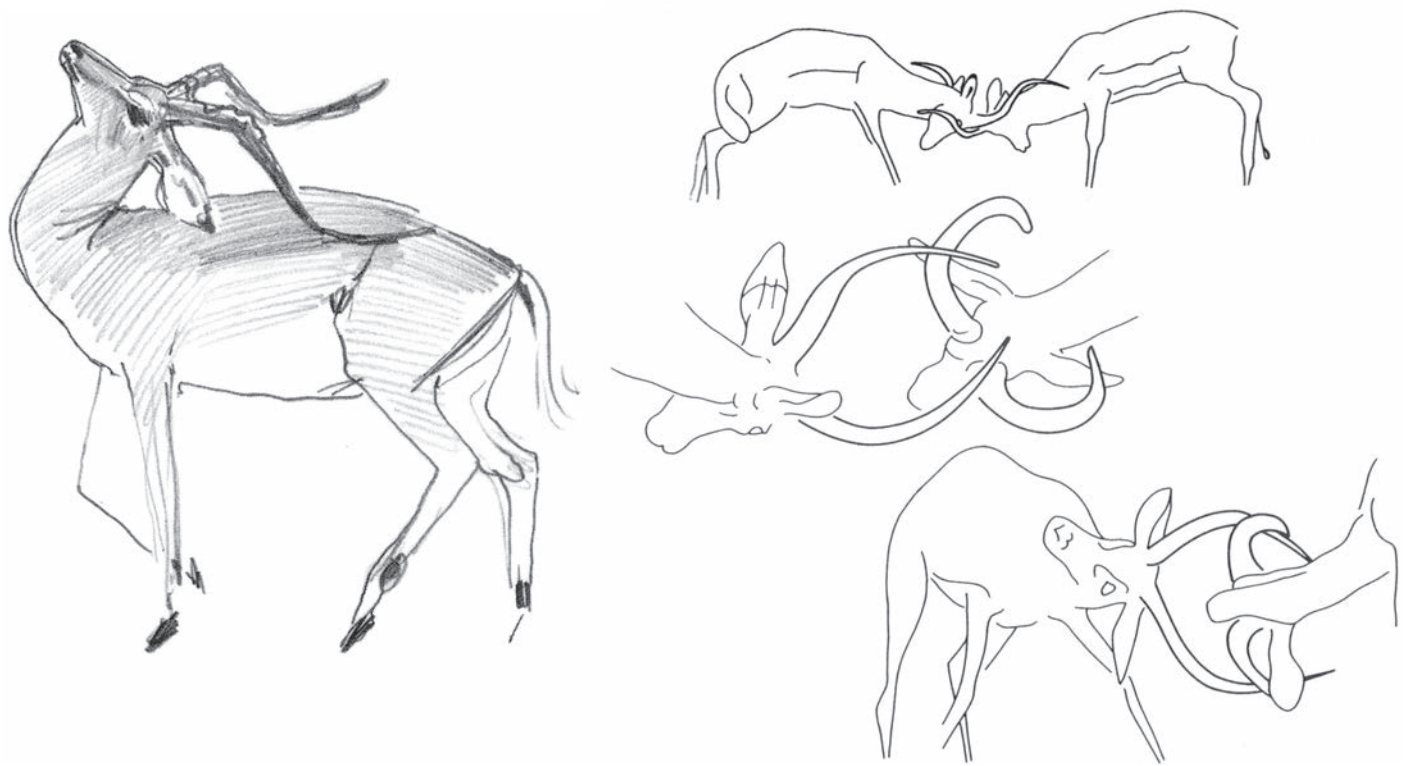
Social and Reproductive Behaviour Impalas are gregarious, forming herds of various sizes depending on the season and the

quality of habitat. In Hwange N. P., group size varies from 4 to 150 individuals with the largest herds found in open habitats (mean group size 15.4 in bush/grassland habitats, 12.2 in grassland and 7.3 in bushland; Bourgarel 2004). It is generally during the wet season, or the beginning of the dry season, that the biggest herds occur (Murray 1981). In N Namibia, Black-faced Impala herds range from 3 to 15 individuals, occasionally up to about 20, with aggregations of larger herds formed during or after the birth season (Joubert 1971).

Impala social organization consists of territorial adult ♂♂ during the rut, bachelor groups and breeding herds. In the Sengwa area, ♀♀ seemed to be in separate, stable clans of 30–120 individuals, occupying discrete home-ranges of 80–180 ha depending on the season (Murray 1982a). Bachelor groups comprise juvenile, subadult and adult ♂♂ that are potentially territorial. An age-based hierarchy exists within bachelor groups. Highly mobile (in Hwange N. P., some marked subadults and adults moved 30 km from where they were born [M. Bourgarel pers. obs.]), bachelor groups tend to occur in lower-quality habitats where intra-specific competition and disturbance are less (especially during the rut). Cohesion within bachelor herds is poor, particularly when adult ♂♂ intending to become territorial become aggressive. After the rut, bachelor ♂♂ often mix with breeding herds. Breeding herds comprise adult, subadult and juvenile ♀♀, and subadult and juvenile ♂♂ that form cohesive herds (average spacing between individuals <1 m) without a true hierarchical structure (Jarman 1979). Except during the rut, breeding herds often include several adult and subadult ♂♂ (mixed herds). Studies of marked individuals in Hwange N. P. and the mid-Zambezi valley showed that daily changes in herd size and composition, and in individual association, are frequent throughout the year (Bourgarel 2004, Gaidet 2005). Big herds may split during the day into smaller groups, and individuals from neighbouring herds can join other herds for a few days. Temporary nursery herds have been frequently observed, especially during months following birth periods.

Herd activities are closely synchronized, especially within a breeding herd. Impalas are primarily diurnal (with some nocturnal activity), spending most of the night lying down generally in an open area, mostly ruminating. During the day, when they are not feeding or moving or disturbed, they rest, ruminate and groom themselves in the shade. Due to fairly tight group structure, local competition between individuals may also contribute to the strong group effect on foraging (Fritz & de Garine-Wichatitsky 1996, Blanchard *et al.* 2008).

Impalas display a frequent and highly reciprocal allogrooming system between adults (♂♂ and ♀♀), but also between adults and young and between young individuals, regardless of sex, kinship or dominance status (Mooring & Hart 1992, 1993, 1997b). However, short self-grooming bouts occur more frequently than allogrooming (Mooring 1995, Mooring & Hart 1995a). For many years, the Impala was the primary model organism for testing the predictions of the 'programmed grooming hypothesis', which postulates that tick-removal grooming by Impalas (and other ungulates, see comparative study by Mooring *et al.* 2004) is regulated by an internal timing mechanism that elicits a grooming action before the tick is able to engorge and cause cutaneous irritation. The programmed grooming model makes a number of predictions known as the vigilance, habitat, body size and tick challenge principles. These predict that breeding ♂♂ will groom more frequently than ♀♀ (vigilance principle), smaller individuals will groom at a higher rate than larger individuals



Impala *Aepyceros melampus*. The illustrations on the right show horn-wrestling postures among males (from photographs).

(body size principle), inhabitants of environments with a high density of ticks will groom more frequently (habitat principle), and seasonal increases in tick threat will result in more frequent grooming (tick challenge principle). All these predictions have been supported in studies on Impalas. The rate of grooming varies both seasonally and by region: Impalas increase their rate of grooming during the wet season when tick density is high (Mooring 1995), and populations in tick-dense habitat groom more frequently compared with those in habitats where ticks occur at lower densities (Hart *et al.* 1992, Mooring & Hart 1997a, b). Maternal allogrooming occurs during nursing bouts, but its frequency declines rapidly after the first week. Young Impalas oral-groom more than adults, and consequently harbour a lower density of ticks than adults (Gallivan *et al.* 1995, Mooring & Hart 1997a, b). On the other hand, territorial ♂♂ groom themselves the least, probably related to the need for vigilance and territorial defence, and carry a higher density of ticks as a result (Mooring & Hart 1995a, b, Mooring *et al.* 1996) (see also Predators, Parasites and Diseases).

Just before the rut, adult members of bachelor herds become aggressive and sensitive to even slight movements and changes of posture in others. Dominant ♂♂ assert their position by walking stiffly in the arrogant posture, displaying their thicker neck and horn development (Jarman 1979). In addition, they occasionally fold the ears back and lift the tail, or face their challengers with head turned away, yawning or tongue flicking. Threat can also be expressed by high, medial or low horn presentation, head-tossing, head-dipping, vegetation-horning or (rarely) ground-horning and by mouthing their own penis. During confrontation, with the high horn presentation posture, the dominant ♂ invites his opponent to sniff his forehead. By sniffing and walking away with the low head attitude, the subordinate confirms his submissive position, which can

also be displayed by walking away while grazing, or by sniffing the under-tail of the dominant ♂ (uncommon).

With equal assertions of dominance between two rivals, the confrontation may end in combat. Whilst rare, a fight more often occurs between two territorial ♂♂ than between ♂♂ with different status. Fatal wounds are rare owing to the presence of a dermal shield of thickened skin that protects the neck and head, those parts of the body exposed during fights or pushing contests (Jarman 1972a). Dominant ♂♂ mark their territory with olfactory and auditory advertising. Sebaceous glands are concentrated on the forehead of dominant ♂♂ and the strong-smelling secretion is used to mark vegetation by frontal-rubbing, thereby contributing to scent-marking of territories. This is particularly common during the rut, and is not practised by ♀♀ (Jarman & Jarman 1974). Urine and faeces seem to have a smaller olfactory function even though urination and defecation are often performed in a ritualized fashion (Jarman 1979). Roaring is the most far-reaching display (up to 2 km) of dominant ♂♂, making rutting Impalas one of the noisiest ungulates. Roaring is used when intruders approach and it is occasionally followed by chasing. Roaring increases in intensity as the peak in the rut approaches.

The intensity of territorial behaviour depends on climatic conditions influencing the breeding season. In East Africa, nearer the Equator, an extended breeding season leads to a very long territorial period covering nearly the full year. However, mating generally occurs during the peak of territoriality at the end of the wet season (Jan–Feb in Serengeti N. P.; Jarman 1979). In southern Africa, the determining proximate factor initiating territorial behaviour and the onset of the oestrous cycle is shortening daylength (Skinner 1971, Skinner *et al.* 1974, Skinner & Van Jaarsveld 1987, Oliver *et al.* 2007). Murray (1982b) found that, during the rut, roaring by ♂♂ is also influenced by the lunar cycle; however, Moe *et al.* (2007) found

no consistent pattern to link conceptions with the lunar cycle in 17 years of data from South Africa and Botswana combined. In southern Africa, the rut occurs only during a short period (two months or less) (Fairall 1983) of the cold/dry season (Apr–Jun). Murray (1982b) found that in Zimbabwe the peak of the rut (centred in May) varied across a 20-day interval in five years.

The body condition and fat reserves of territorial ♂♂ decrease during the rut (Monro & Skinner 1979, Dunham & Murray 1982, Van Rooyen 1993) and so the number of territorial ♂♂, the duration of territorial period and territory size are a function of the seasons, population density, individual aptitude (age) and habitat quality. Generally, the number of territorial ♂♂ is greatest at the beginning of the rut and decreases progressively as food resources and intensity of territorial behaviour decline. At higher population densities, or at the beginning of the rut when competition between ♂♂ is greatest, territories are generally smaller. In Sengwa, where the density was 50–68 ind/km², territory sizes were between 8.5 and 13 ha during the peak with an average annual home-range from 49 to 90 ha according to their age (Murray 1982a), but in Serengeti N. P., where the density was 32 ind/km², mean territory size was 17 ha during maximum territorial activity and 58 ha during the dry season (Jarman 1979). In Limpopo Province, South Africa, Oliver *et al.* (2007) found mean territorial tenure was 67 days (range 23–99 days), compared with 82.5 days (range 5–267) in East Africa (Jarman 1979). Good-quality habitats increase mating opportunities by permitting long-lasting territorial periods and by allowing a territorial ♂ to keep more ♀♀ on his territory.

Compared with results of other studies, the home-ranges of Impalas in Lake Mburo N. P. were larger, and long-distance movements of young ♂♂ and ♀♀ occurred. Mean annual home-range size of female breeding herds was 168 ha, whereas home-ranges of up to 590 ha in young ♀♀ were observed (Averbeck 2002). Mean home-range size in adult ♂♂ varied between 70 and 110 ha, and exceeded values found by Murray (1982a) considerably. In NW Namibia, the home-ranges reported for female Black-faced Impalas (using minimum convex polygon) are the largest recorded for Impalas anywhere, at 33.3 ± 3.2 km², perhaps a reflection of the considerable distances that Black-faced Impala ♀♀ must travel between patches of suitable foraging habitat compared with Common Impalas, which inhabit less arid environments (Matson *et al.* 2007).

The home-range of breeding herds (mean area 297 ha in Serengeti N. P. and 80–180 ha in Sengwa; Jarman 1979, Murray 1982a) is bigger than male territories, and so can overlap several territories. As soon as a territorial ♂ has acquired a breeding herd, he checks intermittently to detect ♀♀ in oestrus by genital smelling and licking, or by smelling their urine on the ground. This act is generally followed by display of flehmen. Pre-mating behaviour is variable (Jarman 1979). Generally, the ♂ approaches and follows oestrous ♀♀ with head lowered and nose held forward. With receptive ♀♀ copulation often occurs after perineal licking. Mounting lasts up to 10 sec, and many consecutive mountings will follow at variable intervals (few seconds to one or two minutes). After successful copulation, ♂♂ frequently snort, roar, or chase bachelors and herd ♀♀. After successful copulation, a ♂ does not display any further interest in that ♀ even if she remains sexually receptive.

The Impala ewe and neonate exhibit behaviour that is between the pure 'hider' and pure 'follower' (Jarman 1976): several hours before parturition the pregnant ♀ isolates and conceals herself (in tall grass or

thick bush). The mother eats the afterbirth (Jarman 1976). How long the young stay hidden is uncertain, but after a day or two, they follow their mothers back to the herds during the day. At night, neonates (less than a week old) stay concealed in cover far from the adults. Often several young stay hidden in the same area. When disturbed, these 2–3-day-old young try to make themselves less conspicuous by laying with their head on the ground, but seven-day-olds are vigilant and run away if a potential threat comes too close (M. Bourgarel pers. obs.). After a week, young are no longer isolated from the herd and display anti-predator behaviour, including the formation of nursery groups, especially where there is a marked annual birth season. The weakness of mother–young bonds is illustrated by the rapid decline of the proximity between mother and young and the formation of groups of juveniles (Mooring & Rubin 1991). At 4–6 months of age, offspring preferentially associate with age-mates, forming crèche groups, which are characteristic for Impala young (Jarman 1979, Estes 1991a). Females remain in the breeding herd for life, while weaned ♂♂ are subjected to aggressive behaviour by dominant ♂♂ and are eventually driven out of the breeding herds. Dispersal distances appear to be fairly low (less than 10 km), although male subadults have been recorded dispersing up to 40 km in Hwange N. P. (M. Bourgarel pers. obs.).

Reproduction and Population Structure Females become sexually mature at age 18 months, whereas ♂♂ are fertile as yearlings, but mate only when they become behaviourally mature and territorial in their fourth year (Kerr 1965). In southern Africa, the ♀ has a maximum of two cycles during the reproductive period, but normally conceives during her first oestrus. The fecundity rate is normally 95% in fully mature ♀♀ (>2 years old) but lower in two-year-olds (Fairall 1983). There is no sign of reproductive senility in animals up to 14–15 years old (Skinner 1969).

The relatively short parturition season takes place at the beginning of the wet season (Nov–Jan) in southern Africa (Skinner & Chimimba 2005); in Chobe N. P. Impala parturition is highly synchronized, with 90% of young born within two weeks in mid-Nov, shortly after the first rains (Moe *et al.* 2007). However, in eastern Africa there is no marked reproductive seasonality, as a consequence of little change of daylength near the Equator and the bimodal rainfall pattern (Jarman 1979). Moe *et al.* (2007) posited that Impalas synchronize births in areas with a highly seasonal food supply, and temporally space births in less seasonal (equatorial) areas to reduce predation risks.

Gestation lasts 27–28 weeks (Fairall 1972), and a single young is born (although twins have been recorded; Kayanja 1969, Joubert 1971). At birth, the lamb has an average mass of about 5 kg, but smaller lambs (3.5 kg) have been captured in Hwange N. P. (Bourgarel 2004). Young grow quickly and weaning occurs between 17 and 25 weeks of age. The asymptotic mass is achieved at 4–5 years, but 75% of mature mass is reached by two years of age (Howells & Hanks 1975, Hanks *et al.* 1976, Brooks 1978, Fairall 1983).

At birth and during the first year, the sex ratio is equal, but at adulthood it is biased towards ♀♀ (65% of adults were ♀♀ in Kruger and Hwange National Parks). In breeding herds in Hwange N. P., 88% of adults are ♀♀. Overall, the age composition is 23% juveniles and this figure increases during the birth season to over 30% (M. Bourgarel pers. obs.). Recruitment appears highly variable, and the juvenile to female ratio seems to change strongly (0.47–0.81) with variations in density-dependent competition for resources

(Gaidet 2005). Averbeck (2002) observed an average ♂ : ♀ sex ratio of 1 : 1.5 in Lake Mburo N. P., while the percentage of adult ♀♀ (38–45%) in the population was greater than that of ♂♂ (21–27%). The proportion of juvenile and subadult Impalas remained almost unchanged throughout the study period, at a level of 5–10%. The ratio of sexually mature to sexually immature animals was 2 : 1, and the ratio of adult to subadult ♀♀ was on average 1 : 1.1 (Averbeck 2002).

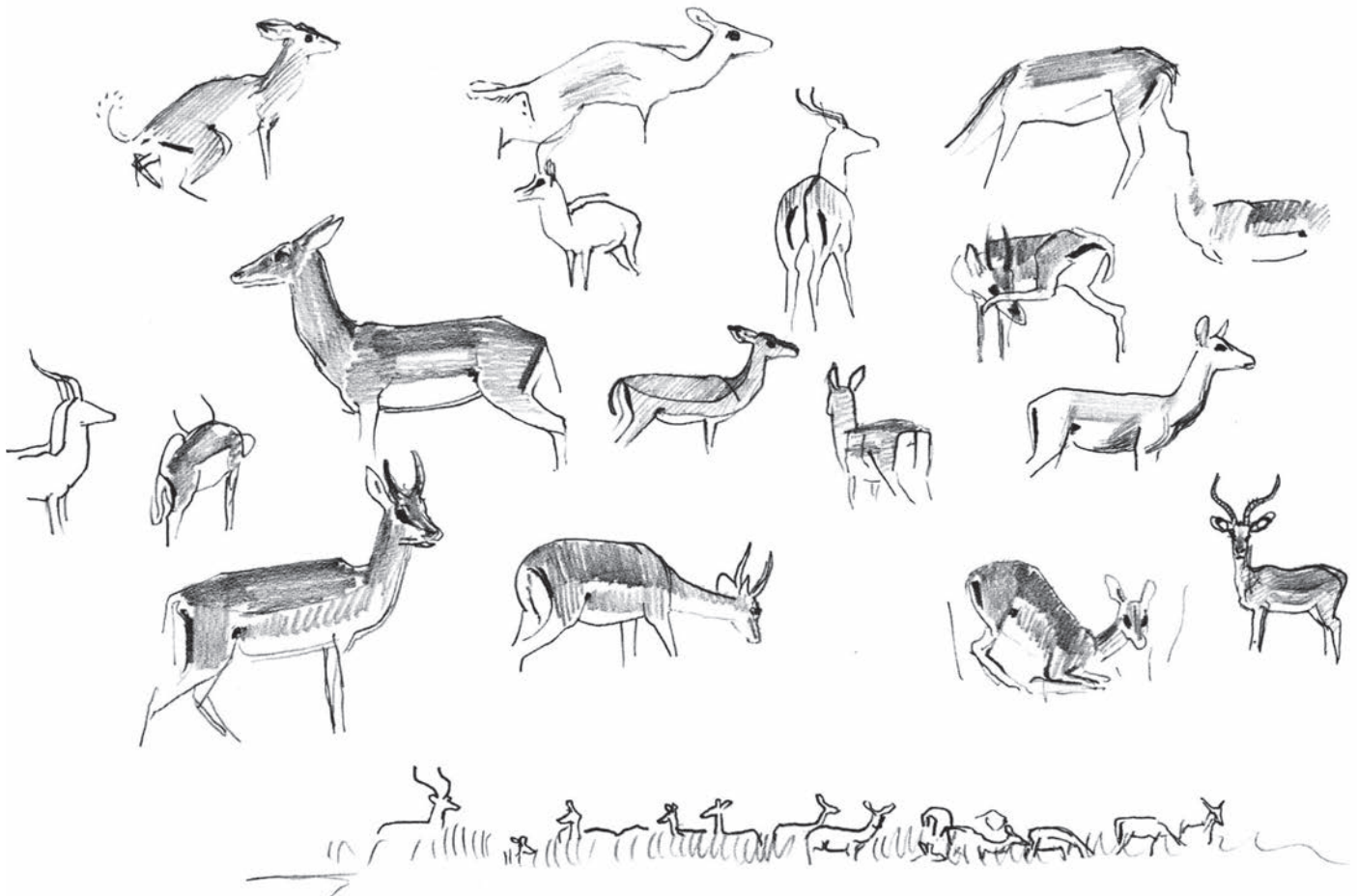
The survival rate depends on the environment, sex and age (Ginsberg & Milner-Gulland 1994): the probability of survival is 0.6 during the first year for both sexes, but mortality occurs mainly during the first month of life (Bourgarel 2004) and reaches 0.95–0.97 at three years old. For ♀♀, the probability stays the same up to 8–9 years old, whereas for ♂♂ it starts to decrease after six years of age to reach zero at 9–10 years of age. Female longevity is 12–14 years in the wild, compared with ten years for ♂♂. Captives have lived to 25 years (Weigl 2005).

Predators, Parasites and Diseases Impalas are prey to all larger predators (including jackals *Canis* spp. and baboons *Papio* spp.), and are often considered as preferred prey for African Wild Dogs *Lycaon pictus*, Leopards *Panthera pardus* and Cheetahs *Acinonyx jubatus* (e.g. Pienaar 1969a, Pole *et al.* 2004, Hayward *et al.* 2006a, b, c). However, as the Impalas taken by predators are on average in poorer condition than the average in the population (Pole *et al.* 2003), it is possible that the rank of the Impala in the prey list of large predators

is density-dependent: when at high density, the proportion of weaker individuals would increase and Impalas would then become the main prey of most large carnivores. As medium-sized predators such as large eagles also prey on young Impalas (see, for example, Mooring 1993), the mortality of newborn Impalas is high, ranging from 15–60% in a study population at Hwange N. P. (H. Fritz pers. obs.). One pack of seven African Wild Dogs in Hwange N. P. ate 4–5 newborns daily for a week (M. Bourgarel pers. obs.). Cheetahs seem also to specialize on young Impalas in the large game ranches in Namibia (Matson 2003).

In woodland (their favourite habitat), Impalas are more vulnerable to predation and so they are extremely alert and prompt to flee. They tend to use more open habitats preferentially when predators such as Lions are in the vicinity (Valeix *et al.* 2009). When disturbed by an intruder that is beyond their flight distance, they snort and move off slowly, but if the intruder is within their flight distance, they often run and leap in all directions, bounding up to 12 m. It is at such times that they commonly kick their hindlegs up, rebounding before landing again (see Adaptations). Seasonal parturition and nursery groups reduce predation risk by diluting the risk among newborns and enhancing vigilance, although this strategy is only likely to be effective against specialist predators (Ims 1990, Moe *et al.* 2007). In general, grooming increases predation risk (Mooring & Hart 1995a).

Ectoparasites of Impalas include ticks, which are also vectors of blood parasites, and lice. Durden & Horak (2004) list five species



Impala *Aepyceros melampus*.

of lice known to parasitize Impalas, including the recently described *Linognathus weisseri*, while numerous studies have investigated tick burdens in Impalas (e.g. Horak 1982, Horak *et al.* 1995b, 2003). The intensity of infestation by ticks depends on the season and Impala density, and varies between individuals: the infestation is greater in subadults and adults than in juveniles, and in adult ♂♂ than in adult ♀♀ (Gallivan *et al.* 1995). Males on their territories harboured six times more adult ticks than did ♀♀, showing the cost of decreased grooming activity (Mooring & Hart 1995a, b). Impalas frequently associate with oxpeckers, *Buphagus* spp., which concentrate their time foraging around the ears, head and neck of Impala, which are the regions supporting the highest density of ticks (Mooring & Mundy 1996, Mooring *et al.* 1996). When oxpeckers are in attendance, Impalas noticeably reduce their own grooming efforts (Mooring & Mundy 1996).

Impalas also harbour numerous endoparasites, and again numerous studies have investigated prevalence, host specificity and seasonal incidence in Impalas (e.g. Horak 1978a, 1981a). In Zimbabwe, 26 nematode, eight cestode and three trematode species have been recovered from Impalas (Jooste 1987). Some of these are definitive Impala parasites and others are occasional. In Zimbabwe, on 20 farms where causes of Impala mortality were studied, 34% of natural deaths were due to predation and 10% to disease (acute fascioliasis, verminous aneurysm/*E. coli* septicaemia or clostridial infection). Endoparasites did not cause death among Impalas and losses associated with ticks and tick-borne diseases were rare (Knottenbelt 1990). Mortality due to anthrax has also been recorded (e.g. Prins & Weyerhaeuser 1987).

Conservation IUCN Category: Least Concern (*A. m. melampus* – Least Concern; *A. m. petersi* – Vulnerable D1). CITES: Not listed.

Although Impalas seem to have been eliminated from some parts of their range (such as Burundi), they are still relatively widespread and common and abundant in numerous protected areas across their range. Owing to its high rate of reproduction and great adaptability, the Impala has become of prime interest for meat production (e.g. Fairall 1983, Bothma 1989), not only on wildlife ranches but also in remote communal areas (e.g. Feron *et al.* 1998, Auerbeck 2001, 2002, Bourgairel *et al.* 2001).

The main threat to Common Impala seems to be active poaching at the edge of, and within, protected areas (with strong influence on densities as well as population structure) combined with agro-pastoral development (Setsaasa *et al.* 2007, Auerbeck *et al.* 2009b). However, the type of hunting may skew sex and age ratios in the population very differently (Setsaasa *et al.* 2007, Auerbeck *et al.* 2009b). Hunting risk is also likely to affect Impala behaviour, such as change in habitat selection or waterhole attendance (Crosmary *et al.* 2012).

Poaching, livestock development and severe drought are considered the main factors for the decline of *A. m. petersi* (Green & Rothstein 1998, East 1999). The introduction of 180 individuals of *A. m. petersi* from Kaokoland to the west of Etosha N. P. between 1968 and 1971 helped promote the conservation of the subspecies, and a few were translocated from Etosha N. P. to private game farms in Namibia. Matson *et al.* (2004) analysed 21 translocations of Black-faced Impalas to 20 Namibian game farms that occurred between 1970 and 2001, with the aim of identifying characteristics of the translocated populations

and the release sites that significantly correlated with the success of the translocations (determined by whether the population had a positive growth rate). Initial population size was paramount to the success of translocations, and populations of over 15 individuals were more successful, while the presence of Cheetahs also influenced the success of translocated populations; in the presence of this predator, smaller translocated populations of Black-faced Impalas were less likely to be viable than larger populations.

The introduction of *A. m. melampus* to ranches and conservancies neighbouring Etosha N. P. may contribute a threat to *A. m. petersi* through hybridization. Green & Rothstein (1998) estimated that about one-quarter of all privately owned Black-faced Impalas occur in mixed herds with Common Impalas. In a recent study, Lorenzen & Siegmund (2004) analysed 127 Black-faced Impala individuals from five subpopulations in Etosha N. P. to determine whether any hybridization had taken place within the park, but could not find any evidence for hybridization between the two subspecies.

Measurements

Aepyceros melampus

A. m. melampus

HB (♂♂): 1402 (1271–1504) mm, n = 5

HB (♀♀): 1352 (1173–1506) mm, n = 55

T (♂♂): 280 (220–340) mm, n = 33

T (♀♀): 258 (205–300) mm, n = 23

HF c.u. (♂♂): 855 (820–905) mm, n = 5

HF c.u. (♀♀): 767 (672–860) mm, n = 55

E (♂♂): 145 (130–157) mm, n = 33

E (♀♀): 140 (130–155) mm, n = 23

WT (♂♂): 45.7 (31.3–61.5) kg, n = 32

WT (♀♀): 38.5 (23.2–60.5) kg, n = 81

Zambezi Valley and Hwange N. P., Zimbabwe (H. Fritz & M. Bourgairel pers. obs.; V. Wilson pers. comm.)

Sh. ht (♂♂): 873 (785–925) mm, n = 28

Sh. ht (♀♀): 800 (790–810) mm, n = 12

WT (♂♂): 56.9 (46.0–64.4) kg, n = 28

WT (♀♀): 42.1 (38.93–45.69) kg, n = 12

Serengeti N. P., Tanzania (Sachs 1967, with slightly different body measurements)

Maximum recorded horn length is 91.7 cm for a pair of horns from the Masai Mara National Reserve, Kenya (Rowland Ward)

A. m. petersi

HB (♂♂): 1350 (1240–1450) mm, n = 7

WT (♂♂): 63.0 kg, n = 10*

WT (♀♀): 50.4 kg, n = 9*

N Namibia (Joubert 1971)

*Range not available

Maximum recorded horn length is 68.0 cm for a pair of horns from Grootfontein, Namibia (Rowland Ward)

Key References Auerbeck 2002; Bourgairel 2004; Dunham 1980; Gaidet 2005; Jarman 1979; Jarman & Jarman 1974; Joubert 1971; Matson 2003; Murray 1981, 1982a, b.

Hervé Fritz & Mathieu Bourgairel

Tribe ALCELAPHINI

Alcelaphines



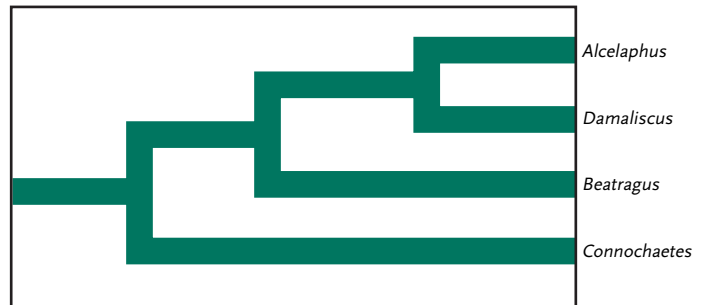
Lichtenstein's Hartebeest
Alcelaphus buselaphus lichtensteinii.

Alcelaphini Brooke, 1876. In: Wallace. Geog. Distr. Anim. p. 224.

The Alcelaphini are a very well-defined and distinctive group of large, long-faced, heavily horned animals. Molecular clocks have suggested that ancestral Alcelaphini might have first diverged from ancestral Hippotragini about 17 mya and from an aepycerotine basal lineage some 20 mya (Hernández Fernández & Vrba 2005). Living genera in this tribe include *Alcelaphus*, *Damaliscus*, *Connochaetes* and *Beatragus*. The Impala *Aepyceros melampus* was once regarded as an early alcelaphine (Gentry 1978, Vrba 1984), an inclusion that has been rendered obsolete by molecular studies that show *Aepyceros* occupies a basal position within the Antilopinae, its ancestral stock having evolved substantially earlier than the supposed emergence of the earliest alcelaphines. Therefore, while the Impala and alcelaphines do share a very ancient common ancestry this does not merit a common taxon.

There are several fossil genera and, judging from their abundance in the fossil record, the group has been ecologically successful for some 8 million years and even spread to India (where they later became extinct). A giant form, *Megalotragus*, was larger than any living species and carried horns that were over a metre long, of an undulating, convex/concave structure and with a wide span. Alcelaphines have very peculiar cranial morphology and radical remodelling of faces and horns has been assisted by horn pedicels and foreheads being hollow. Fossils reveal that the hammer-shaped head of *Alcelaphus* evolved after the formation of a pedicel, a strong downward turn in the muzzle and an extraordinary phylogenetic upward and sideways twisting of the horn axes. For a discussion of the elaboration of horn shapes in Alcelaphini, see Kingdon (1982).

Alcelaphines are nearly always specialist grazers, inhabitants of the African savanna habitat and its fringes and are classified as roughage feeders (Hofmann 1973). The genera have radiated to occupy distinct ecological niches, notably broad, open grassy valleys (*Alcelaphus*); seasonally inundated valley bottoms with rank grass (*Damaliscus lunatus*); flat open pastures with short grass (*Connochaetes*); and dry open savannas (*Beatragus*). Alcelaphines seem to have specialized on the growth form of grasses typical for one part of the wet-dry seasonal cycle: wildebeest (*Connochaetes* spp.), which have no second lower premolar in adults (Attwell 1980), have very broad flat incisors and are adapted for unselective cropping of short grass swards: the population of Common



Tentative phylogenetic tree for Alcelaphini (modified after Arctander *et al.* 1999 and Hassanin *et al.* 2012).

Wildebeest *Connochaetes taurinus* that resides on the short-grass plains of the Serengeti ecosystem is a classic case. *Damaliscus lunatus* feeds most efficiently from medium-length grasses and in doing so selects a high proportion of leaf blades. Hartebeest, with a long pointed muzzle and narrow toothrow, excel at selecting leaf blades and sheaths from long senescent swards in the dry season. At less favoured times of year, all are forced to eat less preferred growth stages (for example, all graze on green flushes at the start of the rains and all will eat senescent swards in times of drought). However, differences in dietary preferences help explain the coexistence of these genera.

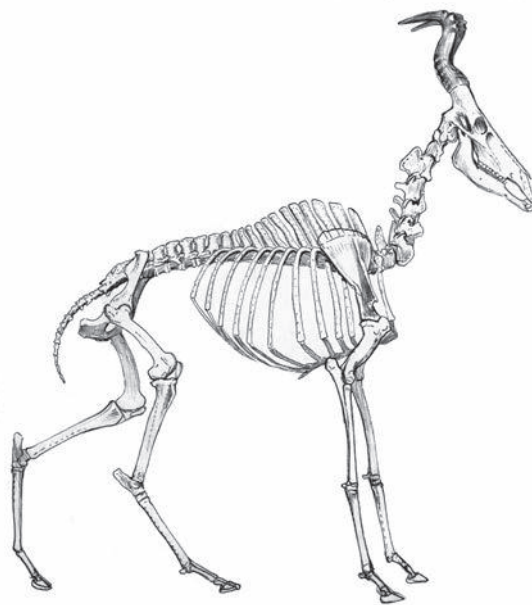
Feeding specializations also explain broad differences in migratory habits and distribution. Thus, wildebeest depend heavily on short green swards, which help fuel the costs of reproduction. Costs are greatest when ♀♀ are lactating and at this time of their reproductive cycle they seek actively growing, short-grass areas where seasonal rainfall has boosted productivity. In the dry season they have to find other reserves of food, so that seasonal pastures are often some distance apart. Spectacular, large-scale migrations such as those of the Serengeti ecosystem are the result. Common Wildebeest and Topis *D. l. jimela* are both dependent on high levels of rainfall with Topis, in particular, relying on sumplands, which, in turn, dictate much of their geographical distribution. By contrast, the feeding style of Hartebeest allows them to select a high-quality diet (in relation to what is available) in the same general area throughout the year: they thus tend to be relatively sedentary. As dry season specialists, Hartebeest can survive in more arid areas, as shown by the existence of Hartebeest in Ethiopia and Eritrea and (until exterminated by modern humans) in North Africa and the Middle East.

Keys to alcelaphine success lie in their adoption of a grass diet out on open valleys and plains, where they withstand intense solar radiation so long as they have access to water. In such habitats their exceptional speed and stamina mitigates their increased exposure to predators. Elongation of the legs (as an anti-predator and enlarged range adaptation) has been matched by elongation of the skull, but not the neck (see figures in Kingdon 1982).

There is little sexual dimorphism although ♂♂ are slightly taller and more heavily muscled, particularly in the neck and shoulders. Females have one pair of inguinal nipples. Both sexes have horns. The shape is similar in the two sexes but those of ♂♂ are heavier and stronger.



Lelwel Hartbeest *Alcelaphus buselaphus lelwel* myology.



Lelwel Hartbeest *Alcelaphus buselaphus lelwel* skeleton.

Males fight by springing forward into a 'clash' of the horns while falling downwards onto their 'knees'. Horn clashes are followed by vigorous 'wrestling' in which ♂♂ try to force the head of the opponent to one side and then hook into its unprotected side using the sharp horn tips. Males may fight for hours and deaths have been recorded.

All alcelaphines have strongly polygynous mating systems, which are shaped by the feeding and reproductive ecology of ♀♀ (Gosling 1986). Females try to maximize food intake and quality for reproduction (the high metabolic costs of lactation are their main problem) by seeking high-quality food. During movements between pastures they minimize the chances of being killed by scanning for predators and by joining groups. Group membership is usually labile although ♀♀ may be accompanied by their offspring for several years. In a few cases group membership is more constant (as in those Topi populations where the territories of ♂♂ are sufficiently large to encompass the entire home-range of female groups and their young). Male mating tactics are determined by the predictability of female movements and the most common outcome, for all alcelaphines, is 'resource-defence polygyny' (Emlen & Oring 1977): ♂♂, therefore, defend areas of grassland that ♀♀ need for food and attempt to mate with them as they arrive. Such territories may be occupied for long periods or only briefly (as in the case of rutting migratory wildebeest, where territories are established for only a few hours or days in the path of the annual migration).

'Lekking', where ♂♂ join clusters and give every appearance of displaying to attract ♀♀, occurs in Topis under quite specific conditions, but has not been seen in any other alcelaphine species. The Topi ♂♂ that achieve the most matings appear to do so because they occupy territories that are preferred by ♀♀, and not because of any individual display characteristics; thus ♀♀ appear to drive this system. However, the lek-like clusters result in highly skewed mating success for the ♂♂. Interestingly, antelopes of the genera *Damaliscus* and *Alcelaphus* do not perform flehmen, and lack the incisive papilla and ducts that constitute the oral connection to the vomeronasal organs (Hart *et al.* 1988).

Scent-marking is well developed in all living alcelaphines. All possess preorbital glands, but these are less prominent than in groups such as the gazelles or Oribi *Ourebia ourebi*. Some species such as the

Topi leave visible deposits of secretion on the tips of grass stems, but most do not have invaginated glands and instead rub the surface of the gland onto twigs, on the ground or on themselves. Pedal glands are well developed on the forefeet of all species, although some have rudimentary glands on the hindfeet; inguinal glands are absent. The most developed expression of marking is piles of dung, which are deposited throughout territories but are largest and most conspicuous where ♂♂ regularly meet their neighbours along boundaries. These encounters are a mixture of agonistic behaviour and scent-marking behaviour with each ♂ sniffing, kneeling, head rubbing and defecating in turn. Boundary dung piles are made even in the tiny lek territories of Topis. Territorial male alcelaphines also 'self-anoint', rubbing the substances used to mark their territories onto their own bodies. Thus, ♂♂ rub preorbital gland secretions onto their shoulders, leaving conspicuous smears, or lie on or even roll in their dung piles. This behaviour may be linked to 'scent-matching', a mechanism that is thought to reduce the cost of territory defence by allowing intruders to match the smell of defenders to that of their territory so that they are more likely to withdraw without risking dangerous combat (Gosling 1982). Territorial ♂♂ also use visual advertisement of their status, including standing on small elevations such as termite mounds.

Over centuries the great biological success of Alcelaphini has been undermined by the intrusion of livestock, especially intensive cattle pastoralism. The survival of alcelaphines, therefore, lies at the heart of the development/conservation debate because livestock compete directly for pasture and alcelaphines are generally displaced once cattle numbers have reached critical levels. Migratory populations have also suffered massive losses when fencing, introduced to enclose stock or control disease, has cut off migration routes. These factors, combined with habitat loss and overhunting, have led to overall decline in alcelaphine populations throughout most of Africa. The only exceptions are in some eastern and southern African localities, where some form of sustainable commercial use has resulted in stable or even locally increased populations.

L. Morris Gosling & Jonathan Kingdon

GENUS *Beatragus*

Hirola

Beatragus Heller, 1912. Smithsonian Misc. Coll. 60 (8): 8.



Hirola *Beatragus hunteri* head myology.

Beatragus is a monotypic genus endemic to SE Kenya and SW Somalia. The generic status of the Hirola has been controversial but it is now recognized as a lineage very distinct from *Damaliscus* and *Alcelaphus*, yet filling an ecological niche similar to *Alcelaphus* (Kingdon 1982, Kumamoto *et al.* 1996, Pitra *et al.* 1998, Grubb 2005). *Beatragus* probably pre-dates the common ancestor of *Damaliscus* and *Alcelaphus* (an alcelaphine that would have closely resembled the extinct genus *Parmularius*) (Gentry 1978). Karyological work supports this conclusion by showing that *Beatragus* is the sister-group of *Damaliscus* + *Alcelaphus*, branching off from the lineage before the latter two genera differentiated. *Damaliscus* + *Beatragus* would be a parapatric and, therefore, unacceptable entity. It now seems that all parties would agree to the treatment of *Beatragus* as a distinct genus.

Beatragus represents a long-lasting phylogenetic lineage dating to ca. 3.1 mya (mid-Pliocene; Kumamoto *et al.* 1996, Pitra *et al.* 1998). The fossil record dates to the early Pleistocene (Gentry 1974, 1978, 1990). *Beatragus* is represented in the fossil record by a larger bodied species, *B. antiquus* (Leakey 1965), which might have approached twice the body weight of *B. hunteri*. Fossils of *Beatragus* have been found at Olduvai, Tanzania (Leakey 1965, Gentry & Gentry 1978), Omo R., Ethiopia (Gentry 1985), Gobaad, Djibouti (Thomas *et al.* 1984), and Elandsfontein, South Africa (Gentry 1974, Gentry & Gentry 1978, Kingdon 1982).

The fossils of *Beatragus* indicate that this genus was widely distributed and probably occupied a tall-grass grazing niche comparable to the one now occupied by *Alcelaphus*. This likely evolutionary history has considerable implications for understanding the biology and management of Hirola. These implications are discussed in the species profile.

Gentry (1974) suggested that *B. antiquus* might be the direct ancestor to *B. hunteri*. As such, *B. hunteri* may represent a somewhat dwarfed



Hirola *Beatragus hunteri* adult male frontal and rear views.

species living in a small, ecologically impoverished area on the fringe of the former range of *B. antiquus*. If so, the exceptionally heavy and disproportionately robust horns of *B. hunteri* (compared with antelopes of similar shoulder height (e.g. Blesbok *Damaliscus pygargus phillipsi* or Addax *Addax nasomaculatus*) might owe as much to larger ancestors as to any current adaptive advantage for hefty horn stems.

Thomas M. Butynski & Jonathan Kingdon



Hirola *Beatragus hunteri* adult male.

Beatragus hunteri HIROLA

Fr. Antilope Hirola; Ger. Hunters Leierantilope

Beatragus hunteri (P. L. Sclater, 1889). Proc. Zool. Soc. Lond. 1889: 58. 'Africam orientalem, in ripis fl. Tana' (East bank of Tana R., Kenya).

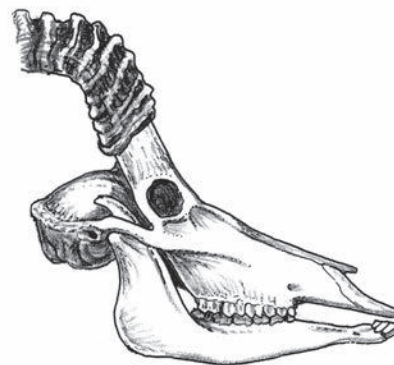


Hirola *Beatragus hunteri*.

See Butynski (2000) for discussion concerning use of the common name Hirola instead of Herola. The vernacular name 'Hunter's Hartebeest' (in honor of H.C.V. Hunter, who collected the type specimen in 1887) is not acceptable as this species is not a Hartebeest *Alcelaphus buselaphus*.

Taxonomy Monotypic. Originally named *Cobus hunteri*. Renamed *Damaliscus hunteri*, and even considered conspecific with the Topi *Damaliscus lunatus* (Haltenorth 1963), but fossil and DNA evidence indicate *Beatragus* has been distinct from *Damaliscus* for ca. 3.1 million years (Pitra *et al.* 1998; and see Kumamoto *et al.* 1996); inclusion in *Beatragus* is now generally supported (Kingdon 1982, Gentry 1990, Grubb 2005). Synonyms: none. Chromosome number: $2n = 44$ (FN = 60). Eight metacentric/submetacentric and 13 acrocentric/telocentric pairs of autosomes; the X and Y chromosomes are acrocentric (Kumamoto *et al.* 1996).

Description Medium-sized antelope similar in appearance to a Hartebeest or Topi, but colour paler, build lighter and more graceful, face less elongated, withers much less elevated above hindquarters, and horns lacking a basal pedicle. Has inverted chevron between the eyes and 'spectacles' around the eyes. Inner ears white. Eyes, nostrils, lips, and tips of the ears black. Overall pelage uniform rufous-tawny becoming slaty-grey with age. Ventrums and insides of legs whitish-



Lateral view of skull of Hirola *Beatragus hunteri*.

tawny. Udder and hooves black. Tail white. Preorbital glands very large. Pedal glands on the forefeet. Inguinal glands absent. Females smaller than ♂♂.

Horns are long, lyrate, sharp-tipped, Impala-like, but much thicker at the base. Dental formula: $I^{0/3}, C^{0/1}, P^{3/2}, M^{3/3} = 30$, with the second lower premolar absent (as in *Connochaetes*).

Geographic Variation None recorded.

Similar Species

Damaliscus lunatus. Reddish-brown to purplish-brown pelage; black patches on outer thigh; tail blackish; lacks inverted white chevron between eyes and white 'spectacles' around eyes. Sympatric (*D. l. topi*) over south-eastern half of Hirola range (Butynski 2000).

Distribution Endemic to Africa. The Hirola has a very restricted natural geographic range, being endemic to SE Kenya and SW Somalia. Confined to a region of grassland, light shrub and woodland that lies parallel to the Indian Ocean and which is bounded by dry *Acacia* scrub to the north-west and by coastal forest and tsetse fly to the south-east (Bunderson 1981).

Historical Distribution The Hirola formerly occurred over a region 40–200 km inland from, and parallel to, the Indian Ocean from Garsen and Bura on the lower Tana R. in SE Kenya north-east to Lag Dere in SW Somalia. The historic geographical distribution covered ca. 17,900 km² in Kenya and ca. 20,500 km² in Somalia. The geographical distribution probably did not change greatly between the time of discovery (1887) and the 1970s (Bunderson 1981, East 1999, Butynski 2000).

Current Distribution In Kenya, the Hirola now occurs between Garsen, Bura and Galma Galla/Kolbio over an area of ca. 8000 km² (Butynski 2000). The current status in Somalia is not known. The small population in Tsavo East N. P., Kenya (not mapped), originated from a translocation of 30 animals from Garissa District conducted in 1963. It is thought that most of these perished soon after release and that the size of the



‘effective founder population’ was only 11–19 animals (Butynski 2000). The extent of occurrence of this population was ca. 500 km² in 2011 (Probert 2011). In this profile, the population in SE Kenya and SW Somalia is referred to as the ‘natural population’, whereas the one in Tsavo East N. P. is referred to as the ‘Tsavo population’.

Habitat Hirola inhabit a flat and gently undulating coastal strip where the mean annual rainfall ranges from 350 mm (north-west) to 600 mm (south-east), and the altitude ranges from 220 m (north-west) to 40 m (south-east). The climate is hot throughout the year, with annual minimum and maximum temperatures averaging ca. 21 °C and ca. 33 °C, respectively. Vegetation varies from waterless dry thorn bush (north-west), to open bushed grassland, to light woodland, to lush savanna grassland (south-east). The preferred habitat is seasonally flooded, open grassland with scattered small shrubs and trees on well-drained white sand soils where the mean annual rainfall is 400–500 mm. Highest densities (7.14 ind/km²) occur where there is a good cover (30–50% cover) of green grass (*Chloris mossambicensis*, *Chloris roxburghiana*, *Dactyloctenium aegyptium*, *Digitaria milanjiana*, *Enteropogon somalensis*, *Sporobolus ioclados* and *Sporobolus pellucidus*) of short to intermediate height (10–50 cm). Hirola prefer short leafy swards of grass formed by fire, or by the combined grazing pressure of wildlife and domestic livestock (Bunderson 1981). Highest densities are attained in areas heavily used by domestic livestock where traditional Somali herding practices are maintained and livestock are highly mobile. However, Hirola avoid herds of livestock, areas of overgrazing, tall dense stands of grass and herbaceous vegetation, thick woodland, and forest. During the dry seasons (Jan–Mar, Jul–Sep) the distribution of Hirola in Kenya is compressed and concentrated in two areas of high-quality forage; one near the Tana R. between Masalani and Bura, and the other in the Galma Galla/Kolbio region (Bunderson 1981).

Competition with livestock and habitat degradation appear to be major problems for the Hirola as the range is presently seriously

overstocked and unsustainably grazed. A survey in 2011 of the entire current natural range of the Hirola found more than 100,000 livestock (sheep, goats, cattle, camels), or 232 livestock per individual Hirola (King *et al.* 2011a).

Abundance The natural population in Kenya during the 1970s was ca. 16,000 animals (Bunderson 1981). The population was estimated at 10,000–15,000 animals from 1973 to 1984, followed by a drastic decline (85–90%) between 1983 and 1985 (Butynski 2000). Ground surveys suggested the population was between 500 and 2000 Hirola in Kenya in 1995/96 (Andanje & Ottichilo 1999, Butynski 2000, Dahiye & Aman 2002). An intensive aerial survey was conducted in January 2011 over a 12,000 km² area that probably included the entire present natural range of the Hirola. A total of 245 individuals were observed, yielding a population estimate of 434 animals (S.D. = 30.2; King *et al.* 2011a). As such, Kenya’s population of Hirola has declined ca. 97% since the 1970s. Probably extinct in Somalia, but small numbers may occur north of Bushbush N. P. and at Lag Dere.

Tsavo East N. P. holds a translocated population that was estimated at 56–76 animals in 1995–96 (Andanje & Ottichilo 1999), 77 animals in 2000 (Andanje 2002), 105 animals in 2006 (S. A. Andanje pers. comm.), 100 animals in 2010 (Kock *et al.* 2010b) and 67 animals in 2011 (Probert 2011).

Adaptations Kingdon (1982) does not consider Hirola to have unusual ecological requirements, suggesting that it derives from a more generalized antelope than either *Alcelaphus* or *Damaliscus*. Since Hirola and *Alcelaphus* are allopatric, he further suggests that survival of the present relict population is due to absence of competition from *Alcelaphus*. *Alcelaphus* is a relatively recently evolved genus, the members of which have probably been kept out of the geographical range of the Hirola by sub-desert to the north, the Indian Ocean to the south-east and the Tana R. to the west.



Hirola *Beatragus hunteri* dorsal view of horns and skin fold on nape.

The structure of the gastrointestinal tract indicates that the Hirola is extremely well adapted to eat dry and coarse grasses, and has an excellent ability to preserve water (Hofmann 1996). Hirola drink water (J. King pers. comm.), but this appears to be a rare event (Butynski 2000). Foraging is concentrated in the post-dawn and pre-dusk hours in order to avoid the hot mid-day temperatures. During the heat of the day, Hirola generally rest in the shade of a shrub or small tree.

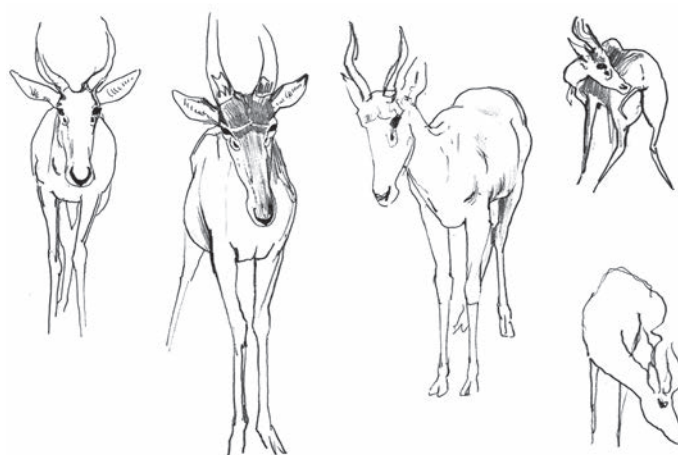
The nape skin of the adult ♂ is exceptionally thick, rolling up into a prominent fold behind the horns when the head is erect and ears pricked. This probably serves as a dermal shield during male horn-fighting. Kingdon (1982) observed that this fold is an accommodation of tough, inflexible skin to the demand for movement of the ears, which, as with many other bovids, are important signalling devices.

Foraging and Food Primarily grazers, Hirola browse on forbs when grass is scarce (Bunderson 1981, Cerling *et al.* 2003). They select short green grass with a high ratio of leaf to stem (Andanje & Ottichilo 1999). The most important grasses in the diet on the natural range probably include *Chloris myristachya*, *Cenchrus ciliaris* and *Digitaria* spp. (Kingdon 1982). In Tsavo, Hirola eat grasses that average 17 cm in height, cropping them at 4–16 cm above the ground. The plant species eaten most frequently here are *Digitaria rivae*, *D. macroblepora*, *Chloris barbaa*, *Sporobolus helvolus* and *Latipes senegalensis* (Andanje & Ottichilo 1999).

Social and Reproductive Behaviour Adult ♂ ♂ vigorously defend territories of good quality pasture. There is no information on size of territories held by ♂ ♂ except that they appear to be several square kilometres in area. Males mark their territory (mainly in the evenings) by kneeling on forelegs and rubbing their preorbital glands on vegetation and soil while slashing vegetation with their horns. This is followed by scratching the ground with the forefeet and by depositing dung. Non-territorial ♂ ♂ may live in bachelor groups of 2–38 animals (Bunderson 1981), sometimes in the company of Coastal Topis *D. lunatus topi*, Plains Zebras *Equus quagga*, Gerenuks *Litocranius walleri* and Giraffes *Giraffa camelopardalis* (Bunderson 1981, Kingdon 1982).

In the natural population, adult ♀ ♀ and their young form stable breeding groups of 5–40 individuals (mean = 8) (Bunderson 1981). In Tsavo, breeding groups ranged in size from 5 to 11 (mean = 7.5, $n = 8$) in one study (Andanje & Ottichilo 1999) and 6–14 (mean = 9.8, $n = 5$) in a later study (Probert 2011). Home-ranges of breeding groups in Tsavo overlap with the territories of 2–3 adult ♂ ♂ and vary in size from 12 to 40 km² (mean = 21 km², $n = 8$; S. A. Andanje pers. comm.). These groups are usually accompanied by one adult ♂ and led by either the adult ♂ or the dominant ♀. The adult ♂ is presumed to be the holder of the territory on which the breeding group is resident. Breeding groups move from one adult male territory to another in search of food.

In Tsavo, two breeding groups moved 3.5–4.5 km/day (S. A. Andanje pers. comm.). However, these groups were probably much more sedentary than groups in the natural population. Subadults leave the breeding group soon after weaning (ca. 9 months of age) when they are chased out by adult ♀ ♀ (S. A. Andanje pers. comm.). They then occupy areas peripheral to breeding groups where they live alone or in small mixed- or single-sex groups of up to three individuals (Andanje & Ottichilo 1999). Mixed aggregations of



Hirola *Beatragus hunteri*.

breeding groups and bachelor groups up to 300 animals have been observed in the natural population at the end of the dry season when isolated showers produce patches of green forage (Bunderson 1981).

Males perform flehmen during mating (Butynski 2000). Flehmen has not been recorded in either *Alcelaphus* or *Damaliscus*. This is probably of considerable taxonomic significance as it supports the concept that the Hirola is an ancient alcelaphine that, like wildebeest, retains the urine testing behaviour found (as far as it is known) in all other bovids (Estes 1991a). Females leave the group, either alone or with an adult ♂, just prior to calving. Calves do not join groups until 1–2 months of age.

On the natural range, Hirola associate most frequently with Beisa Oryxes *Oryx beisa*, Gerenuks and Giraffes (Bunderson 1981). In Tsavo, S. A. Andanje (pers. comm.) found breeding groups of Hirola alone 33% of the time, in association with Peter's Gazelles *Nanger (granti) petersii* 67% of the time, with Common Warthogs *Phacochoerus africanus* 8% of the time, and with Beisa Oryxes 8% of the time. Probert (2011) found Hirola in association with other species 92% of the time ($n = 38$ encounters); association with Peters' Gazelles was most common (28% of encounters), followed by Plains Zebras (12%).

Reproduction and Population Structure Polygamous. Mating takes place primarily from Feb to Mar at the start of the long wet season. Births occur from Aug to Feb during the short wet season (Sep–Nov) and short dry season (Dec–Jan). The birth peak is Oct–Nov (Kingdon 1982, S. A. Andanje pers. comm.). The timing of the birth season means that optimal grazing is available from Nov to Jan for lactating ♀ ♀ and growing calves. In captivity, single calves were born after a gestation of 227–242 days (Smielowski 1987). Each year, about half of the adult ♀ ♀ in Tsavo give birth (S. A. Andanje pers. comm.).

Data on age at sexual maturity in the wild are not available, but captive ♀ ♀ mated successfully at 1.4 and 1.7 months of age (Smielowski 1987). Female Hartbeest are sexually mature at 1.5–2 years of age and generally give birth to their first young at 2–3 years of age. Male Hartbeest are adult-sized at three years of age but probably take at least four years to establish territories and mate (Kingdon 1982). These parameters probably also apply to the Hirola.

There are no data on the age/sex ratios of Hirola on the natural range. In Tsavo, the population of 76 Hirola in 1996 comprised 30 (39%) immatures and 46 (61%) adults. The sex ratio among adults

was 13 (28%) ♂♂ to 33 (72%) ♀♀. For this population as a whole, 45 (59%) of the animals were ♀♀. Of these 76 Hirola, 60 lived in eight herds, while 16 lived alone (five adult ♂♂ and 11 subadult ♂♂ and ♀♀; Andanje 2002). A 2011 study in Tsavo found a population comprising 21 (31%) immatures and 46 (69%) adults, an overall sex ratio of 24 (44%) ♂♂ to 30 (56%) ♀♀, and an adult sex ratio of 16 (35%) ♂♂ to 30 (65%) ♀♀. Of the 24 ♂♂, six were with nursery herds and 16 were either alone or in bachelor herds (Probert 2011).

In Tsavo, there is high mortality among calves 2–4 weeks of age, with about half of the calves dying during their first month (S. A. Andanje pers. comm.). Likewise, in captivity, 32% of 19 calves died before they were three months of age (Smielowski 1987). A captive animal born at Gladys Porter Zoo, Texas, survived 15.2 years (Weigl 2005).

Predators, Parasites and Diseases There is little information on predation of Hirola. Lions *Panthera leo*, Leopards *P. pardus*, Cheetahs *Acinonyx jubatus*, African Wild Dogs *Lycaon pictus* and Spotted Hyenas *Crocuta crocuta* are known predators (Gibbon 2010, King *et al.* 2011b) and jackals *Canis* spp., Yellow Baboons *Papio cynocephalus*, African Rock Pythons *Python sebae* and large eagles probably prey on newborns. Preliminary data suggest that Lions are the main predators of Hirola on the natural range as well as in Tsavo (Gibbon 2010, S. A. Andanje pers. comm.). During 2010, on the 40 km² Ishaqbini Conservancy (see below), almost 15% of the known Hirola were lost to predation, mainly by Lions and African Wild Dogs, but also to Leopards (King *et al.* 2011b). Predation is believed to be one of the primary factors currently suppressing the recovery of the greatly reduced natural population (Gibbon 2010, Kock *et al.* 2010a).

Almost nothing is known concerning diseases. However, like other African bovids, Hirola are susceptible to rinderpest (Kock *et al.* 1999, Butynski 2000). It is not unusual for rinderpest to cause more than 50% mortality in populations of wild ungulates. Confirmed epidemics of rinderpest occurred among cattle in the natural range of the Hirola in 1962–63 and in 1982–83, with a probable epidemic in 1972–74. During 1983–85 the Hirola population experienced a major crash from which it has not recovered. There was severe drought and rinderpest during this period. It is suspected that this combination of factors was responsible for the crash (East 1999, Butynski 2000). Of particular concern is the likelihood that Hirola are susceptible to diseases harboured by domestic livestock, especially goats and cattle; outbreaks of contagious bovine pleuropneumonia, haemorrhagic septicaemia and tuberculosis occur among livestock within the natural range of the Hirola (Magin 1996). In captivity, Hirola have suffered from acidosis, bloat, tuberculosis and mycobacterioses (Smielowski 1987).

No blood parasites were found in samples collected from 40 Hirola in 1996 (R. Kock pers. comm.). There is no information on ectoparasites.

Conservation IUCN Category: Critically Endangered A2acd. CITES: Not listed.

This is one of Africa's most threatened large mammals and perhaps its most threatened antelope; low numbers are due to a combination of poaching, disease, drought, habitat loss, predation and competition with livestock (East 1999, Butynski 2000, Kock *et al.* 2010a, King *et al.* 2011b). In 1979, the natural population in Kenya comprised

ca. 16,000 animals on ca. 17,900 km². By 1995–96, there were only 500–2000 animals on ca. 8000 km². Today, the estimate is 402–466 animals (King *et al.* 2011a). Somalia had ca. 2000 Hirola in 1979, but has few, if any, today (Butynski 2000, King *et al.* 2011a). The introduced population in Tsavo East N. P. is currently fairly static at ca. 75–100 individuals (Kock *et al.* 2010b, Probert 2011).

The situation for the Hirola is grave, given its extremely rapid decline and the severe political and environmental problems that currently prevail over the natural range. The extinction of the Hirola would represent the first extinction in historic times of a genus of mammal endemic to the African continent. There is an urgent need to improve the level of management and protection of the one natural population of Hirola, particularly in Arawale National Reserve and in the Masalani and Galma Galla/Kolbio regions of Kenya, and in the Bushbush N. P. and Lag Dere region of SW Somalia. Community conservation and anti-poaching activities must be established over a large portion of the Hirola's remaining range. However, insecurity for conservation workers is a serious problem, making conservation efforts in this region both risky and expensive.

Consideration should be given to establishing protected areas at Galma Galla and Lag Dere, and to expanding the Tana River Primate National Reserve east to include at least 300 km² of prime habitat for Hirola. Recently, the Ishaqbini Hirola Community Conservancy established the Ishaqbini Conservancy (190 km²), which is contiguous with the Tana River Primate National Reserve to the west. The primary goal of the Ishaqbini Conservancy is to conserve the Hirola. There are ca. 150 Hirola on the Ishaqbini Conservancy, or roughly 25% of the natural population. A priority conservation action at this time is the construction of a 27.7 km² predator-proof sanctuary near the Ishaqbini Conservancy from which all large predators will be removed and within which Hirola numbers can increase. Hirola from this site (the 'Ishaqbini Sanctuary') will be released to supplement the contiguous natural population (Kock *et al.* 2010a).

The population in Tsavo East N. P. should be encouraged to expand at a faster rate. To this end, a predator-proof sanctuary (60–80 km²) is under consideration (King *et al.* 2011b, Probert 2011). New populations need to be founded on at least four additional sites in Kenya, including private ranches. A self-sustaining captive population must also be established among the better zoos of Europe and North America (the last Hirola in captivity died in 2002; Probert 2011). The current research programme on the Hirola needs to move its focus from Tsavo to the natural range. The priorities for research are: (1) to determine what factors are limiting the size of this population, and (2) to find additional ways to promote the growth of this population.

In Kenya, these and other recommendations for the long-term conservation of the Hirola have been put forth in a conservation action plan (Magin 1996) and in a conservation evaluation report (Butynski 2000). These recommendations are now part of the current conservation and management plan for the Hirola in Kenya (Hirola Management Committee 2004) and some of them are being acted upon by the Kenya Wildlife Service in conjunction with the Hirola Management Committee and local conservation NGOs.

Measurements

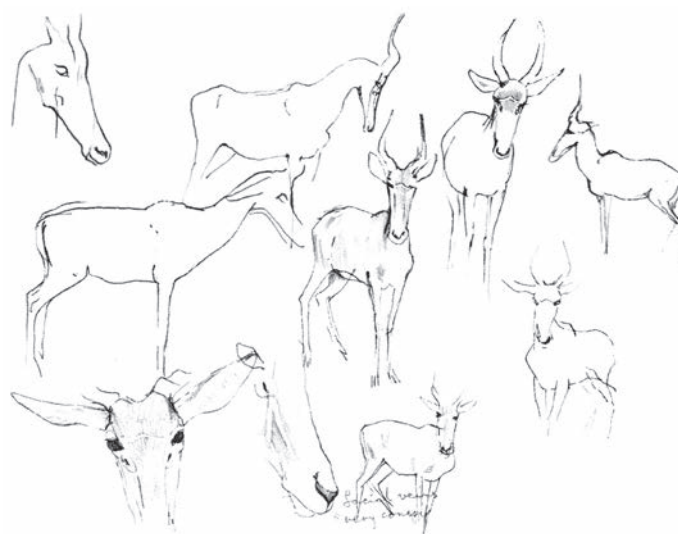
Beatragus hunteri

HB (♀♀): 1740 (1640–1800) mm, n = 4

T (♀ ♀): 390 (360–410) mm, n = 5
 E (♀ ♀): 180, 190 mm, n = 2
 Sh. ht (♀ ♀): 1020 (950–1100) mm, n = 3
 WT (♀ ♀): 92.0 kg, n = 1
 Kenya (R. A. Kock pers. comm., T. M. Butynski pers. obs.)
 Maximum recorded horn length is 72.3 cm for a pair of horns from
 Kenya (Rowland Ward)

Key References Andanje 2002; Andanje & Ottichilo 1999;
 Bunderson 1981; Butynski 2000; Kock *et al.* 2000a.

Thomas M. Butynski



Hirolo *Beatragus hunteri*.

GENUS *Damaliscus*

Damalisks

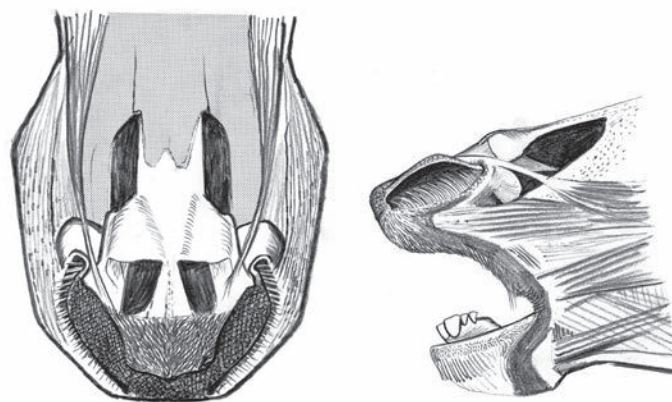
Damaliscus Sclater & Thomas, 1894. Book of Antelopes 1 (part 1): 3, 51.

Two species are recognized, *Damaliscus lunatus* and *D. pygargus*, which are medium-sized antelopes, although the tropical *D. lunatus* are twice as heavy as the southern *D. pygargus*. Within each species there are subspecies that are so distinct that a case could be made for classifying them as different species, and indeed they have been treated as such by several authors (Allen 1939, Grubb 2005; and see Cotterill 2003a). The Tsessebe (*D. l. lunatus*), for example, has quite different horns from the northern Coastal Topi (*D. l. topi*) and Tiang (*D. l. tiang*), and Blesbok (*D. p. philippi*) have much less colour contrast compared with Bontebok (*D. p. pygargus*). Both these 'bastard hartebeests' have characteristic raised shoulders like their close relative the Hartebeest *Alcelaphus buselaphus*.

The pelage of all species is basically brown, chestnut in the north to chocolate in the south, and they have black patches on the head, shoulders and hindquarters. The pelage is characterized by a striking, shiny hue not found in other ungulates. This appears to be an adaptation to reduce heat stress when there is no shade available, as in the treeless Highveld regions of South Africa, and the open grasslands and wetlands of Jonglei District (Sudan). Their colouration is made even more striking by their yellow or white lower limbs, especially in the Bontebok. These adaptations strengthen the visual impact of their ritualized agonistic and sexual displays (see species profiles).

The genus *Damaliscus* evolved in Africa from an ancestor that resembled the Hirolo *Beatragus hunteri* and Impala *Aepyceros melampus*. They are water-dependent grazers that specialize in high-quality grasslands (flood-plains for *D. lunatus* and 'sweetgrass' Highveld for *D. pygargus*). Hartebeest, in contrast, are specialized grazers of low-quality forage: they have lower metabolic rates and are less water-dependent.

Along with the Hartebeest, the genus *Damaliscus* was until recently the most widely distributed of African antelopes and occupied the grasslands and savannas from Senegal to Somalia and the Cape. They are a component of all the major migratory grazing systems,



Topi *Damaliscus lunatus jimela* dissection of nasal cartilage and nostrils. Cartilaginous modelling is shown in white (left).

and dominate the one in the S Sudan. Their mouths are narrow, which gives their head a sharp appearance, and their incisor arcade is narrower relative to their body size than that of the short-grass grazing wildebeest (*Connochaetes* spp.); none the less, they retain the typical bovid dentition of 32 teeth (cf. 30 in *Connochaetes* and *Beatragus*). The adaptations of *Damaliscus* allow them to extract diets of high quality (with a large proportion of green leaf) from senescent swards when that is all that is available: in the southern African winters, *D. pygargus* can survive on senescent sourveld, and in the tropical dry seasons *D. lunatus* survive, and breed, on medium to tall, mature grasslands. Comparing the two *Damaliscus* clusters, Capellini (2006) found that mean annual rainfall was the best predictor of body-size: the rich, sumpland pastures favoured by the larger-bodied *D. lunatus* complex contrasted with the less productive veld and Cape pastures that sustain the smaller-bodied *D. pygargus*. The mouth shape of wildebeest allows them to achieve higher rates of grass intake on short green lawns, from which they can exclude *Damaliscus*: when

they coexist, competition with wildebeest is likely to be a major process determining the abundance of *Damaliscus* species.

The usual mating system of *Damaliscus* is resource territories that ♀♀ use in a transient manner, though in some low-density populations a group of ♀♀ may remain on the same territory for a year or more. In high-density populations, where the scale of the habitats allows the formation of large herds (e.g. in East African flood-plains), most of the animals live in a few large mixed-sex herds, up to 1500 animals. In such circumstances, leks may appear, with ♂♂ spaced as close as

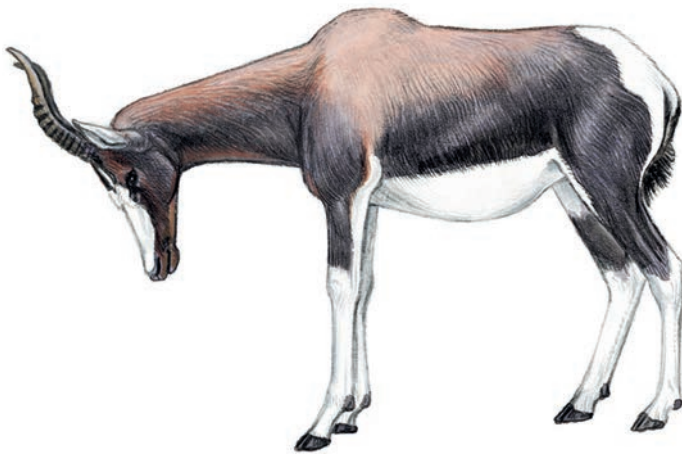
25 m apart on knolls, which the ♀♀ visit when in oestrus. Leks may evolve from groups of successful resource territories, with weaker ♂♂ establishing themselves around the territories of successful ones. The function of these leks is debated: they may result from mate choice by the ♀♀; oestrous ♀♀ may also use the leks to avoid harassment in the mixed-sex herds (Gosling & Petrie 1990, Clutton-Brock *et al.* 1993, Bro-Jørgensen 2003a).

Patrick Duncan

Damaliscus pygargus BONTBOK / BLESBOK

Fr. Bontebok (Blesbok); Ger. Buntbock (Blessbock)

Damaliscus pygargus (Pallas, 1767). Spicil. Zool. 1: 10. No locality. Since restricted to South Africa, Western Cape Prov., Caledon, Swart River (Bigalke 1948).



Bontebok *Damaliscus pygargus pygargus*.

Taxonomy The Bontebok *D. p. pygargus* and the Blesbok *D. p. phillipsi* have been considered as separate species in the past (e.g. Allen 1939; and see Essop *et al.* 1991), but are currently regarded as conspecific (Meester *et al.* 1986, Grubb 2005). The scientific name has been the subject of some confusion, as it has been argued that since a type specimen 'which is indeed a Bontebok' does not exist, the former name *Damaliscus dorcas*, which was used for more than half a century, is invalid (Rookmaaker 1989, 1991). The major reason for the confusion is the fact that the similarly marked Blesbok was discovered on the inland plains of the Free State some 100 years after the Bontebok, and separated by a belt at least 320 km wide at its narrowest from the range of the latter (Bigalke 1955, Skead 1958). The colonists did not distinguish between the two animals. Grubb (1999, 2004, 2005) attributed the original description to Pallas (1766), in which the author redescribed the Bontebok, because of perceived confusion, as *Antelope pygargus*. Grubb (1999) implies, however, that despite the nomenclatural and other problems, Pallas clearly had the Bontebok in mind when he first described *Antelope dorcas* in 1766.

The nomenclatural history of the Blesbok, although also complex, is a little more straightforward. Burchell (1823) wrote of the Blesbok that he had 'taken the liberty of' in effect naming it '*albifrons*', but in Burchell (1836) he synonymized his *Antelope albifrons* with *A.*

pygargus, stating that the species was 'the Blesbok of the Colonists, and sometimes Bontebok'. Harper (1939) recognized that Burchell did not differentiate between the two variations and went ahead and described the Blesbok as *D. phillipsi*. Synonyms: *albifrons*, *dorcas*. Chromosome number: $2n = 38$ (FN = 60); karyotypes have 11 metacentric/submetacentric and seven acrocentric/teleocentric pairs of autosomes, a large acrocentric X and a smaller acrocentric Y (Wurster & Benirschke 1968, Claro *et al.* 1995, Kumamoto *et al.* 1996). Hybrids of *D. p. phillipsi* and the Hartbeest *Alcelaphus buselaphus* have a diploid number of $2n = 39$, and are sterile (Robinson *et al.* 1991). Fabricius *et al.* (1989) used discriminant function analysis to show that the two subspecies and their hybrids can be separated on the basis of colour pattern.

Description Bonteboks and Blesboks are medium-sized antelopes, smaller but similar to the Tsessebe *Damaliscus lunatus lunatus*, although generally considerably darker in colour, standing approximately 0.90–0.95 m at the shoulder. According to Bigalke (1955), the general body colour of the Bontebok 'is a rich dark brown, darker on the sides of the head, the flanks and upperparts of the limbs' (with a purple gloss) compared with the Blesbok with a general body colour of 'a reddish-brown' (without a purplish gloss). Both are white or nearly so on the underparts. Generally, the white blaze on the Bontebok is not divided between the eyes, whereas that of the Blesbok usually is, thus forming a brown bar across the face. However, this character is somewhat variable, as in Bontebok N. P., David (1970) recorded 19% of both sexes with a divided face blaze in a sample of 68 ♀♀ and 47 ♂♂. Whereas the rump patch on the Bontebok is clearly white and extends above the tail, that of the Blesbok is far less extensive and simply paler in colour, but never white. The limbs of the Bontebok, apart from dark stripes on the front of the forelimbs, and occasionally hindlimbs, are white from the knee downwards, whereas on the outer surfaces those of the Blesbok are brown. The precocial young are initially light brown, but develop full adult colouration at approximately eight months. There is little evident colour variation within the area of distribution of the species. There is also little sexual dimorphism, but adult ♂♂ are generally darker in colour and have a conspicuous white scrotum. Both Bontebok and Blesbok have prominent preorbital glands (larger in ♂ than ♀; David 1973,



Blesbok *Damaliscus pygargus phillipsi*.

Lynch 1974), with pedal glands only on the forefeet; there are no inguinal glands.

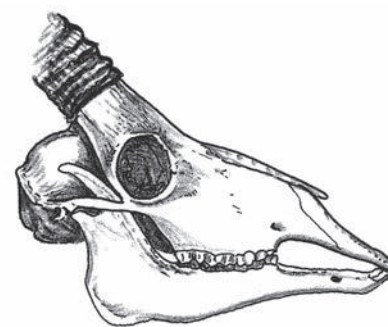
Both sexes have ridged horns that rise from the top of the head, curve backward and outward and then forward towards the unridged tips; horns of ♀ tend to be more slender than ♂. The horns of Bontebok tend to be dark whereas those of Blesbok are considerably lighter (straw-coloured). In Blesboks, horn annuli first appear at eight months of age (Rowe-Rowe & Bigalke 1972), and Watson *et al.* (1991) noted that horns started curving from 15 months onwards. In animals younger than 18 months, horn shape, horn length and horn base circumference can be used to estimate age of subadults fairly accurately.

The first permanent molar is fully erupted and functional at six months and at nine months the second molars erupt with M₂ preceding M². The same tendency occurs with the third molars. The first lower incisor is fully erupted at 18 months, although the deciduous premolars are not yet replaced (Watson *et al.* 1991). By 33 months all permanent teeth have erupted (Ludbrook & Ludbrook 1981).

Geographic Variation

D. p. pygargus (Bontebok): occurs naturally within the south-western portion of the Western Cape, which is a winter rainfall region. Bonteboks, especially adult ♂♂ in good condition, show a beautiful purple bloom on their back and flanks; white face blaze usually continuous, not divided by a transverse brown band between the eyes; rump patch clearly white and extends around base of the tail; basal end of tail white; limbs white from the knee downwards; horns tend to be dark on upper surface of the rings.

D. p. phillipsi (Blesbok): occurs naturally within the true grasslands of the summer rainfall portions of South Africa. Blesboks do not have the purple gloss of the Bontebok and are generally duller in



Lateral view of skull of Bontebok *Damaliscus pygargus pygargus*.

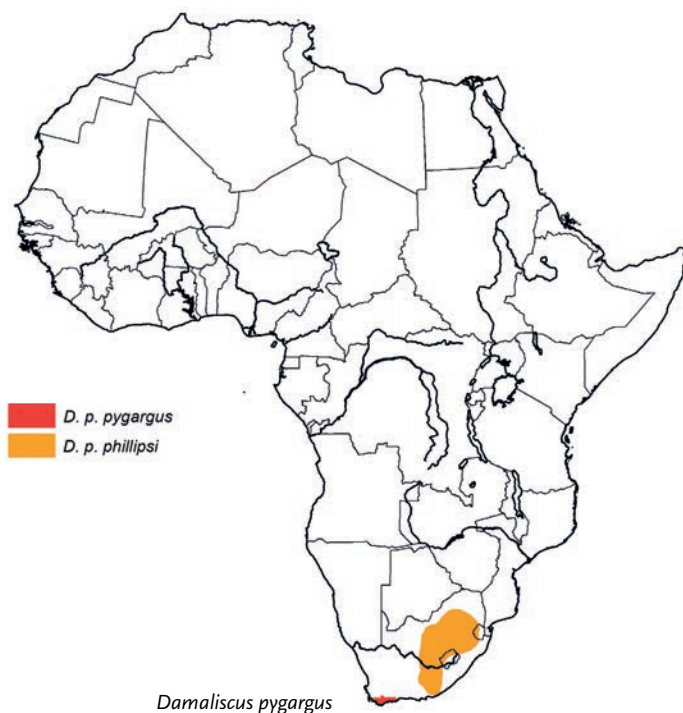
colour; white face blaze divided by a narrow brown band between the eyes; rump patch paler in colour (never white) and basal end of tail is white or pale brown; limbs brown in colour; horns usually straw-coloured.

Similar Species

Damaliscus lunatus. Only the Tsessebe is now sympatric, and then only with the Blesbok, which has been introduced to areas outside its historical (allopatric) range. Similar in shape, having the characteristic high withers and long face, but considerably larger, with no visible white colouration.

Distribution The Bontebok is endemic to the Western Cape of South Africa. Historically, the Bontebok appears to have been restricted to the coastal 'Renosterveld' plain bounded in the west by the Bot R. and probably by the Gouritz R. in the east, although it might have gone a bit further east, until approaching the coastal scrub and forest, which are unsuitable habitats for these grazing antelopes. The northern boundary would have been formed by the mountainous Riviersonderendberg range, the Langeberg range and possibly the Outeniqua Mts; the southern boundary is formed by the sea. This distribution within the Cape Floristic Region ('fynbos') covers practically the same area as the so-called Coastal Renosterveld and Coastal Macchia veld types of Acocks (1953). These represent the areas with the deeper and richer soils and the greatest abundance of grass to be found in the generally grass-impooverished and nutrient-poor 'fynbos' (see Bigalke 1955, Skead 1958, 1980, David 1973, East 1999, Skinner & Chimimba 2005).

The Blesbok, in contrast, occurred naturally in the eastern grasslands of the Northern Cape, the southern grasslands (including the highveld) of the North West and Gauteng Provinces, most of the grasslands of the Free State, marginally in the western and north-western grasslands of KwaZulu-Natal, and the true grasslands of the Eastern Cape (Skead 1980, East 1999, Skinner & Chimimba 2005). Blesboks became extinct in KwaZulu-Natal, probably during the first decade of the twentieth century, but were reintroduced (Rowe-Rowe 1994). Blesboks also formerly occurred in W Lesotho, but were exterminated before 1900 (Lynch 1994). There is no reliable historical evidence of the presence of Blesboks in Swaziland, but they probably occurred marginally in the extreme west and south-west of the country. They have since been introduced to Malolotja N. R. and Milwane Wildlife Sanctuary (Monadjem 1998). Blesbok have been widely reintroduced to private farmland, and also introduced widely outside their natural range; introduced populations occur throughout



much of Namibia, E Botswana and the midlands of Zimbabwe (East 1999).

The natural separation of the two subspecies by some 300 km is speculated to be related to the rise in sea level $\pm 15,000$ years BP after the end of the last ice age, prior to which extensive grasslands are thought to have been available on what is now the eastern Continental shelf. The rise in sea level thereafter resulted in the isolation of one population in the only area rich in grasses within what is today the Cape Floristic Region and another in the current grassland areas somewhat to the north-east, with mountain ranges separating them.

The present-day artificial distribution of both subspecies, largely as the result of pressure from the game industry, is considerably wider than the natural ranges of the two subspecies combined. Despite measures taken to try to minimize the threat of hybridization of the two subspecies, this threat persists in some of the provinces. This has resulted in a procedure for registration of Bontebok populations that have passed a photographically based test (Fabricius *et al.* 1989, Norton & Lloyd 1994). A register of these 'pure' populations is still maintained by the Western Cape and Eastern Cape provinces. Unfortunately, pure Blesbok populations and hybrids are not being monitored as comprehensively.

Habitat Bontebok and Blesbok are exclusively grazers, with a preference for short grass (Skead 1964, Du Plessis 1968, David 1973, Nolte 1973, Skinner & Chimimba 2005), and typically occupy flat or gently undulating grassland areas. Bonteboks are inhabitants of the coastal plain described above (60–200 m), whereas Blesboks are more typically associated with inland grasslands from lower (subcoastal) altitudes to areas up to 2000 m. Water is also an essential habitat requirement.

Abundance Registered Bontebok numbers in South Africa are currently estimated to be in excess of 3500 animals (P. Lloyd pers. obs.), more than 1000 of which are in formal conservation areas;

however, only about 1500 animals actually occur within the native historical range of the subspecies (P. Lloyd pers. obs.). Blesbok numbers are considered to be close to 250,000 (East 1999), with the overwhelming majority (97%) of this population occurring on private land. Many animals are on properties outside the natural range.

Ecologically meaningful densities are difficult to arrive at, since most populations of both Blesboks and Bonteboks are kept at managed densities. In Bontebok N. P., which is home to 250 Bonteboks in about 3000 ha, the density is one animal per 12 ha. In De Hoop (Provincial) N. R., there are 700 Bonteboks in about 5500 ha, yielding a density of roughly one animal per 8 ha.

Adaptations There is speculation that the rich body colour and purple sheen of the Bontebok is related to trace-element metabolism. Much of the natural range of the Bontebok is copper-deficient, and animals are known to suffer from 'sway-back' in the same way that large and small stock are affected, especially in terms of the loss of pigment. Particularly during and after long dry spells, several pale, almost whitish individuals have been observed on De Hoop (Provincial) N. R. The condition is largely reversible and either after treatment or after periods of rainfall, individuals can be seen to have regained their deep colouration. More serious is the poor development or weakening of the bones in copper-deficient areas, as is evidenced by the relatively large number of leg fractures during Bontebok capture operations on nature reserves in the Western Cape (Zumt & Heine 1978). Uncorroborated speculation has also suggested that Bonteboks can store metabolic copper at levels that are toxic to other artiodactyls. Since the Bontebok is effectively endemic to a copper-deficient region, this speculation may warrant further investigation. It is interesting that the Blesbok, endemic to areas with considerably higher copper levels, is the paler of the two subspecies.

Blesboks have a large rumen capacity and intestine length relative to body size, enabling a longer transit time in the gut (necessary due to the lower digestibility of forage consumed) (Klein & Fairall 1986).

The exocrine secretions of the interdigital glands and preorbital glands have been investigated in some detail (Burger *et al.* 1976, 1977, 1999b, c). The interdigital secretions comprise a total of 85 different compounds, including alkanes, alcohols, aldehydes, ketones, fatty acids, phenols, steroids and other compounds. No qualitative differences were found between the secretions of ♂♂ or ♀♀, or from animals from different habitats (Burger *et al.* 1999b). In contrast, the pale yellow preorbital secretions constitute some 42 compounds (19 in common with the interdigital secretions) and qualitative differences between the secretions of ♂♂ and ♀♀ were evident (Burger *et al.* 1999c).

Foraging and Food As stated above, Bonteboks and Blesboks are almost exclusively grazing antelopes, but in freshly burnt areas other grass-like plants, other monocotyledons and even dicotyledons are occasionally utilized (Skead 1964, Langley & Giliomee 1974). Gagnon & Chew (2000), in their review of the dietary classification of African bovids, classed the species as 'variable grazers', taking 60–90% monocots. Studies involving stable carbon isotope analysis confirm that grass dominates the diet (Sponheimer *et al.* 2003b). Species utilized by Bonteboks include *Cynodon dactylon*, *Themeda triandra* (David 1973), *Bromus rigidus*, *Bromus decedrus* (both introduced annual grasses), *Pseudopentameris macrantha*, *Tribolium*

uniolae, *Eragrostis capensis*, *Koeleria cristata*, *Merxmüllera stricta* (Nolte 1973), *Ficinia anceps*, *F. argyropa*, *Restio quinquefarius*, *Helichrysum orbiculare*, *Gnaphalium polycaulon* and *Pentaschistis* sp. (Langley & Giliomee 1974). Skead (1964) observed animals feeding on *Oxalis hirta*. Species utilized by Blesboks include *Themeda triandra*, *Eragrostis curvula*, *E. pseudosclerantha*, *Setaria nigrirostris* and *Chloromelas* sp. (Du Plessis 1968).

A detailed study of Bonteboks' daily activity in Bontebok N. P., during which activity was scored every four minutes for 12 hours per day, showed that on a year-round basis ♀♀ grazed significantly longer than territorial ♂♂ (64.9% : 54.7%) and had significantly less 'other' activity, which related to courtship behaviour and territory defence (4.7% : 12.7%). However, the time spent ruminating and resting was very similar for both sexes (David 1973). A comparison of seasonal differences showed that both sexes grazed for significantly longer in winter compared with summer, although according to Grobler & Marais (1967) the annual rainfall in the park is divided fairly evenly throughout the year, and is not necessarily highest in winter.

The Blesbok shows striking seasonal differences in its foraging behaviour in the summer rainfall regions where it occurs. This is due to the poor nutritional quality of the sourveld grasses on which it feeds during the dry winter months. This in turn leads to the populations in these areas adopting an 'energy-saving' mode of existence during winter, such that the herds reduce all activities to an absolute minimum and go into a state of semi-torpor, while awaiting the advent of the spring rains and the sprouting of fresh green grass (Du Plessis 1968, Lynch 1974).

Social and Reproductive Behaviour Bonteboks and Blesboks are gregarious and territorial animals but, whereas Bonteboks defend their territories throughout the year, Blesboks are territorial only during the rut, from Mar to May. The social organization comprises territorial ♂♂, female herds and bachelor herds. Territorial ♂♂ of both subspecies establish territories that, for Bonteboks in Bontebok N. P., vary in size from about 1 to 4 ha, with a mean size of about 2.5 ha (David 1973), whereas for Blesboks they range from 9 to 41 ha, with a mean size of 25 ha (Novellie 1979). Small herds of adult ♀♀ with their young, averaging only three ♀♀ with a maximum of nine in Bonteboks, and up to 25 with an average of ten in Blesboks, are associated with each territorial ♂ (David 1973, Lynch 1974, Novellie 1975, 1979). These female herds wander at will through the network of territories (female home-ranges typically include 2–3 territories), but in Bonteboks the year-round defence of territories results in a remarkable stability of the social order, since the same group of adult ♀♀ and young will often remain with the same ♂ throughout the year (David 1973, Estes 1991a). As such, territorial Bontebok ♂♂ spend most of their time with ♀♀; for example, four out of 18 ♂♂ studied in Bontebok N. P. were never seen alone in 235 observations and the remaining 14 were seen alone in only about 20% of observations (David 1973). The Blesbok social order is not so stable, since during the winter (Jun–Aug) territories are undefended and large aggregations of both sexes and all age groups (up to 650 animals) may be formed (Lynch 1974, Novellie 1975). Nevertheless, female herds still have well-defined home-ranges. By Sep these aggregations slowly disintegrate, and territoriality among ♂♂ becomes increasingly noticeable from Nov (Lynch 1974).

Bachelor groups form larger aggregations, consisting mostly of younger ♂♂, but also old ♂♂ and recently deposed territorial ♂♂. The young ♂♂ may become territorial at a later stage, but are unlikely to establish a territory, or depose a territorial ♂ from an existing territory, until they are sexually mature at about five years of age. Bachelor groups may also include small numbers of young ♀♀, which usually remain in the herd until they are about two years old. There is no hierarchy within bachelor groups and no aggression between members (David 1973, Novellie 1975).

Territorial ♂♂ advertise their ownership of a territory by assuming a 'proud' posture with head held high, ears extended sideways and by standing on raised ground where they are clearly visible. Males demarcate territories by deposition of secretions from the preorbital glands onto grass and other stems, though David (1973) questioned what role these secretions played in territorial marking. Apparently unique to Bonteboks and Blesboks is the subsequent transfer of these secretions from marked stalks to their horns by means of stroking their horns across the grass with a sideways movement of the head (David 1970, 1973, Lynch 1974). In some territorial ♂♂ this results in deposition of a black waxy substance a few millimetres thick between the horn annuli (Lynch 1974). This behaviour is not unique to territorial ♂♂, and adult ♀♀, bachelor ♂♂ and even young indulge in this 'glandular weaving'. In male Blesboks, secretions from the gland accumulate on the face and stain the white face blaze a yellowish-black (Lynch 1974); such face-staining was not observed in Bontebok (David 1973).

Another method of territory demarcation by territorial Blesboks and Bonteboks is through the creation of dung middens throughout their territories (4.3/ha in the latter in Bontebok N. P., David 1973), while bachelor ♂♂, ♀♀ and young defecate randomly. Territorial ♂♂ usually choose a dung patch to lie on and Blesbok ♂♂ wipe their preorbital glands on the dung patch and then on the neck and shoulder while lying down (Lynch 1974). Although David (1973) attributed no marking function to dung middens because bachelors and other territorial ♂♂ took no notice of them, they are clearly of significance to their owners and may serve as indirect territory markers (Lynch 1974). Novellie (1981) concluded that a territorial dung patch served to communicate its owner's identity to neighbouring territorial ♂♂, as male Bonteboks in captivity could distinguish between their own faecal pellets and those of a stranger. Both Bonteboks and Blesboks also have interdigital glands and so pawing, especially of the dung heaps, by territorial ♂♂ may be an additional factor in marking.

Males defend their territories against bachelor ♂♂ by aggression, and bachelors will always give way when chased or approached by a territory holder. However, against neighbouring territory holders, the territory is defended through a complex series of ritualized displays called a challenge ritual (David 1973, Lynch 1974). Serious fighting, involving ♂♂ dropping on to their knees with their foreheads close to the ground and locking horns in a violent pushing contest (Du Plessis 1968, Lynch 1974), is rare and was only witnessed in 3% of Bontebok challenge rituals (David 1973).

Challenge rituals are a significant daily occurrence in the lives of most territory holders and involve them either entering a neighbouring territory or receiving a neighbouring ♂ for the performance of the ritual. The average duration of Bontebok challenge rituals was 6.5 min, with a range from 1 to 23 min. The most frequent behaviours

seen during a ritual, which include both aggressive and submissive actions, include the following: approach and withdrawal while head-flagging, which involves turning the head and horns away from the opponent; standing flank to flank with the opponent, sometimes in parallel position, but usually in reverse parallel accompanied by mutual anus sniffing; aggressive head-shaking; lateral presentation, in which one ♂ stands sideways in front of the other; glandular weaving, in which the ♂ transfers secretions from the preorbital glands onto grass stalks and then waves his muzzle and horns across the same grass stalks; urination; defecation; soil horning while on the knees; cavorting, which involves a ♂ leaping into the air and kicking out with the hindlegs. Neutral activities such as grazing and grooming also form part of the ritual (David 1973).

Territorial ♂♂ of both subspecies court ♀♀ with a low-stretch display, holding the head low and outstretched with the tail curled over the back (David 1973, Lynch 1974, Estes 1991a, Skinner & Chimimba 2005). Males test the receptivity of ♀♀ by sniffing the vulva (the ♀ standing with tail out), although, unlike most antelopes, neither Bonteboks nor Blesboks exhibit flehmen (a trait shared with *Damaliscus lunatus* and *Alcelaphus*). If a ♂ sniffs the vulva of an unreceptive ♀, she turns to run round him in a tight circle, flank to flank, but always with head held low in a submissive posture.

Females do not isolate themselves from the rest of the female herd during parturition (David 1975, Estes 1991a). Young are capable of walking and following their mothers within half-an-hour (David 1975, Estes 1991a). There is no concealment behaviour, except when mothers are grazing (Langley & Giliomee 1974), and ♀♀ do not eat the afterbirth. Females only suckle their own offspring, driving others away. Young separated from their mother bleat loudly. Young are weaned at about four months. Young ♂♂ leave their mothers of their own accord at about 12 months of age, when the mothers produce their next offspring; they may remain solitary at first, but eventually join bachelor groups until sexually mature.

Associations with other ungulates specifically, and other species in general, are not clear, possibly since hunting during the past two centuries and enclosure within reserves has compromised 'natural' studies, but both subspecies have been associated with species such as the Plains Zebra *Equus quagga* and Mountain Zebra *Equus zebra*, Impala *Aepyceros melampus* and Ostrich *Struthio camelus*.

The only sounds made by Bonteboks during an 18-month study were the explosive alarm snort and a series of grunts emitted by a ♂ when mounting a ♀ prior to copulation (David 1970).

Reproduction and Population Structure Bonteboks and Blesboks are polygamous short-day seasonal breeders, with single young (weight 6–7 kg) being born after a gestation period of ± 240 days (Skinner *et al.* 1974, David 1975). The majority of Bontebok young are born between Sep and Nov (peaking in Oct) after the rut from Jan to mid-Mar (David 1973). Blesbok young, in contrast, are mostly born between Nov and Jan (peaking in Dec), after an autumn rut from Mar to May (Skinner *et al.* 1974). The differing strategies allow Bontebok young to be born in middle to late spring of the winter rainfall areas of the Cape Floristic Region, whereas Blesbok young are born somewhat later in the summer rainfall areas prior to the dry winter months, thereby optimizing the grazing available after the respective wet seasons. Novellie (1986) found that conception

rate was influenced by rainfall, which determines forage quantity and quality prior to the breeding season.

Blesbok ♀♀ mature sexually at about 2½ years of age (Du Plessis 1968), similar to records for Bonteboks that suggest they became sexually mature at about 2¼ years of age (David 1970, 1975). Male Bonteboks apparently reach sexual maturation at about three years of age (Estes 1991a), but only tend to become territorial at about five years. The same is probably true of Blesboks. Oestrous cycle length is 28–32 days (Marais 1988). In captivity, well-fed ♀♀ kept in proximity to a ♂ cycled throughout the year. The introduction of a ♂ to a group of isolated and non-cycling ♀♀ resulted in immediate synchrony of the oestrous cycle, which is likely to result in the bulk of the young being born within a short period of time (Marais & Skinner 1993).

In Bontebok N. P., David (1970) found the sex ratio of yearling and older Bonteboks to be 100 ♂♂ to 87 ♀♀ ($n = 215$) and a separate evaluation of roughly one-year-old young gave a similar ratio of 100 : 88 (26 : 23, $n = 49$).

Under captive conditions, Bonteboks have attained 15 years and seven months of age, compared with Blesboks, which have reached more than 20 years of age (Jones 1993). Historically, in the wild the life-span is likely to have been considerably shorter, but in current times the species is not exposed to predation by large carnivores and many individuals may attain such an age under relatively natural conditions.

Predators, Parasites and Diseases As animals adapted to grassland environments, both Bonteboks and Blesboks could be considered to be subject to predation by typical grassland carnivores. Historically, these would have included Lions *Panthera leo*, Leopards *Panthera pardus*, Spotted Hyaenas *Crocuta crocuta*, African Wild Dogs *Lycaon pictus* and, particularly for Blesboks, Cheetahs *Acinonyx jubatus*. Smaller carnivores include Black-backed Jackals *Canis mesomelas* and Caracals *Caracal caracal*, while other predators potentially implicated in juvenile mortality are Chacma Baboons *Papio ursinus*, the African Rock Python *Python sebae* and some of the larger raptors.

In Bonteboks, two important causes of death that have been recorded are verminosis and copper deficiency (Zumpt & Heine 1978).

Over the course of a ten-year study period in Bontebok N. P., Bonteboks were found to harbour eight species of ixodid ticks, of which *Rhipicephalus glabroscutatum* and *R. nitens* were most abundant (Horak *et al.* 1997); Horak *et al.* (1986) also recorded two louse species (*Damalinia* sp. and *Linognathus* sp.) and the larvae of two oestrid flies (*Gedoelestia* sp. and *Strobiloestrus* sp.). In the same park, Boomker & Horak (1992) amended the list of helminth parasites recovered to one trematode (*Paramphistomum microbothrium*), two cestodes (*Taenia hydatigena* and *Moniezia expansa*) and 19 nematode species, with *Longistrongylus curvispiculum* and *Nematodius spathiger* the most abundant and prevalent (see also Horak *et al.* 1982a).

The helminth and arthropod burdens of Blesboks from various reserves in South Africa were investigated by Horak *et al.* (1982a), who recovered 21 nematodes (*Haemonchus bedfordi* and *Trichostrongylus axei* were present in all regions sampled), two cestodes, six ixodid ticks, two lice and the larvae of five oestrid flies (see also Young *et al.* 1973b, Horak & Butt 1977, Horak 1978b, 1981b).

Conservation IUCN Category: Least Concern (*D. p. pygargus* – Near Threatened; *D. p. philippi* – Least Concern). CITES: Appendix II (*D. p. pygargus* only).

More than 95% of the estimated total population of 250,000 Blesboks occur on private land, with larger protected populations occurring in Suikerbosrand N. R. (Gauteng), and Willem Pretorius G. R., Sterkfontein Dam N. R., Tussen-die-Riviere G. R. and Golden Gate Highlands N. P. (Free State). The two most important conservation areas for the Bontebok are Bontebok N. P. and De Hoop (Provincial) N. R., the former with ± 250 animals and the latter (including the neighbouring privately owned Overberg Test Range, which has conservation as a secondary objective) with nearly 700 animals (making this the largest population of the subspecies). They also occur on Hottentot-Hollands (Provincial) N. R., which has limited suitable habitat, and has around 20 animals (P. Lloyd pers obs.).

Though historical records are lacking, it is likely that, due to its restricted distribution, the Bontebok was never very abundant. So it is perhaps not surprising that, as early as 1830, indiscriminate hunting and the enclosure of the best land for farms by the early settlers in the Western Cape had seriously reduced its numbers, so that the species was in real danger of extinction. Fortunately, enlightened landowners in the Bredasdorp district perceived the threat to the species and enclosed as many as they could on their land. Their timely actions undoubtedly saved the Bontebok for posterity, but numbers were still not very high by the time the first Bontebok N. P. was proclaimed near Bredasdorp in 1931 with a paltry total of 17–22 animals (Bigalke 1955, Barnard & Van der Walt 1961, Van der Merwe 1968).

This first park was not a success due to its small size and poor quality grazing and the decision was eventually taken to look for a wholly new park. After a long search a suitable site was found for the present park near the town of Swellendam and, in March 1960, 84 sedated animals were transferred by truck, of which 61 survived the critical first three days in the new park. The introduced Bonteboks thrived in their new environment and quickly improved both in condition and number (Barnard & Van der Walt 1961, Van der Merwe 1968). Today, the numbers in the park, which is about 3000 ha in size, have stabilized at around 250 animals. Surplus animals from this park have formed the nucleus of reintroduced populations in other protected areas, and have also been introduced outside their former range (for example, to West Coast N. P.).

The greatest threat to both Bontebok and Blesbok is deliberate or accidental hybridization at the intra-specific level (mixture of the subspecies). Despite some provinces taking measures to try to prevent such activities, such hybridization has unfortunately occurred and represents a threat to both the pure Bontebok and the pure Blesbok. Attempts are being made to ensure that such animals may not be translocated, may only be sold as venison, and should not be maintained in close proximity to pure animals of either subspecies.

Measurements

Damaliscus pygargus

D. p. pygargus

HB (♂): 1480 mm, n = 1

T (♂): 330 mm, n = 1

E (♂): 140 mm, n = 1

Sh. Ht. (♂): 988 mm, n = 1

South Africa (Roberts 1951)

Skinner *et al.* (1980) recorded adult Bontebok ♂♂ with a mean mass of 61.0 kg (range 59.6–63.6; n = 24)

Maximum recorded horn length for a Bontebok is 42.6 cm for a pair of horns from the former Cape Province, South Africa (Rowland Ward)

D. p. philippi

HB (♂): 1580 mm, n = 1

HB (♀): 1393 mm, n = 1

T (♂): 215 mm, n = 1

T (♀): 177 mm, n = 1

E (♂): 139 mm, n = 1

E (♀): 127 mm, n = 1

Sh. ht (♂): 912 mm, n = 1

Sh. ht (♀): 840 mm, n = 1

South Africa (Roberts 1951)

Maximum recorded horn length for a Blesbok is for a pair of horns from Vryburg, Northern Cape, South Africa, which measured 52.4 cm (Rowland Ward)

Key References Bigalke 1955; David 1973, 1975; Du Plessis 1968; Lynch 1974; Novellie 1975, 1979.

Jeremy David & Peter Lloyd

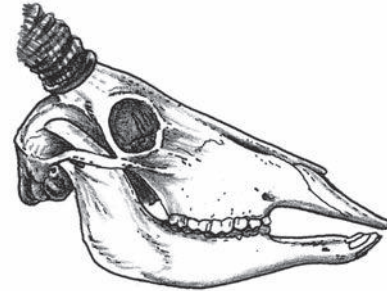


Bontebok *Damaliscus pygargus pygargus*.

Damaliscus lunatus TOPI / TSESSEBE / TIANG / KORRIGUM

Fr. Damalisque; Ger. Leierantilope

Damaliscus lunatus (Burchell, 1824). Travels in Interior of Southern Africa 2: 334[1824]. South Africa, Northern Cape Prov., Kuruman Dist., 'Makkwarin' (Matlhwareng) River.

Tsessebe *Damaliscus lunatus lunatus*.Lateral and palatal views of skull of Tsessebe *Damaliscus lunatus lunatus*.

Taxonomy Polytypic, with as many as seven recognized subspecies (Haltenorth 1963, Ansell 1972). There are obvious differences between the southern *lunatus* and the other subspecies, for instance the horns of *lunatus* being crescent- rather than lyre-shaped (see also Geographic Variation). Consequently, while traditionally only a single species has been recognized (e.g. Grubb 1993c), a convincing case can be made for splitting the species into two, as has been done by some authors (Allen 1939, Grubb 2005).

More recently, Cotterill (2003c) examined specimens of *D. lunatus* from south-central and East Africa and distinguished between Tsessebés from C Zimbabwe, Botswana and southern Africa, and those in NE Zambia in the southern Bangweulu Flats, which he described as a new species *Damaliscus superstes* based on differences in cranial morphology and pelage (and see Ansell 1978). Cotterill (2003c) proposed considering animals from south-central Africa (south of, and including, Angola, Zambia and S DR Congo) as *D. lunatus* (with the exception of *D. superstes*), and all other populations from East Africa and the remainder of the range provisionally as *D. korrigum* (the approach subsequently followed by Grubb 2005). Analyses of mitochondrial DNA of Tsessebés from Botswana and East African Topis reveal some degree of genetic divergence between the two clades (Arctander *et al.* 1999). In this sense, the isolated population in Bangweulu represents something of an anomaly, the two clades otherwise being separated across the southern Tanganyika and Rungwe Rifts in SW Tanzania and neighbouring Zambia (Cotterill 2003d).

As with Hartbeest *Alcelaphus buselaphus*, further taxonomic investigation is needed, and pending the availability of more detailed studies using both molecular and morphological data – and in contrast to the classification presented by Grubb (2005), who regards *korrigum*, *lunatus* and *superstes* as distinct species – we adopt a conservative approach, treating the entire group under an interim scheme in which there are currently six subspecies (described below). This complex may well be eligible for treatment as a superspecies.

Synonyms: *korrigum*, *eurus*, *floweri*, *jimela*, *jonesi*, *korrigum*, *lyra*, *phalius*, *purpureus*, *reclinis*, *selousi*, *senegalensis*, *superstes*, *tiang*, *tiangriell*, *topi*, *ugandae*. Chromosome number: $2n = 36$ (FN = 60) in *D. l. lunatus* and *D. l. jimela* (Van der Veen & Penzhorn 1987, Kumamoto *et al.* 1996). Karyotypes of *D. l. jimela* have 12 metacentric/submetacentric and five acrocentric/telocentric pairs of autosomes. The X chromosome is the largest acrocentric element, and the Y is a small acrocentric (Kumamoto *et al.* 1996). This is in contrast to the karyotype of *D. l. lunatus* described by Van der Veen & Penzhorn (1987), where the X chromosome was submetacentric.

Description Medium-sized antelope with high shoulders and lower hindquarters. Muzzle is narrow and head long. Chestnut pelage is short, with a purplish bloom that shows a cline, being strongly marked in eastern and only slight in western populations. Dark, near black, patches on head, shoulders and hindquarters. Limbs are bright yellow and hooves black. Tail with a dark brown tassel of long hair at tip. Blaine (1914) described the visual impact of these animals as follows: 'A herd of korrigum presents a striking and beautiful colour-effect. They change from mauve to purple-red and black, against a background of brilliant emerald-green as the sunlight plays spectrally on their glossy painted skins.' Young are sandy coloured for first two months, and very similar to young Hartbeest. There are well-developed preorbital glands, and pedal glands between front hooves, particularly well developed on forefeet; there are no inguinal glands. Males slightly darker and larger (110–120% of the female body mass), but sexes are difficult to distinguish at a distance.

The horns, which occur in both sexes, are lyre- or crescent-shaped, deeply corrugated for nearly their entire length (only the tips being smooth), measuring up to 60 cm in the northern populations.



Topi *Damaliscus lunatus jimela*.

Males generally have thicker and longer horns than ♀♀, although horn length in ♂♂ decreases with age perhaps due to attrition from soil honing (Anthony & Lightfoot 1984). Horn size also increases from the southern *D. l. lunatus* (the Tsessebe) towards the northern subspecies (Estes 1991a).

Geographic Variation

- D. l. lunatus* (Tsessebe or Sassaby): central and southern Africa. Horns lunate (crescent-shaped) in profile, bending outwards in a uniform curve, then inwards and slightly forwards. Dark reddish-brown in colour, with lower parts of shoulders, upperparts of fore- and hindlegs, and thighs conspicuously darker than body colour; back of ears, hind-parts of rump, inside of hindlegs and abdomen, and base of tail all yellowish-white; lower parts of legs brownish-yellow, forelegs with a narrow band of dark brown on the front (Skinner & Chimimba 2005).
- D. l. superstes* (Bangweulu Tsessebe): Bangweulu Flats in NE Zambia; extinct in Katanga Pedicle of DR Congo. Larger than Tsessebe, horns thicker and wider spread, with a broader pedicle. In adults of both sexes, horns grow symmetrically outwards with tips curving inwards to form a sphere (distinct from the semi-lunate profile characteristic of Tsessebe *D. l. lunatus*). Larger body size, chocolate-brown pelage and spherical horn profile all appear as diagnostic in the field (Cotterill 2003c).
- D. l. korrigum* (including *purpurescens*) (Korrigum): West Africa, in the Sudanian and Sahelian zones, from Senegal, Gambia and Mauritania to Cameroon and W Chad. The border between Korrigum and Tiang is formed by a line from the Chari R. to the north, along the Logone R., in W Chad. Largest of the races with the longest horns. Pelage bright reddish-orange, paler below; lower legs from knees to hooves are fawn, banded with greyish-brown. Face greyish-black, speckled with white.

D. l. tiang (including *lyra*) (Tiang): SE Chad to SW Ethiopia and NW Kenya. Horns more slender than Korrigum. Redder in colouration than Korrigum, and the coat has a distinct reddish-purple tinge. There is often a faint dark stripe from the ear to below the eye.

D. l. topi (Coastal Topi): East Africa in Kenya and S Somalia. Medium length horns with pronounced lyrate curves.

D. l. jimela (Topi or Nyamera): East Africa in the Great Lakes region. Horns smaller than in other races, rounder in cross-section, and having the curve less pronounced (with only a slight inclination back at the tips). Darker in colour than Tiang, being a rich rufous cinnamon with a strong purplish iridescence. Dark facial markings are better defined than in Tiang.

Similar Species

Damaliscus pygargus. Historically, geographically separate (though now introduced outside its former range), with the Blesbok (*D. p. phillipsi*) living in C and S South Africa, and the Bontebok (*D. p. pygargus*) in the Western Cape.

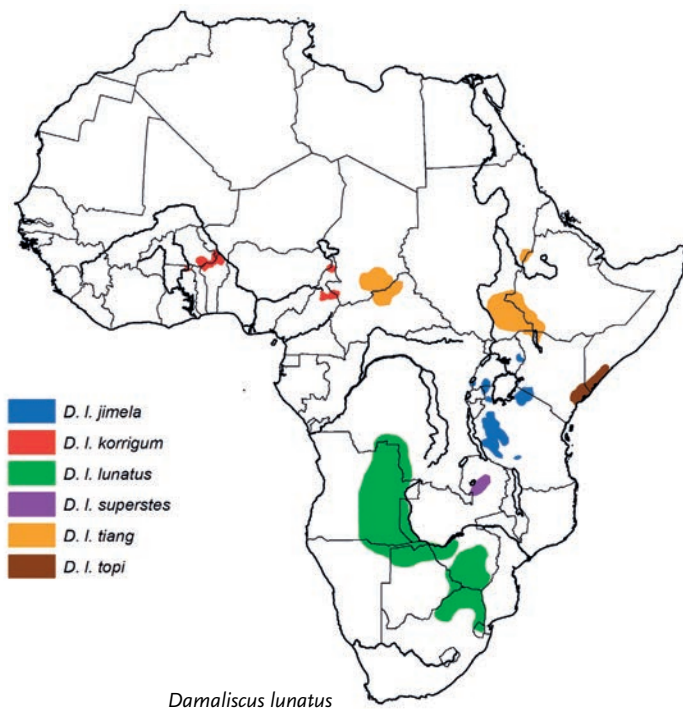
Alcelaphus buselaphus. Various subspecies of Hartbeest overlap in parts of their ranges with *D. lunatus*, but these subspecies are fawn-coloured, and readily distinguishable from *D. lunatus*. The only exceptions are the Red Hartbeest in N Botswana and Korkay in Ethiopia, which also have dark colouring and black patches on the flanks. Hartbeest further are distinguished by the presence of the pedicel supporting the horns (except for Lichtenstein's in south-east Africa) and by their complex, inverted horn shape.

Distribution Endemic to Africa, south of the Sahara, *D. lunatus* was, along with the Hartbeest, one of the most widely distributed African antelopes. The species formerly occurred from the Atlantic coast of West Africa from C and N Senegal and S Mauritania across the Sahel and Sudanian savanna to Ethiopia and Somalia, and south throughout the high-rainfall eutrophic and dystrophic savannas in all the countries of East and central Africa to South Africa, where it was replaced by the congeneric Blesbok in the Highveld and the Karroo (C and N South Africa), and the Bontebok in the Cape. The historical distribution of the species in southern and south-central Africa is discussed in detail by Cotterill (2003d). It has never been found, either as fossil remains or historically, in North Africa.

Historical Distribution The Korrigum formerly occurred in S Mauritania, C and N Senegal, Gambia, C Mali, Burkina Faso (excluding the south-west), N Ghana, N Togo, N Benin, S Niger, N Nigeria and widely on the Adamaoua Plateau in N Cameroon to W Chad (East 1999, Chardonnet 2004).

The Tiang occurred throughout S Chad (where it undertook extensive seasonal movements), in open seasonally inundated grasslands in N Central African Republic, and was formerly widespread in savanna and flood-plain grasslands in S and C Sudan. From there, its range extended into the south-western lowlands of Ethiopia and extreme NW Kenya (East 1999).

The Coastal Topi formerly occurred in S Somalia in riverine grasslands on the lower Shebelle and Juba Rivers and the area around Bush Bush N. P. In Kenya, it occurred in Lamu, Garissa and Tana River districts (East 1999). The Topi (locally distinguished as Nyamera) occurred in SW Kenya and NW and W Tanzania (on seasonally inundated grasslands within *Acacia* and *Combretum* savannas, and in



Brachystegia woodlands), E and SW Uganda, NE Rwanda and the eastern flood-plains and savanna grasslands of Burundi (East 1999).

The Bangweulu Tsessebe formerly occurred in the Bangweulu Flats in NE Zambia, bounded to the north by the Chambeshi and Luapula Rivers, and the Muchinga Escarpment to the south; it was formerly present in the Katanga Pedicle of DR Congo (Cotterill 2003c).

The Tsessebe formerly occurred across E Angola, and in Zambia was restricted to open plains and woodland edges west of the Zambezi R. In Namibia, it is naturally confined to the Caprivi Strip, while in Botswana it occurred widely in the north and east. In Zimbabwe, it occupied parts of the highveld plateau and the south, south-east and north-west, and occurred throughout parts of S Mozambique. In South Africa, it formerly occurred in the Limpopo, North West, Mpumalanga and Northern Cape Provinces (the original specimen on which the description of the species is based was collected just north-east of Kuruman). It also occurred in N KwaZulu–Natal where the last remaining herd was seen around 1925 (East 1999, Skinner & Chimimba 2005).

Current Distribution The species has undergone a drastic reduction in its range, largely due to hunting, competition from livestock and general encroachment. This range reduction has been most marked in the Korrigum in West Africa, where the species now no longer occurs in Mauritania, Mali (1970s), Senegal (pre-1930), or Gambia (early 1900s). An important population survives on the borders of Burkina Faso, Benin and Niger, in the large W–Arly–Pendjari complex of protected areas. Although believed exterminated in Ghana by the 1970s (East 1999), a relic population was reported recently still surviving in the Red Volta River valley in NE Ghana (J. Mason pers. comm.). The Korrigum probably no longer occurs in N Togo, where it was known until the late 1980s, except as vagrants (Grubb *et al.* 1998, East 1999). Further east, another relict population of the Korrigum survives in N Cameroon with a marginal occurrence in NE Nigeria (whereas they once occurred widely in the

northern savanna regions), mainly due to movements of populations from Waza N. P. in Cameroon (East 1999, Chardonnet 2004). Observations of animals in W Chad are likely due to vagrants from Bouba Ndjida N. P. in Cameroon (Chardonnet 2004).

The Tiang still occurs in S and SE Chad, in the basin of the rivers Bahr Aouk, Bahr Keita and Bahr Salamat, reaching Manda N. P. to the west and including Zakouma N. P. (Chardonnet 2004). The range in NW Central African Republic adjoins that in Chad, mainly the plains along the Aouk R., Bamingui R., Manovo R., Koumbala R., Gounda R. and St Floris plains (Chardonnet 2004). Most surviving animals are restricted to the Manovo–Gounda–St Floris N. P. In Sudan, East (1999) noted that it has been eliminated from most of the northern part of its former range (but that a small population survived in Dinder N. P.) and that Tiangs still occurred in large numbers in the south-east; recent surveys across a large part of S Sudan confirm they survive in good numbers particularly in the Jonglei area and in Boma N. P. (Fay *et al.* 2007). In Ethiopia, they still occur in good numbers in the south-west, while in Kenya they are confined to Sibiloi N. P. in NW Kenya (Marsabit district) (East 1999).

The current distribution of the Coastal Topi in S Somalia is not known, but it is now confined to isolated patches in its former range (East 1999); its range in Kenya is largely unchanged. The *jimela* subspecies (Topi) is abundant around L. Victoria, especially in the Serengeti–Mara where there were about 100,000 in 1989 (Sinclair 1995; though see East 1999), and is found southwards to L. Rukwa. In Uganda, it survives only in three areas in the east and south-west, with a very marginal extension into E DR Congo on the Rwindi–Rutshuru plain to the south of L. Edward, and in Rwanda only in the north-east (Akagera N. P.). It is extinct in Burundi.

The Bangweulu Tsessebe still occurs in the southern Bangweulu Flats in NE Zambia, but is extinct in the Katanga Pedicle in DR Congo (Cotterill 2003c). The Tsessebe occurs in a large number of fragmented populations in the countries to the south of Tanzania, and still occurs in small numbers throughout its former range in Zambia, west of the Zambezi. It also occurs in extreme SE Angola, NE Namibia, including the Caprivi Strip, but is now mainly found in the north in Botswana, particularly in the Okavango Delta, and in scattered localities in central parts of Zimbabwe and south of the central plateau. The Tsessebe became extinct in Mozambique around the late 1970s or early 1980s (having once occurred in the south) (East 1999); there are plans to reintroduce them to Gorongosa N. P. In South Africa, a small population lives in the northern part of Kruger N. P., mostly north of the Letaba R. (see Conservation), and, as elsewhere in southern Africa, they have been reintroduced to many parts of their former range from which they were eliminated, including in Swaziland, where the indigenous population is extinct (East 1999; and see Cotterill 2003d).

Habitat *Damaliscus lunatus* is a flood-plain species: two of its local names mean ‘mud’, and all the major populations are centred on wetlands. The importance of flood-plains to this species is exemplified by the decline in the population living around L. Rukwa (Tanzania) when a rise in the water level caused a reduction in the area of the flood-plain (Vesey Fitzgerald 1960, Rodgers 1982). The Jonglei District area of the Sudan is the supreme example of a flood-plain population of *D. lunatus*, where about half a million animals migrate between the wetlands of the Sudd in the dry season and the woodlands, bushlands and grasslands to the east (Boma N. P.) and the south. This

population interacts, in ways yet to be studied, with very much smaller resident herds that live year-round in favourable pockets. The species is not as specialized as the Southern Lechwe *Kobus lechwe*, and can be found in a wide range of grasslands, bushlands and woodlands, though it does better in open grasslands (Yoaci & Van Orsdol 1981); it does not occur in forests, arid or montane habitats (above 1500 m).

Damaliscus lunatus uses catena ridges in the wet seasons and sumps in the dry seasons, tracking medium-height (10–20 cm sward surface), semi-mature grasses whose flowering heads are just beginning to appear. It uses regenerating grasses in flood-plains after fire to a greater extent than other species (Wisley 1996). Densities in the habitats available to *D. lunatus* are predictable from the structure of the grasslands, so abundance is strongly affected by rainfall, grazing pressure and fire (Duncan 1975).

The spatial scale of movements by *D. lunatus* during the annual cycle of habitat use is closely linked to the geographical scale of the catenary sequence. When this is hundreds of kilometres, as in S Sudan, the Tiang migration covers some 400 km (Hillman & Fryxell 1988). The Serengeti ecosystem, like most savannas, is dissected by streams and rivers, so the scale of the catena is much smaller. In the central woodlands, the annual foraging cycle from the ridges to the sumps of the catenas occurs within a few kilometres, and the home-ranges of Topis are only a few square kilometres in size. Between these extremes, in the larger-scale landscapes of the western Serengeti ecosystem (in the flood-plains of the Grumeti and Mbalageti rivers), the animals move over tens of kilometres between sumps and ridges, and home-ranges cover tens of square kilometres (Duncan 1975).

Adaptations *Damaliscus lunatus* is a fast-moving antelope, and Selous claimed that the Tsessebe and the Hartebeest were the most difficult antelopes to run down on horseback (cited in Estes 1991a). The species shows no particular adaptations to wetlands, like the elongated hooves of the Sitatunga *Tragelaphus spekii*. Its most striking feature is its glossy bloom, apparently an adaptation for thermoregulation, and the species has behavioural and physiological adaptations for water conservation (e.g. timing of feeding, resting posture, orientation of the long axis to reduce solar radiation, and water retention from faeces; Jarman 1973). Though water-dependent, animals can go for months without drinking in the dry season if they are feeding on growing grass. These adaptations may be the basis of the species' wide historical distribution in the often treeless plains of the Sahel and the S Sudan, where wildebeest do not occur at all.

Abundance This was perhaps the most abundant African antelope before it suffered a drastic collapse in numbers and range, particularly in West Africa (see Conservation). East (1999) estimated total current population numbers for the species as a whole (correcting for undercounting bias in aerial surveys) at around 300,000, comprising 3000 Korrigums, 75,000 Tiangs, 100,000 Coastal Topis, 93,000 Topis and 30,000 Tsessebes. The total for the Tiang included an estimated 50,000 animals in S Sudan, which East (1999) acknowledged could be a gross underestimate; recent aerial surveys carried out during the dry season of S Sudan in 2007 indicate a population exceeding 155,000 (Fay *et al.* 2007), a large reduction from the more than 350,000 animals estimated by Mefit-Babtie (1983) in the northern part of the Jonglei. Chardonnet (2004) revised the estimate of the global population of Korrigums to 1850–2650, with perhaps 800 in W–Arly–Pendjari

complex and 800–1600 in Waza N. P. in N Cameroon, and estimated the number of Tiangs in central Africa at 3200. Based on East (1999; Appendix 4), numbers of Bangweulu Tsessebe are ~3500.

Population densities vary greatly. High densities (up to 45 ind/km²) are found in flood-plain systems (e.g. in the Ishasha Plain, Jewell 1972; and in the western Serengeti, Duncan 1975). Densities in woodland and bushland habitats are lower, ca. 5/km² in the central woodlands of Serengeti N. P. (Duncan 1975). In the dystrophic savannas of southern Africa, Tsessebes are widespread but rare, with for instance <0.1/km² in the northern third of Kruger N. P. (Dunham *et al.* 2005).

Foraging and Food *Damaliscus lunatus* is nearly exclusively a grazer (99% of the rumen contents in Serengeti N. P., 98% in the Lamu District, Kenya, Duncan 1975; and see Gagnon & Chew 2000b). These observations are confirmed by studies involving stable carbon isotope analysis (Cerling *et al.* 2003, Sponheimer *et al.* 2003). *Damaliscus lunatus* uses a wide variety of species, from species of the family Cyperaceae in wetlands to short grass species on the high ground. Their principal grass species in the Masai Mara include *Themeda triandra*, *Cynodon dactylon* and *Sporobolus* spp. (Hansen *et al.* 1985). In the woodlands of Serengeti N. P., *Digitaria macroblephara* is an important species, and in the western corridor *Setaria sphacelata* and *Echinochloa haploclada* and the wetland *Panicum* spp. are important in the dry seasons (P. Duncan pers. obs.); here, Topis switch their preferences between grass species according to the changes in the plants' structure, particularly the lengths of their leaves (see below). Animals do occasionally browse a few plants, such as *Dicrostachys*, *Combretum* and *Scleeryocarya*.

Damaliscus lunatus is a green leaf specialist, and its narrow muzzle and incisor arcade allow it to feed very selectively. These animals are capable of extracting diets with 75% green leaf from senescent swards that contain only 12% green leaf (Duncan 1975, Murray & Brown 1993) and are thus able to extract diets from such swards with higher metabolizable energy than are wildebeest (Murray & Illius 2000). However, on short leafy swards (<5 cm), where bite sizes are small, they are not as able to compensate by increasing bite rates as are wildebeest, so they are unable to maintain high levels of food intake. On senescent swards where green leaf is sparse, they are less selective than Hartebeest (Murray & Brown 1993).

As a result of its highly selective feeding habits, *D. lunatus* may be particularly susceptible to competition from other grazers such as Common Wildebeest *Connochaetes taurinus*, African Buffalo *Syncerus caffer* and cattle. Common Wildebeest should achieve higher rates of grass intake on short green lawns since they have higher bite rates and broader mouths, allowing them to obtain their maintenance requirements from 2 cm high swards, 1 cm shorter than the minimum height for *D. lunatus* (Bell 1971, Murray & Brown 1993, Murray & Illius 2000). Common Wildebeest may, therefore, be able to exclude *D. lunatus* competitively. In the central woodlands of Serengeti N. P., the density of resident Topis dropped from 4.4/km² to 0.8/km² in a week when a large concentration of Common Wildebeest ate 90% of the grass, and the sward surface dropped from >50 cm to <5 cm (P. Duncan pers. obs.). They returned within a month, so the competition may have been for space, rather than for resources (Duncan 1975). Competition, during a period of low rainfall, has been suggested to be the cause of a 70% decline in the Tsessebe population of a 436 km² ranch in Zimbabwe (Dunham *et al.* 2003). Inter-specific, as well as intra-specific competition may be a process determining the abundance

of *D. lunatus* in ungulate communities where resources are limiting. Topis are virtually absent from the short-grass plains in the south-east of Serengeti N. P., the wet season concentration area of the migratory wildebeest, zebras and gazelles.

The ability of *D. lunatus* to use a wide range of habitats in this flexible manner means that in ecosystems with flood-plains, their food is of high quality throughout the year, so they maintain good body condition throughout the year, grow quickly and breed fast (see below).

Social and Reproductive Behaviour It was in Topi that it was first noted that antelope mating systems can be very variable within and between populations (Monfort-Braham 1975). In most of its range, the ♂♂, as in many antelopes, defend resource territories where ♀♀ come for food, water or shade. These are up to 1 km in diameter, and ♀♀ move across the boundaries of a number of territories in small groups of up to a dozen ♀♀ with their young. Non-territorial ♂♂ from one year of age associate in bachelor herds, which also move through the mosaic of territories, but are vigorously separated from ♀♀, especially oestrous ones, by the territorial ♂♂. In Tsesebees, bachelors have been observed to live in herds of 2–22 individuals in Zimbabwe (Grobler 1973), and 2–31 in N Botswana (average = 8; Child *et al.* 1972).

Territorial Topi ♂♂ mark their territories by static optic displays on vantage points, and as in other antelopes, they also mark their territories with scent using urine, faeces and glandular secretions (Gosling 1986). Rubbing their heads on the ground spreads the secretions of the preorbital glands on the ground, and in the wet season can leave the ♂♂ with large amounts of mud on their heads and horns. Large dung heaps are another obvious visual indicator of this olfactory marking (Gosling 1987). Males and ♀♀ have interdigital glands between their front hooves, and both sexes mark grass stems with secretion from their well-developed preorbital glands. When the culms have flower heads, the animals bite off the flowers and carefully lower their heads on to the culms, which enter the gland and emerge with about half a centimetre of sticky secretion clearly visible. The secretions of these glands in the Bontebok/Blesbok, and presumably in *D. lunatus* too, are chemically complex and show qualitative and quantitative differences between ♂♂ and ♀♀ in the preorbital, but not the interdigital, glands (Burger *et al.* 1999c). The richness of olfactory communication in this species contrasts with their meagre acoustic communication. Apart from the alarm snort and distress squeaks of young, the only vocalizations used by *D. lunatus* are 'quacking and grunting calls', as in Hartbeest (Estes 1991a).

Territorial defence involves dominance and threat displays – lateral presentation in erect posture, nodding/head-casting, horn-sweeping, cavorting, ground-horning and head-shaking. Fighting involves dash-fighting, ramming, front-pressing and twist-fighting. Defensive and submissive displays involve the head-in posture, head-low posture and lying-out (Estes 1991a). The most striking display is by territorial ♂♂, which adopt the erect posture and lift their heads almost to the horizontal, with their ears down and tail held stiffly and horizontally, while walking stiffly with the front legs lifted high. When trying to stop ♀♀ leaving their territories this display can be carried out at the gallop – impressive though that is to the observer, it does not detain a determined ♀♀ for long.

When the spatial scale of the catena is fine and a single ♂ can defend both wet and dry season habitat in his territory, a group of ♀♀ may

stay year-round on the territory. At such times, the mating system comprises a single ♂ and a harem of 5–8 ♀♀, which may stay together for years (Duncan 1975). Such a mating system is probably exceptional in the Serengeti ecosystem, but common in low-density populations (e.g. Kruger N. P.; Joubert 1972). In the high-density flood-plain populations, a few groups of up to 100 ♂♂ defend tiny territories, usually on a knoll. These territories are small, 50–100 m across, and ♀♀ come to the leks principally for mating (and for resting), since there are no other resources (such as water, shade or food) on these leks or 'breeding arenas'. Even the ♂♂ have to leave their territories to obtain their food. Such leks have been found in Akagera N. P. (Monfort-Braham 1975), the western Serengeti N. P. (Duncan 1975) and the Masai Mara (Gosling & Petrie 1990). A similar mating system was described in Queen Elizabeth N. P. (Uganda, Jewell 1972): on the 80 km² Ishasha Plain, most of the 3700 Topis moved about in one or two large herds. A temporary territorial system, with ♂♂ spaced at about 50 m intervals, was set up wherever the large herds were. The ♂♂ were not known individually, so whether a particular individual defended one or multiple areas is uncertain.

Around Topi leks are resource territories through which herds of up to 1500 Topis of all ages and both sexes move. Males on the central territories of the leks obtain more matings than ♂♂ on resource territories or on peripheral lek territories; the tenure of the ♂♂ on the central territories is short, and is measured in days compared with the tenure of ♂♂ on resource territories of weeks, months or years. 'Of all the diverse mammalian mating systems, leks are the most bizarre' (Clutton-Brock *et al.* 1993). Leks are found in birds, bats and in a few mammals, but are commonest in ungulates, where they have been found in Fallow Deer *Dama dama*, Sika Deer *Cervus nippon*, Southern Lechwe and Kobs *Kobus kob* as well as Topis (Clutton-Brock *et al.* 1993). This mating system raises three questions: why do oestrous ♀♀ leave their usual groups, why do they aggregate on leks and why do they collect on particular territories? In such high-density populations it is clearly not possible for a ♂ with a resource territory to separate an oestrous ♀♀ from the non-territorial ♂♂, and it is likely that this system allows oestrous ♀♀ to reduce harassment by ♂♂, as in some other high-density ungulate populations (Clutton-Brock *et al.* 1993; but see Bro-Jørgensen 2003b). It has also been suggested that female Topis choose certain territories for the quality of the ♂ ('hotshots', see Gosling & Petrie 1990, Bro-Jørgensen 2003a, Bro-Jørgensen & Durant 2003) and perhaps also for their ecological characteristics (resources and risk of predation, Balmford *et al.* 1992).

The highly synchronized rut in Topi is a good model to study interactions between the sexes. The rut lasts c. 1.5 months, when individual ♀♀ come into oestrus for roughly one day, mate with four ♂♂ on average (range 1–13), with c. 11 intromissions from each partner (Bro-Jørgensen 2007). Most ♀♀ mating with central lek ♂♂ also mate with other ♂♂, resulting in intense sperm competition. Although data on actual fitness consequences of the different tactics are not yet available, detailed studies have used this model system to show that male Topis use a wide range of tactics to keep oestrous ♀♀ on their territories for as long as possible, thereby securing mating opportunities. These tactics include threatening young calves, which then bleat and attract their mothers (Gosling *et al.* 1986), and active signal falsification, of alarm snorts, to deceptively retain receptive ♀♀ in their territories (Bro-Jørgensen & Pangle 2010). It has also been suggested that ♀♀ which mate



Courting ♂♂ approach ♀♀ in the high-stepping walk, with ears dropped and tail raised. *Damaliscus* spp., along with

dry-season birth season. In more mobile populations the young generally follow their mothers, though they may hide at night and

some ♀♀ may leave the large herds for some weeks around the birth (Estes 1991a).

Damaliscus lunatus in low-density populations commonly associate with other species, such as the Impala *Aepyceros melampus* and Common Wildebeest. The function of such multi-species groups is, as in primates, probably anti-predator.

Reproduction and Population Structure *Damaliscus lunatus* is usually a strictly seasonal breeder, with the young being born after an eight-month gestation period within just a couple of months, in the dry season (e.g. Feb–Mar in the Sudan, Hillman & Fryxell 1988; Aug–Nov in the Serengeti ecosystem, Duncan 1975 and DR Congo, Mertens 1985; Jul–Aug in Zambia's Northern Plateau, Ansell 1960a; and Sep–Dec in Zimbabwe, Botswana and South Africa, Fairall 1960, Child *et al.* 1972). This timing corresponds with the season when flood-plain populations are on the highest quality food, but the savanna populations are on poor-quality, senescent grass at this time. The breeding season can vary within a population: the Tana R. population had two peaks at nine-month intervals in 1973–74, and in the Virunga population the birth period was Sep–Nov in the 1970s, but Mar–May in the 1960s (Mertens 1985). Offspring were apparently born to all adult ♀♀ (>2 years old) each year in the Serengeti and Lamu populations, and to a very high proportion of the two-year-olds (about 80%, Duncan 1975). In Tsessebes, about 97% of adult ♀♀ have offspring; two-year-olds occasionally breed (Huntley 1972), but usually do not (Child *et al.* 1972, Dunham *et al.* 2004). Female Topis (but not Tsessebes), therefore, mate at an earlier age than Hartbeest (but not before the third year; Stanley Price 1978a); in Common Wildebeest the proportion of second-year animals mating varies with the abundance of resources (about 40% do when resources are abundant, 6% when they are not; Mduma *et al.* 1999).

Mothers give birth to a single young, and birth-weight is 10–12 kg in Tsessebes (Child *et al.* 1972). In Topis, the young get their black patches by three months, when their shoulder height is about half that of the adults; at six months their horns have one or two rings and are about 12 cm long. Their coat develops the chestnut colour of the adults by about one year, when their horns have 6/7 rings and are about 24 cm long (Mertens 1984). Tsessebe horns are about 20 cm long at 12 months, and ca. 30 cm at 18 months (Child *et al.* 1972, Huntley 1973, Anthony & Lightfoot 1984). Their sharp seasonal breeding season allows the ages of young animals to be determined easily by reference to the development of their teeth (see Fig. 5, Child *et al.* 1972, which is based on a sample of 82 individuals collected over three years).

Growth rates in Topis are fast, and ♀♀ can reach 70% of their adult weight at nine months when resources are abundant (Duncan 1975). In Tsessebes, data from N Botswana suggest that the ♀♀ grow more slowly, reach adult weight at three years and breed only then; the weight of the testes suggests that ♂♂ mature in time for the rut in their third year (40–42 months; Child *et al.* 1972). Sex ratios are female-biased, with adults (>1 year old) in Topis and Tsessebes consisting of only 30–40% ♂♂ (Mertens 1985, Monfort-Braham 1975, Dunham *et al.* 2005).

Data on the vital rates of *D. lunatus* populations are sparse. The only life-table is based on the ages of skulls found in Virunga N. P. (DR Congo), Rwenzori Mountains N. P. (Uganda) and Akagera N. P. (Rwanda). Ages were determined by tooth replacement and wear (Mertens 1984), assuming two cementum rings per year in

the roots of the M1 teeth. It seemed that virtually all the animals died before the age of seven years, apparently from predation and poaching, and the life expectancy at birth was calculated as 2.4 years for ♂♂, 2.3 years for ♀♀ (Mertens 1985). The life expectancy of Tsessebes in N Botswana, using an approximation, was calculated to be a little longer (3.0 years; Child *et al.* 1972). Even this value seems very low for animals of their size, and in a species that feeds on flood-plain grasslands the assumption of two cementum rings per year is a weak one that needs to be checked with animals of known ages. In captivity, the life-span of animals that live to three years is 8–9 years with no significant difference between ♂♂ and ♀♀ (see Bro-Jørgensen & Durant 2003); some animals have lived to 23–24 years of age (Weigl 2005). In some populations, survival rates must be higher, since in favourable circumstances Topi populations can grow fast. In the western Serengeti N. P. they increased after the eradication of rinderpest from about 10,000 to about 50,000 in the ten years between 1966 and 1976 (Sinclair 1995).

Few data are available on the limitation of *D. lunatus* populations. The Kruger N. P. Tsessebe population (South Africa) has declined and is close to extinction: survival rates of adults and juveniles have declined in the last 20 years. Low rainfall, in interaction with a density dependent effect on adult survival, may be responsible for the decline (Dunham *et al.* 2005; see also Owen-Smith & Mason 2005); inter-specific competition and predation may also be involved (see below).

Predators, Parasites and Parasites Though vulnerable to many predators (newborn animals can be killed by jackals *Canis* spp.; Estes 1991a), *D. lunatus* appears to suffer low predation rates compared with other species. For example, in the Savuti ecosystem (Botswana), Spotted Hyaenas *Crocuta crocuta* preferred Plains Zebra *Equus quagga* foals to Tsessebes when the migratory zebras were present, and preferred Impalas *Aepyceros melampus* to Tsessebes when the zebras were not (Cooper 1990). In the Serengeti–Mara system, Topis are an important, if not a preferred, prey of Lions *Panthera leo* and Spotted Hyaenas (Kruuk 1972, Schaller 1972, Cooper *et al.* 1999). None the less, it is likely that the Topis in the woodlands of the central part of Serengeti N. P. have been predator-limited (Sinclair 1995).

Cleaveland *et al.* (2005) isolated bovine tuberculosis, caused by *Mycobacterium bovis*, from one out of a sample of nine Topis sampled systematically in 2000 during a meat cropping programme in Serengeti N. P. Steinberg (1988) reported on Johne's disease (*Mycobacterium paratuberculosis*, also known as paratuberculosis) in a captive Topi. Anthrax was reported from Tiangs in S Sudan (Ramachandran *et al.* 1988). Tsessebes appear not to be susceptible to, or to carry, *Cowdria ruminantium* (the tick-borne causative agent of heartwater in domestic ruminants) either by infection from ticks or by injection (Peter *et al.* 1999), although Kock *et al.* (1995) obtained positive samples from healthy, free-ranging Tsessebes in Zimbabwe taken during translocation from areas harbouring *Amblyomma* ticks. Jardine (1992) reported on a natural, fatal case of theileriosis (cytauxzoonosis) in Tsessebes.

In Zambia, three Tsessebes sampled on a game ranch in Central Province had six species of ixodid ticks, including *Amblyomma variegatum*, *Boophilus decoloratus*, *Rhipicephalus appendiculatus*, *R. evertsi*, *R. kochi* and *R. lunulatus* (Zieger *et al.* 1998a). In addition, two trematode and cestode species were recovered (*Calicophoron* sp., *Avitelinea centripunctata*) and four species of nematodes (*Agriostomum cursoni*, *Dictyocaulus* sp., *Gaigeria pachysclis* and *Impalaia* sp.). Two species of botfly were also

recovered: *Gedoelestia cristata* and *Oestrus variolosus* (Zieger *et al.* 1998b). A single Tsessebe in Kruger N. P. harboured helminths from the genera *Haemonchus*, *Trichostrongylus*, *Longistongylus*, *Cooperia*, *Impalaia*, *Parabronema* and *Skrjabinema* (Boomker *et al.* 1986). The most prevalent and abundant nematodes recovered from Tsessebés shot at Nylsvley N. R. in South Africa were *Cooperia hungi*, *Impalaia tuberculata* and *Trichostrongylus falculatus*. The nematodes *Trichostrongylus colubriformis sensu lato*, *T. thomasi* and *Haemonchus bedfordi* and trematodes of the genus *Paramphistomum* were also present (Reinecke *et al.* 1988).

Conservation IUCN Category: Least Concern (*D. l. korrigum* – Vulnerable C1+2a(i); *D. l. topi* – Near Threatened; *D. l. jimela*, *D. l. lunatus*, *D. l. tiang*, *D. l. superstes* – Least Concern); CITES: Appendix III (Ghana).

The history of the West African Korrigum exemplifies the fragility of this highly productive species, which has been severely reduced by overhunting/poaching across all of its range, as well as by other threats such as competition with livestock and loss of habitat. Once ranging over at least 1 million km² from Senegal to W Chad, by 1979 it had been reduced to one population in Mali, and another of a few thousand individuals around the W–Arly–Pendjari complex (SE Burkina Faso, SW Niger, N Benin; Sayer 1982, East 1999). Although the population in Mali has since died out, Korrigums still survive in and around the W–Arly–Pendjari complex (800 animals). The largest population occurs in Burkina Faso, with the range comprising Arly Total Reserve, Pama Faunal Reserve, Singou Game Ranch, Madjoari Faunal Reserve, Wamou and Arly Hunting Areas, Kourtiagou Faunal Reserve, W N. P. and Tapoa Djerma Hunting Area. Movements to the west are restricted by the man-made L. Kompienga, and movements to the north are only possible during the rains (Jun–Sep), though no such movements have been seen for several years (Chardonnet 2004). In Niger, the range is entirely restricted to W N. P., while in Benin the main stronghold is Pendjari N. P. and adjacent hunting areas of Pandjari, Atakora and Konkombri (Chardonnet 2004). Korrigums also survived in a small population in N Togo in Keran N. P. in the late 1980s, though this population has probably since been exterminated (East 1999), and the only animals likely to occur in N Togo are vagrants from the W–Arly–Pendjari complex (Chardonnet 2004). Another small population was observed in NE Ghana in 1999 (J. Mason pers. comm.), but no further information is available on the status of this population. Elsewhere, Korrigums also still occur in N Cameroon, with their stronghold in Waza N. P. (where the population is estimated at between 800 and 1600, down from 20,000 in 1962) and in smaller numbers (ca. 250) in Bénoué and adjoining hunting zones (East 1999, Chardonnet 2004). From here vagrants move into neighbouring NE Nigeria (into Chugurma–Dugurmi N. P.) and Chad (Chardonnet 2004).

Around one-quarter of the population of Tiangs occurs in protected areas (East 1999), including: Zakouma N. P. and Salamata Faunal Reserve and Aouk hunting areas (Chad), Manovo–Gounda–St Floris N. P. (Central African Republic), Boma N. P. (Sudan), Omo and Mago National Parks (Ethiopia) and Sibilo N. P. (Kenya); however, while Zakouma N. P. has the largest population in central Africa (1300), the population in Manovo–Gounda–St Floris continues to decline. There is no information on their status in Dinder N. P. in Sudan, where they may now number no more than a few dozen individuals (Chardonnet 2004). The large surviving population in the Jonglei remains unprotected.

Most Coastal Topis occur outside of protected areas, but Boni and Dodori National Reserves (Kenya) represent an important stronghold for this subspecies. Elsewhere, Virunga N. P. (DR Congo), Queen Elizabeth N. P. (Uganda), Akagera N. P. (Rwanda), Masai Mara National Reserve (Kenya) and Serengeti N. P. (Tanzania) for Topis (more than 90% of which occur in protected areas), and Liuwa Plain (Zambia), the Okavango and Chobe N. P. (Botswana) and Kruger N. P. (South Africa) for Tsessebés (40% in protected areas), represent important strongholds for this species (East 1999). However, many of these populations have been declining in recent years, such as those in Queen Elizabeth and Virunga National Parks (East 1999). Numbers of animals in Akagera N. P., the last effective stronghold for the Topi in Rwanda, declined from around 7500 in 1990 to an estimated 770 in the late 1990s following the reduction in size of the park from 2500 km² to 732 km² in 1997 (Williams & Ntayombya 1999), although the population has since recovered (Apio & Wronski 2011). Even the population in Kruger N. P., among the best-protected areas on the continent, doubled from about 500 to 1000 between 1975 and 1986, and then declined to 220 in 1996 (Dunham *et al.* 2005), while numbers in Masai Mara National Reserve declined ~70% between 1977 and 2007 (Ogutu *et al.* 2011).

Bangweulu Tsessebés survive in good numbers in Bangweulu, and have been translocated to a number of private game ranches in Zambia (Cotterill 2003c). The latter author called for the translocation of a population to Kasanka N. P. east of the Luombwa R.

The species is a generalist in terms of habitat and food requirements. Provided it is not excessively hunted and suitable habitat is available, its fast growth and reproductive rates mean that numbers build up quickly in eutrophic savannas. In dystrophic savannas, the densities of Tsessebés are so low that very large areas are required to maintain viable populations. The species has been successfully (re)introduced to many areas with a wide range of ecological conditions in South Africa, such as Marakele and Pilanesberg National Parks (East 1999) and Itala G. R. in N KwaZulu–Natal (Rowe–Rowe 1994), Swaziland (Mkhaya G. R.; Monadjem 1998) and Namibia (Etosha N. P.; Van der Walt 1989), and to private land both in South Africa and in the northern farming districts of Namibia.

Measurements

Damaliscus lunatus

D. l. jimela

TL (♂ ♂): 2230 (2075–2355) mm, n = 30

TL (♀ ♀): 2090 (1965–2210) mm, n = 17

T (♂ ♂): 528 (400–585) mm, n = 30

T (♀ ♀): 464 (380–520) mm, n = 17

HF c.u. (♂ ♂): 502 (475–515) mm, n = 30

HF c.u. (♀ ♀): 477 (462–505) mm, n = 17

E (♂ ♂): 194 (185–205) mm, n = 30

E (♀ ♀): 182 (165–200) mm, n = 17

Sh. ht (♂ ♂): 1150 (1040–1260) mm, n = 30

Sh. ht (♀ ♀): 1130 (1050–1180) mm, n = 17

WT (♂ ♂): 130.0 (112.0–147.0) kg, n = 30

WT (♀ ♀): 109.0 (91.0–130.0) kg, n = 17

Serengeti N. P., Tanzania (Sachs 1967)

Maximum recorded horn length for *D. l. jimela* is 61.9 cm for a pair of horns from Bugungu, Uganda (Rowland Ward)

D. l. lunatus

TL (♂♂): 2160 (2070–2290) mm, n = 21

TL (♀♀): 2130 (1900–2260) mm, n = 45

T (♂♂): 450 (400–520) mm, n = 20

T (♀♀): 420 (360–510) mm, n = 44

E (♂♂): 1960 (1840–2060) mm, n = 21

E (♀♀): 1920 (1770–2090) mm, n = 46

Sh. ht (♂♂): 1260 (1160–1340) mm, n = 21

Sh. ht (♀♀): 1250 (1080–1320) mm, n = 44

WT (♀♀): 127.0 kg

WT (♂♂): 140.0 kg

N Botswana (Child *et al.* 1972)

Maximum recorded horn length for *D. l. lunatus* is 46.9 cm for a pair of horns from Angola

A pair of horns of *D. l. korrigum* from the Central African Republic measured 84.1 cm – the longest on record for the species; maximum recorded horn length for *D. l. tiang* is 67.3 cm for a pair of horns from Nyala, Sudan (Rowland Ward)

Key References Bro-Jørgensen 2003a, b, 2007; Child *et al.* 1972; Duncan 1975; East 1999; Gosling & Petrie 1990; Joubert 1972; Mertens 1984, 1985.

Patrick Duncan

GENUS *Alcelaphus*

Hartebeest

Alcelaphus de Blainville, 1816. Bull. Sci. Soc. Philom., Paris 1816: 75.

The genus *Alcelaphus*, the Hartebeest, appeared in the fossil record less than a million years ago, with the earliest fossil record dated at ca. 740,000 years BP (Gentry 1978, Vrba 1995), and is thus the most recently evolved of antelopes.

Hartebeest are specialist grazers and quickly radiated across the entire African savanna from the Cape to Morocco, apparently outcompeting and replacing previous forms (including relatives of the now rare *Hirola Beatragus hunteri*). According to the most recent molecular phylogeny (Flagstad *et al.* 2001), early populations became restricted to two refugia, one north and one south of the Equator, perhaps separated by the expansion of the central African rainforest belt in a period of global warming about 500,000 years BP. The subsequent radiations from these refugia now comprise the two most distantly separated groups of taxa within the genus. These clades meet in STanzania where Coke's Hartebeest *A. buselaphus cokii*, whose range is mainly in Kenya and Tanzania, adjoins that of Lichtenstein's Hartebeest *A. b. lichtensteinii*, a form characteristic of the extensive miombo woodland of south-eastern Africa including Mozambique, Zambia and Zimbabwe. About 400,000 years BP the northern clade divided into an eastern clade, giving rise to the modern forms *cokii*, *swaynei*, *tora* and *lelwel*, and a western clade, yielding *major* and the extinct *buselaphus*. The southern group consists only of *caama* and *lichtensteinii*, which, in contrast to accounts that place *lichtensteinii* into a separate species or genus (Vrba 1979), appear to be closely related having diverged only about 200,000 years BP (Flagstad *et al.* 2001). There is considerable morphological variation within taxa and a number of intergrade forms, perhaps hybrids, indicating that the genus is still in a state of rapid evolution (at least until recent times).

Here, as an interim measure, we take the view that these eight recent taxa are subspecies of *Alcelaphus buselaphus*, a scheme that is essentially consistent with that adopted by Sclater & Thomas (1894), even though these authors regarded the taxa as species of the synonym *Bubalis*. However, the scheme adopted is provisional and important problems remain: more detail is needed of genetic structure within the eight taxa to extend the findings of Arctander *et al.* (1999) and Flagstad *et al.* (2001); the taxonomic position of the Hartebeest (probably *A. b. buselaphus*) that extended across North Africa and into the Middle-East needs to be confirmed. Are the

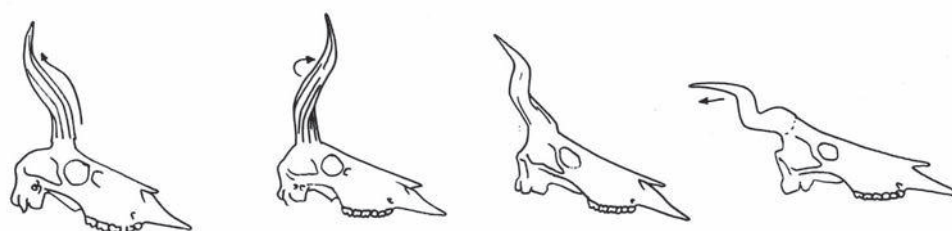
descendants of the northern and southern clades separate species (as suggested by Flagstad *et al.* 2001)? Do any other taxonomic divisions merit specific status? Further taxonomic studies are thus urgently needed and they will almost certainly result in important changes to our interim scheme.

This genus exemplifies a rare pan-African distribution for a large mammal, a fact that may be linked to some critical feeding adaptations. The key to the Hartebeest's success may be the ability to extract high-quality food from tall senile grass swards and to survive on relatively low intakes: Hartebeest use their long thin muzzle to extract leaf blade from dry swards (Murray 1993, Murray & Brown 1993) and can even nibble off leaf sheath from grass stems (Stanley Price 1974). These traits allow Hartebeest to feed successfully during the dry season, the most challenging time for grazing antelopes, and may have been the key that allowed Hartebeest to occupy such vast areas of grassland across Africa, over a wide variety of climatic regimes, and to displace preceding forms.

The long thin legs and face take a trend found in the Alcelaphini to an extreme. The long thin legs are probably an anti-predator adaptation in an animal that lives on the open plains, in grassland clearings or across grassland/woodland ecotones. Hartebeest are vulnerable to both coursing-predators such as African Wild Dogs *Lycaon pictus* and, particularly when they come to drink, to ambush-predators, such as Lions *Panthera leo*. Hartebeest are notably alert animals with highly developed brains (Oboussier 1970b) and can run for very long distances at a fast canter. The long thin muzzle is an adaptation to feeding selectively (*Alcelaphus* retains the typical bovid dentition of 32 teeth), but the high placement of the eyes allows grazing animals to monitor their surroundings even with the nose thrust into a tall sward.

Hartebeest have one of the most varied and complex horn shapes of the bovids and these define the main taxa – and the hybrids that sometimes occur between them. The horns are fighting weapons and their different parts are co-adapted with their often violent combat. There are three basic parts to the horn: (i) a base that protects the top of the head from the horns of an opponent, either by catching the horn in a narrow 'v' or by enlargement into a spatulate boss in the case of Lichtenstein's Hartebeest; (ii) an intermediate part, sometimes

Fossil skulls illustrate evolution of *Alcelaphus* 'horn-twist'. From left, *Parmularius*, *Rabaticeros* proto-*Alcelaphus*, Lelwel Hartbeest *Alcelaphus buselaphus lelwel*.



incurred, which catches and in some cases locks the opponent's horns; and (iii) sharp horn tips that are used to stab the opponent when its head has been forced to one side and that may sometimes inflict fatal wounds (Gosling 1975). The remarkable shapes that combine these functions were determined by an extraordinary rotation of the horns during evolutionary history, and particularly in the transition from a damaliscine ancestor via a fossil genus *Rabaticeros* (Gentry 1978, Kingdon 1982); the horns of this antelope first show the rotation that produced the remarkable horn structure of modern Hartbeest. In most taxa the horns are placed on top of a tall pedicel, which provides further protection as ♂♂ engage in violent 'clashes'; the exception is Lichtenstein's Hartbeest in which the spatulate base of the horns may provide a functional equivalent. 'Folded' bone around the squat pedicels in Lichtenstein's Hartbeest has been interpreted as evidence for their phylogenetic 'collapse' from a previously taller condition (Kingdon 1982).

Like most ungulates, the mating system of Hartbeest is shaped by the movements of ♀♀ in relation to vegetation quality and abundance and by female sociality; these factors determine the potential for polygyny or the number of ♀♀ that ♂♂ can potentially monopolize (Gosling 1986). In most areas ♂♂ solve the problem of access to ♀♀ by defending against other ♂♂ a part of the food

resource that ♀♀ need; in other words, resource-defence polygyny (Emlen & Oring 1977). Breeding ♂♂ spend much of their time in such territories and try to mate with and retain ♀♀ when they visit. When female densities are very low, and when they range over large areas, ♂♂ are forced to adopt another strategy: that of 'following' ♀♀ throughout their home-range.

While behaviour has been studied to a variable extent on particular subspecies, there has been no systematic attempt to compare details across the entire radiation. The information in hand suggests some basic similarity. For example, one of the most conspicuous displays is the 'head-in' posture of subordinate ♂♂ in which the chin is drawn in and the tail recurved while the ♂ utters juvenile 'quack' vocalizations and moves in an exaggerated high-stepping gait (Gosling 1975). This striking display occurs when subordinate ♂♂ are threatened by territorial ♂♂, and probably has an appeasement function. Exactly the same display occurs in Coke's Hartbeest and Red Hartbeest (L. M. Gosling pers. obs.), representatives of the northern and southern clades, respectively, which suggests that this display originated at least half a million years ago when, according to Flagstad *et al.* (2001), these taxa diverged.

L. Morris Gosling

Alcelaphus buselaphus HARTEBEEST

Fr. Bubale; Ger. Kuhantilope

Alcelaphus buselaphus (Pallas, 1766). Misc. Zool. p. 7. Morocco. No locality cited but the name is based on 'Le bubale' of Buffon, 'en Barbarie & dans toutes les parties septentrionales de l'Afrique', and on other sources. Restricted to Barbary by designation of the 'Vache de Barbarie' of Perrault as the lectotype (Ruxton & Schwarz 1929: 575), and further restricted to Morocco by Lydekker (1914: 5).

Taxonomy Hartbeest are exceptionally variable morphologically, particularly in horn shape and coat colour, and up to the time when the destructive impact of man interfered (within the last 200 years) they were still in a state of dynamic evolutionary change. Hybrid or intergrade populations are common, particularly in the regions between relatively homogeneous types, and, as a result, the taxonomy of the group has been confused, with numerous races and subspecies described (see Ansell 1972).

Our understanding of Hartbeest taxonomy has improved in recent years through molecular phylogenies based on variation in mitochondrial DNA sequences (Arctander *et al.* 1999, Flagstad *et al.* 2001). These authors have suggested three principal Hartbeest clades arising from three geographic refugia: a southern clade (*caama*, *lichtensteinii*), a western clade (*major*, *buselaphus*) and an eastern clade (*lelwel*, *cokii*, *swaynei*, *tora*). The eastern and western clades may have originated from an earlier, single northern clade. On

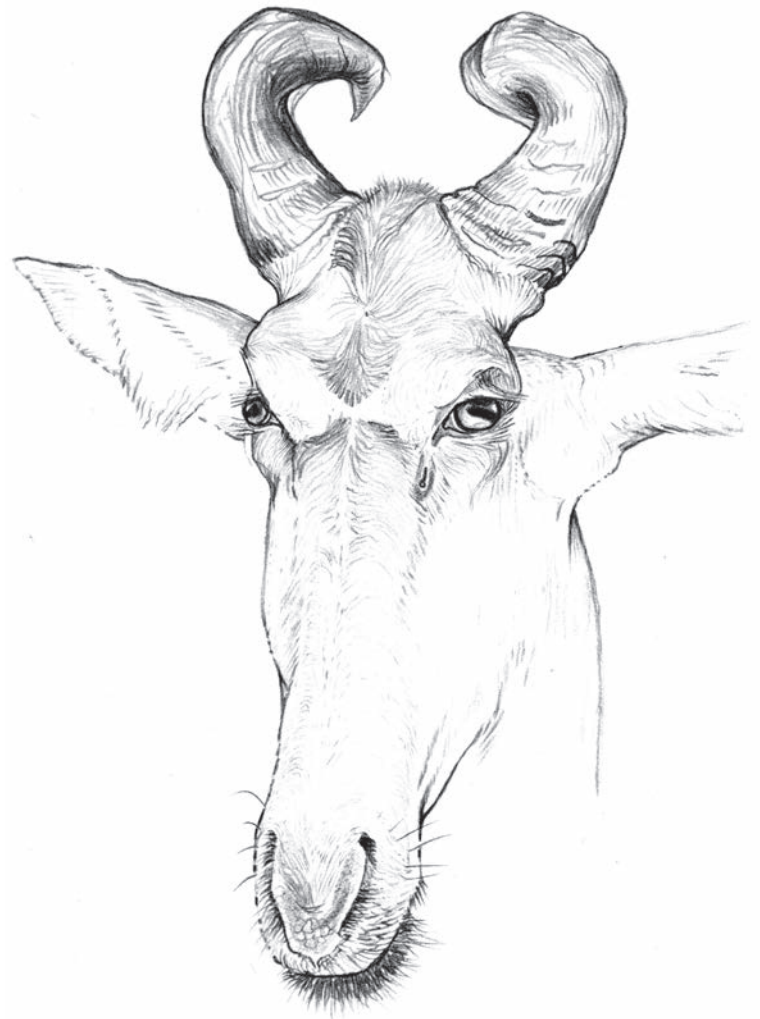
this evidence, *caama* is most closely related to *lichtensteinii* and should not be more closely allied to the East African forms as in some recent classifications; further, while *lichtensteinii* is clearly morphologically distinct from *caama* in many respects, molecular evidence (Matthee & Robinson 1999a) suggests that it should not be given separate specific or generic status (*Sigmoceros*), as had been argued previously (Roberts 1951, Vrba 1979, Meester *et al.* 1986, Grubb 1993c).

Further taxonomic investigation is needed, based on these recent findings, but, until this is available – and in contrast to the classification presented by Grubb (2005), who regards *caama*, *lichtensteinii* and *buselaphus* as distinct species – it seems most sensible to retain an interim scheme that recognizes eight subspecies (described below). While nomenclature and taxonomic level have changed in most cases, the subdivision of Hartbeest into eight main forms is consistent with the scheme adopted many years ago by Sclater & Thomas (1894). This has the advantage of allowing a coherent approach to

the Hartebeest adaptive radiation, although the main disadvantage of treating Hartebeest as one entity is that if the numbers of all the local forms are summed it suggests that Hartebeest are still quite abundant and leads to misplaced complacency about their conservation status. In fact, Hartebeest are declining rapidly almost everywhere (except in parts of southern Africa) and valuable local forms and 'hybrid' populations have disappeared (*buselaphus*, *nakurae*, possibly *tora*; see below) or are severely threatened (*swaynei*, *jacksoni*, *keniae*). Thus, it is important to emphasize the importance of local taxa and populations and the importance of conserving this variation (see Conservation).

Synonyms: *ambiguus*, *bangae*, *basengae*, *boselaphus*, *bubalinus*, *bubalis*, *cama*, *caama*, *cokei*, *cokii*, *cookei*, *deckenii*, *dieseneri*, *digglei*, *dorcas*, *evalensis*, *frommi*, *gendagendae*, *godonga*, *godowiusi*, *gombensis*, *gorongozae*, *grotei*, *hennigi*, *heufferi*, *heuglini*, *inkulanondo*, *insignis*, *invadens*, *jacksoni*, *janenschii*, *kangosa*, *keniae*, *konzi*, *lachrymalis*, *lademanni*, *lelwel*, *leucopymnus*, *leupolti*, *lichtensteinii*, *lindicus*, *luzarchei*, *major*, *matschiei*, *mauretanicus*, *modestus*, *montanus*, *munzneri*, *nakurae*, *neumanni*, *niediecki*, *niedieckianus*, *niedieki*, *noacki*, *obscurus*, *oscar*, *petersi*, *prittwitzii*, *rahatensis*, *rendalli*, *roosevelti*, *rothschildi*, *rowumae*, *rukwa*, *saadanicus*, *sabakiensis*, *schillingsi*, *schmitti*, *schusteri*, *schulzi*, *selbornei*, *senegalensis*, *senganus*, *shirensis*, *stierlingi*, *swaynei*, *tanae*, *tendagurucus*, *tora*, *tschadensis*, *tunisianus*, *ufipae*, *ugala*, *ulanga*, *ungonicus*, *ungoniensis*, *uwendensis*, *wiesei*, *wembaerensis*, *wintgensii*. Synonyms based on names of hybrids or integrades include: *digglei*, *keniae*, *kongoni*, *nakurae*, *neumanni*, *rahatensis*, *ritchii*, *rothschildi*. Chromosome number: $2n = 40$ (Hsu & Benirschke 1975, Robinson *et al.* 1991). Hybrids between *A. buselaphus* and *Damaliscus pygargus* are known and characterized by $2n = 39$ and are sterile (Robinson *et al.* 1991).

Description Medium-sized antelope with long and slender legs. Conspicuous hump over the shoulders is due to the long dorsal processes of the vertebrae in this region; it is sometimes stated, incorrectly, that the forelegs are longer than the hindlegs or that the vertebral column slopes. Hair of face, neck, back, sides and upperparts of limbs ranges from sandy-brown to deep red-brown in the Red Hartebeest *A. b. caama* to deep purplish tinge in Swayne's Hartebeest *A. b. swaynei*. Dark 'blaze' down front of face from horn-base to nose in more deeply coloured Red and Swayne's subspecies. There is typically a horizontal 'eyebrow' stripe of lighter, contrasting colour to that of face; for example, Coke's Hartebeest *A. b. cokii* has pale dun-coloured eyebrow on darker brown face and the Red Hartebeest has chestnut-brown eyebrow contrasting with its black 'blaze'. Inside of ear has black hairless pattern consisting of four radiating branches, surrounded by long white hair. All forms have whitish underparts, extending down back of legs, with pale rump below a line level with base of tail. Dark grey or black patches occur on shoulders and flanks of the Red Hartebeest and Swayne's Hartebeest, taxa that have been separated for a very long time. Occurrence of these striking patches together with deeply coloured pelage suggests action of more intense sexual selection in these two subspecies than in others. Patches are reminiscent of those in related alcelaphines, *Damaliscus lunatus* and Blesbok/Bontebok *Damaliscus pygargus*, and could thus reflect ancestral patterns. Tails generally covered with short pale hair with long tuft of black hair at end; the Red Hartebeest has thick black hair along entire length of tail. Both sexes have preorbital glands (larger in ♂♂); glands are very active in Lichtenstein's Hartebeest *A. b. lichtensteinii*,



Frontal view of Lichtenstein's Hartebeest *Alcelaphus buselaphus lichtensteinii* face.

which sometimes have a patch of secretion on their side that is left when they rub the side of the face on their own body (Dowsett 1966). Both sexes have large, active pedal glands with an anterior opening in the forefeet; Reiter *et al.* (2003) investigated the constituents of the interdigital secretion of the Red Hartebeest and identified 53 compounds. No inguinal glands. Males about 15% heavier than ♀♀ and neck and forequarters are more heavily muscled as an adaptation to fighting.

With the exception of Lichtenstein's Hartebeest, horns are supported on a sometimes heavy, bony pedicle that varies in height between subspecies and may vary individually in putative 'hybrid' zones. In Lichtenstein's Hartebeest, cross-sections of skulls suggest that the heavily 'bossed' horns of this form may represent the phylogenetic 'collapse' of a previously tall pedicel, such as is found in the closely related Red Hartebeest (Kingdon 1982). Like all alcelaphines, ♀♀ also have horns, although they are more slender and less angular than those of ♂♂. Horns are grey/black and their length ranges from 30–39 cm in *buselaphus* to 50–70 cm in *major* and *lelwel*; they have a thick basal portion, a sloped, deeply ridged (though less so in *lichtensteinii*), intermediate portion, and sharply pointed, smooth horn tips (see also Adaptations).

Geographic Variation

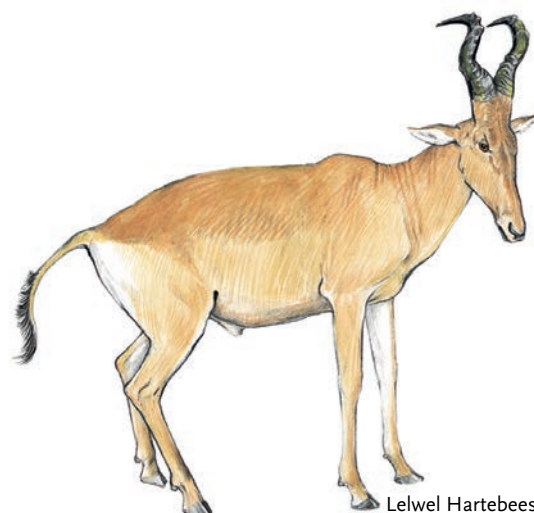
A. b. buselaphus (Bubal Hartebeest): North Africa, from Morocco to Israel. Extinct. The Bubal was the smallest subspecies. Pelage was uniform pale brown with pale underparts, but lacked the pale rump below the tail-base that occurs in all other subspecies. Horns had a 'U'-shaped appearance from the front, being similar to those of the Western Hartebeest.

A. b. major (Western Hartebeest or Kanki): West Africa, from Senegal, Gambia and Guinea to about Cameroon. A very large subspecies with golden or mid-brown pelage, lighter underparts and lighter rump; colour gradations are gradual and gives the impression of uniform brown colouration; pale eyebrow stripe and pale shape under the eye. Horns diverge from the base before curving upwards then backwards into long sharp horn tips; 'U'-shaped from the front (only the extinct Bubal shares this characteristic). Horns are unusual in leaving an area of unprotected skull between the base of the horns, suggesting that fighting in this subspecies may emphasize horn-locking and 'wrestling' rather than 'clashes' (see Adaptations below). This may also be the case in Lichtenstein's Hartebeest, and both subspecies also have a raised bump on the forehead, perhaps as an adaptation to this form of combat.



Western Hartebeest
Alcelaphus buselaphus major.

A. b. lelwel (including *jacksoni*) (Lelwel Hartebeest): SE Chad and N Central African Republic east to SE Ethiopia and south to N Kenya and NW Tanzania. A large subspecies with rich mid-brown pelage. No distinctive coat patterns. Has the usual pale underparts and rump (below the level of the tail-base). Horns have high 'V'-shaped appearance from front; set on a very tall pedicel, with sharp horn tips projecting backwards.



Lelwel Hartebeest
Alcelaphus buselaphus lelwel.

A. b. swaynei (Swaine's Hartebeest or Korkay): Rift Valley of Ethiopia; extinct in Somalia. Reddish-brown pelage, which becomes deep purplish-black in some adult ♂♂, particularly on the face, neck and sides. In the darkest ♂♂ the eyebrow stripe is lost except for a spot above each eye. Dark patches on flanks and shoulders. Horns resemble those of Coke's Hartebeest in having a bracket shape in front view, but the bends between the three sections of each horn are more rounded giving a lyrate shape and the horns are more widely spread.

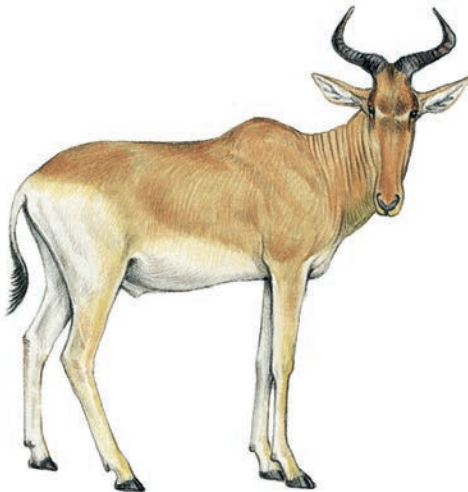


Swaine's Hartebeest
Alcelaphus buselaphus swaynei.



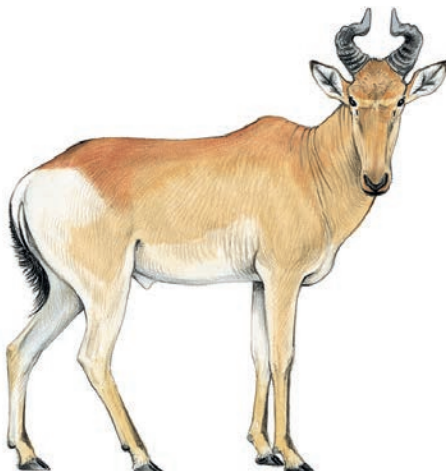
Tora Hartbeest
Alcephalus buselaphus tora.

A. b. tora (Tora Hartbeest): NW Ethiopia and SW Eritrea, and adjacent parts of Sudan. Pelage reddish-ochre to fawn with pale rump. Horns rather like Swayne's Hartbeest, a lyrate and widely spread version of the basic bracket shape; base and mid-section form a flattened 'V' from the front.



Coke's Hartbeest
Alcephalus buselaphus cokii.

A. b. cokii (Coke's Hartbeest or Kongoni): S Kenya and N Tanzania. Pelage mid-brown, light underparts and pale rump; pale eyebrow stripe. Distinguished by bracket-shaped horns with almost right-angle bends in front view; divided into short vertical basal section, horizontal mid-section and backward-pointing sharp horn tips.



Lichtenstein's Hartbeest
Alcephalus buselaphus lichtensteinii.

A. b. lichtensteinii (Lichtenstein's Hartbeest or Nkonzi): miombo woodland regions of south-central Africa. A large subspecies with mid-brown pelage, light underparts and pale rump, sometimes almost white under the tail-base; darker brown 'saddle' along back to tail-base. Sometimes a narrow pale eyebrow stripe, but this is often absent; sometimes pale marks over and under each eye. The side of the body behind the shoulder often has a dark mark caused by rubbing of the preorbital gland. The lack of a pedicel is diagnostic amongst Hartbeest as is the distinct bump on the forehead (Western Hartbeest have a less prominent version of this structure). Horns are short and distinctive in having a spatulate basal section that protects the top of the skull with a hook-shaped mid-section.

A. b. caama (Red Hartebeest or Khama): southern Africa. Distinctive striking chestnut-brown pelage, black facial 'blaze' and dark patches on shoulders and flanks; some animals have 'saddle' of dark hair along the back as occurs in Lichtenstein's Hartebeest. Only Swayne's Hartebeest in Ethiopia has such striking colouration. Horns resemble those of the Lelwel Hartebeest with a high 'V' shape on a tall pedicel, but also have a slight double-bending reminiscent of Lichtenstein's Hartebeest.

Intergrade populations occur between *lelwel* and *cokii* (Kenya Hartebeest: *keniae*; extinct Nakuru Hartebeest: *nakurae*), and have been reported between *lelwel* and *swaynei* and between *lelwel* and *tora* (*neumanni*, *rothschildi*, *digglei*, *rahatensis*) (Ruxton & Schwarz 1929), but these may be less extensive than previously supposed and in some cases may represent clinal variation in the main forms (Bolton 1973); Yalden *et al.* (1984) believe that the Blue Nile may have been an effective barrier between *lelwel* and *tora*.

Similar Species

Damaliscus lunatus. Similar distribution to the Hartebeest, but never occurred in North Africa and is absent from south-west Africa. Characterized by simple, scimitar-shaped horns about the same length as the head that sweep backwards or, in the case of Tsessebe *D. l. lunatus*, slender bracket-shaped horns with rounded curves that lack the angular appearance of Hartebeest horns; they lack the presence of a pedicel supporting the horns. Pelage is generally deeper in colour than that of Hartebeest, being typically deep chestnut-brown with various patterns, including black shoulder patches in the Topi *D. l. jimela*; however, Swayne's Hartebeest and Red Hartebeest also have deep chestnut pelage and dark patches.

Beatragus hunteri. Restricted to NE Kenya, where the Hartebeest does not occur, and probably has been exterminated in S Somalia where it was once abundant. The Hirola is distinguished from the Hartebeest by its long, Impala-like, lyrate horns and the lack of a pedicel.

While adult species of the genus *Beatragus* and *Damaliscus* can be readily distinguished from adult Hartebeest, this is not necessarily the case for the young. For the first few months of life, before adult features such as the pedicel of Hartebeest start to appear, the young of these three genera are virtually indistinguishable, reflecting their close phylogenetic links. In contrast, the brown young of wildebeest *Connochaetes* spp., with their characteristic low head position, are quite distinct.

Distribution Hartebeest formerly ranged from North Africa and the Middle East throughout the savannas and grasslands of sub-Saharan Africa and the miombo woodlands of south-central Africa down to the tip of southern Africa, being absent from desert and forest, notably the Sahara and the western rainforest.

Historical Distribution In North Africa, the Bubal Hartebeest occurred in Morocco (Loggers *et al.* 1992, Aulagnier *et al.* 2001), the steppes of the Hauts Plateaux and nearby mountains in Algeria (Kowalski & Rzebik-Kowalska 1991, De Smet & Smith 2001), the mountains of S Tunisia (Smith *et al.* 2001), Libya (where knowledge of their former range is unclear; Hufnagl 1972, Khatibi & Mallon 2001), and parts of the Western Desert in Egypt (Osborn & Helmy 1980, Saleh 2001). Numerous hartebeest remains have been found in excavations



Red Hartebeest
Alcelaphus buselaphus caama.

of fossils in Egypt and the Middle East, especially Israel and Jordan, and these, together with illustrations of hartebeest in the tombs of ancient Egyptians, are assumed to be *A. b. buselaphus*. The precise former southern limits of distribution of the Bubal Hartebeest are not known (Ansell 1972).

The Western Hartebeest occurred in the savanna woodlands of West Africa, from S Senegal, E Gambia, Guinea-Bissau and N Guinea eastwards through SW Mali and N Côte d'Ivoire to N Cameroon and W Central African Republic and SW Chad (Grubb *et al.* 1998, East 1999).

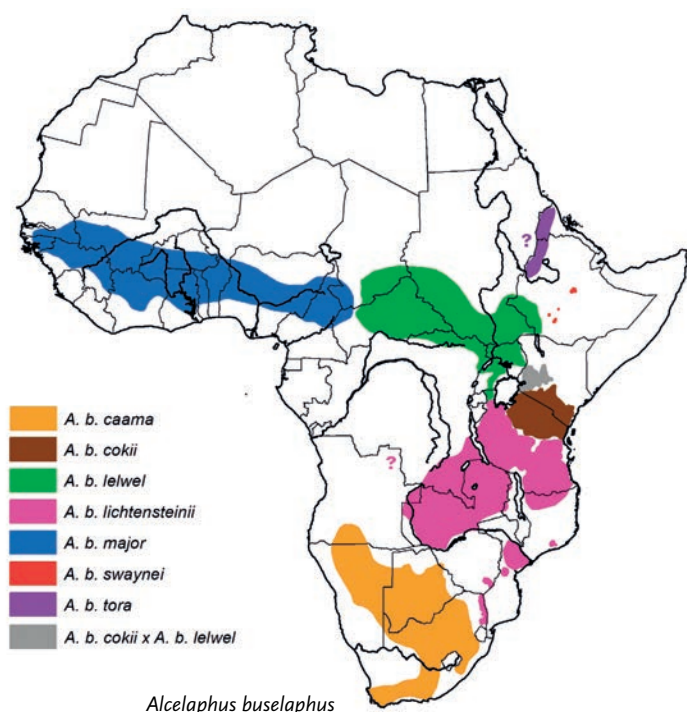
Tora Hartebeest formerly occurred in the western and south-western savannas of Eritrea, the north-western lowlands of Ethiopia and in the adjacent border regions of Sudan, while Swayne's Hartebeest occurred throughout the Rift Valley in Ethiopia into NW Somalia (Yalden *et al.* 1984, East 1999). Lelwel Hartebeest ranged from SC and SE Chad through N and E Central African Republic, SW and SE Sudan, the northern and north-eastern savannas of DR Congo, the south-western lowlands of Ethiopia, NW Kenya, much of N Uganda and extreme NW Tanzania. Coke's Hartebeest occurred widely throughout S Kenya and N and NE Tanzania (Stewart & Stewart 1963, East 1999).

Lichtenstein's Hartebeest formerly occurred widely in the miombo woodlands of south-central Africa, from W and S Tanzania, SE Burundi and SE DR Congo south to S Mozambique and NE South Africa (probably as far south as N KwaZulu-Natal; see discussion in Milstein 1989).

Except where they were replaced by Lichtenstein's Hartebeest (e.g. Mozambique, most of Zimbabwe, NE South Africa), Red Hartebeest occurred throughout much of southern Africa (with a marginal intrusion into S Angola near the Namibian border), except in the more arid regions of W Namibia and South Africa, and parts of N and E Botswana; they occurred only marginally in W Zimbabwe.

Current Distribution The range and numbers of Hartebeest have declined markedly and become increasingly fragmented, due to hunting, and the expansion of cultivation and livestock farming.

The Bubal Hartebeest is now extinct. The last report from SE Morocco was in 1945 (Panouse 1957), and the last animals were



shot between 1945 and 1954 in Algeria (De Smet 1989) and 1902 in Tunisia at the edge of the great Eastern Erg, south-west of Tataouine (Lavauden 1926b).

Western Hartebeest no longer occur in Gambia (though migrants may enter from Senegal), and have disappeared from much of their former range in this region, surviving mainly in and around protected areas; they are still reported to occur, albeit at low densities, in W N. P. in SW Niger (Hibert *et al.* 2004). Populations outside parks have generally declined, one well-documented example being the sharp decline outside Niokolo-Koba N. P. in Senegal (Galat-Luong & Galat 2001). They remain marginal or absent in extreme W Central African Republic and Chad.

There is limited recent information on the status of Tora Hartebeest, but they may survive in low numbers in the W and SW savannas of Eritrea and some inaccessible parts of Ethiopia (East 1999) although recent short surveys have failed to confirm their presence (Heckel *et al.* 2008, Heckel 2009); they are probably extinct in Sudan.

Swayne's Hartebeest survive in three isolated localities in the Southern Rift of Ethiopia, in Senkele Wildlife Sanctuary, Nechisar N. P., and the newly designated Mazie N. P. (East 1999, Flagstad *et al.* 2000, Refera 2005, Antonínová *et al.* 2008); they no longer occur in either Awash N. P. or Yavello Sanctuary (Antonínová *et al.* 2008). Swayne's Hartebeest is extinct outside Ethiopia.

Lelwel Hartebeest have undergone dramatic reductions in numbers, particularly in Uganda and Central African Republic, where they were once particularly abundant but are now reduced to a handful of protected areas; their status in NW Tanzania (around the Rumanyika Orugundu-Ibanda Arena Game Reserves) is not known.

Coke's Hartebeest have lost half of their former range in Tanzania, but populations still occur in Serengeti and Tarangire National Parks in Tanzania, and Tsavo N. P. and the Masai Mara National Reserve in Kenya (East 1999).

Lichtenstein's Hartebeest have been eliminated from many parts of their former range, and now occur mainly in wildlife areas in Tanzania, Mozambique and Zambia. In Zimbabwe, they remain confined to the south-east, while in Malawi they are largely or entirely restricted to Kasungu N. P. and Vwaza Marsh G. R.; the subspecies is extinct in Burundi, and probably in Angola (East 1999).

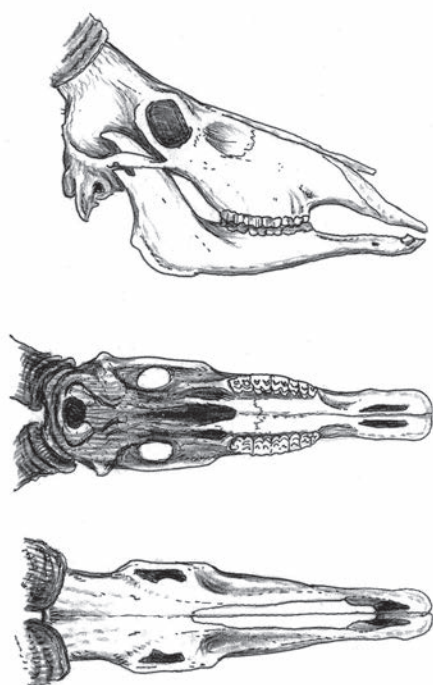
The range of Red Hartebeest was greatly reduced due to overhunting by European colonists, and they survived only in the Northern Cape Province of South Africa and in Namibia. They are now expanding again as they have been reintroduced into many protected areas and private game farms, and they have also been introduced outside their former range (e.g. to Swaziland in Malolotja N. R. and to private game farms in Zimbabwe). The Red Hartebeest remains extinct in Lesotho, while its current status in Angola is not known (East 1999).

Habitat Hartebeest are associated with grassland, but are rarely found in the centre of extensive grassland plains. In open areas, such as the grassland of Serengeti N. P. in Tanzania, they are typically found around the edge of woodland. When in woodland areas, such as the wooded savanna of West Africa or the miombo woodland of south-eastern Africa, they are typically associated with grassland clearings. They thus appear to be an edge or ecotone species (Booth 1985), generally avoiding more closed woodland. The remarkable variety of savanna habitats occupied, from woodland to the dry savannas of Ethiopia, vary substantially in primary production, climatic seasonality, habitat structure and openness (Bourlière 1983). Hartebeest body size varies in relation to differences in habitat primary production, such that subspecies in more productive habitats are significantly larger than those in less productive ones (Capellini & Gosling 2007). Throughout their range, Hartebeest are dependent on the availability of surface drinking water. They have been recorded at 3700–4000 m on Mt Kenya (Young & Evans 1993).

Hartebeest may be outcompeted in open grassland by specialized short-grass feeders such as Common Wildebeest *Connochaetes taurinus*. This relationship was illustrated by a 'natural experiment' in Nairobi N. P. in the 1960s. Before the 1962/63 drought, Common Wildebeest dominated the plains ungulate community and kept grassland in a short cropped form that was optimum for themselves and too short for Hartebeest. The severe 1960/61 drought reduced the Common Wildebeest population to low levels and the subsequent heavy rains in 1962 allowed grassland to increase to a height that Hartebeest could utilize more efficiently. Hartebeest thus increased in numbers and replaced Common Wildebeest as the dominant savanna ungulate (Gosling 1975). However, predation was also involved in this transition because Common Wildebeest were killed at a higher rate than expected from their relative numbers and this helped drive their numbers down. This situation persisted into the late 1960s when Hartebeest numbered around 1500 and wildebeest around 250 in the 144 km² area. In drier areas, with coarser grasses, Hartebeest may sometimes have dominated the central areas of grassland plains. Thus, in the Haut Plateau in N Somalia, Swayne observed that Hartebeest (of the subspecies that was subsequently named after him) literally covered the open plains; a dozen herds were in sight at one time with each herd consisting of 300–400 animals (shortly afterwards these herds were decimated by rinderpest [Hunt 1951], and Swayne's Hartebeest is now extinct

in Somalia). According to Lavauden (1926b), in North Africa the now extinct Bubal Hartebeest occurred in sub-desert steppe and semi-forested habitats, preferring rocky habitats to dunes (and see also Heim de Balsac 1936); however, by the start of the twentieth century, Bubal Hartebeest had been overhunted for centuries and may already have been forced away from their preferred habitat.

Abundance The most recent survey of Hartebeest abundance (East 1999) paints a picture of overall decline and fragmentation of the surviving populations, now mainly restricted to protected areas, many of which are poorly managed. An exception is the Red Hartebeest in southern Africa, which is currently increasing in numbers (see Conservation). The abundance of Hartebeest is best summarized with reference to the three main clades identified by Flagstad *et al.* (2001). The total number of the Western clade (*major*) is about 36,000 (correcting for undercounting bias in aerial surveys), but they are declining nearly everywhere because of illegal hunting. The more diverse Eastern clade (*lelwel*, *cokii*, *swaynei*, *tora* and intergrades) totals about 115,750 and is generally declining. Nearly all of this total consists of *Lelwel* (70,000) and *Coke's* (42,000) Hartebeest; *Tora* Hartebeest may already be extinct and both *Swayne's* (less than 800, with most in the Senkelle Sanctuary and Mazie N. P. in Ethiopia; Antonínová *et al.* 2008) and the Kenya (*cokii* × *lelwel*; 3500) Hartebeest are at dangerously low levels (East 1999). The *Lelwel* Hartebeest may have undergone a major decline since the 1980s, when total numbers were estimated to be >285,000, mainly in Central African Republic and S Sudan. Little information is available on its current status in Sudan, although recent survey work conducted in the dry season estimated totals of 1070 and 115 animals for Southern N. P. and Boma N. P., respectively (Fay *et al.* 2007); the latter is a significant decline from the >50,000 animals estimated in the dry season in 1980 by Fryxell (1980).



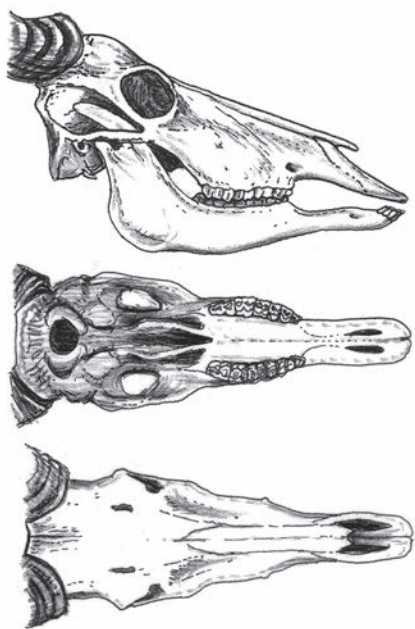
Lateral, palatal and dorsal views of skull of Lelwel Hartebeest *Alcelaphus buselaphus lelwel*.

Lichtenstein's Hartebeest in the southern clade totals about 82,000, with sizeable populations surviving only in Tanzania, particularly in the Selous ecosystem, and Zambia, in Kafue N. P. and the Luangwa Valley. The other member of the southern clade, the Red Hartebeest, totals about 130,000 and is increasing mainly due to reintroduction for consumptive use such as sport hunting.

The overall total for the species at the time of East's summary was about 360,000 animals. However, this total is strongly influenced by the contribution of the managed populations of Red Hartebeest in southern Africa. It is also a tiny proportion of historical numbers, and conceals the fact that Hartebeest are declining almost everywhere and that this rate of decline is accelerating with the increase in illegal hunting for the bushmeat trade. For example, Sournia & Dupuy (1990) gave the population of Western Hartebeest for the important Niokolo-Koba N. P. in Senegal as over 5000. When surveyed in 1990–93, the population was ca. 2325, and by 1994–98 it was ca. 1175 (A. Galat-Luong, G. Galat & M. Mbaye pers. comm.). Likewise, in Comoé N. P. in Côte d'Ivoire numbers declined by 60% from 18,300 in 1984 to an estimated 5200 in 1998 (Fischer & Linsenmair 2001a).

Densities of Hartebeest, like those of other African ungulates, must be considered with some reservations. Few populations are monitored sufficiently closely to know whether they are at carrying capacity. Many contemporary populations, including those in protected areas, are under severe hunting pressure or affected by fencing. While early explorer accounts were often exaggerated, few areas now seem even remotely close to the picture they gave of ungulate abundance. In addition, Hartebeest have specific habitat preferences and are never found at uniform densities across censused areas. With these caveats, Hartebeest density has been measured in a number of places: *Coke's* Hartebeest averaged 2.6/km² in the Athi/Kapiti plains in Kenya before the severe 1961 drought and 0.8/km² after it (Stewart & Zaphiro 1963); Western Hartebeest were recorded at 0.3/km² in 1990–93 and 0.01/km² in 1994–98 in Niokolo-Koba N. P. (Galat *et al.* 1998), 1.01/km² in Ali N. P., Upper Volta (Green 1979), 0.45/km² in Comoé N. P. (Fischer & Linsenmair 2001a), and 1.66/km² in Bénoué N. P., Cameroon; densities of Lichtenstein's range from 0.2 to 3.5/km² (Booth 1985).

Adaptations The skull of the Hartebeest is long and thin and the incisor row narrow (ca. 5 cm), probably as an adaptation to selective feeding. Hartebeest crop short green swards and green flushes that follow burning, when they are available, but they are most notably adapted to feeding selectively within medium and tall swards. The thin muzzle is pushed into the sward and is used to select grasses with a high proportion of leaf blade; Hartebeest can even nibble sheath from grasses that have had their leaves removed (Stanley Price 1978a, Murray & Brown 1993). This selectivity can be readily observed as Hartebeest lift their heads to look around while chewing (an anti-predator adaptation), often with the grass selected protruding from the mouth. Perhaps the most remarkable aspect of Hartebeest feeding is the ability to extract high-quality food from senescent swards (Murray & Brown 1993). Where Hartebeest and Roan Antelopes *Hippotragus equinus* overlap in West Africa, the two species graze on similar plants except in the driest time of year; at this point Roan Antelopes are forced to switch to browse while Hartebeest continue to feed on senescent grasses (Schuette *et al.* 1998). Hartebeest are thus particularly well adapted to survival in arid grasslands and in dry seasons and droughts.



Lateral, palatal and dorsal views of skull of Lichtenstein's Hartebeest
Alcelaphus buselaphus lichtensteinii.

The digestibility of dry matter and organic matter in the Hartebeest is higher, and the intake lower, than other alcelaphines (Arman & Hopcraft 1975, Stanley Price 1978a, Murray 1993). The combination of an ability to select high-quality components from senescent swards, coupled with low appetite and high digestive efficiency, could be the key suite of adaptations that allowed the Hartebeest to outcompete and replace more generalist alcelaphine precursors.

The horns and skulls of all male antelopes are adapted to fighting, but those of the Hartebeest show some unique features. They are also highly variable across Africa, probably reflecting different adaptations to fighting. In general, Hartebeest fight by pushing forward with the hindlegs into a horn 'clash', falling down onto their 'knees' as they do so. The horns meet with great violence and the 'bang' can be heard from hundreds of metres away. The horns then tend to interlock during 'wrestling' (see Social and Reproductive Behaviour), a phase of fighting in which animals push and twist their horns, trying to push the head of the opponent to one side. If they succeed, they disengage the horns and stab the face, neck and shoulder of the opponent with a backward hooking movement. Deep horn wounds are common in areas where competition is intense, and population densities high, and sometimes these wounds result in death (Gosling 1975).

Horns consist of three main sections: a finely ridged short but thick basal section, a deeply ridged middle section and a smooth, sharply pointed tip. Observation of fighting and wear facets on horns shows that the middle section is used to catch the blow of an opponent, and the sharp tip is for stabbing. The parts are angled so that the horns interlock during 'wrestling'. This angling has been achieved by rotational twisting and a complete reversal of the horns during a species-specific evolutionary development that is possibly reiterated during ontogenetic growth (Kingdon 1982); variations in this process are partly responsible for the characteristic variation in horn

shape across the different extant (and extinct) forms of Hartebeest. This angling reaches its most extreme in Lichtenstein's Hartebeest, where the middle-section and tip forms an incurved hook that catches the horns of the opponent and prevents it disengaging. In Coke's Hartebeest, the middle horn section is horizontal and catches the blow of an opponent above the head. In other Hartebeest, but at its most extreme in Lelwel's, the middle section is oblique and guides the horn of an opponent into the narrowing 'V' shape between the base of the horns, again stopping the blow above the head. In Lichtenstein's Hartebeest, the basal section is broad and spread over the top of the head to protect it. In all forms, except Lichtenstein's Hartebeest, the basal sections are set on a bony pedicel that again probably functions to extend the leverage and stop an opponent's horns well away from the brain. All of these structures are strong and heavy and designed to withstand heavy blows and violent 'wrestling'. Differences in fighting intensity between different Hartebeest taxa have not been quantified.

Hartebeest are renowned for their vigilance and for their speed and endurance. They can run at a fast canter for many kilometres and hunters report that they continue to run even when badly wounded. Presumably these traits were originally anti-predator adaptations in animals that live in open savanna environments (see Predators, Parasites and Diseases). However, their behaviour may also have been shaped by humans. The first Hartebeest appeared less than a million years BP in an area where stone tools made by successive *Homo* species have been abundant for 2.4 million years. The long dorsal processes probably function to support the powerful shoulder muscles and absorb the shocks of a fast prancing gait, but may also serve to increase the body surface in lateral displays to competitors and mates (see Social and Reproductive Behaviour).

Hartebeest thermoregulate by panting rather than sweating. In experiments to measure this response under natural solar radiation, Coke's Hartebeest started to pant at 32–34 °C; discounting the heat lost by re-radiation (80%) and convection, Hartebeest lose 61% of absorbed and metabolic heat by panting (Finch 1972). When individuals are hydrated, increased panting appeared to be a response to skin temperature but, when dehydrated (15% weight loss), the response was triggered at 39.5 °C by core (rectal) temperature (Finch & Robertshaw 1979). When dehydrated, Hartebeest thus accept an increase in body temperature in order to conserve water. Brain damage is presumably prevented, as in other antelopes, because blood that has been cooled by panting in the nasal mucosa removes heat from the blood entering the brain in the counter-current heat exchanger of the rete mirabile (Taylor 1969). These mechanisms allow a degree of water independence in the dry season. Under natural conditions, some Hartebeest seek shade to reduce exposure to solar radiation (Gosling 1975) and experiments (Finch 1972) confirm the physiological benefits. It is thus interesting that not all Hartebeest seek shade; some rest in the sun and some even stand on termitaria and other mounds in exposed positions. Perhaps this is because of the risks of predation from Lions *Panthera leo* and Cheetahs *Acinonyx jubatus* in areas where cover from trees and shrubs provides shade: Hartebeest might thus trade off the costs of thermoregulation against the risks of predation.

Foraging and Food Hartebeest feed mainly on grass (Stewart & Stewart 1970) and studies involving stable carbon isotope analysis

support field observation and faecal analysis in showing that they are almost exclusively grazers (Cerling *et al.* 2003, Sponheimer *et al.* 2003b). None the less, Hartbeest do browse, as evidenced by direct observations and the occurrence of browse in stomach contents (Van Zyl 1965, Wilson 1966c, Kok & Opperman 1975, Booth 1985; and see Gagnon & Chew 2000). Hartbeest feeding specializations may be the key to their explosive evolution that occurred at the expense of less-specialized grazing antelopes, notably the *Hirola Beatragus hunteri* and allies (Kingdon 1982). Hartbeest have long narrow noses and incisor rows that are adapted to feeding selectively within tall grass swards. They are particularly well adapted to taking bites with a high proportion of leaf blade from senescent swards and in feeding trials they rejected poor quality components of the diet at a higher frequency than wildebeest and Topis (Murray 1993). They can also scrape the leaf sheath off the stem in defoliated swards (Stanley Price 1974). Hartbeest cannot increase their bite size in taller swards and their intake rate is lower than that of Common Wildebeest and Topis (Murray 1993). Their low intake is probably because they have a lower metabolic rate than other extant alcelaphines and this, in combination with their ability to select a high quality diet and high digestibility (Arman & Hopcraft 1975, Murray 1993), gives them an important advantage in the dry season, a limiting time for many species. In the wet season they feed less selectively from short green flushes.

Seasonal changes in their feeding can follow a classic catenary sequence. In Nairobi N. P. they feed from short green grasses on the catena apex in the rains, then progressively shift to longer, coarser grasses in or near sumps as the dry season advances (Gosling 1975). This may be the basis of their ecotone habit (Lamprey 1973): they are ecologically poised to take advantage of a shift from one preferred food to another. Significantly, when the resource-defence territories of ♂♂ are subdivided between two competing ♂♂, the split generally occurs at right-angles to the grass zones within the original territory: each ♂ thus retains access to the full spectrum of seasonally optimum grass communities (Gosling 1975).

A number of ecologists have investigated the basis of possible niche separation between Hartbeest and other grazing ungulates. Bell and others (Gwynne & Bell 1968, Bell 1970) showed that grazing ungulates in Serengeti N. P., including Hartbeest, selected different plant parts from grass swards, and more recent feeding trials (Murray 1993, Murray & Brown 1993) suggest that specialization on particular growth stages of grass may be the fundamental reason why a diversity of grazers can co-exist. These specializations have a spatial dimension as well as a temporal one since tall dry swards can persist for longer in some areas than rapidly growing and more nutritious growth stages. Thus, Hartbeest can remain as residents when other alcelaphines such as wildebeest that are dependent on more ephemeral growth stages are forced to migrate to seek food elsewhere. This specialization also gives Hartbeest the ability to live in relatively arid grasslands and explains the fact that they extended further north, into Ethiopia, Eritrea, North Africa and the Middle East, in contrast to the more restricted distributions of the wildebeest and *D. lunatus*. However, they do not penetrate truly arid areas such as the Sahara. Their ability to extract a high-quality diet from senescent swards also gives them considerable commercial potential since they can exploit dry swards on a year-round basis more efficiently than any competitors, both alcelaphine or cattle.

The grass species eaten by Hartbeest have been documented in a number of studies using direct observation in the field and analysis of stomach contents and faeces. In Coke's Hartbeest in Tanzania, Lamprey (1973) found that grass occurred in the diet of Hartbeest at a frequency (96%) greater than in any other large herbivore in the area; 12 grass species were seen being eaten, the most common being *Cynodon dactylon*, *C. plechtostachyu* and *Cenchrus ciliaris*. In studies using faecal analysis in Kenya (Casebeer & Koss 1970, Stewart & Stewart 1971), the most common species detected were *Themeda triandra* and *Ischaemum afrum*. *Pennisetum mezianum* was avoided in the wet season although it was one of a number of grasses eaten at higher frequencies in the late dry season. Red Hartbeest also favour *T. triandra*, eating it throughout the year; other grasses eaten by this species in N South Africa include *Eragrostis* spp., *Panicum stapfianum*, *Cynodon dactylon*, *C. hirsutus* and *Sporobolus* spp. (Kok & Opperman 1975). Red Hartbeest are the only subspecies known to eat significant amounts of browse, but this only occurs in the dry season of particularly dry years (Skinner & Chimimba 2005). Swayne's Hartbeest appear to select grasses not only on the basis of nutrients, but also on water content and this may explain why they can survive in areas where no apparent free water is available (Matravers Messina 1993).

Daily activity patterns are similar to those of many other species of plains ungulates. At dawn in Kenya, a few Hartbeest are still lying at the end of a resting period. However, most are already grazing in medium or long grass areas and this activity predominates until the temperature rises in mid-morning and animals move to short grass areas where they rest. Early morning grazing may be particularly important for this water-dependent species, because grass is often wet with dew at this time. At the start of resting, often between 10:00 and 11:00h, many animals stand, sometimes in the shade of trees or shrubs and ruminate; as time goes on, progressively more lie down, so that by 13:00–16:00h most are resting in this way. As it cools at around 16:00h animals start to move towards long grass areas, grazing as they do so (Gosling 1975). This basic pattern of activity is similar in Red Hartbeest (Ben Shahar & Fairall 1987). In Coke's Hartbeest, grazing continues for one to two hours after sunset, when another resting period commences. There is at least one further grazing period before a resting phase just before dawn. However, activity at night needs further investigation. Movement to short grass areas during the day for resting seems likely to be an anti-predator adaptation, but the relationship between such movements at night and activity cycles is poorly known. Activity also varies seasonally with more grazing during the middle of the day in the rains (Gosling 1975).

Social and Reproductive Behaviour Like most of the plains antelopes, the primary determinant of the Hartbeest mating system appears to be the movements of ♀♀ in relation to food and water (Gosling 1986). Females invest most in offspring, particularly during pregnancy and lactation, and their ecology is thus shaped by selection to maximize nutrient intake for reproduction. There is no known post-natal care of their offspring by ♂♂. As noted already, ♀♀ have horns, and there is a moderate level of agonistic behaviour between adult ♀♀. This sometimes results in fights with violent horn contact and, as a result, a few ♀♀ are seen with broken horns. The context of agonistic behaviour between ♀♀ has not been studied

but it seems to occur when they come into close contact during drinking, earth-eating or feeding. One animal generally proves to be dominant in such encounters and the role of these dominance relations in mediating the access of ♀♀ to limiting resources is a priority for future study (for polygynous antelopes in general, as well as for Hartbeest). Sometimes ♀♀ seem to compete where no obvious resource is under dispute. For example, after rain, Red Hartbeest ♀♀ lie down and rub their face and neck in wet soil. Females engaged in this behaviour are sometimes approached and chased away by dominant animals (L. M. Gosling pers. obs.). Such behaviour seems linked to the establishment or reinforcement of dominance rather than to competition for a resource. The role of these dominance interactions in competition for access to mates is unknown (as is the existence of choice of mates, below).

Females aggregate into groups that are more or less well defined. These groups split and reform as ♀♀ move about the landscape and the only consistent associations are between a ♀ and her offspring. This association becomes looser as new calves are born. In Coke's Hartbeest, up to four successive offspring can sometimes be seen clustered with their mother and typically the distance from the mother to each offspring increases with its age.

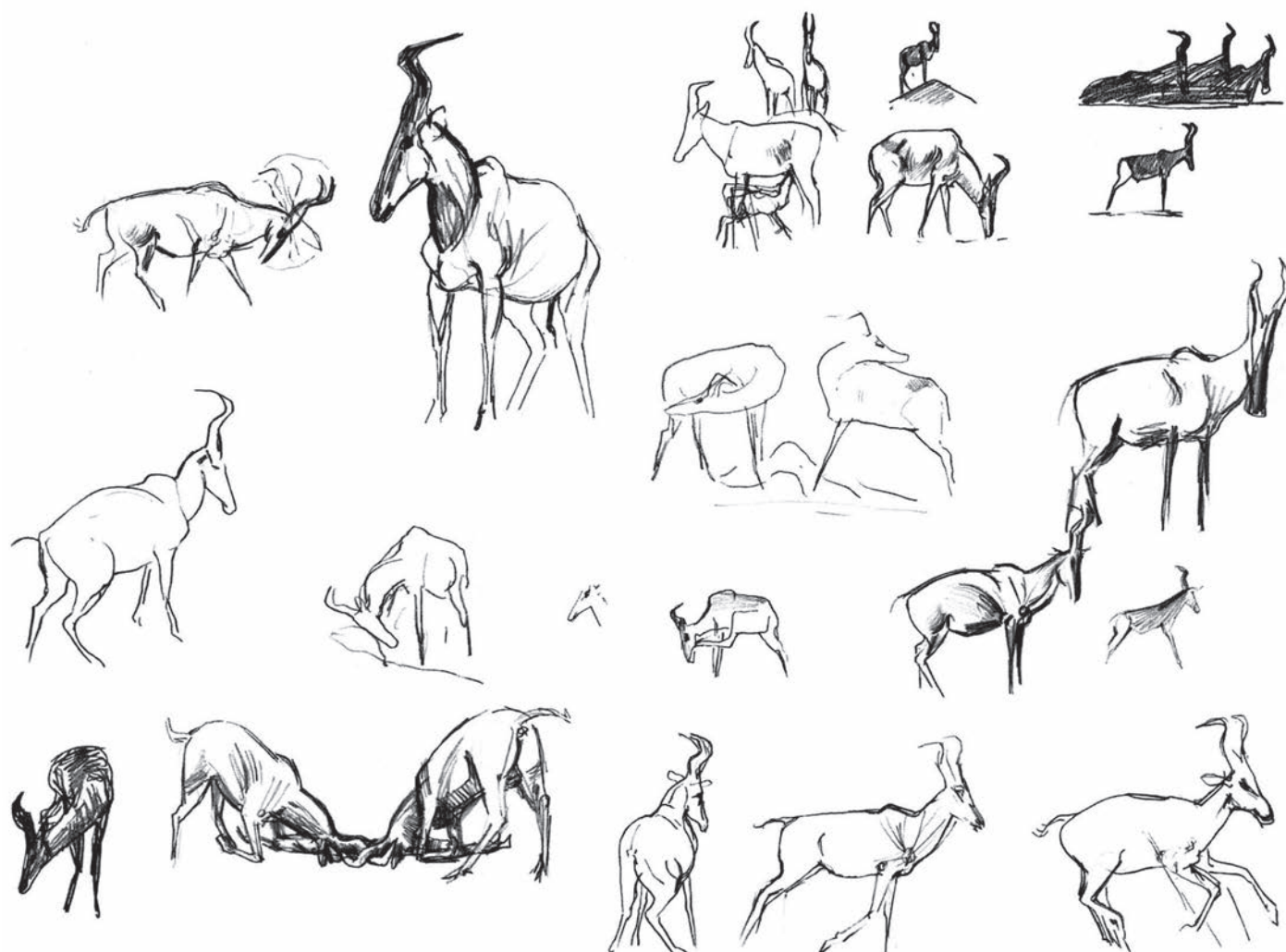
The wide-scale movements of groups of ♀♀ are dictated by differences in the growth and persistence of different grass communities throughout the seasons and by movements during the day between resting and feeding locations. Hartbeest are water-dependent and, in the dry season, movements to permanent water sources become increasingly important. The savanna environment has a regular pattern of vegetation productivity in relation to rainfall and, in general, female movements are quite predictable. As a result, sedentary, 'sit-and-wait' mating strategies are a viable option for ♂♂ (Gosling 1986). Males compete to defend the areas that most ♀♀ visit and establish defended areas known as resource-defence territories; 38% of adult ♂♂ occupied territories in a three-year study of Coke's Hartbeest (Gosling 1975), indicating that an average of up to three ♂♂ may potentially compete for each territory. As a result of this competition, territories that attract most ♀♀ are smaller and tenure is shorter for their owners; lower-quality territories have fewer ♀♀, but they are held for longer periods (Gosling 1974). Territories provide a spatial reference for dominance, their owners being dominant over all other ♂♂ while in residence. This becomes particularly important during mating and, as far as is known, only territorial ♂♂ (or dominant ♂♂ that follow groups of ♀♀, see below) mate. When ♂♂ leave their territories, for example to drink, they are subordinate to ♂♂ resident in territories that they pass through. Males temporarily outside their territories are generally dominant over non-territorial ♂♂, although not always. The behavioural state of dominance in territorial ♂♂ thus appears to be under central nervous system control and can be turned on and off as they cross the boundary of their territory.

While Hartbeest do use the preorbital glands to some extent for marking objects in their territories, territories are scent-marked mainly by dung piles and these are particularly large at boundaries where resident ♂♂ interact with neighbouring territorial ♂♂; the interdigital secretion also probably plays a role in demarcation of territories (Reiter *et al.* 2003). Neighbours meet regularly in agonistic encounters, particularly where territories are relatively small. These encounters consist of much grooming (possibly to

avoid head-on orientations) and are marked by head-high postures with facing away. The focus of most encounters is ritualized scent-marking. Males sniff a dung pile, paw it, kneel, rub their head and horns, stand and defecate. The opponent then moves to the same position, noses the faecal pellets left by the preceding ♂ and repeats the actions. Repetitions of these sequences can go on for some time, sometimes with vigorous pawing that scatters the faeces and results in a depression at regularly used sites. In general, Hartbeest do not lie down in their dung piles during boundary encounters (in contrast to wildebeest) although they do lie on their own dung piles when resting (possibly a form of self-anointing with the odour used to mark their territory; Gosling 1982). Hartbeest break shrubs and dwarf trees such as *Acacia drepanolobium* with their horns then rub the surface of the preorbital gland on the end of broken branches; such marking sites are generally 1–3 cm in diameter (Gosling 1975). Males also 'self-anoint' by rubbing the secretion of the preorbital gland on their own sides leaving a distinct mark in the case of Lichtenstein's Hartbeest (Dowsett 1966). This area is sniffed and sometimes nibbled by opponents during agonistic encounters and these animals may be assessing their opponent (as a territory owner) by matching the smell on the pelage with that of scent marks in the territory (Gosling 1982). In the case of Lichtenstein's Hartbeest in Zimbabwe, self-marking increases in Sep just before the rut (Booth 1985); however, this behaviour occurs in all age and sex classes, which is curious and needs further investigation. Booth (1985) saw a territorial ♂ Lichtenstein's Hartbeest marking a ♀ on its rump just before mounting.

Horn contact behaviour usually starts with 'horn-tangling' (light butting and twisting against the opponent's horns). Serious fighting is generally absent during boundary encounters and also from most interactions with intruders. It occurs principally to determine ownership of a territory and at such times ♂♂ fight with great violence and are sometimes killed (see Adaptations); Dowsett (1966) reported one fight lasting more than an hour. Inter-individual body orientation is also very important in interactions between male Hartbeest. During encounters ♂♂ often orientate in the parallel or reverse parallel orientation. Encounters end with the ♂♂ gradually and reciprocally turning the head away after a period in the forward parallel orientation and eventually moving directly away from each other. They often graze at this point. Some interactions even consist almost entirely of two ♂♂ grazing next to each other ('grazing encounters') with subtle and reciprocated changes in body orientation.

Agonistic behaviour with intruding ♂♂ varies according to the dominance status of the intruder. Encounters with high status ♂♂ can contain many of the elements that occur between neighbouring territorial ♂♂, including escalation to horn contact. In rare cases, such interactions can escalate to full-blooded fights that become takeover attempts. However, the great majority of encounters with non-territorial ♂♂ end in the early flight of the intruder. Sometimes intruders simply turn and run as an owner approaches. Sometimes owners stand with the head erect and facing away. The intruder may then walk away with a lowered head. However, quite often the intruder approaches the owner and sniffs its cheek and neck, sometimes even nibbling down its neck. This behaviour ('neck-sliding') may function to smell the odour of the owner and test if it is the same animal that made the scent marks (dung piles) in the territory (the 'scent-



Hartebeest *Alcelaphus buselaphus*.

matching' hypothesis; Gosling 1982). Sometimes owners overtake the intruder as it walks or runs away and, turning in front of the retreating animal, perform a characteristic bucking lateral display: the intruder responds by a low head toss and accelerated withdrawal.

The bald fact that most breeding Hartebeest ♂♂ occupy resource-defence territories conceals a great deal of variation. In low and moderate population densities, territories are often large. For example, Dowsett (1966) recorded territories of 1.55–5.2 km² for Lichtenstein's Hartebeest in Zambia and Backhaus (1959) observed the behaviour of a Lelwel Hartebeest ♂ in a territory of at least 3 km². In both of these cases, small groups of ♀♀ remained for long periods within one territory; in Dowsett's study there were 1–9 ♀♀ in a sample of 11 such groups, while there were three ♀♀ in the group observed by Backhaus. In Uganda (Kidepo), several Lelwel ♀♀ were generally present in each male's territory (4–10 km²), but this female distribution pattern was very variable according to season and year due to massive emigration and immigration (J. Kingdon pers. comm.). At higher population densities, territories are much smaller. In a high-density population in Kenya, Coke's Hartebeest territories averaged 0.31 km² in a sample of 73 territories observed

over three years; territories in preferred ecotone habitats that attracted most ♀♀ were smaller than those in scrubland territories (Gosling 1974). In Nairobi N. P., at the time of these observations, ♀♀ had home-ranges of ca. 5 km² and these included 20–30 male territories. Female ranges may thus include from one (or a small number of territories) to over 30, a fact that must affect the potential for mate choice.

Some ♂♂ occur in quite dense clusters, particularly around short grass clearings (Gosling 1974: Coke's Hartebeest; Mattravers Messana 1993: Swayne's Hartebeest). In such cases ♂♂ rest on the short grass areas and also graze them intensively when green flushes occur after rainfall. However, Hartebeest are classic edge species and they graze into long grass areas in the evenings, and increasingly as the dry season progresses. These clusters of resource territories are sometimes so dense that it has been suspected that they might have similarities to a 'lek', an arena where clustered ♂♂ display and ♀♀ choose mates. However, the quality of the food supply is always critically important in attracting ♀♀ to such territories, and thus in the mating success of the male owners. Thus, while small, such territories should probably be regarded as resource territories; they

are not lek territories in the sense of the tiny territories on Topi leks. However, the clusters of territories found in Coke's and Swayne's Hartbeest would make it easier for ♀♀ to choose between territorial ♂♂; but variation in the degree of mating skew has not been measured.

Perhaps the best evidence for the role of sexual selection on male characteristics is sexual dimorphism in fighting structures (horns, pedicel and skull robustness). Not only do the sexes invest to a different extent in these traits, but the degree of difference between ♂♂ and ♀♀ varies across subspecies. This variation appears to be mainly a response to differences in the length of the breeding season. Species with shorter breeding seasons and thus a higher polygyny potential are relatively more dimorphic in horn dimensions, pedicel height and skull weight (Capellini & Gosling 2006). Sexual selection might also have favoured the occurrence of deep colouration together with other conspicuous patterns in the pelage of Red and Swayne's Hartbeest. There are indications that competition might be intense in these two subspecies with breeding restricted to a short annual breeding season in Red Hartbeest and restricted spatially in Swayne's Hartbeest in the territory clusters described by Mattravers Messana (1993). There may be enhanced male intra-sexual competition in both cases and, possibly, enhanced opportunities for female choice. However, more work is needed to fully explain variation in coat colouration, including the absence of conspicuous colouration in the two woodland subspecies, the Lichtenstein's Hartbeest and Western Hartbeest.

However, Hartbeest do show flexibility in male mating tactics: when they are at very low densities breeding ♂♂ follow groups of ♀♀ around their entire home-range. A well-authenticated case occurred in Amboseli N. P. where an individually known ♂ accompanied a group of ♀♀ throughout an 11 km² area (D. Western pers. comm.). Similar behaviour appeared to occur in Masai Mara National Reserve, where L. M. Gosling (pers. obs.) observed another low-density population in the late 1980s. 'Following' strategies may arise when resources are very unpredictable so that a ♂ is forced to follow ♀♀ in order to ensure that he is with them when they become receptive. However, neither Amboseli nor the Mara were particularly unpredictable habitats and it is more likely that a low density of ♀♀ and reduction in the level of competition between ♂♂ was critical in the appearance of following tactics. Males in resource-defence territories should generally win against following ♂♂ because of the benefits of owner advantage in a small scent-marked territory. Thus, 'following' can probably only succeed when there is a very low density of male competitors.

When ♀♀ enter a territory, ♂♂ stand at the boundary, circle behind them as they pass by and nose the vulva. Sometimes ♀♀ respond by urinating and ♂♂ sniff the urine as it falls and on the ground. However, remarkably (in view of its widespread occurrence amongst ungulates), Hartbeest do not show the oestrus testing display known as flehmen (a trait shared with *Damaliscus*). If ♀♀ are in oestrus, mating behaviour becomes prolonged. Again, body orientation is important: ♂♂ often stand in front of ♀♀ or even walk away from them to look intently at non-existent objects away from the ♀. These behaviours appear to be a subtle attempt to threaten the ♀ into stopping as she walks away but not to alarm her so that she starts to run. When near to the ♀ the ♂ employs the 'ear-down' posture with nose raised, ears down and the tail stiffly curved (Gosling

1974). In general, a ♀ can escape a male's attentions if she runs away quickly but if she is in oestrus, the ♂ will gallop hard to intercept her and bring her back, even if the ♀ has run into the neighbouring territory. When mating is in progress, neighbouring ♂♂ sometimes run into the territory and gallop at full speed through the group, trying to scatter it. This tactic presumably increases the chance that the oestrous ♀ will be displaced into its own territory. Copulation occurs repeatedly with the male's forelegs just in front of the female's haunches and the head dropped vertically over the female's shoulders. Most copulation in Coke's Hartbeest appears to be around mid-day, perhaps as an anti-predator adaptation since mating animals must be very vulnerable; Hartbeest are generally resting in short grass areas at mid-day and predators are usually inactive.

Parturient ♀♀ usually isolate themselves and retire to scrubland to give birth. Female Coke's Hartbeest eat the afterbirth and the calf stands about 30 min after birth (Gosling 1969a), considerably slower than wildebeest, which are more vulnerable in an open habitat. Young hide in long vegetation for about two weeks after birth (lying-out), emerging only to be suckled and for their mother to consume their urine and faeces; presumably this removes odours that might attract mammalian predators. Such hiding behaviour also occurs in Lichtenstein's Hartbeest (Mitchell 1965, Ansell 1970) and Red Hartbeest (Kok 1975). Variation in development of the young and lying out behaviour require more detailed study. It might be predicted that Hartbeest with a more synchronized calving period, such as Red Hartbeest, would stand more quickly after birth, if, as is believed, such calving distributions are shaped by predation pressure.

Males that fail to occupy resource territories live in groups. Males join male groups from about ten months of age up to two or three years of age. This timing depends partly on when they are separated from their mothers and thus, to some extent, on when the mother has further offspring. The mother keeps previous offspring further away from a new calf and, in the case of ♂♂, this makes the offspring more exposed to aggression from the territorial ♂. Further, when a young ♂ is chased away by a territorial ♂, the mother is more likely to intervene and to flee with it if the ♂ is her only offspring. Once young ♂♂ are separated from their mothers, territorial ♂♂ chase them with exceptional severity and try to horn them as they flee. As a result young ♂♂ are sometimes found isolated and are sometimes injured. When young ♂♂ join male groups they may also be chased by adult members of the group; as a result they sometimes cluster with other young ♂♂ in subgroups at the edge of groups of older ♂♂.

Such 'male groups' (sometimes called bachelor herds) comprise about 62% of the adult male population in Coke's Hartbeest (Gosling 1975). They occupy areas outside territories or, more usually, little-used parts of territories. It is not economically possible for territorial ♂♂ to keep all parts of their large territories free of non-territorial ♂♂. Rather, they tend to chase any intruder that comes too close to them, wherever they might be in their territory. Active defence is also more likely during cooler times of the day. References in the literature to male groups defending territories are certainly an error: single high-status non-territorial ♂♂ may sometimes establish a small temporary territory, but groups never do so. Groups of non-territorial ♂♂ vary in size from one to over a hundred individuals. Single non-territorial ♂♂ are common (particularly when high status ♂♂ isolate to try to find a vacant territory) and so it is impossible

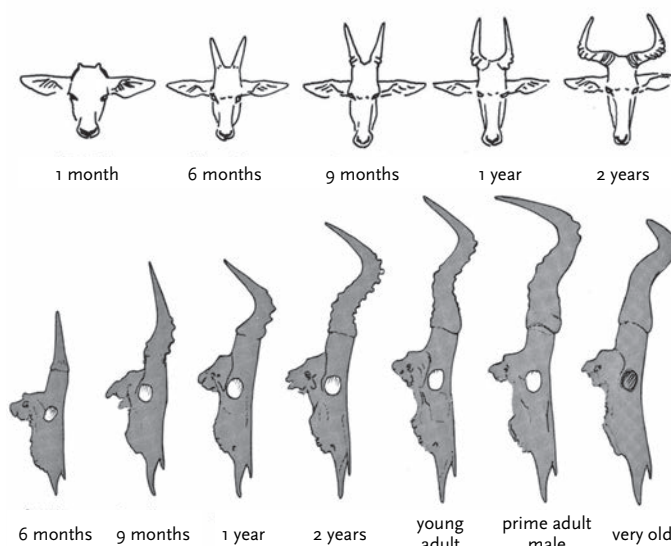
to tell if a lone adult ♂ is territorial or not without observing its behaviour, preferably for a number of days.

By far the most common social behaviour in male groups is agonistic behaviour and ♂♂ form dominance relationships. When they reach high dominance status they leave the groups and wander about looking for vacant territories. If they have previously held a territory they return to the same area and sometimes succeed in taking it back, or in taking over an adjacent territory. Sometimes they occupy a territory when the owner is temporarily away, for example to drink, and an ownership contest occurs when the owner returns. Fights for territory ownership are by far the most severe type of contest. They consist of repeated violent clashes and often result in severe injury and sometimes in death. When a ♂ is defeated it may be pursued for several kilometres.

There are few vocalizations. The most distinctive is the 'quack'-like sound made by young calves. Significantly, the same call is produced by half-grown or young adult ♂♂ when they show the subordinate 'head-in' posture as they move away or flee from approaches or aggression by a territorial ♂ (Gosling 1974). The alarm snort is used in anti-predator contexts (below).

Reproduction and Population Structure The seasonal distribution of reproduction varies between different parts of Africa and appears to be adapted to seasonal patterns of rainfall/primary production. In Nairobi N. P., where there are two seasons of rains, there are two peaks of calving by Coke's Hartebeest. These peaks occur before the two seasons of rain so that the late phases of lactation, when ♀♀ need most food, coincide with the production of fresh green grass. This grass is also available as the young start to wean and it is not clear which of these two events is most important for this timing. Where there is only one season of rain there is only one breeding season. Thus, Lichtenstein's Hartebeest calve from Jul–Sep in Zambia, Mozambique and Zimbabwe (Ansell 1960a, Mitchell 1965, Wilson 1966c, Booth 1985), although Ansell (1960a) gives a season of Oct–Nov for the low-lying Luangwa Valley. In Namibia, there is a corresponding unimodal pattern of calving for Red Hartebeest with a peak in Nov and Dec, a month or two before the start of the rains (L. M. Gosling pers. obs.).

In Coke's Hartebeest, the seasons of calving are quite widely spread, reflecting the distribution of rainfall (Gosling 1969a). Thus, it seems likely that selection for the timing of mating reflects the timing of water-dependent primary production. However, in the case of Red Hartebeest in Namibia the calving peak is considerably sharper than that of rainfall. The general reason for sharp calving peaks is probably that young born outside the peak are more likely to be killed by predators so that natural selection favours calving within the peak (Estes 1966, Gosling 1969a). Coke's Hartebeest may be free of this constraint because young hide alone in long grass for the first two weeks of life (Gosling 1969a) and thus rely on crypsis rather than on saturating predation pressure. Under such circumstances, there could even be advantages in producing young when there are few others about to avoid the formation of 'prey images' by predators such as baboons and hyaenas. It is not entirely clear why Red and Lichtenstein's Hartebeest have such sharp calving peaks, but perhaps young rely to a lesser extent on crypsis; like Coke's Hartebeest, Lichtenstein's Hartebeest calves hide after birth (Ansell 1970), but duration and variation have not been quantified.



TOP: Coke's Hartebeest *Alcelaphus buselaphus cokii* horn development (from Gosling 1975)

ABOVE: Lelwel Hartebeest *A. b. lelwel* horn development (courtesy of J. Bindernagel pers. comm.).

Gestation is about eight months (Skinner *et al.* 1973). A single calf is born weighing about 15 kg (Wilson 1966c). Calves are weaned at about 7–8 months of age (Kok 1975). Most Hartebeest ♀♀ probably conceive for the first time between 15 months and two years old, although this may depend on condition due to variation in grassland production. Lichtenstein's Hartebeest ♀♀ are sexually mature at 16–18 months (Mitchell 1965, Wilson 1966c) and Red Hartebeest at 28 months (Skinner *et al.* 1973). Physiological maturity in ♂♂ may also be reached at about 18 months; ♂♂ of around this age have been seen crouching and ejaculating after sniffing or attempting to mount ♀♀ (Gosling 1975). However, ♂♂ do not mate until they have acquired a territory, probably not before three years of age, at least in moderate- to high-density populations. It is possible that territories are acquired earlier in low-density populations where male intra-sexual competition is lower, but there are no data.

Like most of the plains antelopes, Hartebeest generally have an adult sex ratio biased towards ♀♀. In Coke's Hartebeest, while the ratio at birth does not differ from unity ♂♂ comprise only 42% of adults (over 20 months old). The main cause of this difference is mortality indirectly caused by male competition. In particular, young ♂♂ chased away from their mothers by territorial ♂♂, and old ♂♂, excluded from high-quality territories, are often injured and isolated in scrubland. Such animals are vulnerable to predation, particularly by Lions (Gosling 1974).

A life-table, based on a sample of aged skulls from natural mortality in a population of Coke's Hartebeest, shows a typical mammalian pattern with high mortality over the first two years of life, relatively low annual mortality up to six years, and then accelerating mortality up to 12 years; ♀♀ outnumber ♂♂ in the oldest year classes and some probably live up to about 15 years (Gosling 1974, 1975). Weigl (2005) gives longevity record as 22–23 years in captivity, and Flower (1931) reports 19 years for a Bubal Hartebeest.

Predators, Parasites and Diseases Lions are the main predators of adult Hartebeest (Mitchell *et al.* 1965, Schaller 1972, Gosling

1975). Adults are occasionally killed by Cheetahs, although the only case confirmed in a long-term study of Coke's Hartebeest was an instance of four Cheetah ♂♂ hunting together (L. M. Gosling pers. obs.); Cheetahs do, however, kill large numbers of calves. Leopards *Panthera pardus* are known to kill calves in Serengeti N. P. (Bertram 1979) and probably kill small numbers throughout the species' range. The alert response of adult Hartebeest ♀♀ to jackals *Canis* spp. and baboons *Papio* spp. suggest that they kill very young calves. Adult and juvenile Hartebeest are also hunted and killed by Spotted Hyenas *Crocuta crocuta* (Kruuk 1972, Mills 1990, Di Silvestre *et al.* 2000) and African Wild Dogs *Lycaon pictus* (Creel & Creel 1995).

Predation on Hartebeest may be affected by the abundance of alternative prey. In Serengeti N. P., when migratory ungulates, such as Common Wildebeest and Plains Zebras *Equus quagga*, move into an area, Lions feed mainly on the migrants and pressure on resident species, including Hartebeest, is temporarily reduced (Bertram 1979). Hartebeest are extremely vigilant and respond to predators, particularly Lions, at great distances. When alarmed, Hartebeest face the predator directly with the head at maximum elevation, the nose drawn in and the ears directed forwards. They seek any rise in the ground to obtain a better view. At intervals related to the apparent level of danger, they make characteristic loud snorts by rapidly forcing air through the nostrils. They may approach and even follow a moving predator such as a Lion or Cheetah to keep it in sight and thus under sensory control. Hartebeest respond sensitively to the alarm behaviour of other nearby animals. Gosling (1975) observed an isolated territorial ♂ in scrubland respond to its neighbour's alarm snorting by snorting itself and adopting the same body orientation, even though it could not see the predator (a Lion) that the first animal had detected. The main function of belonging to groups is probably due to the benefits of selfish-herd membership (detection and dilution effects). When disturbed by predators, lone territorial ♂♂ in scrubland move closer to each other. Members of other species, for example wildebeest, sometimes take advantage of the extreme vigilance of Hartebeest by seeking refuge within Hartebeest groups when predators are detected. Flight distances appear to be related to vulnerability. In a group watching a predator, ♀♀ with young calves keep to the rear of the group and are usually the first to flee, running straight away from the back of the group. Active defence against predators is rare although young Hartebeest ♂♂ have been seen attacking Black-backed Jackals *Canis mesomales* after the jackals had killed a young gazelle (L. M. Gosling pers. obs.).

Hartebeest carry a large number of disease organisms, but there are few records of them showing any clinical symptoms of disease. Large-scale mortality may instead be generally due to starvation when food resources are exhausted within range of permanent water; examples include the die-off of Coke's Hartebeest in 1973 in Nairobi N. P. in Kenya (Hillman & Hillman 1977) and of Red Hartebeest in the Kalahari in 1985 (Knight 1995a).

Hartebeest generally have low susceptibility to rinderpest virus infection (Plowright 1982). For example, in the great pandemic of 1889–97, while *Damaliscus* spp. amongst other antelopes died in large numbers, Red Hartebeest were relatively unaffected (Scott 1970). However, sometimes Hartebeest were severely affected by rinderpest, as in the case of Swayne's Hartebeest in Somalia in 1897 (Simon 1962) and the Western Hartebeest in 1913–17 (Pecaud 1924, in Plowright 1982). Hartebeest typically live at lower

density than the most susceptible species (African Buffalo *Syncerus caffer* and wildebeest) and it would be interesting to know how far density explains this variation: Swayne's Hartebeest were known to reach high densities on open grassland before their numbers were reduced by overhunting. Antibodies have also been detected against bluetongue virus in Western Hartebeest (Formenty *et al.* 1994) and Red Hartebeest (Simpson 1978), against bovine ephemeral fever in Coke's Hartebeest (Devies *et al.* 1975) and bovine virus diarrhoea in Lichtenstein's Hartebeest (Anderson & Rowe 1998). Alcelaphine herpes virus-2 has been identified in a number of subspecies; it is closely related to alcelaphine herpes virus-1, which is carried by wildebeest and causes malignant catarrhal fever (Reid *et al.* 1975, Seal *et al.* 1989) but has not been linked to clinical MCF in Hartebeest.

Hartebeest have relatively low susceptibility to the anthrax bacillus, but they do die in moderate numbers when infected; examples are the 1999 and 2000 outbreaks in Mago N. P., Ethiopia, involving Lelwel Hartebeest (Shiferaw *et al.* 2002). The haemoprotezoan *Theileria* sp. has been isolated from the serum and from ticks carried by Red Hartebeest (Spitalska *et al.* 2005), but there were no clinical signs of theileriosis. *Trypanosoma brucei*, the protozoan parasite that causes African sleeping sickness, has been detected in Western (Jamonneau *et al.* 2003) and Coke's (Geigy & Kaufmann 1973) Hartebeest. However, Hartebeest are not favoured by tsetse flies (*Glossina* spp.) and were not detected as hosts in a sample of 13,145 blood meals collected throughout Africa (Clausen *et al.* 1998).

Most, perhaps all, adult Hartebeest carry a moderate number of ticks, including *Amblyomma* spp., *Boophilus* spp., *Haemaphysalis aciculifer*, *Hyalomma truncatum* and *Rhipicephalus* spp. (Hoogstraal 1956, Matthyse & Colbo 1987, Walker *et al.* 2000, Ntiamoa-Baidu *et al.* 2005). These are vectors of a number of viral diseases (see below and an overview in Walker *et al.* 2003). Ticks sometimes occur in clusters, notably around the edges of the ears. Records of the infestation of various wild bovid hosts suggest that Hartebeest are remarkably free of ticks compared with such species as Impala *Aepyceros melampus*, wildebeest and African Buffalo (Walker *et al.* 2000). This finding is supported by studies of the numbers of ticks per individual in relation to body size, which show that Hartebeest carry less ticks and have a smaller proportion of engorged ticks than would be expected (Olubayo *et al.* 1993). This may be linked to effective grooming with the incisors and hindfeet and also to their relatively open habitat. Oxpeckers *Buphagus* spp. rarely feed on Hartebeest. In a study of Coke's Hartebeest, oxpeckers sometimes attempted to land, but were nearly always immediately driven away (L. M. Gosling pers. obs.); in another study that included Coke's Hartebeest, none was seen feeding (Koenig 1997). The low incidence of ticks means that Hartebeest are probably little affected by tick parasitosis (direct damage due to wounds and blood loss). Hartebeest are sometimes infected by *Sarcoptes scabiei*, the mite causing sarcoptic mange (Pence & Uekermann 2002).

Gastrointestinal parasites of Hartebeest include helminths and nematodes (e.g. Bindernagel 1972, Boomker *et al.* 2000). Nematode faecal egg counts of Hartebeest in N Kenya were higher in drought years than non-drought years (Ezenwa 2004b), possibly due to nutritional stress.

Most adult Hartebeest appear to be infested with nasal botfly larvae, including those of *Oestrus ovis* (Howard 1977, Wetzel 1984, Mbassa 1986). These flies lay eggs in the nose and the larvae migrate upwards into the nasal cavity. L. M. Gosling (pers. obs.) once saw

a Coke's Hartbeest ♂ in Nairobi N. P. sneeze out a larvae and on inspection it proved to be *O. ovis*. Some individuals contain large numbers of these larvae and in necropsy of a Red Hartbeest ♂ in Namibia, L. M. Gosling (pers. obs.) was able to confirm that these penetrate even into the cavity of the pedicel. It is sometimes said that the larvae penetrate the brain, but evidence is lacking. Hartbeest sometimes sneeze unexpectedly and this could be a response to botfly larvae; the alarm snort is similar but is accompanied by alert behaviour, focused on a predator.

Conservation IUCN Category: Least Concern (*A. b. buselaphus* – Extinct; *A. b. cokii* – Least Concern; *A. b. lelwel* – Endangered A2acd; *A. b. swaynei* – Endangered C2a(i); *A. b. tora* – Critically Endangered C2a(i); *A. b. major* – Near Threatened; *A. b. lichtensteinii* – Least Concern; *A. b. caama* – Least Concern). CITES: Not listed.

The feeding habits of Hartbeest bring them into direct conflict with grass-eating livestock and, as numbers of livestock have increased, Hartbeest numbers have declined everywhere except in a few protected areas. Hartbeest also are valued for their high-quality meat and as the bushmeat trade escalates out of control, partly fuelled by the increase in modern guns, many Hartbeest populations are being hunted to extinction. Hartbeest are thus declining in most parts of their range and are now rare outside protected areas, many of which are too small to support viable populations.

Protected areas holding important populations of Hartbeest include: Niokolo-Koba N. P. (Senegal), although this population declined by half in the 1990s alone (Galat *et al.* 1998); Comoé N. P. (Côte d'Ivoire), Mole and Digya National Parks (Ghana) and Pendjari N. P. (Benin) for Western Hartbeest; Zakouma N. P. (Chad), Manovo-Gounda-St Floris N. P. (Central African Republic), Southern N. P. (Sudan), Mago N. P. and surrounds (Ethiopia) and Murchison Falls N. P. (Uganda) for Lelwel Hartbeest; Mazie N. P. and Senkelle Wildlife Sanctuary (Ethiopia) for Swayne's Hartbeest; Tsavo N. P. and Masai Mara National Reserve (Kenya) and Serengeti and Tarangire National Parks (Tanzania) for Coke's Hartbeest; the Selous ecosystem and Ruaha-Rungwa-Kisigo complex (Tanzania), Kafue N. P. and Luangwa Valley (Zambia), and Niassa G. R. (Mozambique) for Lichtenstein's Hartbeest; and, for Red Hartbeest, Kgalagadi Transfrontier Park (South Africa/Botswana), Etosha N. P. (Namibia) (East 1999) as well as various nature reserves and conservancies, such as the expanding population of Red Hartbeest of about 18,000 animals in the 400,000 ha Seeis Conservancy in E Namibia (H. Förster & B. Förster pers. comm.).

The failure to protect Hartbeest adequately is particularly tragic because there is poor recognition of local variation among Hartbeest populations and even less recognition of their evolutionary importance as the outstanding model of a mammalian adaptive radiation in the savanna environment. Many local variants have disappeared (*buselaphus*, *nakurae*). Hartbeest were kept in captivity by the ancient Egyptians, illustrated in the tombs of the pharaohs, and used for ceremonial purposes. However, the wild populations from which these animals were taken are now extinct, perhaps partly because of habitat destruction in the Mediterranean region, but mainly due to hunting. Bubal Hartbeest in North Africa were similarly reduced and probably died out around the 1950s (see Distribution); groups in zoos (including London and Paris) that could have ensured their survival were allowed to die out. The intergrade populations of the Kenya Rift

Valley were displaced by intensive farming and shot by settlers and troops; the last surviving Nakuru Hartbeest (a remnant of a once abundant intergrade population between *A. b. cokii* and *A. b. lelwel* in the Kenya Rift Valley), a ♂, was seen and photographed in 1967 (Gosling 1969b). Other subspecies and intergrades are severely threatened or may already have disappeared (*swaynei*, *jacksoni*, *keniae*, *tora*); there are now less than 800 Swayne's Hartbeest (Antonínová *et al.* 2008) and Tora Hartbeest have not been seen for some 10–15 years in any part of their range. The Hartbeest are the most important example of an antelope adaptive radiation in which most members still just survive; they illustrate better than any other group an adaptive radiation into varied savanna habitat and the evolutionary consequences of long-term climatic change. They thus represent an opportunity to conserve the spectacular manifestation of an evolutionary process rather than a museum collection of isolated taxa in protected areas. There is also a case for conservation at a local level. For example, the declining Kenya Hartbeest is a unique local race and should be a conservation priority in a country that values its wildlife and depends on it economically.

An important exception to the pattern of decline is the Red Hartbeest in southern Africa, which is important for various forms of sustained use such as trophy hunting. The latter case is a remarkable example of the success of the southern African approach to wildlife conservation, which involves the transfer of ownership of wildlife and thus any financial profit from its use to the landowner. So long as such practices continue on a rational basis, Red Hartbeest populations will remain secure; indeed its numbers are expanding. Lichtenstein's Hartbeest also seems to be relatively secure, partly because there are several very large reserves within their range (which is tsetse country) and perhaps because this species is exploited to a lesser extent. The lesson from population changes between Hartbeest taxa across Africa is that populations with consumptive use are stable or expanding while the others are plunging to short- or medium-term extinction. Future conservation measures should attempt to expand and improve the operation and sustainability of sustainable use schemes. However, they should also be combined with non-consumptive exploitation in properly guarded protected areas. A further obstacle to be overcome is that unless income from consumptive and non-consumptive use is shared by local communities, Hartbeest will not survive in the medium term. Their meat is highly regarded and they will be poached to extinction except where tangible economic benefits for entire communities outweigh the individual's short-term need or taste for food.

The expanding Hartbeest populations in southern Africa are descended from the small number of survivors of the slaughter of the seventeenth to nineteenth centuries by European colonists. Hartbeest were eradicated from most of their range (Skead 1980, 1987) and much genetic variation was undoubtedly lost at this time. For example, even though its taxonomic status is uncertain, the Hartbeest known as the Cape Red Hartbeest (and believed at the time to be a subspecies) was completely exterminated by hunting and only those known as Northern Red Hartbeest survived around the Kalahari and in what is now known as Namibia (Harper 1945). However, the survivors are numerous again and expanding as the considerable economic potential of the species is appreciated and exploited. The main conservation problem in southern Africa is that animals are sold and translocated to new areas without regard to natural spatial patterns of genetic variation. Local legislation needs to be revised, if only because populations are

most likely to thrive if introduced into areas to which they are locally adapted, that is, their natural range. There is an urgent need for an Africa-wide conservation strategy for the Hartebeest, one that transcends local custom and makes use of best-practice across the continent. Hopefully, before it is too late, conservationists at least will become aware of the impending loss of the finest existing example of a pan-African large mammal radiation.

Measurements

Alcelaphus buselaphus

A. b. caama

TL (♂♂): 2144 (2073–2200) mm, n = 8
 TL (♀♀): 2096 (2070–2110) mm, n = 3
 T (♂♂): 470 (404–504) mm, n = 8
 T (♀♀): 472 (430–500) mm, n = 3
 HF c.u. (♂♂): 557 (534–572) mm, n = 8
 HF c.u. (♀♀): 524 (503–545) mm, n = 3
 E (♂♂): 195 (192–201) mm, n = 8
 E (♀♀): 185 (175–192) mm, n = 3
 WT (♂♂): 152.0 (137.0–156.0) kg, n = 8
 WT (♀♀): 120.0 (105.0–136.0) kg, n = 3
 Botswana (Smithers 1971)

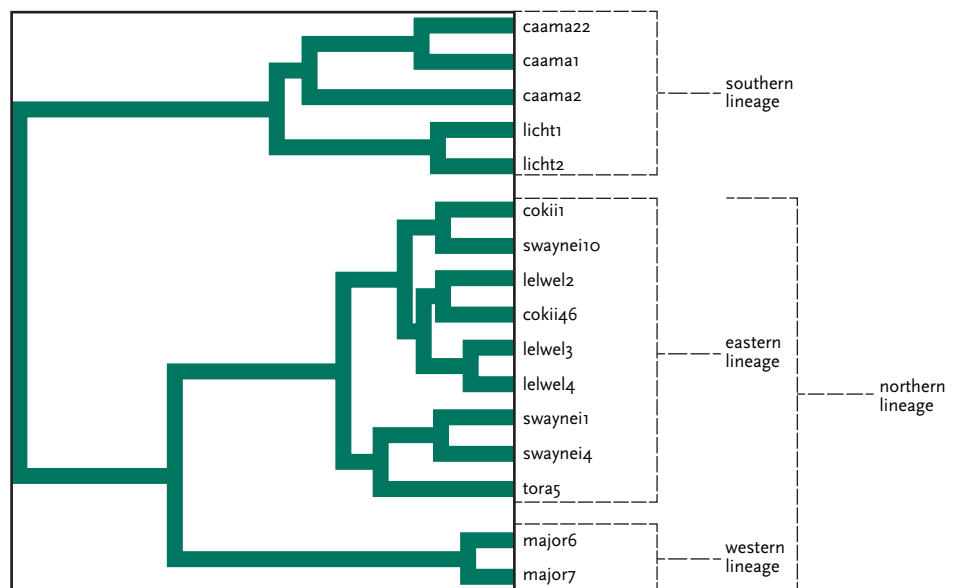
A. b. lichtensteinii

TL (♂♂): 2380 (2090–2540) mm, n = 6
 TL (♀♀): 2360 (2010–2420) mm, n = 5
 Sh. ht (♂♂): 1230 (1220–1360) mm, n = 6
 Sh. ht (♀♀): 1250 (1190–1300) mm, n = 5
 WT (♂♂): 177.1 (156.7–203.9) kg, n = 10
 WT (♀♀): 166.3 (160.4–181.2) kg, n = 10
 Zambia (Wilson 1966c)

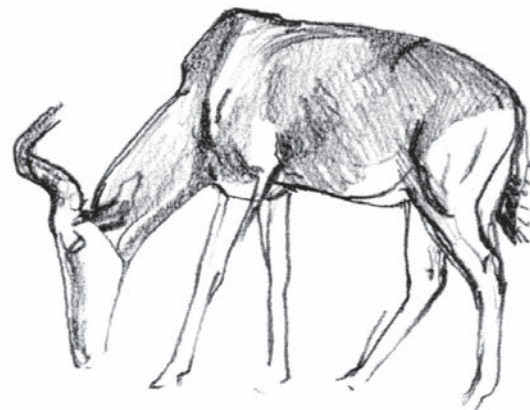
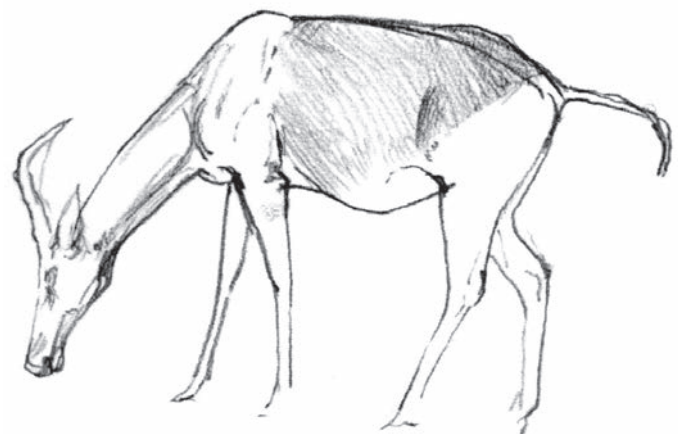
A. b. cokii

TL (♂♂): 2327 (2210–2460) mm, n = 5
 TL (♀♀): 2205 (2105–2275) mm, n = 5
 T (♂♂): 515 (490–545) mm, n = 5
 T (♀♀): 497 (460–515) mm, n = 5
 HF c.u. (♂♂): 505 (500–520) mm, n = 5
 HF c.u. (♀♀): 492 (480–500) mm, n = 5
 E (♂♂): 201 (190–213) mm, n = 5
 E (♀♀): 186 (180–195) mm, n = 5
 Sh. ht (♂♂): 1170 (1130–1180) mm, n = 5
 Sh. ht (♀♀): 1120 (1110–1160) mm, n = 5
 WT (♂♂): 142.5 (129.0–159.8) kg, n = 5
 WT (♀♀): 126.2 (116.0–135.0) kg, n = 5
 Serengeti N. P., Tanzania (Sachs 1967)

Maximum recorded horn lengths for the subspecies are: 74.9 cm for *A. b. caama* for a pair of horns from Windhoek, Namibia; 61.9 cm length for *A. b. lichtensteinii* for a pair of horns from Mumbwa, Zambia; 61.0 cm for *A. b. cokii* for a pair of horns from Kenya; 73.0 cm for *A. b. major* for a pair of horns from Nigeria; 70.1 cm for *A. b. lelwel* from the Aouk R., Chad; 58.1 cm for *A. b. tora* from the Sudan; and 51.4 cm for *A. b. swaynei* from Somalia



Tentative phylogenetic tree for *Alcelaphus* as estimated from cytochrome *b* data (after Flagstad *et al.* 2001).



Lelwel Hartebeest *Alcelaphus buselaphus lelwel* female (top) and male (bottom).

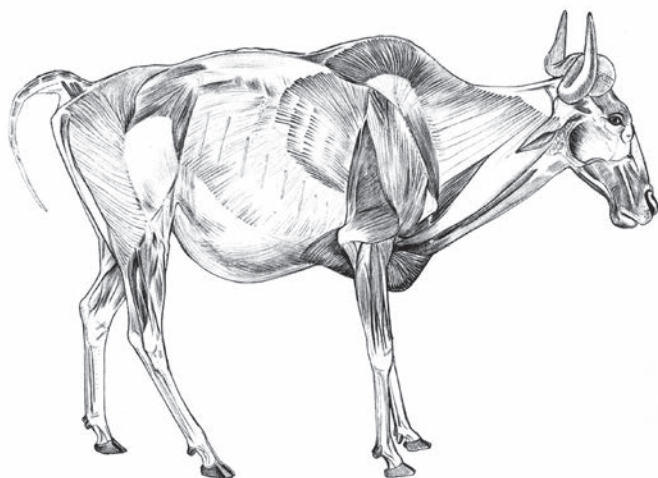
Key References Dowsett 1966; Gosling 1969a, 1975, 1986; Kok 1975; Mattravers Messana 1993; Wilson 1966c.

L. Morris Gosling & Isabella Capellini

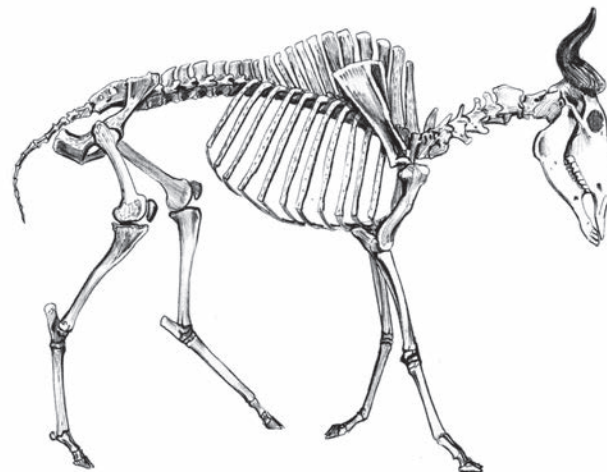
GENUS *Connochaetes*

Wildebeest

Connochaetes Lichtenstein, 1812. Mag. Ges. Naturf. Fr. Berlin 6: 152.



Common Wildebeest *Connochaetes taurinus* myology.



Common Wildebeest *Connochaetes taurinus* skeleton.

There are two recognized species, the Common Wildebeest *Connochaetes taurinus* and the Black Wildebeest or White-tailed Gnu *C. gnou*. While the latter is monotypic, there are five distinctive subspecies of *C. taurinus*, at least one of which (*C. t. mearnsi*) may be different enough to be considered a separate species (Georgiadis 1995). Black Wildebeest ranged the temperate Highveld and Karoo of South Africa, from where *C. gnou antiquus* was described. *Connochaetes taurinus* is known from fossil remains in North and East Africa, and from lower, middle, and upper Pleistocene beds in South Africa. According to mtDNA analyses (Arctander *et al.* 1999), the Common Wildebeest shows a pattern of colonization going from southern Africa toward East Africa, probably following the expansion of savanna habitat during the past 2.5 million years. While the related *Alcelaphus* and *Damaliscus* species continued their pan-African distribution, western and northern *Connochaetes* populations disappeared and the species now only survives in the southern refugium, from mid-Kenya southwards.

The adaptations of the two wildebeest species to their respective savanna ecosystems made them the keystone species among guilds of grazing ungulates. Although their size and conformation are very different (the mass of an adult Common Wildebeest is 250 kg compared with a 157 kg Black Wildebeest), they share traits that help explain their success. The distributions of the two species overlapped periodically after the speciation of the Black Wildebeest ca. 1 mya (Corbet & Robinson 1991), but habitat preferences and behavioural differences have contributed to reproductive isolation (Brink 2005). However, the two species are also genetically close enough to produce viable hybrids (Fabricius *et al.* 1988), and indeed hybridization and introgression now pose significant risks to the Black Wildebeest due to injudicious translocations that have brought the species into contact with each other at numerous localities in South Africa (Grobler *et al.* 2011).

Wildebeest are adapted to exploit extensive grasslands that can support great concentrations of grazing antelopes, producing highly nutritious green pastures during growing seasons (Estes 1991a). Productivity is maintained by recycling of the manure distributed by the massed animals. Both species are equipped with broad incisor

arcades to take large bites of short grasses (in both species, the dental formula is $I^{0/3}, C^{0/1}, P^{3/2}, M^{3/3} = 30$, with the second lower premolar absent, as in *Beatragus*). They are bulk rather than selective feeders. The Common Wildebeest is virtually a pure grazer, whereas the Black Wildebeest also browses to some extent on karroid shrubs. Both species are territorial, which represents the original sedentary-dispersed social organization shared by all but a few antelopes in the subfamily Antilopinae. In the resident phase, the Black Wildebeest defends a far larger territory than its congener. In the migratory phase, the Common Wildebeest defends temporary, very small territories. How close migrating Black Wildebeest territorial ♂♂ would tolerate one another is unknown: there has been no migratory population since the species was nearly exterminated in the late 1800s. Though efforts to restore the species have been outstandingly successful, the thousands of Black Wildebeest now live in isolated herds on farms and ranches in the Highveld and also outside their natural range as far afield as Namibia.

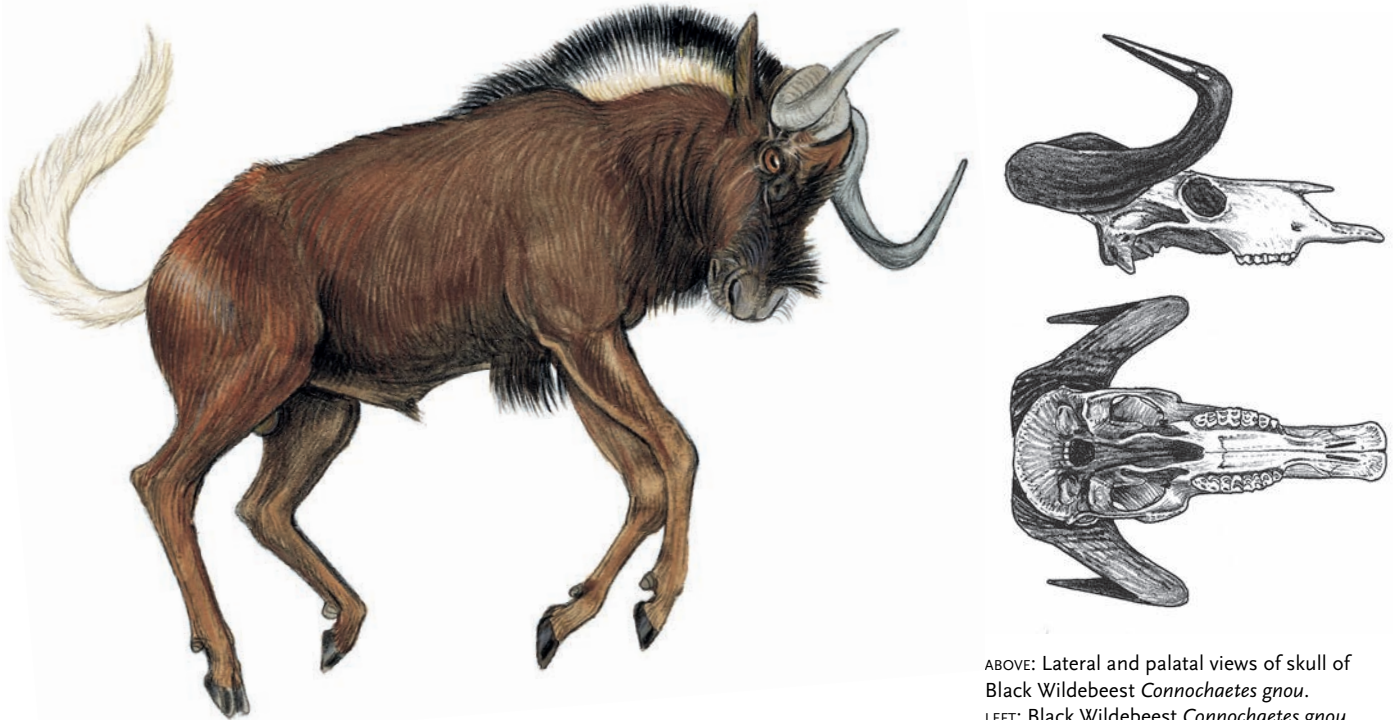
What sets wildebeest apart from all other antelopes – and must contribute to their dominance of competing migrants – is their reproductive system. They have abandoned the ancestral system wherein newborn calves go through a hiding stage (for example, Hartbeest *Alcelaphus buselaphus*) that lasts days and even weeks, during which mothers must remain in attendance. In highly mobile aggregations, selection would favour reducing or even eliminating the hiding stage. Wildebeest abandoned it altogether and evolved an entirely new follower-calf system. The main features are extreme precocity of the newborn, which gain mobility within minutes of birth, aggregations of pregnant ♀♀ on calving grounds, a short peak during which some 80% of the calf crop is born, and associations of mothers and calves in maternal herds (Estes 1976, Estes & Estes 1979). In this way, not only are predation and predators limited, but herds with older calves provide essential cover for neonates (substituting for high grass) during the first day or two when they are most vulnerable.

Richard D. Estes

Connochaetes gnou **BLACK WILDEBEEST (WHITE-TAILED GNU)**

Fr. Gnou à queue blanche; Ger. Weisschwanzgnu

Connochaetes gnou (Zimmermann, 1780). Geogr. Gesch. Mensch. Vierf. Thiere 2: 102. South Africa, 'Die lander der Caffern, ziemlich tief ins land vom Cap gerechnet in grossen Waldern ohnheit der Uchtermanns Brenjes hogde und Camdebo'; since selected as Eastern Cape Prov., Somerset East Dist., Agterbruintjieshoogte (Grubb 1999).



ABOVE: Lateral and palatal views of skull of Black Wildebeest *Connochaetes gnou*.
LEFT: Black Wildebeest *Connochaetes gnou*.

The moniker Gnu derives from the Khoikhoi (aka Hottentot) descriptive term for the bellowing snort the animal gives when alarmed (Skinner & Chimimba 2005).

Taxonomy Monotypic, with no subspecies recognized. Synonyms: *capensis*, *connochaetes*, *gnou*, *gnu*, *operculatus*. Chromosome number: $2n = 58$ (Wurster & Benirschke 1968, Corbet & Robinson 1991). Hybridization with Common Wildebeest has been recorded, and hybrids are fertile (Fabricius *et al.* 1988).

Description Similar in appearance to its close relative the Common Wildebeest *Connochaetes taurinus*, but smaller in size, with strongly built forequarters sloping to more slender hindquarters. Rich, dark-brown colour; mature ♂♂ have a black face and a darker, almost black appearance; newborn calves are fawn-coloured. Head and face is less elongated than in Common Wildebeest, with a broad muzzle, erect facial tuft, preorbital glands and distinct tuft of hair under the chin. Further tuft of hair found on the chest, between the forelegs. Stiff, upright, trim mane, creamy-white with dark tips. Horse-like tail is creamy white but dark at base, almost reaching the ground. Pedal glands are present on front hooves and excrete a sticky substance; inguinal glands are absent. Males larger than ♀♀.

Horns, present in both sexes, are smooth with expanded bases, directed forward and downwards before curving up sharply. Adult ♂♂ have heavy horns with prominent bosses, while horns of ♀♀

are slighter. Calves have long spike-like horns that start to curve at approximately nine months; ♂♂ attain full horn shape at 4–5 years (von Richter 1971b). In addition to the differences in horn shape and horn base architecture, the skull of the Black Wildebeest can be distinguished from that of the Common Wildebeest in being generally smaller, shorter and dorsoventrally flattened. The angle of the braincase to the face is greater in the Black Wildebeest than the Common Wildebeest, the orbits are absolutely and proportionally enlarged, while the frontal suture is fused (Brink 2005). These features appeared progressively over the last million years, and can be observed in rudimentary form in the earliest fossil populations of ancestral Black Wildebeest (Brink 1993, 2005). All molar teeth are erupted by the third year of age, with the upper third and fourth premolars erupting at 28–30 months; patterns of tooth eruption are discussed in detail by von Richter (1971b).

Geographic Variation None recorded.

Similar Species

Connochaetes taurinus. Larger, greyish in colour with dark brindle stripes on the neck and shoulders; head and face elongated; chin with long beard and limp hair, and shaggy mane of long black hair under the throat; black tail almost reaching the ground; horns smooth, arising from swollen bosses and directed outwards and slightly downwards before curving up; horn tips pointed



inwards and often slightly backwards. Although the ranges of the two species formerly barely overlapped (with Black Wildebeest confined to the temperate, treeless Highveld and Karoo regions of South Africa, Swaziland and Lesotho), stocking of both species outside their natural range has led to fertile hybrids where the two species are kept on the same property (Fabricius *et al.* 1988).

Distribution Black Wildebeest are endemic to southern Africa. According to von Richter (1974) they formerly migrated in large numbers in both east–west and north–south directions, probably following the onset of rains and changing vegetation cycles.

Historical Distribution Formerly confined to the central inland plateau of South Africa, specifically the Highveld regions of Free State, Gauteng and North West Provinces, parts of the Eastern Cape and Northern Cape provinces, and marginally in the grassveld regions of western KwaZulu–Natal, in the foothills of the Drakensberg Range (von Richter 1974). It has been suggested that their occurrence in the western parts of KwaZulu–Natal may have been due to a local movement from the Free State during the winter months in search of better feeding grounds. Black Wildebeest were also recorded seasonally in grassland areas of W Swaziland and the western parts of Lesotho (where they were exterminated before 1900). A detailed discussion of the historical distribution of the species is given by von Richter (1971a).

Current Distribution Black Wildebeest have been widely reintroduced to areas within their former distribution range, as well as to farmland and reserves well outside their natural range. For example, although they do not occur naturally in Namibia, they have been introduced and now occur widely throughout Namibia's farming districts (East 1999). They have also been reintroduced in Lesotho (in Sehlabathebe N. P.) and in Swaziland in Malolotja N. R. (East 1999).

Habitat A species characteristic of the open plains Highveld grasslands (the Highveld BZ) and Karoo shrublands (the Karoo subzone) of southern Africa. The high central plateau grasslands are characterized by flat to rolling hills, and mountainous areas with altitudes ranging from 1350 to 2150 m. These areas are dominated by a single layer of grasses, with cover dependent on rainfall and the degree of grazing.

Abundance Several thousand are all that remain of the millions that once roamed South Africa's Highveld and Karoo regions. The total population is estimated at more than 18,000 animals (including the introduced population in Namibia), 80% of which occur on private land and 20% in protected areas. However, population size is increasing, especially on private land, with a large extralimital population now established in Namibia, where importations from South Africa led to a dramatic rise in the estimated total numbers, from 150 in 1982 to more than 7000 in 1992 (East 1999).

Adaptations Black Wildebeest actively condition their own preferred habitat by persistent grazing and trampling (von Richter 1974, Kok & Vrahimis 1995), especially applicable to sub-optimal areas, where territorial ♂♂ open up fairly dense vegetation. These ♂♂ are closely attached to their territories throughout the year; here, vegetation horning during demonstrative-threat displays plus sustained grazing in the immediate vicinity of the stamping ground keeps the grass in the favoured short state, thereby enhancing visibility (Kok & Vrahimis 1995).

Although scattered trees may be found in concentration areas, animals rarely use trees for shade and shelter. Generally these darkly coloured ungulates are exposed to direct solar radiation and other, often extreme, climatic conditions. During early morning and late afternoon, when temperatures are lower, animals present the long axis of their bodies to the sun to facilitate heat uptake (Vrahimis & Kok 1992). Conversely, during the heat of day, animals orientate themselves to expose the smallest surface to direct sunlight, thereby compensating for excessive heat load. In summer, when the hottest time of the day usually coincides with the highest windspeed, it is more likely that animals orientate with respect to wind direction, thus maximizing amount of airflow over the entire length of their bodies (Vrahimis & Kok 1992). Additionally, animals prefer lying down to standing during the heat of the day, thereby reducing the intake of reflected radiation from the ground.

Although they are subjected to high ambient temperatures during the day, the brain temperature in Black Wildebeest is usually within 0.2 °C of arterial blood temperature. Selective brain cooling is absent, even though brain temperature may rise to 42.0 °C (Jessen *et al.* 1994). Jessen *et al.* (1994) established that heat storage as a thermoregulatory tactic is relatively unimportant for Black Wildebeest. The Black Wildebeest may be considered to have extraordinary homeothermic capacity, the key being the insulation provided by its fur. Furthermore, due to enlarged evaporative surfaces in the long snout of the genus *Connochaetes*, heat is also dissipated by panting. Even in a thermal environment characterized by large contrasts between day and night, the circadian variation of body temperature in the Black Wildebeest appears to reflect an endogenous rhythm rather than a reaction to cyclic thermal loads. In addition, it was recorded that increased metabolic rate, as during

episodes of chasing, increases blood temperature (1.3 °C within 4 min). Without free access to water, heterothermy may be obligatory (Jessen *et al.* 1994).

However, regarding selective brain cooling, it has been established that the mammals with the greatest capacity for such brain cooling possess carotid retes, bilateral networks of arterioles in, or just outside the cranial cavity, in the main arterial blood supply to the brain (Gillilan 1974 and Simoens *et al.* 1987, in Mitchell *et al.* 2002). In the artiodactyls, the retes have a thermoregulatory function and are heat exchangers in which the arterial blood destined for the brain is cooled by venous blood returning from the evaporating surfaces of the nasal cavity (Baker 1982 and Mitchell *et al.* 1987, in Mitchell *et al.* 2002). Studies conducted in a free-living Black Wildebeest revealed that, as one would normally expect for artiodactyls, selective brain cooling could develop, but, unexpectedly, seldom actually did in their natural habitats (Jessen *et al.* 1994). Thus, Jessen *et al.* (1994) found that at a brain temperature that exceeded 42 °C, established under induced intense exertional hypothermia, selective brain cooling was abandoned and brain and blood temperatures were similar.

Foraging and Food The Black Wildebeest is predominantly a grazer and prefers short grassveld (von Richter 1974). A feeding study listed 41 plant species utilized, and showed that 63% of the Black Wildebeest's main diet consisted of grass and 37% of karroid shrubs (Van Zyl 1965). Grasses such as *Sporobolus* spp., *Themeda triandra* and *Cynodon dactylon* formed the bulk of their diet. Karroid shrubs were browsed during the colder months of the year, probably correlating with the decline in the nutritional value of the grass. Roberts (1963) found that, in the central Free State, 86.8% of the diet consisted of grasses, especially *Eragrostis lehmanniana* (31.3%), *Themeda triandra* (25.3%), *Panicum coloratum* (20.3%) and *Cynodon dactylon* (9.9%). Research conducted on feed utilization and digestion in Golden Gate Highlands N. P. in the Free State indicates that the diet of Black Wildebeest consisted of 80% grass and karroid shrubs and that the relatively high fermentation rate is due to suitable substrate for microbial activity found in that area (Van Hoven & Boomker 1981). These observations of grass predominating in the diet are borne out also by studies involving stable carbon isotopes (Sponheimer *et al.* 2003b).

The feeding preferences of a tame Black Wildebeest cow were investigated over a two-year period (S. Vrahimis pers. obs.). This animal was hand-reared, but subsequently integrated into a free-ranging herd. Results obtained during the free-ranging stage showed that this animal utilized grass (93.7%), karroid shrubs (3%) and herbs (3.3%). While mainly a non-selective grazer there was evidence of some preference for certain grass species. This was evident due to the fact that the animal would feed on a specific grass species for quite some time (approx. 20 min.), before moving on and feeding on another grass species, once again for a period of time. All social groups exhibit a typical bimodal feeding pattern with high-intensity grazing peaks during the early morning and late afternoon (Vrahimis & Kok 1993). Generally, ♂♂ spend more time grazing than ♀♀. For territorial ♂♂ this is perhaps explicable on the basis of their intensive involvement in territorial behaviour and, therefore, greater energy costs, while in the case of bachelor herds, which usually occupy marginal areas with poor grazing (often to avoid harassment by territorial ♂♂), the animals have to feed longer. In addition, the

two categories of grass plants found in grasslands described by Low & Rebelo (1996), namely, sweet grasses having a lower fibre content which maintain nutrients in winter (palatable), and sour grasses having a higher fibre content which tend to extract nutrients during winter (unpalatable), will also determine the time spent feeding during winter in different grassland areas. Black Wildebeest are dependent on water and drink regularly, mainly in the late afternoon.

Social and Reproductive Behaviour Black Wildebeest are gregarious, their social groups comprising female herds, bachelor herds and territorial ♂♂. Average size of a female herd is 28 animals (range 14–49; n = 144) and comprises adult and subadult ♀♀ and calves, and in most cases an attending territorial bull. A number of yearling ♂♂ are usually also found in these herds. Bachelor herds contain ♂♂ of various ages, including yearlings, with an average of 21 individuals (range 11–32; n = 52). Tolerance of the ♂♂ towards one another is notable in these groups (von Richter 1971b). Two types of territorial ♂♂ are recognized: isolated, solitary bulls, usually older animals, and those found in a territorial network. Definite dominance hierarchies are evident in such a territorial system where most matings take place. Home-range and size of territories is largely dependent on the density of animals and the size of the available area and available food source.

Von Richter (1971c) described territorial ♂♂ displaying vigorously, defending their territories and challenging neighbouring bulls or intruders throughout the year in the Free State. Territoriality is a prerequisite for reproduction, as non-territorial ♂♂ are excluded from the rut. Encounters between territorial ♂♂ are highly ritualized and resemble those of Common Wildebeest (von Richter 1974). Estes (1991a) records standing in erect posture, a rocking canter, calling, defecation preceded by pawing, kneeling, ground horning, rolling on stamping ground, herding and chasing as the means of advertising territories. The territories of neighbouring ♂♂ are separated by distances of 180–450 m (von Richter 1972). Agonistic behaviour between territorial ♂♂ is comprised of dominance-threat displays, defensive-submissive displays and fighting (ramming horns). In several instances, carcasses of ♂♂ with interlocked horns have been found.

Black Wildebeest are among the most vociferous of all antelope species. Territorial ♂♂ have a very specific call, best described as a loud 'woink', which carries over a long distance and is heard day and night. Calling is more intense at night, and the fact that this is the main signal available after dark is well demonstrated during full moon (when covering of the moon by a cloud leads to more intensive calling). When this call is made, the head jerks back and the mouth opens wide. Males respond to each other's calls.

Observations conducted during the mating season include the recording of interactions between territorial ♂♂ and ♀♀. Interactions consist of herding, chasing, inspecting for receptiveness and mating. On a daily basis, a build-up of interactions was evident from 13:00 to 18:00h; 39–66% of all interactions consisted of inspections of the receptiveness of ♀♀, while chasing comprised a third of all activities. Most matings observed were between 14:00 and 18:00h, but it is suspected that mating often occurs at night.

Female herds move from one territory holder to another and the time spent with each can vary from a few hours to several days. Herd movements occur mainly at night. When approaching a territorial

♂, the herd is usually met by the ♂ at the periphery of the territory, performing a typical, stiff-legged gait, which Estes (1991a) referred to as a 'rocking canter'. Once the herd has entered his territory, the ♂ moves about in the herd inspecting ♀♀ at random. When approached within a herd, ♀♀ lift and swish their tail. Heads are often held at an angle-horn position (agonistic behaviour – readiness for combat) and circling of the ♂ and ♀ then follows. Occasionally ♀♀ drop their heads and interlock horns with the ♂. Urination on demand and urine testing (flehmen) continuously take place (Estes 1991a). When about to mate, the ♂ approaches in the typical low-stretch posture (Estes 1991a), resting his chin on the female's rump, stands bipedally, and mates. Most matings take place on the periphery of the herd where the ♂ normally stands separately; a receptive ♀ usually approaches the ♂ here with her tail lifted and swishing.

Parturition takes place within the herd and all births witnessed were between 08:00h and 12:00h (S. Vrahimis pers. obs.). Females about to calve become very restless, lying down and standing up continuously. During the final stage the ♀ lies flat on the ground. Whether the ♀ eats the afterbirth, as sometimes occurs in Common Wildebeest, is unknown. Von Richter (1974) recorded an average of 9 min elapsing before a calf can stand on its feet.

Throughout the day, lying down dominates (85%) all categories of activities for calves 1–3 months of age. During subsequent months this activity stabilizes to a much lower level (55–56%) of the diurnal time budget. The most noteworthy development in diurnal activities involves a progressive increase in the time spent feeding (4–33%). From the second month, the formation of nursery or crèche groups is evident, showing synchronized activity distinct from the main body of the herd, such as playing and exploring. At approximately three months, aggregations of calves are more pronounced, with the young spending the largest part of the day together, indicating the start of the weakening of the mother–calf bond (Vrahimis & Kok 1994).

Regarding associations with other species, the distribution range of Black and Common Wildebeest (Aylward 1881, Sidney 1965, Skead 1987) was known to overlap slightly, especially in the Free State and regions of the Highveld. Associations of Black Wildebeest with the now extinct Quagga *Equus quagga quagga* were recorded (Bryden 1889, Sclater 1900/1901, Lydekker 1926). Ostriches *Struthio camelus* also co-existed with both wildebeest species. Early explorers and hunters passing through the central open plains of South Africa described huge aggregations of wildebeest, Quaggas, Plains Zebra *Equus quagga*, Blesbok *Damaliscus pygargus phillipsi*, Hartbeest *Alcelaphus buselaphus* and Springbok *Antidorcas marsupialis* (Cumming 1980 [1850], Bryden 1893).

Reproduction and Population Structure Black Wildebeest are seasonal breeders, and breeding appears to be triggered by shortening daylength (Skinner *et al.* 1973). The majority of calves are born within a three-week period (von Richter 1971c), from mid-Nov to end Dec. Generally, the peak mating season is from mid-Mar to end Apr. Most ♀♀ conceive at the age of 16 months and calve when they are two years old (S. Vrahimis pers. obs.), after a gestation period of approximately 8.5 months (Skinner *et al.* 1973). Males can mate successfully at the age of 16 months, but first have to secure a territory before being allowed to mate. In one area all adult ♂♂ were removed, leaving only young ♂♂ (16–18 months)

present during the mating season. These ♂♂ mated successfully, but the calving percentage was not as high as expected (68%). Average age of territorial ♂♂ is four years, but in areas where excessive hunting occurs, two-year-old ♂♂ were territorial.

A single calf is born (there being no records of twins; von Richter 1974, S. Vrahimis pers. obs.) and the average birth-weight recorded is 14 kg (range 12.5–15.5 kg; n = 4). Calves are weaned at 6–8 months; the composition of the mother's milk is discussed by Van Zyl & Wehmeyer (1970). Birth rates are generally high, ranging from 72 to 97% (S. Vrahimis pers. obs.). Von Richter (1971c) recorded lower reproductive rates (47–68%) in some areas of marginal habitat suitability, and stated that the reproductive performance, in a specific area, can be variable and is linked to seasonal climatic conditions, as 86% and 100% of cows were recorded birthing in the same area on different occasions. A lack of predators in the enclosed areas where Black Wildebeest are held today lowers mortality. The current primary cause of mortality is separation of calves from their mothers during game capture operations. Von Richter (1971c) recorded 5–11% mortality in two different areas, also ascribed to separation of cows and calves.

Wildebeest have a unique reproductive system, which includes a short, sharply defined calving season that generates a superabundance of newborn calves (Estes 1991a). Connected to the species' former migratory habits, there is a tendency to concentrate in large numbers, a preference for short grass and calves follow their mothers shortly after birth, all of which are incompatible with a concealment strategy. Although Black Wildebeest are no longer able to migrate and no longer permitted to occur in large concentrations, this could be a vestige of behaviour important for the survival of wild animals in the past.

Today, Black Wildebeest are extensively managed in protected areas that do not allow the formation of natural population structures. In most areas animals are captured and removed annually, depending on the animal numbers, climatic conditions and grazing. Attempts are made to maintain a balance, with sex ratios kept close to parity and equal representation of all age classes. Pre-natal sex ratio of 91 fetuses examined showed 1.17 ♂♂ : 1 ♀. Von Richter



Black Wildebeest *Connochaetes gnou*.

(1972) reported that game-capture operations changed sex ratios, whereas in one national park, from which no animals were removed, the sex ratio was near parity. Weigl (2005) gives a longevity record in captivity of 21.8 years, although in the wild longevity is estimated at approximately 14 years (based on the known age of a single animal; S. Vrahimis pers. obs.).

Predators, Parasites and Diseases Presently, in South Africa, these animals are confined to nature reserves and private farmland, where major predators no longer occur. In historical times, explorers and hunters described instances where large numbers of animals died as the result of the outbreak of diseases, apparently scabies or mange (Harris 1840, Cumming 1980 [1850], Bryden 1889). Von Richter (1974) suspected that rinderpest and foot and mouth disease, which seriously affected Common Wildebeest, could have had an influence on Black Wildebeest. Fatal, sporadic outbreaks of anthrax in Black Wildebeest were recorded up to 1943 (Neitz 1965). Black Wildebeest are also asymptomatic carriers of the virus that causes malignant catarrhal fever, a disease deadly to cattle. A survey conducted in 1988 to establish the extent of malignant catarrhal fever in the Free State showed that there were 13 confirmed cases recorded from 1977 to 1987. The survey involved 205 landowners that had either Black or Common Wildebeest, or both species on their properties (Vrahimis & Prinsloo 1988). As a result of malignant catarrhal fever outbreaks in South Africa restrictions were placed on the relocation of both Black and Common Wildebeest in 1982 and no new introductions were allowed. Malignant catarrhal fever was then also listed as a notifiable disease and all cases had to be reported. Due to the fact that it was later found that malignant catarrhal fever was not a significant problem, these restrictions were lifted in April 1993, once again allowing for free movement of both wildebeest species in South Africa.

The endo- and ectoparasite burdens of Black Wildebeest have been investigated at two localities in South Africa, which revealed a small number of species and relatively small number of helminths and ticks at both localities (Horak *et al.* 1983b). This was ascribed to fairly cold climates prevailing in the survey regions and the fact that Black Wildebeest appear to be fairly resistant to parasitic infestation. The nematode burden of Black Wildebeest examined in another survey was found to be extremely low when compared with that recorded by Horak *et al.* (1983b) and was also perceived to be a reflection of the adverse climatic conditions, namely hot summers and cold winters with low rainfall during either season (Boomker *et al.* 2000).

In Black Wildebeest, as in the Common Wildebeest, larvae of oestrid botflies inhabit the sinuses and nasal septa, apparently without causing obvious harm to the host. Horak *et al.* (1983b) observed an erratic, but progressive, increase in the numbers of first stage larvae of *Gedoeletia* spp. on the dura mater of Common Wildebeest calves until they reach the age of approximately 13 months; likewise, Horak (2005) noted that large numbers of first instar larvae of *G. hassleri* appeared to accumulate on the dura of Black Wildebeest in the Eastern Cape from June to August. Flies of the genus deposit first instar larvae on the cornea or conjunctiva of the eyes of their hosts from where they migrate either via the optic nerve tract or artery to the subdural cavity and dura mater, and then via anterior routes to the nasal passages where they moult to the second instar (see Horak & Butt 1977).

Conservation IUCN Category: Least Concern. CITES: Not listed.

By 1900 the Black Wildebeest was nearly exterminated by hunting and the reduction of available habitat due to human settlement (von Richter 1971a, 1974), as well as the periodic outbreak of diseases. Fisher *et al.* (1969) stated that Black Wildebeest were subjected to constant unregulated persecution for more than a century, culminating in slaughtering of immense numbers for their skins in the 1870s. Millais (1895) expressed concern, fearing the extinction of the species, as formerly, 'tens of thousands of these wildebeest had been scattered in troops of from twenty to fifty over the face of the Southern Transvaal and Free State Highveld, and after careful inquiries, there were hardly more than 550 in existence'. These animals were exterminated throughout the greater part of their former distribution range and recorded as being extinct in the wild (Stevenson-Hamilton 1917, Fitzsimons 1920, Shortridge 1934). Fortunately, the species was saved from extinction by conservation-minded farmers, especially in the Free State, by protecting herds on their farms.

Following the turn of the nineteenth century, Black Wildebeest numbers started to increase rapidly (Fitzsimons 1920). However, the drought in 1933 had a severe impact on this species, and von Richter (1971a) provides information from one population where only 15–20 animals, mainly ♂♂, survived out of a population of approximately 400 animals. According to Fisher *et al.* (1969), until 1936 the only Black Wildebeest surviving were all on private land, and later that same year animals were released into the then Free State G. R. (Somerville). When the Free State G. R. was abolished, the herd was transferred to Willem Pretorius G. R. in 1956, where numbers had increased to 370 animals by 1966. Gradually, over the years, reintroductions took place on a large scale. Translocations were mainly carried out from the small number of original herds in the Free State and to a lesser extent from a herd in the North West Province, as well as from the De Beers estate in the Northern Cape (von Richter 1971a).

Although it is now supposedly safe from extinction, Black Wildebeest numbers are still relatively low. Presently, the largest threat to the species is hybridization with the Common Wildebeest. Sidney (1965) mentions the occurrence of hybrids between Black and Common Wildebeest in KwaZulu–Natal, which is probably one of the first recorded instances. Fabricius *et al.* (1988) provide evidence that hybrids are fertile. As most recorded instances of hybridization have been Common Wildebeest ♂♂ cross-breeding with Black Wildebeest ♀♀, Corbet (1991) speculates that this could be due to the larger size of the former species being able to dominate the latter. The external appearance of hybrids can vary, with the most prominent and reliable feature being the shape of the horns. Although first generation hybrids are easily identified, hybrids interbred with pure stock Black Wildebeest are difficult to recognize on appearance alone and advanced backcrosses are hard to detect (Grobler *et al.* 2011); Ackermann *et al.* (2010) discuss several anomalous cranial morphological characteristics of hybrids. It has always been believed that hybridization only occurs under artificial conditions, but, recently, in a protected area (approx. 6000 ha) in KwaZulu–Natal where large herds of both Black and Common Wildebeest were housed together, all the wildebeest had to be destroyed because of hybridization.

For several years Tussen-die-Riviere N. R. in the Free State had large populations of both Black and Common Wildebeest together, with no apparent problem of hybridization. It was decided in the early 1990s that these animals should be separated and that preference should be given to Black Wildebeest (being endemic to central South Africa) and all Common Wildebeest were removed from the reserve. At one stage, this was one of the largest populations of Black Wildebeest in South Africa, but annual hunting on the reserve resulted in almost the entire Black Wildebeest population being concentrated in a narrow area south of the Orange R., causing serious habitat degradation. After all the Common Wildebeest on the reserve were culled, Black Wildebeest from other protected areas in the Free State were subsequently translocated back to Tussen-die-Riviere N. R.

Measurements

Connochaetes gnou

HB (♂ ♂): 1800 (1700–1880) mm, n = 92
 HB (♀ ♀): 1660 (1530–1750) mm, n = 53
 T (♂ ♂): 540 (460–610) mm, n = 92
 T (♀ ♀): 500 (420–560) mm, n = 53
 HF c.u. (♂ ♂): 470 (440–500) mm, n = 92
 HF c.u. (♀ ♀): 450 (430–480) mm, n = 53
 E (♂ ♂): 170 (150–190) mm, n = 92
 E (♀ ♀): 160 (140–180) mm, n = 53
 WT (♂ ♂): 160.0 (134.0–200.0) kg, n = 253
 WT (♀ ♀): 131.0 (117.0–149.0) kg, n = 64
 Free State, South Africa (S. Vrahimis pers. obs.)
 Maximum recorded horn length is 74.6 cm for a pair of horns from the Free State, South Africa (Rowland Ward)

Key References Estes 1991a; von Richter 1971b, c, 1974.

Savvas Vrahimis

Connochaetes taurinus COMMON WILDEBEEST

Fr. Gnou bleu; Ger. Streifengnu

Connochaetes taurinus (Burchell, 1824). Travels in Interior of Southern Africa 2: 278 (footnote) [1824]. Apparently 'Kosi Fountain', but lectotype came from South Africa, North West Prov., Vryburg Dist., 'Chue Spring, Maadji Mtn [Klein Heuningvlei]'; see Grubb (1999).



Common Wildebeest *Connochaetes taurinus albojubatus*.

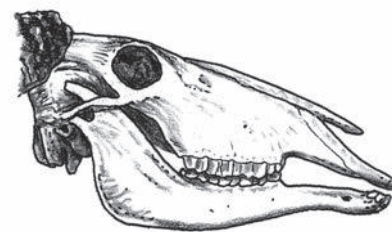
According to Skinner & Chimimba (2005), the now uncommon name Gnu applies to the Black Wildebeest *C. gnou* and derives from the Khoikhoi (aka Hottentot) descriptive term for 'the bellowing snort they give when alarmed'. But as an onomatopoeic term, it sounds more like the territorial advertising call 'GA-nou!'. 'Wildebeest' is the misnomer bestowed on both species – first the Black – by the Dutch colonists because of a fancied resemblance to the 'wild ox' of Eurasia.

Taxonomy Five subspecies are usually recognized (Ansell 1972, Grubb 2005). Synonyms: *albojubatus*, *babaulti*, *borlei*, *cooksoni*,

corniculatus, *fasciatus*, *gorgon*, *hecki*, *henrici*, *johnstoni*, *lorenzi*, *mattosi*, *mearnsi*, *reichei*, *rufijianus*, *schulzi*. Chromosome number: 2n = 58 (Wallace 1978b, Corbet & Robinson 1991).

Description A large, long-faced antelope with cow-like horns, heavy-set body but thin legs, and forequarters higher than hindquarters. Head large, muzzle broad, with wide incisor row and flexible lips; nostrils covered with skin flap. Eyes obscured by long lashes, iris yellow, tapetum reflection greenish. Ears narrow, ca. 200 mm; frontal mask black (but subject to individual and subspecific variation). Neck short and thick, with mane upstanding or lax, and beard from chin to forelegs. Coat short, glossy with vertical 'stripes' of longer, dark hair on neck, shoulders and chest. Colouration of torso blue-grey, tan, or brown with vertical stripes of longer, dark hair on neck and thorax (subject to partial moult, most developed in breeding season, making individuals look darker). Tail, mane, backs of ears and facial blaze black; beard black, tan, or off-white. Lower legs lighter coloured. Calves fawn to tan, mask, beard, dorsum and tail black (but up to one in ten has blond crown). Change to adult colouration complete in third month. Hooves with little taper; false hooves well-developed. Tail hock-length with long hair reaching to heels (widely used as a fly whisk). Preorbital glands are developed in both sexes, but larger in ♂, and covered with hair, the central duct absent or vestigial, and the secretion appears as a clear oil. Pedal glands are present on the forefeet, but rudimentary on hindfeet (Pocock 1910, Ansell 1969). The secretion of the pedal glands is black, pungent and detectable to the human nose (resembling fresh tar); the constituents of the secretion have been examined by Wood (1998). Inguinal glands are absent.

Horns cowlike, present in both sexes, unridged and extend sideways with tips pointing inward; horns of ♂ are wider and thicker,



ABOVE: Lateral view of skull of Common Wildebeest *Connochaetes taurinus*.

LEFT: Common Wildebeest *Connochaetes taurinus taurinus*.

with well-developed bosses beginning in third year. Attwell (1980) considered the loss of the second lower premolar in adults (which retain only the third and fourth premolars) as representative of an advanced stage of evolution in ungulate dentition. Adult dentition is complete by just over three years; Attwell (1980) discussed age determination based on tooth eruption, attrition and cementum layers. Horn development to 24 months is illustrated in Kingdon (1982: 530) and herein.

Geographic Variation

- C. t. taurinus* (Blue Wildebeest or Brindled Gnu): Namibia and South Africa, north of the Orange R., to Mozambique and from Mozambique to Zambia south of the Zambezi R., and from SW Zambia, west of the Kafue R., to SE and S Angola. Bluish-grey coat, black beard and upstanding black mane. Also commonly called the Brindled Gnu because of the stripes of darker hair on the neck and shoulders extending back to about the middle of the body.
- C. t. cooksoni* (Cookson's Wildebeest): restricted to the Luangwa Valley, Zambia; believed to have ranged, but only as vagrants, onto the adjacent plateau into C Malawi (Ansell & Dowsett 1988). Browner than other races.
- C. t. johnstoni* (Nyassa, Johnston's or White-banded Wildebeest): north of Zambezi R. in Mozambique to east-central Tanzania, and formerly in S Malawi, but now extinct there (Ansell & Dowsett 1988). Sometimes referred to as the 'White-banded Wildebeest' for the pale chevron between its eyes (often absent in the Tanzania population). Distribution largely confined to *Acacia* savanna of

major river valleys within the miombo (*Brachystegia*) woodland zone. Former northern distribution limit Wami R., Tanzania.

- C. t. albojubatus* (Eastern White-bearded Wildebeest): N Tanzania to C Kenya just south of the Equator, west to the Gregorian Rift Valley; southernmost point in recent past (1950s) at least to the Handeni–Kondoa road (5° 30' S) (J. Kingdon pers. obs.). Lighter grey than *C. t. mearnsi*, larger and about 50 kg heavier, with wider horns but less-developed boss; beard white to tan.
- C. t. mearnsi* (Western White-bearded Wildebeest): N Tanzania and S Kenya west of the Gregorian Rift Valley, reaching L. Victoria at Speke Bay. This is the smallest, darkest and most numerous race – the Common Wildebeest of the Serengeti Plains. Horns shorter but boss most developed; beard white to tan. Male territorial advertising call distinctively different from other races: resonant croak with mouth closed repeated many times, compared with more metallic series of 6–12 calls with mouth open of other races. Female mimicry of male secondary characters includes a penile tuft of adipose tissue, rarely if ever present in other subspecies (Estes 1991b). Often unrecognized as a subspecies distinct from *C. t. albojubatus* (Heller 1913b, Allen 1939, Kingdon 1982), yet DNA studies support the phenotypical differences and indicate that *mearnsi* is the longest isolated, and genetically most unlike the other races (Arctander *et al.* 1999). A small resident population of *C. t. mearnsi* existed in the Gregorian Rift Valley near L. Naivasha, but was eliminated by fencing and shooting by the end of World War I (Roosevelt & Heller 1915). The only known place of potential contact now is via the Rift Wall opposite L. Natron, which is sometimes traversed by *albojubatus* (D. Peterson pers. comm.).

Similar Species

Connochaetes gnou. Fossil evidence indicates the two species separated ca. 3 mya (Gentry 1978, Vrba 1979, Flagstad *et al.* 2001); although the ranges of the two species formerly barely overlapped (with Black Wildebeest adapted to the temperate, treeless Highveld and Karoo), stocking far outside its natural range (Botswana, Namibia, Zimbabwe) has led to fertile hybrids where the two species are kept on the same property (Fabricius *et al.* 1988). These are much smaller, darker antelopes with more evenly developed limbs, dangerous horns that project forward like meathooks, and a white tail.

Distribution Endemic to Africa, historically ranging in short grasslands and open bushland and woodland from N and E Namibia, Botswana, N South Africa (generally, north of the Orange R., in the Northern Cape, North West, Limpopo, Mpumalanga, Gauteng, Free State and NE KwaZulu–Natal Provinces) and Mozambique to ca. 38° E (Chuyulu Hills) in S Kenya, west to L. Victoria at ca. 01° S. Palaeontological evidence indicates that *C. taurinus* lived in the Saharan region in the late Pleistocene (Gentry 1978), and more recently in West Africa, possibly in a ‘bovid’ western refugium (Arctander *et al.* 1999).

In pre-colonial times, Common Wildebeest dominated the teeming assemblages of plains game in most of the Acacia savanna ecosystems of eastern Africa. Migratory populations rivalling those of the Serengeti Plains existed in Kenya’s Athi-Kapiti Plains; in Tanzania, stretching from the Gregorian Rift Valley to Mt Meru, mainly comprising S Masailand; and in much of Botswana. Populations in the order of 25,000–50,000 inhabited the broad river valleys incised in the miombo (*Brachystegia*) woodlands of SE Tanzania and N Mozambique (*C. t. johnstoni*), the Liuwa Plains of Barotseland, SW Zambia, extending into SE Angola; the Limpopo Valley between Zimbabwe and Mozambique; South Africa from the lowveld of the Limpopo and Mpumalanga provinces west into the foothills of the Drakensberg; and in NE Namibia, Common Wildebeest migrated between Etosha G. R. into

adjacent Botswana and Angola, before a game-proof fence was erected along the Namibia–Botswana border, followed by fencing of the eastern border of Etosha N. P. Loss of range outside of protected areas has resulted in the replacement of migratory populations with smaller more sedentary populations within protected areas, as in the case of Etosha N. P. (Berry 1997, East 1999).

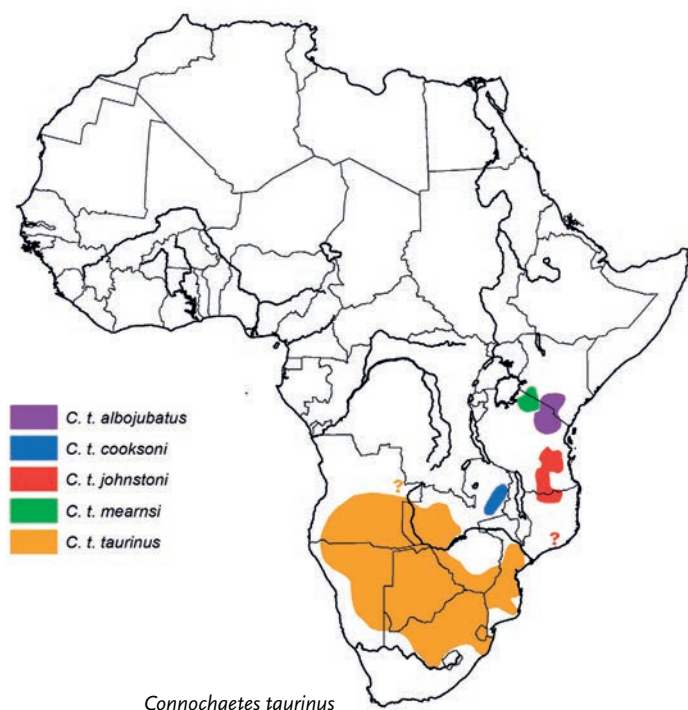
The only range state in which the Common Wildebeest has been exterminated is Malawi. According to Sidney (1965), the Nyassa Wildebeest’s range in Malawi used to be bounded by L. Malawi on the north, the Shire R. on the west and the Zambesi on the south. The alluvial plains of the river and Lakes Chilwa and Chuita must once have supported a sizeable population. But as one of the best agricultural regions of the country, it was capable of supporting a dense human population; the few animals that persisted at the south end of L. Chilwa were finally shot out in 1925 (Sweeney 1959; see also Ansell 1982, Ansell & Dowsett 1988).

Common Wildebeest have also been introduced to regions outside their former distribution range, including the Eastern Highlands of Zimbabwe, parts of KwaZulu–Natal and private farmland in Namibia.

Habitat A quintessential plains antelope preferring open short grassland, and closely associated with *Acacia* savanna. Rainfall averages between 400 and 800 mm across its range. Migratory populations disperse over the arid part of the range during the wet season, and concentrate in higher-rainfall areas with permanent water during the dry season. Prefers well-drained soils with firm footing, avoiding wetlands and waterlogged soil, although their dry season range typically includes extensive areas of black-cotton soil associated with *Acacia drepanolobium*, *A. seyal* and *Balanites aegyptica*. They are rarely found above 1800–2100 m (e.g. floor of Ngorongoro Crater in Tanzania), but may be transient in montane grassland and hilly terrain (e.g. movement between seasonal pastures; Estes & Small 1981, Estes 2002a, Musiega & Kazadi 2004).

Abundance During the late 1990s, the global population was estimated at around 1,298,000 (correcting for undercounting biases in aerial surveys; East 1999), with the migratory Serengeti–Mara population representing about 70% of global species numbers (942,000, having dropped below 1 million following the severe 1993 drought). Other population estimates were: Blue Wildebeest, 150,000 (with about half in protected areas, and one-quarter on private land and conservancies); Cookson’s Wildebeest, 16,000 (about 60% in protected areas); Nyassa Wildebeest, 96,000 (about two-thirds in protected areas, particularly Selous G. R.); and Eastern White-bearded Wildebeest, 94,000 (with about two-thirds in and around protected areas).

The most recent estimate of the total population size of Common Wildebeest is around 1,550,000 (Estes & East 2009), largely due to the rebounding of the Serengeti population of Western White-bearded Wildebeest to about 1,300,000 (Thirgood *et al.* 2004); other subspecies populations are estimated at 130,000 Blue Wildebeest, 5000–10,000 Cookson’s, and 50,000–75,000 Nyassa. However, the latest estimates of Eastern White-bearded Wildebeest indicate a steep decline in the subspecies’ populations to a current level of perhaps 6000–8000 animals. While the Common Wildebeest remains one of Africa’s most abundant game species at present, these figures highlight both the significance of the migratory Serengeti population and the vulnerability of the species to further adverse developments, such as those that



have affected the Eastern White-bearded subspecies during the last decade (Estes & East 2009).

Maximum densities of 35/km² have been recorded in the Serengeti and Ngorongoro Crater populations (Runyoro *et al.* 1995), although the Ngorongoro population density was closer to 55/km² up until 1980 (mean of 14,000/250 km²; Estes 2002a). Elsewhere, population densities estimated by aerial surveys are lower: less than 0.15/km² in areas such as Kafue N. P. (Zambia), Hwange N. P. (Zimbabwe) and Etosha N. P. (Namibia) and the southern Kalahari, to 0.6–1.3/km² in Kruger N. P. (South Africa) and North Luangwa N. P. (Zambia), Selous G. R. and Kajiado (see East 1999).

Adaptations The size, proportions and shape of the Common Wildebeest are all adapted to the species' migratory habits, including the ability to sustain a canter with minimal energetic cost, facilitated by high shoulders and slender legs (Alexander 1977, Pennycuik 1979, Christiansen 2002).

Common Wildebeest have a number of physiological adaptations including the ability to minimize water loss by allowing body temperature to rise in hot weather and by seeking shade (Taylor 1970a, Ben-Shahar & Fairall 1987). When body temperature rises above ca. 40°C, animals dissipate heat by nasal panting. However, the Black Wildebeest is more heat- and cold-tolerant than Common Wildebeest, and Hofmeyr (1981) found the latter to be at a disadvantage compared with Hartbeest *Alcelaphus buselaphus*, as its thin pelage and dark skin fail to provide significant protection against solar heat gain. In areas

devoid of shade, Common Wildebeest orientate their bodies to minimize insolation; they also face into the wind (Berry *et al.* 1984). Common Wildebeest are considered water-dependent, able to go without drinking for several days on green pasture, but no more than two days while subsisting on dry grass. Daily requirement has been estimated at 10 litres under arid conditions (Taylor 1968b). However, in Botswana's Kalahari Desert, Common Wildebeest go for months without drinking in sandveld areas where local rains have produced abundant plant growth such as tsama melons *Citrullus vulgaris* and tubers (Estes & East 2009). This suggests greater adaptability to environmental conditions than commonly supposed.

The rumino-reticulum of the Common Wildebeest is comparable with that of African Buffalo *Syncerus caffer* or cattle in proportion to size, with average capacity of 40 litres. Its wide muzzle, wide incisor arcade and flexible lips are adapted for non-selective bulk grazing, preferably on grasses in an early growth stage, between 3 and 10 cm, and green with more leaf than stem (Talbot & Talbot 1963, Bell 1970, Hofmann 1973, Gordon & Illius 1988).

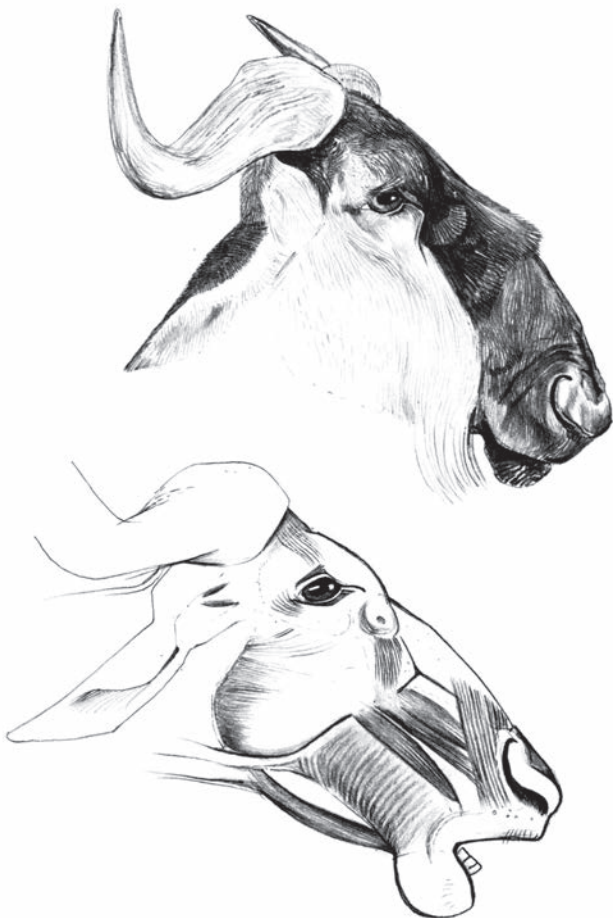
Foraging and Food Classed as a variable grazer by Gagnon & Chew (2000) in their review of the dietary preferences of African bovids, and studies using stable carbon isotopes suggest that Common Wildebeest have such a high component of grass in their diet that they are best considered as hypergrazers (Cerling *et al.* 2003, Sponheimer *et al.* 2003b); Hofmann & Stewart (1972) classify them as a fresh-grass grazers dependent on water.

During the wet season in the Serengeti ecosystem, Common Wildebeest concentrate on the highly nutritious, productive short-grass plains, which sustain very high herbivore densities. In the dry season they pursue a rotational-passage grazing system as they move rapidly through medium and tall grassland in search of green pastures (McNaughton & Banyikwa 1995, Wilmshurt *et al.* 1999b). Grasses with the most leaf and least stem are selected. A comparative study of selectivity and feeding rate of Common Wildebeest, Hartbeest and Topis *Damaliscus lunatus jimela* in Serengeti N. P. showed that the Common Wildebeest has the fastest bite rate on swards with low biomass and high protein content of green leaf (Murray & Brown 1993).

Preferences for species and growth stages vary depending on season and availability and in different populations and ecosystems (Berry 1980, Ben-Shahar 1991, Ben-Shahar & Coe 1992, Murray 1993, Bodenstein *et al.* 2000, Ego *et al.* 2003). Shallow-rooted colonial species that carpet the ground are preferred (Bell 1970). Favourites include *Cynodon dactylon* (probably most important overall; Andere 1981), *Brachiaria brizantha*, *Sporobolus marginatus*, *Cenchrus ciliaris*, *Eragrostis superba*, *Digitaria milanjiana*, *D. macroblephara* and small sedges in short grassland (e.g. *Kyllinga*). Many other species are eaten in early growth stages or when preferred decreaser species are rare, such as *Themeda triandra*, *Chloris gayana*, *Pennisetum mesianum* and *Panicum maximum*.

Food availability is often limited in the late dry season following extensive wildfires. Forty years' worth of data collection prove conclusively that the Serengeti population is limited by food supply (Mduma *et al.* 1999). Nomadic/migratory movements are discussed further under Social and Reproductive Behaviour.

Social and Reproductive Behaviour The following account is based mainly on the author's observations of *C. t. mearnsi* in



Common Wildebeest *Connochaetes taurinus albojubatus* head and myology.

Ngorongoro Crater and Serengeti N. P. between 1963 and 2006, supplemented with information from other populations as indicated.

The Common Wildebeest is a highly social species, with a grouping and mating system based on male territoriality. Migratory populations move in vast herds and aggregate in dense concentrations on green pastures. Actively territorial ♂♂ segregate yearling and older non-territorial ♂♂ from ♀♀ and young, making three distinct social classes: female or nursery herds of ♀♀ and young; all-male (bachelor) herds; and territorial ♂♂ – the latter the only class normally ever found alone.

The Common Wildebeest has two related but different dispersion patterns: (a) sedentary/dispersed and (b) migratory/aggregated. The former is representative of most social, territorial antelopes; the latter, derived state is adapted to migratory habits. Depending on environmental variables, one form can change into the other, either way. In the sedentary/dispersed state, nursery herds of ♀♀, calves and attached (mainly female) yearlings occupy preferred grazing grounds, which competing bulls divide into a network of individual territories. The intolerance of breeding (= territorial) ♂♂ keeps bachelors in less favourable, lightly or undefended habitat. Female herds, comprised of 2 to ca. 25 cows and young (with a mean number of ten in Ngorongoro Crater), represent semi-exclusive associations derived from the tendency of ♀♀ with young calves to band together, and also due to durable mother–daughter bonds (which persisted two years in the case of a marked barren mother; Estes 1966). Strangers attempting to join resident herds in the Ngorongoro Crater were generally rejected, chased out by the attendant bull if treated with hostility by the cows. Each herd acted largely independently and remained within a restricted home-range, often less than 100 ha during the wetter half of the year (Nov–May), encompassing the territories of four or five resident territorial ♂♂. Captive migrating ♀♀ kept in a 25 ha enclosure behaved in the manner of resident herds, including establishment of a dominance hierarchy (A. Moss pers. comm.).

In Ngorongoro Crater, as pastures stopped growing after the rains ended, known female herds began to aggregate on the remaining green pastures. At the end of the day, each herd returned to its accustomed home-range (Estes 1966). However, as the dry season intensified, the small herds stayed in aggregations on the remaining greenbelts and within a few weeks apparently lost their separate identity. Nevertheless, when the short rains rejuvenated the Crater pastures, some of the known animals returned to the same home-ranges (Estes 1966, 1969, 1976).

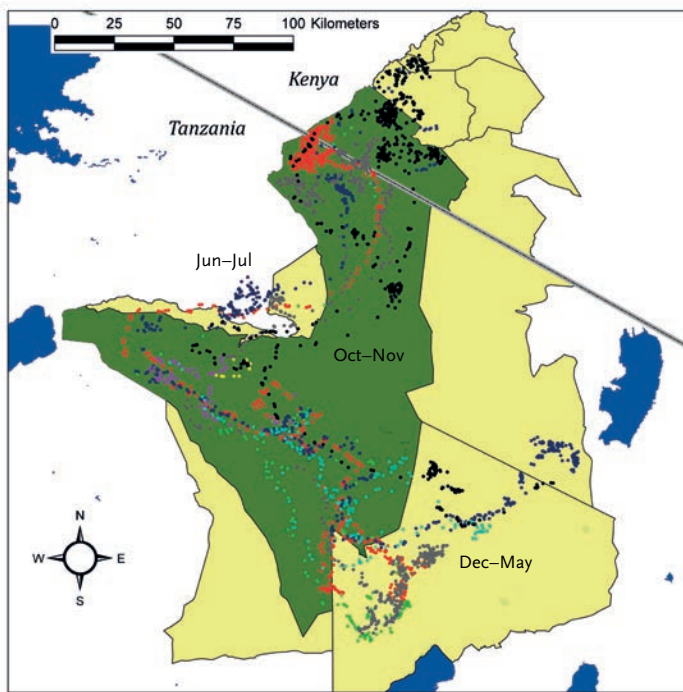
Bachelor herds include ♂♂ of all ages from yearlings to old bulls, with herd sizes ranging from two to thousands, depending on the size of the population and openness of the habitat: the more open the habitat, the larger the herds – as usual in social ungulates (Estes 1974, 1991a). Competition between bachelors is much less spirited than in male herds of Topis, Hartebeest and most other African antelopes (Estes 1969). This relatively unaggressive behaviour contrasts with the behaviour of territorial bulls. Males mature and become territorial at 5–6 years of age (Watson 1969). Rarely, a bull of three years can participate (briefly) in the rut (Estes 1966, 1969). In resident populations, bulls may hold the same territories for years, either continuously or discontinuously, depending on variable grazing conditions and proximity of ♀♀ (Talbot & Talbot 1963, Estes 1969). In Ngorongoro, average spacing between bulls is roughly 60 m in areas frequented by small herds, but even there bulls were alone 80% of the

time (Estes 1969). Except for the rut, territorial competition is most intense early in the rains (Nov/Dec) when rangeland abandoned in the dry season is reoccupied by ♀♀. The fact that mating opportunities are virtually non-existent so near the calving season suggests that the psychological advantage of established ownership promotes year-round occupancy where competition is strong.

Serious fights mostly involve attempts to establish a territory, which territorial neighbours fiercely resist. Rather than contest the territory of an established bull, a newcomer's best strategy is to win rights to a small plot between territories by wearing down the resistance of the neighbours, and then gradually enlarging it. Creating a 'stamping ground' is one of the first acts in laying claim to a space. It is created by pawing, kneeling and horning the ground, defecating, lying and rolling. These bare patches, centrally located and strewn with dung, are the olfactory foci of the territory; there may be several on a property, but usually one where the bull spends most of its inactive time. Female herds when present also frequently rest on the stamping ground. Fights between established bulls are uncommon, but neighbours engage in elaborate daily challenge rituals that serve to reaffirm the fitness of each bull to hold property. The ritual includes mutual urine testing with the vomeronasal organ. Male–male urine testing is highly unusual, as the primary function of this organ in ungulates is to detect female reproductive status through assaying hormone breakdown products in their urine (Estes 1969, 1972, Krieger *et al.* 1999). When a territorial bull leaves his property, he reverts to the status of a bachelor male as soon as he has passed beyond the territories of his immediate neighbours (Estes 1969).

The mobile/aggregated state is adapted to migratory and nomadic movements in extensive savanna ecosystems with a rainfall gradient from ca. 200 to 800 mm. Wilmshurst *et al.* (1999b) found that movements of Common Wildebeest are broadly similar to those of other large herbivores that migrate in response to resource gradients. In Serengeti N. P., the short, colonial grasses found in the lower-rainfall areas are kept growing by frequent rain and fertilized by herbivore concentrations, whose manure is buried overnight by hordes of dung beetles. Equally important, colonial grasses only 2–4 cm high virtually carpet the ground (Bell 1970, McNaughton 1984), unlike the medium and longer grasses in the higher-rainfall areas where wildebeest circulate in the dry season seeking swards of intermediate-height and greenness that offer the optimal combination of bulk and digestibility (Fryxell 1991, Morrison & Bolger 2012). Wolanski *et al.* (1999) suggest that excessive salinity triggers the migration of Common Wildebeest and Plains Zebras off the Serengeti short-grass plains.

Eight Common Wildebeest collared and monitored for 1086 wildebeest days in the Serengeti ecosystem moved an average 4.47 km/day (S.D. 5.26 km, maximum in one day 57.5 km). Daily movements increased from Mar–Jun with a peak in May (Thirgood *et al.* 2004, Hopcraft 2010). The structure and composition of aggregations vary according to habitat conditions, season, time of day, prevailing activity and level of territorial behaviour. The tendency of Common Wildebeest to associate in peer subgroups (see later) means that distribution is not random – which makes sampling to determine sex ratio and recruitment difficult, even though immature age classes are distinct (♂♂ to 3–4, ♀♀ to 2.5 years). Most samples of the Serengeti population suggest an equal adult sex ratio (Watson 1967, 1969, 1970, Sinclair 1979, Mduma 1996), whereas samples of resident populations generally indicate a female bias in the order of 1 : 1.5 or 1 : 2 (R. D.



The annual migratory route of eight female Common Wildebeest *Connochaetes taurinus* in the Serengeti-Mara ecosystem (each series of coloured dots represents the movement of one animal tracked using a GPS collar). Common Wildebeest retreat to the Mara River in the north-west during the dry season, often detouring via the (unprotected) Western Corridor on their way. Green corresponds to Serengeti National Park (Tanzania) and Masai Mara National Reserve (Kenya); yellow corresponds to surrounding buffer zones (map courtesy J. Grant, C. Hopcraft, Frankfurt Zoological Society and the University of St Andrews).

Estes pers. obs.). Common Wildebeest aggregations on the Serengeti short-grass plains are typically dispersed with wide individual spacing. But when feeding in tall swards, aggregations are compact with minimal individual spacing, possibly from fear of Lions *Panthera leo*.

Except during several months of the dry season when territorial activity is attenuated, mature bulls accompanying the migration space out and become active as soon as an aggregation stops moving. In short order they round up ♀♀ and weed out the bachelors, enforcing the same kind of segregation as in resident populations: nursery herds contained in a territorial network with bachelor ♂♂ on the periphery. Such groups have been called 'pseudo-herds', as the association of ♀♀ is merely temporary (Watson 1969). Only cows with young of the year keep together. They begin to separate after nine months, but female and some male yearlings are frequently associated with nursery herds, at least some of which continue to trail their mothers. When on the move in files or columns, both sexes and all ages join together. However, when the movement is halted by an obstacle (river crossing, tall vegetation, defile), bulls come to the forefront and are the first to risk going forward (R. D. Estes pers. obs.). When Common Wildebeest are in tree savanna they cluster in the shade during the hottest hours. At night, aggregations gather on the shortest available grassland and rest/ruminate in 'bedding formations', which may contain hundreds of animals but being linear, with enough separation to permit individuals to move in or out, can disperse immediately when alarmed, as when tested by hunting hyaenas (Estes & Estes 1979).

Territorial ♂♂ are capable of reproducing at any time and for a good six months of the year have continuing but declining mating

opportunities, as some 20% of ♀♀ fail to breed during the rutting peak; a few breed as much as five months later. The onset of the rut is marked by a peak of noise and activity. No other African wildlife event can match the spectacle of the Serengeti rut, which occurs during the migration from the short-grass plains into the woodland zone. An idea of the intensity of sexual competition can be gained from the number of territorial bulls in dense concentrations: up to 250/km² (R. D. Estes pers. obs.). This remarkably close packing of territorial bulls facilitates synchronous breeding of cows in migrating hordes: no ♀ in oestrus is likely to go undetected for long. The rutting uproar continues day and night, reaching a crescendo when aggregations are on the move.

As long as ♀♀ are present, territory holders neither rest nor feed but exert every effort to detain ♀♀, prevent raids by their nearest rivals, and seize opportunities to break up a neighbour's herd. Herding bulls do not engage in challenge rituals, but frequently butt heads. Tightly clustered herds within a network of single bulls is a hallmark of the rut clearly visible from an airplane or hilltop. Considering that up to half-a-million cows are mated during the rut, it is surprising how seldom copulations are witnessed. By far the most effort exerted by territorial bulls goes into herding, chasing and fighting. Their efforts may look, but are not, futile, as having a herd improves a bull's chances of gaining a cow in heat, because ♀♀ suffer less sexual harassment by going into a group rather than stopping with a lone ♂ (R. D. Estes pers. obs.). The more cows a bull encounters, the more mating opportunities. Bulls that establish territories in the main stream of a migrating horde obviously are fitter than bulls with peripheral territories where most passers-by are bachelor ♂♂. Good locations also vary with time of day or night. Bulls under a broad shade tree may have up to 100 ♀♀ and young during the hottest hours while unshaded neighbours have a few or none. Bulls that stay put on territories in a close-cropped, abandoned pasture may be rewarded come evening, when an aggregation returns to spend the night on short grassland.

In the hurly-burly of the rut, it is not unusual for a bull to overlook the presence of an oestrous ♀ in his herd, but having detected one, a bull copulates with her dozens of times, up to three or four mounts with ejaculation in a minute when not distracted by the need to repel invading neighbours. A preference to continue mating with the same bull is shown by ♀♀ in heat, which will follow and even solicit copulation. But if forced to leave, oestrous ♀♀ have been seen to copulate with a succession of bulls until no longer receptive (Estes 1991a). Oestrus lasts at most one day. While the energetic costs of rutting are rigorous for actively competing bulls, interludes when no ♀♀ are in the immediate vicinity enable them to rest and feed. Bulls that have been active over a sustained period may take a day or two off in a bachelor herd (R. D. Estes pers. obs.). Accordingly, the Common Wildebeest rut leaves breeding ♂♂ less spent than ungulates of the Northern Temperate Zone that persevere to exhaustion. However, serious injuries – to hooves, legs, horns, eyes – incapacitate possibly 0.05% of the competing bulls. Those with broken horns can hold their own as long as they have the bosses to absorb the impact of butting. But a bull that has lost a whole horn can no longer stand up to an intact rival. The end of the rut is marked by reduced intensity and volume of calling and by the presence in resting herds of adults of both sexes. The fat deposits bulls accumulate in the months prior to the rut are depleted by the end of it (Sinclair 1977b).

The fact that 80% of the annual calf crop is born within three weeks is linked to the evolution of 'follower young', a key adaptation to the mobile/aggregated state of migratory populations. Apart from the two wildebeest species and the Blesbok/Bontebok *Damaliscus pygargus*, the young of all other antelopes go through a hiding or lying-out stage of varying length. Selection for follower young born in a short time stems from the Common Wildebeest habit of massing on short, green grass. Tan calves are conspicuous among dark-coloured adults. As aggregations rapidly deplete pastures and move on, mothers guarding 'hider calves' adapted for concealment in tall, tan grass would be left behind. Changing to follower young led Common Wildebeest to lose all aspects of the ancestral hider strategy. Calves have lost the hiding instinct and accompany their mothers as soon as they can stand. This takes as little as 3 min (mean of 7 min), and the feeble stage when neonates cannot keep up with a herd is over within about two days (Estes 1976, Estes & Estes 1979). A drastic speed-up in the development of locomotory skills is key to this precocity. Common Wildebeest calves have almost adult muscle/bone length ratios at birth, whereas hider calves have only two-thirds the adult muscle/bone ratio at birth (Grand 1991). Common Wildebeest calves may be the most precocious of all ungulates.

Actual parturition is described in detail in Estes & Estes (1979). Mothers only lick their calves in the first hour postpartum; neonates neither receive nor need the stimulation of anogenital licking to void wastes. Mothers recognize their newborns by scent, and aggressively reject any but their own (Estes & Estes 1979). Calves may be seen to eat dung within a few days, presumably acquiring rumen bacteria. They start sampling grass within a week. Within a day or two mother and calf are mutually imprinted. Calves rest in crèches or lie alone while their mothers feed. Some mothers leave sleeping calves to join wildebeest filing to water. This practice came to light while following Ngorongoro cows returning from drinking, which were acting as though they had lost calves – running and bawling, sometimes joining forces and inspecting every herd with calves. After going some 3 km in this manner, several distraught mothers found their calves – just where they had left them. Up until then, a lone wildebeest calf was assumed to be orphaned and doomed (R. D. Estes pers. obs.) Associative behaviour is manifested within days of birth, in crèche formation and group play (chasing, cavorting, head-butting). Beginning as yearlings, peer subgroups of the same sex and age are discernible even in huge Serengeti aggregations. The annual calving season promotes further subdivisions into groupings of ♀♀ in the same reproductive state. In the months before and after calving the following subgroupings can be observed, in addition to the aforementioned divisions: pregnant ♀♀, maternity groups of cows with calves, non-pregnant ♀♀, and cows that have lost calves (both these often found grouped in male aggregations) (Estes & Estes 1979).

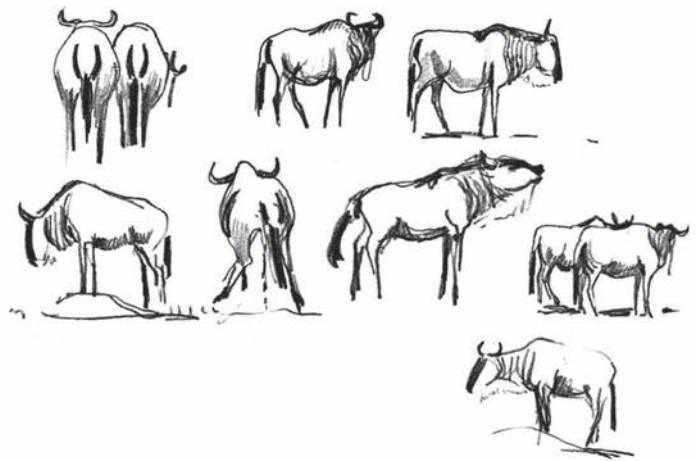
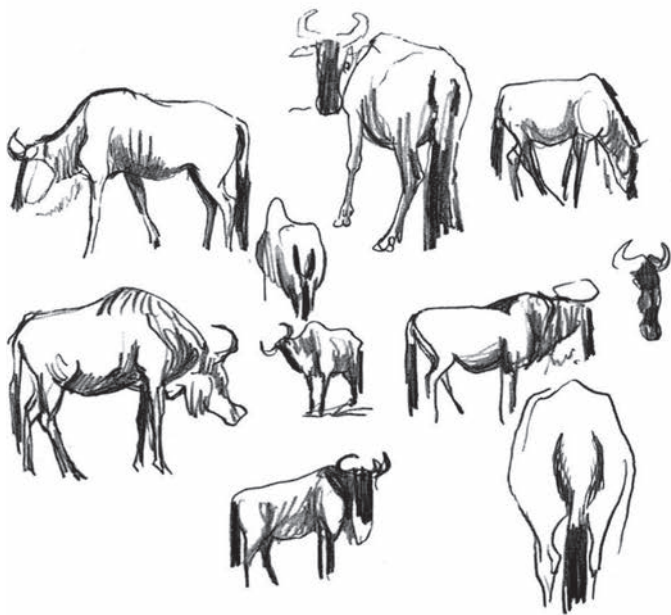
While resting, inter-individual spaces of approximately one metre keep herd members beyond horn reach. Only mother and calf lie in contact. Star-formations can be seen in small herds that enable members to monitor a full 360 degrees. Such circles form through settling back-to-back facing away rather than head-to-head. Bachelor herds can be discerned at a distance by their more regular individual spacing. Rubbing the muzzle or head on the rump or shoulder of another wildebeest, commonest between ♀♀, is also performed during the territorial challenge ritual. It appears sociable, although

these contacts apparently often include depositing secretions of the preorbital glands, which might be an assertion of dominance (Estes 1969, 1991a). Comfort behaviours such as lying down and rolling (rare or unknown in other ruminants) are most commonly seen in territorial bulls (though Common Wildebeest cannot roll over completely like zebras).

Common Wildebeest also have the habit of rubbing their preorbital glands on branches and trunks of trees, usually as the prelude to horning bouts. Olfactory communication is involved, as marking and horning are directed especially at sites that have already been marked and horned; and bouts begin with sniffing of the site. The behaviour is also infectious as Common Wildebeest will line up and take turns rubbing and thrashing the same tree. However, vegetation horning is primarily an activity of adult ♂♂; other animals horn much less often and vigorously. Bouts may last anywhere from 15 seconds or less to as long as five minutes. It is clearly aggressive in character and may either be directed, as in encounters between territorial bulls, or an undirected display of aggressive mood. What is extraordinary and generally overlooked is the environmental impact of Common Wildebeest horning in large populations. Data collected on the incidence and effects of horning beginning in 1979, in 1980–81, 1986, 1998 and 2003 show that on the Serengeti Plains and in tree savanna of the woodland zone two out of three young trees of suitable size and accessibility have been horned, many repeatedly over a period of years. In numerous cases the stems and branches of trees (especially *Acacia* spp. and *Balanites aegyptica*) have been destroyed every time they produced stems of thrashable size; the resulting growth in the case of *A. tortilis*, a dominant tree, is a supine hedge, within which a main stem of up to 10 cm diameter may be found. The evidence suggests that destruction of woody vegetation by Common Wildebeest was second only to fire and elephants in transforming Serengeti savanna woodlands into tree grassland during the 1970s and 1980s (Estes *et al.* 2008).

In undisturbed herds or aggregations of Common Wildebeest, the advertising calls of territorial bulls are the source of virtually all vocalizations. Calling by other classes is common in moving aggregations and consists mainly of exchanges between mothers and their offspring, which reach a crescendo when they become separated, as when massed at waterholes, crossing terrain that funnels many animals close together, or when stampeded by predators. Whereas differences in the advertising calls of *C. t. mearnsi* are discernible from other subspecies, the higher-pitched calls of other classes sound the same. Yet, mothers and dependent offspring recognize one another's calls. It enables nearly all separated pairs to reunite, facilitated by remaining at the separation site and running back and forth bawling (R. D. Estes pers. obs.).

With a dozen or more ungulate species in savanna herbivore communities, the Common Wildebeest inevitably is often found in the same place and time with some of them, especially with other grazers. The Plains Zebra *Equus quagga*, which eats many of the same grasses (Bell 1970, Casebeer & Koss 1970, Ben-Shahar & Coe 1992) is popularly believed to be closely associated, and indeed it is common to find aggregations that include both species. Research on the incidence and basis of association between Common Wildebeest and eight other grazing ungulates (Plains Zebra, Grant's Gazelle *Nanger (granti) granti* and Thomson's Gazelle *Eudorcas thomsonii*, Topi, Hartbeest, Waterbuck *Kobus ellipsiprymnus*, Impala *Aeypceros melampus* and Common Warthog *Phacochoerus africanus*) of the Serengeti



Common Wildebeest *Connochaetes taurinus albojubatus*.

ecosystem found a large overlap in distribution with the Common Wildebeest and that most species were eating the same plants in the same vegetation types (Sinclair 1985). Most species were found closer to Common Wildebeest than expected if distribution was random. In the wet season, 71% of the Plains Zebra population could be found near the main Common Wildebeest concentrations, but on the leading edge where they could graze before the sward was eaten down by the latter. But in the dry season, after migrating to the Masai Mara part of their range, the Plains Zebras avoided inter-specific competition by staying further away from the Common Wildebeest and grazing in taller grassland. The results of this study strongly suggest that the basis of the association is mutual protection against predators. As the Common Wildebeest is the preferred prey of all the large carnivores, the other species are safer in proximity to this most abundant herbivore. The conclusion: 'In general, predation appears to play as important a role as inter-specific competition in structuring this community' (Sinclair 1985: 916; and see Hopcraft 2010). Despite proximity, behavioural interaction and communication with associated ungulates are surprisingly limited. They get out of one another's way and respond to each others' alarm signals, but largely ignore their species-specific displays. Most ungulates react to the alarm signals of other species, including monkeys and baboons, jackals *Canis* spp., oxpeckers *Buphagus* spp. and other birds.

Reproduction and Population Structure The timing of calving and rutting is geared to the climate so that both occur under favourable conditions (Sinclair *et al.* 2000). Onset of the annual rut varies from year to year by as much as three weeks, under the influence of variable climatic conditions. For example, following the great East African drought of 1960, when most cows lost their calves, *C. t. mearnsi* and *C. t. albojubatus* calved two months earlier than normal; Estes 1966). In East Africa, the rut comes after the rains (Jun) when the animals are in top condition, thus ensuring an adult conception rate normally better than 90%. Some ♀♀ breed as yearlings (ca. 20% in the Serengeti ecosystem), but most conceive a year later (ca. 28 months). In the 1960s and 1970s, while the

Ngorongoro and Serengeti populations were increasing at the rate of 10% a year, the yearling conception rate was closer to 80% (Estes 1966, Watson 1969, 1970, Estes & Estes 1979, Sinclair *et al.* 2000).

Research conducted in the Grumeti Reserves bordering Serengeti N. P. in 2002–2004 on 17 captive ♀♀ (Monfort *et al.* 2001) yielded new information about the reproductive physiology of the species (Clay 2007, Clay *et al.* 2010). Regular assays of faecal hormones excreted by each ♀ revealed their reproductive-endocrine rhythms and determined that Common Wildebeest are seasonal, polyoestrous, spontaneous ovulators. The duration of oestrous cycles and luteal phases were quantified, and a gestation period of eight months was confirmed (Clay *et al.* 2010). The average duration of postpartum anoestrus was 100 days. No significant correlation was found between lunar phase and the timing of luteal phases as proposed by Sinclair (1977b). How the oestrous cycles of ♀♀ are synchronized has long been a subject of speculation (Rutberg 1987, Sinclair 1977b, Sinclair *et al.* 2000). A major objective of this study was to test the author's hypothesis that chorusing of bulls, which reaches a peak during the rut, serves this function (R. D. Estes pers. obs.). A month prior to the 2003 Serengeti rut, recordings of rutting calls were played to two groups of captive cows continuously for three weeks, one of which included a bull, while a third control group was kept isolated. Faecal progesterin assays showed that the oestrous cycles of the two exposed groups were synchronized more closely than in the control group. This research provides the first evidence of an auditory cue that modulates reproductive timing in the Bovidae (Clay 2007).

Calving occurs typically ca. two months before the period of most rain and maximum grass production (Talbot & Talbot 1963). Common Wildebeest calving is more tightly synchronized than that of any other African ungulate, comparable to the birth peak of Caribou *Rangifer tarandus* (Dauphiné & McClure 1974). The Serengeti migratory population usually calves in Feb, between short and long rains, but the resident population in the Western Corridor is subject to the wetter climate associated with L. Victoria and calves 1–2 months earlier. In southern Africa, the calving season is generally Nov/Dec (though sometimes later; Attwell 1977), but in

Liuwa Plains, SW Zambia, calving occurs in late Oct to early Nov just before the rains start (Howard & Conant 1983). Calves weigh between 14 and 25 kg at birth, with calves in southern Africa being larger (Talbot & Talbot 1963, Attwell 1977).

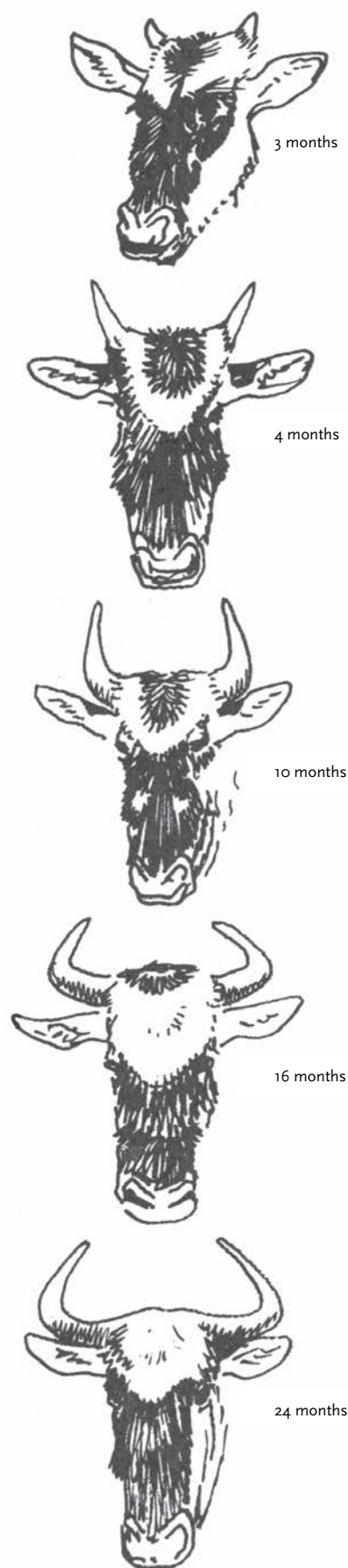
Maternal stress is considered to be most severe during early to mid-lactation (Eltringham 1979, Altmann 1980, Murray 1982b). During the abbreviated feeble stage, calf survival depends on the presence of harder-to-catch calves a few days older, which serve as cover for newborns. The more calves in a maternity herd, the higher the calf survival rate. Survival in the first month averages ca. 70% in migratory aggregations vs. 50% or less in resident small herds (Estes 1976). A calf's only defence is its own mother, which is quite effective against a single Spotted Hyaena *Crocuta crocuta* (Estes & Estes 1979). Young of the year begin to form separate groups at about nine months, following weaning at around eight months (Watson 1967). However, some continue to follow their mothers until the next calf crop is born. The potential payoff is that cows that lose calves allow their yearlings to nurse. Estimated calf survival to yearling stage in the Serengeti population in nine years between 1965 and 1994 averaged 22.9% (12.3–35.1) (Mduma 1996, Appendix 2).

Weigl (2005) gives a longevity record for the species in captivity of 24.3 years, which is about five years longer than maximum longevity recorded by Attwell (1977) in KwaZulu–Natal (1982). But the oldest animals recorded in Etosha N. P. were 13–14 years (Berry 1980) and individuals of over 12 years in Serengeti N. P. were considered very old (Mduma 1996).

For information on sex ratios see Social and Reproductive Behaviour.

Predators, Parasites and Diseases Common Wildebeest are typically the preferred prey of Lions and Spotted Hyaenas wherever they occur (Kruuk 1972, Schaller 1972, Elliott *et al.* 1977, Mills & Shenk 1992, Scheel 1993b). The fact that they tend to be the dominant large herbivore in savanna ecosystems may largely explain this preference. But there is also quantitative evidence that wildebeest are less vigilant than most associated prey species, including Plains Zebras, the second most-preferred prey (Scheel 1993b).

Aggregations are easier to approach than singles and small herds, probably because each individual feels and is safer in a large group. Observations of scanning rates showed that rates declined with increasing herd size, including herds containing individuals of different species (e.g. zebras) (Scheel 1993a). Scanning rates were also influenced by light and cover. Common Wildebeest scanned more at twilight and on moonlit nights than during the day. Scanning rate also correlated with nearby cover large enough to conceal hunting Lions. Greater vigilance, as indicated by increased scanning rates, would be expected in bushy habitat and tall grass, but oddly enough, wildebeest scanned less in such places than in more open habitat. Likewise animals in the interior of a group tend to scan less than those on the periphery. This is usually explained by the fact that animals on the outside are more vulnerable (Elgar 1989, FitzGibbon 1990a), but having their view blocked by other animals could explain reduced scanning rates of individuals inside a herd. Similarly, thick cover that renders the ability to detect approaching predators problematic could explain reduced scanning rates in such habitats (Scheel 1993a). Of eight species in the study, Common Wildebeest and Common Warthogs were the least vigilant, and both were preferred by Lions. Hence these species were at greatest predation risk (Scheel 1993b). However, Common Wildebeest and Plains



Common Wildebeest *Connochaetes taurinus* horn development.

Zebras were considered equally vulnerable to Lions in Kruger N. P., and no selection by season or sex was noted (Mills & Shenk 1992).

Although the hunting technique of the Spotted Hyaena is adapted to selecting the most vulnerable individuals, a single adult hyaena is capable of running down and killing a healthy full-grown Common Wildebeest (Wasson 1990). The hyaena's specialization on newborn calves during the calving season is a major factor in maintaining the short peak, as mortality of calves born before the peak is virtually total (Estes 1976). Cheetahs *Acinonyx jubatus* and African Wild Dogs *Lycaon pictus* as well as Lions partake of the birth bonanza. Jackals very rarely prey on wildebeest calves. The birth of thousands of calves during the short peak completely glut the predator market (Rutberg 1987, Ims 1990, Sinclair *et al.* 2000).

The infamous pan-African rinderpest epizootic of the 1890s, a virus transmitted from cattle brought into Somalia around 1887 during the Italian campaign, caused the mortality of up to 90% of the continent's cattle, African Buffalo, tragelaphines *Tragelaphus* spp. and wildebeest. No other livestock or wildlife disease has had such widespread mortality, and the survivors of the rinderpest pandemic, with at least partial immunity, mostly recuperated within one to two decades (Simon 1962). Called the 'yearling disease' because older Common Wildebeest calves were vulnerable to rinderpest in lean years (Talbot & Talbot 1963), rinderpest disappeared from the Serengeti population in 1963 (Dobson 1995). The population then increased five-fold from 250,000 to 1,250,000 by the mid-seventies (Sinclair 1979). Apart from such rare epidemics, studies of Common Wildebeest and African Buffalo suggest that disease rarely kills animals in good body condition. But disease, like predation, can cull animals in poor condition (Sinclair 1977a, Prins 1996). Common Wildebeest are carriers of malignant catarrhal fever (sometimes referred to as 'snotsiekte'), a viral disease fatal to cattle. The Masai have to keep their herds away from the short-grass plains during and after the Common Wildebeest calving season, to avoid pastures contaminated by afterbirths (Homewood *et al.* 1987). Anthrax, an endemic disease of African wildlife (Prins 1996), most prevalent in arid ecosystems, has been implicated as a major cause of the decline of the Common Wildebeest population in Etosha N. P. (Berry 1993). Protecting cattle from foot and mouth disease has been the justification for the veterinary cordon fences criss-crossing Botswana in total disregard of their effects on the wildlife, so that the ruling oligarchy of cattle barons can continue to profit from the European Union (EU) subsidized export of beef to Europe (Williamson & Williamson 1985a, Williamson 1994b; and see Conservation). Cleaveland *et al.* (2005) isolated bovine tuberculosis, caused by *Mycobacterium bovis*, from two of 18 migratory Common Wildebeest samples in the Serengeti system in 2000.

Similarly, healthy animals are hardly affected by external and internal parasites, but can be further weakened when in poor health. Ticks are the most serious external parasites, and botflies (oestrid flies) are common parasites of Common Wildebeest throughout their range (Howard & Conant 1983). Larvae of *Gedoelestia* spp. are typically deposited on the cornea of the eyes, and then make their way to the nasal/sinus cavities via the ocular-cranial route or ocular-vascular-pulmonary route. Larvae of *Oestrus* spp. are deposited in the nostrils. The larvae develop to mature larvae in the sinus cavities and then crawl out to pupate. Botflies do not seem to cause Common Wildebeest any harm, although *Gedoelestia* larvae have been found in the braincase and on the dura mater (Talbot & Talbot 1963, Horak *et al.* 1983b). Horak

et al. (1983b) recovered parasites from 55 Blue Wildebeest in Kruger N. P. and recorded 13 nematodes (particularly *Haemonchus bedfordi*), four cestodes, one trematode, the larvae of five oestrid flies, three lice, seven ixodid ticks, one mite and the nymphae of a pentastomid species (*Linguatula nuttalli*, indicative of the large number of Lions in Kruger N. P., the final hosts of the pentastomid). Remarkably, they recovered very few adult ticks of any species. Only one species, the lungworm *Dictyocaulus viviparus*, was attributed to any ill-effects observed in Common Wildebeest, causing fairly extensive pulmonary lesions, though seemingly not severe enough to cause death.

Conservation IUCN Category: Least Concern. CITES: Not listed.

Reductions in historical geographic range have been relatively minor, with only the elimination of *C. t. johnstoni* from Malawi being perhaps most notable. However, all the major Common Wildebeest populations except the Tanzania populations of *C. t. mearnsi* and *johnstoni* have undergone declines, some by as much as 90%. Fences that blocked migration between wet- and dry-season ranges have had the most obvious impact. Denying access to water and to higher-rainfall refuges during severe droughts have caused mass die-offs. But many other anthropogenic factors have taken their toll: ever-expanding settlement, mechanized agriculture, overstocking with cattle and habitat degradation, elimination of water sources through watershed deforestation and expropriation for irrigation, poaching, bushmeat trade, armed conflicts – and last but not least, game eradication programmes in failed efforts to eliminate the wild hosts of sleeping sickness (nagana) and other diseases of domestic livestock.

The decline in numbers and episodes of mass mortality of Common Wildebeest in Botswana caused by veterinary cordon fences that blocked drought-induced migrations received considerable notoriety, particularly after thousands died at L. Xau in the north-east of the Kalahari Desert in 1980 (Owens & Owens 1980), followed by other large die-offs in subsequent years (Williamson & Williamson 1985a, Parry 1987, Estes & East 2009, Gadd 2012). But Spinage (1992) documents historical evidence that the decline actually began much earlier. Archive records show that there was at one time a significant migration every winter east and south-east from the southern Kalahari to the Molopo R. into South Africa through the unfenced boundary between Tsabong and Khuis (with Common Wildebeest moving as much as 40 km per day). Wildebeest here were once so numerous that they were regarded as a menace by local farmers because they competed with local cattle for grazing and transmitted malignant catarrhal fever. Large-scale killing of Common Wildebeest followed, at least until 1961, when the species was classified as a game animal that could only be hunted with a licence.

Fencing of national park boundaries caused Common Wildebeest populations to crash in Kruger N. P. (Whyte & Joubert 1988) and Etosha N. P. (Berry 1997). Mechanized farming, cattle ranching and fencing of the Loita Plains wet-season range of the Masai-Mara population of *C. t. mearnsi* led to a decline of 75% between 1977 and 1997 (Homewood *et al.* 2001, Ottichilo *et al.* 2001, Serneels & Lambin 2001, Ogutu *et al.* 2011). Progressive fencing of the Athi-Kapiti Plains keeps reducing the range available for wildlife; the Kitengela corridor between the plains and Nairobi N. P. is now so tortuous that Common Wildebeest rarely come into the park, which was formerly an important dry-season concentration area. Completing the fencing of the park by closing the connection to the Athi-Kapiti Plains is now advocated by many (Cowie 2004).

The migratory population of the Western White-bearded Wildebeest defines, and is largely conserved in, the Serengeti ecosystem, including Ngorongoro Conservation Area and the Masai Mara National Reserve. Thirgood *et al.* (2004) radio-tracked eight Common Wildebeest during 1999–2000 in relation to protected area status in different parts of the ecosystem, and found that the collared animals spent 90% of their time within well-protected core areas. However, two sections of the migration route – the Ikoma Open Area and the Mara Group Ranches – currently receive limited protection and are threatened by poaching or agriculture. Comparing current Common Wildebeest migration routes with those recorded during 1971–73 indicates that the western buffer zones appear to be used more extensively than in the past. Thirgood *et al.* (2004) suggest that the current development of community-run Wildlife Management Areas as additional buffer zones around the Serengeti represents an important step in the conservation of this UNESCO World Heritage Site.

The Serengeti migration was seriously threatened in 2010 by the proposed construction of a paved highway from Musoma on L. Victoria to Tanga on the Indian Ocean coast across the northern part of Serengeti N. P. Intended to transport oil, minerals and produce to the coast from landlocked countries to the west and north, this road would have carried thousands of vehicles a day and permitted roadside development along the route, threatening sooner or later to truncate the migration. International outcries by scientists (e.g. Dobson *et al.* 2010; and see Holdo *et al.* [2011], who predicted a decline in the wildebeest population by one-third), conservationists, tour operators, UNESCO and IUCN finally persuaded President Jakaya Kikwete to accept an alternative route south of the Park and to construct only a gravel road across the northern Serengeti, as proposed in the original 2005 plans. However, in Sep 2011, the Minister of Transport announced plans for a railway across the Serengeti along the same route, pledging that, despite opposition, the project will be completed or reach advanced development within the next five years.

Priorities for research and conservation in the future include: (1) identifying, restoring and maintaining access to water and drought refuges for Common Wildebeest, zebras and other water-dependent herbivores; (2) maintaining corridors and dry season refuges, and promoting Transfrontier Conservation Areas (TFCA) that enlarge and protect viable ecosystems; (3) applying pressure from national and international conservation organizations to stop the EU from subsidizing beef exports from Botswana to Europe at above-market prices (Williamson 1994b); and (4) enforcing separation of Black and Blue Wildebeest introduced on ranches in South Africa, Botswana and Namibia to prevent hybridization.

Existing TFCAs of potentially great importance for restoring Common Wildebeest populations to something approaching their former abundance include: the Kavango–Zambezi TFCA, spanning an area of approximately 287,000 km² at the confluence of Namibia, Angola, Zambia, Zimbabwe and Botswana and including the Caprivi Strip, Chobe N. P., the Okavango Delta and the Victoria Falls; the Great Limpopo N. P. connecting Zimbabwe, Mozambique and South Africa, facilitating the doubling of the size of Kruger N. P. by adding an adjoining section of Mozambique and the Gonarezhou N. P. in Zimbabwe; and the Kgalagadi Transfrontier Park, which combines South Africa's Kalahari Gemsbok N. P. with Botswana's Gemsbok N. P. Serengeti wildlife would also benefit from the proposal to incorporate the Mara range in a TFCA. Efforts are also under way to

link Selous G. R. in STanzania with Niassa G. R. in N Mozambique via Selous–Niassa Wildlife Corridor. Another promising conservation initiative is establishment of private wildlife conservancies adjoining and extending protected areas, as exemplified by Sabi Sand G. R., and the Timbavati and Klaserie Private Nature Reserves on the western boundary of Kruger N. P.

Measurements

Connochaetes taurinus

C. t. mearnsi

TL (♂ ♂): 2495 (2330–2760) mm, n = 40
 TL (♀ ♀): 2346 (2270–2415) mm, n = 11
 T (♂ ♂): 623 (565–730) mm, n = 40
 T (♀ ♀): 587 (550–635) mm, n = 11
 HF c.u. (♂ ♂): 501 (470–540) mm, n = 40
 HF c.u. (♀ ♀): 489 (462–510) mm, n = 11
 E (♂ ♂): 202 (183–230) mm, n = 40
 E (♀ ♀): 195 (187–207) mm, n = 11
 Sh. ht (♂ ♂): 1226 (1110–1340) mm, n = 40
 Sh. ht (♀ ♀): 1171 (1070–1230) mm, n = 11
 WT (♂ ♂): 201.1 (171.0–242.0) kg, n = 40
 WT (♀ ♀): 163.0 (140.8–242.0) kg, n = 11
 Serengeti N. P., Tanzania (Sachs 1967)

WT (♂ ♂): 210.0 kg, n = 40
 WT (♀ ♀): 165.0 kg, n = 43
 Western Masailand (Talbot & Talbot 1963)

C. t. cooksoni

WT (♂ ♂): 235, 241 kg, n = 2
 WT (♀ ♀): 219, 224 kg, n = 2
 E Zambia (Wilson 1968)

C. t. albojubatus

WT (♂ ♂): 243.0 (222.0–271.0) kg, n = 10
 WT (♀ ♀): 192.0 (179.0–208.0) kg, n = 10
 S Kenya (Ledger 1964)

C. t. taurinus

Sh. ht (♂ ♂): 1472 (1410–1565) mm, n = 17
 Sh. ht (♀ ♀): 1353 (1290–1410) mm, n = 17
 WT (♂ ♂): 237.2 kg, n = 98
 WT (♀ ♀): 190.4 kg, n = 95
 KwaZulu–Natal (Sh. ht: Attwell 1977; WT: Hitchins 1968)

WT (♂ ♂): 251.7 kg, n = 97
 WT (♀ ♀): 214.8 kg, n = 106
 Kruger N.P. (Braack 1973)

Maximum recorded horn length in the species is 86.0 cm for a pair of horns from Messina, Limpopo Province, South Africa (Rowland Ward)

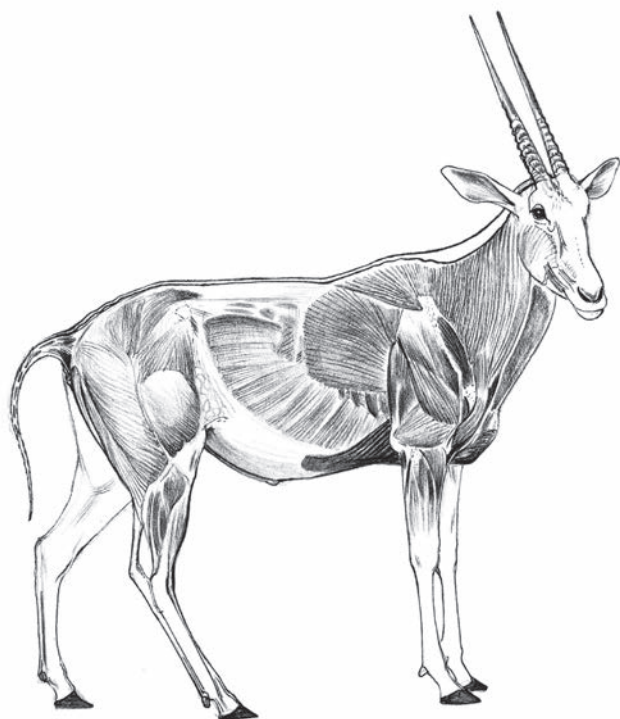
Key References Attwell 1977; East 1999; Estes 1966, 1969, 1976, 1991a; Estes & East 2009; Hopcraft 2010; Mduma *et al.* 1999; Sinclair 1979; Sinclair *et al.* 2000; Talbot & Talbot 1963; Watson 1967, 1969.

Richard D. Estes

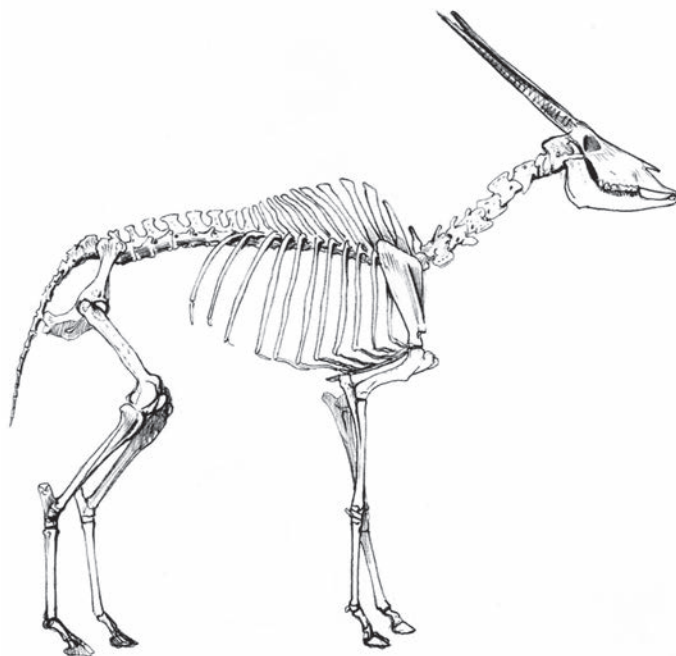
Tribe HIPPOTRAGINI

Horse-like Antelopes

Hippotragini Sundevall, 1845. Öfversigt. Kongl.-Vetensk. Akad. Förhand. for 1845, parts 2 and 3, p. 31.



Beisa Oryx *Oryx beisa* myology.



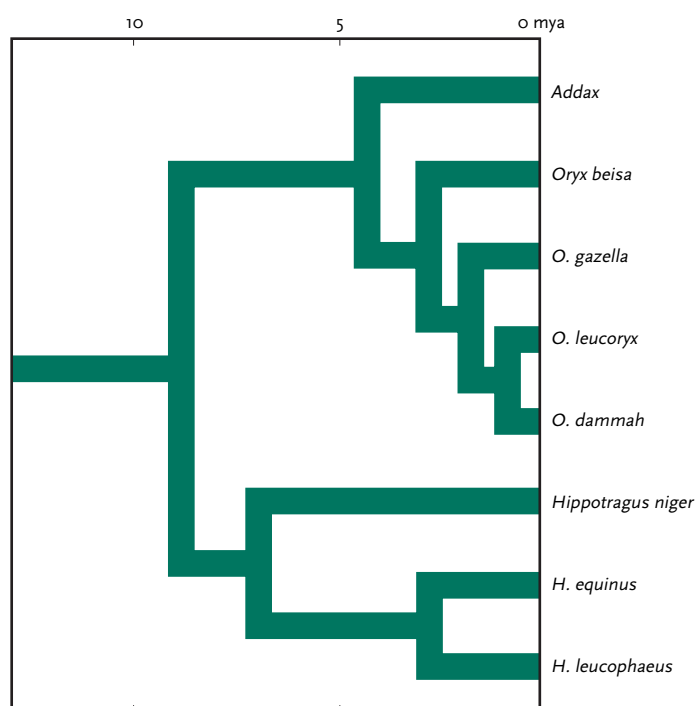
Beisa Oryx *Oryx beisa* skeleton.

Hippotragini are large, barrel-bodied antelopes with long, slender and well-annulated horns, long ears and broad, heavy hooves (with well-developed pedal glands on all four feet). The tribe is represented by six extant African species in three genera, *Hippotragus*, *Oryx* and *Addax*, and a seventh species (the Arabian Oryx *Oryx leucoryx*) in Arabia. Four of these are desert or near-desert species, and the morphology of both fossil and living forms confirms the common ancestry of all hippotragines and the likelihood of an early accommodation to heat, desiccation and a marked trend towards grass-eating (Gentry 1978). False hooves are particularly well developed in the oryxes and the Addax *Addax nasomaculatus*. The coat is sleek, in various shades of tan, white and black and the face is striped rather like a goat or gazelle. The thick, tapering necks and mane earned these antelopes their tribal name Hippotragini, which means 'horse-goat'. Sexes are similar, but males are heavier and have thicker horns. Preorbital glands are absent, although they are vestigial in some species (for example, in *Hippotragus* and Scimitar-horned Oryx *Oryx dammah*); inguinal glands are absent. Pedal glands are present on all four feet. Females of all species have two pairs of inguinal nipples.

The earliest hippotragine fossils are difficult to separate from the earliest caprines and the earliest alcelaphines (Gentry 1978), which is consistent with the three tribes emerging from a common stock during the early Miocene (Hassanin *et al.* 2012). Fossils from India and Europe indicate that hippotragines were once more widespread and might even have penetrated Africa from a Eurasian source (Simpson 1953, Gentry 1978, both authors who allied this tribe with the preeminently Eurasian Bovinae, whereas

Kingdon [1982] associated hippotragines with caprines). Molecular studies have confirmed a relationship with Caprini, but suggest an even closer affinity with the Alcelaphini (e.g. Gatesy *et al.* 1997, Matthee & Davis 2001, Hassanin & Douzery 2003, Hassanin *et al.* 2012). As for geographic and ecological origins, incipient deserts in mid-Miocene North Africa or even outside Africa are possible centres of endemism or evolutionary origin. In as much as caprines almost certainly originated in Asia, there could also be a continental dimension for Hippotragini, fossils of which were first found in Eurasia and might signify a non-African emergence, possibly as the larger-bodied, lowland branch of a proto-Caprine lineage (Kingdon 1982). An early accommodation by ancestral hippotragines to cooler, drier climates (and more grass in their diets) might have begun during a marked trend towards global cooling and increasing aridity in Africa at about 14 mya (Cerling *et al.* 1997a, Retallack 2001, Zachos *et al.* 2001).

Because deserts make considerable demands on the physiology of any animal it is certain that such adaptations were acquired incrementally by the ancestors of Hippotragini. Lineages that have a head-start in any set of favourable adaptive traits tend to retain their advantages in suitable habitats. In the case of other Antilopinae lineages, adaptations to drought were first made by small-bodied animals at around the Oligocene/Miocene boundary, but there is no certainty that the immediate ancestors of Hippotragini were as well suited. Indeed, Kingston & Harrison (2007) have shown that Pliocene Hippotragini were still less than wholly committed to a grass (C4) diet than the contemporary species. None the less, it seems likely

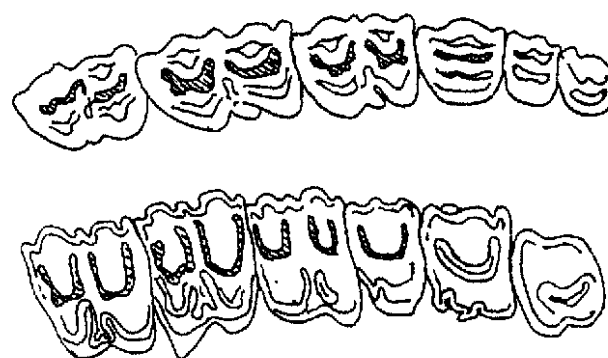
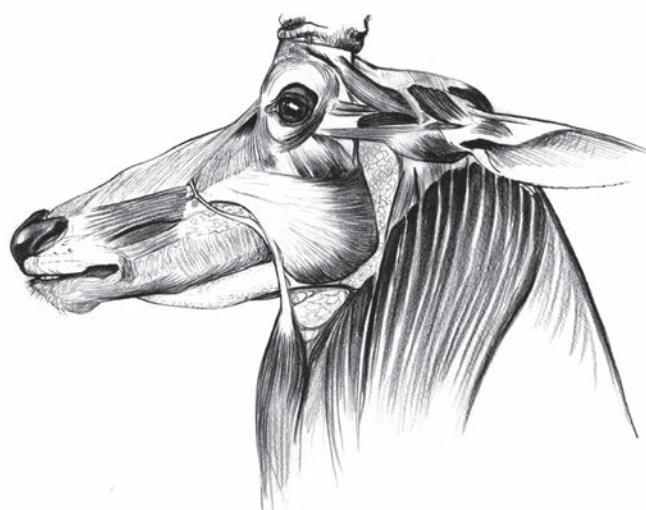


Tentative phylogenetic tree for Hippotragini (modified after Hassanin & Douzery 2003 and Hassanin *et al.* 2012).

that the hippotragine trend towards large-bodied grazers coping with desiccation might have begun in the mid-Miocene, either in North Africa or neighbouring areas of western Asia.

This period well preceded the divergence between *Hippotragus* and *Oryx*, which has long been known to have been early (Kingdon 1982), but molecular studies have now narrowed this divergence down to the mid-Miocene (approximately 10.5 mya) followed by a surprisingly early divergence (8.5 mya) between *Hippotragus niger* and *Hippotragus equinus* (Hernández Fernández & Vrba 2005). By 10.5 mya, hippotragines must have been well established in Africa and a predominantly northern African focus for proto-*Oryx*/*Addax* and a southern focus for proto-*Hippotragus* would seem likely. This was a particularly benign period (also marked by a major exchange of fauna with Eurasia), but a dry south-west African focus would have already existed. It is therefore very interesting that a recently extinct hippotragine, the Bluebuck *Hippotragus leucophaeus*, shared characteristics of both the Roan and Sable Antelopes, but was smaller than either of them. This relic species survived in the Cape of Good Hope, a dry but cool region, until 1779. Its affinities were closer to *H. equinus* than to *H. niger* but it seems to have retained more generalized features than either. It may also be significant that Sable Antelope populations have been found to have the greatest intra-specific genetic diversity known for any mammal (more than 18% of divergent maternal ancestry, Pitra *et al.* 2002), with almost imperceptible differences in general morphology. Perhaps this level of genetic divergence has been influenced by a lineage history of more than 8 million years since the *H. niger* lineage diverged from the morphologically very similar *equinus/leucophaeus* lineage.

It is significant for our broader understanding of hippotragine evolution that the 8+ mya split between *H. niger* and *H. equinus* (if the molecular clock calibration is correct) took place a mere 2 million years after the probable north/south split between proto-*Hippotragus*

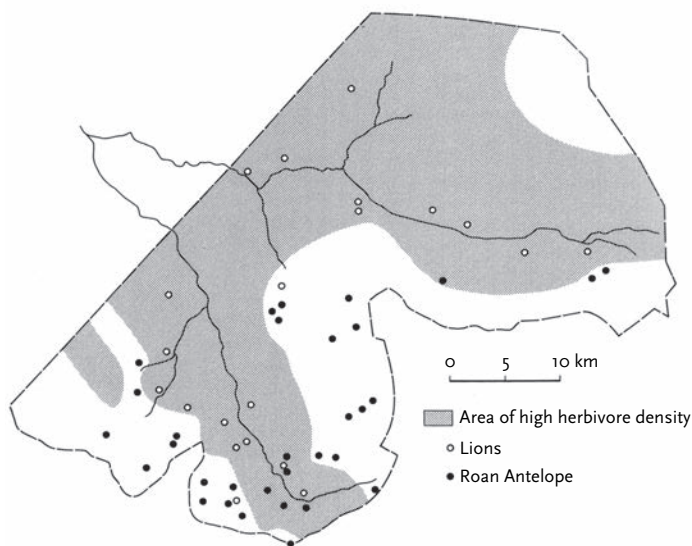


TOP: Facial myology of Sable Antelope *Hippotragus niger*.

ABOVE: Upper-right tooththrows of Scimitar-horned Oryx *Oryx dammah* (above) and Roan Antelope *Hippotragus equinus* (below).

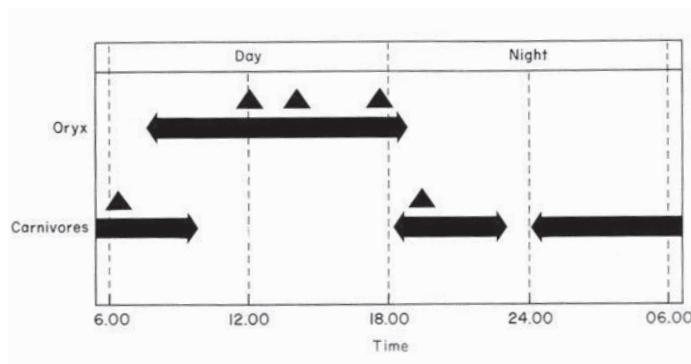
and the proto-*Oryx*/*Addax* lineage. This is consistent with benign conditions having continued over much of tropical and southern Africa during the late Miocene, but this ended with the closing of the Straits of Gibraltar and the beginning of the Messinian (6.5–5.3 mya), when the Sahara Desert first spread over the whole of northern Africa. Before the Messinian was over, at least two hippotragine lineages of true desert antelopes had evolved, but the ancestors of *Addax* were clearly the earliest and best equipped large herbivore to have adapted to the very driest conditions of the Sahara. This left *Oryx* to find a slightly less extreme niche across a wider range of deserts and desert fringes. *Oryx* species differentiated during other periods of intense aridification in the late Pliocene and Pleistocene. Ancestral Gemsboks took advantage of one of these arid periods in the later Pleistocene to colonize south-west Africa by means of an arid corridor that connected Somalia with the Namib and Kalahari deserts.

Today, Hippotragini are broad-spectrum grazers with broad, heavily crenellated teeth, well adapted to cope with tough foods (see Figure above). Their selection of food plants also shows few signs of being particularly specialized. All hippotragines, but most subtly, *Hippotragus* species, have specialized in exploiting zones with an impoverished fauna and flora. Their narrowed choice, even within



Map of Kidepo Valley N. P. showing area of high herbivore density with records of Lions *Panthera leo* and Roan Antelopes *Hippotragus equinus* over 23 months (Kingdon 1982 from data collected by I. Ross).

the tropics, is marked by an attachment to particular localities in which they build up intimate knowledge of large home-ranges (which includes systematic avoidance of areas with numerous predators and competitors). Rigours of the environment are often sufficient to explain why *Oryx* occupy areas with few other herbivores, but this is insufficient to explain why Roan and Sable Antelopes also shun apparently suitable areas in spite of rainfall being relatively high and plant productivity also being good, even if seasonal. Powerful, long-horned hippotragines are certainly not excluded from pastures by aggression from competing species, so their apparently voluntary spatial restriction must be guided by environmental clues that are not readily apparent to a human observer. It has been demonstrated, in several localities, that Roan, Sable and Beisa *Oryx* *Oryx beisa* avoid areas with high densities of other herbivores (Kingdon 1982). Why should hippotragines be limited to small localities or discontinuous vegetation belts in which the density of other herbivores is markedly lower than in neighbouring areas? Early studies of predation revealed that Roan and Sable Antelopes were disproportionately susceptible to predation by Lions *Panthera leo*, even when their numbers were already low (Pienaar 1969a, Harrington *et al.* 1999, McLoughlin & Owen-Smith 2003). Likewise, Beisa *Oryx* time their visits to water



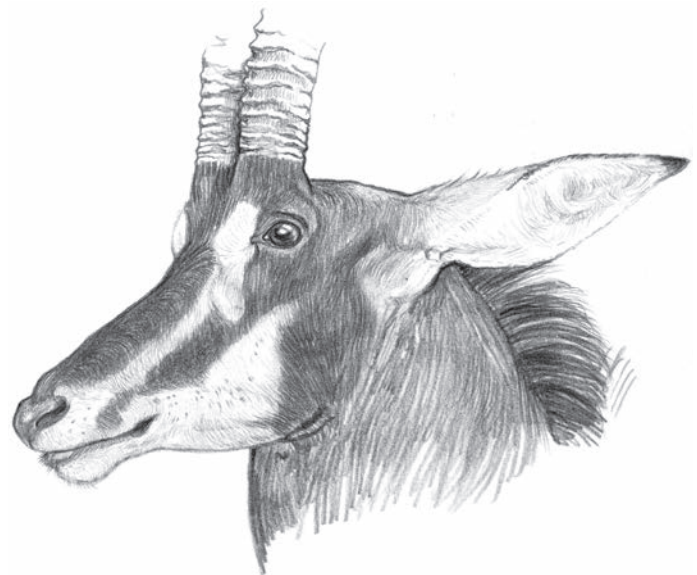
Dry season visits to artificial waterholes in Tsavo N. P. showing temporal separations between Beisa *Oryx* *Oryx beisa* and carnivores. Arrows indicate peaks of visits (from Ayeni 1975).

to coincide with least likelihood of predator activity (Ayeni 1975). In Kidepo Valley N. P., Uganda, Roan Antelopes very seldom intruded into areas with a high density of grazers and, concomitantly, such areas supported numerous Lions. Thus, over a two-year period, Roan consistently preferred drier, better-drained ground where both predators and potential competitors were fewer (see Kingdon 1982). This suggests that predation can be the decisive force in shaping habitat-choice for vulnerable species and that food resources, as well as direct competition for those resources, may be less influential in determining local dispersal over the landscape. The role of predation in selecting for detailed and species-specific patterns of habitat-choice may be operating at both the direct, ontogenetic level as well as at a genetic level. In the first instance, direct attrition as a result of sustained predation could bring about such patterns. In the second instance, survivors could have been selected for their ability to choose habitat in response to a wide variety of environmental clues that, over many generations, effectively reduced their chances, or their offspring's chances, of being taken by a predator.

Behaviour, modes of communication, social structures, ecological dispersal patterns and anatomy have probably all been influenced by an ancestral exposure to dry impoverished habitats. Young animals, once emerged from their 'hider' phase, are exceptionally social and active. They spend much of their time playing or rushing around with stylized gaits, horning objects or mock-fighting. Hippotragines are unusual in that the ♀♀ have horns that are as long as those of the ♂♂. Female social units tend to have closed membership and horns provide them with the means of excluding outsiders from scarce resources and resisting any attempts by ♂♂ to limit their movement or threaten their offspring.

Hippotragines pose special challenges for conservation, not least because of their extensive ranges. As agricultural and 'development' interests continue to excise, diminish, constrict or obliterate conservation areas, many local populations will be extirpated, as has already happened in many areas.

Jonathan Kingdon



Sable Antelope *Hippotragus niger kirkii* adult male.

GENUS *Hippotragus*

Roan and Sable Antelopes

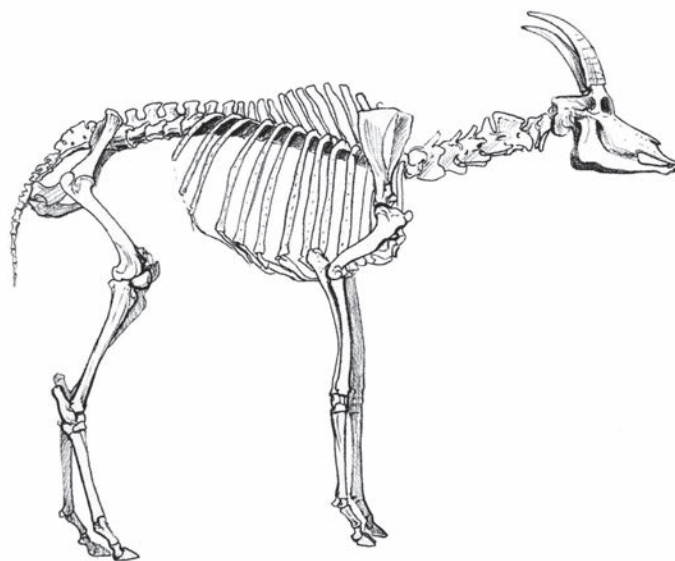
Hippotragus Sundevall, 1845. Öfversigt. Kongl.-Vetensk. Akad. Förhand. for 1845, parts 2 and 3, p. 31.

Polytypic genus with two extant species: the Roan Antelope *Hippotragus equinus*, in both savanna woodlands and grasslands of sub-Saharan Africa, and the Sable Antelope *Hippotragus niger*, confined to the southern savanna regions of Africa and, more particularly, to the miombo (*Brachystegia* dominated) woodlands.

Judging from their relatively abundant representation in Pliocene fossil beds, *Hippotragus*, or its close allies, were more common then than they are today and, supposedly, more ecologically diverse. For example, a very large type of Roan Antelope, *H. gigas*, is known from Sterkfontein and other late Pliocene deposits and a closely related genus, *Praedamalis daturi*, is known from upper Pliocene beds at Laetoli (Kingston & Harrison 2007). These authors have attributed the apparent decline of *Hippotragus* and hippotragines to competition from more recently evolved grazers, notably alcelaphines, but the susceptibility of *Hippotragus* to predation can only have accelerated the decline of this genus and could be the single most significant factor defining the ecological niche of *Hippotragus* within the African antelope spectrum (Kingdon 1982). Roan and Sable Antelopes are subject to less predation in the miombo woodlands they occupy, while also minimizing competition with the diverse array of other large grazers that live in surrounding savannas (see discussion in Sable profile under Adaptations). Likewise, other members of the tribe escape competition by occupying the most arid habitats.

When the carbon profiles of teeth from eight hippotragine specimens from Pliocene beds at Laetoli were compared with those of contemporary *Hippotragus* (and *Oryx*), the living species were confirmed to be unambiguously grass-eaters, with predominantly C₄ diets, whereas the Pliocene species were all much less exclusively C₄ dominated, indicating that they were mixed feeders, relying more on C₃ browse than contemporary species (Kingston & Harrison 2007). That carbon profiles may reflect the gross diet but fail to show up some subtleties of actual foraging patterns should, however, be borne in mind. For example, in his studies of Sable Antelopes in several localities, R. D. Estes (pers. obs.) has found that during the dry season animals eat quite a lot of foliage and forbs. Even so, the findings of Kingston & Harrison (2007) clearly reveal differences that could be interpreted in more than one way: (1) the fact that the fossil samples come from Pliocene populations could be indicative of a wider spectrum of dietary types within *Hippotragus*; (2) a preponderance of C₃ browsers in the Pliocene samples could be taken as evidence for less grass-dominated habitats; and (3) the fact that several tribes of the Antilopinae, notably Hippotragini, Alcelaphini and Reduncini, have all become progressively more and more specialized for grass-eating strongly suggests a phylogenetic dimension. It seems likely that the three explanations may all be correct and are probably not easily disentangled.

Although Roan and Sable Antelopes are the sole survivors of this genus, the now extinct Bluebuck *Hippotragus leucophaeus* was a relict species, which lived along the south-western coast of the Cape Province from about Caledon to Plettenberg Bay (Ansell 1972, Meester *et al.* 1986). Considered by Haltenorth (1963) to be a dwarfed subspecies of Roan Antelope, molecular studies have placed the divergence



Roan Antelope *Hippotragus equinus* skeleton.

between *H. leucophaeus* and *H. equinus* in the region of 3 mya (Hernández Fernández & Vrba 2005). This molecular clock dating suggests that gigantism in the *H. equinus* lineage arose after this divergence. The delicate build, smaller size and peculiar colouring of *H. leucophaeus* could represent morphological responses to the impoverished or chemically peculiar soils of the Cape or they could signify conservative retentions in a formerly more widespread precursor within the ancestral lineage of *H. equinus*. The last individual Bluebuck was shot around 1800, the first African antelope to be hunted to extinction by European settlers (Klein 1974). Detailed reviews of the species are provided by Mohr (1967) and Klein (1974), and see Smithers (1983) for a synopsis.

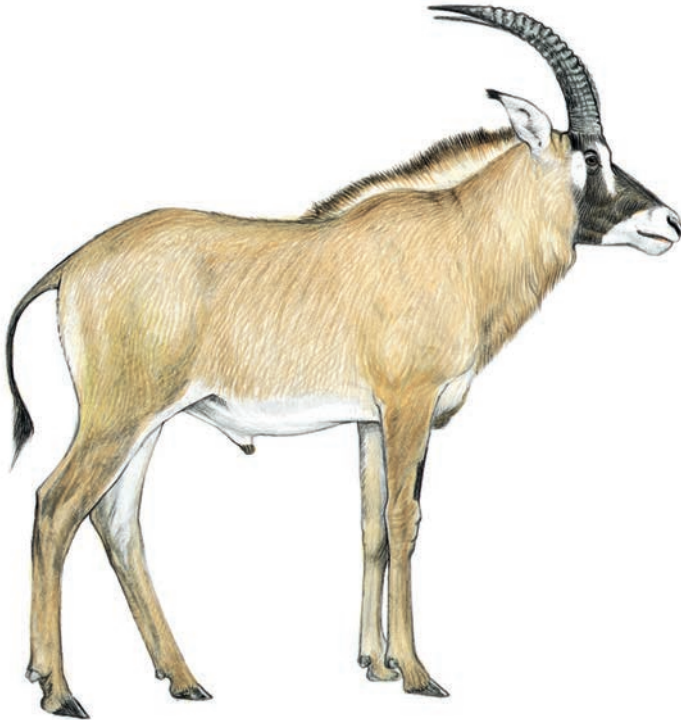
Of special interest are recent revelations of hybridizations between Roan and Sable Antelopes in Kruger N. P., South Africa (Estes & Whyte 2006) and the discovery that several members of the Giant Sable herd in Cangandala N. P., Angola, are clearly hybrids sired by a Roan Antelope bull (Vaz Pinto 2006). A major question, and one that is of crucial importance for the conservation of *Hippotragus* species, is whether Roan–Sable hybrids are viable. While Robinson & Harley (1995) have described such hybrids as viable it is the genetic details that matter. The lineages of *H. niger* and *H. equinus* are estimated to have remained separate in spite of having maintained partially sympatric ranges for at least a portion of their estimated 8.5 million year existence as separate lineages (as determined by molecular clock, Hernández Fernández & Vrba 2005). This reinforces the urgent need to study the genetics of currently known hybrids to determine whether any danger exists that they might contaminate the *H. niger variati* genotype, a potential catastrophe for this very distinctive population that is already on the brink of extinction.

Richard D. Estes & Jonathan Kingdon

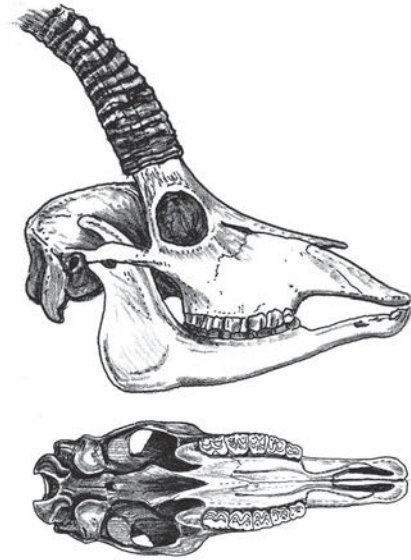
Hippotragus equinus ROAN ANTELOPE

Fr. Hippotrague rouan; Ger. Pferdeantilope

Hippotragus equinus (É. Geoffroy Saint-Hilaire, 1803). Cat. Mamm. Mus. Nation. Hist. Nat. p. 259. 'Inconnue'; now thought to be South Africa, Western Cape Prov., Plettenberg Bay (Grubb 1999). For dating the name to É. Geoffroy Saint-Hilaire, 1803 see Grubb (2001b, 2004, 2005).



Roan Antelope *Hippotragus equinus*.



Lateral and palatal views of skull of Roan Antelope *Hippotragus equinus*.

Taxonomy Ansell (1972) distinguished six subspecies, based primarily on morphology. Matthee & Robinson (1999b) analysed the mitochondrial DNA population structure of 13 samples representing four of Ansell's subspecies (*H. e. equinus*, *H. e. cottoni*, *H. e. langheli* and *H. e. koba*) and confirmed the existence of at least four, well-delineated maternal clades (of course, mtDNA relates only to maternal lineages). Subsequently, Robinson & Alpers (2001) investigated both mtDNA and nuclear DNA patterns (via microsatellites), and greatly expanded the sample database from the earlier work. Their results distinguished several geographically defined genetic groupings. First, there is a clear genetic separation, both mitochondrial and nuclear, of the western African assemblage (based on samples from Benin, Ghana and Senegal). This group is referable to Ansell's *H. e. koba*. Second, three other assemblages are recognized: the north-eastern assemblage with N Tanzania, Kenya and Uganda; the south-eastern assemblage with Zimbabwe, Zambia, Malawi and S Tanzania; and the south-western assemblage with Namibia, Botswana and South Africa (the 'Kruger National Park lineages' are not included in this assemblage because of probable previous genetic mixing with animals from elsewhere). Third, the authors reported that Ansell's *H. e. charicus* (from Nigeria, Cameroon, Chad, Central African Republic) should not be considered part of an eastern and southern clade, nor of the western clade. It seems that there is still no definitive support for a central clade, which *H. e. charicus* and *H. e. bakeri* (from Sudan)

might belong to. With the exception of *H. e. koba* representing the western African assemblage, there is no exact correspondence between Ansell's subspecies and results based on DNA. Other Roan populations form a geographically diverse assemblage with no clear genetic correspondence between subspecies. Alpers *et al.* (2004) distinguish two evolutionarily significant units (per Ryder 1986) for the Roan: the western African group, and a 'rest-of-Africa' group (including *cottoni*, *equinus* and *langheli* subspecies), but noted that more work is needed to clarify the status of *charicus* and *bakeri* subspecies.

Synonyms: *aethiopica*, *aurita*, *bakeri*, *barbata*, *charicus*, *cottoni*, *docoli*, *dogetti*, *gambianus*, *jubata*, *koba*, *langheli*, *rufopallidus*, *scharicus*, *truteri*, *typicus*. Chromosome number: $2n = 60$ (Robinson & Harley 1995). Despite very different phenotypes, and subtle differences in chromosomes (Fordyce-Boyer *et al.* 1995), the Sable *Hippotragus niger* and Roan Antelope are genetically close enough to produce viable hybrids (Robinson & Harley 1995; see Estes & Whyte 2006, Vaz Pinto 2006, and *Hippotragus niger* species profile for further discussion).

Description Large-sized antelope, the second tallest after the Common Eland *Tragelaphus oryx*, and third heaviest after the Common Eland and the Bongo *Tragelaphus eurycerus*. Horse-like body-shape with short, stiffly erect, greyish-brown mane edged with black extending from neck to withers. Pelage uniform sandy-fawn, or light reddish-fawn to grey, or dark rufous. Conspicuous facial mask with striking colouration comprising white parts on cheeks, muzzle, chin and on two oblique and parallel stripes along each eye, contrasted against deep dark black background. Face pattern varies both individually and regionally, with black markings more extensive in

north, and light markings in south. Black patches of facial mask become greyish with age, even turning whitish in very old individuals. Ears long and narrow and terminate in tufts 3–5 cm long. Shoulders higher than hindquarters. Legs long and hooves large; false hooves prominent. Tail reaches heels, with black tassel on lower half. Preorbital glands are vestigial and there are pedal glands on all feet; inguinal glands are absent.

Both sexes have paired ringed horns that rise steeply and curve evenly backwards with diverging tips. Horns strongly ridged for most of the length, but tips are smooth. Sexual dimorphism is weak, ♂♂ being only slightly heavier than ♀♀, while horns, head and neck are slightly thicker in ♂♂ than ♀♀.

Geographic Variation As noted above, six subspecies have been identified by Ansell (1972); however, the validity of some of these subspecies is still in doubt, and recent genetic studies have shown that only the western African subspecies (*koba*) constitutes a genetically separate group from those inhabiting the rest of Africa (Robinson & Alpers 2001, Alpers *et al.* 2004).

Western populations:

H. e. koba: Senegal to Benin. General colour pale tawny, although specimens from West Africa tend to be reddish; forehead chestnut in both sexes.

Central populations:

H. e. charicus: E Nigeria, Cameroon, Chad and Central African Republic. No discernible differences with *H. e. koba*.

H. e. bakeri: Sudan. Browner than the other races; forehead blackish in ♂♂, reddish-brown in ♀♀; chest pale, as are ears and front of pasterns.

Eastern and southern populations:

H. e. langheldi: S Sudan, Ethiopia, N DR Congo, Uganda, Kenya, Tanzania, Rwanda, Burundi. General colour pale reddish; forehead reddish-brown in both sexes.

H. e. cottoni: S DR Congo, Angola, Zambia, C and N Malawi, N Botswana. No discernible differences with *H. e. equinus* (see below), except they are redder than other specimens.

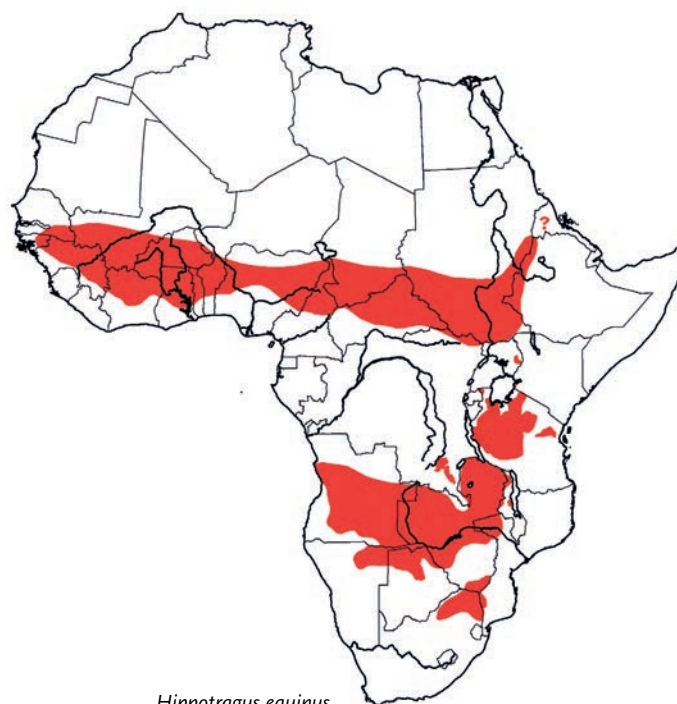
H. e. equinus: Zimbabwe, South Africa and Mozambique. General colour greyish, with forehead black in both sexes.

Similar Species

Hippotragus niger. Sympatric through most of the southern savannas.

These two grazing species tend to remain in different vegetation types, the Sable being a species less of grassland/tree-savanna and more of open miombo woodland. The Sable is smaller on average, characterized by sexually dimorphic colouration – deep black pelage in adult ♂♂ (sorrel to chestnut in ♀♀ and young); horns are longer, commonly exceeding 1 m.

Distribution Endemic to Africa. Formerly one of the most widely ranging of African antelopes, found throughout savanna woodlands and grasslands of sub-Saharan Africa, but now greatly reduced in range (East 1999), though remarkably still locally abundant in parts of West Africa (Poché 1974). Roan were probably present in Egypt until 2000 BC (Osborn & Osbornová 1998).



Historical Distribution In West Africa, Roan Antelopes ranged from C and S Senegal, Gambia, S and E Guinea-Bissau and S Mauritania east through SW Mali, N Guinea, N Côte d'Ivoire, Burkina Faso, Ghana, Togo, N and C Benin, SW Niger, and C and N Nigeria. From there, they ranged eastwards through N Cameroon (from L. Chad to the Adamaoua Plateau), S Chad, Central African Republic and N DR Congo and S Sudan to the western lowlands of Ethiopia in the Sudanian region between latitudes 15 and 19°N; they ranged as far north as the south-western savannas of Eritrea. Southwards they ranged through NE and SW Uganda, S Kenya, Tanzania, NE Rwanda and Burundi to Angola (except in Cabinda and the arid south-west), S DR Congo, NE Namibia, Botswana (where older records evidence that they formerly occurred much further south than they do today; Smithers 1971) and Mozambique (East 1999). In South Africa, an observation dating to 1778 suggests that a population of Roan Antelope formerly inhabited the Western Cape in the vicinity of Plettenberg Bay (consistent with the fossil record), but were likely extirpated from the region during the late 1700s (Faith 2012). In recent times, their range has extended only as far as the bushveld/lowveld regions of the North West, Limpopo and Mpumalanga Provinces, and the Northern Cape.

Current Distribution The range of the Roan Antelope has contracted greatly since the beginning of the twentieth century, and they have been eliminated from parts of their former range surviving mainly in and around protected areas as well as in non-protected areas with low densities of people and livestock (East 1999). A striking feature in the distribution of the Roan Antelope is a clear contrast between West and central Africa, where it remains one of the most common antelopes, and East and southern Africa where it is one of the rarest.

In West and central Africa, its range has contracted in the face of hunting and habitat degradation although the species remains locally common. On one hand, Roan Antelopes have disappeared

from areas lying on the fringe of the typical habitat such as Mauritania, Gambia (where they now occur only as vagrants in the east), N Sierra Leone, N Liberia, C Mali and C Niger; on the other hand, they remain locally abundant in the heart of typical habitat such as SE Senegal, SE Burkina Faso, N Benin, SW Niger, N Cameroon, SE Chad and N and E Central African Republic (East 1999). Dowsett & Dowsett-Lemaire (1989) give Roan Antelopes as occurring in the savanna of Congo, based on records from two localities – Les Grandas and Lefini; however, the species is certainly no longer recorded there.

In East and north-east Africa, the Roan Antelope is extinct in Eritrea and in Burundi, but still survives in W Ethiopia (e.g. in Gambella N. P.) and in SW and SE Sudan (J. O. Heckel pers. comm.). In Kenya, Roan Antelopes are present only in Ruma N. P., where they are entirely surrounded by cultivation (East 1999). In Uganda, East (1999) reported them surviving only in Pian-Upe G.R. They are still widely present, albeit patchily, in Tanzania (notably Biharamulo, Moyowosi, Kigosi, Katavi, Rukwa, Rungwa). In Rwanda, they are restricted to Akagera N. P., although they have been in perpetual decline since the park's boundaries contracted (Williams & Ntayombya 1999, Apio & Wronski 2011).

In southern and south-central Africa, Roan Antelopes are still widely distributed in Zambia, where they survive mainly within protected areas and game management areas, including the Luangwa Valley and Kafue N. P. In Angola, there is limited information, but they are reported to survive in some areas (P. Vaz Pinto pers. comm.). In Malawi, they are now confined mainly to four protected areas in the north and south, with the largest population in the small Nyika N. P. (East 1999). In Mozambique, there are two locations with very limited populations of Roan Antelopes: in the hunting areas of western Tete Province and in Great Limpopo Transfrontier Park (East 1999); there are also plans to reintroduce them to Gorongosa N. P. In Namibia, the present 'natural range' of the Roan Antelope includes the East and West Caprivi Strip, Khaudom G. R. and Nyae Nyae Communal Conservancy. They were introduced to Etosha N. P. in 1970 and to Waterberg Plateau Park in 1975. However, the Kaross area in the west of Etosha, where the main Roan population is located, falls below the 300 mm rainfall isohyet and the population has not thrived (Martin 1983). Roan Antelopes are today confined to the northern savannas of Botswana, while in Zimbabwe they have disappeared from the Highveld but are still present in limited numbers in the Hwange ecosystem, in the mid-Zambezi valley and in patches of the lowveld (East 1999).

The Roan Antelope is among the most threatened antelopes in South Africa. The species still survives in the north of Kruger N. P. (but see later), and has been reintroduced elsewhere, including Marakele N. P. in Limpopo Province. A breeding population of Roan is maintained in Percy Fyfe N.R. in Limpopo Province. Although there is no evidence that Roan Antelopes formerly occurred in KwaZulu-Natal, they have been introduced to reserves such as Weenen and Karloof Nature Reserves (Rowe-Rowe 1994). The indigenous population that formerly occurred in NE Swaziland is extinct, but Roan Antelopes have since been introduced to Mkhaya G. R. (Monadjem 1998).

Habitat The Roan Antelope is usually present in dystrophic (nutrient-poor) savannas, such as miombo woodland, and inhabits

gently undulating terrain of open woodlands and savannas with long grass, low tree density and canopy cover (Pienaar 1963, Joubert 1976, Wilson & Hirst 1977, Dörgeloh 1998a, b, Perrin & Taolo 1999b). Cover of high grasses and woody plants plays an important role for both grazing and calving (Taolo 1995, Dörgeloh 1998a). Calving ♀♀ select habitats with long grass and woody plants, which provide shelter for the newly born calves (Allsopp 1979, Dörgeloh 1998b). The highest densities of Roan Antelopes are found in areas with an average rainfall of around 1000 mm, where soils are mainly infertile and support grazing of low quality. They tend to avoid areas of short grass and woodland where the trees form a closed canopy or where the bush forms thick, closed stands (Heitkönig & Owen-Smith 1998). Permanent water is important. Shrub encroachment seems to have a negative effect on Roan Antelopes (Joubert 1976, Wilson & Hirst 1977), even though they tolerate low shrub growth (Ben-Shahar 1990).

In Comoré N. P., Côte d'Ivoire, Roan Antelopes are notably present in woodlands during the wet season. They do not cover great distances, but range over different types of altitude and vegetation depending on the season. At the beginning of the wet season they leave the plains bordering the rivers and migrate towards higher areas, where they are frequently observed in the open woodlands (Steinhauer-Burkart 1987). In Bouba Ndjida N. P., N Cameroon, situated in the savanna woodland belt and receiving an average annual precipitation of 1200 mm (falling mainly from May to Oct), Roan Antelopes occur in *Terminalia laxiflora* wooded savanna. The trees of this habitat do not exceed 3 m in height and grass cover consists mainly of tall perennial Andropogoneae. These grasses grow up to 3 m high during the wet season and constitutes the principal forage for the majority of large herbivores. Roan occur to a lesser extent in the *Isoberlinea doka* savanna woodland, but seem to avoid fringing forest (Van Lavieren & Esser 1979). In Bénoué N. P., Cameroon, Roan Antelopes prefer *Burkea-Detarium* open savanna rather than *Isoberlinea* woodland and *Anogeissus* riparian forest during the dry season. During the wet season, *Burkea-Detarium* open savanna is still the preferred habitat, but they also occur in *T. laxiflora* and *T. macroptera* open savannas (Stark 1986b). In Zakouma N. P., Chad, Roan often occur in the Combretaceae wooded savannas (52% of observations) or in the *Acacia seyal* savannas. They are less frequently observed in more open areas (Dejace *et al.* 2000). In Kenya's Lambwe valley, Allsopp (1979) observed that Roan selected open *Themeda/Setaria* grassland, and never observed them in *Hyparrhenia* grassland or in dense continuous thickets.

In the Waterberg region in Limpopo Province, South Africa, part of the moist savanna biome dominated by woody plant species such as *Terminalia sericea*, *Burkea africana* and *Combretum* spp. and characterized by abundant and perennial water-courses and rivers, Roan Antelopes occupy an area of flats with sandy acidic soils and low rock cover. They also venture onto rocky slopes further away from water resources (Ben-Shahar 1990). In Kruger N. P., favoured habitat is on slightly undulating land consisting of heavy clay soils derived from basalt; hillier areas on clay-loam soils derived from dolerite are also used to a lesser extent (Joubert 1976).

Abundance East (1999) estimated the total population of Roan Antelopes at about 40,000, although correcting for undercounting bias in aerial surveys gives a slightly higher estimate of 76,000 animals,

of which 60% occur in and around protected areas. According to East (1999), the largest populations survive in Burkina Faso (>7370), Cameroon (>6070), Zambia (>5080) and Tanzania (>4310). Winter (1997) noted that more than 50,000 Roan Antelopes survived in S Sudan in the 1970s, including 4100 in the Jonglei region and 2000 in the Boma region. Spinney (1996) commented that Roan Antelopes in Sudan survived locally in relatively stable numbers. During recent surveys conducted during the dry season of S Sudan, only 21 individuals were counted in Southern N. P., with a small group sighted in the Jonglei and two other sightings in Boma N. P. (Fay *et al.* 2007).

Historical accounts indicate that the Roan Antelope was extremely rare in certain localities but could reach considerable densities in areas where environmental factors were favourable, for example in parts of West Africa (Poché 1974). Densities vary greatly across their distribution, but the average density is quite low (Wilson & Hirst 1977). In natural conditions, the density does not exceed 4/km², even in areas where nutrients are not deficient (Wilson & Hirst 1977). But under intensive management, Roan Antelopes may be stocked at high densities of up to 20/km² (Dörgeleh *et al.* 1996). For example, in Nylsvley N. R. (South Africa) density could reach about 8/km² (Dörgeleh 1998b). Effective management could explain why, in the 18 years preceding 1992, the Roan population in South Africa grew at approximately 1% per year. The result of the national inventory in 2001 was 1237 animals.

Aerial surveys provide estimated population densities of 0.007/km² in Kruger N. P. (Kröger & Rogers 2005), 0.2–0.6/km² in Pendjari N. P. (Benin) (Chardonnet 1995, Rouamba & Hien 2002), and 0.8–1.5/km² in Pama–Arly–Singou (Burkina Faso) (Lungren *et al.* 2004). Aerial surveys of Arly N. P., where the species is common, have produced densities of 1.1/km² (Barry & Chardonnet 1998) and 0.34/km² (Bouché *et al.* 2004). Aerial surveys of Bouba Ndjida N. P. gave a density between 0.2 and 0.6 herds/km² with a mean herd size between 4.2 and 6.9, producing a total population size estimated at 4114 (Van Laveren & Esser 1979).

Ground surveys provide densities ranging from 0.03 to 0.10/km² in areas like Manda N. P. (Chad) (Chai 1996), Comoé N. P. (Fischer 1996, Fischer & Linsenmair 2001a) and Dinder N. P. (Sudan) (Hashim *et al.* 1998). In Waza N. P., where Roan densities have been monitored over several decades, they declined from 2.4/km² (1960s, following 20 years of above-average rainfall and effective protection) to 0.7/km² (mid-1990s, following droughts and transmission of disease by livestock) to 0.2/km² (early 2000s, following increased poaching) (Scholte *et al.* 2007). In Konkoumbouri Hunting Area (Burkina Faso), density was 3.9/km² (Bouché & Lungren 2004), which is considerably higher than the density of 0.27/km² recorded in the same area based on aerial surveys (Bouché *et al.* 2004).

Adaptations Roan and Sable Antelopes share common arid-adapted ancestors with other hippotragines. These ancestors came from North African or western Asian biomes (Kingdon 1982) and probably came to occupy both northern and southern savannas following a dry period in the mid-Miocene (Hernández Fernández & Vrba 2005). Since semi-arid savannas were already occupied by several ungulate species, it is possible that *Hippotragus* had to adapt themselves to broad-leaved deciduous woodlands and grasslands of the mesic savanna that were freer from large herbivore competitors.

Changes contingent on latitudinal shifts probably had consequences for their social organization: territoriality in ♂♂, traditional home-ranges for herds of ♀♀, spatial segregation of bachelor ♂♂. Habitat changes were accompanied by morphological changes such as lengthening of the head and an increase in gape and the incisor–molar diastema, changes presumably well adapted for feeding on tufted perennial grasses. It has been suggested that the Roan Antelope's occupation of large home-ranges, dependence on water and relatively slow gait might all be symptomatic of derivation from a still larger, giant-sized ancestral stock (Kingdon 1997). Roan kept the typical hippotragine ability to walk long distances daily, which allows them to reach remote feeding grounds beyond the reach of most competitors; furthermore, being less water-dependent than many potential competitors, such as Kobs *Kobus kob*, they have access to good quality forage further away from water and away from other herbivores (with the exception, of course, of the Savanna Elephant *Loxodonta africana*).

Foraging and Food Roan Antelopes are considered to be predominantly grazers, taking only a small amount of browse. In their review of the dietary preferences of African bovids, Gagnon & Chew (2000) classified Roan as variable grazers, while studies involving stable carbon isotope analysis (from southern Africa only) are consistent with observations (e.g. Joubert 1976, Heitkönig 1993) that suggest that grass predominates in their diet (Sponheimer *et al.* 2003b). However, although Joubert (1976) found that browse did not contribute significantly to the diet (less than 5% of total intake), several other authors have mentioned that browse could play an important role during critical periods of the year, especially in the late dry season (Poché 1974, Wilson & Hirst 1977). In Zimbabwe, Child & Wilson (1964) showed that Roan Antelopes used to feed from browse plants such as *Diplorhynchus mossambicensis* (leaves), *Capparis tomentosa* (leaves), *Piliostigma thoningii* (fruit), *Diospyros kirkii* (fruit), *D. mespiliformis* (fruit) and bamboo (flowers). Schuette *et al.* (1998) studied the diet of Roan Antelopes in West Africa by means of microhistological analysis of faeces and found that Roan Antelopes switched from being predominantly grazers (>95% grass) in the wet season to mixed feeders (<50% grass) in the dry season.

Several studies, especially in South Africa, have shown that Roan Antelopes are quite selective, feeding only on a restricted number of grass species that represent as much as 90% of the year-round diet (e.g. Joubert 1976, Wilson & Hirst 1977, Heitkönig 1993, Dörgeleh 1998a,b, Perrin & Taolo 1999a), and remain so even under stressful conditions (Wilson & Hirst 1977). Studies in Kruger N. P. have found that these antelopes appear to be ecologically separated from common grazers where they feed selectively on tall grasses growing in the drainage line grassland during the critical dry months (Knoop & Owen-Smith 2006). Roan usually prefer inflorescent tips of mature grasses ranging in height from 5 to 30 cm, and favour taller and ranker perennial grasses. In Kruger N. P., Roan Antelopes selectively graze patches of nutrient-rich grasses (Wilson & Hirst 1977, Senft *et al.* 1987, in Kröger & Rogers 2005) in the boundary between savanna and wetland (Kröger & Rogers 2005). The greatest contributor to the diet throughout the dry and wet seasons is *Themeda triandra* (Joubert 1976). Other grass species most consumed in the dry season are *Eragrostis curvula*, *Melinis* spp., *Panicum maximun* and

Sporobolus fimbriatus, and during the wet season, *Hyparrhenia* spp. and *Heteropogon contortus*. Roan Antelopes would occasionally browse on trees and shrubs, particularly *Colophospermum*, *Grewia*, *Thylacium*, *Lonchocarpus* and *Kigelia*.

In the Nylsvley N. R., in South Africa's Limpopo Province, a spatial segregation exists between the breeding herd and bachelor ♂♂. During the wet season (Oct–Mar), breeding herds select the lower floodplain and the *Eragrostis pallens*–*Burkea africana* savanna where the mean grass height is the highest (around 45 cm). Selection of flood-plains may be partly explained by the fact that they contain higher levels of sodium than any other plant community (Dörgeleh 1998a). However, the drying of the floodplain in autumn with a corresponding decrease in forage quality and availability forces the Roan Antelope to move away. During winter (dry season, Apr–Sep) breeding herds select the *Aristida bipartita*–*Setaria sphacelata* grassland where there are large amounts of forage and a high calcium content for pregnant and lactating ♀♀ (the southern winter is the calving and lactating season, a period when ♀♀ have to maximize their intake of quality food to avoid calcium deficiency). Adjacent grassland dominated by *Tristachya rehmannii*–*Digitaria monodactyla* and the *Rhus leptodictya*–*Combretum apiculatum* complex were selected to a lesser extent (Dörgeleh 1998a). *Eragrostis pallens*–*B. africana* savanna is utilized to a large extent and may serve as a calving area in winter where the long grasses (mean = 48.3 cm) and woody plants (mean = 45.4%) provide cover for the newborn calves. Bachelor ♂♂ usually occur in suboptimal habitats, consisting of plants of low forage quality and high woody plant densities (Allsopp 1979, Esser 1980, Dörgeleh 1998a). Bachelor ♂♂ use the flood-plain in both summer and winter, and *Cymbopogon plurinodis*–*Combretum apiculatum* communities during winter (Dörgeleh 1998b). Differential utilization of plant communities between seasons as a consequence of reduced forage quality and palatability during the dry season has also been recorded in Dinder N. P. (Sudan) (Hashim 1987) and in Nyika N. P. (Malawi) where Roan leave the central plateau for miombo woodlands and valleys (though some remain when highly nutritive forage is maintained through dry season patch burning; Munthali & Banda 1992). On Nylsvley, Roan (both social groups) were highly selective of burnt areas, especially the flood-plain and the *A. bipartita*–*S. sphacelata* grassland, although spatial segregation between social groups could still be observed to some extent. The flood-plain showed the highest increase in percentage nitrogen, while the *A. bipartita*–*S. sphacelata* grassland and the *A. bipartita*–*S. sphacelata* savanna had the highest increase in calcium and phosphorus, respectively, when burnt (Dörgeleh 1998a,b).

Studies in Kruger N. P. and Nylsvley N. R. demonstrate the remarkable contrast that exists between the numerous studies on 'rare Roan' in southern Africa, and the very few studies on 'common Roan' in West and central Africa. In West and central Africa, the diet of the Roan Antelope might well comprise a slightly higher share of browse than documented in East and southern Africa, as suggested by the studies of Schuette *et al.* (1998) and De Stefano (2004). Interestingly, fewer browsers inhabit the West and central African regions, so that Roan Antelopes have comparatively less competition for browse than for grazing in these particular regions.

Limiting factors for Roan Antelopes are related to habitat quality, availability and utilization. Animals characteristically spend several

days at a time within an area of less than 5 ha (activity area) before moving on to another small section within their overall home-range. The activity areas of these antelopes vary from one month to another, the surface of which apparently bear little relation to the size of the herd using the area but is probably more closely related to the degree of food availability, food palatability and distance to water (Wilson & Hirst 1977).

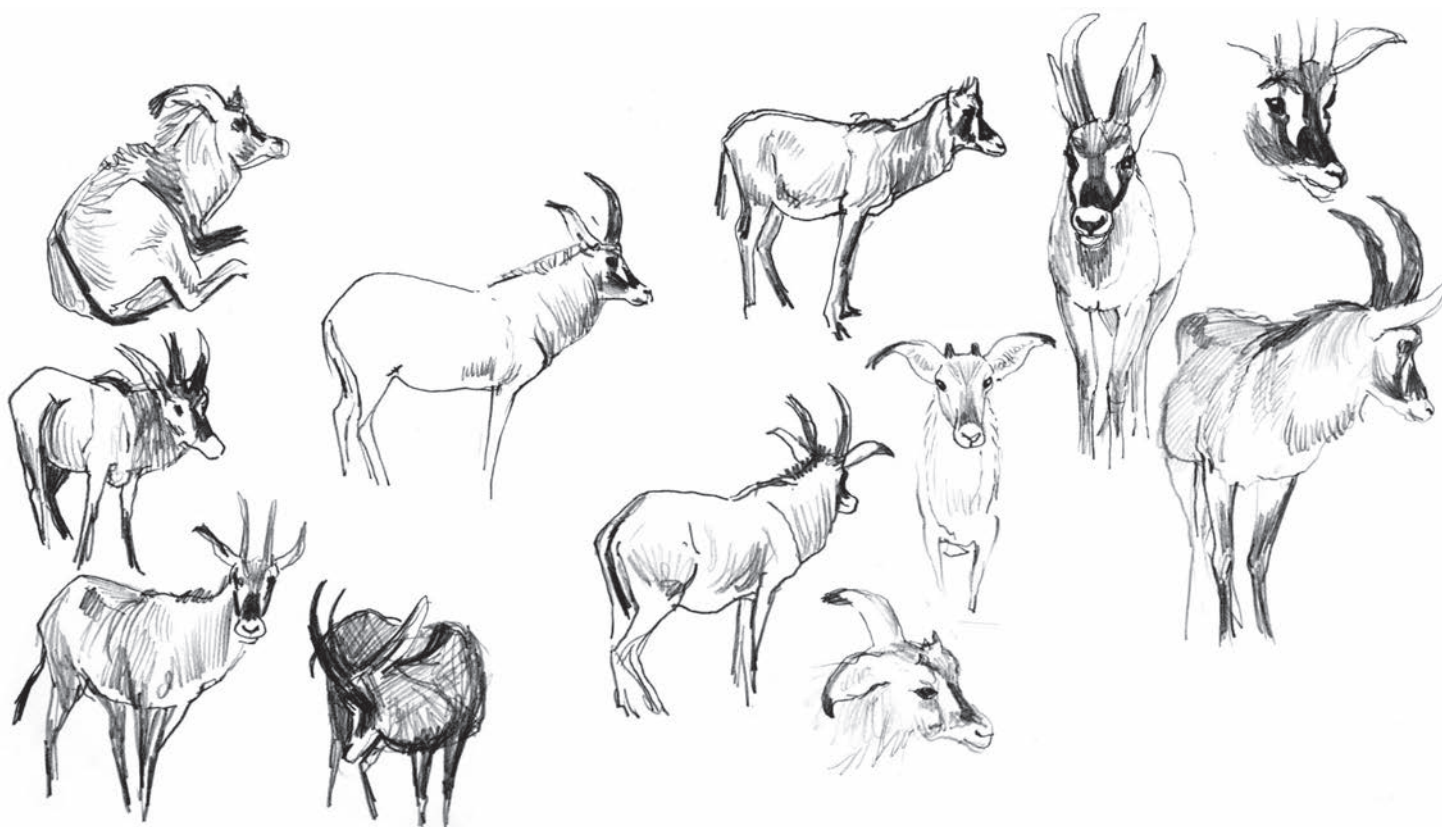
By means of radio-tracking in W Transfontier Park, Cornelis *et al.* (2006) recorded Roan Antelopes making large daily movements (15–20 km), even where poaching pressure was low. Herds graze in the early morning and late afternoon and are for the most part inactive during the remainder of the day, ruminating, resting and socializing. They commonly drink in the late morning, but introduced animals in a park outside their natural range were frequently seen at water at any time of the day, though mainly towards mid-day (Perrin & Taolo 1998). Animals usually kneel while drinking, and display a preference for drinking on open banks. Similarly, ruminating and resting occurs in the shade of a tree preferably in open areas. Like Sable, Roan Antelopes regularly visit salt or mineral licks. Child & Wilson (1964) recorded an unusual observation of two Roan Antelopes feeding on *Equisetum* sp. in water 0.6 m deep, which, to reach, required the antelopes to totally immerse their heads (and see Gewalt 1987).

Social and Reproductive Behaviour The Roan Antelope is regarded as a semi-gregarious, generally sedentary, species. The social organization is dominated by a ♂, with nursery herds typically comprising 4–18 ♀♀ and young. In Comoé N. P., the average size of the herd varies depending on the time of year: at the beginning of the dry season (Oct–Dec) the herds average 2.5 and at the beginning of the wet season (Apr–Jul) 5.6 (Mühlenberg & Roth 1985). When density is high, herds reach about 20–25 individuals, and sometimes even up to 60 animals. Temporary aggregations of 150 animals are also known (Kingdon 1982).

The dominant ♂ evicts young ♂♂ at 2.5–3 years of age, and sometimes also ♀♀ as they reach sexual maturity. Evicted young ♂♂ either become solitary or form bachelor groups of two to more than 20 individuals, until they become socially mature at 6–7 years old. At this time ♂♂ then either remain solitary or are integrated into stable groups after taking over a female herd or ousting a dominant ♂. Lone ♂♂ remain outside of the main home-range, although occasionally an adult ♂ can temporarily join a splinter group of ♀♀ (Joubert 1970).

The alpha-female plays a leading role in initiating group activities such as feeding, drinking, moving and fighting, and even the dominant ♂ will follow her. This can lead to friction between the dominant ♀ and the next ♀ in line, which may gradually drift away from the main herd with her subgroup. These subgroups and the ejected young ♀♀ that form new herds assist dispersal within a population.

Males exhibit territorial behaviour (Joubert 1976). At low densities, Roan Antelopes are not strictly territorial, since a single ♂ can only defend an area of 200–600 m diameter around a mobile herd of cows. Allsopp (1979) studied two groups in the Lambwe valley, one of which comprised 45 individuals and the other 36, with home-ranges of 15–20 km² and 25 km², respectively, and which were probably the size of the male's territory. These results differed from those of Child & Wilson (1964) and Joubert (1970)



Roan Antelope *Hippotragus equinus*.

in southern Africa, where home-ranges were estimated at 48 km² and 60–100 km², respectively. In Waterberg N. P., Namibia, Erb (1993) estimated the home-range size of an introduced population at 48 km² for two clans and 12 km² for one ♂, using the minimum convex polygon method. Opinions differ on the degree to which home-ranges overlap. According to Joubert (1976), the various herds' home-ranges do not overlap, and marking is accomplished by both visual and olfactory means. Allsopp (1979) noted that mixing between herds may occur. Radio-collared Roan Antelopes in W Transfontier Park exhibited some temporary mixing of herds and overlapping of home-ranges (Cornelis *et al.* 2006).

Mating behaviour is initiated by the herd's dominant ♂ and includes dominance postures, sniffing the vulva area, an olfactory test of the female's oestrous status (flehmen), leg lifting (laufschiag) and mounting if the ♀ is receptive. Mounting duration is short and occurs many times before successful intromission. Low intensity fights are common within the bachelor herd and consist of head-long rushes, which usually stop just short of contact, but sometimes results in a clash of horns, followed by sparring from a kneeling position (Allsopp 1979). Such intra-specific aggression may lead to some fatalities (Wilson & Hirst 1977).

Females leave the herd to calve, but usually return the day after parturition. Newly born calves are hidden in dense vegetation and may be as far as 2 km from the herd for an extended period of up to six weeks (Wilson *et al.* 1974). This is a period of high mortality. The calf is almost odourless, effectively camouflaged and remains nearly motionless. The calf is left unattended throughout the day,

except in the early evening and early morning hours when suckling occurs (Beudels *et al.* 1992a). Most of the calves are weaned while food availability is declining (Beudels *et al.* 1992a). Communication between mother and calf is both visual and auditory, with slight but regular sharp shrills being emitted by both. Calves are kept in isolation for up to 4–6 weeks after which they join a group of a similar age within the main herd. When alarmed, these juvenile groups stay together, following the leadership of a single ♀ rather than joining their own mothers.

Roan Antelopes tend to avoid large concentrations of other grazing species (Joubert 1976), probably because they are susceptible to local competition (Wilson & Hirst 1977, Brown & Allen 1989, Harrington *et al.* 1999, Kröger & Rogers 2005). However, this may not be the prime reason, and Kingdon (1982) suggests that Roan Antelopes are absent from areas of high herbivore density because of the selective preference for these antelopes by more numerous predators. Large herds of Common Wildebeest *Connochaetes taurinus*, African Buffalo *Syncerus caffer* and Plains Zebras *Equus quagga* (their most likely ecological competitor), in particular, can keep the grass low and unsuitable for Roan Antelopes (Joubert 1976). For example, the Roan population of Kruger N. P. was almost driven into extinction in the early 1990s by reduction of grass cover through overgrazing (see Conservation) and in Kidepo Valley N. P. it was found that the distribution of Plains Zebras and Roan Antelopes rarely overlapped (Kingdon 1982). However, they are sometimes found associating with other grazers. For example, in Pendjari N. P., as

well as in W Transfrontier Park, Roan Antelopes may be associated with Western Hartebeest *Alceaphus buselaphus major* or Korrigums *Damaliscus lunatus korrigum* (Delvingt *et al.* 1989). In Central African Republic, Roan Antelopes may be seen with Lelwel Hartebeest *A. b. lelwel* or Giant Elands *Tragelaphus derbianus*, especially at saltlicks. Roan Antelopes may also be associated with smaller herds of oryx, Common Wildebeest, African Buffalo, Plains Zebras and Ostriches *Struthio camelus* in other regions.

Reproduction and Population Structure Roan Antelopes could be regarded as prolific breeders based on their reproductive potential (one calf every 10–10.5 months) (Joubert 1976). Single calves, with a birth-weight of 12–18 kg, are born after a gestation of 268–286 days (mean = 270) and 2–3 weeks after parturition ♀♀ enter a postpartum oestrus (Wilson & Hirst 1977). Females first conceive at two years of age (Joubert 1976). The calving season is not well defined: in Akagera N. P., a peak in births was recorded in May/Jun and Dec/Jan at the end of both wet seasons (Beudels *et al.* 1992a); in Central African Republic, the peak occurs in Apr and Dec (Delvingt & Lobão Tello 2004); and in South Africa's Limpopo Province most calves are born Jan–Mar (Wilson 1975).

Joubert (1976) counted 42 calves per 100 adult ♀♀ in Kruger N. P. where recruitment was calculated as 0.12 sexually maturing ♀♀ annually entering the breeding segment of the population. Also in Kruger N. P. the cow : calf ratio was about 0.5 while the population was stable (Mason 1990b), although this decreased to 0.42 on average between 1983–93 when the population was declining (Harrington *et al.* 1999), with an average adult female survival of 0.73 during the same period of decline (Harrington *et al.* 1999). In Nylsvley N. R., Dörgeloh (1998b) estimated recruitment at 0.33 sexually mature ♀♀ per breeding adult ♀♀. In Percy Fyfe N. R., Wilson *et al.* (1974) calculated a birth rate ranging between 0.32 and 0.47 calves per female per year (mean = 0.39). Factors influencing birth rate are essentially related to the quality and quantity of food.

In Akagera N. P., the highest juvenile mortality occurs at the beginning of each wet season when stable groups are most fragmented, and consequently when juveniles unaccompanied by adults may therefore be most vulnerable to predation (Beudels *et al.* 1992a). These authors calculated an annual calf survival of 0.89 for ♀♀ and 0.78 for ♂♂. In Nylsvley N. R., the mortality rates were estimated around 77% for calves aged 0–6 months, 70% for calves 6–12 months and around 81% for calves aged 0–12 months (Dörgeloh 1998b). In Kruger N. P., Joubert (1976) estimated a mortality rate of 67.5% during the first few weeks of life. Both studies showed no differences in mortality between sexes during the first two years. In Nylsvley N. R., the density and diversity of predators are not as high as in Kruger N. P., so the high mortality of calves during the first weeks may be due to other causes such as nutritional stress during winter when calves are born, or cytauxzoonosis, a disease caused by a blood parasite that causes high mortality among stressed Roan Antelopes (Wilson & Hirst 1977). Wilson *et al.* (1974) calculated a calf mortality rate of 80% within the first 12 weeks after birth in the Percy Fyfe N. R. and in other provincial reserves of N South Africa. Population viability analysis carried out on Nylsvley N. R. showed that newborn calf mortality was the most critical population parameter influencing extinction risk, especially in female calves (Dörgeloh 1998b).

In Kruger N. P., Joubert (1976) calculated male : female sex ratio among calves at 1 : 1.13 and 1 : 1.58 among yearlings. Mortality affects more subadult ♂♂, which should result in a biased adult sex ratio in favour of ♀♀. For example, the Roan Antelope population of Nylsvley N. R. presents an adult sex ratio of 1 : 1.89 (Dörgeloh 1998b), which is quite similar to the adult sex ratio found by Joubert (1976) in Kruger N. P. (1 : 1.8), although Munthali & Banda (1992) recorded an adult sex ratio of 1 : 0.83 in Nyika N. P.

Captive Roan Antelopes have lived to more than 25 years (Weigl 2005), although longevity is certainly shorter in the wild.

Predators, Parasites and Diseases The most significant predators are Lions *Panthera leo*, Spotted Hyaenas *Crocuta crocuta*, African Wild Dogs *Lycaon pictus* and Nile Crocodiles *Crocodylus niloticus*. Calves may also be preyed upon by Leopards *Panthera pardus* and Black-backed Jackals *Canis mesomelas*. There is one report of an adult Roan bull being killed by Cheetahs *Acinonyx jubatus* in East Africa (Spinage 1986). Juveniles unaccompanied by adults may be most vulnerable to predation (Beudels *et al.* 1992a). Lion predation has been implicated as a potential cause for the population decline observed in Kruger N. P. (Harrington *et al.* 1999).

In small protected areas artificially high densities build up, and, in the absence of dispersal opportunities, cause an increase in the rates of transmission of pathogens, thus contributing to some of the high mortalities seen among Roan Antelopes (Dörgeloh 1998b). In South Africa, mortality is sometimes attributed to tick overburdens brought about by good rains, in particular of the species *Rhipicephalus appendiculatus*, *R. evertsi* or *Boophilus decoloratus*. No fewer than four pathogens have been implicated in the death of juveniles: *Cytauxzoon* spp. (infection rates can reach 31.2% in young calves; the parasites are thought to be transmitted by *R. appendiculatus*), *Babesia*, *Chlamydia* and *Pneumocystis carinii*. Two helminth parasites were recovered from Roan Antelopes on Percy Fyfe N. R., namely *Skrjabinema ovis* and *Ostertagia* spp. (Wilson & Hirst 1977). Roan Antelopes are highly susceptible to anthrax, which can cause dramatic declines in the population (Pienaar 1960, 1961), and rinderpest (Chardonnet & Kock 2001), and they may be susceptible to malignant catarrhal fever (Gulland *et al.* 1989).

Conservation IUCN Category: Least Concern. CITES: Not listed.

As noted already, there are contrasts in the conservation status of the Roan Antelope throughout its distribution range. It currently remains common in some areas of West and central Africa, but is becoming increasingly rare in most areas of East and southern Africa. Overall, the Roan Antelope tends to disappear from transformed habitats and areas with human settlements and this helps explain its withdrawal from large parts of its historical distribution. Nevertheless, in West and central Africa, the Roan Antelope continues to thrive in areas where other antelopes are decreasing. This is probably due to its ability to withstand illegal hunting pressures better than many other large herbivores, especially the more water-dependent and more sedentary species, which are more exposed to poaching. However, some populations in West Africa are in decline, such as that in Comoé N. P. where numbers have declined by about 70% between 1978 and 1998 to

around 500 animals (Fischer & Linsenmair 2001a), and in Mole N. P. (Ghana), where numbers have declined from an estimated 1010 in 1993 to 160 in 2004 (East 2006). Elsewhere, Roan have disappeared from several areas because of the opening up of farms, fencing and settlement, and poaching. Illegal hunting probably contributed to the demise of the Roan Antelope in Masai Mara National Reserve in Kenya in the 1970s (Hofer *et al.* 1996). In the Karoi area, in Zimbabwe, Roan Antelopes were systematically exterminated by government tsetse control hunters: 2862 Roan Antelopes were shot on tsetse control between 1924 and 1945 (Best *et al.* 1970).

Harrington *et al.* (1999) have proposed different explanations to understand the decline of the Roan population and its lack of subsequent recovery in South Africa, specifically in the Kruger N. P. (450 animals in 1986 to around 30 in 2001; Grant *et al.* 2002): (i) extreme deterioration of habitats caused by a long period of low rainfall; (ii) substantial influx of Plains Zebras and Common Wildebeest into Roan range, increasing competition for grazing resources; and (iii) enhanced predation by Lions, following the influx of Plains Zebras and Common Wildebeest. Despite the high-density conditions, and the probable competition for resources, predation pressure following the influx of grazers seems to be the main factor responsible for the drastic decline of Roan Antelopes in Kruger N. P. (Knoop & Owen-Smith 2006; and see McLoughlin & Owen-Smith 2003). Evidence seems to suggest that ecological disturbances set off by 'ecosystem manipulation' through the extensive provision of water-points in this region facilitated the build-up of Plains Zebra and Common Wildebeest numbers. The increase of common grazing ungulates might explain the decrease of uncommon grazing ungulates relying on a feeding strategy based upon the selection of the highest quality plant parts in the most remote areas from water sources. Although the closure of 13 artificial water points (including one large dam) within the Roan Antelope's range in Kruger N. P. in 1995–96 resulted in an initial recovery in the Roan population, this recovery has not continued and the population still remains well below historical numbers (R. Harrington pers. comm.), suggesting that other factors in addition to those mentioned above may be influencing the population. Kröger & Rogers (2005) suggest that fine spatial scale dietary resource requirements (wetland boundary) by Roan Antelopes may make them experience the effects of habitat deterioration first, before other ungulates.

Dörgeloh (1998b) proposed that, in South Africa in particular, habitat management and calf mortality should be primary issues in designing a management plan for the Roan Antelope. Management procedures must aim at modifying or supplementing missing habitat factors. Management recommendations include, in South Africa, the maintenance of the important plant communities, mainly flood-plains and the *Aristida bipartita*–*Setaria sphacelata* grassland type. The hydrology of the flood-plain should be maintained to supply sufficient quality forage throughout the wet season. Bush encroachment onto the latter plant community should be controlled. Patch-burning throughout the dry season will increase the forage quality for the Roan Antelope. The carrying capacity can be increased by enlarging protected areas. It can also be increased by introducing an artificial feeding programme, which should enhance the condition of animals during winter and

control their parasite load. Another management option could be to reduce the population size, which will improve the population growth rate, and may also improve calf survival and the condition of animals (Dörgeloh 1998b). The decrease of the Roan population in Kruger N. P. shows that protected areas are not necessarily the 'safest' option and that the risk of extinction should be minimized by having populations in different areas with different management strategies (Dörgeloh 1998b). Interestingly, the highest densities and largest populations of Roan Antelopes appear to remain in West and central Africa with light management interventions, while the conservation status of Roan Antelopes is degrading in southern Africa with intensive management.

The current strongholds of Roan Antelopes are predominantly focused in West and central Africa: Dulombi, Corrubal and Boé areas (Guinea-Bissau); all the northern regions of Guinea (only occurs seasonally in National Park of Upper Niger, according to Brugière *et al.* 2005); Niokolo-Koba N. P. and Falémé Hunting Zone (Senegal); Comoé N. P. (Côte d'Ivoire); Arly and W National Parks and Nazinga Game Ranch and all surrounding gazetted Hunting Areas (Burkina Faso); Mole N. P. and Digya N. P. (Ghana); Pendjari and W National Parks and surrounding gazetted Hunting Zones (Benin); W N. P. and Tamou Faunal Reserve (Niger); Waza, Faro, Bénoué and Bouba Ndjida National Parks and all surrounding gazetted Hunting Zones (Cameroon); Manovo–Gounda–St Floris and Bamingui–Bangoran National Parks and the very extensive areas gazetted as Hunting Areas (Central African Republic); and Zakouma N. P. (where the population was estimated at about 1300; Mackie 2004), Siniaka-Minia Faunal Reserve and Aouk Hunting Areas (Chad). In the remainder of the range, among the largest surviving populations are those in the North and South Luangwa and Kafue National Parks (Zambia), Nyika N. P. (Malawi) and in N Botswana (East 1999).

In extreme situations with small populations, the planned exchange of animals between reserves might be needed to counter inbreeding. However, in the early 1990s another threat appeared in the mixing of distinct taxa of Roan Antelope, notably the importation of Roan Antelopes from West and central Africa to southern Africa where this species is one of the most expensive wild animals for sale, reaching prices as high, and even higher, than Black Rhinoceros *Diceros bicornis*. In May 2000, the South African Minister of Environmental Affairs and Tourism requested a moratorium on the importation of non-indigenous subspecies of Roan Antelope, in view of the dangers that hybridization poses to the threatened South African subspecies *H. e. equinus*. The trade of Roan Antelopes in southern Africa is also a threat to West and central African wildlife where this particular antelope is one of the few distinct major natural assets. Long-term conservation of the Roan Antelope in West and central Africa relies on safeguarding its value for all stakeholders. For local communities, attention needs to be paid to management that brings tangible benefits (notably employment by safari operators and returns from sustainable use of wildlife). For government agencies that must plan land-use, their decisions need to be based on the most efficient rural development tools (e.g. cotton farming is making rapid encroachment on Roan natural habitat), while for private operators with monetary motives, the depletion of a large antelope such as the Roan acts as a disincentive for investment in all kinds of wildlife tourism.

Measurements*Hippotragus equinus*

HB (♂ ♂): 2593 (2360–2840) mm, n = 19
 Sh. ht (♂ ♂): 1459 (1370–1610) mm, n = 19
 WT (♂ ♂): 277.8 (232.0–313.0) kg, n = 19
 N Benin (Coatmellec 2004).

TL (♂): 2730 mm, n = 1
 TL (♀): 2630 mm, n = 1
 T (♂): 540 mm, n = 1
 T (♀): 530 mm, n = 1
 HF c.u. (♂): 620 mm, n = 1
 HF c.u. (♀): 600 mm, n = 1

E (♂): 310 mm, n = 1

E (♀): 290 mm, n = 1

Caprivi (Rautenbach 1982)

In E Zambia, Wilson (1968) gave the mean weight for 12 ♂ ♂ as 280.0 kg (range 241.0–298.1) and for 8 ♀ ♀ as 258.2 kg (range 222.4–280.0)

Maximum recorded horn length is 99.0 cm for a pair of horns from Tokwe Valley, Zimbabwe (Rowland Ward)

Key References Allsopp 1979; Dörgeleh 1998a, b; East 1999; Heitkönig 1993; Joubert 1976; Wilson 1975; Wilson & Hirst 1977.

Philippe Chardonnet & William Crosmary

***Hippotragus niger* SABLE ANTELOPE**

Fr. L'Hippotrague noir; Ger. Rappenantilope

Hippotragus niger (Harris, 1838). Athenaeum 535: 71. 'The great mountain range in the county of Mataveld', and 'On the northern side of the Cashan range of mountains, about a degree and a half south of the tropic of Capricorn', since specified as South Africa, North West Prov., Krugersdorp and Rustenburg, Magaliesberg (Grubb 1999).



Sable Antelope *Hippotragus niger*.

Common name derived from a heraldic colour and the black pelage of adult ♂ ♂. Not to be confused with a fur-bearer of the weasel family, the Sable *Martes zibellina*.

Taxonomy Polytypic, with four recognized subspecies. Mitochondrial DNA studies by Pitra *et al.* (2002) and Pitra *et al.* (2006), involving more comprehensive sampling than that undertaken by Matthee & Robinson (1999b), confirmed the distinctness of the subspecific lineages, the boundaries of which broadly conform with recognized subspecies boundaries (Ansell 1972). The most recent genetic research by Jansen van Vuuren *et al.* (2010) not only confirms that all four subspecies are significantly differentiated from each other, but clearly demonstrates that the western Zambian sable, despite the close resemblance of some individuals to the Giant Sable in facial markings and coat colour, is not referable to *H. n. variani*. Most striking is the fact that none of the haplotypes detected in the western Zambian sable specimens were shared with those from Angola, nor were *H. n. niger* haplotypes detected in the Angolan population. Had there ever been interbreeding between the two populations, it should be revealed in the mtDNA analysis (Jansen van Vuuren *et al.* 2010). Instead, the most closely related haplotypes to *variiani* are found in the southern region of central Tanzania (a distance of some 2000 km). This suggests that the peripheral populations of *H. n. niger* in Angola and STanzania were founded during the Pleistocene by episodic long-distance colonizations from a common source population (Pitra *et al.* 2002, 2006).

Synonyms: *anselli*, *harrisi*, *kaufmanni*, *kirkii*, *niger*, *roosevelti*, *variiani*. Chromosome number: 2n = 60 (Wurster & Benirschke 1968, Claro *et al.* 1993). Despite very different phenotypes, and subtle differences in chromosomes (Fordyce-Boyer *et al.* 1995) the Sable Antelope and the Roan Antelope *H. equinus* may be genetically close enough to produce viable hybrids (Robinson & Harley 1995). In the latter instance, a hybrid ♀ was born into a Sable herd in the Satara area of Kruger N. P. (South Africa) in the late 1980s. A Roan bull had joined this herd in about 1987, though it was unclear where the bull came from as there were no Roan herds in that area. As it was clearly a hybrid, the animal was captured and put in a large enclosure (1 km × 1 km) in the Pretoriuskop area of the Park

where no other Sable or Roan Antelopes were present. This was to prevent her from breeding with the pure Sable stock of the Park (though it is fairly certain that she was sterile). The animal died in early 2006 at an estimated 19 years of age (Estes & Whyte 2006). Subsequently, multiple instances of hybridization have occurred in Cangandala N. P. in Angola (Vaz Pinto 2006, Walker 2010; and see Conservation).

Description A large, heavy-set antelope with long, arched horns, narrow pointed ears and sexually dimorphic colouration. Brown or black bridge to the nose bordered by a preorbital patch of white connecting with a white stripe that extends to the white upper lip. Narrow dark orbital stripe down the side of the face separates this white stripe from the white forecheek and chin. Inside surfaces of the elongated ears have white hair; backs are light russet-brown. Muzzle elongated, mouth with wide gape and diastema, and a small dewlap under throat. Neck is thick, with an upstanding mane. Short, glossy pelage, ♀♀ and young sorrel to chestnut, becoming deep black in adult ♂♂. Similar contrasting white markings in both sexes, including rump patch, belly and facial markings. Mane and tail hairs black. Conspicuous pendant penile sheath white with black tip. Calves up to two months are tan with indistinct markings. Rudimentary preorbital glands are present under the white 'eyebrows', and there are pedal glands on all feet, the constituents of which have been examined by Wood (1998); inguinal glands are absent.

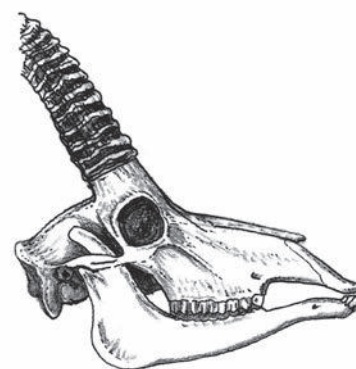
Horns are well developed in both sexes, but thicker, longer, more sickle-shaped in ♂♂. Horns are laterally compressed and strongly ringed for most of their length. The pattern of horn growth in relation to age for known-age individual Sable Antelopes has been quantified for *H. n. roosevelti* in the Shimba Hills by Ross (1984). Age determination based on patterns of tooth eruption is discussed by Grobler (1980a), the first permanent tooth (M_1) erupting at 6–10 months and the first premolars at about 34–42 months.

Geographic Variation

H. n. niger (Black-black Sable): south of the Zambezi R. in Mozambique, Zimbabwe, NE South Africa, N Botswana, Caprivi Strip (NE Namibia), Zambia west of Zambezi and SE Angola. The only race in which ♀♀ become nearly black, mimicking the main male secondary character; young begin turning dark as yearlings.

H. n. kirkii: north of the Zambezi R. in Mozambique, Malawi, Zambia, SE DR Congo, E Angola and W Tanzania, west of the Eastern Arc Mts. Highly significant genetic separation between W Tanzania populations and Kenya/East Tanzanian populations (*H. n. roosevelti*) suggests long isolation of the different lineages on either side of the Eastern Arc Mts (Pitra *et al.* 2002).

H. n. roosevelti (Roosevelt Sable): patchy distribution in coastal hinterland of Kenya and Tanzania, associated with extension of miombo-type woodland into Kenya, where now found only in Shimba Hills National Reserve. Isolated relict populations in Tanzania except in and adjacent to Selous G. R., its one stronghold (estimated population of 3900 in 1998). The population is highly differentiated along approximately the 38th degree of longitude. Usambara Mts and Pangani R. are obvious geographic barriers cutting across the northern parts of its range and the Rufiji R. further south. The Eastern Arc Mts appear to mark the western boundary of its range,



Lateral view of skull of Sable Antelope *Hippotragus niger*.

but clear morphological differences across this genetic divide have yet to be found.

H. n. variani (Giant Sable): limited to two reserves in C Angola south of Malange – Cangandala N. P. and Luando Integral Reserve of the Giant Sable. Distinguished from other races by facial mask lacking white stripe bordering the nose and retention of tan hocks by adult bulls. 'Giant' designation derives from male's horns, which average ca. 30 cm longer than in other races.

Similar Species

Hippotragus equinus. Sympatric through most of the southern savannas.

The Roan Antelope is less of a woodland and more of a grassland/tree-savanna species, tolerating taller grassland and higher elevations (Estes 1991a, Dörgeleh 1998a). Averages 40 kg heavier with a conspicuous black and white mask, but grey to rufous coat that is similar in both sexes; robust curving horns in both sexes are much shorter (average = 75 cm) and heavier than those of the Sable.

Distribution Endemic to Africa. Confined to the southern savanna regions of the continent, with a particular association with the miombo (*Brachystegia*) woodland communities.

Historical Distribution Their natural distribution extends from the Caprivi Strip and E and SE Angola, west throughout Zambia, and south of the Zambezi R. in N and NE Botswana, throughout Zimbabwe, Mozambique (except the extreme south-east) and northwards through SE DR Congo, Malawi and W, NE and SE Tanzania (East 1999). The northern limit of Sable distribution formerly extended near or to the Somalia border (I. Parker pers. comm.) in a 5000 km² expanse of miombo-like *Diospyros* lowland woodland lying inland from the Kenya coast, extending west to the border of Tsavo N. P. (Estes & Estes 1969a). In South Africa, they occurred in the bushveld and lowveld areas of the North West, Limpopo and Mpumalanga Provinces; the historical southern limit was the Komati R., at ca. 26° S (Pienaar 1963) and the Magaliesberg Mts. An isolated population (the Giant Sable) occurred in C Angola, between Cuanza and Luando R. and north of the Cuanza R. (East 1999, Crawford-Cabral & Veríssimo 2005).

Current Distribution Sable Antelopes have been eliminated from large parts of their former range and now survive mainly in protected



areas and on private land. Their range reduction has been particularly marked in Mozambique, where they survive in good numbers only in Niassa G. R. in the north, and in the western Gaza province. In SE DR Congo, they have been eliminated from most of their range (but survive in Upemba N. P. and Kundelungu N. P.). Similarly, they have been eliminated from much of their range in NE Tanzania, but still survive at low to moderate densities in the miombo woodlands of W and S Tanzania; the population in the Selous ecosystem probably represents the largest free-ranging population in Africa. The northerly limit of their range now extends to SE Kenya (Shimba Hills National Reserve).

Sable Antelopes have been reintroduced to many parts of their former range, but have also been introduced to areas where they never naturally occurred, including to Swaziland (Mkhaya Private Reserve; Monadjem 1998), widely on private farmland (and to the Waterberg Plateau Park) in Namibia, and various provinces in South Africa (Free State, KwaZulu–Natal, Eastern Cape, Northern Cape) (East 1999).

Habitat Apart from Lichtenstein's Hartebeest *Alcelaphus buselaphus lichtensteini*, no large mammal is more closely identified with the miombo woodland zone than the Sable Antelope. This broad-leaved, deciduous open woodland is dominated by *Brachystegia*/*Julbernardia*/*Isoberlinia* spp. growing on leached granitic and sandy soils. Currently covering a large part of the interior of southern Africa, this vegetation type is maintained by annual fires that burn off the grasses and much of the undergrowth. These woodlands are open enough to support an understorey of grasses and forbs and are interspersed with edaphic grasslands and flood-plains. The Sable Antelope is an 'edge' species that frequents the woodland/grassland ecotone. It spends the wet season in woods open enough to support an understorey of grasses no more than 30 cm high on well-drained soils, and in the dry season emerges onto the grasslands in search of green grass and forbs.

Sable Antelopes occur in three drier vegetation types south of the miombo ecotype (Wild & Barbosa 1967):

- Rhodesian teak (*Baikiaea plurijuga*) woodland, associated with *Pterocarpus angolensis*, *Guibourtia coleosperma* and *Ricinodendron* and sparse grass cover of tall *Aristida* spp., *Triraphia schlechteri*, *Tristachys rehmannii*, *Digitaria* spp. and *Eragrostis* spp.
- Dry early deciduous savanna woodland (lowland). Mopane woodland mixed with *Kirkia acuminata*, *Sterculia africana*, *Commiphora* and *Combretum* spp. in varying proportions. Associated grasses include *Stipagrostis uniplumis*, *Digitaria milinjiana*, *Panicum kalaharens* and *Pogonarthria squarrosa*.
- Deciduous dry tree savanna (on Kalahari sand). Dominant trees include *Baikiaea plurijuga*, *Colophospermum mopane*, *Dialium englerianum*, *Erythrophloeum africanum*, *Pterocarpus angolensis*, *Ricinodendron rautanenii* and *Azelia quanzensis*. Important grasses: *Aristida stipitata*, *A. pilgeri*, *Tristachya rehmannii*, *Eragrostis* spp., *Andropogon schirensis*, some *Hyparrhenia dissoluta* and *H. filipendula*.

Sable populations currently reach their highest densities (4/km²) in W Zimbabwe and N Botswana, in the transition zone between mopane and mixed deciduous savanna woodland, growing on Kalahari sands (type c above), where the average rainfall is 625 mm or less, falling Dec–Mar (Wilson & Hirst 1977).

The miombo woodland zone receives an annual rainfall of 750–1125 mm in a single wet season lasting 6–7 months. However, from Zambia to Botswana the climate becomes progressively drier, as noted above. The southern limit of Sable distribution in Botswana coincides quite closely with the 500 mm rainfall isohyet, in *Terminalia* deciduous tree-savanna. Summer temperature and humidity are high (up to 40 °C) in the region and winter temperatures frequently drop below freezing in Zimbabwe and Botswana.

The Central African plateau lies at an altitude of 1000–1500 m, but most of the miombo woodland grows on an ancient upland plateau with little relief. In the Southern Highlands of Tanzania and the Chimanimani Mts of E Zimbabwe, Sable Antelopes occur in montane grassland; also in wooded hills of Mozambique's Gorongosa N. P., and among low hills fronting the Cuanza R. in the Luando Reserve, Angola. At their north-eastern limit they inhabit Kenya's coastal Shimba Hills, which consist of a forest/grassland mosaic.

Abundance The most recent estimate of total population size is 53,365 animals, although correcting for undercounting bias in aerial surveys gives a slightly higher estimate of 75,000 animals (East 1999). The largest populations survive in Zimbabwe (>19,690), Tanzania (>10,680), Namibia (7100) and Mozambique (4270) (East 1999). According to an unsubstantiated report of the Kissama Foundation printed in the December 1997 issue of *Safari Times*, newsletter of the Safari Club International, at least 253 and probably many more Giant Sable Antelopes survived the 25-year civil war, greatly reduced from an estimated 2000–3000 in the late 1960s (Estes & Estes 1974, East 1999).

Like other ungulates of the miombo woodlands, the Sable Antelope occurs at low density in comparison with ungulate densities in semi-arid savanna. In what Wilson & Hirst (1977) considered the best Sable habitat in southern African, the Matetsi area of SW Zimbabwe, the estimated density was 4/km². In Kenya's Shimba Hills National

Reserve, the estimated year-round density was $1.4/\text{km}^2$ (Estes & Estes 1969a, Sekulic 1977). However, this island population now numbers less than 200 individuals (Ross 1984, K. Ross pers. comm.). A density of $4/\text{km}^2$ was estimated in Zambezi N. P., Zimbabwe, in the 1969 dry season, but represented the concentration of animals from a much wider area (Estes & Estes 1969b). Earlier road-strip counts by Dasmann & Mossman (1962) in this Park also gave a density of $4/\text{km}^2$. In the Luando Reserve, the wet season range of a herd of 32 Sable Antelopes observed for a year was ca. 20 km^2 , a density of $1.6/\text{km}^2$; its dry-season range was ca. 12 km^2 , amounting to a density for the year of $1/\text{km}^2$ (Estes & Estes 1974). Density estimates based on aerial surveys are much lower, usually ranging from 0.01 to $0.10/\text{km}^2$, reaching 1.2 – $1.3/\text{km}^2$ in areas where Sable Antelopes are particularly common (East 1999).

Adaptations According to Kingdon (1982) the Sable and Roan Antelopes share arid-adapted ancestors with *Oryx* and *Addax*. Thus, the adaptive radiation of species from North African biomes extended into the northern and southern savannas, and, according to Hernández Fernández & Vrba (2005), most likely followed a dry period in the mid-Miocene. A diverse array of semi-arid savanna ungulates left little room for large, arid-adapted antelopes. However, the broad-leaved deciduous woodlands and grasslands of the mesic savanna were occupied by few ungulates and hardly any the size of Roan or Sable Antelopes. So, like the oryxes and *Addax*, which occupy deserts and sub-deserts where they have no competitors among large antelopes, Roan and Sable Antelopes found niches in the mesic savanna, thereby avoiding competition with most other large antelopes. Here there were also fewer Lions *Panthera leo* and other large predators, which could have been another factor promoting their choice of these less-productive and mineral-depleted ecotypes (Kingdon 1982).

In the process of adapting to the mesic savanna, *Hippotragus* gave up nomadic habits and became dependent on habitats that provide free water. They adopted the social organization typical of a sedentary life-style, with territorial ♂♂, female herds resident in traditional home-ranges and segregated bachelor ♂♂. Actually, these changes were not as radical as might be supposed, for Gemsboks *Oryx gazella* will drink and bulls will stake territories where water is available – and in the Kalahari even where it is not (Williamson & Williamson 1985b). More radical were the morphological changes that culminated in the *Hippotragus* phenotype. Perhaps most significant was the lengthening of the head and the increase in gape and the incisor–molar diastema, which are well adapted for feeding on tufted perennial grasses.

It is plausible to suppose that the Roan Antelope, which has a much wider geographic range and occupies more open savannas, evolved before the Sable, which is limited to the southern savanna and closely linked to the miombo woodland zone. The Roan Antelope's relatively small degree of sexual dimorphism would seem to place it closer to *Oryx* and *Addax* and their arid-adapted, nomadic ancestors. As the only member of the tribe with conspicuous sexual dimorphism, the Sable Antelope is arguably the most recent and niche-specialized hippotragine. However, the Black-black Sable (*H. n. niger*) affords an example of how selection can lead to reduced sexual dimorphism when socio-ecological circumstances warrant. This race lives in the driest region of the species' range, extending south of the miombo biome. During a Pleistocene dry epoch both natural and sexual

selection favoured female mimicry of male colouration as a means of reducing aggression toward male offspring and allowing them access to scarce green pastures. Had this counter-selection continued and the population become increasingly migratory, it could have led to unimorphism and sexually integrated herds, as among oryxes and the *Addax*, where minimal sexual dimorphism is seen as the end result of this process of female mimicry of male secondary sexual characters (Estes 1991b, 2000).

Foraging and Food Studies from several areas have confirmed that Sable Antelopes are both graminivorous and folivorous (Glover 1969, Estes & Estes 1969a, b, 1974, Grobler 1974, 1981a, Wilson 1975, Sekulic 1977, Wilson & Hirst 1977, Ross 1984). About 15–20% of the diet consists of herbs, forbs and woody vegetation, and Gagnon & Chew (2000), in their review of the dietary preferences of African bovids, classified the Sable Antelope as a variable grazer. For example, the leaves of *Diplorhynchus condylocarpon*, an understory shrub abundant in miombo woodland, especially on termite mounds, is a favourite browse plant in all studied miombo woodland habitats (Estes & Estes 1974). However, grass forms the primary component of the diet, as borne out by studies involving stable carbon isotopes, which suggest that they are almost entirely grazers (Cerling *et al.* 2003, Sponheimer *et al.* 2003b).

Studies of Sable Antelope food habits by Wilson & Hirst (1977) indicated that, like the Roan, the Sable is highly specific in choice of food plants, specializing on a small number of available species at any one time. Marked preferences were shown for *Setaria perennis*, *Themeda triandra*, *Eragrostis gummiflua* and *Heteropogon contortus*. The last-named was most utilized, followed by *Themeda triandra*. Grobler (1981a) noted that the Sable Antelopes he observed in Matopos N. P., Zimbabwe, preferred a grass sward below 160 mm and cropped plants between 40 and 140 mm above ground.

A grazing herd keeps moving from tuft to tuft of preferred grass and usually shifts feeding grounds from day to day. After staying in a small part of the home-range for several days at a time, a herd will likely move 2–4 km and settle in another area. In the Matetsi area of NW Zimbabwe, Sable Antelopes foraged in an area of 37 ha inside a 260 ha annual home-range during the dry season (Wilson & Hirst 1977). In Zambezi N. P., a herd of 125 Sable Antelopes remained on Chamabonda Vlei within an area of about 250 ha from early Jun until at least late Jul and could usually be found less than 1 km from the previous day's location (Estes & Estes 1969b); the following summary of Giant Sable seasonal feeding habits also applies to other populations (Estes & Estes 1974).

The Sable Antelope's preference for bunch grasses at a tender growth stage largely determines its seasonal habitat preferences. Preferred grasses and browse are found in woodland during the rains, especially on termite mounds and on the woodland/grassland border. Here the grasses stay short, the ground remains comparatively firm and there is little undergrowth. In Apr upland woodland grasses begin to dry, and the Sable Antelopes then move onto the edaphic vlei and drainage-line grasslands (*mulolos* = *dambos* of Zambia, = *mbugas* of East Africa), where pastures are still green. As the rains end in May, bringing low humidity and freshening winds, the drying trend accelerates. Woodland grasses have all dried up and most trees have shed their leaves. Only lower parts of the catena around marshes, swamps and springs, along streams and drainage lines retain enough

moisture to support growth. Tall *Hyparrhenia* grass species become dominant in these pastures late in the rains. A Sable Antelope grazing bunch grasses gathers in a clump of blades with dextrous lip movements, then bites off and chews a length up to 36 cm. Herds subdivide as Sables move between patches, still seeking clumps of green grass they can crop in mouthfuls, rather than trying to select green shoots sprouting from bases of otherwise dry tufts. In Jun fires burn woodland undergrowth and adjacent *anhara* grasslands. The woods remain barren until the next rains, but the *anhara* grasslands flush within a fortnight, attracting Sables into the open starting in late Jun and early Jul. They may feed on post-burn flushes of 5 cm or even less (however, Sable Antelopes in the Shimba Hills only moved onto burn flushes when they reached 15 cm high, meanwhile continuing to feed on standing hay; Estes & Estes 1969a). Finally, the grasslands lowest in the catena burn and quickly respond with new growth, the wetter the ground the lusher the growth. A succession of herbs and shrubs springs up once the grasses are removed (Estes & Estes 1974).

The extended burning season produces a mosaic of pastures at different stages of regrowth. If not for fires, the Sable Antelopes would have to hunt harder and harder for green pasture until forced to subsist on dry hay (and see Parrini & Owen-Smith 2009). The Giant Sables stayed in good condition with sleek coats even at the end of the dry season, whereas Sables observed in Zambezi N. P. a year earlier, subsisting on dry grass, were mostly in fair to poor condition with staring coats. However, in Shimba Hills National Reserve, where the grasslands are burnt repeatedly as a management tool, Ross (1984) noted that such regular annual burns favour fire-resistant grass species in the long run. Over time these grasses become less palatable, and have a significantly lower mineral and protein content than grasses that are burnt less frequently. Whilst the post-burn green flush is attractive to Sable Antelopes, the grasses become unpalatable within six months and the Sables then move on to areas that have not been burnt. This emphasizes the need for patchy burns to create a grassland mosaic, and shows the benefit of having coarse-grass feeders such as zebras *Equus* spp. and African Buffalo *Syncerus caffer* present, whose choice of grass length benefits Sable Antelopes by removing the taller clumped grasses thus making available the short green leaves that Sables prefer (Ross 1984).

Although Sable Antelopes are considered water-dependent, some live in areas that are waterless for much of the dry season (P. Vaz Pinto, pers. comm.). However, most drink daily, and even during the rains they visit waterholes frequently. Sables prefer to drink from pans and waterholes rather than flowing rivers (Estes & Estes 1969b). Their feeding peaks are typical of most African ungulates, being early morning and late afternoon. Herds settle to rest and ruminate by 09:00h. Herds of Giant Sables were observed to stop feeding at dusk and move some distance in the dark before lying down to ruminate. After resting for several hours, they fed up until about midnight and sporadically afterward (more on moonlit, less on dark nights), but were inactive the last couple of hours until dawn. Daily ranging in the order of 1–2 km while on green pasture increased in the dry season, often involving movements up to 10 km as herds searched for remaining patches of green grass. Sable Antelopes often visit waterholes and salt licks after the morning and before the late-afternoon feeding peak.

Sable regularly chew bones (producing a white froth) in the Shimba Hills (Sekulic & Estes 1977). All populations frequent mineral licks

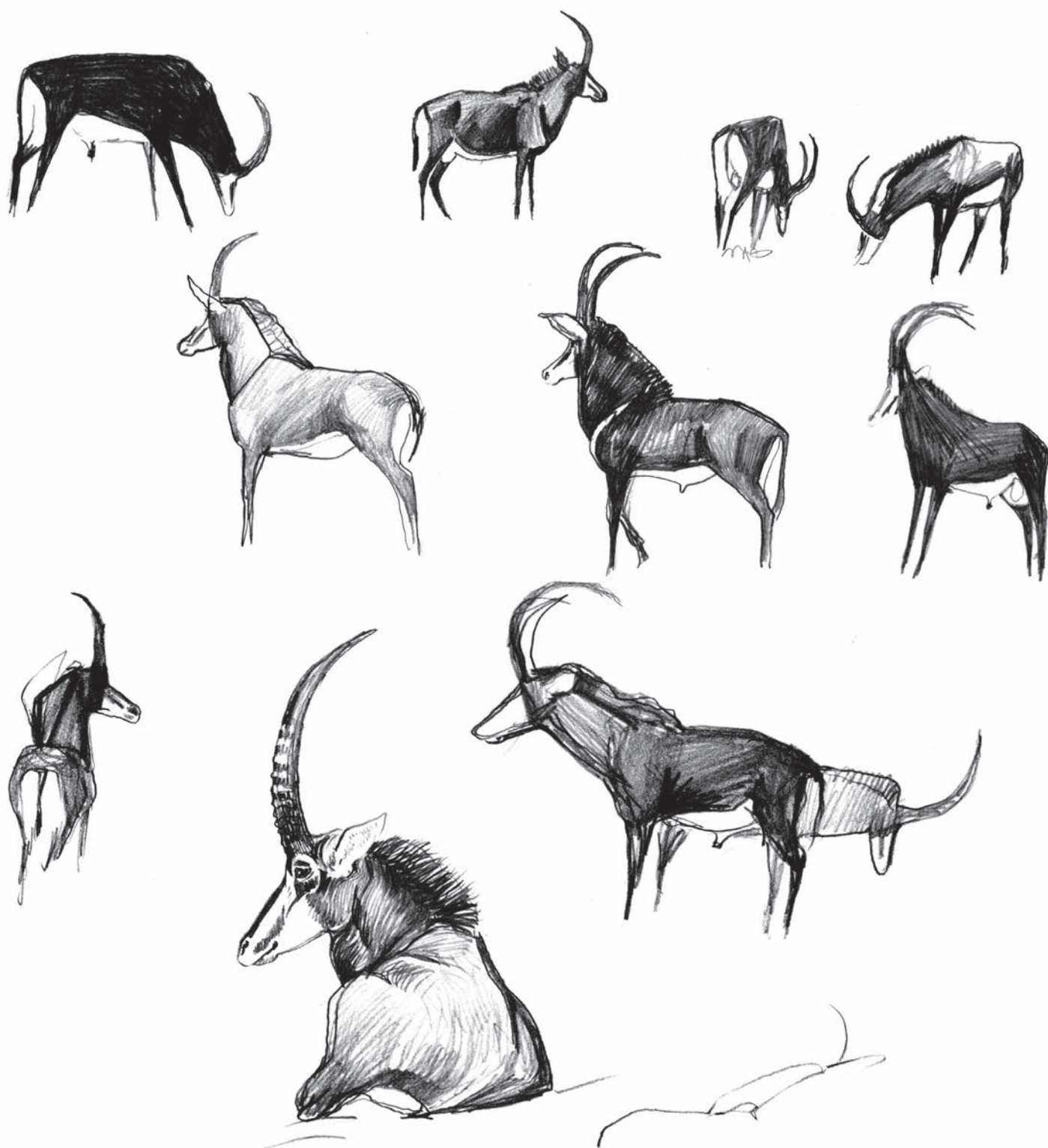
at the bases of termite mounds and saline pans. Sterile soils deficient in essential elements such as potassium, calcium, iron, selenium and salt would account for these habits (detailed in Wilson & Hirst 1977, Sutton *et al.* 2002). Samples collected at five different licks used by Giant Sables tested very high in calcium, medium-high in phosphorous, medium-high to very high in magnesium, and very low to high or very high in potassium, ammonia, nitrate and aluminium (Estes & Estes 1974).

Sable Antelopes in Zambezi N. P. fed on a prostrate perennial herb, *Blepharis bainesii*, which resembles and is as prickly as a thistle, and which grew abundantly among the annual grasses they were consuming at the time. A Sable Antelope would gingerly close its mouth over a flowering head, grip the wiry stem with its lips and pluck it. Then, standing with head outstretched and tilted to one side, mouth gaping, it would proceed to ensalivate the ball until it was soft enough to swallow. At the same time, *Brachiaria* grass the Sables were eating often came up by the roots with an attached clod of dried clay, which they removed with vigorous head shakes or ejected by gaping and pushing with their tongues (Estes & Estes 1969b).

Social and Reproductive Behaviour Sable Antelopes are gregarious with three different classes: breeding herds of ♀♀ and young, bachelor herds, and territorial ♂♂. In addition, ♀♀ with hidden calves may form maternity subgroups. Numbers in breeding herds vary: in *H. n. niger*, 21 (maximum 125, from an average of 57 herds in eight different Parks of Zimbabwe, Botswana and South Africa [Estes & Estes 1969b]); in *H. n. kirkii*, 15.2 (average of 93 nursery herds all over Zambia, sighting records of Zambia Dept of Wildlife, Fisheries and National Parks, 1957–1968); in *H. n. roosevelti*, 19.6 (range 7–48, average of five herds [Estes & Estes 1969a]); and in *H. n. variani*, 22.5 (range 13–69, average of 13 herds). Numbers in bachelor herds are usually under ten ♂♂ (rarely up to 25) from 3 to 5 years old.

Breeding herds comprise what are presumably related ♀♀ occupying a traditional home-range with an age-graded dominance hierarchy. The senior cow usually leads herd movements and is the most vigilant individual (except for low-ranking peripheral ♀♀). Dominance is frequently reinforced with aggressive behaviour ranging from simple supplanting, rubbing head/horns on the opponent's body, lateral-presentation, medial- and low-horn presentation, prodding and chasing (Estes 1991a, Thompson 1993). Individual distances of 3–4 m are maintained even in a resting herd. Large herds frequently subdivide and may range separately for hours, days and even weeks. Mothers and calves may end up in different groups. When different, unrelated herds meet, as at water-holes, they are mutually hostile.

Home-ranges vary greatly in area in different populations and among herds of the same population, depending on the nature of the habitat and herd size. In the Shimba Hills open grassland habitat, several herds remained the whole year in ranges of 10–25 km², which overlapped by up to 20%. A herd of 70 animals had the largest range. In typical miombo woodland, herds may be separated by kilometres of unoccupied but perfectly suitable-looking habitat. For example, in the Luando Reserve, spacing between nearest neighbours for six known herds averaged 7.5 km (range 5–10 km) (Estes & Estes 1974). Four herds studied for 27 months in Matopos N. P. had annual home-ranges of 2.4–2.8 km² (Grobler 1974), whereas two herds in different South Africa nature reserves had ranges of 9.2 and 17.7 km²



Sable Antelope *Hippotragus niger*.

(Wilson & Hirst 1977). Joubert (1974) recorded home-ranges of only 0.2–0.4 km² in Kruger N. P. In contrast, using GPS collars, Rahimi & Owen-Smith (2007) recorded much larger annual home-range sizes covering 118 km² and 65 km² for two herds numbering 15 and 6 animals (excluding adult bulls), respectively, in the same park. One Giant Sable herd stayed the whole year in an area of ca. 12 km², while its neighbour 'migrated' 15 km from the grasslands where both herds spent the dry season to a separate wet-season range in wooded habitat (Estes & Estes 1974).

The seasonal grouping and movement patterns of Sable Antelopes may be summarized as follows (Estes & Estes 1974): (1) concentration during the dry season in the open, within 2–4 km of water; (2) break-up early in the rains into smaller sections, which sooner or later settle down in relatively stable groups in a wooded part of the home-range; (3) increased movement at the end of the rains and fragmentation of herds prior to the calving season; and (4) reformation of stable herds of ♀♀ after the new calves leave concealment.

The amplitude of seasonal movement is related to climate and water distribution. In general, Sable Antelopes move further in low than in high rainfall areas. Where their needs are adequately met, herds may remain the whole year in small home-ranges, as noted above. But the Sable Antelopes in Gorongosa N. P. had entirely different dry- and wet-season ranges: at the height of the dry season most herds stayed on the Rift Valley floor, then withdrew to the miombo woodland on the higher, dissected plateau during the rains (Tinley 1977). Verheyen (1951) observed movements of 40 km between wet- and dry-season ranges in Upemba N. P. (DR Congo). In NW Zimbabwe and adjacent Botswana, wet-season dispersal covers a still larger area. Herds of up to 100, putatively representing wet-season dispersers, were seen in the Kisuma Pans area 65 km south-west of Victoria Falls in early Jun (Estes & Estes 1969b).

To participate in breeding, ♂♂ must own territories, but are only ready to compete for space when they mature at five or six years (Estes & Estes 1974). Territory size ranges from 4 to 9 km² in the Shimba Hills National Reserve (Sekulic 1978, 1983). Grobler (1974) estimated the size of defended territories at 0.25–0.4 km². In Zambezi N. P., minimum spacing between territorial bulls was 1–2 km and 2–3 km among six territorial Giant Sable bulls in the study area (Estes & Estes 1974). Between the time they are driven away from the breeding herds by territorial bulls as three-year-olds, subadult bulls often roam alone if there is no bachelor herd in the area. In any case, a young adult prospecting for a territory tends to isolate himself from other ♂♂ and to haunt a particular locality, which he proceeds to patrol and demarcate by scraping the ground with his forefeet then defecating, on a patch of bare ground or on a road, and by thrashing small trees with his horns. In time he lays claim to a piece of land wherein he may mate with any receptive ♀♀ that enter.

Very little information on territorial tenure is available. Two known bulls in Matopos N. P. occupied the same pieces of real estate for at least two years (Grobler 1974). In Shimba Hills National Reserve, where large territories were maintained with very low turnover, eight territorial ♂♂ were known to occupy the same territories between two and four or more years, with an average of 2.8 years (Sekulic 1978). There is a link between territory size and habitat quality, as noted by Ross (1984), with prime territories being smaller than those in more marginal habitats, and equally territorial tenure is shorter in the prime locations.

Sable territoriality is unusual in that not all territorial bulls are equal. As observed both in the Shimba Hills National Reserve and in the Luando Reserve, there are 'master bulls' that can invade and supplant their neighbours (Estes & Estes 1974, Estes 1991a). For example, a known bull without a herd invaded a herd that was accompanied or tended by a neighbouring ♂ and, after intense displays and a brief fight (in kneeling attitude), took over the herd. However, he only stayed for a day before returning to his own territory and the displaced bull came back. In other instances, a bull whose efforts to prevent a herd from exiting his land by threat and dominance displays and chasing were unavailing, crossed over with them and the neighbour bull acknowledged subordinate status by keeping a respectful distance. The most likely explanation for such territorial inequality is dominance based on seniority: younger territorial bulls continue to acknowledge the dominance of seniors who intimidated them in their bachelor days. In Matopos N. P., Grobler (1974) divided territorial ♂♂ into three different classes: central, peripheral and outer territorial ♂♂. Only the central ♂♂ were in regular contact with the female herds.

All observed territories included woodland, into which bulls often withdrew when alone. They are surprisingly inconspicuous standing in the shade, considering how a bull stands out in a herd of ♀♀ and young, especially while actively herding, urine-testing and dominating the cows and adolescent ♂♂. When his herd is on the move, the bull brings up the rear but can dictate the direction by performing such dominance and threat displays as lateral presentation, head-shaking, horn-sweeping and low-horn presentation (head lowered, chin in, horns pointing towards opponent) (Estes 1991a). But when a herd is resident for an extended period in one territory, the proprietor is often absent, either patrolling and marking his boundaries or remaining solitary in the woods.

Research in the Shimba Hills National Reserve noted that female and calf Sable herds typically moved through the territory of 8–10 different bulls during their annual foraging through their home-range (Ross 1984). As noted, bulls have access to oestrous ♀♀ only when they are within their own territory. Ross (1984) quantified the amount of times different ♀♀ were in the territory of different bulls, since herds often split up into smaller groups that ranged in different areas of their home-range. Certain ♀♀ exhibited distinct 'territorial preferences', spending a disproportionate amount of time with a 'preferred' bull. Most interestingly, such ♀♀ returned to their 'preferred territory' to give birth. Since ♀♀ in the Shimba Hills exhibit postpartum oestrus, these ♀♀ are mated immediately by the resident bull. It seems likely that this preference allows the calf and mother greater protection from the bull, since in all likelihood the calf is the offspring of the territorial bull (Ross 1984).

When a herd bull's urine testing detects a cow in pro-oestrus, he begins courtship displays, following her in lowstretch (neck and chin outstretched), lateral presentation of the body in the erect posture, and laufsclag (or foreleg lifting). Should the ♀ prove unreceptive, running away or circling to avoid contact, a bull may become aggressive, hitting her with his horns and chasing her, even roaring. Cows, when persistently chased, scream their distress and end by lying prone in total submission (Estes & Estes 1974). Such unusually aggressive behaviour was also observed by Grobler (1974), Kingdon (1982) and in a captive herd by Buechner *et al.* (1974). A receptive cow stands performing the submissive head-in display with

tail out in response to foreleg lifting, whereupon the bull mounts and completes copulation within a few seconds (Estes & Estes 1974).

Urine-testing, which enables ♂♂ of most ungulates to monitor female reproductive status, is also performed very frequently by ♀♀ and even young calves in this species (likewise in Roan Antelopes and probably in the whole tribe). Research into the behaviour and reproductive physiology of captive ♀♀ has shown that urine testing can serve to synchronize reproduction among associated individuals (Thompson 1995, Thompson & Monfort 1999).

Behaviour of Sable Antelope mothers and calves is typical of the 'hider' system prevalent among antelopes (Estes 1991a). A cow preparing to calve typically seeks seclusion and grass tall enough to conceal a calf during the 2–3 week hiding period. Exceptionally, however, a cow may remain in her herd and calve on bare ground (Sekulic 1978). A mother remains on guard within the area where the calf is hiding but may not know its exact location and has to search for it when retrieving and suckling it two or more times a day (Thompson 1996). Following these activity periods, during which a calf may have social contact with other calves if the mother leads it to her herd, it seeks and remains in a new hiding place until retrieved again. Calves are sometimes found hiding together (Grobler 1980b). After calves join the herd at 2–4 weeks (Thompson 1998), they associate together in crèches and only seek out their mothers to nurse. They have even less contact after weaning but continue to associate with their peers in definable subgroups. The bond between calves is so much closer than the maternal bond that calves often end up separated from their mothers, a situation promoted by the tendency of crèches to lag behind the rest of the herd (Estes 1991a). Calves born after the annual peak may not join a crèche but instead rest with the herd (Thompson 1998).

Usually silent, ♀♀ and young exchange surprisingly high, bird-like calls when searching for one another. When hotly pursued by a bull, ♀♀ and young ♂♂ emit a harsh scream, and bulls emit a braying roar when chasing other Sables. Sable Antelopes are rarely found closely associated with other ungulates.

Reproduction and Population Structure The Sable Antelope is an annual, seasonal breeder throughout most of its range, which lies almost wholly in the single wet-season zone. Mating occurs toward the end of the dry season and calving occurs over a period of several months at the end of the rains. As fecundity is strongly influenced by nutrition, mating should occur when the breeding population is in peak condition. Recorded conception rates have been nearly 100% (Wilson & Hirst 1977). Yet Sable Antelopes unable to find green pasture at the end of the dry season are likely to be in only fair to poor condition. One natural and one anthropogenic occurrence may raise the Sable's nutritional plane: the regrowth of foliage a month or more before the rains in the miombo 'spring' and green pasture resulting from burning. Calving late in the rains is a time of plenty, when tall grassland provides secure hiding places during the concealment period. Most calves (ca. 80%) are born during a two-month calving peak: Feb–Apr in Zimbabwe (Child & Wilson 1964, Grobler 1974, Wilson 1975); Jan–Feb in N Botswana (Child 1968); Feb–Mar in Kruger N. P. (Fairall 1968); and May–Jun in Giant Sable reserves (Estes & Estes 1974). In Kenya, with two wet seasons characteristic of the equatorial region, the Sable Antelope has no fixed breeding season. Like the Roan, ♀♀ have a postpartum

oestrus and may reproduce every 9–10 months (Sekulic 1978, Ross 1984). Males are fertile all year round (Wilson & Hirst 1977).

Gestation period has been given as 240–248 days (Wilson & Hirst 1977) and 259–272 days (mean = 266; Grobler 1980b). Mean birth mass for ♂♂ has been recorded as 19 kg (range 13.5–19.8; n = 26) and for ♀♀ 20.3 (range 13.5–22.5; n = 22) (Grobler 1980b). The faded tan colour and markings of newborn calves change to the adult form within two months, by which time the horns are 2–3 cm long. Both sexes of *H. n. niger* begin to darken in their first year and become progressively darker with age, to the point where mature cows can be mistaken for bulls. In the other races ♀♀ may become a richer, chestnut colour with age, but only ♂♂ turn black, beginning in their fourth year and proceeding from forequarters to hindquarters. The horns grow straight up, becoming twice ear-length in yearlings and beginning to curve in the second year. Calves are weaned at about eight months; the milk composition of free-ranging Sable Antelopes has been investigated by Osthoff *et al.* (2007), and seems comparable to that of ovines.

Males become adolescent and capable of breeding by 1.5 years (Wilson & Hirst 1977). Their horns are thicker than those of ♀♀ but do not become longer and more curved until the third year, by which time (2.5 years) ♀♀ are fully grown and pregnant (although ♀♀ in captivity may calve at two years). Males continue growing for another two years, becoming larger and dominant over ♀♀ and developing much thicker, longer horns of more pronounced curvature.

As in virtually all sociable, territorial bovids, the adult sex ratio is skewed in favour of ♀♀, in consequence of male sexual competition and selective predation. The fact that female offspring are philopatric while ♂♂ are driven from the maternal herd and home-range when they develop obvious male secondary characters is the main reason. For instance, the adult sex ratio in a subpopulation of 415 animals in Victoria Falls was 36 : 64 (Estes & Estes 1969b). In Matopos N. P., Grobler (1974) calculated a 1 : 1 yearling sex ratio, compared with a 1 : 2.18 to 1 : 2.38 overall adult sex ratio. Territorial ♂♂, spaced out on their territories, typically comprise 10–12% of the population (R. D. Estes pers. obs.).

Survival and recruitment rates, based on percentage of immature animals to adult ♀♀ were assessed in the Shimba Hills National Reserve, Victoria Falls and Luando Reserve during a two-year study (Estes & Estes 1969a, b, 1974):

| | Shimba Hills | Victoria Falls | Luando |
|---------------|--------------|----------------|--------|
| Calves (%) | 86.5 | 47.5 | 75.2 |
| Yearlings (%) | 37.8 | 35.0 | 53.1 |
| 2-yr-olds (%) | 18.9 | 26.4 | 39.8 |

Weigl (2005) gives a longevity record for *H. n. niger* in captivity of 22 years and three months. Females more than ten years of age have been recorded calving (Grobler 1980b).

Predators, Parasites and Diseases Predator density is low in the miombo woodland zone, reflecting the low density of prey species. Leopards *Panthera pardus* and Spotted Hyaenas *Crocuta crocuta* are the main predators, followed by African Wild Dogs *Lycaon pictus*, mainly through predation on calves and juveniles. The tendency of the young to associate in crèches, which regularly lag behind the herd, increases their vulnerability. In the southern, drier parts of the

Sable Antelope's range there are more Lions, Spotted Hyenas and African Wild Dogs, but the presence of abundant and preferred prey species such as Plains Zebras *Equus quagga* and Common Wildebeest *Connochaetes taurinus* usually buffers the Sable – though apparently not in Kruger N. P. (Pienaar 1969a). There may also be some hesitation to take on the adults, as the Sable can defend itself more effectively than most antelopes, especially by stabbing backward and sideways with its scimitar horns, a fighting technique rarely deployed against conspecifics except in sparring matches (Estes 1991a). If it proves to be a habit, moving from feeding grounds to a resting/ruminating spot after dark could be an additional anti-predator strategy (Estes 1991a).

In the Shimba Hills National Reserve (Ross 1984), a Sable bull was observed defending a calf from a Leopard attack. By roaring loudly and charging the Leopard, the bull successfully frightened the Leopard off the calf, which only sustained a few scratches. The incidence of 'female territory preference' described earlier suggests that the bull could in fact have been defending his own calf, despite the fact the Sable herds typically move so freely through different territories in the course of the year (Ross 1984).

The tall grasslands utilized by Sable Antelopes in the dry season are often heavily infested with ticks, especially clusters of hundreds of larval 'pepper ticks' in the inflorescences. Various species of ixodid ticks have been recorded from Sable: in the Central Province of Zambia, Zieger *et al.* (1998b) recovered five species from a single animal, namely *Amblyomma variegatum*, *Boophilus decoloratus*, *Rhipicephalus appendiculatus*, *R. evertsi* and *R. lunulatus*.

Sable Antelopes react to the alerting calls of associated oxpeckers (*Buphagus* spp.), which play an important role in reducing tick loads, especially concentrations around the tail, ears and neck. Observations of different Sable populations in Zimbabwe suggested that the more oxpeckers present the less heavy tick loads and associated sores were in evidence. In Zambezi N. P., where there were few oxpeckers compared to Hwange N. P., tick loads were noticeable especially in lactating ♀♀, which were in the poorest condition. Some animals had missing eartips, probably caused by infected tick bites (less likely due to occasional freezing temperatures). In Matopos N. P., where oxpeckers had been largely eliminated through cattle-dipping and reduced wildlife in surrounding areas, the Sable Antelopes were not only in mostly poor condition but some were seriously infested with ticks and had large sores resembling mange (Estes & Estes 1969b).

The parasites of Roan and Sable Antelopes were investigated in Percy Fyfe N. R. by Wilson & Hirst (1977). Four protozoal parasites of the blood and organs were implicated in the deaths of juvenile Sable and Roan, including *Cytauxzoon* sp. and *Babesia* sp., both tickborne diseases, *Chlamydia* sp., a chronic disease of domestic calves, and *Pneumocystis carinii*. A rapid loss rate of calves only a few days old from cytauxzoonosis infection was explained by the finding that *Cytauxzoon* sp. could be transmitted by the mother via the placenta. Helminthiasis (eight species identified) was only a secondary problem and not an important factor by itself in Sable mortality. Exceptional worm burdens could lead to some loss of condition but were far outweighed by primary deficiencies in diet. However, infection by *Haemonchus* spp. was suspected as a main cause of mortality in Sable Antelopes in Zimbabwe under particularly moist conditions (Grobler 1981b). Thomas *et al.* (1982) report

infections of Sable Antelopes by *Babesia*, *Theileria* and *Anaplasma* spp. Sable Antelopes have been reported to be more resistant to anthrax (caused by *Bacillus anthracis*) than are Roan (Pienaar 1961).

Conservation IUCN Category: Least Concern (*H. n. variiani* – Critically Endangered A2cd; C2a(i)). CITES: Appendix I (*H. n. variiani* only).

Distribution and numbers of Sable Antelopes have been reduced by loss of habitat (to settlement, cultivation, development schemes) and poaching. Range and numbers were severely reduced during Mozambique's civil war, while the effects of recent wholesale poaching in Zimbabwe are not yet fully known or realized. A 2004 aerial survey of Liuwa N. P. and surroundings in SW Zambia (Barotseland) indicates that both Sable and Roan Antelopes have been eliminated from the region (P. Viljoen pers. comm.). A former stronghold of Sable in N Botswana, near the Caprivi border, has been severely impacted by the construction of the Northern Buffalo Fence, which has affected their access to water, causing significant mortality.

Of the total Sable population estimated by East (1999), about half were estimated to occur in and around protected areas. Major protected populations of the species occur in Selous (probably the largest in Africa), Moyowosi-Kigosi, Ugalla River, Katavi-Rukwa, and Ruaha-Rungwa-Kisigo-Muhesi Game Reserves (Tanzania); Kafue N. P. (Zambia); Liwonde N. P. (Malawi); Niassa G. R. (Mozambique); Hwange N. P. (Zimbabwe); Chobe N. P., Moremi and Okavango-Linyanti Game Reserves (Botswana); and South Africa's Kruger N. P. (where in decline either due to habitat degradation or high predation pressure; Grant & Van der Walt 2000, Owen-Smith *et al.* 2012) (East 1999).

In Kenya, the only major population (representing Roosevelt Sable) occurs in the Shimba Hills National Reserve. A nucleus herd from this population could be translocated as foundation stock to create a second reserve in one of the places where Sable Antelopes formerly occurred. Possible sites include Mwangea Hill near Vitengeni west of Malindi, Jombo Hill or Mrima Hill south of the Shimba Hills, and the South Coast near Lunga Lunga. In addition to reducing the risk of having only one population in the limited area of the Shimba Hills National Reserve, protecting another example of the indigenous fauna and flora of the *Brachystegia/Diospyrus* ecotype of the coastal hinterland would be highly desirable for the preservation of Kenya's biodiversity.

Sable have been widely reintroduced on private land and provincial nature reserves in South Africa, Swaziland, Zimbabwe, Botswana and Namibia (East 1999). Many of these reintroduced populations are small, and this poses a genetic threat to Sable. In a survey of 136 ranches in Zimbabwe with Sable Antelope, 35% had fewer than 50 individuals and 20% of all populations had less than 10 animals (du Toit, R. F. 1992). Consequently, inbreeding, evidenced by increased calf mortality, is a major risk in many of the smaller, privately owned herds (Grobler & Van der Bank 1994).

Luando Reserve and Cangandala N. P. are the essential strongholds for Giant Sable. Expeditions mounted in 2002 and 2004 established that herds still survived in both protected areas – despite near-to-total absence of protection during and after Angola's 28-year civil war (Estes 2002b, Goering 2002, Walker 2004, Baldus 2005, O'Keefe 2005, Vaz Pinto 2006). However, now that peace has come

to Angola, the Giant Sable may be more threatened than ever (Estes 2002b, Walker 2004). Virtually all of the 25,000 or more people who lived in the Luando Reserve during the mid-1970s moved out and took refuge in cities and towns during the fighting. By 2002, Angolans were flooding back into the areas they had evacuated. Unless the government can strictly limit the number of people coming back into Luando and other protected areas, the habitat available to wildlife will be increasingly limited. Unscrupulous foreign trophy hunters prepared to pay almost any price to hunt Giant Sable may come in considerable numbers. The best hope for the Giant Sable's survival is a National Park that encompasses both the Luando Reserve and Cangandala N. P., wherein conserving Sable habitat has top priority (Estes 1983). Unless the Angola Government underwrites this alternative in the near future, it may be too late for this iconic animal.

Although instances of hybridization with the congeneric Roan Antelope are extremely rare in the wild (see Taxonomy), camera-trap photos taken in Cangandala N. P. in 2005 revealed the presence of hybrids of the Critically Endangered Giant Sable with Roan. Hybrid animals were identified by their unusually long, floppy ears and uncharacteristic facial markings. In Jan 2006, a Roan bull was seen leading the Sable herd, further evidence that cross-breeding between the single Roan bull and the Sable cows was taking place, apparently in the absence of a mature Sable bull and/or absence of Roan cows (Vaz Pinto 2006). Survey work revealed that only 10, elderly Giant Sable cows survived in Cangandala N. P., and that they produced only hybrids (called robles) after 2005. A total of 10 robles were born up until 2010 at the rate of one every six months or so. The hybrids included two ♂♂, which developed into large bulls. In 2009, a 400-ha captive-breeding enclosure was established in Cangandala N. P. and in Jul and Aug of 2009, the nine surviving Sable cows (the tenth had since died of old age) – of estimated ages 8–14 years – were transferred to a holding boma in the enclosure, later to be joined by a bull airlifted 100 km from the Luando Reserve. Unfortunately, expectations that the captive cows would produce a bumper crop of calves were dashed when only three calves were born in 2010.

In 2010, photographic evidence of a two-month-old hybrid calf in Cangandala N. P., accompanied by its hybrid mother, proved that hybrids were fertile after all, although it was unclear whether hybrids were breeding among themselves, or whether the calf was the outcome of a Sable or Roan backcross with a hybrid. This spurred a second capture operation in 2011, which included doubling the size of the fenced sanctuary to 3400 ha, hopefully large enough to

enable two herds with two territorial bulls to coexist. In Jul and Aug, a capture team logged over 100 helicopter hours flying over the Luando Reserve and Cangandala N. P. and found no Sable in the southern part of Luando, where Unita troops based at Mulondo had probably killed all resident herds (numerous poachers camps indicated continuing heavy commercial poaching). However, four different herds (the largest numbering 24) were recorded in the northern part of the Luando Reserve near Cunga Palanca, each accompanied by a territorial bull. In addition, three, solitary, territorial bulls were sighted, yielding a total of 60 animals (7 bulls, 21 cows, 11 calves, 12 yearlings and 9 two-year-olds). Three ♀♀, one two-year-old ♂ and one solitary territorial bull were translocated to the enlarged sanctuary in Cangandala N. P. At the same time, in Cangandala N. P., all of the known hybrid robles were darted one at a time. The two mature bulls and a sub-adult ♂ were castrated, and the six roble cows had their udders removed to prevent them rearing young. In summary, fewer than 100 Giant Sable, and more likely 60–70 animals, are all that survive in Luando Reserve. Thus, the *in situ* captive-breeding efforts in Cangandala are do or die for the Giant Sable.

Measurements

Hippotragus niger

HB (♂♂): 1924 (1877–1985) mm, n = 4

T (♂♂): 465 (425–515) mm, n = 4

HF c.u. (♂♂): 524 (457–550) mm, n = 4

E (♂♂): 237 (225–265) mm, n = 4

WT (MM): 191.0, 260.0 kg, n = 2

Botswana (Smithers 1971)

Haltenorth & Diller (1980) give Sh. ht. as 1270–1430 mm for ♂♂ and 1170–1350 mm for ♀♀. In E Zambia, Wilson (1968) gave the mean weight for 15 ♂♂ as 234.7 kg (range 212.0–262.7) and for 10 ♀♀ as 217.9 kg (range 203.9–231.0). Grobler (1974) estimated the mass of six ♂♂ darted in Matopos N. P. at between 155.0 and 270.0 kg

Maximum recorded horn length is 164.8 cm for a pair of horns of a Giant Sable from Angola (Rowland Ward)

Key References East 1999; Estes 1991a; Estes & Estes 1969a, b, 1974; Grobler 1974, 1980a, b; Ross 1984; Wilson & Hirst 1977.

Richard D. Estes

GENUS *Addax**Addax*

Addax Laurillard, 1841. In: d'Orbigny, Dict. Univ. Hist. Nat. I, p. 619.

Addax is a monotypic genus containing the *Addax nasomaculatus*, a desert antelope that originally ranged so widely over the Sahara that it represented a single gene-pool and even the most assiduous splitters have been unable to argue convincingly for recognition of subspecies. This taxonomic detail is a good biological indicator of the absence of physical or ecological boundaries in open deserts, even when that desert is as extensive as the Sahara. It is also an indicator of the extent of movements made by these animals and of their former great numbers. Of course, there have been more humid periods when the Sahara became a mosaic in which stretches of arid land became interspersed with more savanna-like habitats. At such times there may well have been some tendency for subpopulations to become distinct; none the less, these periods would seem not to have lasted long enough to allow subspeciation.

Both morphological and genetic studies cluster *Addax* and members of the genus *Oryx* (e.g. Hassanin *et al.* 2012), with the latter speciating more recently; indeed, these genera have been known to hybridize (Ruhe 1993), presumably with sterile offspring. The *Addax* is known to have taken adaptation to heat-stress, solar radiation and total drought further than any other large antelope and this implies that its lineage must have made a very early start in making the necessary physiological modifications (the Arabian *Oryx leucoryx*, which most resembles the *Addax* in size and colouring, may well match it in resistance to heat and drought, but these adaptations are more recently evolved). Molecular clocks suggest that the *Addax* and *Oryx* lineages diverged about 5 mya (Hernández Fernández & Vrba 2005), which broadly corresponds with the later Messinian (6.5–5.3 mya) when the Mediterranean dried out and deserts, especially the Sahara, spread as the world became cooler and drier. Within the hippotragines, which first appear in the African fossil record at about 6.5 mya, the joint *Addax*–*Oryx* lineages' divergence from *Hippotragus* has been calculated

at over 10 mya (Hernández Fernández & Vrba 2005; and see discussion under Hippotragini). Although the latter are not desert animals today, there is much to suggest that all hippotragines share a common arid-adapted heritage, possibly beginning in Asia as the large-bodied branch of a proto-caprine lineage (Kingdon 1982). The *Addax* could, therefore, represent the culmination of some 10–14 million years of life in arid lands.

The many remarkable characteristics that are so authoritatively described in the profile of *Addax nasomaculatus* imply that even at the beginning of the 'Messinian Crisis', the ancestors of this species were probably already the best equipped large herbivores to adapt to a prolonged 'ordeal by drought'. Their survival, until very recently, in the driest fastnesses of the Sahara represents a period of refinement to the many challenges of the Sahara that is probably as old as the desert itself, so much so that no other free-ranging large mammal can approach it for efficient utilization of the Sahara's scarce and scattered resources.

While concern was voiced in the 1930s about impending extirpation of this unique genus (In Tanoust 1930, Brocklehurst 1931), the crass ineptitude of deaf colonial powers has been augmented by their successors and by many contemporary international policy-making bodies, notably those concerned with promoting livestock and so-called 'development'. Together with the armed, motorized men that have done most of the killing, all these institutions suffer a selective myopia towards the ecological and evolutionary processes that have enabled useful and beautiful organisms to make their livings in the remotest and most difficult regions of the world. The casual emptying of naturally adapted life out of the Sahara exposes the shallowness and brutality of our cultures and institutions; it will be among the many severe indictments of our generation.

Jonathan Kingdon

Addax nasomaculatus ADDAX

Fr. *Addax*; Ger. *Mendesantilope* oder (*Addax*)

Addax nasomaculatus (de Blainville, 1816). Bull. Sci. Soc. Philom., Paris 1816: 75. No type locality given. Lydekker (1914: 148) stated it was 'probably Senegambia', but Grubb (2005) noted that it was more probable that British hunters or collectors obtained *Addaxes* from the Tunisian Sahara, to which he restricted the type locality.

The *Addax* probably takes its name from the vernacular Arabic *agas* or *adas*. The specific name *nasomaculatus* – meaning 'spotted nosed' – refers to the contrasting white patches on the otherwise darker head.

Taxonomy On the basis of differences in pelage between museum specimens from Tunisia and Sudan, Lydekker (1908) suggested the possibility of two subspecies, *A. n. nasomaculatus* and *A. n. addax*. However, this was rejected by Flower (1932) on the basis of observed seasonal differences in pelage throughout the *Addax*'s range, and although Allen (1939) attempted to reopen the debate, the issue was put to rest by Ellerman & Morrison-Scott (1951) and Setzer (1956) following examination of original and current specimens. Ansell

(1972) treated the *Addax* as monotypic. Synonyms: *addax*, *gibbosa*, *mytilopes*, *suturosa*. Chromosome number: 2n = 58; the first pair of autosomes are submetacentric, while all other chromosomes are acrocentric (Wurster & Benirschke 1968). Their chromosomes share many common features with other Hippotragini (Claro *et al.* 1996). *Addax* and Scimitar-horned *Oryx* *Oryx dammah* hybrids are known and reported to resemble *Addaxes* in European zoos (Ruhe 1993). Hybrids born at Bou-Hedma N. P. in Tunisia (believed to be sired by an oryx ♂) were large bodied like oryx, with typical oryx horn shape, but with obvious *Addax* body colouration and body shape (R. Molcanova pers. comm.).



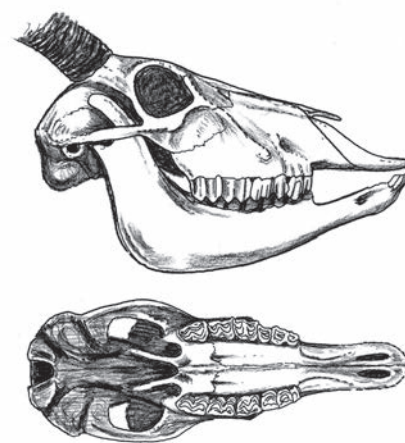
Addax *Addax nasomaculatus*.

Description A predominantly white, stocky-bodied, medium-sized antelope inhabiting the sand seas and gravel plains of the Sahara. Head light grey or beige, with contrasting white patches in front of the eyes, linked across the bridge of the muzzle. Small white patches behind the eyes. Nose beige, lips and chin white. Crown and forehead sporting a prominent, wig-like tuft of dark brown hair. Ears white with a long basal tuft of pale hairs. With the exception of the throat and chest, which are beige, overall body colour is bright matte white. During the hot season (Apr–Oct) pelage is short, but in the colder months (Nov–Mar) it lengthens on the neck, chest, shoulders, back and flanks, becoming greyer, a characteristic especially obvious in Addaxes held in zoos with cold winter climates (Renshaw 1902). Adults of both sexes develop a beige fringe of variable length on the lower neck. Legs white with beige patches on knees. Hooves broad and splayed. Tail short and white, sporting a sparse tuft of dark terminal hairs. Other than slight differences in size, weight and horn development in adults, sexes are essentially similar. Pedal glands are present on all four feet.

Both sexes bear corkscrew-shaped horns, which grow upwards and outwards, reaching over one metre in length. The horns of the adult ♂ are stockier than those of the ♀, often having two to two-and-a-half turns to the female's one-and-a-half to two. Horns are heavily annulated over the first two-thirds of their length in both sexes. Over time, and with violent sparring, the horns of the ♂ may become lost, damaged or blunted.

Geographic Variation None recorded (and see Taxonomy above), although Addaxes inhabiting colder, North African climates tend to maintain a longer and darker pelage than sub-Saharan populations, a characteristic shared by animals kept in northern zoos.

Similar Species The Addax's size, colouration and habitat preferences leave little chance of misidentification in the field. However,



Lateral and palatal views of skull of Addax *Addax nasomaculatus*.

lack of familiarity with the animal due to its rarity, together with long flight distances, makes comparison desirable with the Scimitar-horned Oryx *Oryx dammah* and the Dama Gazelle *Nanger dama*, both of which have in the past been sighted in close proximity to Addaxes.

Oryx dammah. Now extinct in the wild. Larger, averaging 150 kg; off-white with rusty-red neck and cape instead of pure white; scimitar-shaped horns; occupies sub-desert steppe rather than true desert.

Nanger dama. Smaller (60 kg); white and rusty rather than pure white colouration; short, lyrate horns; occupies sub-desert steppe and wadis rather than true desert.

Distribution Endemic to the Sahelo-Saharan region of Africa, west of the Nile Valley. As with other ungulates of the Sahelo-Saharan fauna, the Addax has undergone an unprecedented reduction in its geographical range over the past century, and although the issue's gravity is only just being seriously considered by the international conservation community, authors in the 1930s (In Tanoust 1930, Brocklehurst 1931) had already raised the alarm, identifying excessive offtake and motorized hunting as the prime cause of the Addax's decline.

Historical Distribution Their presence in prehistoric times is reflected in rock engravings and paintings (Hugo & Bruggmann 1999), as well as on walls of tombs in the Nile Valley from the Sixth Dynasty (In Tanoust 1930, Heim de Balsac 1931), although there is no solid proof of the Addax occurring east of the Nile R. (Manlius 2000b). They are depicted in North African mosaics from Roman times. Historically widespread, and present in suitable habitats in all countries sharing the Sahara Desert (Nachtigal 1879–89, In Tanoust 1930, Kock 1970, Newby 1984a, Beudels-Jamar *et al.* 2005a). The coastal Atlantic deserts of Mauritania and ex-Spanish Sahara, extending as far north as the Moroccan Drâa Valley and the southern edge of the Atlas Mts formed the western and north-western limits to the Addax's distribution (Marçais 1937, Morales Agacino 1950, Valverde 1957, Loggers *et al.* 1992). In the central Sahara, the great ergs and hamadas (Lhote 1946, Walter & Breckle 1986, Kowalski & Rzebik-Kowalska 1991) and further east, the Western Desert of Libya and Egypt (Hufnagl 1972, Osborn & Krombein 1969, Osborn & Helmy



1980), were all former Addax strongholds. In the southern Sahara and bordering Sahelo-Saharan steppes, the Addax was formerly numerous along a several thousand kilometre front, stretching from Mauritania to C Sudan via Mali, Niger and Chad (Brocklehurst 1931, Shaw 1945, Lhote 1946, Brouin 1950, Audas 1951, Monod 1958, Gillet 1969, Kock 1970, Wilson 1980, Lamarche 1987, Heringa 1990).

Current Distribution Although already long extinct in Morocco, Tunisia (1932) and Egypt (ca. 1900), and extremely rare in Libya and Algeria (Lavauden 1926a, Brocklehurst 1931, Cabrera 1932, Flower 1932, Bigourdan & Prunier 1937, Blancou 1958a, b, Dupuy 1967, Hufnagl 1972), the Addax was still present in fair numbers in Mauritania, Mali, Niger and Chad up until the late 1960s and early 1970s (Monod 1958, Hue 1960, Edmond-Blanc *et al.* 1962, Gillet 1964). Massed herds, drawn together by exceptional grazing, could then still be found in Chad, Mauritania and Mali (Newby 1978a, Lamarche 1980). Monod (1961, 1990), on his fourth voyage across Mauritania's Majabat sand sea in 1960, counted the tracks of more than 5000 Addaxes in a single day and over 11,000 in the space of a week.

Today, the Addax is confined to two to three sparsely inhabited areas of E Niger and W Chad, lying between the Termit/Tin Toumma area of the former and the Djourab of the latter (Grettenberger & Newby 1990, Thomassey & Newby 1990, East 1999, Mallon & Kingswood 2001a, Claro & Sissier 2003, Monfort *et al.* 2004, Newby *et al.* 2004, Planton & Ascani 2004, Wachter *et al.* 2004a, Beudels-Jamar *et al.* 2005a, Wachter *et al.* 2008, 2009, Wachter & Newby 2010). Possible rare vagrants from these areas may be seen in N Niger, S Algeria and Libya. They are rumoured to persist in former strongholds straddling the Mali–Mauritania (Majabat Al Koubra) frontier and in Egypt, but there is no recent supporting evidence (Hoath 2003, F. Claro pers. comm.). Aerial and ground surveys carried out in the Erdis and Mourdi of NE Chad in late-2005 recorded no Addaxes. In early

March 2007, the fresh tracks of about 15 Addaxes were seen in C Mauritania, in an area where they had not been seen for over 20 years (R. Vernet pers. comm.).

Habitat The most desert-loving large ungulate, frequenting areas of extreme temperature (range -5 to $+60^{\circ}\text{C}$) and aridity (less than 100 mm annually). With the exception of truly mountainous areas, the Addax has been recorded from all major Saharan habitat types, ranging from gravelly and sandy plains, to dune fields, sandy basins and depressions, pans and wadi systems (In Tanoust 1930, Newby 1978a, Lamarche 1980, Giazzi 1996). Their preference is for harder, packed sands and flatter areas within and between dune fields that support perennial vegetation. Although not a mountain species, Addaxes use wadi beds to penetrate Saharan massifs in search of food and shade. Their local distribution is heavily influenced by the presence of suitable pasture and shade during the hottest months (Apr–Aug), when Addaxes may move into the more wooded sub-Saharan grasslands during periods of drought, or when attracted by rainfall and any resulting pastures (Gillet 1964, 1965, Newby 1978a).

Abundance Probably fewer than 300 animals survive in the wild, distributed unevenly along a narrow, 600 km-long band lying between Termit/Tin Toumma in Niger and the Djourab sand sea in Chad. The main population is in Niger, probably numbering around 200 individuals. Otherwise, they are found in widely separated small groups, typically singletons or small herds of 2–3 animals (Ama *et al.* 1998, Lamarche & Hamerlink 1998, Barmou & Oumarou 2000, Scholte 2001, Amadou 2002, Monfort *et al.* 2004, Wachter *et al.* 2004a). In the Termit/Tin Toumma area, M. Ascani (pers. comm.) reported the tracks of a group of 57 Addaxes during the cold season of 2001–2002. In the same area, Claro & Sissier (2003) observed 34 in 2002 (and see Claro 2004) and a systematic survey carried out by Wachter *et al.* (2004a) recorded 26 Addaxes and estimated a population size of 227 (with 95% CI between 93 and 555) for the area of 8814 km² sampled. In September 2004, a total aerial count of some 93,000 km² of prime Addax habitat to the east of the Termit Massif returned a total of 128 Addaxes (Keita 2004, Planton & Ascani 2004). Ground and aerial surveys in 2005 in N Chad (Beudels-Jamar *et al.* 2005a) turned up only one, all-adult group of nine Addaxes. In May 2007, more than 60 animals were again spotted in the Termit/Tin Toumma area of Niger (T. Rabeil pers. comm.). In November 2007, 71 Addax were spotted in Tin Toumma during a combined ground and air survey. Statistical treatment of data suggests a population size of around 200 animals (Wachter *et al.* 2008, 2010).

Addaxes have been reintroduced to fenced sectors of protected areas in Tunisia (Bou-Hedma N. P.) and Morocco (Souss-Massa: 70 animals released 1994–97 increased to ca. 550 by 2007; Cuzin *et al.* 2007). During 2007, 33 Addax from Bou-Hedma N. P. and zoos in Europe and the United States were introduced to enclosures in Tunisia's Djebel and Senghar National Parks in the Great Eastern Erg (Molcanova & Wachter 2010). Addaxes from Souss-Massa N. P. in Morocco have also been released into a small, 600-ha enclosure at Safia just north of the Morocco–Mauritania border (T. Abaigar pers. comm.).

In comparison with the situation in the wild, *ex situ* presence and status is healthy, with over 600 Addaxes in Europe, North America, Japan and Australia in managed breeding programmes. At least 1000

more individuals are held in private collections and ranches in the United States and the Middle East (Engel & Brunsing 1999, D. Noble pers. comm., T. Correll pers. comm.).

Adaptations The Addax displays a large number of morphological, physiological and behavioural adaptations to life in a hot, dry environment, including pale colouration to reflect radiant heat, pelage length and density to assist with thermoregulation, barrel-bodied shape to reduce surface area/volume ratio, and large, splayed and spongy hooves for moving in a hot and sandy environment.

The Addax has a highly efficient moisture extraction and retention system. The rumen and omasum are important in water economy and conservation (Ruckbush & Thivend 1979), and faeces are exceptionally dry. Consumption of plants, such as *Boerhavia repens* or *Limeum viscosum*, may be the source of the fine mucilaginous film coating the faeces that assists ejection (Gillet 1965). The Addax likely exhibits physiological heat and moisture control measures described in other large desert-living mammals, including urine concentration (Monod coined the term 'addaxite' for the rock-hard aggregation of sand and Addax urine!), osmoregulation and sodium retention, high tolerance to thermal stress, low metabolic rate, high switch-on point for sweating and the presence of an efficient blood temperature cooling system in the nasal sinuses (Taylor 1969, Taylor & Lyman 1972, Cloudsley-Thompson 1977, Schmidt-Nielsen 1979, Louw & Seeley 1982). Research on free-ranging Arabian Oryxes in Saudi Arabia (Ostrowski *et al.* 2003) has demonstrated a high degree of heterothermy, up to $4.1 \pm 1.7^\circ\text{C}$ per day, permitting an estimated water economy of more than 0.5 l per day in thermoregulation. It is likely that a similar adaptation exists in the Addax.

Behavioural adaptations include feeding during cooler hours and at night, and sheltering and resting during the heat of the day. Seasonal distribution and frequency of traditional resting sites is often influenced by presence of shade (Newby 1981). Animals have been recorded excavating shelter behind vegetation or on the shade side of dunes using both hooves and horns (Lamarche 1980, Dragesco-Joffé 1993).

Foraging and Food The Addax is a grazer, the diet of which is based almost exclusively on the small number of plants able to prosper under the desert's harsh regime. Staples include the xerophytic grasses *Stipagrostis vulnerans* and *S. acutiflora*, and the prickly succulent *Cornulaca monacantha*. *Stipagrostis vulnerans* and *C. monacantha* are particularly favoured, their distribution and quality often defining the Addax's local presence, foraging behaviour and movements (Monod 1958, Gillet 1964, Lamarche 1980, Monfort *et al.* 2004, Wachter *et al.* 2004a). Addaxes may remain for weeks or months in areas of good grazing. As plants dry out, or begin to green after a period of drought, Addaxes will clamber on to tussocks, pawing away sand and dead vegetation to reach new or remaining green shoots and leaves.

As temperatures in the open desert rise (shade temperatures during the hot season regularly exceed 45°C), or the quality of vegetation diminishes, Addaxes will move towards the sub-desert steppes or mountainous areas where surface rainfall run-off or subterranean seepage allow the growth of vegetation and the maintenance of sparse trees and shrubs. At times like this, plants such as *Panicum turgidum*, *Aristida mutabilis*, *Moltkiopsis ciliata* and

Indigofera spp. are eaten. As with all Sahelo-Saharan ungulates, as well as Ostriches *Struthio camelus*, the succulent, but bitter, wild melon *Citrullus colocynthis* is especially sought, containing as it does a rare source of moisture. It is at these times that Addaxes will also browse on shrubs, such as *Leptadenia pyrotechnica*, *Capparis decidua*, *Maerua crassifolia* and *Acacia tortilis*, eat the long fleshy parasite *Cistanche phelypaea* (Lamarche 1980, Wachter *et al.* 2008) – a habit that may have given rise to the belief held by the bedu that the Addax eats snakes – and strip *P. turgidum* grasses of their seed heads (Gillet 1964).

Although tropical rainfall in the Addax's domain is a rare event, it does happen occasionally, giving rise not only to temporary standing water but also to rich, ephemeral pastures known as *jizu* or *eshoob* by the Arabs. Jizu pastures, which are often extensive, are composed of only a small number of perennial species (such as *S. acutiflora*, *Astenatherum forskalii*, *Limeum* sp., *Heliotropium* sp., *Cyperus conglomeratus* and *Tribulus* sp.), but are highly attractive to Addax and other desert fauna (Newby 1978a, 1984a, Wilson 1978, Poilecot 1996). The Sahara is also prone to winter rainfall from Mediterranean weather fronts. If insufficient to leave standing water, the combination of drizzle plus cold night-time temperatures (regularly as low as $1\text{--}2^\circ\text{C}$) favours plant growth and the greening of perennials. Since the Addax very rarely has access to free water, its diet must provide both food and moisture. With adequate grazing, animals are able to survive for long periods, possibly years, without drinking. However, under conditions of poor grazing and high temperatures they lose condition and eventually succumb. On occasions when it is available, Addaxes will drink water in large quantities.

Social and Reproductive Behaviour The Addax is nomadic, wandering over large areas in search of grazing. Movement and duration of stay within any one locality is dictated by quality of grazing, and in the hotter months, to a certain extent by shade. It will remain in the general vicinity of good grazing for long periods. Although not a migrant in the true sense of the word, the Addax undertakes local, seasonal movements in relation to vegetation and climatic conditions. In the relatively uniform desert and sub-desert lands of the Sahel, movements tend to be north–south in direction, i.e. from the more arid desert to the less arid sub-desert and Sahel (Gillet 1965, Newby 1978a). In C Niger, movement may also be east–west, i.e. from the open desert towards the better-wooded and more varied habitats of the Air and Termit mountains (Hue 1960). In Mali and Mauritania, seasonal movements are north-west to south-east, between the dunes of the Mreyye and the better vegetated Aklé (Lamarche 1980, 1987).

Addaxes generally live in small herds of up to 15 animals, comprising ♂♂ and ♀♀ of all ages (Lhote 1946, Lamarche 1980, Walters 1981, Mackler 1984). The larger groups observed in the past, sometimes numbering several hundred, were probably the result of many smaller herds congregating seasonally and temporarily in areas of exceptional grazing (Nachtigal 1879–89, In Tanoust 1930, Monod 1961, Newby 1978a). With increasing persecution, and as a result of mortality due to the severe droughts of the past four decades, average Addax herd size today is rarely more than half a dozen (Dragesco-Joffé 1993). In Niger, between 1980 and 1991, average herd size was 2.2 (range 1–5, $n = 27$) (Rapant 1992, Poilecot 1996). In the wild, herds are generally led by an adult cow (Lamarche 1980), although Mackler (1984) observed male dominance under captive

conditions. During the rut, the alpha-male interacts aggressively with challengers, engaging in long bouts of horn wrestling, and chasing off younger ♂♂ (Newby 1978a, Lamarche 1980, Mackler 1984). In captivity, ♂♂ have been observed to engage in flehmen and lausschlag to assess oestrus in ♀♀ and to elicit receptivity for copulation (Mackler 1984).

Shortly before parturition, the ♀ moves away from the herd, possibly to avoid the attentions of the dominant bull. The young is born in a shallow scrape, often in the shelter of vegetation if available, the cow and calf joining the herd after 3–4 days. For the first few days, the cow leaves her calf to join the herd to feed, often moving considerable distances in doing so (In Tanoust 1930, Lamarche 1980).

Reproduction and Population Structure In the wild, frequency of births and resulting calving periods depend on pasture condition. Under good conditions ♀♀ demonstrate postpartum oestrus and can breed throughout the year (Dolan 1966a, Dittrich 1986). In times of severe drought or periods of poor grazing, reproduction is disturbed and ♀♀ may either abort, abandon young calves, or not calve at all until pasture improves (Newby 1978a, Lamarche 1980). In general, however, ♀♀ have one young per year, usually calving during the cooler months (Sep–Mar).

The gestation period is between 34.5 and 38.5 weeks, and a single calf is born weighing between 5.0 and 8.6 kg (mean = 7.0; n = 96 from animals in captivity, Ferrell *et al.* 2001; see also Puschmann 1989, Engel & Brunsing 1999). Calves are rusty-beige at birth, progressively taking on the adult pelage over the first year of its life (Lamarche 1980). Calves are weaned after 6–10 months and reach sexual maturity between 24 and 30 months (Densmore 1986, Dittrich 1986). In captivity, the reproductive behaviour of Addaxes has been well studied (Manski 1991) as has their reproductive endocrinology (Asa *et al.* 1996, Hall-Woods *et al.* 1999). Mean oestrous cycle length at St Louis Zoo was 32.3 days. Longevity under zoo conditions is in the order of 25–28 years (Jones 1993, Weigl 2005).

Predators, Parasites and Diseases A healthy adult Addax has no natural predators. Young calves are harassed and taken by Golden Jackals *Canis aureus* (Lamarche 1980, J. Newby pers. obs). Other potential predators, before their almost total extirpation in the Sahara, included Cheetahs *Acinonyx jubatus*, Striped Hyenas *Hyaena hyaena* and African Wild Dogs *Lycan pictus*.

Diseases in the wild are little known, although Addaxes are reported to be susceptible to rinderpest (Brouin 1950). In captivity, Addaxes have been identified as the hosts of a wide range of bacterial, viral and intestinal organisms, including Johne's disease (Burton *et al.* 2001), yersiniosis (Raverty 2002), encephalomyocarditis (Citino 1995), clostridium (Gulland & Parsons 1987) and roundworms (Craig 1993).

Conservation IUCN Category: Critically Endangered A2cd; C1+2a(ii). CITES: Appendix I. CMS: Appendix I.

Along with other large Sahelo-Saharan mammals, including the Slender-horned Gazelle *Gazella leptoceros* and Dama Gazelle, the plight of the Addax has been largely overlooked by the conservation community. The Scimitar-horned Oryx *Oryx dammah* is already 'Extinct in the Wild' and the species mentioned above are all down to highly fragmented populations of less than 500 individuals at best. With the notable exceptions of a CMS project, funded by the French

government (FFEM) and the European Union, and the establishment in 2004 of the Sahara Conservation Fund (SCF), direct support for conservation to the region is extremely limited.

The decline and extirpation of the Addax, along with the other large ungulates of the Sahara and Sahel, can be attributed primarily to a murderous combination of the motor vehicle, the modern rifle and man's cupidity (Newby 1980, 1981, 1982, 1988). The further impacts of civil war, severe drought (1969–72, 1983–84) and the extension of pastoralism into desert lands, thanks to the increase in wells, have also taken a heavy toll on wildlife. During the recent past, a new and potentially disastrous threat from hunters from the Gulf states has also emerged (*Le Sahel* 2002, BBC 2003, *El Watan* 2003, UNEP/CMS 2004), a phenomenon earlier addressed by Newby (1990a) and Cloudsley-Thompson (1992). Lastly, the exploration for oil (and the construction of wells and pipelines for its exploitation) in Niger's Tin Toumma desert is having a major impact on Addax distribution and access to grazing, as well as leaving them vulnerable to opportunistic hunting by military detachments providing security to the oil workers (Sahara Conservation Fund 2010).

Establishment of protected areas for the Addax and other Sahelo-Saharan species, and designating the Addax as a strictly protected species in all range states, has been a case of too little too late. Although massive reserves, such as the Ahaggar (4,400,000 ha) and Tasilli (1,140,000 ha) in Algeria, the Aïr/Ténéré (7,736,000 ha) in Niger, the Ouadi Rimé–Ouadi Achim (7,795,000 ha) in Chad, and the newly established Wadi Howar N. P. in Sudan cover areas where the Addax formerly occurred, they are under-resourced or no longer harbour Addaxes (Newby 1982, 1984b, 1991, UNESCO 1998, Monfort *et al.* 2004, Newby *et al.* 2004). In early 2012, Niger established the Termit and Tin Toumma National Nature Reserve, a 97,000 km² tract of desert and sub-desert land specifically designed and managed to protect Addax and other threatened species. In the short term, the only way of saving the Addax from extinction in the wild is to multiply efforts on the ground to protect it and its remaining critical habitat. Given the terrain and the political instability in the Addax's remaining range, this is a significant task. Continued support for gazetted reserves in Chad and Niger, together with the establishment of new protected areas, especially along the Mali/Mauritania frontier (Majabat) and Chad (Bodélé, Eguey), will only succeed if adequately supported and combined with programmes to create incentives for the local people to protect wildlife wherever it is found (Newby *et al.* 1987, Newby 1990b, 1992, 2002). Addax, together with other Sahelo-Saharan ungulates, should be the subject of a binding, inter-governmental, regional agreement and action plan under the Bonn Convention. International efforts and diplomacy are needed to ensure that foreign hunters behave responsibly, respect local and international laws, and contribute to wildlife conservation and restoration programmes. To combat the threat from oil activities, far better communication and cooperation between ministries and operators in the same country are essential.

In Morocco and Tunisia, reintroduction schemes are beginning to bear fruit (Engel & Brunsing 1999, Cano *et al.* 2001, Wakefield & Molcanova 2001, Anonymous 2003, Molcanova & Wachter 2010), and these are providing valuable lessons and experience needed for reintroduction and local captive-breeding initiatives in countries where the Addax is still extant (Dixon *et al.* 1991). Luckily, a number of zoos in Europe and the United States are maintaining genetically robust stocks of Addax ready for reintroduction. Like



Addax *Addax nasomaculatus*.

all reintroductions, however, efforts will come to nothing unless the root causes for the Addax's extinction are addressed beforehand (Spalton *et al.* 1999, Dunham 2001).

Ultimately, as In Tanoust (1930) said in his authoritative work on Saharan wildlife, the desert itself is the Addax's best protection: 'l'addax est une pauvre bête, facile à tuer, et qui n'a qu'une protection: le desert' [the addax is a sorry beast, easy to kill, and with only one protection: the desert itself].

Measurements

Addax nasomaculatus

HB (♂ ♂): 1600, 1700 mm, n = 2

HB (♀ ♀): 1540, 1580 mm, n = 2

T (♂): 340 mm, n = 1

T (♀ ♀): 260, 280 mm, n = 2

HF c.u. (♂ ♂): 95, 95 mm, n = 2

HF c.u. (♀ ♀): 95, 100 mm, n = 2

E (♂ ♂): 200, 200 mm, n = 2

E (♀ ♀): 175, 185 mm, n = 2

Sh. ht (♂ ♂): 1060, 1140 mm, n = 2

Sh. ht (♀ ♀): 1060, 1080 mm, n = 2

WT (♂ ♂): 101.0, 125.0 kg, n = 2

WT (♀): 82.0 kg, n = 1

Air Mts, Niger (Brouin 1950)

WT (♂ ♂): 94.4, 104.0 kg, n = 2*

WT (♀ ♀): 94.7 (87.1–108.9) kg, n = 3*

WT (unsexed): 104.0 (91.0–115.0) kg, n = 4**

Captivity (*St Louis Zoo [Fischer *et al.* 1993]; **The Living Desert [T. Correll pers. comm.])

Maximum recorded horn length from the native range is 91.4 cm from the Sudan, although an animal in Texas, USA, had horns measuring 103.2 cm (Rowland Ward)

Note: A wealth of information on the dimensions of the skull, skeleton and brain of the Addax can be found in von Oboussier (1974)

Key References Beudels-Jamar *et al.* 2005a; In Tanoust 1930; Gillet 1964; Lamarche 1980; Mallon & Kingswood 2001a (and chapters therein); Newby 1978a.

John Newby

GENUS *Oryx*

Oryxes

Oryx de Blainville, 1816. Bull. Sci. Soc. Philom., Paris 1816: 75.

The genus *Oryx* embraces several forms of desert antelope, including the Gemsbok *Oryx gazella*, the Arabian Oryx *O. leucoryx* and the Scimitar-horned Oryx *O. dammah*. Until recently, the north-east African Beisa Oryx *O. beisa* was commonly subsumed as a subspecies of the Gemsbok, but most authors now regard Beisa as a distinct species (Grubb 2005; and see Osmers *et al.* 2012). The latter course has been followed in this work.

The genus *Addax* has many resemblances with *Oryx*, but the two lineages diverged some 5.3 mya (Hernández Fernández & Vrba 2005). It would appear that while *Addax* became specialized to exploit the driest areas of the Sahara, *Oryx* maintained sufficient versatility to adapt to (literally) more marginal areas of the four great desert regions of Afro-Arabia. Thus, the Scimitar-horned Oryx formerly flourished in a broad swathe around the Sahara, both to the north and to the south. The Beisa Oryx inhabited extensive areas

of semi-desert around the Horn of Africa, and the Gemsbok spread widely throughout the Namib and Kalahari arid region. The Scimitar-horned Oryx is, perhaps, the more wholly desert-adapted of the three African species, sharing its white colouring and diminished size with both the Arabian Oryx *Oryx leucoryx* and the Addax *Addax nasomaculatus*.

As animals from regions where predators are few, young oryxes seem to be consistently susceptible to heavy predation in spite of occasional examples of protective threats by adults (Tilson *et al.* 1980, Mills 1990, Molcanova *et al.* 2001, M. Stanley Price pers. comm.). It can be suspected that there are similar vulnerabilities to parasites and diseases to which other antelopes are immune. Thus, desert-acquired susceptibility to predators and diseases are likely to be major selective forces confining *Oryx* to dry open areas with few other antelopes or carnivores and where recruitment can keep up with mortality.

Whether the Arabian Oryx ever occurred on the African mainland, west of Sinai, has been a matter of some conjecture. This species formerly occurred through most of the Arabian Peninsula, north to Kuwait and Iraq, but the last populations were hunted out by 1972. A concerted reintroduction programme was initiated in 1982 (Stanley Price 1989). The probable presence of this species in the Sinai during prehistoric times (see Osborn and Osbornová 1998) raises the question as to whether the species could have got through the Isthmus of Suez and colonized the Egyptian deserts to the east of the Nile R. In reviewing the question of whether the Arabian Oryx occurred in Egypt during pharaonic times, Manlius (2000c)

focused attention on a desert hunting scene depicted in a fresco from the walls of Neferhotep's tomb of Drab Abul Neggah, near Thebes. Neferhotep lived during the XVIIIth Dynasty, from 1427 to 1392 BC. The hunting scene depicts an oryx whose morphology and coat colouration closely resembles that of an Arabian Oryx. This is not irrefutable evidence of the presence of Arabian Oryxes in the Eastern Desert, and the pharaonic fresco might equally be evidence that Egyptians went hunting in Arabia (T. Wachter pers. comm.).

Jonathan Kingdon

Oryx gazella GEMSBOK (SOUTHERN ORYX)

Fr. Gemsbok; Ger. Südafrikanischer Spiessbock

Oryx gazella (Linnaeus, 1758). Syst. Nat., 10th edn 1: 69. 'India'; understood to be South Africa (Thomas 1911: 152).

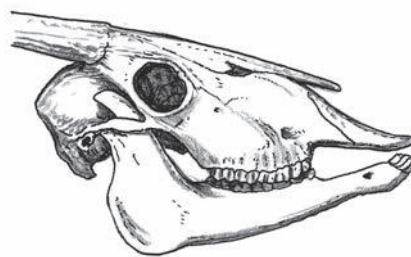


Gemsbok *Oryx gazella*.

The origin of the name Gemsbok is obscure, but appears to be a combination of the German word 'gems' for the European chamois and the Dutch word 'bok' for buck.

Taxonomy Monotypic species including only those animals from southern Africa (following Kingdon 1997, East 1999, Grubb 2005, Osmers *et al.* 2012), and excluding forms *beisa*, *gallarum*, *annectens* and *callotis* (and other allied forms) from the East and north-eastern parts of Africa (contra Ansell 1972, Grubb 1993c).

Synonyms: *aschenborni*, *bezoartica*, *blainei*, *capensis*, *nec*, *onyx*, *oryx*, *pasan*, *recticornis*. Chromosome number: $2n = 56$ (Hsu & Benirschke 1968, Wurster 1972, Gallagher & Womack 1992, Kumamoto *et al.* 1999). One male $2n = 57$ specimen deviated from the normal complement due to aneuploidy; this animal died from maternal



Lateral view of skull of Gemsbok *Oryx gazella*.

neglect on the day of birth, although post-mortem investigations did not reveal any congenital abnormalities (Kumamoto *et al.* 1999). The X chromosome is a large acrocentric and the Y chromosome is a small acrocentric (Kumamoto *et al.* 1999). Gray (1972) reports hybridization in captivity between the Beisa Oryx *Oryx beisa* and Gemsbok, which produced viable offspring.

Description A large, thick-necked, monomorphic antelope with long straight horns aligned with the muzzle, large and oval ears, and a distinctly marked body pattern. Muzzle tip white with characteristic bold black facial strips extending from the horns to the dark muzzle ring, all set on a white background. Belly bright white, with a contrasting black flank strip that extends to the elbow and hindquarters; lower legs have characteristic white stockings and black hooves. Remaining upper body a distinctive pale cream-grey, with a thin dark brown mane from shoulders to mid-back, widening after into saddle above rump and narrowing again towards tail. Tail is long, black and hangs to below the hocks. Pelage short and sleek, body hairs about 35 mm long. Like all oryx species, neck and shoulders are enveloped in an exceptionally thick, inelastic and dense skin. Distinctive dewlap at throat, with a dark brown line down the mid-line to between the forelegs. Newly born Gemsbok pelage is light brown to reddish in colour without any distinctive markings. Juveniles start to develop adult colouration at six months, when horns also start to become more prominent. Pedal glands are present on all feet; the constituents of these glands have been investigated by Wood (1997b); preorbital and inguinal glands are absent. Sexes are difficult to tell apart, except that adult ♂♂ are heavier set.

Horns present in both sexes, ♂♂ with shorter, stockier horns. The first third of the cylindrical horns is ribbed, remainder being long, smooth and ending in notably sharp tips.

Geographic Variation There is no obvious geographical variation, but Angolan animals are distinguished by their narrower black markings.

Similar Species

Oryx beisa. Allopatric, occurring in East Africa only. Slightly smaller, with a more brown-grey coat colour and less prominent flank strips and upper leg markings, and lacks a black muzzle ring. A particular subspecies, *O. b. callotis*, in SE Kenya and NE Tanzania has prominent black-haired ear fringes.

O. dammah. Saharan species, now extinct in the wild. Smallest of the African species; characteristic apricot-brown forequarters and white body coat, with no dark facial or flank patterning; long, characteristically arched horns.

Distribution Endemic to southern Africa, south of the Cunene and Zambezi Rivers, formerly with a marginal intrusion into SW Angola.

Historical Distribution Formerly occurred widely in the semi-arid and arid bushland and grassland of the Kalahari and Karoo and adjoining regions of southern Africa (East 1999). Gemsboks ranged well south of the Orange R. in South Africa into Namaqualand and the central Karoo and marginally into Limpopo Province of South Africa. They ranged throughout Namibia and Botswana, though largely absent from parts of N and NE Namibia (including the Caprivi Strip) and within and to the north of the Okavango Delta in Botswana (as well as parts of the south and south-east). Extended peripherally into NW Zimbabwe, at the eastern limit of the Kalahari sand areas north and south of Hwange N. P. (Smithers & Wilson 1979) and SW Angola, north to about 75 km inland of Benguela (Crawford-Cabral & Veríssimo 2005).

Current Distribution Gemsboks remain widely, albeit patchily, distributed in south-western southern Africa, although populations in SW Angola are now considered extirpated, even from the former stronghold in Iona N. P. (East 1999). The species does not range as far south into the Karoo and Namaqualand as it once did, but it has been reintroduced in parts of its former range in the Northern Cape, largely onto private land and some national reserves such as Karoo N. P. There have been widespread reintroductions elsewhere within the former range, and Gemsboks have also been introduced in several areas, including onto private land in Zimbabwe (some of these populations may now have been extirpated) and in Limpopo Province of South Africa (East 1999).

An apparently viable population has become established on the White Sands Missile Reserve, New Mexico, USA.

Habitat Gemsboks prefer open arid to semi-arid grasslands with intermittent wooded or karroid shrublands receiving less than 500 mm annual rainfall. In Botswana and Namibia, they occur in open savanna and light woodlands, but at the arid extreme of their distribution they range into extensive dune fields and arid mountainous areas. In the arid Kalahari system, they prefer *Acacia*-



Oryx gazella

dominated savannas in combination with scattered pans. The pans and dry river beds are particularly important for their mineral licks sites, which offer important mineral supplements to the animals' generally poor-quality Kalahari diets. Furthermore, it has been suggested that the mineral licks may also be an important source of clay, crucial in neutralizing the effects of acidosis, in addition to minimizing the effects of plant secondary compounds in the rumen (Kreulen & Jager 1984). Gemsboks penetrate moister *Baikiaea* and Mopane *Colophospermum mopane* woodlands in the eastern areas of their range.

Abundance In the southern Kalahari, Gemsbok densities ranged between 0.45 and 0.87 animals/km². With the demise of migratory Common Wildebeest *Connochaetes taurinus* and Red Hartebeest *Alcelaphus buselaphus caama* populations in the Kalahari, there appears to have been an increase in Gemsbok numbers in the central Kalahari system; their independence of surface water and non-migratory behaviour seems to have helped them survive the adverse effects of the veterinary cordon fences that have had such a detrimental impact on populations of migratory game (Spinage & Matlhare 1992). In 1997, the Gemsbok population in the southern Namib was estimated to be 10,400 strong, at a density of 0.17 ind/km², which appeared to be down from the estimate of 0.53 ind/km² in 1984 (Kilian 1997). Population estimates are available for almost all of this species' range, with Namibia (187,000), Botswana (125,000) and South Africa (13,000) collectively harbouring about 320,000 of a combined total population of 330,000 animals. However, actual numbers are probably higher because of an unknown level of undercounting bias in aerial surveys. East (1999), assuming an average correction factor for undercounting bias of 1.3, produced a total population estimate of 373,000.

Adaptations Gemsboks are extremely well adapted to surviving in hot and arid environments. Their pelage is well suited to reflect radiant heat, there is evidence that they show adaptive heterothermy

in extreme desert conditions, they are able to conserve body water more efficiently than virtually all other artiodactyls, they can regulate their brain temperature, and they have a range of thermoregulatory behaviours.

Taylor (1969) proposed that brain temperature regulation, especially during exercise, was achieved by counter-current heat exchange between the cool venous sinus blood derived from the nasal veins and the network of carotid artery blood vessels, known as the carotid rete situated at the base of the brain. Recent work by Maloney *et al.* (2002) on free-ranging Gemsboks has demonstrated that brain cooling, as in all other ruminants that have been studied, is a component of routine thermoregulation. The system completely shuts down during times of extreme exercise or stress, and is triggered most often in the late afternoon when the animal's body temperature is in the rising phase of its circadian rhythm. Its effect may be to reduce evaporative water loss. During exercise the animal rids itself of excess heat through panting (which increases the air flow over the capillaries of the veins in the nasal passages) or sweating.

Behavioural adaptations are a key part of the Gemsbok's ability to survive in arid environments. It is able to survive without drinking water by selecting for higher quality foods through its more selective feeding on succulent plant parts (facilitated by its relatively narrower muzzle than expected for an animal of its size), shifting to better quality browse in the dry months, making extensive use of water-rich melons and tubers, and by feeding predominantly in the cooler evenings (Knight 1991, 1995b). Furthermore, they lie up in cool sand and make extensive use of shade, spending up to 40% of the day in the shade, 10% more than Common Wildebeest in the Kalahari. Gemsboks also reduce water loss while foraging during daylight hours by actively orientating their body in such a way as to reduce the surface area directly exposed to the sun's rays. This behaviour was noticeably more common in the hot dry season. Gemsboks are also up to 13% less active than Common Wildebeest, which in itself saves both energy and water. Moreover, it appears that activity budgets and feeding rates of Gemsbok are shaped more by external factors such as air temperature, vegetation height and group size, than by sex and reproductive differences (Ruckstuhl & Neuhaus 2009).

Water turnover rate is the lowest known (85 ml/kg per day) (Macfarlane *et al.* 1971). The Gemsbok's kidneys are relatively efficient in their water retention ability as reflected in their ability to handle water with 1.8% total dissolved salts (Giddings 1990). Furthermore, the stomach of the Gemsbok also shows morphological adaptation to conserving water. The colon ascendens makes up 80% of the length of the colon; this is the main site of water reabsorption and reduces water content from 82% in the proximal gut to 56% or less in the faeces (Reiðig 1995). Finally, the Gemsbok can moderate its breathing to reduce the loss of moisture in the respiratory tract.

Foraging and Food Gemsboks have a great capacity to digest high-fibre diets—a further adaptation to surviving in their arid environment (Hofmann 1973, Reiðig 1995). Although they are predominantly grazers (80–93% of diet), they broaden their diets in the dry season to include a greater proportion of browse, ephemerals and *Acacia* pods, which make up 6% of their diet at this time (Knight 1991). In the Kalahari, they prefer productive short-grass habitats associated with pan edges and dry river beds in the wet season, moving into the taller, less palatable longer grasslands in the dry season.

Gemsbok tend to be rather generalist in their selection of grasses and forbs, feeding on *Stipagrostis ciliata*, *Eragrostis lehmanniana* and *Tribulus terrestris* throughout the year, but switching to more resilient and fibrous *S. amabilis* and *S. uniplumis* and water-rich Tsama Melon *Citrullus lanatus*, when available, during the dry season. They appear to avoid the prolific annual grass *Schmidtia kalahariensis* when it is green during the wet season, probably because of a chemical irritant produced by this grass, but they do feed on it in the dry season. Gemsboks also feed extensively upon protein-rich pods of *Acacia erioloba* and *A. haematoxylon* during the dry seasons. Overutilization of *A. erioloba* pods is known to cause prussic poisoning in Gemsboks. By virtue of their narrower muzzle and use of browse, Gemsboks are able to select for a better quality diet, particularly in the dry season, than similar-sized, broad-mouthed grazers such as Common Wildebeest.

Stomach contents have a very high moisture content (82%), so much so that Bushmen used the rumen juice as a source of water, squeezing and straining the liquid through grass into skin containers (Skinner & Chimimba 2005). To supplement their required daily water intake (which Knight [1995b] estimated at 2.5–4 litres depending on weather conditions), Gemsboks make extensive use of water-rich fruits such as the Tsama Melon in the Kalahari and Nara *Acanthosicyos horridus* in the Namib. They also excavate the tuber of the astringent-tasting Gemsbok Cucumber *A. naudinianus* during the dry months, as well as others such as *Brachystelma* spp., *Cucumella cinerea*, *Neorautanenia brachypus* and *Talinum tenuissimum* (Williamson 1987, Knight 1995b). The Gemsbok Cucumber appears to be a more predictable source of water than the Tsama Melon, which varies considerably between areas and years in its abundance. Dieckmann (1980) recorded Gemsboks digging for the roots of *Grielum humifusum* during the dry season in Namaqualand. When freshwater is available individuals will drink up to 21 litres every five days (Dreyer 1987). Introduction of drinking water to the South Africa side of the Kgalagadi Transfrontier Park appeared to result in a higher density of Gemsboks than the adjacent, but waterless, Botswana side of the Park. As an energy-saving tactic, Gemsboks are considerably less active than other large herbivores such as Common Wildebeest. Daily foraging distances average 9 km for both sexes.

Social and Reproductive Behaviour Gemsboks are gregarious, occurring in mixed herds (averaging about eight animals) and nursery herds, although solitary ♂♂ are also common. Herds are usually relatively small, up to 30, but larger herds of as many as 300 can form in the wet season (Knight 1991). Although the ♂♂ are territorial, they show some degree of tolerance towards other adult ♂♂. Solitary territorial bulls have territory sizes ranging between 14 and 30 km² in the southern Kalahari, while adult female home-ranges vary between 260 and 530 km² depending upon environmental conditions (Knight 1991). Some territories have been held by the same individual for as long as three years (Knight 1991). By contrast, non-territorial bulls may range over areas of 3600 km². In the absence of access to drinking water, home-ranges of adult ♀♀ vary between 1400 and 3074 km² (Knight 1991). In the central Kalahari G. R., female home-ranges varied from 52 to 212 km²; five ♂♂ (probably territorial) had annual ranges of 10–16 km² (Williamson & Williamson 1988). In Namaqualand in the Northern Cape, the mean size of territories was 7.6 km², and tended to be delimited by drainage lines and kopjes (Dieckmann 1980).

Adult ♂♂ mark their territories with piles of dung that they deposit in a characteristic low crouch. The dung piles are often left under or adjacent to large trees or bushes, predominantly around the periphery of the territory (Dieckmann 1980, Knight 1991). The territories appear to be patrolled on a regular basis. The ♂♂ defend their territories from other ♂♂ through threat-like behaviour that includes ground pawing, horning of shrubbery and head-on clashes (Dieckmann 1980). Such aggressive behaviour constitutes about 20% of all social interactions. In comparison with other antelopes, Gemsboks appear to show relatively high levels of aggression as reflected in the high incidence of broken or damaged horns. The most dangerous fighting movement is an over-the-shoulder horn thrust, made when contestants are standing alongside each other, and it can result in death. The territorial bull will herd mixed and/or nursery herds into his territory. Non-territorial ♂♂ do not form bachelor groups but remain with mixed herds. When approached by adult ♂♂, subadults normally hang and shake their heads in submission and move off. Under lower rainfall regimes (less than 100 mm of rain) the territorial system is replaced with a 'following' system with ♂♂ tagging onto breeding herds. However, in favourable habitats, such as along the vegetated dry river beds in the Namib, adult ♂♂ are more sedentary. Adult ♂♂ with symmetrical horns appear to be more successful in maintaining their territories and breeding, as are adult ♀♀ in breeding (Møller *et al.* 1996).

Courtship and mating is the prerogative of the territorial bull and occurs throughout the year; non-territorial ♂♂ very rarely succeed in mating. Males test the reproductive status of ♀♀ regularly and exhibit flehmen after inserting the nostrils into the stream of a female's urine. If the ♀ is in oestrus, lauschlag may follow and if the ♀ is receptive she will stand and allow the ♂ to copulate. The ♀♀ stay with the herd during parturition or leave to give birth. The young are hidden for up to six weeks after birth, after which time the mother and young will join either a mixed or nursery herd. The effectiveness of their hiding behaviour led early colonists to think that the calves were born with horns (the horns growing some 200–300 mm during the period of concealment). Nursing of young tends to follow periods of rumination.

Reproduction and Population Structure Although single calves are born at any time of the year, there tend to be peak periods such as Aug–Sep in the Kalahari (Knight 1991) and North West Province (Skinner *et al.* 1974) and May–Jul in the Namib, which coincides with the peak wet season (J. W. Kilian pers. comm.). Gestation period is about 8.5 months; Fringe-eared Oryxes *O. b. callotis* have a postpartum oestrus, but it is not known whether the same holds true for Gemsboks. Calves are weaned at about five months. Females become sexually mature at the age of two years and first conceive at 29–33 months (Dieckmann 1980). Maximum longevity in captivity has been given as just less than 24 years (Weigl 2005). Adult ♂ to ♀ sex ratios averaged 1.0 : 1.4; adult ♀ to calf ratios averaged 1 : 0.28 (Knight 1991).

Predators, Parasites and Diseases Lions *Panthera leo* and Spotted Hyaenas *Crocuta crocuta* are the main predators of adults and calves, although Cheetahs *Acinonyx jubatus* will also prey on calves. Mills (1990) found Gemsboks made up between 32% and 52% of Lion and Spotted Hyaena kills, respectively, and Gemsboks were also

the most important food item in the overall diet of two groups of Spotted Hyaenas studied in the Namib Desert by Tilson *et al.* (1980). Spotted Hyaenas' success rate is higher (82%) for Gemsbok calves vs. 14% for adults. Adult Gemsboks often back into *Acacia* thickets as a defence strategy against attack by Spotted Hyaenas.

Simpson (1978) recorded serological evidence of bluetongue antibodies in Gemsboks in Botswana. Gemsboks are also prone to ticks in wetter areas, which may account for their inability to survive in higher rainfall areas. The ticks notably attack the udder regions in adult ♀♀. Horak *et al.* (1992a) examined 48 Gemsboks from Etosha N. P. and Hardap Dam G. R. in Namibia and recorded four ixodid tick (*Hyalomma marginatum*, *H. truncatum*, *Rhipicephalus evertsi* and an unidentified *Rhipicephalus* sp.) and two lice (*Haematopinus oryx* and *Linognathus oryx*) species. Boomker *et al.* (1986) recorded a number of helminths from an animal taken in Kgalagadi Transfrontier Park, including a number of new host records: *Haemonchus contortus*, *Longistrongylus meyeri*, *Paracooperia serrata*, *Impalalia nudicollis* and *Agriostomum equidentatum*, and Boomker (1986) later also added *Trichostongylus auriculatus*. Boomker & Durette-Desset (2003) remark on the presence of *Teladorsagia hamata* in the species.

In response to reports from game farmers regarding mortalities among Gemsboks that had been introduced in Free State, Fourie & Vrahimis (1989) conducted a study on Tussen-die-Riviere G. R. and established that the Karoo paralysis tick *Ixodes rubicundus* was responsible for paralysis and mortalities amongst the Gemsboks. The mean burden of female Karoo paralysis ticks on paralysed subadult Gemsboks was 0.83 ticks/kg host body mass (range 0.26–2.12) compared with a burden of 0.12 ticks/kg host body mass (range 0.03–0.18) on healthy adult animals. Gemsboks with high tick burdens were therefore more likely to suffer paralysis compared with Gemsboks with lower tick burdens. Paralysed animals were found during May and Jun of each year, corresponding closely with the peak period of activity of the Karoo paralysis tick.

Conservation IUCN Category: Least Concern. CITES: Not listed.

Despite having experienced a range contraction and decline in numbers in the nineteenth and twentieth centuries, Gemsboks remain widespread and are present in a number of well-managed protected areas (about 35% of the population), including Etosha N. P. and Namib-Naukluft N. P. (Namibia) and the mega Kgalagadi Transfrontier Park between South Africa and Botswana. Furthermore, about 45% of the entire population resides on private land (East 1999). In Namibia alone the population on private land increased from 55,000 in 1972 to >164,000 in 1992, indicative of the important role this sector of society is playing in the conservation of the species (East 1999). The Gemsbok's ability to meet its survival needs within a relatively small area of semi-arid or arid savanna, even during severe droughts, enables it to occupy much smaller mean annual ranges than migratory species such as the Common Wildebeest and Red Hartebeest. Furthermore, their independence of surface water and non-migratory behaviour have enabled it to largely escape the adverse effects of veterinary cordon fencing (East 1999). The Gemsbok's future is secure so long as protection within southern African reserves and private lands continues. Provided illegal hunting is controlled, the Gemsbok's desirability as a hunting trophy could promote further increases in population size and might extend the species' distribution.

Measurements*Oryx gazella*

HB (♂ ♂): 1995 (1220–2460) mm, n = 14

HB (♀ ♀): 2140 (1700–2400) mm, n = 15

T (♂ ♂): 418 (320–520) mm, n = 14

T (♀ ♀): 435 (400–525) mm, n = 15

HF c.u. (♂ ♂): 510 (460–580) mm, n = 14

HF c.u. (♀ ♀): 508 (450–545) mm, n = 15

E (♂ ♂): 191 (180–205) mm, n = 14

E (♀ ♀): 199 (185–225) mm, n = 15

WT (♂ ♂): 240.0, 245.0 kg, n = 2

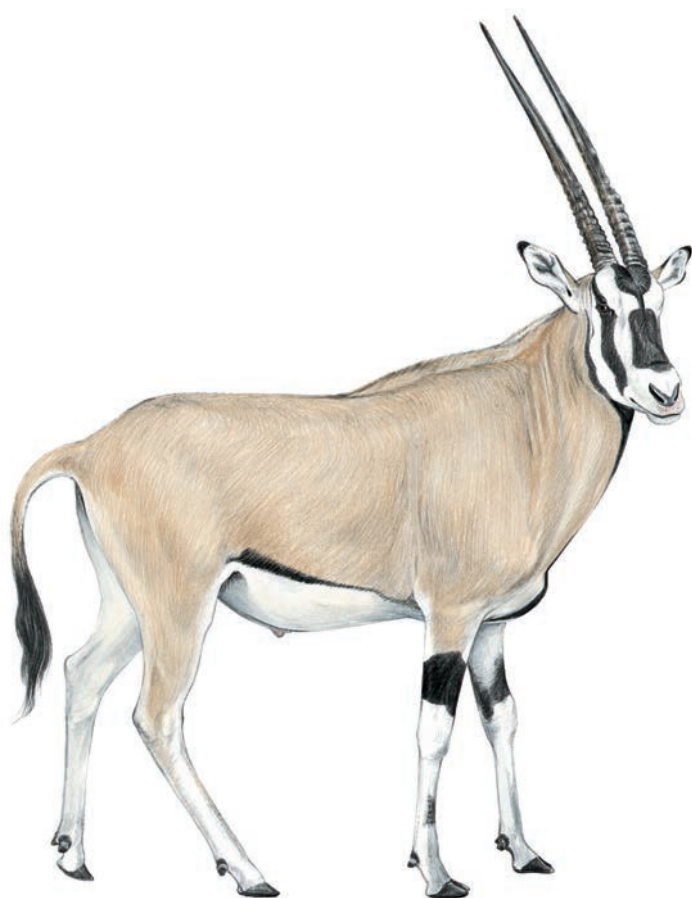
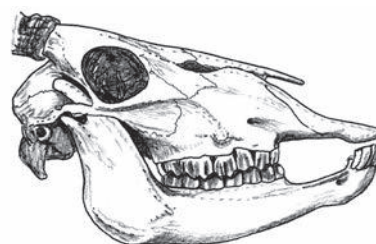
WT (♀ ♀): 200.0, 230.0 kg, n = 2

Kalahari (Smithers 1971, M. Knight pers. obs.)

Maximum recorded horn length is 125.7 cm for horns of a ♀ from the Northern Cape, South Africa (Rowland Ward)

Key References Dieckmann 1980; East 1999; Knight 1991.**Michael Knight*****Oryx beisa* BEISA ORYX (FRINGE-EARED ORYX)**Fr. *Oryx beisa*; Ger. Eritrea-Spiessbock (Swahili Choroa)

Oryx beisa (Rüppell, 1835). Neue Wirbelt. Fauna Abyssin. Gehorig, Säugeth., p. 14, pl. 5. Eritrea, 'in den Niederungen der Küstenlandschaft bei Massaua' (Red Sea coast west of Massawa).

Beisa Oryx *Oryx beisa*.Lateral view of skull of Beisa Oryx *Oryx beisa*.

Taxonomy The Beisa Oryx has frequently been treated as a subspecies of the southern African Gemsbok *Oryx gazella* (Ansell 1972), but has since been restored to full species status (Kingdon 1997, Grubb 2005), a view supported by karyotypic (Kumamoto *et al.* 1999) and molecular data (Osmers *et al.* 2012). Two morphologically recognizable subspecies of *O. beisa* are found on either side of the Tana R. in East Africa: the Beisa Oryx *Oryx beisa beisa* to the north and the Fringe-eared Oryx, *O. b. callotis* to the south (see

below). Molecular genetic investigation based on mtDNA control region and cytochrome *b* sequences from 21 *O. b. beisa* from Samburu and Marsabit in Kenya and 39 *O. b. callotis* from S Kenya and Tanzania confirmed significant genetic differentiation and historical isolation of the two subspecies, but with the complication that overall three equally distinct genetic lineages can be detected within modern East African oryx. One lineage clearly corresponds to Fringe-eared Oryx. The other two lineages are found together within oryx of Samburu and Marsabit, interpreted as evidence that what we call *O. b. beisa* today represents an ancient introgression between two of three originally differentiated subpopulations of East African oryx (Masembe *et al.* 2006). Synonyms: *annectens*, *aschenbonni*, *callotis*, *gallarum*, *reticornis*, *subcallotis*, *typica*. Chromosome number: $2n = 58$; the X chromosome is a large acrocentric and the Y chromosome is a small acrocentric. The two subspecies have indistinguishable karyotypes (Claro *et al.* 1996, Kumamoto *et al.* 1999). Gray (1972) reports hybridization in captivity between *O. gazella* ($2n = 56$) and *O. beisa*, which produced 'viable' offspring.

Description A large, thick-necked, brownish to greyish antelope with long straight horns and distinctively patterned head and ears. Face boldly striped in black and white in adults. Muzzle tip white, with black mask over bridge of nose and a black shield-shaped blaze mark on forehead overlaying a whitish background (or pale sandy buff in Fringe-eared Oryx). Mask and blaze may or may not be joined by a narrow black line and fine details of face-mask pattern are often individually distinctive at close range. Vertical black facial stripes extend from horn bases across eye to corner of mouth. Narrow black line extends down centre of throat to chest. Body

colour pale brownish-grey and pelage is dense, short and sleek. Tight, inconspicuous mane of the same colour extends from head to mid-back. Belly white (usually sandier in Fringe-eared Oryx), with a narrow black flank-stripe from elbow to just above knee. Lower legs white (sandier in Fringe-eared Oryx), and hooves and false hooves black; prominent black markings above knees of forelegs. Tail matches body colour, carrying an extensive brush of black hairs. Mature Fringe-eared Oryxes display distinctive terminal ear tassles, sometimes very prominent. Occasionally, hair loss in old Fringe-eared Oryxes may lead to extensive mottled patches of blackish skin colouration showing through on flanks and body. Hair loss may also result in appearance of all-black ear linings with no fringes. Sexes are superficially similar in the field, especially among younger age classes. Adult ♂♂ have thicker necks and deeper shoulders than ♀♀. Mature ♂♂ may sometimes be recognized at a distance by a combination of the massive neck, heavy horns and weary head-low gait adopted when walking in a typical 'controlling' position just behind a moving group. Mature ♂♂ develop a relatively enlarged scrotum compared with subadult ♂♂. For reliable separation from the more round-bellied, lighter-necked and thinner-horned ♀♀, ♂♂ are distinguished by the black penis sheath under the mid-belly or the scrotum (seen from between the hindlegs). Pedal glands are present on all four feet; preorbital and inguinal glands are absent.

The newborn calf has a uniform sandy or orange-brown body colour (almost cinamon-toned when very young) with weakly developed face pattern in tawny and buff, and a dark brown tail tuft. Body colour and pattern develops to adult tones in a continuous process from 2–6 months of age. Notably the face mask is last to develop full adult colouration, with the blaze patch at the base of the horns retaining tawny colouration longest, becoming fully black typically between 24 and 36 months of age in the Fringe-eared Oryx (Wacher 1986).

In adults, the cylindrical horns are annulated over the basal third to two-thirds of their length, but become progressively smoother and end in very hard and sharp, black shiny tips. Horns are rather straight (a more female trait), or slightly backswept (more masculine trait). Male horns are thicker and, in older individuals, often shorter, than those of ♀♀. Observation of known individuals (Arabian Oryx *Oryx leucoryx* and Fringe-eared Oryx) over time shows that full grown horns may shorten with age. This applies particularly to ♂♂, the result of splintering, breaks and tip damage in fighting, and also perhaps from wear accruing as the result of the specific behaviour of stabbing at termite mounds and soil: conceivably this serves to sharpen (and incidentally clean) the horns as well as perform a display function. Broken, misshapen horns may occur, resulting in asymmetrical, sometimes bizarre, shapes and single-horned animals, especially under managed conditions.

At birth, horn buds are present but scarcely observable in the field. At four months of age horns are approaching ear length, and have grown to match head length by about nine months. Through this period the horns typically lack annulations and appear smooth and blunt tipped, being encased in a fibrous keratinous sheath. This keratinous layer is most obvious when flaking off patchily to reveal the hard sharp adult horn material beneath. The period of this exfoliation occurs variably among individuals and in some cases for relatively extended periods between 6 and 24 months of age (Wacher 1986).

Inspection of the incisiform dentition on a series of known-age skulls (n = 46) and known-age live Fringe-eared Oryxes (n = 76

observations made on 40 or so individuals) on the Galana Ranch in Kenya indicated full sets of milk teeth up to 12 months of age. Successive eruption of the permanent incisiform dentition follows, commencing between 12 and 18 months of age, with completion occurring between 2.5 and 3.5 years of age (Wacher 1986).

Geographic Variation

O. b. beisa (Beisa Oryx): arid parts of Ethiopia and Horn of Africa, extreme SE Sudan and Kenya. Ears with small black tip; body colour tends to greyer cleaner tones (e.g. Samburu).

O. b. callotis (Fringe-eared Oryx): SE Kenya (south of the Tana R.) and NE Tanzania. Ears with long, pendulous, black-haired tips that are variable in size, developing with age; body colour tends to duller, sandier tones (e.g. Tsavo).

Similar Species

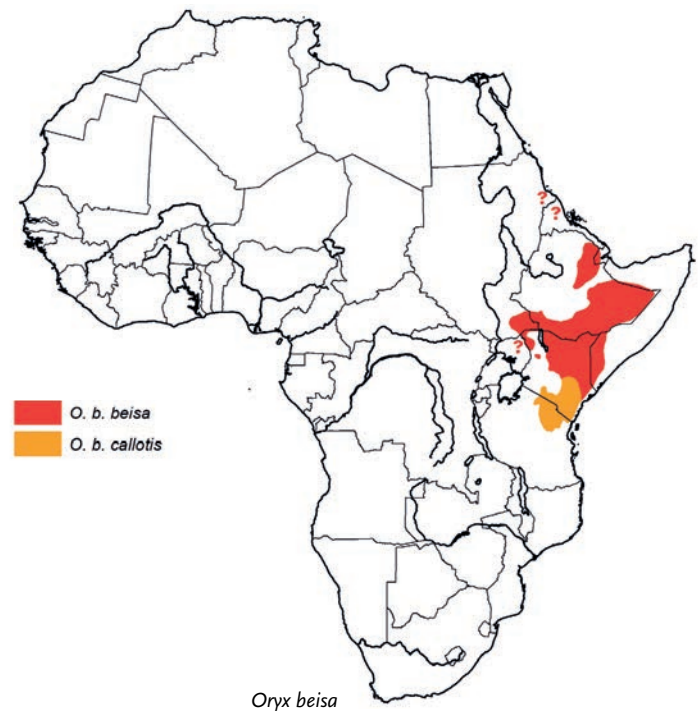
Oryx dammah. Allopatric Saharan species, now extinct in the wild. Smallest African member of genus, with characteristic apricot-brown forequarters and white body, much less contrasting facial and flank patterning, and long, characteristic arched horns.

O. gazella. The most similar species, but allopatric, occurring in south-west Africa only. Larger and brighter, with more extensive black markings, particularly on hindlegs, and a diagnostic dark patch over the upper rump; more rounded ears; horns typically more widespread.

Hippotragus equinus. Marginally sympatric in some areas (for example, SE Sudan). Much larger, somewhat redder antelope with shaggy coat and heavy curved horns

H. niger. Probably only marginally sympatric where the southern range of the Fringe-eared Oryx meets the northern part of the range of the Sable. Similar-sized antelope with reddish or black body colour and white belly and facial markings; arched horns.

Distribution Endemic to Africa.



Historical Distribution Formerly widespread in north-east Africa, from NE Sudan throughout arid areas of Eritrea, Ethiopia, NE Uganda and Kenya to Djibouti, Somalia and NE Tanzania.

Current Distribution The distribution of the species has declined markedly, especially at the margins of its range (East 1999). There is no current information on the population status of Beisa Oryxes in NE Sudan, but they survive in the south-east, mainly in Boma N. P. Likewise, in Eritrea there is no reliable recent information on their status. In Djibouti, they were restricted to the Gammaré Plateau on the Ethiopia border by the mid- to late 1980s. In Somalia, they were believed to be eliminated from the coastal plain north of Mogadishu by the late 1970s (T. Thurow pers. comm.) and survive only, as far as is known, in the south, where a population was noted in the Lag Dhere area in the 1980s (J. Sale pers. comm.). Beisa Oryxes still occur widely in Ethiopia and N Kenya. They are possibly extirpated in Uganda, although formerly common in the Bokora Corridor and Metheniko Game Reserves.

Fringe-eared Oryxes are distributed entirely south of the Tana R. in E Kenya and NE Tanzania, with a major centre of distribution in Tsavo (East) and the Galana Ranch region (Cobb 1976), spreading west and south to Mkomazi, Amboseli and sporadically appearing in Serengeti N. P. (Walther 1978c).

Habitat Beisa and Fringe-eared Oryxes prefer arid and semi-arid grasslands and bushlands, but avoid tall grass in the wet season and dense dry bush in the dry season. The condition of grazing and state of the soil influence seasonal movements. They move out of waterlogged and soft-soiled depressions and up onto higher ground during the rains, but make many cyclic peregrinations in some parts of their range. During the driest periods, and in the most arid parts of their range, movements are irregular. They occur to altitudes of 1700 m in Ethiopia (Yalden *et al.* 1996).

A radio-tracking study of range and habitat use by Fringe-eared Oryxes in the eastern lowlands of Kenya, on the Galana Ranch and Tsavo East N. P. boundary area (Wacher 1986), found significant differences in range use between some largely solitary adult ♂♂ (apparently occupants of territories) and the rest of the population (which ranged more widely) (see Social and Reproductive Behaviour below). In a generally flat landscape, characterized by a habitat sequence from lateritic and bushy red soils down through wooded and bushed grasslands on grey soils to black cotton grassland-drainage lines, analysis of radio locations on a 1 km² grid indicated a significant general association with those grid cells characterized by a mixture of habitats. This suggests that oryxes tend to remain close to the ecotone between major red soil and grey soil habitat associations in this region. Both mixed-sex herds and solitary ♂♂ showed a significant tendency to use open grassland habitats during feeding bouts in morning and evening, while moving into denser habitats to find shade in the hot middle hours of the day. Oryx herds used the open grassland habitats more in seasons of green growth while bushier red soils were frequented more often in the dry season. Individual animals made extensive movements to new grazing zones (up to 45 km recorded directly) in response to rainfall at the end of dry periods, although known solitary ♂♂ observed in these periods did not move.

During dry months, radio-collared Fringe-eared Oryxes on the eastern border of Tsavo East N. P. showed interesting behaviour in

relation to their need for water. At this time, the Galana R. becomes the main available surface water for a few weeks following the drying up of waterholes. Under these conditions herds tend to drink towards mid-day and show great caution wherever riverine thickets overlook the sand banks most favourable for drinking, but with a potential for ambush from Lions *Panthera leo* or Leopards *P. pardus*. After a trek of 10–15 km to the Galana R. bank, members of the herd stagger their drinking so that some animals are alert and always have their heads up, while others kneel to drink. Groups do not loiter or rest in such an area, rather they remain the minimum possible time and set off to march directly back within a couple of minutes of arriving, just as soon as drinking is complete. By contrast, herds visiting the open, nearly treeless banks of the artificial Aruba Dam in neighbouring Tsavo East N. P. were noted spending time resting beside the water. Solitary adult ♂♂ are also known to come to the river to drink at dusk (B. R. Heath pers. comm.) and, indeed, this was noted in the case of a radio-collared territorial ♂, who during one dry season once visited water at dusk (arriving back on his territory 12 km north at 23:00h). However, this single instance is contrasted with six other daytime excursions when the same individual arrived to drink in the middle of the day and returned to his territory before dusk. This same territorial ♂ and two adult ♀♀ with calves were observed daily throughout the late dry season month of Mar 1983. During this period all three animals were based ca. 10 km north of the river around Lali hills but never associated in the same social group. Observations confirmed that the territorial ♂ and adult ♀ with older calf trekked to the river and back once every 4–5 days throughout the month, maintaining the 10 km distance from the river during all non-drinking days. By contrast, a ♀ with a young calf and lactating more heavily, moved progressively closer to the river during the same period, and drinking intervals became shorter, diminishing from five to three days through the month. At the onset of rainfall towards the end of the month all movements to the river ceased for all three animals, as widespread small water pools became available. It has also been noted that managed oryxes supplied with water on a daily basis may also drink only at 4–5 day intervals (Stanley Price 1985b).

Abundance Densities are typically low, with aerial surveys giving densities of 0.05–0.1/km² in the Awash Valley and 0.15–0.2/km² in areas such as Mkomazi G. R. and Tarangire N. P. (East 1999; and references therein). Higher local densities were recorded in known centres of distribution in the 1970s: 0.26/km² for Marsabit in the 1970s (aerial survey KREMU data), 0.31–0.69/km² in Tsavo East N. P. (ground survey by Leuthold & Leuthold 1976), 0.54/km² in Isiolo in Kenya (Leuthold & Leuthold 1976) and up to 1.2–1.4/km² for Fringe-eared Oryxes (aerial survey of Galana Ranch in the 1970s; M. Stanley Price pers. comm.). However, it is notable that more recent estimates for some of these key areas have reported lower figures, for example, 0.05–0.1/km² in Tsavo in the 1990s (Butynski *et al.* 1997a).

Correcting for an undercounting bias in aerial surveys, East (1999) used an average density of 0.05/km² to estimate a total population of 50,000 Beisa Oryxes and 17,000 Fringe-eared Oryxes.

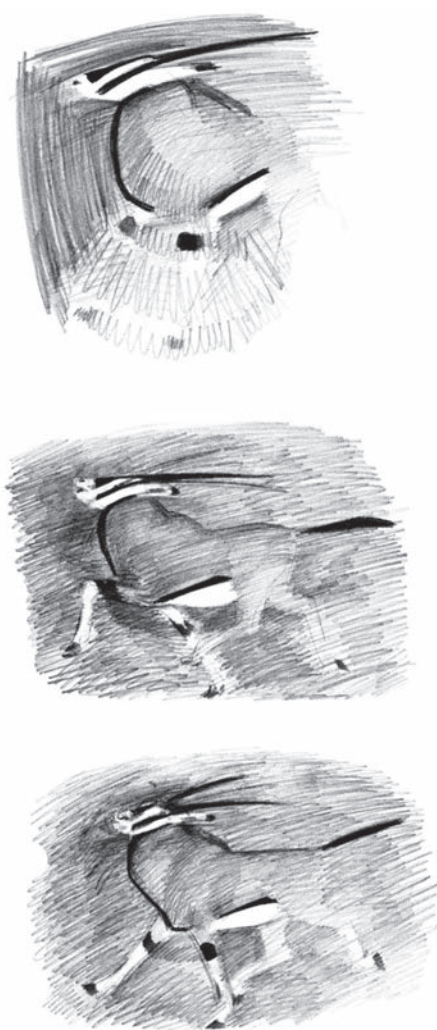
Adaptations Taylor (1969) studied oryxes to investigate their adaptation to arid environments and showed that these antelopes

have various physiological devices to reduce heat stress. Such adaptations have been shown to be widely shared by many, less obviously arid-adapted antelope and livestock species (King 1983), but are well developed in oryxes and gazelles. In dry conditions, dehydrated oryxes are known to conserve body water by allowing the body temperature to rise, storing heat through the day instead of sweating (Taylor 1970a). The brain is protected by a counter-current heat exchange system between the blood vessels draining the nasal mucosa and those travelling toward the brain (the carotid rete), which is believed to sustain the brain at normal temperature while the rest of the body warms. Under experimental conditions dehydrated oryxes are reported to have successfully sustained body temperatures in the vicinity of 45 °C for several hours (Taylor 1970b). More recent studies of this phenomenon in free-ranging oryxes are reported by Maloney *et al.* (2002).

Fringe-eared Oryxes were subject to unusually detailed research in the 1970s and 1980s at the Galana Game Ranch Research Project in SE Kenya, where a series of studies on physiological and behavioural traits were conducted on captive and semi-free-range animals kept in the heart of the species' natural distribution. These studies established that Fringe-eared Oryxes are comparatively efficient in managing their water economy. In trials, animals drank from 2.2 to 3.6 litres per head per day (Stanley Price 1985a), with individuals typically obtaining their water intake by drinking once every 4–5 days. In a comparative trial with five other species – camels, cattle, Common Eland *Tragelaphus oryx*, sheep and goats – body water turnover rate measured in free-ranging Fringe-eared Oryxes using injections of tritiated water was the lowest, measured at 35 ml/kg per day compared with the next lowest (camels) at 41 ml/kg and was highest in goats at 94 ml/kg (King *et al.* 1975, King 1979, 1983). These antelopes probably function without access to free water for protracted periods in some parts of their range, managing on moisture from food selection alone. There is currently no scientific confirmation of this with the Beisa Oryx, but it has been speculated on in older literature (Taylor 1968a), and given the survival of these oryxes during particularly long and widespread droughts their ability to go without surface water is probably tested periodically in the drier parts of their range. There is also evidence that the combined effect of unusually efficient body heat management and water economy, sets oryxes at an advantage. They can remain active and graze their fill during hot daytime periods more easily compared with other species (Lewis 1975).

Behavioural adaptations also help explain the ability of oryxes to survive aridity. For example, like many other mammals, they pant when water is available and are able to survive without drinking surface water by selecting comparatively succulent species or the most succulent parts of plants when feeding or the best times to feed (see Food and Foraging). They also reduce temperature and water loss by 'shading' and orientating their body to minimize areas exposed to the sun and possibly by scraping away hot surface soil and materials before lying down. The strong, splayed triangular hooves are adapted for both sandy and hard stony ground, but are ill suited to soft, muddy ground.

The peculiar facial and forequarter markings come into great visual prominence during a highly ritualized run that is characteristic of oryxes and has been dubbed the 'tournament' (Kingdon 1982) or 'runplay' (Lewis 1974). This performance starts with one or more



Beisa Oryx *Oryx beisa* head-wags and hackney gait during 'tournament' display.

animals running round the herd in broad circles. A galloping spurt builds sufficient momentum for the runner to suddenly switch into a long, high-stepping pace like a hackney pony. Simultaneously, the animal pulls its bunched neck back, throws its chin into the air and jerks its head from side to side in perfect opposite rhythm with the pace of the forelegs, an action that further emphasises the length of the horns and body colouring highlights. Bouts of high-stepping/head-flagging may simply slow and break into a normal run or they may climax in a sudden feint or actual clash of horns with a standing individual in the herd, usually followed by instantly darting away in a normal run to prevent escalation. The individual may then return to circling round, breaking back into the extended gait and initiating the sequence again, perhaps with a different member of the herd. Sometimes, excitement can spread and many members of the group may run around their herd with frequent, but mostly brief, horn clashes or feints. Oryxes of all ages may be observed using this gait, younger animals may be particularly prone to it, and on occasion comparatively young oryxes may initiate interaction with older and larger animals in the course of these displays (Wacher 1986).

Lewis (1975) noted that outbreaks of the displays in semi-captive oryxes seemed to be associated with sudden changes in environmental conditions (for example, after showers of rain early in the wet season and shortly after release from the night boma at the same time of

year). The displays are infrequently observed in wild oryxes, but on Galana Ranch have also been associated with bright mornings in the early wet season or on one occasion directly following a brief, but heavy, shower of rain. Speculation on possible functions of this display include a ritual testing of rank order (minimizing the risks of damage in such dangerously horned animals) or possibly a device for focusing attention on landmarks as an aid to navigation (Kingdon 1997). But data are lacking and further research is needed.

Connected to fighting and conflict, both Beisa and Fringe-eared Oryxes show marked sexual dimorphism in skin thickness over the forequarters and over the forehead and front of the face. The skin of a male Fringe-eared Oryx forms a 'dermal shield' up to 2.5–3 cm thick over the neck and shoulders, while the equivalent area on an adult female hide is also slightly thickened relative to the rest of the body, but only to about 1 cm depth (Wacher 1986). In terms of body mass, the skin of oryx ♂♂ was found to comprise 8.7% of live weight (substantially the highest proportion among 11 antelope species reported, including heavier species such as Waterbuck *Kobus ellipsiprymnus*, Common Wildebeest *Connochaetes taurinus* and Common Eland), but only 4.8% in ♀♀ (Ledger 1968). This adaptation is not unique to oryxes, and is quite widespread in horned ungulates (e.g. Jarman 1972a), but appears to be unusually well-developed in this fiercely armed species. As well as increasing protection against stabbing horn tips during fighting, the heavy dermal shield presumably also serves to increase bulk, visual display and weight for ♂♂.

Foraging and Food Both Beisa and Fringe-eared Oryxes are preferentially grazers, and they eat a wide range of grass species and growth stages, taking a succession of small cropping bites. Recorded grasses include species of the genera *Aristida*, *Sporobolus*, *Setaria*, *Brachiaria*, *Schoenfeldia* and *Chrysopogon*, but the actual number of species is probably very great (Kingdon 1982). In the dry season oryxes browse more often (Cobb 1976), taking species of the genera *Grewia*, *Indigofera*, *Acacia* and, reportedly, *Adenium*, which is known to be a very poisonous plant. It has been suggested that by means of selective feeding by time of day (and particularly at night) oryx may take advantage of free water obtained hygroscopically from the atmosphere by food plant species such as the dwarf shrub *Disperma* sp., which under the right conditions of temperature and humidity can increase in water content from 2% to 40% (Taylor 1968a).

Direct observations of tame Fringe-eared Oryxes feeding in natural habitat reported diet selection consisting of 83.3% grass items, 8.5% herbs and 7.9% browse (Field 1975). When grazing they were observed to be more selective of protein-rich leaves than larger-mouthed species such as African Buffalo *Syncerus caffer* and cattle. Grasses form a higher proportion of the diet in drier conditions and important species taken by oryx at Galana Ranch include *Brachiaria deflexa*, *Schoenfeldia transiens* and *Botriochloa* spp. in wetter conditions, with *Enneapogon cenchroides* and *Chloris roxburghiana* increasingly important in the dry season. Fringe-eared Oryxes were also noted making use of the moisture-rich herb *Commelina* sp. when available. Low level of browse use is persistently observed, but most notably towards the end of rainy periods when dwarf shrubs such as the legume *Indigofera schimperi* and shrubs such as *Grewia tristis* are utilized (Field 1975).

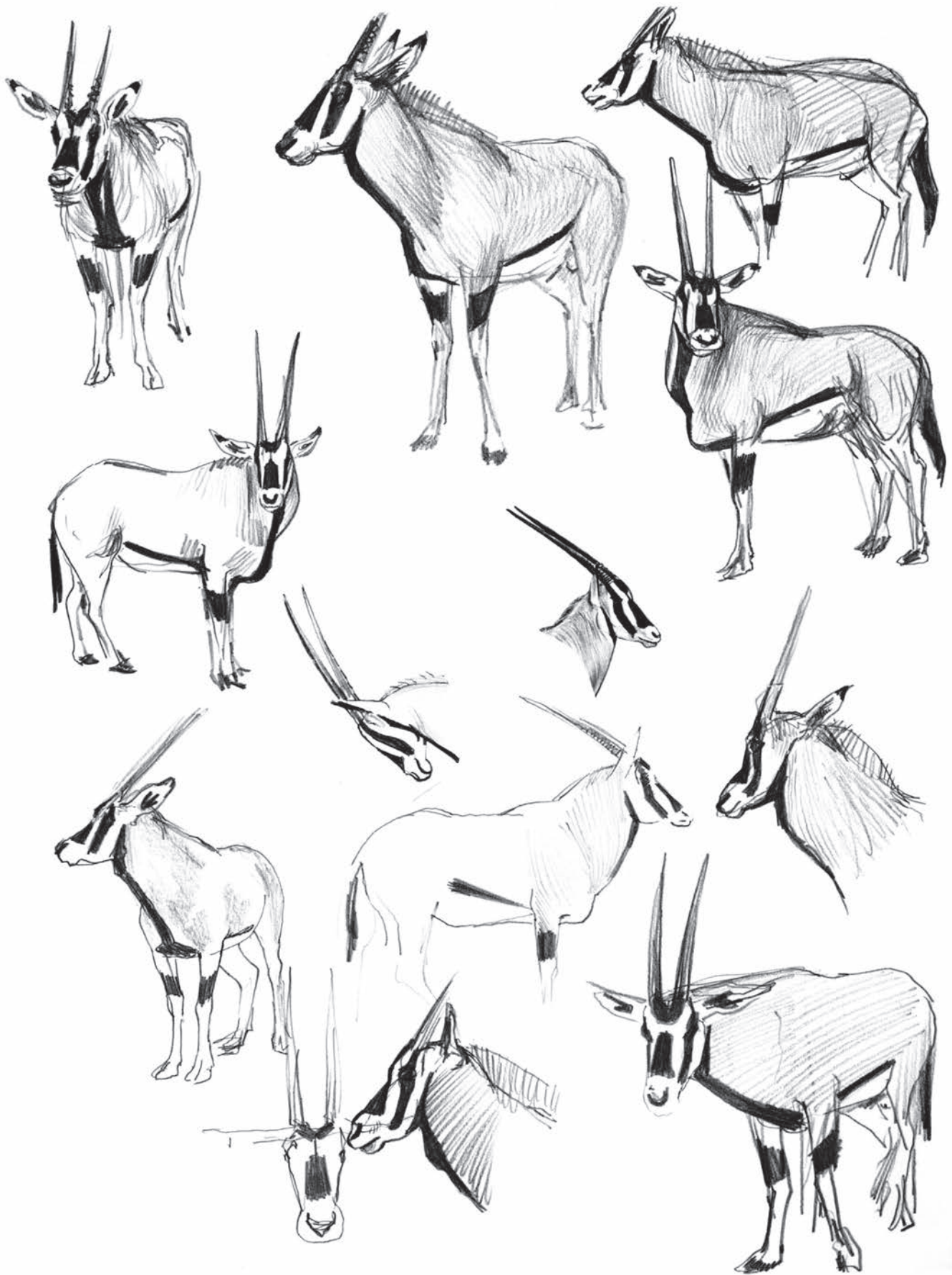
An analysis of their diet, based on stable carbon isotopes, again reported that although oryxes are primarily grazers (with 88% C₄ diet), they also take a small, but significant, fraction of browse (Cerling *et al.* 2003). Food intake rates in comparative feeding trials were measured at 2.2–2.5 kg/day (Stanley Price 1985a). During droughts they will occasionally walk long distances to water but may also dig deeply for potentially water-rich tubers and swollen underground stems of *Thunbergia guerkeana* and gouge the hugely swollen surface stems of *Pyrenacantha malvifolia* with horn and hooves before consuming broken off pieces (Root 1972). Fringe-eared Oryxes have also been seen on rare occasions chewing on bleached animal bones (osteophagia), presumably in response to mineral needs (Field 1975). In comparative trials at the Galana Ranch it was noted that oryx preference for abundant grasses coupled with physiological tolerance to heat allowed them to flourish under a daytime-only foraging regime (no opportunity for nocturnal feeding) imposed by a domestication management trial, in contrast to the browsing and heat-sensitive Common Eland (Lewis 1975).

Where conditions are favourable, oryxes can remain in a limited locality over several seasons, but cyclical movements over long distances and nomadism have been recorded in several areas (Percival 1928, Cobb 1976). Large numbers congregate in a locality one year, only to switch to another in other years. They avoid flooded areas during the wet season, when they prefer higher, drier ground. In the dry season they often join other herbivores on the black cotton soils that were avoided in the rains, the principal attraction being grassy regrowth.

Individually known adult female and herd-living male Fringe-eared Oryxes were measured moving over ranges measuring 250–300 km² during the course of 1–2 years of radio-tracking at Galana Ranch, with indications that with longer data sets individual home-ranges could be much larger (Wacher 1986). Female and non-territorial male oryxes move around these ranges in a series of stages, settling in locally smaller areas for periods of days or weeks. Some of the longest transitions between areas coincide with the onset of rains when exploration for fresh pasture is undertaken.

Social and Reproductive Behaviour The Beisa Oryx is a gregarious species and herds commonly number 20–60 animals of mixed sex, although temporary aggregations of more than 200 have been observed (Kingdon 1982). Solitary individuals are generally ♂♂ (although ♀♀ that have recently given birth spend much time away from herds). Very expansive wandering is known to take place, but the extent of such movements, principally by young ♂♂, has yet to be studied in detail.

Radio-tracking studies of wild Fringe-eared Oryxes on Galana Ranch (Wacher 1986) indicate that they live in a relatively complex social environment, characterized by socially dynamic mixed-sex herds of variable size and composition. In green conditions and at high local densities, groups may occur in loosely structured assemblies, typically with the majority of all of the younger animals aggregated in one group, perhaps resting, while older animals are grouped at a distance feeding. Long-term social relationships between individuals are likely to exist, but hard to detect. Observations from this population are summarized below, but it should be noted that this location represents one of the most resource-rich habitats used by any oryx species, and therefore reflects behaviour exhibited under relatively benign and high-density conditions.



Beisa Oryx *Oryx beisa*.

Adult ♀♀ spend the majority of their time in herds. Relatively brief periods of constant group composition are regularly disrupted by episodes of splitting or fusion with group-size changing regularly even within 24 hours in high-density populations. Major factors influencing group size and composition for ♀♀ are the time elapsed since calving, and season (Wacher 1986). On Galana Ranch the largest aggregations of oryx (100–300) were recorded exclusively in wet season periods on large areas of fresh grazing. Mean group size from a count sample of oryx groups over all seasons averaged 10–11, but group size experienced by individuals ranged from 1 to >200 for all radio-collared ♀♀ followed longer than a few months. Although large aggregations occur in seasons of green grass growth, ♀♀ that calve in green conditions usually still persist in isolation and form consortships in the immediate postpartum period.

At calving, experienced adult ♀♀ tend to isolate themselves to give birth to a cryptic calf that adopts a solitary hiding defence strategy over the first 2–3 weeks of life. In the Fringe-eared Oryx this behaviour was observed consistently in radio-collared wild animals, and in the semi-captive Galana herd it was notable that adult ♀♀ showed a sharp peak in tendency to run away back to the wild in the month of calving. Most ♀♀ come into postpartum oestrus within 1–2 weeks, and so often attract the attention of adult ♂♂. Small group sizes of 1–3 individuals (typically some combination of a lactating cow, neonate and consorting adult ♂) are most typical (but not invariable) in this period and calving interval data indicate that there is a high probability that healthy adult ♀♀ will conceive within this period. Females may also intermittently join herds while the calf lies out (Kingdon 1982). During the period 2–6 months postpartum, adult ♀♀ are most likely to be found in mixed-sex herds (10–15% adult and subadult ♂♂) of variable size, with a range of calves and younger age groups also present. Crècheing among calves and cohorts of young may be apparent, and on occasion a lactating cow may move as far as 10–12 km away from her own calf and back again in the course of a single day when, for example, travelling to a water source to drink in the dry season. During the period 6–9 months postpartum, adult ♀♀ become more likely to be found in mixed groups composed mainly of adults and subadults only, with a marginally higher proportion of ♂♂ (20–30%). This is not an absolute change, but it appears that progressively less time is spent in the immediate company of her own or other young in the period of later pregnancy leading up to isolation for birth of the next calf. A tendency of Fringe-eared Oryx herds to form group types characterized by the presence or absence of young was also noted independently in Tsavo East N. P. (Leuthold & Leuthold 1975b).

The majority of maturing, and some fully adult, ♂♂ are also found in mixed-sex herds and information from individuals suggests that their ranging and foraging behaviour operates on a similar wide scale to that seen in ♀♀ (see above). All-male groups of Fringe-eared Oryx bulls were only identified on six occasions in the course of a three-year study (setting aside the common phenomenon of solitary adult ♂♂). Known radio-collared territorial bulls were present on five of these occasions, confirming the group was a temporary association. On the sixth occasion, the largest all-male group recorded (five individuals found walking to the river) included a tagged wild ♂ who was known to have been a member of a mixed-sex group of 96 animals the day before and who was next seen in a mixed-sex group of 57 two weeks later.

However, some adult ♂♂ behave very differently, distinguished by spending the majority of their time alone and in comparatively restricted areas. In the Galana–Tsavo border zone, the best documented solitary male home areas (territories) were placed along the ecotone between red and grey soils, straddling grassland and woodland habitats preferred by herding oryxes. Two radio-collared solitary bulls in this area restricted their movements to separate 5–8 km² zones over study periods of 1–3 years. They were seen to patrol boundaries in parallel with neighbouring adult ♂♂ with some evidence for a degree of spatially determined reciprocal dominance between neighbours. These ♂♂ make visual displays by a ritualized sequence of squatting defecation, associated only with adult male oryxes (castrated adult male oryxes did not develop this behaviour on Galana Ranch). This involves walking directly to a known dung site, scenting the ground and/or older dung piles, scraping the ground or dung pile with a front hoof before squatting low on the haunches while defecating, in the process creating a strikingly vertical visual display apparent at long range to other oryxes. Dung piles were not usually dropped exactly on top of one another, but scattered around a patch of bare soil. Sometimes 3–4 dung sites may be visited and re-marked in direct succession in the course of a morning ‘patrol’. Midden sites (n = 61 observations of active dung site use at 50 different dung site locations) mapped for one radio-collared bull were found to be scattered throughout his area of residence, with no indication of clustering towards the margins (Wacher 1986). More than 80% of sites had been used previously with 3–6 older dung piles (maximum ten) evident at most sites when inspected immediately after use.

Tellingly, the most common social grouping of solitary ♂♂ when not alone was to be seen in groups with a single adult ♀ (with or without new calf present), although larger mixed-sex groups move through territories fairly frequently, when the local resident may or may not join them temporarily. Consortships between solitary ♂♂ and oestrous ♀♀ are normal, often lasting 3–5 days and sometimes as long as three weeks. Radio-collared cows with neonates mostly consorted with 2–3 different ♂♂ over the postpartum period. Solitary bulls attempt to herd and control movement of consorting ♀♀ using passive body positions and posture, and active horn threats, chases and lunges. This usually results in the ♀ remaining near the centre of the territory, but not always. Oestrous ♀♀ can and do escape to another solitary bull, or even back to herds on some occasions. Under these conditions, with dams in view on a neighbouring territory, it is notable that on three separate occasions one well-known, solitary, radio-collared bull was seen vigorously herding and threatening single calves (on one occasion galloping at full speed to head off the running calf) to prevent them moving towards their dams and retain them on his own side of the boundary. On one of these occasions a ♀ was seen returning to her calf on the radio-tracked male’s territory. Adult ♂♂ have frequently been noted to be attentive to young calves, whether encountered in small or larger groups. In most situations this takes the form of herding and nudging the calf towards its mother (but in Arabian Oryx calves have been seen tossed through the air with a rough sweep of the adult male’s horns). Whilst these activities may confer a certain protective advantage to these calves in normal situations, it seems probable that a prime motivation of the ♂ is to manipulate the calf as a means of influencing movements of the mother while she is receptive to mating.

Relations between solitary and herd-living ♂♂ visiting the territory can be surprisingly calm and tolerant in the absence of receptive ♀♀. Territorial bulls may exert dominance to newly arrived ♂♂ by means of a head-low march followed by ritualized lateral head-nod or 'ear-point' display across the front of the recipient (Walther 1978c, and see full description below). On other occasions they may not even bother to approach a mixed-sex visiting group in plain view on the territory. Prolonged and serious clashes between adult ♂♂ do occur, but are relatively rare. In the Galana study, this was only seen between pairs of ♂♂ unknown to the observer. A limited number of observations of a well-known resident solitary bull dealing with mixed-sex groups on his area that included a sexually receptive ♀ suggested that the resident bull had little difficulty retaining social dominance and probably mating advantage also over the visiting herd ♂♂. On such occasions, active herding and chasing is directed primarily at the ♀, but also at other members of the herd by the resident bull. Visiting ♂♂ may also attempt to court and mount the ♀ while the resident is occupied or elsewhere. On one radio-collared male's territory, mountings by all adult male oryxes made during herd visits to the territory were scored as 'successful' or 'unsuccessful' depending on whether the ♀ involved stood still or walked forward as intromission was attempted. Summing over five different occasions when receptive ♀♀ were courted by both the resident and visiting ♂♂ in groups on the territory, the resident bull was scored 'successful' on 5/22 mountings observed while the visiting ♂♂ achieved 0/20 successful mountings and were commonly seen to be submissive when approached and threatened by the resident bull. The circumstances of these observations raise interesting questions about female options to control mating and mate choice.

However, because the social system is dynamic and flexible it seems very probable that not all ♀♀ mate exclusively with solitary territorial ♂♂. Receptive ♀♀ in large mixed-sex groups are sometimes observed, and the level of harassment and chasing by several ♂♂ on one cow can be intense on such occasions. This suggests that solitary territoriality is unlikely to be the only mating strategy used by oryx at Galana. In drier areas, used by Beisa Oryxes in N Kenya and Ethiopia, and at the margins of the oryx range, it seems even more probable that alternative, more mobile, or herd-based mating strategies might be expected to predominate.

In Serengeti N. P., one herd of 15 Fringe-eared Oryxes travelled 17 km in one day, and a lone bull walked 4 km in a straight line within one hour; on the other hand, another Serengeti herd remained localized in a 20 km² area for three weeks (Walther 1978c). In these conditions it is possible that ♂♂ may attempt to detain ♀♀ groups when local grazing conditions allow, but may alternatively attach themselves to more determinedly mobile groups if food or other resources do not attract sufficient isolated calving ♀♀ to their chosen areas. It is therefore possible that oryxes are able to adjust social relations to resident or nomadic conditions and observed mating activities appear to exhibit features of both resource-defence and mate-defence options. It is also noted that in more recent studies of reintroduced Arabian Oryxes in harsh desert conditions of S Saudi Arabia, the oldest adult ♂♂ developed very large-scale spatial segregation relative to each other, where they were comparatively sedentary, not emulating younger ♂♂ who wandered widely in search of dispersing ♀♀ following rare rainfall events. These

observations hint at an unproven possibility that male oryxes may adjust their mating strategy according to circumstance, age and perhaps body size.

Studying free-ranging groups of Fringe-eared Oryxes in a semi-domesticated and resident state, Stanley Price (1978b) found that some of these groups had a closed membership that was of long standing. In such groups there was an alpha-male and often a beta-male immediately below this dominant individual. All adult ♀♀ were arranged in a hierarchy below these ♂♂, but they were dominant over any other adult ♂♂. The ability of ♀♀ to hold social status in this way allows them to control their immediate grazing space effectively among conspecifics in mixed-sex herds. Besides providing a level of defence against predators (see below) this may be a further selective advantage for the existence of fully developed horns on ♀♀ in oryxes generally. Oryxes are notable as a group for specializing in habitats where resources can be scattered and rare, ♀♀ are adapted to breed at a high rate with simultaneous lactation and early pregnancy commonplace, and effective intra-specific defence of energy resources via social status may be at a premium.

The vivid markings may well facilitate social interactions in that even the slightest gestures are amplified by the patterning. Thus, when an adult ♂ expresses routine dominance to subordinates using the 'head nod' or 'ear point' display he walks across the front of the target animal with head and horns held high, slightly turned to one side and ears forward. At the last moment the horns are tilted over in a ritualized (but undelivered) slow motion lateral 'blow' to the air in front of the recipient, the main gesture being created by movement of the brightly marked head, with profile of neck and shoulders clearly shown off. The ritualized submissive response also emphasizes head movement; the receiving animal stands at first with head low, horns pressed protectively down along the neck, before half jumping, half turning away with a shake of the head as the stylized 'blow' is delivered. Captive ♀♀ in this situation have been seen to lie down and bawl (Kingdon 1982).

In addition to these ritualized exchanges, low-key social signalling is an ongoing feature at a range of intensities among oryx groups. Individuals may use a selection of simple stares, positional displacements and avoidance, horn and head gestures in incremental intensities while interacting during grazing or movement. In this context it is notable that adult ♀♀ make use of horns and gestures to maintain status and position while grazing in a similar way to ♂♂. The occurrence of dramatic prancing 'tournaments' is described above. At close range, frequent soft grunts may be heard, notably from cows approaching young calves, or between courting pairs, while calves may bawl vociferously when denied suckling.

In conflict, horn-to-horn clashes may develop with increased intensity among older animals. Fighting takes place face to face with antagonists alternatively 'kneeling' and standing to push against each other between sharply delivered head blows and horn swipes. With rising intensity fighting oryxes may swing round and lean together in a side-to-side position with horns crossed and over-the-shoulder stabbing actions aimed at the neck and shoulder region of the opponent. Fights usually end with one individual breaking away and running, pursued for a short distance by the victor who often then turns away and may indulge in a squat defecation display a short time later. But fatal outcomes do occur in other oryx species (Arabian Oryx) and may also be expected as a rare event in Beisa and Fringe-eared Oryx.

Courtship consists of prolonged bouts of nose-to-tail circling, the ♀ initially repeatedly stepping away from the male's attempts to press his forequarters to her hindquarters, sniff and rub the female's perineal area, kick (laufsclag) or mount. Females may also respond by producing urine, which the courting ♂♂ will sample through typical flehmen. Unreceptive ♀♀ may on occasion repel the ♂ with repeated frontal clashes or may also lie down to discourage attention. But ♂♂ may also initiate courtship bouts by pawing at lying ♀♀ to get them to their feet during rest periods. As circling intensifies the pair break into occasional excursive and rather slow circular or figure-of-eight marches led by the ♀ to and from a more or less fixed point, as the bull follows directly behind. Mounting is rapid, with the male's head held high to avoid the female's horns and intromission is achieved with a single firm thrust.

Reproduction and Population Structure Births occur throughout the year, but well-defined birth peaks may emerge in some conditions (Leuthold & Leuthold 1975b). As ♂♂ tend to mate ♀♀ during their postpartum oestrus, and the gestation period is in the region of 8.5 months (see below), the timing of birth peaks remains difficult to understand (Kingdon 1982). Birth months were not synchronized among six radio-collared breeding ♀♀ captured from the same population on Galana Ranch where newborn calves were found in all seasons and nearly all months (Wacher 1986). Stanley Price (1978b) found that cows matured at about two years. Ages at first mating recorded from five captive, but partially free-range, female Fringe-eared Oryxes at Galana Ranch ranged from 2 years 49 days to 2 years 227 days. Age at first calving from this sample ranged between 2 years and 339 days and 3 years and 194 days, with at least one of these ♀♀ failing to conceive at first oestrus.

Modal gestation period indicated by counting last recorded mating to parturition was 255–259 days (8.5 months, $n = 24$ pregnancies) on Galana Ranch (Wacher 1986). The modal interval from birth to postpartum oestrus (indicated by mating) was 15–19 days after parturition ($n = 32$ births recorded from 18 individuals). The modal inter-calving interval from a sample of 68 births recorded from 19 individual female Fringe-eared Oryxes was 275–279 days (9.1 months); individual ♀♀ were recorded maintaining a ca. 9 month inter-calving interval under semi-captive natural range conditions over a period of six years on Galana Ranch (Wacher 1986). A radio-tracked wild ♀ was detected calving precisely at a 288-day interval, well within the typical range of calving intervals recorded from tame oryx. Observations of four other radio-collared wild ♀♀ also supported maintenance of a 9-month inter-calving interval (Wacher 1986). Based on semi-captive Fringe-eared Oryxes at the Galana Ranch, male calves average 10.5 kg at birth ($n = 12$) and females 11.5 kg ($n = 7$) (R. K. Ngowah & M. Stanley Price pers. comm., Galana Game Ranch Research Project).

Predators, Parasites and Diseases Cheetahs *Acinonyx jubatus* are known to run down young animals, and hyaenas, Leopards and smaller predators are likely to take calves. Lions kill adults where both species are common, but such large predators are generally scarcer in the very arid areas that these oryxes prefer (Kingdon 1982). African Wild Dogs *Lycaon pictus* have also been recorded hunting Fringe-eared Oryxes in the Tsavo–Galana area of E Kenya with variable results. A radio-collared solitary adult bull



Beisa Oryx *Oryx beisa* in subordinate head-low posture.

known to be blind in one eye was killed and eaten by a pack of seven African Wild Dogs. A pack of five African Wild Dogs were observed approaching a herd of 21 oryxes in open grassland, including a single small calf around one month of age. They ran up to the oryxes and began walking intently forward, focusing their gaze on the calf located near the centre of the group. The adult oryxes formed a concave semi-circle facing the dogs; when the dogs were no more than 10 m from the oryx herd, the largest adult male oryx suddenly leapt forward at the lead dog making a tossing lunge with his horns. The dogs retreated at once, circled past the herd and continued on their original direction without further interest. The adult bull in this case was also radio-collared, from which it was known he was usually alone on his territory while the other 20 animals with him were newly arrived in the area and at best only intermittent associates. In a third incident, the fresh skeletonized carcass of an adult female oryx was found in front of a fallen *Commiphora* tree, which had clearly been used as a protective background support while attempting to defend herself with horns when turning to face attackers after a period of pursuit (a characteristic defence strategy of hippotragines). The oryx skull was notable for the fact that the incisiform dentition was worn down to an incomplete row of rounded pegs level with the gum, suggesting a very old animal probably poorly fed. The intact body of a dead African Wild Dog was photographed lying a few yards from the oryx skeleton, marked only by a deep stab wound consistent with an oryx horn entering the body cavity at the angle

of the hindleg. A pack of 12 live and heavy-bellied African Wild Dogs was located resting in the shade 500 m away.

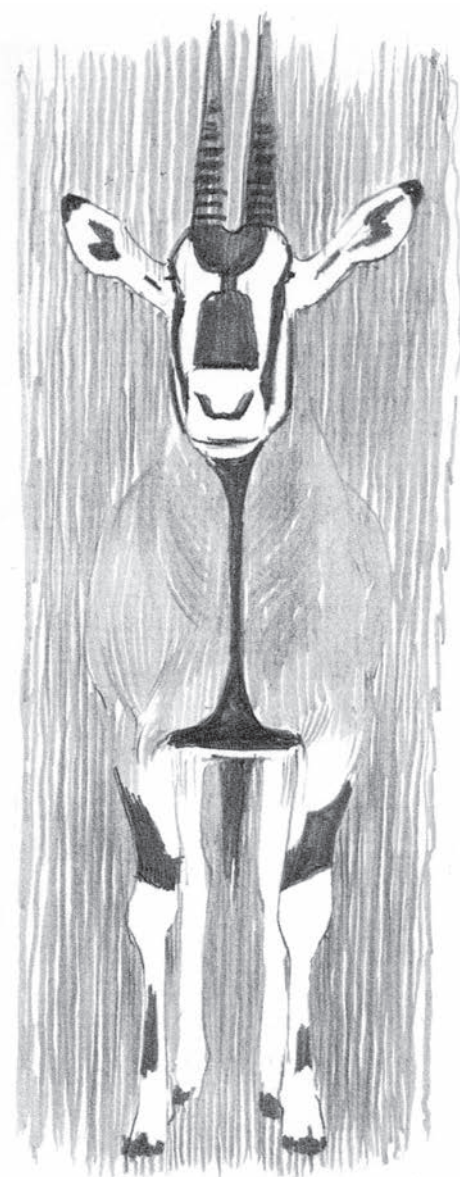
Virus neutralizing antibodies to malignant catarrhal fever virus were found in the blood sera of 50 Fringe-eared Oryxes (Mushi & Karstad 1981). Antibodies to *Brucella abortus* bacterial infection have also been reported (Paling *et al.* 1988).

Conservation IUCN Category: Near Threatened (*O. b. beisa* – Near Threatened; *O. b. callotis* – Vulnerable C1). CITES: Not listed.

Although this species has declined markedly in numbers and range, it remains common in areas where livestock densities are low, with several large populations surviving in protected areas, such as Awash N. P. (in the Awash Valley), and Omo and Mago National Parks (in the south of Ethiopia), Sibiloi, Meru and Tsavo National Parks (Kenya) and Tarangire N. P. and Mkomazi G. R. (Tanzania) (East 1999). Boma N. P. is the only protected area for this species in SE Sudan (Fay *et al.* 2007). Where they have been hunted traditionally it has usually been for the good quality of their meat and the practical value of the very tough hide. The species remains susceptible to the effects of hunting and competition with livestock, since so many remaining populations are outside protected areas: according to East (1999), only 17% of Beisa Oryxes and about 60% of Fringe-eared Oryxes occur in protected areas. The most recent review of local population status within N Kenya compared aerial survey data and found continued substantial (>50%) reductions in density at important population centres in Samburu District over the period of the mid-1990s to 2008, though noting a more stable situation within Laikipia (Woodfine & Parker 2011). More effective protection and management of the remaining populations in areas where the species still occurs in substantial numbers, but is in decline, such as the Awash Valley, Omo-Mago-Chew Bahir, N Kenya and Tsavo, would greatly enhance the long-term survival prospects of this species (East 1999).

The absence of karyotypic sterility barriers (Kumamoto *et al.* 1999) suggests that, in captivity, all oryx taxa may be vulnerable to hybridization, which from a conservation perspective is highly undesirable among these distinctive and naturally allopatric antelopes. Genetic evidence supporting the historical isolation between *O. b. callotis* and *O. b. beisa* led to a direct recommendation that conservation efforts should be directed towards preserving the genetic integrity of each group on the grounds that they may have distinct evolutionary potential (Masembe *et al.* 2006). As noted already, hybridization in captivity between this species and the Gemsbok has produced 'viable offspring' (Gray 1972). Opportunities for either subspecies to hybridize with the Scimitar-horned Oryx *Oryx dammah* and Arabian Oryx and for mixing between the two subspecies of Beisa Oryx exist in some captive collections.

Comparatively small zoo-managed populations of both the Beisa and Fringe-eared Oryxes exist in zoos outside Africa, mainly in Europe and North America (EEP/SSP). Given the downward trend of wild Beisa populations in particular, and the successful role captive breeding has played for two other members of the taxon (Arabian and Scimitar-horned), the efficient long-term management and planning of captive Beisa groups may prove to be important in the future, especially if this is set up within range states where meta-population management of divided and semi-captive populations in conjunction with National Parks may become an increasing necessity.



Beisa Oryx *Oryx beisa* adult male in confrontational posture showing linear geometry of patterning.

Measurements

Oryx beisa

O. b. callotis

HB (♂ ♂): 1800 mm, n = 1

HB (♀ ♀): 1700 mm, n = 1

Sh. ht (♂ ♂): 1100 (1050–1150) mm, n = 8*

Sh. ht (♀ ♀): 1110 (1050–1150) mm, n = 20*

HF c.u. (♂ ♂): 380 mm, n = 1

HF c.u. (♀ ♀): 410 mm, n = 1

Galana Ranch, Kenya (T. Wachter pers obs., Galana Game Ranch Research Project)

*Semi-captives (all animals >36 months of age)

The average weight at maturity (ca. 3–4 yr of age) of semi-captive Fringe-eared Oryxes has been estimated at 165.0 kg for adult ♂ ♂ (n = 19) and 146.0 kg for ♀ ♀ (n = 34) (Carles *et al.* 1981). The

maximum weight recorded for a ♀ on Galana Ranch is 180.0 kg; the heaviest semi-captive ♂ weighed in excess of 210 kg (T. Wachter pers. obs.). Ledger (1968) recorded average weights of wild *O. beisa* as 176.4 kg (range 167.8–209.4, $n = 10$) for ♂♂ and 161.5 kg (range 116.0–188.4, $n = 10$) for ♀♀. Available data from semi-captive Fringe-eared Oryxes suggest that full male body size and neck development are attained after 4–5 years of age, well after the age of physiological sexual maturity. This poses further interesting questions for potential differences in reproductive strategies operating in

individuals of differing body size in this complex and fascinating species. Maximum recorded horn length for *O. b. beisa* is 109.2 cm from Ethiopia; the record for *O. b. callotis* is 110.2 cm for a pair of horns from L. Magadi in Kenya (Rowland Ward).

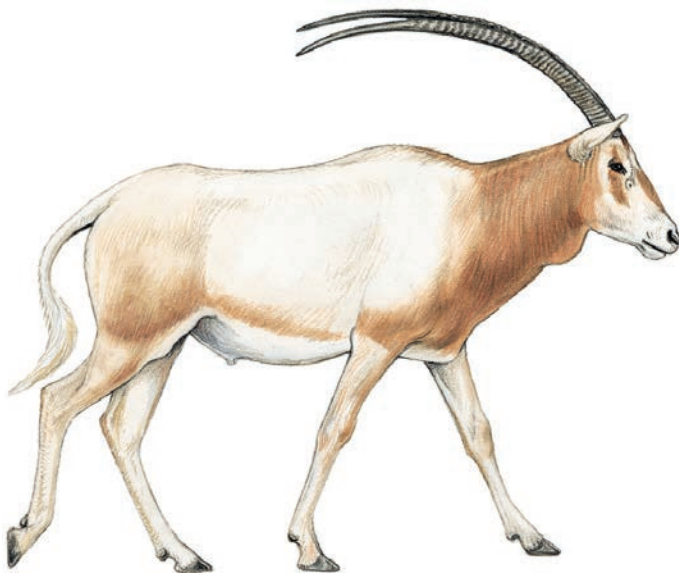
Key References East 1999; Cobb 1976; Kingdon 1982; Lewis 1975; Stanley Price 1978b; Wachter 1986.

Tim Wachter & Jonathan Kingdon

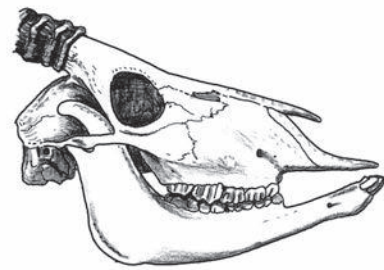
Oryx dammah SCIMITAR-HORNED ORYX (SCIMITAR ORYX)

Fr. Oryx algazelle (Algazel); Ger. Säbelantilope (Nordafrikanischer Spießbock)

Oryx dammah (Cretzschmar, 1827). In: Rüppell, Atlas zu der Reise im nördlichen Afrika von Rüppell, pt 1, Säugethiere, p. 22. Sudan, Northern Kordofan Prov., 'bewohnen die grossen Steppen von Haraza [vicinity of Jebel Haraza]'. The year of original publication is 1827, not 1826 (see Grubb 2005).



Scimitar-horned Oryx *Oryx dammah*.



Lateral view of skull of Scimitar-horned Oryx *Oryx dammah*.

Taxonomy Monotypic. Has frequently been called *Oryx leucoryx* (which is restricted to the Arabian Oryx), and *O. algazel*, which is invalid (see Grubb 2005). Ansell (1972) and Corbet (1978) discuss use of *O. dammah* over *O. tao*. Synonyms: *algazel*, *bezoartica*, *ensicornis*, *nubica*, *senegalensis*, *tao*. Chromosome number: $2n = 56-58$ (Wurster 1972, Gallagher & Womack 1992, Claro *et al.* 1994, Kumamoto *et al.* 1999). Majority of specimens have $2n = 58$ with fixed centric fusion of chromosomes 1 and 25; variation in diploid number (i.e. $2n = 56-57$) is the result of centric fusion polymorphisms of chromosomes 2 and 15 (Kumamoto *et al.* 1999). Sex chromosomes, X and Y, are acrocentric (Kumamoto *et al.* 1999). Scimitar-horned Oryx and Addax *Addax nasomaculatus* hybrids are known and reported to resemble the Addax in European zoos (Ruhe 1993). Hybrids born at Bou-Hedma N. P. in Tunisia (believed to be sired by an oryx ♂) were large-bodied like oryx, with typical oryx horn shape, but with obvious Addax body colouration and body shape (R. Molcanova pers. comm.).

Description A large, robust antelope, with long horns arched over the back in both sexes, and striking rufous and white coat colouration. Cream to whitish body pelage contrasts with reddish-brown colouration on neck, shoulders and upper legs. Seasonal variation in coat length and colour quite marked, with animals appearing whitest in short bright summer coat, while long winter coat is duller and creamier and may reveal faint reddish-brown lateral flank-stripe and reddish tones on rump. Head is elongated, cream with face 'mask' of reddish-brown across muzzle and blaze on forehead, and reddish-brown eye-stripe from base of horn across eye and cheek. Eyes, nostrils, lips and inner ears black. Ventral surface and insides of legs creamy-white, hooves black. Tail long (ca. 39% of HB), and cream with brown-black terminal hairs. Pedal glands present on all four feet, but there is also a small preorbital gland (not present in other *Oryx* species); inguinal glands absent. Sexes superficially similar, but adult ♂♂ larger, with heavier neck and shoulders and thicker horns at all ages. Individuals may be reliably identified by small variations in horn shape and at close range by variation in details of face-mask pattern.

The distinctive horns are long, ridged (lower one-half or one-third marked by 30–60 annulated corrugations), sharp-tipped and curved backwards in a shallow arc (80–150 cm), giving rise to the common name. Female horns are longer and thinner, with less prominent annulations; male horns are noticeably thicker at the base, generally more robust and often shorter in older individuals. Differences in horn circumference at the base are apparent in calves at an early stage and can be useful for determining sex. Hard and sharp adult

horn tips develop after sloughing off the outer keratinous sheaths that cover the horns of young animals.

Geographic Variation None recorded.

Similar Species

Oryx beisa: allopatric in East and north-east Africa only. Horns more or less straight; neck and shoulders lacking reddish-brown colouration; preorbital gland absent.

O. gazella: southern Africa only. Horns more or less straight; neck and shoulders lacking reddish-brown colouration; preorbital gland absent.

Distribution Formerly widespread in semi-arid Sahelo-Saharan zones north and south of the Sahara Desert from the Atlantic Ocean to the Nile R., but not north of the Grand Atlas Mts. Range countries include Egypt, Libya, Tunisia, Algeria, and Morocco north of the Sahara and Mauritania, Mali, Niger, Senegal, Burkina Faso, Nigeria, Chad and Sudan in sub-Saharan Africa.

Historical Distribution In Egypt, the historical range included most of the Western Desert, west of the Nile R., but mostly on oases and wadis. Oryxes were recorded in Siwa and Kharga Oases, El Faiyum area, western Giza and Wadi El Natrun (Osborn & Helmy 1980, Saleh 2001). They were reportedly hunted to extinction in the mid-1800s, with the latest records dating from the 1850s or 1860s; however, there is a record of an individual observed in 1975 in the north-west (Kock 1970, Osborn & Helmy 1980, Saleh 2001). In Libya, the species was described as widespread in the Fezzan (south-west) and Kufra (south-east) regions (Khattabi & Mallon 2001), near known populations in N Chad and the Western Desert of Egypt, respectively; there are unconfirmed historical reports of Scimitar-horned Oryx in NE Libya, from Wadi Jerari (Hufnagl 1972, Khattabi & Mallon 2001). They reportedly became extinct in the 1940s due primarily to illegal, motorized hunting and habitat degradation due to overgrazing by livestock (Newby 1988), although Hufnagl (1972) quotes a possible sighting from NW Libya in 1964.

Late nineteenth-century accounts suggest that the Scimitar-horned Oryx may have occurred at least sporadically in S Tunisia, but some doubted that an established population still existed and none were able to provide first-hand information or reliably sourced specimens (Johnston 1898, Sclater & Thomas 1894–1900, Lavauden 1920, 1926b). All published descriptions, including the presence of a stuffed oryx calf in a private museum near Tunis in 1898 (said to have been received alive from the southern frontier), could equally be explained by contact with trans-Saharan traders or the occasional appearance of wandering individuals (Devillers & Devillers-Terschuren 2005). In Algeria, oryxes inhabited the sub-desert and steppe regions north and south of the Sahara. They were reportedly hunted to extinction in the 1960s, and the last animals were shot in the Tassili region in 1987, though these may have been vagrants from the Sahel (De Smet & Smith 2001). Oryxes were widely distributed in S Morocco and the Western Sahara, south of the Oued Drâa (Loggers *et al.* 1992, Aulagnier *et al.* 2001). They were reported as extinct in Morocco in the 1930s and have not been sighted in Western Sahara since the 1950s, except for a single individual seen in 1973 (Le Houérou 1992).



Oryx dammah

Their historical range is not well documented in Senegal, but they probably occurred throughout the Sahel zone of N Senegal (East 1999), and were hunted to extinction by 1914 (Sournia & Dupuy 1990). In Mauritania, they formerly inhabited the south and western regions, along the Western Saharan frontier (Trotignon 1975, East 1999); they were hunted to extinction by the 1960s (Trotignon 1975, Newby 1988). In Mali, oryxes inhabited the sahel zone in C Mali and north into the desert zone (East 1999). They are presumed extinct since perhaps 1983 (Newby 1988), although a pair was sighted on the Burkina Faso border in 1986 (Duvall *et al.* 1997). In Burkina Faso, they ranged into the sahel zone in the north, but were hunted to extinction in the 1950s (East 1999).

Scimitar-horned Oryxes were widely distributed in sub-desert and sahel zones of C and S Niger and probably occurred in the northern desert zone with seasonal rainfall and good pasture availability (East 1999). The last reported sighting of oryxes in Niger was in 1986 (Millington *et al.* 1991). Overhunting, the introduction of deep permanent water bores for livestock excluding them from prime habitat, and desertification of the Sahel probably caused their extinction by 1989 (Dixon *et al.* 1991). Recent surveys report no evidence of live animals in the Termit region and Tin Toumma (Wacher *et al.* 2004a, 2008, 2009, 2010, Claro 2004). Oryxes formerly inhabited only extreme NE Nigeria, possibly only as a seasonal vagrant (East 1999).

Oryxes were historically abundant and widely distributed in the sub-desert and northern Sahel zones of C and N Chad, extending north into the desert zone (East 1999). Reports of migratory herds of hundreds or even thousands of animals in the sub-desert steppe habitat across NC Chad were common during the twentieth century (Gillet 1966a, Newby 1974). A population of >3500 survived under active protection in the Ouadi Rimé–Ouadi Achim Faunal Reserve between 1973 and 1978 (Bassett 1975, Newby 1980), but by 1988 it was reported that only a few dozen survived in the wild (Dixon *et al.* 1991) and repeated surveys since 1990 have failed to find any evidence

of surviving animals (Monfort *et al.* 2004, Devillers & Devillers-Terschuren 2005, Wacher *et al.* 2011).

In Sudan, Scimitar-horned Oryxes were distributed throughout the entire Sahelian zone of the Darfur and the Kordofan (Devillers & Devillers-Terschuren 2005), and were abundant in the Wadi Howar region near the Chad border. They were reportedly extinct by the mid-1970s (Newby 1988).

Current Distribution Today, the Scimitar-horned Oryx is listed as Extinct in the Wild in all former range countries (Devillers & Devillers-Terschuren 2005). However, semi-captive populations have been established within areas of natural habitat (ranging from 20–80 km²) in several former range states (mapped), including Tunisia (Bou-Hedma N. P., Sidi Toui N. P., Oued Dekouk N. R. and Dghoumès N.P.), Morocco (Souss-Massa N. P.; extralimital) and Senegal (Guembeul Wildlife Reserve and Ferlo-Nord Wildlife Reserve).

In Tunisia, Bou-Hedma N. P. covers 16,448 ha of mountainous and undulating steppe east of Gafsa, and has fenced Total Protection Zones, which are patrolled (Smith *et al.* 2001). Habitat restoration, particularly of the *Acacia raddiana* woodland, was very successful (Kacem *et al.* 1994). In 1985, ten captive-born, young oryxes (five ♂♂, five ♀♀) were translocated from European zoos to a 10 ha acclimatization area. The animals were released into a Total Protection Zone (2400 ha) 18 months later (Bertram 1988, Gordon 1991). In 1999, an additional adult ♂ from Europe was added to the population, individually managed to ensure he bred with established ♀♀, with the aim of increasing the genetic diversity (Molcanová 2004). The population has steadily increased from ten in 1985 to 70 in 1996 (Smith *et al.* 2001), peaking at an estimated 130 in 2005 (T. Gilbert pers. comm.), but had fallen to 73 by 2007 and below 50 in April 2011 (Molcanova & Wacher 2011a).

Sidi Toui N. P. lies in SE Tunisia near the Libyan border. The oryx area, established in 1993, covers 6135 ha encircled by a double fence-line. The landscape of low hills surrounded by open plains, small dunes and dry sandy wadis represents typical pre-Saharan steppe (Karem *et al.* 1993), characterized by a variety of shrubs and dwarf shrubs and a complete absence of tree cover. In 1999, 14 Scimitar-horned Oryxes selected from European zoos to represent a separate genetic line to those at Bou-Hedma N. P. were transported to Sidi Toui N. P. Ten animals (one ♂, 9 ♀♀) were released, while the remaining animals were sent to Bou-Hedma N. P. and Oued Dekouk National Reserve (Molcanova *et al.* 2001). Initial growth of this population peaked at 33 in 2005, but subsequently declined from 2005–2008 coincident with an unexpected swing to a male-biased sex ratio in a classic small population effect. As of 2011, the population size stood at 31 animals (Molcanova & Wacher 2011b).

Oued Dekouk N. R., located near Tataouine, is another fenced reserve covering 6000 ha. In 1999, three animals (one ♂♂, two ♀♀) from European zoos were transferred to Oued Dekouk with two further ♀♀ transferred from Sidi Toui N. P. to Oued Dekouk in 2003 (Molcanova 2006). The population had grown to 21 in 2008 and 26 in 2011 (Molcanova & Wacher 2008, 2011a). In February 2007, eight Scimitar-horned Oryx were translocated from Bou-Hedma N.P. to Dghoumès N.P. (8000 ha), close to Tozeur.

In Morocco, a captive population has been established at Souss-Massa N. P., which covers 33,800 ha in the Atlantic oceanic Sahara region, south of Agadir, but which is outside the original distribution range of

the species. The fenced 1500 ha Arrouais Reserve consists of bush and tree savanna, stony and sandy ground and migrating sand dunes with 5 ha pre-release enclosures (Müller & Engel 2004). Three shipments consisting of a total of 29 oryxes (17 ♂♂, 12 ♀♀) from European zoos were released between 1995 and 1997 (Engel *et al.* 2001, Müller & Engel 2004). The population had increased to 50 in 2000 (Müller 2002) and an estimated 240 in 2005 (T. Gilbert pers. comm.).

In Senegal, captive populations have been established at Guembeul and Ferlo-Nord Wildlife Reserves. In 1999, eight Scimitar-horned Oryxes (three ♂♂, five ♀♀) from the Hai-Bar Wildlife Reserve in Israel were transported to an 8 ha enclosure within the Guembeul Wildlife Reserve (720 ha) at Saint Louis in the north-west region of Senegal (Clark & Bovee 2000). The population had increased to 23 in 2002 with births and the addition of two imported oryxes from Paris Zoo (Clark 2002). Guembeul serves as an acclimatization site for release into the Ferlo-Nord Wildlife Reserve (487,000 ha of sahelian savanna grassland and bushland on gently rolling sandy terrain in NE Senegal). In 2003, eight oryxes were transferred from Guembeul Wildlife Reserve to a fenced core area of 600 ha in Ferlo-Nord (Gueye 2004); all eight animals were born in Senegal and have since produced calves. In 2004, the estimated reintroduced population in Senegal was 30, 18 at Guembeul and 12 at Ferlo-Nord (Gilbert 2004b).

Habitat Climatic changes during the last 5000 years left the Scimitar-horned Oryx population divided north and south of the central Sahara Desert. The African Sahel, the sub-Saharan steppe of hardy grasses, shrubs and drought-resistant trees that fringed the southern limits of the desert from Sudan to Senegal, constituted the most important habitat (Newby 1988). A gregarious species, its herd size varied with season, food availability, reproductive activity and human presence. Oryxes exhibited a seasonal, cyclical pattern of movement, driven by the requirement for grazing, water and shade. Grazing resources were dependent entirely on an unpredictable and variable rainfall (100–400 mm annually). In countries south of the Sahara, during the single Sahelian wet season (Jun–Sep), Scimitar-horned Oryxes used to follow the rains, migrating north to graze on freshly sprouted grasses and to areas with access to water. During the cooler months (Nov–Feb), the oryxes reached the Saharan Desert fringes and their winter grazing pastures. With the onset of the hot dry season (Mar–Jun) the grasses desiccated and the oryxes migrated south to the Sahelian dunes in search of perennial species, such as *Panicum turgidum* and *Aristida mutabilis*, fallen *Acacia* pods and persistent foliage of shrubs and herbs (Gillet 1966a, Newby 1974, Dragesco-Joffé 1993). The wooded wadis (ephemeral desert streams) and inter-dunal depressions provided essential shade during the hottest periods, when shade temperatures could reach 40–45°C, and, as a result, peak feeding activity was at dawn and dusk. Dense shade trees, such as *Maerua crassifolia*, were particularly sought after, while in sparsely wooded regions even a clump of *Panicum turgidum* could provide shade (Gillet 1966a). In Chad, the pattern of seasonal movements consisted of annual migrations greater than 600 km (Newby 1988).

Abundance Formerly abundant throughout the Sahelian zone, there were probably more Scimitar-horned Oryxes south of the Sahara than in the northern range countries (Newby 1988). Historically, aggregations of several hundred or even thousands congregated at favourable pasture or during the seasonal migrations

(Brocklehurst 1931, Edmond-Blanc 1955, Gillet 1966a, Newby 1974). Oryxes were still considered common throughout northern Africa in the mid-1900s, but herds have not been observed since the 1970s. As late as 1985 there were an estimated 500 animals in Chad and Niger, but by 1988 it was reported that only a few dozen survived in the wild and since then there have been no confirmed reports of any surviving wild oryxes. Sadly, the prediction by John Newby (1978b) that 'the Scimitar-horned Oryx will be extinct in the wild before the end of the century' turned out to be true.

Adaptations Although the physiology of the Scimitar-horned Oryx has not been subject to investigation like that of its southern or East African counterparts, it is likely that many of the adaptations to survival in arid environments detailed for the Gemsbok by Knight in this volume also hold true for the Scimitar-horned Oryx. They have the ability to survive for months without drinking, obtaining most of their moisture requirements through their food, but will drink freely when water is available. Physiological adaptations and behavioural mechanisms help them control water balance. For example, the light-coloured coat helps reflect and reduce radiant heat and they are inactive during the heat of the day. In extreme heat they seek shade or lie in shallow scrapes in the sand (Newby 1974, R. Molcanova pers. comm.). The coat is short and thick, and grows longer during the winter (Dolan 1966b, Gordon & Wachter 1986). Studies on the related Beisa Oryx *Oryx beisa* found that dehydrated animals conserve moisture by storing heat during the day (body temperature may exceed 45 °C for eight hours with no apparent ill effect); during the cooler night the heat is transferred back to the environment (Taylor 1969). Body temperature fluctuations are normal in hippotragine antelopes (Kock & Hawkey 1988). Milk analysis of a sample taken three days post-partum consisted of 12.7% fat, 5.4% protein and 24.5% non-fat milk solids (Mayor 1983). Such highly concentrated milk is consistent with the requirement to conserve water in an arid environment.

A nomadic species with movements adjusted to seasonal rains, oryxes used to walk long distances to exploit newly sprouted vegetation and water. They have a highly developed sense of sight and smell, sensing changes in the atmospheric humidity (Gillet 1966a) or responding to distant lightning and the 'smell' of the rains on the winds (Newby 1974). They have large hooves adapted to walking great distances over sandy or loose, stony terrain, and walk at an amble, nodding their heads while walking fast. Captive animals have adapted readily to life in temperate zones.

Foraging and Food Scimitar-horned Oryxes are ruminants and show a pronounced preference for grazing, but also browse. Gagnon & Chew (2000) in their review of the dietary preferences of African bovids classified them as variable grazers. They graze predominantly on a wide variety of grasses, legumes and perennials that vary seasonally in their availability (Gillet 1966a, b, Newby 1974, R. Molcanova pers. comm.). Plants with a high moisture content are selected, such as the leaves and fruit of the wild desert melon *Citrullus colocynthis*, a characteristic species of the Sahelian sub-desert steppes and an important forage species with its leaves and stems staying green well into the hot season (Newby 1974). The animals graze in the early morning, evening and at night, when plants have been observed to collect small droplets of moisture on the leaves (Gillet 1966a, b).

Plants of the genera *Aristida*, *Brachiaria*, *Dactyloctenium*, *Echinochloa*, *Fagonia*, *Indigofera*, *Panicum*, *Requienia*, *Stipagrostis* and *Tephrosia* were important food sources in Chad, as were high protein *Acacia* pods, particularly for lactating ♀♀ (Gillet 1966a, b, Newby 1974). Sahelian populations also fed on foliage from persistent shrubs, including *Cornulaca monacantha*, *Chrozophora senegalensis* and *Cassia italica*, and a few herbs, such as *Heliotropium strigosum* (Newby 1974, Dragesco-Joffé 1993). Animals returned to Tunisia fed primarily on grasses, including the drought-resistant *Cenchrus* sp., used their horns to hook down *Acacia* branches and explored a range of small herbs and shrubs. They showed exploratory tasting behaviour of a range of plant species that were unfamiliar when they were first introduced to natural range. They also avoided the toxic species *Peganum harmala* and *Pergularia tormentosa* (Gordon 1991, T. Wachter pers. comm.). A list of species known to be eaten by the Scimitar-horned Oryx both in the wild and at release sites for reintroduction programmes is provided by Gilbert & Woodfine (2004).

Social and Reproductive Behaviour The most detailed observations of Scimitar-horned Oryx behaviour are those of Gillet (1966a, b) and Newby (1974, 1988) in the wild in Chad and more recent studies in semi-captive conditions in Tunisia (Molcanova & Wachter 2010, 2011a,b, Molcanova *et al.* 2011). Herd sizes in Chad typically ranged from 10–30 (Talbot 1960, Gillet 1966a, Newby 1974, Wilson 1980). The average of 37 herds observed was 14.8 (range 6–28). Typical herds were mixed sex, comprising at least one old ♂, with subadult ♂♂, ♀♀ and juveniles (Newby 1974). Observations from Tunisia show a similar predominantly mixed-sex structure with a mean herd size of 12 (range 2–30) (Molcanova & Wachter 2011b).

Within herds, linear social hierarchies exist, typically with the largest adult ♂♂ dominant to adult ♀♀, but herd movements are usually initiated by an older dominant ♀ (Newby 1974, Knowles & Oliver 1975, Pfeifer 1981, Mayor 1983, Gordon *et al.* 1989, Engel 1997, Molcanova *et al.* 2001, C. Morrow pers. obs.). Generally tolerant relations between ♂♂ in mixed-sex herds have been reported in Chad (Newby 1974) and Tunisia. Dominance is primarily established with ritualistic displays. Both ♂♂ and ♀♀ use spatial displacement, erect posture and lateral horn presentation, often combined with tilting the head to aim the horns toward an opponent. Submission is expressed by turning away with a brief lowering of the head (or, in extreme cases, lying down). Displaying ♂♂ may thrash the ground or vegetation with horns from a standing or kneeling position. If ritualized displays are insufficient, equally matched ♂♂ fight initially face to face, sometimes kneeling, or swinging round side by side, enabling vigorous over-the-shoulder stabbing (Molcanova & Wachter 2011b), the loser breaking off to run away. Fighting may cause horn breakages. Serious injury and/or death has been recorded (Gordon 1989, Blumer *et al.* 1992, Molcanova & Wachter 2007, 2011a,b). Damage or loss of horns results in reduction in social rank in some circumstances, although some long term territory-holders in Tunisia were also one-horned.

Solitary wild ♂♂ were encountered in Chad; although not known to patrol or demarcate territorial boundaries, they did make vigorous attempts to keep ♀♀ together as a herd (Newby 1974). In semi-captive conditions (Tunisia), territorial behaviour by solitary ♂♂ has been described in detail by Molcanova & Wachter (2010, 2011a,b). Territorial ♂♂ occupied restricted areas (typically around 8 km²), in

some cases held for periods of more than six years. These ♂♂ were frequently alone and areas were defended against ♂♂ of similar status. On territory they expressed dominance by characteristic squat defecation displays; on rare excursions off territory (for example, to visit the single drinking point), they defecated in normal standing posture. When herds move onto territories, resident ♂♂ are comparatively tolerant of submissive subordinate ♂♂ in the absence of receptive ♀♀, using ritualized displays to confirm status. Cases of sub-adult ♂♂ transitioning to territoriality, associated with a change from herd-based to a more solitary existence and development of restricted movement in an exclusive area have also been recorded.

Courtship follows a highly ritualistic pattern: the ♂ approaches the ♀ with head high, sniffs the anogenital region and may perform flehmen. A non-oestrous ♀ will continue grazing or walk away, the ♂ losing interest. A ♀ coming into oestrus may lower her head and run a short distance, the ♂ following. Oestrous ♀♀ walk and vocalize more, eat less and solicit attention from the ♂. The ♂ will perform flehmen in response to urination (sampling mid-stream or from the ground). The pair engage in lateral head-to-tail circling ('mating circles') and the ♂ will repeatedly perform laufschiag ('foreleg lift') to test for female receptivity before attempting to mount. Laufschiag may be performed from directly behind the ♀, from the side or on an angle, with the ♂ facing the female's tail. The ♂ will also lean heavily and/or push on the female's hindquarters to test for receptivity. If the ♀ stands during the hindquarter pushing and laufschiag he will perform repeated mounts (82 ± 13 , mean \pm SEM, range 3–155 in artificially synchronized captive ♀♀) followed by a strong pelvic thrust in which his hindfeet may leave the ground. Bouts of courtship activity (4.7 ± 0.7 , mean \pm SEM, range 1–8 in synchronized ♀♀) are interspersed with other activities (grazing, walking, resting).

Females separate from the herd for a few days prior to and following parturition. During labour, ♀♀ exhibit increased walking and alternating periods of standing and lying. Calves can stand and follow their mothers within hours of birth. Ano-genital licking and grooming is the most common mother–calf interaction and occurs independently of suckling. If in good condition, ♀♀ frequently come into post-partum oestrus during this period of isolation. They are usually joined by (or find their way to) an adult ♂ and form mating consortships (usually with territorial ♂♂) over several days in semi-captive populations. Courtship bouts are frequent and the ♂ may also tend the calf assiduously at this time, working to keep the mother-calf pair within his territory. Female oryx may choose to associate with different ♂♂ during the post-partum period. This can involve running to escape blocking manoeuvres by the ♂, and may not be without risk. Fresh stab injuries have been noted on ♀♀ following successful transition between territorial ♂♂ (Molcanova & Wachter 2011b).

Between periods of suckling, calves spend most of their time lying out hidden in vegetation with other calves of similar age for 3–8 weeks (Newby 1974, Gill & Cave-Browne 1988). Females typically return to herds with their calves within 2–3 weeks. Older calves may kneel on carpal joints while suckling. Social play in captive calves of both sexes from 2–15 weeks of age consists of running in circles, leg kicking, head tossing, sparring, circling and pawing the ground (Pfeifer 1985). Once returned to herds, older calves often associate together, forming distinctive crèches (for example, resting at one

side while adults graze), or two or three calves may keep company with one adult ♀ (Molcanova & Wachter 2011a).

Scimitar-horned Oryxes make a variety of sounds: ♂♂ and ♀♀ vocalize more when ♀♀ are in oestrus and ♀♀ are more vocal with calves at foot; ♂♂ grunt. Six vocalizations were distinguished from sonograms: adult contact, juvenile contact, adult alarm snorts, calf 'moans' and mother 'purr' calls (Gill & Cave-Browne 1988).

Reproduction and Population Structure Limited data on reproduction exist for Scimitar-horned Oryxes in the wild (see Table 9), but comprehensive research on captive populations has provided data on ovarian cycles, seasonality and assisted reproductive technologies (ovulation induction, semen collection and cryopreservation procedures) (see Morrow 1997, Morrow *et al.* 1999, 2000 for reviews). Captive oryxes are seasonally polyoestrous, spontaneous ovulators with a 23.4 ± 1.3 day ovarian cycle (luteal phase 18–20 days) and intermittent, short, 8–12 day cycles; oestrus lasts 3–41 hours (Morrow 1997). A loosely synchronized spring anovulatory interval of 36–95 days was recorded in a small captive herd (Morrow *et al.* 1999). Ultrasonography and elevated periovulatory and luteal phase oestrogen concentrations suggests follicular recruitment throughout the ovarian cycle.

Gestation ranges from 222 to 257 days (median 250 days) in captivity and 258 to 274 days in the wild (Table 9). Twin births are uncommon (0.7%; North American Studbook), and twin litters have a high mortality rate (56%), reflecting anatomical limitations imposed by a duplex uterus. Postpartum oestrus occurs in wild (Newby 1974), reintroduced (Gordon 1991, Molcanova & Wachter 2007) and captive (Knowles & Oliver 1975, Nishiki 1992) populations. Oryxes in Chad and those re-established in Tunisia exhibit asynchronous breeding in favourable climatic and nutritional conditions with births every 8–10 months (Gillet 1966a, Newby 1988, Gordon 1991, R. Molcanova pers. comm.). At Sidi Toui N. P., over the course of seven years ($n = 40$ births), calvings peaked in Mar and Oct, with births recorded in all except the hottest two months of Jun and Jul (Molcanova 2006). In captivity, calves have been born every month of the year (Table 9) and it is recommended that the breeding ♂ be removed at certain times of the year to manage births. However, analysis of North American Studbook records of unmanaged breeding herds confirm an 8–11 month reproductive periodicity; ♀♀ that calved in the winter/spring had a longer inter-birth interval than ♀♀ that calved in the summer/autumn (Morrow *et al.* 1999). Median inter-birth interval was 277 days with 75% of intervals less than 11 months.

Calves average about 8–9 kg at birth (range 5–11 kg), and are a light gingery brown colour for the first 2–3 months, with a narrow whitish area on the belly, and faint hint of adult face pattern. The cryptic colouring serves as an anti-predator adaptation during the lying-out phase. Horn buds are visible at birth. Adult colouration is attained between three and 6 months of age, and weaning occurs between six and ten months (Molcanova & Wachter 2010). Estimates of age of sexual maturity range between 10 and 27 months for ♀♀ and 22 and 30 months for ♂♂ (Table 9). Although no comparative data exist for wild animals, in a semi-captive population a ♀ reproduced at 17 years (Molcanova & Wachter 2011b) and captive ♀♀ in good health can continue to reproduce past the age of 20 years. The high reproductive potential is due to a combination of low

Table 9. Reproductive data for Scimitar-horned Oryx.

| Popn | Location | Latitude | Birth season | Oestrous cycle (d) | Gestation (d) | Sexual maturity F | M | References |
|----------------|--------------------|----------|---|-------------------------|-----------------------|-------------------|-------|--|
| Wild | Sudan | 14° N | May | | 274 | | | Brocklehurst 1931 |
| Wild | Chad | 13–16° N | Jul–Aug | | 274 | | | Gillet 1966a, b |
| Wild | Chad | 14–17° N | 8–10 month peaks
Jan–Feb, Sep–Oct, May–Jun | | 258 | >24 | 22–30 | Newby 1974 |
| Wild | Ennedi, Chad | 15–18° N | Jan–Apr | | | | | Edmond-Blanc 1955 |
| <i>In situ</i> | Bou-Hedma, Tunisia | 34° N | Mar, Apr, Jul, Sep, Nov | | | | | Gordon 1991 |
| <i>In situ</i> | Sidi Toui, Tunisia | 32° N | Dec, Mar, Apr, Aug, Sept | | 277, 289 | | | R. Molcanova pers. comm. |
| <i>Ex situ</i> | Hai Bar, Israel | 30° N | Aug–Apr | | | | | Yoffe 1980 |
| Captive | Edinburgh, UK | 55° N | All year | | 222–253 | 18–25 | | Gill & Cave-Browne 1988 |
| Captive | Germany | 52° N | | | 242–256 | 27 | | Dittrich 1972 |
| Captive | London, UK | 51° N | All year ^a | 24.4 ± 2.2 ^b | | | | ^a Zuckerman 1953, Anonymous 1961, Kirkwood <i>et al.</i> 1987, ^b Shaw <i>et al.</i> 1995 |
| Captive | Ohio, USA | 41° N | | | 247 | | | Pope <i>et al.</i> 1991, Morrow <i>et al.</i> 2000 |
| Captive | Virginia, USA | 38° N | Mar–Aug | 23.8 ± 1.3; short 8–12 | 247, 249 | 11–27 | | Morrow & Monfort 1998, Morrow <i>et al.</i> 1999, 2000 |
| Captive | Tokyo, Japan | 35° N | Nov–Mar | | 247.6 | 22 | | Nishiki 1992 |
| Captive | San Diego, USA | 32° N | | 21–22 | | 11 | | Durrant 1983 |
| Captive | New Zealand | 43° S | | 22.7 ± 1.1 ^a | 253, 257 ^b | > 12 ^a | | ^a Bowen & Barrell 1996, ^b Garland <i>et al.</i> 1992 |

mortality, adult longevity and an 8–11 month inter-birth interval. A captive animal was still alive after 27 years (Weigl 2005). Although sex ratios in small captive populations have been reported to be nearly 1 : 1 (Yoffe 1980, Gill & Cave-Browne 1988, Nishiki 1992), an analysis of 1129 births suggested that sex ratios in North America (1985–94) were male-biased (1 : 0.84) (Morrow *et al.* 1999).

Predators, Parasites and Diseases Few large predators inhabited the arid environment of the Scimitar-horned Oryx, but there were once overlaps in range. Spotted Hyaenas *Crocuta crocuta*, Striped Hyaenas *Hyaena hyaena*, African Wild Dogs *Lycaon pictus*, Cheetahs *Acinonyx jubatus*, Golden Jackals *Canis aureus* and Lappet-faced Vultures *Torgos tracheliotus* were likely predators of young and infirm animals (Gillet 1966a, Newby 1974). Death of adults and calves from hunger, heat exhaustion and disease was common during droughts (Newby 1988). Although survival of calves in the wild was high, calf abandonment was also high during drought conditions (Newby 1988). In reintroduced semi-captive populations, calf deaths have resulted from starvation (mismothering or insufficient lactation; Gordon 1991, Molcanova *et al.* 2001), predation by Golden Jackals (Molcanova *et al.* 2001, Molcanova 2002) and aggression by dominant ♂♂ (Gordon 1991). In captivity, calves have in some cases suffered high mortality attributed to inbreeding (Mace & Pemberton 1988, Nishiki 1992).

Normal haematological and serum chemistry values have been examined in captive populations (Bush *et al.* 1983, Hawkey & Hart 1984, Ferrell *et al.* 2001, Flach 2004a). Deaths from *Parelaphostrongylus tenuis* (meningeal worm) infection (Ferrell *et al.* 1997), disseminated intravascular coagulation (Pearce *et al.* 1985), perforation of the large bowel (Mayor 1983), bovine spongiform encephalopathy (Kirkwood

& Cunningham 1999), and serious internal injuries from horn punctures (C. Morrow pers. obs.) have been reported for captive individuals. Tuberculosis is also a potential problem in captivity (Greth *et al.* 1994). Clinical malignant catarrhal fever, bovine viral diarrhoea virus, yersiniosis, gastrointestinal helminths, coccidial oocysts, acidosis, copper deficiency and hoof problems have been reported (Flach 2004a). Reported deaths of Scimitar-horned Oryxes at Hai-Bar N. R., Israel, have included coccidiosis, mouth tumour, parturition and worms (Yoffe 1980).

Immobilization and anaesthesia protocols are well established (Kock & Hawkey 1988, Pearce & Kock 1989, Roth *et al.* 1998, Morrow *et al.* 2000, Flach 2004b). Because of the ability of desert antelopes to accumulate body reserves, individuals may be prone to obesity in captivity. Common veterinary treatments include trauma (broken horns, puncture wounds, lacerations) and hoof/joint disorders (lameness).

Conservation IUCN Category: Extinct in the Wild. CITES: Appendix I. CMS: Appendix I.

The reasons for the catastrophic decline of the Scimitar-horned Oryx are well documented and include habitat loss (desertification due to repeated droughts, development of permanent boreholes and resulting competition with domestic stock and human disturbance), civil war and exploitation through motorized hunting (Newby 1978b, 1980, Mallon & Kingswood 2001a, Devillers & Devillers-Terschuren 2005). Their meat and hide was prized by local people, the thick hide being used for ropes, bags, shoes and shield coverings. They were ruthlessly hunted for their magnificent horns by trophy hunters (Gillet 1966a, Barrett 1967, Newby 1978b). Hunting parties using all-terrain vehicles and modern firearms replaced the

traditional method relying on spears and camels, horses and/or dogs (Brocklehurst 1931, Talbot 1960). Between 1973 and 1978 a wild population flourished (>3500) under active protection in Ouadi Rimé–Ouadi Achim Faunal Reserve in Chad (Bassett 1975, Newby 1980), but between 1978 and 1986 protection in the Reserve was abandoned because of political unrest.

The last known photograph of wild Scimitar-horned Oryx, a group of four, was taken by John Newby in the Air–Ténéré of Niger in May 1980 (Newby *et al.* 2004). As with other ‘last observations’ in Algeria and Egypt (see Distribution), it seems likely that these individuals may have been wandering far from normal locations. Despite sporadic casual reports, no wild Scimitar-horned Oryxes have been confirmed alive in the last 15-odd years. Extensive surveys dedicated to detection of Sahelo-Saharan antelopes carried out in Chad and Niger have produced only five fragments from former haunts in the Ouadi Rimé–Ouadi Achim Faunal Reserve and the central Termit Mts of Niger (Newby *et al.* 2004, Wacher *et al.* 2004a, 2011). No evidence of living oryxes has been obtained.

The Scimitar-horned Oryx has thrived in captivity, and in 2008 it was estimated that there were 1675 animals in 204 institutions (Gilbert 2008). There are perhaps more than 4000 in private collections. However, despite being well represented in captive populations, almost all individuals are derived from a genetic base of fewer than 40–50 founders captured in Chad in the 1960s (Bertram 1988, Dixon *et al.* 1991). A large population of Scimitar-horned Oryxes (>2000) in private collections in the United Arab Emirates are descended from animals captured in N Sudan representing a separate genetic line than the European Endangered Species Programme (EEP) and American Zoos and Aquariums’ Species Survival Plan (SSP) populations (R. Molcanova pers. comm.). In captivity, small, fragmented populations are vulnerable to losses in genetic diversity and fluctuations in size, age and sex ratios. This vulnerability was recognized in the early 1980s, and breeding plans were instituted in North America (SSP; Species Survival Plan), the United Kingdom and Europe (EEP; Europäisches Erhaltungszucht Programm), and Australasia (ASMP; Australasian Species Management Plan) to maximize genetic variation from different founder lineages. Despite being well organized on a regional and global basis, the conservation of this species presents a paradox to zoo managers and conservation biologists. Existing genetic management strategies necessitate the exchange of valuable breeding stock; however, insufficient funding and enclosure space can preclude breeding among genetically valuable pairs. Reproductive technology (e.g. artificial insemination) has proven potential for overcoming the risk and expense of transporting live animals, and for optimizing the use of limited enclosure space, while simultaneously preserving gene diversity (Garland *et al.* 1992, Morrow *et al.* 2000).

Largely due to the success of rearing this species in captivity, populations of Scimitar-horned Oryxes have been re-established in protected, fenced enclosures in Tunisia, Senegal and Morocco (details provided in Distribution). While successful, these populations represent an intermediate stage between captivity and true reintroduction in range countries. Conservation of aridland antelopes

by necessity requires protection of large areas that could never be fenced to accommodate the seasonal migratory behaviour to pastures following the rains. Human encroachment, overgrazing, reduction of tree cover (shade) and the lack of resources have hampered efforts to create protected areas for Scimitar-horned Oryxes (Wacher 2001, Devillers & Devillers-Terschuren 2005). Plans to establish founder populations and a metapopulation management plan within range countries with the ultimate goal of restoring free-living, self-sustaining populations outside of protected areas are gaining momentum (Houston 2003, Wakefield 2003, Woodfine & Engel 2004).

The conservation of this species and other Sahelo-Saharan antelopes was the focus of a workshop convened by the Secretariat of the Convention on the Conservation of Migratory Species and the Institut Royal des Sciences Naturelles de Belgique at Djerba, Tunisia in 1998. This workshop developed an Action Plan for the Conservation and Restoration of Sahelo-Saharan Antelopes and adopted the Djerba Declaration for improving the conservation status of these species (UNEP/CMS 1998, 1999). In 2003, a second seminar on the Conservation and Restoration of Sahelo-Saharan antelopes and their habitats was held at Agadir, Morocco, to review and update the activities and projects in the previous five years (UNEP/CMS 2004).

The Sahelo-Saharan Interest Group (SSIG) was established in 2000 as a network of institutions and individuals keen to conserve Sahelo-Saharan wildlife and the habitats they require for survival (Monfort 2000). The SSIG works to maintain living, healthy deserts that sustain both the wildlife and people who rely on those ecosystems for their livelihood and survival (Monfort & Correll 2004). The SSIG holds an annual meeting and members are actively involved in conservation, research and training across the Sahelo-Saharan regions. In 2005, the SSIG unveiled the Sahara Conservation Fund, an international, non-governmental organization committed to conserving the wildlife of the Sahara and bordering Sahelian grasslands. SCF is spear-heading an initiative to reintroduce Scimitar-horned Oryxes to their former stronghold in Chad, Ouadi Rimé–Ouadi Achim Faunal Reserve.

Measurements

Oryx dammah

HB (♀ ♀): 1360 (1200–1620) mm, n = 31

T (♀ ♀): 530 (440–600) mm, n = 26

Sh. ht (♀ ♀): 1150 (1060–1210) mm, n = 31

WT (♀ ♀): 151.0 (129.0–177.0) kg, n = 19

WT (♂ ♂): 153.0 (144.0–166.0) kg, n = 3

North American captive population (C.J. Morrow pers. obs.; calf data NZP/CRC records 1980–1992)

Maximum recorded horn length is 127.3 cm for an animal from Fada, Chad (Rowland Ward)

Key References Devillers & Devillers-Terschuren 2005; Gilbert & Woodfine 2004; Gillet 1966a, b; Mallon & Kingswood 2001a (and chapters therein); Morrow *et al.* 1999, 2000; Newby 1974, 1988.

Catherine Morrow, Renata Molcanova & Tim Wacher

Tribe CAPRINI

Sheep, Goats

Caprini Gray, 1821. London Med. Repos. 15: 307.

The Caprini are a large tribe of bovids with 34 living species (Grubb 2005). They are largely native to Eurasia and the Rocky Mts, and form a monophyletic unit in morphological and molecular phylogenies (Hernández Fernández & Vrba 2005, Ropiquet & Hassanin 2005a, Hassanin *et al.* 2012). The latter authors have constructed a molecular tree that presents an improved picture of how the species and genera are related to one another within the tribe.

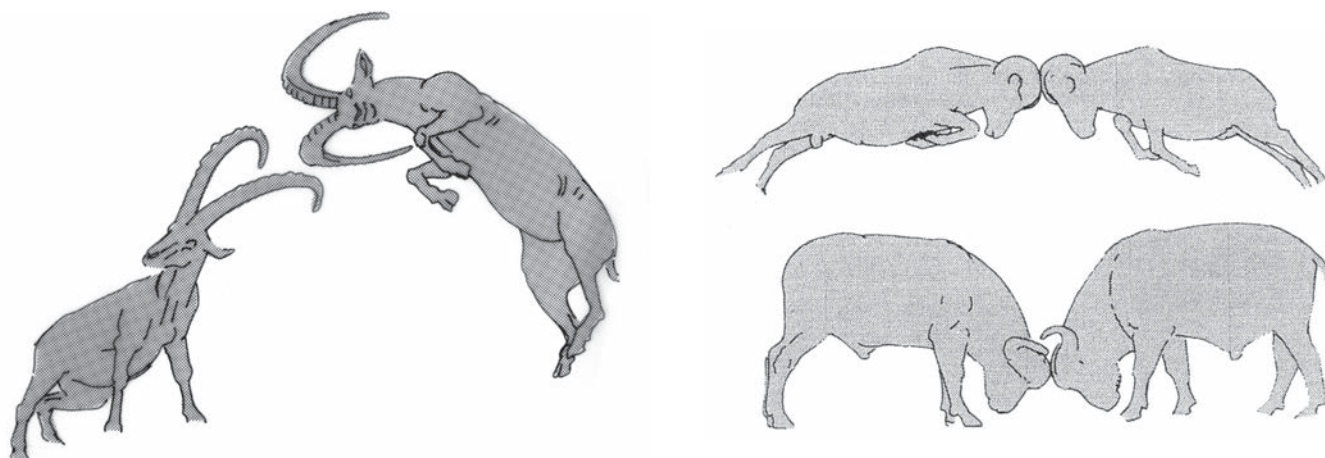
Some taxonomists prefer to place caprines in their own subfamily, but we have followed previous practice and Ropiquet & Hassanin (2005a) in assigning a tribal level to this diverse and interesting group. In earlier treatments, as a subfamily, several tribal subdivisions were recognized. The most recent classification by Grubb (2005) recognized four tribes: (1) Naemorhedini, including *Capricornis* (serows) and *Naemorhedus* (gorals); (2) Ovibovini, including *Ovibos* (Muskox) and *Budorcas* (Takin); (3) Caprini, including *Capra* (goats and ibexes), *Ammotragus* (Barbary Sheep), *Hemitragus* (tahrs), *Pseudois* (Blue Sheep), *Ovis* (sheep), *Rupicapra* (chamois) and *Oreamnos* (Rocky Mountain Goat); and (4) Pantholopini, including *Pantholops* (Chiru or Tibetan Antelope). However, the molecular results of Ropiquet & Hassanin (2005a) indicate that all tribes classically defined in the literature are not monophyletic, thereby supporting the inclusion of all caprine species into a unique enlarged tribe Caprini (and see Hassanin *et al.* 1998, 2012, Hassanin & Douzery 1999). This phylogeny also supports the inclusion of the Chiru *Pantholops hodgsoni* in the caprines (and see Gatesy *et al.* 1997, Vrba & Schaller 2000).

Only three caprines are found in Africa, namely Nubian Ibex *Capra nubiana*, Walia Ibex *Capra walie* and the Aoudad or Barbary Sheep *Ammotragus lervia*. Of these, only the Walia Ibex can be regarded as non-Palaearctic. Himalayan Tahr *Hemitragus jemlahicus*, a species native to the Himalaya of China, N India and Nepal, were introduced to the Western Cape Province of South Africa around 1930 (see below).

Outside Africa, caprines range in size from around 30 kg (*Naemorhedus* spp.) to as much as 350 kg (Muskox *Ovibos moschatus*); ♀♀ may attain only about 60% of the body weight of adult ♂♂. As with other bovids, the presence of horns is marked by strong inter-specific, inter-sexual and individual variation; male horns are often

long or large, notably in the sheep and goats. Sinuses within the frontal bones spread far up the length of the horn cores. This is an obvious weight-reducing benefit for agile animals in which the ♂♂ fight by ramming and clashing their horns (Schaffer & Reed 1972), although similar fighting techniques also occur in living Bovini (cattle). Pelages include fine undercoats that become the woollen fleece of domestic sheep or the 'pashm' of Kashmir (cashmere) goats. Males often have ruffs, manes, fringes or beards. There are no face, pedal or inguinal glands, and ♀♀ have a single pair of inguinal nipples. The molar teeth have a simple clear-cut occlusal pattern. They are extremely similar in sheep and goats despite the former being primarily a close-cropping grazer and the latter more catholic in its diet. Metapodials are often shortened and the body conformation is stocky. Chromosome numbers differ among the various species karyotyped to date, ranging, for example, from $2n = 60$ in *Capra*, $2n = 52-58$ among members of the genus *Ovis* (and $2n = 58$ in the Barbary Sheep *Ammotragus*) and $2n = 42$ in the Mountain Goat *Oreamnos americanus* (e.g. Schmitt & Ulbrich 1968, Wurster & Benirschke 1968, Nadler *et al.* 1974).

Schaller (1977) described caprines as generalized and flexible feeders, living in habitats of simple structure and in areas of low primary productivity. He pointed out that they are often the only ruminant in a particular area or habitat: thus, caprines have a demonstrable association with mountain ranges, high plateaux, precipitous cliffs, uneven hilly country or jebels. Some of these habitats may be wooded, but they are more often barren, rocky, open and of low productivity. Each regional caprine tends to be an adaptable, medium-sized herbivore with a broad niche in a simple, impoverished habitat. Caprines have not flourished in the richer Eurasian habitats, where they are generally replaced by deer (which have made ecological radiations comparable to those of some African antelopes). Some Eurasian caprine distributions look like a relict pattern resulting from withdrawal in the face of human exploitation. While this may often be true, the animals' anatomical peculiarities and agility on rocky terrain reflect long-term adaptation to such habitats. Their pre-human distributions were more likely an evolutionary response to competition from other ungulates (Kingdon 1982).



Bovine fighting techniques: *Syncerus* (below right) compared with *Ovis* (top right) and Nubian Ibex *Capra nubiana* (left).

Fossils of Caprini are reasonably well known from Eurasia and sometimes occurred additionally in North Africa. It would seem that from about 12 mya onwards, different bovids throughout Eurasia, for example *Aragoral* and *Protoryx*, were gradually acquiring characters of the diverse Caprini that later inhabited the same land mass (Gentry 2000). Parallel evolution was evidently rife in the acquisition of characters such as anterior keels on the horn cores or shorter metapodials. Extinct relatives of *Ovibos* were widespread in the later Pliocene, even into North America, and Caprini had entered Africa by the start of the Pliocene. Better-known examples include the South African later Pliocene ovibovine *Makapania broomi*, a Pliocene species of *Budorcas* from Ethiopia, and the puzzling *Nitidarcus asfawi* from the Pleistocene of Ethiopia (Vrba 1997).

Although Pliocene and Pleistocene sheep are not very common and are unknown in Africa, goats or goat-like forms are known from Ethiopia in the middle Pleistocene (*Bouria angettyae*; Vrba 1997) and from North Africa in the later Pleistocene.

It is thought that humans began exerting some control over herds of wild Caprini many millennia ago, perhaps around 8000 BC in Africa, and evidence of domestic sheep is known from the southern tip of Africa about 500 years BC.

In the early 1930s, Groote Schuur Zoological Gardens, situated on the slopes of Devil's Peak, Table Mountain, near Cape Town in the

Western Cape Province of South Africa, obtained a pair of Himalayan Tahrs from the National Zoological Gardens, Pretoria. The pair escaped from their enclosure and established themselves either on Devil's Peak or on Table Mountain. In 1972, there were an estimated 330 individuals (Lloyd 1975), by which time Himalayan Tahrs occurred across much of the north/north-west and south/south-east faces of both Devil's Peak and Table Mountain (and the Saddle linking them) and the north-west faces of the Twelve Apostles range. This uncontrolled increase in the numbers of Himalayan Tahrs, within a Nature Reserve and especially a reserve with a unique flora, posed a serious threat and the local conservation authority, Cape Nature Conservation, initiated a research study to investigate the problems involved. This survey recommended that, as total eradication was probably impossible, there should be a drastic reduction in the population (Lloyd 1975). Between 1975 and 1981 over 600 tahrs were removed by Parks and Forestry officials and members of Cape Nature Conservation. A survey conducted by the Mountain Club and officials of the Parks and Forestry showed that at the end of this period, 88 tahrs were still living on Table Mountain (see Skinner & Smithers 1990 for further discussion).

Michael Hoffmann & Jonathan Kingdon

GENUS *Ammotragus*

Aoudad

Ammotragus Blyth, 1840. Proc. Zool. Soc. Lond. 1840: 13.

Ammotragus includes only the Aoudad *Ammotragus lervia*, which inhabits montane desert habitats in northern Africa. The classification of the Aoudad has changed over the years since it was first included in the genus *Antelope*, with its affinities with *Ovis* and *Capra*, in particular, having been widely discussed in the literature. Several taxonomic works have included the species in the genus *Capra* (Ansell 1972, Corbet 1978), with which it shares a series of morphological traits. Aoudads may interbreed with domestic goats and produce live and fertile offspring (Petzsch 1957, Van Gelder 1977b), although this hybridization does not occur readily. However, Aoudads also share a series of sheep-like characteristics with *Ovis* (Valdez & Bunch 1980), and one author has suggested it is related to the common ancestor of both goats and sheep (e.g. Geist 1971), due to its unique morphological and behavioural characteristics, which, along with fossil remains, would place it near the origin of the Palaearctic sheep lineage, close to the rupicaprids. Analysis of proteins has only served to confuse matters, with seroprotein (Schmitt 1963) and immunoglobulin (Curtain & Fudenberg 1973) analyses revealing a closer relationship to *Ovis* than to *Capra*, while the sequence of amino acids of several haemoglobin chains (Manwell & Baker 1975) showed a closer relation to *Capra* as well as some unique characteristics. Immuno-diffusion studies by Hight & Nadler (1976) paradoxically establish a closer relationship between *Ovis* and *Capra* than between either of them and *Ammotragus*.

A study on phylogenetic relationships based on the comparison of 12S rDNA sequences between eight caprine species, including *Ammotragus*, *Pseudois*, *Capra aegagrus* and five *Ovis* species, show two distinct clusters, one formed by all *Ovis* species and another grouping the other three genera together (Ludwig & Fischer 1998). A complete estimate of the phylogenetic relationships in the Ruminantia unequivocally supports the grouping of *Ammotragus* with the goats and tahrs (*Hemitragus*) (Hernández Fernández & Vrba 2005), although its own morphological, biological, ecological and behavioural characteristics suggest that it should be placed in its own genus *Ammotragus*. A molecular phylogeny of caprines groups *Ammotragus* with *Capra*, *Hemitragus* and *Pseudois* (Ropiquet & Hassanin 2005a), with *Ammotragus* most closely allied with the Arabian Tahr *Arabitragus jayakari* (Ropiquet & Hassanin 2005b).

Common names referring to either sheep (genus *Ovis*) or goats (genus *Capra*) are misleading and names of an Arabic origin should preferentially be used, for example, Aoudad or Arrui. *Ammotragus* differs from goats and sheep in its long face and sharply bent-down braincase, long neck fringe and relatively long tufted tail. It differs additionally from sheep in that the wrinkling on horns does not form prominent ridges, the horns are not keeled, in the presence of a beard and the absence of preorbital and interdental glands.

Peter Grubb & Michael Hoffmann

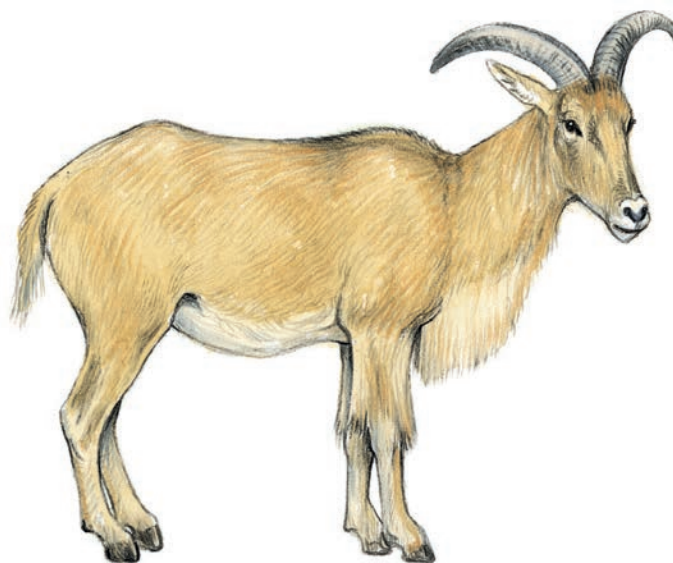
Ammotragus lervia AOUDAD (BARBARY SHEEP, ARUI)

Fr. Mouflon à manchettes; Ger. Mähnspringer (Mähnschaf)

Ammotragus lervia (Pallas, 1777). Spicil. Zool. 12: 12. 'Africae borealori propria'; restricted to Algeria, Department of Oran (Harper 1940).



Aoudad *Ammotragus lervia* male.



Aoudad *Ammotragus lervia* female.

Taxonomy Polytypic species, with six subspecies described (Allen 1939, Ansell 1972, Gray & Simpson 1980), though not without controversy (see, for example, Ellerman & Morrison-Scott 1951). The somewhat vague morphological differences between them (see below), the fact that most of the subspecies were defined from a few specimens, and the presence of several potential areas of hybridization, makes it difficult to expound reliably on the ranges of the different subspecies. A reassessment of subspecies boundaries is clearly necessary. Synonyms: *angusi*, *barbatus*, *blainei*, *fassini*, *jaela*, *ornata*, *sahariensis*, *tragelaphus*. Chromosome number: $2n = 58$, with a large acrocentric X chromosome and a minute bi-armed Y chromosome (Nadler *et al.* 1974, Bunch *et al.* 1977), identical to that of *Ovis aries cycloceros* and *O. a. vignei*.

Description The Aoudad is goat-like in proportions, with head relatively long, legs short and stocky, and tail long and naked underneath. A characteristic feature is the mane, which extends down from under the throat along the front of the neck to the chest, and continuing down each of the forelegs in mature animals. This hair pattern on the legs is referred to as leggings or chaps. A mane is also found in wild sheep such as *Ovis orientalis* and *O. aries*, but chaps are unique to Aoudads. They do not have a typical goatee, and, like some wild sheep, they have a haired chin and a short erect dorsal fringe extending from the neck to the middle of back. The genus name *Ammotragus* means 'sand goat', probably in reference to the colour of the pelage, which is pale, tawny-brown grading to a whitish underside with dark brown areas about the head and shoulders, although variability in colour tones is notable among the subspecies (see below). Unlike sheep, the Aoudad lacks preorbital, interdigital and flank glands, but it has subcaudal glands. The lack

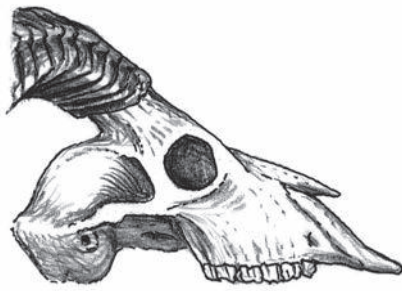
of these glands lends support to the argument that *Ammotragus* is a distinct genus.

Both sexes have horns, relatively large and moderately long (even in ♀♀, compared with goats and sheep), with a somewhat high spiral angle. Horns are elliptical and keeled in cross-section, with a broad frontal surface, and have numerous shallow and uniform sulci as well as periodic growth checks or annuli (Ogren 1965, Schaffer & Reed 1972). The horns curve outwards, backwards and point inwards towards the neck, tending to converge over the nape in mature ♂♂.

The skull is distinguished by the placement of the foramen magnum beneath the horn bases, shaping the cranium accordingly, and the presence of sinuses covering most of the brain as well as complex septa. Aoudads share this advanced skull pattern with the Himalayan Tahr *Hemitragus jemlahicus*, bharals *Pseudois* spp. and *Ovis ammon*. Also, along with the Himalayan Tahr, Aoudad horn bases are displaced behind the eye orbit, while in most Caprini they are usually placed above its posterior half. Finally, the species is characterized by extensive cornual sinuses. All these characteristics are less pronounced or moderate in ♀♀ compared with ♂♂ (Schaffer & Reed 1972).

Geographic Variation

- A. *l. lervia* (Atlas or Moroccan Aoudad): Morocco (and possibly Western Sahara), N Tunisia and N Algeria. Horns scarcely, if at all, depressed; face with an indistinct dark median stripe; beard uniform sandy; body mid-tawny.
- A. *l. ornata* (Egyptian Aoudad): formerly quite widespread throughout the Eastern and Western Desert of Egypt. Horns strongly depressed, turning sharply downwards before bending



Lateral view of skull of Aoudad *Ammotragus lervia*.

backwards; face with no stripe; beard uniform sandy; body sandy rufous.

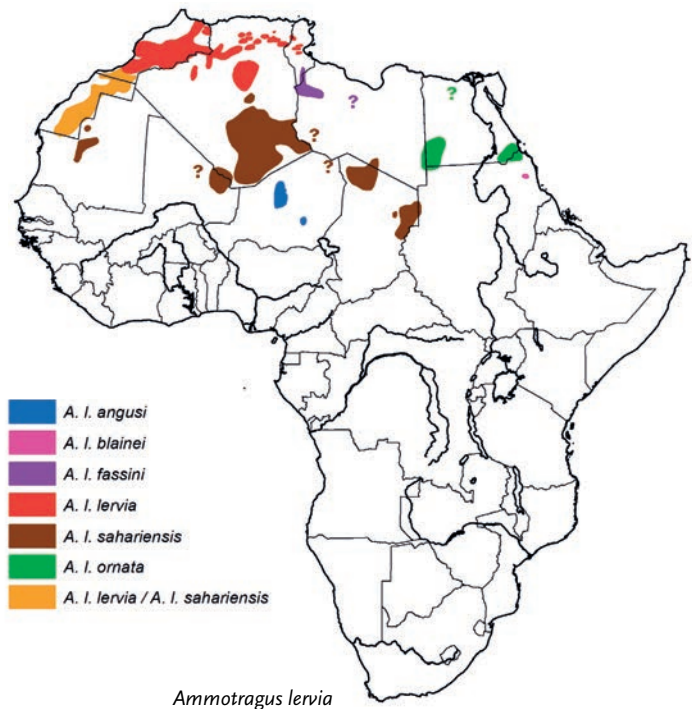
- A. l. sahariensis* (Saharan Aoudad): C and S Algeria, SW Libya, Mauritania, Mali and Tibesti Massif and Ennedi Plateau in Chad; presumed to be the subspecies in Western Sahara, but limits with *A. l. lervia* unclear. Horns like *A. l. ornata*; face with no stripe; ears with a white patch below; beard uniform sandy; body pale sandy rufous.
- A. l. blainei* (Kordofan Aoudad): E Sudan. Horns strongly depressed but not bent backwards so much as in previously named subspecies; face with no stripe, but dark owing to admixture of blackish hairs; beard on sides of lower jaw nearly black; body brownish-grey, less rufous than any previously named subspecies; mane brownish.
- A. l. angusi* (Air Aoudad): originally in Air Massif (Niger) and Termit Massif. Horns much more upright on head than previously named subspecies and curving further backwards and inwards; face with no stripe; beard on sides of lower jaw cinnamon-rufous; body very deep rufous, darker than *A. l. ornata*, dorsal fringe mixed with black, more strongly on front half; chaps sparse.
- A. l. fassini* (Libyan Aoudad): originally in extreme S Tunisia and Libya. Horns less depressed than *A. l. ornata* and *A. l. sahariensis* and more backward-turned than *A. l. blainei*; face with no stripe, but dark due to mixture of brownish and rufous hairs; ears with a dark patch below; beard black, and on lower jaw mixture of tawny and brown; body light tawny-reddish, more rufous than *A. l. sahariensis* and *A. l. blainei*.

Similar Species

Capra nubiana. Confined to Egypt, Sudan and Eritrea, its distribution may overlap with that of the Aoudad, particularly in some mountainous areas of the western coast of the Red Sea: at the edge of the Egyptian Eastern Desert, and a few areas in Sudan (see below). Similar in size to the Aoudad (♂♂ weighing around 90 kg), but shows a characteristic long goatee in mature ♂♂, lacking any mane or the like; male horns are long (up to 1400 mm in some individuals), projected upwards and forming a semi-circle over its back, whereas the ♀ of this species has shorter horns that grow only up to 380 mm in length.

Distribution Endemic to North Africa.

Historical Distribution Formerly widespread in any rugged and mountainous terrain from deserts and semi-deserts to open forests in North Africa (Brentjes 1980, Shackleton 1997). Known also within its present range from late Pleistocene fossils, Holocene rock art and Ancient Egyptian mummified remains.



Current Distribution The distribution of the six subspecies, while imperfectly known, can be summarized as follows.

Atlas or Moroccan Aoudads are found in the mountains of Morocco, except the western half of the Rif (Aulagnier & Thévenot 1997, F. Cuzin pers. comm.), as well as the northern part of Algeria (Kowalski & Rzebiak-Kowalska 1991, De Smet 1997b) and Tunisia (De Smet 1997a), where more than 30 years ago the Aoudad was approaching extinction (Schomber & Kock 1960). The boundary between this subspecies and the Saharan Aoudad in Morocco/Western Sahara is unclear. It has been presumed to be the subspecies imported to European zoological gardens at the end of last century, and from there to American zoos about 1900 (Gray 1985). This subspecies would then form the basis of free-ranging populations inhabiting the S USA (Gray 1985). However, no conclusive evidence to support the notion that this was the sole subspecies used in extralimital transplants has been found (J. Cassinello pers. obs.). On the contrary, Ogren (1965: 9) stated that the pelage of some of the individuals introduced to New Mexico resembles each of the six recognized subspecies, which suggests the existence of hybrid forms. Gray (1985) also supposes that this is the subspecies introduced in the Sierra Espuña mountains of Murcia (Spain), a population that has expanded throughout the whole south-east of the country (Cassinello 2000, Cassinello *et al.* 2004).

The Egyptian Aoudad is native to deserts in Egypt (see Gray 1985), and was assumed to be extinct (Amer 1997). However, there are reports of its continued presence in remote areas, including herds located in the extreme southern region of the Egyptian Eastern Desert (mainly within the boundaries of the Gebel Elba Protected Area) and the Gebel El Uwieinat and Gilf El Kebier Plateau (Western Desert, at the extreme southern corner of the country) (M. A. Saleh pers. comm.). In addition, Wachter *et al.* (2002, and references therein) also report evidence of the presence of Aoudads in both the Elba Protected Area and the Western Desert between 1997 and 2000. Manlius *et al.* (2003) and Manlius (2009) provide further information on their distribution in these remote areas.

The Saharan Aoudad has a very large geographic distribution that, according to Gray (1985), includes parts of S Morocco and Western Sahara (the boundary with the Atlas Aoudad is unclear; see also Aulagnier & Thévenot 1997), the Sahara of S Algeria (Kowalski & Rzebik-Kowalska 1991; although De Smet 1997b only accounts for *A. lervia* in Algeria), SW Libya (see also Shackleton & De Smet 1997), the mountains of the Adrar de Iforas in Mali (Lamarche 1997a), N Niger (although Magin & Newby 1997 only account for *A. l. angusi* in Niger), and Mauritania (Lamarche 1997b). According to Mekonlaou & Daboulaye (1997), this subspecies used to be widespread in Chad, but today it is probably restricted to the sandstone massifs in Ennedi (Alados *et al.* 1988 reported this population as *A. l. blainei*) and the Tibesti Massif in NW Chad. The species was recently reported from Western Sahara (Cuzin 2003), where there have been no reliable reports of Aoudad since the surveys of Valverde (1957). This is presumably the subspecies that has been successfully breeding in captivity in a public research institute in SE Spain since 1975 (EEZA, CSIC, Almería, Spain, see, for example, Alados *et al.* 1988).

The Kordofan Aoudad was once relatively widespread from W Sudan to the Red Sea coast, but currently is probably restricted to the Red Sea hills of E Sudan (Nimir 1997). According to Alados *et al.* (1988), and contrary to Mekonlaou & Daboulaye (1997), this is the subspecies that may occur in the Ennedi and Uweinat mountains in NE Chad. This may be the form in SE Libya. In 1923, *A. l. blainei* was introduced into the Sabaloka reserve on the Sixth Cataract of the Nile (Gray 1985), where it no longer survives.

The Air Aoudad inhabits the Air Massif in Niger (Magin & Newby 1997). There is a small but apparently viable population that inhabits the Termit Massif region in Niger, isolated from others geographically and probably since long ago, thus of extreme interest both from conservation and taxonomic perspectives (J. Newby pers. comm., T. Rabeil pers. comm; see also Claro & Sissier 2003, Claro 2004, Wachter *et al.* 2008). According to Alados *et al.* (1988) this is the form in the Tibesti in Chad, not *sahariensis* (see above).

The Libyan Aoudad is found in Libya (Hufnagl 1972, Shackleton & De Smet 1997) and in the extreme southern part of Tunisia (Gray 1985, De Smet 1997a). Like the Saharan Aoudad, this subspecies was introduced into the EEZA, but the whole population was moved into the Barcelona Zoo, also in Spain, in the late 1980s.

As noted above, Aoudads have been successfully introduced as a game species in mountainous desert regions of Texas, New Mexico and California (USA), N Mexico and S Spain.

Habitat Aoudads tend to inhabit rocky and precipitous terrain, from near sea level up to the summits of the Air Mts in Niger, which may reach 2100 m (Magin & Newby 1997) and to snow-free areas at about 4100 m in the Atlas Mts (Cuzin 2003). They also require at least some tree cover for shade, and might wander far from water sources for long periods of time. No detailed studies have been carried out in Africa, but empirical data obtained from populations introduced in USA (Johnston 1980) and Spain (Cassinello 2000) revealed the following habitat preferences according to season: open lands and protective rocky slopes during the breeding season (spring), woodlands during summer and grasslands during rutting (autumn) and winter, although in dry regions Aoudads can also be seen in dry forest areas during rutting. A recent study on habitat suitability of the exotic free-ranging population inhabiting SE

Spain shows an impressive expansion potential and adaptation to different environmental conditions, but constrained by low winter precipitation, high altitude, high terrain slope and the presence of forest (Cassinello *et al.* 2006).

Abundance There are no total population estimates available, but numbers are probably in the order of 5000–10,000 individuals. The total population in Morocco has been estimated at between 800 and 2000 individuals (Cuzin *et al.* 2007), which is higher than that suggested by Aulagnier & Thévenot (1997) at 800–1000. Several thousand individuals survive in Algeria (De Smet 1997b), while low numbers occur in Chad (Mekonlaou & Daboulaye 1997), the Adrar des Iforas in Mali (Lamarche 1997a), and in Mauritania (Lamarche 1997b). In Niger, some 3520 Aoudads were estimated to be present in Air Ténéré National N. R. in 1989 (making this the most important stronghold for wild Aoudad on the continent), and 670 outside the limits of the reserve (Poilecot 1991). Numbers are suspected to be increasing in protected areas in the Air mountains, but declining elsewhere in Niger (Magin & Newby 1997). Aoudads seem to be locally numerous in the Eastern and Western Deserts of Egypt (M. A. Saleh pers. comm.), where they were once thought extinct. There are no estimates for Lybia (Shackleton & De Smet 1997) or Tunisia (De Smet 1997a); there also are no estimates for Sudan, where they are very rare and declining (Nimir 1997).

Small groups scattered irregularly over large ranges are the typical pattern of the distribution of the species in the wild, so that obtaining population estimates in the field is difficult. Free-ranging populations in USA and Spain vary in group composition and density both monthly and yearly (Gray & Simpson 1982a, Cassinello 2000).

Adaptations This is a mountain-dwelling caprine perfectly adapted to inhabiting rocky and steep terrains. There is no convincing explanation for the existence of its conspicuous mane, but given that it is a sexually dimorphic character, the most likely explanation is that the mane is used for display purposes by ♂♂ and it is possible that it may act as a dispenser of scent from squirts of urine. Ogren (1965) postulates that it might provide protection against sand storms, by covering the face; it would also prevent flies from disturbing the animal while foraging. Finally, the mane might also contribute to display in agonistic and sexual contexts; captive adult ♂♂ have been seen waving their manes by twisting their heads, raised on their hindlegs while laying the forelegs on fences confronted with other all-male enclosures (T. Abáigar pers. comm.). They use their horns as shovels when sand bathing, a common behaviour probably related to protection against ectoparasites or, as Ogren (1965) suggests, to homeothermy.

Foraging and Food Little data on food habits have been reported from the wild (see Poilecot 1991, Chaveas 2000). This species is a generalist herbivore combining grazing with browsing. In Spain their diet comprises all kind of shrubs, succulent and non-succulent forbs, creepers, dwarf shrubs and grasses, depending on seasonal availability (Miranda *et al.* 2012). In the Air Massif, and probably elsewhere, the green seed pods of acacia trees (*Acacia tortilis raddiana*, *A. ehrenbergiana*) are much sought after by Aoudads; they are even reported butting tree trunks to make the pods fall (J. Newby pers.

comm.). Aoudads can survive without drinking water for long periods, eating just succulent forbs, but if they have the chance they will drink daily from ponds or wells. They probably make small migratory movements in relation to food availability, but there is no specific information.

Social and Reproductive Behaviour The Aoudad is a gregarious species. There is limited information from the wild, but their behaviour is well documented in exotic, free-ranging herds in the USA and Spain. Gray & Simpson (1982a) found that ♀♀ lead the group when adults of both sexes are present, while group composition and group size vary seasonally. Six group types can be distinguished in free-ranging populations: solitary; nursery (females, young and juveniles); mixed; all-male; all-female; and all-juvenile (Gray & Simpson 1982a, Poilecot 1991, Cassinello 2000, Chaveas 2000). Mixed groups are mostly found during rutting, and nursery groups during spring and summer. Adult ♀♀ and juveniles are the sex–age classes most commonly observed. Yearly fluctuations in group dynamics in the same areas are evident, but generally are characterized by a prevalence of adult ♀♀, followed by subadults and finally a lower percentage of adult ♂♂ (Cassinello 2000). However, the percentage of adult ♂♂ observed in the Tirghist Reserve in Morocco is slightly higher than that of subadults (Chaveas 2000).

From the meagre information available (e.g. Dupuy 1966, Chaveas 2000), group size in populations in the wild resembles that in free-ranging populations in USA and Spain. In their Spanish range, herds tend to be small, the majority of groups consisting of less than 11 individuals (Bigalke 1986, Cassinello 2000). In the Texan population, mean group size can oscillate from 5 to 20 individuals (Gray & Simpson 1982a). The mean home-range size ranges from 259 to 3367 ha, and dispersal is particularly accentuated in summer (Simpson *et al.* 1978, Dickinson & Simpson 1980). The species is not territorial, and ♂♂ that reach adulthood leave maternal herds to create their own all-male group or to join existing ones.

Social rank determines each individual's position in a hierarchical order. In captivity, the rank of an adult ♀ may vary according to proximal factors, such as mating, parturition and weaning of young (Cassinello 1995). Aoudad fighting techniques present a variety of forms (Katz 1949, Haas 1959, Ogren 1965, J. Cassinello pers. obs.), some of them ancestral in Caprini, from reverse-parallel pushing to horn-locking; although horn clashing is also present, they do not rise on their hindlegs (as goats do) and they usually clash from short distance, so that collision is not as violent as in wild sheep. Typically, the contestants approach with heads lowered in a threat posture, and when closer they bring the heads down even further, thus directing the bases of the horns forward. Contestants then run toward each other and collide, the blow being delivered with the base of the horns, the force of the collision producing a loud sound that can be heard as far as 300 m away (Habibi 1987). Even infants display all fighting forms when playing (Haas 1959, J. Cassinello pers. obs.).

Courtship is carried out by the most dominant ♂♂ and follows a conspicuous and ritualized display, similar to that of other caprines, with low-stretch posture, tongue-licking and female chasing; also, a sort of guarding behaviour has been observed in dominant ♂♂ following copulation with a ♀ (see Habibi 1987). Females in good

condition bias their investment towards their sons, allocating their resources preferentially (the suckling rate of sons is significantly higher than daughters) and producing more sons than daughters (Cassinello 1996, Cassinello & Gomendio 1996). Mother–offspring conflict during weaning has been investigated. There seems to be a progressive cessation of investment, with no behavioural conflict arising between mother and offspring, except when she resumes sexual activity before weaning has taken place (Cassinello 1997a). Sporadic allosuckling events have been reported in captivity, carried out by alien young of a similar age to that of the allo-mother's true offspring (Cassinello 1999).

Aoudads may produce up to six types of vocalizations: sheep and goat-like bleats (the only sound youngsters produce), short nose snorts, mouth blows, rasping screeches, and grunts (see Gray & Simpson 1982b).

Reproduction and Population Structure Males and ♀♀ can be regarded as sexually mature when aged 14 months and 9 months, respectively (Cassinello 1997b). The mating season peaks from Sep to Nov, and the average gestation period is 22 weeks (Gray & Simpson 1980). In captivity, twins may be produced as frequently as once every four or five births; triplets have been reported in free-ranging populations (ARMAN 1991). Young weigh about 4.5 kg at birth. Singletons are heavier than twins, and high-ranking mothers tend to produce heavier young than low-ranking mothers. Birth-weights also increase with maternal age (see Cassinello 1997b, Cassinello & Alados 1996, Cassinello & Gomendio 1996). Inter-birth intervals average 10 months in captivity, and weaning takes place at a mean age of 8.2 months. The population sex ratio seems to be 1 : 1.

Studies in captivity have shown that variation in female reproductive success is determined first by longevity, followed by fecundity, offspring survival at one month and age at first parturition. Among the factors that affect the components of reproductive success, longevity depends on physical condition, fecundity is higher in top-ranking ♀♀, offspring survival increases with birth-weight, and age at first parturition increases with population density and inbreeding coefficients (Cassinello & Alados 1996).

Aoudads may live up to 20 years in captivity (Ogren 1965, Weigl 2005), but longevity probably rarely exceeds 10 years in the wild (Gray & Simpson 1980).

Predators, Parasites and Diseases Presumably, Lions *Panthera leo* and Leopards *Panthera pardus* were among the natural predators of the species in the past, but today Striped Hyaenas *Hyaena hyaena*, Golden Jackals *Canis aureus* and feral domestic dogs may be the most common natural predators. Also, raptors may predate newborns and young, as reported in Aoudad populations in Spain (accounts from forest rangers of the Golden Eagle *Aquila chrysaetos* taking young). The free-ranging populations in S USA seem to be remarkably free of disease and parasites (Ogren 1965, Pence 1980).

Conservation IUCN Category: Vulnerable C1. CITES: Appendix II.

The lack of surveys carried out in North Africa make determining the precise current status of the species difficult. In its native habitat,

the major threats are habitat loss, competition with livestock and poaching (Alados & Shackleton 1997), resulting in a steady decrease in numbers throughout its range and increasing isolation of populations. Some populations or subspecies are at serious risk of extinction, and the confirmation of the presence of *A. l. ornata* in Egypt (Wacher *et al.* 2002; M.A. Saleh pers. comm.) lends support to the dire need for population surveys in other areas, and clarification on the taxonomic status of the recognized subspecies.

The degree to which Aoudads are legally protected across their range varies. For example, Aoudads have been fully protected in both Morocco and Tunisia since 1966, while in Niger hunting has been banned since 1964; on the other hand, they receive no formal protection in Mali, and although they are listed under Schedule II as a protected species in Sudan, they can still be shot by anyone with the appropriate licence. Aoudads occur in a number of protected areas, including: Takherkhort Hunting Reserve (established in 1967 specifically to conserve this species), the adjacent Toubkal N. P., and Eastern High Atlas N. P. (Morocco); Belezma, Tassili n' Ajjer, and Ahaggar National Parks, and in Djebel Aissa State Forest (Algeria); Fada-Archei Faunal Reserve (Chad); Adrar Mouflon Partial Faunal Reserve (Mauritania); and the vast Aïr Ténéré National N. R. (Niger) (see Shackleton 1997 and chapters therein). The population in Djebel Chambi N. P. in Tunisia was reintroduced in 1987; some animals escaped and a wild population has survived (De Smet 1997; K. de Smet pers. comm.). A few Aoudads are held in captivity in Djebel Bou-Hedma N. P. (De Smet 1997a), and the species was also released in Oued Dekouk N. R. (K. De Smet pers. comm.). Aoudads were introduced into Tripoli N. R. in Libya (Shackleton & De Smet 1997).

In contrast to the situation in the wild, introduced US and Spanish populations are either well established or steadily

increasing (Gray 1985, Cassinello *et al.* 2004). However, it is a priority to register and keep information on subspecific origins of captive and introduced populations and prevent undesirable hybridization events, particularly if reintroduction programmes are to be implemented.

Measurements

Ammotragus lervia

HB (♂ ♂): 1490 (1050–1760) mm, n = 18

HB (♀ ♀): 1290 (1040–1500) mm, n = 41

T (♂ ♂): 190 (170–210) mm, n = 3

T (♀ ♀): 170 (160–190) mm, n = 4

Sh. ht (♂ ♂): 960 (890–1050) mm, n = 3

Sh. ht (♀ ♀): 780 (760–800) mm, n = 4

WT (♂ ♂): 86.0 (50.0–132.0) kg, n = 17

WT (♀ ♀): 42.0 (12.0–68.0) kg, n = 39

Free-ranging population, New Mexico, USA (Ogren 1965), except HB and WT, which correspond with sexually mature individuals (♂ ♂ older than 1.5 yr; ♀ ♀ >1 yr) from the captive population at EEZA (CSIC), Almería, Spain (Cassinello 1997b)

Maximum recorded horn length is 88.0 cm for a pair of horns from the Ennedi Mts, Chad; however, record horn length from an extralimital population introduced in Colorado, USA, is 90.1 cm (Rowland Ward)

Key References Cassinello 1998, 2000; Cassinello *et al.* 2004, 2006; Chaveas 2000; Gray & Simpson 1980, 1982a, b; Ogren 1965; Shackleton 1997 (and chapters therein).

Jorge Cassinello

GENUS *Capra*

Ibexes

Capra Linnaeus, 1758. Syst. Nat., 10th edn, 1: 68.

Capra is a polytypic genus that includes eight species: Markhor *C. falconeri*, Goat *C. hircus* (wild populations commonly called *C. aegagrus*) and the ibexes (Nubian Ibex *C. nubiana*, Walia Ibex *C. walia*, Siberian Ibex *C. sibirica*, Alpine Ibex *C. ibex*, Spanish Ibex *C. pyrenaica* and Tur *C. caucasica*) (Grubb 2005). There is no agreement on the true number of species recognized, and as few as two (*hircus* and *falconeri*; Haltenorth 1963) and as many as nine have been recognized (the Tur sometimes being split into two species, *C. caucasica* and *C. cylindricornis*) (Heptner *et al.* 1961).

The genus is distributed from the Iberian Peninsula, the Alps and the Caucasus Mts through the Middle East, south into Egypt, Sudan, Ethiopia and the Arabian Peninsula and east across Iran, Afghanistan and Pakistan into the Hindu Kush, Pamirs, Tien Shan and Altai Mts of central Asia, in upland precipitous habitats. There is a substantial Pleistocene fossil record in Europe; only the supposed Pliocene *C. primaeva* (doubtfully in this genus) is recorded from Africa. Only two species, the Walia Ibex and Nubian Ibex, occur in Africa: the former is found only in and around Simien Mountains N. P. in Ethiopia, while the latter is found in Egypt, east of the Nile, NE Sudan, N Eritrea,

Israel, Jordan, SE Oman, Saudi Arabia and SE Yemen (and extinct in Lebanon and Syria). Analysis of mitochondrial cytochrome *b* and Y chromosome DNA sequences suggests that the two species form a monophyletic clade, although the Walia Ibex potentially has been isolated for up to 0.8 million years from Nubian Ibex (Gebremedhin *et al.* 2009).

Members of the genus are robust animals with stout limbs, short hoofs and short tail. The rhinarium is hairy, and there is a beard on the chin. Long hair extends over forequarters in the Markhor, but not in other species. Males and ♀ ♀ are strongly sexually dimorphic; ♂ ♂ are larger with large horns, ♀ ♀ with relatively small, slender horns. Horns grow during life but growth is seasonal, forming rings or checks during the quiescent phase, which aids ageing individuals in the field. There is a wide range in size between species and sexes (50–130 kg). The skull is characterized by a short narrow facial region, but is broad across the frontals, with tubular orbits; the skull is strengthened by secondary bony deposition leading to disappearance of the nasofrontal suture, though the naso-maxillary suture remains open.



Nubian Ibex *Capra nubiana* male with tightly curved horns.

Capra nubiana NUBIAN IBEX

Fr. Bouquetin de Nubie; Ger. Nubischer Steinbock

Capra nubiana (F. Cuvier, 1825). In: E. Geoffroy Saint-Hilaire and F. Cuvier, Hist. Nat. Mammifères 6, pt 50, 'Bouc sauvage de la Haute-Egypte', p. 2, pl. 397. Egypt, 'de la Haute-Égypte ... ou de Nubie'; Nubia (Lydekker 1913: 153; G. M. Allen 1939: 549) or Upper Egypt (Ellerman & Morrison-Scott 1951: 407), which are virtually synonymous; restricted by Grubb (2005) to Sudan, Northern Prov., Nubian Desert, east of Nile R.



Nubian Ibex *Capra nubiana*.

Species are differentiated by size, form of the horns in ♂♂ (much variation between species), length of pelage and colour pattern. Along the anterior surfaces of the horns, ibexes have prominent bosses (secondarily lost in some populations of Tur and Spanish Ibex). African ibexes (Nubian and Walia) have contrasting black-and-white leg markings and horns that are long and semi-circular in outline, placed further forward on the skull compared with other ibexes, associated with the development of a swelling on the frontal bones just below the horn bases. They differ from each other in size and horn features (slender or robust, strongly or slightly laterally compressed).

Ansell (1972) included the Barbary Sheep or Aoudad *Ammotragus lervia* in this genus, but this has not been followed here and is in conflict with molecular data (Ludwig & Fischer 1988, Ropiquet & Hassanin 2005a).

Peter Grubb & Michael Hoffmann

Taxonomy Monotypic. Considered a subspecies of *Capra ibex* (Ellerman & Morrison-Scott 1951, Ansell 1972, Corbet 1978, Harrison & Bates 1991), but treated as distinct by Uerpmann (1987) and Grubb (1993c, 2005). Synonyms: *arabica*, *beden*, *mengesi*, *sinaitica*, *typical*. Chromosome number: $2n = 60$ (Schaller 1977).

Description Tan to greyish, mid-sized ungulate of mountainous desert terrain, with prominent horns and striking black and white leg markings. Mature ♂♂ much larger and heavier than ♀♀, with dark beards and scimitar-shaped horns. During the rut, breeding ♂♂ develop enlarged necks and dark pelage on chest, shoulders and flanks. Both sexes have whitish belly, inner legs and buttocks, and short dark tails. Nostril, mouth and orbits outlined in black. Eyes have amber irises and horizontal black pupils. Chin and hairs surrounding mouth and nostrils are usually whitish. Darker band extends from eye to edge of mouth. Nasal area may be rufous-brown. Ear backs grey, and fronts have black centres with contrasting white edges. Summer body pelage of adults and young comprises short, tan guard hairs (replaced in winter by brown to grey guard hairs with underfur). Mid-dorsal band of longer hairs extends from nape to base of tail, and is dark in ♂♂. Belly whitish, partially edged with a dark band in many adults. Fronts of upper and lower foreleg black, with white band above grey knee callus. White fetlocks and pasterns contrast with black hooves on fore- and hindlegs. Dark band above fetlock extends to leading edge of hindleg.

The flattened face of the male horns has as many as 30 prominent horizontal knobs; female horns are short and slender and bear narrow growth rings, but no knobs. Male horn dimensions vary among populations (Habibi 1994).



Capra nubiana

Geographic Variation None recorded.

Similar Species

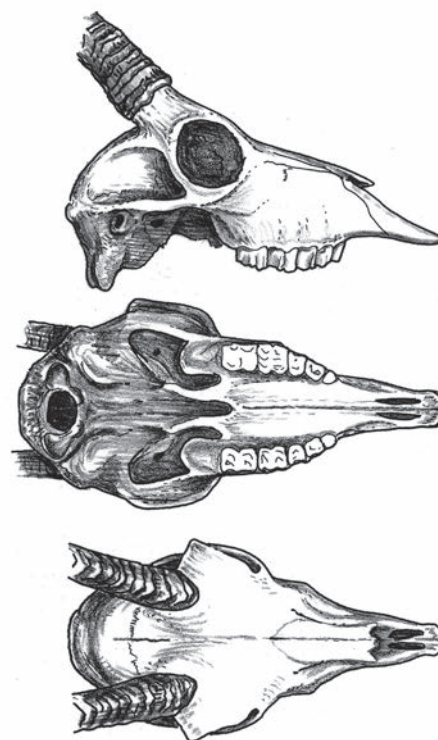
Capra walie. Restricted to the Simien Mts in Ethiopia. Larger and stouter body, more robust horns and darker pelage.

Distribution Once widely distributed in north-east Africa, east of the Nile R., Sinai, the Near East and the Arabian Peninsula, but decimated by relentless hunting and habitat encroachment in much of their original range (see, for example, Manlius 2001). Nubian Ibexes in Africa exist mainly as small isolated populations in the Eastern Desert and Red Sea Mts of Egypt, and in the Red Sea hills of Sudan.

Locations of confirmed recent occurrences in Egypt's Eastern Desert include: Gebel Ataq, Gebel El Galâla El Bahariya (North Galala Plateau), and Gebel El Galâla El Quiblia (South Galala Plateau) (M. Saleh pers. comm.). Nubian Ibexes also occur throughout the Red Sea Mts of Egypt, from Gebel Ghârib in the north to Elba near the Sudan border. Krausman & Shaw (1986) rediscovered a population surviving in the Wadi el Assuti and Wadi Habib, where ibexes had not been seen since 1927. Recent records in Egypt's Sinai Peninsula are from Gebel El Maghara, Gebel El Halal and Gebel Yalag in N Sinai, the Gebel El Tih in C Sinai and at many sites in the mountains of S Sinai (Saleh & Basuony 1998). Manlius (2001) provides a detailed discussion of the historical ecology and biogeography of the Nubian Ibex in Egypt from 1800 to the present day.

In Sudan, small Nubian Ibex populations were observed around Erkowit, Jebel Ashat and Jebel Sherik Gebel during a 1990 survey (Nimir 1997), and the species likely occurs elsewhere in the country's Red Sea hills as far north as the Gebel Elba (Nimir 1997, I.M. Hashim pers. comm.).

No confirmed recent records are available for Eritrea, where the species had been recorded near the Sudan border (Hillman & Yohannes 1997, D. Zinner pers. comm.). Nubian Ibexes had been reported in



Lateral, palatal and dorsal views of skull of female Nubian Ibex *Capra nubiana*.

extreme N Ethiopia (Yalden *et al.* 1984), but the only recent record is an unconfirmed report from the Tendaho Estates area in EC Ethiopia near the Djibouti border (Hillman *et al.* 1997).

Extralimital to Africa, Nubian Ibexes occur in Israel, Jordan, Oman, Yemen and Saudi Arabia, but are now extinct in Lebanon and Syria (Shackleton 1997, and chapters therein; Grubb 2005).

Habitat Mountains, cliffs, hills and associated plateaux, canyons and wadis. Supports arid and semi-arid vegetation, including annual forbs and grasses dependent on seasonal rainfall, geophytes, woody shrubs and stands of *Acacia*, *Populus* and *Pistacia* trees. Dense herbaceous vegetation at runoff sites and springs are important foraging habitat. Steep slopes provide vital escape cover, especially for ♀♀ and young (Kohlmann *et al.* 1996). Springs or other open freshwater are essential. Human pressures force Nubian Ibexes to remote and inaccessible locations, and livestock grazing degrades foraging and watering sites (Alados & Shackleton 1997).

Abundance Recent African records are from opportunistic observations by biologists (e.g. Krausman & Shaw 1986) and reports by local inhabitants. Three populations in Sinai comprised 300–400 animals in the 1970s (Baharav & Meiboom 1981). About 200 Nubian Ibexes inhabit the Gebel El Galâla El Bahariya Plateau (M. Saleh pers. comm.), and small groups are reported elsewhere in E Egypt (Amer 1997). Numbers in Egypt appear stable (M. Saleh pers. comm.). Isolated bands exist in the Red Sea hills of Sudan, but populations may be declining (Nimir 1997, I.M. Hashim pers. comm.).

Adaptations A stocky body, short legs and exceptional equilibrium enable Nubian Ibexes to negotiate rugged terrain. Wide

hooves with large flexible pads may promote stability on narrow ledges and absorb shock when they jump. They respond to threats by rapidly scaling or descending steep slopes, and routinely use narrow, precarious trails. They have excellent distance vision, and group living enhances vigilance (D. Saltz pers. comm.). Their pelage is very cryptic in most desert habitats. Nubian Ibexes lack strong physiological adaptations for water conservation or thermoregulation. They obtain preformed water from plants, but require non-saline drinking water (Shkolnik *et al.* 1979). During hot summers, Nubian Ibexes are active during early morning and dusk. They avoid activity, and seek shade, during mid-day (Baharav & Meiboom 1982), and may also forage at night. In cool winters they shift their daily activity to sunlit slopes, and are active longer during the day. Nubian Ibexes have a low basal metabolic rate, perhaps reducing their energy requirements in arid environments (Chosniak *et al.* 1984).

Foraging and Food Nubian Ibexes consume a wide array of herbaceous and woody plants. Specific diet varies by locality and season. Woody browse consumed in Egypt included *Acacia raddiana*, *Lindenbergia sinaica*, *Lycium shawii*, *Capparis spinosa* and *Ficus pseudosycamoros* (Osborn & Helmy 1980). Herbaceous species eaten were *Phragmites australis*, *Imperata cylindrica*, *Juncus rigida*, *Alhagi manifera* and excavated roots of *Lotus arabicus*. In Sinai, important perennial plant foods in winter were: *Globularia arabica*, *Helianthus lipii*, *Ephedra foliata*, *Zilla spinosa*, *Thymus decussatus*, *Gymnocarpus decander* and *Echinops glaberrimus* (Baharav & Meiboom 1982). Protected Nubian Ibex populations have eaten landscape plantings and agricultural crops in Israel (Hakham & Ritte 1993).

In the Negev Desert, mature ♂♂ relied on low-quality fibrous browse during most of the year (Gross 1991). They took large bites, and had high intake rates and long rumination bouts (Gross *et al.* 1995b, 1996, S. Kohlmann pers. comm.). By contrast, the smaller ♀♀ and young ♂♂ sought higher quality, but scarcer, herbaceous forage throughout the year. Smaller animals chewed food thoroughly, and spent more time actively foraging than did the large ♂♂.

Social and Reproductive Behaviour Nubian Ibex are highly social (Habibi 1994, Gross *et al.* 1995a), typically occurring in female-based bands that include young and male juveniles to three years of age. Mature ♂♂ more than seven years of age represent a second group type, while ♂♂ 4–6 years old may form more transitory associations of six or more individuals. In a protected Negev population, adult ♀♀ maintained a stable linear dominance hierarchy throughout the year (Greenberg-Cohen *et al.* 1994), and female-based groups averaged more than 20 individuals (Gross *et al.* 1995a). Nubian Ibex bands are significantly smaller in the face of intense hunting pressure and habitat degradation. In hunted Egyptian and Saudi Arabian populations, groups averaged less than six animals (Osborn & Helmy 1980, Habibi & Grainger 1990).

Mature ♂♂ disperse in late summer, and may travel long distances to join female groups during the 6–8 week autumn rut. A travel corridor between Israel populations used by breeding ♂♂ was ≥60 km long (Shkedy & Saltz 2000). They court ♀♀ using characteristic approach behaviour, with neck outstretched, tail-up and displaying flehmen (Habibi 1994). Unreceptive ♀♀ ignore, threaten or flee persistent suitors. Younger ♂♂ also court ♀♀, but are easily displaced by mature ♂♂. Closely-matched breeding ♂♂

engage in dramatic horn clashes in which winning ♂♂ often attain higher elevations to increase the downward force of their attack (S. E. Kohlmann pers. comm.).

Neonates remain hidden for about a week after birth, and then follow their mothers who rejoin female-based groups. Kids are adept climbers and gambol and play in precarious sites. In protected populations, Nubian Ibexes have formed temporary nurseries of many young associated with only few ♀♀ (Hakham 1985, Levy & Bernadsky 1991). Young have been confined for several days or more in a natural topographical ‘trap’ in which they were visited by their mothers until they managed to escape (Müller *et al.* 1995).

Reproduction and Population Structure Females breed by two years of age. Following a 20-week gestation period, they give birth in spring (Mar–Apr) to one or two offspring at secluded sites in rough terrain. Nubian Ibexes are short-lived, rarely exceeding 12 years of age in the wild, even in protected populations (P. Alkon pers. obs.). Sex ratios at birth are even, but adult ♀♀ usually outnumber ♂♂ (Habibi 1994). Annual fluctuations in protected populations are probably regulated by yearly changes in environmental conditions as well as density-dependent mechanisms (Alkon & Kohlmann 1990). The dispersion of breeding ♂♂ among distant female-based groups during the rut (Shkedy & Saltz 2000) may promote high genetic diversity in protected populations (Stuwe *et al.* 1992).

Predators, Parasites and Diseases On the African continent the only likely predator is the Leopard *Panthera pardus*, although, on the Arabian Peninsula, Grey Wolves *Canis lupus* may occasionally prey on them (Harrison & Bates 1991, G. Ilani pers. comm.). Attacks by large raptors are rare. Parasites of wild Nubian Ibexes include nematode lungworms, coccidia and arthropods (Solomon *et al.* 1996, Yeruham *et al.* 1999). Captive animals have succumbed to sarcoptic mange (Yeruham *et al.* 1996).

Conservation IUCN Category: Vulnerable C1+2a(i). CITES: Appendix II.

The main threats to the Nubian Ibex include competition with livestock and camels in Egypt, where the availability and distribution of waterholes is likely to be a major factor in the condition of populations (Amer 1997). Hunting is also a threat in Egypt and Sudan (Amer 1997, Nimir 1997), and is implicated in the disappearance of this species from some parts of its range in Egypt (Manlius 2001).

Egypt and Sudan have enacted protective wildlife laws and established wildlife reserves, but resources for surveys and enforcement are limited. Armed conflicts also have disrupted conservation measures in parts of north-east Africa. In Egypt, Nubian Ibexes are legally protected and their hunting is totally forbidden under articles of the Agricultural Law. Nature Reserves in which they occur are Gebel Elba Conservation Area (disputed Sudan Government Administration area) and the Wadi el Assuti in the Eastern Desert, and Gebel Mûsa and Gabel Katerîna Wildlife Reserve in south central Sinai (Amer 1997). Nubian Ibexes appear to have maintained their number and range in Egypt over the past several decades (M. Saleh pers. comm.). In Sudan, Nubian Ibexes are a Schedule II species under the Wildlife Conservation Act. Hunting was banned between 1989 and 1992, since when the ban has been lifted and animals can be hunted under special permit (Nimir 1997).

Protected areas in which they occur include Tokar G. R., Sinkat-Erkawit Game Sanctuary and Erkawit Game Sanctuary, totalling 829,500 ha. No hunting of wildlife has been recently permitted in Eritrea. The Yob Wildlife Reserve (2658 km²) along the Sudanese border encompasses past Nubian Ibex range in that country (Hillman & Yohannes 1997).

Future conservation measures should include placing the Nubian Ibex on Schedule I of the Wildlife Conservation Act in Sudan to ensure full protection (Nimir 1997), government control of the area that includes the Wadi el Assuti and its junction with the Wadi Habib (one of the few places outside the Sinai where good numbers of Nubian Ibexes survive) and making Gebel Elba a National Park (requiring cooperation between Egyptian and Sudanese governments) (Amer 1997, Nimir 1997). Nubian Ibexes respond strongly to effective protection, which bodes well for future conservation measures (Habibi 1994, 1997, Alkon 1997, M. Saleh pers. comm.). Within a generation, newly protected Nubian Ibexes reduced flight distances from humans, returned to abandoned range and formed larger groups. The largest extant Nubian Ibex populations (≥ 1600 animals) are in Israel, where they are very tolerant of humans following four decades of protection.

Measurements

Capra nubiana

HB ($\sigma \sigma$): 1370 (1190–1590) mm, n = 20

HB ($\phi \phi$): 1092 (920–1210) mm, n = 25

T ($\sigma \sigma$): 116 (80–170) mm, n = 20

T ($\phi \phi$): 91 (65–160) mm, n = 27

HF c.u. ($\sigma \sigma$): 290 (260–390) mm, n = 13

HF c.u. ($\phi \phi$): 272 (240–300) mm, n = 20

E ($\sigma \sigma$): 168 (135–200) mm, n = 20

E ($\phi \phi$): 153 (130–175) mm, n = 28

WT ($\sigma \sigma$): 64.2 (42.0–85.0) kg, n = 16

WT ($\phi \phi$): 31.4 (25.0–39.5) kg, n = 30

Negev Desert, Israel (P. U. Alkon *et al.* unpubl.); ages of all $\sigma \sigma \geq 4$ years, and all $\phi \phi \geq 3$ years

Maximum recorded horn length is 138.4 cm for an animal from Khartoum Zoo in Sudan (Rowland Ward)

Key References Gross 1991; Habibi 1994; Harrison & Bates 1991; Manlius 2001; Osborn & Helmy 1980; Shackleton 1997 (and chapters therein).

Philip U. Alkon

Capra walie WALIA IBEX (ETHIOPIAN IBEX)

Fr. Bouquetin d'Ethiopie (Le Wali); Ger. Aethiopischer Steinbock (Walia-Steinbock)

Capra walie Rüppell, 1835. Neue Wirbelt. Fauna Abyssin. Gehörig, Säugeth. 1: 16; 40 pp, 14 pl. 'die höchsten felsigten Gebirge Abyssiniens ... in den Provinzen Simen und Godjam'; restricted to Ethiopia, mountains of Simien (Lydekker 1913: 156).



Walia Ibex *Capra walie*.

walie, *wali*. Chromosome number: not known, but probably $2n = 60$, as for other karyotyped *Capra* species.

Description Mid-sized ungulate of robust build with outstanding rock-climbing abilities. Less massive and sleeker than the Alpine *Capra ibex* and the Siberian Ibex *Capra sibirica*, but stouter and heavier than its more elegant northern neighbour, the Nubian Ibex *Capra nubiana*. Back and upper body chestnut-brown, the chin, throat, belly and the inner surfaces of the legs whitish for both sexes. A black stripe extends down the front of each leg, a white band just above the knee cuts across the black stripe on the forelegs. This black and white pattern is less pronounced in young $\sigma \sigma$ and $\phi \phi$ than it is in $\sigma \sigma$ aged three years or older. Males aged 4–6 years have small beards, which turn into long beards from about the seventh year, at which age their chest darkens and the black streak on their back becomes more pronounced. Females and young $\sigma \sigma$ do not have beards (Nievergelt 1981, Nievergelt *et al.* 1998). Adult $\sigma \sigma$ are larger than $\phi \phi$ and have semi-circular, massive horns with transverse knobs on the front. Females have small and slightly curved horns.

Geographic Variation None recorded.

Similar Species

Capra nubiana. Occurs in Egypt, Sudan and W Eritrea, extending into the Near East and the Arabian Peninsula. Slender and smaller, dominant colour of coat bright and sandy, and horns of $\sigma \sigma$ thinner and more curved.

Taxonomy Monotypic. Originally named as a species (Rüppell 1835, Lydekker 1913, Harper 1945), it has been considered a subspecies of *Capra ibex* (Haltenorth 1963, Schaller 1977) and of *Capra nubiana* (Heptner *et al.* 1961). Now usually treated as a distinct species (Ansell 1972, Yalden & Lagen 1992, Grubb 1993c, 2005), which appears to be supported by genetic data that reveal that the differentiation between *C. walie* and *C. nubiana* is similar to the differentiation observed between the Alpine Ibex *C. ibex* and the Spanish Ibex *C. pyrenaica* (Gebremedhin *et al.* 2009). Synonyms: *wali*,



Distribution Endemic to Ethiopia. The Walia Ibex is found only in and around Simien Mountains N. P. in the North Gonder Administrative Zone of NW Ethiopia. As far as historical records go, its range seems to have always been very restricted and the total population remains small and vulnerable (Nievergelt 1981, Yalden & Lagen 1992, Hillman *et al.* 1997). Considering available records and looking at the topographic and climatic features of the heterogeneous and often fractured country, it may be assumed that the extremely deep and arid lowland-channel with the Tekeze R. is a natural border in the north and east. In the north-west, west and south, Walias probably occurred in the spurs of high Simien, ranging from Adi Arkay towards Debarq and perhaps Dabat.

Habitat The Simien Mts are remarkable for the impressive escarpments that separate the hilly high plateaux from the terraced lowlands, the original flora of which is a dense and diverse mountain forest with species such as *Juniperus procera*, *Olea africana*, *Syzygium guineense* up to roughly 3000–3200 m. An ericaceous belt dominated by the tree heather *Erica arborea* and St John's Wort *Hypericum revolutum* occurs at 3200–3800 m, and the whole of the vegetation above the timberline consists of afroalpine grassland with the megaphytic *Lobelia rhynchopetalum*. Inatye Mountain within the National Park reaches 4070 m, and the adjoining mountains Bwahit and Ras Dejen are 4430 and 4543 m, respectively. Seasonal changes in vegetation are determined by the wet season, from Jun until Sep/Oct, but variations in diurnal temperature exceed by far the variations entailed by seasonal changes.

Today, farmers have turned a large part of the original vegetation of the lowlands into terraced fields (Klötzli 1977, Nievergelt 1981, Hurni 1982, 1986, Nievergelt *et al.* 1998, Hurni & Ludi 2000) and livestock have also encroached into the forest. The higher escarpments and plateaux are intensively used as pasture for cows, sheep, goats and horses but they are too cold for agriculture.

The steep and rocky areas in the alpine and ericaceous belts along the escarpment as well as the mountain forest belt are the main habitat of the Walia Ibex. War in this region gave rise to indiscriminate hunting mainly in the western parts of the National Park, and the Walias adapted to living and ranging in adjoining habitats as well. There is reasonable evidence to suggest that Walias not only found refuge among rocks and in the denser mountain forest in lower altitudes, but that most animals of the small population moved into the escarpment towards the slightly higher and less disturbed eastern region (although it lies outside the National Park). The areas south of Bwahit Mountain were the main retreat during this critical period. They included parts of the escarpment, but also cliffs, steep slopes with almost no forests and an extensive high plateau, where the alpine steppe is so scarce that there is almost no competition from livestock. The use of flat, plateau-like areas as feeding grounds is rather untypical for most ibexes, but its use by the Nubian Ibex has been observed. This habitat preference of the Walias in the Bwahit area indicates that rich alpine steppe on the slightly lower plateaux within the National Park are suitable Walia Ibex habitat, too, provided there is no disturbance by man or livestock (Nievergelt 2012).

Abundance The population size of Walia Ibex numbered 150–300 animals between 1966 and 1969, increasing slowly until 1983 when there were possibly more than 500 animals, and then decreasing again during the period of civil unrest during the early 1990s. In 1994 and 1996, the population was estimated at 200–250 animals, but it subsequently increased, reaching about 500 animals in 2004 (Nievergelt 2012). The earlier recovery of the population after 1971 can be regarded as a positive response to the introduction of an effective control system with several outposts of game wardens. Along with this recovery, the animals slowly became less shy, and were even seen in habitats close to footpaths. In addition, a notably higher proportion of older ♂♂ was observed. After the war the animals became extremely shy again, hiding in naturally well-protected places (Hillman *et al.* 1997, Nievergelt *et al.* 1998). The more recent recovery took place exclusively in the eastern corner of the National Park, the Chennek area, and was even more pronounced in the adjoining Bwahit–Mesarerya–Digowa range outside the National Park (Ludi 2005, 2006) where, in the 1960s and 70s, no Walias could be observed at all. The most recent estimate (2009) puts the total population at ca. 750 animals (Alemayeh *et al.* 2011).

Adaptations As with all members of the genus *Capra*, the Walia Ibex is an outstanding rock-climber with strong and relatively short legs; it is more sure-footed than almost any other African ungulate, and moves safely up and down sheer cliffs. The ♀♀ give birth in extremely inaccessible places and the young learn to climb immediately. The characteristic afroalpine climate requires adaptation to cold, but this regime is also the basis of rich pastures and – between roughly 2300 and 2700 m – the dense and protective evergreen montane forest. The diurnal activity pattern shows a peak of foraging and social activities in the morning and again towards the evening.

Foraging and Food The diet of the Walia Ibex includes a great variety of herbaceous and woody plants (Dunbar 1978, Nievergelt

1981). Among the abundant trees and shrubs dietary staples include *Erica arborea* (twigs) and *Lobelia rhynchopetalum*, but they seem to be partial to a number of green herbs, such as *Simenia acaulis*, *Alchemilla rothii*, *Arabis alpina*, *Swertia* sp. and *Scabiosa columbaria*. There is little evidence of them foraging on members of the family Papilionaceae, and no reports of them foraging on Labiatae. Most herbs are foraged mainly around their respective flowering seasons. According to direct observation, fresh plants were usually selected by ♂♂ at the beginning of their flowering period, while ♀♀ favoured them at the end of this period when the plants produce highly nutritious fruits.

Social and Reproductive Behaviour Like other ibexes, Walias are highly social animals (Dunbar & Dunbar 1974b, 1981, Nievergelt 1974, 1981). They have varied social units, such as female-based groups that include young and juvenile ♂♂ until they are about two or three years, groups of adult ♂♂ and mixed groups. As can be expected from the low density, most groups are relatively small. In earlier studies, the largest group recorded included 24 animals (♀♀ and young, including ♂♂ up to three years); in 2004, in the open area east of the National Park borders, a herd of 54 Walias was observed (Ludi 2006).

Sexual segregation is pronounced, mostly during parturition and lactation. In keeping with the rutting peak (see below), the highest occurrence of mixed groups can be observed from Mar to May. The clear rank order amongst ♂♂ correlates closely with their age, body size and horn length. The linear dominance hierarchy observed in several *Capra* species can be expected in Walia ♀♀ as well. Open groups and established hierarchies give the social system its structure. Individuals are occasionally involved in fights or play-fights if the sparring partner is of similar age or rank. It is remarkable that quite a number of fights were observed between ♀♀ and ♂♂ of one or two years, when the ♂♂ attain or surpass the body weight of adult ♀♀ and start to leave the female-based groups. As has been observed in other ibexes, there seems to be no sign of territoriality. Based on seven individually known animals it is presumed that individuals or small groups usually remain for several months in areas of less than 0.5 km², but adult ♂♂ often range in larger areas.

Courting ♂♂ lower their horns while approaching receptive ♀♀, and display flehmen, lifting their tail into an almost horizontal position. Newborns stand within the first hours after birth, and follow their mother closely. Within the female-based groups, the young remain in close contact with their mothers.

Reproduction and Population Structure In contrast to the ibex species living in temperate latitudes, where winter dictates a discrete annual reproductive cycle, rutting behaviour and newborns can be observed throughout the year. However, there is a clear rutting peak between Mar and May, and, in keeping with the gestation period of five months, births peak accordingly after the wet season in Sep/Oct. Older ibexes, both ♂♂ and ♀♀, have a more synchronized cycle. Although ♀♀ could well be both fertile and sexually receptive earlier, ♀♀ younger than four years of age are only exceptionally observed with a newborn (Nievergelt 1972). This late breeding corresponds to the slow growing process of this mountain ungulate. Data on life expectancy are lacking. Based on findings concerning other caprines (Geist 1971, Nievergelt 1966),

and the examination of horns, the maximum age in the wild was estimated to be around 15 years.

Predators, Parasites and Diseases Leopards *Panthera pardus* and Spotted Hyenas *Crocuta crocuta* are potential resident predators, but there have been no direct reports of attacks by these animals. A number of direct observations indicate that numerous large birds of prey such as Verreaux's Eagle *Aquila verreauxii*, Tawny Eagle *A. rapax* and Martial Eagle *Polemaetus bellicosus* may take young (Nievergelt 1974). In samples of faeces the following intestinal parasites have been identified: *Trichostrongyloides* spp., *Nematodirus* spp., *Strongyloides* spp., *Trichuris* spp. and *Bunostomum* spp. The samples were collected after the reported death of five Walias, with symptoms of diarrhoea, in the eastern part of the range and at the end of the wet season in 2004 (Berhanu Gebre *et al.* 2004).

Conservation IUCN Category: Endangered B1ab(iii), D. CITES: Not listed.

Walia Ibexes are protected by Ethiopian law, and cannot be hunted except under a Special Permit for Hunting Game Animals for Scientific Purposes. The species has survived a period of war, and the main current threats to it now are posed by human and livestock pressure on the habitats in and around Simien Mountains N. P. (13,600 ha). The latter was gazetted by the Simen National Park Order No. 59 (1969) and has been a World Heritage Site since 1978 (when most of the people living in the lowland areas where resettled outside). The Park is administered by the Parks and Wildlife Administration Authority of the Regional Government, and has attracted increasing international attention since the World Heritage Committee placed the Park on the List of World Heritage in Danger in 1996 because of decline in the population of the Walia Ibex due to human settlement (most of the people resettled outside of the park in 1978 have returned once again and now reside either within or outside the Park), grazing and cultivation. Walia Ibexes are excluded by cultivation of the lowland terraces right up to the timberline and are further displaced by the practice of allowing domestic animals to graze at the higher altitudes. Despite the existence of national and regional legislation, the remoteness of the area, coupled with the existence of people living within and outside of the Park prior to its establishment as a Conservation Area, makes legislation difficult to enforce. Only the sheer inaccessibility of major parts of its habitat has protected the Walia from total extinction. Proposed conservation measures include: (1) extend the National Park area towards the Bwahit region so as to establish a buffer zone and increase the effective area of the Park with natural movement corridors along the escarpment range (as proposed by Hurni 1986); (2) reduce human and livestock impact in the National Park; (3) prohibit all hunting within the Park and enforce regulations effectively; (4) exclude all possibility of hybridization by prohibiting free-ranging domestic goats from the area; (5) initiate a captive-breeding programme to reduce the risk of extinction (there currently are no Walia Ibexes in captivity anywhere in the world); and (6) establish a monitoring programme that includes systematic assessment of conservation measures (Brown 1969b, Hurni 1986, Hillman *et al.* 1997, Shackleton 1997, Nievergelt *et al.* 1998).

The Walia Ibex is used by the Ethiopian Wildlife Conservation Organization (EWCO) and the Ethiopian Wildlife and Natural

History Society (EWNHS) as their emblem, and frequently features elsewhere in other Ethiopian symbolism (including the national football team, who are nicknamed ‘The Walya Antelopes’).

Measurements

No reliable body measurements are available, although Haltenorth & Diller (1980) report measures as: HB: 1500–1700 mm; T: 200–250 mm; Sh. ht (♂♂): 1000–1100 mm; Sh. ht (♀♀): 900–1000 mm; and WT (♂♂): 100–125 kg; WT (♀♀): 80–100 kg

Maximum recorded horn length is 118.1 cm for a pair of horns from Ethiopia (Rowland Ward)

Key References Dunbar & Dunbar 1974b, 1981; Hillman *et al.* 1997; Nievergelt 1972, 1974, 1981; Nievergelt *et al.* 1998.

Bernhard Nievergelt

Glossary

abbrev. = abbreviation

adj. = adjective

cf. = *confer*, compare with; as opposed to

Lat. = Latin

n. = noun

pl. = plural

q.v. = *quod vide*, 'which see'

v. = verb

acetabulum: the concave socket (fossa) in the pelvic bone in which the head of the femur articulates.

acrocentric: describes a chromosome that has the centromere (*q.v.*) very near one end and that therefore appears to have only one arm (= telocentric (*q.v.*) for practical purposes).

ad libitum: (*Lat.*) as much as one likes; having unrestricted access to a resource (e.g. water or food).

aestivate: state of torpor (*q.v.*) induced by cold or drought; usually associated with a reduced metabolic rate and inactivity.

aFN: the total number of chromosomal arms in the autosomal chromosome complement of a species (*cf.* fundamental number [FN], which includes the chromosomal arms of the sex chromosomes as well as those of the autosomal (*q.v.*) chromosomes). Each metacentric (*q.v.*), submetacentric (*q.v.*) or subtelocentric (*q.v.*) chromosome is given a value of 2; each acrocentric (*q.v.*) chromosome is given a value of 1. *See also* fundamental number.

afroalpine: describes habitats and/or vegetation occurring above the treeline on African mountains. Includes montane grassland and heathlands.

afromontane: refers to mountainous regions in Africa, e.g. afromontane forests and afromontane grasslands.

agouti: having an even mixture of pale- and dark-tipped hairs on the pelage creating a grizzled, speckled or 'pepper and salt' appearance.

Albertine Rift Valley: *see* Rift Valley (*q.v.*).

alisphenoid: bone in the skull.

Allee effect: a scenario in which populations at low numbers are affected by a positive relationship between population growth rate and density, which increases their likelihood of extinction.

allele: an alternative form of a gene. A diploid organism carries two alleles (which may be same or different) for each gene locus. At any one locus, there may be several possible alleles (although only two are present in a single organism).

Allelomimetic behaviour: behaviour in social animals in which each animal does the same thing as those nearby.

Allen's Rule: A rule that states that structures in endotherms such as limbs (which are more prone to heat loss) are reduced in size by means of natural selection over time in cooler climates (to reduce heat loss).

allogrooming: grooming behaviour directed at another individual. *cf.* autogroom (*q.v.*).

allomothering: non-parental mothering; caring for young by individuals (male or female) that are not the parents of the young.

allopatry (*adj.* **allopatric**): the situation where populations of the same or different species have non-overlapping geographic ranges; refers also to populations of the same, or different, species that are geographically separated. *cf.* sympatry (*q.v.*); syntopy (*q.v.*).

allozyme: one of a number of forms of the same enzyme having different electrophoretic properties and that are encoded by alternate alleles at the same genetic locus.

altimontane: collective term for the belts of ericaceous and afroalpine vegetation on the high mountains of tropical East Africa (White 1983).

altricial: describes young born in an undeveloped state. *cf.* precocious (*q.v.*).

altruism: behaviour that enhances the reproductive and genetic fitness of another individual at the expense of its own.

alveolus (*pl.* **alveoli**, *adj.* **alveolar**): small cavity; socket that houses the root of a tooth.

angular process: process at the posterior lower corner of the mandible; situated ventral to the coronoid process (*q.v.*).

ante-orbital (= **anteorbital**): in front of the orbit (*q.v.*).

antebrachial: anterior to the arm (forelimb).

anterior palatal foramina: the two foramina (*q.v.*) on the ventral part of the skull.

apomorphy (*adj.* **apomorphic**): situation in which a novel character evolves from a pre-existing character. In cladistics (*q.v.*), an apomorphic character shared among two or more species (synapomorphy [*q.v.*]) indicates shared descent from a common ancestor and hence monophyly (*q.v.*). *cf.* plesiomorphy (*q.v.*).

arboreal: living above the ground (in trees and shrubs). *cf.* scansorial (*q.v.*); terrestrial (*q.v.*).

auditory bulla: *see* tympanic bulla.

auditory meatus (*pl.* **auditory meati**): the external opening of the ear; the passage leading from the tympanic membrane (ear drum) to the external ear.

autapomorphy: derived trait uniquely characteristic of a taxon.

autogroom: grooming behaviour in which an individual grooms itself. *cf.* allogroom (*q.v.*).

autosomal: pertaining to any chromosome other than the sex chromosomes.

bachelor herd: a herd comprised entirely of males, usually mature, but of mixed age.

baculum (*pl.* **bacula**, *adj.* **bacular**): the os penis, or penis bone, which supports the penis in some mammals.

bai (*pl.* **bais**): an opening or clearing.

basal metabolic rate: metabolic rate required for survival in the thermal neutral zone (*q.v.*); a state that requires the lowest expenditure of energy when at rest.

basicranium: the base of the skull.

basisphenoid: cranial bone in middle of base of skull; the median posterior part of the sphenoid bone, forming part of the floor of the braincase.

Bergmann's Rule: The theory that the size of a warm-blooded animal in a single, closely related, evolutionary line, increases along a gradient from warm to cold temperatures.

bicuspid: having two points or cusps (particularly of teeth).

bifid: divided by a shallow notch.

bilophodont: describes cheekteeth having two transverse ridges.

bipedal: body supported by the two hindlimbs; movement not using the forelimbs.

blastula: a hollow ball of undifferentiated cells (derived from a fertilized ovum by cell division), which represents one of the earliest stages of embryonic development.

BP: (*abbrev.*) before the present.

brachydont: describes a premolar or molar tooth with low crowns. *cf.* hypsodont (*q.v.*).

braincase (= cranium): that part of the skull housing the brain; the part of the skull posterior to the front line of the orbits. *cf.* rostrum (*q.v.*).

buccal: On the cheek side of the mouth or teeth or penetrating to the cheek or sometimes used broadly as pertaining to the cavity of the mouth.

bullae: *see* tympanic bullae.

bunodont: describes molar teeth, entirely covered by enamel, that have low, rounded, hill-like cusps (as opposed to sharp, pointed cusps). (*cf.* hypsodont, lophodont).

bushmeat: meat for human consumption derived from non-domesticated mammals, birds and reptiles taken from their natural habitats and domiciles.

bushveld: savanna vegetation type characterized by a grassy ground layer and a moderately dense upper layer of shrubs and scattered trees.

BZ: (*abbrev.*) Biotic Zone.

C or c: (*abbrev.*) canine tooth; upper case denotes adult dentition, lower case denotes deciduous dentition (milk teeth). *See also* canine.

c.u.: (*abbrev.*) (*Lat. cum unguis* = with nail) measurement of the hindfoot when length of the nail on the claw is included in the measurement. Usually hindfoot is measured without the claw because claws may be broken or worn. When length of claw is included, it is conventional to record as 'HF c.u.'. *cf.* s.u. (*q.v.*)

caecum (pl. caeca): a blind-ending pouch in the alimentary canal (often enlarged as a fermentation chamber) located at the junction of the small and large intestines.

canine: the most anterior tooth on the maxilla bone and in a similar position on the mandible; situated immediately posterior to the incisors; if incisors are absent, the most anterior tooth in the jaw. Unicuspid; tall and pointed in most mammals. Never more than one canine on each side of each upper and lower jaw; absent in some taxa.

caniniform: having shape and appearance of a canine tooth.

carnassial shear: Found in some carnivores and formed by the blade-like cusps of the fourth upper premolar teeth and first lower molar teeth, which, occluding together like the blades of a pair of scissors, provide a shearing action for cutting through tough skin or bone. Sometimes referred to as the carnassials.

carotid: pertaining to the carotid artery located in the front of the neck through which blood from the heart flows to the brain.

cauda epididymides: the ducts of the epididymides at the posterior end of the testes that carry sperm from the testes to the vas deferens, which, in turn, carries sperm to the penis. Sometimes used to store sperm prior to copulation.

caudal: pertaining to the tail; in the direction of the tail.

Cenozoic (= Cenozoic Era): geological era, ca. 65 mya to today, comprising the Quaternary and Tertiary Periods: the Age of Mammals.

central Africa: Cameroon (south of the Sanaga R.), Central African Republic (but only south of ca. 7° N), Equatorial Guinea, Gabon, DR Congo (except SE). Mainly rainforest habitats and rainforest–savanna mosaics.

centromere: the part of a chromosome where sister chromatids are linked together during mitosis.

cerebellum: the part of the hindbrain that controls and coordinates motor movements, posture, balance and muscle tone.

cerebrum (= cerebral hemispheres): the anterior part of the brain that is involved in voluntary movements, processing sensory information, olfaction, learning, memory, communication and other functions.

cervical: pertaining to the neck.

cf. (in general usage): compare or compare with. In the context of descriptions, implies a difference or contrast: e.g. 'In *Elephantulus edwardii*, first lower premolar single-rooted (*cf.* *E. myurus* in which the first lower premolar is double-rooted).'

cf. (in taxonomy): precedes the specific name if there is uncertainty in the assignment.

cheekteeth: the premolar (*q.v.*) and molar (*q.v.*) teeth combined.

choana (pl. choanae): the openings of the internal nostrils on the skull, situated immediately posterior to the bony palate.

chromosome: one of the thread-like bodies within the nucleus of a cell, which carry the genes (genetic material) in linear order; each chromosome is composed of one long molecule of DNA (and two long molecules at cell division). Chromosomes occur in pairs (one from each parent) and are visible as rod-like bodies in cells that are dividing. The total number of chromosomes in a cell is expressed as the diploid number (2n).

CI: condyloincisive length; the length of the skull from the anterior end of the longest incisor tooth to the posterior end of the occipital condyles. *cf.* GLS.

cingulum (pl. cingula): ridge around the base of the crown of a tooth.

CITES (abbrev.): Convention on International Trade of Endangered Species of Wild Fauna and Flora; an international treaty set up to ensure that international trade in wild animals and plants does not threaten the survival of species in the wild. It accords varying degrees of protection to more than 33,000 species of animals and plants. Appendix I lists species that are the most endangered among CITES-listed animals and plants. Appendix II lists species that are not necessarily now threatened with extinction but that may become so unless trade is closely controlled. Appendix III is a list of species included at the request of a Party that already regulates trade in the species and that needs the cooperation of other countries to prevent unsustainable or illegal exploitation.

- clade:** branch of a phylogenetic tree containing the set of all organisms descended from a common ancestor.
- cladistic (analysis):** a methodology that provides a classification in which organisms are grouped in terms of the time when they had a common ancestor.
- cline** (*adj.* **clinal**): in context of geographic variation, a gradual and sequential change of a character(s) without a significant break such as would justify division into separate subspecies or species.
- CMS:** Convention on Migratory Species of Wild Animals (also known as the Bonn Convention). An intergovernmental treaty, concluded under the aegis of the United Nations Environment Programme, concerned with the conservation of migratory terrestrial, aquatic and avian migratory species throughout their range. Migratory species threatened with extinction are listed on Appendix I; Migratory species that need or would significantly benefit from international co-operation are listed in Appendix II.
- CNL:** condylo-nasal length; measurement from the most anterior part of the nasal bone to the most posterior part of the occipital condyle (exoccipital) on the same side of the skull; a similar measurement to 'greatest length of skull'.
- cochlea** (*pl.* **cochleae**, *adj.* **cochlear**): a hollow structure, spirally coiled like a snail's shell, situated in the skull and containing the internal organ of hearing.
- competitive exclusion:** the principle that two different species cannot indefinitely occupy the same ecological niche.
- concatenation:** a chain of linked elements.
- concave:** having a curvature that curves inwards; having an outline or a surface curved like the interior of a circle or sphere. *cf.* convex (*q.v.*).
- concavity:** a concave depression in an outline or surface.
- conceptus:** embryo prior to implantation.
- conductance:** in thermal biology, the rate at which heat passes across a temperature gradient, e.g. the density and thickness of the pelage affects the rate at which body heat passes from the body to the outside. Thick pelage, which traps and holds air, results in low thermal conductance.
- condylar process:** process at the posterior upper corner of the mandible, which forms the lower hinge of the jaw articulation; fits into the glenoid fossa (*q.v.*) of the skull.
- condylarth** (*adj.*): as in the Condylarthra, an extinct order of mammals.
- condyle:** a rounded process on a bone that articulates with a socket-like concavity in another bone.
- condylobasal length:** the length of a skull, measured from the anterior points of the premaxilla (*q.v.*) to the posterior surfaces of the occipital condyles (*q.v.*).
- congeneric:** belonging to the same genus.
- conspecific:** belonging the same species. *cf.* heterospecific (*q.v.*).
- contiguous:** touching; sharing a boundary (as in geographic ranges).
- convex:** having a curvature that bulges outwards; having an outline or a surface curved like the exterior of a circle or sphere. *cf.* concave (*q.v.*).
- coprophagy:** the eating of faeces. Includes the eating of an individual's own faeces as they are voided from the anus.
- copulatory plug:** plug formed in the vagina of the female after copulation; formed from seminal fluids of the male. Prevents or reduces the chance of sperm from another male(s) entering the female reproductive tract if the female copulates again soon after copulation with the first male.
- coronoid canal:** a foramen (canal) in the coronoid process (*q.v.*) of the mandible.
- coronoid process:** angular pointed process on the upper margin of the mandible, situated anteriorly to the condylar process (*q.v.*); does not participate in the jaw articulation.
- corpus luteum** (*pl.* **corpora lutea**): a glandular mass of tissue on the surface of an ovary, that develops after the extrusion of an ovum from a Graafian follicle (*q.v.*); secretes the hormone progesterone.
- cotype:** originally synonymous with syntype but now used as synonym of paratype (*q.v.*).
- CR:** (*abbrev.*) *see* crown–rump length.
- cranial profile:** the shape of the cranium (the part of the skull that surrounds the brain) when viewed from the side.
- craniodental:** pertaining to the skull and teeth.
- cranium:** that part of the skull housing the brain. Also called braincase.
- crepuscular:** at, active in, twilight, when light intensity is higher than at night but lower than during the day. *cf.* diurnal (*q.v.*); nocturnal (*q.v.*).
- Cretaceous Period:** period (within the Mesozoic Era); 146–65 mya.
- crown:** (1) top of head; (2) exposed part of a tooth (visible above gum), especially the grinding surface.
- crown–rump length (CR):** distance from the crown of head to the rump of a foetus (i.e. maximum length of a foetus in its natural form).
- cuckolding:** when an intruding male mates with an oestrous female without her mate being aware of the event.
- cursorial:** pertaining to running.
- cuspid** (*adj.* **cuspidate**): a prominence or sharp point, such as on the occlusal surface of some teeth. *See also* t.
- cutaneous:** (*adj.*) pertaining to the skin.
- Cyrenaica:** a region of North-East Libya. Includes the Cyrenaican Plateau and that part of the Mediterranean Coastal Biotic Zone between the plateau and the sea, as well as drier terrain south of the plateau.
- cytochrome b:** a protein involved in electron exchange in the mitochondria. It is the product of a gene in the mitochondrial genome. The sequence of this gene is often compared between species in phylogenetic studies to infer relatedness.
- cytogenetics** (*adj.* **cytogenetic**): the study of the microscopic structure of chromosomes, especially the mapping of genes.
- cytonuclear:** (*adj.*) pertaining to the nucleus and the cytoplasm of a cell.
- Dahomey Gap:** the geographic region where savanna habitat extends southwards to the West African coast in E Ghana, Togo, Benin (formerly Dahomey) and extreme SW Nigeria. The presence of savanna forms a break (or gap) in the extensive Rainforest Biotic Zone, which extends along the West Africa coast from Sierra Leone to Cameroon. The Dahomey Gap is an important biogeographical barrier separating the faunas to the east and west of the Gap.
- deciduous teeth:** *see* milk teeth (*q.v.*).

- Dega:** Ethiopian word for the temperate agricultural/economic altitudinal zone, about 2300–3000 m, warm enough for cereal-based agriculture.
- delayed implantation:** a means of lengthening the interval between copulation and parturition by delaying the implantation of the blastula (*q.v.*), so that both copulation and parturition can occur in the most optimal seasons. Development to blastula stage is followed by a period of halted development lasting several weeks or months; then the blastula implants and embryonic development proceeds normally, usually without any further interruption, until the young is born.
- deme:** a unit of population that is interbreeding and is separate from any other such population.
- dental formula:** a simple numerical method of denoting the number of incisor (I), canine (C), premolar (P) and molar (M) teeth on one side of the upper jaw and lower jaw, and the total number of teeth. For example, the dental formula of a primitive mammal is $I^{3/3}, C^{1/1}, P^{4/4}, M^{3/3} = 44$, which means there are three incisors, one canine, four premolars and three molars on each side of the upper jaw and also the lower jaw, making a total of 44 teeth. The formula may also be expressed in the form $^{3143}/_{3143} = 44$. Each incisor, premolar and molar is numbered according to its position in the tooth row; superscript numbers indicate upper jaw, subscript numbers indicate lower jaw (mandible) e.g. P^4 (upper fourth premolar), M_2 (lower second molar).
- dentine:** the substance, also known as ivory, comprising tusks (*q.v.*) and the interior hard part of vertebrate teeth. Lies under the enamel of teeth (but may be exposed if the enamel wears) and surrounds the pulp chamber and root canals.
- diastema:** space in the mouth between the incisor teeth and cheekteeth in those mammals that feed on grasses, herbs etc. (e.g. rodents, hares, rabbits, ruminants, etc.).
- dichromatism:** condition in which members of a species show one of only two distinct colours or colour-patterns.
- dilambdodont:** molar tooth with W-shaped ridges. *cf.* zalambdodont (*q.v.*).
- dimorphism:** *see* sexual dimorphism.
- diphyly:** the derivation of a taxon from two separate lines of descent. *cf.* monophyly (*q.v.*).
- diploid number (2n):** total number of chromosomes (including sex chromosomes) in a somatic cell of an organism.
- distal:** the end of any structure furthest away from the mid-line of the body or furthest from the point of its attachment. *cf.* proximal (*q.v.*).
- diurnal:** at, active in, daytime; when light intensity is high. *cf.* crepuscular (*q.v.*); nocturnal (*q.v.*).
- DNA hybridization:** technique of comparing the similarity between two DNA molecules by reassociating single strands from each molecule and determining the extent of double-helix formation. In phylogenetics, this technique is used to determine the relatedness of two or more taxa.
- DNA:** (*abbrev.*) deoxyribonucleic acid; the very large self-replicating molecule that carries the genetic information of a chromosome; each molecule is composed of two complementary chains of DNA.
- dorsoventral (dorsoventrally):** from dorsal to ventral surface; from back to belly of an animal.
- E:** (*abbrev.*) length of external (outer) ear (= pinna), measured from tip of ear to the posterior point of the ear conch). Length and shape usually affected by preservation.
- East Africa:** Kenya, Uganda, Rwanda, Burundi and Tanzania.
- eastern Africa:** SE Sudan, Ethiopia, Eritrea, Djibouti, Somalia, Kenya, Uganda, Tanzania, Malawi (but only south of L. Malawi and east of the Shire R. Valley) and Mozambique (but only east of Malawi and north of the Zambezi R.).
- echolocation:** the use of reflected ultrasonic pulses of sound to perceive the surroundings (including obstacles, prey and other animals).
- ecotype:** a genetically distinct geographic variety or population within a species, which is adapted to specific environmental conditions.
- ectoparasite:** a parasite that lives on the exterior of an organism (e.g. ticks, fleas, lice). *cf.* endoparasite (*q.v.*).
- ectotympanic:** a bony element within the middle ear that supports the tympanic membrane or eardrum.
- edaphic:** influenced by conditions of soil or substratum.
- emargination:** a distinct notch or indentation.
- embryo number:** number of foetuses within the uterus or uteri of the female (as assessed by autopsy). Expressed as mean number (with range from minimum to maximum, and sample size). *cf.* litter-size (*q.v.*).
- enamel:** hard material that forms a cap over the dentine component of a tooth; usually the most visible part of a tooth.
- encephalization quotient (EQ):** a measure of comparative brain size or weight defined as the ratio of the actual brain weight to the expected brain weight predicted for an animal of a given body weight.
- endemic:** restricted to, peculiar to, or prevailing in, a specified country or region.
- endoparasite:** a parasite that lives in the interior of an organism (e.g. nematodes, cestodes, blood parasites). *cf.* ectoparasite (*q.v.*).
- entoconid cusp:** the posterior cusp on the lingual (inner) side of a lower molar tooth.
- entotympanic:** an independent ossification found in the floor of the tympanic cavity in various extant and extinct eutherian groups, including, for example, Scandentia, Chiroptera, Dermoptera, Hyracoidea, Pholidota, Xenarthra, Carnivora, and Macroscelidea.
- Eocene:** geological Epoch (within the Tertiary Period); 55–38 mya.
- epiphysis (pl. epiphyses):** any part of a long bone that is formed from a different centre of ossification and that later fuses with the bone to form its terminal part.
- epitympanic recess:** a hollow located on the roof of the middle ear.
- erg:** a large, relatively flat area of desert covered with wind-swept sand with little or no vegetation cover (sometimes referred to as a dune sea).
- evaporative water loss:** the loss of water from the body through the skin and/or the lungs. A mechanism used by mammals to reduce T_b (*q.v.*) when T_a (*q.v.*) is high. Excessive evaporative water loss may lead to dehydration if free (drinking) water is unavailable.
- exfoliating:** shedding flakes (e.g. of bark), or breaking into relatively thin slabs (e.g. of granitic rock).
- exoccipital condyles:** a pair of projections from the occipital bone on either side of the foramen magnum (*q.v.*), which articulate with the first of the spinal vertebrae.

extant: living at the present time. *cf.* extinct.

F. R.: (*abbrev.*) Forest Reserve.

facultative: having the capacity to switch from one mode of life or action to another depending on conditions or circumstances. *cf.* obligate (*q.v.*).

female-defence polygyny: a mating system in which males control access to females directly, usually by virtue of female gregariousness (Emlen & Oring 1977).

fenestra (*pl.* **fenestrae**): opening in a bone, or between two bones.

flank: the side of the body of a mammal.

flehmen: an act performed by many species of mammals whereby an adult male sniffs the vulva and urine of a female to test for oestrus. The head of the male is raised, the nose pointed upwards, the lips retracted and the nose wrinkled. This muscular contraction opens the *ductus incisivus* ensuring that scent molecules reach the Jacobsen's organ for olfactory analysis.

FN: (*abbrev.*) *see* fundamental number.

foliaceous: (*adj.*) resembling the leaf of a plant.

folivore (*adj.* **folivorous**): an animal that eats leaves.

foramen (*pl.* **foramina**): an aperture (which is usually small, round or elliptical) in a bone, or between bones, for the passage of a nerve, blood vessel or muscle.

foramen magnum: the large opening at the posterior end of the skull through which the spinal cord passes.

form: a neutral term for a single individual or taxonomic unit that may be employed without reference to the formal taxonomic hierarchy of categories; one of the varieties found in a polymorphic species.

forest island: *see* relict forest.

fossa (*pl.* **fossae**): a depression or hollow usually in a bone (e.g. glenoid fossa, preorbital fossa)

fossorial: adapted for digging; burrowing. *cf.* subterranean (*q.v.*).

founder effect: the loss of genetic diversity that occurs when a new isolated population is derived from a very small number of individuals.

fovea: small pit or depression.

frontal bone: one of a pair of bones forming the anterior part of the braincase.

frugivorous: fruit-eating.

fundamental number (FN): an ambiguous term sometimes defined as (1) the total number of chromosomal arms in the full chromosomal complement of an organism (i.e. including the sex chromosomes), or (2) the total number of chromosomal arms found in the autosomal chromosomes only (i.e. excluding the sex chromosomes). When only the autosomal chromosomes are included, some authors (but not all) use aFN instead of FN to avoid ambiguity. For further details, *see* aFN.

fusiform: elongated and tapering at both ends.

fybos: the heath shrublands characteristic of the Cape Floristic Kingdom (within the South-West Cape Biotic Zone) of South Africa. Dominant plants are sclerophyllous, evergreen, low (<3 m), bushy and fine-leaved, but there are also scattered taller bushes and, less often, very widely spaced trees. Contains an exceptionally high number of endemic species of plants. The three main components on nutrient-poor sandy soils are species of Ericaceae, Restionaceae and Proteaceae. Also includes 'renosterveld' (*q.v.*) (dominated by species of Asteraceae) on nutrient-rich silt or clay soils.

G. R.: (*abbrev.*) Game Reserve.

gallery forest: type of forest outlier (in a savanna region) found in narrow sheltered valleys and ravines on hillsides, where soils are moist enough, and conditions humid enough, to support rainforest trees (Rosevear 1953).

garrigue: a type of short, Mediterranean shrubland (White 1983).

genetic drift: in population genetics, refers to changes in the frequencies of genes in small, isolated populations that occur with time, as a result of random sampling events as opposed to natural selection.

genotype: genetical term to describe the genetic constitution of an individual inherited from its parents. *cf.* phenotype (*q.v.*).

genus (*pl.* **genera**): taxonomic division superior to species and subordinate to family.

geocarpic: having fruit that mature underground.

geophagy (= **geophagia**): the eating of saline or calcareous soil.

gestation: the development of embryo/foetus, which takes place in the uterus; the period during which this development takes place. The gestation period is defined as the interval between conception and parturition (birth). Strictly speaking, the gestation period is not the interval between copulation (mating) and parturition (birth), although many authors take it to be this interval. The gestation period (*sensu stricto*) may be lengthened by reproductive delays, such as delayed implantation (*q.v.*).

glans penis: the bulbous tip of the penis.

glenoid (= **glenoid fossa**): the cavity (fossa) in the squamosal bone of the skull for the articulation of the condyle of the mandible (lower jaw) in mammals; visible on lateral and/or ventral views of skull depending on the taxon.

GLS: (*abbrev.*) greatest length of skull, measured from anterior end of incisor teeth or nasal bone (whichever is most anterior) to the posterior end of the skull (occiput, occipital condyles or auditory bullae, whichever is most posterior).

Gondwana (= **Gondwanaland**): the southernmost of the two Mesozoic (*q.v.*) supercontinents that later fragmented (as a result of continental drift) into the landmasses of Africa, Madagascar, Antarctica, Australia, South America, the Indian subcontinent and the Arabian peninsula.

Graafian follicle: the structure in the mammalian ovary that contains the developing ovum and from which the ovum is released at the time of ovulation.

gracile: lightly built. *cf.* robust.

graminivore (*adj.* **graminivorous**): feeding on grasses.

granivore (*adj.* **granivorous**): an animal that eats grains and seeds.

graviportal: having limbs adapted to bearing great weights (as in elephants).

gregarious: living together in groups, flocks, herds.

Gregorian Rift Valley: *see* Rift Valley.

guard hair: long thin bristle-like hairs, mainly on the back and flanks that project beyond the soft hairs of the pelage; when present, conspicuous but never as numerous as soft hairs; probably tactile in function.

gular: pertaining to the upper part of the throat (the gula) as in gular gland, gular pouch, gular region.

GWS: (*abbrev.*) greatest width of skull, usually measured across the widest point of the zygomatic arches (*q.v.*).

- haematopoietic** (*n.* **haematopoensis**): pertaining to the formation of blood cells from stem cells.
- hallux**: the first digit of the hindlimb.
- hammada**: flat plain covered with pebbles of various sizes on a hard substrate in an arid environment. Much of the Sahara Desert is formed of hammada.
- haplotype**: the set of alleles borne on one of a pair of homologous chromosomes; a group of genes that is inherited together from a single parent.
- HB**: (*abbrev.*) length of head and body (measured from the tip of the nose to the most posterior point of the pelvis (anterior to the first tail vertebra)).
- hemidiaphragm**: half of the diaphragm, the muscle that separates the chest cavity from the abdomen and that serves as the main muscle of respiration.
- hermaphrodite** (*adj.* **hermaphroditic**): an individual having both male and female reproductive organs.
- heterospecific**: (*adj.*) belonging to different species. *cf.* conspecific (*q.v.*)
- heterothermic**: condition when the body temperature fluctuates in relation to the ambient temperature T_a (*q.v.*). *cf.* homeothermic (*q.v.*).
- heterozygosity**: a measure of the genetic variation in a population, expressed through the presence of different alleles (*q.v.*) at one or more loci on homologous chromosomes.
- HF**: (*abbrev.*) length of hindfoot (measured from the 'ankle bone' to the tip of the longest digit usually without including the claw). *See also* c.u.; s.u.
- hibernaculum** (*pl.* **hibernacula**): a place, domicile or roost where an animal hibernates.
- hibernation**: a state of inactivity accompanied by a reduction in metabolic rate (below basal metabolic rate [*q.v.*]), lower T_b , and slow breathing. Occurs when T_a is low and food is scarce; usually lasts for weeks or months; not common in African mammals (*cf.* torpor).
- high forest**: rainforest that has matured, stabilized and reached the climax stage of succession.
- highveld**: high plateaux characteristic of inland southern Africa, dominated by grasses.
- Holocene**: geological Epoch (within the Quaternary Period) (*q.v.*) following the Pleistocene Epoch (*q.v.*); ca.11,000 mya to today. Sometimes referred to as the 'Recent' Epoch.
- holotype** (= **type**): the single specimen designated or indicated by the original author of the original description of a new species or subspecies, to be the standard reference to the essential characters of the new taxon. *see also* cotype (*q.v.*), lectotype (*q.v.*), neoparatype (*q.v.*), neotype (*q.v.*), paratype (*q.v.*), syntype (*q.v.*), topotype (*q.v.*) and type locality (*q.v.*).
- home-range**: the area (expressed in square metres, or square kilometres) routinely used by an animal for its day-to-day activities and requirements, and that contains the resources required for survival and reproduction. Within the home-range there may be a 'core area' or 'centre of activity' that is utilized more frequently than other parts (e.g. 80% or 90% of known time-based observations). *cf.* territory (*q.v.*).
- homeothermic**: describes an organism having a body temperature that is maintained at a constant level (within limits), independently of the ambient temperature T_a (*q.v.*). For the limits, see upper and lower critical temperatures [*q.v.*]. *cf.* heterothermic (*q.v.*).
- homoplasy**: similarity between different organisms or taxa resulting from evolution along similar lines (e.g. convergent evolution) rather than descent from a common ancestor.
- homozygous** (*n.* homozygosity): describes a diploid organism that has inherited the same allele of any particular gene from each of its parents. *cf.* heterozygous.
- hyoid**: a small bone or bones in the throat located at the base of the tongue and supporting the muscles of the tongue.
- hyperthermia**: elevation of body temperature above normal limits due to increase in T_a (*q.v.*) or increase in metabolic rate. *cf.* hypothermia (*q.v.*).
- hypoconulid**: the most posterior cusp on the lingual (inner) side of a lower molar tooth.
- hypogeal**: living or growing underground.
- hypothermia**: drop in body temperature below normal limits; occurs in some small mammals when T_a (*q.v.*) falls, and is a means of conserving energy in cold weather. *cf.* hyperthermia (*q.v.*).
- hypsodont**: describes a premolar or molar tooth with high crowns; has short roots. *cf.* bunodont, lophodont.
- I or i**: (*abbrev.*) incisor (*q.v.*) tooth or teeth; upper case denotes adult dentition, lower case denotes deciduous dentition (milk teeth). *See also* incisor.
- I.** (*pl.* **Is.**): (*abbrev.*) Island.
- I¹-M³**: (*abbrev.*) the length of the upper toothrow from the anterior end of the first upper incisor to the posterior end of the last molar. In taxa where the last molar is M¹ or M² (instead of M³), the measurement is I¹-M¹ or I¹-M².
- implantation**: the embedding of a blastula (*q.v.*) in the lining of the uterus.
- incertae sedis**: (*Lat.*) refers to a taxon of uncertain status and that is perhaps taxonomically invalid.
- incisive foramen** (*pl.* **foramina**): paired foramina located at the anterior end of the bony palate, just posterior to the incisor teeth.
- incisor**: tooth rooted in the premaxillary bone (most anterior bone of upper jaw) and in an equivalent position in the mandibular bone (lower jaw); always anterior to the canine teeth, if present. The number and form of the incisor teeth varies in different species. *See also* dental formula (*q.v.*).
- infraorbital foramen** (*pl.* **foramina**): foramen that connects the orbit (eye-socket) with the rostrum (premaxilla and maxilla bones); this foramen contains the masseter medialis muscle in some taxa. Also referred to as anteorbital foramen and antorbital foramen.
- infrasonic**: describes sounds with frequencies below the range that can be heard by humans.
- infundibulum**: a funnel-shaped cavity or depression.
- inguinal**: situated in the groin, that is the area between the lower lateral part of the abdomen and the thigh.
- inner**: nearest to mid-line of body, e.g. inner incisor, inner margin of ear.
- insectivore** (*adj.* **insectivorous**): an animal that eats insects.
- inselberg**: isolated rocky hill; term used mainly in western Africa. *See also* jebel (*q.v.*); kopje (*q.v.*), krantz (*q.v.*).
- inter-aural**: between the ears.
- inter-digital**: between the digits (e.g. interdigital gland).

- inter-orbit (= inter-orbital constriction):** narrowest part of the skull between the orbits when viewed dorsally at the level of the frontal bones.
- inter-parietal:** bone (not paired) on dorsal surface of the skull, lying between and partly posterior to the parietal bones.
- inter-pterygoid region:** the region between the two plate-like pterygoid bones (*q.v.*) that form part of the roof of the mouth.
- inter-specific:** between different species.
- intra-specific:** within one species; between members of the same species.
- intromission:** insertion of the penis into the vagina during copulation.
- invagination:** the formation of a cavity by the in-sinking of the outside wall or surface of a tissue or structure, thereby drawing an exterior layer into the interior of the structure to form the lining of the cavity; a cavity formed by the process of invagination.
- Isoptera:** taxonomic order containing the termites (within the phylum Insecta).
- isozyme:** any one of several different forms of an enzyme encoded by the same or different genes and that each differ in properties such as optimum pH or isoelectric point.
- iteroparous:** repeated reproduction throughout a season or a lifetime (*cf.* semelparous – reproduces once and then dies).
- ivory:** *see* dentine.
- jebel (= gebel):** isolated rocky hill in savanna and arid habitats; term used mainly in northern Africa. *See also* inselberg (*q.v.*); kopje (*q.v.*).
- jugal:** bone of the skull that forms the middle part of the zygomatic arch (*q.v.*); anteriorly joins the maxillary process (*q.v.*) of the maxilla bone and posteriorly joins the squamosal process of the squamosal bone.
- K-selection:** selection for characteristics suitable in stable environments (slow development of young, small litter size, relatively long time to maturity, relatively long life span) *cf.* r-selection (*q.v.*).
- Kaokoveld:** area of sandstone and lava hills of the Namib Desert (Biotic Zone 11b) in NW Namibia, inland from the Skeleton Coast.
- Karoo:** southern African term for grassy dwarf shrubland on the semi-arid central plateau of the western half of South Africa at altitudes of 500–2000 m.
- karyogram:** a photographic representation of a karyotype (*q.v.*) as it appears at mitosis. Individual chromosomes are arranged in pairs from largest to smallest.
- karyological:** pertaining to the nucleus and chromosomes.
- karyotype:** the chromosomes in the cell of an animal. *See also* karyogram.
- kloof:** a deep, narrow valley or gorge.
- kopje:** rocky hill with boulders, rock crevices and sparse vegetation; term used mainly in southern Africa. *See also* inselberg (*q.v.*); jebel (*q.v.*); kranz (*q.v.*).
- krantz (pl. krantzes):** a wall of rock encircling a mountain or summit; hence any precipitous or overhanging wall of rocks.
- L.:** (*abbrev.*) Lake.
- labial:** pertaining to the lips; situated near the lips; on the outer side of the teeth within the mouth. *cf.* lingual (*q.v.*).
- labially:** in the direction of the lips. *cf.* linguallly (*q.v.*).
- lachrymal bone:** small bone in skull situated at the upper anterior margin of the orbit, near the lachrymal (tear) gland.
- lambdoid crest:** *see* supraoccipital crest.
- lamina (pl. laminae):** in the context of premolar and molar teeth, a transverse row of cusps (e.g. t1, t2 and t3, or t4, t5 and t6, etc.) that, when worn, form a transverse ridge of bone and dentine across the tooth.
- larynx (= voice box):** the structure in the throat of mammals that produces sound.
- lauschlag:** a courtship behaviour in antelopes in which the male touches the female's underside with a stiff foreleg, placing it either under her flank from the side or between her hind legs from behind. Also termed the mating kick or foreleg kick.
- Laurasia:** the northernmost of the two Mesozoic (*q.v.*) supercontinents that later fragmented (as a result of continental drift) into the landmasses of Europe, Asia (excluding the Indian subcontinent) and North America.
- lectotype:** a specimen chosen from syntypes (*q.v.*) to stand as 'the type' of a species or subspecies when no holotype (*q.v.*) was designated by the author who described the new species or subspecies.
- lek:** a traditional site where males gather for the sole purpose of attracting and courting females, and to which females come for the sole purpose of mating with the male of their choice.
- limiting factor:** the principle that the growth or functioning of an organism is limited when any essential factor (or resource) is lacking or in short supply, regardless of the quantity available of any other factor (or resource). The principle may also be applied to the proliferation and/or distribution of a population or species.
- lingual:** pertaining to the tongue; situated near the tongue; on the inner (tongue) side of the mouth. *cf.* labial (*q.v.*).
- lingually:** in the direction of the tongue. *cf.* labially (*q.v.*).
- litter-size:** number of young born to a female. Expressed as mean number (with range from minimum to maximum, and sample size). *cf.* embryo number (*q.v.*).
- localized movements:** movements of an animal within part or all of its home-range within a single day or within a limited period of time. *cf.* migration (*q.v.*); nomadic movements (*q.v.*).
- longitudinal:** lengthwise; running in a head to tail direction. *cf.* transverse (*q.v.*).
- lophodont:** molar teeth having the crowns formed in transverse crests or ridges (*cf.* bunodont).
- lordosis:** dorsi-flexion of the spine, often performed by females prior to copulation.
- lower critical temperature:** the lowest ambient temperatures at which the animal must increase its metabolic rate to maintain a constant body temperature. If ambient temperature decreases further, and the animal is unable to increase its metabolic rate sufficiently to maintain a constant body temperature, it will enter hypothermia and may eventually die. *cf.* upper critical temperature.
- lowveld:** savanna at lower altitudes below the Great Escarpment of South Africa, with vegetation consisting of a grassy lower layer and a woody upper layer of shrubs and/or trees, at either high density (woodland) or intermediate density (bushveld, *q.v.*).
- lumbar:** describes vertebrae between the thoracic vertebrae and the sacrum; vertebrae of the lower back in humans.

lyrate: having curvature suggestive of a lyre.

M: (*abbrev.*) molar tooth or teeth. *See also* molar (*q.v.*).

Maghreb: *see* North-West Africa (*q.v.*).

malleus: the most external bone of the three ossicles of the middle ear, the handle of which is joined to the ear drum.

mandible: lower jaw.

mandibular ramus: one of the two branches (sides) of the mandible (*q.v.*); the two rami are joined at the mandibular symphysis (*q.v.*).

mandibular symphysis: the junction, marked by a small vertical ridge, where the left and right sides of the mandible are fused.

masseter muscle: one of the muscles that raises the lower jaw, e.g. during chewing. Particularly well developed and powerful in herbivores.

mastoid: one of a pair of bones, often with a prominent process, situated near the posterior end of the skull behind the auditory meatus (*q.v.*).

matriarchal; describes social groups dominated and/or led by a female (often one of the oldest females in the group).

maxilla (*pl. maxillae*): one of the pair of bones in the skull that forms that part of each upper jaw in which the canine (*q.v.*) (if present) and cheekteeth (premolars and molars) (*q.v.*) are rooted.

maxillary process: projection of bone from the maxilla that forms the anterior portion of the zygomatic arch (*q.v.*); usually orientated vertically to the anterior–posterior line of the skull.

maxillary: pertaining to the maxilla (*q.v.*).

meatus: a passage or channel; the opening of a passage.

medial: situated in the middle.

melanistic: having an abnormally large amount of black or dark pigment in pelage and skin.

mesa: Ethiopian word for the microhabitat (usually on slopes) within afroalpine moorlands and grasslands, where it is higher and drier than surrounding areas, so dominated by (usually) *Alchemilla*.

Mesozoic (= Mesozoic Era): geological era; ca. 250–ca. 65 mya, comprising the Triassic, Jurassic and Cretaceous Periods; the Age of Reptiles.

metabolic rate: *see* basal metabolic rate (*q.v.*).

metabolic water: water produced by oxidative processes within the body; an important source of water for arid-adapted mammals when free (drinking) water and water within the food is in short supply or unavailable.

metacarpals: the long bones of the hand, situated between the carpal bones of the wrist and the proximal phalanges of the fingers.

metacentric: describes a chromosome with the centromere (*q.v.*) at or very near the middle of its length, so there are two arms of equal or almost equal length (ratio not greater than 1 : 1.1). *cf.* submetacentric (*q.v.*).

metacone: the posterior labial (external) cusp of an upper molar tooth.

metacromion: a process projecting backward and downward from the acromion (the lateral triangular projection of the spine of the scapula that forms the point of the shoulder and articulates with the clavicle of the scapula) of some mammals.

metapopulation: in population dynamics and ecology, a group of spatially separated populations of the same species that interact at some level.

metatarsal gland: scent glands on the outside lower hind leg. In the Bovidae, only the Impala *Aepyceros melampus* possesses metatarsal glands.

metatarsals: the long bones of the foot, situated between the tarsal bones of the ankle and the most proximal phalanges of the toes.

microcomplement fixation: in molecular evolutionary studies, species can be compared by the extent to which antibodies to the proteins of one species cross-react to the proteins of another species. The extent of cross-reaction is indicative of the similarity of the proteins and, by inference, the evolutionary affinity of the two species. Albumin is a protein commonly used for these studies.

microsatellite locus (*pl. microsatellite loci*): a region within a DNA sequence where short sequences of one, two, three or four of the nucleotides (A [adenine], T [thiamine], G [guanine] and C [cytosine]) are repeated consecutively; e.g. ACACAC, CAACAA. The number of times a sequence is repeated varies between individuals, within populations of a species, or between species, which makes microsatellite loci useful tools in systematics (*q.v.*).

migration: movements of species that travel, predictably and more-or-less directly, from one habitat to another (and back again), along predetermined routes, in response to seasonal changes in climate, food supply or any other resource. *cf.* localized movements (*q.v.*); nomadic movements (*q.v.*).

milk teeth: teeth occurring in newborn mammals, or appearing soon after birth, and preceding the permanent teeth of the adult animal. Also called deciduous teeth.

Miocene: geological Epoch (within the Tertiary Period); ca. 23–5 mya.

miombo: a vernacular name applied to trees in the genus *Brachystegia*; a type of savanna woodland in the Zambezi region where *Brachystegia* spp. are the commonest trees or one of the commonest trees.

Mistbelt: foothills along the eastern Great Escarpment that experience regular fogs, with vegetation comprising mainly grasslands and patches of afroalpine forest in protected valleys and ravines.

mitochondrial DNA: the small amount of DNA contained within the mitochondria of a cell.

molar: grinding or cutting tooth rooted in the maxilla bone and the mandible; there are usually one, two or three molar teeth in each ramus of the jaw. Together with the premolars, if present, they form the 'cheekteeth'. The number and form of the molar teeth varies in different species. Not preceded by deciduous (milk) teeth.

molariform: similar in form to a molar tooth; used to describe the form of the premolar teeth in some taxa.

monoestrous: Generally, having one oestrus cycle (*q.v.*) during a single reproductive season. In some taxa, having one litter per year. *cf.* polyoestrous (*q.v.*).

monogamy (*adj. monogamous*): a mating system in which one male mates with one female. Neither sex has the opportunity of monopolizing additional members of the opposite sex. Fitness often maximized through shared parental care (Emlen & Oring 1977). *cf.* polygyny (*q.v.*).

monophyletic: describes a taxonomic group descended from a common ancestor that was itself a member of that taxonomic

- group, and including *all* the descendants of that ancestor (Groves 2001). *cf.* paraphyletic (*q.v.*); polyphyletic (*q.v.*).
- monophyly**: derivation of taxa from a common ancestor. *cf.* diphyly (*q.v.*), polyphyly (*q.v.*).
- monospecific**: describes a genus containing only one known species. *See also* monotypic (*q.v.*).
- monotocous**: normally having only one young per litter (twinning, if it occurs, is very rare and abnormal). *cf.* polytocous (*q.v.*).
- monotypy** (*adj.* **monotypic**): describes a taxon containing only one immediately subordinate taxonomic unit, e.g. a monotypic family contains only one genus; a monotypic genus contains only one species. *cf.* polytypy (*q.v.*).
- mopane**: a vernacular name applied to the tree *Colophospermum mopane*; a type of savanna woodland in the Zambezi region in which *C. mopane* is the commonest species of tree.
- Mt**: (*abbrev.*) Mount.
- mtDNA**: (*abbrev.*) mitochondrial DNA (*q.v.*).
- Mts**: (*abbrev.*) Mountains.
- multiparous**: describes either the birth of more than one offspring at once, or a female that has given birth two or more times.
- muzzle**: the snout; the nose and jaws of a mammal.
- MW**: (*abbrev.*) *see* mastoid width.
- mya**: (*abbrev.*) millions of years ago.
- myrmecophagy** (*adj.* **myrmecophagous**): the eating of ants and/or termites.
- mystacine vibrissae**: vibrissae (*q.v.*) resembling a moustache.
- n. d.**: (*abbrev.*) no data.
- N. P.**: (*abbrev.*) National Park.
- N. R.**: (*abbrev.*) Nature Reserve (not National Reserve).
- naris** (*pl.* **nares**): a nostril.
- Neogene Period**: geological period and system; 23.03 ± 0.05 to 2.5 mya, comprising the second part of the Cenozoic Era.
- neonate**: a newly born animal.
- neoparatype**: any specimen described at the same time as the neotype (*q.v.*).
- neotype**: a specimen selected as the type in cases where the primary types are definitely known to be lost or destroyed.
- nipple**: external opening of mammary gland. Nipple number and position vary according to the taxon, but are consistent within a species. Nipples arranged in pairs, one of the pair on each side of body.
- nocturnal**: at, active in, the night; when light intensity is at its lowest; between sunset and sunrise. *cf.* crepuscular (*q.v.*); diurnal (*q.v.*).
- nomadic movements**: irregular and unpredictable movements, from one locality to another, made by species living in unpredictable habitats. *cf.* localized movements (*q.v.*); migration (*q.v.*).
- nomen dubium**: when the available evidence is not sufficient to permit the identification of a species, its name is considered to be a *nomen dubium* and therefore not available for taxonomic purposes.
- nomen nudum**: a name that is not valid because, when it was originally published, the organism to which it referred was not adequately described, defined or sketched. The name is therefore invalid because it is impossible to associate it indisputably with any specific organism.
- nominate subspecies**: the subspecies that bears the name of the species to which it belongs (e.g. *Otocyon megalotis megalotis*), only brought into existence by the creation of one or more other subspecies in the same species (e.g. *Otocyon megalotis virgatus*).
- North Africa**: those parts of Mauritania, Morocco, Algeria, Tunisia, Libya and Egypt that are north of the Sahara Desert.
- North-Central Africa**: Southern Chad and southern Sudan, west of the Nile R. and south of the Sahara. Mainly savanna habitats.
- North-West Africa (= Mahgreb)**: those parts of Mauritania, Morocco, Algeria, Tunisia and NW Libya that are north of the Sahara Desert.
- nuchal**: pertaining to the nape of the neck.
- nulliparous**: not having given birth.
- obligate**: obligatory; limited to one mode of life or action irrespective of conditions or circumstances. *cf.* facultative (*q.v.*).
- occipital condyles**: the pair of smooth, rounded processes of the occipital bone at the posterior end of the skull on either side of the occipital foramen that acts as a hinge between the head and the neck.
- occiput**: the posterior part of the skull, above the foramen magnum (*q.v.*).
- occlusal**: pertaining to the biting surface of a tooth.
- oestrous cycle**: the reproductive cycle in most non-pregnant female mammals, comprising recurring physiological changes induced by reproductive hormones.
- oestrus** (*adj.* **oestrous**): The period when a female is sexually receptive.
- Oligocene**: geological Epoch (within the Tertiary period), ca. 38–23 mya.
- omnivore** (*adj.* **omnivorous**): an animal that eats a wide range of foods.
- orbit**: bony cavity (eye-socket) in which the eye is situated.
- oscillogram**: a visual representation (graph) of sound waves in which amplitude (sound wave pressure) is plotted on the vertical axis, and time on the horizontal axis (*cf.* sonogram *q.v.*).
- osmetrichia**: hairs structurally specialized for the dispersal of scent.
- osteophagia**: the chewing on bones engaged in by herbivorous animals suffering from a deficiency of phosphorus and calcium in their diet.
- outer**: furthest from the mid-line of the body.
- ovulation**: the release of female gametes (ova, eggs) from the ovary.
- ovum**: the female gamete or egg cell.
- owl pellets**: waste material, normally in an egg-like shape, regurgitated by owls, which contains undigested fragments of bone, hair, feathers and scales etc. from the prey; for mammalogists, useful in determining indirectly the species of small mammals in a habitat.
- P or p**: (*abbrev.*) premolar tooth or teeth; upper case denotes adult dentition, lower case denotes deciduous dentition (milk teeth). *See also* premolar.
- pachyosteosclerosis**: a thickening of the bones of the ribs and vertebrae, resulting in unusually solid bone structure with little to no marrow.
- Palaeartic**: a zoogeographic region comprising Europe, North Africa and Asia (except for southern portion of the Arabian Peninsula and tropical and sub-tropical parts of the Oriental Region).
- Palaeocene**: geological Epoch (within the Tertiary Period); 65–55 mya.

- palatal foramen** (*pl.* foramina): a foramen (*q.v.*) in the palatine bone.
- palate**: the roof of the mouth. The anterior part (hard palate) comprises the bony palate (formed by the premaxillae, maxillae and palatine bones), and a covering mucous membrane. The posterior part (soft palate) is composed only of muscular tissue covered by a mucous membrane.
- Paleogene**: geological period and system; 65.5 ± 0.3 to 23.03 ± 0.05 mya, comprising the first part of the Cenozoic Era.
- papilla** (*pl.* papillae, *adj.* papillate): a small projection or protuberance.
- paraoccipital process**: narrow strut-like bone that projects ventrally from the paraoccipital bone on the posterior part of the skull.
- parapatry** (*adj.* parapatric): the situation where two or more species have geographic ranges that are contiguous (*q.v.*) but do not overlap. This abutting may be along a line of habitat discontinuity, ecotone, or altitudinal/climatic contour, but may also arise from competitive exclusion of one (or both) by the other.
- paraphyletic**: describes a taxon containing units that have evolved from a single ancestral taxon but that do not contain all of the descendents of the most recent common ancestor.
- paratype**: a specimen collected at the same time and place as the holotype (*q.v.*) and designated by the original authority as such. There may be one or more paratypes.
- parietal**: one of the pair of bones forming the vault of the braincase, situated between the frontal and the occipital bones.
- parous**: having given birth.
- partim**: in taxonomy, used in context of taxon names and synonyms to indicate that not all material that has been referred to the name is currently considered to belong to that name. e.g. *auritus* (partim) is listed as a synonym of *Plecotus christii* because only some of the specimens, which were earlier identified as *Plecotus auritus*, are now considered to represent *P. christii*.
- parturition**: the act of giving birth.
- pectoral**: pertaining to or situated on the chest.
- pedal glands**: glands that are situated in the feet opening between the hooves.
- pelage**: the hairy, woolly or furry covering of the body in mammals. The pelage variously consists of hairs, guard hairs and underfur according to the species.
- petrophily** (*adj.* petrophilic): occupying habitats dominated by large boulders.
- phalanx** (*pl.* phalanges): one of the bones in a finger.
- pharynx** (*adj.* pharyngeal): the passage leading from the oral and nasal cavities in the head to the oesophagus and larynx (*q.v.*).
- phenotype**: the visible characters of an individual resulting from the interaction between the genotype (*q.v.*) and the environment.
- philopatry**: the tendency to remain in or consistently return to the place where one was born.
- philtrum**: a medial vertical cleft or groove in the rhinarium (*q.v.*) extending from between the nostrils to the upperlip.
- phylogenetics**: pertaining to the line of descent of a taxon; a method of classification that attempts to show the evolutionary relatedness of organisms.
- phylogeny** (*adj.* phylogenetic): the evolutionary history and line of descent of a species or higher taxonomic unit.
- piloerection**: the erection of hairs that occurs as a means of conserving heat (*see* temperature regulation) and, in some mammals, as a threat display.
- pinna** (*pl.* pinnae): the external (outer) ear.
- placental scars**: scars on the inner surface of the uterus of a mammal; the site where a placenta was attached during pregnancy. The number of placental scars can give an indication of the number of litters that a female has had (when the average number of young/litter is known).
- placentation**: the formation, type and structure of the placenta; the arrangement of placentae.
- plantar**: of the sole of the foot.
- plantigrade**: describes locomotion during which the entire sole of each foot touches the ground.
- Pleistocene**: geological Epoch (within the Quaternary Period); ca. 1.7 mya to 10,000 year ago.
- plesiomorphy** (*adj.* plesiomorphic): in cladistics (*q.v.*), describes a pre-existing character state across a wide taxonomic grouping. Sharing of that state (symplesiomorphy [*q.v.*]) amongst a subset of taxa within the wider grouping is not indicative of monophyly (*q.v.*). *cf.* apomorphy (*q.v.*).
- pleural cavity**: the body cavity occupied by the lungs.
- Pliocene**: geological Epoch (within the Tertiary period), ca. 2–5 mya.
- poikilothermic**: the condition when the body temperature varies with the surrounding ambient temperature.
- pollex**: digit 1 ('thumb') of forefoot ('hand').
- polygyny** (*adj.* polygynous): a mating system in which one male mates with several females. *See* resource-defence polygyny; female-defence polygyny. *cf.* monogamy (*q.v.*).
- polymorphism** (*adj.* polymorphic): the existence, within a species or population, of individuals having different forms (colour, size, shape etc.).
- polyoestrous**: Generally, having two or more oestrous cycles (*q.v.*) during a single reproductive season. In some taxa, having more than one litter/year. *cf.* monoestrous (*q.v.*).
- polyovulation**: production of many ova (and hence many corpora lutea) during a single oestrus; sometimes called 'superovulation'; recorded in some species of sengis.
- polyphyletic**: describes a taxon derived from two or more ancestral sources; not of a single, immediate line of descent (Mayr *et al.* 1953). *cf.* monophyletic (*q.v.*).
- polyphyly**: derivation of a taxon from two or more ancestral sources. *cf.* monophyly (*q.v.*).
- polytocous**: normally or often having more than one young per litter. *cf.* monotocous (*q.v.*).
- polytypy** (*adj.* polytypic): a taxon that has several taxa in the next lower taxonomic category, e.g. a polytypic family contains two or more genera, a polytypic genus has two or more species. *cf.* monotypy (*q.v.*).
- postauricular**: behind the external ear (pinna).
- postorbital process**: the bony projection arising from upper rim of orbit and projecting outwards and downwards around the posterior of the orbit.
- postorbital**: behind (posterior to) the orbit.
- postpartum oestrus**: an oestrus cycle immediately after (or very soon after) parturition and while lactating.

- precocious** (= **precocial**): describes young born in a well developed state enabling them to move around and forage soon after birth. *cf.* altricial (*q.v.*).
- premaxilla** (*pl.* **premaxillae**): one of a pair of bones at the anterior end of the skull that bears the incisor teeth.
- premolar**: tooth on the maxilla bone situated immediately anterior to the molar teeth; usually preceded in time by deciduous (milk) tooth; multi-cusped. Structure and function of premolar teeth vary according to species.
- preorbital fossa**: a bilateral depression in the skull, located anterior to the eye.
- preorbital**: anterior to the eye.
- prepuce** (*adj.* **preputial**): the skin surrounding and protecting the head of the penis; foreskin.
- preputial gland**: a gland situated adjacent to the penis or vaginal opening.
- primiparous**: a female that has given birth only once. *cf.* multiparous (*q.v.*).
- promiscuity**: a mating system in which each male mates with several females and each female mates with several males.
- pronking**: *see* stotting.
- protocone**: The main inner (lingual) cusp of an upper molar tooth.
- protuberant**: projecting forward (bulging) beyond the surrounding surface.
- proximal**: nearest to the body or to the mid-line of the body; nearest to the point of attachment. *cf.* distal (*q.v.*).
- proximate cause**: a cause that produces an effect directly without any intervening agency.
- pterygoid process**: one of a pair of narrow, ventrally projecting processes of the pterygoid bones situated immediately posterior to the bony palate and forming the walls of the mesopterygoid fossa (*q.v.*).
- pterygoid**: one of a pair of cranial bones forming part of the roof of the mouth.
- pubic bone**: anterior inferior part of the pelvis, articulating with its opposite number in the anterior midline at the pubic symphysis.
- Quaternary Period**: period within the Cenozoic Era; 2 mya to today, comprising two epochs: the Pleistocene and Holocene (Recent) (*q.v.*).
- r-selection**: selection for characteristics suitable in unstable fluctuating environments (rapid development of young, large litter size, relatively short time to maturity, relatively short life span) *cf.* K-selection (*q.v.*).
- R.**: (*abbrev.*) River.
- radius**: one of the two bones of the lower forelimb between the humerus (upper arm) and the wrist.
- ramus**: one half (left or right) of the lower jaw or mandible.
- range length**: distance between the most distant captures (by live-trapping) of an individual; a rough method of assessing home-range (*q.v.*).
- Recent**: *see* Holocene (*q.v.*).
- relict forest**: a forest that persists where local conditions are favourable after the disappearance of forest from the surrounding area as a result of climate change or human activity. Relict forests include those at the base of inselbergs that are watered by rainwater running off the inselberg, and forests growing in graveyards and sacred sites that are protected. Sometimes known as forest islands.
- relict population**: one that persists where local conditions are favourable after the extinction of the species from at least part of its former range.
- Renosterveld**: a dominant vegetation type in the Cape Floristic Region (*q.v.*), and characterized by the dominance of members of the Daisy Family (Asteraceae), specifically one species - Renosterbos *Elytropappus rhinocerotis*, from which the vegetation type gets its name.
- reproductive capacity**: number of young produced by a female during the breeding season.
- reproductive chronology**: the timing and duration of events, such as spermatogenesis, copulation, ovulation, gestation, parturition, lactation and reproductive inactivity, throughout the year.
- reproductive strategy**: the strategy adopted to maximise reproductive success, determined primarily by litter-size and reproductive chronology (*q.v.*).
- resource-defence polygyny**: a mating system in which a male controls access to several females indirectly, by monopolizing critical resources (Emlen & Oring 1977).
- retarded embryonic development**: a means of lengthening the interval between copulation and parturition so that both events can occur in the most optimal seasons. The implanted embryo enters a period of retarded (slowed) growth that may last 4–8 months, after which development proceeds normally.
- reticulation** (*adj.* **reticulated**): having a net-like pattern.
- rhinarium**: area of naked moist skin surrounding the nostrils.
- ridge** (= **commissure**): in teeth, a ridge connecting two cusps.
- Rift Valley**: deep valley extending from the Red Sea through Ethiopia and East Africa to Malawi; formed ca. 12 mya by subsidence of the valley floor and uplifting of the edges to form mountains and highlands. Four parts: (1) Ethiopian Rift Valley dividing the Ethiopian plateau into two parts; (2) Albertine Rift Valley (Western Rift Valley) in Uganda, E DR Congo and W Tanzania; (3) Gregorian Rift Valley (Eastern Rift Valley) in N Kenya, C Kenya and N Tanzania; (4) Malawian Rift Valley – the extension of the Albertine Rift Valley in Malawi. The Rift Valleys are noted for their many deep and beautiful lakes.
- riparian**: growing on or living on the banks of streams or rivers.
- riverine forest**: forest growing along the banks of a river or stream where conditions are moister than in the surrounding area. Sometimes referred to as ‘fringing forest’.
- Robertsonian fusion**: a chromosomal event involving the apparent fusion of non-homologous single armed (telocentric *q.v.*) chromosomes to form a bi-armed (metacentric *q.v.* or submetacentric *q.v.*) chromosome. Modern studies have revealed that all chromosomes have two arms, even if the smaller one is not detectable by light microscopy. Consequently, the term Robertsonian translocation is becoming more commonly used than Robertsonian fusion.
- rostral**: pertaining to the rostrum.
- rostrum**: that portion of the skull anterior to the front line of the orbits and supporting the upper part of the muzzle, comprised of the nasals, premaxillae and maxillae bones.
- rupicolous**: rock-living.
- s.u.**: (*abbrev.*) (*Lat. sans unguis* = without claw) sometimes added as a suffix to the hindfoot measurement to emphasize that HF has been

- measured without the claw. However, since this is the standard method of measurement, most authors write 'HF', not 'HF s.u.'. *cf.* c.u. (*q.v.*).
- sacrum** (*adj.* **sacral**): the fused vertebrae to which the pelvic girdle is attached.
- sagittal crest**: longitudinal crest of raised bone on the mid-dorsal line of the cranium.
- scansorial**: climbs or scrambles over logs and in low vegetation close to the ground. *cf.* terrestrial (*q.v.*); arboreal (*q.v.*).
- scapholunar bone**: a bone formed by the coalescence of the scaphoid and lunar in the carpus of Carnivora.
- sclerophyllous**: describes vegetation having hard leaves that are resistant to drought.
- scrotal**: pertaining to, or within, the scrotum (*q.v.*).
- scrotum**: an external sac containing the testes and epididymides in male mammals.
- sebkha**: A geological feature, in North Africa, that is a smooth, flat, plain usually high in salt (also sabkha).
- sectorial**: adapted for cutting.
- selenodont**: molar teeth having longitudinal crescent-shaped ridges.
- Senegambia**: Senegal and Gambia.
- sensu lato**: (*Lat.*) in a broad sense.
- sensu stricto**: (*Lat.*) in a strict sense.
- sensu**: (*Lat.*) in the sense of.
- septum**: a dividing wall separating two cavities.
- sex ratio**: the number of males to the number of females, usually expressed as a proportion to one male, e.g. 1 : 1 (equal numbers of males and females), 1 : 0.5 (= twice as many males as females), 1 : 2 (= twice as many females as males).
- sexual dimorphism**: observable (phenotypic) difference(s) (e.g. in colour, size or form) between the males and females of a species or higher taxon.
- Sh. Ht.**: (*abbrev.*) shoulder height (in ungulates, usually taken to be between the pegs, but sometimes measured over the curve).
- sibling species**: pairs or groups of true species that are reproductively isolated, but genetically closely related and so similar in appearance that they are difficult to separate solely on the basis of morphological characters.
- side-stripe**: longitudinal stripe(s) of contrasting colour on each flank, usually from shoulder to rump or upper part of hindlimbs. May be bordered by additional side-stripe above and below.
- singleton**: a neonate that is born singly as opposed to being one of a larger litter.
- sister species**: species that are thought to have arisen from a single dichotomous splitting event.
- sonogram**: a visual representation (graph) of sound in which frequency is plotted on the vertical axis, and time on the horizontal axis; can be analysed manually or with computer programs (*cf.* oscillogram *q.v.*).
- sounder**: a group of pigs.
- South-Central Africa**: Angola, SE DR Congo, Zambia and Malawi (but only west of L. Malawi and the Shire R. Valley).
- southern Africa**: south of the Cunene and Zambezi Rivers, i.e. Namibia, Botswana, Zimbabwe, southern Mozambique and South Africa (after Smithers 1983).
- spatulate**: like a spatula, i.e. narrow at the base but wider, flat and parallel-sided distally.
- species**: population(s) of closely related and similar organisms, which are capable of interbreeding freely with one another and cannot or typically do not interbreed with members of other species.
- sperm storage**: storage of sperm in the cauda epididymides (*q.v.*) of males for some time before copulation, or in the reproductive tract of females for an extended period before ovulation takes place. A type of reproductive delay that, in females, lengthens the length of gestation (*q.v.*).
- sperm**: any male gamete; the male cell that fuses with a female gamete (ovum, egg cell) to produce a fertilized egg or zygote from which an embryo will develop.
- spermatogenesis**: the formation of sperm in the testes.
- stotting**: bouncing up and down with legs held stiffly. Also referred to as pronking.
- sub, sub-**: prefix meaning under, signifying beneath or ventral to (as in anatomical features) or south of (as in sub-Saharan); less than (as in subsonic); not quite, nearly, almost, somewhat (as in subequal, subtriangular). In taxonomy, indicates a group just below the status of the taxa immediately following it (e.g. a genus may contain two or more subgenera).
- subauricular**: below the ear.
- subcaudal**: below the tail.
- subdermal**: just below the skin.
- submetacentric**: describes a chromosome with the centromere (*q.v.*) somewhat nearer one end than the other, so there are two arms of somewhat unequal length (ratio 1 : 1.2–1.9). *cf.* metacentric (*q.v.*); subtelocentric (*q.v.*).
- subspecies**: a geographically localized and isolated subdivision of a species, which differs genetically, morphologically and taxonomically from other subdivisions of the species.
- subtelocentric**: describes a chromosome with the centromere (*q.v.*) much nearer one end than the other, so there are two arms of very unequal length (ratio 1 : >2).
- subterminal**: just below the end or tip.
- subterranean**: living permanently below the ground; *cf.* fossorial (*q.v.*).
- suckling**: the act of a mother giving milk directly from her breast (mammary glands) to her young. Mothers suckle; their young suck.
- sulcus** (*pl.* **sulci**): a groove, fissure or furrow.
- superovulation**: *see* **polyovulation** (*q.v.*).
- supinate**: to turn or rotate the hand or forearm, or the hindlimb and foot.
- supracaudal**: above the tail.
- supraoccipital crest**: ridge of bone, orientated transversely across the back of the skull, at the junction of the parietal and/or supraoccipital bones and the occipital bone. Sometimes referred to as the lambdoid crest.
- supraorbital ridge**: ridge of bone along upper rim of orbit (eye-socket).
- supraorbital**: above (dorsal to) the orbit.
- supraordinal**: describes a taxon above the level of the order.
- sympatry** (*adj.* **sympatric**): the situation where populations of two or more different species have overlapping geographic ranges; refers also to populations of two or more species whose geographic ranges are partly or wholly overlapping. They may or may not interact. *cf.* allopatry (*q.v.*); syntopy (*q.v.*).

- symplesiomorphy**: a primitive or ancestral character shared by two or more groups, which is inherited from ancestors older than the last common ancestor.
- synanthropic**: associated with humans and/or their houses and other buildings.
- synapomorphy** (*adj.* **synapomorphic**): situation in which a homologous character is present in two or more taxa and is thought to have originated in their most recent common ancestor. *See also* apomorphy.
- syndactyly**: of digits; whole of part fusion of two or more digits (e.g. Digits 2 and 3 of the hindfoot in otter-shrews).
- synonym**: one or more of different names for the same taxonomic unit. A synonym may be a 'senior synonym' (the oldest name), or a 'junior synonym' (a more recent name) that is no longer considered as valid. May be used to refer to all names that have been associated, at some time in the past, with the taxonomic unit as currently understood.
- syntopy** (*adj.* **syntopic**): describes the situation where two or more species use the same or similar habitats and activity times. They may or may not interact. *cf.* allopatry (*q.v.*); sympatry (*q.v.*).
- syntype**: any specimen, or one of a series of specimens, used to designate a species when a holotype (*q.v.*) and paratype(s) (*q.v.*) have either not been selected, or have been lost or destroyed.
- systematics**: the science of arranging organisms in a way that reflects their evolutionary relationships; such relationships may be expressed as a phylogeny (*q.v.*). Often defined (somewhat incorrectly) as a synonym of taxonomy (*q.v.*).
- T**: (*abbrev.*) length of tail, measured from anterior of the first caudal vertebra to the posterior end of the last caudal vertebra (excluding any tufts, bristles etc. at tip of tail).
- T_a**: (*abbrev.*) ambient temperature; the temperature in which an animal is living. *cf.* T_b (*q.v.*).
- Ta**: ambient temperature; the temperature in which an animal is living. *cf.* T_b (*q.v.*).
- talonid**: heel at the posterior end of a lower molar tooth.
- tapetum lucidum**: light-reflecting layer behind or in the retina of the eyes of some vertebrates that reflects light back through the retina thereby increasing the sensitivity of the eye to dim light.
- taxon** (*pl.* **taxa**): any defined unit (e.g. family, genus, species, subspecies) in the classification of organisms.
- taxonomy**: the science of biological nomenclature; the study of the rules, principles and practice of naming and classifying species and other taxa. Sometimes considered as an integral part (and near synonym) of systematics (*q.v.*).
- T_b**: (*abbrev.*) body temperature; the temperature of the core (central) part of an animal. *cf.* T_a (*q.v.*).
- telocentric**: describes a chromosome that appears to have a terminal centromere (*q.v.*) and therefore only one arm. Modern studies have revealed that all chromosomes have two arms but the smaller arm of telocentric chromosomes is not visible under a light microscope.
- temporalis**: a broad radiating muscle arising from the coronoid process (*q.v.*) of the lower jaw and attaching to the upper part of the skull.
- termitarium** (*pl.* **termitaria**): a place where termites (Insecta: Isopoda) live. Often a large mound of modified hard soil. The shape and size of a termitarium is unique to each species of termite.
- terrestrial**: living on the ground. *cf.* arboreal (*q.v.*); scansorial (*q.v.*).
- territory**: an area defended by an individual against certain other members of the species, usually by overt aggression or advertisement; territory is marked by the urine, faeces or glandular secretions of the territory's owner. *cf.* home-range (*q.v.*).
- Tertiary Period**: geological period, 65–2 mya, comprising five epochs: Palaeocene, Eocene, Oligocene, Miocene and Pliocene (*q.v.*); followed by the Quaternary Period (*q.v.*).
- testes**: the male gonads, or testicles, in which spermatozoa are formed and in which the male hormone is produced.
- Tethys Sea**: the sea separating the two supercontinents, Gondwana (*q.v.*) and Laurasia (*q.v.*) during much of the Mesozoic Era before the opening of the Indian and Atlantic oceans during the Cretaceous Period (*q.v.*).
- thermal conductance**: a measure of the ability of substances (including pelage) to transfer heat.
- thermolability** (*adj.* **thermolabile**): the ability of a homeotherm (e.g. camel) to allow its body temperature to vary over a 24-hour period, without either hibernating or aestivating.
- thermoneutral zone**: the range of body temperatures within which an animal does not have to increase its metabolic rate to increase T_b (*q.v.*) (when T_a (*q.v.*) is low) and reduce T_b (when T_a is high).
- thermoregulation**: regulation of body temperature, either by metabolic or behavioural means (or both simultaneously) so that T_b (*q.v.*) is kept more or less constant.
- thoracic**: pertaining to, or situated upon, the chest.
- through-put time**: time taken for food to pass through the digestive tract.
- tibia** (*pl.* **tibiae**): one of the two bones forming the lower leg (the shin bone); part of hindlimb between knee and ankle.
- TL**: (*abbrev.*) total length from tip of snout to posterior end of tail. Equivalent to the head and body length and tail length added together. *See also* HB (*q.v.*) and T (*q.v.*).
- toothrow**: Generally, the row of teeth from the most anterior incisor tooth to the most posterior molar. In golden moles, the row of teeth from the canine to the most posterior molar. Sometimes used in contexts of specific types of teeth, e.g. premolar toothrow, molar toothrow.
- topotype**: any specimen from the type locality (*q.v.*), i.e. the same locality as that from which the holotype (*q.v.*) was taken.
- topotypical**: pertaining to the type locality (e.g. a topotypical population is one found at the type locality).
- torpor** (*adj.* **torpid**): a state in which there is a (usually short-term) reduction of metabolic rate and a lowering of T_b (*q.v.*) when T_a (*q.v.*) declines; arousal from torpor occurs when T_a increases and without high energy costs to the individual. Torpor is associated with a state of inactivity and reduced responsiveness to stimuli. Torpor lasts for only short periods of time (hours or days). *cf.* hibernation.
- tragus**: a cartilaginous structure, usually small, projecting from the inner side of the external ear just anterior to the auditory meatus (*q.v.*).
- transverse**: in a direction across the body from side to side. *cf.* longitudinal (*q.v.*).
- Triassic Period**: period (within the Mesozoic Era); 248–208 mya. The first mammals appeared in this period.

triconid: describes a molariform tooth having three cusps.

tricuspid: having three points or cusps (particularly of teeth).

trifid: divided into three by two emarginations (*q.v.*).

tubercle: a small rounded protuberance.

tusks: long, continuously growing incisor or canine teeth that protrude (usually in pairs) beyond the mouth in some mammals including elephants (in which the tusks are incisors), and warthogs and other pigs (in which the tusks are canines); comprised of dentine (ivory). Some mammals, e.g. hyraxes, have 'tusk-like' incisors.

tympanic bulla (*pl. tympanic bullae*): one of a pair of usually rounded bony capsules, on underside of skull (one on each side), housing structures of the middle and inner ear in many mammals. Also called auditory bulla (*q.v.*).

type description: the original description of a species; the original description of the holotype (and paratype[s] if included).

type locality: the locality from which a holotype (*q.v.*), lectotype (*q.v.*) or neotype (*q.v.*) was collected. Also called topotypical locality.

type population: the population from which the holotype was selected.

type series: the holotype and all specimens collected at the same place and time and used, together with the holotype, to describe a new species.

type species: usually the species that was the first to be described under the name of a new genus. Not all genera had a designated type species when they were first created; in such cases, other rules determine which species will be the type species.

type specimen: *see* holotype.

underfur: dense and often woolly layer of the pelage, situated close to the skin and below the soft hairs and guard hairs; usually short and present in those species that experience lower T_a .

unicuspid: having one cusp or point (particularly of teeth).

upper critical temperature: the highest ambient temperatures at which the animal must increase its metabolic rate to maintain a constant body temperature. If the ambient temperature increases above the upper critical temperature and the animal is unable to cool itself, it will enter hyperthermia and may eventually die. *cf.* lower critical temperature.

uvula: the conical projection from the posterior edge of the soft palate that plays a role in the articulation of sounds and the closing the nasopharynx during swallowing.

vagility: the ability to move about, disperse or migrate.

vagrant: an individual that has been found well outside the normal geographic range of its species, e.g. a bat or bird that has been wind-borne, or an animal that has been transported as a stowaway on a ship, to a distant locality.

vascularized: infiltrated with capillaries.

vasoconstriction: constriction of the capillaries of the blood system near the surface of the skin in order to reduce the rate of heat loss through the skin; a mechanism used by many mammals to conserve heat when T_a (*q.v.*) is low. *cf.* vasodilation (*q.v.*).

vasodilation: the dilation (or opening) of the capillaries of the blood system near the surface of the skin in order to increase the rate of heat loss through the skin; a mechanism used by many mammals to cool themselves when T_a (*q.v.*) is high. *cf.* vasoconstriction (*q.v.*).

veld: Afrikaans word, used mainly by southern African biologists, to refer to a wide variety of grassland vegetation types typically used for grazing. *See also* bushveld, highveld, lowveld.

vertebra (*pl. vertebrae*): any of the bones that make up the backbone.

vertebral formula: the number of vertebrae in each part of the spine, from anterior to posterior: the parts are cervical (C), thoracic (T), lumbar (L), sacral (S), caudal (Ca).

vestigial: small and imperfectly developed; a structure having a smaller and more simple form than the corresponding structure in an ancestral species.

vibrissa (*pl. vibrissae*): long stiff hairs on the face, especially around nostrils and lips; often associated with the perception of tactile sensation; 'whiskers'.

vlei: southern African term for a marsh or swamp, either permanent or seasonal.

wadi: a desert valley, usually dry at the surface except after heavy rainfall.

water turnover: the rate at which water (fluids) is utilized and replaced in the body per unit time (normally expressed as ml/kg body weight/day); the amount of water an animal processes through its body each day. Water turnover is related to water availability, the urine concentrating ability of the kidney, amount of protein in the diet and T_a (*q.v.*). Water turnover rates are characteristically low in arid-adapted mammals when compared with non arid-adapted mammals.

West Africa: ca. south of 18° N from Senegal to the Sanaga R. in Cameroon, and Bioko I. (Equatorial Guinea) (Rosevear 1965).

WT: (*abbrev.*) weight (mass) of an individual, usually expressed in grams (g) or kilograms (kg).

xiphisternum: The posterior segment, or extremity, of the sternum (sometimes called the xiphoid process).

zalambdodont: cheekteeth with three main cusps connected by crests (ectolophs) forming a V-shape; largest cusp is at the apex of the V (on the lingual or tongue side of the tooth); assumed to be derived from the primitive tribosphenic teeth found in some extinct early mammals. *cf.* dilambdodont (*q.v.*).

ZW: (*abbrev.*) *see* zygomatic width.

zygomatic arch: one of a pair of cheekbones, formed of the maxillary process anteriorly, jugal bone medially and squamosal bone posteriorly. Ranges from massive, broad, widely flared and bony, to frail, slender and cartilaginous. When present, provides protection to the eyes and orbits. Also called zygoma.

zygomatic width (ZW): greatest width between the outer aspect of one zygomatic arch to the equivalent position on the opposite zygomatic arch. *See also* GWS.

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